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RESEARCH PAPER

Icriocarcinidae: a family of portunoid crabs from the Upper Cretaceous of North America

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Abstract Icriocarcininae Števčić, 2005, an extinct North American subfamily of portunoid decapods, is elevated to family level to contain two Late Cretaceous genera—*Icriocarcinus* Bishop, 1988, from the Pacific Coast, and *Branchiocarcinus* Feldmann and Vega, 1995, from the Gulf of Mexico and Atlantic Coast Plain. The family is centered on *Icriocarcinus xestos* Bishop, 1988, described from the Late Campanian of Baja California. Closely allied with this species are: "*Eryma*" *flecta* Rathbun, 1926, originally described from the latest Campanian of Tennessee and now known to occur throughout the Maastrichtian of the adjoining Mississippi; *Branchiocarcinus cornatus* Feldmann and Vega, 1995, from the Maastrichtian of San Luis Potosí, Mexico; and undescribed material from the latest Maastrichtian of New Jersey. The Gulf and Atlantic populations compose a single new species—*Branchiocarcinus flectus* (Rathbun). Provisionally regarded as a lobster, on the basis of a single, eroded chela, *B. flectus* is now known from complete bodies found at several locations in the eastern US. The additional material also clarifies the identity of *B. cornatus*, which is based on a distorted external mold of a lone dorsal carapace. Members of the family lack the typical portunoid flattened fifth pereiopod but share other characters that enable placement within the Portunoidea.

Keywords Icriocarcinidae · Crustacea · Upper Cretaceous · Pacific and Gulf Coast

Kurzfassung Icriocarcininae Števčić, 2005, eine ausgestorbene nordamerikanische Unterfamilie von portunoiden Dekapoden, wird auf Familienniveau gehoben und beinhaltet die zwei oberkretazischen Gattungen *Icriocarcinus* Bishop, 1988, von der pazifischen Küste und Branchiocarcinus Feldmann und Vega, 1995, vom Golf von Mexiko und der atlantischen Küstenebene. Die Familie zentriert sich um *Icriocarcinus xestos* Bishop, 1988, beschrieben aus dem Obercampanium von Baja California. Nahe verwandte Arten sind: *"Eryma" flecta* Rathbun, 1926, ursprünglich beschrieben aus dem obersten Campanium von Tenessee, heute bekannt aus dem gesamten Maastrichtium des angrenzenden Mississipi; *Branchiocarcinus cornatus* Feldmann und Vega, 1995, aus dem Maastrichtium von San Luis Potosi, Mexiko; sowie unbeschriebenes Material aus dem obersten Maastrichtium von New Jersey. Die Populationen vom Golf und Atlantik stellen eine einzige neue Art dar: *Branchiocarcinus flectus* (Rathbun). Aufgrund von ungenügenden Merkmalen ursprünglich als Hummer angesehen, ist *B. flectus* heute in Form von vollständigen Körpern aus verschiedenen Lokalitäten der östlichen Vereinigten Staaten bekannt. Das zusätzliche Material klärt auch die Identität von *B. cornatus*, welcher auf einem deformierten Häutungshemd eines dorsalen Karapax basiert. Mitgliedern dieser Familie fehlt das charakteristische portunoide flache fünfte Pereiopod, aber sie besitzen

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andere Merkmale, die eine Platzierung in die Portunoidea rechtfertigen.

Schlüsselwörter Icriocarcinidae · Crustacea · Oberkreide · Pazifische- und Golfküste

Introduction

Foundational work on Upper Cretaceous decapod assemblages in the Pacific Coast and southeastern US regions was accomplished mainly through the efforts of Mary J. Rathbun (deceased, formally with the US National Museum) and Gale A. Bishop (Georgia Southern University). Among the many species each documented from Cretaceous deposits of North America, both reported the same peculiar brachyuran propodi from the Maastrichtian of the central Gulf Coastal Plain. Rathbun (1926) described a single, eroded propodus from the Coon Creek Tongue in Tennessee, suggesting a lobster affiliation (*Eryma* von Meyer, 1840) in naming it. However, Rathbun (1926, p. 188) added a cautious caveat: “There will be doubt about the generic position of this species until other portions of the animal are found.” The author may have later observed similar material in samples assembled by Stephenson and Monroe (1940) from the Prairie Bluff Formation in Mississippi. Rathbun (in Stephenson and Monroe 1940) referred to this unillustrated material as belonging to “a genus of family Portunidae, akin to *Charybdis*.” The only portunoid then and since described from the Upper Cretaceous of the Southeast is *Ophthalmoplax stephensoni* Rathbun 1935, suggesting the possibility that Rathbun’s undescribed material from the Prairie Bluff may be related to the Coon Creek specimen. As discussed below, Rathbun’s Prairie Bluff material is from essentially the same location as many well preserved specimens used in this study.

After discovering similar isolated propodi in the Coon Creek Tongue of Mississippi, Bishop (1983) also expressed doubt about the *Eryma* affiliation, and, although initially indecisive about how to refer to these incomplete remains (Bishop 1983, 1985, 1986a), he eventually acknowledged their portunoid nature (Bishop 1986b).

In a brief review of the genus, Feldmann and Titus (2006) proposed removal of fragment-based assignments from *Eryma* von Meyer made by Rathbun (1923, 1926, 1935), including “*Eryma*” *flecta* Rathbun 1926, until more complete material became available. In the past several years, the writers have identified bodies with associated chelipeds from the type and other localities in the Gulf of Mexico and Atlantic Coastal Plain and now affiliate them with the portunoid genus *Branchiocarcinus*. Finally, there does not seem to be a relationship between Rathbun’s (1926) “*E.*” *flecta* and other chelae-based species attributed by Rathbun (1923, 1935) to *Eryma* von Meyer.

Bishop (1988) described *Icriocarcinus xestos* from the Late Campanian Point Loma Formation near Carlsbad, San Diego County, California, and placed it into the Portunoidea Rafinesque, 1815, as part of the Family Carcineretidae Beurlen, 1930. Vega and Feldmann (1991) and Vega et al. (1997) suggested that the genus should be placed into the Xanthoidea MacLeay, 1838. Schweitzer et al. (2002) assigned *Icriocarcinus* Bishop, 1988, to the Goneplacidae MacLeay, a placement sustained by several others (Karasawa and Kato 2003; Schweitzer and Karasawa 2004; Schweitzer and Feldmann 2005; Karasawa and Schweitzer 2006; Castro 2007; Schweitzer et al. 2007, 2010; Karasawa et al. 2008; De Grave et al. 2009; Hyžný 2011). Števčić (2005, p. 69) erected the subfamily Icriocarcininae to be questionably placed within the Goneplacidae (Goneplacoidea). We suggest that this taxon should remain within the Portunoidea and be raised to the family level.

We propose that the Icriocarcinidae contain the genera *Icriocarcinus* Bishop, 1988, and *Branchiocarcinus* Vega, Feldmann and Sour-Tovar, 1995. *Branchiocarcinus cornatus* Feldmann and Vega, 1995 (in Vega et al. 1995) was described from the Maastrichtian Cárdenas Formation of San Luis Potosí, NE Mexico, on the basis of a single, partial carapace, and included as part of the Carcineretidae, a position followed by several authors (Vega et al. 2001, 2006; Feldmann and Villamil 2002; Sepkoski 2002; De Grave et al. 2009; and Schweitzer et al. 2010; among others). Although the dorsal carapaces of *Icriocarcinus* and *Branchiocarcinus* have clearly similar carapace shape, dorsal carapace regions, venter, and pereiopods, they were often placed in different superfamilies (De Grave et al. 2009; Schweitzer et al. 2010). Even less clear taxonomically was “*E.*” *flecta* Rathbun (1926), which is here assigned to *Branchiocarcinus* as *Branchiocarcinus flectus* new combination.

Geologic setting and age

The material discussed herein was recovered from several different units and disparate locations in southern North America—*Icriocarcinus* from California and Baja California, and *Branchiocarcinus* from Tennessee, Mississippi, New Jersey, and San Luis Potosí.

Icriocarcinus. Specimens of *Icriocarcinus xestos* Bishop were recovered from the Rosario Formation of Punta San Tomás, Baja California Norte, Mexico (Fig. 1). The Upper Cretaceous beds at Punta San Tomás are immediately

