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NEW GENUS OF CRAB (BRACHYURA: RANINOIDA: NECROCARCINIDAE) FROM THE UPPER CRETACEOUS OF WEST ANTARCTICA, WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT

A new genus of crab from the Late Cretaceous of Antarctica increases diversity within Necrocarcinidae Förster, 1968, and demonstrates what appear to be gradual evolution and sympatric speciation in the southern high latitudes. New taxa include ***Hadrocarcinus tectilacus*, new genus, new species**, as well as **two new combinations, *Hadrocarcinus carinatus* (Feldmann et al., 1993) and *Hadrocarcinus wrighti* (Feldmann et al., 1993)**. Necrocarcinidae was paleogeographically widespread by the middle Early Cretaceous, but the geographic distribution and diversity of the group increased even further by the middle Late Cretaceous, perhaps as a result of high sea levels and elevated global temperatures at that time. The paleogeographic range and diversity of necrocarcinids decreased during the latest Cretaceous and into the earliest Paleocene (Danian), possibly due to decreases in sea level and global temperatures, restricting the family to the northern high latitudes. Alternatively, apparent diversity trends in Necrocarcinidae may simply reflect available rock volume.

Key Words: Antarctic Peninsula, Decapoda, Gustav Group, Hidden Lake Formation, James Ross Basin, Marambio Group, Santa Marta Formation

INTRODUCTION

In late 2009, one of us (Lamanna) participated in a brief paleontological reconnaissance of exposures of the Upper Cretaceous (Coniacian) Hidden Lake Formation between Cape Lachman and Brandy Bay, northwestern James Ross Island, Antarctica. Among the fossils discovered was a nearly complete, three-dimensionally preserved decapod. We describe the specimen as the holotype of a previously unrecognized genus and species of Necrocarcinidae.

GEOLOGIC SETTING

The Hidden Lake Formation is the uppermost unit of the "middle" Cretaceous Gustav Group, which is exposed along the northwestern margin of James Ross Island, immediately east of the northern tip of the Antarctic Peninsula, and also sporadically in this area of the Peninsula itself (Ineson et al. 1986; Riding and Crame 2002; Crame et al. 2006) (Fig. 1). The Hidden Lake Formation consists of volcaniclastic conglomerates, sandstones, siltstones, and mudstones, and attains a maximum thickness of at least 400 m (Ineson et al. 1986; Riding and Crame 2002; Whitham et al. 2006). The formation is regarded as early Late Cretaceous (Coniacian) in age on the basis of strontium isotope chemostratigraphy (McArthur et al. 2000) as well as palynostratigraphy (Riding and Crame 2002) and ammonite biostratigraphy (Kennedy et al. 2007). It overlies the Whisky Bay Formation and is conformably overlain by the lowermost unit of the Marambio Group, the Santa Marta Formation (Ineson et al. 1986; Crame et al. 2006).

The Hidden Lake Formation was deposited in a marine paleoenvironment (Whitham et al. 2006). Multiple facies occur in the unit and are interpreted as representing shelf, base of slope, fan delta, and basin floor settings, respectively (e.g., Pirrie et al. 2004; Whitham et al. 2006). Fossils reported from the Hidden Lake Formation to date include palynomorphs (e.g., Baldoni and Medina 1989; Riding et al. 1992; Barreda et al. 1999; Riding and Crame 2002; Crame et al. 2006), wood (Baldoni and Medina 1989; Crame et al. 2006), fern, conifer, bennettitalean, and angiosperm foliage (Hayes et al. 2006), corals (Whitham et al. 2006), brachiopods and bryozoans (Crame et al. 2006), gastropods (Ineson et al. 1986; Crame et al. 2006), bivalves (Ineson et al. 1986; Baldoni and Medina 1989; Crame et al. 2006), belemnites (Crame et al. 2006), ammonites (Ineson et al. 1986; Crame et al. 2006; Kennedy et al. 2007), elasmobranch teeth and vertebrae (Crame et al. 2006; Whitham et al. 2006), "reptile bones" (Crame et al. 2006), a distal tibial fragment of a non-avian theropod dinosaur (Molnar et al. 1996), and numerous trace fossils

