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Corresponding author:
Carrie E. Schweitzer;
Email: cschweit@kent.edu

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Differentiation of *Tehuacana* and *Hyphalocarcinus* new genus from similar forms in Palaeoxanthopsidae (Decapoda, Brachyura, Eubrachyura, Carpilioidea)

Carrie E. Schweitzer[1], Adiël Klompmaker[2] and Javier Luque[3]

[1]Department of Geology, Kent State University Stark Campus, 6000 Frank Ave. NW, North Canton, OH 44720, USA
[2]Department of Museum Research and Collections and Alabama Museum of Natural History, University of Alabama, 313 Mary Harmon Bryant Hall, Box 870340, Tuscaloosa, Alabama 35487, USA
[3]Department of Zoology, Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Abstract

The brachyurans *Tehuacana tehuacana* Stenzel, 1944 and *Dromilites americana* Rathbun, 1935 have historically been difficult to place in families. A reevaluation of type and referred material from several institutions suggests that the two species are referrable to separate genera in Palaeoxanthopsidae. *Hyphalocarcinus* new genus is erected to accommodate *H. americanus* new combination, and *Tehuacana* remains a distinct genus. Palaeoxanthopsidae evolved and radiated in the Atlantic Ocean, ranging from Late Cretaceous (Maastrichtian) to early Eocene (Ypresian) in age. This work adds to the known diversity of Palaeoxanthopsidae and demonstrates that the family survived and thrived in the Atlantic Ocean in the wake of the end-Cretaceous extinction. Differential preservation of specimens must be evaluated carefully when placing superficially similar taxa at the family, genus, and species level.

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Non-technical Summary

The true crabs *Tehuacana tehuacana* and *Dromilites americana* have historically been difficult to place in families. A reevaluation of type and referred material from several institutions suggests that the two species are referrable to separate genera within the family Palaeoxanthopsidae. *Hyphalocarcinus* is a new genus erected to accommodate *H. americanus*, and *Tehuacana* remains a distinct genus. Palaeoxanthopsidae, the family to which these genera belong, evolved and radiated in the Atlantic Ocean, ranging from Late Cretaceous (Maastrichtian) to Eocene in age. This work adds to the known diversity of Palaeoxanthopsidae and demonstrates that the family survived and thrived in the Atlantic Ocean after the end-Cretaceous extinction. Differing preservation styles, including broken margins, loss of cuticle, and abrasion of specimens, must be evaluated carefully when placing superficially similar taxa within a family, genus, and species.

Introduction

Investigation of the impact of the end-Cretaceous extinction on the origins, evolution, diversity, and radiation of brachyuran crabs during the Cenozoic is pivotal to expanding our understanding of the fossil record of true crabs during the Paleocene, their post-Mesozoic radiation, and their phylogenetic relationships (Klompmaker et al., 2016; Luque et al., 2019, 2024; Schweitzer and Feldmann, 2023; Van Bakel et al., 2023).

When decapod fossils are incomplete or differentially preserved, it can be difficult to distinguish between and among related taxa. The presence or absence of cuticle or some cuticular layers can render specimen appearance very different, even those of the same species (Waugh et al., 2009; Klompmaker et al., 2015; Schweitzer et al., 2024). Such complications have affected interpretation of various taxa, including the Paleocene forms *Dromilites americana* Rathbun, 1935 and *Tehuacana tehuacana* Stenzel, 1944. Generic and suprageneric placement of *D. americana* has been previously questioned, noting that it was likely not a member of Dromiidae (Guinot, 2008; Schweitzer and Feldmann, 2010). *Tehuacana* had been placed in Goneplacidae and Mathildellidae previously (Stenzel, 1944; Karasawa and Kato, 2003). Furthermore, the two species had been synonymized, with *Tehuacana americana* becoming the senior synonym (Armstrong et al., 2009). Although the two taxa have many similarities, we investigated their proposed synonymy and their generic and suprageneric placement by statistical and morphological analyses, considering differential preservation.

Geological settings

Specimens in Alabama were collected from the upper Danian Porters Creek Formation localities (Mancini and Tew, 1989; Pietsch et al., 2016). These include the Black Bluff (massive claystones), Tombigbee River, Sumter County, Alabama, of the Porters Creek Formation, upper Danian (ALMNH loc. 5). The UF specimen was collected from the upper Danian Porters Creek Formation in Furman, Wilcox County, Alabama. The USNM specimens were collected from Pine Barren Creek + Prairie Creek and Allenton + Prairie Creek and Pine Barren section, Wilcox County, Alabama, of the Porters Creek Formation, upper Danian (Rathbun, 1935).

Specimens in Texas were collected from localities of the upper Danian–Selandian Wills Point Formation (Armstrong et al., 2009). The MMNS and non-type NPL specimens were collected from Hansen Quarry, Limestone County, Texas, of the Wills Point Formation, Mexia Clay Member, upper Danian (Armstrong et al., 2009). The type specimen of *Tehuacana tehuacana* was collected from Tehuacana Creek, Limestone County, Texas, of the Wills Point Formation (no member specified), upper Danian–Selandian (Stenzel, 1944).

Materials and methods

Materials and preparation. Some specimens were whitened with ammonium chloride before photography with a Nikon D7200 camera with an AF Nikkor 28-105 mm lens. Measurements were taken with Mitutoyo analog calipers to the nearest tenth of a millimeter or derived from photos with a ruler placed at the same height as the specimen. Incomplete specimens were measured as half of the measurement where possible and then doubled. T-tests and Mann–Whitney tests were performed in Past 4.08 (Hammer et al., 2001), all at $p = 0.05$, to compare several carapace ratios (carapace length/carapace width, fronto-orbital width/carapace width, intestinal length/carapace length) of specimens of *Dromilites americana* versus *Tehuacana tehuacana*. Images were toned in Adobe Photoshop 23.1.0 before making figures in Adobe Illustrator 26.0.2. Photos of ALMNH and MMNS specimens were taken using a Canon EOS 90D camera with a 60 mm lens in an Ortech Photo-e-Box Plus lightbox.

Materials. *Dromilites americana*, holotype, USNM PAL 371688; paratypes USNM 335993A–D, USNM PAL 795622–795626; UF 17090; ALMNH:Paleo:21474–21481, MMNS IP-7402; UT NPL 31165. *Tehuacana tehuacana*, holotype UT BEG 21289 (cast and photos); USNM PAL 794470, 795627–795629; MMNS IP-7399 (four specimens).

Repositories and institutional abbreviations. Types, figured, and other examined specimens in this study are deposited in Alabama Museum of Natural History Paleontology Collection, University of Alabama, Tuscaloosa, Alabama, USA (ALMNH:Paleo:); Cátedra de Geología Histórica, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina (GHUNLPam); Georgia Southern Museum, Georgia Southern University, Statesboro, Georgia, USA (GSCM); Department of Earth Sciences, Kent State University (KSU D); Geologisk Museum, University of Copenhagen, Copenhagen, Denmark (MGUH); Mississippi Museum of Natural Science, Jackson, Mississippi, USA (MMNS IP); Muséum National d'histoire naturelle, Paris, Collection de Paléontologie, France (MNHN); Institut für Palaöntologie, Universität Bonn, Germany (UBIP); Florida Museum, University of Florida, Gainesville, Florida, USA (UF); United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM PAL); Jackson School Museum of Earth History, Non-Vertebrate Paleontology, University of Texas, Austin, Texas, USA (UT). Other institutional abbreviations are: Colección de Paleontología, Museo del Desierto, Saltillo, Coahuila, Mexico (CPC); Museo de Paleontologia, Instituto de Geologia, Universidad Nacional Autonoma de Mexico (GM).

