



Identification of the polyp stage of three leptomedusa species using DNA barcoding

Authors: Schuchert, Peter, Hosia, Aino, and Leclère, Lucas

Source: Revue suisse de Zoologie, 124(1) : 167-182

Published By: Muséum d'histoire naturelle, Genève

URL: <https://doi.org/10.5281/zenodo.322675>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Identification of the polyp stage of three leptomedusa species using DNA barcoding

Peter Schuchert^{1*}, Aino Hosia² & Lucas Leclère³

¹ Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Switzerland

² The Natural History Collections, University Museum of Bergen, Allégaten 41, 5007 Bergen, Norway

³ Sorbonne Universités, UPMC Univ. Paris 06, CNRS, Laboratoire de Biologie du Développement de Villefranche-sur-mer (LBDV), 181 chemin du Lazaret, F-06230 Villefranche-sur-mer, France

* Corresponding author; E-mail: peter.schuchert@ville-ge.ch

Abstract

DNA sequence data of hydromedusae and hydroids collected in the fjords near Bergen, Norway, permitted to connect three leptomedusae to three thecate hydroids with hitherto unknown life cycles. For all three species pairs, identical 16S and 18S sequences could be found. For comparisons, estimates of intraspecific variation of 16S sequences of other leptomedusa species were determined by comparing specimens collected at different localities. The sequence comparisons allowed us to conclude that *Ptychogena crocea* Kramp & Dumas, 1925 is the medusa stage of the hydroid *Stegopoma plicatile* (M. Sars, 1863), *Earleria quadrata* (Hosia & Pages, 2007) the medusa of *Racemoramus panicula* (G.O. Sars, 1874), and *Cyclocanna welshi* Bigelow, 1918 the medusa of *Egmundella producta* (G.O. Sars, 1874). Due to non-matching geographic distribution patterns of the medusa and hydroid phases, as well as the possibility that other related medusa species may have morphologically identical hydroids, the identities of *Stegopoma plicatile* and *Racemoramus panicula* are considered ambiguous. These nominal species likely refer to species complexes. Their names are therefore considered as partial synonyms of the medusa-based names and the latter should remain in use despite being more recent. *Cyclocanna welshi* and *Egmundella producta* are recognised as synonyms, and the species should from now on be referred to as *Cyclocanna producta* (G.O. Sars, 1874) n. comb.

Keywords: Cnidaria - Hydrozoa - Leptothecata - marine - hydromedusae - hydroids - life cycles.

INTRODUCTION

The life cycles of many hydromedusae and hydroids remain unknown because they are rare or difficult to cultivate. DNA barcodes, namely mitochondrial 16S and COI sequences, have recently emerged as a useful tool to unravel hydrozoan life cycles through matching sequences obtained from medusae and hydroids. Two recent papers have thus identified the polyp stage of *Oceania armata* Kölliker, 1853 (Schuchert, 2016b) and connected the polyp *Boreohydra simplex* Westblad, 1937 with the medusa *Plotocnide borealis* Wagner, 1885 (Pyataeva *et al.*, 2016).

During the last decade, the authors have sampled hydroids and medusae in Norway, mostly in the fjords near Bergen. The specimens were used for various taxonomic and systematic research, including DNA based phylogenetics and constructing barcode databases for the molecular identification of hydrozoans. A recent sampling in the deep waters of Korsfjord and Raunefjord

yielded three leptomedusa species whose 16S and 18S sequences matched those of polyp stages collected in the same region.

Here we present a synthesis of these results with a re-evaluation of the life cycle and taxonomy of the three Leptothecata species.

MATERIAL AND METHODS

Thecate hydroids were collected on various substrates by dredging. Leptomedusae were collected from various depths and locations using plankton nets of different sizes (details on the new material are given in Appendix 1). For depths below 70 m, a modified WP3 plankton net with a non-filtering cod-end and 750 µm mesh size was used. For species identification we used Kramp (1959), Cornelius (1995) and other works mentioned in the Taxonomy part.

DNA extracts and 16S sequences were obtained as

given in Schuchert (2005, 2016b). Most 18S sequences were determined as described in Leclère *et al.* (2009), except for three (marked with § in Appendix 1) which were retrieved by BlastN from transcriptome assemblies (L. Leclère, C. Dunn, and C. Munro, unpublished data). Alignments and phylogenetic analyses were performed as given in Schuchert (2005, 2016b). The aligned 16S sequences were trimmed to the position of the 3' ends of the primers SHA/SHB which were used for this study (Cunningham & Buss, 1993). The aligned 18S sequences were trimmed to the shortest available sequence. Differences between sequence pairs were quantified using p-distances (uncorrected base-pair differences in %, Collins *et al.*, 2012) using the software Bioedit (Hall, 1999).

In order to have a wider spectrum of species for comparisons, all suitable 16S sequences of leptomedusae (excluding Campanulariidae) found in the GenBank database were also included in the analyses (GenBank accession numbers can be taken from Figs 1-2). The Campanulariidae form a distinct, separate clade (Leclère *et al.*, 2009; Maronna *et al.*, 2016) and were excluded from our analysis as they do not contribute additional information. Additional sequencing of COI and 16S was carried out at the CCDB (<http://ccdb.ca/resources/>) for some medusa specimens, with the sequences deposited in the BOLD database (Appendix 2). As these 16S sequences represented the same haplotypes as given in Appendix 1, they were not included in the final analysis in order to avoid dense, unreadable phylogenetic trees.

Abbreviations

BOLD	The Barcode of Life Data System (see Ratnasingham & Hebert, 2007), http://boldsystems.org
CCDB	Canadian Centre for DNA Barcoding
GenBank	Genetic sequence database of the National Institute of Health, USA, http://www.ncbi.nlm.nih.gov/genbank
MHNG	Muséum d'histoire naturelle de Genève, Switzerland

RESULTS AND DISCUSSION

Maximum likelihood analyses

16S and 18S sequence data were used to obtain Maximum Likelihood trees (Figs 1-2) which graphically visualise inter- and intraspecific sequence divergences. Comparing the length of the branches separating the samples allows rapid identification of identical or highly similar sequences found for polyp and medusa stages (Figs 1-2, highlighted in red), as well as the visualisation of the intraspecific distances seen in a few other species (highlighted in blue).

The mitochondrial 16S gene sequence tends to be a reliable marker for Hydrozoa (Miglietta *et al.*, 2007,

2009, 2015; Schuchert, 2005, 2016b; Zhang *et al.*, 2015), but for species-level relationships it is advisable to include also a nuclear marker in order to exclude misleading effects of past introgressions or hybridisations on the mitochondrial markers (e. g. like in Miller *et al.*, 2012). We used the nuclear 18S gene sequence to complement the results obtained using the 16S data, as they were available from other studies for a good number of the species and samples used here. Although 18S is not an ideal barcoding marker due its relatively low interspecific variability, in the present data set the species were sufficiently well separated and the polyp-medusa matches were also seen in with the 18S sequences (Fig. 2, Table 2), thus adequately complementing the 16S results. Neither 16S nor 18S resolves satisfactorily the phylogenetic relationships at the family level. However, this was not the aim of this study and will be the subject of a forthcoming publication using more markers and taxa (L. Leclère, unpublished data).

16S and 18S intraspecific variation

The substitution rate of the mitochondrial 16S gene varies considerably within the Leptothecata subclades (Leclère *et al.*, 2009; compare also Cunha *et al.*, 2016 for COI). To quantify the extent of intraspecific variation within the leptomedusae, we calculated maximum p-distances for available pairs of conspecific specimens from different localities (Table 1). The observed values ranged from 0.34 to 1.18% and are lower than values observed for other hydrozoans [up to 4.4 % in Oceaniidae (Schuchert, 2016b); 5.5% in Corynidae (Schuchert, 2005); 19.6% in Plumularia setacea (Schuchert, 2014), but the Plumulariidae have a higher substitution rate (Leclère *et al.*, 2009) and *P. setacea* could be a species complex]. For the 18S sequence only four preliminary estimates for the intraspecific divergences could be obtained (Table 2). These values allow evaluating sequence divergences other than perfect matches between polyp and medusa samples (Table 3).

Ptychogena crocea and *Stegopoma plicatile*

16S sequences obtained from three *P. crocea* medusae (Fig. 3) and two samples of the hydroid *Stegopoma plicatile* (Fig. 4), all collected in the vicinity of Bergen (Appendix 1), were identical. Likewise, also 18S and COI sequences were identical (COI: GenBank JN109191, BOLD specimens HYPNO_314 & HYPNO_286). These results indicate that the hydroid identified as *Stegopoma plicatile* is the polyp stage of *P. crocea*. In the 16S tree, its congener *Ptychogena lactea* appeared as a sister-species, although well separated from *P. crocea*. Other members of the Laodiceida clade (Maronna *et al.*, 2016), such as *Modeeria rotunda*, clustered nearby.

