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Systematic notes on some leptomedusa species with a description of *Neotima galeai* n. spec. (Hydrozoa, Cnidaria)

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Abstract: This work reports upon observations and identifications of 18 leptomedusae, mostly documenting specimens which have been used for previous molecular phylogenetic studies. All species are illustrated, for some of them links to electronically archived photos are provided. The taxonomy of some genera and species is discussed. The diagnosis of the genus *Neotima* Petersen, 1962 is modified to accommodate the new species *Neotima galeai*, the only member of the genus with subdivided gonads. *Eutima sapinhoa* Narchi & Hebling, 1975 is transferred to the genus *Neotima* as *Neotima sapinhoa* (Narchi & Hebling, 1975) n. comb. *Helgicirrha schulzii* Hartlaub, 1909 and *Tima plana* Neppi, 1910 are both regarded as junior synonyms of *Helgicirrha cari* (Haeckel, 1864). *Eirene octonemalis* Guo, Xu & Huang, 2008 is a new junior synonym of *Eirene hexanemalis* (Goette, 1886).

Keywords: Marine hydromedusae - Leptothecata - taxonomy - DNA barcoding - new species - digital archive.

INTRODUCTION

This work reports upon observations and identifications of a number of leptomedusae I have examined during recent years. Many of the animals were used to extract DNA for molecular genetic analyses that have been published elsewhere (e.g. Leclère *et al*., 2009; Schuchert *et al.*, 2017) or have simply been deposited in GenBank, and for which it was desirable to have more published details on their identification. Comparing DNA sequences (barcodes) has opened many new possibilities in hydrozoan systematics (e.g. Schuchert, 2016; Schuchert *et al.*, 2017, and references therein). However, for many DNA sequences of hydrozoans deposited in GenBank, no information on the species identification is available. This causes sometimes considerable problems when new sequences result in conflicting taxonomic identities and one must assume that a misidentification could be at the origin of the conflict. Ideally, these problems can be resolved relatively easily if voucher specimens are available in public collections and they are cited in the GenBank record. Especially for small hydromedusae, however, it is often not possible to deposit a voucher as the whole specimen is used to extract the DNA for the subsequent sequencing. Photos or drawings of such specimens are thus the only available proof for a correct identification. These illustrations can be deposited e.g. in the BOLD database together with the COI sequences derived from these samples. This possibility is not readily available for other sequence types deposited in GenBank and it is unfortunate that the identities of many sequences in GenBank remain uncertain and not re-examinable (a parallel problem exists for distributional records, comp. Lindsay *et al*., 2017). In a taxonomic/systematic context, it is thus essential that the species identifications of published DNA sequences can be verified either by depositing voucher material, publishing descriptions and illustrations of the material, or by submitting photos or drawings to electronic archives. These archives can be institutional libraries, open or commercial archiving services etc. Important in this context is that a DOI number is obtained for the dataset and that a long period of digital preservation is guaranteed. With a DOI number, the documented specimens can be cited and if needed their taxonomy revised in the future.

Hydromedusae collected with plankton nets are rarely obtained in perfect condition. Mostly they are damaged or at least deformed and they do not lend themselves to take publication-quality photos. In such cases, drawings are still one of the best tools to document and publish the identification process. However, also lesser quality photos, which cannot be published in a scientific publication, may still be valuable for other specialists and may serve as proof of a correct identification. This type of data is best submitted as electronic archival material as mentioned above and as it has been done

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for several samples of this study and also of previous publications (see Table 1). The DOI numbers can even be cited in the GenBank entries (see e.g. KX355450), thus creating an easy way to verify the identity of a sample. The current repository of any electronic document with a DOI number can easily be accessed by adding the text "https://doi.org/" in front of the DOI code and using the whole string as an address in a web browser. More such archived illustrations will be deposited in future and it is hoped that other systematists who generate and publish DNA sequences – or, by the way, also distribution records – might also adopt this approach (*cf*. Whitlock, 2011; Roche *et al*., 2015 and references therein).

MATERIAL AND METHODS

For collecting and examining hydromedusae see e.g. Russell (1953), Brinckmann-Voss (1970), Bouillon (1978b), Cornelius (1995), Schuchert (2012), Schuchert *et al.* (2017).

The molecular genetic methods used are described in Schuchert (2005, 2016) and Schuchert *et al.* (2017). DNA isolate numbers refer to DNA extracts in TE buffer kept in the DNA collection of the MHNG. Sequences can be retrieved from GenBank via https://www.ncbi.nlm.nih.gov/nucleotide/.

Medusae were either drawn after living or formalin-preserved material and do not necessarily represent an individual but a composite of several specimens. Inspired by the style of Mayer (1910), schematic illustrations was here preferred over a realistic depiction of the preserved specimen which often obscures the proportions.

Drawings were always made with pencil and then later inked using the image editor software GIMP (www.gimp.org).

Not all family and genus diagnoses and synonyms are given here. These can be found in Schuchert (2017a). Although all known synonyms are given for each species, only the most important citations and references are provided. Usually a source with a more complete list is included.

For the photos and the specimen data (Table 1), pdf files were created using MS Word and then deposited in the ZENODO archive, a free repository of research data (http://about.zenodo.org/).

Abbreviations:

NHMD	Natural History Museum of Denmark
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
NIWA	National Institute of Water and Atmospheric Research, Wellington, New Zealand
GenBank	Genetic sequence database of the National Institute of Health, USA http://www.ncbi.nlm.nih.gov/genbank/

Table 1. Accessory material (photos of specimens) of selected leptomedusae.

Family	*species*	locality	DNA isolate	DOI (with links)
Campanulariidae	*Clytia gregaria*	USA, San Juan Islands	920 & 1169	https://doi.org/10.5281/zenodo.495304
Campanulariidae	*Clytia islandica*	Norway, Raunefjord	1112	https://doi.org/10.5281/zenodo.495407
Campanulariidae	*Clytia* spec.	Norway, Korsfjord	1183	https://doi.org/10.5281/zenodo.165754
Eirenidae	*Eutima gracilis*	Sweden, Kristineberg	1063	https://doi.org/10.5281/zenodo.495383
Eirenidae	*Eutima gegenbauri*	Sweden, Kristineberg	1062	https://doi.org/10.5281/zenodo.495387
Eirenidae	*Tima bairdii*	Norway, Fanafjord	1116	https://doi.org/10.5281/zenodo.495392
Eireniidae	*Eutonina indicans*	Norway, Fanafjord	1110	https://doi.org/10.5281/zenodo.495355
Laodiceidae	*Laodicea undulata*	Sweden, Kristineberg	1137	https://doi.org/10.5281/zenodo.46237
Laodiceidae	*Laodicea undulata*	France, Villefranche-sur-Mer	1151	https://doi.org/10.5281/zenodo.165741
Laodiceidae	*Staurodiscus gotoi*	New Zealand , Hauraki Gulf	126	https://doi.org/10.5281/zenodo.55257
Laodiceidae	*Staurostoma mertensii*	Norway, Fanafjord	1114	https://doi.org/10.5281/zenodo.495373
Melicertidae	*Melicertum octocostatum*	Norway, Korsfjord	1161	https://doi.org/10.5281/zenodo.165766
Mitrocomidae	*Cosmetira pilosella*	Norway, Korsfjord	1165	https://doi.org/10.5281/zenodo.165761
Mitrocomidae	*Halopsis ocellata*	Norway, Raunefjord	1111	https://doi.org/10.5281/zenodo.495359
Mitrocomidae	*Mitrocomella polydiademata*	Scotland, Dunstaffnage Bay	1133	https://doi.org/10.5281/zenodo.495337
Mitrocomidae	*Mitrocomella polydiademata*	Norway, Fanafjord	1115	https://doi.org/10.5281/zenodo.495350
Mitrocomidae	*Tiaropsis multicirrata*	Norway, Raunefjord	437	https://doi.org/10.5281/zenodo.495413

BOLD	The Barcode of Life Data System, see Ratnasingham & Hebert (2007).
DOI	Digital Object Identifier
COI	Cytochrome Oxidase I
16S	16S mitochondrial ribosomal RNA gene sequence

TAXONOMY

Family Melicertidae L. Agassiz, 1862
Genus *Melicertum sensu* L. Agassiz, 1862

Melicertum octocostatum (M. Sars, 1835)
Fig. 1A-B

Oceania octocostata M. Sars, 1835: 24, pl. 4 fig. 9a-d.
Melicertum campanula. – Agassiz, 1862: 349. – Mayer, 1910: 207, pl. 23 figs 4-5, pl. 24 fig. 5. – Naumov, 1969: 350, figs 215-216. [not *Medusa campanula* Fabricius, 1780 = ? *Catablema vesicarium*]
Melicertum octocostatum. – Kramp, 1919: 52, pl. 1 fig. 10, pl. 3 fig. 8. – Kramp & Damas, 1925: 294. – Russell, 1953: 245, figs 138-142, pl. 13 figs 2-4. – Kramp, 1959a: 134, fig. 152. – Kramp, 1961: 136. – Kramp, 1968: 63, fig. 164. – Arai & Brinckmann-Voss, 1980: 79, figs 44-45. – Bouillon, 1984: 87. – Cornelius, 1995: 124, fig. 17. – Okuizumi & Kubota, 2003: 39, fig. 1. – Wang *et al.*, 2014: 99, fig. 16.

Material examined: MHNG-INVE-48744, 3 specimens 4-5 mm wide and with up to 40 larger tentacles; Norway, Raunefjord, 60.2731°N 5.20728°E, 10 m depth; collection date 14.06.2006; one specimen used for DNA extraction, DNA isolate 433, 16S sequence FJ550510, 18S FJ550595, 28S FJ550451. – MHNG-INVE-94100, one of >4 specimens; Norway, Korsfjord, 60.1846°N 5.196°E; one other specimen used to obtain DNA isolate 1161, 16S KY363951, 18S KY363981, for archived photos see Table 1, remaining medusae used to extract RNA for transcriptome analysis.

Diagnosis: Umbrella 5-20 mm wide and high, conical to pyriform with thick, solid apex and thinner sides; per octant 3-7 fine, radial, subumbrellar tissue-thickenings with or without nematocysts (may be absent, or present in fully grown animals only); 40-80 large tentacles alternating with as many small ones, with distinct basal bulb formation; no ocelli, no cirri. Stomach short and broad, octagonal, mouth with 8 small lips when fully grown. 8 sinuous, linear gonads covering almost the full length of the 8 radial canals, getting thicker towards periphery. Colours: stomach and gonads yellow.
For polyp stage see Cornelius (1995).

Remarks: No subumbrellar nematocysts could be seen in the present animals which were relatively young (small). The tissue thickenings were present though.

Distribution: A strictly coastal species occurring in cooler waters of the North-western Atlantic from The English Channel to the Arctic Ocean; Iceland; North America from Woods Hole to Halifax and western coast of Greenland. Also present in the Pacific from Japan to the Arctic Ocean and British Columbia (Kramp, 1961; Arai & Brinckmann-Voss, 1980; Okuizumi & Kubota, 2003; Wang *et al*., 2014). An unexpected record is also known from Papua New Guinea (Bouillon, 1984). Type locality: Coastal region of Bergen, Norway.

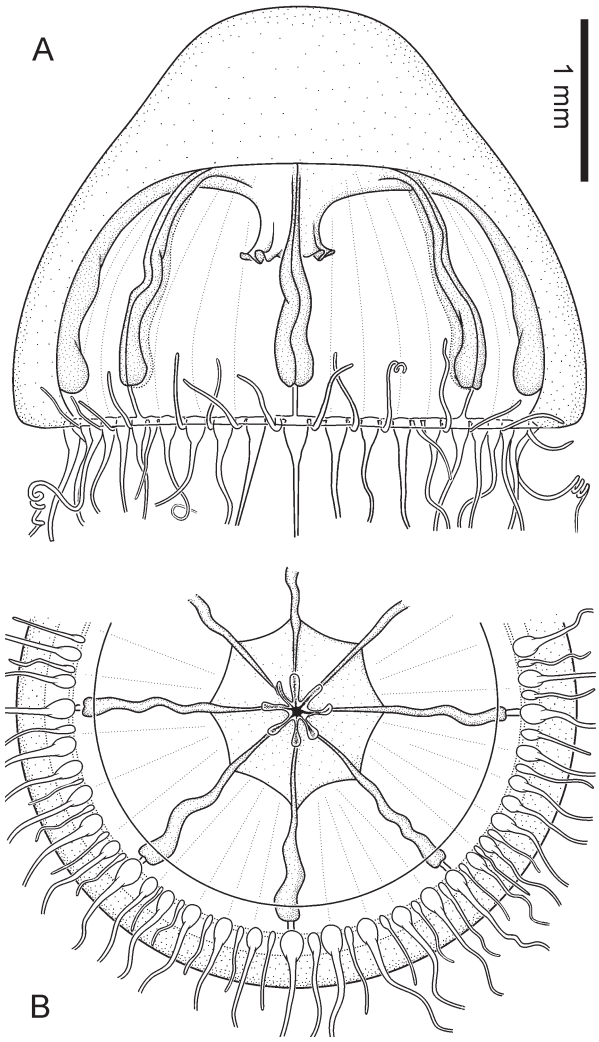

Fig. 1. *Melicertum octocostatum* after photos of living medusae from Norway. (A) Lateral view, tentacles cut. (B) Oral view.

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

Laodicea undulata (Forbes & Goodsir, 1853)
Fig. 2A-C

? *Medusa cruciata* Forsskål, 1775: 110, pl. 33 figs A, a1-a2.
? *Medusa crucigera* Gmelin, 1788: 3158, new name for *Medusa cruciata* Forsskål, 1775.

