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Revision of and additions to early Cenozoic Brachyura (Crustacea: Dromiacea: Eubrachyura) from the USA

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Abstract

A new genus *Vincentdromia* accommodates *Vincentdromia americana* (Roberts, 1956) new combination. The age for the species is revised to earliest Eocene (Ypresian) from Eocene (Roberts, 1956) or Paleocene (Schweitzer et al., 2012), based upon reinterpretations of microfossil zones and updates to the International Chronostratigraphic Chart. *Eriosachila orri* Schweitzer and Feldmann, 2000, is reported for the first time from Eocene rocks of California. Newly referred specimens expand the range of morphological variation, the age, and the geographic range for *Stevea martini* Feldmann et al., 2014.

Key words: Dromiidae, Aethridae, Hexapodidae, Eocene, Paleocene

1. Introduction

Paleocene and Eocene crabs of North America are important in understanding the diversity of and the radiation among eubrachyuran crabs after the end-Cretaceous extinction (Schweitzer and Feldmann, 2023). This report adds to the generic diversity of early Cenozoic crabs, in addition to expanding the geographic and geologic range of some species. 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), documented here for both Dromiacea and Eubrachyura.

2. Materials and methods

Most specimens were whitened with ammonium chloride prior to photography and photographed using a Leica Z6 APO macroscope with PLANOPO 0.5xWD lens and SPOTFLEX digital camera, or a Leica M125C microscope with PLANOPO 1X lens and K3C camera, with LASX z-stacking software. Images were toned in Adobe Photoshop 23.1.0 prior to making figures in Adobe Illustrator 26.0.2. Lynn Dorwalt, Wagner Free Institute of Science supplied images of the holotype of *Dromiopsis americana*, unwhitened.

Measurements were taken with Mitutoyo analog calipers to the nearest tenth of a millimeter. Incomplete specimens were measured as half of the measurement where possible and then doubled.

Repositories and institutional abbreviations: United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM PAL); WFIS, Wagner Free Institute of Science, Philadelphia, Pennsylvania, USA.

3. Systematic Paleontology

Infraorder Brachyura Linnaeus, 1758
Section Dromiacea De Haan, 1833

Superfamily Dromioidea De Haan, 1833

Family Dromiidae De Haan, 1833

Included genera: Fossil taxa as in Schweitzer et al. (2012) and Schweitzer and Feldmann (2024), and extant taxa as in Poore and Ahyong (2023) and DecaNet (2024).

Diagnosis: as in Schweitzer et al. (2012).

Discussion: *Dromiopsis americana* Roberts, 1956, may be referred to Dromioidea based upon its carapace shape, differentiated anterolateral and posterolateral margins, lack of an augenrest, and all three main carapace grooves well-developed. Among the families of Dromioidea, *Dromiopsis americana* is best placed within Dromiidae, based upon its cervical groove weaker than the stronger branchiocardiac groove; deep, small, rimmed orbits; and suborbital spine visible in dorsal view. All of these are diagnostic for Dromiidae (Schweitzer et al., 2012). Sphaerodromiidae Guinot and Tavares, 2003, have similarly developed carapace grooves, but the lateral margins of members of this family are distinctly rimmed, whereas those of *D. americana* are not and instead have distinct, discrete spines. In Dynomenidae Ortmann, 1892, most of the suborbital margin is usually visible in dorsal view, and the orbital margins are long and sloped so as to be directed anterolaterally. Basinotopidae Karasawa et al., 2011, have anterolateral spines of similar arrangement as in *D. americana*, but the cervical groove is about the same depth as the branchiocardiac and extends onto the flank of the carapace, not seen in *D. americana*. Diaulacidae Wright and Collins, 1972, have much weaker carapace grooves and anterolateral spines than in *D. americana*. Xandarocarcinidae Karasawa et al., 2011, also have weaker carapace grooves than *D. americana,* and they have long outer-orbital spines, lacking in *D. americana*.

