

**DECAPODA (CRUSTACEA) OF THE COON CREEK  
FORMATION (MAASTRICHTIAN) OF MISSISSIPPI  
AND TENNESSEE**

**Krystyna M. Kornecki, Rodney M. Feldmann, and  
Carrie E. Schweitzer**



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# DECAPODA (CRUSTACEA) OF THE COON CREEK FORMATION (MAASTRICHTIAN) OF MISSISSIPPI AND TENNESSEE

Krystyna M. Kornecki<sup>1,2</sup>, Rodney M. Feldmann<sup>2</sup>, and Carrie E. Schweitzer<sup>3</sup>

## ABSTRACT

The Upper Cretaceous (Maastrichtian) Coon Creek Formation of Mississippi and Tennessee possesses a diverse and abundant assemblage of decapods including lobsters, ghost shrimp, and crabs. The formation lies in a temporally and paleogeographically significant location, situated between the Atlantic Coastal Plain and the Western Interior Seaway, shortly before the closing of the seaway and the K-Pg mass extinction. Coon Creek decapods have been little studied since the fauna was first described in the 1920s. A large collection of specimens, ranging in preservation from poor to excellent, has recently become available for study.

Analysis of the elemental composition of the sediment and cuticle of six species of decapods from six families (Palinuridae, Nephropidae, Callianassidae, Dakoticancridae, Raninidae, and Retroplumidae) collected at the Blue Springs locality in Mississippi reveals phosphatic replacement of cuticle and trace amounts of iron and sulfur in the surrounding sediment. Concretions bearing decapods and a decapod burrow were observed in thin section and were mapped for elemental distribution using Energy-dispersive X-Ray spectroscopy and dot mapping indicating consistent elemental results with the surrounding sediment. The six species of decapods were analyzed using the same techniques and suggest diagenetic affects in cuticular structure and the presence of silica forming on the cuticle of a single specimen. Taphonomic data supports preservation ranging from well preserved phosphatization to secondary alteration to silica-rich exterior and weathering clay minerals. Because the silica is not replacing the phosphatized exocuticle and microscopic structure of cuticle in cross section is not preserved in the silica layer, the cause of this alteration is uncertain.

The systematics and taxonomy of the decapod species from the Coon Creek Formation were reassessed. Sixteen species are identified, including two new species: *Hoploparia tennesseeensis*, *Hoploparia mcnairyensis*, *Linuparus keyesi* sp. nov., *Linuparus* sp., *Palaeopetrochirus enigmus*, *Seorsus wadei*, *Bournelyreidus ericksoni* sp. nov., *Cristipluma mississippiensis*, *Lithophylax flectus* new combination, *Hoploparia georgeana*, *Mesostylus mortoni*, *Tetracarcinus subquadratus*, *Avitelmessus grapsoideus*, *Cretacorantina testacea*, *Dakoticancer australis*, *Prehepatus harrisi*, and ?*Latheticocarcinus atlanticus*, as well as two fragments belonging to the Majidae. This decapod fauna has species in common with correlative units of the Western Interior Seaway, the Gulf Coastal Plain, and the Atlantic Coastal Plain, supporting the hypothesis that the Mississippi Embayment is an ecotone for North American decapods.

**Key words:** Cretaceous, Decapoda, Coon Creek Formation, *Linuparus keyesi* sp. nov.; *Bournelyreidus ericksoni* sp. nov.; *Lithophylax flectus* new combination.

<sup>1</sup>Department of Earth and Environmental Science, Rensselaer Polytechnic Institute, Troy, NY 12180, USA <kornek2@rpi.edu>

<sup>2</sup>Department of Geology, Kent State University, Kent, OH 44242, USA

<sup>3</sup>Department of Geology, Kent State University at Stark, 6000 Frank Ave. NW, North Canton, OH 44720, USA

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### INTRODUCTION

The paleontology of the Coon Creek Formation (Maastrichtian, of Tennessee and Mississippi) has been a popular area of study since the 1920s, beginning with a thorough assessment by Bruce Wade (1926). These descriptions of marine invertebrate taxa have been the starting point for all subsequent paleontological research of the fossil invertebrates of the formation. The Coon Creek Formation is fossiliferous, with excellent preservation of a diverse assemblage of decapod taxa, first described by Rathbun (*in* Wade, 1926). An assemblage of so many fossil decapods is a rarity, both in quantity of specimens as well as diversity. The vertebrate taxa (Whetstone, 1977; Carpenter et al., 2003; Stringer, 2003; Gibson et al., 2008), ichnofossils (Hall and Savrda, 2008), and associated sediments have been addressed from the formation or correlative units within the associated seas of North America. However, little has been done to study the decapods of the formation as a whole since Wade's original work, except for those publications by Bishop (1983; 1985; 1991) and Bishop et al. (1998), which focused heavily on the Dakoticancridae, nor to compare them with the decapods of correlative units in the region.

This work aims to compile all known decapod taxa of the Coon Creek Formation and to present the taxa in a recent systematic framework.

The second aim of this work is to compare these taxa to correlative units in the Western Interior Seaway, the Atlantic Coastal Plain, and the Gulf Coastal Plain in order to address the hypothesis that the Mississippi Embayment represents an ecotone for the North American decapod fauna. A third objective for this work incorporates a taphonomic description of the unit.

#### TECTONIC SETTING

The Cretaceous-Paleogene gulf, known as the Mississippi Embayment, was located on the southern margin of North America during the Maastrichtian. It comprises a southwestward plunging trough that has been filled with about 1.5 kilometers of Cretaceous and Cenozoic sediments. The embayment is underlain by an early Paleozoic graben and basin fault complex (Cox and Van Arsdale, 2002). The subsidence of the embayment is attributed to forming the Gulf of Mexico, but Cox and Van Arsdale (2002) proposed that because sea floor spreading ceased in the Gulf of Mexico 60 million years before the formation of the embayment, the subsidence was caused by the passage of the faulted crust over the Bermuda hotspot during the mid-Cretaceous. The associated volcanism began around 115 million years ago and ended around 65 million years ago in central Mississippi (Cox and Van Arsdale, 2002).

## STRATIGRAPHY

The Coon Creek fauna was dated as early Maastrichtian by Russell and Parks (1975), but Bishop (1986:119) interpreted it to be latest Campanian to earliest Maastrichtian, based on the *Baculites reesidei* zone (Obradovich and Cobban, 1975) as the base of the Maastrichtian boundary.

The beds containing the Coon Creek fauna are located in northern Mississippi and southern Tennessee, near what was then the northern end of the Mississippi Embayment at around 30 – 35° N (Mancini et al., 1995; Fig. 1). Mancini et al. (1995) described the Late Cretaceous section through the region as a succession of coastal regression and transgression cycles, with the Coon Creek beds comprising part of a progradational to regressive cycle (Smith, 1989; Mancini et al., 1995). In simplified terms (temporarily setting aside some nomenclatural complications), the section enclosing the Coon Creek beds is comprised of some basal chalks and marls (the Demopolis Formation) that become more argillaceous up-section (the Coon Creek Formation), which in turn pass up into non-calcareous and non-glaucconitic, mainly fluvial sands and clays (the McNairy Sand). Wade (1917) described the Coon Creek beds as consisting specifically of a lower clay zone (the “Transitional Clay” of Conant, 1941 that grades down into the Demopolis marls below) and an upper “ferruginous clay horizon” that presages the overlying sands. In its type area of Coon Creek, in McNairy County of Tennessee, the Coon Creek Formation consists of about 58 meters of marine sandstone and shale. Being at the end of a comparatively long and narrow embayment, the section is predominantly (but not entirely) siliciclastic, particularly compared to same-age beds that were deposited farther from the coast. The Coon Creek Formation passes southward into marine sands, clays and limestones of the Ripley Formation, while it grades and pinches northward into the McNairy Sands (Smith, 1989). The Coon Creek beds have at various times and places been regarded as a clay-rich tongue of the Ripley Formation. Mancini et al. (1995; 1996) identified the chalk as the maximum flooding surface, the

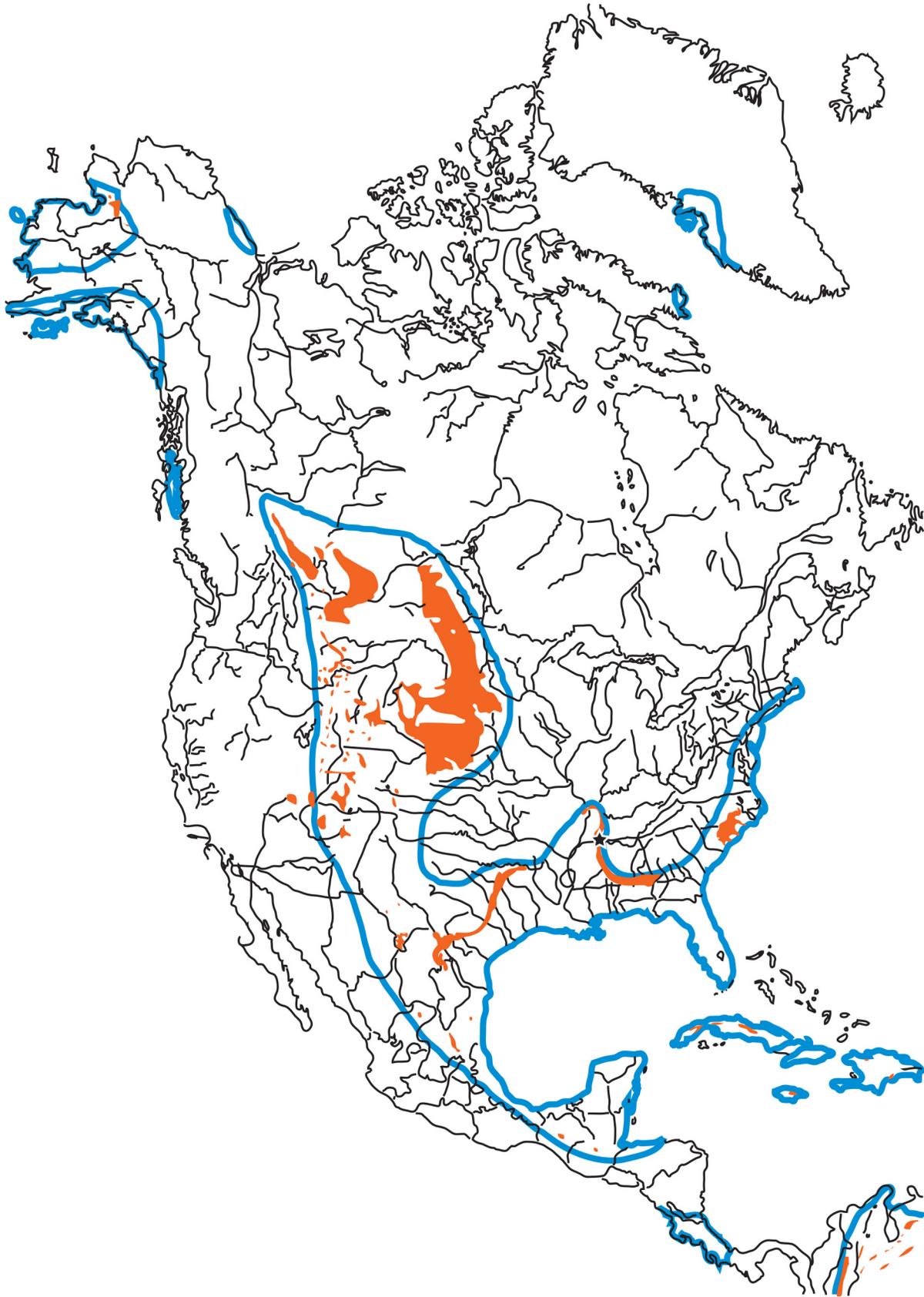
shales as progradational during highstand, and the sands as progradational and regressive prior to the next transgression (Smith, 1989).

The stratigraphic nomenclature applied to this sequence has some complications, especially regarding the question of whether the Coon Creek beds rank as a formation (the Coon Creek Formation), or as a member (the Coon Creek tongue of the Ripley Formation). Russell and Parks (1975:A35) provided a detailed summary of the early literature. Even so, since Russell and Parks (1975), both Coon Creek Formation and Coon Creek tongue have been used in the literature for the same set of beds. For simplicity, this paper will refer throughout to “the Coon Creek Formation” and localities will be noted as to whether they are in Tennessee or Mississippi.

## METHODS AND MATERIALS

This study primarily examined Dr. Gale Bishop’s Collection, on loan from the South Dakota School of Mines and now repositied in the the Florida Museum of Natural History at the University of Florida, and newly collected material of roughly 500 specimens from the Blue Springs locality, New Albany, Mississippi (Fig.1), collected over the course of four days during December, 2012 and May, 2013. These specimens were compared to previously published studies and to other collections of fossil decapods, including material at Kent State University. Comparisons were made during two visits to the U.S. Museum of Natural History in Washington, D.C. Collections from both the Pink Palace Natural History Museum in Memphis, Tennessee, and the Mississippi Museum of Natural History in Jackson, Mississippi were obtained through loan for further study at Kent State University and have been described and illustrated where appropriate. All specimens were prepared (when necessary), whitened, and photographed with a Nikon D3100 digital camera.

All Coon Creek species were compared to age equivalent species from the Gulf Coastal Plain, the Western Interior Seaway, and the Gulf of Mexico, using the revised taxonomy of Schweitzer et al. (2010).



**Figure 1.** Maastrichtian outcrops, orange. Intercontinental seaway outlined, blue. Blue Springs locality marked by black star (modified from Schuchert, 1955).

Taphonomic and sedimentologic studies were conducted by petrographic analysis, scanning electron microscopy (SEM), and energy dispersive x-ray spectrometry (EDX). For use in the SEM and EDX, specimens were sectioned and polished to 1200 grit scale after impregnation in epoxy and drying in a vacuum chamber when necessary. Particularly difficult specimens were re-impregnated and vacuumed multiple times. Specimens were mounted on aluminum stubs using double sided carbon tape tabs. They were then carbon coated twice to ensure even and thick coating. One sample was gold coated to permit more detailed observations of *Dakoticancer australis* cuticle morphology using scanning electron microscopy. Further experimentation is needed for impregnation of specimens for future SEM and EDX work.

#### LOCALITIES

“Ft. Pierre Locality,” Pierre Shale Formation – North section line of sec. 21 to the south section line of sec. 26, T. 6 N., R. 29 E., Stanley County, South Dakota in the Upper Cretaceous Pierre Shale, from the zone of *Baculites grandis* Hall and Meek (Bishop, 1972:3823).

Pierre Shale Formation (holotype location for *Plagiophthalmus izetti*) – NE ¼, NE ¼, sec. 25, T.3 N., R. 17 W., Grand Co., Colorado (USGS Locality D8090); *Baculites scotti* zone (index fossil to upper Campanian rocks) (Bishop, 1988:377).

Pierre Shale Formation (paratype location for *Plagiophthalmus izetti*) – SE ¼, SE ¼, sec. 29, T.2 S., R. 70 W., Jefferson County, Colorado (Bishop, 1988:377).

Prairie Bluff Formation (collection site by Mr. Ralph Harris, 1982 of *Prehepatus harrisi*) – sec. 3, T8S, R3E, Union County, Mississippi (Bishop, 1985:1030).

Fox Hills Formation (holotype location for *Latheticarcinus shapiroï*) – Grand River, Corson County, South Dakota; two paratypes collected from either Red Bird, Wyoming, or from the Fox Hills of Central South Dakota; paratypes are either Campanian or Maastrichtian (lacking any other more specific record) (Bishop, 1988:378).

Bearpaw Shale Formation – The locality is

found near Fort Peck, Montana, and the Fort Peck Dam on the Missouri River (Feldmann et al., 2012).

Coon Creek type section – On Coon Creek, 1.6 km south of Enville, Coon Creek Formation, lower lithofacies. Dark greenish gray, glauconitic sandy silt. McNairy County, Tennessee. Index fossils: Nanno-assemblage 23a *Nostoceras hyatti*, *B. undatus*, *B. claviformis* (Ebersole, 2009:31).

Blue Springs locality – Lower Maastrichtian Coon Creek Formation (34°24'30.14" N, 88°53'08.36" W). Unvegetated roadcut at the exchange of new U.S. Highway 78 and Mississippi Highway 9, approximately 22 km northwest of Tupelo, Mississippi and 2.5 km southwest of the village of Blue Springs. Also referenced as locality GAB 37; E ½, NW ¼, sec. 16, T8S, R4E, Union County, Mississippi. Six meters of sandy, glauconitic and phosphatic light olive gray mudstone. Also includes an interval of phosphatic nodules (Bishop, 1983:417).

Coon Creek Formation (collection site by Mr. Ralph Harris, 1982 of *Prehepatus harrisi*) – sec. 9, T8S, R4E, Union County, Mississippi (Bishop, 1985:1030).

Coon Creek fauna locality – Known as “Dave Weeks Place” on Coon Creek. Located in northeastern McNairy County, Tennessee, 3.5 miles south of Enville, 7.5 miles north of Adamsville, and 1/8 of a mile east of the main Henderson-Adamsville Road. Best exposed fossil beds are in the valley 250 yards east of Dave Weeks’ house, along the headwaters of Coon Creek. Coon Creek is a small stream flowing northward into White Oak Creek, a tributary of the Tennessee River (Wade, 1926:9).

“Thompson Farm Fossil Bed” – Coon Creek Formation, along Melton Creek near Enville, Tennessee (Conover, 1990, in Dunagan and Gibson, 1993).

Merchantville/Marshaltown Formation Spoils or Railroad Bridge Spoils – located on the north side of the canal near a railroad bridge, 39°32'49" N, 75°42'57" W, New Castle County, Delaware (Feldmann et al., 2013).

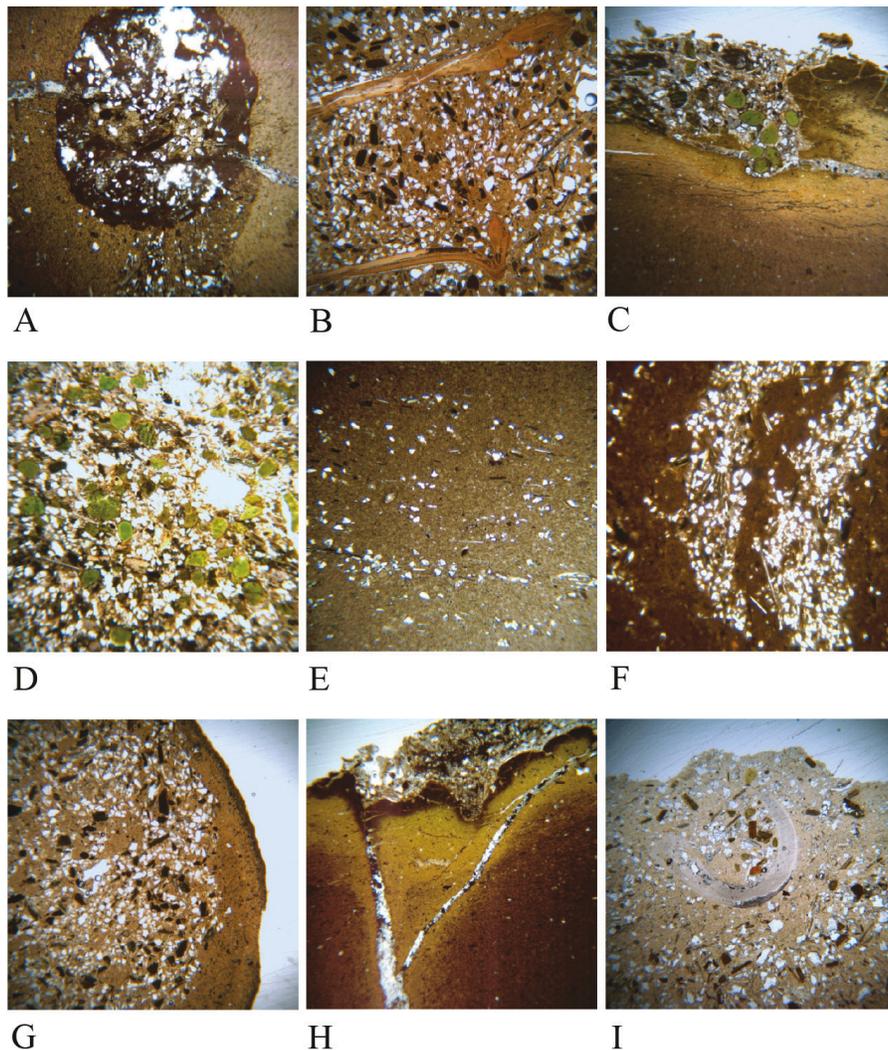
Deep Cut locality – located about one kilometer east of Delaware Route 896 on the C and

D Canal, New Castle County, Delaware, 39°32'44" N, 75°42'57" W. Contains *in situ* material from the Merchantville, Marshalltown, and Englishtown Formations (Feldmann et al., 2013).

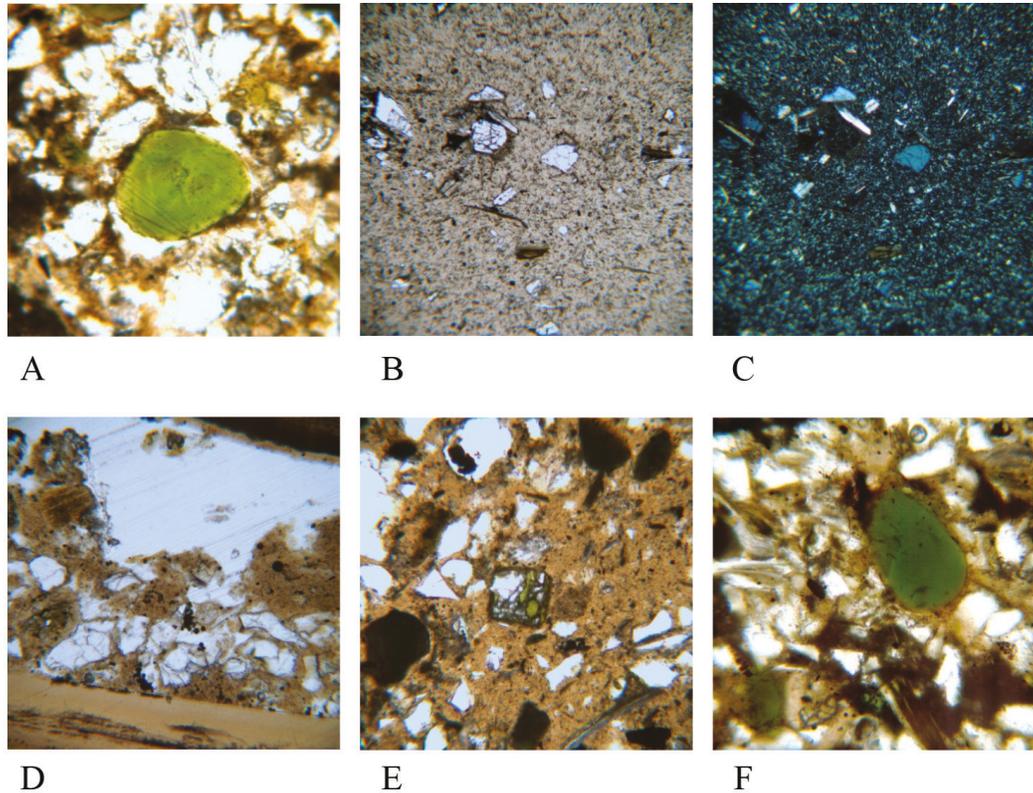
#### INSTITUTIONAL ABBREVIATIONS

**USNM**, United States National Museum of Natural History, Smithsonian Institute, Washington, District of Columbia; **MMNS**, Mississippi Museum of Natural Science, Jackson, Mississippi;

**MPPM**, Memphis Pink Palace Museum, Memphis, Tennessee; **GAB**, Gale A. Bishop Collection, loaned from South Dakota School of Mines; **B**, Gale A. Bishop Collection, loaned to Kent State University without specimen numbers, material collected at the Blue Springs Locality; **KSU**, Kent State University, Kent, Ohio; **SDSM**, South Dakota School of Mines, Rapid City, South Dakota; **GSUM**, Georgia Southern University Museum, Statesboro, Georgia (referenced as



**Figure 2.** Examples of cuticle preservation and concretions from the Blue Springs locality in thin section. Burrow at center of flat concretion with larger grains, KSU-005 (A); cuticle in light concretion, KSU-007 (B); outer edge of concretion with dark, fine grained rind and larger sediment lightly cemented to the outside, KSU-005 (C); glauconite grains in sediment, KSU-003 (D); fine grains in concretion, KSU-005 (E); cross section of burrow, KSU-006 (F); fine grained rind of a concretion with coarse grains internally, KSU-007 (G); concretion from image A with calcite infilling crack to the burrow at center, KSU-005 (H); light colored concretion with coarse grains, KSU-003 (I). Thin section images at magnification 10 X 0.4.



**Figure 3.** Mineralogy and cuticle preservation in thin section, continued. Unaltered glauconite grain in matrix, KSU-003 (A, F); concretion internal matrix in plain light (B) and cross polarized light (C), KSU-007; cuticle horizontal across bottom, porous space, and surrounding grains, KSU-004 (D); and coarse grains and cuticle fragments with grain altering to glauconite, KSU-003 (E). Thin section images, magnification 10 X 20.

GSCM or Georgia Southern College Museum in Bishop, 1988); **MGUH**, Museum Geologicum Universitatis Hauniensis, Copenhagen, Denmark; **MHN LM**, Musée d'Histoire naturelle ("Musée Vert"), Le Mans (Sarthe), France; **UF**, Florida Museum of Natural History, University of Florida, Gainesville.

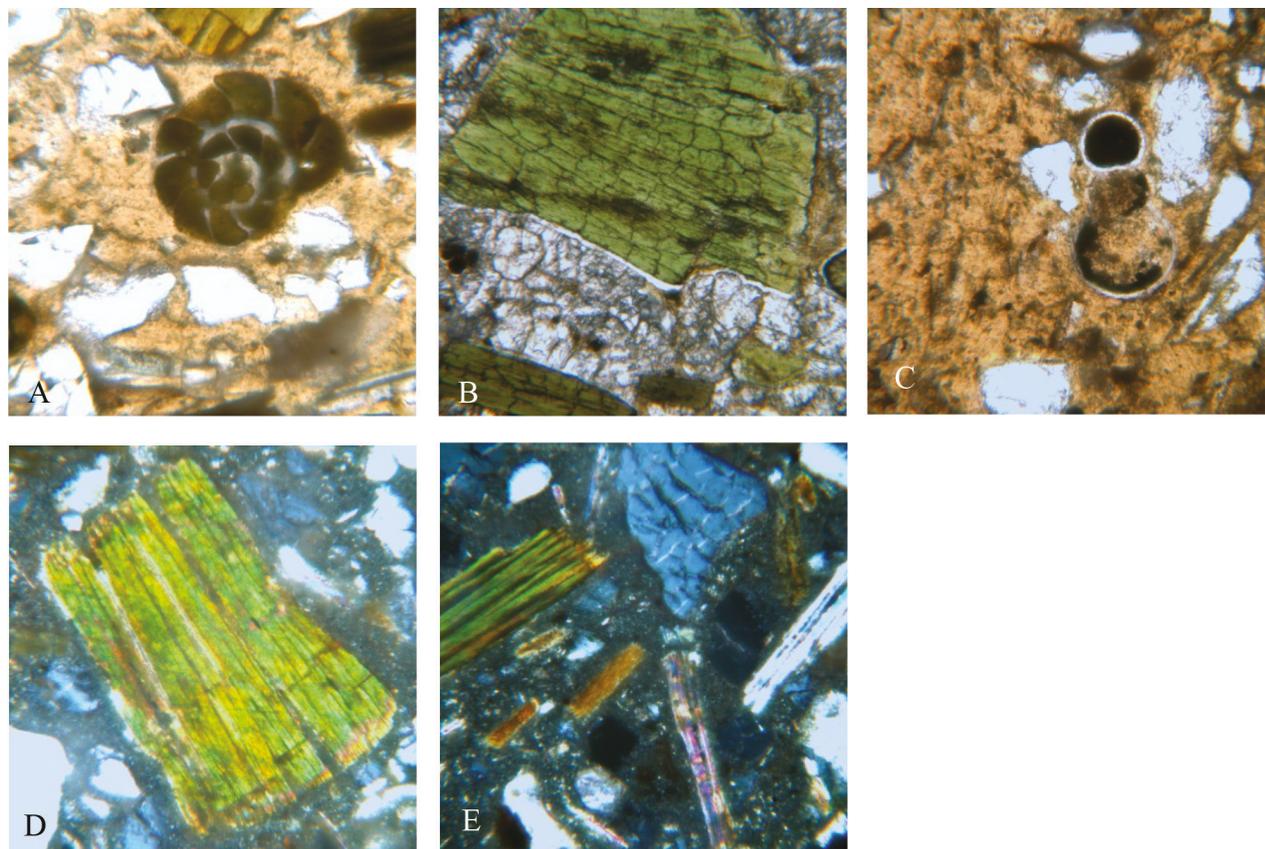
### SEDIMENTOLOGY

The lithology was studied at the Blue Springs locality outcrop in New Albany, Union County, Mississippi, just off exit 73B on Route 78. The unit is massively bedded. In hand sample, the rock is a very micaceous, glauconitic, clay-rich sandy siltstone, with common burrows and small concretions. It is grey-brown to grey-green (Munsell color values 5Y 5/4 and 5Y 4/4). It is weakly cemented with calcite. Some layering is visible in hand sample that is not seen in the outcrop, which may be highlighted or

even caused by weathering and re-cementation (Fig. 2D–E). Study of thin sections shows that the rock consists of approximately 10% pore space, and (recalculating the remaining components to 100%), 40% muscovite (ca. 0.25 mm), 50% clay (< 0.063 mm), 9% glauconite (ca. 0.25 mm), and 1% organics (0.13 to 0.25 mm).

The glauconite occurs as large and well rounded cryptocrystalline grains that results in a bimodal grain-size distribution (Figs. 2D, 3A, 3F). Some glauconite grains are fractured. In some cases, glauconite has clearly replaced fecal pellets, and possibly also foraminiferal tests, given poor resemblance of some grains to tests (Fig. 4A, 4C). Fragments of dark brown, opaque organic material are ubiquitous (Fig. 3E).

Many concretions are black or green on the outside, some are beige. Freshly broken surfaces react vigorously to HCl, and cracks in



**Figure 4.** High magnification images of glauconite formation and alteration in rock sample, KSU-003. Foraminifera test with glauconite infilling chambers (A); weathering mineral grain into mica (B); gastropod protoconch with glauconite inside whorls (C); weathered mineral grain into mica in cross polarized light (D); mineral grains in cross polarized light without preferred orientation (E); Thin section images at magnification 10 X 40.

the concretions have infillings of calcite cement. Many show round pits and long, thin burrow-like features on their surfaces. Compositions are given in Table 1. In the example of the dark concretions that was studied in thin section, the external color zone was different from the inside primarily in its color, although the outer zone had large micas and more pores, with a central hollow with secondary calcite infilling (Fig. 2A, 2C, 2H). In the example of the lighter concretions that was studied in thin section, the concretion also had a dark, dense, external rind. It contained glauconite, although the grains of glauconite are sparser and less rounded than those in the host bedrock (Fig. 2G). Its nucleus consisted of large fragments of crab cuticle (Fig. 2B). The fragments are brown, and are layered

with considerable pore space between them and around them. Some concretions contain claws and associated fragments of the mudshrimp *Mesostylus*.

