



Paleocene decapod Crustacea from northeastern Mexico: Additions to biostratigraphy and diversity



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ARTICLE INFO

Article history:

Received 21 November 2016

Received in revised form

2 January 2017

Accepted 10 January 2017

Available online 11 January 2017

Keywords:

Crustacea

Decapoda

Paleocene

Northeastern Mexico

ABSTRACT

New decapod specimens from mid-Paleocene shallow marine deposits of NE Mexico represents an important addition to the diversity, paleobiogeography and evolution of the Crustacea record. In this work, we describe additions to the decapod assemblage from the Paleocene (Selandian) Rancho Nuevo Formation (Difunta Group, Parras Basin, Coahuila). Due to the evident size differences with other decapod assemblages, we compare the new assemblage with those from the Lower Paleocene (Danian) Mexia Clay Member of the Wills Point Formation, Texas, and the Lower Eocene (Ypresian) El Bosque Formation in Chiapas. Species reported from the mid-Paleocene (Selandian) assemblage of the Porters Creek Formation (Alabama), are correlatable to the decapod species from NE Mexico in age, size and systematic composition. The erymid lobster *Enoploclytia gardnerae* (Rathbun, 1935) is represented by several carapaces and chelae remains. One isolated palm of Callianassidae is included. Numerous carapaces of *Linuparus wilcoxensis* Rathbun, 1935 are described, representing the most abundant lobster. A new record for the raninid *Notopoides* sp., and presence of *Quasilaeviranina* sp. cf. *arzignagnensis* and *Quasilaeviranina ovalis* are here reported. New raninids, *Claudioranina latacantha* sp. nov. and *Claudioranina* sp. (Cyrthorhininae) are also part of this assemblage. *Paraverrucoides alabamensis* (Rathbun, 1935), and *Tehuacana americana* (Rathbun, 1935) are represented by several carapaces exhibiting intraspecific morphological variation. Different sizes among the Early and Middle Paleocene and Early Eocene decapod populations suggests a possible effect of variation in seawater temperatures and/or a Lilliput effect after the K/Pg event.

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1. Introduction

The Late Cretaceous/Early Paleogene (K/Pg) event has received wide attention (Schulte et al., 2010; Brusatte et al., 2015). Post extinction conditions and recovery periods are less well known to date (Cope et al., 2005; Schweitzer and Feldmann, 2005; Keller and Abramovich, 2009; Sessa et al., 2012), nor is the development of strategies to confront stressful environmental post-extinction conditions (Keller, 1989; Harries and Knorr, 2009; Keller and

Abramovich, 2009; Smith et al., 2009; Martínez-Díaz et al., 2016). Paleocene decapod crustaceans of Northeastern Mexico studied by Vega et al. (2007) suggest important changes in the pre- and post K/Pg extinction faunal composition of decapod assemblages. Similar crustacean assemblages were also reported by Rathbun (1935) for the Paleocene (lower Selandian) Porters Creek Formation (previously Sucarnoochee beds) of Alabama (Mancini and Tew, 1988) and another rich and diverse assemblage of small decapod crustaceans from the Lower Paleocene (Danian) Mexia Clay Member, Wills Point Formation, Texas (Armstrong et al., 2009). The Rancho Nuevo Formation in the northeastern Mexican state of Coahuila offers an opportunity to compare changes in decapod

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composition and the establishment of new decapod communities, especially after the K/Pg event. The new material documented here is characterized by specimens of *Enoploclytia gardnerae* (Rathbun, 1935), *Linuparus wilcoxensis* Rathbun, 1935, one callianassoidea, additional specimens of the mathildellid crab *Tehuacana americana* (Stenzel, 1944), and the paleoxanthopsid *Paraverrucoides alabamensis* (Rathbun, 1935) which, show evidence of intraspecific variation. New species of raninid crabs are also reported here and compared with similar raninoids from the Lower Eocene (Ypresian) El Bosque Formation of Chiapas, SE Mexico. Finally, possible causes are discussed for survival after the K/Pg event, successful establishment of new decapod communities, and persistence of some groups.

2. Geological setting

Based on the occurrences of the nautiloids *Cimomia haltomi* (Aldrich, 1931) and *Hercoglossa* sp., Murray et al. (1959) first documented the presence of Paleocene strata in Coahuila, north-eastern Mexico, while Hasseltine (1968) presented details of the stratigraphy of the sediments. McBride et al. (1974) defined a 4000 m thick deltaic sequence of Campanian/Paleocene sediments deposited in the Parras and La Popa basins, as the Difunta Group, and proposed the youngest unit in eastern Parras Basin, as the Rancho Nuevo Formation. This later unit conforms an approximate 60 m sequence of sandstone, mudstone, limestone and conglomerate. Wolleben (1977) and Vega and Perrilliat (1995) described invertebrates from the Rancho Nuevo Formation and the equivalent upper Potrerillos Formation (La Popa Basin). Vega et al. (1999) reported Early Paleocene ostreid banks from the upper part of the Las Encinas Formation, which underlies the Rancho Nuevo Formation. The K/Pg boundary was placed within the upper part of the Las Encinas Formation (Murray et al., 1960; Weidie and Murray, 1967; Hasseltine, 1968; McBride et al., 1974; Wolleben, 1977; Lawton et al., 2009; Stinnesbeck et al., 2016). The Upper Mudstone Member of the Potrerillos Formation in the adjacent La Popa Basin can be correlated to the Rancho Nuevo Formation (Lawton et al., 2009); both units include black to brownish mudstone as the main lithology, where invertebrates (mollusks and crustaceans) are found in concretions. Klosterman et al. (2007) reported rhynchonellid brachiopods from a Paleocene carbonate lenticle of the Upper Mudstone Member of the Potrerillos Formation, and based on $^{87}\text{Sr}/^{86}\text{Sr}$ measurements from the calcitic shells of brachiopods, the authors suggested an age of 57.4 Ma for the sediment containing the brachiopods. Correction to the international stratigraphic chart (Cohen et al., 2016; updated), suggests that this age may be now equivalent to 58.1 Ma, which corresponds to the Late Paleocene (Selandian–Thanetian). Based in the relative position of the studied outcrop on the upper portion of the Rancho Nuevo Formation, we suggest that the reported assemblage of crustaceans is best assigned to the Middle Paleocene. The material herein examined comes from a locality known as “Rancho Las Moras”, located at about 50 km NE of Saltillo, Coahuila (Fig. 1). Here, the Rancho Nuevo Formation consists of alternating dark olive-gray mudstones and brown coarse sandstone. Crabs are mainly preserved in concretions, but without cuticle. Wood remains and nautiloid shell fragments are also present, as well as abundant serpulid worm tubes assigned to *Rotularia* sp.

Specimens referred to in this study are deposited at Museo del Desierto, Saltillo, Coahuila, Mexico, under acronym CPC (Colección Paleontológica de Coahuila); Colección Nacional de Paleontología, Instituto de Geología, UNAM, under acronym IGM; Museo de Múzquiz, Múzquiz, Coahuila, under acronym MUZ; United States National Museum, Washington, DC, under acronym USNM; Texas Natural Science Center, Austin, Texas, under acronym NPL.

3. Systematic paleontology

Order Decapoda Latreille, 1802

Suborder Pleocyemata Burkenroad, 1963

Infraorder Glypheidea Winckler, 1882

Superfamily Erymoidea Van Straelen, 1925

Family Erymidae Van Straelen, 1925

Genus *Enoploclytia* McCoy, 1849

Type species: Astacus leachi Mantell, 1822, by original designation.

Enoploclytia gardnerae (Rathbun, 1935)

Fig. 2.A-2.C, 2.F-2.I

Archaeocarabus (?) *gardnerae* n. sp.; Rathbun, 1935, p. 75, pl. 16, Figs. 19–21.

Enoploclytia gardnerae (Rathbun, 1935); Vega et al., 2007, p. 1432, Fig. 4.1–4.4.

Description.—Astacid of large size; cephalothorax triangular, elongated, ornamented by uniformly spaced large spines and small tubercles; deep postcervical groove, curved forward on lower portion of carapace. Two prominent tubercles closely behind of rostrum, separated at same distance of rostrum base width. Strong oblique line of spines behind cervical groove. Postcervical groove with two close separated lines of strong spines curvedly aligned. Branchiocardiac groove closely to midline of carapace. All specimens are covered with strong truncated tubercles, alternating in most carapace with small spiny tubercles or punctae. Small tubercles closely spaced and randomly distributed. Size of tubercles decrease in size from dorsal to ventral. Chelae much longer than carapace; subequal but of similar length, heavily ornamented with large, acute spines and tubercles. Merus one-fifth the total length of cheliped; rectangular in lateral view, becomes wider at union with carpus; outer surface nearly flat, covered by uniformly spaced, similarly sized tubercles; inner surface flat, with small tubercles; upper surface nearly flat; inner margin with evenly spaced, oblique, large acute spines; outer margin with smaller spines, spaced about half distance as on inner marginal spines. Lower margin of merus proximally acute, becoming wider at union with carpus, covered by four large, acute spines and numerous small tubercles; distal margin of merus with slightly curved, deep, transverse groove, extends obliquely outward, terminates as long, large, acute spine that reaches proximal margin of carpus. Carpus slightly shorter than merus, about one-seventh the total length of cheliped; subquadrate in lateral view; outer surface concave, covered by numerous, evenly spaced tubercles; inner surface flat, covered by small tubercles and scarce small spines; lower margin slightly concave, with strong tubercles and rows of spines on each side; upper margin covered by small tubercles; distal margin marked by shallow groove near articulation with propodus. Right propodus rectangular in lateral view, nearly one-fifth total cheliped length; outer surface concave, covered by numerous, evenly spaced tubercles; inner surface nearly flat, covered by small tubercles and three longitudinal rows of large, acute tubercles; upper margin sharp. Left propodus rectangular in lateral view, one-fourth longer than right propodus and one-fourth total cheliped length; outer surface concave, covered with numerous tubercles; inner surface flat, covered by small tubercles and three rows of sharp spines; lower margin broad, rounded, with numerous tubercles; upper margin broad, with numerous small tubercles. Left and right fixed fingers straight, about equal length, equivalent to nearly half the total length of cheliped; lower proximal portion ornamented with tubercles, otherwise smooth; proximal portion slightly wider, becoming narrow to about one third of total length; occlusal surface with scarce spines from midlength to distal part of fixed finger. Moveable finger practically identical in form and size to fixed

