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ABSTRACT

The extent to which the Cretaceous-Paleogene (K-Pg) extinction event impacted decapod crustaceans has yet to be tested rigorously due to a lack of studies at the outcrop scale. We comprehensively describe an early but not earliest Danian assemblage from Mussel Creek, central Alabama, United States, based on collecting of decapod carapaces and appendage remains at the roadcut part of this site since 2010. The specimens were recovered chiefly from silty, micaceous mudstones of the Pine Barren Member within the Clayton Formation, *c.* 8 m above the K-Pg boundary. Microfossil analysis indicates that the decapods originate from the lower middle part of the NP2 nannofossil zone, *c.* 600-700 ka after the K-Pg boundary. Based on 354 identifiable specimens, we recognize eight species: 1) four Brachyura: *Alahexapus martini* (Feldmann, Schweitzer & Portell, 2014) n. comb., *Costacopluma nicksabani* n. sp., *Raninoides danicus* n. sp., and an indeterminate representative of Palaeoxanthopsidae Schweitzer, 2003; 2) three Axiidea: *Alphacheles zeta* (Rathbun, 1936) n. comb., *Ctenocheles* sp., and *Eucalliaxiopsis alabamensis* (Rathbun, 1935a) n. comb.; and 3) one Paguroidea: "*Paguristes*" *johnsoni* Rathbun, 1935a. Two new genera are described: *Alahexapus* n. gen. and *Alphacheles* n. gen. The assemblage is dominated by specimens of *C. nicksabani* n. sp. (52% of identifiable specimens) and *E. alabamensis* n. comb. (31%). Three specimens of *C. nicksabani* n. sp. preserve rare gonopods. A rarefaction analysis indicates that (nearly) all species were collected. This assemblage represents the most diverse early Danian decapod assemblage from North America thus far, and provides a basis for further study of decapods across the K-Pg boundary.

KEY WORDS
Alabama,
Anomura,
Axiidea,
Brachyura,
Crustacea,
Danian,
Decapoda,
Paleocene,
new combinations,
new genera,
new species.

RÉSUMÉ

Systématique, biodiversité et paléoécologie d'un assemblage de crustacés décapodes du Danien inférieur de l'Alabama, États-Unis.

L'ampleur de l'impact de l'extinction du Crétacé-Paléogène (K-Pg) sur les crustacés décapodes n'a pas encore été rigoureusement évaluée en raison du manque d'études à l'échelle des affleurements. Nous décrivons de manière exhaustive un assemblage du Danien inférieur, mais pas le plus ancien, provenant de Mussel Creek, dans le centre de l'Alabama, aux États-Unis, sur la base de la collecte collecte de restes de carapaces et d'appendices de décapodes dans un talus routier depuis 2010. Les spécimens ont été principalement collectés dans des mudstones limoneux et micacés du Membre Pine Barren au sein de la Formation Clayton, à environ 8 m au-dessus de la limite K-Pg. L'analyse des microfossiles indique que les décapodes proviennent de la partie inférieure moyenne de la zone à nannofossiles NP2, environ 600 à 700 ka après la limite K-Pg. Sur la base de 354 spécimens identifiables, nous reconnaissons huit espèces : 1) quatre Brachyura : *Alahexapus martini* (Feldmann, Schweitzer & Portell, 2014) n. comb., *Costacopluma nicksabani* n. sp., *Raninoides danicus* n. sp. et un représentant indéterminé de la famille des Palaeoxanthopsidae Schweitzer, 2003 ; 2) trois Axiidea : *Alphacheles zeta* (Rathbun, 1936) n. comb., *Ctenocheles* sp. et *Eucalliaxiopsis alabamensis* (Rathbun, 1935a) n. comb. ; et 3) un Paguroidea : "*Paguristes*" *johnsoni* Rathbun, 1935a. Deux nouveaux genres sont décrits : *Alahexapus* n. gen. et *Alphacheles* n. gen. L'assemblage est dominé par des spécimens de *C. nicksabani* n. sp. (52 % des spécimens identifiables) et *E. alabamensis* n. comb. (31 %). Trois spécimens de *C. nicksabani* n. sp. conservent des gonopodes, ce qui est rare. Une analyse de raréfaction indique que (presque) toutes les espèces ont été collectées. Cet assemblage de décapodes du Danien inférieur est le plus diversifié d'Amérique du Nord connu à ce jour et fournit une base pour la poursuite des études sur les décapodes à travers la limite K-Pg.

MOTS CLÉS
Alabama,
Anomura,
Axiidea,
Brachyura,
Crustacea,
Danien,
Decapoda,
Paléocène,
combinaisons nouvelles,
genres nouveaux,
espèces nouvelles.

INTRODUCTION

The degree to which decapod crustaceans experienced extinction during the Cretaceous-Paleogene mass extinction event remains an open question as analyses have been done largely at a global scale and at different taxonomic levels (e.g., Schweitzer & Feldmann 2005, 2023; Klompmaker *et al.* 2016). Early Paleocene (Danian) decapod crustaceans provide insights into their biodiversity after this extinction event. Such assemblages have been described from multiple continents including Antarctica (Feldmann & Tshudy 1989), Europe (Jakobsen & Collins 1997; Robin *et al.* 2017), North America (Rathbun 1935a; Collins & Wienberg Rasmussen 1992; Armstrong *et al.* 2009), and South America (Feldmann *et al.* 1995). The stratigraphic position of these assemblages within the Danian is critical to evaluate the biodiversity of decapods after the mass extinction.

The Clayton Formation is a lower Danian unit exposed in the southeastern United States known to yield decapods. Decapods or their burrows have been reported from the Clayton Formation from Illinois (Cope *et al.* 2005), Arkansas (Rathbun 1935a; Martínez-Díaz *et al.* 2016), and Alabama (Feldmann *et al.* 2014, 2019; Martínez-Díaz *et al.* 2016; Foster *et al.* 2020), but these papers focused on selected taxa for the purposes of their studies or reported on a limited number of specimens.

The goal of this paper is to comprehensively describe an early Paleocene (early Danian) decapod assemblage from the Pine Barren Member of the Clayton Formation in central Alabama, United States. Based on collecting efforts spanning 15 years, we clarify the taxonomy of some previously reported taxa; report multiple new records and taxa; and discuss the stratigraphic and paleobiogeographic implications, paleoecology, and diversity of this assemblage.

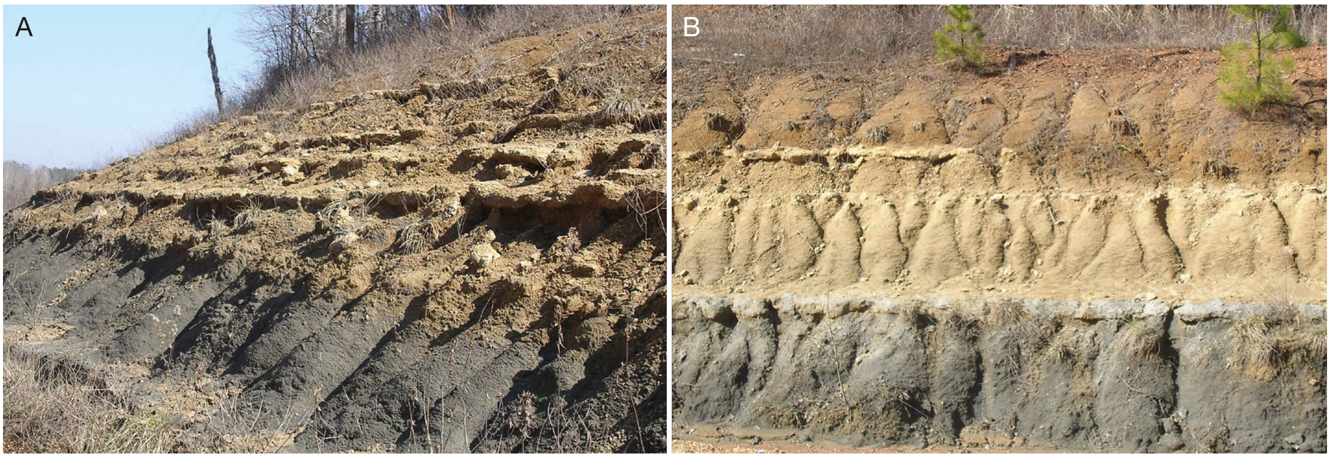

Fig. 1. — Images of the roadcut of Mussel Creek, Lowndes County, Alabama, exposing the lower Danian Pine Barren Member (Clayton Formation): **A**, East side; **B**, West side. Most of the soft, tan layers have grown over since photos were taken in 2010. The main hard limestone layer (layer 13, *c.* 8 m above the K-Pg boundary in Figure 2 corresponds to layer 18 of Udgata & Savrda 2016) is barely visible in the lower left corner of **A** but clearly visible in the lower third of **B**. Credits: photos by P. George Martin.

GEOLOGICAL SETTING

The lower Paleocene (Danian) Clayton Formation in Alabama is divided into a lower (Pine Barren) and upper (McBryde Limestone) members in central Alabama. Toulmin (1977) first documented the macroinvertebrate content of the Pine Barren beds in Alabama (Butler and Wilcox counties). Several localities or cores from central Alabama with Pine Barren sediments have been described including but not limited to the Antioch Church Core (Schulte & Speijer 2009), Braggs (e.g., Jones *et al.* 1987; Bryan & Jones 1989; Zachos *et al.* 1989), Mooseland (Larina *et al.* 2016), Moscow Landing (e.g., Smith 1997; Hart *et al.* 2013; Savrda *et al.* 2020), and Mussel Creek (Hart *et al.* 2013; Udgata & Savrda 2016). Thus, the age of these sediments is generally well constrained.

The roadcut at Mussel Creek (ALMNH loc. 3) is in the southern part of Lowndes County, Alabama, United States (Fig. 1). Here, *c.* 5.5 m of section of the lower Danian Pine Barren Member of the Clayton Formation is exposed and another 1 m can currently be cored with an auger until hitting a limestone layer (Fig. 2). These sediments, all within nannofossil zone NP2, comprise an alternation of gray to tan, carbonaceous, glauconitic calcareous, variably sandy micaceous mudstones and harder lime- to marlstone layers (Hart *et al.* 2013; Udgata & Savrda 2016). Udgata & Savrda (2016) interpreted these layers to represent a highstand systems tract, and these limestones to have formed diagenetically below marine flooding surfaces. Macrofossils from this roadcut include plant remains, asteroid ossicles, bivalves, gastropods, a nautiloid, echinoid spines, bryozoans, a crinoid, decapods, shark and ray teeth, holocephalan teeth, bony fish teeth and vertebrae, crocodile bones and teeth, turtle, and some trace fossils (Figs 3; 4). Among these macrofossils, four decapod species (Feldmann *et al.* 2014, 2019) and two lamniform shark species (Cicimurri *et al.* 2020; Ebersole *et al.* 2024) were formally reported, but many other fossils remain to be studied. Nearly all decapod specimens studied herein originate from the lower middle part of NP2 nannofossil zone (Fig. 2).

Older, earliest Danian layers exposed in the stream cut of Mussel Creek have yielded reported macrofossils such as echinoids, bivalves, bryozoans, and burrows such as *Thalassinoides* Ehrenberg, 1944 (Savrda 1993; Udgata & Savrda 2016; Zachos 2017).

MATERIAL AND METHODS

In total, 354 identifiable decapod specimens (excluding 30 Axiidean indet. and 25 Decapoda indet.) were collected at the Mussel Creek roadcut (31°58'17"N, 86°42'15"W) in Lowndes County, Alabama, from 2010-2024 during one or multiple trips each year. Most specimens were collected by PGM (2010-2024) and many others by AAK (2021-2024). The specimens were often found loose on the surface, having weathered out of the mudstones and limestones; some specimens were discovered embedded in the rock. The specimens were largely collected from the mudstones above and below the most prominent limestone layer (layer 13 in Figure 2) currently visible at the roadcut (layer 18 of Udgata & Savrda 2016), which is *c.* 8 m above the K-Pg boundary exposed within the creek bluff based on our measurements. Specimens were prepared using air scribes and hardened with Paraloid B-72 as needed. Specimen photography was done using a Canon EOS 90D camera with a 60 mm lens in an Ortech Photo-e-Box Plus lightbox. Closeup pictures were made using a Swiftcam 18 MP camera mounted on a microscope and using an MP-E 65 mm lens on a Canon EOS 90D camera. Postprocessing of specimen images such as stacking occurred in Adobe Photoshop. A D3D-s (model S2) 3D scanner was used to create 3D models of specimens of new species with the help of Polyga PointKit Scan software. All specimens used are reposited in the museum collections listed below. Specimens only identifiable to high taxonomic ranks (Axiidea indet.: ALMNH:Paleo:5920 [3 specimens], ALMNH:Paleo:5922 [1 specimen], ALMNH:Paleo:13536 [1 specimen], and ALMNH:Paleo:21556 [25 specimens]; Decapoda indet.: ALMNH:Paleo:21557 [21 specimens], UF 303812 [1 specimen], UF 303815 [1 specimen], UF 303819 [1 specimen], and UF 303866 [1 specimen]) are not treated further below. Coordinates of localities, where available, use the datum WGS 84 standard.

Non-decapod macrofossils were identified with the assistance of comparative material in the ALMNH and MMNS collections and multiple references (Gardner 1935; Toulmin 1977; Cicimurri *et al.* 2020; Garvie 2021; Ebersole *et al.* 2024).

In the discussion, we compare the diversity of early Danian decapod assemblages globally. We recognize there are younger Danian assemblages (e.g., upper Danian Porters Creek Formation [Rathbun 1935a]; middle Danian Faxe Formation [Jakobsen & Collins 1997; Jakobsen *et al.* 2020; Klompmaker *et al.* 2022a]; upper Danian Mexia Clay Member of the Wills Point Formation [Armstrong *et al.* 2009]), but they are outside the envisioned scope of the discussion.

NANNOFOSSIL ANALYSES

Thirty-two samples were collected throughout *c.* 6 m of outcrop section exposed at the roadcut of Mussel Creek. The samples were carefully selected across all lithologies; thus, samples were collected in both the intervals of mudstone and beds of limestone/marl. The calcareous nannofossils were studied under cross-polarized light and phase contrast at 1000X magnification, using a Zeiss Axiophot light microscope (LM). The samples were prepared for LM observation using a routine smear slide technique. Samples were analyzed quantitatively to identify biostratigraphic events and establish a nannofossil zonation for the section, and to document nannofossil-assemblage changes throughout the early Danian. Quantitative analysis involved counting 300 nannofossil specimens from random fields of view. In general, reaching a count of 300 specimens required observation of between 1-2 traverses. However, samples marked by very low nannofossil abundances would sometimes require viewing of up to five traverses. The abundances of each species were also recorded using the following categories: SA (super-abundant) = > 75 specimens, A (abundant) = 21-75 specimens, C (common) = 9-20 specimens, F (few) = 4-8 specimens, and R (rare) = 1-3 specimens.

The biostratigraphic interpretation of the samples utilized the nannofossil biozonation of Martini (1971), and the associated numeric ages of zonal boundaries and nannofossil bioevents are derived from Gradstein *et al.* (2012). We use the terms "Base" for the first or lowest stratigraphic occurrence of a species, and "Top" for the last or highest stratigraphic occurrence. The terminology for abundance-based bioevents includes the following: "increase" = frequent-common; "influx" = abundant; "major influx" = super-abundant; "acme" = acme, or absolute highest abundance. Of taxonomic and biostratigraphic note is that although *Cruciplacolithus tenuis* (Stradner, 1961) is the traditional and official index species representing Zone NP2, we acknowledge the serious taxonomic problem (e.g., cross bar with "feet-like" terminations) associated with the use of Base *C. tenuis* as the zonal marker defining NP2. In this study, we follow the historical taxonomic concept/biostratigraphic approach used by others (Perch-Nielsen 1985; Van Heck & Prins 1987; Varol 1989; Bown *et al.* 2023). As such, we consider Base *Cruciplacolithus intermedius* Van Heck & Prins, 1987, the bioevent and substitute zonal marker defining Zone NP2. We consider Zones NP1-NP2 to represent the "lower"/"early" Danian here informally. Slides with nannofossils are stored at the Geological Survey of Alabama.

INSTITUTIONAL ABBREVIATIONS

ALMNH	Alabama Museum of Natural History paleontology collection, University of Alabama, Tuscaloosa, Alabama;
GSA	Geological Survey of Alabama, Tuscaloosa, Alabama;
MGSB	Museu Geològic del Seminari de Barcelona, Barcelona;
MMNS IP	Mississippi Museum of Natural Science Invertebrate Paleontology collection, Jackson, Mississippi;
NPL	Non-vertebrate Paleontology lab, Jackson School Museum of Earth History, University of Texas at Austin, Austin, Texas;
UF	Florida Museum of Natural History (Invertebrate Paleontology), University of Florida, Gainesville, Florida.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder AXIIDEA de Saint Laurent, 1979

Family CTENOCHELIDAE Manning & Felder, 1991

INCLUDED GENERA. — *Ahazianassa* Karasawa, Kishimoto, Ohara & Ando, 2019; *Alphacheles* n. gen.; *Ctenocheles* Kishinouye, 1926; *Cretagourretia* Ossó, Charbonnier, Hyžný, Van Bakel, Devillez, Bover-Arnal & Moreno-Bedmar, 2024; *Ctenocheloides* Anker, 2010; *Dawsonius* Manning & Felder, 1991; *Gourretia* de Saint Laurent, 1973; *Kiictenocheloides* Sakai, 2013; *Laurentgourretia* Sakai, 2004; *Paragourretia* Sakai, 2004.

Genus *Alphacheles* n. gen.

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TYPE SPECIES. — *Callianassa zeta* Rathbun, 1936 (*Callianassa alpha* Rathbun, 1935a; *non Callianassa alpha* Stenzel, 1935), by present designation.

ETYMOLOGY. — The genus name is a combination of "alpha", referring to the homonymous species name *Callianassa alpha*, and "cheles" meaning "claw". Gender: masculine.

DIAGNOSIS. — As for the type species.

REMARKS

Shortly after the description of *Callianassa alpha* Rathbun, 1935a, it was revealed that the name had already been used by Stenzel (1935) for yet another fossil ghost shrimp assigned to *Callianassa*. A rectification was published in the following year, renaming *C. alpha* to *C. zeta* Rathbun, 1936.

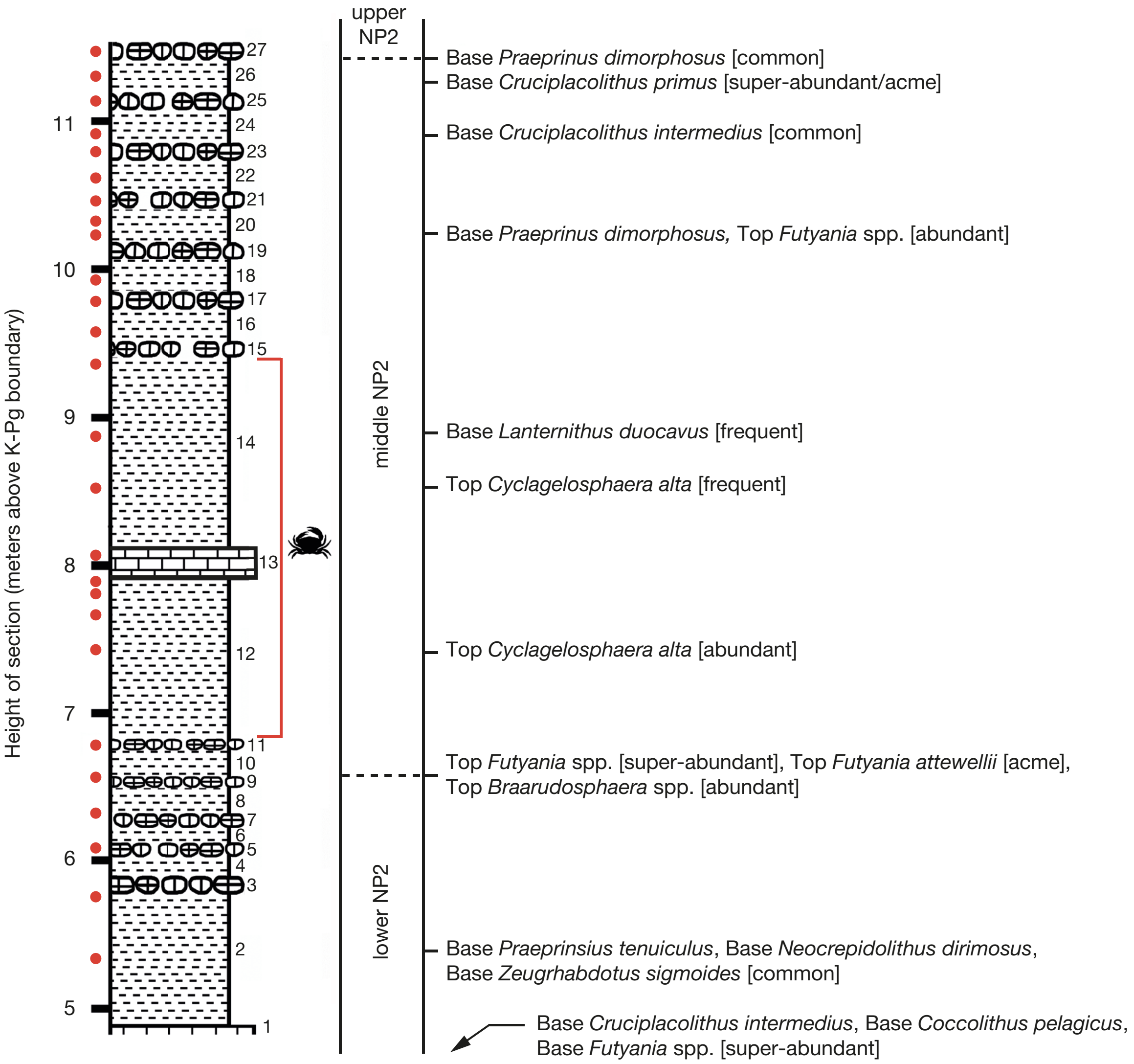

FIG. 2. — Stratigraphic column of the Mussel Creek roadcut relative to the K-Pg boundary within the creek, nannofossil zonation and key species based on microfossil samples (**red dots**), and layers in which nearly all decapods were found.

Callianassa zeta differs from all known extant and extinct ghost shrimp taxa by its tuberculate area ("densely punctate excrescence" *sensu* Rathbun [1935a]; "triangular patch of granules" *sensu* Feldmann *et al.* [2019]) at the base of the fixed finger which is present at the outer and inner lateral surfaces. This character has been considered a diagnostic feature of this species (Rathbun 1935a; Feldmann *et al.* 2019). Its taxonomic significance is herein elevated to the genus level, and hence a new genus is proposed to accommodate this species.

So far, only propodi and dactyli are known for *Alphacheles zeta* (Rathbun, 1936) n. comb. Most specimens represent major claws, whereas in one case also a minor claw is identified (Fig. 5O). Their morphology is rather close to that of extant species of *Gourretia* and *Paragourretia*, based on which the new genus is classified within the family Ctenochelidae. Nevertheless, the familial placement of *Alphacheles* n. gen. should be considered preliminary until more complete material is found. *Alphacheles* n. gen. shares with the above-mentioned genera the following set of characters: major cheliped propodus distinctly longer than high and subrectangular in outline, relatively long fingers exceeding half of the propodus palm length, and dactylus occlusal surface with simple dentition (cf. Le Loeuff & Intès 1974; Sakai 2002, 2004; Ngoc-Ho 2003). These characters are shared also with *Cretagourretia*, an exclusively fossil genus known from the Early Cretaceous (Albian) of Spain. This set of characters mentioned above is rarely seen in other ghost shrimp families (Poore & Ahyong 2023). As mentioned above, *Alphacheles* n. gen. differs from all ghost shrimp genera known to date by the presence of a tuberculate area at the base of the fixed finger. It differs also from yet another exclusively fossil ctenochelid genus, *Ahazianassa*, from the Late Cretaceous (Maastrichtian) of Japan. Additionally, *Alphacheles* n. gen. possesses a more elongate palm than *Ahazianassa* does.

