Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 2026
doi: https://doi.org/10.18257/raccefyn.4030

Original article

Rediscovery and redescription of *Ostraconotus spatulipes* A. Milne-Edwards, 1880 (Crustacea: Decapoda: Anomura: Paguridae), and its affinity within the Paguroidea

Redescubrimiento y nueva descripción de *Ostraconotus spatulipes* A. Milne-Edwards, 1880 (Crustacea: Decapoda: Anomura: Paguridae), y su afinidad dentro de los Paguroidea

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Inaugural article from Rafael Lemaitre as correpondant member of the Academia Colombiana de Ciencias Exactas, Físicas y Naturales

Abstract

The taxonomic history of the pagurid hermit crab *Ostraconotus spatulipes* A. Milne-Edwards, 1880, is reviewed, and the morphology of the species is documented in detail, within the context of modern systematic knowledge of the Paguroidea. Molecular knowledge remains limited, as only the H3 gene was successfully amplified. The available H3 sequence, however, is consistent with placement of *O. spatulipes* within Paguridae, but does not resolve its internal phylogenetic position. Full anatomical details, illustrations, and coloration are provided, all of which are necessary for phylogenetic studies, given the importance attributed to this intriguing species in the evolution of the Paguroidea in general, and the family Paguridae in particular. This morphologically exceptional, carcinized, minute hermit crab (< 5.0 mm in carapace length) was known exclusively from specimens collected between 1872 and 1879 in the Gulf of Mexico and off Barbados. Surprisingly, despite numerous faunal surveys and expeditions conducted since then in the region, no more specimens of *O. spatulipes* had been obtained until one of us (DLF) captured a single female off the west coast of Florida in 2014. More fresh specimens are required to expand molecular genetic analyses that can accurately place this unique species within the Anomuran Tree of Life.

Keywords: Paguridae; *Ostraconotus*; redescription; taxonomy; molecular evidence; DNA.

Resumen

Se revisa la historia taxonómica del cangrejo ermitaño pagurídeo *Ostraconotus spatulipes* A. Milne-Edwards, 1880, y se documenta la morfología de la especie en detalle en el contexto del conocimiento sistemático moderno de los Paguroidea. El conocimiento molecular sigue siendo limitado, ya que solo el gen H3 fue amplificado con éxito. Sin embargo, la secuencia H3 disponible respalda la ubicación de *O. spatulipes* dentro de Paguridae, pero no resuelve su posición filogenética interna. Se proporcionan detalles anatómicos completos, ilustraciones y coloración, todos necesarios para los estudios filogenéticos dada la importancia atribuida a esta intrigante especie en la evolución de los Paguroidea en general, y de la familia Paguridae en particular. Este pequeño cangrejo ermitaño morfológicamente excepcional y carcinizado (< 5,0 mm de longitud de caparazón) se conocía exclusivamente por ejemplares recolectados entre 1872 y 1879 en el

Citation: Lemaitre R, et al. Rediscovery and redescription of *Ostraconotus spatulipes* A. Milne-Edwards, 1880 (Crustacea: Decapoda: Anomura: Paguridae), and its affinity within the Paguroidea. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 2026 Sep 21. doi: https://doi.org/10.18257/raccefyn.4030

Editor: Hernando Campos

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Received: January 14, 2026
Accepted: August 25, 2026
Published on line: September 21, 2026

Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 2026
doi: https://doi.org/10.18257/raccefyn.4030

Golfo de México y frente a Barbados. Sorprendentemente, a pesar de numerosas prospecciones faunísticas y expediciones realizadas desde entonces en la región, no se habían obtenido más ejemplares de *O. spatulipes* hasta que uno de nosotros (DLF) capturó una sola hembra frente a la costa oeste de Florida en 2014. Se requieren más especímenes frescos para ampliar los análisis genéticos moleculares que puedan situar con precisión a esta especie única dentro del Árbol de la Vida de Anomuros.

Palabras clave: Paguridae; *Ostraconotus*; redescripción; taxonomía; evidencia molecular; ADN.

Introduction

During the pioneering dredging program conducted in the Gulf of Mexico and the Caribbean Sea by the United States Coast and Geodetic Survey steamer *Blake* (**Agassiz**, 1888a, 1888b), several specimens of a unique hermit crab were collected. **Alphonse Milne-Edwards** (1880) considered them to be so remarkable that he placed them in a new monotypic genus for a species he named *Ostraconotus spatulipes*, a new taxon he briefly described without including any illustrations. A few years later, **Milne-Edwards and Bouvier** (1893) used the same specimens reported in the original description, as well as others collected on the USC&GS *Blake*, to provide an expanded illustrated description of this strange-looking paguroid. The morphology included a large, calcified carapace, paddle-like dactyls on pereopods 2 and 3, a broadened, plastron-like propodus on pereopod 4, and a minuscule pleon not contained within any protective housing. A. Milne-Edwards did not indicate the etymology of the generic and specific names, but clearly these were chosen in reference to the unusually calcified or shell-like (Gr. *ostrakon*) condition of the cephalothorax and spatulate or flat shape (Gr. *spathe*) of the second and third pereopods. In his narrative of the *Blake* cruises, **Agassiz** (1888b: 42) considered *O. spatulipes* to be "the most aberrant of all the hermit crabs", with a "tail" (pleon) so rudimentary that females held their eggs with the "feet" (pereopods), and that lived without evidence of a house. **Wolff** (1961) and **Russell** (1962) later considered this species to be free-living.

Since *O. spatulipes* was first documented by **A. Milne-Edwards** (1880) and **A. Milne-Edwards and Bouvier** (1893), this paguroid has been mentioned in numerous studies discussing its unusual morphology, living habitats, and its relatedness or similarities with other paguroids. Carcinologists were intrigued mostly by the unusually strong calcification and development of the cephalothorax along with the extreme reduction of the pleon, which **Borradaile** (1961) subsequently attributed to the process of carcinization; the flattened, blade-shaped dactyls of pereopods 2 and 3, which suggested a swimming ability or perhaps facilitated rapid locomotion over soft bottoms, and the apparent lack of housing, at least not the typically expected gastropod shells, to protect the pleon. To **Rabaud** (1941), the extreme reduction of the pleon in *O. spatulipes* suggested that this part of the body was so small that it could not contain any internal organs as in other pagurids. Morphological similarities have been noted, and in some cases evolutionary relationships have been suggested, between *Ostraconotus* and various paguroid genera. **Agassiz** (1888b), **A. Milne-Edwards and Bouvier** (1893) and **Russell** (1962) suggested a relationship with, or at least a shared general body form between this species and galatheoids. **A. Milne-Edwards and Bouvier** (1893) also mentioned a similarity in carapace development and calcification with *Tylaspis* Henderson, 1885 (recently reassigned from the Parapaguridae to Probeebidae) and *Porcellanopagurus* Filhol, 1885. Early studies (**Borradaile**, 1916; **Forest**, 1951; **Wolff**, 1961; **Roberts**, 1972) have frequently compared the similarities of *Ostraconotus* with the latter genus, although providing ambiguous or inconclusive results regarding phylogenetic relationships. Subsequent studies (**Türkay**, 1986; **Lemaitre**, 1993; **Richter & Scholtz**, 1994; **Poupin & McLaughlin**, 1996; **McLaughlin & Lemaitre**, 2007; **Anker & Paulay**, 2013) have continued to emphasize similarities and relationships between *Ostraconotus* and *Porcellanopagurus*. Modern studies that have used molecular data (**Tsang *et al.***, 2011;

Bracken-Grissom *et al.*, 2013) to investigate paguroid phylogeny have not included *O. spatulipes* in their genetic analyses because of the rarity and lack of high-quality genetic material among the few preserved historical type specimens available.