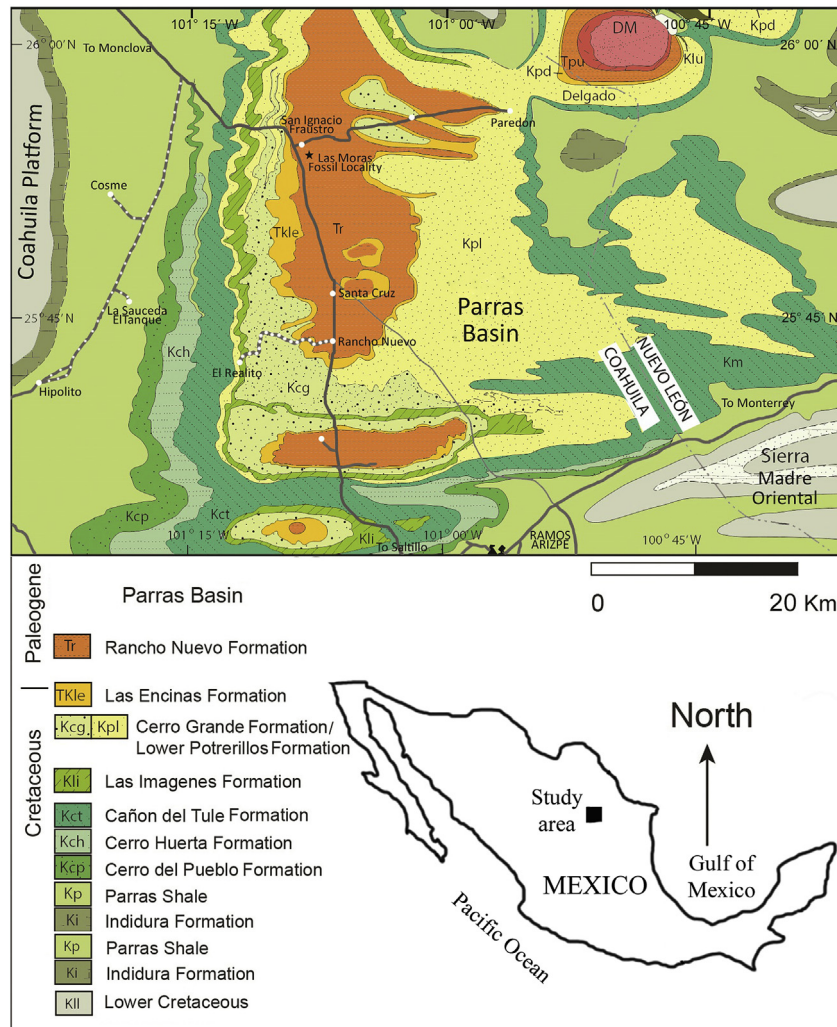


Fig. 1. Location map of Las Moras locality and stratigraphic units of the Parras Basin. Modified from Lawton et al., 2009.

finger, several spines at distal portion of occlusal surface, otherwise surface smooth.

Material examined.—Eight nearly complete carapaces, fragments of carpus, merus, and articulated fingers: hypotypes CPC1981 to CPC1991.

Measurements.—See Table 1.

Discussion.—*Enoploclytia gardnerae* was originally described as *Archaeocarabus* (?) *gardnerae* by Rathbun (1935), based on carapace and chelae fragments from the middle Paleocene (Selandian) of Alabama. Although Stenzel (1945) considers the fragment reported by Rathbun as “unidentifiable”, questioning its generic position, Vega et al. (2007) placed that species in *Enoploclytia*, based on similarities of carapace and palm. The specimens here reported allow us to confirm this affinity, and some additions to the morphology of the species are given based on nearly complete carapace remains, fragments of chelae, and the large pair of chelae (Fig. 2F) previously illustrated by Vega et al. (2007, Fig. 4.1). An incomplete, medium-sized cephalothorax was also reported by Vega et al. (2007, Figs. 4.5, 4.6) as *Enoploclytia* sp., but the morphology of the carapace suggests affinities with *Hoploparia* sp. Intraspecific variation in chelipeds of erymids has been documented (Hyžný et al., 2015). The new specimens from Rancho Las Moras include numerous dactyli and cheliped fragments, but the present material is too fragmentary to document morphometric

variation. Large sized Cretaceous *Enoploclytia* spp. specimens have been reported from SE US and NE Mexico, from sediments of the Pflugerville Member (Campanian) of Texas (Beikirch and Feldmann, 1980), and the Dessau Formation, (Austin Group, Campanian) of Coahuila, NE Mexico (Vega et al., 2013) (Fig. 2D, 2E). These data suggest that the genus was established in the area from Late Cretaceous to Early Paleogene times.

Infraorder Axiidea De Saint Laurent, 1979

Family Callianassidae Dana, 1852

Fig. 2. J

Description.—Smooth inner surface of right palm, fixed finger short, triangular.

Material examined.—One complete palm: hypotype CPC1992.

Measurements (in mm).—Hypotype CPC1992, palm maximum length, 10.1; maximum height, 8.0.

Discussion.—Callianassids are relatively scarce in the Paleocene deposits of the Rancho Nuevo Formation relatively scarce when compared to Late Cretaceous and Early Eocene assemblages from Mexico. Vega et al. (2007) reported only two incomplete palms. This may be the result of preservation and/or collecting bias, but slow recovery from the K/Pg event must be also considered as a cause of this unusual scarcity.

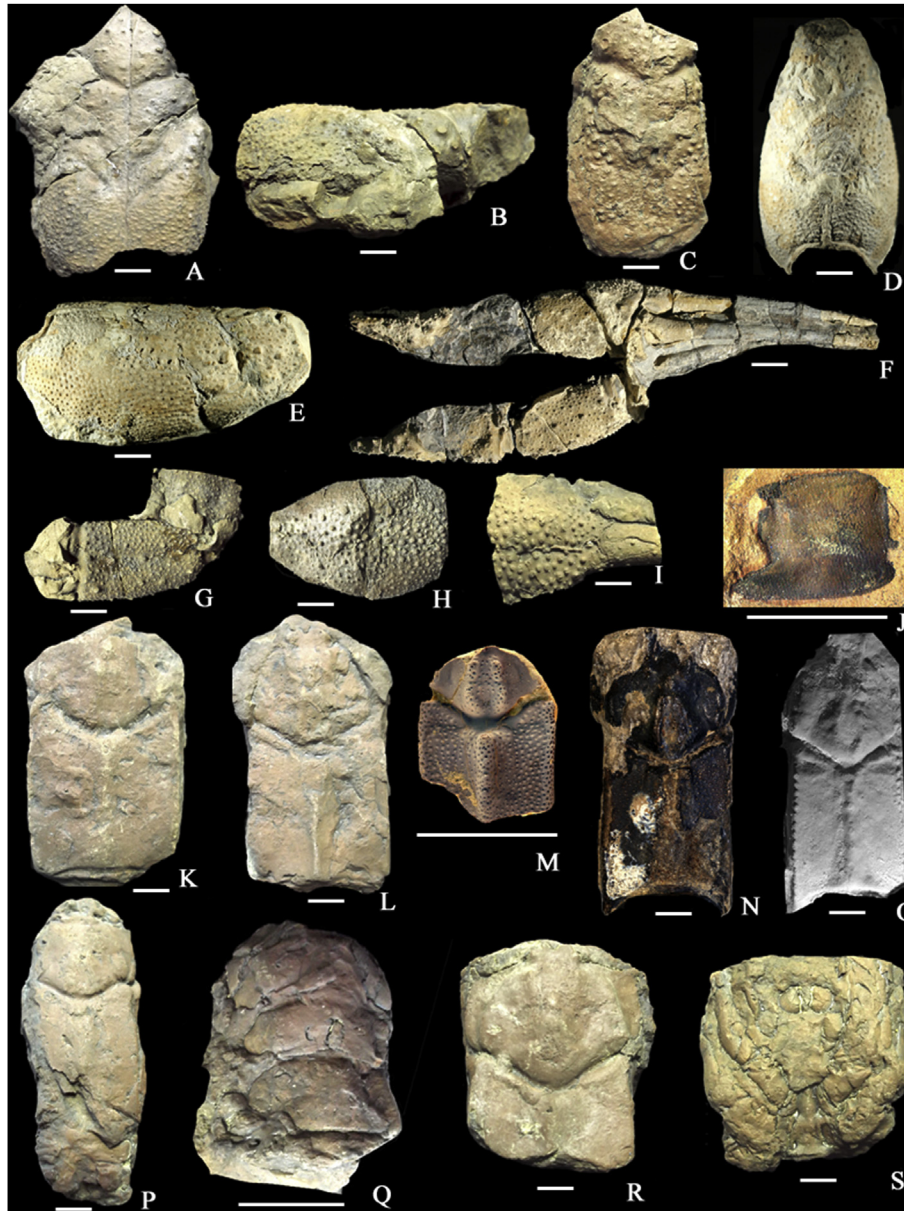


Fig. 2. A–C, F–I, *Enoploclytia gardnerae* (Rathbun, 1935), Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; A, Dorsal cephalothorax, hypotype CPC1982; B, right lateral view of cephalothorax, same specimen; C, Dorsal cephalothorax, hypotype CPC1981; F, Large pair of chelae, IGM-9095; G, Carpus, hypotype CPC1989; H, Incomplete palm, hypotype CPC1990; I, Distal portion of palm with partial fixed and movable fingers, hypotype CPC1991. D, E, *Enoploclytia tepeyacensis* Vega et al., 2013, Campanian, Dessau Chalk, Coahuila; D, Dorsal cephalothorax, holotype MUZ-825; E, Right lateral view of cephalothorax, same specimen. J, Callianassidae, hypotype CPC1992, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila. K–S, *Linuparus wilcoxensis* Rathbun, 1935; K, L, Dorsal view of cephalothorax, hypotypes CPC2004 and CPC2011, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; M, Plastic cast of dorsal cephalothorax, hypotype CPC1993, latest Maastrichtian, Las Encinas Formation, Coahuila; N, Dorsal view of cephalothorax, holotype USNM371499, Paleocene (Selandian), Prairie Creek Formation, Alabama; O, Partial dorsal carapace, hypotype NPL31150, Paleocene (Danian), Wills Point Formation, Texas; P, Dorsal view of carapace, hypotype CPC2006, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; Q, Dorsal view of abdomen, hypotype CPC2005, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; R, Partial dorsal cephalothorax, hypotype CPC2013, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; S, Ventral view of cephalothorax, same specimen. Scale bars = 10 mm.

