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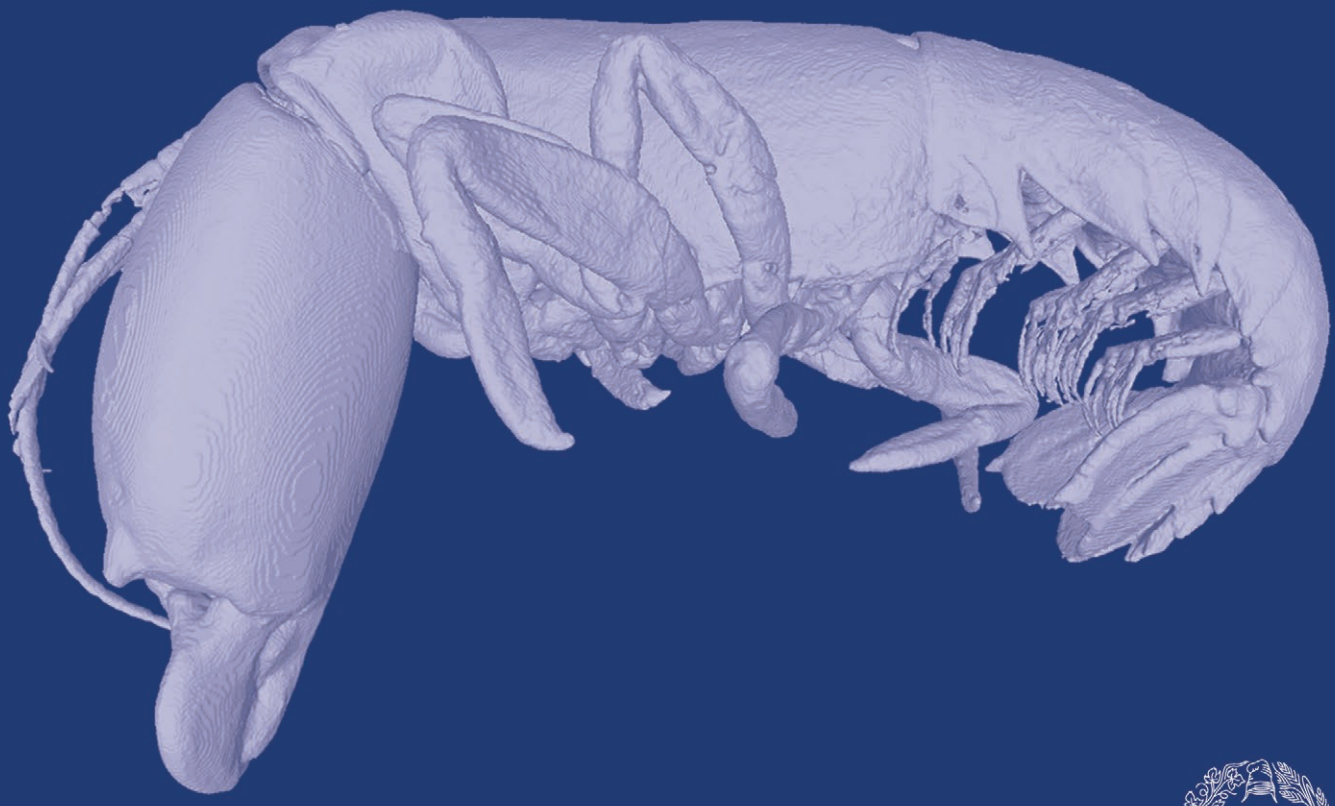

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Couverture / *Cover* :
Lateral view of *Synalpheus idelisae* n. sp., non-ovigerous individual (PR24-6202-21).

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A new eusocial species of snapping shrimp, *Synalpheus idelisae* n. sp. (Decapoda, Alpheidae), with a review of caste differentiation in eusocial shrimp

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ABSTRACT
Snapping shrimp in the genus *Synalpheus* Spence Bate, 1888 are the only marine organisms known to exhibit eusociality, a social structure characterized by colony-living and a reproductive division of labor. Here we describe a new species of eusocial sponge-dwelling snapping shrimp, *Synalpheus idelisae* n. sp., based on material collected from Puerto Rico and the Dominican Republic. Phylogenetic analyses (based on mitochondrial 16S and COI loci) and morphological traits place *S. idelisae* n. sp. within the *Synalpheus rathbunae* Coutière, 1909 species complex, which includes several other eusocial species. *Synalpheus idelisae* n. sp. can be distinguished from its close relatives by the shape of the anterodorsal spine on the major chela, the morphology of the pleura, and the number of setal combs on the fifth pereopod. Like many other eusocial species in the genus *Synalpheus*, *S. idelisae* n. sp. exhibits traits such as direct larval development and a second pereopod with a four-segmented carpus. Notably, we document several colonies of *S. idelisae* n. sp. in which queens replace the major snapping chela with a second minor chela, a pattern linked to morphological caste differentiation in *Synalpheus* shrimps. Finally, we review the occurrence of this pattern across other eusocial and putatively eusocial *Synalpheus* species. With the addition of *S. idelisae* n. sp., there are now a total of seven eusocial species in the West-Atlantic *S. rathbunae* species complex.

KEY WORDS
Crustacea,
Caridea,
Dominican Republic,
Puerto Rico,
new species.

RÉSUMÉ
Une nouvelle espèce eusociale de crevette pistolet, Synalpheus idelisae n. sp. *(Decapoda, Alpheidae), avec une révision de la différenciation des castes chez les crevettes eusociales.*
Les crevettes pistolet du genre *Synalpheus* Spence Bate, 1888 sont les seuls organismes marins connus pour être eusociaux, c'est à dire présenter une structure sociale caractérisée par la vie en colonie et une division du travail en matière de reproduction. Nous décrivons ici une nouvelle espèce de crevette pistolet eusociale vivant dans les éponges, *Synalpheus idelisae* n. sp., à partir de spécimens collectés à Porto Rico et en République dominicaine. Les analyses phylogénétiques (basées sur les loci mitochondriaux 16S et COI) et les caractères morphologiques placent *S. idelisae* n. sp. au sein du complexe d'espèces *Synalpheus rathbunae* Coutière, 1909, qui comprend plusieurs autres espèces eusociales. *Synalpheus idelisae* n. sp. se distingue de ses proches parents par la forme de l'épine antérodorsale de la grande pince, la morphologie des pleures et le nombre de peignes de soies sur le cinquième péréiopode. Comme de nombreuses autres espèces eusociales du genre *Synalpheus*, *S. idelisae* n. sp. présente des caractéristiques telles qu'un développement larvaire direct et un second péréiopode à carpe quadrisegmenté. Notamment, nous décrivons plusieurs colonies de *S. idelisae* n. sp. où les reines possèdent, à la place de la grande pince, une seconde pince mineure, un schéma lié à la différenciation morphologique des castes chez les crevettes du genre *Synalpheus*. Enfin, nous examinons la fréquence de ce schéma chez d'autres espèces eusociales et présumées eusociales du genre *Synalpheus*. Avec l'ajout de *S. idelisae* n. sp., le complexe d'espèces *S. rathbunae* de l'Atlantic Ouest compte désormais sept espèces eusociales.

MOTS CLÉS
Crustacés,
Caridea,
République dominicaine,
Porto Rico,
espèce nouvelle.

INTRODUCTION

Eusociality is a complex form of social organisation that has evolved over twenty times across animals (Crozier & Pamilo 1996; Barden & Engel 2020). This condition is defined by a reproductive division of labor, cooperative brood care, and overlapping generations (Wilson 1971). The only marine examples of eusociality are found in *Synalpheus* Spence Bate, 1888, a genus of sponge-dwelling pistol shrimps (Duffy 1996). *Synalpheus* exhibits a range of social behaviors. These have been categorized into: 1) pair-living species, in which a single mated pair typically resides in a sponge; 2) communal species, in which multiple mated pairs cohabitate in a sponge; and 3) eusocial species, in which one (or a few) ovigerous females, i.e. "queens" reside in a colony with many non-ovigerous individuals, i.e. "workers" (Chak & Rubenstein 2015; Chak *et al.* 2015, 2017; Hultgren *et al.* 2017). These fortress defenders perform cooperative colony defense using their robust major chelae (Duffy *et al.* 2002). *Synalpheus* species primarily produce swimming larvae that disperse planktonically, but eusocial species typically have direct development, with crawling larvae that do not disperse (Duffy & Macdonald 2010; Chak *et al.* 2017; Hultgren *et al.* 2021).

The *Synalpheus gambarelloides* (Nardo, 1847) species group is distributed throughout the West Atlantic and is the most studied clade within *Synalpheus*. This lineage radiated between 5-8 million years ago and contains at least four independent eusocial origins (Duffy *et al.* 2000; Ashrafi & Hultgren 2023). Within the *S. gambarelloides* species group, the four independent origins occur in three separate species complexes (clades): the *S. rathbunae* Coutière, 1909 complex, the *S. brooksi* Coutière, 1909 complex, and the *S. paraneptunus* Coutière, 1909 complex (fig. 4 in Chak *et al.* 2017). Recent work by Ashrafi & Hultgren (2023) have identified two new eusocial species in the Indo-West Pacific, indicating at least six different origins of eusociality worldwide.

The *Synalpheus* system is unique among eusocial taxa given their many, recent eusocial origins and spectrum of social states. In contrast, "classic" eusocial taxa such as corbiculate bees, ants, termites, and vespids combined represent only a quarter of all known eusocial transitions; some insect origins date to over 100 million years ago, and most lack closely related non-eusocial species (Crozier & Pamilo 1996; Barden & Engel 2020).

