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Systematic revision of *Chone* Krøyer, 1856, *Dialychone* Claparède, 1870 and *Paradialychone* Tovar-Hernández, 2008 (Sabellidae: Annelida) in Norwegian waters

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Preface

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Cover photo: Mugga/Fredrik Pleijel.

Chone sp. (See *Chone* sp. 1 under 3.5 Morphological analysis)

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May the worms be with you.

Tuva Bongard Munkeby,

15th May 2018

Abstract

The species of *Chone, Dialychone* and *Paradialychone* (Sabellidae: Annelida) in Norwegian waters are assessed using morphological and molecular data. The monophyly of *Chone, Dialychone, Paradialychone* and *Euchone* is tested and discussed. Sixty- six morphological characters are obtained by different means of microscopic techniques, Scanning Electron Micrographs (SEM) and photography. Fifty-seven sequences of the mitochrondrial gene Cytochrome oxidase 1 (CO1) are included of which 25 sequences are newly sequenced, the rest obtained from GenBank. Molecular analyses of molecular data are conducted, including Bayesian inference, Maximum Likelihood, genetic distances and statistical parsimony haplotype network. Results from Bayesian Inference and Maximum Likelihood appear consistent, and the presence of 7 clades is indicated, some well supported. Morphologically distinct members of genera that are currently considered as different appear as sistergroups with very low genetic distance. Neither *Chone*, *Dialychone* nor *Euchone* appear monophyletic considering the current classification. *Paradialychone* is only represented by one sequence in the dataset, but morphological diagnostic features of this genus appear in other clades. Alternatives to diagnostic characters are discussed. At least 3 species that are morphologically and genetically distinct are new to science. A key based on the dataset of this study is provided to the species present in Norwegian waters, including the 3 new species. This indicates that there are 9 species of *Chone* and 4 species of *Dialychone* present in Norwegian waters. This study provides new data to these groups, which indicates that current classifications of these genera are not congruent with molecular characters.

Sammendrag

En revisjon av arter i slektene *Chone, Dialychone* og *Paradialychone* (Sabellidae: Annelida) i norske farvann er gjennomført med utgangspunkt i gjeldende taksonomiske beskrivelser og molekylære data. De fylogenetiske slektskapsforholdene mellom *Chone, Dialychone, Paradialychone* og *Euchone* testes og diskuteres. 66 morfologiske karakterer er samlet ved hjelp av ulike mikroskopiteknikker, Scanning Electron Micrographs (SEM) og fotografi. 57 sekvenser av det mitokondrielle genet cytochrome oxidase 1 (CO1) er anvendt i fylogenetiske analyser, hvorav 25 sekvenser er sekvensert i denne studien, og resten nedlastet fra GenBank. Fylogenetiske analyser av molekylære data inkluderer Bayesiansk analyse, Maximum Likelihood, samt genetisk distanse og haplotypenettverk. De to fylogenetiske trærne viser like slektskapsforhold, hvor sju avgrensede grupper vises, noen med høy støtteverdi. Individer med tydelige morfologiske forskjeller vises som søstergrupper med lav genetisk divergens. Hverken *Chone, Dialychone* eller *Euchone* fremstår som monofyletiske ved implementering av genetiske analyser sammenlignet med gjeldende slektsbeskrivelser. Bare én sekvens av *Paradialychone* er tilgjengelig, men karakterer i slektsdiagnosen oppstår også i andre grupper i de fylogenetiske trærne. Alternativer til beskrivende karakterer for slektene diskuteres. Molekylære data er brukt for denne gruppen for første gang. Minst tre arter som er morfologisk og genetisk forskjellige er oppdaget som nye for vitenskapen. Basert på resultatene er det laget en nøkkel til artene i norske farvann, inkludert de tre nye artene. Resultatene indikerer at de gjeldende morfologiske slektskarakterene ikke samsvarer med genetisk slektskapsforhold, og viser at det er ni arter av *Chone* og fire arter av *Dialychone* i norske farvann.

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Abbreviations

aprl	Anterior peristomial ring lobe
abd	abdomen
abdunc	Abdominal uncini
chinv	Chaetal inversion
cr	crown
CO1	Cytochrome oxidase 1
dl	Dorsal lips
dpa	Dorsal pinnular appendages
gr	Glandular ridge
mf	Main fang
rt	Radiolar tip
pin	Pinnules
pyg	pygidium
SEM	Scanning Electron Micrograph
thcc	Thoracic capillary chaeta
thunc	Thoracic uncini
vsc	Ventral shield of collar
vc	Ventral cirri (Ventral radiolar appendages, Ventral filamentous appendages)

1 Introduction

1.1 Marine biodiversity

Planet earth is the foundation of our existence. It provides a home, food and resources that are essential for our survival. This is a complex system that has evolved for millions of years, and all the components are needed for the functioning of this planet as a whole. Extensive research and technological progress has enabled us to discover and map interactions within- and between organisms, which broadens our understanding of biodiversity and the importance of it (Walker 1992, Burger & Shaffer 2008, Cooke 2008). The biggest part of the biosphere is the ocean which covers 75% of the Earth's surface (Reece et al. 2011). The ocean plays a critical part in the regulation of our climate. Life originated in the ocean (Snelgrove 2010). Evolution in a relatively stable environment for billions of years has led to extreme diversity in many taxa (Grosberg et al. 2012). The diversity of the marine ecosystem is also one of the most unknown scientific areas, with perhaps as many as two- thirds of marine species still being undescribed (Appeltans et al. 2012). Taxonomic work is therefore urgently needed in order to be able to implement sufficient monitoring of marine ecosystems.

Benthic habitats are distinct areas of seafloor with different substrate and depths (Harris & Baker 2011). Inhabited by invertebrates like molluscs, amphipods, foraminifers, annelids, crustaceans, cnidarians and microorganisms, specific species compositions constitute ecosystems adapted in response to the physical and chemical environment at different depths of the seabed. Epibenthic species are sedentary species that live on the surface of the seafloor, while inbenthic species are burrowers adapted who's niche is within the sediments. Benthic ecosystems consist of organisms from different trophic levels, like predators, scavengers, suspension- feeders and decomposers. In this way, benthos provide important bioturbation processes (Hutchings 1998). Bioturbation is particle turnover and nutrient cycling of sediment matter which regulates the functioning of ecosystems, and rate of recycling is found to correlate with species richness and species density (Solan et al. 2004, Braeckman et al. 2010, Kristensen et al. 2012, Solan et al. 2013).

Many factors affect and threaten the functioning of benthic ecosystems. Chemical pollution, plastic waste, climate change, eutrophication, translocation of invasive species, habitat destruction and fragmentation are examples of perturbations that may lead to a loss of species, which in turn makes the ecosystem more susceptible to invasive species and reduce ecosystem functioning(McNulty 1961, Gray et al. 1990, Muir et al. 1992, Solan et al. 2004). The problem of plastic microparticles is also increasing and is negatively affecting the fitness of marine benthos, with future consequences yet to be assessed (Besseling et al. 2012, Von Moos et al. 2012). Species composition may also have an impact on affect economic factors like the marine industry, such as aquaculture and fossil fuel extractions, but most importantly the consequences of a decline in biodiversity may have a negative effect on our survival through the loss of ecosystem services provided by marine biotopes (Worm et al. 2006).

1.2 Annelida/Sedentaria/Sabellidae

Annelida is an incredibly diverse group of invertebrates. There are currently more than 17 000 described annelid species, which include the commonly known earthworm and the leeches. One comprehensive monophyletic clade defined within the annelids is Sedentaria. According to molecular analysis, the Sedentaria includes the sedentary bristle worms, or polychaetes, but also the clitellates where we find the earthworms (Weigert & Bleidorn 2016). Although bristle worms are not well known to the public, except for the observant diver or the ambitious fisher, their species diversity and function makes the group fascinating. They play an important role in marine ecosystems and can be useful as ecological indicators of ecosystem status (McNulty 1961, Hutchings 1998, Dean 2008). Within Sedentaria are the fan worms (Sabellidae Latreille, 1825), also known as feather-duster worms or sabellids. Sabellids inhabit most marine environments from the littoral to the deep ocean sediments. A few species have also colonized freshwater habitats. They are important members of the fouling communities and may be susceptible to unintentional translocation in ballast water, ship hulls etc. Tracing of such species can be detected with genetic markers (Capa et al. 2013, Capa & Murray 2016). In some cases species have been reported as invasive, while others as especially adaptable to areas with anthropogenic impacts (Giangrande et al. 2012, Arias Rodríguez et al. 2013). Especially the Arctic Sea is susceptible to ecosystem degradation due to climate change and species invasions (Cheung et al. 2009). It is important to increase our knowledge about these organisms in order to assess their ecological demands, impact as potential pests and response to environmental changes.

Sabellids are sedentary tube- dwellers. Some species construct a tube by using particles from the water column mixed with self- produced mucous secreted from the buccal cavity and epidermis. In other species the formation of tubes happens while burrowing (Bonar 1972). The worms’ tube serves as a home, protecting the worm against rough environmental conditions and predators. They bear a feather/snowflake- like structure at the anterior end of their body which is particularly fragile. This is called the radiolar crown (see Figure 1), and is formed by straight appendages, called radioles, arranged in semicircles or spirals. The radiolar crown, well irrigated with a vascular system, functions as the worms' branchia, i.e. its respiratory organ (Capa et al. 2014). Some species also bear radiolar eyes in the crown, containing photoreceptor cells that can detect alterations of light. Small heavily ciliated projections in the radioles, called pinnules, create small currents that allow the worm to collect particles from the water column and lead them down to the mouth (Bonar 1972, Rouse & Pleijel 2001). These particles are then sorted and can be rejected, used as food, or used as material for the tube-building (Capa et al. 2014, Bok et al. 2016). In addition to having these essential physiological purposes, the radiolar crown is an elegant and beautiful organ, often colorful, or bearing pigmented areas reflecting sunlight. It sways gently in the water and serves as a pleasant sight for the lucky observer, or as inspiration for the environment in science fiction (e.g. the touch-sensitive plants in *Avatar* (Cameron)).

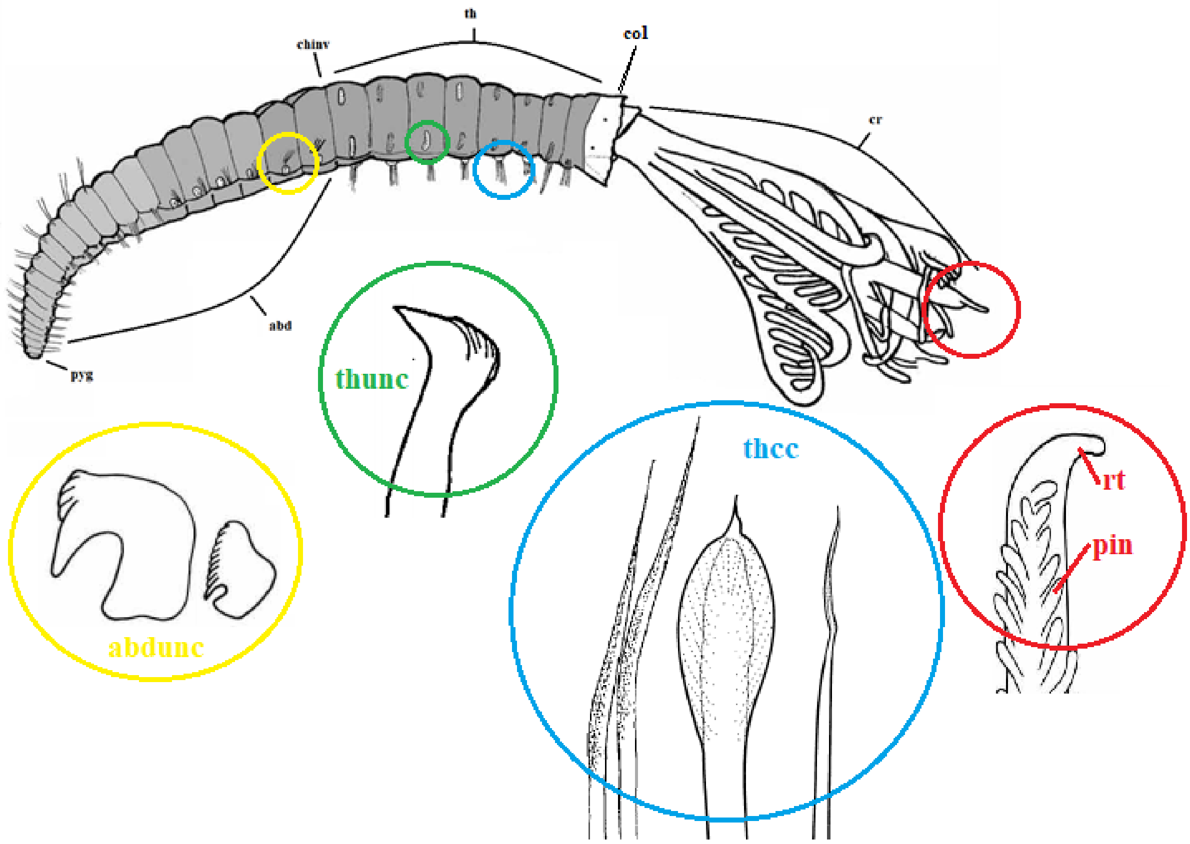


Figure 1: General sabellid morphology. Abbreviations: cr, crown; rt, radiolar tip; pin, pinnule; col, collar; th, thorax; thcc, thoracic capillary chaeta; thunc, thoracic uncini; chinv, chaetal inversion; abd, abdomen; abdunc, abdominal uncini; pyg, pygidium. Modified from (Tovar-Hernández et al. 2007) Fig 5; (Giangrande 1992) Fig 2; (Fitzhugh 1989) Fig 23.

The trunk of sabellids is split in two parts: the thorax and the abdomen, separated by the chaetal inversion in which the trunk is rotated 180 degrees. Both parts are segmented, with 8 thoracic segments and number of abdominal segments which vary between species and with developmental stage. Each segment is equipped with two kinds of chaeta: capillary chaetae, which are bristle-like, and uncini, which are hook-like. These chaetae are motile and used for movement within the tube. The worms can sense alterations in the water current and, in some species that possess photoreceptors in the crown or the trunk, alterations in light. Alterations in current or light may be signs of a predator or danger nearby, and the worm responds by retracting inside its tube at a surprisingly high speed. By doing so, its fragile crown is quickly protected by the safety of the tube. Once the danger or threat has subsided, it crawls out again, exposing its crown once more to feed and breathe.

Forty genera and over 400 species of sabellids are described in the literature (Capa et al. 2014), however, studies suggest that there might be as many as 490 species (Rouse & Pleijel 2001). Thirty- seven taxa within the sabellid family are found within Norwegian waters (Artskart , DBIF , Hansson 1998) These reports are however inconclusive because updated diagnoses, thorough morphological characterization and information about their geographic distribution is scarce and needs revision in some cases (Cochrane 2000). With the increasing use of DNA technology and DNA barcoding this may provide a useful tool. The utilization of both morphological and molecular data, i.e. integrative taxonomy, has been implemented in some genera and waters (Knight-Jones 1983, Capa et al. 2013, Capa & Murray 2015b, Capa & Murray 2015a, Capa & Murray 2016). Some genera have only a few or no DNA sequences available in GenBank (Benson et al. 2008) and Barcode Of Life Data Systems (BOLD) (Ratnasingham & Hebert 2007). Also, information about the intraspecific genetic variability or genetic structure among populations is scarce. More detailed molecular data may provide a deeper understanding of the phylogeny of sabellids, uncover cryptic species and allow us to assess the status of widespread species.

The first three subdivisions of Sabellidae was first described as Fabriciinae, Sabellinae and Myxicolinae (Rioja 1923). Subsequent revisions led to only two subfamilies: Fabriciinae and Sabellinae where Fabriciinae included 12 genera and Sabellidae 33 genera (Fitzhugh 1989, Rouse & Pleijel 2001). These numbers include the taxa Fitzhugh (1989) transferred from Fabriciinae to Sabellinae (*Euchone*, *Chone*, *Desdemona*, *Jasmineira*, *Myxicola* and *Fabrisabella*). Sabellinae is characterized by having a radiolar skeleton with at least two rows of cells, otherwise a morphologically heterogenous group. Molecular analysis later suggested subfamily Fabriciinae to be considered as family Fabriciidae, and Sabellinae is therefore currently accepted as Sabellidae (Kupriyanova & Rouse 2008, Capa et al. 2011a). The phylogeny of Sabellidae is disputed and different methods suggest different phylogenetic relationships. A cladistic analysis based on morphological characters shows a clade including *Claviramus*, *Chone*, *Euchone*, *Fabrisabella*, *Jasmineira*, *Myxicola*, *Panomethus* and *Panousea* (Fitzhugh 2003). On the other hand, a preliminary study of reproductive strategy and the 28S rRNA reveals three main groups, of which one group includes only *Myxicola*, *Chone* and *Euchone* (Patti et al. 2003), which is partly supported by analysis of 28S,18S and H3 which resulted in *Myxicola*, *Chone*, *Euchone* and *Amphicorina* forming a clade (Kupriyanova & Rouse 2008). Furthermore, a cladistic analysis by Cochrane (2003) suggests *Euchone* as a paraphyletic group based on the length and distribution of pinnules, and the form and number of segments of the anal depression. This might indicate that both molecular and morphological data is useful when assessing phylogeny.

1.3 Study area

The study area is based on current literature describing oceanography in the respective areas (Blindheim & Rey 2004, OSPAR 2010, Yashayaev et al. 2015, Nygren et al. (In review)). The Nordic Seas (Greenland, Iceland and Norwegian Seas) represent the most northern part of the Atlantic Ocean and constitute the connection to the Arctic Sea, north of Svalbard, see Figure 2 (Oug et al. 2017). The North Sea represents the southern areas of this study. The material is sampled from 0-608 m, sampled from five areas, which are defined below with designated area code.

The Barents Sea (Area I) is described as cold water shelf sea areas. In the western areas and along the coasts of Troms and Finnmark, it is influenced by North Atlantic Waters (Ingvaldsen & Loeng 2009). Material from nine locations within this area is studied, including the White Sea.

The Greenland Sea (Area II) is described as cold water areas, with influxes from the Arctic ocean caused by the East Greenland Current. It ranges from east of Iceland, past Jan Mayen to Svalbard (Blindheim & Rey 2004, Yashayaev et al. 2015). Material from two locations within this area is studied.

The Norwegian coast (Area III) represents coastal areas over a depth of 200 m, ranging from Egersund to Loppa. These are a mix of North Atlantic Water masses and the less saline

Norwegian Coastal Current (Sætre 2007). Material from five locations within this area is studied.

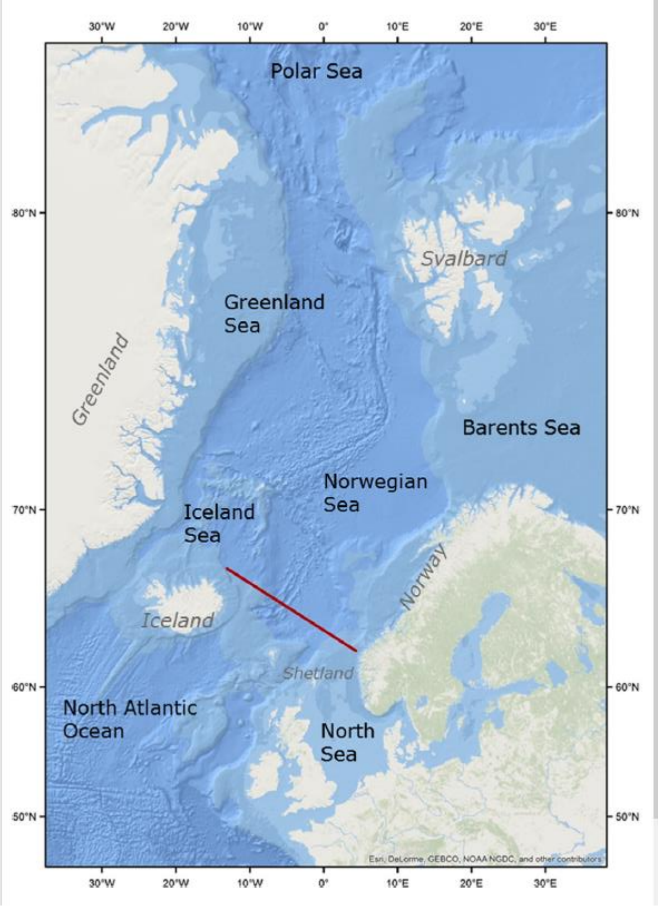


Figure 2: Barents Sea, Greenland Sea, Norwegian Sea and North Sea, From (Oug et al. 2017).

The Norwegian Continental Shelf (Area IV) describes deeper areas between 200 and 600 m off the Norwegian coast and fjord areas which are influenced by North Atlantic Water inflow (Blindheim & Rey 2004). Material from one location within this area is studied.

The North Sea (Area V) is described as shallow shelf areas, except for the Norwegian Trench along the southern coast of Norway, which acts as a channel to the Norwegian Sea. It is influenced by the Norwegian Coastal current in the northern parts, and warm North Atlantic water masses in the southern parts (Rodhe et al. 1996, Hjøllo et al. 2009). Material from eight locations within this area is studied.

The number of polychaete species decline towards the deep oceans outside the shelves, indicating a need for more extensive research (Kongsrud et al. 2011). Such results indicate that finer biogeographical definitions including these deep areas are required (OSPAR 2010, Watling et al. 2013, Yashayaev et al. 2015).

