

# Resolving a 200-year-old taxonomic conundrum: neotype designation for *Cephalothrix linearis* (Nemertea: Palaeonemertea) based on a topotype from Bergen, Norway

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The taxonomic identity of the palaeonemertean *Cephalothrix linearis* (Rathke, 1799) has been obscure for nearly two centuries, because its original description applies to almost any congeners, including *Cephalothrix filiformis* (Johnston 1828) and *Cephalothrix rufifrons* (Johnston, 1837), which occur commonly in the North Sea and adjacent waters. In this paper, I redescribe *C. linearis* based on two topotypes from Bergen, one herein designated as the neotype for *C. linearis*, because Rathke's original material is not extant; I invoke Article 70.3.2 of the International Code of Zoological Nomenclature to fix *Planaria linearis* Rathke, 1799 as the type species of *Cephalothrix* Örsted, 1843 for the sake of stability. From the neotype, I determined sequences of the 28S rRNA, 16S rRNA, and cytochrome *c* oxidase subunit I (COI) genes. Using the COI sequence, I inferred the phylogenetic position of *C. linearis* along with 316 cephalotrichid sequences currently available in public databases. A tree-based species delimitation analysis detected 43 entities among them, with 34 in *Cephalothrix* and nine in either *Balionemertes* or *Cephalotrichella*. I apply valid species names to 12 of the 34 entities in *Cephalothrix*. I tabulated a total of 36 nominal species that are likely the members of the genus; the following five were excluded even though their specific names were originally combined with *Cephalothrix*: *Cephalothrix armata* Ulyanin, 1870 [Monostilifera, possibly *Emplectonema gracile* (Johnston, 1837)], *Cephalothrix fragilis* Bürger, 1892 [now *Cephalotrichella signata* (Hubrecht, 1879)], *Cephalothrix signata* Hubrecht, 1879 [now in *Cephalotrichella*], *Cephalothrix unipunctata* Parfitt, 1867 [now *Tetrastemma melanocephalum* (Johnston, 1837) (Monostilifera)], and *Cephalothrix viridis* Chapuis, 1886 [possibly Heteronemertea]. The five names *cephalothrix* Diesing, 1850 (as *Borlasia cephalothrix*), *kroyeri* Diesing, 1850 (as *Cephalothrix kroyeri*), *linearis* Diesing, 1850 (as *Borlasia linearis*), *lineata* Claparède, 1862 (as *Cephalothrix lineata*), and *oerstedi* Diesing, 1850 (as *Cephalothrix oerstedi*) are declared nomenclaturally unavailable.

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## INTRODUCTION

Nemerteans, or ribbon worms, are mostly marine, benthic invertebrates that constitute the phylum Nemertea, which is closely related to Phoronida, Brachiopoda, Mollusca, and Annelida (Luo *et al.* 2018). So far, about 1300 species of nemerteans have been described and named from world oceans (Gibson 1995; Kajihara *et al.* 2008; Norenburg *et al.* 2018). They are classified into three major taxa: Palaeonemertea, Pilidiophora, and Hoplonemertea (Thollesson & Norenburg 2003; Strand *et al.* 2018).

It was once believed that nemerteans could be differentiated from each other by examining internal morphology, chiefly based on serial transverse sections (e.g., Gibson 1985). While it is true that higher taxa (e.g., Palaeonemertea *versus* Hoplonemertea) can be distinguished by internal anatomy, specialists have been increasingly aware that this is not true for different species within less inclusive taxa, such as families or genera, where the members are almost uniform in internal anatomical structure. Artefacts derived from fixation and histological preparation can obscure inter-specific morphological differences, even if such differences were present in the first place (cf. Sundberg 1979). Here, traditional name-bearing type specimens in the form of serial transverse sections, which has been common for nemertean taxonomy since the 20th century, are insufficient, if not useless, for the purpose of identifying a specimen of interest by morphological comparison in the sense of the International Code of Zoological Nomenclature (hereafter the Code) (International Commission on Zoological Nomenclature (hereafter ICZN) 1999). At the moment, objective anchoring of species names is best achieved with so-called barcode sequences, mostly represented by the cytochrome *c* oxidase subunit I (COI) gene (e.g., Chen *et al.* 2010; Sundberg *et al.* 2016), but also the 16S rRNA gene to some extent (e.g. Hiebert & Maslakova 2015). For many of the species newly established since the middle of 2000s, such barcode sequences have been generated and published at the time of species description (e.g., Strand *et al.* 2005; Maslakova & Norenburg 2008; Taboada *et al.* 2013). However, an overwhelming majority of the species established before the 21st century have not yet been anchored to such sequences. Even when barcode sequences are available in public databases, their taxonomic reliability can be doubtful (e.g., Bridge *et al.* 2003). On the other hand, it has become evident that external characters in living state are more informative than previously expected for nemertean species identification (Strand *et al.* 2014). For accurate species-name allocation, therefore, it is important to provide with as many species as possible a combination of *i*) scientific name, *ii*) barcode sequence(s), and *iii*) high-quality images taken in life, each derived from a reliably identified specimen, ideally collected at type localities, with voucher material (tissue and/or DNA) deposited in research institutes.

The identity of the palaeonemertean *Cephalothrix linearis* (Rathke, 1799) (Figure 1A) has been confused and in need

of clarification for more than 200 years (see the following subsection *Taxonomic history* for further details). In the North Sea and adjacent waters, two additional species of *Cephalothrix* Örsted, 1843 commonly occur: *Cephalothrix filiformis* (Johnston, 1828), with uniformly whitish body; and *Cephalothrix rufifrons* (Johnston, 1837), having a yellowish body with a characteristic reddish hue at the tip of head. The original description of *C. linearis* was so vague that it could apply to almost any cephalotrichid, let alone *C. filiformis* and *C. rufifrons*. Later authors regarded *C. linearis* as either synonymous with *C. filiformis* (Bürger 1904) or *C. rufifrons* (Stephenson 1911: 6–10; cf. Hylbom 1957), or distinct from both *C. filiformis* and *C. rufifrons* (Wijnhoff 1913; Gibson 1982, 1994).

The problem is complicated by the facts that *i*) the original description of *C. linearis* applies to both *C. filiformis* and *C. rufifrons*, *ii*) the type locality of *C. linearis* is encompassed by the areas of distribution of both *C. filiformis* and *C. rufifrons*, and *iii*) *C. linearis* has nomenclatural precedence over *C. filiformis* and *C. rufifrons*. The type material of *C. linearis*, even if it were extant, would never serve to solve the problem, because morphology would be unlikely to diagnose the species and no DNA sequence could be obtained from material collected in the 18th century. Here exists the “exceptional need”—in the sense of Article 75.3 of the Code (ICZN 1999)—for a neotype of *C. linearis*, and especially for barcode sequence(s) from it. However, from European waters, there has been no report of any nemertean decidedly referable to *C. linearis* and decidedly different from *C. filiformis* and *C. rufifrons*.

I identified one of the 12 species of nemerteans (Figures 1B–N, 6A–D) that I collected during my short visit to Bergen in 2006 as *C. filiformis*. Partially based on the Bergen material, I reported three types of rhynchocoel blood vessels in 26 specimens representing 14 species of *Cephalothrix* (Kajihara 2010). Among them, Type C was only found in a couple of specimens of *C. filiformis* from Bergen. On the other hand, Beckers *et al.* (2013) applied the name “*Procephalothrix filiformis*” to a uniformly white form having a long pre-oral region from Sylt (Germany), which possesses a Type-B rhynchocoel vessel (evident on 74–80 of 501 slices of transverse sections available at [https://www.morphdbase.de/?P\\_Beckers\\_20130201-M-15.1](https://www.morphdbase.de/?P_Beckers_20130201-M-15.1)). After thorough literature survey and genetic analysis, I concluded that I had made a misidentification and the Bergen specimens should represent *C. linearis*, rather than *C. filiformis*.

The purpose of this paper is to enable objective usage of the name *C. linearis* by designating a topotype from Bergen as a neotype. To better establish the taxon concept, I provide a brief description of its external feature and internal anatomy. I inferred the phylogenetic position of *C. linearis* among other congeners, for which COI sequences were available in the public databases. I performed a species delimitation analysis and tried to apply valid species names wherever possible to each ‘species’ detected by the analysis. In addition, I went through