The most detailed discussion of the morphology and relationships of *O. spatulipes* can be found in studies by **de Saint Laurent-Dechancé** (1966) and **de Saint Laurent** (1968), who documented and illustrated anatomical details that had not been mentioned in the original description or any other subsequent study, including the existence of sexual tubes in this peculiar species. De Saint Laurent concluded that *Ostraconotus* was closest phylogenetically to *Catapaguroides* (**A. Milne Edwards & Bouvier**, 1892) and *Decaphyllus* (**de Saint Laurent**, 1968), based on several shared characters such as the presence of 10 pairs of gills, loss of all pleopods in the male, shape of antennules and mouthparts, and the presence of a right sexual tube in males. These three genera were considered by de Saint Laurent to represent a homogeneous or "*Ostraconotus* group", with *Ostraconotus* showing the more specialized adaptations, such as enlargement and calcification of the cephalothorax, drastic reduction of the pleon, and transformation of the propodi of pereopods 4 into incubating laminae. **De Saint Laurent** (1966) pointed out that in highly specialized paguroids such as *Ostraconotus*, the adaptive characters often result from convergence that can mask true phyletic relationships. However, since De Saint Laurent's studies of *Ostraconotus* more than half a century ago, the number of known paguroid species and genera has more than doubled, most discoveries being in the Paguridae, including numerous forms with a bewildering variety of sexual tubes and modified pleons, and equally remarkable carcinized forms such as *Solitariopagurus* Türkay, 1986 and *Patagurus* Anker & Paulay, 2013. Furthermore, the knowledge of paguroid characters, genetics, and evolution has increased so significantly that a new analysis is required to at least somewhat clarify the phylogenetic relationships of *Ostraconotus*.

The unique anatomical features and presumed unorthodox mode of living for *O. spatulipes* have led various carcinologists to mention this rare paguroid as an example of extreme body adaptation and carcinization (**Forest**, 1951; **Wolff**, 1961; **Russell**, 1962; **de Saint Laurent-Dechancé**, 1966; **Richter & Scholtz**, 1994; **McLaughlin & Lemaitre**, 1997; **Anker & Paulay**, 2013). Yet, several aspects of the anatomy and the biology of this paguroid have remained incomplete, and its precise phylogenetic position among paguroids remains uncertain. This uncertainty is due, in part, to the lack of available fresh specimens to perform anatomical examinations and obtain quality tissue for DNA analysis. Remarkably, no specimens of this paguroid had been collected since it was discovered in the late 19th century, until **Willems *et al.*** (2015) reported material presumably of *O. spatulipes* obtained during ecological studies off Suriname. Regrettably, the deposition of that new material is unknown and is thus unavailable for examination.

After one of us (DLF) had been four decades studying the decapod fauna from the Gulf of Mexico and the Caribbean, including intense ship-based deep-water dredging and inshore collecting in virtually all the ecological regions and habitats of these two regions with a variety of sampling methods, it was puzzling that no specimens of *O. spatulipes* had been obtained. Finally, however, with the help of sampling gear used aboard the historical vessel USCGS *Blake*, one female specimen was collected in 2014 off the coast of southwest Florida. This new specimen has provided the opportunity not only to report the rediscovery and redescribe in detail the morphology of this unusual paguroid, but also to make the first attempts at molecular genetic analyses. Based on our study of the newly collected *O. spatulipes* specimen type material, we present a redescription and detailed discussion of its morphology, along with limited molecular genetic insights into relationships of this species within the Paguridae.

Materials and methods

Collections, specimen deposition, and morphology

The single *O. spatulipes* specimen recently obtained by one of us (DLF) off the southwest coast of Florida in the Gulf of Mexico aboard the R/V *Pelican* was collected using hemp "tangles" attached to a custom-built benthic skimmer like the one used by **Pequegnat *et al.***

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doi: https://doi.org/10.18257/raccefyn.4030

(1970: 18 fig. 2–1). These hemp "tangles" or "rope tails" were modeled after those used by earlier naturalists (**Agassiz**, 1888a: 24) to collect the only known specimen of *O. spatulipes* known before the one obtained on the R/V *Pelican* that we report here.

The specimens used for this study are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ), the Muséum national d'Histoire naturelle, Paris, France (MNHN), and the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM). The most recently collected specimen was originally deposited in Lafayette Zoological Collections (ULLZ) at the University of Louisiana, which have recently been transferred in their entirety to the USNM. The corresponding ULLZ catalog number is included with the newly issued corresponding USNM number. Details on station data of the historical specimens deposited in MCZ and MNHN can be found in **Peirce & Patterson** (1879).

The morphological terminology used in our study departs from that of some paguroid specialists (**McLaughlin**, 2003: fig. 2l, m, n; **Tudge *et al.***, 2012: fig. 70.5G) in the numbering of cephalothoracic sternites, and follows instead the system used in **Lemaitre *et al.*** (2017). As in the latter study, and to avoid confusion, sternites are referred to only by the pereopod pairs between which they are ventrally positioned, thereby also identifying which of the posterior five thoracic somites they are derived from. Otherwise, the common paguroid terminology is used as summarized by **McLaughlin** (2003). The following measurements (to the nearest 0.1 mm) were used: shield length (sl), from the tip of the rostrum to the midpoint of the posterior margin of the shield; carapace length (cl), from the tip of the rostrum to the posterior midpoint of the carapace, and carapace width (cw) along the widest part of the carapace. All measurements are in millimeters (mm). Other abbreviations used are: sta, station; ov, ovigerous females; USCGS, United States Coast & Geodetic Survey steamer; HBG, Heather D. Bracken-Grissom.