? *Medusa cacuminata* Modeer, 1791: 26, new name for *Medusa cruciata* Forsskål, 1775.
Laodicea crucigera. – Lesson, 1843: 294, new genus.
Thaumantias undulata Forbes & Goodsir, 1853: 313, pl. 10 figs 7a-d.
Thaumantias confluens Forbes & Goodsir, 1853: 314, pl. 10 fig. 8a-d.
Thaumantias mediterranea Gegenbaur, 1857: 237, pl. 8 figs 1-3.
Laodicea calcarata L. Agassiz, 1862: 350.
Cosmetira punctata Haeckel, 1864: 334. – Haeckel, 1879: 132, synonym.
? *Cuspidella costata* Hincks, 1868: 210, pl. 40 fig. 5. – Watson, 2005: 501, fig. 3A-B.
Laodice ulothrix Haeckel, 1879: 133, pl. 8 figs 5-7.
? *Ptychogena longigona* Maas, 1893: 64, pl. 6 figs 7-9. – Browne, 1907: 474. – Kramp, 1919: 35, doubtful species.
Laodicea bigelowi Neppi & Stiasny, 1911: 396. – Neppi & Stiasny, 1913: 38, pl. 3 figs 30-31. – Kramp, 1961: 142.
Laodice cruciata. – Mayer, 1910: 201, figs 104-105, pl. 21 figs 4-5, pl. 22 figs 2-6, pl. 23 figs 1-3. – Neppi & Stiasny, 1913: 37, pl. 3 figs 27-29.
Laodicea undulata. – Russell, 1936: 581, figs 1-7, hydroid stage. – Russell, 1953: 230, figs 123-131, pl. 14 figs 1-3. – Kramp, 1959a: 135, fig. 153. – Kramp, 1961: 141. – Goy, 1979: 272, fig. 12. – Pagès *et al*., 1992: 28, fig. 29. – Ramil & Vervoort, 1992: 28, fig. 2w-g. – Cornelius, 1995: 99, fig. 22.

Material examined: MHNG-INVE-31753, originally 2 specimens in ethanol, one used for DNA extraction; France, Villefranche-sur-Mer, Ligurian Sea, Mediterranean, 43.686°N 7.317°E, depth 2-70 m; collection date 11.05.2001; DNA isolate 125; 16S sequence FJ550471, 18S FJ550390. – 3 specimens; France, Villefranche-sur-Mer, 43.686°N 7.317°E, depth 0-70 m; collection date 04.04.2005. – 2 specimens; France, Villefranche-sur-Mer, 43.686°N 7.317°E, depth 0-70 m; collection date 28.04.2014; used for RNA extraction. – 1 specimen; Sweden, Kristineberg, 58.24385°N 11.43230°E, 0 m depth, collection date 03.10.2014; DNA isolate 1137; 16S sequence KY363963, COI MF000514, 18S KY363985. – 1 specimen; France, Bay of Villefranche-sur-Mer, 43.6963°N 7.3075°E; collection date 25.04.2016; DNA isolate 1151; 16S KY363967.
For archived photos of specimens see Table 1.

Diagnosis: Umbrella 10-37 mm wide, usually 10-20 mm; flatter than hemisphere; stomach quadratic, short, with four folded lips; four long, sinuous gonads along radial canals, contiguous with stomach; 100-300 tentacles, basal bulbs faintly developed, with abaxial spur; adaxial ocellus usually on every third to fifth tentacle; spiral cirri, usually one between successive tentacles; cordyli distinctly club-shaped, without nematocysts, usually one between successive tentacles, no statocysts.
For polyp stage see Cornelius (1995).

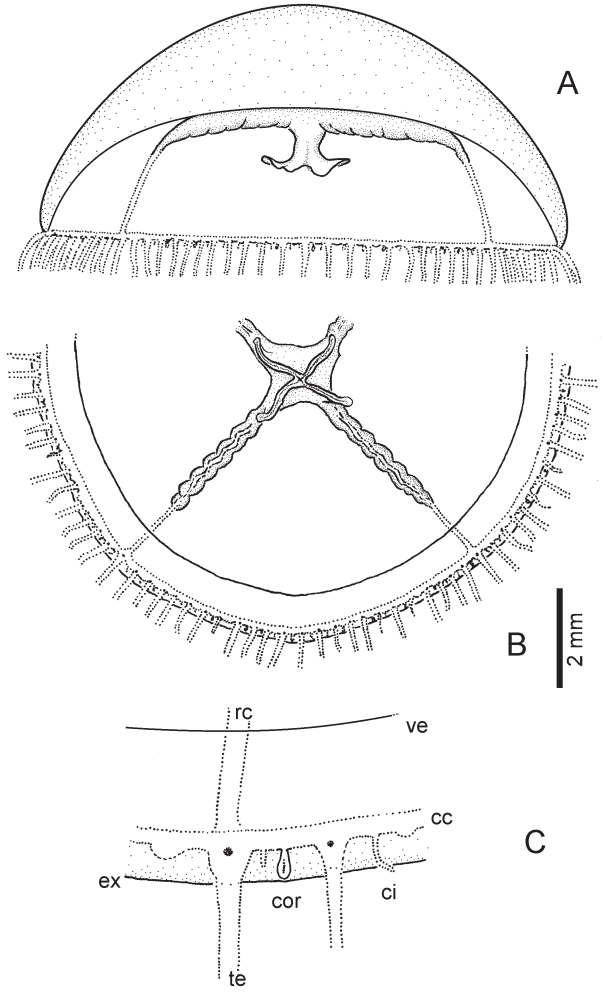

Fig. 2. *Laodicea undulata* after living medusa from the Mediterranean. (A) Lateral view. (B) Oral view. (C) Bell margin seen from oral side. Abbreviations: ci – cirrus, cc – circular canal, cor – cordylus, ex – exumbrella, rc – radial canal, te – tentacle.

Remarks: The specimens from the Mediterranean had 60-80 tentacles, the North Sea specimen 280.

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 (Pages *et al*., 1992) require a re-evaluation (Kramp, 1955b: 253; see also below under *L. indica*). Type locality: The Minch, Scotland.

Laodicea indica Browne, 1905

Fig. 3

Laodice indica Browne, 1905b: 136, pl. 1 fig. 5, pl. 4 figs 7-11.
Laodicea indica. – Mayer, 1910: 202, synonym of *L. cruciata*. – Kramp, 1953: 268, type specimen, synonymy. – Kramp, 1961: 140. – Kramp, 1968: 66, fig. 172. – Bouillon, 1978a: 152, fig. 9. – Bouillon, 1984: 61, revision, life

cycle. – Bouillon, Boero & Fraschetti, 1991: 151, figs 1-3, life cycle.

Laodice fijiana var. *indica*. – Maas, 1905: 25, pl. 2 figs 14-15, pl. 5 figs 32-35. – Kramp, 1953: 270, is probably *L. indica*. [not *Laodicea fijiana* Agassiz & Mayer, 1899]

Laodice maasii Browne, 1907: 466, new name for *Laodice fijiana var. indica* in Maas, 1905. – Kramp, 1953: 270, is *L. indica*.

? *Laodice fijiana.* – Maas, 1906: 89. – Kramp, 1953: 270.

Material examined: MHNG-INVE-25646; 1 specimen in ethanol, originally fixed in formalin; Seatoun jetty, Miramar Peninsula, Wellington, New Zealand, 41.31855°S 174.8304°E, depth 0-2 m; date collected 22.03.1994. – MHNG-INVE-54671; 5 badly preserved specimens; Bay of Ambon, Moluccas, Indonesia; expedition Bedot & Pictet 1890; material described in Maas (1906).

Diagnosis: Like *L. undulata*, but Indo-Pacific occurrence, tentacle number in mature specimens lower with 30-200. For polyp stage see Bouillon (1984), identical to *L. undulata*.

Remarks: There is currently no trait known that would reliably distinguish *L. indica* from the Atlantic *L. undulata.* Also the polyps appear identical (Bouillon, 1984; but see Bouillon *et al.*, 1991). Some authors (e.g. Mayer, 1910; Bouillon, 1984) have therefore synonymised the two names, but Kramp (1953, 1961, 1968) continued to regard them as separate. I also refrained from synonymising the two because some preliminary molecular data indicate that the Pacific *Laodicea* could be rather distinct from the Atlantic ones (10% difference of 16S sequence, unpublished, comp. FJ550471, JQ715946, JQ715947, KY363963).

The medusa from New Zealand had a relatively high number of tentacles (about 200), but which is only slightly higher than the maximal number of 180 given in Kramp (1968).

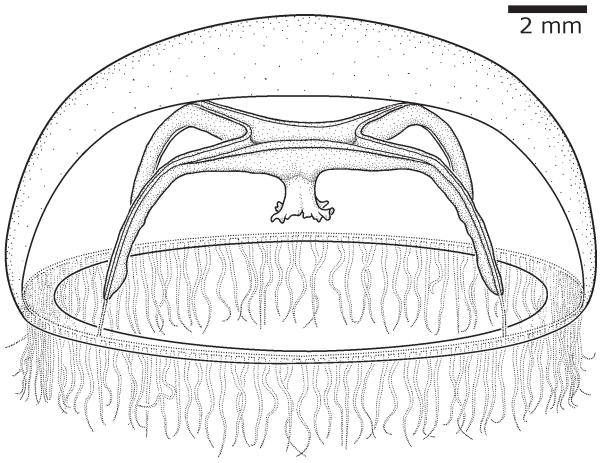

Fig. 3. *Laodicea indica,* schematic drawing after a preserved specimen from New Zealand.

The material identified by Maas (1906) as *L. fijiana* was re-examined for this study. It is not well preserved, but evidently the radial canals lack the diagnostic outgrowths which are characteristic for *Laodicea fijiana* (see Agassiz & Mayer, 1899). The tentacle number is about 60 and it is likely *L. indica* as already suspected by Kramp (1953).

Distribution: Tropical to temperate regions of the Indian Ocean and the western Pacific Ocean (Kramp, 1968). Type locality: Mutwal Island, West Coast of Ceylon.

Genus *Ptychogena* A. Agassiz, 1865

Diagnosis: Laodiceidae medusae with large, prismatic manubrium, 4 radial canals connected to stomach via large, funnel-shaped, mesentery-like basal extensions of the manubrium. Along radial canals lateral, transverse, fold-like diverticula on which the gonads are located; bell margin with club-shaped cordyli, no cirri, no ocelli. Hydroids where known like *Stegomoma plicatile* (M. Sars, 1863). Colony erect, branching, polysiphonic, with tendency to ramification in one plane. Hydrothecae on stem and branches, all pedicellate. Hydrothecae tubular, curved outwards gradually narrowing downwards, ending in a gable-shaped operculum. Gonothecae larger than hydrothecae, elongated, almost completely adnate with branches and axis, with or without operculum.

Remarks: The diagnosis given in Kramp (1959a) and subsequent authors (e.g. Bouillon *et al.*, 2006) had to be slightly modified. Based on observations on *Ptychogena lactea* A. Agassiz, 1865, influential authors like Haeckel (1879), Mayer (1910), and Kramp (1919, 1933) interpreted the perradial funnel-shaped structures bearing the gonadal folds as widened proximal parts of the radial canals. However, especially in the case of *P. crocea*, these structure are intuitively better interpreted as pockets of the manubrium as seen in many other hydromedusae [see also Russell (1953: 224) who expressed the same opinion for the similar *Chromatonema rubrum* Fewkes, 1882]. These pouches have the same characteristic colour and tissue density as the manubrium, while the radial canals connecting the end of the funnel to the circular canal are thin and transparent like the latter. Whatsoever, they are gastrodermal structures and as such homologous. Interpreting the funnels as radial canals was perhaps influenced by the general diagnosis of the leptomedusae which should have gonads on the radial canals.

The only *Ptychogena* species for which the polyp stage is known is *Ptychogena crocea* (Schuchert *et al.*, 2017), but the other species of the genus could have a similar or identical hydroid.

The medusae of this genus are rather similar or hardly distinguishable from the genera *Modeeria* Forbes, 1848 and *Chromatonema* Fewkes, 1882, although the latter genus has been placed in a separate family, Tiarannidae

Russell, 1940. Currently, the only feasible trait to distinguish *Chromatonema* from *Ptychogena* is the shape of the cordyli: they are club-shaped in *Ptychogena* and spindle-shaped in the *Chromatonema*. It is possible that there are significant differences in the polyp-stage, but the polyps of *Chromatonema* remain unknown. Molecular phylogenies have to re-address the problem. Preliminary data (figs 1-2 in Schuchert *et al.*, 2017) suggest that they are closely related.

Ptychogena crocea Kramp & Dumas, 1925
Fig. 4A-C

Ptychogona crocea Kramp & Dumas, 1925: 290, pl. 1 figs 1-7. – Kramp, 1933: 558, fig. 21. – Russell, 1940: 519, figs 18-19. – Rees, 1952: 5. – Kramp, 1959a: 137, fig. 158. – Kramp, 1961: 146. – Schuchert *et al*., 2017: 168, figs 3-4.

? *Ptychogona crocea*. – Léon *et al.*, 2007: 57, photo 1.

in part *Lafoea plicatilis* M. Sars, 1863: 31.

in part *Stegopoma plicatile*. – Kramp, 1913: 15, figs 1-2. – Broch, 1918: 26, fig. 8. – Edwards, 1973a: 590. – Cornelius, 1995: 114, fig. 25. – Schuchert, 2001: 51, fig. 37A-E. – Schuchert *et al.*, 2017: 168, fig. 4.

Material examined: MHNG-INVE-94101, 1 fully grown, formalin preserved specimen of a catch of about 10 specimens; Norway, Korsfjord, 60.1846°N 5.196°E, 0-600 m depth; collection date 14.06.2016; other, younger specimens were used to extract DNA and RNA; sample DNA sample 1163 giving 16S sequence KY363953, 18S KY363983; DNA sample 1195 resulting in 16S sequence KY363958; DNA sample 1196 giving 16S sequence KY363959 (16S all identical, see Schuchert *et al.*, 2017).

Diagnosis: Umbrella up to 25 mm wide, height 15 to 25 mm but often flatter than a hemisphere (depending on state of contraction and health). Jelly thick, apical jelly about one third of bell height. Stomach relatively large, prismatic, attached to subumbrella via cross-shaped base, mouth wide, irregular. Four radial canals, transparent but relatively thick in distal half or third of radius, connected to stomach via a funnel-shaped, laterally compressed, mesentery-like basal outgrowth of the manubrium, this structure bears on both sides up to 7 thick, large transverse folds, their upper end not connected to subumbrella and covered by the gonads in a thick layer. Bell margin with up to 80 bulbs of different sizes, about 30 developed into tentacles, others mere marginal warts or rudimentary tentacles and all intermediate stages to fully developed tentacles. Between pairs of tentacles 2-4 cordyli, some attached to bell margin, many also on small marginal warts/rudimentary bulbs. Cordyli club-shaped, with few (<10) nematocysts (about 16 µm long spindle-shaped microbasic mastigophores). Colour: stomach, basal extensions, and gonads all with a characteristic, intense yellow-orange colouration; bulbs whitish; canals slightly opaque.

