FIRST REPORT OF *COSTACOPLUMA* COLLINS AND MORRIS, 1975 (DECAPODA: BRACHYURA: RETROPLUMIDAE) FROM THE EOCENE OF ALABAMA, U.S.A.

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ABSTRACT

Nine specimens of retroplumid crabs collected from the late early or early middle Eocene Tallahatta Formation in southern Alabama form the basis for description of a new species, *Costacopluma grayi*. The discovery confirms the extension of the range of the genus into the Eocene and represents the first occurrence of *Costacopluma* in the United States. As a result of the geologic range extension, the genus is now known to be contemporary with two other retroplumid genera, *Retrocypoda*, and *Retropluma*.

INTRODUCTION

The Retroplumidae Gill, 1894, is a relatively small family of decapod Crustacea which was originally named for a single extant genus of deep-water crabs from the Indo-Pacific region. Subsequently, another extant genus has been recognized and as many as five genera, known only from the fossil record, have been assigned to the family. The stratigraphic range has been extended into the Late Cretaceous as a result. The family has been re-evaluated by de Saint Laurent (1989), Vega and Feldmann (1992), and Schweitzer and Feldmann (2001), and the position of the extinct genera has been debated.

One of the genera that is most widely distributed both geographically and stratigraphically is Costacopluma Collins and Morris, 1975. Species of the genus have been reported from Niger (West Africa), India, Argentina, Brazil, Venezuela, Mexico, and Greenland in rocks ranging in age from Late Cretaceous to Paleocene. One specimen of questionable identity has been reported from the Eocene of Hungary. Thus, the discovery of nine specimens, referable to a new species of Costacopluma from Eocene rocks in Alabama, U.S.A., is noteworthy because it extends the geographic and stratigraphic range of the genus. The specimens that form the basis for this work are typically found as carapaces with adhering claystone within a glauconite-rich quartz sand. Most of the carapaces exhibit some degree of compaction fractures; however, the cuticle tends to be well preserved. Although carapace, sternum, and abdomen material is preserved in some specimens, only fragments of the appendages are found.

GEOLOGY, STRATIGRAPHY, AND AGE

In south central Alabama, *Costacopluma grayi* carapaces, documenting a new species of crab, were collected by wet sieving (5 mm mesh) at low water level (1-2 m depth) from outcrops along the southeastern bank of the Conecuh River just behind Point A Dam, in Covington County (Fig. 1). Here, nearly 10 m of sediments ranging from glauconite-rich

quartz sands to micaceous sandy claystones were mapped within seven distinct beds (see Copeland, 1966: 50-51). These shallow-marine sediments are part of a transgressionrelated condensed section in the lower Tallahatta Formation of Eocene age.

The name "Tallahatta" was first applied by W.H. Dall (1898: 344) as a replacement for the colloquial name "Buhrstone." Dall, at the suggestion of E. A. Smith, renamed the formation after the Tallahatta Hills in Choctaw County, Alabama, which exhibited the lithologic character and fauna of the unit.

In Alabama, the Tallahatta Formation is the basal member of the lower to middle Eocene Claiborne Group which also consists (in ascending order) of the Lisbon Formation and Gosport Sand. Typically, the Tallahatta is disconformably underlain by either the lower Eocene Hatchetigbee or Bashi formations (upper Wilcox Group). Elsewhere in the eastern Gulf Coast Plain, the Tallahatta Formation has been mapped in Mississippi and Georgia. In Alabama, the unit typically consists of massive siliceous claystone (buhrstone) interbedded with layers of glauconitic sand and sandy clay. According to Raymond et al. (1988: 83) the thickness of the Tallahatta Formation in southern Alabama ranges from about 38 m in the west thinning to 17 m in the east.

