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New records of mesopelagic siphonophores (Cnidaria, Hydrozoa) from the Colombian Caribbean collected during offshore exploration cruises

Cristina Cedeño-Posso[1*], Edgar Fernando Dorado-Roncancio[1]

1 Programa de Biodiversidad y Ecosistemas Marinos, Línea de Inventarios, Taxonomía y Biología de Especies, Instituto de Investigaciones Marinas y Costeras, Playa Salguero, Santa Marta, Magdalena, Colombia • CCP: cristina.cedeno@invemar.org.co https://orcid.org/0000-0001-8622-2947 • EFDR: edgar.dorado@invemar.org.co https://orcid.org/0000-0002-0321-5416

* Corresponding author

Abstract. Five species of siphonophores are newly recorded in the Colombian Caribbean Sea: the physonects *Athorybia rosacea* (Forsskål, 1775), *Nanomia bijuga* (Delle Chiaje, 1844), and *Agalma okenii* Eschscholtz, 1825 and the calycophores *Amphicaryon ernesti* Totton, 1954 and *Hippopodius hippopus* (Forsskål, 1776), from samples collected with deep-water trawls in six hydrocarbon exploration areas (GUA OFF 3, COL 1, COL 2, COL 3, COL 4; COL 10) where research projects were undertaken in 2013 and 2018 by the Marine and Coastal Research Institute "Jose Benito Vives de Andreis" in agreement with the National Hydrocarbon Agency.

Keywords. Biodiversity, Calycophorae, distribution, Physonectae

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Introduction

Siphonophores are colonial, oceanic, holoplanktonic animals not permanently attached to a substrate, with the exception of those in the family Rhodaliidae which are epibenthic. Siphonophores present three types of body plans, according to their suborder (Dunn et al. 2005). The most common and easily recognizable suborder is Calycophorae, which has two nectophores (anterior and posterior) but no pneumatophore. The suborder Cystonectae has a gas-filled float, called a pneumatophore, and a long-stemmed siphosome, and the suborder Physonectae bears a pneumatophore, a nectosome with multiple swimming units (nectophores), and a long-stemmed siphosome (Mapstone 2014; Dunn et al. 2005).

Apart from the typical siphonophore that is well recognized (*Physalia physalis* cystonect), the study of siphonophores in Colombian waters has been limited because there are few researchers dedicated to the taxonomy of this group; siphonophores are polymorphism and, like all gelatinous plankton, they are also extremely fragile organisms and have the ability to autotomize as a defense mechanism, a phenomenon that occurs when they are collected with plankton nets, making their identification and classification difficult (Dunn et al. 2005; Haddock et al. 2005). For this reason, the taxonomy of this group is often based on parts of the colony, such as its bracts, pneumatophores, or young colonies (Dunn et al. 2005).

The characterization of planktonic communities is an essential component of environmental baseline studies. Given the dependence of these communities on their fluid environment, these planktonic organisms are reliable indicators of an ecosystem's state and health (Vides 2019). In the Colombian Caribbean Sea, 23 species of siphonophores have been reported in the latest checklist by Oliveira et al. (2016). Most of these species were collected for zooplankton studies in coastal areas using horizontal plankton trawls to depths of 50 m.

Since 2013, through agreements between Marine and Coastal Research Institute "Jose Benito Vives de Andreis" (Invemar) and the National Hydrocarbons Agency (ANH), plankton have been sampled in exploration blocks in the Colombian Caribbean using vertical plankton trawls to obtain samples at various depths in the water column, down to 1000 m, with more attention paid depths below 70 m. In the resulting samples, we found five siphonophore species (from two suborders) which are newly recorded from the Colombian Caribbean Sea. These results highlight the need to train specialists in this group and continue sampling not only in the epipelagic zone (0–200 m) but also in the mesopelagic zone (200–1000 m).

Methods

Zooplankton samples have been obtained in seven exploration blocks in the Colombian Caribbean (GUA OFF 3 [2013], COL 4 and 5 [2014], COL 2 [2015], COL 1 [2016]; COL 3 [2017]; COL 10 [2018]) for a total of 61 stations, mostly during the rainy season (November–December), except for COL 1 which was taken during the dry season. Invemar, as an entity linked to Ministerio de Ambiente y Desarrollo Sostenible (Art.18, Law 99 of 1993), does not require a permit to collect specimens (Paragraph 1. Art. 2.2.2.2.8.1.2., Decree 1076 of 2015). Vertical stratified trawls of zooplankton were carried out at the 61 stations at four depth ranges (0–60 m, 70–140 m, 170–340 m, 540–1000 m) using a General Oceanic double trip mechanism, with 200 μm and bongo nets and a 0.6 m mouth diameter. The samples were narcotized with 10% magnesium chloride and fixed with formaldehyde and neutralized with sodium tetraborate (borax), leaving the solution at a 5% concentration.

