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Hydromedusae observed during night dives in the Gulf Stream

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Abstract: Hydromedusae were photographed and collected during 75 night-time dives in the Gulfstream off Florida. Most of the collected material was used to obtain DNA extracts and subsequently to determine part of the mitochondrial 16S rRNA gene, a barcode marker preferentially used for hydrozoans. The morphological data and the 16S barcodes permitted us to identify 46 species and 6 additional species nameable only to the genus level. Photos and descriptions are provided for all of them and the taxonomy and species status discussed. Six new species are described: *Pandeopsis prolifera* n. spec., *Zanclea mayeri* n. spec., *Corymorpha floridana* n. spec., *Staurodiscus luteus* n. spec., *Octophialucium irregularis* n. spec., *Solmaris flavofinis* n. spec. The new family Wuvulidae is proposed for the genus *Wuvula* Bouillon, Seghers & Boero, 1988. The new name *Aequorea neocyanea* is introduced for *Zygodactyla cyanea* L. Agassiz, 1862 to avoid a secondary homonymy with *Aequorea cyanea* de Blainville, 1834. *Zygodactyla cyanea* was considered to be a synonym of *Aequorea forskalea* Péron & Lesueur, 1810 for most of the 20th century, but we present arguments that it should be kept distinct from the latter and it must be transferred to the genus *Aequorea*. The genus *Otoporpa* Xu & Zhang, 1978 is regarded here as congeneric with *Pegantha* Haeckel, 1879 and its type species *Otoporpa polystriata* Xu & Zhang, 1978 is therefore changed to *Pegantha polystriata* (Xu & Zhang, 1978) new comb. *Dipleurosoma brooksii* Mayer, 1910 is recognized as a new synonym of *Staurodiscus kellneri* (Mayer, 1910); *Staurodiscus heterosceles* Haeckel, 1879 as a new synonym of *Staurodiscus tetrastaurus* Haeckel, 1879; *Orchistoma agariciforme* Keller, 1884 and *Tetracannota collapsum* Mayer, 1900 both as new synonyms of *Orchistoma pileus* (Lesson, 1843). The following Indo-Pacific species are newly recorded for the Atlantic Ocean: *Pandeopsis ikarii* (Uchida, 1927), *Aequorea taiwanensis* Zheng *et al.*, 2009; *Zygocanna apapillatus* Xu, Huang & Guo, 2014; *Gastroblasta timida* Keller, 1883; *Cunina becki* Bouillon, 1985; and *Pegantha polystriata* (Xu & Zhang, 1978). The 16S sequences also permitted us to discover several new links with polyp stages, this for *Cirrhitiara superba* (Mayer, 1900), *Euphysilla pyramidata* Kramp, 1955, *Zancleopsis dichotoma,* and *Melicertissa mayeri* Kramp, 1959. Detailed, high resolution photos of living medusae were found to be very useful for taxonomic purposes and are mostly preferable to preserved, damaged specimens obtained with plankton nets. Photos of living animals also permit us to better document material used to determine 16S barcodes and make the latter useable for taxonomic revisions.

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

INTRODUCTION

Identifying hydromedusae can be a challenge, notably because the most important and still heavily used monographs of Kramp (1959a, 1968) have become somewhat dated. This not only because many new species have been discovered meanwhile, but also because the taxonomy has evolved and new diagnostic traits are being used. Whatsoever, there are no modern, comprehensive monographs with ocean-wide scopes like Kramp's and these remain an essential tool for taxonomists and plankton ecologists. Even the monograph of Mayer (1910) remains indispensable for systematists as it summarizes the entire older literature.

It is unlikely that in the near future comparable monographs will ever be published, above all because of copyright problems and because modern electronic databases offer more possibilities and flexibility, provided that they cover all species comprehensively. An outstanding example for such a taxonomic database is the AntWeb (AntWeb, 2021) and its taxonomic companion AntCat (Bolton, 2021). A comparable website for marine organisms is the "World Register of Marine Species"

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(WoRMS Editorial Board, 2021; Schuchert, 2020). However, there is still a long way to go until the WoRMS database can replace taxonomic monographs because it is still very incomplete. Although the currently accepted species names of Hydrozoa are nearly all entered in the WoRMS database, only a minority of species have suitable illustrations and/or links to recent publications with descriptions and figures. This absence cannot easily be overcome as for many hydrozoan species there exist simply no suitable illustrations. Above all, we generally lack good photos of living hydromedusae, photos showing sufficient details that can be used for taxonomic comparisons and that represent citable works that can be used as a permanent reference. More photos will allow for a better comparison of populations and assessment of geographic variation. There exist many good photos of hydromedusae in the internet, but they are too ephemeral for scientific purposes. A way to overcome this has been presented in Schuchert (2017a, b) who suggested creating archived electronic documents with a DOI number for specimens used to obtain DNA sequences published in GenBank. While this approach is useful especially for non-specialists, it is highly desirable to have many more published photos of living medusae identified by experts and accompanied by DNA barcodes (comp. e.g. Lindsay *et al*., 2017; Schuchert, 2017a, 2018). Unfortunately, many 16S barcodes deposited in GenBank lack information on how the animal was identified or no voucher specimen is available, too often not even the provenance is given (Marques *et al*., 2013). It is thus impossible to verify these identifications and the sequences get valueless if they are in conflict with more recent results.

Photos of living medusae – whole animals and details – present clear advantages over drawings and reconstructions made from preserved material collected with plankton nets (see e.g. Larson *et al*., 1991; Mills *et al*., 1996; Wrobel & Mills, 1998; Raskoff *et al.,* 2003, 2005; Lindsay *et al*., 2008, 2017; Schuchert, 2018). Net-collected samples are nearly always damaged or distorted, the subsequent preservation lets the specimens shrink, the colours fade, the statocysts regularly get dissolved, and the DNA is usually destroyed. This renders morphological comparisons often rather difficult.

The aim of the present work was therefore to document, identify, DNA barcode, and discuss the taxonomy of hydromedusae observed and photographed *in situ* off the coast of Florida.

As many medusae make diel vertical migrations (Mills, 1983; Buecher & Gibbons, 2003; Benovic *et al*., 2005 and references therein), these species can only be seen by SCUBA divers during night-time (black water dives, comp. Hammer, 1975; Raskoff *et al*., 2003; Madin *et al*., 2013). This method is indeed very promising and several rarely reported medusae species were encountered [see *e.g.* also Nonaka *et al.* (2021) for a similar study on fish larvae].

MATERIAL AND METHODS

Sampling and photographing

All photography and sampling in Florida were done by RC during drift dives beginning at about sunset (civil twilight). The starting point was always approximately 5.5-12 km east of Palm Beach (USA, Florida) at approximately 26.7°N latitude. Starting bottom depths were between 150-200 m. Specimens were collected between the surface and 20 m depth with the great majority collected at 8-12 m. The divers drifted in a Northerly direction for 80 to 120 minutes, resulting in drifts of 2 to 17 km, depending on the drift time, strength of the current and relative location of the Gulf Stream. The average drift was about 8 km, diving depth 10-12 m. The approximate WGS84 coordinates are 26.70, -79.94 to 26.78, -79.94.

All specimens were photographed 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.

Specimens were collected in numbered (BFLA numbers), disposable, zip lock bags and preserved for DNA analysis in 95% ethanol or in 4% formaldehyde solution for voucher specimens (UF numbers). The material was then deposited in the Florida Museum of Natural History (USA, FL, Gainsville) and made available to PS.

For the medusae which were photographed but could not be collected, the size was estimated by RC. However, for most specimens photographed but not collected, especially prior to February 2019, estimates were not recorded and are thus not provided here.

Only a selection of the photos taken are shown here. The whole set has been deposited in both the Florida Museum of Natural History and the Muséum d'Histoire naturelle of Geneva (MHNG) where they will be entered in their collection management database.

The observed specimens are listed separately for each species in the section "Examined material". Each record starts with the field number (BFLA) if collected, or with the observation date if not collected. Sometimes a part of or the whole specimen was also preserved in formalin and deposited as voucher in the Florida Museum of Natural History. The catalogue numbers are given as UF-######. Because formalin-fixed voucher material is only available for a minority of the specimens, the field numbers (BFLA) in this work are used to refer to a particular sample. All specimens and observations for which no locality is specified came from the area given above. For some additional comparison material the provenance is given.

Species identifications

Published works used to identify the species are given in the synonymies. Only studied publications are given. In the paragraph entitled "Observations" the actual observations and characteristics of the available specimens(s) are given, it is not a generalized description of the species. Not all observed species are reported here. Specimens that were not identifiable to species level and were also not collected for DNA barcoding have been omitted. In this study, only hydromedusae are presented. The Siphonophorae will be treated in a separate publication.

DNA barcoding

Methods for obtaining about 600 bp of the mitochondrial 16S gene as well maximum likelihood analyses are given in Schuchert (2014, 2018, 2019). The DNA extracts are kept by the Muséum d'Histoire naturelle of Geneva in their DNA collection (kept at -20°C, dissolved in TE buffer).

All new sequences have been deposited in the GenBank database with the accession numbers MW528627 to MW528734. The obtained 16S barcode sequence 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 of the sequences. For individual pairwise sequence comparisons, the two sequences were a ligned using 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 pairwise percent identities (p-values) were calculated using the corresponding function in BioEdit.

Additional examined comparison material

Aequorea forskalea Péron & Lesueur, 1810

Alcohol preserved sample MHNG-INVE-0055261; Mediterranean; collected before 1900; diameter ca. 10 cm, much fragmented, with gonads, about 100 radial canals. – Alcohol preserved sample MHNG-INVE-0055271; Mediterranean, Bay of Villefranche-sur-Mer; collected before 1895; det. C. Hartlaub; immature, 23 mm, ~48 radial canals.

Aequorea spec.

Pieces from two alcohol preserved medusae obtained from L. Leclère; Mediterranean, Bay of Villefranche-sur-Mer; collected 15-MAR-2017; 4-5 cm diameter, about half as many tentacle bulbs as radial canals; DOI of photos 10.5281/zenodo.4298436 and 10.5281/zenodo.4298454; used to obtain 16S sequence MW528733 and MW528734.

Aequorea macrodactyla (Brandt, 1834)

Alcohol preserved sample MHNG-INVE-55440; ca. 5 damaged specimens; Indonesia, Bay of Ambon; collected 1890; Material of Maas (1905).

Aequorea vitrina Gosse, 1853

One living, much damaged medusa obtained from J. J. Soto Angel and L. Martell; collected 27-MAR-2019; Norway, Hordaland, near Bergen, WGS84: 60.4567, 4.9339; ca. 10 cm diameter, >100 radial canals, about 5 times as many tentacles as radial canals; used to obtain 16S sequence MW528629.

GENERAL RESULTS AND DISCUSSION

Using close-up photos taken during 75 dives in the time period from 19 September 2018 to 18 June 2020 (123.5 hours total diving time) combined with the 16S RNA gene sequences it was possible to distinguish at least 56 species of hydromedusae. Of these 56 species, 52 are treated in the following taxonomic part, but 6 of them could only be identified to genus level (Appendix 1). Six new species are described. Four morphotypes are not treated here as either not enough data and/or material was available to identify them.

The approach to take several photos *in situ* and then use a tissue sample for DNA barcoding proved to be very satisfactory. Good photos taken at several angles and distances mostly permited us to see all relavant taxonomic traits of these transparent animals. As in preserved samples, it is of course important that the animals are sufficiently mature, *viz*. gonads are present. Such photos were actually often more useful than preserved specimens. Preserved medusae, notably those obtained with plankton nets, are regularly distorted and damaged and often only suitable for schematic drawings that need to be based on several specimens. Photos of living specimens are always preferable as they can provide taxonomically important information which is not well conveyed in drawings, e.g. colours and tissue opaqueness. Also the bell shape, mesoglea thickness, and the proportions are better examined in living material as they aremostly not well preserved. A disadvantage of the photographic/*in situ* approach is that microscopic details – like statocysts, nematocyst groups, and cirri – are less well visible and examinable. Sometimes these details could be examined in the alcohol preserved sample before DNA extraction. Another drawback, but which is also a problem in net-material, is the low number of specimens and the absence of fully mature animals making it regularly impossible to obtain a complete idea of the morphological variability of a species (comp. *Aequorea* species).

Recent molecular analyses showed that many hydroids have a very high genetic diversity and are likely species complexes (Moura *et al*., 2008; Schuchert, 2014; Montano *et al*., 2017; Maggioni *et al*., 2018, 2020; Postaire *et al.,* 2017; Miglietta *et al.,* 2018a; Boissin *et al*., 2018). Our medusa samples were all collected in a quite narrow region, but several morphospecies proved to be composed of two or more deeply separated molecular clades (*Zancleopsis dichotoma*, *Laodicea undulata, Orchistoma* *pileus*, *Pseudaegina rhodina*) or they were split here into sister species if the clades correlated with morphological differences (*Pandeopsis ikarii* and *P. prolifera* n. spec., *Proboscidactyla ornata* and *P. gemmifera*). An explanation for high intraspecific variation could be that the animals brought to the collecting site by the Gulf Stream originated from far apart sites and populations (see discussion under *Zancleopsis dichotoma*).

Our observations also revealed the presence of several Indo-Pacific species which have so far not been seen in the Atlantic Ocean: *Pandeopsis ikarii*, *Aequorea taiwanensis*, *Zygocanna* cf. *apapillatus*, *Gastroblasta timida*, *Cunina becki*, and *Pegantha polystriata*. *Thecocodium quadratum* was also found, but this surprising occurrence has already been reported by others (Kubota & Meldonian, 2016).

The new barcodes also permitted us to find similar sequences in GenBank obtained from hydroids and which are potentially the polyp stage of these medusae, or at least they will resemble them strongly (comp. Schuchert, 2016, 2018; Schuchert *et al.*, 2017). The 16S sequence of *Cirrhitiara superba* (Mayer, 1900) matched very closely the one obtained of a hydroid from Panama identified as *Thecocodium* spec. The 16S of *Euphysilla pyramidata* Kramp, 1955 matched closely a published sequence of a *Sphaerocoryne* polyp collected in the Maldives archipelago. The 16S barcodes of *Zancleopsis dichotoma* (Mayer, 1900) were related to ones of *Astrocoryne*

Table 1. 16S haplotype p-distances (% base pair differences in aligned sequence pairs) and number of haplotypes observed in the examined material. Only the species for which such a comparison was possible are listed.

species	p-distance within examined population	number of haplo-types	p-distances compared to haplotypes of the same species available in GenBank [GB number, locality]
Cytaeis tetrastyla	1.0-2.2	3	-
Pandeopsis ikarii	-	1	3.5 [MG136757, Japan]
Pandeopsis prolifera n. spec	2.3	2	-
Turritopsis nutricula	0.5	2	1.4-1.9 [EU624348, New England; MH029857 Panama]
Thecocodium quadratum	0.5	2	4.3-4.5 [FN422379, W Indian Ocean]
Proboscidactyla ornata	0.4-1.0	4	6.7-7.5 [EU305481, Caribbean; JQ715911, China]
Euphysilla pyramidata	0.2	2	-
Zanclea mayeri n. spec.	0.8-1.2	4	-
Zancleopsis dichotoma	0.5-6.2	5	-
Laodicea undulata	0.2-10.6	4	5.5-8.1[FJ55047, KY36396, KY36396; European coasts]
Staurodiscus kellneri	0.2-0.5	3	-
Staurodiscus tetrastaurus	0.2	2	-
Orchistoma pileus	0.5-8.1	7	-
Wuvula ochracea	0.2	2	-
Aequorea neocyanea	0.3-2.1	8	3.7-5.2 [MW528733, MW528734, Mediterranean]
Aequorea spec. 1	0.2-1.0	5	-
Aequorea taiwanensis	0.2-0.5	3	0.2-0.64 [JQ716019, JQ716019, Taiwan Strait]
Octophialucium aphrodite	0.8	2	-
Pseudaegina rhodina	0.2-7.8	4	-
Pegantha martagon	0.2-1.4	3	25 [MG979374, California]
Solmaris corona	1.7-3.2	3	-
Solmaris flavofinis	0.2	2	-
Solmundella bitentaculata	-	1	8.6-10.5 -14 [KX355407, Mediterranean; KF97740, China Sea; EU293998, Antarctica]
Aglaura hemistoma	0.9	2	2.0-5.0 [KP776748, Mediterranean; EU293984, Japan]
Rhopalonema velatum	0.2	2	0.2-4.3 (EU29399, Mediterranean; EU293993, Tierra del Fuego)
Geryonia proboscidalis	-	1	0.17-1.2 [KX355451, Mediterranean; EU293979, Japan; KT809331, Sea of Cortez]
Olindias tenuis	-	1	0.5 [MG979369, U.S. Virgin Islands]

cabela Maggioni *et al*., 2017*,* a hydroid found in the Red Sea and the Maldivian Archipelago. *Hebella venusta* (Allman, 1877) is likely the hydroid of *Melicertissa mayeri* Kramp, 1959 as their 16S are sufficiently similar. These results demonstrate again the value of 16S barcodes and well documented entries in GenBank for hydrozoan systematics. A taxonomically sound reference sequence database is also a prerequisite for new approaches using next generation sequencing of environmental DNA to monitor the biodiversity of a habitat [see e.g. Ames *et al.* (2021) for an eDNA study on jellyfish].

TAXONOMIC PART

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

Synonymy: See Schuchert (2007).

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 spec.

Fig. 1A-B

Examined material: BFLA3826; 1 specimen, 14-NOV-2018; bell height 5 mm; photographed and then preserved in alcohol for DNA extraction; 16S sequence MW528641.

Observations: Bell 5 mm high, higher than wide, mesoglea thick, apical mesoglea 1/4 of bell height, apex rather flat. Manubrium with cruciform base, oral region tubular, widest at base and thus like an inverted cone; four perradial oral tentacles arise well above mouth rim, trunk long, branched about 3 to 4 times, ending in spherical nematocyst knobs. Four gonads, male, interradial, encircling stomach entirely. Four radial canals and marginal bulbs, bulbs D-shaped (Fig. 1B), each with about eight filiform tentacles; dark, round ocelli on adaxial side of tentacle base.

16S Data: A blastn search with the partial 16S gene sequence (MW528641) did not give a close match, but the best five matches were *Bougainvillia* species. The sequence with the highest similarity (94% identity) was EU305470, obtained from a *B. fulva* collected in Japan (Kirsten Jensen, Kansas University, pers. com.). Others were *B. triestina* and *B. carolinensis* with about 92% identity. *Bougainvillia muscus* sequences differed even more, reaching only 87% identity.

Remarks: This *Bougainvillia* medusa could not be identified reliably. Morphologically, it resembles *B. carolinensis* (McCrady, 1859) and *B. muscus*

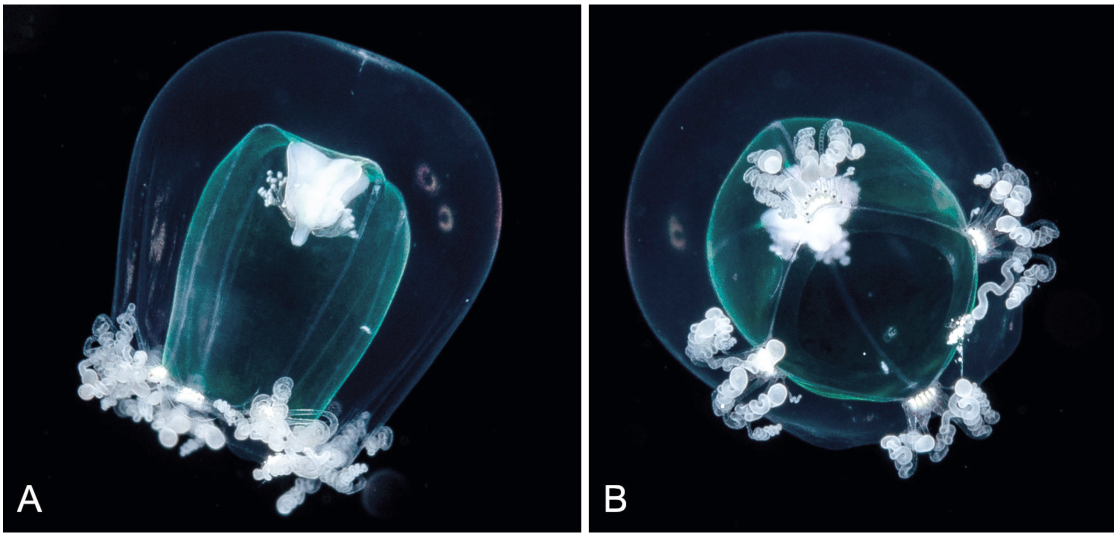

Fig. 1. *Bougainvillia* spec. of 14-NOV-2018, bell height 5 mm (A) Lateral view of whole animal. (B) Oral view.

(Allman, 1863). It differs from *B. carolinensis* (see descriptions in Mayer, 1910; Kramp, 1959a; Calder, 1971) in lacking the characteristic shape of the manubrium, which is widening from the aboral end towards the mouth. The manubrium of the present medusa is widest at the aboral end (Fig. 1A). *Bougainvillia muscus* medusae (for a description see Schuchert, 2007) differ in being smaller (1-4 mm), they have less tentacles per bulb (2-6), and the oral tentacles branch less (0-2).

Also, the 16S data argue against *B. carolinensis* and *B. muscus*. There are several 16S sequences of *B. muscus* available in GenBank (e.g. AM183126, AM411411), covering populations from Europe to New Zealand and with an intraspecific divergence of up to 1.5% base pair differences. The *Bougainvillia* medusa from Florida differed from *B. muscus* in 13% of the base pairs, and was thus far beyond the intraspecific divergence. The single available sequence from a *B. carolinensis* from Brazil (MG791827) did also not match (90% identity only). No morphological data are available for this sample and its identification cannot be verified.

Other *Bougainvillia* medusae known from the region can also be excluded based on their morphology. *Bougainvillia niobe* Mayer, 1894 buds medusae from the manubrium. These might not always be present, especially in mature animals (compare fig. 90 in Mayer, 1910), but the gonads are reportedly adradial and not interradial (Kramp, 1959a: 12). *Bougainvillia rugosa* Clarke, 1882 has medusae with unbranched oral tentacles and only 3 tentacles per bulb (Migotto, 1996).

The observed medusa thus likely belongs to an unnamed species, or a hydroid-based nominal species for which the adult medusa is not known yet. Using the 16S sequence will certainly in the future permit the identification of the hydroid (comp. Schuchert *et al.*, 2017; Schuchert, 2019), as well as additional growth stages and the females of the medusa, and thus give a more solid base for the description as a new species.

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

Synonymy: See Schuchert (2007).

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-C

Cytaeis tetrastyla Eschscholtz, 1829: 104, pl. 8 fig. 2. – Schuchert, 2007: 275, fig. 32, synonymy, references, taxonomic details.

Examined material: BFLA4066; 1 specimen; 10-APR-2019; size 2 mm; preserved in ethanol for DNA extraction; 16S sequence MW528664. – BFLA4069; 1 specimen; 11-APR-2019; size 1.5 mm; photographed and preserved in formalin and deposited as UF-013780. – BFLA4073; 1 specimen; 11-APR-2019; 2 mm; preserved in ethanol for DNA extraction; 16S sequence MW528667. – BFLA4418; 1 specimen; 28-MAY-2020; size 4 mm; preserved in ethanol for DNA extraction; 16S sequence MW528725. – 16-NOV-2017; 1 specimen photographed, not collected.

Observations: *Cytaeis* medusa with bell height 1.5-2 mm, apical jelly not much thickened and without apical process, but often with apical funnel-like depression; subumbrella with shallow gastric peduncle. Manubrium spindle-shaped, reaching to velum level, with more than 10 capitate tentacles originating distinctly above mouth margin; in upper third of manubrium several medusa buds, in lower two thirds apparently with developing gonad. Four perradial tentacles, fully contracted about as long as bell height, solid, bases widened to ovoid bulbs which adhere just above bell margin, giving the impression of the tentacles being connected by a flared end (Fig. 2B); the tentacle arises at an acute angle to the bulb and curve towards aboral.

Distribution: Circumglobally in tropical to subtropical seas, partly oceanic (Schuchert, 2007). Type locality: Atlantic Ocean, south of Equator.

16S Data: The three obtained 16S haplotypes have a maximal divergence of 2.2% and are thought to represent intraspecific variation (Table 1). Blastn searches in GenBank did not yield matches at species-level identities. The closest matches were with several samples of *Cytaeis uchidae* Rees, 1962 from Japan (about 95% identity), followed by other *Cytaeis* species, though with lower identity values.

Remarks: The taxonomic situation and identification of *Cytaeis* medusae is currently not resolved (see discussion in Schuchert, 2007). The opinion of Bouillon *et al.* (2004) that the "*Cytaeis tetrastyla*-like"medusae should not be given a specific name until the taxonomy has been sorted out properly is still valid, in particular if they do not come from the tropical Atlantic Ocean. However, the current material does come from the same tropical waters of the Atlantic Ocean as the type material and no named or distinct *Cytaeis* polyps are known from this region. We can thus be reasonably sure that *Cytaeis tetrastyla* is most likely the correct name.

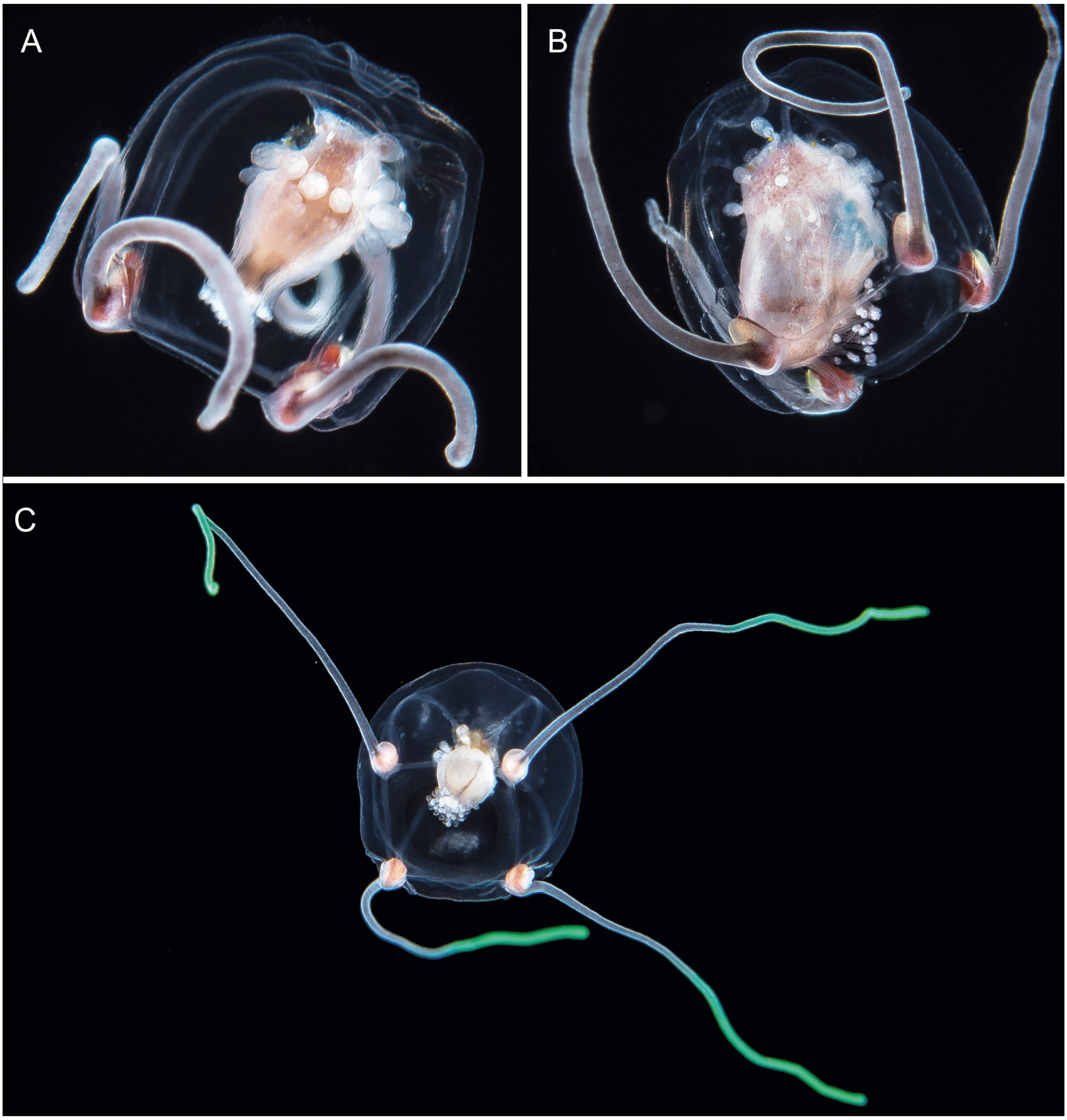

Fig. 2. *Cytaeis tetrastyla*, bell height 2 mm. (A) Lateral view, note medusa buds on upper part of manubrium, BFLA4066. (B) Lateral view with focus on the frontal exumbrella showing the typical flared tentacle bases of *Cytaeis* medusae, BFLA4073. (C) BFLA4069, note green tentacle tips, a colour likely due to interference effects and not pigments.

The taxonomic ambiguity relating to *C. tetrastyla* needs to be resolved using DNA sequence data of several populations and the present samples will hopefully contribute to this end.

Many cytaeidid medusae have a quite characteristic connection of the tentacles to the bell margin. The proximal ends of the tentacles are widened to an ovoid bulb which adheres along its long axis to the exumbrella just above bell margin, giving the impression of the tentacle being connected to the exumbrella by a flattened end (Fig. 2B).

The hydroid stage of this species is not known. A potential candidate is the *Cytaeis* hydroid from Bermuda Island described by Calder (1988).

Family Pandeidae Haeckel, 1879
Genus *Amphinema* Haeckel, 1879

Synonymy: See Schuchert (2007).

Diagnosis: Medusa with two long opposite tentacles; with or without ocelli; gastric peduncle absent; mostly 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, *Amphinema biscayana* (Browne, 1907)], 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 turrida (Mayer, 1900)
Figs 3A-D

Dissonema turrida Mayer, 1900: 44, pl. 2 figs 3-4. – Mayer, 1910: 116, pl. 10 fig. 1, pl. 22 fig. 1.
Stomotoca turrida. – Mayer, 1915: 199, pl. 1 fig. 1.
Amphinema turrida. – Schuchert, 2007: 312, fig. 48.

Examined material: 02-JUL-2018; 1 specimen photographed; approximately 6 mm; not collected.

Observations: *Amphinema* medusa, approximately 6 mm high, with elongated, folded gonads that extend along 5/6 of radial canals (Fig. 3A-B); manubrium about half the height of the subumbrella, simple cruciform mouth with a few folds; two opposite tentacles, long, hollow, base laterally compressed and clasping bell margin, no abaxial spur, large red abaxial ocellus; about 12 rudimentary bulbs on bell margin, each with a large, red ocellus (Fig. 3B). Adradial and interradial rudimentary bulbs bearing a thin cirrus originating in the middle of the bulb (Fig. 3C).

Distribution: Florida and Bahamas; Mediterranean; Torres Strait; Papua New Guinea; Japan; Pacific Side of Mexico; Chile (Schuchert, 2007). Type locality: USA, Florida, Dry Tortugas archipelago.

Remarks: *Amphinema turrida* has recently been redescribed and discussed by Schuchert (2007). Most Pacific populations lack the cirri and their status needs to be re-evaluated using genetic data.

Genus *Cirrhitiara* Hartlaub, 1914

Cirrhitiara Hartlaub, 1914: 284; type species *Tiara superba* Mayer, 1900, by monotypy.

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; 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 unknown.

Cirrhitiara superba (Mayer, 1900)
Figs 4A-D, 5

Tiara superba Mayer, 1900: 34, pl. 16 fig. 39.
Tiara pileata var. *superba*. – Mayer, 1910: 126, pl. 27 fig. 8, pl. 28 figs 3-4.
Tiara pileata f. *superba*. – Vanhöffen, 1913a: 416.
Cirrhitiara superba. – Hartlaub, 1914: 284, fig. 237. – Kramp, 1959a: 121, fig. 122. – Kramp, 1961: 97. – Kramp, 1968: 39, fig. 101.
not *Cirrhitiara superba*. – Thiel, 1938: 296, fig. 2. – Kramp, 1953: 267. – Van der Spoel & Bleeker, 1988: 167, fig. 8.

Examined material: BFLA4087; 1 specimen; 07-MAY-2019; preserved in ethanol for DNA extraction; 16S sequence MW528672. – 30-JUL-2018; 1 specimen photographed; not collected.

Observations: Pandeid medusa 7 mm high and 5 mm wide, bright pink manubrium and tentacle bulbs, apical process of variable size present, apical exumbrella with perradial furrows. Manubrium filling more than half of the volume of the subumbrella, mouth rim complexly folded. Gonads on stomach forming folds diverging from interradial, in each quadrant two adradial series of folds that are connected interradially by a transverse fold. Four broad radial canals, connected to stomach via funnel-like widenings. Four long, tapering, perradial tentacles, base laterally compressed and clasping bell margin, no abaxial spur, large red abaxial ocellus near abaxial end. Alternating with the tentacles three small bulbs, each with an abaxial ocellus and a thin cirrus usually originating laterally from bulb. All small bulbs of equal size.

16S Data: The partial 16S gene sequence (MW528672) obtained was used to search for similar sequences in GenBank using the blastn function. Similar sequences found were mostly from *Leuckartiara* species and other Pandeidae, giving sequence identities in the 90% range. However, there was also one sequence (MH361354) which had only a single mismatch in 599 aligned bases (99.8% identity, = 0.2 % divergence), a value which certainly represents intraspecific variation (reference values for Pandeidae acc. Schuchert, 2018, table 2). The matching sequence was obtained from a hydroid originating from Caribbean Sea close to Panama and identified as *Thecocodium* spec. (Miglietta *et al.*, 2018b). The hydroid is described and depicted in the supplementary material of Miglietta *et al.* (2018b).

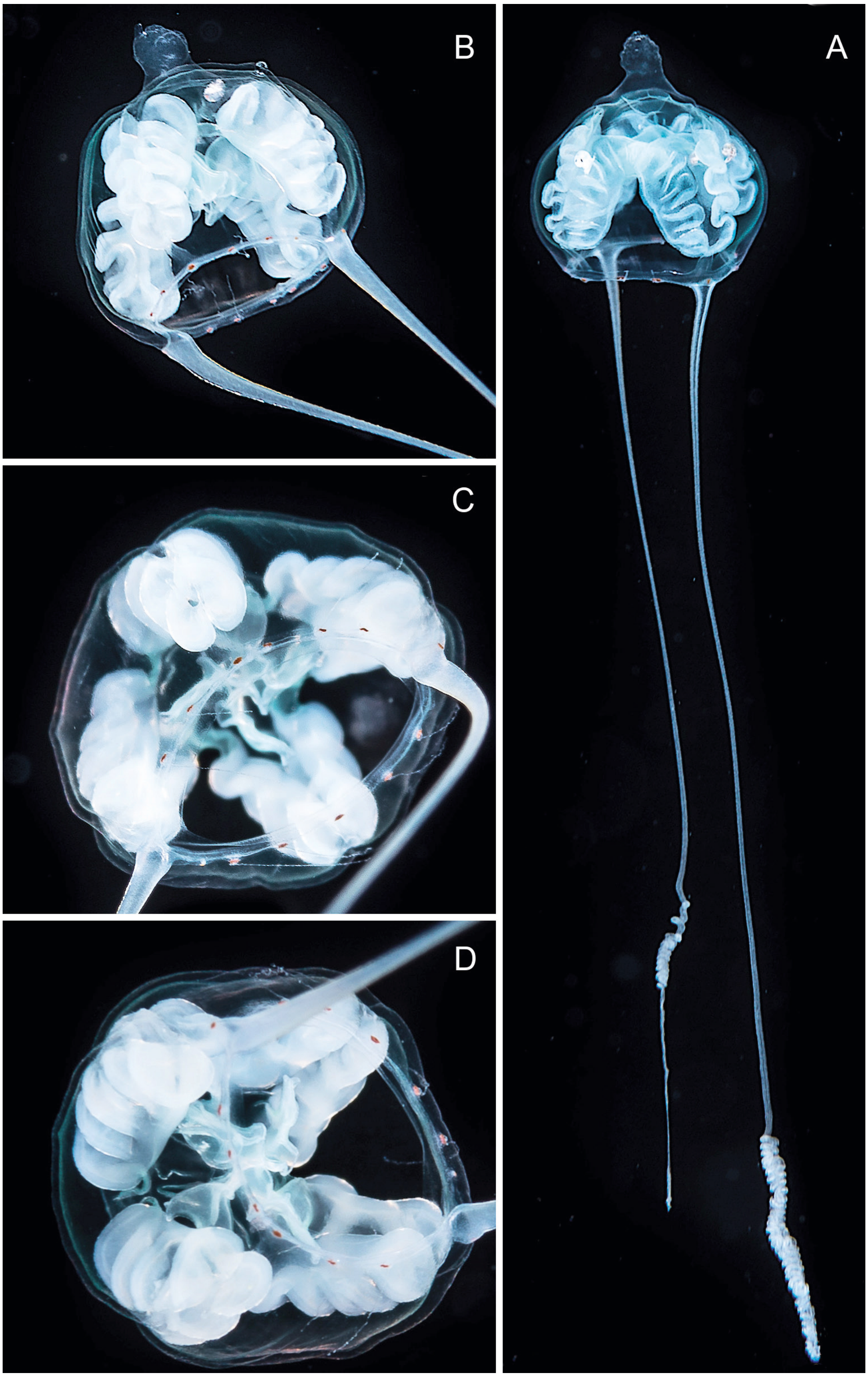

Fig. 3. *Amphinema turrida*, bell height approximately 6 mm. (A) Lateral view. (B-D) Oblique views from oral side, note the presence of thin cirri.

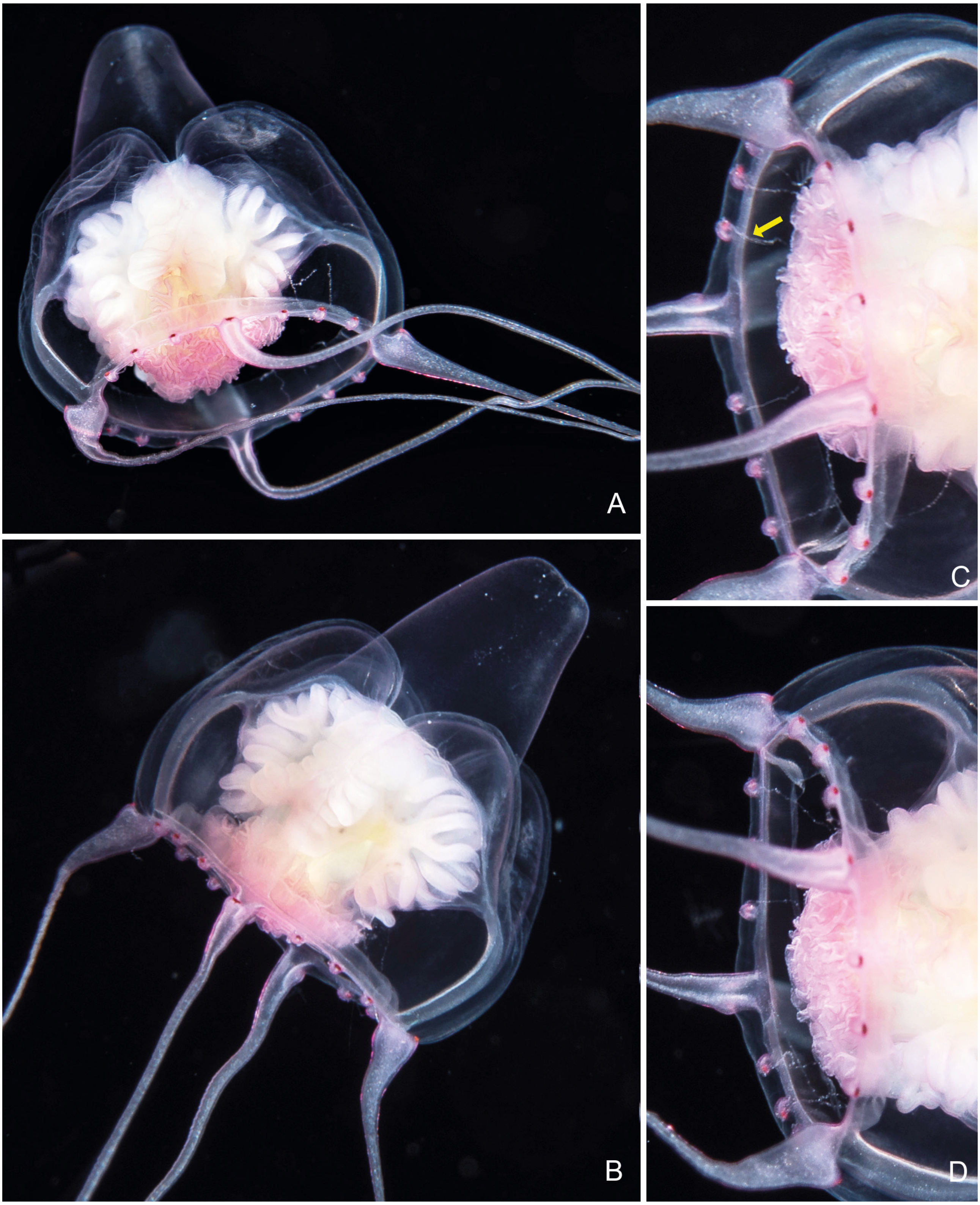

Fig. 4. *Cirrhitiara superba*, specimen BFLA4087, bell height 7 mm. (A-B) Lateral view. (C-D) Close up of bell margin, note cirri (arrow in C).

Fig. 5. *Cirrhitiara superba*, specimen observed in 2018 but not collected. The cirri are barely visible.

It is a polyp lacking tentacles. The typical capitate dactylozooids of the genus *Thecocodium* were not observed, which means that it could also belong to other genera with hydroids lacking tentacles, e.g. *Hydrichthys* (Pandeidae, see Schuchert, 2007).

The obtained 16S sequence did not cluster with any other genus of Pandeidae for which there were sequences available (Fig. 8), but this is due to the poor resolving power of the 16S marker above the genus level.

Remarks: *Cirrhitiara superba* has only rarely been reported. The identity of the present material is beyond doubt as it matches very well the descriptions in Mayer (1900, 1910). Moreover, it comes from the same region and the same continental shelf region as the type material.

Thiel (1938) identified a small (1 mm) juvenile medusa from Brazil as *C. superba*. His specimen had eight tentacles, the interradial ones being less developed. There were also 8 to (?) 16 rudimentary bulbs, each with a lateral cirrus. The presence of interradial tentacles – even less developed – argues against this being *C. superba.* Neither Mayer (1900, 1910) nor we observed interradial tentacles in *C. superba.* Vanhöffen (1913a), who had mostly young medusae obtained from Mayer, speaks of 8 tentacles in his largest medusae, but he was likely referring to both types of tentacles, *viz.* four large ones and four cirri.

Kramp (1953) thought that two medusae collected near the eastern coast of Australia belonged to *C. superba* despite they lacked cirri. Additionally, the interradial bulbs were larger than the adradial ones and no ocelli were observed. This makes the identification rather doubtful. The medusae are perhaps referable to *Leuckartiara fujianensis* Huang, Xu, Lin & Qiu, 2008 or *Leuckartiara neustona* Xu & Huang, 2004.

The medusa shown in Van der Spoel & Bleeker (1988: fig. 8) originating from Indonesia had thick cirri and 8 long tentacles and thus unlikely belong to the present species.

Distribution: Florida, Bahamas (Mayer, 1910). Records from Brazil (Thiel, 1938), north-eastern Australia (Kramp, 1953), and Indonesia (Van der Spoel & Bleeker, 1988) are likely misidentifications (see above). Type locality: USA, Florida, Dry Tortugas archipelago.

Genus *Merga* Hartlaub, 1914

Merga Hartlaub, 1914: 249; type species *Pandea violacea* Agassiz & Mayer, 1899 by original designation.

Tiarula Hartlaub, 1914: 253; type species *Tiara tergestina* Neppi & Stiasny, 1912 by original designation.

Mergintha Hartlaub, 1914: 250; type species *Mergintha lobianci* Hartlaub, 1914 by monotypy.

Janiopsis Bouillon, 1980: 328; type species *Janiopsis costata* Bouillon, 1980 by monotypy; invalid junior homonym of *Janiopsis* Rovereto, 1899 [Gastropoda, Buccinidae].

Diagnosis: Pandeid medusae with smooth or granulate adradial or interradial gonads, with mesenteries, stomach with cross-shaped base, manubrium not twisted, with simple or faintly crenulated oral lips; four, eight, or more tentacles, with or without rudimentary bulbs or tentacle-stumps, with or without ocelli.

Hydroids, where known, colonial, arising from tubular, ramified hydrorhiza, cauli slightly branched or not, with or without pseudohydrotheca, when present not enveloping tentacles, one whorl of filiform tentacles. Medusa buds arise from stems or stolons.

Merga violacea (Agassiz & Mayer, 1899)

Fig. 6A-E

Pandea violacea Agassiz & Mayer, 1899: 160. – Mayer, 1900: 34, pl. 1 fig. 1. – Bigelow, 1909: 205, pl. 41, figs 10-11. – Mayer, 1910: 119, text fig. 64, pl. 11 fig. 7, pl. 12 fig. 1.

Mergintha lobiancoi Hartlaub, 1914: 250, fig. 205. – Kramp, 1953: 265, synonym.

Merga violacea. – Hartlaub, 1914: 249, fig. 204, new combination. – Kramp, 1953: 265. – Kramp, 1959a: 116, fig. 106. – Kramp, 1961: 107. – Kramp, 1968: 41, fig. 104. – Schuchert, 2007: 355, fig. 69.

? not *Merga violacea*. – Menon, 1932: 7, pl. 1 fig. 10. [? = *Pandeopsis ikarii*]

Examined material: BFLA4006; 1 specimen; 26-NOV-2018; size 12 mm high, 10 mm wide, pink colour; photographed and preserved in ethanol for DNA

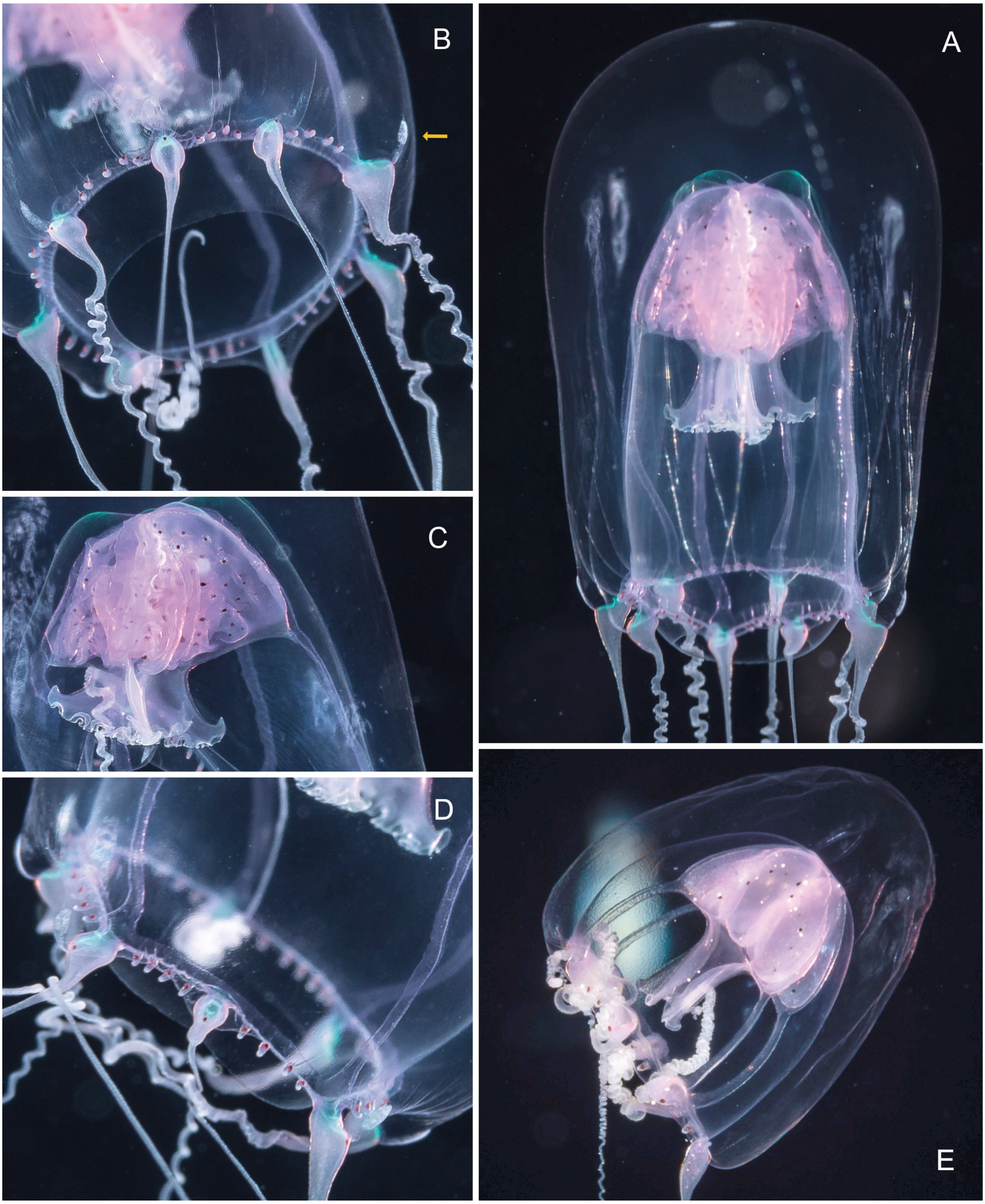

Fig. 6. *Merga violacea*. (A-D) Specimen BFLA4006, bell height 12 mm. (A) Lateral view of whole animal, note that the bell is somewhat contracted and more elongate than normal. (B) Bell margin seen from oral, note the flat abaxial spurs above some of the tentacle bulbs (arrow). (C) Lateral view of stomach. (D) Bell margin, note rudimentary bulbs with short tentacle stumps. (E) Lateral view of younger animal observed 30-Jun-2018, size approximately 7 mm.

extraction; 16S sequence MW528650. – 30-JUN-2018; 1 specimen photographed; size approximately 7 mm, pink, only 2 rudimentary bulbs between tentacle pairs; not collected. – 09-AUG-2018; 1 specimen photographed; size approximately 10 mm, pink; not collected.

Observations: Typical medusa of the genus *Merga*, up to 12 mm high, characteristic light pink-purple colour of manubrium and tentacles (Fig. 6A-E), without apical process but when fully grown with a thick apical jelly, shallow subumbrellar pockets present. Manubrium about half the height of subumbrella, very wide, connected for about half its length along the radial canals; stomach base and mouth cruciform, mouth rim slightly folded. Gonads on interradial surfaces of stomach, thin, smooth and not folded. Four radial canals broad, connected to stomach in its upper parts as mesenteries. Eight long, tapering tentacles, base laterally compressed and clasping bell margin, may be continued on exumbrella as an atypical, flat, abaxial spur (Fig. 6B); large red abaxial ocellus near abaxial end of bulb. Rarely also 9 tentacles observed. Alternating with the tentacles 2-5 small bulbs (max. total 34) with a short, blunt tentacle stump, all the same size and also with a red ocellus. Usually with brown pigment dots in the stomach wall (Fig. 6C, E).

Distribution: Circumglobal in tropical to subtropical waters (Schuchert, 2007). Type locality: Fiji Islands.

16S Data: The partial 16S gene sequence (MW528650) obtained was used to search for similar sequences in GenBank using the blastn function. Other similar sequences found were as expected of Pandeidae species but had only identities below 89%. The similarities with the *Pandeopsis* species described below were also relatively low (<86%, see also Fig. 8).

Remarks: The species has recently been redescribed and discussed by Schuchert (2007), but the problem with the type locality remains unresolved. No type material could be located in the Harvard Museum of Zoology (A. Baldinger, pers. com. June 2019), the museum Agassiz and Mayer were associated with.

Agassiz & Mayer (1899) introduced the name *Pandea violacea* in a paper reporting on medusae collected in the Fiji archipelago. In the description – no figure was given – they state that they have also found indistinguishable medusae at the Dry Tortugas Islands which they intended to illustrate in a subsequent publication. Notwithstanding, the paper dealt with specimens from Fiji and therefore the Fiji Archipelago should be considered as the type locality of the species. This could be taxonomically important if future genetic studies show that the two populations belong to separate species.

In one of our specimens (BFLA4006), some tentacle bulbs had atypical abaxial spurs formed by thickening of the exumbrellar epithelium (Fig. 6B). Several specimens also had brown dots in the stomach wall (Fig. 6A, C). There seem to be differences between Pacific and Atlantic individuals, including the colouration (comp. Bigelow, 1909; or Schuchert, 2020: photos of Australian *Merga violacea*).

Genus *Pandeopsis* Kramp, 1959

Pandeopsis Kramp, 1959b: 39; type species *Pandeopsis scutigera* Kramp, 1959 by original designation.

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.

Remarks: The only tangible difference of *Pandeopsis* and *Merga* is the more quadratic stomach base in the former. While some *Pandeopsis* specimens examined here indeed had a wide, quadratic stomach base (Fig. 7C), the difference to *Merga* is not always distinct and both genera could therefore be regarded as congeneric. The 16S phylogenetic tree (Fig. 8) suggests that the two genera are not closely related, but this needs confirmation with additional markers.

Pandeopsis ikarii (Uchida, 1927)

Fig. 7A-C

Tiaranna ikarii Uchida, 1927a: 208: fig. 35.

Pandeopsis ikarii. – Kramp, 1961: 444. – Kramp, 1965: 39, synonymy. – Kramp, 1968: 41, fig. 105. – Schuchert, 1996: 73, fig. 43a-b. – Buecher *et al.,* 2005: 43. – Kubota *et al*., 2011: 57, figs 1-3. – Suehiro & Kubota, 2015: 73, fig. 1, pl. 1.

Pandeopsis scutigera Kramp, 1959b: 232, fig. 7, Gulf of Thailand. – Kramp, 1961: 113, 444. – Kramp, 1968: 41, synonym.

? not *Pandeopsis ikarii*. – Bouillon, 1980: 336. – Bouillon, 1985: 257, fig. 6, life cycle. [? = *Pandeopsis prolifera* n. spec.]

Examined material: BFLA4088; 1 specimen; 07-MAY-2019; size 2.5 mm, faintly greeninsh gastrodermis, no dots on manubrium seen; preserved in ethanol for DNA extraction; 16S sequence MW528673. – 08-AUG-2018; 1 specimen photographed; size approximately 5 mm, greenish manubrium, dots present; not collected.

MHNG-INVE-0092017; Japan, Mie Prefecture, Toba City; WGS84 34.4781, 136.8670; collector and donor

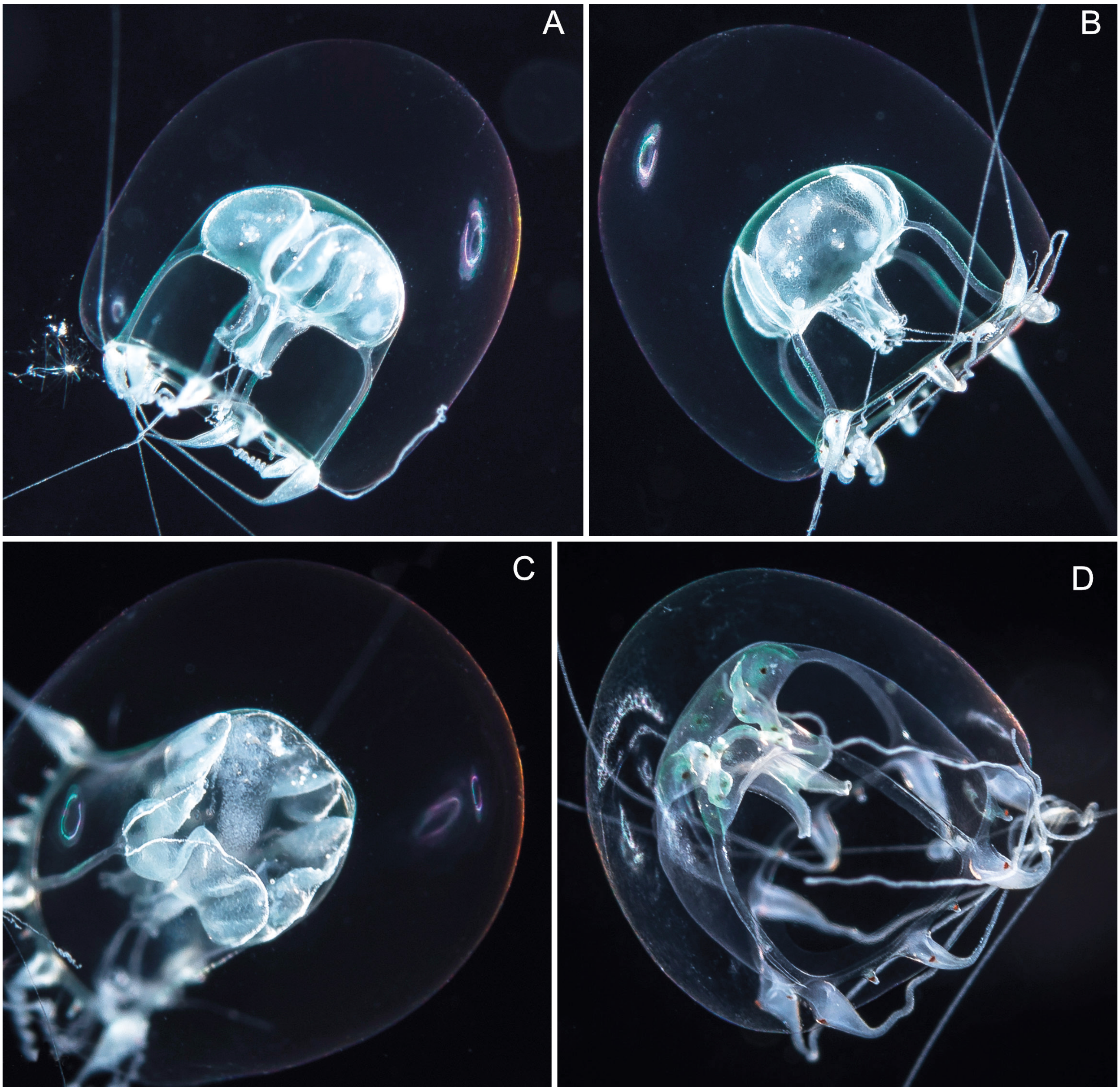

Fig. 7. *Pandeopsis ikarii*. (A-C) Specimen BFLA4088, size 2.5 mm, presumable incipient oocytes are visible in the stomach wall. (D) Specimen collected 08-AUG-2018, size 5 mm, the identification is somewhat unreliable as there is no sequence data available.

Takanori Suehiro; year 2015; 12 medusae cultivated from a polyp stage collected on sand, age about 3 months, examined alive and preserved, size 4 mm, 12 tentacles; 16S sequence MG136757.

Observations: Sample BFLA4088, bell height 2.5 mm, bell top rounded, lower lateral walls straighter, mesogoea thick, at apex nearly 1/2 of bell height, smooth. Manubrium large, base square-shaped, wide upper half, narrower lower part with cross-shaped section, mouth drawn out into four lips with smooth rim; colour greenish, no pigment dots; wall of upper half of manubrium apparently with layer of numerous developing oocytes (Fig. 7A). Radial canals forming mesenteries along upper half of manubrium, smooth, greenish. Eight tentacles, long, tapering, with red abaxial ocellus at base. Eight adradial rudimentary bulbs with a very short, stump-like tentacle, with abaxial red ocellus (Fig. 7B). Individual collected 08-AUG-2018 similar but larger (5 mm), with dots on manubrium (Fig. 7D).

16S Data: An blastn search with the partial 16S gene sequence (MW528673) was used to search for similar sequences in GenBank. The closest match with 3.5 % sequence divergence was with sequence MG136757

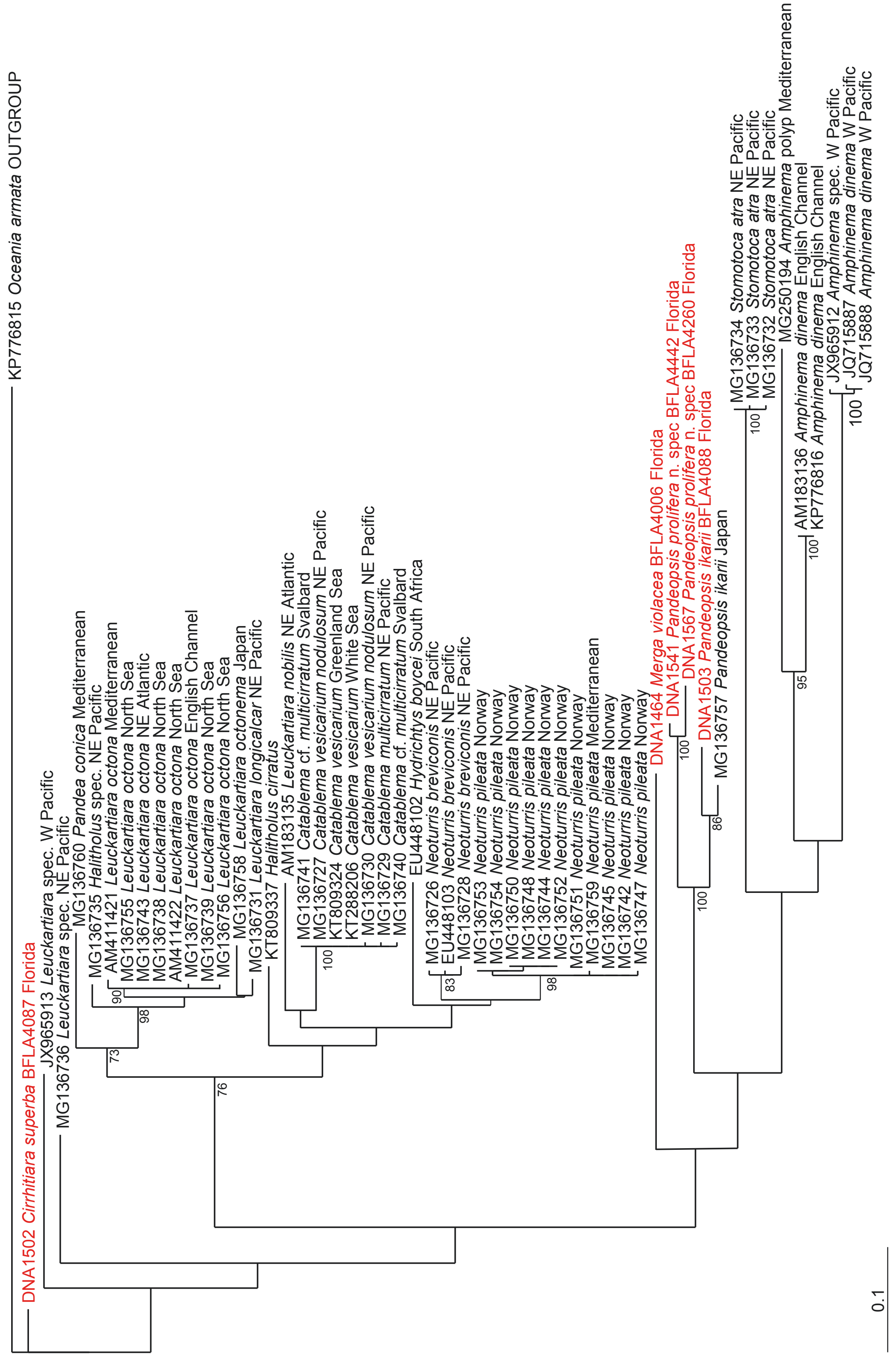

Fig. 8. 16S rRNA maximum likelihood phylogenetic tree of Pandeidae species obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Red labels are new sequences from this study. 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.

obtained from a *Pandeopsis ikarii* sample from Japan (see also Fig. 8 and the discussion of the next species).