Some other concretions are even lighter grey-brown in color; these are weakly cemented, micaceous, and silty to sandy, and do not contain fossils (Figs. 2I, 3B, 3C, 3E). A flat concretion was observed in thin section. Its outer rim is dark and fine, brownish-black in color. Some of the rock sample is lightly cemented to the concretion, giving it an outer zone of glauconite, clay, and mica, while internally it consists of very fine clay with some larger muscovite grains (Fig. 4B, 4D, 4E), with a central hollow that has been filled with some clay, mica, and organic fragments. This was likely a burrow (Fig. 2A). No glauconite is present

**Table 1.** Percent composition of Coon Creek Formation lithology and included concretions.

	Bedrock	Flattened concretion	Light concretion	Dark concretion
Clays and fines	39	70	44	50
Coarse muscovite	40	30	44	40
Glaucinite	10	—	<1	—
Organics	11	—	10	—
Fossils	—	—	<1 (shell and cuticle fragments)	10 (foraminifera)

in the concretion: it consists of 60% clay and fine muscovite and 20% coarser muscovite (0.13–0.25 mm).

Some annelid worm burrows are present. These are tube-shaped with pointed ends and wrinkle-like features on their surfaces. Crescentic microstructure is visible in thin section. They share the same colors as the concretions, some being black, hard, and dense, and others being light beige with weakly cemented exteriors. In thin section the burrows have dense outer rinds as seen in the concretions, so they presumably all represent an early phase of diagenesis. Cross-sections of burrows show layers of different lithologies, alternating between coarse grains and fine grains, arranged in crescents parallel to the convex margin of the specimen (Fig. 2F).

Fossil preservation will be covered in detail in the Discussion section.

### SYSTEMATIC PALEONTOLOGY

See Rathbun (1918) for schematic of brachyuran morphology.

#### Order DECAPODA LATREILLE, 1802

#### Infraorder ASTACIDEA LATREILLE, 1802

#### Superfamily NEPHROPOIDEA DANA, 1852

#### Family NEPHROPIDAE DANA, 1852

#### Subfamily NEPHROPINAE DANA, 1852

#### Genus *HOPLOPARIA* MCCOY, 1849

Type species.—*Astacus longimanus* Sowerby, 1826, by subsequent designation of Rathbun (1926:129).

Included species.—*Hoploparia albertaensis*

Tshudy et al., 2005; *H. alpines* (Van Straelen, 1936c) as *Homarus alpinus*; *H. antarctica* Wilckens, 1907; *H. arbei* Aguirre-Urreta, 1989; *H. aspera* Harbort, 1905; *H. bearpawensis* Feldmann, Bishop and Kammer, 1977; *H. belli* McCoy, 1849; *H. benedeni* Pelseneer, 1886; *H. bennetti* Woodward, 1900; *H. beyrichi* Schlüter, 1862; *H. biserialis* Fritsch and Kafka, 1887; *H. blossomana* Rathbun, 1935; *H. buntingi* (Feldmann and Holland, 1971) as *Nephrops buntingi*; *H. catalunica* Garassino, Artal and Pasini, 2009; *H. calcarifera* Schlüter, 1879; *H. collignoni* (Van Straelen, 1949) as *Palaehomarus Collignoni*; *H. columbiana* Beurlen, 1938; *H. corneti* Van Straelen, 1921; *H. dentata* (Roemer, 1841) (= *H. prismatica* McCoy, 1849; *Palaeno roemeri* Robineau-Desvoidy, 1849); *H. dentonensis* Rathbun, 1935a; *H. edwardsi* (Robineau-Desvoidy, 1849) as *Nephrops samviensis*; *H. eocenica* Lörenthey in Lörenthey and Beurlen, 1929; *H. falcifer* Fritsch and Kafka, 1887; *H. fraasi* (Böhm, 1891) as *Homarus fraasi*; *H. gabbi* Pilsbry, 1901; *H. gadzicki* Feldmann and Crame, 1998; *H. gammaroides* McCoy, 1849 (= *H. belli* McCoy, 1849; *H. victoriae* Quayle, 1987); *H. georgeana* Rathbun, 1935; *H. gladiator* Pilsbry, 1901; *H. groenlandica* Ravn, 1903; *H. hakeleensis* (Fraas, 1878) as *Pseudostacus hakeleensis*; *H. hemprichi* (Mertin, 1941) as *Paleohomarus hemprichi*; *H. heterodon* (Bosquet, 1854) as *Oncopareia Bredai*; *H. horrida* Schweitzer, Feldmann et al., 2003; *H. intermedia* Secretan, 1964; *H. johnsoni* Rathbun, 1935; *H. kamimurai* Kato and Karasawa, 2006; *H. kamuy* Karasawa and Hayakawa, 2000; *H.*

*klebsi* Noetling, 1885 (= *H. knetschii* Zimmermann, 1944 [imprint 1942]); *H. lehmanni* Haas, 1889; *H. longimana* (Sowerby, 1826) (type) (= *H. granulosa* Bell, 1863; *H. punctulata* Bell, 1863; *H. sulcirostris* Bell, 1863); *H. mcNairyensis* Rathbun, 1926a; *H. mesembria* Etheridge, Jr., 1917; *H. minima* Tribolet, 1876; *H. miyamotoi* Karasawa, 1998; *H. muncki* Pelseneer, 1886; *H. natsumiae* Karasawa, Ohara and Kato, 2008; *H. nephropiformis* Schlüter, 1879; *H. pelseneeri* (Van Straelen, 1936a) as *Homarus pelseneeri*; *H. percyi* Beneden, 1872; *H. pusilla* Secretan, 1964; *H. riddlensis* Feldmann, 1974; *H. saxbyi* McCoy, 1849; *H. scabra* Bell, 1863; *H. schluteri* Tribolet, 1876b; *H. sculpta* Secretan, 1964; *H. senonensis* Forir, 1887; *H. seucica* Schlüter, 1879; *H. tennesseensis* Rathbun, 1926a; *H. triboleti* Borrisiak, 1904; *H. trigeri* (A. Milne-Edwards, 1886) as *Ptychodus trigeri*; *H. tshudyi* Schweitzer and Feldmann, 2001a; *H. victoriae* Quayle, 1987; *H. wardi* Quayle, 1987.

Generic diagnosis.—“Cephalic ridges and spines developed to varying degrees; well-developed rostrum with or without spines; cervical groove extends about half the distance to the dorsal surface; postcervical groove extends from the dorsal surface to curve around and merge with the cervical groove; well developed hepatic groove; branchial regions with granules, scabrous ornamentation, or keels; exopod of the uropod with a diarsis; chelae clearly differentiated into crushers and cutters,” (Feldmann et al., 2007:703).

Discussion.—This genus has been referred to as a “wastebasket” (Tshudy and Sorhannus, 2003). However, the species within it are strikingly similar, with many characters in common. One might hope that a pattern would emerge to further differentiate among nearly 50 species, but no such pattern has been recognized (Feldmann et al., 2007). *Hoploparia* occurs widely geographically and ranges from the Early Cretaceous to the Miocene (Feldmann et al., 2007).

***HOPLOPARIA TENNESSEENSIS***  
**RATHBUN, 1926**

Figure 5A–F

Diagnosis.—Postorbital keel with large spine at anterior margin. Lacking ornamentation on thorax.

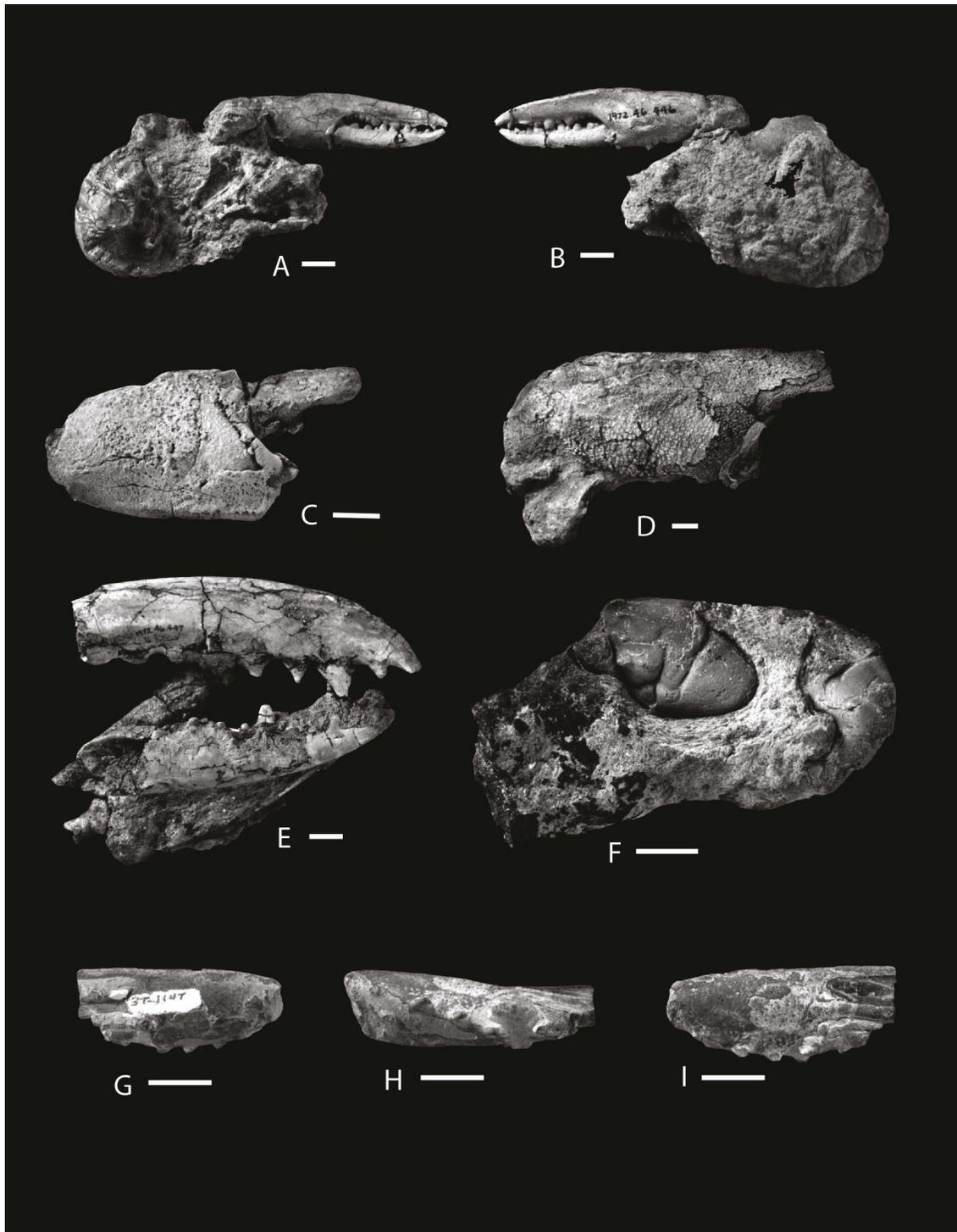
Cephalon with post antennal spines and postorbital spines. Cuticle granular on cephalothorax. Pleura with sulcus on posterior margin. Chelae long and slender with large denticles.

Description of material.—Carapace narrow and laterally compressed. Cuticle granular. Rostrum short with small, spinose keels on either side of midline. Postrostral carina with small spines decreasing in size posteriorly. Two well defined antennal spines; one suborbital spine and one, well defined postorbital spine at anterior end of postorbital keel. Inferior groove, cervical groove, intercervical groove, and postcervical groove deep and well defined with faint continuation in a concave upward arc between the cervical and postcervical groove. Terga weakly granular or punctate with a small node on anterior margin at the transition point between the first tergum and pleuron; posterior margin of pleura with arcuate sulcus. Pleural ventral margin sigmoidal, terminating in an acute point at posterior edge. Chelae with robust and pustulose palm becoming wider distally; fingers slightly arcuate to straight and elongate with very low, flat denticles proximally, becoming pointed distally.

Material examined.—Carapace UF 252087 length 72 mm, width 41 mm; carapace UF 252088 length 35 mm, width 8 mm. Other specimens include UF 252086; MPPM 72.46.445; MPPM-007; MPPM-003; MPPM-004; MPPM-005; MPPM-007; MPPM 1972.46.446; MPPM 1972.46.447.

Occurrence.—GAB Blue Springs locality 37 and the type locality at “Dave Weeks Place”. Other localities include the state line cut on the Southern Railway in McNairy County, Tennessee, one mile northwest of Wenasoga, Mississippi; on the line between Selma and Ripley Formations as well as a few hundred yards west of the station near Wenasoga, Mississippi (Rathbun *in* Wade, 1926 p. 187) as well as in Union County at Lee’s old mill, (34°32’29.32” N, 88°54’43.13” W), located 2 miles northeast of Keownville on the road to Molino (Rathbun, 1935:25).

Discussion.—In Rathbun’s initial description of *Hoploparia tennesseensis* (*in* Wade, 1926:187), few carapaces were preserved and described.



**Figure 5.** *Hoploparia tennesseensis* Rathbun, 1926; specimen MPPM 1972.46.446. View of inner surface of left lateral cutting claw and segments of pleon (A), view of outer surface of left lateral cutting claw (B). *H. tennesseensis* Rathbun, 1926; crushing claw; specimen MPPM 005 (C). *H. tennesseensis* Rathbun, 1926; crushing claw; specimen MPPM 004 (D). *H. tennesseensis?* Rathbun, 1926; cutting claw; specimen MPPM 1972.46.447 (E). *H. tennesseensis* Rathbun, 1926; carapace and pleon; specimen UF 252086 (F). *Hoploparia georgeana* Rathbun, 1935; claw; specimen UF 252091 (G, H, I) Scale bars = 1 cm.

The lengths of specimens in the present study are congruent to those in the original sample, the type measuring a total of 48.6 mm and study material being of similar size. Like Rathbun's material, the Blue Springs locality specimens are cracked along the midline and possess a cervical and inverted, Y-shaped hepatic groove that are also well defined.

The presence of more material aids in verification of the species and illustrates variation between individuals. Most notably, specimens from the Blue Springs locality vary considerably in size. Most carapaces are about the same size as those Rathbun illustrated and described, but two carapaces are preserved in a different orientation than those of Rathbun; they are more inflated and larger than those described by Rathbun. The Blue Springs specimens are found preserved lying on their side; though this may be due to a morphological trait, there is nothing to indicate such and therefore no reason to assess the Blue Springs specimens to be different than those Rathbun described. A number of claws were also found, though they are not articulated with any carapaces.

Claws also show a range in size and forms and some illustrate cuticle ornamentation. Robust, potentially crushing claws possess a long, large palm that increases in size distally. These large specimens of palms possess flat tubercles on their outer surface. Dactylus and propodus of these claws are broken either at the base or proximal to the base. Claw segments likely belonging to cutting claws of the dactylus and/or propodus, on the other hand, possess long, slender, and weakly arcuate fingers with pronounced denticles that become very sharp distally. One claw, preserved on specimen MMNH 1972.46.446 (Fig. 5A–B) illustrates this form, fully articulated. Another, impressive specimen MMNH 1972.46.447 (Fig. 5E), does not possess the palm of the claw but is, even so, extremely large and likely the cutting claw of the species. The type specimen of *Hoploparia tennesseensis* is in fact a claw and was not associated with a carapace. Most notably, this claw possesses broad, flat tubercles on the cuticle that become oblong punctae on the finger. Denticles are not present. Rathbun also described carapaces that match the form of *Hoploparia*

*tennesseensis* from the Coon Creek Formation in a later publication (1935) that she referred to as this species. Though there is a paucity of original material, the flat tubercles present on the type specimen as well as Blue Springs specimens and the later inclusion of the carapaces by Rathbun supports the inclusion of these specimens as *Hoploparia tennesseensis*.

#### ***HOPLOPARIA MCNAIRYENSIS* RATHBUN, 1926**

**Diagnosis.**—Ornamentation granular, keels at base of rostrum (Feldmann et al., 2007). Rathbun (*in* Wade, 1926) did not provide a diagnosis.

**Description.**—“Carapace behind the cervical groove is granulated. Granulation is scarce immediately in front of the cervical groove, becoming more crowded and flattened toward the front and middle of the carapace. There is also a spine near the orbit. A second specimen also has granulation and a long rostrum. The carapace has a median carina with a lateral carina on either side. The lateral carinae are slightly more prominent and irregular, possessing spines and tubercles where as the median carina do not. There is also a blunt, uneven ridge that extends from the orbital angle to the cervical suture with two interruptions,” (Rathbun, *in* Wade, 1926:187).

**Material examined.**—No. 10272 (specimen from Vanderbilt University?, described by Rathbun, 1926, only); USNM 73118.

**Occurrence.**—Half a mile northwest of Gravel Hill, McNairy County, Tennessee, on the line between Selma and Ripley Formations; State Line cut, in McNairy County, Tennessee, near Wenasoga, Mississippi; Coon Creek Formation, Maastrichtian.

**Discussion.**—Rathbun (*in* Wade, 1926) stated her uncertainty that the two specimens of *Hoploparia mcnairyensis* belonged to the same species, citing a need for more material. Having observed specimen USNM 73118, and without access to the Vanderbilt University specimen, it remains uncertain that any material from this study, including all material from the Blue Springs locality, is representative of *H. mcnairyensis*.

**HOPLOPARIA GEORGEANA RATHBUN, 1935**

Figure 5G–I

1935. *Hoploparia georgeana*. Rathbun, Geological Society of America Special Papers, 3:25, pl. 9, figs. 9–12.

2010. *Hoploparia georgeana*. Schweitzer et al., Crustaceana Monographs, 10:29.

Diagnosis.—Carpus of left and right claw, cuticle granular. Upper surface of claw possessing anteriorly directed spines; first two spines form a pair parallel to the point of articulation with the carpus, the outermost of which is directed laterally, followed by a row of three spines that form the upper keel of the claw, beginning at outer margin of upper surface continuing to end at the inner margin, close to the articulation of the dactylus. Lower margin becoming increasingly narrow from the upper margin, becoming keeled toward proximal margin. Articulated joint of merus and carpus (?) possessing widely spaced spines (direction and placement of fragment indiscernible).

Material examined.—UF 252089, length: 25.92 mm, height: 15.3 mm; UF 252090, length: 21.44 mm, height: 13.72 mm, UF 252091, length: 40.74 mm, height: 16.98 mm; UF 252092, length: 27.02 mm, height: 14 mm, width: 10 mm; UF 252093, length: 25.7 mm, height: 13.7 mm.

Occurrence.—Rathbun (1935:26) described the holotype from Maryland at an erosional exposure at Brightseat, Prince Georges County from the Monmouth Formation, Upper Cretaceous. Specimens described herein occurred at the Blue Springs locality, Coon Creek Formation, Union County, Mississippi, Maastrichtian.

Discussion.—The identification of these claw fragments extends the geographic range of *Hoploparia georgeana* from the Atlantic Coastal Plain to the Mississippi Embayment and is the second species of *Hoploparia* found at the Blue Springs locality. These specimens can clearly be differentiated from *Hoploparia tennesseensis* in that they possess spines that are not observed on chelae of *H. tennesseensis*. Because there are no articulated claws with *H. mcnairyensis*, it is not impossible that the claws of *H. georgeana* are a junior synonym of *H. mcnairyensis*, but ornamentation of *H. mcnairyensis* does not possess

such pronounced spines. More specimens are needed to confirm that *H. mcnairyensis* and *H. georgeana* are not the same species.

**Infraorder AXIIDEA****DE SAINT LAURENT, 1979****Superfamily CALLIANASSOIDEA DANA, 1852****Family CALLIANASSIDAE DANA, 1852****Genus MESOSTYLUS BRONN AND****ROEMER, 1852**

Type species.—*Pagurus faujasi* Desmarest, 1822.

Included species.—*Mesostylus faujasi* (Desmarest, 1822); *Mesostylus mortoni* (Pilsbry, 1901) as *Callianassa mortoni*.

Generic diagnosis.—“Merus of major cheliped longer than high, upper margin convex, lined with large granules; large knob on distal margin articulating with carpus. Carpus longer than high, distal margin concave, serrate, lower distal margin with flange extending onto outer surface in weak rim separated from distal margin by prominent sulcus, distal margin of flange serrate. Proximal margin of manus at 100–110° angle to lower margin; upper and lower margins finely serrate; fingers with stout teeth on occlusal surfaces. Major chela exhibiting notable dimorphism; chelae stouter and more rectangular in presumed males, chelae more slender and higher proximally in presumed females. Minor chela longer than high, highest proximally; fingers with parallel ridges. Pleonal somites apparently smooth.” (Schweitzer and Feldmann, 2012:17).

**MESOSTYLUS MORTONI (PILSBRY, 1901)**

Figure 6A–B

1901. *Callianassa mortoni*. Pilsbry. Proceedings of the Academy of Natural Sciences of Philadelphia:112, pl. 1, figs. 1–7.

1926. *Callianassa mortoni*. Rathbun In B. Wade (ed.), The fauna of the Ripley Formation of Coon Creek, Tennessee. U.S. Geological Survey Professional Paper, 137:188, pl. 67, figs. 1, 2, 4–9.

1935. *Callianassa mortoni*. Rathbun, Geological Society of America (Special Paper), 2(i–viii):29.

1941. *Protocallianassa mortoni* (Pilsbry, 1901). Mertin, Nova Acta Leopoldina, 10 (68):208.

1962. *Protocallianassa mortoni* (Pilsbry, 1901). Roberts, New Jersey Geological Survey Bulletin, 61:169, pl. 81,

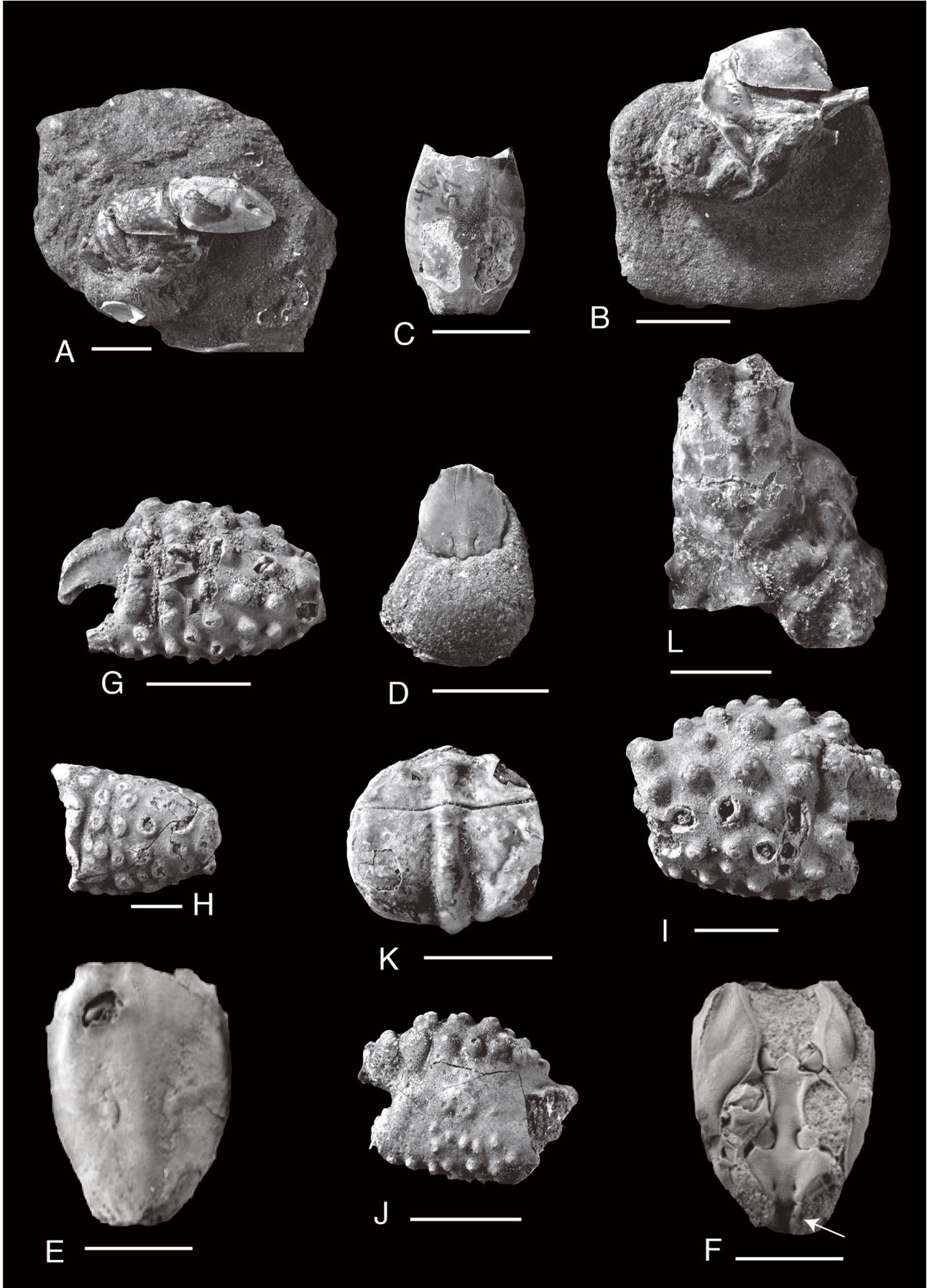


fig. 8, pl. 83, figs. 1–6.

1991. *Protocallianassa mortoni* (Pilsbry, 1901). Bishop, Mississippi Geology, 12 (1):12–13.  
 2012. *Mesostylus mortoni* (Pilsbry, 1901). Schweitzer and Feldmann, Bulletin of the Mizunami Fossil Museum, (38):19.  
 2013. *Mesostylus mortoni* (Pilsbry, 1901). Feldmann et al., Bulletin of the Mizunami Fossil Museum, (39):12–15.

Description.—“Merus longer than high, upper surface convex; proximal margin at about 60° angle to lower margin, with projection near lower margin articulating with ischium; lower margin nearly straight; distal margin concave, articulating with long projection of carpus; outer margin convex, with row of large granules, very large swelling ornamented with tubercles distally, knob on distal margin articulating with carpus. Carpus longer than high, with sinuous proximal margin, with projection at upper margin to articulate with merus, marked concavity below it, then becoming convex at lower margin; lower margin sloping downward distally so that entire carpus becomes higher distally; upper margin weakly convex, serrate; distal margin concave, serrate where articulating with manus; at lower distal corner, flange projecting anteriorly, extending onto outer surface as weak ridge separated from distal margin by prominent sulcus, distal margin of flange serrate; strongly vaulted on outer surface, slightly depressed on inner surface. Manus longer than high, strongly vaulted on outer surface; proximal margin sinuous, with weak projection centrally for articulation with carpus, lined with setal pits, entire margin oriented at about 100° angle to lower margin; lower and upper margins serrate, rimmed, nearly straight, manus becoming slightly less high

distally; distal margin straight where intersecting upper margin, then directed slightly obliquely to intersection with fixed finger, serrate; inner surface of manus flattened, with row of setal pits along upper margin. Fixed finger with triangular central spine; movable finger with basal blunt spine and long, blunt tooth centrally; outer surface of movable finger with two rows of setal pits; row of setal pits along upper margin of inner surface of movable finger. Movable finger of minor chelae with two or three granular keels with rows of setal pits or granules between them. Ischia of other pereopods longer than high, smooth. Abdominal somites poorly known, smooth,” (Schweitzer and Feldmann, 2012:19).

Description of material.—Specimens are of chelae and carpus, some of which bear both major and minor claws. Merus and carpus longer than high; narrow. Cuticle smooth. Dactyl and fixed finger edentulous; proximal margin of carpus greater than 90°, top and bottom margin of carpus and merus finely serrate, distal outer margin of carpus with finely serrate keel or flange extending from lower margin upward and proximally from the distal margin of the carpus ¼ of total height; row of tubercles on the lower margin of the merus.

Material examined.—UF 252094, length of merus (l): 15.58 mm, height of merus (h): 13.92 mm; MPPM 1974.35.16, l: 17.48 mm, h: 15.28 mm; MPPM 72.46.456, l: 15.93 mm, h: 12.38 mm; MPPM 020, h: 17.22 mm; MPPM 019, l: 20.28, h: 15.4 mm; MPPM 023, l: 21.52 mm, h: 17 mm; MPPM 021, (major claw) l: 19.34, h: 18.26, (minor claw) l: 16.04, h: 14.45 mm; UF 252095, l: 11.66 mm, h: 10.14 mm; MPPM 024, l: 15.64 mm, 13.94 mm; UF 252096, (major claw) l: 13.64 mm, h:

← **Figure 6.** *Mesostylus mortoni* (Pilsbry, 1901); specimen MPPM 72.46.456 (A). *Mesostylus mortoni* (Pilsbry, 1901); specimen MPPM 1974.35.16 (B). *Bournelyreidus ericksoni* sp. nov.; specimen MPPM 1972.46.157 (C). *Bournelyreidus ericksoni* sp. nov.; specimen MMNS IP 3140 (D). *Bournelyreidus ericksoni*; holotype UF 252131 (E). *Bournelyreidus ericksoni*; holotype UF 252131; venter with arrow indicating location of hook (F). *Prehepatus harrisi* Bishop, 1985; MPPM 1972.46.448 (G). *Prehepatus harrisi* Bishop, 1985; specimen MPPM 1972.46.448 (H). *Prehepatus harrisi* Bishop, 1985; specimen KSU 2219 (I). *Prehepatus harrisi* Bishop, 1985; specimen KSU 2219 (J). Majid (?) fragment 1; specimen MMNS 4016 (K). Majid (?) fragment 2; Specimen MMNS 4108 (L). Scale bars = 1 cm except in E and F. For these two, scale bars = 0.5 cm.

12.69 mm, (minor claw) l: 9.4 mm, h: 8.78 mm; UF 252097, h: 16 mm.

Occurrence.—Early Campanian to Maastrichtian throughout the Atlantic and Gulf Coastal Plains and the Mississippi Embayment (Schweitzer and Feldmann, 2012; Feldmann et al., 2013).

Discussion.—Schweitzer and Feldmann (2012) proposed to restrict *Protocallianassa* to *Protocallianassa archiaci*, the type species, and referred *Protocallianassa mortoni* to *Mesostylus* because it possesses the well developed flange on the lower distal margin of the carpus, the proximal margin of the merus is at an angle greater than 100°, and it has a ridge of large tubercles on the merus (Schweitzer and Feldmann, 2012:17). The tubercles on the merus of the Blue Springs specimens are not well preserved and generally are observed as pits, but are verified as tubercles on specimen MPPM 019. Modern studies such as Tsang et al. (2008) and Sakai (2011) have reevaluated the systematics of extant Axiidea, but necessary morphology for classification is not preserved in the fossil record. Because of this, the placement of *Mesostylus mortoni* has been maintained in this study and reflects that of Schweitzer and Feldmann (2012) and Feldmann et al. (2013). This species of mud shrimp is relatively wide spread geographically and ranges from New Jersey to Tennessee and Mississippi (Feldmann et al., 2013).

### Infraorder ACHELATA SCHOLTZ, 1995

#### Superfamily PALINUROIDEA LATREILLE, 1802

#### Family PALINURIDAE LATREILLE, 1802

#### Genus *LINUPARUS* WHITE, 1847

1847. *Linuparus*. White, List of Specimens of Crustacea in the Collection of the British Museum, London:40.

1849. *Podocratus*. Becks MS., in Geinitz, Das Quadersand-Steingebirge oder Kreidegebirge in Deutschland, Freidberg:96.

1862. *Podocrates*. Schlüter, Deutsche geol. Gesell. Zeitschr, 14:710.

1897. *Linuparus* (part). Ortmann, Am. Jour. Sci., 4<sup>th</sup> ser., 4:296.

Type species.—*Palinurus trigonus* von Siebold, 1824.

