Unusual Albian (Early Cretaceous) Brachyura (Homoloidea: Componocancroidea New Superfamily) from Montana and Wyoming, U.S.A.

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INTRODUCTION

Chance collection of specimens of decapod crustaceans has often led to the discovery of new species and occurrences of decapods in rock units not previously known to yield them. The discovery of two fossil crabs in rocks of the Shell Creek Shale in southern Montana by Robert Feldman represents just such a serendipitous discovery. When the material was made available to us for study, it became clear that one of the specimens represented a truly unique taxon. Search of the literature on the Shell Creek Shale disclosed a tangential reference to some decapod specimens that had been collected in Bighorn County, Wyoming, during PhD research by Don Eicher. That material, which had been tentatively identified in 1957 by Henry B. Roberts, U.S. National Museum of Natural History, was deposited in the collections of the Peabody Museum, Yale University. Those specimens, in addition to material collected by Robert Feldman, form the basis for the description of two new species of brachyurans and the definition of a new superfamily, family, and genus within Heterotremata to embrace one of them.

The specimens in this study were collected from two sites in southern Montana and northern Wyoming. In Montana, two crabs were collected from the Shell Creek Shale about 30 m (100 ft) above the Muddy Sandstone. The original designation of the collecting site, by Robert Feldman in August 1982, was “... about 20 yards northwest of road south of Duck Creek in SE, NE, NW, NE, Sec. 5, T4S, R25E, Yellowstone County, Montana (USGS Mossmain SW Quadrangle, 7.5’ Series)” (Feldman, personal communication, 2004). The site was re-occupied by two of us (RMF and CES) accompanied by Feldman and a GPS location of 45°31'13.6"N, 108°39'19.5"W was determined. During that visit, no additional specimens were collected, although trace fossils of indeterminate affinities, an oyster, and a fish scale were collected from the otherwise fairly unfossiliferous layers.

In Wyoming, eleven specimens were collected from the Shell Creek Shale in an ironstone concretionary bed 57 m (187 ft) above the base of this unit at a locality in badlands about 3 miles west from the old Cloverly Post Office and 13 miles northeast from Greybull, Big Horn County, Wyoming. The locality is designated as site IP (Invertebrate Paleontology collection, Yale Peabody Museum) A00822. The specimens were collected by Karl M. Waage and Don L. Eicher. Of this lot, eight specimens are identifiable brachyurans and three remain indeterminate.

The stratigraphic history of the Shell Creek Shale was outlined by Eicher (1962). The unit was named by Eicher (1960) for what had previously been referred to as the “Upper Thermopolis” by Mills (1956) who included it within the Mowry Shale, or as the unnamed upper part of the Thermopolis Shale (Mobery, 1960). The Shell Creek Shale lies above the Muddy Sandstone and below the Mowry Shale (Eicher, 1962). The unit was interpreted by Eicher (1960) to have been deposited in a deepening-upward basin in which the salinity increased upward. Twelve species of foraminifers have been identified from the Shell Creek Shale (Eicher, 1960, p. 27) but the macrofossil record is sparse. Perhaps most notable is the presence of the ammonite Neogastroplites haasi Reeside and Cobb, 1960, which places the unit within the lowest zone of Neogastroplites in the Lower Cretaceous (Reeside in Eicher, 1960, p. 27). The brachyurans collected from the Formation in Wyoming were sent to Henry Roberts, then at the U.S. National Museum of Natural History, who identified eight of the specimens as Homolopsis sp. and two as Dakoticancer sp. Until today, those specimens were not re-evaluated.

All specimens used in the study are deposited in the Peabody Museum of Natural History, Yale University, New Haven, CT (YPM).
SYSTEMATICS

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Homoloida De Haan, 1839
Homolidae De Haan, 1839
Zygastrocarcinus Bishop, 1983

Type Species.—Zygastrocarcinus griesi Bishop, 1983, by original designation.