In Covington County, behind Point A Dam, the approximately 1 m thick crab-bearing horizon at the base of Bed 5 of Copeland (1966: 50-51) consists of very coarse to medium grained quartz sand with glauconite, clay clasts, and fine clay particles. Here, evidence of bioturbation is abundant throughout the entire stratigraphic section. The bluish-green sediments of Bed 5, contain a diverse assemblage of fossils, consisting mainly of remains of sharks and other fishes. Teeth of shark and ray species collected in situ with *Costacopluma* grayi included Lamna lerichei (Casier, 1946), Galeocerdo latidens (Agassiz, 1843), Nebrius thielensis (Winkler, 1873), Striatolamia macrota (Agassiz, 1843), Abdounia recticonus (Winkler, 1873), Carcharias hopei (Agassiz, 1843), Carcharocles auriculatus (de Blainville, 1818), Dasyatis sp., Rhinobatis sp., Aetobatus sp., and Myliobatis sp. Additionally, remains of freshwater turtles (trionychids and emydids), a terrestrial snake (*Tallahattaophis dunni* Holman and Case, 1988), an estuarine snake (*Palaeophis virginianus* Lydekker, 1888), and crocodiles (crocodylids) were found (see also Holman and Case, 1988). Furthermore, the small solitary coral, *Balanophyllia desmophyllum* H. Milne Edwards and Haime, 1848 and small fragments of silicified wood occur.

Based on the molluscan assemblage, Toulmin (1977) placed the Tallahatta Formation in the lower middle Eocene. Later, Bybell and Gibson (1985) used calcareous nannofossils to refine the age of the Tallahatta Formation in Alabama to calcareous nannofossil zones NP12 to NP14 of Martini (1971). They examined sediments from the Point A Dam section referred to in Copeland (1966) and, based on the presence of *Discoaster sublodoensis* Bramlette and Sullivan, 1961, *Lophodolithus mochlophorus* Deflandre *in* Deflandre and Fert, 1954, and *Lophodolithus nascens* Bramlette and Sullivan, 1961 and the absence of *Rhabdosphaera inflata* Bramlette and Sullivan, 1961, referred this part of the unit to lower zone NP14. Their work suggests either a late early or early middle Eocene age for sediments containing these crabs.

Systematics

Order Decapoda Latreille, 1802 Section Heterotremata Guinot, 1977 Superfamily Retroplumoidea Gill, 1894 Family Retroplumidae Gill, 1894

Type Genus.—Retropluma Gill, 1894.

Included Genera.—*Archaeopus* Rathbun, 1908; *Bathypluma* de Saint Laurent, 1989; *Costacopluma* Collins and Morris, 1975; *Cristipluma* Bishop 1983; *Loerenthopluma* Beschin, Busulini, De Angeli, and Tessier, 1996; *Retrocypoda* Via Boada, 1959; *Retropluma* Gill, 1894.

Remarks.—A diagnosis of the family has recently been given (Schweitzer and Feldmann, 2001) and will not be repeated herein. They considered all genera within the family with the exception of *Retrocypoda*. That genus has been described and well illustrated by Via (1969), Beschin et al. (1996), and De Angeli and Beschin (2001). The morphology of the dorsal carapace of *Retrocypoda almelae* Vía Boada, 1959, documents the possession of a short, downturned, axially sulcate rostrum, ovoid outline, flattened carapace, and transverse ridges, all diagnostic of the Retroplumidae. Likewise, the sternum exhibits the characteristic beaded, transverse keels. The genus is distinguished from other genera within the family by having four transverse ridges, rather than two or three as is characteristic of the others.

Archaeopus originated in the Cretaceous and is the oldest of the genera assigned to the family. Today, the family is represented in the Indo-Pacific region by *Retropluma* and *Bathypluma*.

Genus Costacopluma Collins and Morris, 1975

Type Species.—*Costacopluma concava* Collins and Morris, 1975, p. 823, pl. 97, figs. 1–9, by original designation.

Included Species.—Costacopluma australis Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995; C. bifida



Fig. 1. Location map showing the *Costacopluma* collecting area along the southeastern bank of the Conecuh River behind the Point A Dam in Covington County, Alabama.

Collins, Higgs, and Cortitula, 1994; *C. binodosa* Collins and Rasmussen, 1992; *C. bishopi* Vega and Feldmann, 1992; *C. concava* Collins and Morris, 1975; *C. mexicana* Vega and Perrilliat, 1989; *C. nordestina* Feldmann and Martins-Neto, 1995; *C. salamanca* Feldmann, Rodriguez, Martinez, and Aguirre-Urreta, 1997; *C. senegalensis* (Rémy in Gorodiski and Rémy, 1959), as *Archaeopus*.