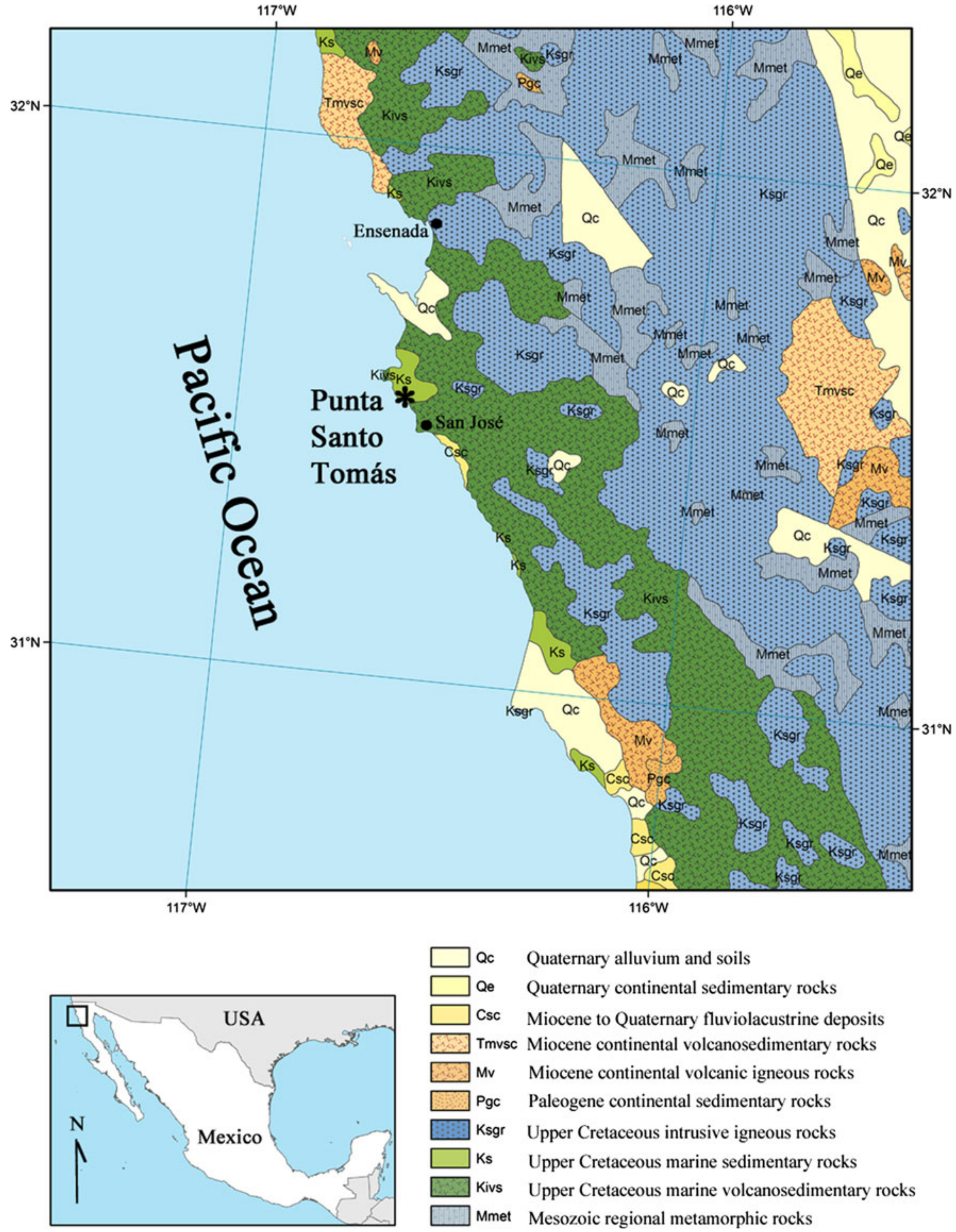


Fig. 1 Geologic map of NE portion of Baja California, Mexico, near the border with the USA. Note Upper Cretaceous deposits (*Ks*) along the Pacific coast, mostly from the Campanian Rosario Formation. Specimens here reported were collected at Punta Santo Tomás, NE of San José town. From Ferrari et al. (2007)

adjacent to the Punta San José section, which has been studied by Kilmer (1966), Gastil et al. (1975), Filmer and Kirschvink (1989), Backus (1998), and Ward et al. (2012). The Rosario Formation crops out along the Pacific Coast of northern Baja and is principally composed of siltstone, fine sandstone, and channel-fill conglomerates. Bishop (1988) reported the xanthid brachyuran *Xandaros sternbergi* (Rathbun, 1926) from this unit in the Punta San José section.

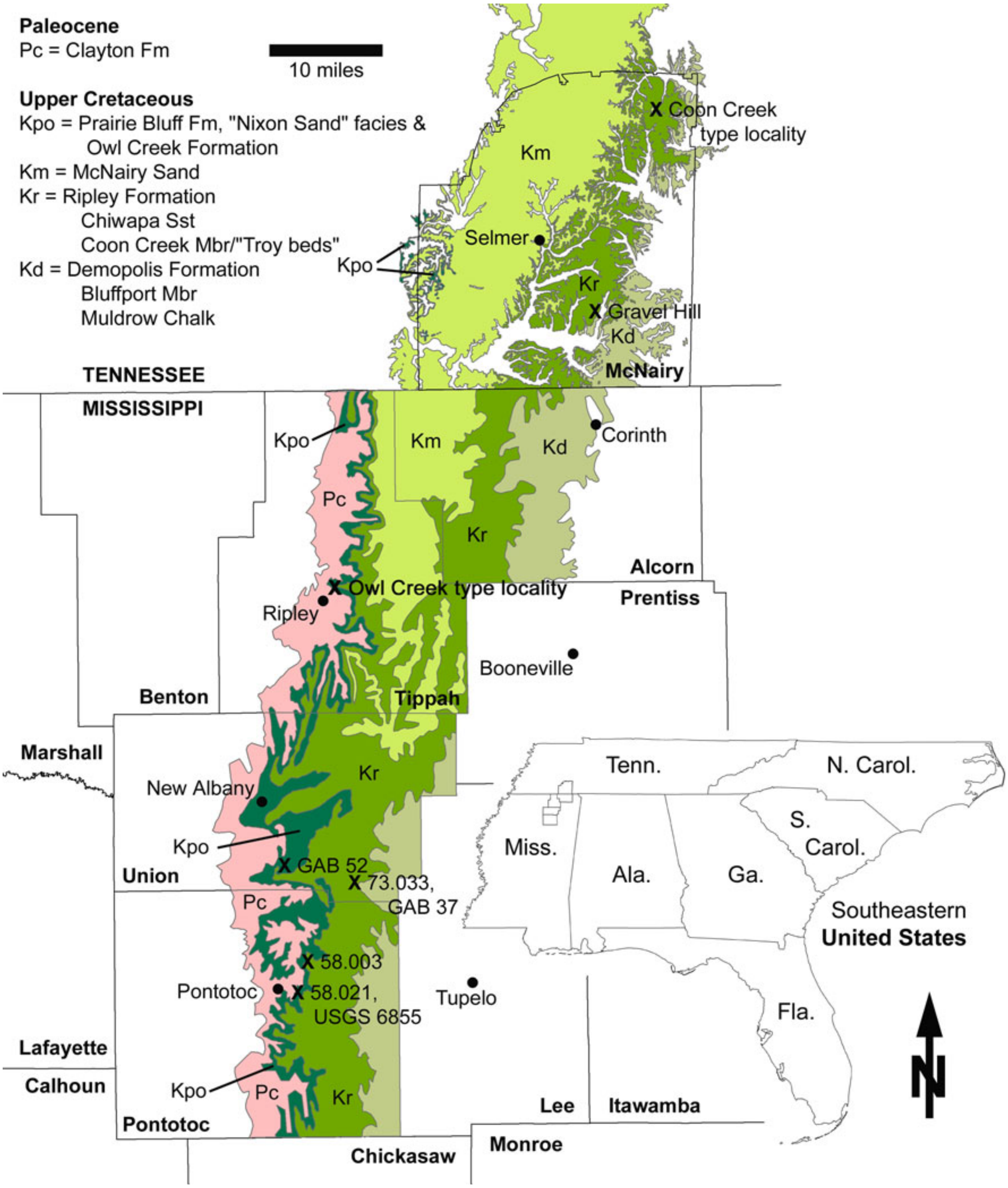


Fig. 2 Map of the Maastrichtian beds in northeast Mississippi and adjacent Tennessee. Fossil localities are marked with *X*s; cities denoted with *solid circles*; county names in *bold*. Bishop's (1983) locality GAB 37 is equivalent to MMNS locality MS.73.033; Stephenson and Monroe's (1940) locality USGS 6855 is equivalent to MMNS locality MS.58.021. All samples were collected from the Early Maastrichtian Coon Creek beds (Ripley Fm), except those collected at GAB 52 and the Pontotoc sites, which are exposures of the Late Maastrichtian "Nixon sand". Map created in ArcMap™ 9.2 (©1999–2006, ESRI). Mississippi and Tennessee geologic shape files based on Bicker (1969) and Parks and Russell (1975), respectively. Bicker (1969) mapped beds as contiguous across their surface intersect, inferring continuity in the subsurface, whereas Parks and Russell (1975) accounted for Quaternary alluvial dissection. Precise details of the Mississippi localities are available upon request from the Mississippi Museum of Natural Science

Up the coast in adjoining California and north of Sand Diego is the type locality of *Icriocarcinus xestos* Bishop, 1988, which occurs in the Point Loma Formation at Carlsbad. The Point Loma Formation consists of interbedded fine-grained sands and clays (Kennedy and Moore 1971). As is the case in the Rosario Formation, the Point Loma also contains *X. sternbergi* (Bishop, 1988).

Branchiocarcinus. Decapod remains have been recovered throughout the Upper Cretaceous section in the northern Gulf of Mexico Basin, but the Coon Creek Tongue in Mississippi and Tennessee can be locally rich and diverse in them (Rathbun 1935; Bishop 1983, 1985, 1986a). The brachyuran *Branchiocarcinus* occurs in several lithofacies in the Maastrichtian section of the eastern Mississippi Embayment, including the Coon Creek Tongue of Wade (1926) and Sohl (1960), the Prairie Bluff Chalk of, e.g., Sohl (1960), the Nixon Sand of Phillips (2010), and the Owl Creek Formation of, e.g., Sohl (1960). *Branchiocarcinus* also occurs in the Late Maastrichtian Tinton Formation of the Atlantic Coastal Plain, the macrofaunal content of which was discussed by Landman et al. (2007).

The lowest observed stratigraphic occurrence of *Branchiocarcinus* is in the Coon Creek Tongue of Tennessee and Mississippi (Figs. 2, 3). The Coon Creek Tongue, treated as the lower member of the Ripley Formation in north Mississippi, is a complex of glauconitic clayey and sandy lagoonal beds containing variably winnowed fossil-rich lags with a fauna similar to that of the younger Owl Creek Formation. *Branchiocarcinus* also occurs in all the Late Maastrichtian lithofacies in Mississippi. Moving northward in the Mississippi Embayment and on the eastern side, the laterally changing surface sequence begins to the south with the typical chalk/marl of the Prairie Bluff Formation (west-central Alabama and east-central Mississippi), which is gradually replaced by increasingly terrigenous sediments that may be regarded as member units: the superjacent Nixon Sand (sandy marl facies of Phillips (2010)) and the laterally adjacent "4th Street" facies (including clayey, sandy, and slightly aragonitc layers). Overlying and gradually replacing the Nixon Sand is the Owl Creek Formation.

