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A new homolid crab, *Zygastrocarcinus carolinasensis* n. sp., from the Cretaceous (Campanian) of NE Mexico: implications for paleobiogeography

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Abstract

A new species of the homolid crab, *Zygastrocarcinus carolinasensis* n. sp., is reported from the Upper Cretaceous (upper Campanian) strata of Coahuila, NE Mexico. Only the anterior part of the ~8 mm wide carapace was preserved in addition to a part of the sternum (sternites 1-6). The sternum is the oldest figured example of a fossil homolid sternum, and also of the entire section of fossil Homoloida. The sternum seems to be similar to extant homolids in general outline, and to an earlier described Eocene homolid. Hitherto, *Zygastrocarcinus* spp. were only known from the northern part of the USA (Wyoming, Montana, and South Dakota). Thus, the new species extends the geographic range of the genus during the Cretaceous to much of North America. Additionally, this is the second fossil homolid known from Mexico.

Keywords: Crustacea, Decapoda, Brachyura, Campanian, Mexico, *Zygastrocarcinus*.

Resumen

Se reporta una nueva especie del cangrejo homólido, Zygastrocarcinus carolinasensis n. sp., en estratos del Cretácico Superior (Campaniano superior) de Coahuila, NE de México. Únicamente se preservó la porción anterior del caparazón de ~8 mm de ancho, además de parte del esternón (esternitos 1-6). El esternón es el ejemplar ilustrado más antiguo para un homólido fósil, así como para toda la sección de los Homoloida fósiles. El esternón es muy parecido a los de homólidos existentes en cuanto a su forma general, y a un homólido del Eoceno descrito previamente. Hasta ahora, se conocían Zygastrocarcinus spp., solamente en la región norte de los EUA (Wyoming, Montana, Dakota del Sur). Por lo tanto, la nueva especie amplía la distribución geográfica del género durante el Cretácico a gran parte de Norteamérica. Además, éste es el segundo homólido fósil reportado para México.

Palabras Clave: Crustacea, Decapoda, Brachyura, Campaniano, México, Zygastrocarcinus.

1. Introduction

Homolid crabs appeared in the Late Jurassic, were fairly common in the late Early and Late Cretaceous, and are only marginally known from the Cenozoic with the exception of extant homolids (*e.g.*, Karasawa *et al*., 2011, fig. 13). The less common occurrence of homolids in Cenozoic marine sediments may be related to a migration to deeper waters after the Cretaceous (Schweitzer *et al*., 2004) in the Early Cenozoic (Collins, 1997), because deep water strata are not often preserved in the fossil record. Extant homolids generally inhabit waters of 100-1000 m depth, although many species of *Homologenus* A. Milne-Edwards *in* Henderson, 1888, live in even deeper waters (Guinot and Richer de Forges, 1995, fig. 76). Members of the homolid family are believed to have originated from Late Jurassic prosopid crabs (Collins, 1997). The genus *Laeviprosopon* Glaessner, 1933, seems to play a crucial role in the discussion as this genus has been assigned to both the Prosopidae (Glaessner, 1933; Schweitzer and Feldmann, 2008) and the Homolidae (Patrulius, 1966; Wright and Collins, 1972; Collins and Wierzbowski, 1985; Wehner, 1988). The central discussion point is the presence or absence of a *linea homolica*, a longitudinal line of weakness near the lateral margins where the carapace breaks during the molting process. Recently, Klompmaker (2013) suggested that mid-Cretaceous (late Albian) species of *Laeviprosopon* from Spain may exhibit a *linea homolica*, although the number of specimens was limited. Currently, *Laeviprosopon* is placed within the Prosopidae (Schweitzer *et al*., 2010; Karasawa *et al*., 2011). Given the current placement of *Laeviprosopon*, it may be speculated that early species of *Laeviprosopon* could have given rise to the first true homolids. Here, we report on a new species of a different homolid genus, *Zygastrocarcinus*, exhibiting an unambiguous *linea homolica*. The discovery of the new species has implications for paleobiogeography. Additionally, the specimen exhibits a sternum, very rarely preserved in fossil Homoloida.

