Journal of Paleontology, page 1 of 18

0022-3360/25/1937-2337
doi: 10.1017/jpa.2024.25

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

Ontogenetic morphology changes in a crab assemblage (Crustacea, Decapoda, Brachyura, Dakoticancroida) from the Late Cretaceous (Maastrichtian) of the Mississippi Embayment, USA†

Carrie E. Schweitzer,[1]* Rodney M. Feldmann,[2] and Jillian Findling[2]

[1]Department of Earth Sciences, Kent State University at Stark, North Canton, Ohio 44720, USA <cschweit@kent.edu>
[2]Department of Earth Sciences, Kent State University, Kent, Ohio 44242, USA <jfindlin@kent.edu>

Non-technical Summary.—Differences in crab body shape among and between juveniles and adults, as well as differences between males and females, are not well studied among extinct crabs. Although differences between males and females in the "tail" and the claws are well documented in living crabs, sexual differences in the carapace, or shell, receive less attention. The three extinct crab species *Tetracarcinus subquadratus* Weller, 1905, *Dakoticancer australis* Rathbun, 1935, and *Seorsus wadei* Bishop, 1988 are here recognized as being a continuum of body shapes of the same species, representing males and females and/or juveniles and adults, on the basis of examination of dozens to hundreds of specimens of each from the same collecting locality. A new genus, *Synoriacarcinus*, is named to embrace two species previously referred to *Seorsus* Bishop, 1988. Two families of extinct crabs, Dakoticancridae and Ibericancridae, were widespread on coastal North America during the Late Cretaceous but became extinct in the end-Cretaceous event.

Abstract.—Differences in brachyuran morphology among and between juveniles and adults as well as sexual dimorphism are not well studied among extinct brachyuran crabs. Carapace dimorphism and morphological changes during growth have received little attention in fossil crabs. *Tetracarcinus subquadratus* Weller, 1905, *Dakoticancer australis* Rathbun, 1935, and *Seorsus wadei* Bishop, 1988 are herein synonymized on the basis of examination of dozens to hundreds of specimens of each from the same locality. *Synoriacarcinus* new genus is named to embrace two species previously referred to *Seorsus* Bishop, 1988, *Synoriacarcinus millerae* (Bishop, 1992), new combination, and *Synoriacarcinus kauffmani* (Feldmann et al., 2013), new combination. Both Dakoticancridae and Ibericancridae were well established on coastal North America during the Late Cretaceous but became extinct in the end-Cretaceous event.

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Introduction

Dakoticancrid crabs are well represented in the decapod fauna of the Late Cretaceous of North America. The family has been well studied (Bishop et al., 1998), but because the fossils are found in large assemblages of a single species, paleobiological studies not usually available to decapod paleontologists are possible.

Ontogeny and growth in extant Brachyura have been well summarized recently by McLay (2015), noting allometric growth in particular among features that could be observed in fossils.

Ontogenetic changes in collections of extinct brachyurans have been studied in Cretaceous raninoid crabs of Brazil, noting a proportional widening of the carapace with overall increase in size (Matos et al., 2021). Extinct spider crabs were shown to exhibit allometry among collections of the same species from Neogene rocks of the Caribbean (Klompmaker et al., 2015). Within Decapoda, clear changes during growth can be observed in the pereiopods of axiidean and gebiidean ghost shrimps (Hyžný and Klompmaker, 2015). Thus, recognition of changes during growth in fossil decapods is receiving increasing attention.

Study of several hundred specimens from a single locality suggested that three dakoticancroid taxa, *Tetracarcinus subquadratus* Weller, 1905 (Weller, 1905a), *Dakoticancer australis* Rathbun, 1935, and *Seorsus wadei* Bishop, 1988, might be synonymous. Morphological examination, measurements, and statistical analysis demonstrate this, with *T. subquadratus* as the senior synonym. We propose that the form previously assigned to *Tetracarcinus subquadratus* represents the smaller, possibly juvenile or sexually immature members, of the species (Fig. 1.1). The *Dakoticancer australis* morphology represents the larger, probably adult and sexually mature forms of the species (Fig. 1.3). Those specimens assigned to *Seorsus wadei* seem to occupy a position of intermediate size and intraspecific variability, with slightly

*Corresponding author.
†Guest editor: Adiel Klompmaker.

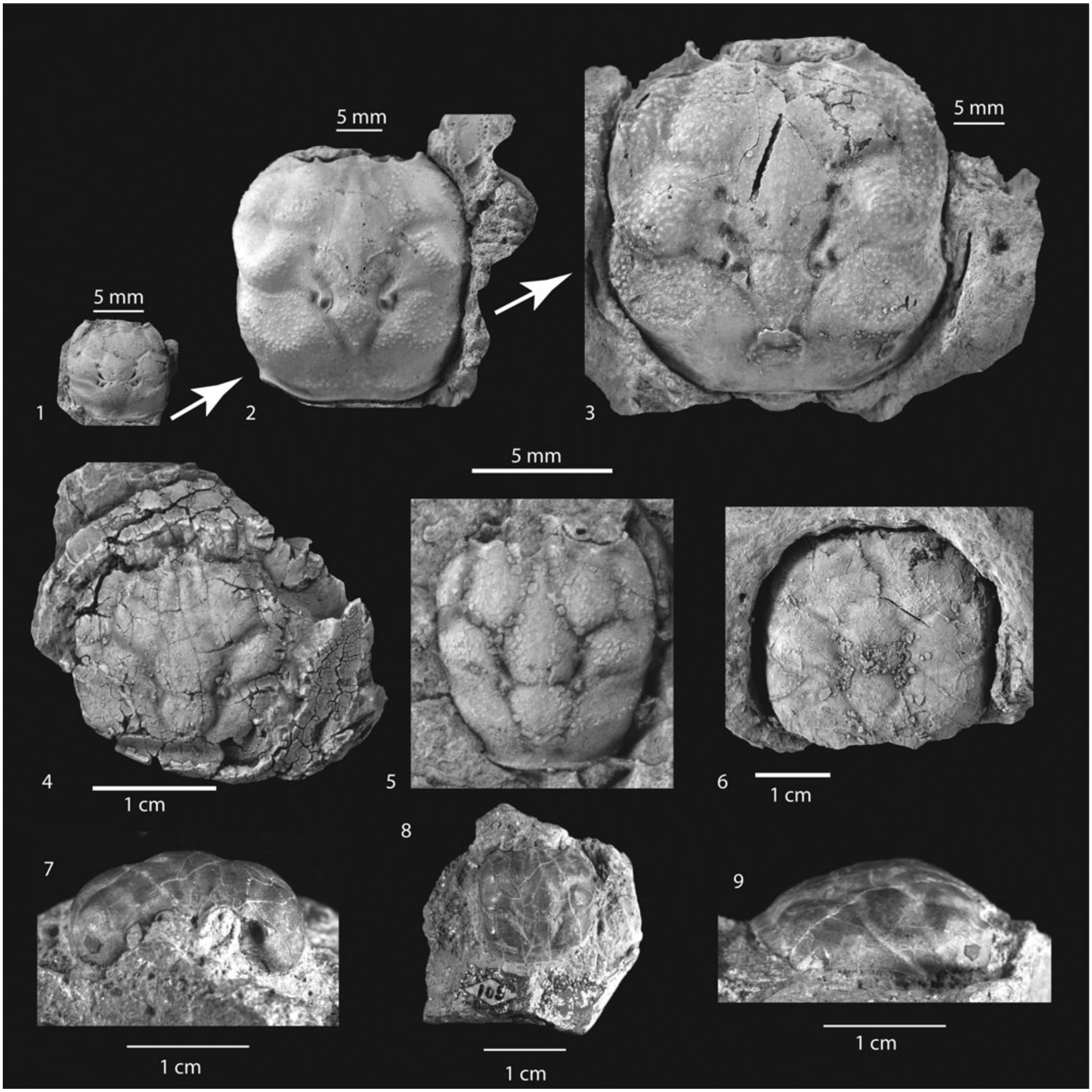

Figure 1. *Tetracarcinus subquadratus* Weller, 1905. (**1–3**) *Tetracarcinus subquadratus* from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation, growth series: (**1**) dorsal carapace MMNS-IP-11911, *Tetracarcinus*-type morphology; (**2**) dorsal carapace MMNS-IP-11891, *Seorsus*-type morphology; (**3**) dorsal carapace MMNS-IP-11895, *Dakoticancer australis*-type morphology. (**4–6**) *Tetracarcinus subquadratus* from New Jersey: (**4**) NJSM 23337, Woodbury Clay Formation; (**5**) NJSM 23339, Woodbury Clay Formation; (**6**) KSU D 2097; New Jersey specimens from near type locality for species illustrated for comparison with Blue Springs material (**4–6** originally illustrated by Feldmann et al., 2013, fig. 13). (**7–9**) *Tetracarcinus subquadratus*, cotype NJSM 7788: (**7**) anterior view; (**8**) dorsal view; (**9**) right lateral view (unwhitened, photos by R. Pellegrini, NJSM).

narrower carapaces that are not statistically significantly different in size or shape from *D. australis* (Fig. 1.2). For ease of discussion herein, we will use the original species name associated with the different morphologies we now consider conspecific in our discussion of the synonymy of the forms. These morphologies are defined specifically in the following, but in general, smaller, presumably younger specimens exhibit the *T. subquadratus* morphology; larger, presumably older specimens exhibit the *D. australis* morphology; and *Seorsus* specimens are generally intermediate in size between *D. australis* and *T. subquadratus* and are slightly narrower overall.

Materials and methods

Material and preparation.—Approximately 850 specimens of *Tetracarcinus subquadratus*, including those originally placed

https://doi.org/10.1017/jpa.2024.25 Published online by Cambridge University Press

in *T. subquadratus*, *Seorsus wadei*, and *Dakoticancer australis*, were collected by C.E.S., R.M.F., and several colleagues over four total days in December 2012 and March 2013 at approximately 34.39251°N, 88.88563°W, the Blue Springs, Mississippi, locality (Kornecki et al., 2017). Numbered specimens, those measured and/or illustrated, are MMNS-IP-11870 through 11974. Incomplete specimens were measured as half of the measurement where possible and then doubled. Specimens were prepared with Paleotools microjacks and whitened with ammonium chloride before photography with a Nikon D7200 camera with an AF Nikor 28–105 mm lens. Measurements were taken with Mitutoyo analog calipers to the nearest tenth of a millimeter (Supplementary Data tables 1, 6, 7, 8). Charts were prepared in Excel. One-way ANOVA (Supplementary Data tables 2, 3, 4, 5) and t-tests (Supplementary Data tables 9, 10) were performed in Past 4.08 (Hammer et al., 2001), all at $p = 0.05$. Images were toned in Adobe Photoshop 23.1.0 before making figures in Adobe Illustrator 26.0.2.

Other material examined.—Dakoticancer australis, holotype, USNM PAL 73840, USNM PAL 335991a–d, acc. no. 215705, loc. 18628. *Tetracarcinus subquadratus*, NJSM 7788, cotype; USNM PAL 73716; USNM PAL 794463–794469, from the C and D canal, Delaware, locality. KSU D 1165 and 1170, casts of GAB-37-1158 and GAB 37-1170, respectively, specimens collected by G.A. Bishop from the Blue Springs locality and originally referred by him to *Dakoticancer australis.* KSU D 2091, 2092, *Tetracarcinus subquadratus*, from C and D Canal, Delaware, Campanian. LP 108 and 130 and KSU D 715, collected from the Maastrichtian Potrerillos Formation (Vega and Feldmann, 1991).

Repositories and institutional abbreviations.—Types, figured, and other examined specimens in this study are deposited in the Mississippi Museum of Natural Sciences (MMNS); Department of Earth Sciences, Kent State University (KSU D); New Jersey State Museum, Trenton, NJ (NJSM); United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM PAL).

