

# The Dakoticancridae (Decapoda, Brachyura) from the Late Cretaceous of North America and Mexico

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## Contents

Introduction .....	237
Diagnosis of the family Dakoticancridae .....	239
Biology .....	239
General .....	239
Reproductive structures .....	239
Intersexuality of <i>Dakoticancer overanus</i> Rathbun, 1917 .....	239
Sensory apparatus .....	240
Feeding and food gathering .....	240
Burrowing .....	241
Decoration .....	241
Color patterns .....	241
Genera and species .....	241
Systematic keys to genera and species .....	246
Carapace key .....	246
Chelipede key .....	246
Cladistic analysis .....	246
Paleoautecology .....	247
General .....	247
Paleoautecology of <i>Dakoticancer overanus</i> .....	247
Paleoautecology of <i>Dakoticancer australis</i> .....	248
Paleoautecology of <i>Avitelmessus grapsoides</i> .....	249
Paleoautecology of <i>Tetracarcinus subquadratus</i> .....	250
Dakoticancroid crab assemblages .....	250
Origin of the Dakoticancridae .....	251
Cretaceous paleogeography .....	252
General .....	252
Western Interior Seaway .....	252
Mississippi Embayment .....	252
Northern Atlantic Coastal Plain .....	253
Western Gulf Coastal Plain and Mexico .....	253
Biogeographic range of dakoticancrids .....	254
Interpretation .....	254
References .....	254

## Abstract

The podotrematous crab family Dakoticancridae includes four genera: *Dakoticancer* Rathbun, *Tetracarcinus* Weller, *Avitelmessus* Rathbun, and *Seorsus* Bishop, all known solely from the Late Cretaceous of North America. *Lathelicocarcinus* Bishop, originally referred to the family, must be reassigned. Fine details of anatomy, preserved on specimens of *D. overanus* Rathbun and *A. grapsoides* Rathbun, permit description of genital openings and interpretation of functional morphology of appendages. Although one species, *D. australis* Rathbun, has been found associated with burrow structures, all were probably vagrant epifaunal animals on fine- to medium-grained siliciclastic substrata. Food was probably obtained by generalized low-level predation and scavenging. Results of a cladistic analysis are consistent with the stratigraphic data suggesting that *T. subquadrata* Weller is nearest the rootstock of the family and that other taxa within the family are derived from it.

## Introduction

The Dakoticancridae comprise a small, homogeneous group of podotrematous crabs that thrived in North America during the Late Cretaceous. They are sufficiently distinctive that they remain the sole family in the Dakoticancroidea. The name of the Dakoticancridae is derived from the family's type genus, *Dakoticancer*, which in turn is a name derived from the occurrence of the type species in South Dakota, (Dakota + Cancer = *Dakoticancer* – Dakoticancridae).

Weller described the first dakoticancroid crab in 1905 when he described *Tetracarcinus subquadratus* from New Jersey figured in 1905a, figs. 4, 5, and 6, and again in 1905b (same figures but

with 5 and 6 reversed) and four specimens figured in 1907 (Pl. III, figs. 16, 17, 18, and 19). Weller did not assign the crabs to a family at the time of definition (Weller, 1905a: 328) but subsequently referred it to the family Dromiacea (sic) (Weller, 1907: 852). He designated no holotype. These specimens were probably available to Henry B. Roberts (1962), who, as first revisor, designated the specimen illustrated by Weller, 1907, fig. 17 (NJSM #7788) and refigured by Rathbun, 1935 (pl. 10, fig. 16) as the best preserved of the “three syntypes”. This specimen can be considered the lectotype.

The family was named by Rathbun in 1917. She described *Dakoticancer overana* Rathbun, 1917, based upon specimens sent to the National Museum by W.H. Over, of the University of South Dakota, from collections made in Pennington County, South Dakota from rocks of the Upper Cretaceous Pierre Shale. In 1935, Rathbun (1935: 40) cited the type locality as being “West side, Missouri River, a short distance below Mobridge, eastern Corson County...”. In that same work, she described a new subspecies, *Dakoticancer overana australis* Rathbun, 1935, from the Ripley Formation, Union County, Mississippi. Rathbun (1937: 26) subsequently described *Dakoticancer olsoni*, but Bishop (1988a: 75) pointed out that this taxon did not belong in *Dakoticancer*.

In 1923, Rathbun described *Avitelmessus grapsoideus* from a large male specimen (USNM #31895) collected from the Peedee Formation by L.W. Stephenson (Coll. #3452) “Near Hudlers Landing, Cape Fear River, 30 1/2 miles above Wilmington...”. Rathbun assigned this crab to the Family Atelecyclidae (1923: 403). She subsequently (1926: 190-191, pls. 69-70) described and illustrated several additional specimens from western Tennessee. Kesling & Reimann (1957) further enhanced our knowledge of *Avitelmessus grapsoideus* by their description and illustration of a magnificently prepared specimen from the Coon Creek Formation, Coon Creek, Tennessee (Univ. Mich. Museum Paleont. #33406) that preserves the dorsal, anterior, and lateral aspects of the carapace and proximal pereopods, including both chelipedes. This specimen was described in great detail and illustrated by nine figures. A color pattern was

discerned and described. The assignment to the Atelecyclidae was maintained by their allusion to Rathbun’s assignment and by a comparison to the atelecyclid *Bellia picta* Edwards from the coast of Peru. It must be noted that subsequently *Bellia* has been assigned to the Bellidae and is no longer referred to the Atelecyclidae. *Avitelmessus* was subsequently assigned to the Dakoticancriidae (Glaessner, 1960). The genus remains a significant one in that it may be ancestral to another family. Glaessner (1969: 440) said: “A derivative of the Cancridea from a form like the Upper Cretaceous *Avitelmessus* (Dakoticancriidae, originally placed in Atelecyclidae) seems possible”.

To this list of taxa, Bishop added two additional genera: *Lathelicocarcinus* Bishop, 1988b, and *Seorsus* Bishop, 1988a. Both were based upon specimens collected from lower Maastrichtian deposits in Mississippi. The former genus is probably referable to a different family and the latter is known only from the type material. Subsequent work on the family has resulted in the elevation of *Dakoticancer overana australis* to species rank (Bishop, 1983b), as well as enhancement of our understanding of the biology and biogeography of the included species.

As presently understood, the group is small and of limited geologic and geographic scope, although specimens are abundant in fossil Lagerstätten in North America. Nonetheless, Glaessner (1980) suggested that the family might figure prominently in the evolutionary history of the decapod crustaceans and applied the taxonomy of Guinot (1977, 1978) that distinguished three major groups of crabs, the Podotremata, Heterotremata, and Thoractotremata, into which were integrated the traditional families of brachyurans. Glaessner’s interpretation of the evolution of the Brachyura documented three major times of adaptive radiations: Middle and Upper Jurassic, Mid-Cretaceous, and the Late Cretaceous-Early Paleogene. Implied, but not cited in the text description is a fourth radiation in the Eocene. No mention is made of the Dakoticancriidae on Glaessner’s chart, nor in its description; however, Glaessner (1980: 188) did cite it earlier in his text: “A similarity of the carapace with that of *Avitelmessus* Rathbun does not apply to its [*Pororaria eocenica* Glaessner, 1980] median portion

which shows a corystoid pattern. *Avitelmessus* is very close to *Dakoticancer*. [*Pororaria eocenica* has since been referred to the Portunidae (Feldmann & Maxwell, 1990)]. As Guinot (1978) remarked, these genera should not be assigned to the Dromiacea". This is an interesting situation, especially since Glaessner called attention to the Dakoticancridae as an unanswered problem (1960: 47): "... (3) the Upper Cretaceous Dakoticancridae including *Avitelmessus grapsoides* Rathbun and their relation to a group of large-eyed American crabs comprising *Archaeopus antennatus* Rathbun, "*Plagiolophus*" *vancouverensis* (Woodward), *Carcineretes* and *Ophthalmoplax*. Within this incompletely known group may lie the key to the genetic relationships of the Dorippidae and other Oxyrhynga, the Ocypodidae, and possibly the Portunidae". If, as Glaessner suggests, they are not assignable to the Dromiacea, where do the dakoticancroids belong? and, what was their origin? Guinot (1993) considered the Dakoticancridae to be the sole family within the Dakoticancroidea; this superfamily she considered to be separate and apart from both the Dromiacea and Archaeobrachyura.