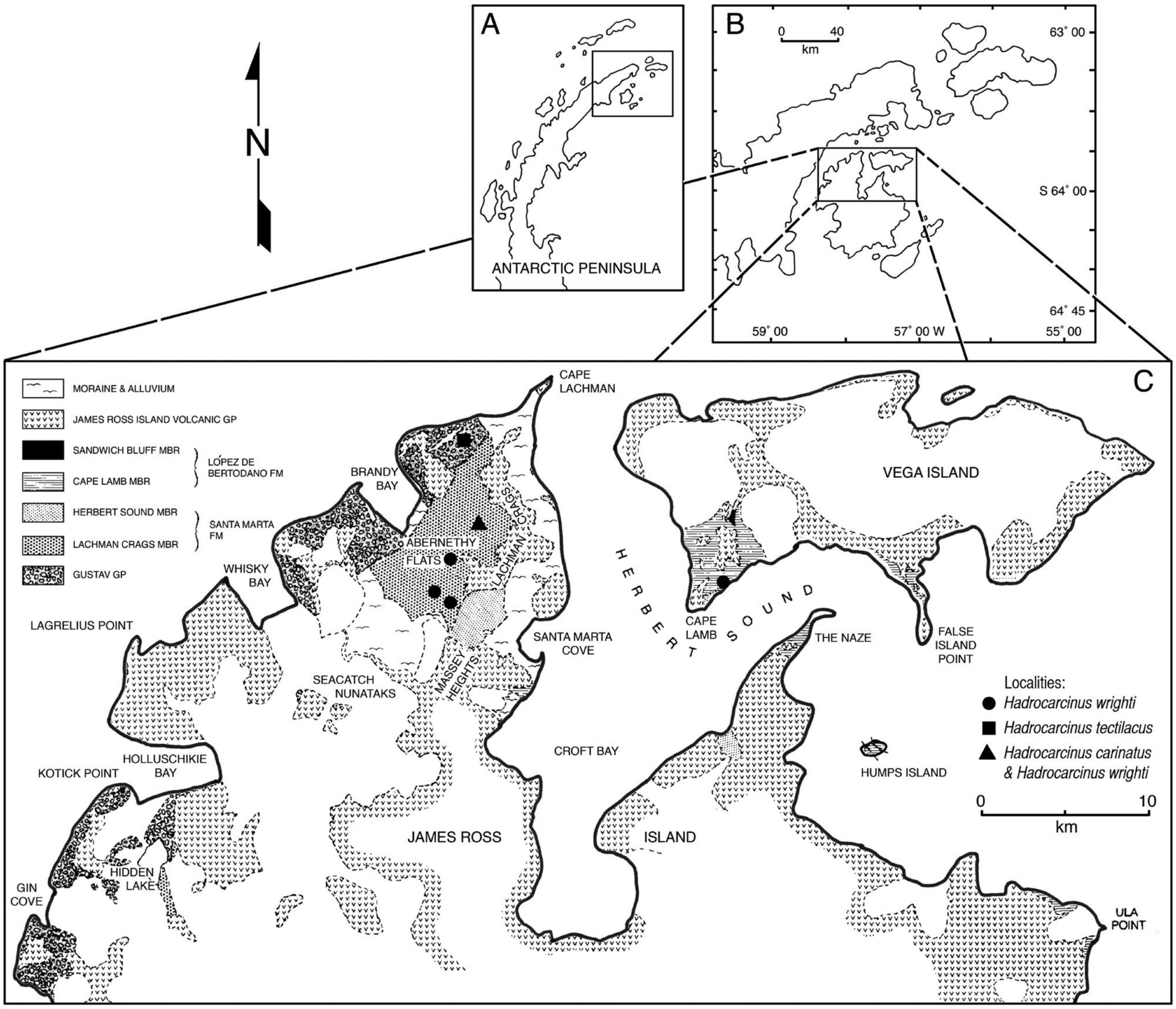

Fig. 1.—Fossil localities of *Hadrocarcinus*. **A,** map of Antarctic Peninsula showing location of James Ross Island area (indicated by rectangle); **B,** map of James Ross Island area showing location of northern James Ross and Vega islands (rectangle); **C,** geologic map of northern James Ross and Vega islands, showing localities that have yielded *Hadrocarcinus* spp. (*H. tectilacus*, square; *H. wrighti*, circle; *H. carinatus* and *H. wrighti*, triangle). Fig. 1A and 1B modified from Feldmann et al. (1993:fig. 1); Fig. 1C modified from Crame et al. (1991:fig. 3) and Feldmann et al. (1993:fig. 1).

(Buatois and López Angriman 1992; Buatois 1995; Buatois et al. 2009) including the brachyuran decapod trackway *Foersterichnus rossensis* (Pirrie et al. 2004). The crab reported herein is thus the first decapod body fossil yet recovered from the Hidden Lake Formation.

Institutional abbreviations.—**BAS**, British Antarctic Survey, Invertebrate Type Collection, Cambridge, U.K.; **CIRGEO**, Centro de Investigaciones en Recursos Geológicos, Buenos Aires, Argentina; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **KSU D**, Decapod Comparative Collection, Department of Geology, Kent State University, Kent, Ohio, U.S.A.; **SM**, Sedgwick Museum, Cambridge University, Cambridge, U.K.; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758

Section Raninoida Ahyong et al., 2007

Diagnosis.—“Carapace longer than wide or about as wide as long, generally ovate, usually vaulted transversely, regions poorly defined; usually with well-developed rostrum

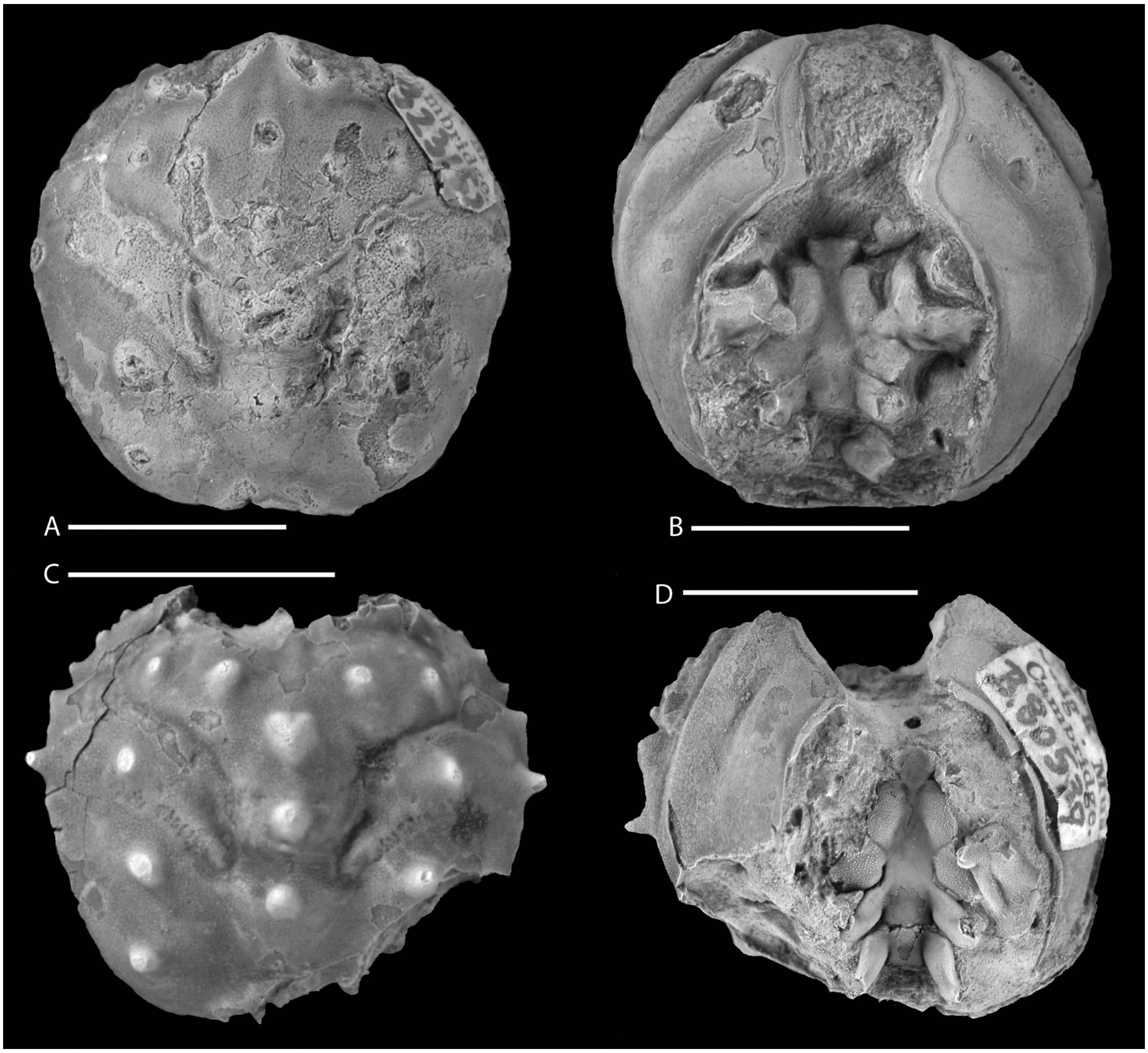

Fig. 2.—Necrocarcinidae, *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835). **A–B,** SM B 23152: **A,** dorsal carapace; **B,** sternum. **C–D,** SM B 80539: **C,** dorsal carapace showing deep cervical groove, well-defined protogastric and axial regions and small anterolateral spines; **D,** sternum. Scale = 1 cm.

and orbital spines; branchiocardiac groove developed as boundary for urogastric region; maxilliped 3 elongate, merus long; thoracic sternum narrow, sternites 1–3 generally fused, sternites 7 and 8 often reduced and at lower level than other sternites; where known, pleon narrow in males and females, showing reduced but clear dimorphism; genital openings coxal, spermatheca present" (Karasawa et al. 2011:549).