Molecular analyses: DNA extraction, PCR, sequencing, and BLAST

Total genomic DNA (gDNA) was extracted from muscle tissue of one individual using the Qiagen DNeasy® blood and tissue kit (USNM 1549510, HBG12188). Total genomic DNA quality was visualized using 2% agarose gels run at 100 V for 90 min, and concentration was measured using a dsDNA HS assay kit on the Qubit 2.0 fluorometer (Invitrogen, Waltham, MA, USA). One partial mitochondrial gene and one nuclear protein-coding gene were selected. These included the 16S large ribosomal subunit (~550 base pairs (bp)) and histone H3 (~350 bp) using the primers 16SL2/L9 and 16S1472, 16SF, and 16S1472 (**Palumbi *et al.***, 1991; **Crandall & Fitzpatrick**, 1996; **Schubart *et al.***, 2000s) and H3AR and H3AR (**Colgan *et al.*** 1998). Despite numerous attempts, only the H3 gene was successfully amplified by means of a polymerase chain reaction (PCR) on the thermal cycler (Pro-Flex PCR System). All downstream results solely included the successfully amplified H3. PCR amplifications were performed in 25 µl volumes containing 1 µl of Taq polymerase, PCR buffer, 2.5 mM of deoxyribonucleotide triphosphate mix dNTPs, 0.5 µM forward and reverse primer, and extracted DNA. Thermal profiles of the PCR reaction included: initial denaturing for 2 min at 94 ˚C; annealing for 35 cycles: 30 s at 94˚C, 45 s at 50˚ C, 1 min at 72 ˚C; final extension 2–3 min at 72 °C. PCR products were sent to GENEWIZ® NextGen Sequencing service (South Plainfield, NJ, USA) for sequencing. All sequence data were confirmed by sequencing both strands (forward and reverse directions). Consensus sequences were generated within Geneious Prime 2020 9.1.7 (Biomatters, NJ, USA). Primer regions at the beginning of the sequences were manually removed before multiple sequence alignment. All reading frames for the H3 gene were examined to ensure the proper reading frame was used and to confirm the alignment contained no pseudogenes. Nucleotide sequences were queried against the NCBI nucleotide (nt) database using BLASTn (BLAST+ v2.16.0). Searches were performed with an E-value threshold of 1×10^{-5} using default scoring parameters and low-complexity filtering enabled. Hits with the highest query coverage were examined for identity. All obtained sequences were deposited in the GenBank database.

Results

Systematic account

Order **Decapoda** Latreille, 1802
Suborder **Pleocyemata** Burkenroad, 1963
Infraorder **Anomura** H. Milne Edwards, 1832
Superfamily **Paguroidea** Latreille, 1802
Family **Paguridae** Latreille, 1802
Genus ***Ostraconotus*** A. Milne-Edwards, 1880

Ostraconotus A. Milne-Edwards, 1880: 45 (type species by monotypy: *Ostraconotus spatulipes* A. Milne-Edwards, 1880); Henderson, 1888: 52; Alcock, 1905: 26 (key), 191; Borradaile, 1916: 122, fig. 13c; Balss, 1924: 763; Melin, 1939: 13; Bouvier, 1940: 114; Forest, 1951: 185; Gordan, 1956: 321; Wolff, 1961: 26, fig. 11c; de Saint Laurent-Dechancé, 1966: 259; de Saint Laurent, 1968: 1114; Roberts, 1972: 390; de Saint Laurent, 1972: 100; Türkay, 1986: 140; Lemaitre, 1993: 18; García-Gómez, 1994: 11, tbl. 3; Richter & Scholtz, 1994: 193; McLaughlin & Lemaitre, 1997: 112, tbl. 2 [character matrix]; McLaughlin, 2003: 118 [key], 124; McLaughlin & Lemaitre, 2007: 38; McLaughlin et al., 2010: 31; Tudge et al., 2012: 231; Anker & Paulay, 2013: 283, tbl. 1; Poore & Ahyong, 2023: 332; Felder, 2026: (in press).

Diagnosis. Ten pairs of biserial phyllobranch gills, no pleurobranch on somite XII (thoracomere 7, above pereopod 4). Rostrum prominent. Ocular acicles simple. Crista dentata on third maxilliped with few strong teeth, lacking accessory tooth. Cephalothorax vaulted, strongly calcified except for portions of branchiostegites; with distinct cardiac grooves and linea lateralis, cardiac sulci weakly marked; cephalic shield and posterior carapace fused, well delimited by cardiac grooves and linea lateralis; posterior carapace much broader than long, not appreciably reduced. Chelipeds subequal in length, unequal in strength, right distinctly stronger, left weaker and slender. Pereopods 2 and 3 (ambulatory legs) with lanceolate paddle-like dactyls. Sternite of somite XI (thoracomere 6, pereopods 3) with short, broad subrectangular anterior lobe. Pereopod 4 with broadly expanded and flattened propodus, lacking propodal rasp; dactyl elongate, simple. Pereopod 5 subchelate. Male with long sexual tube on coxa of right pereopod 5; coxa of left lacking sexual tube or with papilla; without pleopods on either side, or rarely with unpaired left pleopods 2 and 3. Female with paired gonopores and unpaired left pleopods 2–4. Pleon considerably reduced, partially bent under thorax. Uropods symmetrical. Telson with terminal margin entire or weakly divided.

Gender. Masculine.

Species. A monotypic genus, *Ostraconotus spatulipes* A. Milne-Edwards, 1880.

Remarks. **Poupin & McLaughlin** (1996) discussed the unclear or inconsistent description of the female pleopod condition provided in the original diagnosis of *Ostraconotus* by **A. Milne-Edwards** (1880) and the subsequent expanded diagnosis and illustrations by **A. Milne-Edwards & Bouvier** (1893). **Poupin & McLaughlin** (1996) determined, and we herein confirm, that there are three pleopods (pleopods 2–4) in females on the left side. These authors also pointed out that **Russell** (1962) mistakenly reported the number of pleopods as four. The pleopod condition in males was not mentioned by **A. Milne Edwards**, although subsequent carcinologists (**de Saint Laurent**, 1968; **McLaughlin**, 2003) have indicated that males lack pleopods. During this study, one male was found to have pleopods 2 and 3 on the left side, so there appears to be some variability in the male pleopod condition.

As previously mentioned in the Introduction, this genus has been used in numerous studies as an example of extreme evolutionary adaptation or carcinization among the Paguridae. Its phylogenetic relationships have been hypothesized by some carcinologists to be closest to *Porcellanopagurus* whereas others have proposed a closer relationship to *Catapaguroides* and *Decaphyllus* (see references in Introduction).

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Ostraconotus spatulipes A. Milne-Edwards, 1880
Figs 1–6

Ostraconotus spatulipes A. Milne-Edwards, 1880: 45 (type locality: "Blake", sta 50, 26°31'N, 85°53'W [off central west coast of Florida, Gulf of Mexico]); Agassiz, 1888b: 42; A. Milne-Edwards & Bouvier, 1893: 169, pl. 12, figs 1–24; Alcock, 1905: 191; Balss, 1924: 763, figs 20, 21; Rabaud, 1941: 191, fig. 11; Gordan, 1956: 321; Wolff, 1961: 28; Russell, 1962: 19, fig. 14; de Saint Laurent, 1968: 1114, figs 54–57; Türkay, 1986: 222; Abele & Kim, 1986: 32, 359, 389, unnumbered fig. a; Poupin & McLaughlin, 1996: 222; McLaughlin & Lemaitre, 1997: 87, figs 6c, 12e; McLaughlin et al., 2005: 244; McLaughlin & Lemaitre, 2007: 39; Felder et al., 2009: 1070; McLaughlin et al., 2010: 31; Tudge et al., 2012: 314; Willems et al., 2015: 28, tbl. 2 [list]; Poore & Ahyong, 2023: 332; Felder, 2026 (in press: figs 2.155, 2.156 with accompanying text).