Genus *Vincentdromia* new genus

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Type species: *Dromiopsis americana* Roberts, 1956, by original designation.

Etymology: The genus name is derived from the Vincentown Formation, from which the specimens were collected, and *Dromia*, a common stem in the family. The gender is feminine.

Diagnosis: Carapace ovate-rectangular; slightly wider than long, longest at about half the distance posteriorly; suborbital spine blunt, visible in dorsal view; anterolateral margin with one spine excluding outer-orbital protuberance anterior to intersection of cervical groove, one at approximately the intersection of the cervical groove, and two between the intersections of the cervical and branchiocardiac grooves; spines sharp, with rounded cross-sections, well-separated from one another; cervical, post-cervical and branchiocardiac grooves deep; mesogastric and metagastric regions transversely inflated with medial interruption.

Discussion: *Dromiopsis americana* is herein removed from *Dromiopsis* Reuss, 1858 [imprint 1857]. Species of *Dromiopsis* are quite variable, thus, each species of the genus should be reevaluated for generic placement. The type species of *Dromiopsis*, *D. rugosus*, is granular overall; has deep cervical, branchiocardiac, and postcervical grooves, the former two of which extend deeply onto the flanks; spinose lateral margins; and a carapace that narrows distinctly posteriorly. *Dromiopsis americana* was referred to the genus because of its similarity to some of the smoother species referred to the genus, *D. laevior* Reuss, 1859, and *D. elegans* Reuss, 1858 [imprint 1857] (Roberts, 1956). *Dromiopsis laevior*, as illustrated by Reuss (1859, pl. 3, figs. 4–6) is very similar in all regards to *D. rugosa*, except that it lacks granulation. *Dromiopsis elegans* is also quite similar to these two species, except that it seems to be somewhat wider compared to the length than those two (Reuss, 1859, pl. 4, figs. 1, 2).

Dromiopsis americana differs from the type species of *Dromiopsis* in lacking overall granular ornamentation; in having discrete, distinct lateral spines instead of a regularly spinose anterolateral margin; in lacking a cervical groove extending onto the lateral flank, and in having a carapace that narrows only weakly posteriorly, so that the posterior end of the carapace is rectangular in shape. Thus, *D. americana* cannot remain in *Dromiopsis*.