Systematic paleontology

Infraorder Brachyura Linnaeus, 1758
Section Dakoticancroida Rathbun, 1917
Superfamily Dakoticancroidea Rathbun, 1917
Family Dakoticancridae Rathbun, 1917

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

Diagnosis.—Carapace quadrate, wider than long to longer than wide; rostrum narrow, bilobed; orbits well developed, usually rimmed; eyes sheltered by orbits when retracted; anterolateral margins entire; posterior margin nearly straight; medial part of cervical groove weakly developed; gastric regions poorly to moderately separated from cardiac and intestinal regions; branchiocardiac groove well developed; pleural sutures located on sides of carapace; fifth pereiopods very reduced; sternum broad, sternites visible to posterior of carapace, sternite 4 sometimes with ridge parallel to anterior end, sternites 5, 6, and 7 with or without 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 rounded triangular; female pleon wide, with long epimeres, all pleonites free; coxae of pereiopods at same level as sternum; first pereiopods isochelous (modified from Feldmann et al., 2017).

Remarks.—Dakoticancridae has been well studied (Bishop et al., 1998; Kornecki et al., 2017). The family is unusual in being known from two large assemblages of several hundred specimens of two separate species, one of which is composed of *Dakoticancer overanus* Rathbun, 1917 at Mobridge, South Dakota (Jones et al., 2022). The other large collection of specimens is composed of those formerly referred to *Dakoticancer australis* Rathbun, 1935; *Seorsus wadei* Bishop, 1988; and *Tetracarcinus subquadratus* Weller, 1905a, all three of which we herein refer to *Tetracarcinus subquadratus* Weller, 1905a, at Blue Springs, Mississippi. Sexual dimorphism and intersex individuals are well documented from the *Dakoticancer overanus* population from South Dakota (Jones et al., 2022). *Avitelmessus grapsoideus* is documented from several Gulf Coastal states (Rathbun, 1935). This study provided an opportunity to examine hundreds of specimens and to compare and contrast morphologies known from forms that had been referred to separate genera and species.

Dakoticancridae are podotrematous crabs, with gonopores on coxae of the pereiopods in both males and females, which is the basal condition in Brachyura and indeed Decapoda as a whole (Schram and Koenemann, 2021). The family originated and flourished in the Late Cretaceous but became extinct at the end of the Cretaceous, probably due to its location primarily in the Western Interior Seaway and Gulf Coastal North America proximal to the Chicxulub impact site (Schweitzer and Feldmann, 2023). Dakoticancroids are superficially similar to the more derived heterotrematous crabs, which have gonopores on the sternum in females, in having a flattened carapace as wide as or wider than long with very wide sterna, which is unusual among the podotrematous crabs. The dakoticancrid morphology may have been "experimental" in becoming wider than long and acquiring a body form like heterotrematous crabs, which preferentially survived the end-Cretaceous events (Schweitzer and Feldmann, 2023). *Callichimaera* Luque et al., 2019 and *Componocancer* Feldmann et al., 2008 similarly document unique brachyuran body forms that appeared and went extinct in the Cretaceous. This pattern deserves more study.

Genus *Dakoticancer* Rathbun, 1917

Type and sole species.—Dakoticancer overanus Rathbun, 1917, by monotypy.

Diagnosis (modified from Jones et al., 2022).—Carapace quadrate, wider than long, length/width (L/W) about 75%; rostrum narrow, bilobed; orbits well developed, rimmed, without spines, fronto-orbital width (FOW) about 48%

carapace width; eyes sheltered by orbits when retracted; anterolateral margins entire, anteriorly with tiny sharp spines; with weak row of granules extending from anterolateral margin onto hepatic region; broad, granular ridge extending from lateral margin onto epibranchial region, epibranchial region forming transverse ridge nearly perpendicular to axis; narrow, granular rim extending from lateral margin onto branchial region, branchial region with broad inflation parallel to epibranchial region; gastric regions poorly separated from cardiac and intestinal regions; pereiopods 5 reduced; sternum broad, sternites visible to posterior of carapace, sternite 4 with ridge parallel to anterior end, sternites 5, 6, 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 rounded triangular; female pleon wide, with long epimeres, all pleonites free; coxae of pereiopods at same level as sternum; pereiopods 1 isochelous.

Remarks.—Dakoticancer overanus differs in several significant ways from specimens referred to *Dakoticancer australis* (Table 1). *Dakoticancer overanus* generally is about 75% as long as wide, whereas individuals referred to *D. australis* are about as wide as long, with L/W ratios ranging from about 0.98 to 1.08. This difference is statistically significant (Table 2). *Dakoticancer overanus* has an intestinal region reduced to a very short area between the cardiac region and the posterior rim, whereas specimens of *D. australis* have an intestinal region occupying about 22% the maximum length of the carapace. The long intraorbital and outer-orbital spines seen in *D. australis* individuals are lacking in *D. overanus.* The epibranchial ridge in *D. overanus* is transverse and more or less perpendicular to the axis, whereas that of specimens of *D. australis* is oblique to the axis. *Dakoticancer overanus* also has a transverse swelling on the branchial region that is weaker in *D. australis* individuals. Sternal ornamentation is well developed as rows of granules in *D. overanus*, whereas in *D. australis,* there are few or no granules on the sternum.

These differences in morphology are not typical of allometric growth or difference in life stage. Each of the differences is noted in both males and females of each species, and the morphology of *Dakoticancer overanus* is remarkably consistent across individuals of various sizes (Jones et al., 2022). Thus, *D. overanus* is retained as the only member of *Dakoticancer*. As will be discussed in the following, allometric changes and changes in development of ornamentation are documented for *Tetracarcinus*, and *D. australis* will be shown to represent larger individuals of *Tetracarcinus.*

A specimen of *Dakoticancer overanus* reported by Rathbun (1935) from New Jersey was transferred by Roberts (1962) to *Tetracarcinus.* Rathbun (1926) reported a ventral specimen of *D. overanus* from the Coon Creek unit in Tennessee; it is probable that this specimen is actually *Tetracarcinus subquadratus*. Thus, *Dakoticancer overanus* is known primarily from South Dakota (Rathbun, 1917; Bishop, 1981; Jones et al., 2022; Klompmaker et al., 2022), with some occurrences in North Dakota (Tucker et al., 1987), restricted to the northern Western Interior Seaway. All occurrences are Campanian–Maastrichtian.

Genus *Tetracarcinus* Weller, 1905a

1905a *Tetracarcinus* Weller.
1905b *Tetracarcinus* Weller.
1917 *Dakoticancer* Rathbun (partim).
1986b *Parapaguristes* Bishop.
1988 *Seorsus* Bishop.

Type and sole species.—Tetracarcinus subquadratus Weller, 1905 (Weller, 1905a), by monotypy.

Diagnosis.—Carapace about as wide as long, L/W = 0.95–0.97, square; upper orbital margin with short inflection or spine medially, outer-orbital spine short or long, suborbital spine long, FOW 50–58% carapace width; lateral margins with beaded rims on hepatic, epibranchial, and branchial regions; epibranchial region oblique, composed of two distinct

Table 1. Differences between dakoticancrid species discussed here; *Dakoticancer overanus* data from Jones et al. (2022). Taxon names in the table are those used historically, to highlight morphological differences. *Tetracarcinus subquadratus*, *Seorsus wadei*, and *Dakoticancer australis* are herein synonymized as *T. subquadratus*.

Characteristic	*Tetracarcinus subquadratus*	*Seorsus wadei*	*D. australis*	*D. overanus*
Overall carapace width (mm)	9.6–20.6, n = 34	9.9–33.6, n = 12	17.3–42.1, n = 59	Female mean 19.8, n = 90; Male mean 20.9, n = 176
L/W carapace mean, median, n	1.03, 1.05, 36	1.04, 1.06, 9	1.01, 1.02, 23	0.78, 0.78, 52
FOW/W mean, median, n	0.61, 0.62, 22	0.49, 0.51, 9	0.52, 0.52, 38	
IL/L median, n	0.15, 0.15, 14	0.22, 0.22, 8	0.22, 0.22, 27	Intestinal barely developed
Thin keel posterior to epibranchial	Present	Sometimes present	Absent	Absent
Orbits with beaded rim	Present	Absent	Absent	Present
Suborbital spine	Long	Moderate length	Moderate length	?
Intraorbital spine	Blunt projection	Well developed	Well developed	Absent
Outer-orbital spine	Blunt projection	Well developed	Well developed	Blunt projection
Pits along axial region	Deep	Reduced	Reduced	Deep
Ridges of granules on hepatic, epibranchial, branchial	Narrow	Broad	Broad	Broad
Fourth sternite	Broad rim anteriorly	Sharp rim anteriorly	Sharp rim anteriorly, interrupted axially in males	Broad rim anteriorly in female, sharper rim in male
Epibranchial	flattened	With oblique ridge	With oblique ridge	Transverse ridge
Branchial	Flattened	With weak oblique swelling	With weak oblique swelling	Transverse swelling
Granules on sternites	Few	Few to none	Few to none	Arranged in transverse rows

https://doi.org/10.1017/jpa.2024.25 Published online by Cambridge University Press

Table 2. Statistical results for comparisons of carapace length to carapace width (L/W) ratios of specimens assigned to *Dakoticancer australis*, *Seorsus wadei*, and *Tetracarcinus subquadratus*, as well as *Dakoticancer overanus*. Significant results shaded gray. Measurements in Supplementary Data tables.

One-way ANOVA: test for equal means of L/W ratio	Sum of squares	df	Mean square	F	p (same)
Between groups:	1.92563	3	0.641877	290.4	9.39E-54
Within groups:	0.256388	116	0.00221	Permutation p (n = 99,999)	
Total:	2.18202	119	1.00E-05		
Dunn's post hoc test for equal means of L/W ratio; Raw p values, uncorrected significance					
	L/W *D. australis*	L/W *Seorsus*	L/W *Tetracarcinus*	L/W *D. overanus*	
L/W *D. australis*		0.5336	0.3439	2.42E-16	
L/W *Seorsus*	0.5336		0.2177	2.60E-08	
L/W *Tetracarcinus*	0.3439	0.2177		1.13E-09	
L/W *D. overanus*	2.42E-16	2.60E-08	1.13E-09		
Kruskal–Wallis test for equal medians					
H(chi^2): 89.22					
H_c (tie connected): 89.22					
P (same): 3.221E-19					
There is a significant difference between sample medians					
Mann–Whitney pairwise					
	L/W *D. australis*	L/W *Seorsus*	L/W *Tetracarcinus*	L/W *D. overanus*	
L/W *D. australis*		0.2278	0.08733	2.032E-15	
L/W *Seorsus*	0.2278		0.05386	2.049E-06	
L/W *Tetracarcinus*	0.08733	0.05386		7.795E-12	
L/W *D. overanus*	2.032E-15	2.049E-06	7.795E-12		

segments; intestinal region from 11% to 22% length of carapace, may form a flattened area, especially in larger individuals; sternite 4 weakly inflated anteriorly, sternites with sparse granules not arrayed into rows; male pleon with all somites free, lateral terminations on pleonites rectangular, telson rounded–triangular; female pleon wide, with long epimeres, all pleonites free; coxae of pereiopods at same level as sternum; pereiopods 1 isochelous or weakly heterochelous.

Remarks.—*Tetracarcinus* is known from only one species, *T. subquadratus*. It was originally described from New Jersey and has been subsequently reported from many other Atlantic coastal and Gulf coastal North American locations. The age difference between the New Jersey and Delaware Atlantic coastal specimens of *T. subquadratus* (Santonian, Campanian) and those of the Gulf coastal Coon Creek localities (Maastrichtian) is notable. Therefore, we considered whether the specimens from each region should be referred to different species of *Tetracarcinus*. Specimens referred by Bishop (1988) and Kornecki et al. (2017) to *Tetracarcinus subquadratus* from the Coon Creek localities, as well as the small specimens herein, seem to share several similarities with the material figured by Weller (1905a, b, 1907), Rathbun (1935, pl. 10, fig. 16), and Roberts (1962, pl. 87, fig. 6). The specimen illustrated by Rathbun and Roberts cited here is one of Weller's cotypes, NJSM 7788, and illustrated here also (Fig. 1.7–1.9). Note that the cotype of Weller is an eroded carapace, and the ridges and fine detail of the cuticle are visible only under extreme magnification of the image. The specimens of Bishop (1988) and Kornecki et al. (2017) and those we sorted into *T. subquadratus* have the square carapace, the wide posterolateral margin, the thin keel bounding the posterior margin of the epibranchial region, and the granular ornamentation seen in the specimens of Weller (1905a, b, 1907).