The typical Prairie Bluff Formation, or "Prairie Bluff chalk" (Sohl 1960), is a deep inner shelf (or shallow middle shelf) deposit representing the deepest marine facies occurrence of *Branchiocarcinus*. The Prairie Bluff is a fine-grained marl (not a true chalk), although there are thin, condensed intervals where the quartz sand is significant. The Prairie Bluff does not preserve aragonitic shells but contains a diverse and abundant moldic fauna (Sohl 1960, 1964) and calcitic shells. Moving northward and updip, the Nixon Sand (Phillips 2010) is a texturally and faunally distinctive bed of calcareous sand to sandy marl lying intergradationally (laterally and vertically) between the middle shelf deposits of the Prairie Bluff Formation and the shallower Owl Creek Formation (Stephenson and Monroe 1940). The Nixon Sand is an even-textured wackestone or packstone and contains little to no glauconite. The Nixon Sand preserves moldic mollusks (no aragonite), calcitic pterioid bivalves, decapod remains, and abundant

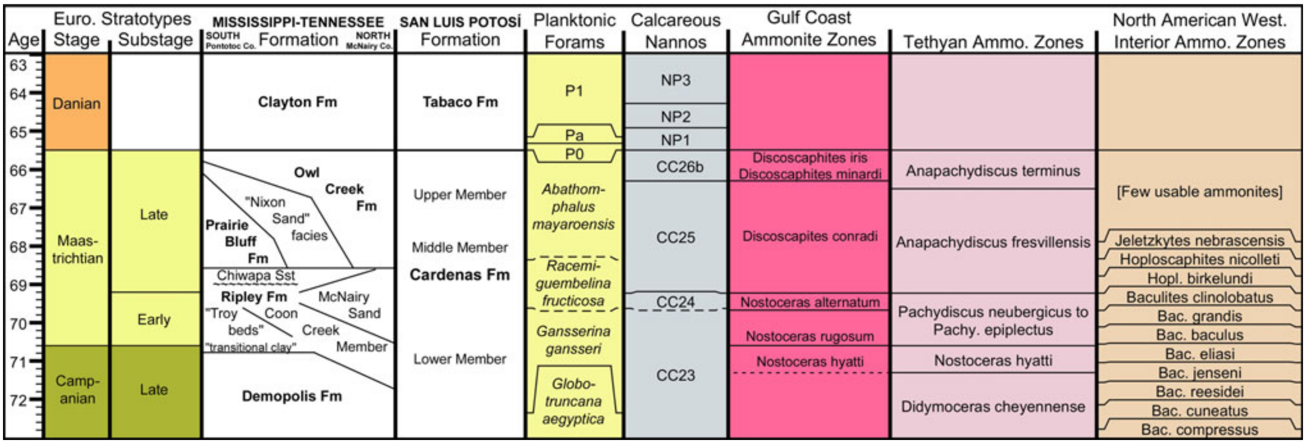


Fig. 3 Stratigraphic chart correlating the Maastrichtian of Mississippi with that of San Luis Potosi. Basic chart chronostratigraphy and most of the biostratigraphic columns were created in TS (TimeScale) Creator (©2005–2010, A. Lugowski and J. Ogg). All ages are standardized to the Geologic Time Scale 2004 and the Concise Geologic Time Scale compilation of the International Commission on Stratigraphy and its Subcommission on Stratigraphic Information. The stratigraphic data used in TS Creator are based on numerous events borrowed from many global and regional reference sections and integrated time scales. The Gulf Coast ammonite zones and their correlative ages are based on Cobban (1974), Cobban and Kennedy (1991a, b, 1993, 1995), and Landman et al. (2004). The position of the stage and substage boundaries is based primarily on the work of Sohl and Koch (1986) and the ammonite zones defined by the aforementioned authors. The informal units "Nixon Sand", "Troy beds", and "transitional clay" were introduced by Phillips (2010), Swann and Dew (2008, 2009), and Sohl (1960), respectively. Correlation of the San Luis Potosí section with the Mississippi section is approximate and thus tentative. The Coon Creek beds are time-transgressive, the Campanian–Maastrichtian boundary being located higher in the section in the northern part of the outcrop belt (Tennessee). A major unconformity is recognized at the base of the Chiwapa Sandstone, separating it, in sequence stratigraphic terms, from the remainder of the subjacent Ripley Formation. Foraminiferal zonation in the Gulf Coast defines the Campanian–Maastrichtian boundary as coincident with the transgressive surface marking the base of the Chiwapa Sandstone (Mancini et al. 1995; Puckett 2005)

echinoids and bryozoans. *Branchiocarcinus* was encountered regularly in this lithofacies. Also in the updip, and still further north, the typical Prairie Bluff Formation becomes multiple thin facies of calcareous sands and sandy marls, each with a distinctive fossil composition, (at least) one of which contains some aragonitic preservation and another an echinoid-bearing calcareous sand. This sandy bedded series, the "4th Street" facies (named for type locality MS.73.041), lies below the Nixon Sand, contains more siliceous clay and glauconite, and floatstone layers, including a phosphatic, fossil-rich lag and a shell bed of calcitic pseudomorphs. Fragmentary *Branchiocarcinus* are found as fragmentary steinkerns occurring in the phosphatic lag.

Similar in many respects to the Coon Creek Tongue, the Owl Creek Formation consists of glauconitic, fine sandy siliceous clay beds containing both aragonitic and calcitic mollusks (including well-preserved shells of *Discoscaphites* Meek, 1870), decapod remains, and small burrowing echinoids. Within both the Owl Creek Formation and the 4th Street facies of the Prairie Bluff Formation, *Branchiocarcinus* occurs with the retroplumid *Costacopluma* Collins and Morris, 1975. The macrofauna in the Owl Creek of Mississippi is very similar if not near identical with that of the Tinton Formation of New Jersey, including the presence of *Pinna laqueata* (Conrad, 1858); *Tenuipteria argentea* (Conrad, 1858); *Eubaculites carinatus* (Morton, 1834); *Discoscaphites iris* (Conrad, 1858); *Schizaster variabilis* (Slocom, 1909), and *B. flectus* (Rathbun, 1926) new combination.

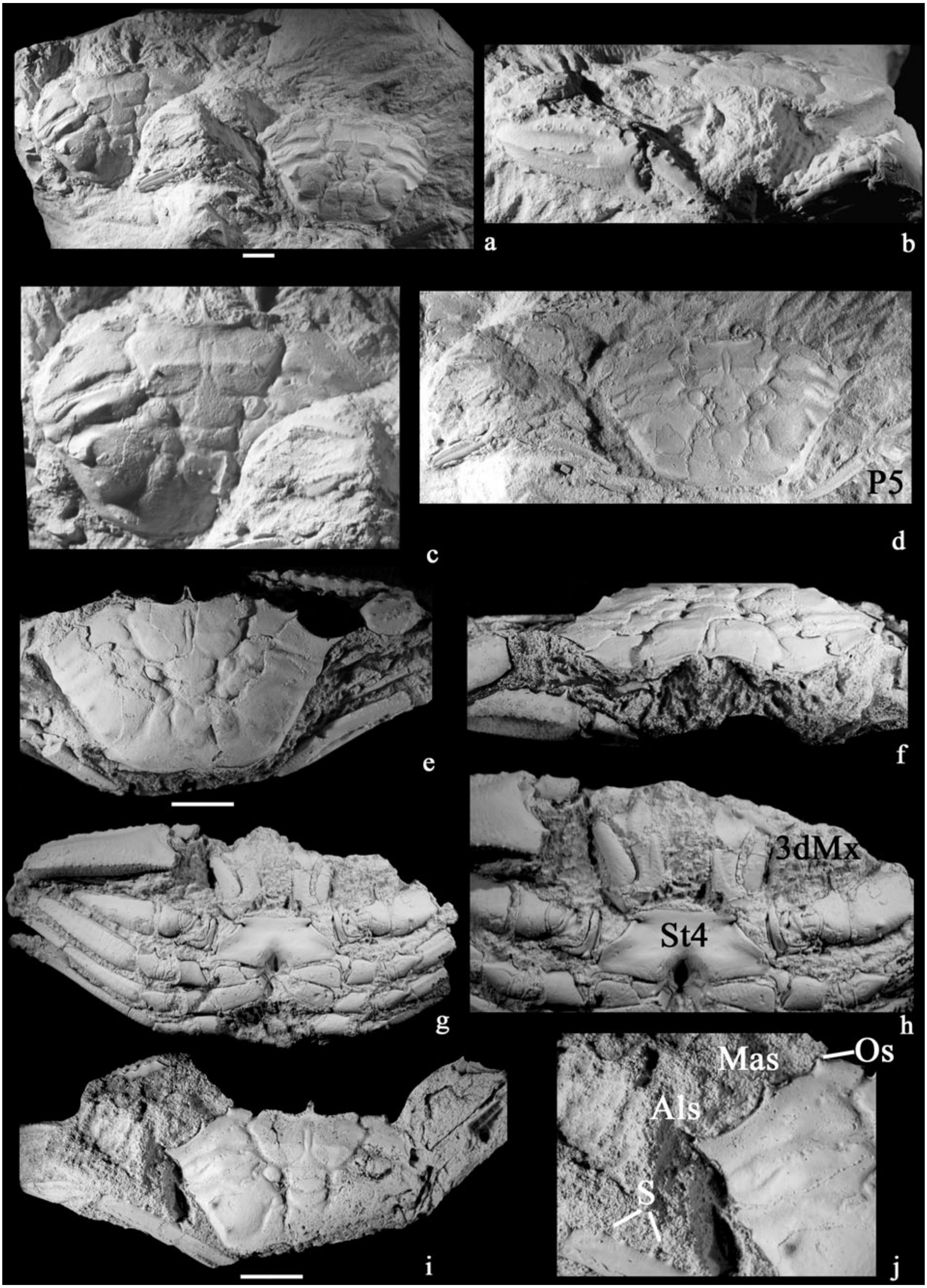
The Cárdenas Formation (Böse 1906) is a sequence of mainly terrigenous sediments that crops out on the western margin of the Sierra Madre Oriental in San Luis Potosí, east-central Mexico. A diverse invertebrate fauna has been described from a variety of localities and a lagoonal paleoenvironment has been interpreted for most of the sequence (Böse and Cavins 1927; Burckhardt 1930; Müllerried 1930; Myers 1968; Hurtado-González 1984; Vega et al. 1995; Alencáster et al. 1999; Caus et al. 2002; Ifrim et al. 2005; Baron-Szabo et al. 2006; Schafhauser et al. 2003, 2007; Omaña et al. 2008; Ifrim and Stinnesbeck 2010; among others). From the Montebello section (locality IGM 2616) in San Luis Potosí, Vega et al. (1995) reported callianassid remains, a questionable majid carapace, several specimens of *Dakoticancer australis* Rathbun, 1935; *Costacopluma bishopi* Vega, Feldmann and Sour-Tovar, 1995, and *B. cornatus*.

Age. On the basis of ammonite biostratigraphy, magnetostratigraphy, and absolute ages obtained from strontium isotopes of ammonite aragonite, Ward et al. (2012) suggested a Middle to Early Late Campanian age for the Rosario Formation at Punta San José. Foraminiferal studies suggest a Middle Campanian to Early Maastrichtian age for the Point Loma Formation in the vicinity of Carlsbad (Sliter 1968; Kennedy and Moore 1971; Bukry 1994). Specimens of *I. xestos* described initially by Bishop (1988) and later by Schweitzer et al. (2007) were collected from the Point Loma Formation, from strata that are probably correlatable and contemporary with the crab-bearing beds of the Rosario Formation at Punta Santo Tomás.