The hydroid stage of this species is *Stegomoma plicatile* (M. Sars, 1863) (Schuchert *et al.*, 2017).

Remarks: The nematocysts have been described in Russell (1940). The yellow colour is lost in preserved animals. For the difference to *Chromatonema rubrum* and other similar medusae see Schuchert *et al.* (2017).

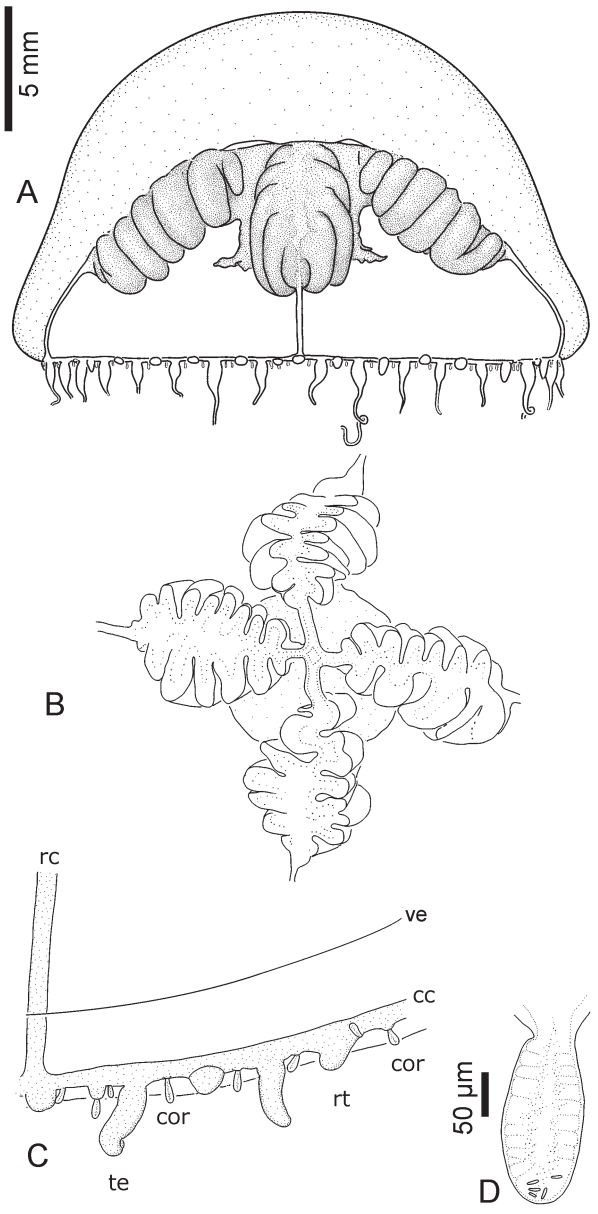

Fig. 4. *Ptychogena crocea,* after living and preserved specimens from Norway. (A) Lateral view. The slight concave lateral walls are a typical sign of beginning deterioration. (B) Stomach and gonads in aboral view. (C) Bell margin seen from oral side (not to scale with A). Abbreviations: cc – circular canal, cor – cordylus, ex – exumbrella, rc – radial canal, rt – rudimentary tentacle or marginal wart, te – tentacle, ve – velum. (D) Cordylus.

Distribution: Deep waters (0-1000 m) of Norway. (Kramp & Damas, 1925; Kramp, 1961) and off the south-west coast of Scotland (Fraser, 1974). A single, much damaged specimen has also been recorded from deep waters of the Cape Verde Islands and three specimens from the Gulf of Maine (Léon *et al.*, 2007). Type locality: Norway, Romsdal, deep waters of Moldefjord.

Ptychogena lactea A. Agassiz, 1865
Fig. 5

Ptychogena lactea A. Agassiz, 1865: 137, figs 220-224. – Mayer, 1910: 215, fig. 109. – Kramp, 1919: 31, pl. 3. – Kramp, 1959a: 137, fig. 157. – Kramp, 1961: 146. – Kramp, 1968: 67, fig. 175. – in part Naumov, 1969: 321, figs 90, not hydroid. – Arai & Brinckmann-Voss, 1980: 83, fig. 46. – Miyake *et al.*, 2004: 40, fig. 5.

Ptychogena pinnulata Haeckel, 1879: 148. – Haeckel, 1882: 7, pl. 2. – Mayer, 1910: 215, synonym. – Kramp, 1955a: 157.

Ptychogena pinnulata var. *intermedia* Linko, 1905: 217.

not *Ptychogena lactea*. – Calder, 1970: 1512, pl. 3 fig. 1, hydroid.

Material examined: MHNG-INVE-82311; 1 subadult specimen, 20 mm diameter, formalin preserved; Canada, British Columbia, Vancouver Island, 49.36667°N 124.08517°W, depth 0-238 m; date collected 15.06.2012; leg. Moria Galbraith.

Diagnosis: Umbrella in mature animals 15-70 mm in diameter, but exceptionally up to 90 mm wide and 30 mm high, bell hemispherical to flatter than a hemisphere (depending on size, state of contraction and health). Jelly thick, apical jelly about one third of bell height. Stomach relatively large, prismatic, attached to subumbrella via cross-shaped base, mouth wide, irregular, rim in folds. Four radial canals, relatively thick, in proximal half connected to stomach via a funnel-shaped, laterally compressed, mesentery-like basal outgrowth of the manubrium. On both sides of each radial canal up to 30 relatively thin, transverse lamellar folds, their upper end connected to subumbrella. The lamellar folds also present distal to the perradial basal outgrowths of the manubrium. Gonads covering lamellar folds. Large animals with papillae along edges of lamellar folds and some folds branched. Bell margin with 70-300 (max. 500) tentacles, no marginal warts or rudimentary tentacles. Between pairs of tentacles 1-3 club-shaped cordyli attached to bell margin.
Colour: gonads, radial canals, and tentacles characteristic milk-white (but also with a peachy or greenish tint, Schuchert *et al*., 2017).
Hydroid unknown (Schuchert *et al.*, 2017).

Distribution: A predominantly Arctic species that penetrates into Boreal zones of the Atlantic and Pacific Oceans. Its southern limits in the Atlantic Ocean are

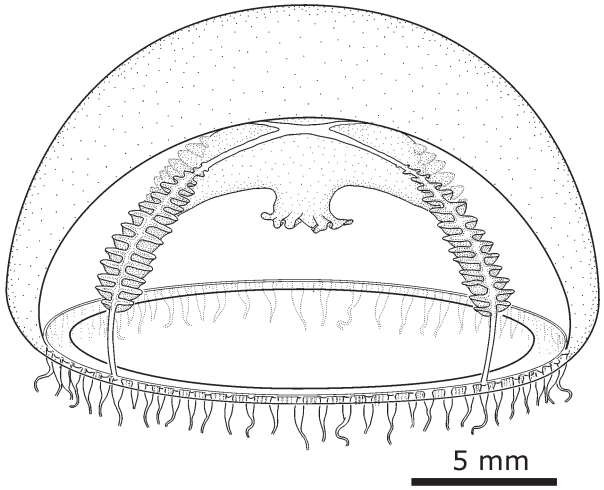

Fig. 5. *Ptychogena lactea,* subadult, schematic after MHNG-INVE-82311.

Cape Cod and the Faroe-Shetland Channel, in the Pacific Ocean northern Japan and British Columbia. Often collected at depths of over 250 m but may be found near the surface where the water is very cold (Arai & Brinckmann-Voss, 1980; Fraser, 1974). Type locality: Nahant, Massachusetts Bay, USA, Atlantic Ocean.

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

Staurodiscus gotoi (Uchida, 1927)
Fig. 6A-C

Staurodiscoides gotoi Uchida, 1927: 165, figs 1-2.

Staurodiscus gotoi. – Kramp, 1961: 147. – Kramp, 1965: 56. – Kramp, 1968: 70, fig. 183. – Xu & Zhang, 1974: 20, fig. 9. – Bouillon, 1984: 65. – Bouillon & Barnett, 1999: 87, fig. 85. – Xu *et al.*, 2014: 577, fig. 455.

Material examined: MHNG-INVE-33467, >30 specimens of various developmental stages; New Zealand, Hauraki Gulf, Devonport, Narrow Neck Beach, 36.8123°S 174.8025°E, 0 m; collection date 26.07.2002; DNA isolate 126, 16S sequence FJ550472, COI MF000510, 18S sequence FJ550535, 28S sequence FJ550391; for photos of living specimens see Table 1.

Diagnosis (NZ material): Umbrella somewhat higher than hemisphere, diameter 5-8 mm, jelly thick, at apex about half the bell height. Manubrium moderately long, cruciform in section, four simple lips. Four radial canals and circular canal rather broad. Radial canals in proximal half thick and on both sides with 2-4 lateral outgrowths, outgrowths thick, not strictly opposite, covered by gonad tissue, longer ones curved towards bell margin but not connected to circular canal. Bell margin with four large perradial bulbs tapering into

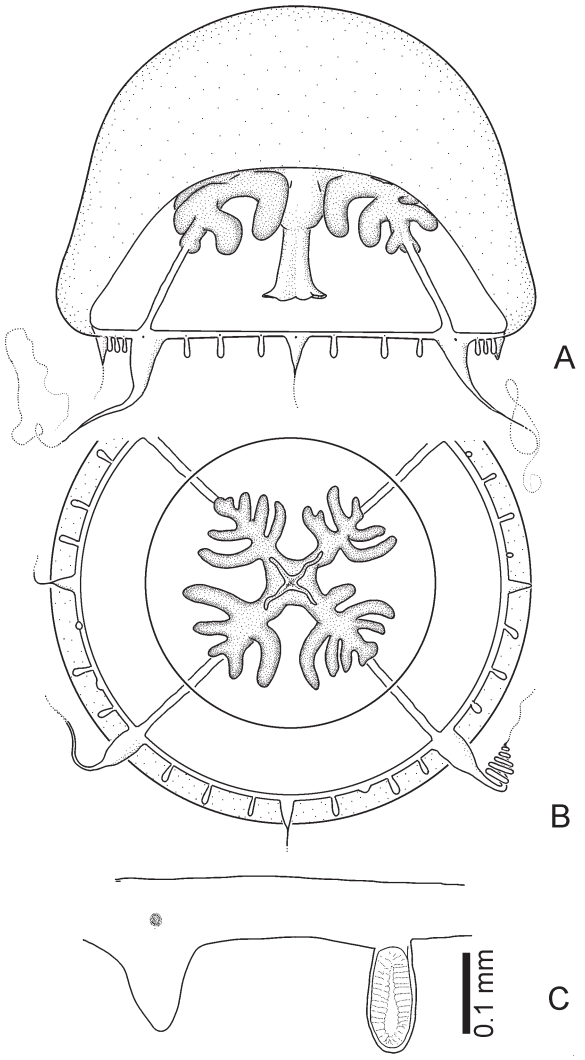

Fig. 6. *Staurodiscus gotoi* subadult, schematic composite drawing made after photographs of living specimens and preserved specimens. Diameter of bell approximately 6 mm (A) Lateral view. (B) Oral view. (C) Circular canal with tentacle-less bulb and a cordylus shown in optical section.

long tentacles. Interradial tentacle bulbs present, in fully mature animals tapering into tentacles but these shorter than the perradial ones. All tentacle bulbs with a black abaxial ocellus. Occasionally some additional, very small adradial bulbs. Between perradial- and interradial bulbs usually three cordyli. Cordyli relatively large, hollow, cylindrical gastrodermal cells, with a few nematocysts at the tip. Some of the cordyli also with an ocellus near their origin.
Polyps unknown.

Variation: Young medusae have only two tentacles and very small lateral outgrowths of the radial canals. Xu & Zhang (1974) depicted an animal with 16 tentacles.

Distribution: Japan, China, Papua New Guinea, Indonesia, North Island of New Zealand (Kramp, 1965; Bouillon, 1984; Bouillon & Barnett, 1999). Type locality: Japan, Shizuoka Prefecture, Shimizu Bay.

Remarks: The identification of this material as *St. gotoi* was largely influenced by Bouillon & Barnett (1999) who used also material provided by the author. There are nevertheless some differences of the New Zealand medusae to those of Japan and China: there are fewer cordyli (24-26 versus up to 88), the bell diameters are smaller (4-8 versus up to 15), the interradial tentacles are often small or absent, the mesogloea is much thicker, and the lateral outhgrowths are limited to the proximal half of the tentacles. It is assumed that these are population differences. Additionally, it was noted that the mesogloea shrinks in formalin-preserved animals. A later transfer into 70% ethanol makes the mesogloea disappear completely, resulting in a condition where the lateral outgrowths cf. the radial canals reach the bell margin. It is possible that some published illustrations of *Staurodiscus* species are actually based on such material with a shrunken bell.

Family Eirenidae Haeckel, 1879
Genus *Eirene* Eschscholtz, 1829

Diagnosis: Eirenidae medusa with distinct, broad gastric peduncle; cirri absent; with or without excretory pores; 4-6 simple radial canals; gonads on subumbrellar part of radial canals, not extending to gastric peduncle; numerous statocysts (>8).
The hydroids of '*Campanulina*', '*Campanopsis*' or '*Eugymnanthea*' type (see Bouillon *et al.*, 2006).

Remark: *Clytia* species with a short gastric peduncle like *Clytia gregaria* (see below) are formally not distinguishable from *Eirene* species. Thus, some nominal *Eirene* species (Schuchert, 2017a; see Du *et al.*, 2010 for a key to the species) with a shallow peduncle and no excretory papillae could therefore also be *Clytia* species. Life-cycle studies or DNA barcodes (Schuchert *et al.*, 2017) have to confirm the identity of *Eirene pentanemalis* Lin, Xu & Huang, 2013, *Eirene brevistylus* Huang & Xu, 1994, and other similar species.

Eirene viridula (Péron & Lesueur, 1810)
Fig. 7A-C

Oceania viridula Péron & Lesueur, 1810: 346, English Channel.
Geryonia pellucida Will, 1844: 70, pl. 2 figs 8-12.
Geryonopsis delicatula Forbes, 1848: 39.
Geryonopsis forbesii Van Beneden, 1867: 87, pl. 3 figs 1-7. – Haeckel, 1879: 202, synonym.
Tima willi Neppi, 1909: 368, figs 3, 4, 7, 8, 12, 13, 15, 16, 18-25, 28-45, 47.
Phortis pellucida. – Neppi & Stiasny, 1913: 49.
Perigonimus nudus Stechow, 1919: 16, fig. D. – Schuchert, 2007: 273, synonym.

