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SHORT COMMUNICATION

NEW MATERIAL OF *CHELUS COLOMBIANA* (TESTUDINES; PLEURODIRA) FROM THE LOWER MIOCENE OF COLOMBIA

EDWIN CADENA,[*,1] CARLOS JARAMILLO,[1] and MARIA E. PARAMO[2]; [1]Center for Tropical Paleoecology and Archeology, Smithsonian Tropical Research Institute, Balboa, Ancon AA 0843-03092, Panama; [2]Instituto Colombiano de Geología y Minería, Museo Geológico José Royo y Gomez, Bogotá, Colombia.

The pleurodire genus *Chelus* contains three species: the extant type species *C. fimbriata* (Schneider, 1783), which lives in most major drainages in northeastern South America (Fig. 1); the late Miocene *C. lewisi* Wood, 1976, from the Urumaco Formation of Venezuela (Wood, 1976); and the middle Miocene *C. colombiana* (Wood, 1976), from the Villavieja Formation of Colombia. *C. colombiana* also has been reported from upper Miocene strata at Estado do Acre, Brazil (Bocquentin, 1988; Bocquentin and Rodrigues dos Santos, 1989). *Chelus* species are differentiated by shell features, because skulls are not known for either fossil congener. Sanchez-Villagra, Linares et al. (1995) examined the diagnostic utility of shell features by performing a morphometric analysis of all three *Chelus* species. They concluded that although the shape and size of the first neural and entoplastron were too variable to be reliably used to differentiate species (contra Wood, 1976), other features such as the shape and size of the carapace, the relative heights of knobs along the dorsal ridges on the carapace, the proportions of the bridge, and the position of the intergular scale were reliable. No previous workers have considered whether the shapes and positions of scars for contact of the axillary and inguinal buttresses on the ventral surface of the carapace and of the ilium, ischium, and pubis on the dorsal surface of the plastron are useful for differentiating species of *Chelus*.

In this article, we describe newly discovered lower Miocene shell material of *Chelus colombiana* from central Colombia that represents the geologically oldest, unequivocal record for the genus and we re-interpret the specific affinities of upper Miocene *Chelus* material previously reported (Bocquentin, 1988; Bocquentin and Rodrigues dos Santos, 1989) from Estado do Acre, Brazil. We also document the pattern and distribution of iliac, pubic, ischial, axillary, and inguinal scars among all three *Chelus* species. We argue that those features are useful for differentiating *Chelus* species and we incorporate them into the first cladistic analysis of intra-generic relationships for the genus.

Institutional Abbreviations—**CURS**, Colección Alcaldía de Urumaco, Rodolfo Sánchez, Urumaco, Estado Falcón,Venezuela; **GMB** and **M1MP**, Museo Geológico José Royo y Gómez, paleontological collection INGEOMINAS (Instituto Colombiano de Geología y Mineria), Bogotá, Colombia; **MCNC**, Museo de Ciencias Naturales, Caracas, Venezuela; **MNHN**, Muséum national d'Histoire naturelle, Paris, France, laboratoires: **AC**, Anatomie Comparée, and **Z**, Zoologie des Reptiles et Amphibiens; **MPV**, Museo Paleontológico de Villavieja, Departamento del Huila, Villavieja, Colombia; **UCMP**, University of California Museum of Paleontology, Berkeley, U.S.A.; **UFAC**, Universidade Federal do Acre, Rio Branco, Acre, Brazil; **UMA**, University of Massachussets Museum of Natural History, Massachussets, U.S.A.; **UNEFM**, Múseo de la Universidad Nacional Experimental Francisco Miranda, Coro, Estado Falcón, Venezuela.

Comparative Material and Sources—*Chelus colombiana*: type description (Wood, 1976); unpublished photographs of holotype shell (UCMP 78762); paratype xiphiplastron (GMB 1891); and a nearly complete, unpublished shell (GMB Royo-*Chelus*). *C. lewisi*: type description (Wood, 1976); unpublished photographs of holotype shell (MCNC 239); and unpublished xiphiplastra (UNEFM 1424 and UNEFM 1442). *C. fimbriata*: complete shells (MNHN AC 1930-365, 1973-8381, 1991-2581A, A5171, A5200, A5176, and MNHN Z 9406) and computed tomography images (Maisano, 2002) of complete skeleton (UMA R-1376).

SYSTEMATIC PALEONTOLOGY

TESTUDINES Treviranus, 1802
PLEURODIRA Cope, 1864
CHELIDAE Gray, 1825
CHELUS Dumeril, 1806

Type Species—*Chelus fimbriata* (Schneider, 1783).

Other Species—*Chelus lewisi* Wood, 1976, and *C. colombiana* (Wood, 1976).

Distribution—Early Miocene–Recent, northern South America (e.g., Wood, 1976; Ernst and Barbour, 1989; Iverson, 1992; this study).