Fig. 4 *Icriocarcinus xestos* Bishop, 1988. **a** Concretion containing two dorsal carapaces with limbs (IGM-6625-1 and IGM-6625-2), Rosario Formation, Punta Santo Tomás, Baja California, Mexico. **b** Frontal view of specimen IGM-6625-1, whitened. **c** Dorsal view of same specimen, whitened. **d** Dorsal view of carapace IGM-6625-2, whitened. **e** Dorsal view of carapace IGM-7722, whitened, Rosario Formation, Punta Santo Tomás, Baja California, Mexico. **f** Frontal view of same specimen, whitened. **g** Ventral view of same specimen, whitened. **h** Ventral detail of same specimen to show left third maxilliped (*3dMx*) and sternite 4 (*S4*), whitened. **i** Dorsal view of carapace IGM-7957, whitened, Rosario Formation, Punta Santo Tomás, Baja California, Mexico. **j** Left dorsal carapace detail of same specimen to show orbital (*Os*), middle anterolateral (*Mas*) and anterolateral (*Als*) spines and spines on dorsal edge of P4 (*S*), whitened. *Scale bars* = 10 mm ▶

The Coon Creek Tongue in Tennessee is regarded as latest Campanian in age at the type locality on the basis of a distinctive ammonite assemblage containing several heteromorphs, including the index species *Nostoceras hyatti* Stephenson, 1941 (Cobban and Kennedy 1995; Larson 2003). However, from the Coon Creek Tongue to the south in Mississippi, Cobban (1974) reported *Nostoceras alternatum* (Tuomey, 1854), which is indicative of an Early Maastrichtian age (Cobban and Kennedy 1995). Therefore, the Campanian–Maastrichtian boundary lies within the Coon Creek Tongue, the boundary dropping in the section southward upon entering Mississippi (Figs. 2, 3). Ostracod and foraminiferal biozonations for the southeastern US indicate an early Late Maastrichtian age for the Prairie Bluff and Owl Creek formations (Mancini et al. 1995), and thus their intervening facies (Nixon Sand and 4th Street). Ammonite zonation also suggests a Late Maastrichtian age for these units, and identifications by Neil Landman, American Museum of Natural History, indicate an overlapping and gradually younging succession for these facies, with the Prairie Bluff dominated by the oldest Late Maastrichtian scaphitid-baculitid assemblage and the Owl Creek by the youngest (or younger) one (Landman et al. 2004). Finally, in the Atlantic Coastal Plain, the age of the Tinton Formation is latest Maastrichtian (Landman et al. 2007). Therefore, in North America, *Branchiocarcinus* occurs in the northern Gulf of Mexico and Atlantic Coastal Plain in deposits ranging in age from latest Campanian to Late Maastrichtian and is found essentially throughout the Maastrichtian section in Mississippi (Figs. 2, 3).

The presence of *Exogyra costata* Say, 1820, in the Cárdenas Formation at Montebello (IGM 2616; Vega et al.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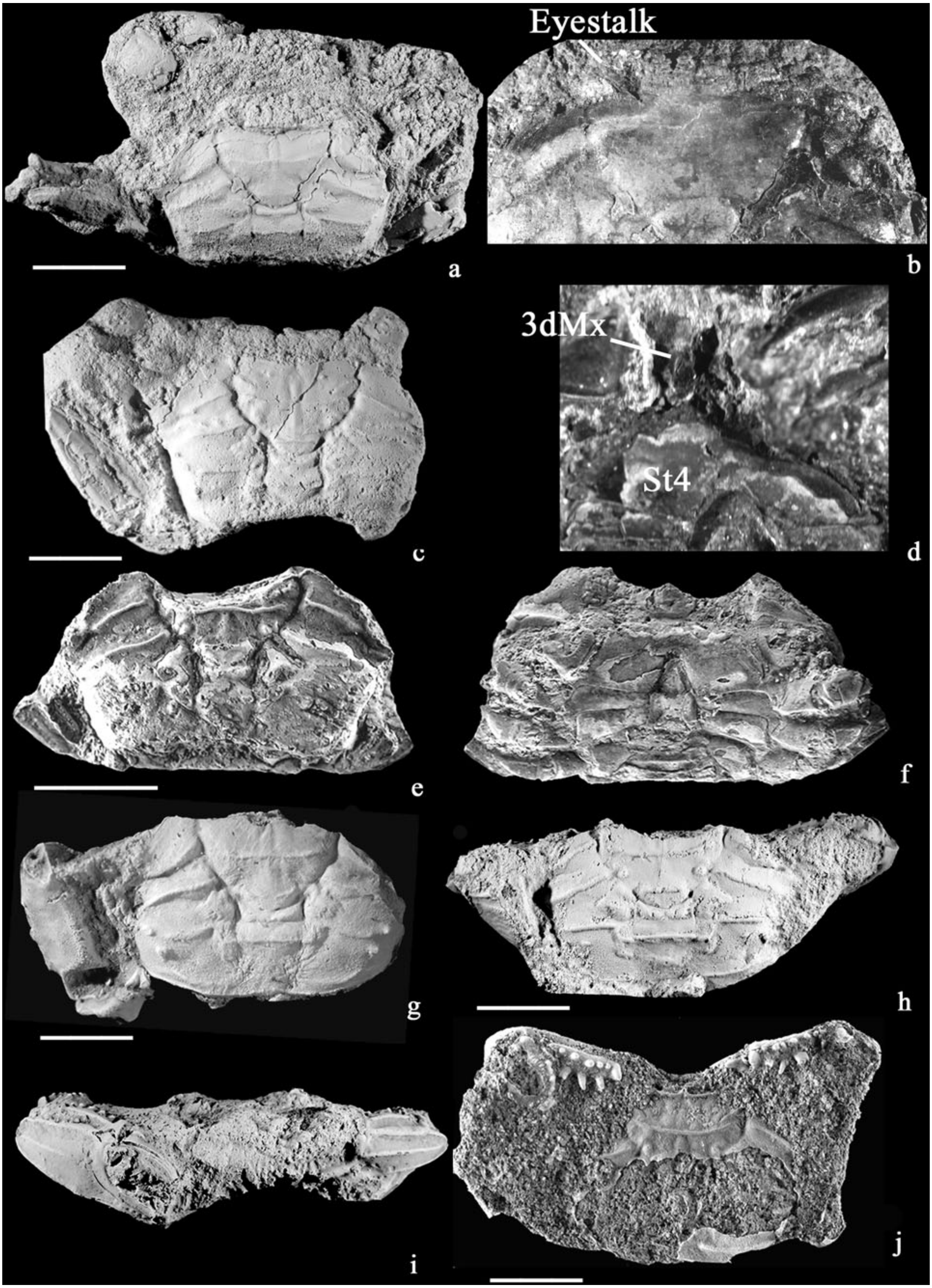
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◀ **Fig. 5** *Branchiocarcinus flectus* (Rathbun 1923), new combination. **a** MPPM 1972.46.459, dorsal view of carapace with limbs, whitened, Coon Creek Tongue, Coon Creek type locality, McNairy County, Tennessee. **b** Detail of front view of same, showing right eyestalk. **c** MMNS IP-2813, dorsal view of carapace with limbs, whitened, Coon Creek Tongue, locality MS.73.033, Union County, Mississippi. **d** Detail of ventral view of same with exposed third maxillipeds (*3dMx*) and partial sternite 4 (*St4*). **e** USNM 543041, dorsal view of carapace with partial limbs, Owl Creek Formation, Owl Creek type locality, Tippah County, Mississippi. **f** Ventral view of same, male with partial abdomen, sternum and P1–P4 coxae. **g** MMNS IP-3014, dorsal view of carapace with partial limb, whitened, Coon Creek Tongue, locality MS.73.033, Union County, Mississippi. **h** Epitype/chorotype MPPM 1972.46.452, dorsal view of carapace with limbs, whitened, Coon Creek Tongue, Coon Creek type locality, McNairy County, Tennessee. **i** Frontal view of same showing both chelipeds, whitened. **j** MMNS IP-2966, dorsal view of partial carapace with limbs (note rows of spines on dorsal surface of right palm), Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. *Scale bars* = 10 mm

1995) suggests a Maastrichtian age for the sediments containing *B. flectus*.

Methods and materials

Ammonium chloride (NH_4Cl) smoke was used to enhance the specimens in Figs. 4b–j, 5a, b, g–i, 6d–l, 7a, b. All other specimens were photographed uncoated under artificial light.

Material used in this study is housed in the Paleobiology Collection at the National Museum of Natural History, Washington, DC (USNM); the Pink Palace Museum in Memphis, Tennessee (MPPM); the Colección Nacional de Paleontología, Instituto de Geología, UNAM, Mexico City, Mexico (IGM); the Mississippi Museum of Natural Science, Jackson, Mississippi (MMNS); the Gale A. Bishop decapod collection at the South Dakota School of Mines and Technology, Rapid City, South Dakota (GAB); the American Museum of Natural History (AMNH); and the Monmouth Amateur Paleontologists Society, West Long Branch, New Jersey (MAPS).