2. Locality

The study locality is situated in the northern edge of the Parras Basin Coahuila (Figure 1) and exposes siliciclastic sediments of the upper Campanian Cerro del Pueblo Formation (Eberth *et al*., 2004; Lawton *et al*., 2009; among many others). A previous study (Rodríguez de la Rosa and Cevallos-Ferriz, 1998) reported on plant remains, invertebrates, and vertebrate remains from the El Pelillal locality, which yields beds of about the same stratigraphic level and is located 3.6 km NE of the locality reported on here (26°06′06.11″ N, 101°09′22.33″ W). Rodríguez de la Rosa and Cevallos-Ferriz (1998, p. 751) suggested a tide-influenced, freshwater environment for the El Pelillal locality. The specimen of this study is found in association with the ammonite *Sphenodiscus* sp. and other marine invertebrates, and thus was likely a marine decapod, which is consistent with extant and other fossil homolids.

3. Systematic Palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Homoloida Karasawa, Schweitzer and Feldmann, 2011
Superfamily Homoloidea De Haan, 1839
Family Homolidae De Haan, 1839
Genus *Zygastrocarcinus* Bishop, 1983

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

Other Species. *Zygastrocarcinus cardsmithi* Bishop, 1986; *Z. griesi* Bishop, 1983; *Z. mendryki* (Bishop, 1982); *Z. waagei* Feldmann *et al.*, 2008, *Z. carolinasensis* Klompmaker, Ventura, and Vega n. sp.

Zygastrocarcinus carolinasensis Klompmaker, Ventura, and Vega n. sp.
Figures 2, 3

Diagnosis. Carapace small; exhibiting tumid regions, tubercles, and strong grooves; moderately convex transversely; lateral side subvertical. Rostrum axially downturned. Front with large concavity adjacent to rostral area. Confluent hepatic and protogastric regions exhibiting four tubercles arranged in a diamond shape with most prominent angle directed posteriorly. Epibranchial region exhibits strong, directed anterolaterally spine. Strong cervical groove broadly V-shaped, anterolaterally directed, straight until approaching epibranchial region. Sternites 1 and 2 forming minute triangle; larger sternite 3 exhibiting raised, laterally directed episternites; sternite 4 larger than sternite 3, exhibiting raised, posterolaterally directed episternites.

Description. Carapace small (width ~8 mm); exhibiting tumid regions, tubercles, and strong grooves; moderately convex transversely; lateral side subvertical.

Rostrum axially downturned, without spines. Front with large concavity adjacent to rostral area in which eye can rest as is typical of extant homolids (see Guinot and Richer de Forges, 1995). Epigastric regions defined by two rounded tubercles adjacent to tip of long anterior process of mesogastric region, anteriormost one being smallest. Pyriform mesogastric region tumid in posterior portion due to three swellings arranged in a triangle pointing anteriorly in dorsal view, anterior process and posterior portion separated by depression at narrowest part, with two setal pits just lateral to axis of posteriormost portion. Confluent hepatic and protogastric regions exhibiting four tubercles arranged in a diamond shape with most prominent angle directed posteriorly. Uro- and/or metagastric region as wide as mesogastric region. Epibranchial region with strong,