The morphological variation within eusocial and non-eusocial *Synalpheus* species creates an ideal system to study the evolutionary morphology of social animals. In the eusocial species *Synalpheus regalis* Duffy, 1996, larger non-breeding workers display more defensive behavior (Duffy *et al.* 2002), and weapon polymorphism also occurs in workers of several eusocial species. In the eusocial species *S. chacei* Duffy, 1998, some larger workers possess a longer chela with falcate fingers, indicating dimorphism in major chela development (Duffy 1998). In many eusocial species, some larger workers often possess larger major chelae (relative to size) when compared to nestmates (Tóth & Duffy 2008).

Reproductive division of labor, an intrinsic feature of eusociality, is also a potential driver of morphological evolution in social *Synalpheus* species. Eusocial queens (reproductive females) have proportionally smaller chelae than pair-living females (Tóth & Duffy 2008). The pinnacle of morphological variation, observed originally in queens of *S. filidigitus* Armstrong, 1949, is the loss of the major chela (Duffy & Macdonald 1999). These reproductive queens bear two minor chelae, losing an important weapon used in colony defense. Across eusocial species, there are many instances of queens

with two minor chelae, but there is no systematic review of this pattern in recent literature.

Within the eusocial lineages of the *S. gambarelloides* group, the monophyletic *S. rathbunae* complex is the most diverse clade of eusocial species, with six currently described species: *S. rathbunae; S. regalis*; *S. filidigitus; S. elizabethae* (Rios & Duffy, 2007); *S. chaki* Ashrafi & Hultgren, 2022; and *S. corbariae* Ashrafi & Hultgren, 2022. In this study, we describe a new species of *Synalpheus*, *Synalpheus idelisae* n. sp., from the *S. rathbunae* complex. Several colonies of our new species have queens with two minor chelae, and we survey the literature and our collections to review cases of queens or workers with the same morphological feature. This species was uncovered while conducting field excursions in Puerto Rico and the Dominican Republic, adding to our existing knowledge of social snapping shrimps in the Caribbean. Through our examination of morphological differences between closely allied species and our analysis of molecular material, we document the distinctness of this new eusocial species.

MATERIAL AND METHODS

Specimens used in our study were collected during two expeditions focusing on sponge-dwelling shrimp, one to Puerto Rico (March 2024) and one to the Dominican Republic (June 2024). Whole sponges were collected via scuba diving from coral reefs at 9-23 m depth, with a focus on sponges known to host *Synalpheus* species in the West Atlantic (Macdonald *et al.* 2006; Hultgren & Duffy 2012), primarily the sponge species *Agelas clathrodes* (Schmidt, 1870), *A. dispar* Duchassaing & Michelotti, 1864, and species of *Hyrtios* Duchassaing & Michelotti, 1864. Sites in the Dominican Republic included Peñon (18°15'10"N, 68°46'44"W, *c.* 12 m depth) and Dominicus Reef (18°20'38"N, 68°49'58"W, 15.5 m depth). In Puerto Rico, *S. idelisae* n. sp. was only found at our deepest site (Deep Shelf Reef, 17°53'45"N, 66°58'11"W, 4.23 m depth), though we collected and searched the same host sponges at several other sites, including Mario site (17°57'10"N, 67°3'21"W, 9-12 m depth), Pelotas (17°57'32"N, 67°4'1"W, 9 m depth), Turromote (17°56'5"N, 67°1'8"E, 12-15 m depth), and Enrique (17°57'21"N, 67°3'10"W, 9 m depth). At all sites, whole sponges were collected underwater in mesh bags, and kept in aerated seawater until processing. The sponges were individually dissected in seawater, and the macrofauna was removed, identified to species, counted and sexed, and preserved in 95% EtOH or RNAlater.

Type specimens are deposited at the University of Florida Natural History Museum (FLMNH) and the MNHN, and all other material is housed temporarily at Denison University, Ohio. All specimens will ultimately be deposited at the Florida Museum of Natural History (FLMNH).

DR (Dominican Republic) and PR (Puerto Rico) numbers represent field numbers; for body size, we measured carapace length in mm from the posterior margin of the carapace to the base of the rostrum. Exact sexing of non-ovigerous workers in eusocial species of *Synalpheus* is difficult without the use of scanning electron microscopy (Tóth & Bauer 2007). In the species description, we refer to non-ovigerous colony members as males (♂), although sexual composition of non-ovigerous colony members investigated using scanning electron microscopy indicates equal ratios of non-ovigerous males and females, and some intersex individuals, in other eusocial species (Tóth & Bauer 2007).

We extracted DNA from eggs or leg tissues of specimens using a DNeasy Blood and Tissue Kit (Qiagen) following the standard manufacturer's protocol, and amplified two mitochondrial loci, 16S rRNA (16S, *c.* 500 bp) and cytochrome oxidase I (COI, 658 bp, 5' barcoding region). For COI, we initially used the polyHCO/polyLCO primer pair (Brasier *et al.* 2016) to amplify 658 bp, or a combination of primers that amplified a shorter region (mlCOIintF/jgHCO2198), using annealing temperatures and PCR conditions in the reference papers (Geller *et al.* 2013; Leray *et al.* 2013). We amplified 16S using the 16sar/16S-1472 primers and PCR conditions described previously (Hultgren *et al.* 2014). We purified PCR products using a shrimp alkaline phosphate exonuclease protocol (EXO-SAP, ThermoFisher, Waltham, MA, USA), sequenced forward and reverse sequences at MCLab (South San Francisco, CA, USA) using an ABI 3730XL sequencer, and generated cleaned consensus sequences (forward and reverse) on Sequencher (GeneCodes, Ann Arbor, MI, USA). We aligned sequences for each locus in the MEGA program (Stecher *et al.* 2020) using MUSCLE (Edgar 2004), and calculated appropriate nucleotide substitution models using jModelTest2 (Darriba *et al.* 2012). We constructed a concatenated Bayesian tree using COI and 16S, using MrBayes 3.2.7a (Ronquist *et al.* 2012), implemented on CIPRES (Miller *et al.* 2010), coding gap positions as missing data. In MrBayes, we ran Markov Chain Monte Carlo (MCMC) searches with four chains for 1×10^9 generations, sampling every 1000 generations and discarding the first 25% of the samples as burn-in (final standard deviation of split frequencies = 0.000606). We calculated distance within and between different species in the *S. rathbunae* complex (% COI divergence, K2P model) in MEGA X (Stecher *et al.* 2020).

Two specimens (PR24-6202-01, and PR24-6202-21) were imaged (Figs 4; 5; Supplementary materials 1; 2) using X-ray computed tomography (CT) at the New Jersey Institute of Technology Otto H. York Center for Environmental Engineering and Science. Specimens were scanned in 0.5 mL Eppendorf microtubes suspended in 95% ethanol using a Bruker SkyScan 1275 micro-CT scanner. The specimens consist of an ovigerous queen and a non-ovigerous worker from a single colony in Puerto Rico. The queen specimen was scanned at a voltage of 30 kV and a current of 150 µA for 138 ms exposure times averaged over 5 frames per rotation with a voxel size of 8.25 µm. The worker specimen was scanned at a voltage of 36 kV and a current of 175 µA for 70 ms exposure times averaged over 5 frames per rotation with a voxel size of 6.85 µm. We used NRecon (Micro Photonics, Allentown, PA) to generate Z-stacks, and we used 3D Slicer v5.8.1 (Fedorov *et al.* 2012) to reconstruct 3D models and export .stl files.

ABBREVIATIONS

Institutions

DU	Denison University, Granville;
FLMNH	Florida Museum of Natural History, Gainesville;
FUNDEMAR	Dominican Foundation for Marine Research; Bayahíbe;
MNHN	Muséum national d'Histoire naturelle, Paris;
UF	University of Florida, Bayahíbe.

Other abbreviations

CIPRES	Cyberinfrastructure for Phylogenetic Research;
CL	carapace length;
CT	computed tomography;
DR	Dominican Republic;
EtOH	Ethanol;
EXO-SAP	shrimp alkaline phosphate exonuclease;
K2P	Kimura 2-parameter;
m	metres;
ms	milliseconds;
PCR	Polymerase chain reaction;
PR	Puerto Rico.

SYSTEMATICS

Family ALPHEIDAE Rafinesque, 1815
Genus *Synalpheus* Spence Bate, 1888

Synalpheus idelisae n. sp.
(Figs 1-7)

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TYPE MATERIAL. — **Holotype**. **Dominican Republic** • ♂ (CL 2.9 mm); Peñon; ; 15.XI.2024; in the sponge *Agelas dispar* on a coral reef; K. M. Hultgren and S. C. Chak (DR24-5417); FLMNH UF Arthropoda 74183.
Allotype. **Dominican Republic** • 1♀ queen (CL 4.6 mm); Peñon; 15.XI.2024; in the sponge *Hyrtios* sp. on a coral reef; K. M. Hultgren and S. C. Chak (DR24-5501); FLMNH UF Arthropoda 74182.
Paratypes. **Dominican Republic** • 1♂ (CL 3.3 mm); same data as the holotype (DR24-5420); MNHN-IU-2025-167 • 1♂ (CL 3.1 mm); same collection data as the holotype (DR24-5312); GenBank 16S: PX552077; FLMNH UF Arthropoda 74183.
Puerto Rico • 1♂ (CL 3.1); Deep Shelf Reef; 15.III.2024; in the sponge *Agelas dispar* on a coral reef; K. M. Hultgren and S. C. Chak (PR24-4803); GenBank COI: PX572955, 16S: PX552075; FLMNH UF Arthropoda 74185.