Besides *Callianassa alpha*, Rathbun (1935a) described also "*C. alpha* var." from the Upper Eocene Jackson Group of Mississippi. A new variety of *C. alpha* is based on a single incomplete propodus and a pleon found at the same locality.

Fig. 3. — Non-decapod body macrofossils from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**, Crocodylia vertebra (ALMNH:Paleo:21546); **B**, Crocodylia osteoderm fragment (ALMNH:Paleo:21538); **C**, Crocodylia tooth (ALMNH:Paleo:22081A); **D**, anterolateral shark tooth of *Mennerotodus mackayi* Cicimurri, Ebersole & Martin, 2020 (ALMNH:Paleo:21532); **E**, (para-)symphyseal shark tooth of *Mennerotodus mackayi* (ALMNH:Paleo:21523); **F**, turtle femur (ALMNH:Paleo:21547); **G**, wood fragment (ALMNH:Paleo:21534); **H**, lateral shark tooth of *Palaeohypotodus speyeri* (Dartevelle & Casier, 1943) (ALMNH:Paleo:21524); **I**, vomerine with some teeth of bony fish cf. *Pycnodus* sp. (ALMNH:Paleo:21543); **J**, molariform tooth of bony fish cf. *Pycnodus* sp. (ALMNH:Paleo:21522); **K**, vertebra of bony fish (ALMNH:Paleo:21545); **L**, bivalve *Cucullaea* (?) sp. (ALMNH:Paleo:21530); **M,** right oyster valve of *Ostrea crenulimarginata* Gabb, 1860 (ALMNH:Paleo:21520); **N**, left oyster valve of *Gryphaeostrea vomer* (Morton, 1828) (ALMNH:Paleo:21533); **O**, right oyster valve of *Gryphaeostrea vomer* (ALMNH:Paleo:21535); **P**, left valve of bivalve cf. *Eomiltha* sp. (ALMNH:Paleo:21544); **Q**, bivalve *Callocardia* sp. (ALMNH:Paleo:21541); **R**, bivalve *Venericardia (Baluchicardia)* sp. (ALMNH:Paleo:21519); **S**, bivalve *Crassatella* cf. *C. ioannes* Gardner, 1935 (ALMNH:Paleo:21539). Scale bars: A, B, F, L, Q-S, 10.0 mm; C, D, G-I, K, M-P, 5.0 mm; E, J, 2.0 mm. Credits: photos by Adiël A. Klompmaker.

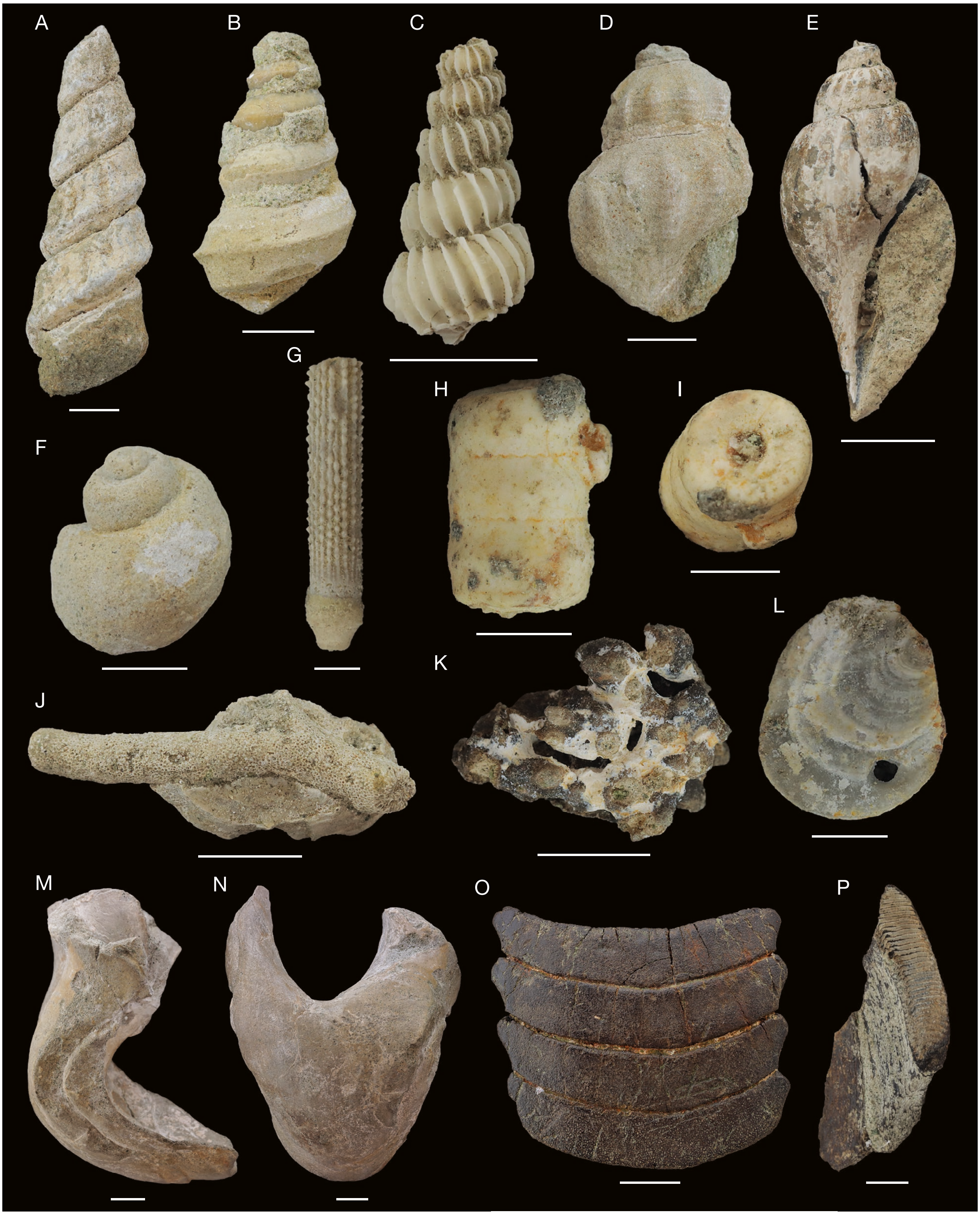

Fig. 4. — Non-decapod body and trace macrofossils from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**, gastropod *Kapalmerella* sp. (ALMNH:Paleo:21526); **B**, gastropod *Mesalia* cf. *M. hardemanensis* (Gabb, 1860) (ALMNH:Paleo:21515); **C**, gastropod *Straticostatum* (*Paginacosta*) sp. (ALMNH:Paleo:21516); **D**, gastropod Fasciolariidae Gray, 1853 (ALMNH:Paleo:21525); **E**, gastropod *Volutocorbis* cf. *V. rugatus* (Conrad, 1860) (ALMNH:Paleo:21521); **F**, gastropod Naticidae Guilding, 1834 (ALMNH:Paleo:21540); **G**, echinoid spine of Cidaroida Claus, 1880 (ALMNH:Paleo:21537); **H**, **I**, Crinoidea Miller, 1821 (ALMNH:Paleo:21527); **J**, Bryozoan *Heteroconopeum damicornis* (Canu & Bassler, 1920) (ALMNH:Paleo:21531); **K**, Clionid sponge boring trace (infilling) *Entobia* isp. (ALMNH:Paleo:21529); **L**, oyster Gryphaeidae Vialov, 1936 (Pycnodontinae) with drill hole (*Oichnus paraboloides* Bromley, 1981) by predatory gastropod (ALMNH:Paleo:21536); **M**, **N**, Nautiloid *Hercoglossa* sp. (ALMNH:Paleo:22082); **O**, four ray teeth of *Myliobatis* sp. (ALMNH:Paleo:9737); **P**, Holocephalian *Ischyodus williamsae* Case, 1991 (ALMNH:Paleo: 9739). Scale bars: A-C, E, F, J, K, P, 5.0 mm; D, M-O, 10.0 mm; G-I, L, 2.0 mm. Credits: photos by Adiël A. Klompmaker.

Fig. 5. — Type specimens of *Alphacheles zeta* (Rathbun, 1936) n. comb. from the upper Danian Porters Creek Formation of the Prairie Creek region, Wilcox County, Alabama: **A**-**D**, outer, inner, upper marginal, and lower marginal views of major right propodus of holotype (USNM MO 371506); **E**, **F**, outer and inner views of left major propodus of paratype (USNM PAL 336022 A); **G**, frontal view of holotype; **H**, lower margin view of paratype (USNM PAL 336022 A); **I**-**L**, outer and inner views of left major propodi of paratypes (USNM PAL 336022 B); **M**, outer view of right major propodus of paratype (USNM PAL 336022 B); **N**, **O**, outer and inner views of right major propodus of paratype and minor propodus with dactylus (USNM PAL 336022 B). Scale bars: 2.0 mm. Credits: photos by Adiël A. Klompmaker.

Because the isolated propodus does not appear to show a densely tuberculate area at the base of the fixed finger, "*C. alpha* var." is not considered closely related to *Alphacheles zeta* n. comb. Given the large temporal separation of *c.* 25 million years, these specimens might represent a new species, but a restudy of the specimens is needed.

Alphacheles zeta (Rathbun, 1936) n. comb.
(Figs 5; 6)

Callianassa zeta Rathbun, 1936: 37. — Feldmann *et al.* 2019: 284, 293, 294, fig. 3E, F.

Callianassa alpha Rathbun, 1935a: 67, pl. 15.23-15.25, 15.27. — non *Callianassa alpha* Stenzel, 1935: 391, pl. 15.1, 15.2, 15.7, 15.8.

Type material. — **Holotype. United States** • Alabama, Wilcox County, Prairie Creek region; Porters Creek Formation; Paleocene (upper Danian); USNM MO 371506.
Paratypes. United States • 1 specimen; same as for the holotype; USNM PAL 336022 A • 10 specimens; idem; USNM PAL 336022 B.

Additional material examined. — **United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21511 (propodus) • 1 specimen; idem; ALMNH:Paleo:21512 (propodus) • 1 specimen; idem; ALMNH:Paleo:21513 (propodus) • 2 specimens; idem; MMNS IP-7255 (2 specimens, partial propodus and dactylus and propodus and dactylus) • 1 specimen; idem; UF 303822 (propodus).

Type horizon. — Porters Creek Formation (Sucarnoochee beds in Rathbun 1935a), upper Danian.

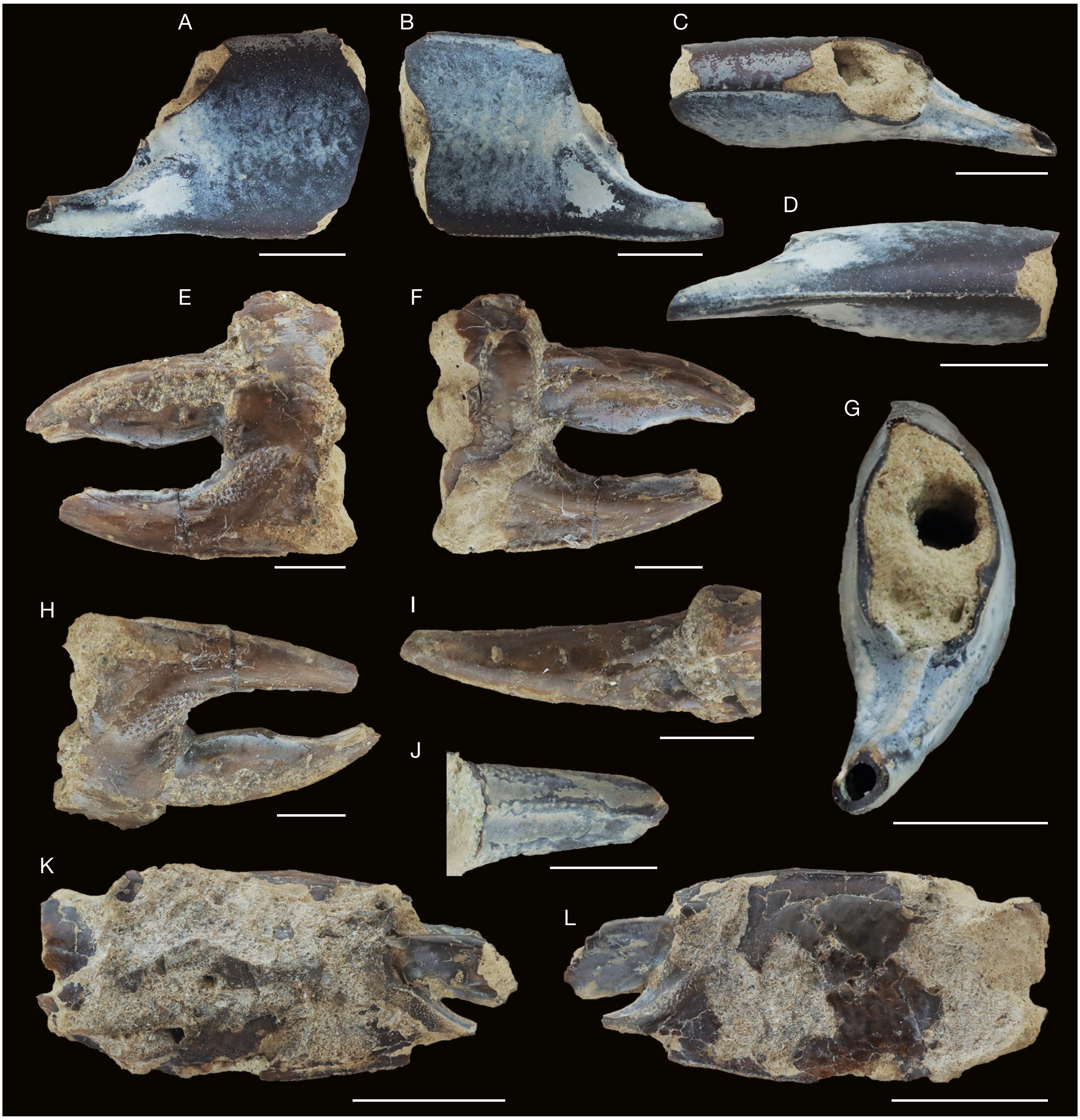

FIG. 6. — *Alphacheles zeta* (Rathbun, 1936) n. comb. from the lower Danian Pine Barren Member (Clayton Formation) at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**D**, outer, inner, upper marginal, and lower marginal views of major left propodus (ALMNH:Paleo:21511); **E**, **F**, outer and inner views of partial propodus and dactylus (MMNS IP-7255.1); **G**, frontal view of major left propodus (ALMNH:Paleo:21511); **H**, partial occlusal view of dactylus (MMNS IP-7255.1); **I**, upper marginal view of dactylus (MMNS IP-7255.1); **J**, occlusal view of fixed finger (UF 303822); **K**, **L**, outer and inner views of propodus and partial dactylus (MMNS IP-7255.2). Scale bars: A-J, 2.0 mm; K, L, 5.0 mm.Credits: photos by Adiël A. Klompmaker.

TYPE LOCALITY. — Prairie Creek region, Wilcox County, Alabama, United States.

DIAGNOSIS. — Major cheliped propodus palm slightly longer than high (L/H = 1.1-1.3), upper and lower margins carinate, subparallel with each other, inner and outer surfaces with densely tuberculate, sharply delineated areas at base of fixed finger, forming part of broad longitudinal ridges; fixed finger approximately 0.7 as long as upper palm length, slender, occlusal surface with continuous row of microdenticles; major cheliped dactylus upper margin convex, occlusal margin sinuous.

MEASUREMENTS. — Palm length in mm: ALMNH:Paleo:21511: *c.* 5.0, USNM MO 371506: 6.8.

DESCRIPTION

Major cheliped propodus palm slightly longer than high: 1.1-1.3 as long as high (measured at upper margin), highest at palm mid-length; proximo-lower corner rounded; upper and lower margins subparallel with each other, lower margin

Fig. 7. — Pectinate finger of *Ctenocheles* sp. from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**D**, outer, inner, lower margin, and occlusal views (ALMNH:Paleo:21514). Scale bar: 5.0 mm. Credits:

with slight concavity at junction with fixed finger; upper and lower margins sharply carinate, carinae accompanied with rows of small setal pores on both sides (inner and outer); outer lateral largely surface smooth, with few setal pores and two densely tuberculated, sharply delineated areas: circular patch of tubercles positioned below articulation with dactylus and oval patch of tubercles forming broad longitudinal ridge at base of fixed finger; inner lateral surface with similar tuberculate longitudinal ridge and several scattered tubercles close to articulation with dactylus.

Fixed finger approximately 0.7 as long as upper palm length, slender, subcircular in cross section, distal half bent slightly upward; occlusal surface with continuous row of microdenticles. Major cheliped dactylus upper margin convex; outer and inner lateral surfaces with rows of setal pores along upper margin and occlusal margin; occlusal margin sinuous forming elongate convexity proximally and slightly shorter concavity distally. Minor cheliped propodus palm 1.4 as long as high (measured at upper margin), upper and lower margin subparallel; fixed finger presumably as long as palm, occlusal surface with one tooth at mid-length; dactylus slender, occlusal margin continuous.

Remarks

Rathbun (1935a: pl. 15.23-15.25, 15.27) figured two specimens, one of which is the holotype (USNM MO 371506). The Smithsonian Institution assigned USNM PAL 336022 A to the figured propodus considered a paratype and USNM PAL 336022 B to 10 other paratype propodi specimens, verified by AAK in 2018. This totals 12 specimens rather than the 11 specimens Rathbun (1935a) mentioned.

Genus *Ctenocheles* Kishinouye, 1926

Type species. — *Ctenocheles balssi* Kishinouye, 1926, by monotypy.

Diagnosis. — See Poore *et al.* (2019: 119).

Ctenocheles sp.
(Fig. 7)

Material examined. — **United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21514 (finger).

Measurement. — Finger length: 12.0 mm.

Description

Incomplete pectinate finger, thin, rounded to slightly oval in cross-section, somewhat curved in lateral and occlusal views. Teeth on occlusal surface of at least three sizes; with smaller ones in between larger ones, number of which varies. Inner, outer, and lower sides with small, variably sized pits.

Discussion

Tshudy & Sorhannus (2000) and Hyžný & Dulai (2014) pointed out that pectinate claws evolved in multiple, often distantly related decapod lineages including Astacidea Latreille, 1802 (Nephropidae Dana, 1852: *Acanthacaris* Bate, 1888 [extant], *Oncopareia* Bosquet, 1854 [Early Cretaceous-Paleocene], *Thaumastocheles* Wood-Mason, 1874 [extant], *Thaumastochelopsis* Bruce, 1989 [extant]); Astacidea (Stenochiridae Beurlen, 1928: *Stenochirus* Oppel, 1861 [Early to Late Jurassic]); Axiidea (Ctenochelidae: e.g., *Ctenocheles* [Early Cretaceous-Holocene]); Brachyura Latreille, 1802 (Iphiculidae Alcock, 1896 [Miocene-Holocene] and Leucosiidae Samouelle, 1819 [Eocene-Holocene]); Glypheidea Van Straelen, 1925 (Litogastroidae Karasawa, Schweitzer & Feldmann, 2013: *Lissocardia* von Meyer, 1851 [Middle Triassic]); and Polychelida (Palaeopentachelidae Ahyong, 2009: *Palaeopentacheles* von Knebel, 1907 [Late Jurassic]). Thus, uncritical assignment of isolated claw elements to any of these is not justified, but a combination of stratigraphic and geographic occurrence can narrow down possibilities substantially. The stratigraphic occurrence of the aforementioned taxa excludes most taxa, leaving Ctenochelidae and *Oncopareia* as possibilities. Tshudy *et al.* (2022) revised *Oncopareia* to include European records only, making assignment of ALMNH:Paleo:21514 to this taxon unlikely. Within Ctenochelidae, some representatives of multiple genera bear pectinate claws including *Ctenocheles*, *Ctenocheloides*, and *Kiictenocheloides*. Of these, only *Ctenocheles* is recognized in the fossil record thus far. Therefore, we assign the specimen to *Ctenocheles* with some provision. This early Danian specimen differs from the late Danian *Ctenocheles cookei* (Rathbun, 1935a) from Alabama because the teeth of *C. cookei* are more similar in size and the pits on the sides are more aligned. It also differs from the late Danian *Ctenocheles cultellus* (Rathbun, 1935a) from Alabama in that

C. cultellus has an oval rather than a rounded cross-section of the finger. In the absence of more complete specimens with both fingers and a propodus preserved, we refer the specimen to *Ctenocheles* sp.

Family EUCALLIACIDAE Manning & Felder, 1991

Type genus. — *Eucalliax* Manning & Felder, 1991.

Remarks

The family has a well-documented fossil record with a stratigraphic span reaching back to Late Cretaceous (Cenomanian) (Charbonnier *et al.* 2017). The assignment of the fossil material consisting of isolated cheliped elements to various eucalliacid genera was discussed in several studies (Hyžný 2012; Hyžný & Hudáčková 2012; Hyžný & Gašparič 2014). However, recent revisions of extant representatives based both on molecular and morphological characters (Poore *et al.* 2019; Robles *et al.* 2020; Poore 2021) call for re-evaluation of the fossil record of these animals.

Genus *Eucalliaxiopsis* Sakai, 2011

Type species. — *Eucalliax cearaensis* Rodrigues & Manning, 1992, by original designation and monotypy.

Included fossil species. — *Eucalliaxiopsis alabamensis* (Rathbun, 1935a) n. comb.; *E. pseudorakosensis* (Lőrenthey *in* Lőrenthey & Beurlen, 1929).

Diagnosis. — See Sakai (2011: 503, 504).

Remarks

The assignment of *Callianassa alabamensis* Rathbun, 1935, to *Eucalliaxiopsis* is based on the combination of the following characters: a subquadrate manus, a triangular fixed finger with an oblique longitudinal ridge, and a smooth lower margin of cheliped merus. The oblique longitudinal ridge is also present in *Calliaxina* Ngoc-Ho, 2003 (Hyžný 2012; Poore 2021), but it is accompanied by a lateral concavity in the minor chela in this genus (Hyžný 2012), a character which is not identified in *C. alabamensis*. In *Calliaxina*, the lower margin of the cheliped merus has denticles (Poore 2021), whereas it is smooth in *C. alabamensis*. The observed variation of two morphotypes of cheliped dactylus in *C. alabamensis* corresponds to differences between major and minor claws as exemplified in extant species of *Eucalliaxiopsis* (Poore 2021).

At least some fossil species of *Eucalliax* Manning & Felder, 1991, as listed by Schweitzer *et al.* (2010) and Hyžný & Klompmaker (2015), probably belong to *Eucalliaxiopsis*. This is because they were assigned to *Eucalliax* largely based on similarities with some extant species, previously classified within *Eucalliax*. Recent revisions (Poore *et al.* 2019; Robles *et al.* 2020; Poore 2021) recognized the genus *Eucalliax* to be monotypic, with the only extant representative being its type species, *E. quadracuta* (Biffar, 1970), while the species previously treated under *Eucalliax* were reassigned to other eucalliacid genera. In this respect, Hyžný & Dulai (2021) reassigned *Eucalliax pseudorakosensis* (Lőrenthey in Lőrenthey & Beurlen, 1929) from the Miocene of Central Europe to *Eucalliaxiopsis*. Other fossil species of *Eucalliax* are still pending revision.

Eucalliaxiopsis alabamensis (Rathbun, 1935a) n. comb.
(Figs 8-10)

Callianassa alabamensis Rathbun, 1935a: 70-71, pl. 15.7-15.10.