Revised Diagnosis (shell only)—Differs from all other chelids in the following combination of three derived carapace features: (1) costovertebral tunnel sensu Gaffney et al. (2006:628) on underside uniformly wide along its entire length, versus costovertebral tunnel absent; (2) dorsal surface ornamented with three prominently raised, longitudinal ridges, one bearing five knobs and extending along midline of carapace and other two ridges each bearing four knobs and extending across medial portions of costals, versus three knobby longitudinal ridges absent and dorsal surface instead bears microvermiculate ornament; and (3) scar on ventral surface for contact of inguinal buttress restricted to fourth costal, versus inguinal scar spans fourth and fifth costals in *Hydromedusa tectifera* and spans fifth and sixth costals in primitive chelids and some modern species such as *Phrynops*

[*]Corresponding author. Current address: Department of Geology, University of Florida, Florida Museum of Natural History, Gainesville, Florida 32611, U.S.A., ecadena@ufl.edu

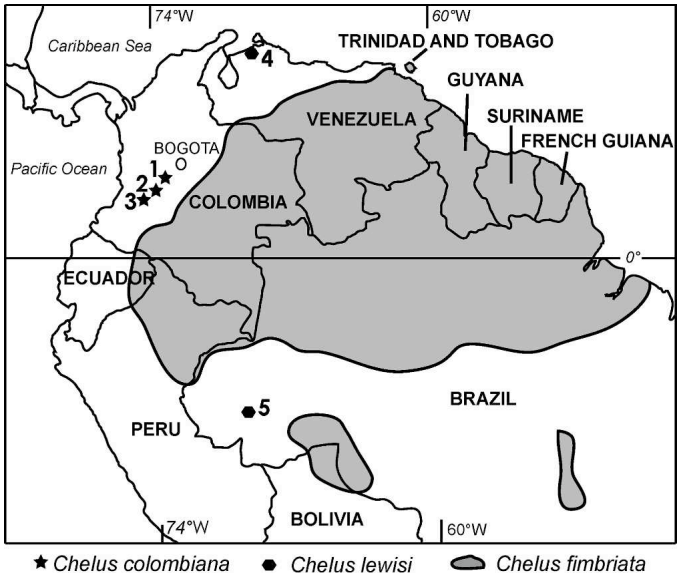

FIGURE 1. Map of northern South America showing distribution of extant *Chelus fimbriata* (shaded) and select Miocene *Chelus* occurrences (Arabic numerals). **1**, *C. colombiana*, costals and xiphiplastron (this study) from the Pubenza locality, Colombia; Barzalosa Formation; early Miocene. **2**, *C. colombiana*, plastral bones (Wood, 1976) from the Coyaima locality, Colombia; Villavieja Formation; middle Miocene. **3**, *C. colombiana*, shells (including holotype) and carapace and plastral plates (Wood, 1976) from the Villavieja locality, Colombia; Villavieja Formation; middle Miocene. **4**, *C. lewisi*, shells (including holotype), xiphiplastron, and vertebra (Wood, 1976) and two unpublished xiphiplastra from localities near Urumaco, Venezuela; Urumaco Formation; late Miocene. **5**, *C. lewisi*, carapace and plastral bones, previously referred to *C. colombiana* by Bocquentin and Rodrigues dos Santos (1989), from Estado do Acre, Brazil; late Miocene.

vanderhaegei, *Emydura macquarri*, and *Acanthochelys pallidipectoris*.

Remarks—The specific epithets '*colombianus*' and '*fimbriatus*' have been used incorrectly by many authors. According to the International Commission on Zoological Nomenclature (1999:Art. 30.1.2), "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". The word 'chelus' means 'turtle' and is feminine in standard Greek dictionaries. Because '*Chelus*' is a feminine generic name, its associated specific epithets must also be feminine, in these cases '*colombiana*' and '*fimbriata*', as correctly used by, for example, Gaffney (1977), Iverson (1992), and Bonin et al. (2006).

CHELUS COLOMBIANA (Wood, 1976) emended spelling

(Fig. 2A–H, Fig. 3)

Chelus colombianus Wood, 1976:2–6, fig. 1, pls. 1–3 (original description).

Holotype—UCMP 78762, nearly complete shell (Wood, 1976:pls. 1, 2) from near Villavieja, upper Magdalena River Valley, Colombia; Villavieja Formation; late Miocene in age.

Referred Specimens—Shells and plastron and carapace bones (GMB and UCMP collections) listed by Wood (1976:2, 3) from various localities in the upper Magdalena River Valley, Colombia; Villavieja Formation; late Miocene in age. Two complete shells (MPV collections) referred by Sanchez-Villagra, Linares et al. (1995). Newly referred specimens described below are a xiphiplastron (M1MP60505-79) and costals (M1MP60505-41, -44, -46, and -61), all from the Pubenza locality (4° 24′ 21″ N, 74° 42′ 12″ E), Cundinamarca Department, upper Magdalena River Valley, Colombia; Barzalosa Formation; early Miocene in age, within palynological zone 34 of Jaramillo and Rueda (2004) and Jaramillo et al. (2006) or zone 27 of Muller et al. (1987). Our list excludes the upper Miocene carapace bones, xiphiplastra, and ilium (UFAC collections) from Estado do Acre, Brazil, that Bocquentin and Rodrigues dos Santos (1989) assigned to *Chelus colombiana*, because for reasons given below we interpret those specimens as belonging to *C. lewisi*.

