

Crabs (Decapoda, Brachyura) from the lower Paleocene of Alabama, USA

R.M. Feldmann, C.E. Schweitzer & R.W. Portell

Feldmann, R.M., Schweitzer, C.E. & Portell, R.W. Crabs (Decapoda, Brachyura) from the lower Paleocene of Alabama, USA. *In*: Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M. & Van Bakel, B.W.M. (eds.), Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geologica*, **147**: 135-151, 2 figs., 2 tables, 3 pls., Leiden, October 2014.

Rodney M. Feldmann, Department of Geology, Kent State University, Kent, Ohio 44242, USA (rfeldman@kent.edu); Carrie E. Schweitzer, Department of Geology, Kent State University at Stark, 6000 Frank Ave NW, North Canton, Ohio 44720, USA (cschweit@kent.edu); Roger W. Portell, Division of Invertebrate Paleontology, Florida Museum of Natural History, 1659 Museum Rd., University of Florida, Gainesville, Florida 32611, USA (portell@flmnh.ufl.edu).

Key words – Retroplumidae, Hexapodidae, Gulf Coast, systematics, new species.

The present record of two species of brachyurous decapod crustaceans, *Costacopluma grayi* Feldmann & Portell, 2007 and *Stevea martini* sp. nov., from the lower Paleocene Pine Barren Member (Clayton Formation) in south-central Alabama, constitutes an extension of the range of the former and the sole occurrence of the latter. Previously, *C. grayi* was described from the middle Eocene Tallahatta Formation in Alabama. *Stevea martini* sp. nov. constitutes only the second species of the genus and the sole fossil occurrence known to date.

Contents

Introduction	135
Occurrence, stratigraphy and depositional setting	135
Systematic palaeontology	136
Acknowledgements	144
References	144

Introduction

Decapod crustaceans from the lower Paleocene Clayton Formation are quite rare. Cope *et al.* (2005) recorded *Hoploparia tennesseensis* Rathbun *in* Wade, 1926, *Linuparus canadensis* (Whiteaves, 1885), *Mesostylus* *sensu lato*, cf. *M. mortoni* (Pilsbry, 1901), *Paguristes johnsoni* Rathbun, 1935 and *Paguristes* sp. from a small exposure of this formation in southern Illinois. These occurrences represented the first notice of decapods from that unit to our knowledge. Thus, the presence of two other species of decapods from this formation is noteworthy. The purpose of the present work is to record the second occurrence of the genus *Costacopluma* Collins & Morris, 1975 from Alabama and the first occurrence of *Stevea* Manning & Holthuis, 1981 in the fossil record.

Occurrence, stratigraphy and depositional setting

Fourteen well-preserved carapaces of *Costacopluma grayi* Feldmann & Portell, 2007 and two carapaces of *Stevea martini* sp. nov. were surface collected during 2011-2013

near Mussel Creek in Lowndes County, south-central Alabama (Fig. 1). Here, over 8.5 m of exposed glauconitic sand, mud, and carbonate attributed to the lower Paleocene Pine Barren Member of the Clayton Formation unconformably overlies > 1.0 m of exposed Upper Cretaceous Prairie Bluff Chalk (see Savrda, 1993; Udgata, 2007). The crabs were found weathered from near the top of the approximately 6.0 m section of the Pine Barren Member exposed above road level adjacent to the creek. Udgata (2007, pp. 31, 32) provided a detailed measured section of this outcrop and identified seventeen distinct beds of variable thickness (informal units 14–30). The crabs originated from his uppermost informal units 19–30; however, none can be placed in any particular bed with confidence.

The Clayton Formation (Midway Group) occurs in an arc-shaped belt from southern Tennessee, to eastern Mississippi and into southeast Georgia (Bryan, 1987; Mancini *et al.*, 1989). A small exposure has also been recognised in southern Illinois (Cope *et al.*, 2005). In central Alabama, the unit is divided into a lower (Pine Barren) and an upper member (McBryde Limestone). The former consists of up to 46 m of alternating, unconsolidated to indurated beds of grey calcareous silt, glauconitic sands, and sandy limestone (mrddata.usgs.gov). The latter is comprised of up to 15 m of yellow to grey clayey limestone (mrddata.usgs.gov). Udgata (2007, p. 21) stated that the Clayton Formation in Alabama was primarily deposited, ‘in a passive-margin marine shelf setting under variable water depths and energy regimes controlled by sea-level dynamics and distance to the paleo-shoreline.’ Savrda (1993) and Udgata (2007) concluded that the Pine Barren Member of the Clayton Formation at the Mussel Creek locality represented a shallow-marine, shelf deposit.

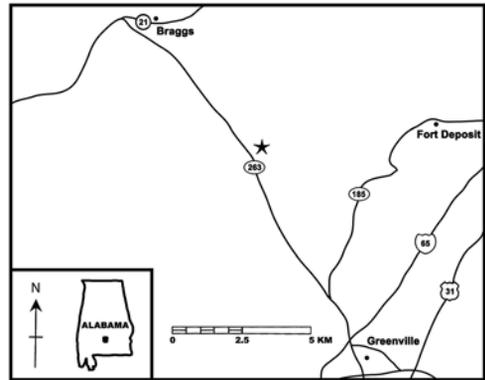


Fig. 1. Location map showing the site in Lowndes County, Alabama (denoted by star) from which *Costacopluma grayi* and *Stevea martini* sp. nov. were collected.

Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Brachyura Latreille, 1802

Section Heterotremata Guinot, 1977

Superfamily Retrolumoidea Gill, 1894

Family Retrolumidae Gill, 1894

Genus *Costacopluma* Collins & Morris, 1975

Type species – *Costacopluma concava* Collins & Morris, 1975, by original designation.