OTHER MATERIAL EXAMINED. — **Dominican Republic** • 5♂ (CL 2.28-3.49 mm); Dominicus Reef; K. M. Hultgren and S. C. Chak; 13.XI.2024; in the sponge *Hyrtios* sp.; (DR24-402); DU • 6♂ (CL 2.34-3.48 mm); Peñon; K. M. Hultgren and S. C. Chak; 15.XI.2024; in the sponge Ham sponge (DR24-5507); DU • 5♂ (CL 2.03-3.17 mm); Peñon; K. M. Hultgren and S. C. Chak; 15.XI.2024; in the sponge *Hyrtios* sp. (DR24-6001); DU • 5♂ (CL 3.09-3.39 mm); Tortuga; K. M. Hultgren and S. C. Chak; 15.XI.2024; in the sponge *Hyrtios* sp. (DR24-7102); DU • 4♂ (CL 2.72-3.17 mm); Dominicus Reef; K. M. Hultgren and S. C. Chak; 13.XI.2024; in the sponge *Hyrtios* sp. (DR24-902); DU.
Puerto Rico • 1♀ queen (CL 4.04 mm); Deep Shelf Reef (PR24-4801); DU • 12♂ (CL 1.86-2.7 mm); Deep Shelf Reef; K. M. Hultgren and S. C. Chak; 15.III.2024; in the sponge *Agelas dispar* (PR24-4802); DU • 3♂ (CL 2.18-2.8 mm); Deep Shelf Reef; K. M. Hultgren and S. C. Chak; 15.III.2024; in the sponge *Agelas dispar* (PR24-4901); DU • 3♂ (CL 2.69-2.91 mm); Deep Shelf Reef; K. M. Hultgren and S. C. Chak; 15.III.2024; in the sponge *Agelas clathrodes* (PR24-5101); DU • 4♂ (CL 2.83-2.98 mm); Deep Shelf Reef; K. M. Hultgren and S. C. Chak; 15.III.2024; in the sponge *Agelas clathrodes* (PR24-5202); DU • 1♀ queen (CL 3.3 mm); Deep Shelf Reef (PR24-5401); DU • 7♂ (CL 1.9-2.89 mm); Deep Shelf Reef; K. M. Hultgren and S. C. Chak; 15.III.2024; in the sponge *Agelas clathrodes* (PR24-5412); DU • 1♀ queen (CL 3.27 mm); (PR24-6201); DU • 6♂ (CL 1.95-2.69 mm); Deep Shelf Reef; K. M. Hultgren and S. C. Chak; 15.III.2024; in the sponge *Agelas dispar* (PR24-6202); DU.

ETYMOLOGY. — This species is named after Idelisa Bonnelly de Calventi, a marine biologist from the Dominican Republic, often referred to as the mother of marine conservation in the Caribbean region, and the founder of the Dominican Foundation for Marine Research (FUNDEMAR) which helped facilitate our field work.

DISTRIBUTION. — Western Atlantic: Dominican Republic and Puerto Rico (localities within).

COMPARATIVE MATERIAL. — *Synalpheus rathbunae*: **Panama (West Atlantic)** • 1♂; Bocas del Toro; K. M. Hultgren and J. E. Duffy; 9.XI.2007; in the sponge *Neopetrosia rosariensis* (Zea & Rützler, 1983); CL 2.6 mm; P07-6203; DU • 1♂; Bocas del Toro; K. M. Hultgren; 28.II.2008; in the sponge *N. rosariensis;* P08-11507-03; DU • 1♂; Bocas del Toro; K. M. Hultgren; 9.XI.2007; in the sponge *N. rosariensis*; P07-5801; DU • 1♂; Bocas del Toro; K. M. Hultgren; 9.XI.2007; in the sponge *N. rosariensis;* P07-5303-2; DU • 1♂; Bocas del Toro; K. M. Hultgren; 28.II.2008; in the sponge *N. rosariensis;* P08-6801-2; DU • 1♂; Bocas del Toro; K. M. Hultgren; 28.II.2008; in the sponge *N. rosariensis;* P08-7701-2; DU • 1 ♂; Bocas del Toro; K. M. Hultgren; 28.II.2008; in the sponge *N. rosariensis;* P08-11102-3; DU • 2♂; Bocas del Toro; K. M. Hultgren and J. E. Duffy; 9.XI.2007; in the sponge *N. rosariensis*; CL 2.7 mm; P07-6402; GenBank COI: MZ323465; 16S: PX438786; DU.
Synalpheus filidigitus: **Panama (West Atlantic)** • 1♂; Bocas del Toro; K. M. Hultgren; 22.II.2008; in the sponge *Neopetrosia* cf. *proxima* (Duchassaing & Michelotti, 1864); P08-14601-31; DU.
Belize • 1♂; Sand Bores; K. M. Hultgren and K. S. Macdonald; 27.VII.2009; in the sponge *N.* cf. *proxima*; CBC09-4203-2; DU • 2♂; Sand Bores; K. M. Hultgren and K. S. Macdonald; 27.VII.2009; in the sponge *N.* cf. *proxima*; CBC09-7604; DU.

DESCRIPTION (BASED ON ALL MATERIAL EXAMINED)

Body

Subcylindrical; carapace smooth, sparsely setose, pterygostomian corner with broad acute angle, posterior portion with distinct cardiac notch.

Frontal margin (Figs 1A, B; 3C)

Rostrum narrower than orbital hoods, about as long as orbital hoods, and separated from hoods by deep sinus. Orbital hoods hoof-shaped. Stylocerite broad, with bluntly acute tip, distinctly shorter than first segment of antennular peduncle. First antennular segment with two basal ventral processes. Basicerite with strong, sharp spine on dorsal margin; length of longer lateral spine of basicerite variable, nearly reaching or slightly exceeding 2nd segment of antennular peduncle. Lateral spine of basicerite about 50-80% length of scaphocerite. Scaphocerite without blade, with robust lateral spine, reaching or overreaching distal end of 3rd article of antennular peduncle. Mouthparts not dissected, apparently typical externally for the genus.

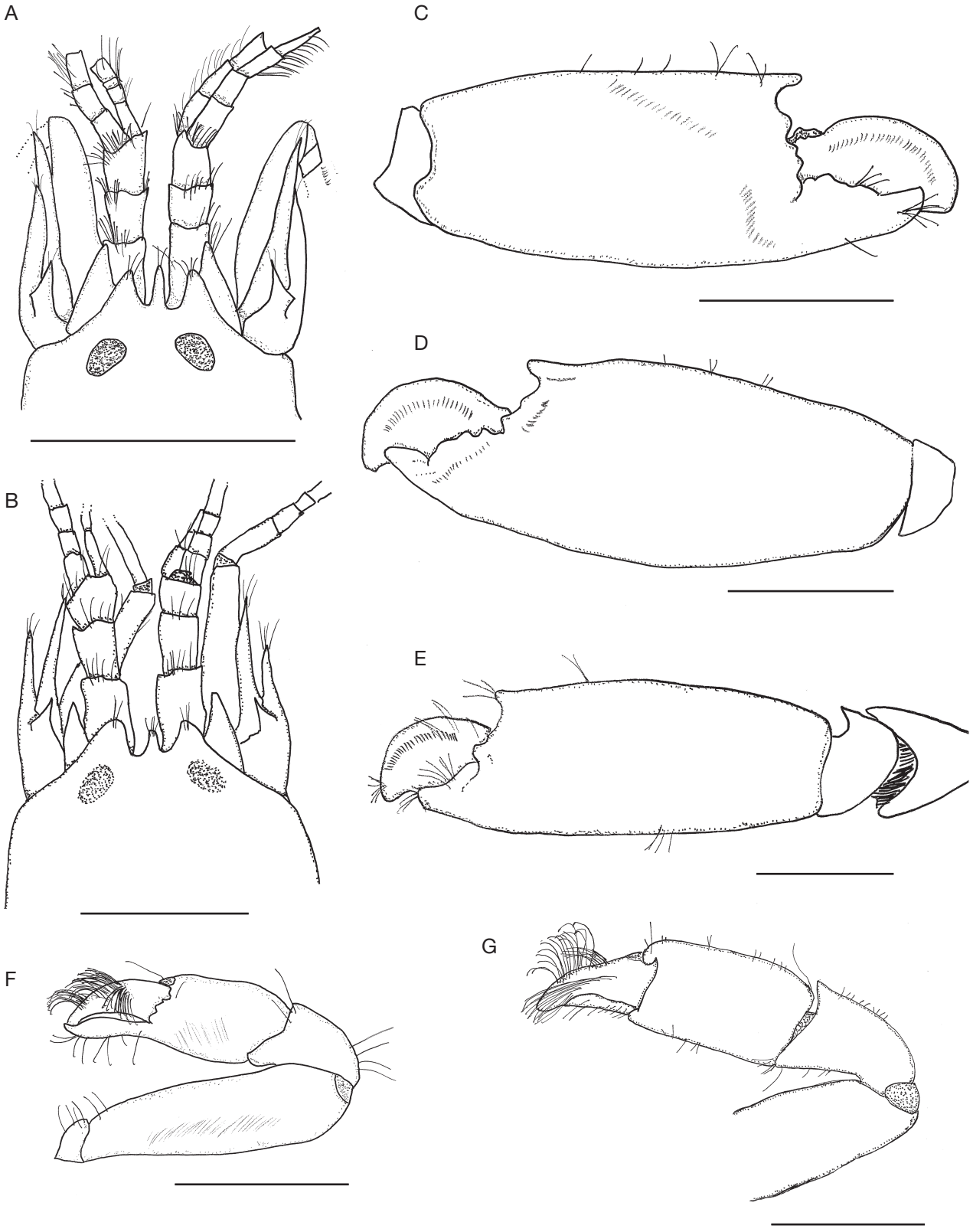

FIG. 1. — *Synalpheus idelisae* n. sp.: **A**, **C**, **D**, **F**, holotype, non-ovigerous individual (FLMNH UF Arthropoda 74183); **B**, **E**, **G**, allotype, female queen (FLMNH UF Arthropoda 74182): **A**, frontal region, dorsal view; **B**, frontal region, dorsal view; **C**, major chela, lateral view; **D**, major chela, mesial view; **E**, major chela, lateral view; **F**, minor chela, lateral view; **G**, minor chela, dorsomesial view. Scale bars: 1 mm.