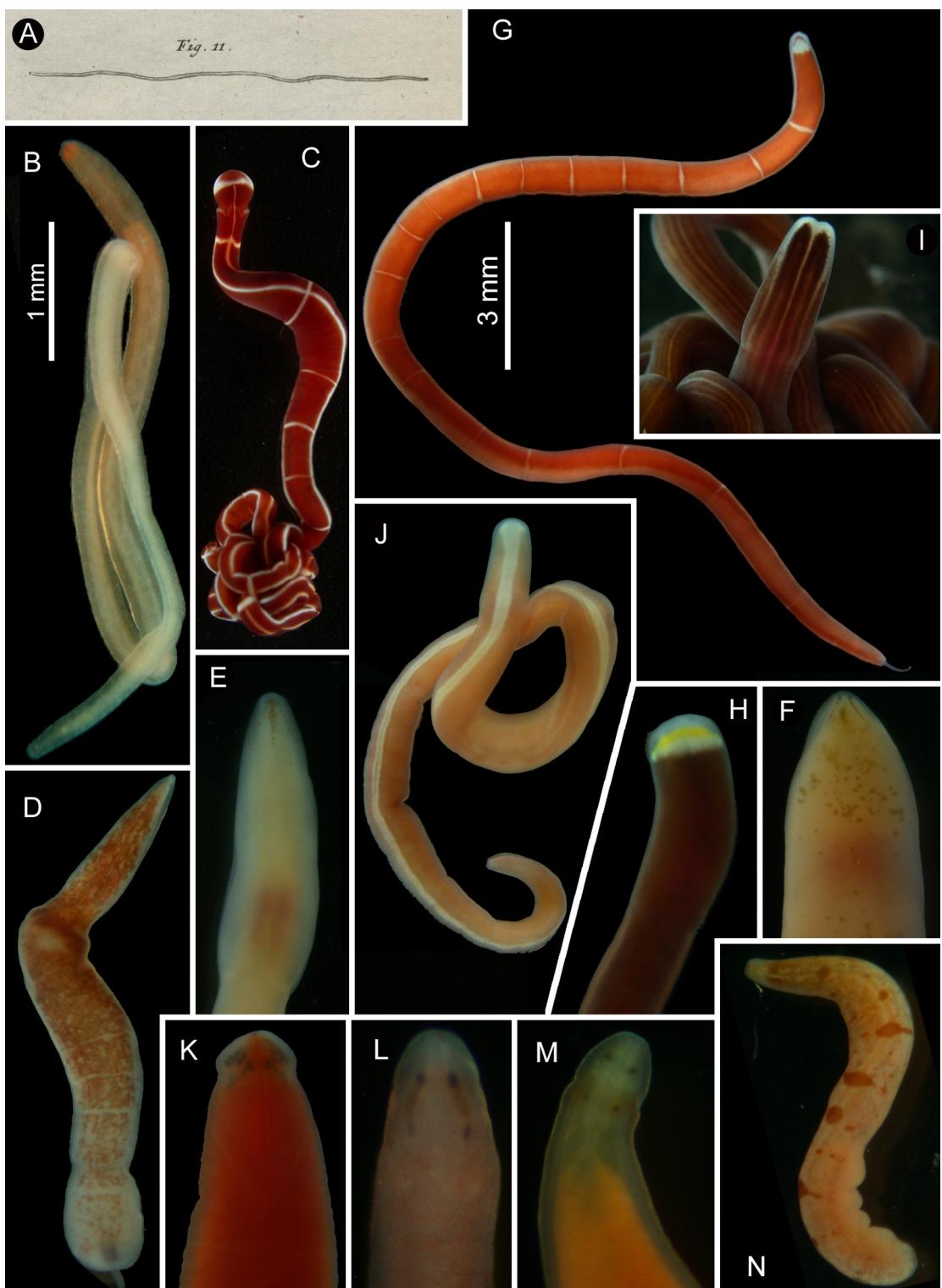


Figure 1. Nemerteans from Bergen: A, *Planaria linearis*, reproduced from Rathke (1799); B, *Cephalothrix rufifrons* (Johnston, 1837); C, *Tubulanus annulatus* (Montagu, 1804); D–F, cf. *Cerebratulus fuscus* (McIntosh, 1874); G, *Micrura fasciolata* Ehrenberg, 1828; H, *Micrura purpurea* (Dalyell, 1853); I, *Lineus longissimus* (Gunnerus, 1770); J, *Lineus bilineatus* (Renier, 1804); K, *Nipponnemertes pulchra* (Johnston, 1837); L, cf. *Tetrasistema vermiculus* (Quatrefages, 1846); M, cf. *Tetrasistema candidum* (Müller, 1774); N, *Oerstedia dorsalis* (Abildgaard, 1806).

old names, especially ones that were once synonymized with *C. linearis*. Some of those turned out to be nomenclaturally unavailable, while others were not members of *Cephalothrix* and are briefly commented upon in this paper.

## Taxonomic history

*Cephalothrix linearis* was originally established in the now-triclad-platyhelminth genus *Planaria*. The entire original description (Rathke 1799: 84) reads as follows: “Den liniedannede, med smal fladtrykt Krop, afstumpet i begge Ender (*linearis, corpore elongato depresso, utrinque truncato*) Tab. III. Figure 11. Ved Bergen fik jeg et beskadiget Exemplar, der var over 6 Tom. langt men neppe halvanden Linie bredt. Ved Stat et mindre, der var meer mørk rustfarvet, omrent 3 Tom. langt og 1/2 Lin. bredt, og fandtes i Fiæren eller Ebbetiden paa Stene mellem Tang og Sertularier, af hvilke sidste den synes søge sin fornemste Næring”. [The ‘line-shaped’, with narrow, flat-compressed body, truncated in both ends (linear, body elongated, flattened, both ends truncated) pl. III, fig. 11. In Bergen, I obtained a damaged specimen that was over 6 inches (= ~16 cm; 1 Norwegian inch = 26.1 mm) long but hardly half a line (= ~1 mm; 1 Linie = 1/12 inches = 2.18 mm) wide. In Stat (possibly Stathelle or Stadt, Statt, or Statlandet; M.V. Sørensen, Natural History Museum of Denmark, Copenhagen, pers. comm.), I got a smaller one, which was darker, rusty-coloured, about 3 inches (= ~8 cm) long and 1/2 lines (= ~1 mm) wide, and found at low tide between rocks and kelps and ‘Sertularier’, on which it seems to best feed.]

Örsted (1843: 573) established the genus *Cephalothrix* for the two new species *Cephalothrix bioculata* Örsted, 1843 (type locality: south to the island of Ven [Hven or Hveen], Sweden) and *Cephalothrix coeca* Örsted, 1843 (between Copenhagen and Trekroner, Denmark). In doing so, Örsted (1843: 573, 1844: 82) suggested *Planaria linearis* Rathke, 1799 might belong to *Cephalothrix*. Rathke’s (1799) original figure (Figure 1A) shows *P. linearis* with a slender body, which is typical in *Cephalothrix*.

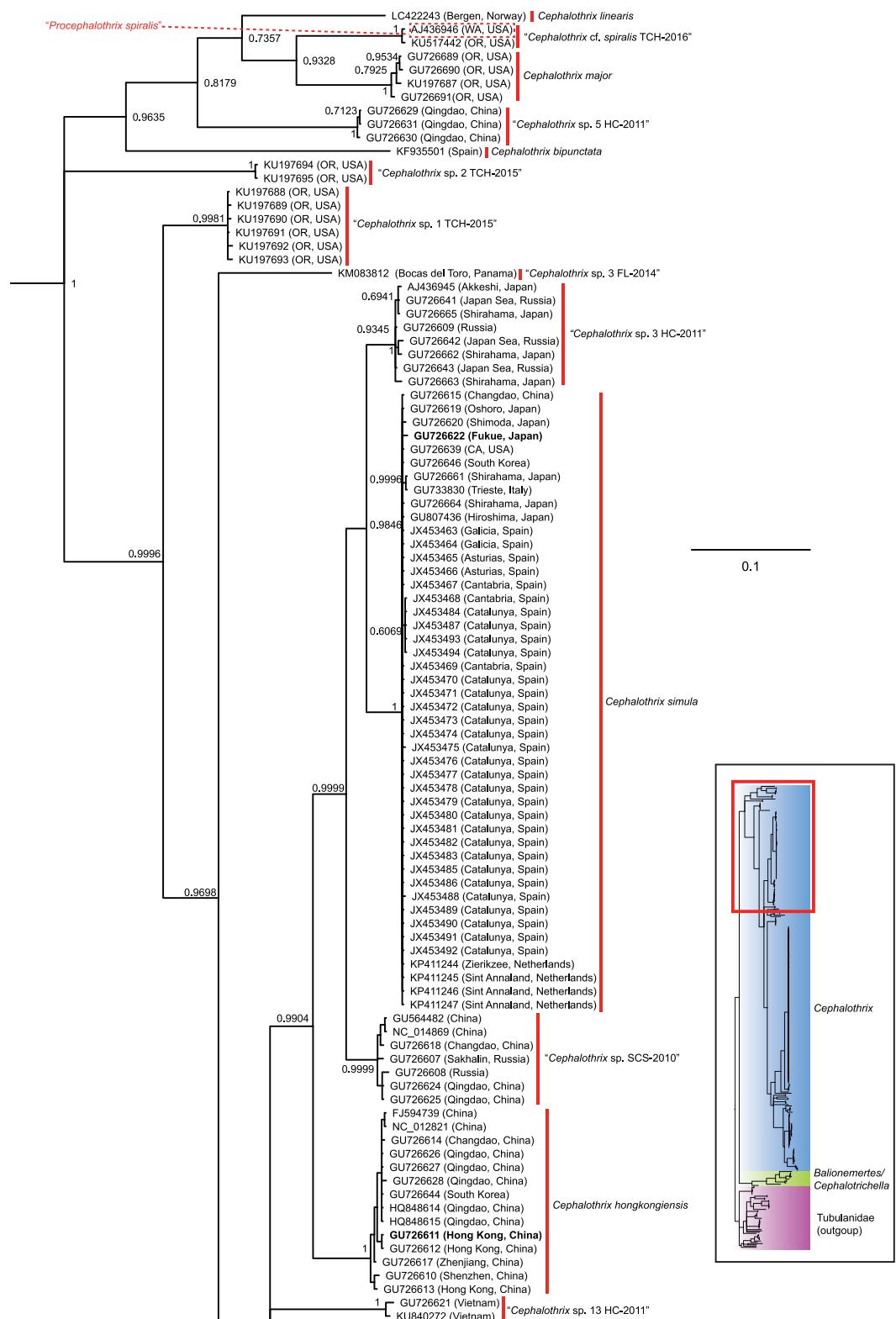
McIntosh (1873–1874) synonymized 10 nominal species known by that time from various places in European waters—*Astemma longum* Örsted, 1843 (type locality: between Frederikshavn and Skagen, Denmark), *Cephalothrix longissima* Keferstein, 1862 (type locality: Saint-Vaast-la-Hougue, France), *Cephalothrix ocellata* Keferstein, 1862 (type locality: Saint-Vaast-la-Hougue, France), *Gordius gracilis* Dalyell, 1853 (type locality: Scotland), *Nemertes rufifrons* Johnston, 1837 (type locality: Britain), and *Planaria filiformis* Johnston, 1828 (type locality: Britain), in addition to *C. bioculata* and *C. coeca*—and referred to it as *C. linearis* along with his Scottish material. Jensen (1878) challenged McIntosh’s (1873–1874) synonymization and applied the name *C. longissima* to the Norwegian taxon; Jensen (1878) even doubted that Rathke’s (1799) two original specimens might have represented two different species. However, Bürger (1904) retained *C. longissima* Keferstein, 1862 in the synonymy of *C. linearis* (Rathke, 1799), along with *P. filiformis* Johnston, 1828, *A. longum* Örsted, 1843, *C. coeca* Örsted, 1843, and *G. gracilis* Dalyell, 1853.

Wijnhoff (1910, 1913) reviewed the genus *Cephalothrix*. Before Wijnhoff’s (1913) taxonomic revision, the species name *C. linearis* had appeared in Lankester (1866), Hubrecht (1879), Langerhans (1880), Oudemans (1885), Chapuis (1886), Joubin (1890, 1902), Bürger (1892, 1895, 1904), Riches (1892), Verrill (1892), Bergendal (1900), Coe (1901, 1905), and Wijnhoff (1910). Wijnhoff (1913) distinguished *C. linearis* from *Cephalothrix bipunctata* Bürger, 1892, *Cephalothrix buergeri* Wijnhoff, 1913, *C. rufifrons*, *Cephalotrichella signata* (Hubrecht, 1879), *Procephalothrix aliena* (Punnett, 1903), and *P. filiformis* (Johnston, 1829). However, Wijnhoff’s (1913) taxonomic treatment was problematic, essentially failing to distinguish *C. linearis* from *C. rufifrons* and *C. filiformis*.