Included species – *Costacopluma australis* Feldmann, Casadío, Chirino-Gálvez & Aguirre-Urreta, 1995 (lower Paleocene [Danian], Argentina), *C. bifida* Collins, Higgs &

Cortitula, 1994 (Paleocene, Venezuela), *C. binodosa* Collins & Wienberg Rasmussen, 1992 (Campanian, West Greenland), *C. bishopi* Vega & Feldmann, 1992 (Maastrichtian, Mexico), *C. concava* Collins & Morris, 1975 (?Maastrichtian, Nigeria, India), *C. grayi* Feldmann & Portell, 2007 (Eocene, Alabama, USA), *C. mexicana* Vega-Vera & Perrilliat, 1989 (Maastrichtian, Mexico), *C. nordestina* Feldmann & Martins-Neto, 1995 (Paleocene, Brazil), *C. salamanca* Feldmann, Rodriguez, Martinez & Aguirre-Urreta, 1997 (lower Paleocene [Danian], Argentina), *C. senegalensis* (Remy in Gorodiski & Remy, 1959, as *Archaeopus*; Paleocene, Senegal), *C. squiresi* Nyborg, Vega & Filkorn, 2009 (Paleocene, California, USA) and *C. texana* Armstrong, Nyborg, Bishop, Ossó-Morales & Vega, 2009 (Paleocene, Texas, USA).

Diagnosis — Small rectangular to ovoid carapace, wider than long; carapace surface distinctly flattened and traversed by three elevated, granular ridges, the anteriormost being complete and typically biconvex forwards; posterior two ridges converging axially defining depressed, triangular to rectilinear, smooth mesobranchial region. Carapace flanks distinct, nearly perpendicular to dorsal surface and separated from it by beaded rim. Sternum with well-defined sternites; sternites 4-7 each with prominent transverse, beaded ridge. Transverse ridges also present on pleonal somites.

Stratigraphic range – Campanian (Late Cretaceous) to Eocene.

***Costacopluma grayi* Feldmann & Portell, 2007**

Pls. 1, 2.

2007 *Costacopluma grayi* Feldmann & Portell, p. 92, figs. 2A-E, 3A-D.

Type series – Holotype, a complete dorsal carapace, is UF 113749; paratypes are UF 113748, 113750, 114747, 115672 and 115793-115796, all 'collected from the upper lower to lower middle Eocene Tallahatta Formation behind Point A Dam, SW1/4, NE1/4, Sec. 35, T5N, R15E, River Falls Quadrangle, USGS 7.5' Series (1984), Covington County, Alabama.' (see Feldmann & Portell, 2007, p. 92) and deposited in the Invertebrate Paleontology Division of the Florida Museum of Natural History, University of Florida, Gainesville.

Additional material – UF 228989, 228990, 235556-235560 and 235562-235568, all from the lower Paleocene Pine Barren Member, Clayton Formation, SW1/4, NW1/4, Sec. 31, T12N, R14E, Fort Dale Quadrangle, USGS 7.5' Series (1981), Lowndes County, Alabama, and deposited in the Invertebrate Paleontology Division of the Florida Museum of Natural History, University of Florida, Gainesville.

Emended description – Sternum wider (9.1 mm) than long (5.5 mm); ovoid outline. Greatest width at posterior corner of sternite 5; length measured from anterior of sternite 3 to posterior margin of sternite 7. Sternite 8 not preserved. Sternite 3 straight anteriorly, bilobate posteriorly, axially depressed and fused to sternite 4. Sternite 4 broadening posteriorly, with prominent episternal projections extending almost to posterior of sternite 5. Deep axial depression of male extending to anterior margin of somite 4 and

continues widening posteriorly to sternite 7. Sternites 5 and 6 similar; sternite 5 with episternal projection extending almost to posterior of sternite 6; outer margins of sternites 6 and 7 broken. Sternal suture 3/4 straight, fused. Sutures 4/5, 5/6 and 6/7 extending to margin of axial depression. A narrow, longitudinal slit in the axial depression at level of crest of somite 6. Sternites 4-7 bearing prominent, sharp, beaded transverse crests paralleling posterior margin of sternites.

Male pleon poorly preserved, with transverse crests on at least somites 5 and 6. Telson apparently triangular.

Discussion – Feldmann & Portell (2007) described *Costacopluma grayi* on the basis of a suite of nine moderately well-preserved specimens collected from the Eocene Tallahatta Formation in southern Alabama. Although the dorsal carapace was well preserved, the sterna and pleons were not well represented. The venters of two male specimens exhibited parts of the sterna and pleons. Certainly, enough of the morphology of the specimens was available to recognise them as representing a new species.

Recently, additional specimens referable to *Costacopluma* were recovered from the lower Paleocene Pine Barren Member of the Clayton Formation in Alabama (Pls. 1, 2). These specimens also retain most, or all, of the dorsal carapace and, furthermore, they display well-preserved sterna. Although differing in age by an estimated 20 myr, the specimens are morphologically indistinguishable from the type series of *C. grayi* and, therefore, are referred to that species. Measurements of length, width, frontal width

Table 1. Measurements and ratios determined on *Costacopluma grayi* and morphologically similar species. L = maximum length; W = maximum width; FW = frontal width; FOW = fronto-orbital width; CW = cardiac width, L/W = length/maximum width; FOW/W = fronto-orbital width/maximum width; UF = Florida Museum of Natural History, University of Florida, Gainesville, Florida; CPBA = Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina; UnG = Departamento de Geociências, Universidade de Guarulhos, São Paulo, Brazil; * = approximate measurement. Previously published measurements from Feldmann & Martins-Neto (1995), Feldmann *et al.* (1997) and Feldmann & Portell (2007).