Eirene viridula. – Russell, 1953: 321, text. figs. 201-205, pl. 20 figs 3-4. – Kramp, 1959a: 158, fig. 215. – Kramp, 1961: 191. – Kramp,1968: 90, fig. 243. – Cornelius, 1995: 223, fig. 51.

Material examined: Several mature specimens; France, Villefranche-sur-Mer, Mediterranean, 43.686°N 7.317°E, 0 m depth; collection date 04.05.2001; DNA isolate 010; 16S sequence KY363937. – 1 specimen; France, Normandy, Luc-sur-Mer, English Channel, 49.31985 °N 00.34965°W, 0 m depth; collection date 17.08.2005; DNA isolate 388; 16S sequence FJ550502, 18S FJ550588, 28S FJ550445.

Diagnosis: Umbrella up to 30 mm wide, nearly hemispherical, middle portion fairly thick; peduncle broad, projecting beyond bell margin, shape variable. Velum narrow. 4 radial canals. Stomach fairly small, with four pointed lips and crenulated margin; gonads linear, extending from bell margin to base of peduncle. Up to 70 tentacles of different sizes, large and small frequently alternating, tentacles fine, bulbs conical with distinct adaxial excretory papilla projecting into subumbrella; 50 or more statocysts, each with 1-4 concretions. No cirri. Colourless except for green tinge of manubrium.

Polyp stage see Cornelius (1995).

Distribution: North-western Europe; Mediterranean; west coast of Africa; east coast of Africa; Ceylon, Papua New Guinea. Type locality: English Channel.

References: Russell (1953), Cornelius (1995).

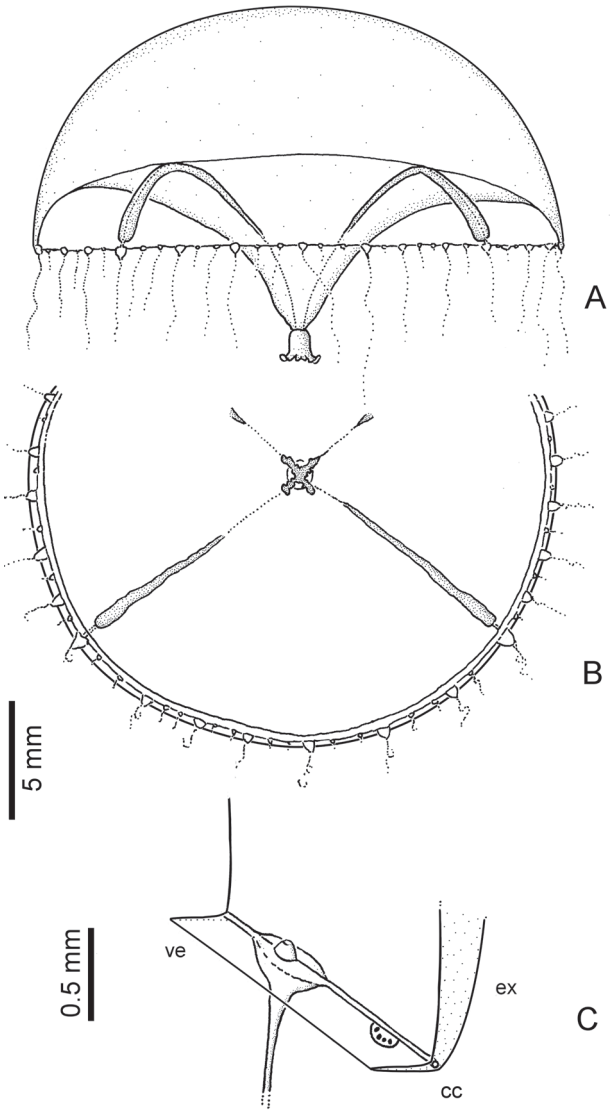

Fig. 7. *Eirene viridula,* after living Mediterranean specimens. (A) Lateral view. (B) Oral view. (C) Marginal bulb in adaxial view, note conical excretory papilla on subumbrellar side of tentacle bulb. Abbreviations: cc – circular canal, ex – exumbrella, ve – velum.

Eirene hexanemalis (Goette, 1886)

Fig. 8A-C

Irenopsis hexanemalis Goette, 1886: 832. – Browne, 1905b: 142, pl. 1 fig. 4, pl. 3 figs 5-8. – Maas, 1905: 37, pl. 6 figs 38-40. – Mayer, 1910: 310, figs 171, 171a. – Vanhöffen, 1911: 229, fig. 19.

Phortis pellucida forma *hexanemalis.* – Vanhöffen, 1913: 17.

Phortis pellucida forma *pentanemalis* Vanhöffen, 1913: 18.

Eirene hexanemalis. – Kramp, 1936: 248, bibliography, synonymy. – Kramp, 1953: 281, fig. 5, variation, seasonality. – Kramp, 1961: 188. – Kramp, 1965: 77, fig. 5, variation. – Kramp, 1968: 91, fig. 245. – Bouillon, 1983: 421, figs 1-3, life cycle, ecology. – Bouillon, 1984: 39, fig. 6, hydroid, nematocysts.

Eirene octonemalis Guo, Xu, & Huang, 2008: 61, fig. 1. **new synonym**

? *Eirene pentanemalis* Lin, Xu & Huang, 2013 in: Lin *et al*., 2013: 756, figs 1-3.

Material examined: MHNG-INVE-53565; 22 formalin-preserved medusae, fertile males and females; Abu Dhabi, 24.4666°N 54.3272°E, depth 0 m; collection date 20-26.08.2006; one individual with 12 radial canals; leg. H. Galea.

Diagnosis: Mature medusa 10-18 mm in diameter, bell hemispherical, thick apical jelly, gastric peduncle broad, length variable but usually not reaching beyond velum level. Velum narrow. Manubrium six-rayed in cross-section, perradial corners of the mouth drawn out as lips, mouth margin with many folds. Majority of individuals with six radial canals, in a minority with other numbers varying from 4 to 12. Gonads thin, more or less straight, along radial canal from base of peduncle to circular canal. 40-60 short tentacles on small bulbs, bulbs with adaxial, conical excretory papilla. In-between 2 tentacle bulbs 1-2 rudimentary bulbs (marginal warts) and 2-4 round statocysts with one concretion (occasionally 2-4, Browne, 1905b).

Polyp planktonic, solitary, see Bouillon (1983).

Distribution: Coastal waters from South- and East Africa to Australia, Indonesia, China, and Japan (Kramp, 1965). Type locality: Zanzibar, East Africa.

Remarks: This is a well-known species, the only new information is the existence of a specimen with 12 radial canals which was mixed with the 22 specimens with 6 radial canals. Until now, the maximal number of canals was 11. The variation in the number of radial canals has been summarized by Kramp (1965) and Bouillon (1983). A minority of individuals of a particular population can have from 4 to 12 tentacles.

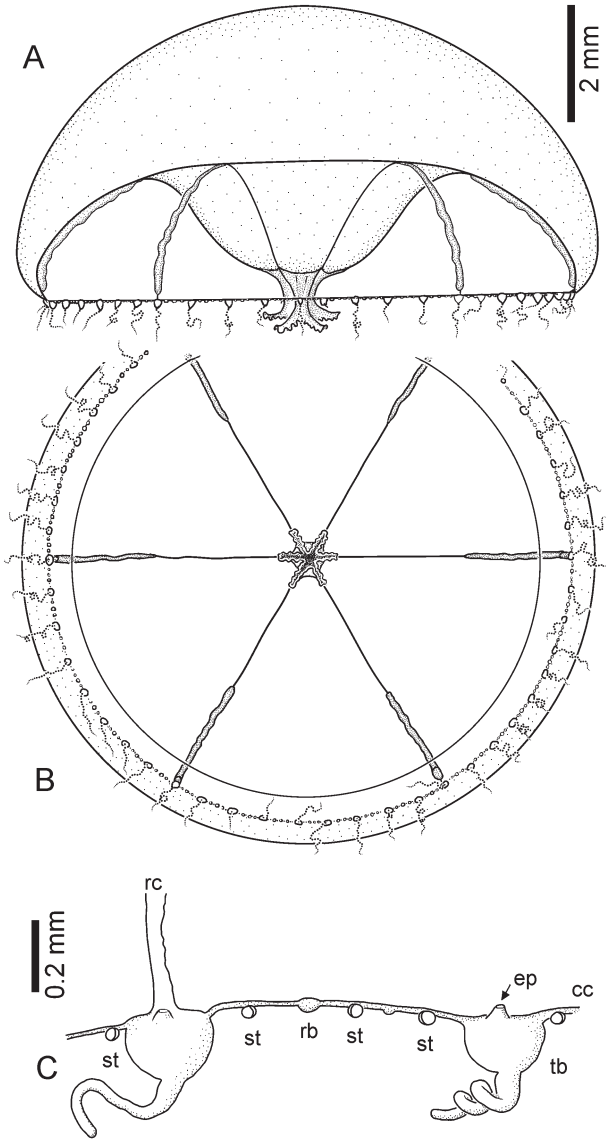

Fig. 8. *Eirene hexanemalis,* after preserved material. (A) Lateral view. (B) Oral view. (C) Schematic view on circular canal from adaxial side. Note presence of conical excretory (arrow). Abbreviations: cc – circular canal, ep – excretory papilla, ex exumbrella, rb – rudimentary bulb, rc – radial canal, st – statocysts (shown without concretion).

It is thus evident that *Eirene octonemalis* Guo, Xu, & Huang, 2008 must be regarded as not separable from *E. hexanemalis*. The former species differs from the latter in having 8 radial canals. The only peculiarity of *E. octonemalis* is that all four known specimens had 8 radial canals. This could, however, be a population specific trait.

Likewise, *Eirene pentanemalis* Lin, Xu & Huang, 2013, which is characterised by five radial canals and the purported absence of excretory papillae, could also be a young *E. hexanemalis*. The species is based on badly mutilated material for which a reliable observation of the excretory papillae appears doubtful.

References: Browne (1905b), Kramp (1936, 1953), Bouillon (1983).

Genus *Helgicirrha* Hartlaub, 1909

Helgicirrha cari (Haeckel, 1864)

Fig. 9A-D

Tima cari Haeckel, 1864: 332.

Tima pellucida. – Schulze, 1874: 138, pl. 2 figs 6a-b. [not *Geryonia pellucida* Will, 1844 = *Eirene viridula* (Péron & Lesueur, 1810)]

Geryonia pellucida. – Haeckel, 1879: 201, pl. 12 figs 1-2. [not *Geryonia pellucida* Will, 1844 = *Eirene viridula* (Péron & Lesueur, 1810)]

Helgicirrha schulzii Hartlaub, 1909: 86. **new synonym**

Eirene viridula. – Mayer, 1910: 311, fig. 172. [not *Eirene viridula* (Péron & Lesueur, 1810)]

Tima plana Neppi, 1910: 165, figs 2, 2a-b. **new synonym**

Helgicirrha schulzei. – Kramp, 1936: 254 [subsequent incorrect spelling]. – Russell, 1953: 328, figs 206-212, pl. 20 figs 1-2. – Kramp, 1959a: 159, fig. 218. – Kramp, 1961: 192. – Bouillon, 1971: 362, pl. 7-8, fig. 12. – Brinckmann-Voss, 1973: 68, figs 4-5. – Pagès *et al.,* 1992: 27, fig. 28. – Cornelius, 1995: 238, fig. 55.

Helgicirrha cari. – Kramp, 1936: 253. – Kramp, 1959a: 160, fig. 219. – Kramp, 1961: 191.

Material examined: 1 specimen; France, Bay of Villefranche-sur-Mer, 43.6856°N 7.3178°E, 0 m depth; collection date 29.04.2016; DNA isolate 1153; 16S sequence KY363968, COI MF000519, 18S KY363989.

Diagnosis: Umbrella diameter 20-50 mm when mature, distinctly flatter than a hemisphere, apical jelly about 1/3 of total height, gastric peduncle broad, conical, length about bell-height (Fig. 9A). Stomach small, with cruciform mouth opening, drawn out into perradial lips to variable length, mouth margin folded to a variable degree. Velum narrow. 4 radial canals. Gonads thin, extending from stomach to close to bell margin. 40-50 larger bulbs each with a short and fine tentacle, between these bulbs 2-3 small bulbs that occasionally bear tentacle stumps. Most marginal bulbs with a pair of lateral cirri and a conical excretory papilla pointing into the subumbrella (Fig. 9D). 50-100 statocysts, each with 2-3 concretions.

Hydroid stage an athecate polyp with lateral medusa budding, for more details see Brinckmann-Voss (1973) and Bouillon (1971).

Distribution: North-western Europe south of Norway, Mediterranean, coast of West Africa, Benguela Current (Pages *et al.*, 1992). Type locality: Nice, Mediterranean.

Remarks: Kramp (1936) revised the genera *Eirene* and *Helgicirrha* and kept *H. cari* distinct from the better known *H. schulzii* based on the presence of longer mouth lips in *H. cari*. As this is usually a rather variable character and not used to distinguish species of leptomedusae, it is rather doubtful that the two species are really distinguishable. Moreover, in Schulze's (1874) illustration of the species, on which Hartlaub (1909) based the new name *H. schulzii*, the mouth lips are not significantly smaller than the ones observed here (Fig. 9C). These facts indicate that both nominal species are indistinguishable. Additionally, Laakmann & Holst (2013) published COI sequences of *H. schulzii* collected in the North Sea (GenBank numbers KC440021 and KC440025). The two haplotypes differed in one base pair. The COI sequence of the Mediterranean specimen in the present study also had only one nucleotide difference with the sequences from the North Sea. A difference of one base pair represents therefore evidently only an intraspecific variation (comp. also Laakmann & Holst, 2013; Schuchert, 2014, 2016; Zheng *et al.,* 2014; Schuchert *et al*., 2017 for intraspecific COI variation in Hydrozoa).

To conclude, *H. schulzii* Hartlaub, 1909 must be regarded as a synonym of *H. cari* (Haeckel, 1864), with the latter having precedence.

The specific epithet of *H. schulzii* (original spelling) was modified to *H. schulzei* by Kramp (1936), arguing that the name refers to Schulze. However, this is incorrect as the epithet was likely meant to represent the Latinised form Schulze, which is Schulzi. The second i comes from the genitive declension. Although many subsequent authors used Kramp's spelling, the correct spelling remains *H. schulzii*.