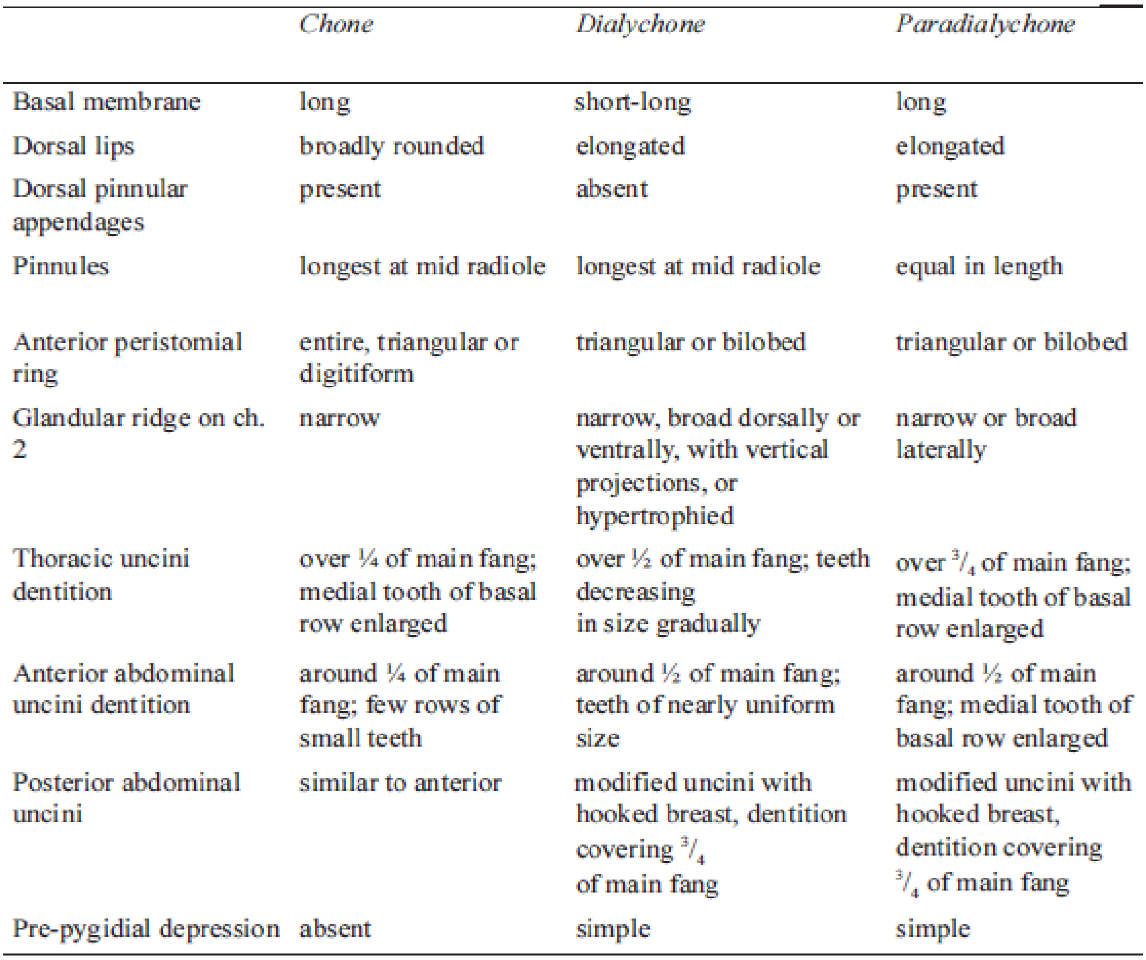
1.4 *Chone* Krøyer, 1856, *Dialychone* Claparède, 1868 and *Paradialychone* Tovar-Hernández, 2008

Recent cladistics analysis of *Chone* reveals that this does not entail one, but three different genera: *Chone*, *Dialychone* and *Paradialychone* (Tovar-Hernández 2008). However, it has been a long and winding road to this taxonomic classification and they are currently some of the least understood sabellid genera (Cochrane 2003).

These three genera have been characterized by having a palmate membrane connecting the lower part of the radioles, i.e. melted crown (Krøyer 1856), a ventrally intact collar and dorsally fused branchial lobes. *Chone* is based on the synapomorphies of dorsal lips broadly rounded, thoracic uncini with a large tooth above the mf, located in midline, and thoracic and anterior abdominal uncini with dentition covering one- quarter of the mf. *Dialychone* is currently based on lacking dorsal pinnular appendages, pinnules longest mid- radiole, elongated dorsal lips, ventral shield undifferentiated, dentition of thoracic uncini slightly diminishing in size posteriorly, unequal in size, abdominal uncini modified posteriorly and having a simple anal depression. *Paradialychone* is based on having elongated dorsal lips, dorsal pinnular appendages present, pinnules similar in length along entire radiole, ventral shield undifferentiated, enlarged second tooth of uncini and a simple anal depression (Tovar-Hernández 2008).

A summary of the diagnostic features of the three genera is shown in Table 1. Deviations from these features have been found in some species (Capa & Murray 2015b).

Table 1: Diagnostic features of *Chone*, *Dialychone* and *Paradialychone* (Modified from Capa & Murray (2015)).



	Chone	*Dialychone*	*Paradialychone*
Basal membrane	long	short-long	long
Dorsal lips	broadly rounded	elongated	elongated
Dorsal pinnular appendages	present	absent	present
Pinnules	longest at mid radiole	longest at mid radiole	equal in length
Anterior peristomial ring	entire, triangular or digitiform	triangular or bilobed	triangular or bilobed
Glandular ridge on ch. 2	narrow	narrow, broad dorsally or ventrally, with vertical projections, or hypertrophied	narrow or broad laterally
Thoracic uncini dentition	over ¼ of main fang; medial tooth of basal row enlarged	over ½ of main fang; teeth decreasing in size gradually	over $^{3}/_{4}$ of main fang; medial tooth of basal row enlarged
Anterior abdominal uncini dentition	around ¼ of main fang; few rows of small teeth	around ½ of main fang; teeth of nearly uniform size	around ½ of main fang; medial tooth of basal row enlarged
Posterior abdominal uncini	similar to anterior	modified uncini with hooked breast, dentition covering $^{3}/_{4}$ of main fang	modified uncini with hooked breast, dentition covering $^{3}/_{4}$ of main fang
Pre-pygidial depression	absent	simple	simple

Chone currently entails 21 valid species worldwide, of which 7 species have been registered, in the study area: *C. duneri* Malmgren, 1867, *C. fauveli* McIntosh, 1916, *C. paucibranchiata (Krøyer, 1856)*, *C. filicaudata* Southern, 1914, *C. infundubuliformis* Krøyer, 1856, *C. heterochaeta* Hofsommer, 1913 and *C. kroyerii* Sars, 1862 (Tovar-Hernández 2008, Read 2018). Within the genus *Dialychone* there is 18 valid species, with 2 species which reported in the area of study: *D. collaris* (Langerhans, 1881) and *D. normani* (McIntosh, 1916) (Tovar-Hernández 2008, Nishi et al. 2009, Tovar-Hernández & Dean 2010, Selim et al. 2012, Read 2018). *Paradialychone* entails 16 valid species, of which none are reported in the study area (Hansson 1998, Tovar-Hernández 2008, Nishi et al. 2009, Tovar-Hernández & Dean 2010, Capa & Murray 2015b, Read 2018).

1.5 Aims

The aims of this thesis are to (i) assess whether the current taxonomic classifications of species of *Chone, Dialychone, Paradialychone* in Norwegian waters are congruent with the molecular data, (ii) test the monophyly of *Chone*, *Dialychone*, *Paradialychone* and *Euchone* using molecular data and (iii) discuss possible solutions to any incongruent taxa.

To answer morphological research questions I have studied in detail the morphology of specimens in museum collections and collected material in Trondheim, Bergen and the White Sea. By using different microscopic techniques, morphological descriptions and images of the material available, a character matrix has been generated. One gene (CO1) has been sequenced from material, or downloaded from GenBank. Phylogenetic analyses and pairwise distances have been calculated using molecular data. Distribution information has been revised, and a key to species present in Norwegian waters is provided. The data have been compared in order to assess indications of discrepancy between current morphological classification and molecular analyses.

This has been done because to have an accurate number of species and know how to identify them is essential when working with biology. The consequence of a poorly revised group is a lack of knowledge in biodiversity, which is the foundation of monitoring and assessing fauna. Knowing whether they are morphologically and genetically distinct and assessing the intergeneric genetic relationship between genera can help increase our understanding of the group.

2 Materials and methods

2.1 Material borrowed and collected

The specimens used in this project were either collected and studied alive before fixation, or preserved specimens were borrowed from collections in natural history museums and research institutions. Live specimens were collected in the Trondheimsfjord at Sletvik Biological Station (NTNU), in Raunefjord at the Marine Biological Station Espegrend of the University of Bergen (UiB) and the White Sea Biological Station (WSBS) of Moscow State University. Material was collected by scuba diving or grab. Specimens and tissue samples for molecular analysis were fixed and preserved in 96 % Ethanol (EtOH), while other specimens used for morphological studies and long term preservation were fixed in 10 % Formalin (FA) and preserved in 75 % EtOH or fixed in Bouin solution and preserved in 75 % EtOH.

The collections at the NTNU University Museum, the University Museum of Bergen and the White Sea Biological Station were examined. Some specimens were also supplemented from the Mediterranean Sea from Mallorca. The material was either preserved in 96 % EtOH or fixed in 10 % FA and preserved in 75 % EtOH.

2.2 Morphological studies

Material was studied using a Leica MZ APO Stereomicroscope (Leica 10472648). Staining patterns of glandular tissue was studied using methyl blue. Photographs of live and fixed specimens were taken using a Leica DFC 290 with Leica Application Suite software attached to a stereomicroscope Leica M 165 C. Live animals were sedated using Magnesium chloride in order to inhibit movement and get clear, detailed photographs.

Parapodia in fixed specimens, usually 2nd, 7th, 9th and posteriormost segments, were removed using forceps or scalpel and mounted with glycerin and immersion oil was used on glass slides for studying chaetae with Leica DM LB2 Microscope. Drawings of the chaetae were made to scale using a camera lucida. Digitalization of the drawings were made using GNU Image Manipulation Program (GIMP) 2.8.22 (Montesanto 2015).

Selected specimens were dehydrated in Acetone, critical point dried and coated with silver (Ag) and examined under scanning electron microscopy (SEM) using HITACHI S405-A using a filament source (see Figure 3) at the White Sea Biological Station, or coated with Gold palladium and examined using Teneo Valumsko 106 8566 LO VAC with a FEG source at the Cellular & Molecular Imaging Core facility (CMIC) at NTNU.

Figure 3: Scanning Electron Micrograph, HITACHI S405-A, at the White Sea Biological Station (Photo: Tuva Bongard Munkeby).

2.3 Formatted descriptions and key

A character matrix was built in Description Language for Taxonomy using morphological data from direct study of specimens (DELTA Editor, v 1.02, 2011) (Dallwitz et al. 1999). This was done in order to produce formatted descriptions and species key. The matrix included characters and states previously used in literature (Banse 1972, Cochrane 2000, Tovar-Hernández & Sosa-Rodríguez 2006, Tovar-Hernández et al. 2007, Tovar-Hernández 2008), with some additions and modifications in order to assemble all characters defined for these genera. Unordered multistate, real numeric and absence/presence coding methods were used. Action command translate into natural language was used in order to compute descriptions.

2.4 DNA extraction, amplification and purification

Tissue samples from the radioles, or trunk when crown was missing, were sampled from 63 specimens of approximately 12 species of 3 genera. Forceps and scalpel was cleaned between each sample using EtOH96 and a glass alcohol lamp. DNA extraction and amplification (Polymerase Chain Reaction, PCR) was conducted at the genetics lab at the NTNU University Museum. DNA extraction was performed using DNeasy Tissue Kit (Qiagen, GmbH, Hilden, Germany) following the manufacturer's instructions. To amplify the mitochondrial gene CO1, the following reagents were used: 2.0 µl DNA template, 2.5 µl PCR buffer (Qiagen, Hilden, Germany), 2.0 (10 mM) µl dNTP mix (TaKaRa, Shiga, Japan) , 1.0 (100 µM) µl Fprimer, 1.0 (100 µM) µl Rprimer , 0.13 µl TaKaRa Ex Taq HS (TaKaRa, Shiga, Japan) and 16.37 µl

dH_2O (a total volume of 25 µl). PCR amplification was performend using BioRad T100 or BioRad C1000 thermal cycler (BioRad Laboratories) using two primers: LCO1490/HCO2198 (Folmer 1994) of 650 basepairs and ArF5/ArR5 (Gibson et al. 2014) of about 300 basepairs. PCR cycles for LCO1490/HCO2198 started at 95°C for 3 minutes. Then 40 cycles at 95°C for 30 seconds, 48°C for 30 seconds and 72°C for 1 minute followed, with a final extension of 72°C for 7 minutes. PCR cycles for ArF5/ArR5 primers started at 95°C for 3 minutes. Then 40 cycles at 94°C for 30 seconds, 46°C for 30 seconds and 72°C for 30 seconds followed, with a final extension of 72°C for 7 minutes. This was conducted on a total of 111 samples in a total of 7 PCR runs. 15 specimens were sent to sequencing from Bergen, 4 of these were successful sequences but deemed contaminated and not included in the analysis.

Protein detection of PCR products was carried out using gel electrophoresis. An agarose mix of 1.25% agarose in 1x TAE buffer was made, colored with 0.0033% SYBR green. In each well 1.5 µl DNA Loading dye and 4 µl sample was added. For every 10th well, 3 µl of DNA Ladder was added. Power for electrophoresis was set to 120V using a 300V Power Source (VWR, Radnor, PA). Images were acquired using GeneSnap from SynGene software (Version 6.08, Cambridge, England). The final PCR products were cleaned with illustra ExoProStar 1-Step (GE Healthcare, Little Chalfont, UK), and sent to the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario, Canada.

2.5 Phylogenetic analysis

Consensus sequences (contigs) of the forward and reverse sequence strands were made and edited using Sequencher v 4.8 (Gene Codes Corporation, Ann Arbor, MI USA), and a sequence similarity search was performed using the Basic Local Alignment Search Tool (BLAST) in Genbank (Benson et al. 2008), which resulted in 25 uncontaminated viable sequences of the COI gene. Published and unpublished sequences in the Barcode of Life Data System (BOLD) (Ratnasingham & Hebert 2007) and GenBank were also BLASTed, which resulted in 29 sequences, including two sequences of *Euchone*. Two outgroups, *Myxicola* and *Amphiglena*, were chosen based on the phylogenetic analysis of Capa et al. (2014) because these genera are closely related to, but does not fall within, the ingroup. Three sequences were included from the outgroups, which gave a total of 57 sequences in the analysis. The homologous sites of the sequences were aligned using MAFFT version 7, using the default option L-INS-I method, which is one of the most accurate multiple sequence alignment options (Katoh & Toh 2010, Katoh et al. 2017). Eight sequences of 28S ribosomal RNA were also downloaded from from BOLD, BLASTed and aligned similarly as the COI sequences, and a separate preliminary analysis was performed on these sequences using *Amphiglena mediterranea* as outgroup. These sequences were considered uninformative and not included in the analyses because they were from two different regions of the 28S gene, and the sequences were short and alignment produced gaps.

The aligned sequence file was converted from FASTA to NEXUS using ALTER (Glez-Peña et al. 2010). The best fitted substitution model with AIC values were calculated using JModeltest (Darriba et al. 2012). A Bayesian inference tree with posterior probabilities was calculated using MrBayes v3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003), using substitution model GTR+I+G (AIC=15359.382080) and 2 000 000 generations in the Markov Chain Monte Carlo with a sampling frequency of 1000, reaching a standard deviation of frequencies= 0.006842. A Maximum Likelihood tree with bootstrap values was calculated using RaxML Blackbox (Stamatakis et al. 2008). Trees were rooted in *Amphiglena mediterranea* using FigTree (Rambaut 2017) and visually edited using GIMP.

2.6 Genetic distances

The sequences were trimmed 12 base pairs at beginning and end of sequence (= 657 bp) and gaps were replaced with N using BioEdit (Hall 1999). Pairwise distance between groups were calculated using MEGA 7 (Kumar et al. 2016) on 54 sequences, excluding the outgroups (See Table 1 for group definitions). Two calculations of pairwise distance were calculated using no variance estimation method, including transitions and transversions, homogenous pattern among lineages and pairwise deletion of missing data. One was calculated using P- distance substitution model and uniform rate variation among sites. The second using the Maximum Composite Likelihood model (Tamura et al. 2004) and Gamma distributed rate variation among sites (shape parameter= 1). Codon positions included were 1^{st}+2^{nd}+3^{rd}+Noncoding. All ambiguous positions were removed for each sequence pair. The within group mean distance values were also calculated. The results are presented in Table 3 in Appendix II.

2.7 Haplotype networks

The sequences were trimmed 40 base pairs at the beginning and 90 base pairs at the end (=530 bp) in order to minimize amount of missing data using BioEdit. The FASTA file was converted to PHYLIP using ALTER. Haplotype networks were calculated using a 95% connection limit using TCS (Clement et al. 2000) on 54 sequences and visualized using PopART (Leigh & Bryant 2015). Visualizations of results were made using GIMP.

Table 2: List of sequences of *Chone*, *Dialychone*, *Paradialychone* and *Euchone*, and the clades which they belong to in Figure 4. Terminal number equals CO1 accession number in BOLD (underlined) for published data, and terminal number for unpublished data. Species name and grouping for genetic distance is given. Voucher ID is given for material available.

Clade	**Terminals/ CO1**	**Taxa**	**Voucher**	**Group number genetic distance**
1	POLNB1857-15	*C. kroyerii*	ZMBN98851	4
1	LABBI018-09	*C. mollis*	-	3
1	ARCMI387-14	*C. mollis*	-	3
1	ARCMI381-14	*C. mollis*	-	3
1	ARCMI380-14	*C. mollis*	-	3
1	TB23	*C. paucibranchiata*	NTNU-VM	2
1	TB01	*C. infundibuliformis*	NTNU-VM	1
1	TB02	*C. infundibuliformis*	NTNU-VM	1
1	TB03	*C. infundibuliformis*	NTNU-VM	1
1	TB04	*C. infundibuliformis*	NTNU-VM	1
1	TB05	*C. infundibuliformis*	NTNU-VM	1
1	TB06	*C. infundibuliformis*	NTNU-VM	1
1	TB12	*C. sp.* y	NTNU-VM	5
2	KBPOL573-11	*C.* sp	-	6
2	KBPOL562-11	*C.* sp	-	6
2	POLNB1443-15	*C. fauveli*	-	7
2	TB48	*C. sp.* 1	NTNU-VM	8
2	NBPOL375-08	*C. infundibuliformis*	-	9
2	TB07	*C. fauveli*	NTNU-VM	10
2	TB09	*C. fauveli*	NTNU-VM	10
2	TB10	*C. fauveli*	NTNU-VM	10
3	BCPOL965-10	*C.* sp	-	11
3	BCPOL964-10	*C.* sp	-	11
3	CMBIA168-11	*P. ecaudata*	-	12
3	BCPOL320-08	*C. magna*	-	13
3	BCPOL382-08	*C. magna*	-	13
3	BCPOL21-08	*C. magna*	-	13
3	BCPOL319-08	*C. magna*	-	13
3	BCPOL316-08	*C. magna*	-	13
3	BCPOL217-08	*C. magna*	-	14
3	BCPOL123-08	*C. magna*	-	14
3	BCPOL813-10	*C. magna*	-	14

3	BCPOL216-08	*C. magna*	-	14
3	BCPOL820-10	*C. magna*	-	14
3	BCPOL730-10	*C. magna*	-	14
3	BCPOL194-08	*C. magna*	-	14
3	BCPOL036-08	*C. magna*	-	14
4	BCAS068-14	*E. rosea*	-	15
4	TB40	Sabellidae gen. sp.	NTNU-VM	16
4	TB26	*C.* cf *duneri*	NTNU-VM	17
4	TB27	*C.* cf *duneri*	NTNU-VM	17
4	CCANN894-09	*C.* sp	-	18
4	TB34	*D. sp.* 1	NTNU-VM	19
5	POLNB1854-15	*E. sp.* 2	-	20
5	TB44	*E. sp.* 1	NTNU-VM	21
6	TB55	*D. collaris*	NTNU-VM	22
6	TB56	*D. collaris*	NTNU-VM	22
6	TB57	*D. collaris*	NTNU-VM	22
6	TB58	*D. collaris*	NTNU-VM	22
6	TB60	*D. normani*	NTNU-VM	23
6	TB59	*D. sp.* 2	NTNU-VM	25
6	TB61	*E sp. chiade*	NTNU-VM	26
6	TB62	*D. sp.* 3	NTNU-VM	24
7	POLNB1863-15	*C. duneri*	-	27

3 Results and discussion

In this chapter the results of the molecular analyses will be presented in three parts: 3.2 Genetic distances and 3.3 Haplotype networks. A summary of these results are written for each clade in 3.4 Summary of molecular results. Results of the morphological analysis, including discussion of species according to morphological and molecular data, are formulated in 3.5 Morphological analysis. In light of these findings, an evaluation of the phylogenetic status of Chone, Dialychone, Paradialychone and Euchone and possible resolutions is discussed in 3.6 Monophyly of genera. A key based on the morphological characters of the material studied is given in 3.7 Key to species of *Chone* and *Dialychone* in Norwegian waters. Finally, a discussion of morphological characters is given in 3.8 Discussion of characters.

3.1 Phylogenetic analysis

The phylogenetic results are found in the Bayesian inference tree in Figure 3, and Maximum Likelihood in Figure 26 Appendix I. These show a presence of seven clades, which are based on the maximum number of specimens in the same genus based on taxonomic classification. The two trees are congruent, and recover the same clades, some well supported.

All of the species that have more than one specimen are monophyletic except for *C. duneri, C. infundibuliformis, C. magna* and *C. fauveli*. These species give reason for caution and will be discussed further under 3.5 Morphological analysis. All of the genera with more than one specimen appear paraphyletic, this will be discussed further under 3.6 Monophyly of genera.

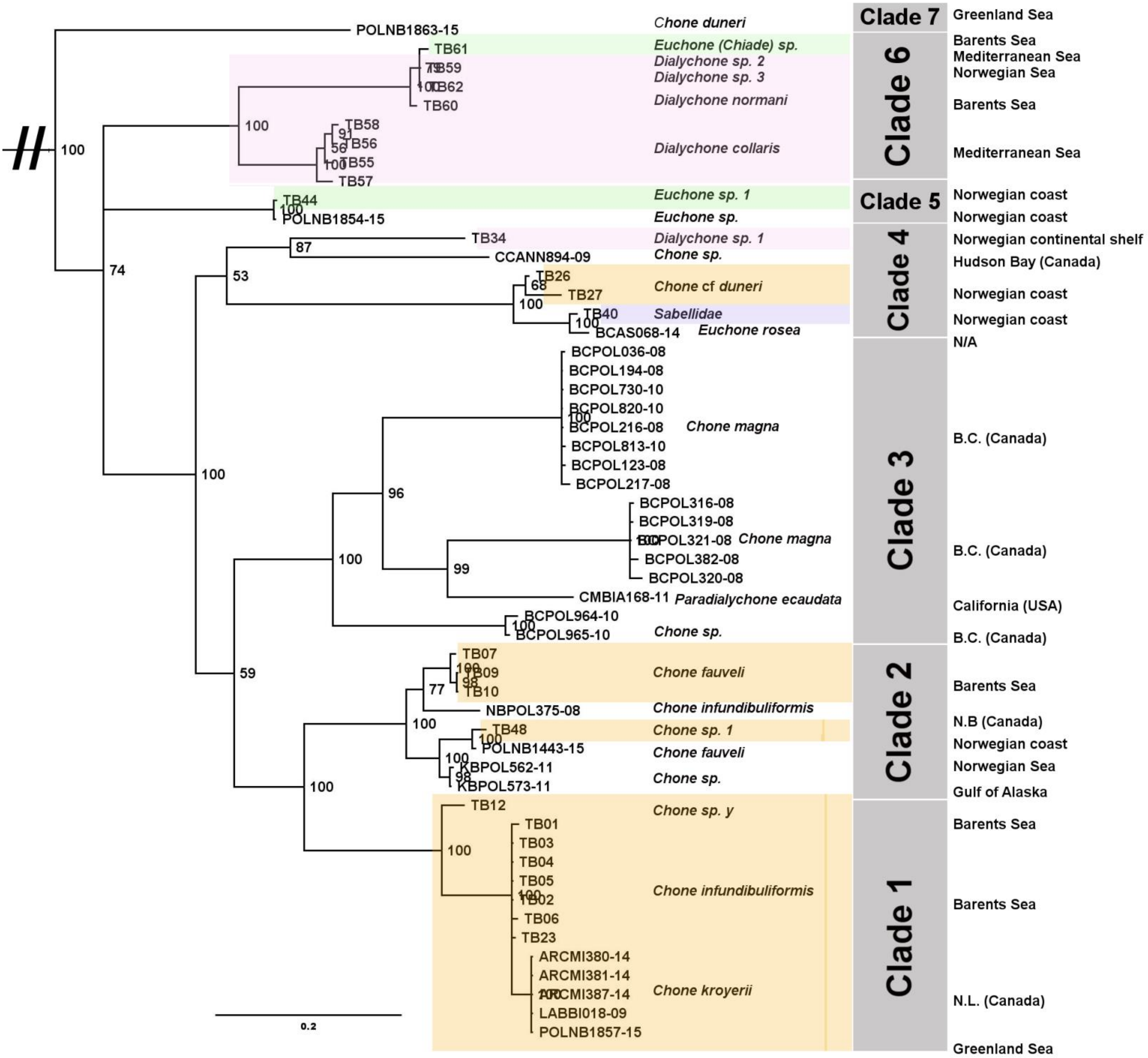


Figure 4: Bayesian inference tree of CO1 fragment of *Chone*, *Dialychone*, *Paradialychone* and *Euchone*. The analysis included a total of 57 sequences. The sequences where material was available for morphological studies is marked in colors according to current classification (*Chone* orange; *Dialychone* pink; *Euchone* green; Sabellidae blue). Species name and sampling site indicated to the right of each terminal. The outgroups were included in the analysis but is not represented in this figure in order to make the ingroup visual. Including node labels showing posterior probabilites and branch length values.

