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New Brachyura (Crustacea: Decapoda: Raninoida: Eubrachyura) from the earliest Eocene of New Jersey, USA

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Abstract

Earliest Eocene carbonates of the Vincentown Formation, New Jersey, yield a limited but notable brachyuran fauna. *Arcticocarcinus americanus* new species marks the first Cenozoic record of Necrocarcinidae (Raninoida) in North America. Three different epibionts colonize the carapace of the holotype of *A. americanus* new species. *Feldmannicarcinus* new genus documents a preference for carbonate environments within Tumidocarcinidae (Carpilioidea), unusual among members of the family. *Feldmannicarcinus sturgeoni* (Feldmann et al., 1998) new combination and *Feldmannicarcinus hajzeri* new species document the new genus from Ypresian through Bartonian rocks of east coastal North America. Mounting evidence suggests that Paleocene carbonate localities of the North Atlantic served as a Cenozoic refugium for many decapod lineages that originated in the Cretaceous (Schweitzer and Feldmann, 2023).

Key words: Vincentown Formation, epibionts, Necrocarcinidae, Carpilioidea, Tumidocarcinidae, Ypresian

1. Introduction

The Paleocene and early Eocene were times of notable transition in brachyuran faunas (Schweitzer and Feldmann, 2015, 2023). Some podotrematous lineages, including Homoloidea De Haan, 1839; Lyreididae Guinot, 1993; Raninidae De Haan, 1839; and Dromioidea De Haan, 1833, survived the end-Cretaceous extinction and experienced a renewed peak of diversity during the Eocene (Artal et al., 2022; Hartzell et al., 2022; Schweitzer and Feldmann, 2023; Shaffer and Schweitzer, 2024). Others, such as Longodromitidae Schweitzer and Feldmann, 2009; Necrocarcinoidea Förster, 1968; and Etyoidea Guinot and Tavares, 2001, persisted into the Cenozoic, but their diversity sequentially dropped until their extinction during the middle Cenozoic (Schweitzer and Feldmann, 2023). Of the eubrachyuran fauna, Carpilioidea Ortmann, 1893, originated in the Cretaceous and radiated extensively by Eocene time when it peaked in diversity. The Vincentown Formation yields a limited but distinct brachyuran fauna that contains each of these three categories of brachyuran crab, a dromioid, a necrocarcinoid, and a carpilioid (Schweitzer, 2024).

The Vincentown Formation of New Jersey is composed of fossiliferous carbonate sand. Its age as determined by nannofossils is earliest Eocene (summarized in Schweitzer, 2024; Cohen et al., 2013, ICC chart 2024/12). The fossils reported here were collected from the North Branch of the Rancocas Creek, Vincentown section, in Southampton Township, Burlington County, New Jersey, USA. *Vincentdromia americana* (Roberts, 1956), is a member of Dromiidae, a dromiacean family that diversified in the Eocene and is extant (Schweitzer, 2024). New specimens recovered from the Vincentown Formation and described here document lineages that survived the end-Cretaceous extinction only to become extinct by the Miocene.

2. Materials and methods

Specimens were colored with water soluble dye and whitened with ammonium chloride prior to photography. Imaging was done with a Leica Z6 APO macroscope with PLANOPO 0.5x lens and SPOTFLEX digital camera or a Nikon D7200 with Tamron 28x105 mm lens. Enlargements of the epibionts were imaged with a Leica M125C microscope with PLANOPO 0.5x lens and K3C camera with LASX z-stacking software. Images were toned in Adobe Photoshop 23.1.0 prior to composing figures in Adobe Illustrator 26.0.2. Measurements were taken with Mitutoyo analog calipers to the nearest tenth of a millimeter.

Repositories and institutional abbreviations: The specimens are deposited in the New Jersey State Museum (NJSM), Trenton, NJ, USA. Other institutional abbreviations for material examined include CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Paleontology Collections, Brussels, Belgium; LO, Department of Geology, Lund University, Lund, Sweden; MPEF, Museo Paleontologico Egidio Feruglio, Trelew, Chubut, Argentina; UT, Jackson School Museum of Earth History, Non-Vertebrate Paleontology, University of Texas, Austin, Texas, USA.

3. Systematic Paleontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Raninoida Ahyong, Lai, Sharkey, Colgan and Ng, 2007
Superfamily Necrocarcinoidea Förster, 1968

Family Necrocarcinidae Förster, 1968

Included genera: *Arcticocarcinus* Schweitzer et al., 2016; *Elektrocarcinus* Schweitzer et al., 2016; *Hadrocarcinus* Schweitzer et al., 2012; *Necrocarcinus* Bell, 1863; *Thelecarcinus* Böhm, 1922.