Distribution—Early–late Miocene, Colombia.

Revised Diagnosis—Differs from *Chelus fimbriata* and *C. lewisi* in the following shell features: midline length of largest known carapaces approximately thirty percent greater (derived condition); posterior process of xiphiplastron shorter and approximately twice as wide (primitive condition); and pubic scar on dorsal surface of xiphiplastron oval in outline and with posterior end broader (derived condition). Differs from *C. fimbriata* (condition unknown in *C. lewisi*) in having contact for axillary buttress (i.e., axillary scar) on ventral surface of carapace extending across anteromedial part of second costal and posterolateral part of first costal and almost reaching peripherals (derived condition), versus contact limited to first costal in *C. fimbriata*. Resembles *C. fimbriata* in having knobs on dorsal ridges of carapace prominently developed and posterior knobs higher than anterior knobs when seen in lateral view (intermediate condition), versus knobs less prominent and height more uniform along length of carapace (derived condition) in *C. lewisi*. Resembles *C. lewisi* in having one or more supernumerary scales sensu Wood (1976:5) separating intergular scale from anterior margin of plastron (derived condition), versus supernumerary scales absent and intergular scale broadly contacts anterior margin of plastron in *C. fimbriata*. Differs from *C. lewisi* and, to a lesser extent, *C. fimbriata* in having lateral end of femoroanal sulcus on ventral surface of xiphiplastron marked by modest-sized femoroanal notch in lateral margin of bone (primitive condition); this notch is present, but not nearly as well developed in *C. fimbriata*. Differs consistently from *C. lewisi* and some *C. fimbriata* in having dorsal outline of carapace quadrangular and with lateral sides approximately parallel (intermediate condition); in all known *C. lewisi* specimens the carapace is expanded posteriorly and the posterolateral edges flare outwards (derived condition), whereas in *C. fimbriata* the carapace is either quadrangular in Amazonian populations or expanded posteriorly in Orinoquian populations (Sanchez-Villagra, Linares et al., 1995).

Remarks—Many workers (e.g., Sanchez-Villagra, Pritchard et al., 1995, and references therein) have questioned the taxonomic value of the intergular scale, because certain attributes of this scale are highly variable within and among extant populations of *Chelus fimbriata*. Despite admittedly extensive intraspecific variation in the shape and length of the intergular scale and its contacts with the gular scales, in all *C. fimbriata* specimens previously described or known to us the intergular scale broadly contacts the anterior margin of the plastron and no supernumerary scales are present. This differs from the condition in the fossil species *C. colombiana* and *C. lewisi*, in which two or three supernumerary scales are present and these completely or almost completely separate the intergular scale from the anterior margin of the plastron. Two arrangements are seen in the fossil species. In the first arrangement, the intergular scale is hexagonal in shape and two supernumerary scales are in front of the gulars. In plastra exhibiting the first arrangement, the supernumerary scales completely separate the intergular from the anterior margin of the plastron in *C. colombiana*, whereas in *C. lewisi* the anteriormost tip of the intergular scale extends between the supernumerary scales and barely contacts the anterior margin of the plastron. In the second arrangement, the intergular scale is orthogonal in shape and is completely separated from the anterior margin of the plastron by three supernumerary scales.

