Master's thesis

NTNU
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Department of Natural History

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Integrative Taxonomy Reveals Hidden Diversity in the Genus *Chaetozone* (Annelida, Cirratulidae) in Norwegian Waters

Master's thesis in Biology
Supervisor: Torkild Bakken
May 2019

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Kunnskap for en bedre verden

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Abstract

The polychaetes of the family Cirratulidae (Annelida) are common inhabitants in offshore benthic sediments and considered as an important group in environmental monitoring. Amongst them, the genus *Chaetozone* is the most species-diverse worldwide. Seven species of *Chaetozone* have been recorded in Norway, although these records should be considered cautiously as species delineation is challenging with morphological means. In order to determinate the number of species present in Norway and their distribution, 306 specimens from Norwegian and adjacent waters were DNA sequenced (the universal mitochondrial barcoding region COI, and D1-D2 regions of the nuclear 28S rDNA) and datasets investigated after phylogenetic and species delimitation analyses such as ABGD, mPTP and GMYC. These molecular analyses were used as a frame to re-examine the morphological diagnostic features of each of the species.

Over 130 new COI barcodes are obtained, and a total of 16 species are recovered in the analyses. This includes sequences from specimens of the type locality of the type species of the genus, *Chaetozone setosa*, and its distribution was confirmed to be limited (in Norway) to Arctic waters. The morphology and nomenclature of all species are discussed.

This is a first molecular approach to resolve the species delineation, evolutionary relationships and geographic structure of members of *Chaetozone*, a genus which taxonomy has proven to be difficult. It provides a tool for both molecular and morphological identification and demonstrates the considerable underestimation of the diversity of *Chaetozone*, in the North East Atlantic. This also gives a taste of what is to be expected for the rest of the elusive systematics of the family Cirratulidae.

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List of abbreviations

br	Branchiae
cO	Ciliated organ
dCr	Dorsal crest
dT	Dorsal tentacles
nuO	Nuchal organ
per	Peristomium
pr	Prostomium
Seg	Segment
Set	Setiger (= chaetiger)
vGr	Ventral groove

1 Introduction

1.1 Twenty Thousand Leagues Under the Seas, the Adventure Continues

In the 21st century, it might seem that no exploration is left to be done on Earth. The new mysteries to be solved are now that of Space, and the new explorers target Mars. There is however still one exciting adventure ongoing on lands and (20 000 leagues) under seas, as grand and noteworthy as the exploration of outer space, and that is the quest of discovering and inventorying the incredible and fascinating variety and of living organisms on Earth.

Though estimates of the biodiversity on Earth vary (Mora et al. 2011), most studies agree that a majority of it remains to be discovered and described. This is especially true in the marine environment (Appeltans et al. 2012), as it is more challenging to explore (Earle 1991), in a way similar to space conquest when it comes to its deepest parts. However, quite unlike the Moon, we do find, if not aliens, a number of uncommon and enigmatic creatures under the sea. Bryozoans, corals, ascidians, hydrozoans, molluscs, annelids, and even the occasional mud dragons are but a few examples of the often poorly known but wonderful world hidden under the surface of the ocean.

Systematics is the study of biological diversity, a process that includes taxonomy, the science that aims to describe, name and classify organisms, and phylogeny, that investigates evolutionary relationships between them (Simpson 1961, Mayr 1969, Wilson 1985, Winston 1999). To name something is the first step towards understanding it. Therefore, and though the pursuit of knowledge of all organisms around us is a worthy and noble goal in itself, taxonomy is a fundamental basis to biology research. Whether it is to investigate the history of life, or understand the global and complex ecosystem in which we live, being able to accurately identify organisms is crucial.

The increasing availability of molecular data such as DNA sequences has transformed taxonomy and systematics, opening new perspectives for species discovery, delineation and identification (Bickford et al. 2007). Mitochondrial and nuclear genes sequences, such as the now omnipresent barcode (Hebert et al. 2003a,b) combined with bioinformatics have become

a primary tool to assess the delimitation of species, defined as "separately evolving metapopulation lineages" (De Quieroz, 2007). These tools allow us to investigate the diversity of various groups for which the morphological characters visible to human eye (even under a microscope) may not reflect the aforementioned lineages, and thus lead to a classification that do not represent an evolutionary history nor reality (Schander & Willassen 2005).

When the species boundaries recovered through careful analyses of DNA sequences are then combined to detailed morphological analyses we refer to a work of integrative taxonomy (e.g. Dayrat 2005, Padial et al. 2010, Schlick-Steiner et al. 2010). They can be used as a reference to study a number of morphological characters and potentially find the ones that reliably reflects the different lineages and will make possible the morphological identification of the different species.

1.2 Annelida - Cirratulidae

Annelida, or segmented worms, is a vast and diverse group that includes, amongst others, earthworms, leeches, echiurids, sipunculids and polychaetes. The polychaetes, or bristle worms, are a paraphyletic group which segments typically bear, as their name indicates, many bristles (also called chaetae or setae). They are a very diverse group of mostly marine animals, coming in all shapes, sizes and colors, with or without eyes or jaws, a variety of tentacles, cirri or branchiae, and of course all kinds of bristles.

Polychaetes belonging to the family Cirratulidae Ryckholt, 1851 (Fig. 1) are elongate worms. Their parapodia (the part on both side of each segment bearing the chaetae, or bristles) are in most cases very little developed, looking like simple ridges or bumps along the segments. Their most striking features are the long filament-like branchiae that most bear on many segments and their grooved dorsal tentacles (Fig. 1& 2). The tentacles can either be numerous tentacular filament, or a pair of thick tentacular palps, and are used for feeding. Along them is a ciliated groove, used to bring food particles to the mouth (Blake & Magalhães 2017).

They are deposit feeder, collecting particles around them with their tentacles, and all but one genus that lives in holes it bores in calcareous structures, live in sediments from the shallow

inter-tidal area to the abyss (Chambers & Woodham 2003). Cirratulidae are typically burrowed just under the surface of the sediments, with only their branchiae and tentacles exposed above the surface, and some species are known to build tubes (Blake & Magalhães 2017). They are amongst the most common and abundant polychaetes in offshore habitats and are also often present in great numbers in organically rich sediments, and can be used as indicators of organic pollution (Pearson 1976, Pearson & Rosenberg 1978, Rygg 1985).

Cirratulidae are mostly placed in two distinct, though unofficial, groups depending on the nature of their tentacles. The grooved tentacles of the genera *Cirratulus* Lamarck, 1818, *Cirriformia* Hartman, 1936, *Timarete* Kinberg 1866, *Fauvelicirratulus* Çinar & Petersen, 2011 and *Protocirrineris* Czerniavsky, 1881, take the shape of numerous tentacular filaments arising from one or several anterior segments. These genera are referred to as "multitentaculate" Cirratulidae (Fig. 1). They typically have a broad and wedge-shaped prostomium (the anterior part of the head), and include the largest specimens of the family, up to 20cm long.

The tentacles of the genera *Aphelochaeta* Blake, 1991, *Caulleriella* Chamberlin, 1919, *Chaetocirratulus* Blake, 2018, *Chaetozone* Malmgren, 1867, *Kirkegaardia* Blake, 2016 and *Tharyx* Webster & Benedict, 1887, arise as two long thick processes, usually from the back or the posterior margin of the peristomium (the posterior part of the head), owning them the name of "bitentaculate" Cirratulidae (Fig. 1). They usually have a narrow and conical prostomium, and are smaller worms that rarely size above a couple of centimeters.

One genus in the family, *Dodecaceria*, Ørsted, 1843, is left in his own group as it bores into calcareous structures like shells. It's tentacles are also a pair thick processes, but arising laterally. Cirratulidae belonging to this genus are thus often referred to as the "hard-bottom bitentaculate" Cirratulidae (Fig. 1), as opposed to the "soft-bottom" bitentaculate Cirratulidae.

These genera are the ones traditionally included in Cirratulidae and fitting the current description of the family. However, the few molecular studies providing information about the phylogeny of Cirratulidae show that the Ctenodrillidae (Kennel 1882) are nested within Cirratulidae (Weidhase et al. 2016). Despite these results, the family and its description have yet to be revised. There is no information on the monophly (or paraphyly) of these groups.

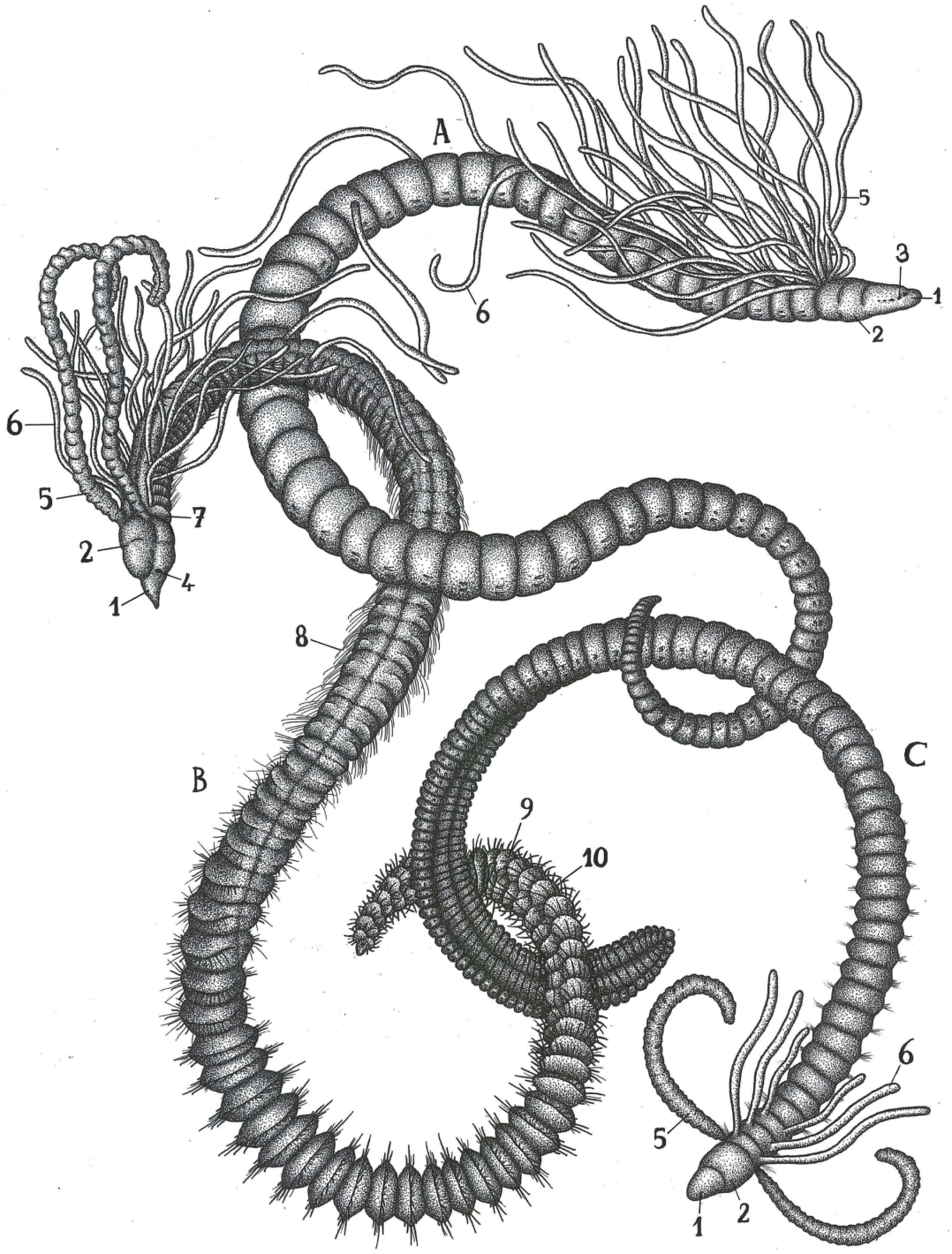


Figure 1 – Family Cirratulidae, main morphotypes and characteristics: A, multitentaculate Cirratulidae (*Cirratulus* sp.); B, soft-bottom bitentaculate Cirratulidae (*Chaetozone* sp.); C, hard-bottom bitentaculate Cirratulidae (*Dodecaceria* sp.); 1, prostomium; 2, peristomium; 3, eyes; 4, nuchal organ; 5, grooved tentacles (various shapes); 6, branchiae; 7, parapodia; 8, capillary chaetae; 9, modified posterior segments (cinctures); 10, acicular spines. (Maël Grosse, original illustration).

1.3 Bitentaculate Cirratulidae – *Chaetozone*

Amongst the 304 extant species of Cirratulidae, 201 are bitentaculate (Read & Fauchald 2019), with no less than 80 species and one new genus described in the past 10 years, and many species probably left to discover (e.g. Elías et al. 2017, Munari et al. 2017), including in the North East Atlantic (Chambers 2000, Chambers & Woodham 2003).

Of the six genera of bitentaculate Cirratulidae, *Chaetozone* is the most diverse with 62 species worldwide. *Chaetozone* is distinguished from the other bitentaculate Cirratulidae by having posterior segments modified into cinctures created by elevated parapodia bearing fascicles of numerous unidentate spines (Fig. 1&2), sometimes with a few bidentate hooks (Fig. 2) (Blake 2018). The nature and arrangement of chaetae are the main characters differentiating the bitentaculate genera as *Aphelochaeta* bears only smooth capillary chaetae (Fig 2), *Kirkegaardia* bears both smooth and serrated capillary chaetae (Fig 2), *Caulleriella* bears capillary chaetae and bidentate hooks (Fig. 2), *Tharyx* bears capillary chaetae and knobby tipped spines (Fig. 2) and *Chaetocirratulus* bears capillary chaetae and a few unidentate spines not arranged in cinctures (Blake 2018, Blake and Magalhães 2017).

Important characters for species identification include the general shape of the body, the presence or absence of a dorsal or a ventral groove or ridge along all or part of the body, the shape of the prostomium and of the peristomium, the nature of the first segment, the position of the paired tentacles, the position of the first branchiae, the nature and arrangement of the chaetae, the shape of the posterior modified segments or the shape of the pygidium (Blake 2017).

Seven species of *Chaetozone* are recorded in Norwegian waters by the Norwegian Biodiversity Information Center: *C. setosa* Malmgren, 1867, *C. christiei* Chambers, 2000, *C. jubata* Chambers & Woodham, 2003, *C. gibber* Woodham & Chambers, 1994, *C. vivipara* (Christie, 1984), *C. abranchiata* (Hansen, 1878), *C. caputesocis* (De Saint-Joseph, 1894). *Caulleriella zetlandica* (McIntosh, 1911) has previously been described within *Chaetozone* (McIntosh 1911, Southern 1914) and is also reported from Norway.

However, geographical and historical considerations incite then to caution regarding these records. Indeed, the understanding of the group's morphology and number of characters employed to describe and diagnose the different species has significantly increased since the first description of *Chaetozone setosa*. The boundaries and definition of the bitentaculate genera has been the subject of many changes and discussions (e.g. Hartman 1961, Blake 1991, Blake 2018), and many species have now been placed in a different genus than the one they were originally described in (examples in Table 1). In the light of today's knowledge of the group, their description is also often too succinct for accurate and confident identification. *Chaetozone setosa* for instance, has been reported from nearly all over the world (Chambers 2000), but is now believed to be probably only present in arctic and sub-artic waters, while the other records would be of different species (Blake 1996).

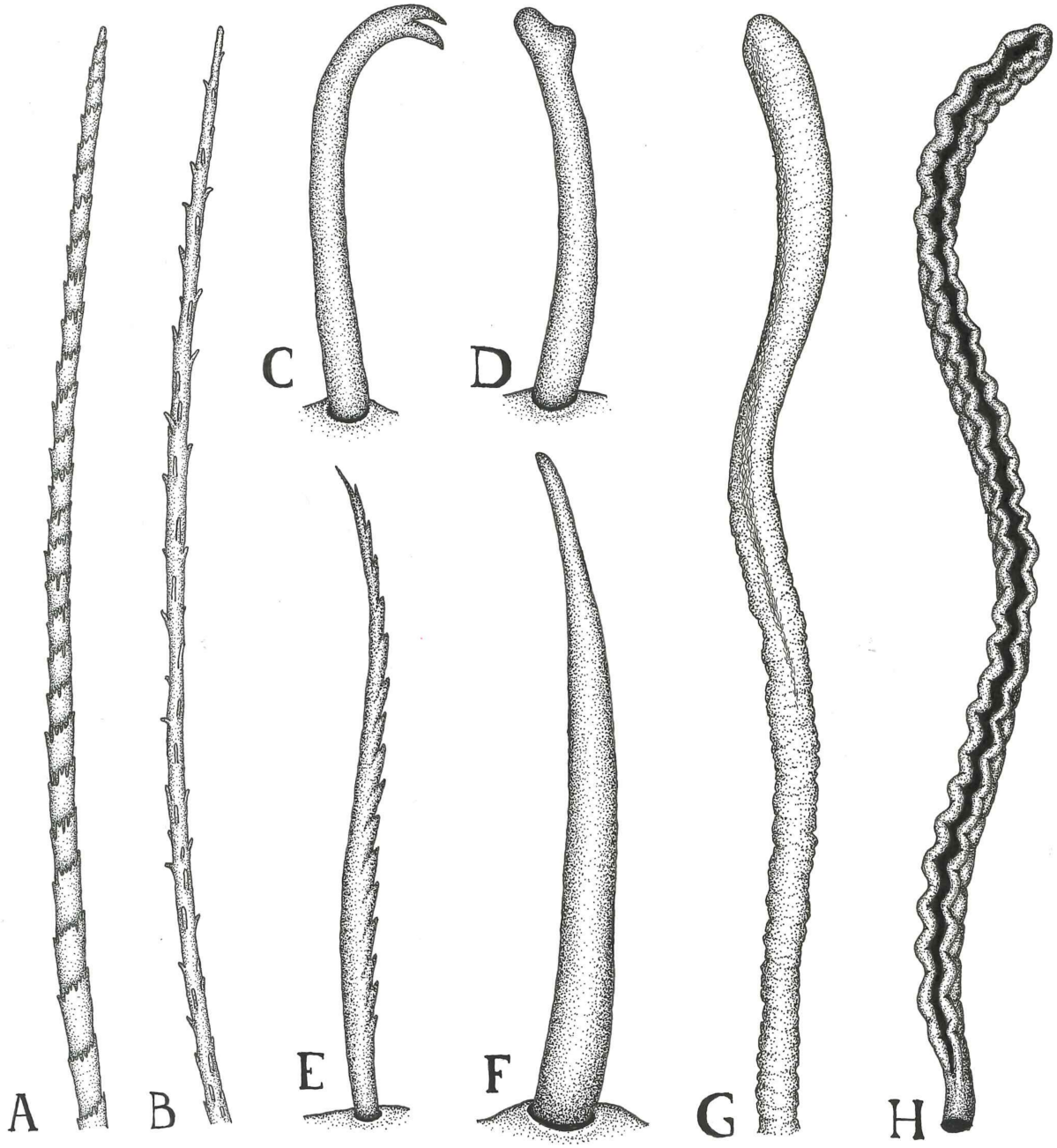


Figure 2 – Cirratulidae chaetae and processes: A, Segmented capillary chaetae (~100µm); B, Smooth capillary chaetae (~100µm); C, Bidentate hook (~15µm); D, Knobby tipped spine (~15µm); E, serated capillary chaetae (~70µm); F, unidentate spine (~70µm); G, Detail of a branchia (~ 1mm); H, Grooved tentacle (of a bitentaculate Cirratulidae, ~2mm) (Maël Grosse, original illustration).

Table 1 – Species of *Chaetozone* recorded in Norway: Author, date of publication, type locality, location of type material. MNHN: Museum National d'Histoire Naturelle; NMSZ: National Museums of Scotland; NMWZ: National Museums of Wales; BMNHN: British Museum (Natural History); SMNH: Ssedish Museum of Natural History,.

Name	Author	Original placement	Type locality	Type material
	Hansen, 1878	*Cirratulus*	West Norway	Unknown
Chaetozone caputesocis	De St Joseph, 1894	*Heterocirrus*	Off Dinard, North France	Syntypes: MNHN-IA-TYPE0938 to 0949
Chaetozone christiei	Chambers, 2000	*Chaetozone*	Off Newton by the Sea, East England	Holotype: NMS.Z.1998.122 Paratypes: NMS.Z.1998.123, NMW.Z 1999.016.006
Chaetozone gibber	Woodham & Chambers, 1884	*Chaetozone*	Off Folkestone, Kent, South East England	Holotype: NMS.Z.1992.87 Paratypes NMS.Z.1992.88, BMHN 1992.427 to 432, NMW.Z 1993.009, MNHN-IA-TYPE0629
Chaetozone jubata	Chambers & Woodham, 2003	*Chaetozone*	Faeroe-Shetland Channel	Holotype: NMSZ. 1999.237.0001 Paratypes: NMSZ 1999.237.0002 to 0005.
Chaetozone setosa	Malmgren, 1867	*Chaetozone*	Isfjorden, Svalbard	Lectotype: SMNHN 1493-03 Paratypes: SMNHN 1493-04 to 175
Chaetozone vivipara	Christie, 1984	*Tharyx*	Off Newcastle upon Tyne, East England	Holotype: BMNHN ZB 1984:1 Paratypes: BMNHN ZB 1984:2 to 29

Valid nominated species need to have a representative specimen, or type, deposited in a public institution (Table 1). A type specimen links the species to which it belongs to a species name that can then be given to any specimen identified as belonging to the same species as the type. This type is then of crucial importance to accurately identify material. This type specimen can be accompanied by other specimens from the type locality (the place from which the type specimen originates and from which the species is described) used in the original descriptions of the species, called paratypes. Though they do not have the function of name-bearer, having an almost certain probability to belong to the same species as the type specimen, these paratypes are also extremely valuable in the identification of new material.

1.4 Molecular Data and Associated Species Delimitation Tools

From single genes to whole genomes, a wide range of molecular data is now available for Biosystematics. Many studies have revealed unknown or "cryptic" diversity in different polychaete groups using molecular data for taxonomical investigation following the process of integrative taxonomy described earlier (e.g. Nygren 2014, Nygren & Pleijel 2011, Brasier et al. 2016, Capa et al. 2013, Aguado et al. 2019). Typically, DNA sequences of one or several gene fragments, also called markers, are used to recover information about lineages. Several of this gene fragments are widely used across organisms, like mitochondrial gene cytochrome oxidase I (COI) which is the "universal barcode" (Hebert et al. 2003a, b), or parts of the 28S rRNA nuclear gene.

Many methods have been designed to use the information contained in this DNA to study evolutionary relationships between species, and specifically for taxonomy. Though the methods differ, the motivation behind them is always the same: statistically differentiate two or more separately evolving lineages. Distance based methods assume that, due to the presence of gene flow within one lineage and the absence of it between lineages (which is the meaning of "separately evolving" and equivalent to the absence of reproduction between members of two distinct species), molecular markers will show distinctly less variability within species than between species. Different tree based methods use the branch lengths and

topology of a previously inferred tree to establish a threshold between intra- and inter-specific relationships.

In the family Cirratulidae, the multitentaculate genus Timarete has been the subject of some molecular studies at the species level (Magalhães et al. 2014, Seixa et al. 2017, Choi et al. 2018), in complement of morphological descriptions. No such technique however, has been used to investigate bitentaculate Cirratulidae.

1.5 Aims

The main aims of this study is (i) to assess the numbers of species of the genus *Chaetozone* in Norwegian waters using molecular data. This includes (ii) testing the monophyly of *Chaetozone*, by (iii) producing a phylogeny of the family Cirratulidae with said molecular data. The last aim is to (iv) re-examine the diagnostic features of each species found.

2 Material and Methods

2.1 Specimens and Study Area

Around 1500 specimens were examined in this study, most from the collections of the University Museum of Bergen (ZMBN) and NTNU University Museum (NTNU-VM). This material was either fixed and preserved in 96% ethanol or fixed in 10% formalin and preserved in 75% ethanol.

Material from the Mediterranean Sea (Mallorca, Spain) were also made available for the study. This material was collected by grab and fixed and preserved in 96% ethanol.

Additional specimens were collected for this study in the Trondheimsfjord by dredging of sediments and fixed in 96% ethanol.

The study area covered by these specimens was divided in six biogeographic regions according to their different oceanographic and topographic characteristics (Blindheim & Rey 2004, OSPAR 2010, Yashayaev et al. 2015, Nygren et al. 2018). The Greenland Sea (Fig. 3, cyan stars) is a deep cold water area and the Barents Sea (Fig. 3, purple dots) is a shallow cold water area. The Norwegian coast and shelf (Fig. 3, red pentagons), the Skagerrak (Fig. 3, orange triangles) and the North Sea (Fig. 3, blue squares) are shallow waters areas (<600m) with warmer water, while the Norwegian Sea (Fig. 3, green diamonds) is a deep water area.

Type material of *Chaetozone setosa*, *C. christiei*, *C. gibber*, *C. jubata*, *C. vivipara* and *Caulleriella zetlandica* (McIntosh 1911) was made available by the Swedish Natural History Museum, Stockholm, Sweden (SMNH), the National Museums of Scotland, Edinburgh, UK (NMSZ) and the British Museum (Natural History), London, UK (BMNH).