3.2 Genetic distances

Table 3 in Appendix II shows the calculated genetic distances between groups according to. Within group distance values are marked in red and low between group pairwise distance values (<0.027) are marked in blue. The value of 0.027 is based on studies by Hebert et al. (2003) and is not used as a threshold for delimiting species in this study, but as a supplement to the molecular and morphological dataset. The terminals are divided in 27 groups based on morphological differences. The intergenetic distance ranges from 0.0- 75.3 %, and the intragenetic distance from 0.0- 2.7 %. These values are somewhat similar to or higher than what is found in other polychaetes. (Nygren et al. 2009, Nygren et al. 2010).

3.3 Haplotype networks

The haplotype network analysis resulted in 37 haplotypes and 18 networks. Results are shown in Figure 5 with Clade and group number (as used in Genetic distances), singletons or networks with less than three (< 3) sequences are not presented. Bars between haplotypes indicate number of mutations. The results are congruent with the phylogenetic analyses.

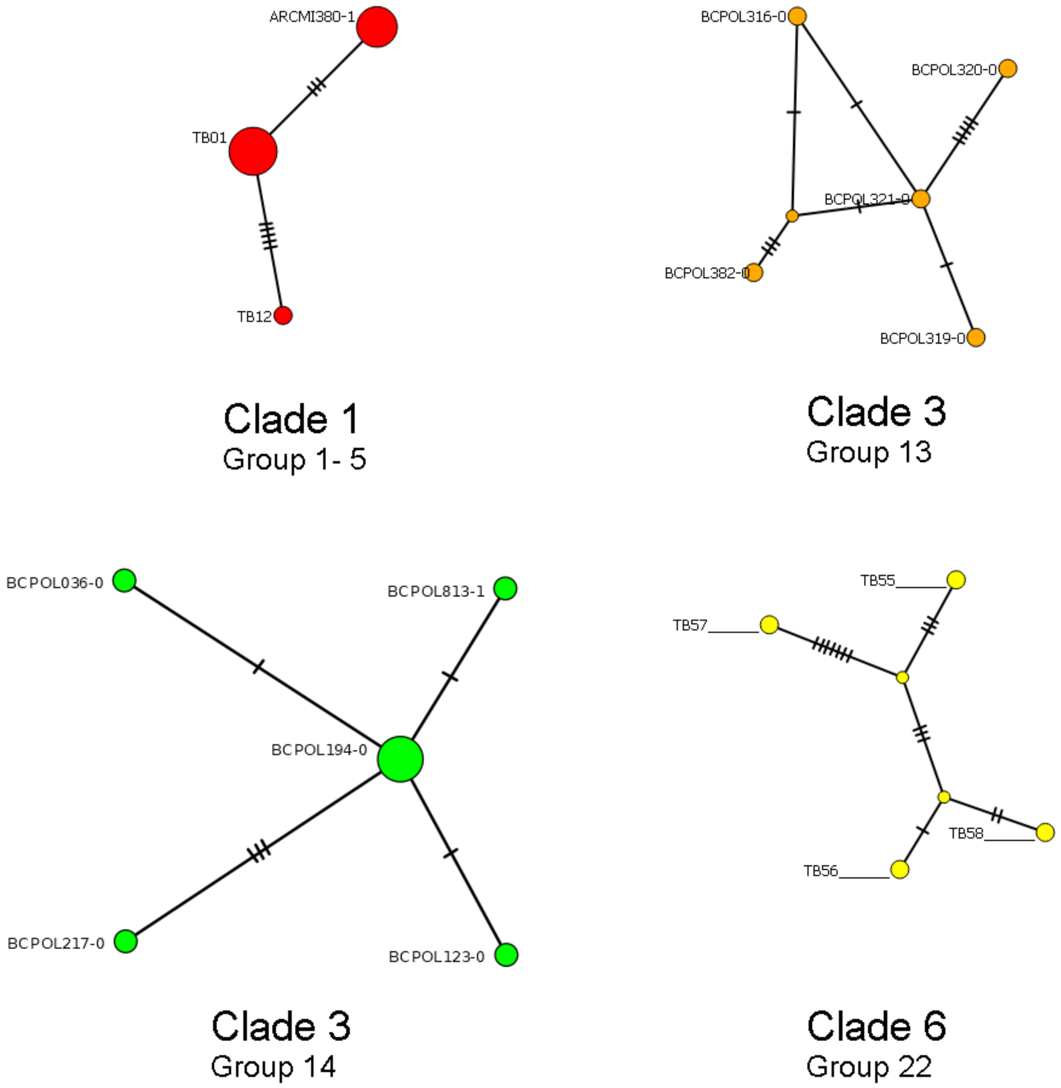


Figure 5: Haplotype network for CO1 of *Chone* and *Dialychone*. Each bar across a line connecting two specimens denotes one mutation. For terminals within groups see Table 2.

3.4 Summary of molecular results

Clade 1 This clade is well supported (pp=100, bs=98). It gathers 13 terminals, 3 haplotypes, 1 network and 3 species, namely *C. kroyerii* (within pairwise distance 0.0 %), *C. infundibuliformis* (0.2 %) and *C.* sp. y. The intergenetic divergence ranges from 0.3- 4.8 %. The material unavailable for this study are ARCMI380-14, ARCMI381-14, LABBI018-09 and ARCMI387-14. These are from Canada, originally identified as *C. mollis.*

Clade 2 This clade is well supported (pp=100, bs=99). It gathers 8 terminals, 6 haplotypes, 4 networks and at least 2 species, namely *C. fauveli* (within pairwise distance 0.4 %) and

C. sp. 1. The material unavailable for this study is NBPOL375-08, POLNB1443-15 and KBPOL562-11+KBPOL573-11 (0.2 %).The intergenetic divergence ranges from 2.8- 8.6 %, except for between *C.* sp. 1 and POLNB375-08 where it is 0.9 %. They are the same haplotype.

Clade 3 This clade is well supported (pp=100, bs=99). It gathers 16 terminals, 11 haplotypes, 4 networks and 3 species, namely *C. magna* (within pairwise distance 0.2- 0.7 %), *P. ecaudata* and *C.* sp. (0.9 %). The intergenetic variance ranges from17.2- 22.4 %. None of the material was available for this study.

Clade 4 This clade is poorly supported (pp=53, bs=55). It gathers 6 terminals, 6 haplotypes, 4 networks and 2 species, namely *C.*cf *duneri* (within pairwise distance 2.7 %) and *D.* sp. 1. The material unavailable for this study is CCANN894-09 and BCAS068-14. The intergenetic divergence in this clade ranges from 5.5- 28.6 %, except for the divergence between TB40 and BCAS068-14 which is 1.4 %.

Clade 5 This clade is unresolved when using Bayesian inference, and poorly supported when using Maximum Likelihood (bs=56). It gathers 2 terminals, 2 haplotypes, 1 network and 1 or 2 species. The intergenetic variance is 0.2 %. The material unavailable for this study was POLNB1854-15.

Clade 6 This clade is well supported (pp=100, bs=100). It gathers 8 terminals, 6 haplotypes, 3 networks and 5 species, namely *D. collaris* (within pairwise distance 1.3 %), *D. normani, D.* sp. 2, *D.* sp. 3 and *Euchone* (Chiade) sp. All of this material is available for this study. Intergenetic divergence ranges from 0.2- 16.4 %.

Clade 7 This clade is separated at the basal node of the ingroup and is well supported (pp=100, bs=100). It gathers 1 terminal, 1 haplotype and 1 network. This material is unavailable for this study.

3.5 Morphological analysis

In this chapter the analyses of the morphological analyses are presented followed by a discussion of morphological and molecular results for each species. Distribution range is based on documented distribution presented by Horton et al. (2018).

Chone Krøyer, 1856

Chone Krøyer, 1856, p.13; Sars, 1862, p.119; Malmgren, 1866, p.404; Langerhans, 1881, p.111; Hofsommer, 1913, p.332; McIntosh, 1923, p.287; Fauvel, 1927, p.334; Day, 1967, p.776; Banse, 1972, p.460; Fitzhugh, 1989, p.67; Giangrande, 1992, p.518; Tovar-Hernández and Sosa-Rodíguez, 2006, p.36–37.

Parachonia Kinberg, 1867, p.355.

Megachone Johnson, 1901, p.430.

Metachone Bush in Moore, 1904, p.190.

Type species

Chone infundibuliformis Krøyer, 1856, by original designation (redescribed by Tovar-Hernández and Sosa-Rodríguez 2006).

Diagnosis - Large-bodied sabellid species. Branchial lobes fused dorsally. Radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges present. Dorsal lips broadly rounded, as long as wide, without mid-rib, vascularized by plexus of small blood vessels derived from basal branchial blood vessels; dorsal lips with hyaline cartilage, but without branchial skeleton extensions. Longest pinnules at midradiole. Ventral lips present, broadly rounded. Dorsal and ventral pinnular appendages present. Anterior peristomial ring lobe entire, triangular or digitiform. Posterior peristomial ring collar present. Narrow glandular ridge on chaetiger 2. Ventral shields absent. Notopodia in chaetiger 1 with two groups of elongate narrowly hooded chaetae in C-shaped arrangement. Notopodia in chaetigers 2–8 with superior group of chaetae in two irregular rows, all elongate, narrowly hooded; inferior group with one anterior row of short bayonet chaetae, two posterior rows with symmetrical, mucronate (or with very fine hairs instead) paleate chaetae. Thoracic neuropodia bearing acicular uncini with teeth above main fang unequal in size, median tooth of basal row enlarged, hood present, handles long. Dentition of thoracic uncini occupying one-quarter of the main fang length. Anterior abdominal segments with two transverse rows of elongate, narrowly hooded chaetae, chaetae from the anterior row shorter than chaetae in posterior row;

uncini with well developed rectangular breast, handles absent, main fang well developed, few rows of small teeth covering one-quarter of the main fang length; intrafascicular variation: older uncini, located dorsalmost in torus, smallest in size, younger uncini, located abdominal uncini by shading. ventralmost in torus, biggest in size. Posterior abdominal segments with very elongate, narrowly hooded chaetae; uncini shape and intrafascicular variation similar to those in anterior abdominal segments (From Tovar-Hernández (2008): 2216- 2218).

Remarks – According to the analyses of CO1 fragment, the current classification makes this genus appear paraphyletic. Possible diagnostic features for the clades in the present study, based on the molecular results and the material available are further discussed under 3.6 Monophyly of genera. According to the results the following genus description amendments should be considered: Pinnules longest at mid- radiole, i.e. snowflake- shaped, or similar in length along entire radiole, i.e. featherduster- shape. Dorsal pinnular appendages absent, or present. ventral cirri absent, or present. Anterior margin of collar smooth. Dorsal and ventral incisions of collar absent. Dentition of thoracic uncini second tooth enlarged, or teeth slightly diminishing in size posteriorly, covering from one- quarter to three- quarters of the mf length. Inferior thoracic notochaeta paleate or pseudospatulate. Abdominal uncini with teeth of nearly uniform size, or second tooth enlarged, covering from one- quarter to three- quarters of the mf length. Peristomial eyes and glandular ridge on anterior abdominal segments absent. Anal depression, pygidial eyes and pygidial cirrus absent.

Chone kroyerii Sars, 1862

Chone kroyerii Sars, 1862: 35-37.; Cochrane, 2000: 144- 145.; Tovar-Hernández, 2007: 45-47.

Material examined – The Greenland Sea (Area II): Svalbard, 78.2072’N 13.9333’E, 1 September 2009, 157 m, 1. September 2009 (1 specimen). 69.48375’N 53.93836’W, 16 September 2013, 10 m (1 specimen). The Barents Sea (Area I): Finnmark, 70.62533’N 30.51400’E, 14 April 2014, 89-91 m (1 specimen).

Description – Size 6- 7 mm. Palmate membrane extending two- thirds to three- quarters of the branchial crown length. Number of pair of radioles 11. Radiolar pigmentation white spots within skeleton cells. Radiolar flanges broad. Radiolar tips length up to one- eighth of the branchial crown length, tips tapering, or broad. Pinnules length longest mid- radiole, i.e. snowflake- shape. Dorsal lips broadly rounded, as long as wide. Dorsal pinnular appendages present. ventral cirri present. Length of the basal lamina of the branchial crown shorter than collar segment (median area in lateral view).

Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarrectangular, swollen. Mid- dorsal collar gap narrow. Dorsal pockets well developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe triangular, covered by collar margin. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation present. Dorsal glandular epithelium does not stain with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini in a single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate, medium mucro. Dentition of thoracic uncini enlraged second tooth, covering a half of the mf length.

Ventral, glandular pattern in bands on posterior abdomen. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior and posterior abdominal uncini squared. Dentition of anterior and posterior abdominal uncini teeth slightly diminishing in size posteriorly, covering a half of the mf length. Posterior margin of pygidium rounded.

Remarks – The molecular analysis indicate that *C. kroyerii* is genetically identical to *C. mollis* (Figure 4, Clade 1). *C. kroyerii* is characterized by having a rectangular ventral shield of collar(horseshoe in *C. mollis*), broad dorsal gap (narrow in *C. mollis*), broad radiolar tips (filiform in *C. mollis*) and paleate notochaeta with medium mucro (absent or minute mucro in *C. mollis*) (Tovar-Hernández 2007, Tovar-Hernández 2007). Both *C. kroyerii* and *C. mollis* is described as dentition of thoracic uncini covering a quarter of the mf length, second tooth enlarged. In this material *C. kroyerii* has a swollen vsc, which is described for *C. mollis* (Tovar-Hernández 2007). *C. mollis* is distributed in California, Western Mexico and the Pacific coast of Panama (Tovar-Hernández 2007).

The voucher specimens for the sequences of *C. mollis* in this analysis are collected on the East coast of Canada. Photographs of these specimens show broad radiolar tips (ARCMI381-14, ARCMI387-14, LABBI018-09). In order to assess the possibility of *C. kroyerii* and the *C. mollis* sequences to be the same species investigation of chaetae, dorsal gap and radiolar tips in the voucher specimens of the Canadian specimens is encouraged. If this is the case, *C. kroyerii* has a wider distribution than currently assumed. It appears in the same haplotype network as *C. infundibuliformis* and *C.* sp. y, but is morphologically different.

Distribution –Norwegian coast. *Amendment:* Greenland Sea, Barents Sea.

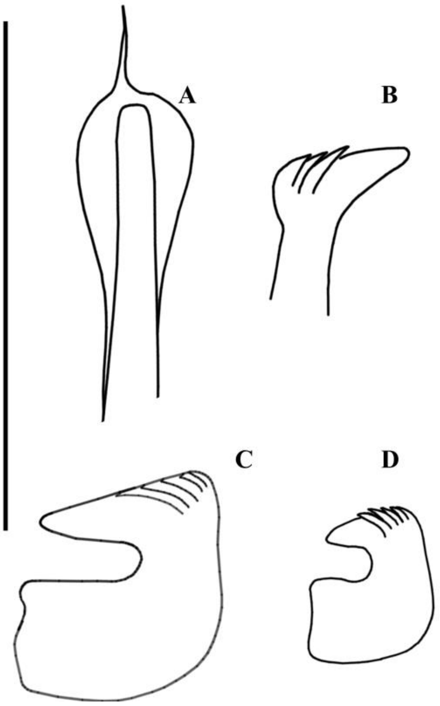


Figure 6: *Chone kroyerii* (POLNB1857-15). (A) Thoracic inferior, paleate notochaeta; (B) thoracic uncini; (C) anterior abdominal uncini; (D) posterior abdominal uncini. Scale 0.1 mm.

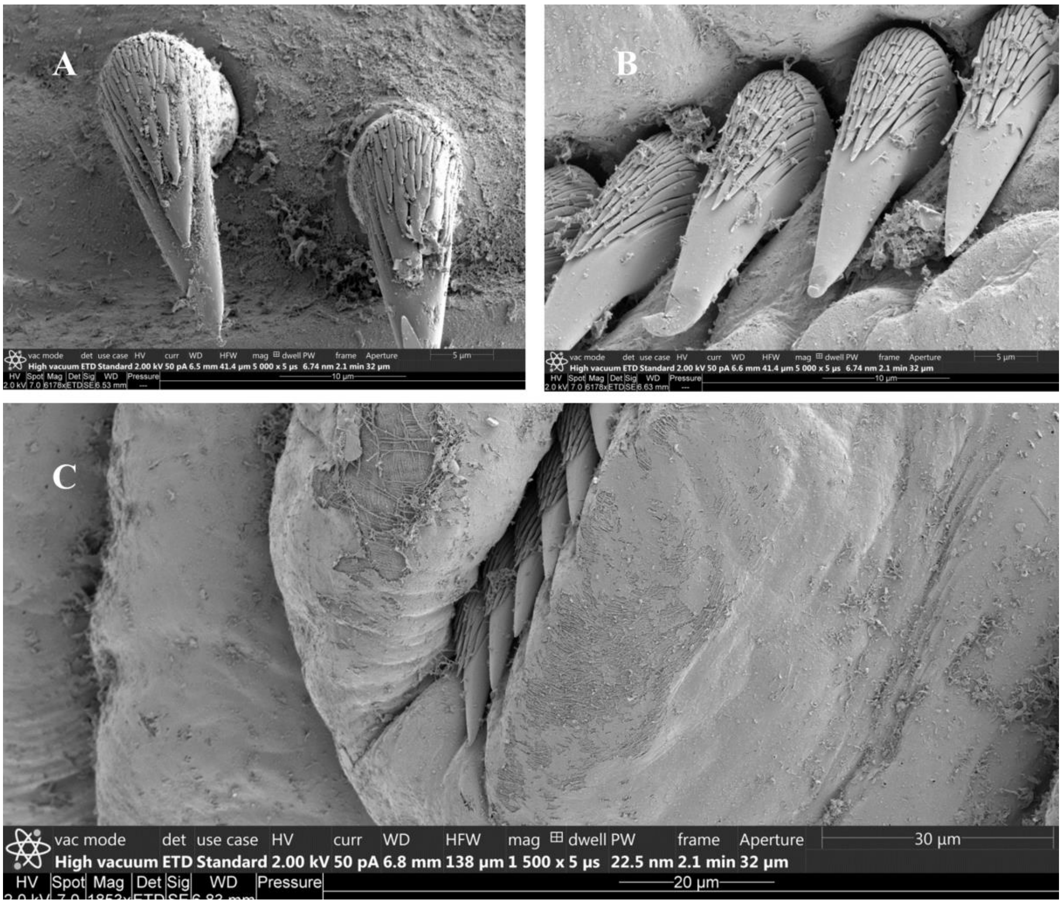


Figure 7: *Chone kroyerii* (A) Thoracic uncini; (B) anterior abdominal uncini; (C) posterior abdominal uncini.

Chone paucibranchiata (Krøyer, 1856)

Sabella paucibranchiata Krøyer, 1856: 22- 23.

Chone paucibranchiata Krøyer, 1856: 22- 23.; Banse, 1972: 465- 466.; Cochrane, 2000: 146-147.

Material examined – The Barents Sea (Area I): 70.97683’N 8.7735’W, 109 m, Grab, 14 September 1999 (4 specimens, TB23). 70.64783’N 9.37217’W, 599 m, RP sledge, 17 September 1999 (1 specimen). 70.60317’N 9.34533’W, 313 m, RP sledge, 17 September 1999. 73.03067 N 73.03067 E, 213 m, Beamtrawl, 9 June 2015 (5 Specimens). The North Sea (Area V): 58.1828’N 10.0413’W, 327- 240 m, 13 May 2009 (1 specimen). 58.9545’N 10.5733’W, 125- 226 m, 18 May 2009 (10 specimens). 58.6203’N 10.3254’W, 256- 290 m, 15 May 2009 (5 specimens). 68.3187’N 10.3245’W, 389. 408 m, 13 May 2009 (1 specimen). 58.6801’N 10.3997’W, 178- 238 m, 16 May 2009 (4 specimens). 58.5118’N 10.4186’W,275-289 m, 14 May 2009 (5 specimens). 58.9983’N 10.6599’W, 440- 442 m, 18 May 2009 (1 specimen). 58.5716’N 10.3793’W, 243- 277 m, 14 May 2009.

Description - Palmate membrane extending less than one- quarter of the branchial crown length. Number of radioles three pairs. Radiolar pigmentation absent. Radiolar flanges narrow. Radiolar tips length up to one- eighth of the branchial crown length, tapering. Pinnules length similar in length all along, i.e. featherduster- shape. Dorsal lips broadly rounded, as long as wide. Dorsal pinnular appendages present. ventral cirri absent. Length of the basal lamina of the branchial crown as long as collar segment.

Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view same as first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap narrow. Peristomium covered when collar is flat. Anterior peristomial ring lobe bilobed, exposed above collar margin. Ventral thoracic shields differentiated. Biannulate thoracic segments present ventrally, absent dorsally. Posterior-bending dorsal thoracic biannulation absent. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium present. Thoracic pre- chaetal and post-chaetal lobe well developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta short broadly hooded. Inferior thoracic notochaetae paleate. Anterior margin of inferior chaetae medium mucro. Dentition of thoracic uncini teeth slightly diminishing in size posteriorly, covering three- quarters of mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior and posterior abdominal uncini squared. Dentition of anterior and posterior abdominal uncini series of teeth in nearly uniform size covering three quarters of the mf length. Posterior margin of pygidium rounded.

Remarks – According to the molecular analysis *C. paucibranchiata* (TB23) is genetically similar to *C. infundibuliformis* (Figure 4, Clade 1). *Chone paucibranchiata* is characterized as small in size, having three pairs of radioles (more than three pairs in *C. infundibuliformis*), pinnules in similar length along entire length of radiole(longest mid- radiole in *C. infundibuliformis*), bilobed anterior peristomial ring lobe(triangular in *C. infundibuliformis*) and differentiated thoracic ventral shields (undifferentiated in *C. infundibuliformis*) (Banse 1972, Cochrane 2003, Tovar-Hernández & Sosa-Rodríguez 2006). Studies have noted that *C. paucibranchiata* and *C. murmanica* might be the same species (Cochrane 2000). In this material, *C. paucibranchiata* have peristomial eyes absent (present in *C. murmanica*) (Tovar-Hernández 2007). Feather- duster shape of pinnules, bilobed anterior peristomial ring lobeand elongated dorsal lips (the latter present in this material, not mentioned in previous descriptions) are currently diagnostic characters of *Paradialychone* (Tovar-Hernández 2008). Ventral patch of cilia has previously been noted in *P. ecaudata* and *D. trilineata* by (Tovar-Hernández 2008), and in *C. duneri* by (Cochrane 2000). Figures of chaeta of *C. paucibranchiata* have previously not been made due to the fact that the type specimen had broken chaeta. Here, drawings and SEM of the material have been made.

Chone paucibranchiata has characters that are in disagreement with *Chone.* When investigating the sequence it is identical to *C. infundibuliformis* (TB01- 06). For these reasons, it is likely that this sequence has been contaminated, and named as such in Figure 4, but the possibility that the morphological characters are homoplastic or this species undergoes comprehensive developmental stages cannot be dismissed based on these results. The status of *C. paucibranchia* cannot be assessed in relation to molecular data.

Distribution –Norwegian coast. *Amendment:* Barents Sea, North Sea.

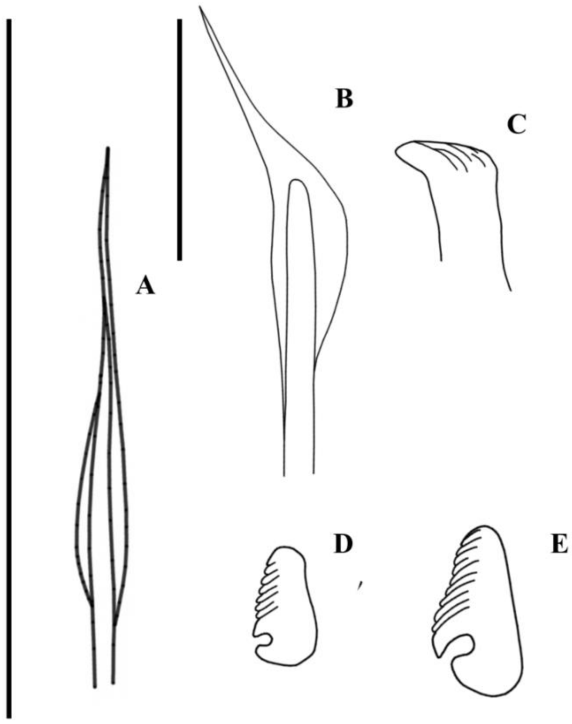


Figure 8: *Chone paucibranchiata* (TB23). (A) Thoracic inferior, broadly hooded, notochaeta; (B) thoracic inferior paleate, notochaeta; (C) thoracic uncini; (D) anterior abdominal uncini; (E) posterior abdominal uncini. Scale (A) 0.1 mm, scale (B, C, D, E) 0.025 mm.

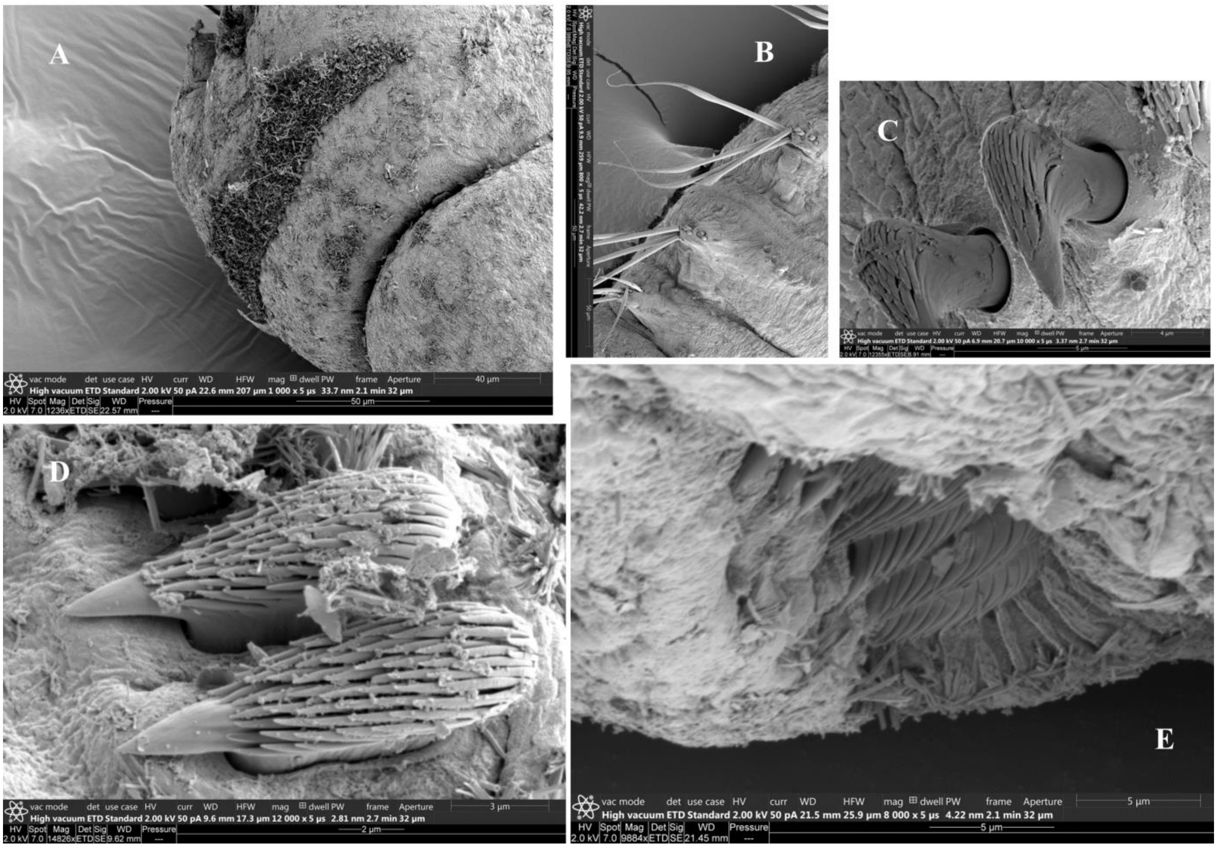


Figure 9: *Chone paucibranchiata* (TB23). (A) Ventral patch of cilia; (B) thoracic inferior notochaeta; (C) thoracic uncini; (D) anterior abdominal uncini; (E) posterior abdominal uncini.

Chone infundibuliformis Krøyer, 1856

Chone infundibuliformis Krøyer, 1856: 33.; Malmgren, 1866: 404-405, Pl. 28, Fig 87.; Malmgren, 1867: 116.; Cunningham & Ramage, 1887: 670, Pl. 44, Fig 32.; McIntosh, 1916: 35, Pl. 2, Fig 9.; Fauvel, 1927: 334, Fig 116a–o.; Wesenberg-Lund, 1950, 58.; Banse, 1972: 461–465, Fig 1a–l.; Hartmann-Schröder, 1996: 550, Fig.168a–h.; Tovar-Hernández & Sosa-Rodríguez, 2006: 37- 52.

Chone suspecta Krøyer, 1856: 33; Tovar-Hernández, 2007: 44.

Material examined - The Barents Sea (Area I): White Sea, Kandalaksha Bay, Velikaya Salma Strait, 66.642300`N 33.188272’E, 5- 20 m depth, Diving, 5, 12, 13 and 21 September 2017, Substrate: rock in mud (19 specimens)(TB01-06). 73.45-76.15’N 33.30’E, 138- 155 m, September 2013 (3 specimens).

Description – Size 3- 7 cm. Palmate membrane extending two- thirds to three- quarters of the branchial crown length. Number of pair of radioles 13. Radiolar pigmentation white spots within skeleton cells. Radiolar flanges broad. Radiolar tips length up to one- eighth of the branchial crown length, tips broad. Pinnules longest mid- radiole, i.e. snowflake- shape. Dorsal lips broadly rounded, as long as wide. Dorsal pinnular appendages present, connected by palmate membrane. ventral cirri present. Basal lamina of the branchial crown shorter than collar segment (median area in lateral view).

Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap very pronounced delineated faecal groove, almost resembling a dorsal split. Dorsal pockets well developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe triangular, covered by collar margin. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation present. Glandular ridge on second segment not intact dorsally. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini in two irregular rows. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate, with medium length mucro. Dentition above mf of thoracic uncini teeth slightly diminishing in size posteriorly, covering a half of the mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior abdominal uncini squared, dentition in a series of teeth of nearly uniform size above mf, covering a quarter of the mf length. Breast of posterior abdominal uncini squared, handles absent, dentition in a series of teeth similar in size, covering a quarter of the mf length. Pygidial uncini dentition teeth of nearly uniform size covering three- quarters of the mf length. Posterior margin of pygidium triangular.

Coloration – Crown entirely red, except for one or several white circles and white radiolar pigmentation (Figure 12A). Dorsal pinnular appendages with white pigmentation (Figure 12A and C), ventral cirri red. Dorsal lips red (Figure 12C). Body cream colored, glandular ridge on second segment pale (Figure 12D), gradually more opaque posteriorly (Figure 12G).

Remarks –Chone infundibuliformis is characterized by having short radiolar tips, vc, dorsal pinnular appendages connected by a palmate membrane, ventral shield of collarhorseshoe-shaped, glandular ridge of second segment not intact dorsally, thoracic uncini distributed in irregular double rows (except in juveniles), abdominal uncini similar in shape anteriorly and posteriorly, with a squared breast and dentition covering less than half of the mf length (Tovar-Hernández & Sosa-Rodríguez 2006). The specimens studied in this study possess a prominent delineated faecal groove extending along the entire thorax (Figure 12A and E). This character was conspicuous in both live and fixed material (both FA and EtOH), see Figure 12F, and has been previously observed for *C. infundibuliformis* (Cochrane 2000).

The molecular analyses indicate that these specimens share a genetically distinct lineage, and that the two most closely related species are *C. kroyerii* and *C. sp.* y (Figure 5, group 1-5; Figure 4, Clade 1). Haplotype network analysis shows that *C. kroyerii* is more closely related to *C. infundibuliformis* than to *C.* sp. y, and vice versa (Figure 5, group 1-5).

I would like to amend the description as follows: Dorsal gap varying from narrow dorsal collar gap extending as narrow, deep faecal through all thoracic segments, to broad collar gap extending as broad, deep faecal groove through all thoracic segments. Pygidial uncini with teeth of nearly uniform size, covering three- quarters of the mf length.

Distribution –South of Bering Strait; Greenlandic and Alaskan part of Arctic ocean; Western part of the North Atlantic Ocean; Norwegian coast; Irish coast; Portugese coast; Mediterranean Sea. *Amendment:* Barents Sea.

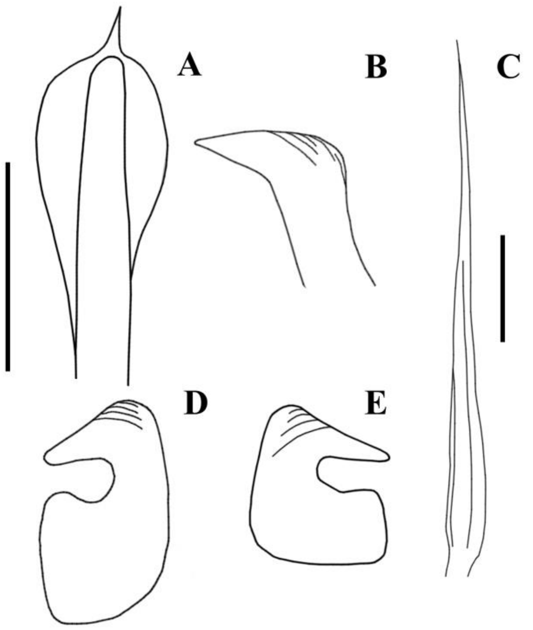


Figure 10: *Chone infundubuliformis* (TB02). (A) Thoracic inferior, paleate notochaeta; (B) thoracic uncini; (C) anterior abdominal uncini; (D) posterior abdominal uncini; (E) abdominal neurochaeta. Scale 0.1 mm.

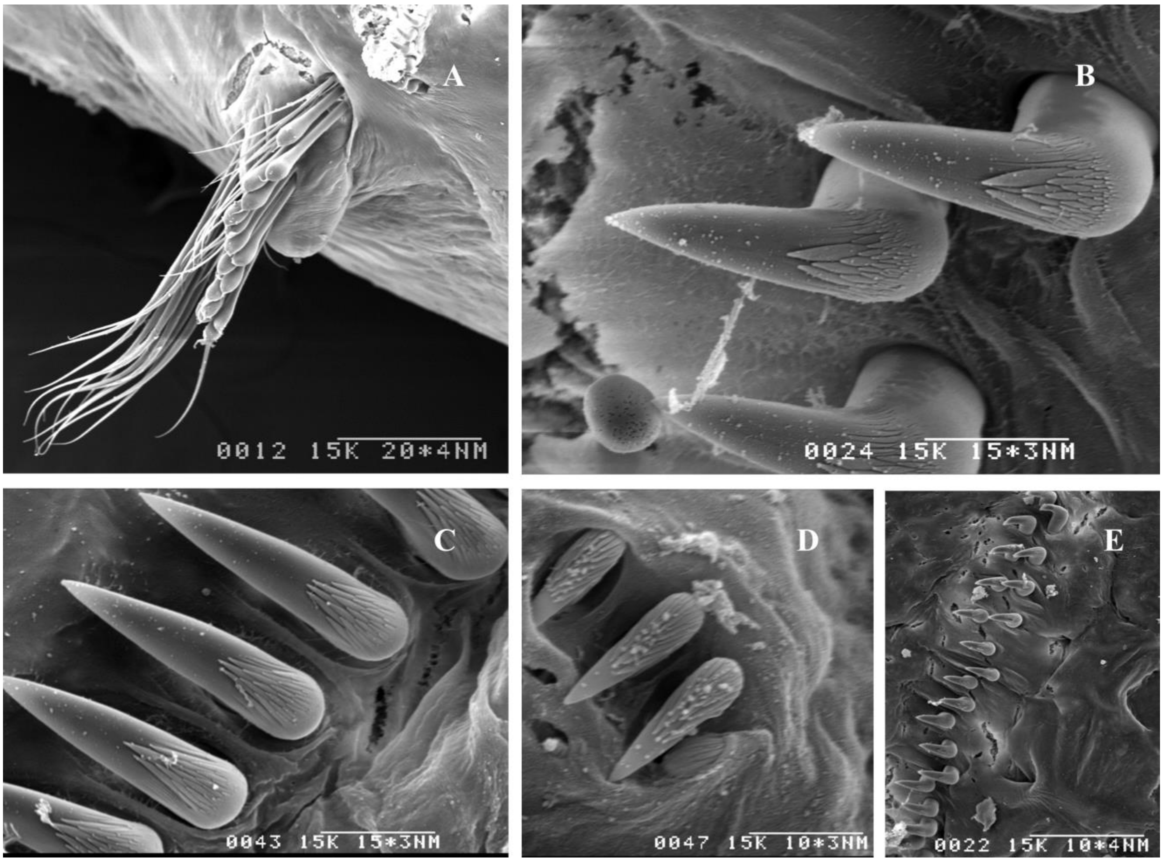


Figure 11: *Chone infundibuliformis* (TB02). (A) Thoracic notochaeta; (B) thoracic uncini; (C) abdominal uncini; (D) pygidial uncini; (E) thoracic distribution of uncini.

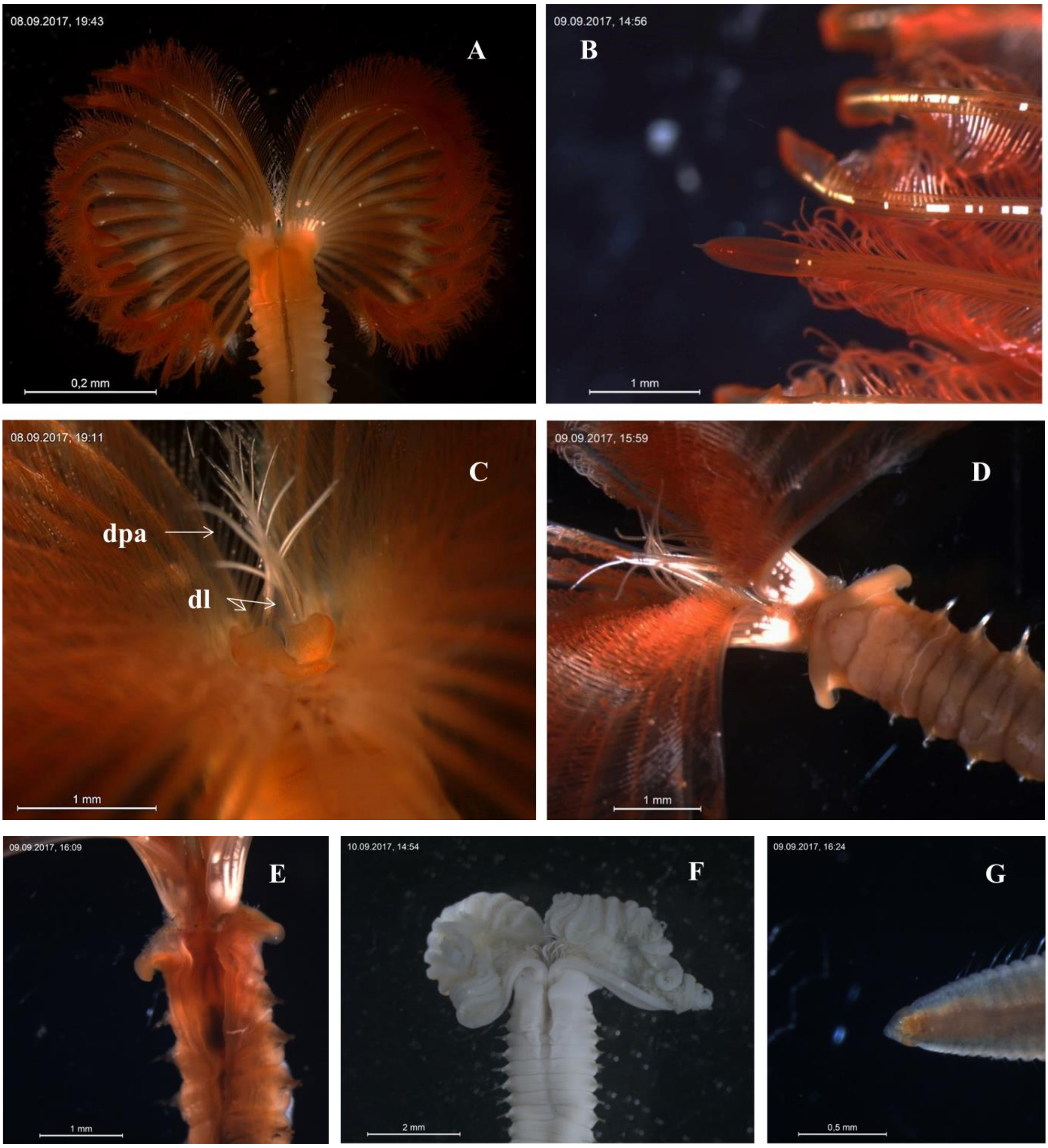


Figure 12: *Chone infundibuliformis* (TB02). (A) Radiolar crown and thorax, dorsal view; (B) radiolar tips; (C) crown internal structure, ventral view; (D) crown and thorax, ventral view; (E) thorax, dorsal view; (F) thorax, dorsal view, fixed material; (G) pygidium. Abbreviations: dpa, dorsal pinnular appendages; dorsal lips, dl (Photo: Tuva Bongard Munkeby).

Chone sp. y *sensu* Cochrane, 2000

Chone sp. y Cochrane 2000:136- 142, Fig 2.6.5 and 2.6.6.

Material examined – The Barents Sea (Area I): 71.19025 N 32.24985 E, 226- 224 m, RP-sledge, 10 August 2013 (1 specimen, radiolar crown missing).

Description - Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap narrow. Dorsal pockets poorly developed, or well developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe triangular, covered by collar margin. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present ventrally, absent dorsally. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium does not stain with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe not developed. Distribution of thoracic uncini in a single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae short, broadly hooded. Dentition of thoracic uncini teeth slightly diminishing in size posteriorly, covering half of the mf length.

Ventral, glandular pattern on abdomen band on posterior abdomen. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior and posterior abdominal uncini squared. Dentition of anterior and posterior abdominal uncini series of teeth similar in size, covering three- quarters of the mf length. Posterior margin of pygidium rounded.

Remarks – This species has not been formally described, but it has appeared in a PhD thesis (Cochrane 2000). *Chone* sp. y was described based on a character combination of long tapering radiolar tips, pinnules of equal length along entire radiole, ventral cirri present, elongate dl, partial biannulation of thoracic segments, superior notochaeta “narrowly swollen”, inferior thoracic notochaeta “short broadly swollen, tapering with long tips” (interpreted here as short, broadly hooded), abdominal uncini with squared breast and dentition of unequal size, similar in size along entire abdomen. The specimen studied has partial biannulation, narrowly and broadly hooded notochaeta, abdominal uncini similar in shape posteriorly, breast of abdominal uncini squared. Elongated dorsal lips and feather-duster shaped pinnules of radiole are currently diagnostic features of *Paradialychone* (Tovar-Hernández 2008). This is neither confirmed nor refuted in this study because of poorly preserved material. Figures and SEM of chaeta has not previously been made, but is presented here.

Even though this specimen bear characters that contradict with the synapomorphies of *Chone* noted by Tovar-Hernández (2008), molecular analysis supports its placement within Clade 1 (Figure 4) and within the same haplotype network as two well- described *Chone*- species.

