A NEW GENUS AND SPECIES OF DROMIID CRAB (DECAPODA, BRACHYURA) FROM THE MIDDLE EOCENE OF SOUTH CAROLINA

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ABSTRACT

A new genus and species of brachyuran decapod crustacean of the family Dromiidae, *Quinquerugatus holthuisi*, is described from the middle Eocene Tupelo Bay Formation and Santee Limestone in South Carolina. The new genus and species is morphologically similar to the dromiid *Cryptodromia* spp. but differs from them in having a more rounded carapace, well developed triangular rostrum, better defined grooves, and strong lateral spines.

RÉSUMÉ

Un nouveau genre et une nouvelle espèce de crustacé décapode brachyoure de la famille des Dromiidae, *Quinquerugatus holthuisi*, sont décrits de l'Eocène moyen de Tupelo Bay Formation et Santee Limestone en Caroline du Sud. Ce genre et cette espèce, sont morphologiquement similaires aux Dromiidae *Cryptodromia* spp. mais ils en diffèrent par une carapace plus arrondie, un rostre triangulaire bien développé, des sillons mieux définis et de fortes épines latérales.

INTRODUCTION

The middle Eocene Atlantic and Gulf Coast formations yield an exceptional decapod fauna. Rathbun (1935) described 10 families and more than 50 species from different formations on the Atlantic and Gulf Coast but only one family and three species from the Tupelo Bay Formation. Blow & Manning (1996)

Studies on Malacostraca: 255-267

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published diagnoses of 25 species in 23 genera of decapods from Eocene rocks in North Carolina and South Carolina. Feldmann et al. (1998) described 10 species of brachyuran decapods, including four new species, from the Eocene Castle Hayne Formation in North Carolina.

The purpose of the present work is to describe a new genus and species that occurs in both the Tupelo Bay Formation and Santee Limestone in South Carolina. Charles Lyell (1845) is considered the first to have recognized the calcareous marine deposits as Santee Limestone in South Carolina. In 1952, Cooke & MacNeil redefined the Santee Limestone and McBean Formation, restricting them to the *Cubitostrea sellaeformis* zone. All of these papers used the name Santee Limestone to refer to the hard, moldic middle Eocene limestone in South Carolina. The softer, younger limestone that was called Castle Hayne by Cooke & MacNeil (1952) was referred to as the Cross Member of the Santee Limestone by Campbell (1995).

Sanders & Katuna (2000) informally proposed that the Cross Member be elevated to the rank of formation. Geisler et al. (2005) proposed the name Tupelo Bay Formation to embrace both the Cross Member and an additional unit called the Pregnall Member. The Cross Member of the Tupelo Bay Formation overlies the Santee Limestone and is overlain by the late Eocene Pregnall Member of the Tupelo Bay Formation and the Harleyville Formation (Geisler et al., 2005) (fig. 1).

The Santee Limestone is exposed in the Martin Marietta Jamestown Quarry (fig. 2) and is composed of highly fossiliferous limestone that grades into yellowish sands and thin sandstones of the McBean Formation (Colquhoun et al., 1969). The Santee Limestone is indurated and very moldic, with common glauconite (Campbell, 1995). It is typically gray with orange iron stains and has an abundant fauna represented by bivalves, gastropods, bryozoans, echinoids, brachiopods, corals, and crabs, as well as some vertebrates (mainly shark teeth) (Bishop & Palmer, 2006).

The Tupelo Bay Formation (fig. 1) is exposed in the Martin Marietta Berkeley County Quarry (fig. 2) (across from the Martin Marietta Orangeburg Quarry) and is mainly represented by a highly fossiliferous limestone. The Tupelo Bay Formation is less indurated than the Santee Limestone, and unlike the Santee Limestone, has a creamy white color. Boulders often have a thin, black coating, and probably because of its poor induration, it has fewer well-preserved molds of decapods than the Santee Limestone (Campbell, 1995). In both the Santee Limestone and Tupelo Bay Formation, bryozoans are the most common faunal element in the formation represented by more the 60 species

Ma	Series/ subseries		European Stage	NP Zone	Carbonate Units on South Carolina Coastal Plain
35 -		LATE	Priabonian	21	Drayton Formation Parker's Ferry Formation
				18	Harleyville Formation
					75 11 3 7 1
40-	EOCENE	MIDDLE	Bartonian	17	Pregnall Member Cross Member Lubelo Bay Formation
			Lutetian	16	Santee Limestone
45 –				15	Warley Hill Formation
				14	

Fig. 1. Chronostratigraphic sequence of middle and upper Eocene carbonate units on the Coastal Plain of South Carolina. Modified from Geisler et al. (2005).