### Diagnosis of the family Dakoticancridae

Carapace rectangular to transversely ovoid, almost as wide as long; rostrum narrow, bilobed; orbits well developed, rimmed; eyes sheltered by orbits when retracted; median part of cardiac groove weak, gastric regions hardly separated from cardiac intestinal region, branchiocardiac groove well developed, pleural sutures located on carapace sides; genital openings on coxae, female on third leg and male on the fifth; fifth legs much reduced. Sternum of female without longitudinal grooves. Chelae equal. (Rathbun, 1917: 385; Glaessner, 1969; Bishop, 1983c: 424.)

### Biology

#### General

Because of the absence of living forms, all inferences regarding the biology of the Dakoticancridae

must be made by interpretation of functional morphology, occurrence, and associations with other organisms. Where not stated, observations have been made on *Dakoticancer overanus* and are extended to the family. The number of specimens of that species and the completeness of that material far exceeds those of the other species.

#### Reproductive structures

The genital structures of *Dakoticancer overanus* lie on the coxae of the pereopods (Figs 1.4, 1.5); the oviduct perforations on the coxa of the third pereopod and the seminal ducts on the coxa of the fifth pereopods (Bishop, 1984b). The oviduct perforations are small oval openings near the posterior-proximal corner of the coxa, just in front of the articulator with the sternum. The orifice is nearly surrounded by a raised rim separating abundant setal pits on the outside from smooth exoskeleton on the inside. A specimen approximately 15.63 mm wide has oviduct perforations 0.15 mm in diameter. The seminal duct is small and usually not visible, normally being pressed against the second somite of the abdomen. Only when the coxa is flexed the seminal duct is visible.

Bishop and Sturgeon (in preparation) have demonstrated that the gonopores of *Avitelmessus grapsoides* are carried on the coxae of pereopod 3 (oviducts) or pereopod 5 (seminal duct). The oviduct perforations are small openings situated near the posterior articulation of the coxal articulation with the sternum and the seminal duct openings are found on the proximal side of the coxal articulation, often hidden if pereopod 3 is in a relaxed position.

#### *Intersexuality of Dakoticancer overanus Rathbun, 1917*

Primary and secondary sexual characteristics of *Dakoticancer overanus* and two known intersexes have been described by Bishop (1974, 1983a). These include the characteristics summarized in Table I.

Table I. Sexual characters observed on specimens of *Dakoticancer overanus*.

	Primary sexual characteristics	Secondary sexual characteristics
Females	Oviduct perforation in coxa of P <sub>3</sub>	Abdomen wide and ovate Sternum gently dished Sternal somites granulate on distal edges and a few along midline of each somite
Males	Seminal duct on coxa of P <sub>5</sub>	Abdomen narrow and rectangular Sternum medially troughed Sternal somites granulate mesially from distal edge to abdominal groove
Intersex 1	Oviduct? perforation on left P <sub>3</sub>	Abdomen intermediate and rectangular Granulate as in males
Intersex 2	Oviduct on coxae P <sub>4</sub> Seminal duct on coxae P <sub>5</sub>	Abdomen intermediate, rectangular Granulate as in males

### Sensory apparatus

The orbits of specimens referred to *Dakoticancer overanus* are inclined forward and outward and in front view are divided into two fossae, emarginated into anterior margin. The orbits are bounded by the rostrum mesially, by the extraorbital spine distally, and by a suborbital spine ventrally. They are rimmed, and the inner orbital fossa is defined by a separate, tuberculate inner orbital ridge extending from edge of rostrum to the inner orbital septum. It is set somewhat inside the outer orbital rim. The inner orbital fossa is larger than the outer fossa and bears spines on its lower and outer border, and has a suborbital drain or trough between. The eyestalks reach into the second fossa and taper medially; they are completely retractable for protection. Bishop (1984b) described a reticulated inner orbital sensory structure, the *orbital bulla reticularis*, situated on the outer surface of the inner orbital fossa.

One joint of the antenna has been seen just below the origin of the eye and is granulated. The second antenna is smaller and lies between first antenna and suborbital spine.

In *Avitelmessus grapsoideus* the orbital width is 44% of the total carapace width. The orbits are deeply incised into the anterior margin with the two fossae, rimmed by granulate emarginations; the inner orbital fossa is set ahead of the outer fossa and is separated from it by a trough, bounded

laterally by extraorbital and ventrally by suborbital spines. The eyestalks are long, bulbous proximally, and fold completely into the orbits.

### Feeding and food gathering

The chelipedes and claws of *Dakoticancer overanus* are equal, the palms are twice as long as high, fingers downturned. The third maxillipedes are broad and spatulate; the exognath is half as wide as the endognath, with ischia reaching beyond the line of the rostrum. The inner exopod margins are granulate. The endopods do not meet closely, are longitudinally grooved, and are finely granulate especially along the inner margin. The buccal frame margin is raised into a very narrow rim; the sides are parallel. The third maxillipede coxa/basis buttresses against the anteriormost, trapezohedral sternal somite and the carapace edge, where the buccal frame meets the pterygostomial margin.

In *Tetracarcinus subquadratus*, the chelae are equal, bulbous, and small, commensurate with carapace size. The palm is longer than high and smooth, except for the granulate upper surface.

The chelipedes of *Avitelmessus grapsoideus* are symmetrical, the claws are as long as high, with equal fingers carrying three molariform proximal teeth and a cutting edge distally. The merus, carpus, propodus, and dactylus are very granulate to spiny, especially on the outer surfaces.

### Burrowing

Evidence for burrowing by dakoticanrid crabs is equivocal. Bishop (1981) observed that, although *Dakoticanter overanus* is frequently associated with a few concentrically layered straight burrows, the burrows are neither abundant enough to be their domiciles nor are they large enough. He concluded, therefore, that the species was not an obligatory burrower.

However, molds of *D. australis* have been found inside burrows in the Portrerillos Formation in Nuevo León, Mexico. The diameters of the burrows range from 7 to 12 cm. These crabs, inferred by Vega & Feldmann (1991) to be exuviae, are preserved within burrows and have preserved appendages that remain articulated, but show dislocation of the ventral side of the carapace. To date, more than 20 specimens of *D. australis* have been collected at this locality, all within galleries and all with dislocated plastrons. This suggests a behavior of molting within burrows, which is uncommon for most brachyurans as molting inside burrows has not been observed frequently in extant crabs (Vega & Feldmann, 1991). *Dakoticanter australis* specimens from the Cardenas Formation in San Luis Potosí, east-central Mexico, are not found associated with burrows, and most of them possessed articulated appendages. It is possible that these latter specimens are corpses, rather than molts, or that the observed differences in preservation between assemblages of Nuevo León and San Luis Potosí reflect different taphonomic histories, rather than different molting behavior (Vega et al., 1995).

### Decoration

The pereopods of *Avitelmessus grapsoides* consist of the large chelipedes, three pairs of large, long, flattened, similarly-sized walking legs P2, P3, and P4, and a much reduced, ?subdorsal fifth pair of pereopods P5. Pereopods 2, 3, and 4 apparently are similar in size and shape. Each has a long merus which extends to be on line with the midpoint of the carpus on the chelipede. Each of these pereopods is flattened and oriented with the blade slanting backward and downward. The

leading and trailing edges of the meri are very spiny and their lower and upper surfaces (the surfaces that have to slide past as the crab walks) are smooth. The carpus and propodus of these ambulatory legs must have been about the same length as the merus. The fifth legs are much smaller than the others and appear to have been held posteriorly or even above the carapace, suggesting the possibility for carrying behavior in these crabs. The last pair of legs in *Dakoticanter overanus* are also slender and much reduced in length. They were probably carried in a subdorsal position as well.