The supposed distinction by Wijnhoff (1913) between *C. linearis* and *C. rufifrons* is incomprehensible. Earlier, Wijnhoff (1910) examined the voucher slides of ‘*C. linearis*’ by Bergendal (1900), which had a “starkare röd nosspets” [strong red tip of snout] when alive (Bergendal 1900: 593), a characteristic feature in *C. rufifrons*. Later, Wijnhoff (1913) diagnosed *C. rufifrons* as having a red cephalic tip and, at the same time, also diagnosed *C. linearis* (and *C. filiformis* too) as not having a red cephalic tip. However, Wijnhoff (1913) regarded Bergendal’s (1900) *C. linearis* (with a red tip) as conspecific with Rathke’s (1799) taxon (supposed to lack a red tip), not with *C. rufifrons* (with a red tip). Hylbom (1957: 554) noted that “Because of this variability in the pigmentation of the head and the great uniformity in the anatomy of *C. rufifrons* and *C. linearis* there is a tendency to confuse the two species”.

The purported difference by Wijnhoff (1913) between *C. linearis* and *C. filiformis* has later turned out to be baseless. As stated above, Bürger (1904) regarded *C. filiformis* as a junior synonym of *C. linearis*. However, Wijnhoff (1913) opposed this synonymization, and established the genus *Procephalothrix* for *Planaria filiformis* Johnston, 1829 (and for *Cephalothrix aliena* Punnett, 1903 as well), arguing that it differs from *Cephalothrix* by possessing a body-wall inner circular muscle layer, while *Cephalothrix* lacked the one. That is, *C. filiformis* and *C. linearis* were supposed to be distinguishable by the presence/absence of the inner circular muscle layer. However, an inner circular muscle layer is actually present in *C. rufifrons* (Kajihara 2010), which is supposed to belong to *Cephalothrix* s.str. This finding supports Sundberg *et al.*’s (2003) synonymization of *Procephalothrix* with *Cephalothrix*.

Outside the North Sea, many taxa initially identified as *C. linearis* turned out to be different species: Wijnhoff (1913) established *C. buergeri* for *C. linearis* sensu Bürger (1892, 1895) from Naples (Italy); Coe (1943) regarded *C. linearis* sensu Verrill (1892) from northeast USA (Connecticut, Massachusetts, Maine) as synonymous with *C. spiralis*; specimens identified as *C. linearis* from Japan (Takakura 1898; Yamaoka 1940; Iwata 1951; Ali *et al.* 1990; Noguchi *et al.* 1991) have been reported to accumulate high concentration of tetrodotoxin (Asakawa *et al.* 2000, 2013), which are now regarded as *Cephalothrix simula* (Iwata, 1952) (Kajihara 2007a; Kajihara *et al.* 2013).



**Figure 2.** Bayesian phylogenetic tree of 317 cephalotrichid COI sequences (1 of 4); horizontal bars on the right of OTU labels indicate the results of the PTP species delimitation analysis. GU726622 and GU726611 have been designated as “quasi name-bearing sequences” for *C. simula* and *C. hongkongiensis*, respectively (Kajihara *et al.* 2013). “*Cephalothrix cf. spiralis* TCH-2016” turned out to be different from *C. spiralis* s.str. in the sense of this paper.

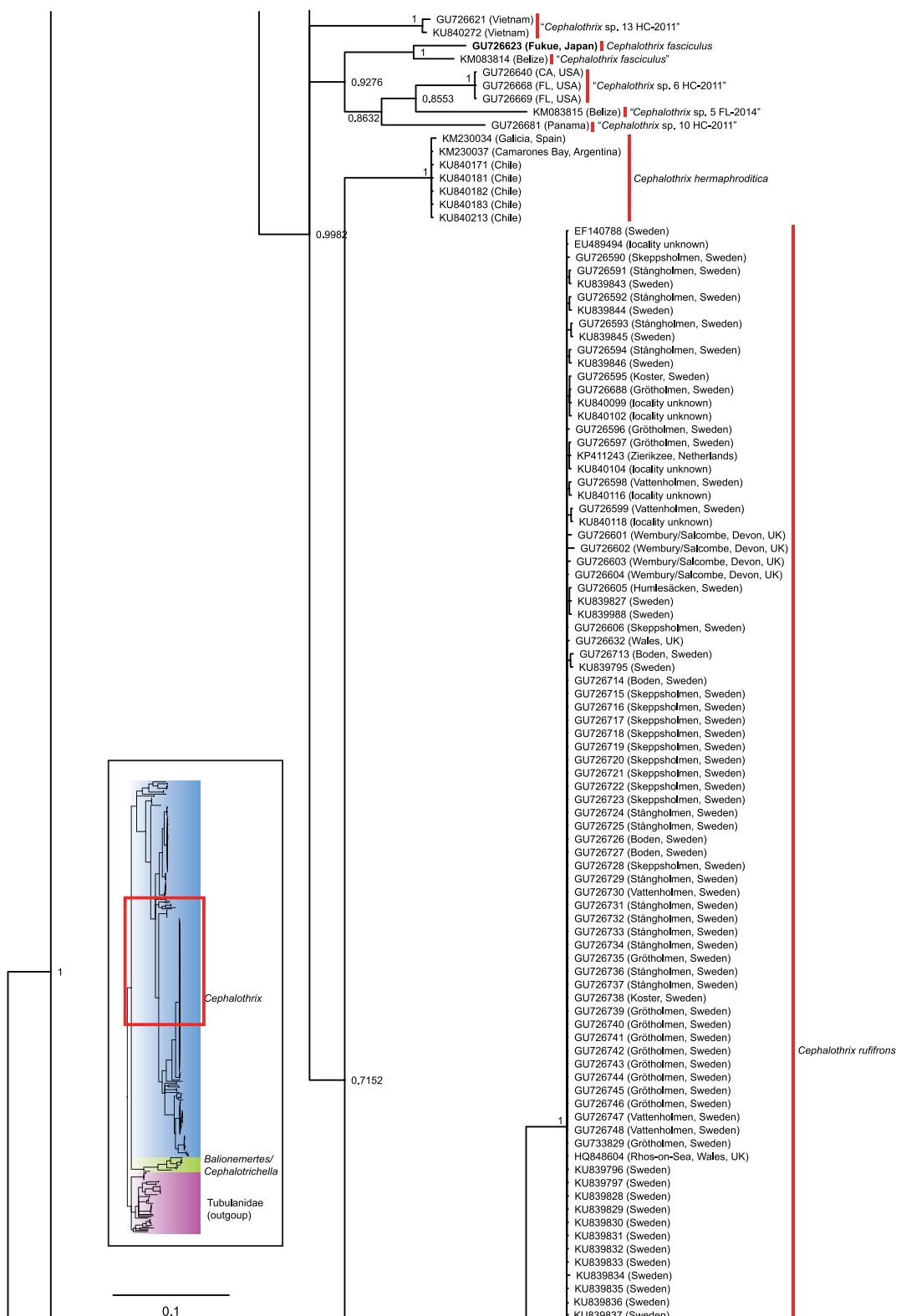


Figure 3. Bayesian phylogenetic tree of 317 cephalotrichid COI sequences (2 of 4); horizontal bars on the right of OTU labels indicate the results of the PTP species delimitation analysis. GU726623 has been designated as a “quasi name-bearing sequence” for *C. fasciculus* (Kajihara *et al.* 2013).

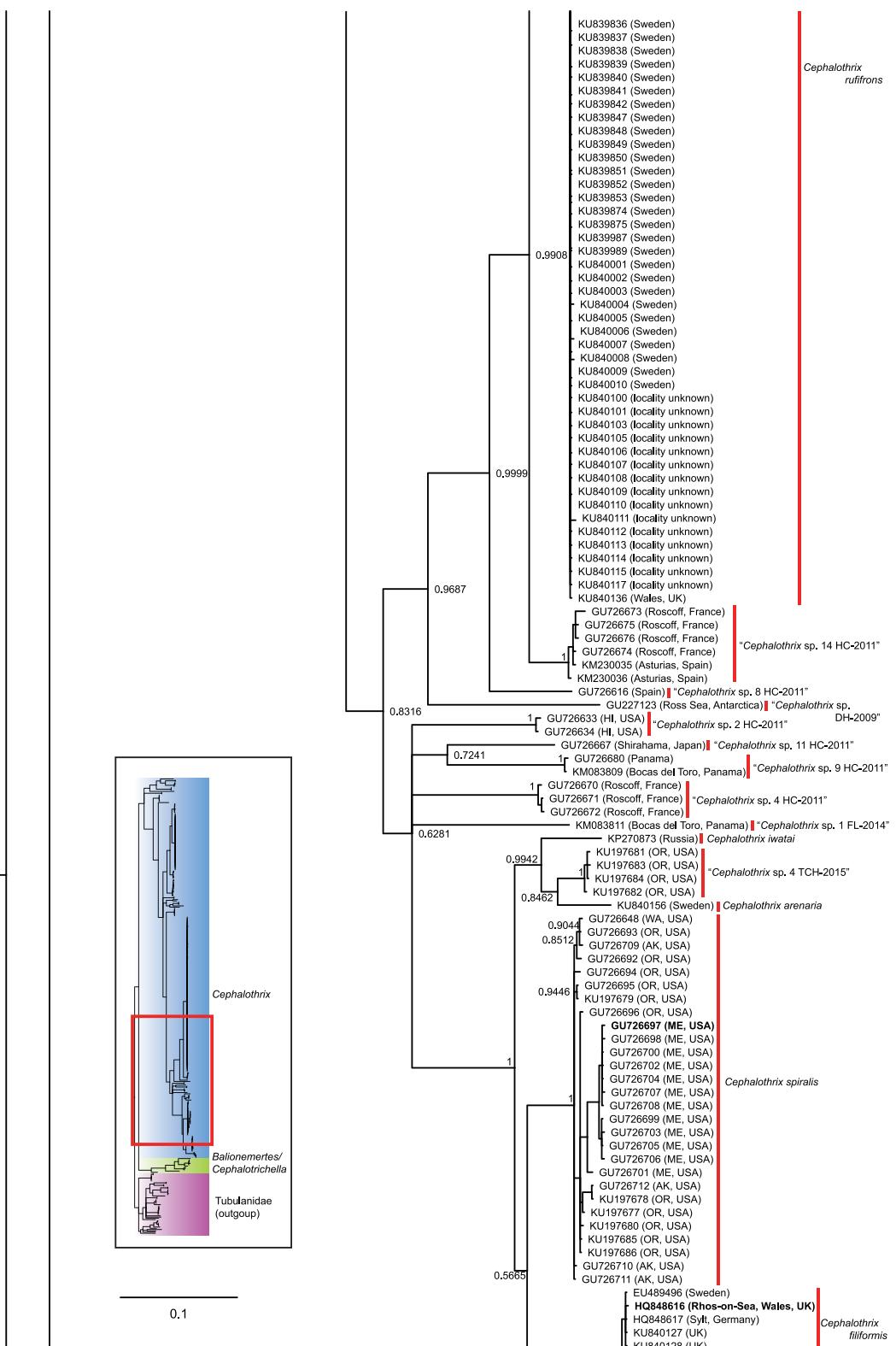


Figure 4. Bayesian phylogenetic tree of 317 cephalotrichid COI sequences (3 of 4); horizontal bars on the right of OTU labels indicate the results of the PTP species delimitation analysis. GU726697 and HQ848616 are regarded as an ‘anchor point’ for *C. spiralis* and *C. filiformis*, respectively, in this paper.