Siphonophores were separated and identified with a Leica M205A stereomicroscope and dissected with a Zeiss Primo Star light microscope. We contrasted their specific taxonomic characters with current literature to confirm the taxonomic identities of each specimen (Totton and Bargmann 1965; Pugh 1999; Licandro et al. 2017). The specimens were deposited in the Cnidaria reference collection with their respective catalog numbers of Museo de Historia Natural Marina de Colombia (MHNMC) of Invemar (institution code INV CNI). Some specimens were too deteriorated to be included in this reference collection, but they can be located with the museum's consecutive number in the plankton section (ZOOP). The catalog numbers of each specimen are listed in the material examined section, along with the identification section which has information on how the species was recognized.

Results

Of the seven exploration blocks and 61 stations analyzed, only 16 stations showed the presence of 23 specimens of siphonophores that had not been previously recorded for the Colombian Caribbean. Three species belong to the suborder Physonectae and family Agalmatidae: *Athorybia rosacea* (Forsskål, 1775) was found at four stations (COL 3–E 564; COL 10–E 617; GUA OFF 3–E 358, E 372); *Nanomia bijuga* (Delle Chiaje, 1844) was found at 3 stations (COL 1–E 437, E 446; GUA OFF 3–E 357); *Agalma okenii* Eschscholtz, 1825 was found at 3 stations (COL 1–E 456, E 466; GUA OFF 3–E 358). Two species belong to the suborder Calycophorae and the families Prayidae and Hippopodiidae: *Amphicaryon ernesti* Totton, 1954 was found at seven stations (COL 1–E 437, E 466, E 467; COL 2–E 418, E 431; COL 4–E 380; COL 10–E 617; GUA OFF 3–E 358) and *Hippopodius hippopus* (Forsskål, 1776) was found at 6 stations (COL 1–E 467; COL 10–E 600, E 617; COL 2–E 421; COL 4- E 380, E 383) (Fig. 1).

Systematic account

Suborder Physonectae Haeckel, 1888

Family Agalmatidae Brandt, 1834

***Athorybia rosacea* (Forsskål, 1775)**

Figure 2A

Material examined. COLOMBIA – Caribbean Sea • offshore, exploration block GUAOFF 3 - E 358; 12° 50′28″N, 073°34′34″W; 170–340 m depth; 20.XI.2013; INV CNI4613 • GUAOFF 3 - E 372; 12°18′25″N, 073° 31′5″W; 0–60 m depth; 11.XII.2013; INV CNI4614 • COL 3 - E 564; 11°58′57″N, 074°59′38″W; 70–140 m depth; 4.X.2017; consecutive number: 62016 • COL 10 - E 617; 13°30′22″N, 072°40′25″W; 0–60 m depth; 1.VI. 2018; consecutive number: ZOOP 66374.

Identification. There are two accepted species of *Athorybia* Eschscholtz, 1829, *A. rosacea*, and *A. lucida* Biggs, 1978 (Schuchert 2022). Two of the most distinguishing characteristics of these genus is the large, red-pigmented pneumatophore, making up almost the entire volume of the colony (Fig. 2A) and the absence of nectosomes. Four colonies observed in this study (not all of them were in good condition and were not deposited in the reference collection) had an average width of 10 mm. There are few bracts attached along the short stem, giving the colonies a typical rose-petal shape.

***Nanomia bijuga* (Delle Chiaje, 1844)**

Figure 2B

Material examined. COLOMBIA – Caribbean Sea • offshore, exploration block GUAOFF 3 - E 357; 12°50′ 46″N, 073°50′24″W; 70–140 m depth; 19.XI.2013; INV CNI4615 • COL 1 - E 437; 12°35′0″N, 074°7′30″W; 70–140 m depth; 10.IV.2016; consecutive number: ZOOP 56181. COL 1 - E 446; 12°45′0″N, 074°52′30″W; 70–140 m depth; 14.IV.2016; consecutive number: ZOOP 56189.