Diagnosis.—Small, rectangular to ovoid carapace; wider than long; with distinctly flattened surface crossed by three elevated ridges, the anteriormost complete and the medial and posterior ridges converging mesially to define depressed, triangular mesobranchial region. Carapace flanks distinct, nearly perpendicular to dorsal surface. Sternal plates well defined; sternites 4-7 each with prominent transverse, beaded ridge. Transverse ridges also present on abdominal somites.

Remarks.—Costacopluma is a well constrained genus that is distinguishable from other genera within the family on the basis of the number, shape, and conformation of the transverse carapace ridges. Vega and Feldmann (1992) examined the relationships between genera within the Retroplumidae. They noted that, in general, members of the family were characterized by possession of three transverse ridges. In the presumed ancestral form, Archaeopus, the ridges were broad and discontinuous. In Costacopluma, the ridges tended to be broad and the anteriormost ridge was continuous, whereas the posterior two ridges joined near the anterior end of the cardiac region. The other genera were characterized by reduction of one of the ridges. In Cristipluma, the anterior ridge was developed only in the axial region, and in Retropluma and Bathypluma, the medial ridge was reduced or absent, and the remaining two ridges became very narrow

and sharply crested. In the analysis done by Vega and Feldmann (1992), *Retrocypoda* Vía Boada, 1959, was not considered; that genus was not adequately illustrated in the original description and Via Boada (1969) was overlooked. *Loerenthopluma*, which was not named until 1996, follows the same pattern of reduction of the medial ridge as do *Retropluma* and *Bathypluma*, whereas *Retrocypoda* possesses four narrow transverse ridges uniformly distributed along the carapace.

Costacopluma grayi new species Fig. 2A-2E, 3A-3D

Diagnosis.—Typical *Costacopluma* with strongly downturned, triangular rostrum with beaded surface; sharp, distinctly beaded lateral margin; nearly circular posterior element of mesogastric region.

Description.—Carapace small to moderate size for genus; subovate, wider than long, length about 80 percent maximum width measured at midpoint of mesobranchial region; flattened transversely and longitudinally; lateral flanks distinct, downturned at right angles to carapace surface; three transverse ridges of which anteriormost is complete; posterior and medial ridges converge in advance of cardiac region.

Front narrow, about 17 percent maximum carapace width; rostrum strongly downturned, triangular, axially sulcate; surface pustulose. Orbits deep, concave, forward-directed, rectangular when viewed from front; bounded dorsally by distinct, beaded rim. Fronto-orbital margin about 65 percent maximum width. Anterolateral margin straight to weakly convex with distinct beaded rim extending from outer-orbital corner to merge with more convexly rounded, rimmed posterolateral margin. Posterolateral corner and posterior margins poorly preserved, appearing to be gently convex.

Epibranchial regions transversely elongate, swollen, separated by axial sulcus extending onto rostrum. Protogastric and hepatic regions not distinguishable, depressed. Mesogastric region circular, swollen, beaded, 27 percent maximum width, bounded laterally by deep, broad arcuate depressions. Metagastric and urogastric region indistinct, narrow, with subtle longitudinal axial elevation. Cardiac region transversely ovoid, 40 percent maximum width. Urogastric region elongate-oval, inflated, separated from posterior margin by shallow depression. Epibranchial and mesobranchial regions depressed.

Transverse ridges distinct, elevated well above remainder of carapace. Anterior-most ridge a sinusoidal curve, concave axially and convex laterally, surface beaded; medial ridge straight, beaded, extending posteromesially to anterior end of cardiac region where it merges with concave forward, beaded, anteromesially-directed posterior ridge; medial and posterior ridges define a triangular mesobranchial region.

Surface of exocuticle very finely beaded, nearly smooth. Surface of endocuticle with coarser, evenly spaced pustules.