Diagnosis: as in Schweitzer et al. (2016, 2018a, 2024).

Discussion: The new specimen fits the diagnostic characters of Necrocarcinidae in possessing orbits set above the anterolateral margin, a rounded carapace that is about as wide as long, distinct cervical and branchiocardiac grooves, and spinose anterolateral margins.

The long anterolateral spine on the new specimen is reminiscent of the long spine of the orithopsid genus *Cristella* Collins and Rasmussen, 1992. Orithopsidae Schweitzer et al., 2003, do not have the anterolateral margin placed below the level of the orbits, as in Necrocarcinidae and the new specimen. Orithopsids are more flattened and less vaulted than necrocarcinids, and they usually have strongly ornamented orbital areas. The new specimen is damaged in the orbital area but yields no evidence of spinose orbits or a produced rostrum. The outer-orbital angles of *Cristella* are produced into triangular spines, which in the new specimen, are blunt and short. The new specimen is therefore placed within Necrocarcinidae with members of which it shares diagnostic carapace features.

Arcticocarcinus Schweitzer, Karasawa, Luque and Feldmann, 2016

Type species: *Necrocarcinus insignis* Segerberg, 1900, by original designation and monotypy.

Other species: *Arcticocarcinus americanus* new species.

Diagnosis: As in Schweitzer et al. (2016, 2018a).

Discussion: The single specimen here referred to *Arcticocarcinus* is poorly preserved. However, it retains some distinctive features that suggest referral to *Arcticocarcinus.* The position of the orbits is above the anterior portion of the anterolateral margin, so that the anterolateral margin extends upward and posteriorly from its origin at the orbits. This is diagnostic for most necrocarcinids (Schweitzer et al., 2016). The specimen has a very large, stout anterolateral spine directed anterolaterally, diagnostic of *Arcticocarcinus*. It also has a stout posterolateral spine that differs from the type species of *Arcticocarcinus* in being situated further anteriorly than that of *A. insignis*. In addition, the cervical and branchiocardiac grooves are present but weak in the new specimen, and the ornamentation and development of carapace regions is similar to *Arcticocarcinus insignis*. A difference is that the branchial regions have a weak longitudinal keel with a few tubercles, whereas in *A. insignis*, large tubercles are arrayed linearly but not on a ridge.

The new specimen differs from species in all other genera of Necrocarcinidae in possession of long anterolateral and posterolateral spines. Other genera have lateral spines, but they are much shorter. The position of maximum width at the position of the long anterolateral spine is also unique to *Arcticocarcinus* and the new specimen. Although the specimen has some differences from the type species of *Arcticocarcinus*, it is most similar to *Arcticocarcinus* and its poor preservation precludes naming a new genus for it.

Arcticocarcinus americanus **new species (Figs. 1.1–1.4)**

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Etymology: The species name is derived from the country of origin, as it is the first Cenozoic member of Necrocarcinidae found in the Western Hemisphere.

Diagnosis: Anterolateral and posterolateral margins with one long, stout spine each; protogastric region ornamented with two tubercles; hepatic region smooth; branchial regions with tubercles on a weak longitudinal ridge; surface overall densely and evenly granular.

Description: Carapace about as wide as long, moderately vaulted transversely and longitudinally. Outer-orbital margins thickened but otherwise broken, fronto-orbital width about half carapace width. Anterolateral margins set below level of orbits anteriorly, with one spine just distal to outer-orbital margin, one long, stout, anterolaterally-directed spine at about maximum carapace width. Posterolateral margin long, apparently with one stout spine (broken base only preserved) and at least one more tiny spine just anterior to posterior margin. Posterior margin concave, broadly rimmed. Carapace surface covered with small, densely and evenly spaced granules where cuticle preserved.

Mesogastric region short, with a tubercle on anterior process and one tubercle centrally in widened posterior area. Metagastric region about as long as wide, with central tubercle. Urogastric region short, slightly depressed below level of other axial regions. Cardiac region long, narrowing posteriorly, with tubercle anteriorly. Protogastric regions wide, more or less confluent with hepatic regions, with two tubercles, one along axis and one laterally. Cervical and branchiocardiac grooves weak, delineating arcuate epibranchial region which is ornamented with two tubercles. Branchial regions weakly inflated, with longitudinal keel parallel to the axis, with a few tubercles.

Measurements: Measurements (in mm) taken on the carapace of NJSM 28659, the holotype of *Arcticocarcinus americanus* new species: carapace length, 15.6; carapace width, 15.7; fronto-orbital width, 7.9.