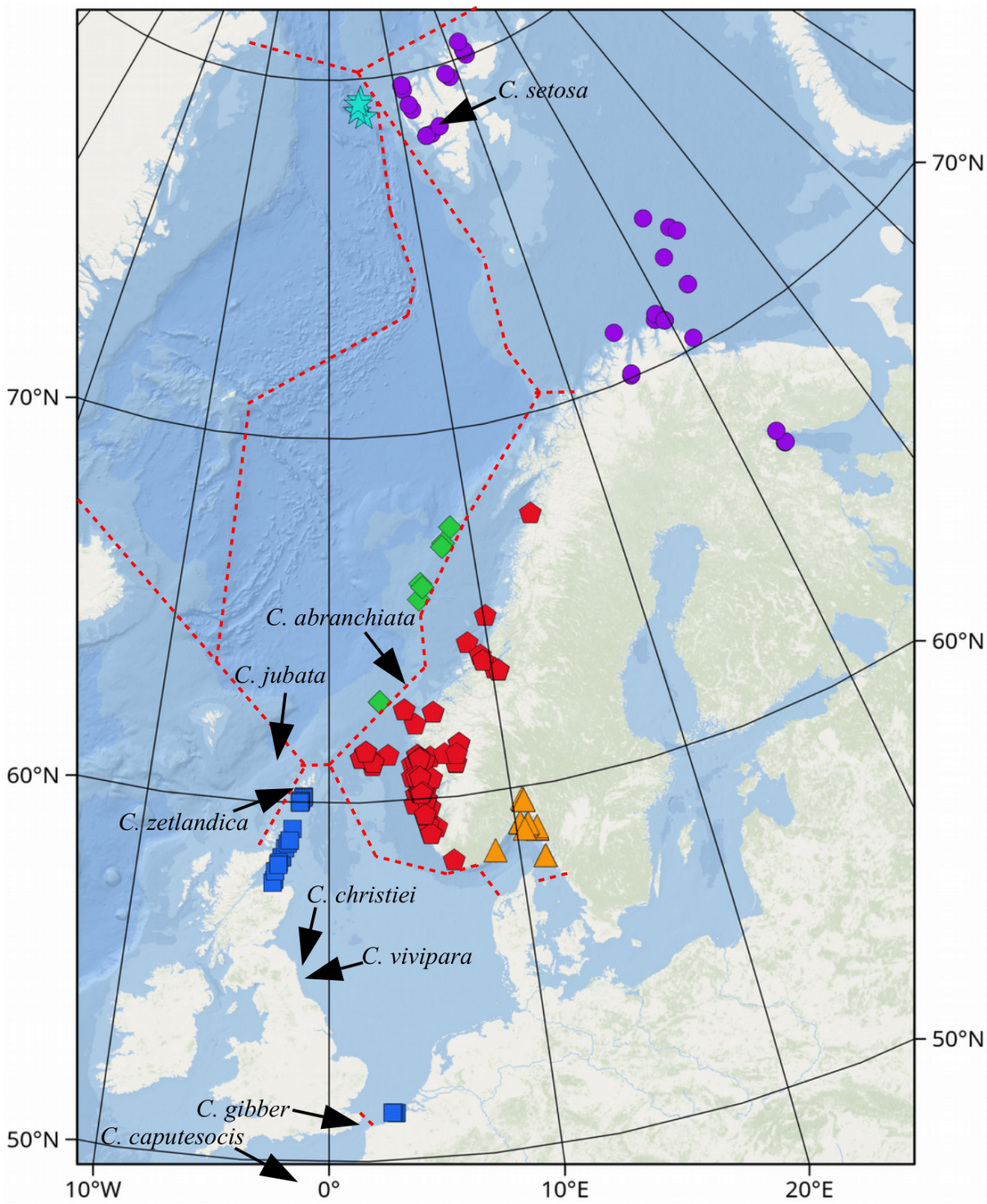


Figure 3 - Sampling sites for molecular studies and biogeographic regions: Delimited by red lines; Greenland Sea (cyan stars), Barents Sea (purple dots), Norwegian Sea (green diamonds), Norwegian coast and shelf, (red pentagons), Skagerrak (orange triangles), North Sea (blue squares). Type localities of *Chaetozone. setosa*, *C. christiei*, *C gibber*, *C. caputesocis*,*C. jubata*, *C. abranchiata*, *C. vivipara* and *Caulleriella zetlandica* are indicated by black arrows.

2.2 Molecular data retrieval

In total, 306 ethanol fixed specimens were selected for molecular work across the geographic area (see above) and across the range of depth covered by the different materials (from 6 to 1256m).

Tissue samples of 95 of these specimens were sent to the Canadian Center for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario, that performed sequencing on both strands using the primer pairs polyLCO/polyHCO or ZplankF1_t1/ZplankR1_t1 (Table 2). The rest of the samples were processed in the facilities of the NTNU University Museum as follow.

To extract DNA from the specimens, a few parapodia, or a few of the posterior-most segments for the smallest specimens, were placed into 50µL of QuickExtract (Epicentre) and heated at 65°C for 60 minutes followed by 3 minutes at 95°C in a thermos-shaker at 300 rpm.

The method above produces very impure DNA extracts potentially containing high concentration of PCR inhibitors, and the manufacturer indicates a very short preservation time of the raw extracts. Diluting these extractions in EB buffer was a solution to both problems. Testing of the most efficient dilution was done with qPCR (quantitative polymerase chain reaction) over 16 extractions. These samples were used undiluted, diluted 1:5 or diluted 1:10 in EB buffer. qPCR mixes contained 1µL of each primer jgLCO1490 or jgHCO2198, 1µL of SYBRgreen, 7µL of MQ-H_20, 12µL of MyTaq Red Mix (Bioline) and 3µL of DNA template, either not diluted, diluted 1:5 or diluted 1:10, for a total volume of 25µL. The 1:5 dilution resulted a much higher number of successful products than using the undiluted samples and showed a much earlier amplification than using the undiluted or diluted 1:10 samples. As a results, all extractions were eluted in 200µL EB buffer.

Amplification of the markers was done by Polymerase Chain Reaction (PCR). PCR mixes contained 0.30µL of each primers, 1.4µL of DNA template and 10µL of RedTaq 1.1x MasterMix 2.0mM $MgCl_2$ (VWR) for reaction volume of 12µL. The different pairs of primers

used (jgLCO1490/jgHCO2198, CirrCOIF/CirrCOIR, polyLCO/polyHCO, 28SC1'/28SD2) are presented with their respective cycles in Table 2.

1.5µL of each PCR products was run for 45 minutes on a 1% agarose gel electrophoresis containing SYBR safe (Invitrogen) for DNA detection and visualized using GeneSnap from SynGene software (Version 6.08, Cambridge, UK). All the successful PCR products left were purified with illustra ExoProStar 1-Step (GE Healthcare, Litlle Chalfont, UK). Cycle sequencing was performed on both strands by Eurofins Genomics DNA Sequencing Department (Ebersberg, Germany).

218 published and unpublished sequences of COI (209 sequences) and 28S D1-D2 (9 sequences) were downloaded from the Barcode of Life Data (BOLD, Ranasingham & Hebert 2007) and GenBank (Benson et al. 2008). These sequences were from specimens identified as belonging to the genera *Aphelochaeta*, *Caulleriella*, *Chaetozone*, *Cirratulus*, *Cirriformia*, *Ctenodrilus*, *Dodecaceria*, *Kirkegaardia*, *Protocirrineris*, *Raricirrus*, *Tharyx*, and *Timarete*. Most of these sequences belong to specimens not collected in the area of interest in this study. They were however included in the analyses in order to get a better overview of the diversity and phylogeny of the family.

The whole dataset is presented in table Appendix I. To facilitate the use of two different genes for several specimens in some analyses, specimens are, whenever possible, referred to by their voucher number. When no voucher is provided to accompany a sequence, either GenBank or BOLD accession number is used (when such a sequence is used, no other sequence coming from the same voucher can be found).

Table 2 – PCR Primers: The different primer pairs used to amplify both markers used in this study and their respective cycles.

Region	Name	Length	Source	Sequence 5'-3'	Cycle
COI	jgLCO1490	~650bp	(Geller et al. 2013)	TITCIACIAAYCAYAARGAYATTGG	3min 96°C
	jgHCO2198		(Geller et al. 2013)	TAIACYTCIGGRTGICCRAARAAY(	60s 95°C
				34x	60s 48°C
					60s 72°C
					5min 72°C
	CirrCO1F	~650bp	(Weidhase et al. 2016)	TTTTTCTACTAACCATAAAGACATTG	60s 96°C
	CirrCO1R		(Weidhase et al. 2016)	CCGAGGAAGTGTTGAGGGA	60s 94°C
				34x	60s 53°C
					60s 72°C
					5min 72°C
	polyLCO	~650bp	(Carr et al. 2011)	GAYTATWTTCAACAAATCATAAAG	60s 96°C
	polyHCO		(Carr et al. 2011)	TAMACTTCWGGGTGACCAAARA	40s 95°C
				5x	40s 46°C
					60s 72°C
					40s 94°C
				35x	40s 51°C
					60s 72°C
					7min 72°C
	ZplankF1_t1	~650bp	(Prosser et al. 2013)	tgtaaaacgacggccagtTCTASWAATC ATAARGATATTG	60s 95°C
	ZplankR1_t1		(Prosser et al. 2013)	caggaaacagctatgacTTCAGGRTGR CCRAARAATCA	40s 94°C
				29x	40s 51°C
					60s 72°C
					5min 72°C
28S (D1-D2)	28SC1'	~900bp	(Le et al. 1993)	ACCCGCTGAATTTAAGCAT	60s 96°C
	28SD2		(Le et al. 1993)	TCCGTGTTTCAAGACGG	30s 95°C
				29x	60s 62°C
					60s 72°C
					7min 72°C

2.3 Phylogenetic Analyses

2.3.1 Alignments and Datasets

Forward and reverse reads were merged into consensus sequences using Geneious 11.0.5 (https://www.geneious.com).

COI fragments sequences were aligned with MUSCLE (Edgard 2004) implemented in Aliview (Larson 2014). 28S D1-D2 fragments were aligned on MAFFT online version (Katoh et al. 2017) with the algorithm Q-INS-i, that considers the secondary structure of RNA, using the 200PAM/k=2 scoring matrix and a gap penalty of 1.53.

The complete COI dataset contains all 436 sequences either produced for this study and downloaded from BOLD or GenBank. The complete 28S dataset contains all 153 sequences either produced for this study and downloaded from Genbank (Table 3).

To perform distance-based species delimitation analyses, all sequences in the dataset must share a common domain as no distance can be calculated between two specimens for which sequences cover two different non-overlapping parts of the gene. Some short sequences were removed from the complete COI dataset to create a dataset suitable for distance analyses.

One species delimitation method requires that all sequences in the alignment are unique. To that effect, some sequences were removed from the complete COI dataset and the complete 28S dataset to produce two additional datasets (Table 3).

All five dataset had some missing data in flanking regions, and the 28S datasets presented several ambiguous regions where no satisfactory alignment and homology statement could be made. The softwares Gblocks (Castresana 2000) removes positions missing a certain amount of data, and/or poorly aligned. It was used on all COI datasets with default parameters, and on the 28S datasets with softest parameters, to produce five additional datasets allowing us to test the influence of this missing data (Table 3).

A combined dataset was obtained by concatenating the complete COI and 28S alignments. Some sequences were removed from this dataset to produce a second combined dataset with only unique sequences.

Norwegian species of *Chaetozone* were identified through analyses of all these datasets (COI, 28S, combined, with and without removing the poorly aligned positions and divergent regions with Gblocks). Some conflicts detected between both genes were identified as possible contamination. In these cases vouchers were re-examined to verify their identity. While a mislabeled or contaminated sequence does not affect phylogenetic inference over a single gene, these conflicts locally created poorly supported topologies and branch length in combined phylogenetic analyses, which in turn affect downstream species delimitation analyses. The aforementioned sequences were removed to perform additional analyses of the combined dataset without them.

Outgroups included in the alignments for ML inference were *Glyphanostomum* sp., *Flabelliger affinis* and P*olycirrus cf eximius* (Weidhase et al. 2016, Rouse & Pleijel 2001). No outgroups were included the the datasets for Bayesian inference (Drummond & Bouckaert 2015).

2.3.2 Data Partition And Model Selection

PartitionFinder2 (Lanfear et al. 2016, Guindon et al. 2010) was used to test partitions and find the best model for phylogenetic analyses using the Bayesian Information Criterion for both markers.

2.3.3 Maximum Likelihood

Maximum Likelihood inference was performed with PhyML (Guidon et al. 2010), on the 28S dataset before and after Gblocks, to test the impact of the missing data and ambiguous positions, as well as on the complete COI dataset also before and after Gblocks, to test the importance of missing data in species delimitation analyses, and on the COI dataset with short terminals removed, to compare the different species delimitation analyses, distance and tree based, also before and after Gblocks with default parameters, again to see the effect of missing data. A GTR+Γ model with 4 four category count was used for the COI dataset and an TN93+Γ model with four Γ category counts was used for the 28S dataset. Support values were estimated with a 100 bootstrap replicates.

Analysis of the concatenated datasets were performed with IQ TREE on Cypres Science Gateway (Miller et al. 2010), A GTR+Γ model with four Γ category count was used for the COI partition and an TN93+Γ model with four Γ category counts was used for the 28S partition. Each partition was allowed to have its own set of branch length. Support values were estimated with a 1000 bootstrap pseudoreplicates.

Trees were visualized and edited using FigTree 1.4.4 (Rambaut 2018) and LibreOffice Draw.

This makes a total of eight analyses, four with the COI data, two with the 28S data, one on the complete combined dataset, and one with the combined dataset of Norwegian *Chaetozone*.

2.3.4 Bayesian Inference

Bayesian inference was performed with BEAST2 (Bouckaert et al. 2014) on Cypres Science Gateway (Miller et al. 2010), on the 28S dataset before and after Gblocks, with duplicate sequences removed, on the COI dataset before and after Gblocks, with duplicate sequences removed, and on the combined dataset of all COI sequences and all 28S sequences with duplicate sequences removed. A GTR+Γ model with four Γ category count was used for the COI dataset/partition and an TN93+Γ model with four Γ category counts was used for the 28S dataset/partition. A strict clock was assumed for both datasets/partitions. A Yule model was used as Tree Prior with a default Γ distribution as birth rate prior for both datasets/partitions. A lognormal distribution with M=1.0 and S=1.25 for kappa parameters prior of the 28S dataset/partition (Drummond & Bouckaert 2015). Trees of both partitions were linked for the combined analysis. All analyses were run with a chain length of 50000000.

Convergence of each run and parameter was checked using Tracer 1.7.1 (Rambaut et al. 2018). A maximum clade credibility was obtained with Treeannotator (Bouckaert et al. 2014) after discarding 10% of the trees as burnin for single gene trees, and 20% for the combined analysis.

Trees were visualized and edited using FigTree 1.4.4 (Rambaut 2018) and LibreOffice Draw.

This makes a total of six analyses, two with the COI data, two with the 28S data, one on the complete combined dataset (Table 3), and one and the Norwegian *Chaetozone* combined dataset.

Table 3 – Molecular datasets: Characteristics of the datasets and analyses performed with them. For the combined datasets, the number of terminal in the complete combined datasets is indicated first, then the number of terminals in the Norwegian *Chaetozone* combined datasets.

Dataset	Characteristics				Analyses					
	Number of Terminals	Number of positions	Number of partitions	Best model	ML	BI	ABGD	GMYC	mPTP	STACEY
Complete COI	436	658	1	GTR+Γ	x				x	
Complete COI Gblocks	436	453	1	GTR+Γ	x				x	
COI No Duplicates	331	658	1	GTR+Γ		x		x	x	
COI Gblocks No Duplicates	199	453	1	GTR+Γ		x		x	x	
Distance COI	423	658	1	GTR+Γ	x		x		x	
Distance COI Gblocks	423	457	1	GTR+Γ	x		x		x	
Complete 28S	153	919	1	TN+Γ	x		x		x	
Complete 28S Gblocks	153	679	1	TN+Γ	x		x		x	
28S No Duplicates	92	802	1	TN+Γ		x		x	x	
28S Gblocks No Duplicates	84	679	1	TN+Γ		x		x	x	
Combined	492 - 225	1610 - 1491	2	COI: GTR+Γ 28S: TN+Γ	x				x	x
Combined No Duplicates	383 - 182	1460 - 1436	2	COI: GTR+Γ 28S: TN+Γ		x		x	x	

2.4 Species Delimitation

Four different species delimitation methods were used in this study, one distance method and three different tree based methods. COI was the selected target gene for species delimitation analyses and the three methods primarily chosen are designed for single gene analyses (e.g. Vogler & Monaghan 2006, Vitecek et al. 2017, Nygren et al 2018, Aguado et al. 2019). 28S was selected to try to infer a fully resolved robust phylogeny (e.g. Rousset et al. 2007, Osborn & Rouse 2011). As many sequences of 28S were obtained for *Chaetozone*, these analyses were also tested on this gene, and an additional multi-loci tree based species delimitation method was tested.

2.4.1 ABGD

The Automatic Barcode Gap Discovery (ABGD, Puillandre et al. 2012) is a method designed to find the "barcode gap" within a dataset, following the assumption that interspecific variability is significantly higher than intraspecific variability (Hebert et al. 2003). This means that the genetic distance between two individuals in a dataset belongs to one of two distinct set of values, one composed of small short distances, representing intraspecific variability, and one composed of higher distances, representing interspecific variability, with no intermediate values. As this model was proposed on what is now used as the "universal barcode", this absence of intemediate values allowing us to discriminate between the intraspecific and interspecific variation is called the "barcode gap".

ABGD calculates simple pairwise distances or substitution-corrected distances (using either JC69 or K2P models) between aligned sequences and tests a range of prior intraspecific divergence to infer a limit to intraspecific variability. The barcode gap is the first significant gap detected after this limit. The data is partitioned a first time using this barcode gap and the method is then repeated inside each partition found to refine the partitions. The partitions found after this step are the species hypotheses.

ABGD was used with a range of 30 priors from 0.001 to 0.5 on JC69 distance matrixes from the two COI datasets for distance analyses, and on the two complete 28S datasets.

2.4.2 mPTP

The multi-Rate Poisson Tree Process (mPTP, Kapli et al. 2017) is a tree based species delimitation method. It partitions a tree into sets of tips. The branch lengths of each species is fit to an exponential distribution that can be different for each set. It then finds the partition of the dataset that maximizes the likelihood score of the partition of branch lengths.

mPTP was applied through its on-line version to all 14 trees inferred previously (Table 3).

2.4.3 GMYC

The General Mixed Yule Coalescent method (GMYC, Fujisawa and Barraclough 2013) is a tree based species delimitation method that maximizes the likelihood score of an ultrametric tree by separating the branches of this tree between within-species-branches (coalescent events) and between-species-branches (speciation events) under the GMYC model (Pons et al. 2006).

GMYC was implemented in R (R Core Team 2015) with the packages ape (Paradis & Schliep 2018), MASS (Venables & Ripley 2002), Paran (Dino 2018) and splits (Ezard et al. 2017) on the six ultrametric Bayesian trees inferred previously (Table 3). Both the single and (experimental) multiple threshold methods were tested.

2.4.4 STACEY

Species Tree And Classification Estimation, Yarely (STACEY, Jones 2014) is a species delimitation method under the multi-species coalescent model. It is a Bayesian inference of a species tree from gene trees where tips can be merged into “minimal clusters” or species.

Stacey was implemented as a species package in BEAST2. A GTR+Γ model with four Γ category count was used for the COI dataset/partition and an TN93+Γ model with four Γ

category counts was used for the 28S dataset/partition. A strict clock was assumed for both datasets/partitions with a lognormal prior. The tree prior was a fossilized birth/death model. The collapse height was of 1e-4. The collapse weight was estimated with a beta prior (1,1) around [0,1] and a start value of 0.5. A 1/X prior was used for the Growth rate. A lognormal distribution with M=1.0 and S=1.25 was used for kappa parameters prior of the 28S dataset/partition and the population scaling factor (Drummond & Bouckaert 2015, Vitecek et al. 2017). The chain length was of 300000000.

STACEY was used on the combined dataset of Norwegian *Chaetozone.*

Convergence of each run and parameter was checked using Tracer 1.7.1 (Rambaut et al. 2018).

2.5 Morphological Analyses

The material was examined a first time to make a preliminary sorting in order to select specimens from all different morphologies present for DNA sequencing. After the molecular analyses, the DNA vouchers were examined more carefully in order to look for morphological patterns representative of each species.

The aim of this second analysis was not to write formal complete species descriptions or re-descriptions, but to find, when possible, diagnosis characters enabling researchers to sort and distinguish the different species, even though it may not be possible to name them yet.

All specimens were examined using a Leica M165C stereomicroscope and a Leica DM250 compound microscope. Detailed pictures of specimens were taken with a Leica MC170HD camera mounted on a Leica M165C stereomicroscope or Leica DFC420 camera mounted on a Leica MZ16A stereomicroscope. All specimens were stained in a solution of Shirlastain A (SDL International LTD). Shirlastain A is used to enhance contrast at the surface of the specimens and allow an easier and more precise observation of the external morphology. Some specimens were stained in a solution of Methyl Blue. Methyl Blue, like Methyl Green, stains glandular tissues that may be present following a distinct pattern in some species.

Parapodia of some specimens, usually an anterior and a posterior one, or complete segments, were mounted on slides in Euparal and photographed with a Leica DFC420 camera mounted on a Leica DM60000 B compound microscope.

Some specimens were examined with a Zeiss SUPRA 55VP scanning electron microscope (SEM) at the electron microscopy lab of the University of Bergen. To be certain to link the right morphological characters to the right species previously determined through molecular analyses, some of the DNA vouchers had to be used. The specimens were critically point dried with a Polaron critical point dryer (Watford, England) and coated with gold (40%) and palladium (60%) with a Polaron SC502 coater.

Figures, pictures and ink handmade illustrations were edited with with GIMP 2.10 (GNU Image Manipulation Program), LibreOffice Draw and an Intuos3 Pen Tablet (Wacom).

2.6 Specimens Occurrences

Specimens occurrences and species distributions were investigated with QGIS 2.14 (QGIS Development Team 2016).

3 Results

3.1 Molecular Analyses

3.1.1 Data Retrieval, Partition and Model Selection

A total of 144 new 28S (58%) and 177 new COI sequences (57%) were obtained. PCR success was of 67% for 28S and 69% for COI. Sequencing success was of 86% for 28S and 82% for COI.

Partition Finder 2 found a GTR+Γ as the best model for the COI partition. No additional codon partition was found within the COI alignment. A TRN+ Γ was found as the best model for the 28S partition and no additional codon partition was found within the 28S alignment either.

3.1.2 Phylogeny of Cirratulidae – Monophyly of *Chaetozone*

In both the Maximum Likelihood and Bayesian Inference of the combined dataset (COI+28S), *Chaetozone* is recovered monophyletic with strong support (posterior probability of 1 and bootstrap value of 89) (Fig. 4).

Ctenodrillus and *Raricirrus* are also recovered monophyletic and strongly supported as such in both combined analyses (with respective posterior probabilities of 0.8819 and 0.9999 and bootstrap values of 99 and 95) (Fig. 4).

Dodecaceria is supported as monophyletic in the Maximum Likelihood analysis (bootstrap value of 74), but not in the Bayesian Inference (posterior probability of 0.3648) (Fig. 4).

Cirratulus is supported as monophyletic only in the Bayesian Inference. In the Maximum likelihood analysis, it is paraphyletic in regard to *Cirriformia* and *Timarete* but only one terminal falls out of *Cirratulus*, with very low support (Fig. 4).

However, *Aphelochaeta* and *Tharyx* are recovered paraphyletic and mixed with one another. *Cirriformia* and *Timarete* are in the same situation (Fig. 4).

The Bayesian Inference strongly supports both the bitentaculate Cirratulidae (*Chaetozone*, *Aphelochaeta* and *Tharyx*) and the multitentaculate Cirratulidae (*Cirratulus*, *Cirriformia* and *Timarete*) as monophyletic (with respective posterior probabilities of 0.9735 and 1). *Dodecaceria*, *Ctenodrillus* and *Raricirrus* form a third supported monophyletic group (with a posterior probability of 0.9921). The relationship between these three groups is unresolved (Fig. 4).

The Maximum Likelihood analysis however, supports *Chaetozone* as sister to the rest of Cirratulidae. *Dodecaceria*, *Ctenodrillus* and *Raricirrus* are again supported as a monophyletic group, as well as the multitentaculate Cirratulidae (*Cirratulus* with *Cirriformia* and *Timarete*) (with respective bootstrap values of 79 and 100). The relations of these two groups together and with the group formed by *Aphelochaeta* and *Tharyx* are unresolved (Fig 4.).

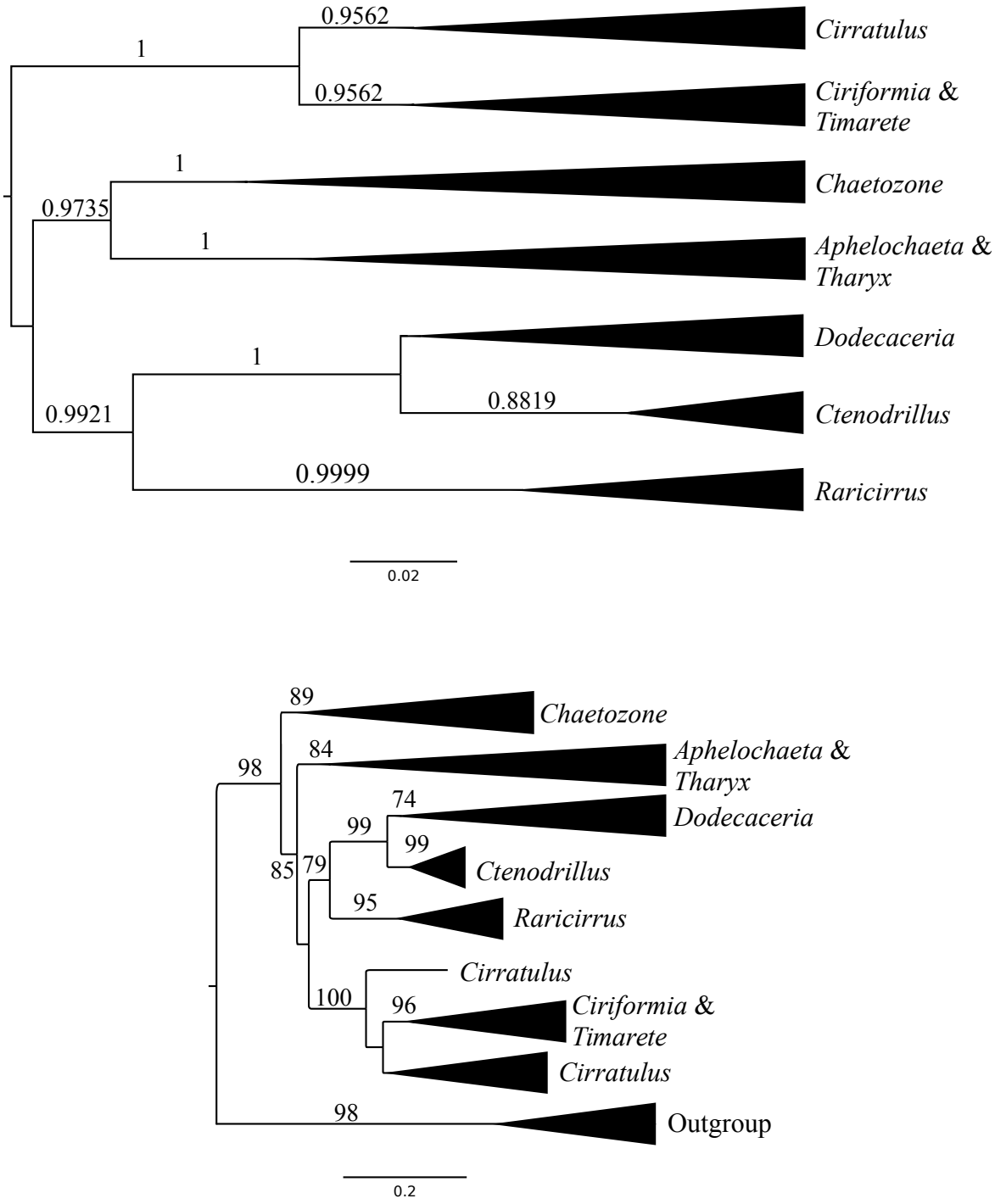


Figure 4 - Phylogeny of Cirratulidae: A, Bayesian Inference of the complete combined dataset, posterior probabilities above 0.6 are indicated above branches. B, Maximum Likelihood inference of the complete combined dataset, bootstrap values above 60 are indicated above/under branches.