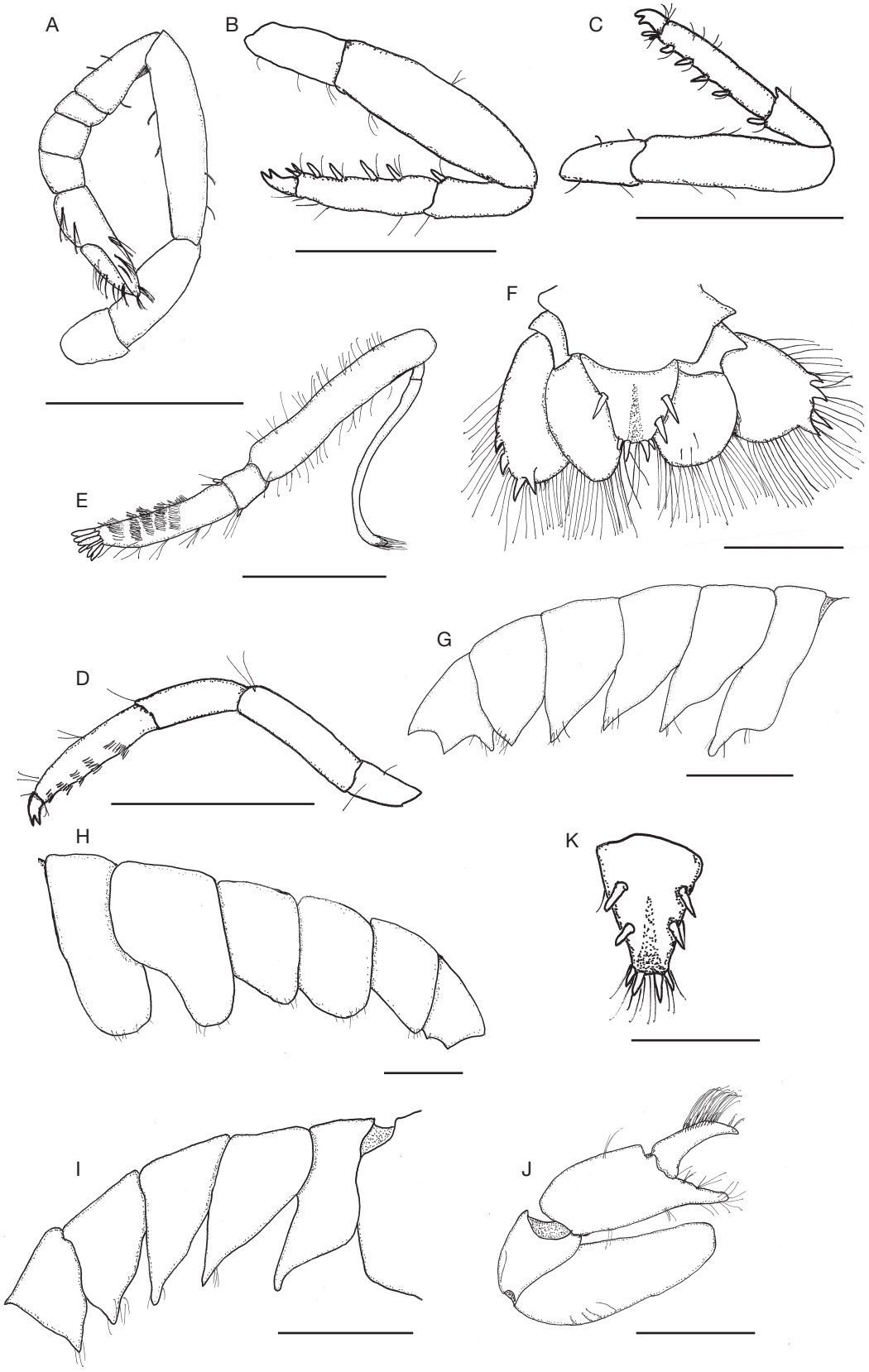

FIG. 2. — *Synalpheus idelisae* n. sp.: **A**-**G**, holotype, non-ovigerous individual (FLMNH UF Arthropoda 74183); **H**, allotype, female queen (FLMNH UF Arthropoda 74182); **I**, **J**, paratype, non-ovigerous individual (DR24-5303); **K**, non-ovigerous individual (DR24-6014): **A**, second pereopod; **B**, left third pereopod; **C**, left fourth pereopod; **D**, left fifth pereopod; **E**, left third maxilliped; **F**, telson and uropods, dorsal view; **G**, right pleura, lateral view; **H**, left pleura, lateral view; **I**, right pleura, lateral view; **J**, minor chela, open; **K**, telson, dorsal view, uropods omitted. Scale bars: A-J, 1 mm; K, 0.5 mm.

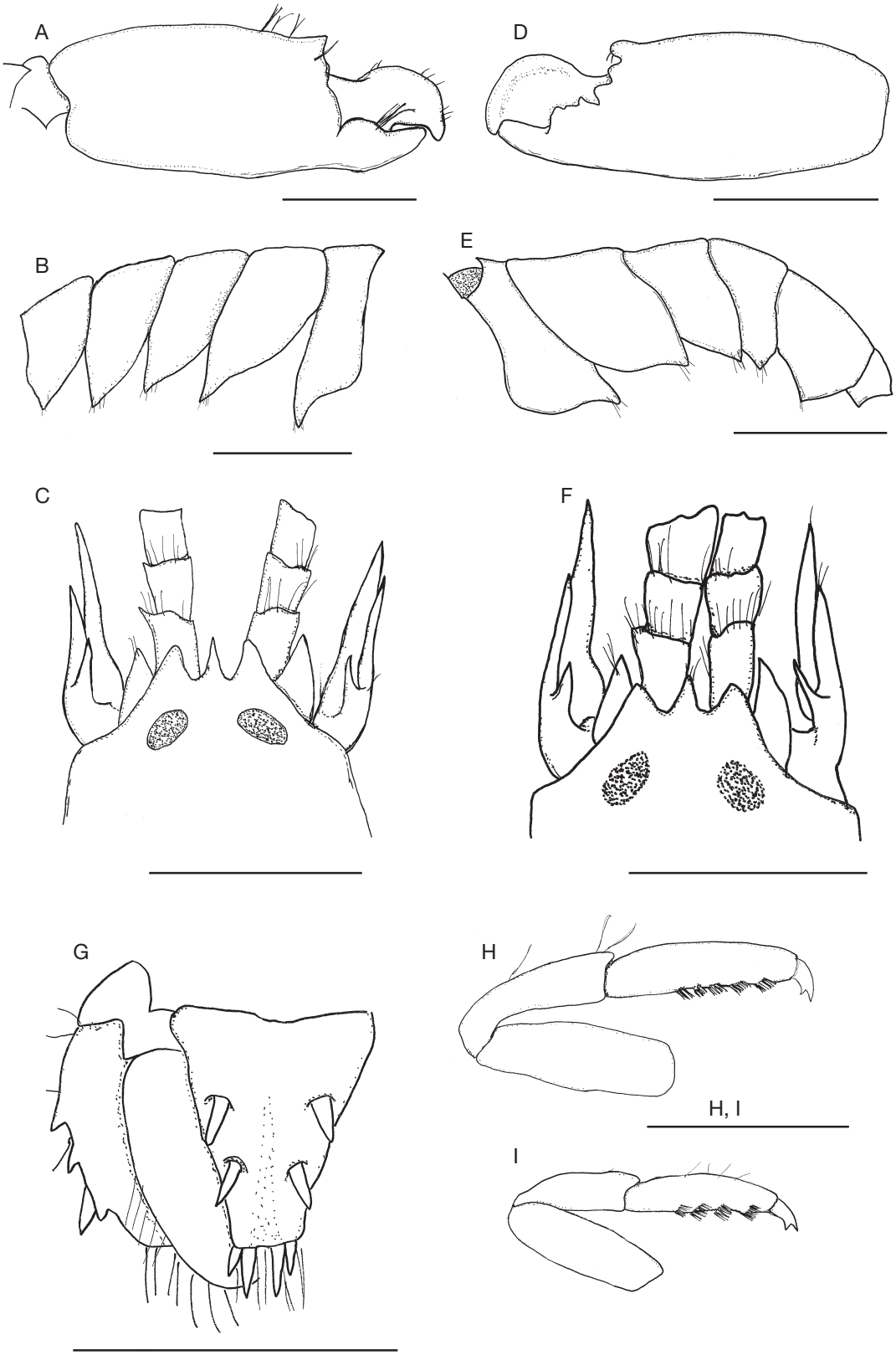

FIG. 3. — *Synalpheus idelisae* n. sp.: **A**, paratype, non-ovigerous individual (FLMNH UF Arthropoda 74185); **B**, **C**, paratype, non-ovigerous individual (MNHN-IU-2025-167); **H**, non-ovigerous individual (DR24-5313): *Synalpheus rathbunae*: **D**, non-ovigerous individual (P07-6402); **E**, **F**, **G**, non-ovigerous individual (P07-6203); **I**, non-ovigerous individual (P08-6801-2): **A**, major chela, lateral view; **B**, right pleura, lateral view; **C**, frontal region, dorsal view (antennal appendages omitted); **C**, frontal region, dorsal view (antennal appendages omitted); **D**, major chela, mesial view; **E**, left pleura, lateral view; **F**, frontal region, dorsal view (no antennal appendages); **G**, telson and right uropod, dorsal view (left uropod omitted); **H**, fifth pereopod; **I**, fifth pereopod. Scale bars: 1 mm.