Distribution: Japan, Philippines, Gulf of Thailand, Java Sea, New Zealand, Indian Ocean, Red Sea. Type locality: Seto (Wakayama), Japan.

Remarks: This is the first record of this species for the Atlantic Ocean. Notably sample BFLA4088 (Fig. 7A-C) matched very well the existing descriptions of this species given above in the synonymy. The only difference being the absence of pigment dots on the stomach wall. They might develop later only (comp. Suehiro & Kubota, 2015). Another observed specimen (Fig. 7D) had such spots, but as no sequence information is available for this specimen the identification remains somewhat uncertain.

Pandeopsis ikarii has been widely reported in the Indian- and Pacific Oceans, but some of these records might belong to a distinct species. Bouillon (1980: 336) observed that his animals from the Bismarck Sea had a dense proliferation of medusa buds on the manubrium and developed up to 14 tentacles. The budding was sometimes already present in young animals with four tentacles only. The maximal size was up to 10 mm, thus quite larger than usually reported (4.5 mm in Kramp, 1968). Another detail mentioned by Bouillon is a band of chordoid cells along the four corners of the manubrium ending in nematocysts clusters, an element neither observed here nor mentioned in other descriptions of the species. The budding was also observed by Navas (1971, cited in Bouillon, 1980) in animals collected in the Indian Ocean, but not by any other observer. Dr Shin Kubota (pers. com.) informed us that he never observed medusa buds in Japanese *P. ikarii*. It is therefore very likely that Bouillon's material belonged to another species, perhaps even *Pandeopsis prolifera* n. spec described below.

***Pandeopsis prolifera* n. spec.**

Fig. 9A-E

Holotype: BFLA4442; collected 07-JUN-2020; size 8 mm; part of specimen preserved in formalin and deposited in Florida Museum of Natural History, catalogue number UF-014057; before formalin fixation, about 1/4 of animal was cut and preserved in ethanol for DNA extraction (MHNG-INVE-0137381); 16S sequence MW528727.

Other examined material: BFLA4260; 1 specimen; 07-MAY-2019; size 5 mm; preserved in ethanol for DNA extraction; 16S sequence MW528695.

Type locality: USA, Florida, 5.5-12 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Diagnosis: *Pandeopsis* medusa with medusa budding on manubrium wall in mature animals, eight tentacles, approximately 24 rudimentary bulbs; stomach base square-shaped in younger animals.

Description: Bell size up to 8 mm, bell higher than wide (Fig. 9A), bullet-shaped, jelly very thick, apical jelly takes up about 1/3 of total height, lateral walls also thick. Exumbrella smooth. Manubrium large, square-shaped base in younger individual, more cross-shaped in older specimen (Fig. 9C); manubrium with wide upper part (stomach) filling nearly half the subumbrella and attached to it via mesenteries, narrower lower part of manubrium with cross-shaped section, mouth drawn out into four lips with slightly undulated rim; manubrium colourless but with pigment dots (Fig. 9D). In holotype interradial stomach wall densely beset with a layer of medusa buds of different developmental stages, about 50 per quadrant, white, in some buds red pigment dots of developing ocelli. Radial canals thick, smooth. Eight tentacles, long, tapering, not much laterally compressed, with red abaxial ocellus at base. 24 adradial rudimentary bulbs with a very short, stump-like tentacle, with abaxial red ocellus (Fig. 9B, D).

16S Data: See Fig. 8, Table 1, and below under Remarks.

Distribution: Type locality only.

Remarks: Our main argument to separate *P. prolifera* from *P. ikarii* is the distinct separation in the phylogenetic analysis (Fig. 8). The observed base pair differences between the two clades were 7.2 to 8.9 %, which is rather large in comparison to the intraspecific variation seen in the other Pandeidae (comp. Fig. 8) but could also be in part due to generally longer branches in this cluster.

However, there are also morphological differences between the animals identified here as *P. prolifera* and *P. ikarii*:

- medusa buds on manubrium (Fig. 9A) versus no buds on manubrium (Fig. 7A-B),
- three rudimentary bulbs between tentacle pairs even in younger medusae (Fig. 9D) versus one only (Fig. 7B),
- colourless manubrium (Fig. 9) versus greenish manubrium (Fig. 7).

We acknowledge that all these differences could be due to a low sample number bias and not fully-grown individuals. More samples could blur the differences and require that both morphotypes be regarded as conspecific. The high intraspecific genetic divergence would be surprising though.

Genus *Larsonia* Boero, Bouillon & Gravili, 1991

Stomotoca (*Stomotocanna*) Haeckel, 1879: 52; type species *Stomotoca pterophylla* Haeckel, 1879 by monotypy.

Larsonia Boero, Bouillon & Gravili, 1991: 198; type species *Stomotoca pterophylla* Haeckel, 1879 by original designation.

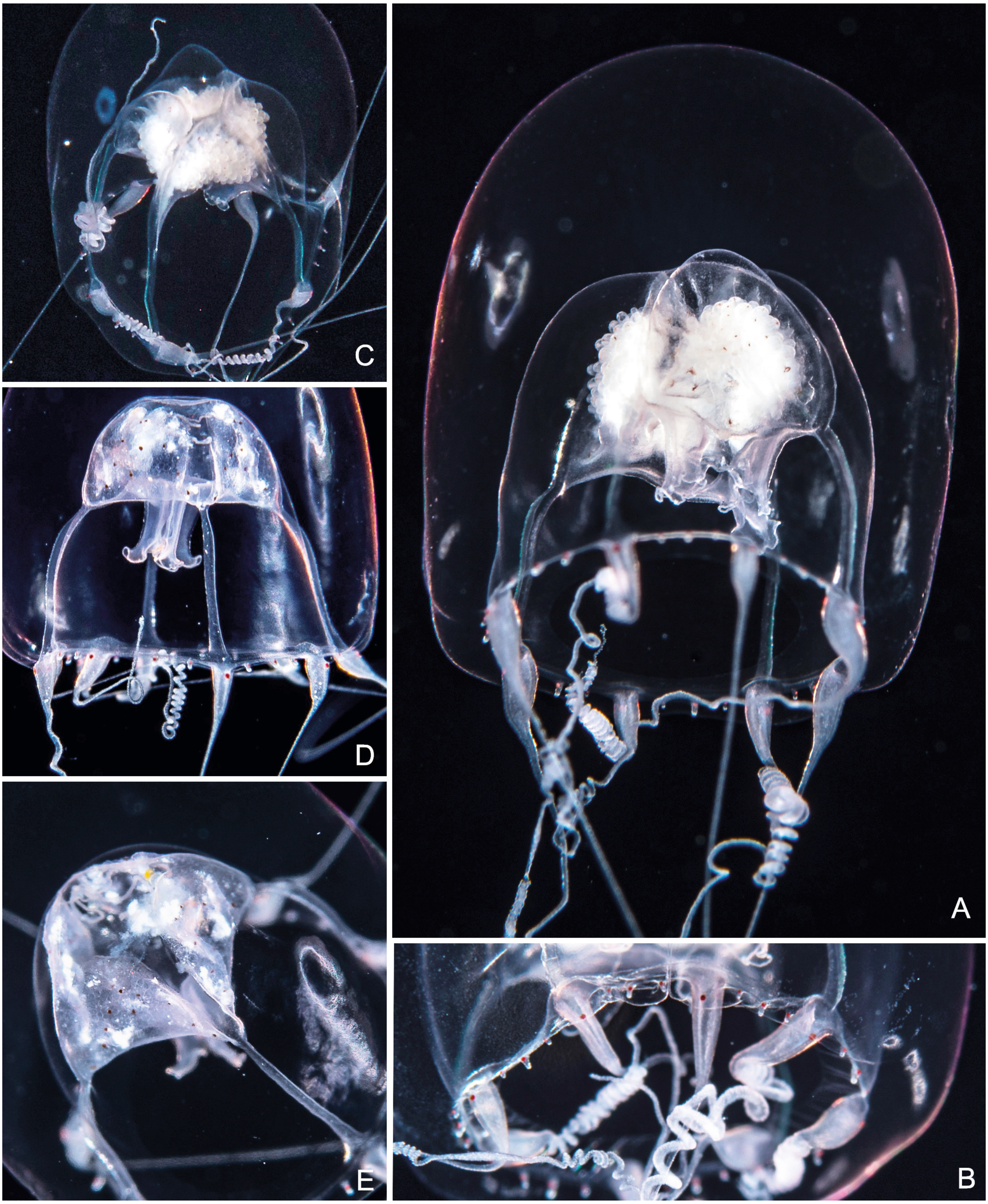

Fig. 9. *Pandeopsis prolifera* n. spec. (A-C) Holotype, BFLA4442, bell height 8 mm. (D-E) BFLA4260, size 5 mm. (A) Lateral view. (B) Bell margin in oral view. (C) Oblique view on aboral part, note shape of manubrium base which is not obviously square-shaped. (D) Lateral view. (E) Oblique view on aboral part, base is square-shaped, some incipient oocytes are visible, food items are in the lumen.

Diagnosis: Medusa with thick apical mesoglea and usually pointed apex; manubrium large, attached to a broad gastric peduncle, extending well beyond bell margin, mouth with crenulated lips; gonads in 8 adradial rows on manubrium, complexly transversely folded; two opposite perradial tentacles, numerous rudimentary bulbs on bell margin; no ocelli.
Hydroid parasitic on fish, with plate-like naked hydrorhiza, hydranth with no tentacles; gonozooid branched, producing at ends medusa buds.

Remarks: Larson (1982) reared medusae released from a parasitic hydroid of the genus *Hydrichthys* Fewkes, 1887 and could identify them as *Stomotoca pterophylla* Haeckel, 1879. Because Larson's hydroid showed little host specificity and many *Hydrichthys* polyps are rather similar, Larson concluded that they will also produce medusae referable to the genus *Stomotoca* L. Agassiz, 1862. Therefore, he suggested to synonymize *Hydrichthys* and *Stomotoca*. This was contested by Boero & Bouillon (1989) who could show that the type species of *Stomotoca* – *S. atra* L. Agassiz, 1862 – had a polyp stage that was completely different from *Hydrichthys* (free living, with scattered tentacles). Moreover, the polyp of a tentatively identified *Hydrichthys mirus* Fewkes, 1887 – type species of the genus *Hydrichthys* – produced a *Leuckartiara*-like medusa (Boero *et al.*, 1991). Because *Stomotoca pterophylla* and *Stomotoca atra* have different polyps, Boero *et al.* (1991) proposed the new genus *Larsonia* for *S. pterophylla*. Boero *et al.* must have overlooked that Haeckel (1879) had already introduced a subgenus name for *S. pterophylla*, namely *Stomotocanna* Haeckel, 1879. As a subgenus level name automatically also becomes available at the genus level, *Larsonia* Boero, Bouillon & Gravili, 1991 is a junior synonym of *Stomotocanna*. However, because Haeckel's name has not been used since its introduction and in the interest of nomenclatural stability, it should not be reactivated (ICZN, paragraph 23.9.1.1.)

Larsonia pterophylla (Haeckel, 1879)
Fig. 10A-D

Stomotoca (Stomotocanna) pterophylla Haeckel, 1879: 52, pl. 4 fig. 10.
Stomotoca pterophylla.– Mayer, 1910: 113, pl. 29 figs 3-5, pl. 30 fig. 7. – Bigelow, 1918: 372, synonymy, discussion of species. – Uchida, 1940: 284, fig. 3. – Kramp, 1959a: 119, fig. 115. – Kramp, 1961: 115. – Kramp, 1968: 44, fig. 113. – Larson, 1982: 433, fig. 183. – Wedler & Larson, 1986: 97, fig. 11a-b, hydroid, young medusa.
Stomotoca divisa Maas, 1897: 11, pl. 1 figs 1-9. – Vanhöffen, 1913b: 14, synonym.
Larsonia pterophylla. – Boero *et al*., 1991: 198, new combination. – Woodstock *et al.,* 2019: fig. 1, hydroid.
Stomotoca atra. – Vanhöffen, 1913b: 14, pl. 2 figs 12-16. – Stampar & Kodja, 2007: 55, figs 2-3. [not *Stomotoca atra* L. Agassiz, 1862]

Examined material: BFLA4453; one formalin fixed specimen deposited under catalogue number FU-014064; collected 08-JUN-2020; height 27 mm. – 08-AUG-2018, 1 specimen photographed; not collected...

Observations: Medusa 27 mm, with low umbrella and big, conical, pointed apical process; subumbrella shallow; with broad gastric peduncle reaching to velum level; 4-5 ribbon-like radial canals; two opposite tentacles, long, whitish, with swollen base clasping bell margin, no ocelli; about 80-100 atentaculate bulbs along bell margin, small, wart-like, all about the same size, without ocelli (Fig. 10C); manubrium barrel-shaped, with mouth drawn out into four long perradial lips, margin crenulated; gonads large, covering stomach in eight adradial series of about 10 branched folds directed towards interradial, pairs of adradial fold series connected perradially by a thick, vertical fold; adradial folds branching with up to four ends (Fig. 10B). Gonads and manubrium colour golden-brown or brown.

Distribution: American coasts from Gulf of Maine to Brazil, West Africa, Pacific coasts of Panama to Peru, Japan, Papua New Guinea, Indian Ocean (Kramp, 1968; Bouillon, 1980; Navas-Pereira & Vannucci, 1991; Stampar & Kodja, 2007, as *Stomotoca atra*). Type Locality: Caribbean Sea, 20.60°N 79.00°W.

Remarks: The observed specimens agreed well with existing descriptions of *Larsonia pterophylla*, except that one had five radial canals instead of four. This surplus radial canal was interpreted as a developmental aberration or variation without taxonomic significance. Also other tetraradial hydromedusa species occasionally show three or five radial canals (see *Clytia* spec.).
Stomotoca atra L. Agassiz, 1862 is a very similar species and Vanhöffen (1913b) thought that they could be conspecific. However, *S. atra* is distinct from *L. pterophylla*, notably they have different polyp stages (comp. Larson, 1982 and Boero & Bouillon, 1989). The medusae are distinguishable: in *L. pterophylla* the mouth margin is crenulated and perradially drawn out into long lips, in *S. atra* it is not crenulated and the perradial lips are short. Additionally, the transverse gonad folds are branched several times in *L. pterophylla*, while they are mostly unbranched in *S. atra* (comp. Schuchert, 2017b) or in loops in very mature animals (comp. Bigelow, 1918; Arai & Brinckmann-Voss, 1980). The Brazilian medusae depicted in Stampar & Kodja (2007) and identified as *S. atra* must thus belong to *L. pterophylla*.

Family Oceaniidae Eschscholtz, 1829
Genus *Turritopsis* McCrady, 1857

Synonymy: See Schuchert (2020).

Diagnosis: Medusae with high bell, proximal portion of radial canals swollen through vacuolated gastrodermal

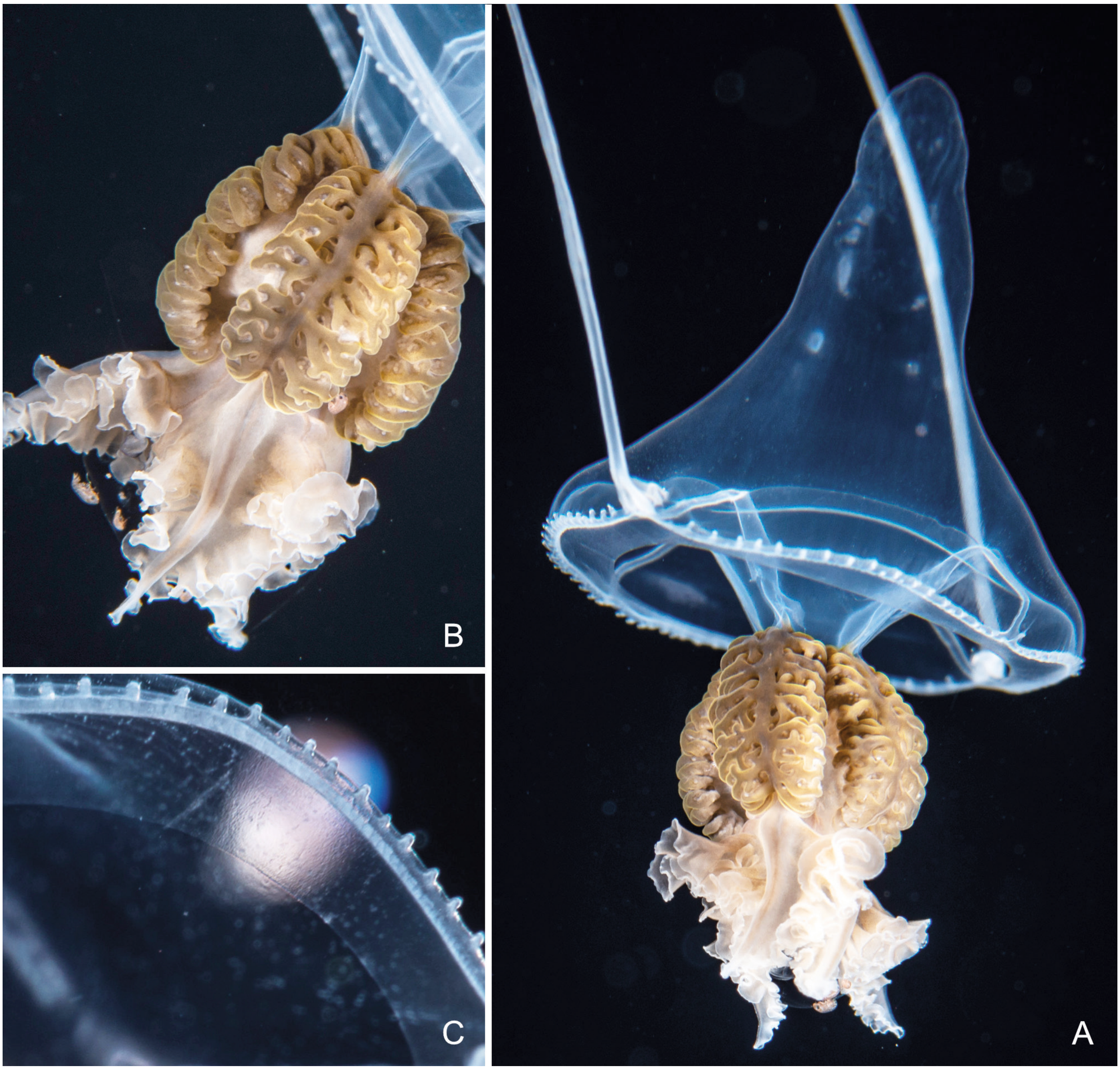

Fig. 10. *Larsonia pterophylla.* (A) BFLA4453, lateral view of animal, size 27 mm. (B) BFLA4453, close up of manubrium in lateral view. (C) Animal photographed 08-AUG-20181 part of bell margin in aboral view showing rudimentary tentacle bulbs (warts).

cells, forming a peduncle-like mass on top of manubrium, in larger animals continued on manubrium as perradial ribs. Tentacles numerous and evenly distributed. Mouth four-lipped, fringed with numerous spherical nematocyst clusters, these with or without a distinct stalk. Ocelli adaxial on tentacle base.

Polyp stage forming erect, branching colonies, side-branches and hydranth pedicels adnate for some distance, perisarc tubes not nested. Hydranths spindle- to club-shaped; filiform tentacles scattered over much of hydranth body. Gonophores develop on the hydrocauli in perisarc covered region and are liberated as medusae.

Remarks: The genera *Turritopsis* McCrady, 1857 and *Oceania* Péron & Lesueur, 1810 are morphologically not separable (comp. Schuchert, 2016). The purported difference of the stalked oral nematocyst buttons in *Oceania* is not tenable as also *T. nutricula* has stalked clusters (see below). However, to avoid unnecessary taxonomic changes, the two genera should not be synonymized until a comprehensive molecular phylogeny using several marker genes confirms this.

Turritopsis nutricula McCrady, 1857

Fig. 11A-D

Oceania (Turritopsis) nutricula McCrady, 1957: 55, pl. 4 figs 1-10.

Turritopsis nutricula. – Brooks, 1883: 465. – Brooks, 1886: 388, pl. 37. – Brooks & Rittenhouse, 1907: 429, pls 30-35, development. – Mayer, 1910: 143, figs 10-13, pls 14-15. – Goy, 1979: 270, fig. 4. – Wedler & Larson, 1986: 86, fig. 5B. – Schuchert, 2004: 327, figs 2A-B, 3D-E, revision. – Miglietta *et al.,* 2018a: fig. 2. – Calder, 2019: 12, fig. 1e.

Modeeria multitentaculata Fewkes, 1881: 149, pl. 3 figs 7-9.

Examined material: BFLA4391; 1 specimen; 17-MAY-2020; size 3 mm; preserved in alcohol for DNA extraction; 16S sequence MW528718. – BFLA4416; 1 specimen; 28-May-2020; size 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528724.

Observations: Typical *Turritopsis* medusae, bell heights up to 3 mm, manubrium yellow, blocks of vacuolated cells at manubrium base with deep interradial clefts, thus clearly separated (Fig. 11B-C), tentacle numbers about 50, base with an adaxial ocellus, tentacle tips swollen in life. Nematocyst buttons lining the mouth margin with stalks like in *Oceania armata*.

16S Data: The two 16S sequences obtained had only 0.5% base pair divergence. In order to compare them

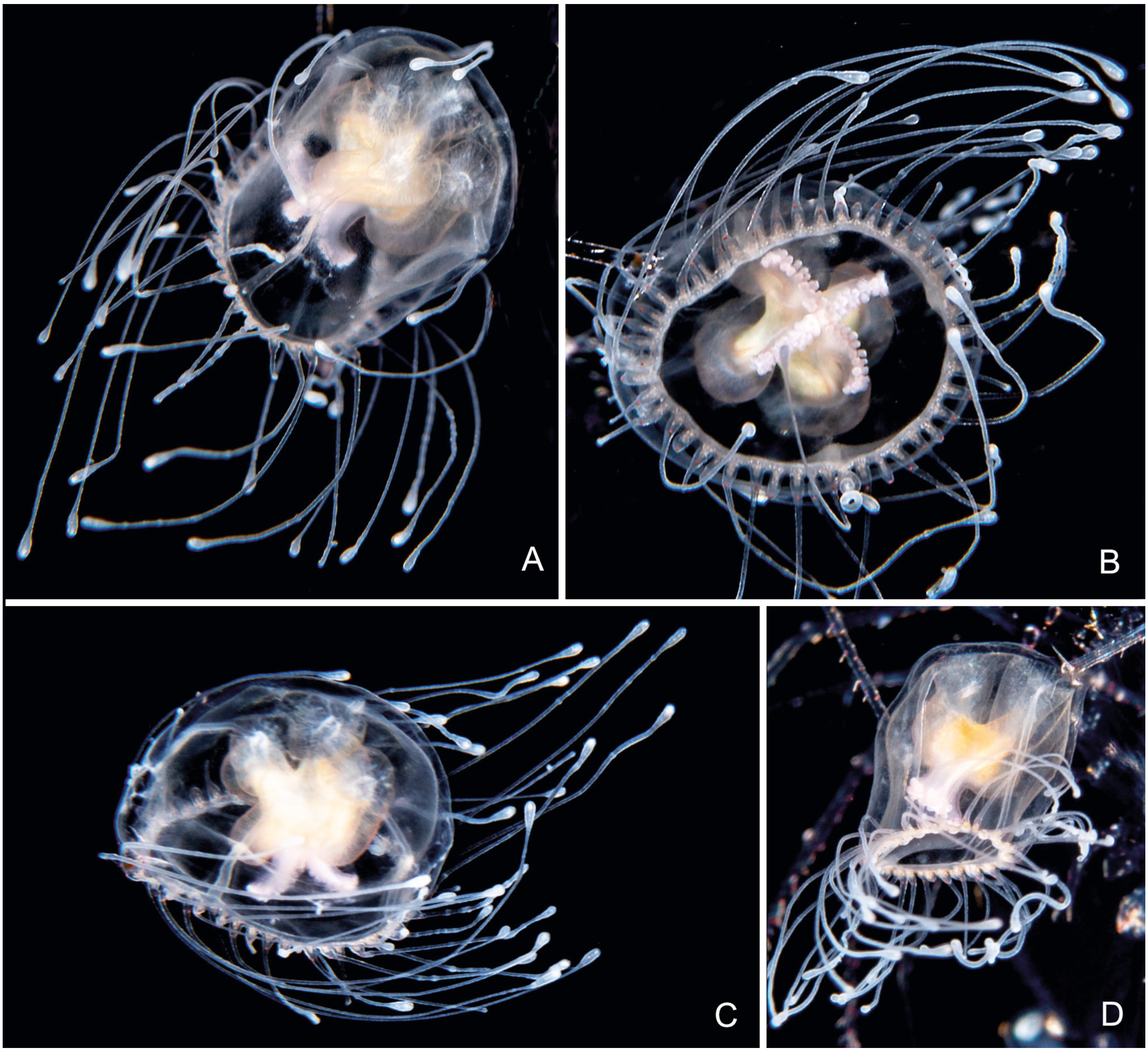

Fig. 11. *Turritopsis nutricula*. (A-C) Specimen BFLA4416, bell height 2 mm. (D) Specimen BFLA4416, 3 mm height. (A) Oblique view of animal. (B) Oral view, note nematocyst clusters along mouth margin and the interradially separated blocks of vacuolated cells at manubrium base. (C) Oblique view. (D) Lateral view, in the background some appendages of a decapod.

to other existing sequences, they were added to the set of sequences used in Miglietta *et al.* (2018a) and a maximum likelihood phylogenetic analysis was made (results not shown). Both sequences of this study clustered with sequences of *T. nutricula* from Woods Hole (GenBank numbers EU624349 and EU624348) and others from Panama (e.g. EU62435), thus fall within the clade of *T. nutricula* of Miglietta *et al.* (2018a).

Distribution: Temperate to tropical coastal regions of the western Atlantic Ocean from Woods Hole to Brazil, Gulf of Mexico, Caribbean Sea. Type locality: Atlantic Ocean, USA, South Carolina, Charleston Harbor.

Remarks: The samples examined here matched unambiguously *Turritopsis nutricula* in the restricted sense of Schuchert (2004). The yellow manubrium and particularly the interradially split blocks of vacuolated cells at the manubrium base are diagnostic for *Turritopsis* medusae of this region. Moreover, the sampling site is in the same biogeographic region as the type locality, the latter being about 800 km away. There can thus be little doubt that these specimens represent the true *T. nutricula*.

Species delimitation in the genus *Turritopsis* was difficult and until the revision of Schuchert (2004) most authors assumed that there is only a single, circum-globally occurring species named *T. nutricula*. Schuchert (2004) using morphological data showed that this is not the case and re-established several previously synonymized names. This was then later confirmed using genetic data [see summary in Miglietta *et al.* (2018a) and references therein]. However, so far it was not clear which of the molecular clades corresponded to the true *T. nutricula*. Although the studies of Miglietta *et al.* included specimens identified as *T. nutricula*, their identity was uncertain because they were either based on young medusae or polyps. Both of them are not unambiguously identifiable. The results of the present study confirm the correct identification of the *T. nutricula* clade in Miglietta *et al.* (2018a).

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

Heterotiara Maas, 1905: 19, invalid junior homonym of *Heterotiara* Pomel, 1883 (Echinodermata).

Protiaropsis Stechow, 1919: 150, nom. nov. pro *Heterotiara* Maas, 1905, type species *Heterotiara anonyma* Maas, 1905 by original designation.

? *Kanaka* Uchida, 1947: 304, type species *Kanaka pelagica* Uchida, 1947 by monotypy.

? *Gymnogonium* Xu & Huang, 1994: 152, type species *Gymnogonium zhengzhongii* Xu & Huang, 1994 by original designation.

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.

Remarks: For a key to the currently known species see Du *et al.* (2018).

Protiaropsis anonyma (Maas, 1905)
Fig. 12 A-C

Heterotiara anonyma Maas, 1905: 19, pl. 3 figs 19-21. – Bigelow, 1909: 216, pl. 41 figs 12-14. – Vanhöffen, 1911: 211, pls 12-13. – Bigelow, 1918: 382. – Bigelow, 1928: 287. – Russell, 1940: 516, figs 5-7. – Kramp, 1959a: 17, 125, fig. 131. – Kramp, 1961: 122. – Kramp, 1965: 41. – Kramp, 1968: 53, fig. 138. – Schmidt, 1973: 22. – Schmidt & Klinker, 1974: 34. – Bouillon, 1980: 314. – Brinckmann-Voss & Arai, 1989: 41, figs 1b, 1e.

not *Heterotiara anonyma*. – Bigelow, 1913: 25, records North Pacific. [= *Bythotiara depressa* Naumov, 1960]

in part *Heterotiara anonyma*. – Arai & Brinckmann-Voss, 1980: 69, fig. 40. [in part *Bythotiara depressa* Naumov, 1960]

Protiaropsis anonyma. – Stechow, 1919: 150, new combination. – Schuchert, 2010: 338.

? *Kanaka pelagica* Uchida, 1947: 103, fig. 5. – Kramp, 1961: 123. – Kramp, 1968: 58, fig. 153. – Schmidt, 1973: 22, could be a young *Heterotiara anonyma*. – Bouillon, 1980: 316, could be *Heterotiara anonyma*.

Examined material: BFLA4037; 1 specimen; 26-MAR-2019; size 12 mm high; part preserved in formalin and deposited as UF-013457, small part in alcohol for DNA extraction; 16S sequence MW528657.

Observations: Bythotiaridae medusa 12 mm high, bell cylindrical, not compressed laterally, mesoglea thick, especially apical jelly which is about 1/3 of the total bell height; bell margin with regular furrows in which lie the tentacles. Manubrium 2/3 the height of the subumbrella, shaped like inverted cone, section cross-shaped, interradial wall smooth, mouth cruciform, rather small, four red strands run along the interradial corners of the manubrium. Four thin radial canals, no mesenteries; circular canal thin. 10 tentacles, length about half the height of the bell, originating from under circular canals without formation of a distinct tentacle bulb but with an epidermal swelling at the junction of tentacle and circular canal, proximal part of tentacles curving adnate around bell margin in furrows, tapering only slightly distally, ending in bright orange, spherical to ovoid knob, diameter about 0.3 mm. No ocelli.

16S Data: A blastn search in GenBank with the sole 16S (MW528657) gave mostly species of Filifera/Anthoathecata, but all below 90% identity and thus precluding any conclusions on relationships.

Distribution: Widespread in warm parts of the Atlantic, Indian, and Pacific Oceans, usually in depths of 0 to 600 m (Arai & Brinckmann-Voss, 1980; corrections in Brinckmann-Voss & Arai, 1989). Type locality: Indonesia, 0.2933°S, 129.2418°E, 0-1000 m depth.

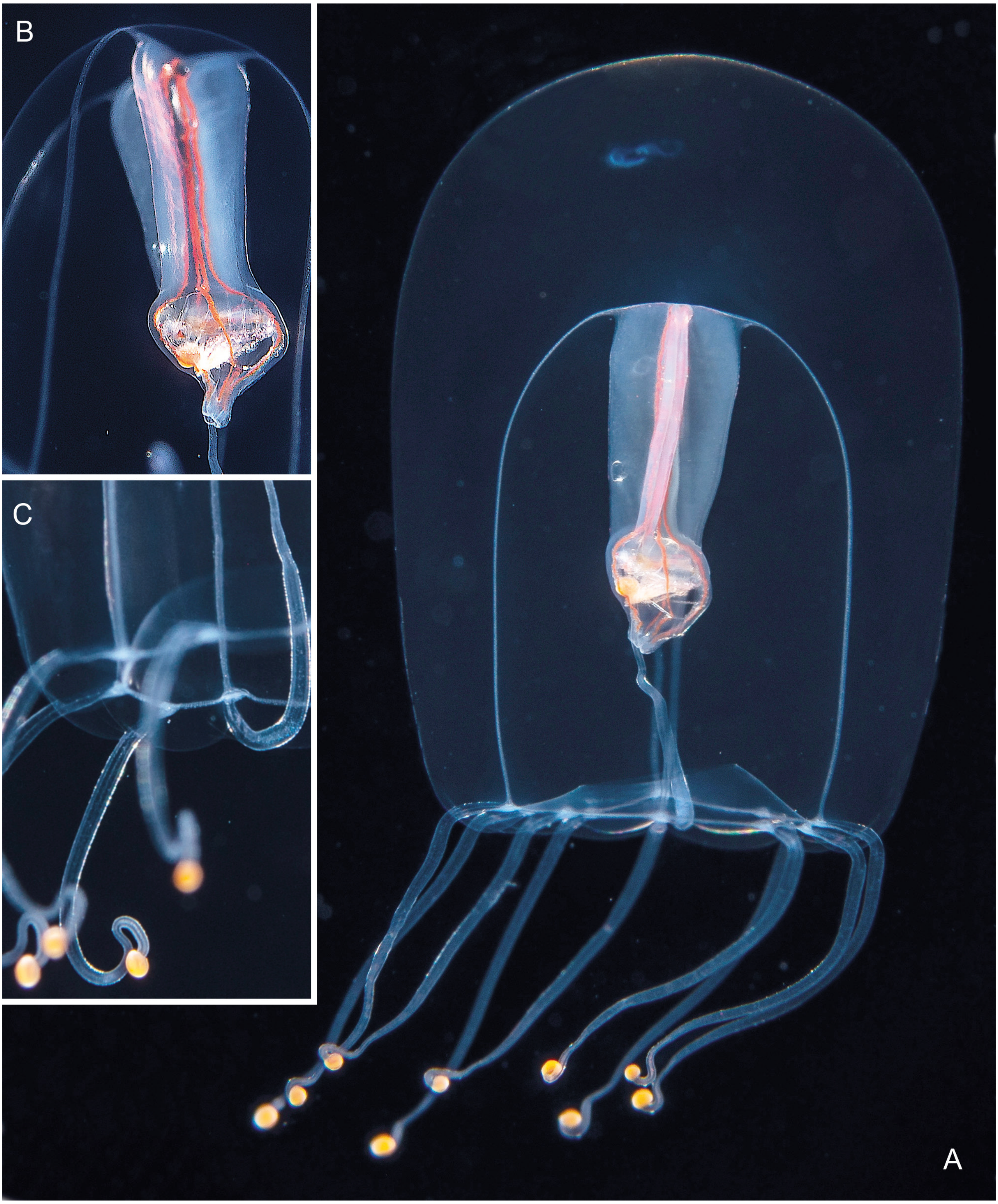

Fig. 12. *Protiaropsis anonyma,* specimen BFLA4037, bell height 12 mm. (A) Lateral view of animal with amphipod prey in its stomach. (B) Manubrium at other angle, note cruciform base. (C) Bell margin.

Remarks: Most illustrations of this species do not show the terminal swellings of the tentacles (e.g. in Kramp, 1959a, 1968), a typical character of Bythotiaridae medusae. These are almost invariably lost in specimens caught with a plankton net, but they are normally present in this species (see Kramp, 1948, 1965; Schmidt, 1973; Arai & Brinckmann-Voss, 1980).

The size of the examined medusa was at the lower end of the range usually given for this species (12-20 mm, Maas, 1905; Bigelow, 1909; Vanhöffen, 1911). Bigelow (1918) also found somewhat smaller (up to 13 mm) in the nearby Bermuda region, likewise Bouillon (1980) in animals from Papua New Guinea.

The interradial red strands are rather conspicuous in the living and preserved animal (Fig. 12A-B), but they have been mentioned only rarely so far. Only Vanhöffen (1911) observed them in an animal caught near the Nias Islands (Indonesia).

The nematocysts have been described by Russell (1940) and Bouillon *et al.* (1988a). The species has large desmonemes which are typical for the family Bythotiaridae.

The taxonomic scope of *Protiaropsis anonyma* is not yet fully clear as there are other similar species, some of which which could prove to be conspecific (see also discussions in Schmidt, 1973).

Protiaropsis minor (Vanhöffen, 1911) is somewhat smaller (6-12 mm), has perhaps a shorter manubrium, and 16 to 24 tentacles (see description by Pagès *et al.*, 1992). Bouillon *et al.* (1988a) found both morphotypes in sympatry and kept them distinct.

Kanaka pelagica Uchida, 1947 has eight tentacles but is much smaller (1.8 mm). It was based on a single specimen which was likely a juvenile. Kramp (1953) thought it might belong to *P. minor*, while Schmidt (1973) and Bouillon (1980) think it is referrable to *Protiaropsis anonyma*.

Gymnogonium zhengzhongii Xu & Huang, 1994, is small (2.2 mm), has a short manubrium, and a pair of branched radial canals, resulting in six canals in total. The manubrium of the only observed specimen had gonads. Bouillon *et al.* (2006: 182) thought that it could belong to *Protiaropsis anonyma*. As the the species is based on a single specimen, it cannot be excluded that the branched radial canals were a developmental aberration. New material has to prove the validity of the species, but as the type specimen was apparently mature at 2.2 mm, the genus and species should be retained as valid for the moment.

Bouillon (1980) thought that also *Bythotiara depressa* Naumov, 1960 could be conspecific with *P. anonyma* as he found intermediate forms. *Bythotiara depressa* differs from *P. anonyma* in having an irregularly folded surface of the gonads. Brinckmann-Voss & Arai (1989) examined the problem in detail and they worked out diagnostic differences of the two species (see also Xu *et al.*, 2016). Some of the previous records of *P. anyonyma* from colder waters of the North Pacific Ocean were actually *B. depressa*.

All these ambiguities underline the need for a comprehensive dataset of 16S DNA barcodes which will hopefully improve the species delimitations.

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

Thecocodium Bouillon, 1967: 1119; type species *Thecocodium brieni* Bouillon, 1967 by original designation.

Diagnosis: Medusa with lobed bell margin, with marginal nematocyst ring from which usually arise several centripetal nematocyst bands or exumbrellar 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)
Fig. 13A-B

Ptilocodium quadratum Werner, 1965: 11, figs 4-5. – Werner, 1984: 139, fig. 85.

Thecocodium quadratum. – Jarms, 1987: 59, fig. 8.1-8.4. – Kubota, 1993: 89, fig. 1. – Akiyama *et al.,* 2013: 113, figs 1-2.

Thecocodium aff. *quadratum*. – Kubota *et al*., 2018: 7, fig. 2A-B.

Thecocodium spec. – Kubota & Meldonian, 2016: 77, fig. 1.

Examined material: 21-JUL-2018, 1 specimen photographed; not collected. – BFLA4461; 1 specimen; 13-JUN-2020; size 5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528730. – BFLA4466; 1 specimen; 13-JUN-2020; size 4 mm; preserved in alcohol for DNA extraction; 16S sequence MW528731.

MHNG-INVE-0039477; schizoholotype, polyps obtained from original culture of Werner (courtesy Dr G. Jarms), origin of material Kenya; cultivated and reared medusae, preserved in Feb-2006; 16 sequence FN422379.

Observations: Medusa with bell-shaped umbrella, up to 5 mm, mesoglea thick, including lateral walls, height of apical jelly at least 1/3 of total height, not delimited as apical process. Bell margin with deep perradial clefts continued as canal-like furrows to mid-

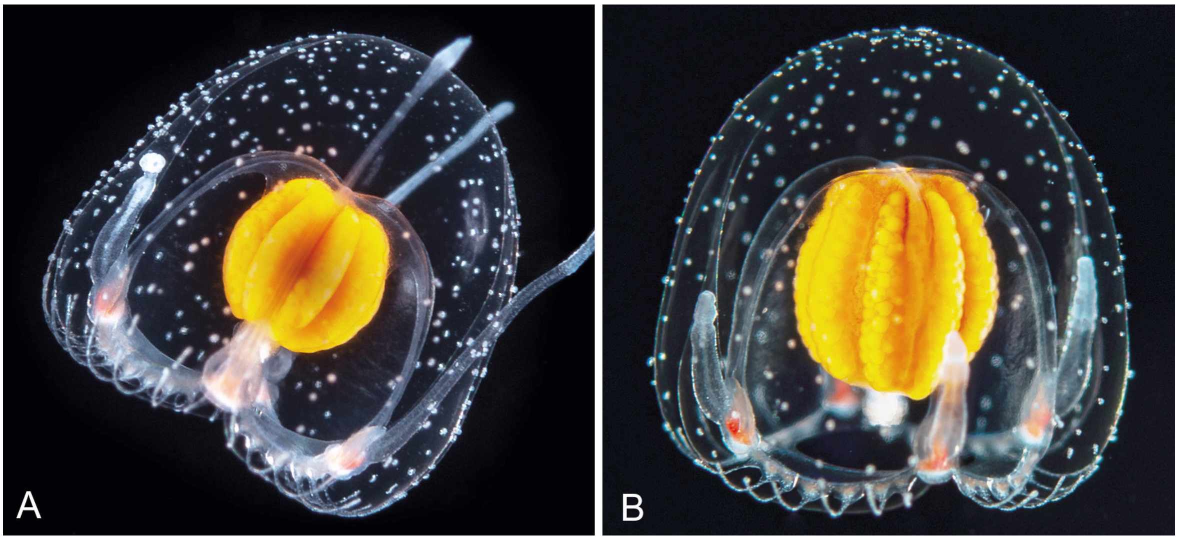

Fig. 13. *Thecocodium quadratum*, females. (A) Specimen photographed 21-JUL-2018. Lateral view of whole animal. (B) BFLA4461, an apparently fully mature female.

height of bell and housing tentacle. Bell margin appears lobed through the clefts, between the furrows on each lobe 5-7 meridional nematocyst tracks originating from near circular canal and curving around bell margin to exumbrella and then dissolving into arrays a few isolated nematocysts clusters, >100 additional nematocyst buttons scattered on entire exumbrella. Four smooth radial canals widened to funnels at the junction to the manubrium. Four tentacles, directed upwards, lying in the canal-like exumbrellar furrows, usually contracted to length shorter than bell height, but able to extend to length at least >3 times the bell height. Tentacles at origin with a small bulb with a pink to red colour, bulb adnate to exumbrella; main trunk of tentacles appears chordoid and is transparent, tapering to tip which is whitish-opaque and sometimes slightly swollen. Manubrium large, with a spherical stomach and a small neck-like oral region, small cruciform mouth; gonads much developed surrounding the manubrium entirely, with a brilliant, intense yellow-orange colour, subdivided in 8 adradial, vertical bulges (Fig. 13B), the whole appearing like a peeled orange composed of 8 wedges, perradial and interradial clefts deep. Females with > 200 eggs.

Distribution: Coast of Kenya (Jarms, 1987); Japan (Kubota, 1993); Taiwan (Kubota *et al*., 2018); Florida (Kubota & Meldonian, 2016; this study). Type locality: Indian Ocean, NE of Mombasa (hydroid, substrate unknown).

16S Data: The two obtained 16S haplotypes differed in 0.5% of their base pairs, the divergences to the type material were 4.3 to 4.5% (Table 1).

Remarks: The descriptions of this species (Werner, 1965; Jarms, 1987) were based on a cultivated hydroid colony and its released medusae reared to subadult stage. It was therefore with some hesitations that subsequent findings of the medusa in the plankton where attributed to this species or they were even only identified to genus level (see synonymy above). The observed specimen from Florida differed from the type material in having a slightly higher umbrella and many more exumbrellar nematocysts clusters. Moreover, the gonads are much more developed. The species has been recorded from Florida waters before (Kubota & Meldonian, 2016). Like Kubota & Meldonian (2016) we are also aware that the identification of the Florida specimens as *Thecocodium quadratum* is to some degree questionable for biogeographic reasons. However, comparing our photos with a medusa from Taiwan published by Kubota *et al*. (2018) it is evident that there are no taxonomically significant differences and this morphotype has likely a very widespread distribution. The 16S sequences from the Florida specimens differed about in 4.5% of the base pairs compared to the type specimen (Table 1). In comparison with other medusae this appears to us as intermediate between intraspecific or interspecific variation, but these few samples and just one marker alone cannot provide conclusive information. Because the morphology of Pacific and Atlantic medusae match, we think it should be attributed to *T. quadratum* until more detailed genetic data prove the contrary.

Family Proboscidactylidae Hand & Hendrickson, 1950

Genus *Proboscidactyla* Brandt, 1835

Synonymy: See Schuchert (2009).

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 and opposite to nematocyst cluster; gonozooids and dactylozooids without tentacles, mouth-less and smaller than gastrozooids; medusa buds close to gonozooid tip.

Remarks: Species delimitation in this genus has a long history of discussions and especially the status of the various variants of *P. ornata* are unclear [comp. Schuchert (2009) and references therein]. The medusae of *P. ornata* are quite variable and a number of species and subspecies have been proposed, mainly based on the presence and position of vegetative medusa buds. Kramp (1957, 1965) examined numerous specimens and concluded that these variants likely belong to the same species, the number of canal ramifications and the place of medusa budding being variable even within the same population.

However, as seen in other medusa-based species – e.g. *Clytia* or *Zanclea* – once also the polyp stage is considered, many morphospecies can sometimes be distinguished (for *Zanclea* see e.g. Boero *et al*., 2000). Hand (1954), using complete data of the medusa and polyp stage of Pacific *Proboscidactyla* species as well as host data of the polyp colony, found that they differ in minute details. This makes it likely that other widely distributed *Proboscidactyla* species which are solely based on the medusa stage could represent species complexes. DNA sequence results obtained in this study indeed indicate that this seems to be the case for at least *P. ornata*.

***Proboscidactyla ornata* (McCrady, 1859)**

Fig. 14A-G

Willsia ornata McCrady, 1859: 149, pl. 9 figs 9-11.

Proboscidactyla ornata. – Mayer, 1910: 189, pl. 20 figs 1-10, text fig. 100.

Material examined: BFLA4349; 1 specimen; 11-MAR-2020; size 4 mm, 17 tentacles, presumably a mature male; preserved in alcohol for DNA extraction; 16S sequence MW528709. – BFLA4354; 1 specimen; 11-MAR-2020; size 4 mm, 18 tentacles, with green subumbrella; preserved in alcohol for DNA extraction; 16S sequence MW528710. – BFLA4356; 1 specimen; 13-MAR-2020; size 4 mm, 21 tentacles, mature male; preserved in alcohol for DNA extraction; 16S sequence MW528711. – BFLA4357; 1 specimen; 13-MAR-2020; size 5 mm, 21 tentacles, mature female; preserved in alcohol for DNA extraction; 16S sequence MW528712 – BFLA4454; 1 specimen; 11-JUN-2020; size 5 mm, 19 tentacles; preserved in formalin and deposited as FU-014065. – BFLA4455; 1 specimen; 11-JUN-2020; size 6 mm, 18 tentacles, mature male; preserved in formalin and deposited as FU-014066. – 13-MAR-2020; 1 specimen photographed, not collected; 4 mm, 16 tentacles.

Observations: Medusae with the characteristics of the genus, bell as wide as high, 4-6 mm, apical jelly about 1/3 of total height. Exumbrella with more or less linear arrays of nematocyst patches of variable length, starting from bell margin and alternating with tentacles, some reaching beyond mid part of bell, patches with up to 10 nematocysts, patches often lost in preserved animals. Manubrium rather broad, cruciform base giving impression of four (rarely 5) peradial basal pouches, gonads covering entire interradial wall of stomach, separated perradially, smooth surface; mouth rim much folded but not clearly with four lips, rim with nematocysts. Four (rarely 5) thin radial canals originate from basal manubrium pouches, branching dichotomously so that 4 to 5 ends reach circular canal (= solid strand). Tentacles only at ends of radial canals, 16-21 in mature animals, oviform basal bulb, tapering in much extensible tentacles; abaxial side of bulb gastrodermis with a dark pigment, lost in formalin preserved animals.

16S Data: See Table 1 and Fig. 16. The sequences of this study were quite divergent from *P. ornata* sequences from other regions, showing p-distances of up 7.5% and separating into distinct mitochondrial lineages. The lineage of Florida *Proboscidactyla ornata* without medusa buds is also clearly different from those here identified as *P. gemmifera* (see below).

Distribution: Reportedly circumglobal in tropical and temperate waters, but in view of the genetic data presented below, the known distribution must be restricted to the coastal waters of the NE Atlantic. Type locality: USA, South Carolina, Charleston Harbor.

Remarks: The present material (Fig. 14) agreed well with the descriptions given in McCrady (1859) and Mayer (1910) who had material from the same biogeographic region (warm temperate and tropical northwestern Atlantic; Spalding *et al.,* 2007). The observed differences concerned the tentacle numbers which were 16 to 21, thus more variable than the 16 given in Mayer (1910). Our material observed in situ

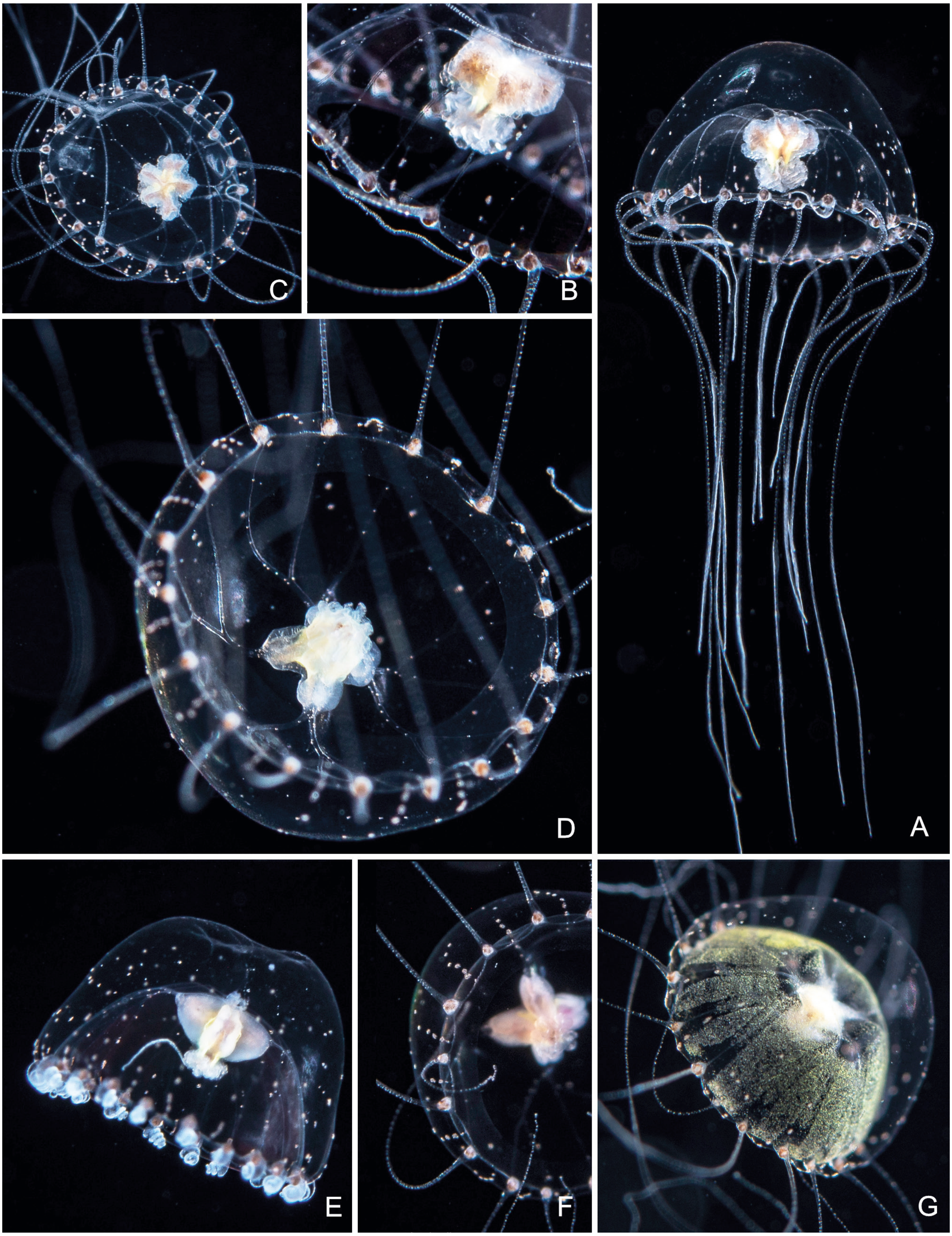

Fig. 14. *Proboscidactyla ornata*. Note that the usage of a flash brightens very much the exumbrellar nematocysts. (A-C) BFLA4357, bell size 5 mm, mature female, note that there are five radial canals leaving the manubrium. (D) BFLA4349, bell size 4 mm, subadult (?). (E) BFLA4356, bell size 4 mm, male. (F) Medusa photographed 13-MAR-2020, not collected, bell size 4 mm, note regular arrangement of exumbrellar nematocysts patches. (G) BFLA4354, bell size 4 mm, a layer of unidentified green particles is covering the subumbrella.

also had more nematocyst patches on the exumbrella, however, these are apparently lost rapidly in preserved material (likely also in net caught material). The maximum likelihood tree (Fig. 16) strongly suggests that our current concept of *P. ornata* comprises several mitochondrial lineages, *viz*. most likely species. This is also the reason why we separated the morphotype with medusa buds into a separate species (see below). Our medusae *P. ornata* were all rather fully grown, at least some with developed gonads. Because vegetative medusa budding might only occur in immature specimens, we cannot exclude that also *P. ornata* can have such a medusa budding. In this context, an observation noted by Mayer (1910) is interesting. He states that the budding variety of *P. ornata* is confined to the region south of South Carolina, while the non-budding form occurs from Florida up north to New England. Agassiz (1865, Buzzards Bay), Fewkes (1882a, Tortugas), and Calder (1970, Virginia) raised the medusa and did not report vegetative budding. This can be interpreted as two species with differing distributions being present. The northern limit of the budding form must be corrected to at least North Carolina as the type specimen of *P. gemmifera* (Fewkes, 1882) came from Beaufort Inlet.

Proboscidactyla gemmifera **(Fewkes, 1882)**

Fig. 15A-F

Willia gemmifera Fewkes, 1882b: 300, pl. 1 fig. 24.
Proboscidactyla gemmifera. – Browne, 1905: 727.
Dyscannota gemmifera. – Mayer, 1900: 47, pl. 8 fig. 17.
Proboscidactyla ornata var. *gemmifera*. – Mayer, 1910: 192, fig. 101a, pl. 21, figs 1-3.

Material examined: BFLA4285; 1 specimen; 06-DEC-2019; size 3 mm, 19 tentacles, with medusa buds; preserved in alcohol for DNA extraction; 16S sequence MW528699. – BFLA4321; 1 specimen; 24-JAN-2020; size 2.5 mm, 17 tentacles, with medusa buds; preserved in alcohol for DNA extraction; 16S sequence identical to MW528699. – BFLA4338; 1 specimen; 07-FEB-2020; size 3 mm, 18 tentacles, with medusa buds; preserved in alcohol for DNA extraction; 16S sequence identical to MW528699. – 24-JAN-2020; 1 specimen photographed, not collected; 3 mm, 14 tentacles, with medusa buds.

Observation: Medusae as described for *P. ornata* but somewhat smaller, 2.5-3 mm, though none of them appear sexually mature, tentacle numbers 14-19, more nematocyst patches on exumbrella, these often quite irregular and some not in linear arrays, no dark pigment in gastrodermis of tentacle bulbs. The most notable difference is the presence of four blastostyles (Fig. 15C) at each of the proximal-most branching points of the radial canals. Blastostyle resembling a polyp with one short capitate tentacle (visible in Fig. 15A, C) and bearing one to several medusa buds of different development stages.

16S Data: See Table 1 and Fig. 16.

Distribution: NE Atlantic from Cape Hatteras to Florida, likely more widely spread but identifications are unreliable (see *P. ornata*). Type locality: USA, North Carolina, Beaufort Inlet.

Remarks: Although the three samples used to obtain 16S sequence data were collected at different dates they all proved to be identical and clearly distinct from *P. ornata* (Fig. 16). This clade seems to be about equally distant from *P. ornata* as it is from the Pacific *P. flavicirrata* Brandt, 1835. This evident barcoding gap argues for it representing a distinct species.

The observed morphological differences to the sympatric *P. ornata* are listed above. It must be noted that *P. gemmifera* were found during the winter months, while the mature *P. ornata* were seen from March to June.

Proboscidactyla gemmifera was described based on a single medusa which was probably not fully developed as it had only eight tentacles (Brooks, 1880; Fewkes, 1882b). Mayer (1900, 1910) later supplemented more detailed descriptions of more advanced specimens from Florida. These descriptions do not agree with our specimens concerning the position of the blastostyles. Fewkes and Mayer found them at the junction of the radial canal to the manubrium, while in our samples they were located at the first bifurcation of the radial canals (Fig. 15A). This is not necessary a significant difference. Kramp (1957, 1962) found the blastostyles in every possible position along the radial canals, this in various populations from the Pacifc (identified as *P. ornata*). He regarded this variation as without any systematic importance.

Uchida & Sugiura (1975) examined the medusa bud development in a Japanese form of *P. ornata* and found that the position of the blastostyles is variable, depending on the developmental age (size) of the medusa. Smaller ones had them at the corners of the stomach, larger ones at the branching points. They also found that sexually mature medusae can continue budding medusae.

Although with some hesitation, we therefore referred our medusae to *Proboscidactyla gemmifera*.

Suborder Capitata

Family Sphaerocorynidae Prévot, 1959

Genus *Euphysilla* Kramp, 1955

Euphysilla Kramp, 1955b: 245; type species *Euphysilla pyramidata* Kramp, 1955 by monotypy.

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

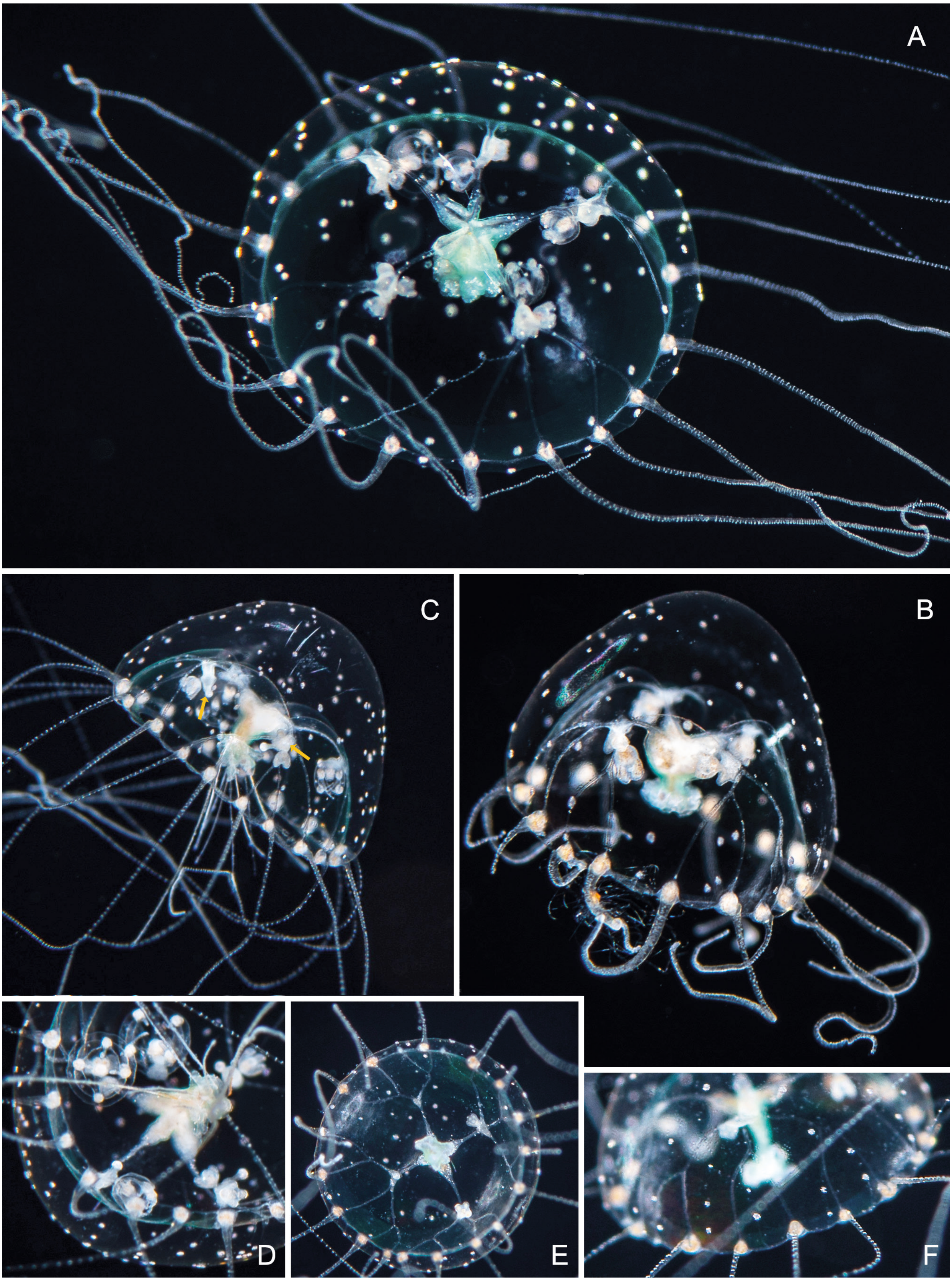

Fig. 15. *Proboscidactyla gemmifera.* Note that the usage of a flash brightens very much the exumbrellar nematocysts. (A) BFLA4338, diameter 3 mm. (B) Medusa photographed 24-JAN-2020, not collected, diameter 3 mm. (C) BFLA4285, lateral view, diameter 3 mm, arrows point to blastostyles (D) BFLA4285, oral view. (E) BFLA4321, aboral view. (F) BFLA4321, lateral view of bell margin, diameter 2.5 mm, note regular arrangement of exumbrellar nematocysts patches.