Catalogue number	L	W	FW	FOW	CW	L/W	FOW/W
<i>Costacopluma grayi</i>							
UF 113748	--	*6.2	--	4.8	--	--	0.77
UF 113749	>8.1	10.3	--	*6.6	--	>0.79	0.64
UF 113750	11.8	14.4	--	*8.8	--	0.82	0.61
UF 114747	*8.6	10.5	--	--	--	>0.82	--
UF 115672	>7.9	10.3	--	--	--	>0.77	--
UF 115793	>8.7	10.8	--	--	--	>0.81	--
UF 228989	8.2	11.4	1.2	7.6	4.8	0.72	0.67
UF 228990	>10.3	11.9	1.9	8.4	4.7	>0.87	0.71
<i>Costacopluma salamanca</i>							
CPBA 17376 holotype	14.8	17.3	--	9.5	--	0.86	0.56
CPBA 17372 paratype	>12.5	14.6	--	8.2	--	>0.86	0.56
CPBA 17373 paratype	15.0	17.6	--	9.8	--	0.85	-0.56
CPBA 17377 paratype	8.8	10.6	--	6.9	--	0.83	0.65
<i>Costacopluma nordestina</i>							
UnG IT-046	14.5	15.7	--	10.0	--	0.92	0.64

and fronto-orbital width demonstrate that overall size, as well as ratios of frontal dimensions to maximum width, fall well within the range determined for the type series. Comparison of the measurements of *C. grayi*, including the Clayton Formation specimens, with other morphologically similar species documents recognisable differences (Table 1).

Criteria cited in the diagnosis of the genus provide a broad spectrum of features that clearly distinguish *Costacopluma* from other genera within the Retroplumidae. These comparisons were articulated in Feldmann & Portell (2007) and will not be repeated here. Distinctions between species within the genus also are based upon a broad range of characters. Among these, general carapace outline, position of the widest part of the carapace, breadth of the transverse ridges, form of the rostrum and relative proportions of the front and fronto-orbital margin to maximum width of the carapace may be considered the most significant and most frequently cited points of comparison. Among these, general carapace outline is considered to be the least reliable. The cuticle of extant retroplumids is relatively thin, and we infer that extinct retroplumids also had such cuticle. In fact, fossil retroplumids commonly display distortion of the carapace consistent with thin, poorly calcified cuticle that may have been a result of compaction, which may have affected the outline in such a way that some specimens appear to be quadrate whereas others appear to be more ovoid. This deformation may also affect perception of the position of maximum width of the specimen. The deformity can make it appear that the maximum width is in the middle, in the anterior third, or the posterior third, whereas reconstruction of an undeformed carapace often shows that the maximum width was in an entirely different position. However, the nature of features on the dorsal surface of the carapace, such as ridges and concavities, do not deform in terms of their general width, granulation, or in whether they intersect one another, and provide a more reliable basis for interspecific comparison.

Among the species of *Costacopluma*, *C. salamanca* and *C. nordestina* are most closely similar to *C. grayi* in the configuration of the transverse ridges. These three species have ridges intermediate in width between those that have the narrowest ridges, *C. concava* and *C. senegalensis*, both from Africa, and the remaining species, from Texas, Mexico, California, Argentina and Greenland. The last-named lot share the character of having much broader transverse grooves and correspondingly narrower mesobranchial regions. Further, the posterior pair of transverse ridges on most of the species with broad ridges tends to be near parallel with one another. The consequence of this is that the ridges are less clearly conjoined axially or are not conjoined at all. Thus, the mesobranchial regions are not only narrower, but are also rectilinear rather than triangular.

The granular nature of the transverse ridges appears to be quite variable when inspecting illustrations of the various species. Although the size and density of the granules may vary, it seems that granulation is present wherever cuticle is preserved. Some specimens, such as *Costacopluma australis*, *C. bifida*, *C. bishopi*, *C. squiresi* and *C. texana* lack cuticle and exhibit no granulation.

The overall form of the transverse ridges varies, as noted above. There seems to be a biogeographic pattern of variation evident in the breadth and orientation of the ridges. *Costacopluma concava*, from the Maastrichtian of Nigeria (Collins & Morris, 1975) and India (Gaelani *et al.*, 1983) and *C. senegalensis* from the Paleocene of Senegal exhibit extremely narrow ridges, and the posteriormost two converge axially and are

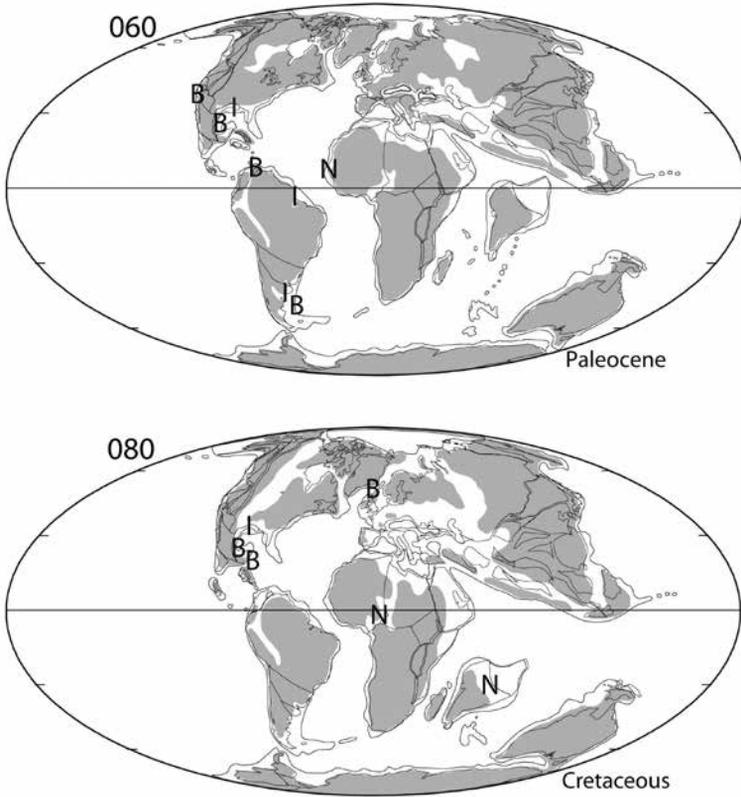


Fig. 2. Middle Late Cretaceous and middle Paleocene palaeogeographic maps (modified from Scotese, 2006), showing the approximate location of species of *Costacopluma*, identified by the width of dorsal carapace ridges (see Table 2). N = narrow width; I = intermediate in width; B = broad width.