Identification. There are two accepted species of *Nanomia* A. Agassiz, 1865, *N. cara* Agassiz, 1865 and *N. bijuga* (Delle Chiaje, 1844) (Totton and Bargmann 1965; Schuchert 2022). Three colonies were observed in this study (not all of them were in good condition and were

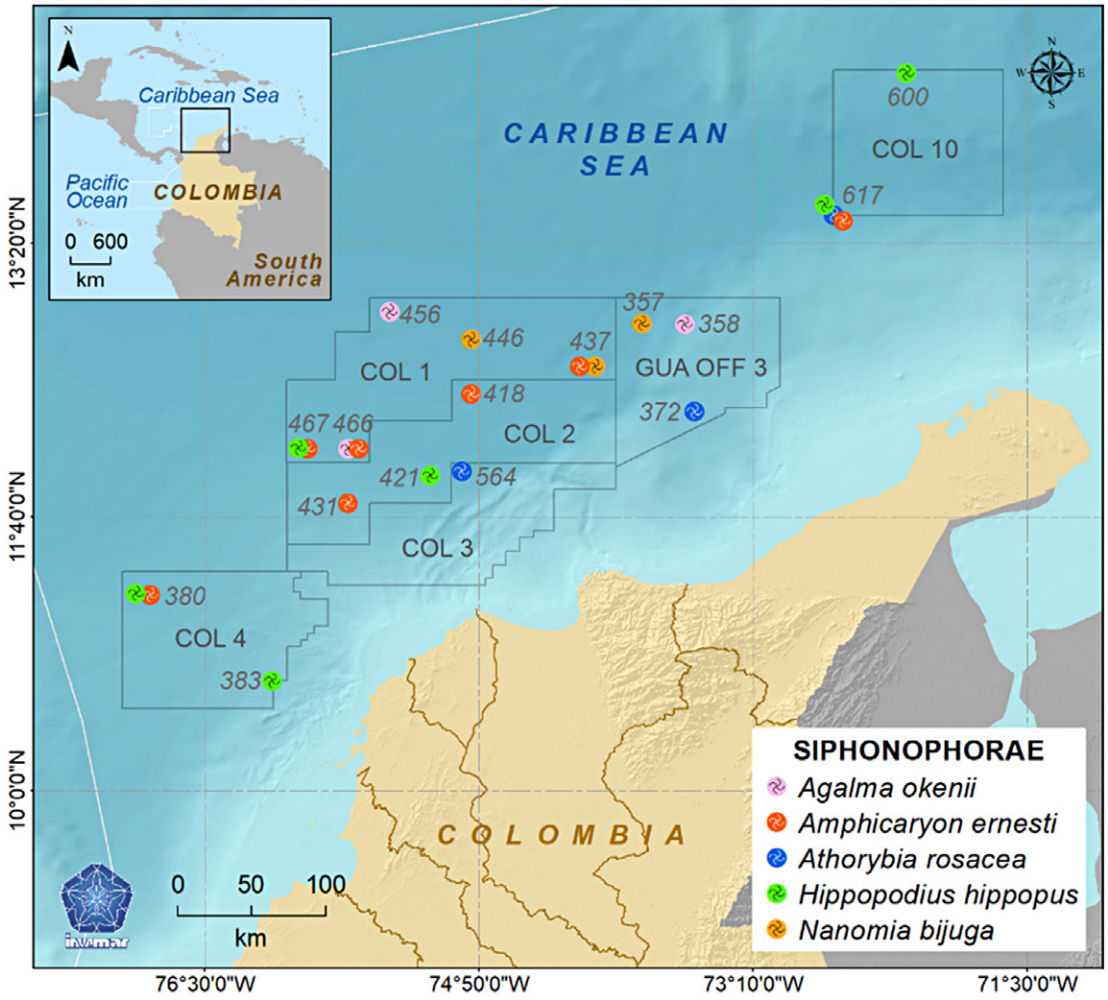

Figure 1. Location of the stations and exploration blocks where siphonophores were collected in 2013 and 2018. Map produced by the Invemar LabSIS information systems laboratory.

not deposited in the reference collection). One of them was a young colony with a width of 12 mm; adult colonies reach 100–450 mm long when in a state of contraction, according to Totton and Bargmann (1965). The nectophores of the colony were deteriorated or lost during collection; their identification was based on the bracts and the unicornuate tentilla at the base of the involucre (Fig. 2B) (Alvariño 1981).