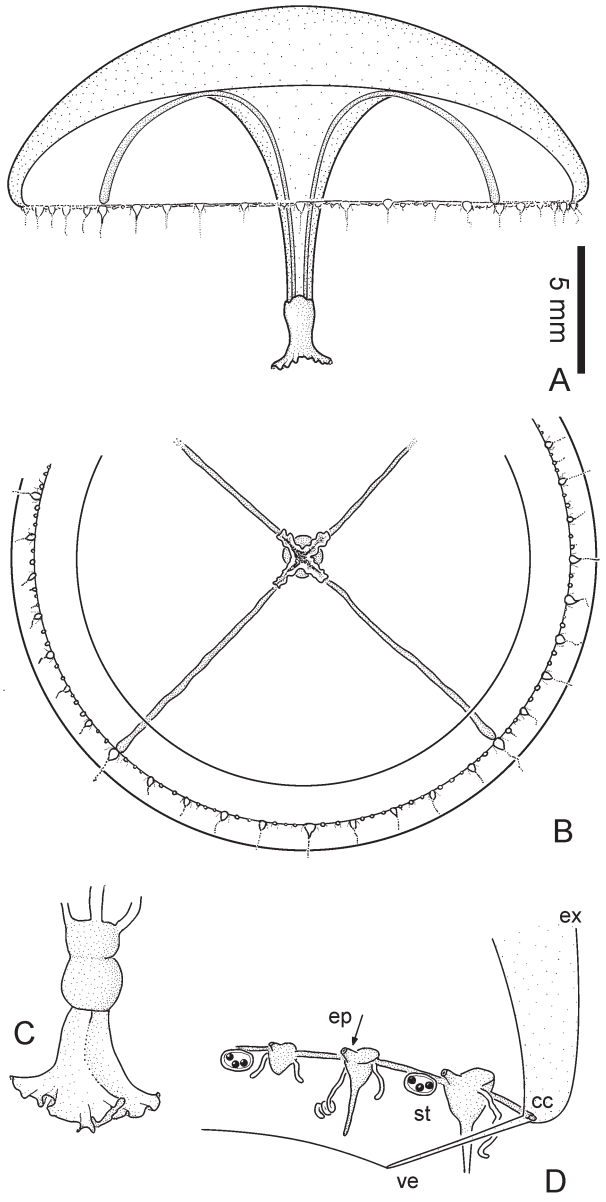

Fig. 9. *Helgicirrha cari,* after living Mediterranean specimen. (A) Lateral view. (B) Oral view. (C) Manubrium. (D) Schematic view on bell margin from adaxial side. Note the presence of conical excretory papillae that project into subumbrella (arrow). Abbreviations: cc – circular canal, ep – excretory papilla, ex exumbrella, ve – velum.

Genus *Eutima* McCrady, 1859

Remarks: See Vannucci (1957) and Bouillon (1984) for a discussion and comparison of species.

According to Migotto *et al.* (2004), *Eutima sapinhoa* Narchi & Hebling, 1975 lacks cirri and in the adult medusa the gonads stretch from the manubrium to close to the bell margin. Using the classification of Bouillon *et al.* (2006), the species must therefore be transferred to the genus *Neotima* as *Neotima sapinhoa* (Narchi & Hebling, 1975) **n. comb.**

Eutima gegenbauri (Haeckel, 1864)

Fig. 10A-B

Octorchis gegenbauri Haeckel, 1864: 331. – Russell, 1953: 367, fig. 233-23, pl. 22 fig. 4.

Eutima gegenbauri. – Neppi & Stiasny, 1913: 48. – Kramp, 1959a: 161, fig. 221. – Kramp, 1961: 195. – Cornelius, 1995: 228, fig. 52.

Eutima (*Octorchis*) *gegenbauri.* – Kramp, 1933: 588, fig. 58. – Russell, 1970: 260, figs 23s-24s.

Liriopsis campanulatus Claus, 1877: 11.

Octochandra canariensis Haeckel, 1879: 198, pl. 13 fig. 1.

Octochandra germanica Haeckel, 1879: 198, pl. 13 figs 3-8.

Material examined: MHNG-INVE-31748; 2 specimens; France, Villefranche-sur-Mer, Ligurian Sea, Mediterranean, 43.686°N 07.317°E, 0 m depth; collection date 04.05.2001; DNA isolate 009; 16S sequence FJ550515, COI MF000489, 18S FJ550600, 28S FJ550456. – MHNG-INVE-89881; >10 specimens; Sweden, Kristineberg, 58.243849°N 11.432305°E, 0 m depth, collection date 03.10.2014; DNA isolate 1062; 16S sequence KY363964, COI MF000515; for archived photos see Table 1.

Diagnosis: Umbrella 10-20 mm wide when mature, almost hemispherical. Apical jelly thick (up to 1/2 of bell height), gastric peduncle very long, 2-3 times the bell height, conical, with very broad base. Velum narrow. 4 radial canals. Stomach tubular, with four lips, rim with a few folds. Elongate gonads along radial canals subdivided, 4 on peduncle beginning near stomach, 4 gonads on subumbrellar parts of radial canals reaching to bell margin, thus a total of 8 gonads. 8-16 tentacles without distinct bulbs, relatively thick and stiff, not coiling; between tentacles marginal warts, about 60-80 in total, with nematocysts, each wart with an adaxial, conical papilla, usually 1-2 lateral cirri, but these often rudimentary or lost, with a few nematocysts. Papillae with nematocysts. 6-8 statocysts, irregularly placed, with 6-12 concretions.
No distinct colours or denser tissues greenish.
Polyp stage: see Cornelius (1995).

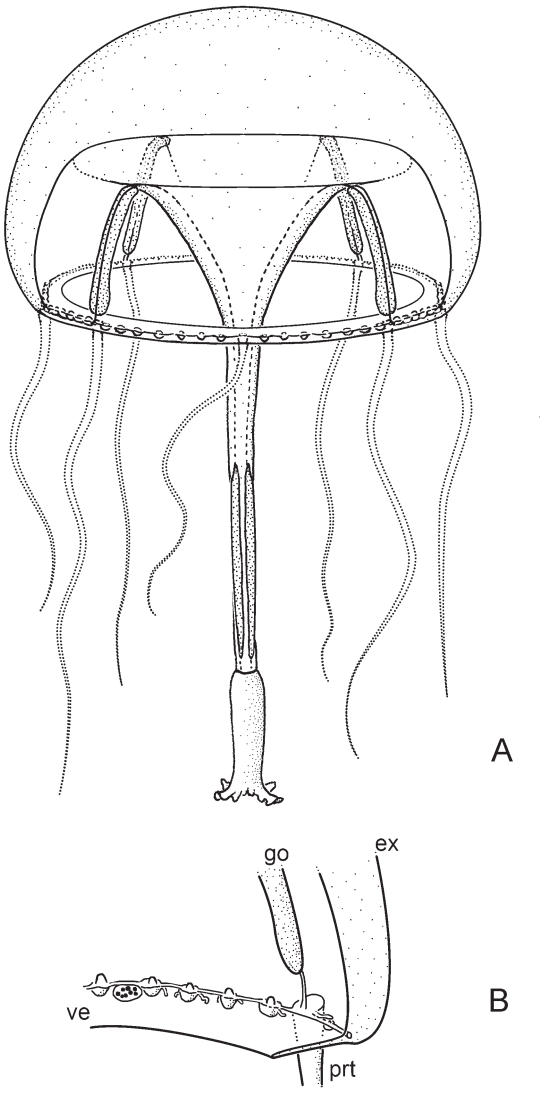

Fig. 10. *Eutima gegenbauri,* after living Mediterranean specimen. (A) Lateral view. (B) Schematic drawing of bell margin seen from adaxial.

Distribution: North-western Europe up to mid-Norway; Mediterranean; Canary Islands; Morocco, North Carolina. Type locality: Nice, Mediterranean.

Remarks: The marginal warts have an easily visible adaxial, conical papilla. They have reportedly no excretory pore, but this could not be verified in the present material and needs further examination by histological sections (comp. Russell, 1953: 372).
Vannucci (1957) thought that *Eutima curva* could be conspecific with *E. gegenbauri*, a proposal which was not followed by subsequent authors. DNA sequences of material of *E. curva* from New Zealand were clearly distinct from *E. gegenbauri* (Leclère *et al.*, 2009; Schuchert *et al.*, 2017).

Genus *Neotima* Petersen, 1962 emended

Diagnosis: Eirenidae medusa with large gastric peduncle, four radial canals, 4-8 statocysts, tentacle bulbs or bell margin without cirri, bulbs without excretory papillae, without cordyli, with marginal warts, gonads on entire length of radial canals, either undivided or interrupted in middle part. Hydroid unknown.

Remarks: It was necessary to modify slightly the diagnosis of this genus (Bouillon *et al.*, 2006) in order to accommodate the new species described below which has subdivided gonads. The alternative solution, to propose a new genus name, seemed less desirable. Moreover, other genera of the family, like *Eutima*, are also composed of species with entire or subdivided gonads.
The genus *Eutima* McCrady, 1859 differs from the genus *Neotima* by the presence of lateral cirri on the marginal warts (Bouillon *et al.*, 2006). The generic subdivision of the Eirenidae Haeckel, 1879 is likely highly artificial and needs a taxonomic revision.

Neotima galeai new species
Fig. 11A-B

Holotype: MHNG-INVE-93201; 1 mature medusa in ethanol, originally preserved in formalin; Persian Gulf,

Abu Dhabi, 24.4666°N 54.3276°E, 0 m depth, collected 26.08.2006; leg. H. Galea.

Paratypes: MHNG-INVE-53566; 4 intact and 1 dissected mature medusae in ethanol; otherwise same data as holotype.

Type locality: 24.4666°N 54.3276°E, 0 m depth.

Diagnosis: *Neotima* medusa with gonads along radial canals interrupted for some distance, resulting thus in eight gonads in total.

Etymology: The species is dedicated to the collector of the type material, Dr Horia Galea, in appreciation of his admirable work on hydrozoan systematics.

Description: Medusa nearly hemispherical, diameter 9-11 mm. Aboral jelly thick, 1/3 or more of total height, with a broad gastric peduncle of about the same length as the bell height, basal diameter about half the diameter of the bell, tapering in an even curve to a diameter slightly smaller than stomach diameter. Manubrium small, 1.2 mm high, bell-shaped, mouth opening cruciform as margin drawn out into four perradial lips, entire mouth margin in numerous folds. 26-28 tentacles of which 4 always perradial, contracted 6-7 mm, not coiled, bases laterally compressed, no bulbs, no longitudinal furrows. Between each pair of tentacles 2-7, mostly 4-6, marginal warts, sizes variable but apparently not developing into tentacles, without adaxial papillae. Observed statocyst numbers 6-8, likely normally 8, number of concretions unknown. Cirri absent. Gonads along the four radial canals, reaching from close to junction with circular canal to manubrium, but interrupted for a stretch in middle of the peduncle, gonads thus subdivided into a total of eight gonads, diameter of gonads relatively small compared to other leptomedusae, not much thicker than tentacle base.
Nematocysts: small haplonemes, abundant on tentacles, (6-7)x(2) µm; larger haplonemes, relatively rare, along circular canal and in marginal warts, (11-14)x(3) µm.
Colours: Transparent, gonads whitish.
Polyp unknown.

Distribution: Known from type locality only (United Arab Emirates).

Remarks: The number of concretions in the statocysts could not be determined as these were missing due to the initial preservation in formalin.
The new species matched the diagnosis for the genus *Neotima* Petersen, 1962 (see also Bouillon *et al.*, 2006), except for the subdivided gonad (see remarks above). It resembles *Neotima lucullana* (Delle Chiaje, 1823), but this Mediterranean species is much larger (diameter up to 87 mm), has a thin aboral jelly, about twice as many tentacles, the tentacles have an abaxial groove, and the gonads are undivided (Petersen, 1962). The only other known *Neotima* species, *Neotima peterseni* Bouillon, 1984, has a similar size and tentacle number as the new species, but the bell shape and thickness of the mesogloea are different, as well as the gonads being undivided (comp. Bouillon, 1984: table 3).
Neotima galeai can potentially be confused with *Eutima hartlaubi* Kramp, 1958, a species occurring in the same biogeographic zone. However, the latter species is distinguishable by having marginal warts with lateral cirri, only 12-14 tentacles, and an abaxial spur at the tentacle base (Kramp, 1958; 1968).
The gonads of *Neotima galeai* are relatively thin and one is tempted to regard the observed medusae as subadult. However, the other *Neotima* species also have thin gonads and this seems to be a characteristic trait of the genus and also many other species of the family Eirenidae.

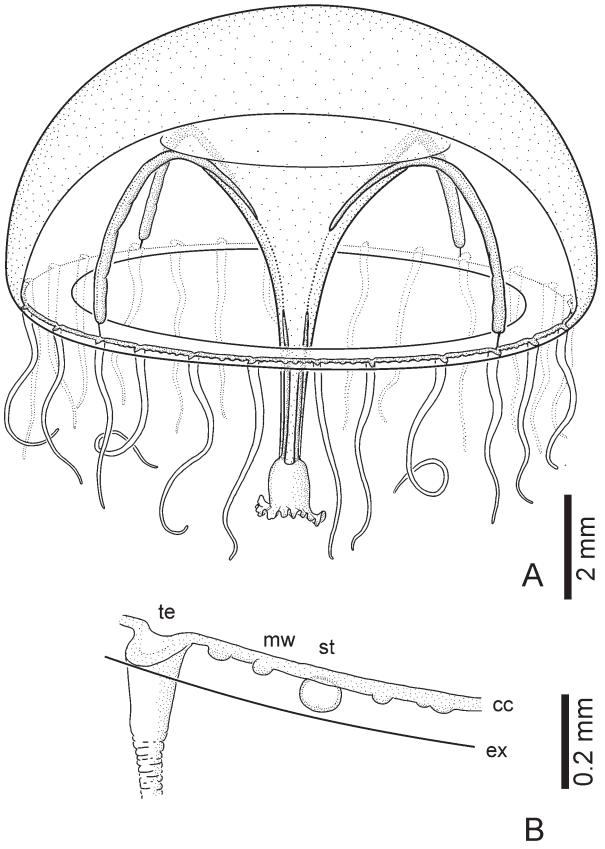

Fig. 11. *Neotima galeai* new spec., schematic drawings after preserved specimens. (A) Lateral view. (B) Bell margin, oblique view from abaxial, concretions of statocyst not shown. Abbreviations: cc – circular canal, ex – exumbrella, mw – marginal wart or rudimentary bulb, st – statocyst, te – tentacle.