Included superfamily.—Raninoidea De Haan, 1839.

Geologic range.—Early Cretaceous (Berriasian)–Recent.

Superfamily Raninoidea De Haan, 1839

Diagnosis.—As for section.

Family Necrocarcinidae Förster, 1968

Diagnosis.—Carapace circular or ovate, about as long as wide or slightly wider than long, widest at position of last anterolateral spine, moderately vaulted longitudinally and transversely; regions well defined, usually with longitudinal ridges or rows of tubercles on axial and branchial regions; rostrum narrow, sulcate at tip or with small spines;

orbits small, circular, with two fissures, directed forward; inner-orbital, intra-orbital, and outer-orbital spines well developed; fronto-orbital width typically between 30–45% maximum carapace width but rarely over half in some species; anterolateral margins long, usually with numerous spines; posterolateral margin entire or with spines; cervical and branchiocardiac grooves well developed, usually parallel to one another. Sternum narrow, sternites 1–3 fused and quadrate; anterior portion of sternum at low angles to one another, sternum deep posteriorly, with flanks at high angle to one another, lateral margins raised and granular; sternite 4 long, with widely raised lateral margins, axially deep, episternal projections short, suture 4/5 incomplete; sternal suture 4/5 deep, concave posterolaterally, becoming straight and oriented parallel to axis of animal axially; sternite 5 wider than long, articulating with pereiopod 2, directed laterally; sternite 6 similar to sternite 5; sternite 7 directed ventrolaterally; sternite 8 directed ventrolaterally, much smaller than sternite 7; sternal sutures 5/6 and 6/7 complete. All pleonites free, with blunt axial spines, somite 6 much longer than wide, telson long; pereiopods 4 and 5 apparently reduced in size (after Karasawa et al. 2011:551).

Included genera.—*Necrocarcinus* Bell, 1863; *Corazzatocarcinus* Larghi, 2004; *Cristella* Collins and Rasmussen, 1992; *Hadrocarcinus,* new genus; *Paranecrocarcinus* Van Straelen, 1936; *Polycnemidium* Reuss, 1859; *Pseudonecrocarcinus* Förster, 1968; *Shazella* Collins and Williams, 2004.

Material examined.—In addition to that listed in Karasawa et al. (2011), *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835), SM B23152, 23210, B80539; Atelecyclidae Ortmann, 1893, *Atelecyclus umdecimdentatus* (Herbst, 1783), USNM 123248; Trichopeltariidae Tavares and Cleva, 2010, *Trichopeltarion nobile* A. Milne-Edwards, 1880, USNM 1000834, lot containing males and females; *Podocatactes hamifer* Ortmann, 1893, USNM 72481, 72485; Homolidae De Haan, 1839, *Homola barbata* (Fabricius, 1793), USNM 344628 (female), 152623 (male); Homolodromiidae Alcock, 1900, *Homolodromia paradoxa* A. Milne-Edwards, 1880, USNM 285279; Cyclodorippidae Ortmann, 1892, *Tymolus japonicus* Stimpson, 1858, USNM 45836, 45844.

Remarks.—Placement of genera in the Necrocarcinidae is reasonably stable. Recently, however, Vega et al. (2010) suggested that *Corazzatocarcinus* bears characteristics reminiscent of Cenomanocarcinidae. Vega (pers. comm., 2011) noted the similarity of the sternum and abdomen of *Corazzatocarcinus hadjoulae* (Roger, 1946) to that of *Cenomanocarcinus vanstraeleni* Stenzel, 1945. However, the preservation of the sternum of *Corazzatocarcinus hadjoulae* is poor. Until the type material of *Corazzatocarcinus* can be examined, we will sustain Larghi's (2004) placement of the genus in Necrocarcinidae.

The new taxon is referable to the Necrocarcinidae due to its possession of most of the diagnostic features given here (Fig. 2). It differs from other genera within the family in having rather well-developed carapace regions and protruding, well-differentiated anterolateral spines, yielding a superficial similarity to some eubrachyuran genera, especially *Trichopeltarion* A. Milne-Edwards, 1880, of Trichopeltariidae, and members of the Atelecyclidae, to which we compared it. However, the sternum, pleon, cervical, and branchiocardiac grooves, and carapace ornamentation all clearly indicate placement within Necrocarcinidae. The new genus possesses a deep, narrow sternum with sternites 1–3 fused and a long, axially deep sternite 4 with steep lateral sides; the abdominal somites have an axial keel and somite 6 is very long; the orbits and rostrum are set well above the anterolateral margin; and the cervical and branchiocardiac grooves are both well developed with the cervical being the better developed of the two. The carapace is ornamented with rather large tubercles, some on an axial keel. These are all key features of Necrocarcinidae.

Camarocarcinidae Feldmann et al., 2007, and Cenomanocarcinidae Guinot et al., 2008, are also families within Raninoidea that bear superficial resemblance to Necrocarcinidae. The new genus is excluded from Camarocarcinidae based upon its possession of a strong cervical groove that is stronger than the branchiocardiac groove; in Camarocarcinidae, the opposite is true. In addition, camarocarcinids have endocuticular pillow-like structures that are clearly visible with the naked eye; these are not seen in *Hadrocarcinus*. Cenomanocarcinidae have five spines on the rostrum as compared with three on *Hadrocarcinus*; weak cervical and branchiocardiac grooves whereas both are strong in *Hadrocarcinus*; and a broader, more broadly concave, axially shallower sternum than that of *Hadrocarcinus* (Karasawa et al. 2011:550).

The new genus is easily excluded from other sections in which the carapace grooves are well developed, such as Dromiacea De Haan, 1833, and Homoloida Karasawa et al., 2011 (both formerly referred to Podotremata Guinot, 1977), because it lacks an augenrest structure. In addition, the pleonites that are present appear to include the sixth somite which lacks triangular epimeres, and the carapace lacks a well-developed postcervical groove. These features are usually or always present within families in Dromiacea and Homoloida (Karasawa et al. 2011:534, 545). Thus, placement within Raninoida and Necrocarcinidae is clearly indicated.