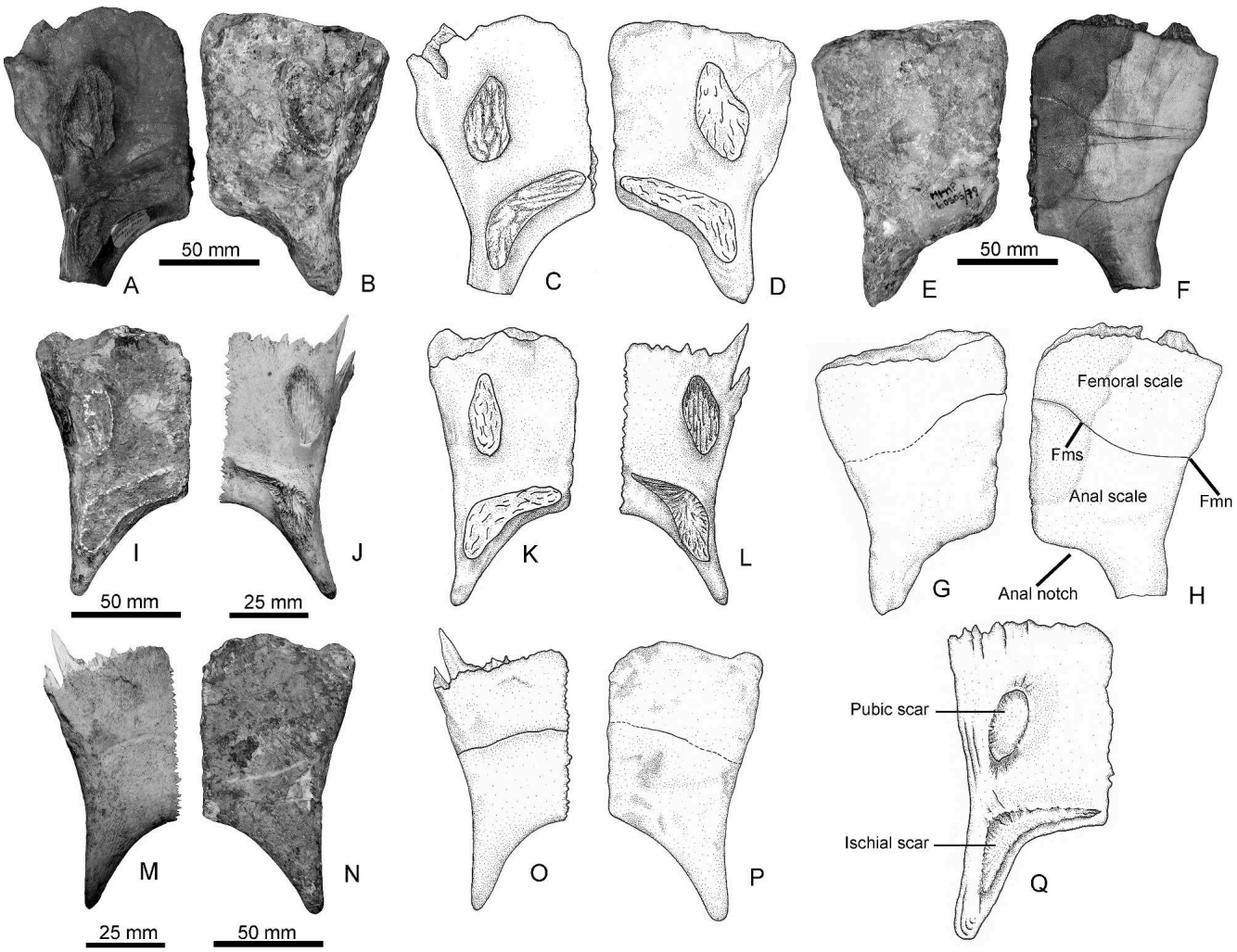

FIGURE 2. Representative xiphiplastra of the three *Chelus* species. **A**, **C**, **F**, **H**, GMB 1891, left xiphiplastron of *C. colombiana*, in dorsal (**A**, **C**) and ventral (**F**, **H**) views; Coyaima locality, Colombia; Barzalosa Formation; middle Miocene. **B**, **D**, **E**, **G**, M1MP60505-79, right xiphiplastron of *C. colombiana*, in dorsal (**B**, **D**) and ventral (**E**, **G**) views; Pubenza locality, Colombia; Barzalosa Formation; early Miocene. **I**, **K**, **N**, **P**, UNEFM 1442, left xiphiplastron of *C. lewisi*, in dorsal (**I**, **K**) and ventral (**N**, **P**) views; near Urumaco, Venezuela; Urumaco Formation; late Miocene. **J**, **L**, **M**, **O**, MNHN AC 1930-365, right xiphiplastron of *C. fimbriata*, in dorsal (**J**, **L**) and ventral (**M**, **O**) views; Amazon Basin; Recent. **Q**, UFAC 1578, left xiphiplastron of *C. lewisi*, previously referred to *C. colombiana* by Bocquentin and Rodrigues dos Santos (1989), in dorsal view; Estado do Acre locality, Brazil; late Miocene (modified from Bocquentin and Rodrigues dos Santos, 1989:fig. 2B). **Abbreviations**: **Fmn**, femoroanal notch; **Fms**, femoroanal sulcus.

DESCRIPTION OF LOWER MIOCENE *CHELUS COLOMBIANA* SHELL BONES FROM PUBENZA, COLOMBIA, AND ASSESSMENT OF SHELL CHARACTERS FOR DIFFERENTIATING SPECIES OF *CHELUS*

Plastron

The sole plastron bone available from Pubenza is a complete right xiphiplastron (M1MP60505-79; Fig. 2B, D, E, G). The bone is widest anteriorly, narrows posteriorly, and terminates in a horn-shaped posterior process that is relatively short and wide. The form of the xiphiplastral posterior process on M1MP60505-79 is primitive for chelids, because its proportions are similar to *Yaminuechelys maior* (Bona and de la Fuente, 2005:fig. 4B) from the early Paleocene of Argentina and only slightly larger than *Lomalatachelys neuquina* (Lapparent de Broin and de la Fuente, 2001:fig. 5B, D), which is a primitive chelid and a possible member of the *Chelus* group from the Santonian of Argentina, and *Bonapartemys bajobarrealis* (Lapparent de Broin and de la Fuente, 2001:fig. 2B) from the Turonian–Campanian of Argentina. In contrast, *C. lewisi* and *C. fimbriata* have the longest and narrowest posterior xiphiplastral process among chelids, a condition that we consider derived. On the ventral face of M1MP60505-79 (Fig. 2E, G), the femoroanal sulcus is clearly visible as an anteriorly convex line extending across the medial half of the bone; the lateral half of this sulcus is partially covered by a thin layer of gypsum. The lateral end of the femoroanal sulcus is marked by a shallow femoroanal notch in the lateral edge of the bone. This notch is less pronounced in *C. fimbriata* (in fact, it is not obvious in the xiphiplastron depicted in Fig. 2J, L, M, O) and it is absent in *C. lewisi*. We interpret the femoroanal notch as a primitive feature, because it occurs in primitive chelids such as *B. bajobarrealis*. The pubic and ischial scars are perfectly preserved on the dorsal surface of M1MP60505-79 (Fig. 2B, D). The pubic scar is somewhat oval-shaped, with the wider end directed posteriorly. The anterior part of the medial rim of the pubic scar is straight and parallels the medial edge of the xiphiplastron, whereas the anterior part of the lateral rim of the scar is medially