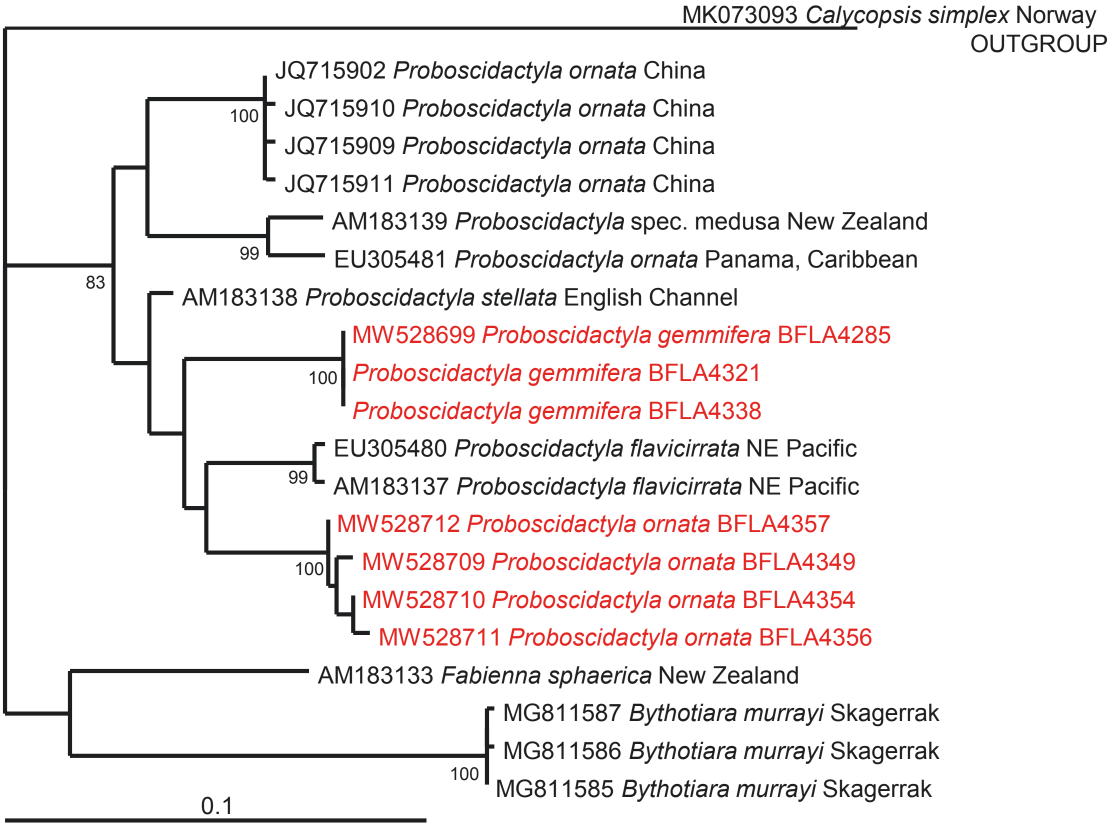

Fig. 16. 16S maximum likelihood phylogenetic tree of Proboscidactylidae and related taxa obtained with PhyML (GTR+G model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). All sequence labels start with the GenBank numbers permitting the retrieval of more information. Red labels are new sequences from this study. All samples are based on medusae.

terminal nematocyst knob; no gastric peduncle; mature gonads circular, surrounding manubrium; no ocelli. Usually with groups of medusa buds in middle part of manubrium.

Remarks: The diagnosis of *Euphysilla* of Bouillon *et al.* (2006) was here slightly modified by adding "with apical chamber" (see below). *Euphysilla pyramidata* appears indistinguishable from the genus *Sphaerocoryne* except for the medusa budding and the absence of ocelli. It is here associated with the Sphaerocorynidae following Petersen (1990, as suborder Sphaerocorynida incerta sedis).

Euphysilla pyramidata Kramp, 1955

Fig. 17A-I

Euphysilla pyramidata Kramp, 1955b: 245, pl. 1 fig. 1, pl. 2 fig. 3. – Kramp, 1959a: 90, fig. 42. – Kramp, 1961: 39. – Kramp, 1965: 4. – Kramp, 1968: 17, fig. 33. – Vannucci & Santhakumari, 1969: 40. – Schmidt, 1973: 16. – Hamond, 1974: 554, figs 4-6. – Segura-Puertas, 1984: pl. 2 fig. 2. – Petersen, 1990: 135, fig. 7B. – Xu & Huang, 2004: 560, fig. 9.

? not *Euphysilla pyramidata*. – Bouillon, 1978b: 259, figs 7 & 8.1-2.

Examined material: BFLA4396; 1 specimen; 17-MAY-2020; size 2.5 mm; preserved in ethanol for DNA extraction; 16S sequence MW528719. – BFLA4397; 1 specimen; 17-MAY-2020; size 2 mm; preserved in ethanol for DNA extraction; 16S sequence MW528720. – BFLA4402; 1 specimen; 26-MAY-2020; size 3 mm; preserved in formalin and deposited as UF-014043. – BFLA4468; 1 specimen; 17-JUN-2020; size 3 mm; preserved in formalin and deposited as UF-014073. – BFLA4478; 1 specimen; 18-JUN-2020; size 4 mm; preserved in ethanol for DNA extraction; 16S sequence identical MW528719.

Observations: Umbrella 2-4 mm in height, oviform, with apical thickening of very variable height, lateral walls thin, exumbrella with scattered nematocysts. Above manubrium an apical chamber, without apparent connection to gastric cavity, size variable depending on size of apical process (Fig. 17A-C). Manubrium an inverted cone, as long as bell cavity, base broad and cruciform in life (Fig. 17D), more square-shaped when preserved, upper part of manubrium cylindrical, narrowing to tubular lower part of manubrium ending in small, circular mouth. All observed medusae were budding medusae, buds in groups on all four perradial sides of the manubrium in about the middle of the manubrium. Gonad-like opaque tissue layer covers manubrium above buds. Colour of manubrium intensively yellow-orange. Radial canals connected to manubrium by apparent short mesenteries (giving cruciform manubrium base), thin; circular canal more rectangular than circular. Four tentacles, contracted about half the length of the bell height, each with 8-12 crescent-shaped, clasping nematocyst pads, all in one row on adaxial side, terminal button ovoid, as wide as rest of tentacle. Four tentacle bulbs relatively small, orange-yellow, without well visible ocelli, but a faint reddish spots may be present on abaxial tentacle base (Fig. 17A).

Nematocyst (Fig. 17F-I, preserved tissue, sizes approximative): small stenoteles (7x10 µm), large stenoteles (12x13 µm), desmonemes (4x9 µm), spherical microbasic eurytele with barbed filament, shaft appears without barbs (7x10 µm).

16S Data: The three obtained 16S sequences represented two haplotypes, differing in only one base pair of 588. A blastn search in GenBank singled out a sequence (LT714182) with very high similarity (99.3%, Fig. 21). The sequence was obtained from a *Sphaerocoryne* polyp collected in the Maldives archipelago.

Distribution: Circumglobal in tropical seas. Western Africa (Kramp, 1955b); Gulf of Mexico (Segura-Puertas *et al*., 2003); Indian Ocean (Kramp, 1965; Vannucci & Santhakumari, 1969; Hamond, 1974); Red Sea (Schmidt, 1973); Bismarck Sea (Bouillon, 1978b); Taiwan Strait (Xu & Huang, 2004); tropical eastern Pacific Ocean from Peru to Mexico (Segura-Puertas, 1984). Type locality: Atlantic Ocean, Gulf of Guinea, off the coast of Bénin; WGS84 6.01667, 2.35000; depth 0-10 m.

Remarks: *Euphysilla pyramidata* has not been recorded frequently, this despite its apparent circumglobal distribution. Kramp's type specimen had no medusa buds, but he states that it had developed gonads. *Euphysilla pyramidata* with medusa buds were then reported in nearly all descriptions subsequent to Kramp (1955b, 1965) (see synonymy above). Hammond (1974) found both forms. Except for the medusa buds, our specimens matched Kramp (1955b) quite well, including the yellow manubrium colour, although in Kramp's formalin preserved material the remaining colour had become faint. The differences of our specimens and Kramp's description in the shape of the manubrium (quadratic versus cruciform manubrium base, wide mouth versus narrow) can easily be attributed to fixation artefacts, *viz*. the type specimen having been preserved with an inflated stomach. Moreover, the stomach base depicted by Kramp (1955b: pl. 2 fig. 3) is more cruciform than quadratic. Kramp (1955b) did not mention an apical chamber, but his figure 1 on plate 1 shows such a chamber, although only faintly.

Euphysilla pyramidata medusae reported from the Pacific Ocean by Bouillon (1978b) have some differences to our material. First, the apical thickening, hence likely also the apical chamber, is absent and the umbrella is more spherical, thus unlike the type specimen figured in Kramp (1955b). Second, Bouillon (1978b) also describes the colour of the manubrium as rose-orange and the one of the bulbs as having a hue of red. Whether these are species level or population level differences remains to be investigated by genetic examinations. Perhaps Bouillon's medusae are referrable to *Euphysilla tubularia* Huang, Xu & Lin, 2015, from which they appear not objectively separable. The tubular part of the manubrium in the mouth region in *Euphysilla tubularia* is certainly only a fixtion artefact. We observed the same in the present material.

It is thus probable that *E. pyramidata* as currently perceived is a complex of species. As in other genera, including information on the polyp stage might change its scope.

The 16S sequences gave a surprising match with a hydroid of the genus *Sphaerocoryne* from the Maldives (LT714182, Maggioni *et al*., 2017). The author of this sequence, Dr Davide Maggioni, kindly let us know that a publication describing this colony is currently in preparation.

Family Zancleidae Russell, 1953

Genus *Zanclea* Gegenbaur, 1857

Synonymy: See Schuchert (2010).

Diagnosis: Newly liberated medusae with two opposite tentacles, umbrella bell-shaped, four perradial exumbrellar 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 macrobasic euryteles; mouth simple, circular; gonads inter-radial; no ocelli.

Hydroid stage colonial, with stolonal hydrorhiza, polyps sessile or with pedicels, 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 tentacles; gonozooids and dactylozooids, when present, resembling reduced gastrozooids. Gonophores liberated as free medusae or rarely medusoids. Cnidome includes stenoteles and macrobasic euryteles, the latter type may be absent in the polyp stage.

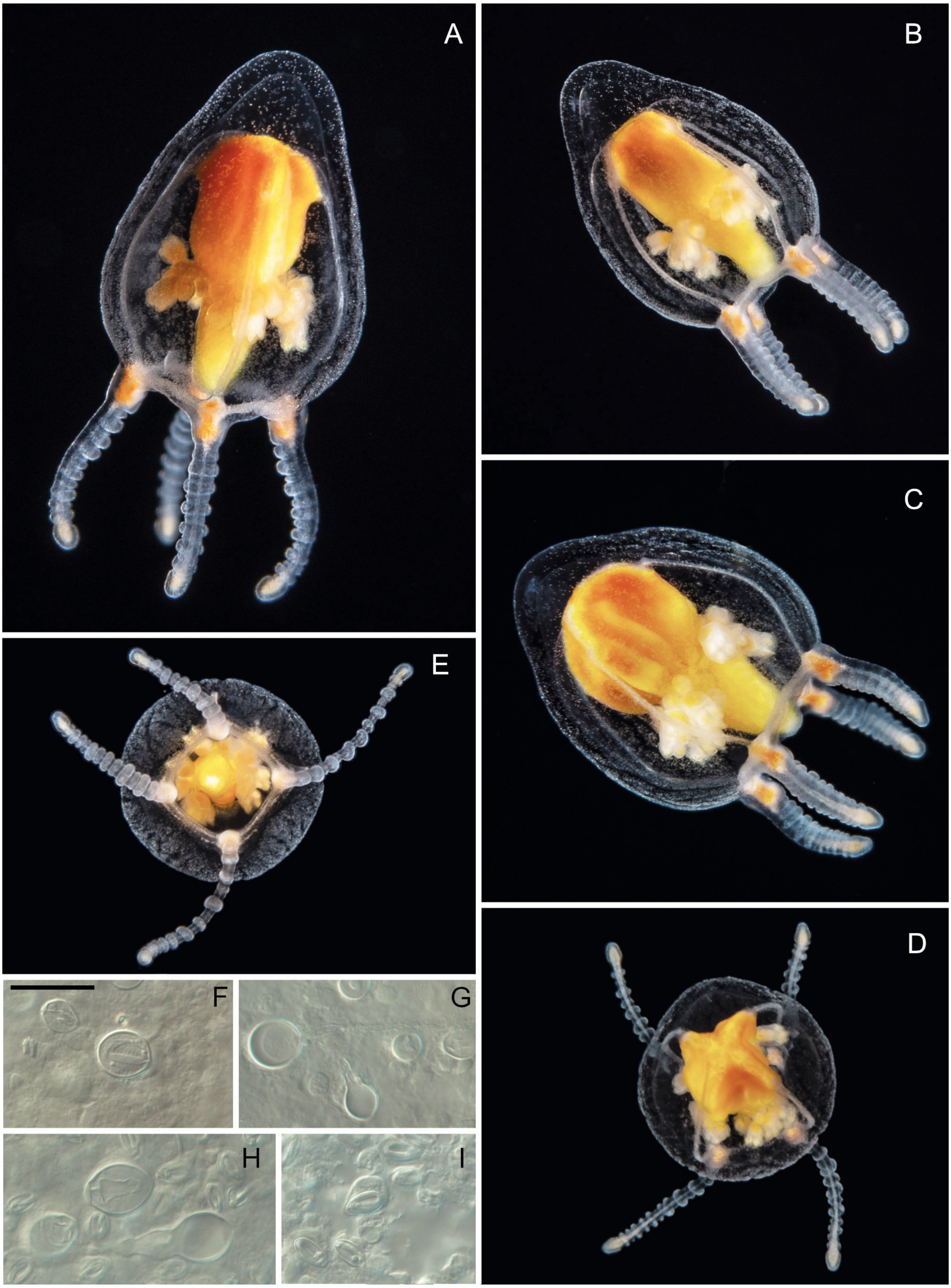

Fig. 17. *Euphysilla pyramidata*. (A-B) BFLA4396, bell height 2.5 mm. (C-D) BFLA4468, bell height 3 mm. D in aboral view, note cruciform manubrium base. (E) BFLA4397, oral view, bell height 2 mm. (F-I) Nematocysts of alcohol preserved tissue, scale equals 20 µm, valid for F to I. (F) Undischarged microbasic eurytele. (G) Discharged microbasic eurytele, stacked photo. (H) Intact and discharged large stenotele. (I) Desmonemes.

Remarks: For the identification of many *Zanclea* species it is usually necessary to know the hydroid stage (Boero *et al*., 2000; Puce *et al*., 2002; Maggioni *et al*., 2018; Schuchert, 2010). Some Teisseriidae hydroids also produce *Zanclea*-like medusae, but they have ocelli.

Boero *et al*. (2000) critically reviewed all known *Zanclea*, *Zanclella*, and *Halocoryne* and described several new species. Subsequently, a bewildering number of new species were described, based either solely on the medusa or the polyp stage (e. g. Gershwin & Zeidler, 2003; Puce *et al.,* 2002; Galea, 2008; Puce *et al*., 2008; Xu *et al.,* 2008; Pantos & Bythell, 2010; Hirose & Hirose, 2012; Varela, 2012; Montano *et al*., 2015; Pica *et al*., 2017). A molecular phylogeny was provided by Maggioni *et al.* (2018). It is now clear that the genus *Zanclea* is enormously diverse and the lumping of several nominal species into *Zanclea costata* as in Russell (1953) or Kramp (1959a, 1968) is not tenable anymore.

Zanclea mayeri n. spec.

Figs 18A-E, 19A-H

Zanclea costata. – Mayer, 1910: 87, pl. 8 fig. 6, perhaps also 2, 3, 7. [not *Z. costata* Gegenbaur, 1857]

Holotype: BFLA4061; photographed (Fig. 18A-E) and collected 10-APR-2019; 6 mm high, 3 mm wide; preserved in alcohol and used entirely for DNA extraction; frozen DNA solution deposited in MHNG under the catalogue number MHNG-INVE-0137375; 16S sequence MW528663.

Paratypes: BFLA4219; 1 specimen; 27-SEP-2019; height 5 mm; preserved in alcohol for DNA extraction; frozen DNA solution deposited as MHNG-INVE-0137377; 16S sequence MW528687. – BFLA4281; 1 specimen; 06-DEC-2019; height 7 mm; preserved in alcohol for DNA extraction; frozen DNA solution deposited as MHNG-INVE-0137378; 16S sequence MW528697. – BFLA4297; 1 specimen; 09-DEC-2019; height 6 mm, width 4 mm; preserved in alcohol for DNA extraction; frozen DNA solution deposited as MHNG-INVE-0137380; 16S sequence MW528703.

Type locality: USA, Florida, 5.5-12 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Etymology: The name honours Alfred Goldsborough Mayor [Mayer] who described this species in his outstanding work of 1910 (for a biography see Stephens & Calder, 2006).

Description: Mature medusa 4 to 7 mm high and 3-4 mm wide, bell bullet-shaped, apex rounded, lateral wall straight. Mesoglea relatively thick, thicker at apex. Exumbrella with four thick, white perradial nematocyst bands, protruding from surface, reaching from circular canal to apex, two opposite bands often recurved at apex (Fig. 18A-C). Subumbrella with interradial pockets projecting into apical mesoglea (Fig. 18A-B). Manubrium large, composed of a larger upper part and a thinner, short, cylindrical mouth region. Upper part of manubrium with cruciform cross-section (Fig. 19B), gonads cover surface entirely as a thin layer, but separated perradially. Radial canals smooth. Only two tentacles, opposite, other two perradial positions without bulbs. Tentacles at base thick, without bulb formation, evenly tapering to very fine end, very contractile or extensible to more than 35 mm (Fig. 18E). Tentacles with abaxial row of cnidophores, these relatively large, spherical, with long, contractile stalk (Figs 18E, 19D). No ocelli present. Colours: manubrium orange (females) or faintly orange (males), tentacles faint pink-orange. Nematocysts: macrobasic euryteles and stenoteles (Fig. 19F-H).

One medusa (Fig. 19E) with a hydroid colony growing on upper part of manubrium, polyp with one whorl of few capitate tentacles, stolon-like processes in the manubrium tissue. It is not evident if this hydroid is derived from medusa or if it is a parasitic hydroid.

16S data: The four available samples gave four different 16S haplotypes with divergences of 0.8-1.2%. A blastn search in GenBank with the obtained sequences yielded numerous *Zanclea* sequences, but all with less than 92% identity. A maximum likelihood tree using part of the 16S sequence data of Maggioni *et al.* (2018) did not associate the sample with any other (Fig. 21).

Remarks: Mayer (1910) described and figured a single *Zanclea* medusa from Florida which he attributed to *Zanclea costata* Gegenbaur, 1857. His figure (pl. 8 fig. 6) obviously depicts the same medusa as shown here in Figs 18-19. Also, the size was the same (6 mm) and the umbrella shape matches. The scope of *Z. costata* has changed since then, although the identity of Gegenbaur's medusa from the Mediterranean is still not entirely resolved (Brinckmann-Voss, 1970; Boero *et al.*, 2000; Cerrano *et al.*, 1997; Schuchert, 2010; Maggioni *et al.*, 2018). Gegenbaur's medusae were relatively big (2-5 mm), had four tentacles, and the nematocyst bands reached up to the apex. However, medusae that exactly matched Gegenbaur's medusa have never been found again and the current scope of *Z. costata* goes back to Brinckmann-Voss (1970). The Mediterranean *Z. costata* has four marginal bulbs even in younger stages and with optimal growth it will develop four tentacles (Gegenbaur, 1857; Brinckmann-Voss, 1970; Schuchert, 2010). *Zanclea mayeri* is even larger than *Z. costata* but has only two tentacles and two bulbs. The divergence of the 16S from *Z. costata* (GenBank entry FN687559) is 9% and 8.5% from an unidentified Mediterranean *Zanclea* with four tentacles (GenBank entry KP776810). *Zanclea mayeri* is distinct and does not match any of the

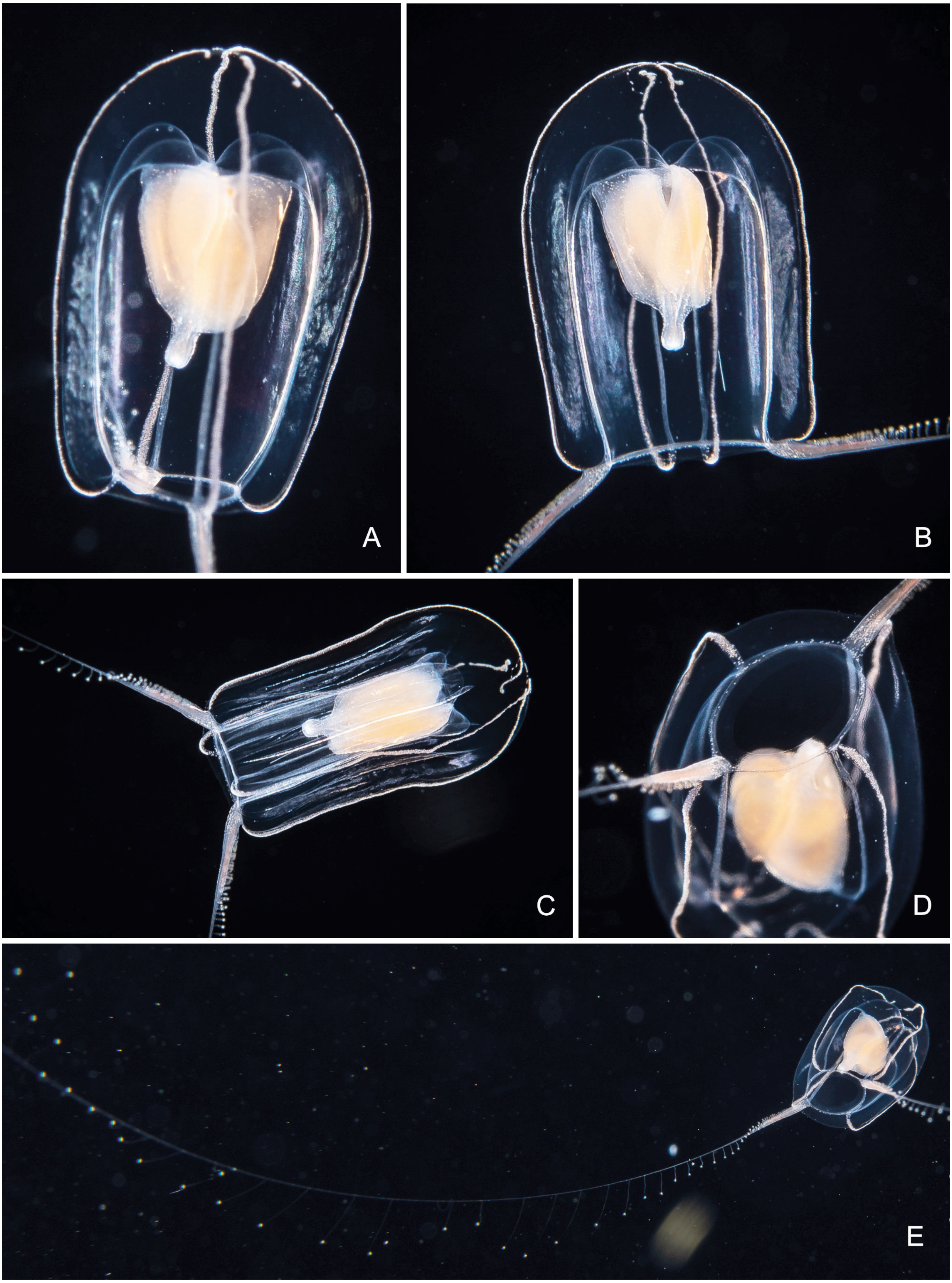

Fig. 18. *Zanclea mayeri* n. spec., living holotype specimen, BFLA4061, bell height 6 mm (A-C) Lateral views. (D) View on umbrella opening. (E) Animal with one tentacle fully extended.

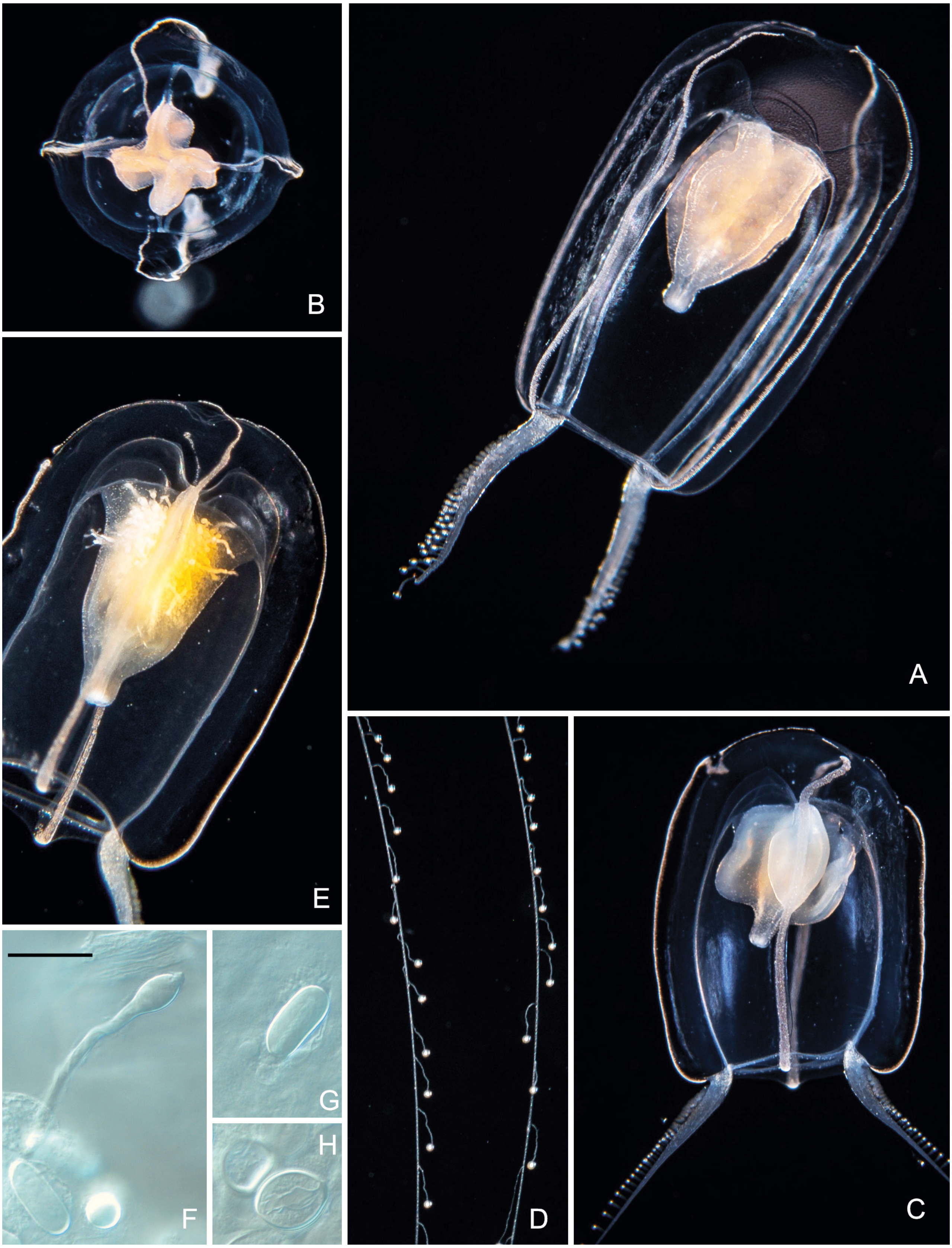

Fig. 19. *Zanclea mayeri* n. spec. (A) BFLA4281, female with oocytes in gonad, height 7 mm. (B) BFLA4281, view from aboral side. (C) BFLA4297, height 6 mm. (D) BFLA4219, part of extended tentacles. (E) BFLA4219, note the capitate polyps growing in the upper part of the manubrium wall, height 5 (F-G) BFLA4219, alcohol preserved nematocysts; scale bar 20 µm. (F) Discharged macrobasic eurytele. (G) Intact macrobasic eurytele, stacked photo. (H) Stenotele.

known nominal *Zanclea* species. We therefore introduce it as a new nominal species.

The holotype specimen of *Zanclea mayeri* n. spec. was used entirely to extract its DNA. The deposited type material is thus not a preserved specimen but only part of it as an extract of its genomic DNA in a buffered solution. A DNA solution serving as type specimen has so far not been used for any hydrozoan, but it is in accordance with the International Code of Zoological nomenclature as it can be regarded as a part of the type specimen (Article 72.5.1). Moreover, photos of the living holotype specimens are given in Fig. 18A-E and applying article 72.5.6 of the ICZN the depicted specimen becomes the type specimen.

Zanclea spec.

Fig. 20A-B

Examined material: BFLA4278; 1 specimen; 06-DEC-2019; height 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528696.

Observations: *Zanclea* medusa, height 2 mm, bell as wide as high, apical part a flat cone. Four exumbrellar nematocyst bands reaching from tentacle bulbs to level of manubrium base (ca. 4/5 of bell height). Manubrium relatively small, bottle-shaped, in upper part with several polyps, these sessile, partly embedded, cylindrical body, with up to three whorls of capitate tentacles. Gonads apparently not yet developed. Four equally well-developed marginal tentacles with stalked cnidophores, no distinct bulb formation, tentacles evenly tapering from origin to distal. No ocelli present. Upper, broader part of manubriumas well as tentacles intensively green.

16S Data: A maximum likelihood tree using part of the 16S sequence data of Maggioni *et al.* (2018) did not associate the sample with any other (Fig. 21). The sequence is rather distinct from those of *Z. mayeri* n. spec. as it shares only 91% identical base pairs.

Remarks: Only one immature animal of this striking *Zanclea* species was observed. The green colour, the four tentacles, and the hydranths on the stomach make it rather unique. Although it is likely an undescribed species, we nevertheless renounced on naming it as we think that we do not have enough photos showing more details for a complete description. It is also immature and the polyps could be a parasite or some teratological development and not a normal feature of the species.

The animal resembles *Zanclea medusopolypata* Boero, Bouillon & Gravili, 2000 from Papua New Guinea, but the latter has only two tentacles. Although tentacle numbers can be variable in *Zanclea* species (Brinckmann-Voss, 1970; Altuna, 2016) it should not be referred to *Z. medusopolypata* for biogeographic reasons and because its polyp stage remains unknown.

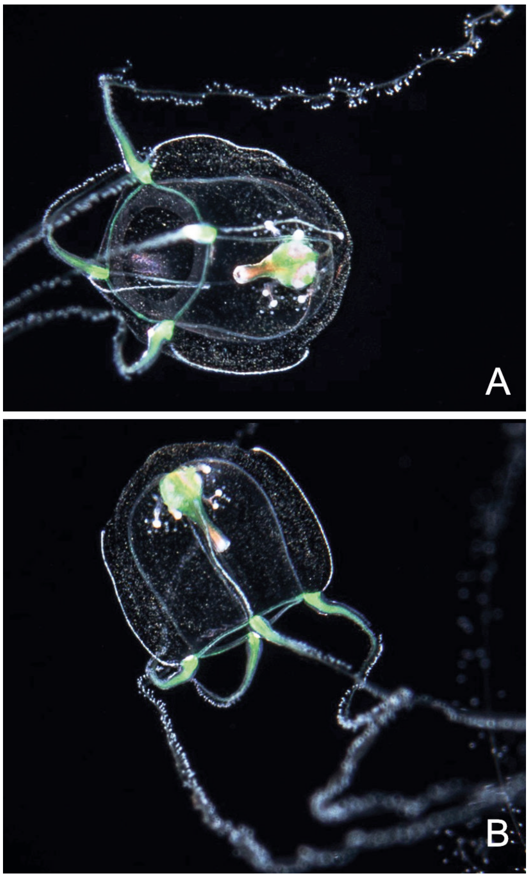

Fig. 20. *Zanclea* spec. (A-B) BFLA4278, bell height 2 mm.

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

Diagnosis: Medusa with or without apical projection; four tentacles, either two long, opposed, capitate tentacles with capitate side branches and two opposed, shorter, simple capitate tentacles, or with four simple capitate tentacles; marginal tentacular bulbs clasping umbrella margin, bulbs with large hemispherical adaxial bulges covered with nematocysts, with abaxial ocelli; manubrium flask-shaped; mouth more or less cruciform, with or without simple lips; gonads interradial to adradial, smooth with interradial cleft or more adradial pads or vertical folds. Polyp stage unknown.

Remarks: The affinities of this genus were obscure for a long time. Hartlaub (1907) placed it in the Zancleidae, Mayer (1910) and Kramp (1961) in the Cladonematidae, Kramp (1965, 1968) in the Pandeidae. It was only when Bouillon (1978b) examined the cnidome it became clear that the presence of stenoteles excluded the Pandeidae, while the desmonemes excluded the Zancleidae. Because also the Cladonematidae differ considerably, Bouillon (1978b) proposed the new family Zancleopsidae to accommodate it. The family currently

Fig. 21. 16S maximum likelihood phylogenetic tree of Zancleidae and related taxa 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%). All sequence labels start with the GenBank numbers permitting the retrieval of more information. Red labels are new sequences from this study.

also includes the genus *Dicnida* Bouillon, 1978b (Bouillon *et al.*, 2006), but it is unclear if it belongs to the suborders Capitata or Aplanulata. Our results presented below show that the family belongs to the Capitata.

The species delimitations within the genus *Zancleopsis* are not well worked out, despite the comparisons or keys given in Bouillon (1978b, 1985) or Wang *et al.* (2016). The differences are mostly either due to mutilated- or to juvenile specimens having not yet developed diagnostic traits (Bouillon, 1978b).

Zancleopsis dichotoma (Mayer, 1900)

Figs 22A-F, 23A-F

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

Zancleopsis dichotoma. – Hartlaub, 1907: 115, fig. 105. – Mayer, 1910: 91, pl. 8 fig. 1. – Bigelow, 1938: 102, figs 1-2. – Kramp, 1959a: 95, fig. 53. – Kramp, 1961: 56. – Kramp, 1965: 25, correction of Kramp, 1959a. – Kramp, 1968: 39. – Bouillon, 1978b: 290. – Bouillon, 1985: Table 1.

Cnidotiara gotoi. – Kramp, 1959a: 12, pl. 1 figs 7-8. [misidentification, not *Zancleopsis gotoi* (Uchida, 1927)]

? *Zancleopsis dichotoma*. – Xu *et al*., 2014: 363, fig. 228, juvenile specimen.

Examined material

Small form: BFLA4170; 1 specimen; 09-AUG-2019; size 3 mm; preserved in alcohol for DNA extraction; 16S sequence MW528683. – BFLA4171; 1 specimen; 09-AUG-2019; size 3 mm; preserved in alcohol for DNA extraction; 16S sequence MW528684. – BFLA4248; 1 specimen; 23-NOV-2019; size 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528692. – 13-AUG-2019, 3 mm, 1 specimen photographed, not collected. – 16-OCT-2019, no size estimate, 1 specimen photographed, not collected.

Large form: BFLA4408; 1 specimen; 26-MAY-2020; height 15 mm, 5 mm wide, male; preserved in alcohol for DNA extraction; 16S sequence MW528723. – BFLA4436; 1 specimen; 07-JUN-2020; height 12 mm, female; preserved in formalin and deposited as UF-014054. – BFLA4467; 1 specimen; 17-JUN-2020; height 15 mm, 5 mm wide, female; preserved in formalin and deposited as UF-014072, part of broken tentacle preserved in alcohol for DNA extraction; 16S sequence MW528732. – 11-APR-2019; 1 specimen photographed; size 10-15 mm, with male gonads; not collected.

Observations

Small form (Fig. 22): Total bell height up to 3 mm, 1/4 to 1/3 of the height taken by pointed apical process; umbrella bell-shaped to conical, relatively thick walls, with shallow interradial subumbrellar pockets, tip of apical process green (Fig. 22A, E). 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, shallow gonad folds, folds mostly adradial, irregular. Radial canals not forming mesenteries, smooth. 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 25 short, abaxial, side branches ending in nematocyst knobs, size of knobs gradually increasing towards distal (Fig. 22F). The other tentacle pair very short, ending in spherical nematocyst knob. In youngest animals observed these short tentacles either missing or just beginning to develop (Fig. 22E). All tentacle bases with a red ocellus on abaxial side.

Nematocysts (alcohol preserved tissue, BFLA4171): 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].

Large form (Fig. 23): Much larger than small form, height 8 to 15 mm and 5 mm diameter, apical process larger reaching 1/2 of total height, tip of apical process whitish, gonads always present, more and larger vertical gonad folds, approximately up to 15, 2-3 folds adradial, brownish, oocytes yellow (Fig. 23A), tentacle bulbs with intense yellow colour, shorter tentacle pair longer than in small form, sometimes terminal knob missing (Fig. 23B).

16S Data: The haplotypes of the small form differed in 0.5-0.8% of the base pairs, in the large form 0.3%. The maximal divergence observed between the two forms was 6.2% base pair difference.

The maximum likelihood analysis (Fig. 21) identified *Astrocoryne cabela* Maggioni *et al.*, 2017 polyps from the Red Sea and the Maldives Islands as relatively closely related, if not conspecific.

Distribution: Florida, Bermuda Islands, mid North Atlantic, Brazil (Kramp, 1959a; Navas-Pereira, 1980). Type locality: USA, Florida, Dry Tortugas archipelago. The record for the China Sea (Xu *et al.*, 2014) is based on a juvenile, indeterminable animal.

Remarks: This is a rare species of which only a few specimens have been reported. Our samples separated into two size categories which also had slight morphological differences, but explainable by different developmental stages being present. The smaller (bell size up to 3 mm) corresponded more to Mayer's (1910) description, while the larger ones corresponds to Bigelow's (1938) specimen. The only difference to Bigelow's material was the length of the tentacles and the presence of terminal knobs in the shorter pair of tentacles. However, this is easily explained by damage during the collecting process of Bigelow's material. Also Kramp (1965: 25) observed that the distal parts of the tentacles are often lost in net material. In one of our specimens, one knob was also missing (Fig. 23B). Mayer (1900) described *Gemmaria dichotoma* based on several, but apparently all immature medusa of 3 mm bell height. He characterised them as having only a single pair of branched tentacles. This is certainly attributable to the rather young stages he had. Also in some of our younger stages the short tentacles were either just developing or absent (Fig. 22E).

Were it not for the 16S results, we would have attributed without hesitation the two forms to two different developmental stages of the same species. The 16S barcode sequences separated the large and small forms into two distinct lineages (Fig. 22) which differed maximally in 6.2% of their aligned bases. We have no reference values of what constitutes intraspecific variation for this family, but the value is quite high compared to other species (comp. Table 1).

Due to the absence of any other diagnostic feature, we preferred for the moment to regard these two forms as belonging to the same species and representing younger and older stages. Many hydromedusae are known to continue their growth even when their gonads get mature. Note also that both forms were found at different times of the year (August to October versus April to June). If the two forms belong to the same species, then the differences in the 16S sequences deserves nevertheless some thoughts, beyond the possibility that they are simply stochastic variations observed in the small number of specimens. It can be argued that the larger forms are certainly also older and have thus spent more time in the current of the Gulfstream. This would then imply that the two forms come from quite different localities, the different 16S haplotypes might therefore come from separate populations.

Kramp (1968: 39) suspected that *Z. dichotoma* and *Z. tentaculata* are conspecific [for descriptions of *Z. tentaculata* see Kramp (1965, 1968) and Bouillon (1978b)]. Bouillon (1978b; 1985) kept them distinct, but he also had some doubts about the suitability of the distinguishing traits. Some of them are linked to the developmental stage (size and shape of bell, position and shape of the gonads, length and form of tentacles), others are clearly due to damages and losses during the collecting process (tentacle lengths and terminal knobs).

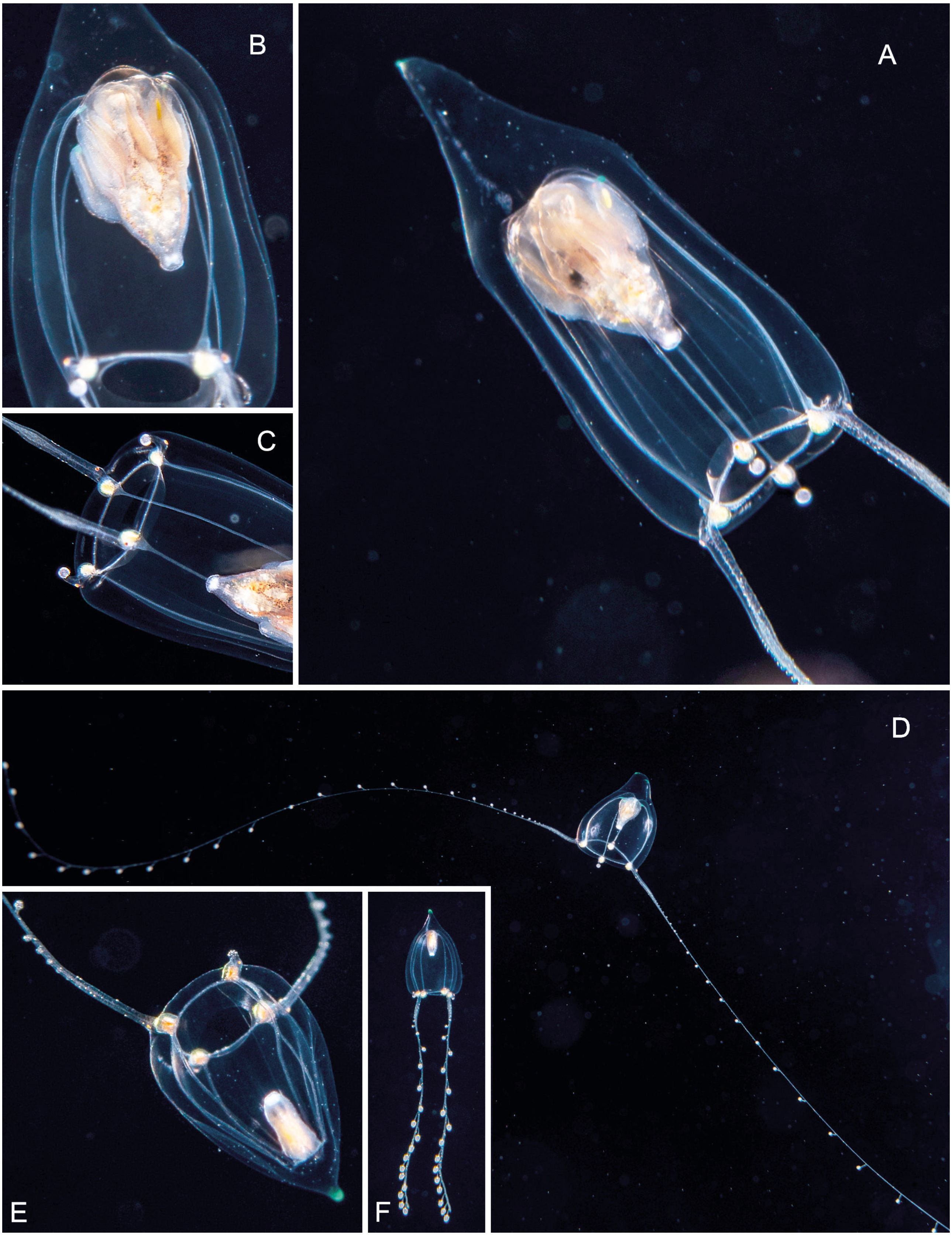

Fig. 22. *Zancleopsis dichotoma,* small form. (A-C) BFLA4171, bell height 3 mm, stomach filled with prey items, note well developed short tentacles. (D) BFLA4170, bell height 3 mm, gonads just begin to develop. (E-F) BFLA4248, bell height 2 mm, immature, note that one of the short tentacles (upper one) is only just developing, while the opposite bulb appears to be devoid of a tentacle.

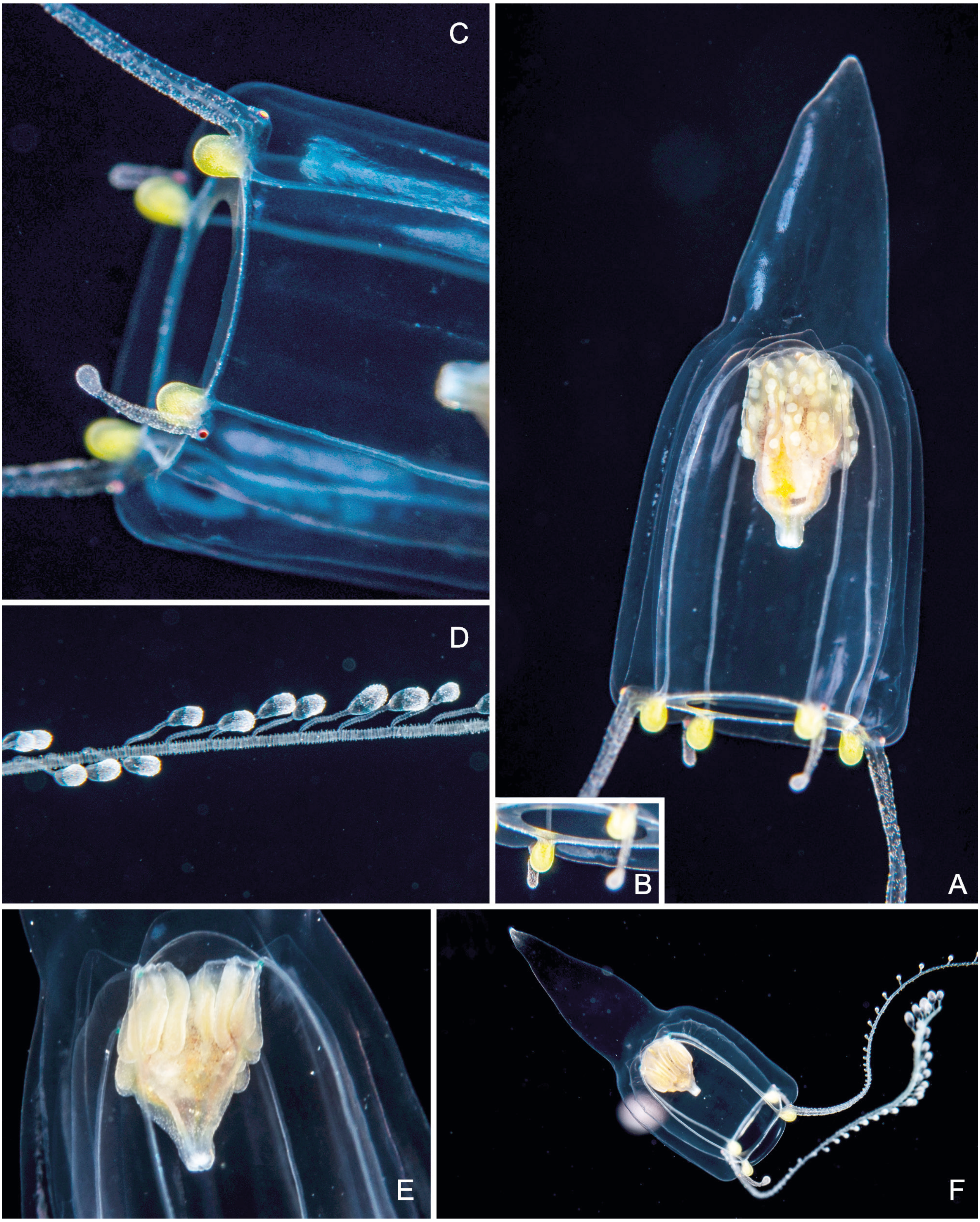

Fig. 23. *Zancleopsis dichotoma,* large form, sizes refer to the total bell height, including the apical process. (A-C) BFLA4467, size 12 mm, female, note in B that one of the short tentacles lacks a terminal knob. (D) BFLA4436, size 10 mm, part of long tentacles with capitate side branches. (E) BFLA4408, size 15 mm, close up of manubrium with male gonads. (F) Animal observed 11-APR-2019, size approximately 10-15 mm.

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

Synonymy: See Schuchert (2010).

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.

Remarks: *Corymorpha* species usually have a rather simple medusa and a more complex hydroid stage offering more discriminating details. *Corymorpha* species that are solely based on the medusa stage are thus potentially species complexes which could be split into several species once their polyp stages become known. This is particularly pertinent for species with suspiciously wide distributions like *C. forbesii*.

Corymorpha forbesii (Mayer, 1894)
Fig. 24A-B

Hybocodon forbesii Mayer, 1894: 236, pl. 1 fig. 1. – Mayer, 1910: 42, pl. 1 fig. 8, pl. 2 fig. 3. – Vanhöffen, 1913a: 414. – Uchida, 1927a: 193, fig. 30.
Hybocodon forbesi. – Kramp, 1959a: 87, fig. 36. – Kramp, 1961: 42. – Kramp, 1968: 13, fig. 22. [incorrect spelling]
Hybocodon forbessi. – Nair, 1951: 50, pl. 1 fig. 1. [incorrect spelling]
Vannuccia forbesii. – Brinckmann-Voss, 1967: 1, figs 1-6. – Brinckmann-Voss, 1970: 14, figs 9-11, pl. 1 figs 1-2. – Schmidt, 1973: 17. – Bouillon, 1978b: 268. – Bouillon *et al.*, 2004: 93, fig. 49K-L.
Vannuccia forbesii f. *kanti* Bouillon, 1978a: 136.
Corymorpha forbesii. – Schuchert, 1996: 103, fig. 60a-c. – Schuchert, 2010: 386, fig. 15, synonymy, redescription.

Examined material: BFLA4045; 1 specimen; 01-APR-2019; preserved in ethanol for DNA extraction; 16S sequence MW528642. – 24-JUN-2019; 1 specimen photographed, with male gonads, not collected.

Observations: Umbrella bell-shaped, height size 2 mm, higher than wide, no apical process or a slight apical thickening, no exumbrellar nematocysts. Manubrium spindle-shaped, length about 2/3 of subumbrellar height, simple mouth, gonads encircle manubrium without interruption. Four large marginal bulbs, all of similar size or bulb opposite tentacle larger than the two other atentacular bulbs, bulb surface covered with

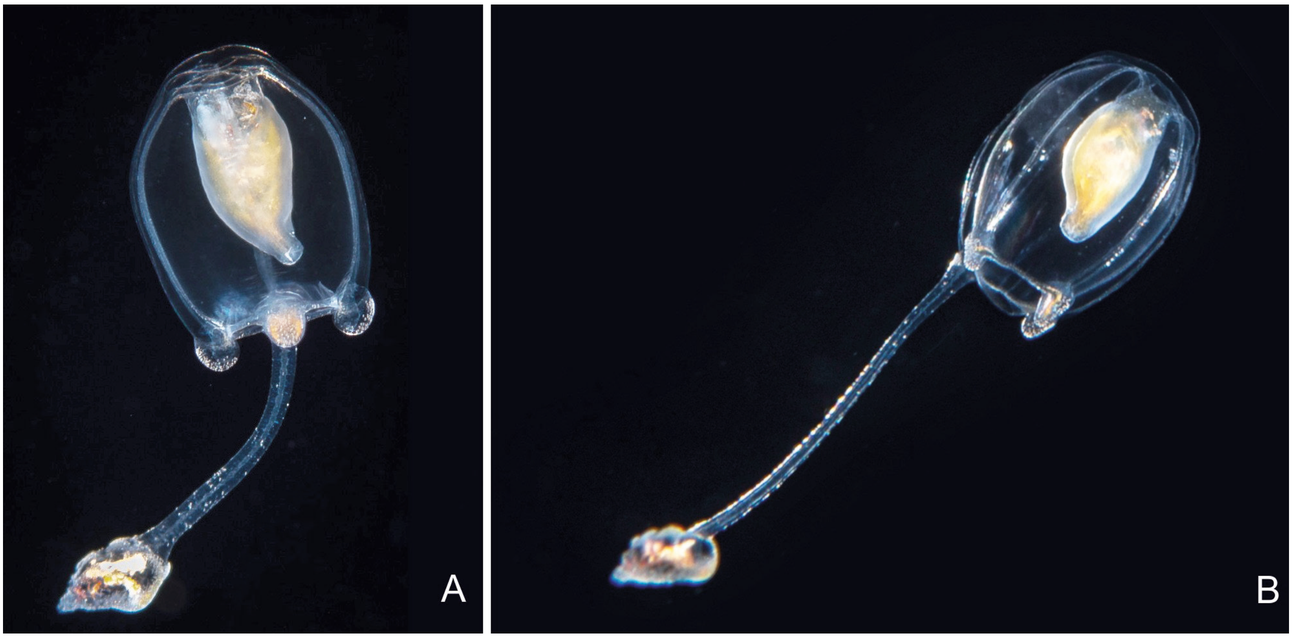

Fig. 24. *Corymorpha forbesii*, bell size ca. 2 mm (A) BFLA4045. (B) Specimen photographed in 24-JUN-2019.

nematocysts. Only one single tentacle, rather stiff, length 1.5 the bell height, 2/3 of length isodiametric and with only few nematocysts, distal third a club-shaped terminal swelling with numerous nematocysts.

16S Data: A blastn search in GenBank using the sole 16S indicated *Corymorpha glacialis* as best match, although with only 84% identity. This species was followed by other *Corymorpha* and Aplanulata species with similar low identify scores.

Distribution: Florida, Bahamas, Brazil, Mediterranean, Red Sea, Seychelles, India, Vietnam, Papua New Guinea, southern Japan, and New Zealand (Schuchert, 2010). Type locality: Bahamas; Nassau Harbour.

Corymorpha gracilis (Brooks, 1883)

Fig. 25A-B

Steenstrupia gracilis Brooks, 1883: 144.
Steenstrupia rubra. – Mayer, 1910: 31, pl. 1 fig. 7. [not *Steenstrupia rubra* Forbes, 1848 = *Corymorpha nutans* M. Sars, 1835]
Euphysora gracilis. – Kramp, 1959a: 89, fig. 40a. – Kramp, 1961: 40. – Goy, 1979: 269, fig. 2.
Corymorpha gracilis. – Nagata *et al*., 2014: 299, fig. 9.
not *Euphysora gracilis* – Pagès *et al.,* 1992: 20, fig. 18.

Examined material: BFLA4368; 1 specimen; size 4 mm; preserved in ethanol for DNA extraction; 16S sequence MW528715. – BFLA4401; 1 specimen; size 6 mm; preserved in ethanol for DNA extraction; 16S sequence identical to MW528715.

Observations: Umbrella bell-shaped, height 4 to 6 mm, about two times higher than wide, with very large, pointed apical process, often of the same size as the umbrella. No gastric peduncle. Manubrium tubular with some tapering towards mouth, length about 1/2 to 4/5 of the subumbrellar height, with long, conspicuous apical canal entering apical process (Fig. 25A-B), distal end often somewhat thickened and yellow in colour. Gonads wrapping manubrium entirely without perradial interruptions. Marginal tentacles of distinct types, one long, extensible tentacle with up to 7 large, oblong nematocyst clusters encircling tentacle entirely, some smaller annular nematocyst, clusters can be present, terminal cluster oblong and slightly thicker than annular ones. The annular clusters may be absent and only a few small clasping clusters can be present (likely in regeneration after tentacles loss). Other tentacles reduced to mere cones, the one opposite the longer tentacle about twice as long as the other two. Radial canals fine, but well visible due to white-yellowish pigmentation. Gastrodermis of tentacles with some red hues.

16S Data: A blastn search in GenBank using the sole 16S indicated *Corymorpha nutans* as best match, although with only 89% identity. This species was followed by other *Corymorpha* and Aplanulata species with similar low identity scores.

Distribution: Atlantic cost of the USA from New England to Florida (Brooks, 1883; Kramp 1959); Brazil (Kramp, 1959; Nagata *et al.,* 2014); South Atlantic (Goy, 1979). Doubtful records from the Benguela current (Pagès *et al*., 1992). Type locality: USA, North Carolina, Newport River.

Remarks: The specimen depicted by Pagès *et al.* (1992) and identified as *Euphysora gracilis* (syn. *Corymorpha gracilis*) lacked the typical large apical projection with the gastrodermal process in it. It is therefore not unambiguously attributable to *Corymorpha gracilis.*

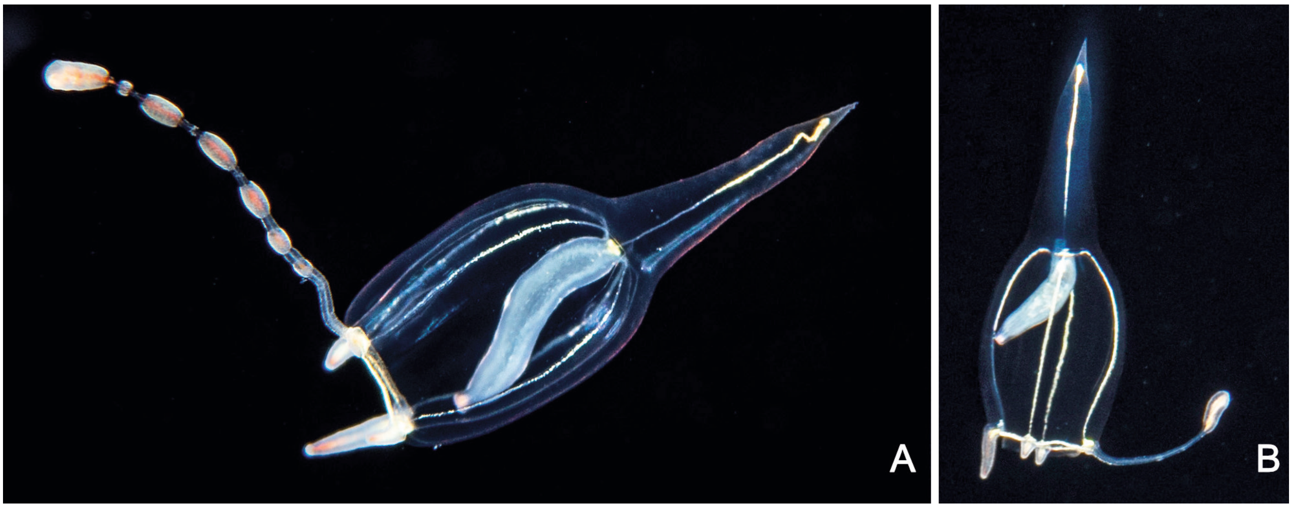

Fig. 25. *Corymorpha gracilis.* (A) BFLA4368, total bell size 4 mm. (B) BFLA4401, size 6 mm.

Corymorpha floridana n. spec.

Fig. 26A-E

Holotype: BFLU4371; 1 formalin preserved male medusa deposited as FU-014026; collected 16-MAR-2020; bell height 3 mm.

Other examined material: BFLA4362; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence MW528714. – BFLA4363; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence identical to MW528714. – BFLA4364; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence identical to MW528714. – BFLA4365; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence identical to MW528714. – BFLA4437; 1 specimen; 07-JUN-2020; preserved formalin and

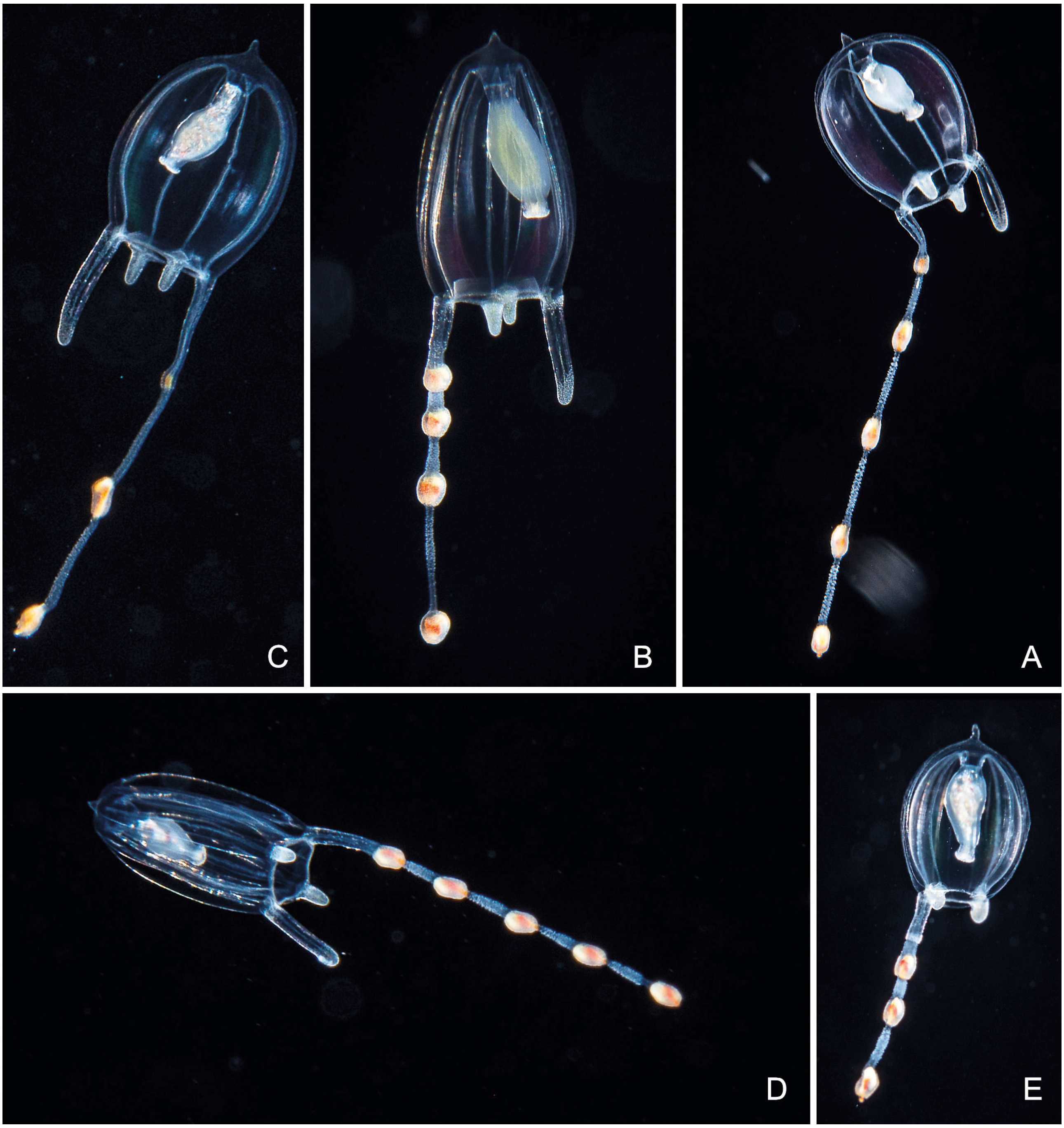

Fig. 26. *Corymorpha floridana* n. spec (A) Holotype, BFLA4371, bell height 3 mm. (B) 01-APR-2019; photographed but not collected; mature male, 2 mm. (C) 11-MAR-2020; photographed but not collected; 2 mm. (D) BFLA4363; bell height 2 mm. (E) BFLA4362; 2 mm; note that part of the long tentacle and the entire intermediate length tentacle are missing.

submitted as FU-014055; 4 mm bell. – 13-MAR-2020; 1 specimen photographed, not collected; 2 mm. – 16-MAR-2020; 2 specimens photographed, not collected; 2 mm.