Ptychogena crocea is a distinct and conspicuous medusa

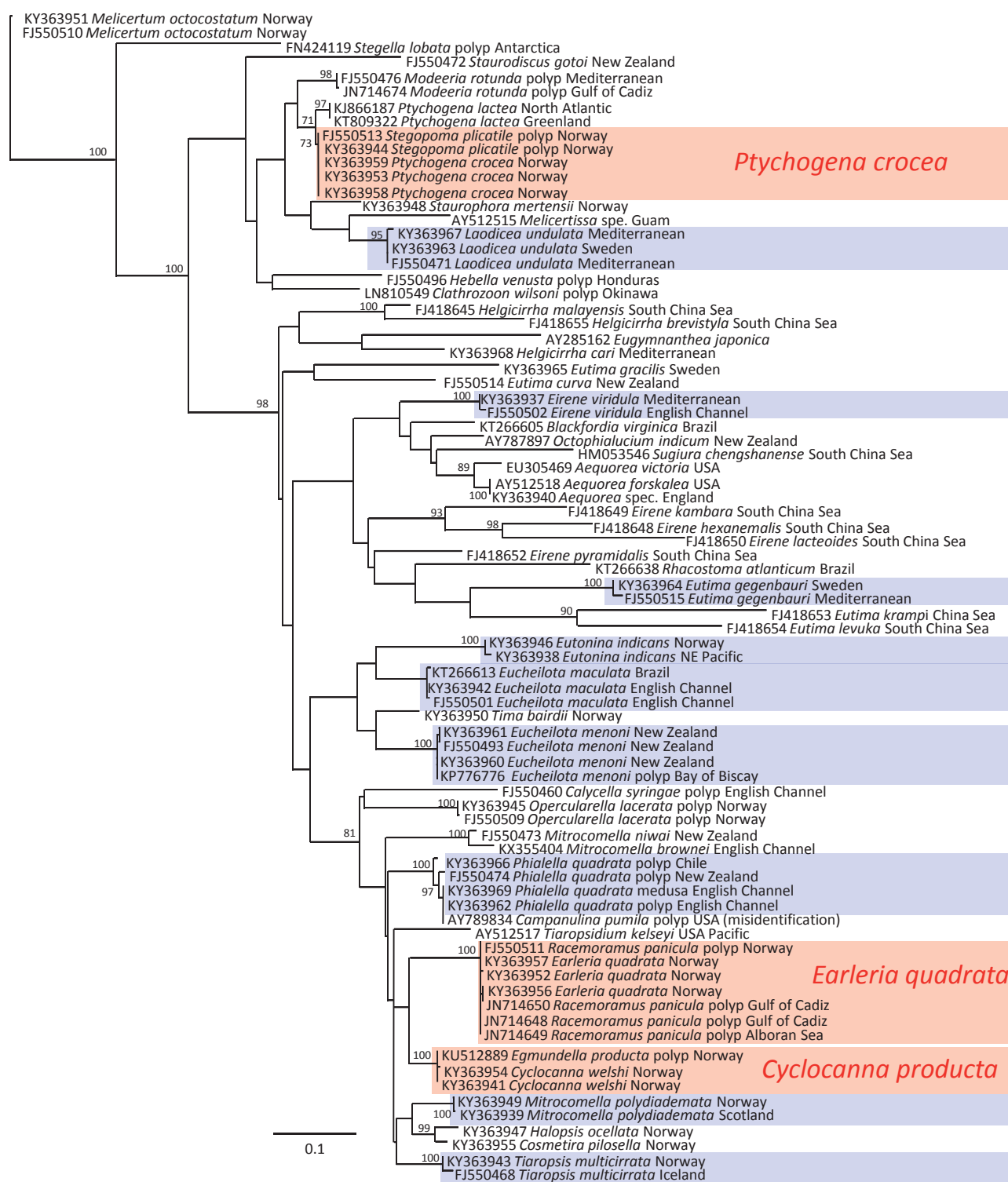


Fig. 1. 16S maximum likelihood phylogenetic tree of leptomedusan species obtained with PhyML (GTR+G+I model) and based on 605 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details see text and Appendix 1.

Samples based on the polyp stage are indicated, all others are medusa samples. Highlighted in red are matching medusa and polyp stage samples. Highlighted in blue are samples used to estimate intraspecific variability (Table 1).

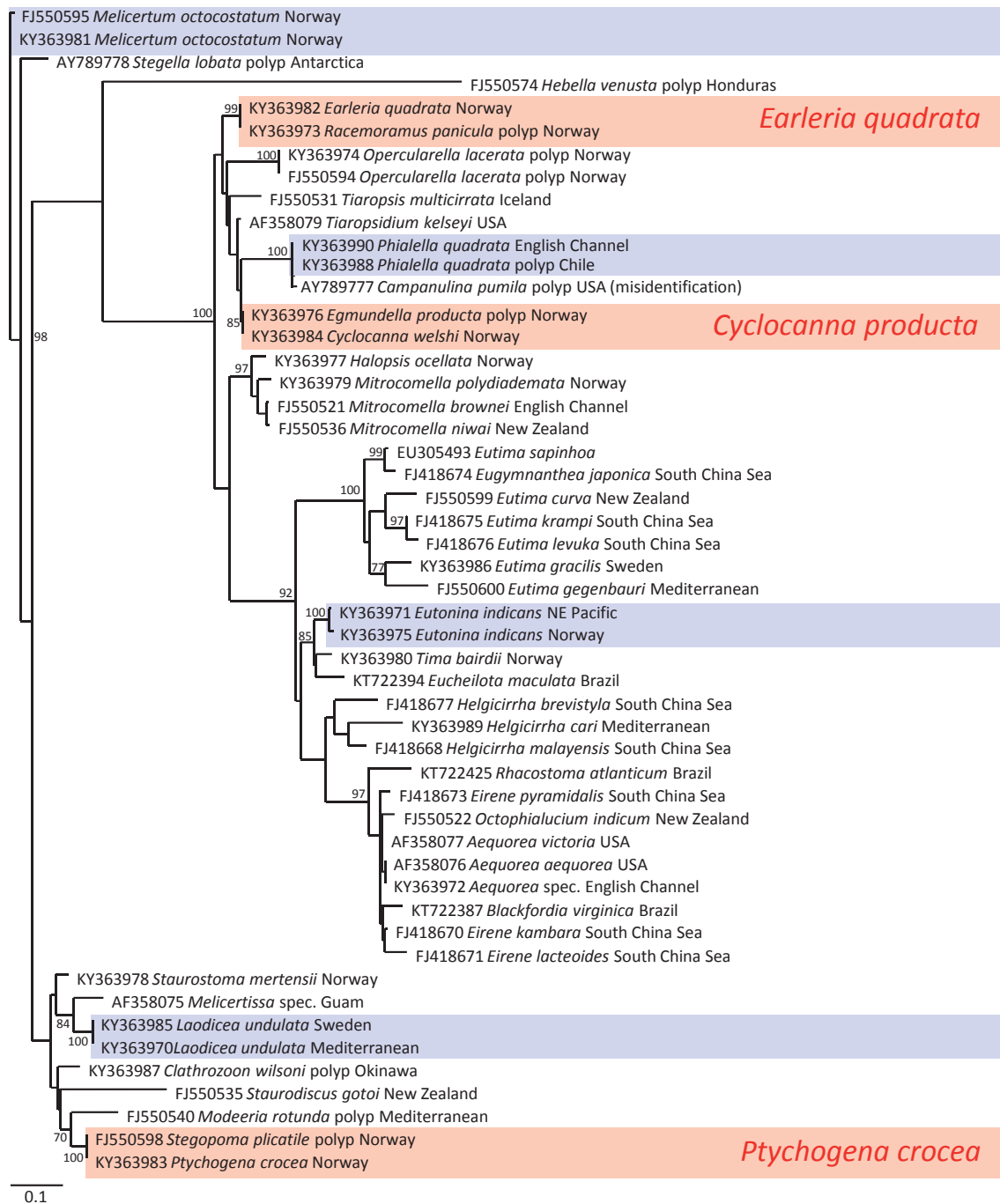


Fig. 2. 18S maximum likelihood phylogenetic tree of leptomedusan species obtained with PhyML (GTR+G+I model) and based on 1665 bp positions of the nuclear 18S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details see text and Appendix 1.

Samples based on the polyp stage are indicated, all others are medusa samples. Highlighted in red are matching medusa and polyp stage samples. Highlighted in blue are samples used to estimate intraspecific variability (Table 2).

Table 1. Maximal observed intraspecific p-distance values (%) of 16S sequences of Leptothecata with a medusa stage.

species and localities	distance
<i>Eirene viridula</i> Villefranche KY363937 - English Channel FJ550502	0.51
<i>Eucheilota maculata</i> Brazil KT266613 - English Channel FJ550501	0.51
<i>Eucheilota menoni</i> New Zealand FJ550493 - Bay of Biscay KP776776	0.34
<i>Eutima gegenbauri</i> Mediterranean FJ550515 - Sweden KY363952	0.84
<i>Laodicea undulata</i> Sweden KY363963 - Mediterranean FJ550471	0.50
<i>Mitrocomella polydiademata</i> Norway KY363949 - Scotland KY363939	0.17
<i>Phialella quadrata</i> New Zealand FJ550474 - Chile KY363966	1.18
<i>Tiaropsis multicirrata</i> Iceland FJ550468 - Norway KY363943	0.84

Table 2. Selected examples of maximal observed intraspecific p-distance values (%) of the 18S marker.

species and localities	distance
<i>Eutonina indicans</i> Norway KY363975 - NE Pacific KY363971	0.24
<i>Laodicea undulata</i> Sweden KY363985 - Mediterranean KY363970	0
<i>Melicertum octocostatum</i> Norway, intrapopulation, KY363981 - FJ550595	0.12
<i>Phialella quadrata</i> English Channel KY363990 - Chile KY363966	0

Table 3. Observed minimal and maximal p-distances in %, for details of the used species and samples see Appendix 1.

species or species pairs	16S	18S
within <i>Ptychogena crocea</i> (KY363953, KY363959, KY363958)	0	one sample
within <i>Stegopoma plicatile</i> (FJ550513, KY363944)	0	one sample
<i>Ptychogena crocea</i> - <i>Stegopoma plicatile</i>	0	0
within <i>Earleria quadrata</i> (KY363952, KY363957, KY363956)	0.17 - 0.34	one sample
within <i>Racemoramus panicula</i> (JN714650, FJ550511, JN714649, JN714648)	0 - 0.39	one sample
<i>Earleria quadrata</i> - <i>Racemoramus panicula</i>	0 - 0.17	0
within <i>Cyclocanna welshi</i> (KY363954, KY363941)	0.17	one sample
within <i>Egmundella producta</i> KU512889	one sample	one sample
<i>Cyclocanna welshi</i> - <i>Egmundella producta</i>	0 - 0.17	0

and easily identifiable. Its intensively orange-yellow manubrium and gonad pouches makes it very visible in plankton samples, even young stages (Fig. 3D). In addition to its yellow-orange colour, the characteristic lateral perradial stomach diverticula (gonad pouches, Fig. 3B) are very large and not attached to the subumbrella. Preserved material can nevertheless be confused with *Modeeria rotunda* (Quoy & Gaimard, 1827) and *Chromatonema rubrum* Fewkes, 1882, which also occur in deep waters of the North Atlantic (see Kramp, 1919, 1920, 1959; Russell, 1953; Edwards, 1973; Bleeker & van der Spoel, 1988; Cornelius, 1995; Schuchert, 2001; Pagès *et al.*, 2006).