Infraorder Achelata Scholtz and Richter, 1995

Family Palinuridae Latreille, 1802

Genus *Linuparus* White, 1847

Type species.—*Palinurus trigonus* von Siebold and von, 1824, by original designation.

Linuparus wilcoxensis Rathbun, 1935

Fig. 2.K–2.S

Linuparus wilcoxensis n. sp.; Rathbun 1935, p. 74, pl. 16, figs. 11–14; Vega et al. 2007, p. 1436, fig. 4.8–4.10.

Linuparus sp. cf. *wilcoxensis* Rathbun 1935; Armstrong et al. 2009, p. 747, fig. 3.3.

Description.—Carapace of medium size, cephalothorax rectangular, elongated, with V-shaped, deep cervical groove. Submarginal posterior groove of carapace wider medially than laterally. Median ridge sharp, elevated. Lateral ridges fine-edged, slightly raised. Lateral region between median and lateral ridges weakly concave, covered by coarse, scalelike granules. Lateral margins smooth, straight, forming an inverted 45° angle with the lateral ridges. Gastric area anterior to cervical groove with two low, rhombshaped

Table 1

Measurements (in mm) for Paleocene *Enoploclytia gardnerae* (Rathbun, 1935) and *Enoploclytia* sp. specimens from NE Mexico. L = Maximum carapace length; W = Maximum carapace width; L/W = Length/Width ratio; H = Maximum carapace height.

Referred taxa	Catalog number	L	W	L/W	H
<i>Enoploclytia gardnerae</i> (in Vega et al., 2007)	Hypotype IGM-9095	56.1	28.5	1.97	52.0
<i>Enoploclytia</i> sp. (in Vega et al., 2007)	Hypotype IGM-9097	40.7	27.9	1.46	28.1
<i>Enoploclytia gardnerae</i> (This work)	Hypotype CPC1981	115	79.8	1.44	45.3
	Hypotype CPC1982	179	82.3	2.17	50.7
	Hypotype CPC1983	80.5	43.1	1.87	35.0
	Hypotype CPC1984	85.1	51.3	1.66	25.3
	Hypotype CPC1985	78.5	47.5	1.65	30.8
	Hypotype CPC1986	65.0	50.3	1.29	34.0
	Hypotype CPC1987	60.7	49.4	1.23	30.2
	Hypotype CPC1988	79.3	46.5	1.71	27.2
Mean		92.9	56.3	1.63	35.9

ridges; distal part of each ridge bears a forward-projected, small spine, short ridge just anterior of rhomb-shaped ridges. Cervical groove curved axially, with large, acute spine about 5 mm proximal to cervical groove. Lateral flanks oblique, with prominent swellings bearing two stout tubercles. First sternite triangular, swollen; sternites 2–5 rectangular, becoming wider posteriorly, with lateral margins raised. Coxae of pereopods 1–4 subtrapezoidal. Epistomal area exhibits small lateral granules. Third maxillipeds rectangular, elongated. Pleon coarsely punctate especially on the median and lateral elevations. Segments 3–6 of similar length.

Material examined.—Thirty two specimens represented by complete and fragmentary carapaces: hypotypes CPC1993 to CPC2024.

Measurements.—See Table 2.

Discussion.—The new material allows us to confirm the affinity of the Rancho Nuevo Formation specimens to *Linuparus wilcoxensis*. A small cephalothorax fragment was reported by Armstrong et al. (2009) as *Linuparus* sp. cf. *wilcoxensis*, from the Danian of Wills Point Formation in Texas (Fig. 2.M). The small specimen from Texas exhibits granules on the dorsal surface of the carapace, which makes it most similar to *L. wilcoxensis*, from the mid-Paleocene of Alabama (Fig. 2.N). A medium-sized cephalothorax from the upper Las Encinas Formation (latest Maastrichtian, approx. 66.2 Ma, immediately underlying the Rancho Nuevo Formation), is similar in carapace shape (Fig. 2.O) to that of *L. wilcoxensis*, with crowded granules on lateral ridges (Kornecki, 2014), but more and more complete specimens are needed in order to confirm this specific placement. Cope et al. (2005) documented *Linuparus canadensis*

Table 2

Measurements (mm) for Late Cretaceous–Early Paleogene *Linuparus wilcoxensis* specimens from NE Mexico.*For juvenile specimens. L = Maximum carapace length; W = Maximum carapace width; L/W = Length/Width ratio; H = Maximum carapace height.

Referred taxa	Catalog number	L	W	L/W
<i>L. wilcoxensis</i> Maastrichtian Las Encinas Fm. (this work)	Hypotype CPC1993	51.0	23.6	1.93
<i>Linuparus</i> cf. <i>wilcoxensis</i> Paleocene Rancho Nuevo Fm. (in Vega et al., 2007)	Hypotype IGM-9099	42.0	26.1	1.61
<i>L. wilcoxensis</i> Paleocene Rancho Nuevo Fm. (this work)	Hypotype CPC1994	54.1	34.5	1.57
	Hypotype CPC1995	61.7	35.0	1.76
	Hypotype CPC1996	64.5	43.8	1.47
	Hypotype CPC1997	58.3	30.4	1.92
	Hypotype CPC1998	57.7	37.0	1.56
	Hypotype CPC1999	67.2	39.8	1.69
	Hypotype CPC2000	54.3	30.6	1.77
	Hypotype CPC2001	43.4	34.5	1.26
	Hypotype CPC2002	61.6	38.8	1.59
	Hypotype CPC2003	47.5	42.0	1.13
	Hypotype CPC2004	76.2	47.3	1.61
	Hypotype CPC2005	95.5	44.0	2.17
	Hypotype CPC2006	80.5	25.5	3.16
	Hypotype CPC2007	48.8	26.9	1.81
	Hypotype CPC2008	66.1	36.4	1.82
	Hypotype CPC2009	56.4	35.6	1.58
	Hypotype CPC2010	69.8	37.4	1.87
	Hypotype CPC2011	79.2	46.0	1.72
	Hypotype CPC2012	42.3	33.2	1.27
	Hypotype CPC2013	57.0	41.4	1.38
	Hypotype CPC2014	51.3	34.3	1.50
	Hypotype CPC2015	80.4	49.3	1.63
	Hypotype CPC2016	56.7	48.4	1.17
	Hypotype CPC2017	46.6	43.4	1.07
	Hypotype CPC2018	62.8	42.5	1.48
	*Hypotype CPC2019	27.5	26.1	1.05
	*Hypotype CPC2020	27.4	25.7	1.07
	*Hypotype CPC2021	30.4	30.0	1.01
	*Hypotype CPC2022	28.8	25.0	1.15
	*Hypotype CPC2023	32.2	18.3	1.76
	*Hypotype CPC2024	32.7	16.3	2.01
Mean (CPC1994–2024)		55.0	35.2	1.58

(Whiteaves, 1884) as a possible Maastrichtian survivor species in the Paleocene (Danian) Clayton Formation of southern Illinois. The specimens from NE Mexico shows differences with *L. canadensis*, from the Maastrichtian of British Columbia, Alberta, South Dakota, Tennessee and Louisiana (Mertin, 1941; Schweitzer et al., 2003), but the single specimen from the Las Encinas Formation show differences with that species. *Linuparus* is represented by 4 extant and 35 fossil species. The genus appears in the Early Cretaceous and presents a peak in diversity during the Late Cretaceous (Feldmann, 1981; Tsoi et al., 2011).

Infraorder Brachyura Latreille, 1802

Section Raninoidea De Haan, 1839 [in De Haan, 1833–1850]

Superfamily Raninoidea De Haan, 1839

Family Raninidae De Haan, 1839

Subfamily Raninoidinae Lörenthey in Lörenthey and Beurlen, 1929

Genus *Notopoides* Henderson, 1888

Type species.—*Notopoides latus* Henderson, 1888, by monotypy.

Notopoides sp.