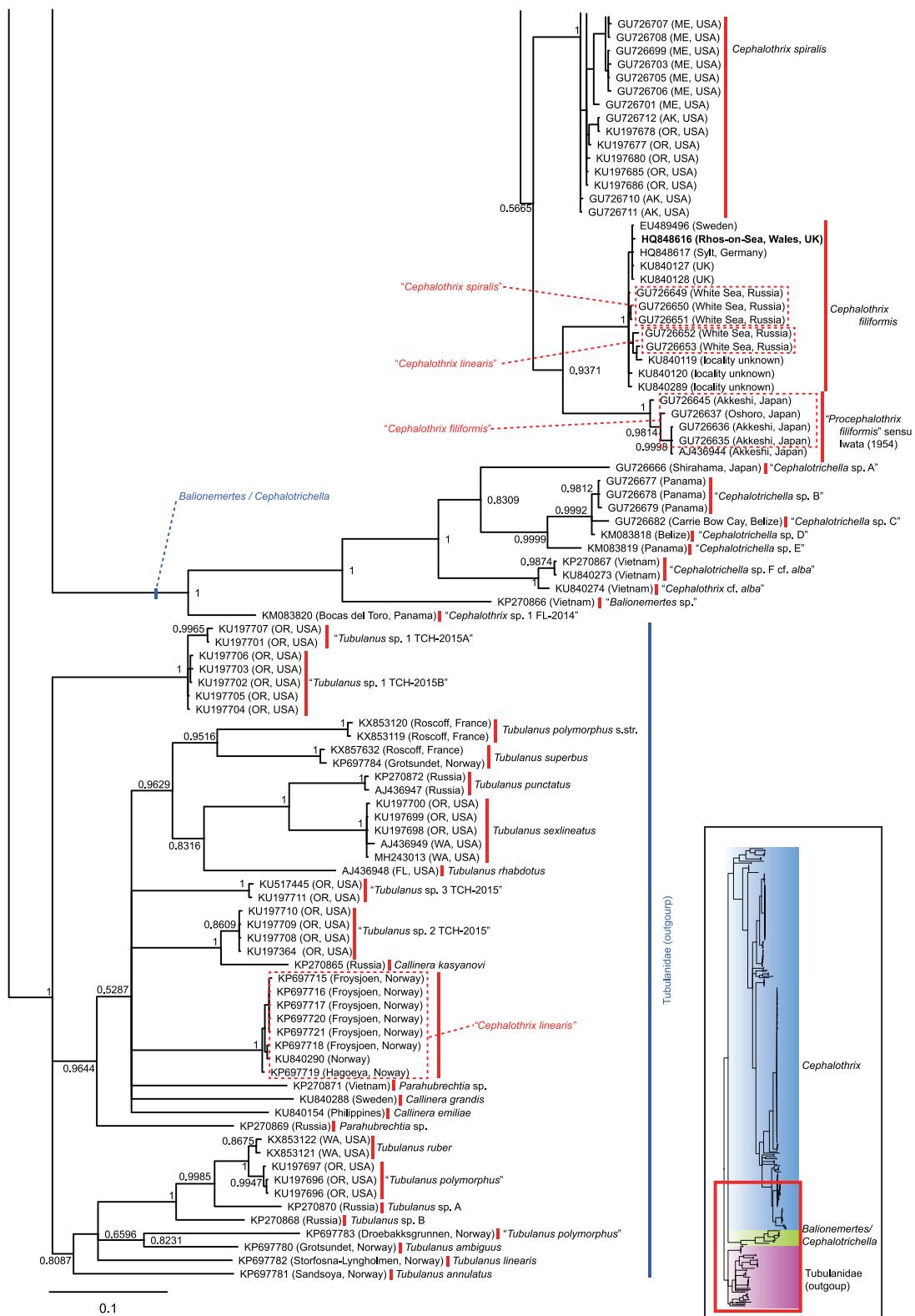


Figure 5. Bayesian phylogenetic tree of 317 cephalotrichid COI sequences (4 of 4); horizontal bars on the right of OTU labels indicate the results of the PTP species delimitation analysis. HQ848616 is regarded as an ‘anchor point’ for *C. filiformis* in this paper. *Cephalothrix filiformis* in the sense of this paper is represented by sequences originally identified as not only *C. filiformis* but also *C. linearis* and *C. spiralis*.

Gibson (1994, 1995) regarded *C. linearis* and *P. filiformis* as two distinct taxa. The distinction between *C. linearis* and *C. filiformis/C. rufifrons* has remained uncertain up to now, while the latter two can be readily distinguished from each other. Meanwhile, Beckers *et al.* (2013) applied the name *C. linearis* to a form from Roscoff/Brittany (France). However, the external feature in the French specimen (Beckers *et al.* 2013: Figure 3b) looks similar to *C. simula*, especially that of Faasse & Turbeville (2015: Figure 3), in that the body is ochre to olive green and the pre-oral region is short (cf. Fernández-Álvarez & Machordom 2013: Figure 2; Kajihara *et al.* 2013: Figures 2–4). Anatomically, the French specimen possesses a Type-A rhynchocoel vessel (evident on 85–95 of 183 slices of transverse sections available at [https://www.morphdbase.de/?P\\_Beckers\\_20130201-M-14.1](https://www.morphdbase.de/?P_Beckers_20130201-M-14.1); Kajihara 2010), as with *C. simula* (Kajihara *et al.* 2013). No molecular sequence is currently available from Beckers *et al.*'s (2013) French specimen, which could have been of a great help in understanding the true nature of the specimen.

## MATERIAL AND METHODS

Specimens were obtained by dredging at two localities near the Espeland Marine Biological Station (EMBS), University of Bergen, Norway: *i*) Bukkasundet, from 60°14.150'N, 5°12.300'E (30 m deep) to 60°14.100'N, 5°12.400'E (16 m deep); and *ii*) Vatlestraumen, about 60°20.200'N, 5°11.100'E (11–18 m deep). Sampling was made by the *R/V Aurelia* on 20 and 23 October 2006. The sediment obtained from Bukkasundet was sand with pebbles (up to 10 cm in diameter) and fragments of bivalve shells. The one from Vatlestraumen was a mixture of shells of dead bivalves and echinoderms, both heavily covered with tubes of sedentarian polychaetes. The dredged material was left in plastic containers at the Marine Biological Station half filled with seawater for 48 hrs before nemerteans crawled out from the sediment. Nemerteans were photographed alive by a Nikon E995 digital camera. After anaesthetized in MgCl<sub>2</sub> solution isotonic to seawater, specimens were cut into two pieces. The anterior fragment was fixed in Bouin's fluid for histological sectioning; the posterior one in 99% EtOH for DNA extraction. Histological sections were cut at 8 µm in thickness and stained by the Mallory's trichrome method (Gibson 1994). Type specimens are deposited at the Invertebrate Collection of the Hokkaido University Museum (ICHUM), Sapporo, Japan.

Total DNA was extracted by using DNeasy Blood and Tissue Kit (Qiagen). Three markers, the nuclear 28S rRNA gene, and the mitochondrial 16S rRNA and COI genes, were amplified by the primer pairs LSU5 (Littlewood 1994)/rd5b (Schwendinger & Giribet 2005), 16Sar-L/16Sbr-H (Palumbi *et al.* 1991), and LCO1490/HCO2198 (Folmer *et al.* 1994), respectively. Annealing temperature was set to 50°C for 28S and 16S. For COI, a touchdown PCR (Don *et al.* 1991) was performed, starting from 57°C down to 51°C. In terms of sequencing, the same primer pairs were used for 16S and COI;

for 28S, the following internal primers were also used: D2F (Littlewood 1994), 28Sa (Whiting *et al.* 1997), 28Z (Hillis & Dixon 1991), and LSU3 (Littlewood 1994). Three sequences generated *de novo* have been deposited in DDBJ/EMBL/GenBank.

To infer the phylogenetic position of the Bergen species, a Bayesian phylogenetic inference based on COI was performed by MrBayes ver. 3.2.6 (Ronquist *et al.* 2012) using the newly determined one (LC422243), along with 316 cephalotrichid sequences currently available in DDBJ/EMBL/GenBank; 47 tubulanid sequences were used as an outgroup (Table in Appendix 1). Sequences were aligned using MEGA ver. 7 (Kumar *et al.* 2016) so that translated protein sequences (using the general invertebrate mitochondrial code) were straightforward. The dataset consisted of 699 bases including gaps. PartitionFinder ver. 2.1.1 (Lanfear *et al.* 2017) was used for the best-fit substitution model; GTI + I + G was selected for every codon position. The Bayesian inference consisted of two independent runs, each with four Markov chains of 12,000,000 generations; trees were sampled every 100 generations. Run convergence was assessed by the average standard deviation of split frequencies (0.010701), minimum estimated sample size of all tree lengths ( $2.011281 \times 10^3$ ), and potential scale reduction factor of all tree lengths (1.000633). Burn-in fraction was set to 0.25. The resulted Bayesian tree was used for a species delimitation analysis based on the Poisson Tree Process (PTP) method (Zhang *et al.* 2013), implemented on the bPTP web server (<https://species.h-its.org/ptp/>).

Wherever possible, a valid species name was allotted to each species detected by the PTP analysis. Allocation of valid names was based on the database entry. When more than two different species names were found in a single species, the name of the sequence from the type locality was considered appropriate. For species represented by sequence(s) without valid name, a provisional name (such as "Cephalothrix sp. 3 HC-2011") was allotted. When more than two different provisional names were included in the same species, the 'principle of priority' was applied.