A collection of specimens from the C and D Canal, Malicks collection, in the USNM was measured, USNM 794463–69. This canal is in Delaware, directly across the Chesapeake Bay from New Jersey, close to the type locations for *T. subquadratus*, which are Santonian and Campanian (Weller, 1905a, b, 1907). Decapod specimens collected from the C and D Canal are Campanian in age (Feldmann et al., 2013) (Fig. 1.4–1.6). Comparison of the Delaware specimens and the Maastrichtian Coon Creek, Mississippi, specimens referred to the *Tetracarcinus* morphology studied here showed no differences in carapace morphology, nor were the L/W and FOW/W width ratios significantly different (Tables 3–5). Thus, comparison of the Coon Creek specimens with those collected very near to the type

Table 3. Results of t-tests for carapace ratios of *Tetracarcinus subquadratus* from Blue Springs, Mississippi, locality and C and D Canal, Delaware, locality. Measurements in Supplementary Data tables.

t-tests for equal means: carapace L/W	
Blue Springs	C and D Canal
N = 30	N = 7
Mean: 1.0081	Mean: 0.98567
95% confidence: (0.98801, 1.0282)	95% confidence: (0.97239, 0.99894)
Variance: 0.0028988	Variance: 0.000206
Difference between means: 0.022446	
95% confidence interval (parametric): (–0.019622, 0.064515)	
95% confidence interval (bootstrap): (0.0005606, 0.043628)	
t: 1.0832	
p (same mean): 0.28612	Critical t-value (p = 0.05): 2.0301
Unequal variance t: 1.9992	p (same mean): 0.053611
Monte Carlo permutation: p (same mean): 0.2808	
t-tests for equal means: carapace FOW/W	
Blue Springs	C and D Canal
N = 26	N = 4
Mean: 0.60742	Mean: 0.55797
95% confidence: (0.58576, 0.62909)	95% confidence: (0.47304, 0.6429)
Variance: 0.0028769	Variance: 0.00285
Difference between means: 0.049452	
95% confidence interval (parametric): (–0.0095269, 0.10843)	
95% confidence interval (bootstrap): (–0.0031931, 0.094276)	
t: 1.7175	
p (same mean): 0.096926	Critical t-value (p = 0.05): 2.0484
Unequal variance t: 1.724	p (same mean): 0.15993
Monte Carlo permutation: p (same mean): 0.0971	

https://doi.org/10.1017/jpa.2024.25 Published online by Cambridge University Press

Table 4. Statistical results for comparisons of fronto-orbital width to carapace width (FOW/W) ratios of specimens assigned to *Dakoticancer australis*, *Seorsus wadei*, and *Tetracarcinus subquadratus*, as well as *Dakoticancer overanus*. Significant results shaded gray. Measurements in Supplementary Data tables.

One-way ANOVA: test for equal means of L/W ratio	Sum of squares	df	Mean square	F	p (same)
Between groups:	1.92563	3	0.641877	290.4	9.39E-54
Within groups:	0.256388	116	0.00221	Permutation p (n = 99,999)	
Total:	2.18202	119	1.00E-05		
Dunn's post hoc test for equal means of L/W ratio; raw p values, uncorrected significance					
	L/W *D. australis*	L/W *Seorsus*	L/W *Tetracarcinus*	L/W *D. overanus*	
L/W *D. australis*		0.5336	0.3439	2.42E-16	
L/W *Seorsus*	0.5336		0.2177	2.60E-08	
L/W *Tetracarcinus*	0.3439	0.2177		1.13E-09	
L/W *D. overanus*	2.42E-16	2.60E-08	1.13E-09		
Kruskal–Wallis test for equal medians					
H(chi^2): 42.83					
H_c (tie connected): 42.83					
P (same): 2.67E-09					
There is a significant difference between sample medians					
Mann–Whitney pairwise					
	FOW/W *D. australis*	FOW/W *Seorsus*	FOW/W *Tetracarcinus*	FOW/W *D. overanus*	
FOW/W *D. australis*		0.3372	1.32E-08	0.03724	
FOW/W *Seorsus*	0.3372		5.68E-05	0.858	
FOW/W *Tetracarcinus*	1.32E-08	5.68E-05		1.10E-06	
FOW/W *D. overanus*	0.03724	0.858	1.10E-06		

locality reveals that they are not different, supporting referral of the Coon Creek specimens to the same species of *Tetracarcinus*. Thus, we maintain all of the specimens within *T. subquadratus*.

Some of the New Jersey specimens are Santonian in age, which ranges from 86.3 to 83.6 Ma, and some are Campanian, which ranges from 83.6 to 72.1 Ma (ICC 2022.02; Cohen et al., 2013) (Table 6). The Coon Creek specimens are Maastrichtian, making them between 72.1 and 66 Ma (ICC 2022.02; Cohen et al., 2013). At most, this would be a species range of 20 million years. Stringer et al. (2020) refined the age of the Coon Creek to early Maastrichtian, which may narrow the species range even more. Reported average lifespans for species range from about 1 to 16 million years (Lamkin and Miller, 2016), placing *Tetracarcinus* at the upper limit. For comparison, the life span of a genus in another group of podotrematous brachyurans, Raninoida Ahyong et al., 2007, ranges from 4 to 37 million years (Hartzell et al., 2022), with 20 million years for a species falling within this range.

Parapaguristes has previously been shown to be a junior synonym of *D. australis*, representing the claw morphology of specimens referred to that taxon (Kornecki et al., 2017). The synonymy of *Dakoticancer australis*, *Seorsus wadei*, and *Tetracarcinus subquadratus* is documented in the following, with *T. subquadratus* as the senior synonym. We propose that the form previously assigned to *Tetracarcinus subquadratus* represents the smaller, possibly juvenile or sexually immature, members of the species (Fig. 1.1). The *Dakoticancer australis* morphology represents the larger, probably adult and sexually mature

Table 5. Statistical results for comparisons of intestinal region length/carapace length (IL/L) and carapace width of specimens assigned to *Dakoticancer australis*, *Seorsus wadei*, and *Tetracarcinus subquadratus*. Significant results shaded gray. Measurements in Supplementary Data tables.

One-way ANOVA: test for equal means of IL/L ratio	**Sum of squares**	**df**	**Mean square**	**F**	**p (same)**
Between groups:	0.04957	2	0.024785	42.3	3.78E-11
Within groups:	0.026954	46	0.000586	Permutation p (n = 99,999)	
Total:	0.076523	48	1.00E-05		
Dunn's post hoc test for equal means of L/W ratio; raw p values, uncorrected significance					
	IL/L *D. australis*	IL/L *Seorsus*	IL/L *Tetracarcinus*		
IL/L *D. australis*		0.8848	4.20E-07		
IL/L *Seorsus*	0.8848		9.97E-05		
IL/L *Tetracarcinus*	4.20E-07	9.97E-05			
One-way ANOVA: test for equal means of carapace width	**Sum of squares**	**df**	**Mean square**	**F**	**p (same)**
Between groups:	4,706.53	2	2,353.27	85.51	3.91E-22
Within groups:	2,669.36	97	27.5193	Permutation p (n = 99,999)	
Total:	7,375.89	99	1.00E-05		
Dunn's post hoc test for equal means of carapace width; raw p values, uncorrected significance					
	D. australis	*Seorsus*	*Tetracarcinus*		
D. australis		0.01028	2.10E-16		
Seorsus	0.01028		3.53E-03		
Tetracarcinus	2.10E-16	3.53E-03			

Table 6. Occurrences of *Tetracarcinus subquadratus*, based on revisions here.

Original referral	Author/reference	Current referral	Formation	Age
Tetracarcinus subquadratus	Weller (1905a, b; 1907); Roberts (1962)	*Tetracarcinus subquadratus*	Magothy Formation (as Cliffwood), New Jersey	Santonion
Tetracarcinus subquadratus	Weller (1905a, b; 1907); Roberts (1962)	*Tetracarcinus subquadratus*	Woodbury Formation, New Jersey	Campanian
?*Tetracarcinus subquadratus*	Rathbun (1935)	?*Tetracarcinus subquadratus*	Lewis Shale, Wyoming	Campanian to Maastrichtian
Tetracarcinus subquadratus	Bishop (1988); Kornecki et al. (2017)	*Tetracarcinus subquadratus*	Coon Creek Formation, Mississippi	Maastrichtian
Dakoticancer overanus	Rathbun (1926)	*Tetracarcinus subquadratus*	Coon Creek Formation, Tennessee	Maastrichtian
Dakoticancer overanus	Rathbun (1935)	*Tetracarcinus subquadratus*	Magothy Formation (as Cliffwood), New Jersey	Santonion
Dakoticancer australis	Rathbun (1935); Bishop (1988); Kornecki et al. (2017)	*Tetracarcinus subquadratus*	Coon Creek Formation, Mississippi	Maastrichtian
Dakoticancer australis	Rathbun (1935)	*Tetracarcinus subquadratus*	Navarro Group, Texas	Maastrichtian (Condon and Dyman, 2006)
Seorsus wadei	Bishop (1988)	*Tetracarcinus subquadratus*	Coon Creek Formation, Mississippi	Maastrichtian
Dakoticancer australis	Vega and Feldmann (1991)	*Tetracarcinus subquadratus*	Potrerillos Formation	Maastrichtian
Dakoticancer australis	Schweitzer et al. (2019)	*Tetracarcinus subquadratus*	Prairie Bluff Formation, Mississippi	Maastrichtian
Dakoticancer australis	Schweitzer et al. (2019)	*Tetracarcinus subquadratus*	Marlbrook Marl, Arkansas	Maastrichtian
Dakoticancer australis	Schweitzer et al. (2019)	*Tetracarcinus subquadratus*	Wolfe City Formation, Texas	Maastrichtian
Tetracarcinus subquadratus	Schweitzer et al. (2019)	*Tetracarcinus subquadratus*	Prairie Bluff Formation, Alabama and Mississippi	Maastrichtian
Tetracarcinus subquadratus	Schweitzer et al. (2019)	*Tetracarcinus subquadratus*	Demopolis Formation, Mississippi	Maastrichtian
Tetracarcinus subquadratus	Schweitzer et al. (2019)	*Tetracarcinus subquadratus*	Eutaw Formation, Mississippi	Maastrichtian

forms of the species (Fig. 1.3). Those specimens assigned to *Seorsus wadei* seem to occupy a position of intermediate size and intraspecific variability, with carapaces that are slightly narrower but not statistically significantly different in size or shape from *D. australis* (Fig. 1.2; Tables 2, 4, 5).