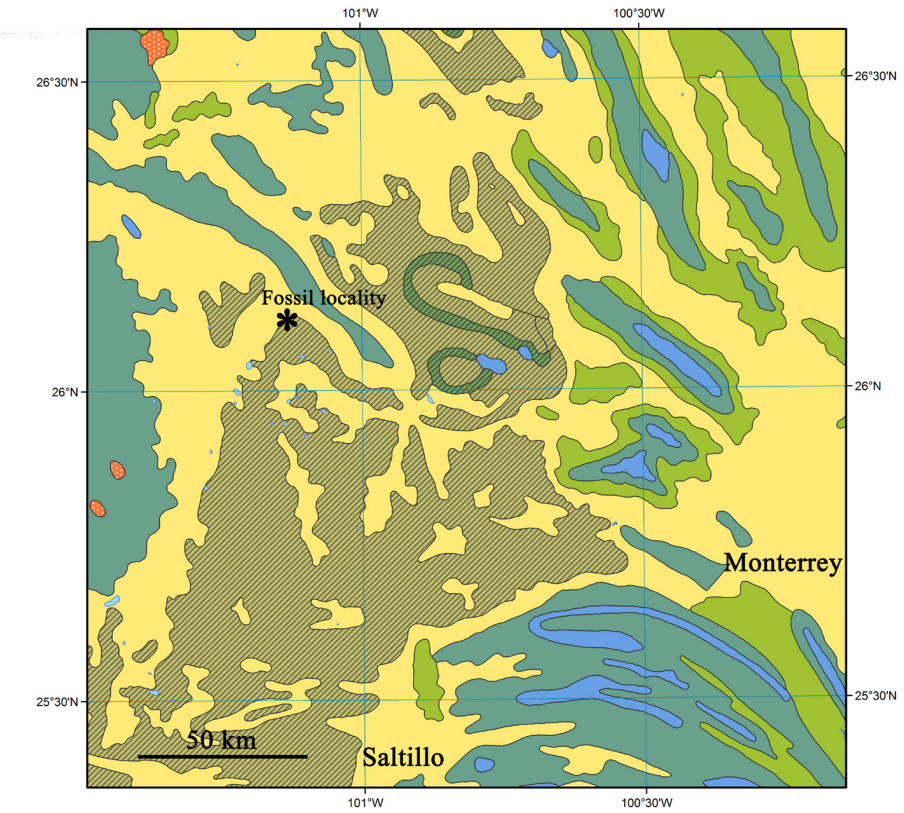

Figure 1. 1, Map of locality where the specimen was found near Exhacienda de Carolinas, Ramos Arizpe County, Coahuila. 2, Landscape of study locality.

