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Additional observations on hydromedusae during night dives in the Gulf Stream

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Abstract: This work is a supplement of our previous study (Schuchert & Collins, 2021) on hydromedusae observed and collected during night-time dives in the Gulf Stream off Florida. Close-up photos and collection of selected specimens for DNA extraction and 16S barcode sequencing permitted us to distinguish 49 distinct morphotypes or species of hydromedusae. Eighteen of them are new additions to the ones reported in our 2021 paper. Seven potential species of the 49 were only identified to the genus level, one to the family level. Two new species are described: *Zancleopsis grandis* sp. nov. and *Melicertum tropicalis* sp. nov. 16S sequences permitted us to identify the previously unknown subadult medusa of *Podocoryna martinicana* Galea & Ferry, 2013. Three species are new records for the Northwest Atlantic: *Leuckartiara adnata* Pagès, Gili & Bouillon, 1992, *Corymorpha valdiviae* (Vanhöffen, 1911), and *Cnidocodon leopoldi* Bouillon, 1978. The 16S data indicated the potential presence of cryptic species in *Thecocodium quadratum* (Werner, 1965), *Laodicea undulata* (Forbes & Goodsir, 1853), *Orchistoma pileus* (Lesson, 1843), and *Pseudaegina rhodina* (Haeckel, 1879).

Keywords: Cnidaria - Hydrozoa - Florida - blackwater diving - 16S DNA barcodes - taxonomy.

INTRODUCTION

This work is a complement to our publication Schuchert & Collins (2021). It summarises observations and results obtained from September 2020 to February 2023. For the scientific framework please consult the Introduction of our 2021 publication.

MATERIAL AND METHODS

Sampling

For the diving and sampling technique, localities, sample treatment, and deposition of voucher and DNA samples please see Schuchert & Collins (2021). All sampling drifts started 6 to 7 miles east of Palm Beach, with the approximate WGS84 coordinates 26.74, -79.94 used for the locality data in GenBank. BFLA sample numbers (= field numbers) refer to a single specimen if not stated otherwise. Sizes were estimated underwater or measured after collection in a tray. Formalin preserved voucher samples have been deposited in the Florida Museum of Natural History (FMNH) and were not re-examined, only the alcohol preserved samples used for DNA extraction were examined.

For this study, photographing and sampling was mainly done by RC, with substantial contributions by Deb Dever, Linda Ianniello, and Andrea Whitaker.

Photographic and fluorescence technique

Specimens were photographed *in situ* using a Nikon D800e with a Nikon AF Micro-NIKKOR 60 mm f/2.8D lens. The camera housing was Nauticam D800, with 2 Ikelite DS161 strobes and two FixNeo 1500 lumen lights.

Autofluorescence patterns in hydroids and medusae could potentially offer new species discriminating traits useable while collecting (comp. Kubota *et al.*, 2008, 2010; Kubota, 2010; Prudkovsky *et al.*, 2016; Maggioni *et al.*, 2020a). In June of 2022, RC added a Light & Motion Sola Nightsea brand light for stimulating fluorescence (Nightsea Inc., Hatfield, Pennsylvania; blue light, wavelength output primarily in the 440-460 nm range). The light is normally used with a yellow dive mask filter to search for strongly fluorescing animals. Some photos

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were taken in situ with blue excitation filters on the strobes and a Tiffen Yellow #12 filter on the camera. Lab photos were taken with the blue light and Tiffen Yellow #12 filter at high ISO settings. These photos are green only. More often, the author used the light to search for fluorescing specimens and then photographed them with a combination of white strobes and the blue Sola light.

Species identifications and taxonomy

Taxa are arranged principally alphabetically with some adaptations to bring resembling species closer together. Except for taxa treated already in Schuchert & Collins (2021), consulted works used to identify the species are given in the synonymies. In the paragraph entitled "Description" the actual observations and characteristics of the available specimens(s) are given, it is not a generalised description of the species. Not all observed species are reported here. Animals that were not identifiable to species level and were not collected for DNA barcoding have been omitted with a few exceptions. In this study, only hydromedusae are presented. The Siphonophorae will be treated in a separate publication.

DNA barcoding

Methods for extracting DNA, obtaining about 600 bp of the mitochondrial 16S gene, as well as maximum likelihood analyses are given in Schuchert (2014, 2018, 2019). The frozen DNA extracts in TE buffer are kept by the Muséum d'histoire naturelle of Geneva (MHNG) in their DNA collection. All new 16S sequences have been deposited in the GenBank database with the accession numbers OQ975685 to OQ975727.

For a limited number of samples, including some of our previous study, we could also sequence part of the COI gene. Fragments of about 848 bp of the mitochondrial cytochrome oxidase subunit I (COI) were amplified using the forward primer COF (TGAGTATTTTCAACTAATCAYAAAGA) and the reverse primer CoR (AAGTAAGCTCTAGTATCAA-CRTCCAT) (Schuchert, 2018). The PCR cycling profile for the COI fragment was: 5 cycles with 50 sec 94°C, 50 sec 45°C, and 120 sec 70°C; followed by 30 cycles with 50 sec 94°C, 50 sec 50°C, and 120 sec 70°C. The obtained COI sequences have been deposited in GenBank under the accession numbers OQ975002 through OQ975025.

A fragment of about 750 bp spanning the region of the ITS (Internal Transcribed Spacer) of the tandemly repeated ribosomal genes of *Pseudaegina rhodina* samples was amplified using the primers IFs (GTCGCTACTACCGATTGAATGG) and IRs (CGCTTCACTCGCCGTTACTAGG) (shortened primers of Martinez *et al.*, 2010). The PCR cycling profile for the ITS fragment was: 24 cycles with 20 sec 94°C, 45 sec 51°C, and 90 sec 72°C. The sequences have been deposited in GenBank under the accession numbers OQ991147 through OQ991157.

The obtained 16S or COI barcode sequences were compared to existing sequences in GenBank using the blastn search function (Johnson *et al.*, 2008) as implemented in the website of GenBank (https://blast.ncbi.nlm.nih.gov). The resulting list was then sorted according to the percent identity to the tested sequence. For individual pairwise sequence comparisons, the two sequences were aligned using the Bioedit Sequence Alignment Editor (Hall, 1999) and the integrated ClustalW tool using default settings (Larkin *et al.*, 2007). After truncation to eliminate single stranded ends, the percentage of base pair differences (p-values, Srivathsan & Meier, 2012) were calculated using the corresponding function in BioEdit. The branch lengths in the maximum likelihood phylogenetic trees are not percentage values, but the number of substitutions per site calculated by the selected model of DNA evolution.

GENERAL RESULTS AND DISCUSSION

Close-up photos taken during 91 drift dives (total dive time about 155 hours) and collection of selected specimens for DNA extraction and 16S barcode sequencing permitted us to distinguish 49 species of hydromedusae. Eighteen of them are new additions to the 56 reported in our 2021 paper. Seven potential species of the 49 were only identified to the genus level, one to the family level. Two new species are described: *Zancleopsis grandis* sp. nov. and *Melicertum tropicalis* sp. nov. Three species are new records for the Northwest Atlantic: *Leuckartiara adnata* Pagès, Gili & Bouillon, 1992, *Corymorpha valdiviae* (Vanhöffen, 1911), and *Cnidocodon leopoldi* Bouillon, 1978. Using 16S sequence data it was possible to identify the so far unknown subadult medusa of *Podocoryna martinicana* Galea & Ferry, 2013.

For the updated checklist of hydromedusae species recorded or potentially present in the coastal region from Cape Hatteras to Florida and the whole Gulf of Mexico see appendix 1.

Substantial 16S differences indicated the potential existence of cryptic species in *Pandeopsis ikarii* (Uchida, 1927), *Thecocodium quadratum* (Werner, 1965), *Laodicea undulata* (Forbes & Godsir, 1853), *Orchistoma pileus* (Lesson, 1843), and *Pseudaegina rhodina* (Haeckel, 1879).

Although indicative, divergent 16S lineages in morphospecies do not always signal the presence of more than one biological species. There are many factors that can lead to divergent intraspecific clades, like: hybridisation and introgression, selectively maintained ancient polymorphisms, marker errors like amplification of nuclear copies of the mitochondrial genome, and statistical problems like inadequate sample size that does not cover the complete intraspecific genetic diversity (comp. Moritz & Cicero, 2004; Morgan-Richards *et al.*, 2017; Thielsch *et al.*, 2017; Phillips *et al.*, 2022).

To prove the existence of cryptic species one needs considerably more samples and more detailed genetic analyses. For some samples close to *Aequorea neocyanea* Schuchert & Collins, 2021, the 16S sequence are rather distant from the other samples and their specific identity was difficult to assess. For this case, the same limits to the barcoding technique apply as stated above. For several samples belonging to the genera *Aequorea, Bougainvillia*, *Clytia*, *Cunina*, *Leuckartiara,* and *Zanclea* we did not make a species-level identification. While they are possibly new species, some of them were juveniles or offered not enough details for an appropriate description as a new species.

TAXONOMIC PART

Order Anthoathecata
Suborder Filifera
Family Bougainvilliidae Lütken, 1850
Genus *Bougainvillia* Lesson, 1830

Diagnosis: Medusa with four perradial marginal bulbs bearing two or more identical tentacles, bulbs with or without ocelli; four perradial oral tentacles, usually branched and ending in nematocyst clusters; gonads interradial or adradial on manubrium, sometimes also along basal perradial extensions of the manubrium.

Hydroid colony stolonal or branched, more rarely hydranths sessile; perisarc terminating at base of hydranth or extending onto hydranth as pseudohydrotheca; hydranth cylindrical to spindle-shaped, tentacles in one or two closely approximated whorls, tentacle-bases never enveloped by pseudohydrotheca, tentacles alternately inclined up- and downward (amphicoronate). Gonophores develop into free medusae, arising singly or in clusters from stem, branches, or stolons.

Bougainvillia sp.
Fig. 1A-B

Bougainvillia spec. – Schuchert & Collins, 2021: 241, fig. 1A-B.

Examined material: BFLA4494; 10-Oct-2020; size ~7 mm, female; preserved in ethanol for DNA extraction, 16S sequence OQ975688, COI sequence OQ975010. – **BFLA4499**; 14-Dec-2020; size ~6 mm, female; preserved in ethanol for DNA extraction; specimen lost. – **BFLA4500**; 14-Dec-2020; size

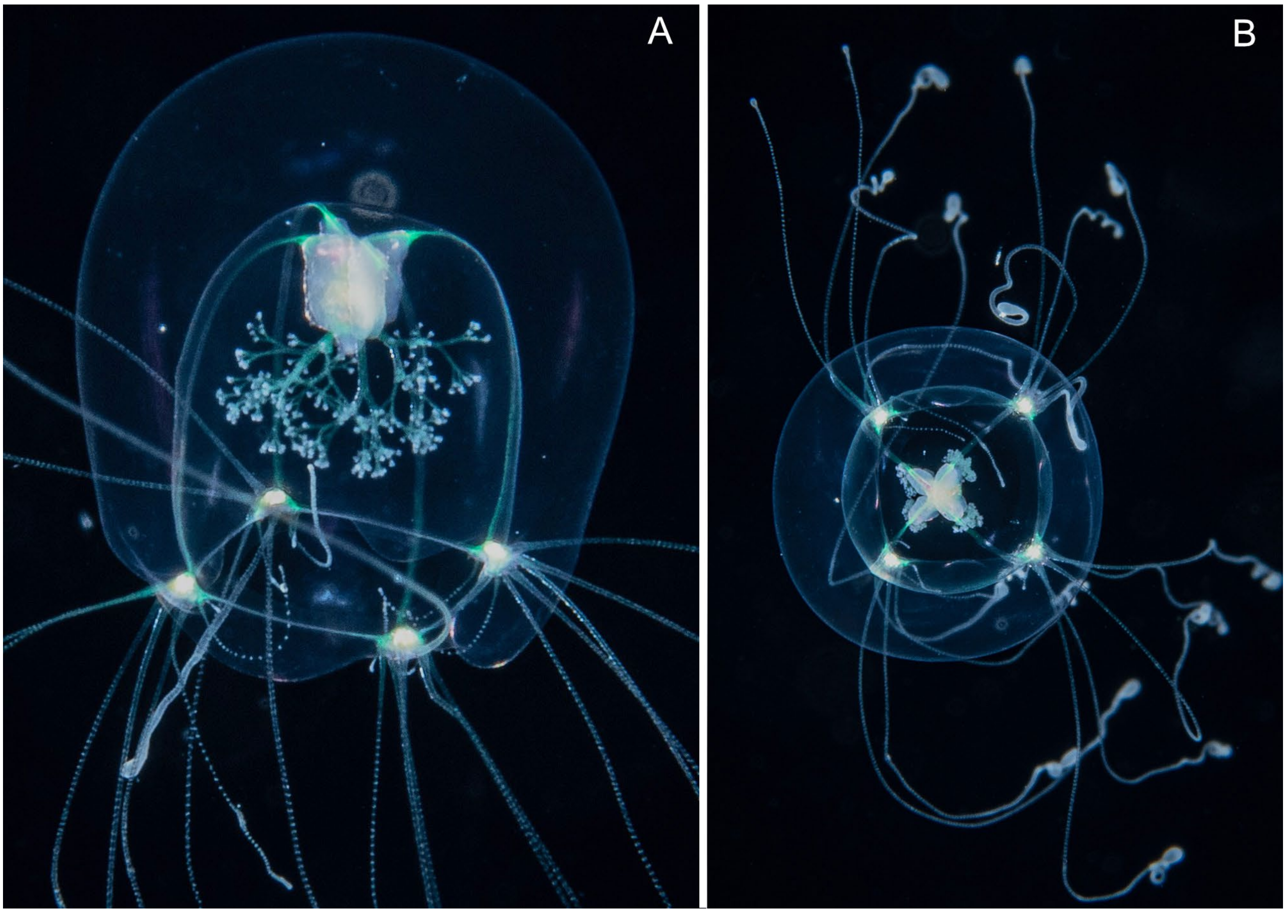

Fig. 1. *Bougainvillia* sp. BFLA4494, bell size 7 mm. (A) Lateral view, note the extensive branching of the oral tentacles, visible only when they are extended. (B) Oral view, the oral tentacles are completely contracted. Photos by Linda Ianniello.

~6 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975688, COI sequence OQ975011. – **BFLA4849**; 06-Oct-2022; size ~3 mm; preserved in ethanol for DNA extraction; deposited in FMNH as UF-017273.

Description: Bell up to 7 mm high, slightly higher than wide, mesogloea thick, apical mesogloea ¼ of bell height. Manubrium cruciform in cross-section except for short tubular oral part; cruciform part in mature animals roughly isodiametric (Fig. 1A), in less developed animals more conical. Four perradial oral tentacles arise well above mouth rim, trunk long, branched up to 4 times, ending in spherical nematocyst knobs (Fig. 1A). Gonads flat pads on stomach, interrupted perradially, interradial vertical cleft interradial (Fig. 1B). Four radial canals and marginal bulbs, bulbs D-shaped, each with 5-8 filiform tentacles; dark, round ocelli on adaxial side of tentacle base.

Sequence Data: 16S sequences of two out of four samples could be determined. The new haplotypes differ only in one to two base pairs to the previously reported one (MW528641, p-distances 0.14 and 0.28%).

Remarks: See Schuchert & Collins (2021) for discussion and reasons why we did not name it as a new species.

Family Cytaeididae L. Agassiz, 1862
Genus *Cytaeis* Eschscholtz, 1829

Diagnosis: Medusa with spherical to oblong bell, four or more capitate oral tentacles arising well above mouth margin, medusa budding from manubrium. With four marginal tentacles, solid, tapering, in adults with broad, enlarged base adhering to exumbrella just above bell margin, no ocelli.
Hydroids monomorphic, arising from reticulate stolons covered by perisarc. Hydranths sessile, with one whorl of filiform tentacles below conical hypostome; base of hydranths often with a perisarc collar. Gonophores develop from stolons, liberated as medusa with four tentacles.

Cytaeis tetrastyla Eschscholtz, 1829
Fig. 2A-G

Cytaeis tetrastyla Eschscholtz, 1829: 104, pl. 8 fig. 2. – Schuchert, 2007: 275, fig. 32, synonymy, references, taxonomic details. – Schuchert & Collins, 2021: 242, fig. 2A-C.

Examined material: BFLA4520; 16-Apr-2021; size ~2 mm; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank MW528725. – **BFLA4558**; 27-May-2021; size ~5 mm; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank MW528664. – **BFLA4590**; 10-Jul-2021; size ~4 mm; preserved in ethanol for DNA

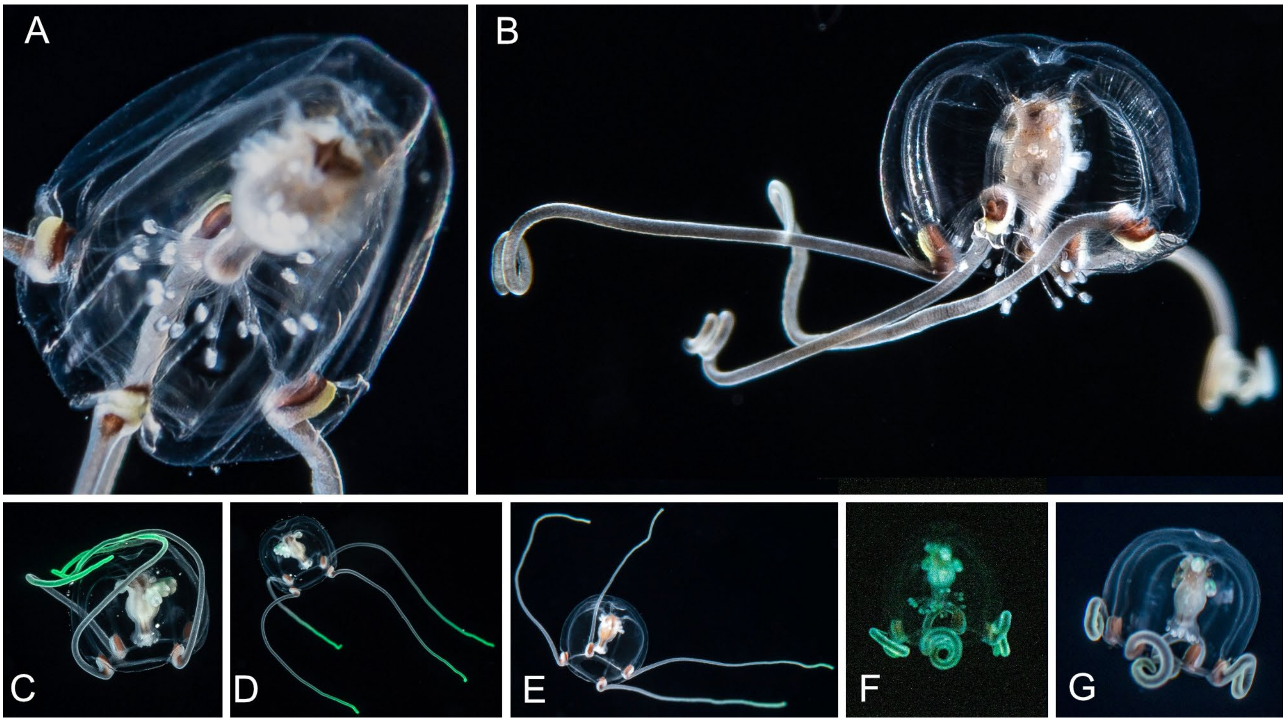

Fig. 2. *Cytaeis tetrastyla.* (A-B) BFLA4558, bell 5 mm. (C-D) BFLA4592, 5 mm bell, normal light (E) BFLA4520, bell 2 mm. (F) BFLA4797, bell 4 mm, autofluorescence, in situ, underexposed with ~1500 lumen white light, no flash. (G) BFLA4797, white light and flash.

extraction; PCR failed. – **BFLA4592**; 10-Jul-2021; size ~5 mm; preserved in ethanol for DNA extraction; PCR failed. – **BFLA4797**; 05-May-2022; size ~4 mm; preserved in ethanol for DNA extraction; deposited in FMNH as UF-016270. – 1 specimen photographed 24-Feb-2022; size estimated 4 mm; not collected. – 1 specimen photographed 15-May-2022; size estimated 4 mm; not collected.

Description: See Schuchert & Collins (2021).

Sequence Data: The two obtained 16S sequences corresponded to two known haplotypes (see above).

Remarks: In some of the observed animals the ends of the tentacles showed a green luminescence even with standard illumination (Fig. 2C-E), while other were more pigmented (Fig. 2A-B). The autofluorescence pattern is shown in Fig. 2F-G.

Family Bythotiaridae Maas, 1905
Genus *Protiaropsis* Stechow, 1919

Diagnosis: Bythotiaridae medusae with thick umbrella, four simple radial canals; no centripetal canals; gonads interradial, no transverse folds; no secondary tentacles; no ocelli.
Hydroid unknown.

Protiaropsis anonyma (Maas, 1905)
Fig. 3

Protiaropsis anonyma. – Schuchert & Collins, 2021: 257, fig. 12A-C.

Examined material: BFLA4536; 25-Apr-2021; size: 12 mm; part preserved in ethanol for DNA extraction, 16S sequence OQ975695, COI sequence OQ975013; rest of animal preserved in formalin and deposited as voucher UF-015243.

Description: As in Schuchert & Collins (2021), but with only nine tentacles instead of 10. The red interradial strands were also present in this specimen (Fig. 3).

Sequence Data: The new 16S haplotype differed only in one base pair (p-distance 0.2%) from our previously published one (GenBank MW528657).

Distribution: See Schuchert & Collins (2021).

Remarks: The interradial, longitudinal red strands in the manubrium were also present in this specimen and are likely a constant feature of this species.

Family Hydractiniidae L. Agassiz, 1862

Remarks: Several genera of the Hydractiniidae have been redefined by Miglietta *et al.* (2010, 2012) based on molecular phylogenies. Many of these genera are now no longer diagnosable solely using morphological traits. Moreover, not all species were included in the phylogeny and thus for some *Hydractinia* species it is unclear to which genus they belong.

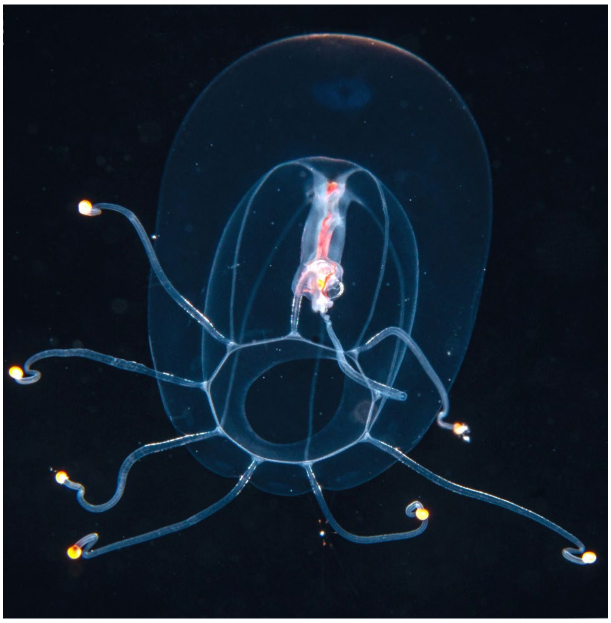

Fig. 3. *Protiaropsis anonyma* BFLA4536, oblique view from oral side, size 12 mm, note that one tentacle tip is tucked inside mouth, a feeding action often seen in hydromedusae.

Genus *Podocoryna* sensu Miglietta *et al.* (2010, 2012)

Podocoryna M. Sars, 1846: 4; type species *Podocoryna carnea* M. Sars, 1846, by monotypy.

Dysmorphosa Philippi, 1842: 37; type species *Dysmorphosa conchicola* Philippi, 1842 by monotypy.

Rhizocline Allman, 1864: 355; type species *Hydractinia areolata* Alder, 1862 by original designation.

Corynopsis Allman, 1864: 353; type species *Podocoryne alderi* Hodge, 1863 by original designation, hydroid only (see Calder, 1988: 27).

Podocoryne Lütken, 1850: 33, incorrect subsequent spelling.

Cytaeandra Haeckel, 1879: 79; type species *Hydractinia areolata* Alder, 1862 by designation of Schuchert (2008).

Hydractomma Stechow, 1921: 250; type species *Hydractinia pruvoti* Motz-Kossowska, 1905 by original designation.

Diagnosis: Hydractiniidae producing free-swimming, feeding medusae, or exceptionally medusoids as in *Podocoryna pruvoti* (Motz-Kossowska, 1905).

Remarks: This is a provisional diagnosis as not all Hydractiniidae medusae were included in the study of Miglietta & Cunningham (2012). It basically agrees with Kramp's (1961) diagnosis, except for *Podocoryna pruvoti*. Galea & Ferry (2013) provide a tabular review of all known *Podocoryna* species.

Podocoryna martinicana Galea & Ferry, 2013
Fig. 4A-B

Podocoryne martinicana Galea & Ferry, 2013: 579, fig. 1, pls 1-2.

Examined material: BFLA4487; 14-Sep-2020; size: 2 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975687. – 1 specimen photographed 09-Sep-2021; size 3 mm; not collected.

Description: Medusa spherical, diameter 2-3 mm, mesogloea evenly thick, apex somewhat flattened, no apical process. Manubrium about half the height of the subumbrella, composed of large, ovoid upper part ("stomach") and smaller, cylindrical mouth region; mouth margin with four small, inconspicuous, perradial lips. Gonads apparently developing on stomach wall. Four radial canals, connected to manubrium via flat, funnel-shaped widenings (Fig. 4A), resembling small mesenteries. Up to nine large tentacles, with slight size differences suggesting a successive development, all short and tightly coiled like a snail shell; bases of tentacles slightly swollen where joined to bell margin, but basal bulbs not much developed, only discernible through pigmentation. In addition to large tentacles, four small, short tentacles lacking bulbs, partially coiled. Colours: stomach, tentacle bases and tips orange-brown. Without interradial pigment spots on aboral end of manubrium.

Sequence Data: The 16S sequence obtained of sample BFLA4487 differed only in 3 base pairs (p-distance 0.5%) from GenBank entry KP776813 *Podocoryna martinicana,* a hydroid collected from the coast of Martinique island and identified by Horia Galea, one of the original authors of this species.

Distribution: Martinique island (Galea & Ferry, 2013), Florida (this study). Type locality: Martinique, 14.6386°N 61.1396°W, depth 10 m, hydroid exclusively on hermit crab *Iridopagurus caribbensis*.

Remarks: The present samples were identified as belonging to *Podocoryna martinicana* solely on the close similarity of the 16S sequences (see above). Only the newly released medusae of this species were known so far (four-tentacle stage, Galea & Ferry, 2013). *Podocoryna martinicana* deviates in many aspects from its congeners, e.g., the multiple whorls of tentacles in the feeding zooids, the bright pigmentation of the tentacles and hypostome of polyps, and that of the distal half of marginal tentacles of the medusa (see colour photos in Galea & Ferry, 2013). The 16S sequence is likewise not clustering with any clade or hydractiniid species for which there is 16S sequence data available (Maximum Likelihood analysis, results not shown). A more detailed genetic analysis using more markers will likely show the need for a new genus name.

Family Pandeidae Haeckel, 1879

Remarks: For a taxonomic discussion of the family see Schuchert (2007). A maximum likelihood phylogenetic tree of 16S sequences of Pandeidae is shown in Fig. 5. Several genera appear to be polyphyletic, but the relationships of the genera are only poorly resolved. For this study, only the clustering into nominal species is of importance. While the species usually come out as clades, this is not the case for nominal *Catablema* species. For this genus the COI marker seems to be the better choice (see discussion in Schuchert, 2018).

Genus *Amphinema* Haeckel, 1879

Diagnosis: Medusa with two large opposite tentacles; with or without ocelli; gastric peduncle absent; mostly

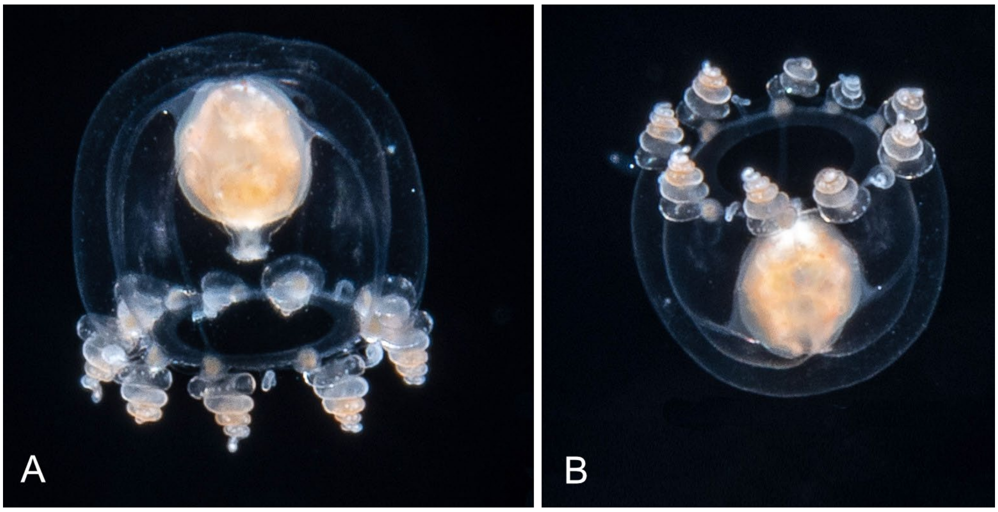

Fig. 4. *Podocoryna martinicana* BFLA4487, size 2 mm. (A) Lateral view. (B) Oblique oral view. Photos by Linda Ianniello.

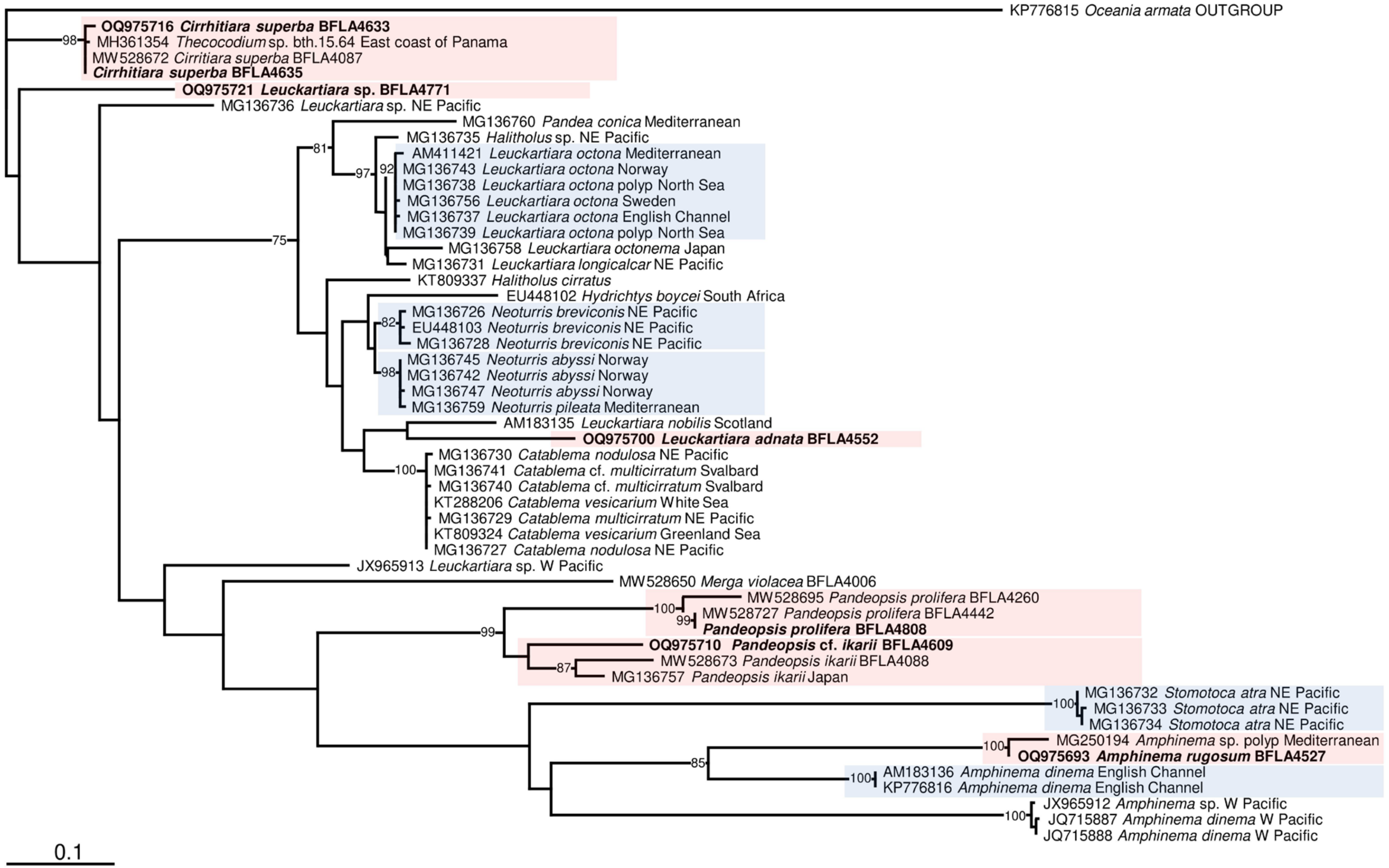

Fig. 5. 16S maximum likelihood phylogenetic tree of Pandeidae species obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Taxa in bold are from this study. Species clades of this study are highlighted in red, other resolved species clades in blue. All sequence labels start with the GenBank numbers, permitting the retrieval of more information. For more details see text and Schuchert (2018). Samples based on the polyp stage are indicated, all others are medusa samples.

with a considerable apical projection; with or without additional marginal small cirri or marginal rudimentary bulbs; with or without mesenteries; four simple oral lips, not or not much crenulated. Gonads on manubrium in adradial or interradial position, occasionally extending to the radial canals.

Hydroid colonies usually stolonal (except for one species of uncertain affinity), hydranths with a well developed caulus, caulus longer than hydranth, covered by perisarc; hydranths without pseudohydrotheca, spindle-shaped, conical hypostome, one whorl of filiform, amphicoronate tentacles. Polyps bend over when disturbed. Gonophores arise either from cauli, stolons or both, released as free medusae.

Amphinema rugosum **(Mayer, 1900)**

Fig. 6A-E

Stomotoca rugosa Mayer, 1900a: 4, pl. 2 fig. 5.

Amphinema rugosum. – Schuchert, 2007: 309, fig. 47, synonymy, redescription.

Examined material: BFLA4527; 1 male specimen; 16-Apr-2021; size ~2.5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975693, COI sequence OQ975012.

Description: *Amphinema* medusa with total height 2.5 mm, umbrella slightly wider than high, on top an ovoid apical process, top of umbrella with slight perradial furrows, with shallow subumbrellar pockets. With four broad radial canals with slightly irregular

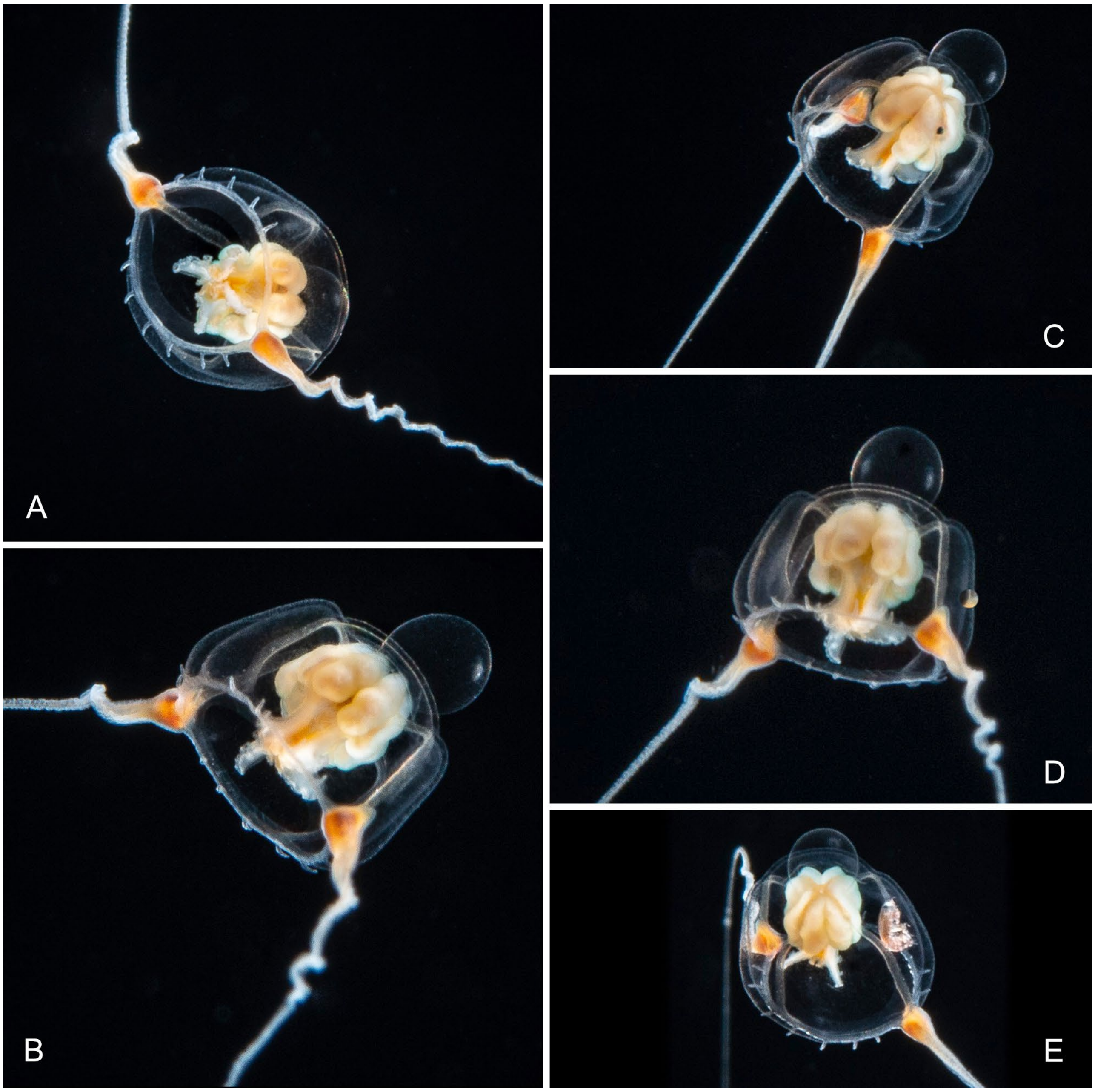

Fig. 6. *Amphinema rugosum,* BFLA4527, size 2.5 mm. (A-E) Views at various angles.

and smooth margins, without mesenteries. Two diametrically opposed tentacles with thick base, evenly tapering and extended up to 40 mm long; additionally, 14 small tentaculae along bell margin. Manubrium reaching almost to the velum, cross-shaped in section, mouth with four prominent, slightly recurved lips, mouth margin partly smooth, partly with some folds. Eight large male gonads covering adradial walls of manubrium, each with two shallow transverse constrictions leading to a structure composed of three bulbs. Ocelli not present. Colour of marginal tentacle bulbs and stomach brownish yellow to orange, tentaculae colourless.

Sequence Data: The partial 16S gene sequence (OQ975693) obtained was used to search for similar sequences in GenBank using the blastn function. The closest match was an *Amphinema* polyp from the Mediterranean with a p-distance of 1.8% (GenBank MG250194, see also Fig. 5). Likewise, the partial COI gene (GenBank OQ975012) singled out the COI sequence of the same polyp (GenBank MG237874, p-distance 1.1%). The *Amphinema* polyp was collected by one of us (PS) and it conformed to the hydroid stage of *A. rugosum* (see Rees & Russell, 1937; summary in Schuchert, 2007).

Description and Distribution: See Schuchert (2007).

Remarks: The single observed medusa matched Mayer's (1900a) description rather well, except for the somewhat less furrowed gonads.

Genus *Cirrhitiara* Hartlaub, 1914

Diagnosis: Pandeid medusa with solid apical projection; 4 or 8 large hollow marginal tentacles alternating with rudimentary marginal bulbs, each carrying a single lateral cirrus on one side; all marginal bulbs with ocelli; gonads adradial, with diverging folds directed perradially, with interradial transverse fold connecting the adradial groups of gonads; with long mesenteries.

Hydroid imperfectly known, stolonal hydroids lacking tentacles (Schuchert & Collins, 2021).

Cirrhitiara superba (Mayer, 1900)

Figs 7A-F, 8A-E

Tiara superba Mayer, 1900b: 34, pl. 16 fig. 39.

Cirrhitiara superba. – Schuchert & Collins, 2021: 244, figs 4A-D, 5, synonymy, description, hydroid.

Examined material: BFLA4633; 04-Aug-2021; size 10 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975716. – **BFLA4635**; 04-Aug-2021; size 10 mm; preserved in ethanol for DNA extraction, 16S sequence identical to MW528672; voucher UF-015298 in 4% formalin. – **BFLA4841**; 19-Aug-2022; size 14 mm; part preserved in ethanol for DNA extraction, part in 4% formalin, both deposited in FMNH as UF-017269. – **BFLA4842**; 1 female; 19-Aug-2022; size 12 mm; part preserved in ethanol for DNA extraction, part in 4% formalin, both deposited in FMNH as UF-017270. – 1 specimen photographed 10-Jul-2022; not collected. – 1 specimen photographed 19-Aug-2022; size 13 mm; not collected.