Tetracarcinus subquadratus Weller, 1905a
Figures 1–8

1905a *Tetracarcinus subquadratus* Weller, p. 328, figs. 4–6.
1905b *Tetracarcinus subquadratus*; Weller, p. 136, pl. 15.
1907 *Tetracarcinus subquadratus*; Weller, p. 852, pl. 111, figs. 16–19.
1926 *Dakoticancer overana* Rathbun, 1917; Rathbun, p. 189, pl. 67, fig. 3.
1929 *Dacoticancer* [sic] *overanus*; Glaessner, p. 134.
1935 *Dakoticancer overanus australis* Rathbun, p. 40, pl. 10, fig. 20.
1935 *Tetracarcinus subquadratus*; Rathbun, p. 41, pl. 10, figs. 16, 17.
1958 *Tetracarcinus subquadratus*; Holland and Cvancara, p. 496.
1962 *Tetracarcinus subquadratus*; Roberts, p. 184, pl. 87, figs. 3–6.
1969 *Dakoticancer overanus australis*; Glaessner, p. R491, fig. 303,2b.
1969 *Tetracarcinus subquadratus*; Glaessner, p. R491, fig. 303,1.
1983 *Dakoticancer australis*; Bishop, p. 426, figs. 3G, H, 6A–C, 7.
1983 *Paguristes whitteni* Bishop, p. 420, figs. 3E, F, 4A–I.
1985 *Dakoticancer australis*; Bishop, p. 1028.
1986a *Dakoticancer australis*; Bishop, p. 292.
1986b *Parapaguristes whitteni*; Bishop, p. 605, fig. 5B.
1988 *Seorsus wadei* Bishop, p. 72, fig. 1A–F.
1988 *Dakoticancer australis*; Bishop, fig. 1I, M.
1988 *Tetracarcinus subquadratus*; Bishop, fig. 1G, K.
1991 *Dakoticancer australis*; Bishop, p. 8, fig. 33G, H.
1991 *Dakoticancer australis*; Vega and Feldmann, p. 165, figs. 4, 5.
1995 *Dakoticancer australis*; Vega, Feldmann, and Villalobos-Hiriart, p. 240.
1998 *Dakoticancer australis*; Bishop et al., p. 242, fig. 1.6–1.9.
2010 *Dakoticancer australis*; Schweitzer et al., p. 57.
2010 *Seorsus wadei*; Schweitzer et al., p. 57.
2010 *Tetracarcinus subquadratus*; Schweitzer et al., p. 58.
2013 *Tetracarcinus subquadratus*; Feldmann et al., p. 28, fig. 13.
2013 *Seorsus wadei*; Feldmann et al., p. 29.
2016 *Dakoticancer australis*; Bishop, p. 13.
2017 *Dakoticancer australis*; Kornecki et al., p. 292, fig. 8C–I.
2017 *Tetracarcinus subquadratus*; Kornecki et al., p. 300, fig. 8A, B.

Holotype.—Syntypes are NJSM 7788 and 9532.

Diagnosis.—As for genus.

Occurrences.—Because of the similarities between and among the various species of *Dakoticancer* and *Tetracarcinus*, species

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occurrences have been reassigned over time (Table 6). Weller's (1905a, b, 1907) original localities were from the Cliffwood Clay (now Magothy Formation, Santonian) (USGS Magothy) and Woodbury Formation of Campanian age (USGS Woodbury). Rathbun (1935) later referred a specimen from the Campanian to Maastrichtian Lewis Shale of Wyoming (Gill et al., 1970) to *T. subquadratus*. Her image (Rathbun, 1935, pl. 10, fig. 17) looks like a member of *Tetracarcinus*, but the actual specimen (USNM PAL 73716) is quite fragmental. It may belong to a different taxon.

Previously reported Maastrichtian occurrences for *Dakoticancer australis* are in Arkansas (Schweitzer et al., 2019), Mississippi, and Texas (Rathbun, 1935), USA, and several locations in Mexico (Vega and Feldmann, 1991). *Seorsus* is known only from the type locality in Mississippi. Thus, *Tetracarcinus subquadratus* as defined here ranges from Santonian to Maastrichtian and is found in Alabama, Arkansas, Delaware, Mississippi, New Jersey, Tennessee, and Texas, USA, as well as northern Mexico (Table 6).

Description (notable differences between smaller, Tetracarcinus*-type, and larger,* Dakoticancer australis*-type, individuals in bold).*—**Carapace about as wide as long or slightly wider than long (smaller, usually <17 mm, L/W = 1.01, n = 14, Fig. 2.5, 2.6; larger, usually >17 mm, L/W averaging 1.04, n = 34, Figs. 2.1–2.4, 6.2)**, square, moderately vaulted transversely and longitudinally. Rostrum parallel-sided at base, narrowing distally, axially sulcate, with marginal beaded rim in smaller individuals. **FOW about 58% carapace width in smaller individuals (Fig. 2.5), 50–52% in larger individuals (Figs. 2.1, 6.4) (statistically significant; Table 4)**; orbits directed forward, upper-orbital margin biconcave, **inflection at boundary between orbit and augenrest in smaller individuals (Fig. 3.1), with intra-orbital spine in larger individuals (Fig. 3.2, IO) that is attenuated into long spine in large individuals (Fig. 3.2–3.4, IO)**; **outer-orbital spine barely projected in smaller individuals (Fig. 3.1, OO), spine well developed in larger individuals (Fig. 3.2–3.4, OO)**; lower orbital margin with long narrow spine (Fig. 3, SO). **In smaller individuals, orbital margin beaded, a second beaded keel diverging from orbit and bounding a flattened area posterior to orbital margin; in larger individuals, beaded rims absent and orbital margin with broad rim.**

Lateral margins weakly convex, with beaded rim extending from outer-orbital angle to intersection of cervical groove with margin, beaded rim connecting with a row of granules on hepatic region form a U-shaped granular structure (Fig. 2). Beginning just posterior to cervical groove intersection, a weak beaded rim arcs from paralleling the margin onto epibranchial region (Fig. 2). A narrow ridge extends from the lateral margin paralleling and bounding the posterior margin of the epibranchial region. Posterior to it, a beaded ridge extends obliquely onto the branchial region, terminating just short of the cardiac region (Fig. 2). Posterior margin with well-defined, beaded rim. **In smaller individuals, a narrow ridge extends from the lateral margin paralleling and bounding the posterior margin of the epibranchial region (Fig. 2.5, K), narrow ridge sometimes weakly expressed in larger individuals (Fig. 2.3, K).**

Mesogastric region with elongate anterior process widened posteriorly, posterior margin biconcave. Metagastric region widest anteriorly, narrowing posteriorly, posterior margin bounded by marked groove. Urogastric region developed only as a groove; cardiac region elongate, granular; intestinal area not well defined, **intestinal region about 11% carapace length in smaller individuals and 22% carapace length in larger ones (Fig. 6.3)**. Very deep pits/muscle scars bounding lateral margin of metagastric region, just lateral to anterior edges of cardiac region, and at anterior corners of metagastric region.

Protogastric region long, quadrate; hepatic region long, narrow, with arcuate beaded rim. Epibranchial region flattened, composed of two segments oriented at sharp angle to one another, bounded anteriorly by cervical groove that extends in straight segment from lateral margin obliquely toward axis, then turning sharply and obliquely toward mesogastric region; bounded posteriorly by branchiocardiac groove more or less parallel to cervical groove but not as strongly angled. **Remainder of branchial region not differentiated in smaller individuals; branchial region inflated transversely at about midlength, corresponding to arcuate granular ridge in larger individuals (Fig. 2.2)**.

Chelae with short manus, ornamented with rows of granules on outer surface; fingers thin, upper surface keeled; left and right of similar size or possible weakly heterochelous (Kornecki et al., 2017).

Only proximal portions of pereiopods 2–5 preserved; ischium and coxa (basis) fused, best and most often preserved; coxa of pereiopod 1 largest, pereiopod 2 and 3 coxae smaller, coxa 3 bearing female gonopore (Fig. 4.3), visible on some specimens; pereiopod 4 coxa only slightly smaller in length; pereiopod 5 coxa much reduced, often not visible.

Male sternites 1 and 2 triangular; sternite 3 very short, with lateral nodes just posterior to and on either side of triangular-shaped sternites 1 and 2 (Fig. 5.3), crescent-shaped swelling lies on sternite 3 between the nodes; **sternites 1–3 directed dorsally at high angle to other sternites in smaller specimens and at a lower angle in larger specim**ens. Sternites 4–7 with sparse granules, posterolateral edge of sternites 4–7 with episternal projections; each sternite depressed axially to accommodate pleon, creating narrow, deep sterno-pleural cavity. Sternite 4 inflated along anterior margin, **inflation stronger in larger individuals**, rectangular before becoming axially depressed, longest of all sternites, **with broad rim bounding anterior margin of sterno-pleonal cavity in smaller individuals, ridge in larger individuals** (Fig. 5.2, 5.4); sternite 5 widest of all sternites, rectangular, directed laterally; sternite 6 same shape as sternite 5, but slightly less wide, directed slightly posterolaterally; sternite 7 directed posterolaterally, **with sharp granules along sterno-pleonal depression in small individuals**; sternite 8 smallest, usually fully covered by pleon; all sternal sutures axially interrupted. Male pleon elongate, narrowing distally with 7 free somites; somites 1–5 rectangular, with sparse granules; somite 2 widest; somite 6 same length as other somites; rounded telson; pleon extending about one-quarter the length of sternite 4.

Female sternites 1 and 2 triangular; sternite 3 with lateral nodes just posterior to and on either side of triangular sternites 1 and 2 (Fig. 4.4, 4.5), crescent-shaped swelling lying between

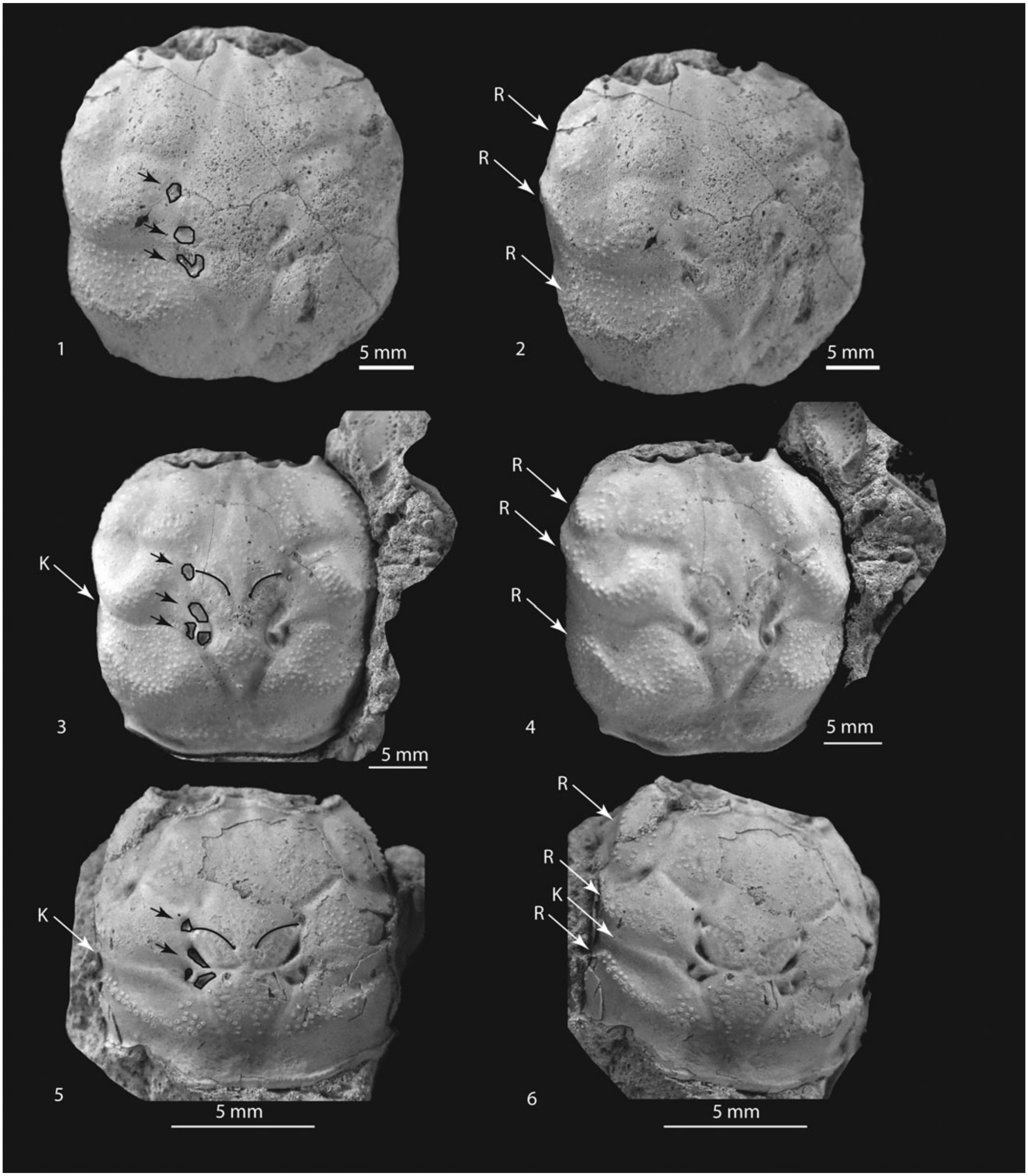

Figure 2. Comparative morphology of variously sized carapaces of *Tetracarcinus subquadratus* from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation: (**1**) large specimen MMNS-PI-11874, dorsal view, arrows indicate deep muscle scars outlined in black; (**2**) oblique left lateral view of specimen MMNS-PI-11874; (**3**) intermediate-sized specimen MMNS-PI-11891, arrows indicate deep muscle scars outlined in black; (**4**) oblique left lateral view of specimen MMNS-PI-11891; (**5**) small specimen MMNS-PI-11911, arrows indicate deep muscle scars outlined in black; (**6**) oblique left lateral view of small specimen MMNS-PI-11911. R = beaded rim; K = narrow keel bounding posterior margin of epibranchial region.