Family Mitrocomidae Haeckel, 1879
Genus *Mitrocomella* Haeckel, 1879

Mitrocomella brownei (Kramp, 1930)
Fig. 12A-B

Trissocoma brownei Kramp, 1930: 23, fig. 9-11.

Mitrocomella brownei. – Kramp, 1932: 341, figs 9, 37, revision. – Rees & Russell, 1937: 75, figs 9-10, life cycle. – Russell, 1953: 261, figs 150-155, pl. 15 fig. 4. – Kramp, 1959a: 142, fig. 169. – Kramp, 1961: 155. – Pagès *et al.,* 1992: 32, table. – Bouillon, 1995: 236. – Cornelius, 1995: 140, fig. 31. – Bouillon & Barnett, 1999: 91, fig. 91.

Material examined: 3 medusae; France, Roscoff, 48.73°N 04.00°E, 0-20 m depth, collection date April 1998; DNA isolate N119; 16S sequence KX355404, COI MF000485, 18S FJ550521, 28S FJ550374.

Diagnosis: Umbrella diameter 4-7 mm, umbrella usually somewhat flatter than a hemisphere, lateral jelly rather thin, apical jelly somewhat thickened, no gastric peduncle. Velum width 1/3 to 1/4 of radius. Manubrium short, cruciform cross-section, base not much larger than oral end, mouth simple, four perradial, slightly recurved lips. Radial canals 4, narrow, straight. Gonads oval, somewhat more elongate in females, situated near the ends of the radial canals, in younger animals more towards middle. Marginal tentacles typically 16, range in adults 11-24, with basal bulbs, 5-7 cirri between adjacent tentacles, coiling spirally. Typically 8 large, adradial statocysts (range 8-11), each with 5-7 concretions in a u-like arrangement. Colours: manubrium greenish, pink, or ochreous yellow.

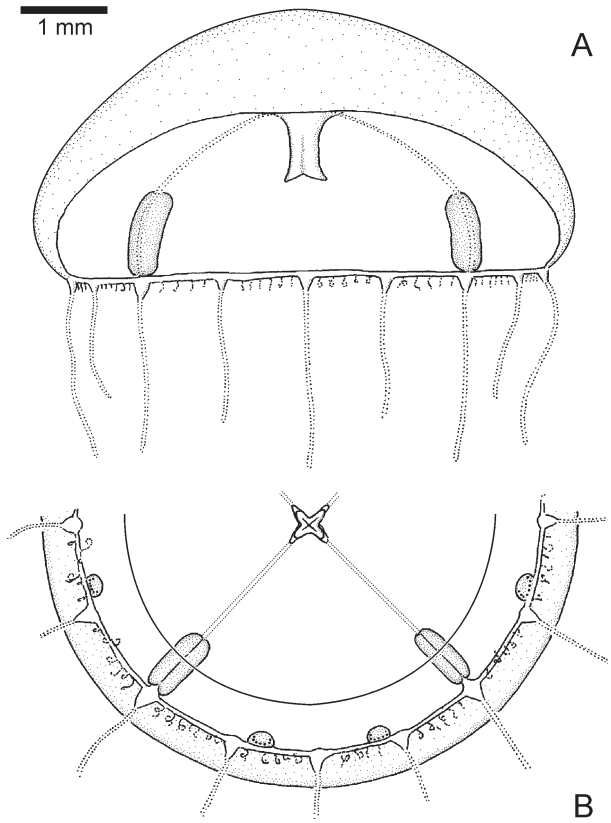

Fig. 12. *Mitrocomella brownei*, male, after life. (A) Lateral view. (B) Oral view.

Polyp stage tiny, of "*Cuspidella"* type, see Cornelius (1995).

Distribution: British Isles, Brittany, Mediterranean, New Zealand. Type locality: North Sea.

References: Russell (1953), Cornelius (1995), Bouillon & Barnett (1999).

Mitrocomella polydiademata **(Romanes, 1876)**
Fig. 13A-D

Tiaropsis polydiademata Romanes, 1876a: 274, nomen nudum.
Tiaropsis polydiademata Romanes, 1876b: 526. – Romanes, 1877: 194, pl. 15 fig. 3.
Mitrocomella polydiademata. – Kramp, 1932: 346, text-figs 3, 5, 11, 18, 29, 30, 40, pl. 10 figs 3-4. – Russell, 1953: 257, figs 147-149. – Naumov, 1969: 326, fig. 193. – Edwards, 1973b: 601, figs 1-2, life cycle. – Arai & Brinckmann-Voss, 1980: 93, figs 51-52. – Pagès *et al.*, 1992: 32. – Ramil & Vervoort, 1992: 38, fig. 6a-i. – Cornelius, 1995: 143, fig. 32.
? *Cuspidella grandis* Hincks, 1868: 210, pl. 40, fig. 4.
Cuspidella polydiademata. – Naumov, 1969: 327, fig. 194.
Mitrocomella fulva Browne, 1904: 17, pl. 1 fig. 3, pl. 3 figs 1-2. – Kramp, 1932: 344. – Kramp, 1961: 156. – Edwards, 1973b: 601, synonym. – Pagès *et al*., 1992: 32.

Material examined: 1 specimen; Scotland, Firth of Lorn, Dunstaffnage Bay, 56.455°N 05.434°E, 0 m depth, temperature 8-10°C; collection date 11.05.2004; DNA 1133; 16S sequence KY363939, COI MF000501; archived document see Table 1. – >2 specimens; Norway, Fanafjord, 60.24079°N 05.22941°W, 0 m depth; collection date 23.04.2015; DNA isolate 1115; 16S sequence KY363949, COI MF000508, 18S KY363979; archived document see Table 1.

Diagnosis: Umbrella diameter 9-30 mm, mostly around 10-12 mm, umbrella usually hemispherical or slightly higher, apical jelly thickened, no gastric peduncle. Top of subumbrella sometimes rather flat. Velum width about 1/4 of bell radius. Manubrium short, small, cruciform cross-section, base not much larger than oral end, mouth simple, four perradial, slightly recurved lips. Radial canals 4, relatively thick close to manubrium. Gonads elongate in females, covering 2/3 of radial canals, separated from circular canal and manubrium, when fully developed pendant and usually in zig-zag (Fig. 13D). Marginal tentacles typically 28-36 (reportedly up to 64) when mature, with basal bulbs, some bulbs without tentacles, 5-9 cirri between adjacent tentacles, coiling spirally. 16 large statocysts, each with numerous concretions aligned in two curved rows. When irritated, the medusa emits a greenish light.
Polyp stage tiny, of "*Cuspidella*" type, see Cornelius (1995).

Distribution: Northern boreal species, known from North Atlantic and NE Pacific. Type locality: Cromarty Frith, Scotland.

References: Russell (1953), Arai-Brinckmann-Voss, 1980, Cornelius (1995a).

Family Lovenellidae Russell, 1953
Genus *Eucheilota* McCrady, 1859

Eucheilota maculata Hartlaub, 1894
Fig. 14A-C

Eucheilota maculata Hartlaub, 1894: 193. – Hartlaub, 1897: 499, pl. 20 figs 4-8. – Russell, 1953: 311, text-figs 193-195. – Kramp, 1959a: 154, fig. 206. – Kramp, 1961: 174. – Werner, 1968: 136, figs 2-20, life cycle. – Russell, 1970: 256, figs 19s-20s. – Cornelius, 1995: 157, fig. 35. – Nagata *et al.,* 2014: 304, figs 17-18, Brazil.

Campanulina hincksii Hartlaub, 1897: 496, pl. 21, pl. 22 fig. 11. – Cornelius, 1995: 157, fig. 35.
Campomma hincksi. – Stechow, 1921: 255.
? *Eucheilota maculata.* – Goy, 1979: 277, fig. 16.

Material examined: About 50 specimens; France, Normandy, Luc-sur-mer, 49.32102°N 00.3443527°W, 0 m depth, collected 18.05.2005; DNA isolate 386, 16S sequence FJ550501, 18S FJ550587, 28S FJ550444; DNA isolate of second specimen DNA1136, 16S KY363942.

Diagnosis: *Eucheilota* medusa with a large black dot on each of the four interradial sides of the stomach. Umbrella diameter about 13 mm (range 10-20 mm),

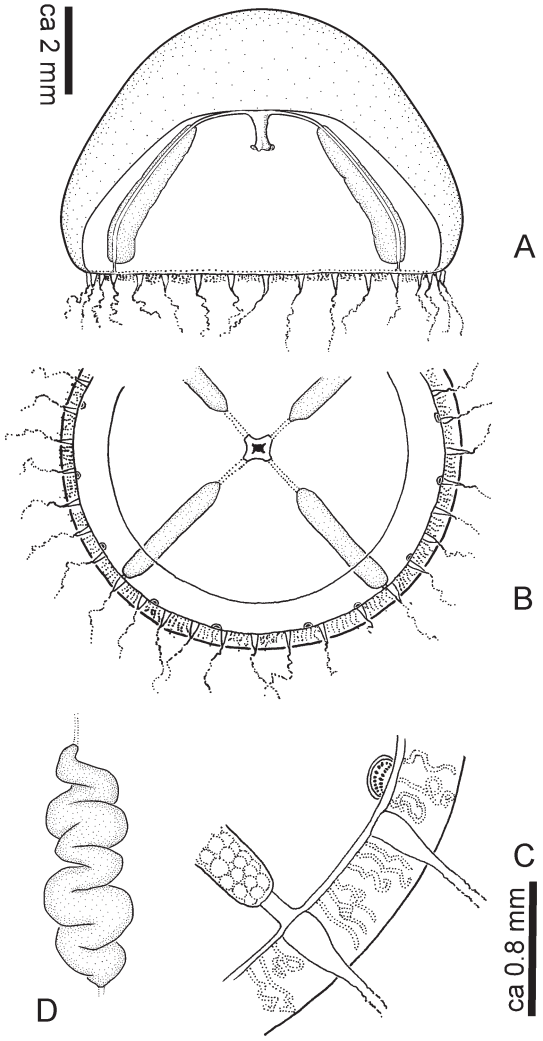

Fig. 13. *Mitrocomella polydiademata*, gonads not fully developed, after life combined from several specimens. (A) Lateral view, diameter about 10 mm. (B) Oral view. (C) Enlarged bell rim showing tentacle bulbs, cirri, and one statocyst. (D) Fully developed gonad, oral view.

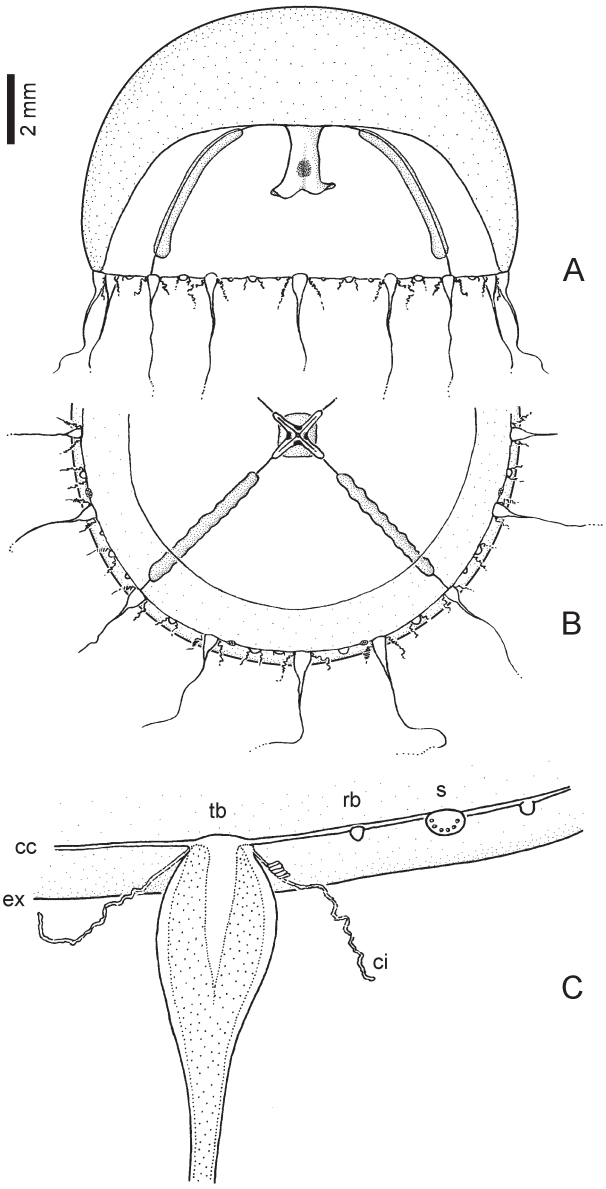

Fig. 14. *Eucheilota maculata*, after life. (A) Lateral view. (B) Oral view. (C) Enlarged bell rim in oral view, showing tentacle bulbs (tb), cirri (ci), and one statocyst (s); cc – circular canal, ex – exumbrella, rb – rudimentary bulb.

usually hemispherical or slightly higher, apical jelly somewhat thickened, no gastric peduncle. Top of subumbrella rather flat. Velum width ca 1/5 of bell radius. Manubrium short, cruciform cross-section, base not much larger than oral end, mouth simple, four perradial, slightly recurved lips. Radial canals four, narrow. Gonads elongate in females, covering 2/3 of radial canals, separated from circular canal and manubrium, when fully developed slightly wavy. Marginal tentacles typically 16 (occasionally 20) when mature, with distinct basal bulbs, between each pair of tentacles 1-3 small, rudimentary bulbs without tentacles. Tentaculate bulbs and sometimes also rudimentary bulbs with a lateral spiral cirrus on each side. Eight closed statocysts with 5-6 concretions each.
Polyp stage forming branched colonies of the "*Campanulina*" type, see Werner (1968) or Cornelius (1995).

Distribution: Southern North Sea, western Baltic Sea, English Channel, Argentina, Brazil, and southwest of India (Cornelius, 1995; Nagata *et al*., 2014). Type locality: North Sea, Helgoland.

References: Russell (1953), Cornelius (1995).