Fig. 3. B–3.D

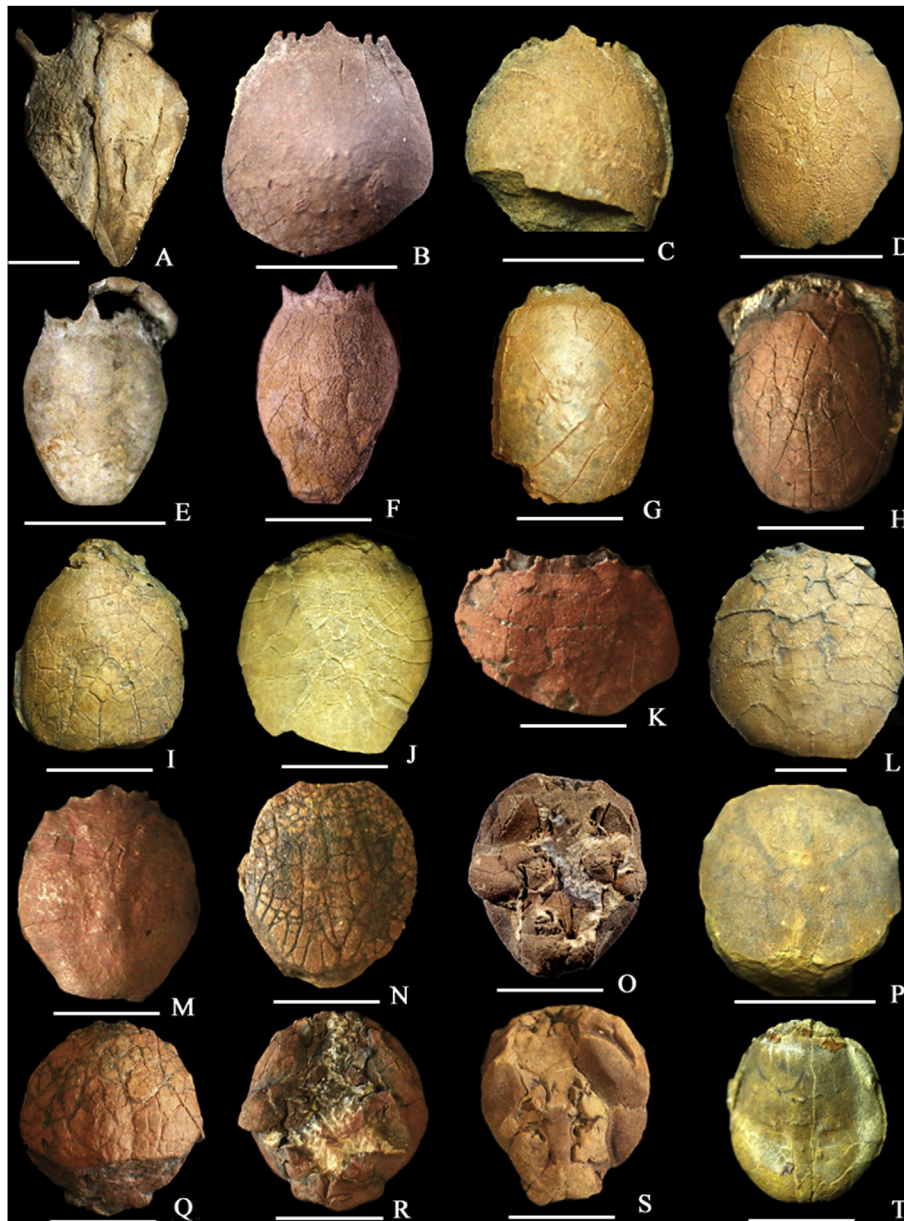


Fig. 3. A, *Macroacaena venturari* Vega et al., 2007, dorsal view of carapace, holotype IGM-9101, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila. B–D, *Notopoides* sp., Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; B, dorsal view of carapace, hypotype CPC2026; C, dorsal view of carapace, hypotype CPC2027; D, dorsal view of carapace, hypotype CPC2425. E, F, *Notopoides exiguus* Beschin et al., 1988; E, dorsal view of carapace with right cheliped, holotype 11879, Lower Eocene, Chiampo Valley, Vicenza, Italy; F, dorsal view of carapace, hypotype IHNFG-3018, Lower Eocene, El Bosque Formation, Chiapas. G–I, *Quasilaeviranina* sp. cf. *arznagnensis* Beschin et al., 1988, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; G, dorsal view of carapace, hypotype CPC2030; H, dorsal view of carapace, hypotype CPC2028; I, dorsal view of carapace, hypotype CPC2029. J, K, *Quasilaeviranina ovalis* (Rathbun, 1935), Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; J, dorsal view of carapace, hypotype CPC2031; K, dorsal view of carapace fragment, hypotype CPC2032. L–S, *Claudioranina latacantha* n. sp., Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; L, dorsal view of carapace, paratype CPC2035; M, dorsal view of carapace, holotype CPC2033; N, dorsal view of carapace, paratype CPC2037; O, ventral view of carapace same specimen; P, dorsal view of carapace, paratype CPC2038; Q, dorsal view of carapace, paratype CPC2034; R, ventral view of carapace same specimen; S, ventral view of carapace same specimen; T, *Claudioranina* sp., dorsal view of carapace, holotype CPC2039 Paleocene (Selandian), Rancho Nuevo Formation, Coahuila. Scale bars = 10 mm.

Description.—Carapace obovate, longer than wide, with lateral margins convex. Fronto-orbital margin narrow, about half as wide as the maximum carapace width; rostrum short but slightly extending beyond the outer orbital spine, sub-triangular, with a broad base ending in the inner orbital spine; orbits sub-horizontal, bearing two short and wide orbital fissures; intra-orbital spine short, nearly truncated; outer orbital spine short, single, directed forward, and with its outer margin directed antero-mesially. Anterolateral margin lacking spines. Cuticle not preserved in the studied material.

Material examined.—Two nearly complete carapaces, one fragment: hypotypes CPC2025 to CPC2027.

Measurements (in mm).—Hypotypes CPC2025, maximum carapace length, 24.8, maximum carapace width, 19.8; CPC2026, maximum carapace length, 14.8, maximum carapace width, 13.9.

Discussion.—The first raninoid reported from the Paleocene of Coahuila is *Macroacaena venturai* Vega et al., 2007 (Fig. 3A). The material herein reported as *Notopoides* sp. differs from any *Macroacaena* species by its more ovate carapace, the lack of anterolateral spines (one large anterolateral spine present in *Macroacaena*), the compact frontal margin (enlarged in *Macroacaena*), and the lack of a longitudinal ridge (present in some *Macroacaena*) (Tucker, 1998; Schweitzer et al., 2003; Schweigert et al., 2004; Vega et al., 2007; Karasawa et al., 2014). Instead, the ovate carapace with convex anterolateral margins lacking spines, and the overall construction of the fronto-orbital margin, rather suggest affinities to the genus *Notopoides*. The new material from the Paleocene (Selandian), Rancho Nuevo Formation, Coahuila (Fig. 3B–3D), assigned to *Notopoides* sp., differs from *Notopoides exiguus* Beschin et al., 1988, from the Early Eocene of Italy and Mexico (Fig. 3E, 3F, respectively) in the shorter rostrum, the narrower fronto-orbital margin, and the less pronounced angle between the outer orbital spine and the anterolateral margin (Beschin et al., 1988; Vega et al., 2008). *Notopoides* sp. shares with *N. nantoensis* Beschin et al., 2013, from the Middle Eocene of Italy, the obovate carapace margin and narrow fronto-orbital region, but differs by its larger size. Unfortunately, the poorly preserved fronto-orbital margin of *N. nantoensis* does not allow for more detailed comparison. *Notopoides? pflugervillensis* Beikirch and Feldmann, 1980 from the Campanian of Texas, also shows a poor preservation of the frontal region, which impedes direct comparison with the Paleocene material reported here. *Notopoides* sp. shares several characters with *N. latus*, the only extant of this genus species known, such as the general ovate carapace outline, the triangular rostrum, a narrow fronto-orbital margin, the outer orbital spines directed anteromesially, and the lack of spines on the anterolateral margin, but they differ by the absence of granulated anterolateral margins, present in *N. latus*. *Notopoides latus* is distributed throughout the Indo-Pacific region (Dawson and Yaldwyn, 2002).

Genus *Quasilaeviranina* Tucker, 1998

Type species.—*Ranina simplicissima* Bittner, 1883, by original designation.

Quasilaeviranina sp. cf. *arznagnensis* (Beschin et al., 1988)

Fig. 3.G–3.I

Notosceles arznagnensis Beschin et al., 1988, Fig. 10.

Quasilaeviranina arznagnensis (Beschin et al., 1988), Tucker, 1998, p. 356; Schweitzer et al., 2010, p. 75; Karasawa et al., 2014, p. 257.

Description.—Carapace elongated, oval, slightly domed and curved to lateral margins. Post-frontal region depressed, making the fronto-orbital region to lie below the dorsal carapace, forming a post-frontal escarpment parallel to the fronto-orbital margin. No cuticular traces are preserved; only a few fine granules on the dorsal

surface immediately posterior to fronto-orbital margin.

Material examined.—Three nearly complete carapaces: hypotypes CPC2028 to CPC2030.

Measurements (in mm).—Hypotypes CPC2028, maximum carapace length, 30, maximum carapace width, 21.2; CPC2029, maximum carapace length, 18.9, maximum carapace width, 13.7; CPC2030, maximum carapace length, 22.5, maximum carapace width, 19.3.

Discussion.—Among raninoids, the overall elongate ovate outline of the carapace, the shape of the fronto-orbital margin, the anterolateral margin with one or no spines, and particularly the terraced postfrontal region, are traits commonly seen among genera of the subfamily Raninoidea like *Quasilaeviranina*; a widespread genus known so far from Paleocene and Eocene fossils (Tucker, 1998; Van Bakel et al., 2012; Karasawa et al., 2014). The Paleocene specimens from Mexico herein referred to as *Quasilaeviranina* sp. cp. *arznagnensis* exhibit similar features with *Q. arznagnensis* from the Eocene of Italy and USA (as *Raninoides ovalis* pro parte in Rathbun, 1935; pl. 18, Fig. 6), like the elongated shape of carapace, the relatively narrow fronto-orbital margin with respect to the maximum width of the carapace, the short rostrum, and the short triangular outer orbital spines. Despite this, the new material differs from *Q. arznagnensis* in the more sub-parallel outer orbital spines instead of straight and converging anteromesially, and the apparently wider orbital fissures, although the latter feature may be an artifact due to the missing cuticle. The Paleocene specimens also differ from other species of *Quasilaeviranina* in its narrower fronto-orbital margin; a trait only shared with *Q. arznagnensis*. Another species, *Quasilaeviranina pororariensis* (Glaessner, 1980) from the late Eocene of New Zealand, also seems to have a narrow fronto-orbital margin, but unfortunately the front in the holotype is poorly preserved (Glaessner, 1980; Feldmann and Maxwell, 1990), impeding a more reliable comparison at this time. Despite this, *Q. pororariensis* also differs from the Paleocene material in the broader and sub-horizontal anterior margin between the outer orbital fissure and the anterolateral spine, and its much wider shield-shaped carapace. *Quasilaeviranina keyesi* (Feldmann and Maxwell, 1990) from the Late Eocene of New Zealand, *Q. ombonii* (Fabiani, 1910) from the Early Eocene of Italy, and *Q. simplicissima* (Bittner, 1883) from the Eocene of Italy and Hungary, differ from the Paleocene material from Mexico by the presence of anterolateral spines, and a more urn-shaped carapace. The new material also differs from *Q. eocenica* (Rathbun, 1935) from the Eocene of Alabama, USA, by the narrower anterior carapace resulting in more parallel lateral margins (Rathbun, 1935; Tucker, 1998; Karasawa et al., 2014). *Quasilaeviranina ovalis* (Rathbun, 1935), also from the Eocene of Alabama, USA, differs from the new material in the wider carapace. *Quasilaeviranina miniscula* Beschin et al., 2012, from the Eocene of Italy, differs from the Paleocene Mexican material by the more produced fronto-orbital margin, and the presence of a well developed anterolateral spine (Beschin et al., 2012).

Quasilaeviranina ovalis (Rathbun, 1935)

Fig. 3.J–3.K

Raninoides ovalis n. sp.; Rathbun, 1935, p. 81, pl. 18, Figs. 1–8.

Laeviranina ovalis (Rathbun, 1935); Glaessner, 1960, p. 16.