Type locality: USA, Florida, 5.5-12 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Etymology: The name refers to the Florida Peninsula were the species was found.

Diagnosis: *Corymorpha* species with one long moniliform tentacle, one much shorter filiform tentacle opposite, and two tentacle stumps. Long tentacle with up to five orange, round to oblong nematocyst rings, including a terminal button. Bell with very small, pointed apical projection, no apical canal. Manubrium simple, on short gastric peduncle.

Description: Medusa with umbrella 2-3 mm high and about 1.6 mm wide (Fig. 26A-E), evenly bell-shaped, jelly relatively thin, not much thickened at apex, regularly with a small, pointed projection, not much varied in size. Manubrium on short gastric peduncle, spindle shaped, about half or somewhat more of the height of the subumbrella, mouth circular, with white rim. Gonads encircle nearly whole manubrium as relatively thin layer, without folds or perradial interruption. Four radial canals and circular canal thin, smooth. No tentacle bulbs or ocelli. Four tentacles of three types. One long tentacle, much extensible, contracted about two bell heights long, thick, only slightly tapering; nematocysts concentrated in three to five nematocyst rings, one knob in terminal position, rings more or less equidistant and well separated, shape round to oblong when tentacle extended, colour orange. Tentacle opposite the long tentacle about half the length of the bell-height, evenly thick, end rounded, without nematocyst buttons, with some nematocysts at base and at end. Other two tentacles short, length about 1/3 of filiform tentacle, conical, with scattered nematocysts.
Variation: the mid-length tentacle was missing in one specimen (Fig. 26E), otherwise morphology rather uniform.
Corymorpha floridana, like other *Corymorpha* species, has a rather distinctive zigzag swimming style due to its unbalanced tentacle arrangement.

16S Data: A blastn search in GenBank using the sole 16S indicated *Corymorpha nutans* as best match, although with only 88% identity. This species was followed by other *Corymorpha* and other Aplanulata species with similar low identify scores.

Remarks: We were unable to identify our material with any of the described *Corymorpha* species (Schuchert, 2020) and therefore introduce it here as a new nominal species. With its tentacle configuration it conforms with the scope *Euphysora* Maas, 1905, a genus synonymized with *Corymorpha* M. Sars, 1835 by Petersen (1990). Some authors continue to regard it as valid, *e.g.* Bouillon *et al.* (2006).
Corymorpha floridana n. spec. resembles three other species, but can easily be distinguished from them:

- *Corymorpha bigelowi* (Maas, 1905): has a long tentacle with adaxial nematocyst clasps and not in rings, also larger apical projection; Indo-Pacific distribution (Schuchert, 2010; Madkour *et al*., 2019).
- *Corymorpha annulata* (Kramp, 1928): has a distinct apical canal, a larger apical projection, many more (up to 17) nematocyst rings and these much narrower and not round or oval; Indo-Pacific distribution (Kramp, 1968).
- *Corymorpha crassocanalis* (Xu & Huang, 2003): has a long tentacle with adaxial nematocyst clasps and not in rings, no apical canal, broad and indistinct apical projection, broad radial canals (coasts of China).

Although distinct, *Corymorpha floridana* n. spec. is a rather simple medusa from a genus with a much more complex polyp stage. There is thus a danger that more than one polyp could be found that produce the same medusa (e.g. as for many *Clytia* species) and the species will thus become unrecognizable. However, through the available 16S sequence data this problem is likely resolved. To our knowledge, there is only one polyp-based *Corymorpha* species that is endemic to the NW Atlantic, namely *Corymorpha pendula* L. Agassiz, 1862, but this species does not produce free medusae. The polyp of the medusa *Corymorpha bigelowi* was described by Sassaman & Rees (1978).

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

Laodicea Lesson, 1843: 294, type species *Medusa crucigera* Gmelin, 1788 by monotypy.
Laodice Lesson, 1843: 294, invalid non-Latin name.
Octorhopalon von Lendenfeld, 1885: 919, type species *Octorhopalon fertilis* von Lendenfeld, 1885 by monotypy.

Diagnosis: Medusa with four simple radial canals; gonads along radial canals; with marginal cordyli, with or without marginal cirri, with adaxial ocelli, without statocysts.

Laodicea undulata (Forbes & Godsir, 1853)
Fig 27A-E

Laodicea undulata. – Schuchert, 2017a: 353, fig. 2A-C, redescription, complete synonymy.

Examined material: BFLA3797; 1 specimen; 13-OCT-2018; size 6 mm; preserved in alcohol for DNA extraction; 16S sequence MW528645. – BFLA3806; 1 specimen; 19-OCT-2018; preserved in alcohol for DNA extraction; 16S sequence MW528646. – BFLA3812; 1 specimen; 20-OCT-2018; size 8 mm; preserved in alcohol for DNA extraction; 16S sequence MW528647. – BFLA3836; 1 specimen; 19-NOV-2018; size 6 mm; preserved in alcohol for DNA extraction; 16S sequence MW528648. – BFLA4126; 1 specimen; 06-JUN-2019; size 10 mm; has one branched radial canal, thus 5 radial canals in total; preserved in alcohol for DNA extraction; 16S sequence identical to MW528648. – 04-MAR-2019; 1 specimen photographed, with one radial canal joining another radial canal instead of manubrium, not collected.

Observations: *Laodicea* medusae with umbrella up to 10 mm wide, all individuals not fully grown; stomach quadratic, short, with four folded lips. Gonads contiguous with stomach and spreading along proximal half to 2/3 (depending on bell size and age) of widened radial canals (= basal stomach pouches or extensions), flat leaf-like, pendant, sinuous. Up to 100 tentacles; small tentacle bulbs that taper gradually into tentacle, bulb usually with an adaxial ocellus, usually one marginal cirrus between successive tentacles; usually one cordylus between successive tentacles.

16S Data: A blastn search in GenBank with the four obtained sequences gave always as best match one of the European *Laodicea undulate* sequences, although the similarities were rather low (92-95%). The haplotypes from Florida showed high divergence values of up to 10.6% (Table 1), while the three European haplotypes have only 0.5% bp differences. A maximum likelihood tree separated the sequenced into three distinct lineages (Fig. 28).

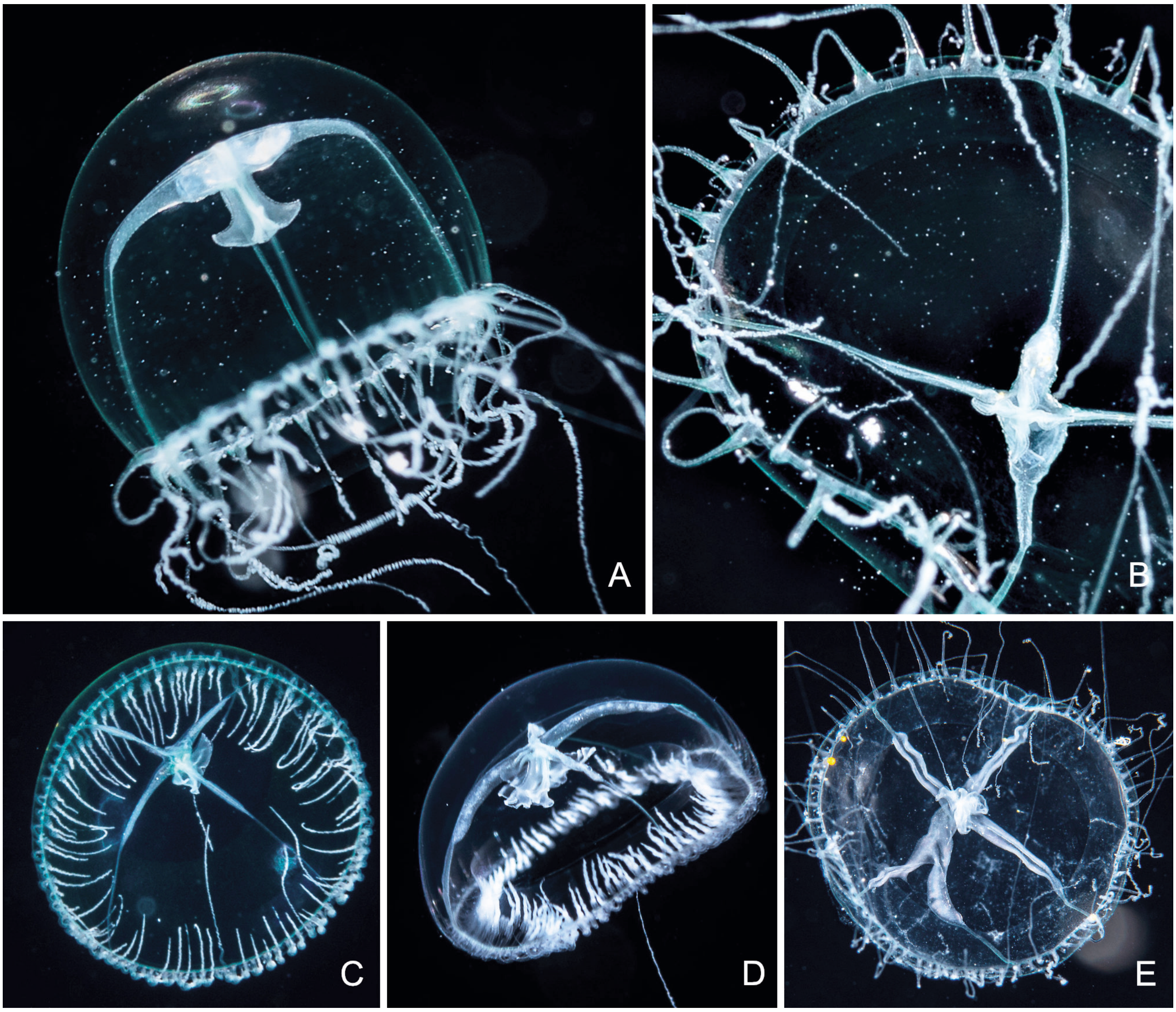

Fig. 27. *Laodicea undulata*, all not fully grown. (A-B) BFLA3836, size 6 mm, subadult. (A) Lateral view of whole animal, bell contracted and therefore higher than when relaxed. (B) Aboral view showing bell margin, cirri and cordyli are visible. (C) BFLA3836, size 6 mm. (D) BFLA3812, size 8 mm. (E) BFLA4126, size 10 mm, note the aberrant, branched radial canal.

Distribution: Eastern Atlantic and adjacent waters from Iceland and northern Norway to South Africa; western Atlantic from Nova Scotia to Tierra del Fuego; Mediterranean (Kramp, 1968). Some occasional records from the Indo-Pacific require a re-evaluation (Schuchert, 2017a). Type locality: The Minch, Scotland.

Remarks: It is arguable if the widened radial canals with the gonads (Fig. 27) should not better be interpreted as basal perradial extensions or pouches of the manubrium.

Although the animals of this study were morphologically not separable, some of their 16S sequences were very divergent, suggesting the presence of cryptic species (Fig. 28). *Laodicea undulata* has a complex synonymy. It includes also a nominal species of the NE Atlantic, namely *Laodicea calcarata* L. Agassiz, 1862 (see Agassiz, 1865), but this nominal species is currently not separable from *L. undulata* (comp. Cornelius, 1995; Schuchert, 2017a). Mayer (1900) described *Laodicea neptuna* from Florida. As it has only eight tentacles it

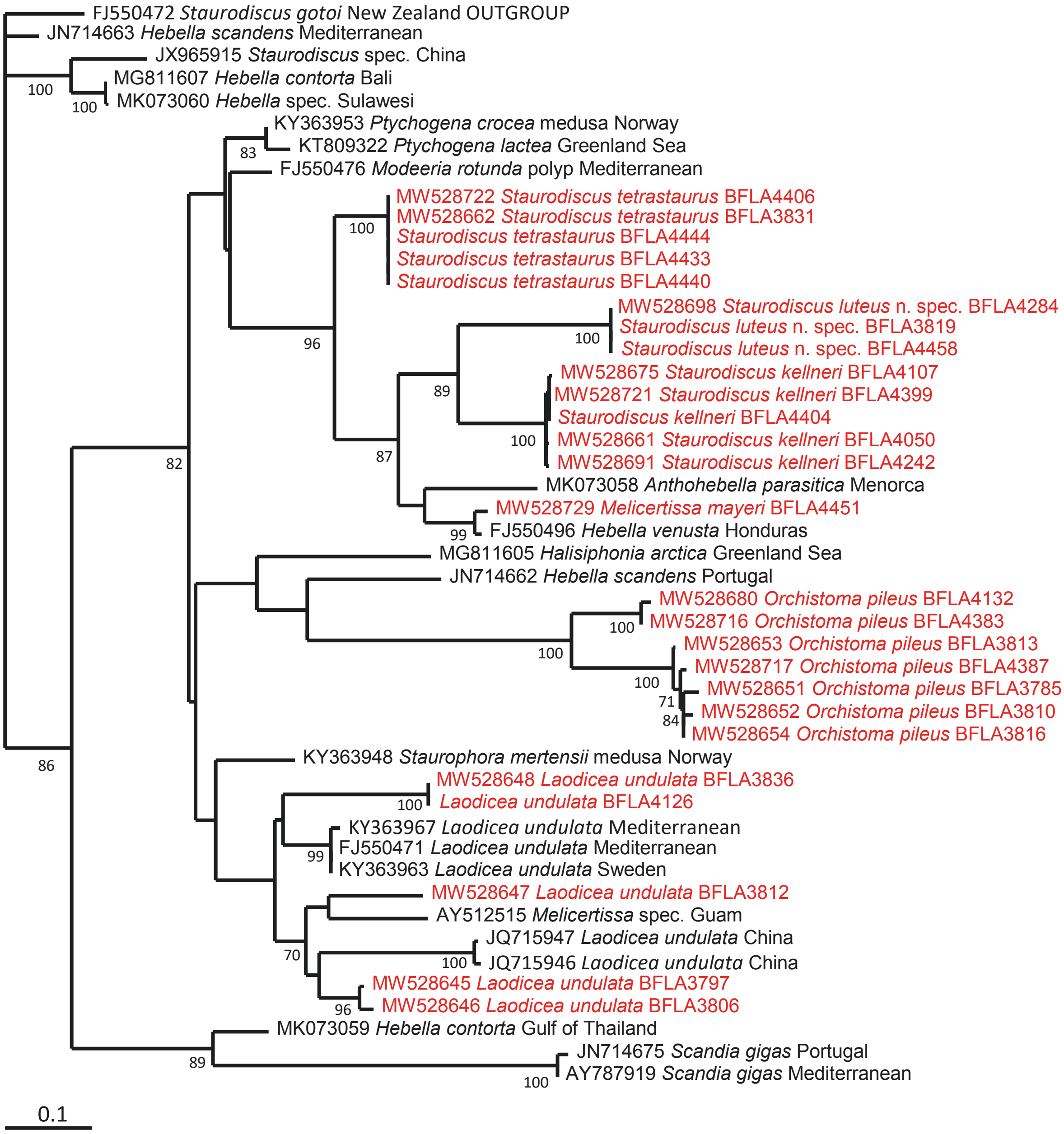

Fig. 28. 16S maximum likelihood phylogenetic tree of Laodiceidae, Hebellidae, and Orchistomatidae, obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). All sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Red labels are new sequences from this study.

cannot be one of the *Laodicea* observed here. Kramp (1959a) regarded it as a *species inquirenda*.

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

Melicertissa Haeckel, 1879: 135; type species *Melicertissa clavigera* Haeckel, 1879 by monotypy.
Melicertella Haeckel, 1879: 134; type species *Melicertella panocto* Haeckel, 1879 by monotypy.

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.

Remarks: See Uribe-Palomino *et al.* (2018: 26, table 1) for a synopsis of the species.

Melicertissa mayeri Kramp, 1959
Fig. 29A-C

Melicertissa clavigera. – Mayer, 1910: 210, pl. 24 figs 2-3. [not *Melicertissa clavigera* Haeckel, 1879]
Melicertissa mayeri Kramp, 1959a: 139, fig. 162, new name. – Kramp, 1961: 144. – Uribe-Palomino *et al.*, 2018: 26, table 1.
? *Lafoea venusta* Allman, 1877: 11, pl. 6 figs 3-4. [possible synonym]
? Hebella venusta. – Calder, 1991: 41, fig. 25. – Boero *et al.,* 1997: 39, species inquirenda. – Galea, 2010: 13, fig. 4E-G. – Calder, 2013: 17, fig. 5a. – Calder, 2019: 33, fig. 8a.

Examined material: BFLA4451; 1 specimen; 08-JUN-2020; size 10 mm; part preserved in formalin and deposited as UF-014062, part preserved in alcohol for DNA extraction; 16S MW528729.

Observations: *Melicertissa* medusa with nearly hemispherical bell, diameter 10 mm, apical jelly thickened. Manubrium relatively small, cross-section an eight-rayed star, mouth with eight simple lips, base star-shaped and widened, continued as eight basal perradial stomach extensions, leaf-like, replacing about 2/3 of radial canal, continued after this as thin, unbranched radial canal. Gonads on distal part of basal stomach extensions, flat and leaf-like on both sides of extension, occasional folds present (Fig. 29B). Eight perradial and eight interradial tentacles fully developed, three adradial small tentacles, total number thus 19. Tentacle bulbs conical to ovoid. Between each pair of tentacles 1-3 cordyli, totally about 35. Adaxial ocelli on circular canal opposite each tentacle bulband cordylus. Cirri absent. Mostly colourless, gonads white, sides of tentacle bulbs with green hue.

16S Data: A blastn search in GenBank with the obtained sequences gave a good match of 98.7% similarity with the sequence FJ550496 obtained from the hydroid *Hebella venusta* (Allman, 1877). The maximum likelihood tree also shows the close relationship (Fig. 28).

Distribution: Florida (Kramp, 1959a); ?Indian Ocean (Navas-Pereira & Vannucci, 1991; a single individual only). Type locality: USA, Florida, Dry Tortugas archipelago.

Remarks: Mayer (1910) identified *Melicertissa* medusae from Florida as *M. clavigera* Haeckel, 1879 despite them having 16 tentacles instead of 8 as for typical *M. clavigera*. He considered this as intraspecifc variation with possibly *M. clavigera* being a younger form. Nair (1951) questioned this, mainly based on the assumption that Haeckel described *M. clavigera* has having 24 cordyli at a size of 10 mm, while Mayer (1910) depicted his medusa with only 16 cordyli at a diameter of 7 mm. If Mayer's specimens were older and had more tentacles, then they should not have fewer cordyli (although they might have been lost, they break away easily). Kramp (1959a) adopted Nair's suggestion and introduced the new name *Melicertissa mayeri* for Mayer's specimens. However, both Nair and Kramp must have overlooked comments in Mayer (1910: 211) in which he described the variation of tentacle numbers and cordyli. Some interradial tentacles may be replaced by a cordylus (resulting thus in less than 16 tentacles). Some octants of the bell may have two tentacles and three cordyli, others had three tentacles and 2 cordyli. The number of tentacles and cordyli is thus variable and Mayer's (1910) conclusion that *M. clavigera* is conspecific with the Florida population is understandable and needs re-examination using genetic methods.

Our specimen had 19 tentacles and about 35 cordyli, deviating thus somewhat from the scope given in Mayer (1910) and Kramp (1959a). Only very few specimens of both *M. clavigera* and *M. mayeri* have been described so far and it is very likely that the intraspecific variation of the tentacle- and cordylus numbers has been underestimated. Therefore, we nevertheless identified the present medusa as *M. mayeri*.

The 16S sequence matched rather closely (1.3% base pair differences, Fig. 28) to a sequence obtained from the hydroid *Hebella venusta* (Allman, 1877) collected in Honduras and growing on the hydroid *Thyroscyphus marginatus* (Fig. 30). The type material of *Hebella venusta* came from Loggerhead Key, Florida. Recent descriptions of *Hebella venusta* are given by Galea (2010) and Calder (2013, 2019). It is a nominal species with very few diagnostic traits and Boero *et al.* (1997) are right considering it a *species inquirenda* as our current concept of it could include several species (viz. the same hydroid morphotype but producing different medusae). It is therefore not clear if the material from which the sequence FJ550496 was obtained corresponds really to the *H. venusta* at the type locality.

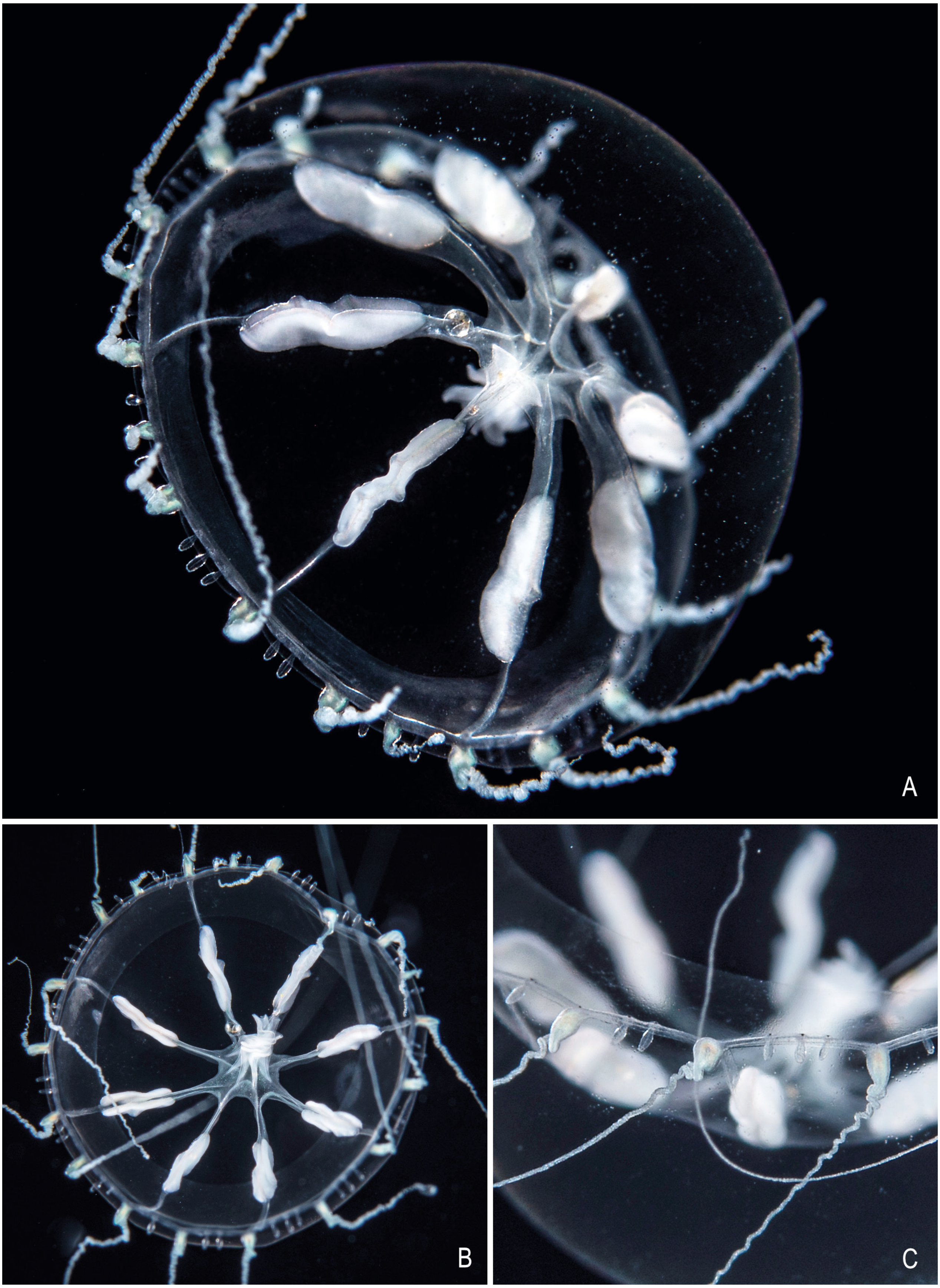

Fig. 29. *Melicertissa mayeri,* BFLA4451, size 10 mm. (A) Oblique view of whole animal. (B) Oral view. (C) Bell margin, note cordyli and ocelli.

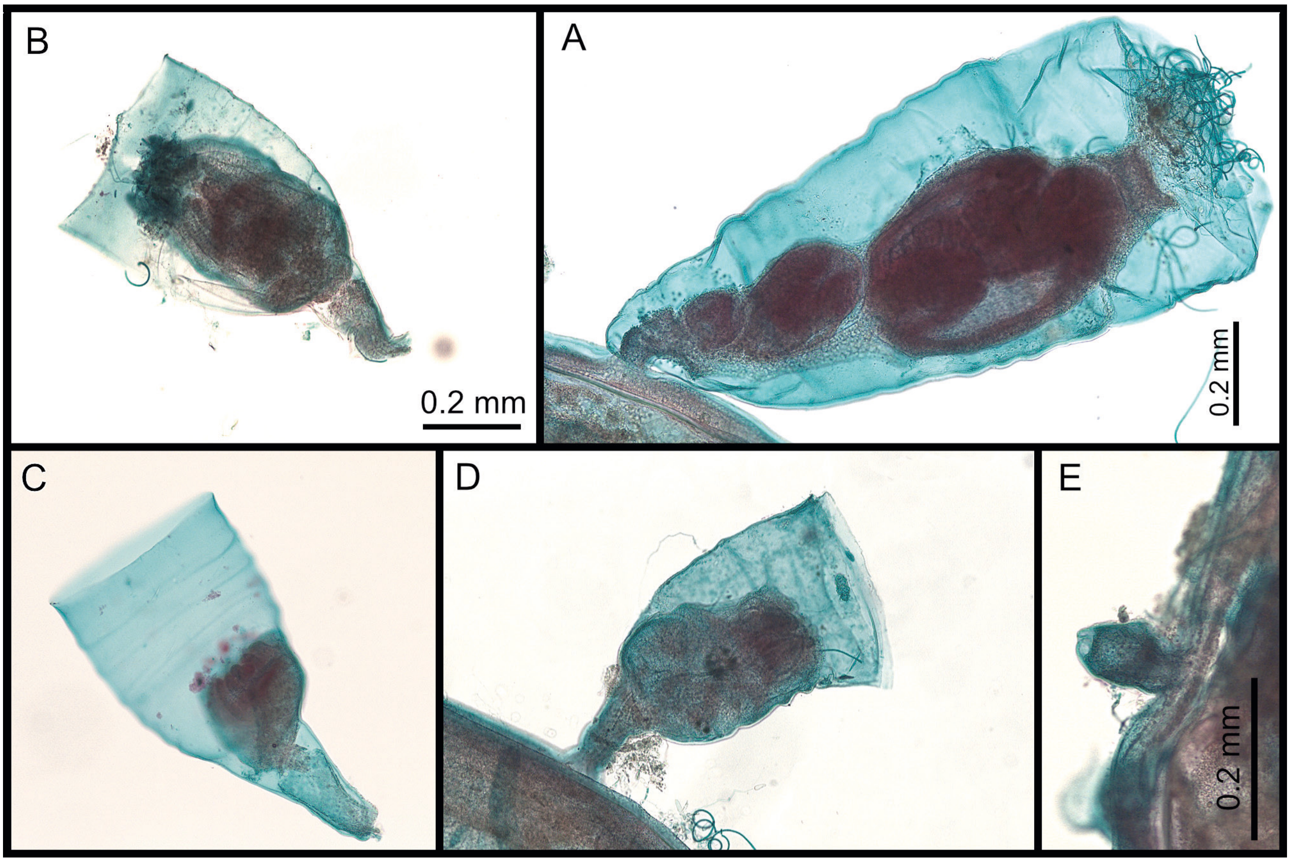

Fig. 30. Hydroid *Hebella venusta*, MHNG-INVE-0035476, from Honduras, stained slide preparation, voucher specimen of 16S sequence FJ550496. (A) Gonotheca with medusa buds, ocelli are faintly visible. (B) Hydrotheca with hydranth, rim with four shallow cusps. (C-D) Hydrothecae with smooth rim. (E) Unidentified structure resembling a nematotheca, but it could also be a rest of a broken caulus.

However, *Melicertissa mayeri* is clearly not a member of the Laodiceidae (Fig. 28) but must be transferred to the Hebellidae (comp. also Migotto & Andrade, 2000). According to the tree (Fig. 28) it appears even congeneric with *Staurodiscus*.

Genus *Staurodiscus* Haeckel, 1879

Staurodiscus Haeckel, 1879: 145, type species *Staurodiscus tetrastaurus* Haeckel, 1879 (Kramp, 1961: 147).

Staurodiscalma Haeckel, 1879: 145, type species *Staurodiscus tetrastaurus* Haeckel, 1879 by monotypy.

Staurodiscema Haeckel, 1879: 146, type species *Staurodiscus heterosceles* Haeckel, 1879 by monotypy.

Toxorchis Haeckel, 1879: 157, type species *Toxorchis arcuatus* Haeckel, 1879 by monotypy.

Staurodiscoides Uchida, 1927b: 165, type species *Staurodiscoides gotoi* Uchida, 1927 by monotypy.

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).

Remarks: See Kramp (1962) and Bouillon (1984b) for emended diagnosis and synopsis of the species. For the life cycle see Migotto & Andrade (2000).

Staurodiscus kellneri (Mayer, 1910)

Fig. 31A-H

Toxorchis kellneri Mayer, 1910: 229, pl. 28 figs 1-2. – Vanhöffen, 1913a: 421. – Bigelow, 1917: 306. – Bigelow, 1926: 54. – Kramp, 1959a: 141, fig. 167. – Kramp, 1961: 150.

Dipleurosoma brooksii Mayer, 1910: 227, fig. 118a-b, **nov. syn**.

Toxorchis brooksi. – Kramp, 1959a: 141, fig. 168b. – Kramp, 1961: 147.

Hebella furax. – Migotto & Andrade, 2000: 1873, figs 1-5. [? not *Hebella furax* Millard, 1957]

? *Toxorchis milleri* Bouillon, 1984b: 71, fig. 20.

? not *Staurodiscus kellneri*. – Bouillon *et al*., 2004: 152, figs 82A-D.

Examined material: BFLA4050; 1 male; 01-APR-2019; size 20 mm; preserved in formalin (UF-013450) and small part in alcohol for DNA extraction; 16S sequence MW528661. – BFLA4074; 1 specimen; 11-APR-2019; size 13 mm; preserved in formalin (UF-013784) and small part in alcohol for DNA extraction; 16S sequence identical to MW528721. – BFLA4107; 1 specimen; 27-MAY-2019; size 10 mm, only 9 radial canals; preserved in formalin (UF-013794) and small part in alcohol for DNA extraction; 16S sequence MW528675. – BFLA4242; 1 specimen; 11-NOV-2019; size 7 mm; preserved in formalin (UF-013835, sample macerated, only debris left) and part in alcohol for DNA extraction; 16S sequence MW528691. – BFLA4399; 1 specimen; 17-MAY-2020; size 11 mm; preserved in formalin (UF-014041) and small part in alcohol for DNA extraction; 16S sequence MW528721. – BFLA4404; 1 specimen; 26-MAY-2020; size 8 mm; preserved in alcohol for DNA extraction; 16S sequence identical to MW528721. – BFLA4424; 1 specimen; 28-MAY-2019; size 9 mm; preserved in formalin (UF-014050) and small part in alcohol for DNA extraction; 16S sequence MW528726. – BFLA4452; 1 specimen; 08-JUN-2020; size 14 mm; preserved in formalin and deposited as UF-013450. – 30-MAY-2020; 1 specimen; photographed but not collected; 10 mm, 9 radial canals, juvenile.

Observations: Umbrella diameter 10-20 mm, hemispherical or slightly flatter than hemisphere, lateral jelly thin but gradually thickening towards apex, the latter moderately thick. Manubrium rather flat, mouth wide open or a short tube with variable number of folded lips, manubrium base much enlarged and drawn out star-like into up to 12 basal extensions which may branch into two or three radial stomach extensions and reaching almost to circular canal, continued as short radial canals (about 1/6 of bell radius) and these all connected to circular canal, no blind ending radial canals or stomach extensions, 16-19 radial canals. Branching pattern variable and irregular, some radial canals not branching. Gonads develop on lateral walls of stomach extensions, reaching from branching points to beginning of radial canals, colour pale reddish-brown or brown-yellow. Tentacles 23-32, with distinct ovoid marginal bulb, black ocellus on adaxial side where joined to umbrella. Marginal bulbs independent of radial canals. Between each pair of tentacles usually one, sometimes 2-3 (especially in smaller animals) elongate cordyli, cordyli with a few terminal nematocysts, at attachment site on adaxial side a black ocellus. No statocysts.

16S Data: The six 16S sequences obtained represented four haplotypes with only 0.16 to 0.5% base pair differences. In the maximum likelihood tree (Fig. 28) they are well separated from the other *Staurodiscus* species and also *Melicertissa* of this study.

Distribution: Florida and Gulf of Maine (Kramp, 1959a). Type locality: USA, Florida, Dry Tortugas archipelago. The Mediterranean occurrence given in Bouillon *et al.* (2004) is based on records of the hydroid *Hebella furax* Millard, 1957 and is most likely incorrect because the medusa is not known to occur in this well investigated area. It is by no means evident that the simple hydroid *Hebella furax* corresponds to *Staurodiscus kellneri* in all regions it has been reported. It is highly probable that *Hebella furax* represent a species complex (see also Remarks below).

Remarks: This is a rare medusa, only a few individuals have been described so far and the variation of the number of tentacles, radial canals, and the branching of the stomach extensions were not well known. Migotto & Andrade (2000) reared medusae released from a hydroid they collected in coastal waters of Brazil and identified as *Hebella furax* Millard, 1957. The resulting adult medusae were clearly identifiable as *S. kellneri,* although the authors hesitated somewhat with this identification, presumably because the branching pattern of the radial canals/stomach extensions were more variable than documented before. This trait was rather variable in our specimens too (Fig. 31A-G) and confirms the observations of Migotto & Andrade (2000). However, *Hebella furax* cannot simply be synonymized with *Staurodiscus kellneri. Hebella furax* [see Millard (1975) and also Boero *et al*. (1997)] was originally described from South Africa and is a widespread, rather simple hydroid offering few diagnostic features. It is very likely that it does not produce *S. kellneri* medusae over its whole distribution range, just like the "*Campanulina*"-type hydroids produce medusae belonging to different genera (see Schuchert *et al.*, 2017 for similar cases).

Staurodiscus brooksii (Mayer, 1910) (see description in Kramp, 1959a) from the Bahamas appears very similar to *S. kellneri.* The former has fewer tentacles and also fewer radial canals because four radial canals are unbranched. BFLA4399 had exactly this condition (Fig. 31F), while others like BLFA4050 (Fig. 31A) had it partially. Mayer (1910) described *S. brooksii* based on drawings made by

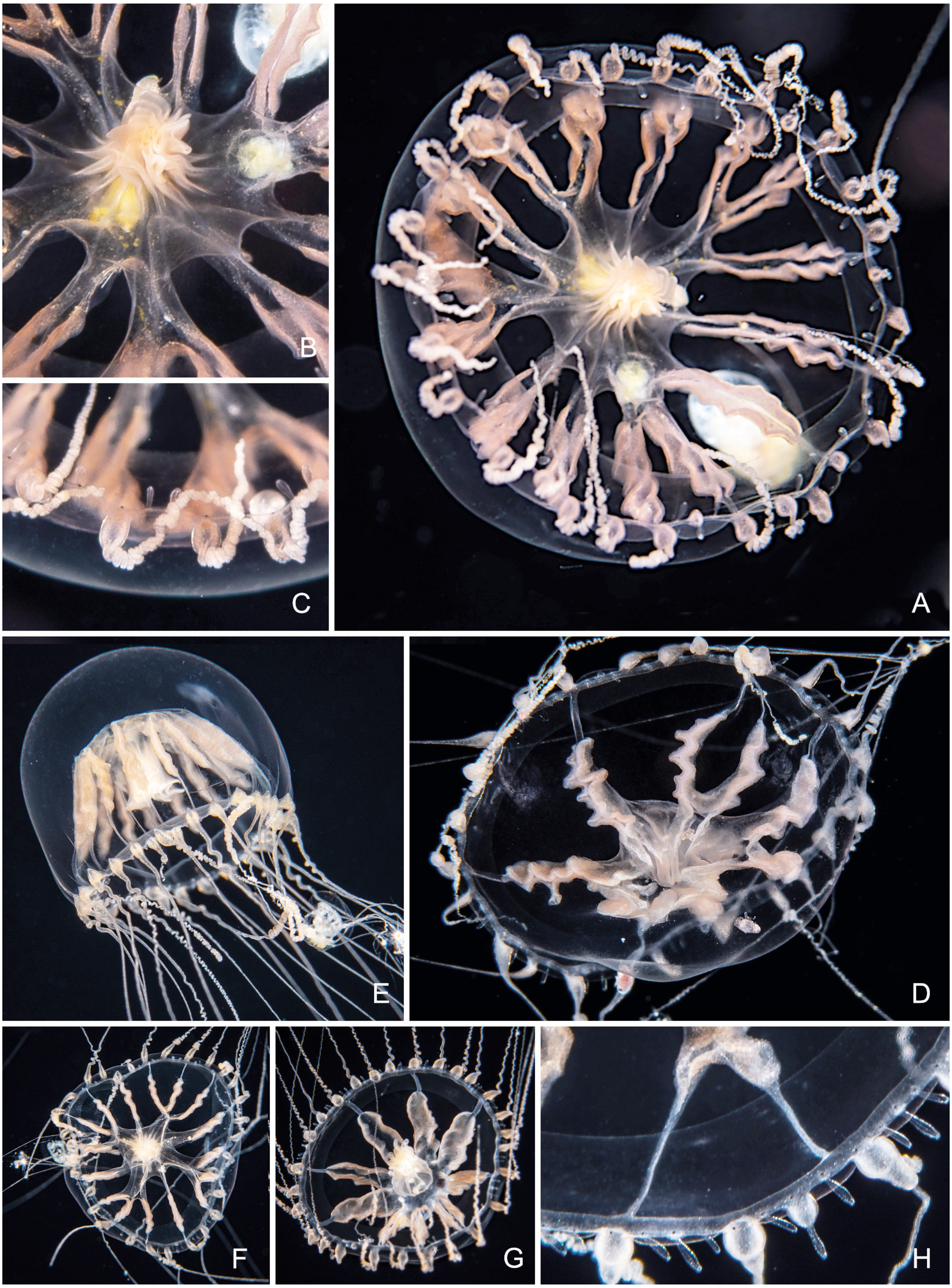

Fig. 31. *Staurodiscus kellneri*. (A-C) BLFA4050, size 20 mm. (A) Oral view, the oval, white body is a crustacean on the exumbrella. (B) Mouth part. (C) Bell rim, ocelli and cordyli are visible. (D) BFLA4107, size 10 mm, young animal with only nine radial canals reaching the circular canal. (E) BFLA4399, contracted bell, lateral view, size 11 mm. (F) BFLA4399, oral view, not all radial extensions are branched. (G) Animal photographed 12-OCT-2020, 10 mm, juvenile with 9 radial canals. (H) BFLA4242, bell diameter 7 mm, bell margin with bulbs and cordyli.

the late William K. Brooks of a medusa collected from Nassau, Bahama Islands. The drawing did not show ocelli, but they were probably overlooked by Brooks as they are rather small and not well visible (Fig. 31H). Kramp (1959a) pointed out that also the cordyli were also not mentioned in Mayer (1910), but they are shown in Mayer's figure (1910: 118aA). *Staurodiscus brooksii* must evidently be a younger stage of *Staurodiscus kellneri* and we regard both as conspecific. Both names were introduced in Mayer (1910), with *S. brooksii* appearing on page 227, *S. kellneri* on page 229. As the current ICZN does not enforce page precedence for synonymized names appearing in the same work, acting as first revisors we prefer to use the name *Staurodiscus kellneri* for the present species. It is the better and more precisely known nominal species and has been reported subsequently, while *S. brooksii* is incompletely described and has not been reported anymore (based on Kramp, 1961).

With the new data on the variability of the radial canals and their branching pattern in *Staurodiscus kellneri*, *S. milleri* (Bouillon, 1984b) becomes hardly distinguishable. They could well be conspecific. The only tangible difference remaining being the smaller size of *S. milleri* (up to 8.5 mm versus 10-20 mm). Although we think that both names should be synonymized, we hesitate to do so for biogeographic reasons. *Staurodiscus milleri* is only known from the Bismarck Sea, thus both nominal species have a very disjunct distribution.

***Staurodiscus tetrastaurus* Haeckel, 1879**

Figs 32A-D

Staurodiscus tetrastaurus Haeckel, 1879: 145, pl. 9 figs 1-3. – Mayer, 1910: 214, pl. 22 figs 7-8, pl. 25 fig. 5, pl. 26 figs 10-11. – Uchida, 1927b: 167. – Menon, 1932: 14, pl. 2 figs 14, 19. – Nair, 1951: 60. – Kramp, 1959a: 140, fig. 165. – Kramp, 1961: 148. – Kramp, 1962: 321. – Kramp, 1968: 70, fig. 182. – Migotto & Andrade, 2000: table 6.

Staurodiscus heterosceles Haeckel, 1879: 146. **syn. nov.**

Examined material: BFLA3831; 1 specimen; 15-NOV-2018; size 7 mm; preserved in ethanol for DNA extraction; 16S sequence MW528662. – BFLA4406; 1 specimen; 26-MAY-2020; size 8 mm; preserved in ethanol for DNA extraction; 16S sequence MW528722. – BFLA4433; 1 specimen; 30-MAY-2020; size 5 mm; preserved in ethanol for DNA extraction; 16S sequence identical MW528722. – BFLA4440; 1 specimen; 07-MAY-2020; size 10 mm; preserved in ethanol for DNA extraction; 16S sequence identical to MW528662. – BFLA4444; 1 specimen; 07-MAY-2020; size 15 mm; part preserved in formalin and deposited as UF-014059, small part preserved in ethanol for DNA extraction; 16S sequence identical to MW528662. – 11-DEC-2017; 1 specimen photographed; juvenile, gonads not yet developed, not collected.

Observations: Bell hemispherical, 8 to 15 mm when mature, apical jelly about 1/3 of total height. Manubrium composed of central, cylindrical part and four basal, perradial extensions each with two lateral outgrowths in about middle of bell. Central part of manubrium tubular, with cruciform mouth opening drawn into four lips, margin slightly undulated. Basal, perradial extensions of stomach reaching almost to circular canal and thus length of radial canals to circular canal is short (1/4); stomach outgrowths relatively thick, giving off lateral diverticula in about the middle, these paired outgrowths opposite or not, oblique to radial axis or slightly curved, towards ends somewhat irregularly folded or undulating, not connecting to circular canal. Gonads in walls of stomach outgrowths. Mature animals with 23-30 tentacles and 1-3 cordyli between each pair of tentacles. Young animal with four perradial tentacles only and 7-9 cordyli per quadrant (Fig. 32A). Tentacles with conical bulbs. Small, inconspicuous ocelli present on adaxial side of tentacles bulbs and attachment sites of cordyli (Fig. 32F). Animal colourless or with greenish tint. Amphipods appear often to associate with the medusa (Fig. 32).

16S Data: The five obtained 16S sequences represented 2 haplotypes differing only one position (an insertion/deletion). In the maximum likelihood tree (Fig. 28) they are well separated from the other *Staurodiscus* species and also *Melicertissa* of this study. It is part of a well supported clade comprising the *Staurodiscus* species of this study and some Hebellidae.

Distribution: Canary Islands, Florida, Caribbean Sea, coast of Mozambique, coasts of India, Singapore, Taiwan Strait, Bismarck Sea (Kramp, 1959a, 1968; Bouillon 1978a, 1984b; Navas-Pereira & Vannuci, 1991; Zhang, 1999; Segura-Puertas *et al.*, 2003). Type locality: Atlantic Ocean, Canary Islands, near Lanzarote.

Remarks: Haeckel (1879) introduced two nominal *Staurodiscus* species, *S. tetrastaurus* and *S. heterosceles*, both collected at the same time and near Lanzarote Island. The former had 8-16 tentacles, 48 cordyli, and a bell diameter of 4-6 mm, the latter 8-32 tentacles, 40-80 cordyli, and a bell diameter of 6-8 mm [note that the figures in Kramp (1959a, 1968) depict a juvenile *S. tetrastaurus* with four tentacles, compare Fig. 32A]. Additionally, Haeckel distinguished both nominal species based on the branching pattern of the radial canals (= actually basal extensions of the manubrium, comp. Fig. 32A, E, G): *S. tetrastaurus* has opposite pairs, while they were not opposite in *S. heterosceles.* Haeckel (1879) also observed intermediate forms and explicitly expressed doubts that they are "*bona species*", but nevertheless named both forms [Haeckel used an artificial, typological species concept and did not distinguish biological species, comp. comments in Haeckel, 1879: XXV, 109]. Kramp (1962, 1968) too thought that both names refer likely to the same species.

One of our specimen (BFLA3831) was also intermediate as it had the size and tentacle numbers of *S. heterosceles,* but the outgrowths of the stomach had opposite side-branches (Fig. 32E). Others (Fig. 32G) had a variable branching pattern. The observed juvenile specimen (Fig. 32A) had three opposite and one alternate pairs of side-branches. It is thus quite clear that *S. tetrastaurus* and *S. heterosceles* must be regarded as conspecific, *S. tetrastaurus* being the valid name. Medusae identified as *Staurodiscus heterosceles* have – to our knowledge – not been recorded anymore since Haeckel's time.

Andrade & Migotto (1997) reared the initial stages of medusae released from a hydroid referable to *Hebella scandens* (Bale, 1888) and found that they resembled our *S. tetrastaurus.* Our 16S phylogeny (Fig. 28) also suggests a more close relationship to Hebellidae than to Laodiceidae. *Staurodiscus tetrastaurus* is the type species of the genus, thus decisive to which family the genus belongs.

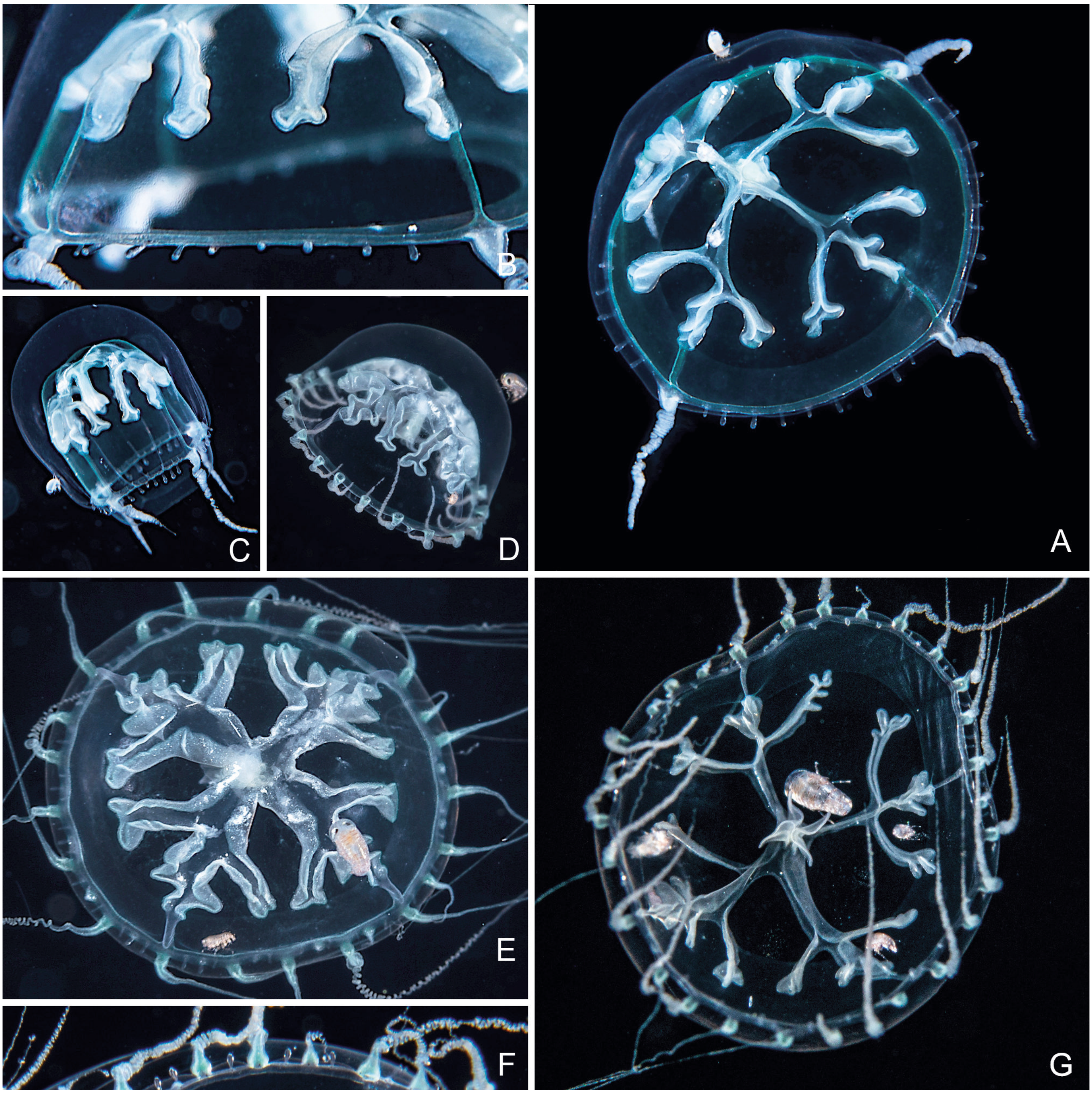

Fig. 32. *Staurodiscus tetrastaurus*. (A-C) Young animal observed 11-DEC-2017. (D-E) BFLA3831, size 7 mm. Some amphipods are associated with the animal. (F) BFLA4440, size 10 mm, bell margin seen from adaxial side, ocelli are barely visible. (G) BFLA4440, oral view, note variation of position of lateral diverticula.

***Staurodiscus luteus* n. spec.**

Fig. 33A-H

Holotype: BFLA4284; 1 specimen; collected off Palm Beach, Florida, 06-DEC-2019; size 6 mm, ~32 tentacles; bell fragments preserved in formalin and deposited as UF-013842, fragment in alcohol used for DNA extraction (MHNG-INVE-0137382); 16S sequence MW528698.

Other examined material: BFLA3819; 1 specimen; 24-OCT-2018; size ~2.5 mm, ~36 tentacles; preserved in ethanol for DNA extraction; 16S sequence identical to MW528698. – BFLA4458; 1 specimen, no photos taken; 11-JUN-2020; size ~8 mm; preserved in ethanol for DNA extraction; 16S sequence identical to MW528698. – 06-MAY-2017; 1 specimen photographed; 8 mm; not collected. – 26-JUL-2018; 1 specimen photographed; size ~5 mm ~38 tentacles; not collected. – 11-APR-2019; 1 specimen photographed; damaged, 8 mm, ~24 tentacles; not collected. – 27-MAY-2019; 1 specimen photographed; juvenile, ~2 mm, ~9 tentacles; not collected. – 27-MAY-2019; 1 specimen photographed; juvenile, 2.5 mm, ~6 tentacles; not collected. – 17-MAY-2020; 1 specimen photographed; ~4 mm, ~24 tentacles; not collected. – 13-JUN-2020; 1 specimen photographed; 5 mm, ~17 tentacles; not collected.

Type locality: Atlantic Ocean, USA, Florida, approximately 6.5 km east of Palm Beach, WGS84 rectangle between 26.70, -79.94 and 26.78, -79.94, occurrence depth 8-10 m.

Diagnosis: Similar to the sympatric *Staurodiscus kellneri*, but smaller (<10 mm), with intensively yellow colour of stomach and its radiating extensions, and marginal bulbs; more radial canals (up to 30 and more) due to more branching, stomach extensions narrower, radial canals broader.

Description: *Staurodiscus* medusa with bell somewhat flatter than hemisphere, largest diameter observed 8 mm, apical jelly thick, about half the umbrella height (Fig. 33D). Conspicuous, opaque, intensively golden-yellow colour of stomach, radial canals and marginal bulbs, colour fading in peripheral regions of radial canals; colour is partially preserved in alcohol. Stomach wide, up to half the diameter of the subumbrellar diameter, shallow, base irregularly star-shaped, turning into basal stomach extensions which taper radially and branch irregularly 0 to 3 times and changing gradually into 30 to 40 radial canals which all reach the circular canal, radial canals very short. Gonad tissue (gametes) could not be seen in the preserved material, thus animals likely not reproductive. About 24 to 38 tentacles, long, contracted tightly coiled, their bulbs ovoid, clearly separated from rest of tentacles. Marginal bulbs positioned independently of radial canals. Usually only one cordylus between pairs of tentacles, also in younger individuals, sometimes cordylus on a marginal bulb without tentacle. Small, brown ocellus on base of adaxial side of bulb or on radial canal at attachment sites of cordylus. On aboral side of manubrium the cross-like marks of an original state with only four radial canals can be seen (Fig. 33E). Branching of the radial stomach extensions must occur early in development. Amphipods appear occasionally to associate with the medusa.

Etymology: The Latin adjective *luteus* means yellow and refers to the striking yellow colour of this medusa.

16S Data: The three 16S sequences obtained in this study were all identical. *Staurodiscus kellneri* haplotypes have about 9% base pair differences to the one of *S. luteus*. The two species are clearly separated in the maximum likelihood tree (Fig. 28).

Distribution: Known from type locality only.

Remarks: The opaque, yellow or golden-yellow colour renders *S. luteus* rather conspicuous (Fig. 33), although it resembles otherwise *S. kellneri* and *S. milleri* (Bouillon, 1984b). The latter has about the same size and is thus even more similar. The radial canals are more branched in *S. luteus*, resulting in 30 to 40 canals, while *S. milleri* has up to 18. Bouillon (1984b) usually also observed living animals for his studies in the Hansa Bay and he would certainly have noted any conspicuous colour as it is present in *S. luteus*. We therefore assume that *S. milleri* was not pigmented.

It is though possible that formalin preserved material – which loses colours after some time – has previously been mis-identified as *S. kellneri* in the western Atlantic. Both species can be separated based on their size, branching patterns of the radial canals, and proportions. The identification is more secure if 16S data are used.

Family Orchistomatidae Bouillon, 1984

Genus *Orchistoma* Haeckel, 1879

Orchistoma Haeckel, 1879: 138; type species *Mesonema pileus* Lesson, 1843 (Kramp, 1961).

Tetracannota Mayer, 1900: 46; type species *Tetracannota collapsum* Mayer, 1900 by monotypy.

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.

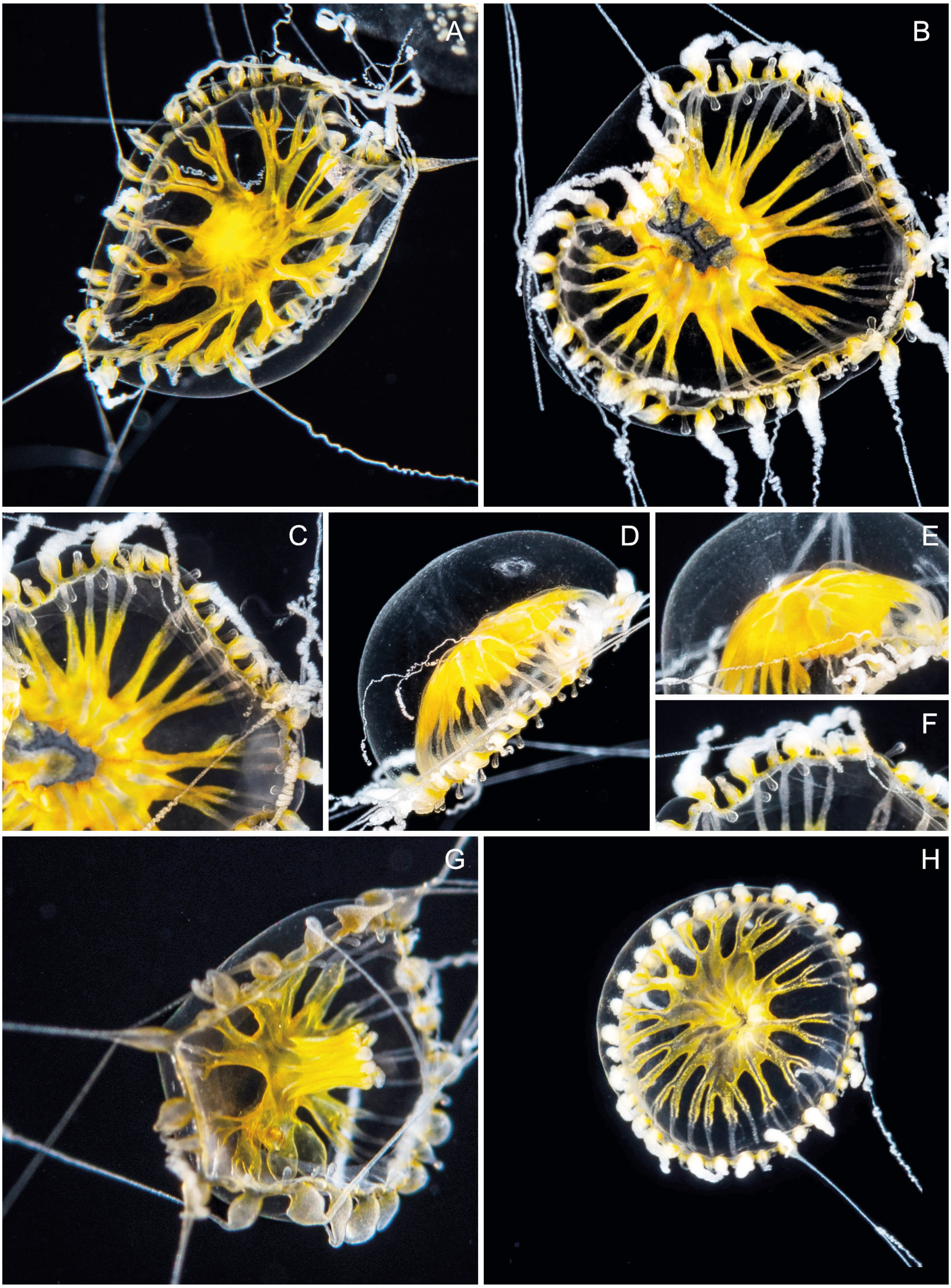

Fig. 33. *Staurodiscus luteus* n. spec. (A) Holotype, BFLA4284, 6 mm diameter, oblique view on oral side. (B-F) BFLA3819, size 2-3 mm. (B) Oral view. (C) Oral view. (D) Lateral view. (E) Oblique view on aboral part, note cross-shaped mark of original radial canals. (F) Bell margin from oral side, cordyli and ocelli are visible. (G) Juvenile, 4 mm, oral view, photographed 17-MAY-2020. (H) Photo taken 26-JUL-2018, aboral view.

Orchistoma pileus (Lesson, 1843)

Figs 34A-F & 35A-G

Mesonema pileus Lesson, 1843: 317, pl. 6 fig. 1.

Orchistoma pileus. – Haeckel, 1879: 139. – Kramp, 1959a: 139, fig. 163. – Kramp, 1961: 144. – Segura-Puertas *et al.*, 2009: 376. – Bouillon, 1984b: 90. – Gershwin *et al.*, 2010: table 7.

Orchistoma steenstrupii Haeckel, 1879: 139, pl. 15 figs 3-5. – Mayer, 1910: 211, pl. 25 figs 1-4. – Kramp, 1955a: 157, re-examination of type specimens, synonym.

Orchistoma agariciforme Keller, 1884: 418, pl. 21 figs 1-3. **n. syn.**

Orchistoma agariciforme. – Kramp, 1959a: 140. – Kramp, 1961: 144. – Bouillon, 1984b: 88, figs 29-30, redescription. – Bouillon *et al.*, 2004: 170, fig. 91E. – Gershwin *et al.*, 2010: table 7.

Tetracannota collapsum Mayer, 1900: 46, pls 7-8 figs 14-16. **n. syn.**

Dipleurosoma collapsum. – Mayer, 1910: 226, pl. 27 figs 1-3 & 7. – Kramp, 1961: 134. – Goy, 1979: 274, fig. 11. – Kramp, 1959a: 132, fig. 147.

Dipleurosoma collapsa. – Vanhöffen, 1913a: 420.

Orchistoma collapsum. – Bouillon, 1984b: 90, genus transfer. – Pagès *et al.*, 2006: 373, fig. 7A-C. – Gershwin *et al.*, 2010: table 7.