Other Species.—Zygastrocarcinus cardsmithi Bishop, 1986; Zygastrocarcinus mendryki (Bishop, 1982); Z. waagei n. sp.

Diagnosis.—Carapace slightly longer than wide; ornamented with large tubercles that may themselves be granular; extra-lineal areas typically well-preserved; sub-hepatic regions highly inflated; rostrum turned down; cervical and branchiocardiac grooves deep, about equally developed; cardiac region long, narrow; carapace widest in posterior one-third; male pleomeres apparently all free; telson with sinuous lateral margins, with longitudinal depression near tip; somite 5 widest, somites narrowing anteriorly; merus of pereiopods with spines.

Remarks.—Bishop (1983) originally erected Zygastrocarcinus for two Cretaceous species. Subsequently, he described a new species (Bishop, 1986) and referred two other species to the genus, Paleohomola gorrelli Rathbun, 1926, and Homolopsis richardsoni Woodward, 1896. Collins (1997) indicated that the two last-named species did not belong to Zygastrocarcinus with which Schweitzer et al. (2004) later concurred. They referred Homolopsis richardsoni to a new genus, Rhinodromia, and placed it and Paleohomola within Homolodromiidae due to their lack of lineae homolicae. Bishop and Brannen (1992) placed Homolopsis etheridgei (Woodward, 1892) from the Albion of Australia within Zygastrocarcinus. Collins (1997), however, erected a new genus for this species, Lignihomola. We concur with Collins (1997) that the species is sufficiently distinctive to warrant generic placement differentiating it from both Homolopsis and Zygastrocarcinus. Lignihomola and Zygastrocarcinus share several features, including preservation of extralinal portions of the carapace as well as appendages and pleons, not seen in most other Cretaceous homolids. In addition, both taxa are ornamented with large granules and lack the lateral ridges extending from the cardiac region onto the branchial region (MR [= metabranchial ridge] of Schweitzer et al., 2004) seen in many homolids, both extinct and extant. However, the two genera can be differentiated because Lignihomola displays markedly sinuous lateral margins, giving the carapace a bulbous appearance. The carapace of Zygastrocarcinus is more or less rectangular overall. In addition, the chelipeds of Lignihomola are distinctly short, whereas those of Zygastrocarcinus appear to have been much longer than the carapace itself.

Zygastrocarcinus differs from other Cretaceous genera in several ways. Few other taxa within Homolidae have well-preserved extra-lineal areas, and nearly every specimen of Zygastrocarcinus spp. possesses at least part of this area. This suggests that the extra-lineal regions of Zygastrocarcinus were either especially well calcified or especially tightly attached to the rest of the carapace. The latter seems to be likely in any case, because specimens of both Z. griesi and Z. waagei possess elements of the sternum and appendages as well. Thus, the entire exoskeleton was apparently strongly articulated by arthroplial membranes and other materials. In other genera such as Latheticocarcinus Bishop, 1988, known from Cretaceous through Danian rocks, usually only the dorsal carapace between the lineae homolicae is known. It is uncommon to find other exoskeletal elements in fossil homolids.

Zygastrocarcinus differs from many other homolids in lacking lateral ridges extending from the cardiac region onto the branchial region (MR of Schweitzer et al., 2004). Such ridges are seen to be prominent in both Latheticocarcinus and Homola Leach, 1815, an extant genus known from fossil occurrences in Eocene rocks of western North America (Schweitzer, 2001; Schweitzer et al., 2006). Homolopsis Bell, 1863, collected from Cretaceous rocks in a number of localities world wide (Schweitzer et al., 2004), is widest at mid-length and also lacks these ridges but does possess marked lateral projections at mid-length on the lateral margin along the lineae homolicae. Species of Zygastrocarcinus, by contrast, are widest in the posterior one-third of the carapace, both including and excluding the extra-lineal portions, and lack such lateral projections at mid-length. Thus, Zygastrocarcinus is a distinct genus.