Systematic paleontology

Infraorder **Brachyura** Linnaeus, 1758
Section **Eubrachyura** de Saint Laurent, 1980
Superfamily **Carpilioidea** Ortmann, 1893
Family **Palaeoxanthopsidae** Schweitzer, 2003

Included genera. *Hyphalocarcinus* new genus; *Jakobsenius* Schweitzer, 2005; *Lobulata* Schweitzer, Feldmann, and Gingerich, 2004; *Palaeoxantho* Bishop, 1986; *Palaeoxanthopsis* Beurlen, 1958; *Paraverrucoides* Schweitzer, 2003; *Remia* Schweitzer, 2003; *Rocacarcinus* Schweitzer, 2005; *Tehuacana* Stenzel, 1944; *Verrucoides* Vega et al., 2001.

Diagnosis. Carapace usually wider than long but can be about as long as wide, widest about 65% of the distance posteriorly, strongly vaulted longitudinally, moderately vaulted transversely; carapace regions moderately to strongly inflated, often ornamented with large swellings, strongly delineated; front triangular and axially notched, with spines on either side of notch and with inner-orbital spines; frontal width about 20% maximum carapace width; orbits square, with two fissures; fronto-orbital width about half maximum carapace width; anterolateral margins long, convex, with straight segment followed by three spines, the last spine longest, stout, directed posterolaterally; posterolateral margins short, sinuous; swellings on epibranchial and branchial regions forming transverse ridges; carapace usually about as long as wide or wider than long; female gonopores very large, ovate, positioned centrally on sternite 5 just lateral to the axis (adapted from Schweitzer et al., 2018, p. 10).

Remarks. Palaeoxanthopsidae embraces a somewhat superficially heterogeneous group of genera that are united by several diagnostic characters. The carapace is usually wider than long or about as wide as long, and ornamentation is somewhat variable, with carapace regions ranging from moderately inflated to bearing very large, spherical swellings (Schweitzer et al., 2018).

However, the family is united by (1) the presence of well-defined regions, (2) the presence of a transverse ridge or swelling on the branchial regions, (3) orbits bearing two fissures, (4) anterolateral margins with discrete, well-separated spines, separated from the outer-orbital angle by a straight segment, (5) a quadrilobed front with two medial lobes sometimes projected beyond the orbits, (6) a moderately wide sternum with a Y-shaped groove pattern on sternites 3 and 4, and (7) strong lateral swellings on sternite 4 (Fig. 1). The two genera, *Tehuacana* and *Hyphalocarcinus* new genus, possess all of these features. They differ from Palaeoxanthopsidae