Included species.—*Linuparus adkinsi* Rathbun, 1935a; *L. africanus* Glaessner, 1932a;

*L. bererensis* Secretan, 1964; *L. bigranulatus* Glaessner, 1930; *L. canadensis* (Whiteaves, 1885) as *Hoploparia? canadensis* = *L. atavus* Ortmann, 1897; *L. carteri* (Reed, 1911) as *Thenops carteri*; *L. dentatus* Van Straelen, 1936a; *L. dulmenensis* (Geinitz, 1849–1850) (Schlüter, 1899) as *Podocrates dulmenensi*; *L. dzheirantuiensis* Feldmann, Schweitzer et al., 2007; *L. eocenicus* Woods, 1925; *L. euthymei* (Roman and Mazeran, 1920) as *Podocrates euthymei*; *L. grimmeri* Stenzel, 1945; *L. hantscheli* Mertin, 1941; *L. japonicas* Nagao, 1931; *L. kleinfelderi* Rathbun, 1931a; *L. korura* Feldmann and Bearlin, 1988; *L. laevicephalus* Mertin, 1941; *L. macellarii* Feldmann and Tshudy, 1988; *L. petkovici* Bachmayer and Marković, 1955; *L. pustulosus* Feldmann in Feldmann et al., 1977; *L. richardsi* (Roberts, 1962) as *L. (Podocratus) richardsi*; *L. schluteri* (Tribolet, 1874) as *Podocrates schluteri*; *L. scyllariformis* (Bell, 1858) as *Thenops scyllariformis*; *L. spinosus* Collins and Rasmussen, 1992; *L. stolleyi* (Haas, 1889) as *Podocrates stolleyi*; *L. straili* (Forir, 1887) as *Thenops straili*; *L. somniosus* Berry and George, 1972; *L. sordidus* Bruce, 1965; *L. tarrantensis* Davidson, 1963; *L. texanus* Rathbun, 1935a; *L. trigonus* Siebold, 1824 as *Palinurus trigonus*; *L. vancouverensis* (Whiteaves, 1885) as *Hoploparia (?) canadensis*; *L. watkinsi* Stenzel, 1945; *L. wilcoxensis* Rathbun, 1935a.

Generic diagnosis.—“Carapace sub-rectangular with three longitudinal keels; rostrum absent; supraorbital spines close to median line, fused to form plate or separated by indentation; well marked cervical groove; longitudinal median carina extends from posterior margin to cervical groove; prominent ridges form swelling of flank just posterior to cervical groove. Pleon with variously spinose margins on pleurae and keeled terga. Pereiopod 1 stout; pereiopods 2–5 long, slender; telson sub-rectangular,” (Feldmann et al., 2013:15).

Discussion.—Specimens from the Coon Creek possess all diagnostic characters of the genus. Important features not preserved on Rathbun’s (*in* Wade, 1926) specimen are observed including keeled terga, inflated flanks (stridulating

region or *appareil stridulant* of Secretan, 1964), and spines on the margins of the pleura. *Podocratus* is herein treated as a junior synonym of *Linuparus*. Subgeneric diagnoses are not included in the following discussion and are not utilized in classification because they lack utility as suggested by Feldmann et al. (2007) because features used to determine subgeneric placement are not mutually exclusive.

**LINUPARUS KEYESI SP. NOV.**

Figure 7A–G

1926. *Podocratus canadensis* (partim). Rathbun, in Bruce Wade, U. S. Geologic Survey Professional Paper 137:185, pl. 63, figs. 12, 16.  
 1983a. *Linuparus canadensis* (partim). Bishop, Journal of Crustacean Biology, 3(3):417–430.  
 1986. *Linuparus canadensis*. Bishop, Journal of Crustacean Biology, 6(3):345–346.  
 1991. *Linuparus canadensis*. Bishop, Mississippi Geology, 12(1, 2):8–17.

Zoobank Nomenclatural Act.—D3D73DD7-B27A-42AE-A9FC-99AC1D970234.

Diagnosis.—Large to medium sized carapace for the genus. Gastric region aristate. Pleurae with three spines on lateral keel and ventral margin, one or two pustules at center of pleura.

Description.—Carapace sub-rectangular. Rostrum distinct, bifid; supraorbital spines close to midline and separated, single pair of post-supraorbital spines. Cephalic region with marginal keel possessing three or more forward directed spines and antennal keel possessing 4 or more forward direct spines. Cephalic region slightly inflated with aristate gastric region outlined by five large, forward directed spines and a variable range of small spines in between the larger ones. Cephalic region sparsely granular. Cervical groove parabolic, deep and well defined. Thoracic region with three longitudinal keels with numerous, anteriorly directed spines of nearly equal size. Axial keel possesses seven to nine spines, lateral keels with 10 to 15 spines. Slightly inflated flank posterior to cervical groove indicating *appareil stridulant* (of Secretan, 1964). Nearly vertical ventral walls of carapace. Flank with prominent, finely granular marginal rim. Thoracic region uniformly granular. Pleon sub-rectangular and coarsely punctate. Axial

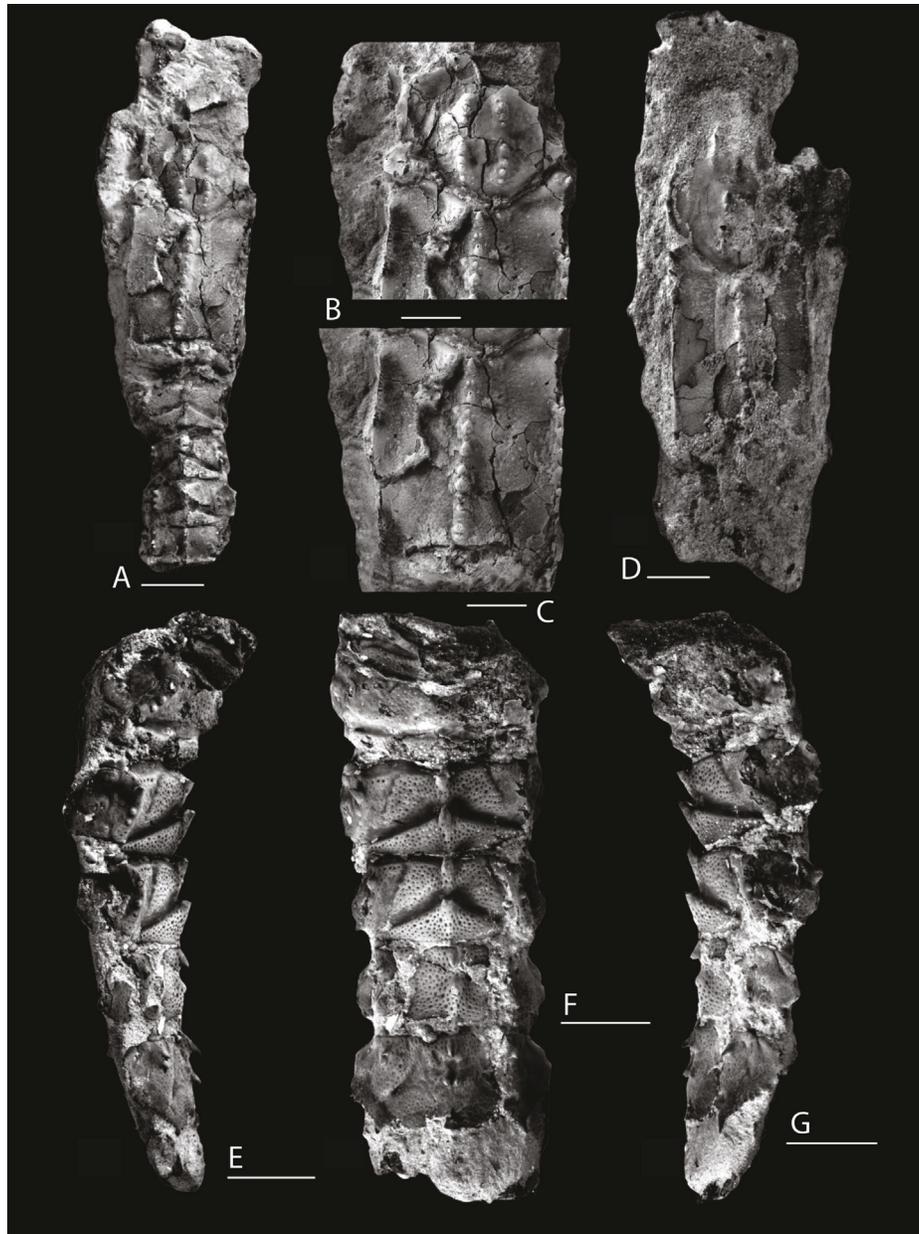
keel of pleon with pair of anteriorly directed spines with smooth, posteriolaterally sloping sulcus rising between the two spines on the first through fourth somite, spines on fifth and sixth somite posteriorly directed. Angular demarcation between terga and pleura with three outward projecting spines, declining posteriorly. Pleura with 3 spines at ventral margin and two pustules at the center of the second and third pleura, with only one on fourth pleuron. Basal antennal segment spinose on margin and on central keel of dorsal surface. Right mandible rectangular with small, arcuate, anterior process.

Etymology.—Latinization of Keyes, “*keyesi*” pays recognition to Mr. Richard Keyes, whose generosity and knowledge of the area aided in the identification the species. We also recognize him for his donation of the paratype USNM 610401 from his personal collection.

Type material.—Holotype: MMNH 2000.1.11 carapace length 55 mm, width 26 mm, pleon length 20 mm, width 12 mm; Paratypes: USNM 610401, length: 69 mm, width: 23 mm; 1972.2.444 (carapace) length 65 mm, width 35 mm; MPPM-002 carapace length 85 mm, width 35 mm, pleon length 105 mm, width 35 mm; KSU 2224 pleon length 10 mm width 25 mm. Other specimens: MPPM-001, UF 260960, UF 260962, UF 260964, UF 260965, UF 260963, UF 252100, and UF 260961.

Occurrence.—Blue Springs locality, Mississippi, Coon Creek Formation; Maastrichtian, Late Cretaceous. Other specimen (No. 10272) collected ½ mile northwest of Gravel Hill, McNairy County, Tennessee (Rathbun, in Wade, 1927:186).

Discussion.—Rathbun (in Wade, 1926:185; pl. 63, figs. 12, 16) described the specimen as *Podocratus canadensis*. Her description of the available material conforms to the morphology of the new specimens from the Coon Creek Formation. That being said, Rathbun’s material consisted only of the thoracic region of the carapace. The fragmented carapace is tricarinate behind the cervical groove and the keels possess irregularly-sized spines. The median keel has nine spines with the third to last being double (Rathbun in Wade, 1926:185). Rathbun also noted that the Coon Creek specimen possessed a longitudinal sulcus or furrow around the median keel as was described from the



**Figure 7.** *Linuparus keyesi* sp. nov. Dorsal view of carapace, MMNH 2000.1.11 (A, B, C), dorsal view of carapace, MPPM 001 (D), lateral and dorsal view of pleon, USNM 610401 (E, F, G), scale bars = 1 cm.

specimens of *Linuparus canadensis* from Alberta, Canada. The longitudinal furrow was not observed in the studied material, but if the cause of this furrow is in fact post-mortem deformation (which it almost certainly is), then the character is not of taxonomic significance.

When compared to descriptions of more complete specimens of *L. canadensis*, the Blue Springs *Linuparus keyesi* is different in size, form of gastric region, and nature of the pleura. There

are only a few species of *Linuparus* from North America. *L. canadensis* is possibly the most widely distributed in the Cretaceous (Feldmann and McPherson, 1980:12). Feldmann and McPherson (1980) suggested that *L. canadensis* occurs from Alberta, Canada to Louisiana, USA; however, observations from this study lead to the conclusion that this distribution should exclude the material from the Coon Creek Formation of Mississippi.

Because of the fragmental nature of decapod

preservation, only portions of the whole animal are sometimes used to describe new species. *Linuparus* species infrequently have the pleon available for comparison, yet some species are described solely on the pleon, such as *Linuparus texanus* Rathbun, 1935. Because the Coon Creek Formation specimens possess both the carapace and the pleon, the specimens can be compared to the morphology of most previously described species (Table 2).

Stenzel (1945) noted the close similarity and relationship of *L. canadensis* with *Linuparus watkinsi*. *Linuparus watkinsi* also possesses three keels on the thorax, but the median keel has seven spines. Though, Stenzel (1945) noted that these are the major spines and that a few accessory spines also exist. Lateral keels of *L. watkinsi* possess 12 major spines. Both *L. canadensis* and *L. watkinsi*, therefore, have about seven to eight prominent spines on the median keel (illustrated in Stenzel, 1945, pl. 34 and described in Table 2 of Feldmann et al., 2007:709), similar in character to the nine median spines on the Coon Creek specimens (Fig. 7A–D). The lateral keels have twelve spines on Rathbun's Coon Creek specimen as well, just as in *L. watkinsi*.

Whiteaves (1885) initially described *Hoploparia? canadensis* as having large conical tubercles on three keels on the cephalon with five tubercles forming an isosceles triangle of the gastric region. Rathbun (1935) also described the gastric region of *L. canadensis* as having five spines that form an isosceles triangle. Stenzel (1945) described the cephalon of *L. watkinsi* in great detail. The cephalon of *L. watkinsi* has nine keels, three of which make the oval shaped gastric region, much like the Coon Creek specimens. The antennal keels (beginning at the fronto-lateral margin), the supraorbital keels, and the suborbital keels (gently curving and spreading posteriorly) are also spinose.

The pleon of *L. watkinsi* also has three spinose keels, like the thorax. The lateral keels have only two spines on each lateral somite, except for the first segment, which has none. The median keel has one central spine on the first and second segment, two laterally compressed spines on the

third segment, four spines on the fourth segment and two simple spines on the fifth segment. The telson has one spine and the uropods are narrow with sigmoidal edges. The upper surface of each pleonal segment of *L. canadensis* has a tubercle in the center, on its anterior edge, and another one on the margin of each of the sides at the tergal-pleural margin.

*Linuparus texanus* is a specimen of the pleon only (Rathbun, 1935:73). Each segment has two median spines as well, the pleura are rounded, and the edge of each pleuron is separated from the tergum by a smooth, blunt ridge that terminates in a stout and conical spine, pointing anteriorly.

*Linuparus wilcoxensis* has lateral keels with "crowded granules" and a median ridge with granules that becomes spinose with age (Rathbun, 1935:74). The pleon is coarsely punctate, but lacks carinae sloping toward the pleura and lacks pleural spines characteristic of the Coon Creek specimens. *Linuparus wilcoxensis* also possesses one to two spines rather than three on the ventral margin of the pleura. Specimens included in NMNH 371498 (103 fragmented specimens) of *L. wilcoxensis* from the Eocene of the Prairie Creek Formation possess a rectangular mandible with an anterior process and spines on the pleonal segments pointing both anteriorly and becoming posteriorly, as *L. keyesi* sp. nov. does.

*Linuparus grimmeri* has a median keel bearing about nine spines and lateral keels with about 20 small spines (Stenzel, 1945). The lateral keels on the terga have two spines per somite, except for the first, which has none. *Linuparus grimmeri* is generally narrow and a more finely ornamented species and is very small for the genus.

*Linuparus richardsi* Roberts, 1962 (Feldmann et al., 2013:15), was collected from the Graham Brick Company pit, Maple Shade, Burlington County, New Jersey from the Merchantville Formation. Another specimen had been collected from the Marshalltown/Merchantville spoils along the C and D Canal, Delaware. The species is diagnosed as having supraorbital spines that are close and fused, but lacking post-supraorbital spines. The gastric region is triangular and outlined

**Table 2.** Table of *Linuparus* species characters of the most similar species to *Linuparus keyesi* sp. nov.

Species	Size	Gastric Region	Median keel # of spines	Lateral keel # of spines	Ornament	Pleura
<i>L. canadensis</i>	Large	Triangular (5)	9	12	Coarse	1 lateral spine, 1 spine on pleural margin
<i>L. watkinsi</i>	Small	Oval (5 major, plus accessory)	7 major, plus accessory	12	Coarse	2 lateral spines (except 1 <sup>st</sup> somite)
<i>L. grimmeri</i>	Very Small	Oval	9	20	Fine	2 lateral spines
<i>L. texanus</i>	Small	N/A	N/A	N/A	Fine	1 lateral spine
<i>L. wilcoxensis</i>	Small	Triangular	Small, granular	Small, granular (becoming spines with age)	Fine	1-2 pleural spines
<i>L. richardsi</i>	Large	Triangular (5)	Decrease in size posteriorly	12-14	Coarse	N/A
MPPM 002	Large	Triangular/Oval (>5)	10-12?	12-13?	Coarse	N/A
UF 252100	Medium	Oval/Aristate (>5)	N/A	N/A	Coarse	N/A
MPPM-001	Medium	Oval/Aristate	9	14	Coarse	N/A
2000.1.11	Medium	Oval/Aristate	8-9?	11?	Coarse	3 lateral spines, 3 pleural spines, 2 central pustules on pleura
UF 260959	Medium	Oval/Aristate	N/A	N/A	Fine?	N/A
USNM 610401	Large	N/A	N/A	N/A	Coarse	3 lateral spines, 3 pleural spines, 2 central pustules on pleura
UF 260960	Medium	Oval/Aristate	7	13	Coarse	3 lateral spines, 2 pleural spines, no pustules visible
UF 260961	Medium	Oval/Aristate	7	13	Coarse	3 lateral spines, 3 pleural spines, no pustules visible
UF 260962	Medium	Oval/Aristate	9	N/A	Coarse	N/A
UF 260963	Medium	Oval/Aristate	N/A	N/A	Coarse	N/A
UF 260964	Medium	Oval/Aristate	N/A	N/A	Coarse	N/A
UF 260965	Small	Oval/Aristate	9	>10	Coarse	N/A

by five large spines. The lateral keels on the thoracic region possess spines that decrease in size posteriorly. The cephalic region is smooth rather than granular (Feldmann et al., 2013:15).

The carapace of one specimen of *L. keyesi* sp. nov., MPPM 002, has a more triangular gastric region and is generally large in overall size, but it does not possess irregularly granular ornamentation, and it is not apparent that the spines on the keels decrease in size posteriorly. The poor nature of preservation of the specimen makes comparison difficult. Both MPPM 001 (Fig. 7D) and MMNS 2000.1.11 (Fig. 7A–C) are both slightly smaller than MPPM 002 as is the specimen from New Jersey, *Linuparus richardsi* (Feldmann et al., 2013:15, fig. 5). One cannot help but find MPPM 002 to be very reminiscent of *L. richardsi* and could easily be mistaken for *L. canadensis* due to its preservation.

Though the material from the Coon Creek Formation was determined to be *L. canadensis* by Rathbun (*in* Wade, 1926) and Bishop (1991), newly available specimens have more morphological characters preserved. The new Coon Creek specimens cannot be assigned to *L. canadensis* because of the gastric region and ornamentation on the pleura (Fig. 7E–G).

*Linuparus watkinsi* has a distinct rostrum that is nearly identical to those preserved on small specimens of *L. keyesi* sp. nov. *Linuparus watkinsi* is also a smaller species, but lacks the same number of spines on the lateral keel of the terga, and the pleura do not have pustules at the center as *L. keyesi* sp. nov. does. *Linuparus grimmeri* possesses many similarities of the carapace, but the species is much smaller with finer ornamentation and generally less ornamentation on the pleura compared to *L. keyesi* sp. nov.

Stenzel (1945:410) contrasted *L. watkinsi* and *L. canadensis*, citing the shape of the gastric region, the number of accessory spines on the gastric region, and the medial keel of the thorax as being the main differences. Because of this, the characters of the Coon Creek specimens document a new species, sharing characters with each of *L. watkinsi* and *L. canadensis*, as well as

possessing unique characters. Table 2 illustrates key differences between closely related species of *Linuparus*. Though specimens observed possess a range in number of thoracic spines, we believe the variable nature of preservation of the carapaces affects approximations of numbers of thoracic spines. Because of this, we do not believe that the thoracic keel characters are sufficient to describe *L. keyesi* sp. nov. as they vary by specimen, possibly due to age or the individual. For example, specimen UF 260965 may be an example of a juvenile of *L. keyesi* sp. nov. It has acutely pointed, well pronounced spines, and is a great deal smaller than other specimens with nearly identical morphology other than having a slightly larger number of thoracic spines. Though the thoracic spines vary, the gastric region and pleurae sculpture are sufficiently different to distinguish *L. keyesi* sp. nov. from other *Linuparus*.

#### **LINUPARUS SP.**

Description of material.—Carapace medium sized, sub-rectangular, and narrow. Pair of supraorbital spines and pair of protogastric spines, slightly granular and rounded in form. Two or three spines on cephalic margin but generally smooth. Gastric region elliptic to ovate, slightly inflated with rounded, blunt spines outlining the narrow region and connecting to the bluntly granular median cephalic carina. Antermost spine is reduced and located between the protogastric spines. Gastric region slopes steeply toward the cervical groove. Thoracic region with three longitudinal keels; axial keel poorly preserved and not obviously spinose; lateral keel finely nodose with three larger nodes at posterior margin. Somites coarsely punctate with two anterior directed median spines on second and third somite. Sulcus connecting anterior margin of second spine to the tergal-pleural margin.

Material examined.—UF 260959, width: 1.7 cm, length: 5.2 cm.

Occurrence.—Blue Springs locality Mississippi, Coon Creek Formation; Maastrichtian, Late Cretaceous.

Discussion.—This specimen of *Linuparus* lacks key features to be assigned to any of the most closely related species (Table 2). Because

the preservation of the specimen is incomplete – gastric region is compromised, pleurae are not visible or present, specimen is crushed and anterior of cephalon is distorted – it is inappropriate to use the available characters to assign it to a new species or to an existing one. The most similar species is *Linuparus kleinfelderi* Rathbun (1931), but the wide carinae are smooth, rather than spinose. Specimen USNM 2009820, *Linuparus* sp., of the Eagleford Formation from the University of Dallas roadcut in Irving, Texas, also has wide keels, but the keels are granular. The gastric region of the specimen from the Eagleford Formation is also similar in nature to *Linuparus* sp. of the Coon Creek Formation in that it is aristate, but other similar morphology cannot be confirmed.

**Infraorder ANOMURA MACLEAY, 1838**  
**Superfamily PAGUROIDEA LATREILLE, 1803**  
**Family DIOGENIDAE ORTMANN, 1892**  
**Genus PALAEOPETROCHIRUS BISHOP, 1991**

Type species.—*Palaeopetrochirus enigmus* Bishop, 1991.

Included species.—*Palaeopetrochirus enigmus* Bishop, 1991.

Generic diagnosis.—As for species.

***PALAEOPETROCHIRUS ENIGMUS* BISHOP, 1991**

Diagnosis.—“Left cheliped robust; merus long, triangular in cross section, flattened on bottom and front; posterior edge with en-echelon crinkles; carpus short; claw longer than high, outer face convex, lower margin level but slightly sinuous, upper margin strongly arched; fixed finger relatively short, stout, and triangular; dactylus relatively long, narrow, and curved,” (Bishop, 1991:11).

Description of material.—Left claw; lower margin straight, upper margin forming continuous arc with dactylus when fingers are closed; weakly convex outer surface. Outer surface with distally directed nodes. Nodes coarsest at lowermost and uppermost margin of propodus.

Material examined.—The holotype, 1700 MGS is illustrated in Bishop (1991:15) and is the sole specimen of the species. Its current

whereabouts are unknown.

Occurrence.—Bishop (1991) stated that the specimen did not occur with any written information on locality, etc. by the collector, but specimens associated in the box of material left by the collector, Ralph Harris, and described by Bishop, were likely from the Blue Springs locality, New Albany, Mississippi according to Bishop (1991) and would therefore be Maastrichtian.

Discussion.—The specimen described by Bishop (1991) has not been referenced since the publication and the Diogeninae Ortmann, 1892, genus, and species were not recognized by Schweitzer et al. (2010). The species was described in a less widely circulated journal, *Mississippi Geology*. Possibly because of this, the species has gone unreported since its initial description. The singular specimen is likely from the Coon Creek Formation, but there is no significant evidence to give us justification to include this potential hermit crab claw, especially without the presence of any other material. Bishop (1991:11) diagnosed the new genus as having “equal or subequal” claws with the possession of a single specimen of left claw, of which one can only observe the outer surface and part of the lower margin (Bishop, 1991:15, figs. 5A, 5B, and 5C). Bishop also illustrated the “lower edge of merus” (Bishop, 1991:15, fig. 5D), but did not reference it in his description.

There are many specimens of *Paguristes* Dana, 1851 in the fossil record, and one species of *Parapaguristes* Bishop, 1986, *Parapaguristes tuberculatus*. *Palaeopetrochirus enigmus* is tentatively retained in the Diogenidae, though there is no way of knowing that this species is left-handed. We have not been able to locate the specimen.

**Infraorder BRACHYURA LATREILLE, 1802**  
**Section DAKOTICANCROIDA RATHBUN, 1917**

**Family DAKOTICANCRIDAE RATHBUN, 1917**

Included genera.—*Dakoticancer* Rathbun, 1917; *Tetracarcinus* Weller, 1905; *Avitelmessus* Rathbun, 1923.

Included species.—*Dakoticancer overanus* Rathbun, 1917; *Dakoticancer australis* Rathbun,

1935; *Tetracarcinus subquadratus* Weller, 1905; *Avitelmessus grapsoides* Rathbun, 1923.

Family diagnosis.—“Carapace quadrate, as wide as long or longer than wide; rostrum narrow, bilobed; orbits well developed, rimmed; eyes sheltered by orbits when retracted; anterolateral margins entire; posterior margin nearly straight; medial part of cervical groove weakly developed; gastric regions poorly separated from cardiac and intestinal regions; branchiocardiac groove well developed; pleural sutures located on sides of carapace; fifth pereopods very reduced, subdorsal; sternum broad, sternites visible to posterior of carapace, sternite 4 with ridge parallel to anterior end; sternites 5, 6, and 7 with granular transverse ridges; sternum of female without longitudinal grooves; lateral portion of posterior part of sternites visible; male pleon with all somites free, lateral terminations on pleonites rectangular, telson subtriangular; female pleon wide, with long epimeres, all pleonites free; coxae of pereopods at same level as sternum; first pereopods isochelous,” (Karasawa et al., 2011:556).

#### Genus *DAKOTICANCER* RATHBUN, 1917

Type species.—*Dakoticancer overanus* Rathbun, 1917.

Included species.—*Dakoticancer overanus* Rathbun, 1917; *Dakoticancer australis* Rathbun, 1935.

Generic diagnosis.—“Carapace rectangular to transversely ovoid, length and width about equal, front narrow, rostrum bilobed; orbits well developed; median part of cardiac groove weak, gastric regions hardly separated from cardiac-intestinal region, branchiocardiac groove well developed, pleural sutures on carapace sides; genital openings on coxae: female’s on third leg and male’s on fifth; fifth legs much reduced. Chelae equal,” (Bishop et al., 1998:5).

Discussion.—*Dakoticancer* is the type genus of the Dakoticanidae. Bishop et al. (1998) addressed the reproductive structures, intersexuality, functional morphology, feeding structures, and life habit of species of the Dakoticanidae where material was available. These topics will be expanded upon

by species, where applicable, below.

#### *DAKOTICANCER OVERANUS* RATHBUN, 1917

1917. *Dakoticancer overana*. Rathbun, Proceedings of the United States National Museum, 52:385–391.
1929. *Dakoticancer overanus*. Glaessner, Fossilium Catalogus I: Animalia, pars 41:134.
1930. *Dakoticancer overana*. Rathbun, Proceedings of the United States National Museum, 78:1–10, pls. 1–6.
1935. *Dakoticancer overana*. Rathbun, Geological Society of America Special Paper 2:160.
1969. *Dakoticancer overanus*. Glaessner in Moore (ed.), Treatise on Invertebrate Paleontology, R (4) (2):R400–R533, R626–R628.
1972. *Dakoticancer overanus*. Bishop, Journal of Paleontology, 15(3):631–636.
1974. *Dakoticancer overanus*. Bishop, Crustaceana, 26(2):212–218.
1977. *Dakoticancer overanus*. Bishop, Journal of Sedimentary Petrology, 47(1):129–136.
1977. *Dakoticancer overanus*. Feldmann et al., Journal of Paleontology, 51(6):1161–1180.
1981. *Dakoticancer overanus*. Feldmann, Géobios, 14 (4):449–468.
1981. *Dakoticancer overanus*. Bishop, the GSC Museum Contributions to Natural History:383–414.
1983. *Dakoticancer overanus*. Bishop, Journal of Crustacean Biology, 3(3):417–430.
1983. *Dakoticancer overanus*. Bishop, Crustaceana 44(1):23–26.
1984. *Dakoticancer overanus*. Bishop, Journal of Crustacean Biology 4.3 (1984):514–517.
1985. *Dakoticancer overanus*. Bishop, Journal of Paleontology, 59(3):605–624.
1986. *Dakoticancer overanus*. Bishop, Published in: Gore, R.H., and K.L. Heck: Crustacean Biogeography. Crustacean Issues 4. A.A. Balkema, Boston:111–141.
1986. *Dakoticancer overanus*. Bishop, Journal of Crustacean Biology, 6(3):345–346.
1987. *Dakoticancer overanus*. Tucker, Feldmann, Holland, and Brinster, Annals of Carnegie Museum, 56(7):275–288.
1991. *Dakoticancer overanus*. Bishop, Mississippi Geology, 12(1,2):8–17.
1991. *Dakoticancer overanus*. Bishop, Mississippi Geology, 12 (1,2):14.
1993. *Dakoticancer overanus*. Dunagan and Gibson, Tennessee Academy of Science Journal, 68(3):87–93.
1998. *Dakoticancer overanus*. Bishop et al., Contributions to Zoology, 67(4):237–255.
2011. *Dakoticancer overanus*. Karasawa et al., Journal of Crustacean Biology, 31:523–565.
2013. *Dakoticancer overanus*. Jones, Thesis, Kent State University, December, 2013.

Diagnosis.—“Carapace of moderate size,

rectangular, slightly wider than long, widest across epibranchial regions, sides sinuous, slightly convergent posteriorly; high, moderately arched; grooves deep, cervical groove prominent, relatively continuous except across continuous sagittal ridge; pits present at junction of cervical and antennal grooves. Tumid regions granulate, hind margin nearly width of carapace, not developed into a shelf, raised and granulate. Chelae equal, twice as long as high," (Bishop et al., 1998:6).

Occurrence.—Pierre Shale in South Dakota, North Dakota, and Montana; Maastrichtian.

Discussion.—*Dakoticancer overanus* does not occur in the Mississippi Embayment in Tennessee or Mississippi, but is very common in correlative units of the Pierre Shale of South Dakota, North Dakota, and Montana within the Western Interior Seaway (Bishop et al., 1998). *Dakoticancer overanus* also illustrates a number of intersex forms that are not observed in any other species of the family (Jones, 2013).

#### **DAKOTICANCER AUSTRALIS RATHBUN, 1935**

Figure 8C–I

1926. *Dakoticancer overana*. Rathbun, in Bruce Wade, U. S. Geological Survey Professional Paper 137, p. 189, pl. 67, fig. 3.
1935. *Dakoticancer overana australis*. Rathbun, Geological Society of America Special Papers, 2:1–160.
1969. *Dakoticancer overanus australis*. Glaessner in Moore (ed.), Treatise on Invertebrate Paleontology, R(4) (2):R400–R533, R626–R628.
1983. *Dakoticancer australis*. Bishop, Journal of Crustacean Biology, 3(3):417–430.
1983. *Paguristes whitteni*. Bishop, Journal of Crustacean Biology, 3(3):420.
1985. *Dakoticancer australis*. Bishop, Journal of Paleontology, 59(5):1028–1032.
1986. *Dakoticancer australis*. Bishop in Gore and Heck (eds.), Crustacean Biogeography, Crustacean Issues 4, A. A. Balkema, Rotterdam, The Netherlands:292.
1986. *Dakoticancer australis*. Bishop, Journal of Crustacean Biology, 6(3):345–346.
1991. *Dakoticancer australis*. Feldmann and Vega, Annals of Carnegie Museum, 60 (2):165.
1991. *Dakoticancer australis*. Bishop, Mississippi Geology, 12(1, 2):8–17.
1991. *Parapaguristes whitteni* (Bishop, 1983). Bishop, Mississippi Geology, 12(1–2):13.
1995. *Dakoticancer australis*. Vega et al., Journal of Paleontology, 69(2):fig. 4.

1998. *Dakoticancer australis*. Bishop et al., Contributions to Zoology, 67(4):237–255.