Agalma okenii Eschscholtz, 1825

Figure 3A

Material examined. COLOMBIA – Caribbean Sea • offshore, exploration block COL 1 - E 456; 12°55′00″N, 075°22′30″W; 70–140 m depth; 17.IV.2016; INV CNI4616 • GUAOFF 3 - E 358; 12°50′28″N, 073°34′34″W; 170–340 m depth; 20.XI.2013; consecutive number: 63100 • COL 1 - E 466; 12°05′00″N, 075°37′30″W; 540–1000 m depth; 20.IV.2016; consecutive number: ZOOP 56211.

Identification. It is the type species of *Agalma* Eschscholtz, 1825; there are three accepted species: *A. clausi* Bedot, 1888, *A. elegans* (Sars, 1846) and *A. okenii* (Totton and Bargmann 1965; Schuchert 2022). Four colonies were observed in this study (not all of them were in good condition and were not deposited in the reference collection). Two of colonies were young and had an average width of 13 mm; the nectophore height reaches 12 mm in adult colonies according to Pugh (1999). The nectophores of the colonies had deteriorated during their collection; their identification was based on the bracts, which have four distal facets, and the tricornuate tentilla, which have an ampulla and two terminal filaments (Fig. 3A) (Pugh 1999).

Suborder Calycophorae Leuckart, 1854
Family Prayidae Kölliker, 1853
Subfamily Amphicaryoninae Chun, 1888

Amphicaryon ernesti Totton, 1954

Figure 3B

Material examined. COLOMBIA – Caribbean Sea • offshore, exploration blocks; COL 4 - E 380; 11°10′41″N, 076°50′11″W; 70–140 m depth; 23.X.2014; INV CNI 4617 • COL 2 - E 418; 12°25′0″N, 074°52′30″W; 70–140 m depth; 25.XI.2015; INV CNI4618 • COL 10 - E 617; 13°30′22″N, 072°40′25″W; 70–140 m depth; 1.VI.2018; INV CNI4619 • COL 1 - E 437; 12°35′0″N, 074°7′30″W; 70–140 m depth; 10.IV.2016; consecutive number: ZOOP 56181 • COL 1 - E 466; 12°05′00″N, 075°37′30″W; 70–140 m depth; 20.IV.2016; consecutive