Quasilaeviranina ovalis (Rathbun, 1935); Schweitzer et al., 2010, p. 75; Karasawa et al., 2014, p. 257.

Description.—Carapace elongated, oval, slightly domed and curved to lateral margins. Post-frontal region depressed, making the fronto-orbital region to lie below the dorsal carapace, forming a post-frontal escarpment parallel to the fronto-orbital margin. No cuticular traces are preserved; only a few fine granules on dorsal surface immediately posterior to fronto-orbital margin.

Material examined.—One nearly complete carapace and one fragmented carapace: hypotypes CPC2031, CPC2032.

Measurements (in mm).—Hypotype CPC2031, maximum carapace length, 15.7, maximum carapace width, 15.1.

Discussion.—This specimen shares with *Quasilaeviranina* the barrel-like ovate carapace, rather than the distinctive urn-shaped carapaces of other quasilaeviraninid species. Given the overall carapace outline and geographic proximity, we assign the specimen to *Q. ovalis*.

Subfamily Cyrtorhininae [Guinot, 1993](#)

Genus *Claudioranina* [Karasawa et al., 2014](#)

Type species.—*Cyrtorhina oblonga* [Beschlin et al., 1988](#).

Claudioranina latacantha sp. nov.

Fig. 3.L-3.S

Diagnosis.—Carapace ovate, slightly longer than wide, widest posterior to mid-length. Rostrum short and broad, simple, triangular, weakly sulcate; fronto-orbital margin about half the carapace maximum width; orbital margins oriented horizontal. Anterior carapace lacking terraces or coarse tubercles; frontal margin set at a lower level than the rest of the carapace. Anterolateral margin bearing two conspicuous, short, simple, sub-triangular spines (excluding outer-orbital spine), with the more anterior spine usually better developed or preserved than the more posterior spine. Pterygostome ridged; junction between the pterygostome and sternite 4 very narrow; sternites 1–3 fused, sub-triangular, crown-shaped; sternite 4 longer than wide, flattened mesially, with elongated sub-parallel episternites projecting backwards; sternites 5 and 6 with well developed linea media; sternite 6 short, rhomboid. Cheliped coxa broad; merus stout, inflated, concave anteriorly, strongly convex posteriorly.

Description.—Carapace ovate in outline, moderately vaulted, slightly longer than wide, widest posterior to mid-length. Rostrum short and broad, simple, triangular in shape, weakly sulcate; fronto-orbital margin about half the carapace maximum width, slightly depressed with respect to the rest of the dorsal carapace; orbital margins oriented horizontal; inner and outer orbital fissures, and the inner-orbital, supra-orbital, and outer-orbital spines, are not clearly preserved in the material studied. Outer-orbital spines short with rounded tips jointed in some cases. Anterolateral margin convex, bearing two conspicuous, short, simple, sub-triangular spines (excluding outer-orbital spine), with the more anterior spine usually better developed or preserved than the more posterior spine; posterolateral margin nearly straight, slightly convex anteriorly, becoming slightly convex posteriorly towards posterior margin; junction between anterolateral and posterolateral margins indistinct; posterior margin slightly shorter than fronto-orbital margin, and slightly less than half the carapace maximum width. Anterior carapace lacking terraces or coarse tubercles, with frontal margin set at a lower level than the rest of the carapace. Pterygostome ridged; junction between pterygostome and sternite 4 very narrow, recessed. Thoracic sternum narrow; sternites 1–3 fused, sub-triangular, widening posteriorly, about twice as wide as it is long; sternite 4, longer than wide, broader than in other Cyrtorhininae taxa, flattened mesially, with concave sub-parallel lateral margins, wider anteriorly at the level of the anterolateral extensions that form the pterygostome/sternum junction; episternite 4 poorly preserved, but apparently elongate, sub-parallel anteriorly, oblique postero-laterally; sternite 5 the widest, wider anteriorly, becoming considerably narrower posteriorly near junction with sternite 6, with a well developed linea media, lateral margins concave, raised; suture 4/5 indistinct; sternite 6 short, somewhat rhomboid, nearly twice as wide as long, wider mesially, with slightly concave anterior margins, and more

concave posterior margins, bearing a well developed axial linea media. Sternites 7–8, and episternites 5–8 unknown. Cheliped coxa broad; merus stout, inflated, concave anteriorly, strongly convex posteriorly. Cuticle not preserved in all specimens. Carapace surface covered with fine granulations closely separated.

Etymology.—The name refers to the features of carapace and fronto-orbital spines. From Greek ‘lata’ (flattened) and ‘acantha’ (spines).

Material examined.—Three nearly complete and three incomplete carapaces: holotype CPC2033; paratypes CPC2034 to CPC2038.

Measurements.—See [Table 3](#).

Remarks.—[Guinot \(1993\)](#) erected the subfamily Cyrtorhininae to receive the extant species of *Cyrtorhina* [Monod, 1956](#); a genus that markedly differs from most raninoidean clades, except for Symethinae [Goetze, 1981](#), as first suggested by [Serène and Umali \(1972\)](#), and supported by [Guinot \(1993\)](#). Recent revisions of Raninoidea by [Van Bakel et al. \(2012\)](#), [Guinot et al. \(2013\)](#), and [Karasawa et al. \(2014\)](#), also reinforced the proximity between Cyrtorhininae and Symethinae, both forming a monophyletic clade. The similarities in the sternal architecture between taxa of Cyrtorhininae and Symethinae is remarkable, in particular the very narrow junction between the pterygostome and the fourth sternite, the narrow sternite 4 with elongated sub-parallel episternites projecting backwards, and the rhomboid shape of the sixth sternite (see also [Guinot, 1993](#); [Feldmann and Schweitzer, 2007](#); [Van Bakel et al., 2012](#); [Luque, 2015](#)). [Tucker \(1995, 1998\)](#), following the view of [Monod \(1956\)](#), considered *Cyrtorhina* as closer to *Ranina* De Haan, 1839, but this proximity was the result of the exclusion of *Symethis* [Weber, 1795](#). Her phylogenetic analysis was based on the assumption that symethids were too different from other raninoids to be included in the family Raninidae, thus resulting in a long-branch attraction between *Cyrtorhina* and *Ranina*. Despite the poor preservation of the material herein studied, the general ovoid carapace outline, the shape of anterolateral margin, the frontal margin set at a lower level than the rest of the carapace, the robust and curved merus of the cheliped, the rhomboid shape of the sixth sternite, the ridged pterygostome, the very narrow junction between the pterygostome and fourth sternite, the architecture of the thoracic sternum, and the inflated and stout convex merus of the cheliped, indicate that *Claudioranina latacantha* sp. nov. lies in close proximity to genera within Cyrtorhininae. The anterior sternites of *C. latacantha* sp. nov. are considerably wider than in *Antonioranina* [Van Bakel et al., 2012](#), or *Claudioranina* [Karasawa et al., 2014](#), and especially *Cyrtorhina*, although more reminiscent to those seen in *Symethis* yet wider. This results in the coxae of the chelipeds to be more separated from each other, in sharp contrast to all other known Cyrtorhininae species. This is not surprising, taking into account that the new taxon is older than any other Cyrtorhininae or Symethinae taxon, and likely sharing more plesiomorphic conditions with their most recent common ancestor than any of the more

Table 3

—Measurements (mm) for Paleocene *Claudioranina latacantha* sp. nov. specimens from NE Mexico. L = Carapace maximum length; W=Carapace maximum width.

Referred taxa	Catalog number	L	W
<i>Claudioranina oblonga</i> (Beschlin et al., 1988)	Holotype MCZ 1100 numbered KSU D 14	24.1	20.1
<i>Claudioranina latacantha</i> sp. nov.	Holotype CPC2033	16.1	18.4
	Paratype CPC2034	26.8	23.6
	Paratype CPC2035	31.5	35.7
	Paratype CPC2036	26.8	27.6
	Paratype CPC2037	16.2	18.0
	Paratype CPC2038	16.4	15.3
Mean (except <i>C. oblonga</i>)		22.3	23.1

derived taxa. The sixth sternite of *Claudioranina latacantha* n. sp. is very similar to that of *Cyrtorhina* and *Symethis*, all sharing a wide rhomboid shape, but markedly different from the sub-triangular sixth sternite seen in *Antonioranina* and *Claudioranina*. The anterolateral margin of *Claudioranina latacantha* sp. nov. bears one conspicuous short and simple sub-triangular spine, and a less conspicuous and smaller second spine in a more posterior position. *Claudioranina oblonga* (Beschin et al., 1988) also possesses two anterolateral spines, whereas *Antonioranina globosa* (Beschin et al., 1988), *A. fusselsi* (Blow and Manning, 1996), and *A. ripacurtae* (Artal and Castillo, 2005) have two to four spines (see also Feldmann et al., 1998; Van Bakel et al., 2012; Karasawa et al., 2014). *Cyrtorhina granulosa* Monod, 1956, and *C. balabacensis* Serène, 1971, have three anterolateral spines, with a fourth spine in *C. granulosa* described by Serène and Umali (Serène and Umali, 1972) as an hepatic spine, equivalent to a conical tubercle in *C. balabacensis* (see Serène and Umali, 1972, p. 50). Regarding the dorsal ornamentation, the material is strongly eroded, making it impossible at this point to determine the type of cuticular microstructures. *Claudioranina latacantha* sp. nov. from the Paleocene Rancho Nuevo Formation of Mexico, is the oldest confirmed member of the subfamily Cyrtorhininae, and the oldest known representative of the clade Cyrtorhininae + Symethinae. Its geographic occurrence and age challenge previous assumptions that cyrtorhinids originated and diversified in Europe, and indicate that the most recent common ancestor for this clade must have originated in pre-Paleocene times (Table 4).