Systematic paleontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Icriocarcinidae Števčić, 2005 new status

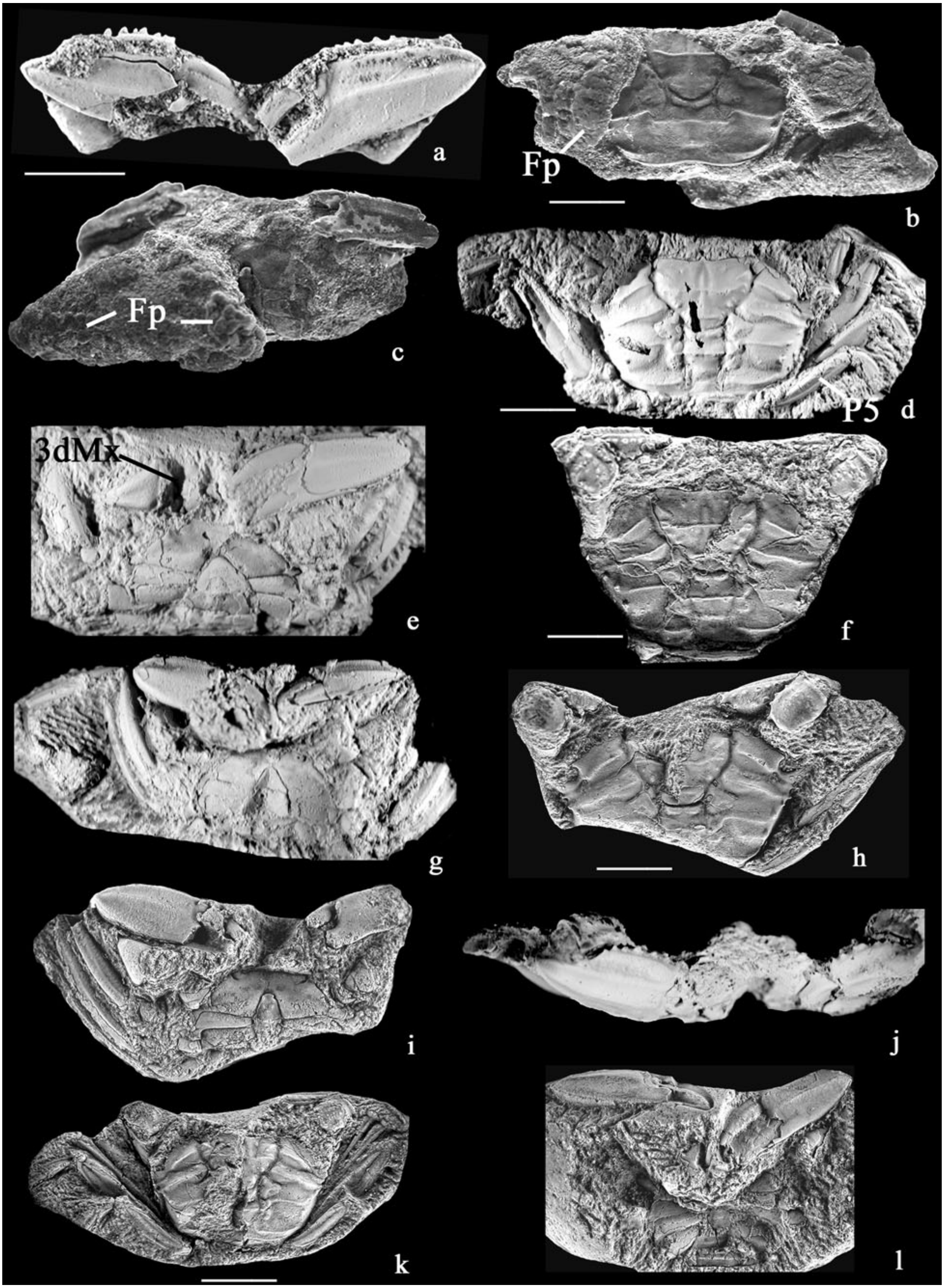
Icriocarcininae Števčić, 2005, p. 69.

Type genus. *Icriocarcinus* Bishop, 1988.
Genera included. *Icriocarcinus* Bishop, 1988; *Branchiocarcinus* Vega, Feldmann, and Sour-Tovar, 1995.

Diagnosis. Carapace small to medium, inverted subtrapezoidal, twice as wide as long, widest at level of sharp, front-directed anterolateral spines; anterior margin straight, pseudorostrum narrow, long, downturned; eyestalks long and slender, distal portion reaches anterolateral spine; orbits wide, ovate with short, anterolaterally projected spine; anterolateral margin short, arched with small middle spine; strong, slightly curved anterolateral spine divides anterolateral from posterolateral margin; posterolateral margin long, steep, two-thirds maximum carapace length with three small sharp, evenly-spaced tubercles; posterior margin nearly straight, one-third the maximum carapace width; dorsal carapace regions marked by strong transverse ridges and deep cervical groove; sharp transverse ridges on proto, meso, meta, and urogastric, and epi, meso, and metabranchial regions; sternum wide, transversely subovate, widest at midlength, sternite 3 transversely subtrapezoidal, sternite 4 subtrapezoidal, sternite 5 transversely subrectangular, sternite 6 similar to sternite 5, sternite 7 rectangular, sternite 8 small and subquadrate; episternal process of sternites 4–6 inverted, triangular; male abdomen triangular, telson triangular, somite 6 subtrapezoidal, somite 5 subrectangular, somites 4 and 3 similar to somite 5; endopodite of third maxilliped inverted subtrapezoidal; chelipeds slightly unequal, right chela slightly larger than left; meri with row of tubercles on ventral surface, carpus with spines on dorsal surface; palm of both chelipeds robust, subrectangular elongated, with strong longitudinal ridges on external surface, dorsal surface of palm with two three rows of sharp spines, ventral margin with fine tubercles; dorsal surface of dactylus with row of longitudinal spines; P2–P5 long, slender, dactylus unciform.

Discussion. Števčić (2005) erected the subfamily Icriocarcininae to be questionably placed within the Goneplacidae and to include only the type genus *Icriocarcinus*. *Branchiocarcinus*, originally placed in the Carcineretidae, shares nine features with *Icriocarcinus*:

1. an inverted subtrapezoidal carapace that is wider at the level of the anterolateral spines;
2. slender eyestalks;
3. narrow and projected pseudorostrum;
4. sharp, projecting anterolateral spines;
5. sharp, short, slightly inclined transverse ridges on the dorsal carapace;
6. a few small tubercles along the posterolateral margin;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◀ **Fig. 6** *Branchiocarcinus flectus* (Rathbun 1923), new combination. **a** MMNS IP-2966, frontal view of partial carapace with chelipeds, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **b** MMNS IP-3141, dorsal view of carapace with chelipeds, Coon Creek Tongue, locality MS.73.033, Union County, Mississippi. **c** Ventral view of same with row of fecal pellets (*Fp*). **d** MMNS IP-4388, dorsal view of carapace with limbs, including fifth pereiopod (*P5*), whitened, Owl Creek Formation, Owl Creek type locality, Tippah County, Mississippi. **e** Ventral view of same showing both chelipeds and third maxilliped (*3dMx*), whitened. **f** MMNS IP-4389, dorsal view of carapace with limbs, whitened, Owl Creek Formation, Owl Creek type locality, Tippah County, Mississippi. **g** Ventral view of same showing both chelipeds, whitened. **h** MMNS IP-4390, dorsal view of incomplete carapace with partial limbs, whitened, Owl Creek Formation, Owl Creek type locality, Tippah County, Mississippi. **i** Ventral view of same showing both chelipeds, whitened. **j** Frontal view of same showing both chelipeds, whitened. **k** MMNS IP-4391, dorsal view of carapace with limbs, whitened, Owl Creek Formation, Owl Creek type locality, Tippah County, Mississippi. **l** Ventral view of same showing both chelipeds, whitened. *Scale bars* = 10 mm

7 subovate sternum, slightly wider than long, with interrupted sutures 4/5;
8 well developed chelipeds with longitudinal carinae on the outer surface of the palms, two rows of spines on the dorsal surface of the palms, and a short, curved dactylus; and
9 slender pereiopods 2–5, each with an unciform dactylus.

Unique morphological features shared by *Icriocarcinus* and *Branchiocarcinus* indicate they belong to a discrete portunoid family. Although some similarities are shared with the Lithophylacidae, both families have features sufficiently peculiar to each to keep them separated, possibly as some of the most primitive Portunoidea (Karasawa et al., 2008).

Schweitzer et al. (2010) included *Icriocarcinus* in the Goneplacidae MacLeay (1838) and described the goneplacoid affinities (Schweitzer et al. 2002) of *Icriocarcinus* on the basis of its apparent similarities to the goneplacoid genus *Ommatocarcinus* White, 1852. Schweitzer et al. (2007, fig. 3e, f) illustrated a specimen of *O. macgillivrayi* White, 1852 to show those similarities. However, these similarities should be contrasted with the differences that exist between *Icriocarcinus* and *Ommatocarcinus*. Included among these more important differences are:

1 the eyestalks of *Ommatocarcinus* are extremely large and the orbital spines do not correspond to the anterolateral spines of *Icriocarcinus*;
2 the dorsal carapace in *Ommatocarcinus* is nearly smooth, except for a continuous, transverse ridge that is not equivalent to any of the ridges seen for *Icriocarcinus*;
3 *Icriocarcinus* has a short, projected pseudorostrum, not seen for *Ommatocarcinus*;
4 the sternum of *Ommatocarcinus* is much wider than long, whereas for *Icriocarcinus* it is only slightly wider;
5 sternite 4 of *Icriocarcinus* is longer and narrower than that of *Ommatocarcinus*;
6 the chelipeds of *Ommatocarcinus* are slenderer and lack spines and there are no longitudinal ridges on outer surface of palm; and
7 the dactyli of *Icriocarcinus* are curved and shorter.

In goneplacoids, the carapace and chelipeds are usually smooth whereas in the Icriocarcinidae the carapace has well-defined dorsal regions and the chelipeds are spiny.