### Color patterns

Kesling & Reimann (1957: 8) described patterns on the exoskeleton of *Avitelmessus grapsoides* as remnants of color markings or patterning, with the comment that “We strongly suspect that the colors have changed somewhat, but that the pattern has been faithfully retained”. The pattern described consisted of “...a medium background, dark spots and blotches, and light lines” ... with ... “preserved parts of the exoskeleton on the carapace...lighter on the mesogastric area and the ridges of the protogastric area...”. The carapace has dark umber spots, differing in size and shape, being larger and more elongate in concave parts on the protogastric, epibranchial, and hepatic regions. The carapace pattern has a microscopic pattern of labyrinthic light lines, seen only with magnification. The meri of the chelipedes are lighter below than above, the carpi are lighter on the side near the body and have dark blotches on their upper and distal surfaces and rosettes of small spots on their proximal surfaces. The chelae are lighter on the side near the body. The walking legs are lighter below with transverse dark blotches on their sides. These patterns are consistent with counter shading seen in many decapods that live in shallow water.

### Genera and species

As it is presently understood, the family Dakoticanteridae embraces four genera and five species known only from the continental interior and Atlantic and Gulf coastal plains of North America.

***Dakoticancer* Rathbun, 1917**

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 on third leg and male on the fifth; fifth legs much reduced. Chelae equal (after Bishop, 1983b: 424).

Type. – The type species of *Dakoticancer* Rathbun, 1917 is *D. overanus* by original designation.

Range. – *Dakoticancer* is known from 80 specimens in northeastern Mexico, 1 specimen from Bexar County, Texas on the western Gulf Coastal Plain, and is very abundant in the Mississippi Embayment and Western Interior Seaway in rocks of Campanian and Maastrichtian age and from Mexico (Vega & Feldmann, 1991; Vega et al., 1995).

Included species. – Two species have been described. *Dakoticancer overanus* Rathbun, 1917 is abundant in the Western Interior Seaway (ca. 5,000 specimens) and *Dakoticancer australis* Rathbun, 1926 is abundant (ca. 1,000 specimens) in the Mississippi Embayment and present in Texas and Mexico.

***Dakoticancer overanus* Rathbun, 1917**

(Figs. 1.1 - 1.5)

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.

Types. – The holotype (USNM 32055) and paratypes (USNM 32055a; 32056b-1) are deposited in the collection of the United States National Museum of Natural History, Washington, D.C. 20560.

Range. – *Dakoticancer overanus* is known from the Campanian and Maastrichtian Pierre Shale or equivalents in South Dakota, North Dakota, and Montana. The earliest known specimens are from the Zone of *Exiteloceras jenneyi* after which *D. overanus* assemblages become quite common in the mid-late Campanian and early Maastrichtian.

***Dakoticancer australis* Rathbun, 1935**

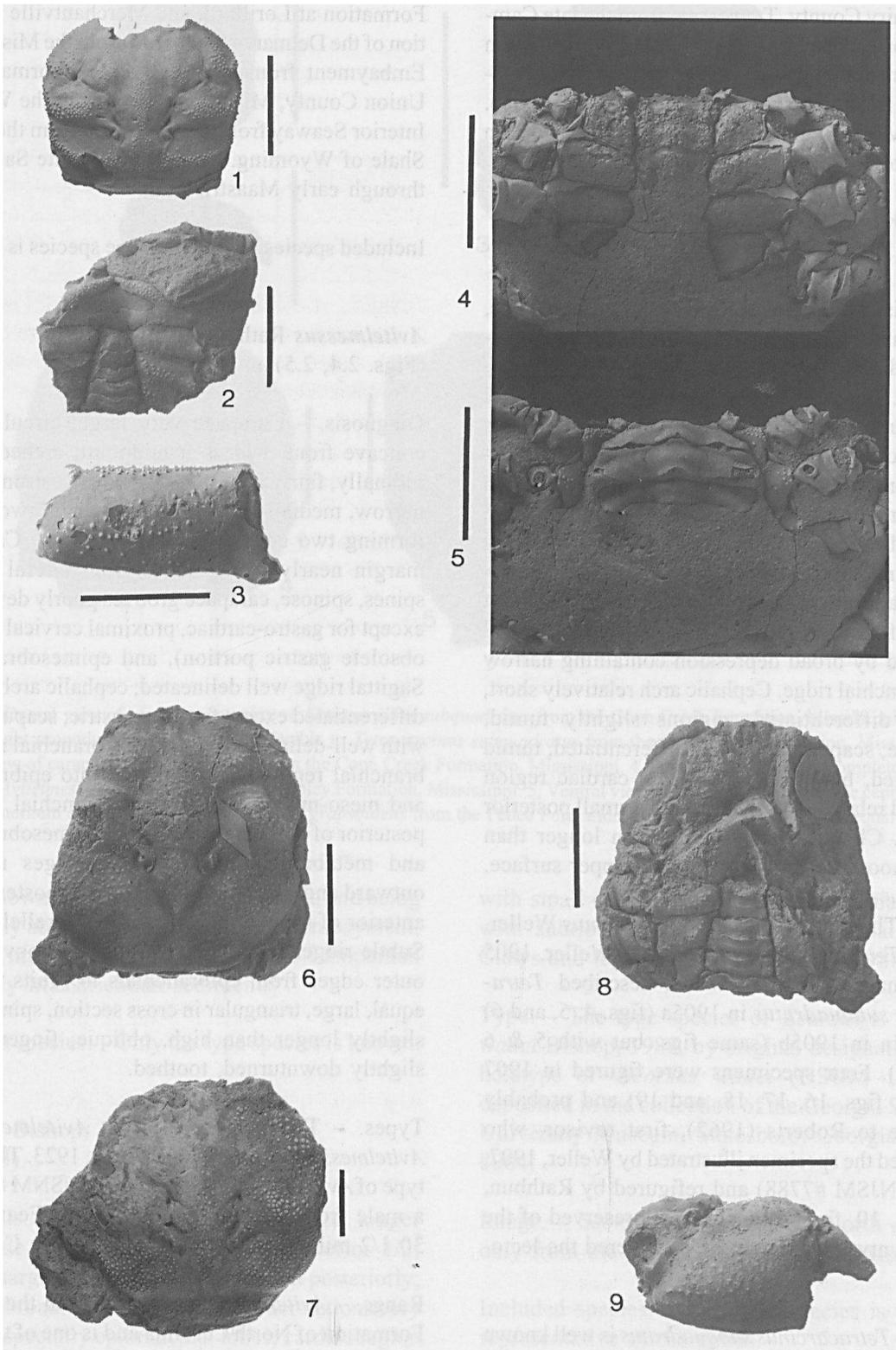
(Figs. 1.6 - 1.9)

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 produced into a 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, 1983b: 426).

Types. – The holotype (USNM 73840) and five paratypes (USNM 73840) are deposited in the collection of the United States National Museum of Natural History, Washington, D.C. 20560.

Range. – *Dakoticancer australis* is abundant in the Mississippi Embayment in the early Maastrichtian Coon Creek Formation in the Union and Pontotoc

→  
 Fig. 1. *Dakoticancer* spp.: 1 - 5, *Dakoticancer overanus* from the Pierre Shale, Mobridge, South Dakota, U.S.A.: 1, Dorsal view of nearly complete topotype carapace. 2, Ventral view of sternum and abdomen of male. 3, Outer view of right propodus. 4, Ventral view of male showing gonopore openings on coxae of fifth pereopod. 5, Ventral view of female showing gonopore openings on coxae of third pereopod. 6 - 9, *Dakoticancer australis* from the Coon Creek Formation, Blue Springs, Union County, Mississippi, U.S.A.: 6, Dorsal view of nearly complete holotype male carapace. 7, Dorsal view of complete paratype carapace showing prominent posterior shelf. 8, Ventral view of nearly complete holotype male carapace. 9, Outer view of nearly complete right carpus, propodus, and dactylus. Scale bars equal 1 cm.



counties, Mississippi, from the early Maastrichtian of McNairy County, Tennessee, from the late Campanian or early Maastrichtian Navarro Formation near Castroville, Bexar County, Texas, the Maastrichtian Difunta Group, in Coahuila State, Mexico, and the Maastrichtian Portrerillos Formation in San Luis Potosí State, Mexico.