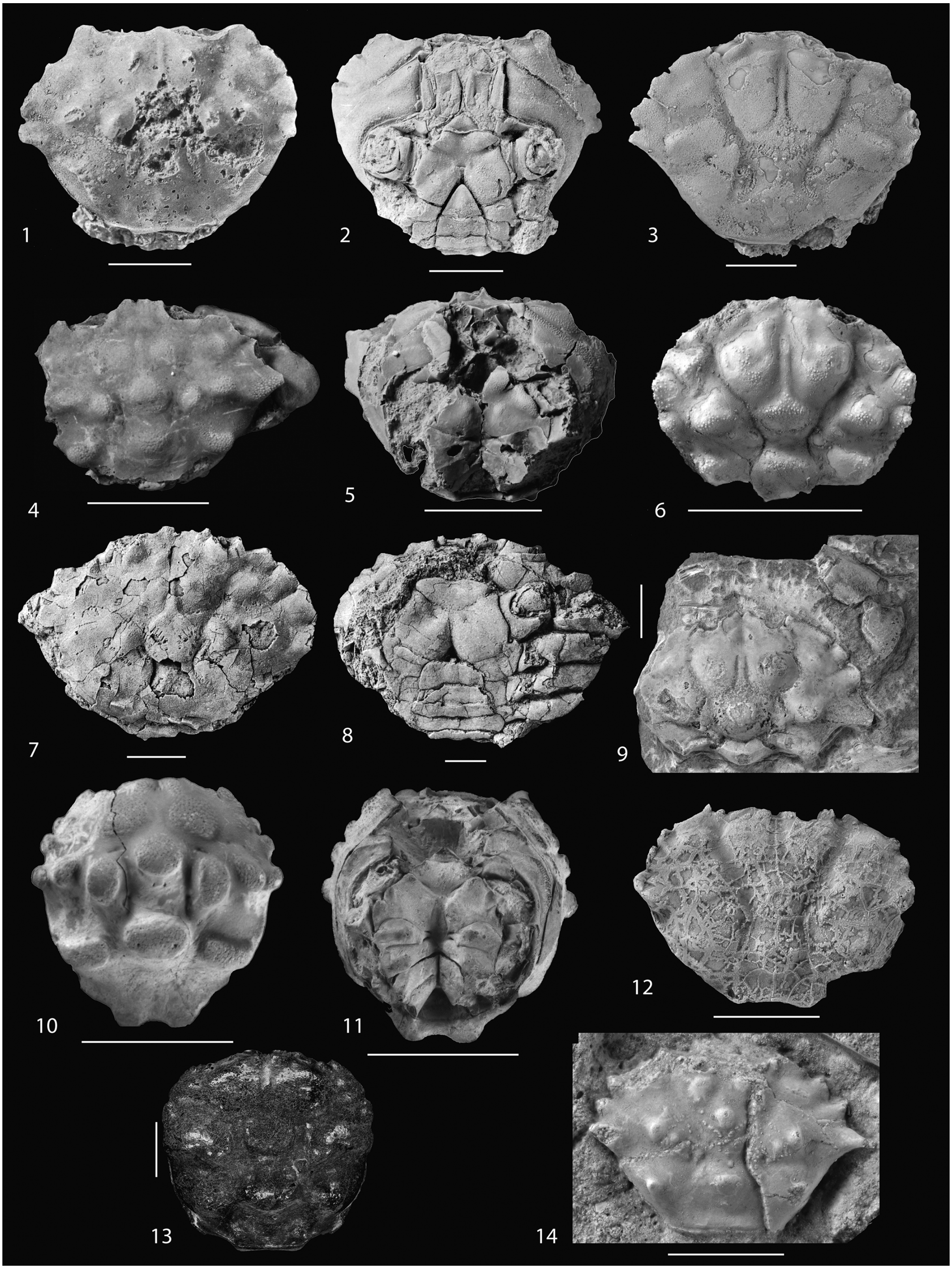

Figure 1. Palaeoxanthopsidae. (**1, 2**) *Lobulata lobulata* (Feldmann et al., 1995), holotype GHUNLPam 7001: (**1**) dorsal view; (**2**) ventral view (Feldmann et al., 1995, fig. 7.1, 7.2). (**3**) *Jakobsenius cretaceus* (Segerberg, 1900), KSU D 37, cast of holotype MGUH 2483. (**4, 5**) *Paraverrucoides alabamensis* (Rathbun, 1935): (**4**) dorsal view of holotype USNM PAL 371718; (**5**) ventral view of paratype USNM PAL 371707. (**6**) *Palaeoxantho libertiensis* Bishop, 1986, holotype GSCM 1692. (**7, 8**) *Rocacarcinus gerthi* (Glaessner, 1930), holotype Glaessner 1, UBIP: (**7**) dorsal view; (**8**) ventral view (Feldmann et al., 1995, fig. 9.3, 9.4). (**9**) *Palaeoxanthopsis cretacea* Rathbun, 1902, syntype USNM PAL 73709. (**10, 11**) *Hyphalocarcinus americanus* (Rathbun, 1935) n. comb., paratype USNM PAL 335993B: (**10**) dorsal view; (**11**) ventral view. (**12**) *Remia africana* (Remy in Remy and Tessier, 1954), KSU D 1100, cast of holotype MNHN R03885. (**13**) *Tehuacana tehuacana* Stenzel, 1944, holotype BEG021289 (photo by S. Skwarcan). (**14**) *Verrucoides verrucoides* (Collins and Rasmussen, 1992), KSU D 1803, cast of holotype MGUH 21.612. (**1–12, 14**) Scale bars = 1.0 cm; (**13**) scale bar = 5.0 mm. All except (**10, 11, 13**) appear in Schweitzer et al. (2018).

as diagnosed by Schweitzer et al. (2018) in being about as wide as long rather than wider than long and hexagonal. The carapace of *Hyphalocarcinus* new genus is much more strongly domed than other genera in the family. These differences are distinctive; but in all other ways, these two genera possess the diagnostic characters of the family.

Hyphalocarcinus new genus is erected to accommodate *Dromilites americana* (Rathbun, 1935), originally considered as a member of the podotrematous Dromiidae De Haan, 1833. *Dromilites americana* cannot be referred to *Dromilites* Milne Edwards, 1837 for several reasons, the most important of which is that *D. americana* is not a dromiid or even a podotrematous crab, as revealed by its thoracic sternum, which exhibits typical eubrachyuran sternal features, including the size, the width, and the shape of the sternites, the interrupted sternal sutures 4/5 and 5/6, and a median line on sternites 7 and 8 (Schweitzer et al., 2024) (Fig. 1.11).

Tehuacana was originally placed within Goneplacidae on the basis of its flattened rectangular shape (Stenzel, 1944). Later, the genus was moved to Mathildellidae Karasawa and Kato, 2003, where it has remained. Similarities with other genera of Mathildellidae include a flattened carapace, dorsal regions weakly to moderately defined, an ovate sternum, and posterolateral reentrants. The holotype of *Tehuacana tehuacana* is not well preserved, so placement of the taxon is difficult. Because of the superficial similarities with *Dromilites americana* and the carapace swellings and morphology that are diagnostic for Palaeoxanthopsidae, the two genera are referred together to the same family, noting that each diverges somewhat from other palaeoxanthopsids.

Dromilites americana has many superficial similarities with genera within Aethridae Dana, 1851. It has a well-developed sternal locking mechanism on sternite 5, sternal sutures 4/5 and 5/6 are incomplete, and sternal sutures 6/7 and 7/8 are complete, seen in Aethridae but also many other eubrachyurans (Guinot, 1979). The dorsal carapace of *Dromilites americana* has affinities with some taxa within Aethridae. Among extinct and extant aethrids, several genera have strongly inflated carapace regions (Schweitzer and Feldmann, 2019; Poore and Ahyong, 2023). However, most extant and many extinct aethrids have very strongly convex anterolateral margins, not seen in *D. americana.* Thus, we consider Palaeoxanthopsidae as the best placement for the new genus for *D. americana* at this time. Members of the family are already known from the Late Cretaceous through Eocene of the Gulf Coastal Plain, so neither the geologic nor geographic range is extended by these referrals.

Hyphalocarcinus new genus

1935 *Dromilites* Milne Edwards, 1837 (partim); Rathbun, p. 79.
1966 *Dromilites* Milne Edwards (partim); Davidson, p. 211.
1986 *Dromilites* Milne Edwards (partim); Bishop and Whitmore, fig. 1D.
2005 *Marydromilites* Števčić, 2005; nomen nudum (ICZN, 1999, Article 13.1).
2008 *Dromilites* Milne Edwards (partim); Guinot, p. 21.
2009 *Tehuacana* Stenzel, 1944 (partim); Armstrong et al., p. 753.
2010 *Dromilites* Milne Edwards (partim). Schweitzer et al., p. 64.
2010 *Dromilites* Milne Edwards (partim); Schweitzer and Feldmann, p. 422.
2010 *Dromilites* Milne Edwards (partim); Franţescu et al., p. 264.
2016 *Dromilites* Milne Edwards (partim); Klompmaker et al., table S9.
2017 *Tehuacana* Stenzel, 1944 (partim); Luque et al., p. 46.
2017 *Tehuacana* Stenzel, 1944 (partim); Martinez-Díaz et al., p. 77.
2018 *Tehuacana* Stenzel, 1944 (partim); Vega et al., fig. 5.

Type species. *Dromilites americana* Rathbun, 1935, by original designation.

Diagnosis. Carapace longer than wide; protogastric, metagastric, epibranchial, cardiac, and mesobranchial regions with strongly inflated, spherical, densely granular swellings; anterolateral margins with four conical blunt spines with densely granular tips; posterior margin with triangular projections on each end; thoracic sternum longer than wide, pleonal locking mechanism on sternite 5; sternal sutures 4/5 and 5/6 incomplete, suture 6/7 and 7/8 complete, median line on axis of sternites 7 and 8.

Etymology. The genus name is a combination of the Greek words *hyphalo*, meaning under the sea, secret, and *karkinos*, a common stem for crab, in reference to the difficulty in placing this taxon within a family. The gender is masculine. The name suggested by Števčić (2005), *Marydromilites*, is a nomen nudum under ICZN Article 13.1 (ICZN, 1999; see also Franţescu et al., 2010).

Remarks. *Dromilites* was considered a member of Dromiidae by Rathbun (1935), but since then it has been referred to another dromiacean family, Sphaerodromiidae Guinot and Tavares, 2003. Notably, both families include crabs exhibiting the podotrematous condition, with gonopores of both males and females on the pereiopod coxae, and they have distinctive sterna consisting of narrow sternites with reduced episternal projections (Schweitzer et al., 2024, fig. 122). Schweitzer and Feldmann (2010) restricted *Dromilites* to just four species, and they noted the affinities of *D. americana* with eubrachyuran crabs.

Dromilites americana cannot be referred to *Dromilites* for several reasons, the most important of which is that it is not a podotrematous crab. Its sternum exhibits features of a eubrachyuran, including the size, width, and shape of the sternites and the interrupted sternal sutures with a median line on sternites 7 and 8 (Figs 1.11, 2.6). Sternite 4 is longer than it is wide in *D. americana*, as in most eubrachyuran crabs, whereas *Dromilites* sensu stricto have a long anterior projection on sternite 4. No podotrematous crabs have a sternum like that of *D. americana.* Other differences between *Dromilites americana* and *Dromilites* sensu stricto are the presence of strong cervical, post-cervical, and branchiocardiac grooves in *Dromilites*, all of which are absent in *D. americana. Dromilites* has crispate lateral margins, lacking in *D. americana.* The carapace swellings of *D. americana* are large and spherical, whereas those of *Dromilites* are more subdued and not granular.