Type: The holotype of *Arcticocarcinus americanus* new species is NJSM 28659.

Discussion: The specimen is rather incomplete. The outer-orbital angles are visible, but the orbits and front are broken. Similarly, some portions of the anterolateral and posterolateral margins are complete but other segments are broken. However, a sufficient number of diagnostic characters remain to place the specimen in *Arcticocarcinus*. The new species differs from *Arcticocarcinus insignis* (Fig. 1.5) in having fewer lateral spines and in having much smaller dorsal tubercles. In addition, the hepatic region in the new species lacks strong ornamentation, whereas in *A. insignis*, there are several tubercles.

Preservation of the specimen is poor and rather odd. The matrix itself displays calcite crystals, and a calcite coating with visible crystal cleavage lies on the left orbital area of the specimen of *Arcticocarcinus americanus* new species. Other calcite coatings obscure detail on the posterior margin. The calcite recrystallization obviously happened post-deposition but it is not known when. Across the anterior part of the mesogastric and right protogastric region lies a probable serpulid worm tube (Figs. 1.1, 1.2, 1.4). Just anterior to the worm tube lies a foraminiferan (Figs. 1.2, 1.4). Lateral to the left side of the urogastric region lies an encrusting bryozoan, possibly a calloporid membraniporiform cheilostome (M. Key, personal communication, December 2024) (Figs. 1.1, 1.2, 1.3). The axial locations of these encrusting organisms are outside of the area of the carapace that can be groomed by many crabs (Tashman et al., 2018), so the encrusters could have colonized the carapace before or after death. Similar epibionts including worm tubes and bryozoans have been illustrated on Paleocene decapods (Jakobsen and Feldmann, 2004), and bryozoans encrusting decapod crustaceans in general have been well documented (Key and Schweitzer, 2019).