Type material. — **Holotype. United States** • Alabama, Wilcox County, Prairie Creek and Pine Barren section; Porters Creek Formation; Paleocene (upper Danian); USNM MO 371505.
Paratypes. United States • 1 specimen; same as for the holotype; USNM PAL 327231 A • 5 specimens; idem; USNM PAL 327231.

Additional material examined. — **United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21509 (partial propodus) • 1 specimen; idem; ALMNH:Paleo:21510 (base fixed finger) • 1 specimen; idem; MMNS IP-7251 (cheliped) • 1 specimen; idem; ALMNH:Paleo:21549 (fixed finger and dactylus) • 1 specimen; idem; ALMNH:Paleo:21552 (fixed finger and dactylus) • 2 specimens; idem; ALMNH:Paleo:21548 (dactyli) • 16 specimens; idem; ALMNH:Paleo:21551 (dactyli) • 22 specimens; idem; ALMNH:Paleo:21554 (dactyli) • 1 specimen; idem; MMNS IP-7256.3 (dactylus) • 8 specimens; idem; MMNS IP-7256.6-13 (dactyli) • 1 specimen; idem; UF 303824 (dactylus) • 1 specimen; idem; UF 303829 (dactylus) • 1 specimen; idem; UF 303830 (dactylus) • 1 specimen; idem; UF 303832 (dactylus) • 1 specimen; idem; UF 303833 (dactylus) • 1 specimen; idem; UF 303834 (dactylus) • 1 specimen; idem; UF 303835 (dactylus) • 1 specimen; idem; UF 303836 (dactylus) • 1 specimen; idem; UF 303837 (dactylus) • 1 specimen; idem; UF 303840 (dactylus) • 1 specimen; idem; UF 303841 (dactylus of ?minor) • 1 specimen; idem; UF 303842 (dactylus) • 1 specimen; idem; UF 303843 (dactylus) • 1 specimen; idem; UF 303844 (dactylus) • 1 specimen; idem; UF 303845 (dactylus) • 1 specimen; idem; UF 303847 (dactylus) • 1 specimen; idem; UF 303848 (dactylus) • 1 specimen; idem; UF 303849 (dactylus) • 1 specimen; idem; UF 303850 (dactylus) • 1 specimen; idem; UF 303851 (dactylus) • 1 specimen; idem; UF 303853 (dactylus) • 1 specimen; idem; UF 303856 (dactylus) • 1 specimen; idem; UF 303857 (dactylus) • 1 specimen; idem; UF 303862 (dactylus) • 1 specimen; idem; UF 303863 (dactylus) • 1 specimen; idem; UF 303864 (dactylus) • 1 specimen; idem; UF 303865 (dactylus of ?minor) • 7 specimens; idem; ALMNH:Paleo:21550 (fixed fingers) • 6 specimens; idem; ALMNH:Paleo:21553 (fixed fingers) • 2 specimens; idem; MMNS IP-7256.4-5 (fixed fingers) • 1 specimen; idem; UF 303823 (fixed finger) • 1 specimen; idem; UF 303825 (fixed finger) • 1 specimen; idem; UF 303826 (fixed finger) • 1 specimen; idem; UF 303827 (fixed finger) • 1 specimen; idem; UF 303828 (fixed finger) • 1 specimen; idem; UF 303831 (fixed finger) • 1 specimen; idem; UF 303838 (fixed finger) • 1 specimen; idem; UF 303839 (fixed finger) • 1 specimen; idem; UF 303846 (fixed finger) • 1 specimen; idem; UF 303852 (fixed finger) • 1 specimen; idem; UF 303854 (fixed finger) • 1 specimen; idem; UF 303855 (fixed finger) • 1 specimen; idem; UF 303858 (fixed finger) • 1 specimen; idem; UF 303859 (fixed finger) • 1 specimen; idem; UF 303861 (fixed finger).

Type horizon. — Porters Creek Formation (Sucarnoochee beds in Rathbun 1935a), upper Danian.

Type locality. — Prairie Creek and Pine Barren section, Wilcox County, Alabama, United States.

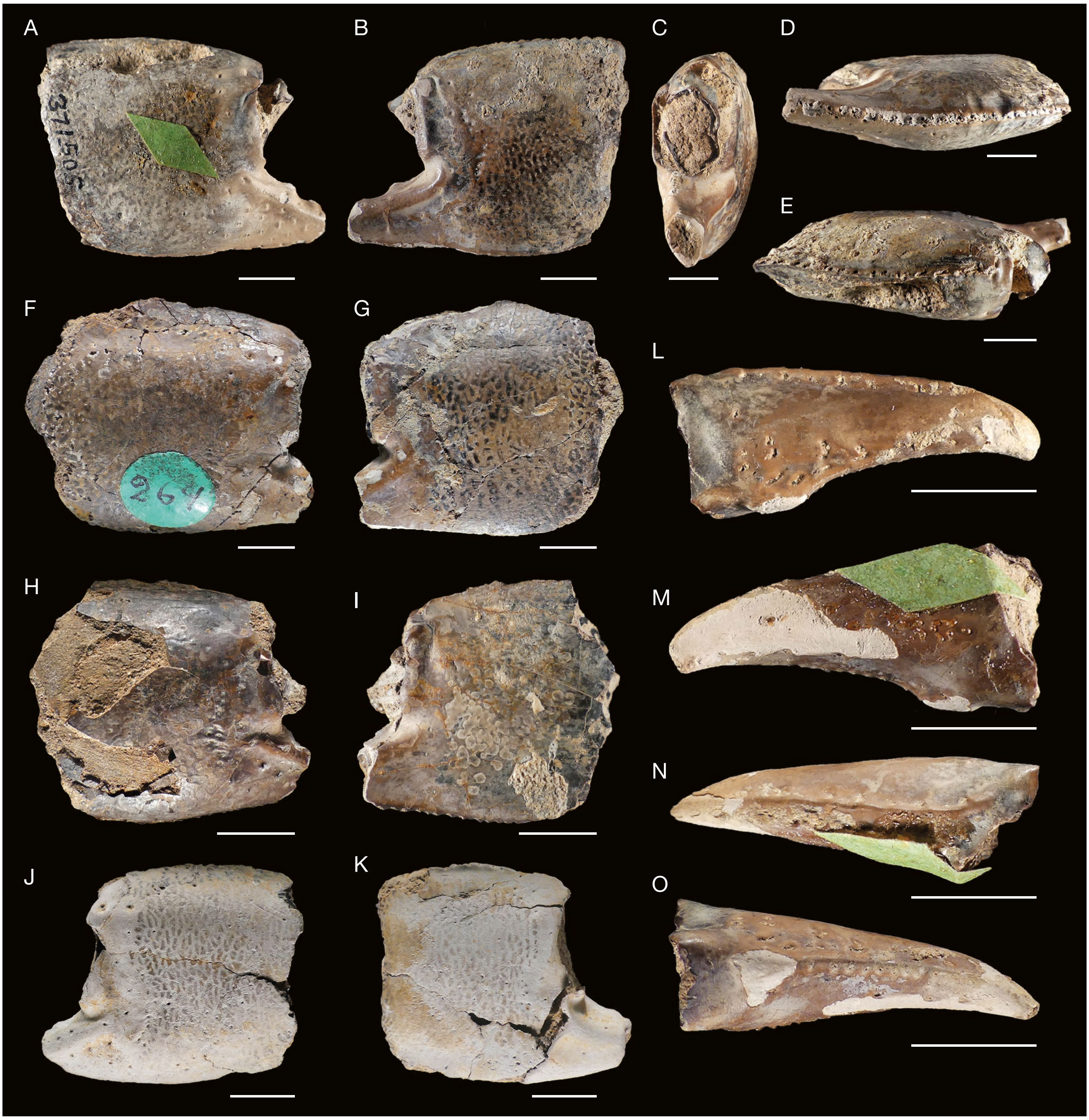

Fig. 8. — Type specimens of *Eucalliaxiopsis alabamensis* (Rathbun, 1935a) n. comb. from the upper Danian Porters Creek Formation from the Prairie Creek and Pine Barren section, Wilcox County, Alabama: **A**-**E**, outer, inner, frontal, lower marginal, and upper marginal views of major right propodus of holotype (USNM MO 371505); **F**-**K**, outer and inner views of right (2×) and left major propodi of paratypes (USNM PAL 327231); **L**-**O**, outer, inner, upper marginal, and occlusal views of right dactylus of paratype (USNM PAL 327231 A). Scale bars: 5.0 mm. Credits: photos by Adiël A. Klompmaker.

Diagnosis. — Cheliped merus 1.6 times as long as high; outer lateral surface with longitudinal ridge at mid-height; lower margin smooth. Cheliped carpus 1.5 times as high as length at upper margin. Cheliped propodus palm approximately as high as length at upper margin; upper and lower margins carinate, carinae accompanied with rows of setal pores on both sides (inner and outer), carina on lower margin forming microdenticles distally (along fixed finger); distal margin of outer lateral surface with blunt tooth just below articulation with dactylus. Fixed finger approximately as long as upper palm length; outer lateral surface with oblique longitudinal ridge; fixed finger occlusal surface with proximal blunt tooth, entire occlusal surface (incl. proximal tooth) with numerous equally sized denticles. Dactylus upper margin straight, carinate; occlusal surface of robust dactylus morphotype with proximal blunt tooth followed with finely denticulated edge; occlusal surface of slender dactylus morphotype without proximal tooth.

Measurements. — Palm length (mm): MMNS IP-7251: 8.9, USNM MO 371505: *c.* 19.0.

FIG. 9. — *Eucalliaxiopsis alabamensis* (Rathbun, 1935a) n. comb. from the lower Danian Pine Barren Member (Clayton Formation) at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**E**, outer, inner, frontal, upper marginal, and lower marginal views of major right propodus (ALMNH:Paleo:21509); **F**-**I**, outer, inner, lower marginal, and occlusal views of left fixed finger (MMNS IP-7256.4); **J**-**M**, outer, inner, upper marginal, and occlusal views of robust left dactylus (MMNS IP-7256.6); **N**-**Q**, outer, inner, upper marginal, and occlusal views of slender right dactylus (UF 303857); **R**-**U**, outer, inner, upper marginal, and occlusal views of elongated, slender left dactylus (MMNS IP-7256.3); **V**, frontal view of right partial propodus and dactylus (ALMNH:Paleo:21549). Scale bars: 5.0 mm.Credits: photos by Adiël A. Klompmaker.

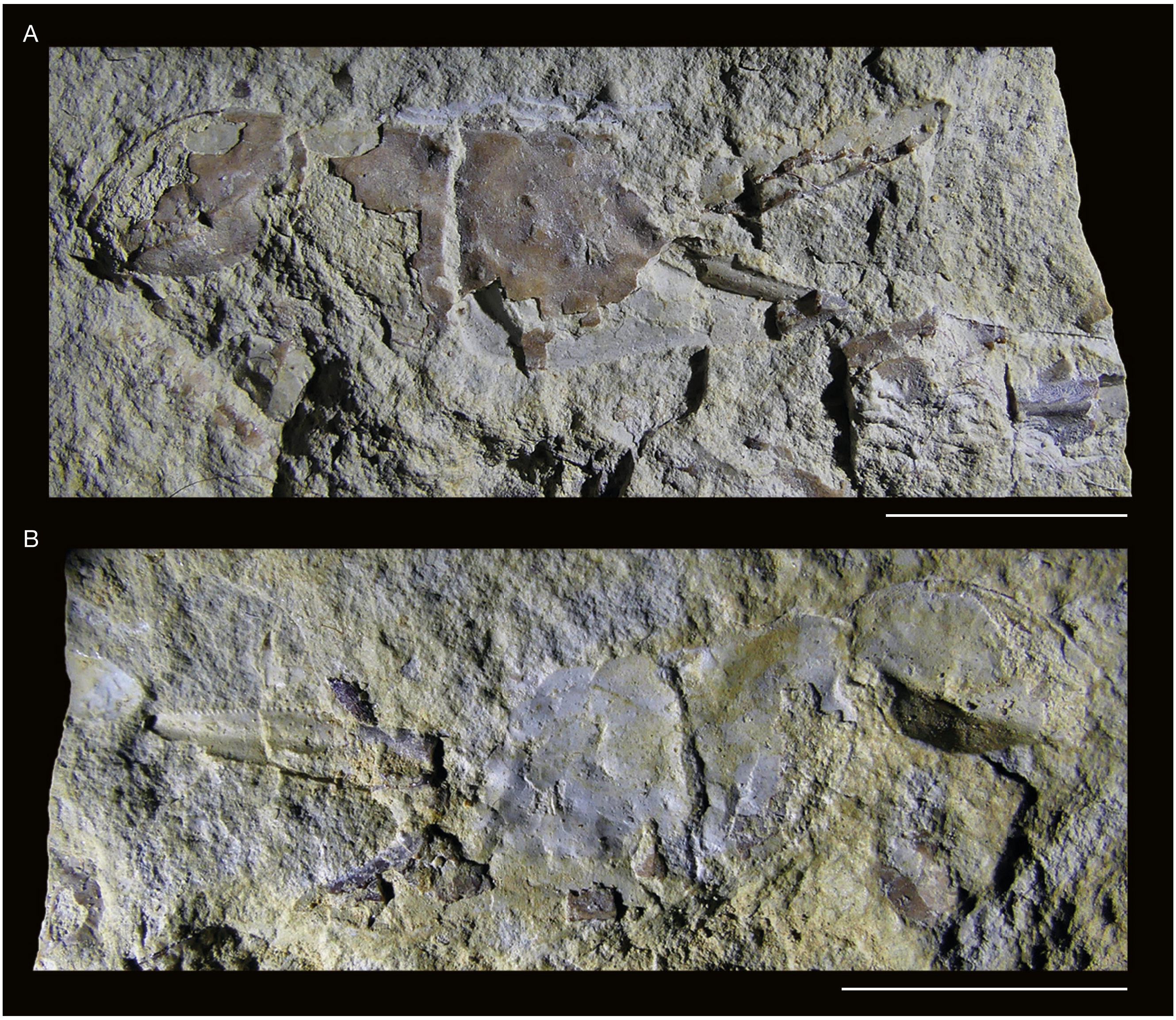

FIG. 10. — *Eucalliaxiopsis alabamensis* (Rathbun, 1935a) n. comb. from the lower Danian Pine Barren Member (Clayton Formation) at the roadcut of Mussel Creek, Lowndes County, Alabama (MMNS IP-7251): **A**, right major cheliped with, from left to right, the merus, carpus, propodus, and dactylus; **B**, counterpart. *In situ* nodule with specimen found *c.* 9.8 m above K-Pg boundary. Scale bars: 10.0 mm. Credits: photos by Adiël A. Klompmaker.

DESCRIPTION

Cheliped merus oval in outline, 1.6 times as long as high; outer lateral surface with longitudinal ridge at mid-height; lower margin distinctly convex, smooth. Cheliped carpus 1.5 times as high as length at upper margin; proximal margin rounded; distolateral margin square at lower angle. Cheliped propodus palm approximately as high as length at upper margin, highest proximally; proximo-lower corner rounded; upper and lower margins carinate, carinae accompanied with rows of setal pores on both sides (inner and outer), carina on lower margin forming microdenticles distally (along fixed finger); inner lateral surface with numerous setal pores concentrated close to distal margin and forming subvertical irregular row; outer lateral surface with setal pores concentrated distally, highest number of pores present close to junction with fixed finger; distal margin of outer lateral surface with blunt tooth just below articulation with dactylus. Fixed finger approximately as long as upper palm length, broadly oval in cross section; outer lateral surface with oblique longitudinal ridge, numerous setal pores scattered below ridge and in row above it along entire fixed finger length; fixed finger occlusal surface with proximal blunt tooth, entire occlusal surface (incl. proximal tooth) with numerous equally sized denticles, tip slightly bent upward. Dactylus upper margin straight, carinate; outer lateral surface with rows of setal pore clusters along upper and occlusal margins; inner lateral surface with several setal pore clusters along mid-length; occlusal surface of robust dactylus morphotype with proximal blunt tooth followed with finely denticulated edge; occlusal surface of slender dactylus morphotype without proximal tooth; dactylus tip slightly bent.

Remarks

Rathbun (1935a: pl. 15.7-15.10) figured two type specimens, the dactylus paratype, which received a new number subsequently (USNM PAL 327231 A), but she also mentioned the presence of more specimens (20 propodi and three fingers). Five additional specimens (USNM PAL 327231) are listed as paratypes in the Smithsonian Institution database and seen by AAK in 2018, but another catalog number used in Rathbun (1935a) (371504) does not return any match in their database. Thus, the whereabouts of 16 original specimens is uncertain.

Newly collected specimens match the type material in most details. Slight differences relate to the mode of preservation. The type specimens are partly abraded hindering the observation of minute details while the cuticular surfaces are better preserved in the newly collected material. For instance, the development of microdenticles on the lower margin of the propodus, the dentition on the occlusal edges of fingers and morphological details of setal pores are not well observable in the type material. Setal pores are arranged in clusters; the clusters are oval, distinctly elongate or V-shaped. Elongate setal pore clusters, oriented perpendicularly to the occlusal margin, are present especially on the outer lateral surface of dactyli, whereas V-shaped clusters are sometimes present on the outer lateral surface of the fixed fingers. The number of setal pores/setal pore clusters slightly varies when comparing the same parts of various specimens.

There are two morphotypes of dactyli identified in the newly collected material: the robust one, with the proximal tooth on the occlusal surface, and the slender one, without the respective tooth. The slender morphotype is interpreted to belong to a minor claw, whereas the robust morphotype is interpreted to belong to a major claw; such differences in the morphology of cheliped dactyli are known also in extant species of Eucalliacidae (Poore 2021). Based on the presence of a proximal tooth on the occlusal surface of the fixed finger, all studied propodi attributed to *E. alabamensis* n. comb. are interpreted to belong to major claws only; such a proximal tooth is missing in minor claws of eucalliacid shrimps (Hyžný 2012; Hyžný & Hudáčková 2012; Poore 2021).

Major chelipeds are sexually dimorphic in representatives of *Eucalliaxiopsis*, with males having the propodus palm proportionally longer than that of females (Poore 2021). The limited number of complete propodi does not allow an evaluation of this dimorphism in *E. alabamensis* n. comb., although one propodus (Fig. 8F, G) indeed appears to be proportionally longer than others and might represent a male individual.

The newly presented material of *E. alabamensis* n. comb. is the second report of the species, originally described nearly a century ago (Rathbun 1935a). It also adds further details to the description of the species, especially the morphology of the carpus and merus, previously unknown for this taxon. The range of the species is expanded from the late Danian to the early Danian.

From fossil congeners, *Eucalliaxiopsis alabamensis* n. comb. differs from *E. pseudorakosensis* mainly in the nature of major dactylus. In *E. pseudorakosensis*, the occlusal margin of the dactylus is armed with a distal tooth (Hyžný & Hudáčková 2012), which is entirely missing in *E. alabamensis* n. comb.

Infraorder ANOMURA MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family ?Diogenidae Ortmann, 1892

Genus ?*Paguristes* Dana, 1851

Type species. — *Paguristes hirtus* Dana, 1851, by subsequent designation (Stimpson 1858: 235).

"*Paguristes*" *johnsoni* Rathbun, 1935a
(Fig. 11)

Paguristes johnsoni Rathbun, 1935a: 78, pl. 14.13-14.18. — Cope *et al.* 2005: 101, pl. fig. 6.2.

Type material. — **Holotype. United States** • Alabama, Wilcox County, Prairie Creek and Pine Barren section; Porters Creek Formation; Paleocene (upper Danian); USNM MO 371705 (right propodus).
Paratype. United States • 1 specimen; same as for the holotype; USNM MO 371706 (left minor propodus and dactylus).

Additional material examined. — **United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21483 (right propodus + base of dactylus) • 1 specimen; idem; ALMNH:Paleo:21484 (left dactylus) • 1 specimen; idem; ALMNH:Paleo:21485 (right dactylus) • 1 specimen; idem; ALMNH:Paleo:21486 (?left fixed finger) • 1 specimen; idem; ALMNH:Paleo:21487 (right dactylus) • 1 specimen; idem; ALMNH:Paleo:21555 (left merus) • 1 specimen; idem; UF 303860 (right dactylus) • 1 specimen; Alabama, Sumter County, Tombigbee River, Black Bluff (32°22'22"N, 88°2'38"W), ALMNH loc. 5; Porters Creek Formation; Paleocene (upper Danian); ALMNH:Paleo:21495 (right propodus) • 1 specimen; idem; ALMNH:Paleo:21496 (right dactylus) • 1 specimen; idem; GSA-I21012 (right dactylus) • 1 specimen; Alabama, Wilcox County; Porters Creek Formation; Paleocene (upper Danian); GSA-I20984 (right propodus).

Type horizon. — Porters Creek Formation (Sucarnoochee beds in Rathbun 1935a), upper Danian.

Type locality. — Prairie Creek and Pine Barren section, Wilcox County, Alabama, United States.

Diagnosis. — Major palm short; about as long as high; tubercles with pit in center; diamond-shaped in cross-section; with sharp, convex upper and lower margins; upper margin shorter than lower margin; rounded ridges on outer and inner sides. Major dactylus with tubercles with pit in center and non-tubercular patches with setal pores on outer, upper, and part of inner sides; occlusal surface with a few large teeth and a smaller tooth on outer side of first tooth proximally, and a row of connected small teeth toward distal end.

Measurements. — Palm length (mm): ALMNH:Paleo:21483: 5.4 (as preserved); USNM MO 371705: 15.6; ALMNH:Paleo:21495: 10.4; GSA-I20984: 10.6 (as preserved).

Description

Reference is made to Rathbun (1935a: 78). Additionally: major dactylus curved inward; tubercles with pit in center and non-tubercular patches with setal pores on outer, upper, and part of inner sides; occlusal surface with a few large teeth and a smaller tooth on outer side of first tooth proximally, and a row of connected small teeth toward distal end.

Remarks

The single right propodus available (ALMNH:Paleo:21483) from Mussel Creek is incomplete but closely resembles the holotype of *Paguristes johnsoni* (USNM MO 371705, right propodus) and other right propodi (ALMNH:Paleo:21495, right propodus; GSA-I20984, right propodus) from the upper Danian Porters Creek Formation in Alabama in terms of overall shape, size, and distribution of the ornamentation, and the ridge on the outer surface.

The base of the dactylus is preserved along with the propodus from Mussel Creek (ALMNH:Paleo:21483), showing the base of the first large tooth and an adjacent small accessory tooth on the outer side that large tooth. This pattern resembles other isolated dactyli from Mussel Creek and dactyli from the Porters Creek Formation (ALMNH:Paleo:21496, GSA-I21012), which allows us to assign these specimens to *P. johnsoni* as well. The sample also contains an isolated finger that could be a fixed finger of this taxon (Fig. 11I, J). It contains a row of small teeth on the occlusal surface and might belong to the minor claw of this taxon because large teeth on the occlusal surface are often seen on both fingers of the major claw in paguroids, whereas small teeth are often seen on the minor claw in paguroids (e.g., Forest *et al.* 2000). The oblique row of small teeth on its inner proximal part matches that of the base of the fixed finger of the propodus (ALMNH:Paleo:21483). Dactyli of the major claw were unknown from this species thus far. A left merus possibly belonging to the same species was also found (ALMNH:Paleo:21555).

This species was briefly discussed in Bishop (1983: 419), citing a personal communication with Jaques Forest, who was in doubt that *Paguristes whitteni* Bishop, 1983, and *P. johnsoni* could be assigned to *Paguristes* or even paguroids. Tubercular propodi do not necessarily imply a paguroid affinity. Indeed, the propodi of *Paguristes whitteni* belong to carapace specimens of the brachyuran crab *Dakoticancer australis* Rathbun, 1935a (see Kornecki *et al.* 2017), also common at the same locality in Mississippi. We cannot assign the tubercular elements herein to a brachyuran carapace from the same assemblage. The dactyli and propodi are too large for *Alahexapus martini* (Feldmann, Schweitzer & Portell, 2014) n. comb. and the (distal) cheliped elements of other brachyuran taxa (see below) do not resemble the propodi/dactyli of *P. johnsoni.* The cheliped elements also cannot be linked to a brachyuran carapace from the Porters Creek Formation. Given the extensive collecting efforts at the Mussel Creek roadcut since 2010, the likelihood of finding other brachyuran taxa to which the claw elements could belong is low. We therefore suggest that the specimens represent a paguroid.