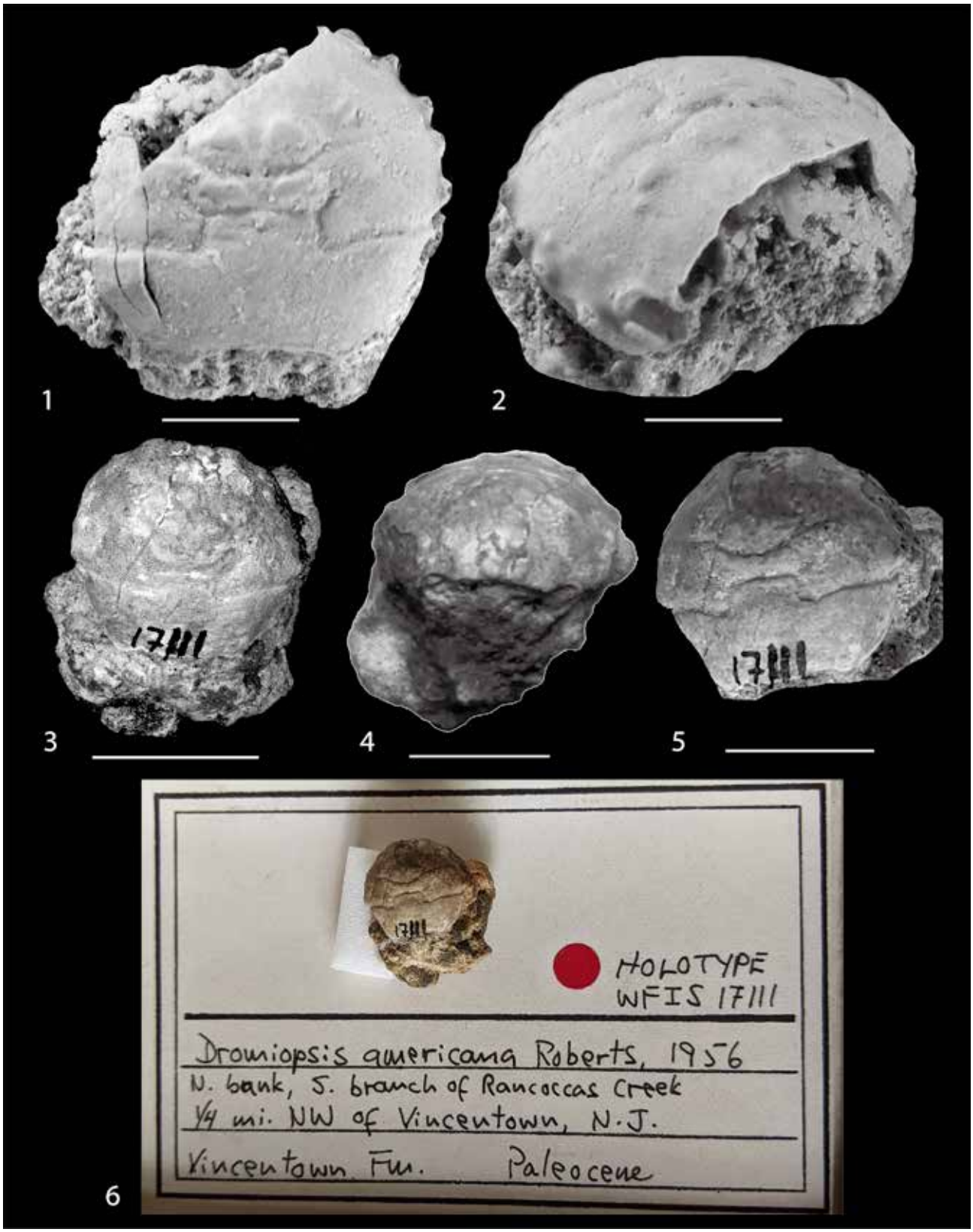

Fig. 1. ***Vincentdromia americana*** **(Roberts, 1956) new combination.** 1–2, USNM PAL 553514, dusted with ammonium chloride, dorsal carapace (1) and oblique frontal view showing orbit (2). 3–6, holotype WFIS 17111, dorsal carapace (3), anterior view showing edges of orbits (4), oblique view showing carapace grooves (5), and specimen with label (6). Scale bars = 5 mm.

Dromilites americana is most similar to species of *Quinquerugatus* Franţescu et al., 2010, *Torodromia* Artal et al., 2022, and *Stimdromia* McLay, 1993, in Dromiidae. The sole species of *Quinquerugatus* from the Eocene of South Carolina has discrete spines as seen in *D. americana*. However, the cervical groove is weak in *Quinquerugatus,* and *Quinquerugatus* has a posterior spine, posterior to the intersection of the branchiocardiac groove with the lateral margin, not present in *D. americana. Torodromia*, from Ypresian rocks of Spain, has anterolateral spines of varying sizes, such that the largest is in a position between the cervical and branchiocardiac grooves intersecting the lateral margin. In *D. americana*, the spines are all about the same size. In addition, *D. americana* has two spines between the intersection of the cervical and branchiocardiac grooves with the margins of the carapace, whereas *Torodromia* has only one. *Torodromia* has three anterolateral spines including the outer orbital spine anterior to the intersection of the cervical groove with the lateral margins, whereas *D. americana* has two. *Dromiopsis americana* has two distinct swellings on the posterior part of the mesogastric region, which do not appear in *Torodromia*. Species of *Stimdromia*, which range from late Eocene to Holocene, are characterized by strong anterolateral spines that are produced on a crispate rim, not present in *D. americana*.