So far, four species of Zygastrocarcinus are known, all from the Western Interior Seaway of North America. The oldest species is the new taxon described below, Z. waagei, collected from Lower Cretaceous rocks of Montana and Wyoming. Both Zygastrocarcinus griesi and Z. cardsmithi are known from Campanian rocks of Montana (Bishop, 1983, 1986), and Z. mendryki was collected from Maas-trichtian rocks of South Dakota (Bishop, 1982). Thus, the genus appears to have been endemic to the area. Of Cretaceous Homolidae, it is the only known genus to be endemic to an epeiric sea. Whereas other genera are found in the Western Interior Seaway (Homolopsis; Latheticocarcinus), they are also known from oceanic environments (Schweitzer et al., 2004).

Zygastrocarcinus waagei n. sp.

Fig. 1A-G

Diagnosis.—Carapace longer than wide; anterior carapace regions with large, granular tubercles; cardiac region much longer than wide; branchial regions finely granular; sub-hepatic regions very inflated; male pleomeres apparently all free, telson with sinuous lateral margins, with longitudinal depression near tip; somite 5 widest, somites narrowing anteriorly; merus of pereiopods with long, forward-directed spines.

Description.—Carapace longer than wide, with large tubercles; moderately vaulted transversely and longitudinally; lineae homolicae well developed anteriorly, more faint posteriorly. Front axially down-turned, triangular; orbits positioned sub-rostrally, fairly large, directed forward. Ocular sheath (terminology of Guinot and Richer de Forges, 1995) with...
marked axial crease, displaced laterally due to crushing. Sub-hepatic region strongly inflated, bounded by deep grooves, ornamented with scattered tubercles, lacking concave area in which eye can rest as is typical of extant homolids; triangular sub-epibranchial region posterior to sub-hepatic region.

Epigastric regions small, circular, inflated. Mesogastric region with long anterior process extending into sulcus
which extends into rostrum; anterior process with longitudinal inflation centrally; region widening posteriorly, with three swellings arranged in a triangle, posterior two swellings larger, all three swellings granular, posterior part of mesogastric region marked by muscle scars where cuticle is decorticated. Meta gastric region wider than long, widest axially, narrowing distally, anterior margin nearly straight, posterior margin convex. Urogastric region short, depressed. Cardiac region longer than wide, with pair of circular swellings anteriorly and one at posterior end, swellings granular. Intestinal region longer than wide, narrow, granular where cuticle retained.

Protogastric regions with three spherical swellings, swellings themselves granular where cuticle is not opalized. Hepatic region very reduced, with at least one swelling. Cervical groove initially nearly straight, obliquely directed from lateral margin to lateral edge of mesogastric region, then curving in concave arc around posterior margin of mesogastric region, with a pit on either side of axis of animal; groove deepest laterally but remaining relatively deep along entire length. Post-cervical groove deep, bounding posterior margin of meta gastric region, extending laterally about one-third the distance to lateral margins. Branchiocardiac groove not well known, parallel to cervical groove laterally, extending axially and outlining lateral margins of cardiac region, two segments becoming parallel posterior to cardiac region and outlining intestinal region.

Epibranchial region oblique, roughly parallel to cervical and branchiocardiac grooves, with lateral, larger swelling and axial, smaller swelling. Remainder of branchial region undifferentiated, broadly inflated. Sub-epibranchial region bounded by ventral extensions of cervical and branchiocardiac grooves; remainder of sub-branchial region broadly inflated, with row of tubercles parallel to and along linea homolica; all sub-dorsal regions oriented perpendicular to dorsal carapace, lateral sides high. Posterior margin rimmed, concave axially, with two broad concavities laterally.

Merus of pereiopod 1 much longer than high, with forward directed spines on upper margin, upper and lower margins relatively straight; ischium of pereiopod 1 short, about as long as high, ornamented on outer surface with scattered tubercles. Coxae of pereiopods 2 and 3 longer than high. Pereiopod 5 appearing to have been sub-dorsal based upon position of small, dorsally directed coxae.