Claudioranina sp.
Fig. 3.T

Description.—Carapace sub-ovate in outline, slightly longer than wide, widest at posterior third. Fronto-orbital margin narrow, about half the carapace maximum width; orbits and rostrum poorly preserved in holotype. Anterolateral margin long, less convex than in other Cyrtorhininae species, bearing two anterolateral spines (excluding outer-orbital spine); anterior anterolateral spine short, triangular, nearly as long as wide, directed forwards, and separating the outer-orbital spine from the rest of the anterolateral margin; posterior anterolateral spine short, directed outwards, positioned anterior to concave posterior portion of anterolateral margin that forms the diagnostic conspicuous carapace constriction; posterolateral margin convex, apparently slightly shorter than anterolateral margin; junction between anterolateral and posterolateral margins much clearer than in other Cyrtorhininae species. A slight concavity is located at the mid length of the carapace, just below the end of the anterolateral margin. The concavity runs across the

widest part of the carapace describing a curve oriented to the posterior margin. Posterior margin poorly preserved in holotype. Dorsal anterior carapace lacking postfrontal terraces, ridges, or coarse tubercles. Traces of cuticle in rostrum, supraorbital and post-cardiac regions; setal pits closely spaced preserved in the cuticular fragments. Rest of carapace covered with small granulations characterizing endocuticle.

Material examined.—One complete carapace: hypotype CPC2039.

Measurements (in mm).—Hypotype CPC2039, carapace maximum length: 22.4; carapace maximum width: 20.6.

Remarks.—The broad and transversally curved carapace of the specimen of *Claudioranina* sp. is short and triangular. Anterolateral spines close to the fronto-orbital margin, as well as its outer ornamentation, are features typically seen among *Claudioranina*. The poorly ornamented anterior carapace, the anterolateral constriction of the carapace, and a carapace widest at the posterior third, differ from other species within *Claudioranina*, but more complete specimens are needed to define the species of the single specimen.

Section Eubrachyura De Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Carpilioidea Ortmann, 1893

Family Paleoxanthopsidae Schweitzer, 2003

Genus *Paraverrucoides* Schweitzer, 2003

Type species.—*Xanthilites alabamensis* Rathbun, 1935, by original designation.

Paraverrucoides alabamensis (Rathbun, 1935)

Fig. 4. A–4.L

Xanthilites alabamensis n. sp.; Rathbun, 1935, p. 91, pl. 20, Figs. 3–16; Toulmin, 1977, p. 177, pl. 9, Fig. 3.

Paraverrucoides alabamensis (Rathbun, 1935); Schweitzer, 2003, p. 1123, Figs. 6.1, 6.3, 6.6; Vega et al., 2007, p. 1438, Figs. 5.3–5.5, 6.1; Armstrong et al., 2009, p. 758, Figs. 6.5–6.9.

Description.—Carapace subhexagonal, maximum width at mid-length; anterior margin broad, two-thirds the maximum width; orbits circular, broad, orbital notch triangular, front bifid, wide, projected beyond front, with four small spines; anterolateral margin inclined, with three spines, anterolateral one being the most developed; posterolateral margin smooth, nearly two-thirds of maximum length; posterior margin straight, about one-half maximum width, with small elevations on lateral sides. Dorsal carapace regions well defined; branchiocardiac groove deep, inclined posteriorly from orbital spine to base of cardiac region; protogastric lobes swollen; mesogastric region semioval, long

Table 4

—List of fossil and extant genera and species within the Subfamily Cyrtorhininae Guinot, 1993, known to date. Classification following Van Bakel et al. (2012), and Karasawa et al. (2014).

Genus	Species	Locality	Age	Source
<i>Claudioranina</i> Karasawa et al., 2014	<i>Claudioranina latacantha</i> sp. nov.	Coahuila, NE Mexico	Paleocene	This work
	<i>Claudioranina</i> sp.			
	<i>C. oblonga</i> (Beschin et al., 1988) (type)	Vicenza, Italy	Eocene [Lutetian–Bartonian]	Beschin et al., 1988; Karasawa et al., 2014
<i>Antonioranina</i> Van Bakel et al., 2012	<i>A. fusselsi</i> (Blow and Manning, 1996)	North Carolina, US	Eocene	Blow and Manning, 1996; Feldmann et al., 1998
	<i>A. globosa</i> (Beschin et al., 1988) (type)	Vicenza, Italy; Istria, Croatia	Eocene [Ypresian–Lutetian]	Beschin et al., 1988; Mikuz, 2010; Van Bakel et al., 2012; Karasawa et al., 2014
	<i>A. ripacurtae</i> (Artal and Castillo, 2005)	Huelva, Spain	Eocene [Early Ilerdiense]	<i>A. ripacurtae</i> (Artal and Castillo, 2005)
<i>Cyrtorhina</i> Monod, 1956	<i>C. balabacensis</i> Serène, 1971	Sulu Sea, Philippines	Recent	Serène, 1971; Serène and Umali, 1972
	<i>C. granulosa</i> Monod, 1956 (type)	São Tomé and Príncipe, Ghana, Gulf of Guinea, Atlantic African Coast	Recent	Monod, 1956; Serène and Umali, 1972; Global Biodiversity Information Facility http://www.gbif.org/species/4382900 (data retrieved May 8, 2016)

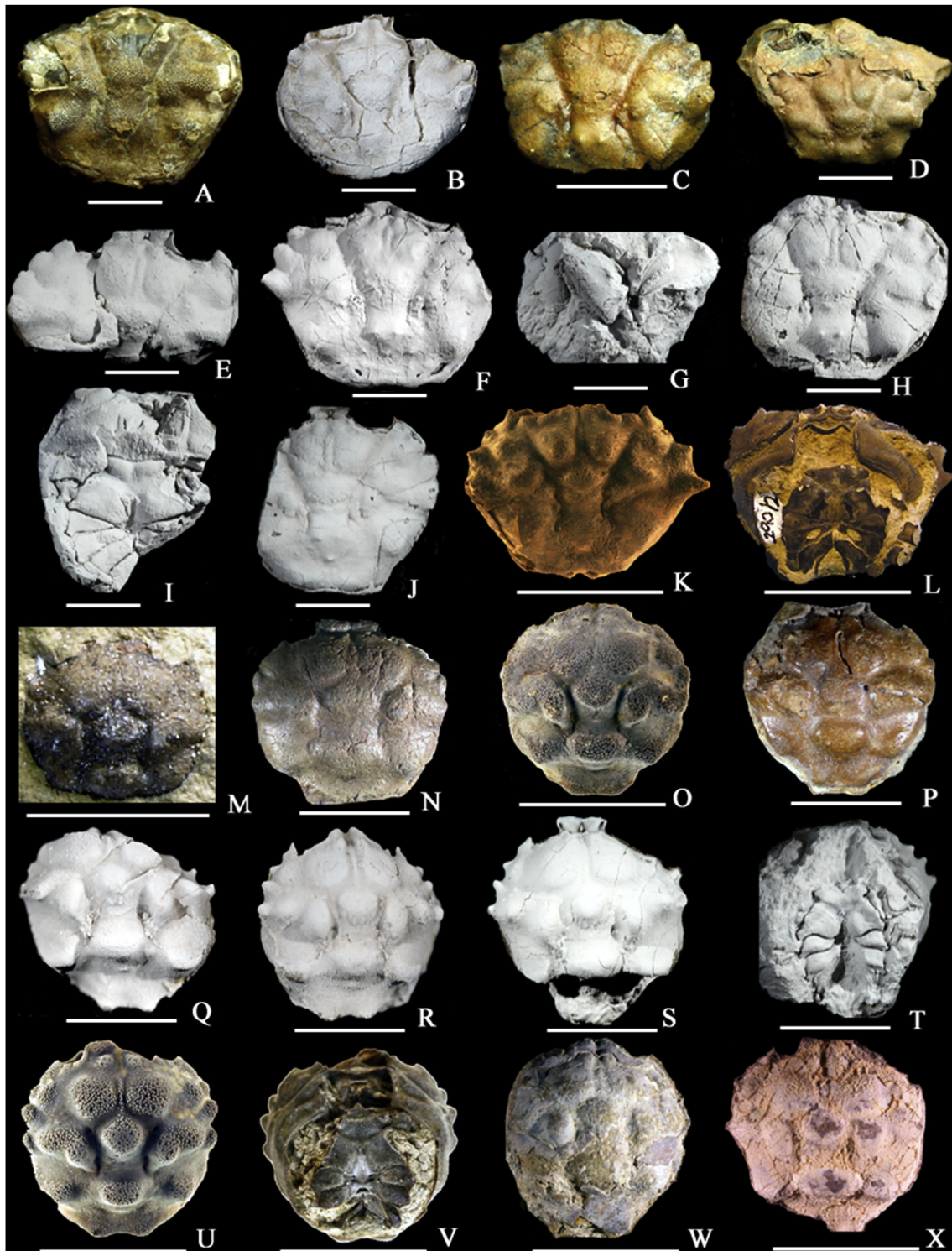


Fig. 4. A–L, *Paraverrucoides alabamensis* (Rathbun, 1935); A, dorsal carapace, hypotype CPC2040, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; B, dorsal carapace, hypotype CPC2041, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; C, dorsal carapace, hypotype CPC2042, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; D, dorsal carapace, hypotype CPC2043, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; E, dorsal carapace, hypotype CPC2044, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; F, dorsal carapace, hypotype CPC2045, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; G, ventral carapace with right chela and impression of left chela, same specimen; H, dorsal carapace, hypotype CPC2046, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; I, ventral carapace with sternum, hypotype CPC2053, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; J, dorsal carapace, hypotype CPC2047, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; K, L, dorsal and ventral carapace (female), hypotype NPL31177, Paleocene (Danian), Wills Point Formation, Texas. M–V, *Tehuacana americana* (Rathbun, 1935); M, dorsal carapace, hypotype CPC2071, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; N, dorsal carapace, hypotype IGM-9105, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; O, dorsal carapace, hypotype NPL31168, Paleocene (Danian), Wills Point Formation, Texas; P, dorsal carapace, hypotype IGM-9106, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; Q, dorsal and ventral carapace with sternum, hypotype CPC2074, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; R, dorsal carapace, hypotype CPC2075, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; S, dorsal carapace, hypotype CPC2076, Paleocene (Selandian), Rancho Nuevo Formation, Coahuila; T, ventral carapace with sternum, same specimen; U, V, dorsal and ventral carapace with sternum, hypotype NPL31164, Paleocene (Danian), Wills Point Formation, Texas. 23, 24, *Tehuacana schweitzeriae* Vega et al., 2008, dorsal carapace, holotype IHNFG-3051 and paratype IHNFG-3053, respectively, Eocene (Ypresian), El Bosque Formation, Chiapas. Scale bars = 10 mm, except in figure M, scale bar = 5 mm.

anterior process projected to base of rostrum; hepatic lobes with a prominent boss; epibranchial lobes distinct, semiovate; meso- and metabranchial areas flat, with prominent boss at midlength of posterolateral margin; metagastric and urogastric regions depressed; cardiac region subhexagonal, inflated with two small tubercles transversely aligned; intestinal region indistinct. Sternum broad, sterno-pleonal depression shallow; surface smooth; sternites 1, 2 form a small triangle; sternite 3 transversely elongate, with lateral projections extending beyond margin of sternum and a median groove, clearly separated from sternite 4 by a deep inclined transverse groove; sternite 4 subtrapezoidal with posterolateral projections, median part longitudinally depressed without any distinct groove; sternite 5 narrowing towards median line; sutures 4/5 and 5/6 medially interrupted; sternite 7 subrectangular; sternite 8 subrectangular, slightly smaller than sternite 7. Chelae robust, palm elongated, nearly rectangular, fixed finger triangular, movable finger slightly longer than fixed finger.