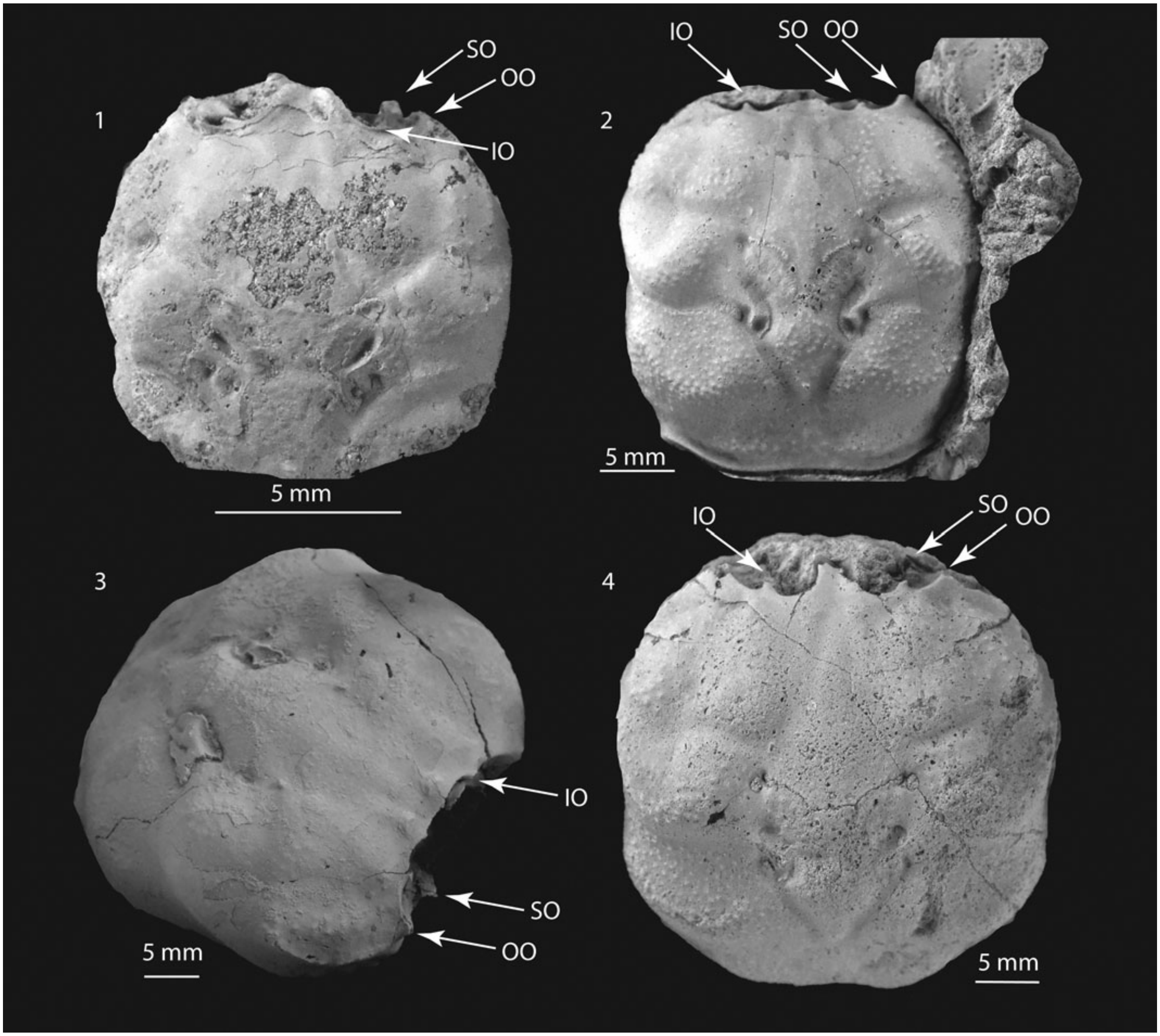

Figure 3. Comparative orbital morphology of variously sized carapaces of *Tetracarcinus subquadratus* from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation: (**1**) dorsal view of small specimen MMNS-PI-11875; (**2**) dorsal view of intermediate-sized specimen MMNS-PI-11891; (**3**) oblique frontal view of large specimen MMNS-PI-11908; (**4**) dorsal view of large specimen MMNS-PI-11874. IO = intraorbital spine; OO = outer-orbital spine; SO = suborbital spine.

nodes; sternites 1–3 directed dorsally, at moderate angle to other sternites. Sternites 4–8 gently slope axially, creating wide, shallow sterno-pleonal cavity to accommodate pleon; episternal projections at posterolateral edge of each sternite; sternites 4–7 flattened and without ornamentation. Sternite 4 rectangular, with granulated, inflated anterior margin, longest of all sternites, **with broad rim bounding anterior margin of sterno-pleonal cavity in smaller individuals, ridge in larger individuals** (Fig. 4.1–4.3); sternite 5 widest of all sternites, transversely rectangular, short; sternite 6 of same shape as sternite 5 only slightly less wide; sternite 7 directed posterolaterally; sternite 8 reduced; all sternal sutures incomplete. Spermathecae circular, occurring at termination of sternal suture 7/8 (Fig. 4.4). Female pleon wide, ovate, narrowing distally into broad triangular telson (Fig. 4.5); somites 1–5 convex with round margins; somite 3 laterally widest; somite 6 flat.

Material examined and occurrence.—See Materials and methods and Table 6.

Remarks.—Bishop (1988) described three different genera and species of dakoticancrid crab from the Blue Springs locality. He noted that only two of 1,500 specimens were referrable to *Seorsus* (Bishop, 1988, p. 75), whereas he referred 28 to *Tetracarcinus subquadratus* and 528 to *Dakoticancer australis* (Bishop, 1983, table 1). Kornecki et al. (2017) recognized no individuals of *Seorsus* when examining hundreds of specimens collected by us from the same locality. In our analysis, we

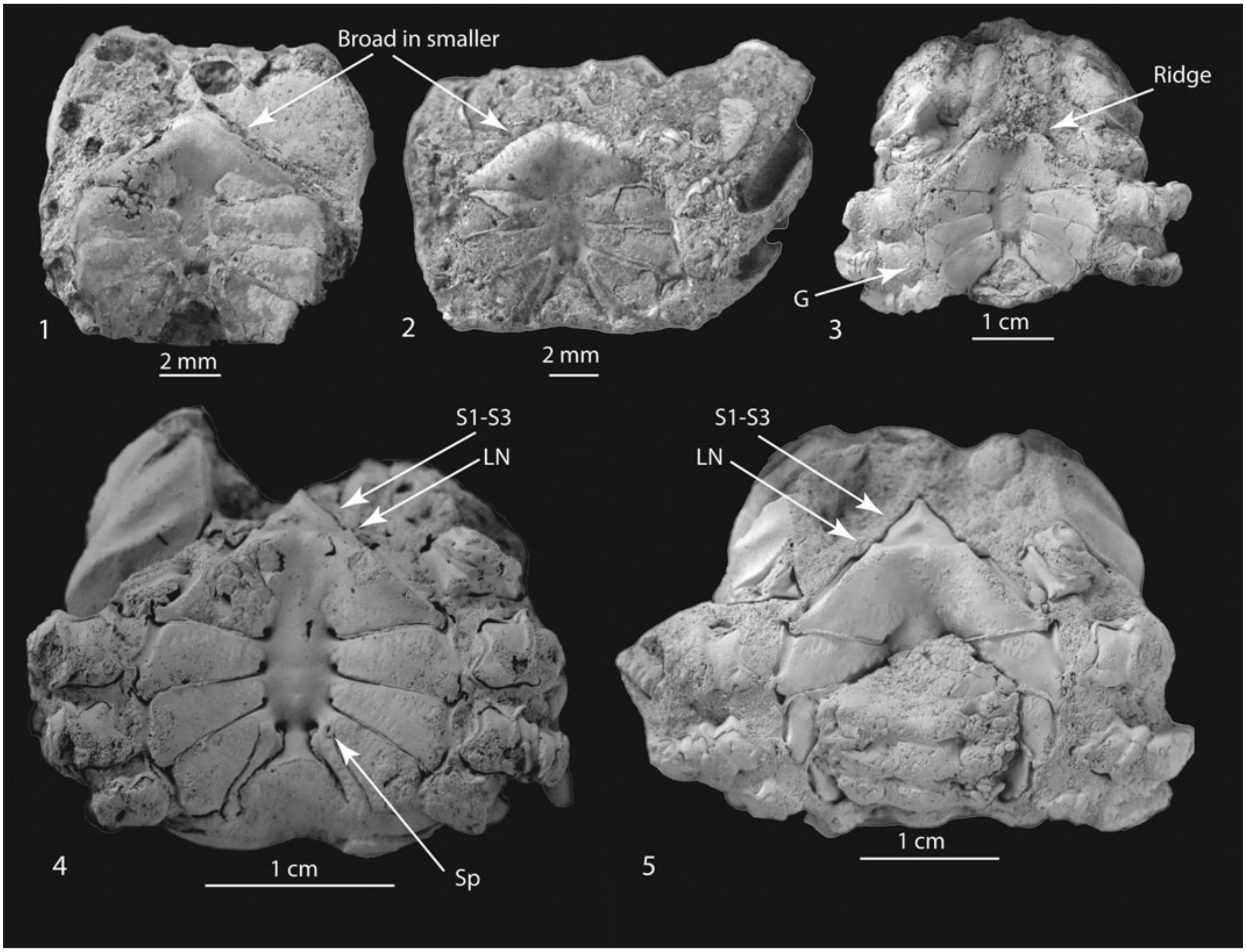

Figure 4. Comparative female ventral morphology of various sizes of *Tetracarcinus subquadratus* from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation: (**1**) sternum of small specimen MMNS-PI-11952 showing broad anterior rim bounding anterior edge of sternopleonal depression on sternite 4; (**2**) sternum of small specimen MMNS-PI-11943 showing broad anterior rim bounding anterior edge of sternopleonal cavity on sternite 4; (**3**) sternum of larger specimen MMNS-PI-11955 showing ridge bounding anterior edge of sternopleonal cavity on sternite 4 and gonopore (G) on coxa of third pereiopod; (**4**) sternum of large specimen MMNS-PI-11965 showing ridge bounding anterior edge of sternopleonal depression on sternite 4 and spermatheca at axial tip of sternal suture 7/8; (**5**) sternum of large specimen MMNS-PI-11951 showing ridge bounding anterior edge of sternopleonal depression on sternite 4 and partial pleon. S1–S3 = sternites 1–3; LN = lateral node.

isolated all of the rectangular, dakoticancroid specimens we collected from the Blue Springs locality. Then we compared the morphology of the specimens to images in Bishop (1988) as well as Weller (1905a, b, 1907), Rathbun (1935), and Roberts (1962) to qualify the characteristics they used to identify *Tetracarcinus*-type morphology. We determined that these characteristics included small, square carapaces (<17 mm wide) (Fig. 1.1); a short intestinal region compared with the overall length of the carapace; a thin keel bounding the posterior margin of the epibranchial region; beaded rims on the orbits and short intra- and outer-orbital spines; a long suborbital spine; very deep pits along the axial regions; and narrow ridges of granules on the hepatic, epibranchial, and branchial regions (Figs. 1.1, 2.5, 2.6, 3.1). We also noted that these specimens often retained cuticle but rarely retained the sternum.