## RESULTS

### Molecular phylogeny, species delimitation, and name allocation

In the COI phylogeny, *Cephalothrix* was recovered as a monophyletic group except '*C. linearis*' sensu Strand (see below). The 317 cephalotrichid COI sequences were classified into 43 species by the PTP analysis, with 34 species in *Cephalothrix* and nine in either *Balionemertes* Sundberg, Gibson & Olsson, 2003 or *Cephalotrichella* Wijnhoff, 1913 (Figures 2–5; Table in Appendix 1). Of the 34 species of *Cephalothrix* detected by the PTP analysis, valid names were applied to the following 12 species: *Cephalothrix arenaria* Hylbom, 1957, *C. bipunctata*, *Cephalothrix fasciculus* (Iwata, 1952), *C. filiformis*, *Cephalothrix hermafroditica* (Gibson, Sánchez &

Méndez, 1990), *Cephalothrix hongkongiensis* Sundberg, Gibson & Olsson, 2003, *Cephalothrix iwatai* Chernyshev, 2013, *C. linearis*, *Cephalothrix major* Coe, 1930, *C. rufifrons*, *C. simula*, and *C. spiralis*. The rest of the 22 species were referred to by provisional names according to the public database entry.

In the phylogenetic tree (Figures 2–5), sequences originally labelled as *C. linearis* appeared in three taxa: *i*) *C. linearis* in the sense of this paper, *ii*) *C. filiformis* in the sense of this paper, with two sequences from the White Sea originally identified as *C. linearis* (GU726652 and GU726653; Chen *et al.* 2010) along with 11 other sequences (which also included sequences labelled as *C. spiralis*), and *iii*) an unidentified tubulanid, possibly in the genus *Callinera*, represented by eight sequences from Froysjøen and Hagoøya, Norway (KP697715–KP697721 and KU840290; M. Strand, unpubl.).

Sequences originally identified as *C. filiformis* and *C. spiralis* appeared in more than one species detected by the PTP analysis. An objective standard was necessary to allot a name uniquely to each species. Fortunately, sequences from the type locality of *C. filiformis* (UK) and *C. spiralis* (Nova Scotia [Canada] to Long Island [USA]) were recovered in each species. “*Procephalothrix filiformis*” sensu Iwata (1954) from Japan also contained sequences originally labelled as *C. filiformis*. In the phylogenetic tree, *C. filiformis* in the sense of this paper and “*Procephalothrix filiformis*” sensu Iwata (1954) appeared as sister species (Figure 5).

Earlier, Kajihara *et al.* (2013) designated a COI sequence from a topotype as a “quasi name-bearing sequence” for *C. simula* (GU726622), *C. hongkongensis* (GU726611), and *C. fasciculus* (GU726623) to guarantee objective name usage; the intent of “quasi” was that actual name bearers are type specimens, not sequences. Likewise, I propose a tentative name-bearer for *C. filiformis* and *C. spiralis* in the following section.

## Taxonomy

### *Cephalothrix* Örsted, 1843

**Type species.** *Planaria linearis* Rathke, 1799, herein fixed under Article 70.3.2 of the Code (ICZN 1999).

**Remarks.** Örsted (1843: 573) established *Cephalothrix* originally including the two nominal species *C. bioculata* Örsted, 1843 and *C. coeca* Örsted, 1843 without type-species designation. Only these two are eligible as the type species, according to Article 67.2 of the Code (ICZN 1999). On the other hand, Gibson (1995: 325) indicated *Cephalothrix linearis* (Rathke, 1799) as the type species of the genus. According to Recommendation 67B of the Code (ICZN 1999), Gibson (1995) should have indicated it by its original binomen, *Planaria linearis* Rathke, 1799. Noting that Gibson’s (1995) designation was irrelevant, Kajihara (2007a: 294) remarked *C. coeca* Örsted, 1843 was the type species. While doing so, however, Kajihara (2007a) overlooked Article 69.2.2 of the Code (ICZN 1999), which states “If an author designates as type species a

nominal species that was not originally included... and if, but only if, at the same time he or she places that nominal species in synonymy with one and only one of the originally included species..., that act constitutes fixation of the latter species as type species of the nominal genus or subgenus”. Gibson (1995) regarded *P. linearis* Rathke, 1799 as synonymous with *C. coeca* Örsted, 1843, but not with *C. bioculata* Örsted, 1843. Therefore, *C. coeca* Örsted, 1843 has been validly fixed as the type species of *Cephalothrix* by Gibson (1995) under Article 69.2.2 of the Code (ICZN 1999). However, the nominal species *Cephalothrix coeca* Örsted, 1843 seems to be included in the taxonomic taxon *Cephalothrix filiformis* (Johnston, 1828) (see below), instead of *Cephalothrix linearis* (Rathke, 1799) as formerly regarded (McIntosh 1873–1874; Bürger 1904; Wijnhoff 1913; Gibson 1995). For the sake of stability, I invoke Article 70.3.2 of the Code (ICZN 1999) to fix *Planaria linearis* Rathke, 1799 as the type species of *Cephalothrix* Örsted, 1843.

The cyanobacterial *Cephalothrix* Da Silva Malone *et al.*, 2015 (Da Silva Malone *et al.* 2015) is a hemihomonym (same name used for taxa in different nomenclature jurisdictions; Shipunov 2011) of *Cephalothrix* Örsted, 1843, which causes trouble in database search.

### *Cephalothrix linearis* (Rathke, 1799) (Figures 6–10)

**Basionym.** *Planaria linearis* Rathke, 1799 (Rathke 1799: 84, pl. III, Figure 11).

**Synonym.** ?*Cephalothrix longissima*, Jensen (1878: 86); *Cephalothrix filiformis*, Kajihara (2010: 2325, Figure 2D).

**Material examined.** Neotype: ICHUM 3509, Bukkasundet, 20 October 2006, 34 slides. Paraneotype: ICHUM 3511, Vatlestraumen, 23 October 2006, 32 slides.

**Sequences.** Determined from the neotype (ICHUM 3509): LC422241, 28S rRNA (1238 bp); LC422242, 16S rRNA (491 bp); LC422243, COI (658 bp).

#### Description.

**External feature.** Neotype (Figure 6A, B) 7 cm in length, about 0.5 mm in width; paraneotype (Figure 6C, D) anterior fragment, 5 cm in length, 0.55 mm in width. Under natural light, pre-oral region being reddish, fading anteriorly to tip of head that appears almost transparent, whereas post-oral region bright orange to pinkish. When irritated, worms often spirally wind their body into corkscrew-shape.

**Body wall and musculature.** Body wall consisting of ciliated epidermis (lost in neotype), connective-tissue basement membrane, outer diagonal muscle, outer circular muscle, and longitudinal muscle (Figures 7A, 8A). Splitting of body-wall outer circular muscle layer near lateral nerve cord not obvious (Figure 8B), but fibres occasionally running medially along lateral nerve cord from body-wall outer circular muscle layer (Figure 8C). Inner circular muscle layer present only in anterior foregut region, abutting on distal wall of lateral blood vessels; no circular muscles confirmed medially to lateral vessels (Figure 8D). Longitudinal muscle plate present between rhynchocoel and alimentary canal, posteriorly extending to intestinal region

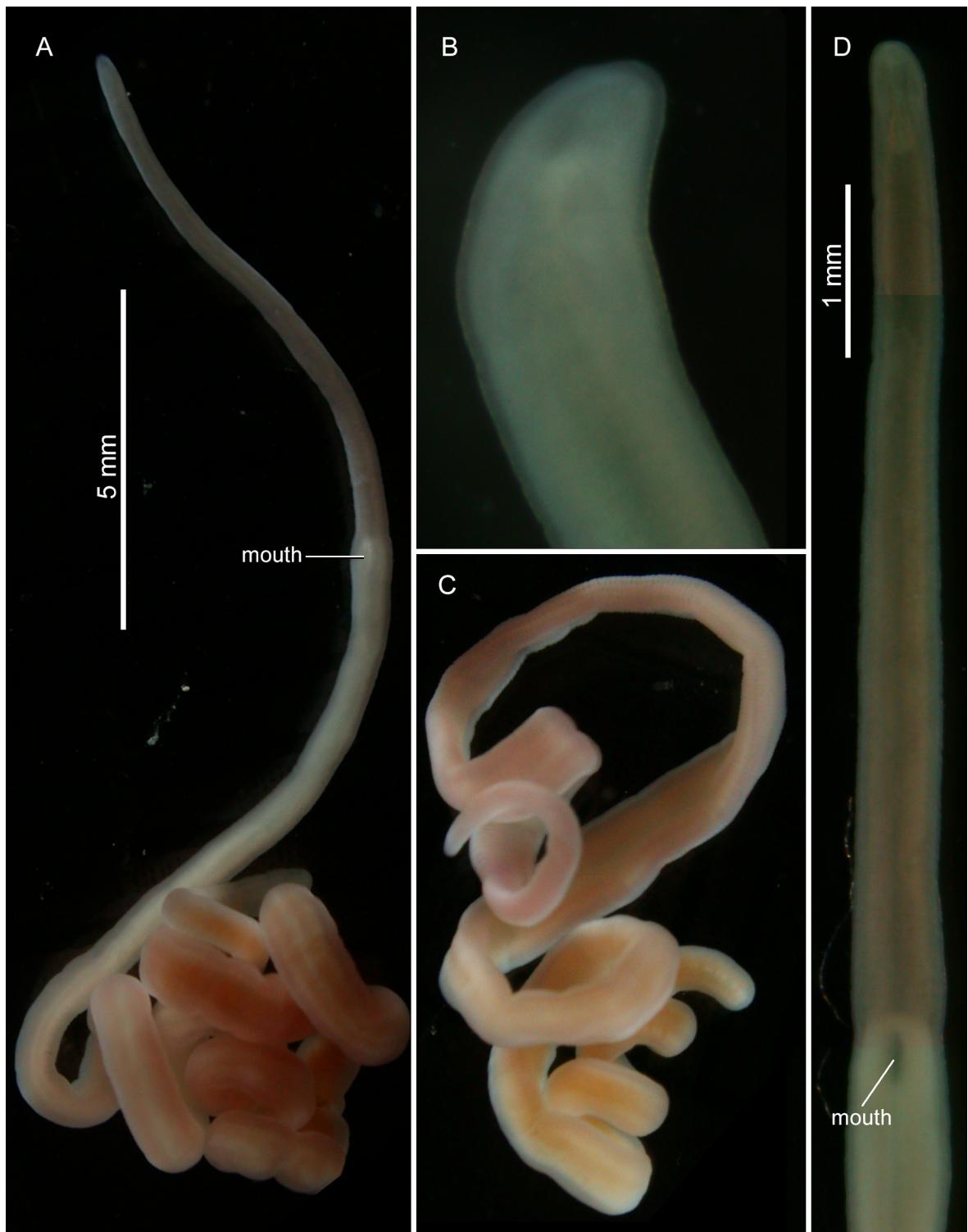


Figure 6. *Cephalothrix linearis* (Rathke, 1799), photographs taken in life: A, ICHUM 3509 (neotype), general appearance of entire body; B, ICHUM 3509 (neotype), magnification of head; C, ICHUM 3511 (paraneotype), general appearance of anterior fragment, showing its posterior portion being helically coiled; D, ICHUM 3511 (paraneotype), magnification of head in anaesthetized state, ventral view, composite photograph.