Material examined.—Twenty three specimens represented by complete and fragmentary carapaces: hypotypes, CPC2040 to CPC2062.

Measurements.—See Table 5.

Discussion.—The new specimens from Coahuila, Mexico, are similar in shape and size to those described and figured by Rathbun (1935) from the Paleocene (late Danian–early Selandian) of Alabama, but much larger than the specimens reported from the Lower Paleocene (Danian) Mexia Clay Member (Armstrong et al., 2009) (Fig. 4K, L). Small specimens of this species, along with *Linuparus wilcoxensis* and *Tehuacana americana* (Rathbun, 1935), suggest that the Early Paleocene (Danian) decapod assemblage from Wills Point, Texas, was affected by dwarfism, either as result of high seawater temperature or due to recovery processes, after the K/Pg event (see Martínez-Díaz et al., 2016). Important similarities are found with the Cretaceous (Maastrichtian) *Palaeoxhantopsis Beurlen, 1958*, from Mexico, Puerto Rico and Brazil (Schweitzer et al., 2008). A lineage from this genus may have given rise to *Paraverrucoides* and *Verrucoides Vega et al., 2001*, in the Paleogene of North America.

Superfamily Goneplacoidea MacLeay, 1838

Family Mathildellidae Karasawa and Kato, 2003

Genus *Tehuacana* Stenzel, 1944 = (*Marydromilites*)

Type species.—*Tehuacana tehuacana* Stenzel, 1944 (*Dromilites americana* Rathbun, 1935), by original designation.

Tehuacana americana (Rathbun, 1935)

Figs. 4.13–4.22

Dromilites americana n. sp.; Rathbun, 1935, p. 79, pl. 17, Figs. 1–6. *Tehuacana tehuacana* n. gen., n. sp.; Stenzel, 1944, p. 546, pl. 93, Figs. 6–9; text-figs 1–3; Glaessner, 1969, p. 527, Fig. 333.9; Bishop and Whitmore, 1986, p. 298, fig. 1F; Vega et al., 2007, 2008, p. 1438, Figs. 5.6 and 5.7, pl. 3, Fig. 7.

Tehuacana americana (Rathbun 1935), new combination; Armstrong et al. 2009, p.153, figs. 4.10–4.16; 5.1, 5.2, 5.4–5.7, 5.9, 5.10.

Description.—Carapace of medium size, slightly longer than wide, highly convex in transversal section. Anterior margin short, one-half of the maximum carapace width, orbits rounded with two supraorbital notches; anterolateral margins broadly curved, with three anterolateral spines, posterior spine being the largest; posterolateral margins convex, about one-fourth of the maximum width, forming a subsquared projection at junction with posterior margin; convex on both sides and straight at middle portion. Protogastric regions subsquare, elevated, bordered by deep cervical groove; mesogastric region subpentagonal with narrow, parallel sided anterior process; hepatic regions small, subtriangular; epi- and mesobranchial lobes fused, bilobed, with a posterior triangular extension adjacent to cervical groove; metabranchial areas elevated from the margin of carapace, subtriangular; meta- and urogastric regions depressed; cardiac lobe subtrapezoidal; intestinal region flat, inclined towards posterior margin. Third maxillipeds short, semirectangular; coxa subtrapezoidal, granulose, one-seventh the length of ischium and half its width; ischium semi-rectangular, elongated, narrow at the base, with longitudinal groove at middle portion, surface granulose, except for that of groove. Sternum broad, sterno-abdominal depression deep; surface covered with small granules; sternites 1 and 2 completely fused without trace of suture in a sharp, small triangle; sternite 3 transversely elongate, clearly demarcated from sternite 2 and 4 by transverse suture, with prominent tubercles on lateral edges; sternite 4 subtrapezoidal, anterolateral margins rimmed, posterolateral projections; suture 3/4 complete, without any prominent depression; posterior margins of sutures 3/4, 4/5 and 5/6 lined with small rounded granules on lateral parts; sternite 4 entire with median part longitudinally depressed but without any distinct groove, posterior part relatively deeper with 2 short, low, rounded, longitudinally curved ridges; sternite 5 complete, narrowing towards median line, with press button of pleonal locking mechanism located at the base of sternite; sutures 4/5 and 5/6 medially interrupted; 7/8 medially interrupted.

Material examined.—Sixteen complete carapaces, and three fragments: hypotypes CPC2063 to CPC2080.

Table 5

Measurements (mm) for Paleocene *Paraverrucoides alabamensis* (Rathbun, 1935) specimens from NE Mexico and SE USA. L = Maximum carapace length; W = Maximum carapace width; L/W = Length/Width ratio.

Referred taxa	Catalog number	L	W	W/L
<i>Paraverrucoides alabamensis</i> (= <i>Xanthilites alabamensis</i> Rathbun, 1935)	Holotype 371 708	17.6	24.8	1.41
<i>P. alabamensis</i>	Hypotype NPL31177	16.5	24.0	1.45
(in Armstrong et al., 2009)	Hypotype NPL31178	13.7	19.0	1.39
<i>P. alabamensis</i>	Hypotype IGM9102	20.9	22.5	1.08
(in Vega et al., 2007)	Hypotype IGM9103	15.1	18.5	1.23
	Hypotype IGM9104	14.1	17.2	1.22
<i>P. alabamensis</i>	Hypotype CPC2040	16.7	21.5	1.29
(This work)	Hypotype CPC2041	20.0	26.4	1.32
	Hypotype CPC2042	15.0	21.2	1.41
	Hypotype CPC2043	10.2	17.3	1.70
	Hypotype CPC2048	13.2	19.2	1.45
	Hypotype CPC2049	14.2	19.2	1.35
	Hypotype CPC2050	13.5	19.0	1.41
	Hypotype CPC2051	14.0	21.8	1.56
	Hypotype CPC2052	18.7	26.9	1.44
Mean		15.5	21.2	1.38

Measurements.—See Table 6.

Discussion.— According to [Armstrong et al. \(2009\)](#) *Tehuacana americana* include specimens previously assigned to *Dromilites americana* [Rathbun, 1935](#), but [Frantescu et al. \(2010\)](#) suggest that those specimens represent two different species. The shape of the sternum in specimens of “*Dromilites americana*” is clearly different from the one of a typical dromiid crab, but identical to that observed for *Tehuacana* (see [Rathbun, 1935](#), Fig. 17.2; [Stenzel, 1944](#), Fig. 2; [Armstrong et al., 2009](#), Fig. 4.11; Fig. 4.O, 4.U, 4.V, this study). Assignment of *Tehuacana* has changed from the Goneplacidae to its actual position within Mathildellidae ([De Grave et al., 2009](#)). The fossil record of *T. americana* has considerably increased since it was reported by [Stenzel \(1944\)](#) based on a single specimen from the Danian Wills Point Formation of Texas ([Vega et al., 2007](#); [Armstrong et al., 2009](#)), with a total of 24 specimens known from Paleocene deposits of southeastern US and NE Mexico. Intraspecific morphological variation was observed in *T. americana* specimens of the Mexia Clay Member (Early Paleocene of Texas) of the Wills Point Formation ([Armstrong et al., 2009](#)). We suggest that variation in dorsal carapace morphology is the result of intraspecific variation, as observed in some extant Mathildellidae (Peter Ng, pers. comm.). The studied material of *T. americana* from the Rancho Nuevo Formation include both carapaces with subrounded shape and short anterolateral spines, and also carapaces slightly longer than wide, with strong anterolateral spines. When compared with specimens from the Danian Wills Point Formation, the ones from Coahuila are twice as big, but same intraspecific variation of the carapace is observed (Fig. 4.M, 4.N, 4.P–4.T). This variation includes not only the strength of anterolateral spines, but also the carapace, which is slightly longer than wide, the strength of bosses on the dorsal surface and bilobed posterior projections, reaching to almost fourth of total carapace length in some specimens. In general, however, the dorsal regions remain identical in placement and shape among the specimens of *T. americana*. Sterna in the specimens preserving the ventral carapace portion are nearly identical.

Tehuacana schweitzeriae [Vega et al., 2008](#), from the Early Eocene (Ypresian) of Chiapas ([Vega et al., 2008](#); [Armstrong et al., 2009](#)) (Fig. 4.W, 4.X), is represented by small carapaces, longer than wide, similar in size to specimens of *Tehuacana americana* from the Wills Point Formation in Texas. Southward migration of some Paleocene genera to SE Mexico (Chiapas) was suggested ([Vega et al., 2008](#)). Change in size of *Tehuacana* might be due to an increase in sea water temperature, since all species from the Ypresian of Chiapas have small size ([Vega et al., 2001, 2008](#)). Gradual reduction in size could explain this observed size-turnover across the Paleocene-Eocene boundary; during this interval, a diminished population (in this case *T. americana*) could have persisted due to reduced corporal size, finally constituting a new species, *T. schweitzeriae*. Gradual reduction in size, on the other hand, differs from the Lilliput effect where populations of same species are able to develop small sizes to confront selective pressures caused by a massive extinction ([Martínez-Díaz et al., 2016](#)).