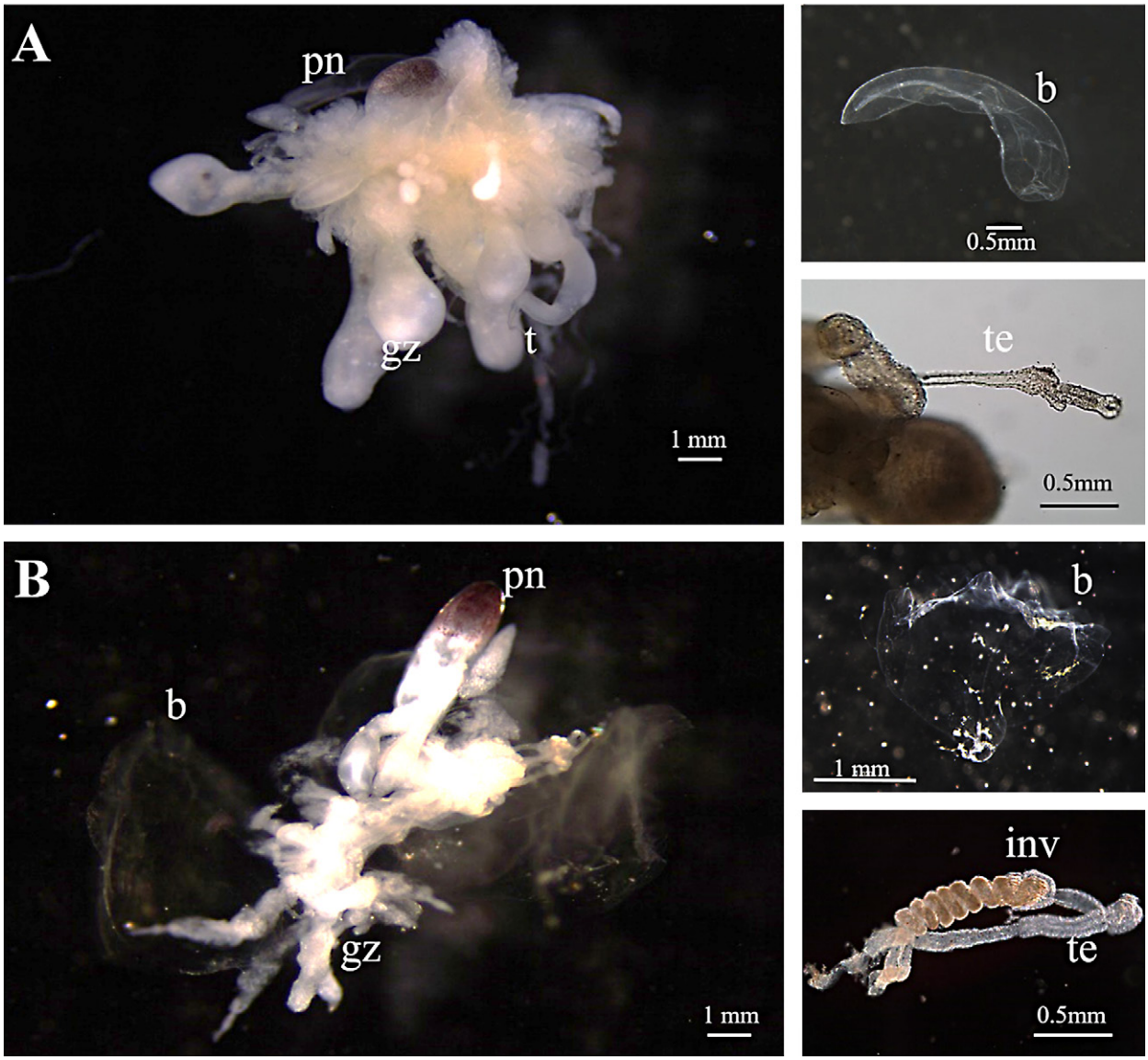

Figure 2. Newly reported siphonophore species from the Colombian Caribbean Sea, collecting. Physonect zooids: **A.** *Athorybia rosacea*, less bracts. **B.** *Nanomia bijuga*. Labels: b = bract; gz = gastrozooid; pn = pneumatophore (float); t = tentacle with tentilla; te = tentilla; inv = involucre.

number: ZOOP 56209 • COL 1 - E 467; 12°05′00″N, 075°52′30″W; 70–140 m depth; 21.IV.2016; consecutive number: ZOOP 56213 • **COL 2 - E 431**; 11°45′00″N, 075°37′30″W; 70–140 m depth; 3.XII.2015; consecutive number: ZOOP 56249.

Identification. There are three accepted species of *Amphicaryon* Chun, 1888: *A. acaule* Chun, 1888, *A. ernesti*, and *A. peltifera* (Haeckel, 1888) (Totton and Bargmann 1965; Schuchert 2022). This study found seven polygastric phases of *A. ernesti* (not all specimens were in good condition, and not all were deposited in the reference collection); these had an average height of 8.5 mm; the nectophore height of adult colonies reaches 8 mm according to Pugh (1999). The specimens were identified by two characteristics: the definitive nectophore is not embraced by the larval one, and the ostium has lost contact with the nectophore surface but is connected by a fine strand of tissue (Fig. 3B) (Mapstone 2009).

Family Hippopodiidae Kölliker, 1853

***Hippopodius hippopus* (Forsskål, 1776)**

Figure 3C

Material examined. COLOMBIA – Caribbean Sea • offshore, exploration blocks; COL 4 - E 380; 11°10′41″N, 076°50′11″W; 170–340 m depth; 23.XI.2014; INV CNI 4620 • COL 4 - E 383; 10°40′4″N, 076°05′21″W; 540–1000 m depth; 27.XI.2014; INV CNI4621 • COL 2 - E 421; 11°55′00″N, 075°07′30″W; 170–340 m depth; 29.XI. 2015; INV CNI4622 • COL 1 - E 467; 12°05′00″N, 075° 52′30″W; 170–340 m depth; 21.V.2016; INV CNI4623 • COL 10 - E 600; 14°22′12″N, 072°13′48″W, 170–340 m depth; 12.VI.2018; INV CNI4624 • COL 10 - E 617; 13° 30′22″N, 072°40′25″W; 170–340 m depth; 1.VI.2018; consecutive number: ZOOP 66375.