The fact that the right propodus is larger than the left propodus (see Rathbun 1935a: pl. 14.13-14.17), if both isolated elements are indeed from the same species, is inconsistent with Diogenidae, members of which usually have a larger left propodus or (sub)equal propodi (e.g., Tudge *et al.* 2012: 305), including *Paguristes*, which is mentioned to have isochelous propodi (Fraaije *et al.* 2015: 590). An exception within diogenids is *Petrochirus* Stimpson, 1858, but this taxon has scabrous ornamentation in the type species *Petrochirus diogenes* (Linnaeus, 1758) (see Hyžný & Dulai 2021: fig. 43.7) not seen in *P. johnsoni* and various fossil *Petrochirus* (Beschin *et al.* 2002, 2006, 2012). The dactyli herein closely resemble a dactylus identified as *Petrochirus* sp. from the Early Miocene of Venezuela (Feldmann & Schweitzer 2004: pl. 1.2-1.4), but this record has more teeth on the occlusal surface. It is likely these species belong to the same genus. We have not found close matches with other *Petrochirus* spp. More complete material with both left and right cheliped would be necessary to further evaluate the genus and family placement. For now, we treat the specimens as "*Paguristes*" *johnsoni* within Paguroidea.

The assignment of our material to *P. johnsoni* implies a range extension into the early Danian in Alabama. Cope *et al.* (2005) ascribed a propodus from the Clayton Formation of southern Illinois to *P. johnsoni*. The level of this specimen within the Clayton Formation was not reported, but potassium-argon dating on glauconite on the oldest sample from the Clayton Formation returned a date of 60.6 ± 1.3 Ma (Reed *et al.* 1977). This date suggests it is not the earliest Danian and that this propodus from Illinois is probably younger than the specimens herein.

Infraorder BRACHYURA Linnaeus, 1758
Section RANINOIDA De Haan, 1839 [in 1833-1850]
Superfamily RANINOIDEA De Haan, 1839 [in 1833-1850]
Family RANINIDAE De Haan, 1839 [in 1833-1850]
Subfamily RANINOIDINAE Lőrenthey
in Lőrenthey & Beurlen, 1929

Genus *Raninoides* H. Milne Edwards, 1837
[in 1834-1840]

TYPE SPECIES. — *Ranina laevis* Latreille, 1825, by monotypy.

INCLUDED SPECIES. — Extant species: *Raninoides benedicti* Rathbun, 1935b; *R. bouvieri* Capart, 1951; *R. crosnieri* Ribes, 1989; *R. hendersoni* Chopra, 1933; *R. intermedius* Dai & Xu, 1991; *R. laevis* (Latreille, 1825); *R. lamarcki* A. Milne Edwards & Bouvier, 1923; *R. longifrons* Chen & Türkay, 2001; *R. louisianensis* Rathbun, 1933; *R. personatus* Henderson, 1888. Exclusively fossil species: *R. acanthocolus* Schweitzer, Feldmann, González-Barba & Cosovic, 2006; *R. araucana* (Philippi, 1887); *R. asper* Rathbun, 1926; *R. borealis* (Collins & Wienberg Rasmussen, 1992); *R. budapestiniensis* (Lőrenthey, 1897); *R. danicus* n. sp.; *R. dickersoni* Rathbun, 1926; *R. eugenensis* Rathbun, 1926; *R. fabianii* (Lőrenthey in Lőrenthey & Beurlen, 1929); *R. fulgidus* Rathbun, 1926; *R. fulungensis* Hu & Tao, 1999; *R. glabra* (Woodward, 1871); *R. goedertorum* (Tucker, 1998); *R. gottschei* (Böhm, 1927); *R. granulofrons* Vega, Nyborg, Garassino, Pasini, Aguilar-Pérez, Borges-Sellén, Arano-Ruiz, Quintero-Vázquez &

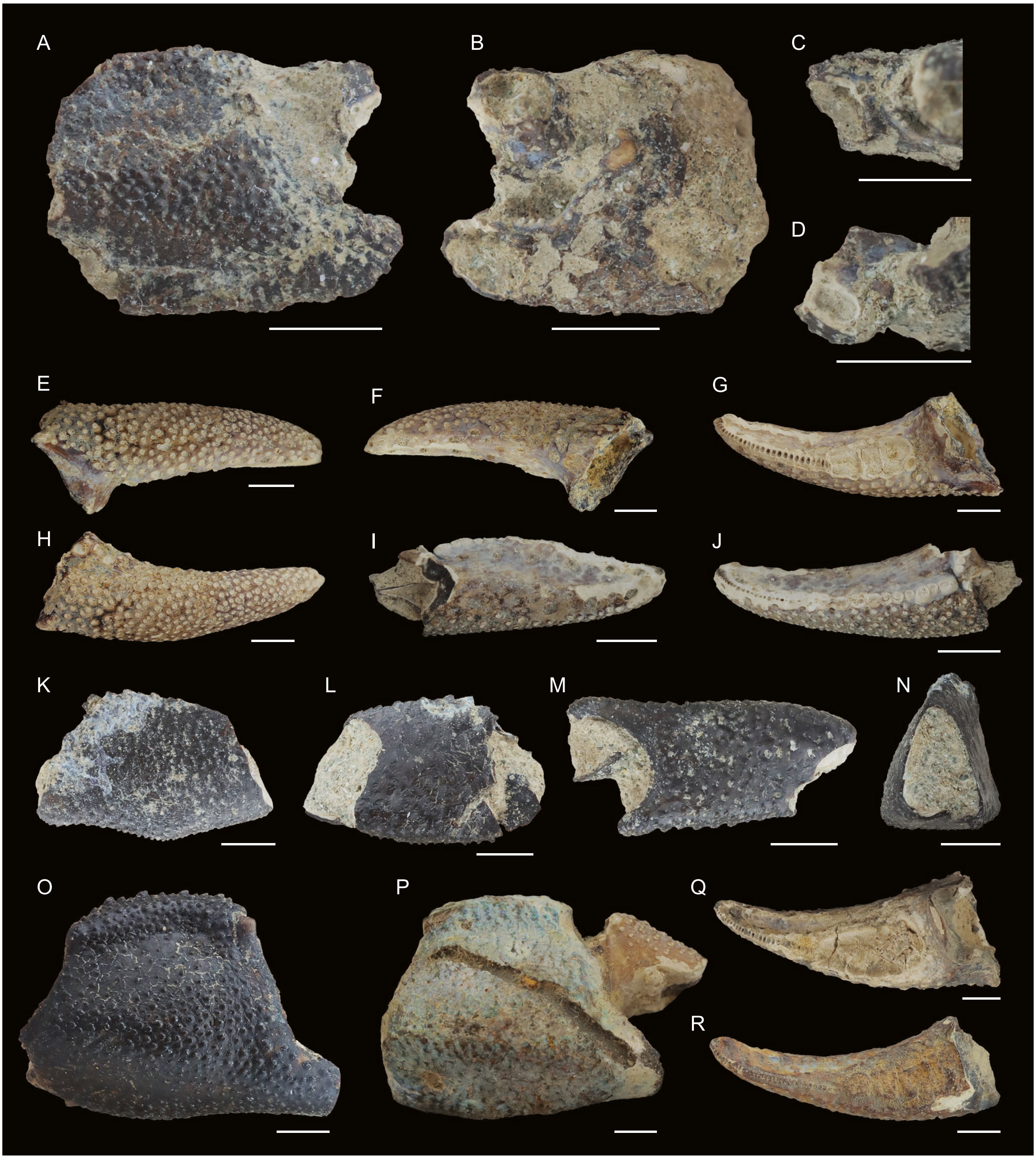

Fig. 11. — "*Paguristes*" *johnsoni* Rathbun, 1935a, from the lower Danian Pine Barren Member (Clayton Formation) at the roadcut of Mussel Creek, Lowndes County, Alabama (**A**-**N**), the upper Danian Porters Creek Formation at Black Bluff, Sumter County, Alabama (**O**, **Q**, **R**), and the upper Danian Porters Creek Formation in Wilcox County, Alabama (**P**): **A**, **B**, outer and inner views of right propodus (ALMNH:Paleo:21483); **C**, **D**, bases of fixed finger and dactylus (ALMNH:Paleo:21483); **E**-**H**, outer, inner, occlusal, and upper margin views of right dactylus (ALMNH:Paleo:21487); **I**, **J**, inner and occlusal views of possible left fixed finger (ALMNH:Paleo:21486); **K**-**N**, outer, inner, lower, and proximal views of left merus (ALMMH:Paleo:21555); **O**, **P**, outer views of right propodi (ALMNH:Paleo:21495 and GSA-I20984); **Q**, **R**, occlusal views of right dactyli (GSA-I21012 and ALMNH:Paleo:21496). Scale bars: 2.0 mm. Credits: photos by Adiël A. Klompmaker.

Gutiérrez-Domech, 2024; *R. hollandica* (Collins, Fraaye, Jagt & Van Knippenberg, 1997); *R. javanus* (Böhm, 1922); *R. madurensis* Beets, 1950; *R. mexicanus* Rathbun, 1930; *R. morrisi* Collins, Lee & Noad, 2003; *R. notopoides* (Bittner, 1883); *R. oregonensis* Rathbun, 1926; *R. perarmata* (Glaessner, 1960); *R. pliocenicus* De Angeli, Garassino & Pasini, 2009; *R. proracanthus* Schweitzer, Feldmann, González-Barba & Cosovic, 2006; *R. pulchra* (Beschin, Busulini, De Angeli & Tessier, 1988); *R. rathbunae* Van Straelen, 1933;

R. rioturbiensis Schweitzer, Feldmann, Casadío & Raising, 2012; *R. sinuosus* (Collins & Morris, 1978); *R. slaki* Squires, 2001; *R. treldenaesensis* Collins & Jakobsen, 2003; *R. vaderensis* Rathbun, 1926 (*Laeviranina lewisana* Rathbun, 1926); *R. toehoepae* (Van Straelen, 1924); *R. washburnei* Rathbun, 1926.

DIAGNOSIS. — See Karasawa *et al.* (2014: 258).

Raninoides danicus n. sp.
(Figs 12; 13; Appendices 1I, J; 2)

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Giulianolyreidus johnsoni (Rathbun, 1935a). — Feldmann *et al.* 2019: 285, fig. 5.

TYPE MATERIAL. — **Holotype. United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21488.
Paratypes. United States • 1 specimen; same as for the holotype; ALMNH:Paleo:5919 • 1 specimen; idem; ALMNH:Paleo:21489 • 1 specimen; idem; ALMNH:Paleo:21490 • 1 specimen; idem; ALMNH:Paleo:21491 • 1 specimen; idem; ALMNH:Paleo:21492.

ETYMOLOGY. — *danicus* refers to the first species of *Raninoides* recognized from the Danian.

ADDITIONAL MATERIAL EXAMINED. — **United States** • 5 specimens; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21493 • 1 specimen; idem; ALMNH:Paleo:21494 • 2 specimens; idem; MMNS IP-7252 • 4 specimens; idem; MMNS IP-7253 • 1 specimen; idem; MMNS IP-8792 • 1 specimen; idem; UF 303873.

TYPE HORIZON. — Pine Barren Member of the Clayton Formation, middle NP2 nannofossil zone, lower Danian.

TYPE LOCALITY. — ALMNH loc. 3: Mussel Creek roadcut (31°58'17"N, 86°42'15"W), Lowndes County, Alabama, United States.

DIAGNOSIS. — Carapace length-width ratio *c.* 1.45 without rostrum and spines. Fronto-orbital width *c.* 70% of maximum width; posterior margin 70% of maximum width. Front with outer orbital spine curving inward to form straight part, lined with tubercles; intra-orbital spine surrounded by deep fissures, outer part top of spine steep-sided and lined with tubercles; outermost part rostral section of front concave, lined with tubercles. Anterolateral margin with one strong spine near outer orbital angle and directed anterolaterally, otherwise mostly straight and lined with tubercles. Sinuous band of tubercles just posterior to frontal margin. Sternite 4 longer than wide.

MEASUREMENTS. — Maximum carapace width (mm): ALMNH:Paleo:21488: 12.3, ALMNH:Paleo:5919: 14.7, ALMNH:Paleo:21490: 12.3, MMNS IP-7252.1: 15.1, MMNS IP-7253.1: 8.8.

DESCRIPTION
Carapace longer than wide (l/w ratio *c.* 1.45 without rostrum and spines), moderately vaulted transversely, weakly vaulted longitudinally, widest around third of length. Fronto-orbital width *c.* 70% of maximum width; posterior margin 70% of maximum width. Front incompletely known, but with outer orbital spine curving inward to form straight part, lined with tubercles; intra-orbital spine surrounded by deep fissures, outer part top of spine steep-sided and lined with tubercles; outermost part rostral section of front concave, lined with tubercles. Suborbital margin lined with tubercles, mostly straight except near outer orbital spines and with single deep fissure. Orbit wider than tall. Anterolateral margin with one strong spine near outer orbital angle and directed anterolaterally, otherwise mostly straight and lined with tubercles; convex transition to mostly straight and longer posterolateral margin lined with tubercles. Convex transition from posterolateral margin to posterior margin, which exhibits a slight concavity axially and is smooth-rimmed. Axis of carapace with weak, rounded ridge. Carapace regions undefined, except for lateral parts of cardiac region in between concave-outward branchiocardiac grooves. Pair of posterior gastric pits in front of branchiocardiac grooves. Cuticle of dorsal carapace with widely spaced deep pits and more dense shallow pits, but with sinuous band of tubercles just posterior to frontal margin. Pterygostome with gentle ridge anteriorly, widening anteriorly, with sinuous buccal collar, with tubercular cuticle, uninterrupted transition to branchiostegite. Sternite 3 small, rounded laterally, with sharp tip and steep front; sternite 4 longer than wide, with concave lateral sides, episternites rounded; sternite 5 about equally long as wide, widening toward sternite 4, with axial groove; sternite 6 widening posteriorly, with concave posterior margin on either side of axis, with axial groove. Sternites 3-4 cuticular surface pitted but with tubercles along margins; tubercles on lateralmost parts of sternites 5 and 6 in dorsal view, and on transition from sternite 5 to 6. Pleurites 4-7 partly visible externally, smooth cuticular surface except for pleurite 4 and spines on pleurites 4-7 containing tubercles; pleurites with rims around pereiopod attachments. Coxae of maxilliped 3 curved forward, adjacent to lateral sides sternite 3. Oval attachment of cheliped pair to venter, circular for second pereiopod pair. Rostrum, pleon, and appendages not preserved.

REMARKS
Feldmann *et al.* (2019) ascribed three carapaces (MMNS IP-7252 [2 specimens] and MMNS IP-8792) to *Giulianolyreidus johnsoni* within Lyreidinae Guinot, 1993. The dorsal carapace is close to this species first described from the upper Danian Porters Creek Formation of Alabama (Rathbun 1935a: pl. 17.12-17.17 [as *Symethis johnsoni*]; Bishop & Whitmore 1986: fig. 1K [not 1G, 1H, 1J]; Waugh *et al.* 2009: fig. 11; Karasawa *et al.* 2014: fig. 12C, D) and later from the upper Danian Mexia Clay Member of the Wills Point Formation in Texas (Armstrong *et al.* 2009: fig. 4.1-4.2 [as *Macroacaena johnsoni*] [identification verified by AAK]), but the axial ridge is more prominent and the pits on the cuticular surface are larger in *G. johnsoni*. Moreover, the ventral side of multiple new specimens (ALMNH:Paleo:5919, ALMNH:Paleo:21488-21490, ALMNH:Paleo:21494) and MMNS IP-8792 show marked differences, revealing an axial groove

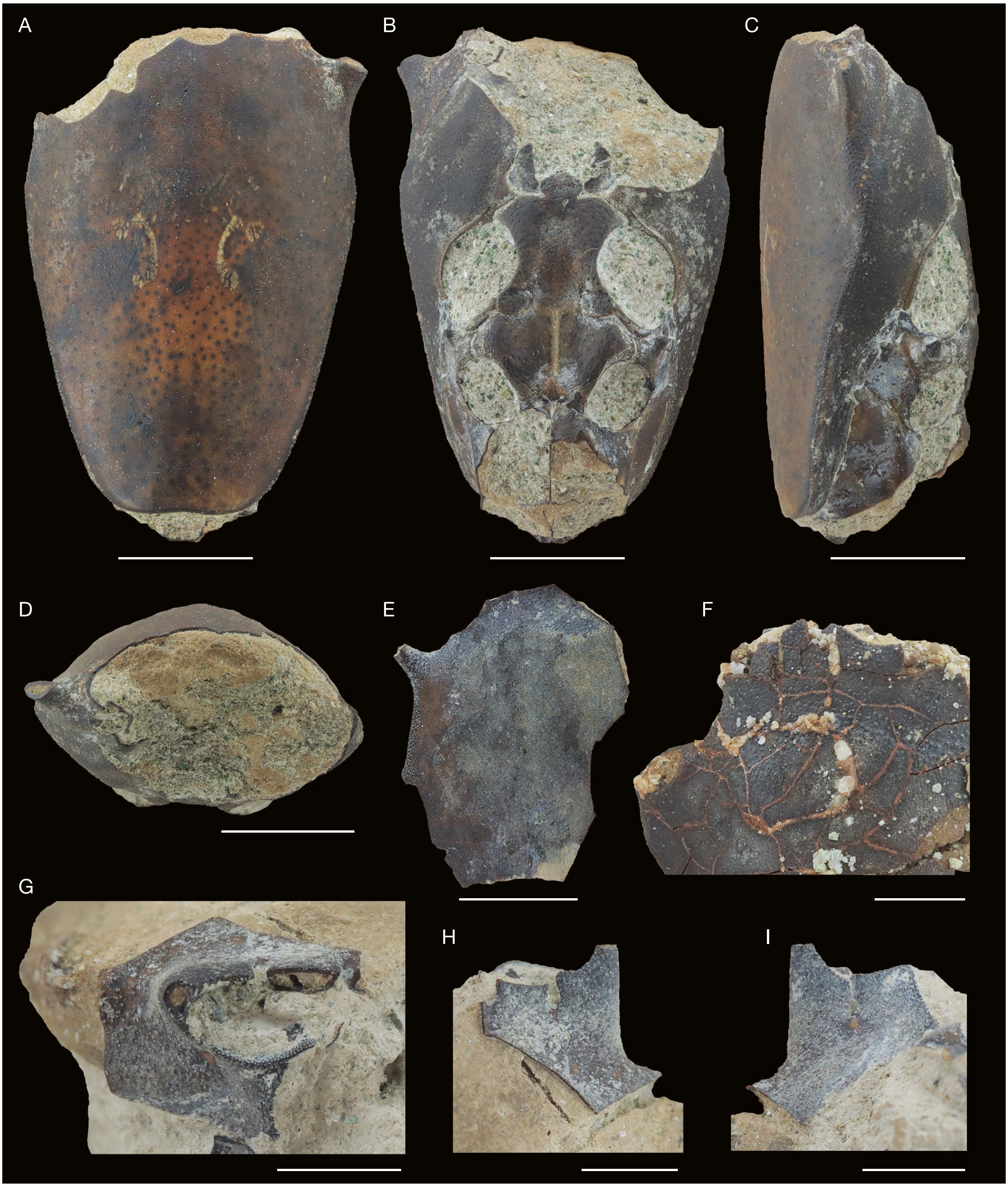

Fig. 12. — *Raninoides danicus* n. sp. from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**D**, dorsal, ventral, right lateral, and frontal views of holotype ALMNH:Paleo:21488; **E**, dorsal view of paratype ALMNH:Paleo:21492; **F**, dorsal view, focused on the left frontal margin, of paratype ALMNH:Paleo:21491; **G**-**I**, right orbital, upper orbital margin, and lower orbital margin views of paratype ALMNH:Paleo:5919. Scale bars: A-E, 5.0 mm; G-I, 2.0 mm. Credits: photos by Adiël A. Klompmaker.

on sternites 5 and 6 (Figs 12B; 13A, which *G. johnsoni* lacks (Rathbun 1935a: pl. 17.12). Comparable dorsal and ventral surfaces are found among Raninoidinae, such as *Notosceles* Bourne, 1922, and *Raninoides*. The main differences between these genera involve the development of the rostrum, orbital fissures, and the outer orbital spines (diagnoses in Karasawa *et al.* 2014, and Schweitzer *et al.* 2018b), but these features are not well-preserved in the specimens from Mussel Creek. Karasawa *et al.* (2014) diagnosed that *Notosceles* exhibits short open fissures, but one specimen herein (ALMNH:Paleo:21491) exhibits fairly deep fissures (Fig. 12F). An additional difference we noted is that the anterolateral spine is substantially larger and more anterolaterally directed in *Raninoides* than in *Notosceles*, in which a small spine is consistently more forwardly directed across all species (see extant species and *Notosceles bournei* Rathbun, 1928, from the Paleocene of Texas, Alabama, and Arkansas, see Rathbun 1935a). Many extant and fossil *Raninoides* have a strong anterolaterally directed spine, consistent with our specimens. This genus is diagnosed to exhibit a bifid outer orbital spine (Karasawa *et al.* 2014; Schweitzer *et al.* 2018b), but this does not apply to all species assigned to this genus because several members have a straight plateau inward from a single spine rather than another spine (e.g., Paleocene *R. borealis*, extant *R. crosnieri*, extant *R. longifrons*, and extant *R. personatus*). None of the fossil specimens studied here have the tip of the outer orbital spine preserved, but two specimens show a straight plateau inward in addition to the base of the outer orbital spine (ALMNH:Paleo:5919 and MMNS-IP7253.2). Thus, we assign the specimens to *Raninoides* with confidence.

Reasons for species separation often include the orientation, size, and location of the anterolateral spine; the development of the frontal margin and post-frontal ridge, and carapace proportions (e.g., Collins *et al.* 2003; Schweitzer *et al.* 2006, 2012; De Angeli *et al.* 2009). The early Danian *Raninoides danicus* n. sp. differs from all other species. The stratigraphically closest species are *R. borealis* from the middle Paleocene (Selandian) of West Greenland and *R. granulofrons* from the late Campanian-early Maastrichtian of Cuba. Based on a study of the type material by AAK, *R. borealis* bears an anterolateral spine that may be farther from the outer orbital margin, this spine is oriented more forward, and the intra-orbital spine is more rounded. *Raninoides granulofrons* bears an intra-orbital spine that is more rounded on top, and the preserved base of the anterolateral spine is smaller, mentioned to be short by Vega *et al.* (2024).