Modeeria rotunda has a reddish-brown manubrium and characteristic interradian subumbrellar pockets giving the impression that the manubrium is partly sunken into the mesogloea.

Chromatonema rubrum has relatively small, white lateral gonad pouches and an orange to brown-reddish manubrium (Kramp, 1919, 1920). In addition, the cnidomes of the species differ: while *P. crocea* has 14-15 µm long microbasic mastigophores, *C. rubrum* and *Modeeria rotunda* have microbasic euryteles (19-20 µm and 25 µm; Russell, 1940).

The congener *Ptychogena lactea* A. Agassiz, 1865, which also occurs in the NE Atlantic, has gonads on thinner

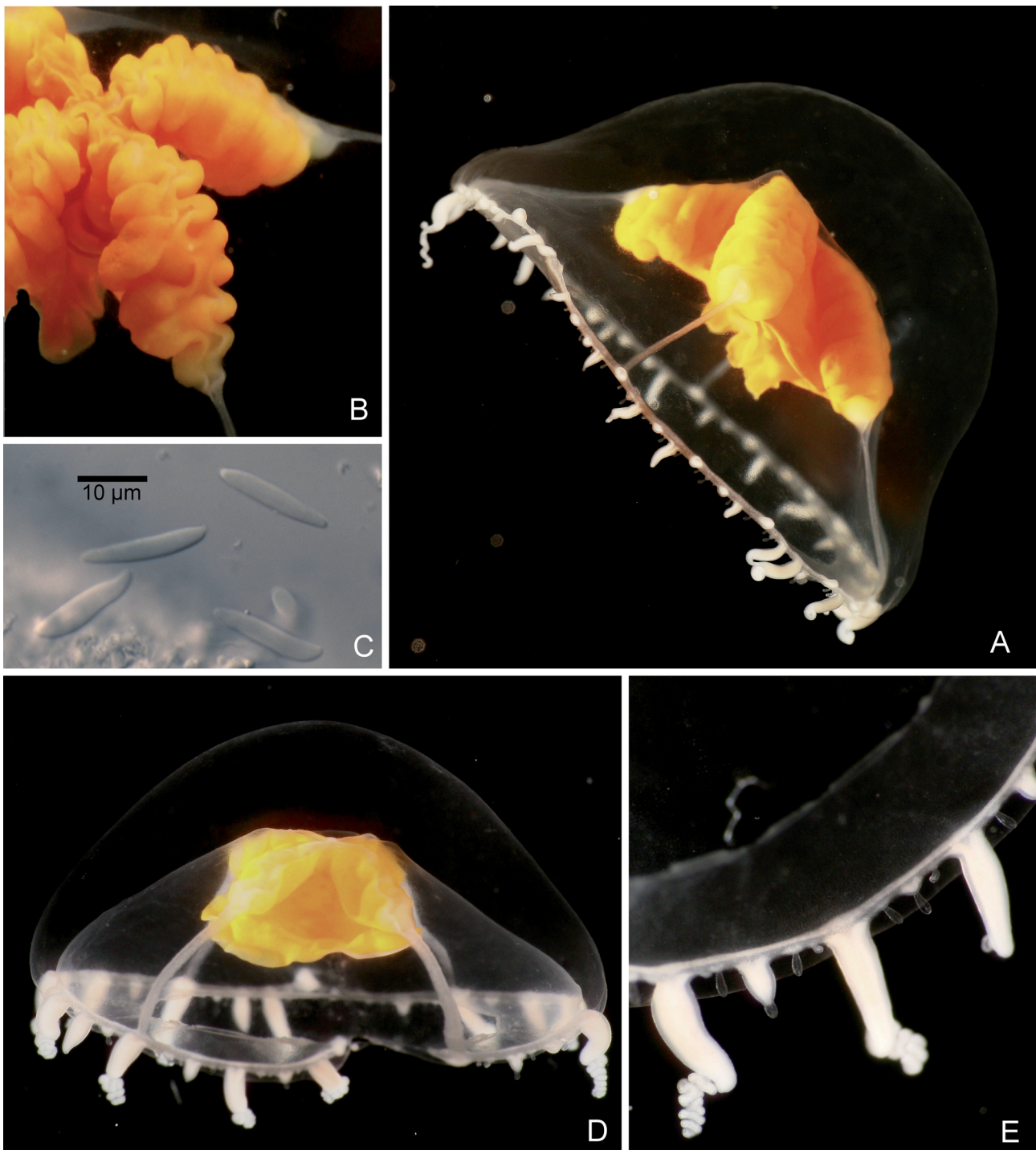
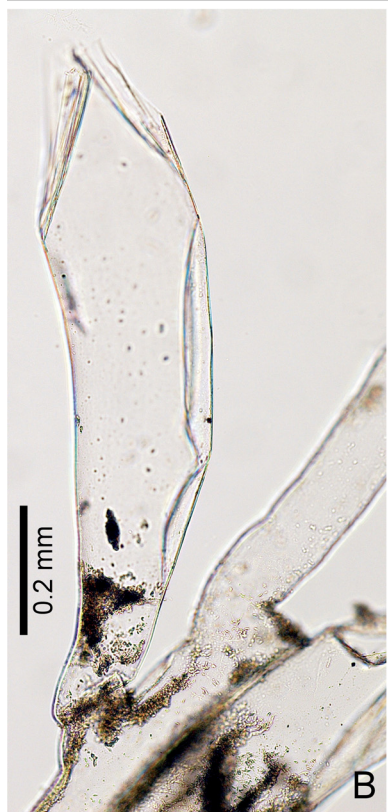


Fig. 3. *Ptychogena crocea* Kramp & Dumas, 1925, living medusae, except C, from Korsfjord, Norway. (A) MHNG-INVE-94101, lateral view, bell diameter 23 mm height 14 mm. (B) Same specimen as in A, close up of gonads. (C) Same specimen as in A, nematocysts. (D) Younger individual, used to obtain DNA isolate 1163. (E) Same as D, close up of bell margin seen from oral side, showing tentacles, tentacle stumps and several cordyli.

Fig. 4. *Stegopoma plicatile* (M. Sars, 1863), preserved sample MHNG-INVE-69614 (yielding DNA isolate 803) from Korsfjord, Norway, 650 m. (A) Whole colony. (B) Hydrotheca. (C) Branch with gonotheca (arrow). ►



and more numerous lateral diverticula that are attached to the subumbrella. Their colour differs also from *P. crocea*, being white, or with a peachy or greenish tint. More details and illustrations of these two *Ptychogena* species will be presented in a forthcoming publication (P. Schuchert, unpublished data).

Ptychogena crocea is a deep-water medusa with a rather restricted distribution and has so far been reported mostly along the Norwegian coast (Kramp & Dumas, 1925; Kramp, 1933, 1961; Rees, 1952; Hosia & Båmstedt, 2007), but there are also records of single specimens from the Cape Verde Islands and from the Gulf of Maine (Léon *et al.*, 2007). However, these two records need to be confirmed by new samples as at least the one from the Cape Verde had an atypical colour and could have been *Chromatonema rubrum*.

In contrast, the hydroid *Stegopoma plicatile* has a very wide, circumglobal distribution (Vervoort, 1972; Edwards, 1973; Cornelius, 1995; Calder, 2012). It is widespread in the Arctic and reaches as far south as Sweden and into deep waters off Brittany. It has also been reported in Boreal and Arctic regions of the Pacific and scattered points in the Southern Hemisphere and Antarctica. The type material came from Norway. Although the species has been described repeatedly, the reproduction of *S. plicatile* remained unknown for a long time until Schuchert (2001) reported for the first time that it releases a medusa. This was also observed for one of the current samples (MHNG-INVE-69614) which produced medusae of about 2 mm in diameter with four perradial tentacles, small interradian bulbs and 1-3 cordyli per quadrant. There were no ocelli or statocysts present. The stomach was distinctly cruciform in cross-section and lacked the yellow colour. Unfortunately, it was not possible to cultivate the medusae for more than two days.