(Figures 7A, 8D). No dorsoventral muscles found.

**Rhynchocoel and proboscis.** Proboscis pore opening subterminally. Rhynchodaeal epithelium containing basophilic glandular cells. Rhynchodaeal sphincter present just in front of proboscis insertion; latter situated just behind ventral commissure (Figures 9A–H, 10A–D). Rhynchocoel wall consisting of inner longitudinal and outer circular muscle layers. Proboscis paratype (Figure 7A); pseudocnidae, about 13 µm long and 5 µm wide, arranged in three (dense central and sparse lateral) rows when examined by squeezed preparation (Figure 10E).

**Alimentary canal.** Ratio of distance between (A) tip of head to ventral commissure and (B) ventral commissure to posterior end of mouth about one to eight (A : B = 1 : 8) measured from serial sections. Ratio of distance between (C) tip of head to centre of mouth and (D) body diameter at mouth opening about 10 to one (C : D = 10 : 1) measured in anaesthetized condition in paratype (Figure 6D). Oesophagus absent. No diverticulum in foregut and intestine.

**Vascular system.** Precerebral vascular system consisting of pair of lateral vessels connecting anteriorly; mid-dorsal vessel absent precerebrally. As they pass through cerebral ring, they connect mid-dorsally above rhynchodaeal sphincter just behind ventral commissure, from where Type-C vessel (Kajihara 2010) runs posteriorly along proboscis (Figures 7B, 9G–H, 10A–D) [in length for 144 µm in neotype, 168 µm in paratype]. Postcerebrally, lateral vessels abutting on dorso-lateral or lateral to alimentary canal, without contacting rhynchocoel. Blood corpuscles present.

**Nervous system.** General structure of nervous system largely conforming to other species (e.g., Kajihara *et al.* 2013). Dorsal commissure 15 µm diameter in neotype (12 µm in paratype), situated 64 µm ahead of ventral commissure in neotype (56 µm in paratype); ventral commissure 29 µm diameter in neotype (20 µm in paratype). Pair of nerves sent off ventral ganglia merging at midline to form foregut nerve stem (Figure 10A–D). Unlike many other congeners, ganglionic tissue of lateral nerve directly abutting on body-wall outer circular muscle layer, and situated laterally to fibrous core (Figure 8B, C), instead of dorsally and ventrally as well, in many other congeners. A few bundles of longitudinal muscle fibres appear to be present lateral to fibrous core of lateral nerve (Figure 8B).

#### Sense organs.

No apical organ, eyes, cerebral organs, lateral organs, or sensory pits recognizable.

**Excretory system.** Not found.

**Reproductive system.** Both neotype and paratype are female; ovaries arranged in row on each side, situated lateral to intestine (Figure 7A).

**Remarks.** The following statements and evidences are meant to satisfy the seven conditions stipulated in Article 75.3 of the Code (ICZN 1999), which qualify a valid designation of a neotype. First, I designate ICHUM 3509 as the neotype with the express purpose of clarifying the taxonomic status of *C. linearis*. *Cephalothrix linearis* can be differentiated from

other congeners by the Type-C vessel that leads from the cephalic vessel and runs posteriorly along the proboscis through the proboscis insertion, and by the absence of body-wall longitudinal muscles lateral to the lateral nerve cord between the body-wall outer circular muscle layer (but *C. germanica* Gerner, 1969 and *C. paragermanica* Senz, 1993 are reported to lack such longitudinal muscles as well). However, in light of the phylogenetic closeness discovered by the present analysis, these features may also be found in *C. bipunctata*, *C. major*, “*Cephalothrix* cf. *spiralis* TCH-2016”, and “*Cephalothrix*

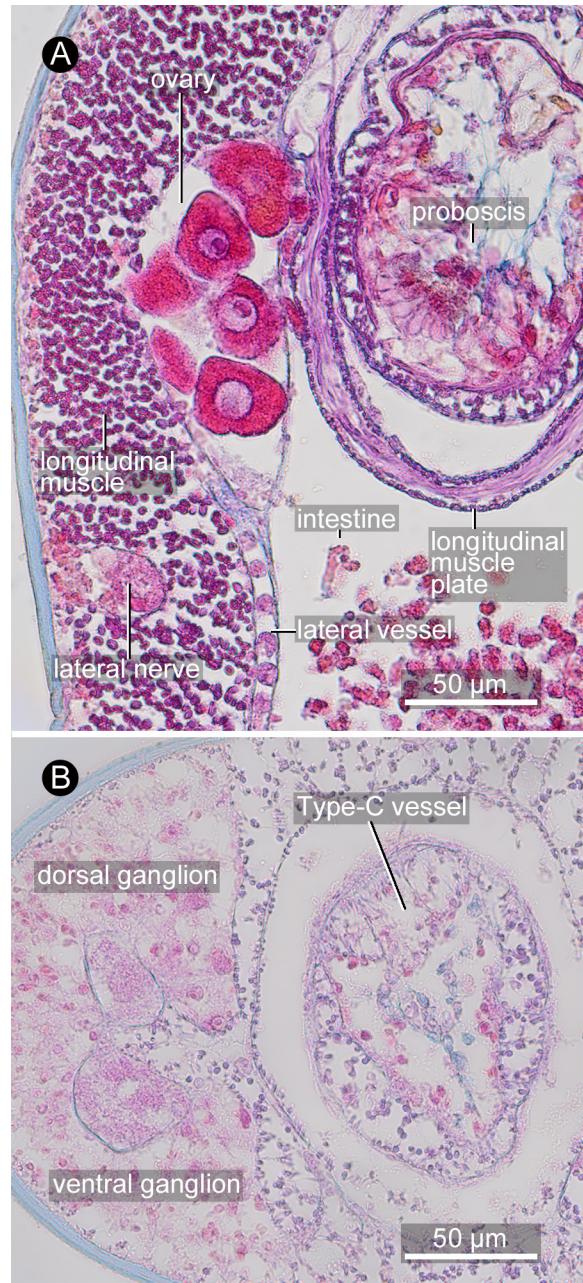


Figure 7. *Cephalothrix linearis* (Rathke, 1799), ICHUM 3509 (neotype), photomicrographs of transverse sections: A, intestinal region; B, brain region.

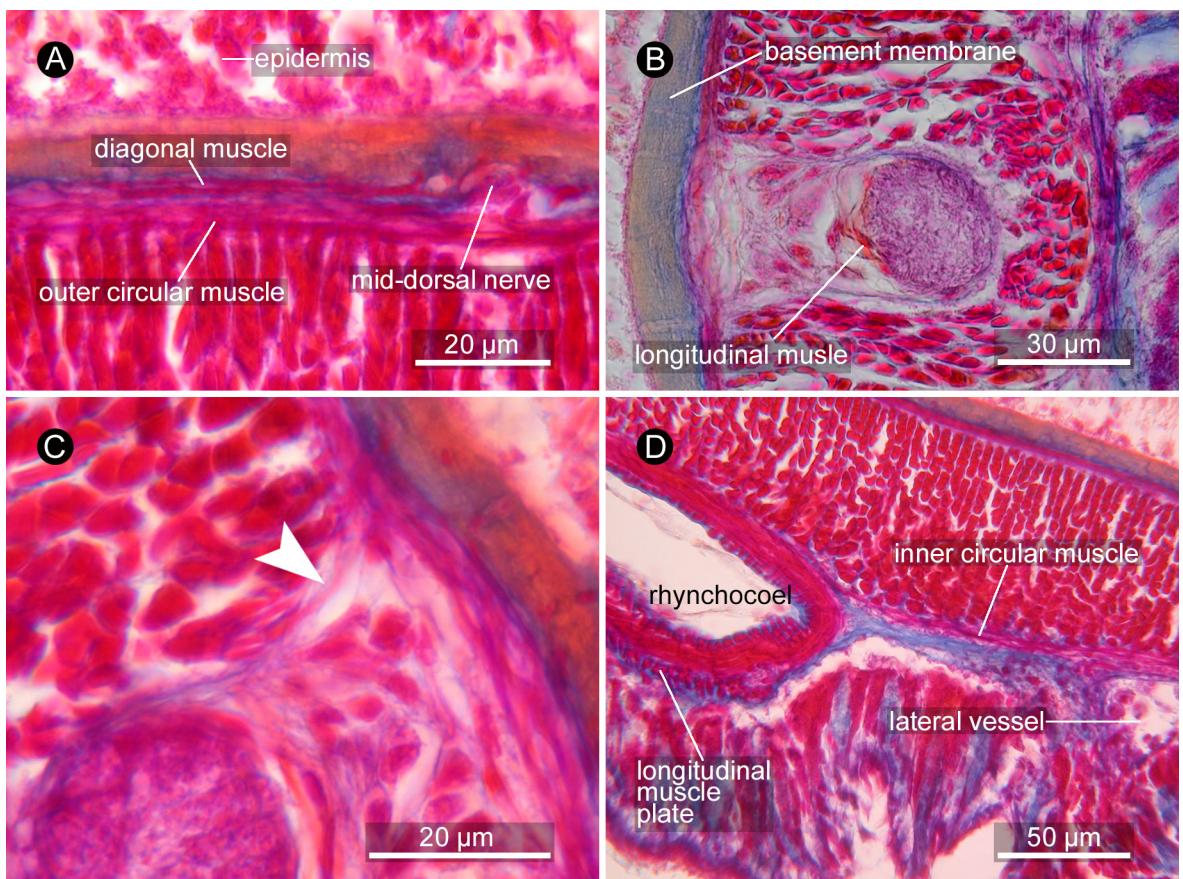


Figure 8. *Cephalothrix linearis* (Rathke, 1799), ICHUM 3511 (paraneotype), photomicrographs of transverse sections through foregut region: A, body wall musculature; B, lateral nerve cord; C, muscle fibre sent out from body-wall outer circular muscle layer to surround lateral nerve cord (indicated by arrowhead); D, longitudinal muscle plate and inner circular muscle layer.

sp. 5 HC-2011". Ultimately, only such genetic characters as sequences of COI (LC422243) or 16S rRNA (LC422242) may be useful in delineating *C. linearis* from other species, as DNA taxonomy is indispensable in *Cephalothrix* systematics (Leasi & Norenburg 2014). Rathke's (1799) original material is unlikely extant. If it were, the most likely place where it would have been deposited would be the Natural History Museum (NHMO) (Oslo, Norway) or the Natural History Museum of Denmark (NHMD) (Copenhagen, Denmark). I contacted a curator in each museum; the reply from both was negative (A.-H. Rønning, NHMO, Oslo; M.V. Sørensen, NHMD, Copenhagen; pers. comm.). The present Bergen specimens (ICHUM 3509, 3511) can be identified as *C. linearis* s.str. because their body colour—anteriorly reddish, posteriorly bright orange or pinkish—does not contradict with what was stated in the original description (“rustfarvet” [rusty-coloured]; Rathke 1799: 84); in comparison to *C. filiformis*, *C. linearis* appears to be more reddish, while the former generally looks whitish. Also, the general body shape depicted in the original illustration (Figure 1A) is concordant with the present material (Figure 6A, C), although the former could apply to most other

species of *Cephalothrix*. The neotype came from Bergen, one of the localities mentioned in the original description (the other being “Stat”). The neotype series has been deposited in the ICHUM, which “maintains a research collection, with proper facilities for preserving name-bearing types, and that makes them accessible for study” (Article 75.3.7).