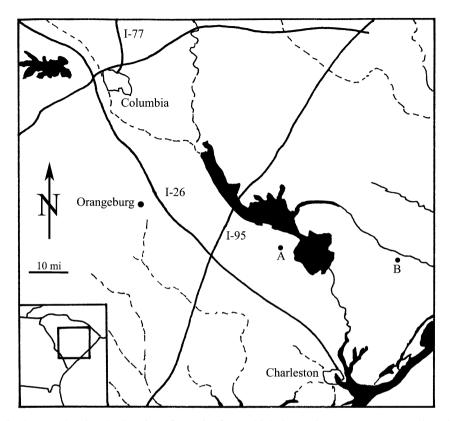


Fig. 2. Map showing the location of quarries from which decapod crustaceans were collected: A, Martin Marietta Berkeley Quarry; B, Martin Marietta Jamestown Quarry. Modified from Campbell (1995).

(Bishop & Palmer, 2006). The Santee Limestone is interpreted to have been deposited in a warm, clear, offshore environment (Bishop & Palmer, 2006).

Within the Santee Limestone, decapods have been collected as broken carapaces, claws, or pereiopod elements. Bishop and Palmer (2006) hypothesized that this was caused by a high energy environment in which the decapod remains could have been fragmented. The decapod fossils described here have a well preserved carapace that has weakly developed grooves, partial orbits, rostrum and the lateral spines.

The classification used follows that of Schweitzer et al. (2010).

COLLECTING LOCALITIES

The decapod crustaceans described here were collected by Billy Palmer in 1996. One of the specimens was collected from the middle Eocene Tupelo Bay Formation in the Berkeley Quarry exposure and the other from the middle Eocene Santee Limestone in the Jamestown Quarry (fig. 2). The quarries are situated in Berkeley County, South Carolina: Martin Marietta Berkeley ("Cross") Quarry on the east side of County Road 59, 2.4 km (1.5 mi) south of South Carolina Routes 6 and 45, USGS Chicora 15' quadrangle, 33°21.6′N 80°13.4′W, and Martin Marietta Jamestown Quarry, 33°16′0.81″N 79°39′13.88″W.

SYSTEMATICS

Order DECAPODA Latreille, 1802

Suborder PLEOCYEMATA Burkenroad, 1963

Infraorder BRACHYURA Linnaeus, 1758

Section DROMIACEA De Haan, 1833

Superfamily DROMIOIDEA De Haan, 1833

Family DROMIIDAE De Haan, 1833

Subfamily DROMIINAE De Haan, 1833

Included fossil genera. — *Ameridromia* Blow & Manning, 1996; *Cryptodromia* Stimpson, 1858; *Dromia* Weber, 1795; *Dromidia* Stimpson, 1858; *Epigodromidia* McLay, 1993; *Kerepesia* Müller, 1976; *Lucanthonisia* Van Bakel, Artal, Fraaije & Jagt, 2009; *Noetlingia* Beurlen, 1928; *Pseudodromilites* Beurlen, 1928; *Quinquerugatus* n. gen.

Diagnosis. — See Guinot & Tavares (2003: 49).