Distribution –Norwegian coast. *Amendment:* Barents Sea.

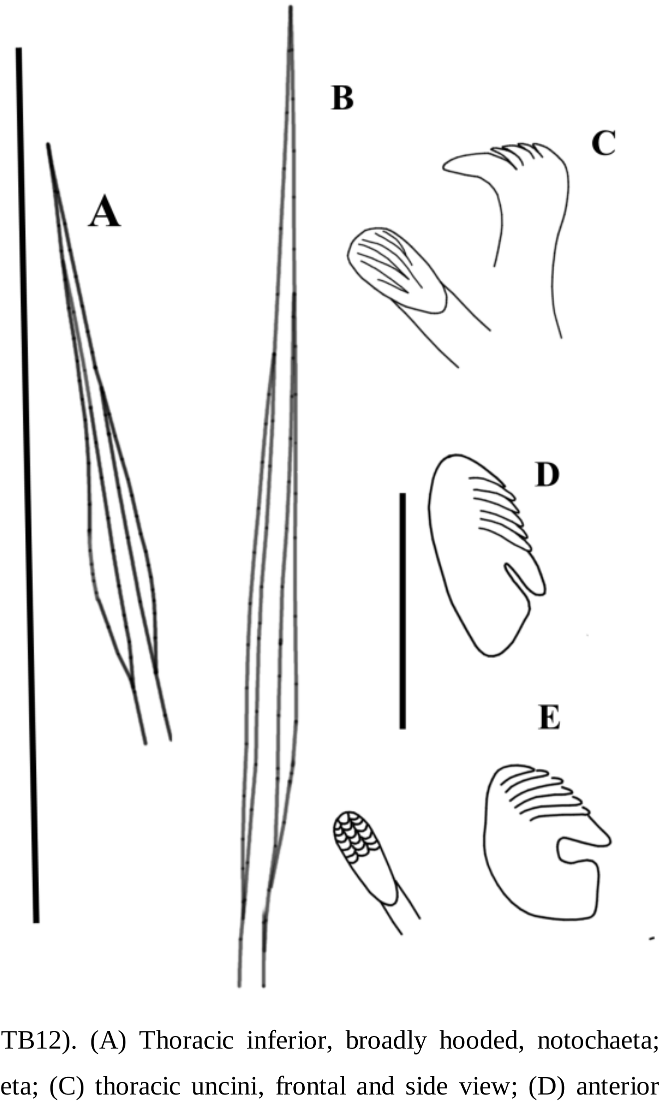


Figure 13: *Chone sp.* y (TB12). (A) Thoracic inferior, broadly hooded, notochaeta; (B) thoracic superior, narrowly hooded, notochaeta; (C) thoracic uncini, frontal and side view; (D) anterior abdominal uncini; (E) posterior abdominal uncini. Scale (A,B) 0.1 mm, scale (C, D, E) 0.025 mm.

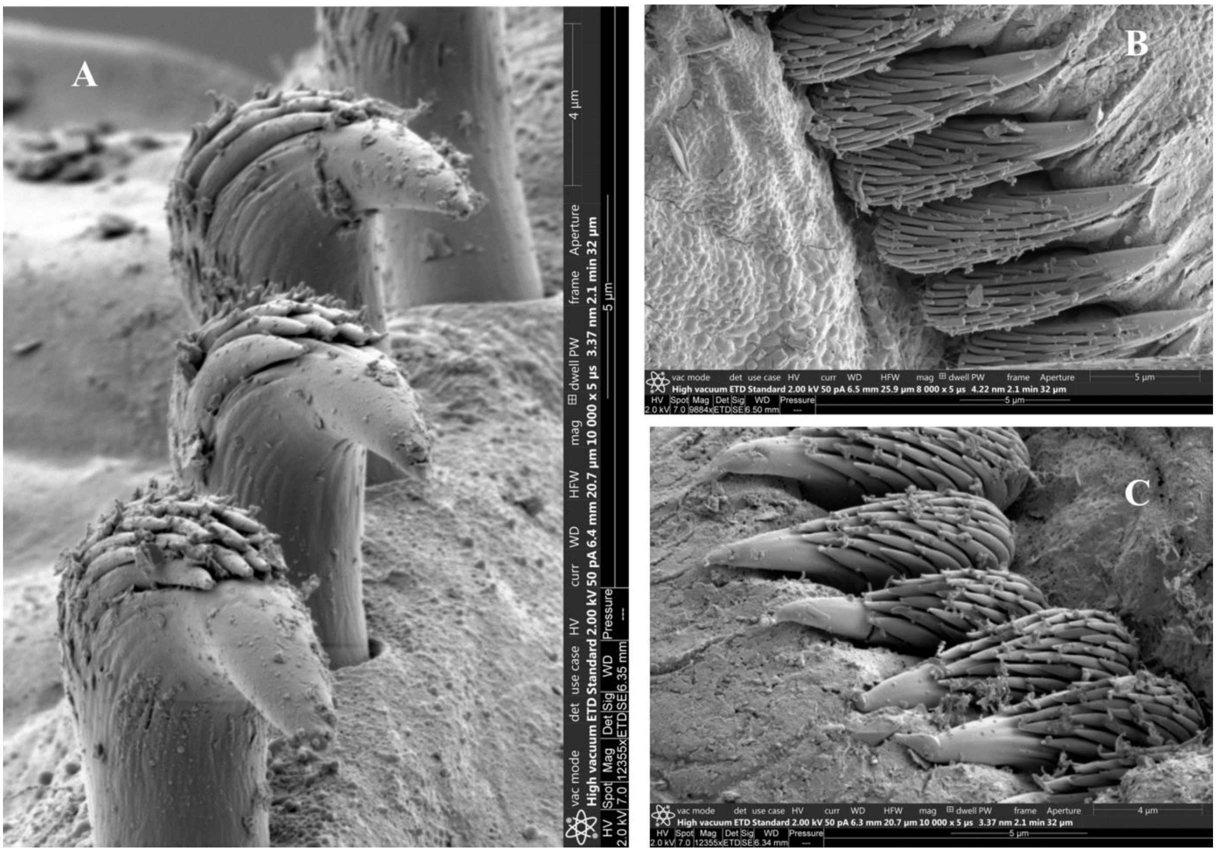


Figure 14: *Chone sp.* y (TB12). (A) Thoracic uncini; (B) anterior abdominal uncini; (C) posterior abdominal uncini.

Chone fauveli McIntosh, 1916

Chone fauveli McIntosh, 1916: 36–42, Pl. 2, Fig 8.; McIntosh, 1923: Pl. 121, Fig 2, Pl. 130, Fig 2.; Knight-Jones 1990: 275, Fig 6.20.; Kirkegaard 1996: 374, Fig 214.; Cochrane 2000: 145.; Tovar-Hernández 2007: 42-44, Fig 6.

Material examined - The Barents Sea (Area I): White Sea, Kandalaksha Bay, Velikaya Salma Strait, 66.642300`N 33.188272'E, 20 m depth, Diving, 17, 18, and 22 September 2017, substrate: mud (7 specimens) (TB07, TB09-10). 71.990917'N 33.02535'E, September 2011 (1 specimen). 73.1626'N 32.93785'E, September 2011 (1 specimen). 73.21500'N 34.32117'E, 205 m, Beamtrawl, 9 June 2015 (1 specimen).

Description – Size 4-6 cm. Palmate membrane extending two- thirds to three- quarters of the branchial crown length. Number of pair of radioles 15. Radiolar pigmentation white spots within skeleton cells. Radiolar flanges broad. Radiolar tips length up to one- quarter of the branchial crown length, tips filiform. Pinnules similar in length all along, i.e. feathershape. Dorsal lips broadly rounded, as long as wide. Dorsal pinnular appendages present, connected by palmate membrane. ventral cirri present. Length of the basal lamina of the branchial crown shorter than collar segment (median area in lateral view).

Angle of collar in lateral view ventral higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarrounded. Mid- dorsal collar gap narrow. Dorsal pockets poorly developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe triangular, covered by collar margin. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation present. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini in a single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae pseudospatulate, short mucro. Dentition above mf of thoracic uncini a large tooth above the mf in midline, followed by a series of smaller teeth, covering three- quarters of the mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior abdominal uncini hooked. Dentition of anterior abdominal uncini a large tooth above the mf in midline, followed by a series of smaller teeth, covering three- quarters of the mf length. Breast of posterior abdominal uncini hooked, or squared. Dentition of posterior abdominal uncini large tooth followed by a series of smaller teeth, covering three- quarters of the mf length. Pygidial uncini which has several teeth in nearly uniform size, covering three- quarters of the mf length. Posterior margin of pygidium triangular.

Coloration – Crown white with two or more broad red circles (Figure 17A). White parts with high proportion of white pigmentation, red circles without white pigmentation. Radiolar tips, ventral cirri and dorsal pinnular appendages white (Figure 17B and C). Dorsal lips red (Figure 17D). Body red and cream- colored in a marble- like pattern, gradually more opaque posteriorly. Glandular ridge on second segment white (Figure 17D, E and F).

Remarks – Molecular analysis indicate that *C. fauveli* (TB07, TB09-10) is a genetically distinct lineage. *Chone fauveli* is characterized by having long radiolar tips, dorsal pinnular appendages united by palmate membrane, ventral cirri present, vertical grooves on collar, ventral shield of collarrounded, thoracic uncini distributed in two irregular rows, thoracic inferior notochaeta paleate, dentition of thoracic uncini second tooth enlarged, covering a quarter of the mf length (Tovar-Hernández 2007). However, Figures by Knight- Jones (1990) resembles pseudospatulate chaeta and Cochrane (2000) noted *C. fauveli* as lacking ventral cirri and having short radiolar tips. In the material studied inferior thoracic notochaeta is clearly pseudospatulate, ventral cirri is present, thoracic uncini is distributed in a single row and all uncini has an enlarged second tooth and dentition covering three- quarters of the mf length in thoracic and abdominal uncini.

The sequence (NBPOL375-08) most closely related to *C. fauveli* (TB07/TB09/TB10) is identified as *C. infundibuliformis* (see Figure 4, Clade 2), but the worm in the picture lacks the conspicuous deep furrow of *C. infundibuliformis*, and the radiolar tips are long. This might indicate that NBPOL375-08 is misidentified (Additional information on *C. fauveli* under *C.* sp. 1).

Distribution – Greenland Sea; Barents Sea; Northeast Atlantic Ocean.

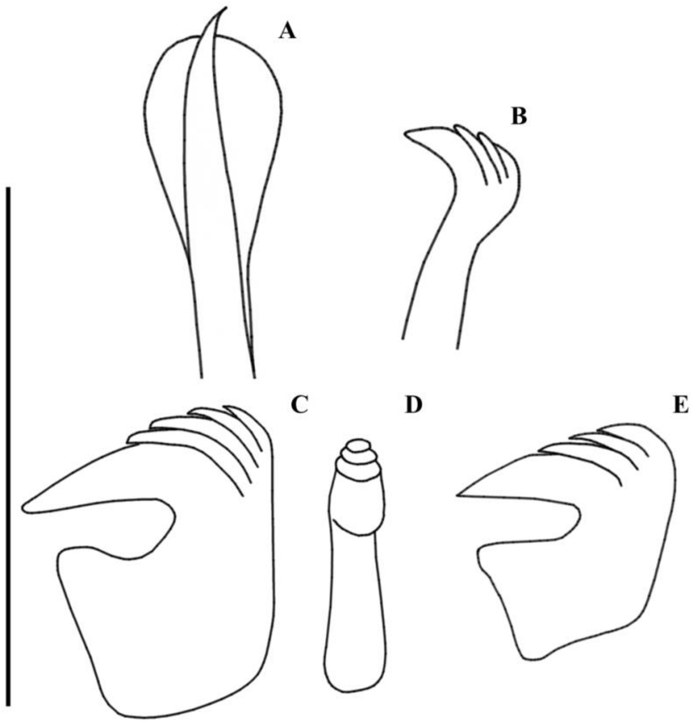


Figure 15: *Chone fauveli* (TB07). (A) Thoracic inferior pseudospatulate notochaeta; (B) thoracic uncini; (C) anterior abdominal uncini, frontal and side view; (D) posterior abdominal uncini; (E) abdominal neurochaeta. Scale 0.1 mm.

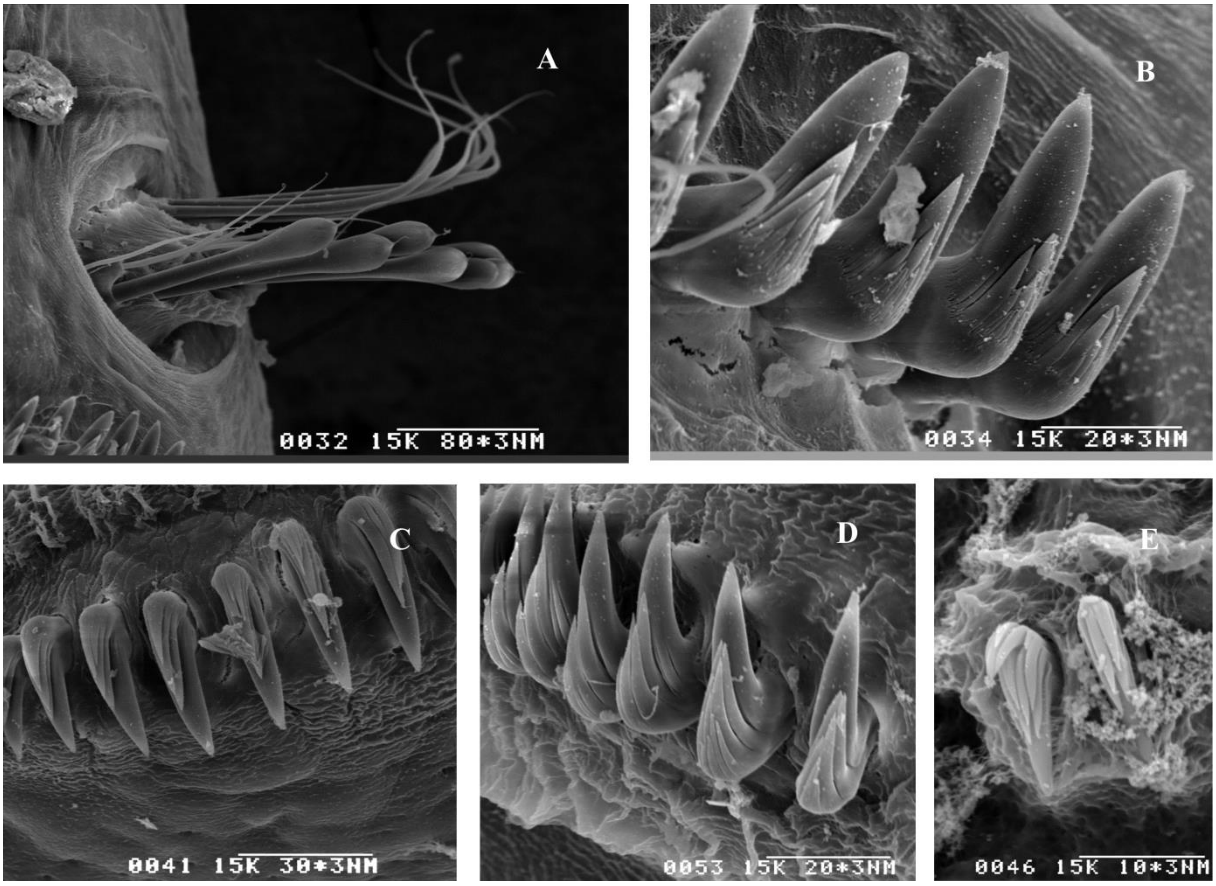


Figure 16: *Chone fauveli* (TB07). (A) Thoracic notochaeta; (B) thoracic uncini; (C) anterior abdominal uncini; (D) psoterior abdominal uncini; (E) pygidial uncini.

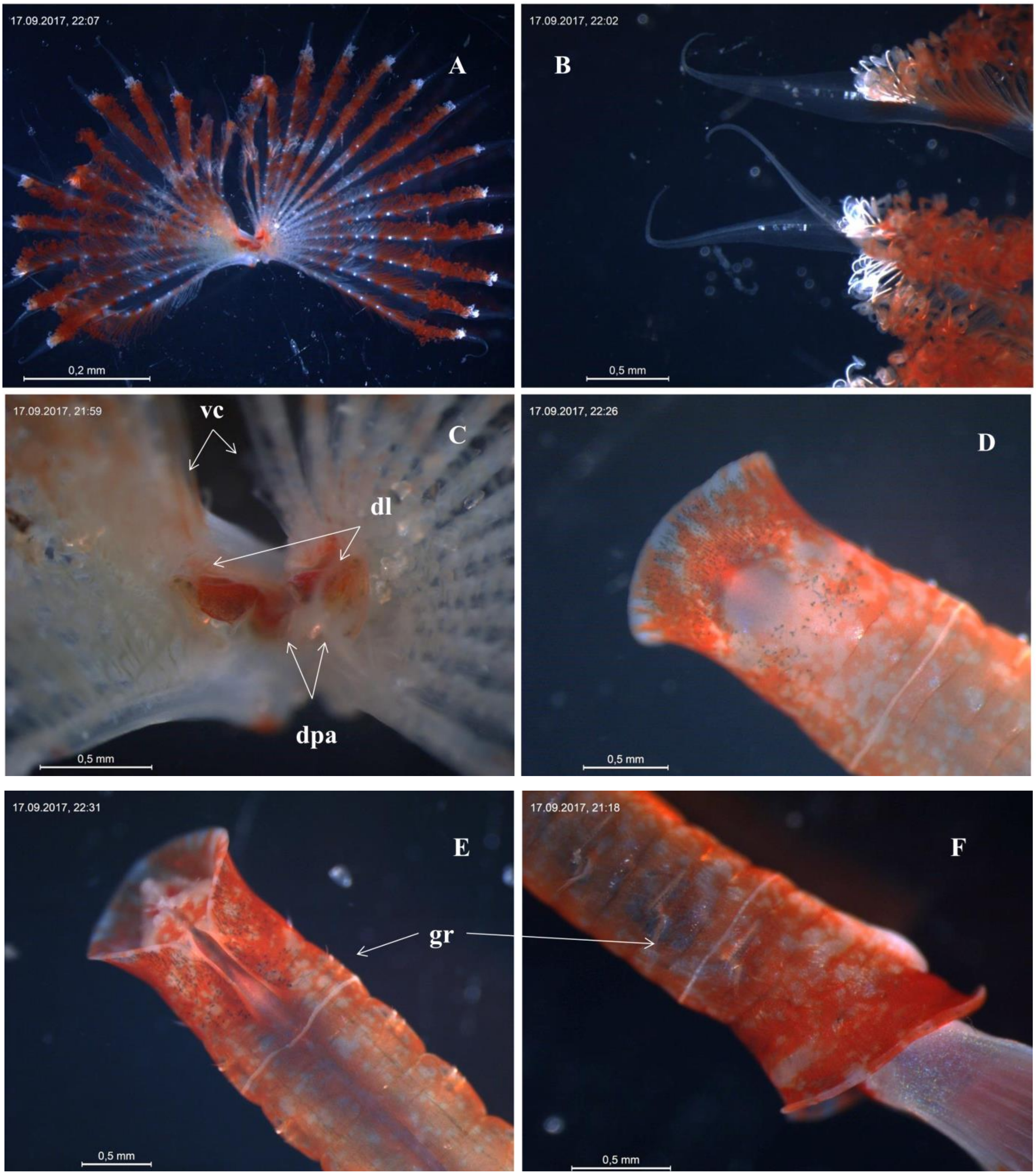


Figure 17: *Chone fauveli* (TB07). (A) Radiolar crown, view from above (B) radiolar tips; (C) crown internal structure, view from above dorsally; (D) thorax, ventral view; (E) thorax, dorsal view; (F) thorax, lateral view; Abbreviations: vc, ventral cirri; dl, corsal lips; dpa, dorsal pinnular appendages; gr, glandular ridge (Photo: Tuva Bongard Munkeby).

Chone cf *duneri* Malmgren, 1867

Chone duneri Malmgren, 1867: 225, Pl. 14, Fig 75a-d; Langerhans, 1880: 114-115, Fig 44a-e.; Hofsommer, 1913: 336-339.; Southern, 1914: 141. ; Wessenberg-Lund, 1950: 58.; Pettibone, 1954: 339. ; Eliason, 1962: 89-91.; Hartmann-Schroder, 1971: 517.; Banse, 1972: 466, Fig 2a-b.; Kirkegaard, 1996: 372-374.; Tovar-Hernández et al. 2007 326-329, Fig 6.

Chone longocirrata Sars, 1872: 406- 417; Hartmann, 1959: 1- 628; Cochrane, 2000: 134-135.

Material examined – The Norwegian coast (Area III): Fanafjorden, 60.2338’N 5.259983’E, 168 m, Large Grab, 6 June 2017, substrate: mud/clay (1 specimen). Fanafjorden, 60.229683’N 5.2509’E, 192 m, Large Grab, 6 June 2017, substrate: mud/clay (1 specimen).

Description - Palmate membrane extending two- thirds to three- quarters of the branchial crown length. Number of pair of radioles 8. Radiolar pigmentation white spots within skeleton cells. Radiolar flanges narrow. Radiolar tips length up to one- quarter of the branchial crown length, filiform. Pinnules length longest mid- radiole, i.e. snowflake- shape. Shape of dorsal lips broadly rounded, as long as wide. Dorsal pinnular appendages present. Ventral cirripresent. Length of the basal lamina of the branchial crown shorter than collar segment (median area in lateral view).

Anterior margin of collar smooth. Angle of collar in lateral view leveled, i.e. even height, or ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view same as first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap narrow. Dorsal pockets well developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe bilobed, exposed above collar margin. Peristomial eyes absent. Glandular ridge on second segment narrow. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate, medium mucro. Dentition above mf of thoracic uncini series of teeth in nearly uniform size, or teeth slightly diminishing in size posteriorly, covering three-quarters of mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior abdominal uncini squared. Dentition of anterior abdominal uncini a series of teeth of nearly uniform size above mf, covering a half of the mf length. Breast of posterior abdominal uncini squared. Dentition of posterior abdominal uncini series of teeth similar in size, covering half of the mf length. Anal depression absent. Posterior margin of pygidium rounded.

Remarks – *C. duneri* has been described as having radiolar tips up to half the length of radiole, bilobed peristiomial lobe projection, smooth anterior margin of collar, peristomium well exposed beyond collar, horsehoe- shaped vsc, inferior notochaeta paleate with medium mucro, dentition of abdominal uncini covering a half of the mf length, breast squared, similar along entire abdomen (Tovar-Hernández et al. 2007). However, the material studied has broad radiolar tips length up to one- quarter, peristomium is covered by the collar, and the inferior notochaeta has a more narrow swelling, distally tapered, than those depicted in *C. duneri*. *Chone duneri* has been synonymized with *C. longocirrata* although type material for *C. longocirrata* was found to have short, broad radiolar tips and inferior notochaeta with a more narrow swelling, distally tapered (Hartman 1959, Cochrane 2000). The characters of the material studied resemble those of *C. longocirrata*, more than those of *C. duneri*. This might indicate that *C. longocirrata* should be considered re- established, which is also noted by Cochrane (2000).