*Tetracarcinus* Weller, 1905  
(Figs. 2.1, 2.2)

Diagnosis. – Carapace relatively small, subquadrate, length nearly equals width, widest across epibranchial regions. Rostrum small, narrow, medially grooved. Lateral margins sinuous; posterolateral margin and posterior margin tend to be a continuous smooth curve on steinkerns or incomplete specimens, complete specimens exhibit slightly expanded posterior margin with bordering rim. Carapace poorly differentiated by grooves; cervical very shallow medially, obsolete distally, groove delineating sagittal ridge broad, smooth, shallow but well defined. Epibranchial and metabranchial separated by broad depression containing narrow mesobranchial ridge. Cephalic arch relatively short, weakly differentiated, regions slightly tumid, granulate; scapular arch well differentiated, tumid and ridged, high areas granulate; cardiac region large and relatively posteriad with a small posterior tubercle. Chelae equal, small; palm longer than high, smooth except for granulate upper surface.

Type. – The type species of *Tetracarcinus* Weller, 1905 is *Tetracarcinus subquadratus* Weller, 1905 by original designation. Weller described *Tetracarcinus subquadratus* in 1905a (figs. 4, 5, and 6) and again in 1905b (same figs. but with 5 & 6 reversed). Four specimens were figured in 1907 (pl. 111, figs. 16, 17, 18, and 19) and probably available to Roberts (1962), first revisor, who designated the specimen illustrated by Weller, 1907, fig. 17 (NJSM #7788) and refigured by Rathbun, 1935 (pl. 10, fig. 16) as the best preserved of the “three syntypes”, now to be considered the lectotype.

Range. – *Tetracarcinus subquadratus* is well known from the Northern Atlantic Coastal Plain from the

Magothy Formation at Cliffwood, Woodbury Formation at Lorillard, and Merchantville Formation of the Delmarva Peninsula; from the Mississippi Embayment from the Coon Creek Formation of Union County, Mississippi; and from the Western Interior Seaway from one specimen from the Lewis Shale of Wyoming. It ranges from late Santonian through early Maastrichtian.

Included species. – Only the type species is known.

*Avitelmessus* Rathbun, 1923  
(Figs. 2.4, 2.5)

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. 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 meso-metabranchial 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.

Types. – The type species of *Avitelmessus* is *Avitelmessus grapsoides* Rathbun, 1923. The holotype of *Avitelmessus grapsoides* is USNM #31895, a male from Hudlers Landing, Cape Fear River, 30 1/2 miles above Wilmington, North Carolina.

Range. – *Avitelmessus* is known from the Peedee Formation of North Carolina and is one of the most common crabs on the eastern Gulf Coastal Plain,

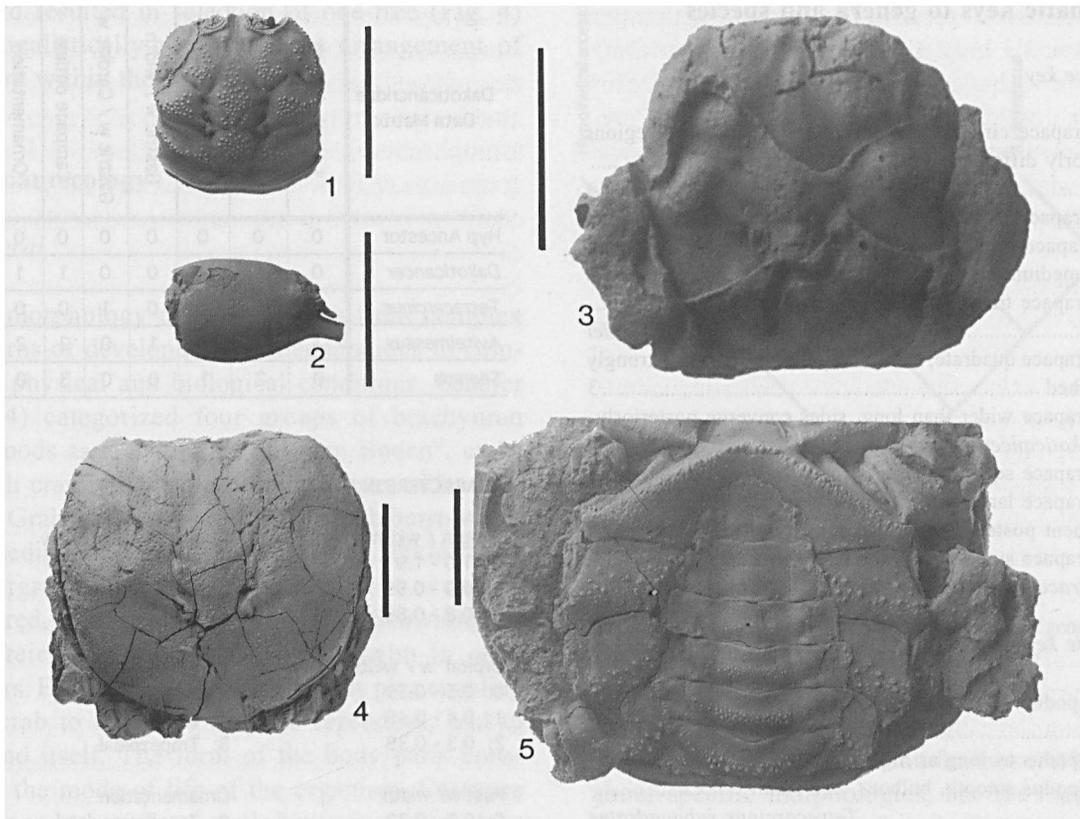


Fig. 2. 1, Dorsal view of complete carapace of *Tetracarcinus subquadratus* from the Coon Creek Formation, Mississippi. 2, Outer view of right propodus interpreted to be referable to *Tetracarcinus subquadratus* from the Coon Creek Formation, Mississippi. 3, Dorsal view of carapace of *Seorsus wadei* from the Coon Creek Formation, Mississippi. 4, Dorsal view of nearly complete carapace of young *Avitelmessus grapsoides* from the Ripley Formation, Mississippi. 5, Ventral view of nearly complete female cephalothorax showing sternum and abdomen of *Avitelmessus grapsoides* from the Pedee Formation, North Carolina. Scale bars equal 1 cm.

being known from Georgia and Alabama, and being extremely abundant in the Mississippi Embayment, ranging into Texas. It is found in late Campanian and early Maastrichtian sediments.

Included species. – Only the type species is known.

***Seorsus*** Bishop, 1988  
(Fig. 2.3)

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, 1988a: 72.)

Type. – The type species of *Seorsus* is *Seorsus wadei* Bishop, 1988, by original designation. The holotype of *Seorsus wadei* (GSUM 1694) is deposited in the collection of the Georgia Southern University Museum, Statesboro, Georgia 30460-8064.

Range. – *Seorsus* is known from North America only from the early Maastrichtian of Mississippi.

Included species. – The type species is the sole representative of the genus.

**Systematic keys to genera and species**

*Carapace key*

- 1a Carapace circular, transversely flat, carapace regions poorly differentiated, thin, spiny, large ..... *Avitelmessus grapsoides*
- 1b Carapace quadrate or trapezohedral, arched, high, carapace regions well differentiated, granulate, small to medium-sized ..... 2
- 2a Carapace trapezohedral, longer than wide ..... *Seorsus wadei*
- 2b Carapace quadrate; sides sub-parallel, sinuous, strongly arched ..... 3
- 3a Carapace wider than long, sides converge posteriorly *Dakoticancer overanus*
- 3b Carapace square or longer than wide ..... 4
- 4a Carapace large, with inflated branchial chambers, prominent posterior shelf ..... *Dakoticancer australis*
- 4b Carapace small with granulate, metabranchial ridges *Tetracarcinus subquadratus*

*Chelipede key*

- 1a Propodus twice as long as high, granulate ..... *Dakoticancer overanus*
- 1b Propodus as long as high ..... 2
- 2a Propodus smooth, bulbous, and small ..... *Tetracarcinus subquadratus*
- 2b Propodus not smooth ..... 3
- 3a Propodus granulate ..... *Dakoticancer australis*
- 3c Propodus spiny ..... *Avitelmessus grapsoides*

**Cladistic analysis**

In order to test the relationships of the genera within the Dakoticancridae, a cladistic analysis was designed and run. The study employed PAUP 3.1.1 to analyze the data matrix (Swofford, 1990). The program was run on a Macintosh computer.