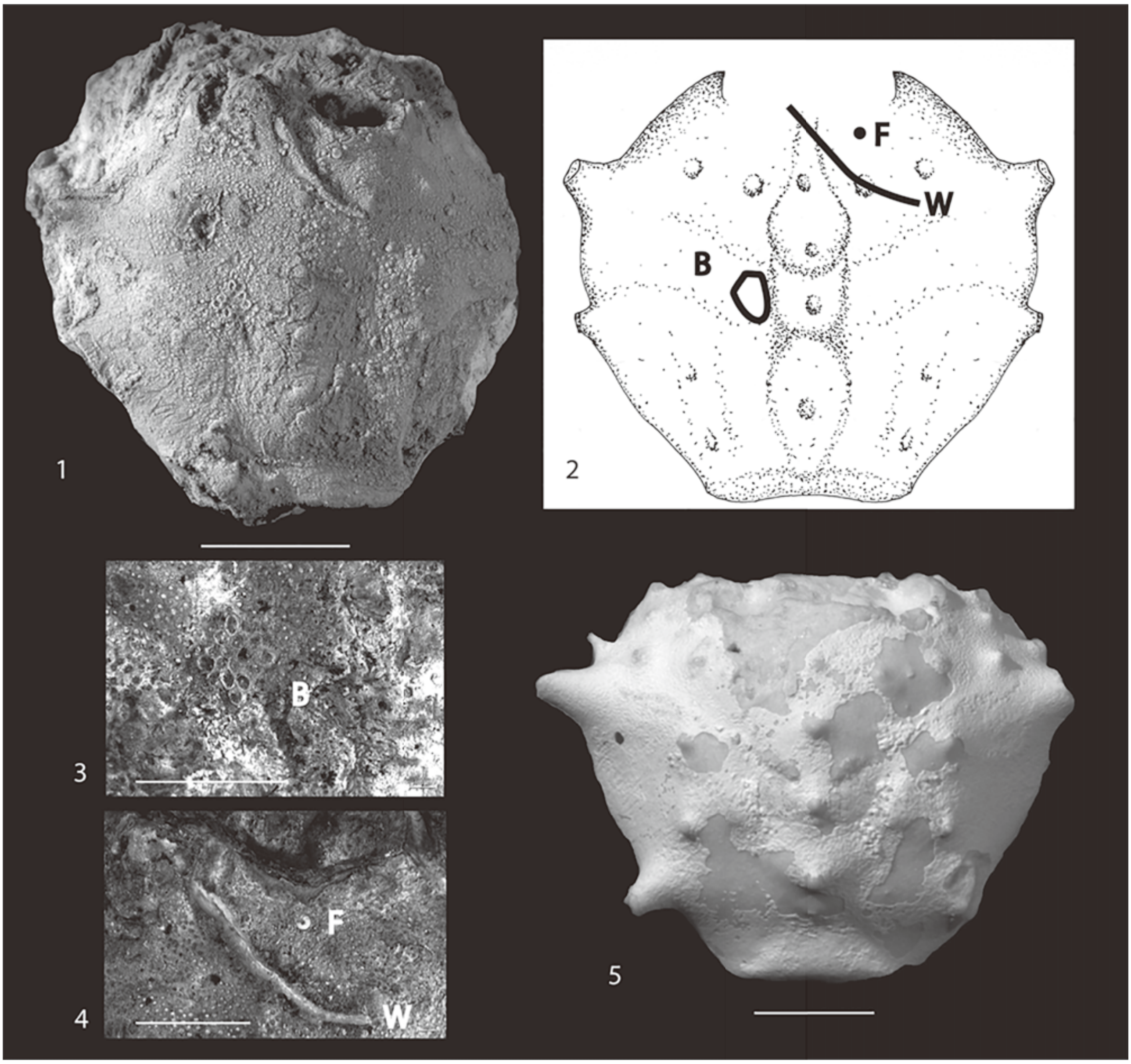

Fig. 1. *Arcticocarcinus* spp. 1–4, *Arcticocarcinus americanus* new species, holotype, NJSM 28659. *1*, dorsal carapace; *2*, schematic line drawing of *A. americanus* new species showing position of epibionts; *3*, enlargement of carapace with bryozoan colony; *4*, enlargement of carapace with foraminiferan and probably serpulid worm tube. **5, *Arcticocarcinus insignis* (Segerberg, 1900)**, holotype, LO1551t (Schweitzer et al., 2018a, fig. 4.2). B = bryozoan colony, F = foraminiferan, W = worm tube. Scale bars 1, 5 = 5 mm. Scale bars 3, 4 = 2 mm.