Identification. *Hippopodius* Quoy & Gaimard, 1827 is monotypic genus (Totton and Bargmann 1965). Two of the most representative characteristics of *H. hippopus*

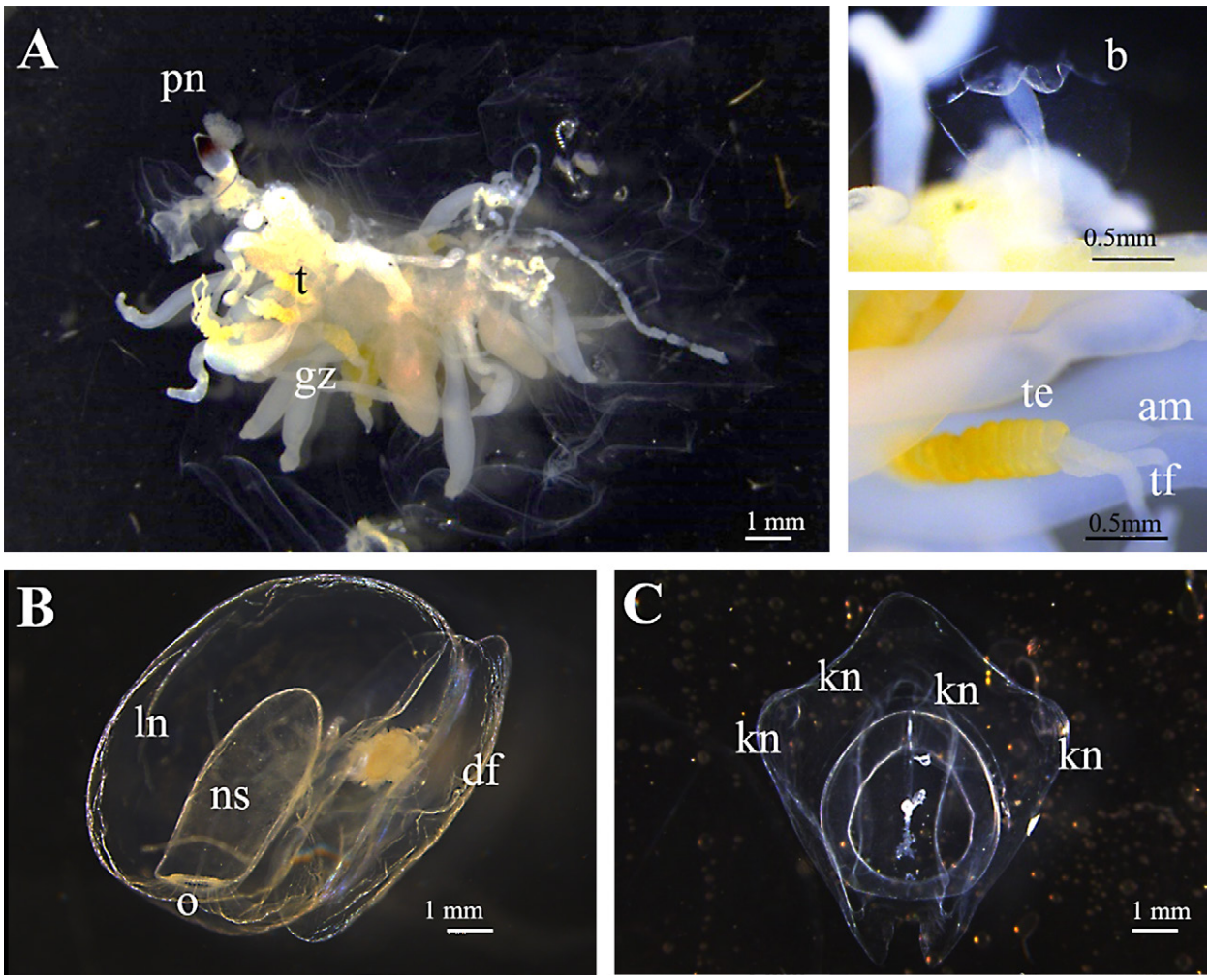

Figure 3. Newly recorded siphonophore species from the Colombian Caribbean Sea. Physonect zooids: **A.** *Agalma okenii*, calycophores. **B.** *Amphicaryon ernesti*, polygastric phase in lateral view. **C.** *Hippopodius hippopus*, nectophore. Labels: b = bract; gz = gastrozooid; pn = pneumatophore (float); t = tentacle with tentilla; te = tentilla; inv = involucre; am = ampulla; tf = terminal filament; ln = larval nectophore; df = defninitive nectophore; ns = nectosac; o = ostium; kn = knob.

are that the nectophore is shaped like a horse's hoof and the four rounded dorsal knobs vary in size and form an arc above the ostium (Fig. 3C) (Totton and Bargmann 1965). Six nectophores observed in this study (not all of them were in good condition and not all were deposited in the reference collection). They had an average height of 8.1 mm; adult colonies reach 20 mm high according to Pugh (1999).