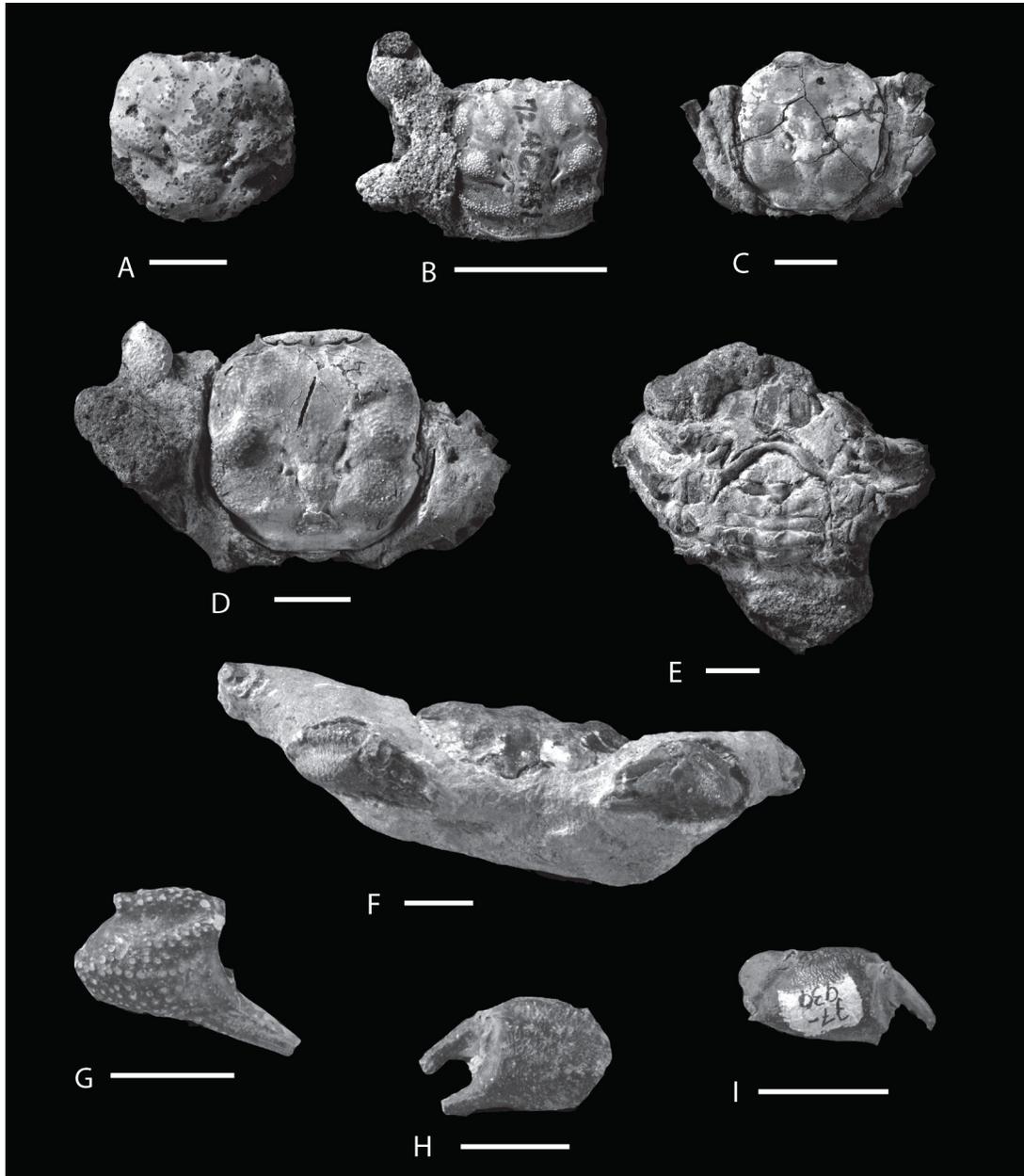
2010. *Paguristes whitteni*. Schweitzer et al., Crustaceana Monographs, 10:54.

Diagnosis.—“Carapace large, slightly longer than wide, widest across branchial and hepatic regions (sides nearly parallel), well differentiated by grooves, ornamented by granules over entire surface. Posterior extending as fairly discrete shelf, not quite at maximum width of carapace, hind margin slightly raised. Chelae equal, short, stout, and crested, carpal articulation very oblique; fingers short, downturned,” (Bishop et al., 1998:6).

Addendum to chelae diagnosis.—Propodus longest at lower margin, fixed finger long, slender, slightly downturned with four denticles. Dactyl long, slender downturned with denticles and tuberculate on top-most surface. Articulation of dactyl to palm of propodus rimmed and triangular. Palm nearly straight on lower margin, slightly convex on upper margin. Horizontal keel at midline of the palm, extending from upper margin of fixed finger to proximal edge of propodus. Keel with distinct row of tubercles, tubercles above keel forming two loosely defined rows. Propodus generally evenly tuberculate on outer margin, slight sulcus below uppermost margin smooth. Carpus oval, longest from proximal to distal margins of articulation with well defined, smooth sulcus at midline; evenly tuberculate on outer surface. Inner surface becoming smooth at margin of articulation.

Material examined.—One hundred and fifty-nine carapaces were measured, length averaging 27.8 mm ranging from 15.6 to 43.1 mm, width averaging 28.2 mm ranging from 15.9 to 46.3 mm, frontal width averaging 3.2 mm ranging from 1.3 to 22.7 mm, frontal orbital width averaging 15.5 mm ranging from 9.9 to 29.2 mm (full list of measured material available online: Kornecki, 2014).

Occurrence.—Coon Creek Formation in Union and Pontotoc counties, Mississippi and McNairy County, Tennessee; Navarro Formation near Castroville, Bexar County, Texas; Difunta Group in Coahuila State, Mexico; Portrerillos Formation in San Luis Potosi State, Mexico. Late Campanian to early Maastrichtian (Bishop et al.,



**Figure 8.** Dakoticantridae of the Blue Springs locality. *Tetracarcinus subquadratus* dorsal carapace, UF 252102 (A); *T. subquadratus* dorsal carapace, MPPM 1972.46.51 (B); *Dakoticancer australis*; UF 252103 (C); *D. australis*; UF 252104 (D); *D. australis* dorsal carapace and segments of first periopod, UF 252105 (E); *D. australis* venter, UF 252106 (F); *D. australis* claw, UF 252107 (G); *D. australis* claw, UF 252108 (H); *D. australis* claw, UF 252109 (I). All scale bars = 1 cm.

1998).

Discussion.—Material forming the basis for interpretations include specimens collected by the authors along with AnnMarie Jones, Dr. Ovidiu Frantescu, Dr. Adina Frantescu, Dr. George Phillips, and members of the Mississippi Gem

and Mineral Society on March 24 and 25, 2012 and December 17 and 18, 2013, as well as those received on loan from the Pink Palace Museum, Memphis, Tennessee; the South Dakota School of Mines and Technology Museum, Rapid City, South Dakota; and the Mississippi Museum of Natural

Science, Jackson, Mississippi. All available specimens of Dakoticancridae were measured and plotted where possible. Ninety specimens of males and females were identified using pleon or sternum morphology. Of these, three specimens have gonopores preserved, none of which possessed intersex characters.

The proportion of females to males is not a 1:1 ratio but rather 28 females and 47 males— a 0.59:1 ratio (Fig. 9). Perhaps this is a relic of preservational bias or sampling bias, but such is unlikely as all material was collected that was found at the outcrop and there are multiple collecting events by many different people over a long time span. Furthermore, a preservational bias is unlikely between males and females due to their apparent similar preservation potential. Decapods tend to have less well calcified cuticle if their lifestyle is to swim, such as shrimp (Amato et al., 2008). This difference in cuticle density is not observed between sexes of the same species without adaptations for swimming. Therefore, the presence of a greater abundance of males than females could indicate that the community preserved is a life assemblage, but that the females had different behavioral or distributional patterns than the males, such as migrating further onshore while brooding their young (Hooper, 1986).

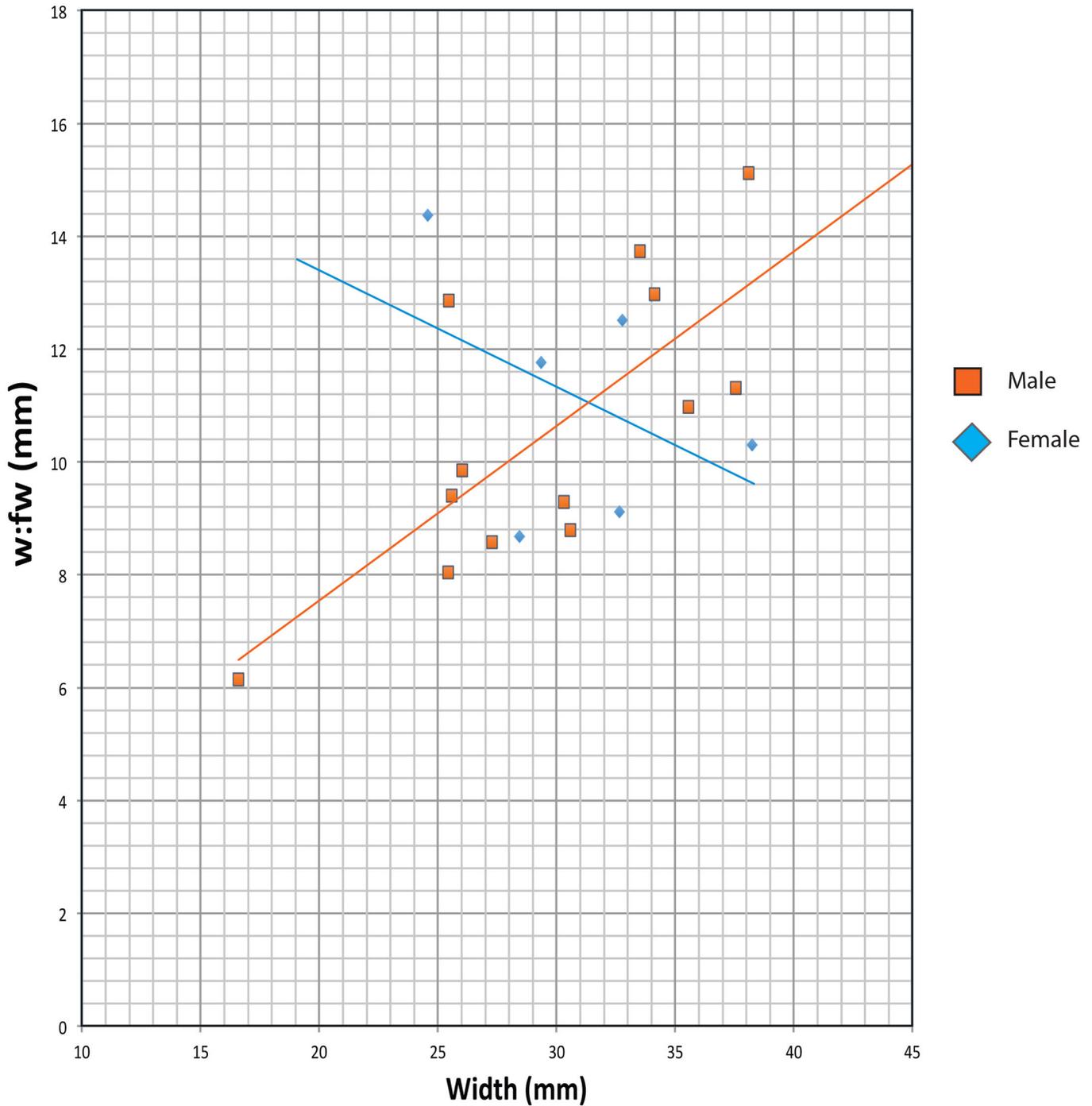
Though some specimens of *Dakoticancer australis* comprised of sterna only or carapace and sternum could be identified as male or female, the majority of them cannot offer data on other measurements of their morphology due to damage or incomplete preservation. Only six specimens of female *Dakoticancer australis* could be quantified for certain comparisons. Measurements of male and female *D. australis* are quantified in Figures 9, 10, and 11. Measurements of width vs. width/frontal orbital width and width vs. frontal width to frontal orbital width were of normal, Gaussian distribution, but measurements of width vs. width to frontal orbital width are Non-Gaussian (Table 3). When tested for similarity between males and females, all p-values indicated a rejection of the null hypothesis, concluding that sexual dimorphism is not present in frontal ratios of *D. australis* (Table 4).

In 1983, Bishop described a new species of hermit crab, *Paguristes whitteni*, based on “major and minor claws of male and female” specimens as well as carpus and manus specimens that possessed a distinct, tuberculate ornamentation. His description (Bishop, 1983:422–423) embraced both articulated specimens of *Dakoticancer australis* as well as disarticulated *Paguristes whitteni*.

Some noteworthy aspects of this description include the reiteration of the short, stout, and downturned dactyl, which is later clarified as being “only the stub of dactylus preserved, but apparently stout and presumably short,” (Bishop, 1983:423). The diagnosis of *Dakoticancer australis* claws by Bishop et al. (1998) stated, “chelae equal, short, stout, and crested, carpal articulation very oblique; fingers short, downturned,” (p. 242 after Bishop, 1983). Without illustration of the morphological differences between claws of *Dakoticancer australis* and *Paguristes whitteni* that Bishop indicates, it is not possible to confirm the morphological differences suggested, utilizing available material of approximately 80 claws, both articulated and disarticulated.

Bishop stated (1983:420–421) that “the specimens representing this taxon [*Paguristes whitteni*] are all claw elements” and that the “preservational bias is consistent with the pagurids because of the heavy mineralization of the claws,” referring to the absence of a carapace. He goes on to state that the claws “seemed to resemble claws of *Dakoticancer australis*; a similarity so striking that I concluded that the large “hermit crab claws” might be nothing more than claws of large specimens of *D. australis*. A search for *D. australis* carapaces with claws attached yielded only four specimens (out of 528) all amongst the largest of the carapaces.”

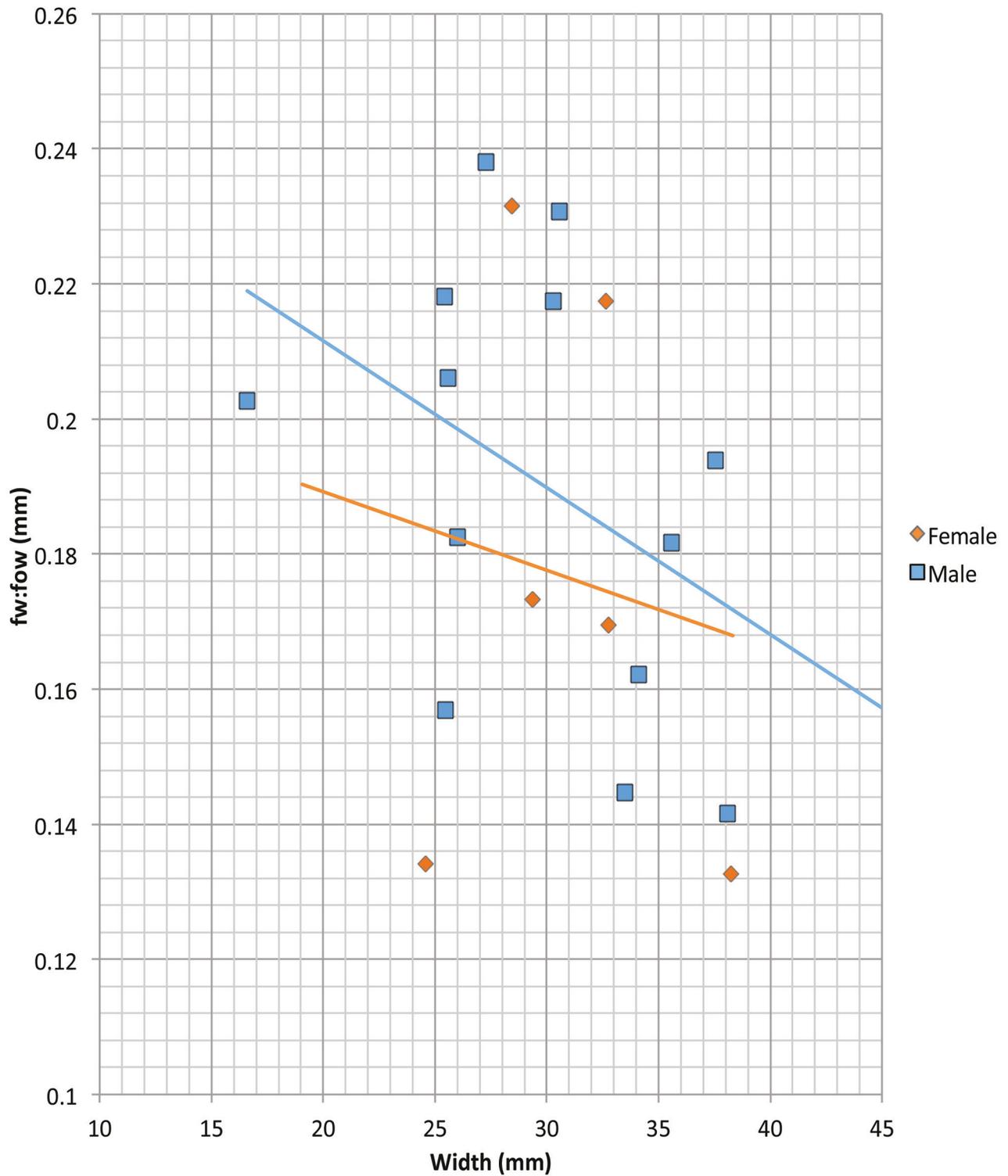
In the collections of Coon Creek Formation material, there were 14 articulated carapaces of *Dakoticancer australis* (KSU 2220, UF 252111–252123), ranging within the intermediate size range available for study; carapaces much smaller as well as much larger are also present in the collection, but lack articulated first pereopods. The data that Bishop (1983:424, fig. 5) illustrated suggests that



**Figure 9.** Male versus female ratios of *Dakoticancer australis* do not illustrate sexual dimorphism when comparing width against ratio of width to frontal width. Male:  $y = 0.3094x + 1.3568$   $R^2 = 0.54062$ . Female:  $y = -0.2066x + 17.53$   $R^2 = 0.19629$ .

he had 26 specimens of *Dakoticancer australis* claws to compare to *Paguristes whitteni* claws, of which he documented measurements for 12 specimens. With only four articulated specimens of *Dakoticancer australis* claws at his disposal

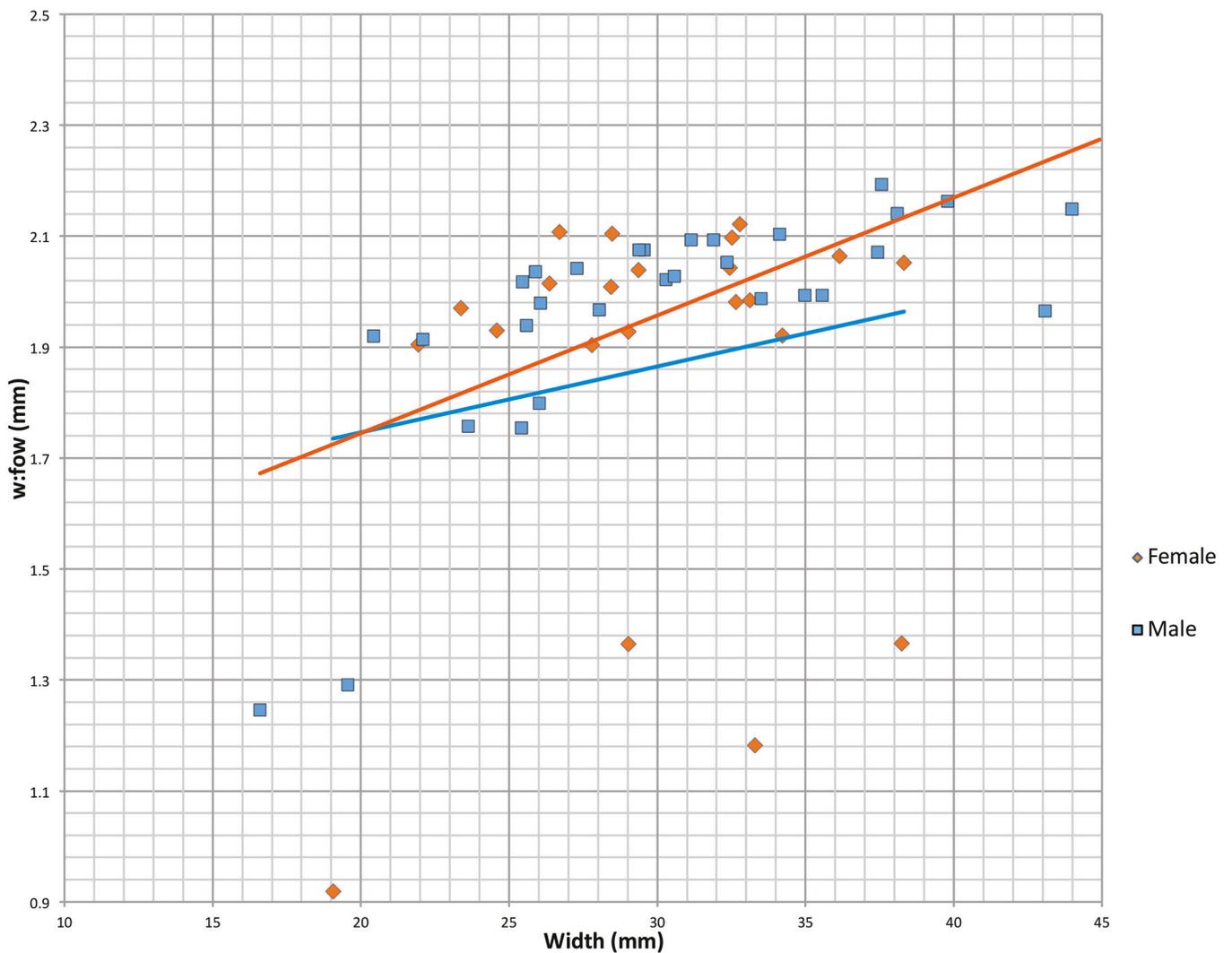
and without illustration of these specimens, it is difficult to reach the same conclusions presented by Bishop (1983). Specimens illustrated in figure 3 (Bishop, 1983:421) and figure 4 (Bishop, 1983:422) do not seem to illustrate morphological



**Figure 10.** Male versus female ratios of *Dakoticancer australis* do not illustrate sexual dimorphism when comparing width against ratio of frontal width to frontorbital width. Male:  $y = -0.0012x + 0.2125$   $R^2 = 0.0737$ . Female:  $y = -0.0022x + 0.255$   $R^2 = 0.1708$ .

**Table 3.** Tests of normality for *Dakoticancer australis* measurements. Results of tests of normality are coded “G” for Gaussian and “N” for non-Gaussian. W = width, FW = frontal width, FOW = frontorbital width.

	Sex	Number of specimens	Test of normality				
			Probability graphs	Chi-squared	Griffiths’ Skewness	Griffiths’ Kurtosis	Kolmogorov Smirnov
W/	Female	6	G	G	G	G	G
W:FW	Male	16	G	G	G	G	G
W/FOW	Female	22	N	N	N	N	N
	Male	40	N	(G-N)	N	N	N
FW/FOW	Female	6	G	G	G	G	G
	Male	16	G	G	G	G	G



**Figure 11.** Male versus female ratios of *Dakoticancer australis* do not illustrate sexual dimorphism when comparing width against ratio of width to frontorbital width. Male:  $y = 0.0211x + 1.3223$   $R^2 = 0.49744$ . Female:  $y = 0.0119x + 1.5086$   $R^2 = 0.03237$ .

**Table 4.** Tests of similarity between males and females of *Dakoticancer australis*. Pooled variance t tests require equal variances, but Welch-Setterthwaite “pooled degrees of freedom” tests are appropriate regardless. All t tests indicate a rejection of the null hypothesis. Thus, there is no statistical difference between males and females. Degrees of freedom = dof.

	F test of variance	Student's t test (pooled variance)	T test (Welch Setterthwaite)	Mann-Whitney- Wilcoxon
W/WFW				
(dof), score, #tails	(15,5), 1.1274, 1	(20), 0.574, 2	(11.2), 0.591, 2	ECRS, 76
p value	0.486	0.572	0.566	0.705
W/FOW				
(dof), score, #tails	(21,30), 2.244, 1	(60), 1.38, 2	(32.5), 1.19, 2	zU, 369, 2
p value	0.486	0.572	0.566	0.705
FW/FOW				
(dof), score, #tails	(15,5), 1.84, 1	(20), 1.0014, 2	(7.97), 0.868, 2	ECRS, 56.5
p value	0.165	0.328	0.414	0.193

differences between the claws of the two taxa, but rather preservational bias in mode of preservation and ornamentation.

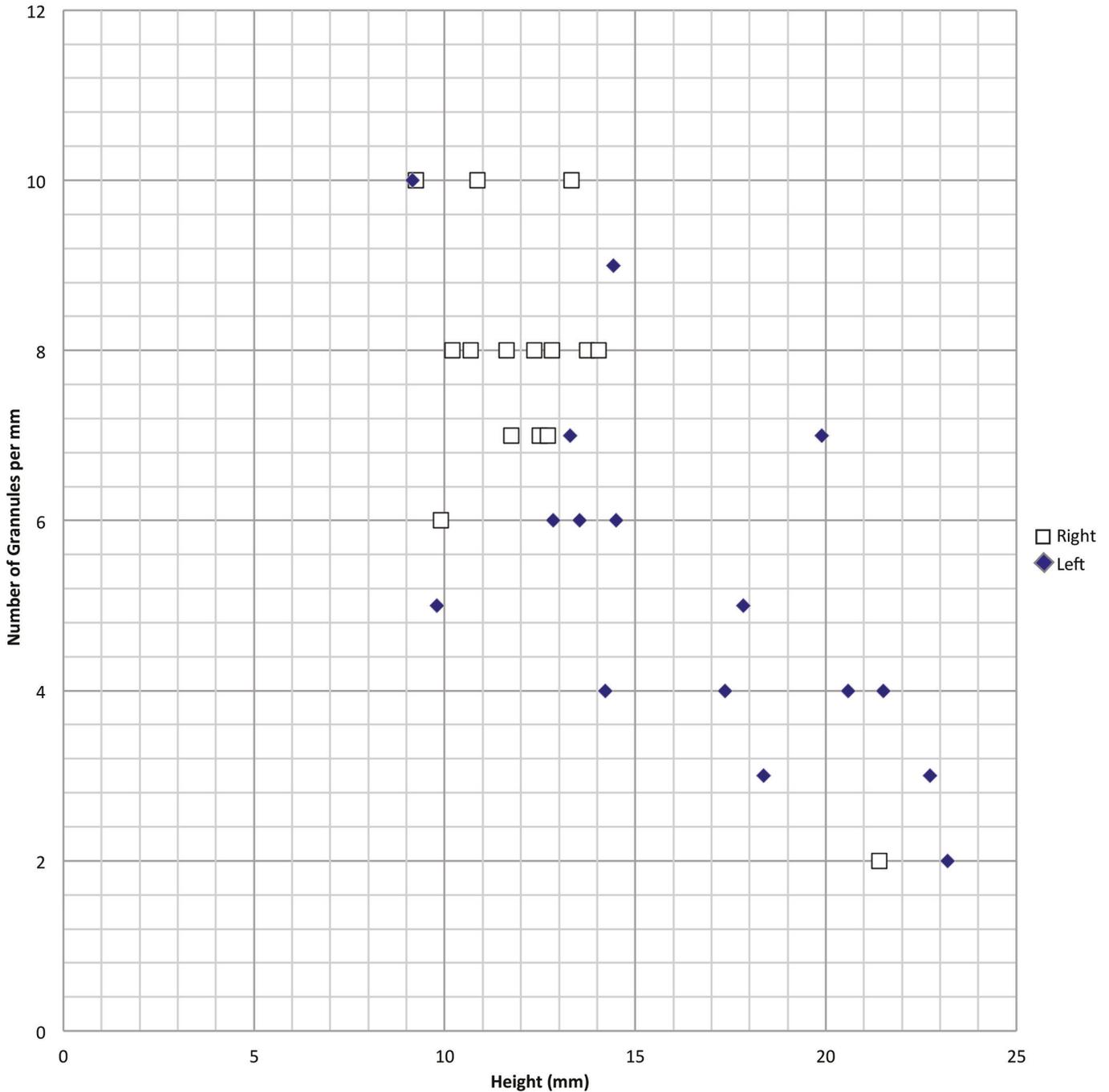
Furthermore, the data does not indicate which data points in the size plots are of a left or right claw, though the plot of *Paguristes whitteni* does group into two distinct sizes (Bishop, 1983) and could be interpreted as heterochelous without more data. Of course, these specimens cannot be associated with a single individual because they are disarticulated and the assessment of heterochely is not necessarily statistically valid.

Bishop's (1983) observation that the claws on articulated specimens of *Dakoticancer australis* are quite small, and that the claws attributed to *Paguristes whitteni* are larger and disarticulated is indeed a preservational bias. To suggest that these morphologically identical forms of different sizes belong to two different species within two different infraorders, the Anomura and the Brachyura, yet occurring in the same locality, would indeed be a dramatic case of convergent evolution. Preservational bias caused by disarticulation is more prominent in specimens with larger claws, perhaps due to decomposition, predation, or transport. The majority of carapaces lack articulation of the first

pereiopods altogether. Thus, *Paguristes whitteni* is herein considered to be a junior synonym of *Dakoticancer australis*.

The range of sizes in these claws is noteworthy; the increase in the size of the propodus correlates with the increase in size of ornamentation and may indicate allometric growth, though the small forms are identical to large forms in all other instances (Fig. 12).

Also of note, Bishop illustrated paratype specimens of *Dakoticancer australis* USNM 73840 (1983:425, fig. 6A; Bishop et al., 1998:243, figs. 1–6, 1-8), a male specimen, and specimen USNM 18628 (1983:425, fig. 6B; Bishop et al., 1998:243, figs. 1-7). These specimens possess noticeably different morphology. USNM 73840 is widest at about 50% of the carapace length, has a larger posterior shelf, is less tumid in the branchial regions and has a less well defined cardiac region. USNM 73840 is narrowest at 50% the carapace length, has very tumid branchial regions, and a well defined cardiac region ending in a sharp point about 75% the carapace length. The specimens of the Coon Creek Formation and Blue Springs locality conform morphologically to the holotype specimen illustrated by Rathbun (1935:134–135, pl. 10, fig.



**Figure 12.** *Dakoticancer australis* claw height versus granule size. Granule size increases as claw size increases, as indicated by decreasing number of granules per mm<sup>2</sup>. Most specimens of right claws are smaller than left claws, but this may be biased by sampling.

20), but do not resemble the paratypes illustrated by Bishop. The paratypes of *Dakoticancer australis* should be re-examined to determine if they represent a different species.

**Genus *TETRACARCINUS* WELLER, 1905**

Type species.—*Tetracarcinus subquadratus* Weller, 1905.

Included species.—*Tetracarcinus subquad-*

*ratus* Weller, 1905.

Generic diagnosis.—“Carapace generally small, subquadrate, length nearly equal to width, widest at position of epibranchial regions; orbits rimmed; lateral margins sinuous; posterior margin rimmed; cervical groove shallow medially and poorly developed distally; regions flattened, weakly inflated; epibranchial and metabranchial regions separated by broad depression enclosing narrow mesobranchial region; epibranchial regions transversely weakly inflated; cardiac region with posterior tubercle; first pereopods isochelous,” (Feldmann et al., 2013:28).

### ***TETRACARCINUS SUBQUADRATUS***

**WELLER, 1905**

Figure 8A–B

1905. *Tetracarcinus subquadratus*, Weller, *Journal of Geology*, 13:324–337.  
 1907. *Tetracarcinus subquadratus*, Weller, *Geology Survey of New Jersey, Paleontological Survey*, 4:846–853.  
 1935. *Tetracarcinus subquadratus*, Rathbun, *Geological Society of America Special Papers*, 2:41, pl. 10, figs. 16–17.  
 1958. *Tetracarcinus subquadratus*. Holland, Jr. and Cvancara, *Journal of Paleontology*, 32(3):496.  
 1991. *Tetracarcinus subquadratus*. Bishop, *Mississippi Geology*, 12 (1, 2):13.  
 1998. *Tetracarcinus subquadratus*, Bishop et al., *Contributions to Zoology*, 67 (4):244, fig. 2.1.  
 2010. *Tetracarcinus subquadratus*, Schweitzer et al., *Crustaceana Monographs*, 10:58.  
 2013. *Tetracarcinus subquadratus*, Feldmann et al., *Bulletin of the Mizunami Fossil Museum*, 39:28.