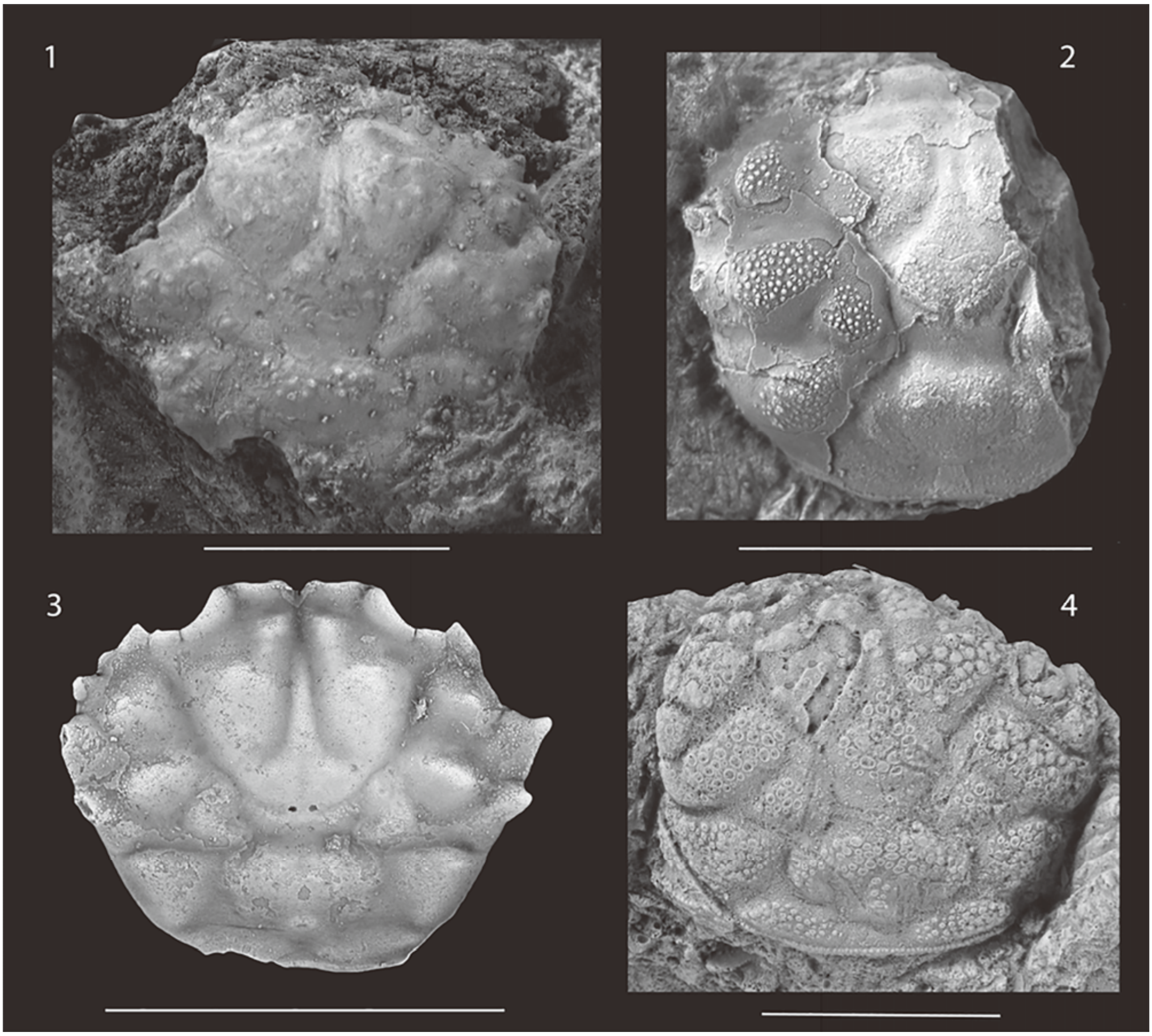

Fig. 2. Tumidocarcinidae. **1, *Feldmannicarcinus hajzeri* new species**, holotype, NJSM 28660. **2, *Nitotacarcinus antipodes* Schweitzer et al., 2012**, holotype MPEF-PI 5410. **3, *Titanocarcinus briarti* (Forir, 1887)**, holotype, IRSNB MI 11011 (image from Schweitzer et al., 2018b, fig. 10.2). **4, *Lobonotus natchitochensis* Stenzel, 1935**, cast of holotype, UT 21168 (image from Schweitzer et al., 2018b, fig. 9.1). Scale bar 1 = 5 mm. Scale bar 2–4 = 1 cm.

Section Eubrachyura de Saint Laurent, 1980
Superfamily Carpilioidea Ortmann, 1893

Family Tumidocarcinidae Schweitzer, 2005

Included genera: as in Schweitzer et al. (2018b, 2024), plus *Feldmannicarcinus* new genus.

Diagnosis: as in Schweitzer et al. (2018b).

Discussion: The new genus fits all of the diagnostic carapace features of Tumidocarcinidae, including the carapace shape and size ratios and the strongly downturned frontal area; small orbits with two weak fissures; and anterolateral margin with five spines. The new specimens are only composed of broken dorsal carapaces, so diagnostic ventral features are not preserved. Tumidocarcinidae is known from the Late Cretaceous to the Miocene, from cosmopolitan occurrences including Eocene localities in East coastal North America (Schweitzer et al., 2018b).

***Feldmannicarcinus* new genus**

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Type species: *Glyphithyreus sturgeoni* Feldmann, Bice, Hopkins, Salva and Pickford, 1998, by original designation.

Included species: *Feldmannicarcinus hajzeri* new species; *F. sturgeoni* new combination.

Etymology: The genus name honors Rodney M. Feldmann, who first identified the type species of the new genus, and who made a monumental contribution to the study of North American fossil decapod crustaceans. Many genera in the family end with -*carcinus*.

Diagnosis: Carapace about 85% as long as wide, strongly downturned anteriorly; regions moderately developed; ornamented with sparse but distinct tubercles; orbits shallow; epibranchial region with distinct, oblique row of tubercles.

Discussion: The new genus (Fig. 2.1) differs from all other genera within Tumidocarcinidae in its moderately defined regions with sparsely tuberculate ornamentation (Figs. 2.2–2.4). The type species of the new genus, *Feldmannicarcinus sturgeoni* new combination (Figs. 3.4, 3.6), was originally placed in *Glyphithyreus* Reuss, 1859, and later moved to *Lobonotus* A. Milne-Edwards, 1863, in a revision of *Glyphithyreus* (Karasawa and Schweitzer, 2004). Although overall similar in carapace relative proportions and regional development to *Lobonotus* (Fig. 2.4), these are family-level characters. *Feldmannicarcinus sturgeoni* differs from species of *Lobonotus* in lacking the densely-spaced, large granules on the regions and the distinctive reniform swellings along the lateral margins of the cardiac region.