Hadrocarcinus, new genus

Type species.—*Necrocarcinus wrighti* Feldmann, Tshudy, and Thomson, 1993, by present designation.

Included species.—***Hadrocarcinus carinatus*** (Feldmann, Tshudy, and Thomson, 1993), **new combination;** *Hadrocarcinus tectilacus*, new species; ***Hadrocarcinus wrighti*** (Feldmann, Tshudy, and Thomson, 1993), **new combination.**

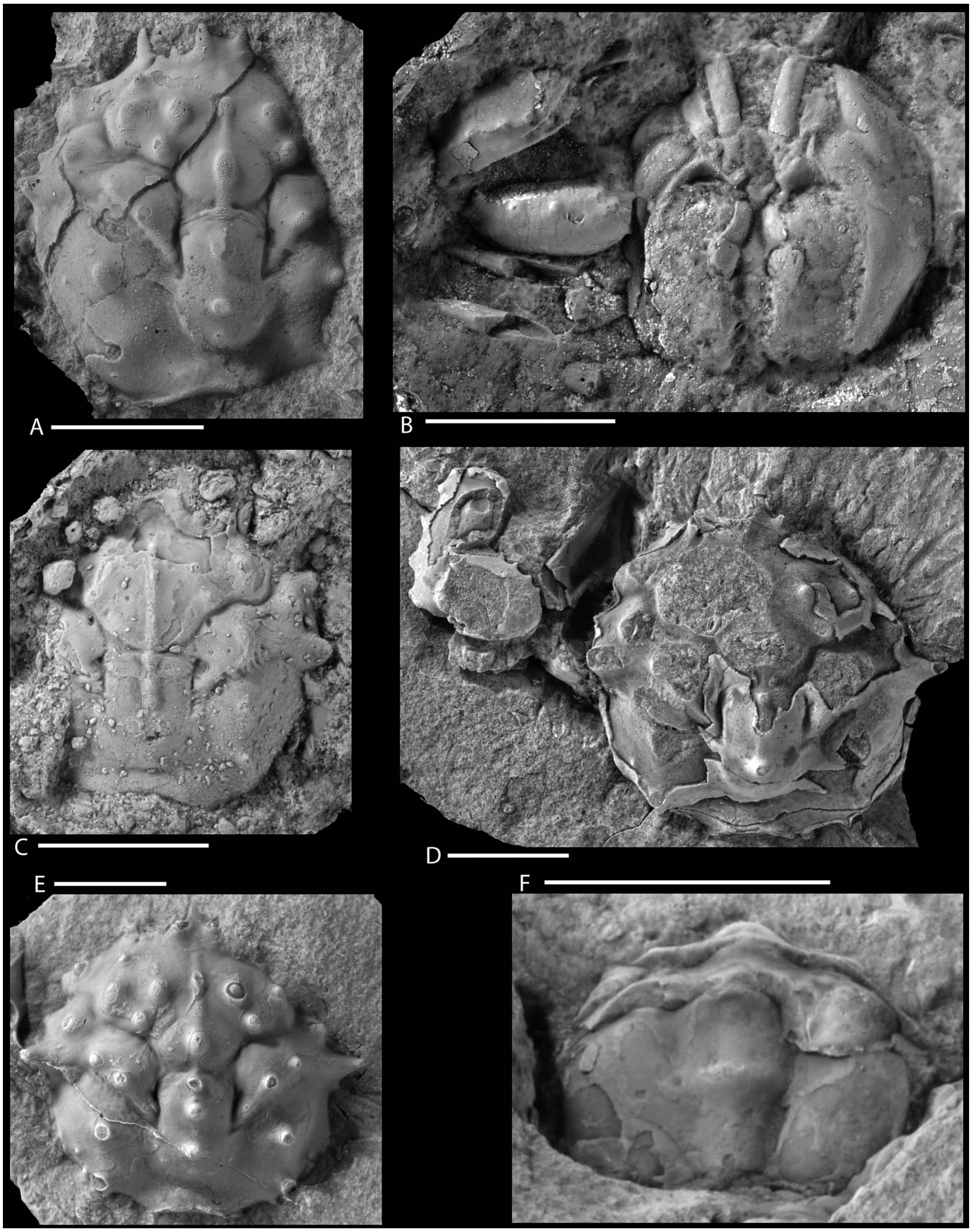

Fig. 3.—Necrocarcinidae, *Hadrocarcinus* spp. **A,** *Hadrocarcinus wrighti*, latex cast (KSU D 1015) of holotype, BAS In. 2237, dorsal carapace showing deep cervical groove, long outer-orbital spine, two intra-orbital spines, and two basal rostral spines; **B,** *Hadrocarcinus wrighti*, latex cast (KSU D 1014) of paratype CIRGEO 882, ventral surface showing maxillipeds, pterygostomial regions, large chelipeds, and sternum with fused sternites 1–3 and sternite 4 with deep axial depression; **C,** *Hadrocarcinus carinatus*, latex cast (KSU D 1016) of holotype BAS In. 2238 showing dorsal carapace with deep cervical groove, strong axial keel, and at least two large anterolateral spines; **D-F,** *Hadrocarcinus tectilacus*, CM 56700, holotype: **D,** dorsal carapace and left chelipeds showing very strong anterolateral spines, strong carapace regions and ornamentation; **E,** Exaflex® cast of internal mold showing very strong ornamentation, rostrum, and deep cervical and branchiocardiac grooves; **F,** female pleon with very long pleonite 6. Scale = 1 cm.

Diagnosis.—Carapace about as wide as long, widest about 40% the distance posteriorly on carapace; rostrum trifid, middle spine downturned, outer two spines directed upward; orbits with two intra-orbital spines and broad outer-orbital spine, outer-orbital spine directed anteriorly or axially; fronto-orbital width about 44% maximum carapace width; anterolateral margins set below level of rostrum and orbits, with between four and six spines excluding outer-orbital spine, most appearing to be broad, triangular; last spine long, directed laterally; posterolateral margin with two spines near posterolateral corner; posterior margin narrow, convex; carapace regions very well defined, most ornamented with stout spines; cervical groove deep, sinuous, bounding posterior margins of protogastric and hepatic regions; branchiocardiac groove shallower than cervical groove, bounding posterior margin of epibranchial region; postcervical groove only present as deep lateral margin of metagastric region; chelipeds appearing to be heterochelous at least in terms of length; sternum deep, narrow; sternites 1–3 fused, long sternite 4 with steep lateral sides, deep axially; pleon with axial keel, somite 6 very long.