The molecular analyses are poorly supported and ambiguous. *Chone* cf *duneri* appears in both Clade 4, and in Clade 7 basally separated from all of the other sequences (Figure 4). However, POLNB1863-15 (Clade 7) was not studied directly and photograph (BOLD) does not allow identification. The material in Clade 4 (TB26-27) was sampled in the same area with a depth interval of 20 m with a moderate intragenetic divergence. There are possibilities that these errors during sequencing occurred, the specimens might be from two populations or they are susceptible for cryptic speciation. A thorough taxonomic revision of this species, its synonymies, and molecular characters is needed. This is also reflected in the distribution range.

Distribution – Atlantic Ocean; Arctic Ocean. *Amendment:* Norwegian coast.

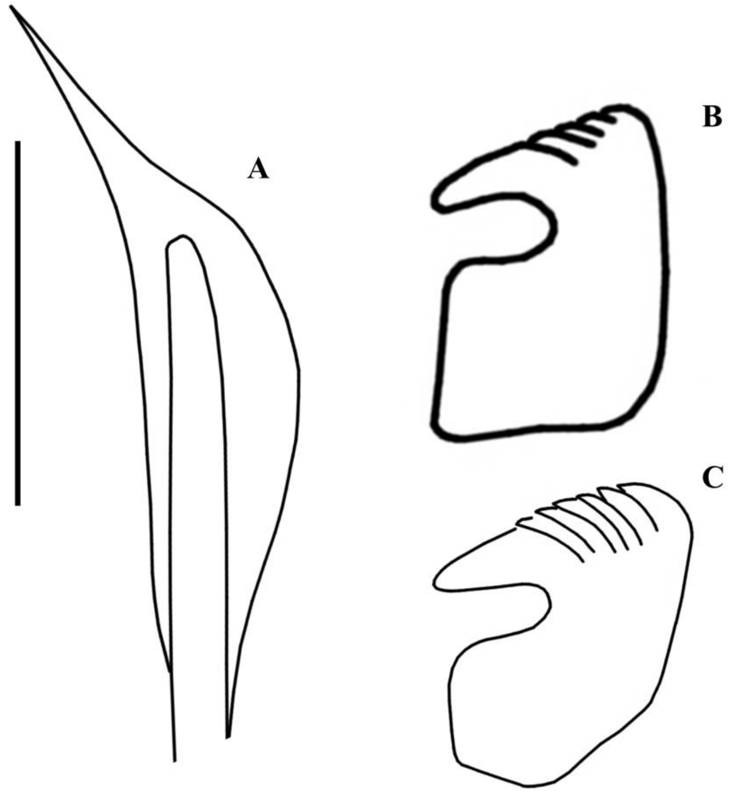


Figure 18: *Chone* cf *duneri* (TB26). (A) Thoracic paleate inferior notochaeta; (B) anterior abdominal uncini; (C) posterior abdominal uncini. Scale 0.025 mm.

Chone sp. 1

Material examined – The Norwegian coast (Area III): Agdenes, Sletvik, Hopavågen, 63.592693’N 9.553166’E. 4 m, Van Veen Grab, 29 August 2017 (1 Specimen) (TB48).

Description – Size 9 mm. Palmate membrane extending two- thirds to three- quarters of the branchial crown length. Number of pair of radioles 6. Radiolar flanges broad. Radiolar tips length up to one- eighth of the branchial crown length, tapering, or broad. Pinnules length longest mid- radiole, i.e. snowflake- shape. Shape of dorsal lips broadly rounded, as long as wide. Ventral cirripresent. Length of the basal lamina of the branchial crown as long as collar segment.

Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap narrow. Dorsal pockets poorly developed. Peristomium partially exposed when collar is flat. Anterior peristomial ring lobe digitiform, exposed above collar margin. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini single row. Dentition of thoracic uncini enlarged second tooth, covering three- quarters of mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini from posterior abdomen slightly modified from those in anterior abdominal segments. Breast of anterior abdominal uncini hooked. Dentition of anterior abdominal uncini enlarged second tooth covering three quarters of mf length. Breast of posterior abdominal uncini hooked. Dentition of posterior abdominal uncini teeth in uniform size covering three- quarters of the mf length. Posterior margin of pygidium rounded.

Remarks – The molecular analysis indicate that this specimen is genetically similar to *C. fauveli* (POLNB1443-15) (Figure 4, Clade 2). However, it has a conspicuous digitiform aprl, whereas *C. fauveli* has a triangular aprl. Digitiform anterior peristomial ring lobehas been inconsistently recorded as absent or present depending on different literature in *C. paramollis, C. mollis* and *P. ecaudata* (Tovar-Hernández 2007, Tovar-Hernández 2008). This specimen has short radiolar tips (long in *C. mollis* and *C. paramollis*) and dorsal lips broadly rounded (elongated in *Paradialychone*). Abdominal uncini are slightly modified, and a similar shape to *C. fauveli* is seen, i.e. a less quadratic impression than *C. infundubuliformis*.

Of all the sequences in Clade 2 (Figure 4), photographs of two live specimens (POLNB1443-15 and KBPOL573-11) have similar coloration to *C. fauveli* (TB07, TB09-10). This is also the case for the *Chone* sp. in the cover photo. The discrepancies of conspicuous characters between the material and the description by Tovar-Hernández (2007), and the result of this study indicate that *C. fauveli* might be several species, where one has ventral cirri present and long filiform radiolar tips and anterior peristomial ring lobetriangular, and the other has ventral cirri absent short radiolar tips and anterior peristomial ring lobedigitiform.

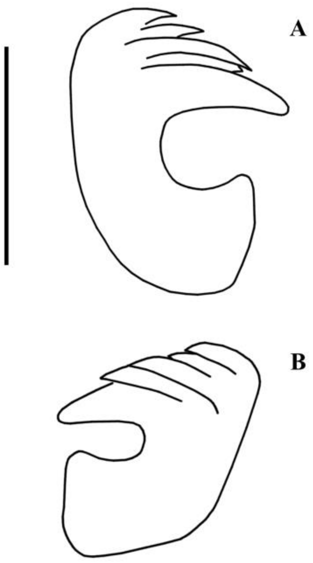


Figure 19: *Chone* sp. 1 (TB48) (A) Anterior abdominal uncini; (B) posterior abdominal uncini. Scale 0.025 mm.

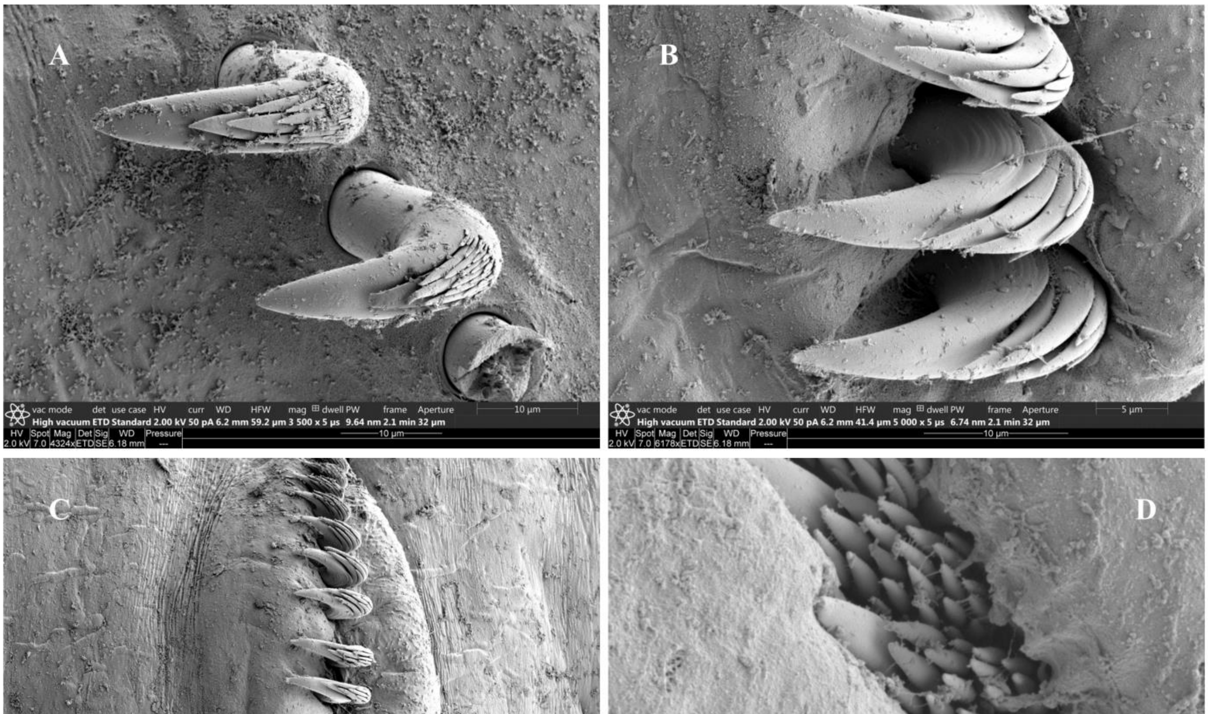


Figure 20: *Chone* sp. 1 (TB48) (A) thoracic uncini; (B) anterior abdominal uncini; (C) anterior abdominal uncini, entire tori; (D) posterior abdominal uncini.

Dialychone Claparedè, 1868

Dialychone Claparède, 1868, p. 499; Lo Bianco, 1893, p.77; Tovar-Hernandèz 2008: 2218-2219.

Type species

Dialychone acustica Claparède, 1870, by original designation (redescribed by Tovar-Hernández et al. 2007).

Diagnosis - Medium to large-bodied sabellid species. Branchial lobes fused dorsally. Radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges present. Dorsal lips elongate, longer than wide, without branchial skeleton extensions. Ventral lips present, broadly rounded. Dorsal pinnular appendages absent. Ventral radiolar appendages present. Longest pinnules at mid-radiole. Anterior margin of anterior peristomial ring triangular or bilobed. Posterior peristomial ring collar present. Glandular ridge on chaetiger 2 narrow, broad dorsally, broad ventrally, broad with vertical projections, or hypertrophied. Ventral shields absent. Notopodia in chaetiger 1 with two groups of elongate, narrowly hooded chaetae in C-shaped arrangement. Notopodia in chaetigers 2–8 with superior group of chaetae in two irregular rows, all elongate, narrowly hooded; inferior group with one anterior row of short bayonet chaetae, two posterior rows with symmetrical, mucronate paleate chaetae. Thoracic neuropodia bearing acicular uncini with teeth decreasing gradually in size away from the main fang; dentition covers one-half of the main fang length, hood present, handles long. Grs on posterior thoracic segments can be present. Anterior abdominal segments with two transverse rows of elongate, narrowly hooded chaetae, chaetae from the anterior row shorter than chaetae in posterior row; uncini with well-developed rectangular breast, handles absent, main fang well developed with a series of teeth of nearly uniform size covering one-half of the main fang length; intrafascicular variation: older uncini, located dorsalmost in torus, smallest in size, younger uncini, located ventralmost in torus, biggest in size. Posterior abdominal segments with very elongate, narrowly hooded chaetae; modified uncini with hooked breast, handles absent and dentition covering three- quarters of the main fang length; intrafascicular uncinal variation similar to those in anterior abdominal segments. Grs on anterior abdominal segments can be present. Pre-pygidial depression simple (From Tovar-Hernández (2008): 2218- 2219).

Remarks – In the analyses of CO1 fragment this genus appear paraphyletic when implementing current diagnostic features. Additional discussion of this matter is given under 3.6 Monophyly of genera. According to this material the following genus description amendments might be considered: Anal depression simple, or absent.

Dialychone collaris (Langerhans, 1881)

Chone collaris Langerhans, 1880: 116, Fig 29 a-f.; Fauvel, 1927: 337, Fig 116 p-x; Day, 1967: 777, Fig 37.7 a-f.; Giangrande, 1992: 524- 525, Fig 13 a-f, 14 a-d.; Tovar-Hernández et al., 2007: 324- 326, Fig 5 a- n.; Selim 2008: 111-113, Fig 2 j-t.

Dialychone collari Langerhans, 1880: 116, Fig 29 a-f.; Tovar-Hernández, 2008: 2219.

Material examined – Mediterranean Sea, Cala Blava, Mallorca, Illes Balears, Spain, 39.488083'N 2.733972'E, 3-5 m, substrate: algae over rocks and Posidonia (4 specimens) (TB55- 58).

Description - Palmate membrane extending half of the branchial crown length. Number of pair of radioles 3–9. Radiolar flanges broad. Radiolar tips length up to one- eighth of the branchial crown length, filiform. Pinnules length longest mid- radiole, i.e. snowflake- shape. Shape of dorsal lips elongate without branchial skeleton extensions. Dorsal lips length three times longer than wide. Dorsal pinnular appendages absent. Ventral cirripresent. Length of the basal lamina of the branchial crown shorter than collar segment (median area in lateral view).

Anterior margin of collar crenulated all around. Angle of collar in lateral view leveled, i.e. even height. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap narrow. Dorsal pockets well developed. Peristomium partially exposed when collar is flat. Anterior peristomial ring lobe bilobed. Exposition of the anterior peristomial ring lobeexposed above collar margin. Peristomial eyes present. Glandular ridge on second segment narrow. Ventral thoracic shields differentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium does not stain with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post-chaetal lobe not developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate. Anterior margin of inferior chaetae short mucro. Dentition of thoracic uncini teeth slightly diminishing in size posteriorly, covering a half of the mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini similar shape along entire abdominal segments. Breast of anterior and posterior abdominal uncini hooked. Dentition of anterior abdominal uncini series of teeth in similar size covering a half of the mf length. Denition of posterior abdominal uncini series of teeth in similar size, covering three- quarters of the mf length. Anal depression simple. Posterior margin of pygidium rounded.

Remarks – *Dialychone collaris* is described as having short radiolar tips, broad radiolar flanges (Selim et al. 2012), pinnules similar in length along entire radiole, collar crenulated all around, peristomial eyes, bilobed preistomial lobe projection, elongated dl, short dpa, abdominal uncini with a squared breast and modified posteriorly (Tovar-Hernández et al. 2007). The material studied here differ in that it has pinnules longest mid- radiole, dorsal pinnular appendages absent and the abdominal uncini are similar in shape along entire abdomen. However, the Figures of the descriptions show pinnules that are shorter towards the end of the radiole, and this is a characteristic feature for *Dialychone*, as is lacking dorsal pinnular appendages (Capa & Murray 2015b). The descriptions describe modifications of abdominal uncini posteriorly, but they have been described as similar in shape in other literature (Giangrande 1992). This material supports the latter. *Dialychone collaris* has previously been described as having the unique character of the collar being crenulated all around (Tovar-Hernández et al. 2007), but this is also found in *D.* sp. 2 (TB59). This might indicate that it is not a unique character for *D. collaris. D. collaris* is, however, the only species in this dataset with peristomial eyes.

Dialychone collaris has been reported from several localities in the Northeast Atlanic and according to Knight- Jones (1990) there are moprhological differences between northern and southern specimens. These specimens are sampled in Mallorca and are recovered as a genetically distinct lineage (Figure 4, Clade 6), in the same haplotype network Figure 5) with distinct morphological characters. The phylogenetic relationship between southern and northern specimens should be investigated in the future as it cannot be assessed with these data. The type material should be studied in order to describe the shape of the radiolar tips, as this is not mentioned in newer literature (Tovar-Hernández et al. 2007).

Distribution –Greenland Sea; Barents Sea; Northeast Atlantic Ocean; Mediterranean Sea; Red Sea; Mosambic coast.

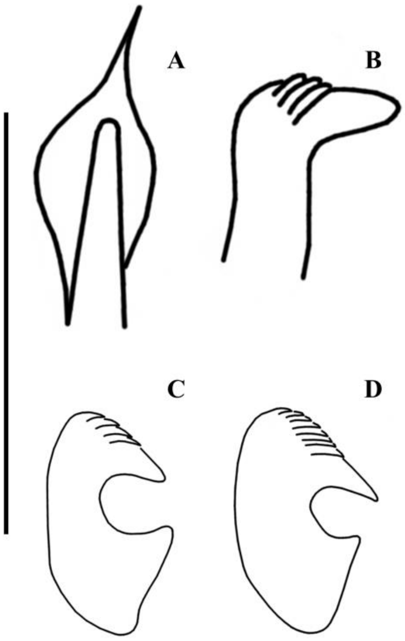


Figure 21: *Dialychone collaris* (TB55). (A) thoracic paleate inferior notochaeta; (B) thoracic uncini; (C) anterior abdominal uncini; (D) posterior abdominal uncini. Scale 0.05 mm.

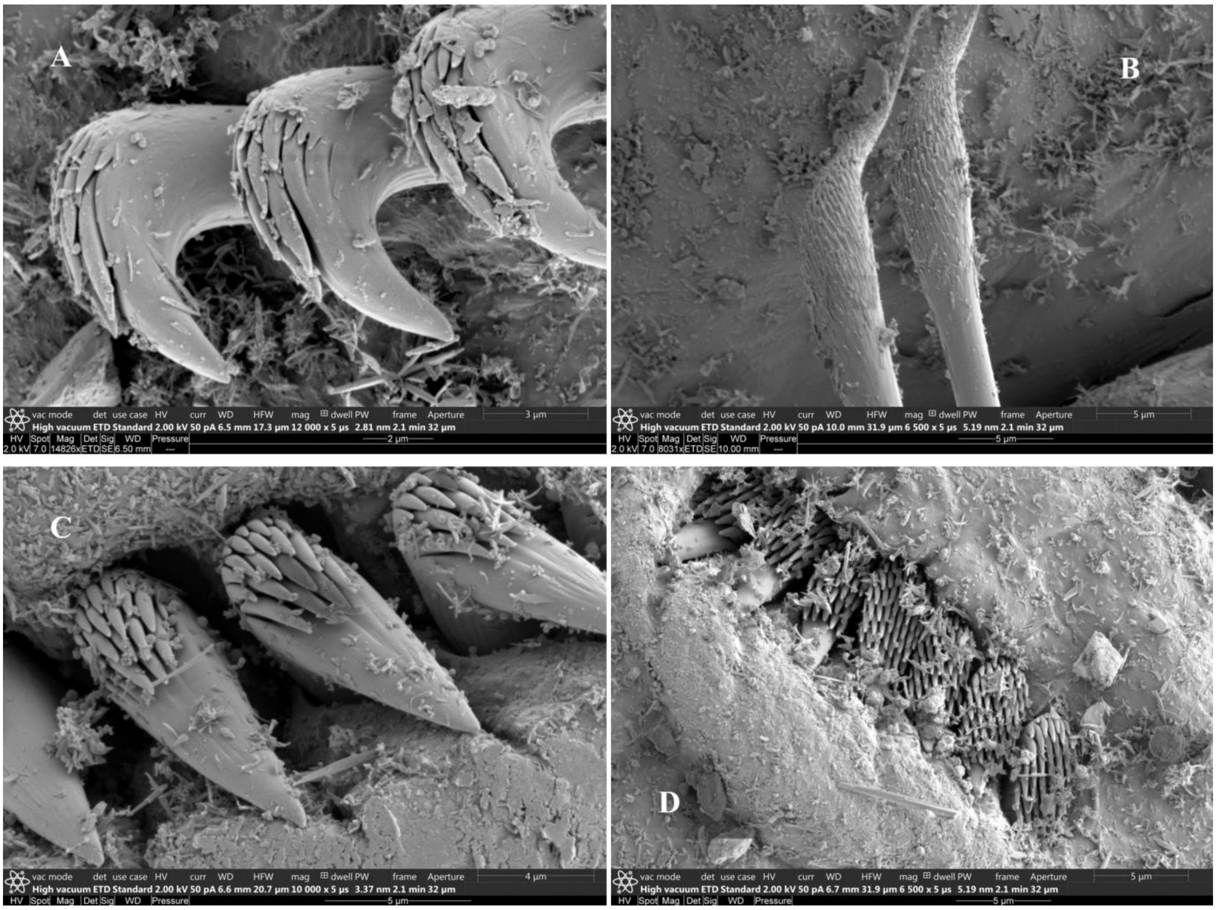


Figure 22: *Dialychone collaris* (TB55). (A) thoracic uncini; (B) thoracic paleate inferior notochaeta; (C) anterior abdominal uncini; (D) posterior abdominal uncini. Scale 0.05 mm.

Dialychone normani (McIntosh 1916)

Chone normani McIntosh, 1916: 65–67, Pl. 2, Fig 13–15, Pl. 3, Fig 14–15.; Tovar-Hernández, 2007: 50- 52, Fig 11.

Dialychone normani Tovar-Hernández 2008: 2219.

Material examined – Mediterranean Sea, Sa Porrassa, Mallorca, illes Balears, Spain, 39.502722’N 2.543889’E, 5 m, algae over rocks (1 specimen) (TB60).

Description - Palmate membrane extending half of the branchial crown length. Number of pair of radioles 5. Radiolar flanges broad. Radiolar tips length up to one- eighth of the branchial crown length, filiform. Pinnules length longest mid- radiole, i.e. snowflake- shape. Shape of dorsal lips elongate without branchial skeleton extensions, three times longer than wide. Dorsal pinnular appendages absent. Ventral cirripresent. Length of the basal lamina of the branchial crown as long as collar segment.

Anterior margin of collar smooth. Angle of collar in lateral view leveled, i.e. even height, or ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe, or sunglass- shaped. Mid- dorsal collar gap narrow. Dorsal pockets well developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe bilobed, covered by collar margin. Peristomial eyes absent. Glandular ridge on second segment narrow. Ventral thoracic shields differentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium does not stain with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate. Anterior margin of inferior chaetae short mucro. Dentition above mf of thoracic uncini series of teeth in nearly uniform size, or teeth slightly diminishing in size posteriorly, covering a half of the mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini from posterior abdomen modified from those in anterior abdominal segments. Breast of anterior abdominal uncini squared, dentition a series of teeth of nearly uniform size above mf, covering a half of the mf length. Breast of posterior abdominal uncini squared, dentition a series of teeth similar in size, covering three- quarters of the mf length (similar to Figure 23). Anal depression absent. Posterior margin of pygidium rounded.

Remarks –The character combination for *D. normani* is medium sized- triangular radiolar tips, broad radiolar flanges, bilobed peristomial lobe projection, dorsal lips rounded, ventral cirri present, smooth anterior margin of collar, peristomium covered by collar, narrow glandular ridge on second segment and abdominal uncini modified posteriorly (Tovar-Hernández 2007). This description does not mention length of dl, but mentions that the length of the ventral lips are ¼ of dl. Dorsal lips have been noted as elongated in other literature (Tovar-Hernández 2008). It has a very close resemblance do *D. dunerificta*, but has broad radiolar flanges (narrow in *D. dunerificta* according to Tovar-Hernández et al. (2007)).