concave and broadly separated from the anterolateral corner of the bone. In *C. lewisi* and *C. fimbriata,* the pubic scar is more nearly oval in shape, relatively narrower, and the anterior part of the lateral rim is not concave; a similar condition occurs in *Y. maior*. The pubic scar is located more centrally on M1MP60505-79 and in xiphiplastra of *L. neuquina* and *Prochelidella portezuelae* (de la Fuente, 2003:fig. 2.3) from the Turonian–Coniacian of Argentina, whereas in *Y. maior*, *C. lewisi*, and especially *C. fimbriata* the pubic scar is closer to the lateral edge of the xiphiplastron. The location of the pubic scar is unknown for *B. bajobarrealis*. The ischialic scar on M1MP60505-79 is broad and asymmetrically triangular in outline, with rounded posterior and anterior ends. The medial rim of the scar is shallowly concave in ventral aspect and parallels the posterior edge of the xiphiplastron. The latter feature is also present in primitive chelids and *C. lewisi*, but in *C. fimbriata* the medial end of the ischialic scar tends to be narrower and is directed away from the posterior edge of the bone. Judging by the broadly concave posterior edge of M1MP60505-79, in life the anal notch formed by the left and right xiphiplastra would have been U-shaped, as in most other chelids. *Yaminuechelys gasparini* (de la Fuente et al., 2001:fig. 2B, G) from the Campanian–Maastrichtian of Argentina differs in having a V-shaped anal notch. All characteristics described above for M1MP60505-79 occur in a left xiphiplastron (GMB 1891; Fig. 2A, C, F, H) that Wood (1976) referred to *C. colombiana* in his type description for that species. The latter specimen is crucial for establishing the specific identity of M1MP60505-79, because in the holotype shell (UCMP 7872) of *C. colombiana* the articulated nature of the shell and the layer of matrix and plaster covering the pelvic girdle mean that only the shape, thickness, and size of the xiphiplastra and the position of the femoroanal sulcus can be determined from the holotype.

Carapace

Four specimens preserving a total of seven costals were collected from Pubenza. These specimens can be reliably assigned to *Chelus*, because each preserves part of the diagnostic dorsal ridge that extends anteroposteriorly across the medial ends of the costals (e.g., Fig. 3G).

M1MP60505-44 preserves nearly complete first and second right costals (Fig. 3A–C). The first costal is slightly wider than long and its lateral margin is broadly convex. A concave indentation in the anterior part of the medial edge of the first costal marks the location of the first neural and indicates that the first neural did not extend far enough posteriorly to contact the second costals. The ventral face bears a prominent axillary scar with a raised rim that extends across the anteromedian part of the second costal and lateral part of the first costal, and almost reaches the contact surface for the peripherals. In *Chelus fimbriata,* the axillary scar typically is limited to the posterior part of the first costal—that is also the condition in *Bonapartemys bajobarrealis* and *Yaminuechelys maior*—but in some *C. fimbriata* individuals the axillary scar may also extend onto the anteriormost part of the second costal. Although the position of the axillary scar can be used to differentiate *C. colombiana* and *C. fimbriata*, at present this feature cannot be used for *C. lewisi* because ventral surfaces of the anterior costals cannot be seen in any specimens of that species.

M1MP60505-46 is a virtually complete, fourth left costal (Fig. 3D–F). The dorsal surface on this bone exhibits the same pattern of ridges described below for M1MP60505-61. More laterally, a shallow and narrow sulcus marks the contact between the second and the third pectoral scales; this sulcus indicates that the specimen is a fourth costal. As in *Chelus fimbriata* and *C. lewisi*, a well-developed and transversely elongate inguinal scar extends along the lateral half of the ventral surface of the costal.

M1MP60505-61 consists of nearly complete sixth and seventh right costals (Fig. 3G–I). About one-third of the distance from their medial ends, the dorsal surface of both costals is crossed anteroposteriorly by the right dorsal ridge. The preserved portions of the dorsal ridge are tall and decrease in height posteriorly: the ridge is 18 mm high at the anterior margin of the sixth costal and only 10 mm high at the posterior margin of the eighth costal. Between the dorsal ridge and the medial ends of the bones, the dorsal surface of each costal is shallowly depressed and crossed by a smaller transverse ridge that divides as it approaches the contact with the neurals. From the base of the dorsal ridge, the sulcus between the third and fourth pleural scale extends transversely across the lateral portion of the sixth costal (Fig. 3G, H).