Examined material: BFLA3785; 1 specimen; 20-SEP-2018; size 12 mm; preserved in ethanol for DNA extraction; 16S sequence MW528651. – BFLA3810; 1 specimen; 20-OCT-2018; size 18 mm; preserved in ethanol for DNA extraction; 16S sequence MW528652. – BFLA3813; 1 specimen; 20-OCT-2018; size 20 mm; preserved in ethanol for DNA extraction; 16S sequence MW528653. – BFLA3816; 1 specimen; 20-OCT-2018; size 10 mm; preserved in ethanol for DNA extraction; 16S sequence MW528654. – BFLA4132; 1 specimen; 11-JUN-2019; size 34 mm; preserved in ethanol for DNA extraction; 16S sequence MW528680. – BFLA4183; 1 specimen; 12-AUG-2019; size 26 mm; preserved in formalin and deposited as UF-013823, no alcohol sample. – BFLA4383; 1 specimen; 09-MAY-2020; size 15 mm; part preserved in formalin and deposited as UF-014033, small part preserved in ethanol for DNA extraction; 16S sequence MW528716. – BFLA4387; 1 specimen; 09-MAY-2020; size 18 mm; part preserved in formalin and deposited as UF-014035, part preserved in ethanol for DNA extraction; 16S sequence MW528717. – 9 specimens, photographed but not collected; dates 10-APR-2019, 26-MAY-2020, 05-MAY-2017, 17-OCT-2017, 28-JUN-2018, 26-MAR-2019, 07-MAY-2019, 20-MAY-2019, 17-MAY-2020; sizes 15-30 mm.

Observations: Medusa bell diameter 10 to 34 mm when mature, almost hemispherical or somewhat shallower (Fig. 34A, D), evenly rounded exumbrella, mesoglea thick, jelly at apex about 2/5 of total height; with thick, tapering gastric peduncle that protrudes through velar opening. Velum broad. Stomach complex, base in centre H- or cross-shaped (Fig. 35A, D), then subdividing dichotomously or irregularly into elongate diverticula attached to the distal part of the gastric peduncle, walls of diverticula contain gonads and are continued on gastric peduncle as radial canals (Fig. 35A-D). Stomach wall follows the branching of the diverticula, mouth opening with complexly folded rim, mouth rim corners at position of diverticula drawn out into lips of variable length, 10 to 16 lips more elongated, sometimes also absent due to apparent damage and subsequent healing (Fig. 35F). Usually several radial canal in formation (Fig. 35E) and not reaching circular canal. Circular canal broad. Along circular canal on adaxial side numerous dark ocelli, not correlated with tentacle positions. 16 to 29 tentacles, extensible but also able to contract to short length (Fig. 34F), tentacles not in phase with the radial canals, with distinct, ovoid tentacular bulbs that taper rapidly into tentacles, bulbs divided bilaterally by a more transparent tissue in median line (Fig. 34C). Between each pair of tentacles 4 to 12, usually around 5 to 6, short thin tentacles (Fig. 34C), these secondary tentacles arise from circular canal, proximal half adnate to or embedded in umbrella, free part with nematocysts, contractile. Colours: stomach and diverticula with gonads can be brown-yellow in some specimens (Fig. 35B, E, F), otherwise whitish or with a yellow hue (Fig. 35D, G).

16S Data: The seven haplotypes found showed high divergence rates (Table 1). The sequences form a monophyletic group in the maximum likelihood tree (Fig. 28) but fell into two well separated subclades with relatively high divergence (up to 8.1%, Table 1), while the differences within the subclades are low.

Distribution: Western Atlantic from Maine (Pagès *et al.*, 2006) to Brazil (Goy, 1979), but mainly Bahamas, Florida and Caribbean (Haeckel, 1879; Vanhöffen, 1913a; Mayer, 1910; Kramp, 1959a), Gulf of Mexico (Segura-Puertas *et al.*, 2009), also Mediterranean (Bouillon, 1984b) and coast of Western Africa. Type locality: West Africa (Haeckel, 1879).

Remarks: Although the 16S data showed that our material separates in two lineages that might qualify as two distinct species (Table 1, Fig. 28), we referred all our samples to *Orchistoma pileus*.

Orchistoma pileus was first described by Lesson (1843), presumably based on a specimen from western Africa (as “mers d’Afrique ?”). Lesson’s drawing was rather simple, but the species is recognizable. He did not show the small tentacles and there are about 30 normal tentacles or their bulbs depicted. Haeckel (1879) restricted the type locality to Western Africa and described concomitantly *O. steenstrupi* based on material from Cuba. The type material of *O. steenstrupi* was later re-examined by Kramp (1955a) and referred to *O. pileus* as it matched Mayer’s (1910) description of this species. Mayer (1910) had material from the Bahamas and Tortugas. Kramp

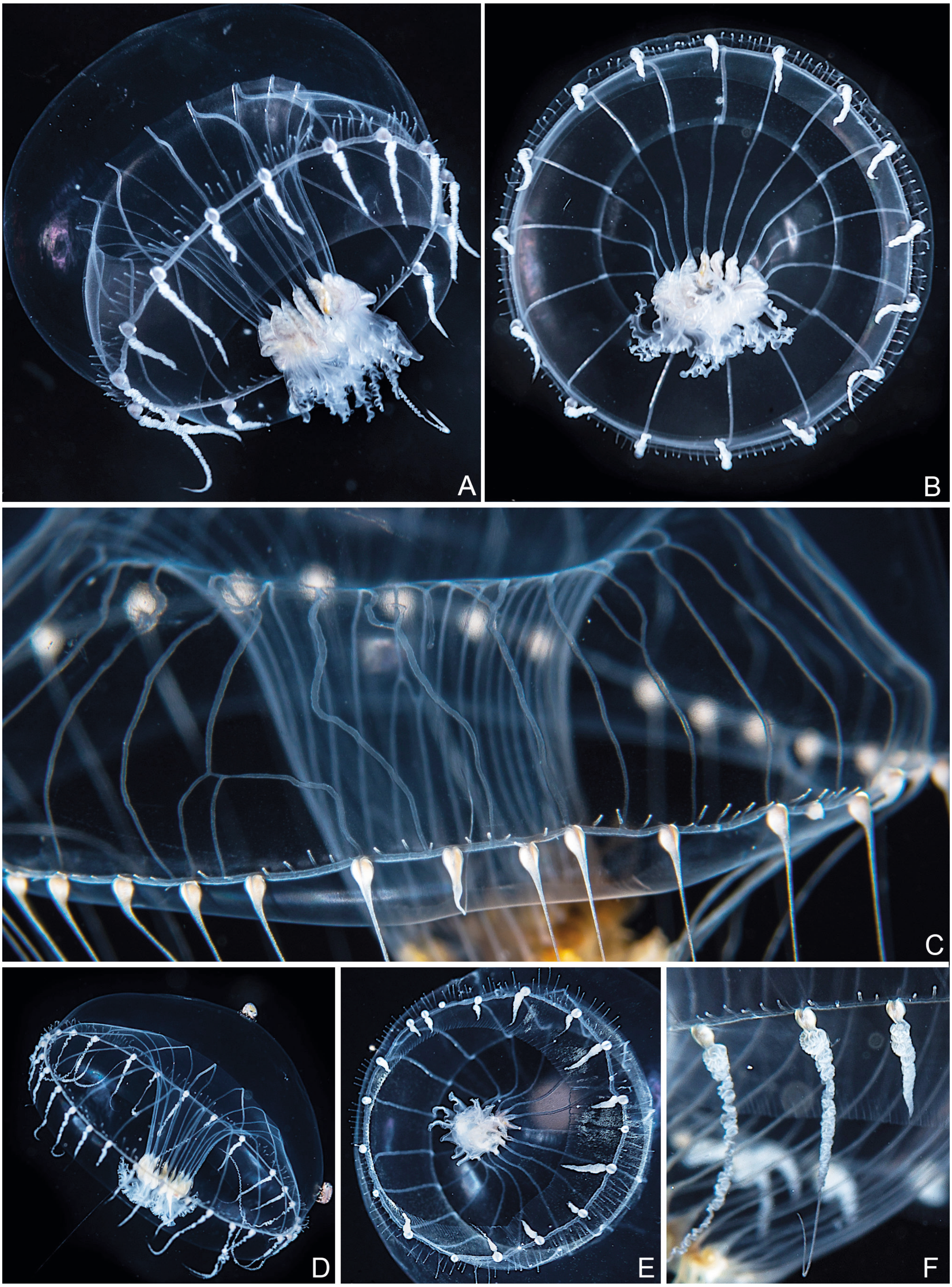

Fig. 34. *Orchistoma pileus*. (A-B) BFLA3785, bell diameter 12 mm, female. (C) BFLA4183, bell diameter 26 mm, bell margin of a mature animal, note irregular radial canals, likely due to healed damage. (D) BFLA3810, bell diameter 18 mm, male. (E) BFLA3813, bell diameter 20 mm. (F) BFLA4132, note curling of long tentacles.

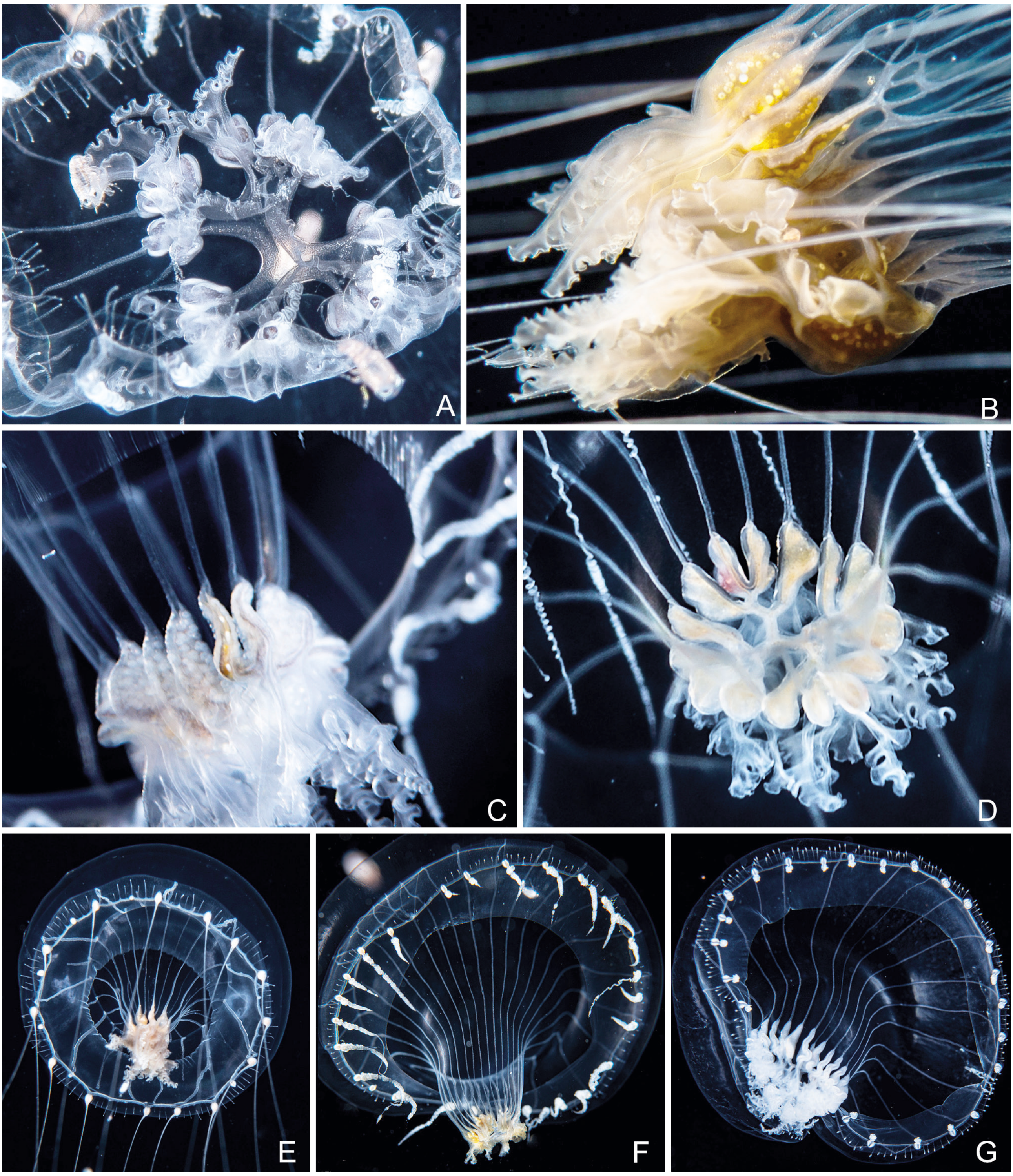

Fig. 35. *Orchistoma pileus*. (A-D) Stomach details. (A) Young animal without gonads, *O. collapsum* stage, oral view, photo 10-APR-2019. (B) BFLA4183, mature female, bell diameter 26 mm, reticulate radial canals are likely due to a healed damage. (C) BFLA3785, bell size 12 mm, subadult female. (D) BFLA3810, bell diameter 18 mm, male, view from aboral side, note branching of radial canals (stomach diverticula), originating from a H-shaped figure, compare to A. (E) BFLA4383, size 15 mm. (F) BFLA4132, size 34 mm, manubrium likely damaged and in process of regeneration. (G) BFLA4387, size 18 mm.

gives the tentacle number as 64, which must be meant as a maximal number because the type specimen of Lesson had only 30.

Tetracannota collapsum was described by Mayer (1900) using medusae from the Tortugas and Bahamas. Despite the strong resemblance to *Orchistoma,* he placed it in a separate genus because it had visibly branched radial canals. His animals were mature but had only 16 tentacles at a size of 7 mm and only 8 manubrial lips. Mayer's branched radial canals are actually the same structure as here described for the stomach diverticula, only that the radial canals showed a grouping into four sets close to the manubrium, but more distally they are evenly distributed (comp. Fig. 35A). Later, Vanhöffen (1913a) found Mayer's species in the West Indies and noted that it is more variable than given in Mayer. Vanhöffen found them to have 16 manubrial lips beginning at a size of 3 mm.

Another nominal species resembling *O. pileus* was described by Keller (1884) as *Orchistoma agariciforme.* He had a single mature medusa from the Mediterranean with only 7 manubrial lips, but which was otherwise similar to *O. pileus*. Bouillon (1984b) described more specimens of *O. agariciforme* from the Mediterranean and considerably widened its morphological scope, notably he observed that the number of the manubrial lips was usually 16. Bouillon concludes that *O. agariciforme* is very close to both *O. pileus* and *O. collapsum.* He gives as distinguishing traits that in *O. collapsum* the radial canals remain in four groups near the manubrium even in adults and it has shorter manubrial lips. *Orchistoma pileus* differs by attaining a larger size of up to 30 to 40 mm, with up to 32 manubrial lips and radial canals as well as up to 64 marginal tentacles.

Gershwin *et al.* (2010) favoured splitting and retention of all these nominal species, even of *O. steenstrupi*, but used outdated values for *O. agariciforme* in their table.

The material we examined in this study was very variable and referable to either *O. pileus* and *O. agariciforme* and we think these names should be synonymized, including also *O. steenstrupi* and *O. collapsum*.

While we had no specimen that exactly matched *O. collapsum* as described by Mayer (1900, 1910), BFLA4383 (Fig. 35E) comes close to it in terms of tentacle and lip numbers. We nevertheless think that this nominal species was based on growth stages of *O. pileus*. Gonads mature in *O. pileus* at a size of less than 12 mm bell size (Fig. 34A) and the medusa continues its growth and the multiplication of radial canals and tentacles. Manubrial lips numbers and sizes are variable, usually there are about 16 somewhat longer lips. The lips can be damaged and regenerated and their number is not a reliable diagnostic feature (Fig. 35F). In general *O. pileus* appears as a rather variable species, mostly due to a long growth and different developmental stages.

This synonymy appears to be to some degree in conflict with the DNA data obtained in this study because the 16S sequences separate into two distinct lineages, although they are sister lineages (Fig. 28). We could not find convincing morphological traits that would allow to identify the lineages, except that in one the manubrium and gonads are brownish-yellow while in the other they are whitish (compare Fig. 35E & 35F versus 35G). BFLA4383 (Fig. 35E) was also in this "yellow" clade and was mentioned above as being close to the morphotype of *O. collapsum*. However, the other sample from this "yellow" clade (BFLA4132, Fig. 35F) is referable to *O. pileus*.

At this stage we cannot resolve the problem of the two lineages. The difference in colour could also be a random result due to low sample numbers. If it can be confirmed by a more detailed genetic analysis of more samples that indeed two species are involved, the two lineages are likely not separable so that they correspond to the nominal species synonymized here.

The high genetic subdivision is reminiscent to the one observed above for *Zancleopsis dichotoma* and *Laodicea undulata*.

Wuvulidae new family

Diagnosis: Medusa with more than four radial canals, sometimes partially ramified; tentacle bulbs and atentaculate bulbs with lateral sac-like appendages; large adaxial excretory papillae on marginal tentacular bulbs. Gonads on radial canals. No ocelli, no statocysts. Hydroid unknown.

Remarks: Bouillon *et al.* (1988b) when introducing the genus *Wuvula* included it in the family Laodiceidae based on the assertion that the appendages of the marginal bulbs resemble cordyli. Pendant cordyli (*e.g.* Fig. 29C) are typical for the Laodiceidae, but they also occur in the Hebellidae. They occur mostly on the bell margin, but may also be placed on marginal bulbs. The hollow appendages in *Wuvula* (Fig. 36F) are clearly not cordyli and also their paired position on the side of bulbs is not known for cordyli in the Laodiceidae. The genus must thus be removed from the Laodiceidae. *Wuvula* lacks ocelli, statocysts, and cordyli and could be related to the Melicertidae Agassiz, 1862 which also lack them. The absence of statocysts and cordyli is, however, likely a plesiomorphy and not suitable for postulating a relationship. Moreover, the 16S data of *W. ochracea* did not indicate relationship to any group (results not shown, but see below).

We therefore propose that the genus is accommodated in a new family Wuvulidae. Its diagnosis is given above and taken from the genus diagnosis.

Genus *Wuvula* Bouillon, Seghers & Boero, 1988

Wuvula Bouillon, Seghers & Boero, 1988b: 247; type species *Dipleurosoma ochraceum* Mayer, 1910 (see below).

Diagnosis: With the characteristics of the family.

Remarks: Bouillon *et al.* (1988b) did not select a type species for this genus. *Dipleurosoma ochraceum* Mayer, 1910 is therefore here designated as type species of the genus.

Wuvula ochracea (Mayer, 1910)

Fig. 36A-I

Dipleurosoma ochraceum Mayer, 1910: 226, pl. 29 figs 1-2. – in part Vanhöffen, 1913a: 421, not fig. A. – Kramp, 1959a: 132, fig. 146. – Kramp, 1961: 134.

Wuvula ochracea. – Bouillon, Seghers & Boero, 1988b: 248, new combination.

Examined material: BFLA4361; 1 specimen; 13-MAR-2020; size 3.5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528713. – BFLA4372 and BFLA4373; 16-MAR-2020; 1 specimen that split into 4 individuals of 3 mm, and some fragments; preserved in formalin and deposited as UF-014027 and UF-014028, fragments in alcohol for DNA extraction; 16S sequence identical MW528713. – BFLA4392; 1 specimen; 17-MAY-2020; size 4 mm; preserved in alcohol for DNA extraction; 16S sequence identical MW528713. – BFLA4470; 1 specimen; 17-JUN-2020; size 3.5 mm; preserved in alcohol for DNA extraction; 16S sequence identical MW528713. – 1 specimen photographed 04-JUN-2019, not collected; size 2.5 mm. – 1 specimen photographed 16-MAR-2020, not collected; size 4 mm.

Observations: Medusa 2.5 to 4 mm in diameter, bell flatter than hemisphere when relaxed, jelly relatively thin, velum very broad. Manubrium rather small, star-shaped in cross-section, mouth with about 6 corners drawn out into lips, mouth rim with no or only few folds. Six radial canals reaching circular canal, in addition up to 5 incomplete, thin radial canals originating from manubrium which do not reach circular canal. Complete radial canals with swelling at about 1/3 distance from manubrium, presumably the place where gonads will develop. Up to 14 relatively short and thin tentacles, all with a small, whitish marginal bulb; additionally up to 55 small, rudimentary bulbs without tentacles. All marginal bulbs with a laterally attached pair of large, club-shaped diverticula and a third sac-diverticulum above the bulb, the latter being a big excretory papilla, all these diverticula with intense yellow colour. Stomach and radial canals also yellow, but less intense than diverticula.

16S data: The partial 16S gene sequence obtained was used to search for similar sequences in GenBank using the blastn function. The results were mostly thecate hydroids, but only with a maximal identity of 83%.

Distribution: Florida. Type locality: USA, Florida, Dry Tortugas archipelago.

Remarks: The observed medusae were smaller (2.5-4 mm) than given in Mayer (1910, 8 mm), but Vanhöffen reported also animals of this size and two of our specimens were actually the result of a fragmentation and regeneration. Mayer (1910) had seen only immature animals. One of ours had bulges on the radial canals that we interpreted as the beginning of the gonad formation (Fig. 36A-D).

The small size and vigorous swimming style made it difficult to get good photographs in the sea and the resulting images are unfortunately not so suitable for seeing more details of the bell margin in the living animals. However, the unique, yellow, lateral appendages of the marginal bulbs are unmistakable and the species is unambiguously identifiable. According to Mayer (1910) the appendages contain symbiotic algae (zooxanthellae). Although Mayer (1910) observed large swarms of this medusa, it is a very rare species. To our knowledge, it was only recorded after its first description by Vanhöffen (1913a), this from near the type locality.

Neither searches in GenBank nor sequence comparisons with a number of Leptothecata gave any hint for relationships with other families (results not shown).

Family Aequoreidae Eschscholtz, 1829

Genus *Aequorea* Péron & Lesueur, 1810

Aequorea Péron & Lesueur, 1810: 334; type species *Aequorea forskalea* Péron & Lesueur, 1810 by subsequent designation by Mayer (1910).

Mesonema Eschscholtz, 1829: 112.

Stomobrachiota Brandt, 1835: 220; type species *Stomobrachiota lenticularis* Brandt, 1835 by monotypy.

Stomobrachium Brandt, 1837: 189.

Mesonema (*Zygodactyla*) Brandt, 1838: 360; type species *Mesonema* (*Zygodactyla*) *coerulescens* Brandt, 1838 by monotypy.

Crematostoma A. Agassiz, 1862: 360.

Rhegmatodes A. Agassiz, 1862: 361.

Aequorea (*Aequoranna*) Haeckel, 1879: 219; type species *Aequorea discus* Haeckel, 1879 by monotypy.

Aequorea (*Aequorella*) Haeckel, 1879: 219.

Aequorea (*Aequoroma*) Haeckel, 1879: 220.

Aequorea (*Aequorissa*) Haeckel, 1879: 221; type species *Aequorea albida* Agassiz, 1862 by monotypy.

Rhegmatodes (*Regmatella*) Haeckel, 1879: 222.

Rhegmatodes (*Regmatissa*) Haeckel, 1879: 223.

Staurobrachium Haeckel, 1879: 224: type species *Aequorea stauroglypha* Péron & Lesueur, 1810 by monotypy.

Mesonema (*Mesonemanna*) Haeckel, 1879: 226.

Mesonema (*Mesonemella*) Haeckel, 1879: 226.

Mesonema (*Mesonemissa*) Haeckel, 1879: 226.

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.

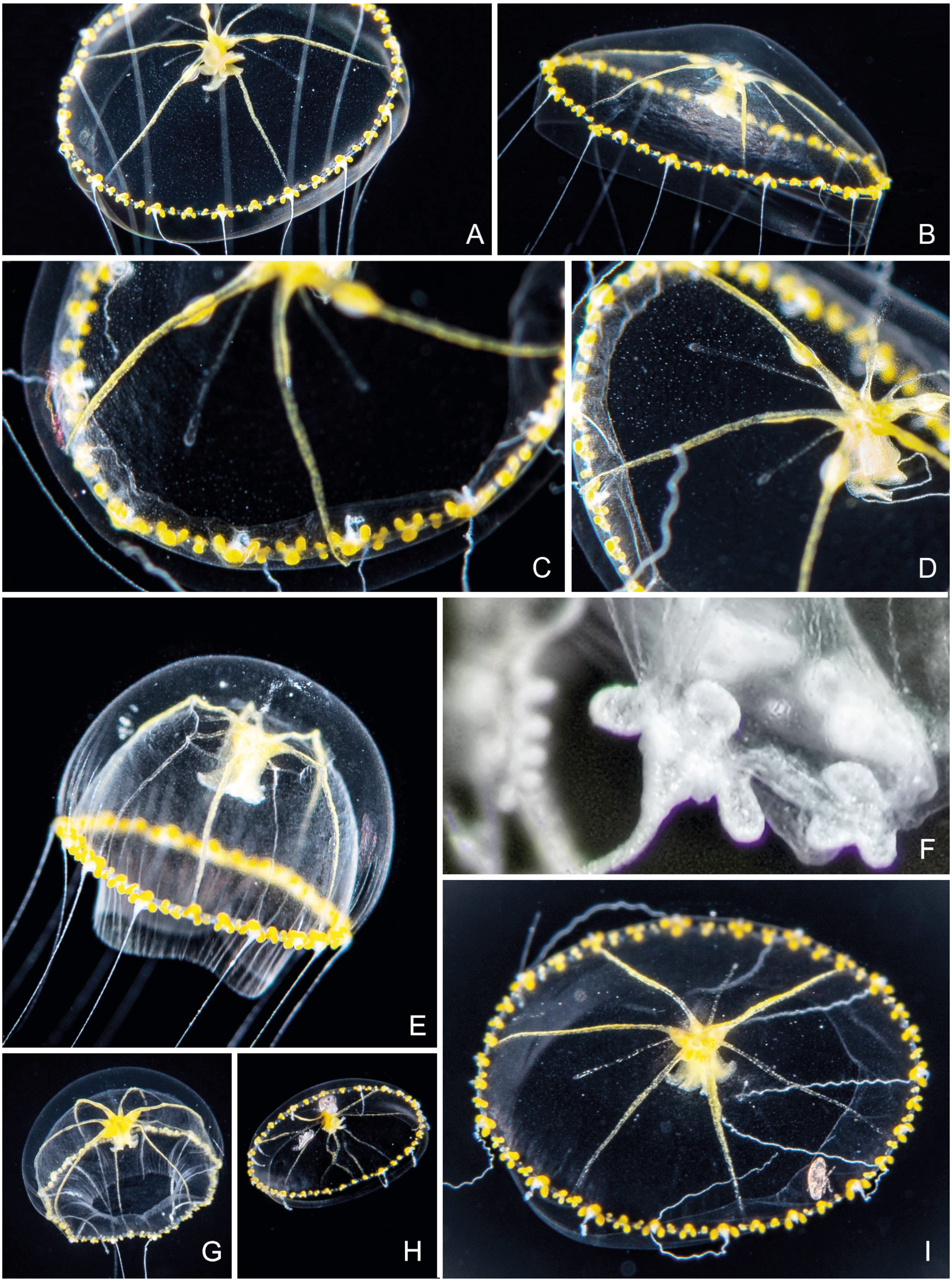

Fig. 36. *Wuvula ochracea*. (A-D) Animal observed 04-JUN-2019, ca. 2.5 mm, different views of the same animal, note beginning gonad development on radial canals. (E) BFLA4392, size 4 mm. (F) BFLA4372, preserved sample, view from adaxial side on a bulb with its appendages. (G) BFLA4470, size 3.5 mm. (H) BFLA4361, size 3.5 mm. (I) Animal observed 16-MAR-2020, not collected, size 4 mm.

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 (see Bouillon *et al*., 2006).

Remarks: *Aequorea* is a difficult genus as can be suspected from the complex synonymy given above. A comprehensive revision of its species is needed (Purcell, 2018). Kramp (1961) plainly expressed "The species are more or less doubtful." Russell (1953) had similar thoughts. However, both experts contributed much in consolidating and establishing a workable species level taxonomy which is still in use today.

Dawson (2004) and Zheng *et al.* (2009, 2014) have begun to study species level systematics using DNA sequences, but we are still missing sequence data for many populations and species and their correlation with morphotypes.

Here, we separated the species first using their 16S data and then searched for suitable names that matched their morphology. A few photographs of fully grown medusae that were not sampled could afterwards also be attributed to nominal species. It seems, however, that the sequence data are not really congruent with described nominal species. While the species level diversity is higher than expected, it is also surprising that some have a much wider distribution than thought before [see also Pruski & Miglietta (2019) for *A. australis* and its occurrence in the Gulf of Mexico].

Some additional species were examined for this study to allow a better comparison and species delimitation. This material is listed above in the section Material and Methods.

Aequorea neocyanea new name

Fig. 38A-I

Zygodactyla cyanea L. Agassiz, 1862: 361. [not *Aequorea cyanea* de Blainville, 1834]

Zygodactyla cyanea. – Agassiz, 1865: 107, fig. 159. – Haeckel, 1879: 227. – Mayer, 1900: 60, pl. 11 fig. 23 & 23a, pl. 15 figs 33-34. – Mayer, 1904: 17, pl. 3 figs 16-17.

in part *Aequorea forskalea*. – Mayer, 1910: 325, *Z. cyanea*as synonym.

? *Mesonema coelum-pensile*. – Vanhöffen, 1913a: 425, fig. C.

? *Aequorea macrodactyla*. – Nogueira *et al*., 2016: fig. 1. [not *Aequorea macrodactyla* (Brandt, 1835)]

Material examined: BFLA3783; 1 specimen; 18-SEP-2018; size 50 mm, with gonads; part preserved in formalin and deposited as UF-013449, part in alcohol for DNA extraction; 16S sequence MW528633 – BFLA3822; 1 specimen; 25-OCT-2018; size 40 mm, with gonads; part preserved in formalin and deposited as UF-013427, part in alcohol for DNA extraction; 16S sequence MW528634. – BFLA3827; 1 specimen; 14-NOV-2018; size 50 mm, with gonads; part preserved in formalin and deposited as UF-013435, part in alcohol for DNA extraction; 16S sequence MW528635. – BFLA4043; 1 specimen; 01-APR-2019; size 50 mm, with gonads; part preserved in formalin and deposited as UF-013436, part in alcohol for DNA extraction; 16S sequence MW528636. – BFLA4082; 1 specimen; 07-MAY-2019; size 55 mm, with gonads; part preserved in formalin and deposited as UF-013787, part in alcohol for DNA extraction; 16S sequence MW528669. – BFLA4083; 1 specimen; 07-MAY-2019; size 42 mm, with gonads; part preserved in formalin and deposited as UF-013788, part in alcohol for DNA extraction; 16S sequence MW528670. – BFLA4085; 1 specimen; 07-MAY-2019; size 60 mm, with gonads; part preserved in formalin and deposited as UF-013789, part in alcohol for DNA extraction; 16S sequence MW528671. – BFLA4236; 1 specimen; 21-OCT-2019; size 30 mm, with gonads; part preserved in formalin and deposited as UF-013844, part in alcohol for DNA extraction; 16S sequence MW528689. – BFLA4304; 1 specimen; 15-JAN-2020; size 90 mm, with gonads; part preserved in formalin and deposited as UF-013881, no tissue sample. – 1 specimen photographed 08-FEB-2017, not collected; size 100 mm, with developed gonads. – 1 specimen photographed 06-JUN-2020, not collected; size 70 mm, with developed gonads.

The formalin samples are mostly strongly fragmented and damaged.

Taxonomy: In order to avoid a secondary homonymy with *Aequorea cyanea* de Blainville, 1834, we propose here the replacement name *Aequorea neocyanea* for *Zygodactyla cyanea* L. Agassiz, 1862. *Zygonema* Brandt, 1838 is a synonym of *Aequorea* Péron & Lesueur, 1810 (Ranson, 1949) and Agassiz' *Z. cyanea* must be transferred to *Aequorea*.

Observations: Typical *Aequorea* medusae, diameters of animals with well developed gonads 50 to 100 mm, sizes of animals without gonads (juveniles) up to 30-40 mm. Umbrella in fully grown animals relatively flat (Fig. 38A), about 1/4 of diameter, in younger ones more spherical. Stomach large, diameter 1/2 of bell diameter, with shallow jelly cone inside. Mouth rim with short fimbriae only (Fig. 38G), same number as radial canals, continued centrifugally as fine rib or streak on stomach and then as radial canal. Radial canals in mature animals 25 to 100, more commonly 60 to 80, lower number might also be due to regeneration from fragments. A few (2-4) incomplete radial canals growing centrifugally can be present, also irregularities like fusions or branching, but these likely of traumatic origin. Gonads along radial canals, spanning from almost the beginning to a short distance from circular canal (Fig. 38A-B), bilamellar, when fully developed large and hanging into subumbrella like a curtain, walls much folded or undulated (Fig. 38A). Fully formed

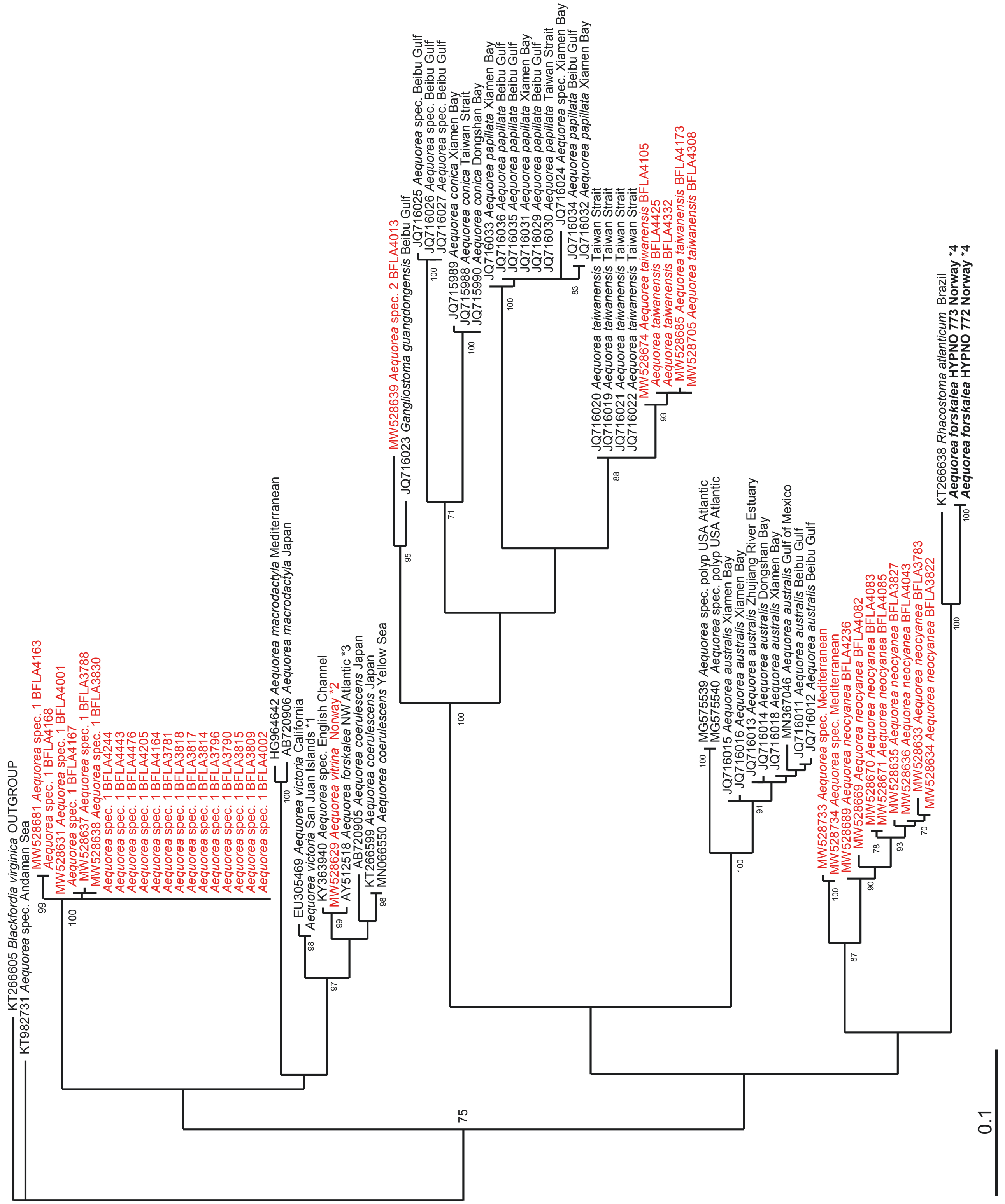

Fig. 37. 16S maximum likelihood phylogenetic tree of the genus *Aequorea* and related genera obtained with PhyML (GTR+G+I model) using about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Red labels are new sequences from this study, for the taxa in bold either a voucher specimen or photos of it have been examined. Notes: *1) Unpublished, L. Leclère, pers. comm. *2) See Material & Methods. *3) Could be a misidentification. *4) Unpublished, A. Hosia & L. Martell, pers. comm., see Fig. 39A.

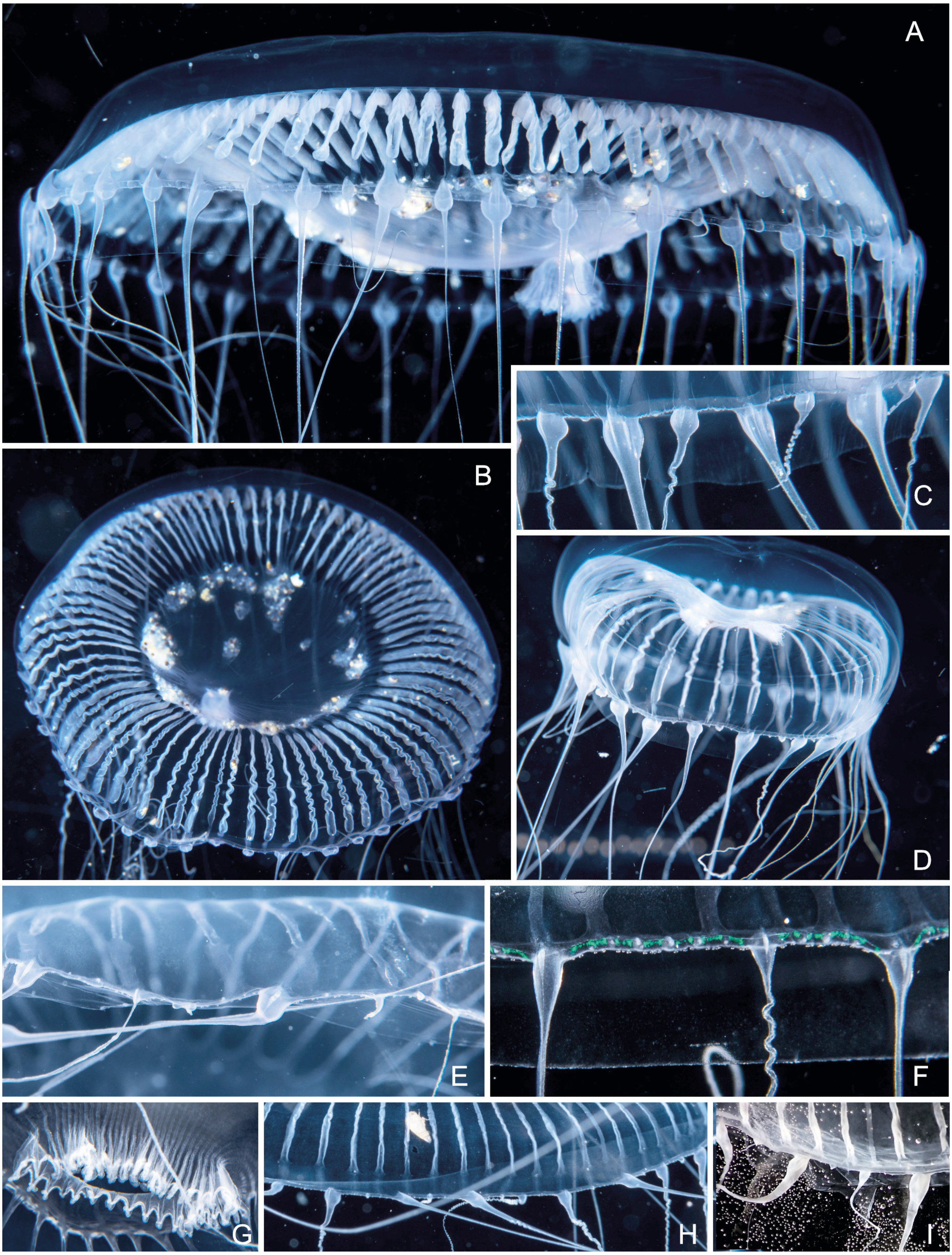

Fig. 38. *Aequorea neocyanea* new name. (A-C) BFLA4085, bell diameter 60 mm. (A) Oblique view from below. (B) Aboral view. (C) Bell margin with tentacles and their bulbs. (D) BFLA4083, bell diameter 42 mm, young animal with beginning gonad development. (E) BFLA4043, bell margin. (F) BFLA4236, bell margin, the green dots are not a pigment but likely due interference effects. (G) BFLA4236, mouth region with short fimbria. (H) BFLA3783, bell margin. (I) BFLA3783, tentacles after fixation in formalin.

tentacles 21 to 50, additionally some small ones or mere bulbs that will likely later also develop into tentacles. Observed ratios of radial canals to fully formed tentacles 1.0-3.0. Tentacles in life nearly always with a swollen base (Fig. 38C, E, F, H) degree of swelling is apparently modifiable and could depend on environment or physiological state as once the animal is preserved the swelling is much reduced (Fig. 38I). Regularly there is a faint abaxial keel, often emphasized or feigned by a whitish line on median of abaxial side (Fig. 38E, F, H) caused by an accumulation of nematocysts, this line only visible in living animals. In swollen bulbs abaxial side or keel often elongated into abaxial spur (Fig. 38A-D), in preserved material much less visible or absent. Excretory papillae absent, excretory pores could not be found reliably in the preserved material. Four or more statocysts (up to 14) between two tentacles or bulbs, 2-3 statoliths per statocyst. Colours: unpigmented, very well grown specimens with a pink hue.

16S data: The eight haplotypes had a range of divergences of 0.3-2.1 % (Table 1, intrapopulation variation). A maximum likelihood tree of the partial 16S sequence (Fig. 37) yielded a diverse but well-defined clade for this species. Its sister clade comprises two samples from the Mediterranean diverging in 3.7-5.2% of their aligned bases (see discussion below). No relationship to *A. forskalea* nor to *A. macrodactyla* is evident though.

Distribution: Florida, Bermuda, perhaps also Brazil and even Mediterranean (see below). Type locality: Atlantic Ocean, USA, Florida, Key West.

Remarks: We think that the present material most likely belongs to the same species identified by Mayer (1900, 1904) as *Zygodactyla cyanea,* although there are some differences. *Zygodactyla cyanea* was first described by L. Agassiz (1862) based on animals from Key West, Florida. His brief description was later expanded (A. Agassiz, 1865) and a figure of a fully-grown animal provided. Agassiz (1865) reported it in great numbers along the Florida Reef. Mayer (1900, 1904) then added more details using material from Florida and the Bahamas, notably also figures of the tentacle bulbs and of younger stages. As Mayer was a collaborator of A. Agassiz, his identification was certainly discussed with the latter. In his 1910 monograph, Mayer then synonymized *Z. cyanea* with *Aequorea forskalea* Péron & Lesueur, 1810 without further discussion.

Our material matches more *Z. cyanea* of Mayer (1900, 1904) and not *A. forskalea* for the following reasons:

1) Mayer found it as very common off the coast of Florida and in our study it was likewise a frequent medusa.
2) The type locality is in the same region and connected by the Gulf stream.
3) Mayer describes and depicts the tentacle bulbs with an abaxial spur, but incorrectly identified it as an exumbrellar excretory papilla (which is unknown in hydromedusae). This corresponds to the bulbs we found (Fig. 38), although this trait is not a unique diagnostic feature for the species as it occurs also in *Aequora* spec. 1 (see below) and others, e.g. *A. krampi* Bouillon, 1984. *Aequorea forskalea* in current understanding has evenly tapering, not much swollen tentacle bases (Fig. 39).
4) The mature animals examined genetically had diameters of 5 to 6 cm, a stomach width of 1/2 the bell diameter, and up to 100 radial canals, thus matching Agassiz' and Mayer's values.

There are also traits that do not match. Notably our maximum tentacle number was about 50 and the ratio of radial canals to tentacles usually in the region of 2. Mayer gives up to 100 tentacles and a ratio of 1. These traits are known to be very variable in this genus and should be used with caution to separate species. Moreover, we found that *Aequorea* medusae often get fragmented and then reconstituted themselves. This vegetative reproduction via fission could account for much of the variation seen in the *Aequorea* (see Stretch & King, 1980).

Contrary to Mayer (1910), we think that Agassiz' medusa should be kept distinct from *A. forskalea*. The 16S sequences of our material were different from

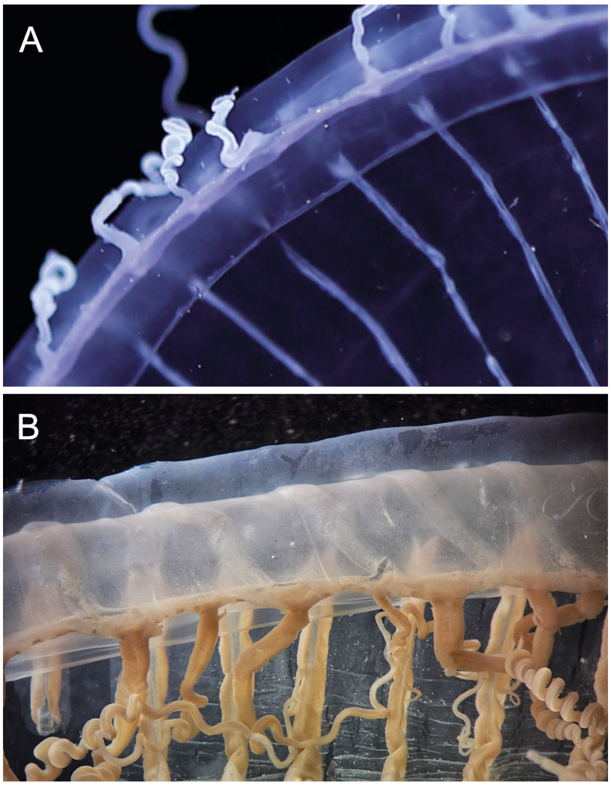

Fig. 39. *Aequorea forskalea.* (A) Living medusa from Norway, bell margin seen from oral side. Photo courtesy of Luis Martell, sample HYPNO 772. (B) Preserved sample from the Mediterranean, MHNG-INVE-0055261.

A. forskalea of the NE Atlantic (Fig. 37), the bell sizes were smaller than for typical *A. forskalea*, and tentacles bases are usually swollen and may have an abaxial keel and spur.

The name *Aequorea forskalea* was introduced by Péron & Lesueur, 1810 to replace the preoccupied name *Medusa aequorea* Forsskål, 1775 and they formally also restricted the type locality to the Mediterranean Sea. Forsskål (1775) provided a good illustration of his medusa which he had seen in the NE Atlantic or the Mediterranean and which we must assume to represent the type specimen. Forsskål's medusa was quite large with a diameter of 23 cm [in his Latin description he states "*Diameter spithamalis*", a spithame being an ancient Greek/Byzantine length unit corresponding to 0.231 m]. Our current scope of the species was outlined by Russell (1953) and Kramp (1959a) who give sizes of up to 175 mm and 60-80 radial canals. The bases of the tentacles are almost invariably given as evenly tapering and not swollen (Fig. 39, see also Kramp, 1959a: fig. 234b). This is clearly different to the ones observed here (Fig. 38) but some cautionary remarks are necessary. The degree of inflation of the tentacle base, the keel formation, and the abaxial spur seem to be variable and a partly transient feature. The swelling depends perhaps on the activity of the animal, the osmotic situation, or the digestive cycle. In preserved animals it is much less pronounced (Fig. 38I), but still apparently different from *A. forskalea*.

The status of the closely related Mediterranean *Aequorea* samples (Fig. 37, MW528733 and MW528734, see Material & Methods) is not clear. They were immature and 4 to 5 cm in size and their tentacle bases resembled the ones shown in Fig. 38E and not Fig. 39B. It could be that they also belong to the present species. The *A. forskalea* of the Mediterranean also differentiate into two morphotypes when examined alive (unpublished observations): one with slender, evenly tapering tentacles as shown in Fig. 39B and another with much swollen bases of the bulbs resembling the ones shown in Fig. 38A-B.

The Brazilian medusae identified as *A. macrodactyla* by Nogueira *et al*. (2016) do not match well the latter species (see Kramp, 1968; Schuchert, 2017a) but conform much better with the scope of *A. neocyanea* as documented here.

The status of the Mediterranean *Aequorea* morphotypes as well as many other populations should be examined using genetic techniques.

Aequorea spec. 1

Fig. 40A-K

Material examined: BFLA3781; 1 specimen; 18-SEP-2018; size 9 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3788; 1 specimen; 24-SEP-2018; no size data, no gonads; preserved in alcohol for DNA extraction; 16S sequence MW528637. – BFLA3790; 1 specimen; 24-SEP-2018; no size data, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631 – BFLA3796; 1 specimen; 13-OCT-2018; size 6 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3809; 1 specimen; 19-OCT-2018; size 10 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3814; 1 specimen; 20-OCT-2018; size 12 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631 – BFLA3815; 1 specimen; 20-OCT-2018; size 10 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3817; 1 specimen; 20-OCT-2018; size 12 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3818; 1 specimen; 24-OCT-2018; size 8 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3830; 1 specimen; 15-NOV-2018; size 7 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence MW528638. – BFLA4001; 1 specimen; 20-NOV-2018; size 13 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence MW528631. – BFLA4002; 1 specimen; 20-NOV-2018; size 17 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA4163; 1 specimen; 06-AUG-2019; fragments 4 and 6 mm, gonads developing; part preserved in formalin and deposited as FU-013813, part preserved in alcohol for DNA extraction; 16S sequence MW528681. – BFLA4164; 1 specimen; 06-AUG-2019; size 8 mm, no gonads; part preserved in formalin and deposited as FU-013814, part preserved in alcohol for DNA extraction; 16S sequence MW528682. – BFLA4167; 1 specimen; 06-AUG-2019; size 6 mm, no gonads; part preserved in formalin and deposited as FU-013815, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528638. – BFLA4168; 1 specimen; 06-AUG-2019; size 6 mm, no gonads; part preserved in formalin and deposited as FU-013816, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528681. – BFLA4205; 1 specimen; 23-AUG-2019; size 4 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA4244; 1 specimen; 11-NOV-2019; size 10 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631 – BFLA4443; 1 specimen; 07-JUN-2020; size 10 mm, no gonads; part preserved in formalin and deposited as FA-014058, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA4464; 1 specimen; 13-JUN-2020; size 9 mm, no gonads; preserved in

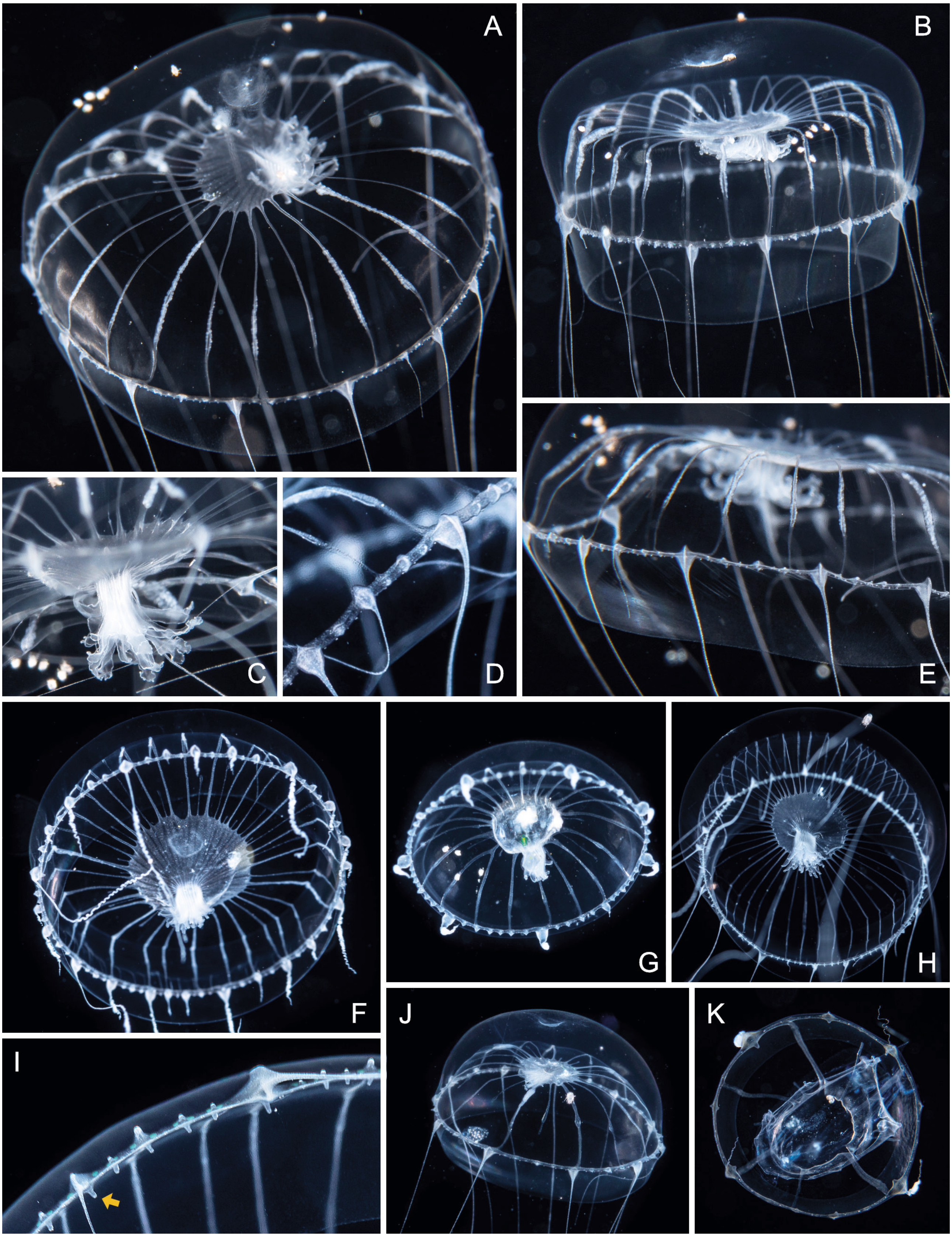

Fig. 40. *Aequorea* spec. 1. (A-B) BFLA4163, size > 10 mm. (C) BFLA4163, manubrium. (D) BFLA3814, close up of bell margin. (E) BFLA4163, close up of bell margin. (F) BFLA3814, size 12 mm. (G) BFLA3788, size not recorded. (H) BFLA4002, size 17 mm. (I) BFLA4002, bell margin from oral side, arrow points to excretory papilla. (J) BFLA3781, size 9 mm. (K) BFLA4476, size 5 mm, youngest observed stage with 6 complete radial canals, a large prey item is in the stomach.

alcohol for DNA extraction; 16S sequence identical MW528681. – BFLA4476; 1 specimen; 18-JUN-2020; size 5 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631.

Observations: Small *Aequorea* medusae with bell diameters reaching 17 mm, only some with beginning gonad development (Fig. 40A-B), gonad development starts at about 9 mm size. Bell in smaller animals nearly hemispherical, larger ones more flattened. Stomach small, in the larger individual diameter ~1/4 to 4/5 of bell diameter. Mouth rim with many broad fimbriae (Fig. 40C). Radial canals thin, up to 46 seen, often also developing centrifugal canals. Gonads developing in some of the radial canals (Fig. 40A), but apparently not fully developed. Up to 25 fully developed tentacles, additionally 1-5 very small tentacles or small bulbs without tentacles. Ratio of radial canals to tentacles 1.3 to 1.8 in individuals with visible gonads, thus always more radial canals than tentacles. Tentacles in life with a distinct, short, conical basal bulb (Fig. 40A-B, D-E), with faint abaxial keel, emphasized or feigned by a whitish line on median of abaxial side (visible in life only), abaxial side of bulb usually continued onto exumbrella as a short abaxial spur (Fig. 40E). Conspicuous excretory papilla on adaxial side of tentacle bulbs (Fig. 40I), pointing into subumbrella. One to two statocysts between tentacles or small bulbs, statocysts with two statoliths.

16S data: The five haplotypes had a range of divergences of below 1.0 % (Table 1, intrapopulation variation). A maximum likelihood tree of the partial 16S sequence (Fig. 37) found no significant relationship to other congeners.

Remarks: This species was delimited by the 16S sequences. Were it not for the 16S data, we would have considered the specimens as juveniles or a smaller form of *A. neocyanea*, this notably for their resembling tentacle bulbs (comp. Figs 38E and 40E). However, the 16S sequence data (Fig. 37) separated them into two unrelated clades. The base pair differences between sequences of the two clades were >8.2%. The two sample sets cannot well be compared morphologically as they represent different developmental stages. None of the specimens of the present species had fully developed gonads. One difference we noted was the presence of a large excretory papilla in a majority of specimens of the present species.

We were initially tempted to identify this lineage as *Aequorea floridana* (L. Agassiz, 1862), a species also reported to be common along the cost of Florida and the Bahamas by Mayer (1900) [for descriptions see Mayer (1910) and Bigelow (1913, 1938)]. Mature *Aequorea floridana* have 16 to 24 radial canals and up to 80-100 tentacles (Mayer, 1910). Sixteen is the prevalent number of radial canals. Our specimens with gonads had 14 to 46 radial canals and consistently fewer tentacles than radial canals. It was mainly the low tentacle number which influenced our decision to reject an identity with *A. floridana*. The lack of fully developed animals and the lack of distinctive features made it advisable not to introduce a new species name. This is an unsatisfactory situation, but 16S data of fully-grown animals and also of typical *A. floridana* morphotypes are needed to solve the problem and to put a name on this lineage.

Aequorea taiwanensis Zheng *et al.*, 2009

Fig. 41A-G

Aequorea taiwanensis Zheng *et al.*, 2009: 110, fig. 1. – Zheng *et al.*, 2014: 63, 16S ML tree.

Material examined: BFLA4105; 1 specimen; 27-MAY-2019; size 27 mm, beginning gonad development; part preserved in formalin and deposited as UF-013793, part preserved in alcohol for DNA extraction; 16S sequence MW528674. – BFLA4173; 1 specimen; 09-AUG-2019; size 30 mm; part preserved in formalin and deposited as UF-013820, part preserved in alcohol for DNA extraction; 16S sequence MW528685. – BFLA4308; 1 specimen; 16-JAN-2020; size 31 mm, gonads visible; part preserved in formalin and deposited as UF-013846, part preserved in alcohol for DNA extraction; 16S sequence MW528705. – BFLA4332; 1 specimen; 31-JAN-2020; size 40 mm, gonads visible; part preserved in formalin and deposited as UF-013890, part preserved in alcohol for DNA extraction; 16S sequence identical MW528705. – BFLA4425; 1 specimen; 28-MAY-2020; size 50 mm, gonads visible; part preserved in formalin and deposited as UF-014051, part preserved in alcohol for DNA extraction; 16S sequence identical MW528705. – 1 specimen photographed 07-FEB-2020, not collected; size 30 mm.

The formalin samples are mostly strongly fragmented and damaged.

Observations: Subadult *Aequorea* medusae with bell diameters 30 to 50 mm, gonad development starts at about 30 mm size. Bell relatively high, apical jelly about 1/2 of bell height. Stomach wide, 7/10 of bell diameter. Mouth rim with numerous, long, thin fimbriae (Fig. 41B). Radial canals thin, 100 to 240, often also with 15 to 100 developing centrifugal canals. 14 to 25 fully developed tentacles, between pairs of tentacles 3-5 small bulbs without tentacles. Ratio of radial canals to tentacles 7.5 to 10, thus always many more radial canals than tentacles. Tentacles in life either with a distinct conical basal bulb with a slight depression of upper side (Fig. 41D) or widened laterally to give a T-shape (Fig. 41C, G). Abaxial spurs absent. Small, abaxial excretory papillae can be present, only seen in preserved material. Tentacle bases in preserved material usually also with lateral expansions (Fig. 41F), but some simply

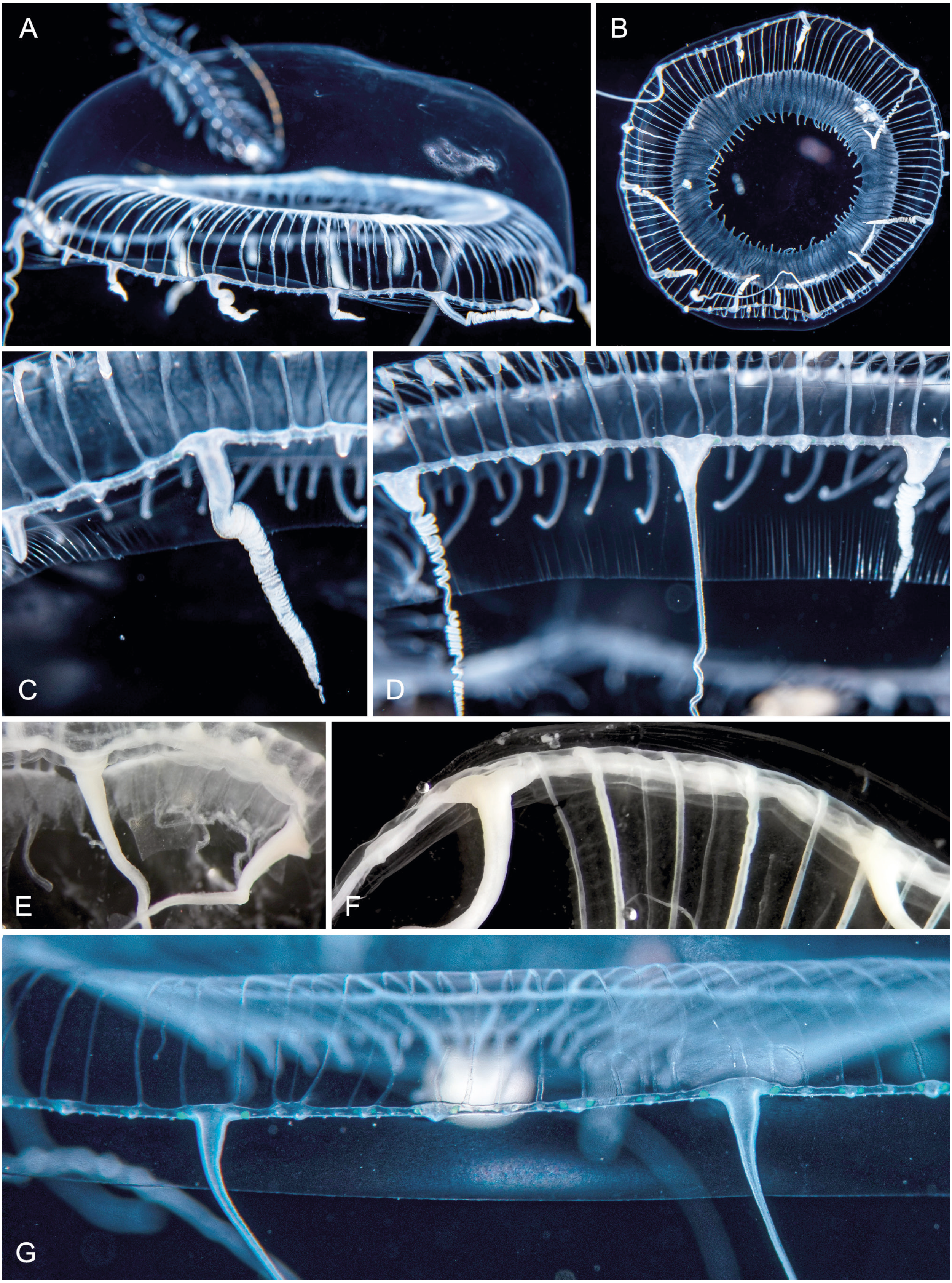

Fig. 41. *Aequorea taiwanensis*. (A-B) BFLA4308, size 31 mm. (C) BFLA4308, bell margin. (D) BFLA4332, bell margin. (E) BFLA4308, bell margin after preservation. (F) BFLA4332, bell margin after preservation. (G) Bell margin of animal photographed 07-FEB-2020, size 30 mm; the green dots flanking the bulbs are likely due to interference effects and not a pigment.

conical (Fig. 41E). Statocysts about as numerous as radial canals but not in phase with them, two statoliths per statocyst.