Discussion

According to the most updated revision of siphonophore species in the Colombian Caribbean (Oliveira et al. 2016), the family Agalmatidae is represented by *Agalma elegans, Halistemma striata, Nanomia cara*, and *Lychnagalma utricularia*, the family Prayidae by *Praya reticulata* and *Rosacea cymbiformis*, and the family Hippopodiidae by *Vogtia pentacantha* and *Vogtia spinosa*. Therefore, the five species of siphonophores reported here are newly recorded in Caribbean Colombian waters. The physonects *Athorybia rosacea*, *Nanomia bijuga*, and *Agalma okenii*, and the calycophores *Amphicaryon ernesti* and *Hippopodius hippopus* have been previously recorded in the western Caribbean Sea and Gulf of Mexico (Gasca 2002, 2009; Pugh and Gasca 2009) and in the Atlantic Ocean (Brazil to Argentina) by Oliveira et al. (2016).

Athorybia rosacea, which was collected at depths of 0–340 m, is an epi- and mesopelagic species found in the water column in the northeastern Colombian Caribbean blocks COL 3, GUA OFF 3, and COL 10, which correspond to the Magdalena River influence zone, the oceanic Colombian zone, and offshore north-east zone (Aruba Passage), respectively (Dorado-Roncancio et al. 2022) (Fig. 1). The records reported here are the first of this short-stem agalmatid species from Colombian Caribbean waters; the species is now known from both the Caribbean Sea and the Pacific Ocean.

Nanomia bijuga was collected at depths of 70–140 m, and it is an epi- and mesopelagic species that undergoes short- and long-distance vertical diel migrations (Barham 1963; Pugh 1999). It was found in the water column in the northeastern Colombian Caribbean in blocks GUAOFF 3 and COL1, which correspond to the oceanic Colombian zone (Dorado-Roncancio et al. 2022; Fig. 1). Previous records Colombian waters were from the Pacific Ocean (Oliveira et al. 2016; Uribe-Palomino et al. 2018).

Agalma okenii is an epi- to mesopelagic species, which was collected at depths of 70–1000 m in the northeastern Colombian Caribbean in blocks GUA OFF 3, COL 1, and COL 2, which correspond to the oceanic Colombian zone (Dorado-Roncancio et al. 2022; Fig. 1). Previous records in Colombia waters were from the Pacific Ocean (Oliveira et al. 2016; Uribe-Palomino et al. 2018).

Amphicaryon ernesti was collected at depths of 70–140 m. It is an epipelagic species, which was collected in the northeastern Colombian Caribbean blocks COL 1, COL 2, COL 4, and COL 10. These areas correspond to the oceanic Colombian zone and offshore northeast zone (Aruba Passage) (Dorado-Roncancio et al. 2022; Fig. 1). Previously, this species has been recorded in Colombian Pacific waters (Oliveira et al. 2016).

Hippopodius hippopus is an epi- and mesopelagic species that undergoes small-scale diel migrations (Pugh 1999). This species was collected at depths between 170 and 1000 m in the northeastern Colombian Caribbean blocks COL 4, COL 2, COL 1, and COL 10. These blocks which correspond to the oceanic Colombian zone and offshore north-east zone (Aruba Passage) (Dorado-Roncancio et al. 2022; Fig. 1). Alvariño (1981) hypothesized that the initial stages of development of *H. hippopus* occur in the mesopelagic or bathypelagic strata, away from the surface waters. Previous records of *H. hippopus* in Colombian waters were from the Pacific Ocean (Oliveira et al. 2016; Uribe-Palomino et al. 2018).

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Authors Contributions

Conceptualization: CCP. Data curation: CCP. Investigation: CCP, EFDR. Methodology: CCP, EFDR. Visualization: CCP. Writing – original draft: CCP. Writing – review and editing: CCP, EFDR.

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