M1MP60505-41 (Fig. 3J–L) preserves nearly complete seventh and eighth left costals, the dorsal surfaces of which exhibit the same pattern of ridges described above. The eighth costal is thicker and its lateral end is broader than the seventh costal. The iliac scar is triangular and slightly elongated in shape and it is almost completely restricted to the eighth costal. In life, the posteriormost portion of the iliac scar would have extended onto the suprapygal. In *Chelus fimbriata,* the iliac scar also occurs on the anterior part of the suprapygal and extends even farther anteriorly onto the seventh costal. Conversely, in the primitive chelids *Lomatachelys neuquina, Bonapartemys bajobarrealis*, and *Yaminuechelys maior* the iliac scar is almost totally restricted to the eight costal. The position of the iliac scar in *C. lewisi* is unknown, because most of the available shells are articulated and infilled with matrix.

TAXONOMIC RE-INTERPRETATION OF UPPER MIOCENE *CHELUS* FOSSILS FROM ESTADO DO ACRE, BRAZIL

Bocquentin and Rodrigues dos Santos (1989) described fragmentary shell material and an ilium from the upper Miocene of Estado do Acre, Brazil. They assigned the shell material to *Chelus colombiana* based on two features: (1) differs from *C. lewisi* in much larger shell size and (2) differs from *C. fimbriata* in having the intergular scale hexagonal in outline, almost enclosed by supernumerary scales, and its anteriormost end only slightly contacting the anterior margin of the plastron. Although maximum shell size is useful for differentiating *C. colombiana* from *C. lewisi* and *C. fimbriata*, in our opinion, the specimens described by Bocquentin and Rodrigues dos Santos (1989) are so fragmentary that they cannot reliably be used to estimate shell size. As for the second feature cited by Bocquentin and Rodrigues dos Santos (1989), the shapes and configurations of the intergular and supernumerary scales seen in their best preserved specimen (UFAC-1546) are almost identical to those in a referred specimen (UNEFM 1415) of *C. lewisi*. Finally, judging from Bocquentin and Rodrigues dos Santos' (1989) drawings and descriptions of xiphiplastra from Estado do Acre (see also here, Fig. 2Q), the shapes of the pubic and ischialic scars and the lack of a femoroanal notch are further evidence that those specimens are more similar to *C. lewisi* than *C. colombiana*. For reasons given above, we thus disagree with Bocquentin and Rodrigues dos Santos (1989) and, instead, interpret the shell material from Estado do Acre material as belonging to *C. lewisi*. Interestingly, those authors noted that the ilium from that site was most similar to *C. lewisi*.

PHYLOGENETIC ANALYSIS

Relationships within *Chelus* are uncertain. Based on differences in contacts of the intergular scale—which was then unknown for the Miocene *C. lewisi*—Wood (1976) suggested that the extant *C. fimbriata* (with a primitively unrecessed intergular) and the Miocene *C. colombiana* (with a derived recessed intergular) belonged to separate lineages. He also suggested that *C.*