We also compared this species to Eocene species, using the papers in which those species were first described and other papers as needed. *Raninoides acanthocolus* bears a shorter anterolateral spine further back on the anterolateral margin and the upper margin of the intraorbital spine slopes inward (Schweitzer *et al.* 2006: fig. 2.7). *Raninoides araucana* bears a smaller anterolateral spine (Philippi 1887: pl. 50.6). *Raninoides budapestiniensis* has an anterolateral spine further back on the anterolateral margin and a stronger postfrontal ridge (Lőrenthey 1898: pl. 1.2). *Raninoides dickersoni,* only known from a venter, has a wider spine on sternite 5 (Rathbun 1926: pl. 20.5). *Raninoides fabianii* apparently lacks anterolateral spines (Lőrenthey & Beurlen 1929: pl. 4.10). *Raninoides fulgidus* has a proportionally smaller anterolateral spine (Rathbun 1926: pl. 23.6; ALMNH:Paleo:5937). *Raninoides glabra* has the axial groove more forward onto the posterior part of sternite 4 (near the center of episternite 4) and sternite 4 is proportionally longer (see Van Bakel *et al.* 2012: fig. 44c, d). *Raninoides goedertorum* and *R. notopoides* exhibit smaller and more forwardly oriented anterolateral spines (Tucker 1998: fig. 13; Hyžný & Zorn 2016: pl. 9.3). *Raninoides gottschei* has a smaller anterolateral spine (Glaessner & Withers 1931: pls 20.1-2, 21.1). *Raninoides perarmata* and *R. rathbunae* have proportionally shorter sternites 4 (Feldmann 1991: figs 2, 4; Feldmann & Schweitzer 2004: fig. 1B). *Raninoides proracanthus* bears a much smaller anterolateral spine (Feldmann & Schweitzer 2004: fig. 2.8). *Raninoides pulchra* exhibits an anterolateral spine that is bifid near its base (Beschin *et al.* 1988: pl. 4.1-3). *Raninoides rioturbiensis* has a longer intraorbital spine narrowing to the front and the base of the anterolateral spine is smaller (Schweitzer *et al.* 2012: fig. 4). *Raninoides sinuosus* exhibits a smaller base of the anterolateral spine and sternite 4 is proportionally shorter (Collins & Morris 1978: pl. 116.4-6). *Raninoides slaki* has a bifid intra-orbital spine and the maximum carapace width is located further posteriorly (Squires 2001: figs 47-55). *Raninoides treldenaesensis* bears a smaller anterolateral spine and sternite 4 is proportionally shorter (Collins & Jakobsen 2003: fig. 4, pl. 3.5). *Raninoides vaderensis* appears close but its anterolateral spine is oriented more forwardly (Rathbun 1926: pl. 22.5; Tucker 1998: fig. 17; Gustafson 2023: figs 16-19). *Raninoides washburnei* has a more forwardly oriented anterolateral spine and its carapace is proportionally wider (Rathbun 1926: pl. 22.6). We did not compare the new species to post-Eocene species because brachyuran species ranging for >32 million years are extremely unlikely and unknown to us.

Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily Retroplumoidea Gill, 1894
Family Retroplumidae 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; *C. bifida* Collins, Higgs & Cortitula, 1994; *C. bishopi* Vega & Feldmann, 1992; *C. binodosa* Collins & Wienberg Rasmussen, 1992; *C. concava* Collins & Morris, 1975; *C. grayi* Feldmann & Portell, 2007; *C. maroccana* Ossó-Morales, Artal & Vega, 2010; *C. mexicana* Vega-Vera & Perrilliat, 1989; *C. mamethioupamei* Hyžný, Perrier, Robin, Martin & Sarr, 2016; *C. nicksabani* n. sp.; *C. nordestina* Feldmann & Martins-Neto, 1995; *C. salamanca* Feldmann, Rodriguez, Martinez & Aguirre-Urreta, 1997; *C. squiresi* Nyborg, Vega & Filkorn, 2023; *C. texana* Armstrong, Nyborg, Bishop, Ossó-Morales & Vega, 2009; *C. senegalensis* (Rémy *in* Gorodiski & Rémy, 1959).

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 often biconvex forwards; posterior two ridges converging axially defining depressed, triangular to rectilinear, smooth mesobranchial region. Rostrum generally narrow, downturned, bilobed. Carapace flanks distinct,

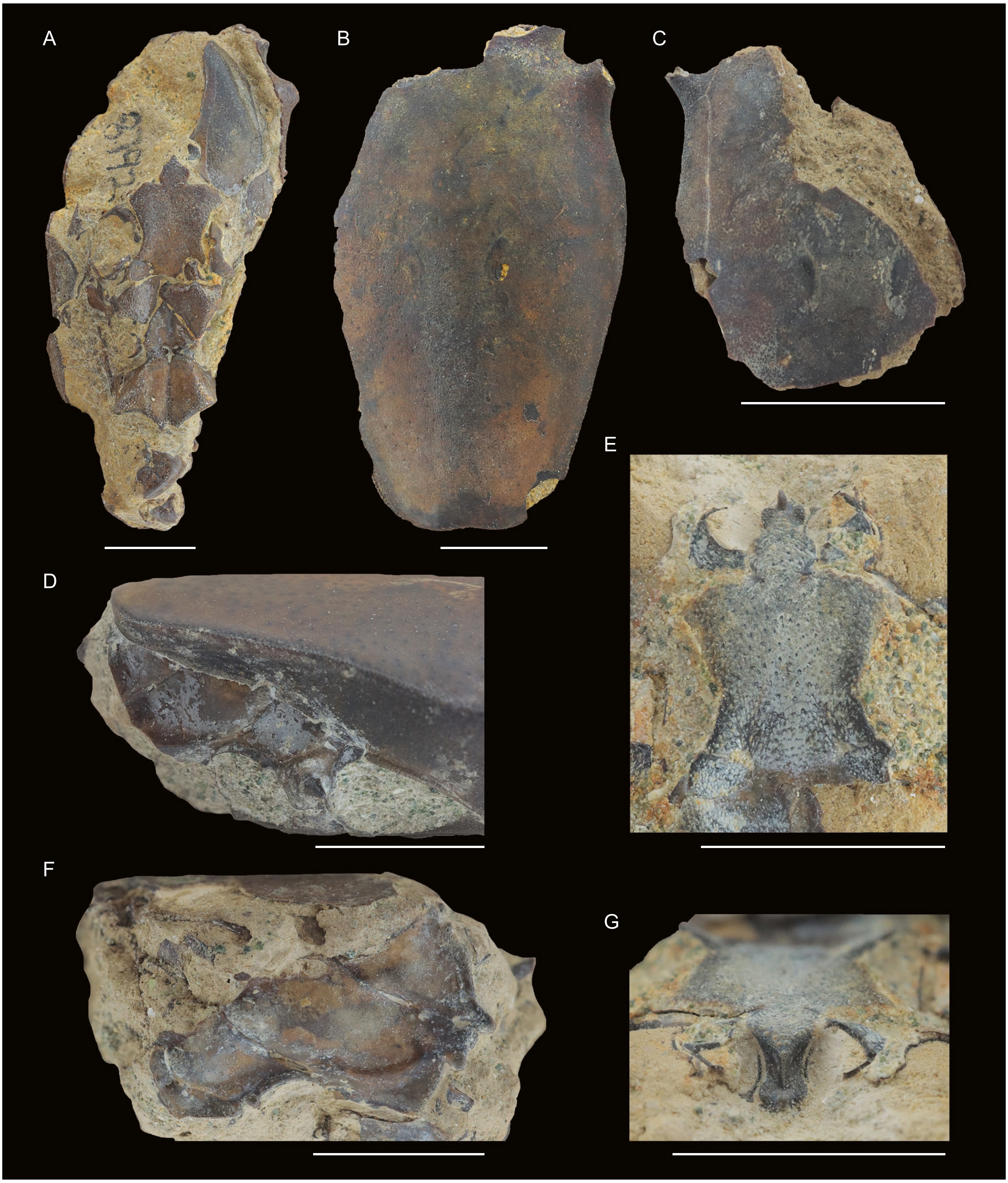

FIG. 13. — *Raninoides danicus* n. sp. from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**, ventral view of MMNS IP-8792; **B**, dorsal view of MMNS IP-7252.1; **C**, dorsal view of MMNS IP-7253.1; **D**, right posterolateral view of holotype ALMNH:Paleo:21488; **E**, ventral view focused on sternites 3-4 of paratype ALMNH:Paleo:21490; **F**, left posterolateral view of paratype ALMNH:Paleo:21489; **G**, frontal view of sternite 3 of paratype ALMNH:Paleo:21490. Scale bars: 5.0 mm. Credits: photos by Adiël A. Klompmaker.

about perpendicular to dorsal surface and separated from it by beaded rim. Sternum broad, with well-defined sternites; sternites 5-7 each with prominent transverse, beaded ridge; male sternopleonal cavity deep, reaching end of sternite 4. Transverse ridges also present on pleonal somites. Pereiopod 5 subdorsal, reduced. Emended from Feldmann *et al.* (2014: 137).

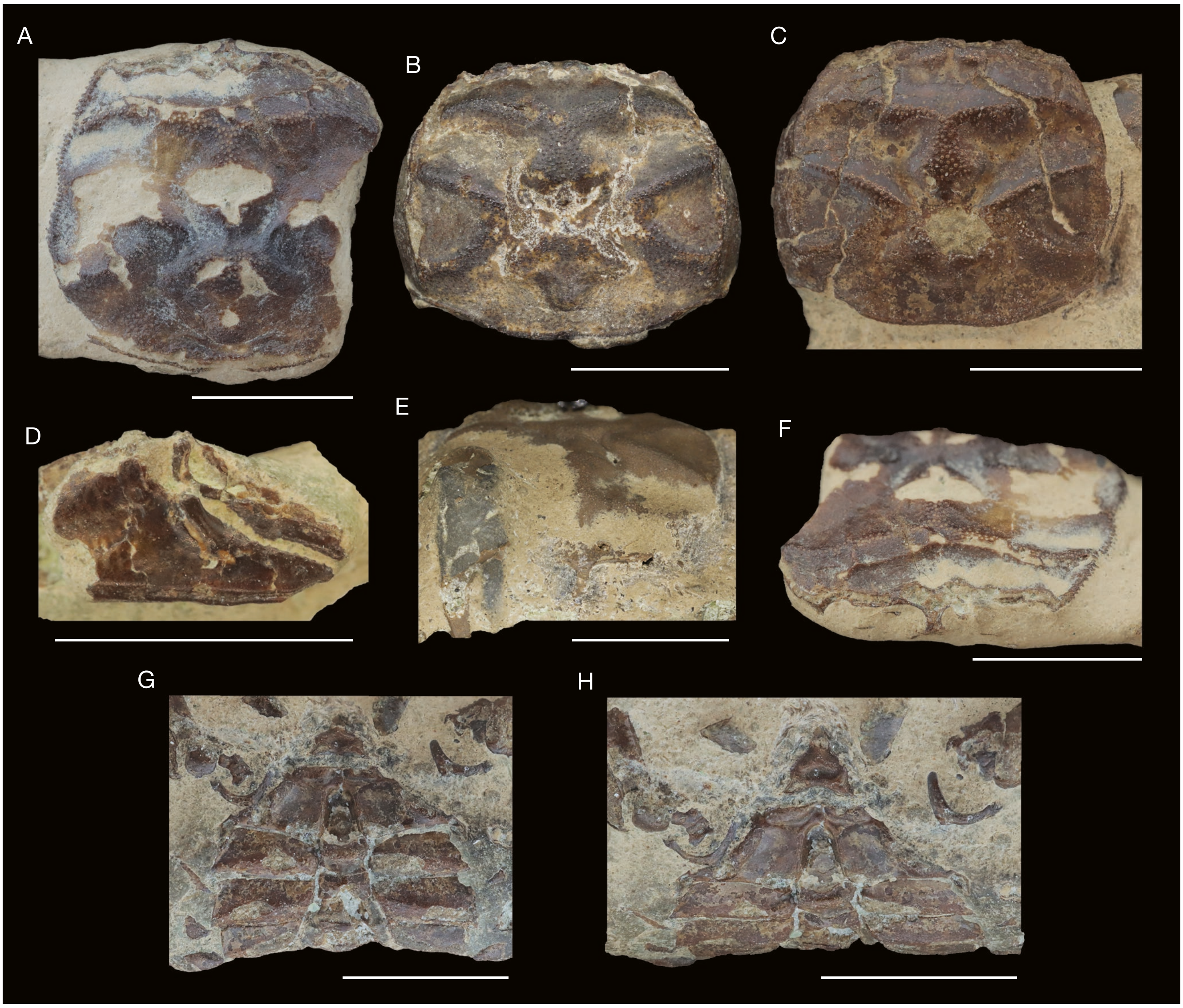

Fig. 14. — *Costacopluma grayi* Feldmann & Portell, 2007, from the Eocene (upper Ypresian-lower Lutetian) Tallahatta Formation in Alabama: **A**-**C**, dorsal views of ALMNH:Paleo:20598B, MMNS IP-10046.1, and MMNS IP-11213; **D**, right propodus and dactylus of UF 287266; **E**, **F**, frontal views of UF 171033 and ALMNH:Paleo:20598B; **G**, **H**, ventral views including male pleon of MMNS IP-11213. Scale bars: 5.0 mm. Credits: photos by Adiël A. Klompmaker.

Costacopluma grayi Feldmann & Portell, 2007
(Figs 14; 15; Table 1; Appendix 1F)

Costacopluma grayi Feldmann & Portell, 2007: 92, figs 2, 3. — Armstrong *et al.* 2009: fig. 6.2-6.3. — Martínez-Díaz *et al.* 2016: fig. 5.9-5.10.

non *Costacopluma grayi* – Feldmann *et al.* 2014: 137, pls 1, 2. (*Costacopluma nicksabani* n. sp.). — Martínez-Díaz *et al.* 2016: figs 5.1-5.8; 6.4. (*Costacopluma nicksabani* n. sp.). — Martínez-Díaz *et al.* 2016: figs 4; 6.4. — Vega *et al.* 2016: fig. 4G, H.

Type material. — **Holotype. United States** • 1 specimen; Alabama, Covington County, Below Point A Dam (31°21'32"N, 86°31'11"W), ALMNH loc. 4; Tallahatta Formation, NP14 nannofossil zone; Eocene (upper Ypresianlower Lutetian); UF 113749.
Paratypes. United States • 1 specimen; same as for the holotype; UF 113748 • 1 specimen; idem; UF 113750 • 1 specimen; idem; UF 114747 • 1 specimen; idem; UF 115672 • 1 specimen; idem; UF 115793 • 1 specimen; idem; UF 115794 • 1 specimen; idem; UF 115795 • 1 specimen; idem; UF 115796.

Additional material examined. — **United States** • 2 specimens; Alabama, Covington County, Below Point A Dam (31°21'32"N, 86°31'11"W), ALMNH loc. 4; Tallahatta Formation, NP14 nannofossil zone; Eocene (upper Ypresianlower Lutetian); ALMNH:Paleo:20598 • 1 specimen; idem; ALMNH:Paleo:21440 • 3 specimens; idem; MMNS IP-6491 • 1 specimen; idem; MMNS IP-6492 • 2 specimens; idem; MMNS IP-10046 • 1 specimen; idem; MMNS IP-11213 • 1 specimen; idem; UF 116615 • 1 specimen; idem; UF 116619 • 1 specimen; idem; UF 142615 • 1 specimen; idem; UF 142616 • 1 specimen; idem; UF 116691 • 1 specimen; idem; UF 171033 • 1 specimen; idem; UF 171034 • 1 specimen; idem; UF 256410 • 1 specimen; Alabama, Conecuh County, Pigeon Creek (T5N, R14E, Sec. 20, NE¼, NE¼); Tallahatta Formation, NP14 nannofossil zone; Eocene (upper Ypresianlower Lutetian); UF 287265 • 1 specimen; idem; UF 287266 • 1 specimen; idem; UF 349284-349310.

Type horizon. — Tallahatta Formation, NP14 nannofossil zone, Eocene (upper Ypresianlower Lutetian).

Type locality. — Below Point A Dam (31°21'32"N, 86°31'11"W), Covington County, Alabama, United States.

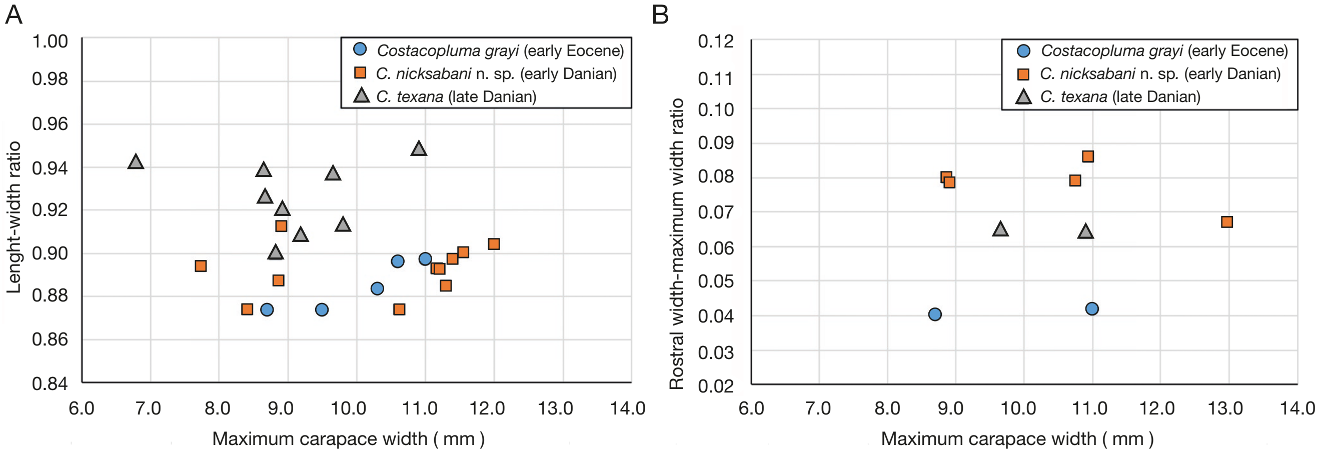

FIG. 15. — Carapace ratios of *Costacopluma* spp. versus specimen size: **A**, length-width ratios; **B**, rostral width-maximum carapace width ratios. See Table 1 for measurements.

DIAGNOSIS. — Carapace relatively small (<15 mm maximum width), subrectangular, wider than long (l/w ratio *c.* 0.9), widest point posterior to mid-length. Fronto-orbital margin *c.* 70% of maximum width; lateral margins somewhat diverging posteriorly, fairly straight, but more convex posteriorly; posterior margin nearly straight. Rostrum inclined downward, slightly longer than wide, minimum width in dorsal view *c.* 4% of maximum carapace width. Outer orbital spine small, triangular, directed forward. Dorsal carapace containing three tubercular transverse ridges of narrow width on average, with rounded tops; anterior ridge sinuous, uninterrupted, diminishes toward but reaches lateral margins. Cardiac region raised, tubercular, with convex and flattened ridge anteriorly and raised extension axially directed posteriorly. Gentle swellings with tubercles just anterior to innermost part of posterolateral margins.

MEASUREMENTS. — See Table 1.

DESCRIPTION

Referral is made to Feldmann & Portell (2007: 92). Additional specimens allow for improved description of rostrum, outer orbital spine, posterior margin, cheliped, sternum, and pleon. Outer orbital spine small, appears directed forward (UF 115796). Partial rostrum narrow, minimally *c.* 4% of maximum carapace width in dorsal view. Posterior margin with one row of small tubercles on top of rim, curving somewhat forward in lateral parts, nearly straight to very slightly concave in axial part (MMNS IP-11213, UF 171033). Outer side propodus (UF 287266) without tubercles as preserved, with a groove near base extending onto fixed finger, with at least four pits on fixed finger close to occlusal surface. Male sternite 4 with distinct, tubercular rim on outer side; less distinct rim on inner side, marking deep sternopleonal cavity for telson; generally smooth on cuticular surface in between. Somites male pleon unfused, with transverse, tubercular keels; telson with rounded tip.

REMARKS

Several papers ascribed early Danian and Maastrichtian specimens to this species (Feldmann *et al.* 2014; Vega *et al.* 2016; Martínez-Díaz *et al.* 2016), but there are several morphological differences between the specimens from the Eocene and these *c.* 18-19 million years older specimens that warrant species-level separation. For the early Danian specimens, referral is made to the new species erected below. The Maastrichtian specimens also represent a different species of *Costacopluma* not treated further herein: they have an outer orbital spine directed anterolaterally instead of forward as in *C. grayi* (UF 115796), are proportionally wider, and have a greater maximum size (see Vega *et al.* 2016; Martínez-Díaz *et al.* 2016).

Specimens with light to dark brown cuticle are embedded in tan/light brown fine sediment with some sand. Others occur in tan-brown sediment with more sand embedded, and a very dark brown cuticle. Finally, some occur in dark gray sediment and have dark brown cuticle. This applies to specimens from Point A Dam and Pigeon Creek. Some are listed as found *in situ* (UF 116615, UF 116619, UF 116691) or found in bed 5 of Copeland (1966) (UF 171033, UF 171034, type series), but the preservation style differs. It is likely that specimens underwent somewhat different taphonomic histories.

Some specimens (MMNS IP-11213 and MMNS IP-10046) are listed to have come from the basal Lisbon Formation in "Bed 5" of Copeland (1966), which Feldmann & Portell (2007) interpreted to be the Tallahatta Formation (see also Savrda *et al.* 2010).

Additional specimens were briefly mentioned in a paper focused on the vertebrate fauna of Point A Dam (Clayton *et al.* 2013). Unfortunately, the whereabouts of those crabs is uncertain (pers. comm. AAK with the Chuck Ciampaglio, November 2023).

Costacopluma texana
Armstrong, Nyborg, Bishop, Ossó-Morales & Vega, 2009
(Fig. 16; Table 1; Appendix 1G, H)

Costacopluma texana Armstrong, Nyborg, Bishop, Ossó-Morales & Vega, 2009: 756, figs 5.14-5.20; 6.1. — Martínez-Díaz *et al.* 2016: figs 5.14, 6.6.

TYPE MATERIAL. — **Holotype. United States** • 1 specimen; Texas, Limestone County, quarry *c.* 2 miles west of Mexia (*c.* 31°40'12"N,

TABLE 1. — Measurements and ratios of *Costacopluma* spp.: *Costacopluma grayi* Feldmann & Portell, 2007, from the Eocene (late Ypresian-early Lutetian) of Point A Dam, Alabama; *C. texana* Armstrong, Nyborg, Bishop, Ossó-Morales & Vega, 2009, from the late Danian of the Hanson Quarry, Mexia, Texas; and *C. nicksabani* n. sp. from the early Danian of Mussel Creek, Alabama. Measurements in mm.

Species	Specimen#	Length from very base rostum (at height orbital margin) to posterior margin along longitudinal axis	Maximum width excluding lateral sides that stick out	Length-width ratio	Minimum rostral width away from base in dorsal view	Rostral width/ maximum width
Costacopluma grayi	UF 171033	7.6	8.7	0.87	0.35	0.040
C. grayi	MMNS IP-11213	8.3	9.5	0.87	–	–
C. grayi	MMNS IP-6491.1	9.5	10.6	0.90	–	–
C. grayi	MMNS IP-10046.1	9.1	10.3	0.88	–	–
C. grayi	ALMNH:Paleo:20598B	9.9	11.0	0.90	0.46	0.042
C. texana	NPL 31172	9.1	9.7	0.94	0.63	0.065
C. texana	NPL 31176	10.3	10.9	0.95	0.7	0.064
C. texana	NPL 31175	6.4	6.8	0.94	–	–
C. texana	NPL 31174	9.0	9.8	0.91	–	–
C. texana	NPL 31173	–	11.3	–	–	–
C. texana	MMNS IP-7396.1	–	10.9	–	–	–
C. texana	MMNS IP-7396.2	8.1	8.7	0.94	–	–
C. texana	MMNS IP-7396.3	8.4	9.2	0.91	–	–
C. texana	MMNS IP-7396.4	7.9	8.8	0.90	–	–
C. texana	MMNS IP-7396.5	8.2	8.9	0.92	–	–
C. texana	MMNS IP-7396.6	8.0	8.7	0.93	–	–
C. nicksabani n. sp.	ALMNH:Paleo:5918A	10.9	12.0	0.90	–	–
C. nicksabani n. sp.	UF 235556	10.2	11.4	0.90	–	–
C. nicksabani n. sp.	UF 228989	–	10.8	–	0.85	0.079
C. nicksabani n. sp.	MMNS IP-7268	7.9	8.9	0.89	0.71	0.080
C. nicksabani n. sp.	MMNS IP-7940.1	8.1	8.9	0.91	0.7	0.079
C. nicksabani n. sp.	MMNS IP-7940.2	10.0	11.2	0.89	–	–
C. nicksabani n. sp.	MMNS IP-7940.3	–	10.9	–	0.94	0.086
C. nicksabani n. sp.	ALMNH:Paleo:21456	–	13.0	–	0.87	0.067
C. nicksabani n. sp.	ALMNH:Paleo:13539	10.4	11.6	0.90	–	–
C. nicksabani n. sp.	ALMNH:Paleo:21497 [#8]	10.0	11.3	0.88	–	–
C. nicksabani n. sp.	ALMNH:Paleo:21504 [#16]	7.4	8.4	0.87	–	–
C. nicksabani n. sp.	ALMNH:Paleo:21504 [#22]	10.0	11.2	0.89	–	–
C. nicksabani n. sp.	ALMNH:Paleo:21453	6.9	7.7	0.89	–	–
C. nicksabani n. sp.	ALMNH:Paleo:21454	9.3	10.6	0.87	–	–
C. nicksabani n. sp.	ALMNH:Paleo:21497 [#5]	8.4	–	–	–	–

96°34'11"W); Wills Point Formation, Mexia Clay Member; Paleocene (upper Danian); NPL 31172.
Paratypes. United States • 1 specimen; same as for the holotype; NPL 31173 • 1 specimen; idem; NPL 31174 • 1 specimen; idem; NPL 31175 • 1 specimen; idem; NPL 31176 • 1 specimen; idem; MGSB 75425.