16S data: The three haplotypes had a range of base pair divergences of 0.2 to 0.5 % (Table 1). The maximum likelihood tree of the partial 16S sequences (Fig. 37) identified them as very closely related to *A. taiwanensis* (p-distances 0.2-0.64%).

Distribution: Taiwan strait, Florida (this study). Type locality: Taiwan Strait.

Remarks: This material resembles very much *Aequorea pensilis* (Haeckel, 1879), only the lateral expansions of the bulbs are shorter and sometimes absent in preserved material, and small excretory papillae can be present. Our identification of the present material as *A. taiwanensis* was based on the strong similarity of the 16S sequences (Table 1). The haplotype divergences to the published sequences from Taiwan Strait were only 0.2 to 0.64%, while within the Florida population we found a maximal value of 0.5%, thus intra- and interpopulation divergences are in the same range. In the ML tree (Fig. 37) the distance of the two population appears higher than the values obtained by pairwise comparisons. This is due to the fact that another substitution model was used for the distance calculation and more importantly, the sequences from the Taiwan Strait specimens were 112 bases shorter at the 3' end, leading to a bias in the ML analysis. While the similarity of our sequences with *A. taiwanensis* almost certainly implies that our material is conspecific, it must be noted that so far no *Aequorea pensilis* 16S sequences are available. It might turn out that *A. taiwanensis* is in fact a synonym of *Aequorea pensilis*. *Aequorea taiwanensis,* according to the description in Zehng *et al.* (2009), resembles *A. pensilis* but lacks the diagnostic long lateral expansions of the tentacle base and it has excretory papillae (comp. Browne, 1905; Maas, 1905; Kramp, 1968: Fig. 268). In our material, the lateral expansions were present, but also not as wide as usually shown for *A. pensilis*. Our material is thus intermediate between *A. pensilis* and *A. taiwanensis*. The specimens of Zheng *et al.* (2009) measured only 25 mm, were thus likely younger than ours, which reached up to 50 mm diameter. Pacific *Aequorea pensilis* reach 100 mm in diameter (Kramp, 1968).

The Atlantic occurrence of a rare *Aequorea* medusa of the Western Pacific Ocean is surprising, but not unparalleled. Pruski & Miglietta (2019) recently found *Aequorea australis* in the Gulf of Mexico, a species formerly only known from the Indo-Pacific Ocean.

The presence of *A. taiwanensis* in the Atlantic Ocean must not be interpreted as a possible recent introduction. While we found three different haplotypes, the four samples from Taiwan Strait (Zheng *et al.*, 2014) represented only a single one. The higher haplotype diversity in the Altantic argues against a recent introduction from the Pacific. The species has likely a wide distribution.

Aequorea spec.2

Fig. 42

Material examined: BFLA4013; 1 specimen; 17-DEC-2018; preserved in alcohol for DNA extraction; 16S sequence MW528639.

Observations: Small, juvenile *Aequorea* medusa, 7 mm, no gonads. Stomach diameter 0.3 of bell diameter. About 30 broad radial canals. Tentacles not all visible, approximate range 18-30. Tentacle bulbs conical, not inflated, without keel or white abaxial line, without abaxial spurs.

16S data: The single sequence proved to be quite closely related to *Gangliostoma guangdongensis* Xu, 1983 (Fig. 37). The base pair differences in the pairwise aligned sequences were 3.6%.

Remarks: We found only one specimen of this lineage and it was too immature for being identified. Additionally, the animal was attempting to swallow a much lager ctenophore and was thus quite distorted. Its 16S sequence resembled the Chinese *Gangliostoma guangdongensis.* The genus *Gangliostoma* is distinguished from *Aequorea* by a papilla situated at the base of the stomach and between each pair of radial canals. This feature is not well documented and it is unclear what it is. No such papillae could be seen in the present specimen.

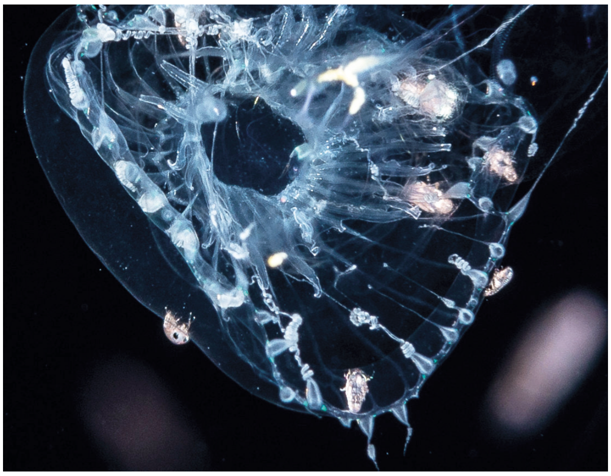

Fig. 42. *Aequorea* spec. 2. (A-B) BFLA4313, size 7 mm, oral view.

Genus *Zygocanna* Haeckel, 1879

Zygocanna Haeckel, 1879: 214, type species *Aequorea pleuronata* Péron & Lesueur, 1810 (Kramp, 1961).

Zygocannota Haeckel, 1879: 215, type species *Aequorea purpurea* Péron & Lesueur, 1810 by monotypy.

Zygocannula Haeckel, 1879: 216, type species *Aequorea undulosa* Péron & Lesueur, 1810 by designation of Mayer (1910: 339).

Diagnosis: Medusa manubrium wide, 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.

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

Fig. 43A-E

Zygocanna apapillatus Xu, Huang & Guo, 2014 in Xu *et al.*, 2014: 912, fig. 344.

Examined material: BFLA4302; 1 specimen; 15-JAN-2020; preserved in alcohol for DNA extraction; 16S sequence MW528704.

Observations: Bell diameter 5 mm, in relaxed state wider than high, relatively flat, apical jelly about 1/3 of height thinning to bell margin. Manubrium relatively small, diameter >1/10 bell diameter, base irregularly star-shaped, wall with radiating vertical folds, these changing into the corners of 7 (9?) simple mouth lips (Fig. 43E). About 10 radial canals originate at manubrium base and some immediately branch once or twice so that about 16 radial canals reach the circular canal. In addition to the complete radial canals about 5 developing centrifugal canals that originate from manubrium or complete radial canal (Fig. 43E). 14 ovoid gonads in about middle of complete radial canals, each with up to 50 oocytes, colour bright yellow with a median colourless, transparent line. 61 long, thin tentacles arising from ovoid bulbs, bulbs bright yellow, few atentaculate, small bulbs also present. One statocyst between pairs of marginal bulbs.

16S Data: The single haplotype (MW528704) was used in a blastn search in GenBank and gave as best match with 94% identity *Cyclocanna producta* (KY570308) followed by several Mitrocomidae and Tiaropsidae with similar scores. A maximum likelihood phylogeny using a wide selection of leptomedusae also associated the sequence with the same families, but with insufficient bootstrap support (tree not shown).

Remarks: This medusa resembles closely *Zygocanna apapillatus* Xu, Huang & Guo, 2014 and it could be conspecific. We were nevertheless reluctant to attribute it to this species for reasons given below. *Zygocanna apapillatus* is a very rare medusa only known from two specimens collected off the coast of Vietnam. The first description is only available in Chinese (Xu *et al.*, 2014), but an English translation and the figures are given in the WoRMS database (Schuchert, 2020; urn: lsid: marinespecies.org: taxname: 828546). Our specimen differs only minimally, having a smaller manubrium diameter, less radial canals, and a higher number of gonads. However, some incomplete, developing radial canals suggest that the final number of radial canals could be higher than observed in the only specimen we had. Based on morphology alone, traditional morphology-based systematics would have treated them as conspecific.

With its small stomach, *Zygocanna apapillatus* is an atypical member of the genus *Zygocanna* and the Aequoridae (comp. Kramp, 1968) and it likely belongs to another family. The comparison of the 16S sequence obtained from our specimen indicated a similarity and possible relationship with several Mitrocomidae and Tiaropsidae but without sufficient bootstrap support due to the poor resolving power of the 16S marker for relationships above the genus level. There was clearly no relationship with Aequoreidae (tree not shown). Mitrocomidae and Tiaropsidae are both characterized by open statocysts, an important taxonomic trait that distinguishes them from most other leptomedusae which have either closed or no statocysts (comp. Bouillon *et al.*, 2006). Unfortunately, we were unable to determine if it had open statocysts (a microscopic examination of living tissue or of histologic sections is needed for this). Without this information a correct identification of the species is impossible. This also holds true for the original description of *Zygocanna apapillatus.* Because of this uncertainty we identified our specimen only as *Zygocanna* cf. *apapillatus.*

Family Malagazziidae Bouillon, 1984a

Genus *Octophialucium* Kramp, 1955

Octophialucium Kramp, 1955b: 256; type species *Octocanna medium* Kramp, 1955 (designation in Kramp, 1961).

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.

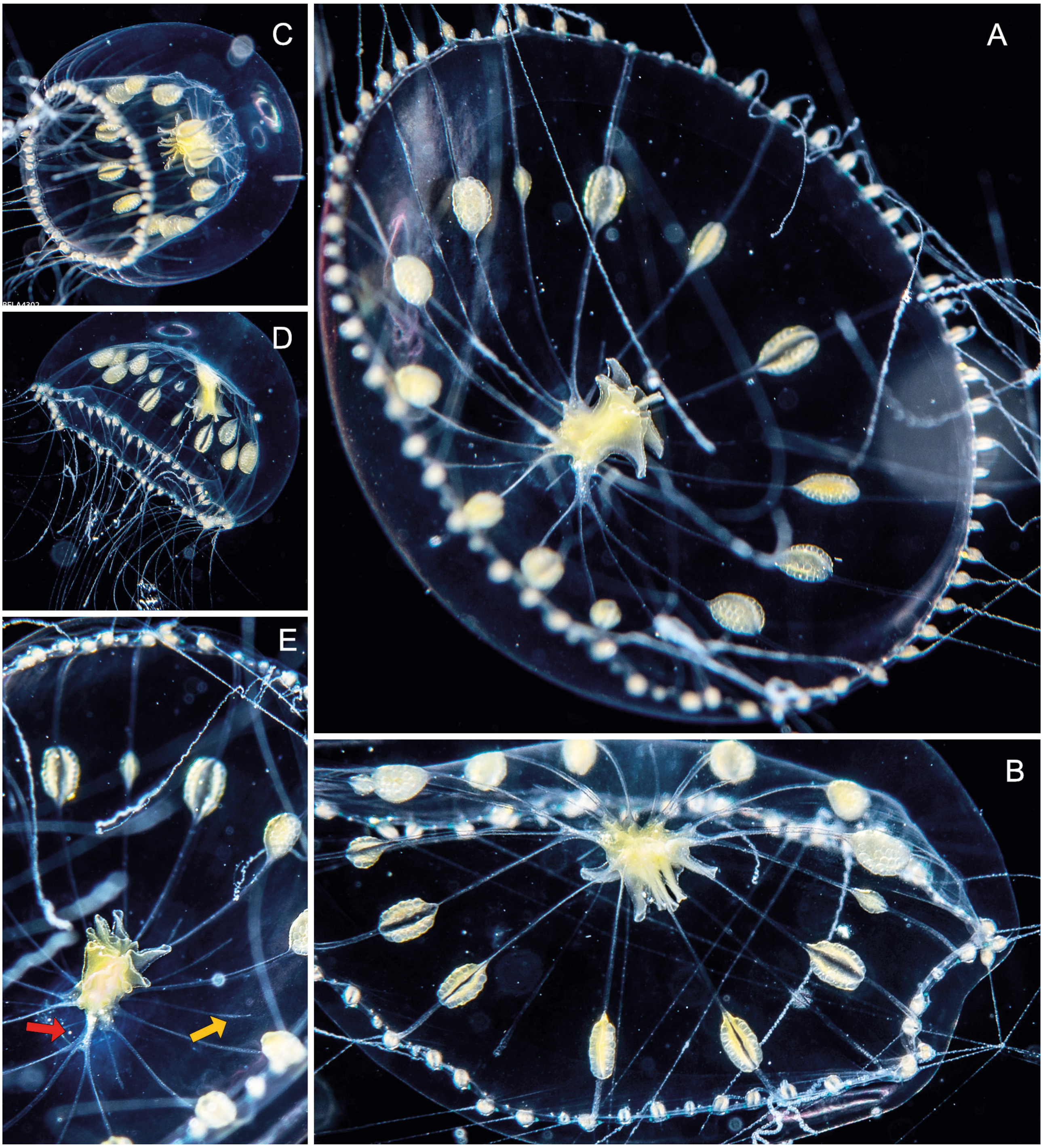

Fig. 43. *Zygocanna* cf. *apapillatus*, bell diameter 5 mm (A) Oral view. (B) Aboral view. (C-D) Lateral views. (E) Oral view, yellow arrow points to a developing radial canal, red arrow points to branching radial canal.

Octophialucium aphrodite (Bigelow, 1928)

Fig. 44A-F

Octocanna polynema. – Maas, 1906: 95, pl. 3 fig. 10. [not *Octocanna polynema* Haeckel, 1879 = indeterminate species]

Octocanna aphrodite Bigelow, 1928: 307, pl. 42 figs 1-2. – Stiasny, 1928: 212, fig. 2.

Octophialucium aphrodite. – Kramp, 1955b: 259, new combination. – Kramp, 1957: 35. – Kramp, 1961: 183. – Kramp, 1968: 89, fig. 239. – Bouillon, 1984b: 81, figs 25-26, life cycle, cnidome. – Wang *et al*., 2018: 108, fig. 3.

not *Octophialucium aphrodite*. – Van der Spoel & Bleeker, 1988: 170, fig. 27.

Examined material: BFLA3823; 1 specimen; 14-NOV-2018; size 24 mm; part preserved in formalin and deposited as UF-013428, part in alcohol for DNA extraction; 16S sequence MW528632. – BFLA3833; 1 specimen; 15-NOV-2018; size 10 mm; preserved in alcohol for DNA extraction; 16S sequence MW528630. – BFLA4130; 1 specimen; 11-JUN-2019; size 26 mm, 10 radial canals; part preserved in formalin and deposited as UF-013806, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528630.
MHNG-INVE-0055283; 2 specimens, badly preserved; Indonesia, Moluccas, Bay of Ambon; collected 27.06.1890-02.09.1890; material described and figured in Maas (1906).

Observations on Florida specimens: Mature medusa diameter up to 26 mm, height about 10 mm, umbrella rather flat, apical jelly about half the height of the umbrella, lateral wall thin. Stomach large, tubular, base an eight-rayed star, mouth with eight long perradial lips, rim crenulated (Fig. 44A, E). Eight to 10 radial canals, tapering somewhat from manubrium to circular canal. Gonads along distal half of radial canals but not reaching to junction with circular canal, serpentine outline (Fig. 44A), in females with numerous small eggs. Tentacles about 90, tentacle-bulbs elongate conical, abruptly tapering into tentacle; most bulbs with a very large excretory papilla protruding into subumbrella from abaxial side above velum (Fig. 44B, arrow), excretory papilla in preserved animals much shrunken and rather small. Left and right of tentacle bulb base often a green spot (Fig. 44B), but which is not due to pigments. Very few incipient bulbs present. Tentacles thin, extensible to long size. One or two statocysts between tentacle pairs (Fig. 44B). Colour: circular canal with a light green tint, green spots flanking tentacle bulbs in living animals, otherwise colourless.

Immature medusa (BFLA3833, Fig. 44C) 10 mm in diameter; radial canals, circular canal, and bulbs green, incipient development of gonads, otherwise similar to adult.

16S Data: Searching GenBank for sequences similar to the obtained 16S sequences indicated a relationship to other leptomedusae, but gave no matches with more than 92% sequence identity. A maximum likelihood analysis of a wide selection of leptomedusae did not identify relationships with sufficient bootstrap support (results not shown). The two haplotypes differed in 0.8% of their base pairs.

Remarks: Morphologically, the adult specimen BFLA3823 matches very well the existing descriptions and figures (Bigelow, 1928; Kramp, 1968; Bouillon, 1984b) of *O. aphrodite.* Also the comparison material from the Moluccas agreed well [specimens described by Maas (1906) as *O. polynema*, later referred to *O. aphrodite* by Bigelow (1928)]. The 16S sequence divergence of 0.8 % for sample BFLA3823 and BFLA3833 was interpreted as intraspecific variation (see Table 1, and Schuchert *et al.*, 2017). BFLA3833 is a subadult specimen and it was thus attributed to *Octophialucium aphrodite* mainly based on 16S sequence similarity.

It is somewhat surprising to find this Indo-Pacific medusa in the NW Atlantic Ocean, but it has already been recorded in the Gulf of Mexico by Canudas Gonzàlez (1979). However, the small size (11 mm), the low tentacle numbers (23-53), and the high number or radial canals (up to 15) given by Canudas Gonzàlez (1979) make this record somewhat doubtful. No illustration was provided. The animal depicted in Van der Spoel & Bleeker (1988) is unlikely *O. octophialucium* as it has only 24 tentacles. It is more likely *O. medium* Kramp, 1955b which has only 16 tentacles, but otherwise resembles *O. aphrodite* very much.

Octophialucium aphrodite resembles also closely *O. funerarium* (Quoy & Gaimard, 1827). The latter occurs in the NE Atlantic and the Mediterranean (Cornelius, 1995) and it appears more probable to be found in the western Atlantic than the Indo-Pacific *O. aphrodite.* Wang *et al.* (2018) have recently discussed some differences of the two species, mostly using the shape of the tentacular bulbs and the average number of statocysts between two fully developed tentacles (1 versus 2). However, there are more differences. Most importantly, the manubrium and the tentacle bulbs of *O. funerarium* are characteristically dark coloured by a black pigment (Quoy & Gaimard, 1827; Kramp & Damas, 1925; Russell, 1953; Cornelius, 1995). Moreover, the jelly is thicker and lentil-shaped, the subumbrella very shallow, the diameter is usually larger (up to 50 mm), and rudimentary bulbs are frequent (rare in *O. aphrodite*).

Bouillon (1984b) remarked that some published illustrations of *O. aphrodite* are based on altered specimens and he provided an excellent figure.

Based on the references given in the synonymy above, the following updated consensus diagnosis for *O. aphrodite* can thus be provided:

Medusa 15-40 mm in diameter when mature, bell flatter than hemisphere, apical jelly about half the height of the

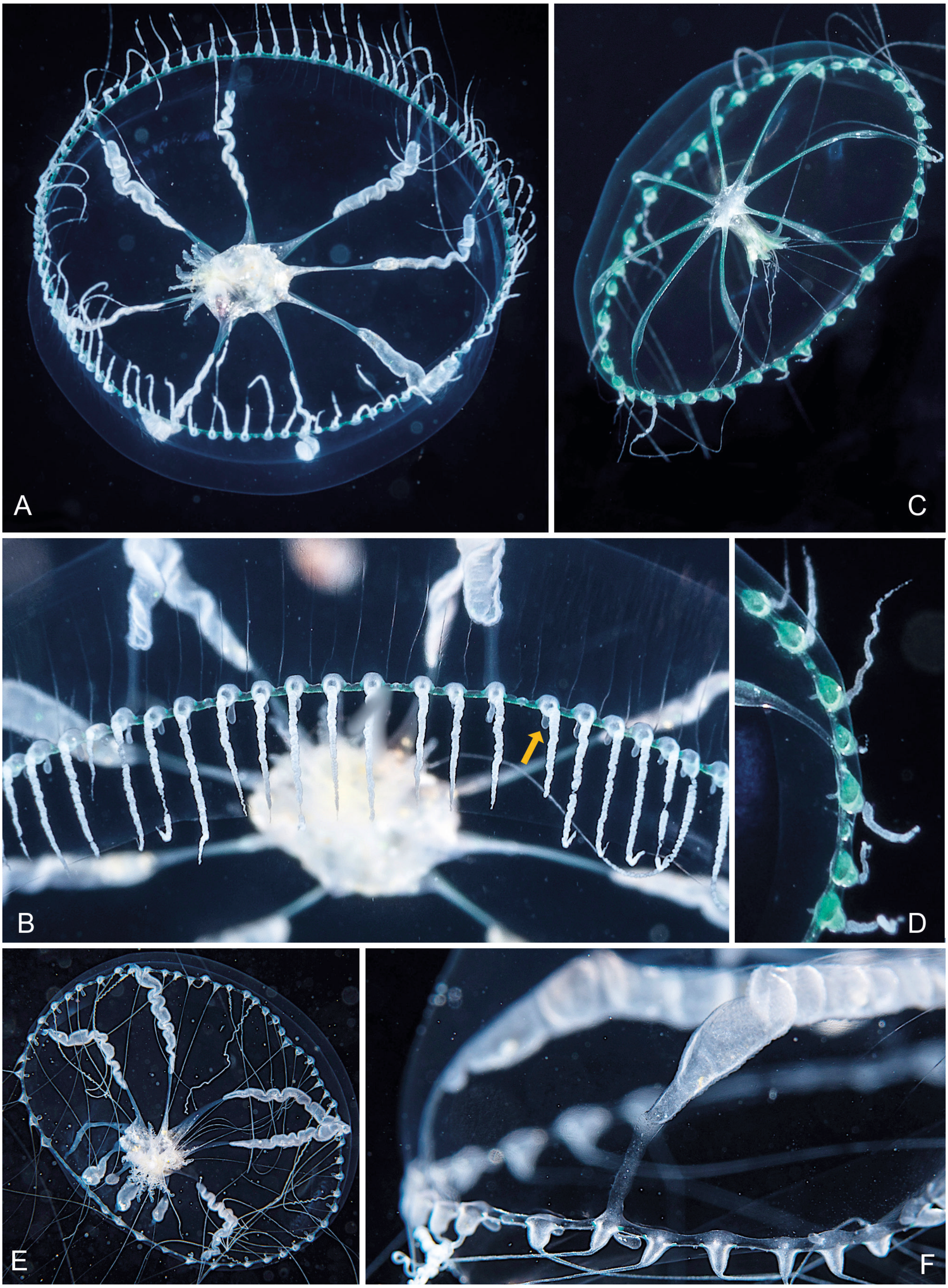

Fig. 44. *Octophialucium aphrodite*, living animals from Florida. (A) Oral view of whole animal BFLA3823, diameter 24 mm. (B) Close up of the bell margin of same animal as shown in A, bell opening facing down. Note the large excretory papillae (arrow) and the green dots flanking the marginal bulbs visible only in life. (C) BFLA3833, oblique aboral, bell diameter 10 mm. (D) Bell margin of medusa shown in C, seen from aboral side. (E) BFLA4130, bell diameter 26 mm, oblique view from oral side. (F) Bell margin of medusa shown in E.

bell, lateral wall thin. Manubrium large, tubular, base an eight-rayed star, mouth with eight perradial lips. Eight radial canals, rarely 7, 9, or 10. Gonads spindle-shaped, along distal 1/5 to 1/2 of radial canals, not reaching to junction with circular canal. 80-120 tentacles and as many bulbs, bulbs distinctly separated from tentacles, only few small bulbs without tentacles present. Excretory papillae tubular, large, in life reaching the same length as the bulbs. One or two statocysts between tentacle pairs, statocysts with two concretions. Colours: colourless or greenish circular canal, without black pigment in manubrium and bulbs.
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.

Distribution: In the Pacific Ocean known from Indonesia, Philippines, Papua New Guinea, and the South China Sea (Kramp, 1968; Bouillon, 1984b; Wang *et al*., 2018); in the Indian Ocean from the Mozambique Channel (Kramp, 1957); in the Atlantic Ocean perhaps in the Gulf of Mexico (Canudas Gonzàlez, 1979) and off Florida (this study). Type locality: Sulu Sea.

Octophialucium irregularis n.spec.

Fig. 45A-G

Holotype: BFLA4290; observed and collected 19-DEC-2019; size 12 mm, with incipient gonads; part preserved in formalin and deposited as UF-013843, part preserved in alcohol for DNA extraction (MHNG-INVE-0137379); 16S sequence MW528701.

Other material: BFLA3829; 1 specimen; 15-NOV-2018; size 4 mm, juvenile; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA3838; 1 specimen; 19-NOV-2018; size 7 mm, without gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4131; 1 specimen; 11-JUN-2019; size 12 mm, without gonads; part preserved in formalin and deposited as UF-013807, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4259; 1 specimen; 30-NOV-2019; size 8 mm, incipient gonads; part preserved in formalin and deposited as UF-013838, much damaged, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4311; 1 specimen; 15-JAN-2020; size 5 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4377; 1 specimen; 18-MAR-2020; size 6 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701.

Description: Bell diameter 8-12 mm for animals with gonads, bell rather shallow, apical jelly about half of height and subumbrella relatively shallow, soft walls and rim deformed easily. Velum narrow. Manubrium cross-section like a multi-rayed star (Fig. 45A-C, G), as many rays as radial canals, multi-rayed outline present from base to mouth, diameter narrowing towards mouth, mouth with about eight lips. Occasionally a secondary manubrium may be present. Radial canals 7-9, originating from manubrium rays, initially broad and then tapering, sometimes also one incomplete centrifugal canal present that does not reach circular canal. Arrangement of radial canals irregular, some irregularly curved, branching once, sometimes coalescing again or fusing with other radial canals, general appearance very variable, irregular, and disordered (Fig. 45A, D, G, F). Gonads arise in middle region of complete radial canals, oblong, slightly pendant (Fig. 45C), fully developed state unknown. Circular canal thin, in larger animals with incomplete centripetal canals arising from non-perradial bulbs, reaching about to mid-subumbrella height (Fig. 45D). Tentacles 27 to 30, on ovoid marginal bulbs which taper rapidly into thin tentacles, these often neatly coiled when contracted (Fig. 45E); bulbs with adaxial excretory papilla pointing into subumbrella, size variable, sometimes relatively large (Fig. 45C). Between tentaculate bulbs 1 to 3 smaller bulbs with very short tentacle (Fig. 45E) or without tentacle. Between successive marginal bulbs 1 to 3 closed statocysts with 2 statoliths (Fig. 45D-E). Colours: orange gastrodermis of tentaculate marginal bulbs, gonads orange; manubrium in younger stages transparent green (Fig. 45G), later whitish, sometimes at base in interradial position orange (Fig. 45A) or a weak interradial, brown pigment band from base to mouth (Fig. 45C).

16S Data: The seven specimens gave all an identical 16S sequence. The single haplotype (MW528701) was used in a blastn search in GenBank and gave as best match with 93% identity an *Octophialucium indicum* from New Zealand (AY787897). The pairwise identities with the 16S of *O. aphrodite* were lower, about 88%. A maximum likelihood tree using a wide selection of leptomedusae did not yield any well supported relationship (tree not shown).

Remarks: There are currently 11 accepted species of *Octophialucium* (Schuchert, 2020). In terms of size and tentacle numbers, the new species resembles only *Octophialucium mollis* Bouillon, 1984b, a species known from the tropical Western Pacific Ocean. *Octophialucium mollis* is also the only *Octophialucium* species that has centripetal canals. *Octophialucium irregularis* differs from *O. mollis* in the following aspects: it lacks the interradial rows of black spots on the manubrium wall (although in some there is a faint brown band, see Fig. 45C), the centripetal canals are longer, and the radial canals are very irregular in appearance and number. The latter feature is the most characteristic trait of this species and its specific epithet

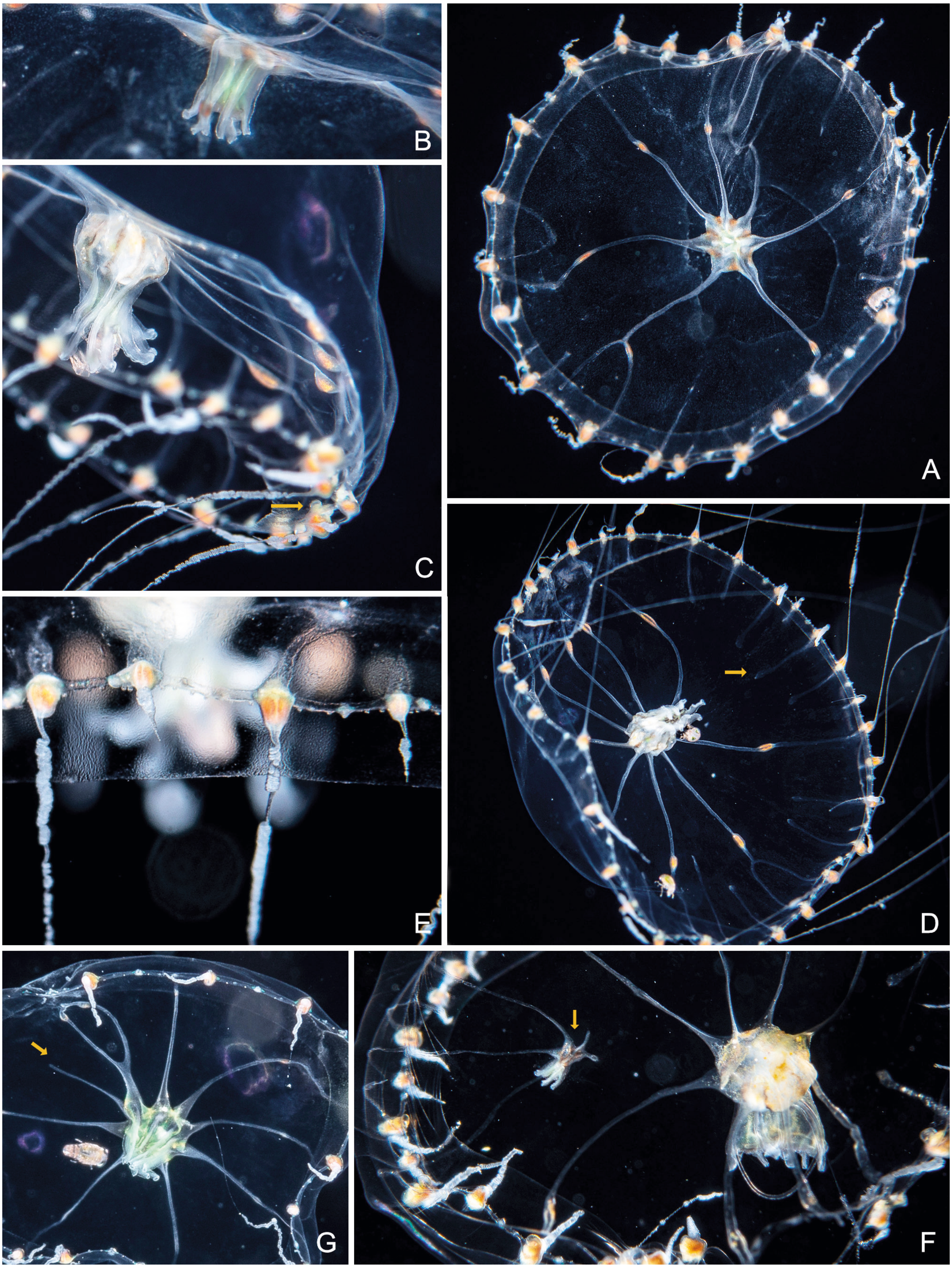

Fig. 45. *Octophialucium irregularis* n. spec. (A) Holotype, BFLA4290, aboral view, 12 mm diam. (B) BFLA4290, lateral view of manubrium. (C) BFLA4259, 8 mm, partial lateral view, arrow points to excretory papilla. (D) BFLA4259, oral view, arrow points to centripetal canal. (E) BFLA4259, bell margin, lateral view. (F) BFLA4131, 12 mm diameter, aboral view, arrow points to secondary manubrium. (G) BFLA3838, 7 mm oral view, arrow points to incomplete centrifugal canal.

irregularis is intended to reflect this. This irregular organisation is likely not only due to genetic factors, but – as irregularities of the bell margin suggest (Fig. 45A, G) – also due to repeated damage and subsequent regeneration.

Family Campanulariidae Johnston, 1836
Genus *Clytia* Lamouroux, 1812

Synonymy: See Calder (1991).

Diagnosis: Medusa with normal, curved umbrella. Manubrium short, with four short perradial lips. Velum present. Normally four radial canals, but some aberrant form 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: Very few nominal species of *Clytia* medusae are unambiguously identifiable. Most morphological characters used to distinguish *Clytia* species fall in the range of variation that can be expected in a single species and having little or no taxonomic value (Lindner & Migotto, 2002; Bouillon *et al*., 2006). Species identification requires usually knowledge of the entire life cycle. A recent extensive molecular phylogeny of the Campanulariidae (Cunha *et al*., 2017) found even more taxonomic inconsistencies, and also provides an excellent framework for barcoding studies. The 16S data set of the latter study was used in a maximum likelihood phylogeny to search for relationships of the sequences obtained in this study. The tree is not shown here due to it size and the sparse results.

Clytia linearis (Thornely, 1900)
Fig. 46A-B

Obelia linearis Thornely, 1900: 453, pl. 44 fig. 6.
Clytia linearis. – Cornelius, 1982: 84, fig. 12. – Medel & Vervoort, 2000: 38, bibliography. – Peña Cantero & García Carrascosa, 2002: 149, fig. 28e-f, synonymy. – Lindner & Migotto, 2002: 541, figs 2-3, life cycle. – Schuchert, 2003: 160, fig. 20, synonymy. – Galea, 2007: 88, figs 20G-I, pl. 2J-K. – Galea, 2008: 20, fig. 4A-B. – Calder, 2013: 55, fig. 15f, record Florida, taxonomy.

Examined material: BFLA4077; 1 specimen; 16-APR-2019; size 3.5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528668.

Observations: Medusa 3.5 mm, bell when relaxed rather flat (Fig. 46A), height about 1/3 of diameter, jelly moderately thick. Manubrium small, four very short, simple perradial lips. Four radial canals, two of them (accidentally?) approximated and therefore not giving a perfectly tetraradial symmetry. Gonads male, very thick and long, sausage shaped, arising at short distance from manubrium and stretching to almost circular canal. 39 tentacles, each arising from a spherical basal bulb, thin and long. 1 to 2 atentaculate, smaller bulbs. At least as many or more statocysts as tentacles. Colour: all tissues with a green hue, transparent.

16S Data: The 16S sequence of our single sample was compared to the 16S dataset of Cunha *et al.* (2017). It was nested within the well supported *Clytia linearis* clade (tree not shown). Its sister clade is made up of the sequences AY789810 and AY346362 from Beaufort NC and the Mediterranean respectively (provenence acc. Govindarajan *et al*., 2006). The sequence divergence from AY789810 is 2.5%.

Distribution: Circumglobal in shallow warm waters (Lindner & Migotto, 2002). Type locality: Papua New Guinea, New Britain, Blanche Bay (Thornely, 1900; hydroid).

Remarks: The identification of this medusa was based solely on its 16S sequence which was nested within a well supported *Clytia linearis* clade. The morphology matched rather well the description of *Clytia linearis* in Lindner & Migotto (2002) which was based on cultivated medusae. It only had slightly more tentacles and much larger gonads, both easily attributable to more optimal growth conditions. Notable were the rather flat umbrella and the small size.

Clytia spec. 1
Fig. 46C

Examined material: BFLA4240; 1 female; 11-NOV-2019; size 7 mm, with gonads; preserved in alcohol for DNA extraction; 16S sequence MW528690. – BFLA4283; 1 specimen; 06-DEC-2019; size 10 mm, with gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528690. – BFLA4342; 1 female; 29-FEB-2020; size 15 mm, with gonads; part preserved in formalin and deposited as UF-013895, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528690.

Observations: Typical *Clytia* medusae, bell slightly shallower than hemisphere, diameters when mature 7 to 15 mm. Manubrium urn shaped, with four long perradial lips, margin undulated. Four radial canals. Gonads thick, ovoid to oblong, in middle of radial canal, about 1/5 of radial canal length. 18 to 22 tentacles arising from ovoid bulbs, 0 to 4 small atentaculate bulbs. Usually 2, sometimes 1 or 3, statocysts between pairs of bulbs, 2 statoliths per statocyst. Colour: radial canals in all three specimens with brilliant green colour.

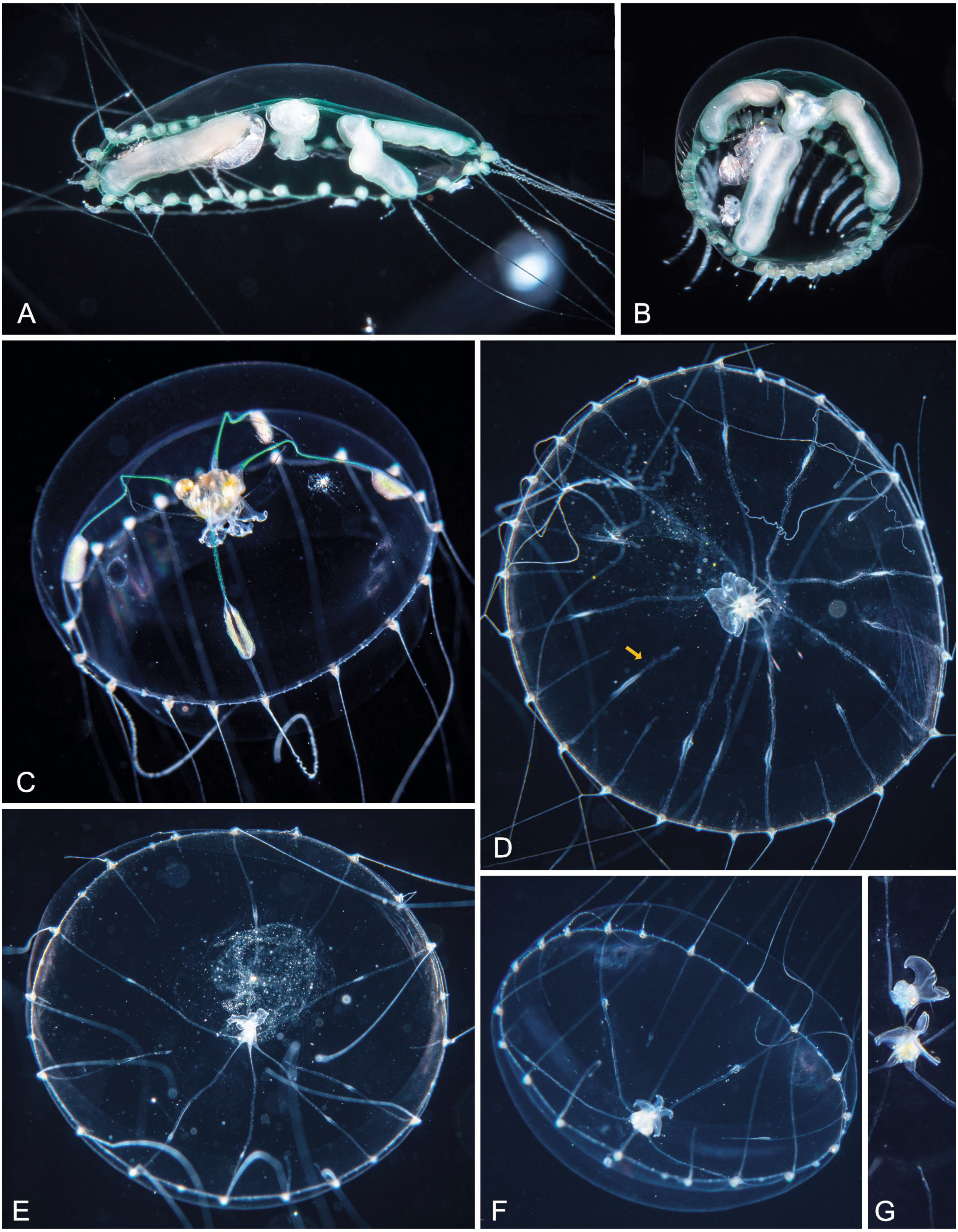

Fig. 46. *Clytia* ssp. (A-B) *Clytia linearis*, BFLA4077, bell dimeter 3.5 mm. (C) *Clytia* spec. 1, BFLA4283, bell diameter 10 mm. (D) ? *Clytia* spec. 2, BFLA4274, 3 mm; arrow points to incomplete centripetal canal. (E) ? *Clytia* spec. 2, BFLA4269, 4 mm. (F) ? *Clytia* spec. 2, BFLA4253, 3 mm, has 5 complete radial canals. (G) ? *Clytia* spec. 2, doubled manubrium of animal photographed 06-DEC-2019, 6 mm bell, not collected.

16S Data: The three samples gave all the same 16S sequence that did not show any sufficiently supported relationship to other *Clytia* medusae in the Campanulariidae 16S dataset of Cunha *et al*. (2017). A blastn search in GenBank gave *Clytia islandica* MF000548 as best match with 91% sequence identity.

Remarks: These medusae look like a typical *Clytia hemisphaerica*. The only notable feature are the green radial canals. This alone, however, cannot be used as a diagnostic feature and it is likely variable as in other hydromedusae. It was not possible to identify the species with any *Clytia* from Florida mentioned in Mayer (1900, 1910). The hydroid stage of this species must first be found to allow a naming and complete description of the species.

? *Clytia* spec.2

Fig. 46D-G

Examined material: BFLA4253; 1 specimen; 23-NOV-2019; size 3 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence MW528694. – BFLA4257; 1 specimen; 23-NOV-2019; size 2 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528694. – BFLA4269; 1 specimen; 04-DEC-2019; size 4 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528694. – BFLA4274; 1 specimen; 04-DEC-2019; size 3 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528694. – 06-DEC-2019; 1 specimen, 6 mm, photographed, not collected; most probably also belongs to this species.

Observations: Umbrella 2 to 4 mm in diameter when gonad development starts, flatter than hemisphere when relaxed, mesoglea moderately thick, thinning towards margin. Manubrium small, urn shaped, with 4 (5?) short perradial lips, margin smooth. Gonads just developing in middle of complete radial canals and also on some incomplete ones. Complete radial canals thin, numbering 5 to 9, originating from manubrium, often irregularly spaced, rarely seen branched, some not entirely straight. With 0 to 15 incomplete centripetal canals originating from circular canal (Fig. 46D), usually from marginal bulbs but not always, not reaching manubrium, length variable from very short to about 3/4 of complete radial canal length. 16 to 22 tentacles arising from small conical bulbs, few atentacular bulbs (3-6) present. Usually 2 statocysts between pairs of bulbs, variable from 1 to 4. Colour: Most specimens without colour, one had pink bulbs. A specimen for which no 16S data is available, but which looked otherwise indistinguishable, had two manubria (Fig. 46G), one being smaller.

16S Data: The four sequenced specimens gave all the same 16S sequence (MW528694). In a maximum likelihood tree (not shown) obtained by comparing it to the Campanulariidae 16S dataset of Cunha *et al*. (2017) it came out as sister lineage to a clade tentatively identified as *Clytia* cf. *stolonifera* Blackburn, 1938 (GenBank KX665270, KX665268) in Cunha *et al*. (2017). The base pair divergence between KX665270 and MW528694 is 7.2%.

Remarks: While the 16S data clearly identified it as a Campanulariidae, finding the correct genus of this material was difficult and is still unsettled. A specimen with five radial canals (Fig. 46F) suggests that it could be *Pseudoclytia pentata* Mayer, 1900, but the presence of centripetal canals is not compatible with this species. Mayer (1910) found and examined an immense number of *P. pentata* over several years and the number of radial canals was somewhat variable, but he never observed centripetal canals. Mayer's medusae rarely had two manubria, just like in our case (Fig. 46G), although we have no 16S data for this specimen to assure that it is the same species as the others examined here.

Our 16S sequence was relatively similar to sequences obtained from two campanulariid hydroids from Belize that resembled the Australian *Clytia stolonifera* (see Cunha *et al*., 2017). The observed divergence of 7.2% represent likely an interspecifc difference when compared to the values of Table 1, but with so few samples the value is currently inconclusive. In the phylogeny of Cunha *et al*. (2017), their hydroids did not cluster within the *Clytia* clade, but had an ambiguous phylogenetic position, frequently placed at the base of Obeliinae. This could mean that a genus other than *Clytia* may be needed for the specimens of Cunha *et al*. (2017) and also the medusa BFLA4253 of this study. DNA sequence information of the type species of *Pseudoclytia* and *Gastroblasta* must be obtained to resolve if one of these genera also belongs to this clade and could be the appropriate genus. For recent discussion of these genera see Gravili *et al.* (2007).

Genus *Gastroblasta* Keller, 1883

Gastroblasta Keller, 1883: 622; type species *Gastroblasta timida* Keller, 1883 by monotypy.

Diagnosis: Medusa when mature with more than one urn-shaped manubrium; up to 20 radial- and as many centripetal canals, some radial canals may be branched; marginal tentacles with bulbs; numerous statocysts, oval gonads developing near the middle of radial canals or also centripetal canals.

Hydroid like in genus *Clytia*, living embedded in sponges (Gravili *et al.*, 2007).

Gastroblasta timida Keller, 1883

Fig. 47A-C

Gastroblasta timida Keller, 1883: 622, pl. 35 figs 1-2. – Mayer, 1910: 279, fig. 151. – Kramp, 1961: 162. – Kramp, 1968: 75. – Gravili *et al.*, 2007: 400.

Examined material: 04-MAR-2019; 1 specimen photographed, not collected.

Observations: Bell diameter 6 mm, circular circumference, flatter than hemisphere, apex rather flat, jelly moderately thick, thickness rather even. Three manubria in middle region of bell, connected by the radiating corners of their bases, urn-shaped, mouth cruciform with four simple lips, not crenulated. 15 broad, band-like radial canals reaching circular canal, 12 incomplete centripetal canals originating from circular canal at the position of bulbs, reaching to variable height but not joined to manubrium. 70 large marginal bulbs with tentacles, tentacles long. About as many statocysts as bulbs. Gonads oval thickenings on radial- and centripetal canals, all about in middle of bell.

Remarks: This medusa matched rather well the description and figures of *Gastroblasta timida* given by Keller (1883) or Mayer (1910). The species was originally described from a number of specimens caught in the Red Sea, but has never been reported subsequently (Gravili *et al.*, 2007).

A closely related and better-known *Gastroblasta* species is the Mediterranean *G. raffaelei* Lang, 1886 (see Gravili *et al.*, 2007). It differs from *G. timida* in having a distinctly elliptical bell.

Multioralis ovalis Mayer, 1910 is the only known medusa species from the western Atlantic having multiple manubria. It has an oval bell and only a single radial canal, even when gonads begin to mature. Although it has been reported several times from different localities (Gravili *et al.*, 2007; Wang *et al.*, 2019), some authors like Kramp (1968) thought it to be an abnormal *Clytia*. Moreover, its structure corresponds to a stage in the development of *Gastroblasta raffaelei* (Gravili *et al.*, 2007).

Although structurally similar to the above described *Clytia* spec. 2 (Fig. 46D-G), the broad radial canals distinguish it immediately from it. Additionally, the general aspect and the tentacle number are different. Both share the presence of centripetal canals originating from tentacle bulbs. Some of them might later join the manubrium. In *Gastroblasta raffaelei* all but two opposite radial canals develop from centripetal canals (Gravili *et al.*, 2007).

We therefore hesitatingly attributed the present sample to *Gastroblasta timida*, despite the wide separation of the occurrences and the somewhat doubtful status of the species.

Distribution: Red Sea, Florida (this study). Type locality: Red Sea, Sudan, Suakin Harbour.

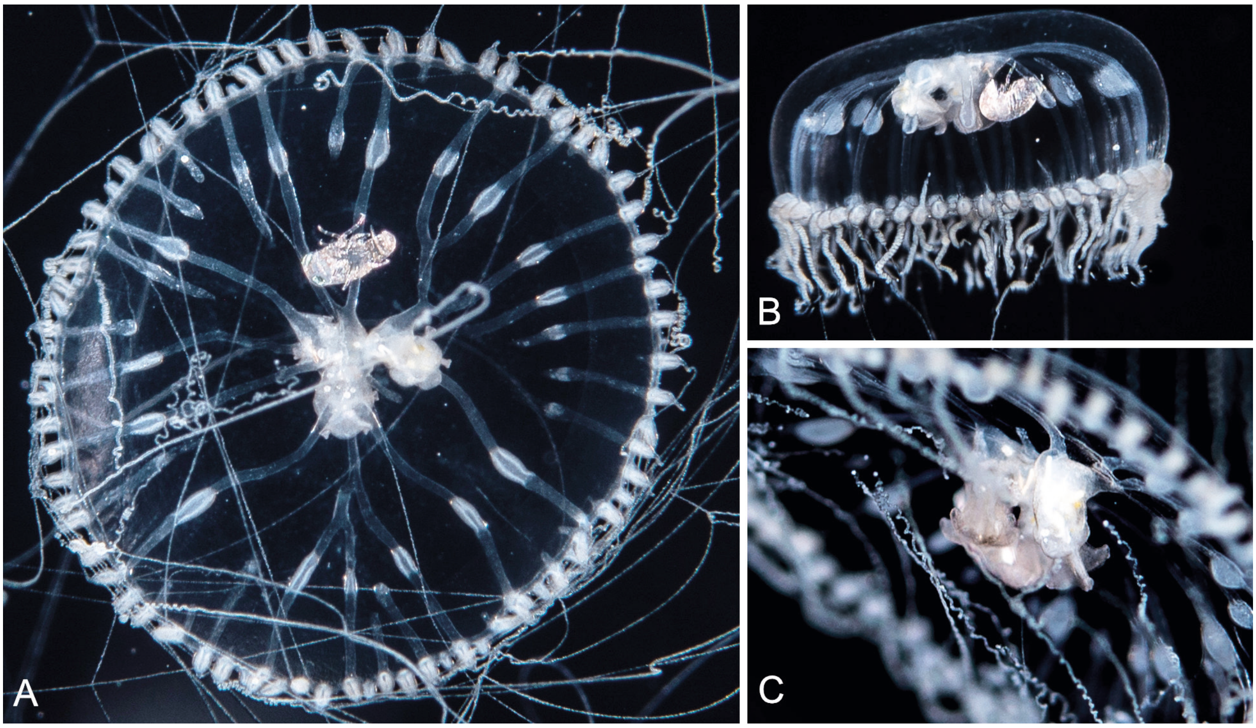

Fig. 47. *Gastroblasta timida*, diameter 6 mm, with crustaceans in subumbrella. (A) Whole animal. (B) Lateral view of contracted animal. (C) Close up of region with stomachs in lateral view.

Order Narcomedusae

Remarks: The families of the Narcomedusae have recently been reorganized by Lindsay *et al.* (2017) using DNA data. Bentlage *et al*. (2018) added more sequences. The 16S sequences of these studies and the ones from the present study were combined to get a maximum likelihood tree (Fig. 48). Although 16S has low resolving power above the genus level, some well supported nodes indicate that the Cuninidae and Solmarisidae are polyphyletic as already found by Bentlage *et al.* (2018). As revision of the families is beyond the scope of this study, we here used the family level taxonomy of Bouillon *et al.* (2006) and Lindsay *et al.* (2017), except for the genus *Otoporpa*.

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

Cunina Eschscholtz, 1829: 116; type species *Cunina globosa* Eschscholtz, 1829 (Kramp, 1961).

Cunoctantha Haeckel, 1879: 31; type species *Cunina octonaria* McCrady, 1859 by designation of Mayer (1910: 460).

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 becki Bouillon, 1985
Fig. 49A-F

Cunina becki Bouillon, 1985: 263, fig. 9.

Examined material: BFLA4022; 1 specimen; 15-FEB-2019; size 14 mm; preserved in formalin and deposited as UF-013444. – BFLA4023; 1 specimen; 15-FEB-2019; size 20 mm; preserved in formalin and deposited as UF-013444. – BFLA4025; 1 specimen; 15-FEB-2019; size 20 mm; part preserved in formalin and deposited as UF-013446, 1/4 part in alcohol for DNA extraction; 16S sequence MW528643.

Observations: Medusae flatter than hemisphere, 14 to 20 mm in diameter, jelly very soft and fragile, margin lobed. Stomach flat, circular, about 1/3 of bell diameter, mouth opening simple, circular (Fig. 49A). 16 band-like manubrial pouches radiating from stomach to the bell margin, pouches slightly widening to about 3/5 of their length, then gradually narrowing again before dividing above tentacle into two narrow peripheral canals or strands (Fig. 49E). The proximal 3/5 of the gastric pockets are more opaque (Fig. 49D) than the rest as the bottom contains the gonad tissue, in the present cases containing numerous, densely packed, small (16 µm), round cells interpreted as oogonia. Tentacles 16, between pairs of tentacles 4 to 7 otoporpae clasping bell margin (Fig. 49E). No peronia.

16S data: The sole 16S sequence clustered within a clade comprising Narcomedusae of different families (Fig. 48).

Distribution: Papua New Guinea, Florida (this study). Type locality: West Pacific, Bismarck Sea, Hansa Bay.

Remarks: *Cunina becki* has so far only been recorded from its type locality in the Bismarck Sea (western Pacific Ocean). It was thus very surprising to find it in the western Atlantic Ocean. The species may have been overlooked as it has a very fragile jelly, which might not withstand usual net collecting. *Cunina becki* is rather unusual for its genus – or even all Narcomedusae – in that the gastric pockets are very narrow and extend to the bell margin, resembling thus radial canals of other hydromedusae. While the main diagnostic features of our medusae – long and narrow gastric pockets, otoporpae, and peripheral canal or strand – match the description given in Bouillon (1985), there are nevertheless some slight differences:

- larger diameter (20 versus 15 mm)
- 16 gastric pockets and tentacles (versus 12-15)
- 4-7 otoporpae between successive tentacles (versus 3-4)
- the gastric pockets narrow gradually distal to the gonads (versus rather abrupt).

Considering the variability of other *Cunina* species (see e. g. Kramp, 1959a, 1968), we think that these differences are due to intraspecific variations and mainly correlated to the somewhat larger size.

With the available material it was not possible to decide if the peripheral canal is really a canal or just a tissue strand. Histological sections are needed to answer this.

Cunina octonaria McCrady, 1859
Fig. 50A-D

Cunina octonaria McCrady, 1859: 211, pl. 12 figs 4-5. – Kramp, 1959a: 199, fig. 307. – Kramp, 1961: 282, synonymy, references. – Kramp, 1968: 128, fig. 347. – Calder, 1971: 77, pl. 8I. – Goy, 1979: 286, fig. 28. – Bouillon, 1987: 197, figs 4A-B, 7A, photos 2-4. – Bouillon *et al.,* 1988a: 223. – Bouillon, 1999: 433, fig. 3.150. – Bouillon *et al*., 2004: 234, figs 144E, 145A, 149A-H. – Galea, 2007: 97, fig. 21O. – Nogueira, 2012: fig. 15. – Nagata *et al.*, 2014: 312, figs 31-32.

Cunina koellikeri Müller, 1861a: 41, pl. 4.

Foveolia octonaria. – A. Agassiz, 1865: 51.

Cunoctanthanparasitica Metschnikoff, 1882: 442.

Cunocantha octonaria. – Brooks, 1886: 361, pls 43-44, life cycle. – Mayer, 1910: 461, text figs 304-305, pl. 55 figs 1-2.

Cunoctantha octonaria var. *köllikeri*. – Mayer, 1910: 464, pl. 54 figs 4-9.

Examined material: 27-May-2019; 1 specimen photographed, not collected; size 7 mm, with beginning gonad maturation. – 27-NOV-2019; 1 specimen photographed, not collected; size 4 mm.

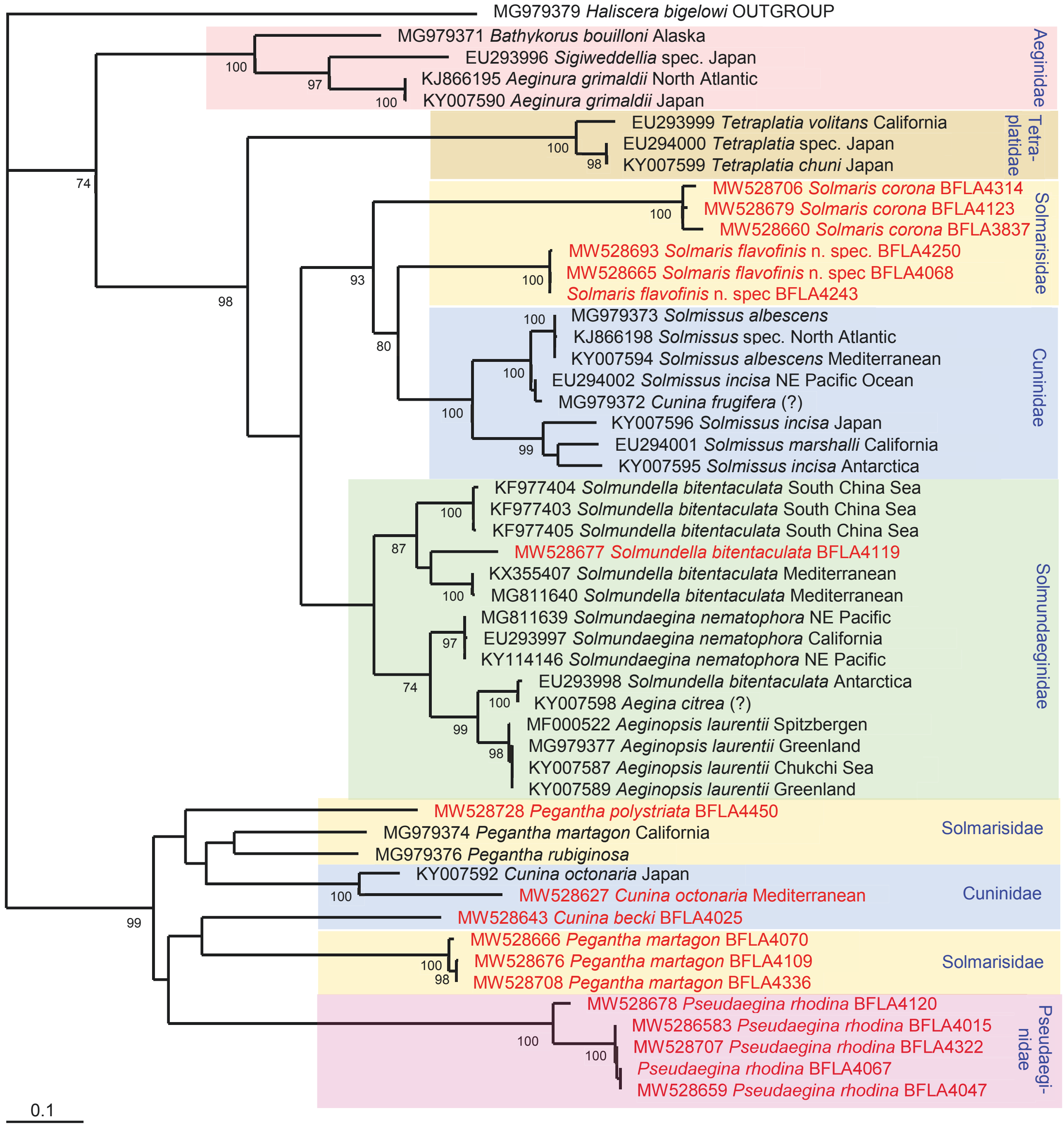

Fig. 48. Maximum likelihood phylogenetic tree of Narcomedusae obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Some proveniences were obtained from Lindsay *et al.* (2017) or through personal communications. Red labels are new sequences from this study. Coloured boxes indicate family affiliations according to the currently used system. (?) Denotes possible misidentifications.

Mediterranean, France, Bay of Villefranche-sur-Mer, 43.6860°N 7.3170°E, depth 0-70 m; 1 specimen collected 24-APR-2016, used for DNA extraction, 16S sequence MW528627.