McIntosh (1873–1874), Bürger (1904), Wijnhoff (1913), and Gibson (1995) placed *Astemma longum* in the synonymy of *C. linearis*. On the other hand, in the original description of *A. longum*, Ørsted (1843: 575) stated in Danish “Munden er engang saa nær ved Enden af Kroppen, som hos den foregaaende Art”, later in German “Der Mund ist noch einmal so nahe am Ende des Körpers, als bei der vorigen Art” (Ørsted 1844: 83) [The mouth is again as close to the tip of the body as in the previous species (= *C. rufifrons*)] (translated by C. Sagorny, University of Bonn, pers. comm.). The body colour was dark gray (“coeruleo-griseo”). It is unlikely synonymous with *C. linearis* in the sense of this paper. It might have not even represented a *Cephalothrix*. Likewise, McIntosh (1873–1874), Bürger (1904), Wijnhoff (1913), and Gibson (1995) placed *Cephalothrix coeca* in the synonymy of *C. linearis*. In the original description of *C. coeca*,

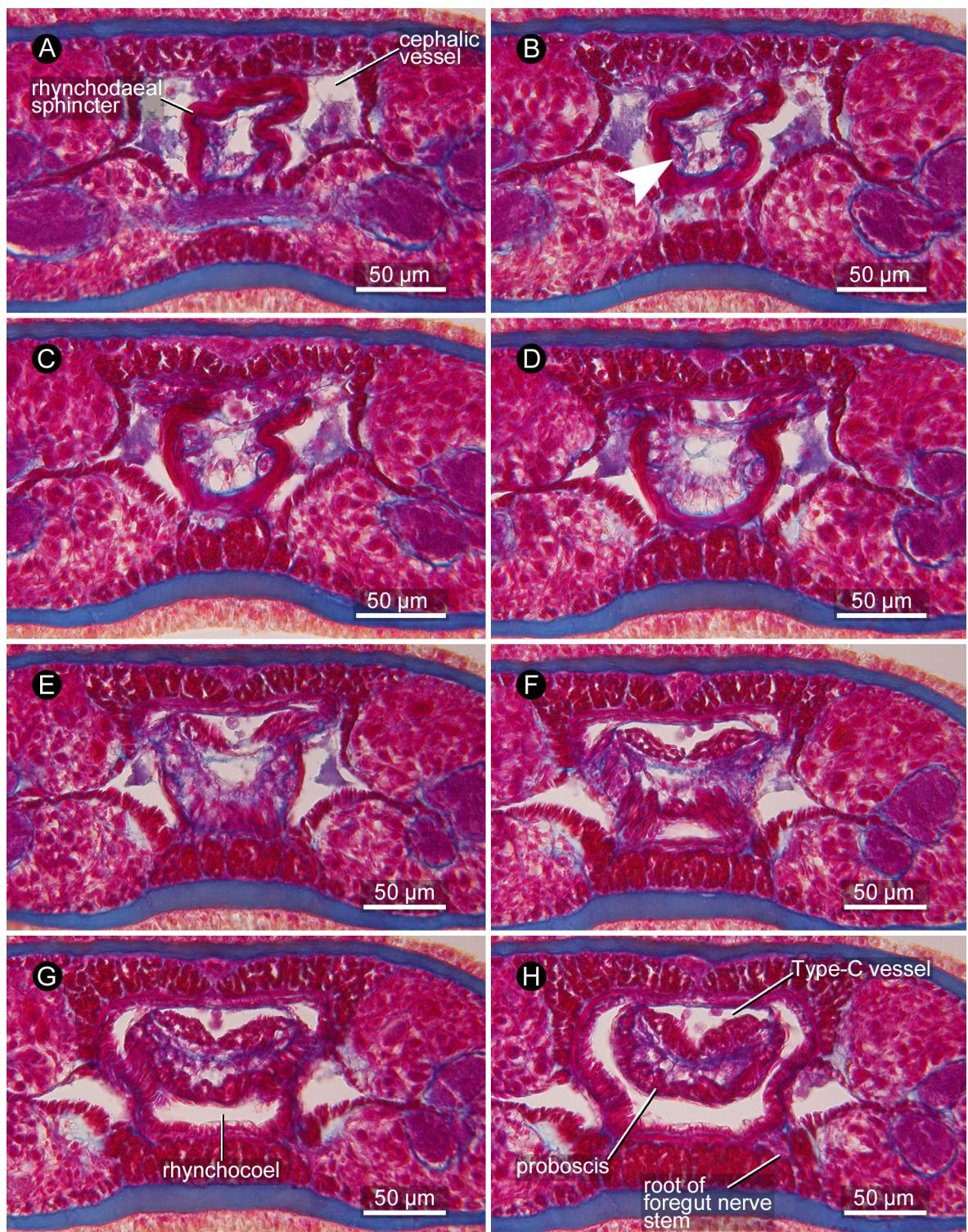


Figure 9. *Cephalothrix linearis* (Rathke, 1799), ICHUM 3511 (paraneotype), A–H, photomicrographs of transverse sections near proboscis insertion.

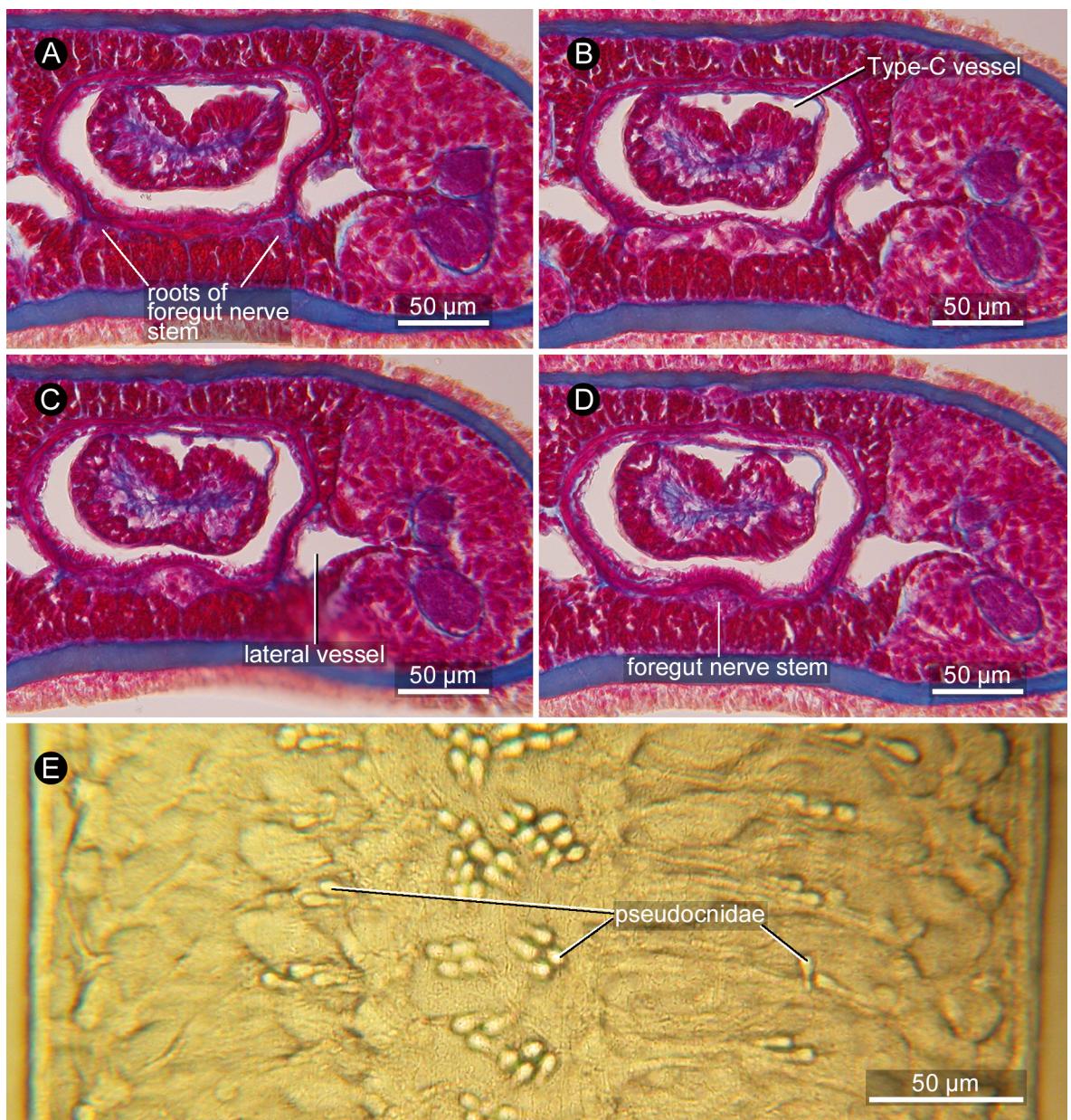


Figure 10. *Cephalothrix linearis* (Rathke, 1799). A–D, ICHUM 3511 (paraneotype), photomicrographs of transverse sections showing pair of nerves from ventral ganglia merging at the midline to form the foregut nerve; E, ICHUM 3509 (neotype), photomicrograph of dissected proboscis in retracted state by squeezed preparation (non-fixed, live tissue), showing arrangement of pseudocnidae.