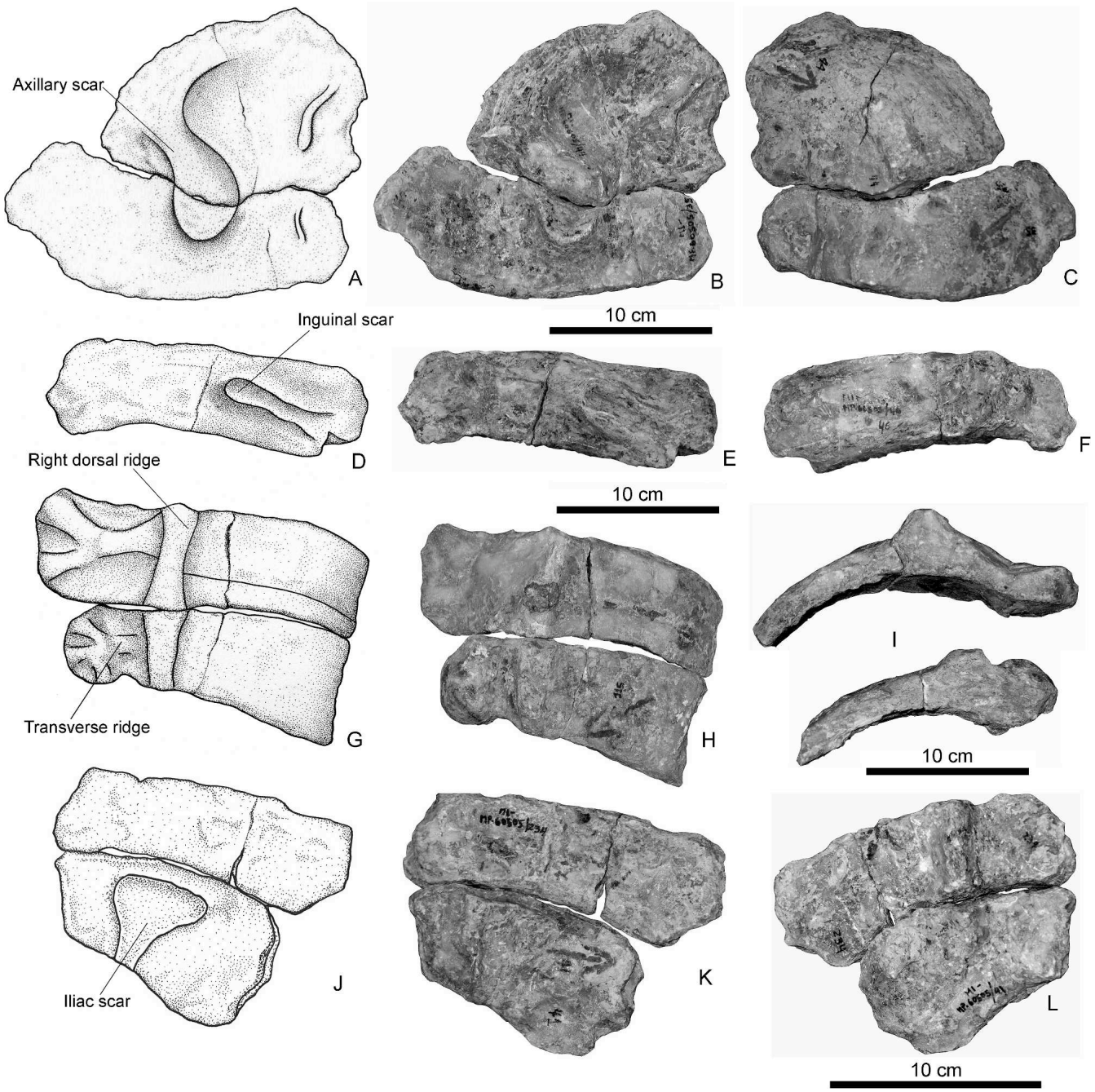

FIGURE 3. Costals of *Chelus colombiana* from the Pubenza locality, Colombia; Barzalosa Formation; early Miocene. **A**–**C**, M1MP60505-44, first and second right costal bones, interpretive drawing (**A**) in ventral view and photographs in ventral (**B**) and dorsal (**C**) views. **D**–**F**, M1MP60505-46, fourth left costal bone, interpretive drawing (**D**) in ventral view and photographs in ventral (**E**) and dorsal (**F**) views. **G**–**I**, M1MP60505-61, sixth and seventh right costal bones, interpretive drawing (**G**) in dorsal view and photographs in dorsal (**H**) and anterior (**I**) views. **J**–**L**, M1MP60505-41, seventh and eighth left costal bones, interpretive drawing (**J**) in ventral view and photographs in ventral (**K**) and dorsal (**L**) views.

colombiana might be ancestral to *C. lewisi*, but he acknowledged "there are at present no compelling reasons to believe this" (Wood, 1979:11). Subsequently Bocquentin (1988) discovered that *C. lewisi* also had a recessed intergular scale and, on the strength of that derived feature, suggested a close relationship between *C. lewisi* and *C. colombiana*. Most recently, Sanchez-Villagra, Linares et al. (1995) suggested that *C. colombiana* and *C. fimbriata* were most closely related, based on similarities in the outlines of their carapaces and sizes of the dorsal ridges, and proposed that the unrecessed intergular in *C. fimbriata* was a reversal.

We examined relationships among the three species of *Chelus* by performing a cladistic analysis using seven shell characters (Appendix 1): three are new (characters 2, 4, and 6) and the other four were adapted from earlier studies (Wood, 1976; Sanchez-Villagra, Linares et al., 1995; Lapparent de Broin and de la Fuente, 2001). We also included three other chelids in our analysis: the fossil species *Bonapartemys bajobarrealis* was used

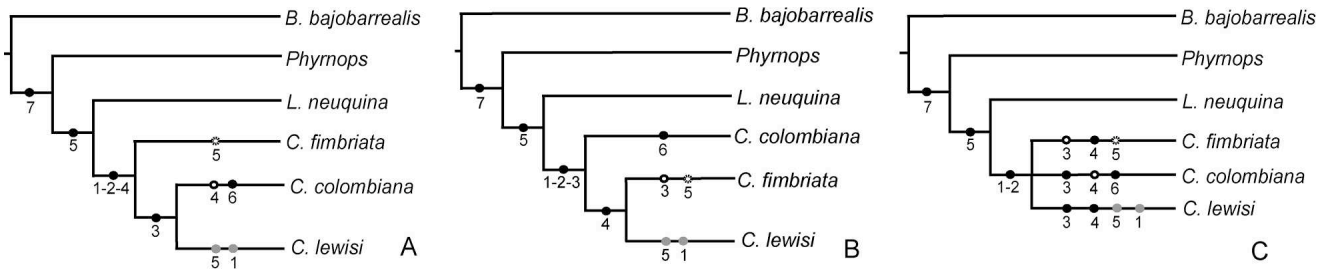

FIGURE 4. Cladograms showing patterns of relationships recovered in our cladistic analysis among the three species of *Chelus* and three other chelid taxa. **A**, **B**, Two shortest trees (11 steps each) showing different arrangements within *Chelus*, with either (**A**) *C. colombiana* + *C. lewisi* or (**B**) *C. fimbriata* + *C. lewisi* as sister taxa. **C**, Strict consensus tree showing an unresolved trichotomy among the three *Chelus* species. Distributions of apomorphies mapped onto all trees using ACCTRAN character state optimization in PAUP version 4.0b10 (Swofford, 2002). Symbols for apomorphies are: white circle, primitive state; black circle, derived state; grey circle, more derived state; and dashed circle, polymorphic state. **Abbreviations**: *B.* = *Bonapartemys*; *C.* = *Chelus*; *L.* = *Lomalatachelys*.