A new genus, *Hyphalocarcinus*, is erected to accommodate *D. americana* and is placed in Palaeoxanthopsidae as discussed. It differs from all other genera in the family in its longer than wide carapace and very large, inflated swellings on the carapace regions. Detailed differences from *Tehuacana* are discussed in the following. At this time, it is monotypic, with occurrences on the Gulf Coastal Plain of North America, late Danian to Selandian in age.

Armstrong et al. (2009) synonymized *Tehuacana tehuacana* Stenzel, 1944, with *Dromilites americana*, resulting in *Tehuacana americana* (Rathbun, 1935) as the species name and *T. tehuacana* as the junior synonym. They attributed the differences in dorsal carapace morphology between and among specimens of *T. tehuacana* and *D. americana* as being intraspecific variation but not sexual dimorphism. This synonymy was maintained by later workers (Luque et al., 2017; Martínez-Díaz et al., 2017; Vega et al., 2018).

To test the validity of this synonymy, we analyzed images and a cast of the holotype of *Tehuacana tehuacana*, and the holotype and paratype specimens of *Dromilites americana*, and other specimens assigned to both species (see Materials and methods). For this study, specimens were attributed to the *Dromilites americana* morphotype if they had a strongly domed carapace; large, spherical, granular carapace swellings; a rostrum with strongly produced axial spines; and/or posterior margins with blunt spines on each end (Fig. 2.2). Specimens were attributed to the *Tehuacana* morphology if they had a flattened carapace and flattened carapace regions without large spherical swellings; blunt short axial rostral spines; and/or lack of blunt spines on the posterior margin (Fig. 2.1).

Statistical analysis of carapace measurement ratios of specimens separated into these two morphologies showed significant differences with both t-test and Mann–Whitney analyses. The carapace length to carapace width ratio, the fronto-orbital width to carapace width ratio, and the length of the intestinal region to carapace length ratio were all significantly different at the $p = 0.05$ level between the two groups in both tests (Table 1; Supplementary Data Tables 1–5). Additional differences include the nature of the anterolateral spines. In the *D. americana* morphotype, the spines are discrete, conical, blunt structures with circular cross sections. In the *Tehuacana* morphotype, the spines are flattened, short, and sharp. The regions of the carapace in *Tehuacana* are granular, as are the large domed inflations of *D. americana*, but this is true of most genera within Palaeoxanthopsidae. *Tehuacana* has large posterolateral reentrants to house the bases of the fifth pereiopods, which are lacking in *D. americana.* In lateral view, the shape of the *linea brachyura* separating the branchiostegite from the pterygostomial region is sinuous in *T. tehuacana* (Fig. 2.7) and strongly arcuate in *D. americana* (Fig. 2.8) (Table 1).

We tested whether the two morphotypes were due to sexual dimorphism or ontogeny. The only specimens of either species for which sex is known are male (N = 1 each), so no evidence of sexual dimorphism is currently available. Moreover, the *T. tehuacana* morphology is not found in Alabama thus far, whereas both morphologies are present in Texas and Coahuila (Mexico). The various features of the carapace discussed here that separate the two groups are present regardless of size; thus, ontogeny does not explain the differences. Although there are superficial similarities between and among specimens referred to these two taxa, enough differences, some of which are statistically significant, exist to retain the two species as separate and in different genera. *Dromilites americana* is placed in a new genus herein, *Hyphalocarcinus*, resulting in

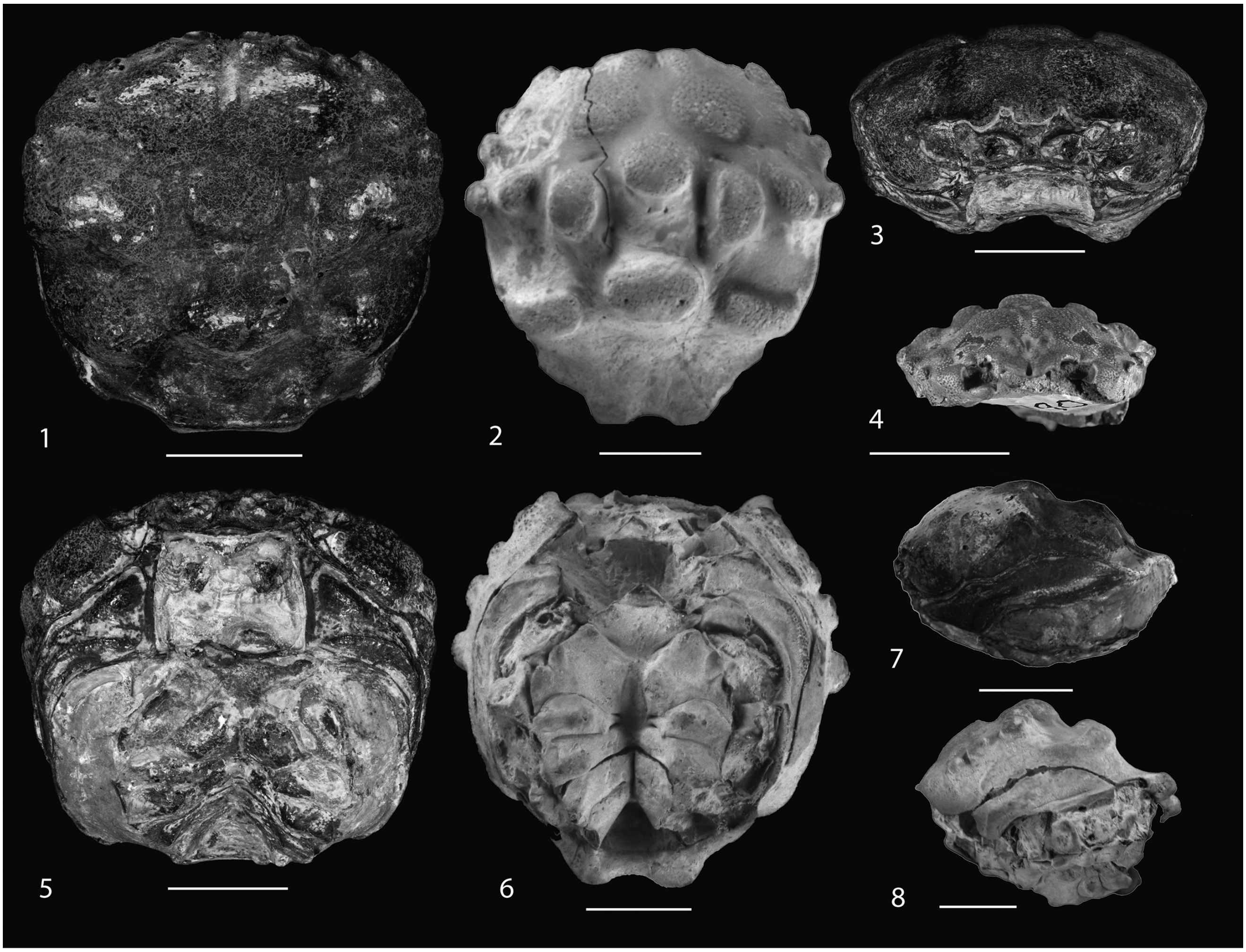

Figure 2. (**1, 3, 5, 7**) *Tehuacana tehuacana* Stenzel, 1944, holotype BEG021289: (**1**) dorsal, (**3**) anterior, (**5**) ventral, and (**7**) lateral views, unwhitened. (**2, 4, 6, 8**) *Hyphalocarcinus americanus* (Rathbun, 1935) n. comb., paratype USNM PAL 335993B: (**2**) dorsal, (**4**) anterior, (**6**) ventral, and (**8**) left lateral views, whitened with ammonium chloride. Photos of *Tehuacana* by Stacie Skwarcan (UT). Scale bars = 5.0 mm.