Description: Pandeid medusa reaching total heights of 14 mm; deep, bell-shaped umbrella. Apical process of variable size present, apical exumbrella with perradial furrows. Manubrium size variable, filling half or entire volume of the subumbrella, mouth rim complexly folded. Gonads on stomach forming branching folds diverging from interradial to adradial, in each quadrant two adradial series of folds that are usually connected interradially by a transverse fold, may be indistinct or short. Four very broad radial canals, margin irregular, canals connected to stomach via funnel-like widenings (mesenteries). Four long, evenly tapering, perradial tentacles, base laterally compressed and clasping bell margin, no abaxial spur, large red abaxial ocellus near abaxial end. Alternating with the tentacles 3 to 5 small bulbs on bell margin, each with a large abaxial ocellus and a thin cirrus usually originating laterally from bulb. Sometimes the cirrus appears to originate more mediolaterally or even medially (Figs 7E, 8C, E, arrows). All small bulbs of equal size. Rarely, a rudimentary bulb in interradial position developing into a small, short tentacle (Fig. 7B-C). Oral part of manubrium usually pink, part underlying gonad region pink or in larger individuals yellow (Fig. 7); gonads colourless, pinkish, or with dark pigment in furrows (Fig. 8D); tentacles with a pink hue, rudimentary bulbs pink; subumbrella and canal system sometimes with pink hue.

16S Data: The two 16S haplotypes found in three individuals are rather similar (p-distance 0.5%, see also Fig. 5).

Remarks: Like many pandeid medusae, *Cirrhitiara superba* is rather variable in form and size of the apical process and the size of the manubrium in relation to the bell cavity (comp. Figs 7A, 8B). Nearly all our animals had four perradial tentacles, except for one which had one small, additional interradial one (Fig. 7B). Cirri arising laterally from rudimentary bulbs (permanent non-tentacular marginal bulbs) are a diagnostic trait for the genus *Cirrhitiara.* While cirri occur also in other Pandeidae [*e.g. Barnettia caprai* Schuchert, 1996; Atlantic *Amphinema turrida* (Mayer, 1900)], the origin lateral to rudimentary bulb and only one per bulb is unique within the Pandeidae. In the photos of the medusa taken for this study, however, some appear to arise mediolaterally or even medially (comp. Fig. 8C-E). This seems often to be due to the base of the cirrus being invisible behind the bulb. However, we should not exclude that at least some originate towards the medial abaxial side of the bulb. This example shows

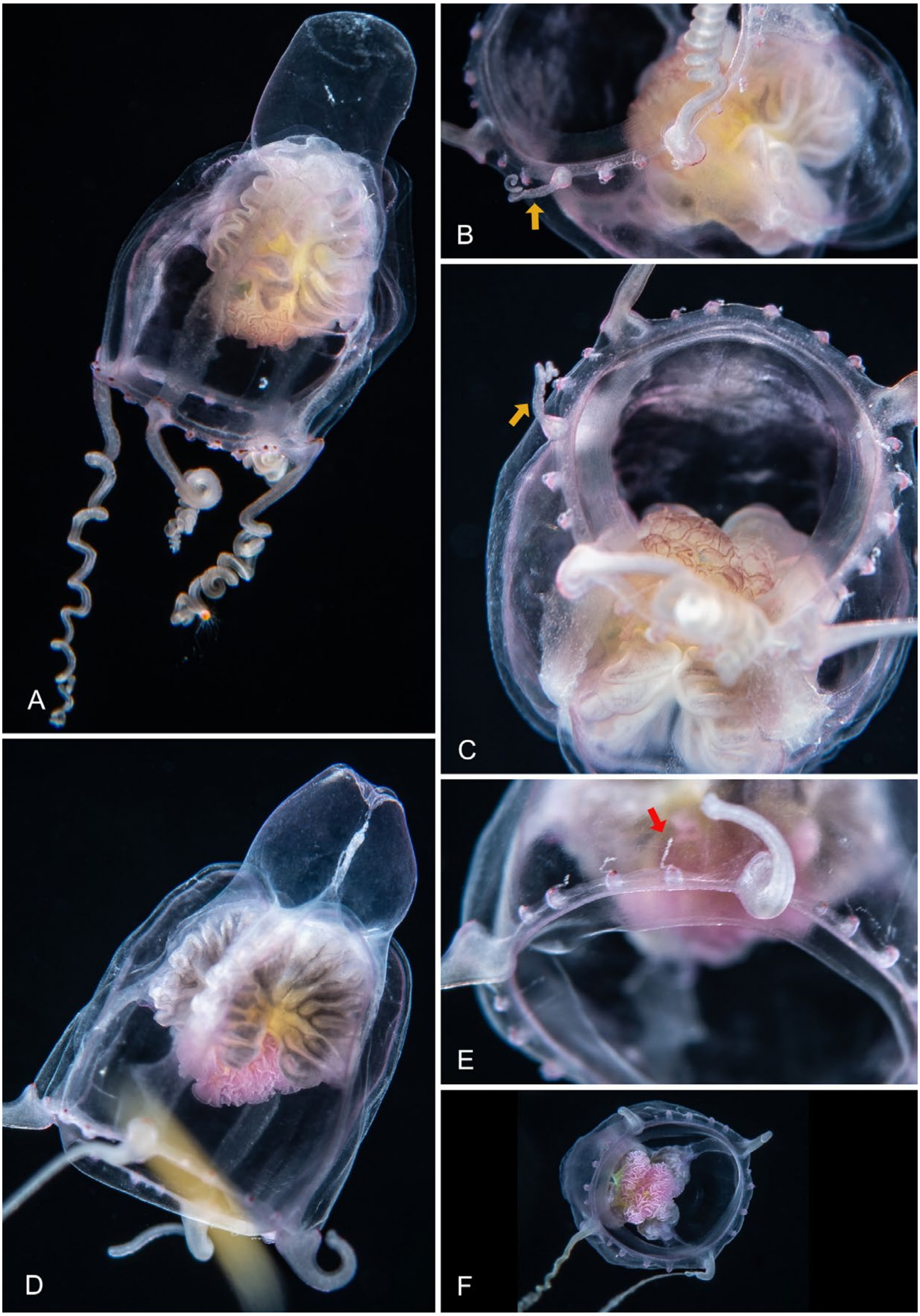

Fig. 7. *Cirrhitiara superba.* (A-C) BFLA4635, size 10 mm. (D-F) BFLA4633, size 10 mm. (A) Lateral view. (B-C) Oral view, note presence of small interradial tentacle (yellow arrow). (D) Lateral view. (E) Oblique view on bell opening, note that cirri sometimes appear not to originate on the side of the rudimentary bulbs (red arrow). (F) Oral view.

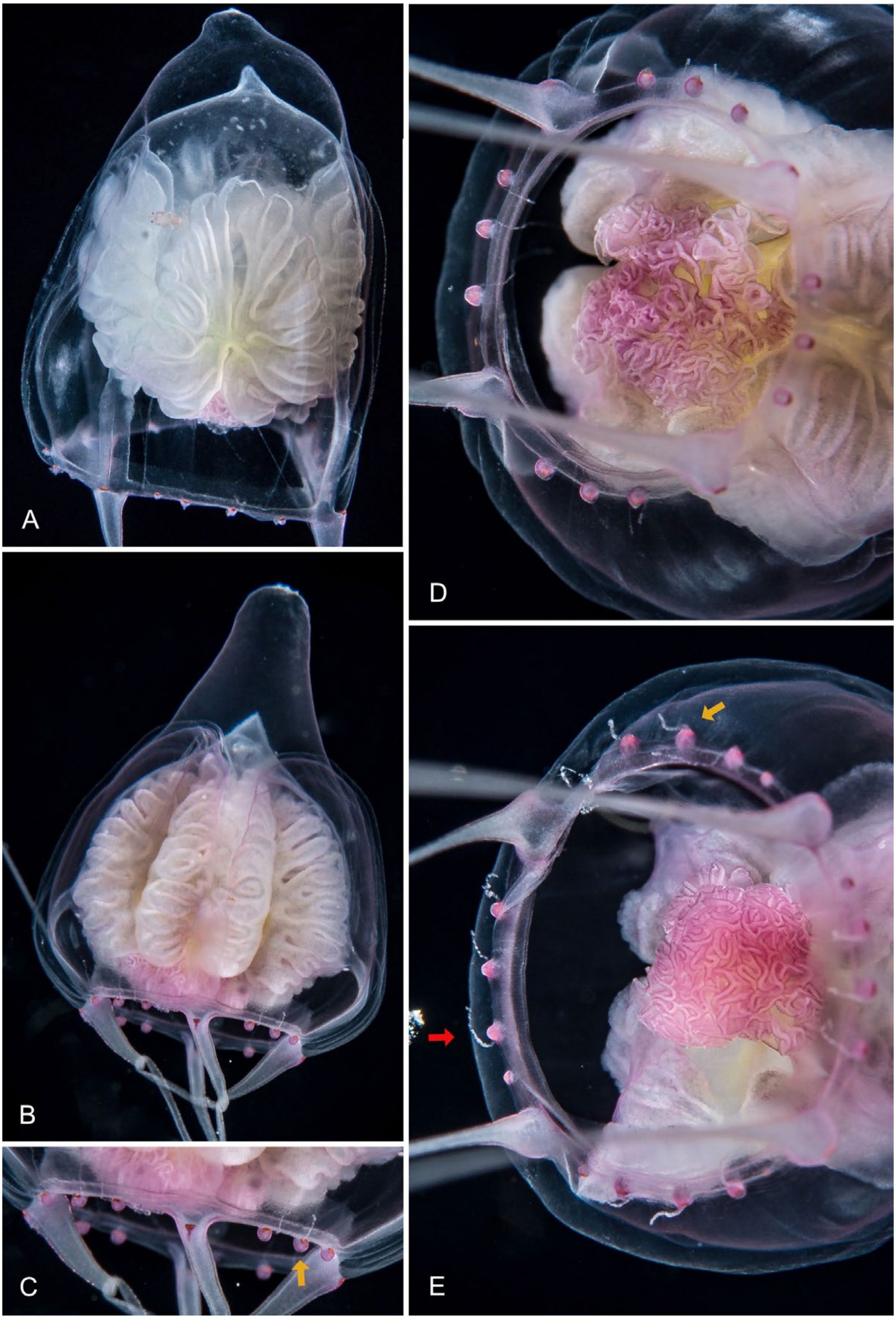

Fig. 8. *Cirrhitiara superba.* (A) BFLA4841, size 14 mm. (B) BFLA4842, size 12 mm. (C) BFLA4842, bell margin, yellow arrow points at apparently median cirrus. (D) BFLA4842, note lateral cirri. (E) Animal photographed 19-Aug-2022; 13 mm; red arrow points at lateral cirri, yellow arrow points at apparently median cirrus.

that also the photographic documentation has its limits in that three-dimensional aspects are often difficult to interpret.

At this place, and with reference to the *Leuckartiara* species described in the following pages, it seems useful to consider the definition of cirri of hydromedusae. Cirri (singular: cirrus) are thin, isodiametric, tentacle-like appendages of the umbrellar margin. They are solid (= not hollow) and usually without a distinctly swollen end. They can arise direct from the bell margin, thus being not associated with marginal bulbs, or they arise immediately adjacent to or on the base of a marginal bulb, the latter bearing a tentacle or not. In a few Anthoanthecata they can be difficult to distinguish from developing or reduced tentacles if there is a distinct separation of the bulb and the tentacle is only gently tapering. Cirri are more commonly found in Leptomedusae where they are often coiled and occuring in groups.

Genus *Eutiara* Bigelow, 1918

Eutiara Bigelow, 1918: 374; type species *Eutiara mayeri* Bigelow, 1918 by original designation.

Diagnosis: Pandeid medusa with simple or branched exumbrellar meridional ridges; blind centripetal canals alternating with radial canals; radial canals wide, with lateral diverticula, with well-developed mesenteries; gonads forming eight series of adradial folds.

Hydroid unknown.

Remarks: Recently, a new *Eutiara* species (*Eutiara decorata* Berberian, Michenet & Goy, 2021) was described which has branched exumbrellar ridges. *Eutiara mayeri* Bigelow, 1918, has radial, unbranched ridges with an underlying gastrodermal canal (Bigelow, 1918: pl. 3 fig. 6). It is currently not known if the other known species of *Eutiara* (*Eutiara russelli* Bouillon, 1981 and *Eutiara decorata*) also have such canals. It can only reliably be seen in histological sections. This character was thus not included in the diagnosis.

Eutiara mayeri Bigelow, 1918

Fig. 9A-E

Eutiara mayeri Bigelow, 1918: 374, pl. 1 figs 1-5, pl. 3 fig. 6. – Kramp, 1959: 14, 123, fig. 129. – Kramp, 1961: 100. – Larson *et al*., 1991: 313.

Neoturris mayeri. – Ranson, 1936: 75, new combination.

Eutiara (*Neoturris*) *mayeri*. – Ranson, 1937: 326, fig. 3, discussion of nematocyst tracks.

Examined material: BFLA4482; 12-Aug-2020; broken specimen 5-10 mm; preserved in ethanol for DNA extraction but specimen was lost. – 1 specimen photographed 03-Jul-2020; size ~15 mm; not collected.

Description: Medusa with umbrella up to 15 mm high, deeply bell-shaped, diameter slightly more than half the height, without or with small apical projection (Fig. 9A). Manubrium large, about ⅔ of subumbrellar height, connected to radial canals via long mesenteries. Mouth margin much crenulated. Gonads eight adradial series of folds, these mostly unbranched. Four radial canals broad, with irregularly branched lateral diverticula (Fig. 9C). Four centripetal canals arising interradially from circular canal, blind-ending, reaching about ⅓ bell height. Four perradial tentacles and four interradial tentacles, all large and similarly developed, lacking ocelli, bases large, laterally compressed, clasping bell margin and continued on exumbrella as thick, somewhat opaque ridges, perradial ones up to apex, interradial ones up half the bell. Tentacles transparent, nematocysts concentrated an adaxial side in a row of globular nematocyst clusters (Fig. 9D, red arrow). Between tentacles on bell margin two to four rudimentary bulbs, each with an ocellus-like pigment spot, spot oblong, parallel to bell margin, without exumbrella ridges. Colour: manubrium, gonads, bulbs, and exumbrellar ridges pink-violet.

For more details see also Bigelow (1918) or Kramp (1959).

Distribution: Off North Carolina, Caribbean Sea, Bahamas, Florida. Type locality: NW Atlantic Ocean; WGS84 35.4500, -73.2333; depth 0-100 m.

Remarks: *Eutiara mayeri* is a very rare medusa. To our knowledge, specimens have been reported in the literature only three times (Bigelow, 1918; Kramp, 1959; Larson *et al*., 1991). The blindly ending interradial canals and the conspicuous exumbrella ridges make this species unmistakable. These ridges are not simply nematocyst tracks, but they are underlain by a gastrodermal tube (Bigelow, 1918). Contrary to the existing descriptions, the bell may have a small apical projection, as it was found in our two samples (Fig. 9A). For both observations we documented, the medusa was associated with a juvenile *Aluterus heudelotii* (Dotterel filefish, Fig. 9A, E) holding the medusa by its mouth. We do not know what this behaviour signifies, but it is most likely not an act of predation, perhaps a kind of acquired defensive behaviour to protect the fish against predation (Greer *et al*., 2016). We saw the same behaviour with filefish using other cnidarians, *e.g. Cirritiara superba*.

Genus *Leuckartiara* Hartlaub, 1914

Synonymy: See Schuchert (2007) for details.

Diagnosis: Medusa mostly with an apical projection of variable size. Manubrium voluminous, connected to radial canals by mesenteries. Mouth with extensively folded and crenulated margin. Gonads on interradial walls of manubrium, bipartite but with broad connection in upper half, with various degrees of folding, no or only few interradial pits. Radial canal broad, often

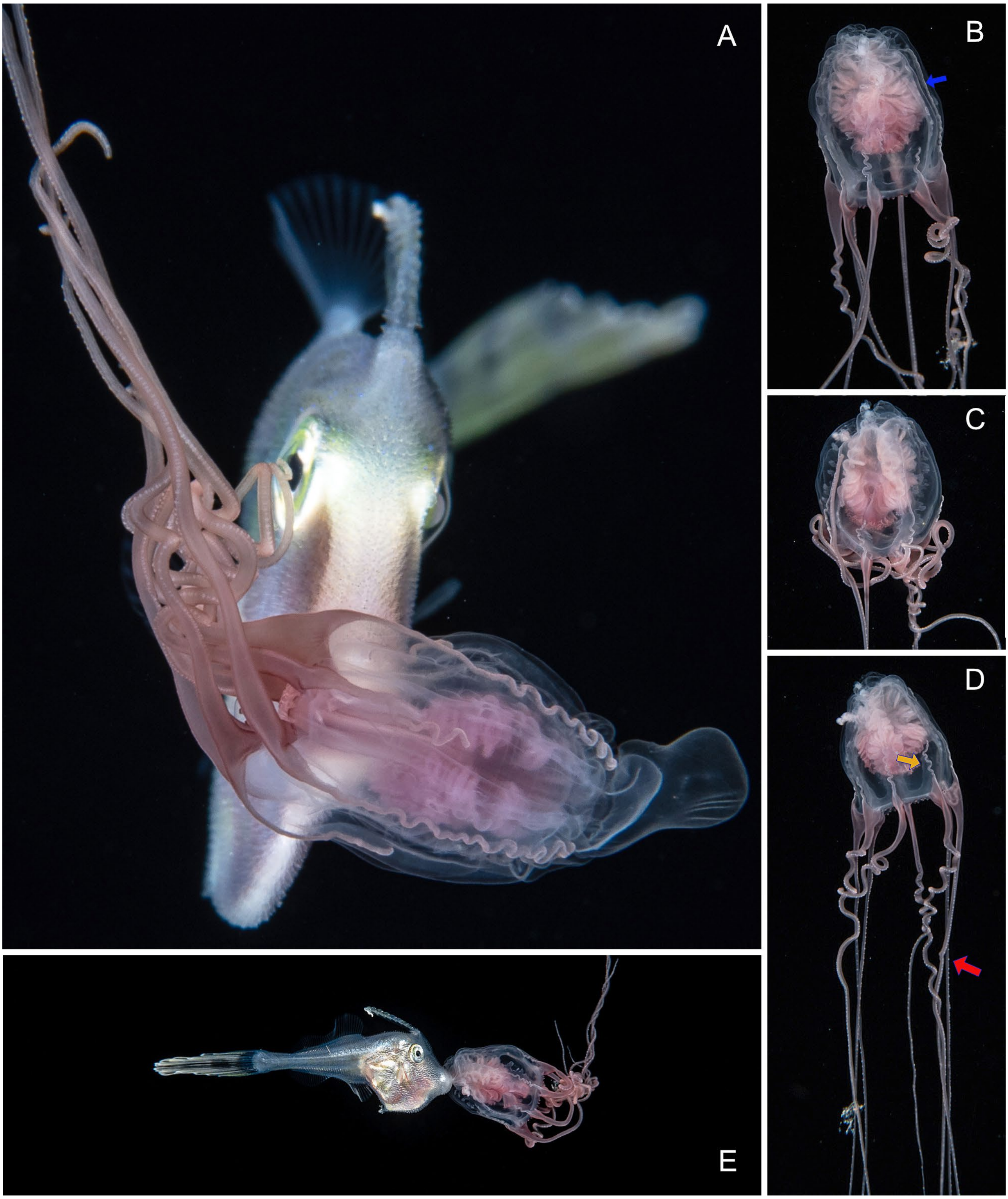

Fig. 9. *Eutiara mayeri.* (A) BFLA4482, ca. 10 mm, with juvenile of *Aluterus heudelotii* in the background. (B-E) Specimen photographed 03-Jul-2020, size 15 mm; blue arrow points to exumbrellar ridge, yellow arrow points to incomplete, centripetal radial canal, red arrow points to nematocyst clusters on tentacles. (E) Animal held by juvenile *Aluterus heudelotii.* Photos by Deb Devers.

jagged. With four or more tentacles, these arising from elongated bulbs, laterally compressed; small bulbs or growth arrested tentacles often present. With ocelli.

Hydroids colonial, arising from creeping stolons; hydrocauli covered by perisarc, not or only sparingly branched, stems monosiphonic. Perisarc extends onto hydranth body as a gelatinous pseudohydrotheca which does not envelop the tentacles. Hydranths with a conical hypostome and one whorl of filiform tentacles. Gonophores develop on cauli or stolons, liberated as medusae.

Leuckartiara adnata Pagès, Gili & Bouillon, 1992

Fig. 10A-D

Leuckartiara adnata Pagès, Gili & Bouillon, 1992: 11, fig. 12A-B. – Hosia *et al*., 2008: 108, fig. 3.

Examined material: BFLA4552; 10-May-2021; size: 10 mm; few tentacles preserved in ethanol for DNA extraction, 16S sequence OQ975700, COI sequence OQ975015; rest of specimen preserved in 4% formalin and deposited in FMNH as voucher UF-015258.

Description: Pandeid medusa 10 mm high; deep, bell-shaped umbrella. Apical process present, relatively small and thin, pointed. Manubrium spanning somewhat more than one third the height of subumbrella, composed of a wide upper stomach region and a smaller, funnel-shaped mouth region (Fig. 10C). Stomach region cubical, upper rim square-shaped, attached to top of subumbrella (Fig. 10C), corners with flap-like protrusions that are connected along the upper half of the radial canals, creating thus large mesenteries. Mouth part of manubrium cross-shaped in section, mouth opening also cruciform, mouth margin drawn out into four perradial lips, not much folded and rather straight. Gonads visible only on the perradial protrusions of the stomach (mesenteries) and not on interradial sides of the stomach, folds oblique, unbranched, sloping in direction of mouth towards the interradii. Four broad radial canals, rim in upper part sinusoid and following the gonad folds, folds becoming small towards junction with circular canal (Fig. 10C). About 21 long, evenly tapering tentacles, base laterally compressed and clasping bell margin, red abaxial ocellus near abaxial end. Between tentacles one or two bulb-like rudimentary tentacles without ocelli. From the bell margin arise about 40 opaque, exumbrellar, meridional ridges, reaching up to upper part of umbrella, lengths variable, some reaching apical process. The ridges are likely nematocyst tracks. The ridges originate from the rudimentary bulbs and the abaxial sides of some of the tentacles, but not all tentacles have them. Some ridges apparently not originating from bulbs or tentacles, these rather short (Fig. 10D).

Mostly colourless, subumbrella with a green hue.

16S Data: The obtained 16S sequence clustered within a subclade of the Pandeidae (Fig. 5) that also contains other *Leuckartiara* species and *Pandea conica*, but otherwise no significantly supported relationships are evident.

Distribution: Off West coast of South Africa, 0-70 m (Pagès *et al*., 1992), central North-Atlantic, 2500 m (Hosia *et al*., 2008), off Florida (this study). Type locality: Off West coast of South Africa, WGS84 -34.5167, 18.0333 [there is likely an error in original publication as Lat. & Long. appear inverted] depth 0-70 m.

Remarks: This is a very rare species and the present observation is a new record for the western Atlantic. A juvenile specimen has been found in the central North Atlantic. Our specimen is somewhat less developed than the type specimens, but doubtlessly the same species. According to the original description by Pagès *et al*. (1992), the specific epithet refers to "adnate rudimentary tentacles" that are continued as ridges on the exumbrella. This must be a misinterpretation as we see these ridges as nematocyst tracks originating from rudimentary tentacles or normal tentacles. Such ridges or nematocyst tracks are also well known in many other pandeids, e. g. *Annatiara affinis* (Hartlaub, 1914), *Eutiara mayeri* Bigelow, 1918, *Leuckartiara gardineri* Browne, 1916, *Merga costata* (Bouillon, 1980), *Neoturris papua* (Lesson, 1843) or *Pandea conica* (Quoy & Gaimard, 1827). The figure of a juvenile specimens in Hosia *et al*. (2008: fig. 2) illustrates well the development of these nematocyst tracks in *L. adnata*.

The gonad of this species is not typical for the genus (comp. next species), but the 16S results do not exclude a relationship with species of the genus (Fig. 5).

Leuckartiara sp.

Fig. 11A-D

Examined material: BFLA4771; 18-Feb-2022; size: 8 x 4.5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975721. – 1 animal photographed 27-Nov-2017; size 6 mm (?); not collected.

Description: *Leuckartiara* species, up to 8 mm in height, 4.5 mm wide, bell-shaped umbrella with distinct but rather short apical projection. Manubrium size variable, filling half or more the volume of the subumbrella, mouth rim complexly folded. Mature animals, gonads on stomach, typical for the genus, 4-5 horizontal folds in adradial position, each fold branched once, diverging from interradial to adradial, the two vertical rows of folds connected interradially by a transverse fold in upper part of the stomach. Four broad radial canals, margin smooth, canals connected to stomach via mesenteries. Four long, evenly tapering,

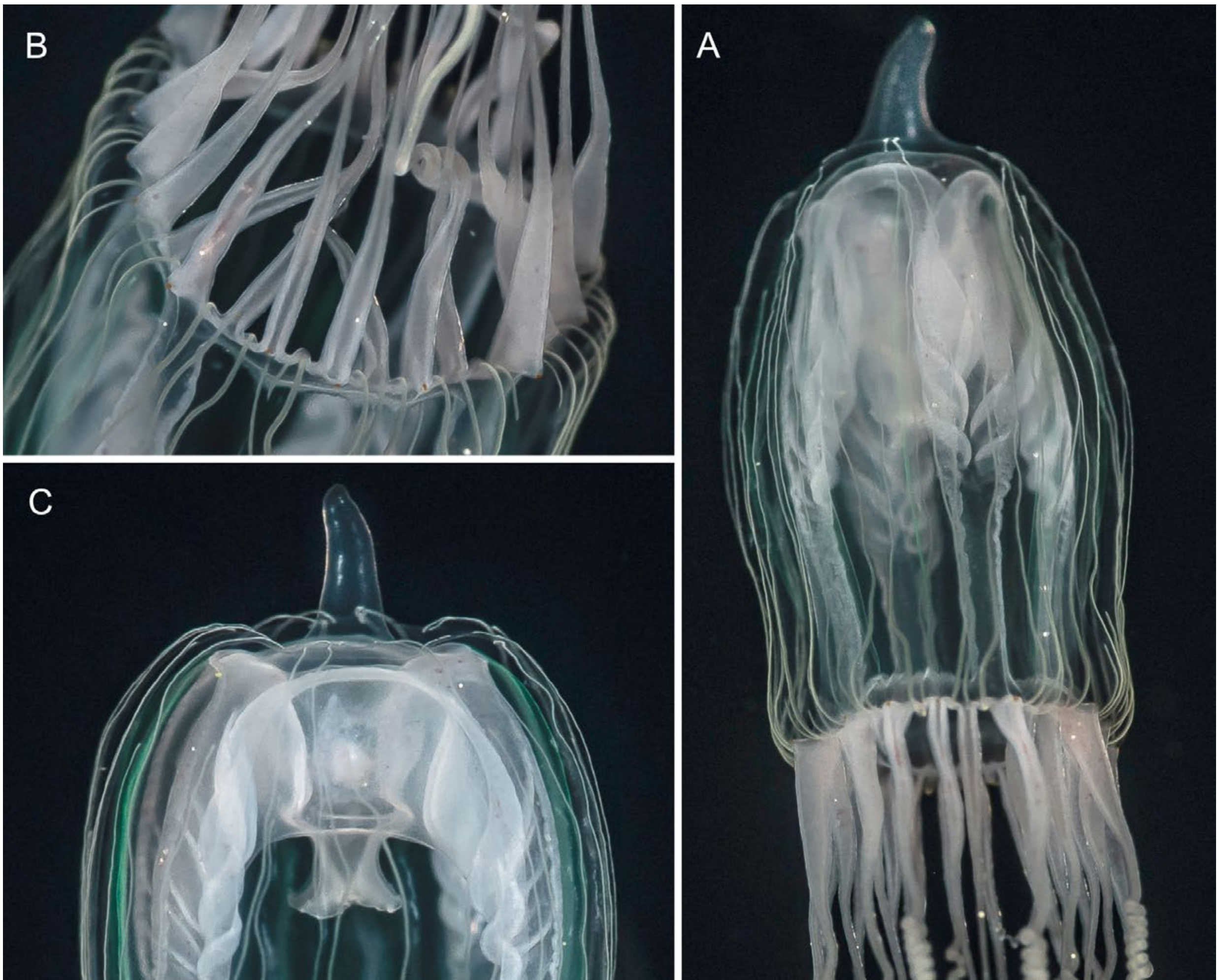

Fig. 10. *Leuckartiara adnata* BFLA4552, height 10 mm. (A) Lateral view of entire animal. (B) Oblique view on bell opening from oral side. (C) Lateral view of bell. (D) Oblique view on bell opening from aboral. Photos by Andrea Whitaker.

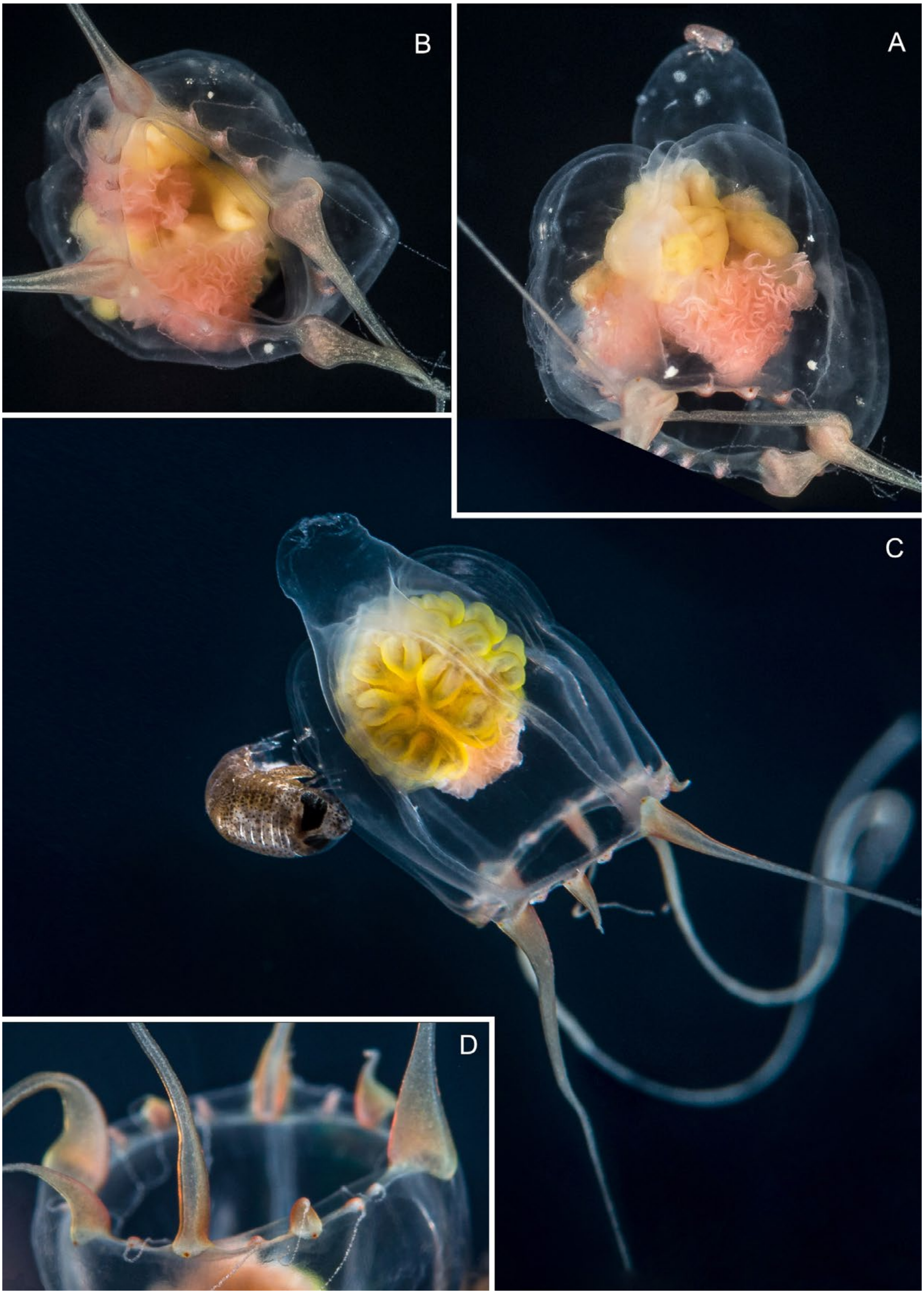

Fig. 11. *Leuckartiara* sp. (A-B) BFLA4771, size 8 mm, somewhat contracted. (A) Lateral view. (B) Oral view, note interradial and adradial bulbs with thin tentacles. (C-D) Animal photographed 27-Nov-2017; size about 6 mm. (C) Lateral view, with hyperiid amphipod on exumbrella. (D) Oblique oral view, note adradial bulbs with thin tentacles, interradial tentacles are larger than adradial ones. Photos by Andrea Whitaker.

perradial tentacles, base laterally compressed and clasping bell margin, no abaxial spur, large red abaxial ocellus near abaxial end. Three to four small bulbs on bell margin alternating with the perradial tentacles, each with a red abaxial ocellus and a thin, long tentacle originating in middle of the bulb, resembling a cirrus but diameter widening gradually at junction with bulb (Fig. 11B). In the second specimen, the interradial bulbs and their tentacles are larger and look like developing normal tentacles. (Fig. 11D). Conspicuously coloured: oral part of manubrium pink, gonad region intensively yellow (Fig. 11A-C), tentacle bases faint brown-red.

Remarks: When observing this species in nature, it can easily be mistaken for *Cirrhitiara superba* due to the similar colouration (comp. Fig. 7A). However, upon closer examination it is evident that the fine tentacles (tentaculae) are unlike the lateral cirri in *Cirrhitiara superba*. They arise medially from the bulbs and their base is enlarged and then tapering towards distal. They are thus like very thin, but normal tentacles. Cirri in pandeids are isodiametric (comp. Fig. 8E). Another important difference is the colour of the gonad. In the present species it is intensively yellow, while in *Cirrhitiara superba* only the gastric wall may be yellow (comp. Figs 7-8). The 16S data also show that the two are distinct (Fig. 5).

The species is not unambiguously attributable to a nominal species of *Leuckartiara* and likely belongs to an unnamed species. The taxonomically important differences to similar *Leuckartiara* species possessing tentaculae are listed in the following.

Leuckartiara acuta Brinckmann-Voss, Arai & Nagasawa, 2005: size is slightly smaller (max. 4.8 mm), four perradial tentacles not laterally compressed and with abaxial spurs, fine tracks of exumbrellar nematocysts originating from all bulbs, occurs only in NE Pacific (Brinckmann-Voss, Arai & Nagasawa, 2005).

Leuckartiara annexa Kramp, 1957: larger (up to 11 mm), lacks apical projection, four perradial and four interradial tentacles of same size, tentaculae unique as without bulbs, basal part adnate on exumbrella for quite a long stretch and then becoming free, distribution Indo-Pacific Ocean (Kramp, 1957).

Leuckartiara eckerti Bouillon, 1985: total height up to 12 mm, overall colour red-orange, gonads rose, two opposite perradial tentacles fully formed, other perradial pair very small (may be age related), between perradial tentacles in each quadrant three rudimentary tentacles lacking basal swelling, distribution in tropical western Pacific Ocean (Bouillon, 1985 and pers. com. Linda Ianniello).

Leuckartiara brownei Larson & Harbison, 1990: small apical projection, four perradial tentacles not laterally compressed, no ocelli, seven reduced tentacles per quadrant, gonads orange-brown, tentacles pink-orange, distribution mainly in cold Antarctic water, but also reported from Mediterranean (Schuchert, 2007).

Leuckartiara foersteri Arai & Brinckmann-Voss, 1980: gonads in parallel and mostly unbranched folds sloping downwards at 45°, colour of gonad with centre fold reddish becoming lighter and more orange towards the sides of the gonad ridges, 2-8 adradial tentacles, these larger than in present material (Arai & Brinckmann-Voss, 1980).

Leuckartiara hoepplii Hsu, 1928: up to 15 mm in total height, interradial tentacles similarly developed as perradial ones, all large tentacles lacking ocelli, per quadrant 6 median cirri on small bulbs (Kramp, 1968).

Leuckartiara gardineri Browne, 1916: conical apex without demarcated apical process, four perradial exumbrellar nematocysts ridges (Kramp, 1968).

Leuckartiara neustona Xu & Huang, 2004: bell 3 mm, lacking apical process, four perradial tentacles with distinct abaxial spurs, two adradial tentaculae per quadrant lacking bulbs and ocelli, in total four interradial club-shaped bulbs with ocelli but no tentacles (Xu & Huang, 2004).

Leuckartiara nobilis Hartlaub, 1914: 8 to 23 fully developed tentacles, many smaller tentacles of different size but these only less developed and not as in current species (Schuchert, 2007).

Leuckartiara zhangraotingae Xu & Huang, 2006: very large apical process, four perradial tentacles lacking ocelli, five tentaculae with ocelli.

The present material does not fit any of these nominal species, while differences are often small or potentially related to different ages. The morphological variability of many nominal *Leuckartiara* species is unknown as they are often only known from a few specimens.

We are convinced that the present material belongs to an undescribed species, but it is difficult to diagnose it solely based on morphological data, while 16S data are not available for most of the other *Leuckartiara* species. It is the opinion of the authors that for establishing new *Leuckartiara* species, like in many other species-rich genera, the use of genetic data is essential. We therefore did not assign this material to a new species. Moreover, the only collected specimen was used for the DNA extraction, which yielded little and only degraded DNA. The conditions for an acceptable type species are not met. We prefer to wait with naming this species until we know more about its variability and until we have more appropriate type material to deposit.

Genus *Pandeopsis* Kramp, 1959

Diagnosis: Pandeid medusae with wide, large manubrium and quadratic base, with long mesenteries;

gonads smooth, sheet-like, covering interradial surface of manubrium, usually with a few dark spots in living or recently fixed specimens; mouth with four simple lips; up to 16 marginal tentacles and up to 24 rudimentary bulbs that may have a very short tentacle stump; tentacular cirri absent; tentacle bulbs without spur, with abaxial ocelli.

Hydroid known only from rearing; colony with common hydrorhiza giving numerous hydranths with one whorl of 3-6 filiform tentacles; medusa buds unknown.

Pandeopsis cf. *ikarii* (Uchida, 1927)

Fig. 12

Pandeopsis ikarii. – Schuchert & Collins, 2021: 249, fig. 7A-C, synonymy, description.

Examined material: BFLA4609; 21-Jul-2021; size 6 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975710, COI sequence OQ975020.

Description: As given in Schuchert & Collins (2021), but three rudimentary bulbs per quadrant instead of one, stomach with red-brown spots (Fig. 12). Medusa buds absent.

DNA Data: The new 16S sequence OQ975710 is rather different from the previously published ones (Fig. 5, GenBank entries MG136757 and MW528673, p-distances 5.0-6.4%), but even more from *P. prolifera* (MW528727 and MW528695, p-distances 7.7-8.9%). For the COI marker, the p-distances were still higher, 9.2% for MG136812 (Japanese sample) and 12.5% for the type specimen of *P. prolifera* (BFLA4442, COI sequence OQ975005).

Remarks: The present sample differs from typical *P. ikarii* in having three rudimentary bulbs alternating with the tentacles (Fig. 12). The number of rudimentary bulbs was given in Schuchert & Collins (2021) as one of the important traits to distinguish *P. ikarii* from *P. prolifera.* The 16S divergence was also unexpectedly high (Fig. 5 and above), but the divergence to *P. prolifera* was even higher. In the ML tree (Fig. 5), the sample BFLA4609 clustered with *P. ikarii*, but with a bootstrap support inferior to 70% (65%). It is also noteworthy that branch lengths within the genus *Pandeopsis* are longer than in other pandeids, which may explain the high divergence values.

Concerning the number of rudimentary bulbs alternating with the tentacles: while one seems to be the usual number (Uchida, 1927; Kramp, 1968), also in Japanese animals there may occasionally be 2 or 3 (see figure 1 in Kubota *et al*., 2011).

The somewhat intermediate position of the BFLA4609 sample between *P. ikarii* and *P. prolifera* questions the validity of the latter nominal species to some degree. The alternative explanation that there are three different species involved appears less plausible. At this stage we cannot draw any definitive conclusions. Considerably more *Pandeopsis* samples must be analysed, preferably using a population genetic approach including nuclear markers.

Fig. 12. *Pandeopsis* cf. *ikarii* BFLA4609, size 6 mm. Note the three rudimentary bulbs alternating with the marginal tentacles.

Pandeopsis prolifera Schuchert & Collins, 2021

Fig. 13

Pandeopsis prolifera Schuchert & Collins, 2021: 252, fig. 9A-E.

Examined material: BFLA4808; 02-Jun-2022; size 6 mm; preserved in ethanol for DNA extraction, 16S sequence identical to MW528727 (= Holotype, BFLA4442).

Description: As given in Schuchert & Collins (2021), but 7 tentacles only, one interradial missing, examination of preserved material confirmed the presence of a few medusa buds on the stomach wall (yellow arrow in Fig. 13).

16S Data: The 16S sequence of the present sample was identical to the one obtained from the holotype (MW528727, Fig. 5).

Remarks: See discussion under *P.* cf. *ikarii* above.

Fig. 13. *Pandeopsis prolifera* BFLA4808, size 6 mm. The yellow arrow points to medusa bud (not well visible), the red arrow points to three rudimentary bulbs alternating with the marginal tentacles, the blue arrow points to a damaged part of bell.