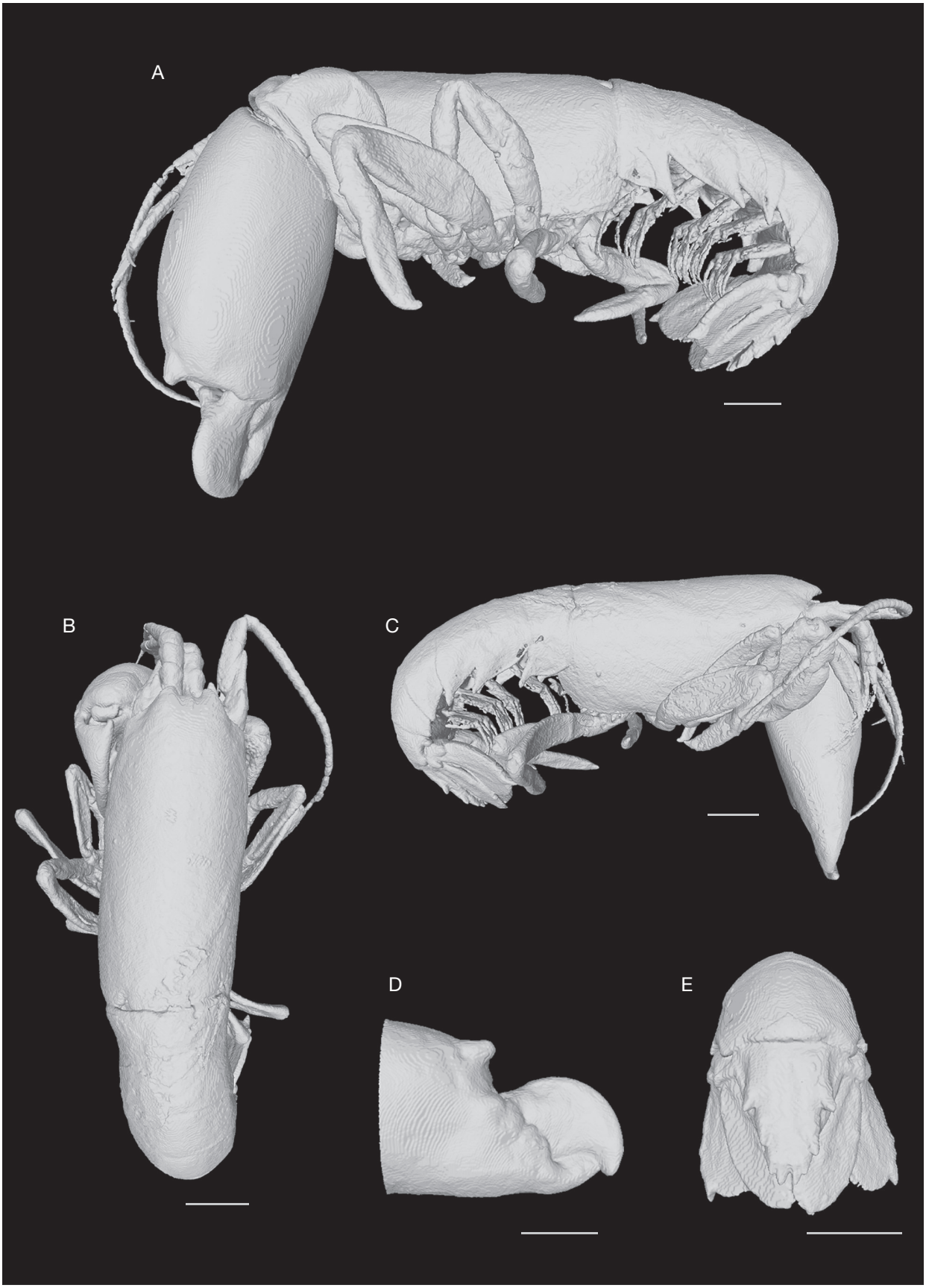

FIG. 4. — *Synalpheus idelisae* n. sp.: **A**-**E**, non-ovigerous individual (PR24-6202-21); **A**, lateral view; **B**, dorsal view; **C**, alternate lateral view; **D**, major chela, frontal region, lateral view; **E**, telson and uropods, dorsal view. Scale bars: 0.5 mm.

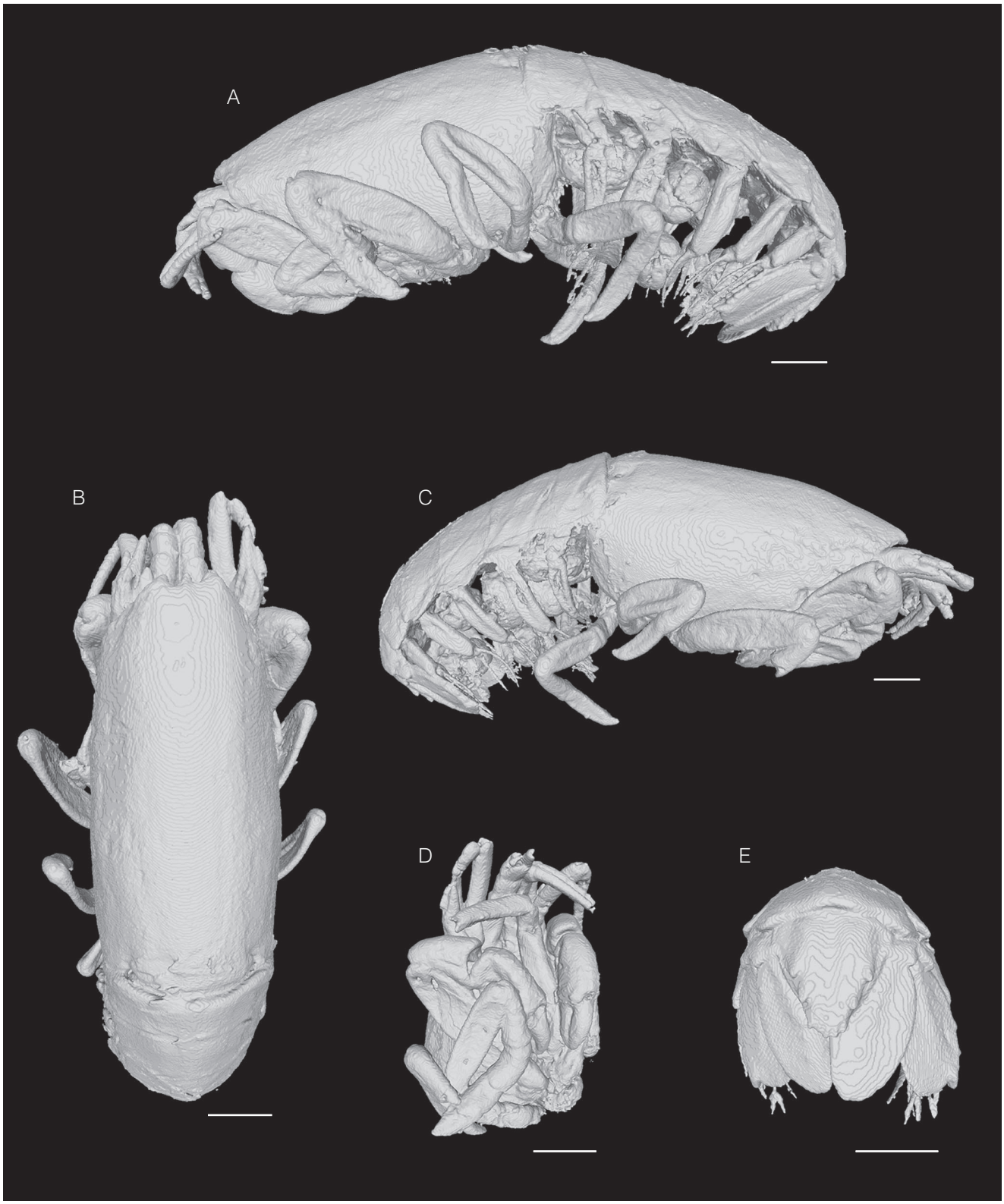

Fig. 5. — *Synalpheus idelisae* n. sp.: **A**-**E**, ovigerous individual (PR24-6202-001); **A**, lateral view; **B**, dorsal view; **C**, alternate lateral view; **D**, anterior portion of carapace and appendages, minor chela pair, ventral view; **E**, telson and uropods, dorsal view. Scale bars: 0.5 mm.