Etymology.—The generic name is derived from the Greek words *hadros*, meaning bulky or stout, in reference to the stout anterolateral spines and well-developed carapace regions, unusual among members of the family, and *karkinos*, meaning crab. The gender is masculine.

Occurrence.—*Hadrocarcinus wrighti* was collected from the Lachman Crags and Herbert Sound members of the Santa Marta Formation (Santonian–Campanian) on northern James Ross Island, as well as the Cape Lamb Member of the Snow Hill Island Formation (Campanian–Maastrichtian) at Cape Lamb on Vega Island (Feldmann et al. 1993; Crame et al. 2004) (Fig. 1C). *Hadrocarcinus carinatus* was collected from the Lachman Crags Member of the Santa Marta Formation (Santonian–Campanian) on northern James Ross Island (Feldmann et al. 1993). *Hadrocarcinus tectilacus,* new species, was collected from the Hidden Lake Formation (Coniacian) on James Ross Island. Thus, the genus appears to span approximately 20 million years.

Remarks.—The new genus, *Hadrocarcinus*, is most similar to *Necrocarcinus*, the type genus of Necrocarcinidae, but differs from it in several substantial ways. The two genera are similar to one another in possessing nearly identical paths of the cervical and branchiocardiac grooves (Figs. 2–3) and in having large tubercles on the dorsal carapace, well-developed axial regions, round, forward directed orbits, and well-defined protogastric regions. However, *Hadrocarcinus* has large, triangular, well-differentiated anterolateral spines that are not seen in any other species of genera within the Necrocarcinidae, in which the spines are otherwise small or developed as small nodes and do not involve the entire carapace being drawn into the spines. In addition, the protogastric, hepatic, and epibranchial regions in *Hadrocarcinus* are much better developed than those of *Necrocarcinus* and other taxa within Necrocarcinidae. *Hadrocarcinus* has two intra-orbital spines, a condition that is unusual among all brachyurans, in which the usual condition is one intra-orbital spine. Thus, the new genus seems clearly warranted.

Hadrocarcinus tectilacus, new species
(Figs. 3D–F)

Diagnosis.—Carapace about as wide as long, widest about 40% the distance posteriorly on carapace; rostrum trifid, middle spine downturned, outer two spines directed upward; orbits with two intra-orbital spines and broad outer-orbital spine, outer-orbital spine directed anteriorly; fronto-orbital width about 44% maximum carapace width; anterolateral margins set below level of rostrum and orbits, with six spines excluding outer-orbital spine; first spine needle-like, short; second and third spines short, broad, triangular; fourth and fifth spines stout, large, broad, triangular; sixth spine directed laterally, needle-like; posterolateral margin with two spines near posterolateral corner; posterior margin narrow, convex; carapace regions very well defined, most ornamented with stout spines; cervical groove deep, sinuous, bounding posterior margins of protogastric and hepatic regions; branchiocardiac groove shallower than cervical groove, bounding posterior margin of epibranchial region; post-cervical groove only present as deep lateral margin of metagastric region; chelipeds appearing to be heterochelous at least in terms of length.

Description.—Carapace about as long as wide, ovate, widest about 40% the distance posteriorly on carapace, strongly vaulted longitudinally and transversely.

Rostrum trifid, central spine longest, with blunt tip, slightly below level of two lateral spines; lateral spines short, directed upward, rostral width about 13% maximum carapace width. Orbits directed forward, orbital margin on same level as rostrum; with two needle-like intra-orbital spines, inner spine directed forward, outer spine directed slightly upward; outer-orbital spine broad at base, appearing to have been bifid at tip, directed axially; fronto-orbital width 44% maximum carapace width; eyestalk wide at base, arcuate, narrowing centrally, extending to outer-orbital spine.

Anterolateral margins set below level of orbits so that there is a nearly vertical segment between outer-orbital spine and first anterolateral spine; first anterolateral spine attenuated, needle-like, followed by two flat, short anterolateral spines; these followed by two much larger, broad, robust triangular spines; last anterolateral spine directed laterally, attenuated, long, for a total of six anterolateral spines not including outer-orbital spine; at least the last two anterolateral spines ornamented with small triangular spines. Posterolateral margin initially weakly convex, entire, then posteriorly with two spines near posterolateral corner; posterior margin narrow, concave.

Mesogastric region with long anterior process, widened posteriorly, posterior portion with large central spine. Protogastric region about as wide as long, with a longitudinal