Family Proboscidactylidae Hand & Hendrickson, 1950

Genus *Proboscidactyla* Brandt, 1835

Diagnosis: Medusa umbrella mostly hemispherical; with exumbrellar nematocyst patches or linear arrays of patches alternating with tentacles; radial canals branched; usually instead of circular canal a solid gastrodermal marginal strand; manubrium base with four, six or more radial gastric pouches, extending along proximal portions of radial canals, pouches in some species inconspicuous; gonads surrounding manubrium and extending onto gastric pouches; tentacles with swollen hollow base connected to the lumen of radial canals.

Hydroid on rims of sabellid polychaete tubes, with creeping, naked stolons; hydranths almost sessile, polymorphic; gastrozooid with rounded hypostome, separated from body by a constriction; hypostome with large pad of nematocysts somewhat displaced onto one side, two filiform tentacles arising close together beneath hypostomial constriction, opposite to nematocyst cluster; gonozooids and dactylozooids without tentacles, mouthless and smaller than gastrozooids; medusa buds close to gonozooid tip.

Proboscidactyla ornata (McCrady, 1859)

Fig. 14A-B

Proboscidactyla ornata. – Schuchert & Collins, 2021: 261, fig. 14A-G.

Examined material: BFLA4491; 17-Sep-2020; size 4 mm; preserved in formalin and deposited in FMNH as UF-015211. – 1 specimen; photographed 10-Mar-2022; size 4 mm; not collected. – 1 specimen observed 08-Dec-2021; size 5 mm; not collected.

Description: Specimens as described in Schuchert & Collins (2021), except for specimen seen 10-Mar-2022 which was a male with fully developed gonads (Fig. 14). In contrast to the other specimens, it had its exumbrellar nematocyst patches confined to a band near the bell margin and not all over the bell.

Distribution: See Schuchert & Collins (2021).

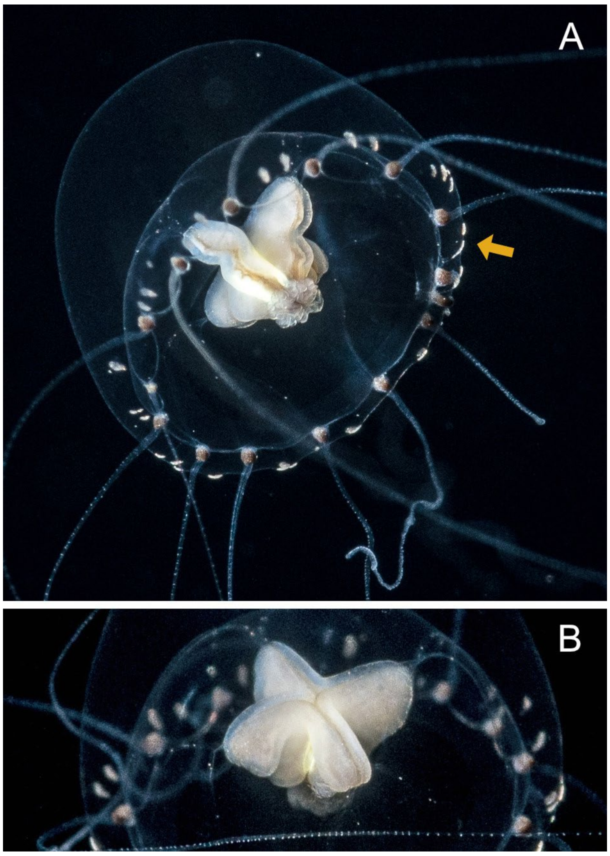

Fig. 14. *Proboscidactyla ornata,* photographed 10-Mar-2022, size 4 mm. (A) Oblique oral view; yellow arrow points to exumbrellar nematocyst patches. (B) Aboral view of manubrium with fully developed male gonads. Photos by Andrea Whitaker.

Remarks: We interpreted the reduced number of exumbrellar nematocyst patches in the mature animal shown in Fig. 14 as an age-related effect.

Family Ptilocodiidae Coward, 1909
Genus *Thecocodium* Bouillon, 1967

Diagnosis: Medusa with lobed bell margin, with marginal nematocyst ring from which usually arise several exumbrellar centripetal nematocyst bands or rows of refringent spots. Four radial canals and hollow circular canal, short mesenteries. Four marginal tentacles with bases embedded in umbrellar furrows, no ocelli. Manubrium with short, perradial lips ending in nematocyst clusters; gonads interradial on manubrium.

Hydroid with reticulate, tubular hydrorhiza, covered by perisarc. Polyps on stolons, sessile, naked, polymorphic, usually with gastro-gonozooids and dactylozooids. Gastro-gonozooids cylindrical or club-shaped, without tentacles, hypostome with nematocysts. Dactylozooids thin, solid gastrodermis, terminal group of capitate tentacles. Gonophores fixed sporosacs or free medusae developing in a single whorl on gonozooids. Cnidome of polyp includes desmonemes.

Thecocodium quadratum (Werner, 1965)

Thecocodium quadratum. – Schuchert & Collins, 2021: 259, fig. 13A-B.

Examined material: BFLA4578; 03-Jul-2021; size 4 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975706, COI sequence OQ975018. – **BFLA4580**; 03-Jul-2021; size 8 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975707, COI sequence identical to OQ975018. – **BFLA4584**; 03-Jul-2021; size 4 mm; preserved in formalin, deposited in FMNH as UF-015275 – **BFLA4812**; 02-Jun-2022; size 4 mm; preserved in ethanol for DNA extraction, deposited in FMNH as UF-016277.

Description: As in Schuchert & Collins (2021).

Sequence Data: Two new 16S haplotypes were found in the present set, although they only differed minimally. The p-distances between samples from Florida were 0.2 to 0.5%, those to the type (GenBank FN422379) 4.3 to 5.2%, thus comparable to the data in Schuchert & Collins (2021: table 1).

A few COI sequences could also be obtained for this study (see above and for sample BFLA4461: GenBank OQ975007). These showed unexpected high divergences of 10.9 to 11.2% (p-distance) to the one obtained from the type specimen (GenBank KT981908).

Distribution: See Schuchert & Collins (2021).

Remarks: Although the morphotype found in Florida seems to be very widely distributed (comp. record from Taiwan in Kubota *et al*., 2018), the considerable divergences to the type specimen seen in the 16S sequences and particularly in the COI sequences, argue in favour of two separate species being involved.

The specimens from Florida differed from the type material (Jarms, 1987) in having a slightly higher umbrella and many more exumbrellar nematocysts clusters. These are arguably rather weak differences, usually relegated to intraspecific variation.

More 16S sequences from the Indian Ocean combined with nuclear markers are needed to justify and substantiate a formal introduction of a new name.

Suborder Capitata
Family Sphaerocorynidae Prévot, 1959
Genus *Euphysilla* Kramp, 1955

Diagnosis: Medusa with pear- to egg-shaped umbrella in life; with apical chamber; manubrium with quadratic base; mouth circular; four equally developed tentacles with adaxial or abaxial nematocyst clasps and a terminal nematocyst knob; no gastric peduncle; mature gonads circular, surrounding manubrium; no ocelli. Usually with groups of medusa buds in middle part of manubrium.

Hydroid like for genus *Sphaerocoryne* (Schuchert & Collins, 2021; Maggioni *et al*., 2021).

Euphysilla pyramidata Kramp, 1955
Fig. 15A-B

Euphysilla pyramidata Kramp, 1955: 245, pl. 1 fig. 1, pl. 2 fig. 3. – Schuchert & Collins, 2021: 265, fig. 17A-I. – Maggioni *et al*., 2021: 504, fig. 4A-L

Examined material: BFLA4759; 21-Jan-2022; size 2 mm; preserved in ethanol for DNA extraction; deposited in FMNH as UF-016248. – 1 specimen photographed 15-May-2022; size 3 mm; not collected.

Description: As in Schuchert & Collins (2021). One specimen (BFLA4759) had a very shallow apical projection and an apical chamber was not visible.

Remarks: The shallow apical process observed in one sample (Fig. 15A) approaches it to populations observed in the Pacific Ocean (see discussion in Schuchert & Collins, 2021). For the polyp stage see Maggioni *et al*. (2021).

Family Zancleidae Russell, 1953
Genus *Zanclea* Gegenbaur, 1857

Diagnosis: Newly liberated medusae with two opposite tentacles, umbrella bell-shaped, four perradial exumbrellar perradial nematocyst patches or tracts containing stenoteles; four radial canals; with two or four marginal tentacles when fully grown, tentacles with numerous abaxial extensile cnidophores containing

Fig. 15. *Euphysilla pyramidata,* BFLA4759, bell size 2 mm. (A) Lateral view. (B) Oblique view on aboral side.

macrobasic euryteles; mouth simple, circular; gonads inter-radial; no ocelli. Medusoids, if present, without tentacles or mouth, but usually with perradial exumbrellar nematocyst patches.

Hydroid stage colonial, with stolonal hydrorhiza, polyps sessile or with pedicels, these usually unbranched, polyps monomorphic or polymorphic, when polymorphic polyps may be differentiated into gastrozooids, gonozooids, and dactylozooids; gastrozooids elongated, cylindrical or claviform, always with capitate tentacles, tentacles usually numerous and scattered over body, in some species reduced to a few or a single tentacle; gonozooids and dactylozooids, when present, resembling reduced gastrozooids. Gonophores liberated as free medusae or rarely as medusoids. Cnidome includes stenoteles and macrobasic euryteles, the latter type may be absent in the polyp stage.

Remarks: A genus once erroneously thought monospecific (Calder, 1988), recent morphological and genetic work show that *Zanclea* comprises an astonishing number of species, many of them morphologically indistinguishable (see references in Schuchert & Collins, 2021 and Maggioni *et al.*, 2018, 2020a, b).

16S data: Our new *Zanclea* 16S sequences were combined with *Zanclea* sequences currently available in GenBank (excluding EU305488, *Zanclea prolifera* due to its long branch divergence) to obtain a maximum likelihood phylogenetic tree (Fig. 16). It is evident that there are at least four distinct species of *Zanclea* in the region.

Zanclea mayeri Schuchert & Collins, 2021

Fig. 17A-C

Zanclea mayeri Schuchert & Collins, 2021: 268, figs 18A-E, 19A-H.

Deposited material: BFLA4650; 05-Sep-2021; size 7.5 mm, presumable male; preserved in 4% formalin, deposited in FMNH as UF-016194. – **BFLA4651**; 05-Sep-2021; size 5 mm, presumable male; preserved in ethanol for DNA extraction, deposited in FMNH as UF-016195. – **BFLA4652**; 05-Sep-2021; size 6.5 mm, female; preserved in 4% formalin, deposited in FMNH as UF-016196. – **BFLA4653**; 05-Sep-2021; size 7 mm; preserved in 4% formalin, deposited in FMNH as UF-016197. – **BFLA4654**; 05-Sep-2021; size 7 mm, presumable male; preserved in ethanol for DNA extraction, deposited in FMNH as UF-016198.

Remarks: See Schuchert & Collins (2021) for the description and other details. For this study, no new DNA sequence data could be determined for *Zanclea mayeri.* The species was thus distinguished from *Z.* cf. *migottoi* and *Zanclea* sp. solely based on its size (5 to 7.5 mm mature), the other two being much smaller.

Zanclea cf. *migottoi* Galea, 2008

Fig. 18A-E

Zanclea costata. – Migotto, 1996: 20, fig. 5A-C. [not *Zanclea costata* Gegenbaur, 1857]

Zanclea cf. *alba*. – Vervoort, 2006: 200, fig. 1A, B, 2.1-2.3. [not *Zanclea alba* sensu Calder, 1988]

Zanclea migottoi Galea, 2008: 14, fig. 3J-L. – Mendoza-Becerril *et al*., 2018: 129. – Mendonça *et al.*, 2022: 8, fig. 3D-F.

Examined material: BFLA4595; 10-Jul-2021; size 1-1.5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975708. – **BFLA4814**; 02-Jun-2022; size 1 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975722, COI sequence OQ975023.

Photos using blue light: See legend of Fig. 19, these specimens were not collected.

Description (collected specimens): Small *Zanclea* medusa with bell height of 1 to 1.5 mm when mature,

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Note added in proof: *Zanclea mayeri* has recently been placed in a new genus as *Apatizanclea mayeri* by Maggioni *et al.* (2023, Systematics and character evolution of capitate hydrozoans. Cladistics, DOI: 10.1111/cla.12567)

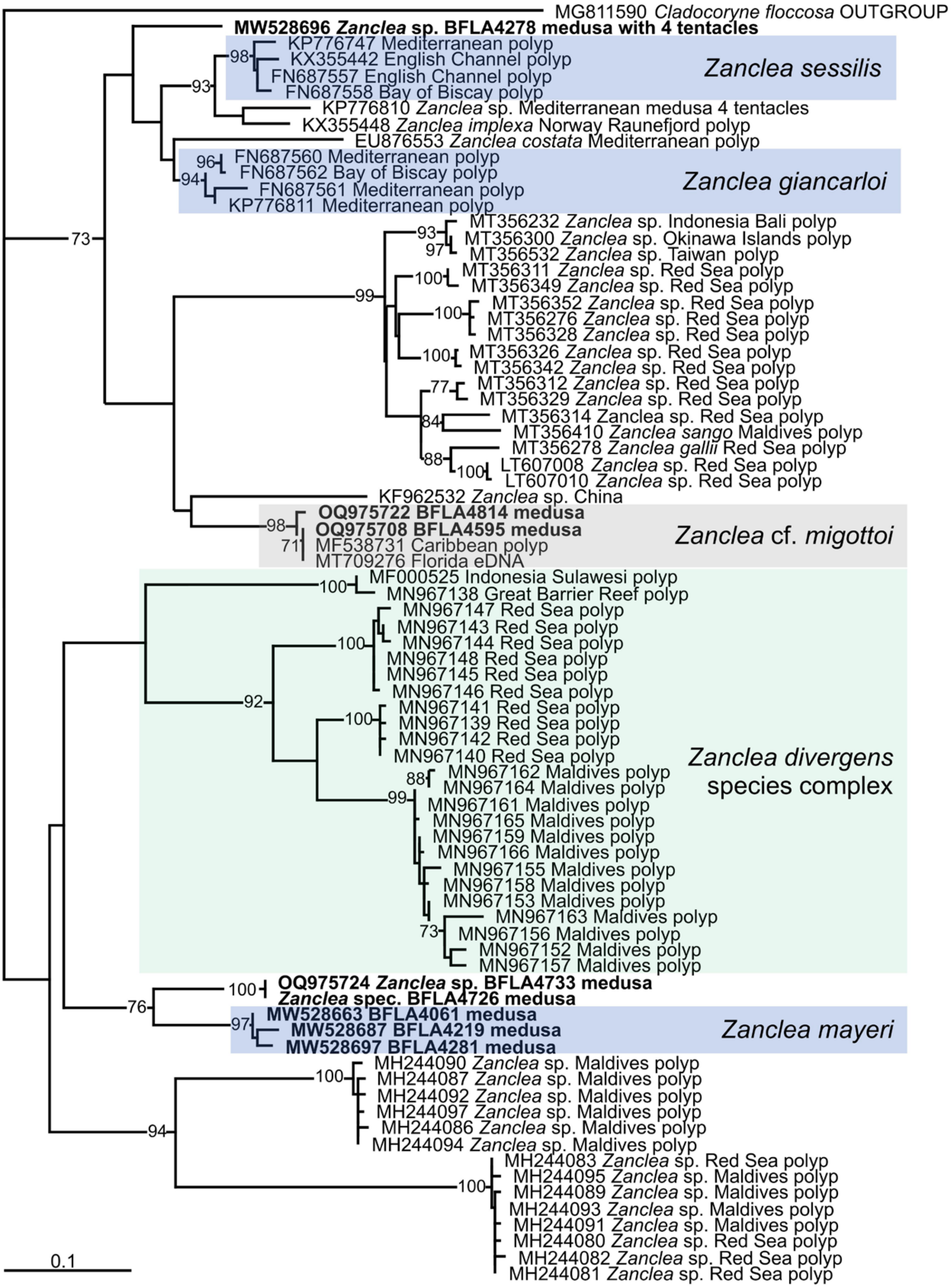


Fig. 16. Maximum likelihood phylogenetic tree of *Zanclea* species obtained with PhyML (GTR+I+G model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Bold labels are sequences from the current study and Schuchert & Collins (2021). Species clades of well-established nominal species are highlighted by a blue background, the *Z. divergens* species complex by a green one, *Zanclea* cf. *migottoi* by a grey one.

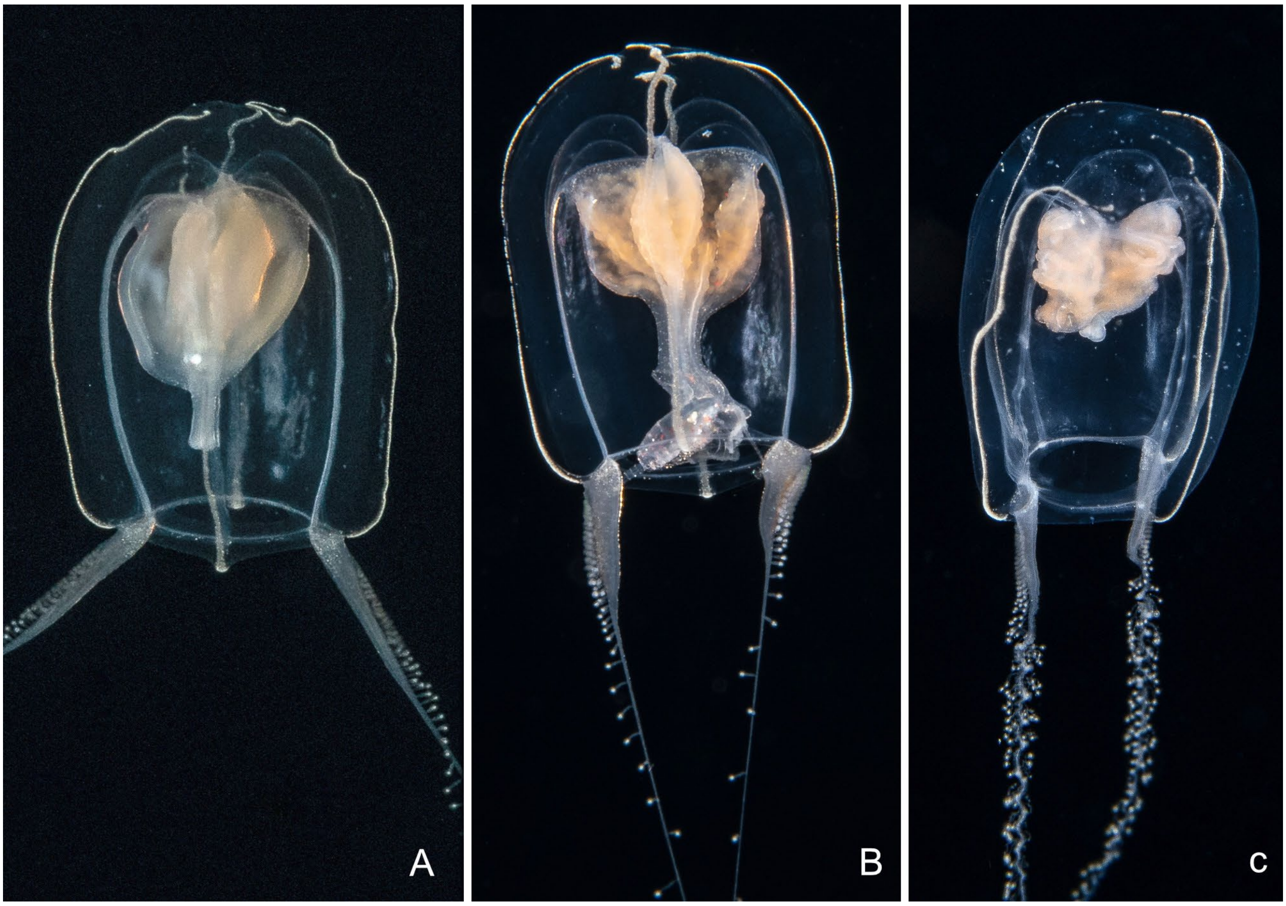


Fig. 17. *Zanclea mayeri.* (A) BFLA4651, size 5 mm, presumably a male. (B) BFLA4652, female, size 6.5 mm. (C) BFLA4654, presumably a male, size 7 mm. Photos by Andrea Whittaker, Linda Ianniello, and Deb Devers.

mesogloea moderately thick, thickness uniform. Top of subumbrella with very small interradial pockets. Exumbrella with four perradial exumbrellar nematocyst tracks arising from bell margin and reaching to upper part of bell but not meeting at apex as in *Z. mayeri* (Fig. 18A-D). Manubrium shaped like inverted bottle, base somewhat cruciform in section, oral part tubular. Gonads surrounding manubrium wall, eggs relatively large (Fig. 18B-D). One pair of marginal bulbs only, tapering into tentacles bearing the typical cnidophores, tentacles extensible to length at least 10 times the bell height. Perradial sites with tentacles alternating with ones lacking bulbs. Manubrium and tentacle base reddish, a useful character to identify it in the water.

Fluorescence observations: The medusa examined under UV light and tentatively assigned to this species showed a strong autofluorescence (Fig. 19A-E). The fluorescence was particularly strong at the top of the manubrium, the gastrodermal part of the marginal bulbs, the lower parts of the radial canal, and the circular canal. The regions of strongest intensity of the fluorescence become better visible if white light is added (Fig. 19A-B).

16S data: Two haplotypes were found, differing by 0.8% (p-distance). One of the sequences (OQ975708) had two polymorphic sites (A/G, ambiguity code = R). One of these combinations matched perfectly the sequence MF538731 deposited in GenBank under the name *Zanclea migottoi*.

Distribution: Guadeloupe and Azores (Galea, 2008), Gulf of Mexico (Mendoza-Becerril *et al*., 2018), coast of Brazil (Galea, 2008; Mendonça *et al*., 2022). Type locality: Guadeloupe, Basse-Terre, Petite Anse.

Remarks: The identification of the present specimens is entirely based on the 16S sequences which are almost identical to a sequence in GenBank (MF538731) published by Mendoza-Becerril *et al*. (2018). This sequence was obtained from a hydroid with medusa buds collected in the Gulf of Mexico and at this moment is identified in GenBank as *Zanclea migottoi*. There is also another, very similar 16S sequence in GenBank (MT709276) obtained from environmental DNA and published by Ames *et al.* (2021). Their identification as *Zanclea migottoi* is also based on the match with the sequence of Mendoza-Becerril *et al*. (2018), thus it is not an independent identification based on morphology.

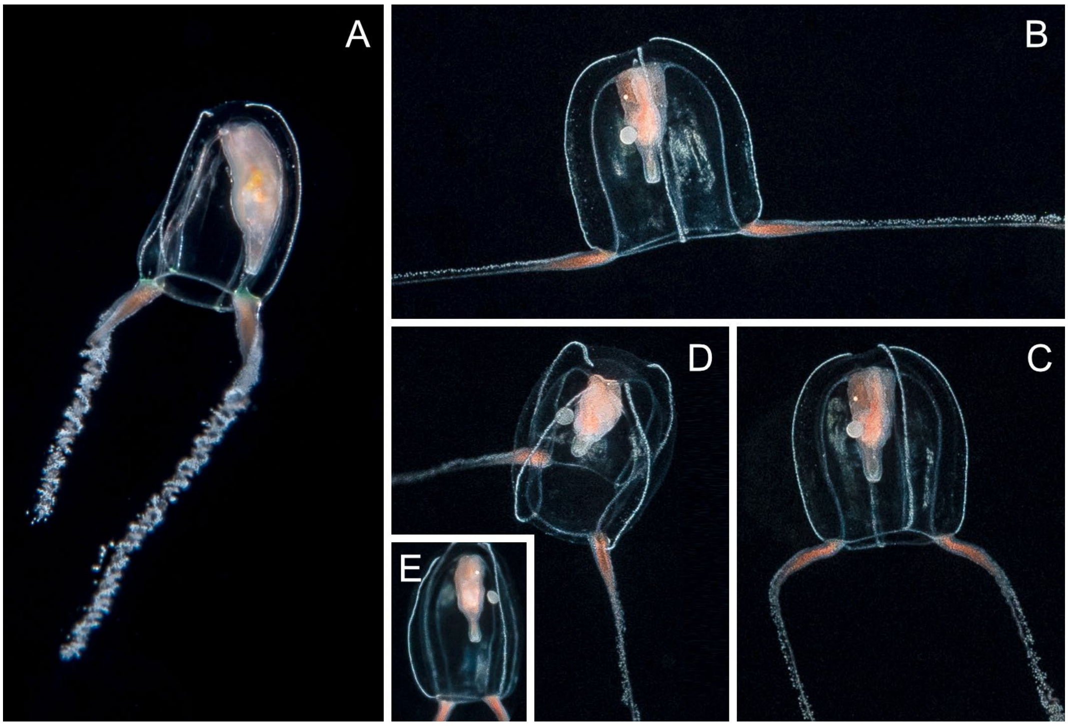


Fig. 18. *Zanclea* cf. *migottoi*. (A) BFLA4814, bell size 1 mm. (B-E) BFLA4595, bell size 1-1.5 mm, the round object on the manubrium was interpreted as an egg, not a medusa bud, in (E) it is seen detached from the manubrium.

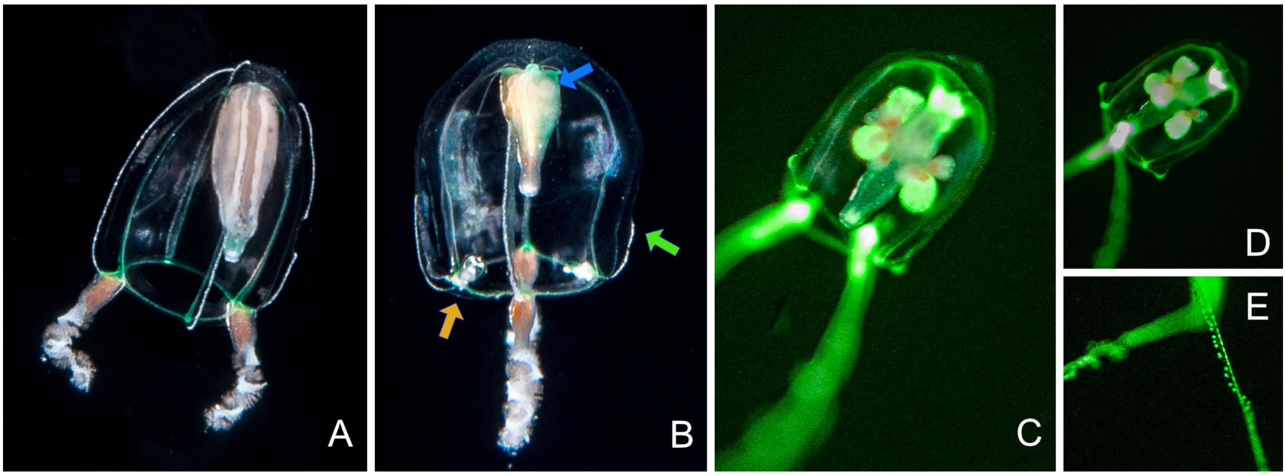


Fig. 19. ? *Zanclea* cf. *migottoi*, all ~2 mm, photographed using a blue light source to stimulate fluorescence and sometimes an additional white light source (see Material and Methods). For the species identification see text. (A) Medusa observed 12-Jun-2022, blue light plus white strobes, no filter. (B) Animal observed 18-Jun-2022, blue light plus white strobes, no filter. The green arrow points to exumbrellar nematocyst track reaching only halfway up the bell; blue arrow points to a presumable egg in the gonad, the yellow arrow indicates a medusa bud on a small, non-tentacular bulb. (C-E) Animal observed 16-Jun-2022; blue light plus yellow filter and blue flash; note the medusa buds on the manubrium, E shows only parts of the tentacles

By using the 16S sequence of Mendoza-Becerril *et al.* (2018) as a reference, both our and Ames' *et al.* (2021) identifications depend on the correct identification of the hydroid by Mendoza-Becerril *et al.* (2018). There are, however, some caveats with the identification of Mendoza-Becerril *et al.* (2018). They collected their hydroid from floating *Sargassum* sp., which is the typical substrate for *Zanclea alba* (Meyen, 1834) (see Calder, 1988, 2013). Subsequently Mendoza-Becerril *et al.* (2020) identified *Zanclea* hydroids from the same region and the same substrate as *Zanclea alba*. *Zanclea migottoi* hydroids differ from *Z. alba* by the possession of macrobasic euryteles, but this was not discussed in these works. The substrate of the type specimen of *Z. migottoi* was given as algae. Dr Maria Mendoza-Becerril was so kind to re-examine the voucher specimen for the sequence MF538731 and she could not find any macrobasic euryteles in the material. Her sample should thus be re-assigned to *Z. alba*, but it cannot be excluded that the macrobasic euryteles had discharged or were otherwise lost during the collection and fixation process. Dr David Maggioni let us know (pers. com.) that he too has found several hydroids attributable morphologically to *Z. migottoi* in the Caribbean and the Indian Ocean. They had macrobasic euryteles – sometimes rather few – and the 16S closely match MF53873 (Maggioni *et al.*, manuscript in preparation), thus supporting the original identification by Mendoza-Becerril *et al.* (2018). This implies that *Z. alba* and *Z. migottoi* are potentially conspecific.

When describing *Z. migottoi,* Galea (2008) could not observe the mature medusa of the material from the type locality. The concept of this species is thus to some degree vague as the presence of macrobasic euryteles alone is not diagnostic, but rather a general feature of the genus. The species appears indistinguishable from *Zanclea implexa* (Alder, 1856) or *Zanclea giancarloi* Boero, Bouillon, & Gravili, 2000 (for recent descriptions see Schuchert, 2010). Identifications of *Z. migottoi* hydroids are thus to some degree arbitrary and it is risky to base molecular identifications on a single, undocumented record.

However, with the present stage of knowledge, we preferred to attribute our medusa to *Zanclea* cf. *migottoi,* with the hope that a dedicated, future study using 16S data will resolve the identity of both *Z. migottoi* and *Z. alba*.

Galea (2008) referred Brazilian hydroids incorrectly identified by Migotto (1996) as *Z. costata* Gegenbaur, 1857 to *Z. migottoi.* Migotto (1996) was able to cultivate medusae released from his hydroid to maturity. His medusae (Migotto, 1996: fig. 5c) were up to 2.5 mm in height, had a slight apical projection, and perradial exumbrellar nematocyst tracks reaching up to the middle of the medusa. They are thus slightly different from the medusae observed by us (Fig. 18). While the size and tentacle number are comparable, ours had longer nematocyst tracks and the shape of the bell is slightly different. The identity of Migotto's (1996) hydroids with our medusa is thus also somewhat questionable, but the morphological differences of the medusae should not be taken as decisive. Cultivated medusae nearly always tend to differ slightly from the ones found in the plankton (unpublished pers. observations).

Some observations made while using a blue light source to stimulate fluorescence deserve being mentioned here, although the specimens were not collected and thus no 16S sequence information is available. We are nevertheless confident that they likely belong to the same species for the following reasons: the size, tentacle number, and nematocyst tracks match; the bulbs were reddish; and they were observed only 10 to 14 days later than specimen BFLA4814. The *Zanclea* sp. treated in the following page appeared only in December and the bell-shape is different.

There is a global fluorescence in the whole medusa (Fig. 19C-E), which is particularly strong at the base of the manubrium, the gastrodermal part of the marginal bulbs, and the circular canal (Fig. 19A-B). Currently, there is only one publication describing species-specific fluorescence pattern in *Zanclea* medusae (Maggioni *et al.*, 2020a). At this stage, any discussions on the differences seem premature as we must first accumulate a set of observation for a larger number of species. However, the animals documented in Fig. 19 are also presenting another intriguing feature. The medusa shown in Fig. 19C-D has medusa buds on the manubrium, the one in Fig. 19B has a medusa bud on one of the tentacle bulbs. At this stage, we cannot say if these buds are a constant feature of the species. It is also not clear if this is a sporadically occurring aberration. In Schuchert & Collins (2021) we described a four-tentacled *Zanclea* with polyps growing out of the manubrium, but which is distinct (see ML tree Fig. 16).

With its medusa buds on the manubrium, the animal is reminiscent of *Zanclea medusopolypata* Boero, Bouillon & Gravili, 2000, a species originally described from Papua New Guinea. *Zanclea medusopolypata* has about the same size (~1 mm), two tentacles, and nematocysts tracks reaching high up the bell. Its diagnostic feature are polyps growing on the side of manubrium, polyps that may also bear medusa buds. Only immature specimens of *Z. medusopolypata* are known. Perhaps the sexually mature do not have the polyps. Interestingly, Boero *et al.* (2000) thought that *Z. medusopolypata* also occurs in the tropical Western Atlantic. They attributed *Zanclea* medusae with polyps described by Rees & Roa (1966, misidentified as *Z. implexa*) from the coast of Venezuela, and by Navas-Pereira (1984, misidentified as *Z. costata*) from Brazil to *Z. medusopolypata.*

Zanclea sp.
Fig. 20A-D

Examined material: BFLA4726; 08-Dec-2021; female, size < 2.5 mm; preserved in ethanol for DNA extraction, 16S sequence same as OQ975724. – **BFLA4733**; 10-Dec-2021; female, size < 4 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975724.

Description: Medusa resembling strongly *Zanclea mayeri* (Fig. 17), but size smaller, 2.5 to 4 mm when mature, mitre-shaped, bell higher than wide (ratio about 3:2), mesogloea of even thickness, only very slightly thicker at apex. Top of subumbrella with very small interradial pockets. Exumbrella with four dense, prominent perradial nematocyst tracks originating from bell margin and reaching to apex, some recurved at apex. Manubrium relatively slender, height about half the subumbrellar height, shaped like an inverted bottle, cross-section only slightly cross-shaped, oral part tubular. Gonads flat pads on interradial parts of manubrium, without folds. Both observed animals female, numerous very small eggs released from gonad but adhering to manubrium (confirmed in preserved animals). One pair of marginal bulbs only, tapering into very extensible tentacles bearing the typical cnidophores. Other perradial sites without bulbs or tentacles. Colours: gastrodermis of manubrium and tentacles brownish-orange, exumbrellar nematocyst track golden.

16S data: The two samples of this study gave identical 16S sequences. The species is obviously a sister species of *Z. mayeri* (Fig. 16), but nevertheless well separated from it. The minimal p-distance divergence between members of the two clades is 5.6%.

Remarks: This *Zanclea* species resembles *Zanclea mayeri,* but the 16S data (Fig. 16) and morphological differences allow us to distinguish them. It is smaller (2.5-4 mm versus 5-7.5 mm bell height when mature), the bell is slenderer and has a more pointed apex, the manubrium is less voluminous and not distinctly cruciform in section (comp. Fig. 17 and Fig. 20). *Zanclea* cf. *migottoi* medusae differ from it in being even smaller (1-1.5 mm), the nematocyst tracks do

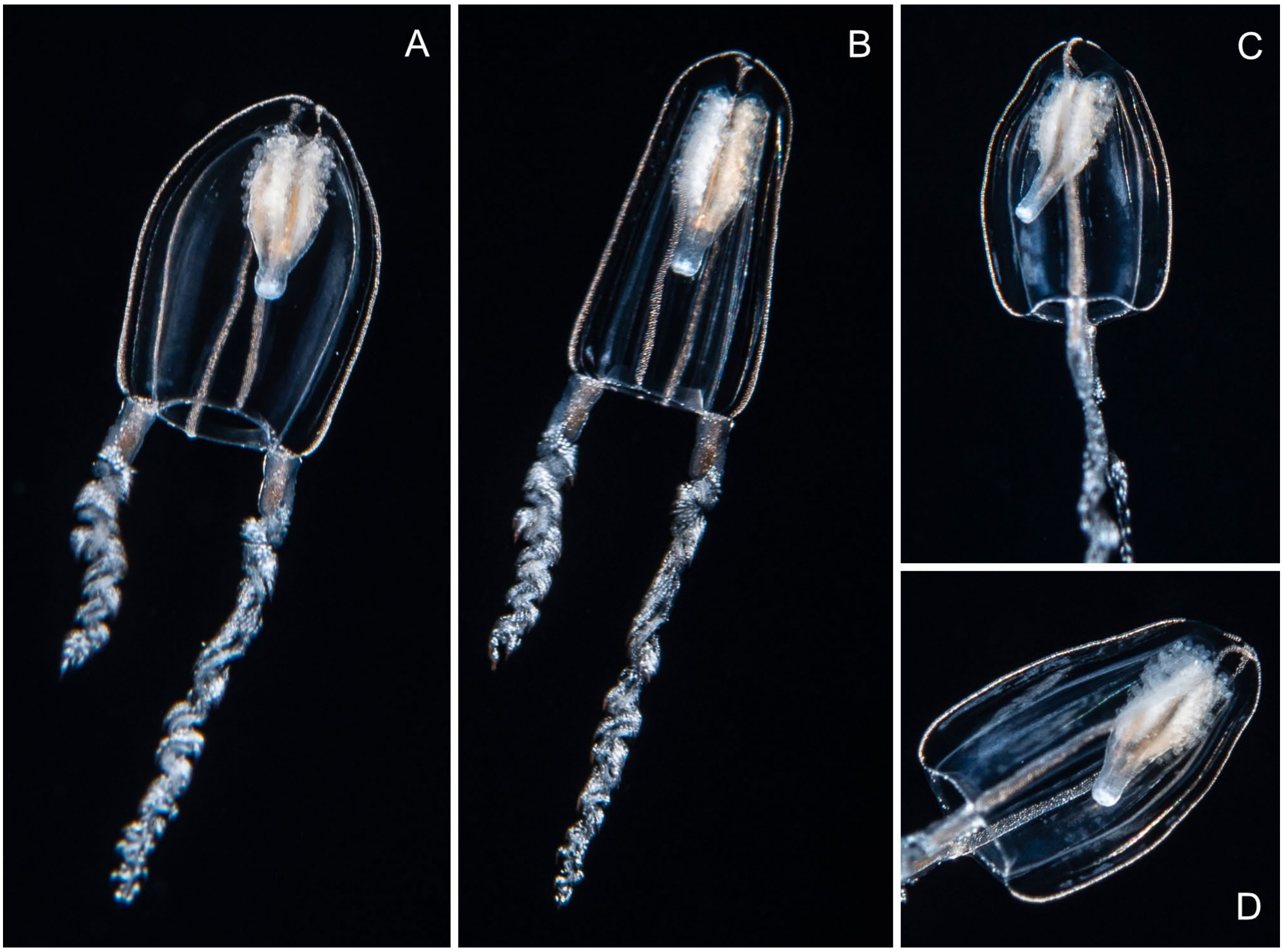


Fig. 20. *Zanclea* sp. Note the liberated small eggs sticking on the manubrium wall. (A-B) BFLA4733, bell size < 4 mm. (B) Bell contracted. (B-D) BFLA4726, bell size < 2.5 mm.

not reach to the apex, the bell apex is flatter, and the manubrium and tentacle bases have a characteristic reddish colour (Fig. 18A-D).

Among the few Zancleidae from other regions that have two tentacles and nematocyst track up to the apex, only *Zanclea medusopolypata* Boero, Bouillon & Gravili, 2000 resembles the present species. The former is a small (1 mm) medusa originally described from Papua New Guinea. It is easily distinguishable through its polyps growing on the side of manubrium, polyps that may also bear medusa buds (see above). The medusa of *Halocoryne frasca* Boero, Bouillon & Gravili, 2000 resembles also the present specimens, but has a flat apex and the cross-section of the bell is somewhat polygonal. Although having a *Zanclea*-like medusa, it was placed in another genus because of its much-reduced polyp stage (Boero *et al*., 2000).

While all observations indicate that this is a new, undescribed species, we prefer not to introduce it here as a new species. Our hesitation is due to the low number of samples we have, and we feel that more details on its growth stages, nematocysts, and its polyp stage are needed to have a better idea of the species. We can also not exclude that *Z. mayeri* is nevertheless morphologically and genetically more variable than previously thought (see comments made in the section "General results and discussion").

Family Zancleopsidae Bouillon, 1978
Genus *Zancleopsis* Hartlaub, 1907

Zancleopsis Hartlaub, 1907: 115, type species *Gemmaria dichotoma* Mayer, 1900 by monotypy.

Cnidotiara Uchida, 1927: 204, type species *Cnidotiara gotoi* Uchida, 1927 by monotypy.

Astrocoryne Maggioni *et al*., 2017: 738, type species *Astrocoryne cabela* Maggioni *et al*., 2017 by monotypy.

Diagnosis: Medusa with or without apical projection; four tentacles, usually two long, opposite tentacles with capitate side branches and two much shorter tentacles, the latter capitate or filiform. Exceptionally also only four equal, short, unbranched capitate tentacles (*Z. gotoi*) or long tentacles without capitate side branches (*Z. oblonga*). On adaxial sides of all tentacles marginal tentacular bulbs clasping umbrella margin, bulbs with large hemispherical adaxial bulges covered with nematocysts. Ocelli on abaxial side of tentacle base. Manubrium flask-shaped; mouth round or cruciform, with or without simple lips; gonads interradial to adradial, smooth with interradial cleft or more adradial pads or vertical folds.

Hydroid stage colonial; hydrocaulus short to moderately long, unbranched, arising from stolons embedded in host sponge; perisarc thin, covering both the hydrorhiza and the hydrocaulus. Hydranth slightly pyriform to cylindrical, with proboscis-like hypostome, tentacles in one or two alternating whorls around broadest part of body, tentacles bicapitate, with a terminal capitulum and a slightly more proximal subterminal nematocyst cluster. Gonophores developing among tentacles and liberated as medusae.