Diagnosis.—As for the genus.

Material examined.—Forty specimens were measured with lengths averaging 13.9 mm ranging from 9.2 to 24.5 mm, widths averaging 13.5 mm ranging 9.2 to 20.2 mm, frontal widths averaging 1.7 mm ranging 1.3 to 2.8 mm, and fronto-orbital widths averaging 8 mm and ranging 6 to 10.4 mm (Supplemental measurements can be found online: Kornecki, 2014).

Occurrence.—*Tetracarcinus subquadratus* occurs at the Blue Springs locality, Coon Creek Formation, New Albany, Mississippi. The species is also known from the Magothy Formation at Cliffwood, New Jersey; Woodbury Formation at Lorillard; Merchantville Formation on the Delmarva

Peninsula; as well as from one occurrence in the Lewis Shale of Wyoming. It ranges from the late Santonian to Maastrichtian (Bishop et al., 1998).

Discussion.—The diagnosis of *Tetracarcinus subquadratus* by Bishop et al. (1998) does not include sternal morphology. It is also of note that Bishop et al. (1998: fig. 2.2) illustrated a disarticulated claw of *T. subquadratus*. Catalogue numbers were not given, thus making it impossible to determine if these specimens were in fact closely associated, though both are stated as being from the Coon Creek Formation, Mississippi. The diagnosis described this claw as “small; palm longer than high, smooth except for granulate upper surface,” (Bishop et al., 1998:244). We have not observed any articulated specimens of *T. subquadratus*, but the claw illustrated by Bishop et al. (1998) does not seem to fit the description, though abbreviated, as “small” as it is nearly the same width as the typical carapace width of the species. Weller (1905a, 1905b, 1907) illustrated carapaces only of the species, and Rathbun (1935) illustrated carapaces of the species and one, disarticulated claw specimen that she assigned to the species as well. Roberts (*in* Richards, 1962) also illustrated *T. subquadratus* without chelae, articulated or disarticulated. He also noted the specimens reported as *T. subquadratus* by Rathbun (1935) of a palm and carapace were not definitively assignable to the species. The specimen of claw illustrated by Rathbun (1935:134–135, pl. 10, fig. 18) does not have any portion of the dactyl preserved and the palm is much shorter than the claw illustrated by Bishop et al. (1998). The claw specimen (Rathbun, 1935:134–135, pl. 10, fig. 18) has no catalogue number but is referenced to be in the New Jersey State Museum and occurred in the Tinton beds, Beers Hill, New Jersey. Rathbun’s other illustrated specimens are from Wyoming and the Cliffwood Clay of Cliffwood Point, New Jersey. This claw is not considered at this time to be that of *T. subquadratus*. There is insufficient evidence to assign it to a new species or any other species at present. The diagnosis by Feldmann et al. (2013) also included a reference to chelae, “first pereopods isochelous,” (p. 28). The specimen illustrated by Feldmann et al. (2013: fig. 13.2),

NJSM 23337, of a “crushed dorsal carapace” may have these pereopods preserved, but there is also no specific reference to a specimen with preserved pereopods or chelae.

Specimens of *Tetracarcinus subquadratus* do not have sterna articulated with carapaces frequently in available material and, therefore, do not provide evidence to correlate carapace morphology with sex. Fewer specimens of *T. subquadratus* are available for study than are of *Dakoticancer australis*. Because the specimens are smaller, this proportion could be related to collecting bias.

Measurements of *Tetracarcinus subquadratus* yielded fairly well constrained data with one clear outlier (Fig. 13). The ratio of the frontal width to the fronto-orbital width of *Tetracarcinus subquadratus* is negatively correlated (Fig. 14A). *Dakoticancer australis* data barely trend with a negative slope and are poorly constrained. The relationship of total width to frontal width in *Tetracarcinus subquadratus* is more positively trending with size than that observed in *Dakoticancer australis* (Fig. 10). The ratio of body width to fronto-orbital width in *Tetracarcinus subquadratus* also trends positively, as is illustrated in *Dakoticancer australis*.

#### Genus *AVITELMESSUS* RATHBUN, 1923

Type species.—*Avitelmessus grapsoides* Rathbun, 1923.

Included species.—*Avitelmessus grapsoides* Rathbun, 1923.

Generic diagnosis.—“Carapace very large, circular with concave front, widest at midpoint; arched longitudinally, fairly level transversely. Rostrum small, narrow, medially grooved. Orbits with two fossae forming two concavities in plan view. Carapace margin nearly forms circle from lateral orbital spines, spinose, carapace grooves poorly developed except for gastro-cardiac, proximal cervical (except obsolete gastric portion), and epimesobranchial [sic]. Sagittal ridge well delineated; cephalic arch poorly differentiated except for mesogastric; scapular arch with well-delineated cardiac and branchial regions, branchial regions differentiated into epibranchial and mesobranchial by epibranchial groove, posterior

of branchial separated into mesobranchial and metabranchial by oblique ridges running outward and backward. Epibranchial posterior and anterior of mesobranchial with subparallel ridges. Subtle ridges parallel gastrocardiac groove along outer edges from epibranchials to orbits. Chelae equal, large, triangular in cross section, spiny; palm slightly longer than high, oblique; fingers long, slightly downturned, toothed,” (Bishop et al., 1998:244).

#### *AVITELMESSUS GRAPSOIDEUS* RATHBUN, 1923

1923. *Avitelmessus grapsoides*. Rathbun, North Carolina Geol. Survey, 5:403–407.

1927. *Avitelmessus grapsoides*. Rathbun in Wade, Geological Survey of Tennessee, Professional Paper 137:190, pl. 69, figs. 1–7, pl. 70, figs. 1–12.

1957. *Avitelmessus grapsoides*. Kesling and Reimann, Contributions from the Museum of Paleontology, 14(1):1–15.

1991. *Avitelmessus grapsoides*. Bishop, Mississippi Geology, 12(1,2):13.

1998. *Avitelmessus grapsoides*. Bishop et al., Contributions to Zoology, 67(4): 249 figs. 2.1–2.5.

Diagnosis.—As for the genus.

Material examined.—*Avitelmessus grapsoides* is not available from collected material at the Blue Springs locality, but specimens of the Coon Creek Formation were observed at the U.S. National Museum of Natural History.

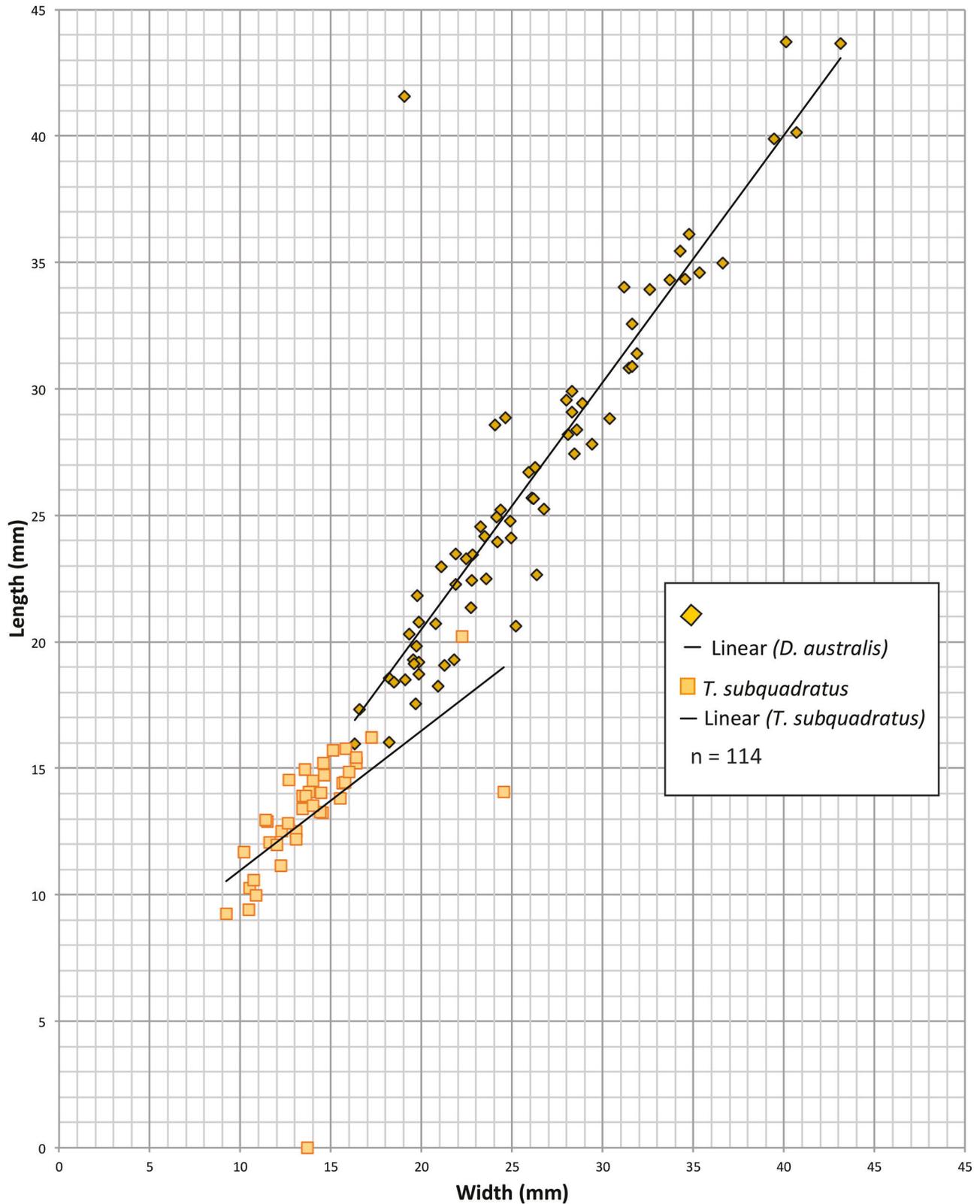
Occurrence.—Peedee Formation of North Carolina as well as from Georgia and Alabama and the Mississippi Embayment into Texas, ranging from Campanian to early Maastrichtian (Bishop et al., 1998).

Discussion.—Rathbun’s description of *Avitelmessus grapsoides* (1923:403–404) and that by Kesling and Reimann (1957:4–11) should be referenced for a complete assessment of the species.

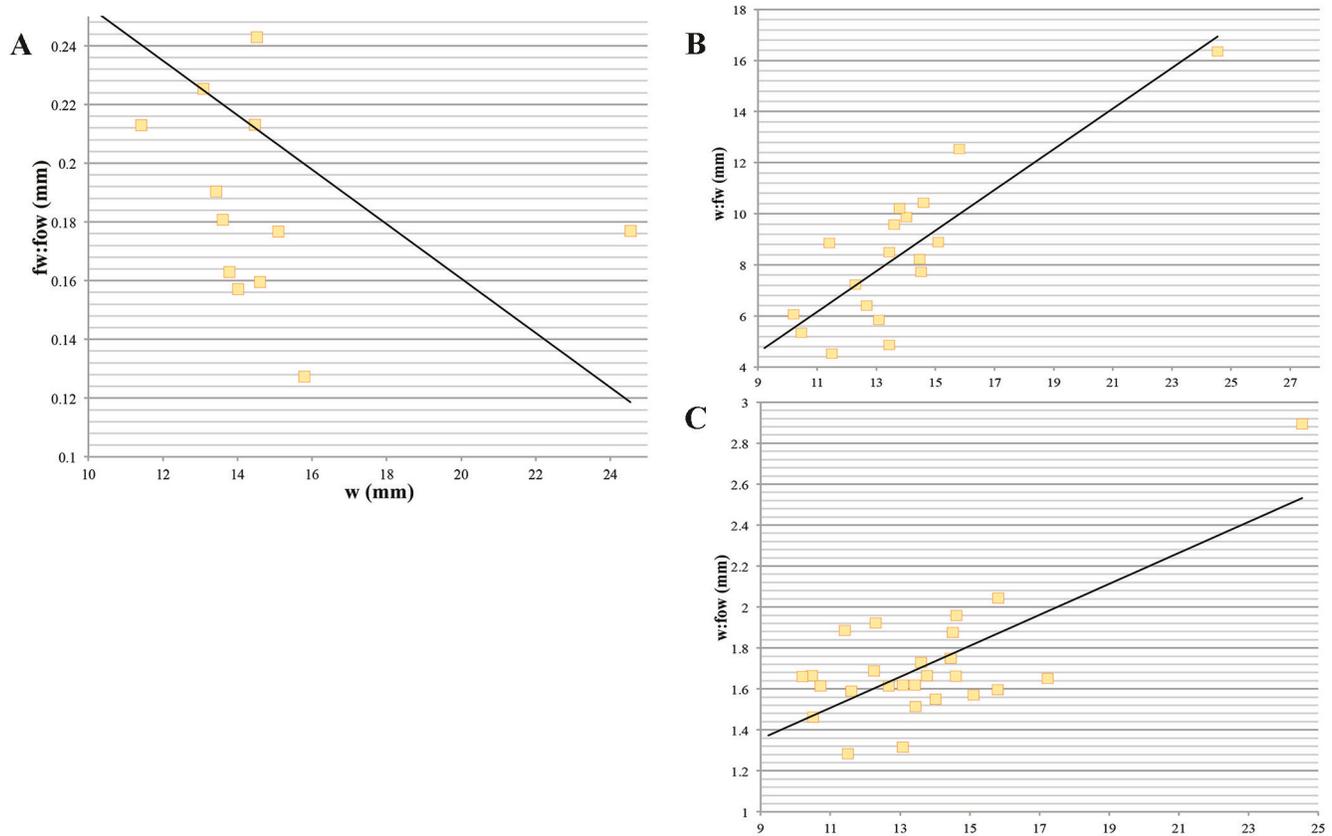
#### Family *IBERICANCRIIDAE* ARTAL ET AL., 2008

Included genera.—*Ibericancer* Artal et al., 2008; *Seorsus* Bishop, 1988; *Sodakus* Bishop, 1978.

Family diagnosis.—“Carapace subrectangular, about as long as wide, generally widest just under half the distance posteriorly but may be at



**Figure 13.** Species of the Dakoticaneridae found at the Blue Springs locality of the Coon Creek Formation illustrating similar ratios of length to width in the *Dakoticaner australis* and *Tetracarcinus subquadratus* throughout ontogeny. *D. australis*:  $y = 0.9764x + 0.9754$   $R^2 = 0.793$ . *T. subquadratus*:  $y = 0.552x + 5.4512$   $R^2 = 0.29766$ .



**Figure 14.** *Tetracarcinus subquadratus* measurements of width against ontogenetic ratios illustrating frontal width to frontorbital width decreases with increase in size (A). Frontal width and frontorbital width increase with increasing body size (B, C).  $y = -0.0093x + 0.3461$  ( $R^2 = 0.26349$ ) (A).  $y = 0.0757x + 0.6754$  ( $R^2 = 0.52701$ ) (B).  $y = 0.7958x - 2.5916$  ( $R^2 = 0.70021$ ) (C).

position two-thirds the distance; rostrum narrow, downturned, bilobed or quadrilobed; orbits square, directed forward, fronto-orbital width ranging from about 40–70% maximum width but usually about half; branchiocardiac groove deep, cervical groove discontinuous; axial regions well defined and distinct; sternum narrow, deep sterno-pleonal cavity, sternite five with pleonal locking mechanism, sterna sutures 4/5 through 7/8 interrupted; female gonopore on coxa of pereopod 3, male gonopore on coxa of pereopod 5, spermatheca of female at sterna suture 7/8; male pleon very narrow, all somites free, female pleon wider, all somites free; pereopods 4 and 5 apparently subdorsal, 5 reduced in size,” (Feldmann et al., 2013:29).

### Genus *SEORSUS* BISHOP, 1988

Type species.—*Seorsus wadei* Bishop, 1988.

Included species.—*Seorsus wadei* Bishop, 1988; *Seorsus kauffmani* Feldmann et al., 2013; *Seorsus millerae* (Bishop, 1992).

Generic diagnosis.—“Carapace slightly longer than wide, width about 93% maximum carapace width, width at position of single anterolateral spine about 40–50% the distance posteriorly on carapace; rostrum long, with four blunt spines including inner-orbital spines; orbits square, rimmed, with intraorbital spine, fronto-orbital width ranging from half to 70% maximum carapace width; well-defined branchiocardiac groove and moderately defined cervical groove,

and well-defined axial regions; sternum narrow, sterno-pleonal cavity narrow, sternites 1-3 fused, sternite 4 long, with concave lateral margins, sterna suture 4/5 incomplete; male pleon with all somites free, subdorsal pereopods 4 and 5; major chela granular; propodus bulbous, two nodes at articulation with carpus; carpus granulated with X-shaped groove; fixed finger and dactylus thin, delicate," (Feldmann et al., 2013:29).

***SEORSUS WADEI* BISHOP, 1988**

1988. *Seorsus wadei*. Bishop, Proceedings of the Biological Society of Washington, 101(1):72, figs. 1A-F.  
 1991. *Seorsus wadei*. Bishop, Mississippi Geology, 12(1/2):13.  
 1998. *Seorsus wadei*. Bishop et al., Contributions to Zoology, 67(4):249, figs. 2.1-2.5.  
 2008. *Seorsus wadei*. Artal et al., Zootaxa, 1907:27.

Diagnosis.—“Carapace of moderate size, longer than wide (L/W=1.10), widest at anterior 1/3; lateral margins distinctively convergent posteriorly; grooves broad, moderately defined; aerolations very tumid, especially epibranchial lobes; cardiac region with small central tubercle; metabranchial region with subtle transverse and submarginal ridges. Claws and legs unknown,” (Bishop et al., 1998:245).

Material examined.—*Seorsus wadei* was not available for observation in the study material. The holotype GSUM 1693, and paratype GSUM 1694 (Bishop, 1988) were collected from the Blue Springs locality.

Occurrence.—GAB 37, Coon Creek Formation, Blue Springs locality, New Albany, Mississippi. Maastrichtian (Bishop et al., 1998).

Discussion.—Bishop et al. (1998) cited two known specimens of *Seorsus wadei*. With the large amount of available new material, it is of interest that *S. wadei* has not occurred more frequently. This species was apparently not numerically abundant within the Mississippi Embayment fauna. *Seorsus kauffmani* occurs in the Turonian Mancos Shale, Semilla Sandstone Member, Sandoval County, New Mexico, and *Seorsus millerae* from spoil piles of the early Campanian Merchantville Formation in Newcastle County, Delaware (Feldmann et al., 2013).

**Section HOMOLOIDA DE HAAN, 1839**  
**Superfamily HOMOLOIDEA DE HAAN, 1839**  
**Family HOMOLIDAE DE HANN, 1839**  
**Genus *LATHETICOCARCINUS* BISHOP, 1988**

Type species.—*Latheticocarcinus shapiro* Bishop, 1988, by original designation.

Included species.—*Latheticocarcinus adelphinus* (Collins and Rasmussen, 1992); *Latheticocarcinus affinis* (Jakobsen and Collins, 1997); *Latheticocarcinus atlanticus* (Roberts, 1962); *Latheticocarcinus brevis* (Collins, Kanie, and Karasawa, 1993); *Latheticocarcinus brightoni* (Wright and Collins, 1972); *Latheticocarcinus centurialis* (Bishop, 1992); *Latheticocarcinus declinatus* (Collins, Fraaye, and Jagt, 1995); *Latheticocarcinus dispar* (Roberts, 1962); *Latheticocarcinus ludvigseni* Schweitzer, Nyborg, Feldmann, and Ross, 2004; *Latheticocarcinus pikeae* (Bishop and Brannen, 1992); *Latheticocarcinus punctatus* (Rathbun, 1917); *Latheticocarcinus schlueteri* (Beurlen, 1928); *Latheticocarcinus shapiro* Bishop, 1988; *Latheticocarcinus spinigus* (Jakobsen and Collins, 1997); *Latheticocarcinus transiens* (Segerberg, 1900).

Diagnosis.—“Carapace longer than wide (width measured between *lineae homolicae*), typically widest just posterior to intersection of cervical groove and *linea homolicae* but relatively uniformly wide through entire length, surface granular, ornamented with discrete, large tubercles; rostrum bifid or singular, sulcate; often with small pseudorostral spines; usually with supraorbital spine; protogastric, hepatic, mesogastric and cardiac regions ornamented with large tubercles; grooves defining lateral margins of mesogastric region deeply incised; cervical groove very deeply incised, arcuate, U-shaped, not typically sinuous, separating the carapace into distinctive anterior and posterior portions; branchiocardiac groove very deep anteriorly, beginning about midway between *linea homolicae* and axis, extending axially, curving around and extending laterally to intersect *linea homolicae*; *lineae homolicae* very well-developed, sub-hepatic and sub-branchial regions rarely preserved; cardiac region with two swellings positioned one beside the other, sometimes with

lateral ridges extending onto cardiac regions; cardiac region not well differentiated from branchial regions by deep grooves,” (Feldmann et al., 2013:17).

**? *LATHETICOCARCINUS ATLANTICUS*  
(ROBERTS, 1962)**

Figure 15E

1962. *Homolopsis atlantica*. Roberts, Bulletin of the New Jersey Division of Geology, 61:179, pl. 89, fig. 4.  
2004. *Latheticocarcinus atlanticus* (Roberts, 1962). Schweitzer et al., Journal of Paleontology, 78:136.  
2010. *Latheticocarcinus atlanticus*. Schweitzer et al., Crustaceana Monographs, 10:68.  
2013. *Latheticocarcinus atlanticus*. Feldmann et al., Bulletin of the Mizunami Fossil Museum, 39:7–37.

Diagnosis.—“Carapace including extralinear flanks; mesobranchial region with one large tubercle posteriorly and two obliquely ovate ones; cardiac region well-defined, with three large tubercles; tubercles ornamenting all regions very large; subepibranchial spine very large and long,” (Feldmann et al., 2013:17).

Description of material.—Carapace fragmented; anterior margin obscured, posterior and posteriolateral margin absent. Rostrum sulcate, appearing singular. Mesogastric region weakly defined by grooves with axial node anteriormost with slightly larger nodes defining protogastric region; pair of nodes lateral to protogastric nodes form hepatic region. Cervical groove well defined; mesogastric region tumid with deepening margin toward the gastric region. Gastric region most tumid with tubercles ending at a small spine. Lateral flanks vertical.

Material examined.—UF 252101, length: 13.18 mm, width: 17.86 mm.

Occurrence.—Coon Creek Formation, Blue Springs locality, Union County, Mississippi, Maastrichtian. Marshalltown/Merchantville spoil pile (Feldmann et al., 2013); Roberts (1962) reported the species from the Merchantville Formation in New Jersey.

Discussion.—The specimen was provided in a collection of material from the Coon Creek Formation collected by Dr. Gale Bishop. The specimen does not possess the Coon Creek locality number assigned by Bishop and is therefore

tentatively described in the assessment of the decapod fauna. As seen in the material examined above, the preservation is also fragmentary. Because of this, the over-all shape of the carapace is unknown as is the anterior and posterior margin morphology. This specimen was likely a molt: the subhepatic and subbranchial regions are not preserved, suggesting that the specimen has broken along the *linea homolica* (*sensu* Collins, 1997). The presence of this feature is also a defining character of the Homolidae. Though the material is quite fragmentary, the cardiac swellings situated beside each other and the distinct separation of the anterior and posterior of the carapace by the cervical groove suggests placement within *Latheticocarcinus*. *Latheticocarcinus atlanticus* also occurs on the Atlantic Coast. Thus, if the identification is confirmed as *Latheticocarcinus atlanticus* in the Coon Creek Formation, the range of this species can be extended to the Mississippi Embayment.

**Section RANINOIDA AHYONG ET AL., 2007  
Superfamily PALAEOCRYSTOIDEA LÖRENTHEY  
IN LÖRENTHEY AND BEURLEN, 1929**

Included families.—Palaeocorystidae Lörenthey *in* Lörenthey and Beurlen, 1929.

Diagnosis.—As for family.

Discussion.—Karasawa et al. (2014) conducted a phylogenetic analysis of the Raninoidea. That classification scheme is followed here.

**Family PALAEOCRYSTIDAE LÖRENTHEY  
IN LÖRENTHEY AND BEURLEN, 1929**

Included genera.—*Alessandranina* Karasawa et al., 2014; *Cenocorystes* Collins and Breton, 2009; *Cretacorantina* Mertin, 1941; *Eucorystes* Bell, 1863; *Ferroranina* van Bakel et al., 2012; *Joeranina* van Bakel, 2012; *Notopocorystes* M’Coy, 1849.

Diagnosis.—“Carapace obovate, usually longer than wide, widest at position of third or fourth anterolateral spine; frontal margin wide; anterolateral margin with 2 to 4 spines; carapace surface ornamented with ridges, straps, tubercles or unornamented; epibranchial region with weak tooth; fronto-orbital margin and orbits wide, orbital

margin with two fissures; rostrum generally long, with two spines at tip; orbits with inner, intra- and outer orbital spines, some of which may be bifid; gymnopleuran condition absent; sternites 1–3 fused, 1 and 2 directed downward; sternite 4 long, pereopod 1 articulating near posterior corner, moderately wide, lateral margins concave; sternal suture 4/5 sinuous laterally, then turning abruptly anteriorly parallel to axis; episternite 4 usually laterally directed but may be posteriorly directed (*Notopocorystes*); sternites 4/5 usually in broad contact (except *Notopocorystes*); sternite 5 long, moderately wide, with double peg structure on episternal projection for attachment of pleon, episternites directed laterally or posterolaterally (*Notopocorystes*); sterna suture 5/6 complete; all female pleonites free, pleonite 6 long, pleonites 2–5 with central spine, entire pleon reaching to level of base of coxae of first pereopods; male pleon narrower, telson triangular, somite 6 long, reaching to level of base of coxae of pereopods 2; pleonal holding mechanism consisting of a double-peg structure; longitudinal furrow on merus of maxilliped 3; chelae with long fingers; female gonopore coxal, small, round; spermatheca at end of suture 7/8, separated from one another; pereopod 5 reduced in size,” (Karasawa et al., 2014:239).

Discussion.—The Palaeocorystidae range from the Early to Late Cretaceous. The family was revised by van Bakel et al. (2012) and later by Karasawa et al. (2014).

### Genus *CRETACORANINA* MERTIN, 1941

Type species.—*Raninella? schloenbachi* Schlüter, 1879.

Included species.—*Cretacoranina denisae* (Secretan, 1964); *C. fritschi* (Glaessner, 1929); *C. testacea* (Rathbun, 1926); *C. trechmanni* (Withers, 1927).

Generic diagnosis.—“Carapace obovate, wide in anterolateral third; posterolateral margin narrowing considerably; rostrum extending beyond orbital margin, tip bifid, with spine just posterior to each spine at tip for a total of four, short spines on either side of rostrum forming inner orbital spines, rostrum sometimes rimmed; intra-orbital spine

bifid, bounded by fissures; outer orbital spine bifid; anterolateral margin with 3 or 4 spines; spines becoming smaller posteriorly, last one nearly obsolete; cervical groove absent; branchiocardiac groove developed as arcs on either side of axis; dorsal carapace ornamentation developed as fungiform pillars overall but ending in indistinct scalloped termination to base of orbital margin or just barely onto orbital margin and anterolateral spines; sternite 3 appearing triangular; sternite 4 wide, episternite 4 wide, in broad contact with sternite 5, directed laterally, suture 4/5 incomplete, straight; sternite 5 narrower than sternite 4,” (Karasawa et al., 2014:239).

Discussion.—van Bakel et al. (2012) limited the genus, though still quite morphologically diverse, to those species with hexagonal ornamentation overall but terminating at the base of the anterolateral spines and those lacking a cervical groove (Feldmann et al. 2014:240). It is not clear that the small pillars forming the texture of the carapace are hexagonal in the Mississippi specimens. The pillar structures do appear to have individual setal pits and to become smaller and closer together at the margins of the carapace. One specimen illustrates exocuticle on the right lateral margin of the dorsal carapace, indicating that these pillars are less distinct when the external layer of cuticle is present, though exocuticle is not commonly observed.

### *CRETACORANINA TESTACEA* (RATHBUN, 1926a)

Figure 15B–D, 15F

- 1926a. *Raninella testacea*. Rathbun, in Wade, ed., U.S. Geological Survey Professional Paper, 137:190.
1929. *Raninella testacea* Rathbun, 1926. Glaessner, in F.J. Pompeckj, ed., Fossilium catalogus, 1, Animalium, 41:370.
- 1935a. *Raninella testacea*. Rathbun, Geological Society of America, Special Paper, 2:50.
1983. *Notopocorystes testacea* (Rathbun, 1926). Bishop, Journal of Crustacean Biology, 3(3):419.
1991. *Raninella testacea*. Bishop, Mississippi Geology, 12(1,2):12.
1998. *Cretacoranina testacea* (Rathbun, 1926). Tucker, Proceedings of the Biological Society of Washington, 111: fig. 5, table 4.
2009. *Cretacoranina testacea*. Waugh et al., Bulletin of the Mizunami Fossil Museum, 35:20.

2010. *Raninella testacea*. Schweitzer et al., Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 256(3):75.
2012. *Cretacorantina testacea*. Van Bakel et al., Zootaxa, 3215:19.
2013. *Cretacorantina testacea*. Feldmann et al., Bulletin of the Mizunami Fossil Museum, 39:25.

Diagnosis.—“Carapace longer than wide, widest about one third the distance posteriorly at position of last anterolateral spine; moderately vaulted transversely and longitudinally. Anterolateral margins convex, with four spines excluding bifid outerorbital spine, shorter than concave posterolateral margins. Outerorbital spines not extending as far anteriorly as bifid intra-orbital spines, intra-orbital spines separated from outerorbital spines and rostrum by open fissures; rostrum triangular, base composed of inner orbital spines, axial spines with axial groove. Surface covered with subhexagonal granules, visible to naked eye. Crescentic furrows at middle of carapace define inner limit of branchial region,” (Feldmann et al., 2013:25).