We can conclude from our sequence analyses that the hydroid from the vicinity of Bergen identified as *Stegopoma plicatile* is the polyp stage of *Ptychogena crocea*. The taxonomic consequences, however, are more difficult to assess. The markedly different distribution patterns of the endemic, medusa-based species *Ptychogena crocea* and the widely distributed polyp-based *Stegopoma plicatile* strongly suggest that the latter is most probably a complex of cryptic species. The morphology of the *Stegopoma* hydroids is rather simple and poor in diagnostic features (see Cornelius 1995; Schuchert, 2001), and it is likely that other medusae related to *Ptychogena crocea* might have nearly identical hydroids. Several Leptothecata are known to have indistinguishable or very similar hydroid stages, but distinct medusae [e. g. “*Cuspidella*”-type hydroids producing medusae of the genera *Cosmetira* Forbes, 1848 or *Mitrocomella* Haeckel, 1879, “*Campanulina*”-type hydroids giving rise to medusae of the genera *Eucheilota* McCrady, 1859 and *Eutonina* Hartlaub, 1897 (Cornelius, 1995)].

The related medusa *Modeeria rotunda* has polyps with hydrothecae identical to those of *Stegopoma plicatile*, but with a colony that remains stolonal according to our current knowledge (Edwards, 1973; Cornelius, 1995; Schuchert, 2001). In the northern Atlantic Ocean, there are two further related medusa species with unknown polyp stages that potentially have a *Stegopoma*-like polyp stage: *Ptychogena lactea* and *Chromatonema rubrum*. Naumov (1969) attributed a “*Cuspidella*”-like hydroid (Bouillon *et al.*, 2006) to *Ptychogena lactea* because he found them to have a similar distribution in the Arctic Sea. This is, however, not a convincing argument and the polyp of *P. lactea* must be considered unknown. *Ptychogena lactea* is primarily an Arctic species and the distribution of *Stegopoma plicatile* (Schuchert, 2001) also matches its occurrence. The morphologically similar *Chromatonema rubrum* is a rare oceanic medusa, but has a much wider distribution (Kramp, 1919, 1959; Bleeker & van der Spoel, 1988). It occurs in deep waters (406-1750 m; Bleeker & van der Spoel, 1988). To our knowledge, the medusa has not been found in coastal waters of Norway, but only far off the continent (Kramp, 1919; Fraser, 1974; Bleeker & van der Spoel, 1988; Licandro *et al.*, 2015). Even if the discussed two medusae do not occur in coastal waters of Norway, they remain candidates for having a *Stegopoma*-like hydroid. So do the other *Ptychogena* medusae known from outside the region of the NE Atlantic: *P. antarctica* Browne, 1907, *P. californica* Torrey, 1909, and *P. hyperborea* Kramp, 1942.

When describing *Stegopoma plicatile*, Sars (1863) had material from four localities reaching from near Bergen, through Tromsø, to the northern tip of Norway in the Barents Sea. To our knowledge, no lectotype has been selected, and thus a more precise type locality cannot be given. *Stegopoma plicatile* was also designated by Totton (1930) as the type species of the genus.

While it is clear that *Ptychogena crocea* medusae are produced by hydroids referable to *Stegopoma plicatile*, it is still possible that even the type material of the latter was composed of several species. We therefore refrain from fully synonymising the two names and applying the senior name *Stegopoma plicatile* to the medusa *Ptychogena crocea* or suggesting a new combination of the two names. Synonymising the two names would lead to a confusing situation in which an endemic medusa has the name of a circumglobally distributed hydroid and which is likely a species complex. In the synonymy given below, *Stegopoma plicatile* is thus taxonomically only considered as a partial synonym. A similar situation was found for the medusa treated in the following.

Earleria quadrata* and *Racemoramus panicula

Earleria quadrata medusae (Fig. 5, GenBank number KY363957) and a *Racemoramus panicula* hydroid

(GenBank FJ550511) from the same region proved to have identical 16S (Fig. 1) and 18S sequences (Fig. 2; KY363982, KY363973¹). Several medusae of *Earleria quadrata* could be examined and they showed low 16S sequence variation of up to 2 bp differences per about 590 bp total length (Fig. 1, Table 3). This is compatible with intraspecific variation observed in other leptomedusan species (Table 1). Interestingly, three 16S sequences derived from *Racemoramus panicula* from the Gulf of Cadiz and the Alboran Sea (identified by C. Moura, JN714648 through JN714650) were very similar to the Norwegian samples, one of them (JN714648) even identical to both the medusa *Earleria quadrata* (KY363957) and the hydroid derived sequence (FJ550511).

Earleria quadrata is unmistakable among Norwegian leptomedusae due to its intensively deep-purple pigmented manubrium with white lips (Fig. 5). The numerous open statocysts (1-3 between each of the up to 40 tentacles) with 6 or more concretions in a single row are also rather characteristic. *Earleria quadrata* is endemic to the coastal waters of Norway and the genus currently comprises six species (Schuchert, 2017). The polyp stage was hitherto only known for the Californian *Earleria corachloae* Widmer, Cailliet & Geller, 2010.

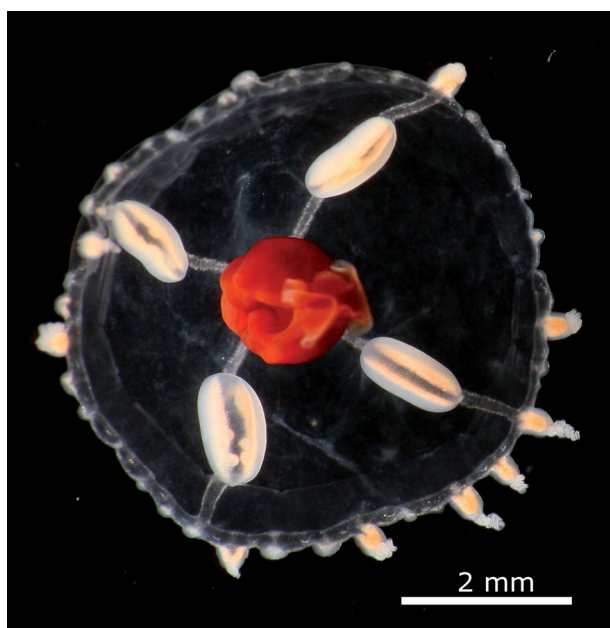


Fig. 5. *Earleria quadrata* (Hosia & Pages, 2007), living medusa from Korsfjord, one individual in a catch of four used to obtain DNA isolate 1162.

1 Resequencing the sample of *R. panicula* used to obtain the 18S sequence FJ550596 showed that it had two possible sequencing errors. Because the new sequence is also longer and the genus name has meanwhile changed, a new GenBank submission was made (KY363973).

While *Earleria quadrata* is only known very locally from deep waters of the Korsfjord south of Bergen (Hosia & Pages, 2007), the hydroid *Racemoramus panicula* has a very wide distribution. It occurs circumglobally in temperate to tropical regions, at depths of 20-5200 m (Schuchert, 2001; Calder, 2012). This extensive range made Calder (2012) doubt whether the observations represent a single species, prompting him to exclude records from the Pacific Ocean and attribute them to *R. denticulata* (Clarke, 1907), a species which so far had often been regarded as conspecific with *R. panicula*. The type locality of *R. panicula* is the Oslofjord (Norway) in a depth of 91-110 m (G. Sars, 1874).

Among the Campanulinidae, *Racemoramus* has a quite unique colony structure, consisting of an unbranched stem from which groups of “*Campanulina*”-like hydrothecae originate at intervals (Fig. 6 and Cornelius, 1995; Schuchert, 2001; Calder, 2012). Calder (2012) therefore proposed to keep it distinct from the genera *Campanulina* van Beneden, 1847 and *Opercularella* Hincks, 1868. No life cycle of any *Racemoramus* species is known so far, although Rees & Rowe (1969) found that *Racemoramus panicula* from Sweden releases a medusa. *Earleria corachloae*, the only hitherto known hydroid of the genus *Earleria*, has branched colonies

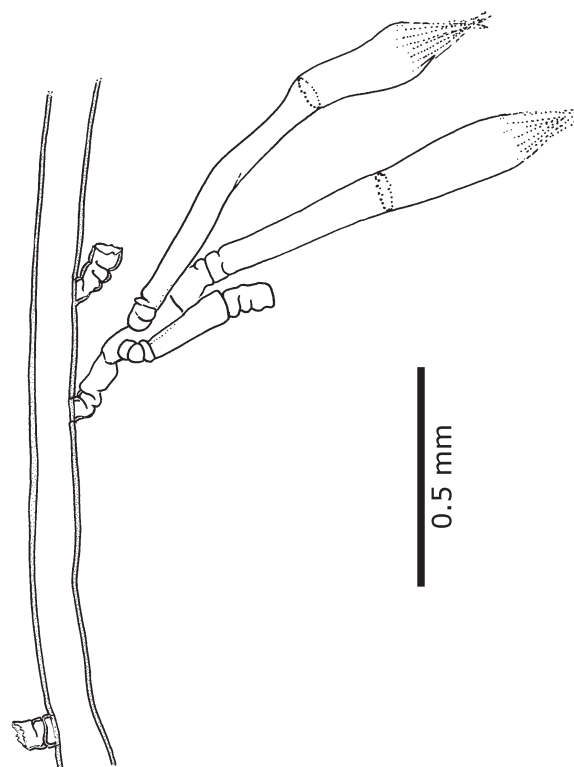


Fig. 6. *Racemoramus panicula* (G. O. Sars, 1874), sample MHNG-INVE-48748 from Korsfjord after DNA extraction, schematic drawing of part of main stem and some side-branches (some broken off).

that correspond with the traditional diagnosis of the genus *Campanulina* van Beneden, 1847 as proposed by Bouillon *et al.* (2006).