The new genus is most similar to *Titanocarcinus* A. Milne-Edwards, 1863, and *Nitotacarcinus* Schweitzer et al., 2007 (Figs. 2.2, 2.3). *Titanocarcinus* spp. are characterized by thickly rimmed orbits with well-defined fissures and overall granular carapace ornamentation, not seen in the new genus (Fig. 2.3). The anterolateral spines of *Titanocarcinus* are more deeply separated from one another, longer, and more triangular than those of the new genus. The regions of *Nitotacarcinus* are densely and finely granular and are much more strongly defined than in the new genus, and *Nitotacarcinus* has weak reniform swellings along the cardiac region (Fig. 2.2). Blow and Manning (1996) named *Titanocarcinus purdyi* from the Eocene (Lutetian-Bartonian) Santee limestone of South Carolina, which was later moved to *Lobonotus* (Schweitzer et al., 2007). It is here maintained in *Lobonotus* based upon its densely granular carapace regions that are subdivided as in those of *Lobonotus*. *Lobonotus* spp. have more differentiated hepatic, protogastric, epibranchial, and branchial regions that are more heavily ornamented than in *Feldmannicarcinus*.

Both species of *Feldmannicarcinus* new genus are known from reef carbonates, which is unlike most other taxa within Tumidocarcinidae. Some of the best known genera within the family, *Tumidocarcinus* Glaessner, 1960; *Pulalius* Schweitzer et al., 2000; and *Nitotacarcinus,* are found in mixed siliciclastics along tectonically active margins (Schweitzer et al., 2018b). Tumidocarcinidae as a family was broadly adapted to many types of environments, but within genera, habitat preferences seem to have been much more restricted.

Feldmannicarcinus hajzeri new species
(Figs. 2.1, 3.1–3.3, 3.5, 3.7)

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Diagnosis: Carapace about 85% as long as wide, strongly downturned anteriorly; anterolateral spines small, without granules or spinelets; carapace regions moderately developed; ornamented with scattered, large, distinct tubercles; orbits shallow; epibranchial region with distinct, oblique row of tubercles.

Etymology: The species name honors Frank Hajzer, New Jersey, who collected and donated the specimens for study.

Description: Carapace hexagonal, length about 84% maximum width, widest about half the distance posteriorly, regions well-defined; strongly vaulted anteriorly and flattened posteriorly and transversely. Front apparently nearly straight, not well preserved; orbits small, shallow, possibly with two shallow closed fissures; fronto-orbital width about 65% maximum carapace width, frontal width about 35% maximum carapace width. Anterolateral margins with five blunt spines including outer-orbital spine; outer-orbital spine short, triangular, about same size as second anterolateral spine; third and fourth anterolateral spines longer, broader, circular in cross-section; fifth spine short, blunt, granular. Posterolateral margin poorly known, weakly convex, posterior margin rimmed.

Epigastric regions rectangular, small, most inflated anteriorly. Mesogastric region with long anterior process ending between epigastric regions, widened posteriorly, with a few tubercles. Metagastric and urogastric regions merging, flattened, mostly smooth, with concave lateral margins. Cardiac region pentagonal, granular anteriorly, narrowing posteriorly; Protogastric regions wider anteriorly, with strong tubercles anteriorly and laterally; hepatic region small, strongly ornamented with large tubercles. Epibranchial region arcuate, composed of two segments, elongate segment directed obliquely from lateral margin anteriorly toward axis, with a weak ridge ornamented with a row of three or four tubercles; second segment triangular, directed at cardiac region, with a few granules; mesobranchial region inflated anteriorly and laterally, with several tubercles; metabranchial region flattened, seemingly without tubercles.

Measurements: Measurements (in mm) taken on the dorsal carapace of specimens of *Feldmannicarcinus hajzeri* new species: holotype NJSM 28660, length, 12.2; width, 14.6; fronto-orbital width ~10, frontal width, 4.4; paratype NJSM 28661, length, >10; width, 11.2; fronto-orbital width, 6.8; frontal width, 4.6.

Types: Two specimens are referred to *Feldmannicarcinus hajzeri* new species, the holotype, NJSM 28660, and a paratype, NJSM 28661.

Discussion: The two specimens of *Feldmannicarcinus hajzeri* new genus and new species are each incomplete but preserve sufficient detail to describe a new species. The holotype (Figs. 3.1–3.3) has well-preserved right anterolateral margins of the carapace, whereas the paratype (Fig. 3.5) has well-preserved branchial regions. Neither has a complete front or posterior margin. The new species differs from *F. sturgeoni* in its much larger and more numerous tubercles on the protogastric, hepatic, mesogastric, branchial, and cardiac regions. By contrast, *F. sturgeoni* has more granular anterolateral spines than those of *F. hajzeri*. *Feldmannicarcinus sturgeoni* is younger, Lutetian-Bartonian in age, than the basal Ypresian *F. hajzeri*. As both species are known from east coastal North America, they are likely end members of a continuous lineage of crabs.