Table 2. Species of *Costacopluma*; their age, geographic occurrence and relative width of their carapace ridges.

Species	Age	Geographic location	Width of carapace ridges
<i>Costacopluma australis</i>	Danian	Argentina	Broad
<i>C. bifida</i>	Paleocene	Venezuela	Broad
<i>C. binodosa</i>	Campanian	West Greenland	Broad
<i>C. bishopi</i>	Maastrichtian	Mexico	Broad
<i>C. concava</i>	?Maastrichtian	Nigeria, India	Narrow
<i>C. grayi</i>	Paleocene, Eocene	Alabama	Intermediate
<i>C. mexicana</i>	Maastrichtian	Mexico	Broad
<i>C. nordestina</i>	Paleocene	Brazil	Intermediate
<i>C. salamanca</i>	Danian	Argentina	Intermediate
<i>C. senegalensis</i>	Paleocene	Senegal	Narrow
<i>C. squiresi</i>	Paleocene	California	Broad
<i>C. texana</i>	Paleocene	Texas	Broad

joined axially, defining a distinctly triangular mesobranchial region. That same orientation of ridges is present in *C. salamanca* (Argentina), *C. nordestina* (Brazil) and *C. grayi* (Alabama, USA).

These three species, however, exhibit ridges that are intermediate in breadth. The remaining species have much broader transverse ridges, with the posterior two ridges tending to be more parallel to one another and defining a narrower, more quadrate mesobranchial region. There is no obvious temporal and little geographic relationship in form of the transverse ridges (Fig. 2). The Cretaceous forms are narrow and broad as are those in the Paleogene. The narrow ridges seem to be restricted to Africa and India, with no occurrence elsewhere. Broad and intermediate ridges extend along the entire western Atlantic coast and broad-ridged forms extend into Europe.

The genus clearly was not affected by the K/Pg extinction event (Fig. 2). The oldest species, *Costacopluma binodosa*, appeared in the Campanian (Late Cretaceous) of West Greenland, and additional species were present in Africa, India and Mexico during the Maastrichtian. Eight of the twelve species known to date are from Paleocene occurrences, and one of these, *C. grayi*, ranged into the Eocene. The genus persisted in the North Atlantic, proximal to the Chixculub impact area, from the Cretaceous into the Paleocene. With the exceptions of outliers in India and California, the genus can be thought of as having an Atlantic Basin distribution.

Superfamily Goneplacoidea MacLeay, 1838

Family Hexapodidae Miers, 1886

Genus *Stevea* Manning & Holthuis, 1981

Type species – *Hexapus williamsi* Glassell, 1938, by original designation.

Diagnosis – ‘Carapace [of female] 1/3 wider than long, subrectangular; posterolateral borders short, slightly convex; anterolateral borders converging anteriorly, passing below exorbital angle. Dorsal surface convex longitudinally; cervical and branchio-cardiac grooves present, faint; 2 round branchio-cardiac depressions. Front depressed, with concave border, widening distally. Eyes movable, cornea narrower than stalk. Mxp3 broad; endopod: ischium mesially expanded, merus flattened, carpus, propodus, dactylus slender, subcylindrical; exopod with flagellum. Female abdomen long, narrow; somite 1 free, somites 2-6 fused, with sutures still distinct on lateral sides, somite 5 with straight lateral margins, somite 6 long, narrow, subhexagonal. Stridulatory apparatus consisting of row of close-set striae. Sternal trenches absent. Chelipeds unequal, propodus of major cheliped large. Other pereopods short.’ (Guinot *et al.*, 2010, p. 285).

Discussion – The description above is focused primarily on characters retained on the carapace and, therefore, more likely to be preserved in the fossil record. The original description (Manning & Holthuis, 1981, p. 177) concentrated on characters of the appendages, reproductive parts and pleon. The illustrations of the species (Manning & Holthuis, 1981, fig. 38; taken from Glassell, 1938, pl. 35) conform to the description by Guinot *et al.* (2010), and further document placement of the Alabama specimens in *Stevea*. Overall form of the carapace of the Alabama specimens, presence of subtle cervical and branchiocardiac grooves, conformation of the eyes and front, as well as size, shape

and striae, comprising the stridulating device, are all consistent with the diagnosis of the genus.

Guinot *et al.* (2010) introduced a new genus, *Holthuissea*, to accommodate *Stevea cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, from the Eocene of northern Italy. The sole species within the new genus lacks cervical and branchiocardiac grooves, has a front that extends well beyond the orbits, rounded orbital margins, a sternum with a punctate surface, and a female pleon with somite 4 widest and tapering proximally and distally, terminating in a small telson. The stridulatory device is small, elevated and with unequal striae. None of these characters is present on specimens from the Paleocene of Alabama. Thus, this new form can be referred to *Stevea* with confidence.

***Stevea martini* sp. nov.**

Pl. 3.

Etymology – The trivial name recognises Mr George Martin, who discovered the specimens and donated them to the Florida Museum of Natural History.

Types – The holotype, UF 228988, and a single paratype, UF 235561, are deposited in the Invertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville.

Locality and horizon – Mussel Creek, SW1/4, NW1/4, Sec. 31, T12N, R14E, Fort Dale Quadrangle USGS 7.5' Series (1981), Lowndes County, Alabama, lower Paleocene, Pine Barren Member, Clayton Formation.

Diagnosis – Carapace with well-developed, beaded rim on anterolateral and posterolateral borders and smoothly rounded transition to flanks on lateral margin. Rostrum downturned with high-angle triangular termination with weak projection on tip; carapace surface densely covered by fine granules.