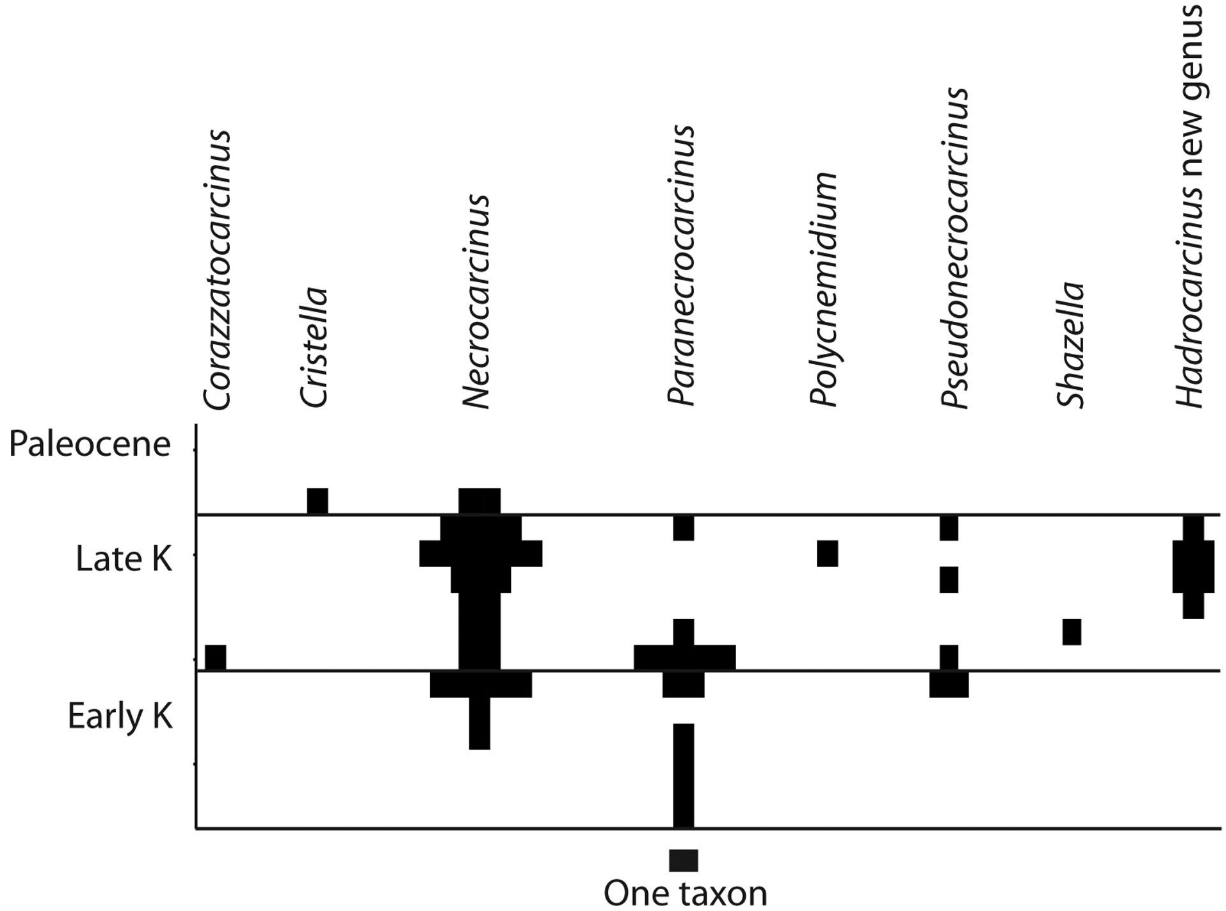

Fig. 4.—Spindle diagram of total number of species per genus of Necrocarcinidae per stage. *Polycnemidium* was reported from the Senonian (i.e., Coniacian-Maastrichtian) by Reuss (1859) and has not since been reported. Since the Senonian spans approximately 25 million years, we placed this genus in the middle of that range (Campanian). Diagram generated by PAST (Hammer et al. 2001) using data from Schweitzer et al. (2010) and references therein.

groove at mid-width, ornamented with at least four spines; hepatic region wider than long, with transverse ridge. Metagastric and urogastric regions confluent, longer than wide, with large central spine; cardiac region with parallel lateral margins, rounded posteriorly, with large central spine; intestinal region flattened.

Cervical groove deep, sinuous, bounding posterior margins of protogastric and hepatic regions; branchiocardiac groove shallower than cervical, bounding posterior margin of epibranchial region; post-cervical groove only present as deep lateral margin of metagastric region. Epibranchial region complex, composed of two separate swellings; innermost swelling oriented obliquely, directed at uro-metagastric region, with finger-like projection at posterior-axial corner, ornamented with two spines; composed of equidimensional swelling that extends to lateral margins and embraces last two anterolateral spines, ornamented dorsally with spine. Remainder of branchial region undifferentiated, with slightly obliquely directed longitudinal keel, originating at spine at about mid-width, and extending in keel to terminate in first posterolateral spine.

Pleonites wide, with broad longitudinal keel; somite 6 longer than wide, with straight lateral terminations.

Right cheliped appearing to be much longer than left; manus of right chela longer than high, becoming higher distally, with two keels on outer surface, one at mid-height and the other closer to lower margin and extending onto fixed finger; fingers appearing to occlude closely.

Left cheliped shorter, with carpus about as long as high, with at least four small, sharp spines on upper surface, spines closer to proximal end of upper surface. Manus longer than high, lower margin with at least three blunt spines, outer surface with spines; upper surface may have been entire.

Etymology.—The trivial name is derived from the Latin words *tectus*, meaning covered or concealed, and *lacus*, meaning lake, in reference to the Hidden Lake Formation, from which the specimen was collected.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the sole specimen of *Hadrocarcinus tectilacus* new genus, new species: maximum carapace width,