Observations: Florida specimens up to 7 mm in diameter, somewhat flatter then hemispherical (Fig. 50B), stomach circular, about half the diameter of bell, without mesoglea cone, with eight broad, manubrial pockets shaped like an isosceles trapezium, region between pockets narrow, band-shaped (Fig. 50A). Eight tentacles originating in middle of pocket base with a short, conical root (Fig. 50C);

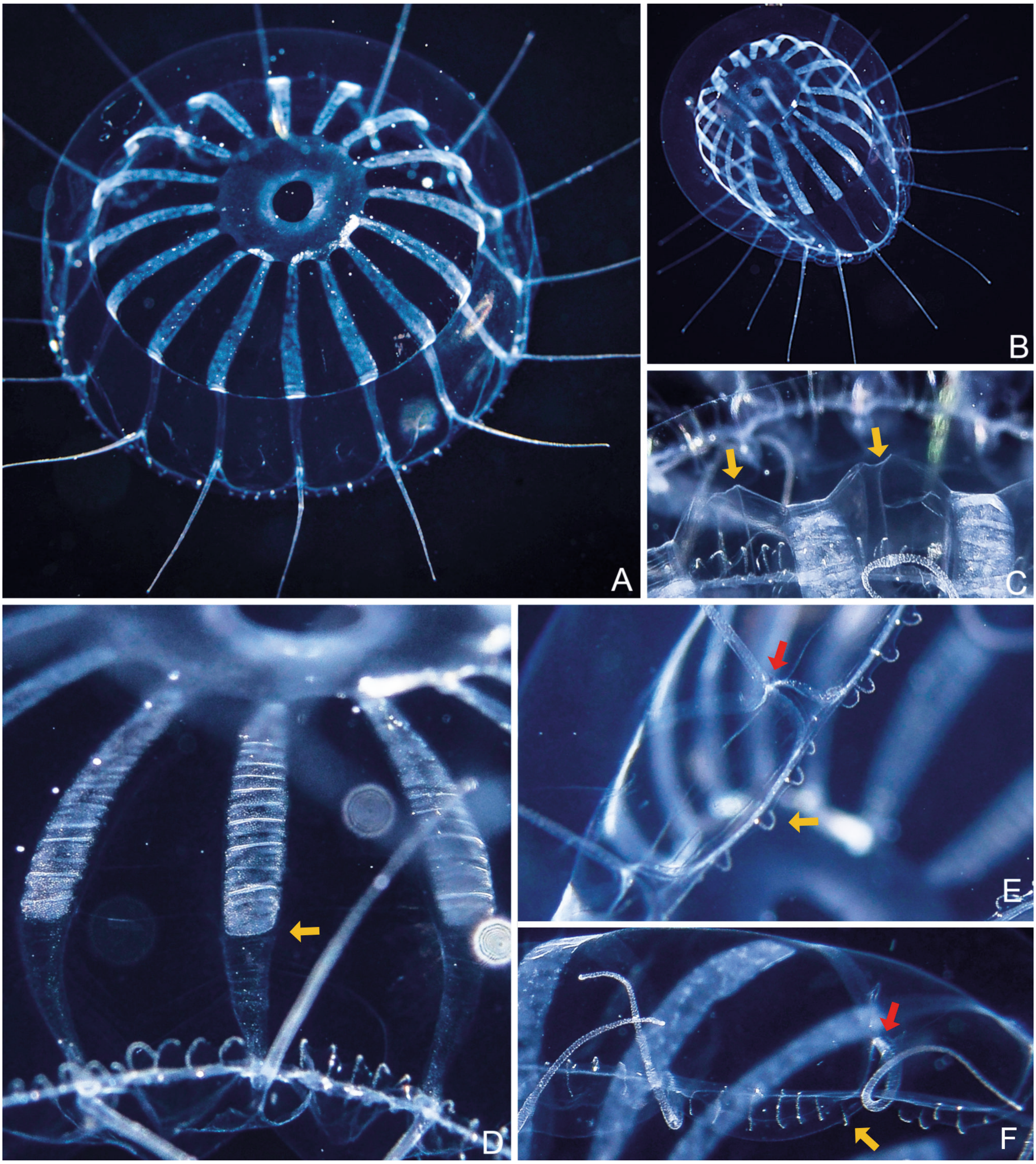

Fig. 49. *Cunina becki*. (A) Aboral view of whole animal, sample BFLA4022, diameter 14 mm. (B) Medusa in contraction phase, sample BFLA4025. (C) BFLA4023, side view showing optical cross-section through gastric pockets (secant plane of bell), oral side is downwards, arrows indicate the lateral margins of one gastric pocket. (D) Gastric pockets seen from above, note transition from the opaque zone with the developing gonads to clear part (arrow). (E-F) BFLA4022, bell margin showing several otoporpae per lappet (yellow arrows) and the bases of tentacles (red arrows).

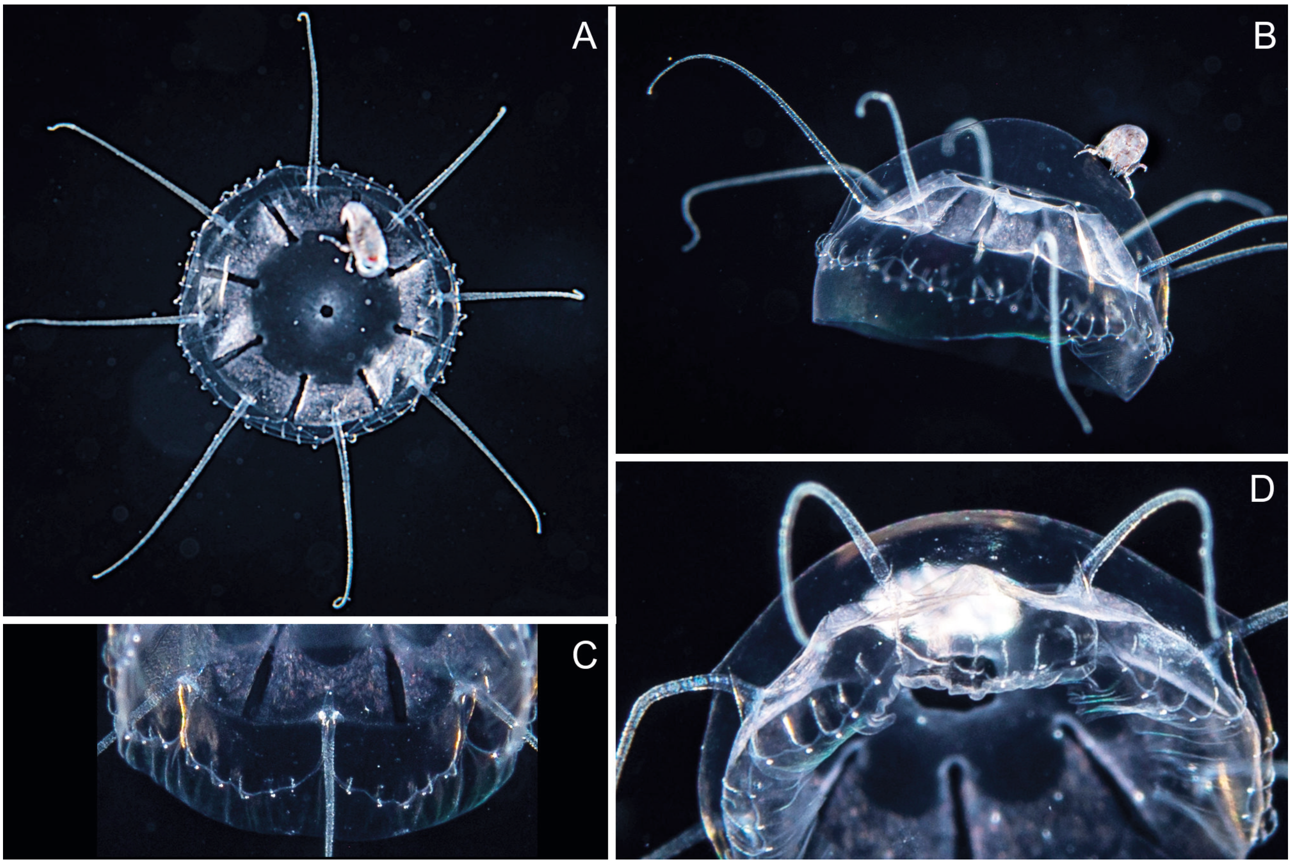

Fig. 50. *Cunina octonaria*, diameter 7 mm. (A) Aboral view of whole animal, with a crustacean on exumbrella. (B) Lateral view. (C) Close up of bell margin, note otoporpae and root of tentacle in middle, the velum is hanging downwards. (D) Oblique view from oral side. The bright spots below the otoporpae are the statocysts.

tentacles projecting from exumbrella at about ¼ between margin and apex of bell. Bell margin between pairs of tentacles lobed, with 4-5 otoporpae and statocysts.

Distribution: Widely distributed in tropical and warm-temperate parts of all oceans, including also the Mediterranean, the Chilean coast, and the South Atlantic (Kramp, 1968; Bouillon, 1999; Bouillon *et al.*, 2004; Galea, 2007; Nagata *et al.*, 2014). Type locality: USA, South Carolina, Charleston Harbor.

Remarks: No DNA samples could be obtained for the Florida specimens. The Mediterranean specimen differed in having 9 or 10 tentacles and pouches (damaged), one statocyst and otoporpe per lappet, manubrial pouches U-shaped.

Family Pseudaeginidae Lindsay, Bentlage & Collins, 2017

Pseudaeginidae Lindsay, Bentlage & Collins, 2017, in Lindsay *et al.*, 2017: 507.

Genus *Pseudaegina* Lindsay, 2017

Pseudaegina Lindsay, 2017 in Lindsay *et al.,* 2017: 507, type species *Aegina rhodina* Haeckel, 1879 by original designation.

Diagnosis: Narcomedusae with interradial manubrial pouches which are subdivied by a short septum in the middle; with peripheral canal system; with primary perradial tentacles alternating with pairs of marginal pouches; tentacle roots recurved orally without penetrating deep into central mesoglea; manubrial pouches begin at points of origin of primary tentacles; deep peronial grooves lined with nematocysts below but not above points of origin of primary tentacles; without secondary tentacles on umbrella margin; without otoporpae.

Pseudaegina rhodina (Haeckel, 1879)

Fig 51A-G, Fig. 52A-B

Aegina rhodina Haeckel, 1879: 338, pl. 20 figs 11-15. – Mayer, 1904: 27, pl. 4 figs 28-29. – Maas, 1905: 71, is Atlantic species. – Mayer, 1910: 452, plate 52, fig. 5; plate 54, figs 11, 11’-11’”.

Aegina canariensis Haeckel, 1879: 339. – Maas, 1905: 71, synonym of *A. rhodina*. – Mayer, 1910: 452, synonym.

Aegina eschscholtzi Haeckel, 1879: 339. – Maas, 1905: 71, synonym of *A. rhodina*. – Mayer, 1910: 453.

Solmundus tetralinus Haeckel, 1879: 351. – Maas, 1905: 71, synonym of *A. rhodina*. – Mayer, 1910: 452, synonym of *A. rhodina*.

? *Aegina lactea* Vanhöffen, 1908: 50, pl. 1 fig. 3.

Aegina citrea. – Bleeker & Van der Spoel, 1988: 244, figs 43-44. – Larson *et al.*, 1989: 789. – in part Kramp, 1959a: 61. [not *Aegina citrea* Eschscholtz, 1829]

Pseudaegina rhodina. – Lindsay *et al.*, 2017: 507, figs 11-13, redescription, new combination.

Examined material

Specimens with 5 tentacles: BFLA4015; 1 specimen; 17-JAN-2019; size 18 mm; part preserved in formalin and deposited as UF-013441, small part in alcohol for DNA extraction; 16S sequence MW528658. – BFLA4047; 1 specimen; 01-APR-2019; size 16 mm; part preserved in formalin and deposited as UF-013451, small part in alcohol for DNA extraction; 16S sequence MW528659. – BFLA4067; 1 specimen; 10-APR-2019; size 20 mm; part preserved in formalin and deposited as UF-013778, small part in alcohol for DNA extraction; 16S sequence identical to MW528659. – BFLA4322; 1 specimen; 24-JAN-2020; size 15 mm; part preserved in formalin and deposited as UF-013887, small part in alcohol for DNA extraction; 16S sequence MW528707. – 13-MAR-2020; 1 specimen; 15 mm; not collected.

Specimens with 4 tentacles: BFLA4120; 1 specimen; 04-JUN-2019; size 9 mm; part preserved in formalin and deposited as UF-013803, small part in alcohol for DNA extraction; 16S sequence MW528678. – BFLA4134; 1 specimen; 15-JUN-2019; size 11 mm; part preserved in formalin and deposited as UF-013809, small part in alcohol for DNA extraction; 16S sequence not determinable. – BFLA4118; 1 specimen; 04-JUN-2019; size 9 mm; part preserved in formalin and deposited as UF-013809, small part in alcohol for DNA extraction, not examined.

Observations

Form with 5 tentacles: Umbrella approximately hemispherical, 15-20 mm, jelly firm, apical mesoglea half the bell height, tentacles issue at about 2/3 of bell height, above tentacles a small bulge (Fig. 51A-B). Velum broad (Fig. 51A). Stomach about half the bell diameter, mounted on a rounded mesogleal cone of the same diameter reaching to level of bell margin (Fig. 51A). Mouth rim can form temporary folds or even a tubular extension with terminal folds (Fig. 51D-F). Five subdivided manubrial pockets (Fig. 51C-D). Manubrial pockets broadly U-shaped, reaching from stomach rim to about half the distance to bell margin (Fig. 51A), in middle a narrow septum which does not reach to the stomach level or level of tentacle origin (Fig. 51C, smp). At bottom of left and right side of the pairs of pouches originates a broad peripheral canal, directed first along peronium towards the bell margin and then following the latter (Fig. 51C). Five tentacles originating in upper half of medusa at about upper level of stomach, the proximal end embedded in an exumbrellar furrow, the tentacle roots rather short, entering the mesoglea, tapering, and curved towards oral (Fig. 51B); tentacle length about 2-3 bell diameters, curved towards oral, nematocysts concentrated on upper side but also present on underside. Below tentacles a deep cleft in exumbrella reaching down to bell margin, its floor with a thickened epidermis containing nematocysts (= peronium, Fig. 51C-G). 48 to ca. 68 statocysts. No otoporpae. Almost colourless, greenish or yellowish cast in daylight.

Form with 4 tentacles: As above, but only four tentacles and four pairs of manubrial pouches, size 9 to 11 mm, 36 to 60 statocysts.

16S data: In the maximum likelihood tree (Fig. 48), all five samples clustered in a lineage that was well separated from most other Narcomedusae. The clade had a distinct internal dichotomy with the single 4-tentacled specimen being rather apart from the 5-tentacled medusae (7.6 to 7.8% base pair differences). The three haplotypes of the 5-tentacled medusae were rather similar (0.18-0.36% divergences, Table 1).

Distribution: Tropical to subtropical Atlantic Ocean (Lindsay *et al.*, 2017). Type locality: Canary Islands, Lanzarote.

Remarks: Haeckel's type material of this species consisted in three specimens. Two of them had four tentacles and a size of 40 mm, one had five tentacles and measured 50 mm. He depicted a mature female with four tentacles. The statocyst numbers were given as two per manubrial hemi-pouch (16-20 in total).

Kramp (1955b, 1961) synonymized this species with the similar *Aegina citrea* Eschscholtz, 1829, an opinion already pondered by Mayer (1910). This view was upheld until Lindsay *et al.* (2017) revised *Aegina citrea* and split it into several species and belonging to separate families, this based on morphological and genetic differences. The main morphological difference to *Aegina* is the shape of the tentacle root. In *Aegina* they are curved towards aboral, in *Pseudaegina* they are curved towards oral.

Our specimens with 5 tentacles matched the description of Lindsay *et al.* (2017) very well as they came from the same region. There are, however, some differences to Haeckel's description. Our specimens were smaller (up to 20 mm) but all immature. The most obvious difference is the number of statocysts: Haeckel saw about 16-20, while we found regularly 60-68.

The haplotype divergence in our sample was high (p-value up to 7.8%) and in the maximum likelihood tree the samples split into two sub-clades (Fig. 48). This separation coincided with two morphotypes: the four- and five-tentacled form (see above). Unfortunately, we could get only one sequence of the four-tentacled form and due

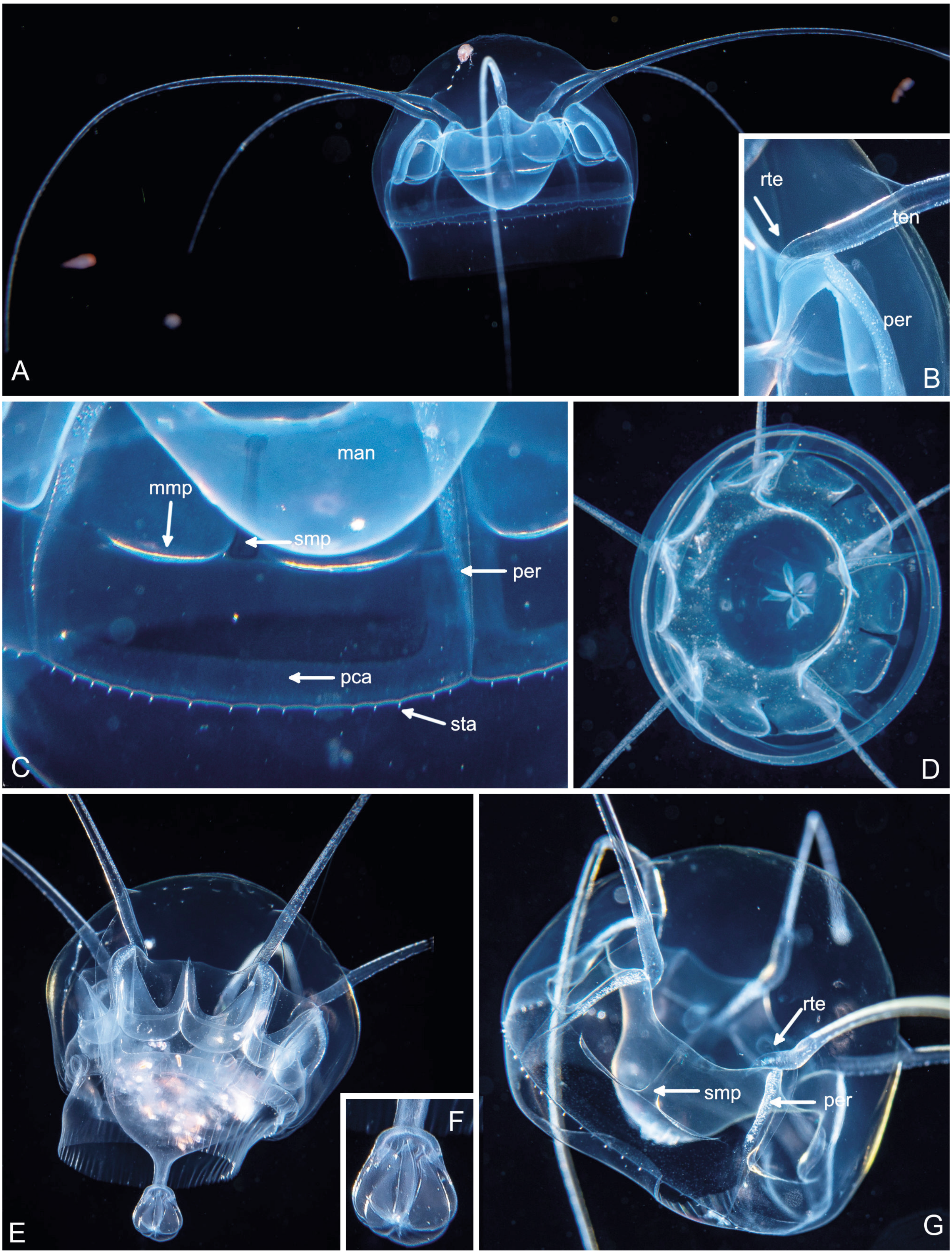

Fig. 51. *Pseudaegina rhodina* with 5 tentacles. (A-C) BFLA4015, size 18 mm. (D) BFLA4047, size 16 mm. (E-F) BFLA4067, size 20 mm. (G) BFLA4322, size 15 mm. (A) Lateral view. (B) Higher magnification of tentacle root (rte, arrow), note inflection towards below (= oral). (C) Details of bell margin. (D) Aboral view, note the (temporary) folding of mouth margin. (E-F) Medusa which has recently fed and its stomach is full of prey. Note the particular, most likely transitory, formation of a mouth tube and folded mouth margin, shown at higher magnification in F. (G). Lateral view. Abbreviations: man – manubrium/stomach covering conical jelly cone, mmp – distal margin of manubrial pouch, pca – peripheral canal, per – peronium, rte – tentacle root, smp – septum in middle of manubrial pouch, sta – statocyst.

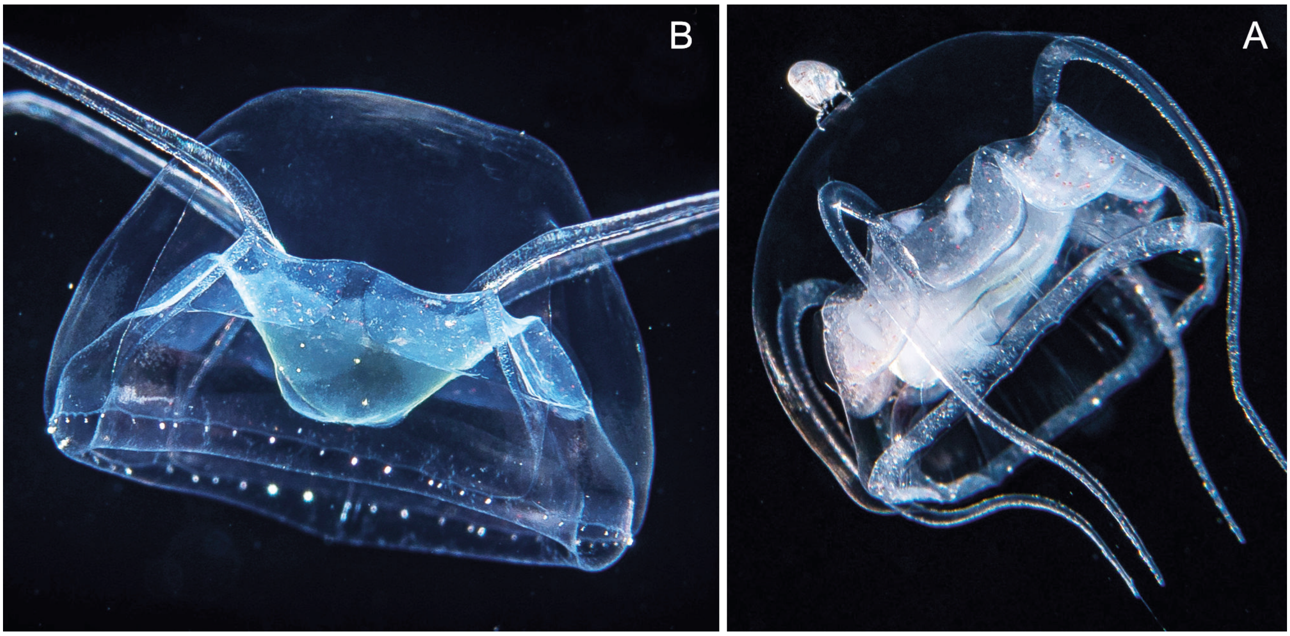

Fig. 52. *Pseudaegina rhodina* with 4 tentacles. (A) BFLA4134, size 9 mm, animal has semi-digested prey items in its gastric system including the peripheral canal system rendering it thus much more visible. (B) BFLA4120, bell size 9 mm, lateral view.

to the low number of samples, this distribution could also be due to mere contingency. The four-tentacled medusae were all smaller than those with five tentacles and it is nevertheless the possible that our material was composed of two sister-species. Because the original material of Haeckel included both four- and five-tentacled forms, it is not possible to use the tentacle number in the diagnosis of a new species without the designation of a lectotype (or a neotype as Haeckel's material is likely lost). A population-genetic study at the type locality combined with the designation of a neotype is thus needed to resolve this taxonomic problem. Because of these unresolved issues and because our samples were monophyletic, we felt it premature to describe one of the clades as a new species.

One particularity not mentioned in previous descriptions concerns the temporary folds of the mouth region (Fig. 51D-F). One of the figures in Lindsay *et al.* (2017: fig. 12C) also shows this ruffling of the mouth margin. In one of our animals the mouth was even drawn out to a tube ending in a flower-like, folded mouth region. The folds disappeared after fixation. It is thus unlikely that they can ever be seen in standard net-plankton samples.

Family Solmarisidae Haeckel, 1879

Genus Pegantha Haeckel, 1879

? *Pegasia* Péron & Lesueur, 1810: 340, type species *Pegasia dodecagona* Péron & Lesueur, 1810 by designation of Haeckel (1879).

? *Polyxenia* Eschscholtz, 1829: 118; type species *Polyxenia cynostylis* Eschscholtz, 1829 by monotypy.

Eurystoma Kölliker, 1853: 322, invalid homonym of *Eurystoma* Rafinesque, 1818 and others.

Pegantha Haeckel, 1879: 332; type species *Pegantha martagon* Haeckel, 1879 (Kramp, 1959a).

Pegantha (*Peganthella*) Haeckel, 1879: 332, no type species designated.

Pegantha (*Peganthissa*) Haeckel, 1879: 332, no type species designated.

Polycolpa Haeckel, 1879: 327, no type species designated. – Kramp, 1957c: 65, synonym.

Solmoneta Haeckel, 1879: 353, no type type species designated. – Mayer, 1910: 439, synonym.

Otoporpa Xu & Zhang, 1978: 50; type species *Otoporpa polystriata* Xu & Zhang, 1978 by original designation. **n. syn.**

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

Remarks: The genus *Otoporpa* Xu & Zhang, 1978 is here regarded as synonym of *Pegantha*. For more details see below under *P. polystriata*.

Pegantha martagon Haeckel, 1879

Fig. 53A-C

Pegantha martagon Haeckel, 1879: 332.

Polycalpa zonaria Haeckel, 1879: 327, Mediterranean.

? *Pegantha simplex* Bigelow, 1904: 260, pl. 5 figs 19-20. – Bigelow, 1909: 83.– Bigelow, 1918: 395, synonym of *P. martagon*.

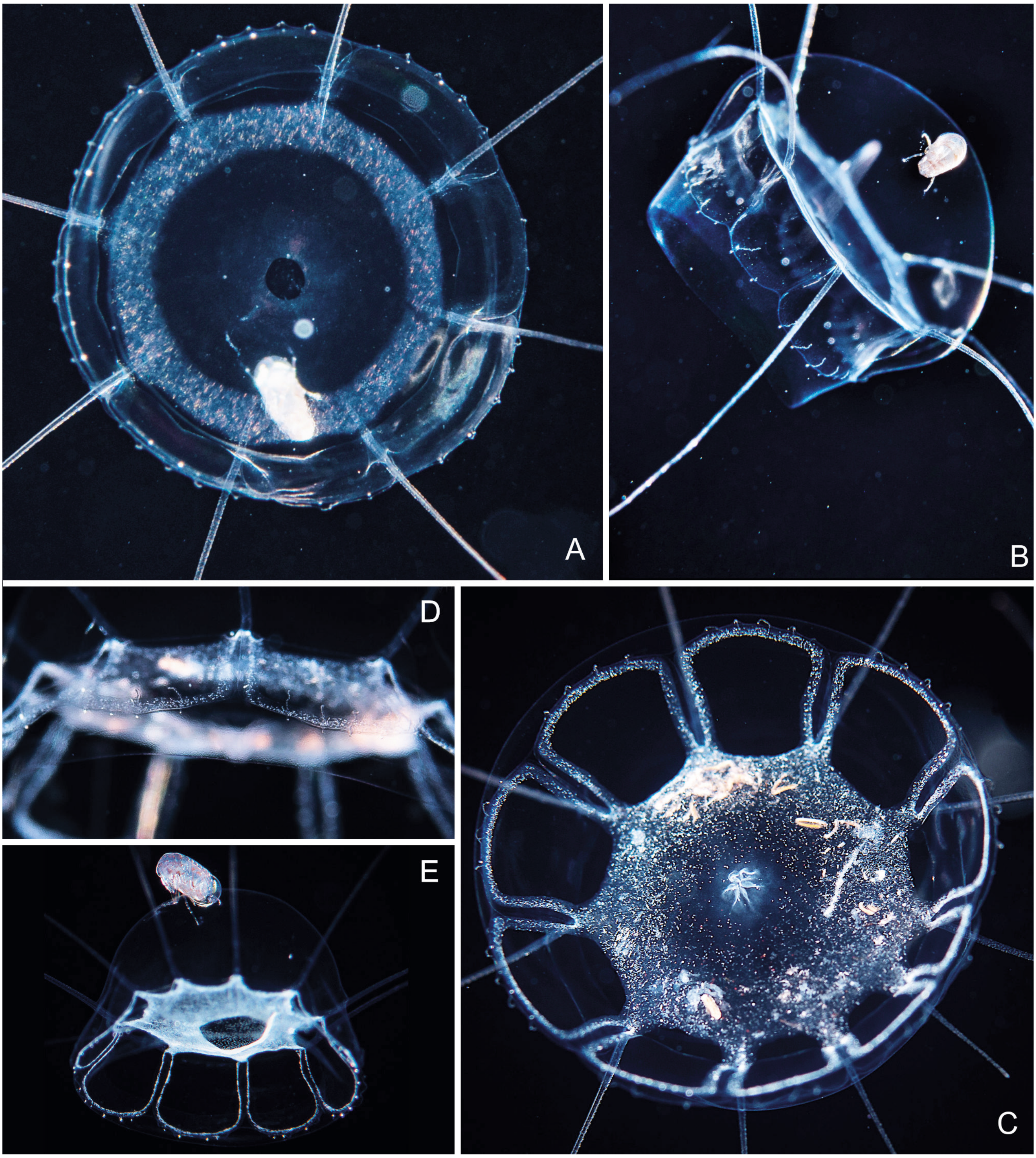

Fig. 53. *Pegantha martagon*. (A-B) Sample BFLA4109, diameter 8 mm. (A) Aboral view, the annular, more opaque structure was interpreted as food debris at the periphery of the stomach, the bright oval element is an out of focus crustacean. (B) Lateral view, note the clearly visible otoporpae and crustacean on the exumbrella. (C-D) BFLA4070, 10 mm. (C) Oral view. The bright, granular material is interpreted as partially digested food which fills the stomach and also the peripheral canal. Note also the closed mouth and the folds of the mouth margin. (D) Lateral view of bell margin. (E) BFLA4336, 6 mm, lateral view, the white matter in the gastric system is likely digested food.

Pegantha martagon. – Mayer, 1910: 443, figs 295-296. – Bigelow, 1909: 83, pl. 18 figs 1-8. – Bigelow, 1918: 396. – Kramp, 1955a: 160. – Kramp, 1957: 67, pl. 6 fig. 1, revision. – Kramp, 1959a: 64, 197, fig. 302. – Kramp, 1961: 274. – Kramp, 1968: 127, fig. 342. – Segura-Puertas, 1984: 45, pl. 14 fig. 1. – Pagès *et al.*, 1992: 41, fig. 49. – Larson *et al.*, 1989: 789, fig. 1A.

Examined material: BFLA4070; 1 specimen; 11-APR-2019; size 10 mm, 10 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528666. – BFLA4109; 1 specimen; 03-JUN-2019; size 8 mm, 8 tentacles; part preserved in formalin and deposited as UF-013796, small part in alcohol for DNA extraction; 16S sequence MW528676. – BFLA4336; 1 specimen; 07-FEB-2020; size 6 mm, 9 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528708. – 26-FEB-2018; 1 specimen photographed, not collected, 9 tentacles.

Observations: Medusae hemispherical or slightly wider than high, diameter 6-10 mm, 8-10 tentacles and marginal lappets (Fig. 53A, C, E), stomach wide, up to 2/3 of bell diameter, no gastric jelly cone (Fig. 53B, E), without manubrial pockets, peripheral canals originating below tentacles (Fig. 53C), first descending parallel along the peronial fold, then along lappet periphery, rather thin (1/6 of lappet width), width constant. Marginal lappets rectangular to rounded, with 4-5 otoporpae (Fig. 53B), these short, max. twice the size of the width of the peripheral canals. Statocysts near otoporpae, about as many as otoporpae. Tentacles curved, tapering, held at approximately 45° upwards, proximal end pointed and horizontal; below tentacles a slight furrow in the exumbrella with the peronium (Fig. 53A).

16S Data: The three obtained haplotypes have only low sequence divergences (Table 1, Fig. 48), but there was no significant relationship to a sequence of *P. martagon* from the Eastern Pacific (GenBank MG979374, Fig. 48).

Distribution: Widely distributed in the tropical and subtropical parts of the Atlantic and Indo-Pacific Ocean (Bigelow, 1909; Kramp, 1959a; Bouillon, 1978c; Bleeker & Van der Spoel, 1988; Navas-Pereira & Vannuci, 1991; Bouillon & Barnett, 1999; Segura Puerta *et al.*, 2003, 2009; Oliveira *et al.,* 2016), surprisingly also in the cold waters around South Georgia and in Antarctic waters (Kramp, 1959a; Toda *et al.*, 2008). Occurs in shallow waters, occasionally from 100 to 300 m depth (Kramp, 1957). Type locality: China Sea.

Remarks: Our samples had apparently not yet developed gonads, being thus not fully mature. The observed tentacle numbers of 8-10 were lower than the 16 given in Kramp (1959a, 1968), but this is a maximal number and most animals have actually only 10-13 tentacles and lappets (Bigelow, 1909; Kramp, 1957, 1959a). According to Bigelow (1909) and Kramp (1959a: 64), the final tentacle number (10-11) is attained early in development, though during further growth some few tentacles and lappets may occasionally be added.

Kramp (1957) observed that the lateral portions of peripheral canal in the lappets are broader than the transverse portions along the bell margin. This was not seen in the present material (Fig. 53C-E).

Pegantha simplex Bigelow, 1904 – a nominal species based on a type specimen from the Maldive Islands – was later synonymized with *Pegantha martagon* by Bigelow himself (Bigelow, 1909, 1918). We think that Bigelow's specimen from the Maldives nevertheless deviates quite strongly from the scope of *P. martagon* as described by later authors (see synonymy above). It was a small (3 mm) medusa but with fully developed, pendant-sac-like gonads. It had 8 tentacles/lappets and reportedly 25 statocysts per lappet, more than twice the number usually seen in *P. martagon*. Later, Bigelow (1909) re-examined this material and had to revise this number. The contraction of the alcohol preserved material feigned the presence of more statocysts. Actually, also Haeckel (1879) in his first description reported 13-15 statocysts per lappet. Because he also had preserved material, Bigelow (1909) assumed that he was likewise mistaken.

The gonads of *P. martagon* are variably described as a simple ring at the periphery of the stomach, or as irregularly lobed, pendant sacs. While it is possible that these two stages are only different developmental stages, we nevertheless suspect that the wide variation of the current concept of *P. martagon* indicates that it comprises several species. Our 16S sequences are very different from a tentatively identified *P. martagon* from California found parasitizing a planktonic polychaete *Tomopteris* (Bentlage *et al.*, 2018).

Pegantha polystriata (Xu & Zhang, 1978) new comb.

Fig. 54A-G

Otoporpa polystriata Xu & Zhang, 1978: 50, pl. 12 figs 65-67.

Examined material: BFL4450; 1 specimen; 08-JUN-2020; size 5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528728. – 02-SEP-2020; 1 specimen photographed, not collected, 2 mm. – Photos of two specimens kindly provided by Linda Ianniello, taken 21-MAR-2020 and 15-SEP-2020 during the same series of dives as for the other medusae of this study.

Observations: Bell diameter 5 mm, solid jelly, thickened aborally, margin subdivided in 8 to 9 U-shaped lappets (Fig. 54A, E), at margin of lappets 3 to 5 statocysts from which originate otoporpae (tracks of thickened epidermis with nematocysts, Fig. 54B, G) that extend almost to bell apex (Fig. 54B),

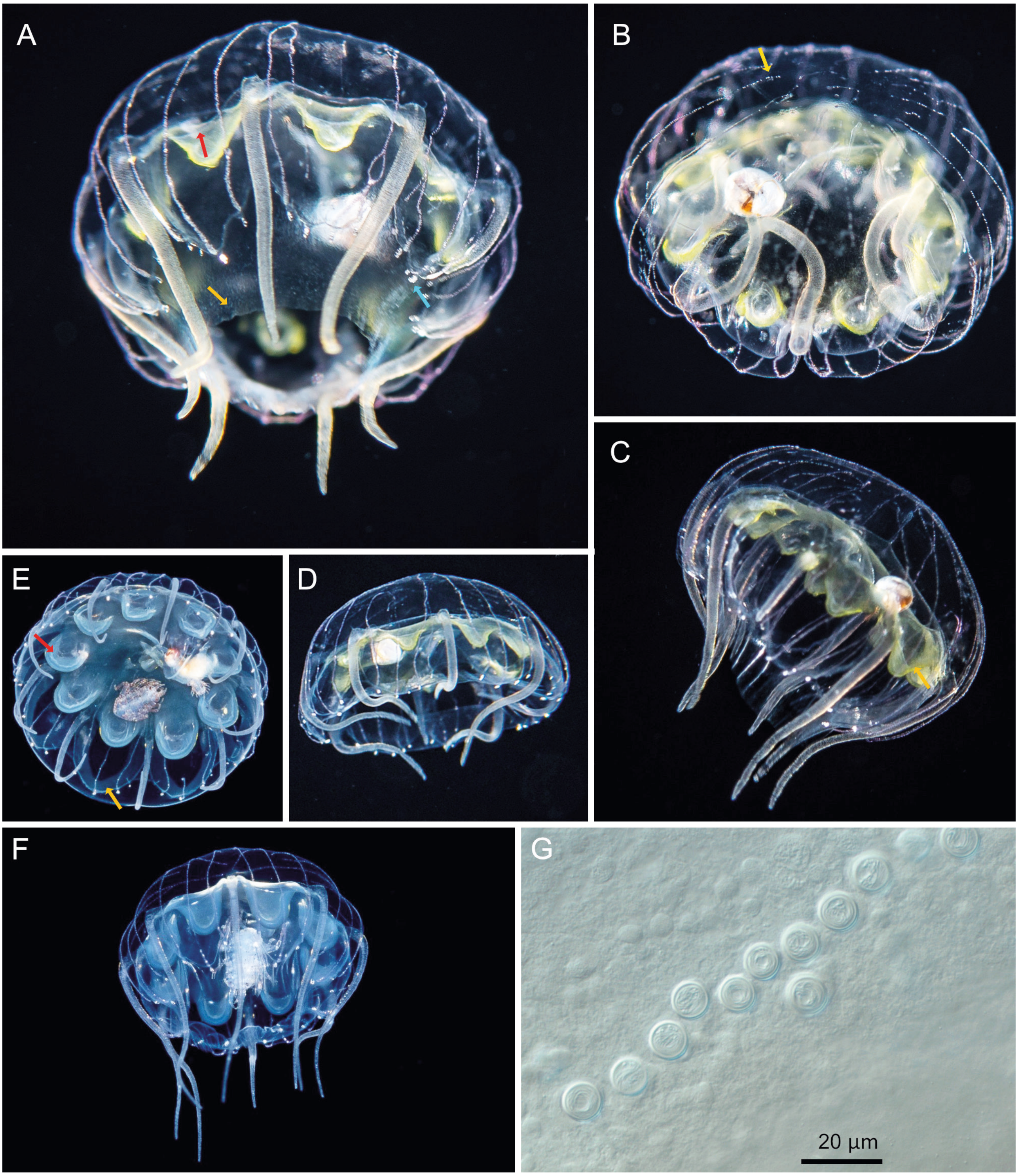

Fig. 54. *Pegantha polystriata*. (A-D) BFLA4450, bell diameter 5 mm. (A) Oblique view from oral side, the blue arrow points to a statocyst, the yellow one to the velum, the red one to the outer margin of the stomach. (B) Oblique view on bell top, arrow indicates otoporpae reaching almost to top of bell. (C-D) Lateral views, the arrow indicates the outer margin of the stomach. (E-F) Photos taken by Linda Ianniello, reproduced with the kind permission of the author. (E) Animal observed 21-Mar-2020 with nine tentacles, yellow arrow indicates peripheral canals, red arrow a gonad diverticulum hanging into subumbrella. (F) Animal observed 15-SEP-2020, the gonad diverticula appear like manubrial pocket. (G) BFLA4450, alcohol preserved, isorhiza nematocysts from exumbrellar otoporpae.

otoporpae sometimes irregular, branching, or not straight. Exumbrella apart of the nematocyst tracks smooth, without radiating keels or furrows. Velum broad (Fig. 54A). Stomach large, circular; near its periphery and positioned interradially 8 to 9 diverticula for the gonads (Fig. 54A-F), originating from stomach floor, in younger animals shallow, in older ones hanging into subumbrella (Fig. 54E); diverticula with thickened walls, dense tissue, sometimes yellow-green tint. Lappets of bell margin apparently with broad peripheral canal, difficult to see and observed only in one animal (Fig. 54E). Eight or nine thick, tapering tentacles originating in about middle of bell height in the bays between adjacent lappets (peronia), tentacles continued at right angles into the jelly as a pointed tentacle-root, tentacles held mostly in oral direction. Statocysts pendant, club shaped, with 2 to 5, usually 3, statoliths in a row, these increasing in size distally. Exumbrellar nematocysts: spherical isorhizas, ca. 10 *µm* (Fig. 54G).

16S data: The single sequence obtained clustered in a clade comprising other *Pegantha* as well as *Cunina* and *Pseudaegina* species, but without resolved internal relationships (Fig. 48).

Distribution: South China Sea, Taiwan Strait (Xu *et al*., 2014), Florida (this study). Type locality: Southern end of Taiwan Strait, 22.5°N, 118.5°E.

Remarks: Our medusae, especially the younger ones (Fig. 54C-D), appear indistinguishable from figures of *Otoporpa polystriata* given in Xu & Zhang (1978) and we are convinced that they are the same, despite this species is so far only known from the South China Sea. However, we think that this species was not classified in the correct family. The genus *Otoporpa* Xu & Zhang, 1978 was originally placed in the family Aeginidae (*sensu* Bouillon *et al.*, 2006) because it had apparently interradial manubrial pouches. The pouches of *Otoporpa* are atypical for Aeginidae as they are rather shallow and most importantly they are not sub-divided by a medium septum (see Fig. 51C, G). Likewise unusual for genera of the former Aeginidae (*sensu* Bouillon *et al.*, 2006), *Otoporpa* has otoporpae (thickenings clasping the bell margin and usually continued as nematocyst tracks on the exumbrella, comp. Figs 50C-D, 53B, D). We think that Xu & Zhang (1978) misinterpreted the developing gonad diverticula typical of the genus *Pegantha* as manubrial pouches. This is understandable as younger stages of these diverticula resemble indeed interradial manubrial pouches (Fig. 54C-D, F).

It is possible that some of the Brazilian specimens described by Tosetto *et al.* (2018) as *Pegantha triloba* Haeckel, 1879 belong to the present species. Tosetto's material lacked the diagnostic radial exumbrellar keels and furrows as shown in Bigelow (1909), it had 8 to 9 lappets and tentacles instead of 12 to 16 (Kramp, 1959a), and the otoporpae continued as nematocyst tracks to almost the top of the umbrella. The otoporpae in *P. triloba* are usually much shorter, but Kramp (1957) found also very long ones like in the present species in young *P. triloba*.

Genus *Solmaris* Haeckel, 1879

Pachysoma Kölliker, 1853: 322, type species *Pachysoma flavescens* Kölliker, 1853 by monotypy; invalid junior homonym of *Pachysoma* Macleay, 1821 [Insecta].
Solmaris Haeckel, 1879: 355, type species *Aequorea rhodoloma* Brandt, 1838 (designation by Kramp, 1961).
Solmaris (*Solmarium*) Haeckel, 1879: 355.
Solmaris (*Solmarinus*) Haeckel, 1879: 357.

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.

Remarks: For a synopsis of species in this genus see Bouillon *et al.* (1991: 408).

Solmaris corona (Keferstein & Ehlers, 1861)

Fig. 55A-C

Aegineta corona Keferstein & Ehlers, 1861: 94, pl. 14, figs 7-9.
Solmaris (Solmarinus) coronantha Haeckel, 1879: 359, pl. 20 figs 7-10, Canary Islands.
? *Solmaris multilobata* Maas, 1893: 45, pl. 4 figs 1-5.
Solmaris corona. – Haeckel, 1879: 358. – Mayer, 1910: 437, figs 288-289. – Russell, 1953: 476, figs 313, pl. 28 fig. 2. – Kramp, 1961: 278. – Pages, Gili, Bouillon, 1992: 42, fig. 51. – Bouillon *et al*., 2004: 236, fig. 147. – Nagata *et al.,* 2014: 313, fig. 33.

Examined material: BFLA3837; 1 specimen; 19-NOV-2018; size approximately 2-3 mm, 18 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528660. – BFLA4123; 1 specimen; 06-JUN-2019; size 9 mm, 25 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528679. – BFLA4314; 1 specimen; 24-JAN-2020; size 2 mm, 15 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528706. – 31-AUG-2018; 1 specimen photographed, 18 tentacles, not collected.

Observations: Umbrella diameter up to 9 mm, jelly lenticular (Fig. 55A), top with a broad, shallow apical projection; periphery with up to 25 lappets, distinctly rectangular (Fig. 55A-C), 1-3 statocysts per lappet (Fig. 55A). Stomach large, more than 2/3 of bell diameter, without gastric pockets, no peripheral canals. Presumable gonad tissue developing as slightly opaque ring on oral side of stomach (Fig. 55A). Up to 25 tentacles, issuing in about middle of bell height, curving upwards, rather stiff, but able to move and even to coil,

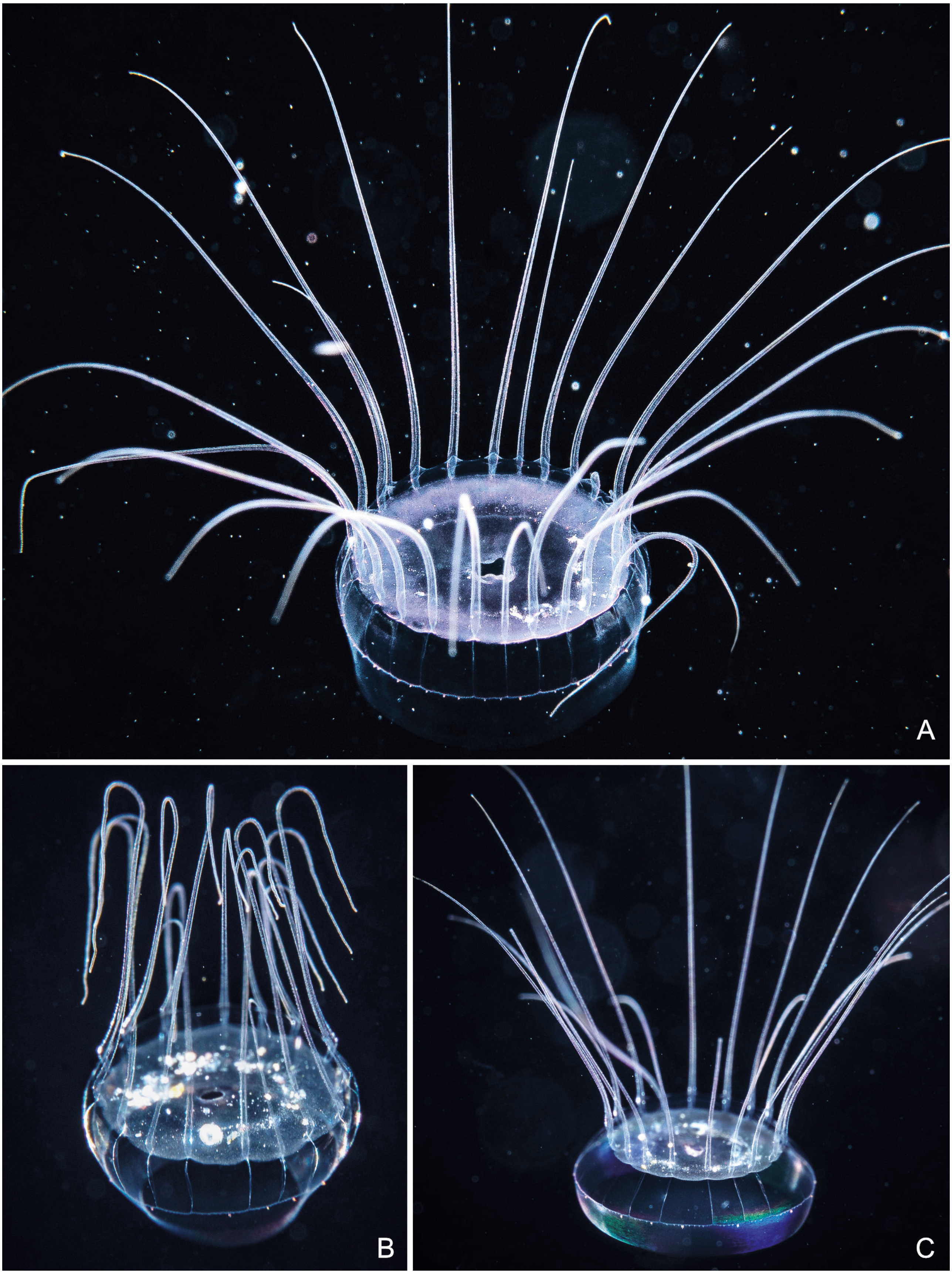

Fig. 55. *Solmaris corona*. (A) Specimen BFLA4123, diameter 9 mm. (B) BFLA4314, diameter 2 mm. (C) BFLA3837, diameter 2-3 mm.

evenly tapering to tip, length about 2-3 bell diameters, root short. Below tentacles no exumbrellar furrows, but thin peronia delimiting the lappets. Colour: stomach and tentacles a purple hue (Fig. 55A), some tentacle tips a very faint yellow (Fig. 55B).

16S Data: See Table 1 and Fig. 48.

Distribution: In the eastern Atlantic, from Norway to South Africa, in the western Atlantic from Florida to Brazil, also Indian Ocean (South Africa) (Pagès *et al.*, 1992; Nagata *et al.,* 2014; this study). Type locality: Mediterranean, Bay of Naples.

Remarks: Our identification as *S. corona* was primarily based on the description given in Russell (1953) and Pages *et al.* (1992). It is somewhat tentative because our specimens were probably not fully grown as they did not attain the maximal tentacle number of 36 and size of 12-15 mm given in Kramp (1953). The observed maximal number of 25 tentacles compares more favourably with the numbers given in the original description for mature animals (27-30, 14 mm diameter; Keferstein & Ehlers, 1861). Russell (1953) provides a table with observed sizes and tentacle numbers for an Irish population and our specimens agree approximately. During the course of its development *S. corona* changes very little in general appearance. There is merely an increase in the number of marginal lappets, tentacles, and sense organs (Russell, 1953).

It was not clear if the opaque ring in the stomach (Fig. 55A) is the developing gonad tissue or some residual, digested food. The slight purple colour let us favour it being the developing gonad tissue.

***Solmaris flavofinis* n. spec.**

Fig. 56A-H

Holotype: BFLA4068, 10-APR-2019; size 9 mm, mature female, 9 tentacles; part preserved in formalin and deposited as UF-013779 (damaged), small part preserved in alcohol for DNA extraction (MHNG-INVE-0137376); 16S sequence MW528665.

Paratype: BFLA4273; 04-DEC-2019; size 9 mm, 8 tentacles; preserved in formalin and deposited as UF-013841.

Other material: BFLA4243; 1 specimen; 11-NOV-2019; size 9 mm, 11 tentacles; preserved in alcohol for DNA extraction; 16S sequence identical to MW528665. – BFLA4250; 1 specimen; 23-NOV-2019; size 8 mm, 10 tentacles, mature female; preserved in alcohol for DNA extraction; 16S sequence MW528693.

Etymology: The specific epithet is derived from the Latin words *flavus* (yellow) and *finis* (end), an allusion to the yellow tentacle tips.

Description: Bell diameter 8-9 mm, height ~4-5 mm, lower part shaped somewhat conical, upper part less steep, with small, rounded apical projection (Fig. 56C); lower third of bell composed of 8 to 11 rectangular lappets (Fig. 56A-F), 1-2 statocysts per lappet (Fig. 56E). Stomach large, 2/3 of bell diameter, flat, without gastric pockets, no peripheral canals. Gonad tissue developing on periphery of oral side of stomach (Fig. 56A, B, F), only females unambiguously identified, forming up to 8 very large oocytes (Fig. 56B), often but not always in perradial position, size estimate ~0.7 mm, flattened lentil-shaped, well visible germinal vesicle (nucleus). 8 to 11 thin tentacles, issuing in about 1/3 of bell height, held upward (Fig. 56C) or downward (Fig. 56A), rather stiff, but able to move and even to coil (Fig. 56F), evenly tapering to tip, length about two bell diameters, root short (Fig. 56G). Below tentacles no exumbrellar furrows, but thin peronia delimiting the lappets. Statocysts bipartite, with inverted cone as base and spherical end with statocysts (Fig. 56H). Colour: colourless except for yellow tentacle tips (Fig. 56A, D).

16S Data: See Table 1 and Fig. 48. The p-distance to *S. corona* was very high (32%).

Remarks: The combination of the traits tentacle number (9-11), size (8-9 mm), and shape of the marginal lobes did not fit any of the known and accepted *Solmaris* species listed in Bouillon *et al.* (1991). Both the 16S and the morphological traits varied only in a relatively narrow range and we are convinced that these medusae represent a distinct species. The species resembling *S. flavifinis* most closely is the Mediterranean *Solmaris flavescens* (Kölliker, 1853) (for a good description see Mayer, 1910: 434, figs 284-286). *Solmaris flavescens* differs in being considerably larger (diameter 15-23 mm) and has more tentacles (usually 13-15, exceptionally 12 or 17). While the yellow tentacle tips of *S. flavifinis* permitted distinguishing it immediately from the co-occurring *S. corona* (see above), this is not a diagnostic trait because it is shared with *S. flavescens* (Kölliker, 1853: 322; Gegenbaur, 1857: 264; Metchnikoff, 1886: 19[257]). Another trait shared with *S. flavescens* is the large size of the oocytes, but several other Narcomedusae also have such large eggs (see table 4 in Bouillon, 1987).

Family Solmundaeginidae Lindsay, Bentlage & Collins, 2017

Solmundinae Haeckel, 1879: 349.

Solmundaeginidae Lindsay, Bentlage & Collins, 2017 in Lindsay *et al.,* 2017: 504.

Diagnosis: Narcomedusae with manubrial pouches interradial, divided into two to four parts; gonads in these pouches; exumbrellar, primary tentacles between marginal lobes; without a peripheral canal system; with two or four primary tentacles leaving umbrella

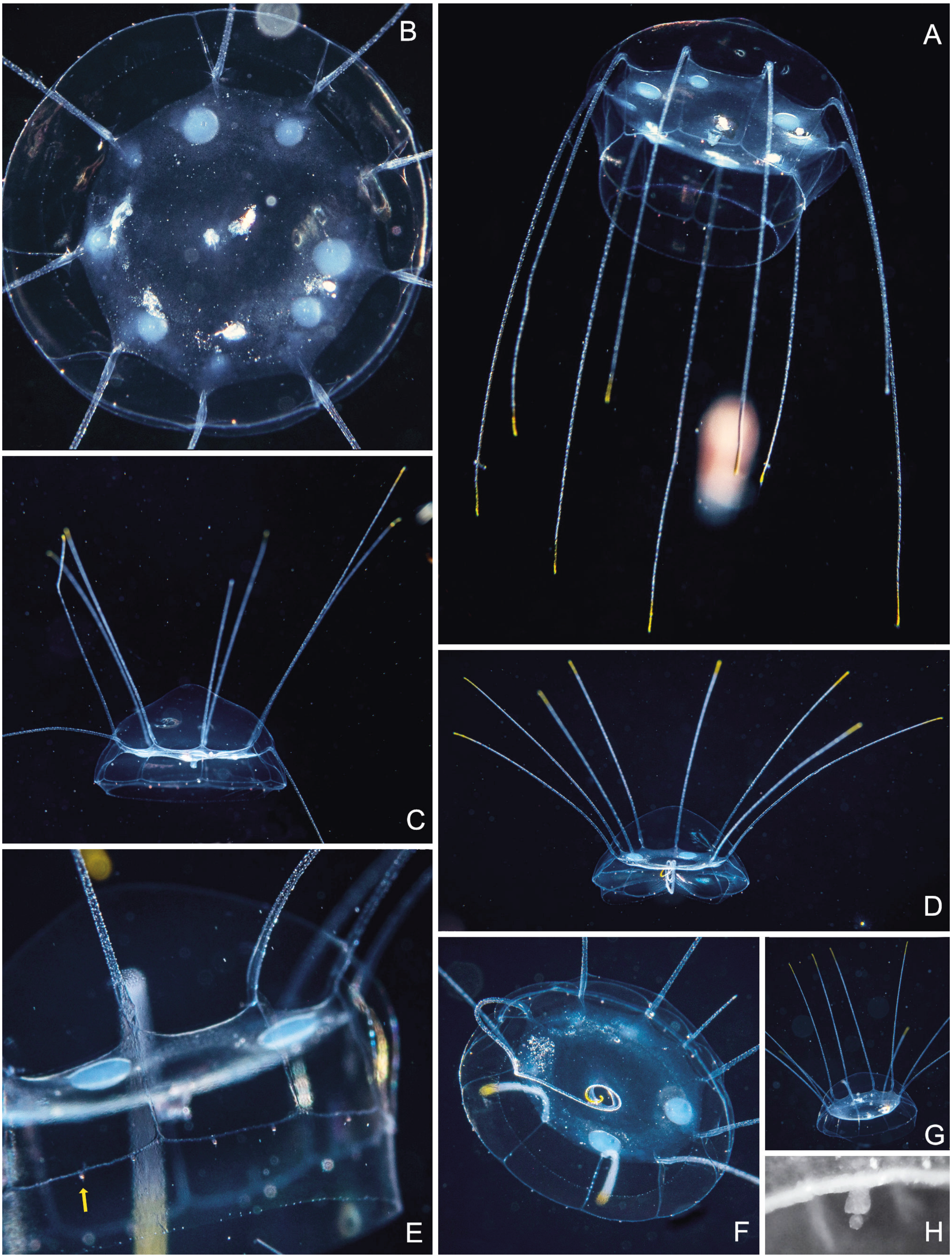

Fig. 56. *Solmaris flavofinis* n. spec. (A-C) Holotype (BFLA4068), diameter 9 mm. (A) Oblique view from aboral side. (B) View from aboral side, note large oocytes with germinal vesicles. (C) Lateral view. (D-F) BFLA4250, diameter 8 mm. (D) Lateral view. (E) Close up of three lappets with statocysts (arrow). (G) BFLA4243, 9 mm. (H) BFLA4273, preserved sample, statocyst enlarged.

in apical half, well above level of stomach pouches; tentacle roots acutely recurved orally; no nematocyst-laden, deep peronial grooves; with peronia, equal or twice as many in number as the primary tentacles; without secondary tentacles on umbrella margin but with rudimentary bulbs; with or without nematocyst patches covering exumbrella. Represented by the genera *Solmundaegina, Solmundella*, *Aeginopsis*, and *Solmundus* (Lindsay *et al*., 2017).

Remarks: When splitting the former Family Aeginidae, Lindsay *et al*. (2017) proposed this new family name based on their new genus *Solmundaegina* and included also the other genera listed above. They may have overlooked that by including the genus *Solmundus* Haeckel, 1879 there is already a family level name for this group available, namely the subfamily Solmundinae Haeckel, 1879, which is also valid at the family level as Solmundidae Haeckel, 1879. However, we agree with Lindsay *et al.* (2017) that the type species of *Solmundus* (*S. tetralinus* Haeckel, 1879) is a doubtful species, perhaps an aberrant *Solmundella bitentaculata* with four tentacles. Family names should not be based on dubious genera and species and it is advisable to remove *Solmundus* from the Solmundaeginidae.

Genus *Solmundella* Haeckel, 1879

Solmundella Haeckel, 1879: 352, type species *Charybdea bitentaculata* Quoy & Gaimard, 1833.

Aeginella Haeckel, 1879: 340, invalid junior homonym of *Aeginella* Boeck, 1861 [Crustacea].

Diagnosis: Narcomedusae with eight manubrial pouches; without peripheral canal system; four peronia, two long tentacles; no secondary tentacles; no otoporpae.

Solmundella bitentaculata (Quoy & Gaimard, 1833)

Fig. 57A-C

Carybdea bitentaculata Quoy & Gaimard, 1833: 295, pl. 25 figs 4-5.

Campanella capitulum Quoy & Gaimard in de Blainville, 1834: 286. – Agassiz, 1865: 169.

Aeginopsis mediterranea Müller, 1851: 277, pl. 11, Mediterranean.

Aeginella dissonema Haeckel, 1879: 340, pl. 20 fig. 16, Canary Islands. – Kramp, 1955b: 308, synonym.

Solmundella muelleri Haeckel, 1879: 352, Canary Islands. – Kramp, 1955b: 308, synonym.

Solmundella henseni Maas, 1893: 55, pl. 5 fig. 11, Florida Current.

Aeginella bitentaculata. – Haeckel, 1879: 341.

Solmundella bitentaculata. – Bigelow, 1909: 77, pl. 2 fig. 3. – Mayer, 1910: 455, fig. 301, record Florida. – Vanhöffen, 1912: 392. – Vanhöffen, 1913a: 428, record Florida. – Kramp, 1959a: 195, fig. 297. – Kramp, 1961: 270. – Rajan, 1963: 314, figs 1-5, larval stages. – Kramp, 1968: 124, fig. 338. – Goy, 1979: 285, fig. 26. – Segura-Puertas, 1984: 44, pl. 13 fig. 3. – Bouillon, 1987: 239, fig. 5, pl. 1 figs 1-5, development. – Pagès *et al.,* 1992: 38, fig. 43. – Buecher *et al*., 2005: 30. – Galea, 2007: 96, pl. 2O. – Wang *et al.,* 2014: 98, fig. 3

Solmundella bitentaculata var. *mediterranea*. – Mayer, 1910: 456, fig. 302, pl. 54 figs 1-3, pl. 55 fig. 4. – Neppi & Stiasny, 1913: 60.

Solmundella mediterranea. – Vanhöffen, 1912: 393, status. – Browne, 1916: 201. – Thiel, 1936: 68, synonym.