Description – Carapace small, rectilinear, much wider (11.1 mm) than long (5.3 mm); length about half carapace width; transversely and longitudinally flattened; regions obscure. Front narrow (1.6 mm), downturned, weakly sulcate when viewed from above resulting in slightly sinuous outline and with weakly projected tip when viewed from front. Orbits quadrate when viewed from above, entire, with beaded rims. Eyes with eyestalks equally broad proximally and distally, constricted mesially. Fronto-orbital margin narrow (3.9 mm), about 35 per cent maximum carapace width, about 56 per cent posterior width. Anterolateral margin smoothly convex to about mid-length, with finely beaded rim separating dorsal surface from nearly vertical flanks. Lateral margin straight, lacking beaded rim and curving ventrally onto flank as smooth arc. Posterolateral margin short, weakly concave, bearing weakly beaded rim. Posterior margin broad, apparently straight, margin broken, about 93 per cent maximum carapace width.

Cervical groove a parabolic arc, moderately well incised axially and becoming obscure, then disappearing as extending towards outer orbital corner. Branchiocardiac grooves weak, diverging posteriorly to define anterior margin of transversely ovoid,

weakly inflated cardiac region. A pair of circular gastric pits situated just postero-laterally to cervical groove. Surface of carapace with closely spaced granules. Where eroded, granules expose endocuticular layer.

Pterygostome weakly granular, with prominent ridge paralleling finely beaded inner margin, and swollen triangular stridulating device bearing about 15 striae oriented postero-laterally. Buccal frame quadrate, wider (2.9 mm) than long (1.5 mm), widening slightly posteriorly. Sternum broad with well-developed, serrated sutures 3/4, 4/5, 5/6, and 6/7 extending into, but not across, triangular axial depression. Axial depression extending nearly to anterior margin of sternite 4. Sternites 1-3 not preserved. Sternite 4 with straight front bounded laterally by two projections separated by sulcus. Lateral margins of sternite 4 sloping posterolaterally to terminate in long, slender episternal projection. Sternite 5 broadening slightly laterally and terminating in well-developed, narrow episternal projection. A small node forming pleonal locking device situated on anterior margin of sternite 5 near margin of axial depression. Sternite 6 similar to 5 but bearing large, circular genital opening axially. Sternite 7 poorly exposed, narrower than 6; sternite 8 not visible.

Female pleon and appendages not preserved.

Discussion – The diagnostic characters serve to distinguish *Stevea martini* sp. nov. from *S. williamsi*, the only other species within the genus. The former has a well-defined anterolateral rim, but one that is not as sharp and beaded as in the type species. The tip of the rostrum in *S. williamsi* is weakly biconcave rather than having straight elements extending to the tip. The carapace surface in the type species is coarsely, rather than finely, granular. In other respects, the two species are similar enough morphologically to warrant placement in the same genus. Van Bakel *et al.* (2006) reported an undescribed species of *Stevea* from northwest Belgium; however, B.W.M. van Bakel (pers. comm., November 2013) has now concluded that it is not referable to that genus.

Stevea martini sp. nov. fits all of the diagnostic criteria for the family listed by Schweitzer & Feldmann (2001, p. 331) in terms of carapace shape. They compiled these criteria in order to distinguish hexapods from other families with similarly shaped dorsal carapaces in fossils. Since that paper was published, four more extinct genera have been added to the family. Of these, *Bellhexapus* and *Holthuisia* fit all of the criteria, except that their fronto-orbital margins occupy the entire width of an arcuate frontal margin instead of partially occupying a straight frontal margin. *Eohexapus* fits all of the criteria except that its front narrows distally instead of widening and its position of maximum width is about one-third the distance posteriorly instead of just anterior to the postero-lateral reentrants. *Eurohexapus* is the most divergent from the 2001 criteria, having a fronto-orbital margin similar to that of *Bellhexapus* and *Holthuisia*, a trapezoidal carapace, and with maximum width occupying the middle one-third of the carapace. Interestingly, with the exception of trapezoidal carapace, none of these divergent features is shared by the other similarly shaped families to which the Hexapodidae was compared, namely the Chasmocarcinidae and Asthenognathidae. In addition, all of the new hexapodid genera, in spite of their differences, do exhibit most of the criteria on the original 2001 list. Thus, the list seems to be generally useful in distinguishing similarly shaped fossil taxa in the Hexapodidae.

Guinot *et al.* (2010) noted that the type specimen of *Stevea williamsi* from Guatemala

and a subsequent specimen from Mexico were considered to be males by Manning & Holthuis (1981), following the initial gender determination of the holotype by Glassell (1938). This resulted in misinterpretation of the second specimen referred to *S. williamsi* by Schweitzer & Feldmann (2001) and questioning of the identification by Guinot (2006). Guinot *et al.* (2010) concluded that the Mexican specimen was a female of *Paeduma cylindraceum* (Bell, 1859). The female of *Stevea* bears a narrow pleon residing within a narrow, triangular axial depression. *Stevea martini* sp. nov. conforms to that configuration, and its gender is well documented by large circular oviducts on the sixth sternite and pleonal-locking nodes on the fifth sternite.

Paeduma and *Thaumastoplax* are genera that are similar in overall form to *Stevea*; however, the greatest distinction is that neither of the aforementioned genera exhibit stridulating structures. With the reassignment of *Stevea cesarii* to *Holthuisia*, *S. martini* sp. nov., from the lower Paleocene of Alabama, represents the oldest fossil representative of the genus.