Table 1. Similarities and differences between *Tehuacana tehuacana* and *Hyphalocarcinus americanus* n. comb.

	Tehuacana tehuacana	*Hyphalocarcinus americanus* n. comb.
Carapace length/carapace width ratio significantly different, t-test, p = 0.012213; Mann–Whitney, p = 0.014079	Mean 0.97449, n = 8	Mean 1.0521, n = 9
Fronto-orbital width/carapace width ratio significantly different, t-test, p = 0.01265; Mann–Whitney, p = 0.04021	Mean 0.67109, n = 7	Mean 0.61528, n = 14
Intestinal length/carapace length significantly different, t-test p = 0.001137; Mann–Whitney, p = 0.005075	Mean 0.14611, n = 6	Mean 0.25722, n = 6
Strongly domed carapace	Absent	Present
Anterolateral spines	Flattened, triangular, short	Large, circular in cross section, granular on tips
Large, granular swellings forming epibranchial, cardiac, protogastric, and metabranchial region	Granular and flattened	Granular and swollen
Narrow posterior margin produced into distinct rounded protuberances at corners	Absent	Present
Large posterolateral reentrants	Present	Absent
Carapace high laterally	Flattened	High
Depressed intestinal region	Present	Present
Regional development	Similar	Similar
Front axially notched	Present	Present
Suborbital area	High	Short
Sternal median line on sternites 7 and 8	Absent	Present

Hyphalocarcinus americanus (Rathbun, 1935) new combination. *Tehuacana tehuacana* remains the type species of that genus.

The specimens of *Tehuacana schweitzerae* Vega et al, 2008 should be reevaluated to determine to which taxon they belong; the specimens are incomplete as illustrated. It should be noted that when the margins of specimens are broken or if the carapace lacks some or all layers of cuticle, the superficial similarities between the two morphologies may be magnified. The discussions of *Dromilites americana*, *T. tehuacana*, and *T. schweitzerae* in many recent publications should be used with caution as they are based either on misidentified specimens as constrained herein or on a combination of specimens referrable to multiple taxa.

Hyphalocarcinus americanus (Rathbun, 1935) new combination
Figs 1.10. 1.11, 2.2, 2.4, 2.6, 2.8, 3

1935 *Dromilites americana* Rathbun, p. 79.
1966 *Dromilites americana*; Davidson, p. 211.
1986 *Dromilites americana*; Bishop and Whitmore, fig. 1D.
2008 *Dromilites americana*; Guinot, p. 21.
2009 *Tehuacana americana* (Rathbun, 1935); Armstrong et al., p. 753.
2010 *Dromilites americana*; Schweitzer et al., p. 64.
2010 *Dromilites americana*; Schweitzer and Feldmann, p. 422.
2010 *Dromilites americana*; Franțescu et al., p. 264.
2016 *Dromilites americana*; Klompmaker et al., table S9.
2017 *Tehuacana americana* (Rathbun, 1935); Luque et al., p. 46.
2017 *Tehuacana americana* (Rathbun, 1935); Martinez-Díaz et al., p. 77, partim.
2018 *Tehuacana americana* (Rathbun, 1935); Vega et al., fig. 5.13, 5.15.

Holotype. Originally identified as *Dromilites americana*, holotype, USNM PAL 371688.

Diagnosis. Diagnosis: As for genus.

Occurrence. Occurrences range in age from the late Danian to Selandian (Paleocene), in Alabama and Texas, USA, and Coahuila, Mexico (Table 2).

Description. Carapace longer than wide, length about 110% width; widest at about 40% distance posteriorly on carapace at position of fourth anterolateral spine (including outer-orbital projection); carapace strongly vaulted longitudinally, moderately vaulted transversely so that it is dome-like; entire surface covered with widely and evenly spaced setal pits. Front projected beyond orbits, notched axially and deeply axially sulcate, with wide granular rim, sides on either side of notch sloping distally, with slight projection at inner orbital angle; orbits broad, with very weak, blunt intraorbital projection bounded on each side by short fissures; suborbital margin projecting beyond upper orbital margin, with sub-inner orbital spine; fronto-orbital width about 60% carapace width. Outer-orbital spine small, anterolateral spines increasing in size posteriorly, projected increasingly anterolaterally, last spine directed laterally, spines with circular cross sections, blunt, ornamented with densely spaced granules on tips. Posterolateral margin initially straight, parallel, then converging posteriorly; posterior margin short, with strong, blunt spines at posterior corners, spines with dense granules on tips; posterior margin weakly concave between spines; posterior width about 32% carapace width.

Epigastric regions small, granular, weakly inflated; protogastric regions moderately inflated, densely granular; hepatic regions much lower than protogastric regions, forming a weakly to moderately inflated ovate swelling along anterolateral margin. Mesogastric region with long, narrow anterior process, greatly inflated posteriorly into spherical region, densely granular on surface; urogastric region depressed well below level of other regions, with concave lateral margins; cardiac region most inflated region of all carapace regions, transversely ovate, densely granular on surface; intestinal region long, depressed well below level of cardiac region, length from posterior edge of cardiac region to posterior margin about 26% carapace length. Epibranchial region arcuate, composed of two swellings, lateral swelling smaller, separated from axial swelling by deep groove, axial swelling ovate and positioned with long axis parallel to axis of carapace; both swellings densely granular on surface; mesobranchial region flattened anteriorly, with very strong transverse ridge at level of cardiac region, ridge densely granular on surface; metabranchial region depressed to level of intestinal region.

Table 2. Occurrences for *Hyphalocarcinus americanus* (Rathbun, 1935) n. comb. Those with asterisks were studied from specimens or high-resolution images provided by museums. Non-asterisked entries are compiled from examination of published images only.

Current placement	Original placement	Material	Formation	Age	State	Reference
**Hyphalocarcinus americanus*	*Dromilites americana*	Holotype USNM PAL 371688 and paratypes USNM PAL 335993A-D	Porters Creek (= Sucarnoochee Beds of Rathbun, 1935)	Late Danian	Alabama	Rathbun (1935); herein
**Hyphalocarcinus americanus*		USNM PAL 795622–795626	Wills Point	Late Danian–Selandian	Texas	Bishop and Whitmore (1986); herein
**Hyphalocarcinus americanus*		ALMNH: Paleo:21474–21481	Porters Creek	Late Danian	Alabama	Herein
**Hyphalocarcinus americanus*		MMNS IP–7402	Wills Point (Mexia Clay Member)	Late Danian	Texas	Herein
**Hyphalocarcinus americanus*	*Tehuacana americana* on label	UT NPL 31165	Wills Point (Mexia Clay Member)	Late Danian	Texas	Herein
**Hyphalocarcinus americanus*		UF 17090	Porters Creek	Late Danian	Alabama	Herein
Hyphalocarcinus americanus	*Tehuacana americana*	NPL 31168, 31164, 31166	Wills Point (Mexia Clay Member)	Late Danian	Texas	Armstrong et al. (2009); Vega et al. (2018)
Hyphalocarcinus americanus	*Tehuacana americana*	IGM–9106	Rancho Nuevo Formation	Selandian	Coahuila, Mexico	Martinez-Díaz et al. (2017)
Hyphalocarcinus americanus	*Tehuacana americana*	CPC2074–2076	Rancho Nuevo Formation	Selandian	Coahuila, Mexico	Martinez-Díaz et al. (2017)

Branchiostegite and pterygostomial region high, linea brachyura wide, very clearly developed; coxae of pereiopods broadly spaced between pterygostome and sternum. Orbital area with pair of axial openings, orbital depression lateral to these openings; second pair of openings directly posterior to/under first pair; epistome a triangular projection between ventralmost pair of openings; endostome with oblique transverse ridges positioned just posterior to suborbital margin.