Thus, *Dromiopsis americana* is placed within a new genus, *Vincentdromia*, resulting in *V. americana* new combination. The Paleocene and early Eocene were times of radiation for dromiacean crabs, well-documented in carbonates of Europe (Beschin et al., 2016; Artal et al., 2022; Miller et al., 2023; Schweitzer and Feldmann, 2023). The occurrence of *Vincentdromia americana* in earliest Eocene carbonates of North America substantiates and broadens this observed pattern.

Vincentdromia americana (Roberts, 1956) new combination (Fig. 1)

1956 *Dromiopsis americana* Roberts, 1956, p. 7.

1992 *Dromiopsis americana* Roberts; Collins and Rasmussen, p. 16.

2009 *Dromiopsis americana* Roberts; Van Bakel et al., p. 56.

2010 *Dromiopsis americana* Roberts; Schweitzer et al., p. 65.

2016 *Dromiopsis americana* Roberts; Robin et al., p. 6.

2023 *Dromiopsis americana* Roberts; Miller et al., p. 127.

Diagnosis: as for genus.

Description: Carapace ovate-rectangular, moderately vaulted transversely and longitudinally, slightly wider than long; front broken; orbits deep, small; upper-orbital margin rimmed, rim forming small outer-orbital protuberance; sub-outer-orbital spine long, blunt, clearly visible in dorsal view; anterolateral margin with one spine excluding outer-orbital protuberance anterior to intersection of cervical groove, one approximately at the intersection of the cervical groove, and two between the intersections of the cervical and branchiocardiac grooves; spines sharp, with rounded cross-sections, well-separated from one another; first and second spines directed anterolaterally; third and fourth spines directed laterally. Posterolateral margin entire, weakly convex; posterior margin broadly concave.

Mesogastric region widened posteriorly, transversely inflated, interrupted axially; protogastric and hepatic regions confluent, with two swellings arranged into an arc just lateral to mesogastric swelling. Cervical groove deep axially, weakening laterally, not extending onto flanks. Metagastric region transversely inflated, with axial interruption, short. Urogastric region short, rectangular. Postcervical groove only developed axially. Cardiac region flattened, triangular. Branchiocardiac groove deepest of three major grooves, very deep laterally and weakening slightly axially, extending onto flank. Epibranchial and remaining branchial regions not well-ornamented. Entire carapace surface covered by densely and evenly spaced punctae.

Measurements: Measurements (in mm) taken on USNM PAL 553514: maximum carapace width, 15.2; carapace length, >12; fronto-orbital width, 10.2.

Material examined: Holotype WFIS 17111 (images only); USNM PAL 553514.

Occurrence: North of Vincentown, New Jersey; Vincentown Formation, composed of carbonate sand (Roberts, 1956). The Vincentown Formation was referred to NP9 of Martini (1971) by Bybell and Self-Trail (1994), of late Paleocene age. A recent update of

the zones of Martini (1971) correlates NP9 with CNP11 of Agnini et al. (2014) and Raffi et al. (2016). CNP11 was placed at 55–56 my, which they considered latest Paleocene (Thanetian) (Raffi et al., 2016). The most recent International Chronostratigraphic Chart places 55-56 mya as very earliest Eocene in age, basal Ypresian (Cohen et al. 2103, ICC chart 2023/09).

Discussion: The holotype WFIS 17111 of *Vincentdromia americana* new combination and the referred specimen from the USNM differ in their superficial appearance. The holotype appears to be a mold of the interior of the carapace and lacks anterolateral spines either due to erosional or cuticle loss (Fig. 1.3–1.5). Specimen USNM PAL 553514 retains some cuticle and has discrete, sharp spines (Fig. 1.1, 1.2). However, the deep axial cervical groove, well-marked post-cervical groove, and deep branchiocardiac groove are nearly identical in the two specimens, as is the rectangular shape of the posterior carapace. The holotype is missing most of the frontal area but has outer edges of the orbits in a similar position as on the USNM specimen (Fig. 1.4). It is well-documented that specimens can appear very different with and without cuticle preservation (Schweitzer et al., 2024). Both were collected from the Vincentown Formation north of Vincentown, New Jersey, USA. All of these features suggest that the specimens are conspecific, but in differing states of preservation, so for now, we refer both to *V. americana*.