Cnidome includes stenoteles, desmonemes, and heteronemes.

16S data: Our new *Zancleopsis* 16S sequences were combined with those published by Maggioni *et al.* (2021) to generate a Maximum Likelihood tree. As outgroup *Euphysilla pyramidata* was chosen (Fig. 21). The three *Zancleopsis* species observed off Florida separated into three distinct clades, assumed to represent three distinct species (see also Maggioni *et al.*, 2021).

Remarks: The discovery of the polyp stage of three *Zancleopsis* species (Maggioni *et al.*, 2021) and the new medusa-based species described herein demanded an update of the genus diagnosis given above. Bouillon (1985) provides a tabular overview on all known *Zancleopsis* at that time, Wang *et al.* (2016) a dichotomic key. These overviews have lost some of their value as we meanwhile know that *Z. dichotoma* sensu Kramp is a species complex. Perhaps also *Z. tentaculata* Kramp, 1928 is an agglomerate of different species.

Currently the genus comprises eight named species, as well as one unnamed clade found in genetic analyses (Maggioni *et al.*, 2021). A list of the accepted nominal species is given in the following together with the useable diagnostic traits for the adult medusa stage.

Z. cabela (Maggioni *et al*., 2017): total bell height 8-15 mm; large apical process; 2 long tentacles with up to 40 abaxial side branches, the latter ending in capitula not larger than the marginal bulbs, two short capitate tentacles; gonads in adradial folds; distribution: NW Atlantic, Indian Ocean, Red Sea; reference: this study.

Z. dichotoma (Mayer, 1900): total bell height 3 mm; large apical process; 2 long tentacles with up to 60 abaxial side branches, the latter ending in capitula not larger than the marginal bulbs, two short capitate tentacles; gonads smooth or in folds; distribution NW Atlantic, tropical W Pacific; reference: this study.

Z. elegans Bouillon, 1978: total bell height 1.7 mm; apical process lacking; 2 long tentacles with 8-10 side branches in distal region, the latter ending in capitula as large as the marginal bulbs, two short capitate tentacles; distribution tropical W Pacific; reference: Bouillon (1978).

Z. gotoi (Uchida, 1927): total bell height up to 8 mm; large apical process; 4 unbranched capitate tentacles, one opposite pair may be longer than the other; gonads smooth, adradial pads; distribution: W Pacific, Indian Ocean; references: Uchida (1927), Kramp (1968), Buecher *et al*. (2005).

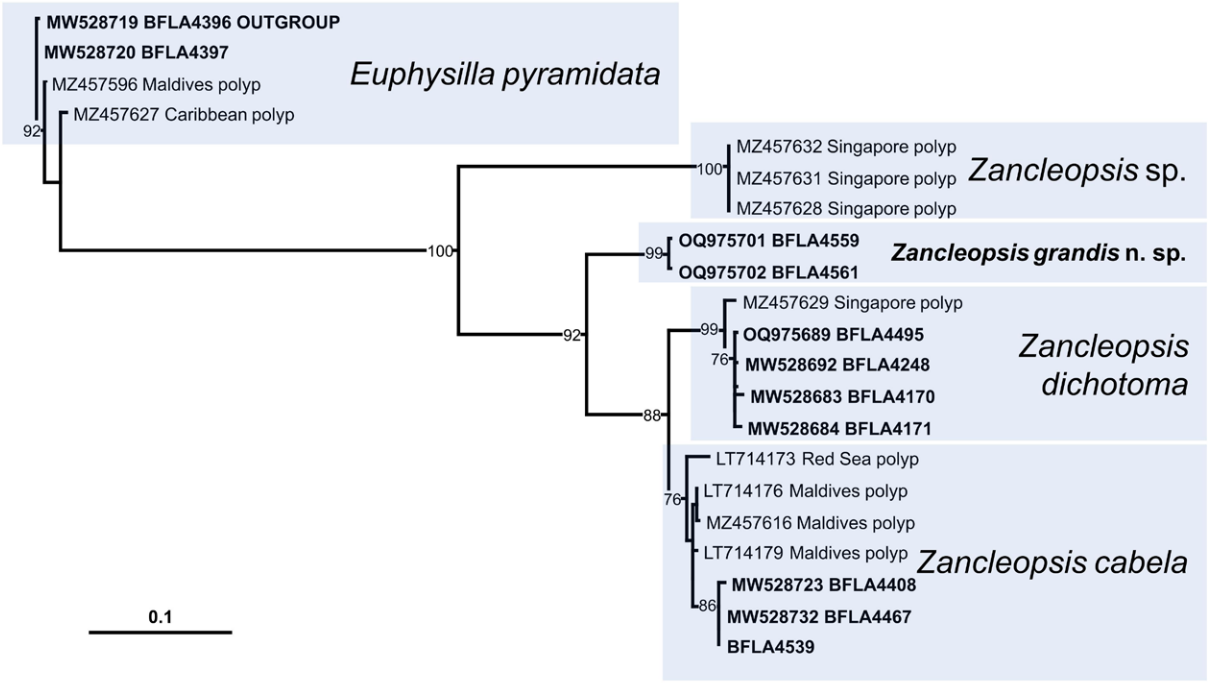


Fig. 21. Maximum likelihood phylogenetic tree of Zancleopsidae species obtained with PhyML (GTR+G model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers permitting the retrieval of more information. Bold labels are sequences from the current study and Schuchert & Collins (2021). Species clades are highlighted by blue boxes.

Z. oblonga Xu, Huang & Wang, 2016 emend.: total bell height 3.5 mm; large apical process; 2 long unbranched tentacles, with up to 65 nematocyst knobs, two short capitate tentacles with small terminal swellings; tentacle bulbs of long tentacles elongate and rather flat, not bulging as in other species; gonads smooth, interradial, shallow groove in middle; distribution: South China Sea (only type specimen known); reference: Wang *et al.* (2016). Taxonomic remark: According to the International Code of Zoological Nomenclature (article 30.1.2), the grammatical gender of genus names with the suffix -*opsis* are feminine. The correct spelling for the original *Zancleopsis oblongus* is therefore *Zancleopsis oblonga*.

Z. symmetrica Bouillon, 1985: total bell height 2 mm; small apical process; no pair of short tentacles, 4 identical, long, tentacles, distally with 7-15 nematocysts buttons, only the distal-most on a short stalk; gonads smooth, interradial; distribution: Papua New Guinea; reference: Bouillon (1985).

Z. tentaculata Kramp, 1928: total bell height 4-25 mm; apical process present, moderate size; 2 long tentacles with up to 15 abaxial side branches, the latter ending in capitula not larger than the marginal bulbs, two short capitate tentacles; gonads in adradial folds or smooth; distribution: tropical W Pacific to Indian Ocean; based on Kramp (1928, 1965, 1968), Bouillon (1978, 1985). Comment: the presence of *Z. cabela* and *Z. dichotoma* in the same region, the implausible size range, and the variable gonad morphology are evidence that the current concept of *Z. tentaculata* likely refers to a species complex.

Z. grandis sp. nov.: total bell height up to 29 mm, large apical process, 2 long tentacles with abaxial side branches, the latter ending in very large capitula, much larger than marginal bulbs, other 2 tentacles comparatively long, tapering, no swollen end or capitulum; gonads in vertical folds.

***Zancleopsis dichotoma* (Mayer, 1900)**

Fig. 22

Gemmaria dichotoma Mayer, 1900b: 35, pl. 17 fig. 40.

Zancleopsis dichotoma. – Hartlaub, 1907: 115, fig. 105. – Mayer, 1910: 91, pl. 8 fig. 1. – Maggioni *et al.*, 2021: 509, fig. 7A-I.

in part *Zancleopsis dichotoma*. – Kramp, 1959: 95, fig. 53. – Kramp, 1961: 56. – Kramp, 1968: 39. – Bouillon, 1978: 290. [refer to two or more species].

Zancleopsis dichotoma small form. – Schuchert & Collins, 2021: 272, figs 22A-F.

not *Zancleopsis dichotoma*. – Bigelow, 1938: 102, figs 1-2. [= *Zancleopsis grandis* sp. nov., see below]

Examined material: BFLA4495; 12-Oct-2020; likely a female, total bell height 3 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975689.

Observations: The single new sample was likely a female with a few flat, incipient eggs on the manubrium (Fig. 22). BFLA4495 had only one short capitate tentacle and the characteristic green tip of the apical process. Tentacle bulbs were not pigmented, appearing white. Long tentacles with up to 50 capitate side-branches.

General description: Includes also observations from Schuchert & Collins, 2021, small form. *Zancleopsis* medusa with total bell height (including apical process) up to 3 mm, ¼ to ⅓ of the height taken by pointed apical process, umbrella bell-shaped to conical, moderately thick walls, with shallow interradial subumbrellar pockets, tip of apical process green (Fig. 22). Manubrium height about half the subumbrellar height when gonads start to develop, pear-shaped, short tubular oral part, mouth rim with four perradial white regions, upper part of manubrium (stomach) ochre coloured, with about 10 longitudinal, indistinct gonad folds, folds mostly adradial, irregular. Radial canals not forming mesenteries, smooth. Four tentacle bulbs all equally developed, almost spherical, placed adaxial of origin of tentacles, white or faintly yellow. Two long, opposite tentacles, much extendable/contractible, with up to 60 short, abaxial, side branches ending in nematocyst knobs, size of knobs gradually increasing towards distal. The other tentacle pair very short, ending in spherical nematocyst knob. In younger animals these short tentacles either missing or just beginning to develop. All tentacle bases with a red ocellus on abaxial side. Nematocysts (alcohol preserved tissue): larger stenoteles [(24-26)x(22-23) µm], smaller stenoteles [(18-21)x(14-17) µm], desmonemes [8.5x5 µm], and macrobasic euryteles [(15-16)x(6-7) µm].

Hydroid as given for genus diagnosis, for details see Maggioni *et al.* (2021).

Fig. 22. *Zancleopsis dichotoma,* BFLA4495, total bell height 3 mm. Photo by Andrea Whitaker.

Sequence Data: The new haplotype (GenBank OQ975689) is very similar to the known ones (Fig. 21), differing only in one to three base pairs (p-distances 0.2-0.5%, Atlantic samples).

Distribution: Tropical NW Atlantic, Singapore (Maggioni *et al.*, 2021).

Remarks: Schuchert & Collins (2021) included in *Zancleopsis dichotoma* two morphologically and genetically distinct forms, called small- and large form. A subsequent, detailed phylogenetic analysis by Maggioni *et al.* (2021), using additional genes and additional samples of hydroids, found that the two forms represent two distinct species. They also described the polyp stages of these two species. The small morph (up to 3 mm with mature gonads) agrees better with the original description of *Z. dichotoma* by Mayer (1900), although some ambiguity remains as Mayer's specimens were likely rather young. In his monograph (Mayer, 1910), he mentions that the gonads are interradial, this for a bell height of 3 mm. The larger form of our previous paper (mature at 8 to 15 mm) had 16S sequences that are like the ones obtained from hydroids from the Red Sea and the Indian Ocean formerly described as *Astrocoryne cabela* Maggioni *et al.*, 2017. The large morph of the medusa was thus renamed *Zancleopsis cabela* (Maggioni *et al.*, 2017) in Maggioni *et al.* (2021).

While fully grown medusae with developed gonads of *Z. dichotoma* and *Z. cabela* have clearly different bell sizes, young *Z. cabela* may easily be mistaken for *Z. dichotoma*. It may thus be necessary to use 16S data to identify *Zancleopsis* medusa that are smaller than 5 mm. (see below). A green tip of the apical projection was found to be a good indicator for *Z. dichotoma,* but not all have it, and the colour may depend on age and developmental stage. Another useful character is the colour of the tentacular bulb. While they are white to faintly yellow or ochre in *Z. dichotoma,* they are intensively sulphur-yellow in *Z. cabela* (comp. Figs 22 and 23).

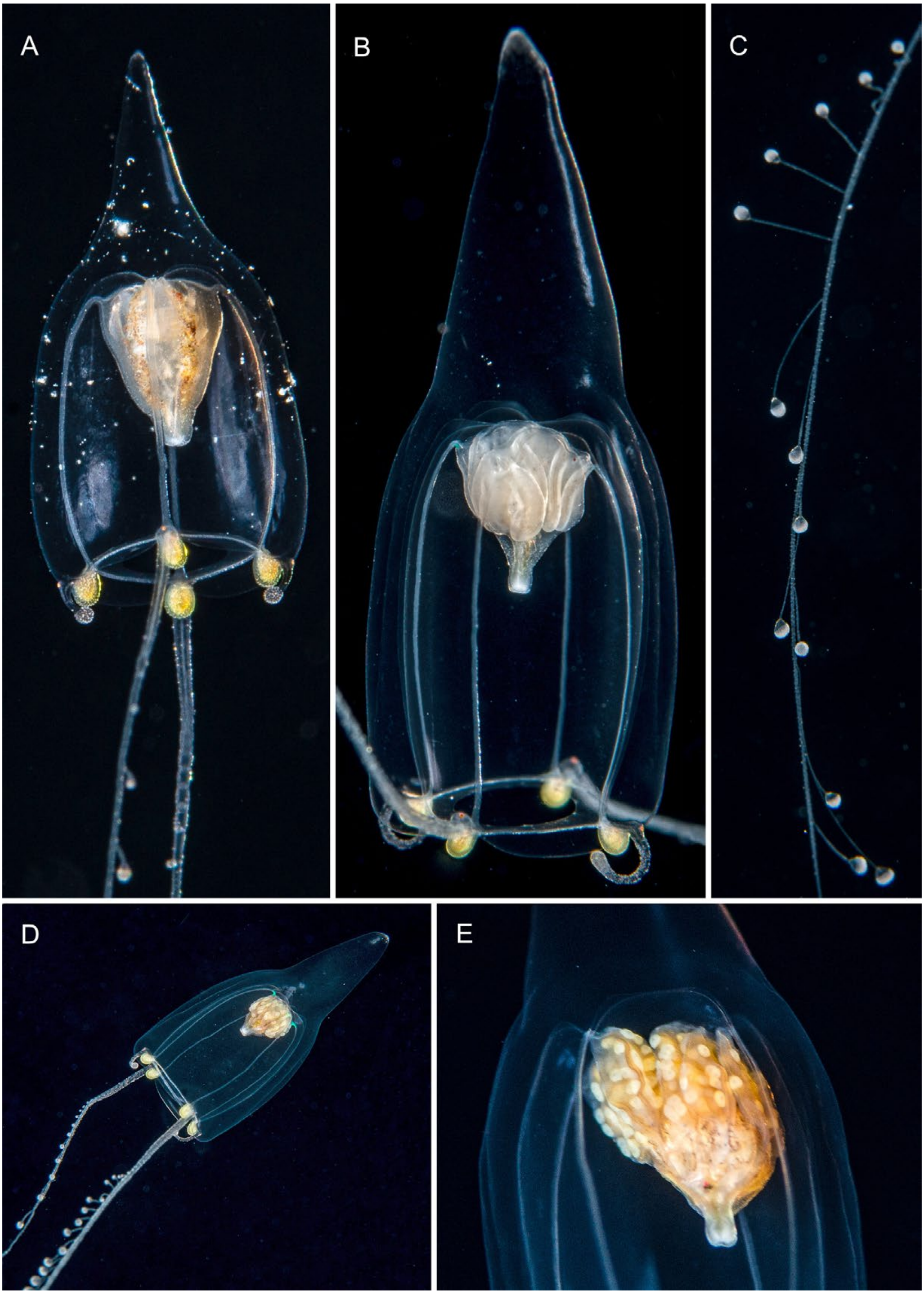


Fig. 23. *Zancleopsis cabela.* (A) BFLA4539, juvenile specimen, total bell height 4 mm, stomach filled with prey, apparently without obvious gonads. (B) Male medusa, observed 15-May-2022, size ~13 mm, note gonad in vertical folds. (C) Part of tentacle of animal shown in B, approximately same magnification, note that the secondary branches are extensible. (D) Female medusa photographed 15-May-2022; size ~13 mm. (E) Manubrium with female gonad, medusa observed 05-May-2022, size ~13 mm, is not the same animal as shown in D.

Zancleopsis cabela (Maggioni *et al.*, 2017)

Fig. 23A-E

Astrocoryne cabela Maggioni *et al.*, 2017: 738, figs 2-4.

Zancleopsis dichotoma large form. – Schuchert & Collins, 2021: 272, fig. 23.

Zancleopsis cabela. – Maggioni *et al.*, 2021: 25, fig. 8A-K, new combination.

Examined material: BFLA4539; 25-Apr-2021; infertile, size 4 mm; preserved in ethanol for DNA extraction, 16S sequence identical to MW528732. – 1 animal photographed 05-May-2022; female, size ~13 mm; not collected. – 1 animal photographed 15-May-2022; male, size ~13 mm; not collected. – 1 animal photographed 15-May-2022; female, size ~13 mm; not collected. – 1 animal photographed 15-May-2022; male, size ~13 mm; not collected.
Uncertain identification: **BFLA4673**; 06-Oct-2021; 4.5 mm, gonads with incipient eggs; preserved in ethanol for DNA extraction, deposited in FMNH as UF-016205, identity is not entirely clear as juvenile, yellow bulbs.

Description: Includes also observations from Schuchert & Collins, 2021, large form. *Zancleopsis* medusa with total bell height (including apical process) 8 to 15 mm and 5 mm diameter, apical process larger reaching ½ of total height, tip of apical process not green, may be slightly opaquer than rest (Fig. 23B), umbrella deeply bell-shaped, higher than wide, mesogloea evenly thick, subumbrella with interradial pockets at top. Manubrium ⅓ to ½ the height of the subumbrella in fully grown animals, cone-shaped, base square, short tubular mouth region. Gonads on the entire interradial sides of the stomach, nearly grown together perradially, in more or less irregular, especially in males, 2-3 adradial, vertical folds (Fig. 23B). Radial canals thin but well visible, not forming mesenteries at junction with manubrium, margins smooth to slightly corrugated. Four equally developed marginal bulbs on bell margin, hemispherical to ovoid, directed downward or slightly towards axis of animal, beset with nematocysts. Tentacles arise on abaxial side of bulbs (Fig. 23B). Two long, opposite tentacles, much extendable/contractible, with up to 40 abaxial side branches ending in spherical capitula, size gradually increasing towards distal (Fig. 23D), capitula not larger than marginal bulbs, mostly much smaller, stalks of capitula also extensible and of variable length (Fig. 23D). The other opposite tentacle pair very short, ending in spherical nematocyst knob. All tentacle bases with a red ocellus on abaxial side. Tentacle bulbs with intense yellow colour, stomach yellowish or light ochre-orange especially in females (Fig. 23D).
Hydroid as given for genus diagnosis, for details see Maggioni *et al.* (2021).

Sequence Data: The only 16S sequence obtained in this study was identical to a previously known haplotype (GenBank MW528732).

Distribution: Tropical NW Atlantic Ocean (Florida), Red Sea, and Indian Ocean. Type locality: Maldives, Magoodhoo Island, Faafu Atoll; 3.0670, 72.9500; depth 25 m.

Remarks: This species was mistaken for *Z. dichotoma* in our previous publication (see discussion above). The small, juvenile (BFLA4539) was initially identified as *Z. dichotoma*, but the 16S sequence identified it clearly as *Z. cabela*. It also had the typical yellow marginal bulbs (Fig. 23A).

Zancleopsis grandis sp. nov.

Figs 24A-F, 25A-D

Zancleopsis dichotoma. – Bigelow, 1938: 102, figs 1-2. [not *Zancleopsis dichotoma* (Mayer, 1900)].

Holotype: BFLA4559; 1 specimen; observed 27-May-2021; total bell height 29 mm, diameter 18 mm; tentacle preserved in ethanol for DNA extraction, frozen DNA solution in TE buffer deposited in MHNG under catalogue number MHNG-INVE-0151847, 16S sequence OQ975701; rest of animal preserved in 4% formalin and deposited in FMNH under catalogue number UF-015262.

Paratype: BFLA4561; 28-May-2021; total bell height 25 mm, diameter 9 mm; fragment preserved in ethanol for DNA extraction, frozen DNA solution in TE buffer deposited in MHNG under catalogue number MHNG-INVE-0151848, 16S sequence OQ975702; rest of animal preserved in 4% formalin and deposited in FMNH under catalogue number UF-015263.

Other material: 1 animal photographed 01-Apr-2019, size not recorded, with gonads; not collected.

Type locality: USA, Florida, about 10 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Etymology: The specific epithet "*grandis*" refers to the relatively large size of this medusa and to the very large capitula of the tentacular side branches.

Diagnosis: *Zancleopsis* medusa with total bell height up to 29 mm, with large apical process, with two long tentacles with abaxial side branches, the latter ending in very large capitula, much larger than marginal bulbs, spherical or ovoid depending on state of contraction, other two tentacles relatively long, tapering, without swollen end or capitulum; gonads in vertical folds.

Description: *Zancleopsis* medusa with total bell height (including apical process) reaching 25 to 29 mm, apical process less than ⅓ of total height, bell higher than wide but proportion variable and depending on state of contraction (Figs 24A, 25A); umbrella bell-shaped, mesogloea evenly thick, subumbrella with interradial pockets at top (Fig. 24B). Manubrium ½ the height of the subumbrella in fully grown animals, flask-shaped, with broad upper stomach part and a more tubular oral part, the latter spanning more than half the height, both parts cruciform in section, especially visible in stomach

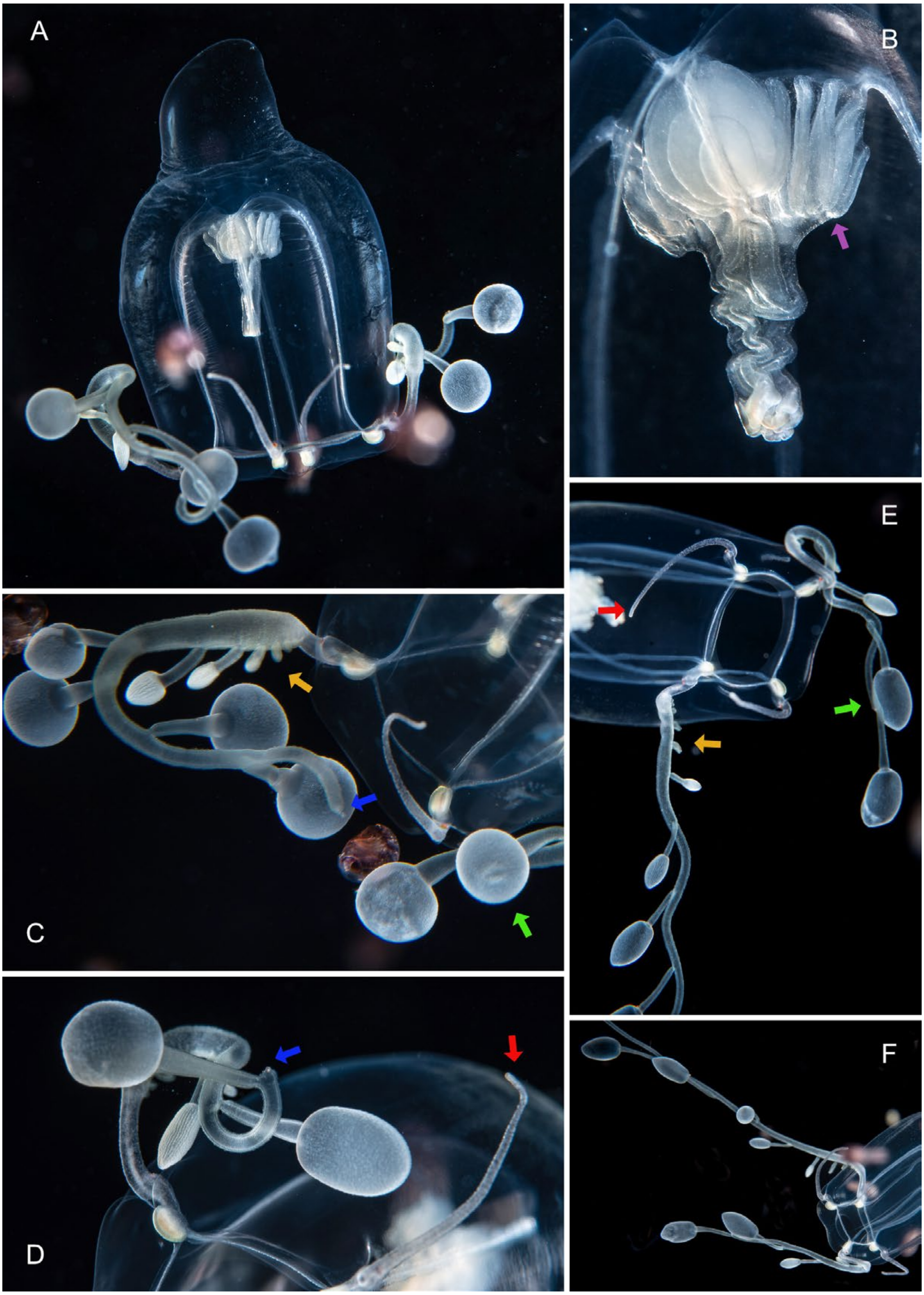


Fig. 24. *Zancleopsis grandis* sp. nov. Holotype, BFLA4559, total height size 29 mm. The brownish objects are crustaceans. Structural details: green arrows – the same individual capitulum; red arrows – filiform tentacles, blue arrows – broken ends of the long tentacles, yellow arrows – developmental zone of the side-branches, purple arrow – gonad folds. (A) Lateral view. (B) Manubrium in lateral view. (C-D) Tentacle details. (E-F) Partially relaxed filiform and branched tentacles, the axis of the medusa is horizontal.

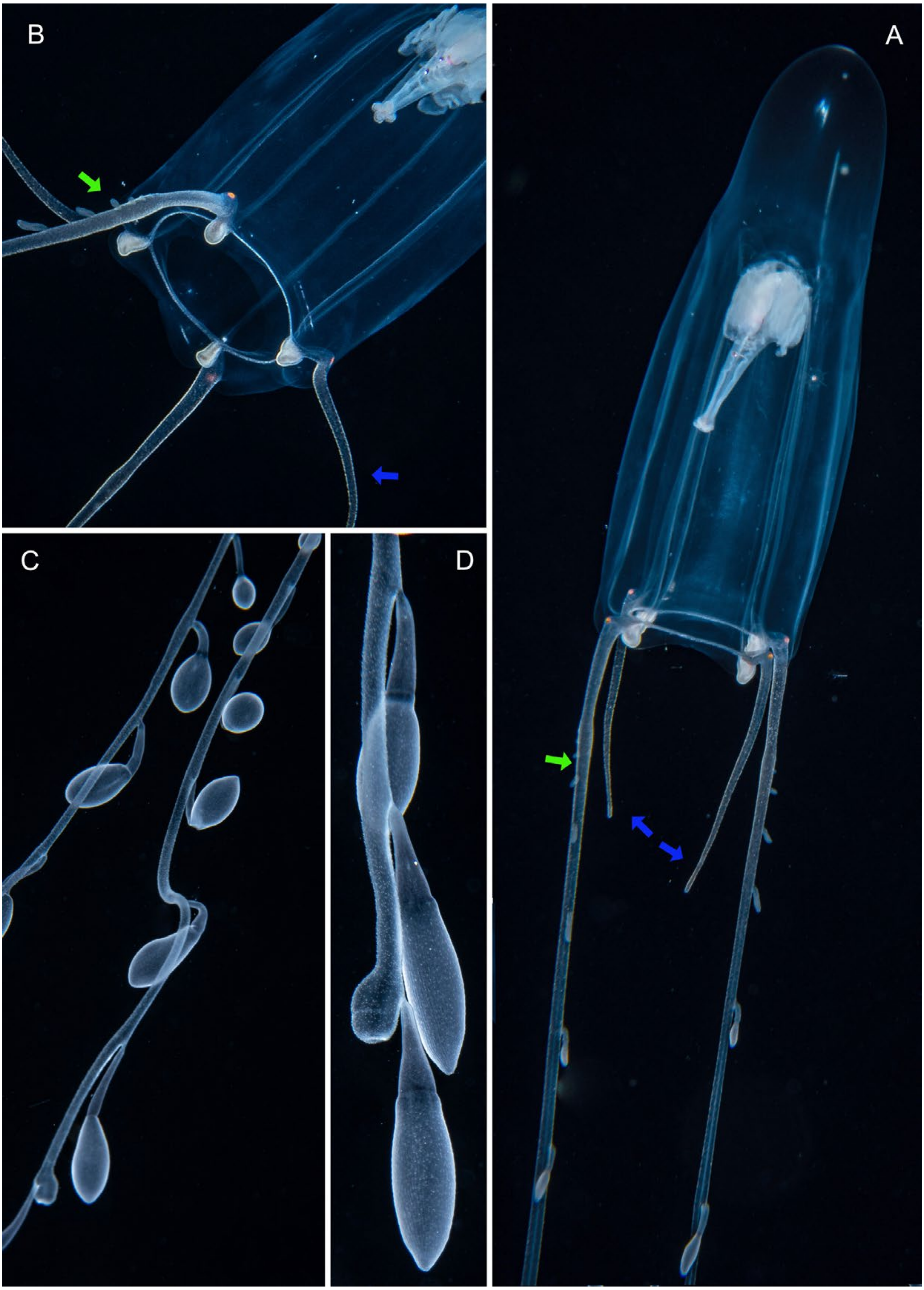


Fig. 25. *Zancleopsis grandis* sp. nov. Paratype, BFLA4561, size 25 mm, tentacles and capitula relaxed; green arrows indicate branched tentacles, blue arrows the shorter, filiform tentacles. (A) Lateral view. (B) View on velar opening, the green arrow points to incipient side-branches of a long tentacle. (C) Long tentacle region with large capitula. (D) Higher magnification of capitula. Photos by Linda Ianniello.

part, base cruciform, mouth likewise and thus forming four small lips (Fig. 25B). Gonads on adradial sides of stomach part of manubrium, in each octant on about four lamellar folds, folds oriented vertically (Fig. 24A-B). Radial canals thin but well visible, not forming mesenteries at junction with manubrium, margins smooth. Four equally developed marginal bulbs on bell margin, bulging, directed downward or slightly towards axis of animal, opaque. Tentacles arise on abaxial side of bulbs, well separated, usually a short distance remaining adnate to bell margin before sharply bending downwards (Fig. 25B); each tentacle with an ocellus in angle of abaxial side of tentacle and exumbrella. Two long, opposite tentacles, much extendable/contractible, with a linear array of abaxial side branches ending in capitula when fully developed, capitula size gradually increasing towards distal (Fig. 24E). The branched tentacles had lengths of > 50 mm when relaxed, but all appear to have their distal parts broken off (Figs 24C-D, 25D) which could be a natural process. The capitula are unique and very large, fully developed capitula are much larger than marginal bulbs, reaching diameters of up to 3.5 mm (calculated from height and width measures of bell); shape variable, depending on degree of contraction or internal turgor, spherical if tentacles contracted and held close to bell (Fig. 24A), or more oblong ovoid to club-shaped in more relaxed tentacles (Figs 24E-F, 25A, C), stalks of capitula also extensible and of variable length. The other opposite tentacle pair relatively long, tapering, without swollen end or capitulum, but end rounded and tip opaquer (Figs 24E, 25A). Colours: red ocelli, otherwise colourless or faintly yellow radial canals and rose/brown manubrium and tentacle bulbs.

Sequence Data: The two samples gave two very similar 16S sequences, the p-distance being 0.3%. The new species is well separated from the other species and a sister clade to *Z. dichotoma* and *Z. cabela*, see Fig. 21.

Distribution: Off Florida (this study), Bermuda (Bigelow, 1938; as *Z. dichotoma*).

Remarks: The large size, the unique giant capitula of the branched tentacles, and the relatively long, filiform other tentacle pair distinguish this new species from all other congeners. Also, the 16S data separate the new species from *Z. dichotoma* and *Z. cabela* (Fig. 21).

The shape differences of the capitula are surprising, but the shape of the capitula can obviously change rapidly (comp. Fig. 24C, E, green arrows indicate the same capitulum). The brief observations we made in situ suggest that a contraction of the tentacles leads to swelling of the capitula and a positioning closer to the bell (Fig. 24A), while relaxed tentacles trail behind the bell (Fig. 25A) and the capitula are elongate. The positioning of the tentacles closer to the bell could be a defensive reaction. It would be rewarding to study this reaction in more detail.

We are convinced that the *Zancleopsis* medusa documented by Bigelow (1938) also belongs to this species and not *Z. dichotoma*. The size (20 mm) and the filiform tentacle do not match our current concept of *Z. dichotoma* (see above). Bigelow's specimen shown in his fig. 1 was damaged and had only some of the proximal tentacular side branches. One of the remaining capitula is clearly larger than those of *Z. dichotoma*. Bigelow (1938: fig. 2) also shows the base of the long tentacles and they are exactly as we have seen for *Z. grandis*: the tentacles become free from the bell margin at some distance from the bulb (comp. Fig. 25B).

Suborder Aplanulata
Family Corymorphidae Allman, 1872
Genus *Corymorpha* M. Sars, 1835

Diagnosis: Medusa bell apex dome-shaped or pointed. Four marginal bulbs present, without long exumbrellar spurs. With a single tentacle or three short tentacles and one long tentacle that differs not merely in size, but also in structure. Manubrium thin-walled, sausage-shaped with flared mouth rim, reaching to umbrella margin. Cnidome comprises stenoteles, desmonemes, and haplonemes.

Hydroids solitary with more or less vasiform hydranth and long caulus. Hydranth with one or several closely set oral whorls of 16 or more moniliform or filiform tentacles and one aboral whorl of 16 or more long, non-contractile filiform tentacles. Hydrocaulus stout, covered by thin perisarc, filled with parenchymatic gastrodermis, with long peripheral canals; aboral end of caulus with papillae turning more aborally into rooting filaments, rooting filaments composed of epidermis and solid gastrodermis, sometimes tips with non-ciliated statocysts. With or without asexual reproduction through constriction of tissue from aboral end of hydrocaulus. Gonophores develop on blastostyles arranged in a whorl over aboral tentacles. Gonophores remain either fixed as sporosacs or are released as free medusae.

Corymorpha floridana Schuchert & Collins, 2021

Corymorpha floridana. – Schuchert & Collins, 2021: 278, fig. 26A-E.

Examined material: 1 specimen; observed 14-Mar-2021; size 2 mm; not collected. – 1 specimen; observed 08-Jan-2023; size 2 mm; not collected.

Corymorpha valdiviae (Vanhöffen, 1911)
Fig. 26

Euphysora valdiviae Vanhöffen, 1911: 198, figs 2, 2a. – Kramp, 1948: 20, footnote, erroneous record from South Atlantic. – Kramp, 1957: 5, correction of Kramp (1948). – Kramp, 1961: 41, diagnosis. – Kramp, 1968: 15, fig. 31.

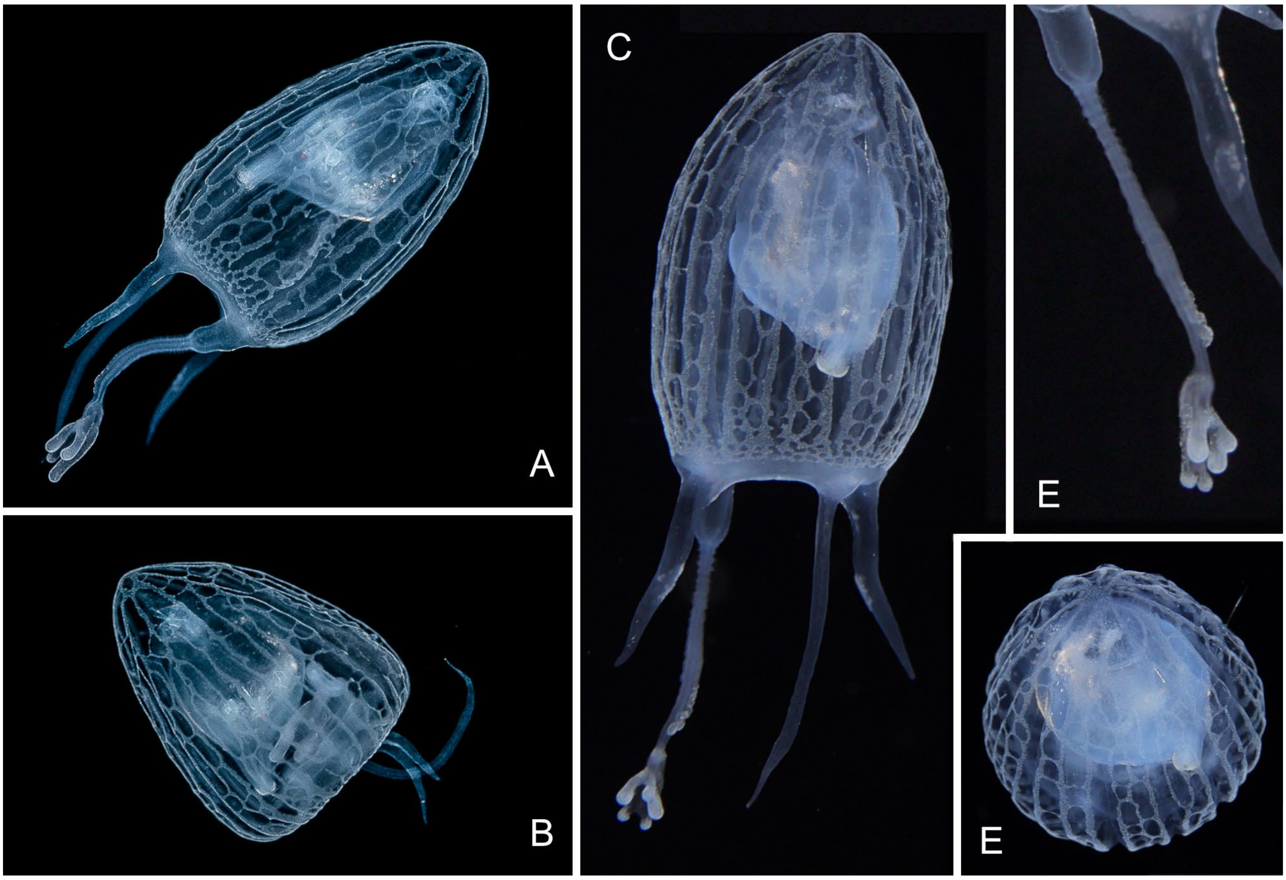


Fig. 26. *Corymorpha valdiviae.* (A-B) Animal from the Gulf Stream. (A) Lateral view with extended tentacles. (B) Large tentacle tucked inside bell and bell rim involuted. (C-E) Photos kindly provided by Ryo Minemizu (Japan); 8 mm sized animal photographed off the coast of Kona, Hawaii, 07-07-2022, depth 15 m. (C) Lateral view. (D) Branched main tentacle, note the five endings. (E) Aboral side of bell. Photos by Andrea Whitaker.

Examined material: 1 specimen; observed 20-Dec-2020; size not recorded; not collected. – Several photographs taken from one animal by Ryo Minemizu (Japan); 8 mm size; Pacific Ocean, Island of Hawaii; WGS84 19.6475, -156.1133; 07-Jul-2022; depth 15 m; not collected.

Description (Atlantic specimen): Bell height not recorded, estimated from photographic limitations of the used lens to be between 3 and 10 mm, mitre-shaped, top bluntly pointed, without apical process, umbrella about two times as high as wide, mesogloea evenly thin, thickened at apex. Exumbrella covered all-over by a characteristic network of nematocyst tracks, these organised as about 10 to 12 radial strands that are connected by sometimes regular transverse strand connecting two meridional strands, but regionally very irregular and resembling a mesh. Manubrium about half the height of the subumbrella, composed of large, ovoid upper part ("stomach") and a short tubular mouth. Apical chamber on top of manubrium likely present. Gonads not seen. Four perradial tentacles, one thicker with branched end, opposite to this an equally long but fine and evenly tapering tentacle, the other opposite pair shorter, thicker, also evenly tapering to a fine point. Largest tentacle with thick, bulb-like base, elongated, continued as isodiametric thinner part, end thickened and branched, the two times dichotomously branched ends resulting in four blunt, finger-like endings (Fig. 26A). At some distance proximal to the thickened terminal region, a region with some more opaque patches on one side of the tentacle. Ocelli absent. The main tentacles can contract strongly and the bell rim can become involuted (Fig. 26B).

Distribution: Indian Ocean, off Sumatra, west of Padang (type locality; Vanhöffen, 1911), Atlantic Ocean, off Florida (new record, this study), Pacific Ocean, off Hawaii (Ryo Minemizu, pers. com.).

Remarks: *Corymorpha valdiviae* is a very rare species, apparently only known from its original description. A later record from the South Atlantic (Kramp, 1948) was subsequently corrected as belonging to *Corymorpha furcata* (Kramp, 1957), differing from Kramp's other samples of *C. furcata* by simply having a contracted tentacle. Kramp (1948) initially emphasised that the difference of *C. valdiviae* to *C. furcata* is, among others, the short main tentacle of the former. The diagnostic difference that separates *C. valdiviae* more reliably from *C. furcata* is the presence of reticulated nematocyst ridges on the exumbrella (Fig. 26).

The type specimen of *C. valdiviae* obviously had much contracted tentacles [see figures in Vanhöffen (1911), copied in Kramp (1968)], but nevertheless, the main tentacle reportedly also differed structurally from our specimen and *C. furcata*. A literal translation of the pertinent part of Vanhöffen's (1911) description is as follows: "The tentacular bulbs are inconspicuous, ocelli are lacking. The main tentacle, characterised by a strong swelling of its base, is stouter than the other tentacles, but not longer than them. Immediately after [distal to] the swelling, it branches in two curved appendages of similar length, of which one is simple, hooked-shaped, whereas the other divides and carries two horse-shaped appendages." According to Vanhöffen (1911), the type specimen had thus a long tentacle that had another side branch distal to the bulb-like swelling. This would be rather unique and very unlike the tentacle in the similar species *C. furcata* and in our specimens.