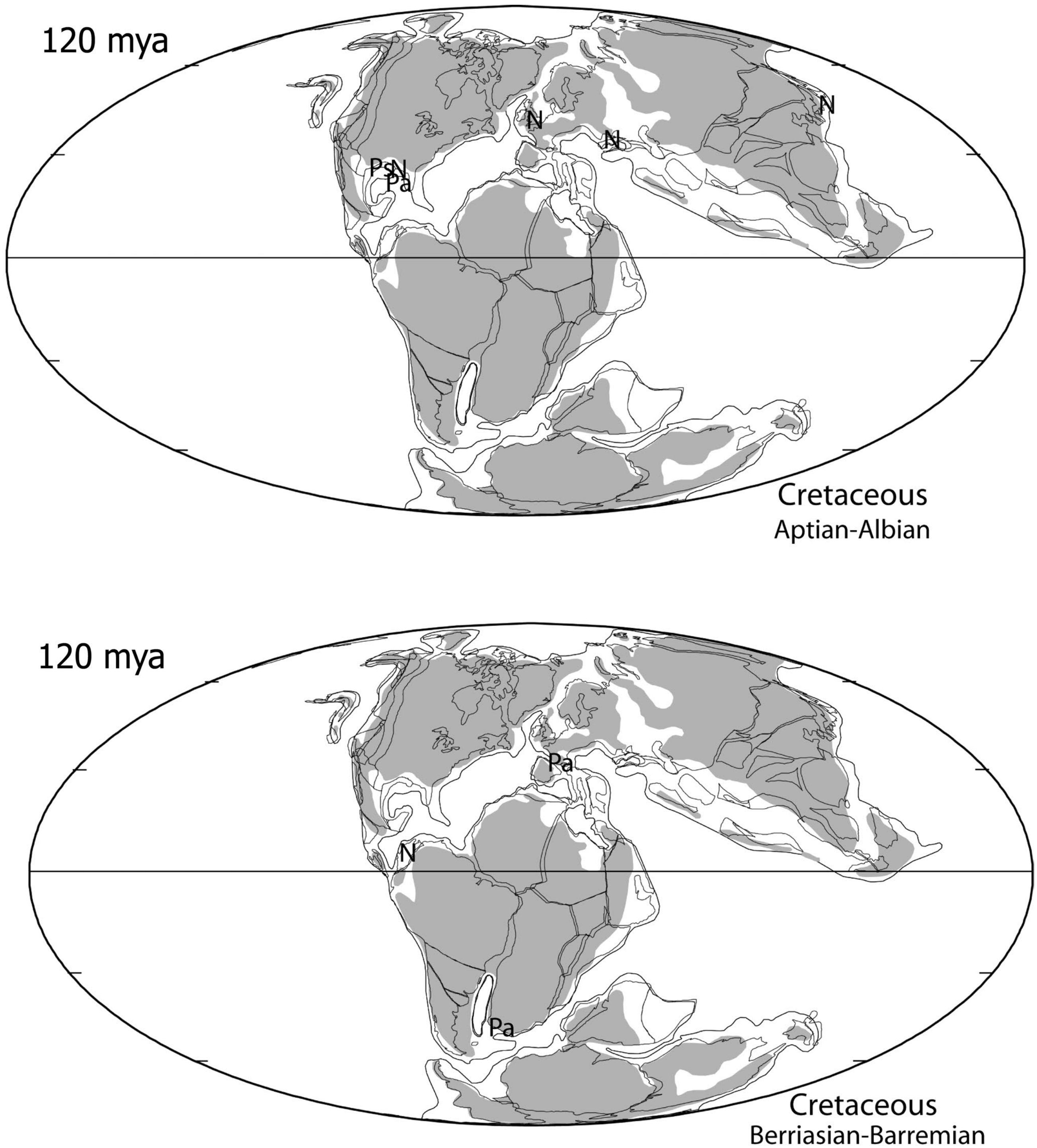

Fig. 5.—Early Cretaceous occurrences of Necrocarcinidae. N = *Necrocarcinus*, Pa = *Paranecrocarcinus*, Ps = *Pseudonecrocarcinus*. Base maps from Scotese (2001) with data from Schweitzer et al. (2010) and references therein.

26.3; maximum carapace length, 26.9; fronto-orbital width, 11.5; rostral width, 3.4; length to position of maximum width, 10.7.

Type.—The holotype and sole specimen is deposited in the Section of Invertebrate Paleontology at Carnegie Museum of Natural History as CM 56700; casts of the specimen are housed at KSU as KSU D2003.

Occurrence.—The specimen was collected by one of us

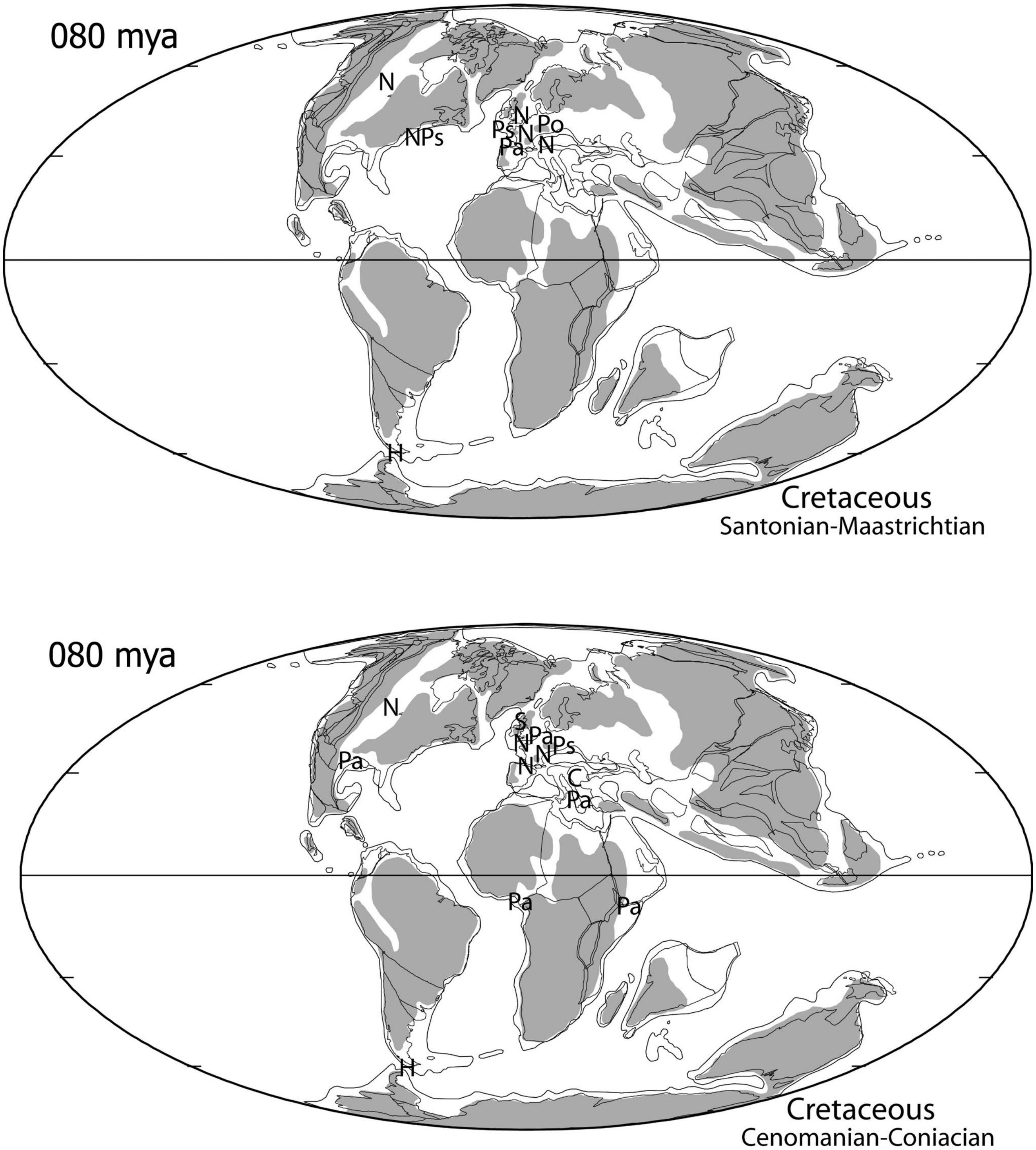

Fig. 6.—Late Cretaceous occurrences of Necrocarcinidae. C = *Corazzatocarcinus*, H = *Hadrocarcinus*, N = *Necrocarcinus*, Pa = *Paranecrocarcinus*, Po = *Polycnemidium*, Ps = *Pseudonecrocarcinus*, S = *Shazella*. Base maps from Scotese (2001) with data from Schweitzer et al. (2010) and references therein.

(Lamanna) from the Coniacian Hidden Lake Formation, on the northern coast of James Ross Island, West Antarctica, west of Cape Lachman, east of Brandy Bay, north of Crame Col, lat. 63º48.540'S, long. 57º52.943'W, on December 8, 2009, associated with inoceramid bivalves.