ADDITIONAL MATERIAL EXAMINED. — **United States** • 6 specimens; Texas, Limestone County, Hanson Quarry; Wills Point Formation, Mexia Clay Member; Paleocene (upper Danian); MMNS IP-7396.

TYPE HORIZON. — Mexia Clay Member of the Wills Point Formation, upper Danian.

TYPE LOCALITY. — Quarry *c.* 2 miles west of Mexia (*c.* 31°40'12"N, 96°34'11"W), Limestone County, Texas, United States.

DIAGNOSIS. — Referral is made to Armstrong *et al.* (2009: 756).

MEASUREMENTS. — See Table 1.

DESCRIPTION

Referral is made to Armstrong *et al.* (2009: 756).

REMARKS

Costacopluma texana is morphologically close to *C. nicksabani* n. sp., but differs in several aspects. For details see the comparisons under *C. nicksabani* n. sp.

Costacopluma nicksabani n. sp.
(Figs 17; 18; Table 1; Appendices 1A-E; 3)

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Costacopluma grayi – Feldmann *et al.* 2014: 137, pls 1-2. — Martínez-Díaz *et al.* 2016: figs 5.1-5.8, 6.4.

TYPE MATERIAL. — **Holotype. United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21453 (carapace).
Paratypes. United States • 1 specimen; same as for the holotype; ALMNH:Paleo:13539 (carapace) • 1 specimen; idem; ALMNH:Paleo:21454 (carapace) • 1 specimen; idem; ALMNH:Paleo:21455 (carapace) • 1 specimen; idem; ALMNH:Paleo:21456 (carapace) • 1 specimen; idem; ALMNH:Paleo:21457 (carapace) • 1 specimen; idem; ALMNH:Paleo:21458 (carapace) • 1 specimen; idem; ALMNH:Paleo:21459 (carapace) • 1 specimen; idem; MMNS IP-7940.1 (carapace) • 1 specimen; idem; UF 247378 (pair of propodi and dactyli).

ETYMOLOGY. — In honor of the legendary American college football coach Nick Saban, who led the University of Alabama team from 2007-2023, winning six national and nine SEC championships with the Crimson Tide. Also, Nick's Kids Foundation has made a tremendous societal impact in Alabama and beyond.

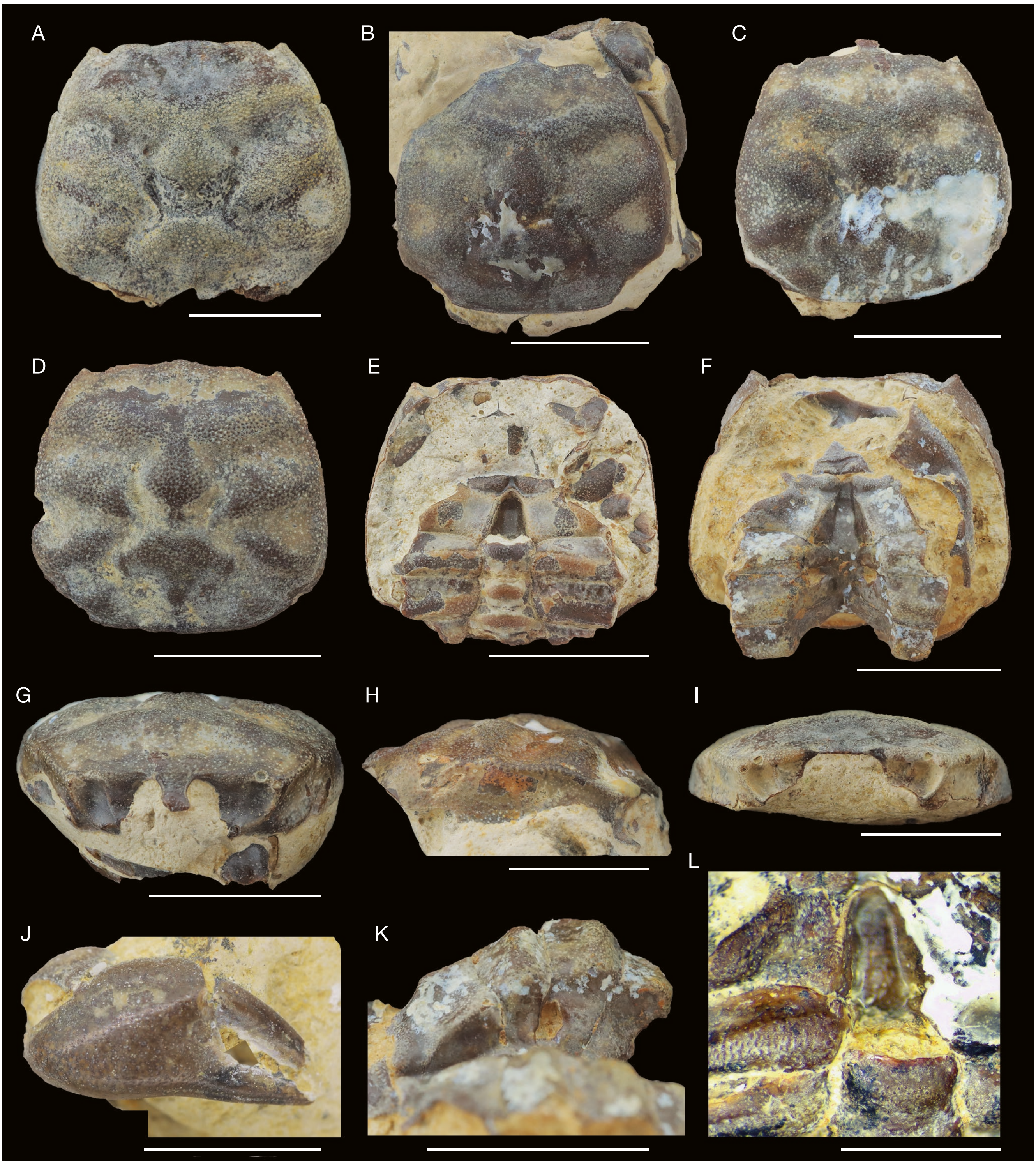

Fig. 16. — *Costacopluma texana* Armstrong, Nyborg, Bishop, Ossó-Morales & Vega, 2009, from the upper Danian Mexia Clay Member (Wills Point Formation) in Limestone County, Texas: **A**-**D**, dorsal views of NPL 31173 (paratype), NPL 31172 (holotype), MMNS IP-7396.3, and MMNS IP-7396.6; **E**, ventral view with male pleon (MMNS IP-7396.2); **F**, ventral view of female individual (MMNS IP-7396.1); **G**, frontal view of MMNS IP-7396.3; **H**, right lateral view of NPL 31176 (paratype); **I**, frontal view of NPL 31173 (paratype); **J**, right propodus and dactylus of NPL 31176 (paratype); **K**, oval oviduct of female individual (MMNS IP-7396.1); **L**, partial ventral view of male individual NPL 31175 (paratype), note small press button on sternite 5 on upper part of slope near sternite 4. Scale bars: A-J, 5.0 mm; K, L, 2.0 mm. Credits: photos by Adiël A. Klompmaker.

Additional material examined. — **United States** • 13 specimens; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:5918 (carapaces/venters) • 51 specimens; idem; ALMNH:Paleo:21497 (51 carapaces/venters) • 1 specimen; idem; ALMNH:Paleo:21498 (propodus) • 1 specimen; idem; ALMNH:Paleo:21499 (carapace with meri and partial carpi)

• 1 specimen; idem; ALMNH:Paleo:21500 (merus) • 1 specimen; idem; ALMNH:Paleo:21501 (carapace) • 1 specimen; idem; ALMNH:Paleo:21502 (venter) • 1 specimen; idem; ALMNH:Paleo:21503 (merus) • 26 specimens; idem; ALMNH:Paleo:21504 (carapaces/venters) • 1 specimen; idem; MMNS IP-6478 (carapace) • 1 specimen; idem; MMNS IP-6479 (carapace) • 1 specimen; idem; MMNS IP-6480 (venter) • 1 specimen; idem; MMNS IP-6481 (carapace) • 13 specimens; idem; MMNS IP-7257 (carapaces, incl. carapace with base cheliped incl. merus) • 1 specimen; idem; MMNS IP-7268 (carapace) • 3 specimens; idem; MMNS IP-7296 (2 carapaces, 1 propodus) • 6 specimens; idem; MMNS IP-7940.2-7 (carapaces) • 1 specimen; idem; UF 235556 (carapace) • 1 specimen; idem; UF 235557 (carapace) • 1 specimen; idem; UF 235558 (carapace) • 1 specimen; idem; UF 235559 (carapace) • 1 specimen; idem; UF 235560 (carapace) • 1 specimen; idem; UF 235562 (carapace) • 1 specimen; idem; UF 235563 (carapace) • 1 specimen; idem; UF 235564 (carapace) • 1 specimen; idem; UF 235565 (carapace) • 1 specimen; idem; UF 235566 (carapace) • 1 specimen; idem; UF 235567 (carapace) • 1 specimen; idem; UF 235568 (carapace) • 11 specimens; idem; UF 235569 (10 carapaces and 1 venter) • 1 specimen; idem; UF 235570 (fixed finger) • 1 specimen; idem; UF 235571 (propodus) • 1 specimen; idem; UF 235577 (carapace with propodus) • 1 specimen; idem; UF 247377 (cheliped propodus) • 1 specimen; idem; UF 254039 (carapace) • 1 specimen; idem; UF 303795 (carapace) • 1 specimen; idem; UF 303796 (carapace) • 1 specimen; idem; UF 303797 (carapace) • 1 specimen; idem; UF 303798 (carapace) • 1 specimen; idem; UF 303799 (carapace) • 1 specimen; idem; UF 303800 (carapace) • 1 specimen; idem; UF 303802 (carapace) • 1 specimen; idem; UF 303803 (carapace) • 1 specimen; idem; UF 303804 (carapace) • 1 specimen; idem; UF 303805 (carapace) • 1 specimen; idem; UF 303806 (venter) • 1 specimen; idem; UF 303807 (carapace) • 1 specimen; idem; UF 303808 (carapace) • 1 specimen; idem; UF 303809 (carapace) • 1 specimen; idem; UF 303810 (carapace) • 1 specimen; idem; UF 303811 (carapace) • 1 specimen; idem; UF 303813 (carapace) • 1 specimen; idem; UF 303814 (carapace) • 1 specimen; idem; UF 303816 (carapace) • 1 specimen; idem; UF 303817 (carapace) • 1 specimen; idem; UF 303818 (carapace) • 1 specimen; idem; UF 303820 (propodus) • 1 specimen; idem; UF 303821 (cheliped).

TYPE HORIZON. — Pine Barren Member of the Clayton Formation, lower middle NP2 nannofossil zone, lower Danian.

TYPE LOCALITY. — ALMNH loc. 3: Mussel Creek roadcut (31°58'17"N, 86°42'15"W), Lowndes County, Alabama, United States.

DIAGNOSIS. — Carapace relatively small (usually <15 mm maximum width), subrectangular, wider than long (l/w ratio *c.* 0.89), widest point posterior to mid-length. Fronto-orbital margin *c.* 70% of maximum width; lateral margins somewhat diverging posteriorly, fairly straight, but more convex anteriorly; posterior margin straight. Rostrum bilobed, inclined downward, slightly longer than wide, minimum width in dorsal view *c.* 8% of maximum carapace width. Outer orbital spine small, triangular, directed forward, about as short as spine on lower orbital margin. Dorsal carapace containing three tubercular transverse ridges of intermediate width on average, with rounded tops; anterior ridge sinuous, uninterrupted, diminishes toward but reaches lateral margins. Cardiac region raised, tubercular, with convex and flattened ridge anteriorly and raised extension axially directed posteriorly. Gentle swellings with tubercles just anterior to innermost part of posterolateral margins. Pleon of male narrow, widening somewhat to posterior; with transverse ridges on somites 3-6; telson and sternite 6 unfused; somites 3-5 fused but with sutures visible. Pleon of female with transverse ridges on somites 2-5; all somites and telson unfused; somites 1-5 much wider than long; somite 6 wider than long; telson triangular with rounded tip.

MEASUREMENTS. — See Table 1.

DESCRIPTION

Carapace relatively small (usually <15 mm maximum width), subrectangular, wider than long (l/w ratio *c.* 0.89), widest point posterior to mid-length, weakly vaulted transversely, moderately vaulted longitudinally. Margins rimmed with granules. Fronto-orbital margin *c.* 70% of maximum width, sinuous; lateral margins somewhat diverging posteriorly, fairly straight, but more convex anteriorly; posterolateral margin slightly concave; posterior margin straight. Rostrum bilobed, inclined downward, slightly longer than wide, minimum width in dorsal view *c.* 8% of maximum carapace width, narrowest point about halfway rostrum, with two lobes distally carrying tubercles, tip concave in dorsal view, lateral margins rimmed and with row of granules. Orbital margin rimmed with tubercles; upper orbital margin somewhat thicker than lateral and lower orbital margins; lower orbital margin with forwardly-directed spine; outer orbital spine small, triangular, directed forward, about as short as spine on lower orbital margin. Orbital cavity subovate but with angle at outer orbital spine, faint ridge of granules dividing outer and inner parts. Eyestalks elongated. Epigastric regions consisting of small, gentle swellings. Dorsal carapace containing three tubercular transverse ridges of intermediate width on average, with rounded tops; anterior ridge sinuous, uninterrupted, diminishes toward but reaches lateral margins; median ridges directed anterolaterally, straight, not connecting axially, reaching lateral margins; posterior ridges directed posterolaterally, not connecting axially, reaching posterolateral margins, curving more laterally in outermost part. Posterior part of mesogastric region raised, tubercular, connecting with anterior ridge where it narrows, with two posterior gastric pits near base. Cardiac region raised, tubercular, with convex and flattened ridge anteriorly and raised extension axially directed posteriorly. Gentle swellings with tubercles just anterior to innermost part of posterolateral margins. Other carapace regions not discernible. Dorsal carapace grooves absent except for short groove lateral to posterior part of mesogastric region ending in ovals pits anteriorly. Cuticular surface of dorsal carapace regions between ridges, in front of anterior ridge, and posterior to cardiac region pitted. Flanks straight; about a quarter in height of maximum carapace width; with groove starting at lateral margin, resulting sometimes in a weak notch, near position where anterior ridge connects to lateral margin; groove curving forward and becoming deeper near base of flank; flank tubercular in posterior part, mostly smooth in anterior third but with some tubercles in anteriormost part.

Pterygostome subtriangular and with posterior extension, with rim posteriorly and inward margin, mostly smooth. Buccal area with pit axially. Maxillipeds not preserved. Sternum suboval, widest at 5th sternite. Sternites 1 and 2 fused, separated by groove, triangular jointly; sternite 1 triangular with sharp tip, with tubercles; sternite 2 much wider than long, with short axial groove, with tubercles, widening toward sternite 3. Sternite 3 fused to sternite 4 but marked by transverse groove, with two lobes on posterior margin on either side of tip of sternopleonal cavity for males but with deep depression axially for females, straight anteriorly, tubercular.

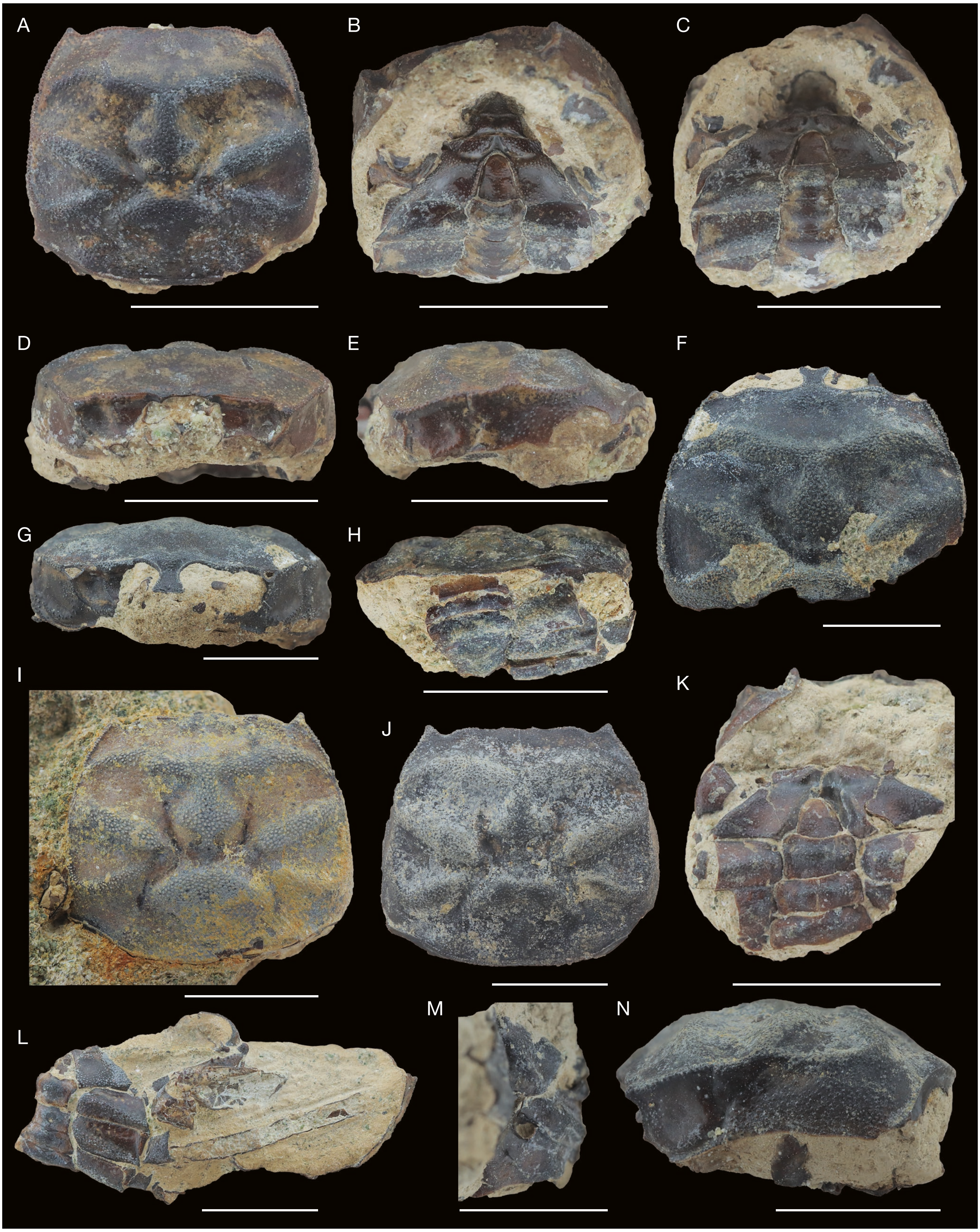

Fig. 17. — *Costacopluma nicksabani* n. sp., from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**E**, dorsal, ventral (2×), frontal, and left lateral views of male individual, ALMNH:Paleo:21453 (holotype); **F**, **G**, dorsal and frontal views of ALMNH:Paleo:21456 (paratype); **H**, posterior view of ALMNH:Paleo:21457 (paratype), showing male somites 1-2; **I**, **J**, dorsal views of ALMNH:Paleo:21454 (paratype) and ALMNH:Paleo:13539 (paratype); **K**, ventral view with female pleon of ALMNH:Paleo:21458 (paratype); **L**, ventral view of carapace and long merus of pereiopod 3 of ALMNH:Paleo:21455 (paratype); **M**, **N**, oval oviduct and left lateral view of ALMNH:Paleo:13539 (paratype). Scale bars: 5.0 mm. Credits: photos by Adiël A. Klompmaker.

Sternite 4 trapezoidal, tubercular, not flattened but concave, widening more laterally; with small anterolaterally oriented projection in anterolateral corner, about straight on anterior side for females and males, not extending much if anything beyond sternite 3. Sternites 5-7 with transverse, tubercular ridge widening inward. Sternites 4-6 with long episternal projections pointing posteriorly, episternal projection not preserved for sternite 7. Sternite 8 poorly preserved. Sternopleonal cavity of male deep, narrow, smooth, with sutures of 4/5, 5/6, and 6/7 extending to base of cavity but not connecting, suture 7/8 partially preserved, axial slit at level of sternite 7; sternopleonal cavity extends to upper part of sternite 4 and marked by clear rim at tip, small press button on sternite 5 on upper part of slope near sternite 4. Sternopleonal cavity of female incompletely preserved, but broader than male; without press button, deep, smooth, with sutures of 4/5, 5/6, and 6/7 extending to base of sternopleonal cavity but not connecting, with flat bottom between sternites 4-6, sternopleonal cavity extends to upper part of sternite 3 and without rim at tip; position of tip of telson marked by granules without forming rim, near base of sternite 3; subcircular oviduct on anterior part of sternite 6 near sternite 5, adjacent to base of sternopleonal cavity. Pleon of male narrow, widening somewhat to posterior; with transverse ridges on somites 3-6, ridge of somite 6 with tubercles, ridges of somites 3-5 pitted; pitted telson triangular with rounded tip; telson and sternite 6 unfused; somites 3-5 fused but with sutures visible; somites 1-2 much shorter than other somites, without ridge in center, with rim on anterior margin for somite 1, with bump in center of somite 2. Pleon of female with pitted transverse ridges on somites 2-5; all somites and telson unfused; somites 1-5 much wider than long; somite 6 wider than long, with tubercles on transverse ridge; telson triangular with rounded tip, pitted. Male pleopod 1 (gonopod 1) curved, open at tip, at position of somite 6.

Chelipeds isochelous or slightly heterochelous. Cheliped propodus without fixed finger wider than tall, upper margin with tubercular rim, lower margin rounded, subtrapezoidal in outer view; outer side convex, with shallow and longitudinal depression near upper margin, mostly pitted cuticular surface but with bands of tubercles near lower and upper margins; inner side flattened to slightly convex, with band of tubercles on lower third; fixed finger taller than wide in cross-section, flat bottom, occlusal surface with poorly preserved teeth decreasing in size to distal part, outer and inner sides with two ridges covered with granules near lower margin separated by groove, setal pits present on outer and inner sides, probably about as long as upper margin. Cheliped dactylus poorly preserved but with two ridges on upper margin of outer side, with setal pits on outer side. Cheliped carpus not preserved. Cheliped merus longer than tall, spines forming ridge on lower margin, scattered granules on convex outer surface, dense granules on upper margin, lower surface flat and mostly smooth. Cheliped ischium triangular, small, surface covered with tubercles, with two spines near articulation with merus. Non-cheliped appendages such as merus appear long; rest of these appendages not preserved.