The holotype of *C. valdiviae* is kept in the Natural History Museum of Berlin under the registration number ZMB Cni 14903. Dr Carsten Lüter, curator of the marine invertebrate collections in the Berlin Museum, was so kind to send us photos of the specimen and to re-examine the long tentacle. The tentacle is difficult to examine because it is strongly contracted, curved, brittle, and tucked into the subumbrella as shown by Vanhöffen (1911: fig. 2), like in Fig. 26B. What appears to be a side branch is in fact rather a fixation artefact related to strong contraction and sharp bending of the tentacle's main trunk. Thus, we interpret the purported side branch of Vanhöffen as a sharp kink of the tentacle. This is also more in accordance with the situation seen in the closely similar *C. furcata.*

Ryo Minemizu (Japan) kindly provided us with photographs of a *C. valdiviae* from the Pacific Ocean (Fig. 26C-E). This medusa, although strikingly similar to the Atlantic specimen, has a main tentacle ending in one bifid and one trifid branching instead of two bifid ones. This is unlikely a population difference but shows that there is more likely some individual variation in the branching pattern. The medusa is apparently quite frequent in Hawaiian waters (Ryo Minemizu, pers. com.).

Aplanulata *incerta sedis*
Genus *Cnidocodon* Bouillon, 1978

Cnidocodon Bouillon, 1978: 256; type species *Cnidocodon leopoldi* Bouillon, 1978 by monotypy.
Ramus Zhang & Wu, 1981: 186, type species *Ramus xiamenensis* Zhang & Wu, 1981.

Diagnosis: Medusa umbrella high, dome-shaped with thick jelly; four narrow radial canals and ring canal; four stout marginal bulbs without ocelli, each with adaxial cushion of nematocysts and with group of four short, capitate tentacles; manubrium cylindrical, shorter than bell cavity; mouth rim circular, without nematocysts; gonad completely surrounding manubrium leaving only oral most part free.
Hydroid unknown (Petersen, 1990).

Remarks: Bouillon (1978) originally placed this genus in the family Corymorphidae, which was contested by Petersen (1990). As long as the hydroid stage is unknown, we prefer to keep it therefore in the informal group "Aplanulata *incerta sedis*".

Cnidocodon leopoldi Bouillon, 1978
Fig. 27A-B

Cnidocodon leopoldi Bouillon, 1978: 255, fig. 4. – Tosetto *et al.*, 2021: fig. 1a-b.
? *Ramus xiamenensis* Zhang & Wu, 1981: 184, fig. 1. – Huang *et al.*, 2008: 412, status.

Examined material: 1 specimen photographed 05-Jan-2023; size 2 mm; not collected.

Description: Medusa with ovoid bell, mesogloea of even thickness, exumbrella rather opaque, finely granulated. Manubrium ovoid with small cylindrical oral part, voluminous, spanning about ⅔ of subumbrella; mouth small, circular. Four radial canals, margin smooth. Four perradial marginal bulbs, with adradial bulge, likely a nematocyst pad, no ocelli. On each bulb a group of four short capitate tentacles.

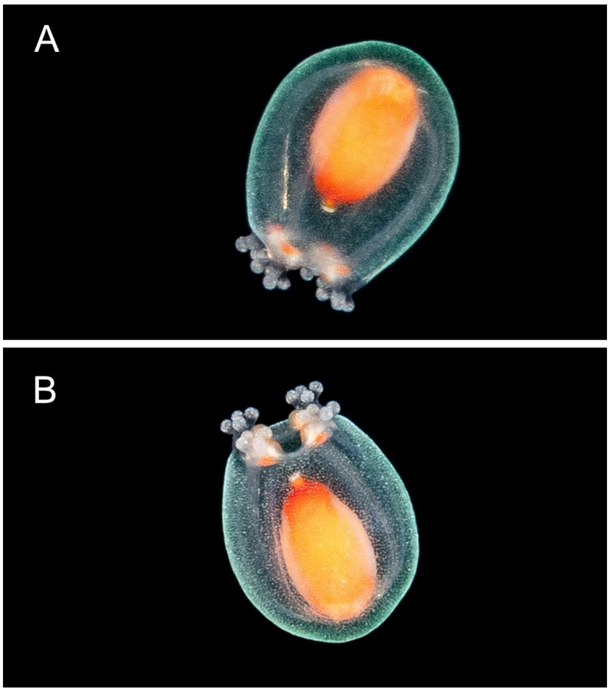


Fig. 27. (A-B) *Cnidocodon leopoldi,* photographed 05-Jan-2023; size 2 mm. Photos by Linda Ianniello.

Colours: umbrella with greenish hue, manubrium intensively orange to red, gastrodermis of marginal bulbs orange.

Distribution: Pacific Ocean (Papua New Guinea, East China Sea), Indian Ocean (coast of India and South Africa), Atlantic Ocean (Brazil) (records reviewed by Tosetto *et al.*, 2021). Type locality: Laing Island, Papua New Guinea.

Remarks: *Cnidocodon leopoldi* has recently been recorded from the Atlantic by Tosetto *et al.* (2021). An earlier record of the genus was from Belize (Larson, 1982, as *Cnidocodon* sp.). Our observed animal matched the original description very well, including the colour.

Order Leptothecata

Remarks: The Leptothecata families are ordered so that they approximately follow the phylogeny (Leclère *et al.*, 2009; Maronna *et al.*, 2016), the statocyst bearing taxa (taxon Statocysta) are separated from those that lack them or have cordyli instead. As the phylogeny of these groups is not sufficiently well known, we refrain from using suprafamilial taxa in this study.

Family Melicertidae L. Agassiz, 1862

Diagnosis: Medusa with broad manubrium base; usually eight simple or bifurcated radial canals; marginal tentacles hollow; no cirri, no statocysts, no cordyli; with or without ocelli.
Hydroid stolonal or sparingly branched, arising from creeping hydrorhiza; perisarc thinning away completely below hydranth base, no hydrotheca; hydranth naked, large, spindle-shaped, amphicoronate tentacles; no intertentacular web; gonophores borne on cauli of hydranths, no gonothecae.

Genus *Melicertum* sensu L. Agassiz, 1862 emend.

Diagnosis: Melicertidae medusae with usually eight radial canals, sometimes up to 10 in some individuals, all arising centrifugally from manubrium, occasionally some radial canals branched; gonads on radial canals, separated from manubrium; no ocelli.
Hydroid phase with the characters of the family.

Remarks: The diagnosis was adapted to account for the observation that some individuals may have more than eight radial canals, even in the type species *Melicertum octocostatum* (M. Sars, 1835) (see below).

DNA sequence data: The new 16S sequences (see below) were combined with *Melicertum* sequences in GenBank to generate a maximum likelihood phylogenetic tree (Fig. 28). As outgroups *Lafoea dumosa* (Fleming, 1820) and *Stegella lobata* (Vanhöffen, 1910) were chosen based on the results given in Leclère *et al.* (2009) and Maronna *et al.* (2016). The samples of *M. octocostatum* included notably animals from the North Atlantic as well as from the North Pacific, both populations showing only low divergences from each other (p-distances 0.7 to 1.2%). The divergence to the new species were much higher (p-distances 5.0 to 5.7%).

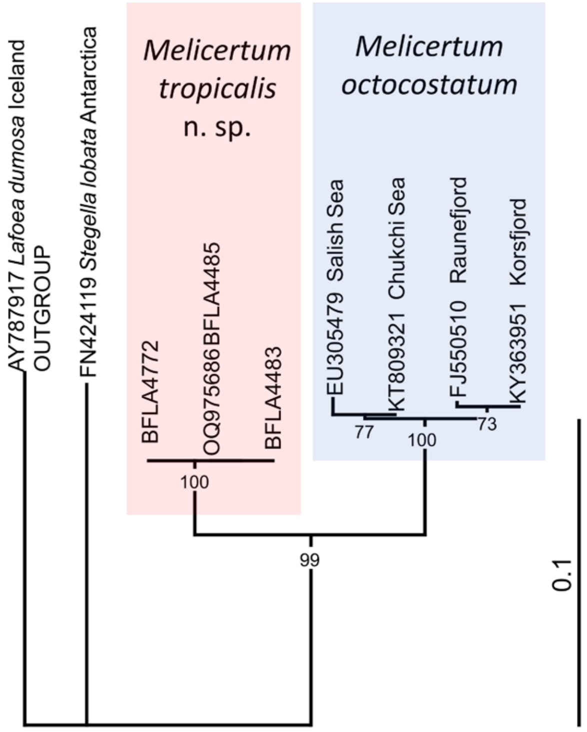


Fig. 28. Maximum likelihood phylogenetic tree of *Melicertum* species obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Species of this study are boxed in red.

Melicertum tropicalis sp. nov.

Figs 29A-E, 30A-B

Holotype: BFLA4483; 1 medusa photographed (Fig. 29A-C) and collected 30-Aug-2020; size 5 mm; preserved in alcohol and part used for DNA extraction, rest in FMNH as UF-015203; frozen DNA solution (DNA1658) deposited in MHNG under catalogue number MHNG-INVE-0151817, 16S sequence OQ975685, COI sequence OQ975008.

Paratypes: BFLA4485; 1 medusa photographed (Fig. 29D-E) and collected 03-Sep-2020; size 6 mm; preserved in alcohol and part used for DNA extraction, rest in FMNH as UF-015204;

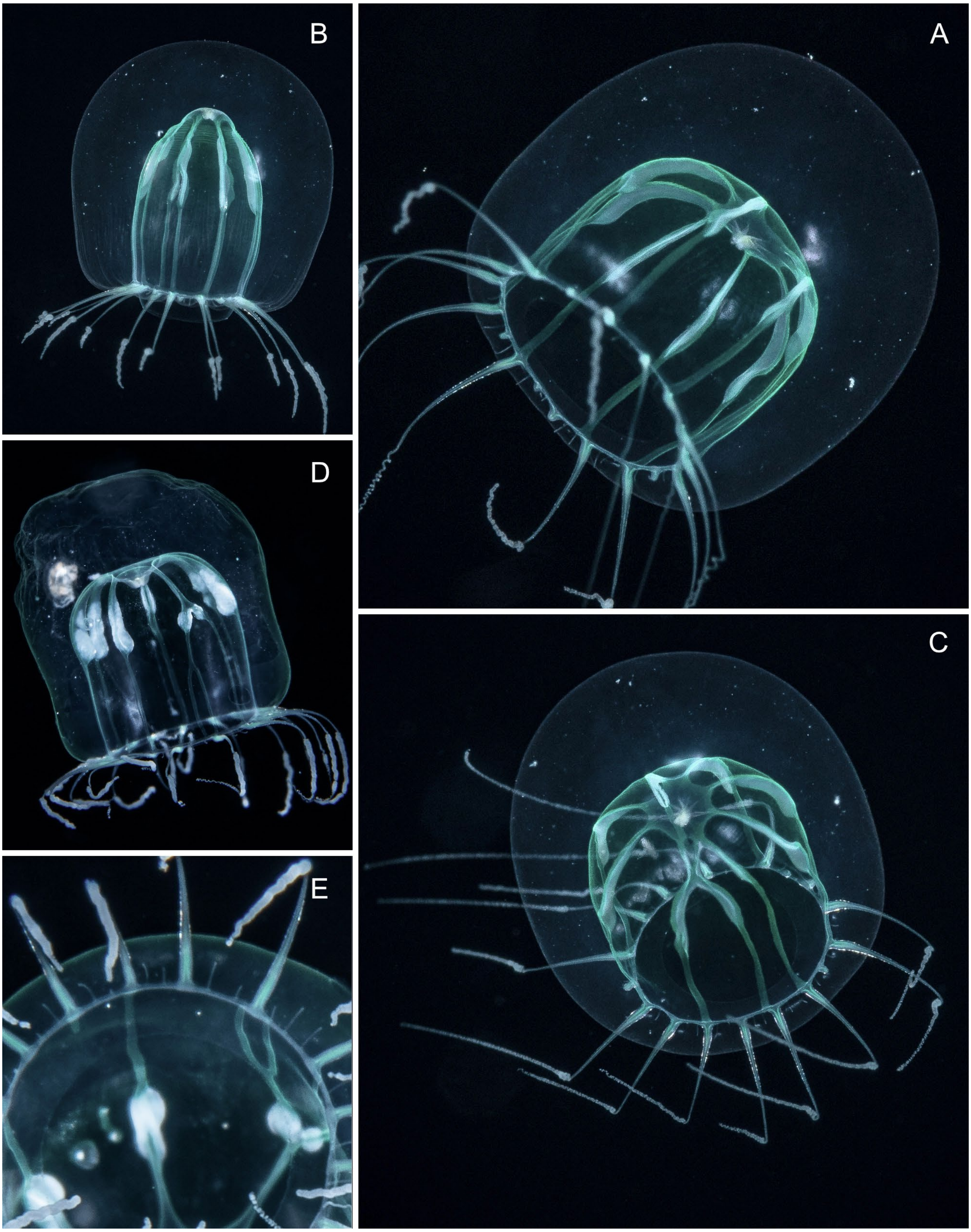


Fig. 29. *Melicertum tropicalis* sp. nov. (A-C) Holotype, BFLA4483; size 5 mm; note branched radial canal in C. (D-E) Paratype, BFLA4485; size 6 mm: note branched radial canal in D, E shows the small tentacles between the long ones. Photos A-C by Andrea Whitaker, D-E by Linda Ianniello.

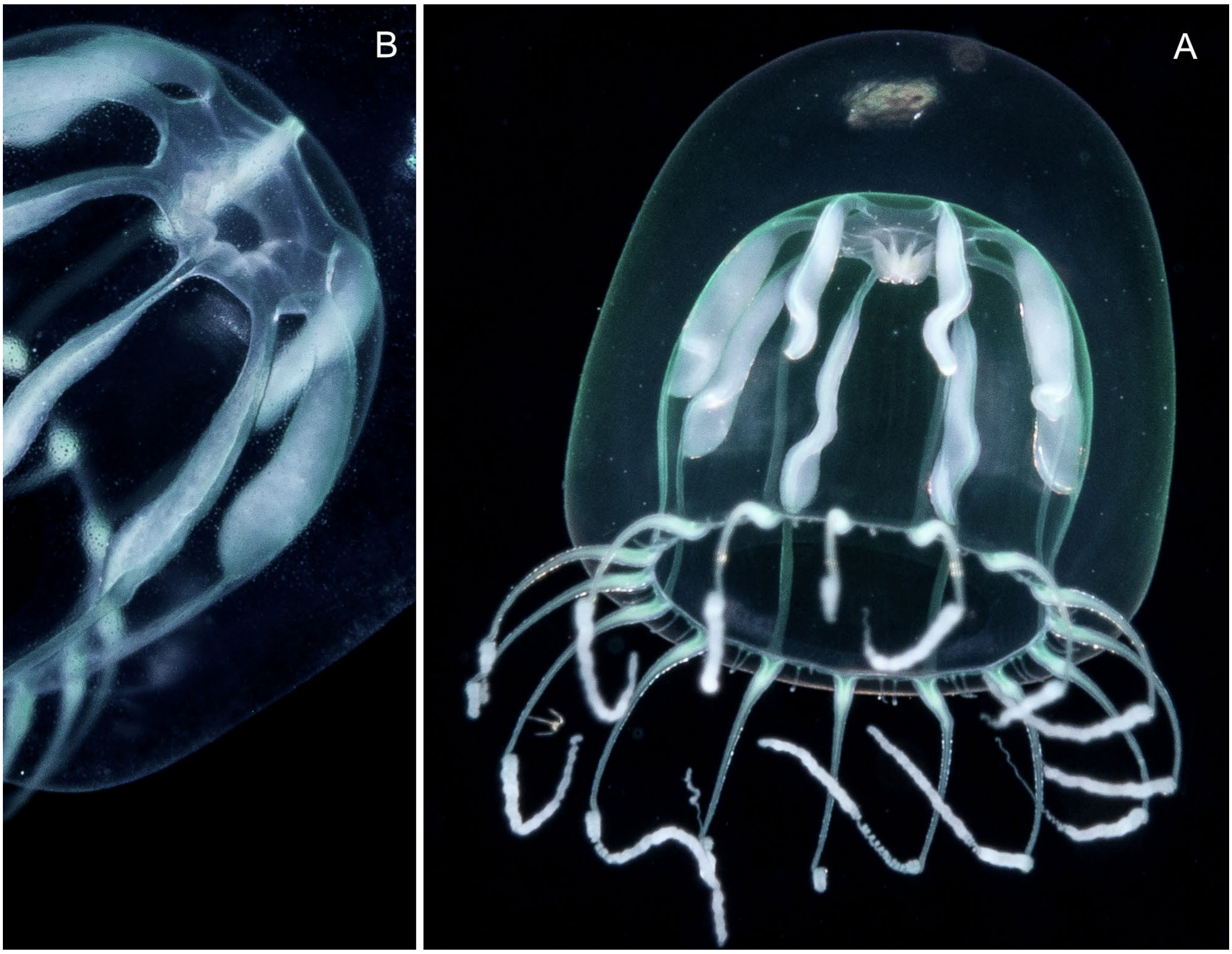


Fig. 30. *Melicertum tropicalis* sp. nov., sizes not recorded, not collected (A) Specimen of 11-Aug-2018, lateral view, apparently fully mature, male. (B) View on stomach from aboral of specimen photographed 09-Aug-2020. Photos by Linda Ianniello.

frozen DNA solution (DNA1660) deposited in MHNG under catalogue number MHNG-INVE-0151818, 16S sequence OQ975686, COI sequence OQ975009. – **BFLA4772**; 1 medusa photographed and collected 18-Feb-2022; size 5 mm; preserved in alcohol and used entirely for DNA extraction; frozen DNA solution (DNA1734) deposited in MHNG under catalogue number MHNG-INVE-0151897, 16S sequence identical to OQ975727, COI sequence OQ975025.

Other material observed: 1 specimen; photographed 08-Dec-2020; size not recorded; not collected. – 1 specimen; photographed 11-Aug-2018; size not recorded; not collected. – 1 specimen; photographed 13-Jun-2019; size not recorded; not collected. – 1 specimen; photographed 09-Aug-2020; size not recorded; not collected. – 1 specimen; photographed 15-Jul-2020; size not recorded; not collected. – 1 specimen; photographed 19-Jul-2020; size not recorded; not collected.

Type locality: USA, Florida, about 10 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Etymology: The specific epithet refers to the species' occurrence in warm waters, in contrast to its congener *M. octocostatum* (M. Sars, 1835), which occurs in cool temperate to cold waters of the Arctic, Atlantic, and Pacific Oceans (some records from warm waters of the Pacific Ocean need a re-evaluation).

Diagnosis: Like *M. octocostatum,* but distinguishable through the following traits [see Schuchert (2017) for a recent treatment of *M. octocostatum*; compare also Figs 29-31]:

- 15 to 18 long tentacles versus 40-80,
- basal bulbs of long tentacles indistinct, absent in small tentacles, both tentacle types clearly distinct and not intergrading as in *M. octocostatum,*
- colourless or in living, younger animals green-blue radial canals and manubrium, versus bright to dark yellow in *M. octocostatum*,
- the 16S sequence differing in at least 5% of the paired bases (COI >9%).

Compared to the population of *M. octocostatum* in the NE Atlantic, the bell is more globular and proportionally higher, while *M. octocostatum* has typically a more conical bell, being widest near the margin (Fig. 31). However, in the NE Pacific, the bell shape can also be as globular as *M. tropicalis* (unpublished pers. obs.). Another difference, although difficult to use as a diagnostic trait, is the length of the gonads, which tend to end farther away from the bell margin in *M. tropicalis*. Besides *M. octocostatum*, there is currently only one other accepted *Melicertum* species (Schuchert, 2023), namely *M. ovalis* Xu, Huang & Guo, 2019. It is immediately distinguishable from the present species – and also *M. octocostatum* – by its oval gonads located close to the bell margin.

Sequence Data: The three obtained 16S sequences of *M. tropicalis* sp. nov. were all identical. The p-distances to *M. octocostatum* sequences (Fig. 28, GenBank numbers and origins: EU305479 Salish Sea, KT809321 Chukchi Sea, FJ550510 Raunefjord Norway, KY363951 Korsfjord Norway) are between 5.0% and 5.7%. For the COI marker (GenBank GQ120071 Norway, KC440073 North Sea, KT809321 Chukchi Sea) the distances are even higher, 9.7% to 11.7%. The maximal intraspecific divergences for *M. octocostatum* are 1.2% for 16S and 3.6% for COI. Although only few sequences are available so far, the interspecific divergences are clearly much higher than the maximal intraspecific ones.

Description (9 specimens): *Melicertum* medusa with bell height up to 6 mm when mature, umbrella bell-shaped to globular, evenly rounded, mesogloea thick, thicker at apex but without apical process, apical jelly about ⅓ of total height. Exumbrella smooth, no visible lines or nematocyst tracks. Manubrium (Fig. 30A-B) short and flat when empty, octagonal in outline, mouth 8-rayed, with 8 small lips. The eight aboral corners of the manubrium continued as radial canals, all joining the circular canal. Sometimes (2 in 9 observed) one radial canal can branch and 9 radial canals reach the circular canal (Fig. 29C, D). Gonads on radial canals, not extending to manubrium, starting from corners of manubrium and extending along radial canal for ½ to ⅔ its length, fully developed lappet-like, undulating, hanging into subumbrella, separated perradially. Sexes not reliably identifiable on photos. 15 to 18 long tentacles, often positioned in phase with or close to junctions of radial canals with circular canals, but in some cases somewhat displaced (Fig. 29A, C), tentacles evenly tapering, no distinct basal bulbs demarcated, proximal most part of tentacle opaquer and giving impression of marginal bulbs. Between each pair of long tentacles 2 to 3 cirrus-like short tentacles (Fig. 29E), very thin, no evident bulb formation. In alcohol-preserved specimens the small tentacles can contract to cordylus-like shape. The two types of tentacles are clearly distinct and not intergrading as in *M. octocostatum.* New long tentacles develop in younger animals from bulb-like swellings (Fig. 29A). Colours: subadults in life with green-blue manubrium, canals, gonads, and proximal part of tentacles; fully adult clear to faintly green, gonads white.

Distribution: Off Florida (this study).

Remarks: The criteria to distinguish *M. tropicalis* sp. nov. are listed above. The DNA results clearly sets it apart from *M. octocostatum.* Although only few sequences are available, the ones available for *M. octocostatum* come from different oceans and are likely providing a good estimation of the intraspecific variability of the 16S and COI marker.

On photos, *Melicertum tropicalis* sp. nov. appears quite distinct from *M. octocostatum,* but easy discrimination criteria that are also applicable to preserved net-plankton are not present, besides the number of tentacles and the geographic separation.

The occasional occurrence of branched radial canals (Fig. 29C, D) was initially rather confusing for finding the correct genus. The genus *Melicertum* has a complicated taxonomic history and its status is not fully resolved. For more details see Kramp (1919) and Arai & Brinckmann-Voss (1980). The concept used after L. Agassiz (1862) is rather unambiguous in its scope and was defined as having eight radial canals (*e.g.*, Bouillon *et al.*, 2006). However, even *M. octocostatum* can occasionally have more than eight radial canals. The specimen shown in Fig. 31B has 10 radial canals. The branching occurs close to corners of the manubrium. The total number of radial canals is thus somewhat variable and the genus diagnosis has therefore been modified to reflect this.

Dipleurosomatidae Boeck, 1868

Diagnosis: Medusa manubrium with narrow base; three, four or more radial canals, radial canals either branched or if not so then irregularly arranged; gonads on radial canals, separated from manubrium; no statocysts, no cordyli, no cirri, only ocelli may be present.

Hydroid *Cuspidella*-like, only known from rearing in *Dipleurosoma typicum* Boeck, 1868 (Cornelius, 1995).

Genus *Dichotomia* Brooks, 1903

Dichotomia Brooks, 1903: 11; type species *Dichotomia cannoides* Brooks, 1903 by monotypy.

Diagnosis: Medusa with four main radial canals bifurcating into two diverging branches, each branching again, all reaching circular canal; gonads adjacent to manubrium, extending outwards along the radial canals and their branches. Hydroid unknown.

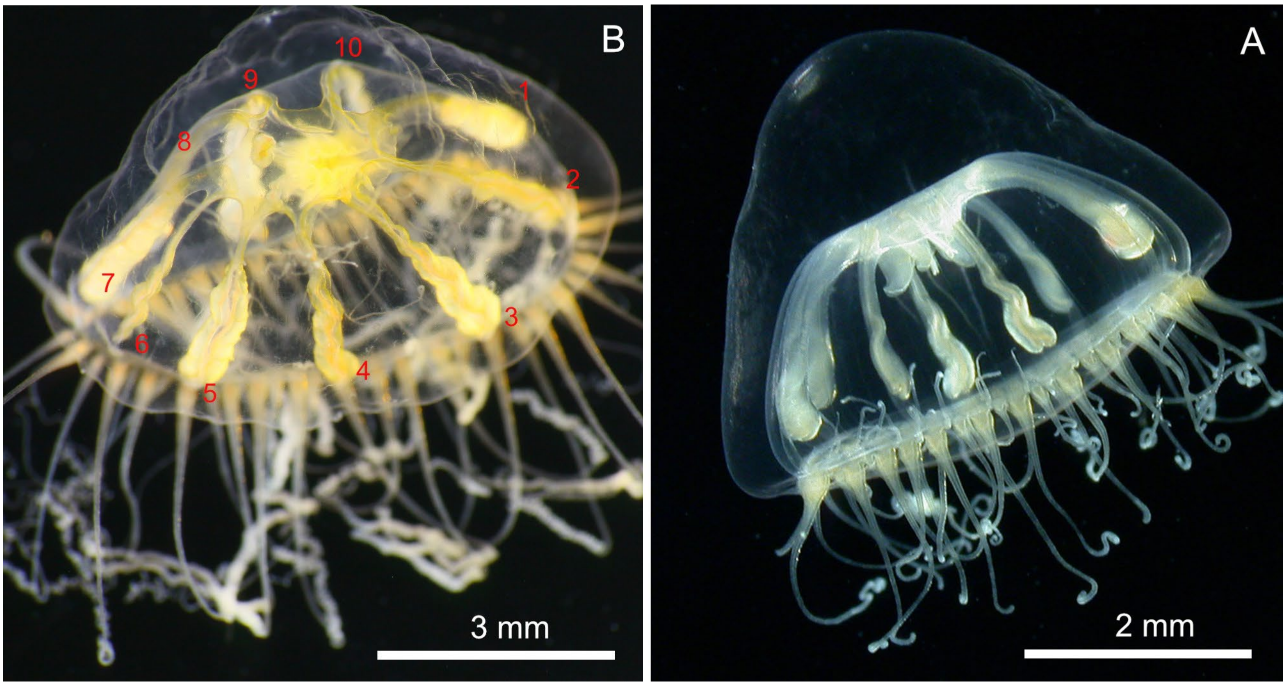


Fig. 31. *Melicertum octocostatum,* both from Norway, close to the type locality. For more details and a link to additional images see Schuchert (2017). (A) Voucher specimen for 16S sequence FJ550510, Raunefjord, 14-Jun-2006. (B) Specimen used to obtain 16S sequence KY363951, Korsfjord, 14-Jun-2016. The red numbers count the radial canals, 10 in this case.

Dichotomia cannoides Brooks, 1903

Fig. 32A-F

Dichotomia cannoides Brooks, 1903: 11, pl. 1 figs 1-3. – Mayer, 1910: 223, fig. 116. – Kramp, 1959: 32, 133, figs 6a-b, 149. – Kramp, 1961: 133. – Xu & Zhang, 1978: 29, figs 5-6. – Bouillon, 1984b: 37, nematocysts. – Pagès *et al.*, 2006: 375, fig. 7D-E.

Examined material: BFLA4610; 22-Jul-2021; size 5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975711, COI sequence OQ975021. – **BFLA4612**; 22-Jul-2021; size 6 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975712, COI sequence OQ975022.

Description: Medusae 5-6 mm high, diameter 3 mm, mitre-shaped bell, umbrella in lower half somewhat cylindrical, in upper half conical (Fig. 32). Mesogloea comparatively thin, thickened at apex and sometimes forming small apical process. Exumbrella smooth. Subumbrella shaped like exumbrella, but more pointed. Stomach large and complexly branched, total height about ⅔ of subumbrella, attached to subumbrella for about half or more of the height of the subumbrella. Stomach attachment at apex H-shaped (Fig. 32B), then subdividing dichotomously to about 16 diverticula which are then continued as radial canals that can branch once again. The stomach walls follow the branching diverticula and forms vertical lappets. Towards the mouth, the manubrium narrows to a cone, lips not observed. Radial canals along half of the subumbrellar height, most of them subdividing close to origin, broad, near circular canal almost as broad as interradial space (Fig. 32C). Gonads on stomach diverticula (Fig. 32A-B). Bell margin contiguously beset with tentacles. Two types of tentacles distinguishable (Fig. 32C, E). Long tentacles up to 24, held downward, evenly tapering, base slightly swollen to form a bulb, distal part curled up, in centre of tentacle a fine line. Between each pair of long tentacles two to four short tentacles that are held upwards, length variable, most at base as thick as long tentacle, but rapidly tapering after some distance, centre with fine line only at proximal end. Colours: manubrium, canal system, and tentacle bases intensively yellow.
Nematocysts are isorhiza or microbasic mastigophore with very indistinct shaft (Fig. 32D), size preserved approx. 13 x 6 µm.

Sequence Data: Two 16S haplotypes obtained from the examined specimens differed only in one base pair (p-distance 0.2%). A blastn search in GenBank did not yield any match above 90% similarity.

Distribution: Western Atlantic from the Caribbean to Gulf of Maine, South China Sea, Papua New Guinea (Pagès *et al.*, 2006). Type locality: Bahamas.

Remarks: Brooks (1903) described the short tentacles as solid. This could not be confirmed by Kramp (1959) and also our photos do not indicate this. Kramp (1959) gives more details on the variation pattern of the radial canals and gastric diverticula. Contrary to Kramp (1959) and Pagès *et al.* (2006), we think that the radial canals in

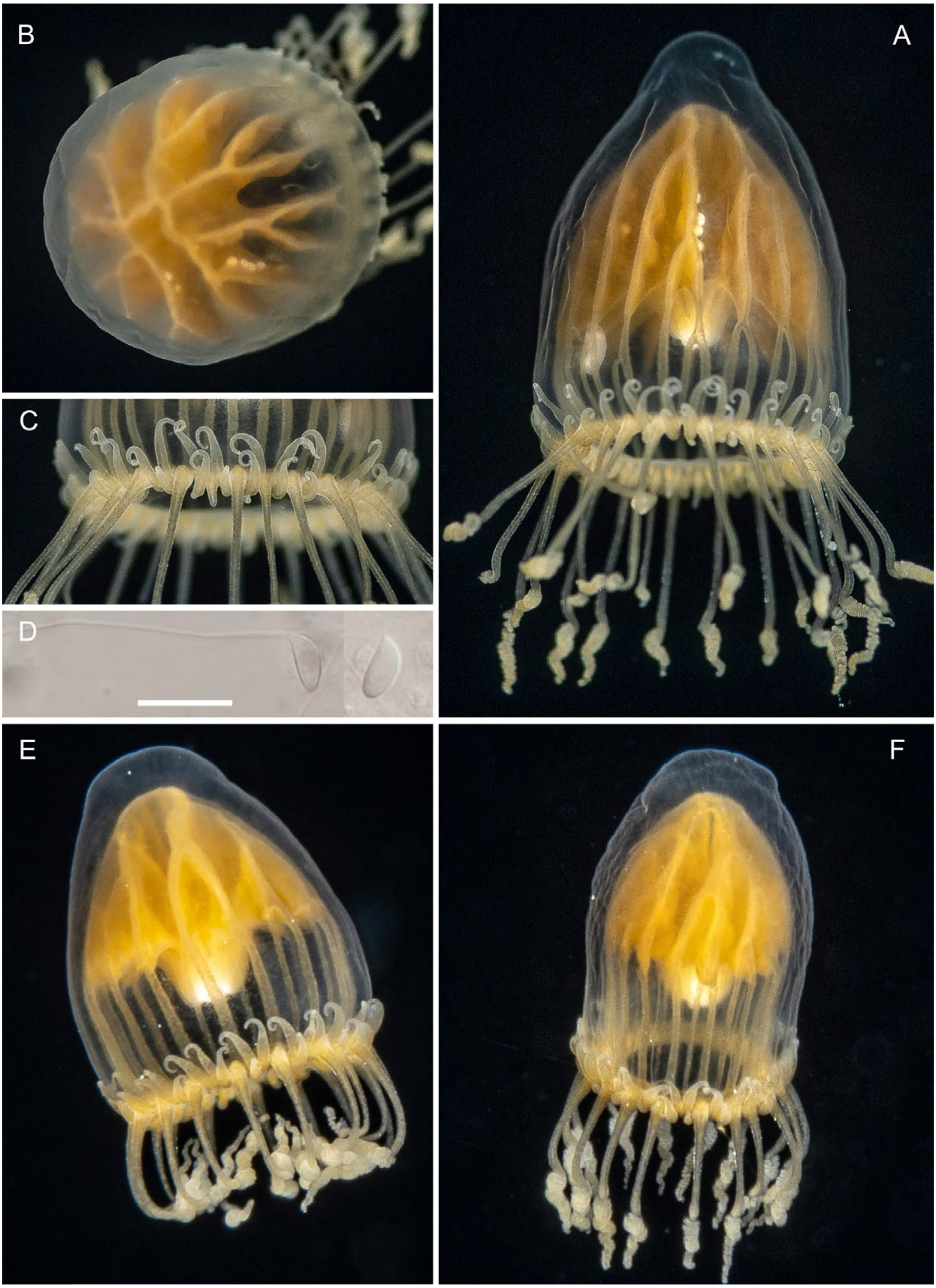


Fig. 32. *Dichotomia cannoides*. (A-D) BFLA4612, size 6 mm, ? female, photos Andrea Whitaker except for D. (A) lateral view, note multiple branchings of the radial canals. (B) View on aboral side, note the branching pattern of the stomach diverticula and radial canals, originating not in a cross but a H-shape at the apex of the manubrium. (C) Umbrella margin with the two types of tentacles. (D) Nematocysts, microbasic mastigophore, right intact, left discharged, scale bar 20 µm. (E-F) BFLA4610, size 5 mm, a younger specimen with less branched radial canals, photos Linda Ianniello.

the strict sense start only below the attachments of the manubrium, above them we named them as branching diverticula of the stomach. Contrary to Pagès *et al.* (2006) we always saw the short tentacles directed upwards and this can thus not be a fixation artefact as they supposed, confirming the observations by Brooks (1906) and Kramp (1959). Although Pagès *et al.* (2006) also photographed a living animal, it had been collected by a net and was quite damaged, especially the long tentacles appear all much truncated. This likely explains why they were not showing their natural behaviour. Bouillon (1984b) found that the medusae contain numerous zooxanthellae, leading likely to the yellow coloration [compare also *Wuvula ochracea* (Mayer, 1910) in Schuchert & Collins (2021), which has a similar colouration].

Although currently classified in different families (Bouillon *et al.*, 2006), *Dichotomia cannoides* resembles formally *Netocertoides brachiatum* Mayer, 1900, especially in having branched radial canals, the same colour, and occurring in the same region (comp. Mayer, 1910). Several photos purportedly showing *Netocertoides brachiatum* currently circulating on the internet are misidentified *Dichotomia cannoides*. According to Mayer (1910), *Netocertoides brachiatum* has a manubrium base in the form of an eight rayed star (= stomach diverticula) from the tips of which originate pairs of radial canals. The radial canals appear thus as only once branched. The medusa has 16 long tentacles and 16 to 25 small ones. To our knowledge, the species has only been reported after its original description without giving any details by Bouillon *et al.* (1986) in the Bismarck Sea and by Segura-Puertas *et al.* (2009) in the Gulf of Mexico.

Netocertoides brachiatum needs a redescription to confirm its distinctness from *D. cannoides*. Both, also need a re-evaluation of their family level classification. They could belong to the Melicertidae. The 16S sequences obtained in this study did not permit us to detect a relationship with other species.

Family Orchistomatidae Bouillon, 1984
Genus *Orchistoma* Haeckel, 1879

Diagnosis: Medusa with short manubrium on large gastric peduncle; mouth with 8-30 sinuous or crenulated lips; eight or more radial canals, simple, ramified, or in groups of four. Up to 64 marginal tentacles; no marginal cirri, but with thin, filiform, tentaculiform structures devoid of marginal bulbs; gonads usually on proximal parts of radial canals; numerous adaxial ocelli; without statocysts, without cordyli, without excretory pores or papillae.

Hydroid phase unknown.

Orchistoma pileus (Lesson, 1843)
Fig. 33A-B

Orchistoma pileus. – Schuchert & Collins, 2021: 231, figs 34A-F & 35A-G, synonymy.

Examined material: BFLA4492; 1 much damaged specimen without manubrium, 26-Sep-2020; size 24 mm; preserved in ethanol for DNA extraction, 16S sequence identical to

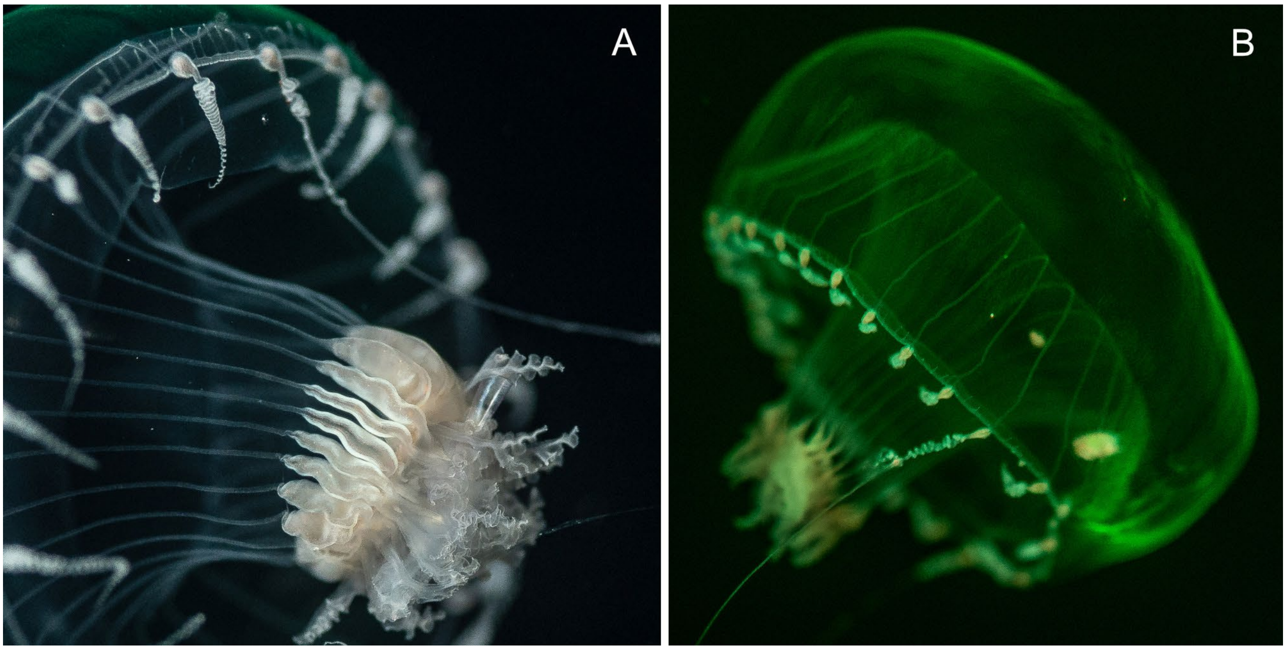


Fig. 33. *Orchistoma pileus.* (A) BFLA4614, size 21 mm, view of manubrium, gastric peduncle and subumbrella. (B) Specimen photographed 16-Jun-2022 using blue light, with yellow filter and blue flash, size not recorded, note the strong green fluorescence (is not the same animal as shown in A). Photo A by Andrea Whitaker.

MW528717 from BFLA4387; voucher in 4% formalin deposited in FMNH under catalogue number UF-015212. – **BFLA4614;** 22-Jul-2021; size 21 mm, manubrium beige; preserved in ethanol for DNA extraction, 16S sequence OQ975713; voucher in 4% formalin deposited in FMNH under catalogue number UF-015290. – **BFLA4807**; 28-May-2022; size 17 mm, juvenile with yellow manubrium; preserved in ethanol for DNA extraction, deposited in FMNH under catalogue number UF-015290. – 1 specimen photographed 08-Jul-2021; size ~3 mm; not collected.
Observations using blue light source to detect florescence pattern, with or without yellow filter, additional blue or white flash: 3 individuals, photographed 12-Jun-2022 and 16-Jun-2022.

Description: See Schuchert & Collins (2021). In addition, the use of a UV light source combined with a yellow filter and a blue flash showed strong green fluorescence of the whole medusa (Fig. 33B).

Sequence Data: The 16S of two new samples could be sequenced. One haplotype proved to be identical to a previously obtained one (see above). There are now 8 haplotypes of the 16S marker known (GenBank MW528651, MW528652, MW528653, MW528654, MW528680, MW528716, MW528717, OQ975713). The maximal intraspecific p-distance is 9.5%.