Sternites 1–2 fused. Sternite 3 long separated from 1–2 by shallow groove. Sternite 4 high, with two rounded swellings along lateral margin and on episternal projection; sternite 5 with sternal locking button on posterior margin; sternites 5, 6, and 7 with transverse ridges; sternites 7 and 8 directed strongly posterolaterally. Sternal sutures 4/5 and 5/6 incomplete; sutures 6/7 and 7/8 complete; sternal median line on sternites 7 and 8.

Materials. *Dromilites americana*, holotype, USNM PAL 371688; paratypes USNM 335993A–D, USNM PAL 795622–795626; UF 17090; ALMNH:Paleo:21474–21481, MMNS IP-7402; UT NPL 31165. Measurements (in mm) on specimens of *Hyphalocarcinus americanus* n. comb. are presented in Table 3 and Supplementary Data Table 1.

Remarks. The morphology of specimens of *Hyphalocarcinus americanus* n. comb. is remarkably uniform across time, space, and size of individuals (Fig. 3). The smallest specimen has a proportionally wider fronto-orbital margin compared with larger specimens (Table 3). Ranges of variation in size of the anterolateral spines and granulation on the carapace swellings are present but not broad. The differences between and among specimens are related mostly to the state of preservation. If cuticle is preserved, ornamentation is observable, and spines appear more distinct than if cuticle is absent or poorly preserved.

Table 3. Carapace measurements (in mm) taken on specimens of *Hyphalocarcinus americanus* (Rathbun, 1935) n. comb. FOW = fronto-orbital width; PW = posterior carapace width; length = maximum length of carapace, including rostrum/front; width = maximum width of carapace taken at the bases of the last anterolateral spines.

Specimen	Width	Length	FOW	PW	Intestinal length
USNM 371688 (holotype)	16.8	17.6	11.2	5.6	—
USNM 35993b (paratype)	17.0	18.7	10.2	5.8	6.1
USNM 35993d (paratype)	12.4	13.3	7.6	4.5	3.6
USNM PAL 795623	16.6	18.9	8.7	5.5	5.7
USNM PAL 795622	15.2	—	10.7	—	—
USNM PAL 795626	10.0	9.5	6.5	—	—
ALMNH:Paleo:21476	21.3	—	11.8	—	—
ALMNH:Paleo:21474	8.6	9.3	5.6	2.7	1.9
ALMNH:Paleo:21475	20.0	—	10.9	—	—
ALMNH:Paleo:21477	15.9	—	9.1	—	—
ALMNH:Paleo:21478	14.5	15.3	8.1	5.2	3.2
ALMNH:Paleo:21479	9.8	10.0	6.1	2.9	—
ALMNH:Paleo:21480	12.0	12.1	6.9	3.8	2.8
ALMNH:Paleo:21481	5.5	—	4.2	—	—
MMNS IP–7402	9.4	9.8	6.4	2.5	1.8

Genus ***Tehuacana*** Stenzel, 1944

Type species. *Tehuacana tehuacana* Stenzel, 1944, by original designation.

Other species. *Tehuacana schweitzerae* Vega et al, 2008.

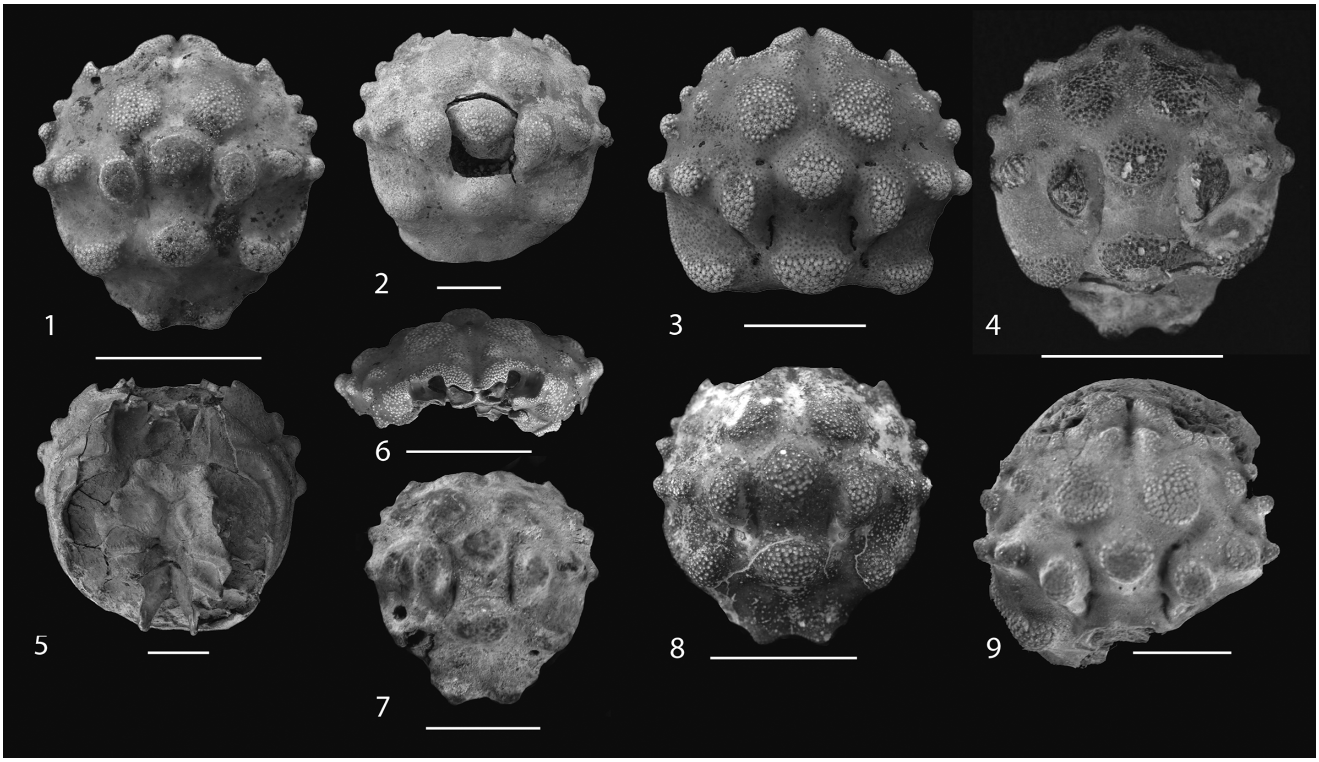

Figure 3. *Hyphalocarcinus americanus* (Rathbun, 1935) n. comb., dorsal carapace except (**5, 6**). (**1**) ALMNH:Paleo:21474. (**2**) ALMNH:Paleo:21475. (**3**) ALMNH:Paleo:21476. (**4**) Holotype USNM PAL 371688 (image from https://collections.nmnh.si.edu/search/paleo/). (**5**) ALMNH:Paleo:21475, ventral view. (**6**) ALMNH:Paleo:21476, frontal view. (**7**) Paratype USNM PAL 335993B. (**8**) MMNS IP-7402. (**9**) USNM PAL 795622. (**1–3, 5–9**) Scale bars = 5.0 mm; (**4**) scale bar = 1.0 cm.