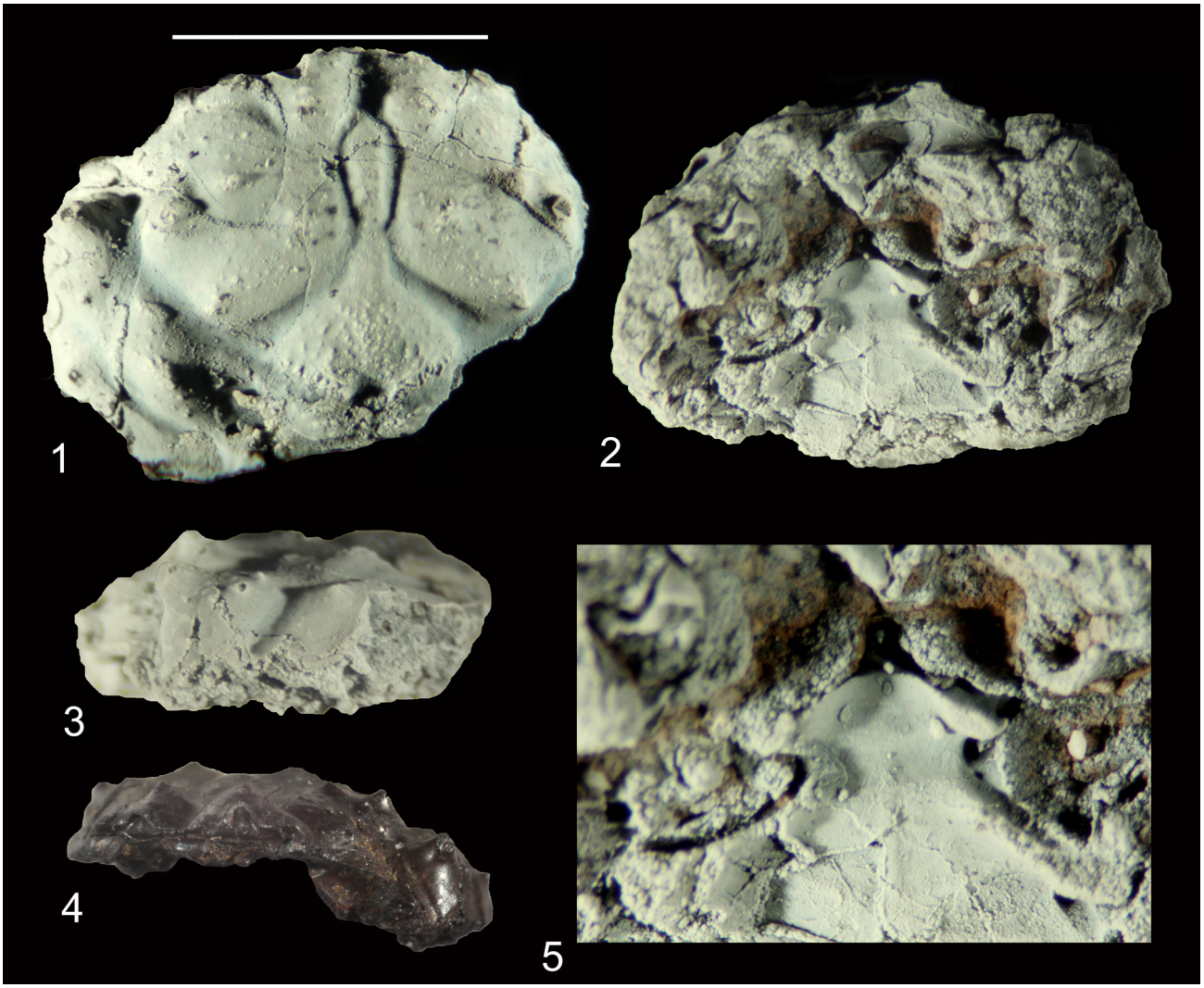

Figure 2. The holotype of *Zygastrocarcinus carolinasensis* n. sp. (CPC-903). 1. Dorsal view. 2. Ventral view. 3. Left-lateral view. 4. Fronto-lateral view. 5. Close up of the first four sternites. Scale bar = 5.0 mm.

anterolaterally directed spine and smaller tubercles posterior to it. Mesobranchial region exhibiting two tubercles lateral to uro- and/or metagastric region, with another branch posterior to uro- and/or metagastric region. Metabranchial region incompletely preserved. Lateral margin rounded.

Grooves generally strong and well developed. Cervical groove broadly V-shaped, directed anterolaterally, straight until approaching epibranchial region, where it bends anteriorly, then curves into anterolateral concavity surrounding anterior part of epibranchial region. Groove defining boundary between epibranchial region and confluent protogastric and hepatic regions connects cervical and branchiocardiac grooves, appears also to be part of longitudinal *linea homolica*, which is also visible on metabranchial region. Post-cervical groove parallels cervical groove axially, but connects to cervical groove at lateralmost position. Branchiocardiac groove equally strong as and parallels cervical groove dorsally, appears to widen

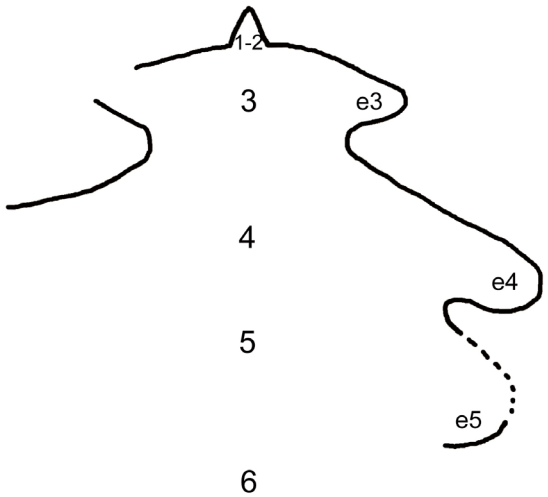

Figure 3. Drawing of the sternum of *Zygastrocarcinus carolinasensis* n. sp., the numbers indicate the sternites, and the e-numbers indicate the episternites.

on lateral side.

Ventral side showing incompletely preserved, triangular sternum. Sternites 1 and 2 forming minute triangle, curving upward at tip in ventral view. Sternite 3 larger, exhibiting raised, laterally directed episternites. Sternite 4 larger than sternite 3, exhibiting raised, posterolaterally directed episternites. Episternites of sternite 5 not well preserved. Central portion of sternites 5 and 6 preserved. All visible sternites appear fused.

Granules (defined as smaller tubercles) present near tubercles on confluent hepatic and protogastric regions, on posterior part of mesogastric region, on uro- and/or metagastric region, and on mesobranchial region.

Posterior carapace, subhepatic region, orbits, cuticle, abdomen, sternites 7 and 8, and appendages not preserved.

Etymology. The species name refers to the Carolinas, an old, abandoned hacienda near the place where the crab was found.

Holotype. CPC-903, Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo, Coahuila, Mexico.

Measurements. Preserved carapace length = 5.2 mm, width = 7.1 mm.