Male pleon apparently with all somites free, filling entire sterno-pleonal cavity. Somite 3 wider than long; somite 4 wider than long but longer than somite 3; somite 5 wider than long, twice as long as somite 4; somite 6 about as wide as long; telson triangular, reaching to base of third maxillipeds, with sinuous lateral margins and longitudinal depression near tip; all somites with broad longitudinal axial swelling and longitudinal lateral depressions parallel to swelling.

Etymology.—The trivial name honors the collector of most of the specimens of the new species, Karl M. Waage. Occurrence.—The holotype and five paratypes, YPM 220103, 220104, 220106, 220107, and 220110, were collected from the Early Cretaceous Shell Creek Shale, near Greybull, Bighorn County, Wyoming, by Karl M. Waage and Don L. Eicher. The sole paratype from Montana, YPM 221135 was collected from the same unit south of Duck Creek, south of Billings, Yellowstone County, Montana, by Robert Feldman.

Remarks.—Zygastrocarcinus waagei n. sp. differs from all other species of Zygastrocarcinus in having less dense ornamentation on the dorsal carapace regions. In particular, the branchial regions are smoother in the new species than in other species of the genus. Whereas some specimens of Z. waagei lack cuticle, enough retain portions of cuticle to indicate that the smoother nature is real and not an artifact of preservation. The specimens display different modes of preservation. The Duck Creek, Montana, specimen is opalized and thus exhibits a smoother carapace that lacks cuticular detail. The specimens collected in Wyoming were preserved within ironstone concretions and exhibit the typical black preservation seen in such occurrences. YPM 220105 consists mainly of replaced cuticle, and the interior of the specimen is infilled with long, narrow fecal pellets.

Remarks.—The specimens assigned to Componocancer roberti new species exhibit a remarkable combination of characters unknown in any other brachyuran taxon and, therefore, warranting designation of a new superfam, family, and genus. In drawing this conclusion, dorsal and ventral morphology of representatives of a broad variety of decapods, including representatives of most families of extant brachyurans, were examined. As will be discussed below, individual features seen on C. roberti were recognized on certain taxa. However, the combination of features, particularly those that have been used as the definitional basis for podotremates and heterotremates, distinguishes this taxon from all others.

The possession of a triangular sternum in which the sternites are unfused laterally is strongly reminiscent of some palinurid and scyllarid lobsters. The strongly reduced sternites 7 and 8 which are directed posteriorly and dorsally...
Diagnosis.—As for the superfamily.

Componocancridae n. fam.

Diagnosis.—As for the superfamily.

Componocancer n. gen.

Type Species.—Componocancer roberti new species, by original designation.

Diagnosis.—As for the superfamily.

Componocancer roberti n. sp.

Fig. 2A-G

Diagnosis.—As for the superfamily.

Description.—Carapace rectangular to hexagonal, length about 90 percent maximum carapace width, widest at 36% the distance posteriorly; moderately vaulted longitudinally, less vaulted transversely, dorso-ventrally compressed.

Front nearly straight, about one-third maximum carapace width; with small, triangular, turned down projection at midpoint that is visible in frontal view. Orbits circular when viewed from front, directed forward; shallow when viewed dorsally; two shallow orbital fissures present in deepest part of orbit; blunt, forward-directed spine at outer orbital corner; fronto-orbital width 81% maximum width. Anterolateral margin convex, sharply defined when viewed laterally, scalloped, with three broad projections, followed by small, forward-directed spine at anterolateral corner; posterolateral margin weakly convex, longer than anterolateral margin. Posterior margin slightly concave, posterior width 66% maximum width.

Regions of carapace defined as slightly more elevated areas with larger and more prominent pitted surfaces. Mesogastric region diamond shaped, with long anterior projection, widest at level of maximum carapace width.