Diagnosis. Carapace wider than long, flattened; anterolateral margins with four wide, triangular, flattened projections; regions well defined, with dense granular ornamentation centrally on each; posterolateral reentrants large; sternum wider than long, sternal median line absent on sternites 7 and 8.

Tehuacana tehuacana Stenzel, 1944
Figs 1.13, 2.1, 2.3, 2.5, 2.7, 4

1944 *Tehuacana tehuacana* Stenzel, p. 546, figs. 1–3, pl. 93, figs. 6–9.
1969 *Tehuacana tehuacana*; Glaessner, p. R527.
2003 *Tehuacana tehuacana*; Karasawa and Kato, p. 138.
2009 *Tehuacana americana* (Rathbun, 1935); Armstrong et al., p. 753.
2008 *Tehuacana tehuacana*; Karasawa et al., p. 97.
2010 *Tehuacana tehuacana*; Schweitzer et al., p. 137.
2017 *Tehuacana americana* (Rathbun, 1935); Martínez-Díaz et al., p. 77, partim.
2018 *Tehuacana americana* (Rathbun, 1935); Vega et al., fig. 5.17.

Holotype. Tehuacana tehuacana, holotype UT BEG 21289.

Diagnosis. As for genus.

Description. Carapace rectangular, slightly wider than long, length about 95% width, widest at about half the distance posteriorly on carapace; moderately vaulted transversely and longitudinally.

Frontal margin with shallow axial notch; frontal margins slope posteriorly to either side of notch. Orbits shallow, with short, blunt intraorbital projection, outer-orbital angle weakly projecting; fronto-orbital width about 67% carapace width. Anterolateral margins convex, with four projections, short with narrowed tips, projections increasing in size posteriorly, not really forming spines, with granular tips. Posterolateral margin weakly convex, with strong posterolateral reentrants; posterior margin including reentrants about 73% carapace width, excluding reentrants about 27% carapace width; posterior margin including reentrants with granular rim, central part of posterior margin straight.

Mesogastric region with long anterior process, widened posteriorly into pentagonal area; protogastric regions wider than long, weakly inflated; hepatic regions triangular, lower than protogastric regions; urogastric region long, depressed; cardiac region wide anteriorly, narrowing posteriorly, pentagonal; intestinal region short, flattened, about 15% carapace length. Epibranchial regions composed of two elongate segments, one directed from last anterolateral projection anteriorly and axially; second directed obliquely posteriorly toward axis and terminating at edge of urogastric region. Remainder of branchial regions undifferentiated, inflated centrally at level of cardiac region and flattened posteriorly. All regions densely granular on highest points.

Buccal frame rectangular, slightly wider than long; branchiostegite granular. Sternites 1 and 2 narrow. Sternite 3 wide, anteriorly with transverse ridge; sternite 4 wide, long, with short episternal projections. Sternites 5 and 6 shorter and wider than sternite 4, directed laterally. No axial line on sternites 7 and 8.

Materials. Tehuacana tehuacana, holotype UT BEG 21289 (cast and photos); USNM PAL 794470, 795627–795629; MMNS IP-7399 (four specimens). Measurements (in mm) taken on *Tehuacana tehuacana* are presented in Table 4 and Supplementary Data Table 2.

Occurrence. Occurrences range in age from late Danian to Selandian (Paleocene), in Texas and Coahuila, Mexico (Table 5).

Table 4. Carapace measurements (in mm) taken on *Tehuacana tehuacana* Stenzel, 1944. FOW = fronto-orbital width; PW = posterior carapace width; length = maximum length of carapace, including rostrum/front; width = maximum width of carapace taken at the bases of the last anterolateral spines.

Specimen	Width	Length	FOW	PW	Intestinal length
KSU 873 cast of holotype	15.3	14.2	10.0	5.3	2.3
USNM PAL 795627	9.6	9.5		1.6	1.1
USNM PAL 795628	10.1	9.0	6.8	—	—
USNM PAL 795629	9.8	—	7.0	—	—
USNM PAL 794470	14.0	14.0	8.8	5.4	2.3
MMNS IP–7399.1	17.0	15.5	11.4		1.5
MMNS IP–7399.2	12.4	12.4	8.0	?	2.1
MMNS IP–7399.3	13.6	13.6	9.2	4.0	2.5
MMNS IP–7399.4	13.0	13.6	—	4.0	1.8

Remarks. Specimens of *Tehuacana tehuacana* look quite different with cuticle as compared with the mold of the interior of the holotype (Fig. 4). Whereas the holotype appears smoother (Fig. 4.1), the cuticle present in other specimens is granular, especially on the margins and raised areas of the carapace (Fig. 4.2–4.4). Specimens of *Tehuacana tehuacana* co-occur with *Hyphalocarcinus americanus* n. comb. in Texas and Mexico but appear to be much less common in Texas, on the basis of the collections studied herein.

Discussion

Palaeoxanthopsidae is already well known from the Late Cretaceous and early Cenozoic of Atlantic Ocean localities (Schweitzer, 2003; Luque et al., 2017; Schweitzer et al., 2018) (Supplementary Data Table 6). The radiation of modern heterotrematous crabs, of which Paleoxanthopsidae is one, began in the Paleocene, diversifying in both reef and siliciclastic environments (Schweitzer and Feldmann, 2023). The new referrals to Palaeoxanthopsidae reinforce this pattern. The oldest palaeoxanthopsid genera are known from the Late Cretaceous, i.e., *Palaeoxanthopsis* from Brazil, Mexico, and Puerto Rico (Rathbun, 1902; Vega et al., 2001; Schweitzer et al., 2008, 2018; Luque et al., 2017); the monotypic genera *Palaeoxantho* from the United States (Bishop, 1986) and *Remia* from Senegal (Remy and Tessier, 1954); Palaeoxanthopsidae sp. from Colombia (Luque et al., 2017) and Jamaica (Morris, 1993; Luque et al., 2017); and the monotypic genera *Lobulata* and *Rocacarcinus* from the late Maastrichtian and early Danian of Argentina (Glaessner, 1930; Feldmann et al., 1995; Schweitzer et al., 2004, 2018; Schweitzer, 2005) (Fig. 5). After the end-Cretaceous mass extinction, the family seems to have persisted during the Paleocene and Eocene across the northern Atlantic into Alabama and Texas in the United States (Rathbun, 1935; Armstrong et al., 2009), Mexico (Vega et al., 2001, 2008), Europe

Table 5. Occurrences of *Tehuacana tehuacana* Stenzel, 1944. Those with asterisks were studied from specimens, casts, or high- resolution images provided by museums. Non-asterisked entries are compiled from examination of published images only.