Occurrence. Upper portion of the Cerro del Pueblo Formation (upper Campanian), Parras Basin, Difunta Group, Coahuila, NE Mexico.

Discussion. The characters of the species fit the genus diagnosis provided by Feldmann *et al*. (2008): the carapace is ornamented with large tubercles, an extra-lineal area is preserved, the cervical and branchiocardiac grooves are deep and about equally well developed, and the rostrum appears downturned. The latter distinguishes it from *Latheticocarcinus* Bishop, 1988, which shows the same general outline of regions and ornamentation, but exhibits a bifid or singular rostrum according to Schweitzer *et al*. (2004).

To distinguish species within *Zygastrocarcinus*, length/width ratios, the widest part of the carapace, tumidity of regions, the ornamentation on the carapace, the cardiac region, the protogastric region, the mesogastric region, and the branchial regions have been used (Bishop, 1982, 1983, 1986; Feldmann *et al*., 2008). Part of these characters cannot be used in this case because the carapace lacks most of the metabranchial and cardiac regions. Consequently, the focus for differentiating *Zygastrocarcinus carolinasensis* n. sp. from other species is on the anterior half of the carapace. A combination of three characters can be used to distinguish *Z. carolinasensis* n. sp. from congeneric species: the distribution pattern of the tubercles on the confluent hepatic and protogastric regions, the course of the cervical groove, and the strong spine on the epibranchial region. The strong tubercles on the hepatic and protogastric regions do not vary in position for species represented by multiple specimens (Bishop, 1983; Feldmann *et al*., 2008, and casts of *Z. waagei* stored at Kent State University # 912), suggesting that intraspecific variation is limited for this character along a growth series. This is also true for other homolids known from multiple specimens such as *Homolopsis edwardsii* (Bell, 1863) and *Latheticocarcinus brightoni* (Wright and Collins, 1972). Thus, this character can be used to distinguish species here. *Zygastrocarcinus carolinasensis* n. sp. contains four tubercles that have a different distribution pattern compared to other species (see Figure 4). Additionally, *Z. waagei* appears to exhibit only three strong tubercles instead of four in other, congeneric species. The course of the cervical groove also appears stable over a growth series (Bishop, 1983; Feldmann *et al*., 2008, and casts of *Z. waagei* stored at Kent State University # 912). The course of the cervical groove adjacent to the mesogastric region is more laterally directed in *Z. griesi* and *Z. cardsmithi* compared to that in *Z. carolinasensis* n. sp. Lastly, *Zygastrocarcinus carolinasensis* n. sp. contains a very strong, anterolaterally directed spine on the epibranchial region. This spine appears less prominent in *Z. cardsmithi* and upwardly oriented in *Z. griesi*.

Many species appear relatively flat on the dorsal carapace compared to *Z. carolinasensis* n. sp., notably *Z. cardsmithi*, *Z. mendryki*, and *Z. waagei*. These are, however, relatively large specimens that cannot be compared directly to the small specimen of *Z. carolinasensis* n. sp. because decapods can become less convex transversely with age (*e.g*., Klompmaker *et al*., 2012; Klompmaker, 2013).

Ventral characters are sparsely known from fossil homolids. From the 41 homolids listed by Schweitzer et al. (2010) plus the new species described herein, *Navarrahomola hispanica* Artal *et al*. (2012) and *'Rathhunopon' atherfieldensis* Wright, 1997, and minus *Rathbunopon tuberculatum* (Van Straelen, 1936) (see Klompmaker *et al*., 2011 for rationale for the latter two), only seven have an abdomen preserved (*Homolopsis chilensis* Förster and Stinnesbeck, 1987; *H. edwardsii*; *H. spinulosa* Glaessner, 1980; *Latheticocarcinus brightoni*; *Zygastrocarcinus griesi*; and *Z. waagei*). This equals 14 % (6/43). On the section level (Homoloida), it is also 14 %