Protaogastric regions weakly developed, rhomboid in shape. Metagastric region triangular with rounded corners, widest anteriorly. Urogastric region indistinct, narrow, wider than long, slightly lower in elevation than other regions. Cardiac region diamond shaped, most prominently inflated of carapace regions, bearing two lateral swellings at level of maximum width and one axial swelling near posterior end of region. Intestinal region undefined. Hepatic regions flattened below level of protaogastric region. Branchial regions large; elongate swollen areas extending posterolaterally; weakly differentiated. Pits on elevated regions of carapace circular, rimmed; larger pits located in regions higher in elevation more prominently developed on endocuticle than on exocuticle surface.

Sub-hepatic region inflated, situated just ventral to orbit, separated from the pterygostomian by distinct groove. Pterygostomian large, longer than high, narrowing distally, convex on the posterior margin, fused with sub-branchial region, inflated area on the posterior half.

Third maxilliped longer than wide, not well preserved, does not appear to close completely the buccal cavity which is rectilinear, wider than long, widest anteriorly. Mandibles isosceles triangular, longest edge aligned axially; right mandible slightly larger than left.

First and second thoracic sternites fused into isosceles-triangular segment, axially depressed in posterior half; short edge separated from third somite by suture. Third sternite short and narrow, axially depressed, convex along posterior margin. Fourth sternite fused axially and sutured laterally to third somite, third and fourth sternites strongly depressed axially. Fourth sternite largest, more than twice size of any other sternite, lateral region highly inflated as oval protuberances; fourth and fifth sternites fused axially and free laterally. Fifth sternite small medially, lateral regions oval shaped, nearly flat, long axis directed slightly posterolaterally. Sixth sternite sutured to fifth and seventh sternites, large oval-shaped openings on sternum of female occur on the lateral edges of medial region. Sixth and seventh sternites appear unfused. Seventh sternite short and narrow, lateral regions directed posterolaterally. Eighth sternite fused axially to seventh somite, very narrow in axial area, lateral regions directed dorsally and posterolaterally.

Pleon of female about 34% maximum carapace width, widest at somite 6. Proximal somites not visible. Somites 4 and 5 short and broad, concave toward posterior, margin rounded. Somite 6 large, rectangular, about twice as wide as long, weakly elevated axially and laterally. Telson triangular with rounded apices, slightly wider than high.

Basal articles of pereiopods 1-3 large, becoming slightly smaller from pereiopod 1 to pereiopod 3. Basal elements of pereiopods 4 and 5 not preserved.

Measurements.—Measurements (in mm) taken on specimens of Componocancer roberti are given in Table 1.

Etymology.—The trivial name recognizes the collector of the holotype, Robert Feldman, of Billings, Montana, who generously made the specimen available for study by the authors, guided us to the collecting site, and permitted deposit of the specimen in the Peabody Museum.
Types.—The holotype, YPM 221136, consists of the carapace and sternum of a female. The paratypes, YPM 220096 and 220102, consist of the carapace and sternum of a male specimen and the carapace and pleon of a female, possibly immature, specimen, respectively.

Occurrences.—The holotype was collected from the Shell Creek Shale (Albian, Early Cretaceous) near Duck Creek, Yellowstone County, Montana, by Robert Feldman. The paratypes were collected from the same unit near Greybull, Bighorn County, Wyoming, by Karl M. Waage and Don

Fig. 2. Componocancer roberti n. gen., n. sp. A-D, Dorsal (A), frontal (B), left lateral (C), and ventral (D) view of holotype, YPM 221136. The sternum exhibits prominent vulvae on sternite 6, indicating that it is a female. E, F, Dorsal (E) and ventral (F) view of paratype, YPM 220096, bearing a broad pleon indicating that it is possibly an immature female. G, ventral view of paratype, YPM 220102, bearing a sternum of a male specimen. Scale bars equal 1 cm.
L. Eicher. All of the specimens of *Componocancer roberti* are preserved as ironstone replacements from within concretionary horizons in the Shell Creek Shale. One paratype from Wyoming, YPM 220102, has a partially decorticated exoskeleton and the interior of the crab is packed with very small, cylindrical fecal pellets which suggests that the organic matter within the exoskeleton was scavenged early in its taphonomic history.