3.1.3 Species Delimitation in Norwegian *Chaetozone*

All analyses performed on the COI datasets recovered the same number and composition of 16 species. The 28S datasets did not respect the assumption of the barcode gap and ABGD failed to produce meaningful results on these datasets. Tree based analyses of the 28S dataset recover between 4 and 8 species, not counting the important number of singletons or cluster of 2-3 specimens made within two of the species recovered by analyses of the COI datasets. No 28S sequences were obtained for three of the species recovered by analyses of the COI datasets. Tree based analyses of the combined dataset recover between 11 and 16 species, not counting the important number of singletons or cluster of 2-3 specimens made within two of the species recovered by analyses of the COI datasets in some of them (Fig. 5). The few sets of priors tested for STACEY did not allow it to converge and so no result is presented here. The use of Gblocks to remove missing data in some datasets had no impact on the general tree topologies or the species delimitation within Norwegian *Chaetozone*.

A consensus of 16 species is made from the different species delimitation analyses (Fig. 5):

- Species 1 (21 specimens) is recovered with all analyses but for mPTP on Maximum Likelihood analysis of 28S where is is lumped with species 2, 3, 14, 15 and 16.

- Species 2 (13) is recovered with all analyses, but for mPTP on Maximum Likelihood analysis of 28S where it is lumped with species 2, 3, 14,15 and 16. It is also further divided in GMYC with multiple threshold on Bayesian Inference of 28S.

- Species 3 (14 specimens) is recovered in all COI analyses and mPTP analyses of both the Maximum Likelihood and Bayesian Inference of the combined dataset. It is lumped with species 1, 2, 14, 15 and 16 in mPTP on Maximum Likelihood analysis of 28S, and with species 14 only in GMYC and mPTP on Bayesian Inference of 28S and GMYC on Bayesian Inference of the combined dataset.

- Species 4 (10 specimens) is recovered in all COI analyses and combined analyses but for GMYC with single threshold on Bayesian Inference of the combined dataset where it is lumped with species 5. It is also further divided in GMYC with multiple threshold on Bayesian Inference of 28S. No 28S sequences were obtained in this species.

- Species 5 (3 specimens) is recovered in all COI analyses and combined analyses but for GMYC with single threshold on Bayesian Inference of the combined dataset where it is lumped with species 4. No 28S sequences were obtained in this species.

- Species 6 contains one specimen for which only a COI sequence was obtained, and two specimens for which only a 28S sequence was obtained. These three specimens form a monophyletic group in all combined analyses. GMYC and mPTP on the Bayesian Inference of the combined dataset cluster these specimens together. mPTP on the Maximum Likelihood analysis of the combined dataset separates them. Without any common marker to link them, it difficult assess the status of these specimens as one or two species. It is decided to leave them as a single species until more data corroborating one or the other hypothesis can be obtained.

- Species 7 (69 specimens) is recovered in all COI analyses. It is lumped together with species 8 in GMYC on the Bayesian Inference of the combined dataset, and divided in two sister groups in mPTP on the Bayesian Inference of the combined dataset. It is divided in a number of singletons or groups of a few specimens, sometimes paraphyletic with species 8 in analyses of 28S and in mPTP on the Maximum Likelihood analysis of the combined dataset.

- Species 8 (42 specimens) is recovered in all COI analyses. It is lumped together with species 7 in GMYC on the Bayesian Inference of the combined dataset, and mostly recovered in mPTP on the Maximum Likelihood Inference of the combined dataset. It is divided in a number of singletons or groups of a few specimens, sometimes paraphyletic with species 7 in analyses of 28S and mPTP on the Bayesian inference of the combined dataset.

- Species 9 (5 specimens) is recovered in all COI analyses and combined analyses but for GMYC with single threshold on the Bayesian Inference of the combined dataset where it is lumped with species 10. Is also lumped with species 10 in all analyses of the 28S datasets.

- Species 10 (11 specimens) is recovered in all COI analyses and combined analyses but for GMYC with single threshold on the Bayesian Inference of the combined dataset where it is lumped with species 9. Is also lumped with species 9 in all analyses of the 28S datasets.

- Species 11 (2 specimens) is recovered in all COI analyses and combined analyses but for GMYC with single threshold on the Bayesian Inference of the combined dataset where it is lumped with species 12. Is also lumped with species 12 in all analyses of the 28S datasets but for GMYC with multiple threshold.

- Species 12 (21 specimens) is recovered in all COI analyses and combined analyses but for GMYC with single threshold on Bayesian Inference of the combined dataset where it is lumped with species 11. Is also lumped with species 11 in all analyses of the 28S datasets but for GMYC with multiple threshold.

- Species 13 (4 specimens) is recovered in all COI analyses and all combined analyses. No 28S sequence was available for this species.

- Species 14 (2 specimens) is recovered in all COI analyses and mPTP on both the Maximum Likelihood and Bayesian Inference on the combined dataset. It is lumped with species 1, 2, 3, 15 and 16 in mPTP on the Maximum Likelihood analysis of 28S, and with species 3 only in GMYC and mPTP on the Bayesian Inference of 28S and GMYC on the Bayesian Inference of the combined dataset

- Species 15 and 16 are each composed of a unique specimens for which both COI and 28S sequences were obtained. They are recovered in all analyses but for mPTP on the

Maximum Likelihood analyses of 28S where they are lumped together with species 1,2,3 and 14.

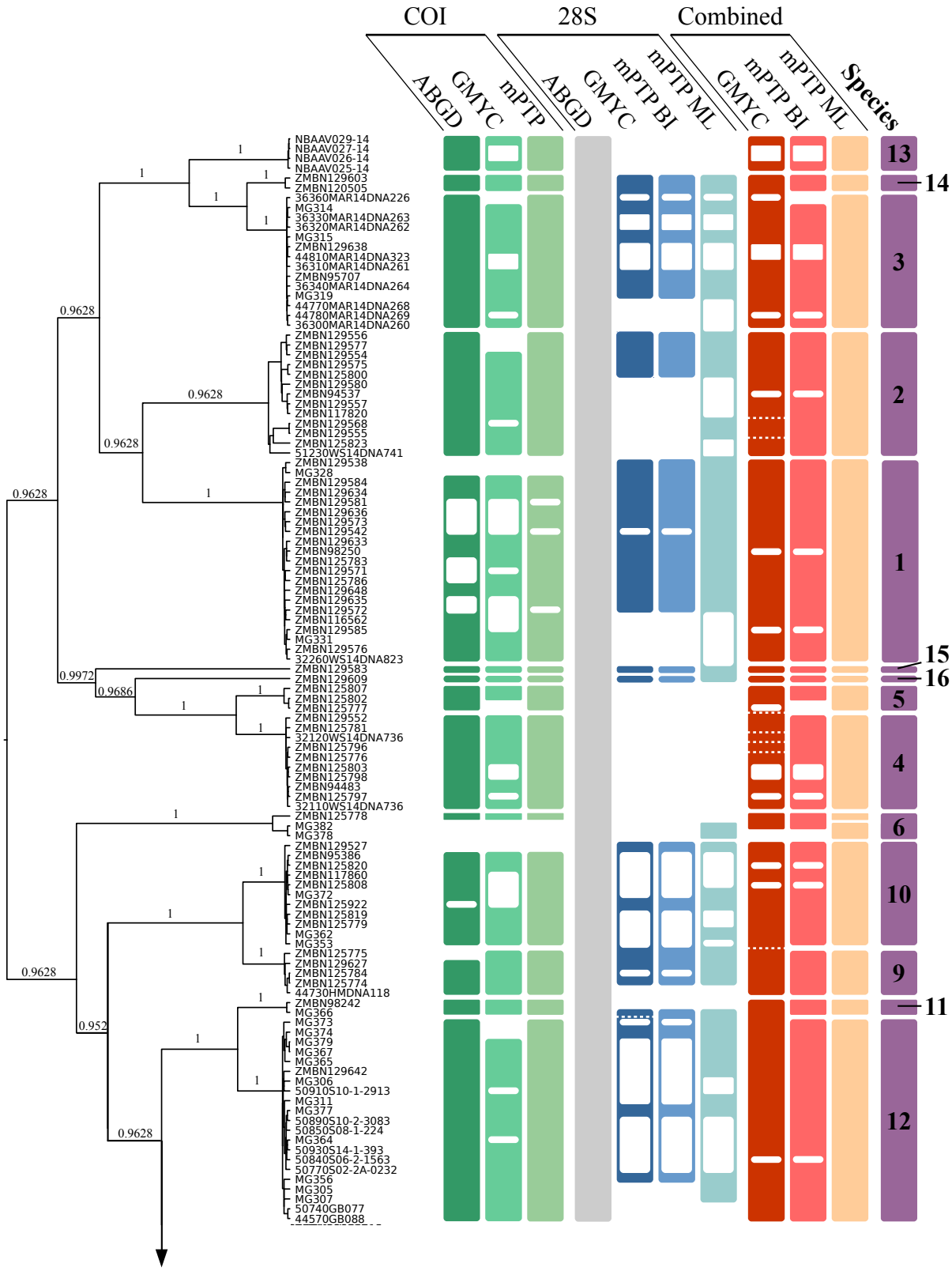

COI
28S
Combined
ABGD
GMYC
mPTP
ABGD
GMYC
mPTP BI
mPTP ML
GMYC
mPTP BI
mPTP ML
Species
NBAAV029-14
NBAAV027-14
NBAAV026-14
NBAAV025-14
ZMBN129603
ZMBN120505
36360MAR14DNA226
MG314
36330MAR14DNA263
36320MAR14DNA262
MG315
ZMBN129638
44810MAR14DNA323
36310MAR14DNA261
ZMBN95707
36340MAR14DNA264
MG319
44770MAR14DNA268
44780MAR14DNA269
36300MAR14DNA260
ZMBN129556
ZMBN129577
ZMBN129554
ZMBN129575
ZMBN125800
ZMBN129580
ZMBN94537
ZMBN129557
ZMBN117820
ZMBN129568
ZMBN129555
ZMBN125823
51230WS14DNA741
ZMBN129538
MG328
ZMBN129584
ZMBN129634
ZMBN129581
ZMBN129636
ZMBN129573
ZMBN129542
ZMBN129633
ZMBN98250
ZMBN125783
ZMBN129571
ZMBN125786
ZMBN129648
ZMBN129635
ZMBN129572
ZMBN116562
ZMBN129585
MG331
ZMBN129576
32260WS14DNA823
ZMBN129583
ZMBN129609
ZMBN125807
ZMBN125802
ZMBN125777
ZMBN129552
ZMBN125781
32120WS14DNA736
ZMBN125796
ZMBN125776
ZMBN125803
ZMBN125798
ZMBN94483
ZMBN125797
32110WS14DNA736
ZMBN125778
MG382
MG378
ZMBN129527
ZMBN95386
ZMBN125820
ZMBN117860
ZMBN125808
MG372
ZMBN125922
ZMBN125819
ZMBN125779
MG362
MG353
ZMBN125775
ZMBN129627
ZMBN125784
ZMBN125774
44730HMDNA118
ZMBN98242
MG366
MG373
MG374
MG379
MG367
MG365
ZMBN129642
MG306
50910S10-1-2913
MG311
MG377
50890S10-2-3083
50850S08-1-224
MG364
50930S14-1-393
50840S06-2-1563
50770S02-2A-0232
MG356
MG305
MG307
50740GB077
44570GB088
1
0.9628
0.9972
0.9686
0.952
13
14
3
2
1
15
16
5
4
6
10
9
11
12

Figure 5: Species delimitation in Norwegian *Chaetozone*: From left to right: Bayesian tree from the combined dataset; Results of the different analyses on the COI datasets (green), 28S datasets (blue) and combined datasets (red); Final species hypotheses. White indicates missing data. Grey bars indicate division in a high number of singletons or groups of few specimens. Posterior probabilities are indicated above branches.

3.2 Morphological and Geographical Analyses

In total, 9 morphogroups could be identified in the material. Each one of the genetic species 1, 3, 5, 6, 11 and 12 described above presents a unique combination of diagnostic characters allowing its morphological identification. The species 7 and 8 together form a seventh morphogroup or species complex. The species 2, 4 and 13 together form an eighth morphogroup or species complex. The species 9 and 10 together form a ninth morphogroup or species complex.

Two of the species complexes above can be further delimited by geographical analyses. Species 7 and 8 have different distribution areas, which allow their identification to species. Though species 2 and 4 are present in the same localities, species 13 lives in a different area at a different depth, which allows its identification to species.

Species 14, 15 and 16 were revealed in later analyses and the vouchers of species 15 and 16 were not examined and are not described here. The unique voucher of species 16 could be superficially examined and present a distinct morphology from all other species but is not described here.

In total, 11 genetic species are identifiable using to a combination of morphological and geographical data.

Only one species could be assigned a name. The name *Chaetozone setosa* is assigned to species 8.

A diagnosis or description of each species previously recorded in Norway is given first. A brief description of the different species or species complexes found in this study is then given.

Chaetozone Malmgren, 1867

Chaetozone Malmgren, 1867: 96, pl.14, Fig: 84; Chambers 2000: 588-589; Blake 2015: 504; Blake 2018: 69.

Type species - *Chaetozone setosa* Malmgren, 1867, by monotypy.

Diagnosis – (From Blake 2018: 69). "Prostomium blunt to conical, peristomium elongate to short, usually lacking eyespots, with a pair of small nuchal slits or depressions at posterior edge; with a single pair of grooved dorsal tentacles arising from posterior edge of peristomium, or sometimes more posterior on an asetigerous anterior segment, or rarely on an anterior setiger. First pair of branchiae arising from an achaetous segment or first setiger; sometimes with first two pairs of branchiae on a single anterior segment. Body usually expanded anteriorly and narrowed posteriorly, rarely with middle or posterior body segments beaded or moniliform; posterior end often expanded. Setae include capillaries on most setigers and sigmoid acicular spines in neuropodia and notopodia, with spines typically concentrated in posterior segments forming distinct cinctures with spines carried on elevated membranes; cinctures with few to many spines sometimes encircling entire posterior end, accompanied with none to many alternating capillaries; bidentate spines sometimes present in juveniles or occasionally in ventral-most position of far posterior setigers of adults, accompanying unidentate spines in cinctures; some species with long, natatory-like capillary notochaetae, sometimes limited to gravid individuals. Pygidium a simple lobe, disk-like, or with long, terminal cirrus."

Remarks – SEM revealed the presence of ciliated branchiae on all the species examined with this method. The branchiae usually appear divided in two parts. They are cylindrical and horizontally wrinkly in their proximal half, and flattened in their distal half, with a row of cilia along each edge (Fig. 7 B). One mention of these cilia is made for *Chaetozone* by De Saint-Joseph (1894). There are no references about the function of these cilia. Small, round ciliated organs were revealed using SEM on all the specimens. They are around 4 to 6 µm, present on the surface of nearly the whole body and particularly abundant on the head (Fig. 7 C-D). Their function is unknown.

3.2.1 Species Previously Recorded in Norway

Chaetozone (?) *abranchiata* (Hansen, 1879)

Cirratulus (?) *abranchiata* Hansen, 1879: 10-11, Pl VII Fig 3-7.
Chaetozone (?) *abranchiata* : Moore, 1903: 470-471.

Description – (From Hansen 1882: 40). "Three specimens, measuring 14mm in length and 3mm in breadth. Body, oblong and pointed at the extremities, built up of slender segments, bearing long, delicate bristles. The head a small obtuse cone, without either eyes or appendages; posterior to the head 1 broad and 2 narrow, naked segments, which along with the head constitute an acuminate projection on the posterior broader bristle-bearing segments. The buccal aperture on under surface of the head. Each bristle bearing segment having on either side an elongate projection, furnished with a small mammilliform tubercle both at the upper an lower extremity, in which are seen the two fascicles of exceedingly long, slender and perfectly smooth capillary bristles. There is no separate pharynx; the intestine passes straight through the body to which it is attached by slender membranous filaments. No blood-vessels were detected, or segmental organs.

Of the branchiae distinguishing this genus, there is indeed not a trace in the animal here described; but it general structure nevertheless brings it nearest to the Cirratulidae."

Remarks – Moore (1903) examined material from the Pacific coast of Japan, that he judged similar to that of Hansen's from the Norwegian Sea, but placed them within *Chaetozone*. This placement was obviously uncertain. The type material was not available for this study and neither Hansen's nor Moore's materials were examined. The status of this species is still uncertain. None of the Norwegian material examined fit Hansen's description.

Chaetozone caputesocis (De Saint-Joseph, 1894)

Heterocirrus caput esocis De Saint-Joseph, 1894: 53-54, Pl. III, Fig. 58-60.
Chaetozone caputesocis Petersen 1999.

Description – (Translated from De Saint-Joseph, 1894: 53-54). " Often collected during dredging. The body slightly yellowish brown, 15 to 17mm long and 0.8mm large for 84 segments. The very characteristic head has the shape of a pike snout slightly flattened at the front with two big black eyes placed on the posterior part, on the cerebral ganglions. On each side of the head, slightly lower than the eyes and near to the limit of the the buccal segment, a small vibrating depression opens. The buccal segment, elongated and achaetous, is followed by a second achaetous segment, barely distinct from it and that bears on its dorsal part two big muscular tentacles with a ciliated groove, 1.70 mm long, reminding of the tentacles of the spionids. Under each tentacle there is a branchial filament three times thinner which has two vessels, while the tentacles have only one as we previously said. The short and bilobed trunk comes sometimes out of the mouth when the animal is compressed. The 3rd segment, which is chaetigerous, and the the next have nearly all, but for the 14-26 last, shortly above the dorsal chaetigerous mount, a pair of ciliated branchial filaments, thin and long, lacking more often when going further from the head. Each segment have in their upper mount 8-9 very thin capillary chaetae, to which joins in the last 23 segments 1 to 4 acicular chaetae, less curved and shorter than the acicular crotchets from the ventral mount described next. The lower mount has in the 10 to 12 first segments simple chaetae thicker than that of the dorsal mount and slightly curved, which, in the next segments, take the shape of shorter acicular chaetae, slightly more curved and ending in a little hook, barely marked; first there are 2, then 5 to 7, and from the 30th segment there are 9; everywhere these chaetae alternate with capillary chaetae.

The anal segment, smooth on the dorsal side, is divided in five lobes on the ventral side (Fig. 60). The intestine is full of sand.

I often find the *H. caput esocis* full of grey eggs or spermatozoa. The eggs, that have a diameter of 0.12mm, show from the 14th segment and lack in the last 18.

The specimens arrived at perfect maturity have in their upper mount 4 to 5 chaetae thinner and four times longer that the others.

The pair of big segmental anterior organs, 0.96mm long, each composed of two branches interiorly ciliated, curved and joined together, occupying the five first chaetigerous segments, opens on each side of the body on the ventral side of the first chaetigerous segment. One of these branches, colourless, opens on a vibrating auricle in the inside of the body at the second achaetous segment and the other, slightly brown, communicates with the exterior through a ciliated pore.

This species is neighbour to the *Heterocirrus multibranchis* Gr., but this one only has capillary chaetae."

Remarks – This is a direct translation of the original description by De Saint-Joseph and his description was not interpreted in terms of modern knowledge and terminology. The paragraph at the end describing "the pair of big segmental organs" is particularly confused and convoluted in the original work.

The status of this species is unclear (Woodham & Chambers, 1994). This species was moved to *Chaetozone* by Petersen (1999), in a table's footnote, without further detail than: "The species is in good agreement with the genus *Chaetozone* as defined by Blake (1996)". Though the type material of this species was not examined during this study, none of the Norwegian material examined seems to fit its description or accompanying illustrations.

Chaetozone christiei Chambers, 2000

Chaetozone christiei Chambers, 2000: 592-594, Fig. 2.

Material examined – Three specimens. North Sea: Holotype, 55.32'N, 1.36'W, 3 November 1982 (1, NMSZ.1998. 122), paratypes, (2, NMSZ.1998.123).

Description – (From Chambers, 2000). "Largely based on the holotype (NMSZ, 1998.122) and other material from the type locality. Maximum body length 12 mm for 110 chaetigers. Body surface smooth, narrowly pointed anterior region widens to mid-body and posterior region. Ventral surface flattened with a longitudinal groove. Anterior dorsal surface rounded, gradually flattening posteriorly. Segments narrow and crowded in anterior region, difficult to distinguish, becoming wider and more obvious in posterior region. Segment divisions in posterior 30 segments slightly narrow 4-5ths width of segment, to give stretched 'concertina-like' appearance. Color of material preserved in alcohol creamy white with iridescent sheen.

Prostomium conical with long acutely pointed tip and a pair of shallow nuchal grooves above the mouth. No eyes. Peristomium achaetous, smooth, partially divided into three annuli, with a ventral mouth, pair of grooved tentacular palps originating from dorsal surface of posterior annulus extending approximately a third of the total body length. The first pair of branchiae arising on the first chaetiger and only slightly posterior and lateral to the bases of the tentacular palps, and extending approximately a third of the body length. Second pair of branchiae arising behind first pair of branchiae on second chaetiger and dorsal to notopodial lobes. Branchiae occurring on every chaetiger in anterior region, occurring less regularly in mid-body region and absent posteriorly from approximately 40th segment. Branchial filaments simple.

Parapodia all biramous with notopodial and neuropodial chaetae, parapodial lobes flattened ridges hardly extending from the body wall. Notopodial and neuropodial lobes separated in mid-lateral line with chaetae arranged in a single fan-shaped row. Chaetae directed posteriorly and laterally in anterior and mid-body region and both anteriorly and posteriorly in the posterior region.

Chaetae all simple, unidentate of three types: (1) awl-shaped capillaries in both notopodia and neuropodia on anterior body region to approximately 50th segment; (2) fine capillaries, 2–3 times longer than awl-shaped capillaries, 3–4 present in notopodia and neuropodia from approximately 20th chaetiger to end of body; (3) spines, 2–3 present in notopodia and neuropodia from 30th segment; 4–5 spines alternating with capillaries in notopodia and neuropodia in posterior body from approximately 50th segment. Pygidium rounded flattened leaf-like lobe, anal opening dorsal."

Remarks – The holotype of *Chaetozone christiei* is conform to the original description by Chambers (2000). The first pair of branchiae arise from the first chaetiger, which is also the first segment, just under the tentacles. The tentacles arise from the posterior margin of the dorsal crest (hinted at but not clearly described in the original description), and slightly overlapping the first segment. A thin marked dorsal groove is present on the anterior half of the specimen. One of the paratypes is also close to the original description. On the second paratype however, another pair of branchiae is present beside and slightly anterior to the tentacles and anterior to the first chaetiger. It is unclear however whether these branchiae arise between the peristomium and the first chaetiger, which would then also be the first segment, or whether they arise from an indistinct achaetous first segment. This second paratype is more similar to a population described by Christie (1985) from Holy Island (Susan Chambers, personal communication).

Chaetozone gibber Woodham & Chambers, 1994

Chaetozone gibber Woodham & Chambers, 1994: 308-310, Fig. 1& 3.

Material examined – Three specimens. Channel: Paratypes (3, NMSZ.1992.88).

Description – (From Woodham & Chambers 1994). "Length of body up to 20 mm for approximately 200 segments. Body surfaces smooth; dorsal surface swollen anteriorly between chaetigers 7-30 approximately, giving a characteristic hump-backed appearance; ventral surface flattened with a longitudinal groove; posterior region bluntly tapered, dorso-ventrally compressed with lateral surfaces somewhat flattened giving almost rectangular shape in cross section. Segments broad, short and crowded in anterior region, becoming narrower and longer posteriorly, without intersegmental constrictions. Colour of preserved material (in alcohol) creamy white.

Prostomium conical with acutely pointed tip. Pair of subdermal eyes, round to elongate, near lateral posterior margins; shallow nuchal groove below and behind each eye. Peristomium achaetous, smooth, partially divided into 3 annuli, pair of grooved tentacular palps originating from dorsal surface of posterior annulus, measuring approximately 1/3 of body length. First pair of branchiae arising immediately posterior to tentacular palps, on first chaetiger. Mouth ventral.

Parapodia all biramous with notochaetae and neurochaetae; parapodial lobes flattened mounds, extending further from the body posteriorly. Pair of branchiae arising dorsal to notopodial lobes on every chaetiger in anterior region, occurring less regularly in mid-body region and absent posteriorly (precise occurrence of branchiae uncertain as frequently only scars remain in preserved specimens); branchial filaments simple, cylindrical and smooth, of variable length up to approximately 2mm, thickest and longest in anterior region.

Notopodia and neuropodia slightly separated with chaetae arranged in single dorsal-ventral rows. Chaetae directed laterally in anterior and mid-body regions and more anteriorly in

posterior third of body. Chaetae of three types: i) slender capillaries in both rami of all chaetigers; ii) stout awl-shaped capillaries in notopodia between approximately segments 40 and 90 iii) spines with unidentate tips in notopodia from mid-body (segments 90-100) to end of body and in neuropodia from anterior region (segments 50-80) to end of body; number of spines in each ramus increasing posteriorly from 1 to 4; each ramus in posterior region of body typically with four unidentate spines and four slender capillaries alternating with each other; left and right chaetal rows well-separated, spines not forming complete rings around segments.

Pygidium with small ventral lobe."

Remarks – Three specimens designated as paratypes of C. gibber were made available for this study. All three of them were very fragile, in several pieces and in overall poor condition. The anterior end of one of them could not be found. Detailed examination was made difficult by their fragility, but one of them seemed to fit the original description by Woodham and Chambers (1994).

Chaetozone jubata Chambers, 2003

Chaetozone jubata Chambers, 2003: 43-45, Fig. 2.

Material examined – Two specimens. Faroe-Shetland channel: Paratypes, 61.5.57'N, 2.4093'W, July 1996, 710 m (2, NMSZ.1999.237.4-5).

Description – (From Chambers, 2003). "Mostly based on holotype (NMSZ.1999.237.0001) and paratype material (NMSZ.1999.237. 0002 and 0003). Body length up to 8 mm for about 50 chaetigers. Body surfaces smooth; anterior and mid-body regions wider than posterior region; ventral surface rounded with longitudinal groove; dorsal surface flattened in anterior and mid-body regions. Chaetigers in anterior and mid region easily distinguished; posterior 10 chaetigers well-separated with obvious constrictions between them. Colour of preserved material (in alcohol) creamy white.

Prostomium conical with pair of shallow nuchal grooves above mouth (not seen using light microscopy but obvious with scanning electron microscopy). No eyes. Peristomium achaetous, smooth and very indistinctly divided into three annuli; pair of grooved tentacular palps (only bases present in holotype) originating from dorsal surface of posterior margin of posterior annulus. Mouth ventral. First pair of branchiae arising on first achaetous segment and directly behind palps. Parapodia all biramous with notochaetae and neuro-chaetae. Pair of branchiae arising dorsal to notopodia and occurring on every chaetiger in anterior region, more sporadically in mid-body; absent in posterior body region. Branchial filaments simple. In anterior region, parapodial lobes low ridges hardly extending from body wall; notopodial and neuropodial lobes very slightly separated in mid-lateral line with chaetae arranged in fan-shaped rows. In posterior region, parapodial lobes very thin and antero-posteriorly flattened. Chaetae all simple, unidentate of three types:

1. Very long capillaries, length two to three times anterior body width, width at base approximately 4.2 μm; 4–10 present in notopodia only from second chaetiger to about 25th chaetiger, gradually reducing in number to 1–2 in posterior chaetigers.