Discussion. — Placement of some fossil genera either in Dromiidae or Dynomenidae is very difficult because of the absence of preservable diagnostic characters of the abdomen, sternum and pereiopods that clearly distinguish these families. The key characters that can differentiate the two families are the small fifth pereiopod with an extra small dactylus and four epipodites (McLay, 1999), but these characters are applicable only to living specimens. The fossils typically do not have these appendages preserved. The main feature preserved on the dorsal carapace that can provide a distinction between these two families lies in the orbits. In Dromiidae, the lower orbital margin is not visible except possibly as a lower orbital spine, whereas in Dynomenidae, the lower orbital margin extends beyond the upper orbital margin and is visible when viewed

dorsally. The specimens described here reveal only a lower orbital spine when viewed in dorsal aspect. Placement of fossil genera either in Dromiidae or in Dynomenidae is still contentious because of the absence of clear additional carapace distinctions between these two families.

The new genus described here has been placed in the Dromiidae because it has a pentagonal carapace, it is convex transversally and longitudinally, lateral margins marked with teeth, and has well developed branchial grooves. The frontal margin is broadly triangular, and the carapace is as wide as long, smooth, and moderately convex, characters that make the new genus and species close to *Cryptodromia* spp. The anterolateral margin of *Quinquerugatus holthuisi* n. gen., n. sp., is similar to the anterolateral margin of *Cryptodromia* because both margins are slightly convex, and bear three, small spines. The branchiocardiac groove is poorly defined, subparallel to the cervical groove, and extends onto the flanks. All these are characteristics of *Cryptodromia*. However, *Quinquerugatus* differs from *Cryptodromia* in having a well developed tridentate rostrum, a better defined cardiac region, greater distance between the cervical and branchiocardiac groove, and just one small spine on the subhepatic region.

Quinquerugatus n. gen.

Type species. — *Quinquerugatus holthuisi* n. gen., n. sp., by monotypy. Included species. — *Quinquerugatus holthuisi* n. gen., n. sp.

Diagnosis. — Pentagonal carapace; short, triangular rostrum with three spines; weakly developed cervical groove, more defined axially than laterally, concave forward; branchiocardiac groove defined most strongly on the lateral third, subparallel to cervical groove, curving around the posterior margin of the cardiac region; five lateral spines including outer orbital spine.

Etymology. — The generic name is derived from the Latin words *quinque* which means pentagonal and *erugatus* which means smooth, to reflect the outline of the carapace and the lack of ornamentation.

Discussion. — Specimens of the new taxon have a series of characters which make them stand apart as a new genus. The carapace in *Quinquerugatus* is pentagonal and inflated transversally and longitudinally, subhepatic region is well defined and slightly inflated with one small spine. *Dromilites* has a subpyriform outline, is moderately arched transversely and almost flat longitudinally, and the subhepatic lobes are prominent with four tubercles laterally. The carapace outline in *Quinquerugatus* is different from that of *Noetlingia*, which has an ovoid outline and is strongly inflated, and *Epigodromia*, which

has a carapace that is longer than wide. In *Noetlingia*, the rostrum is long, and the central rostral spine is well developed and more elongated than the lateral spines. In *Quinquerugatus*, the rostrum is short, bearing two small nodes at the base forming, with the tip, an equilateral triangle. *Epigodromia* has well defined regions covered with small granules, a tridentate rostrum with a small median spine, prominent lateral spines, and it is rounded and covered by granules.

The rostrum is better developed in *Quinquerugatus* than in *Cryptodromia*. The branchiocardiac groove is almost a straight line close to the margin of the carapace in *Quinquerugatus* whereas in *Cryptodromia* spp. it is oriented toward the anterior. The distance between the cervical groove and branchiocardiac groove is much greater in *Quinquerugatus* n. gen. than in *Cryptodromia* spp.

The new genus *Quinquerugatus* is very close to *Lucanthonisia* Van Bakel, Artal, Fraaije & Jagt, 2009, in having a similar tridentate rostrum, similar orbits, and the same number and position of lateral spines. *Quinquerugatus* differs in having a more rounded outline, a less tumid carapace, a more pitted carapace, and more poorly defined grooves than does *Lucanthonisia*. The outer orbital spine is smaller in *Quinquerugatus* and more developed in *Lucanthonisia*. The cardiac region is moderately well defined, pentagonal with its apex oriented posteriorly, and bearing three low nodes in *Quinquerugatus* whereas in *Lucanthonisia* the cardiac region is not defined. All these distinct characters justify the specimens described to be assigned to a new genus. The similarity of *Quinquerugatus*, *Lucanthonisia* and *Cryptodromia* confirm the placement of *Lucanthonisia* in Dromiinae (Schweitzer et al., 2010).