Eight characters were selected as the basis for developing the data matrix (Fig. 3). These characters were those of the dorsal carapace and were selected because they reflected significant differences between the taxa and they were well enough preserved in each of the taxa to be measured. Each of the characters reflected an aspect of the morphology of the crabs that was judged to be sufficiently independent of the others that they would not be redundant. The hypothetical ancestor, against which the taxa were featured, was assigned character states judged to be most primitive.

Dakoticancridae Data Matrix	Length / width	Orbital w / width	Post w / width	Gastric w / width	Gastric w / Cardiac w	Carapace outline	Ornamentation	Greatest width
Hyp Ancestor	0	0	0	0	0	0	0	0
<i>Dakoticancer</i>	0	0	2	0	0	1	1	2
<i>Tetracarcinus</i>	0	0	0	0	1	0	0	0
<i>Avitelmessus</i>	1	1	1	1	0	2	2	1
<i>Seorsus</i>	0	2	1	0	0	3	0	0

**CHARACTERS IN DATA MATRIX**

- Length / width
  - 0: 1.0 - 1.9
  - 1: 0.9 - 0.99
  - 2: 0.8 - 0.89
- Orbital w / width
  - 0: 0.5 - 0.59
  - 1: 0.4 - 0.49
  - 2: 0.3 - 0.39
- Post w / width
  - 0: 0.3 - 0.39
  - 1: 0.4 - 0.49
  - 2: 0.5 - 0.59
- Gastric w / width
  - 0: 0.3 - 0.39
  - 1: 0.2 - 0.29
- Gastric w / Cardiac w
  - 0: 1.5 - 1.99
  - 1: 1.0 - 1.49
- Carapace outline
  - 0: Square
  - 1: Rectangular
  - 2: Circular
  - 3: Trapezoidal
- Ornamentation
  - 0: Zoned granulate
  - 1: Overall granulate
  - 2: Spiny
- Greatest width
  - 0: Epibranchial area
  - 1: Midlength
  - 2: Branchial area

Fig. 3. Data matrix and list of character states used in the cladistic analysis of genera of Dakoticancridae.

Because the number of taxa and the resulting data matrix was small, an exhaustive search was performed. The search resulted in a total of 15 trees of which 5 were equally parsimonious. For each, the consistency index was 1.000, the retention index was 1.000, and the homoplasy index was 0.000.

Examination of these five revealed that four of the trees shared the common character of placing *Tetracarcinus* at the base of the tree. As a result, and because *Tetracarcinus* is the first of the dakoticancrids to appear in the fossil record, the sole tree in which that genus appeared to be more derived was excluded from consideration. Using the criterion of order of appearance in the fossil

record resulted in selection of one tree (Fig. 4) that realistically represents the arrangement of genera within the family.

## Paleoautecology

### General

The morphology of crabs results from complex patterns of development and adaptations to complex physical and biological conditions. Schäfer (1954) categorized four groups of brachyuran decapods as: 1) “Laufers auf dem Boden”, crabs which crawl and run on the substrate surface, 2) “des Grabens im Boden”, crabs which burrow into the sediment, 3) “des Kletterns auf zerklüftetem Untergrund”, crabs which climb on vertical, fissured, hard substrates, and 4) “des Schwimmens im freien Wasser”, crabs which swim in open waters. Each has a characteristic body plan enabling the crab to move, to feed, to reproduce, and to defend itself. The form of the body parts constrain the mode of life of the organism. Carapace shape and proportions, angle between sagittal plane and sternites, arrangement of sternites, lateral cross section, and other body aspects vary in a general way with mode of life.

The carapace of “Laufers”, epifaunal crawlers, is subquadrate, reflexed, with serrated or toothed front. The angle between the sagittal plane and the sternites is  $76^\circ$ . Sternites are somewhat radial relative to the sagittal plane leading to sideways movements of the legs. Lateral cross sections show that these crabs have a convex bottom with the body embedded within the legs. Chela are always formed so as to fit against the cephalothorax. Walking legs become longer in deep-sea forms and setose with the weight borne by folding the dactyli over forming “snow-shoes.”

The pincers, or chelae, of crabs serve multiple functions and hence are highly variable in their size and morphology. Those with specific functions may have longitudinal shearing teeth, flat molariform crushing teeth, comb-like raking teeth, or club-like exterior projections for breaking into shells. Schäfer (1954) discussed the morphology of chelae of crabs and distinguished seven morphotypes of

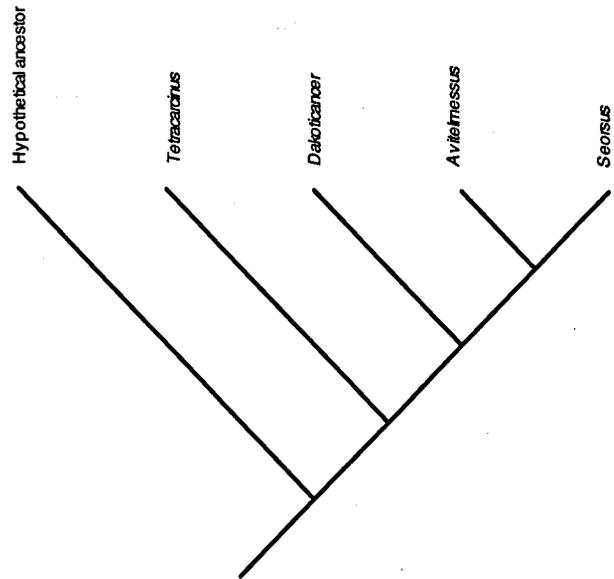


Fig. 4. Cladogram showing inferred relationships of genera within the Dakoticancridae.

teeth. Sometimes obvious conclusions can be made about specific morphologies, but for most crabs the claws are generalized tools for many roles.

### Paleoautecology of *Dakoticancer overanus*

The morphological characteristics of *Dakoticancer overanus* including its rectangular shape, long, slender equally-sized legs P2-P4, claws of similar size and shape held free from the carapace margin with modest-sized, small-toothed downturned fingers, and functional-sized corneas on the eyestalks is consistent with the conclusion that *Dakoticancer* was a generalized epifaunal crawler that lived on the soft substrates of the mud bottoms of the Western Interior Cretaceous Seaway. By reduction of P5, the hind-most legs may be evidence for a possible carrying and covering behavior exhibited by some modern crabs with reduced hind legs. Dactyli on P2-P4 are elongate and triangular, fully capable of folding over into “snow shoes” for walking across the soft substrate. Of all the observable characteristics, none can be cited which clearly establish the mode of life of this primitive crab.

*Dakotancer overanus* is associated with a few concentrically layered straight burrows. Not only are they not abundant enough to have been *Dakotancer* domiciles, they are too small. The preservation of burrows (probably assignable to the thalassinoid *Protocallianassa cheyennensis*) in the *Dakotancer* assemblages indicates that if *Dakotancer overanus* was a burrow dweller, its burrows would likely be preserved in some abundance. Because they were not, Bishop (1981) concluded that *Dakotancer overanus* was not an obligatory burrower.

The consistent association of *Dakotancer overanus* with segmented burrows and fecal pellet packed burrow trails led Bishop (1987: 325) to the conclusion that the presence and preservation of *Dakotancer overanus* was linked through a positive feedback cycle to population explosions of benthic worm populations. If this conclusion is valid, benthic worms may have been the preferred food item for *Dakotancer overanus*, a conclusion further supported by this decapod's delicate downturned fingers armed with small teeth that would be useful in capturing and pulling worms from the substrate. As with most crabs, *Dakotancer overanus* was not an obligatory feeder, but rather would have been a generalized omnivorous browser capable of rapidly responding to periodically burgeoning food resources.