Buccal frame broad, widening anteriorly, bounded by inflated and beaded pterygostomial regions. Ischium of third maxilliped generally rectangular, tapering slightly anteriorly; surface smooth.

Sternites 1-3 forming isosceles triangle, directed dorsally; sutures 1-2, 2-3, and 3-4 fused but elevated and distinct in position. Sternite 4 much wider than sternite 3 with

prominent anterolaterally directed projection. Lateral margin of sternite 4 elevated into rim. Sutures between somites 4-5, 5-6, and 6-7 appear to be unfused laterally and obscurred by abdomen axially. Somite 5 directed laterally; somites 6 and 7 directed posterolaterally; each with prominent nodose keel. Somite 8 not exposed. Axis of somites 2-7 deeply depressed, weakly rimmed on somite 4. Male abdomen apparently unfused throughout, each abdominal somite transversely keeled, telson triangular, extends onto depression in sternal somite 3.

Pereiopods represented by slender, flattened, beaded, dissociated elements.

Measurements.—Measurements, in millimeters, taken on specimens of *Costacopluma grayi* are given in Table 1.

Etymology.—The trivial name honors Mark M. Gray, for bringing the first specimens to the attention of the authors and for generously donating his specimens to the Florida Museum of Natural History (FLMNH).

Types.—The holotype, UF 113749, and paratypes, UF 113748, 113750, 114747, 115672 115793, 115794, 115795, and 115796, are deposited in the Invertebrate Paleontology Division at the FLMNH, University of Florida, Gainesville, Florida.

Occurrence.—The type series was 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.

DISCUSSION

Costacopluma grayi conforms to the diagnostic features of the carapace of the genus in all regards. The ventral surface of the carapace is not preserved on six of the nine specimens and only the pterygostomial region and one of the maxillipeds is preserved on one specimen. Two specimens exhibit parts of the sternum and abdomen of male specimens so it is possible to describe the morphology. The morphology of the sternum and abdomen, coupled with that of the dorsal carapace, makes placement within *Costacopluma* and the Retroplumidae certain.

A single specimen, UF 115793, retains the exocuticule over much of the dorsal carapace (Fig. 3A, B). As is the case with many decapods, the sculpture exhibited by the exocuticle is different from that seen on the surface of the endocuticle, which is visible when the exocuticle is exfoliated. Therefore it is important to note which surface that observations of sculpture are made, if possible. The contrast in ornamentation is even more striking when comparing the sculpture of the cuticular surfaces with that of the mold of the interior as seen on UF 113750 (Fig. 2E), which lacks ornamentation at a fine scale. These observations provide a note of caution when employing fine details of surface ornamentation in systematic work.

The family affinities are even more secure when the dorsal and ventral morphology of *C. grayi* is compared with that of the extant *Retropluma chuni* Doflein, 1904 (= *Ptenoplax dentata* MacGilchrist, 1905) (Fig. 3E, F). Although the outline of sternites 5-7 is poorly exposed in



Fig. 2. A-E, *Costacopluma grayi* new species. A, dorsal view of holotype, UF 113749. B, oblique frontal view of paratype, UF 113748, showing the downturned, rimmed, pustulose rostrum (arrow), rectangular orbit, and steep lateral flanks. C and D, dorsal and ventral views of paratype, UF 115672, illustrated at the same scale and showing well developed carapace regions and, on the ventral surface, pterygostomial regions and left mxp3. E, dorsal view of worn and exfoliated paratype, UF 113750, on which the carapace ornamentation is not in evidence. F, dorsal view of *Costacopluma senegalensis* Rémy, 1959, holotype, RO 3785, deposited in the Muséum national d'Histoire naturelle, Paris. Scale bars = 1 cm.

the fossil, the general form of the sternum, with narrow, triangular sternites 1-3, significantly broader sternite 4, and keeled sternites, is quite similar in the two species. In addition, the similarity in outline of the dorsal carapace, con-

formation of the rostrum, and presence of keels on the dorsal carapace of both taxa is striking. Although *Retropluma* is typically described as having two transverse ridges, careful examination under oblique illumination reveals a very subtle