Type material. Lectotype herein selected: male cl = 3.3 mm, cw = 3.3 mm, off central west coast of Florida, Gulf of Mexico, USCGS *Blake*, sta 50, 26° 31' N, 85° 53' W, 218 m, [between December 1877 and March 1878, see Remarks], coll. A. Agassiz, MCZ 4104.

Paralectotypes, Gulf of Mexico: 16 males cl = 3.0–3.7 mm, cw = 2.9–3.9 mm, 5 females cl = 3.1–3.6 mm, cw = 3.4–3.9 mm, 8 ov females cl = 3.3–3.6 mm, cw = 2.8–3.9 mm, same data as for lectotype, MCZ 4104; 1 male cl = 3.4 mm, cw = 3.4 mm, 2 females cl = 3.7, 4.3 mm, cw = 3.7, 4.5 mm, Sand Key, Florida, USCGS *Bache*, [no coordinates], 137–234 m, 27 March 1872, coll. W. Stimpson, MCZ 3026.

Other material. 1 female sl = 2.9 mm, cl = 3.7 mm, cw = 4.5 mm, off southwest coast of Florida, Gulf of Mexico, R/V *Pelican*, cruise GoMRI-V, sta GoMRI-V-12, 25° 29' 31" N, 84° 27' 46" W, 352–361 m, 9 September 2014, shell, sand, hemp "tangles" on benthic skimmer, USNM 1549510 (= ULLZ 15843); 1 male cl = 4.1 mm, cw = 4.2 mm, 1 female cl = 3.3 mm, cw = 3.7 mm, Florida, [probably same data as for lectotype], 218 m, MCZ 4105; 4 ov females cl = 3.1–3.9 mm, cw = 3.2–4.2 mm, 2 males cl = 3.5–4.9 mm, 2 exuviae, Antilles, USCGS *Blake*, MNHN-IU-2014–23845 (= MNHN-Pg 461); 1 male, [not examined, apparently lost, see Remarks], off Barbados, *Blake*, sta 299, 13° 05' 00" N, 59 39' 40", 10 March 1879, 256 m, museum deposition uncertain.

Redescription. Cephalothorax (**Figures 1, 2, 3A**) approximately as long as broad, broadest between spinose lateral extremes of posterior carapace; dorsal surface finely granulate, lateral margins sharply defined by row of small spines increasing in size anteriorly on posterior carapace and decreasing in size anteriorly on shield; cardiac sulci on posterior carapace each with shallow pit anteriorly, sulci weakening posteriorly, disappearing before reaching posterior margin; branchiostegite membranous except for calcified hourglass-shaped median plate (**Figure 3B**). Shield subhexagonal, defined by distinct cardiac grooves and linea lateralis, approximately 0.7 times as long as broad; dorsal surface lacking setae; gastric region slightly elevated, usually with anteromedian median pair of clusters of small tubercles; anterior margins concave to either side of rostrum, anterolateral projections terminating in strong spine; anterolateral margins diverging posteriorly, minutely spinose; lateral margins minutely spinose, with large spine distally. Rostrum bluntly subtriangular, slightly excavated dorsally, not reaching distally to level of lateral projections.

Ocular peduncles (**Figures 1, 2, 3A**) relatively short, stout, approximately 0.4 times as long as shield, naked, with dorsodistal lobe often bearing minute spines or tubercles; corneas swollen, dilated. Ocular acicles acutely subtriangular, terminating in spine, mesial margins minutely spinulose.

Antennular peduncles (**Figures 1, 2**) slender, exceeding distal margins of cornea when fully extended by approximately one-half or more length of penultimate segment. Segments naked or with scattered short setae; basal segment with rounded ventromesial distal angle, lacking spines. Dorsal and ventral flagella reduced, with relatively few articles (dorsal flagellum with 6–8 articles, ventral flagellum with 4 or 5 articles).

Antennal peduncles (**Figures 1, 2, 3B, C**), when fully extended, exceeding distal margin of corneas by approximately 0.7 to full length of fifth antennal segment. Fifth segment slender, lateral and mesial margins with minute, sharp spines (sharper on lateral

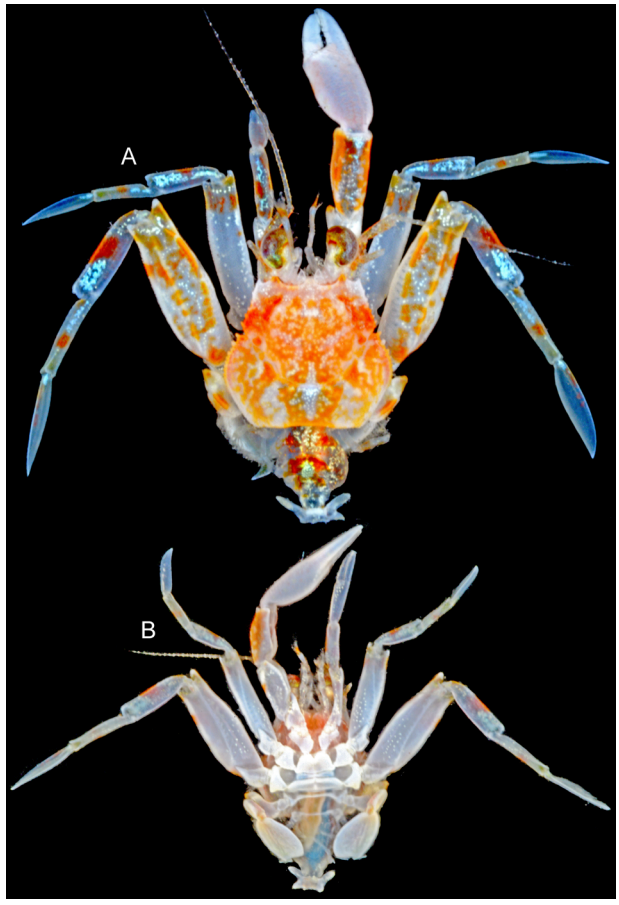

Figure 1. *Ostraconotus spatulipes* A. Milne-Edwards, 1880: female sl = 2.9 mm, cl = 3.7 mm, cw = 4.5 mm, off the southwest coast of Florida, Gulf of Mexico, R/V *Pelican*, sta GoMRI-V-12, USNM 1549510 (= ULLZ 15843). **A.** Habitus dorsal; **B.** habitus ventral