Lithologic evidence from the bentonitic claystone of the Pierre Shale in which *Dakotancer overanus* is preserved, usually in phosphatic concretions distributed through one to three meters of section and the associated fauna including inoceramid bivalves, baculitid cephalopods, often diverse foraminiferal suites (over 100 species at some localities) and mosasaurs, all indicate *Dakotancer overanus* lived in brackish to fully marine water of the Western Interior Cretaceous Seaway.

#### *Paleoautecology of Dakotancer australis*

*Dakotancer australis* from the Mississippi Embayment is similar to *D. overanus* in gross morphology but significantly larger, more robust, with a higher, more strongly ridged carapace that is more granulated and with a thicker cuticle. Pereiopods

P2-P4 are subquadrate and stout, longer than the carapace is wide. The last pair of legs P5 are reduced and possibly carried in a raised position. The dactyli are triangular. The chelae are shorter through the propodus, more robust, and more granulated on their outer surface with fingers more downturned than *D. overanus* and probably were capable of considerable cutting pressure. No epizoans have been observed except for one specimen carrying an oyster attached to its carapace. The lithology of the Coon Creek indicates a shallow nearshore shelf habitat. Associated fossils of the Coon Creek facies include a very diverse and abundant marine fauna, attesting to the normal marine conditions of these sedimentary environments. The *Dakotancer australis* assemblage from the Coon Creek Formation of the Mississippi Embayment occurs in a muddy sandstone associated with abundant marine invertebrates including *Exogyra*, *Sphenodiscus*, *Turritella*, and many other invertebrates. Trace fossils include sparse *Thalassinoides*, leading to the conclusion that *D. australis* in the Coon Creek was not a burrow-dwelling decapod.

*Dakotancer australis* assemblages from the Potrerillos Formation in Nuevo León, Mexico, were found by Vega & Feldmann (1991) mainly in two types of lithofacies. At one locality, molds were found without any articulated appendages, with carapace material very weakly preserved and frequently lost. The lithology is represented by light-gray sandstone, with the layer containing the crabs situated one meter above a massive oestrid bank composed by *Pycnodonta mutabilis* and *Exogyra costata*. The second locality comprises a fine-grained lithology, with a great diversity of molluscan species preserved, mainly infaunal bivalves. Burrows filled with brown sandstone are conspicuous within the rather gray sandy shales. Here, molds of *D. australis* were found inside galleries with diameters ranging from 7 to 12 cm. These crab remains, inferred by Vega & Feldmann (1991) to be exuviae, are preserved within burrows and have preserved appendages that remain articulated, but show dislocation of the ventral side of the carapace. To date, more than 20 specimens of *D. australis* have been collected at this locality, all within galleries and with dislocated plastrons. This

suggests a molting behavior within burrows, a behavior uncommon for most brachyurans, as molting inside burrows has not been observed frequently in extant crabs (Vega & Feldmann, 1991). Nevertheless, *D. australis* specimens from the Cardenas Formation in San Luis Potosí, east-central Mexico, and those from the Coon Creek of the Mississippi Embayment, are not found associated with burrows, and most of them showed articulated appendages. It is possible that the difference in the molting behavior between assemblages of Nuevo León and San Luis Potosí reflect different taphonomic histories, rather than different molting behavior (Vega et al., 1995). It is also important to note that the mean size of the specimens from San Luis Potosí is bigger than the mean size reported for the Poterillos and Coon Creek Formations. However, the dakoticantrids of Maastrichtian deposits from Mexico are sparse, compared to some localities of the United States, such as the Coon Creek Formation, where Bishop (1986a) reported 637 specimens, compared to no more than 80 specimens of this species that had been collected in the Potrerillos and Cardenas Formations. Once again, we must consider differences in paleoenvironment, taphonomic histories, preservational histories, and collecting biases to explain such differences in size and number of individuals. Most samples, both from Potrerillos and Cardenas Formations are exuviae, evidenced by the displaced position of plastron and/or the altered height of the carapace. Bishop (1981: 401, fig. 13-12) has observed similar squashing phenomena resulting in sternal displacement and telescoping of the carapace and sternum, pointing out that these phenomena may be the result of cuticle weakening of the pleural suture during either exuviation or decomposition of a corpse. Most samples from Nuevo León (except those found preserved within burrows) show disarticulated appendages suggesting some transportation in a low-energy environment. It is possible that *D. australis* was a crawler in the intertidal zone, feeding on some mollusks, breaking their shells with rather strong chelae. In fact, compared to other fossil crabs from the Maastrichtian of northeastern, southern, and east-central Mexico, *D. australis* seems to have the heaviest and strongest carapace, with robust

legs that could have been useful in occasional incursions onto the supratidal zone.

#### *Paleoautecology of Avitemessus grapsoideus*

The morphological characteristics of *Avitemessus grapsoideus* include an unusually large size, a carapace which is large, oval, and armored with spines along the front margin, long, flattened appendages with rows of sharp spines along the dorsal edges, equant and very spiny chelipedes with cutting teeth on occlusional surfaces, deeply incised orbits with large eyestalks, divided orbits with trough between, compact antennules, a broad mouthframe with broad spatulate third maxillipedes, and large mandibles. Morphologically, *Avitemessus grapsoideus* is especially unusual because it is significantly larger than any other North American Cretaceous crab and its cross-sectional shape is flat, suggesting these animals inhabited a unique niche, perhaps sheltering by tightly pressing their flattened bodies against the mud-sand bottoms on which they lived on the shallow shelf. In addition to a flattened carapace with spines on the dorsal shield margin, *Avitemessus* also is patterned and counter-shaded. One specimen from North Carolina is encrusted with bryozoans on its legs, but not its carapace nor venter.

*Avitemessus* is known from a few specimens in North Carolina (holotype plus 13 specimens) and great numbers (i.e., thousands) of specimens in the Mississippi Embayment and Eastern Gulf of Mexico. The pattern of distribution and local abundance of *Avitemessus grapsoideus* suggests that this crab was opportunistic and capable of rapid fluctuations in population size in response to as yet undetermined ecological parameters. *Avitemessus grapsoideus* is usually found in muddy lithologies, muddy sands of the Ripley Formation in the Eastern Gulf and Mississippi Embayment associated with abundant marine invertebrates and in papery shale at Graham, Mississippi, and from the muddy sandstones of the Peedee Formation of North Carolina where it is associated with marine vertebrates and invertebrates.

All of these attributes led to the conclusion that *Avitemessus* was an opportunistic crab that lived epifaunally as a "Laufer" on muddy-sand bottoms,

feeding omnivorously most of the time but capable of exploiting rapidly expanding local food resources. Locally, this crab probably inhabited the very nearshore and lagoonal habitats.

#### *Paleoautecology of Tetracarcinus subquadratus*

*Tetracarcinus subquadratus* is a diminutive crab with a small, highly sculptured and granulated carapace that is relatively rectangular and high standing. Orbits are deeply inset and rimmed by a turberculate ridge, eyestalks thin and fold back into outer orbital fossae. Pereiopods are still poorly known, preserved ischium? and merus? on one specimen are thin and round. Chelae are equant, carpus massive in dorsal aspect, quite long and stout, anterior surface granulate. Claws with enlarged bulbous propodi and thin fingers. *Tetracarcinus subquadratus* is unusual because of its diminutive size, seldom larger than ca. 13 mm in width, contrasting rather sharply with *Dakoticanca* and the giant *Avitelmessus*. The small size of this animal and the specialized claws, particularly the tweezer-like pincers, may indicate *Tetracarcinus* was adapted to a specialized mode of life, perhaps as an epizoan on plants or animals such as sponges. This hypothesis remains unsubstantiated by data at this time. These crabs are associated with a relatively normal marine fauna. *Tetracarcinus* is the common crab in the Merchantville Formation of the C & D Canal on the Delmarva Peninsula and is a secondary element in the *Dakoticanca australis* assemblage from the Coon Creek Formation of the Mississippi Embayment in Union County, Mississippi. Only one specimen is known from the Western Interior Basin, that from the Lewis Shale of Wyoming. *Tetracarcinus* is unknown from the Gulf Coastal Plain west of the Mississippi Embayment.