2. Short capillaries, less than a quarter the length of long capillaries, width at base approximately 4.2 μm; 1–2 in notopodia and 4–8 in neuropodia from 2nd chaetiger to end of body.

3. Spines, width at base approximately 6.3 μm, present in notopodia and neuropodia from about 25th chaetiger, alternating with capillaries; gradually increasing from 2–4 in the mid-body region to 12–14 in each ramus of posterior chaetigers.

Pygidium with ventral, thin, scoop-shaped lobe (Fig. 2D); anal opening terminal."

Remarks – The paratypes were only superficially examined but seem conform to this description.

Chaetozone setosa Malmgren, 1867

Chaetozone setosa Malmgren, 1867: 96, pl.14, Fig: 84; Chambers 2000: 589–591, Fig. 1; Blake 2015: 504-507, Fig. 1&2.

Material examined – Svalbard: lectotype, Isfjord, 06 June 1864, 55m (1, SMNH 1493-03), paratypes (172, SMNH 1493-04 to 175).

Description – (From Blake 2015: 504-507). "A moderately sized species, lectotype a complete ovigerous female, 20.2 mm long, 1.7 mm wide for 90 setigerous segments; complete paralectotypes up to 28 mm long, 2 mm wide for 94 setigerous segments.

Body of most preserved specimens curled into a C-shape, but not strongly coiled. Body thickened in middle, narrowing anteriorly and posteriorly. Anterior setigers short, wide, becoming up to 2 times longer in middle body segments, but always narrower than wide except for some segments on ovigerous specimens. Dorsal groove weakly developed, narrow, often limited to anterior setigers; ventral groove well-developed, visible along most of body, absent in far posterior cinctured segments. Color in alcohol brown or grey; no distinct pigmentation.

Prostomium conical, narrow, bluntly pointed anteriorly; eyes absent; nuchal organs narrow diagonal slits, not pigmented. Peristomium with two large, distinct rings best visible laterally, overlain dorsally by swollen peristomial crest with peristomial annulations weakly developed or not apparent on crest, crest overlapping prostomium anteriorly, narrowing posteriorly, extending to near anterior margin of achaetous segment. Dorsal tentacles arising from notch at posterior margin of peristomium; first pair of branchiae typically positioned posterior to tentacles on posterior margin of incomplete achaetous segment; second pair of branchiae on setiger 1.

Setiger 1 of approximately same size as preceding achaetous segment and subsequent setigers; parapodial lobes reduced, inconspicuous ridges in anterior and middle setigers; enlarged with elevated ridges in posterior cinctured segments bearing conspicuous armature;

posterior segments separated by deeply cut intersegmental furrows and with highly elevated membranous podial lobes from which spines and capillaries emerge, forming full cinctures; notopodial spines directed ventrally, neuropodial spines directed dorsally.

Noto- and neurochaetae from setiger 1, setae of anterior segments all limbate capillaries, numbering about 7–10 per fascicle; long, natatory-like notochaetae present from about setiger 18–21, continuing posteriorly. Capillaries thin throughout, some with fibrils along edge, but not consistent; natatory-like setae capillaries, very long, flattened in cross section numbering 2–5 per notopodium mainly restricted to lower part of setal fascicle. Based on data from 16 types in Table 1, with 63–93 setigerous segments (mean = 83.9 ± SD 7.7), acicular spines begin from setiger 35–65 in neuropodia (mean = 51.7 ± SD 7.6) and setiger 43–71 in notopodia (mean = 58.7 ± SD 7.1). Lectotype with neuroacicular spines from setiger 57 and notoacicular spines from setiger 63. Spines numbering 1–3 at first, accompanied by narrow limbate capillaries, increasing to 10–13 in each ramus in fully developed and complete posterior cinctures, with 20–26 spines on a side with alternating capillaries; spines sometimes overlapping at dorsal midline; when long natatory-like setae occur within posterior cinctures, they accompany ventral-most notopodial spines and sometimes dorsal-most neuropodial spines. Spines brownish or brassy in appearance, round in cross section with weak narrow notch at point of emergence, with slightly curved or sigmoidal shape narrowing to a bluntly pointed tip; shafts with thick borders and fine internal striations.

Last few cinctured setigers tapering to narrow posterior end; pygidium with terminal anus and small flattened ventral lobe."

Remarks – The lectotype and paratypes agree with that description. The dorsal crest however is rarely as distinct and prominent as on Blake's (2015, Fig. 1,2) illustrations.

Chaetozone vivipara (Christie, 1984)

Tharyx vivipara Christie, 1984: 70, Fig. 1&2.

Chaetozone vivipara Petersen, 1999.

Material examined – 29 specimens. North Sea: holotype, 55.06'N, 1.257'W, 4 April 1978, 3.5-7m (1, BMNHN1984.1), paratypes (10, BMNH 1984.2-11); paratypes 55.84'N, 1.31'W, 31 October 1978, 9-13m (10, BMNH 1984.12-21); paratypes, 55,202'N, 1.349'W, 31 October 1978, 1-4m (4, BMNH 1984.22-25); paratypes, 54.378'N, 1.97'W, 24 September 1981 (2, BMNH 1984.26-27); paratypes, 53.353'N, 0.50'W, July 1982, 3m (2, BMNH 1984.28-29).

Description – (From Christie, 1984: 70). "The holotype is 8.5mm long and 1.0 mm wide, with 44 setigers and is complete except for some missing palps and branchiae. The body is short and spindle-shaped; it is broadest in the middle and tapers anteriorly and posteriorly. Prepygidial segments are not inflated. The prostomium is a small, acutely pointed, lobe without eyes. The buccal region consists of three asetous segments; segmentation is visible laterally but the dorsal surface is slightly inflated and smooth. A pair of tentacular palps arises on the posterior margin of segment III. When attached, the palps are relatively short and rarely exceed one half of the body length. Branchiae begin on segment IV; branchial scars on each segment indicate their presence along the entire body. They are attached directly above the notopodial idge and there is never more than one pair to each segment.

Anterior and posterior segments are short and narrow whereas middle segments are longer and wider. Notopodia and neuropodia are separate, throughout the body; all setae are short capillaries. Anterior and middle segments possess slender capillary setae with finely tapering tips; posterior segments possess slightly thicker capillary setae with abruptly tapering tips. In anterior segments, the notopodia and neuropodia possess 6-8 an in posterior segments 3-6 setae. The pygidium is short and round with a dorsal anus and a small ventral lip.

The middle segments of mature specimens are swollen due to the presence of numerous embryos within the coelom. Just prior to the release of the embryos, the epithelium becomes very thin and in preserved specimens is often ruptured revealing the embryos beneath."

Remarks – The holotype fits the description an illustration by Christie (1984). However, he describes the peristomium as three achaetous segments, rather than with three annular rings which based on Day (1967) is not correct (see discussion). He also states that the first pair of branchiae arise from "segment IV" (first segment), but the holotype and some of the paratypes show clear branchial scars arising from the posterior margin of the peristomium, or between the peristomium and the first segment, just below the tentacles. These scar is sometime only present on one side, like on the holotype. Some of the paratypes lack this pair of branchiae. It is unknown whether this shows the presence of several species or intraspecific variation.

This species was moved to the genus *Chaetozone* by Petersen (1999), in a table's footnote with the following explanation: "Posterior segments of smaller specimens contain slender acicular chaetae alternating with the capillaries, as in *Chaetozone*; The species has also been identified as *Chaetozone* because of its general appearance." Though the chaetae in the posterior segments are spread in a distinct fascicle or armature creating a slightly elevated membrane and low incomplete cinctures, no spine or chaetae thicker than the others were observed in the type material.

The parapodia of this species are characteristic in that each neuropodia and notopodia is a short, small rounded lobe rather than a low straight mount or ridge.

Chaetozone (?) *zetlandica* (McIntosh, 1911)

Chaetozone zetlandica McIntosh 1911: 161

Chaetozone zetlandica Southern 1914: 115, Pl. 12-13, Fig. 29 A-K.

Caulleriella zetlandica Woodham & Chambers 1994: 311, Fig. 2 & 4.

Material examined – One specimen. St Magnus Bay, Shetland, UK: holotype, 170m (1, BMNH 1921.5.1.3232).

Description – (From Woodham & Chambers 1994). "Length of body up to 24 mm for approximately 154 segments. Body surfaces smooth, slightly iridescent. Dorsal surface of anterior half of body rounded, becoming flatter posteriorly ; ventral surface flattened with longitudinal groove; posterior region bluntly tapered, dorso-ventrally compressed to give an oval shape in cross section. Segments of relatively even length, without intersegmental constrictions.

Prostomium conical with long, acutely pointed tip. Pair of subdermal eyes, round to elongate, near lateral posterior margin; shallow nuchal groove posterior to each eye. Peristomium achaetous, smooth, partially divided into three annuli, pair of tentacular palps originating from dorsal surface of posterior annulus (only stumps present on all specimens). First pair of branchiae originate immediately posterior to tentacular palps, on first chaetiger. Mouth ventral.

Parapodia all biramous with neurochaetae and notochaetae; parapodial lobes flattened mounds, extending further from body posteriorly. Pair of branchiae arising dorsal to notopodial lobes and occurring on every chaetiger in anterior region then irregularly in mid-body and posterior regions (precise occurrence of branchiae uncertain as frequently only scars remain in preserved specimens); branchial filaments simple, smooth, of variable 1ength up to approximately 4 mm.

Notopodia and neuropodia slightly separated, with chaetae arranged in single dorsal-ventral rows, directed latero-posteriorly in anterior and mid-body regions and more anteriorly in

posterior third of body. Chaetae of 5 types: i) slender capillaries in notopodia only in ail chaetigers; ii) stout awl-shaped capilIaries of medium length, occurring in both rami of all chaetigers; iii) short stout awl-shaped capillaries, in mid-body neuropodia only; iv) spines with unidentate tips in neuropodia of posterior region; v) spines with bidentate tips in neuropodia of juvenile or small specimens only. Spines with bidentate tips found in individuals 4-5 mm long, although those in dorsal position of same neuropodia approach unidentate forms. All spines in larger individuals with unidentate tips only.

Pygidium with small ventral button-like lobe."

Remarks – This species was originally described as *Chaetozone zetlandica* from a posterior fragment that is in poor condition and lacks most chaetae. One neuropodia is complete and shows spines arranged in a distinct armature on an elevated membrane. Nothing could be seen from the notopodia. Southern (1914) describes a number of whole specimens from Scotland he identified as *Chaetozone zetlandica* based on the original fragment from McIntosh. Woodham and Chambers (1994) also examined material from Scotland that they attributed to this species, but placed it in the genus *Caulleriella*. They formed this new combination as they did not see any spines on the notopodia, and observed some bidentate spines in neuropodia of small specimens. They however show what they called "awl-shaped" capillary chaetae, as thick as the acicular spines, but longer, and indeed terminating into thin capillary instead of having a blunt tip. These "awl-shaped" capillary chaetae are also shown arranged in a distinct armature, with alternating capillary chaetae on an elevated membrane. As Blake (2018) states that the chaetae of *Caulleriella* are not arranged in cinctures and as the "awl-shaped" capillary chaetae of this species might indeed just be spines, *Caulleriella zetlandica* is strongly suspected to actually be *Chaetozone* zetlandica. Moreover, two of the species found in this study (9 and 10) closely resemble *Caulleriella zetlandica* (and indeed some specimens were identified as such in the collections) and are sister to some species clearly fitting the diagnosis of *Chaetozone*. In particular, they show the same type of long spines thinning into a capillary-like shape distally as is figure in Woodham and Chambers (1994).

The materials examined by Southern (1914) and Woodham and Chambers (1994) has however not been examined in this study and in any case the status of *Chaetozone* (?) *zetlandica* needs to be re-assessed. As stated previously, the diagnosis of either or both *Chaetozone* and *Caulleriella* might need revision.

3.2.2 Species Found in Norwegian Waters

Species 1

Material examined – Six specimens. Norwegian coast and shelf: 59.56729'N, 5.21568'E, 26 April 2017, 328m (1, ZMBN125786); 62.35117'N, 6.16178'E, 21 July 2012, 243m (1, ZMBN125783); 60.2593'N, 5.13703'E, 13 June 2017, 248m (1, ZMBN116562); 61.37705'N, 2.11215'E, 280m (1, ZMBN98250); 59.99'N, 5.35'E, 27 June 2007, 250m (2, MG332, MG334, NTNU-VM unregistered).

Description – A big species, ~2cm long, ~1.5mm wide ~56 segments. Body elongate, larger anteriorly, narrowing towards the head and in posterior half, oval to flattened oval in cross section anteriorly, round in cross section posteriorly. Anterior segments narrow and crowded, 5-6 times as high and wide as long, lengthening and enlarging progressively after the first 10-15 segments to two times as high as long in posterior segments. A light dorsal groove over the first 10-15 segments (Fig. 6 H).

Prostomium conical blunt, as long as peristomium, fused with peristomium. Peristomium short, long like 3 segments, without any rings, in continuity of prostomium, in large specimens much narrower than first segments giving the whole head a characteristic "drop shape" clearly set off the rest of the body. Nuchal organs lateral slits on anterior end of the peristomium. Paired tentacles on achaetous first segment, not completing on top, in large specimens, larger than peristomium but not as wide as second segments which can cover it on the side so that it is only "facing forward". 1st pair of branchiae on second achaetous segment, aligned with following ones. 2nd pair of branchiae on third chaetiger, dorsal to notopodia, subsequent branchiae similarly placed (Fig 6 A).

Parapodia biramous, low mount or ridges in anterior segments, developping into full cintures in posterior segments, with deep constrictions between the segments (Fig. 6 F,H).

Very long capillary chaetae present in notopodia from the 3rd-4t^{h} setiger until the 25th, segmented, each segment like a cylinder diagonally cut in cross section, difficult to see with light microscopy but obvious with SEM, ~7 in anterior notopodia (Fig. 6 B). Smooth short

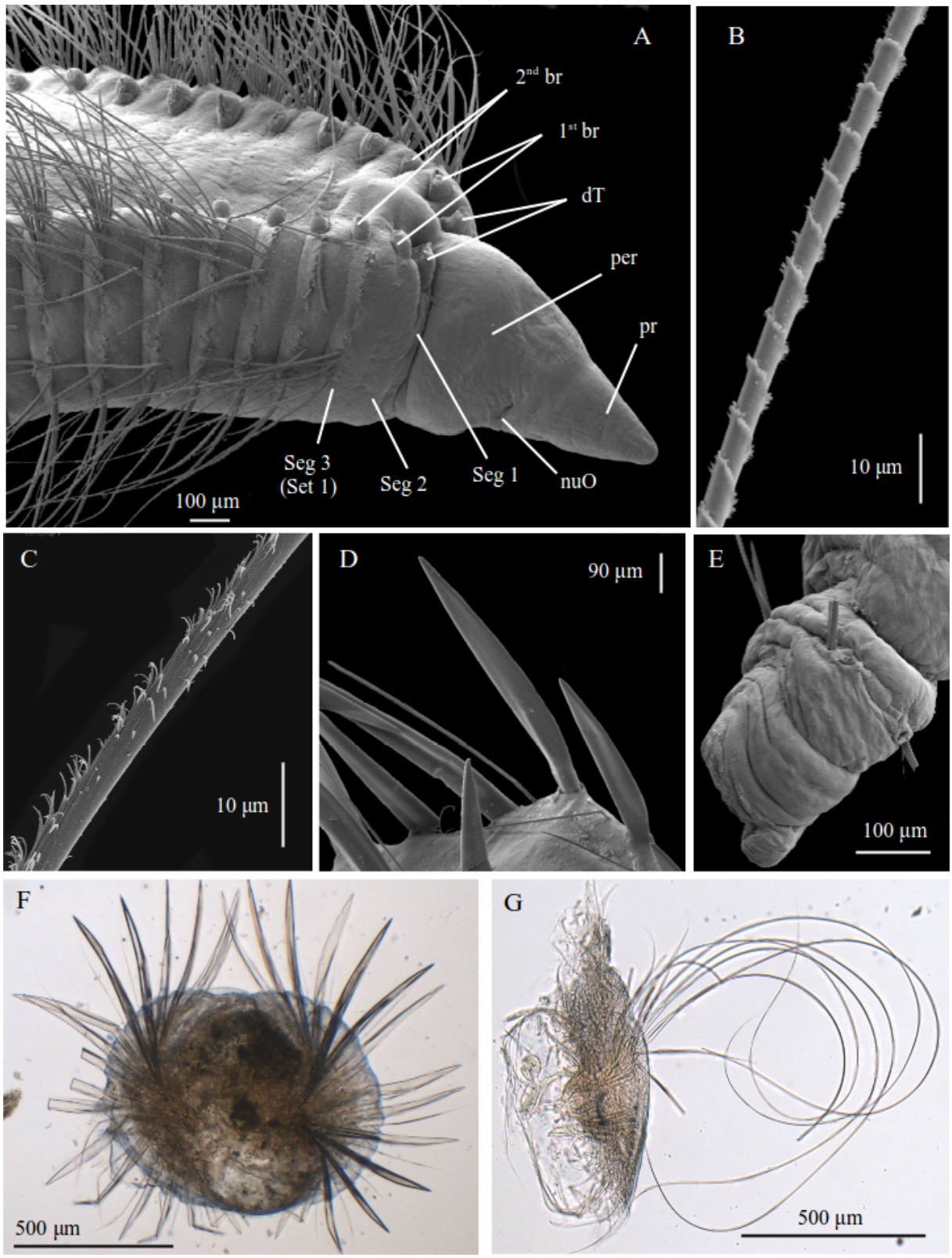
capillary chaetae present in neuropodia and notopodia of all setigers, ~7 to 12 in anterior neotopodia, ~12 in anterior neuropodia (Fig 6 C,G). Acicular spines long, with a broad flattened elongated leaf shaped blade, slightly folded along the length, up to 20 per parapodia in posterior segment with alternating short capillary chaetae, nearly totally encircling them, spines of left and right notopodia crossing over dorsum (Fig 6 D, F).

Pygidium with a rounded ventral lobe. (Fig. 6 E)

Methyl Blue staining pattern – None.

Remarks – The size and volumes of the head and the first segments varies in some specimens, which don't exhibit the characteristic "drop shaped" head and enlarged anterior segments shown on Fig. 6, or sometimes only slightly. The prostomium and peristomium are however always fused, and the pattern of implementation of the paired tentacles and firsts pairs of branchiae is always the same. This species is in that regard similar to species 2 and 4, and is distinct from them by its characteristics segmented chaetae.

This species is found on the Norwegian Coast ans shelf, offshore and in the Fjords, South of Trondheim around 200-300m deep.


A
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100 µm
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10 µm
D
90 µm
E
100 µm
F
500 µm
G
500 µm

Figure 6 - Species 1: A-E SEM. F-G, : light photography. A, head in lateral view; B detail of long segmented notocapillary; C, detail of smooth capillary; D, notopodial spine; E, Pygidium in lateral view; F cross section of posterior modified segment; G, anterior parapodia; H, full specimen in lateral view.

Species 2 & 4

Material examined – 12 specimens. Norwegian coast and shelf: Species 2: 61.42736'N, 7.47479’E, 18 November 2012, 332m (1, ZMBN125800); 62.48183'N, 4.46550’E, 10 March 2012, 211m (1, ZMBN125823); 61.0501’N, 5.40055’E, 03 May 2017, 1236m (1, ZMBN117820); 62.482'N, 4.466’E, 03 October 2012, (1, ZMBN94537); 61.11299'N, 5.14124’E, 22 July 2012, 354m (1, MG329). Species 1: 61.42736'N, 7.47479’E, 18 November 2012, 332m (3, ZMBN125796-125798); 61.21307'N, 5.03809’E, 14 July 2015, 379m (1, ZMBN 125776); 64.804'N, 10.111’E, 08 October 2013, 378m (ZMBN94483); 62.06827'N, 5.03811’E, 20 July 2012, 334m (1, ZMBN125781). 61.11299'N, 5.14124’E, 22 July 2012, 360m (2, MG326, MG333, NTNU-VM unregistered).

Description – This species are in all aspects similar to Species 1, but for the presence of smooth long chaetae instead of segmented long chaetae. Though none of the specimens available in these two species present the degree of enlargement of the first segments that can be observed in some specimens of species 1, there is too much intraspecific variability for these differences to be significant. The prostomium and peristomium in species 4 may also appear more distinctly separated than in the other species but not significantly so (Fig. 7).

Methyl Blue staining pattern – None.

Remarks – Species 2 and 4 are both found on the Norwegian coast and shelf, offshore and in the Fjords where they occupy a wide range of depth from around 200 to 1200m deep. They can sometimes be found at the same stations.

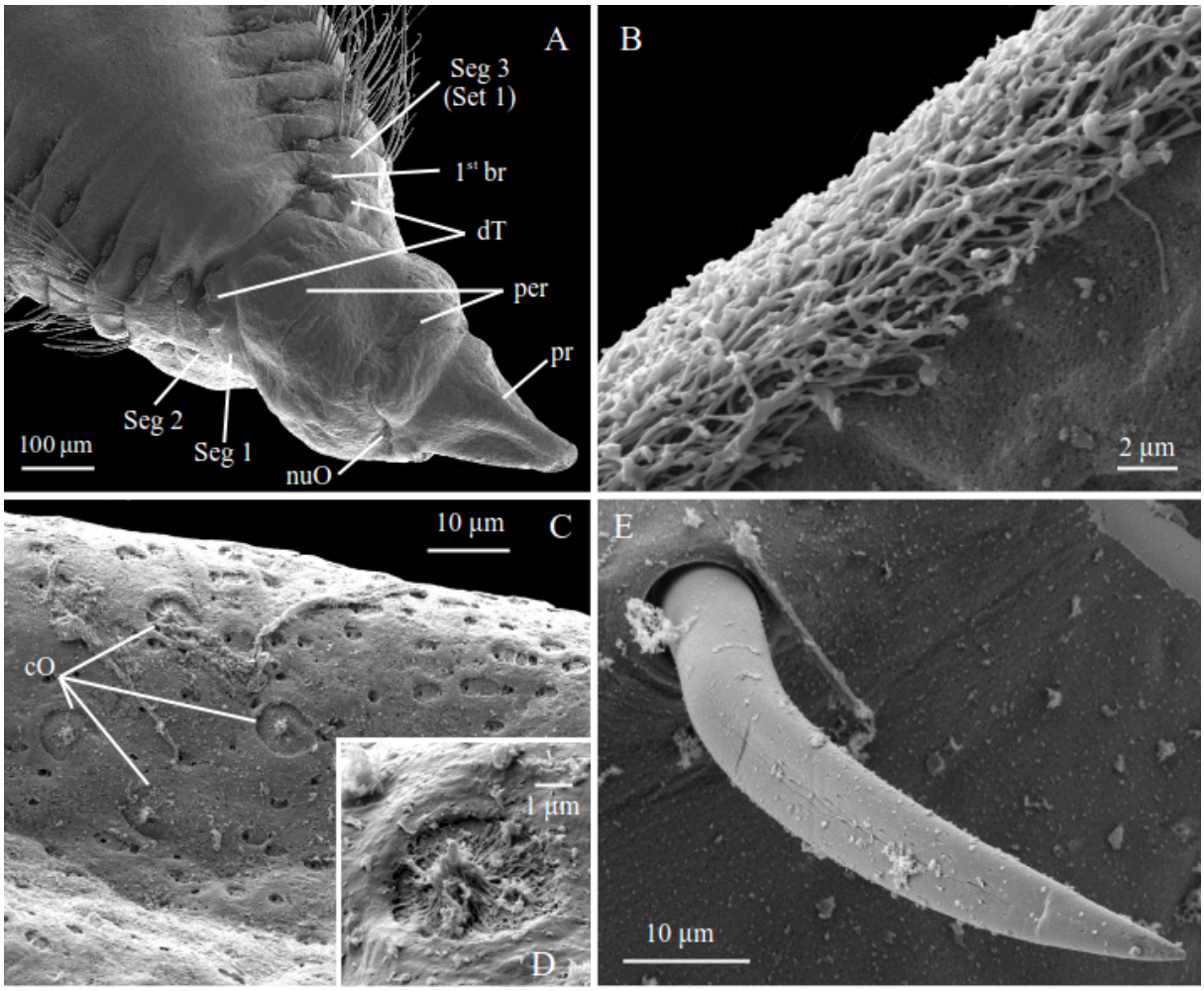

Figure 7 - Species 4: A-D SEM; A head in dorsal view; B detail of a branchiae lateral row of ciliae; C, detail of the head epidermis; D, detail of ciliated organ; E, neuropodial spine.

Species 3

Material examined – 13 specimens. Norwegian coast and shelf: 60.173'N, 5.003’E, 22 April 2011, 6m (1, ZMBN95707). Barents Sea: 71.056'N, 29.655667’E, 21 Avril 2014, 337m (9, MG316-324, NTNU-VM unregistered); 71.187833'N, 28.943167’E, 23 April 2014, 380m (2, MG312-313, NTNU-VM unregistered).

Description – A small species, 4-5mm long, 1/4mm large for 46 segments. Body elongate, without any distinct enlargement, rather round in cross section, flattening a bit in posterior half, anterior segments 4 times as high as long, posterior segments two times as high as long, posterior most segments developing in full cinctures. Dorsal groove on posterior half, ventral ridge all along (Fig. 8 A).

Prostomium conical as long as peristomium, twice as long as high. Peristomium short, long as two segments, sometimes appears partially divided in two rings, one anterior to the mouth and one bearing the mouth. Nuchal organs present on both sides, posterior to prostomium. Paired tentacle arising from first achaetigerous segment, very distinct from peristomium. First pair of branchiae arising from second achaetigerous segment, often undistinct from the first and third segments. 2nd pair of branchise arising dorsal to notopodia on chaetiger 1 (Fig. 8 B). Subsequent branchiae similarly placed. Branchiae or branchial scars present on most segments until apparition of cinctures.

Parapodia biramous, low mount or ridge in anterior and middle part, arising to full complete cinctures with elevated membranes in posterior segments (Fig 8 A,C).

Smooth short capillary chaetae present in neuropodia and notopodia of all setigers, ~13 per parapodia. Some long chaetae in anterior notopodia. Acicular spines with a flattened blade, slightly curved, up to ~22 per parapodia in posterior segment, with alternating capillaries (Fig. 8 C).

Methyl Blue staining pattern – None.

Remarks – Though no egg was observed, the presence of long chaetae (several times the body width) may indicate that the specimens were mature (Blake 2018) which would mean that this species is indeed quite small.

This species is found in the Barents Sea, around 400m deep. One specimen is from the Norwegian coast at 6m deep.