Although no unique portunoid features were found among the Icriocarcinidae, some frequent portunoid characters are:

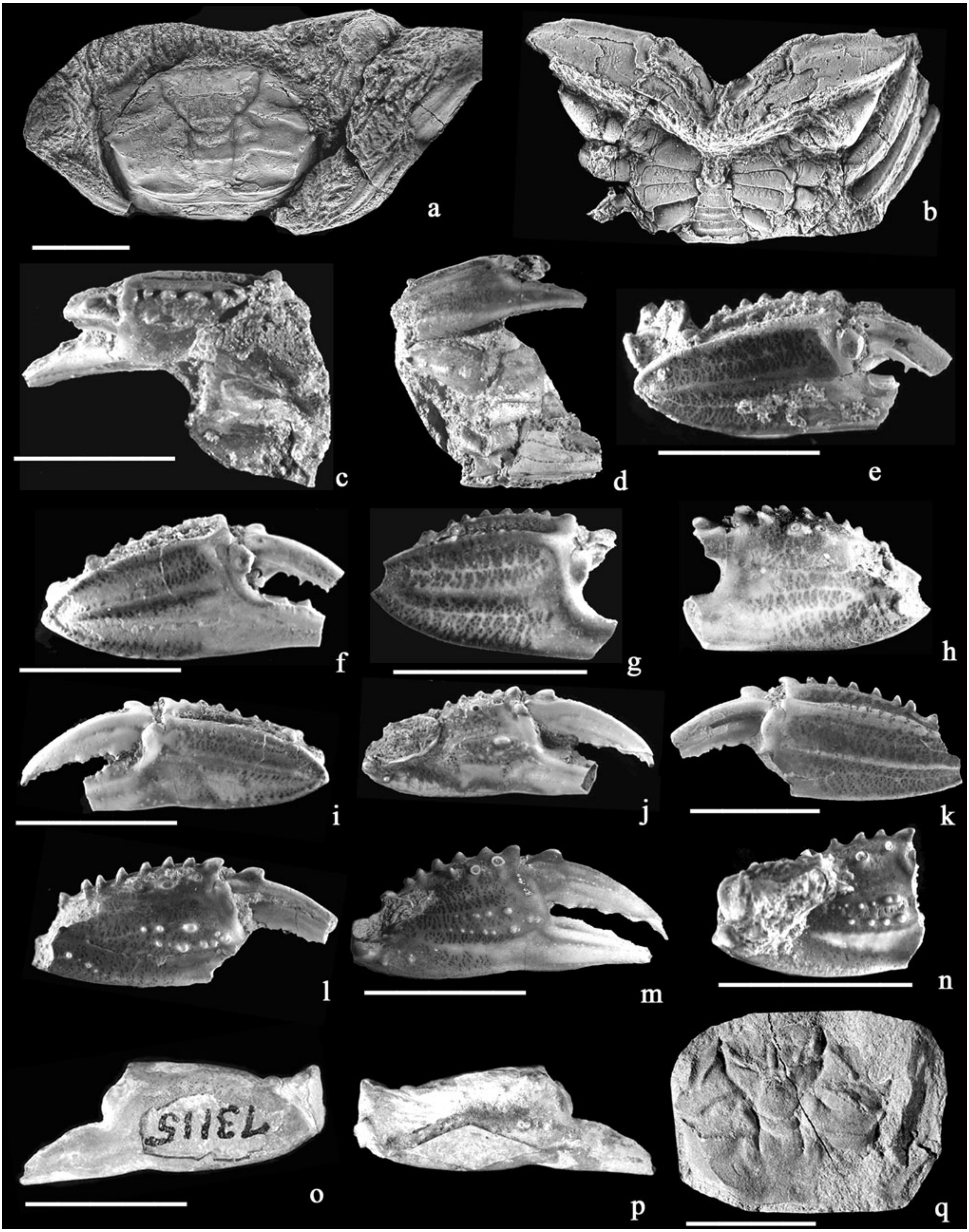
1 a carapace wider than long, the dorsal surface marked by sharp ridges and deep grooves;
2 calcified eyestalks, long and slender; and
3 spiny chelipeds, the meri with a row of spines on the ventral keel, the palm with strong longitudinal carinae on the outer surface, and the dactyli with curved spines on the dorsal surface.

Although the fifth pereiopod is not flattened on either of these genera, a thin, slender P5 with unciform dactylus may reflect a primitive condition within the Portunoidea.

Schweitzer et al. (2007) indicated possible affinities of *Lithophylax* with the Goneplacidae, but later Schweitzer et al. (2010) placed the family Lithophylacidae Van Straelen, 1936, in the Portunoidea. *Lithophylax* bears many similarities with *Icriocarcinus* and *Branchiocarcinus*:

- inverted subtrapezoidal carapace;
- sharp anterolateral spines;
- slender, projected pseudorostrum;
- ridges and grooves on the dorsal carapace;
- elongate, subrectangular third maxillipeds; and
- transverse keels on the abdominal somites.

However, the differences between *Lithophylax* and the icriocarcinids are notable. *Lithophylax* has more rounded ridges and bosses in the dorsal carapace. Its anterior margin is straight, whereas that of icriocarcinids has a small notch that breaks the frontal line. The posterolateral margin is smooth whereas in the Icriocarcinidae it bears small spines. In *Lithophylax*, sternite 6 is more reduced than sternite 5 whereas these same sternites have a similar shape and size in *Branchiocarcinus*. *Lithophylax* has a reduced P5 (according to Guinot and Breton 2006) and has chelipeds that are not spiny on the dorsal surface, with weak median transverse keel on the anterior surface of the palm (Guinot and Breton 2006). Similarities between *Lithophylax* (Cenomanian of Europe) and the Icriocarcinidae (Campanian–Maastrichtian of North America) may be explained in one of several ways: convergence an ancestor–descendant relationship (most probably), in which icriocarcinids redeveloped the fifth pereiopod (if I was reduced indeed in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◀**Fig. 7** *Branchiocarcinus flectus* (Rathbun 1923), new combination. **a** MMNS IP-4392, dorsal view of carapace with limbs, whitened, Owl Creek Formation, Owl Creek type locality, Tippah County, Mississippi. **b** Ventral view of same showing both chelipeds, whitened. **c** MMNS IP-2868, dorsal view of partial carapace with right cheliped, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **d** Ventral view of same. **e** MMNS IP-2726.1, frontal view of right chela, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **f** MMNS IP 2376.2, frontal view of right chela, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **g** MMNS IP-3592, frontal view of right chela, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **h** Inner view of same. **i** MMNS IP-2376.1, frontal view of left chela, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **j** Inner view of same. **k** MMNS IP-2027, frontal view of left chela, Nixon sand, locality MS.58.003, Pontotoc County, Mississippi. **l** Inner view of same. **m** MMNS IP-2999.1, inner view of left chela, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **n** MMNS IP-2726.3, inner view of left chela, Nixon sand, locality MS.58.021, Pontotoc County, Mississippi. **o** Holotype USNM 73115, outer view of left chela, Coon Creek Tongue, Gravel Hill locality, McNairy County, Tennessee. **p** Inner view of same. **q** *Branchiocarcinus cornatus* Feldmann and Vega, 1995, IGM-6244, dorsal view of incomplete carapace, Cárdenas Formation, locality IGM 2616, Montebello, San Luis Potosí, Mexico. *Scale bars* = 10 mm

Lithophylax) or possibly even rarefaction whereby the observed occurrence and diversity of these types of crab is much lower than actual.

Karasawa et al. (2008) suggested a basal position of the Lithophylacidae within the Portunoidea. Similarities between the Icriocarcinidae and the Lithophylacidae may reveal a close relationship, but morphological differences are enough to keep them as separate families. If the presence of a well developed P5 in *Lithophylax* is confirmed in the near future, it may be possible that the Icricarcinidae and the Lithophylacidae are part of the same family, so they may both become subfamilies within the Lithiphylacidae, but for the moment, reduced P5 in *Lithophylax*, among other features, prevents inclusion of Icriocrcinidae as part of the Lithophylacidae.

The sole known specimen of the carcineretid *Cancrixantho* Van Straelen, 1934, from the Campanian of Spain, is similar to the Icriocarcinidae in its anterior margin, pseudorostrum, and dorsal carapace. It also has spines on the posterolateral margin, but the original shape of the carapace has been lost, as a result of unskilled preparation of the specimen, and the anterolateral margins are not preserved. More complete specimens may reveal that *Cancrixantho* (currently in the Carcineretidae) may instead belong to the Icriocarcinidae, thus extending the paleobiogeographic and biostratigraphic range of the family.

Distributed on both coasts of North America (and possibly in Europe also) during the Late Cretaceous (Campanian–Maastrichtian), the Icriocarcinidae became extinct at the end of the period.

Genus *Icriocarcinus* Bishop, 1988

Type species: *Icriocarcinus xestos* Bishop, 1988, p. 247, figs. 2a–d, 3a–d.

Species included: *Icriocarcinus xestos* Bishop, 1988.

Icriocarcinus xestos Bishop, 1988, fig. 4

Icriocarcinus xestos Bishop, 1988, p. 247, figs. 2a–d, 3a–d; Vega et al., 2006, p. 88, fig. 2.6; Schweitzer et al., 2007, p. 32, figs. 3a–d, 4.

Additions to description. The following details can be added to the complete description published by Bishop (1988, p. 247) and Schweitzer et al. (2007, p. 32): pseudorostrum downturned, long, slightly wide at distal tip; anterolateral spine small, anterolaterally directed; frontal line broken and small, median notch; episternal process of sternites 4–6 inverted triangular; chelipeds equal; P2 to P5 long, slender, with lanceolate dactylus; coxa of cheliped with subcircular outer margin; basis small, inverted subtriangular; ischium subcylindrical, wider at midlength; dorsal surface of palm with three ridges with strong spines; dorsal surface of dactylus with small spines; coxae of P2 to P5 subcylindrical, wider at base; ischium of P2 subtriangular, with sharp, small spine on anterior margin, merus spiny; ischia of P3 and P5 subtriangular, slightly smaller than ischium of P2; meri of P2 to P5 with evenly spaced spines on dorsal edge.

Hypodigm. Hypotypes IGM-6625-1 and IGM-6625-2, pair of articulated carapaces in a single piece of fine grey sandstone (Fig. 4a–d); IGM-7722, eroded carapace (Fig. 4e–h); IGM-7957, eroded carapace (Fig. 4i, j), Rosario Formation, middle Campanian, Punta Santo Tomás, Baja California, Mexico.

Measurements. Carapace dimensions, *L*/*W* (in mm): min = 18.1/25.2, max = 25.4/34.1, *n* = 8.

Discussion. Schweitzer et al. (2002) reported, without illustration, a dorsal carapace of *I. xestos* (IGM-7956, Colección Nacional de Paleontología, Instituto de Geología, UNAM) (Fig. 4h) from sea cliffs directly west of Victors Ranch, Punta Santo Tomás, Baja California, probably from the Rosario Formation. Thus, specimens reported herein represent the second occurrence of this species in Mexico. Schweitzer et al. (2002, p. 21) wrote: “It is suggested here that *Icriocarcinus* may be best placed within the Goneplacidae, based upon the broad orbits; narrow rostrum; posteriorly sloping orbital margins; long, attenuated, laterally directed outer-orbital spine at the anterolateral corner; transverse ridges on the epigastric region; and slender pereiopods. *Icriocarcinus* differs from other members of the Goneplacidae in possessing well-developed carapace regions; goneplacids typically have poorly developed carapace regions.”

Genus *Branchiocarcinus* Vega, Feldmann and Sour-Tovar, 1995

Type species: *Branchiocarcinus cornatus* Feldmann and Vega, 1995, p. 345, fig. 5.

Species included: *Branchiocarcinus cornatus* Feldmann and Vega, 1995; *B. flectus* (Rathbun, 1926), new combination.