#### *Dakoticanca* crab assemblages

Decapod-dominated assemblages were described by Bishop (1981, 1983c) in terms of associated taxa, distribution, and mode of preservation. He (1981) described ca. 5,000 fossil decapods collected from six localities at five stratigraphic levels in

the Upper Cretaceous Pierre Shale of South Dakota. The decapod-dominated assemblages are preserved in apatite concretions distributed through thin intervals of shale (3 to 7 m) that are continuous over large areas (15 to 1500 km<sup>2</sup>). As decapods were buried as molts and/or corpses, the thin intersegmental membranes rapidly decomposed allowing the decaying corpses to be filled by mud. The organic-rich sediment was ingested by deposit-feeding organisms as evidenced by filled and open burrows and ubiquitous masses and strings of fecal pellets (Bishop, 1975). Compression due to weight of overburden flattened, broke, and rearranged parts of some decapods. Concentration of phosphates in the fecal pellets combined with the chemical micro-environments of the enclosed spaces within the crabs causing the precipitation of the apatite concretions led to preservation of the decapods. The uniformity of distribution, uniformity of faunal composition, and uniform mode of preservation of the faunas led to the conclusion that they are the preserved portions of recurrent decapod communities.

The *Dakoticanca* community was dominated by the crab *Dakoticanca overanus* (75.0%), baculitid cephalopods and inoceramid bivalves. Less common preserved taxa are the decapods *Homolopsis punctata* (0.8%); *Necrocarcinus pierrensis* (7.6%); *Raninella oaheensis* (0.3%); *Sodakus tankayotankaensis* (0.1%); *Zygotrocarcinus mendryki* (0.05%); *Palaeonephrops browni* (0.4%); and *Protocallianassa cheyennensis* (0.5%) as well as numerous gastropods, bivalves, non-baculitid cephalopods, foraminifera, ostracodes, bony fish, sharks and reptiles. The decapod-dominated community, the *Dakoticanca* association, periodically inhabited the Western Interior Cretaceous sea bottom when conditions in the unstable environment were favorable. Populations of the crabs, representing opportunistic species, colonized the bottom over favorable areas. When conditions became unfavorable (for yet unknown reasons) the crab populations declined to previous low levels. The periodic explosion of crab populations were thus superimposed upon the stable, equilibrium populations of mollusks that characterize the typical fossil assemblages of the Pierre Shale. During non-favorable times the faunal elements of the *Dakoticanca* association were random elements pre-

served in the molluscan assemblages. During favorable times the crab populations rapidly increased and became dominant and their record overprinted the molluscan assemblages.

The accumulated data suggest that crab assemblages may represent opportunistic species capable of rapid population growth, perhaps to exploit burgeoning worm populations, followed by a less rapid decline as a positive taphonomic short cycle becomes operative (Bishop, 1986b; Bishop & Williams, 1986; Bishop, 1987). These opportunistic crab “communities” seem in many cases to be overprinted on “normal” molluscan thanatocoenoses or biocoenoses (Bishop, 1986b). The process that led to the preservation of the decapod-dominated faunas (Bishop, 1986a, 1986b) is thought to have been initiated by aberrant and destabilizing physicochemical conditions (like volcanism) that exterminated most living organisms, resulting in a nutrient flood onto and into the substrate. This flood of nutrients was exploited by an explosion of worm populations providing a resource opportunity for organisms capable of harvesting the abundance of worms. The decapod crustaceans, always present in small numbers, were suited to exploit the food resource provided by the worm communities and underwent population explosions in response to the resource availability provided by the worms. As death took decapods back into the substrate, they in turn provided an opportunity for extension of the worm community providing a decreasing feedback system of worms-decapods-worms-decapods-etc. It is unknown if the decapod community fractions (= assemblages) described by Bishop were always present but in small numbers or, if they represent assemblages that formed only during times of maximal resource supply.

Two types of paleobiogeographic records are thus defined, one based on the fortuitous presence of decapod remains in molluscan assemblages (which will always be limited in numbers of specimens and taxa) and another based on periodic blossoming of opportunistic species of decapods that may form decapod-dominated fossil assemblages. This observation, if true, would mean that the geological record of opportunistic decapod species would be better than that of equilibrium species, which would be preserved as random elements in molluscan assemblages and easily ‘lost’ to

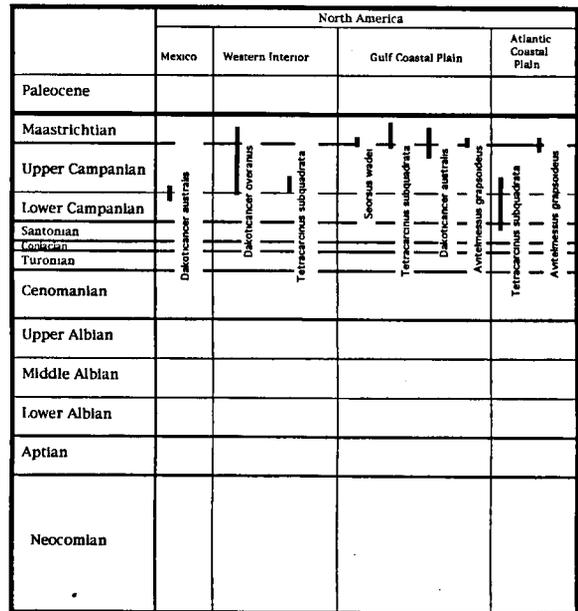


Fig. 5. Stratigraphic ranges of species of dakoticancriids arrayed by biogeographic provinces.

science unless large collections are made. Interpretations based on these different types of records could easily distort our understanding of the geologic history of the decapods.

### Origin of the Dakoticancriidae

The oldest known species within the Dakoticancriidae is *Tetracarcinus subquadratus* from the Northern Atlantic Coastal Plain (Fig. 5). *Tetracarcinus subquadratus* occurs in the late Santonian through the mid-early Campanian. In the Mississippi Embayment *Tetracarcinus subquadratus* occurs in the early Maastrichtian. One specimen has been described from the early-late Campanian of Wyoming in the Western Interior (Bishop, 1986a). *Dakoticancer australis* is found in abundance in the Coon Creek Formation of Maastrichtian age in Mississippi, from the Maastrichtian of Texas, and from Mexico. *Dakoticancer overanus* has been collected from the mid-Campanian to Maastrichtian of the Western Interior in great abundances from *Dakoticancer* assemblages described by Bishop (1981). *Avitelmessus grapsoides* is found in the Maastrichtian Peedee Formation of North Carolina

(Bishop and Sturgeon in prep.) and the late Campanian to Maastrichtian Ripley and Coon Creek of the Eastern Gulf Coastal Plain.

## Cretaceous Paleogeography

### General

Kauffman (1977) has presented a model of Cretaceous paleogeography and paleoclimatology as the supercontinent of Pangea broke up and the Atlantic Ocean opened. A circum-equatorial ocean, the Tethys Seaway, dominated world paleogeography, stretching across America, northern Africa, and southern Europe into the Paleo-Indian Ocean (where India was still a drifting subcontinent). Branching off this east-west ocean were several north-south epicontinental seaways including the Western Interior Seaway and the Northern Atlantic Seaway, both stretching from the Tethys northward into the paleo-Arctic Ocean. The Western Interior Seaway was characteristically a shallow, epicontinental seaway, perhaps little more than a hundred meters deep while the northern Atlantic was a true oceanic area floored by oceanic crust extruded along the mid-Atlantic Ridge as the ocean basin opened by sea floor spreading. The Atlantic Ocean was certainly a deeper, more oceanic body of water less prone to the vagaries of local climate and tectonic activity. Within this setting the primitive decapods underwent several major adaptive radiations and formed the lineages leading to modern decapod faunas.

### Western Interior Seaway

The Western Interior Seaway as described by Kauffman (1977) is a complex epicontinental sea extending about 4,800 km from Arctic Canada to the Tethys Seaway and approximately 1,600 km wide from a mobile belt along its western edge in Nevada and Utah to a stable shallow shelf along its east side. Within this basin, water depths were variable and are inferred by Kauffman (1977) to have been in the order of 100 m, a value accepted by most Cretaceous workers. Other authors cite much deeper conditions (Eicher, 1969). The active

western margin was the source of coarse clastics deposited in rapidly prograding deltaic complexes into rapidly subsiding basins, resulting in a complex series of clastic wedges. Farther to the east the Western Interior Seaway was a stable platform which received the suspended fine clastics from the western part of the basin and surrounding low-lying hills of eastern North America deposited as thick units of mudstone and resulting in classic interfingering patterns with coarser clastics to the west as tectonism pulsed throughout the Cretaceous. Paleocurrent patterns for the Tethys Seaway and the Western Interior Seaway were presented by Kauffman (1977: fig. 10) in assessing distribution of larvae throughout the basin.