Fig. 3. A-D, *Costacopluma grayi* new species. A, dorsal view, unwhitened of paratype, UF 115793, on which exocuticle and endocuticle are exposed in different parts of the carapace, Scale bar = 1 cm. B, enlargement of part of mesogastric and epibranchial regions showing the different sculpture exhibited on surface of exocuticle and endocuticle. Scale bar = 1 mm. C, ventral view of paratype, UF 115794, showing nearly complete sternum and male abdomen. Scale bar = 5 mm. D, ventral view of paratype, UF 115796, showing posterior part of sternum and proximal segments of male abdomen. Scale bar = 1 cm. E, F, *Retropluma chuni* Doflein, 1904 (= *Ptenoplax dentata* MacGilchrist, 1905). E, dorsal view of female. Scale bar = 1 cm. F, ventral view of female. Scale bar = 1 cm.

elevation separating the mesobranchial region from the metabranchial region; thus, the distinction between the ridge pattern of *Retropluma* and *Costacopluma* is one of degree.

Species within the genus are distinguished from one another on the basis of shape of the rostrum, development of granulation on the carapace elevations, carapace outline, and various dimensional ratios including length/width, posterior width/maximum width, and frontal width/maximum width. Because the margins of the Alabama specimens are not completely preserved, it is difficult to employ these ratios with certainty; however, morphological features of the surface of the carapace are well exhibited so that detailed comparisons can be made. Examination of types, or illustrations of types, of all other species within the genus confirms that the form of the carapace ridges, shape of the rostrum, and outline of the posterior element of the

Table 1. Carapace measurements (mm). Key: maximum length (L), maximum width (W), fronto-orbital width (W1). (*) indicates that the measurement is an approximation due to incomplete specimen. (>) indicates a measurement greater that measured. (-) indicates a measurement could not be taken.

FLMNH Specimen UL Number	L	W	W1
113748	_	*6.2	4.8
113749	>8.1	10.3	*6.6
113750	11.8	14.4	*8.8
114747	*8.6	10.5	
115672	>7.9	10.3	_
115793	>8.7	10.8	_
115794	_	_	_
115795	_	>8.2	_
115796		9.6	—

mesogastric region provide ample evidence that C. gravi is unique. All species within the genus, except C. concava, C. senegalensis, and C. gravi, possess ridges that are broadly rounded. The three exceptions have narrower, more sharply defined, granular ridges. Among these three species, only C. senegalensis and the new species have downturned, triangular rostra. Costacopluma concava, as with all other species of the genus for which the rostrum is known, bears a rostrum that is broadened or clearly bifid distally. All species of Costacopluma, with the exception of C. senegalensis and C. grayi, have rostra that are substantially narrower proximally than it is distally. Costacopluma grayi can be readily distinguished from C. senegalensis because the former exhibits a beaded rostral surface, a distinctly beaded lateral margin, and a nearly circular posterior element of the mesogastric region. The posterior part of the mesogastric region on C. senegalensis is transversely ovoid and lacks beaded ornamentation.

Species of *Costacopluma* have been described previously from Late Cretaceous rocks in Greenland (Collins and Rasmussen, 1992), Mexico (Vega and Feldmann, 1992; Vega et al., 1994, 1995), and West Africa (Collins and Morris, 1975). Paleocene occurrences have been recorded from Argentina (Feldmann et al., 1995, 1997), Brazil (Feldmann and Martins-Neto, 1995), Venezuela (Collins et al., 1994), Kashmir (Gaetani et al., 1983) and West Africa (Rémy in Gorodiski and Rémy, 1959). A questionable reference to an indeterminate species of Costacopluma from the late Eocene of Hungary (Müller and Collins, 1991) is based upon one fragmentary specimen. Vega and Feldmann (1992) suggested that Costacopluma was derived from Archaeopus and most likely first appeared in Mexico. Subsequent to that, Costacopluma spp. radiated into the North Atlantic and Tethys. The recognition of Costacopluma grayi from Eocene rocks in Alabama represents both a new geographic and a stratigraphic record. The genus has never been noted in the United States and has not previously been recognized in the Eocene. Based upon the description of this new species, the genus had its latest appearance in North America.

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