Acknowledgements

This contribution is dedicated to Dr Pál Müller, good friend and colleague of ours for three decades. His contributions to the palaeontology of European decapods have been enormous. George Martin collected the above-mentioned Mussel Creek crabs and kindly donated them to the Florida Museum of Natural History, University of Florida. J. Bryan (Northwest Florida State College, Niceville) and S. Roberts (Florida Museum of Natural History, University of Florida) provided several critical references regarding the geology of southern Alabama and drafted Figure 1, respectively. Constructive reviews by C. McLay (Canterbury University, Christchurch, New Zealand) and Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart, Germany), as well as editorial comments by John W.M. Jagt (Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands) substantially improved the manuscript. This is University of Florida Contribution to Paleobiology 665.

References

- Armstrong, A., Nyborg, T., Bishop, G.A., Ossó-Morales, A. & Vega, F.J. 2009. Decapod crustaceans from the Paleocene of central Texas, USA. *Revista Mexicana de Ciencias Geológicas*, **26**: 745-763.
- Bell, T. 1859. Description of a new genus of Crustacea, of the family Pinnotheridae; in which the fifth pair of legs are reduced to an almost imperceptible rudiment. *Journal of the Proceedings of the Linnean Society of London (Zoology)*, **3**: 27-29.
- Beschin, C., Busulini, A., De Angeli, A. & Tessier, G. 1994. I crostacei eocenici della Cava «Boschetto» di Nogarole Vicentino (Vicenza – Italia settentrionale). *Lavori – Società Veneziana di Scienze Naturali*, **19**: 159-215.
- Bryan, J.R. 1987. *Macrofaunal changes across the Cretaceous-Tertiary boundary, Braggs, Lowndes County, Alabama*. Unpublished M.Sc. thesis, University of Florida, Gainesville, Florida: 101 pp.
- Collins, J.S.H., Higgs, R. & Cortitula, B. 1994. A new crab, *Costacopluma bifida* (Crustacea, Decapoda) from the Palaeocene of Venezuela. *Bulletin of the Mizunami Fossil Museum*, **21**: 29-34.
- Collins, J.S.H. & Morris, S.F. 1975. A new crab *Costacopluma concava* from the Upper Cretaceous of Nigeria. *Palaeontology*, **18**: 823-829.
- Collins, J.S.H. & Wienberg Rasmussen, H. 1992. Upper Cretaceous-Lower Tertiary decapod crustaceans from West Greenland. *Grønlands Geologiske Undersøgelse, Bulletin*, **162**: 1-46.

- Cope, K.H., Utgaard, J.E., Masters, J.M. & Feldmann, R.M. 2005. The fauna of the Clayton Formation (Paleocene, Danian) of southern Illinois: a case of K/P survivorship and Danian recovery. *Bulletin of the Mizunami Fossil Museum*, **32**: 97-108.
- Feldmann, R.M. & Portell, R.W. 2007. First report of *Costacopluma* Collins & Morris, 1975 (Decapoda: Brachyura: Retroplumidae) from the Eocene of Alabama, U.S.A. *Journal of Crustacean Biology*, **27**: 90-96.
- Feldmann, R.M. & Martins-Neto, R.G. 1995. *Costacopluma nordestina* n. sp. (Decapoda: Retroplumidae) from the Maria Farinha Formation (Paleocene) of Brazil. *Journal of Paleontology*, **69**: 610-611.
- Feldmann, R.M., Rodriguez, M.F., Martinez, G.A. & Aguirre-Urreta, M. 1997. *Costacopluma salamanca* new species (Decapoda, Retroplumidae) from the Salamanca Formation (Danian) of Patagonia, Argentina. *Journal of Paleontology*, **71**: 125-130.
- Feldmann, R.M., Casadio, S., Chirino-Galv ez, L. & Aguirre Urreta, M. 1995. Fossil decapod crustaceans from the Jag uel and Roca formations (Maastrichtian-Danian) of the Neuqu en Basin, Argentina. *The Paleontological Society Memoir*, **43**: 1-22.
- Gaelani, M., Nicera, A., Silva, I.P., Feis, E., Garzanti, E. & Tintori, A. 1983. Upper Cretaceous and Paleocene in Zanskar Range (NW Himalaya). *Revista Italiana Paleontologia e Stratigrafia*, **89**: 81-118.
- Gill, T. 1894. A new bassalian type of crabs. *American Naturalist*, **28**: 1043-1045.
- Glassell, S. 1938. New and obscure decapod Crustacea from the west American coasts. *Transactions of the San Diego Society of Natural History*, **8**: 411-454.
- Gorodiski, A. & Remy, J.-M. 1959. Sur les D ecapodes  oc enes du S en egal occidental. *Bulletin de la Soci et  g eologique de France*, (**7**)**1**: 315-319.
- Guinot, D. 1977. Propositions pour une nouvelle classification des Crustac es D ecapodes Brachyours. *Comptes Rendus hebdomadaires des S ances de l'Acad mie des Sciences Paris*, **D285**: 1049-1052.
- Guinot, D. 2006. Rediscovery of the holotype of *Paeduma cylindraceum* (Bell, 1859) and description of a new genus of Hexapodidae (Decapoda, Brachyura). *Zoosystema*, **28**: 553-571.
- Guinot, D., De Angeli, A. & Garassino, A. 2010. *Holthuisia*, a new genus from the Eocene of Italy (Decapoda, Brachyura, Hexapodidae): 283-304. In: Fransen, C.H., De Grave, S. & Ng, P.K.L. (eds.), *Studies on Malacostraca, Lipke Bijdeley Holthuis Memorial Volume*. Koninklijke Brill NV, Leiden.
- Latreille, P.A. 1802-1803. *Histoire naturelle, g n rale et particuli re, des crustac es et des insectes*, **3**: 1-468. F. Dufart, Paris.
- MacLeay, W.S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith, A., *Illustrations of the Annulosa of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa."*: 53-71. Smith, Elder and Company, London.
- Mancini, E.A., Tew, B.H. & Smith, C.C. 1989. Cretaceous-Tertiary contact, Mississippi and Alabama. *Journal of foraminiferal Research*, **19**: 93-104.
- Manning, R.B. & Holthuis, L.B. 1981. West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, **306**: 1-379.
- Miers, E.J. 1886. Report on the Brachyura collected by H.M.S. Challenger during the years 1873-1876: 1-362. In: Wyville Thomson, C. & Murray, J. (eds.), *Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873-1876, Zoology*. Johnson Reprints, New York.
- mrdata.usgs.gov/geology/state/sgmc-unit.php?unit=ALPNcl;1. Midway Group; Clayton Formation. United States Geological Survey (accessed October 23, 2013).
- Nyborg, T., Vega, F.J. & Filkorn, H.F. 2009. First described species of *Costacopluma* (Crustacea; Brachyura: Retroplumidae) from the Pacific slope, Paleocene of California, USA. *Bolet n de la Sociedad Geol gica Mexicana*, **61**: 203-209.
- Pilsbry, H.A. 1901. Crustacea of the Cretaceous formation of New Jersey. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **53**: 111-118.
- Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America, Special Paper*, **2**: 1-160.
- Savrda, C.E. 1993. Ichnosedimentologic evidence for a noncatastrophic origin of Cretaceous-Tertiary boundary sands in Alabama. *Geology*, **21**: 1075-1078.