The interfingering Cretaceous lithosomes also received air-transported volcanic ash from volcanos in the tectonically active Rocky Mountains to the west, resulting in deposition of numerous layers of bentonite on the Cretaceous sea bottom. These isochronous, pyroclastic events must have dramatically altered bottom conditions, water chemistry, and atmospheric conditions, leading to dramatic changes in Cretaceous ecosystems and biotas. As Laramide tectonism progressed, the Western Interior Basin was inundated by sediment from the west causing progradation of large deltas and restriction of the basin in Maastrichtian time to a small Paleocene remnant sea centered in North Dakota, the Cannonball Sea.

The Cretaceous sediments of the Western Interior carry extensive and beautifully preserved faunas, primarily encased in concretionary limestone nodules. These faunas include rapidly evolving cephalopod molluscs such as *Baculites*, *Didymoceras*, *Hoploscaphites*, and many other taxa which have been developed into a well-documented chronology based on faunal succession, bentonite stratigraphy, and radiometric dating. This chronology allows other physical and biologic events, such as periodic appearances of decapod Lagerstätten, to be precisely dated.

### Mississippi Embayment

The Mississippi Embayment is a Late Cretaceous and Tertiary seaway that extended from the Tethys Seaway northward into southern Illinois as a well-

defined depositional trough characterized by shallow shelf conditions and relative tectonic stability (Russell et al., 1982). Resultant sediments consist of shelf chalks and muddy chalks and nearshore clastics consisting of basal gravels, sands, and muddy sands. Within these sediments (Stephenson & Monroe, 1940) are contained well-known faunas of the Selma Chalk, Ripley Formation, and the Coon Creek Formations, including several extensive decapod faunas from Blue Springs, Mississippi; Coon Creek, Tennessee; and Braggs, Alabama.

#### *Northern Atlantic Coastal Plain*

The history of the geological study of Cretaceous deposits of the Northern Atlantic Coastal Plain was reviewed by Owens et al. (1970). Geologic studies of these rocks have been hampered by low relief, dense vegetative cover, thick soils, repeated facies, poor preservation of invertebrates, and many other factors. Data and diagrams presented by Owens et al. indicate the Late Cretaceous sediments thin southward and some units pinch out before reaching the Delmarva Peninsula leaving the Merchantville, Englishtown, Marshalltown, and Mount Laurel Sand (oldest to youngest) representing a series of clastic and calcareous clastic lithosomes deposited in nearshore environments along the western margin of the opening Atlantic Ocean. These sediments along the Delmarva Peninsula have yielded a diverse and abundant decapod fauna collected by Harry Mendryk from dredging soil exhumed from the Chesapeake & Delaware Canal during the 1970's, mostly assignable to the early Campanian Merchantville Formation.

#### *Western Gulf Coastal Plain and Mexico*

The depositional history of the Western Gulf Coastal Plain and Mexico during the Late Cretaceous was very similar to that for the Western Interior Seaway. Northeastern Mexico was dominated by prograding deltaic systems through Campanian and Maastrichtian time. Deposition of sediments and local subsidence of basins produced thicknesses up to 1000 m. Dakoticanrid crabs from

Mexico have been reported for the Maastrichtian sediments of the Difunta Group (Vega & Feldmann, 1991) and Cardenas Formation (Vega et al., 1995).

The Difunta Group is an Upper Cretaceous-Eocene sequence of terrigenous rocks, located in the states of Coahuila and Nuevo León. Two deltaic systems prograded from the west and northwest, filling the Parras and La Popa basins (McBride et al., 1974). Although Maastrichtian dakoticanrid crabs seem to be more abundant in the shallow calcarenites and sandstones of the La Popa basin, some specimens have been collected recently from the Parras basin. Deposited north of the structural front of the Sierra Madre Oriental, the Difunta Group was affected by a system of NW-SE faults. Diapirs in the La Popa basin were the result of plastic deformation and pressure over the underlying Minas Viejas, anhydrites. It is probable that this feature resulted in local subsidence and basin-filling episodes, which prevailed until early Eocene times (Vega et al., 1989). Uplift of the Sierra Madre Oriental took place through the Late Cretaceous; thus, depositional basins of the Difunta Group were bordered by this feature to the south and southeast, by the Coahuila Platform to the north and northwest, and by the Tamaulipas arch to the east and northeast (McBride et al., 1974).

The southernmost occurrence of dakoticanrid crabs has been recorded from the sandstones and shales of the Maastrichtian Cardenas Formation, on the eastern margin and central portion of the Sierra Madre Oriental, in San Luis Potosí state (Vega et al., 1995). The Cardenas Formation comprises reefal facies in the southern part of its exposure area (Myers, 1968), while to the north it becomes more terrigenous, with an almost uniform lithology of fine sandstones and shales. Terrigenous material was supplied from the west, from the rising occidental margin of Mexico. Uplift of the Sierra Madre Oriental during the Late Cretaceous formed a barrier to the east, thus deposition of Cardenas sands and muds took place in an elongated, nearly north-south corridor-shaped lagoon. Farther east, pelagic sediments of the Mendes Formation were deposited beyond this barrier, onto the Gulf Coastal Plain.

The Difunta Group and Cardenas Formation have closer faunal affinities with rocks of the Mississippi

Embayment than with correlative units of southwest Texas. The Campanian-Maastrichtian Aguja Formation comprises an eastward-thinning series of paralic and marine sandstones interbedded with shale and lignite deposited in a coastal plain environment. Two progradational cycles are represented in these deposits (Lehman, 1986). As a difference of the preservational style with Mexican specimens, decapods from the Big Bend area are phosphatized exuviae of species more closely related to the Western Interior decapod fauna.

### *Biogeographic range of Dakoticancriids*

Three major biogeographic patterns of occurrence of the dakoticancriids are discernable; each dominated by a genus and having relatively discrete boundaries and each with a few known outside occurrences. The occurrences of *Tetracarcinus subquadratus* are largely confined to the Northern Atlantic Coastal Plain and the Mississippi Embayment with one specimen also known from Wyoming. *Avitelmessus grapsoides* is found dominantly in the Mississippi Embayment and Eastern Gulf Coastal Plain but is also known from North Carolina. *Dakoticancer overanus* is endemic to the Western Interior Seaway and *Dakoticancer australis* is abundant in the Mississippi Embayment but is also present in northeastern Mexico. These ranges might be extended by additional collecting, but the coherence of their distributions has remained relatively constant for a significant time, leading us to believe the distributions are real biogeographic patterns, not artifacts of collecting biases.

### Interpretation

The Cretaceous decapods of North America occur either as 1) uncommon remains in molluscan fossil assemblages, 2) as common remains in molluscan-dominated fossil assemblages, or 3) as dominant elements in decapod assemblages, e.g., the *Dakoticancer* assemblage described by Bishop (1981). The occurrence of fossil decapods as rare or occasionally common elements in molluscan assemblages has led to the logical conclusion that the geological record of decapods is very poor. This

conclusion is supported by the disjunct, fragmentary record of fossil decapods. Of the 97 known Cretaceous decapods from North America, 42 species are known from a single specimen, 8 species each are represented by 2, 3 and 4 specimens, and 3 species each are represented by 5, 6 and 7 specimens. Only 18 species are represented by 9 or more specimens and of these only 4 are represented by 100 or more specimens. These data suggest that fossil decapods are scarce and our knowledge of them is very incomplete. If this is true, then our knowledge of their stratigraphic and geographic distribution must be very fortuitous and random (in the sense of being useful for analysis). With this limitation in mind it must be emphasized that, however limited the geologic record, it must be considered in evolutionary and paleoecologic studies.

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