D. normani is a species that has only been recorded from Finnmark. The small distribution range of this species might be due to its resemblance to *C. duneri*, but *D. normani* is different in having elongated dorsal lips and abdominal uncini modified posteriorly. This material is collected in the Mediterranean Sea, which indicates that this species' distribution is wider than previously assumed and is potentially present in more areas of the Northeast Atlantic Ocean. Molecular analysis indicate that this specimen is genetically similar to *D. sp.* 2, *D.* sp. 3 and *Euchone* (Chiade) sp. (Figure 4, Clade 6). *Dialychone normani* has a smooth collar (crenulated in *D*. sp. 2) and broad radiolar flanges and short radiolar tips (narrow and broad in *D.* sp. 3) and anal depression absent (with lateral wings in *Euchone* (Chiade) sp). Because of conspicuous morphological differences, it is likely that it is *D. normani*. However, the molecular evidence do raise a need for caution when deciding this (See * under *D. sp.* 3).

Distribution – Norwegian Coast. *Amendment:* Mediterranean Sea.

Dialychone sp. 1

Material examined – The Norwegian Continental Shelf (Area IV): Skjoldryggen, 65.9477’N 5.84231’E, 608 m, Beamtrawl, 17 June 2013 (1 specimen, radiolar crown and pygidium missing).

Description - Anterior margin of collar smooth. Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view same as first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap attached to peristomium, or narrow. Dorsal pockets well developed. Peristomium partially exposed when collar is flat. Anterior peristomial ring lobe bilobed, exposed above collar margin. Peristomial eyes absent. Glandular ridge on second segment narrow. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation present. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe not developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate. Anterior margin of inferior chaetae medium mucro. Dentition above mf of thoracic uncini series of teeth in nearly uniform size, or teeth slightly diminishing in size posteriorly, covering a half of the mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini from posterior abdomen modified from those in anterior abdominal segments. Breast of anterior abdominal uncini squared. Dentition of anterior abdominal uncini a series of teeth of nearly uniform size above mf, covering a half of the mf length. Breast of posterior abdominal uncini squared. Dentition of posterior abdominal uncini series of teeth similar in size, covering three- quarters of the mf length.

Remarks – This material is characterized by a bilobed peristomial lobe projection, narrow glandular ridge on second segment, dentition of thoracic uncini covering half of the mf length and posterior abdominal uncini modified from anterior. Based on these characters it is possible to identify the specimen to *Dialychone* (Capa & Murray 2015b). Molecular analysis for this specimen is ambiguous and poorly supported (Figure 4, Clade 4). There is a possibility that this specimen belongs to a distinct group that has adapted to a habitat at low depths.

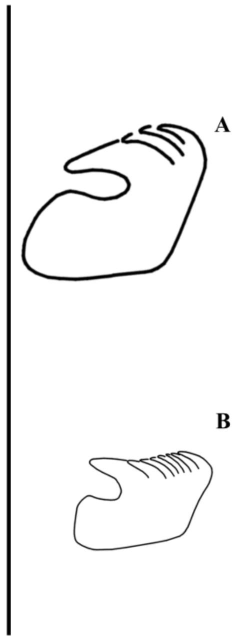


Figure 23: *Dialychone* sp. 1 (TB34). (A) Anterior abdominal uncini; (B) posterior abdominal uncini. Scale 0.1 mm.

Dialychone sp. 2

Material examined **-** Mediterranean Sea, Cala Blava, Mallorca, Illes Balears, Spain, 39.488083’N 2.733972’E, 3-5 m, substrate: algae over rocks and Posidonia (1 specimen) (TB59).

Description - Palmate membrane extending half of the branchial crown length. Number of pair of radioles 4. Radiolar pigmentation absent. Radiolar flanges narrow. Radiolar tips length up to one- eighth of the branchial crown length. Shape of radiolar tips filiform. Shape of dorsal lips elongate without branchial skeleton extensions. Dorsal lips length three times longer than wide. Ventral cirripresent. Length of the basal lamina of the branchial crown as long as collar segment.

Anterior margin of collar crenulated all around. Angle of collar in lateral view leveled, i.e. even height, or ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe, or sunglasses. Mid- dorsal collar gap narrow. Dorsal pockets well developed. Peristomium partially exposed when collar is flat. Anterior peristomial ring lobe bilobed, covered by collar margin. Peristomial eyes absent. Glandular ridge on second segment narrow. Ventral thoracic shields differentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium does not stain with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre-chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta short broadly hooded. Inferior thoracic notochaetae paleate. Anterior margin of inferior chaetae short mucro. Dentition above mf of thoracic uncini series of teeth in nearly uniform size, or teeth slightly diminishing in size posteriorly, covering three- quarters of the mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini uncini from posterior abdomen modified from those in anterior abdominal segments. Breast of anterior abdominal uncini hooked. Dentition of anterioir abdominal uncini a series of teeth of nearly unfiorm size above mf, covering a half of the mf length. Breast of posterior abdominal uncini squared. Dentition of posterior abdominal uncini series of teeth similar in size, covering three- quarters of the mf length. Anal depression absent, or simple. Posterior margin of pygidium rounded.

Remarks – This specimen has the character combination of short radiolar tips, fully crenulated anterior margin of collar, glandular ridge of second segment narrow, short, broadly hooded superior notochaeta, hooked breast of abdominal uncini which are modified posteriorly. It differs from *D. collaris* by having peristomial eyes absent (present in *D. collaris*). No currently species has this combination. For molecular results see * under *Dialychone* sp. 3.

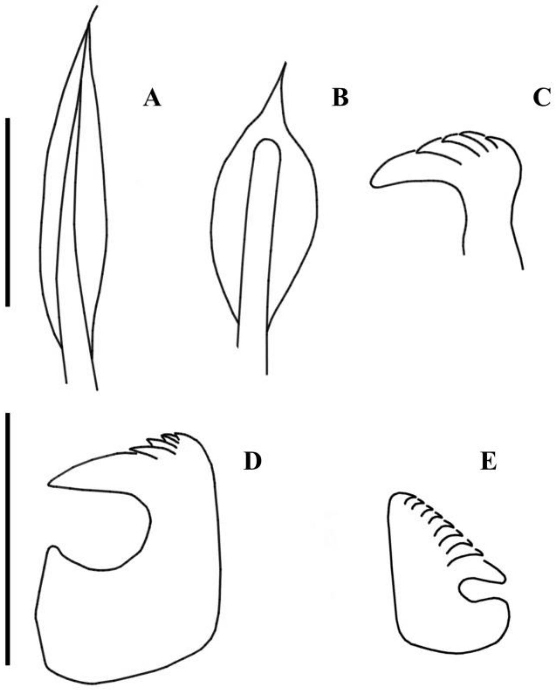


Figure 24: *Dialychone* sp. 2 (TB59) (A) Thoracic superior, broadly hooded, notochaeta; (B) thoracic inferior spatulate, notochaeta; (C) thoracic uncini; (D) anterior abdominal uncini; (E) posterior abdominal uncini. Scale (A, B, C) 0.1 mm, scale (D, E) 0.025 mm.

Dialychone sp. 3

Material examined – The Barents Sea (Area I): Finnmark, 70,29650’N 31,31383’E, 209- 217 m, 8 August 2013 (1 specimen, pygidium missing) (TB62).

Description - Palmate membrane extending half of the branchial crown length, or two- thirds to three- quarters of the branchial crown length. Number of pair of radioles 4. Radiolar pigmentation absent. Radiolar flanges narrow. Radiolar tips length up to half of the branchial crown length, filiform. Pinnules length longest mid- radiole, i.e. snowflake- shape. Shape of dorsal lips elongate without branchial skeleton extensions. dorsal lips length three times longer than wide. Dorsal pinnular appendages absent. Ventral cirripresent. Length of the basal lamina of the branchial crown as long as collar segment.

Anterior margin of collar smooth. Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view two times longer than first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap narrow. Dorsal pockets well developed. Peristomium covered when collar is flat. Anterior peristomial ring lobe bilobed, covered by collar margin. Peristomial eyes absent. Glandular ridge on second segment narrow. Ventral thoracic differentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation absent. Dorsal glandular epithelium does not stain with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini single row.

Remarks – The specimen is similar to “syntype” of *C. filicaudata* regarding the radiolar tips long, peristomial lobe projection bilobed and anterior margin of collar smooth. But it has narrow radiolar flanges (broad in *C. filicaudata*) and a horseshoe- shaped ventral shield of collar(trapezoidal in *C. filicaudata*)(Tovar-Hernández et al. 2007, San Nicolás de los Garza 2017). It resembles *D. longiseta* because of long radiolar tips and a bilobed peristomial lobe projection (Giangrande 1992, Tovar-Hernández et al. 2007), but has narrow radiolar flanges (broad in *D. longiseta*) and a horseshoe- shaped ventral shield of collar(rectangular in *D. longiseta*). The material is poorly preserved and observation of chaeta not available.

* *D. normani*, *D.* sp. 2 and *D.* sp. 3 are recovered as sistergroup to *Euchone* with very low genetic distance (Figure 4, Clade 6). Although these have clear morphological differences, they are in the same haplotype network, and the molecular analysis provides reason for doubt as to whether these specimens are indeed *Dialychone*. This might indicate that this is a group with high phenotypic plasticity. It is not likely that *Euchone* has contaminated the other sequences, because of small differences in sequences. The genetic similarity between the Mediterranean material and the northern material provides evidence that a species may be distributed across these seas.

Sabellidae gen. sp.

Material examined – The Norwegian coast (Area III): Hordaland, 59.75777 N 5.49778 E, 6 August 2014, 60 m, substrate: stones with muddy sand, shell sand (1 specimen, radiolar crown missing) (TB40).

Description - Anterior margin of collar smooth. Angle of collar in lateral view ventral slightly higher than dorsal. Length of the ventral collar segment in lateral view same as first thoracic segment. Shape of ventral shield of collarhorseshoe. Mid- dorsal collar gap attached to peristomium, or narrow. Dorsal pockets well developed. Peristomium partially exposed when collar is flat. Anterior peristomial ring lobe bilobed, exposed above collar margin. Peristomial eyes absent. Glandular ridge on second segment broad dorsally. Ventral thoracic shields undifferentiated. Biannulate thoracic segments present. Posterior- bending dorsal thoracic biannulation present. Dorsal glandular epithelium stains with methyl green. White spots on dorsal and ventral epithelium absent. Thoracic pre- chaetal and post- chaetal lobe well developed. Distribution of thoracic uncini single row. Superior thoracic notochaeta elongate narrowly hooded. Inferior thoracic notochaetae paleate. Anterior margin of inferior chaetae short mucro. Dentition above mf of thoracic uncini series of teeth in nearly uniform size, or teeth slightly diminishing in size posteriorly, covering three- quarters of mf length.

Ventral, glandular pattern on abdomen absent. Abdominal uncini from posterior abdomen modified from those in anterior abdominal segments. Breast of anterior abdominal uncini squared. Dentition of anterior abdominal uncini a series of teeth of nearly uniform size above mf, covering a half of the mf length. Breast of posterior abdominal uncini squared. Dentition of posterior abdominal uncini series of teeth similar in size, covering three- quarters of the mf length. Anal depression absent, or simple. Posterior margin of pygidium triangular.

Remarks – The material has a bilobed peristomial lobe projection, glandular ridge on second segment broad dorsally, dentition of thoracic uncini covering three- quarters of the mf length, posterior abdominal uncini modified from anterior, and anal depression absent or simple. This indicates that this is might be a *Dialychone*. However, molecular analyses indicate that this is genetically similar to *Euchone rosea*. This material does not comply with the description of *Euchone rosea* most apparently by the fact that this specimen has anal depression absent or simple (with lateral wings in *Euchone rosea* by Giangrande & Licciano (2006). The specimen is therefore only identified to family.

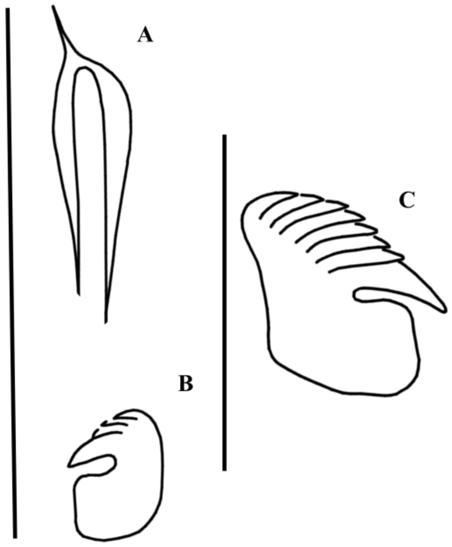


Figure 25: Sabellidae gen. sp. (TB40). (A) Thoracic inferior, paleate, notochaeta; (B) anterior abdominal uncini; (C) posterior abdominal uncini. Scale (A,B) 0.1 mm, scale (C) 0.025 mm.

3.6 Monophyly of genera

These results indicate that the current morphological classifications of *Chone*, *Dialychone*, *Paradialychone* and *Euchone* need revision. The combination of current diagnostic features of the genera and analyses of CO1 provide evidence that none of the genera appear monophyletic.

This is reflected in other studies as well. Capa et al. (2011a) implemented morphological data and multiple genetic markers on several sabellid species and closely related taxa, where *Euchone* do not appear as a monophyletic group. In other studies *Chone* and *Euchone* appear as sistergroups, but these studies have included only one sequence of each (Patti et al. 2003, Kupriyanova & Rouse 2008), whereas Capa et al. (2011a) included two *Euchone*, one *Chone* and one *Dialychone*, where *Dialychone* and *Euchone* appear as sistergroups. This might indicate that even though these genera share some characters (for example internal structure of dorsal lips by Capa et al. (2011b) they might be genetically distant.

The sequences included in the study by Capa et al. (2011a) was one *C.* sp, one *D. perkinsi*, one *E. s.* and one *Euchone variabilis*. This revealed *Euchone* as paraphyletic, where *D. perkinsi* and *E. variabilis* appeared as sistergroups which is congruent with the results in Clade 6 (Figure 4). This means that there is evidence that *Dialychone* and *Euchone* are closely related. However, a cladistics analysis by Cochrane (2003) provided evidence for the paraphyly of *Euchone* based on the length of the pinnules. She proposed to erect a new genus, Chiade, which appears in Clade 6. Chiade was characterized by a snowflake- like crown and an anal depression of three segments. In the study by Cochrane (2003), *E. variabilis* is also included, but it does not appear Chiade- clade. Instead of appearing as a sistergroup to *Dialychone* (as in Capa et al. (2011a)), *E. variabilis* appears as a sistergroup to *Chone*, of which both of them are characterized as having a featherduster- shaped radiolar crown. This is not congruent with the material and results in the present study, where several *Chone*- species have a snowflake- shaped radiolar crown and *Dialychone* and *Euchone* (Chiade) appears as sistergroups. These differences between molecular and morphological results imply that the systematics of these genera is still not fully understood. However, evidence that *Euchone* might be placed in two groups is also given in the present study.

The systematics and phylogenetic relationships within Sabellidae are working progress. The few studies dealing with these issues, and including molecular data have only included a few taxa. Although they are not fully congruent, they have provided new phylogenetic insights to other sabellid genera and annelids (Rousset et al. 2003, Kupriyanova et al. 2006, Capa et al. 2010, Capa et al. 2013, Capa & Murray 2016). Considering that previous morphological studies have indicated paraphyly in *Chone,* it is not unlikely that this might also be the case for *Chone* and *Dialychone* (Fitzhugh 1989, Fitzhugh 1991).

In order for the material comprising the clades in Figure 4 to be taxonomically defined, the current diagnostic features of genera need alteration. Possibilities for synapomorphies for the material in these clades are discussed hereafter. Figure 4 is referred to throughout this chapter.

According to these data, Clade 1 and 2 form a group which is well supported by molecular and morphological data. These would form a monophyletic group based on the following characters; basal membrane long, anterior peristomial ring lobetriangular or digitiform, dorsal pinnular appendages present, glandular ridge on second segment narrow, over ¼ of thoracic uncini covered by dentition, posterior abdominal uncini similar to anterior, anal depression absent (given that TB23 is contaminated). This would entail dismissing diagnostic characters for *Chone*: dorsal lips rounded, pinnules longest mid- radiole, medial tooth of dentition of thoracic uncini enlarged, dentition of abdominal uncini extending around ¼ of mf. In this material the rear end of the abdominal uncini in Clade 2 is rounded, while in Clade 1 it is squared. This might be useful as a character for distinguishing these clades. The morphological data for Clade 3 should be investigated to check if it could also be included. However, the basal node for these three clades have a low support (= 59).

The possibility that Clade 1, 2, 3 and 4 shares the same basal node is present, and in that case the only character that would produce monophyly based on this material is ventral thoracic shield undifferentiated. This would include *C.* cf *duneri* (TB26-27), and be equivalent to Group C, *Chone sensu stricto* in the analysis by Tovar-Hernández (2008). However, *E. rosea* is noted as having ventral thoracic shields differentiated (Giangrande & Licciano 2006).

The most ambiguous genus in this study is *Dialychone*. It is both paraphyletic, and genetically very similar to members of *Euchone*. A character that provides monophyly of the material of Clade 6 are basal membrane short- long, anterior peristomial ring lobe bilobed, dorsal lips elongated, dorsal pinnular appendages absent, pinnules longest mid- radiole, dentition of thoracic uncini slightly diminishing in size posteriorly and differentiated ventral shields. The latter is interesting because *Dialychone* is described as having ventral shields undifferentiated by Tovar-Hernández (2008). This is also noted by Capa et al. (2011a) for *Dialychone* and *Euchone*, which does not comply with the material in this study. If differentiated ventral shields were to be used as a diagnostic character it would include a specimen of a different genus, and dismiss some of the diagnostic features of *Dialychone*, the anal depression and posterior abdominal uncini modified.

Paradialychone is represented by one sequence in the dataset (Clade 3), which is appear as a sistergroup to *Chone*. This contradicts the cladistic analysis of morphological characters by Tovar-Hernández (2008) where *Dialychone* and *Paradialychone* appear as sistergroups. These results indicate that the character combination of pinnules of equal length along entire radiole and elongated dorsal lips are not exclusive for this genus, as these also appear in *C.* sp. y in Clade 1.

Euchone is present in Clade 4, 5 and 6. Investigating the morphological differences *Euchone* is necessary in order to revise the taxonomic status of this genus.

The taxa in Clade 4 and 5 propose difficulties because they have a wide phenotypic variety, consists of 3 genera and are poorly supported by molecular analysis. They do, however, all have a bilobed anterior peristomial ring lobeand length of ventral collar segment same as first thoracic segment. Clade 5 in the Bayesian inference tree displays a more honest result than the Maximum Likelihood because the nodes have a low bootstrap values. It is not included in the Bayesian consensus tree, and needs more data and support in order to assess its position in the tree.

3.7 Key to species of *Chone* and *Dialychone* in Norwegian waters

Based on these results and material available, a short key is provided for *Chone* and *Dialychone* species reported in Norwegian waters:

1. Pygidial cirrus
    a. Sometimes present → *Chone filicaudata* (not confirmed by this study)
    b. Absent → 2.
2. Ventral thoracic shields
    a. Undifferentiated → 3.
    b. Differentiatied → 8.
3. Anterior peristomial ring lobe
    a. Bilobed → 4.
    b. Triangular → 5.
    c. Digitiform → *Chone* sp. 1
4. Abdominal uncini
    a. Similar in shape anteriorly and posteriorly → *Chone* cf *duneri*
    b. Modified posteriorly → *Dialychone* sp. 1
5. Dorsal lips
    a. Elongate → *Chone* sp. y
    b. As long as wide → 6.
6. Radiolar tips
    a. Filiform, up to one-quarter of the length of the branchial crown (OBS: southern specimens may have length up to one-eight of the branchial crown) Ventral shield of collar rounded → *Chone fauveli*
    b. Broad/Tapering, up to one- eight of the branchial crown length → 7.
7. Extension of dentition of abdominal uncini
    a. Up to one- quarter of main fang length → *Chone infundibuliformis*
    b. Up to one- half of main fang length → *Chone kroyerii*
8. Number of pair of radioles
    a. Three pairs → *Chone paucibranchiata*
    b. More than three pairs → 9.
9. Anterior margin of collar
    a. Fully crenulated → *Dialychone collaris*
    b. Smooth → 10.
10. Length of radiolar tips
    a. Up to one- eight of the branchial crown length → *Dialychone normani*
    b. Up to one half of the branchial crown length → *Dialychone* sp. 3

3.8 Discussion of characters

There is an ongoing process of revising the characters used to identify Sabellids, and many characters have been improved. However, this is not the case for older literature. This chapter mentions characters that have shown to be somewhat confusing in descriptions or the material available. Due to variations between descriptions, possibly size- dependent characters, contraction movements of the animal, fixation effects and a lack of standardization of method these characters might be difficult to define (Costa-Paiva et al. 2007, Oliveira et al. 2010).

Some characters have been revised in previous literature, others have not. This is meant as a summary of the morphological challenges that was encountered during this study. It is limited by material available, but a comprehensive glossary by Wong et al. (2014) provides a deeper understanding of the many characters of Sabellidae.

Character: Faecal groove and/or dorsal gap

State: Broad/Narrow

Remark: It is not always included in descriptions whether it refers to the gap (sometimes referred to as dorsal incision) between the collar or an enlarged faecal groove (sometimes referred to as gap in thorax). Some differ between the two (Cochrane 2000) others mention only one (Tovar-Hernández & Sosa-Rodríguez 2006). As noted in the redescription of *C. infundibuliformis* by Tovar-Hernández & Sosa-Rodríguez (2006) it may be size- dependent, and fixation does not not alter its conspicuousness. This might explain why some authors include this character and some don’t. One solution to this might be to include the dorsal state of the glandular ridge on the second segment as consistent (narrow) or dorsally interrupted (broad), and/or specify that this is most apparent in large specimens.

Character: Length of mucro, length of radiolar tips

State: Short/Medium/Long/Extra long

Remark: These are subjective, and uninformative when the identifier is not familiar with the species and the different variations. One solution to this might be to use relative sizes, for example: Mucro of inferior notochaeta absent, one- quarter, one half or more than one half of paleate area/swollen area of chaeta.

Character: Shape of radiolar tips

State: Filiform/Tapering

Remark: It is not clear what the difference is between tapering and short filiform. In this study they have been considered as equal.

Character: Pygidium

State: Triangular/rounded

Remark: This is uninformative when the identifier is not familiar with the species and the different variations. In addition, variation between live specimens has been observed depending on gut movement. One solution might be to refer to merge these two states, and refer to it as rounded.