Description of material.—Carapace obovate, widest at anterolateral 1/3, narrowing posteriorly; bifid rostrum with deep sulcus at axis, arcing laterally to small, inner orbital spine. Two sets of anterolateral spines on either side of rostrum, first of which possesses three short spines, the second two; followed by four anteriorly directed spines on lateral margin, extending half way to the posterior and ending before the carapace narrows, becoming smaller posteriorly. Orbits oval, laterally elongate extending very close to the lateral margin of carapace, vertically compressed. Dorsal carapace evenly covered with fungiform pillars ending abruptly at the proximal margin of the anterolateral spines. Branchiocardiac grooves weakly depressed arcs on either side of axis. Anterior suture of dorsal carapace and venter distinctly grooved, gently arching from lateral margin of rostrum below the slight shelf formed by anterior spines to the most posteriolateral spine; two rows of small spines between anterior spines and suture; second sinuous groove extending parallel to first and more posterior; separated by slightly domed ridge. Some sections

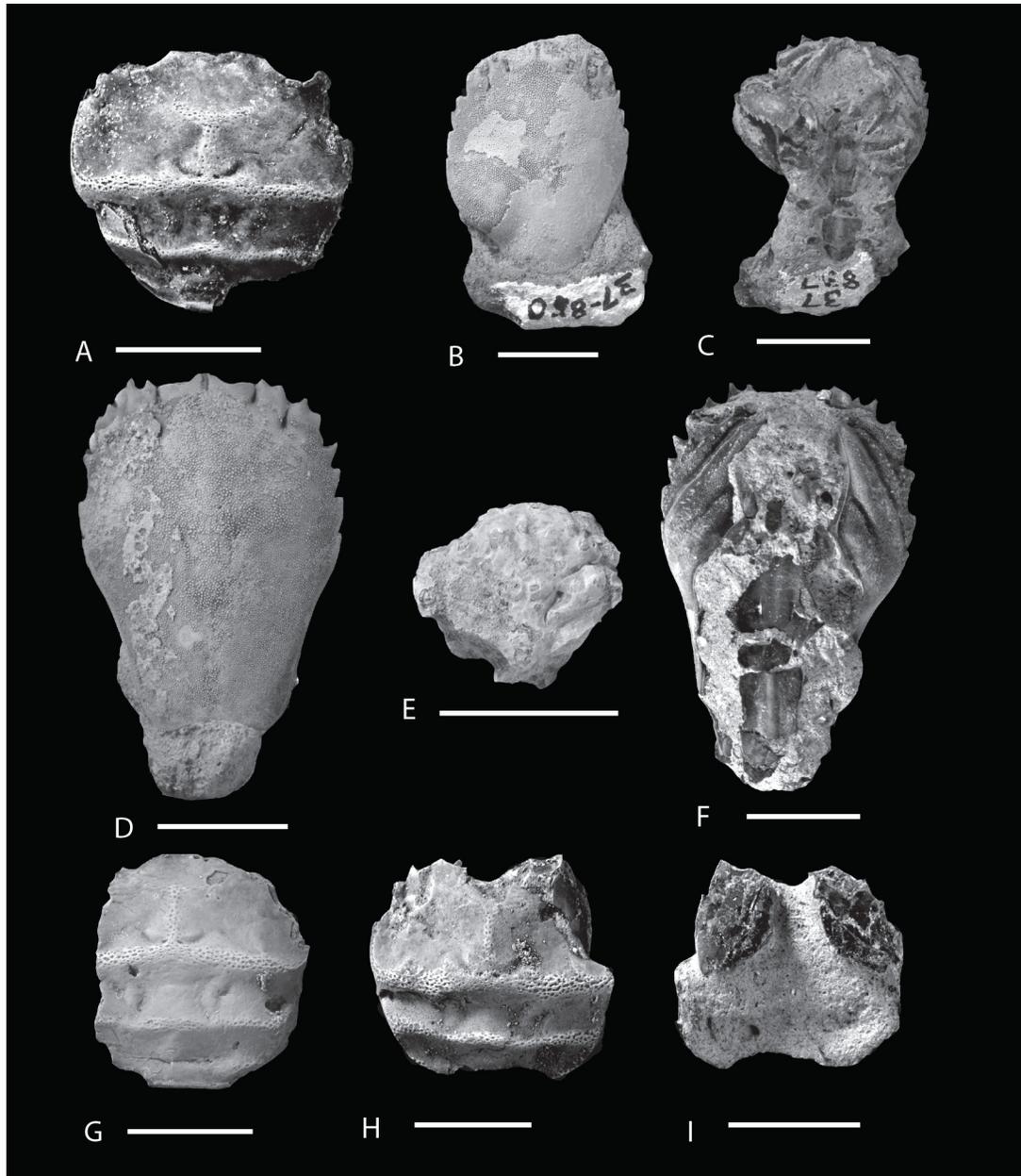
of sternites visible. Sternite 3/4 fused. Sternite four widest at contact with coxae of first pereopods; forms widest portion of sternum. Cuticle of sternum also with smaller, fungiform pillars. Palm of chelae with anteriorly directed spines on ventral and dorsal margin; laterally compressed and much narrower than tall; dactyl about equal in length to anterior margin of palm. Outer face of palm smooth. Fixed finger short, slightly downturned. Segments of first pereopods with rows of anteriorly directed spines.

Material examined.—Thirty specimens were measured, with an average length of 28 mm ranging from 19.8 to 48.8 mm, width averaging 21.8 mm ranging from 15 to 37.1 mm, frontal width average 9.7 ranging from 4 to 16.6 mm, frontal orbital width average 19.1 mm ranging from 16 to 26.5 mm (Supplemental measurements and material available online: Kornecki, 2014).

Occurrence.—Late Cretaceous, Campanian-Maastrichtian. Coon Creek Formation, Tennessee, Blue Springs locality; Coon Creek Formation, Mississippi; Navesink Formation, New Jersey; Marshalltown/Merchantville spoils of the north side of the C and D Canal, Delaware (Feldmann et al., 2013).

Discussion.—Thirty specimens of *Cretacorantina testacea* were observed and measured from the Blue Springs locality of the Coon Creek Formation. Of these, one (UF 252124, Fig. 15B) was preserved with a swelling in the left lateral dorsal carapace in the branchial region, a deformation attributed to infestation by an isopod (Klömpmaker, 2014). This isopod related swelling has been reported in many decapods and has been observed previously in *C. testacea* (Klömpmaker, 2014).

Specimens vary in preservation but are generally excellent, some with articulated claws and ventral portions of the carapace (such as sternites) and some show cuticle texture. Feldmann et al. (2013) noted that the type specimen and the material from New Jersey were incomplete, with the type specimen lacking a rostrum and the posterior portion of the carapace. The Coon Creek Formation specimens from Mississippi present the most complete examples of the species.



**Figure 15.** *Cristipluma mississippiensis*, MMNS IP 2786 (A); *Cretacorantina testacea*; UF 252124, (B); *C. testacea*, UF 252125 (C); *C. testacea*, KSU 2223 (D); *Latheticocarcinus atlanticus* (Roberts, 1962); UF 25211 (E); *C. testacea*, KSU 2223 (F); *C. mississippiensis*, KSU 2222 (G); *C. mississippiensis*, KSU 2222 (H, I). Scale bars = 1 cm.

#### Superfamily RANINOIDEA DE HANN, 1839

Included families.—Lyreiididae Guinot, 1993; Raninidae De Hann, 1839.

Diagnosis.—“Carapace longer than wide or about as wide as long, generally ovate, usually

vaulted transversely, regions poorly defined; usually with well developed rostrum and orbital spines; anterolateral margins usually with one spine but can have none or more than one; posterolateral margin lacking spines; cervical groove not reaching

ventral edge of carapace; branchiocardiac groove indistinct, developed as boundary of urogastric region; branchial ridges absent; junction between sternum and pterygostome usually wide; coxa of third maxilliped small, flattened; sternum narrow, sternites 1–3 generally fused, sternites 5 and 6 with lateral extensions, sterna suture 6/7 complete, sternites 7 and 8 often reduced and at lower level than other sternites; where known, pleon narrow in males and females, showing reduced but clear dimorphism, never reaching sternite 4; genital openings coxal, spermatheca present on endosternite 7/8; branchiostegite reduced; gymnopleuran condition present,” (Karasawa et al., 2014:243).

#### Family LYREIDIDAE GUINOT, 1993

Included Subfamilies.—*Bicornisranininae* Karasawa et al., 2014; *Lyreidinae* Guinot, 1993; *Macroacaeninae* Karasawa et al., 2014; *Marylyreidinae* van Bakel et al., 2012; *Rogueinae* Karasawa et al., 2014.

Diagnosis.—“Carapace much longer than wide, ob lanceolate; dorsal surface smooth or punctate, regions undefined; anterior margin narrow or wide; rostrum trifold, middle spine generally much longer than other two which serve as inner orbital spines; orbit with intra- and outer orbital spines; anterolateral margins may be entire or with one or two spines; sternum-ptyergostome junction poorly to well-developed or absent; gymnopleuran condition present; sternites 1–3 fused, forming a cap-like shape; sternite four large, with lateral extension anteriorly, concave laterally; sternite 5 of similar shape but smaller, with lyreidid hook (Guinot, 1979) and double peg pleonal locking mechanism; sternite 6 much smaller, sometimes with ridge; sternites 7 and 8 much reduced in size, median one reaching sternite 7; pleon narrow in both males and females, telson short, somite 6 long; pleon sexually dimorphic, somites 2 and 5 proportionally wider in females than males, somite 6 proportionally longer in females than males; spermatheca placed on sternite 7, separated by wall; merus of maxilliped three longer than ischium,” (Karasawa et al., 2014: 243–244).

#### Subfamily MARYLYREIDINAE VAN BAKEL ET AL., 2012

Included genera.—*Bournelyreidus* van Bakel et al., 2012; *Hemioon* Bell, 1862; *Heus* Bishop and Williams, 2000; *Marylyreidus* van Bakel et al., 2012.

Diagnosis.—“Carapace much longer than wide, ob lanceolate, widest at about mid-length; dorsal surface smooth, regions undefined, ornamented with upright nodes or fungiform nodes; fronto-orbital margin wide, ranging from about 66% to 80% maximum carapace width; rostrum trifold, middle spine generally much longer than other two serving as inner orbital spines, middle spine bifid; orbit with intra- and outer orbital spines; anterolateral margins with one or two spines; sternum-ptyergostome junction absent; gymnopleuran condition present; sternites 1–3 fused, forming a cap-like shape; sternite 4 narrow, with blunt-triangular episternite directed laterally; sternite 5 with very large lateral projections, arcuate, extending as far as lateral margin of carapace, with lyreidid hook (Guinot, 1979) and double peg pleonal locking mechanism composed of short pegs; sternite 6 much smaller, sometimes with ridge; sternites 7 and 8 much reduced in size; pleon narrow in both males and females, telson short, somite 6 long; spermatheca placed on sternite 7, separated by wall; merus of maxilliped 3 longer than ischium,” (Karasawa et al., 2014:254).

Range.—Early Cretaceous (Albian)-Miocene (Karasawa et al., 2014:254).

#### Genus *BOURNELYREIDUS* VAN BAKEL ET AL., 2012

1992. *Hemioon eysunesensis*. Collins and Rasmussen, Grønlands Geologiske Undersøgelse, Bulletin 162: p. 19.

Type species.—*Hemioon eysunesensis* Collins and Rasmussen, 1992.

Included species.—*Bournelyreidus carlilensis* (Feldmann and Maxey, 1980); *Bournelyreidus laevis* (Schlüter in Von der Marck and Schlüter, 1868); *Bournelyreidus oaheensis* (Bishop, 1988); *Bournelyreidus ericksoni* sp. nov.

Diagnosis.—“Carapace much longer than wide, ob lanceolate, widest at about mid-length;

dorsal surface smooth, regions undefined; fronto-orbital margin wide, ranging about half to two-thirds maximum carapace width; rostrum overall trifold, middle spine generally much longer than other two which serve as inner orbital spines, central spine bifid at tip; orbit with intra- and outer orbital spines; anterolateral margins with two spines; sternum-ptyergostome junction absent, sternite 4 articulating with third maxilliped; sternites 1–3 fused, forming a cap-like shape; sternite four narrow, with short arcuate projections anteriorly, concave laterally, with blunt triangular episternites directed laterally; sternite 5 with moderate lateral projections, arcuate; chelae flattened, lower margin with spines,” (Karasawa et al., 2014:254).

Discussion.—*Bournelyreidus* and *Macroacaena* as described by Van Bakel et al. (2012) and maintained by Karasawa et al. (2014) have very subtle differences; those of the dorsal carapace that are most apparent are the anterolateral spines and anterior margin. *Bournelyreidus* has two anterolateral spines and *Macroacaena* has one spine and may have small protuberance between the anterolateral spine and the outer orbital spine, as well as longer anterolateral spines than *Bournelyreidus* with an anterior margin that is flared anterolaterally. The ventral morphologies of these genera are difficult to compare; the type material of all species of *Bournelyreidus* lack preservation of the venter entirely. *Macroacaena* is limited to “those species with a fronto-orbital width of about 50% maximum carapace width; a carapace reaching maximum width at about the position of the last anterolateral spine and maintaining that width to about 50 or 60% the distance posteriorly on carapace; a fourth sternite with small projections anteriorly; and a fifth sternite with wide projections anteriorly,” (Karasawa et al., 2014:246). *Bournelyreidus* has “sternite four narrow, with short arcuate projections anteriorly, concave laterally, with blunt-triangular episternites directed laterally; sternite 5 with moderate lateral projections, arcuate,” (Karasawa et al., 2014:254).

As can be seen, the difference in preserved morphology that is diagnostic of each genus is subtle. That said, sternite 1–3 is crown-like in

*Macroacaena* and cap-like in *Bournelyreidus*; *Bournelyreidus* has two anterolateral spines and *Macroacaena* may have one node and one spine between anterolateral spines, much longer anterolateral spines, and a flared frontal margin; *Macroacaena* has a longitudinal keel on the dorsal carapace (sometimes) and *Bournelyreidus* does not. The dorsal surface is smooth in *Bournelyreidus* and coarsely punctate in *Macroacaena*. Based upon these observations, we do not recognize all specimens of *Bournelyreidus tridens sensu* Van Bakel et al., (2012) to be referable to *Bournelyreidus*, but rather that all belong to *Macroacaena tridens sensu* Karasawa et al., (2014) except those referred to *Bournelyreidus ericksoni* sp. nov. as discussed below.

#### ***BOURNELYREIDUS ERICKSONI* SP. NOV.**

Figure 6C–F

1991. *Raninella tridens* Roberts, 1962. Bishop, Mississippi Geology, 12(1, 2):13.  
 2012. *Bournelyreidus tridens* (Roberts, 1962). Van Bakel et al., Zootaxa, Monograph 3215:118, fig. 38C–D (part).

Zoobank Nomenclatural Act.—A57FFBA5-9DA9-4C49-ABCA-28773B589326.

Diagnosis.—Carapace small, narrow. Widest medially and nearly equal in width at anterior and posterior margin. Anterior outer-orbital spines forming continuous shelf to rostrum. Rostrum not preserved. Length of anterior spines unknown. Two pairs of small anterolateral spines directed anteriorly; carapace widest at most posterior anterolateral spine. Cuticle smooth to finely punctate. Dorsal carapace axially inflated with weak longitudinal keel; Branchiocardiac grooves bordering cardiac region as weakly depressed arcs on either side of axis. Sternite 1–3 fused, cordate. Sternite four long, narrow; sternite five wide with anterolateral to anteriorly projected and rounded episternites; episternite five with posterior projected hook-like, convex inward processes.

Etymology.—The name is derived from the latinization of “Erickson” in honor of Dr. J. Mark Erickson, advisor and mentor to the first author during her studies at St. Lawrence University and beyond and friend to all three co-authors.

Type material.—Holotype: UF 252131,

length: 12.86 mm, width: 8.42 mm.

Other material examined.—MPPM 1972.46.157, length: 20.64 mm, width: 14.16 mm; UF 252127; UF 252128; UF 252129; UF 252130; KSU 2221; MMNS-IP 3140; MMNS-IP 3140a; MMNS-IP 3140b; MMNS-IP 3140c. Average length: 15 mm, ranging from 12.6 to 20.6 mm, average width: 10.5 mm, ranging from 7.7 to 18.4 mm, and average frontal width: 4.5 mm; ranging from 4.5 to 4.5 mm; Number of specimens: 10.

Occurrence.—Blue Springs locality, Coon Creek Formation, New Albany, Mississippi, Maastrichtian.

Discussion.—*Raninella tridens* was originally described by Roberts (1962) from a single specimen from New Jersey that lacked sternal morphology and lacked details of the anterior margin. Bishop (1991) later referred specimens from Mississippi to this species. The species was later assigned to *Bournelyreidus* by van Bakel et al. (2012), who referenced the type material of *R. tridens* in the diagnosis, as well as referring to specimens from Mississippi. Morphology of the sternum of the Mississippi specimens was included in the diagnosis of *Bournelyreidus tridens*, though the sternal morphology was not available on the type specimen of *Raninella tridens*. Karasawa et al. (2014:246) assigned the type specimen of *Raninella tridens* to *Macroacaena tridens* (Roberts, 1962) as a new combination, which had previously been considered *Bournelyreidus tridens* by van Bakel et al. (2012) and Feldmann et al. (2013). Karasawa et al. (2014) did not include the Mississippi material in this diagnosis and suggested that the placement of this material needed to be assessed and was beyond the scope of their study at the time.

Karasawa et al. (2014) expanded on their explanation, indicating that the assignment of the type specimen of *Raninella tridens* to *Macroacaena tridens* was *Macroacaena tridens sensu* Roberts (1962) and that *Macroacaena* is restricted to those species with fronto-orbital widths of about half the maximum carapace width, that the maximum carapace width is at about the last anterolateral spine, and that the width is maintained about 50 or 60% of the way down the carapace posteriorly,

as well as having sternite 4 with a small projection anteriorly and sternite 5 with wide projections anteriorly. They noted that specimens from Mississippi possessed a hook-like structure on sternite 5, and had an articulation of sternites 4 and 5 similar to that of Lyreidinae and not Marylyreidinae. Specimens observed herein also have a hook-like structure on sternite 5 extending posteriorly to 6, but sternite 5 is widest and extends laterally, and sternite 4 is quite narrow, as is typical of Lyreidinae and Marylyreidinae.

The three described species of *Bournelyreidus* include one from the Upper Cretaceous Pierre Shale of South Dakota, *Bournelyreidus oaheensis* (Bishop, 1978). *Bournelyreidus oaheensis* also has a narrow fourth sternite but has no other sternites preserved. This species also has two tubercles between the anterolateral spine and outer orbital spine and the branchiocardiac grooves continue posteriorly to a weakly concave outward depression on either side of the axis, unlike *Bournelyreidus ericksoni*. It is noteworthy that *B. oaheensis* has tubercles between the anterolateral spines, as is given in the diagnosis of *Macroacaena* by Karasawa et al. (2014), which states that *Macroacaena* “may [have] a small anterolateral protuberance between anterolateral spine and outer orbital spine, (p. 246).

*Bournelyreidus laevis* (Schlüter in Von der Marck and Schlüter, 1868) of Germany also has a relatively unornamented carapace and two anterolateral spines. The specimen illustrated is a line drawing of the carapace. A brief description of the claw is also included; no sternal morphology is preserved. This species does not possess any morphology that is preserved to differentiate it from *Bournelyreidus ericksoni*, but the lack of substantial evidence to confirm it is the same species coupled with the locality of the specimen in Europe suggests that this assessment is not most parsimonious.

*Bournelyreidus carlilensis* (Feldmann and Maxey, 1980) from the Carlile Shale (Turonian) of Kansas, has poorly preserved sternites, but also possesses two anterolateral spines and the slightly sinuous carapace ornamentation of the cardiac region similar to *B. oaheensis*. Specimens UF

252129 of *Bournelyreidus ericksoni* has a faint depression around the cardiac region on some of the larger specimens.

There are no other genera of Lyreidinae described by Karasawa et al. (2014) with the form of the posterior projection of the “lyreidid hook” that is present on the Mississippi specimens, including *Macroacaena*, the genus to which *Bournelyreidus tridens sensu* Roberts (1962) was reassigned. The morphology of the hook on the Mississippi specimens is most similar to *Rogueus orri* Berglund and Feldmann, 1989 (Karasawa et al., 2014: fig. 10), but this species ranges from the Paleocene – Eocene, has a completely different anterior margin, and an incomplete suture between sternites 4 and 5 that “coils” at lateral margins, though this last character superficially looks like episternite 4 on *Bournelyreidus ericksoni* sp. nov.

Specimens referred to Marylyreidinae possess the “lyreidid hook” of Guinot (1979) and Karasawa et al. (2014) but *Bournelyreidus ericksoni* has a hook that is neither quite in the same placement (the hook on *B. ericksoni* sp. nov. is closer to the sixth sternite) nor of the same morphology (*B. ericksoni* sp. nov. is less pointed and does not extend as far from the carapace, Fig 6F) as illustrated by Guinot (1993) and does not possess a distal or subdistal peg. As such, the Mississippi specimens possess unique dorsal and sternal morphology for the genus while conforming to *Bournelyreidus* most obviously by possessing two anterolateral spines. It is not apparent by the phylogeny of Karasawa et al. (2014) that the presence of the lyreidid hook is a particularly indicative morphologic character for any particular genus within the Marylyreidinae, therefore supporting the placement of *B. ericksoni* in the genus *Bournelyreidus* based on all other characters except for the weak axial keel on the dorsal carapace.

**Superfamily CALAPPOIDEA DE HAAN, 1833**  
**Family AETHRIDAE DANA, 1851**  
**Genus PREHEPATUS RATHBUN, 1935A**

Type species.—*Prehepatus cretaceous* Rathbun, 1935.

Included species.—*Prehepatus cretaceous* Rathbun, 1935; *Prehepatus dilksi* Roberts, 1962;

*Prehepatus mexicanus* Schweitzer et al., 2006; *Prehepatus hodgesi* Bishop, 1983; *Prehepatus harrisi*, Bishop, 1985; *Prehepatus pawpawensis* Rathbun, 1935.

Generic diagnosis.—“Left merus triangular, with large nodes on outer surface; carpus longer than high, with nodes arranged into rows of 3 or 4 each parallel to distal margin. Right and left chelae longer than high, becoming higher distally; upper, lower, and outer surfaces ornamented with low, conical spines; proximal margin with distinctive collar, forming articulation with carpus; spines on outer surface generally arranged into rows; inner surface mostly smooth, sometimes with few small tubercles; fixed finger short, directed weakly downward with respect to lower margin of manus, with small tubercles; movable finger with small tubercles at proximal end, keel generally extending from tubercles at least half the distance of the finger,” (Schweitzer et al., 2006:33).

**PREHEPATUS HARRISI BISHOP, 1985**

Figure 6G–J

1985. *Prehepatus harrisi*. Bishop, Journal of Paleontology, 59(5):1028.  
 1991. *Prehepatus harrisi*. Bishop, Mississippi Geology, 12(1, 2):13.  
 2006. *Prehepatus harrisi*. Schweitzer et al., Bulletin of the Mizunami Fossil Museum, 33:33.

Diagnosis.—Chelae only. Merus triangular with large nodes on outer surface; outer surface convex, inner surface flattened with few, smaller nodes. Proximal margin with smooth collar. Upper margin slightly rounded. Outer surface ornamented by five or six approximate rows of tubercles. Tubercles becoming smaller toward upper and lower margins. Fingers short and stout; fixed finger continuing straight from lower margin; dactyl strongly downturned, smooth on inner and outer surface, tubercles present on upper surface.

Material examined.—KSU-2219 (right chelae), length (l): 19.44 mm, height (h): 18.9 mm; MPPM 1972.46.449 (right chela), l: 27.2 mm, h: 23.16 mm; MPPM 1972.46.448 (left chelae), l: 26.38 mm, h: 24.2 mm.

Occurrence.—Blue Springs locality, Coon Creek Formation, New Albany, Mississippi,

Maastrichtian; the early Maastrichtian of northeast Mexico (Vega et al., 1995:247); and the Prairie Bluff Formation, Union County Mississippi, Maastrichtian (Bishop, 1985).

Discussion.—Material from the Blue Springs locality consists of three specimens, one of which is abraded and no longer possesses tubercles or fingers. One specimen is also noteworthy for its smaller size. The largest specimen possesses a nearly complete dactyl, illustrating tubercles on the upper margin, not previously described or preserved in the species.

Schweitzer et al. (2006:32) discussed the placement of *Prehepatus* within higher taxa. The recognition of Hepatidae Stimpson, 1871 as a junior synonym of Aethridae Dana, 1851, was confirmed by Schweitzer et al. (2010:85) and retained in this study. The genus is known only from right and left chelae and one carpus, and is known only from North America. It was originally named by Rathbun (1935) for specimens collected in the Cretaceous Gulf Coastal Plain (Schweitzer et al., 2006). *Prehepatus dilksi* Roberts, 1962, is known from the Cretaceous of New Jersey (Feldmann, et al., 2013).

The only record of the genus not from North America is *Prehepatus weneri* Fraaye and Collins, 1987, from the Netherlands. However, Jagt et al. (2010) proposed that *P. weneri* is a junior synonym of *Necrocarcinus ornatissimus* Forir, 1887 and recommended the combination *Roemerus ornatissimus* (Forir, 1887) after the genus described by Bishop (1983), but which Jagt et al. (2010) refer to as a ‘form genus’. *Prehepatus weneri* may indeed be a junior synonym of *Necrocarcinus ornatissimus*, as the claws of *P. weneri* are very similar to those found in association with *Necrocarcinus ornatissimus* carapaces (Jagt et al., 2010, fig. 1). *Necrocarcinus ornatissimus* is herein considered a senior synonym of *Prehepatus weneri*. This assessment by Jagt et al. (2010) is noteworthy because it limits the genus to North America. Discovery of associated carapaces with material of *Prehepatus* claws in North America will clarify the identification of *Prehepatus* as a uniquely American genus.

**Section HETEROTREMATA GUINOT, 1977**  
**Superfamily RETROPLUMOIDEA GILL, 1894**  
**Family RETROPLUMIDAE GILL, 1894**

Type Genus.—*Retropluma* Gill, 1894.

Included Genera.—*Archaeopus* Rathbun, 1908; *Bathypluma* de Saint Laurent, 1989; *Costacopluma* Collins and Morris, 1975; *Cristipluma* Bishop, 1983; *Loerenthopluma* Beschin, Busulini, De Angeli, and Tessier, 1996; *Retrocypoda* Via Boada, 1959; *Retropluma* Gill, 1894.

Family diagnosis.—“Carapace rectilinear or ovoid, wider than long, ornamented with three transverse ridges, usually positioned on protogastric, epibranchial, and mesobranchial regions. Front narrow, downturned, axially sulcate; orbits broad, margins sinuous, often with blunt projection at midlength; orbits terminating in sharp spine. Sternum with transverse ridges mimicking those on the dorsal carapace,” (Schweitzer and Feldmann, 2001:201).

**Genus CRISTIPLUMA BISHOP, 1983**

Type species.—*Cristipluma mississippiensis* Bishop, 1983.

Included species.—*Cristipluma mississippiensis* Bishop, 1983.

Generic diagnosis.—As for species.

**CRISTIPLUMA MISSISSIPPIENSIS BISHOP, 1983**

Figure 15A, 15G–I

1983. *Cristipluma mississippiensis*. Bishop, Journal of Crustacean Biology, 3(3):428.  
 1985. *Cristipluma mississippiensis*. Bishop, Journal of Paleontology, 59(5):1028.  
 1986. *Cristipluma mississippiensis*. Bishop, Crustacean Issues, 4:111–142.  
 1991. *Cristipluma mississippiensis*. Bishop, Mississippi Geology, 12 (1, 2):12–13.

Diagnosis.—“Carapace ovoid, wider than long, gently arched and poorly differentiated by grooves. Two prominent, continuous transverse ridges crossing carapace; one at midpoint just behind urogastric region, forming widest part of carapace, other behind subtle, crescentic branchiocardiac grooves,” (Bishop, 1983:428).

Description of material.—Carapace ovoid, slightly wider than long, gently arched with steep lateral margins. Two wide, coarsely punctate, transverse ridges intersect urogastric and cardiac regions as well as cardiac and intestinal regions at the midline, continuing laterally and curving slightly anteriorly at margins. Perpendicular and anterior to transverse ridge is a ridge of equal height, continuing anteriorly through mesogastric region, punctate, tapering to smooth surface halfway to anterior margin. Margins of mesogastric region demarcated weakly as elevated, pyriform protogastric region, vanishing anteriorly. Carapace with irregularly distributed nodes on depressed sections. Weak grooves defining cardiac region, nearly equi-dimensional, lateral margins concave axially, bounded by arcuate swellings. Posterior margin straight with narrow rim.

Material examined.—Seven specimens from the Blue Springs locality, Coon Creek Formation, collected December 17 and 18, 2012. Specimens KSU-2222, length: 17.11 mm; width: 23.6 mm; length: 16.24 mm, width: 17.88 mm, frontal width: 11.14 mm; length: 18.9 mm, width: 20.23 mm; length 15.3 mm, width 18.2 mm; length: 16.38 mm, width: 18.2 mm; length: 12.49 mm, width: 16.23 mm; and three specimens on loan: MMNS IP-2786a, length: 20.9 mm, width: 25.3 mm; MMNS IP-2786b, length: 20.22 mm, width: 21.84 mm; MMNS IP-194, width: 19.78 mm.

Occurrence.—Blue Springs locality, Coon Creek Formation, Union County, Mississippi, Maastrichtian.

Discussion.—*Cristipluma mississippiensis* is the only known species of the genus. The genus differs from others in the family in having the anteriormost ridge being developed axially and on to the protogastric region. It is also noteworthy that other genera in the family and previous descriptions of *C. mississippiensis* are referred to as being granulated; specimens of *C. mississippiensis* observed herein are punctate on raised portions of the carapace cuticle and smooth to very weakly and irregularly granulated on the remainder of the dorsal carapace. Few specimens of *Cristipluma mississippiensis* exist; Bishop first described a

single specimen from the Blue Springs locality in 1983. Collecting on December 17 and 18, 2012 yielded seven additional specimens of the species. The above description includes observations of the preserved posterior margin of a carapace of one of these new specimens. Preservation of cuticle is common but specimens are fragmented.

Bishop (1983) discussed the presence of a retroplumid in the Coon Creek Formation at the Blue Springs locality in New Albany, Mississippi, and suggested that the specimen was likely allochthonous because modern species in the family are deep-dwelling. The presence of more specimens of *Cristipluma mississippiensis* found at the Blue Springs locality suggests that it is unlikely that these crabs were in fact living in deeper environments. The preservation is fragmentary which could well indicate extensive transport. It is not parsimonious to hypothesize transport of numerous crab carapaces up the continental shelf from deep waters. It therefore seems likely that this monospecific genus from the Cretaceous could have lived in shallower environments than its modern relatives; a change in preferred habitat within a family is not uncommon over geologic time (Schweitzer and Feldmann, 2000).

#### **Superfamily PORTUNOIDEA RAFINESQUE, 1815**

Included families.—Archaeoportunidae, Artal et al., 2013; Carcineretidae Beurlen, 1930; Carcinidae MacLeay, 1838; Catoptridae, Boralai, 1902; Geryonidae Colosi, 1923; Lithophylacidae, VanStraelen, 1936; Longusorbiidae, Karasawa et al., 2008; Macropipidae Stephenson and Cambell, 1960; Mathildellidae Karasawa and Kato, 2003; Pirimelidae Alcock, 1899; Polybiidae Ortmann, 189; Portunidae Rafinesque, 1815; Psammocarcinidae Beurlen, 1930; Thiidae Dana, 1852.

Diagnosis.—“Carapace hexagonal, subhexagonal, rectangular, or transversely ovate; carapace usually wider than long, usually widest at position of last anterolateral spine; flattened or weakly vaulted; regions poorly or moderately defined; anterolateral margins entire or with up to nine spines including outer orbital spine; front entire or spined; lobe

on endopod of first maxilliped ('portunid lobe') sometimes present; chelipeds usually robust; last pair of pereopods may have ovate dactyls; sternal sutures 4/5, 5/6, 6/7, and 7/8 usually incomplete; sternite 8 usually visible in ventral view, with penial groove (Portunidae); male abdominal somites all free or 3–5 fused, sutures may be visible; gonopod 1 strongly curved, with inflated, strongly hooked base," (Karasawa and Schweitzer, 2006:59).

**Family LITHOPHYLACIDAE VAN STRAELEN, 1936**

Type genus.—*Lithophylax* A. Milne-Edwards and Brocchi, 1879

Included genera.—*Lithophylax* A. Milne-Edwards and Brocchi, 1879.

Diagnosis.—Dorsal carapace transversely hexagonal to inverted trapezoidal, widest at outer-orbital spines. Cuticle weakly granular. Well defined transverse regions lobulated or ridged. Frontal margin straight with narrow, downturned rostrum. Orbits wide, extending posterolaterally to anterolateral spines.

Proto gastric region with distinct, horizontal ridge that slopes gently to the frontal margin; proto gastric and mesogastric regions outlined by singular, deeply incised groove extending toward anterior margin. Mesogastric region with axially directed lanceolate ridge extending to posterior horizontal ridge parallel to the urogastric region. Urogastric region slightly elevated ridge with lateral ends curved toward the anterior margin. Cardiac region with transverse ridge, delimited laterally by deeply incised groove. Intestinal region less defined with weak, horizontal ridge or smooth. Hepatic regions crossed by elevated transverse ridge extending from the groove around the proto gastric region in a posterior direction to the anterolateral margin. Branchial regions inflated with transverse ridge slightly anterior to ridge formed in cardiac region; posterolateral half of branchial region with slightly less inflated area and weak, transverse ridge.