***Branchiocarcinus flectus* (Rathbun, 1926), new combination** (Figs. 5, 6, 7a–p)

Eryma flecta Rathbun, 1926, p. 188, pl. LXIII, figs. 7, 13–15.

Eryma cf. *flecta* Rathbun, 1926. Bishop, 1983, p. 419, fig. 3c; 1986a, p. 121, fig. 7f.

"*Eryma* cf. *flecta*" Rathbun, 1926. Bishop, 1985, p. 1028.

Eryma n. sp. Bishop, 1986a, p. 121, fig. 7d.

Portunid claws indet. (=*Eryma* cf. *flecta* Rathbun) Bishop, 1986b, p. 611, fig. 3b.

Undescribed/unidentified crab of Landman et al. (2007, p. 14, 29, fig. 15a–l).

Description. Carapace small to medium, inverted subtrapezoidal, transversely elongate, maximum width at level of anterolateral spines, twice as wide as long; anterior margin straight, two-thirds the maximum width; pseudorostrum long, downturned, slightly wide at distal end; anterolateral margin rounded, finely serrate, inclined 45° from transverse axis, one-third the maximum carapace length; anterolaterally projected, strong triangular anterolateral spine divides anterolateral from posterolateral margins; posterolateral margin posteriorly inclined, two-thirds the maximum carapace length, with a pronounced tubercle at midlength; posterior margin rimmed, nearly straight, slightly concave at mid width, three-fourths the maximum width; dorsal carapace regions marked mainly by strong transverse ridges; protogastric regions flat, except for a relatively strong transverse ridge that crosses at midlength to reach both sides of protogastric regions; mesogastric process strongly marked, projects toward but does not reach frontal margin; meso and metagastric regions ovate, with a median transverse sharp ridge; urogastric region transversely subovate, with median ridge; cardiac region with a strong transverse ridge, one-third the maximum carapace width; intestinal region flat; posterolateral margins marked by curved ridges; cervical groove deep, extends from limit of antero and posterolateral margins, runs parallel to protogastric regions and is convergent toward meso and metagastric regions and parallel again at level of urogastric region, then extends posterolateral around intestinal region; epibranchial region with posterolaterally inclined (nearly 45°), short ridge; mesobranchial also with inclined, slightly longer ridge, inclined at approximately 20°; metabranchial marked by transverse ridge that extends anterolaterally to base of anterolateral spine. Sternum wide, transversely subovate, widest at midlength, at level of sternite 5; sternites 1 and 2 not preserved; sternite 3 transversely subtrapezoidal, with small tubercle projected on posterolateral margin; sternite 4 subtrapezoidal, one-fourth wider than sternite 3, triangular process extends posteriorly from posterolateral margin to reach midlength of sternite 5; sternite 5 transversely subrectangular, slightly longer at lateral margin, triangular process extends posteriorly from posterolateral margin to reach midlength of sternite 6; sternite 6 similar in shape and length but slightly narrower than sternite 5, also with posterior process that reaches midlength of sternite 7; sternite 7 rectangular, as long but half the width of sternite 6, no posterior process seen; sternite 8 small, subquadrate, one-third the width of sternite 7 and half its length. Male abdomen triangular; telson triangular, extends from base of sternite 4 to midlength of that sternite; abdominal somite 6 subtrapezoidal, slightly wider at its base; abdominal somite 5 subrectangular, twice the width of somite 6 but one-third its length; abdominal somite 4 similar in shape and size to somite 5, but with median transverse ridge extending from side to side; abdominal somite 3 also similar to somite 5 but one-third wider, with a median ridge; remaining somites not observed. Endopodite of third maxilliped subtrapezoidal inverted, with median longitudinal groove. Right chela slightly larger than left; coxae of chelipeds subrectangular, elongate, nearly as long as sternite 4, merus of left cheliped subrectangular, with a row of three tubercles on lower margin, carpus of both chelipeds robust, one-third the length of merus; right propodus robust, subtriangular, with four strong longitudinal ridges on outer surface, ridge on dorsal margin with eight strong tubercles, and an inner parallel row of at least three strong spines; inner surface smooth, fixed finger triangular, middle longitudinal groove on outer surface, with teeth on occlusal surface, dactylus curved, with strong tubercle on proximal dorsal surface, occlusal surface with five teeth of variable size; propodi robust, semi-triangular, elongate, with four strong longitudinal ridges on outer surface, dorsal ridge bearing eight tubercles and a parallel inner row with at least three strong spines, inner palm of left propodus bearing two rows of smaller tubercles, right inner palm smooth, dactyli curved, with longitudinal groove and several teeth on occlusal surface; P2 to P4 of similar length and shape, P5 slightly shorter but not reduced: coxae of P2 to P5 subquadrate, basis short, subcylindrical; ischia subtrapezoidal, meri subrectangular, nearly as long as maximum carapace length; carpi subconical, wider at junction with propodus; propodi elongate, slightly wider at junction with carpus; dactyli uncinate, slightly curved .

Etymology. Although never stated explicitly by the author, Rathbun (1926) chose the species name *flectus* from the

Latin *flect* (=to be bent) because the "finger bends slightly downward from the sinus just behind its origin".

Hypodigm. Holotype: USNM 73115, eroded left cheliped from Gravel Hill, McNairy County, Tennessee (USGS Meso. loc. 10272). Epitype, chorotype: MPPM 1972.46.452, carapace with attached chelipeds from the Coon Creek type locality ("Dave Weeks place"), McNairy County, Tennessee (~USGS Meso. loc. 10198, Wade 1926; ~USGS Meso. loc. 25406, Sohl 1960).

Referred material: MPPM 1972.46.459, carapace with incomplete chelipeds from the Coon Creek type locality; MMNS IP-3141, carapace with chelipeds, and IP-2813, 3014, carapaces with partial chelipeds, from Blue Springs, Union County, Mississippi (MS.73.033a); MMNS IP-2868, 2966, incomplete carapaces with partial chelipeds, and MMNS IP-2027, 2144, 2307, 2376, 2726, 2780, 2999, all propodi, from the town of Pontotoc, Pontotoc County, Mississippi (MS.58.003b, MS.58.021); MMNS IP-3859, 3860, 3911, and 4164, carapaces with and without limbs, from New Albany, Union County, Mississippi (MS.73.041); MMNS IP-3860, carapace with limbs, from New Albany, Union County, Mississippi (MS.73.042); MMNS IP-3723, propodus from Goodfood, Mississippi (MS.58.010); and USNM 543041, carapace with base of limbs, and MMNS IP-3863, 4388-4392, carapaces with limbs, from the Owl Creek type locality, Tippah County, Mississippi (USGS Meso. loc. 25423). The Tennessee specimens are from the Coon Creek Tongue of the Ripley Formation. The Union County, Mississippi, specimens are from the updip Prairie Bluff equivalent (MS.73.041, 4th Street facies) and Owl Creek Formations (MS.73.042). The Pontotoc specimens are from the Nixon sand (sensu Phillips 2010), which is an intervening facies between the Prairie Bluff and Owl Creek Formations. The Goodfood propodus is from the Prairie Bluff Formation (i.e. typical Prairie Bluff "chalk"), and the Tippah County specimens are from the Owl Creek Formation. Bishop's figured propodi are from the Coon Creek Tongue (Bishop 1983, 1986a; GAB 37-909) and Nixon Sand (Bishop 1986a, b; GAB 52-14, Prairie Bluff Formation) of Union County, Mississippi. Refer to map (Fig. 2) and stratigraphic chart (Fig. 3). Material figured by Landman et al. (2007) from the Tinton Formation of Monmouth County, New Jersey, and bearing the catalog numbers MAPS A3329a1–A3329a7, AMNH 50426, and AMNH 50428; plus MMNS IP-4805–4807 from the same locality (Lower Agony Creek, AMNH loc. 3372).

Measurements. Carapace dimensions, *L*/*W* (in mm): min = 10.2/17.3, max = 18.6/26.3, $n = 8$.

Discussion. Rathbun (1926) described *E. flecta* from the Upper Cretaceous of Tennessee on the basis of a single left propodus, indicating that the generic position was uncertain until complementary elements were found. Bishop (1983) illustrated another left propodus (GAB 37-909), from the same unit but in Mississippi, stating that "*E.*" *flecta* was definitely a brachyuran. From a younger unit, Bishop (1986a) illustrated the same propodus plus an additional left propodus with a dorsal row of well-preserved tubercles (GAB 52-14), reporting the latter as "*Eryma* n. sp." Later, this same specimen (GAB 52-14) was re-drawn by Bishop (1986b) as a "portunid(?)" claw. The nature of the portunoid is similar to, and is likely to be the same as, that of *E. flecta*, as was previously suggested by Mary J. Rathbun (USNM) in a species list of the Prairie Bluff Formation prepared by Stephenson and Monroe (1940).

Specimens reported herein from the Maastrichtian of Tennessee, Mississippi, and New Jersey, include dorsal and ventral carapace remains articulated with propodi of the same shape and size as those reported by Rathbun (1926) and Bishop (1983, 1986a, b). The propodi of *Branchiocarcinus* are very distinctive in their tuberculation and overall morphology. As suggested by Rathbun's (1926) epithet for the singular specimen of "*E.*" *flecta*, the fixed finger of *Branchiocarcinus* is flexed, or bent, slightly downward, the point of attachment of the fixed finger and the palm appearing crimped. The propodi of *Branchiocarcinus* have four parallel, longitudinal ridges anteriorly, the dorsal-most of these ridges bearing two rows of well-developed tubercles along its palmar flank. The outer row consists of six or seven short, stout tubercles and the inner row three longer and narrower tubercles, or spines. The left propodus also bears a double row of smaller tubercles on a low, broad ridge dominating the inner palm; palmar tubercles are absent in the right propodus. These tuberculate ridges are only partially preserved on the holotype (USNM 73115) and Bishop's (1983) Coon Creek specimen because of their poor condition.

The carapace morphology is similar to that of *B. cornatus* (type species for the genus) (Fig. 7q) from the lower Maastrichtian of San Luis Potosí, Mexico, but differences in the shape and ornamentation of carapace (see below) suggest that the Mexican species is possibly different, as mentioned below. We suggest that the "*E.*" *flecta* types of Rathbun (1926), the "*Eryma*" and "portunid(?)" material illustrated by Bishop (1983, 1986a, b), and the material introduced herein, all represent a species of the portunoid *Branchiocarcinus*, which by priority principle should be named *B. flectus* (Rathbun, 1926) new combination. Because of its excellent condition and origins, MPPM 1972.46.452 is a key specimen connecting Rathbun's isolated propodus (the holotype) with a body. As it was found in the same unit and very near the type locality, it is a chorotype. Therefore, MPPM 1972.46.452 is erected as the interpretive and main reference type, or epitype.