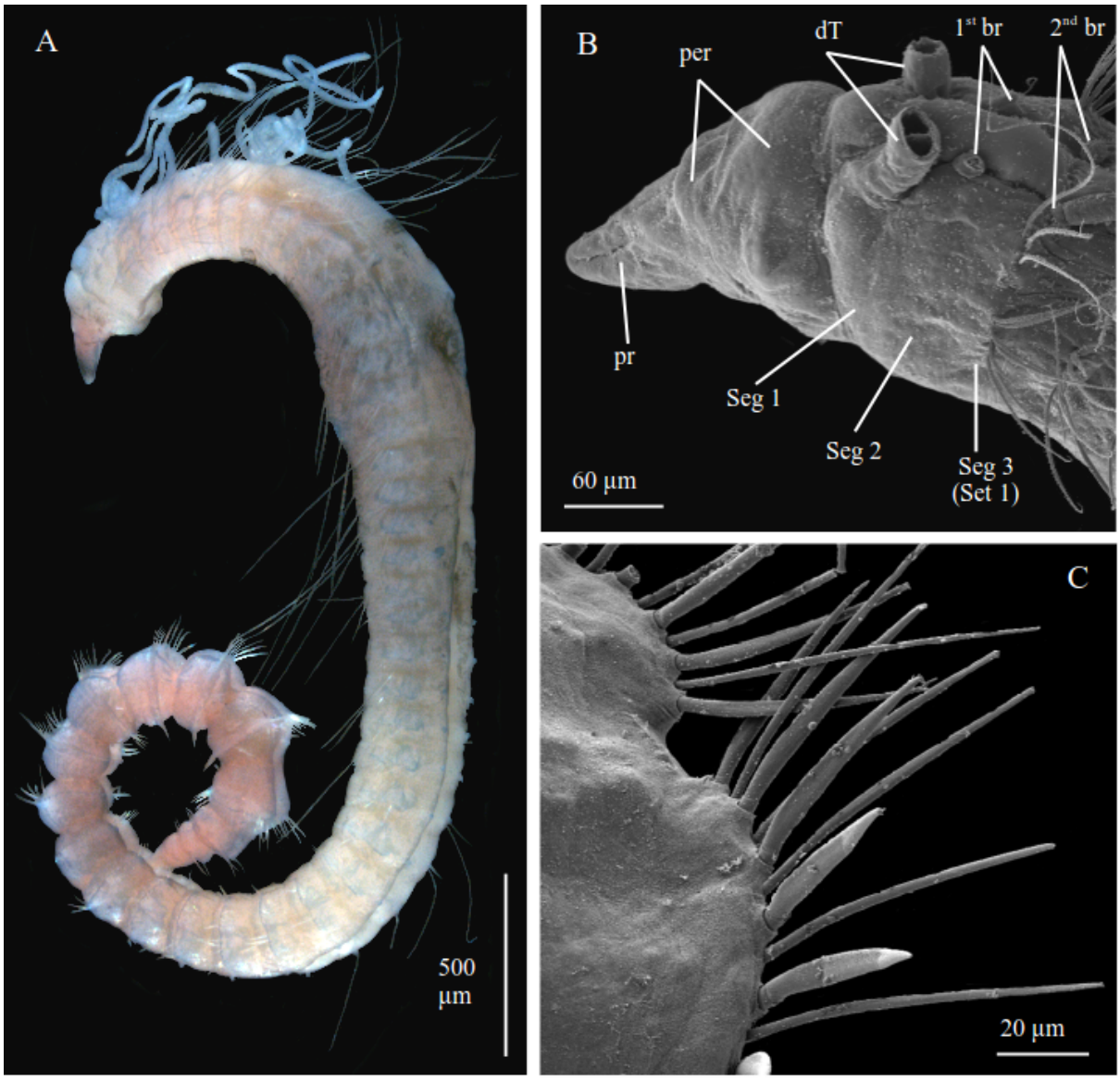

Figure 8 - Species 3: A, D light microscopy, stained with Shirlastain A; B-C SEM; A, full specimen in lateral view; B head in lateral view; C, detail of posterior notopodia.

Species 5

Material examined – Three specimens. Norwegian coast and shelf: 61.04889'N, 4.9723’E, 15 July 2015, 161m (1, ZMBN125777); 60.32652'N, 5.14085’E, 02 September 2014, 75m (1, ZMBN125802); 60.50728'N, 5.00028’E, 30 November 2015, 66m (1, ZMBN125907).

Description – A medium species, ~8mm long, ~1mm large, ~70 segments. Body elongate, narrowing progressively anteriorly, two to three times wider at anterior third than at anterior segments. Round in cross section anteriorly, widening progressively to a flatten oval at anterior third. Anterior segments 5 times higher and wider than long. Mid segments 10 times wider and 5 times higher than long. Posterior segments 2.5 times higher and 3 times wider than long. A thin shallow groove dorsally; a wide shallow ventral groove all along (Fig. 9 C).

Prostomium conical, rounded, nearly as long as the peristomium. Peristomium short, long like 3 segments, 2 times as high and wide as long, 3 distinct rings, middle one complete, long like 1.5 segment, bearing the mouth, anterior one long like one segment ventrally, not completing dorsally, where the middle ring joins the prostomium, posterior one not completing ventrally, overlapping the top of the first segment. Paired tentacles arising from the distinct first achaetigerous segment. First pair of branchiae arising from the second achaetigerous segment, less distinct as partially fused to chaetiger 1. Second branchiae arising from chaetiger 1, dorsal to parapodia (Fig. 9 A). Subsequent branchiae similarly placed. Branchiae or branchial scars present on most chaetigers until posterior modified segments.

Parapodia biramous low mounts or ridges in anterior and middle segments, developing into higher ridges in posterior segments. No specimens is complete so there is no information on the presence or absence of cinctures in posterior segments.

Smooth capillary chaetae present in neuropodia and notopodia of all setigers, ~10-12 per parapodia in anterior segments (Fig. 9 D). Short acicular spines unidentate, 7 per parapodia in available segments (the posterior part of all specimens is missing) (Fig 9 B).

Methyl Blue staining pattern – None.

Remarks – This species is easily differentiable from other species of *Chaetozone* in Norway by its distinct peristomium, which present a complete middle ring, an dorsally incomplete anterior ring, and a ventrally incomplete posterior ring.

This species is found on the Norwegian coast and shelf, around 60 to 160m deep.

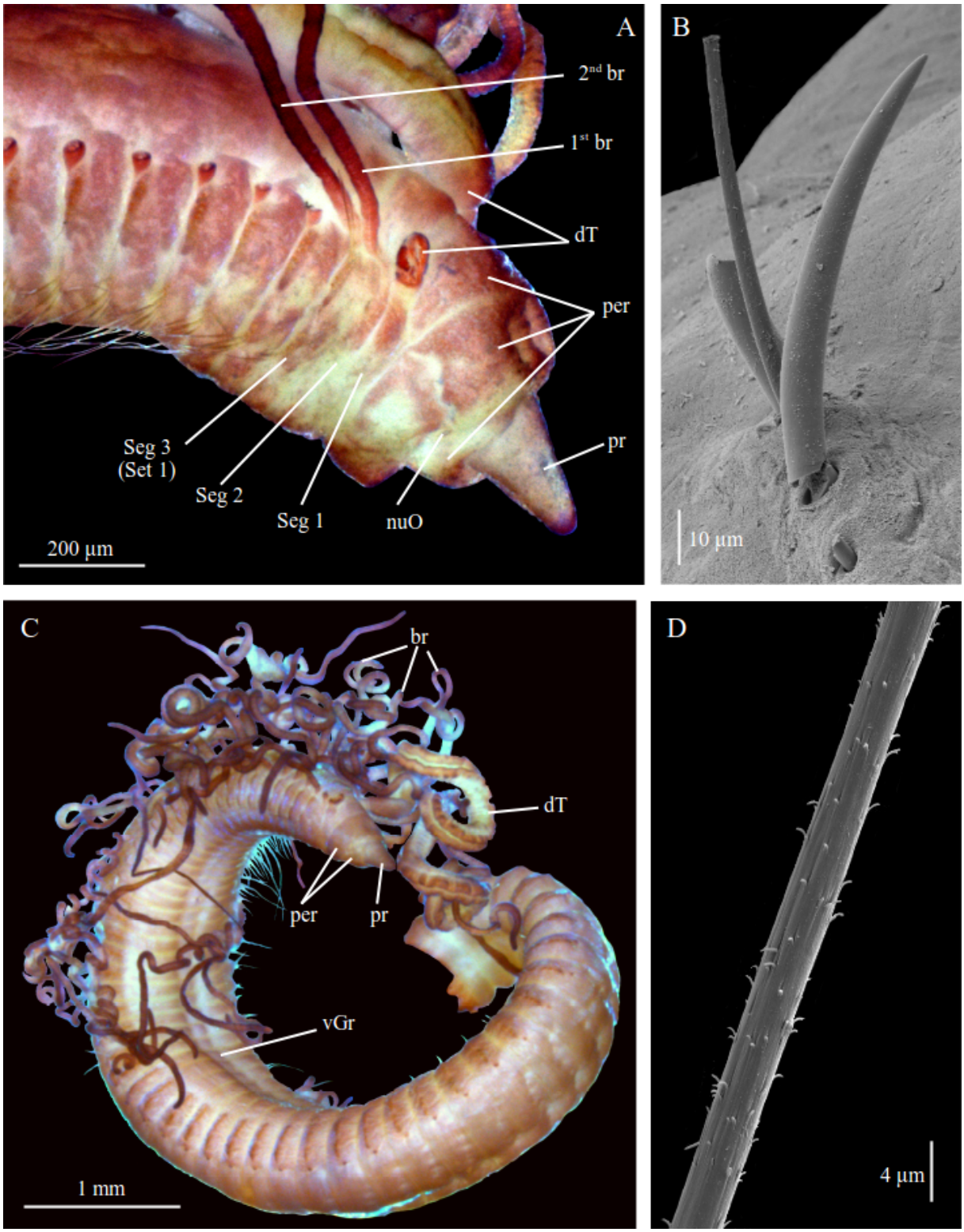

Figure n - Species 5: A,C light microscopy, stained with Shirlastain A; B,D SEM; A, head in lateral view; B, detail of neuropodial spine; C whole specimen in lateral view; D, detail of capillary chaetae.

Species 6

Material examined – One specimen. Norwegian coast and shelf: 60.39590'N, 5.14920'E, 19 May 2014, 171m (1, ZMBN 125778).

Description – An incomplete specimen, small, ~3mm long, ~0.3mm wide, ~60 segments, curled in circle. Anterior segments short and crowded, ~5 times as large as long and 5 times as wide as long, enlarging around 30th chaetiger to twice the length of anterior ones, no distinct dorsal groove or ridge, ventral ridge all along.

Prostomium conical, blunt, long like a third of the peristomium. Peristomium twice as long as wide, long like 7 anterior segments; 3 distinct rings, anterior two as wide as long, posterior one half as long as anterior ones, anterior one slightly enlarged, narrowing towards prostomium, middle one with a small dorsal lobe partially overlapping posterior one, a few weak less distinct annulations along middle ring. Dorsal tentacles arising from the 3rd peristomial ring. First pair of branchiae posterior to tentacles on first achaetigerous segment rather distinct, aligned with following branchiae. Second pair of branchiae on chaetiger 1.

Parapodia biramous, inconspicuous ridges in visible chaetigers. No modified posterior chaetigers present.

Smooth short capillary chaetae present in neuropodia and notopodia of all chaetigers.

Pygidium absent.

Methyl Blue staining pattern – None.

Remarks – Three specimens were clustered in species 6 by molecular analyses. Only one (ZMBN 125778) was examined in detail and is described here from the Norwegian coast.

Species 7

Material examined – 20 specimens. Norwegian coast and shelf: 59.76022’N, 5.49682’E, 08 June 2014, 40m (1, ZMBN125787); 59.02985’N, 5.44881’E, 10 June 2014, 59m (1, ZMBN125789); 60.90389’N, 7.16813’E, 17 November 2012, 115m (1, ZMBN125795); 60.60332’N, 5.09513’E, 6 March 2017, 94m (1, ZMBN125780); 60.21440’N 5.34560’E, 20 January 2016, 65m (1, ZMBN125825); 59.28789’N, 5.32506’E, 08 June 2014, 76m (1, ZMBN125790); 3/2-16, 58.24753’N, 6.53673’E, 03 February 2016, 155m (1, ZMBN125824); 63.26852’N, 10.37638’E, 08 February 2018 (1, MG040); 60.28158'N 5.20288’E 05 December 2007 (1, MG330 NTNU-VM unregistered); 60.269686’N, 5.197750’E, 26 July 2014, 120m (3, MG349-350, MG352, NTNU-VM unregistered). Skagerak: 59.6562’N, 10.6081’E, 20 October 2014, 31m (1, ZMBN 125756); 59.6444’N, 10.6192’E, 21 October 2014, 106m (3, MG343-MG345 NTNU-VM unregistered); 59.05485'N, 10.250467’E, 29 May 2011, 70 m (1, MG341, NTNU-VM unregistered); 58.866667’N, 11.1’E, 2005, 70m (2, MG347-MG348, NTNU-VM unregistered). Barents Sea: 70.262'N 31.083833’E, 16 April 2014, 126m (1, MG325, NTNU-VM unregistered).

Description – These specimens fit the description of Chaetozone setosa by Blake (2015), and are similar to the lectotype and paratypes of this species (Fig. 10).

Remarks – This species is distributed all along the Norwegian coast, the East coast of Sweden and in the North Sea North-East of Scotland, from around 30 to 160m deep. One specimen is recorded from Finmark where it may have a common area with species 8 (Fig. 11 red pentagons).

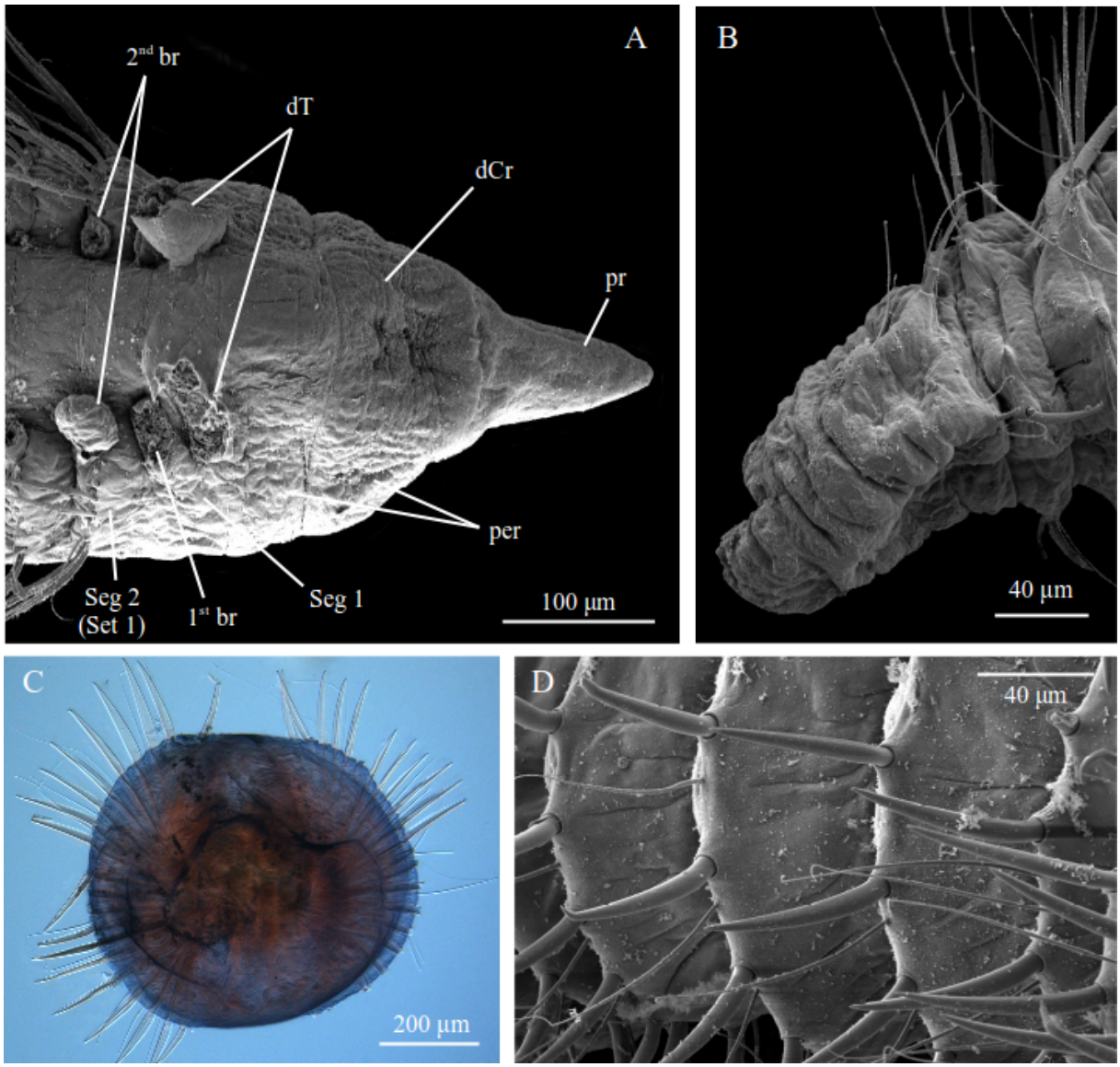

Figure 10 - Species 7: A-B,D SEM. C light microscopy stained with Shirlastain A. A, head in dorsal view; B, Pygidium in lateral view; C cross section of posterior segment, stained with Shirlastain A; D, detail of posterior modified segments and spines.

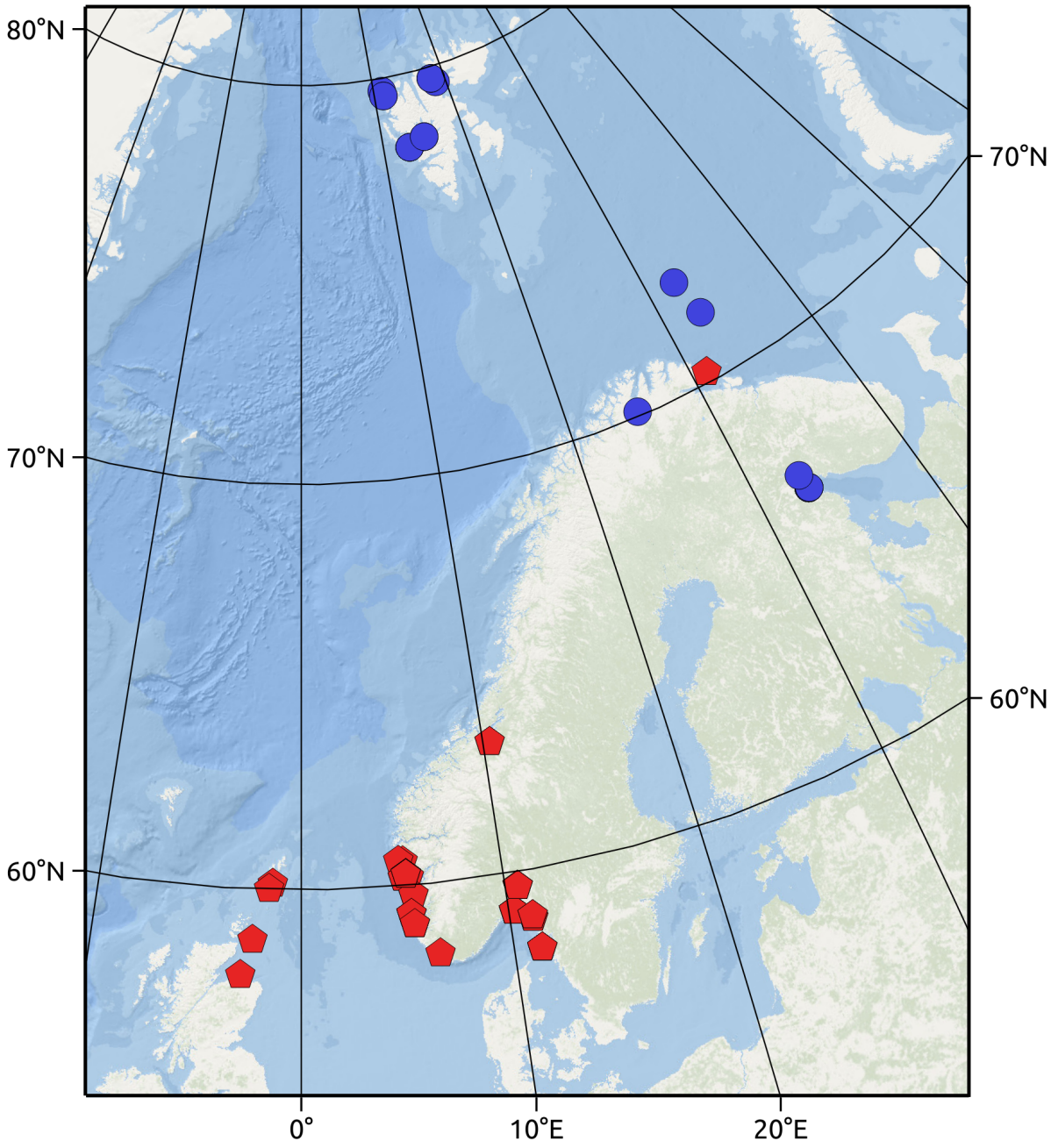

Figure 11 – Distribution of species 7 and 8: Occurence of species 8 (*Chaetozone setosa*) is indicated by blue circles, occurrence of species 7 is indicated by red pentagons.

Species 8

Material examined – 14 specimens. Svalbard: 78.14872'N, 13.12559'E, 13 May 2015 (6, ZMBN125766-125769, 125837-125838); 79.55130N 11.22970E, 30 August 2007, 91m (2, ZMBN125815-125816); 78.32855'N, 15.14712'E, 07 May 2015, 266m (1, ZMBN125811, ZMBN125813); 79.70829'N 18.17362'E, 10 May 2015, 407m (2, ZMBN125817-125818); 79.68089'N 11.13989'E, 09 May 2015, 180m (1, ZMBN125770); 79.58854'N, 18.63483'E, 10 May 2015, 242m (1, ZMBN 125812) – Barents Sea: 71.61528'N 32.99719'E, 9 August 2013, 305m (1, ZMBN 125764);

Description – These specimens fit the description of *Chaetozone setosa* by Blake (2015), and are similar to the lectotype and paratypes of this species (Fig. 12).

Remarks – The specimens belonging to this species are from the Barents Sea only, from around 80 to 400m. All the specimens from Svalbard, the type locality of *Chaetozone setosa*, belong to this species 8 (Fig. 11 blue circles). Other specimens from other areas fit also the description of *Chaetozone setosa* and are similar to its type material, but belong to the species 7. Sequences of specimens from the Canadian arctic identified as *Chaetozone setosa* were present in the dataset and belong to a distinct clade from clades 7 and 8. This is a strong indication that This species 8 is *Chaetozone setosa* and that *C. setosa* is restricted to the Barents Sea. Southern records of *Chaetozone setosa* in Norway are actually of species 7.

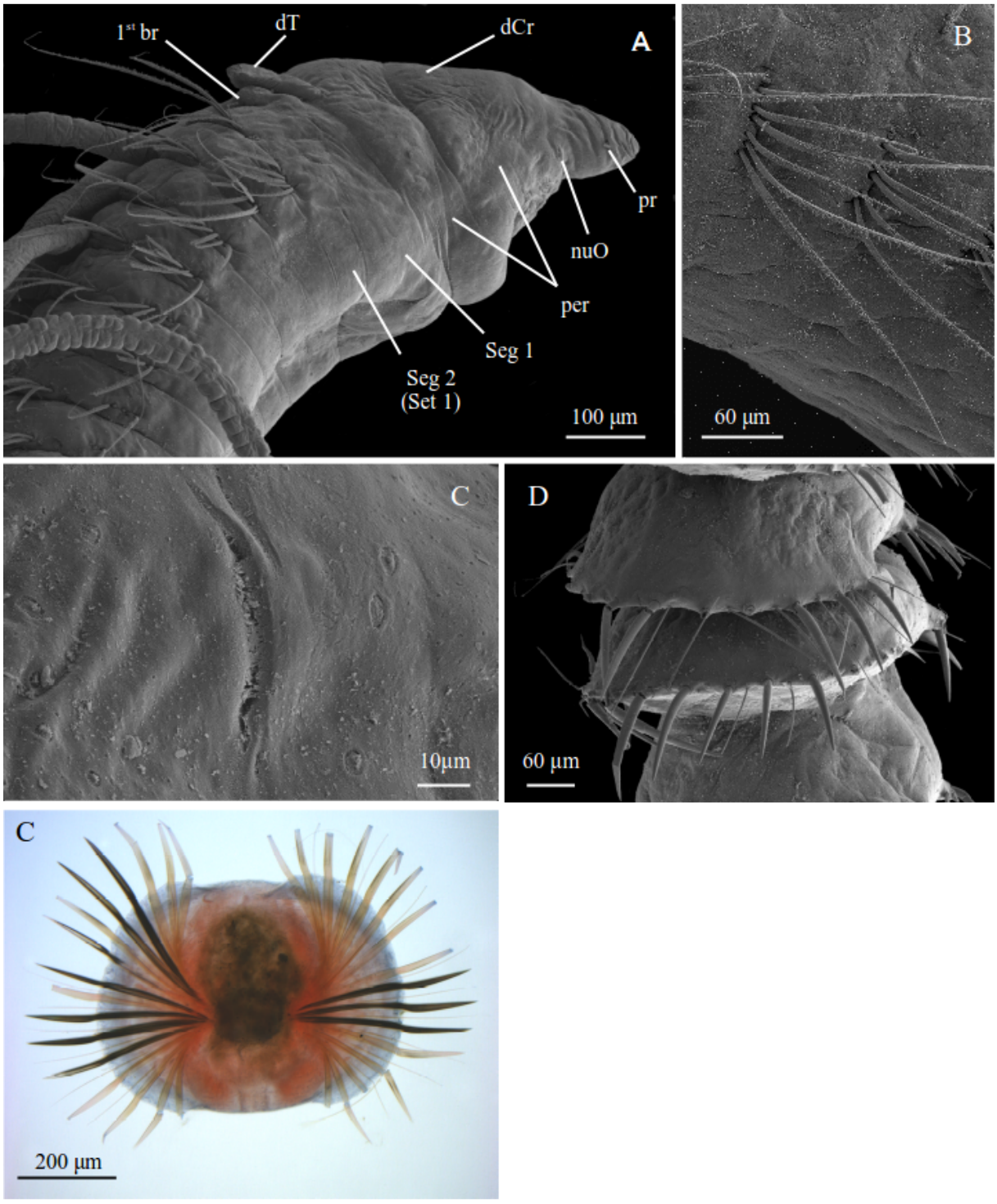

Figure 12 – Species 8: A-D SEM. C light photography. A, head in lateral view; B, detail of anterior neurochaetae; C, detail of nuchal organ; D modified posterior segments; C cross section of modified posterior segments.

Species 9 & 10

Material examined – 7 specimens. Norwegian coast and shelf: Species 9: 59.75777'N 5.49778'E, 08 June 2014, 60m (2, ZMBN 125774-125775). Species 10: 60.54973'N, 5.22897'E, 20 April 2017, 37m (1, ZMBN125779); 60.17295'N, 5.00315'E, 24 April 2014, 6m (2, ZMBN 125819-125820); 60.51035'N, 5.19158'E, 30 November 2015, 32m (1, ZMBN125808); 60.173'N, 5.003'E, 23 April 2014, 6m (1, ZMBN95386).