While it is very probable that Sars' material of *Racemoramus panicula* is the polyp stage of *Earleria quadrata* and the latter is thus a junior synonym, the hydroid *Racemoramus panicula* as used today – even in the restricted sense of Calder (2012) – is most likely a species complex. The disparate distributions of the medusa and the hydroid stage support this hypothesis. Therefore, we prefer to conclude more precisely that the medusa of *Earleria quadrata* has a polyp stage that corresponds to the morphology of *Racemoramus panicula*, but that both names are better not fully synonymised until a world-wide molecular genetic study of *Racemoramus* permits delimiting the different populations and their distributions. We should thus continue to use the name of the medusa for this species for the time being.

As mentioned above, polyps of *Racemoramus panicula* from the Gulf of Cadiz and the Mediterranean had 16S sequences which were identical or very similar to the Norwegian medusa *E. quadrata*. This extends the likely distributional range of this medusa close to that of the morphologically similar Mediterranean medusa *Earleria antoniae* (Gili *et al.*, 1998). It is therefore advisable to molecularly assess the species status of these two *Earleria* species to exclude the possibility of them representing morphologically divergent populations of the same species.

The taxonomic consequences at the family level are discussed in the next section.

Cyclocanna welshi and *Egmundella producta*

The two available samples of the medusa *Cyclocanna welshi* yielded 16S haplotypes differing only in one bp position. One of them was identical to the 16S obtained from the sample of *Egmundella producta* polyp described and figured by Schuchert (2016a). Likewise, the two 18S sequences were identical for polyp and medusa.

Cyclocanna welshi is a highly distinctive medusa. Its four radial canals and the gonads along them make a sharp bend shortly before reaching the circular canal and continue running along the circular canal before giving into it, resulting in a pattern reminiscent of a swastika (Fig. 7). Moreover, there are two types of tentacles: four large perradial tentacles with large bulbs situated at the marginal ends of the radial canals, and many short, papilliform tentacles between these. There are eight open statocysts, each with a linear array of concretions. The genus is monospecific. The collected samples were all reliably identifiable, but deteriorated rapidly so that no satisfactory photos could be made. The specimens appeared to be less pigmented than otherwise described (Bigelow, 1918; Kramp, 1926), but this is likely due to them being smaller (younger) stages.

Cyclocanna welshi is a rare medusa known from a few

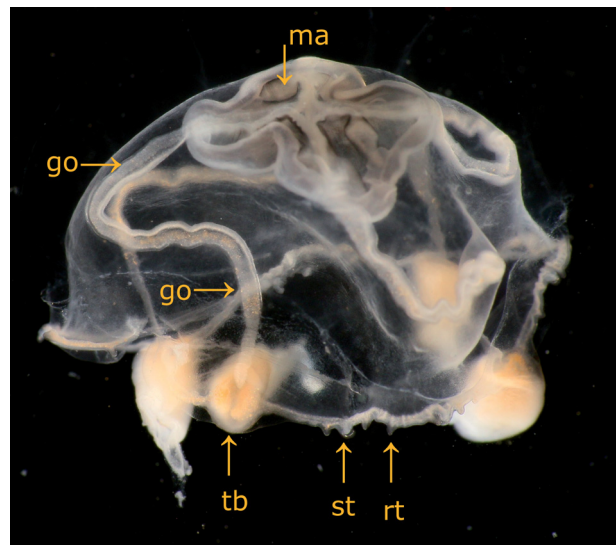


Fig 7. *Cyclocanna welshi*, lateral view, width about 10 mm, living medusa one day after capture, the bell is inverted and has shrunk considerably as it is usual for sensitive hydromedusae. Details: go = gonad, ma = manubrium, rt = short type of tentacle, st = statocyst, tb = bulb of large tentacle type.

specimens only (Kramp, 1926, 1961; Cornelius, 1995). It occurs in cool, deep waters of the North Atlantic. The type locality is off Virginia, USA, in 0-140 m depth.

The polyp *Egmundella producta*, formerly known as *Lovenella producta*, has been redescribed and revised recently (Schuchert, 2016a). It is also rather rare, but its known distribution in the Atlantic matches that of *C. welshi*. Records from the Pacific Ocean (Fraser, 1937) must either be referred to *Egmundella gracilis* Stechow, 1921 or another, as of yet unnamed species (Schuchert, 2016a).

The matching distributions of both medusa and hydroid permit synonymizing the names. The new name must thus be *Cyclocanna producta* (G.O. Sars, 1874) **n. comb.**, as Sars' species name is older. The genus *Egmundella* Stechow, 1921 cannot be synonymised with *Cyclocanna* Bigelow, 1918, as the type species of *Egmundella* is *Egmundella gracilis* Stechow, 1921 and its life cycle – as well as that of any other congener – remains unknown. All the other *Egmundella* species must thus remain in this genus until more is known about their medusae or gonophores.

Kramp (1933) placed *Cyclocanna welshi* in the family Mitrocomidae Haeckel, 1879 and subsequent authors continued to do so, primarily on account of the open statocysts and the absence of ocelli or cirri. According to the diagnosis given in Bouillon *et al.* (2006), the hydroids of this family are of the "*Cuspidella*"-type. With the identification of the hydroid of *Cyclocanna* as an "*Egmundella*"-type, the family diagnosis clearly needs a revision. The genus *Earleria* is also currently placed

in the Mitrocomidae (Arai & Brinckmann-Voss, 1980; Bouillon *et al.*, 2006; as *Foersteria* Arai & Brinckmann-Voss, 1980). The “*Campanulina*”-like hydrothecae of *Earleria corachloae* and the “*Racemoramus*”-like polyp in *Earleria quadrata* add a further argument for the need of a comprehensive revision of the Mitrocomidae and many other related families of Statocysta (Leclère *et al.*, 2009). Such a revision is, however, beyond the scope of the present paper and must be based on a solid, comprehensive molecular phylogeny.

TAXONOMY

Order Leptothecata

Family Laodiceidae Agassiz, 1862

Genus *Ptychogena* A. Agassiz, 1865

Ptychogena A. Agassiz, 1865: 137, type species *Ptychogena lactea* A. Agassiz, 1865 by monotypy.

in part *Stegopoma* Levinsen, 1893: 177, type species *Lafoea plicatilis* M. Sars, 1863 (Totton, 1930).

References: Edwards (1973), Bouillon *et al.* (2006).

Ptychogena crocea Kramp & Dumas, 1925

Figs 3-4

Ptychogona crocea Kramp & Dumas, 1925: 290, pl. 1 figs 1-7. – Kramp, 1933: 558, fig. 21. – Russell, 1940: 519, figs 18-19, nematocysts. – Rees, 1952: 8, record Bergen, Norway. – Kramp, 1959: 137, fig. 158. – Kramp, 1961: 146. – Hosia & Bámstedt, 2007: 116, records Norway, Kors- and Fanafjord.

? *Ptychogona crocea*. – Léon *et al.*, 2007: 57, record Cape Verde Islands.

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

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

Type locality: Norway, Romsdal, deep waters of Moldefjord.

References: For the medusa Kramp & Dumas (1925), for the hydroid Cornelius (1995) and Schuchert (2001).

Family Mitrocomidae Haeckel, 1879

Genus *Earleria* Collins *et al.*, 2006

Foersteria Arai & Brinckmann-Voss, 1980: 88, type species *Halistaura bruuni* Navas, 1969 by original designation, invalid junior homonym of *Foersteria* Szépligeti [Insecta] (Collins *et al.*, 2006).

Earleria Collins *et al.*, 2006: 125, replacement name.

References: Arai & Brinckmann-Voss (1980); Bouillon *et al.* (2006); Collins *et al.* (2006).

Earleria quadrata (Hosia & Pages, 2007)

Figs 5-6

Foersteria quadrata Hosia & Pages, 2007: 180, fig. 5.

in part *Campanulina panicula* G. O. Sars, 1874: 121, pl. 5 figs 9-13.

? *Campanulina panicula*. – Kramp, 1941: 1, figs 1-5. – Cornelius, 1995: 190, fig. 43. – Schuchert, 2001: 56, fig. 41, Iceland.

? not *Opercularella panicula*. – Vervoort, 1966: 104, figs 4-5. – Vervoort, 1972: 40, fig. 11a, Nicaragua (Pacific), Peru. – Leloup, 1974: 4, fig. 3.

? *Racemoramus panicula*. – Calder, 2012: 26, fig. 24.

not *Campanulina panicula*. – Schuchert, 2003: 150, fig. 10, Indonesia.

Type locality: Korsfjorden, 25 km south of Bergen, Norway, > 500 m deep.

References: For the medusa see Hosia & Pages (2007), for the hydroid see Cornelius (1995), Schuchert (2001), or Calder (2012).

Genus *Cyclocanna* Bigelow, 1918

Cyclocanna Bigelow, 1918: 383, type species *Cyclocanna welshi* Bigelow, 1918 by monotypy.

Cyclocanna producta (G.O. Sars, 1874) n. comb.

Fig. 7

Cyclocanna welshi Bigelow, 1918: 384, pl. 3 figs 2-5. – Kramp, 1926: 245, fig. 1. – Kramp, 1933: 571, fig. 35. – Kramp, 1959: 144, fig. 177. – Kramp, 1961: 152. – Cornelius, 1995: 134, fig. 29.

Calycella producta G.O. Sars, 1874: 118, pl. 5 figs 6-8. – Hincks, 1874: 134. – Verrill, 1879: 17. – Storm, 1879: 26. – Broch, 1907: 7.

Lovenella producta. – Segerstedt, 1889: 12. – Jäderholm, 1909: 79. – Kramp, 1935: 140, fig. 57E. – Fraser, 1944: 175, pl. 31 fig. 149. – Schuchert, 2000: 423. – Schuchert, 2001: 54, fig. 39.