4. Discussion

The Late Cretaceous and Early Paleogene have been recognized as significant periods for rapid evolutionary radiation within crustacean decapods ([Schweitzer et al., 2002](#); [Schweitzer and Feldmann, 2005](#)). In NE and SE Mexico, only few genera of Late Cretaceous decapods survived and persisted across the K/Pg (e.g. *Enoploclytia*, *Linuparus*, *Costacopluma*) ([Vega et al., 2016](#)). Considering the particular composition and diversity found in shallow marine deposits in NE Mexico and the southeastern US ([Vega et al., 2007](#); [Armstrong et al., 2009](#)) it seems that the Early Paleocene also corresponds to an adaptive radiation scenario for evolution and establishment of new groups in the SE Gulf Coastal Plain. Recovery dynamics after mass extinctions have been studied in relation to the loss of genera and order levels ([Jablonski, 2002](#)), and to ecological composition of local assemblages during the K/Pg event ([Sessa et al., 2012](#)). Biotic transitions across mass extinctions have

Table 6 Measurements (mm) for Paleocene *Tehuacana americana* ([Rathbun, 1935](#)) specimens from NE Mexico and SE USA. *For juvenile specimens. L = Maximum carapace length; W = Maximum carapace width; L/W = Length/Width ratio.

Referred taxa	Locality	Catalog Number	L	W	W/L	Stage
<i>Tehuacana americana</i> (= <i>Tehuacana tehuacana</i> Stenzel, 1944)	SE USA (Texas)	Holotype	14.5	15.1	0.96	Paleocene
<i>T. americana</i> (= <i>Dromilites americana</i> Rathbun, 1935)	SE USA (Alabama)	Holotype 371,687	18.4	18.3	1.01	
<i>T. americana</i> (in Armstrong et al., 2009)	SE USA (Texas)	Hypotype NPL31164	14.5	14.6	0.99	
		Hypotype NPL31165	13.4	13.1	1.02	
		Hypotype NPL31166	15.3	16.2	0.94	
		Hypotype NPL31167	14.0	15.7	0.89	
		Hypotype NPL31168	10.0	10.7	0.93	
		Hypotype NPL31169	14.6	14.8	0.99	
		Hypotype NPL31171	13.1	12.9	1.02	
		Hypotype IGM9105	13.5	15.0	0.90	
		Hypotype IGM9106	10.1	11.1	0.91	
		Hypotype CPC2063	9.40	12.6	0.75	
<i>T. americana</i> (in Vega et al., 2007)	NE Mexico (Coahuila)	Hypotype CPC2064	11.0	12.0	0.92	
		Hypotype CPC2065	11.6	13.2	0.88	
		Hypotype CPC2066	11.2	14.7	0.76	
		Hypotype CPC2067	11.5	14.4	0.80	
		Hypotype CPC2068	11.7	13.8	0.85	
		Hypotype CPC2069	11.0	14.0	0.79	
		Hypotype CPC2070	10.4	15.7	0.66	
		*Hypotype CPC2071	4.30	5.30	0.81	
		*Hypotype CPC2072	8.00	9.50	0.84	
		Hypotype CPC2073	15.6	17.6	0.89	
		Hypotype CPC2074	18.0	19.8	0.91	
		Hypotype CPC2075	14.8	20.2	0.73	
		Hypotype CPC2076	12.6	13.4	0.94	
		Hypotype CPC2077	13.5	15.5	0.87	
		Hypotype CPC2078	15.9	15.5	1.03	
Mean			12.7	14.2	0.89	

been explained by means of ecological interactions (Miller, 1998), and by the influence of a spatial component to explain differential organismal survivorship (Miller, 1998; Jablonski, 2002). In this sense, the geographical context could have played an important role providing refugia (Harries et al., 1996), that protected small populations from ecological disturbances and by easing the environmental effects of the impact. Thus, survivorship may have been favoured in some sheltered coastal-shallow marine environments. The climatic consequences on the K/Pg impact have been widely discussed (Alvarez et al., 1980; Claeys et al., 2002; Schulte et al., 2010; Vellekoop et al., 2015), but some interpretations suggest less severe effects on Earth's climate (Smit et al., 1992; Pierazzo et al., 1998; Kring and Durda, 2002; Pope, 2002; Morgan et al., 2006; Keller and Abramovich, 2009). Crevice environments, such as those typical of coral reefs or slumped coral blocks (Robin et al., 2016) could have provided a suitable shelter habitat. The above could be an explanation for the prosper settlement of decapod faunas founded in Paleocene localities of the southeastern US (Cope et al., 2005) and NE Mexico. Recent evidence points to phyletic dwarfism as one strategy that may have helped some crabs not only to survive, but also to maintain reduced corporal size and populations (Martínez-Díaz et al., 2016). Climate fluctuations have been proposed as significant factors regarding diversification and speciation rates within extant crustaceans (Davis et al., 2016). During the Early Paleogene (Eocene) temperature fluctuations of sea water (Ho and Laepple, 2016) could have been relevant for the possible surge of survival strategies in shallow marine organisms, such as dwarfism or refugium taxa. The decapod faunas of the Wills Point Formation of Texas (Early Paleocene) and El Bosque Formation (Early Eocene) of Chiapas can be regarded as examples of the above, where a reduction of corporal size is exhibited by all members of the crustacean assemblages. By mid-Paleocene times, individuals of *Enoplocyrtia* and *Linuparus* from the Rancho Nuevo Formation maintained conservative corporal sizes (Tables 1 and 2). *Enoplocyrtia* had a broad ecological range throughout the geological time (Schweitzer and Feldmann, 2014), shifting from low energy siliciclastic to carbonate environments. By the end of the Eocene, *Enoplocyrtia* shows a gradual decline possibly caused by either

niche specialization, food scarcity, competition, and/or habitat shift (Aguirre-Urreta, 1989; Schweitzer and Feldmann, 2014). The decay pattern observed in erymids (Schweitzer and Feldmann, 2014) coincides with a diversity peak reached by other lobster families during Lutetian (Early Eocene). Competition and habitat shift seem to stand out as strong causes for conservative lineages (Hyžný et al., 2015) in *Enoplocyrtia* and *Linuparus*. *Enoplocyrtia* had a broad distribution during the Cretaceous, being more frequent in southern latitudes during the Early Cretaceous and apparently restricted to the Gulf Coast and Europe by Late Eocene times (Aguirre-Urreta, 1989; Feldmann, 1981). The genus *Linuparus* of cosmopolitan distribution during Cretaceous times (Feldmann et al., 2007) seems to have been favoured by temperate climates (Feldmann, 1981; Tsoi et al., 2011). Long range dispersion across the eastern Tethys has been documented for decapods (Hassan-vand et al., 2016). Recent *Linuparus* is restricted to the Indo-West Pacific, considered as a large biogeographic area and center of diversity for some marine species (Briggs, 1999; McLay, 2006). Migration to deep waters of the Indo-West Pacific region could have been another strategy in order to avoid competition of Cretaceous decapod genera (Harries et al., 1996). The Maastrichtian dominant genus *Costacopluma* has never been found in sediments of the Rancho Nuevo Formation, but is represented by numerous individuals in Paleocene and Eocene deposits of southeastern US and Brazil (Armstrong et al., 2009; Martínez-Díaz et al., 2016). Local extinction (Vega et al., 2007), or migration to refugia habitats in response to competition could be an explanation for this enigmatic absence.

5. Conclusion

The Mid-Paleocene decapod fauna of the Rancho Nuevo Formation can be correlated with that of the Porters Creek Formation (previously Sucarnoochee beds) of the Paleocene (late Danian – early Selandian) of Alabama (Mancini and Tew, 1988) (Fig. 5). Size variation of carapaces is evident in comparison between the Early Paleocene (Danian) small decapod assemblage from the Wills Point Formation of Texas and the small crustaceans from the Early Eocene El Bosque Formation, Chiapas SE Mexico. Size variation could have

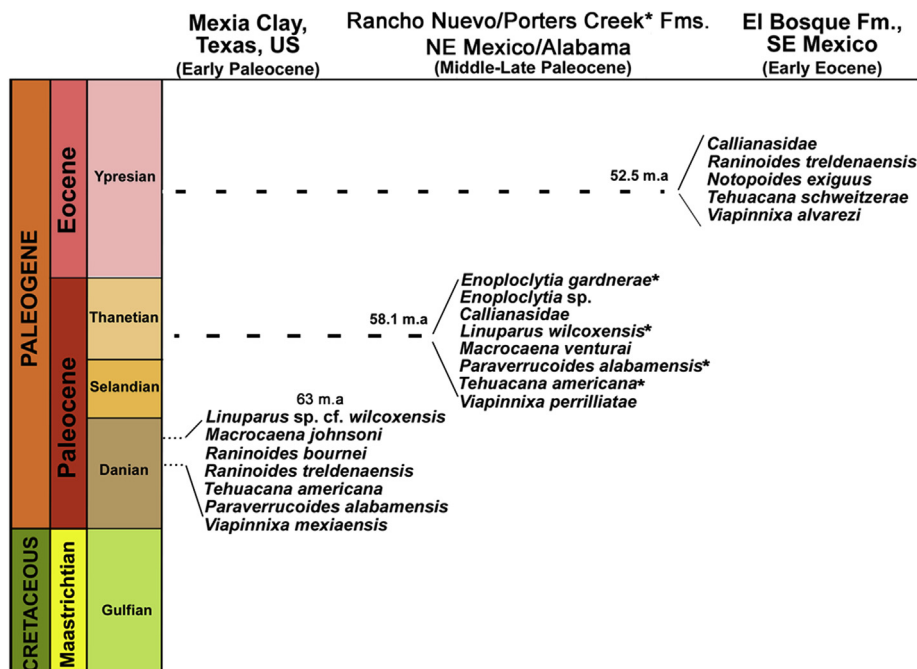


Fig. 5. Stratigraphic position of crustacean taxa from Paleogene assemblages of SE USA and Mexico.

resulted from seawater temperature changes and/or survival strategies, such as the Lilliput effect, particularly in the Mexia Clay Member of the Wills Point Formation in Texas. Increase in seawater temperatures during the Early Eocene (Ho and Laepple, 2016), could explain reduction in size for the Ypresian crustaceans from Chiapas.

Acknowledgments

J.L. Martínez-Díaz wish to thank Posgrado en Ciencias Biológicas, UNAM and Consejo Nacional de Ciencia y Tecnología (CONACYT) for the support to his posgrad studies. Felipe Rodríguez and Daniel Posada collected the material utilized herein. Our gratitude to José Manuel Padilla (Museo del Desierto, Saltillo, Coahuila) for his help in curatorial labours. We thank Wolfgang Stinnesbeck and Alessandro Garassino for suggestions to improve the manuscript. José Flores-Ventura helped with some photographs.

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