Current placement	Original placement	Material	Formation	Age	State	Reference
**Tehuacana tehuacana*	*Tehuacana tehuacana*	UT BEG 21289 holotype	Wills Point	Late Danian–Selandian	TX	Stenzel (1944)
**Tehuacana tehuacana*		MMNS IP–7399	Wills Point (Mexia Clay Member)	Late Danian	TX	Herein
**Tehuacana tehuacana*		USNM PAL 794470, 795627–629	Wills Point	Late Danian–Selandian	TX	Herein
Tehuacana americana	*Tehuacana americana*	IGM 9105	Rancho Nuevo Formation	Selandian	Coahuila, Mexico	Armstrong et al. (2009); Martinez-Díaz et al. (2017); Vega et al. (2018)

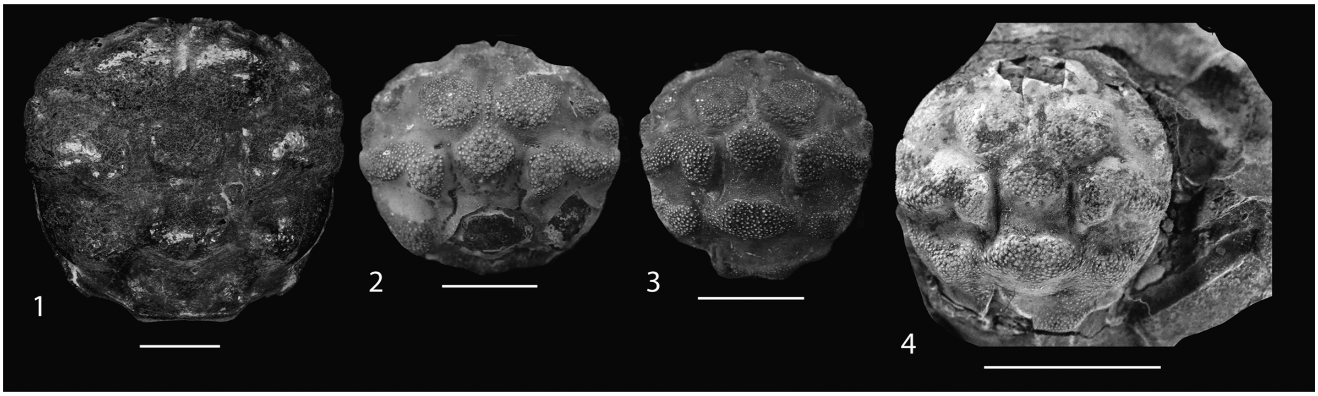

Figure 4. *Tehuacana tehuacana* Stenzel, 1944, dorsal carapace. (**1**) Holotype. (**2**) MMNS IP-7399.1. (**3**) MMNS IP-7399.2. (**4**) USNM PAL 794470. Scale bars = 5.0 mm.

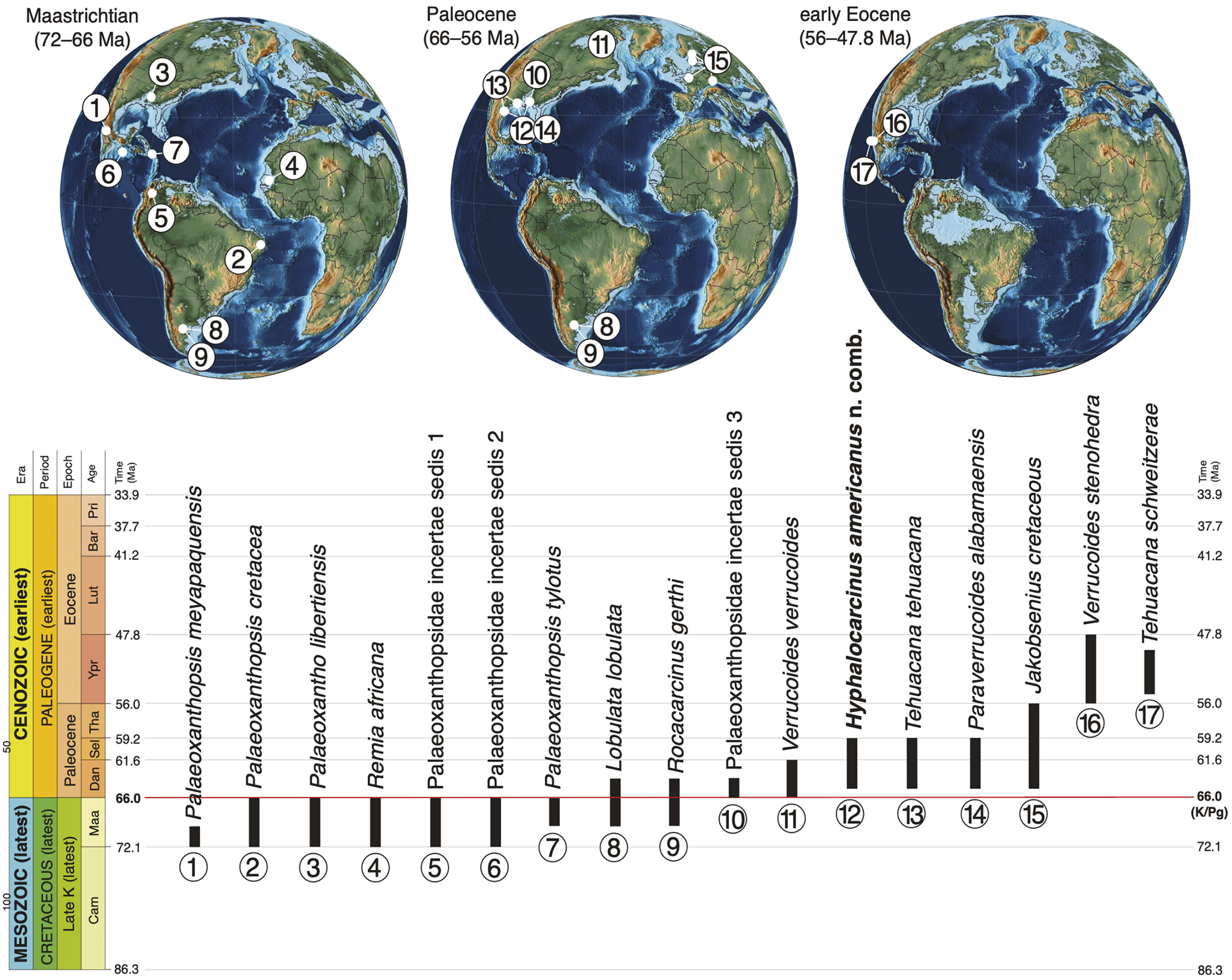

Figure 5. Stratigraphic ranges and paleobiogeographic distribution of palaeoxanthopsid crabs through the Late Cretaceous (Maastrichtian) and early Paleogene (Paleocene to early/middle Eocene). Base map after Scotese (2016).

(Segerberg, 1900; Robin et al., 2017; Miller et al., 2023), and Greenland (Collins and Rasmussen, 1992), possibly filling niches vacated by the end-Cretaceous extinction there, during which well over half of the Gulf Coastal genera became extinct (Schweitzer and Feldmann, 2023). The family disappeared during the Eocene, as indicated by the last known occurrences of palaeoxanthopsids, i.e., *Verrucoides stenohedra* Vega et al., 2001 and *Tehuacana schweitzerae* from the Ypresian of Mexico (Vega et al., 2001, 2008) (Fig. 5; Supplementary Data Table 6).

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Competing interests. The authors declare that they have no known competing interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement. Supplementary Data Tables 1–6 may be found at https://doi.org/10.5281/zenodo.15148347.

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