Campanulina producta. – Bonnevie, 1899: 73. – Bonnevie, 1901: 10. – Broch, 1903: table. – Stechow, 1922: 146.

not *Lovenella producta*. – Fraser, 1911: 44, pl. 3 figs 7-10. – Fraser, 1914: 159, pl. 18 fig. 64. [in part *Egmundella gracilis* Stechow, 1921]

not *Lovenella producta*. – Fraser, 1937: 96, pl. 19 fig. 102.

? *Opercularella producta*. – Vervoort, 1966: 111, fig. 12a. – Vervoort, 1985: 279.

Egmundella producta. – Schuchert, 2016a: 219, figs 1A-D, 2A-C, 3A-F.

Type localities: The syntypes of *Egmundella producta* came from Bodø and the Lofoten (Norway). The type locality of *Cyclocanna welshi* is in the North-West Atlantic, off Virginia, USA, 37.4705°N 74.4214°W, 0-140 m.

References: For the medusa see Cornelius (1995), for the hydroid see Schuchert (2016).

ACKNOWLEDGMENTS

The authors thank the sailors of the Observatoire Océanologique de Villefranche-sur-mer, the Station Biologique de Roscoff, the crew of RV Hans Brattström for their help in collecting polyps and medusae, and the staff at the Espeyrend Marine Biological Station for providing facilities. We are grateful to Casey Dunn and Catriona Munro for providing the RNAseq data, which were used to retrieve some of the 18S sequences. Mrs J. Pralong kindly helped us with the sequencing of the samples. LL was supported by a grant from the Agence Nationale de la Recherche (MEDUSEVO ANR-13-PDOC-0016); AH by the Norwegian Taxonomy Initiative (NTI, project no. 70184233/HYPNO) and ForBio Research School funding from the Research Council of Norway (project no. 248799) and the NTI (project no. 70184215).

REFERENCES

- Agassiz A. 1865. North American Acalephae. *Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College* 2: 1-234. <http://dx.doi.org/10.5962/bhl.title.1837>
- Agassiz L. 1862. Contributions to the natural history of the United States of America. Vol. IV. *Little Brown, Boston*, pp. 1-380, pls 1-19. <http://dx.doi.org/10.5962/bhl.title.12644>
- Arai M.N., Brinckmann-Voss A. 1980. Hydromedusae of British Columbia and Puget Sound. *Canadian Bulletin of Fisheries and Aquatic Sciences* 204: 1-192.
- Bigelow H.B. 1918. Some Medusae and Siphonophora from the western Atlantic. *Bulletin of the Museum of comparative Zoology of Harvard College* 62: 363-442.
- Bleeker J., Van der Spoel S. 1988. Medusae of the Amsterdam Mid North Atlantic Plankton Expeditions (1980-1983) with description of two new species. *Bijdragen tot de Dierkunde* 58(2): 227-258.
- Bonnevie K. 1899. Hydroida. *Norske Nordhavs-Expedition 1876-1878, Zoologi* 26: 1-104, pls 1-8, map.
- Bonnevie K. 1901. Hydroiden. *Die Meeresfauna von Bergen* 1: 1-15.
- Bouillon J., Gravili C., Pages F., Gili J.M., Boero F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle* 194: 1-591.
- Broch H. 1903. Die vom norwegischen Fischereidampfer „Michael Sars“ in den Jahren 1900-1902 in dem Nordmeer gesammelten Hydroiden. *Bergens Museum Aarbog* (1903) 9(3): 1-14, pls 1-4, table.
- Broch H. 1907. Hydroiden und Medusen. *Report of the Second Norwegian Arctic expedition in the "Fram" 1898-1902*, vol. 2(12), pp. 1-12. *Brøgger, Kristiania*. <http://dx.doi.org/10.5962/bhl.title.55607>
- Broch H. 1918. Hydroida. (Part II). *The Danish Ingolf Expedition* 5(7): 1-206.
- Browne E.T. 1907. A revision of the medusae belonging to the Family Laodiceidae. *Annals and Magazine of Natural History* (7)20: 457-480.
- Calder D. 2012. On a collection of hydroids (Cnidaria, Hydrozoa, Hydroidolina) from the west coast of Sweden, with a checklist of species from the region. *Zootaxa* 3171: 1-77.
- Clarke S.F. 1907. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer 'Albatross', from October 1904 to March 1905, Lieut.-Commander L. M. Garrett, U. S. N., commanding. VIII The hydroids. *Memoirs of the Museum of comparative Zoology at Harvard college* 35: 1-18.
- Collins J.S.H., Ross A.J., Genzano G., Mianzan H. 2006. *Earleria* gen. nov. & *Gabriella* gen. nov., replacement names for *Foersteria* Arai & Brinckmann-Voss, 1980 (Cnidaria, Hydrozoa, Mitrocomidae) and *Foersteria* Wehner, 1988 (Crustacea, Decapoda, Prosopidae), junior homonyms of *Foersteria* Szepliget, 1896 (Insecta, Hymenoptera, Bracnidae). *Bulletin of the Mizunami Fossil Museum* 33: 125-126.
- Collins R.A., Boykin L.M., Cruickshank R.H., Armstrong K.F. 2012. Barcoding's next top model: an evaluation of nucleotide substitution models for specimen identification. *Methods in Ecology and Evolution* 3(3): 457-465. <http://dx.doi.org/10.1111/j.2041-210X.2011.00176.x>
- Cornelius P.F.S. 1995. North-west European thecate hydroids and their medusae. Part 1. Introduction, Laodiceidae to Haleciidae. *Synopses of the British Fauna New Series* 50(1): 1-347.
- Cunha A.F., Maronna M.M., Marques A.C. 2016. Variability on microevolutionary and macroevolutionary scales: a review on patterns of morphological variation in Cnidaria Medusozoa. *Organisms Diversity & Evolution* 16(3): 431-442. <https://dx.doi.org/10.1007/s13127-016-0276-4>
- Cunningham C.W., Buss L.W. 1993. Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae. *Biochemical Systematics and Ecology* 21(1): 57-69.
- Edwards C. 1973. The medusa *Modeeria rotunda* and its hydroid *Stegopoma fastigiatum*, with a review of *Stegopoma* and *Stegolaria*. *Journal of the Marine Biological Association of the United Kingdom* 53(3): 573-600.
- Fewkes J.W. 1882. On the Acalephae of the East coast of New-England. *Bulletin of the Museum of comparative Zoology of Harvard College* 9(8): 291-310, pl. 1.
- Forbes E. 1848. A monograph of the British naked-eyed medusae: with figures of all the species. *Ray Society, London*, 104 pp., 13 plates. <http://dx.doi.org/10.5962/bhl.title.10032>
- Fraser C.M. 1911. The hydroids of the west coast of North America. With special reference to those of the Vancouver Island region. *Bulletin from the Laboratories of Natural History of the State University of Iowa* 6(3): 3-91, pls 1-8.
- Fraser C.M. 1914. Some hydroids of the Vancouver Island region. *Transactions of the Royal Society of Canada, 3rd series, section 4* 8: 99-216.
- Fraser C.M. 1937. Hydroids of the Pacific coast of Canada and the United States. *The University of Toronto Press, Toronto*, 208 pp., pls 1-44.
- Fraser C.M. 1944. Hydroids of the Atlantic coast of North America. *The University of Toronto Press, Toronto*, pp. 1-451, pls 1-94.
- Fraser J.H. 1974. The distribution of medusae in the Scottish area. *Proceedings of the Royal Society of Edinburgh* 74: 1-25.
- Gili J.M., Bouillon J., Pages F., Palanques A., Puig P., Heussner S. 1998. Origin and biogeography of the deep-water Mediterranean hydromedusae including the description of two new species collected in submarine canyons of northwestern Mediterranean. *Scientia Marina* 62(1-2): 113-134.

- Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- Hartlaub C. 1897. Die Hydromedusen Helgolands. *Wissenschaftliche Meeresuntersuchungen* 2: 449-536, pls 14-23.
- Haeckel E. 1879. Das System der Medusen. Erster Teil einer Monographie der Medusen. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 1: XX+1-360, 20 plates.
<http://dx.doi.org/10.5962/bhl.title.46856>
- Hincks T. 1868. A history of the British hydroid zoophytes. *John van Voorst, London*, pp. Volume 1: i-lxvii + 1-338, volume 2, pls 1-67.
<http://dx.doi.org/10.5962/bhl.title.99946>
- Hincks T. 1874. Notes on Norwegian Hydroida from deep water. *Annals and Magazine of Natural History* (4)13: 125-137.
- Hosia A., Båmstedt U. 2007. Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. *Marine Ecology Progress Series* 351: 113-127.
- Hosia A., Pages F. 2007. Unexpected new species of deep-water Hydroidomedusae from Korsfjorden, Norway. *Marine Biology Berlin* 151(1): 177-184.
- Jäderholm E. 1909. Northern and arctic invertebrates in the collection of the Swedish state museum (Riksmuseum). IV Hydroiden. *Bihang till Kungliga Svenska Vetenskaps-akademien Handlingar* 45: 1-124, 12 pls.
- Kölliker A. In: Gegenbaur C., Kölliker A., Müller H. 1853. Bericht über einige im Herbste 1852 angestellte vergleichend-anatomische Untersuchungen. *Zeitschrift für wissenschaftliche Zoologie* 4: 299-370.
- Kramp P.L. 1913. Hydroids collected by the "Tjalfe" expedition to the west coast of Greenland in 1908 and 1909. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 66: 1-36.
- Kramp P.L. 1919. Medusae. Pt. 1. Leptomedusae. *Danish Ingolf Expedition* 5(8): 1-111, pls 1-5.
- Kramp P.L. 1920. Anthomedusae and Leptomedusae. *Report of the Scientific results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910* 3(2): 1-14, pl. 1.
- Kramp P.L. 1926. Occasional notes on Coelenterata. 1. *Videnskabelige meddelelser fra Dansk naturhistorisk Forening* 82: 241-247.
- Kramp P.L. 1933. XII Craspedote Medusen III. In: Brandt K. & Apstein C. (Eds), Nordisches Plankton, *Lipsius & Tischer, Kiel*, Lieferung 22: 541-602.
- Kramp P.L. 1935. Polypdyr (Coelenterata) I. Ferskvandspolypyper og Goplepolypper. *Danmarks Fauna* 41: 1-207.
- Kramp P.L. 1941. Notes on the hydroid *Campanulina paniculata* G.O. Sars. *Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Ser. B* 1(2): 1-11.
- Kramp P.L. 1942. The Godthaab Expedition 1928. Medusae. *Meddelelser om Grønland* 81(1): 1-168.
- Kramp P.L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report* 46: 1-283.
- Kramp P.L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom* 40: 1-469.
- Kramp P.L., Damas D. 1925. Les méduses de la Norvège. Introduction et partie spéciale. *Videnskabelige meddelelser fra Dansk naturhistorisk Forening* 80: 217-323.
- Leclère L., Schuchert P., Cruaud C., Couloux A., Manuel M. 2009. Molecular phylogenetics of Thecata (Hydrozoa, Cnidaria) reveals long-term maintenance of life history traits despite high frequency of recent character changes. *Systematic Biology* 58(5): 509-526.
- Leloup E. 1974. Hydropolypes calyptoblastiques du Chili. Report no. 48 of the Lund University Chile Expedition 1948-1949. *Sarsia* 55: 1-62.
<https://dx.doi.org/10.1080/00364827.1974.10411252>
- Licandro P., Blackett M., Fischer A., Hosia A., Kennedy J., Kirby R.R., Raab K., Stern R., Tranter P. 2015. Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. *Earth System Science Data* 7(2): 173-191. <https://dx.doi.org/10.5194/essd-7-173-2015>
- Léon M.E., Hernandez F., De Vera A. 2007. Nota sobre *Ptychogena crocea* Kramp & Damas, 1925 en aguas de Cabo Verde (Laodiceidae: Leptomedusae: Cnidaria). *Vieraea* 35: 57-60.
- Levinsen G.M.R. 1893. Meduser, Ctenophorer og Hydroider fra Grønlands Vestkyst, tilligemed Bemaerkninger om Hydroidernes Systematik. *Videnskabelige meddelelser fra den Naturhistoriske forening i Kjøbenhavn* 4: 143-212, 215-220, appendix, pls 5-8.
- Maronna M.M., Miranda T.P., Peña Cantero A.L., Barbeitos M.S., Marques A.C. 2016. Towards a phylogenetic classification of Leptothecata (Cnidaria, Hydrozoa). *Scientific Reports* 6: 18075. <https://dx.doi.org/10.1038/srep18075>
- McCrary J. 1859. Gymnophthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103-221, pls 8-12.
- Miglietta M.P., Odegard D., Faure B., Faucci A. 2015. Barcoding Techniques Help Tracking the Evolutionary History of the Introduced Species *Pennaria disticha* (Hydrozoa, Cnidaria). *Plos One* 10(12): e0144762.
<http://dx.doi.org/10.1371/journal.pone.0144762>
- Miglietta M.P., Piraino S., Kubota S., Schuchert P. 2007. Species in the genus *Turritopsis* (Cnidaria, Hydrozoa): a molecular evaluation. *Journal of Zoological Systematics and Evolutionary Research* 45(1): 1-88.
<https://dx.doi.org/10.1111/j.1439-0469.2006.00379.x>
- Miglietta M.P., Schuchert P., Cunningham C.W. 2009. Reconciling genealogical and morphological species in a worldwide study of the family Hydractiniidae (Cnidaria, Hydrozoa). *Zoologica Scripta* 38(4): 403-430.
- Naumov D.V. 1969. Hydroids and Hydromedusae of the USSR. *Israel Program for scientific translation, Jerusalem*, pp. 463, 30 pls.
- Miller W., Schuster S.C., Welch A.J., et al. 2012. Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. *Proceedings of the National Academy of Sciences of the United States of America* 109(36): E2382-E2390.
<https://dx.doi.org/10.1073/pnas.1210506109>
- Navas D. 1969. *Halistaura bruuni* sp. nov. (Leptomedusae, Mitrocomidae) with notes on its distribution and ecology. *Marine Biology, Berlin* 2: 307-310.
- Pagès F., Flood P., Youngbluth M. 2006. Gelatinous zooplankton net-collected in the Gulf of Maine and adjacent submarine canyons: new species, new family (Jeanbouillonidae), taxonomic remarks and some parasites. *Scientia Marina* 70(3): 363-379.
- Pyataeva S.V., Hopcroft R.R., Lindsay D.J., Collins A.G. 2016. DNA barcodes unite two problematic taxa: the meiobenthic *Boreohydra simplex* is a life-cycle stage of *Plotocnide*

- borealis* (Hydrozoa: Aplanulata). *Zootaxa* 4150(1): 85-92. <https://dx.doi.org/10.11646/zootaxa.4150.1.5>
- Quoy J.R.C., Gaimard J.P. 1827. Observations zoologiques faites à bord de l'Astrolabe, en mai 1826, dans le Détroit de Gibraltar. *Annales des Sciences naturelles* 10: 5-21, 172-193, 225-239.
- Ratnasingham S., Hebert P.D.N. 2007. BOLD: The Barcode of Life Data System. (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7: 355-364. <https://dx.doi.org/10.1111/j.1471-8286.2007.01678.x>
- Rees W.J. 1952. Records of hydroids and medusae taken at Herdla, Bergen in 1937. *Naturvidenskabelige Raekke, Årbok Universitet i Bergen* 16: 1-8, tab. 1.
- Rees W.J., Rowe M. 1969. Hydroids of the Swedish west coast. *Acta regiae Societatis scientiarum et litterarum Gothoburgensis. Zoologica* 3: 1-23.
- Russell F.S. 1940. On the nematocysts of Hydromedusae III. *Journal of the Marine Biological Association of the United Kingdom* 24: 515-523.
- Russell F.S. 1953. The medusae of the British Isles. *Cambridge University Press, London*, 530 pp., 35 pls.
- Sars M. 1863. Bemaerkninger over fire norske Hydroider. *Forhandlinger i Videnskabs-selskabet i Christiania* 1862: 25-39.
- Sars G.O. 1874. Bidrag til Kundskaben om Norges Hydroider. *Forhandlinger i Videnskabs-Selskabet i Kristiana* 1873: 91-150, pls 2-5.
- Schuchert P. 2000. Hydrozoa (Cnidaria) of Iceland collected by the BIOICE programme. *Sarsia* 85(5-6): 411-438.
- Schuchert P. 2001. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). *Meddelelser om Grønland, Bioscience* 53: 1-184.
- Schuchert P. 2003. Hydroids (Cnidaria, Hydrozoa) of the Danish expedition to the Kei Islands. *Steenstrupia* 27(2): 137-256.
- Schuchert P. 2005. Species boundaries in the hydrozoan genus *Coryne*. *Molecular Phylogenetics and Evolution* 36: 194-199.
- Schuchert P. 2014. High genetic diversity in the hydroid *Plumularia setacea*: A multitude of cryptic species or extensive population subdivision? *Molecular Phylogenetics and Evolution* 76(0): 1-9. <https://dx.doi.org/10.1016/j.ympev.2014.02.020>
- Schuchert P. 2016a. On the gonotheca of *Egmundella producta* (G.O. Sars, 1874) n. comb. (Cnidaria, Hydrozoa). *Revue suisse de Zoologie* 123(2): 219-225. <http://doi.org/10.5281/zenodo.155157>
- Schuchert P. 2016b. The polyps of *Oceania armata* identified by DNA barcoding (Cnidaria, Hydrozoa). *Zootaxa* 4175(6): 539-555. <http://doi.org/10.11646/zootaxa.4175.6.3>
- Schuchert P. 2017. *Earleria* Collins, Ross, Genzano & Manzian, 2006. In: Schuchert P., World Hydrozoa database. Accessed at <http://www.marinespecies.org/hydrozoa/aphia.php?p=taxdetails&id=395323> on 30.01.2017
- Segerstedt M. 1889. Bidrag till Kännedomen om Hydroid-Faunan vid Sveriges Vestkust. *Bihang till Kungliga Svenska Vetenskaps-akademiens Handlingar* 14(4): 1-28, plate.
- Stechow E. 1921. Über Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. *Zoologischer Anzeiger* 53(9-10): 223-236.
- Stechow E. 1922. Zur Systematik der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren. *Archiv für Naturgeschichte* 88(3): 141-155.
- Storm V. 1879. Bidrag til Kundskab om Thronhjemsfjordens Fauna. *Det Kongelige Norske videnskabers selskabs skrifter* 1878: 9-36.
- Torrey H.B. 1909. The Leptomedusae of the San Diego region. *University of California publications in zoology* 6(2): 11-31.
- Totton A.K. 1930. Coelenterata. Part V. - Hydroida. *British Antarctic ("Terra Nova") Expedition, 1910, Natural History Report, Zoology* 5(5): 131-252, pls 1-3.
- Van Beneden P.J. 1847. Un mot sur le mode de reproduction des animaux inférieurs. *Bulletins de l'Académie royale des sciences, des lettres et des beaux-arts de Belgique* 14(1): 448-462, 1 pl.
- Verrill A.E. 1879. Preliminary check-list of the marine invertebrata of the Atlantic coast, from Cape Cod to the Gulf of St. Lawrence. *Tuttle, Morehouse & Taylor, New Haven*, 32 pp.
- Vervoort W. 1966. Bathyal and abyssal hydroids. *Galathea Report* 8: 97-173.
- Vervoort W. 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty geological observatory. *Zoologische Verhandelingen* 120: 1-247.
- Vervoort [Vervoort] W. 1985. Deep-water hydroids. [pp. 267-297]. In: Laubier L. & Monniot C. (Eds.), *Peuplements profonds du golfe de Gascogne: Campagnes BIOGAS. Ifremer, Brest*, pp. 1-629.
- Wagner N. 1885. Die Wirbellosen des Weissen Meeres. Erster Band. Zoologische Forschungen an der Küste des Solowetzischen Meerbusens in den Sommermonaten der Jahre 1877, 1878, 1879 und 1882. *W. Engelmann, Leipzig*, 171 pp., 21 plates.
- Westblad E. 1937. *Boreohydra simplex* n. gen., n. sp., ein Solitärpolyp von der norwegischen Küste. *Arkiv för Zoologi* 29(7): 1-6.
- Widmer C.L., Cailliet G., Geller J. 2010. The life cycle of *Earleria corachloae* n. sp. (Cnidaria: Hydrozoa) with epibiotic hydroids on mid-water shrimp. *Marine Biology* 157(1): 49-58. <https://dx.doi.org/10.1007/s00227-009-1294-y>
- Zhang D., Zheng L., He J., Zhang W., Lin Y., Li Y. 2015. DNA barcoding of hydromedusae in northern Beibu Gulf for species identification. *Biodiversity Science* 23(1): 50-60.