Appendages

Major pereopod 1 (major chela; Figs 1C-E; 3A; Supplement SA1) massive, fingers shorter than half length of palm, fixed finger shorter than dactyl. Palm of chela with distal, superior margin produced into cone-shaped projection, pointing forward or slightly upwards, without an acute spine. Minor

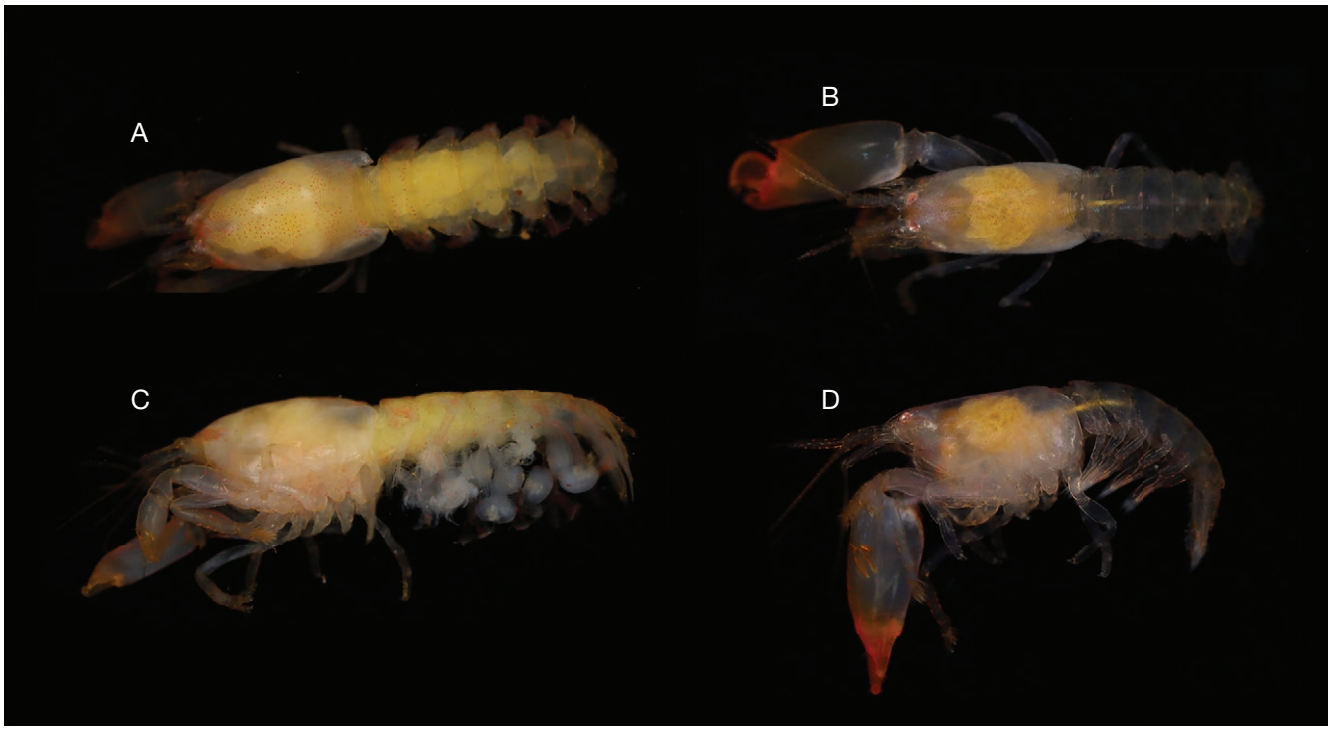

Fig. 6. — *Synalpheus idelisae* n. sp.: **A**, **B**, allotype, ovigerous female queen (FLMNH UF Arthropoda 74182); **C**, **D**, non-ovigerous individual (DR24-5307): **A**, dorsal view; **B**, lateral view; **C**, dorsal view; **D**, lateral view.

pereopod 1 (minor chela; Figs 1F-G; 2J) with palm less than two times longer than high, fingers shorter than palm; dactyl (moveable finger) with flexor margin concave, blade-like, without accessory teeth; conspicuous dorsal brush of setae on extensor side of dactyl; fixed finger mildly concave, with no hint of subdistal tooth. Pereopod 2 (Fig. 2A) with carpus 4-segmented, subequal in length relative to merus. Approximate length ratios for carpal articles of the second pereopod: 1: 0.3: 0.3: 0.6 (from proximal segment to distal segment). Pereopod 3 (Fig. 2B) with biunguiculate dactyl, with flexor unguis about equal (in thickness and length) than extensor unguis, propodus with 4-5 mobile spines on flexor margin and one pair of spines on distal end; carpus with one distal spine on flexor margin; merus without spines on flexor margin. Pereopod 4 (Fig. 2C) similar to 3rd. Pereopod 5 (Fig. 2D; 3H) similar to 4th, but without distal spine on carpus, and with five transverse combs of stiff setae on flexor margin of propodus. Maxilliped 3 (Fig. 2E) with distal circlet of spines on distal segment, lacking ventrodistal spine on antepenultimate segment.

Abdomen

Pleuron 1 of male (Figs 2G, I; 3B) narrow, with anterior corner rounded, posterior corner produced into long slightly hooked projection, with subacute or slightly rounded tip; pleura 2-5 also narrow, with posterior distal corners of pleura 2-5 forming extended, triangular projections. Pleuron 1 of female (Fig. 2H) rounded anteriorly and posteriorly, posterior corners of pleura 2-5 rounded. Telson (Fig. 2F, K; Supplement SA1) with mesial pair of distal telson spines thicker and longer than lateral spines, posterior corners adjacent to distal spines obtuse, distance between distal spines 10-30% width of distal margin. Dorsal telson spines variable, with many individuals (non-ovigerous workers and queens) missing 1-3 dorsal telson spines (see Morphological variations). Uropods (Fig. 2F) with 1-2 marginal fixed teeth on exopod anterior to moveable spine, fixed anterior teeth distinctly removed from fixed tooth.

Color

Nondescript, translucent body with distal tips of chelae tinged orange; ovaries and embryos light yellowish-green (Fig. 6).

First larva

Newly hatched larvae obtained from the allotype, DR24-5501, being crawling megalopae (direct development), similar to direct-developing larvae described for many other eusocial species (Hultgren *et al.* 2021).

Morphological variation

Several female queens from Puerto Rico had two minor chelae, instead of a minor chela and a major chela (e.g., Fig. 5). One of the colonies in the Dominican Republic (DR24 5303-5305) had three workers with two minor chelae. These workers had pleura that were typical of males (e.g., Fig. 2I). Many of the male workers (approximately 58% of the 67 non-ovigerous workers surveyed, from 13 different colonies, including the holotype Fig. 2F) and female queens

TABLE 1. — Species of *Synalpheus* Spence Bate, 1888 sequenced for phylogenetic analysis, including the species identifier, COI and 16S accession numbers, field collection or museum catalog numbers, and country of origin. MNHN indicates the Muséum national d'Histoire naturelle; P09, P07, PR24, DR24, P08, and CBC09 are collection numbers for specimens housed at Denison University.

***Synalpheus* species**	**species identifier**	**COI**	**16S**	**Field or museum number**	**Country**
chaki Ashrafi & Hultgren, 2022	1228	MZ323456	MZ329362	MNHN-IU-2014-1228	Martinique
chaki	1229	MZ323457	MZ329363	MNHN-IU-2014-1229	Martinique
corbariae Ashrafi & Hultgren, 2022	1238	MZ323450	MZ329367	MNHN-IU-2014-1238	Martinique
corbariae	1239	MZ323451	MZ329368	MNHN-IU-2014-1239	Martinique
corbariae	2533	PX572954	PX552074	MNHN-IU-2018-5968	Guadeloupe
corbariae	2537	PX572952	PX552072	MNHN-IU-2021-8137	Guadeloupe
corbariae	2552	PX572956	PX552076	MNHN-IU-2016-1938	Martinique
corbariae	3134	MZ323453	PX438785	MNHN-IU-2019-3134	Martinique
corbariae	3137	MZ323454	MZ329370	MNHN-IU-2019-3137	Martinique
corbariae	4148	MZ323452	MZ329369	MNHN-IU-2016-4148	Martinique
elizabethae (Rios & Duffy, 2007)	137	KU980213	HQ435446	P08-12504	Panama (West Atlantic)
elizabethae	775	PX572959	PX552080	P09-1204	Panama (West Atlantic)
elizabethae	776	PX572960	PX552081	P09-4806	Panama (West Atlantic)
filidigitus Armstrong, 1949	470	KJ595079	HQ435447	CBC09-7603	Belize
filidigitus	779	PX572962	PX552083	P09-6402	Panama (West Atlantic)
filidigitus	783	PX572961	PX552082	P09-7601-2	Panama (West Atlantic)
idelisae n. sp.	2524	PX572955	PX552075	PR24-4803	Puerto Rico
idelisae n. sp.	2526	PX572963	PX552084	PR24-6014	Puerto Rico
idelisae n. sp.	2527	PX572953	PX552073	PR24-6403	Puerto Rico
idelisae n. sp.	2528	PX572951	PX552071	PR24-5614	Puerto Rico
idelisae n. sp.	2561	–	PX552077	DR24-5312	Dominican Republic
idelisae n. sp.	2563	PX572958	PX552079	DR24-5416	Dominican Republic
macdonaldi Ashrafi & Hultgren, 2022	1227	MZ323448	MZ329364	MNHN-IU-2014-1227	Martinique
macdonaldi	2616	PX572950	PX552070	MNHN-IU-2021-8369	Martinique
macdonaldi	2617	PX572957	PX552078	MNHN-IU-2021-8382	Martinique
macdonaldi	4586	MZ323449	MZ329365	MNHN-IU-2016-4586	Martinique
rathbunae Coutière, 1909	771	MZ323465	PX438786	P07-6402	Panama (West Atlantic)
rathbunae	772	PX572964	PX552085	P07-5303	Panama (West Atlantic)
rathbunae	773	MZ323466	PX438787	P07-5801	Panama (West Atlantic)
regalis Duffy, 1996	469	KJ625042	HQ435474	VIMS CBC09-7002	Belize
carpenteri MacDonald & Duffy, 2006	1235	MZ323432	MZ329352	MNHN-IU-2014-1235	Martinique

TABLE 2. — Morphological characters distinguishing different species in the *Synalpheus rathbunae* complex.

	S. elizabethae	***S. filidigitus***	***S. regalis***	***S. rathbunae***	***S. idelisae* n. sp.**	***S. chaki***	***S. corbariae***
Major chela, anterodorsal protuberance	inflated, with spine	inflated, with spine	inflated, with spine	conical point (forwards or upwards)	conical point (forwards or upwards)	inflated, with spine	inflated, typically no spine
Male first pleuron, posterior corner	long hooked projection	short hooked projection	long hooked projection	long acute projection	long hooked projection	short hooked projection	short hooked projection
Pereopod 5, number of rows of transverse setae	4 rows	4 rows	4 rows	4 rows	5 rows	3 rows	5 rows
Second pereopod, distal end of dactyl	simple	filiform	simple	simple	simple	simple	simple
Setae on minor chela	2 rows	brush	brush	brush	brush	2 rows	brush

(33% of the six queens surveyed) had an atypical number of dorsal telson spines – one, two, or three spines (instead of the typical four).