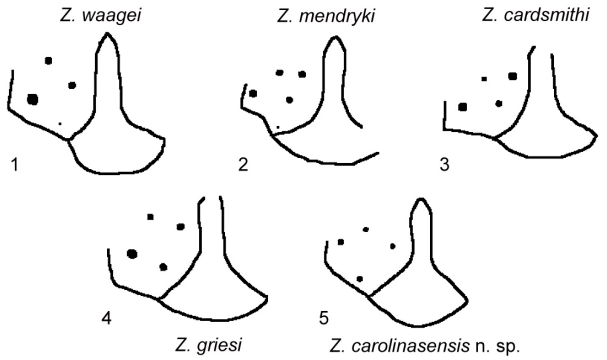

Figure 4. Hepatic and protogastric regions with the tubercles indicated by black dots of *Zygastrocarcinus* spp. The mesogastric region is also outlined. The drawing of *Zygastrocarcinus waageri* is based on Feldmann *et al*. (2008, fig. 1b), *Z. mendryki* based on Bishop (1982, fig. 3a, mirrored horizontally here), *Z. cardsmithi* based on Bishop (1986, fig. 2.2), and *Z. griesi* based on Bishop (1983, fig. 3d).

Table 1. Age, location, and stratigraphic occurrence of *Zygastrocarcinus* spp.

	System	Stage	Country	State(s)	Locality/Localities	Lithologic Unit
Zygastrocarcinus carolinasensis n. sp.	Cretaceous	upper Campanian	Mexico	Coahuila	near the abondoned hacienda Carolinas	Cerro del Pueblo Formation
Z. cardsmithi Bishop, 1986	Cretaceous	middle Campanian	USA	Montana	Twelve Mile Crossing	Pierre Shale, Gammon Ferruginous Member, Zone of *Scaphites hippicrepis* III
Z. griesi Bishop, 1983	Cretaceous	upper Campanian	USA	Montana	Bitter Creek	Bearpaw Shale, Zone of *Didymoceras nebrascense*
Z. mendryki (Bishop, 1982)	Cretaceous	Maastrichtian	USA	South Dakota	Sitting Bull collecting site (Mobridge locality)	Pierre Shale, Mobridge Member, Zone of *Baculites grandis*
Z. waagei Feldmann *et al*., 2008	Cretaceous	Albian	USA	Montana, Wyoming	near Duck Creek, near Greybull	Shell Creek Shale

(7/50) as *Mithracites vectensis* Gould, 1859, has an abdomen preserved as well. Since the abdomen covers the sternum completely in homolids (see Garassino, 2009, p. 6), it is no surprise that no data on the sterna is available from those species. Even less is known about sterna compared to abdomina. Wright and Collins (1972: p. 36) mentioned about the sternum of *Homolopsis spinosa* Van Straelen, 1936, from the Albian of Great Britain that "[…] the sternum, partly seen in a single specimen, is long, tongue-shaped in front and concave in cross section with strongly upturned edges." The sternum is not figured. *Londinimola williamsi* Collins and Saward, 2006, from the Early Eocene of Great Britain is the only figured sternum from a homolid previous to this publication (see their Pl. 1.2b), and appears nearly complete. It is also the oldest known, figured fossil specimen with a sternum preserved from the entire section of the Homoloida until this paper. This Eocene specimen contains a 'homolid press button' on the fourth sternite, a feature to hold the abdomen in place as known from extant homolids (Guinot, 1979; Garassino, 2009). Apparently, this feature had already been developed by the Eocene (Ypresian) ~50 million years ago. The sternum from *Z. carolinasensis* n. sp. is the oldest known figured sternum of homolids, and thus, of particular importance. The general outline of the sternum with the first two sternites forming a small triangle and the third through fifth sternites containing (postero) laterally directed episternites and being subsequently larger to form a triangular sternum, appears similar to the sternum of extant homolids and the sternum of the Eocene *Londinimola williamsi*, suggesting that sternal outline remained fairly stable through time within this family and section. Unfortunately, the homolid press button cannot be seen in this specimen due to preservation of the specimen. No sterna and abdomina are known from the Prosopidae from which the homolids would have originated (Collins, 1997).

The new taxon is of further importance because it is the first species (and specimen) of the genus known outside the USA. Hitherto, *Zygastrocarcinus* spp. was only known from the northern part of the USA (Wyoming, Montana, South Dakota) (Table 1). Thus, *Z. carolinasensis* n. sp. broadens the geographic range during the Cretaceous to a great part of the North American continent. Additionally, this is the second known fossil homolid from Mexico after *Homola bajaensis* Schweitzer *et al*., 2006, from the Eocene of Baja California Sur, northwestern Mexico.

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