Eucheilota menoni Kramp, 1959
Fig. 15A-D

Eucheilota menoni Kramp, 1959b: 248, fig. 14a-b. – Kramp, 1961: 175. – Kramp, 1968: 82, fig. 221. – Bouillon, 1984: 57. – Bouillon *et al.*, 1988: 217, fig. 12, nematocysts. – Bouillon & Barnett, 1999: 89, fig. 80.
? *Mitrocomium assimile* Browne, 1905b: 137, pl. 1 fig. 3.
? *Lovenella assimilis.* – Kramp, 1961: 177. – Kramp, 1968: 80, fig. 216. – Bouillon, 1984: 76, nematocysts. – Bouillon *et al.*, 1988: 220, nematocysts. – Brylinski *et al.*, 2016: 21, fig. 2.
Lovenella assimilis. – Bouillon & Barnett, 1999: 89, Fig. 87.

Material examined: Holotype of *Eucheilota menoni*, 1 female medusa, NHMD-98221; Nancowry Harbour, Nicobar Islands, Galathea station 319; 06.05.1951; det. P. L. Kramp. – MHNG-INVE-29469, about 60 mature medusae; collected at several stations between Auckland and Leigh, New Zealand; February 1997; originally in formaldehyde, pigment almost entirely lost. – MHNG-INVE-33457, 8 specimens; Narrow Neck Beach, Hauraki Gulf, New Zealand, 36.8123°S 174.8025°E, 0 m depth; 03.07.2002; 7 specimens originally in formaldehyde, pigments now faint, one specimen preserved for DNA extraction giving sample DNA072; 16S KY363960. – 10 mature medusae, not in permanent collection; same locality as before but collected 26.07.2002; preserved in 95% ethanol; pigments and statocysts preserved; DNA of one individual sample 1131; 16S sequence KY363961. – Several specimens, not in permanent collection; Motutapu Island, Hauraki Gulf, New Zealand, 36.7443°S 174.9044°E, depth 0-3 m, 30.06.2002; specimens used for examination of life medusae and to extract DNA sample 247; 16S FJ550493, COI KT981899, 18S FJ550570, 28S FJ550427.

Description of New Zealand material: Small medusa (diameter up to 3 mm), bell nearly hemispherical, jelly somewhat thickened at apex, otherwise moderately thin, without apical process. Velum width ca 1/6 of bell radius. Manubrium short, cruciform cross-section, base quadrangular, only slightly larger than oral end, mouth cruciform, simple, four perradial, slightly recurved

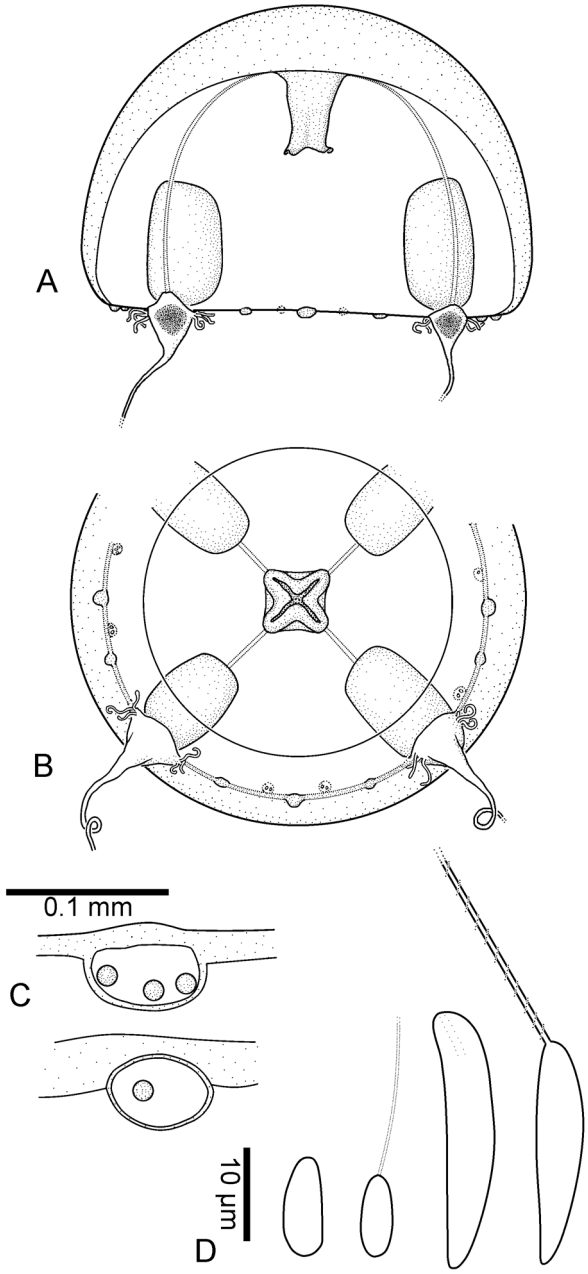

Fig. 15. *Eucheilota menoni* from New Zealand, diameter preserved 1.5 mm. (A) Lateral view. (B) Oral view. (C) Two statocysts, lateral view. (D) Atrichous isorhiza undischarged and discharged, same for large holotrichous isorhizas.

lips. Manubrium without spots of dark pigment. Radial canals four, narrow. Gonads large for the bell-size and already present in small animals (1 mm), covering distal half of radial canals and reaching to level of circular canal; thick, cushion-shaped and projecting deeply into subumbrella, surface smooth, usually without adaxial furrow except in a few animals (and only in 1-2 of the four gonads). Observed egg numbers per gonad about 40. Marginal tentacles 4, between each pair of tentacles 3 small, rudimentary bulbs without tentacles. Tentacles with solid endodermis. Tentaculate bulbs with 3-8 lateral cirri, no cirri on rudimentary bulbs. Tentacular bulbs on abaxial side with a large, conspicuous, black pigment spot. Per quadrant 2-3 statocysts, thus 8-12 in total, each with 1-3 concretions, mostly 2 or 3.
Medusa buds never present.
Nematocysts (preserved material): atrichous isorhizas in tentacles, almond-shaped, size very variable and perhaps 2 size classes, (2.5-3.5)x(7.5-11) µm; mainly in tentacle bulbs, large, curved holotrichous isorhizas, end opposite thread opening pointed, spines of thread tiny and hardly visible under light microscopy, capsule size (4-5.5)x(25-26) µm. Presence of other types cannot be excluded for the examined material (2 medusae).

Distribution: Indian Ocean, Red Sea, western Pacific, eastern Pacific (Altuna, 2009), perhaps introduced in the north-eastern Atlantic (Altuna, 2009; Brylinski *et al.*, 2016). Type locality: Nancowry Harbour, Nicobar Islands.

Discussion: The material from New Zealand was identified as *E. menoni* because DNA sequences of part of the present material have already been published under this name and also because it mostly matched the diagnosis given in Bouillon & Barnett (1999). However, the identity is not entirely clear and it could as well be attributed to *Lovenella assimilis* (Browne, 1905) as has been argued in detail by Brylinski *et al*. (2016). *Eucheilota menoni* and *Lovenella assimilis* are indeed rather difficult to separate (Bouillon, 1984). Bouillon has reportedly seen both species in Papua New Guinea and he summarised the diagnostic differences of *Lovenella assimilis* and *E. menoni* as follows (in brackets the condition observed in the present material):
- 12 to 20 statocysts versus 8 only (8-12)
- no black pigment on the manubrium versus black dots on manubrium (no dots on manubrium)
- gonads with a longitudinal furrow versus smooth gonads (smooth)
- gonads reaching to bell margin versus gonads reaching close to bell margin (to bell margin).

Lovenella assimilis has two concretions per statocyst (Browne, 1905b). Kramp (1959b) could not observe the concretions in his material of *E. menoni,* but in Kramp (1961) he states that there is one concretion only. It could be that he took this from Menon (1932) who described a similar medusa that Kramp thought to be *E. menoni*. The NZ animals had 1-3 concretion, mostly 2-3.

Browne's type material of *Lovenella assimilis* could not be obtained for study, but it is clear from Browne (1905b) that he had a preserved medusa that had lost its pigmentation. This makes *L. assimilis* de facto a "*species inquirenda*", a species that is currently not unambiguously identifiable.
The nematocysts of these two nominal species have been documented by Bouillon (1984), Bouillon *et al.* (1988), Hirano & Yamada (1985), and Altuna (2009). Comparing the results is inconclusive and the interpretation of the capsule types is occasionally subjective.
Bouillon also observed medusa buds in both morphotypes, something never observed by other authors.
To conclude, the present material is not unambiguously attributable to either *E. menoni* or *L. assimilis* and this is also the case for the European material described by Altuna (2009) and Brylinski *et al.* (2016). As already concluded by the latter authors, it is likely that both nominal species as used today are in fact conspecific. Another possibility is that there are more than two species involved and that they all intergrade morphologically. In order to resolve the ambiguity, more specimens of both morphotypes obtained from the western Indian Ocean must be examined morphologically and genetically.
It might seem surprising that two nominal species that are hardly distinguishable have been attributed to two different genera. The medusae of the genus *Lovenella* differ from *Eucheilota* by their number of statocysts, 16-32 versus 4-12 (Kramp, 1968; Bouillon *et al*., 2006). This seems rather arbitrary, but the separation stems from *Lovenella* Hincks, 1868 being polyp-based, while *Eucheilota* McCrady, 1859 is based on a medusa. A re-assessment of the classification is clearly needed (Cornelius, 1995), and *Lovenella* should be regarded a synonym of *Eucheilota*.

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

Octophialucium indicum Kramp, 1958
Fig. 16A-D

Octocanna polynema. – Menon, 1932: 23, pl. 3 fig. 25. [not *Octocanna polynema* Haeckel, 1879 = species inquirenda]
Octophialucium indicum Kramp, 1958: 347, figs 2a-b. – Kramp, 1961: 184. – Kramp, 1965: 72. – Kramp, 1968: 87, fig. 235. – Bouillon & Barnett, 1999: 90, fig. 89. – Xu *et al*., 2014: 623, fig. 510A-B.
Octophialucium funerarium. – Wear, 1965: 7, fig. 3E. [not *Octophialucium funerarium* (Quoy & Gaimard, 1827)]

Material examined: Numerous mature medusae; Greta Point, Evans Bay, Wellington, New Zealand; 41.3055°S 174.8023°E; surface plankton; 15.11.1993 and 02.02.1994; material used in part for the study of Bouillon & Barnett (1999). – MHNG-INVE-29970, 10 medusae; same locality as previous lot; 26.10.1994;

one medusa used to extract DNA sample N126; 16S AY787897, 18S FJ550522, 28S FJ550375; DNA extract of second medusa (sample DNA 1167) resulted in identical 16S as AY787897.

Description of NZ material: *Octophialucium* medusa with bell diameter up to 15 mm, bell flatter than a hemisphere, bell rim somewhat incurved, lateral walls thin and relatively straight, apical jelly thick (1/2 or more of total height). Velum narrow, about 1/10 of radius. Manubrium short, cross-section an eight-pointed star, 8 more or less crenulated lips. Eight radial canals. Gonads short, sausage-shaped, along distal fourth of radial canals but not reaching circular canal. Eight perradial tentacles and 0-8 additional tentacles between perradial tentacles, thus when fully grown usually 16 tentacles in total. Tentacles thin, relatively short. Between each pair of tentacles 3 rudimentary bulbs, small, without tentacle rudiments. All bulbs with very short, conical excretory papilla projecting into subumbrella, difficult to observe. Bulbs without abaxial spurs. Statocysts closed, oval vesicles along circular canal, 32 or more, small, with 2 (occasionally 1 or 3) concretions. Tissues colourless.

Variation: younger stages have only 4 radial canals, the interradial canals develop by outgrowth from the manubrium. Younger stages may have four developing gonads only.

Hydroid unknown.

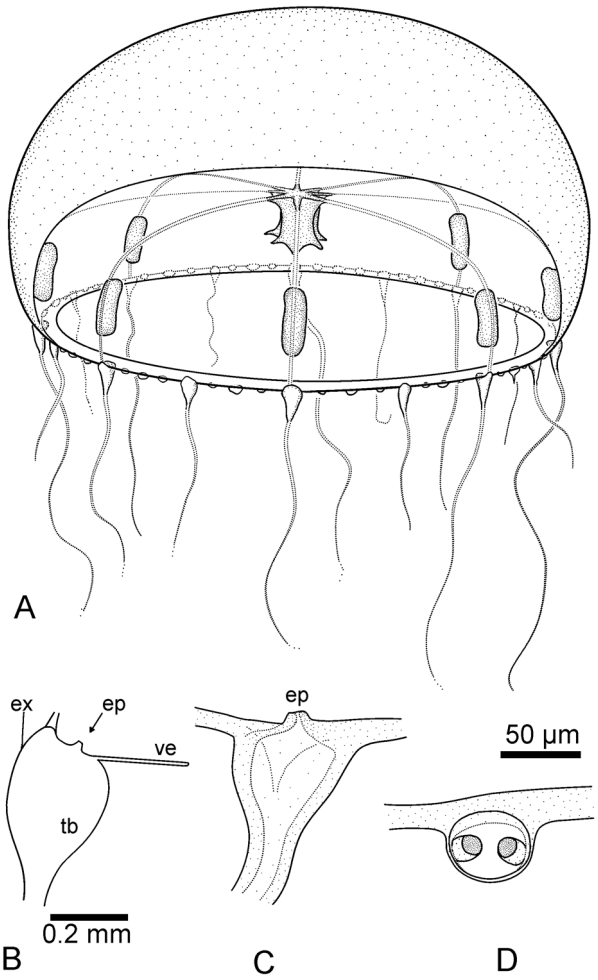

Fig. 16. *Octophialucium indicum*, combined from several preserved specimens. (A) Oblique view, diameter 13-15 mm when alive. (B) Schematic side view of perradial tentacle bulb. (C) Adaxial view of tentaculate bulb in optical section. (D) Statocyst with two concretions. Abbreviations: ep – excretory papilla, ex – exumbrella, tb – tentacle bulb, ve – velum.

Distribution: Tropical Indo-West-Pacific from Madagascar to Tahiti and New Zealand (Kramp, 1965). Type locality: Sittwe (formerly Akyab) Harbour, Burma, surface plankton.