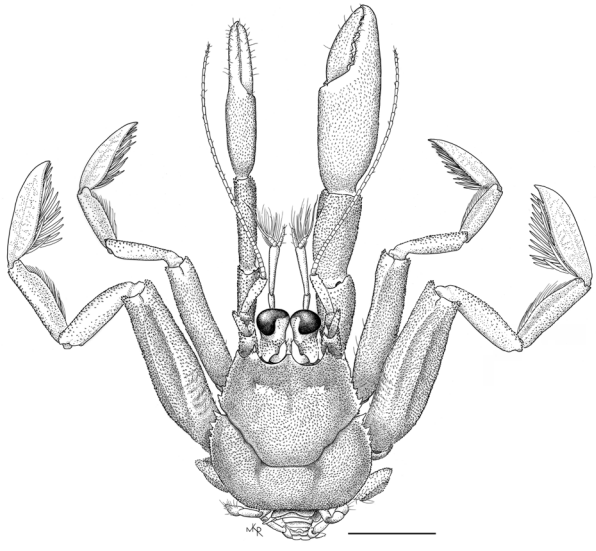

Figure 2. *Ostraconotus spatulipes* A. Milne-Edwards, 1880: lectotype male cl = 3.3 mm, cw = 3.3 mm, dorsal view, USCGS *Blake* Expedition, sta 50, MCZ 4104. Scale bar = 2.0 mm (illustrated by Molly K. Ryan)

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doi: https://doi.org/10.18257/raccefyn.4030

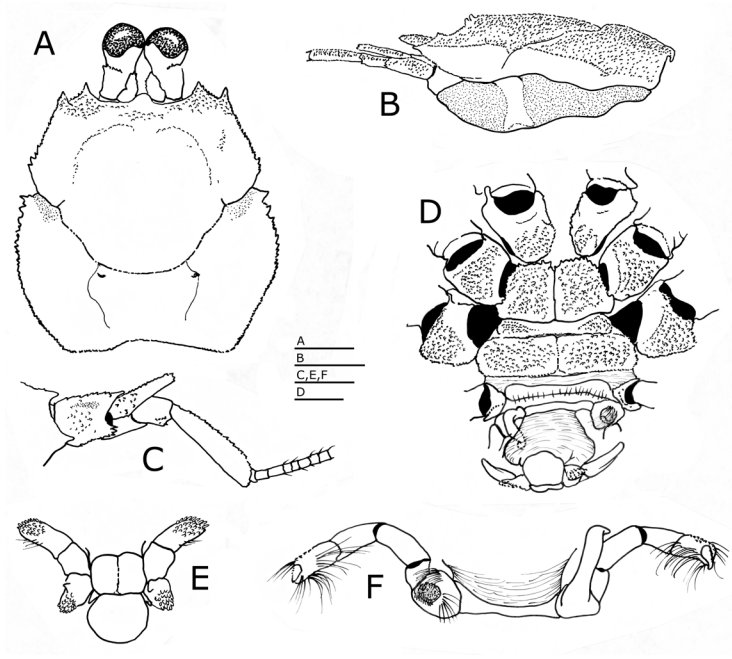

Figure 3. *Ostraconotus spatulipes* A. Milne-Edwards, 1880: **A.** ov female cl = 4.3 mm, cw = 4.5 mm, Sand Key, Florida, MCZ 3026; **B. D.** lectotype male cl = 3.3 mm, cw = 3.3 mm, eastern Gulf of Mexico, USCGS *Blake*, sta 50, MCZ 4104; **C.** ov female cl = 3.6 mm, cw = 3.9 mm, same data as lectotype, MCZ 4104; **E. F.** male cl = 3.7 mm, cw = 3.9 mm, same data as lectotype, MCZ 4104. **A.** Cephalothorax and eyestalks, dorsal view; **B.** left side of cephalothorax with antennal peduncle, lateral view (stippled portion of branchiostegite indicates membranous area). **C.** Right antennal peduncle, lateral view. **D.** Sternum, coxa of pereopods 1-5, pleon, uropods and telson, ventral view. **E.** Uropods and telson, dorsal view. **F.** Pereopods 5 with corresponding sternite, including sexual tube and gonopore, ventral view. Scale bars: 1 mm (**A**, **B**), and 0.5 mm (**C–F**)

margin). Fourth segment short, approximately 0.3 as long as fifth segment, with scattered minute granules. Third segment with sharp spine on ventrodistal angle. Second segment with small spines on lateral and mesial margins; dorsolateral distal angle produced into strong spine-like process; dorsomesial distal angle with distinct spine. First segment hidden under cephalothorax in dorsal view, unarmed except for scattered minute granules. Antennal acicles reaching slightly beyond distal margin of corneas, straight, lateral, mesial margins minutely granulose or spinulose, terminating in blunt tip with minute granules or spines. Flagellum long, reaching distal end of extended chelipeds, nearly naked or with scattered short setae less than 1 flagellar article in length.

Mandible (**Figure 4A**) with edge of incisor process calcareous, edge distally angled and with 1 or 2 obsolete blunt teeth; palp relatively short, distal article with bristle-like setae distally. Maxillule (**Figure 4B**) with endopod slender, external lobe obsolete, internal lobe with 1 or 2 long setae. Maxilla (**Figure 4C**) with endopodite not exceeding distal end of scaphognathite. First maxilliped (**Figure 4D**) with endopodite not exceeding distal endite. Second maxilliped (**Figure 4E**) without distinguishing characters. Third maxilliped (**Figure 4F**) with ischium having weakly developed crista dentata consisting of 2 or 3 calcareous teeth; basis with blunt spine on mesial margin; coxa with distinct distomesial spine. Sternite VIII (of third maxillipeds) divided into 2 lobes by deep V-shaped median sinus, distal margins of lobes armed with small, blunt spines.