Description – Two big species, up to ~2cm long, ~3mm large, ~2mm high ~130 segments. Body elongate, slightly widening after the middle before narrowing and flattening in posterior 1/4th, round-oval in cross section anteriorly; anterior and middle segments approximately all the same length, all very short, ~10 times as high as long; posterior segments 6 times as large as long and 3 times as high as long; A thin dorsal groove and a larger ventral one (Fig. 14 E).

Prostomium short, 1/3rd of peristomium, conical, blunt; nuchal ogans simple slits posterior to prostomium; reddish pigmented spots visible around the nuchal organs with light microscopy, not apparent using SEM. Peristomium short, long as 5 segments, higher than long, dorsum rounded, 2 rings approximately equals, the second one shorter ventrally and extending dorsally posteriorly between paired tentacles, posterior one thinner than a segment. Paired Tentacles arising from first incomplete achaetous segment. First pair of branchiae beside or directly posterior to paired tentacles, on achaetous first segment. Second pair of branchiae on chaetiger 1, just above notochaetae (Fig. 13 A; 14 A,B) subsequent chaetigers with branchiae similarly placed, branchiae or branchial scars on all chaetigers including posterior modified ones.

Chaetiger 1 of approximately same size as following segments. Parapodia biramous, low mounds or ridges in anterior and middle regions, developed in incomplete cinctures encircling only the sides of posterior segments (Fig. 14 C,F).

Smooth short thick capillary chaetae present in neuropodia and notopodia of anterior and middle segments, in tight bundles of 11 to 15 chaetae, arranged in two rows in anterior segments, in notopodia only in posterior segments (Fig. 13 D; 14 D). Smooth short thin chaetae present in neuropodia and notopodia in middle and posterior segments, alternating

with thick capillaries in middle segments, with pointy-tipped acicular spines in posterior neuropodia, and long capillary-tipped acicular spines in posterior notopodia (Fig 13 B, 13 C,F).

Pygidium opening posteriorly, with short ventral lobe and dorsal mound overlapping last two chaetigers.

Methyl Blue staining pattern – On one specimen, lines of small dark blue dots along segment on ventral side could be observed. The peristomium and prostomium stained slightly, but for a distinctly non stained area forming like a "mask" around the "eyes".

Remarks – These species are easily distinguishable from other *Chaetozone* by their typical very narrow segments throughout, the presence of branchiae or branchial scars on all segments, the flat posterior end, and the conspicuous red spots on the side of the peristomium. They both closely resemble *Caulleriella zetlandica* (McIntosh, 1911). See the remarks associated to this species for discussion.

These species are found on the Norwegian coast ans shelf, and in the North Sea North-East of Scotland, from around 6 to 30m deep.

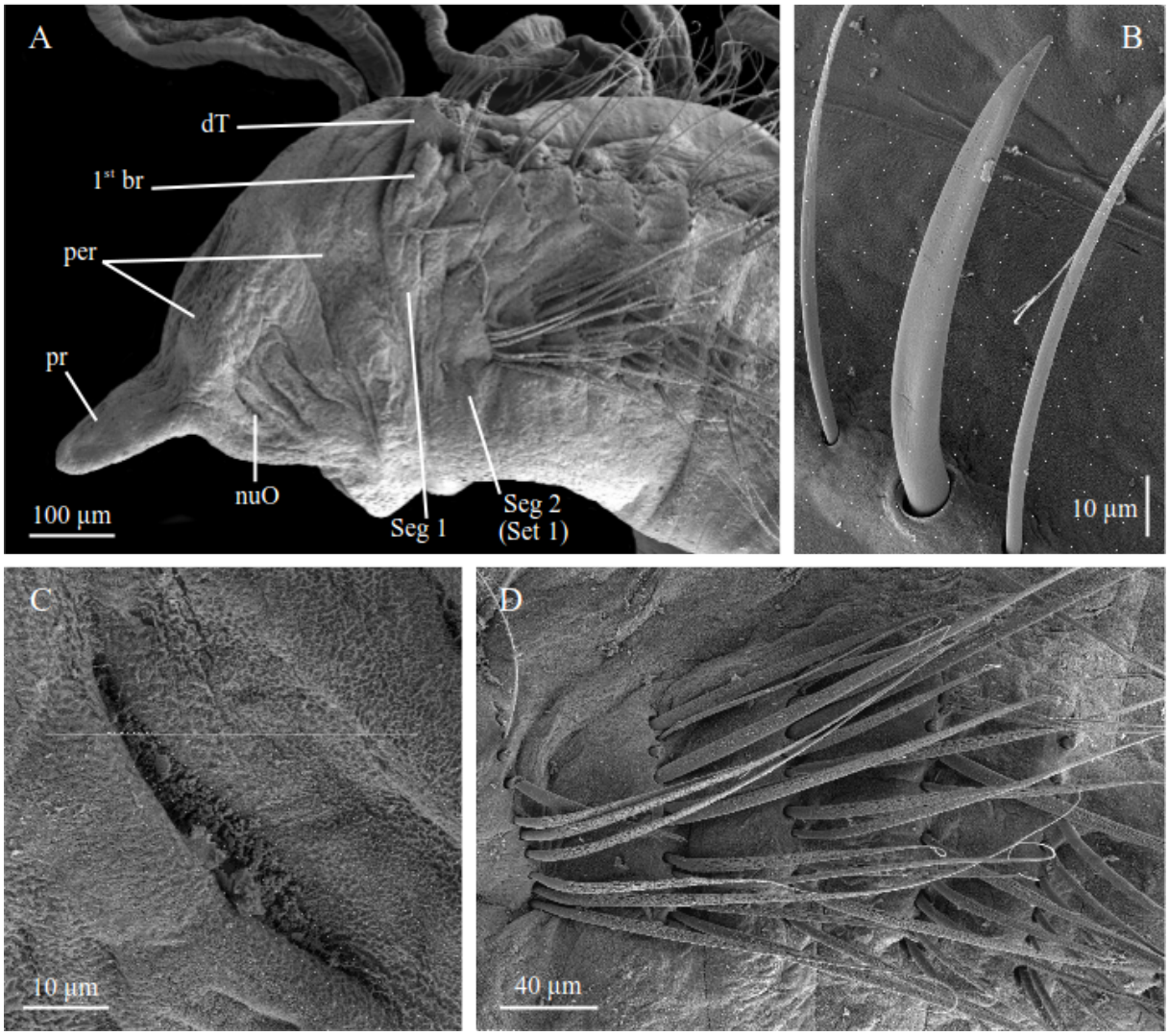

Figure 13 - Clade 9: A-D SEM. A, head in lateral view; B, details of neurospine; C, detail of nuchal organ; D, details of anterior neuropodia.

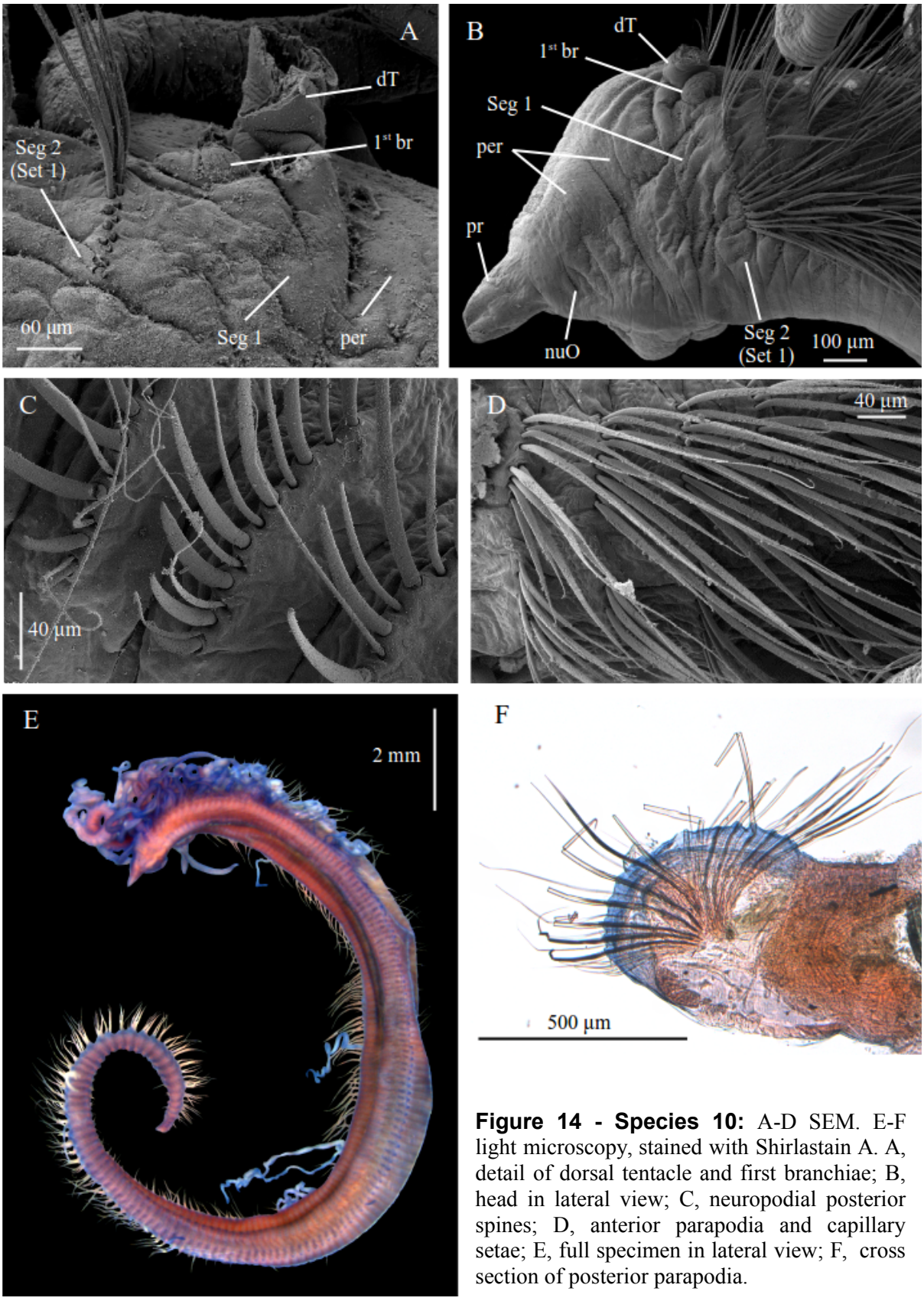

Figure 14 - Species 10: A-D SEM. E-F light microscopy, stained with Shirlastain A. A, detail of dorsal tentacle and first branchiae; B, head in lateral view; C, neuropodial posterior spines; D, anterior parapodia and capillary setae; E, full specimen in lateral view; F, cross section of posterior parapodia.

Species 11

Material examined – 1 specimen. Norwegian coast and shelf: 67.323'N, 14.473E, (1, ZMBN98242).

Description – A moderate sized specimen, ~8mm long, ~1mm large ~76 segments. Body elongate, narrowing anteriorly, thicker in the middle, flattening in posterior 1/4$^{th;}$ Anterior segments about 5 times as wide and high as long; Posterior segments, 3 times as wide as long and as high as long, with slightly deeper grooves between them but no elevated parapodia; Thin shallow dorsal groove anteriorly, wider ventral groove anteriorly.

Prostomium conical, long as 1/3 of peristomium. Peristomium short, long as 5 segments, fused with prostomium, with 2-3 indistinct weakly developed rings laterally, peristomial crest on top, posteriorly overlapping chaetiger 1, distinctly separated from chaetiger 2 on top. Paired tentacles arising from posterior margin of peristomial dorsal crest, above 2nd pair of branchiae. First pair of branchiae arising between the peristomium and the first segment, anterior to tentacles, below tentacles and slightly below 2nd pair of branchiae. 2nd pair of branchiae arising dorsal to notopodia, behind it on chaetiger 1, just below tentacles. Subsequent chaetigers with branchiae similarly placed.

Parapodia biramous, low mount or ridge throughout, covering the whole height of posterior flattened segments, but not highly elevated.

Smooth short capillary chaetae present in neuropodia and notopodia of all chaetigers, ~16 per parapodia. Most of these specimen's chaetae are broken.

Methyl Blue staining pattern – None.

Remarks – The specimen described here is from a littoral of Northern Norway. Another specimen was clustered with this one in molecular analyses, from a littoral of Northern Scotland.

Species 12

Material examined – 5 specimens. North Sea: 51.354333'N, 2.796667'E, 2010, 22m (3, MG308-310, NTNU-VM unregistered); 57.777177'N, 2.905357'E, 17 July 2008, 37m (1, MG367, NTNU-VM unregistered); 58.274250'N, 2.644216'E, 18 July 2008, 56m (1, MG379, NTNU-VM unregistered).

Description – A moderate size species ~13mm long, ~114 segments. Body elongate, narrowing anteriorly and posteriorly, anterior and middle segments 5-6 times as high as wide and long, posterior segments 1.5 times as high as wide and long, dorsum and venter rounded, both with distinct grooves.

Prostomium short, conical, blunt, long like 1/4th-1/3rd of the peristomium; nuchal organs slits at its posterior margin. Peristomium long like 4-5 segments, sometimes with 3 distinct rings, more or less of equal size, anterior lobe slightly overlapping prostomium above nuchal organs, partially fused with 1st chaetiger posteriorly. Dorsal tentacles arising from the posterior margin of the peristomium. First pair of branchiae arising between peristomium and first chaetiger, just beside tentacles; second pair of branchiae arising from posterior margin of first chaetiger, dorsal to notochaetae (Fig 15 B-C). Subsequent setigers with branchiae similarly placed.

Parapodia biramous, low mount or ridges in anterior and middle segments; parapodia developing posteriorly to form low incomplete cinctures in posterior 4th of the body (Fig 15 A,D).

Smooth short capillary chaetae present in neuropodia and notopodia of all chaetigers, ~20 per anterior parapodia, thicker and darkly pigmented anteriorly while the acicular spines appear transparent. Short acicular spines unidentate, pointy, slightly curved, ~13 per parapodia in posterior cinctures, alternating with capillaries up to three times longer than the spines (Fig 15 A,C).

Pygidium with triangular ventral lobe.

Methyl Blue staining pattern – None.

Remarks – These species is recorded from the North Sea North-East of Scotland and off Belgium, and in the Skagerrak, from around 20 to 60m deep.

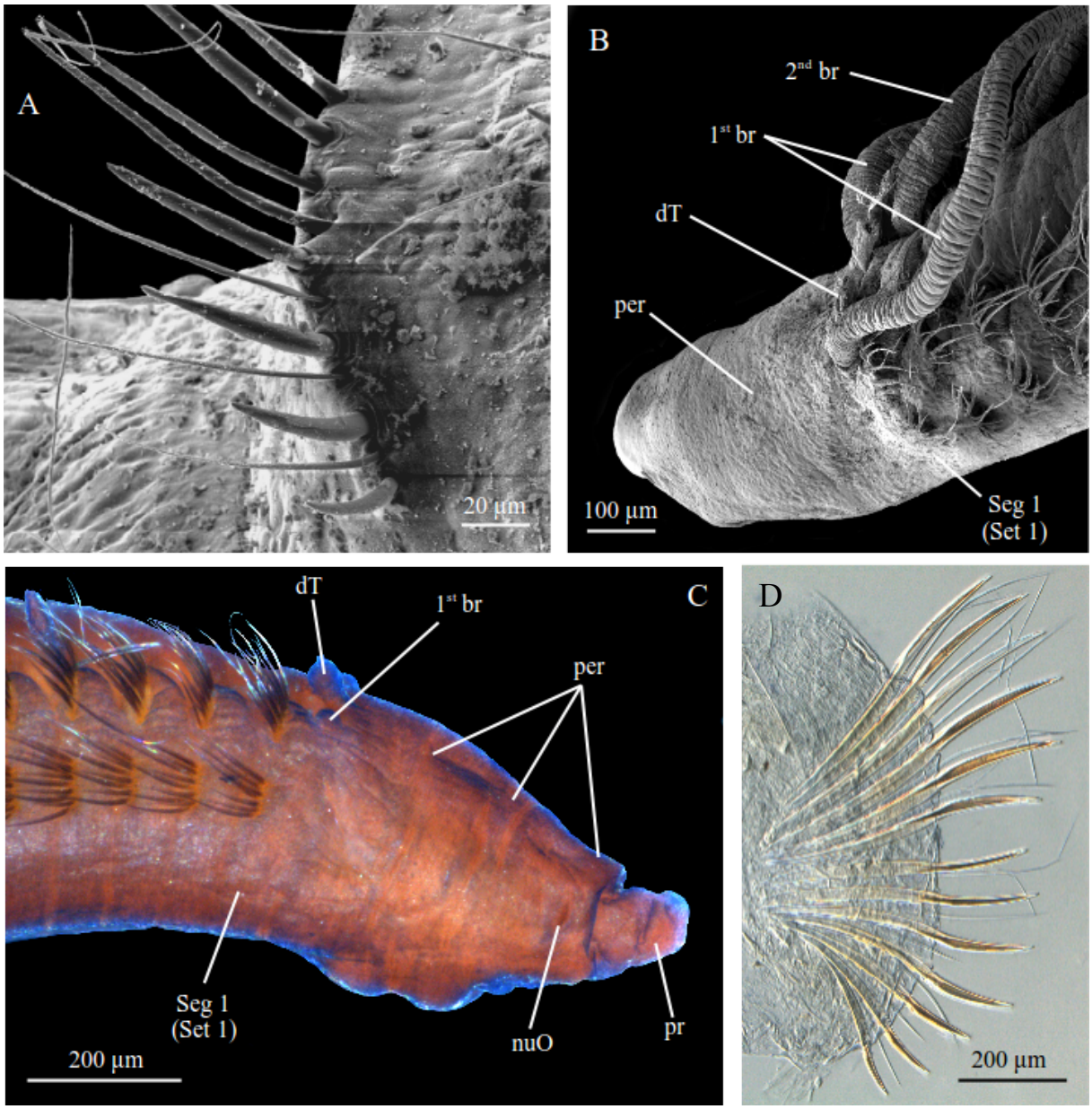

Figure 15 - Species 12: A-B SEM. C-D light microscopy, stained with Shirlastain A. A, detail of posterior neuropodia; B, head in dorso-lateral view; C head in lateral view; D, cross section of posterior parapodia.

Species 13

Material examined – Greenland Sea: 79.06483'N, 4.181'E, 27 June 2016, 2462m (ZMBN unregistered); 79.14028'N, 4.91056'E, 08 July 2016, 1540m (ZMBN unregistered); 79.05616'N, 3.59867'E, 28 June 2016, 3356m (ZMBN unregistered); 78.84983'N, 3.964'W, 01 July 2016, 1970 (ZMBN unregistered); 78.9333'N, 4.64433'W, 01 July 2016, 1548m (ZMBN unregistered); 79.056'N, 3.73067'E, 28 June 2016, 2865m (ZMBN unregistered); 78.98883'N, 5.432'W, 02 July 2016, 995m (ZMBN unregistered).

Description – Due to their small size, whole specimens were used for DNA extractions in previous work, thus no voucher was available to match the sequences. However, the material from which the specimens used for sequencing was selected still contains several specimens probably of the same species, but this material was in too poor condition to produce a useful description. All the specimens are small and incomplete. The arrangement of the tentacles and first branchiae, as well the head general shape seems however most similar to that of species 1, 2 and 4, Though this species appears smaller.

Remarks - Contrary to species 1, 2 and 4, species 13 is a deep sea species (~2500m) from the Greenland sea. It may also be much smaller.

3.2.3 The Specimens from Jan Mayen

Many specimens from Jan Mayen were available in the collection of NTNU University Museum. However these specimens were fixed in formalin and could not be sequenced. As such, they cannot be associated with any of the species above, and though they may present similar morphology to previously described species or species complexes, they cannot be reliably assigned to any of the group identified by molecular method, and are presented separately. Two distinct morphogroups were found in this material

Morphogroup A

Chaetozone setosa Bakken et al. 2010: 11-12.

Material examined – 326 specimens. Jan Mayen: 70.0234'N, 8.4523'W, 14 September 1999, 46m (69, NTNU-VM 36857-36859); 70.5861'N, 8.4641'W, 14 September 1999, 109m (255, NTNU-VM 36852-36856, 36790); 71.0938'N, 8.0663'W, 15 September 1999, 44m (1, NTNU-VM 36860); 70.3887'N, 9.2233'W, 17 Sptember 1999, 599m (1, NTNU-VM 36851).

Description – This group fits the description of *Chaetozone setosa*/species 8 and is similar to its lectotype. It is also similar to species 7.

Methyl Blue staining pattern – None.

Remarks – Though it is likely that all the specimens presenting this morphology in this material belong to one species, it is not possible to know if they belong to *Chaetozone setosa*/species 8, species 7 or a third species presenting the same morphology as these two.

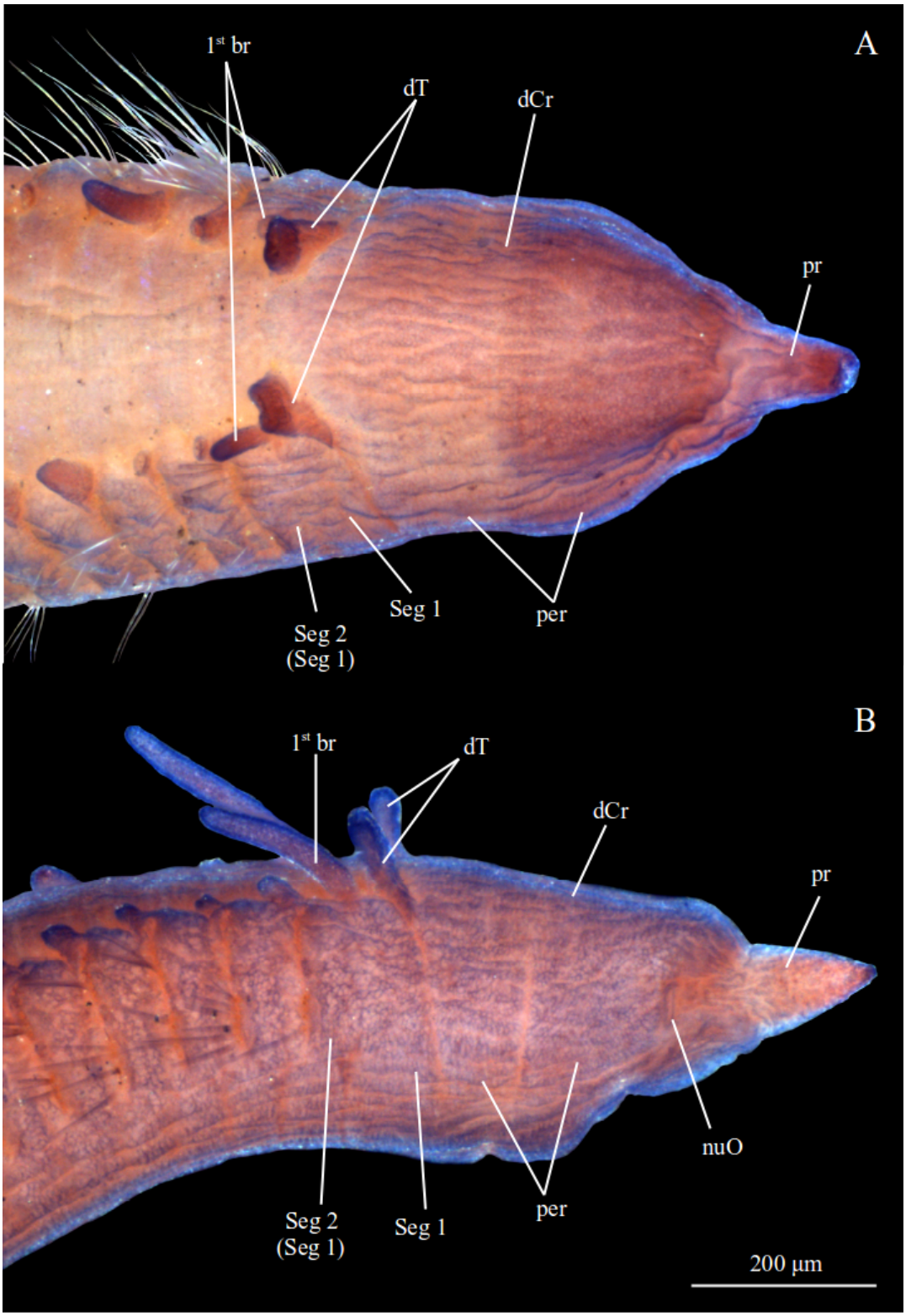

Figure 16 – Morphogroup B: A-B light photography, stained with Shirlastain A. A, anterior end in lateral view; B, anterior end in dorsal view.

Morphogroup B

Chaetozone christiei Bakken et al. 2010: 11-12.

Material examined – 568 specimens. Jan Mayen: 70.0234'N, 8.4523'W, 14 September 1999, 46m (559, NTNU-VM 36788-36789); 70.5861'N, 8.4641'W, 14 September 1999, 109m (2, NTNU-VM 427); 71.0938'N, 8.0663'W, 15 September 1999, 44m (7, NTNU-VM 36786).

Description – This group is similar to species 11 and a paratype of *Chaetozone christiei* showing an additional pair of branchiae between the prostomium and the first segment.

Methyl Blue staining pattern – None.

Remarks - Some variation is observed within this group on the position of the paired tentacles. On some specimens they arise from the peristomial crest directly above the first branchiae, before the first chaetiger, while on other they seem to grow from the peristomial crest all the way to the second chaetiger from where they detach from the body. As this seems to be a continuous variation, this might simply be intra-specific variation, but it is not possible to exclude that this morphogroup is composed of several species.