Rathbun's (1926) small portunid differs from *B. cornatus*, the sole conspecific, in several features. The species from eastern Mexico has a proportionally narrower carapace, a concave and narrower posterior margin, weaker transverse ridges on the dorsal carapace, a stronger protogastric process, a lack of tubercles on the posterolateral margin, and lacks a transverse ridge on the cardiac region. However, one or several of these details could be artifacts of preservation.

Branchiocarcinus cornatus was placed into the Carcineretidae (Portunoidea), on the basis of the presence of transverse ridges of the carapaces and wide anterior margin (Vega et al. 1995, 1997, 2001, 2006; Feldmann et al. 1999; Feldmann and Villamil 2002; Schweitzer et al. 2003; Guinot and Breton 2006; De Grave et al. 2009). In their review of the Carcineretidae, Schweitzer et al. (2007) included only *Carcineretes* Whiters, 1922; *Mascaranada* Vega and Feldmann, 1991; and questionably *Cancrixantho* Van Straelen, 1934, and suggested that *Branchiocarcinus* may have been related with the Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003. Later, Schweitzer et al. (2010, p. 105) placed *Branchiocarcinus* again in the Carcineretidae. We agree with the portunoid affinities of the genus, which differs from other genera of carcineretids in having a much wider carapace, prominent anterolateral spines, sharp transverse ridges, small notch on front of carapace, and spiny chelae. The absence of flattened fifth pereiopods, nearly rectangular carapace, strong transverse ridges on the dorsal carapace, spiny dorsal surface of the palm, and movable fingers all indicate that *Branchiocarcinus* is closely related with *Icriocarcinus*, and should be appropriately united in the portunoid family Icriocarcinidae.

Discussion

Fragmentary *Branchiocarcinus flectus* remains have previously been reported under different names from several different geologic units—the Coon Creek Tongue of Tennessee (Rathbun 1926) and Mississippi (Bishop 1983, 1985, 1986a) and the Prairie Bluff Formation (Bishop 1986b). In addition, M.J. Rathbun identified decapods for Stephenson and Monroe (1940), whose faunal lists included unillustrated material from the Prairie Bluff Formation noted only as a "genus of family Portunidae, akin to *Charybdis*", recovered from USGS Meso. loc. 6855. Included in the material referred to above are propodi and a partial body from the same facies and location (MS.58.021), which subsequent lithologic division has included in the Nixon Sand (Phillips 2010). Bishop's (1986b) Prairie Bluff material is also derived from the Nixon Sand, which is a transitional facies between the Prairie Bluff and the Owl Creek Formations (Fig. 3) but regarded as a member of the former (Phillips 2010). In addition to the Gulf of Mexico, *B. flectus* also occurs in terminal Maastrichtian sediments of the North American Atlantic Coastal Plain. Landman et al. (2007) illustrated both isolated and carapace-associated chelae of an "unidentified" and "undescribed" crab from the uppermost ("*Pinna* layer") of the Tinton Formation of New Jersey. The lithology and fauna in this part of the Tinton is essentially identical with that of the contemporaneous Owl Creek Formation in the northeastern Gulf of Mexico, which also contains *B. flectus*.

Within the Coon Creek Tongue, *B. flectus* occurs with other decapods in primarily two situations:

1. light-colored (light brown), soft, clayey, fine-grained concretions representing original depositional emplacement; and
2. dark (black), hard, phosphatic nodules occurring in winnowed lags representing some degree of condensation (see also Bishop 1986c).

Autochthonous concretions and allochthonous nodules occur with calcitic and aragonitic mollusks and disarticulated vertebrate remains in the medium to dark gray sandy, glauconitic clays and sands typical of the Coon Creek Tongue. The Nixon Sand consists of light-colored, very sandy calcareous marl with a distinctive fauna populated by calcitic and moldic macroinvertebrates. In this unit, *B. flectus* is found in a thin interval densely populated with small, erect bryozoans. Among other characteristics separating this lithofacies from the underlying fine-grained marl (Prairie Bluff) and overlying less calcareous, more terrigenous clay (Owl Creek), the Nixon Sand is further distinguished by an abundance and diversity of well-preserved echinoids and equally abundant remains of the small oyster *Cubitostrea tecticosta* (Gabb, 1860), sea pen axes (Pennatulacea: cf. Virgulariidae), and less common fragments of small crabs, including the isolated propodi of *B. flectus*.

A diversity of decapod skeletal remains is found alongside *Branchiocarcinus* within the Coon Creek Tongue, and recent efforts by the senior writer and colleagues in Mississippi have revealed several new taxa. Published associated genera include *Penaeus* Fabricius, 1798; *Enoploclytia* McCoy, 1849; *Hoploparia* McCoy, 1849; *Linuparus* White, 1847; *Protocallianassa* Beurlen, 1930; *Parapaguristes* Bishop, 1986b; *Dakoticancer* Rathbun, 1917; *Tetracarcinus* Weller, 1905; *Prehepatus* Rathbun, 1935; *Notopocorystes* McCoy, 1849; *Raninella* A. Milne-Edwards, 1862 and *Cristipluma* Bishop, 1983 (Rathbun, 1926, 1935; Bishop, 1983, 1985, 1986a, b). In Mississippi, *Avitelmessus* Rathbun, 1923, occurs in a thin sandstone interval above the other decapod-bearing beds in the Coon Creek Tongue, where it seems to be the dominant decapod. Below the *Avitelmessus* bed (including the lag mentioned earlier), *Dakoticancer* is the most numerous decapod. The senior writer has also collected *Palaeoxanthopsis* Beurlen, 1958, and parts of an unidentified majid from the Coon Creek beds in Mississippi. In addition, carapaces of at least three other new species or species occurrences in this unit remain to be described. Last, Bishop (1986a) lists *Ophthalmoplax* Rathbun, 1935, in the Coon Creek assemblage, but this mention is believed to be a reference to the type specimen of *O. stephensoni* Rathbun, 1935, which is most likely derived from the sandy limestones of the Chiwapa Member ("Keownville Limestone" of Sohl (1960)) of the Ripley Formation. L. W. Stephenson collected the specimen in 1909 (USGS Meso. loc. 6466g), described the section (reinterpreted by Sohl 1960), and referred to the specimen in Stephenson and Monroe (1940) as "*Rhachiosoma*? n. sp." The Chiwapa Sandstone belongs to the younger *Haustator bilira* biozone of Sohl and Koch (1986).

Bishop (1985, 1986b) reported several of the Coon Creek genera as also occurring with *Branchiocarcinus* in the Nixon Sand facies of the Prairie Bluff Formation, namely *Protocallianassa*, *Parapaguristes*, and *Prehepatus*. In addition, Bishop (1986b) illustrated parts of two unidentified brachyurans from the same unit. These have also been recovered by the senior writer from this facies; one is a raninid (new species?) and the other a large-clawed brachyuran of uncertain affinity. Bishop's (1986a) earliest faunal list of the Prairie Bluff Formation suggests an even richer decapod assemblage, but several of the taxa (Atelecyclidae, Macrophthalmidae, and *Raninoides ovalis* Rathbun, 1935) are currently undocumented from the Mesozoic and their presence in the Cretaceous of the northern Gulf has not been observed by the writers. In the Owl Creek Formation, *Branchiocarcinus* co-occurs with *Protocallianassa*, *Prehepatus*, *Notopocorystes*, *Costacopluma*, and Bishop's (1986b) undescribed raninid ("*Raninella*"?; or possibly "*Raninoides ovalis* Rathbun" of Bishop 1986a) from the Prairie Bluff Formation.

Specimen MMNS IP-3141 of *B. flectus* is associated with a row of fecal pellets preserved near the ventral side; these are likely to have been produced by an associated organism that shared the same gallery with IP-3141. Breton (2006) discussed a specimen of *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879, seemingly holding a row of fecal pellets that the author attributed to a different crustacean species. Guinot and Breton (2006) interpreted the pellets associated with the French Cenomanian specimen as having been produced by scavenging organisms, because similar objects were found filling other *L. trigeri* carapaces internally. Guinot and Breton (2006) suggested that *L. trigeri* was not associated with burrows, living in an infralittoral environment with fine-grained soft sediment, where the crab digs to cover itself for protection. Bishop (1988) reported a specimen of *I. xestos* within a sand-filled burrow (see also Schweitzer et al. 2007). No clear evidence has been found to support that *Branchiocarcinus* inhabited burrows. Their abundance in near shore facies suggests that the Icriocarcinidae may have preferred shallow, infralittoral environments, although a single specimen from the chalky facies of the Prairie Bluff Formation indicates tolerance for deeper waters of the inner shelf.

Summary

Icriocarcinus Bishop, 1988, and *Branchiocarcinus* Feldmann and Vega, 1995, represent a family of crabs—the Icriocarcinidae—that lived on the Pacific, Gulf, and Atlantic coasts of North America during the Late Cretaceous (Campanian–Maastrichtian). Both genera share similar portunoid features that are sufficiently distinctive as to warrant placement in a family separate from described portunoid families. *Eryma flecta* Rathbun, 1926, was erected on the basis of a single left propodus from near the type locality of the Coon Creek Tongue in McNairy County, Tennessee (Wade 1926). Originally thought to be a lobster (Erymidae), M.J. Rathbun, in Stephenson and Monroe (1940), may have assigned similar chelae from a sandy facies of the Prairie Bluff Formation in Mississippi to the Portunidae. Also uncertain of their exact placement, Bishop (1983, 1985, 1986a, b) reported additional chelae from the Coon Creek and younger beds of Mississippi and cautiously used similar indefinite and provisional nomenclature to that of M.J. Rathbun. Fortunately, collecting at the Coon Creek type locality in recent decades by the Pink Palace Museum produced two nearly complete articulated exoskeletons—"*E.*" *flecta* chelae attached to bodies. Many more isolated chelae, including several attached to bodies, were recently collected from new Coon Creek localities and younger intervals in Mississippi and New Jersey. These latest discoveries establish the affinity of this crab with *Branchiocarcinus* Feldmann and Vega 1995.

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