Chelipeds robust with elongate propodus; slightly heterochelous with larger right hand. Palm outer surface with weak to strong transverse, medial keel; posterior margin flat or slightly convex; Left

hand slightly more slender. Fingers elongated, several teeth on both prehensile margins.

Sternum oval, flat with punctate cuticle. Sutures 1/2 distinct, suture 2/3 distinct, sternite 4 markedly larger than other sternites, suture 4/5 indistinct axially and distinct laterally. Sutures 5/6 and 6/7 distinct. Suture 7/8 short but distinct, notched at margins. Sternite 7 covered partially by pleon in both males and females. Pleon triangular and extending to middle or anterior margin of sternite 4. Male pleon triangular with broad base and transverse ridges; telson triangular (modified from Guinot and Bretton, 2006, Phillips et al., 2014).

Discussion.—After observing the available material of *Branchiocarcinus cornatus*, *B. flectus*, *B. pacificus*, *Icriocarcinus xestos*, and *Lithophylax triggeri*, we conclude that these species are referable to the same genus, *Lithophylax*, and thus the same family. Icriocarcinidae is therefore considered a junior synonym of Lithophylacidae. Phillips et al. (2014) also recognized and noted the similarities between *Lithophylax*, *Icriocarcinus*, and *Branchiocarcinus* when they elevated the Icriocarcininae to Icriocarcinidae including: an inverted subtrapezoidal carapace; a sharp anterolateral spine; slender, projected pseudorostrum [sic]; distinct ridges and grooves on the dorsal carapace; elongate, subrectangular third maxillipeds; and transverse keels on the abdominal somites.

Examination of excellent material with articulated claws and sternum of *Lithophylax triggeri*, *Icriocarcinus xestos*, and *Branchiocarcinus flectus* indicate that these genera illustrate distinctly lithophylacid morphologies, which has historically been questioned when studying carapace morphology, as it was all that was available at the time. *Lithophylax triggeri*, *I. xestos*, and *B. flectus* have an oval sternum with the pleon extending onto sternite 4, and much of the pleon covering sternites 7 and 8. Their pleons also possess transverse ridges. This link of common sternal morphology between *Lithophylax*, *Branchiocarcinus* and *Icriocarcinus* provides the foundation for relating these three genera to *Lithophylax*.

That said, the dorsal carapace morphology also supports assignment of *Branchiocarcinus* and *Icriocarcinus* to *Lithophylax* and illustrates the same hexagonal to trapezoidal shape, anterolateral spines and large orbits that extend to these spines, a narrow, downturned rostrum, and ridges located in comparable regions but of varying degrees of definition. These three genera are all also heterochelous in nature with similar chela morphology, with a keel on the external face of the palm and elongate fingers.

*Lithophylax* was originally described by A. Milne-Edwards and Brocchi (1879) and formed the basis for erecting Lithophylacidae by Van Straelen (1936). It was retained as the sole genus in the family Lithophylacidae by recent authors (Guinot and Breton, 2006). *Icriocarcinus* was designated type genus of Icriocarcinidae Phillips et al. (2014), which embraced *Icriocarcinus* and *Branchiocarcinus*. They were distinguished from *Lithophylax* because the latter is generally less spinose in nature (lacking spines on the posterolateral margin as well as on the anterior edge of the chelae), it bears more rounded ridges considered to be lobose on the dorsal carapace, and its anterior edge is straight, unlike the notched margins of *Branchiocarcinus flectus*, *Branchiocarcinus cornatus*, and *Icriocarcinus xestos* (Phillips et al., 2014). Phillips et al. (2014) also indicated that *Lithophylax* has a reduced P5 (after Guinot and Breton, 2006), but *B. flectus*, *B. cornatus*, and *I. xestos* do not. Examination of specimen MMNS 4388 (Fig. 8I) of *Branchiocarcinus flectus* appears to have a P5 of similar size and nature to P4, but it is not certain that it is indeed P4 and not P5 based on the arrangement of the preserved pereopods. Examination of illustrations of *I. xestos* by Bishop (1988) suggests that P5 is preserved and only slightly smaller and elevated, much like *B. flectus*. It is important to note that these observations of the nature of P5 are not clear with the available material and the nature of P5 for *I. xestos*, *Lithophylax trigeri*, and *B. flectus* should remain in question. The P5 of *B. cornatus* is unknown based on available material. This morphological character of reduced P5 is cited as a prominent reason for excluding *Lithophylax* from

*Icriocarcinus* and *Branchiocarcinus* by Phillips et al. (2014). This feature certainly raises some uncertainty in higher taxonomic placement, but we conclude that the other morphological evidence is strong enough at this time to include these three genera as *Lithophylax* in the Lithophylacidae, concluding that the reduced P5 of *Lithophylax trigeri* is a specific character or that the nature of P5 for other species is not fully understood.

*Icriocarcinus* was originally assigned to Carcineretidae by Bishop (1988) and was later moved to the Goneplacidae MacLeay, 1839 by Schweitzer et al. (2002) for its similarities to *Ommatocarcinus* White, 1852. Phillips et al. (2014) discussed the differences between *Branchiocarcinus flectus*, *Icriocarcinus xestos*, and *Ommatocarcinus* and we agree with their findings that these genera differ from *Ommatocarcinus* and align more with the Portunoidea than the Gonioplacoidea, given the new information regarding the included genera. These differences are outlined by Phillips et al. (2014:11). Most notably, *Ommatocarcinus* has a bifid rostrum, laterally directed anterolateral spines, wider sternum, and has equal chelae that are much longer and more slender than lithophylacids.

*Branchiocarcinus* was also originally assigned to Carcineretidae by Feldmann and Vega (1995), but was not included in the revision of Carcineretidae by Schweitzer et al. (2007). It was later reassigned to the Carcineretidae by Schweitzer et al. (2010). The original description of *Branchiocarcinus* was based on a very poorly preserved mold of the dorsal carapace. Though the specimen is poor, what is preserved does support placement of *Branchiocarcinus* in *Lithophylax* as it does not possess any characters distinct from *Lithophylax*. The only unique character of the genus as described in *B. pacifica* and *B. flectus* is spines on the posterolateral margin. These are not present on the type species, *B. cornatus*, but are present on *Icriocarcinus xestos*.

#### Genus **LITHOPHYLAX** A. MILNE-EDWARDS AND BROCCHI, 1879

Type species.—*Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879

Included species.—*Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879, *Lithophylax flectus* (Rathbun, 1926), *Lithophylax cornatus* (Vega, Feldmann and Sour-Tovar, 1995); *Lithophylax xestos* (Bishop, 1988); *Lithophylax pacificus* new designation (Nyborg et al., 2014).

Generic diagnosis.—Carapace hexagonal to inverted trapezoidal, one-fourth wider than long, widest portion at anterolateral spines. Orbits extend from narrow, downturned rostrum to anterolateral spines, indicating elongate, mobile eye stalks. Cuticle finely granular.

Protogastric region with transverse ridge or lobes, anterior of region slope gently to the frontal margin; protogastric and mesogastric regions outlined by singular, deeply incised groove extending toward or reaching anterior margin. Mesogastric region axially lanceolate with horizontal ridge parallel to the urogastric region. Urogastric region consisting of slightly elevated ridge. Cardiac region with transverse ridge or lobes, delimited laterally by deeply incised groove. Hepatic regions crossed by pair of elevated transverse ridges or lobes extending from the groove around the protogastric region in a posterior direction toward the anterolateral margin. Branchial regions inflated with transverse ridge slightly anterior to ridge formed in cardiac region; posterolateral half of branchial region also with slightly less inflated area.

First pereopods slightly heterochelous, with larger, less ornamented right claw. Fingers elongate and slender. Medial, transverse keel prominent on external surface of left chela, sometimes less prominent so on right chela. Sternum oval and flat. Sternite 4 much larger, sternite 8 not visible or very reduced on ventral side. Pleon extending nearly to anterior margin of sternite 4 with transverse ridges.

Discussion.—Excluded from the revised diagnosis that originally described *Lithophylax* as a monospecific genus is the stridulating process referred to as the “shutter” (Guinot and Bretton, 2006). The shutter is here considered as species-level feature, unique to *Lithophylax trigeri*, as it is not visible or preserved in other species of *Lithophylax*. *Lithophylax trigeri* has smooth internal

surfaces of palms with 29 striae on inner surface of merus for stridulatory purposes and a counterpart of five striae in front of blunt suborbital tubercles. *Lithophylax flectus* does not have transverse striae, but the tubercles on the internal surface of the palm may be used like the stridulating device of *Psopheticus* Wood-Mason, 1892. The presence and form of stridulating apparatus is also considered to be a specific character, herein.

*Lithophylax flectus* and *Lithophylax xestos* also do not have gonopores as found in *Lithophylax trigeri*, but this is likely due to preservation, and so was not included in the generic diagnosis until it can be verified. Two other characters are also specific to *Lithophylax trigeri*, a much reduced P5 and the absence of spines on the chelae. With more material, it may prove that these characters indeed separate *L. trigeri* from the included species assigned herein, but current observations support these to be specific characters within *Lithophylax*.

*Lithophylax xestos* was originally assigned to *Icriocarcinus* because it lacked a “posterior transverse ridge on the cardiac and mesobranchial regions,” (Bishop, 1988:247). After examining three specimens of *L. xestos* available in the Kent State University collection, it is apparent that *L. xestos* differs from *L. trigeri* in that it is slightly larger and that the transverse ridges on the cardiac and mesobranchial regions are less defined. *Lithophylax xestos* shares a number of characters with *Lithophylax flectus* and *Lithophylax pacificus*, including a regular sized P5, spinose chelae, and spines on the posterolateral margin, though these characters cannot be observed on the type species of *Branchiocarcinus*, *B. cornatus*, because they are not preserved.

A new species, *Branchiocarcinus pacificus* Nyborg et al., 2014 was recently described from the Cretaceous of California. We concur with its association with the lithophylacid species based on its assignment to *Branchiocarcinus*, but propose this species instead belongs to *Lithophylax*, based on its narrow frontal margin, concave posterior margin, and spinose chelae as these are also present in *L. xestos* and *L. flectus*. Thus, we would consider *Branchiocarcinus* a junior synonym of *Lithophylax*.

**LITHOPHYLAX FLECTUS (RATHBUN, 1926)**

## Figure 16

1926. *Eryma flecta*. Rathbun, *In* The Fauna of the Ripley Formation of Coon Creek, US Geological Survey:184–191.
1983. *Eryma cf. flecta* Rathbun, 1926. Bishop, *Journal of Crustacean Biology*, 3:417–430.
1985. “*Eryma cf. flecta*” Rathbun, 1926. Bishop, *Journal of Paleontology*, 59(5):1028–1032.
- 1986a. *Eryma* n. sp. Bishop, *in* Balkema, *Crustacean Biogeography*:111–142.
- 1986b. Portunid claws indet. (= *Eryma cf. flecta* Rathbun). Bishop, *Proceedings of the Biological Society of Washington*, 99:604–611.
2007. Undescribed/identified crab. Landman et al., *Bulletin of the American Museum of Natural History* 303:122.
2014. *Branchiocarcinus flectus*. Nyborg et al., *Scripta Geologica*, 147:4.
2014. *Branchiocarcinus flectus*. Phillips et al., *Paläontologische Zeitschrift*, 87(3):14.

**Diagnosis.**—Carapace small, wider than long with greatest width at anterolateral spines. Dorsal carapace with distinct but fine transverse ridges oriented parallel to the anterior and posterior margins, mesogastric and protogastric regions delimited by well-defined groove extending to the anterior margin. Posterolateral margin of branchial region possessing two spines. Sternite 1 and 2 distinct; sternite 3 indistinct axially and sutures distinct and notched laterally. Pleon extending to anterior margin of sternite 4. Weakly heterochelous with stridulating tubercles on interior surface of left chelae. Chelae spinose on anterior margin.

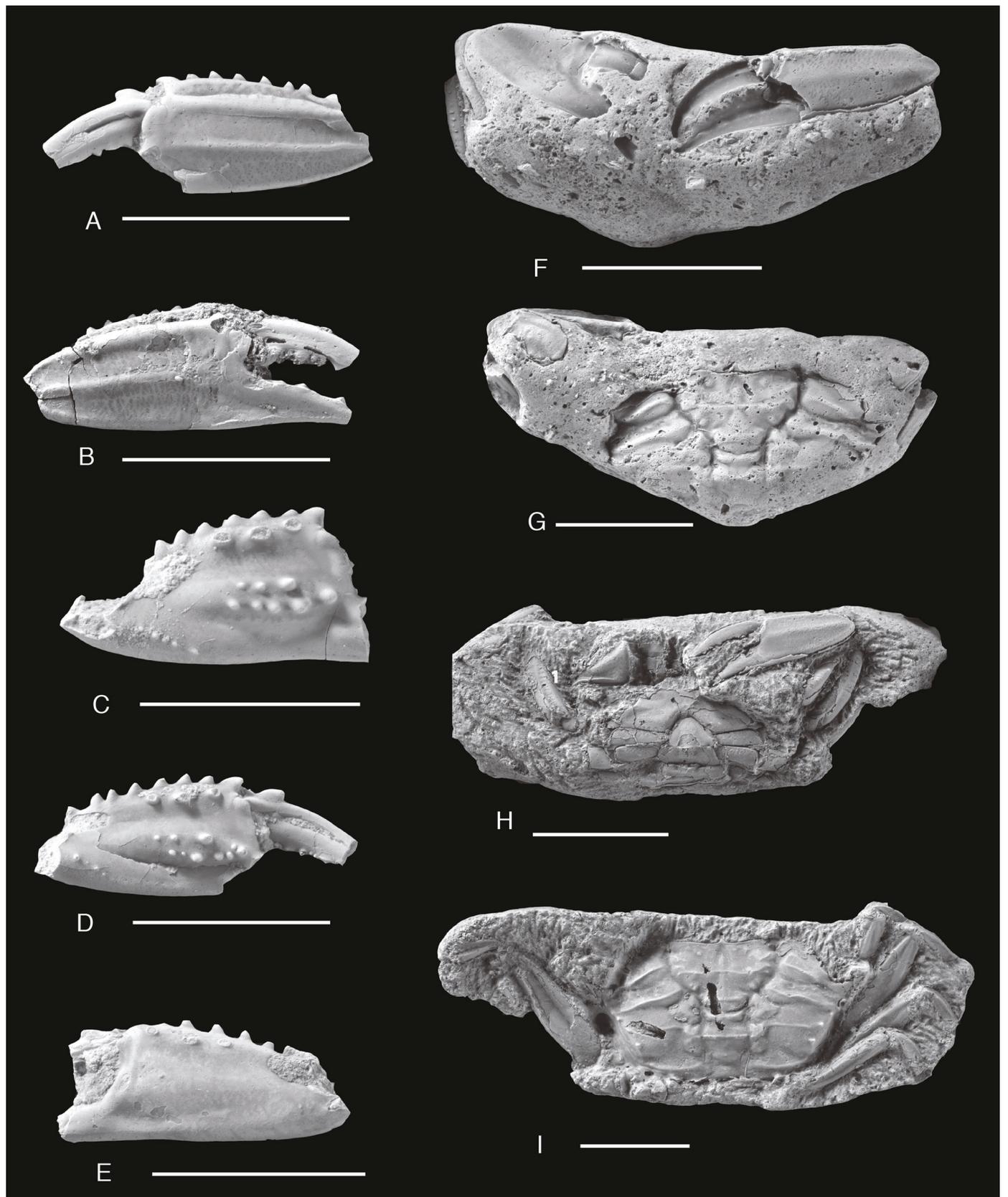
**Description.**—Carapace small, inverted subtrapezoidal; transversely elongated with greatest width at anterolateral spines. Anterior margin straight. Rostrum long, downturned. Large, anteriorly directed anterolateral spine divides anterolateral from posterolateral margins. Dorsal carapace regions marked by strong transverse ridges.

Protogastric region with distinct, horizontal ridge that slopes gently to the frontal margin; protogastric and mesogastric regions outlined by singular, deeply incised groove extending to anterior margin. Mesogastric region axially lanceolate with horizontal ridge parallel to the urogastric region. Urogastric region slightly elevated, transverse ridge with lateral margins of ridge upturned toward the anterior margin. Cardiac region with transverse ridge, delimited laterally by deeply incised groove. Intestinal region less defined with two parallel, horizontal ridges. Hepatic regions crossed by elevated transverse ridge extending from the groove around the protogastric region in a posterior direction to the anterolateral margin. Branchial regions inflated with transverse ridge extending from anterior margin of the urogastric region and a second ridge slightly anterior to ridge formed in cardiac region, both angled posteriorly to the lateral margin; axial portion of branchial region between these two ridges slightly more inflated; posterolateral section of branchial region with slightly less inflated area and distinct transverse ridge and two spines at posterolateral margin. Posterior margin rimmed and slightly concave.

Right chela slightly larger than left (Fig. 8F). Ridge on dorsal surface of chelae with eight tubercles and inner row of three spines. Inner surface of chelae typically smooth on right chela and two rows of small tubercles at center of left chela (Fig. 8C–D); fixed finger elongate and triangular with longitudinal groove on outer surface at midline and single spine closest to articulation on the dorsal surface. Occlusal surface dentition of variable size, dactylus curved slightly toward fixed finger, both fingers elongate and thin.

Sternum transversely subovate. Sternite 1 and 2 distinct, sternite 3 indistinct axially and distinct, notched laterally. Sternite 4 largest; sternites 5, 6,

**Figure 16.** *Lithophylax flectus* new combination. Exterior of left claw, MMNS 2027 (A), specimen MMNS 5067, exterior of right claw (B), specimen MMNS 2144, interior of left claw (C), specimen MMNS 2027, interior of left claw (D), specimen MMNS 3723, interior of right claw (E), specimen MMNS 6115.1, anterior view of carapace with articulated left claw and mold of right claw (F), specimen MMNS 6115.1, dorsal carapace (G), specimen MMNS 4388, venter (H), specimen MMNS 4388, dorsal carapace (I). All scale bars = 1 cm. →



and 7 of similar form, rotating posteriorly, sternites 7 and 8 smaller than 5 and 6. Male pleon triangular, with transverse ridges, covering most of sternites 7 and 8; telson triangular. P5 not appreciably smaller than P4.

Material examined.—MPPM 1972.46.932, length 15.17 mm, width 22.68 mm; MPPM 72.46.459, length 13.82 mm, width 20.02 mm; MMNS 5067; MMNS 3723; MMNS 2027; MMNS2144; MMNS 6115.1; MMNS 4388.

Occurrence.—Blue Springs locality, New Albany, Mississippi, Maastrichtian. Material studied by Phillips et al. (2014) was collected from the Owl Creek type locality in Tippah County, Mississippi, the Nixon Sands and the Prairie Bluff Formation in Goodfood, Mississippi and Pontotoc, Mississippi, and the Tinton Formation in Monmouth County, New Jersey, also Maastrichtian.

Discussion.—Rathbun (1926) named a single, poorly preserved claw from the Coon Creek Formation *Eryma flecta*. Since then, most researchers (Bishop 1983, 1985, 1986; Phillips et al. 2014) have expressed their uncertainty at the assignment of the claw to *Eryma*. Phillips et al. (2014) determined that a claw similar to the one Rathbun (1926) assigned to *Eryma* was articulated with an undescribed species from the Blue Springs locality. Phillips et al. created the new combination, *Branchiocarcinus flectus*. The articulated specimen is clearly brachyuran and is not that of the lobster *Eryma*. Having observed the claw Rathbun (1926) named *Eryma flecta*, it was noted that the specimen lacks much of the detail of claws preserved and articulated with *Branchiocarcinus flectus sensu* Phillips et al. (2014). The original claw described by Rathbun (1926) has a narrow palm and no spines or carina, with only the general outlined shape of the palm and slightly downturned fixed finger, which promoted the trivial name. Though Rathbun's specimen is poor, it is plausible that it belongs to the same species as the specimen described by Phillips et al. (2014).

The Coon Creek species, herein assigned to *Lithophylax*, bears close resemblance to the dorsal carapaces of Cenomanian *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879; the

late Cretaceous *Icriocarcinus xestos* Bishop, 1988; and the Maastrichtian *Branchiocarcinus cornatus* Feldmann and Vega, 1995. Fortunately, one specimen (MMNS 4388) of *Lithophylax flectus* from Coon Creek has a well preserved venter allowing for detailed comparison. It has pleonal segments with transverse ridges; the telson and pleon are triangular. The sternum shape and the pleon extending to the anterior edge of sternite 4 are like those features seen on *Lithophylax trigeri*. The dorsal carapace of *L. flectus* has better definition of the transverse ridges than the lobose ridges of *L. trigeri*, but the location and direction of inflation as well as the deeply grooved areas are consistent. The differences in chela ornamentation and stridulating devices are evidence that *L. flectus* and *L. trigeri* are distinct species but the similarity of other features support assignment to the same genus. The placement of *L. flectus* within *Lithophylax* extends the range of the genus into the Maastrichtian.

#### **Incertae sedis**

##### **Majid (?) Fragment 1**

Figure 6K

Description.—Specimen slightly wider than long, pleonal somite. Indication of single horizontal suture, rounded on all sides. Vertical keel along axis with well defined depressions on either side; inflated laterally.

Occurrence.—Coon Creek Formation, locality MGS173, Union County, Mississippi.

Material examined.—MMNS 4016, height: 14.66 mm, width: 15.38 mm.

##### **Majid (?) fragment 2**

Figure 6L

Description.—Fragmented anterior portion of carapace, only. Frontal margin narrow, extending into wide rostrum formed by two wide projections flared outward. Frontal margin comprising one-third of total carapace width. Medial carina with two spines most anteriorly followed by a pair of two spines directly anterior to well defined cervical groove; groove concave forward axially, turning posteriorly at lateral margins. Branchial region slightly inflated. Mandibles (?) with inward-directed processes.

Occurrence.—Coon Creek Formation, locality MS.73.033a, Union County, Mississippi.

Material examined.—MMNS 4108, height: 26 mm, width: 20.3 mm.

Discussion.—Both specimens are single occurrences from the Coon Creek Formation. This is the first potential documentation of Majidae in the Coon Creek Formation and is a significant occurrence because majids are uncommon in the Cretaceous.

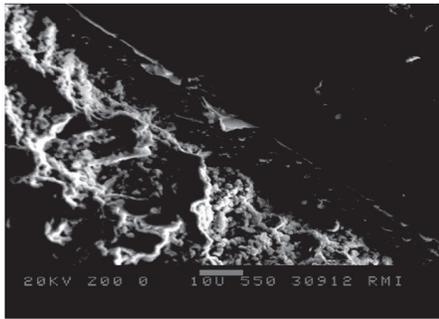
## DISCUSSION

### TAPHONOMY

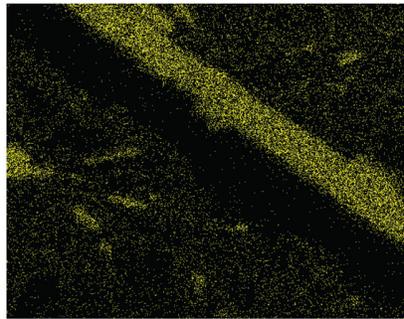
Because of the large volume of decapod material available from the Coon Creek Formation, taphonomic measurements could be conducted on a variety of specimens. Results and interpretations of these investigative approaches are included

here as well as any other otherwise interesting observations from individual taxa or specimens.

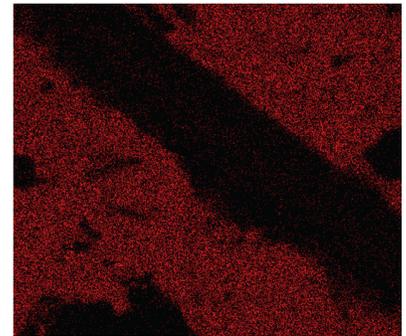
Variation in replacement mineralogy is apparent in specimens of *Tetracarcinus subquadratus* as well as a few specimens of *Linuparus* sp. Most specimens of Coon Creek Formation decapods are preserved as internal molds or are replaced by a phosphate mineral, probably apatite. Few specimens have silica associated with their preservation, and the majority of this type is confined to *T. subquadratus*. Elemental mapping of *T. subquadratus* indicates that specimens preserved with a layer of white, iridescent cuticle possess silica and aluminum (Fig. 17), whereas all other specimens measured are dominantly phosphorous and calcium (Figs. 18–21). Specimens also fluoresced in long and shortwave ultraviolet



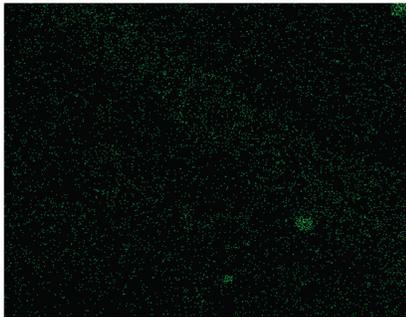
*Tetracarcinus subquadratus*



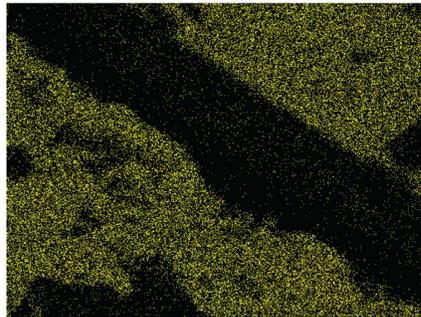
Aluminum



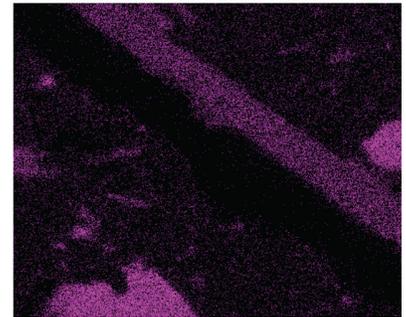
Calcium



Iron

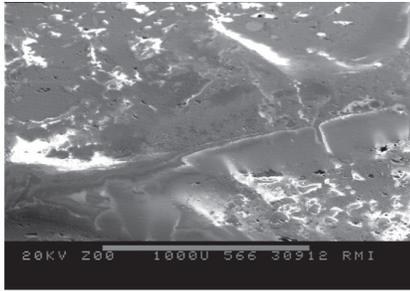
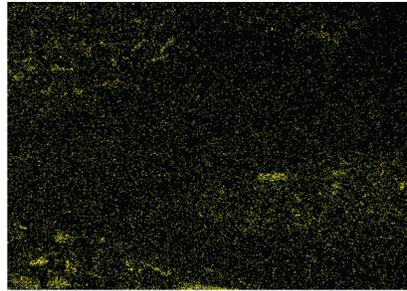


Phosphorous

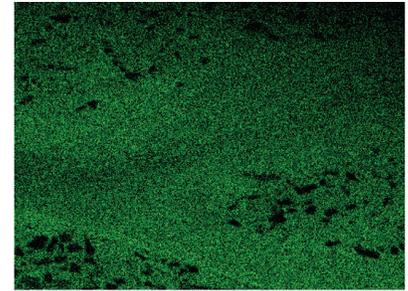


Silica

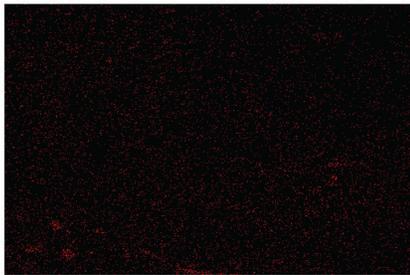
**Figure 17.** Elemental maps of cuticle thin section of *Tetracarcinus subquadratus* (KSU-002). Aluminum and silica are concentrated on the outer margin of the cuticle. Calcium and phosphorous are also present in a relatively high abundance in the surrounding sediment as well as very small traces of iron. The absence of data on the lower margin of the cuticle is likely caused by a shadowing effect from uneven sampling surface.

*Linuparus* sp.

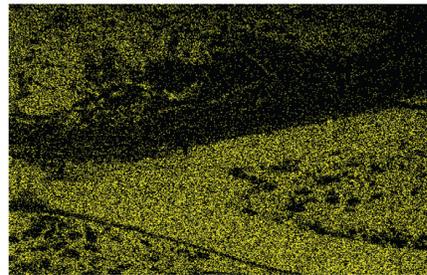
Aluminum



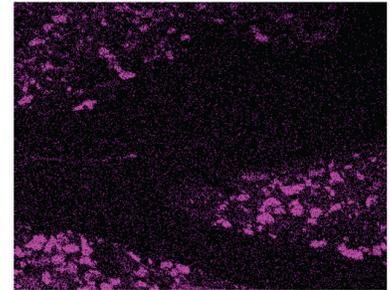
Calcium



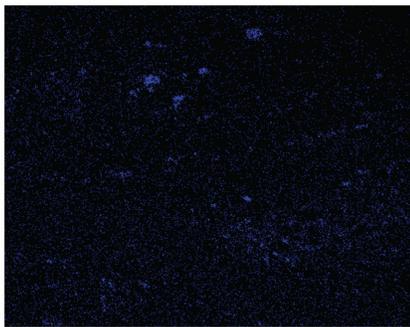
Potassium



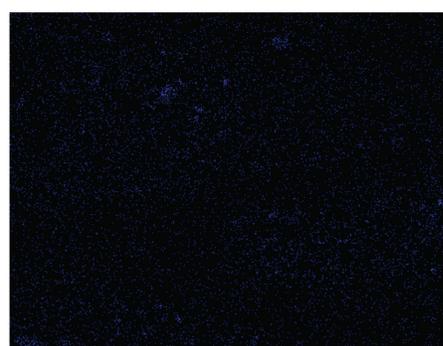
Phosphorous



Silica



Sulfur

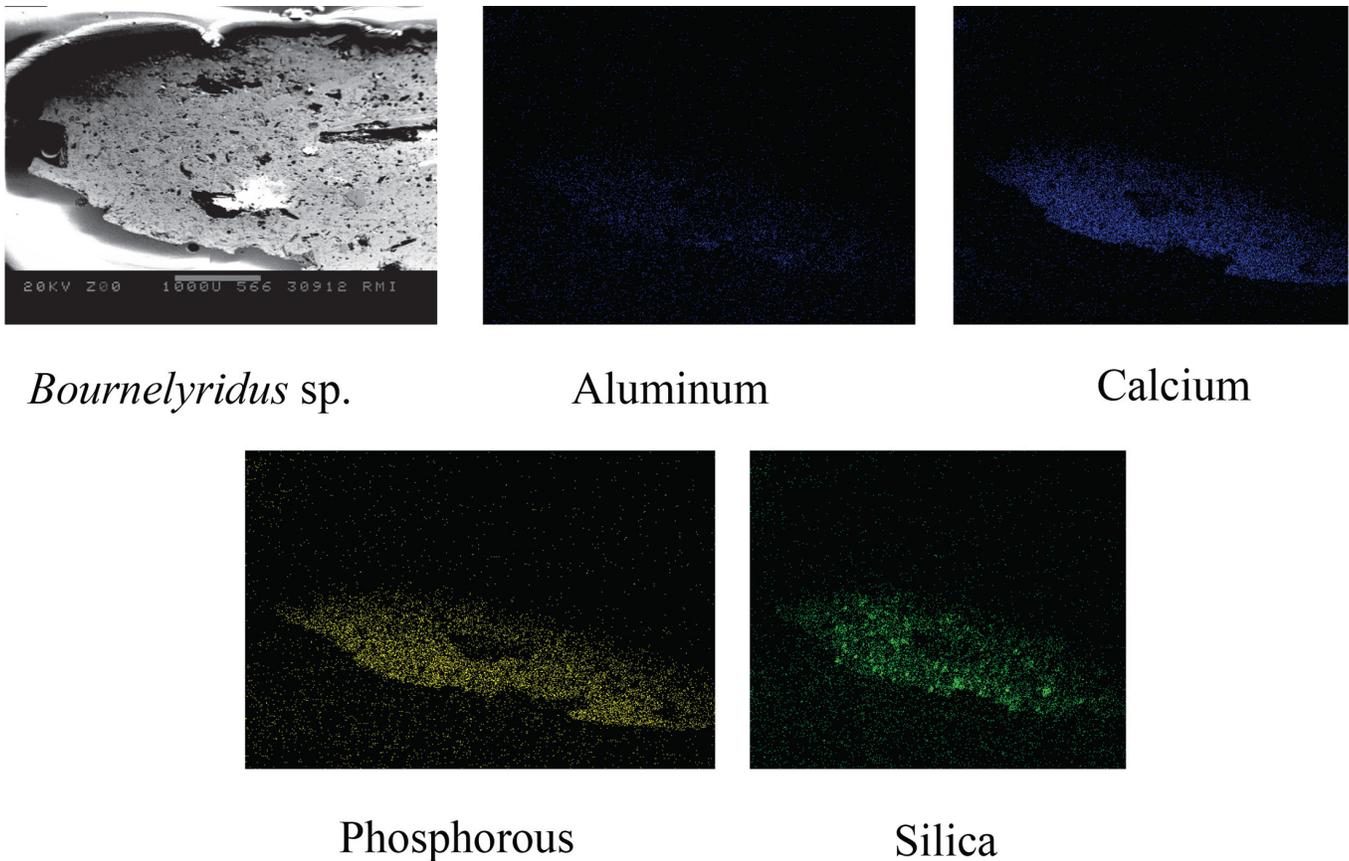


Iron

**Figure 18.** Elemental maps of cuticle thin section of *Linuparus* sp. (KSU-015). Calcium and phosphorous are concentrated in the cuticle, silica and aluminum are also present in a relatively high abundance in the surrounding sediment as well as traces of sulfur, potassium, and iron.

light with a vibrant yellow and orange color in localized places. These specimens also had small flecks that fluoresced bright blue. When the cuticle was observed in thin section, the presence of silica and aluminum is not apparent (Figs. 22–23). Further examination of the location of these minerals in elemental maps indicates that the cuticle is not replaced by silica and aluminum

but rather the exterior of the cuticle is covered in a thin layer of clay minerals (Fig. 18). The highly friable and impervious nature of the included sediments made impregnation of specimens very difficult and resulted in charging of the samples when analyzed in the SEM. We concluded that though the preservational style appears variable in hand sample, these differences are likely relicts



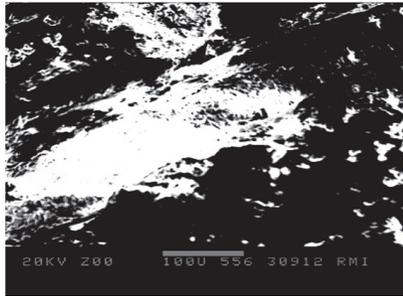
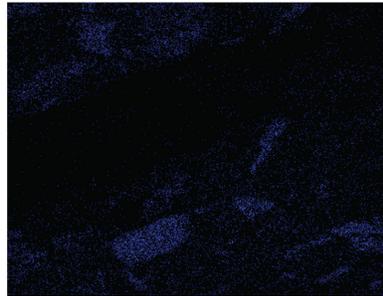
**Figure 19.** Elemental maps of cuticle thin section of *Bournelyridus* sp. (KSU-017). Calcium and phosphorous are concentrated in the cuticle but preservation is of a lesser degree than illustrated in other specimens, silica and aluminum are also present in a lower abundance in the surrounding sediment.

of weathering of phosphatized remains to clay minerals and do not indicate variability due to epibionts, exo- vs. endo-cuticle, taxon, etc. Because of this interpretation, and to avoid further loss of fossil material until more effective methods are developed, further examination of the elemental components of preserved cuticle was not pursued.