as the outgroup to polarize all characters; the extant genus *Phyrnops* was included because it has been identified as the sister-taxon of *Chelus* in several recent molecular phylogenetic analyses (Near et al., 2005; Krenze et al., 2005); and the fossil species *Lomalatachelys neuquina* was included because it potentially is a primitive member of the *Chelus* group (Lapparent de Broin and de la Fuente, 2001). Character descriptions and taxon-character scores are presented in, respectively, Appendices 1 and 2. All characters were treated as unordered and unweighted using the branch-and-bound algorithm in PAUP version 4.0b10 (Swofford, 2002).

We obtained two equally parsimonious trees (Fig 4A, B), each with a tree length of 11 steps, a consistency index of 0.90 (rescaled CI = 0.75), a retention index of 0.83, and a homoplasy index of 0.18. In both trees, monophyly of the *Chelus* clade is supported by the derived states of characters 1 and 2 and *Lomalatachelys neuquina*, *Phyrnops*, and *Bonapartemys bajobarrealis* are placed as successively more distant outgroups to *Chelus*. The first tree (Fig. 4A) identifies a *C. lewisi*-*C. colombiana* clade that is supported by the derived state for character 3 (intergular scale recessed from anterior plastral margin), with *C. colombiana* exhibiting a reversal for character 4. The second tree (Fig. 4B) identifies a *C. lewisi*-*C. fimbriata* clade that is supported by the derived state for character 4 (posterior xiphiplastral process long and narrow), with *C. fimbriata* exhibiting a reversal for character 3. The strict consensus tree (Fig. 4C) recovers an unresolved trichotomy within *Chelus*. Relationships within *Chelus* likely will remain uncertain until informative cranial material is recovered for the two fossil species.

We favor the *Chelus colombiana* (*C. lewis* + *C. fimbriata*) hypothesis, because it is most consistent with the biogeographical distributions of the three species (Fig. 1) and the tectonic history of northern South America. During the middle Miocene, uplifting of the Eastern Cordillera in Colombia separated the trans-Andean basins (Magdalena, Maracaibo, Atrato-Pacific slope, and Panama) from the cis-Andean basins (Orinoco and Western Amazonas) (Hoorn et al., 1995; Albert et al., 2006). This event isolated *C. colombiana* in the present-day Magdalena Valley. Meanwhile, farther to the east in the cis-Andean basins, *C. lewisi* and *C. fimbriata* enjoyed a wider distribution from the proto-Orinoco basin in Venezuela (Sanchez-Villagra, Linares et al., 1995) south to Estado do Acre in southwestern Amazonia (Bocquentin and Rodrigues dos Santos, 1989:fig. 1); extant populations of *C. fimbriata* persist through much of the same region.

In our opinion, the lower Miocene *Chelus colombiana* material described here from Pubenza, Colombia, is the oldest undisputable record for the genus. Broin and de la Fuente (1993) described a seventh cervical vertebra from the Campanian–Maastrichtian of Argentina as belonging to the *Chelus* group, based on its similarity with cervical vertebrae of *C. fimbriata*, but we think that more diagnostic cranial or shell material is required before the Argentine occurrence can be accepted as the oldest record for *Chelus* or the *Chelus* group. At present, all unequivocal occurrences of *Chelus* date from the Miocene to present and are limited to the northern part of South America.

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APPENDIX 1. Shell characters and character states used in cladistic analysis.

1. Condition of three anteroposteriorly aligned ridges on dorsal surface of carapace: 0, absent; 1, present, prominently developed, and become higher towards posterior end of carapace; 2, present, less prominent, and height relatively uniform along carapace.
2. Position of inguinal scar on ventral surface of carapace: 0, across fifth and sixth costals; 1, restricted to fourth costal.
3. Scale pattern on anterior part of plastral lobe: 0, intergular scale contacts anterior margin of plastron and supernumerary scales absent; 1, intergular scale recessed from anterior margin of plastron and two or three supernumerary scales present across anterior margin of plastron, in front of intergular scale and between gular scales.
4. Form of posterior process of xiphiplastron: 0, short and wide; 1, long and narrow.
5. Dorsal outline of carapace: 0, oval; 1, quadrangular, with lateral sides approximately parallel; 2, lateral sides flare outwards toward posterior end.
6. Position of axillary scar: 1, on first costal; 2, on first and second costals.
7. Projection of axillary buttress onto peripherals: 0, reaches contact between second and third peripherals; 1, reaches medial margin of third peripheral or contact between third and fourth peripherals.

APPENDIX 2. Character matrix of six taxa and seven characters used in cladistic analysis.

	12345	67
Bonapartemys bajobarrealis	00000	00
Phyrnops	00000	01
Lomalatachelys neuquina	00001	01
Chelus colombiana	11101	11
Chelus lewisi	21112	?1
Chelus fimbriata	1101a	01

Abbreviation: **a**, polymorphic state (1 or 2).