Similar species: The Atlantic *Octophialucium medium* Kramp, 1955 is very similar, differing only in the more elongated gonads. Another similar species is *Octophialucium sinensis* Huang, Xu, Guo & Qiu, 2010, but this species has only 8 tentacles and smaller bulbs with tentacle rudiments. *Octophialucium funerarium* (Quoy & Gaimard, 1827) from the NE Atlantic has considerably more tentacles, 64-128.

Remarks: The identification of the present material was largely based on Bouillon & Barnett (1999), who also had part of this material at their disposal. However, there is one marked difference of the New Zealand material to the original description given in Kramp (1958): the excretory papillae are not long and conspicuous, they are rather small and very inconspicuous (Fig. 16B-C). Additionally, there are fewer tentacles (max. 16 versus 19-28). While the tentacle number difference is likely not significant for a species level distinction, the different excretory papillae could indicate that we have a distinguishable morphotype and perhaps also a different species or a subspecies.

It is possible that not all known nominal *Octophialucium* species are really distinct. Little is known about the inter-population variation in *Octophialucium* species and only molecular genetic studies can reliably assess the status of the different *Octophialucium* species (for species see Schuchert, 2017b; Kramp, 1955b; 1961).

Family Aequoreidae Eschscholtz, 1829
Genus *Aequorea* Péron & Lesueur, 1810

Aequorea macrodactyla (Brandt, 1835)

Fig. 17A-D

Mesonema (Mesonema) macrodactyla Brandt, 1835: 221. – Brandt, 1838: 359, pl. 4 figs 1-3.

Polycanna purpurostoma Agassiz & Mayer, 1899: 169, pl. 8 figs 26-28.

Aequorea maldivensis Browne, 1905a: 732, pl. 56, figs 4-12.

Mesonema macrodactylum. – Maas, 1905: 40, pl. 8 fig. 52.

Aequorea macrodactylum. – Bigelow, 1909: 174, pl. 36. – Bigelow, 1928: 313, pl. 43 fig. 7.

Aequorea pensilis.– in part Russell, 1953: 355, fig. 220C-D, 225, pl. 33 figs 1-5 [not *Aequorea pensilis* (Haeckel, 1879)]

Aequorea macrodactyla. – Kramp, 1959a: 167, fig. 235. – Kramp, 1961: 207, synonymy. – Kramp, 1965: 87, fig. 8. – Kramp, 1968: 98, fig. 267. – Pagès *et al.*, 1992: 26, fig. 26. – Cornelius, 1995: 208, fig. 48D-E. – Bouillon & Barnett, 1999: 79, fig. 71. – Mizrahi *et al.*, 2015: 59, fig. 1A-D.

? *Aequorea macrodactyla*. – Nogueira *et al*., 2016: fig. 1.

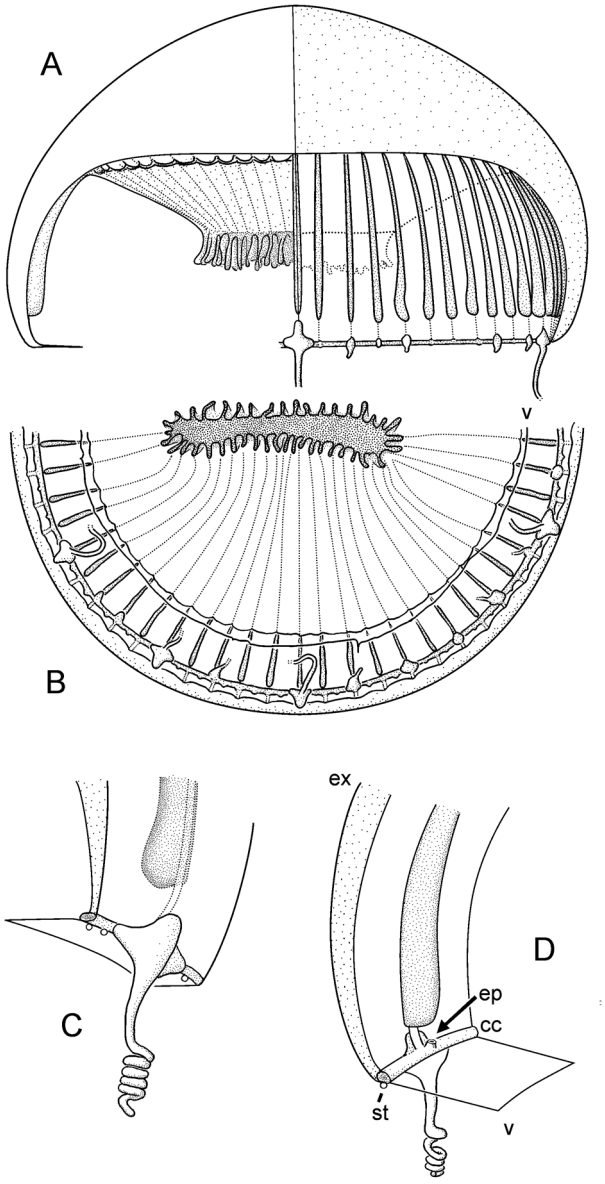

Fig. 17. *Aequorea macrodactyla*, bell diameter about 26 mm, about 70 radial canals, after preserved specimen. (A) Lateral view, left half shown as with umbrella cut away. (B) Oral view. (C) Bell margin seen from outside, note characteristic shape of tentacle bulb. (D) Bell margin seen from inside the bell, note the excretory papilla (arrow, ep). Other abbreviations: cc – circular canal, ex – exumbrella, statocyst, v – velum.

Material examined: NIWA 119801; 8 medusae; from sediment trap in 360 m depth deployed north of Hauraki Gulf, New Zealand, -35.0867°S 174.8833°E, sampling period 28.11.1996 to 05.02.1997; very well-preserved in formalin, 7-30 mm diameter, gonads developed after reaching bell diameters of 20 mm.

Diagnosis: Umbrella diameter when mature 20-75 mm, central jelly thick, lens-shaped, margin thin; with conical jelly filling stomach (1/2 subumbrella height); velum spanning about 1/5 of umbrellar opening. Stomach about 2/3 as wide as umbrella, funnel-shaped, mouth region much folded, about as many folds as radial canals. 60-100 (max. 150) radial canals; gonads extending along radial canals from close to circular canal to base of the stomach (and conical jelly). Much fewer tentacles than radial canals, only 10-30 marginal tentacles of variable lengths, all with conspicuous bulbs of variable sizes, also many bulbs without tentacles, but many radial (>50%) canals end in no bulbs. Marginal bulbs characteristically broad and with rounded abaxial keel clasping the bell margin, with excretory papilla on subumbrellar side. Statocysts below circular canal, numerous, 1-3 between two radial canals, 2-5 concretions per statocyst. Colours: stomach wall pink, gonads greyish-blue or violet (after Kramp, 1965, 1968; Pagès *et al.*, 1992; own observations).
Polyp stage unknown. Nematocysts see Russell (1939, as *A. pensilis*).

Distribution: Circumglobal, widely distributed in tropical and temperate regions of the Indo-Pacific, less common in the Atlantic Ocean, perhaps introduced in the Mediterranean (Kramp, 1965; Pages *et al*., 1992; Mizrahi *et al*., 2015; Nogueira *et al*., 2016, the latter with a map and many references of records). Type locality: Equatorial Pacific.
It is rather frequent at depths from the surface to 2000 m, but even sampling with cable lengths of 4000 m yielded specimens (Kramp, 1965).

Remarks: The relatively low tentacle number combined with the diagnostic broad marginal bulbs with an abaxial keel (Fig. 17C-D) allows a reliable identification of this species, notably to separate it from *A. pensilis* (Haeckel, 1879) and *A. krampi* Bouillon, 1984. Identifying *Aequorea* species is currently rather difficult (comp. e.g. Arai & Brinckmann-Voss, 1980; Gershwin *et al.*, 2010) and a taxonomic revision based on a world-wide study comparing morphotypes and DNA markers is highly desirable.
Aequorea macrodactyla has been recorded from New Zealand before (Kramp, 1965; Bouillon & Barnett, 1999), but the good preservation of the specimens permitted

the illustration of some structural details (Fig. 17A-D). As in other *Aequorea* species, the stomach is very wide but relatively shallow and it almost covers the conical jelly that hangs down from the subumbrella like a gastric peduncle.

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

Clytia gregaria (L. Agassiz, 1862)
Fig. 18A-C

Oceania gregaria L. Agassiz, 1862: 353.
Clytia osterudi Strong, 1925: 389, pl. 37, hydroid.
Phialidium gregarium. – Murbach & Shearer, 1903: 179, pl. 20. – Kramp, 1961: 167, 444. – Kramp, 1962: 25. – Kramp, 1968: 78, fig. 206. – Roosen-Runge, 1970: 217, figs. 2-25, hydroid. – Arai & Brinckmann-Voss, 1980: 104, figs 59-60.
Clytia gregaria. – Bouillon, 1995: 233. – Bouillon & Barnett, 1999: 99, fig. 101.

Material examined: Several specimens; USA, Friday Harbor Laboratories, floating docks, 48.545141°N 123.012059°W, 0.5 m depth; collection date 23.05.2011; DNA was isolated from two individuals, DNA 920 giving the sequences 16S MF000539, COI MF000499; DNA isolate 1169 yielding the 16S sequence MF000540. Specimens without black pigment; archived document see Table 1.

Diagnosis: Umbrella up to 22 mm wide, hemispherical to lens-shaped. Manubrium small, attached on a short gastric peduncle of variable height, manubrium base cross-shaped and attached to peduncle, mouth with 4 long, folded lips. Gonads linear, undulated, along distal half to two-thirds of radial canals, not touching circular canal; females with >100 eggs per gonad. Marginal tentacles 60-80, marginal bulbs nearly globular, few or no bulbs without tentacles when fully grown; 1 statocyst (or rarely 2 or 3) between successive tentacle bulbs, usually 1, sometimes 2 concretions per statocyst. Without colour or gonads pale yellow to salmon. With or without variable amounts of black or dark brown pigment on margin of lips, gonads, marginal bulbs and ring canal.

Distribution: Shallow waters of coastal regions of the NE Pacific Ocean, from British Columbia to Oregon (Arai & Brinckmann-Voss, 1980). Bouillon (1995) and Bouillon & Barnett (1999) recorded it also from New Zealand, mostly in deeper waters. Type locality: Strait of Georgia, British Columbia, Canada, Pacific Ocean.

Similar species: Preserved and damaged material of this medusa can easily be confounded with *Eirene mollis* Torrey, 1909 (see Arai & Brinckmann-Voss, 1980 for description). *Eirene mollis* has up to 180 tentacles and a somewhat more pronounced gastric peduncle. It is not known if it has excretory papillae.

Remarks: A summary on the identity, taxonomy, biology, and distribution of this species is given in Arai & Brinckmann-Voss (1980). This is a locally very common medusa. It has served for a large number of experimental studies (mostly using the superseded name *Phialidium gregariaum*, *e.g.* Dabiri *et al*., 2010; Freeman, 2005; Colin & Costello, 2002; Colin *et al*., 2003; Costello & Colin, 2002; Ridgway & Freeman, 1999; Mills, 1981; and many more references given in these works).

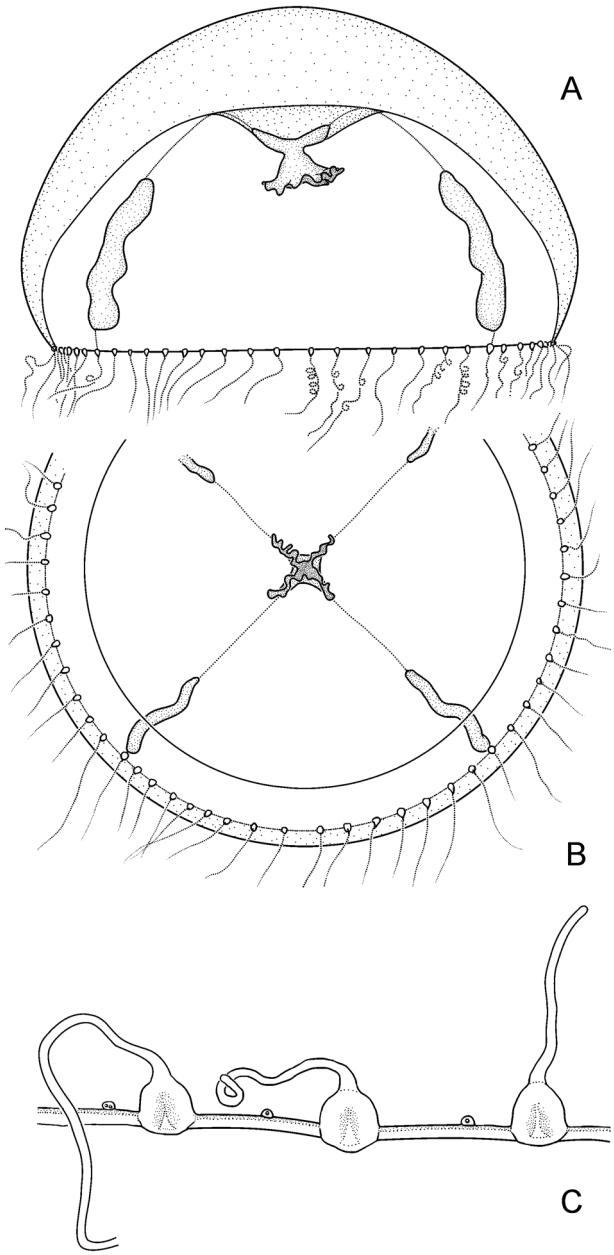

Fig. 18. *Clytia gregaria*, bell diameter about 20 mm, after photographs of living specimens. (A) Lateral view. (B) Oral view. (C) Bell margin in oral view with three tentacles and 3 statocysts.

The hydroid of *Clytia gregaria* has been raised from the medusae several times but it was not possible to relate it to colonies sampled in nature (Arai & Brinckmann-Voss, 1980). The 16S and COI barcode sequence of the present material will hopefully help to identify its polyp stage in nature (*cf.* Schuchert *et al.*, 2017).

Although rather shallow and sometimes absent, the gastric peduncle of *Clytia gregaria* is rather unusual for the genus *Clytia* and makes the medusa very prone to be mistaken for an *Eirene* species, e.g. the sympatric *Eirene mollis* Torrey, 1909. Some *Eirene* species (*cf.* Schuchert, 2017) with a shallow peduncle and no excretory papillae could thus turn out to be *Clytia* species.

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