Distribution: See Schuchert & Collins (2021).

Remarks: Schuchert & Collins (2021: fig. 16) found that the 16S sequences of *O. pileus* formed a clade, but which was divided into two rather divergent subclades, suggestive of a species complex. The minimal p-distance for comparisons of members of the two clades is 7.6%, thus also suggestive for a species complex.
One sub-clade comprised two animals with brownish-yellow manubria and gonads, while the other included animals with whitish or beige gonads. The animal BFLA4614 of this study (Fig. 33A) had beige gonads, but had a 16S haplotype that belongs with the “brownish-yellow” (tree not shown, but comp. to ML tree in Schuchert & Collins, 2021). The colour difference previously observed for the two clades seems thus more likely be due to pure contingency and/or age. Hence, the manubrium colour in *O. pileus* is variable.
However, the two distinct 16S subclades remain a problem. We could also determine three COI sequences for specimens described in our previous publication (GenBank OQ974981, OQ974987, OQ975000). For this marker the minimal distance for the two clades is even higher, namely 14%.
In the absence of diagnostic morphological traits to distinguish the lineages, no new species names should be proposed. *Orchistoma pileus* has a wide distribution and for a correct evaluation of the genetic and morphological variability it is essential to analyse additional populations from other localities, notably from the type localities of the synonyms given in our previous publication. Moreover, species should not be split based solely on mitochondrial markers in the absence of morphological differences. A confirmation using nuclear markers is mandatory.

Family Laodiceidae L. Agassiz, 1862
Genus *Laodicea* Lesson, 1843

Diagnosis: Medusa with four simple radial canals; gonads along radial canals; with marginal cordyli, with or without marginal cirri, with adaxial ocelli, without statocysts.
Hydroid of “*Cuspidella*” type; colony stolonal; hydrotheca tubular, sessile, or exceptionally a poorly delimited pedicel (Bouillon *et al.*, 2006).

Laodicea undulata (Forbes & Goodsir, 1853)

Laodicea undulata. – Schuchert, 2017: 353, fig. 2A-C, redescription, synonymy. – Schuchert & Collins, 2021: 279, fig. 27A-E.

Examined material: BFLA4589; 10-Jul-2021; size 19 mm, female; fragment preserved in ethanol for DNA extraction, 16S sequence identical to MW528648; remaining part preserved in 4% formalin, deposited in FMNH as UF-015278. – **BFLA4664**; 1 specimen; observed 18-Sep-2021; size 9 mm, male; part preserved in ethanol, part in 4% formalin, both deposited in FMNH as UF-016202. – **BFLA4679**; 14-Oct-2021; size 8 mm, male; preserved in ethanol for DNA extraction, deposited in FMNH as UF-016207. – **BFLA4685**; 1 specimen; observed 14-Oct-2021; size: 8.5 mm, male; preserved in 4% formalin, deposited in FMNH as UF-016211.

Remarks: *Laodicea undulata* could be a species complex, see discussion in Schuchert & Collins (2021).

Family Hebellidae Fraser, 1912
Genus *Melicertissa* Haeckel, 1879

Diagnosis: Medusae with eight unbranched radial canals; stomach with eight basal perradial stomach extensions, leaf-like; bulbs and cordyli with adaxial ocelli; with or without cirri.
Hydroid *Hebella*-like.

Melicertissa mayeri Kramp, 1959

Fig. 34A-B

Melicertissa mayeri Kramp, 1959: 139, fig. 162, new name. – Schuchert & Collins, 2021: 282, fig. 29A-C.

Examined material: BFLA4570; 19-Jun-2021; size 11 mm; fragment preserved in ethanol for DNA extraction, 16S sequence OQ975704; rest of bell preserved in 4% formalin and deposited in MHNG as UF-015268. – 1 animal photographed 08-Jul-2021; size 4 mm; not collected.

Sequence Data: The new 16S haplotype had only one base pair difference to the previously reported one (p-distance 0.2%).

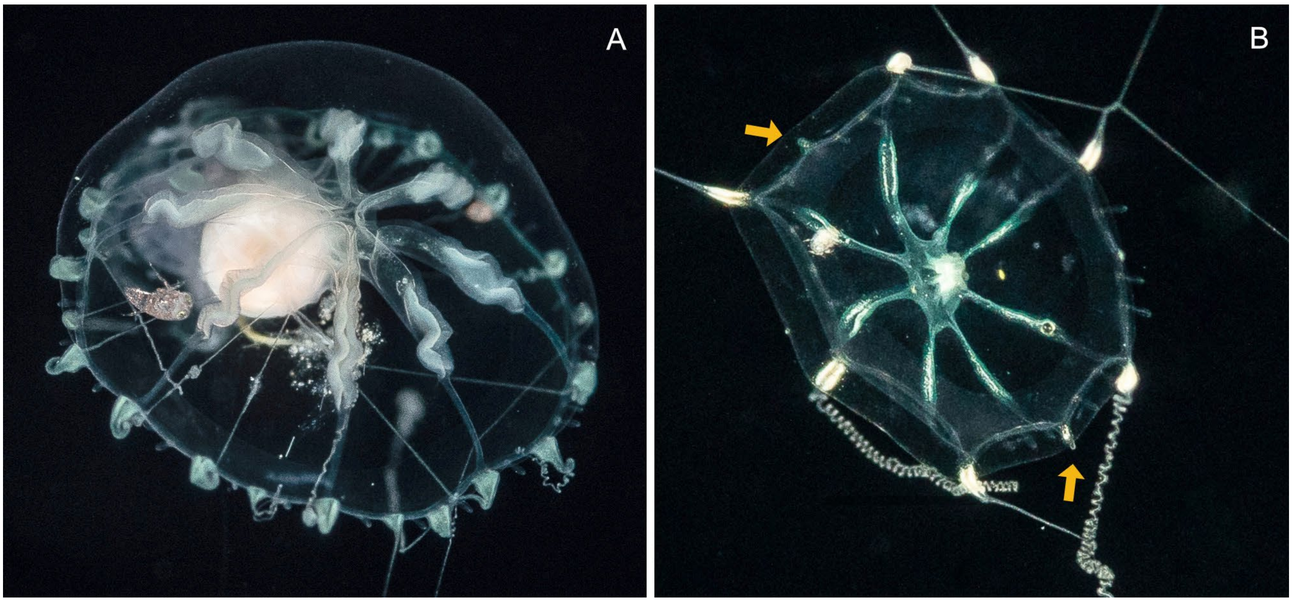


Fig. 34. *Melicertissa mayeri.* (A) BFLA4570, size 11 mm, view from aboral side. The round object below the manubrium is a larval anemone which has been captured by the medusa (B) Animal photographed 08-Jul-2021, size 4 mm, view from oral side; arrows point at developing tentacles. Photos by Andrea Whitaker.

Description: Collected animal generally as in Schuchert & Collins (2021), size 11 mm, about 18-20 tentacles, some in development, mostly one cordylus between tentacles, sometimes two (Fig. 34A). The medusa that was only photographed but not collected (Fig. 34B), was only 4 mm in diameter, had 7 tentacles, plus 2 or 3 just budding, and 1-3 cordyli between tentacles; the gonads were just beginning to develop.

Remarks: With its 7 tentacles (plus 2 beginning to grow), the medusa shown in Fig. 34B matches more *Melicertissa clavigera* Haeckel, 1879 than *M. mayeri* (the former has eight tentacles, the latter about 16, see discussion in Schuchert & Collins, 2021).
However, because its underdeveloped gonads are evidence that it as juvenile, and more tentacles are seen developing, it was here identified as a young *M. mayeri*. Unfortunately, the animal was not collected and no 16S sequence information is available. 16S sequences of typical, mature *M. clavigera* from the Canary Islands (type locality) are needed to evaluate the status of this nominal species.

Genus *Staurodiscus* Haeckel, 1879

Diagnosis: Medusa with 4 or more main primary radial canals, some or all branching one or more times, primary canal and some or all of the branches reaching circular canal; gonads on primary radial canals and branches; numerous tentacles and cordyli; with or without cirri; with or without ocelli.

Hydroid epizootic, *Hebella*-like; hydrothecae almost conical when growing on upper part of the host, cylindrical when growing on lower part of same host; asymmetrical to symmetrical; with everted margin, sharply or slightly oblique, with short to long, wrinkled or annulated pedicels; with membranous diaphragm (sometimes absent) and annular thickening; gonophores as free medusae; gonotheca as big or slightly bigger than hydrotheca, with four opercular flaps, on short pedicel, slightly undulated walls, truncated distally, tapering at base, containing up to three medusae (Bouillon *et al.*, 2006).

Staurodiscus kellneri (Mayer, 1910)

Staurodiscus kellneri. – Schuchert & Collins, 2021: 285, fig. 31A-H.

Examined material: BFLA4548; 07-May-2021; size 8 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975699. – **BFLA4798**; 15-May-2022; size 6 mm; preserved in ethanol for DNA extraction, deposited in FMNH as UF-016271.

Description: As in Schuchert & Collins (2021).

Sequence Data: One new 16S haplotype was found in this study. The minimal p-distance to the previously known haplotypes was 0.3%. The maximum observed intraspecific divergence was recalculated as 0.8% p-distance.

Staurodiscus luteus Schuchert & Collins, 2021

Fig. 35A-B

Staurodiscus luteus Schuchert & Collins, 2021: 289, fig. 33A-H.

Examined material: BFLA4587; 10-Jul-2021; size 5 mm; preserved in ethanol for DNA extraction, 16S sequence identical MW528698, COI sequence OQ975019. – **BFLA4656**; 09-Sep-2021; size 5 mm; preserved in 4% formalin and deposited in FMNH under catalogue number UF-016199. – 1 specimen photographed 04-Nov-2021; size 6 mm; not collected. – 1 specimen photographed 15-May-2022; size 6 mm; not collected. – 1 specimen photographed 28-May-2022; size 4 mm; not collected.

Sequence Data: The single specimen used for sequencing yielded a 16S sequence identical to GenBank entry MW528698. All four so far sequenced samples of *S. luteus* had the same 16S sequence.

Description: As given in Schuchert & Collins (2021). Specimen BFLA4656 is noteworthy as it has a high number of radial canals and tentacles (about 42 radial canals joining the circular canal, 46 marginal bulbs and tentacles), this despite its average size (Fig. 35). Moreover, contrary to our previous material, it seems to be undamaged. The animals are easily damaged and deformed.

Family Aequoreidae Eschscholtz, 1829

Genus *Aequorea* Péron & Lesueur, 1810

Diagnosis: Medusa manubrium very wide, circular; no gastric peduncle, but often with jelly cone within stomach; subumbrella without radial rows of gelatinous papillae. With numerous, unbranched radial canals, new radial canals develop centrifugally from stomach base. Gonads on radial canals, separated from manubrium. Marginal tentacles hollow; usually with excretory pores or papillae on adaxial side of base; no marginal or lateral cirri; statocysts closed; no ocelli.
Hydroid where known of "campanulinid" type, small, usually lacking species-specific characters.

Remarks: As not fully mature *Aequorea* medusae are difficult to distinguish reliably, we report here only specimens for which we obtained 16S sequence information. The new 16S sequences were combined with the dataset used in Schuchert & Collins (2021) and a maximum likelihood phylogenetic tree was calculated. This permitted the new sequences to be matched to the species described in our previous publication. For clarity reasons, Fig. 36 shows only the part of the tree that comprises the new haplotypes obtained in this study, the other newly determined sequences being identical to haplotypes already reported in Schuchert & Collins (2021: fig. 37).

Aequorea neocyanea Schuchert & Collins, 2021

Fig. 37A-B

Aequorea neocyanea Schuchert & Collins, 2021: 297, fig. 38A-I.

Examined material: BFLA4519; 16-Apr-2021; size 10 mm; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528636. – **BFLA4621**; 30-Jul-2021; size 30 mm; part preserved in ethanol for DNA extraction, 16S sequence OQ975714; part preserved in 4% formalin and submitted to FMNH as UF-015291. – **BFLA4622**; 30-Jul-2021; size 30 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975715; part preserved in 4% formalin and

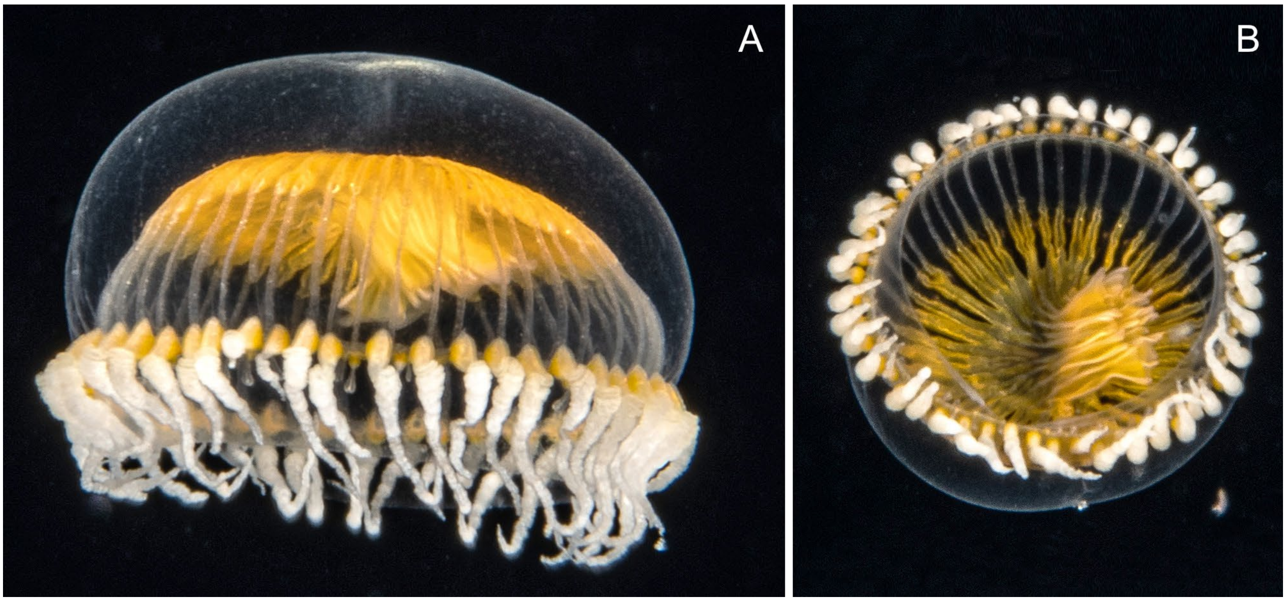


Fig. 35. *Staurodiscus luteus* BFLA4656, size 5 mm. (A) Lateral view. (B) Oral view. Photos by Linda Ianniello.

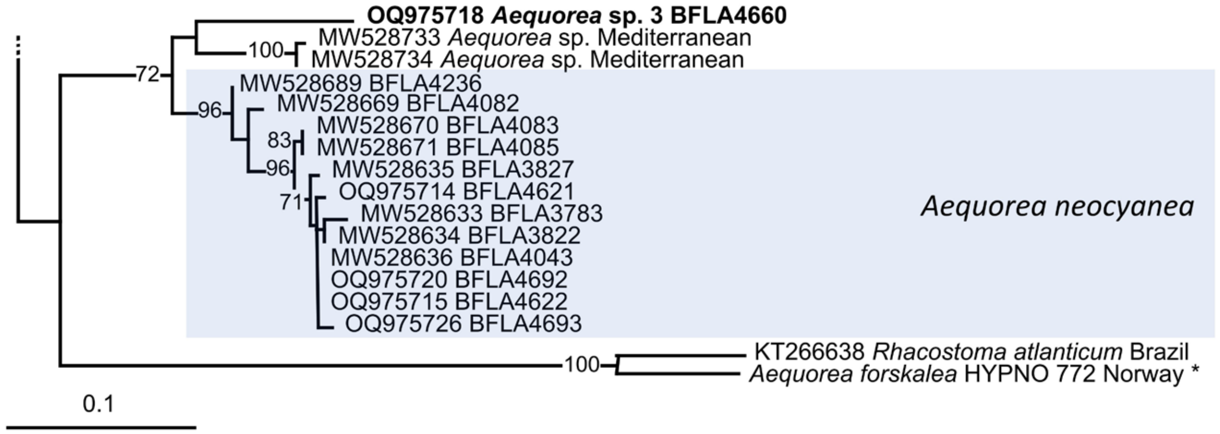


Fig. 36. Cropped 16S maximum likelihood phylogenetic tree of the genus *Aequorea* and related genera obtained with PhyML (GTR+G+I model) using about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers permitting the retrieval of more information. * Unpublished sequence, A. Hosia & L. Martell, pers. comm., see Schuchert & Collins (2021) for more details.

submitted to FMNH as UF-015292. – **BFLA4692**; 22-Oct-2021; size 28 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975720; part preserved in 4% formalin and submitted to FMNH as UF-016212. – **BFLA4693**; 22-Oct-2021; size 48 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975726, COI sequence OQ975024; part preserved in 4% formalin and submitted to FMNH as UF-016213.

Description: As in Schuchert & Collins (2021). For some specimens we observed a ratio of radial canals to tentacles of 5 or 5.5. One of these specimens (BFLA4519, Fig. 37B) was rather small (10 mm), but had about 60 radial canals on which the gonads just began to develop. A peculiar feature were its abaxially protruding tentacle bulbs (Fig. 37B, arrow).

Sequence Data: The five new haplotypes found in this study were compared with our previously determined sequences of this species. For the nine haplotypes we observed a maximal intraspecific p-distance of 2.2% (Fig. 36). Similarly, for the four new COI sequences the p-distances ranged from 0.5 to 2.5%.

Distribution: Florida, Bermuda, perhaps also Brazil and even Mediterranean (Schuchert & Collins, 2021). Type locality: Atlantic Ocean, USA, Florida, Key West.

Remarks: See the discussion under *Aequorea* sp. 3.

Aequorea taiwanensis Zheng *et al.*, 2009

Aequorea taiwanensis. – Schuchert & Collins, 2021: 303, fig. 41A-G.

Examined material: BFLA4681; 4-Oct-2021; size 20 mm, broke apart after capture; small part preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528705; remaining parts preserved in 4% formalin and deposited in FMNH as UF-016208.

Remarks: For description and other data see Schuchert & Collins (2021). No new 16S haplotypes were found.

Aequorea sp. 1

Aequorea spec. 1. – Schuchert & Collins, 2021: 301, fig. 40A-K.

Examined material: BFLA4521; 16-Apr-2021; size 5 mm, immature; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528681 (of BFLA4163). – **BFLA4547**; 07-May-2021; size 8 mm, two manubria, with beginning of gonad development; part preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528681; remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-015253. – **BFLA4569**; 19-Jun-2021; size 10 mm, two manubria, beginning of gonad development; part preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528681; remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-015267. – **BFLA4626**; 31-Jul-2021; size 10 mm, beginning of gonad development; part preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528681; remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-015294. – **BFLA4632**; 04-Aug-2021; size 12 mm, gonads visible, still many incomplete radial canals; part preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528681; remaining part preserved in 4% formalin and deposited in FMNH as UF-015296. – **BFLA4671**; 06-Oct-2021; size 9 mm, gonads visible, still many incomplete radial canals; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528681.

Description: As in Schuchert & Collins (2021). A confirmed regular difference to *A. neocyanea* is the presence of a tubular excretory papilla. Unfortunately, it is often difficult to see, especially in preserved material or when the bulbs are swollen. If a papilla is visible, then this seems to be a good discriminator to separate it

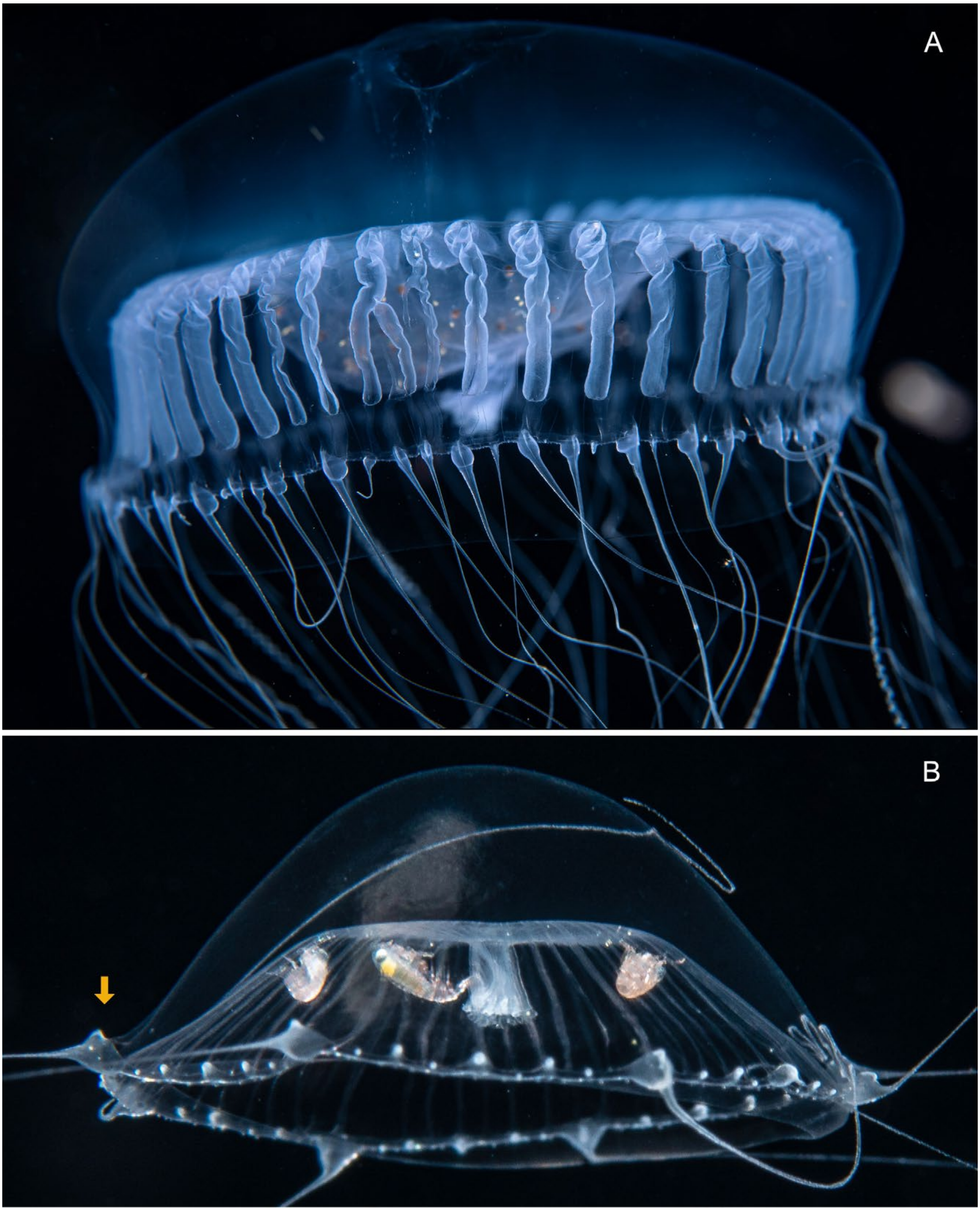


Fig. 37. *Aequorea neocyanea.* (A) BFLA4693, diameter 48 mm; lateral view of the animal, note the fully developed gonads, there are about as many radial canals as tentacles, the exumbrella is damaged. (B) BFLA4519, diameter about 10 mm, juvenile or more likely an animal regenerated from a fragment, identified via 16S sequence, crustaceans are in the subumbrella, note the protruding abaxial part of a tentacle bulb (yellow arrow).

from the similar, but larger *A. neocyanea*. If not visible, this is not diagnostic for *A. neocyanea* and 16S data are necessary to separate the two.

Sequence Data: The six determined 16S sequences were all identical to MW528681 (obtained from BFLA4163, see Schuchert & Collins, 2021: fig. 40A-B).

Remarks: None of the new samples represented a more advanced stage than BFLA4163 documented in Schuchert & Collins (2021). If present, in all these samples the gonads were small and appeared not fully developed. Additionally, some radial canals may lack them, and new radial canals are still forming (presence of incomplete centrifugal canals). We therefore again renounced describing it as a new species. A fully grown specimen is needed to name and describe it appropriately.

Aequorea sp. 3

Fig. 38A-D

Examined material: BFLA4660; 8-Sep-2021; size: 11-12 mm; part preserved in ethanol for DNA extraction, 16S sequence OQ975718; remaining part preserved in formalin and deposited in FMNH as UF-016200.

Description: *Aequorea* medusa 11-12 mm in diameter, bell flatter than hemisphere (Fig. 38B), jelly at top spanning nearly half the bell height. Stomach large, diameter ½ of bell diameter. About 48 complete radial canals, four centrifugal incomplete canals, with regional irregularities of radial canals, such as branching, fusion, or interruptions. Gonads begin development along radial canals, visible as thickenings, reaching from manubrium to ⅔ length of radial canal. Seven bulbs with tentacles, in-between them smaller to tiny bulbs without tentacles (Fig. 38A). Ratios of radial canals to tentacle bearing bulbs about 7. Fully developed tentacle bulbs large, without distinct abaxial keel, without abaxial spur, but abaxial side distinctly protruding and supported by a ledge of the exumbrella (Fig. 38C, yellow arrow). Excretory pores present, on a very small conical papilla (Fig. 38D, red arrow). One statocyst between two bulbs. Colours: the tentacle bulbs and tentacles had a light purple hue in daylight, brownish on photos.

Sequence Data: All new *Aequorea* 16S haplotypes of this study were combined with the dataset used in Schuchert & Collins (2021) and a maximum likelihood phylogenetic tree was calculated (GTR+I+G substitution model). As only a part of the tree differed substantially from fig. 37 in Schuchert & Collins (2021), only this clade is shown here for clarity reasons (Fig. 36).

The minimal p-distance of the 16S sequence of *Aequorea* sp. 3 to *A. neocyanea* was 4.7% (MW528689), to MW528734 *Aequorea* sp. Mediterranean it was 3.5%.

Remarks: The informal species number 3 was chosen in continuation of the unnamed species presented in

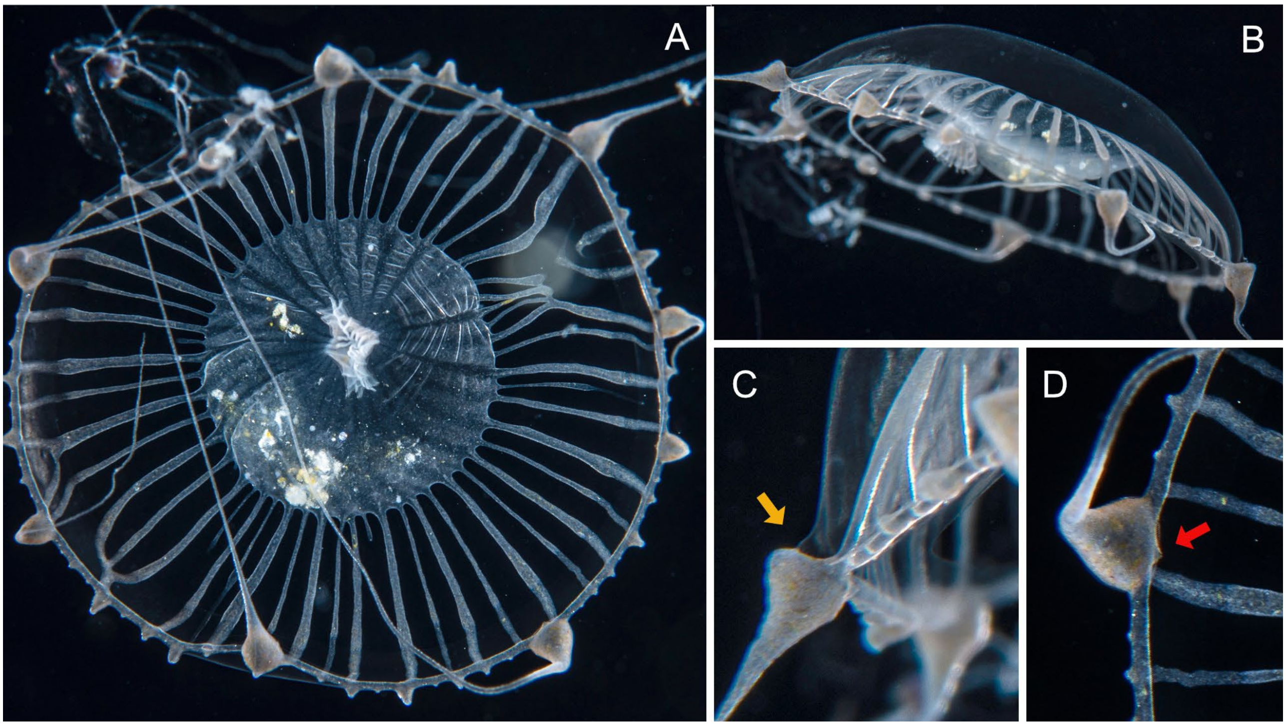


Fig. 38. *Aequorea* sp. 3, BFLA4660, bell diameter 12 mm. (A) View from oral side. (B) Lateral view. (C) Lateral view of tentacle base, the yellow arrow indicates the protruding part of bulb and exumbrella. (D) Tentacle bulb seen from adaxial side, the red arrow points to a small excretory papilla.

Schuchert & Collins (2021). The only sample we had of this medusa was a subadult and it was therefore not possible to identify this medusa with any other nominal *Aequorea* species. Its only particularity are the tentacle bulbs with their protruding abaxial part (Fig. 38C), but a similar situation can occasionally also occur in *A. neocyanea* (Fig. 37B). We suspect that these could be artefacts, or the result of the animals being regenerated from fragmented individuals.

The 16S sequence grouped this specimen closely with *A. neocyanea* and two *Aequorea* specimens from the Mediterranean (Fig. 36). The sequences of the latter two were provided in Schuchert & Collins (2021: 239, 301) who were not sure if they are also referrable to *A. neocyanea*. *Aequorea* sp. 3 complicates the situation even more, at least at this stage with only one specimen available and not knowing its intraspecifc variability.

Aequorea sp. 3 appears different from *A. neocyanea,* but most traits fall within the range of variability also seen in the latter. This includes also the abaxial protrusion of the tentacle bulbs (Fig. 38B). The observed presence of a small excretory papilla and the light purple to brownish colour of the tentacle remain as differences, but are not really convincing. At this stage we are still unable to decide whether the present sample BFLA4660 and the two samples from the Mediterranean that gave the sequences MW528734 and MW528734 (Fig. 36) also belong to *A. neocyanea*.

Species limits in the genus *Aequorea* are unfolding as being very complex and a lot of additional work is essential in order to understand the situation at a global level. It is not enough to sample more specimens from the same site, but specimens from many populations and all seas must be examined and barcoded. The available morphological traits are likely insufficient to separate the species and we like to reiterate the opinion of Kramp (1961), who plainly expressed "The [*Aequorea*] species are more or less doubtful."

Genus *Zygocanna* Haeckel, 1879

Diagnosis: Aequoridae medusa with wide manubrium, no gastric peduncle, subumbrella with or without radial rows of gelatinous papillae. With more than 16 radial canals, at least some branched, new radial canals develop centrifugally from stomach base. Tentacle bulbs usually with excretory papillae. Gonads on radial canals, separated from manubrium.

Hydroids unknown.

Zygocanna cf. *apapillatus* Xu, Huang & Guo, 2014

Zygocanna cf. *apapillatus*. – Schuchert & Collins, 2021: 306, fig. 43A-E.

Examined material: BFLA4877; 02-Feb-2023; size 5 mm; preserved in ethanol for DNA extraction; deposited in FMNH as UF-017277.

Description: As in Schuchert & Collins (2021), mature female with 16 yellow gonads as in previous sample.

Remarks: See discussion in Schuchert & Collins (2021).

Family Malagazziidae Bouillon, 1984
Genus *Octophialucium* Kramp, 1955

Diagnosis: Medusa without gastric peduncle, manubrium with eight lips; usually eight radial canals, variable in some species from 6 to 11; gonads on radial canals, separated from manubrium; tentacle bulbs with adaxial excretory papillae; no permanent atentaculate marginal bulbs, only developing tentacular bulbs; with closed statocysts; no ocelli; no cirri.

Hydroid colony stolonal; hydrotheca pedicellate, with a conical operculum formed by numerous convergent segments that are not clearly demarcated from hydrothecal wall; hydranth with intertentacular web; gonothecae claviform, arising from stolons.

Octophialucium aphrodite (Bigelow, 1928)

Fig. 39A-F

Octophialucium aphrodite. – Schuchert & Collins, 2021: 309, fig. 44A-F.

Examined material: BFLA4575; 24-Jun-2021; size 18 mm, subadult, 8 radial canals; part preserved in ethanol for DNA extraction, 16S sequence OQ975705, COI sequence OQ975017; remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-015270. – **BFLA4840**; 19-Aug-2022; size 26 mm, 8 radial canals, with gonads; part preserved in ethanol and part preserved in 4% formalin, both deposited in FMNH as UF-017268. – **BFLA4848**; 06-Oct-2022; size 15 mm, subadult, only 7 radial canals; some photos made after collection in tray using the full blue light source combined with a yellow filter; part preserved in ethanol and part preserved in 4% formalin, both deposited in FMNH as UF-017272.

Description and distribution: See Schuchert & Collins (2021). One specimen (BFLA4848) had only seven radial canals. Previously we observed eight to ten radial canals.

Sequence Data: The new haplotype obtained in this study differed only in one indel from GenBank MW528632 described in our former publication.

Remarks: Under blue light, the marginal bulbs showed a strong fluorescence, the manubrium and the radial canals produced a weaker signal (Fig. 39E).

Octophialucium irregularis Schuchert & Collins, 2021

Fig. 40A-C

Octophialucium irregularis Schuchert & Collins, 2021: 310, fig. 45A-G.

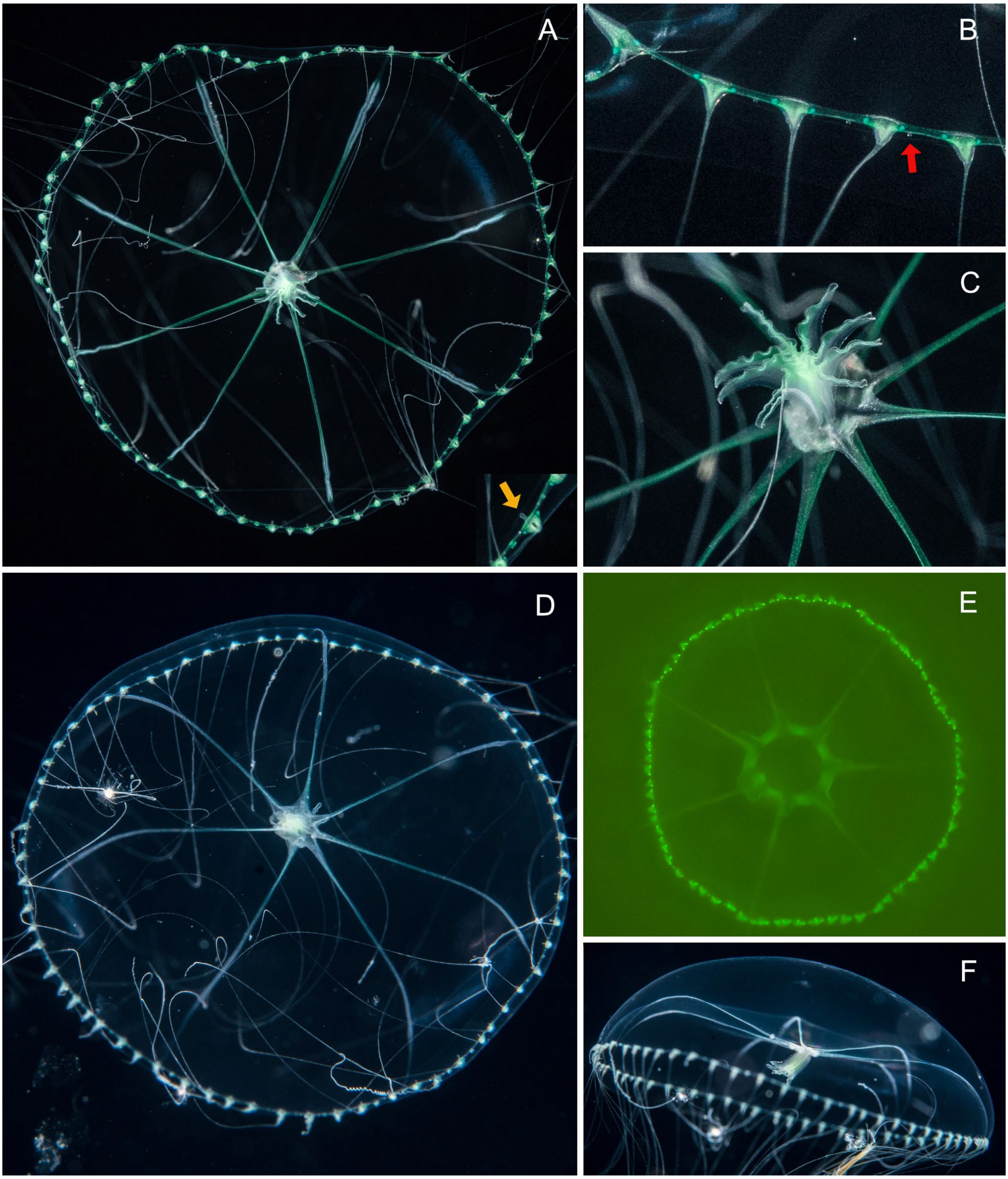


Fig. 39. *Octophialucium aphrodite.* (A-C) BFLA4575, diameter 18 mm. (A) Oral view, inset at bottom right shows enlargement of tentacle bulb with the typical, large excretory papilla (yellow arrow). (B) Bell margin with tentacle bulbs, the statocysts can barely be seen (red arrow). (C) Manubrium in oral view. (D-F) BFLA4848, diameter 15 mm. (D) Oral view, note that it has only 7 radial canals; blue light plus white flash. (E) Oral view under full blue light (plus yellow filter), photo made in the laboratory. The background appears also green because of the white background of the tray. Note the strong fluorescence of the marginal bulbs. (F) Lateral view, blue light plus white flash. Photos A-C by Andrea Whitaker.

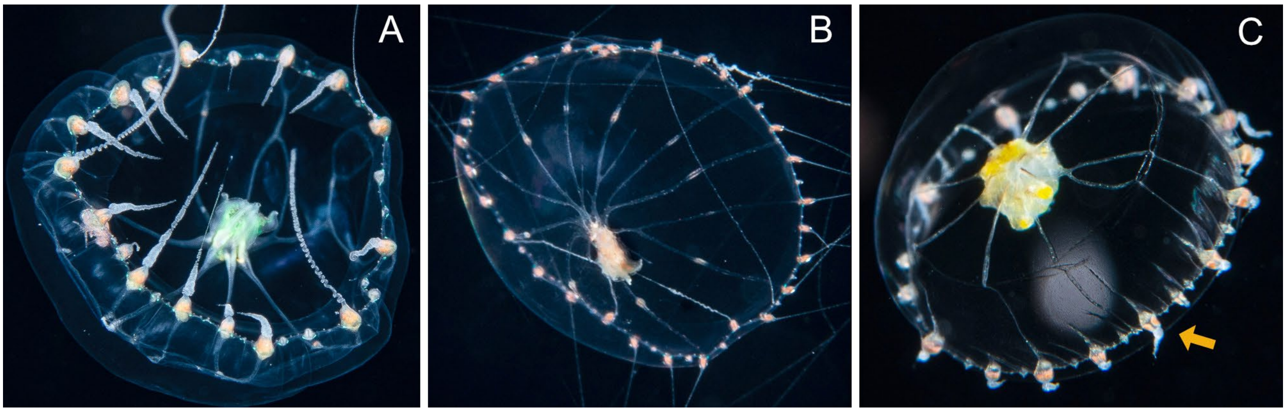


Fig. 40. *Octophialucium irregularis*. (A) BFLA4624, oral view, diameter 8 mm. (B) BFLA4734, oral view, diameter 4 mm. (C) BFLA4661, oblique aboral view, diameter 5 mm, the yellow objects in the stomach are presumably food items. The arrow points at a tentacle bulb with its characteristic orange colour divided into two parts. Photo A by Deb Devers.

Examined material: BFLA4624; 30-Jul-2021; size 8 mm, immature; preserved in 4% formalin and deposited in FMNH as UF-015293. – **BFLA4661**; 18-Sep-2021; size 5 mm, immature; preserved in ethanol for DNA extraction, 16S sequence identical to MW528656 (=BFLA3838). – **BFLA4734**; 10-Dec-2021, incipient gonads; size 4 mm; preserved in ethanol for DNA extraction and deposited in FMNH as UF-016233. – 27-Oct-2021; two animals, size ~5 mm, one with small gonads, one with large ones; not collected, identity unclear. – 21-Jul-2022; 1 specimen, size 12 mm, two manubria; not collected. – **BFLA4709**; 26-Nov-2021; size 6 mm; preserved in ethanol for DNA extraction and deposited in FMNH as UF-016222, identification uncertain as juvenile and no sequence data available.

Description: See Schuchert & Collins (2021).

Distribution: Off Florida only.

Remarks: All eight so far sequenced specimens had an identical 16S sequence and they were collected over a timespan of three years. This uniformity could indicate a recent origin in the region, perhaps a recent colonization by the polyp.

The orange tentacle bulbs are helpful to distinguish the species from *Zygocanna* cf. *apapillatus* (Fig. 40C, arrow).