REMARKS

Specimens from the early Danian of Mussel Creek were previously ascribed to *C. grayi* (Feldmann *et al.* 2014; Martínez-Díaz *et al.* 2016). A restudy of the type and new specimens of *C. grayi* from the Eocene of Alabama and additional specimens from Mussel Creek render this hypothesis untenable. Differences include a proportionally narrower rostrum for *C. grayi* (Figs 12A, F; 13B; 15F, G; Table 1), a narrower median ridge with fewer tubercles (Figs 14; 17), an apparently less tubercular propodus compared to *C. nicksabani* n. sp. (Figs 14D; 18J), and a less tubercular sternite 4.

Costacopluma nicksabani n. sp. differs from all other congenerics as well, compared alphabetically below, using the papers in which those species were first described and other papers as needed. *Costacopluma australis* has an overall similar outline, but the rostrum is protruding less prominently relative to the outer orbital spine than in the new species and the anteriormost transverse ridge appears to be concave forward (Feldmann *et al.* 1995: fig. 16) rather than sinuous. *Costacopluma bifida* has an anterior ridge said to be 'interrupted' medially (Collins *et al.* 1994: 30), which is not the case in *C. nicksabani* n. sp. Moreover, this ridge is mentioned to not reach the lateral margin, but it does in the new species. *Costacopluma bishopi* has much broader transverse ridges (Vega & Feldmann 1992: fig. 4). *Costacopluma binodosa* does not have the front preserved, limiting the number of characters to compare to, but this species has somewhat more prominent nodes just anterior to the posterolateral margins (Collins & Wienberg Rasmussen 1992: fig. 23). Moreover, this species has a posterior portion of the cardiac region that is less raised based on a cast and photos of the type specimen made by AAK. *Costacopluma maroccana* has a more ovate outline resulting from more rounded lateral margins (Ossó-Morales *et al.* 2010: fig. 7; ALMNH:Paleo:20599). *Costacopluma mexicana* has much broader transverse ridges (holotype in Luque *et al.* 2017: fig. 13F). *Costacopluma mamethioupamei* exhibits narrower transverse ridges (Hyžný *et al.* 2016: fig. 5). *Costacopluma nordestina* exhibits a more rounded posterior margin, the lateral margins are more rounded, and the median ridge displays more tubercles (Feldmann & Martins-Neto 1995: fig. 1; Luque *et al.* 2017: fig. 5G, H). *Costacopluma salamanca* is close in terms of ridges and their tubercles, but it is rounder anteriorly so that the fronto-orbital margin takes up a lower proportion of the maximum width (*c.* 63% vs *c.* 70% for *C. nicksabani* n. sp.), and the rostrum appears smaller (see Feldmann *et al.* 1997: fig. 3.2). *Costacopluma senegalensis* has much more rounded lateral margins (Gorodiski & Rémy 1959: pl. 19.1). *Costacopluma squiresi* exhibits a much more pronounced depression between the mesogastric and cardiac regions and the tubercles on the transverse ridges are smaller than in *C. nicksabani* n. sp. (Nyborg *et al.* 2009: fig. 2). *Costacopluma texana* is morphologically, geographically (Texas, United States), and stratigraphically (late Danian instead of early Danian) close to *C. nicksabani* n. sp., so a more detailed comparison is warranted. The median ridge is wider and flatter in *C. texana*, and the anterior and posterior ridges are flatter topped too. Moreover, *C. texana*

Fig. 18. — *Costacopluma nicksabani* n. sp., from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**, **D**, ventral view of female with pleon of MMNS IP-6480; **B**, **E**, frontal and ventral views of male of MMNS IP-7940.4; **C**, **F**, merus and ischium of cheliped of MMNS IP-7257.4; **G**, ventral view of female of ALMNH:Paleo:13539 (paratype); **H**, ventral view with pterygostome and partial buccal area of MMNS IP-7940.2; **I**, male pleopod pair 1 of MMNS IP-7940.1 (paratype); **J**, cheliped propodus of UF 247377; **K**, buccal area of MMNS IP-7940.1 (paratype); **L**, fixed fingers and dactyli of both chelipeds of UF 247378 (paratype); **M**, male pleopod pair 1 of UF 303806; **N**, ventral view of male with small press button on sternite 5 of MMNS IP-7940.2. Scale bars: A, B, D, E, G, H, J, L, 5.0 mm; C, F, I, K, N, 2.0 mm; M, 1.0 mm. Credits: photos by Adiël A. Klompmaker.

has a significantly higher length-width ratio (Mann-Whitney p = 0.0005; Figs 15-18; Table 1), appears to exhibit a thicker upper orbital rim (Fig. 15G, I vs Fig. 16D, G; 17B), has an oval-shaped oviduct rather than subcircular in *C. nicksabani* n. sp. (Fig. 16K vs Fig. 17M), the transverse ridges on sternites 5-6 are taller in at least females, the outer lateral margins of sternite 4 appear more flared up on average, and the press button on males is larger (Fig. 16L vs Fig. 18N).

We did not observe obvious ontogenetic variation, perhaps because of the limited size range of specimens. Sexual dimorphism is not observed on the dorsal carapace, but it is evident on the ventral side (wider female pleon and other characters, see description). Intraspecific variation is limited despite the high number of specimens.

For lesser preserved specimens with cuticle, the tubercles on the transverse ridges are less obvious. Carapace ornamentation is difficult to discern on internal molds (ALMNH:Paleo:21497A, 1 specimen of UF 235569). The sediment surrounding Mussel Creek specimens varies from tan to dark gray and from friable to fully lithified. This observation may indicate differing taphonomic conditions.

The gonopods preserved in three specimens of *Costacopluma nicksabani* n. sp. (ALMNH:Paleo:21457, MMNS IP-7940.1, UF 303806; Fig. 16I, M) resemble those in extant retroplumids (de Saint Laurent 1989). The preservation of gonopods in fossil brachyurans is uncommon (e.g., Karasawa & Schweitzer 2006: 42; Garassino *et al.* 2013: 356), and they had not been recognized within *Costacopluma* and fossil Retroplumidae until this paper. These small pleonal appendages, often taxonomically important for extant crabs, are less calcified than walking appendages and claws and tend to be covered by the pleon within the sternopleonal cavity. Fossil brachyuran species with these structures have been more frequently recognized over the last decade, mostly in specimens that have the pleonal somites incompletely preserved exposing structures underneath (Smirnov 1929; Secrétan 1975; Karasawa & Kato 2001, 2019; Guinot & Breton 2006; Karasawa & Schweitzer 2006; Artal *et al.* 2008; Feldmann *et al.* 2011; Schweitzer & Feldmann 2015; Luque *et al.* 2018, 2019; Pereyra *et al.* 2019; Lima *et al.* 2020; Pereyra & Verde 2020; Hyžný *et al.* 2022; Kovalchuk *et al.* 2023). The preservation of delicate tips of gonopods herein is even rarer.

Superfamily CARPILIOIDEA Ortmann, 1893
Family PALAEOXANTHOPSIDAE Schweitzer, 2003

Palaeoxanthopsidae indet.
(Fig. 19)

MATERIAL EXAMINED. — **United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:21482 (carapace) • 51 specimens; idem; ALMNH:Paleo:21497 (51 carapaces/venters) • 1 specimen; idem; ALMNH:Paleo:21505 (fixed finger) • 2 specimens; idem; ALMNH:Paleo:21506 (fixed fingers) • 1 specimen; idem; MMNS IP-7256.1 (fixed finger) • 1 specimen; idem; UF 303867 (fixed finger) • 1 specimen; idem; UF 303870 (fixed finger) • 1 specimen; idem; ALMNH:Paleo:21507 (dactylus) • 4 specimens; idem; ALMNH:Paleo:21508 (dactyli) • 1 specimen; idem; MMNS IP-7256.2 (dactylus) • 1 specimen; idem; UF 303868 (dactylus) • 1 specimen; idem; UF 303869 (dactylus) • 1 specimen; idem; UF 303871 (dactylus) • 1 specimen; idem; UF 303872 (dactylus).

MEASUREMENTS. — Maximum carapace width (mm): ALMNH:Paleo:21482: 24.6

DESCRIPTION

Preserved carapace *c.* 24.6 mm wide without anterolateral projections, weakly vaulted transversely, moderately vaulted longitudinally. Fronto-orbital width *c.* 55% of maximum width. Anterolateral margin with bases of four projections. Carapace with five large protuberances, one marking base of mesogastric region, two adjacent to anterior part of mesogastric region, and two lateral to cervical groove at level of mesogastric region base. Transverse row of small bumps anterolaterally of posteriormost set of protuberances. On cuticle, tubercles on protuberances and in front of anteriormost protuberances. Pit present in front of each side of posterior part of mesogastric region. Flanks steep. Preserved pterygostome appears subtriangular. Sternite 3 wider than long, separated from sternite 4 by a concave groove. Sternite 4 intersected by narrow sternopleonal cavity, both sides appear square-shaped. Coxa and basis of pereiopod 1, and parts of maxilliped 3 preserved. Sternum and appendages covered by tubercles, except for grooves and sternopleonal cavity. Rostrum, posterior carapace, most of ventral side, pleon, and appendages missing.

Fixed finger robust; curved inward; with row of oval tubercles, variably sized, diminishing in size to tip on average; outer and inner lateral sides with row of pits. Dactylus curved; with strong tubercle on outer side of occlusal surface near base, followed by smaller, similar-sized tubercles toward tip.

REMARKS

The single carapace lacks the posterior portion, the frontal region including the orbital structure and the rostrum, and the projections on the anterolateral margins. The preserved characters fit those of Palaeoxanthopsidae (e.g., Schweitzer 2003; Schweitzer *et al.* 2018a, 2025; Vega *et al.* 2018), including the location of the spherical swellings on the carapace and the anterolateral margins with bases of projections. Specimens of the Maastrichtian genera *Palaeoxanthopsis* Beurlen, 1958, and *Parazanthopsis* Vega, Feldmann, García-Barrera, Filkorn, Pimentel & Avendano, 2001, are morphologically close to the single, incomplete carapace specimen herein. The collection of more complete carapaces is necessary for identification beyond the family level.

We also found various fingers attributable to Palaeoxanthopsidae. Both fixed fingers and dactyli conform well to those seen in Palaeoxanthopsidae such as *Paraverrucoides alabamensis* (Rathbun, 1935a) from the upper Danian Porters Creek Formation of Alabama (GSA-I21006 and GSA-I21010) and *Lobulata lobulata* (Feldmann, Casadio, Chirino-Galvez & Aguirre-Urreta, 1995), from the Maastrichtian-Danian of

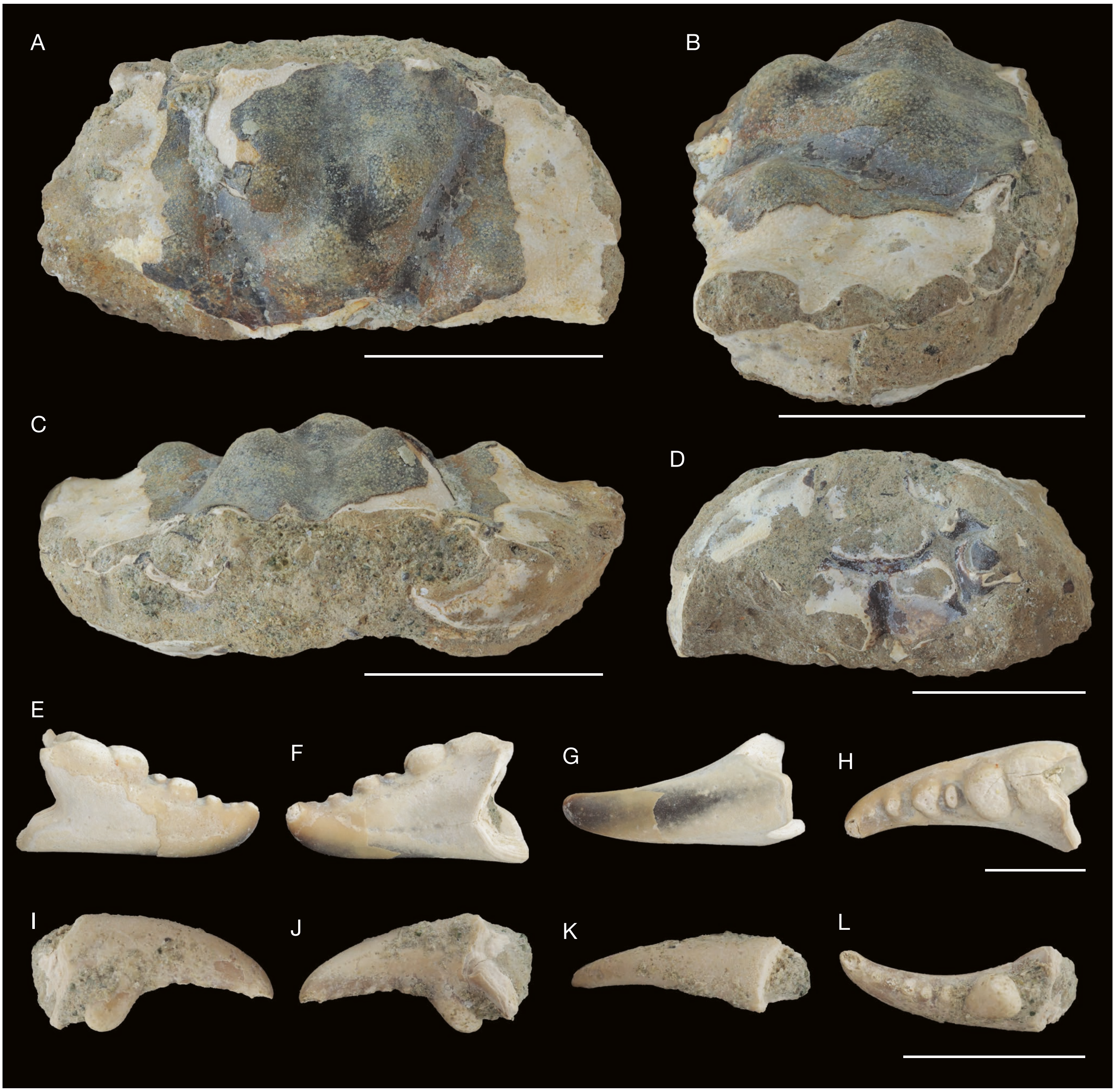

Fig. 19. — Palaeoxanthopsidae indet. from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**D**, dorsal, right lateral, frontal, and ventral views of ALMNH:Paleo:21482; **E**-**H**, outer, inner, lower marginal, and occlusal views of fixed finger of UF 303867; **I**-**L**, outer, inner, upper marginal, and occlusal views of dactylus of ALMNH:Paleo:21507. Scale bars: A-D, 10.0 mm; E-L, 5.0 mm. Credits: photos by Adiël A. Klompmaker.

Argentina (their fig. 7.6). It is very likely that these isolated fingers belong to the same species as the carapace, but associated chelipeds with a carapace are needed for verification.

Superfamily Hexapodoidea Miers, 1886

Family Hexapodidae Miers, 1886

Included genera. — *Bellhexapus* De Angeli, Guinot & Garassino, 2010; *Eohexapus* De Angeli, Guinot & Garassino, 2010; *Eurohexapus* De Angeli, Guinot & Garassino, 2010; *Goniocypoda* Woodward, 1867; *Headonipus* Quayle & Collins, 2012; *Hexalaughlia* Guinot, 2006; *Hexapinus* Manning & Holthuis, 1981; *Hexaplax* Doflein, 1904; *Hexapus* De Haan, 1835 [in 1833-1850]; *Holthuisea* Guinot, De Angeli & Garassino, 2010; *Lambdophallus* Alcock, 1900; *Latohexapus* Huang, Hsueh & Ng, 2002; *Lucahexapus* De Angeli & Caporiondo, 2022; *Mariaplax* Rahayu & Ng, 2014; *Paeduma* Rathbun, 1897; *Palaeopinnixa* Vía, 1966; *Parahexapus* Balss, 1922; *Pseudohexapus* Monod, 1956; *Rayapinus* Rahayu & Ng, 2014; *Rodneyellus* Lima, Alcântara, Aguilera & Tavares, 2025; *Spiroplax* Manning & Holthuis, 1981; *Stevea* Manning & Holthuis, 1981; *Thaumastoplax* Miers, 1881; *Theoxapus* Rahayu & Ng, 2014; *Tritoplax* Manning & Holthuis, 1981.

Genus *Alahexapus* n. gen.

urn:lsid:zoobank.org:act:C230B4E9-59C4-4322-9057-5513F4722A93

TYPE SPECIES. — *Stevea martini* Feldmann, Schweitzer & Portell, 2014, by present designation.

ETYMOLOGY. — *Ala-* refers to Alabama and *-hexapus* refers to the type genus of Hexapodidae. Gender: masculine.

DIAGNOSIS. — As for the type species.

REMARKS

Stevea martini was ascribed to *Stevea* based on a limited number of specimens then available without male and female pleons. Two additional specimens collected since 2014 with male and female pleons preserved suggest assignment to this genus is not tenable. Specifically, the female pleon from the only specimen of *Stevea williamsi*, the type and sole extant species of *Stevea*, was demonstrated to be narrow and have somites 2-6 fused (Guinot *et al.* 2010), whereas the female individual of *Alahexapus martini* n. comb. has proportionally wider pleonal somites 4-6 and these somites are unfused. Additional differences include the anterolateral borders passing below the outer orbital angle rather than joining the outer orbital angle as in *A. martini* n. comb., the rostrum has a concave border rather than a straight border as in *A. martini* n. comb., and the rostrum is widening distally rather than being straight laterally (UF 254042). The degree of fusion of pleonal somites and the pleonal width are considered important characters distinguishing between genera among extant hexapodids (Rahayu & Ng 2014). Other characters frequently used in that paper for genus diagnoses are carapace length-width ratios, cuticle ornamentation, groove development on the carapace, anterolateral margin shape, eye size, maxilliped morphology, ornamentation including stridulatory striae on the pterygostome, cheliped morphology, the degree of sternite and somite fusion, the shape of the pleon, and the shape and reach of the sternopleonal cavity. Many of the same characters are used to define genera present in the fossil record when preserved, but also other characters related to the carapace have been used including the widest point of the carapace, the frontal margin morphology and relative dimensions, and the orbital cavity size and shape (e.g., De Angeli *et al.* 2010; Schweitzer *et al.* 2022).

Key differences between *Alahexapus* n. gen. and exclusively fossil genera exist. *Bellhexapus* is widest at the posterior margin, male somite 6 is longer, and male somites 3-5 are not fused (De Angeli *et al.* 2010: figs 2, 3). In *Eohexapus*, the orbits are circular rather than oval and the dorsal carapace is smooth rather than showing some grooves (De Angeli *et al.* 2010: figs 4-6). *Eurohexapus* exhibits a carapace about as long as wide rather than wider than long, its fronto-orbital width is greater (*c.* 65% of maximum width vs 50% for *Alahexapus* n. gen.), and male somites 2-6 are fused (De Angeli *et al.* 2010: figs 7-9). *Goniocypoda* has a relatively wide fronto-orbital width (*c.* 65% of maximum width vs *c.* 50% for *Alahexapus* n. gen.) (Schweitzer & Feldmann 2001: 335). For *Headonipus*, the “grooves curving from the base of the cardiac region to the middle of the coxigeal incisions isolate elongated intestinal lobes” (Quayle & Collins 2012: 40), are not observed in *Alahexapus* n. gen. Moreover, the posteriormost portion of the carapace of *Headonipus* appears much more depressed and the orbits are subcircular rather than oval (Quayle & Collins 2012: pl. 3.9-3.10; Schweitzer *et al.* 2022: fig. 7.5). For *Holthuisea*, carapace grooves are absent and male somites 3-6 are fused rather than somites 3-5 only (Guinot *et al.* 2010: figs 2-4). *Lucahexapus* has a proportionally greater fronto-orbital width (*c.* 67% of maximum carapace width vs *c.* 50%) and the cervical groove is much wider (De Angeli & Caporiondo 2022: figs 2.5, 3.5). For *Palaeopinnixa*, the carapace is widest just anterior to posterolateral reentrants (e.g., Hyžný & Artal 2018; Schweitzer *et al.* 2022; Gustafson 2023), but *Alahexapus* n. gen. is widest about mid-length and does not widen toward the posterior carapace. Moreover, somites 5-6 in females are fused for the type species *P. rathbunae* and this species does not exhibit stridulating apparatus/striae on the pterygostome (Schweitzer *et al.* 2000: 57). *Rodneyellus* lacks a U-shaped cervical groove and has a lower ratio of fronto-orbital width of maximum carapace width (0.37 vs 0.50).

Key differences also exist with extant genera other than *Stevea* as discussed above, primarily using diagnoses in Manning & Holthuis (1981), Guinot (2006), and Rahayu & Ng (2014). *Hexalaughlia* exhibits a pterygostome without a row of stridulatory striae, and male somite 6 is much longer. *Hexapinus* has a carapace widening posteriorly, the carapace regions are not demarcated except for a poorly defined cardiac region, the orbits are much smaller, and male somite 6 is longer. For *Hexaplax*, the carapace regions are more indistinct, the orbits are larger and are subcircular rather than oval. For *Hexapus*, the carapace regions are less distinct, and the orbits are much smaller. *Lambdophallus* bears much smaller orbits and exhibits a male transverse sternal groove extending laterally from the sternopleonal cavity not seen in *Alahexapus* n. gen. *Latohexapus* has much more distinct carapace regions and its carapace widens posteriorly. *Mariaplax* has a carapace widening posteriorly, smaller orbits, and a much shorter male telson. *Paeduma* exhibits a much longer male somite 6 and carapace grooves are absent to very faint. *Parahexapus* bears a much longer male somite 6 that is narrower than male somites 3-5, and has orbits that are smaller. For *Pseudohexapus,* the pterygostome lacks a row of oblique striae. *Rayapinus* has a carapace without clear grooves, bears a relatively narrow female pleon, has female somites 1-5 fused, and has a male telson almost as long as somite 6. *Spiroplax* exhibits a carapace that is widening posteriorly, and has a much broader male pleon with a triangular telson. For *Thaumastoplax*, the pterygostome lacks a row of oblique striae, the orbits are smaller and circular, and the carapace regions are indistinct. *Theoxapus* has much smaller orbits and a proportionally longer male somite 6. *Tritoplax* has a male telson with a triangular tip, a male pleonal somite 6 that is divided longitudinally, and apparently smaller orbits.

As none of the diagnoses of fossil and extant genera match the species under study, we erect *Alahexapus* n. gen. It is possible additional fossil species may belong to the new genus.

For example, *Palaeopinnixa rocaensis* (Feldmann, Casadío, Chirino-Gálvez & Aguirre-Urreta, 1995), from the Danian of southern Argentina does not widen toward to posterior carapace as for the genus diagnosis of *Palaeopinnixa* (Schweitzer & Feldmann 2001). The fronto-orbital width is similar (45% of maximum width vs *c.* 50% for *Alahexapus* n. gen.), the outline is similar, the flanks for both taxa are straight, the length-width ratio is similar (0.71 vs *c.* 0.67 for *Alahexapus* n. gen.) (Feldmann *et al.* 1995: figs 14, 15). Unfortunately, no cuticle is preserved nor any ventral characters, which hinders further evaluation.

Alahexapus martini
(Feldmann, Schweitzer & Portell, 2014) n. comb.
(Fig. 20; Appendix 1K, L)

Stevea martini Feldmann, Schweitzer & Portell, 2014: 142, pl. 3.

TYPE MATERIAL. — **Holotype. United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); UF 228988. **Paratype. United States** • 1 specimen; same as for the holotype; UF 235561.