Brachyura incertae sedis

Unidentified claw
(Fig. 4)

Material: NJSM 28662.

Description of material: Manus and propodus of right chela, coarsely granular on outer surface, more finely granular on inner surface; propodus about half the length of the manus.

Discussion: The claw resembles some chelae of Dromiidae, such as those of *Epigodromia* McLay, 1993 (Schweitzer et al., 2012, fig. 20.1b). It is similar in being coarsely granular to specimens attributed to taxa now assigned to Goniodromitidae Beurlen, 1932, and Dromiidae (Jagt et al., 2010; Schweitzer et al., 2012) but is generally longer and more slender than those chelae. The dromiid *Vincentdromia americana* (Roberts, 1956) has a generally smooth carapace, and smooth dromiids are associated with chelae without coarse ornamentation (Schweitzer et al., 2012; Schweitzer and Feldmann, 2024). Chelae of members of Tumidocarcinidae are large and smooth (Schweitzer et al., 2018b). Roberts (1956) illustrated several isolated propodi and other cheliped elements, none of which are similar to the one illustrated here. Thus, the identification of the chela remains unknown.

4. Discussion

Arcticocarcinus is known from Danian rocks of Annetorp, Sweden (Segerberg, 1900) and Denmark (Jakobsen and Collins, 1997), and the new occurrence is from earliest Eocene rocks of New Jersey, USA (Schweitzer, 2024). Both *Feldmannocarcinus sturgeoni* new combination and *F. hajzeri* new genus and new species are preserved in coral and bryozoan rich Eocene carbonates (Feldmann et al., 1998; herein), and the morphologically similar *Titanocarcinus* is the only other genus within Tumidocarcinidae mostly found within carbonate environments, primarily in Europe (Robin et al., 2016; Schweitzer et al., 2018b).