Chelipeds subequal in length, distinctly dissimilar in strength, right wider, naked or at most with few scattered short setae on dactyls and fixed fingers. Right cheliped (**Figures 1, 2**) with dorsal surfaces minutely granulose. Chela ovate in outline (dorsal view), approximately 3 times as long as broad, somewhat dorsoventrally flattened, lateral

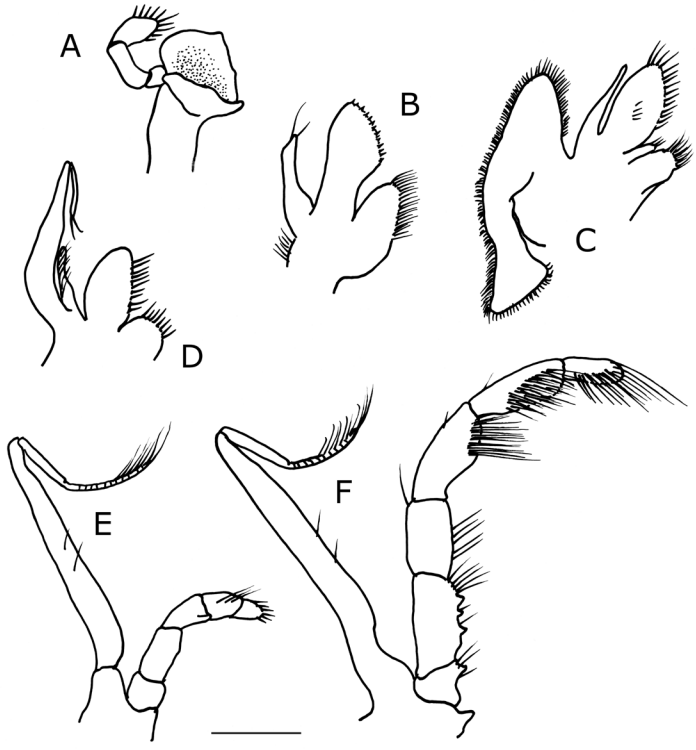

Figure 4. *Ostraconotus spatulipes* A. Milne-Edwards, 1880, male cl = 3.9 mm, cw = 3.7 mm, eastern Gulf of Mexico, USCGS *Blake*, sta 50, MCZ 4104, left mouthparts, internal view: **A.** mandible; **B.** maxillule; **C.** maxilla; **D.** first maxilliped; **E.** second maxilliped; **F.** third maxilliped. Scale bar: 0.5 mm

margin of palm and fixed finger well defined by granulose edge; dorsal surfaces minutely granulose; ventral surfaces glabrous, smooth; mesial margins of dactyl and palm rounded; cutting edges of dactyl and fixed finger each with row of unequal calcareous rounded or subtriangular teeth; dactyl and fixed finger terminating in blunt, inwardly curved calcareous tips overlapping when closed. Dactyl approximately 0.8 times as long as palm, with row of tufts of short setae dorsomesially and ventromesially near cutting edge; mesial margin broadly rounded. Fixed finger with tufts of setae as on dactyl; lateral margin nearly straight. Palm longer than broad, unarmed except for minute granules. Carpus approximately twice as long as broad, unarmed except for minutely granulose dorsal, lateral and mesial surfaces; lateral and mesial surfaces strongly sloping ventrally; ventral surface smooth. Merus subtriangular in cross-section, unarmed except for minutely granulose dorsal, lateral and mesial surfaces; ventral surface smooth. Ischium and coxa unarmed, with row of short setae on ventromesial distal angle.

Left cheliped (**Figures 1, 2**) slender, extending distally to nearly the same level as the right cheliped, naked or at most with few scattered short setae on dactyls and fixed fingers. Chela approximately 5 times as long as broad; somewhat dorsoventrally flattened, lateral margin of palm and fixed finger weakly defined, rounded; dorsal surfaces minutely granulose; ventral surfaces glabrous, smooth; mesial margins of dactyl and palm rounded; cutting edges of dactyl and fixed finger each with row of minute corneous teeth; fingers terminating in inwardly curved calcareous tips overlapping when closed. Dactyl approximately as long as palm. Fixed finger similar to dactyl. Palm approximately 3 times as long as broad, unarmed except for minute granules. Carpus approximately twice as long as broad, unarmed except for minutely granulose dorsal, lateral and mesial surfaces; lateral and mesial surfaces strongly sloping ventrally; ventral surface smooth. Merus subtriangular in cross-section, unarmed except for minutely granulose dorsal, lateral and

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doi: https://doi.org/10.18257/raccefyn.4030

mesial surfaces; ventral surface smooth. Ischium and coxa unarmed, with row of short setae on ventromesial distal angle. Carpus approximately 4.4 times as long as broad, unarmed except for minutely granulose dorsal, lateral and mesial surfaces; lateral and mesial surfaces strongly sloping ventrally; ventral surface smooth. Merus subtriangular in cross-section, approximately as long as carpus, unarmed except for minutely granulose dorsal, lateral and mesial surfaces; ventral surface smooth. Ischium and coxa unarmed, with row of short setae on ventromesial distal angle.

Pereopods 2 and 3 or ambulatory legs (**Figures 1, 2, 5A-D, 6A**) typically positioned with meri, carpi, propodi and dactyls bent to form dipper-shaped outline, dactyls pointing forward; subequal left from right. Dactyl (**Figure 6A**) laterally compressed, blade-shaped or paddle-like, approximately 1.3 times as long as propodus, terminating in sharp corneous

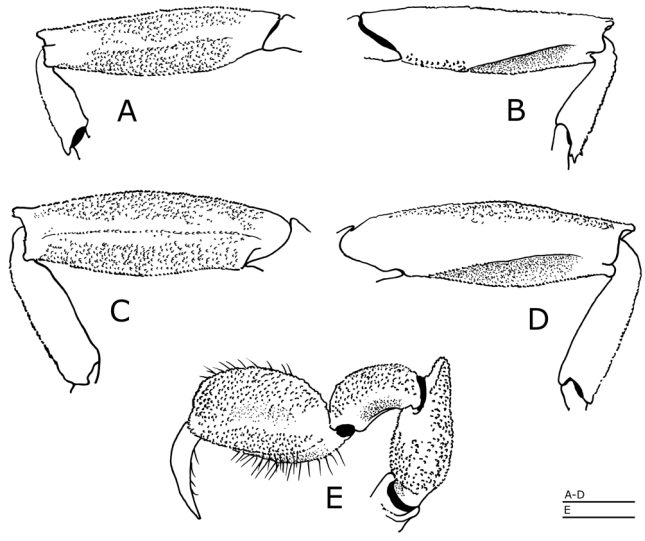

Figure 5. *Ostraconotus spatulipes* A. Milne-Edwards, 1880, lectotype male cl = 3.3 mm, cw = 3.3 mm, eastern Gulf of Mexico, USCGS *Blake*, sta 50, MCZ 4104: **A.** merus and carpus of pereopod 2, lateral view; **B.** same, mesial view; **C.** merus and carpus of pereopod 3, lateral view; **D.** same, mesial view; **E.** pereopod 4, lateral view. Scale bars: 1 mm (**A–D**), and 0.5 mm (**E**)