Seorsus-type morphology was more difficult to define as it appears to be nearly identical to specimens assigned by Bishop (1988) and Kornecki et al. (2017) to *Dakoticancer australis*. The two specimens referred to *Seorsus* by Bishop (1988) seem to be somewhat narrower than those assigned to *D. australis* and may have better-preserved cuticle. Bishop (1988) noted that the main difference between *Seorsus* and other dakoticancrids was its trapezoidal shape; however, that seems to be illusory due to sediment and broken cuticle obscuring the posterolateral part of the carapace (Bishop, 1988, fig. 1A, E) (Figs. 1.2, 2.3, 2.4, 3.2). Otherwise, differences are not notable. Specimens assigned to *Dakoticancer australis* by Rathbun (1935), Bishop (1988), and Kornecki et al. (2017) are characterized by a large, square carapace (>17 mm) (Fig. 1.3), a long intestinal region compared with the overall length of the carapace, lack of a thin keel bounding the posterior margin of the epibranchial region, long intra- and outer-orbital spines, a suborbital spine, shallower pits along the axial regions, and broader ridges of granules on the hepatic, epibranchial, and branchial regions (Figs. 1.3, 2.1,

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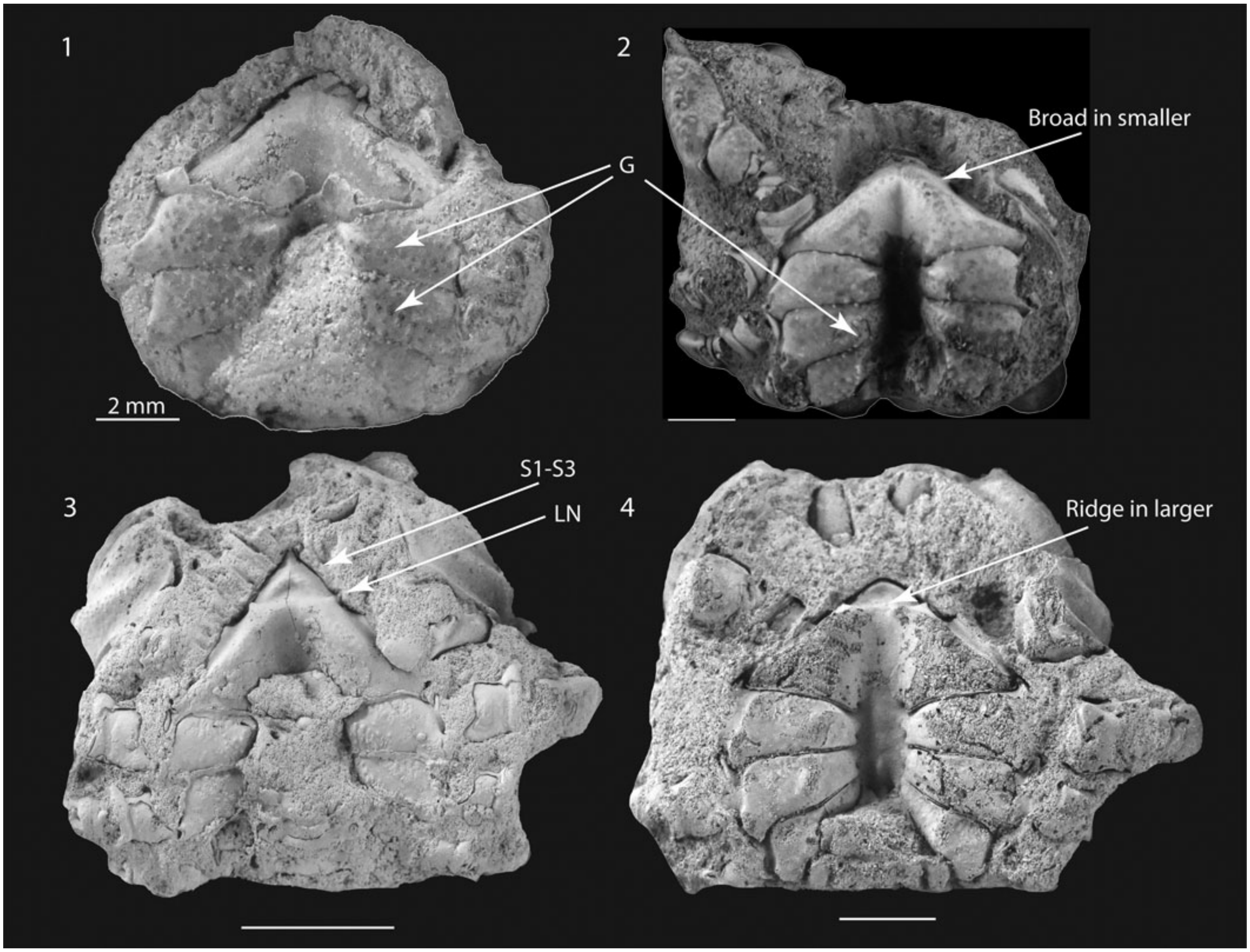

Figure 5. Comparative male ventral morphology of various sizes of *Tetracarcinus subquadratus* from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation: (**1**) sternum of small specimen MMNS-PI-11949; (**2**) sternum of small specimen MMNS-PI-11953 showing broad anterior rim bounding anterior edge of sternopleonal cavity on sternite 4; (**3**) sternum of larger specimen MMNS-PI-11928; (**4**) sternum of large specimen MMNS-PI-11894 showing sharp ridge bounding anterior edge of sternopleonal cavity on sternite 4. G = granules; S1–S3 = sternites 1–3; LN = lateral node. (**2**) Scale bar = 2 mm; (**3, 4**) scale bars = 1 cm.

2.2, 3.3, 3.4). We sorted our specimens according to these criteria to the best of our ability.

To determine whether separation of the specimens into the three different genera and species noted in the preceding was supportable, we quantitatively examined 105 specimens and qualitatively examined several hundred. In terms of size only, larger specimens had historically been referred to *D. australis* and smaller ones to *Tetracarcinus* (Fig. 1). Indeed, in the average carapace width, the three taxa were significantly different from one another (Table 1). In terms of the ratio of carapace length to carapace width, however, there was no significant difference between and among specimens separated into the three taxa using the preceding criteria (Fig. 6.2; Table 2). Thus, although the carapace size was significantly different, the overall shape of the carapace was not, as the individuals maintained a square shape throughout growth. In addition, specimens plotted by carapace width show no distinct clusters, strongly suggesting that these three taxa represent a growth series, not separate species (Fig. 6.1).

The ratio of the FOW to carapace width and the length of the intestinal region as a ratio of the entire carapace length was significantly different between *Tetracarcinus*-type specimens and those referred to the morphologies of the other two genera but was not significantly different between *D. australis* and *Seorsus*-type morphologies (Fig. 6.3, 6.4; Tables 4, 5). The smaller, *Tetracarcinus*-type, and larger, *D. australis*-type, specimens differ in degree of development of carapace ornamentation (Table 1). Smaller specimens have smaller orbital spines, whereas larger ones of *D. australis* morphology have long orbital spines. In smaller specimens, the orbital margin is beaded, whereas in larger specimens, it is rimmed. Smaller specimens have a narrow keel bounding the posterior margin of the epibranchial region, which is missing in most larger specimens. Larger specimens have a more inflated branchial region than smaller specimens.

Sternal differences are evident between *Tetracarcinus* and *D. australis*-type morphologies (Figs. 4, 5). *Seorsus* sterna are uncommon and similar to *D. australis.* In smaller specimens

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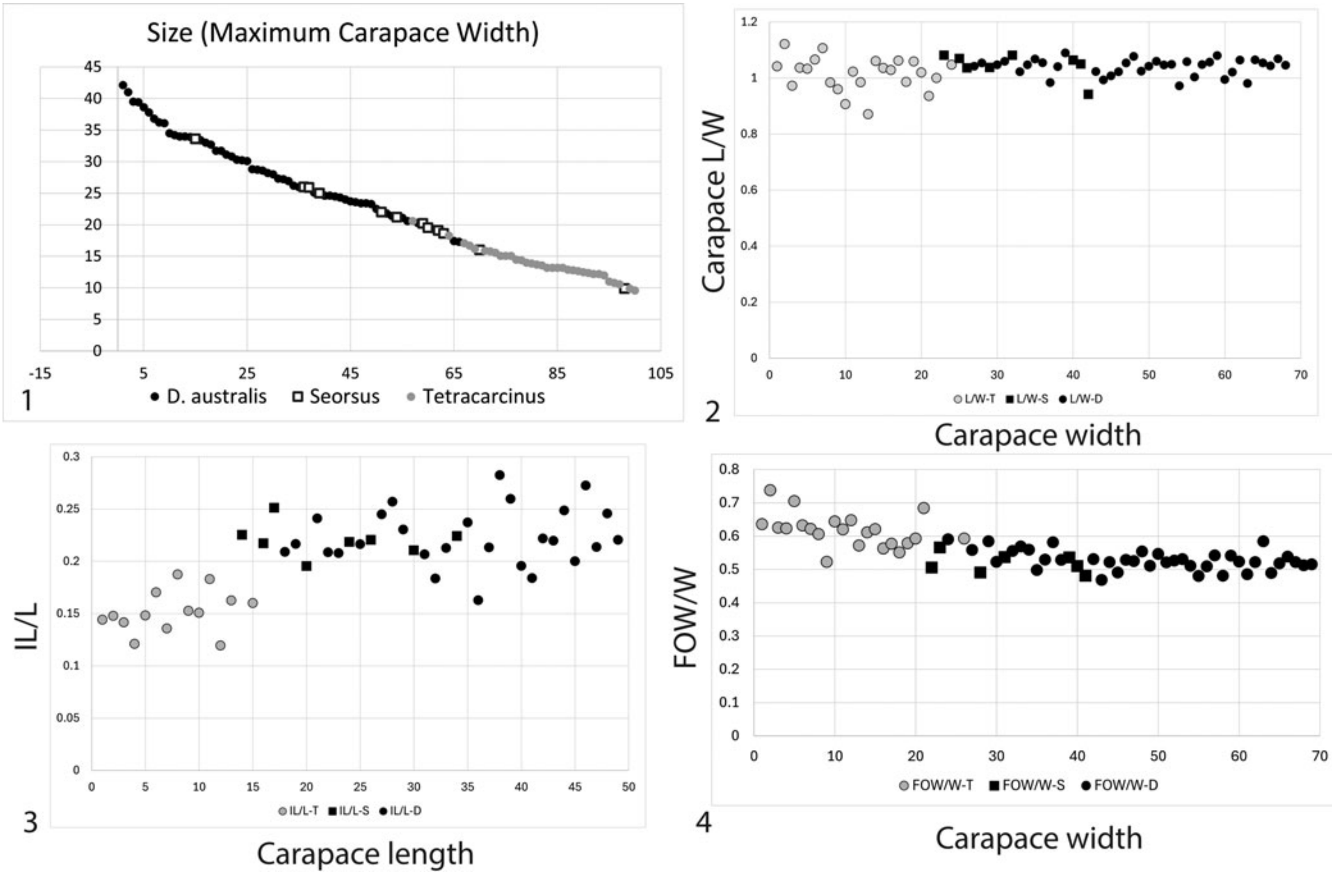

Figure 6. Carapace size and size ratios. Data in Supplementary Data tables 1–6. (**1**) Carapace size of approximately 100 specimens of *Tetracarcinus subquadratus* from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation. Solid black dots indicate specimens sorted into *Dakoticancer australis* morphology; hollow dots indicate specimens sorted into *Seorsus*-type morphology; gray dots indicate specimens sorted into *Tetracarcinus*-type morphology. (**2**) Carapace width plotted against carapace L/W ratio. (**3**) Carapace length plotted against IL/L ratio. (**4**) Carapace width plotted against FOW/W ratio. T = *Tetracarcinus* morphology; S = *Seorsus* morphology; D = *Dakoticancer australis* morphology.