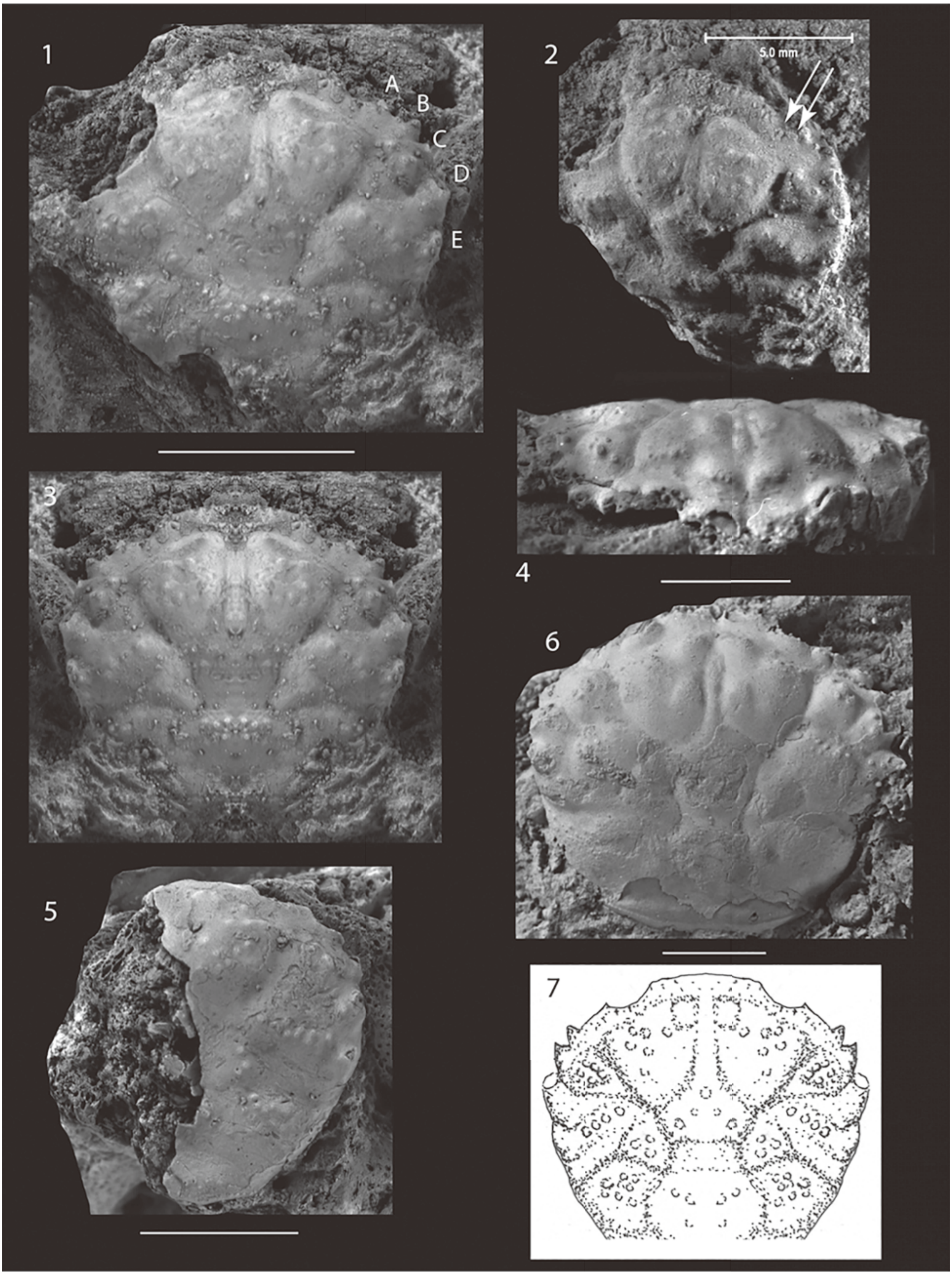

Fig. 3. ***Feldmannicarcinus*** **new genus**. **1–3,** ***Feldmannicarcinus hajzeri*** **new species**, holotype, NJSM 28660. *1*, letters indicate position of five anterolateral spines; *2*, arrows indicate position of orbital fissures; *3*, reconstruction of carapace of *Feldmannicarcinus hajzeri* new species, composed by reflecting right half of carapace. **4, 6,** ***Feldmannicarcinus sturgeoni*** **new combination**, holotype, CM 36036. *4*, anterior view; *6*, dorsal view. **5,** ***Feldmannicarcinus hajzeri*** **new species**, paratype, NJSM 28661. **7,** line drawing of carapace of *F. hajzeri* new species except poorly preserved posterior margin. Scale bars = 5 mm.

The occurrence of *Vincentdromia americana* in Eocene carbonates supports the hypothesis that crabs of Dromiidae radiated beginning in the Paleocene and especially in the Eocene in carbonate sediments (Artal et al., 2022; Miller et al., 2023; Schweitzer, 2024). Thus, the earliest Eocene Vincentown Formation of New Jersey exhibits decapod faunal similarities with Paleocene carbonate localities of the North Atlantic which served as a Cenozoic refugium for many decapod lineages that originated in the Cretaceous (Schweitzer and Feldmann, 2023). The fossiliferous layers of the Vincentown Formation are bryozoan and coralgal debris-rich (Schlanger, 1954; Gallagher, 2003; Zachos, 2017), which may have offered similar niches to the Paleocene carbonates of Denmark and Sweden and other European localities (Collins and Jakobsen, 1994; Robin et al., 2016).

Referral of *Arcticocarcinus americanus* new species to the genus extends its geologic and geographic range, resulting in a generic range of about 10 million years. The generic range of *Feldmannicarcinus* new genus is about 19 million years, given the Lutetian–Bartonian age of *Feldmannicarcinus sturgeoni* (Feldmann et al., 1998; Schweitzer et al., 2018b). Both are well within the generic ranges for brachyuran decapod crustaceans (Schweitzer and Feldmann, 2023).

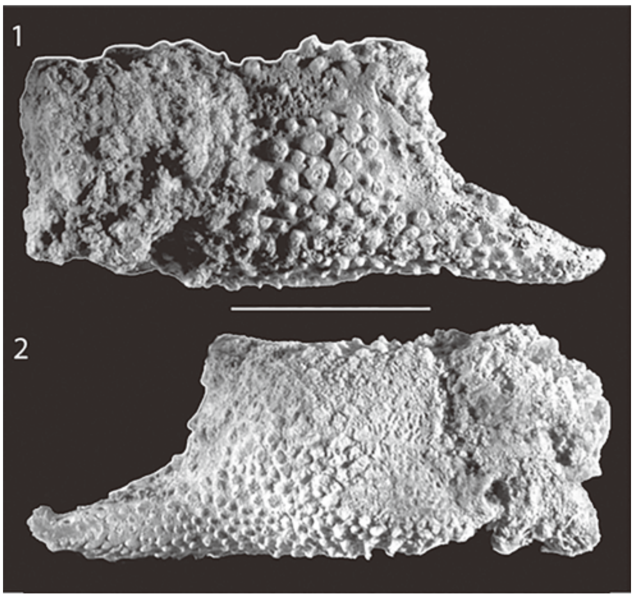

Fig. 4. Unidentified chela, NJSM 28662. Scale bar = 5 mm.

5. Acknowledgements

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