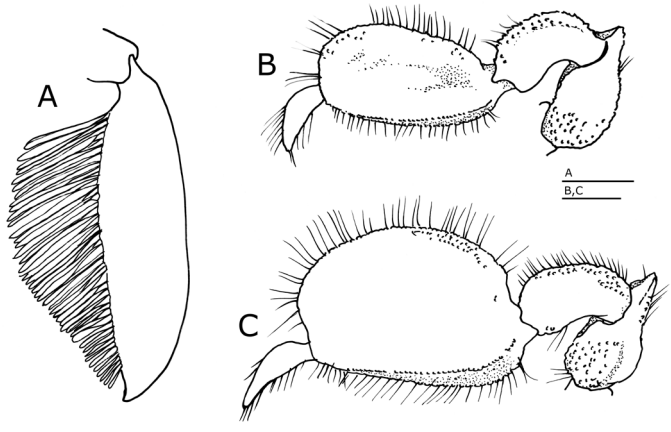

Figure 6. *Ostraconotus spatulipes* A. Milne-Edwards, 1880: **A.** ov female cl = 3.6 mm, cw = 3.9 mm, eastern Gulf of Mexico, USCGS *Blake*, sta 50, MCZ 4104; **B.** ov female cl 4.3 mm, cw = 4.5 mm, Sand Key, Florida, MCZ 3026; **C.** ov female cl 3.7 mm, cw = 3.7 mm, same data as **B. A.** dactyl of left pereopod 3, lateral view; **B. C.** left pereopod 4, lateral view. Scale bars: 0.5 mm

claw; lateral and mesial faces smooth; dorsal margin broadly rounded; ventral margin with distinct fringe of long capsulate setae. Propodus nearly straight, subequal in length to carpus; dorsolateral surface minutely granulose, otherwise smooth; ventral margin with fringe of simple setae. Carpus naked, dorsolateral surface minutely granulose. Merus naked, broad; lateral surface minutely and densely granulose, flat (pereopod 2) or with raised longitudinal median ridge (pereopod 3); mesial surface smooth. Coxae minutely granulose ventrally. Anterior lobe of sternite XI (of pereopods 3; **Figure 3D**) short and broad, naked; surfaces of anterior and posterior lobes minutely granulose.

Pereopod 4 (**Figures 1, 5E, 6B, C**) subchelate, not visible in dorsal view of cephalothorax, carried shield-like appressed against sternum. Dactyl short, less than half length of propodus, narrow basally at juncture with propodus, terminating in small, often obscure corneous claw; dorsal margin sparsely setose, rounded, sometimes slightly bulging dorsally at midpoint; ventral margin sparsely setose, lacking teeth. Propodus laterally compressed, ovate, curved outwardly, and broadly expanded, ranging from 1.3 to 1.9 times as long as high (see **Variations**); lacking propodal rasp; lateral (outer) surface granulose, with lateroventral ridge marked by row of granules; mesial (inner) surface concave, smooth. Carpus arching dorsally, sparsely setose; lateral (outer) surface granulose, mesial (inner) surface smooth. Merus curving outwardly, club-like, broadest basally; terminating dorsodistally in strong, granulose spine-like projection; lateral surface granulose, with dorsal and ventral margins sharply defined. Ischium smooth. Coxa with ventromesial spine-like, granulose projection. Sternite XII (of pereopod 4) rod-like, narrow, entire.

Pereopod 5 (**Figure 3F**) chelate, visible in dorsal view of cephalothorax, slender, typically pagurid-like, significantly shorter than pereopod 4 (approximately half as long). Dactyl sparsely setose, lacking rasp; propodus with poorly developed rasp consisting of few minute spines near juncture with dactyl. Sternite XIII (of pereopod 5) like previous sternite.

Uropods and telson (**Figures 1, 3E**) symmetrical, sparsely setose; exopod and endopod with distinct rasp, endopod with small spine basally. Telson shape somewhat variable, semicircular or subrectangular (longer than broad), lacking lateral indentations; terminal margin undivided or slightly divided by a shallow sinus medially, unarmed.

Male lacking pleopods or rarely with unpaired left pleopods 2 and 3; with long sexual tube (**Figure 3D, F**) arising from coxa of right pereopod 5, directed posteriorly and then curving upwardly behind pereopod 5, with few short setae distally; lacking sexual tube on coxa of left pereopod 5 or with short papilla-like extrusion; gonopore on left coxa (**Figure 3F**) covered with fringe of short setae. Female with unpaired left pleopods 2–4, when ovigerous, each pleopod carrying approximately 20–30 relatively large eggs (~ 0.4 mm in maximum width).

Genetic data. Female sl = 2.9 mm, cl = 3.7 mm, cw = 4.5 mm (USNM 1549510, HBG12811). GenBank PZ817145.

Variations. The morphological variations observed in the studied specimens of this species are minimal compared to the typical broad variations frequently seen in other paguroids and are incorporated in the above redescription. However, a notable exception is the striking sexual dimorphism exhibited by females on the propodus of pereopod 4. The ratio of propodus height/length can be significantly higher in females than in males. In females, this ratio can vary from 1.3 to 1.6 as long as high (*e.g.*, **Figure 6B, C**), whereas in males the propodus is at most 1.3 times as long as high (**Figure 5E**). Propodus height increases with size, especially in egg-carrying females. The telson shape has been found to vary as well from semicircular to subrectangular, although not sex related.

Color. **Figure 1** duplicates the color figure shown in **Felder** (2026, in press: fig. 2.156. The eye corneas are of dark brown pigmentation. Dorsally the cephalothorax, carpus of major cheliped, and broad meri of third pereopods are dominated by mottled orange patches, with lighter reticulations of pale orange, lavender, or powder blue distinct bluish chromatophores. The carapace shield bears a darker red-orange patch laterally near each margin, anterior to each of which there is a light patch of off-white to pale lavender that includes the anterolateral corner. The posterior carapace bears a median longitudinal bar of

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doi: https://doi.org/10.18257/raccefyn.4030

pale blue, crossed by a shorter transverse bar of the same color. To either side of the median bar is a large patch of diffuse pale orange, lighter than most other dorsal areas. While the carpi of both chelipeds are distinctly pigmented by mottled orange with venations of vibrant blue and darker spots of reddish orange, the chelae of both are overall pale lavender marked at most by a blush of pale orange dorsally. The second and third pairs of pereopods have distal articles of predominantly translucent bluish around patches of vibrant blue chromatophores, the latter especially concentrated in the carpi, propodi, and base of the dactyls. Additionally, the carpi and propodi of these appendages each bear a conspicuous patch of red dorsally, most striking on the carpus of the fourth pereopod. Dorsally, the pleon is mottled orange, with several pairs of small but distinct red patches. Ventrally, the overall habitus is semitranslucent pale lavender to faint orange.

Habitat. Epibenthic or demersal, possibly facultatively pelagic or carrying a partially covering thin molluscan shell; outer continental shelf to upper slope, 137–361 m.

Distribution. Western Atlantic: Gulf of Mexico; Barbados; Antilles; Suriname? (See Remarks).