Ecology and colony size (Table 3)

In both the Dominican Republic and Puerto Rico, we have found *S. idelisae* n. sp. living within sponges of the genus *Agelas* (*A. dispar* and *A. clathrodes*), and in the Dominican Republic it was also commonly inhabiting the sponge *Hyrtios* sp. In Puerto Rico, all colonies of *S. idelisae* n. sp. were found in *Agelas dispar* and *A. clathrodes* only from deep sites (23 m depth); *Agelas* host sponges were collected at shallower depths (6-12 m depth), but never contained *S. idelisae* n. sp. In the Dominican Republic, *S. idelisae* n. sp. was found in sponges at shallower depths (12-15.5 m). Colony size ranged from 8-67 individuals (median = 28 individuals), but we did not find queens in every colony, suggesting many colonies may be incompletely sampled. In colonies with queens, there was only a single queen present.

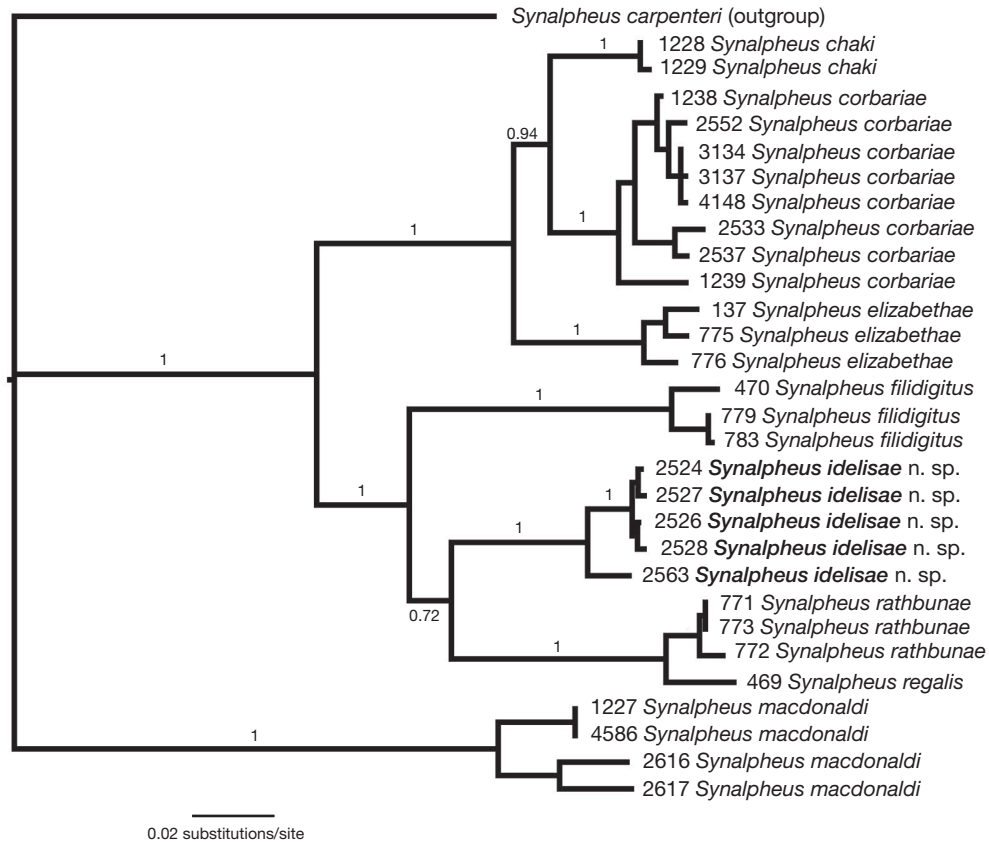

FIG. 7. — Bayesian concatenated tree, constructed using COI and 16S, of the *Synalpheus rathbunae* species complex from the West Atlantic, including *Synalpheus idelisae* n. sp. Numbers above or below each node indicate Bayesian posterior probability values (bpp); bpp below the level of species are omitted. Numbers correspond to the individual specimens in Table 1. *Synalpheus carpenteri* MacDonald & Duffy, 2006 and *S. macdonaldi* Ashrafi & Hultgren, 2022 are the outgroups.

DISCUSSION

Synalpheus idelisae n. sp. has several morphological characters, such as the prominent spine on the dorsal margin of the basicerite and a 4-segmented second pereopod, that in combination clearly distinguish this new species as a member of the *S. rathbunae* species group, bringing the total number of *Synalpheus* species in the *S. rathbunae* species group to seven (Fig. 7). In terms of phylogenetics, *S. idelisae* n. sp. is nested within the *S. rathbunae* species group (Fig. 7), with a mean pairwise interspecific divergence of 12.6% in COI with *S. rathbunae*, which belongs to its sister clade (with *S. regalis). Synalpheus idelisae* n. sp. has a mean pairwise interspecific divergence of 11.2% with *S. regalis.* In contrast, mean intraspecific pairwise genetic divergences in the *S. rathbunae* group ranged from 0% (in *S. chaki*) to 2.58% (within *S. elizabethae*).

Within the *S. rathbunae* complex, *S. idelisae* n. sp. is morphologically most similar to *S. rathbunae* and *S. elizabethae.* It can be distinguished from *S. elizabethae* by several characters, including an anterodorsal spine on the major chela that is conical (vs inflated with an accessory spine in *S. elizabethae)*, a thick transverse brush of setae on the minor first chela (vs two rows of setae in *S. elizabethae*), and five rows of transverse setae on the 5th pereopod (vs four rows of transverse setae in *S. elizabethae*, Figure 2). It can be distinguished from *S. rathbunae* by the shape of the posterior corner of the first pleuron in males (hooked projection in *S. idelisae* n. sp. vs a long acute projection in *S. rathbunae*). The pleura are generally narrower and less overlapping in male individuals of *S. idelisae* n. sp., relative to males in *S. rathbunae*. *S. idelisae* n.sp. can also be distinguished from *S. rathbunae* by the number of transverse combs of setae on the fifth pereopod (five in *S. idelisae* n. sp. vs four in *S. rathbunae*, see Fig. 3H, I; Table 2). The distal telson spines in *S. rathbunae* (Fig. 3G; fig. 51t in Coutière 1909) are similar in width (with mesial telson spines longer than lateral spines), while in *S. idelisae* n. sp., the mesial distal telson spines are thicker and longer than the lateral distal spines (Fig. 2F, K). These species also vary in sponge hosts; *S. rathbunae* is primarily reported from the sponge host *Neopetrosia rosariensis* (Hultgren & Duffy 2012), while *S. idelisae* n. sp. was found in *Agelas clathrodes*, *A. dispar*, and *Hyrtios* sp. Across the rest of the *S. rathbunae* species complex, *S. idelisae* n. sp. can be distinguished from *S. chaki*, *S. regalis*, and *S. filidigitus* by the shape of the anterodorsal projection on the minor chela (conical in *S. idelisae* n. sp., vs inflated with a spine in the other three species); in addition, the distal tips of the dactyl

TABLE 3. — Colony information for *S. idelisae* n. sp. collected in the Dominican Republic and in Puerto Rico; each row indicates a separate colony examined in this study (the queen was not collected for all colonies). Unique colony ID includes the field number, the sponge number, and the sponge species. For the right two columns, the field collection numbers are indicated in parentheses; not all field collection numbers are referenced in the text.

Locality	Unique Colony ID	# Female Queens	# Non-ovigerous individuals
Dominican Republic	DR24-4-Hyrtios sp.	1 (DR24-401)	66 (DR24-402, 403)
Dominican Republic	DR24-9-Agelas clathrodes	1 (DR24-901)	13 (DR24-902, 903)
Dominican Republic	DR24-53-Hyrtios sp.	0	39 (DR24-5302-5316)
Dominican Republic	DR24-54-Agelas dispar	0	13 (DR24, 5402-5406, 5413, 5416-5420)
Dominican Republic	DR24-55-Hyrtios sp.	1 (DR24-5501)	61 (DR24 5502-5508, 5510)
Dominican Republic	DR24-60-Agelas dispar	0	50 (DR24-6001)
Dominican Republic	DR24-71-Agelas clathrodes	0	14 (DR24-7101, 7102)
Puerto Rico	PR24-48-Agelas dispar	1 (PR24-4801)	53 (PR24-4802, 4803)
Puerto Rico	PR24-49-Agelas dispar	0	33 (PR24-4901)
Puerto Rico	PR24-51-Agelas clathrodes	0	20 (PR24-5101)
Puerto Rico	PR24-52-Agelas clathrodes	0	76 (PR24-5201, 5202, 5204-5215)
Puerto Rico	PR24-54-Agelas clathrodes	1 (PR24-5401)	55 (PR24-5402-5416)
Puerto Rico	PR24-62-Agelas dispar	1 (PR24-6201)	40 (PR24-6202, 6203)

of the minor chela in *S. filidigitus* are filiform (vs simple in other species in the *S. rathbunae* complex, Table 2). *S. idelisae* n. sp. can be distinguished from *S. chaki* and *S. corbariae* most easily by the four-segmented carpus of the second pereopod (*S. chaki* and *S. corbariae* have a second pereopod carpus with five segments), and by the shape of the first pleuron in males (long with a hooked projection in *S. idelisae* n. sp., vs shorter with a hooked projection in the other two species, Table 2).