(*Tetracarcinus*-type), the anterior margin of sternite 4 is broadly inflated (Figs. 4.1, 4.2, 5.2), whereas in larger specimens (*D. australis*-type), the margin forms a distinct ridge across the sternum, interrupted axially in males (Figs. 4.3, 5.4). Smaller males and females bear granules on the sternites, sometimes roughly arrayed in rows and sometimes present along the edge of the sterno-pleonal cavity. Larger specimens have few granules in males, and the females are smooth.

Changes in carapace morphology during ontogeny are documented for several species of brachyuran crab. Juvenile, smaller individuals of *Metacarcinus magister* (Dana, 1852) (Eubrachyura, Cancridae) are different in carapace shape and FOW to carapace width compared with larger adults (Hiebert and Rasmussen, 2015) (Fig. 7.5, 7.6). Eyestalks and eyes, and presumably the width of the orbits as well, are commonly relatively larger in juvenile, presumably smaller brachyuran individuals (Marochi et al., 2019). In thoracotreme crabs (Eubrachyura, Thoracotremata), the overall carapace shape changes as the animal grows, such that the posterior part of the carapace changes in overall proportion to the anterior portion (Marochi et al., 2019). In *Callinectes danae* Smith, 1869 (Eubrachyura, Portunidae), the anterolateral and frontal spines were more strongly ornamented in smaller, younger specimens compared with older ones (Shinozaki-Mendes and Lessa, 2019). Analyses of the juvenile crab stage of four different species of panopeid crab (Eubrachyura, Panopeidae, about 1–2 mm width) showed that the FOW/W ratio notably decreased and the anterolateral spines became larger as the animal grew (Martin et al., 1984). For comparison, adult *Panopeus* spp. may reach 15–20 mm in width (Williams, 1984). Comparison of adult *Menippe mercenaria* (Say, 1818) (USNM 1568616) (accessed at https://collections.nmnh.si.edu/search/iz/) and juveniles (accessed at collierseagrant.blogspot.com) indicates that the fronto-orbital width is much wider as a ratio of the carapace width in juveniles (Fig. 7.3, 7.4).

Considering all of this evidence, we propose that the differences between and among the *Dakoticancer australis*, *Tetracarcinus subquadratus*, and *Seorsus wadei* morphologies are of degrees and are most parsimoniously explained by changes in the carapace and sternum during growth (Fig. 7.1, 7.2). Those differences that are significantly different are the result of ontogenetic changes. The types of changes observed across *Dakoticancer australis*, *Tetracarcinus subquadratus*, and *Seorsus wadei* are those documented for many species of extant brachyurans as they grow, including changes in the FOW/W ratio, changes in length of some regions of the carapace, and changes in the size of spines and degree of ornamentation. Thus, these types of differences are well documented as

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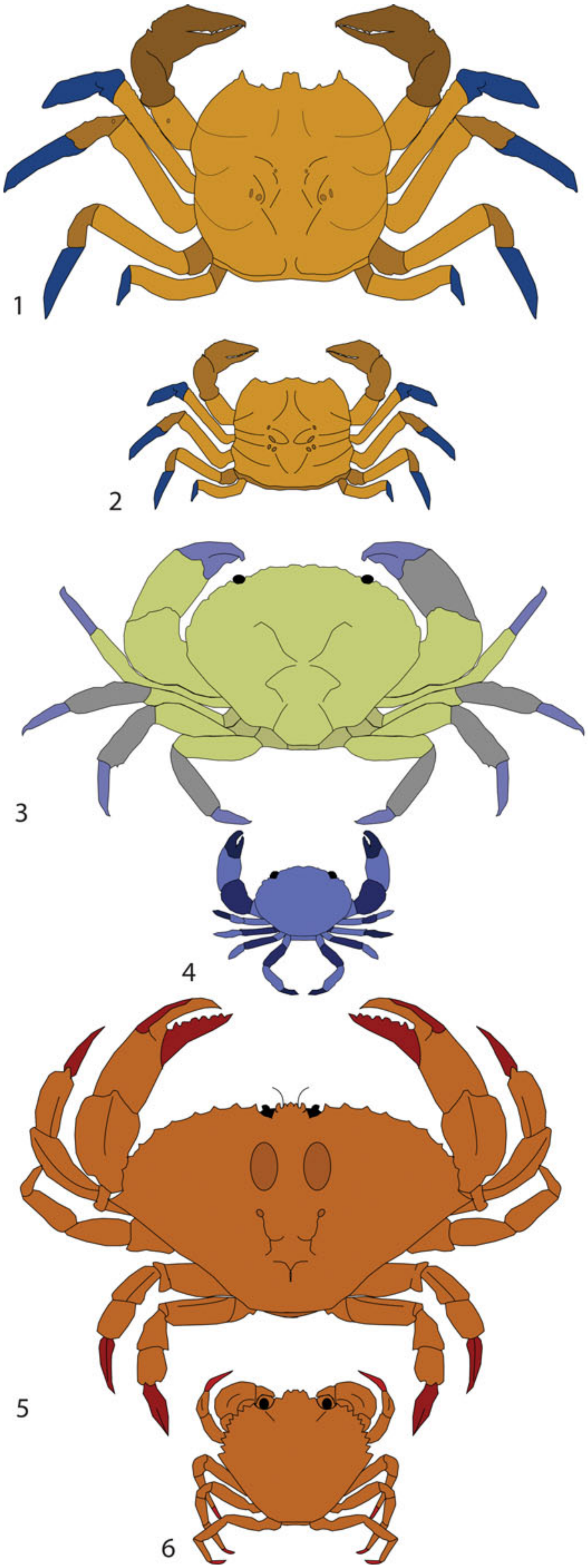

Figure 7. Differences between small and large individuals during ontogeny. Specimens not to scale. (**1**) *Tetracarcinus subquadratus*, morphology of larger individuals, stylized from specimens herein. (**2**) *Tetracarcinus subquadratus*, morphology of smaller individuals, stylized from specimens herein. (**3**) *Menippe mercenaria,* morphology of larger individuals, stylized from image of USNM 1568616. (**4**) *Menippe mercenaria,* morphology of smaller individuals, stylized from image of a juvenile at http://collierseagrant.blogspot.com/2012/11/a-florida-stone-crabs-life-cycle.html. (**5**) *Metacarcinus magister,* morphology of larger individuals, stylized from Hiebert & Rasmussen (2015). (**6**) *Metacarcinus magister,* morphology of smaller individuals, stylized from Hiebert & Rasmussen (2015). Art by J.F.

ontogenetic. These three species, in addition to *Parapaguristes whitteni*, are therefore all referrable to the same species, *Tetracarcinus subquadratus*.

Specimens referred to *Dakoticancer australis* from the Maastrichtian Potrerillos Formation in northeastern Mexico have a slightly different morphology from those documented from the Blue Springs and nearby localities (Vega and Feldmann, 1991; herein) (Fig. 8). They are most similar in size, and thus morphology, to the largest specimens from Blue Springs, which were originally referred to *D. australis*. The Mexican specimens range from slightly wider than long to slightly longer than wide, have more inflated and developed carapace ridges than the larger Blue Springs specimens, and have a more strongly depressed posterior margin than the Blue Springs specimens. The only preserved sternum of the Mexican specimens appears to have sternites 5 and 6 directed posterolaterally (Fig. 8.2); however, this could be because of shearing of the specimen, seen in the dorsal carapace of LP-108 (Fig. 8.3). Although there are some differences between these and the American specimens, we elect to retain them in *Tetracarcinus subquadratus*, most similar to the *D. australis* morphology. Their pronounced ornamentation might be peramorphic in nature.

Family Ibericancridae Artal et al., 2008

Included genera.—*Ibericancer* Artal et al., 2008; *Sodakus* Bishop, 1978; *Synoriacarcinus* new genus; *Tropidicarcinus* Schweitzer et al., 2019.

Diagnosis.—As in Feldmann et al. (2017).

Remarks.—*Seorsus* is herein removed from Ibericancridae and placed into synonymy with *Tetracarcinus* as discussed in the preceding. *Seorsus millerae* (Bishop, 1992) had originally been referred to *Diaulax* on the basis of its elongate-rectangular carapace and inflated epibranchial regions (Fig. 9.1) and was later removed to *Seorsus* (Karasawa et al., 2011). A sternum associated with the carapace of *S. millerae* was subsequently described, demonstrating its affinities with *Ibericancer* in having a very narrow sternum, long sternites 3 and 4, and a deep, narrow sterno-pleonal cavity (Feldmann et al., 2013) (Fig. 9.2). Thus, the bases for placement of *Seorsus* into Ibericancridae were the sternal features of *Seorsus millerae* as the type specimens of *Seorsus wadei*, the type species, did not have sterna. The discovery of dakoticancrid-type sterna with specimens of *Seorsus wadei*, as well as its synonymy with *Tetracarcinus*, necessitate a new genus for *Seorsus millerae* and *Seorsus kauffmani* (Feldmann

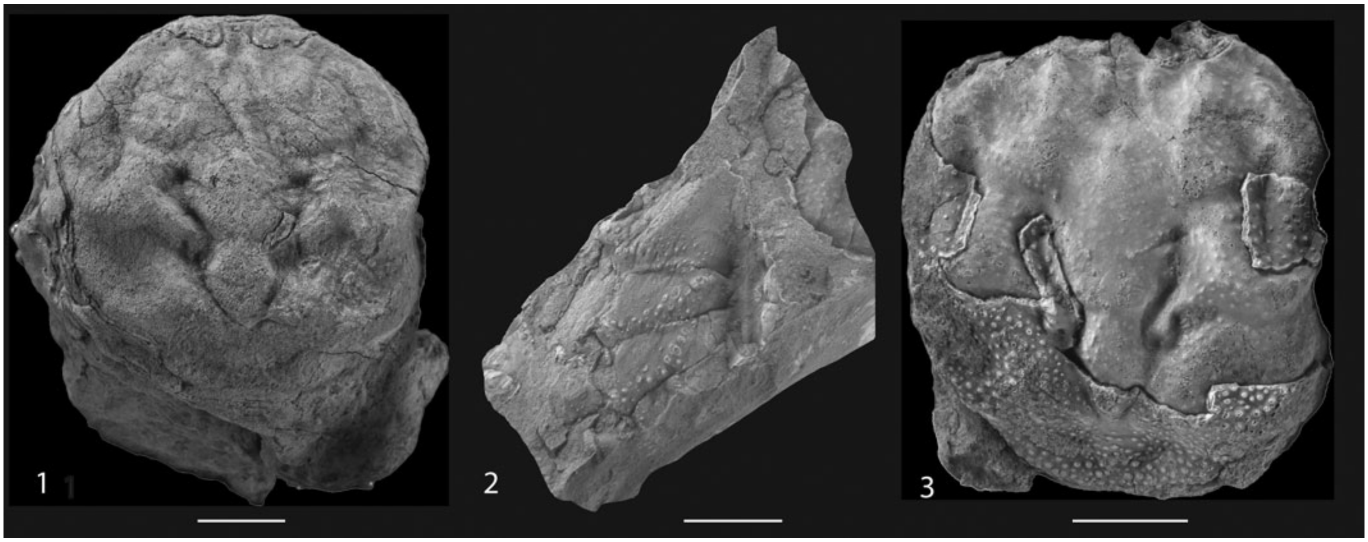

Figure 8. *Tetracarcinus subquadratus* from the La Popa Basin, Mexico, Portrerillos Formation, Maastrichtian. (**1**):LP130, dorsal carapace, cuticle missing. (**2**) KSU D 715, male sternites 4–6. (**3**) LP108, slightly sheared dorsal carapace. Scale bars = 1 cm.

et al., 2013), previously referred to *Seorsus* but now shown to have carapace and especially sternal morphology that ally them with Ibericancridae.