Family Campanulariidae Johnston, 1836

Genus *Clytia* Lamouroux, 1812

Diagnosis: Medusa with normal, curved umbrella. Manubrium short, with four short perradial lips. Velum present. Normally four radial canals, but some aberrant forms may have more. Marginal tentacles >16, with hollow bulbs; without many permanent, small, conical atentaculate bulbs, no excretory papillae. With many statocysts (>16), usually as many or more as tentacles, no ocelli, no cirri. Gonads on radial canals, usually short, not in contact with manubrium.

Hydroid typical for family, colonial, stolonal or erect branched, monosiphonic or polysiphonic. Hydrothecae deep, campanulate, hydrothecal rim sinuous or deeply indented, true hydrothecal diaphragm, gonotheca conical.

Remarks: Because most *Clytia* medusae are not unambiguously identifiable without knowing the polyp stage, only samples for which we could obtain 16S sequence information are treated here, except for *Clytia mccradyi*.

Clytia mccradyi (Brooks, 1888)

Fig. 41A-B

Epenthesis mccradyi Brooks, 1888: 149, pls 13-15.

Oceania mccradyi. – Mayer, 1900b: 50, pl. 31 figs 56-59. – Mayer, 1904: 15, pl. 3 figs 23-24.

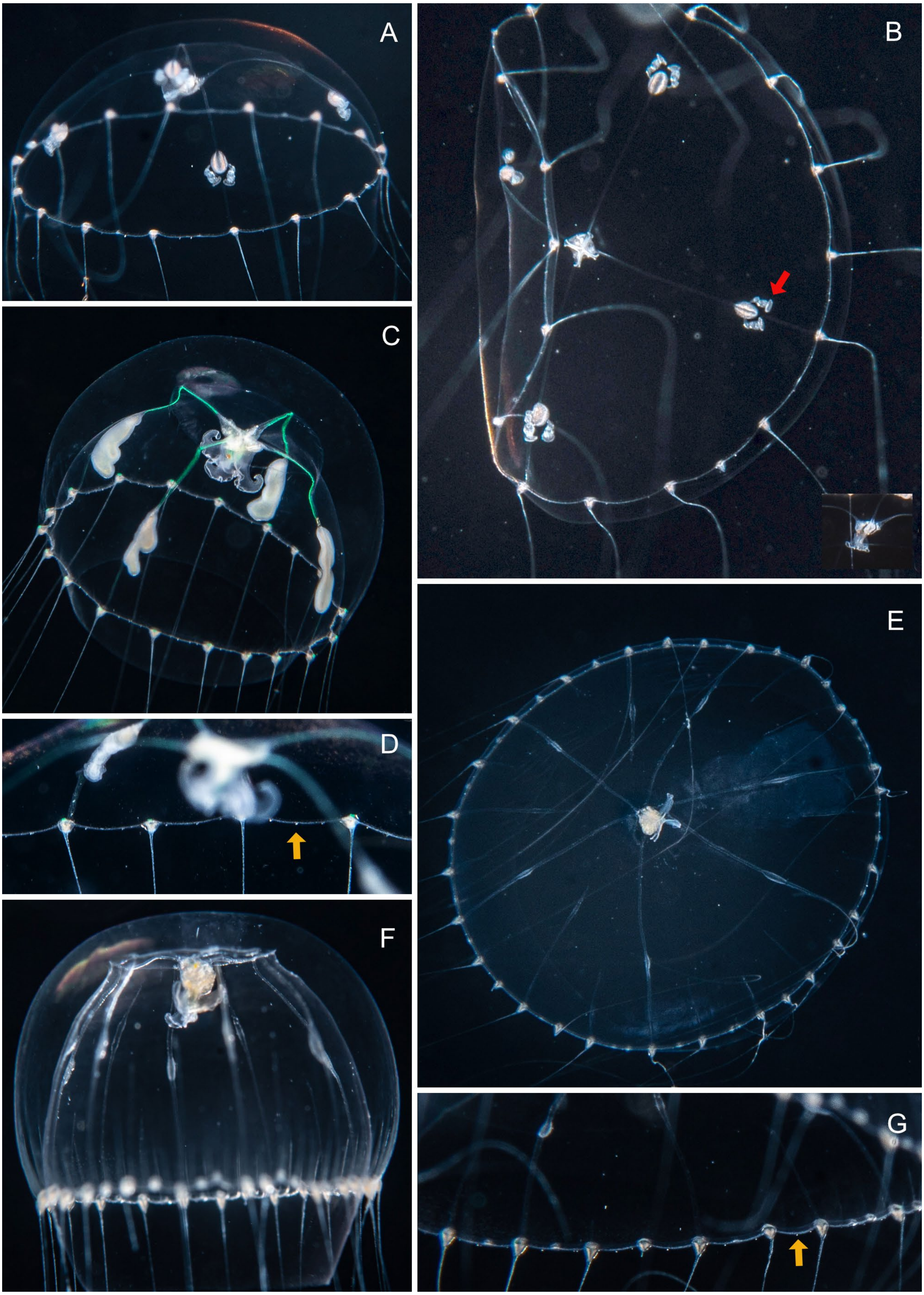
Phialidium mccradyi. – Mayer, 1910: 271, pl. 34 figs 2-3; pl. 35 figs 1-3. – Vanhöffen, 1913: 423. – Kramp, 1959: 149, fig. 188. – Kramp, 1961: 170.

Clytia mccradyi. – Cornelius, 1982: 87, fig. 13. – Goy *et al*., 1991: 113, fig. 33. – Carré *et al*., 1995: 194, figs 1-4.

Examined material: 1 specimen photographed 07-May-2021; size 5 mm; not collected.

Description: *Clytia* medusa, diameter 5 mm, umbrella about half the diameter, mesogloea gradually and evenly

Fig. 41. *Clytia* species. (A-B) *Clytia mccradyi,* size 5 mm. (A) Lateral view. (B) Oral view, red arrow indicates gonothecae growing out of gonads; inset in lower right corner shows manubrium with characteristic pigmentation. (C) *Clytia* sp. 1, BFLA4567, size 11 mm, lateral view, the sharp bends of the radial canal are transitory and due to contraction of the bell. (D) *Clytia* sp. 1, BFLA4573, bell size 9 mm, bell margin, yellow arrow indicates the barely visible statocysts. (E-G) *Clytia* sp. 2, BFLA4550, size 6 mm. (E) Oral view. (F) Lateral view. (G) Bell margin, yellow arrow indicates the barely visible statocysts. ►


A
B
C
D
E
F
G

thickening towards aboral, thickness at apex about ⅙ of total height. Manubrium small, about ⅕ of subumbrellar height, cruciform mouth with four recurved, perradial lips. Four thin radial canals. Gonads small, oval, on radial canals at about ⅔ of their length. On each adradial side of the gonads a small gonotheca, shaped like inverted cone, end truncated and opaque (growth zone). Sixteen thin tentacles on small bulbs, additionally two bulbs without tentacles. Between each pair of tentacles 1 to 2 statocysts. Colours: gonads and marginal bulbs pale pink-orange; interradial walls of stomach with dark vertical band.

Distribution: Along the east coast of the USA from Florida to the Gulf of Maine (Mayer, 1910; Pagès *et al.*, 2006), Caribbean Sea and coast of Mexico (Segura Puertas *et al.*, 2009), Mediterranean (Goy, 1970; Goy *et al.*, 1991; Buecher & Gibbons, 1999), Indian Ocean (Navas-Pereira & Vannuci, 1991), Bismarck Sea (Bouillon, 1984b; Bouillon *et al.*, 1986), Chinese coast estuary (Xu *et al.*, 1985), Pacific coast of Mexico (Segura Puertas *et al.*, 2010). Type locality: Bahamas, Nassau (Brooks, 1888).

Remarks: Although *C. mccradyi* can attain 10 to 15 mm in size (Mayer, 1910; Kramp, 1961), our only observed sample was relatively small and also the gonads were not fully developed. It was thus presumably a subadult. However, it had the diagnostic gonothecae growing out of the gonads (Fig. 41A-B), although these were still in the beginning of their developement. Additionally, the manubrium had the interradial vertical bands of dark pigmentation which are characteristic for the species (Mayer, 1910; Vanhöffen, 1913; Carré *et al.*, 1995).

Clytia sp. 1
Fig. 41C-D

Clytia spec. 1. – Schuchert & Collins, 2021: 312, fig. 46C.

Examined material: BFLA4567; 19-Jun-2021; size 11 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975703, COI sequence OQ975016. – **BFLA4573**; 24-Jun-2021; size 9 mm; preserved in ethanol for DNA extraction, 16S sequence identical to OQ975703.

Description: See Schuchert & Collins (2021).

Sequence Data: The two new 16S sequences were identical and had only one base pair difference to our previously published one of the same species (GenBank MW528690).

Distribution: Off Florida.

Remarks: As noted before, this medusa could formally be attributed to *Clytia hemisphaerica* (Linnaeus, 1767), but the 16S or COI sequences do not match those obtained from typical *C. hemisphaerica* hydroids from the NE Atlantic (*e.g.* GenBank MF000553, or using a blastn search in GenBank).

Clytia sp. 2
Fig. 41E-G

Clytia spec. 2. – Schuchert & Collins, 2021: 314, fig. 46D-G.

Examined material: BFLA4550; 07-May-2021; size 6 mm; preserved in ethanol for DNA extraction, 16S sequence identical to MW528694 (= BFLA4253).

Description: See Schuchert & Collins (2021).

Sequence Data: The 16S sequence of the new sample was identical to our previously determined sequence of this species.

Distribution: Off Florida.

Remarks: With its irregular number of radial canals (Fig. 42E-G) and the occurrence of centripetal canals, this is a highly unusual *Clytia* species. The repeated findings of this morphotype confirms that it is not an accidental aberration. The taxonomic status and the relationships with other Campanulariidae are discussed in Schuchert & Collins (2021).
The 16S sequences of all five samples so far sequenced were identical, despite they were collected at three different dates. This could indicate a quite recent colonization.

Family Lovenellidae *incertae sedis*
Fig. 42A-C

Examined material: BFLA4531; 21-Apr-2021; size 2.5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975694. – **BFLA4541**; 25-Apr-2021; size 5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975697, COI sequence OQ975014.

Description: Umbrella relatively flat, watch-glass shaped, diameter 2.5 to 5 mm, mesogloea thin. Manubrium small, in both specimens with a three-lipped mouth (Fig. 42A, inset). Six to 8 radial canals issued from manubrium, one or two bifurcated more distally, all reaching circular canal. Gonads not fully developed, oblong in about middle region of radial canals. With tentacles and lateral cirri on marginal bulbs. Seven or more long tentacles, fine. Larger marginal bulbs at junctions of radial canals with circular canals, not all bearing tentacles, 2-3 additional bulbs without tentacles present, between two pairs of tentacles up to 5 rudimentary bulbs. At least all tentacular bulbs with lateral cirri, 1 to 3 per side; rudimentary bulbs apparently without cirri. Cirri very thin, but ending in swollen, opaque end (presumably by nematocysts). Cirri very contractile: they can contract so that they become almost invisible (Fig. 42A), but they can also stretch out to almost half the bell diameter (Fig. 42B-C, yellow arrows). Statocysts closed, with 2 to 3 concretions. Colours: clear or faint greenish hue.

Sequence Data: The two obtained 16S sequences differed in 3 base pairs (p-distance 0.5%). Using the

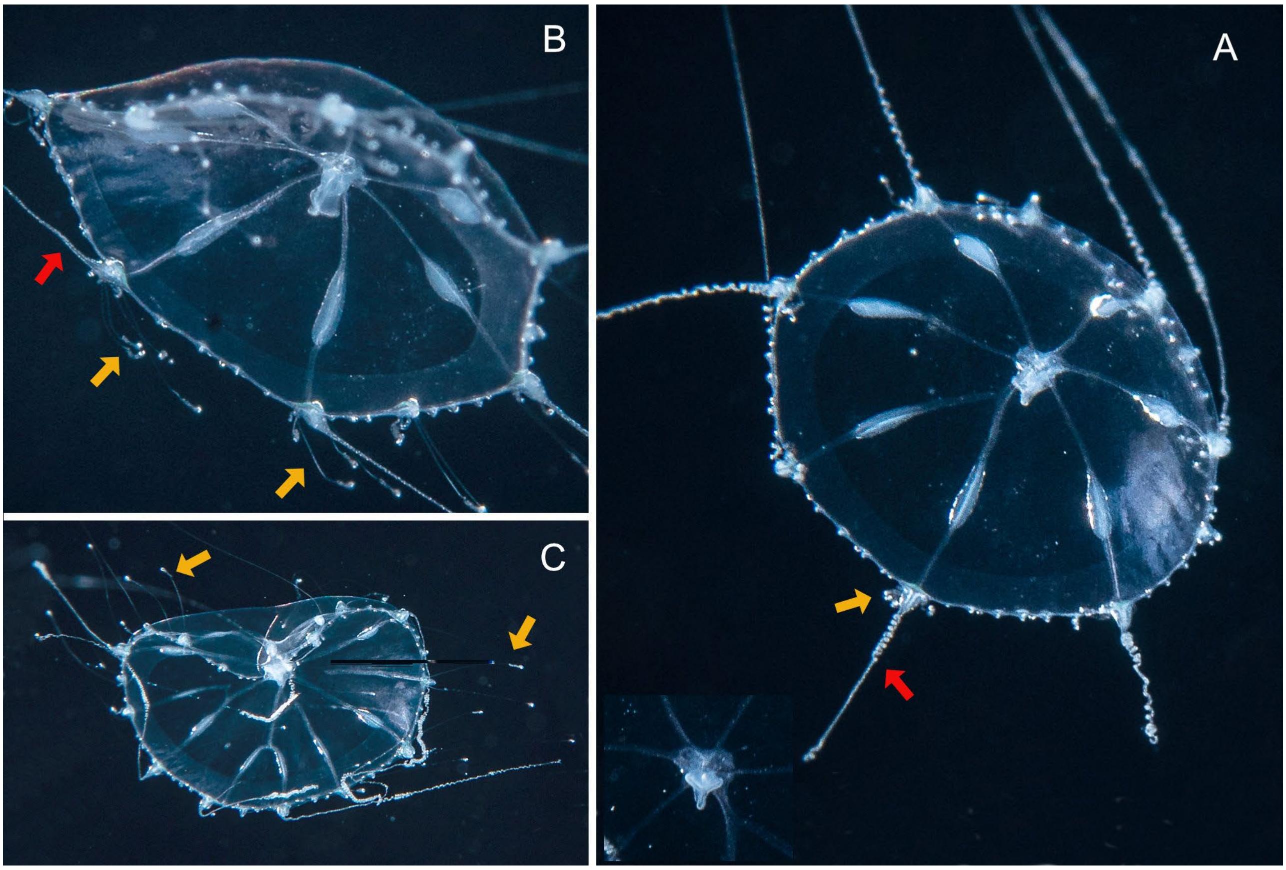


Fig. 42. Lovenellidae *incertae sedis,* yellow arrows indicate cirri, red arrows normal tentacles. (A-B) BFLA4531, size 2.5 mm, oblique aboral view, in A the cirri are contracted, in B stretched out. Inset in lower corner of A shows manubrium in oral view. (C) BFLA4541, size 5 mm, oblique aboral view, many cirri are stretched out.

blastn search engine in GenBank resulted in a long list of leptomedusae, the best matches being all Lovenellidae species, but also *Tima bairdi* (Johnston, 1833). A search for the COI sequence in the BOLD system (Ratnasingham & Hebert, 2007) also gave several *Eucheilota* sp. (Lovenellidae) as matches at the genus level. However, both searches gave only similarities around 92% and no species matches. Using the 16S dataset of Leclère *et al.* (2009) and Maronna *et al.* (2016), supplemented with some new Lovenellidae from GenBank, to generate a Maximum Likelihood phylogenetic tree, associated the present samples also with Lovenellidae and other cirri-bearing leptomedusae, but without yielding any bootstrap node supports higher than 70% (results not shown).

Distribution: Off Florida.

Remarks: The presence of lateral cirri and the absence of a gastric peduncle would place the samples BFLA4531 and BFLA4541 clearly in the family Lovenellidae. However, no known Lovenellidae species has more than four radial canals. There is also no other known genus which combines the traits of lateral cirri with the presence of more than four radial canals (Bouillon *et al.*, 2006). The 16S and COI sequences also indicate a possible relationship with the Lovenellidae, but the results are not conclusive enough due to their poor resolving power above the genus level.

The present medusae could be aberrant forms of a normally four-rayed medusa, *e.g. Lovenella cirrata* (Haeckel, 1879). The finding of two individuals on two different dates argues strongly against the high number of radial canals being solely aberrant forms. If so, a new genus and species must be established and the family diagnosis adapted. However, we deem the available material and information to be insufficient and we prefer to wait for more samples to become available. In particular, the microscopic details of the statocysts and cirri must be described and the variability of the radial canals evaluated.

Order Narcomedusae
Family Cuninidae Bigelow, 1913
Genus *Cunina* Eschscholtz, 1829

Diagnosis: Narcomedusae with as many undivided manubrial pouches as tentacles, gonads in these pouches, primary tentacles positioned in middle of the lower margin of the stomach pouches; with otoporpae, with or without peripheral canal system, without small secondary marginal tentacles.

Cunina octonaria McCrady, 1859

Fig. 44A-C

Cunina octonaria. – Schuchert & Collins, 2021: 316, fig. 50A-D

Examined material: BFLA4497; 16-Oct-2020; size 5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975690 – **BFLA4605**; 15-Jul-2021; size 5.5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975709. – **BFLA4832**; 04-Aug-2022; size 2 mm; preserved in ethanol for DNA extraction, deposited in FMNH as UF-017267. – 1 specimen photographed 06-Aug-2021; size 5 mm; not collected.

Description: See Schuchert & Collins (2021). All examined samples from the Gulf Stream had 8 tentacles.

Sequence data: Two 16S sequences could be obtained. The divergence calculated as p-distance was 1%. In the ML tree (Fig. 43) they formed a well-supported clade with two other *C. octonaria,* one from the Mediterranean, the other from Japan.

Distribution: Widely distributed in tropical and warm-temperate parts of all oceans, including also the Mediterranean, the Chilean coast, and the South Atlantic (Schuchert & Collins, 2021). Type locality: USA, South Carolina, Charleston Harbor.

Remarks: The 16S of *Cunina octonaria* formed a well supported clade (Fig. 43), but the three 16S lineages from different geographic origins were rather divergent. The divergence to the Japanese sequence was 15% (p-distance), to the Mediterranean even 19%. The Japanese sequence diverged 14% from the Mediterranean one. These values are relatively high and perhaps the three populations represent three species or subspecies. The samples from off Florida come from the same biogeographical region as the type specimen, and thus likely representate the "true *C. octonaria*", in case there is more conclusive evidence that there are several species involved.

The available photos lend themselves well to document some structural details of the Narcomedusae and the genus *Cunina* (Fig. 44).

Cunina sp.

Fig. 45A-C

Examined material: BFLA4853; 22-Dec-2022; size 7.5 mm; preserved in ethanol for DNA extraction, deposited in FMNH as UF-017274.

Description: *Cunina* medusa 7-8 mm in diameter, umbrella calotte-shaped, wider than high. Stomach circular, about half diameter of bell, without mesogloea cone. Stomach periphery with 11 gastric pockets, one additional pocket in development (Fig. 45A), gastric pockets relatively narrow but deep, about two times as deep as wide, widening towards periphery, peripheral margin slightly curved, septa between pockets relatively wide, nearly half the width of the gastric pockets, wedge-shaped. Eleven tentacles originating in middle of pocket base with a short, conical root, length of tentacles equals about diameter of bell. Bell margin between pairs of tentacles lobed, these marginal lappets nearly triangular, lateral sides somewhat bulging, at distal edge a single median statocysts and 2 to 3 short otoporpae (Fig. 45A-B). No peripheral canal discernible. Gonads not developed. Colours: crystal clear in tray, hard to see in situ and in the tray, impossible to see without bright light source.

Remarks: Using the identification key in Kramp (1959, 1968) would identify this medusa as *C. peregrina*. However, it is clearly distinct from typical *C. peregrina* as described by H.B. Bigelow (1909, 1918), Kramp (1955, 1957, 1959, 1968), Bouillon (1987), Goy (1979), and Pagès *et al.* (1992). The main difference is the number of statocysts per marginal lappet which was always one only in the present specimen. This cannot be a difference of developmental stage. H.B. Bigelow (1909), when describing the new species *C. peregrina*, fortunately had more than 30 specimens of different developmental stages. Even his smallest animal at 2 mm size had already 3 to 4 statocysts and otoporpae per lappet. Later stages had 4 to 6 otoporpae. Other subtle differences of the present specimens are found in its narrower gastric pockets, the triangular peripheral lappets (in *C. peregrina* more rectangular or rounded, H.B. Bigelow, 1909: pl. 1 fig. 6, pl. 15 fig. 1-2), the gastric pockets are narrower and more elongate, the occlusions separating them wider and triangular. We are therefore convinced that this represents a species distinct from *C. peregrina* and all other currently known *Cunina* species (Schuchert, 2023). We abstain from naming it here because the only specimen was immature and it was not possible for us at this time to get sequence information.

Family Pseudaeginidae Lindsay, Bentlage & Collins, 2017

Genus *Pseudaegina* Lindsay, 2017

Diagnosis: Narcomedusae with interradial, divided manubrial pouches; with peripheral canal system; with primary perradial tentacles leaving umbrella between marginal pouches, in number half that of manubrial pouches; pouches begin at points of origin of primary tentacles; tentacle roots recurved orally without penetrating deep into central mesoglea; deep peronial grooves lined with nematocysts below but not above points of origin of primary tentacles; without secondary tentacles on umbrella margin; without otoporpae.

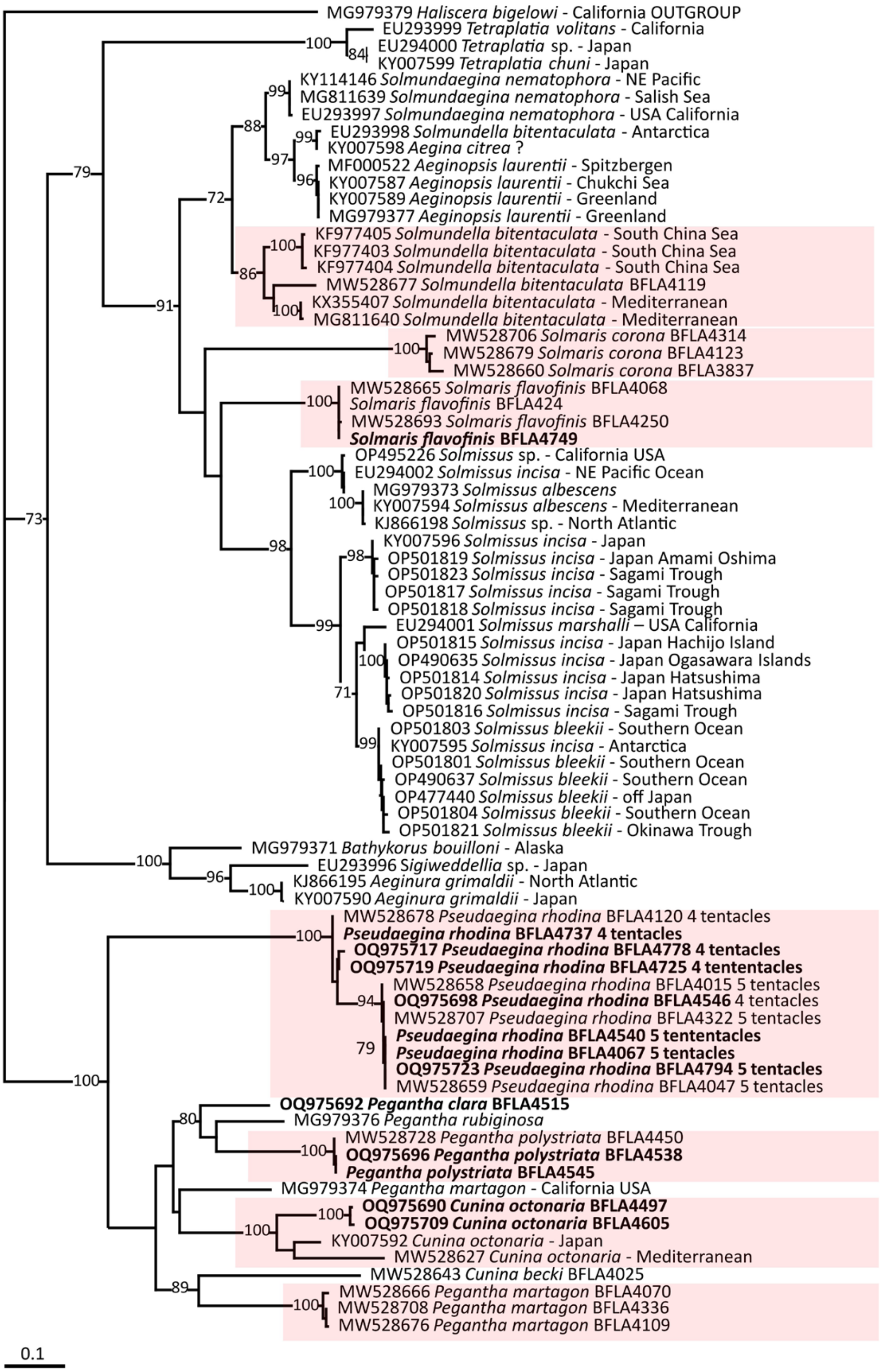


Fig. 43. Maximum likelihood phylogenetic tree of Narcomedusae obtained with PhyML (GTR+G model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Bold names are from this study, coloured boxes mark species clades of the present and our former study.

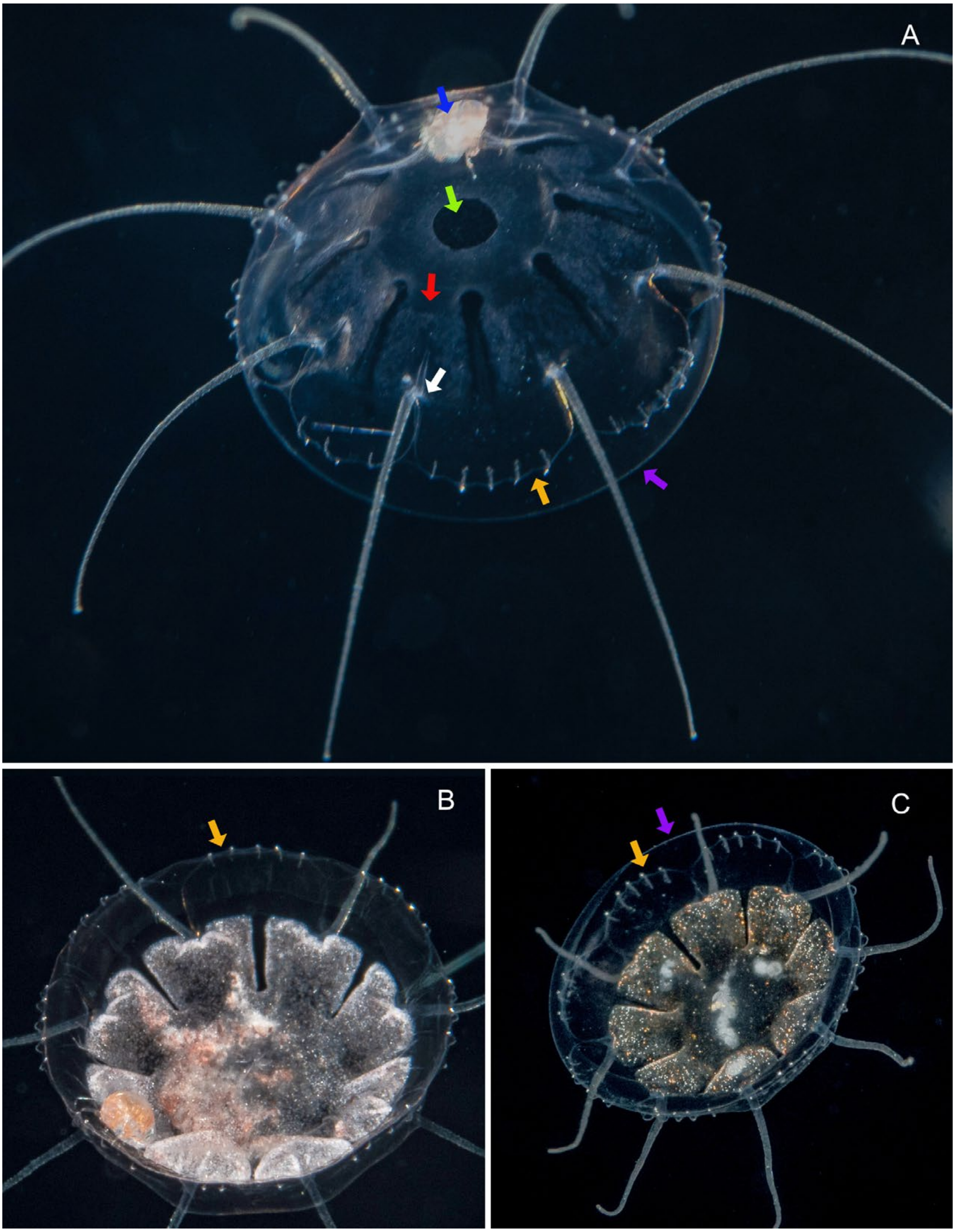


Fig. 44. *Cunina octonaria*. Structural details: green arrow – mouth, seen through apical jelly; blue arrow – crustacean on exumbrella; red arrow – gastric pocket; white arrow – tentacle base, continued in mesogloea as pointed tentacle root; purple arrows – velum rim; yellow arrows – rim of peronial lappet with five otoporpae. (A) Animal of 06-Aug-2021, 5 mm, oblique view on top of umbrella. (B) BFLA4605, size 5.5 mm, view on underside of bell. The gastric system opaque as it is filled with partially digested food. The filled gastric system also shows that there is no peripheral canal running from one tentacle base to the next one along the peronial lappet. (C) BFLA4832, size 2 mm, view on oral side; the stomach is filled with semi-digested food. Photo A by Linda Ianniello, photo C by Andrea Whitaker.

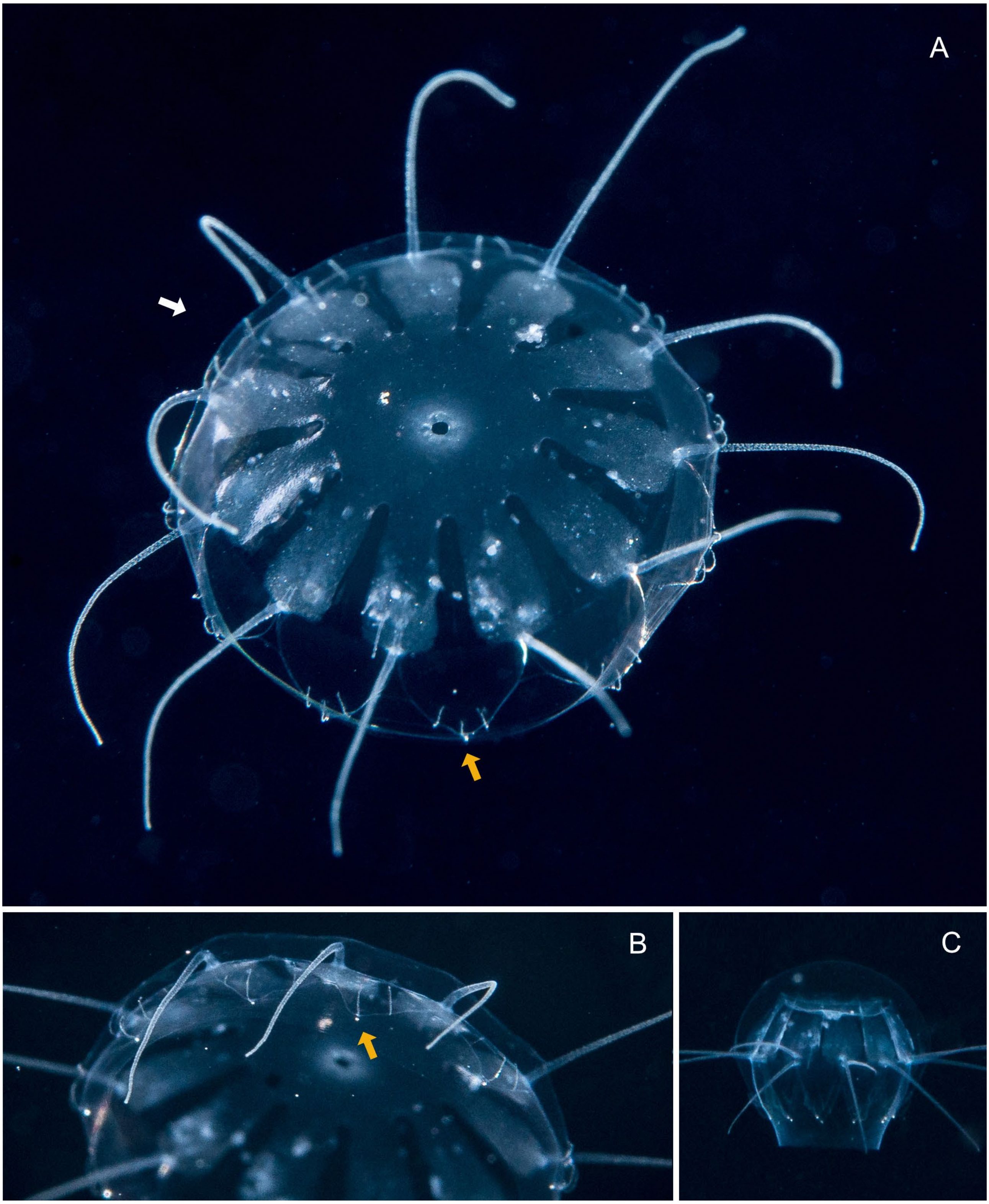


Fig. 45. *Cunina* sp. BFLA4853, diameter 7.5 mm. Details: white arrow – points to developing gastric pocket; yellow arrows – statocysts on peripheral lappets, visible as bright dots. (A) Oblique view on umbrella. (B) Oblique view of underside of bell rim. (C) Lateral view of bell, contracting and expulsing water from the subumbrella, the velum and the lappets are directed towards below.

***Pseudaegina rhodina* (Haeckel, 1879)**

Fig. 46A-D

Pseudaegina rhodina. – Schuchert & Collins, 2021: 319, fig. 51A-G, fig. 52A-B.

Examined material:

With 4 tentacles: **BFLA4546**; 05-May-2021; size 12 mm; part preserved in ethanol for DNA extraction, 16S sequence OQ975698; remaining part preserved in 4% formalin deposited in FMNH as voucher UF-015252. – **BFLA4737**; 10-Dec-2021; size 9 mm; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528678 (=BFLA4120). – **BFLA4778**; 10-Mar-2022; size 6.5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975717. – **BFLA4725;** 08-Dec-2021; 9 mm wide and 5 mm high; preserved in ethanol for DNA extraction, 16S sequence OQ975719. – **BFLA4813**; 02-Jun-2022; size 11 mm; preserved in ethanol for DNA extraction; sequencing failed. – **BFLA4881**; 02-Feb-2023; size 10 mm; preserved in ethanol for DNA extraction, deposited in FMNH as UF-017278. – 1 specimen photographed 08-Jan-2023; size 10 mm; not collected.

All samples appeared to be immature.

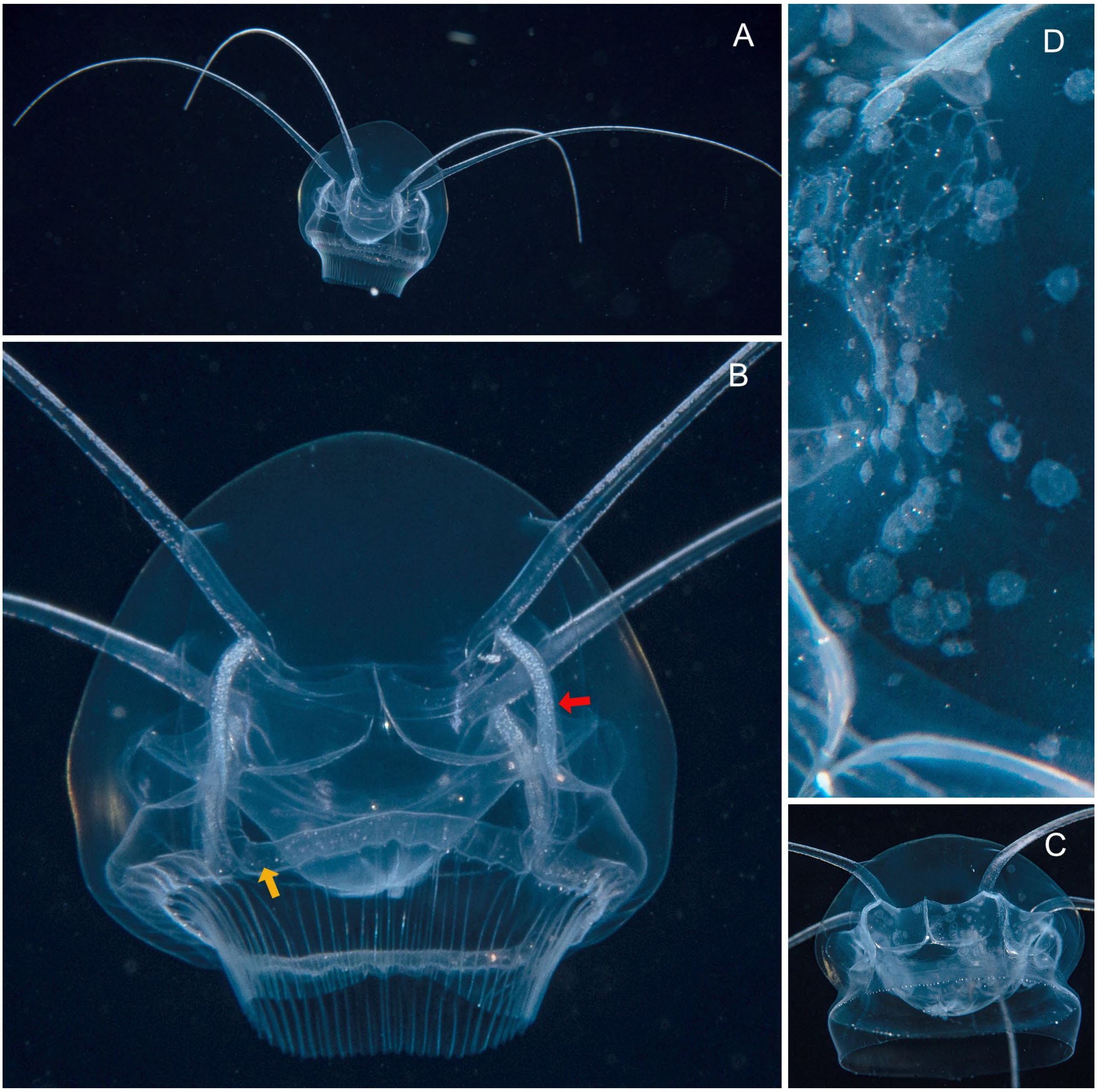


Fig. 46. *Pseudaegina rhodina*. (A-B) BFLA4546, bell size 12 mm, 4 tentacles; lateral views, yellow arrow indicates well visible peripheral canal, red arrow points to a peronium, particularly well visible in this case. (C-D) BFLA4540, bell size 21 mm, 5 tentacles; the stomach contains numerous parasitic juvenile narcomedusae, likely of the genus *Cunina*. Photos A-B by Linda Ianniello.

With 5 tentacles: **BFLA4540;** 25-Apr-2021; size 21 mm wide, ~10 mm high; tentacle preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528659 (= BFLA4047); remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-015246. – **BFLA4794**; 05-May-2022; 17 mm wide, 5 mm thick in tray; part preserved in ethanol for DNA extraction, 16S sequence OQ975723; remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-016268. – 1 specimen photographed 02-Jun-2022; size 12 mm; not collected.
All samples appeared to be immature.

Description and Distribution: See Schuchert & Collins (2021). Updated size ranges are: animals with 4 tentacles 6.5-12 mm, 5-tentacled animals 12-21 mm.
One of the samples was strongly infested with juveniles of another narcomedusa, likely a *Cunina* species (Fig. 46C-D).

Sequence data: All available 16S sequences formed a well separated and supported clade, this as a sister-clade to a clade containing *Pegantha* sp. and *Cunina* sp. (Fig. 43). As noted before, the *P. rhodina* clade has a clear substructure, being composed of an apparent paraphyletic group (with sample BFLA4120) and a more divergent clade (with sample BFLA4015). The p-distances between these two groups are 7.3 to 8.8%, while within each of the two the maximal distances are 2.2% and 0.7%.
For 11 samples we could obtain sequence data for the nuclear ITS region which were then used to generate a ML tree (Fig. 47, GenBank entries OQ991147 through OQ991157). The ITS sequences show the same partition as found for the 16S data (comp. Figs 43 and 47).