Roberts (1956) originally reported that the Vincentown Formation was Eocene in age, but he noted the presence of what he considered Paleocene and Eocene decapod faunal elements.

At the time of publication of Schweitzer et al. (2012) it was considered Paleocene, but as noted above, the age of the Vincentown Formation, and therefore, *Vincentdromia americana*, now appears to be earliest Eocene in age.

Section Eubrachyura de Saint Laurent, 1980
Superfamily Aethroidea Dana, 1851
Family Aethridae Dana, 1851

Genus *Eriosachila* Blow and Manning, 1996

Included species: as in Schweitzer et al. (2010) and DecaNet (2024).

Diagnosis: as in Schweitzer and Feldmann (2019).

Discussion: Species of *Eriosachila* are well-known from North America and the west coast specifically (Schweitzer and Feldmann, 2000, 2019). The specimen here referred to *E. orri* Schweitzer and Feldmann, 2000, is a member of the genus based upon its hexagonal shape, inflated regions, weakly projecting front, and anterolateral and posterolateral margins with blunt projections. The genus has already been reported from Eocene rocks of Baja California Sur, Oregon, and Washington, so an occurrence in California is unsurprising.

***Eriosachila orri* Schweitzer and Feldmann, 2000 (Fig. 2)**

1973 *Zanthopsis rathbunae* Kooser and Orr, 1973, p. 1045.

2000 *Eriosachila orri* Schweitzer and Feldmann, p. 239.

2010 *Eriosachila orri* Schweitzer and Feldmann; Schweitzer et al., p. 85.

Diagnosis: Ovate carapace narrowing posteriorly, with six large domed swellings; anterolateral margin with three blunt projections, posterolateral margin with two projections; blunt projections at posterolateral corners (adapted from Schweitzer and Feldmann, 2000, p. 239).

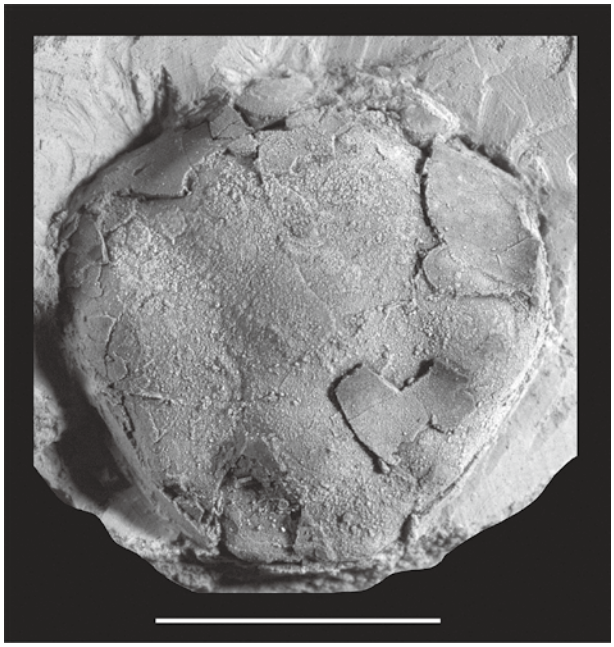

Fig. 2. *Eriosachila orri* Schweitzer and Feldmann, 2000, USNM PAL 372711, dorsal carapace. Scale bar = 5 mm.

Description of material: Carapace about as long as wide, length about 97% maximum width, obovate, narrowing posteriorly, maximum width about 40% the distance posteriorly; moderately vaulted transversely and longitudinally. Only small amounts of cuticle remain, no evidence of ornamentation on it.