Taxonomic remarks

While studying the existing historical material on *O. spatulipes* deposited in MCZ and MNHN, some discrepancies were noticed that merit clarification between the museum records and the listings of specimens published in the original description by **A. Milne-Edwards** (1880) and subsequent report by **A. Milne-Edwards & Bouvier** (1893). **A. Milne Edwards**' (1880) description of *O. spatulipes* was based on specimens from two stations, one from the USCGS *Blake* station 50, off the central west coast of Florida, Gulf of Mexico, and another from the USCGS *Bache* (listed without a station number or coordinates), collected in Sand Key in the Florida Keys, all of which have been found deposited in the MCZ (MCZ 4104, MCZ 3026). As **A. Milne-Edwards** (1880) did not designate a holotype, the specimens from those two stations are to be considered the syntype series, and we have herein selected a lectotype from USCGS *Blake* station 50. In the subsequent report by **A. Milne-Edwards & Bouvier** (1893), where they amplified the description of *O. spatulipes*, specimens were included from the same USCGS *Blake* station 50 listed in **A. Milne-Edwards**'s (1880) description, but they added specimens from three additional stations or localities not listed in **A. Milne-Edwards** (1880), i.e., "Station 299, … Barbade" (one male), "Floride" (3 males and 2 females), and "Antilles" (3 males and four females). The specimen from Barbados has not been located in any museum and appears to be lost. None of the specimens from these three additional stations or localities can be considered part of the original syntype series, as they were not listed in **A. Milne-Edwards** (1880).

Previous discussions on *O. spatulipes* have used the morphological information contained in **A. Milne-Edwards**' (1880) original description and subsequent report by **A. Milne-Edwards & Bouvier** (1893) or have drawn upon **de Saint Laurent-Dechancé** (1966) and **de Saint Laurent**'s (1968) revisionary studies exploring relationships among several pagurid genera. Except for **de Saint Laurent-Dechancé** (1966), no other study that has discussed this unusual pagurid species has stated or given morphological details of the original specimens collected on the USCGS *Blake* or *Bache*. As previously mentioned, **Willems *et al.*** (2015) included *O. spatulipes* in a list of species collected during their ecological study off Suriname, although as previously stated, the fate of that material is unknown, and it has not been possible to reexamine it.

Habitat and morphological adaptations

As previously mentioned, before this study (except for the aforementioned report from Suriname by **Willems *et al.***, 2015), the only known specimens of *O. spatulipes* had been collected in the late 19th century during the pioneering expeditions to the Gulf of Mexico and the Caribbean Sea (**Agassiz**, 1888a, 1888b). This species has most likely been overlooked in deep-water collections because of its small size, the largest specimen so far

measuring only 4.9 mm in carapace length (cl). Known specimens show no indication of what type of habitat this species may use for protecting its body parts, as is the custom in the majority of paguroids. The new specimen reported herein was found entangled in one of four hemp "tangles" attached to the rear box of a "benthic skimmer" dredge like the one used by **Pequegnat *et al.*** (1970). The dredge was deployed at a station near the west Florida escarpment at a depth range of 352–361 m. Contents in the dredge after retrieval included shells and shell fragments (also found attached to the "tangles"), especially empty shells of planktonic cavoliniid pteropods, along with muddy sand. Given that *O. spatulipes* lives, at least on this station, on pteropod shell-rich bottoms, it is possible that the thin, light pteropod shells are used as a means of protection. The reduced pleon, setose paddle-like shape of the dactyls of the anterior appendages (pereopods 2 and 3), and somewhat dorsoventrally flattened body shape, all appear to represent adaptations to enable scurrying over mud bottoms or even swimming. If, as suspected, this species inhabits the lighter and more buoyant pteropod shells, that would also facilitate swimming. Furthermore, the comparatively well calcified, carcinized cephalothorax, reduced pleon, and symmetrical uropods and telson suggest something other than typical paguroid inhabitation of coiled gastropod shells.

Perhaps the most intriguing and unique morphological feature of *O. spatulipes* is the broadened plate-like propodus of pereopod 4. While the propodus is strikingly broad in both sexes, it is distinctly broader in females and particularly in ovigerous females. An earlier naturalist (**Agassiz**, 1888b) suggested, and we agree, that the plate-like propodus serves to enclose and protect the eggs carried on the pleopods by ovigerous females.

Genetic remarks

Despite numerous attempts to obtain mitochondrial and nuclear gene sequences, only the H3 gene of *O. spatulipes* (USNM 1549510, HBG12188) was successfully amplified, yielding a sequence of 304 bp. This gene fragment was queried against the NCBI database using BLAST and showed a 96% identity (288/301 bp) to *Pagurus brevidactylus* (Stimpson, 1859) (GenBank accession number JQ805784), a species of the family Paguridae believed to be broadly distributed in the tropical and subtropical western Atlantic. The genus *Pagurus*, however, is a catch-all genus in need of revision as it currently contains at least 180 known species and is likely polyphyletic. Thus, our molecular analysis can only suggest that the gene sequence generated supports *O. spatulipes* remaining within its current systematic placement as a member of Paguridae. However, this sequence also showed close affinities to other anomurans, such as species of the genera *Phylladiorhynchus* Baba, 1969, a galatheid, and *Lithodes* Latreille, 1806, a lithodid. Clearly, additional individuals and genes (both nuclear and mitochondrial) are required for robust molecular genetic analyses that can definitively place this remarkable species within the Anomuran Tree of Life.

Acknowledgements

The preparation of this work began more than two decades ago when the first author encountered inconsistencies, omission of certain morphological features, and a lack of details of some key body parts in the original description of *Ostraconotus spatulipes*. The only available specimens of this singular species were gathered from the three museums (MCZ, MNHN, and USNM) where they were originally deposited in the late 19th century. The first author studied these historical specimens; one specimen was beautifully illustrated (Fig. 2) by the then illustrator of the Department of Invertebrate Zoology at USNM, Ms. Molly Kelly Ryan, to whom we are grateful. We are most thankful to the following museum colleagues who arranged for loans or provided information: Adam J. Baldinger at MCZ and Laure Corbari and Paula Martin-Lefevre at MNHN. Our co-author DLF is to be commended for his perseverance and tireless efforts to finally obtain at least one specimen of *O. spatulipes*, which allowed the extraction of useful tissue for DNA analysis in HBG's lab. Thanks are due to ULLZ for donating the new specimen of *O. spatulipes* collected by DLF to USNM and to Rose A. Gulledge for preparing the digital versions of

the ink illustrations. Work was supported by funding to DLF from U.S. National Science Foundation grants NSF/BS&I DEB–0315995, NSF/AToL EF–0531603, and the Gulf Marine Research Initiative. This is UL Lafayette Laboratory for Crustacean Research contribution # 229. The molecular work was partly supported by an NSF grant awarded to HBG (DEB 1856667). This is publication # 2177 from the Institute of Environment at Florida International University.

Author contributions

RL: studied museum specimens and performed the taxonomic research and prepared text and ink illustrations; HDGB: extracted tissues for DNA analyses, performed the molecular study and gene-based phylogenetic explorations, and contributed to text preparation; DLF: designed dredge gear to collect the new specimen, directed the cruise to obtain the new specimen, took the color photograph, and contributed to text preparation.

Conflicts of interest

The authors declare no conflict of interests.

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