Remarks.—The new species is readily distinguished from all known species of brachyurans on the basis of the remarkable combination of so-called primitive and derived characters as discussed above. This plexus of characters, especially considering the presence of vulvae on the female sternum, makes it possible to assign the species to new higher taxonomic units within Heterotremata with considerable confidence. However, the question that looms large relates to the evolutionary implications of this morphological array (Feldmann et al., 2007).

Studies of extant brachyurans has led to the quite reasonable probability that the array of characters typifying Heterotremata co-evolved (Guinot, 1977, among others). The combination of characters observed in *Componocancer roberti* new species, however, introduces the possibility that the development of the heterotreme condition evolved by successive steps, one of the first of which was the displacement of the female genital openings from the primitive basal position on the appendages to the sternal position. We know of no a priori reason that this could not be so. If this scenario is correct, *Componocancer roberti* would represent an early intermediary between the dromiaceans and the eubrachyurans.

A second possibility is that *Componocancer roberti* represents a “failed experiment” in morphological combinations -one that did not yield descendant species for some reason. This hypothesis springs from the framework of a scheme developed by Schram (1980; 1983) in defining the Baupläne of eumalacostracans. Schram (1983) designed potential morphological combinations of several characters including development of carapace, presence of uniramous or biramous appendages, and presence or absence of a brood pouch. Examination of living and fossil eumalacostracans revealed three types of occurrences. Many of the combinations could be attributed to known, long-ranging, living and fossil groups. Alternatively, a few enjoyed a brief geological history only to become extinct and a few are known exclusively from modern occurrences. However, there are several combinations of characters within the Baupläne that are not known to be represented either in the fossil or modern record.

It is possible to apply a similar analysis to the history of Brachyura, and when this is done, the same set of combinations arises. Combination of characters in the analysis includes position of genital openings, the podotrematous, heterotrematous, and thoracotrematous conditions defined by Guinot (1977); primitive or derived carapace form, based upon a combination of dorso-ventral compression and development of transverse grooves; presence or absence of a fifth pereiopod carried in a dorsal

Table 1. Measurements, in millimeters, taken on specimens of *Componocancer roberti* n. sp. L = carapace length; W = maximum carapace width; FW = frontal width; FOW = fronto-orbital width; PW = posterior width.

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<td>32.3</td>
<td>~ 7.8</td>
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<td>~ 21.4</td>
<td>23.2</td>
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Fig. 3. Potential Baupläne of Brachyura, based upon the position of genital openings, development of dorsal carapace, position of pleon, and orientation of 5th pereiopods. Boxes outline the morphotypes that are typically exhibited by known groups. 1 = Dromiacea. 2 = Raninoidea. 3 = Newly defined Compononacrinacea. 4 = Some Majoidea. 5 = Most Heterotremata. 6 = Thoracotremata. The morphotypes not delineated by boxes have not been recognized.
position; and position of the pleon, either exposed dorsally or concealed by the carapace (Fig. 3). As in the analysis performed by Schram, not all of the combinations of characters are expressed in known brachyurans. The combination of the heterotreme condition, with a derived carapace, inferred exposed pleon, and dorsal fifth pereiopod is a combination that, until the discovery of *Componocancer roberti*, was unknown.

Considering that this combination of characters is unique and that there are no other specimens representing intermediate conditions (for example, species with all the characteristics of *Componocancer roberti* except possession of a derived carapace form) it is difficult to evaluate the differences between either considering this to be a transitional form between podotremes and heterotremes, or judging the new species to be representative of a novel combination of characters within the landscape of potential brachyuran types. For the time being, it seems more likely that *Componocancer roberti* represents a failed experiment, occupying a niche within the Baupläne of brachyurans that did not successfully establish a long-term lineage.

Acknowledgements


References