Front about 33% carapace width, possibly with axial notch; orbits shallow, circular, directed forward, fronto-orbital width about 60% carapace width. Anterolateral margins not well preserved, no evidence of spines or projections; posterolateral margin nearly straight, with weak protuberance from branchial swelling about two-thirds the distance posteriorly; posterior margin rimmed, straight.

Protogastric regions broadly and weakly inflated. Hepatic regions flattened; mesogastric region with long anterior process between protogastric regions, widening posteriorly into rhomboid-shaped region; urogastric region depressed, short; cardiac region moderately inflated, rounded triangular; intestinal region flattened. Branchial regions with two swellings; anterior-most swelling larger, just posterior to anterolateral corner, broad, spherical; second swelling weaker, smaller, positioned along posterolateral margin.

Measurements: Measurements (in mm) taken on the carapace of USNM PAL 372711: maximum carapace width, 10.4; carapace length, 10.1; fronto-orbital width, 6.2; frontal width, 3.4; posterior width, 3.3; length to position of maximum width, 3.8.

Material examined and occurrence: USNM PAL 372711, Vacaville Shale, Ypresian, Solano County, California, UCMP locality V71128 (originally 3573) (UCMP Locality Search).

Discussion: M. J. Rathbun, on the label accompanying the specimen, identified the specimen as *Hepatiscus* sp. nov. *Hepatiscus* is also a member of Aethridae but is characterized by a smooth carapace that narrows considerably posteriorly. The new specimen is better accommodated in *Eriosachila orri*. The specimen is rather incompletely preserved such that the margins are not well-exposed. Thus, it is difficult to confirm the presence of anterolateral and posterolateral projections. However, all of the other features of the carapace fit the diagnosis for *E. orri*. Because the specimen is incompletely preserved and was found close to the geographic and within the geologic range of *E. orri*, it is referred to that species.

The type material of *Eriosachila orri* was collected from the Lookingglass Formation of Oregon (Kooser and Orr, 1973) and a referred specimen was collected from the Tenmile Member of that formation (Schweitzer and Feldmann, 2000). The Tenmile Member is referable to coccolith zones CP 10 and 11, including the boundary between them of 52.8 Ma (Wells et al., 2000), now placed in the Ypresian (Cohen et al., 2013; Raffi et al., 2016). The specimen herein referred to *E. orri* is also Ypresian in age, from California. Thus, the geographic range for the species is extended south but the stratigraphic range is not extended.

Superfamily Hexapodoidea Miers, 1886
Family Hexapodidae Miers, 1886
Genus *Stevea* Manning and Holthuis, 1981

Stevea martini **Feldmann, Schweitzer, and Portell, 2014 (Fig. 3)**

2014 *Stevea martini* Feldmann, Schweitzer, and Portell, p. 142, pl. 3.

Description of material: Carapace wider than long, length about 64 percent width, rounded rectangular, moderately vaulted longitudinally, flattened transversely; granular overall, granules more densely spaced axially, granules smaller and sparser along anterior margin; surface punctate overall between granules.

Front not preserved. Orbits circular, directed forward, with dense double row of granules forming upper orbital rim, granules and rim weaker on lower orbital margin; fronto-orbital width about 52 percent maximum carapace width. Anterolateral and posterolateral margins confluent, convex, granular rim well-developed anteriorly; posterolateral reentrant well-developed; posterior margin straight; fronto-orbital width about 79 percent posterior width; posterior width about 68% carapace width.

Epigastric regions small, weakly inflated, square. Protogastric regions triangular, bounded laterally by deep groove, not well-differentiated from mesogastric region axially on cuticle, better marked on internal mold; mesogastric with long anterior process, widening posteriorly. Urogastric region very short, deep;

cardiac region trilobate, each apex rounded, two lobes positioned next to one another axially, third directed posteriorly. Urogastric region bounded by deep groove, groove weaking as it bounds cardiac region, with small swelling in groove lateral to anterior cardiac region. Hepatic region not well-differentiated from branchial regions; epibranchial region weakly defined as an oblique, broadly but weakly inflated area.