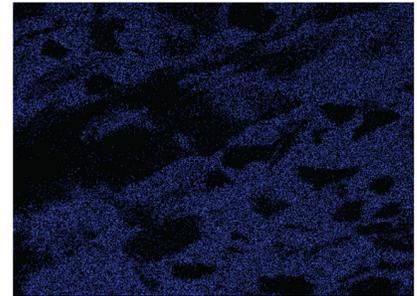
SEM images suggest that internal, microscopic structure of cuticle is preserved in most specimens, regardless of species and physical variability in cuticular morphology or apparent preservation differences (Figs. 17–21). This can be seen as light and dark laminations of cuticle, fibrous, vertical minerals perpendicular to “laminations” of in-filled spaces between pore canals, and microscopic patterns on external surface of cuticle of *Dakoticancer australis* (Fig. 24).

Though some decapods are preserved in concretions and some cuticle illustrates concoidal fracture using scanning electron microscopy, concretions do not show similar qualities to concretions containing decapods found in correlative beds in the Bearpaw Shale of the Western Interior Seaway, indicating dissimilarity in preservation and environment (Feldmann et al., 2012).

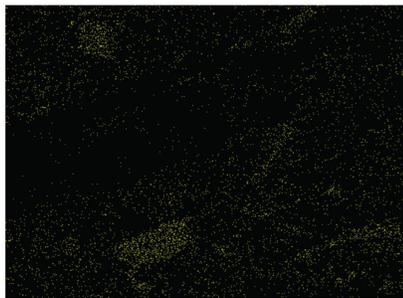
It is common in the fossil record to find specimens of lobsters preserved with the pleon in the contracted state. This is observed as the pleon curled underneath the body and the telson closest to the most anterior portion of the animal. Most specimens of *Linuparus* are not preserved like this but with the pleon outstretched straight behind the body in a single plane. The specimen from Mr.

*Hoploparia tennesseensis*

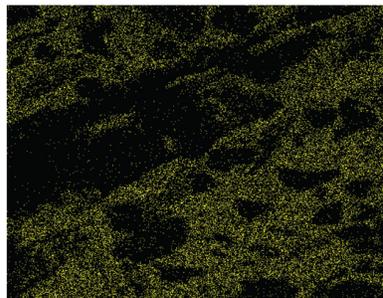
Aluminum



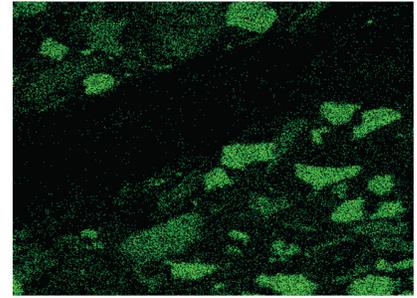
Calcium



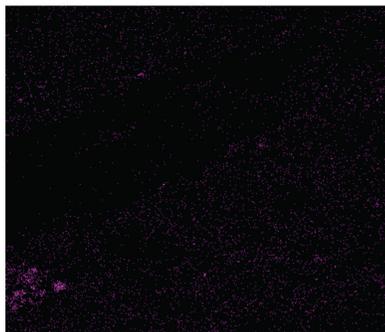
Potassium



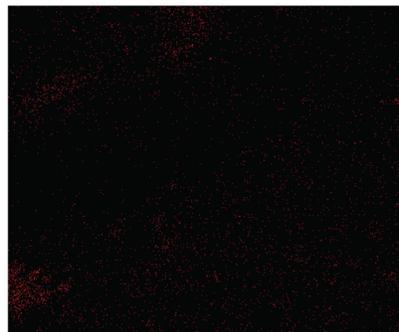
Phosphorous



Silica



Sulfur

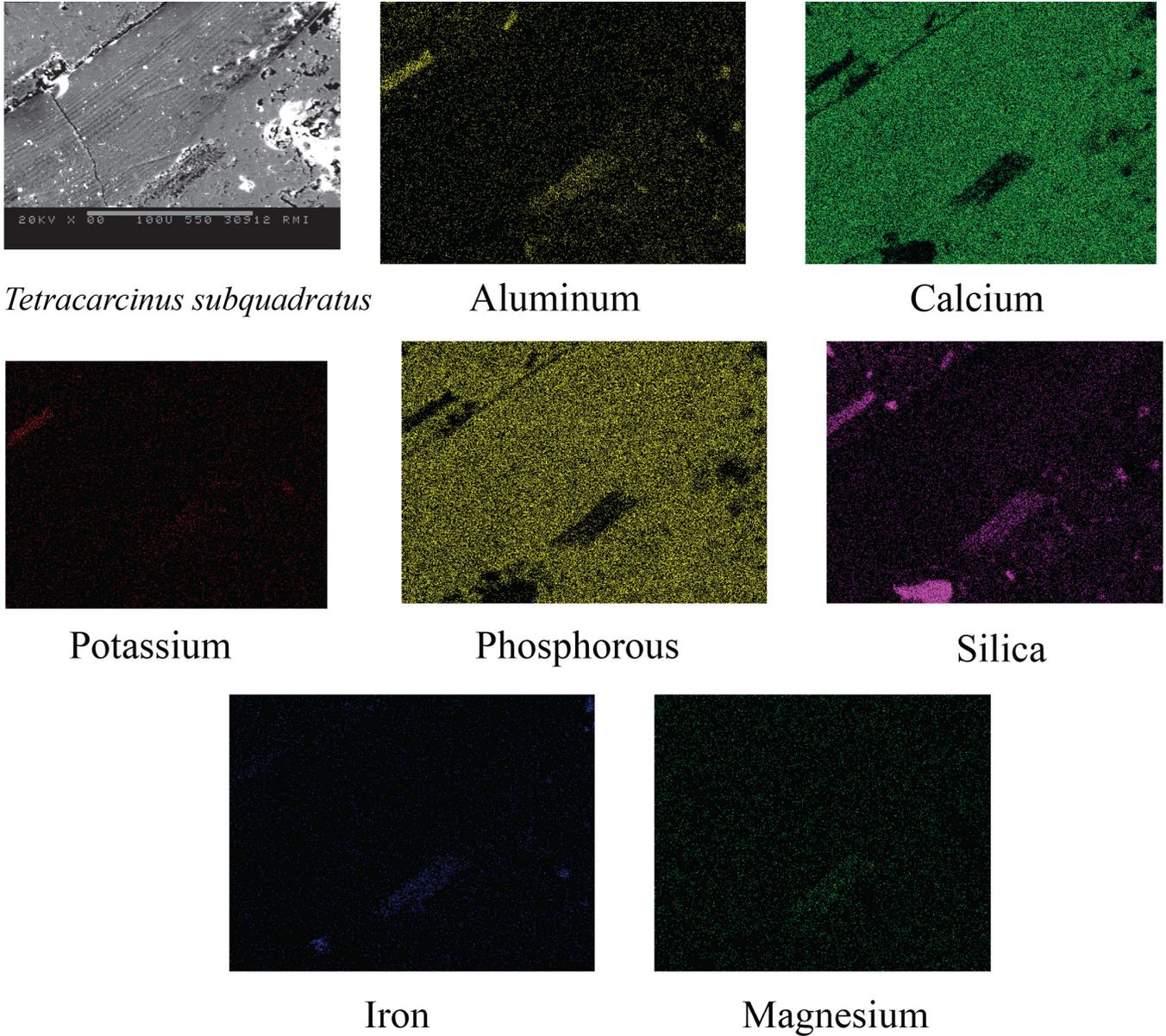


Iron

**Figure 20.** Elemental maps of cuticle thin section of *Hoploparia tennesseensis* (KSU-016). Calcium and phosphorous are concentrated in the cuticle. Large white spot has formed due to charging of the specimen and is therefore causing a shadow in the elemental data. Silica and aluminum are also present in a relatively high abundance in the surrounding sediment as well as traces of sulfur, potassium, and iron.

Keyes's personal collection is even more peculiar because it has both the telson and the most anterior end of the pleon upturned to point dorsally (Fig. 7E–G). This concave upward flexure of the pleon is not possible with the ventral tissue intact. Because of this, fossilization must have occurred post rigor mortis. As the more flexible tissue was broken

down by bacteria, the pleon would be physically capable of bending in the upturned direction. The hypothesis is difficult to confirm because the venter of the pleon is not preserved. The excellent preservation of fine details such as delicate spines makes the identification of this post rigor mortis fossilization even more impressive.

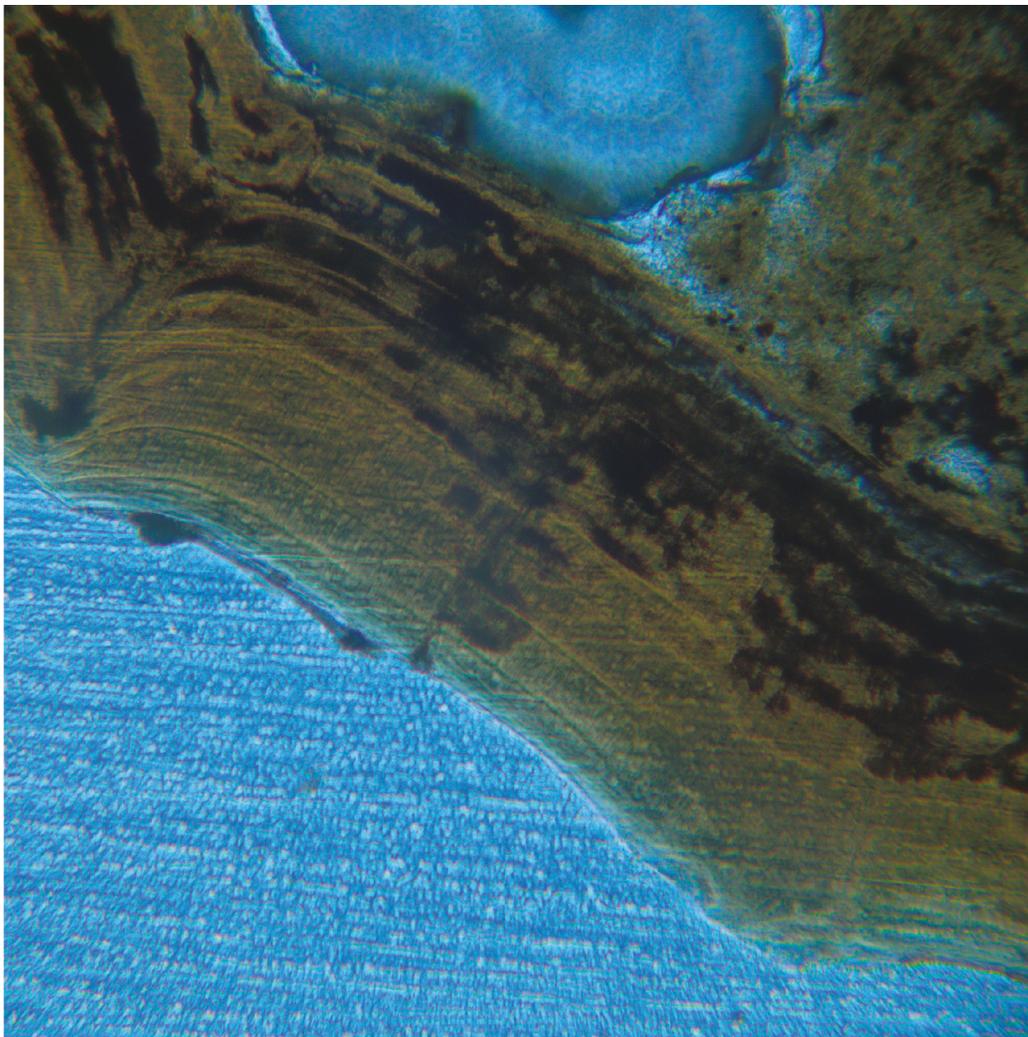


**Figure 21.** Elemental maps of cuticle thin section of *Tetracarcinus subquadratus* (KSU-002). Calcium and phosphorous are concentrated in the cuticle, silica and aluminum are also present in a relatively high abundance in the surrounding sediment as well as traces of magnesium, potassium, and iron.

Fossils found in the outcrop exhibit no preferred orientation. Carapaces of larger crabs sometimes have partial legs attached; it is also common at the Blue Springs locality to find more complete crabs closely associated with disarticulated leg sections. Some carapaces lack the sternum but have claws and legs concentrated in the cavity of the underside of the carapace

where the sternum would be. Many claw and leg fragments are eroded from the outcrop.

Bishop and Williams (1991) discussed the potential for preservation of molts as well as corpses in the fossil record. They suggested that carapaces preserved with attached sterna indicate that they are the remains of corpses, not molts (Bishop and Williams, 1991:458). Bishop (1972)

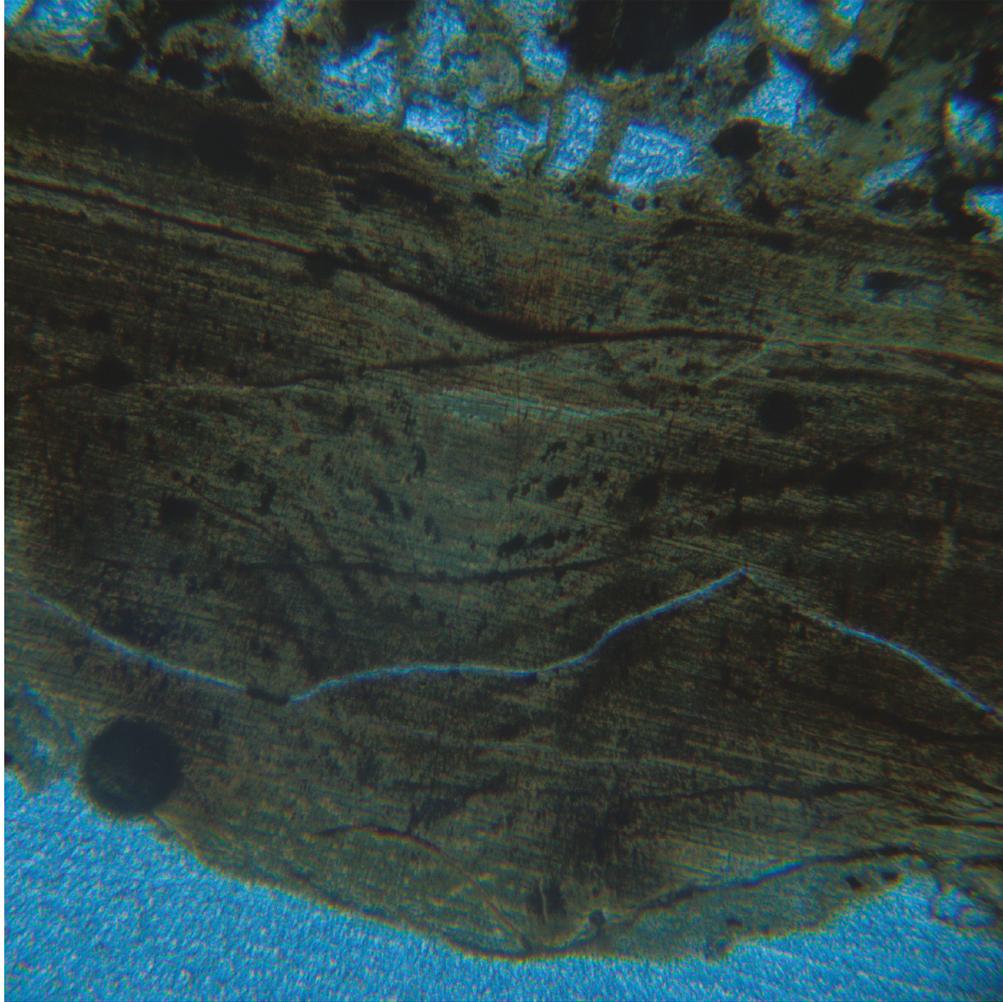


**Figure 22.** Thin section of *Tetracarcinus subquadratus* carapace cuticle, illustrating phosphatization of endocuticle with laminations and pore canal visible (KSU-002). Magnification 10 X 40.

also described a configuration of the carapace, where it is somewhat articulated and indicative of a molt as well, referred to as Salter's position, where the "carapace is lifted and flipped forward, making an angle of about 90° with the sternum. Molts are distinguished from corpses by noting that the carapace has split along the pleural sutures, and the carapace lying outside of the pleural sutures are still attached to the sterna plastron," (Bishop, 1972:633). There are no specimens from the Coon Creek Formation observed in Salter's position, but many specimens are internal molds of the carapace but not the sternum, and therefore may indicate preservation of a molt.

#### PALEOBIOGEOGRAPHIC COMPARISONS

Decapod taxa are compared at the species level throughout correlative units in North America on the basis of general geographic range during the Maastrichtian. Species found only in the Coon Creek Formation (Mississippi Embayment) include: *Hoploparia tennesseensis*, *Hoploparia mcnairiensis*, *Linuparus keyesi* sp. nov., *Linuparus* sp., *?Palaeopetrochirus enigmus*, *Seorsus wadei*, *Bournelyreidus ericksoni* sp. nov., and *Cristipluma mississippiensis*. Species that occur in the Coon Creek Formation as well as the Atlantic Coastal Plain include: *Hoploparia georgeana*, *Mesostylus mortoni*, *Tetracarcinus subquadratus*, *Avitelmessus*

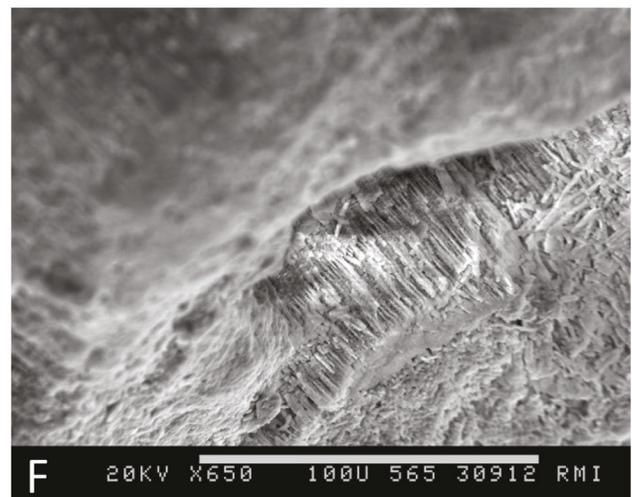
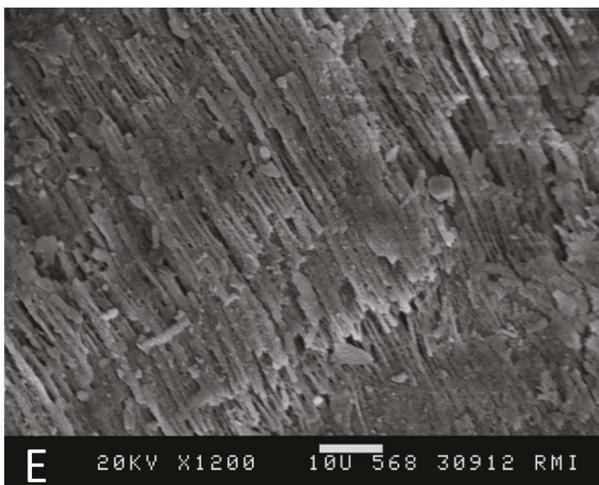
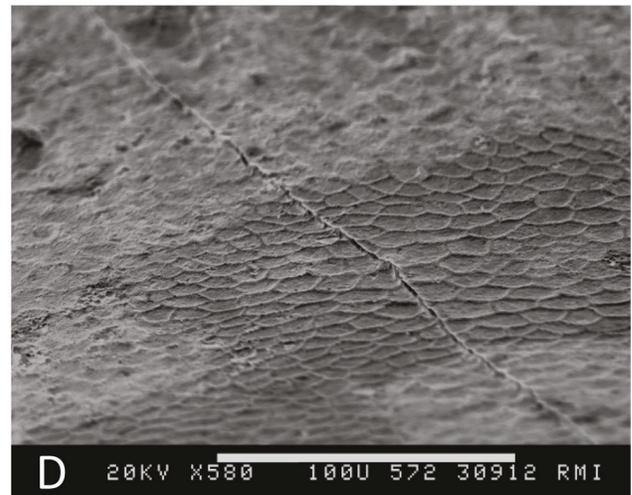
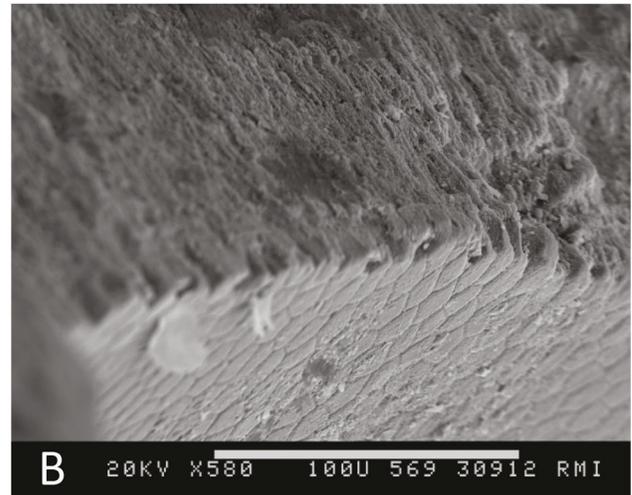
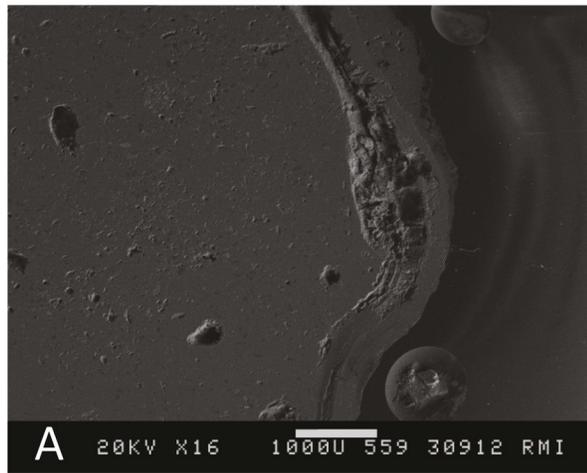


**Figure 23.** Thin section of *Dakoticancer australis* carapace cuticle, illustrating phosphatization of endocuticle with laminations visible (KSU-001). Magnification 10 X 40.

*grapsoideus*, *Cretacorantina testacea*, *Lythophylax flectus*, and *Latheticocarcinus atlanticus*. Species that occur in the Coon Creek Formation as well as the Western Interior Seaway include: *Tetracarcinus subquadratus* and *Avitelmessus grapsoideus*. Species that occur in the Coon Creek Formation as well as the Gulf Coastal Plain: *Mesostylus mortoni*, *Dakoticancer australis*, *Avitelmessus grapsoideus*, and *Prehepatus harrisi*. These shared species from surrounding North American localities supports our hypothesis that the Mississippi Embayment acted as an ecotone during the Maastrichtian.

Schweitzer and Feldmann (2005) discussed the presence of most lineages across the Cretace-

ous–Paleogene boundary. The extinctions present in decapods at this time are actually pseudoextinctions; in fact, the Late Cretaceous is a time of adaptive radiation in Central America. This may be attributed to the composition of decapod exoskeletons, which are more robust to fluctuations in the Carbonate Compensation Depth as opposed to mollusks (Schweitzer and Feldmann, 2005). The Late Cretaceous was rather a time of rapid evolution and faunal turnover, with the greatest number of last occurrences of genera (1/3 of the total genera known from the Late Cretaceous) taking place in the Maastrichtian. About half of these last occurrences were in Central America



**Figure 24.** SEM images of *Dakoticancer australis* claw (KSU-019). Cross section illustrating cuticle on right-hand margin of specimen (A); outer-most layer of endocuticle illustrating micro-ornamentation on lower half of image and pore infilling of endocuticle on upper half of image (B); pore canal opening, dark spot at center of image (C); endocuticle ornamentation (D); mineralization of spaces between pore canals, high magnification (E); and mineralization of spaces between pore canals, low magnification (F).

(Schweitzer and Feldmann, 2005). New species described herein are both first and last occurrences as there are no known specimens from other formations, but finding species that survive across the K–Pg boundary will continue to be difficult due to the paucity of Paleocene rocks.

The presence of species at high and low latitudes, such as *Avitelmessus grapsoideus* and *Tetracarcinus subquadratus*, may be a good example of ecological generalists or eurytypic species surviving in the Western Interior Seaway as well as Atlantic Coastal Plain and Mississippi Embayment. Though geographically diverse, there is no evidence that these mono-specific genera survive the K–Pg extinction.

Cope et al. (2005) described the fauna of the Clayton Formation (Paleocene, Danian) from the northeast of the Mississippi Embayment in Olmsted, Pulaski Co., Illinois. Four genera: *Linuparus*, *Hoploparia*, *Paguristes*, and *Mesostylus*, are reported from the Clayton Formation and also occur in the Coon Creek Formation. Of those four genera, two species, *Hoploparia tennesseensis* and *Mesostylus mortoni*, occur in the Maastrichtian and Danian of the Mississippi Embayment and are the only current evidence for K–Pg survival in this study.

Another noteworthy biogeographic comparison is the absence of intersex characters in the Dakoticanceridae in all other localities and species. Bishop (1974) first described these qualities in *Dakoticancer overanus* of the Western Interior Seaway, which was subsequently studied further by Jones (2013). The species is found only in the Western Interior Seaway and is the only species in the family with this morphological variation.

The first intersex specimen was found at Sitting Bull locality near Mobridge, South Dakota (specimen number USNM 173542) (4-2007) (Bishop, 1974:215). A new example of *Dakoticancer* intersex was discovered in 1976 by Mr. Harry Mendryk at the Mobridge locality. This specimen had female gonopores at the base of the fourth leg and male gonopores at the base of the fifth leg which is different from the previously described intersex configuration (Bishop, 1976:196). Jones

(2013) described other forms of intersex specimens, which were also from Mobridge. Coon Creek Formation specimens of *Dakoticancer australis* yielded 75 specimens with sterna preserved, of which 28 were identified as female and 47 were identified as male. This ratio of more males than females also occurs in the *Dakoticancer overanus* population in Mobridge (Jones, 2013). Of these 78 specimens, none possessed intersex characters. The preservation of Coon Creek specimens was quite different from those of Mobridge; the Mobridge specimens are generally preserved in individual concretions and the Coon Creek specimens, for the majority, weathered out of the rock unit readily. Because of this, gonopores are often damaged or the cuticle from the area is missing entirely. Missing gonopores from the record of Coon Creek material could be forming a preservation bias and could be the reason that this intersex pattern is not observed in Coon Creek specimens of *Dakoticancer australis* at this time.

## CONCLUSIONS

Two new species, *Linuparus keyesi* and *Bournelyridus ericksoni* are described from the Coon Creek Formation. The Coon Creek Formation decapods are very well preserved, possessing ornamentation and cuticle. In some specimens the cuticle of *Tetracarcinus subquadratus* and fragments of *Linuparus* sp. are replaced with silica. These specimens also illustrate fine laminations of cuticle in cross section. The preservational style of decapods in the Coon Creek Formation does not possess the same microbial sheath structure described by Feldmann et al. (2012) from the Western Interior Bearpaw Shale specimens. Seventeen species are recognized from the Coon Creek Formation: *Hoploparia tennesseensis*, *Hoploparia mcnairensis*, *Linuparus keyesi*, *Linuparus* sp., *?Palaeopetrochirus enigmus*, *Seorsus wadei*, *Bournelyreidus ericksoni*, *Cristipluma mississippiensis*, *Hoploparia georeana*, *Mesostylus mortoni*, *Tetracarcinus subquadratus*, *Avitelmessus grapsoideus*, *Cretacorantina testacea*, *Lithophylax flectus*, *Dakoticancer australis*, *Prehepatus harrisi*, and *?Latheticocarcinus atlanticus*. Eight species of decapod occur exclusively in the Coon Creek

Formation. Seven species of decapod co-occur in the Coon Creek Formation and the Atlantic Coastal Plain, four co-occur in the Coon Creek Formation and Gulf Coastal Plain, and two co-occur in the Coon Creek Formation and Western Interior Seaway. The presence of a diverse decapod fauna in the Coon Creek Formation is congruent with the assessment of Schweitzer and Feldmann (2005) that evolution and extinction rates were high in the Late Cretaceous, and rapid faunal turnover, adaptation, and radiation were commonplace in Central America during the Maastrichtian.

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