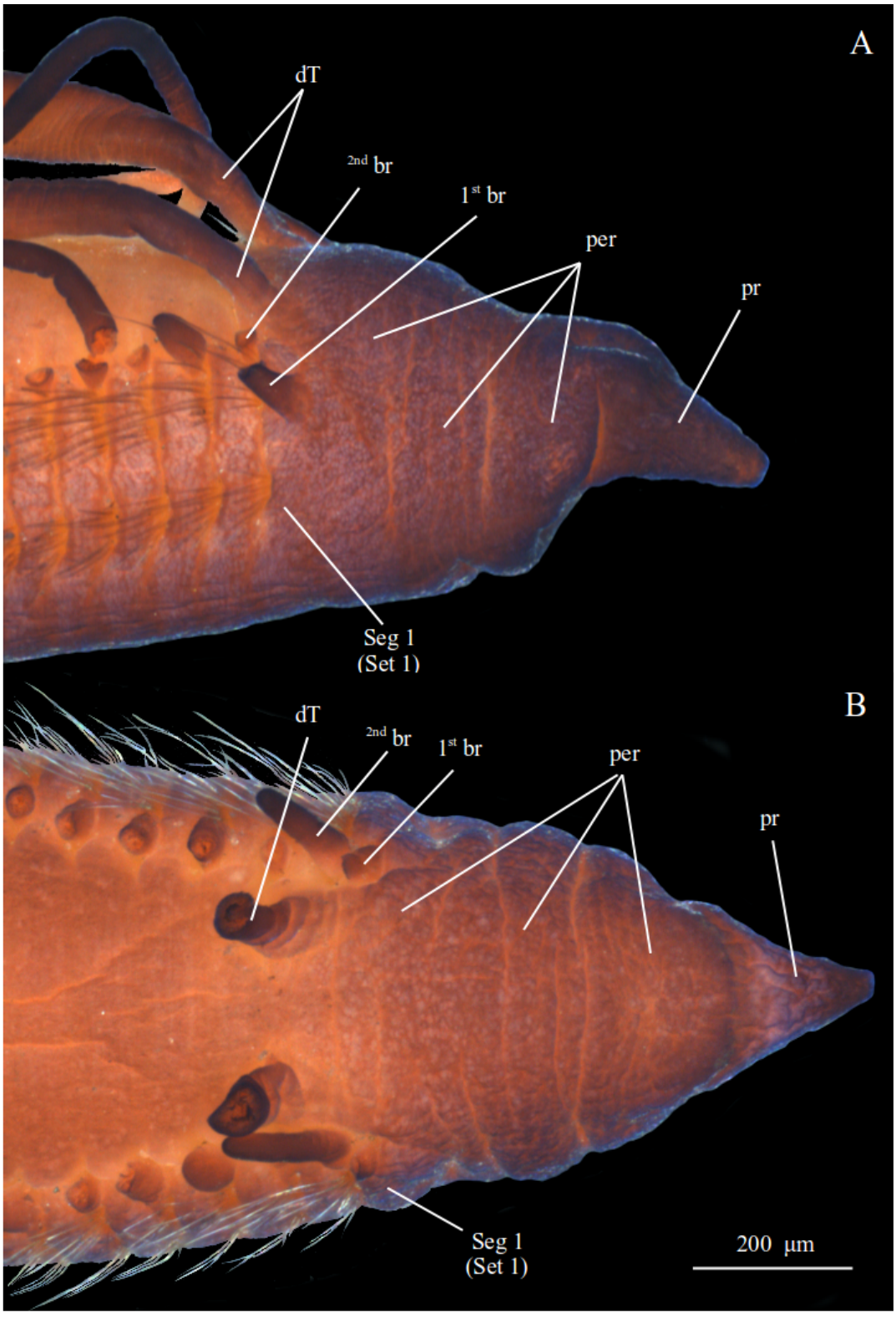

Figure 17 – Morphogroup B: A-B light photography, stained with Shirlastain A. A, anterior end in lateral view; B, anterior end in dorsal view.

4 Discussion

4.1 On the Phylogeny of Cirratulidae

Weidhase et al. (2016), is the most extensive molecular phylogeny of Cirratulidae, using COI sequences of 9 genera. It recovered the multitentaculate Cirratulidae as monophyletic, if including *Raricirrus* (Hartman, 1961) and *Ctenodrillus* (Claparède, 1863), both members of the family Ctenodrilidae (Kennel 1882) and respectively sister to a group formed by the multitentaculate Cirratulidae and to *Dodecaceria*. The sister relationship between *Dodecaceria* and *Ctenodrillus* has been shown in several other studies including Cirratulidae sequences (e.g. Bleidorn et al. 2003, Rousset et al. 2007). In this study, analyzing a combination of two genes, COI and 28S, by both Maximum Likelihood and Bayesian Inference (which are the two analyses referred to in this discussion), *Dodecaceria* and *Ctenodrillus* are also recovered as sister groups. *Raricirrus* is also recovered as part of *Cirratulidae*, but as sister to *Dodecaceria* and *Ctenodrillus* rather than to the multitentaculate Cirratulidae (Fig. 4).

The multitentaculate Cirratulidae (*Cirratulus*, *Cirrifomia* and *Timarete*) are also recovered as monophyletic in this study (Fig. 4). However, they are recovered paraphyletic in the Maximum Likelihood analysis, and while *Cirratulus* is supported as monophyletic in the Bayesian analysis, *Cirriformia* and *Timarete* are also recovered paraphyletic (Fig. 4). The multitentaculate Cirratulidae are nonetheless proposed as a monophyletic group.

In this study bitentaculate Cirratulidae are recovered in the Bayesian analysis, but not in the Maximum likelihood analysis, similar to results found previously (Weidhase et al. 2016). Also, while *Chaetozone* is recovered as monophyletic, *Tharyx* and *Aphelocaheta* are recovered paraphyletic.

However, it must be taken into account that most of the outgroup sequences used in this study (belonging to members of genera outside the scope of the aims) were downloaded from BOLD or GenBank, and therefore their identification could not be verified. As misidentification, even at the genus level, is common in Cirratulidae, it is likely that some of

the sequences used were wrongly labeled and some of the paraphyly within genera described above might be an artifact. Several cases of such probable misidentification were observed throughout the phylogeny. For example, all sequences identified as *Chaetozone* are recovered as monophyletic in this study, but a few sequences labeled differently are nested within this group with very strong support. These sequences include one species identified as *Tharyx* sp., one sequence identified as *Aphelochaeta* sp., and two sequences identified as *Caulleriella* sp. None of these sequences was produced for this study or belong to a specimen from Norwegian waters. The vouchers for the sequences labeled as *Caulleriella* could be checked but were in so poor condition that it was impossible to identify them to genus level, it was then assumed that they were indeed *Chaetozone*. The vouchers for the sequences labeled as *Tharyx* and *Aphelochaeta* could not be checked, but were also assumed to be misidentification.

For many of these sequences, a voucher was not indicated. This is a major issue as linking a sequence (or any type of molecular data) to a specimen makes it available to the scientific community and is crucial for accurate taxonomic work (Funk et al. 2005, Pleijel et al. 2008). The availability of vouchers is particularly important in integrative taxonomy as it allows to link molecular data to morphological data.

Moreover, only seven genera out of the total eleven currently considered valid Cirratulidae genera (Blake and Magalhães), as well as two genera of Ctenodrillidae (which are now known to be part of Cirratulidae even if no formal revision has been made) were included in this study with relatively extensive sampling. Therefore it is possible that the phylogeny of the family described here, or the monophyly of some of the genera or informal groups like multitentaculate Cirratulidae might be challenged when including more taxa.

In further studies, including only sequences from reliably identified specimens, as well as increasing the number of taxa, might be needed to fully resolve the genera relationships within Cirratulidae and potentially revise their boundaries and descriptions if necessary.

4.2 Species Discovery and Identification Through Molecular Analyses, Integrative Taxonomy

One particular marker, COI, and three species delimitation analyses were primarily chosen in this study to investigate the diversity of Chaetozone in Norwegian waters. The choice of the appropriate molecular marker is crucial for accurate species delimitation (Vitecek et al. 2017) and the number and composition of these species is well supported by the three species delimitation methods used on the target gene COI. This shows the robustness of the dataset and gives confidence in this species delimitation. 28S was chosen to infer a well supported and resolved phylogeny at the family level and indeed performed poorly in most analyses when compared to COI. However the number of sequences was also low compared to COI which may account for some of the differences observed. Analyses of the combined datasets were tested with the same methods as for the single genes and are mostly congruent with the analyses of COI.

STACEY has been advocated as an accurate method in some groups when several genes are available (e.g. Jones 2014, Vitecek et al. 2017), and was tested as an additional method in this study but further investigation is required for the use of this method in this group.

mPTP is known to perform poorly in assigning singletons to species when some are present in the dataset (e.g. Kapli et al. 2017, Ahmadzadeh et al. 2017, Aguado et al. 2019). When looking at the results of mPTP on the whole dataset (all Cirratulidae included in this study), it indeed several times fails to discriminate between obviously distant singletons or duos. However, two species composed of only one specimen are present in the Norwegian dataset, and were recovered in all but one analyses by mPTP. The species of *Chaetozone* present in Norway were overall much better sampled that the rest of the family, so despite this drawback of the method, it can still perform well when just a little portion of the dataset is poorly sampled, if the rest is well sampled.

ABGD suggests an inter-specific difference of 3.5 to 3.8%. Effectively, the same number of species of *Chaetozone* in Norwegian waters is recovered from COI with thresholds, effectively barcode gaps, from 2 to 5% difference. Within this group, single barcodes can

indeed be reliably used both for species discovery and specimens identification (Meyer & Paulay 2005). This is particularly interesting in a frame of global DNA barcoding as these species can be integrated in reference libraries and help the molecular identification of a number of specimens, improving the quality of global biodiversity assessments and records.

Molecular methods like DNA barcoding are a great tool for biosystematics (Vogler & Monaghan 2006, Bickford et al. 2007) and in particular for exploring and assessing the largely unknown marine diversity (e.g. Knowlton 1993, Schandler & Willassen 2005, Hardy et al. 2011). However, they should not be an end in themselves or replace traditional taxonomy. Rather, they have to be used in combination with all other methods available, from the traditional light microscopy to the modern SEM techniques or GIS analyses (Geographical Information Softwares), in a frame of integrative taxonomy (e.g. Dayrat 2005, Padial et al. 2010, Schlick-Steiner et al. 2010). Though barcodes alone can be used for assessing a number of species, it has not replaced morphological identification (Will & Rubinoff, 2004), which necessitates formal and accurate species descriptions. Moreover, any further biological study is impossible without a solid taxonomic frame and the possibility to identify properly described and named species.

4.3 Describing Species, Diagnostic Characters

Different methods were used to investigate the morphology of the species of *Chaetozone* found in Norwegian waters, traditional stereo and compound light microscopy, different stains and SEM, with a particular focus on evaluating species diagnostic characters, which are discussed here.

- The presence/absence of long chaetae (several times the width of the body) has often been used as a main diagnostic character for *Chaetozone setosa*. It is now known that in many species these long chaetae are associated with sexual maturity (Blake 2018). In addition, several species in Norway that are not *Chaetozone setosa* possess these chaetae. They can then only be used for identification in combination to other characters.

- Though they are advocated as diagnostic characters (e.g. Chambers 2003), the distribution, and length of the chaetae has not been formally studied here, for several reasons. First, it represents a great amount of work and time that was simply not available. Second, it would require a much larger number of vouchers (specimens in which identity is certain) for potential differences to be significant, especially considering the variations due to the age and maturity of the specimens (e.g. Southern 1914, Woodham & Chambers 1994, Blake 2018). Lastly, such characters are particularly difficult to use when identifying specimens, even more so when most chaetae are broken which is not a rare occurrence (the posterior half of the specimens is simply often missing), and were not considered in priority in the search for diagnostic characters.

- The pattern of implementation of the paired tentacles and the first pairs of branchiae is a more reliable character, as it does not seem to depend on the age of the animal, does not vary with the fixation method, and tentacles or branchial scars are nearly always identifiable (though this may require careful examination and nearly always necessitates the use of Shirlastain A) even when the tentacles or branchiae fell off. However, the variation observed in the type material of *Chaetozone* vivpara, and in a population of Jan Mayen (morphogroup b), questions if intraspecific variation of these characters is possible, and this species should be investigated further. The description of this pattern also relies on the interpretation of the peristomial rings and first few segments of which it can be difficult to make abstraction.

- Many species, like *Chaetozone setosa* are described as having a first achaetous segment just behind the peristomium and before the first chaetiger (which is also then the second segment) from which the the tentacles and/or some branchiae arise (Blake 1996). This segment can be anything from clearly distinct to fused to the peristomium. In this last case, it is often the presence of branchiae that lead to its interpretation as a segment rather than as peristomial ring. Some species have instead a distinct last peristomial ring from which arise the tentacles and/or branchiae. Histological studies by Day (1967) showed that peristomial rings were not segments. However, without

histological examination, naming an achaetous ring as a peristomial ring or as an achaetous segment is left to the interpretation of the taxonomist (Elías et al. 2017) and may not reflect a biological/developmental reality. This appellation must be overlooked when identifying specimens and carefully considered when comparing descriptions. Histology studies of a large number of species might help better understand this segmentation (Elías et al. 2017).

- Methyl green has been extensively used as a diagnostic character for bitentaculate Cirratulidae (e.g. Blake 2015, Blake 2018). Methyl blue, which is an equivalent chemical, was used in this study but failed to reveal any pattern. Not all species exhibit a methyl green/blue pattern so it is possible that no Norwegian species has one. However Blake (2015) describes a methyl green staining pattern in *Chaetozone setosa* which was not observed on the few specimens tested in this study. This might be due to the age of the specimens, the fixation and/or preservation methods, the use of methyl blue instead of methyl green, or simply intraspecific variability. Petersen (1999) reports sexual dimorphism in the staining pattern of an *Aphelochaeta* species. In any case, the use of methyl green/blue is not useful to identify Norwegian species.

- Shirlastain A does not reveal any specific pattern on the specimens, but considerably enhances contrast and allows a much more detailed observation of the "topology" of the specimens. This stains fades away after a few months, and does not prevent DNA extraction and sequencing. Shirlastain A should be used as much as possible when identifying *Chaetozone* species and Cirratulidae in general.

- Petersen (1999) and Christie (1985) describe significant variations between the gametes and eggs of some species or populations. Few individuals with eggs were examined during this study, and the eggs were not examined in detail, but these are characters that could be of interest for species identification and would merit further study.

- The method of fixation was found to have a strong impact on some characters. Ethanol fixed material specimens tend to collapse and wrinkle more than formalin fixed ones. This sometimes make peristomial rings and crest or ventral or dorsal groove or ridge difficult to assess, and must be taken in consideration when identifying material. However this phenomenon is not consistent. Some of the formalin fixed material examined was in so poor condition that no identification or description was possible, while some of the ethanol fixed material was in perfect condition.

As stressed earlier, morphological investigation is mutual with molecular investigation. Morphological identification relies on the diagnosis of characters or combinations of characters that must be specific. A molecular based species delimitation provides a frame to study these characters and distinguish intraspecific variations from inter-specific variation. For several of the species found in this study, no specific set of diagnostic characters was found and form complexes of cryptic species (e.g. Knowlton 1993, Bickford et al. 2007, Nygren 2014). Such cryptic species are commonly found when performing molecular analyses.

4.4 Naming Species

Out of the 16 species of *Chaetozone* found in Norwegian waters in this study, only one could be reliably assigned an existing name, the type species *Chaetozone setosa*. Most of the species recorded in Noway by Artsdatabanken were originally described from Great Britain. Using these species names requires that the species are well described and more importantly, well delimited. Several authors (e.g. Christie 1984, Chambers 2000, Chambers & Woodham 2003, Chambers et al. 2007) mention several undescribed species around the British Islands. Examination of the type material is necessary to reliably identify specimens. However in this case, examination of the type material of *Chaetozone vivipara* and *Chaetozone christiei* only brought more confusion as several distinct morphogroups are present within the paratypes that may be different species. Additionally, Species 12 of this study is found in the North Sea along northern Scotland, but cannot be assigned any name. Finally, the discovery of an unexpected diversity of *Chaetozone* during this study also strongly suggest that many species

are left to be discovered, also in British waters. Considering this, it seems unreasonable to use the names of species described in that area without a revision of the British *Chaetozone*, which is a necessary basis for the descriptions of many North Atlantic species. In particular, the use of DNA barcoding might be necessary to identify and name cryptic species.

Naming cryptic species, as found in several species complexes in this study, is in particular an important question. As argued previously, even if it is possible, identifying and naming a species for which not further diagnostic than a barcode is available is not particularly useful. The question in the case of cryptic species is a bit different. The complex can be morphologically described, and this description is valid for all species within. In that case cryptic species diagnosable only by the used of a molecular barcode can be assigned different names. Though cryptic species are not identifiable through their morphology, it is relevant to examine the ecology, distribution or reproduction of each of them, as they can be useful characters in addition to the molecular barcodes.

4.5 Comments on the Diversity of *Chaetozone* in Norwegian Waters

In total, 16 species of *Chaetozone* present in Norwegian waters were delimited in this study. This is twice the number of species previously recorded for Norway and represent a consequent increase of the diversity of this genus. The majority of *Chaetozone* species (e.g. species 1,2,4,5,6,7,9,10 and 11) occurs on the Norwegian coast and shelf, which present the most important diversity, followed by the North Sea. Species 3 and 8 (*Chaetozone setosa*) are endemic to the Barents Sea, where only three species in total are present. Species 7 is the species with the broadest distribution, from the Barents Sea to the Skagerrak. Species of *Chaetozone* are also distributed differently in the water column. Species 9, 10, 11 and 12 are from relatively shallow waters, from the littoral to around 60m deep. Species 5 and 7 occupy slightly deeper waters, from around 30 to 160m deep, while species 1,2 and 4 occupy deep water from 200 to 1200m deep inside the fjords. These last species are morphologically similar to *Chaetozone jubata*, which has been described as a deep water species (>500m, Chambers 2003, Chambers et al. 2007). A single species has been discovered from the deep waters of the Greenland Sea, and another one from the Norwegian Sea where they are

respectively restricted, but considering the extremely low sampling in these areas, it is not possible to draw ant conclusion about the diversity in these regions.

Knowledge of species distribution, but also the discovery of new species are directly related to the sampling effort (e.g. Nygren et al. 2017). Though the material in this study tried to cover a wide geographic area and a large range of depth, most of the data obtained was from the southern and rather shallow parts of the Norwegian coast and shelf, while several regions, in particular the deeper waters of the North East Atlantic were barely sampled. Even though a much greater number of species than expected was revealed within *Chaetozone* in this work, it is therefore probable that an even higher diversity might be uncovered when studying further these parts of the ocean.

5 Conclusion

In this study, the diversity and phylogeny of the common genus *Chaetozone* (Annelida, Cirratulidae) in Norwegian waters was investigated using a combination of molecular and morphological methods. *Chaetozone* was recovered monophyletic, and 16 species were found in Norwegian waters, which is the double of what was previously recorded. Nine different morphogroups were identified from various morphological analyses. Six species and three species complexes are characterized by a distinct combination of characters allowing their visual identification. The study of the distribution of the cryptic species within these species complexes allow the identification of 3 of them through a combination of morphological and geographical data. The type species of the genus, *Chaetozone setosa*, was identified within the species present in Norwegian waters and is presently restricted to the Barents Sea.

The systematics of Cirratulidae in general and *Chaetozone* in particular is challenging. Molecular data proves to be a reliable tool to discover and identify species in this group. It is a great asset in combination with morphological studies and geographical information, and should be used at a larger scale on this family to unravel its evolutionary history and clarify its complicated classification, as well as exploring its underestimated diversity. Indeed, the unexpected diversity uncovered by this study promises that many species are waiting to be discovered and described. Twenty thousands leagues under the seas, the adventure continues.

6 References

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Appendix I: List of Sequences

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
Itsastk13-P19	BCAS088-14	KT307635		*Chaetozone*
09PROBE-01111	CCANN550-09	GU672355		*Chaetozone*
NUNAV-0075	CCPOL075-07	HQ024281		*Chaetozone*
NUNAV-0193	CCPOL193-07	HQ024275		*Chaetozone*
NUNAV-0194	CCPOL194-07	HQ024276		*Chaetozone*
NUNAV-0236	CCPOL236-07	HQ024277		*Chaetozone*
NUNAV-0238	CCPOL238-07	HQ024278		*Chaetozone*
NUNAV-0241	CCPOL241-07	HQ024279		*Chaetozone*
NUNAV-0242	CCPOL242-07	HQ024280		*Chaetozone*
NUNAV-0271	CCPOL271-08	HQ024284		*Chaetozone*
HLC-30456	CCPOL281-08	HQ024282		*Chaetozone*
HLC-30462	CCPOL282-08	HQ024285		*Chaetozone*
CCPOL311	CCPOL313-08	HQ024283		*Chaetozone*
MBI-SCCWRP-00028	CMBIA028-10			*Chaetozone*
MBI-SCCWRP-00160	CMBIA160-11			*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
MBI-SCCWRP-00161	CMBIA161-11			*Chaetozone*
MBI-SCCWRP-00507	CMBIA374-11			*Chaetozone*
MBI-SCCWRP-00508	CMBIA375-11			*Chaetozone*
WS0086	WSPO086-09	GU672600		*Chaetozone*
WS0095	WSPO095-09	GU672595		*Chaetozone*
WS0096	WSPO096-09	GU672592		*Chaetozone*
WS0102	WSPO102-09	GU672587		*Chaetozone*
WS0103	WSPO103-09	GU672584		*Chaetozone*
WS0105	WSPO105-09	GU672583		*Chaetozone*
WS0108	WSPO108-09	GU672581		*Chaetozone*
WS0109	WSPO109-09	GU672582		*Chaetozone*
WS0111	WSPO111-09	GU672580		*Chaetozone*
WS0112	WSPO112-09	GU672577		*Chaetozone*
WS0276	WSPO276-09	GU672431		*Chaetozone*
VM 68231	PONOR066-13			*Chaetozone*
ZMBN94537	POLNB585-14			*Chaetozone*
ZMBN94483	POLNB646-14			*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
ZMBN94633	POLNB736-14			*Chaetozone*
ZMBN95386	POLNB1149-14			*Chaetozone*
ZMBN95707	POLNB1317-14			*Chaetozone*
ZMBN97115	NBAAV025-14			*Chaetozone*
ZMBN97116	NBAAV026-14			*Chaetozone*
ZMBN97117	NBAAV027-14			*Chaetozone*
ZMBN97118	NBAAV028-14			*Chaetozone*
ZMBN97119	NBAAV029-14			*Chaetozone*
ZMBN95880	POLNB1467-15			*Chaetozone*
ZMBN98242	POLNB1548-15			*Chaetozone*
ZMBN98250	POLNB1556-15			*Chaetozone*
	CRYNO108-15			*Chaetozone*
	CRYNO276-15			*Chaetozone*
	CRYNO285-15			*Chaetozone*
	CRYNO289-15			*Chaetozone*
ZMBN116562	POLNB2219-17			*Chaetozone*
ZMBN117820	POLNB2240-17			*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
ZMBN117860	POLNB2280-17			*Chaetozone*
ZMBN120505	POLNB2475-18			*Chaetozone*
MBI-SCCWRP-00146	CMBIA146-11			*Aphelochaeta*
MBI-SCCWRP-00147	CMBIA147-11			*Aphelochaeta*
MBI-SCCWRP-00148	CMBIA148-11			*Aphelochaeta*
BIOUG06646-F09	HZPLY459-13			*Aphelochaeta*
BIOUG06646-F11	HZPLY461-13			*Aphelochaeta*
BIOUG06646-G01	HZPLY463-13			*Aphelochaeta*
ItsastK13-P127	BCAS120-15	KT307704		*Tharyx*
Itsastk13-P18	BCAS133-15	KT307703		*Tharyx*
08PROBE-272	CCANN361-08	HQ023815		*Tharyx*
08PROBE-0274	CCANN363-08	HQ023816		*Tharyx*
08PROBE-0275	CCANN364-08	HQ023817		*Tharyx*
08PROBE-0280	CCANN369-08	HQ023818		*Tharyx*
08PROBE-0283	CCANN372-08	HQ023795		*Tharyx*
08PROBE-0285	CCANN374-08	HQ023796		*Tharyx*
08PROBE-0287	CCANN376-08	HQ023797		*Tharyx*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
08PROBE-0292	CCANN381-08	HQ023798		*Tharyx*
08PROBE-0295	CCANN384-08	HQ023799		*Tharyx*
08PROBE-0296	CCANN385-08	HQ023800		*Tharyx*
08PROBE-0287	CCANN386-08	HQ023801		*Tharyx*
08PROBE-0298	CCANN387-08	HQ032802		*Tharyx*
08PROBE-0300	CCANN389-08	HQ023803		*Tharyx*
08PROBE-0306	CCANN395-08	HQ023804		*Tharyx*
08PROBE-0310	CCANN399-08	HQ023805		*Tharyx*
08PROBE-0311	CCANN400-08	HQ023806		*Tharyx*
08PROBE-0312	CCANN401-08	HQ023807		*Tharyx*
08PROBE-0314	CCANN403-08	HQ023808		*Tharyx*
08PROBE-0515	CCANN410-08	HQ023809		*Tharyx*
08PROBE-0517	CCANN412-08	HQ023810		*Tharyx*
08PROBE-0518	CCANN413-08	HQ023811		*Tharyx*
08PROBE-0519	CCANN414-08	HQ023812		*Tharyx*
08PROBE-0550	CCANN445-08	HQ023813		*Tharyx*
08PROBE-0567	CCANN462-08	HQ023814		*Tharyx*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
09PROBE-08207	CCANN643-09	GU672122		*Tharyx*
09PROBE-08236	CCANN672-09	GU672146		*Tharyx*
09PROBE-08241	CCANN677-09	GU672152		*Tharyx*
09PROBE-08252	CCANN688-09	GU672161		*Tharyx*
09PROBE-08386	CCANN822-09	GU672260		*Tharyx*
09PROBE-08387	CCANN823-09	GU672259		*Tharyx*
09PROBE-08443	CCANN879-09	GU672304		*Tharyx*
	HZPLY476-13			*Tharyx*
MBI-SCCWRP-00228	CMBIA228-11			*Monticellina*
MBI-SCCWRP-00229	CMBIA229-11			*Monticellina*
ZMBN117880	POLNB2300-17			*Kirkegaardia*
ZMBN117832	POLNB2252-17			*Kirkegaardia*
ZMBN117813	POLNB2233-17			*Aphelochaeta*
ZMBN116564	POLNB2221-17			*Aphelochaeta*
UMBergen_NB_polych487	POLNB1380-14			*Aphelochaeta*
ZMBN95816	POLNB1023-14			*Aphelochaeta*
ZMBN95791	POLNB998-14			*Aphelochaeta*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
ZMBN95780	POLNB987-14			*Aphelochaeta*
ZMBN68238	PONOR073-13			*Aphelochaeta*
ZMBN68237	PONOR072-13			*Aphelochaeta*
		KJ736284		*Chaetozone*
		KJ736283		*Chaetozone*
		KJ736282		*Chaetozone*
		KJ736281		*Chaetozone*
		KJ736280		*Chaetozone*
		KJ736279		*Chaetozone*
		KJ736277		*Chaetozone*
		KJ736278		*Chaetozone*
			DQ779674	*Aphelochaeta*
		KY775641		*Kirkegaardia*
		HQ023811		*Tharyx*
11BIOAK-0917	KBPOL107-11	MF121660		*Cirratulus*
11BIOAK-1197	KBPOL387-11	MF121591		*Cirratulus*
11BIOAK-0912	KBPOL102-11	MF121566		*Cirratulus*