- Schweitzer, C.E. & Feldmann, R.M. 2001. Differentiation of fossil Hexapodidae Miers (Decapoda: Brachyura) from similar forms. *Journal of Paleontology*, **75**: 330-345.
- Scotese, C.R. 2006. Plate tectonic maps and continental drift animations (www.scotese.com).
- Udgata, D.B.P. 2007. *Glauconite as an indicator of sequence stratigraphic packages in a lower Paleocene passive-margin shelf succession, central Alabama*. Unpublished M.Sc. thesis, Auburn University, Auburn, Alabama: 109 pp.
- United States Department of the Interior Geological Survey. 1981. Fort Dale Quadrangle, Alabama. 7.5 Minute Series (Topographic).
- Van Bakel, B.W.M., Fraaije, R.H.B. & Jagt, J.W.M. 2006. Synopsis of Cenozoic decapod crustaceans from Belgium. In: Vega, F.J. (ed.), Special Section. Systematics and paleobiology of fossil Crustacea. *Revista Mexicana de Ciencias Geológicas*, **23**: 370-374.
- Vega, F.J. & Feldmann, R.M. 1992. Occurrence of *Costacopluma* (Decapoda: Brachyura: Retroplumidae) in the Maastrichtian of southern Mexico and its paleobiogeographic implications. *Annals of Carnegie Museum*, **61**: 133-152.
- Vega-Vera, F.J. & del Carmen Perrilliat, M. 1989. Una especie nueva de cangrejo del género *Costacopluma* (Crustacea: Decapoda: Retroplumidae) del Maastrichtiano del estado de Nuevo León. *Universidad Nacional autónoma de México, Instituto de Geología, Revista*, **8**: 84-87.
- Wade, B. 1926. The fauna of the Ripley Formation on Coon Creek, Tennessee. *United States Geological Survey, Professional Paper*, **137**: 1-272.
- Whiteaves, J.F. 1885. Note on a decapod from the Upper Cretaceous of Highwood River, Alberta, Northwest Territories. *Royal Society of Canada Transactions for 1884*, **2**: 237-238.

Plate 1

Costacopluma grayi Feldmann & Portell, 2007.

Figs. 1-3. Dorsal, ventral and frontal views of UF 228989, showing male sternum and partial pleon.

Scale bars equal 5 mm.