Examined material: BFLA4119; 1 specimen; 04-JUN-2019; size 4 mm; preserved in alcohol for DNA extraction; 16S sequence MW528677. – BFLA4422; 1 specimen; 28-MAY-2020; size 2 mm; preserved in alcohol for DNA extraction but specimen was lost. – 24-SEP-2018; 1 specimen; photographed, not collected.
MHNG-INVE-31746; Mediterranean, Bay of Villefranche-sur-Mer; 43.6860°N 7.3170°E; 0-70 m depth; collection date 03-MAY-2001; 2 mature males, 4 mm diameter; part preserved in formalin, part in ethanol in alcohol for DNA extraction; 16S sequence KX355407. – 28-APR-2014; locality as previous sample; 1 specimen, 3 mm diameter, with gonads; preserved in alcohol for DNA extraction; 16S sequence MG811640.

Description: Florida specimens with bell size up to 4 mm, as wide as high, umbrella circumference round (not oval, Fig. 57C), apical jelly thick resembling an apical process (Fig. 57B), evenly rounded and not keeled or oval in transverse section. Stomach wide, up to 7/10 of bell diameter, lenticular, without distinct gastric jelly cone; eight rectangular stomach pouches, no peripheral canal visible. Two opposite tentacles, these thick and long (~18 mm), tapering, originating in middle of bell, held variably upward or downward, held upwards in furrow of exumbrella that reaches almost to top of umbrella, below tentacles also a furrow with peronium, intertentacular peronium indistinct. Bases (roots) of tentacles in mesoglea, tapering, curved towards oral. 14 or more statocysts. Mouth region green, tentacles sometimes with broad yellow regions.

16S Data: See Table 1 and Fig. 48. The available 16S sequences appear polyphyletic, notably the one from an Antarctic medusa is clearly not related to the other ones which all form a well supported clade, but with deep subdivisions.

Distribution: Widely distributed in all oceans, including the Mediterranean, but rare in the northern parts of the Atlantic and Pacific Oceans; circumpolar in Antarctic seas; from surface to fairly deep water (Kramp, 1959a). This species is one of the most widespread of planktonic animals and is found at nearly all latitudes (Larson & Harbison, 1990). Type locality: Pacific Ocean, Banda Sea, Bay of Ambon (Moluccas, Indonesia).

Remarks: The taxonomic history of *Solmundella bitentaculata* is marked by the question whether

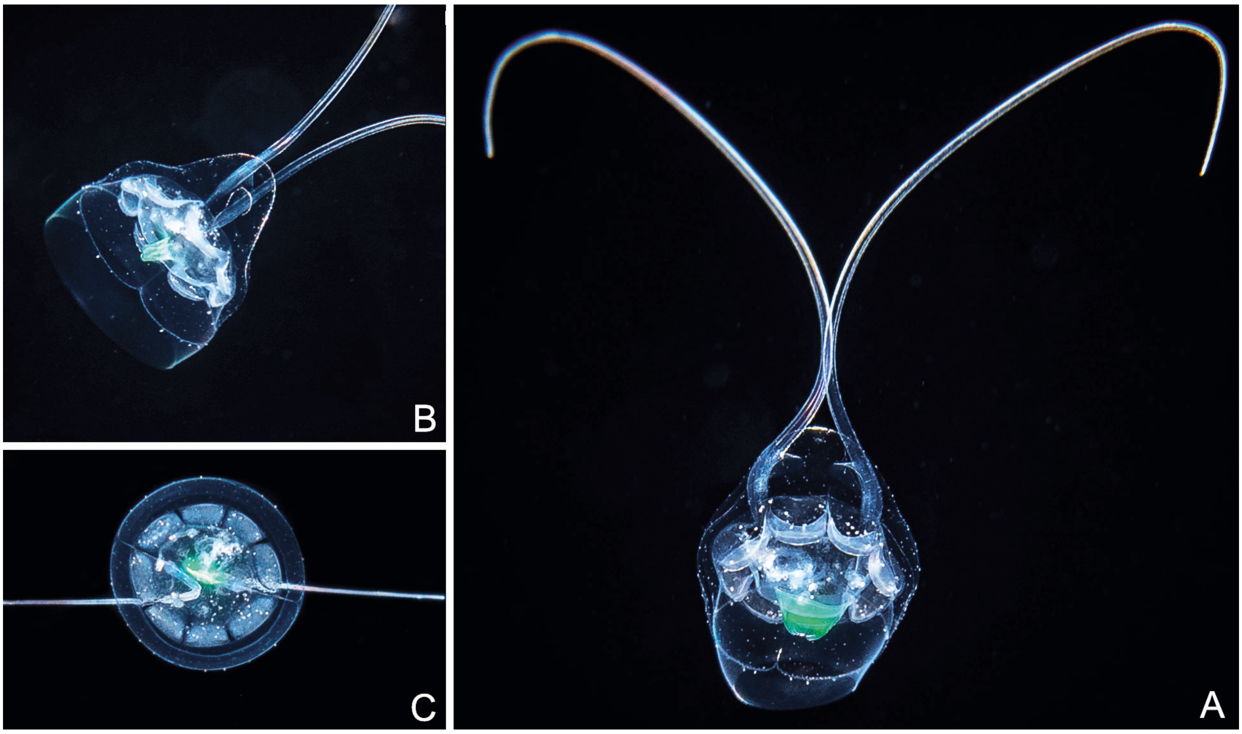

Fig. 57. *Solmundella bitentaculata*, sample BFLA4119, bell diameter 4 mm. (A-B) Lateral views of whole animal, note the green mouth region. (C) Aboral view.

S. mediterranea is distinct from it or conspecific. Summarizing Mayer (1910) and Browne (1916), the two differ by the following traits [in square brackets traits observed in the present study]:

- size when fully mature (12-15 mm *versus* 4-6 mm) [4 mm]
- shape (bell outline, diameter in tentacular axis larger than in intertentacular axis, bell apex keel-shaped *versus* circular bell and apex rounded)[round]
- tentacle length (up to 100 mm versus 10-18 mm) [18]
- peronial furrows (perradial ones deep versus all shallow)[shallow]
- statocysts in fully grown animals (16 versus 8) [14]

Mayer (1910) and Browne (1916) thought that the two names refer to simple variants or growth stages. Thiel (1936) and Kramp (1955b; 1961) listed them as synonyms, this being accepted by subsequent authors. Our Florida specimens matched mostly the *S. mediterranea* morphotype, except for the statocyst number.

Another geographic variation was reported by Vanhöffen (1912) and Browne (1916) for Antarctic populations: they have clusters of nematocysts on the ex-umbrella, especially near the margin.

The maximum likelihood tree (Fig. 48) shows that one sequence (EU293998, from Antarctica according to voucher specimen data) is far apart from the other *Solmundella* which cluster in a monophyletic clade. However, there are possibly some problems with the identification of this specimen as it has almost the same sequence as an *Aegina citrea* of unknown origin (KY007598). The 16S of the Pacific, Mediterranean, and Gulf stream samples formed a well supported clade. The divergences within this clade are high (Table 1) and the three subclades could represent three species. A reconsideration of the morphological differences and the different nominal species in the synonymy listed above is thus warranted. Unfortunately, no morphological data are available for the Pacific specimens used to get the 16S sequences.

Order Trachymedusae
Family Rhopalonematidae Russell, 1953
Genus *Aglaura* Péron & Lesueur, 1810

Aglaura Péron & Lesueur, 1810: 351; type species *Aglaura hemistoma* Péron & Lesueur, 1810 by monotypy.

Lessonia Eydoux & Soulyet, 1852: 643; type species *Lessonia radiata* Eydoux and Soulyet, 1852 by monotypy; preoccupied by *Lessonia* Swainson, 1832 [Aves].

Stauraglaura Haeckel, 1879: 277; type species *Stauraglaura tetragonima* Haeckel, 1879 by monotypy; nomen dubium.

Diagnosis: Rhopalonematidae with slender gastric peduncle; with eight mobile, sausage-shaped gonads attached on peduncle and not on subumbrella; tentacles numerous, all alike; with pendant, club-shaped statocysts on bell margin.

Aglaura hemistoma Péron & Lesueur, 1810

Fig. 58A-D

Aglaura hemistoma Péron & Lesueur, 1810: 351. – Haeckel, 1879: 275, pl. 16 figs 3-4. – Vanhöffen, 1902: 78, synonymy. – Bigelow, 1909: 119, pl. 2 fig. 6, synonymy. – Mayer, 1910: 398, fig. 254, pl. 46 figs 4-5, pl. 49 figs 3-7, pl. 50 fig. 11. – Kramp, 1959a: 192, fig. 291 – Kramp, 1961: 251. – Kramp, 1965: 127, distribution. – Kramp, 1968: 122, fig. 331. – Bouillon, 1978a: 162, cnidome. – Fagetti, 1973: 41, pl. 4 fig. 13. – Goy, 1979: 284, fig. 25. – Pagès *et al*., 1992: 44, fig. 53. – Bouillon *et al*., 2004: 241, fig. 152G. – Nagata *et al*., 2014: 316, figs 36-37.

Lessonia radiata Eydoux & Soulyet, 1852: 643, pl. 2 fig. 16, Pacific Ocean.

Aglaura Peronii Leuckart, 1856: 10, pl. 1 fig. 5, Mediterranean. – Haeckel, 1879: 275, synonym.

Aglantha globuligera Haeckel, 1879: 272, pl. 16 fig. 8, Canary Islands. – Kramp, 1959a: 192, synonym.

Aglaura nausicaa Haeckel, 1879: 274, pl. 16 fig. 1, Mediterranean.

Aglaura laterna Haeckel, 1879: 274, pl. 16 fig. 2, Canary Islands.

Stauraglaura tetragonima Haeckel, 1879: 277, pl. 16 figs 10-11, coast of Australia. – Kramp, 1961: 264, probably *A. hemistoma*.

Aglaura prismatica Maas, 1897: 24, pl. 2 figs 4-5, Gulf of Panama, Pacific Ocean. – Maas, 1906a: 97, pl. 3 fig. 12.

Aglantha octogona Bigelow, 1904: 257, pl. 7 fig. 9, Maldives.

Aglaura ciliata Perkins, 1906: 118, Tortugas.

Examined material: BFLA3808; 4 specimens observed, one collected; 19-OCT-2018; size 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528640. – BFLA4214; 1 specimen; 27-AUG-2019; 2 mm; parts preserved in formalin (UF-013830) and in alcohol for DNA extraction; 16S sequence MW528686. – 20-AUG-2019; 1 specimen photographed; size 3 mm; not collected.

MHNG-INVE-0031745; Mediterranean, Bay of Villefranche-sur-Mer, 43.6860°N 7.3170°E, depth 0-70 m; collection date 03-MAY-2001; numerous specimens collected, some preserved in formalin, one used for DNA extraction, 16S sequence KP776748.

Observations: Specimens from Florida with bell size of 2 mm, cylindrical shape, aboral side with funnel-like depression (Fig. 58C), wall very thin, velum broad, with slender gastric peduncle of 2/3 of subumbrellar height (Fig. 58D). Manubrium protruding through velar opening (Fig. 58A-D), bipartite, upper part sac-like, lower half with cruciform cross-section, ending in four-lipped mouth (Fig. 58B), margins smooth, not crenulated. Gonads eight sausage-shaped apendices in a whorl attached at junction of manubrium to peduncle (Fig. 58A-C). Eight radial canals, thin and very transparent. Seven or eight statocysts (Fig. 58B) on bell margin and about 70 thin tentacles. Mostly colourless, but interference effects often cause iridescence in rainbow colours (Fig. 58A, D).

16S Data: The two haplotypes of this study differed in 0.9% of the base pairs, while the minimal differences to other population were 2 to 5 % (Table 1). In a maximum likelihood tree (not shown) obtained by comparing it to the Trachymedusa 16S dataset of Bentlage *et al*. (2018) and additional trachyline sequences from GenBank, all *Aglaura hemistoma* clustered as a monophyletic group.

Distribution: Widely distributed and common in the warm and temperate parts of the Atlantic-, Indian-, and Pacific Oceans, usually between about 40°N and 40°S including also the Mediterranean, usually in large numbers (Kramp, 1965; Fagetti, 1973; Bouillon, 1978b; Goy, 1979; Navas-Pereira &Vannuci, 1991; Pagès *et al.,* 1992; Nagata *et al.,* 2014). Type locality: Mediterranean Sea, near the town of Nice.

Remarks: Although *Aglaura hemistoma* has numerous synonyms, it is taxonomically rather unproblematic. Providing a tabular comparison of the nominal *Aglaura* species, Vanhöffen (1902) concluded that they are mostly developmental stages or variants of *A. hemistoma*. Moreover, *A. hemistoma* has a very thin jelly which gets deformed quite drastically when preserved (Bigelow, 1909). Our own observations on material from the Mediterranean showed that the bell actually elongates considerably in formalin. Some authors may have misinterpreted this fixation effect as a diagnostic trait and it explains the number of synonyms. The few available 16S sequences are also relatively similar (Table 1).

Genus *Amphogona* Browne, 1905

Amphogona Browne, 1905: 739, type species *Pantachogon apsteini* Vanhöffen, 1902 by monotypy.

Diagnosis: Rhopalonematidae with short, thin gastric peduncle, exumbrella without apical process; eight ellipsoidal or sac-shaped, pendant gonads on radial canals; tentacles thin, all alike, without permanent terminal swelling; statocysts free, club-shaped.

Amphogona apsteini (Vanhöffen, 1902)

Fig. 59A-B

Pantachogon apsteini Vanhöffen, 1902: 65, pl. 10 fig. 18, pl. 11 fig. 28.

Amphogona apsteini. – Browne, 1905: 740, pl. 54 fig. 5, pl. 56 fig. 1, pl. 57 figs 10-15. – Bigelow, 1909: 126, pl. 2 figs 1-2, pl. 34 figs 12-15, pl. 45 fig. 10. – Mayer, 1910: 405, fig. 257. – Kramp, 1959a: 188, fig. 280. – Kramp, 1965: 123, figs 12-13. – Kramp, 1968: 118, fig. 319. – Bleeker & Van der Spoel, 1988: 241, fig. 37.

Examined material: BFLA; 1 specimen; 09-DEC-2019; size 2 mm, juvenile; preserved in alcohol for DNA extraction; 16S sequence could not be obtained as PCR failed repeatedly. – 05-JUL-2019; 2 specimens photographed, 2 mm, not collected.

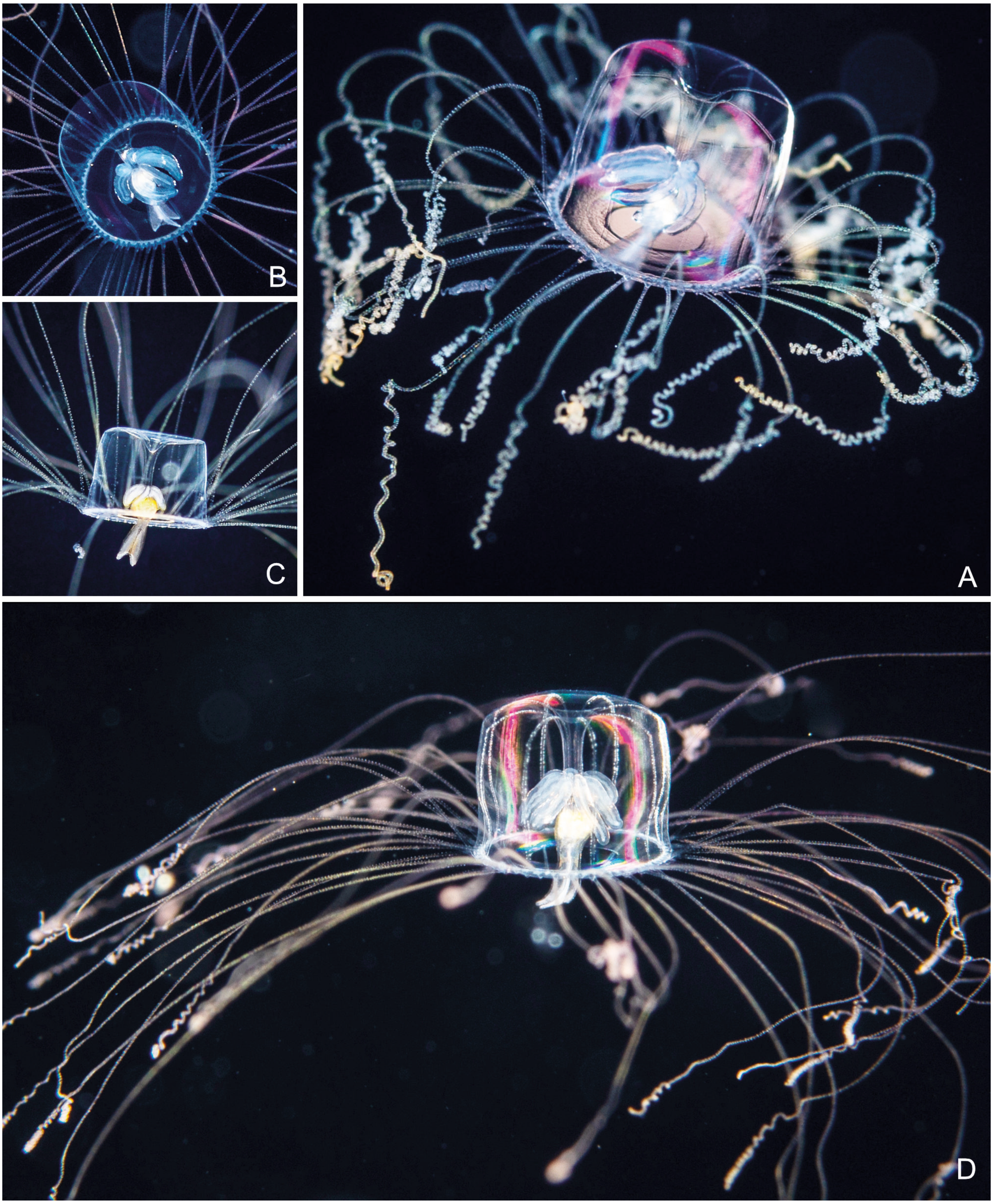

Fig. 58. *Aglaura hemistoma*. (A-B) Sample BFLA3808, bell size 2 mm, oblique views from oral side. The statocysts can be seen in B as tiny, bright spots along the ball margin. (C) Animal photographed 20-AUG-2018, bell size 3 mm. (D) BFLA4214, bell size 2 mm, lateral view.

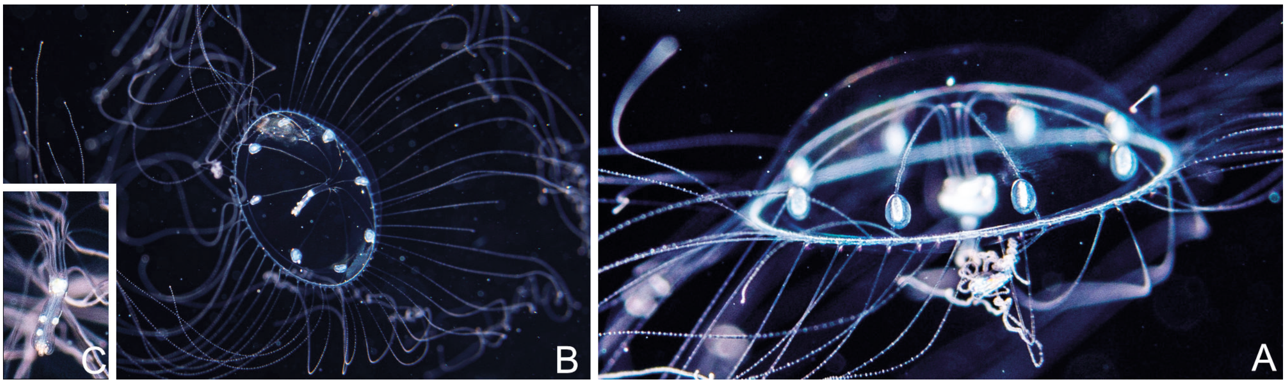

Fig. 59. *Amphogona apsteini*, bell size 2 mm, 09-DEC-2019. (A-B) Two separate individuals. (C) Close up of manubrium and gastric peduncle.

Observations: Bell diameter 2 mm, flatter than hemisphere, jelly relatively thin especially towards margin; with thin gastric peduncle reaching almost to level of velum (Fig. 59B); stomach small, lips inconspicuous. Eight radial canals. Gonads when fully developed ellipsoidal, pendant, close to ring canal, all of equal size or larger ones and smaller ones alternating; long axis of ellipsoidal gonads vertical (Fig. 59A). About 70 tentacles, all the same structure. One to two statocysts per octant.

Distribution: Circumglobal in warm waters. In the Indian Ocean from Indonesia to Moçambique (Kramp, 1953, 1968; Bouillon, 1978a); in the Pacific Ocean from eastern Australia, to the northern Part of the China Sea and Peru (Kramp, 1953, 1965; Bouillon, 1978c; Du *et al*., 2010; Oliveira *et al.,* 2016). In the South Atlantic from Argentina to Brazil and to western Africa (Kramp, 1955b; Nagata *et al*., 2014; Oliveira *et al*., 2016). In the North Atlantic reported from the mid Atlantic to Florida (Bleeker & Van der Spoel, 1988; Larson *et al.*, 1991; this study). Type locality: Indian Ocean, west coast of Sumatra.

Remarks: Kramp (1959a, 1965, 1968) states that the unequal size of the gonads, with small and larger ones alternating, is a characteristic trait of this species. However, this is found only in younger specimens, mature ones seem to have equally developed gonads (Bigelow, 1909; Nagata *et al.,* 2014). Kramp gives also a bell size of 4 to 6 mm. Our specimens were smaller (2 mm). The type material was 2 to 3 mm in size, although perhaps not fully mature. Also Nagata *et al.* (2014) give a bell size of 2 to 3 mm.

Genus *Rhopalonema* Gegenbaur, 1857

Trachynema Gegenbaur, 1854: 53; type species *Trachynema ciliatum* Gegenbaur, 1854 by monotypy.

Rhopalonema Gegenbaur, 1857: 251; type species *Rhopalonema velatum* Gegenbaur, 1857 by monotypy.

Calyptra Leuckart, 1856: 14; type species *Calyptra umbilicata* Leuckart, 1856 by monotypy; invalid junior homonym of *Calyptra* Ochsenheimer 1816 [Lepidoptera] and others.

Marmanema Haeckel, 1879: 261; type species not designated.

Trachyneme Whiteaves, 1901: 29; spelling error.

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 mesoglea when fully developed.

Rhopalonema velatum Gegenbaur, 1857

Fig. 60A-E

? *Trachynema ciliatum* Gegenbaur, 1854: 53, pl. 2 figs 17-23. – Gegenbaur, 1857: 259, pl. 9 fig. 6.

? *Calyptra umbilicata* Leuckart, 1856: 14, pl. 1 figs 9-10. – Mayer, 1910: 378, possibly *R. velatum*.

Rhopalonema velatum Gegenbaur, 1857: 251, pl. 9 figs 1-5. – Bigelow, 1909: 129, pl. 2 fig. 8, pl. 45 fig. 11. – Mayer, 1910: 378, figs 213-222, 224, synonymy. – Russell, 1953: 430, figs 283-284, synonymy. – Kramp, 1959a: 185, fig. 270. – Kramp, 1961: 262. – Kramp, 1968: 114, fig. 307. – Horridge, 1969: 345, figs 3-4, statocysts. – Segura-Puertas, 1984: 38, pl. 10 fig. 4. – Bleeker & Van der Spoel, 1988: 239, fig. 28. – Pagès *et al.,* 1992: 45, fig. 55.

? *Sminthea leptogaster* Gegenbaur, 1857: 246, pl. 9 fig. 11, Mediterranean. – Mayer, 1910: 383, possible synonym.

Trachynema octonarium Haeckel, 1879: 260, Canary Islands. – Mayer, 1910: 378, synonym.

Marmanema tympanum Haeckel, 1879: 262, Mediterranean. – Mayer, 1910: 378, synonym.

Marmanema clavigerum Haeckel, 1879: 263, pl. 17 figs 1-2, Canary Islands. – Kramp, 1961: 262, synonym.

Rhopalonema coerulum Haeckel, 1879: 264, pl. 17 figs 3-6, Canary Islands. – Kramp, 1961: 262, synonym.

Rhopalonema polydactylum Haeckel, 1879: 265, pl. 17 figs 7-1, Mediterranean. – Kramp, 1961: 262, synonym.

Marmanema velatoides Maas, 1893: 13, pl. 1 fig. 6, Atlantic. – Mayer, 1910: 378, synonym.

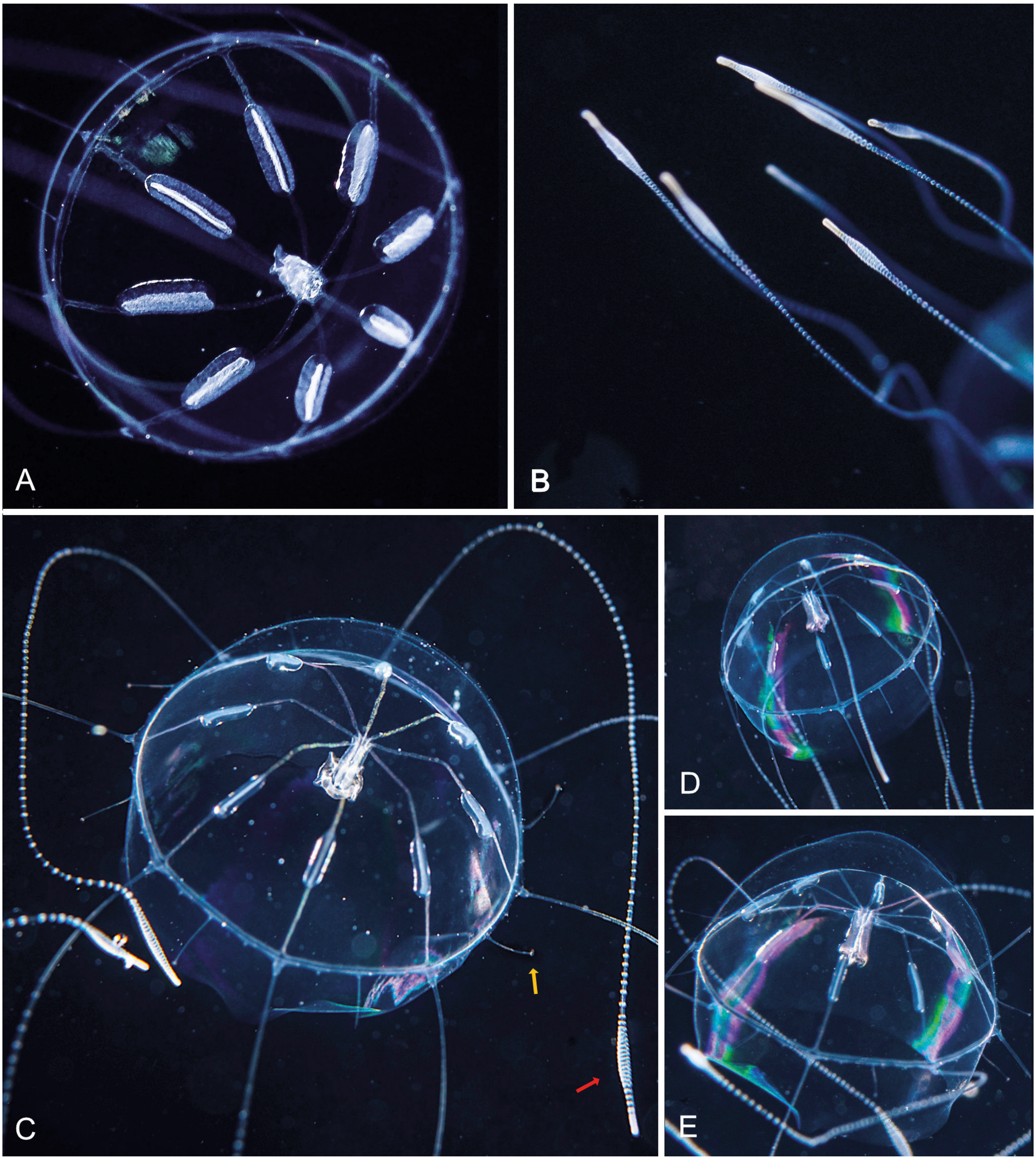

Fig. 60. *Rhopalonema velatum*. (A-B) Specimen of 04-MAR-2019, diameter ca. 11 mm. (A) Oblique view from aboral side. (B) Tentacle tips. (C-E) BFLA4292, 7 mm diameter. (C) Oblique view from aboral side, yellow arrow points to short, interradial tentacle, red arrow points to long, perradial tentacle. (D) Oblique view from oral side. (E) Near lateral view, note the slight apical process.

Rhopalonema striatum Maas, 1893: 15, pl. 1 figs 3-4, Atlantic. – Kramp, 1961: 262, synonym.

Examined material: BFLA4289; 1 specimen; 09-DEC-2019; size 8 mm; no photos taken, preserved in alcohol for DNA extraction; 16S sequence MW528700. – BFLA4292; 1 specimen; 09-DEC-2019; size 7 mm; preserved in alcohol for DNA extraction; 16S sequence MW528702. – 04-MAR-2019; 1 specimen; size 11 mm, photographed, not collected.

Mediterranean, France, Bay of Villefranche-sur-Mer, 43.6860°N 7.3170°E, depth 0-70 m; 3 specimens collected 09-MAY-2001, 04-APR-2005, 29-APR-2014, used for DNA extractions, 16S EU293992 and KP776749.

Observations: Specimens from Florida with bell size of 7-11 mm, bell flatter than hemisphere, at least in some a very shallow apical process visible (Fig. 60E). Velum very broad and hanging down like a curtain. Manubrium small, shorter than bell cavity height. Eight thin radial canals. Gonads on radial canals, elongated ovals, about 1/3 as long as the radial canal, placed in middle of the radial canals. About 16 statocysts, positioned closer to tentacles and not in middle of spaces between tentacles. Eight long, extensible tentacles ending in club-shaped swellings (Fig. 60B, C); eight short, thin tentacles in interradial position, with terminal swelling (Fig. 60B); up to two tentacle stumps in adradial position per octant (Fig. 60C, not well visible).

16S data: The two halplotypes found in the Florida material differ only in one base pair position and likewise also from a Mediterranean haplotype (Table 1). A further haplotype from Tierra del Fuego is more divergent (Table 1).

Distribution: Abundant in the warm and temperate waters of Atlantic, Indian, and Pacific oceans, including also the Mediterranean. Type locality: Mediterranean.

Remarks: The medusa from Florida was identified as *R. velatum* although it differed somewhat from typical specimens as described in Kramp (1959a). There are currently two accepted species in the genus *Rhopalonema*: *R. velatum* and *R. funerarium* Vanhöffen, 1902. *Rhopalonema velatum* differs from the former in having a small apical process, marked off from the rest of the umbrella by a transverse circular furrow or depression. The process varies considerably in size and form (Russell, 1953). *Rhopalonema funerarium* lacks this proces, has long gonads on the distal 2/3 of the radial canals, a very short manubrium, and 32 statocysts. In one of the sample photos (Fig. 60E), a shallow apical process is present. Additionally, the size and position of the gonads and the statocyst number and position matched more *R. velatum*, but the short manubrium was more like in *R. funerarium*. Although the latter species has been regarded as distinct by Kramp (1947, 1959a), others had doubts [see discussion and references in Russell (1953: 435) and Bouillon *et al.* (2004: 244)]. It could well be that *R. funerarium* is only an advanced growth stage of *R. velatum*.

Order Limnomedusae

Family Geryoniidae Eschscholtz, 1829

Remarks: Following Bentalge *et al.* (2018), the Geryoniidae are here classified as Limnomedusae and not Trachymedusae as done traditionally.

Genus *Geryonia* Péron & Lesueur, 1810

Geryonia Péron & Lesueur, 1810: 329, type species *Geryonia hexaphylla* Péron & Lesueur, 1810.
Carmarina Haeckel, 1864b: 466; type species *Carmarina hastata* Haeckel, 1864 by monotypy.
Geryones Haeckel, 1879: 293; type species *Geryones elephas* Haeckel, 1879 by monotypy.
Carmaris Haeckel, 1879: 296, no type species designated.

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 developement.

Remarks: *Geryonia hexaphylla* Péron & Lesueur, 1810, a synonym of *Medusa proboscidalis* Forsskål, 1775, was selected by Haeckel (1879) as type of the genus. Mayer (1910: 424) and Kramp (1961) give as type species *Medusa proboscidalis* Forsskål, 1775 for this genus, but this is incorrect as the name was not part of the original nominal species included in *Geryonia* by Péron & Lesueur.

Geryonia proboscidalis (Forsskål, 1775)

Fig. 61A-B

Medusa proboscidalis Forsskål, 1775: 108, pl. 36 fig. 1.
Geryonia hexaphylla Péron & Lesueur, 1810: 329. – Haeckel, 1879: 295, synonym.
Dianaea endrachtensis Quoy & Gaimard, 1824: 566, pl. 84 fig. 2. – Haeckel, 1879: 295, synonym.
Leuckartiara brevicirrata Haeckel, 1864b: 462. – Haeckel, 1879: 295, synonym.
Leuckartiara longicirrata Haeckel, 1864b: 463. – Haeckel, 1879: 295, synonym.
Geryonia umbella Haeckel, 1864b: 464. – Mayer, 1910: 425, synonym.
Geryonia fungiformis Haeckel, 1864b: 465, new name for *Geryonia hexaphylla* Péron & Lesueur, 1810. – Mayer, 1910: 425, synonym.
Geryonia conoides Haeckel, 1864b: 466.
Carmarina hastata Haeckel, 1864b: 467, pl. 11 figs 1-10. – Mayer, 1910: 425, synonym.
Geryones elephas Haeckel, 1879: 294, pl. 18 fig. 7, South Africa.
Geryonia dianaea Haeckel, 1879: 295. – Mayer, 1910: 425, synonym.
Carmaris umbella Haeckel, 1879: 296. – Mayer, 1910: 425, synonym.
Carmaris Giltschii Haeckel, 1879: 296, pl. 18 fig. 8. – Mayer, 1910: 425, synonym.
Geryones mexicana Agassiz & Mayer, 1902: 149, pl. 4 fig. 17. – Mayer, 1910: 425, synonym.
Carmaris rosea Agassiz & Mayer, 1902: 149, pl. 4 fig. 18. – Mayer, 1910: 425, synonym.
Geryonia fungiformis. – Fol, 1873: 471, figs 1-3, pls 24-25, developement.

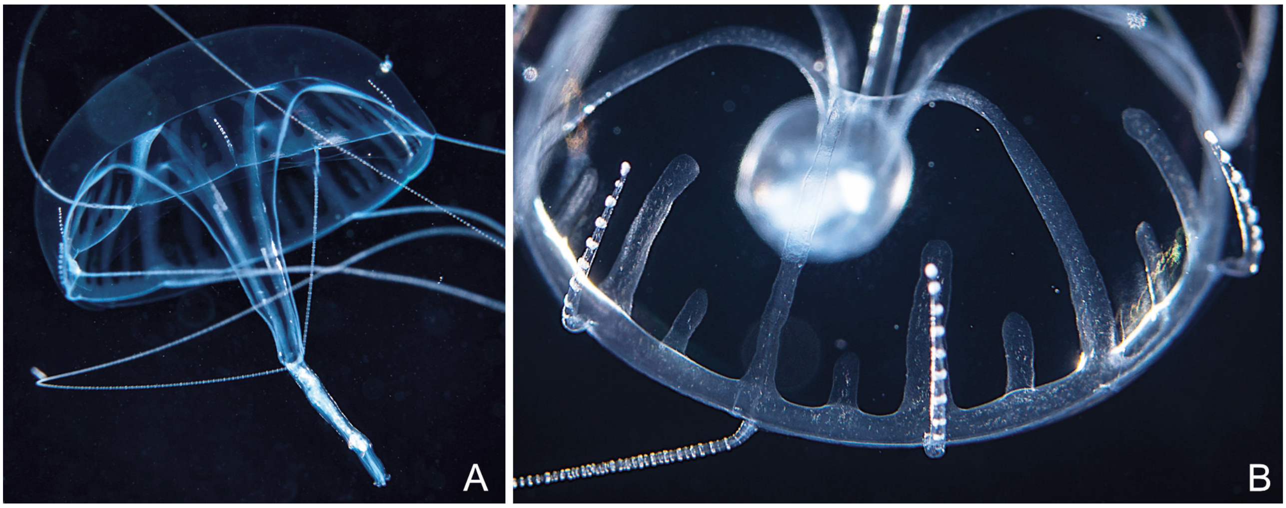

Fig. 61. *Geryonia proboscidalis*. (A) Lateral view of whole, mature animal observed 26-MAR-2019. (B) Bell margin of immature specimen (BFLA4029), bell size approximately 10 mm. Note centripetal canals and the two types of tentacles.

Geryonia proboscidalis. – Haeckel, 1879, 295. – Mayer, 1910: 425, fig. 282, pl. 53 figs 1-3, pl. 43 fig. 10, synonymy. – Berrill, 1950: 296, development. – Kramp, 1959a: 192, fig. 292. – Kramp, 1961: 237. – Kramp, 1968: 122, fig. 332. – Horridge, 1969: 348, figs 5-6, statocysts. – Goy *et al.*, 1991: 119, fig. 47. – Bouillon *et al*., 2004: 237, fig. 150A-C. – Buecher *et al.*, 2005: 35.

Examined material: BFLA4029; 1 specimen; 04-MAR-2019; diameter 10 mm; part preserved in formalin (UF-013448) and part in alcohol for DNA extraction; 16S sequence MW528644. – 26-MAR-2019; 1 specimen photographed, diameter 20 mm, not collected.
Mediterranean, France, Bay of Villefranche-sur-Mer, 43.6963°N 7.3075°E; 25-APR-2016; diameter 70 mm, photos see DOI: 10.5281/zenodo.53890; whole specimen used for DNA extraction, 16S sequence KX355451.

Description of Florida material: Bell almost hemispherical, 10 to 20 mm wide, jelly thick. Stomach small, on a long conical peduncle, peduncle reaching a length of about twice the bell height (Fig. 61A). Six radial canals, 3-7 centripetal canals betwen pairs of radial canals, ending blindly below apex of subumbrella. Gonads along the six primary radial canals, reaching from circular canal to apex of subumbrella, sheet-like, triangular, pointed end towards circular canal. Two types of tentacles. Six long, perradial tentacles with nematocyst rings, and six short interradial tentacles with adaxial nematocyst clusters, often held upwards adnate to subumbrella (Fig. 61B).

16S Data: The 16S sequence (GMW528644) shows few differences to other published sequences of *G. proboscidalis* (Table 1). The p-distance to the Mediterranean specimen was 0.17%, and 0.33% to the one from Japan. More differences where found with sequence KT809331 (1.2%) originating from the Sea of Cortez (Bastian Bentlage, pers. com.).

Distribution: Occurs in tropical and subtropical parts of all three oceans, including also the Mediterranean, approximately between 35° and 35°S (Kramp, 1957, 1965). Type locality: Mediterranean Sea (Forsskål, 1775).

Remarks: With its six radial canals and the two types of tentacles, *Geryonia proboscidalis* is rather reliably identifiable. It is interesting to note the low 16S sequence divergences observed for the sample from Florida, the Mediterranean, and Japan. *Geryonia proboscidalis* could thus be a good example of a hydromedusan species with a truely circumglobal distribution.

Genus *Liriope* Lesson, 1843

Liriope Lesson, 1843: 331; type species *Liriope cerasiformis* Lesson, 1843 (Haeckel, 1979: 288).

Xanthea Lesson, 1843: 333; type species *Xanthea agaricina* Lesson, 1843 by monotypy.

Leuckartia L. Agassiz, 1862: 364; type species *Leuckartia proboscidalis* L. Agassiz, 1862 by monotypy.

Glossocodon Haeckel, 1864b: 460; type species *Liriope eurybia* Haeckel, 1864 by monotypy.

Glossocodon (*Glossoconus*) Haeckel, 1864b: 461; no type species designated.

Liriantha Haeckel, 1879: 286, no type species designated.

Liriantha (*Lirianthella*) Haeckel, 1879: 286; no type species designated.

Liriantha (*Lirianthissa*) Haeckel, 1879: 287; no type species designated.

Liriope (*Liriopella*) Haeckel, 1879: 289; no type species designated.

Liriope (*Liriopissa*) Haeckel, 1879: 290; no type species designated.
? *Pentaradiata* Zamponi & Gezano, 1989: 34; type species *Pentarradiata estuariensis* Zamponi & Genzano, 1989 by monotypy.
? *Heptarradiata* Zamponi & Gezano, 1989: 35; type species *Heptarradiata rioplatensis* Zamponi & Genzano, 1989 by monotypy.
? *Octorradiata* Zamponi & Gezano, 1989: 36; type species *Octorradiata bonaerensis* Zamponi & Genzano, 1989 by monotypy.

Diagnosis: Limnomedusae with long gastric peduncle; stomach small, with 4 lips; 4 radial canals, with additional centripetal canals; 4 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 developement.

Remarks: Rarely, aberrant animals with more than four radial canals and gonads can occur, but the number of oral lips remains rather constantly four (Bouillon *et al*., 2006).

Liriope tetraphylla (Chamisso & Eysenhardt, 1821)

Fig. 62

Geryonia tetraphylla Chamisso & Eysenhardt, 1821: 357, pl. 27 fig. 2.
Liriope tetraphylla. – Russell, 1953: 419, figs 275-282, pl. 24 fig. 2. – Kramp, 1959a: 193, fig. 293. – Kramp, 1961: 239. – Kramp, 1968: 122, fig. 333. – Pagès *et al*., 1992: 43, fig. 52. – Nagata *et al.,* 2014: 315, figs 34-35.
For a complete synonymy see Russell (1953).

Examined material: BFLA4026; 1 specimen; 15-FEB-2019; size 20 mm; preserved in alcohol for DNA extraction; 16S sequence MW528649.
MHNG-INVE-0031754; Mediterranean, Bay of Villefranche-sur-Mer; 43.6860°N 7.3170°E; 70 m depth; collection date 11-MAY-2001; >2 specimens; size 3-4 mm; 1 preserved in formalin, others in ethanol for DNA extraction; 16S sequence MW528628.

Observations: Specimen from Florida with nearly hemispherical bell, 20 mm wide, apical jelly thick, with long, thin gastric peduncle, peduncle length more than two times the bell height. Thin nematocysts tracks on exumbrella, four perradial and four interradial, interradial ones reaching only to base of short tentacles, perradial ones longer. Stomach on long gastric peduncle, relatively small, four indistinct perradial lips. Radial canals four, centripetal canals not visible on photos. Gonads very wide, flat, leaf-like, heart-shaped with pointed side pointing toward periphery. Four long perradial tentacles originating at bell margin, with ring-shaped nematocyst clusters. Four short interradial tentacles originating above bell margin on exumbrella, with adaxial nematocyst clusters.

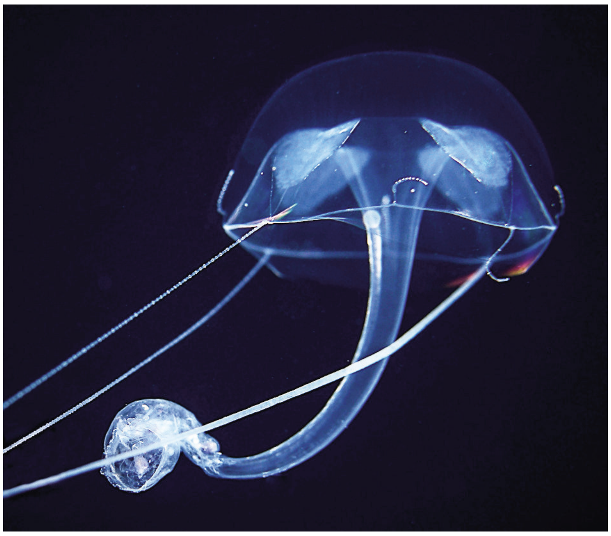

Fig. 62. *Liriope tetraphylla*, BFLA4026, size 20 mm. The stomach is filled with prey items. The larger part of one perradial tentacle is broken off (right).

16S Data: A blastn search in GenBank with the 16S from Florida (MW528649) yielded numerous matches with other *Liriope tetraphylla* samples, but only with identities from 92 to 95.5%. The sequence obtained from the Mediterranean specimen (MW528628) gave identities from 90 to 99 % with other *Liriope tetraphylla* sequences.

Distribution: In Pacific, Indian, and Atlantic ocean, including the Mediterranean, approximately between 40°N and 40°S, in the NE Atlantic reaching to the English Channel (Kramp, 968). Type locality: Indian Ocean (Chamisso & Eysenhardt, 1821).

Remarks: This is a rather unproblematic species, but Collins *et al.* (2008) suggested the existence of cryptic species based on significant divergences in mitochondrial 16S and nuclear sequence data. The high 16S divergences were confirmed in the present study.

Family Olindiidae Haeckel, 1879

Genus *Olindias* Müller, 1861

Olindias Müller, 1861b: 318; type species *Olindias sambaquiensis* Müller, 1861 by monotypy.
Halicalyx Fewkes, 1882a: 277; type species *Halicalyx tenuis* Fewkes, 1882 by monotypy.
Olindioides Goto, 1903: 3, type species *Olindioides formosa* Goto, 1903 by monotypy.

Diagnosis: Olindiidae medusa with 4 radial canals and numerous centripetal canals; numerous tentacles of two kinds: primary ones directed upwards, nematocysts in transverse clasps and often with distal adhesive pads, and secondary ones directed downwards, without adhesive pads, nematocysts in rings. Gonads on papilliform diverticula of radial canals; numerous marginal bulbs which may transform into tentacles, statocysts usually in pairs at base of primary tentacles. Known hydroid either solitary and lacking tentacles, or forming small stolonal colonies and hydranths with a single filiform tentacle.

Remarks: The grammatical gender of the name is male (Calder, 2010). For descriptions of the hydroid see Weill (1936), Patry *et al.* (2014), and Toshino *et al.* (2019). Toshino *et al.* (2019) provide also a tabular overview on the species of this genus and a phylogenetic tree.

Olindias tenuis **(Fewkes, 1882)**

Fig. 63A-C

Halicalyx tenuis Fewkes, 1882: 277, pl. 7 fig. 15.

Olindias tenuis. – Bigelow, 1909: 108. – Mayer, 1910: 354, pl. 47 figs 8-10, pl. 48 figs 1-7. – Kramp, 1959a: 173, fig. 244. – Kramp, 1961: 228. – Larson, 1986: 191, fig. 1.

Olindias phosphorica tenuis. – Bigelow, 1938: 113. – Breder, 1956: 13, pls 1-2.

? *Olindias phosphorica*. – Weill, 1936: 1018, fig., hydroid and larva. [not *Olindias phosphorica,* invalid name for *Olindias muelleri* Haeckel, 1879]

Examined material: BFLA4232; 1 specimen, 21-OCT-2019; size 23 mm; part preserved in formalin (UF-013845) and part in alcohol for DNA extraction; 16S sequence MW528688.

Observations: *Olindias* medusa with bell flatter than hemisphere; diameter 23 mm. No exumbrellar pigment bands. Manubrium as long as subumbrellar height, width uniform, cruciform cross-section, mouth with four simple lips. Four radial canals with gonads along distal half to 2/3. Gonads in development with numerous small oogonia, gonads reaching nearly to circular canal, forming numerous diverticula-like outgrowths along entire length of the gonad (Fig. 63A-C), along the windings of the diverticula runs a purple-pinkish stripe (Fig. 63B). 6 to 8 centripetal canals of different lengths per quadrant (Fig. 63A). Tentacles originating from bell margin without distinct bulb formation, two types present (Fig. 63C): about 34 primary tentacles with scattered nematocyst clusters, part of the clusters with characteristic dark pigment; few secondary tentacles with transverse nematocysts rings (some of these tentacles likely broken off), lacking dark pigment, usually pendant. No exumbrellar tentacles. No adhesive pads on tentacles. Bell margin with about 90 bulbs lacking tentacles, with radial band of nematocysts on abaxial side. One to two round statocysts next to primary tentacles (Fig. 63C). Colours: none except for pink stripes on gonad diverticules.

16S Data: A blastn search in GenBank to find matching sequences to the 16S sequence gave a very close match with MG979369, a sequence from a *O. tenuis* originating from the U.S. Virgin Islands (A. G. Collins, pers. comm.). The sequence divergence was only 0.5%.

Distribution: Florida, Bermudas, Bahamas, Puerto Rico (Mayer, 1910; Kramp, 1959a; Larson, 1986). Type locality: USA, Florida, Key West.

Remarks: The present medusa was identified as *O. tenuis* primarily based on it geographic occurrence, but its traits matched the diagnosis of Kramp (1959a) reasonably well [see Table 5 in Toshino *et al.* (2019)].

The species statuses of *O. tenuis* and *O. sambaquinensis* Müller, 1861 have been questioned by e.g. Bigelow (1938) and Kramp (1959a, 1961), considering them either a subspecies or potentially conspecific with *Olindias muelleri* Haeckel, 1879 (using the incorrect name *Olindias phosphorica*, see footnote). The 16S phylogenetic tree presented in Toshino *et al.* (2019) suggests that the three species are distinct.

Although the names *Oceania phosphorica* and its subsequent combination *Olindias phosphorica* have regularly been attributed to Delle Chiaje, Delle Chiaje (1841) credited "Pér" as author of the binomen and he has thus not established a new species. The correct authority of *Oceania phosphorica* is Péron & Lesueur, 1810 (now recognised as a *Clytia* species, *viz.* a synonym of *Clytia hemisphaerica*). Delle Chiaje's (1841) usage of *Oceania phosphorica* is therefore a misapplication and not a valid name for the common Mediterranean *Olindias* species. The species was first correctly named by Haeckel (1879) as *Olindias muelleri*.

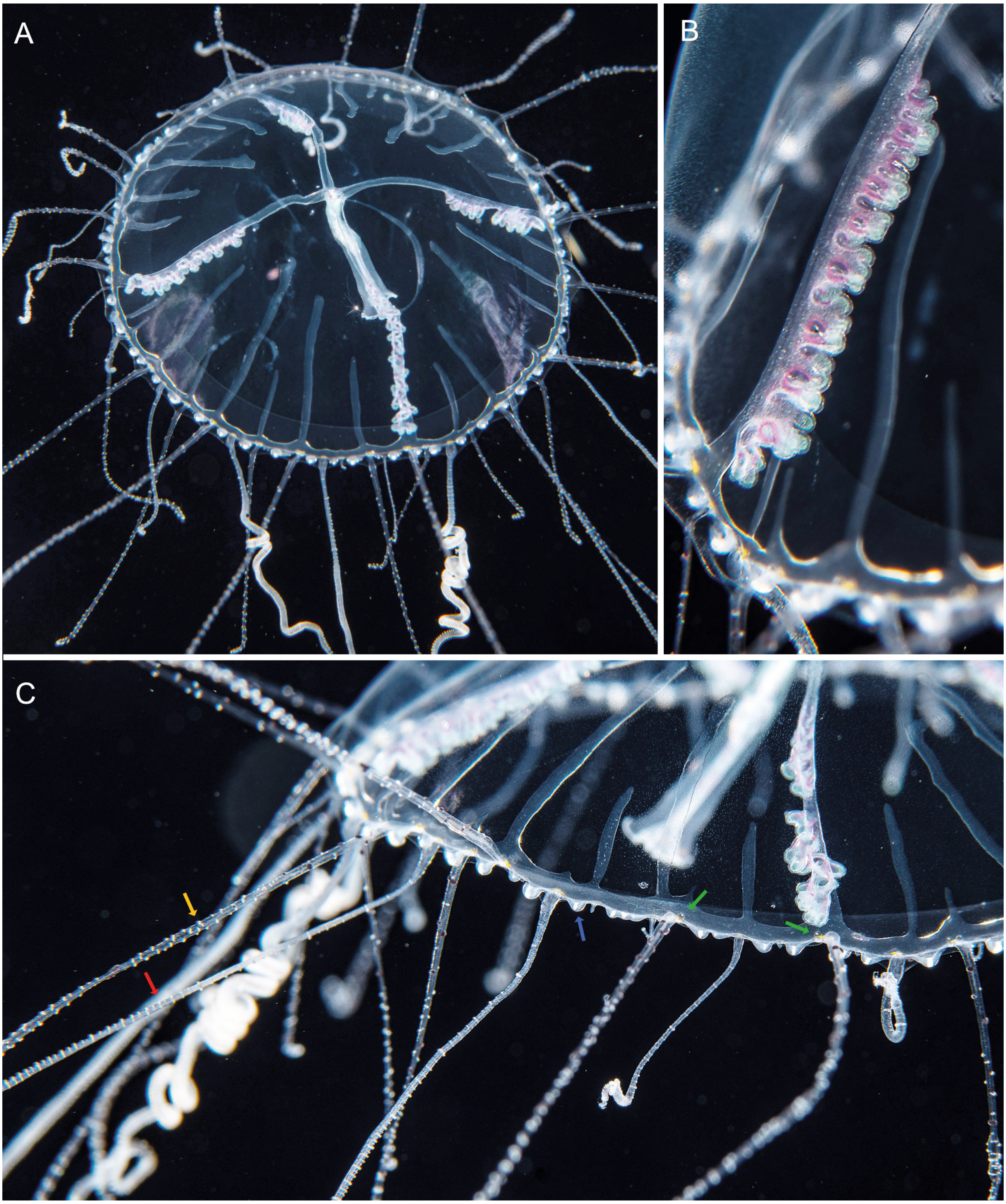

Fig. 63. *Olindias tenuis*, BFLA4232, bell diameter 23 mm. (A) Oblique aboral view of whole animal. (B) Lateral view of radial canal with gonad diverticula. (C) Bell margin with primary tentacles (yellow arrow) and secondary tentacles (red arrow), green arrows point to statocysts. Note the absence of tentacle bulbs, but numerous bulbs without tentacles (blue arrow).

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Appendix 1

Checklist of hydromedusae 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 list without published supporting information for the identifications like descriptions and illustrations. Doubtful species (Kramp, 1961; Schuchert, 2020) 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 is this study. The references for the taxonomic authorities can be found in Schuchert (2020).

species	this study	record source	comments
Suborder Filifera			
Family Bouganvillidae			
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 spec.	yes		
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	
Family Cytaeididae			
Cytaeis tetrastyla Eschscholtz, 1829	yes	3, 4, 5, 11	
Family Hydractiniidae			
Podocoryna americana (Mayer, 1910)		8	barcode id.
Podocoryna borealis (Mayer, 1900)		4	
Podocoryna carnea M. Sars, 1846		4	
Family Niobiidae			
Niobia dendrotentaculata Mayer, 1900		1, 4, 5, 6	

species	this study	record source	comments
Family Oceaniidae			
Oceania armata Kölliker, 1853		2, 4, 5	misidentifications of *T. nutricula* ?
Turritopsis dohrnii (Weismann, 1883)		8	barcode id.
Turritopsis nutricula McCrady, 1857	yes	1, 2, 3, 4, 5, 6, 9, 11	
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)		1, 4, 5, 6, 9, 11	
Amphinema turrida (Mayer, 1900)	yes	1, 2, 4, 5, 6, 11	
Cirrhitiara superba (Mayer, 1900)	yes	1, 6	
Eutiara mayeri Bigelow, 1918		1, 7	
Halitholus intermedius (Browne, 1902)		4, 5	identification doubtful
Larsonia pterophylla (Haeckel, 1879)	yes	1, 2, 4, 5, 6	
Leuckartiara gardineri Browne, 1916		4, 5	identification needs confirmation
Leuckartiara octona (Fleming, 1823)		4, 5	identification needs confirmation
Leuckartiara zacae Bigelow, 1940		4, 5	
Merga violacea (Agassiz & Mayer, 1899)	yes	1, 2, 4, 5, 6	
Pandea conica (Quoy & Gaimard, 1827)		1, 3	
Pandeopsis ikarii (Uchida, 1927)	yes		new record for Atlantic Ocean
Pandeopsis prolifera n. spec.	yes		
Stomotoca atra L. Agassiz, 1862		4, 5	misidentification of *L. pterophylla* ?
Family Proboscidactylidae			
Proboscidactyla gemmifera (Fewkes, 1882)	yes	1, 2, 4, 5, 6	older records include *P. stolonifera*
Proboscidactyla ornata (McCrady, 1859)	yes	1, 2, 4, 5, 6, 9, 11	
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	
Family Rathkeidae			
Lizzia alvarinoae Segura, 1980		9	*Cytaeis* spec ?
Lizzia blondina Forbes, 1848		1, 4, 6, 11	includes *Podocoryna minuta*
Lizzia gracilis (Mayer, 1900)		1, 6	
Podocorynoides minima (Trinci, 1903)		4, 5, 6 ?, 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	

species	this study	record source	comments
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	medusoid
Family Sphaerocorynidae			
Sphaerocoryne agassizii (McCrady, 1859)		1	
Euphysilla pyramidata Kramp, 1955	yes	4, 5	
Euphysilla peterseni Allwein, 1967		11	
Zancleopsis dichotoma (Mayer, 1900)	yes	1, 6, 11	includes *Z. gotoi* records
Family Zancleidae			
Zanclea costata Gegenbaur, 1857		1, 4, 5, 6	= in part *Z. mayeri* + others
Zanclea dubia Kramp, 1959		4, 5	identification ?
Zanclea mayeri n. spec.	yes		new species
Zanclea spec.	yes		
Suborder Aplanulata			
Family Corymorphidae			
Corymorpha forbesii (Mayer, 1894)	yes	1, 2, 4, 5, 6, 11	
Corymorpha gracilis (Brooks, 1883)	yes	1, 4, 5, 6, 9, 11	
Corymorpha floridana n. spec.	yes		new species
Corymorpha furcata (Kramp, 1948)		3, 4, 5	
Corymorpha nutans M. Sars, 1835		5, 8	? misidentifications
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	
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 new name	yes	6	new name
Aequorea taiwanensis Zheng *et al.*, 2009	yes		new record for Atlantic Ocean
Aequorea spec. 1	yes		
Aequorea spec. 2	yes		
Zygocanna cf. *apapillatus* Xu, Huang & Guo, 2014	yes		new record for Atlantic Ocean
Zygocanna vagans Bigelow, 1912		4, 5	
Rhacostoma atlanticum L. Agassiz, 1851		1	

species	this study	record source	comments
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	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*
Clytia linearis (Thornely, 1900)	yes		barcode id.
Clytia mccradyi (Brooks, 1888)		1, 5, 6	
Clytia simplex (Browne, 1902)		4, 5	indeterminable species ?
Clytia spec. 1	yes		
Clytia spec. 2	yes		
Gastroblasta timida Keller, 1883	yes		new record for Atlantic Ocean
Multioralis ovalis Mayer, 1900		1, 6	
Obelia bidentata Clark, 1875		8	barcode id.
Obelia dichotoma (Linnaeus, 1758)		8	barcode id.
Family Cirrholoveniidae			
Cirrholovenia tetranema Kramp, 1959		11	
Family Dipleurosomatidae			
Dichotomia cannoides Brooks, 1903		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, 1864a)		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, 1864a)		4, 11	includes *Helgicirrha schulzii*
Helgicirrha weaveri Allwein, 1967		11	
Family Hebellidae			
Melicertissa mayeri Kramp, 1959	yes	1	
Staurodiscus kellneri (Mayer, 1910)	yes	1, 6	includes *Toxorchis brooksi*
Staurodiscus luteus new species	yes		new species
Staurodiscus tetrastaurus Haeckel, 1879	yes	2, 6	

species	this study	record source	comments
Family Laodiceidae			
Laodicea brevigona Allwein, 1967		5, 11	
Laodicea minuscula Vannucci, 1957		4, 5	
Laodicea undulata (Forbes & Godsir, 1853)	yes	1, 4, 5, 6, 11	
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	
Family Malagazziidae			
Octophialucium aphrodite (Bigelow, 1928)	yes	1, 5	
Octophialucium irregularis n. spec.	yes		new species
Octophialucium medium Kramp, 1955		4, 5	
Malagazzia carolinae (Mayer, 1900)		1, 2, 6, 8	
Family Orchistomatidae			
Orchistoma pileus (Lesson, 1843)	yes	1, 4, 5, 6	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	
Wuvulidae new family			
Wuvula ochracea (Mayer, 1910)	yes	1, 6	
Narcomedusae			
Family Aeginidae			
Aegina citrea Eschscholtz, 1829		3, 4, 5, 9	misidentifications of *P. rhodina* ?
Aeginura grimaldii Maas, 1904		4, 5, 7	
Family Cuninidae			
Cunina becki Bouillon, 1985	Yes		new record for Atlantic Ocean
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	
Cunina peregrina Bigelow, 1909		3, 5, 11	
Solmissus incisa (Fewkes, 1886)		4, 5, 6, 7	
Solmissus marshalli Agassiz & Mayer, 1902		3, 7	
Family Pseudaeginidae			
Pseudaegina rhodina (Haeckel, 1879)	Yes	6, 7	some *A. citrea* records belong to here

species	this study	record source	comments
Family Solmarisidae			
Pegantha clara R.P. Bigelow, 1909		3, 4, 7	
Pegantha martagon Haeckel, 1879	Yes	3, 4, 5	
Pegantha polystriata (Xu & Zhang, 1978) new comb.	Yes		new record for Atlantic Ocean
Pegantha triloba Haeckel, 1879		3, 4, 5	
Solmaris corona (Keferstein & Ehlers, 1861)	Yes	3, 7	
Solmaris flavescens (Kölliker, 1853)		3, 7	
Solmaris flavofinis new spec.	Yes		new species
Family Solmundaeginidae			
Solmundella bitentaculata (Quoy & Gaimard, 1833)	Yes	3, 4, 6, 9, 11	
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	Yes	3, 4, 5, 6, 9, 11	
Amphogona apicata Kramp, 1957		7	mesopelagic
Amphogona apsteini (Vanhöffen, 1902)	Yes	3, 4	
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	
Sminthea eurygaster Gegenbaur, 1857		3, 4, 5	
Order Limnomedusae			
Family Geryoniidae			
Geryonia proboscidalis (Forsskål, 1775)	yes	3, 4, 5	
Liriope tetraphylla (Chamisso & Eysenhardt, 1821)	yes	3, 4, 5, 6, 8, 9, 11	
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)	yes	4, 6	
Scolionema suvaense (Agassiz & Mayer, 1899)		1, 2, 4	
Vallentinia gabriellae Vannucci Mendes, 1948		1, 4	

Sources:

1	Kramp (1959a): Table VII – Neritic species in the West - Atlantic tropical region Cape Hatteras to Florida
2	Kramp (1959a): Table XII – Neritic, predominantly warm water species and their distribution in the three great oceans - West Indies and N. American Warm Water
3	Kramp (1959a): 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 submersable 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)