ID/Voucher	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
11BIOAK-1049	KBPOL239-11	MF121473		*Cirratulus*
11BIOAK-1545	KBPOL735-11	MF121471		*Cirratulus*
11BIOAK-0934	KBPOL124-11	MF121383		*Cirratulus*
11BIOAK-0933	KBPOL123-11	MF121322		*Cirratulus*
11BIOAK-0913	KBPOL103-11	MF121255		*Cirratulus*
11BIOAK-0915	KBPOL105-11	MF121234		*Cirratulus*
11BIOAK-1237	KBPOL427-11	MF121187		*Cirratulus*
11BIOAK-0914	KBPOL104-11	MF121065		*Cirratulus*
11BIOAK-1079	KBPOL269-11	MF121064		*Cirratulus*
11BIOAK-1213	KBPOL403-11	MF121047		*Cirratulus*
11BIOAK-1214	KBPOL404-11	MF121030		*Cirratulus*
11BIOAK-0916	KBPOL106-11	MF121026		*Cirratulus*
08PROBE-0552	CCANN447-08	HQ023478		*Cirratulus*
BAMPOL0375	BCPOL404-08	HM473343		*Cirratulus*
WS0224	WSPO224-09.COI	GU672480		*Cirratulus*
09PROBE-02020	CCANN514-09	GU672325		*Cirratulus*
09PROBE-08327	CCANN763-09	GU672216		*Cirratulus*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
09PROBE-08302	CCANN738-09	GU672197		*Cirratulus*
HLC-30442	CCPOL279-08	HQ024288		*Cirratulus*
08PROBE-0581	CCANN476-08	HQ023479		*Cirratulus*
08PROBE-0106	CCANN195-08	HQ023477		*Cirratulus*
CRBA-9616	GBAN5001-13	JQ048545		*Cirratulus*
WS0230	WSPO230-09	HM417794		*Cirratulus*
LMBP23-002	SFPOM089-11	KR916809		*Cirriformia*
LMBP23-001	SFPOM088-11	KR916808		*Cirriformia*
LMBSAP26-001	PCALN003-10	KR916807		*Cirriformia*
LMBP23-003	SFPOM090-11	KR916806		*Cirriformia*
IBUFRJ-3557	GBAN6444-15	KM192165		*Cirriformia*
IBUFRJ-3557	GBAN6443-15	KM192164		*Cirriformia*
IBUFRJ-3562	GBAN6442-15	KM192163		*Cirriformia*
	GBAN6441-15	KM192162		*Cirriformia*
IBUFRJ-3561	GBAN6440-15	KM192161		*Cirriformia*
		KP096407		*Protocirrineris*
BP2010-329	BCPOL898-10	HQ932659		*Dodecaceria*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
BP2010-154	BCPOL723-10	HQ932543		*Dodecaceria*
BAMPOL0458	BCPOL487.08	HM473361		*Dodecaceria*
BAMPOL0456	BCPOL485.08	HM473360		*Dodecaceria*
BAMPOL0120	BCPOL149-08	HM473359		*Dodecaceria*
BAMPOL0116	BCPOL145-08	HM473358		*Dodecaceria*
BAMPOL0115	BCPOL144-08	HM473357		*Dodecaceria*
BAMPOL0111	BCPOL140-08	HM473356		*Dodecaceria*
BAMPOL0505	BCPOL533-08	HM473355		*Dodecaceria*
BAMPOL0504	BCPOL532-08	HM473354		*Dodecaceria*
BAMPOL0503	BCPOL531-08	HM473353		*Dodecaceria*
BAMPOL0501	BCPOL529-08	HM473352		*Dodecaceria*
BAMPOL0452	BCPOL481-08	HM473351		*Dodecaceria*
BAMPOL0451	BCPOL480-08	HM473350		*Dodecaceria*
BAMPOL0450	BCPOL479-08	HM473349		*Dodecaceria*
BAMPOL0449	BCPOL478-08	HM473348		*Dodecaceria*
BAMPOL0448	BCPOL477-08	HM473347		*Dodecaceria*
BAMPOL0447	BCPOL476-08	HM473346		*Dodecaceria*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
BAMPOL0446	BCPOL475-08	HM473345		*Dodecaceria*
		KP794935		*Dodecaceria*
		KP794934		*Dodecaceria*
	GBAN0672-06	DQ209262		*Dodecaceria*
Cteno10		KT934277		*Ctenodrillus*
Cteno08		KT934276		*Ctenodrillus*
Cteno07		KT934275		*Ctenodrillus*
Cteno06		KT934274		*Ctenodrillus*
Cteno05		KT934273		*Ctenodrillus*
Cteno04		KT934272		*Ctenodrillus*
Cteno02		KT934271		*Ctenodrillus*
Cteno01		KT934270		*Ctenodrillus*
		KP794931		*Dodecaceria*
		MF414725		*Dodecaceria*
		MF414724		*Dodecaceria*
	GBAN4883-13	HE863973		*Raricirrus*
	GBAN4884-13	HE863972		*Raricirrus*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
BIOUG06646-H01	HZPLY475-13			*Dodecaceria*
USNM:IZ:1487023	WIZCO031-18			*Dodecaceria*
USNM:IZ:1487024	WIZCO032-18			*Dodecaceria*
BIOUG06838-G07	HZPLY1000-13			*Cirriformia*
BIOUG06838-G09	HZPLY1002-13			*Cirriformia*
BIOUG06838-G10	HZPLY1003-13			*Cirriformia*
BIOUG06838-H01	HZPLY1006-13			*Cirriformia*
BIOUG06646-G06	HZPLY468-13			*Cirriformia*
BIOUG06646-G07	HZPLY469-13			*Cirriformia*
BIOUG06646-G09	HZPLY471-13			*Cirriformia*
BIOUG06838-D01	HZPLY966-13			*Cirriformia*
LACM:DISCO:3792	DISA326-18			*Timarete*
BIOUG07681-B09	HZPLY1037-13			*Cirratulus*
USNM:IZ:1487042	WIZCO028-18			*Cirratulus*
USNM:IZ:1487043	WIZCO029-18			*Cirratulus*
		MH708233		*Timarete*
		MH708232		*Timarete*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
		MH708231		*Timarete*
		KY061285		*Timarete*
		KY061284		*Timarete*
		KY061283		*Timarete*
		KY061279		*Timarete*
		KY061278		*Timarete*
		KY061277		*Timarete*
		KY061276		*Timarete*
		KY061268		*Timarete*
		KY061267		*Timarete*
		KY061266		*Timarete*
		KY061262		*Timarete*
		KY061261		*Timarete*
		KY061260		*Timarete*
		KY061249		*Timarete*
		KY061248		*Timarete*
		KY061247		*Timarete*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
		KY061238		*Timarete*
		KY061223		*Timarete*
		KY061222		*Timarete*
		KY061221		*Timarete*
		KM192188		*Timarete*
		KM192187		*Timarete*
		KM192186		*Timarete*
		KM192177		*Timarete*
		KM192176		*Timarete*
		KM192178		*Timarete*
		KM192179		*Timarete*
		KM192175		*Timarete*
		KM192174		*Timarete*
		KM192173		*Timarete*
		KM192172		*Timarete*
		KM192171		*Timarete*
		KM192168		*Timarete*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
		KM192167		*Timarete*
			AMW24391	*Cirratulus*
			DQ779683	*Cirratulus*
			AY611443	*Cirriformia*
			AY340388	*Ctenodrillus*
SMNH75830			AY340389	*Dodecaceria*
			AY612631	*Dodecaceria*
			AF1285155	*Dodecaceria*
MG040	POLNB2502-18	not deposited		*Chaetozone*
MG050	POLNB2503-18	not deposited		*Aphelochaeta*
MG057	POLNB2504-18	not deposited		*Aphelochaeta*
ZMBN 125752	POLN2506-18	not deposited		*Chaetozone*
ZMBN 125755	POLNB2509-18	not deposited		*Chaetozone*
ZMBN 125756	POLNB2510-18	not deposited	not deposited	*Chaetozone*
ZMBN 125764	POLNB2518-18	not deposited		*Chaetozone*
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ZMBN 125775	POLNB2529-18	not deposited	not deposited	*Chaetozone*
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ZMBN 125787	POLNB2541-18	not deposited		*Chaetozone*
ZMBN 125789	POLNB2543-18	not deposited		*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
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ZMBN 125796	POLNB2550-18	not deposited		*Chaetozone*
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ZMBN 125800	POLNB2554-18	not deposited	not deposited	*Chaetozone*
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ZMBN 125832	POLNB2586-18	not deposited		*Tharyx*
ZMBN 125833	POLNB2587-18	not deposited		*Tharyx*
ZMBN 125834	POLNB2588-18	not deposited		*Aphelochaeta*
ZMBN 125837	POLNB2594-18	not deposited		*Chaetozone*
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ZMBN129512	not deposited	not deposited	not deposited	*Chaetozone*
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ZMBN129514			not deposited	*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
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MG159	not deposited	not deposited		*Chaetozone*
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ZMBN129526	not deposited	not deposited		*Chaetozone*
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ZMBN129544			not deposited	*Chaetozone*
ZMBN129546	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129547	not deposited	not deposited		*Chaetozone*
ZMBN129549			not deposited	*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
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ZMBN129551	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129552	not deposited	not deposited		*Chaetozone*
ZMBN129553	not deposited	not deposited		*Chaetozone*
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ZMBN129556			not deposited	*Chaetozone*
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ZMBN129575	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129576	not deposited	not deposited		*Chaetozone*

ID/Voucher	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
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ZMBN129580	not deposited	not deposited		*Chaetozone*
ZMBN129581			not deposited	*Chaetozone*
ZMBN129583	not deposited	not deposited		*Chaetozone*
ZMBN129584	not deposited	not deposited		*Chaetozone*
ZMBN129585	not deposited	not deposited		*Chaetozone*
ZMBN129596	not deposited	not deposited		*Chaetozone*
MG026	not deposited	not deposited		*Chaetozone*
MG244	not deposited	not deposited		*Aphelochaeta*
MG246	not deposited	not deposited		*Aphelochaeta*
MG248	not deposited	not deposited		*Aphelochaeta*
MG249			not deposited	*Aphelochaeta*
MG251	not deposited	not deposited		*Chaetozone*
129640	not deposited	not deposited	not deposited	*Chaetozone*
MG266	not deposited	not deposited	not deposited	*Chaetozone*
MG267	not deposited	not deposited		*Chaetozone*
MG268	not deposited	not deposited	not deposited	*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
MG272	not deposited	not deposited	not deposited	*Tharyx*
MG275	not deposited	not deposited	not deposited	*Tharyx*
MG277				*Tharyx*
MG278	not deposited	not deposited	not deposited	*Tharyx*
MG280	not deposited	not deposited	not deposited	*Tharyx*
MG282	not deposited	not deposited	not deposited	*Chaetozone*
MG283	not deposited	not deposited	not deposited	*Chaetozone*
MG289	not deposited	not deposited	not deposited	*Chaetozone*
MG290	not deposited	not deposited	not deposited	*Chaetozone*
MG291	not deposited	not deposited	not deposited	*Chaetozone*
44730HMDNA118	not deposited	not deposited		*Chaetozone*
36800POLYSKAGDNA10517	not deposited	not deposited		*Chaetozone*
50840S06-2-1563	not deposited	not deposited		*Chaetozone*
50890S10-2-3083	not deposited	not deposited		*Chaetozone*
50910S10-1-2913	not deposited	not deposited		*Chaetozone*
50930S14-1-393	not deposited	not deposited		*Chaetozone*
MG302			not deposited	*Tharyx*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
MG303			not deposited	*Tharyx*
MG304			not deposited	*Tharyx*
MG305	not deposited	not deposited	not deposited	*Chaetozone*
MG306				*Chaetozone*
MG307	not deposited	not deposited	not deposited	*Chaetozone*
4457GB088 / MG308	not deposited	not deposited		*Chaetozone*
ZMBN129642	not deposited	not deposited		*Chaetozone*
5074GB077 / MG310	not deposited	not deposited		*Chaetozone*
MG311	not deposited	not deposited	not deposited	*Chaetozone*
4481MAR14DNA323 / MG312	not deposited	not deposited		*Chaetozone*
ZMBN129639	not deposited	not deposited		*Chaetozone*
MG314	not deposited	not deposited	not deposited	*Chaetozone*
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44780MAR14DNA269 / MG316	not deposited	not deposited		*Chaetozone*
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3634MAR14DNA264 / MG320	not deposited	not deposited		*Chaetozone*
3632MAR14DNA262 / MG321	not deposited	not deposited		*Chaetozone*
36310MAR14DNA261 / MG322	not deposited	not deposited		*Chaetozone*
3630MAR14DNA260 / MG323	not deposited	not deposited		*Chaetozone*
36330MAR14DNA263 / MG324	not deposited	not deposited		*Chaetozone*
3613MAR14DNA178 / MG325	not deposited	not deposited		*Chaetozone*
3211WS14DNA736 / MG326	not deposited	not deposited		*Chaetozone*
MG327	not deposited			*Chaetozone*
MG328			not deposited	*Chaetozone*
51230WS14DNA741 / MG329	not deposited	not deposited		*Chaetozone*
31440WS14DNA037 / MG330	not deposited	not deposited		*Chaetozone*
MG331	not deposited	not deposited	not deposited	*Chaetozone*
32260WS14DNA823 / MG332	not deposited	not deposited		*Chaetozone*
32120WS14DNA736 / MG333	not deposited	not deposited		*Chaetozone*
129648	not deposited	not deposited		*Chaetozone*
MG335	not deposited	not deposited	not deposited	*Chaetozone*
MG336	not deposited	not deposited	not deposited	*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
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MG338	not deposited	not deposited	not deposited	*Chaetozone*
MG339	not deposited	not deposited	not deposited	*Chaetozone*
MG340	not deposited	not deposited	not deposited	*Chaetozone*
36770POLYSKAG DNA092MG341	not deposited	not deposited		*Chaetozone*
MG342	not deposited	not deposited	not deposited	*Chaetozone*
30910POLYSKAG 2014-028 / MG343	not deposited	not deposited		*Chaetozone*
30912POLYSKAG 2014-029 / MG344	not deposited	not deposited		*Chaetozone*
30930POLYSKAG 2014-030 / MG345	not deposited	not deposited		*Chaetozone*
ZMBN129641	not deposited	not deposited		*Chaetozone*
ZMBN129647	not deposited	not deposited		*Chaetozone*
3516BE2014 107 / MG349	not deposited	not deposited		*Chaetozone*
35170BE2014 108 / MG350	not deposited	not deposited		*Chaetozone*
MG351	not deposited	not deposited	not deposited	*Chaetozone*
35190BE2014 110 / MG352	not deposited	not deposited		*Chaetozone*
MG353	not deposited	not deposited	not deposited	*Chaetozone*
MG355	not deposited	not deposited		*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
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MG357	not deposited	not deposited	not deposited	*Tharyx*
MG359			not deposited	*Tharyx*
MG362	not deposited	not deposited	not deposited	*Chaetozone*
MG363	not deposited	not deposited	not deposited	*Chaetozone*
MG364	not deposited	not deposited	not deposited	*Chaetozone*
MG365	not deposited	not deposited	not deposited	*Chaetozone*
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MG367	not deposited	not deposited	not deposited	*Chaetozone*
MG368			not deposited	*Tharyx*
MG369			not deposited	*Tharyx*
MG370	not deposited	not deposited	not deposited	*Chaetozone*
MG372	not deposited	not deposited	not deposited	*Chaetozone*
MG373			not deposited	*Chaetozone*
MG374	not deposited	not deposited	not deposited	*Chaetozone*
MG377	not deposited	not deposited	not deposited	*Chaetozone*
MG379	not deposited	not deposited	not deposited	*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
MG380	not deposited	not deposited	not deposited	*Chaetozone*
MG381			not deposited	*Chaetozone*
MG382			not deposited	*Chaetozone*
MG383	not deposited	not deposited	not deposited	*Cirratulus*
MG384	not deposited	not deposited	not deposited	*Chaetozone*
MG385	not deposited	not deposited	not deposited	*Cirriformia*
NTNU-VM 72308	not deposited	not deposited	not deposited	*Cirratulus*
NTNU-VM 72311	not deposited	not deposited	not deposited	*Cirratulus*
MG388	not deposited	not deposited	not deposited	*Chaetozone*
MG389	not deposited	not deposited	not deposited	*Cirriformia*
MG390			not deposited	*Dodecaceria*
MG391	not deposited	not deposited	not deposited	*Dodecaceria*
MG393	not deposited	not deposited	not deposited	*Chaetozone*
MG394	not deposited	not deposited	not deposited	*Aphelochaeta*
ZMBN129620	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129611	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129607	not deposited	not deposited	not deposited	*Chaetozone*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
ZMBN129610	not deposited	not deposited	not deposited	*Chaetozone*
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ZMBN129602	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129603	not deposited	not deposited	not deposited	*Chaetozone*
ZMBN129621			not deposited	*Chaetozone*
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ZMBN129626	not deposited	not deposited		*Chaetozone*
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ZMBN129636			not deposited	*Chaetozone*
BIOUG14667-H10	ARCMI377-14	MG423483		*Flabelligera*
			DQ779688	*Flabelligera*
			DQ209240	*Glyphanostomum*

ID/Voucher/Terminal	BOLD ID COI	GenBank ID COI	GenBank ID 28S	Genus
		DQ209260		*Glyphanostomum*
HUNTSPOL0328	NBPOL328-08	HQ024203		*Polycirrus*
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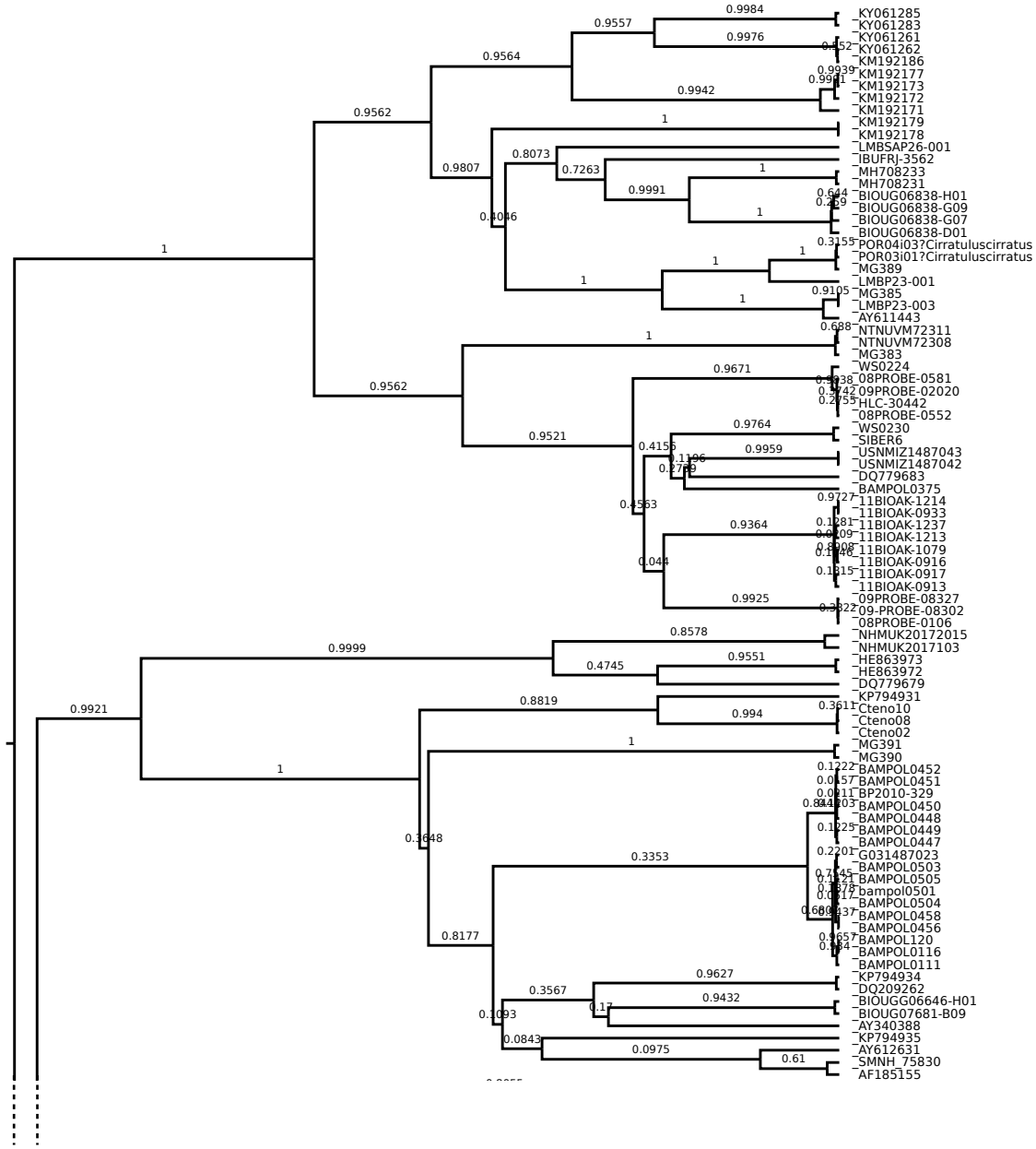
Appendix II: Bayesian Inference (COI+28S) of phylogeny of Cirratulidae

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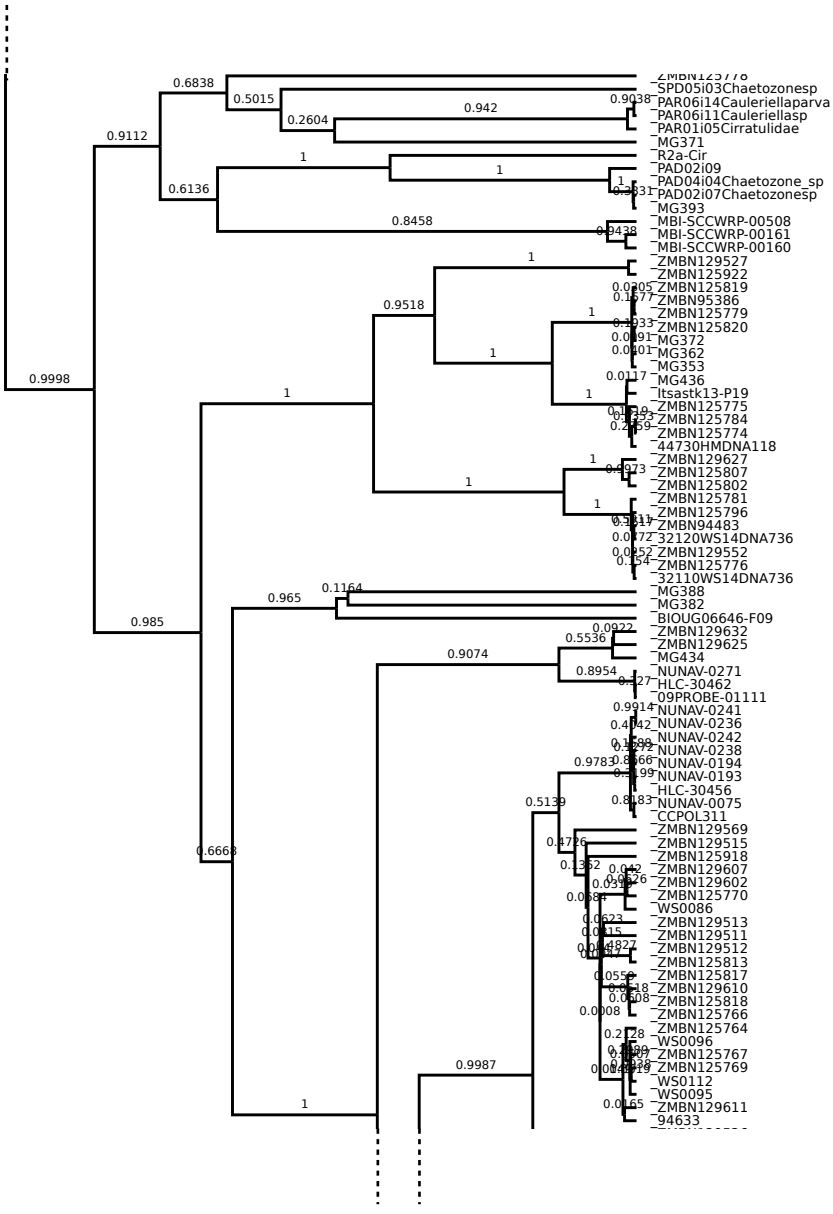
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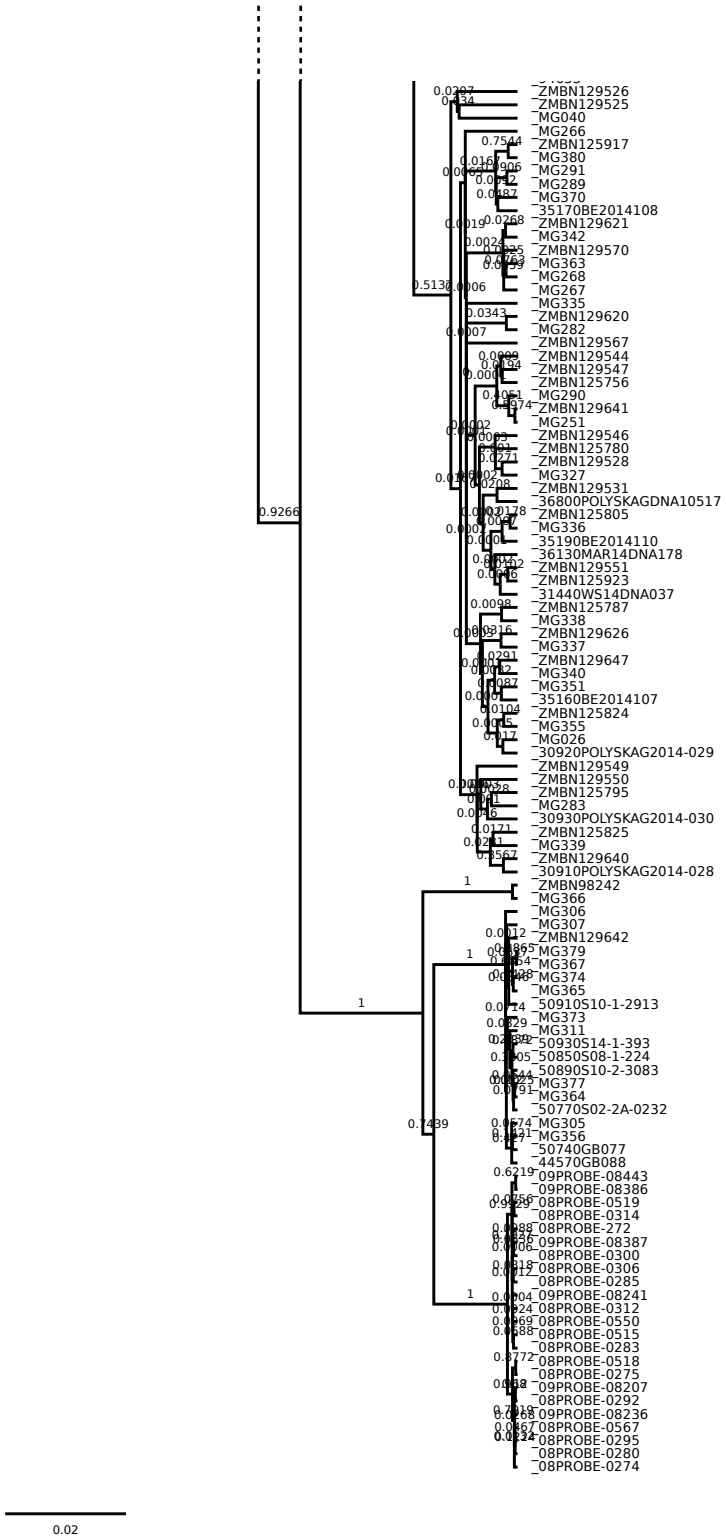
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Maël Ariel Grosse

Integrative Taxonomy Reveals Hidden Diversity in the Genus *Chaetozone* (Annelida, Cirratulidae) in Norwegian Waters

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