ADDITIONAL MATERIAL EXAMINED. — **United States** • 1 specimen; Alabama, Lowndes County, Mussel Creek roadcut (31°58'17"N, 86°42'15"W), ALMNH loc. 3; Clayton Formation, Pine Barren Member, lower middle NP2 nannofossil zone; Paleocene (lower Danian); ALMNH:Paleo:5915 • 1 specimen; idem; ALMNH:Paleo:21464 • 1 specimen; idem; MMNS IP-7939 • 1 specimen; idem; UF 254040 • 1 specimen; idem; UF 254041 • 1 specimen; idem; UF 254042 • 1 specimen; idem; UF 303801.

TYPE HORIZON. — Pine Barren Member of the Clayton Formation, lower middle NP2 nannofossil zone, lower Danian.

TYPE LOCALITY. — ALMNH loc. 3: Mussel Creek roadcut (31°58'17"N, 86°42'15"W), Lowndes County, Alabama, United States.

DIAGNOSIS. — Carapace length-width ratio *c.* 0.67, widest about mid-length. Fronto-orbital width *c.* 50% of maximum carapace width. Orbits of moderate size, oval-shaped. Cervical groove widely U-shaped but diverging, fairly distinct, diminishing near orbits. Branchiocardiac grooves weaker, defining cardiac region laterally. Cuticle of carapace with densely covered fine granules. Pterygostome exhibiting stridulating apparatus with *c.* 15 striae. Female pleon with unfused, much wider than long somites; triangular telson with rounded tip; with gentle axial keel; pitted cuticular surface. Sternopleonal cavity of female appears to reach distal portion of sternite 3. Male pleon narrow, generally narrowing distally; telson longer than wide with rounded tip; somite 6 slightly wider than long, appears unfused, hexagonal, with rimmed lateral margins; somites 3-5 appear fused but with distinct suture marking boundaries; with pitted cuticular surface. Sternopleonal cavity of male appears to reach distal portion of sternite 4.

MEASUREMENTS. — Maximum carapace width (mm): ALMNH:Paleo:5915: 7.1, ALMNH:Paleo:21464: 11.1. UF 228988: 11.1, UF 254041: 8.9, MMNS IP-7939: 11.4.

DESCRIPTION
Referral is made to Feldmann *et al.* (2014: 142-143). Some additional and revised characters are noted in new specimens. Carapace length-width ratio *c.* 0.67. Fronto-orbital width *c.* 50% of maximum carapace width. Sternites with tubercular and pitted cuticular surface; pleonal sternite 2 narrow; sternites 3-4 fused; sternite 4 with curved, anterolaterally directed spine separated by sulcus. Female pleon with unfused, much wider than long somites; triangular telson with rounded tip; maximum width pleon *c.* 30% of maximum carapace width; with gentle axial keel; pitted cuticular surface. Female pleonal somites 1-3 not preserved. Sternopleonal cavity of female appears to reach distal portion of sternite 3; with small press button on sternite 5 on upper part of slope near sternite 4; with subcircular oviduct on sternite 6, adjacent to base of sternopleonal cavity.

Male pleon narrow, generally narrowing distally; telson longer than wide with rounded tip; somite 6 slightly wider than long, appears unfused, hexagonal, with rimmed lateral margins; somites 3-5 appear fused but with distinct line marking boundaries; with pitted cuticular surface. Sternopleonal cavity of male appears to reach distal portion of sternite 4. Third maxilliped partly preserved, with elongated exopod; boot-shaped, tubercular ischium, and about equally wide and long, rounded merus. Appendages not preserved.

REMARKS
This species is rare with only nine individuals reported herein after *c.* 15 years of collecting. This rarity is not primarily caused by the small size of the specimens, making them potentially more difficult to find, because many small specimens of other species were found (see above).

Recently, Schweitzer (2024) ascribed four specimens to *Stevea martini* from a site near Streetman, Freestone County, Texas, United States, originating from the upper Danian-Selandian Wills Point Formation (see Armstrong *et al.* 2009, for age). However, the tubercles on the dorsal carapace are coarser on average and more uniform in the Texan specimens based on all available specimens; sternite 4 has a wider, hexagonal-shaped extension as preserved rather than anterolaterally directed, curved spines as in *A. martini* n. comb. (compare Schweitzer 2024: fig. 3.2 vs Fig. 20E); and the pterygostome does not appear to bear the stridulating apparatus (Schweitzer 2024: fig. 3.6) characteristic for *A. martini* n. comb. (Fig. 20L; Feldmann *et al.* 2014: pl. 3.2) though differential preservation may play a role here. Thus, the specimens from Texas may represent a different hexapodid species warranting further study.

DISCUSSION

BIOSTRATIGRAPHY AND AGE
The lithostratigraphic section analyzed in this study belongs to calcareous nannofossil Zone NP2. The base of NP2 occurs *c.* 2.75 m below the base of the section shown in Figure 2, with the first occurrence/base of *Cruciplacolithus intermedius* (and other bioevents such as the first occurrences of *Coccolithus pelagicus* (Wallich, 1877) and *Futyania* spp. [super-abundant]). A numeric age of 65.50 Ma is assigned to the base of NP2, following the global ages from Gradstein *et al.* (2012). The section has been subdivided into lower-middle-upper NP2

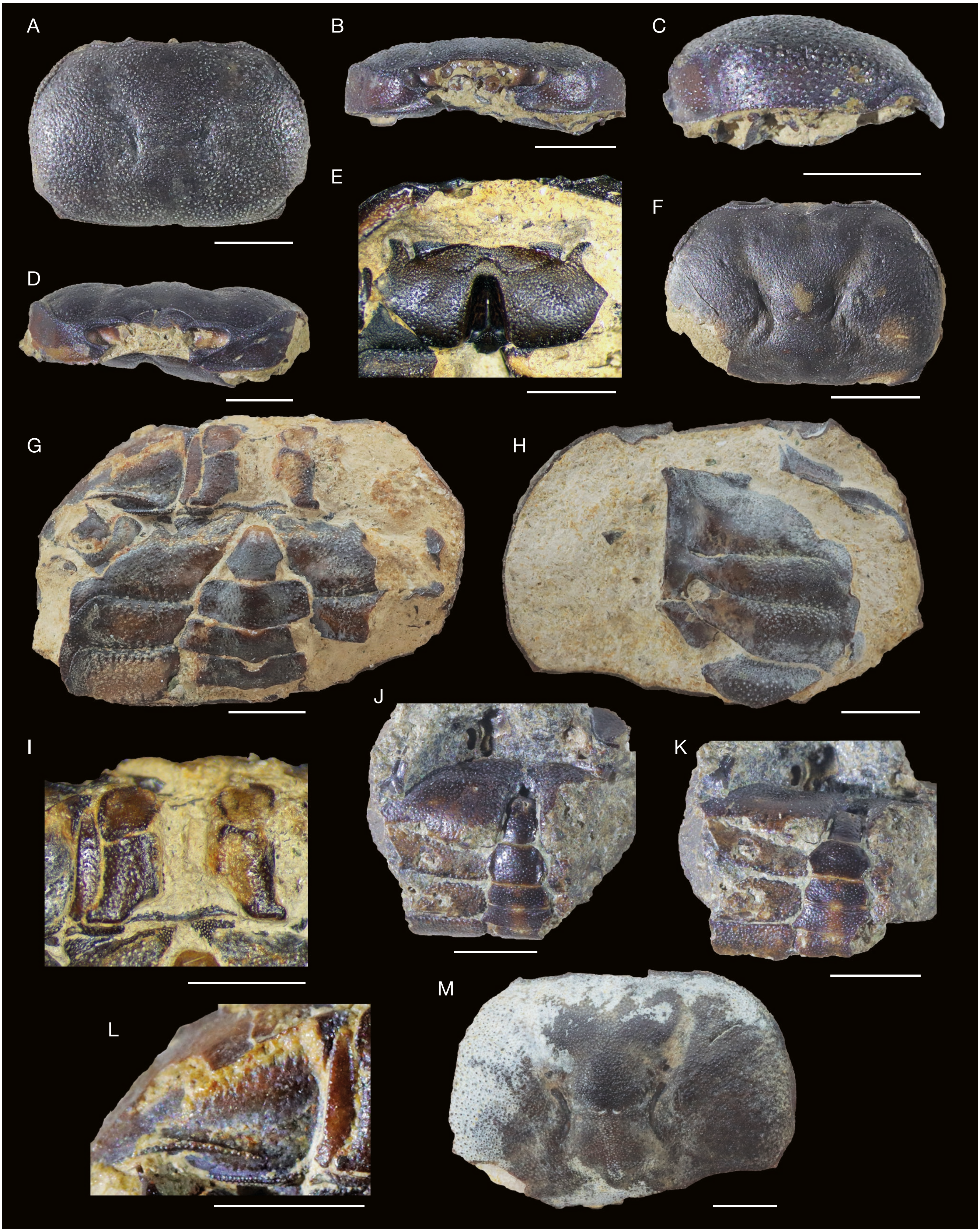

Fig. 20. — *Alahexapus martini* (Feldmann, Schweitzer & Portell, 2014) n. comb. from the lower Danian Pine Barren Member (Clayton Formation) found at the roadcut of Mussel Creek, Lowndes County, Alabama: **A**-**C**, dorsal, frontal, left lateral views of ALMNH:Paleo:5915; **D**-**F**, frontal, partial ventral, and dorsal views of UF 254041; **G**, ventral view of MMNS IP-7939 with female pleon; **H**, ventral view of ALMNH:Paleo:21464; **I**, closeup of maxilliped 3 of MMNS IP-7939; **J**, **K**, ventral views of UF 254040 with male pleon; **L**, view of partially preserved stridulating apparatus (vertical ridges arranged diagonally) of MMNS IP-7939; **M**, dorsal view of ALMNH:Paleo:21464. Scale bars: 2.0 mm. Credits: photos by Adiël A. Klompmaker.

Table 2. — Number of specimens per taxon. Carapaces and isolated appendage elements are all counted as one individual.

Taxon	**Total # specimens**	**Carapaces/venters with or without appendages**	**Propodi with or without dactylus**	**Fixed fingers**	**Fixed finger and associated dactylus**	**Dactyli**	**Meri**	**Cheliped**	**Finger indet.**
Alphacheles zeta (Rathbun, 1936) n. comb.	6	–	6	–	–	–	–	–	–
Ctenocheles sp.	1	–	–	–	–	–	–	–	1
Eucalliaxiopsis alabamensis (Rathbun, 1935) n. comb.	111	–	1	31	2	76	–	1	–
"*Paguristes*" *johnsoni* Rathbun, 1935	7	–	1	–	1	4	1	–	–
Raninoides danicus n. sp.	20	20	–	–	–	–	–	–	–
Costacopluma nicksabani n. sp.	183	174	5	1	–	–	2	1	–
Palaeoxanthopsidae indet.	17	1	–	6	–	10	–	–	–
Alahexapus martini (Feldmann, Schweitzer & Portell, 2014) n. comb.	9	9	–	–	–	–	–	–	–

based on the identification of biostratigraphically useful nannofossil-events used in the zonation schemes of Varol (1989) and Bown *et al.* (2023). The deepest sample analyzed in this study belongs to lower NP2, with the first occurrence/base of *Praeprinsius tenuiculus* (Okada & Thierstein, 1979) (Fig. 2). The middle NP2 is based on the last occurrence/top of *Futyania* spp. [super-abundant], whereas upper NP2 is defined by the first occurrence/base of *Praeprinsius dimorphosus* (Perch-Nielsen, 1977) [common/increase] (Fig. 2). The base of NP3 (64.81 Ma, Gradstein *et al.* 2012) was not observed, as the uppermost sample analyzed is within upper NP2.

The lower middle NP2 nannofossil zone assigned to nearly all decapods and other fossils from the Mussel Creek outcrop, allows us to evaluate the absolute age of the assemblage. Using the astronomically calibrated NP zonation of Hvid *et al.* (2021: fig. 12) and an age model coupled with the NP zonation in Bown *et al.* (2023), we infer an absolute age of 65.4-65.3 Ma for the assemblage. This inference implies the fauna lived *c.* 600-700k years after the K-Pg boundary (66.0 Ma).

Stratigraphic and paleobiogeographic implications of the decapod assemblage

Raninoides danicus n. sp. is the stratigraphically second to oldest species known of the genus after *R. granulofrons*, from the late Campanian-early Maastrichtian of Cuba. This genus has not been reported previously from the fossil record of the southeastern United States. *Eucalliaxiopsis alabamensis* n. comb., *Ctenocheles* sp., and Palaeoxanthopsidae were unknown from the early Danian of Alabama thus far, but they have been reported from the upper Danian Porters Creek Formation of the state (Rathbun, 1935a).

Decapod paleoecology

All decapods appear to have lived in or on the bottom of the muddy substrate. At least one decapod taxon in our assemblage was a likely durophagous predator. Multiple species of Palaeoxanthopsidae, such as *Paraverrucoides alabamensis*, *Lobulata lobulata*, and the indeterminate species in the Mussel Creek assemblage, bear molariform teeth on the fixed finger and a large tooth projecting inward on the dactylus, located more on the outer than inner side of the occlusal surface. This tooth is reminiscent of the more curved and larger tooth that calappid crabs use to break shells (Shoup 1968). Such characters have been ascribed to shell-preying crabs (Schweitzer & Feldmann 2010); thus, we suggest Palaeoxanthopsidae were likely molluscan predators. Mollusks are common at Mussel Creek (Figs 3; 4). The three axiidean species were burrowers (e.g., Hyžný & Klompmaker 2015: table 1), and burrows are commonly found at the Mussel Creek roadcut. As extant hexapodids have been found in burrows (Rahayu & Ng 2014; Naruse 2020), *Alahexapus martini* n. comb. may have had a similar lifestyle. As for extant retroplumids (de Saint Laurent 1989), *Costacopluma nicksabani* n. sp. likely lived on the muddy bottom or burrowed, feeding on organic particles within the sediment. As for nearly all Cenozoic paguroids (e.g., Fraaije & Polkowsky 2016; Pasini *et al.* 2020), specimens of "*Paguristes*" *johnsoni* likely relied on gastropod shells as a domicile, which were common at Mussel Creek (Fig. 4). The carapace shape of *Raninoides danicus* n. sp. suggests it was likely burying in the sediment (e.g., Van Bakel *et al.* 2012). Little is known about the diet of raninoidans, but *Ranina ranina* Linnaeus, 1758, appears to be a scavenger (Baylon & Tito 2012).

Evidence of preserved predation inflicted on decapods is generally rare in the fossil record (Klompmaker *et al.* 2013, for a summary). One of the *Raninoides danicus* n. sp. specimens (MMNS IP-7252.2) figured in Feldmann *et al.* (2019: fig. 5B) bears two elongated depressions diagonally across the carapace. All cuticle is present within these depressions and there is no sign of a tooth impression. They were unsure but suggested biting or crushing by a predator as one explanation. These traces do not match known traces attributed to predation in fossil decapods. We, too, are unsure about the cause.

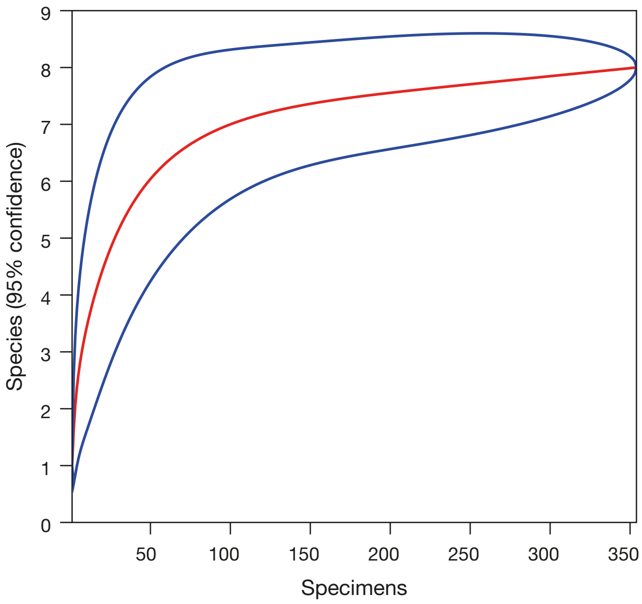

Fig. 21. — Rarefaction analysis using PAST 4.17 (Hammer *et al.* 2001) based on specimens identified at low taxonomic ranks (family-level and lower). The **red** (middle) curve represents the expected number of species for a smaller sample size, whereas the top and bottom (**blue**) curves represent the 95% unconditional confidence intervals. See Table 2 for data.

None of the specimens studied show evidence of *Kanthyloma crusta* Klompmaker, Artal, Van Bakel, Fraaije & Jagt, 2014, the trace fossil attributed to parasitism in the branchial chamber by an epicaridean isopod (see also Klompmaker *et al.* 2022b). Thus, levels of this type of parasitism were low.

Diversity of early Danian decapod assemblages

All to nearly all decapod species of the early Danian Mussel Creek assemblage have been collected as suggested by a rarefaction analysis (Fig. 21; Table 2). The eight species recognized herein make it one of the most diverse early Danian assemblages known relatively soon after the Cretaceous-Paleogene mass extinction. This is partly because of the lack of studies on such assemblages, but also because biostratigraphic data is not always available to place assemblages within a part of the Danian (e.g., Feldmann *et al.* 1993; Robin *et al.* 2017). From the lower Danian Roca Formation at Cerros Bayos in southern Argentina (NP1 nannofossil zone), five decapod species were reported (Feldmann *et al.* 1995). They also reported one species from the early Danian General Roca outcrop, but eight other species came north from there, implying the precise age within the Danian is uncertain. From the early Danian Clayton Formation in Illinois, United States, four species were reported (Cope *et al.* 2005). Finally, Jensen (2013) informally reported on an early Danian assemblage from Sangstrup in Denmark, consisting of 15 species. Although a more thorough study on Sangstrup material is ongoing, alpha diversity appears to be higher than in the assemblage of Mussel Creek.

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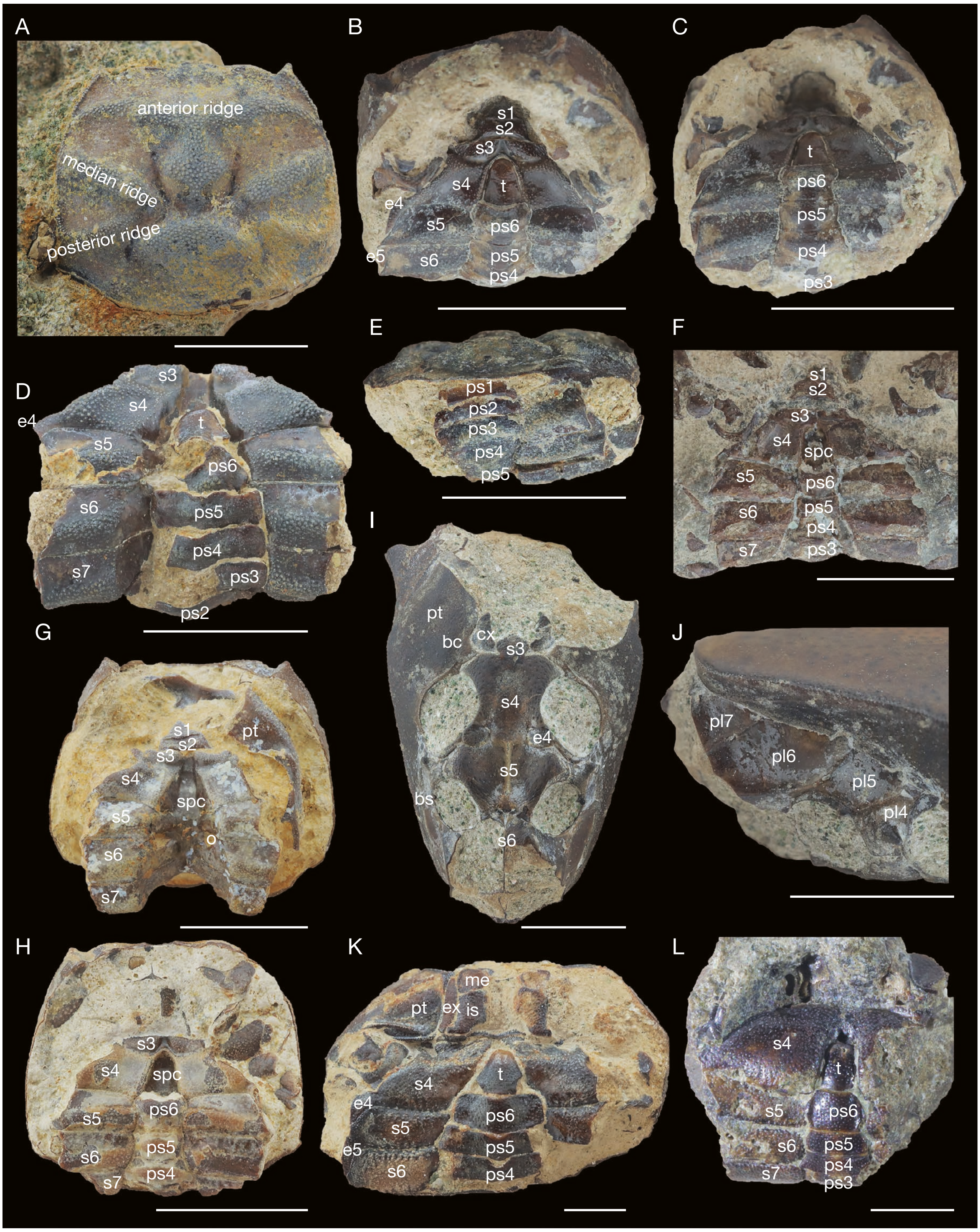
APPENDICES

Appendix 1. — Figure with ventral and some dorsal characters used to describe brachyurans in this study: **A**, dorsal view of *Costacopluma nicksabani* n. sp. (ALMNH:Paleo:21454, paratype); **B**, **C**, ventral views including male pleon of *C. nicksabani* n. sp. (ALMNH:Paleo:21453, holotype); **D**, ventral view including female pleon of *C. nicksabani* n. sp. (MMNS IP-6480); **E**, posterior view of *C. nicksabani* n. sp. (ALMNH:Paleo:21457, paratype); **F**, ventral view including male pleon of *C. grayi* Feldmann & Portell, 2007 (MMNS IP-11213); **G**, ventral view including male pleon of *C. texana* (MMNS IP-7396.2); **H**, ventral view of female individual of *C. texana* (MMNS IP-7396.1); **I**, **J**, ventral and right lateral views of *Raninoides danicus* n. sp. (ALMNH:Paleo:21488, holotype); **K**, ventral view including female pleon of *Alahexapus martini* (Feldmann, Schweitzer & Portell, 2014) n. comb. (MMNS IP-7939); **L**, ventral view including male pleon of *A. martini* n. comb. (UF 254040). Abbreviations: **bc**, buccal collar; **bs**, branchiostegite; **cx**, coxa of maxilliped 3; **e4**, **e5**, episternites 4-5; **ex**, exopod of maxilliped 3; **is**, ischium of maxilliped 3; **me**, merus of maxilliped 3; **o**, oviduct; **pl4-pl7**, pleurites 4-7; **ps1-ps6**, pleonal somites 1-6; **pt**, pterygostome; **s1-s7**, sternites 1-7; **spc**, sternopleonal cavity; **t**, telson. Scale bars: A-J, 5.0 mm; K, L, 2.0 mm. Credits: photos by Adiël A. Klompmaker.



APPENDIX 2. — Link to the 3D model of the holotype of *Raninoides danicus* n. sp. (ALMNH:Paleo:21488): https://zenodo.org/records/17065577

APPENDIX 3. — Link to the 3D model of the holotype of *Costacopluma nicksabani* n. sp. (ALMNH:Paleo:21453): https://doi.org/10.5281/zenodo.17065590