Remarks.—Feldmann et al. (1993) described *Necrocarcinus wrighti* and *N. carinatus* from the Upper Cretaceous of James Ross Island, and, in the case of *N. wrighti*, the Upper Cretaceous of Vega Island as well. Herein, we have placed both of these species within *Hadrocarcinus*. The

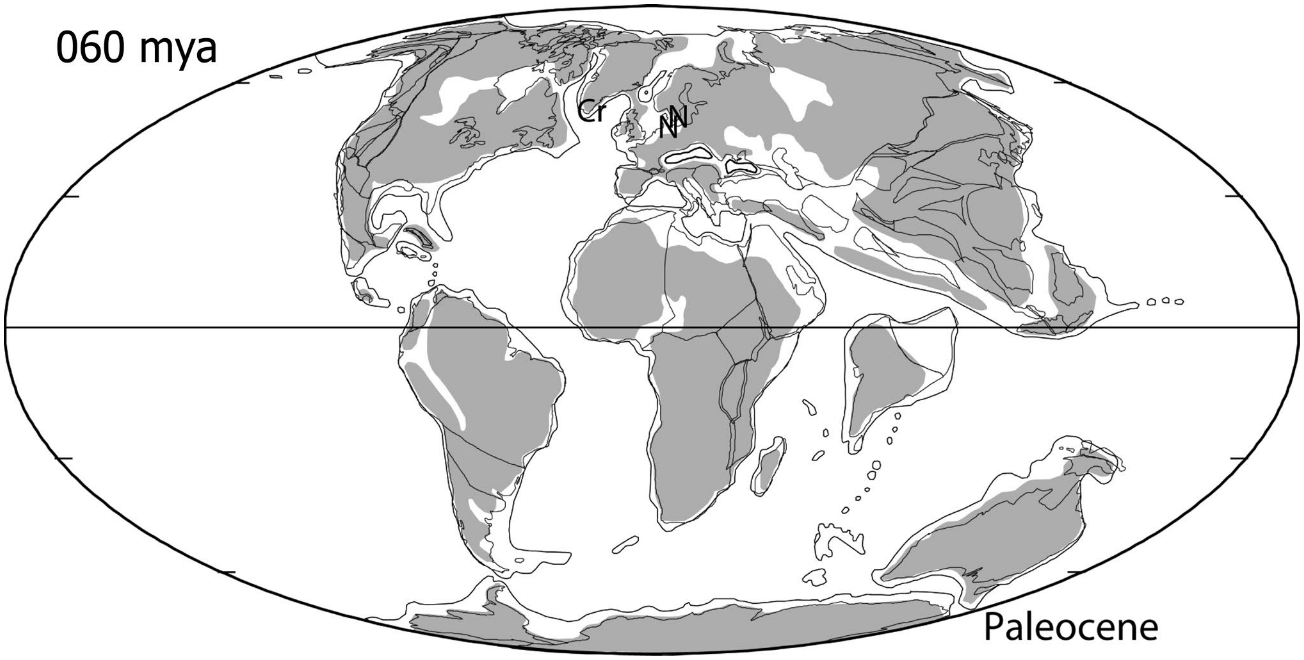

Fig. 7.—Paleocene (Danian) occurrences of Necrocarcinidae. Cr = *Cristella*, N = *Necrocarcinus*. Base maps from Scotese (2001) with data from Schweitzer et al. (2010) and references therein.

new specimen from the Hidden Lake Formation is sufficiently different in morphology and age from these two species to warrant its own species. *Hadrocarcinus tectilacus* differs from *H. wrighti* in possessing larger, longer anterolateral spines; a much more convex posterolateral margin; a long posterolateral spine which is completely lacking in *H. wrighti* (Figs. 3A–B); an axially directed outer-orbital spine whereas that of *H. wrighti* is directed anteriorly; and a narrower posterior margin than that of *H. wrighti*. *Hadrocarcinus carinatus* (Fig. 3C) has carinate axial ornamentation instead of discrete tubercles and more subdued regions than either *H. wrighti* or *H. tectilacus*.

DISCUSSION

The presence of a continuous lineage of *Hadrocarcinus* in the James Ross Basin over the "middle" to latest Cretaceous suggests gradual evolution (anagenesis) of the taxon from Coniacian to Campanian–Maastrichtian time. We are confident in recognizing *H. tectilacus* as a different species from *H. carinatus* and *H. wrighti* based upon the differences enumerated above, as these are easily recognized morphological distinctions that are similar to those used by biologists in recognizing modern brachyuran species (i.e., see McLay [1993] on species within Dromiidae, and Guinot and Richer de Forges [1995] on species within Homolidae). This also suggests that *Hadrocarcinus* was well adapted to the Late Cretaceous paleoenvironment of the Antarctic Peninsula, exhibiting gradual morphological change over approximately 20 million years. Furthermore, the presence of two *Hadrocarcinus* species (*H. carinatus* and *H. wrighti*) in the same locality and stratigraphic unit (the Lachman Crags Member of the Santa Marta Formation of northern James Ross Island) (Fig. 1C) suggests sympatric speciation and niche partitioning in the Antarctic paleoenvironment during Santonian–Campanian time.

Necrocarcinidae is primarily a Cretaceous family, with only a few taxa extending into the earliest Paleocene (Danian) (Fig. 4). Many necrocarcinid genera are monotypic. The family spans all or nearly all of the Cretaceous, with earliest occurrences in the Berriasian–Hauterivian of France (Van Straelen 1936) and the Barremian of South Africa (Wright 1997) and Colombia (Rathbun 1937) (Fig. 5). In the later Early Cretaceous, the family expanded in diversity and paleobiogeographic range (Fig. 5), and by the early to middle Late Cretaceous, necrocarcinids were nearly cosmopolitan in distribution (Fig. 6). The paleogeographic range of the family then constricted to a more antitropical or bipolar distribution by the latest Cretaceous (Fig. 6), and in the Paleocene, necrocarcinids existed only at high latitudes (Fig. 7). This distribution accords well with changing sea level and temperature data for the time, both of which were low during the earliest Cretaceous, increased during the Albian, then increased markedly over the period between about 100–70 million YBP, and then began to drop after about 70 million YBP (Royer et al. 2004; Müller et al. 2008; Wallmann 2008; Leckie 2009). This pattern of diversity also tracks the area of exposure of rocks deposited during these times (Raup 1976; Wall et al. 2009). Thus, it is possible that the observed diversity pattern of Necrocarcinidae simply reflects the increased probability of finding more taxa as the area of stratigraphic exposure increases. It seems unlikely that this diversity pattern is due to collecting bias, because whereas Europe is highly represented, North America is not.

Necrocarcinids appear to have dispersed most widely during times of highest sea level and warmest temperatures, reaching the Antarctic during this time. The high diversity in terms of numbers of genera (Fig. 6) and species of necrocarcinids (Schweitzer et al. 2010) in the middle to higher northern latitudes makes it unremarkable that the family survived the Cretaceous–Paleogene events in that region (Fig. 7), which may have served as a refuge from these events (Harries et al. 1996; Schweitzer and Feldmann 2005).

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