Appendix 1: Specimens and Genbank accession numbers of new sequences (numbers starting with KY) used in this study. Details of the other sequences taken from GenBank and used in Figures 1 and 2 can be found by a GenBank search using the respective accession number. The 18S sequences marked with ^s were obtained from transcriptome assemblies.

DNA isolate	species	Family	Latitude/Longitude	country	locality	depth [m]	date collected	life stage	MHNG INVE voucher	16S accession no.	18S accession no.
1013	<i>Aequorea</i> spec.	Aequoreidae	50.4629 N 3.4814 W	England	Torquay	0	16.06.2007	medusa	-	KY363940	KY363972
774	<i>Clathrozoa wilsoni</i>	Clathrozoidae	26.2838 N 126.866 E	Japan	Okinawa archipelago	126-136	12.11.2009	polyp	69664	LN810549	KY363987
1165	<i>Cosmetira pilosella</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363955	-
1164	<i>Cyclocanna welsli</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363954	KY363984
1200	<i>Cyclocanna welsli</i>	Mitrocomidae	60.2573 N 5.1393 E	Norway	Raunefjord	0-232	01.07.2016	medusa	-	KY363941	-
1162	<i>Earleria quadrata</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363952	KY363982
1193	<i>Earleria quadrata</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363956	-
1194	<i>Earleria quadrata</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363957	-
1097	<i>Egmondella producta</i>	Lovenellidae	60.4083 N 5.1167 E	Norway	Litlesotra Island	100	22.04.2015	polyp	91796	KU512889	KY363976
010	<i>Eirene viridula</i>	Eirenidae	43.686 N 7.317 E	France	Villefranche-sur-Mer	0-75	04.05.2001	medusa	-	KY363937	-
1136	<i>Eucheilota maculata</i>	Eucheilotidae	49.321 N 0.3444 W	France	Luc-sur-mer	0	16.08.2001	medusa	-	KY363942	-
072	<i>Eucheilota menoni</i>	Lovenellidae	36.812 S 174.802 E	New Zealand	Hauraki Gulf	0-1	03.07.2002	medusa	33457	KY363960	-
1131	<i>Eucheilota menoni</i>	Lovenellidae	36.812 S 174.802 E	New Zealand	Hauraki Gulf	0-1	26.07.2002	medusa	-	KY363961	-
1062	<i>Eutima gogenbauri</i>	Eirenidae	58.2438 N 11.4323 E	Sweden	Kristineberg	0	03.10.2014	medusa	89881	KY363964	-
1063	<i>Eutima gracilis</i>	Eirenidae	58.2438 N 11.4323 E	Sweden	Kristineberg	0	03.10.2014	medusa	-	KY363965	KY363986
No15.12	<i>Eutonina indicans</i>	Eirenidae	60.2473 N 5.2268 E	Norway	Fana fjord	0-20	21.04.2015	medusa	-	-	KY363975 ^s
921	<i>Eutonina indicans</i>	Eirenidae	48.545 N 123.012 W	USA	San Juan Islands	0.5	20.05.2011	medusa	-	KY363938	KY363971
1110	<i>Eutonina indicans</i>	Eirenidae	60.2473 N 5.2268 E	Norway	Fana fjord	0-20	21.04.2015	medusa	-	KY363946	-
1111	<i>Halopsis ocellata</i>	Mitrocomidae	60.2748 N 5.2027 E	Norway	Raunefjord	0-20	22.04.2015	medusa	-	KY363947	KY363977
1153	<i>Helgicirrha cari</i>	Eirenidae	43.6856 N 7.3178 E	France	Villefranche-sur-Mer	0-75	29.04.2016	medusa	-	KY363968	KY363989
125	<i>Laodicea undulata</i>	Laodiceidae	43.686 N 7.317 E	France	Villefranche-sur-Mer	2-70	11.05.2001	medusa	31753	FJ550471	KY363970
1137	<i>Laodicea undulata</i>	Laodiceidae	58.2438 N 11.4323 E	Sweden	Kristineberg	0	03.10.2014	medusa	-	KY363963	KY363985
1151	<i>Laodicea undulata</i>	Laodiceidae	43.6963 N 7.3075 E	France	Villefranche-sur-Mer	0-3	25.04.2016	medusa	-	KY363967	-
1161	<i>Melicerium octocostatum</i>	Meliceritidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	94100	KY363951	KY363981
1115	<i>Mitrocomella polydiademata</i>	Mitrocomidae	60.2408 N 5.2294 E	Norway	Fana fjord	0-20	23.04.2015	medusa	-	KY363949	KY363979
1133	<i>Mitrocomella polydiademata</i>	Mitrocomidae	56.455 N 5.434 W	Scotland	Firth of Lorn	0	11.05.2004	medusa	-	KY363939	-
1017	<i>Opercularella lacerata</i>	Campanulinidae	60.2697 N 5.2217 E	Norway	Espesgrend	0	19.05.2012	polyp	89411	KY363945	KY363974
Ros16.5	<i>Phialella quadrata</i>	Phialellidae	48.740 N 3.922 W	France	Roscoff	0-20	10.07.2016	medusa	-	KY363969	KY363990
1012	<i>Phialella quadrata</i>	Phialellidae	54.917 S 68.568 W	Chile	Beagle Channel	20-25	16.03.2007	polyp	54081	KY363966	KY363988
1078	<i>Phialella quadrata</i>	Phialellidae	48.6768 N 3.8861 W	France	Bay of Morlaix	5-30	10.09.2014	polyp	91229	KY363962	-
1163	<i>Psychogena crocea</i>	Laodiceidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363953	KY363983
1195	<i>Psychogena crocea</i>	Laodiceidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363958	-
1196	<i>Psychogena crocea</i>	Laodiceidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363959	-
439	<i>Racemoramus panicula</i>	Campanulinidae	60.1611 N 5.171 E	Norway	Korsfjord	160-80	16.06.2006	polyp	48748	FJ550511	KY363973
1114	<i>Staurostoma mertensii</i>	Laodiceidae	60.2408 N 5.2294 E	Norway	Fana fjord	0-30	23.04.2015	medusa	-	KY363948	KY363978 ^s
803	<i>Siegopoma plicatile</i>	Tiarannidae	60.1673 N 5.2541 E	Norway	Korsfjord	650	04.05.2010	polyp	69614	KY363944	-
437	<i>Tiaropsis multicirrata</i>	Mitrocomidae	60.274 N 5.2035 E	Norway	Raunefjord	10	15.06.2006	medusa	48747	KY363943	-
1116	<i>Tima bairdii</i>	Eirenidae	60.2408 N 5.2294 E	Norway	Fana fjord	0-20	23.04.2015	medusa	-	KY363950	KY363980 ^s

Appendix 2: 16S and COI sequences in the BOLD database determined by CCDB from samples collected in Norway.

Species	BOLD Process ID	Collection date	Locality	16S GenBank accession code	COI GenBank accession code
<i>Cyclocanna welshi</i>	HYPNO179-16*	14.06.2016	Korsfjord	KY570308	KY570317
<i>Earleria quadrata</i>	HYPNO156-16	04.05.2016	Raunefjord	KY570307	KY570316
<i>Earleria quadrata</i>	HYPNO136-16	28.04.2016	Korsfjord	KY570303	KY570312
<i>Earleria quadrata</i>	HYPNO150-16	28.04.2016	Korsfjord	KY570306	KY570315
<i>Ptychogena crocea</i>	HYPNO119-16	04.04.2016	Raunefjord	KY570305	KY570314
<i>Ptychogena crocea</i>	HYPNO172-16	14.06.2016	Raunefjord	KY570304	KY570313
<i>Ptychogena crocea</i>	HYPNO158-16	04.06.2016	Raunefjord	KY570309	KY570318
<i>Ptychogena crocea</i>	HYPNO159-16	04.05.2016	Raunefjord	KY570310	-

* same specimen as isolate 1164 in Appendix 1, others are additional specimens