Among West Atlantic sponge-dwelling species of *Synalpheus* in the *S. gambarelloides* group, *S. idelisae* n. sp. can primarily be distinguished from other species of *Synalpheus* by the 4-segmented carpus of the second pereopod. Outside of the *S. rathbunae* complex, only six other species have a second pereopod with a 4-segmented carpus. *S. ankeri* Hultgren & Brandt, 2015, *S. microneptunus* Hultgren, Macdonald & Duffy, 2011, *S. cayoneptunus* Hultgren & Brandt, 2015, and *S. macdonaldi* Ashrafi & Hultgren, 2022 all have a sparse field of setae on the dactyl of the minor chela (vs a thick brush of setae on *S. idelisae* n. sp.). *S. agelas* Pequegnat & Heard, 1979 is a consistently pair-living species, and has a small blade on the scaphocerite (*S. idelisae* n. sp. has no blade), and *S. barahonensis* Armstrong, 1949 has a tuft of setae on the distal end of the third maxilliped (vs a circlet of spines in *S. idelisae* n. sp. and nearly all other species in the *S. gambarelloides* group).

S. idelisae n. sp. seems to exhibit a great deal of variation in morphology that may be related to colonial life, such as the abnormalities in dorsal telson spines, and the two minor chelae. Abnormal numbers or placement of telson spines were noted in three species in the *S. paraneptunus* Coutière, 1909 complex: the eusocial species *S. riosi* Anker & Tóth, 2008, and the putatively pair-living species *S. brevidactylus* Anker & Tóth, 2008 and *S. paraneptunus* Coutière, 1909 (Anker & Tóth 2008). As far as we have reviewed the literature, there are no reports of abnormal numbers of dorsal telson spines in other eusocial or putatively eusocial species of *Synalpheus*, including *S. elizabethae* (Rios & Duffy 2007), *S. regalis* (Duffy & Macdonald 1999), *S. germanus neptunus* (Banner & Banner 1975), *S. gustavi* (Ashrafi & Hultgren 2023), *S. rathbunae* (Coutière 1909; Chace 1972), or *S. chaki* and *S. corbariae* (Ashrafi & Hultgren 2022).

One product of eusocial evolution is morphological specialisation (Holldobler & Wilson 2009) There is often phenotypic disparity between reproductive and nonreproductive castes in eusocial colonies (Wilson 1971; O'Riain *et al.* 2000; Streinzer *et al.* 2013; Trible & Kronauer 2017; Revely *et al.* 2021). A functional feature of interest in *Synalpheus* is their major chela. Investing less in weaponry could benefit eusocial reproductives given the cost of reproduction and abundance of defensive workers. We surveyed existing literature (Coutière 1909; Chace 1972; Banner & Banner 1975, 1983; Duffy & Macdonald 1999; Tóth & Duffy 2008; Hultgren *et al.* 2017), thirty years of sponge-dwelling shrimp collections from the Caribbean (Duffy, Hultgren, Macdonald, Chak, unpublished data), and recently described eusocial species from Martinique (Ashrafi & Hultgren 2022) to review all known instances of reduced major chelae in eusocial *Synalpheus*. Of the 12 known species of eusocial shrimp, at least seven exhibit major chela reduction in queens. Some eusocial queens have proportionally smaller major chela compared to workers – as in *S. regalis* and *S. chacei* (Tóth & Duffy 2008). Queens with two minor chelae, the most extreme example of major chela reduction, are abundant in eusocial species. Many *S. filidigitus* (Duffy & Macdonald 1999) and *S. rathbunae* (Chace 1972) queens possess two minor chelae; this is also noted in *S. crosnieri* Banner & Banner, 1983, who attributed the unusual sex ratios of this putatively eusocial species to secondary metabolites in their sponge host (Banner & Banner 1983). Other examples of reproductive females with two minor chelae include *S. chacei* (CBC90-207, CBC94-7301, CBC99-7601, CBC03-5401) (Duffy & Macdonald 1999), *S. corbariae* (MNHN-IU-2018-5968, MNHN-IU-2021-8137, MNHN-IU-2016-1938), and *S. macdonaldi* Ashrafi & Hultgren, 2022 (MNHN-IU-2021-8369). One male *S. elizabethae* specimen (CBC01-7202) bearing two minor chelae is also recorded. Reproductive skew, intra-sexual competition, and the energetic trade-off between defensive weaponry and fecundity likely contribute to morphological variation in queen major chela size (Tóth & Duffy 2008; Chak *et al.* 2015; Bornbusch *et al.* 2018).

Synalpheus idelisae n. sp. is morphologically and genetically distinct from other snapping shrimp, and this new species occurs in at least two locations in the West Atlantic. Several individuals, including both queens and workers, possess two minor chelae, a pattern that we continue to document across different eusocial species. In-depth morphological examination of museum specimens and existing collections is necessary to identify additional examples of potential morphological caste differentiation in eusocial *Synalpheus*. Along with two additional recently described species from Martinique (Ashrafi & Hultgren 2022), the discovery of *S. idelisae* n. sp. in Puerto Rico and the Dominican Republic indicates that the *S. rathbunae* species complex is more diverse than originally thought.

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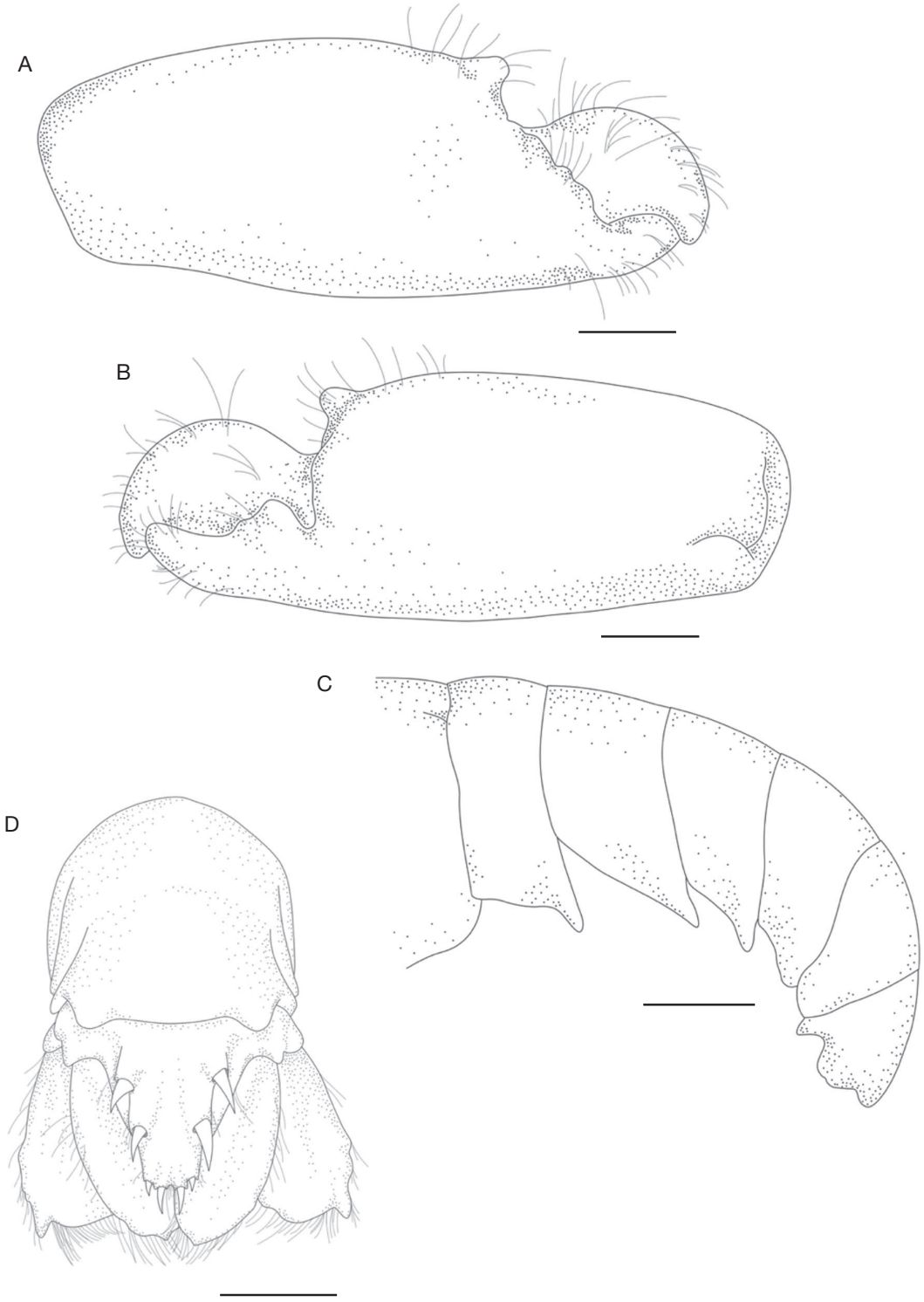
APPENDIX AND SUPPLEMENTARY MATERIALS

APPENDIX 1. — *Synalpheus idelisae* n. sp.: **A**-**D**, non-ovigerous individual (PR24-6202-21): **A**, major chela, lateral view; **B**, major chela, mesial view; **C**, left pleura, lateral view; **D**, telson and uropods, lateral view; lateral uropod spines omitted. Scale bars: 0.5 mm.



SUPPLEMENTARY MATERIAL 1. — STL file of segmented CT scan of non-ovigerous individual PR24-6202-21. https://sciencepress.mnhn.fr/sites/default/files/documents/en/zoosystema2026v48a20_s1.zip. https://doi.org/10.5852/zoosystema2026v48a20_s1

SUPPLEMENTARY MATERIAL 2. — STL file of segmented CT scan of ovigerous individual PR24-6202-001. https://sciencepress.mnhn.fr/sites/default/files/documents/en/zoosystema2026v48a20_s2.zip. https://doi.org/10.5852/zoosystema2026v48a20_s2