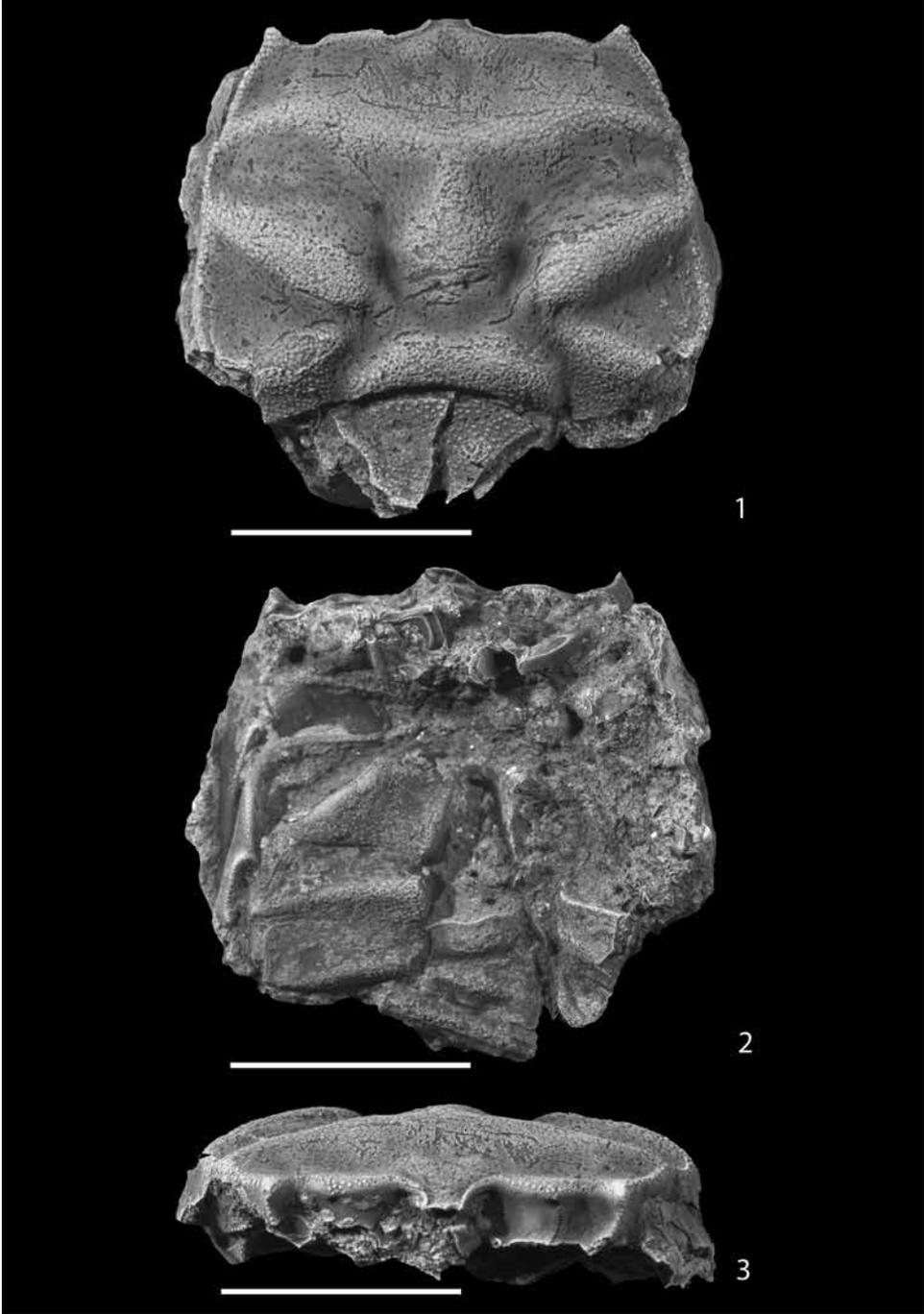


Plate 2

Costacopluma grayi Feldmann & Portell, 2007.

Figs. 1, 2. Dorsal and ventral views of UF 228990, showing male sternum.

Scale bars equal 5 mm.

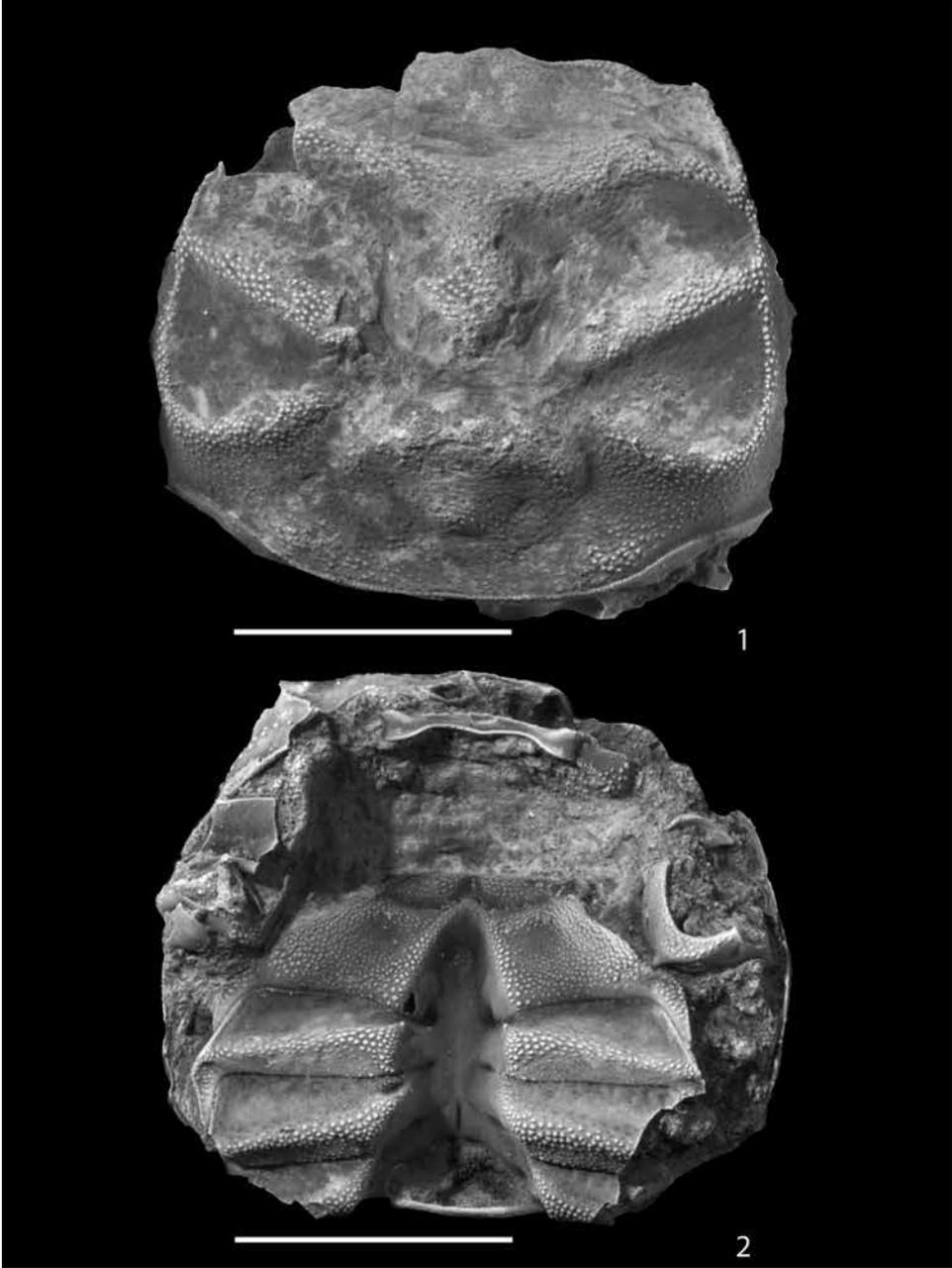


Plate 3

Stevia martini sp. nov.

Figs. 1-3. Dorsal, ventral and frontal views of holotype, UF 228988, showing female sternum.

Fig. 4. Dorsal view of paratype, UF 235561.

Scale bars equal 1 mm.