Quinquerugatus holthuisi n. gen., n. sp. (fig. 3)

Diagnosis. — As for genus.

Description. — Relatively small crab with pentagonal carapace, width of holotype (14.0 mm) 97% of total length (14.4 mm); posterior margin poorly preserved; dorsal carapace inflated transversely and longitudinally, traversed by three transverse, weakly incised grooves; regions poorly developed or undefined. Fronto-orbital width 79% of total width measured at about midlength.

Rostrum short, with two small nodes at base, triangular, sulcate, strongly turned down, slightly depressed axially, spine on tip broken. Orbits small, ovate, with deep, elongate augenrest, separated from orbit by a low ridge.

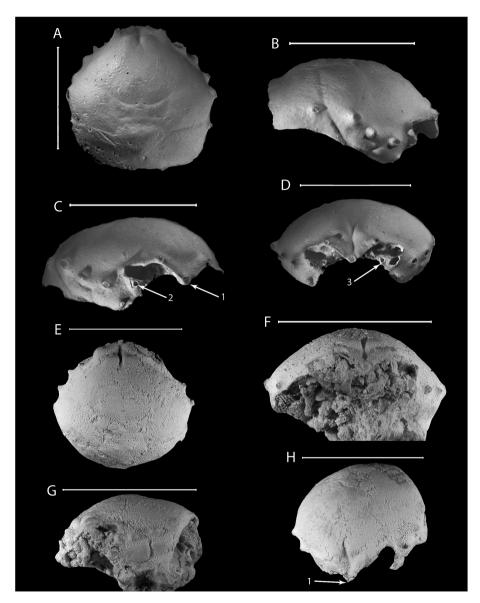


Fig. 3. Quinquerugatus holthuisi n. gen., n. sp.; PI 15222, Holotype; A, dorsal view; B, lateral view; C, anterolateral view; D, anterior view; specimen PI 15206, paratype; E, dorsal view; F, anterolateral view, G, lateral view; H, anterolateral view; arrow 1 = rostrum; arrow 2 = suborbital spine base; arrow 3 = broken suborbital margin. Scale bars equal 10 mm.

Orbits with small upper and lower outer orbital spines, lower orbital spine extends in advance of upper orbital margin.

Anterolateral margin weakly convex with three small, rounded spines excluding outer orbital spine, tips broken; posterolateral margin straight with one large spine just posterior to intersection of branchiocardiac groove with lateral margin; posterior margin poorly preserved, appears slightly concave.

Three transverse weakly incised grooves; cervical groove shallow, concave forward, becomes obscure laterally, more deeply concave axially than laterally; postcervical groove defined as straight line only in axial part of carapace; branchiocardiac groove defined most strongly on lateral third as a straight line curving around the posterior margin of cardiac region axially.

Epigastric regions well defined as two prominent circular nodes; mesogastric region weakly defined posteriorly; not differentiated from protogastric regions laterally; lacking anterior process; two small pits at midline mark gastric muscle insertion points; metagastric region poorly defined, generally rectangular; urogastric region poorly defined; cardiac region moderately well defined, pentagonal with apex oriented posteriorly, with three low nodes, two at midlength of region, other at posterior termination; intestinal region poorly defined, slightly depressed; protogastric and hepatic regions not differentiated; subhepatic region well defined, slightly inflated with one small spine; epibranchial region poorly defined anteriorly and moderately defined posteriorly, very large, almost equal to metabranchial; metabranchial region rectangular, moderately well defined anteriorly, posterior part not preserved.

Flanks subvertical, converge ventrally. Cervical groove continues anteriorly on flank until midheight of flank where it makes sharp postero-ventral turn; branchiocardiac groove extends toward anterior on flank and meets antennar groove.

Abdomen and appendages not preserved.