Male sternites 1–2 fused, suture a granular ridge, sternite 1 triangular, flexed toward dorsal carapace; sternite 2 wider than long, with transverse row of granules parallel to suture 2; sternite 3 wider than long, with short triangular lateral projections; sternite 4 longest of all sternites with anterolateral projections; sternites 1–4 finely granular; sternites 5–7 coarsely granular except in pleonal cavity; sternites 5–7 each wider than long, directed laterally, anterior and posterior margins more or less parallel. Sternopleonal cavity deep, extending to anterior edge of sternite 4; sternal sutures 4/5, 5/6, and 6/7 interrupted, cavity at sternite 6 about 23 percent maximum width of sternum. Male pleonal somite 2? narrow.

Female sternum with sternites 4–7 similar in shape and ornamentation to those of male; large circular gonopore situated just posterior to axial termination of sternal suture 5/6; pleonal cavity wider than that of male, about 36% maximum width of sternum.

Measurements: Measurements (in mm) on specimens of *Stevea martini* are presented in Table 1.

Material examined: USNM PAL 795630–33.

Occurrence: Paleocene (Selandian), Midway Group, Wills Point Formation, 7 miles northwest of Streetman, Freestone Co., Texas, on Highway 7 (Davidson, 1966, p. 213).

Discussion: The new specimens are very similar to the holotype and paratype of *Stevea martini*. They have a granular, rectangular carapace and a beaded anterolateral and posterolateral rim, diagnostic for the species, and the sterna are similar in shape and in possessing granular ornamentation (Feldmann et al., 2014). The new specimens provide new information, adding to our knowledge of the species. Specimen USNM PAL 795633 is known from only a mold of the interior and lacks cuticle, showing the notable difference between specimens with and without cuticle (Fig. 3.7). Specimens USNM PAL 795630 and 795632 show slight differences in ornamentation, with USNM PAL 795632 having slightly smaller, more densely spaced carapace granules (Fig. 3.1). USNM PAL 795632 retains a male sternum (Fig. 3.2), which is narrower than that of the female, known from the holotype. USNM PAL 795630 confirms the placement of the large, ovate gonopores in females (Fig. 3.4).

The type material of *Stevea martini* was collected in Alabama from the Pine Barren Member of the Clayton Formation considered as Danian in age based upon ostracods (Smith, 1978) and foraminiferans (Fluegeman et al., 1990). The specimens reported here were collected from slightly younger rocks of the Selandian Wills Point Formation in Texas, extending the stratigraphic and geographic range, albeit marginally, for the species.

Table 1. Measurements (in mm) taken on specimens of *Stevea martini* Feldmann et al. (2014). W = carapace width; L = carapace length; FOW = fronto-orbital width; PW = posterior width; St L = length of sternites 3–7; St W = width of sternum.

	W	L	FOW	PW	St L	St W	Sex
USNM PAL 795632	12.6	~8	5.9	-	6.5	9.2	male
USNM PAL 795633	13	8.3	7.2	4.5			?
USNM PAL 795631	10.3	6.8	5.4	6.9			male
USNM PAL 795630					>5.4	9.8	female