Character: Notopodial lips(Pre- chaetal and post- chaetal lobe)

State: Present/Absent

Remark: This character has been observed as very conspicuous or not easily discernible in individuals of same species. The possibility that these might be motile or contractible should be investigated.

Character: Dorsal and ventral lips

Remark: Very difficult to discern in small specimens fixed in EtOH.

Character: Anal depression

State: Simple/absent

Remark: This character has been observed as present or absent in individuals of same species in the present study. It has also been observed present in specimens post- fixation of species where anal depression is absent. It is unpredictable/erratic.

Character: Length of collar segment in relation to first thoracic segment

Remark: This requires an exact position of where to measure, and vary with collar level and folding (which varies between specimens of same species) of collar.

Character: Distribution of thoracic uncini

State: Single row/Two irregular rows

Remark: Might be size- dependent (Tovar-Hernández & Sosa-Rodríguez 2006). Observation of live specimens of *C. infundibuliformis* excluded the possibility that this character was a consequence of dorsal- ventral movement, i.e. the thoracic neurochaeta stay put in their own row. It should be noted that Knight- Jones & Perkins (1998) observed movement in other genera.

Character: Dentition of thoracic uncini

Remark: This may vary within tori, for example in *C.* sp. 1 (TB48) See Figure 20.

Character: Pygidial uncini

Remark: In this material there are big differences in dentition and shape between posterior abdominal uncini and pygidial uncin. This means that it might be necessary to pinpoint which segment range that makes up "posterior abdomen".

Character: Anterior peristomial lobe projection

State: Digitiform/Triangular

Remark: Some literature includes character state Digitiform, while others include Elongated triangular.

Character: Number of radioles and segments

Remark: Except for radioles of *C. paucibranchiata*, this may have individual and/or regional variations (Fitzhugh 1989, Cochrane 2000).

Character: Inferior thoracic notochaeta

State: Paleate/Pseudospatulate (Sometimes referred to as Spatulate/Subspatulate)

Remark: Due to ambiguity of this character there has been much confusion (Cochrane 2000). In this material, a clear difference is seen in which the shaft/core of the chaeta stops before the periphery of the tip, paleate, (Figure 10) (Wong et al. 2014), or is continuous and pierces the periphery of the chaeta, pseudospatulate (Figure 15).

Character: Methyl green/blue staining

Remark: It has been observed in this study that the results of staining varies between individuals of same species, methyl blue concentration and the length of the staining period. It is very useful for accentuating diffuse characters (anterior margin of collar, ventral shield differentiation, dorsal lips), but in order to use species specific glandular patterns a standardized method should be made.

Conclusion

The following morphospecies are somewhat congruent with the analyses of molecular data: *C. kroyerii*, *C. infundibuliformis*, *C. fauveli* and *D. collaris*, while the following species give reason for doubt: *C. paucibranchiata*, *C.* sp. y, *C. duneri* and *D. normani*. Some species have morphological differences between them, but are genetically similar. About 3 lineages present in Norwegian waters, genetically distinct and with unique combinations of morphological features, do not match any species description in the literature and are interpreted as new to Science. Some species descriptions have been improved.

Chone, *Dialychone* and *Euchone* do not appear monophyletic in molecular analyses when using current classification. *Paradialychone* remains unsolved, but the current diagnostic features do not appear to be exclusive for this genus. This highlights that the traditional classification might be misleading and that molecular data may provide some more evidence when revising these genera. Possible diagnostic characters for genetically monophyletic clades in this study are discussed.

Other parameters could be implemented in future studies in order to solve this taxonomic mystery, like histology, larval development, ecology, reproduction and differences between sexes. More material from several locations should be collected and evaluated, preferably alive. Several loci should be included in phylogenetic analysis in order to produce statistically significant analyses.

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Appendix I

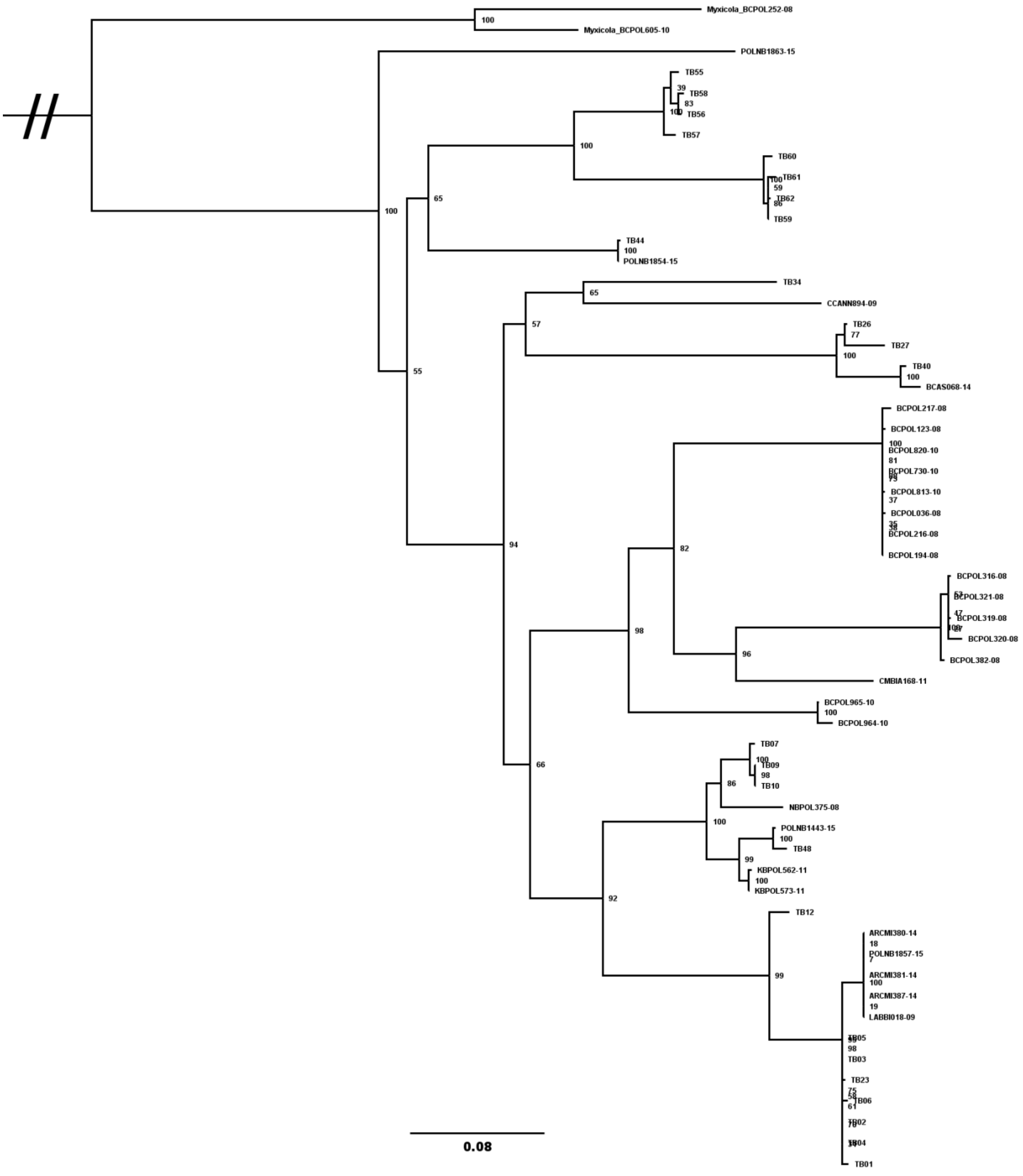

Figure 26: Maximum Likelihood tree of CO1 fragment of *Chone*, *Dialychone*, *Paradialychone* and *Euchone*. The analysis included a total of 57 sequences. Including node labels showing bootstrap values and branch length values.

Appendix Ⅱ

Table 1: Divergences in CO1 fragment using Maximum Composite Likelihood model (Tamura et al. 2004) with gamma distribution (= 1) shown in the lower left corner and p- distance in the upper right corner. Within group distances are marked in red. Low (<0.027) between group distances are marked in blue. The analysis involved 54 nucleotide sequences with a total of 657 positions.

	1	3	4	2	5	10	8	7	6	9	14	13	12	11	26	25	23	24	22	21	20	19	18	17	16	15	27
1	0,002	0,014	0,014	0,003	0,030	0,158	0,156	0,158	0,153	0,159	0,189	0,199	0,729	0,712	0,724	0,725	0,722	0,727	0,709	0,732	0,733	0,715	0,706	0,720	0,713	0,712	0,721
3	0,014	0,000	0,000	0,016	0,045	0,158	0,155	0,157	0,152	0,160	0,193	0,197	0,729	0,710	0,724	0,726	0,721	0,727	0,711	0,731	0,732	0,715	0,706	0,717	0,708	0,706	0,720
4	0,014	0,000	n/c	0,016	0,045	0,158	0,155	0,157	0,152	0,160	0,193	0,197	0,729	0,710	0,724	0,726	0,721	0,727	0,711	0,731	0,732	0,715	0,706	0,717	0,708	0,706	0,720
2	0,003	0,016	0,016	n/c	0,031	0,160	0,156	0,158	0,153	0,160	0,188	0,204	0,726	0,709	0,723	0,722	0,719	0,722	0,703	0,733	0,733	0,712	0,701	0,717	0,717	0,713	0,720
5	0,032	0,048	0,048	0,033	n/c	0,060	0,076	0,076	0,067	0,085	0,152	0,165	0,705	0,676	0,679	0,679	0,674	0,679	0,660	0,710	0,710	0,683	0,665	0,698	0,692	0,683	0,679
10	0,206	0,206	0,206	0,210	0,066	0,004	0,066	0,060	0,049	0,050	0,183	0,178	0,729	0,705	0,720	0,722	0,722	0,725	0,712	0,731	0,730	0,712	0,719	0,712	0,709	0,710	0,721
8	0,204	0,202	0,202	0,204	0,086	0,072	n/c	0,009	0,033	0,078	0,184	0,183	0,736	0,711	0,724	0,726	0,725	0,727	0,717	0,737	0,738	0,718	0,725	0,724	0,721	0,720	0,729
7	0,206	0,203	0,203	0,207	0,086	0,065	0,009	n/c	0,027	0,072	0,181	0,182	0,736	0,710	0,727	0,727	0,728	0,730	0,717	0,740	0,739	0,721	0,725	0,724	0,720	0,720	0,730
6	0,200	0,197	0,197	0,200	0,076	0,053	0,034	0,028	0,002	0,060	0,175	0,189	0,730	0,704	0,721	0,721	0,721	0,724	0,711	0,734	0,733	0,715	0,719	0,717	0,714	0,713	0,724
9	0,211	0,210	0,210	0,212	0,098	0,054	0,086	0,079	0,065	n/c	0,170	0,176	0,747	0,723	0,742	0,742	0,743	0,745	0,732	0,753	0,753	0,737	0,734	0,734	0,731	0,734	0,739
14	0,262	0,270	0,270	0,262	0,201	0,249	0,252	0,247	0,236	0,228	0,002	0,165	0,706	0,681	0,708	0,704	0,705	0,705	0,691	0,706	0,706	0,695	0,688	0,687	0,688	0,686	0,703
13	0,283	0,280	0,280	0,294	0,218	0,243	0,254	0,250	0,264	0,239	0,216	0,007	0,725	0,703	0,726	0,725	0,722	0,725	0,709	0,719	0,718	0,706	0,694	0,705	0,714	0,707	0,710
12	0,260	0,263	0,263	0,253	0,189	0,213	0,227	0,216	0,216	0,216	0,180	0,172	n/c	0,158	0,203	0,198	0,202	0,198	0,197	0,191	0,189	0,180	0,189	0,195	0,184	0,188	0,198
11	0,255	0,254	0,254	0,260	0,203	0,232	0,230	0,223	0,230	0,232	0,214	0,224	0,204	0,009	0,221	0,212	0,212	0,211	0,204	0,184	0,183	0,188	0,181	0,200	0,179	0,173	0,208
26	0,308	0,313	0,313	0,301	0,213	0,261	0,294	0,288	0,279	0,266	0,331	0,297	0,291	0,335	n/c	0,005	0,013	0,005	0,135	0,183	0,182	0,208	0,213	0,225	0,208	0,217	0,205
25	0,296	0,297	0,297	0,295	0,213	0,250	0,283	0,274	0,266	0,252	0,317	0,284	0,281	0,314	0,005	n/c	0,008	0,002	0,127	0,180	0,178	0,198	0,206	0,221	0,207	0,211	0,200
23	0,297	0,300	0,300	0,299	0,228	0,257	0,285	0,280	0,272	0,262	0,326	0,281	0,287	0,313	0,013	0,008	n/c	0,009	0,126	0,178	0,177	0,199	0,205	0,227	0,215	0,215	0,201
24	0,291	0,292	0,292	0,295	0,213	0,243	0,275	0,270	0,262	0,247	0,316	0,284	0,281	0,311	0,005	0,002	0,009	n/c	0,127	0,177	0,176	0,198	0,206	0,222	0,209	0,211	0,200
22	0,296	0,291	0,291	0,308	0,214	0,237	0,266	0,265	0,252	0,252	0,299	0,279	0,276	0,297	0,164	0,152	0,150	0,153	0,013	0,163	0,161	0,191	0,189	0,217	0,205	0,210	0,192
21	0,273	0,276	0,276	0,285	0,181	0,217	0,221	0,225	0,217	0,219	0,297	0,263	0,263	0,254	0,247	0,240	0,238	0,236	0,214	n/c	0,002	0,169	0,185	0,221	0,204	0,201	0,198
20	0,279	0,278	0,278	0,288	0,181	0,224	0,230	0,227	0,220	0,222	0,301	0,260	0,261	0,251	0,245	0,238	0,235	0,233	0,212	0,002	n/c	0,168	0,183	0,219	0,201	0,199	0,197
19	0,260	0,270	0,270	0,266	0,205	0,228	0,244	0,242	0,236	0,231	0,263	0,249	0,245	0,261	0,306	0,285	0,288	0,287	0,268	0,227	0,225	n/c	0,156	0,197	0,190	0,188	0,209
18	0,267	0,273	0,273	0,265	0,201	0,266	0,291	0,284	0,272	0,278	0,266	0,288	0,268	0,244	0,310	0,295	0,292	0,293	0,263	0,253	0,250	0,207	n/c	0,187	0,180	0,175	0,191
17	0,308	0,318	0,318	0,303	0,235	0,330	0,327	0,323	0,319	0,325	0,296	0,325	0,273	0,286	0,347	0,338	0,351	0,340	0,324	0,326	0,322	0,286	0,260	0,027	0,051	0,055	0,230
16	0,281	0,294	0,294	0,259	0,187	0,312	0,308	0,299	0,299	0,298	0,288	0,271	0,253	0,248	0,301	0,301	0,316	0,306	0,300	0,290	0,285	0,274	0,247	0,055	n/c	0,014	0,220
15	0,266	0,278	0,278	0,268	0,194	0,299	0,294	0,285	0,289	0,287	0,282	0,289	0,259	0,236	0,322	0,308	0,314	0,308	0,309	0,283	0,280	0,269	0,236	0,059	0,014	n/c	0,217
27	0,326	0,332	0,332	0,325	0,226	0,280	0,294	0,290	0,291	0,317	0,311	0,316	0,282	0,299	0,290	0,281	0,284	0,282	0,266	0,273	0,270	0,309	0,268	0,350	0,324	0,315	n/c

Appendix III

List of characters and character states included in the DELTA matrix.

#1. Branchial lobes/

1. separate/
2. fused dorsally/

#2. Palmate membrane extending/

1. absent/
2. less than one- quarter of the branchial crown length/
3. one- quarter to one- third of the branchial crown length/
4. half of the branchial crown length/
5. two- thirds to three- quarters of the branchial crown length/

#3. Number of radioles/

1. three pairs/
2. more than three pairs/

#4. Pair of radioles/

#5. Radiolar pigmentation/

1. absent/
2. white spots within skeleton cells/
3. dark spots on flanges/

#6. Radiolar flanges/

1. absent/
2. narrow/
3. broad/

#7. Radiolar tips length/

1. up to one- eighth of the branchial crown length/
2. up to one- quarter of the branchial crown length/
3. up to half of the branchiall crown length/

#8. Shape of radiolar tips/

1. filiform/
2. tapering/
3. broad/

#9. Pinnules/

1. unpaired (alternating)/
2. paired/

#10. Pinnules length/

1. longest mid- radiol, i.e. snowflake- shape/
2. similar in length all along, i.e. feathershape/

#11. Shape of dorsal lips/

1. broadly rounded/
2. elongate, distally tapered with branchial skeleton extensions/
3. elongate without branchial skeleton extensions/

#12. Dorsal lips length/

1. as long as wide/

   2. three times longer than wide/
   3. eight times longer than wide/

#13. Dorsal pinnular appendages/
   1. absent/
   2. present/

#14. Number of dorsal pinnular appendages/

#15. Dorsal pinnular appendages connected by palmate membrane/
   1. absent/
   2. present/

#16. Ventral cirri/
   1. absent/
   2. present/

#17. Parallell lamellae/
   1. absent/
   2. present/

#18. Abscission zone/
   1. absent/
   2. present/

#19. Basal lamina of the branchial crown/
   1. tubular/
   2. cup- shaped/

#20. Length of the basal lamina of the branchial crown/
   1. shorter than collar segment (median area in lateral view)/
   2. as long as collar segment/
   3. longer than collar segment/

#21. Anterior margin of collar/
   1. smooth/
   2. crenulated all around/
   3. crenulated ventrally/

#22. Dorsal incisions of the anterior collar margin/
   1. absent/
   2. short/

#23. Ventral incision of the anterior collar margin/
   1. absent/
   2. short/
   3. long, forming well- developed ventral lappets/

#24. Angle of collar in lateral view/
   1. leveled, i.e. even height/
   2. ventral slightly higher than dorsal/
   3. ventral higher than dorsal/
   4. ventral llower than dorsal/

#25. Length of the ventral collar segment in lateral view/
   1. same as first thoracic segment/
   2. two times longer than first thoracic segment/
   3. three times longer than the first thoracic segment/

#26. Shape of ventral shield of collar/
1. undifferentiated/
2. horseshoe/
3. rectangualr/
4. trapezoidal/
5. rounded/
6. A- shaped/
7. triangular/
8. sunglasses/
9. lung/

#27. Mid- dorsal collar gap/
1. attached to peristomium/
2. narrow/
3. Very pronounced delineated faecal groove almost resembling a dorsal split
4. wide/

#28. Dorsal pockets/
1. not developed/
2. poorly developed/
3. well developed/

#29. Ciliated dorsal pockets/
1. absent/
2. present/

#30. Peristomium/
1. fully exposed when collar is flat/
2. partially exposed when collar is flat/
3. covered when collar is flat/

#31. Ventral peristomial lobe projection/
1. collar/
2. triangular/
3. bilobed/
4. digitiform/

#32. Exposition of the ventral peristomial lobe projection/
1. covered by collar margin/
2. exposed above collar margin/

#33. Vascular loops in peristomium/
1. absent/
2. present/

#34. Peristomial eyes/
1. absent/
2. present/

#35. Glandular ridge on second segment/
1. absent/
2. narrow/
3. broad dorsally/
4. broad ventrally/
5. broad laterally/
6. broad with vertical projections/

   7. hypertrophied/
   8. vestigial/

#36. Ventral thoracic shields/
   1. undifferentiated/
   2. differentiated/

#37. Biannulate thoracic segments/
   1. present ventrally, absent dorsally/
   2. absent/
   3. present/

#38. Posterior- bending dorsal thoracic biannulation/
   1. absent/
   2. present/

#39. Glandular ridges on posterior thoracic segments/
   1. absent/
   2. present/

#40. Dorsal glandular epithelium/
   1. does not stain with methyl green/
   2. stains with methyl green/

#41. White spots on dorsal and ventral epithelium/
   1. absent/
   2. present/

#42. Thoracic pre- chaetal and post- chaetal lobe/
   1. not developed/
   2. well developed/

#43. notopodial lips/
   1. absent/
   2. present/

#44. Distribution of thoracic uncini/
   1. single row/
   2. two irregular rows/

#45. Superior thoracic notochaeta/
   1. short broadly hooded/
   2. elongate narrowly hooded/

#46. Inferior thoracic notochaetae/
   1. absent/
   2. long, broadly hooded/
   3. short, broadly hooded/
   4. paleate/
   5. pseudospatulate/

#47. Anterior margin of inferior chaetae/
   1. convex/
   2. short mucro/
   3. medium mucro/
   4. long mucro/

#48. Dentition above main fang (MF) of thoracic uncini/

1. series of teeth in nearly uniform size/UNEQUAL SIZE??/
2. teeth slightly diminishing in size posteriorly/
3. a large tooth offset from midline, followed by series of smaller teeth/
4. a large tooth above the MF in midline, followed by a series of smaller teeth/
5. one or two large tooth in different positions/

#49. Extension of dentition above mf, thoracic uncini/
1. three- quarters/
2. a half/
3. a quarter/

#50. Glandular ridges on anterioor abdominal segments/
1. absent/
2. present/

#51. Ventral, glandular pattern on abdomen/
1. absent/consistent?/
2. band on posterior abdomen/
3. two round projecting patches per segment/

#52. Abdominal uncini/
1. similar shape along entire abdominal segments/
2. uncini from posterior abdomen modified from those in anterior abdominal segments/

#53. Breast of anterior abdominal uncini/
1. as manubrium/
2. hooked/
3. squared/
4. narrow swelling/

#54. Handles of anterior abdominal uncini/
1. absent/
2. long/
3. short/

#55. Dentition of anterioir abdominal uncini/
1. rasp- shaped plates/
2. a series of teeth of nearly unfiorm size above mf/
3. a large tooth above the MF in midline, followed by a series of smaller teeth/

#56. Extension of dentition in anterior abdominal uncini/
1. crest dentate completely/
2. covering a quarter of the MF length/
3. three quarters/
4. covering a half of the MF length/

#57. Breast of posterior abdominal uncini/
1. as manubrium/
2. hooked/
3. squared/
4. narrow swelling/

#58. Handles of posterior abdominal uncini/
1. absent/

   2. long/
   3. short/

#59. Dentition of posterior abdominal uncini/
   1. rasp- shaped plate/
   2. series of teeth similar in size/
   3. large tooth followed by a series of smaller teeth/

#60. Extension of dentition in posterior abdominal uncini/
   1. crest dentate completely/
   2. covering a quarter of the MF length/
   3. covering half of the MF length/
   4. covering three- quarters of the MF length/

#61. Anal depressio/
   1. absent/
   2. simple/
   3. with lateral wings/
   4. with an anterior margin/

#62. Posterior margin of pygidium/
   1. rounded/
   2. triangular/
   3. pointed/

#63. Pygidial eyes/
   1. present/
   2. absent/

#64. Pygidial cirrus/
   1. absent/
   2. present/

#65. Abdominal growth (addition of segments)/
   1. fixed segment number/
   2. pre- pygidial growth/