Types. — The holotype, PI 15222, and paratype, PI 15206, are housed in the Charleston Museum, Charleston, South Carolina.

Locality and stratigraphic position. — The holotype was collected from the middle Eocene Tupelo Bay Formation in the Martin Marietta Berkeley Quarry, and the paratype was collected from the middle Eocene Santee Limestone in the Martin Marietta Jamestown Quarry.

Etymology. — The trivial name honors the late Dr. L.B. Holthuis in recognition of his encyclopedic knowledge of the Decapoda, meticulous work, and generous personality.

Discussion. — This is the third occurrence of the Dromiidae in either the Santee Limestone or the Tupelo Bay Formation. The specimens described herein have a size and shape close to that of *Cryptodromia* spp., but the

development of the rostrum and the distinction of the carapace grooves make it stand apart as a new genus and species. The high quality of preservation permits distinguishing the weakly developed grooves and all of the small spines of which only one tip is broken. The abdomen, venter, and appendages are not preserved.

Because of the absence of clear distinction of carapace morphology between Dromiidae and Dynomenidae, most of the fossil species described in the Atlantic and Gulf Coast have been assigned to Dromiidae. Rathbun (1935) described a new species, *Dromilites americana*, with a broad distribution in Alabama and Texas. *Dromilites americana* was erected as type species for *Marydromilites* by Števčić (2005) but according to Ng et al. (2008), Števčić's name is not valid. According to the code Article 13.1.1 every new name published must, "be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon". Števčić (2005) does not provide descriptions of the new genus in his paper. Armstrong et al. (2009) revised *Dromilites americana* and placed it in the Goneplacidae MacLeay, 1838, referring this species to *Tehuacana* Stenzel, 1944, but the specimens they illustrated as being *Tehuacana americana* represent more than one species. In the absence of a better placement of *Dromilites americana*, we consider the placement of Rathbun (1935) as being correct.

In their paper, Blow and Manning (1996) described a new genus (*Ameridromia*) and two new species (*Ameridromia hyneorum* and *Dromidia bedetteae*) within the Dromiidae from the Santee Limestone in South Carolina.

Quinquerugatus holthuisi bears several characters that distinguish it from the species that Rathbun (1935) and Blow & Manning (1996) described in their papers. Dromilites americana (Rathbun, 1935) has very well developed and highly inflated mesogastric, protogastric, metabranchial, and epibranchial regions separated by incised grooves. The subrounded shape of the carapace with two inflated projections on the posterior margin in Dromilites americana is also different from the carapace of Quinquerugatus holthuisi which has a pentagonal shape. Dromilites americana has been difficult to place within a family because of the form of the sternum. Ameridromia hyneorum Blow & Manning, 1996, has a subrhombic carapace, narrower posterior margin, forward directed rostrum, fewer spines on the anterolateral margin, and moderately well-defined and more inflated regions compared to Quinquerugatus holthuisi which has a rostrum pointing downward, more spines on the anterolateral margin, and poorly defined regions. Dromidia bedetteae Blow & Manning, 1996, has a relatively longer carapace with spines oriented foreward, a

cardiac region with three small nodes, and a mesogastric region that is not subdivided.

As discussed above, the family-level placement of *Quinquerugatus* must be considered contingent until the fossil Dromiidae and Dynomenidae can be clearly separated. Examination of living decapods and a comparison of fossil Dromiidae, however, suggests no more reasonable placement.

ACKNOWLEDGMENTS

A.E. Sanders, Charleston Museum, Charleston, South Carolina, made the specimens available for study. Comparative material from the South Dakota School of Mines and Technology, Rapid City, South Dakota, and the Natural History Museum, London, United Kingdom, was made available by S. Shelton and C. Mellish, respectively. O. Franțescu, Kent State University, who assisted in the specimen description and gave invaluable assistance in compiling, editing, and formatting this paper. Reviews by C. McLay, University of Canterbury, New Zealand, and B. van Bakel, Oertijdmuseum De Groene Poort, The Netherlands, provided useful comments regarding systematic placement. Our thanks to these individuals. Museum work was funded by NSF EF-0531670 to Feldmann and Schweitzer.

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