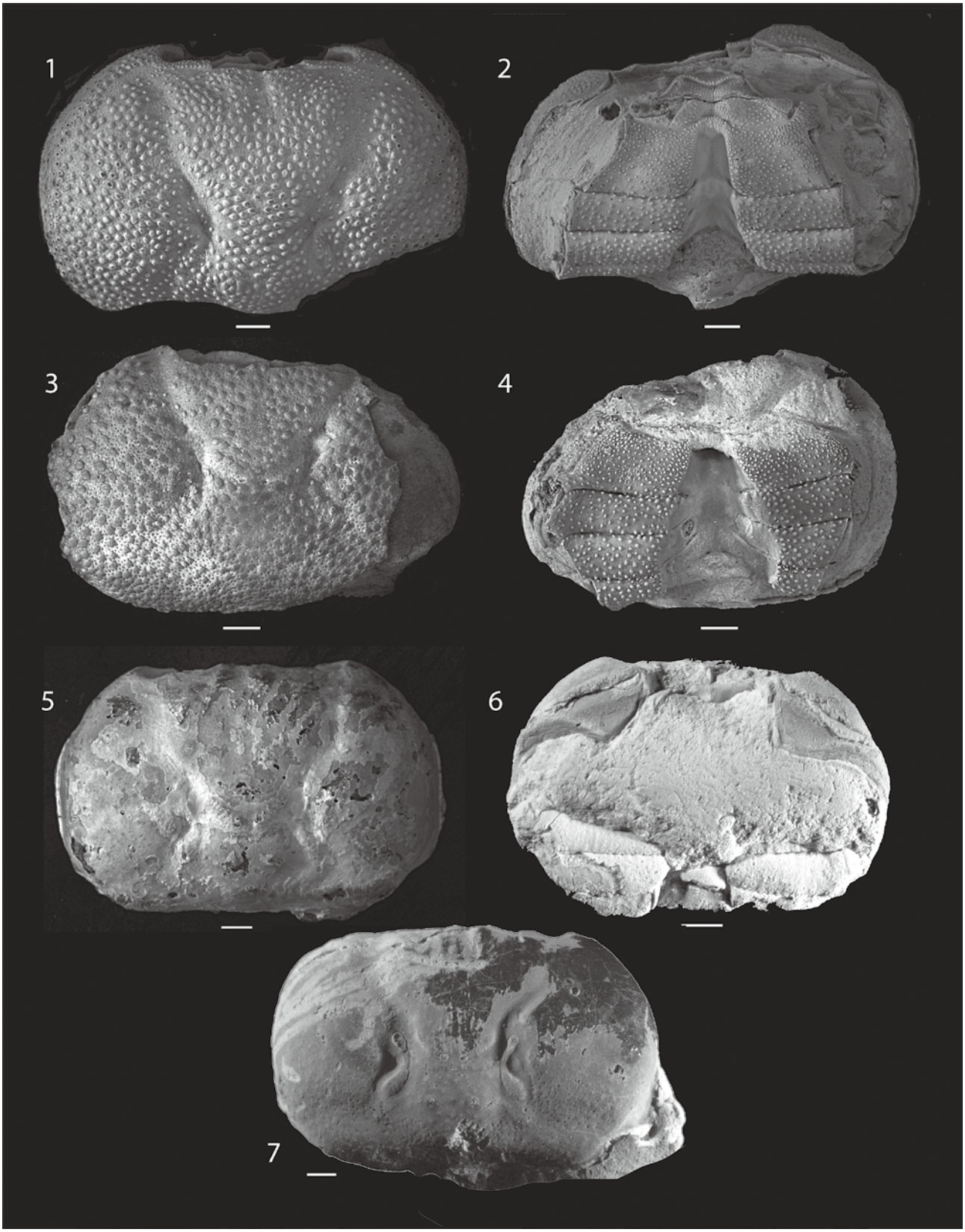

Fig. 3. ***Stevea martini*** **Feldmann, Schweitzer, and Portell, 2014**, dusted with ammonium chloride. 1–2, USNM PAL 795632, dorsal view with fine granules (1) and ventral view of male sternum (2); 3–4, USNM PAL 795630, dorsal carapace with coarse granules (3) and female sternum with clearly exposed gonopores (4); 5–6, USNM PAL 795631, dorsal view of specimen missing cuticular layers (5) and ventral view of posterior sternum and male pleonal somites (6); USNM PAL 795633, mold of the interior, with right posterolateral reentrant well-exposed. Scale bars = 1 mm.

4. Acknowledgements

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