Remarks: The high intraspecific divergences for the 16S marker were already noted in Schuchert & Collins (2021) as they also correlated with tentacle numbers. Admittedly, the result might have been pure coincidence due to the low sample number. While the within-group distances are relatively low, they are high between the groups (7.3 to 8.8%, Fig. 43), a situation recalling two closely related species (see *e.g.*, the case of *Zancleopsis dichotoma* and *Z. cabela*). Now, having more samples, the situation and interpretation has become even more complex. While the 16S data still show two subgroups and most members of each group still differ by their respective tentacle numbers, there is one exception. Sample BFLA4546 had four tentacles but belongs to the clade with otherwise only 5-tentacled medusae. It had even an identical sequence as one of them. Although the tentacle number is thus not diagnostic for the group attribution, the apparently biased distribution of the tentacle numbers remains perplexing and deserves further analysis. There is also a size difference between the two forms, perhaps the two morphotypes are only different growth stages. If not separate species, we could also have perhaps a mixture of two separate populations and BFLA4546 could represent a hybrid. As we have already outlined in the section "General results and discussion", divergent lineages in a monophyletic clade of a nominal species can be indicative of a species complex, but it is not a proof. In order to investigate this in more detail, we analysed the nuclear ITS sequences of samples from both subclades (Fig. 47), this mainly to see if sample BFLA4546 is potentially the result of an hybridisation event between the two sub-clades. The ITS marker also showed a clear partition into two groups, thus mirroring the 16S data. Notably, BFLA4546 clustered again with the sub-clade of 5-tentacled medusae (Fig. 47) and is thus likely not a hybrid. With reservations due to the still relatively small number of examined animals, the results indicate that nuclear and mitochondrial markers do not

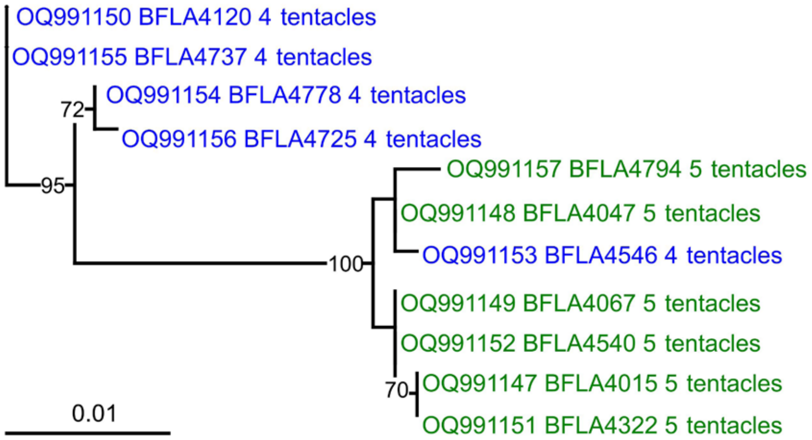


Fig. 47. *Pseudaegina rhodina*. Unrooted maximum likelihood phylogenetic tree obtained with PhyML (JC model) using about 750 bp of the ITS region. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers followed by the BFLA numbers. Medusae with four tentacles shown in blue, those with five tentacles in green.

recombine independently of the clade membership. The two lineages appear thus reproductively isolated and are likely representing different species. However, only a study including more specimens and geographic regions, notably also the Azores as the type locality, can resolve the question reliably. It will likely be necessary to designate a neotype for *Pseudagina rhodina* (see details in Schuchert & Collins, 2021).

Family Solmarisidae Haeckel, 1879

Genus *Pegantha* Haeckel, 1879

Diagnosis: Narcomedusae without manubrial pouches; with peripheral canal system; with gonads on periphery of stomach, ring-like, or covering bulges of the mesogloea, or pendant diverticula; with numerous tentacles leaving exumbrella at the level of manubrium attachment to subumbrella. With otoporpae.

Pegantha clara R.P. Bigelow, 1909

Fig. 48A-B

Pegantha clara R.P. Bigelow, 1909: 80, figs 1-2. – Mayer, 1910: 445, fig. 298A-C. – Bigelow, 1918: 397, synonymy. – Bigelow, 1938: 134, synonymy. – Bigelow, 1940: 305, figs 15-16. – Kramp, 1957: 66, 110, figs 12-13, pl. 6 fig. 3, variation, morphology, review, and revision of genus. – Kramp, 1959: 67, 198, fig. 304. – Kramp, 1961: 272. – Seguera-Puertas, 1984: pl. 13 fig. 4. – Bleeker & Van Der Spoel, 1988: 247, diel vertical migrations. – Bouillon & Barnett, 1999: 110, fig. 120. – Buecher *et al.*, 2005: 34.

Pegantha smaragdina H.B. Bigelow, 1909: 90, pl. 14 figs 1-2, pl. 19 figs 1-9, pl. 22-26. – Kramp, 1961: 272, synonymy.

? *Solmoneta lunulata* Haeckel, 1879: 354. – Kramp, 1957: 66.

Examined material: BFLA4515; 02-Mar-2021; diameter 37 mm, 8 mm height; part without young medusae preserved in ethanol for DNA extraction, 16S sequence OQ975692; rest of medusa preserved in 4% formalin and deposited in FMNH as voucher UF-015227.

Description: Medusa relatively flat, diameter 37 mm, height 8 mm, jelly lens-shaped, stiff mesoglea. Stomach circular, about ¾ the diameter of bell, with mesogloea cone (Fig. 48B), without gastric pockets. Gonads not developed. 19 tentacles, regularly distributed, length very variable, held upwards at an angle of about 45°, curving downward, maximal length equals bell diameter, base penetrating deeply into mesogloea, tentacles where leaving exumbrella on upper side with a buttress-like protrusion of exumbrella. Between each pair of tentacles a marginal lappet, shape quadratic or somewhat more rectangular with variably rounded distal end, curvature likely depending on state of contraction (comp. Fig. 48A and B). Peripheral canals in lappets present, originating next to tentacle bases (Fig. 48B, yellow arrow), first descending parallel along the peronial fold, then along lappet periphery, width ⅕ of lappet width, width more or less constant. Radial peronial fold originating below tentacles inconspicuous (Fig. 48B, brown arrow), peronia at bottom of fold also inconspicuous. 2-4, mostly 3, long and parallel otoporpae on lappet (Fig. 48B, red arrow), majority nearly as long as lappet, some short. 5-6 statocysts along distal rim of lappet (Fig. 48B, pink arrow). Colours: mostly clear with yellow hue along lappet edges in daylight.

Sequence Data: The 16S sequence formed a clade together with a sample of *P. rubiginosa* and sequences of *P. striata* (Fig. 43).

Distribution: Widely distributed in the great oceans between 50°N and 40-50°S (Kramp, 1968). Type locality: Atlantic Ocean, east of New York City, close to Gulf Stream (WGS84 40.0667, -70.33).

Remarks: Kramp (1957) revised all known *Pegantha* species and worked out the suitable characters to distinguish the species. He emphasised the importance of the width of the peripheral canal and the number of otoporpae for distinguishing the species. For *Pegantha clara* he described the width of the radial canal as "narrow" and provided a figure of a lappet with five otoporpae. The same criteria and figure were then used by Kramp (1959) for his key to the species and the diagnosis. It was thus with some initial hesitation that we attributed the present specimen to *P. clara* because its peripheral canals were relatively broad and there were mostly only three otoporpae (Fig. 47B). However, the peripheral canals and numbers of otoporpae of our medusa matched much better the original description and figures of R.P. Bigelow (1909; repeated in Mayer, 1910). R.P. Bigelow (1909) described the peripheral canals as "very wide" and the number of otoporpae per lappet as "2-5, usually 3, long slender otoporpae". The type specimen came notably also from the East coast of the USA. The figure of a Pacific specimen in H.B. Bigelow (1940: fig. 15) matches also our specimen better than Kramp's figure. In our previous publication (Schuchert & Collins, 2021) we also noted a disagreement with Kramp (1957) for the width of the peripheral canals in *P. martagon* Haeckel, 1879. It thus seems that the width of the peripheral canals is perhaps not as reliable as previously thought. It might depend on the examined population or the preservation.

Pegantha polystriata (Xu & Zhang, 1978)

Pegantha polystriata. – Schuchert & Collins, 2021: 324, fig. 54A-G.

Examined material: BFLA4486; 09-Sep-2020; size 1.5 mm; preserved in ethanol for DNA extraction; specimen not in received tube. – **BFLA4538**; 25-Apr-2021; size 5 mm; preserved in ethanol for DNA extraction, 16S sequence OQ975696. – **BFLA4545**; 25-Apr-2021; size 6 mm; preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry

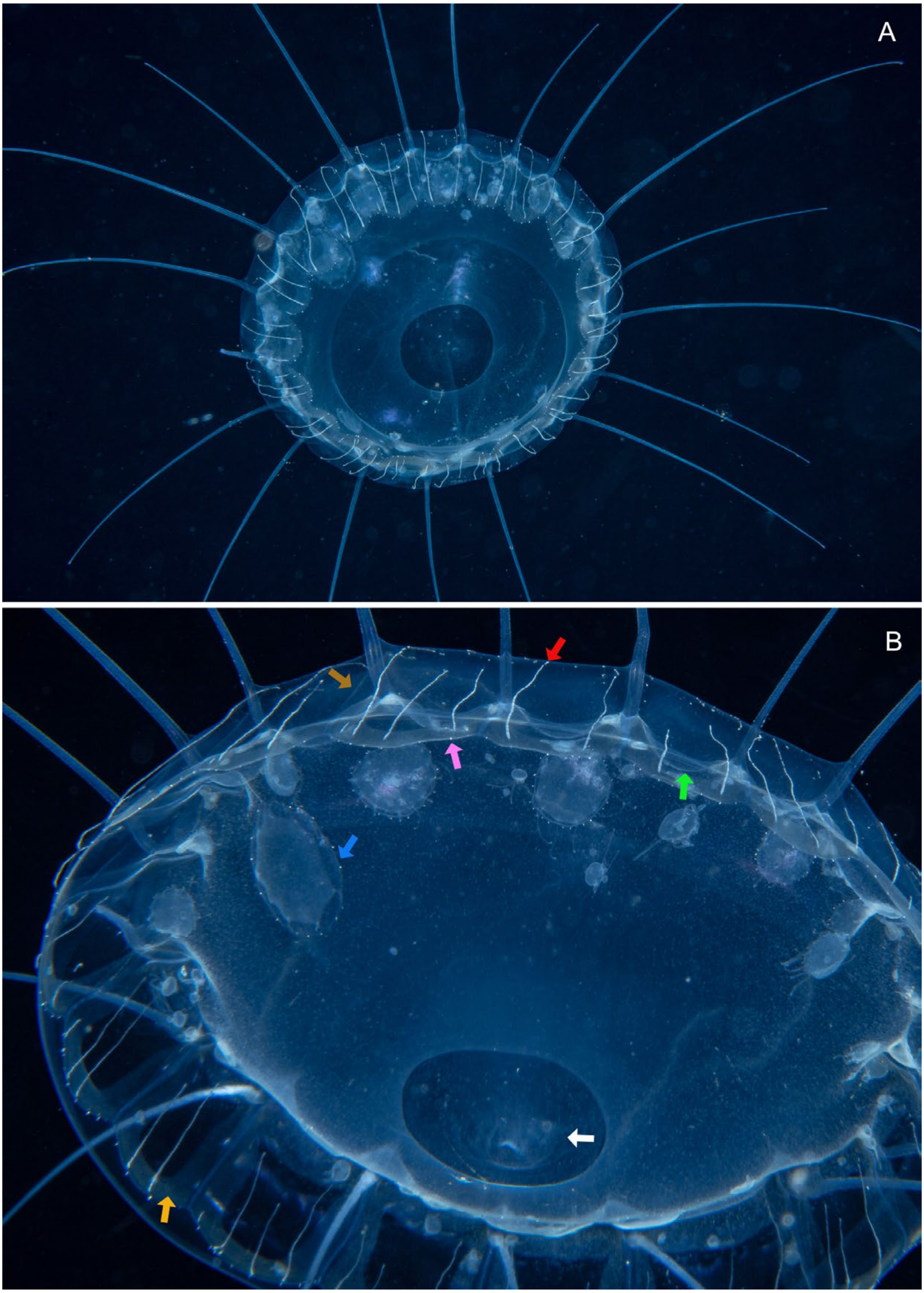


Fig. 48. *Pegantha clara,* BFLA4515, diameter 37 mm. (A) Oral view. (B) Oral view. Structural details: yellow arrow – well visible peripheral canal along lappet rim; white arrow – gastric jelly cone visible through mouth opening; green arrow – peripheral rim of stomach, slightly lowered; red arrow – otoporpa; blue arrow – parasitic narcomedusa in stomach; brown arrow – peronial fold; pink arrow – statocyst. Photos by Linda Ianniello.

OQ975696. – **BFLA4843**; 1 specimen; observed 07-Sep-2022; size 6 mm; preserved in ethanol for DNA extraction; deposited in FMNH as UF-017271. – 1 specimen photographed 14-Sep-2020; size 2 mm; not collected. – 1 specimen photographed 14-Sep-2020; size not recorded; not collected. – 1 specimen photographed 15-Sep-2020; size not recorded; not collected.

Sequence Data: The new 16S haplotype found was only minimally different from the one obtained in our previous publication (MW528728, p-distance 0.3%).

Remarks: For the description and other details see Schuchert & Collins (2021).

Genus *Solmaris* Haeckel, 1879

Diagnosis: Narcomedusae without manubrial pouches; without peripheral canal system; mostly simple annular gonads on manubrial wall; with numerous tentacles leaving exumbrella at the level of manubrium attachment to subumbrella. Without otoporpae.

Solmaris corona (Keferstein & Ehlers, 1861)

Solmaris corona. – Schuchert & Collins, 2021: 326, fig. 55A-C.

Examined material: 1 specimen observed 08-Jan-2023; size 7 mm; not collected.

Remarks: For the description and other details see Schuchert & Collins (2021).

Solmaris flavofinis Schuchert & Collins, 2021

Fig. 49A-B

? *Cunina discoides* Fewkes, 1881: 161, pl. 2 fig. 8; pl. 4 figs 1-2.
Solmaris flavofinis Schuchert & Collins, 2021: 328, fig. 56A-H.

Examined material: BFLA4749; 29-Dec-2021; size 12 mm, 10 tentacles, with gonads; part preserved in ethanol for DNA extraction, 16S sequence identical to GenBank entry MW528665; remaining part preserved in 4% formalin and deposited in FMNH as voucher UF-016241. – **BFLA4857**; 05-Jan-2023; size 10 mm, 10 tentacles, with gonads; preserved in 4% formalin, deposited in FMNH as UF-017275. – 1 specimen; observed 12-Jan-2023; size 8 mm, 10 tentacles, with gonads; not collected.
Identification uncertain: *S.* cf. *flavofinis*, 1 specimen; observed 08-Dec-2022; size not recorded, 15 tentacles, with gonads; not collected.

Description: See Schuchert & Collins (2021) and the remarks below.

Sequence Data: The single new 16S sequence was identical to a previously reported one (GenBank MW528665).

Distribution: Off Florida.

Remarks: The maximal recorded size of the individuals observed in this study was larger than the previously reported ones (up to 12 mm versus 9 mm, Fig. 49A). The tentacle numbers were mostly in the same range (up to 10), except for one animal that was photographed only (Fig. 49B). This medusa had 15 tentacles and the peripheral stomach wall was green-yellow, although it is not clear if this is solely due to the yellow digested food in the stomach. Because we have no 16S data for this animal, we cannot be sure if this specimen really belongs to *S. flavofinis* or is better referred to *S. flavescens* (Kölliker, 1853). A lower tentacle number is one of the diagnostic characters to distinguish *S. flavofinis* from *S. flavescens* (Kölliker, 1853), the latter having 12 to 17 tentacles. In addition to the tentacle number, *S. flavescens* is reportedly also larger than *S. flavofinis* (15-23 mm in the former, in the latter 8 to 12 mm when fertile) and it has a yellow stomach (Kölliker, 1853). The difference is arguably minimal and we agree that both species could turn out to be conspecific. *Solmaris flavescens* is a rarely reported species. It was very inadequately described by Kölliker (1853) based on material observed in the Mediterranean. The only reliable subsequent description based on actual observations of Mediterranean material is Mayer (1910). Because of this uncertainty and the size difference, we prefer for the time being to keep *S. flavofinis* as distinct from *S. flavescens* until genetic data of Mediterranean samples proves the contrary.

Order Trachymedusae
Family Rhopalonematidae Russell, 1953
Genus *Rhopalonema* Gegenbaur, 1857

Diagnosis: Rhopalonematidae without gastric peduncle; gonads along radial canals; marginal tentacles solid, of two kinds: perradial tentacles long, with large, club-shaped ending; inter- and adradial tentacles short with swollen end. Statocysts enclosed in mesogloea when fully developed.

Rhopalonema velatum Gegenbaur, 1857

Rhopalonema velatum. – Schuchert & Collins, 2021: 334, fig. 60A-E

Examined material: BFLA4718; 08-Dec-2021; size 8 mm, mature female; preserved in ethanol for DNA extraction, 16S sequence OQ975725. – **BFLA4861**; 05-Jan-2023; size 8 mm, subadult; preserved in ethanol for DNA extraction, deposited in FMNH as UF-017276. – 1 of several specimens photographed 26-Nov-2021; size 8 mm, mature male; not collected.

Description: The animals looked identical to the ones described in Schuchert & Collins (2021).

Sequence Data: The new 16S haplotype differed only in one base-pair from the two sequences published in our previous report (GenBank entries MW528700, MW528702).

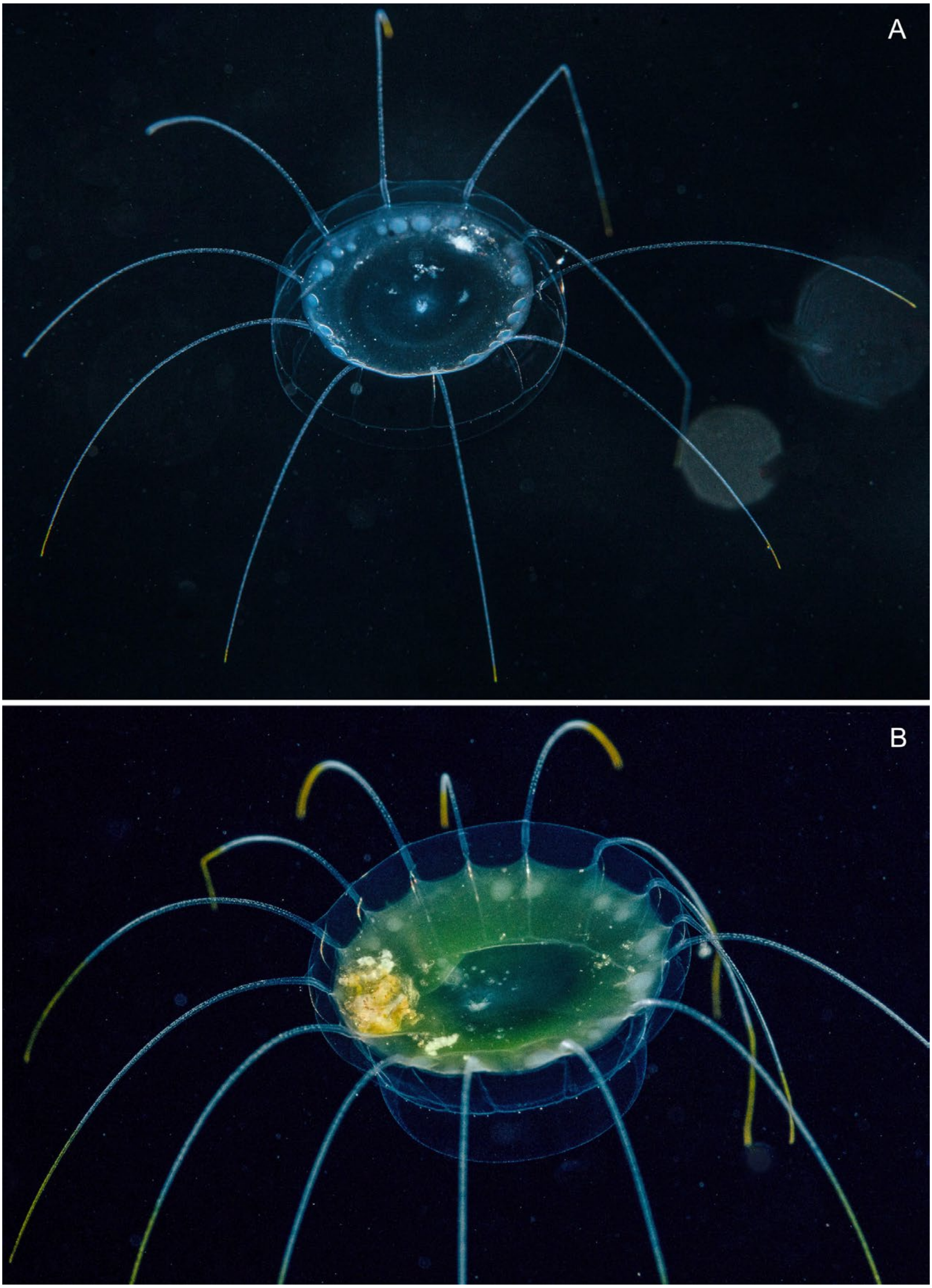


Fig. 49. (A) *Solmaris flavofinis*, BFLA4749, bell diameter 12 mm, oblique view on aboral side, there are numerous disk-shaped gonads along the stomach margin. (B) *Solmaris* cf. *flavofinis*, photographed 08-Dec-2022, size not recorded, oblique view on aboral side, yellow food particles are seen in the stomach. Photo B by Andrea Whitaker.

Distribution: See Schuchert & Collins (2021).

Remarks: *Rhopalonema velatum* is crystal clear and almost impossible to see in daylight. It is a fast swimmer, hard to catch and photograph.

Order Limnomedusae
Family Geryoniidae Eschscholtz, 1829
Genus *Geryonia* Péron & Lesueur, 1810

Diagnosis: Limnomedusae with gastric peduncle; stomach small, with 6 lips; 6 radial canals, with additional centripetal canals; 6 gonads on radial canals, flattened and leaf-shaped; two kinds of marginal tentacles, solid and hollow; ecto-endodermal statocysts enclosed in mesoglea.
No polyp stage, direct development.

Geryonia proboscidalis (Forsskål, 1775)

Geryonia proboscidalis. – Schuchert & Collins, 2021: 336, fig. 61A-B.

Examined material: 1 specimen photographed 07-May-2021; size 50 mm; not collected.

Description: As in Schuchert & Collins (2021), but bell size 50 mm,

Distribution: See Schuchert & Collins (2021).

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Supplemental content S1, DOI: 10.35929/RSZ.0113.S1. List of BFLA samples cited in this and Schuchert & Collins (2021), updated taxon names, GenBank, and museum registration numbers.

Appendix 1
Updated Checklist of hydromedusae and medusoid species recorded or potentially present in the coastal region from Cape Hatteras to Florida and the whole Gulf of Mexico. Note that a number of these records are based on undocumented specimens, simply obtained by re-copying species lists without published supporting information for the identifications like descriptions and illustrations. Doubtful species (Kramp, 1961; Schuchert, 2023) are excluded, but inclusion of a name does not mean that it is a recognizable species. Species determined only to genus level are excluded, except the ones seen in this and our previous study. The references for the taxonomic authorities can be found in Schuchert (2023).

taxon	this study	records source	comments
Suborder Filifera			
Family Bougainvillidae			
Bougainvillia carolinensis (McCrady, 1859)		1, 4, 5, 6, 11	
Bougainvillia frondosa Mayer, 1900		1, 4, 5, 6	
Bougainvillia muscus (Allman, 1863)		4, 5, 8, 9	
Bougainvillia niobe Mayer, 1894		1, 3, 4, 5, 11	
Bougainvillia platygaster (Haeckel, 1879)		1, 2, 3, 4, 5, 9	
Bougainvillia rugosa Clarke, 1882		11	
Bougainvillia triestina Hartlaub, 1911		8	barcode id.
Bougainvillia sp.	yes	12	
Koellikerina elegans (Mayer, 1900)		1, 6	
Koellikerina fasciculata (Péron & Lesueur, 1810)		8, 9	
Nemopsis bachei L. Agassiz, 1849		1, 5, 8, 11	
Thamnostoma tetrellum (Haeckel, 1879)		4, 5	
Family Bythotiaridae			
Bythotiara depressa Naumov, 1960		4, 5	
Bythotiara murrayi Günther, 1903		7	mesopelagic
Calycopsis chuni Vanhöffen, 1911		2	
Calycopsis papillata Bigelow, 1918		1	
Calycopsis simulans (Bigelow, 1909)		4, 5	
Protiaropsis anonyma (Maas, 1905)	yes	1, 3, 5, 12	
Family Cytaeididae			
Cytaeis tetrastyla Eschscholtz, 1829	yes	3, 4, 5, 11, 12	
Family Hydractiniidae			
Podocoryna americana (Mayer, 1910)		8	barcode id.
Podocoryna borealis (Mayer, 1900)		4	
Podocoryna carnea M. Sars, 1846		4	
Podocoryna martinicana Galea & Ferry, 2013	yes		
Family Niobiidae			
Niobia dendrotentaculata Mayer, 1900		1, 4, 5, 6	
Family Oceaniidae			
Oceania armata Kölliker, 1853		2, 4, 5, 14	misidentifications of *T. nutricula* ?
Turritopsis dohrnii (Weismann, 1883)		8	barcode id.
Turritopsis nutricula McCrady, 1857		1, 2, 3, 4, 5, 6, 9, 11, 12	
Family Pandeidae			
Amphinema australis (Mayer, 1900)		1, 6, 11	*species inquirenda*?
Amphinema dinema (Péron & Lesueur, 1810)		1, 4, 5, 6, 9, 11	
Amphinema rugosum (Mayer, 1900)	yes	1, 4, 5, 6, 9, 11	
Amphinema turrida (Mayer, 1900)		1, 2, 4, 5, 6, 11,12	
Cirrhitiara superba (Mayer, 1900)	yes	1, 6, 12	
Eutiara mayeri Bigelow, 1918	yes	1, 7	

taxon	this study	records source	comments
Halitholus intermedius (Browne, 1902)		4, 5	identification doubtful
Larsonia pterophylla (Haeckel, 1879)		1, 2, 4, 5, 6, 12	
Leuckartiara adnata Pagès *et al*., 1992	yes		
Leuckartiara gardineri Browne, 1916		4, 5	identifications need confirmation
Leuckartiara octona (Fleming, 1823)		4, 5	identifications need confirmation
Leuckartiara zacae Bigelow, 1940		4, 5	
Leuckartiara sp.	yes		
Merga violacea (Agassiz & Mayer, 1899)		1, 2, 4, 5, 6, 12	
Pandea conica (Quoy & Gaimard, 1827)		1, 3	
Pandeopsis ikarii (Uchida, 1927)	yes	12	
Pandeopsis prolifera Schuchert & Collins, 2021	yes	12	
Stomotoca atra L. Agassiz, 1862		4, 5	misidentification of *L. pterophylla* ?
Family Proboscidactylidae			
Proboscidactyla gemmifera (Fewkes, 1882)		1, 2, 4, 5, 6,12	older records include *P. stolonifera*
Proboscidactyla ornata (McCrady, 1859)	yes	1, 2, 4, 5, 6, 9, 11,12	
Family Protiaridae			
Halitiara formosa Fewkes, 1882		1, 2, 4, 5, 6, 9, 11	
Paratiara digitalis Kramp & Dumas, 1925		1	
Family Ptilocodiidae			
Thecocodium quadratum (Werner, 1965)	yes	10, 12	
Family Rathkeidae			
Lizzia alvarinoae Segura, 1980		9	= *Cytaeis* sp. ?
Lizzia blondina Forbes, 1848		1, 4, 6, 11	includes *Podocoryna minuta*
Lizzia gracilis (Mayer, 1900)		1, 6	
Podocorynoides minima (Trinci, 1903)		4, 5, 9, 11	
Family Trichydridae			
Trichydra pudica Wright, 1857		5	
Suborder Capitata			
Family Cladonematidae			
Cladonema radiatum Dujardin, 1843		1, 4, 6	
Family Corynidae			
Codonium proliferum (Forbes, 1848)		4, 5	
Coryne eximia Allman, 1859		4	includes *C. gracilis*
Polyorchis karafutoensis Kishinouye, 1910		4, 5	implausible occurrence
Slabberia halterata Forbes, 1846		1, 4, 6	
Slabberia strangulata (McCrady, 1859)		1, 6, 9, 11	
Stauridiosarsia gemmifera (Forbes, 1848)		4, 5	
Stauridiosarsia ophiogaster (Haeckel, 1879)		4, 5	
Stauridiosarsia reesi (Vannucci, 1956)		8	
Family Pennariidae			
Pennaria disticha Goldfuss, 1820		1, 6, 11	
Family Porpitidae			
Porpita porpita (Linnaeus, 1758)		14	
Velella velella (Linnaeus, 1758)		14	
Family Sphaerocorynidae			
Sphaerocoryne agassizii (McCrady, 1859)		1	
Euphysilla pyramidata Kramp, 1955	yes	4, 5, 12	
Euphysilla peterseni Allwein, 1967		11	
Family Zancleopsidae			
Zancleopsis cabela (Maggioni *et al*., 2017)	yes	13	

taxon	this study	records source	comments
Zancleopsis dichotoma (Mayer, 1900)	yes	1, 6, 11, 12	includes *Z. gotoi* records
Zancleopsis grandis sp. nov.	yes		
Family Zancleidae			
Zanclea alba (Meyen, 1834)		14	
Zanclea costata Gegenbaur, 1857		1, 4, 5, 6	incorrect, in part *Z. mayeri* + others
Zanclea dubia Kramp, 1959		4, 5	identification ?
Zanclea mayeri Schuchert & Collins, 2021	yes	12	
Zanclea cf. *migottoi* (Galea, 2008)	yes		
Zanclea sp.		12	with 4 tentacles
Zanclea sp.	yes		with 2 tentacles
Suborder Aplanulata			
Family Corymorphidae			
Corymorpha forbesii (Mayer, 1894)		1, 2, 4, 5, 6, 11, 12	
Corymorpha gracilis (Brooks, 1883)		1, 4, 5, 6, 9, 11, 12	
Corymorpha floridana Schuchert & Collins, 2021	yes	12	
Corymorpha furcata (Kramp, 1948)		3, 4, 5	
Corymorpha nutans M. Sars, 1835		5, 8	? misidentifications
Corymorpha valdiviae (Vanhöffen, 1911)	yes		
Euphysa aurata Forbes, 1848		4	identification doubtful
Family Tubulariidae			
Dicodonium floridana Mayer, 1910		1, 6	
Ectopleura minerva Mayer, 1900		1, 6	
Ectopleura dumortierii (van Beneden, 1844)		1, 8, 9, 11	
Aplanulata *incerta sedis*			
Cnidocodon leopoldi Bouillon, 1978	yes		
Order Leptothecata			
Family Aequoreidae			
Aequorea australis Uchida, 1947		8	
Aequorea floridana (Agassiz, 1862)		1, 4, 6	
Aequorea forskalea Péron & Lesueur, 1810		1, 11	
Aequorea globosa Eschscholtz, 1829		4, 5	
Aequorea macrodactyla (Brandt, 1835)		1, 2, 4, 5, 9, 11	uncertain identifications
Aequorea neocyanea Schuchert & Collins, 2021	yes	6, 12	
Aequorea taiwanensis Zheng *et al.*, 2009	yes	12	
Aequorea spec. 1	yes	12	
Aequorea spec. 2		12	
Aequorea spec. 3	yes		
Zygocanna cf. *apapillatus* Xu *et al.*, 2014	yes	12	
Zygocanna vagans Bigelow, 1912		4, 5	
Rhacostoma atlanticum L. Agassiz, 1851		1	
Family Blackfordiidae			
Blackfordia virginica Mayer, 1910		4, 5, 8	
Family Campanulariidae			
Clytia discoida (Mayer, 1900)		1, 4, 5, 9, 11	identification ?
Clytia elsaeoswaldae Stechow, 1914		8, 14	barcode id.
Clytia folleata (McCrady, 1859)		1, 4, 5, 8, 9	
Clytia gelatinosa (Mayer, 1900)		1, 4, 6, 11	identification ?
Clytia globosa (Mayer, 1900)		1, 4, 6, 11	
Clytia gracilis (M. Sars, 1850)		8	barcode id.
Clytia hemisphaerica (Linnaeus, 1767)		9	id. ?, includes *C. languida*

taxon	this study	records source	comments
Clytia linearis (Thornely, 1900)		12, 14	barcode id.
Clytia mccradyi (Brooks, 1888)	yes	1, 5, 6	
Clytia noliformis (McCrady, 1859)		14	
Clytia paulensis (Vanhöffen, 1910)		14	
Clytia simplex (Browne, 1902)		4, 5	indeterminable species ?
Clytia sp. 1	yes	12	
Clytia sp. 2	yes	12	
Gastroblasta timida Keller, 1883		12	
Multioralis ovalis Mayer, 1900		1, 6	
Obelia bidentata Clark, 1875		8	barcode id.
Obelia dichotoma (Linnaeus, 1758)		8	barcode id.
Obelia geniculata (Linnaeus, 1758)		14	
Obelia hyalina Clarke, 1879		14	
Obelia oxydentata Stechow, 1914		14	
Orthopyxis sargassicola (Nutting, 1915)		14	
Family Cirrholoveniidae			
Cirrholovenia tetranema Kramp, 1959		11	
Family Dipleurosomatidae			
Dichotomia cannoides Brooks, 1903	yes	1, 4, 5	
Netotocertoides brachiatum Mayer, 1900		6	
Family Eirenidae			
Eirene gibbosa (McCrady, 1859)		1, 11	
Eirene lactea (Mayer, 1900)		1, 4, 6	
Eirene pyramidalis (Agassiz, 1862)		1, 4, 5, 6, 9, 11	
Eirene tenuis (Browne, 1905)		4	
Eutima coerulea (Agassiz, 1862)		1, 6	
Eutima gegenbauri (Haeckel, 1864)		11	
Eutima gracilis (Forbes & Goodsir, 1853)		4, 5, 9	
Eutima mira McCrady, 1859		1, 4, 5, 6, 11	
Eutima suzannae Allwein, 1967		11	
Eutima variabilis McCrady, 1859		1, 5, 6, 11	
Eutonina scintillans (Bigelow, 1909)		4	
Helgicirrha cari (Haeckel, 1864)		4, 11	includes *Helgicirrha schulzii*
Helgicirrha weaveri Allwein, 1967		11	
Family Hebellidae			
Melicertissa mayeri Kramp, 1959	yes	1, 12	includes *M. clavigera* from region
Staurodiscus kellneri (Mayer, 1910)	yes	1, 6, 12	includes *Toxorchis brooksi*
Staurodiscus luteus Schuchert & Collins, 2021	yes	12	
Staurodiscus tetrastaurus Haeckel, 1879		2, 6, 12	
Family Laodiceidae			
Laodicea brevigona Allwein, 1967		5, 11	
Laodicea minuscula Vannucci, 1957		4, 5	
Laodicea undulata (Forbes & Goodsir, 1853)	yes	1, 4, 5, 6, 11, 12	
Family Lovenellidae			
Eucheilota comata (Bigelow, 1909)		2	
Eucheilota duodecimalis A. Agassiz, 1862		1, 2, 4, 5, 6, 9, 11	
Eucheilota paradoxica Mayer, 1900		1, 4, 5, 6, 9	
Eucheilota ventricularis McCrady, 1859		1, 6, 9, 11	
Lovenella bermudensis (Fewkes, 1883)		1, 6, 11	
Lovenellidae sp.	yes		

taxon	this study	records source	comments
Family Malagazziidae			
Octophialucium aphrodite (Bigelow, 1928)	yes	1, 5, 12	
Octophialucium irregularis Schuchert & Collins, 2021	yes	12	
Octophialucium medium Kramp, 1955		4, 5	
Malagazzia carolinae (Mayer, 1900)		1, 2, 6, 8	
Family Melicertidae			
Melicertum tropicalis sp. nov.	yes		
Family Orchistomatidae			
Orchistoma pileus (Lesson, 1843)	yes	1, 4, 5, 6, 12	includes *O. collapsum* and *O. agariciforme*
Family Phialellidae			
Phialella parvigastra (Mayer, 1900)		1, 6	
Family Tiarannidae			
Chromatonema rubrum Fewkes, 1882		4, 5	
Modeeria rotunda (Quoy & Gaimard, 1827)		4	
Family Tiaropsidae			
Tiaropsidium roseum (Maas, 1905)		6	
Family Wuvulidae			
Wuvula ochracea (Mayer, 1910)		1, 6, 12	
Order Narcomedusae			
Family Aeginidae			
Aegina citrea Eschscholtz, 1829		3, 4, 5, 9	mostly misidentifications of *Pseudaegina rhodina*
Aeginura grimaldii Maas, 1904		4, 5, 7	
Family Cuninidae			
Cunina becki Bouillon, 1985		12	
Cunina duplicata Maas, 1893		3, 5	
Cunina fowleri (Browne, 1906)		3, 4, 5	
Cunina globosa Eschscholtz, 1829		5	
Cunina octonaria McCrady, 1859	yes	3, 4, 5, 9, 11, 12	
Cunina peregrina Bigelow, 1909		3, 5, 11	
Cunina sp.	yes		similar to *Cunina peregrina*
Solmissus incisa (Fewkes, 1886)		4, 5, 6, 7	
Solmissus marshalli Agassiz & Mayer, 1902		3, 7	
Family Pseudaeginidae			
Pseudaegina rhodina (Haeckel, 1879)	yes	6, 7, 12	most Atlantic *A. citrea* records belong here
Family Solmarisidae			
Pegantha clara R.P. Bigelow, 1909	yes	3, 4, 7	
Pegantha martagon Haeckel, 1879		3, 4, 5, 12	
Pegantha polystriata (Xu & Zhang, 1978)	yes	12	
Pegantha triloba Haeckel, 1879		3, 4, 5	
Solmaris corona (Keferstein & Ehlers, 1861)	yes	3, 7, 12	
Solmaris flavescens (Kölliker, 1853)		3, 7	? in part *Solmaris flavofinis*
Solmaris flavofinis Schuchert & Collins, 2021	yes	12	
Family Solmundaeginidae			
Solmundella bitentaculata (Quoy & Gaimard, 1833)		3, 4, 6, 9, 11, 12	

taxon	this study	records source	comments
Order Trachymedusae			
Family Halicreatidae			
Botrynema brucei Browne, 1908		7	mesopelagic
Halicreas minimum Fewkes, 1882		4, 5, 7	
Haliscera bigelowi Kramp, 1947		5, 7	
Haliscera conica Vanhöffen, 1902		7	mesopelagic
Halitrephes maasi Bigelow, 1909		7	mesopelagic, includes *H. valdiviae*
Family Rhopalonematidae Russell, 1953			
Aglantha elata (Haeckel, 1879)		5	
Aglaura hemistoma Péron & Lesueur, 1810		3, 4, 5, 6, 9, 11, 12	
Amphogona apicata Kramp, 1957		7	mesopelagic
Amphogona apsteini (Vanhöffen, 1902)		3, 4, 12	
Benthocodon pedunculatus (Bigelow, 1913)		7	mesopelagic
Colobonema sericeum Vanhöffen, 1902		4, 5, 7	
Crossota rufobrunnea (Kramp, 1913)		4, 5, 7	
Pantachogon haeckeli Maas, 1893		4, 5, 7	
Persa incolorata McCrady, 1859		3, 5, 9, 11	
Rhopalonema funerarium Vanhöffen, 1902		4, 5	
Rhopalonema velatum Gegenbaur, 1857	yes	3, 4, 5, 9, 11, 12	
Sminthea eurygaster Gegenbaur, 1857		3, 4, 5	
Order Limnomedusae			
Family Geryoniidae			
Geryonia proboscidalis (Forsskål, 1775)	yes	3, 4, 5, 12	
Liriope tetraphylla (Chamisso & Eysenhardt, 1821)		3, 4, 5, 6, 8, 9, 11, 12	
Family Olindiidae			
Cubaia aphrodite Mayer, 1894		1, 4, 6	
Gossea brachymera Bigelow, 1909		1, 2, 4, 5	
Olindias muelleri Haeckel, 1879		1	misidentification ?
Olindias tenuis (Fewkes, 1882)		4, 6, 12	
Scolionema suvaense (Agassiz & Mayer, 1899)		1, 2, 4	
Vallentinia gabriellae Vannucci Mendes, 1948		1, 4	

Sources

1 Kramp (1959): Table VII – Neritic species in the West-Atlantic tropical region Cape Hatteras to Florida

2 Kramp (1959): Table XII – Neritic, predominantly warm water species and their distribution in the three great oceans-West Indies and N. American Warm Water

3 Kramp (1959): Table X – Oceanic species in the epipelagic zone-Atlantic warm water -Eastern and Western, excluding strictly western Atlantic species

4 Segura-Puertas *et al.* (2003): Checklist of Medusa of Mexico

5 Segura-Puertas *et al.* (2009): Medusozoans of the Gulf of Mexico

6 Mayer (1910): Mayer collected hydrozoans extensively along the Atlantic seaboard including the Dry Tortugas from 1892 to 1900. In 1903 he established a marine station on Dry Tortugas, Florida which operated until 1939.* Washed by the Gulf Stream current the Dry Tortugas are approximately 300 nautical miles from the sampling site and perhaps 3 to 10 days drift in Gulf Stream. We place additional emphasis on species collected by Mayer at Dry Tortugas. These entries are not from a checklist.
*Carnegie Institution of Washington Administration Records, 1890-2001, Administration, Carnegie Institution of Washington, Washington D.C.

7 Larson *et al.* (1991): Observations from submersible at Tortugas and Bahamas, surface to 900 m, observations excluded specimens less than 1 cm; New England only observations are excluded here.

8 Pruski & Miglietta (2019): identifications via 16S sequences

9 Martell-Hernández *et al.* (2014)

10 Kubota & Meldonian (2016)

11 Allwein (1967)

12 Schuchert & Collins (2021)

13 Maggioni *et al*. (2021)

14 Calder (2013): Calder's survey covers the same biogeographic region and its Southern boundary overlaps the study location. These entries are not from a checklist.