Genus *Synoriacarcinus* new genus
Figure 9

Type species.—*Diaulax millerae* Bishop, 1992 by original designation.

Other species.—*Synoriacarcinus kauffmani* (Feldmann et al., 2013) new combination; *Synoriacarcinus millerae* new combination.

Diagnosis.—Carapace longer than wide, length about 90% width, widest at position of single, prominent anterolateral spine; orbits square, rimmed, with intraorbital spine; FOW 50–70% carapace width; branchiocardiac groove well defined, cervical groove moderately defined; metagastric region wider than mesogastric region; epibranchial region forming a transverse broad ridge; sternum and sterno-pleonal cavity narrow, sternites 1–3 fused, sternite 4 long, with concave lateral margins, sternal suture 4/5 incomplete; male pleon with all somites free; subdorsal pereiopods 4 and 5; major chela bulbous, granular.

Etymology.—The genus name is formed from the Greek *synoria*, meaning borderland, and *karkinos*, crab, referring to its occurrence on the margins of Cretaceous North America.

Remarks.—The two species referred to *Synoriacarcinus* n. gen. are very similar in terms of the dorsal carapace, with *Synoriacarcinus kauffmani* differing from the type species in its wider fronto-orbital width, 70% as compared with 50% in *S. millerae*, and straighter posterior margin. *Synoriacarcinus*

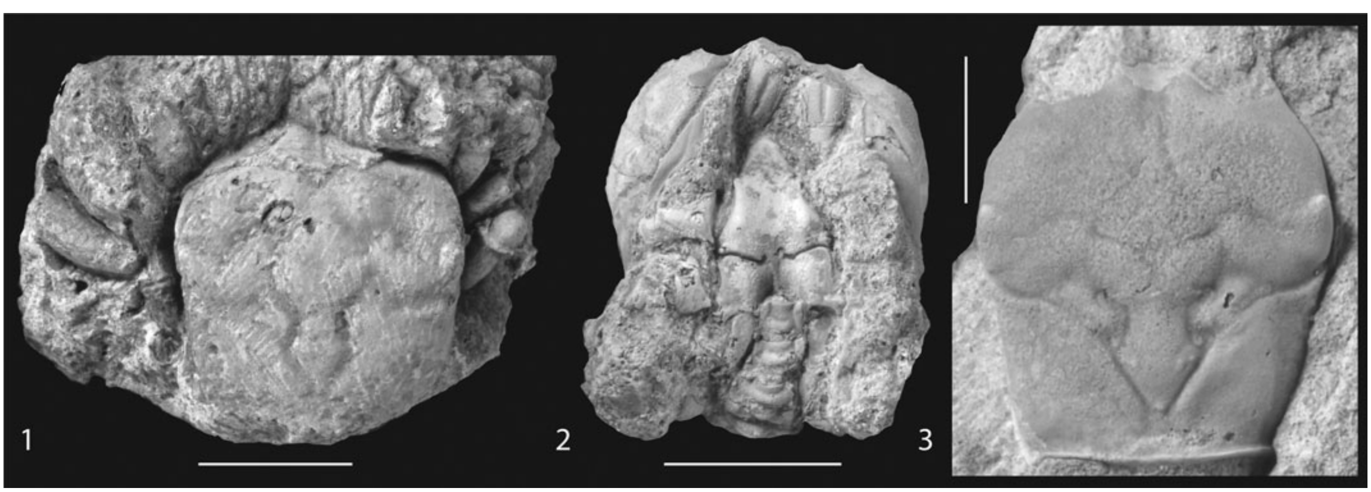

Figure 9. Species of *Synoriacarcinus* new genus. (**1**) *Synoriacarcinus millerae* (Bishop, 1991) new combination, NJSM 23326, dorsal view; (**2**) *Synoriacarcinus millerae* (Bishop, 1991) new combination, NJSM 23318, ventral view of sternum and male pleon. (**3**) *Synoriacarcinus kauffmani* (Feldmann et al., 2013) new combination, USNM PAL 553513, dorsal carapace. Scale bars = 1 cm. All images from Feldmann et al. (2013, fig. 14).

https://doi.org/10.1017/jpa.2024.25 Published online by Cambridge University Press

kauffmani is Turonian in age, from New Mexico, whereas *S. millerae* is Campanian in age, known from New Jersey and Delaware.

Synoriacarcinus differs from *Sodakus* in having a narrower sternum overall, about half as wide, as compared with *Sodakus tatankayotankaensis* Bishop, 1978. *Synoriacarcinus* is widest at about the midlength whereas *Sodakus* is widest in the posterior one-third. *Ibericancer* is nearly as wide as long, whereas *Synoriacarcinus* is longer than wide, and *Ibericancer* lacks regional development as seen on the new genus. *Tropidicarcinus* is squarer and has a wide, arcuate posterior margin differentiating it from *Synoriacarcinus*.

Sodakus is represented by three species in North America, ranging from the Turonian of New Mexico to the Maastrichtian of Mexico and South Dakota, USA. *Ibericancer* is known from the Campanian of Spain. *Synoriacarcinus* is reported from the Turonian of New Mexico and the Campanian of New Jersey. *Tropidicarcinus* is reported from the Campanian and Maastrichtian of Mississippi. Thus, not unlike Dakoticancridae, Ibericancridae was well established on Gulf Coastal and Western Interior North America (Fig. 10).

Figure 11. *Tetracarcinus subquadratus*, MMNS-PI-11950, from the Blue Springs locality, Mississippi, Maastrichtian Coon Creek Formation, internal mold of carapace completely infilled by fecal pellets. Scale bar = 1 cm.

Discussion

Sex ratios are similar in *Dakoticancer overanus* and *Tetracarcinus subquadratus*. The large collection of *Dakoticancer overanus* studied by Jones et al. (2022) exhibited 2.5 males for every one female. Kornecki et al. (2017) examined specimens referred to *D. australis* (now *Tetracarcinus subquadratus*), which showed a similarly skewed ratio of 1.67 males for every one female. Of those specimens that were measurable in this study, 52 were male and 31 were female, similar to the findings of Kornecki et al. (2017). Perhaps this is a feature of populations of Dakoticancridae, as discussed in detail by Jones et al. (2022). Jones et al. (2022) suggested habitat partitioning as a possible reason for the skewed sex ratio in the collection of *D. overanus*. This seems possible for the *Tetracarcinus* specimens from Coon Creek as all the specimens were collected from the same small locality, similar to those of *D. overanus*. Perhaps a different location would yield a higher percentage of females.

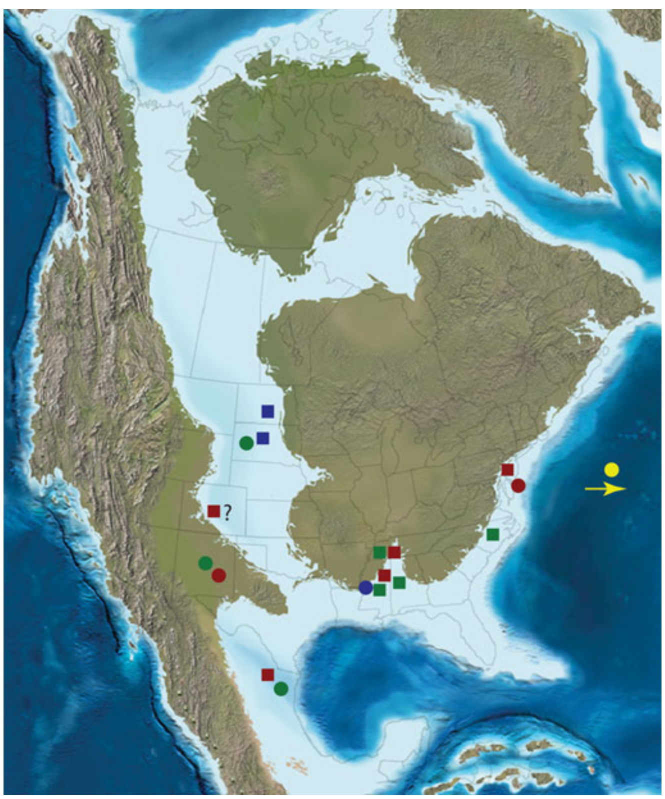

Figure 10. Geographic distribution of Dakoticancridae and Ibericancridae, plotted on a 65 Ma map (earliest Danian). Map by R. Blakey (2012), reproduced under the CC Attribution 1.0 generic license. Red squares = *Tetracarcinus*; blue squares = *Dakoticancer*; green squares = *Avitelmessus*; red circles = *Synoriacarcinus* n. gen.; blue circles = *Tropidicarcinus*; green circles = *Sodakus*; yellow circle = *Ibericancer* (off map, locality in Spain).

The *Dakoticancer overanus* collection of Mobridge, South Dakota, has well-documented intersex individuals, recently summarized and investigated in depth (Jones et al., 2022). Whereas intersex individuals compose a small percentage of the population (<1%), the specimens were readily identifiable as intersex by having male and female gonopores on the same specimen, gonopores on the "wrong" pereiopod, or a sternum morphology of the opposite sex as the gonopore position suggested. No such specimens of *Tetracarcinus subquadratus* have been found. It should be noted that spermatheca are known from only a few specimens (Fig. 4.4), and few gonopores have been identified on coxae of *T. subquadratus*, and those only on females (Fig. 4.3). Thus, at this time, it seems that the intersex population of *D. overanus* must have been unique to either that specific population or the environment in which it lived, not to Dakoticancridae as a group.

In regard to preservation, specimens of *Tetracarcinus subquadratus* from the Blue Springs exhibit a variety of preservations, often depending on size. Smaller individuals often retain cuticle, brownish or tan in color. Larger specimens have black cuticle, often missing the outer layers. Molds of the interior are very common, and one notable specimen is a mold of the interior preserved as fecal pellets (Fig. 11).

https://doi.org/10.1017/jpa.2024.25 Published online by Cambridge University Press

Acknowledgments

Specimens were collected from the Blue Springs locality on two trips, with assistance from O. Franţescu and A. Franţescu (University of Pittsburgh at Bradford), A.R. Jones (UNLV), R. Keyes, K. Kornecki, G. Phillips (Mississippi Museum of Natural Science), and members of the North Mississippi Gem and Mineral Society. Phillips read an earlier draft of the manuscript. E. Lauginiger, Delaware, donated the C and D canal specimens of *Tetracarcinus subquadratus* to the KSU collection. R. Pellegrini, New Jersey State Museum, provided the photos of the cotype of *T. subquadratus*. N. Drew and J. Nakano facilitated access to the paleontological collections at USNM and provided an image of USNM 73716. J.F. was funded by a SURE (Summer Undergraduate Research Experience) stipend awarded by KSU. F.J. Vega (UNAM) collected specimens studied herein from Mexico. A. Hunter, Youngstown State University, helped sort the specimens of *Tetracarcinus* from the Blue Springs locality. Constructive reviews by M. Hyžný (Comenius University, Bratislava, Slovakia), an anonymous reviewer, and Guest Editor A.A. Klompmaker, University of Alabama, Tuscaloosa, Alabama, USA, strengthened this manuscript.

Declaration of competing interests

The authors declare none.

Data availability statement

Supplementary Data tables 1–10 may be found at https://doi.org/10.5281/zenodo.11507484.

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Accepted: 24 July 2024