Örsted (1843: 574) stated that the body was white (“lacteo”). Later, Örsted (1844: 81) used the name *Cephalothrix coeca* in the main text, but *Cephalothrix filiformis* in the figure caption (Örsted 1844: 96). It seems that *C. coeca* is actually synonymous with *C. filiformis*, rather than *C. linearis*.

#### Proposal of tentative name bearers

For each of the following two species, I select a topotype as if it acted as an objective anchor point to the species name. It does not prevent future neotype designation or replacement of unidentifiable name-bearing type under Article 75.5 of the

Code (ICZN 1999) for these species. Needles to say, doing so is beyond the scope of this paper.

#### *Cephalothrix filiformis* (Johnston, 1828)

**Basionym.** *Planaria filiformis* Johnston, 1828 (Johnston 1828: 56–57).

**Type locality.** Britain.

**Proposed material.** Deposited in the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, USA; MCZ DNA105614 (NemPhyl 46), collected in the Rhos-on-Sea (53°18'46"N, 3°44'16"W), Wales (UK), by Per Sundberg on 18

February 2010 (Andrade *et al.* 2012).

**Sequences.** HQ848616 (COI, 654 bp), HQ856842 (28S rRNA, 2665 bp), JF277743 (histone H3, 327 bp), JF277687 (histone H4, 160 bp), JF277594 (16S rRNA, 428 bp), and JF293054 (18S rRNA, 1778 bp) (Andrade *et al.* 2012).

### *Cephalothrix spiralis* Coe, 1930

**Basionym.** *Cephalothrix spiralis* Coe, 1930 (Coe 1930: 101–103, Figures 4–8).

**Type locality.** Nova Scotia (Canada) to Long Island (New York, USA).

**Proposed material.** Deposited in the Smithsonian National Museum of Natural History (NMNH), Washington D.C., USA; NMNH 413.082891.01, collected and identified by Jon L. Norenburg in Mt. Desert Island (Maine, USA).

**Sequence.** GU726697 (COI, 658 bp) (Chen *et al.* 2010).

### Non-*Cephalothrix* nominal species

Table in Appendix 2 summarizes nominal species that are likely contained in the taxon *Cephalothrix*. *Cephalothrix galatheae* Dieck, 1874 is retained in the list, because the proboscis is described as lacking stylets, the mouth is illustrated to lie behind the brain (Dieck 1874: pl. XXI, Figure 16), and the lateral nerve is depicted to be positioned within the body-wall longitudinal muscle layer (Dieck 1874: pl. XXI, Figure 13), although Coe (1902: 432–433) argued it could be synonymous with the decapod-egg parasitic monostiliferan *Carcinonemertes carcinophila* (Kölliker, 1845). Nominal species originally included in *Cephalothrix* but not listed in Table in Appendix 2 are the following five:

### *Cephalothrix armata* Ulyanin, 1870

**Remarks.** Body 25 cm in length, 1.5 mm in width, from the Bay of Sevastopol, Black Sea. Ulyanin (1870: 52) described that the worm was dorsally bright green and the proboscis armature consisted of a curved central stylet. It is undoubtedly a monostiliferous hoplonemertean, possibly *Emplectonema gracile* (Johnston, 1837) or its relative (A.V. Chernyshev, Institute of Marine Biology, Vladivostok, pers. comm.).

### *Cephalothrix fragilis* Bürger, 1892

**Remarks.** From Naples, Italy; body uniformly brown, 3 cm in length, 2–2.5 mm in width. Head yellowish, dorsally with a pair of brown patches, laterally with eyes (Bürger 1892: 149). Bürger (1895: 540) placed it in the synonymy of *Cephalothrix signata* Hubrecht, 1879, which is now in *Cephalotrichella* (Wijnhoff 1913: 299).

### *Cephalothrix signata* Hubrecht, 1879

**Remarks.** From Naples, Italy; body 15 mm in length, dorsally uniformly yellow, ventrally white; head with pair of club-shaped pigment patches dorsally, with white median streak between them, latter posteriorly connected to yellow transverse bar; two identical club-shaped yellow blotches present ventrally; eyes

present (Hubrecht 1879: 297). Wijnhoff (1913) transferred this species to *Cephalotrichella*. The generic name was incorrectly spelled *Cephalothrix* in the original description, but the specific name is deemed to have been published in combination with the correct original spelling, *Cephalothrix*, according to Article 11.9.3.2 of the Code (ICZN 1999); the specific name has been mandatorily changed from *signatus* to *signata* after Articles 31.2 and 34.2 of the Code (ICZN 1999).

### *Cephalothrix unipunctata* Parfitt, 1867

**Remarks.** Parfitt (1867: 213–214) established the species based on George Montagu's unpublished manuscript, which read “Pale yellowish-white, with a lunate black spot before the eyes, the concave part of the luna in front; body filiform, gradually growing thicker towards the head; eyes black, and rather distant; length nearly an inch. Marine. Taken at Tor Cross. Rare”. McIntosh (1873–1874) and Gibson (1995) placed it in the synonymy of the monostiliferous hoplonemertean *Tetrastemma melanocephalum* (Johnston, 1837). The generic name was incorrectly spelled *Cephalothrix* in the original description, but the specific name is deemed to have been published in combination with the correct original spelling, *Cephalothrix*, according to Article 11.9.3.2 of the Code (ICZN 1999).

### *Cephalothrix viridis* Chapuis, 1886

**Remarks.** From Roscoff, France, subtidal; body 2 cm in length, green in colour; no eyes, no lateral cephalic slits. Chapuis (1886: xxii) described that it had a well-developed posterior lobe on each ganglion, which Wijnhoff (1913: 300) interpreted as a cerebral organ. It might represent a valenciniid heteronemertean. The generic name was incorrectly spelled *Cephalothrix* in the original description, but the specific name is deemed to have been published in combination with the correct original spelling, *Cephalothrix*, according to Article 11.9.3.2 of the Code (ICZN 1999).

### Unavailable names

The specific names in the following five binomina are unavailable, and thus should be eliminated from checklists, catalogues, and databases including World Nemertea Database (Norenburg *et al.* 2018).

### *Borlasia cephalothrix* Diesing, 1850

**Remarks.** Diesing (1850: 241) established *Borlasia cephalothrix* Diesing, 1850 as a junior synonym of *Cephalothrix coeca* Örsted, 1843. Gibson (1995: 307) regarded *B. cephalothrix* as an available name, and one of the junior synonyms of *C. linearis*. However, according to Article 11.6 of the Code (ICZN 1999)—which states “A name which when first published in an available work was treated as a junior synonym of a name then used as valid is not thereby made available”—the name *cephalothrix* Diesing, 1850, as published in the binomen *Borlasia cephalothrix*, is not available.

### *Borlasia linearis* Diesing, 1850

**Remarks.** Diesing (1850: 242) established *Borlasia linearis* Diesing, 1850 as a junior synonym of *Planaria linearis* Rathke, 1799. The name *linearis* Diesing, 1850, as published in the binomen *Borlasia linearis*, is thus unavailable under Article 11.6 of the Code (ICZN 1999), although it is listed as an available name by Gibson (1995: 309).

### *Cephalothrix kroyeri* Diesing, 1850

**Remarks.** As Gibson (1995: 324) noted, “Diesing, with no justification, transferred *Tetrastremma bioculatum* Örsted, 1843, to the genus *Cephalothrix* and renamed it”. As with the case of *B. cephalothrix*, the name *kroyeri* Diesing, 1850, as published in the binomen *Cephalothrix kroyeri*, is unavailable, although Gibson (1995: 324) listed it as an available name.

### *Cephalothrix lineata* Claparède, 1862

**Remarks.** Bürger (1904: 18) included *C. lineata* of Claparède in the synonymy of *C. linearis* (Rathke, 1799). Gibson (1995: 325) listed *C. lineata* as an available name, stating that “the systematic position of Claparède’s species remains uncertain”. Originally, Claparède (1862: 150) simply described “Chez le *Cephalothrix lineata* OErst., ..., j’ai trouvé la trompe hérisée de longs poils rigides”. [In *Cephalothrix lineata* OErst., ..., I found the proboscis bristled with long, stiff hairs.] As Gibson (1995: 325) correctly pointed out, “Claparède confusingly gave Örsted as the naming authority for this species, but Örsted never used the name *Cephalothrix lineata*”. Apparently, Claparède had no intention to establish a new taxon, and simply committed two errors, in the spelling of the specific name and in citing the naming authority. Article 33.5 of the Code (ICZN 1999) stipulates “In any case of doubt whether a different subsequent spelling is an emendation or an incorrect subsequent spelling, it is to be treated as an incorrect subsequent spelling (and therefore unavailable), and not as an emendation”. Therefore, the name *lineata* Claparède, 1862, as published in the binomen *Cephalothrix lineata*, should be regarded as unavailable.

### *Cephalothrix oerstedii* Diesing, 1850

**Remarks.** Gibson (1995: 325) listed *C. oerstedii* as an available name and a junior synonym of *C. rufifrons*. However, as with the case in *B. cephalothrix* above, Diesing (1850: 246) tried to replace *Cephalothrix bioculata* Örsted, 1843 with *Cephalothrix oerstedi* Diesing, 1850. The latter is a junior synonym of the former from the beginning. The name *oerstedii* Diesing, 1850, as published in the binomen *Cephalothrix oerstedii*, is thus unavailable according to Article 11.6 of the Code (ICZN 1999).

## DISCUSSION

In this paper, I designated ICHUM 3509 from Bergen as the neotype of *Planaria linearis* Rathke, 1799 (now *Cephalothrix linearis*) to clarify the taxonomic status of the species, especially

in relation to *C. filiformis* and *C. rufifrons*. The barcode sequence from the neotype, along with the redescription, would help establish the taxon concept of *C. linearis*, which has needed clarification for more than 200 years.

So far, 36 nominal species have been established that are likely to be included in *Cephalothrix* (Table in Appendix 2). Every one of these 36 can potentially represent a valid species, while some are arguably synonymous with others. On the other hand, the present PTP delimitation analysis detected 34 species in *Cephalothrix*. I allotted 12 of the 36 available names to them; 22 species detected by the analysis were left unidentified. While most of these 22 are probably undescribed species, some might represent named ones. For instance, “*Cephalothrix* sp. SCS-2010” (China and Russia [Sakhalin]), “*Cephalothrix* sp. 5 HC-2011” (Qingdao, China), and “*Cephalothrix* sp. 3 HC-2011” (Far East Russia and Japan) may represent *Cephalothrix mokievskii* (Korotkevich, 1982) or *Cephalothrix orientalis* (Gibson, 1990). “*Cephalothrix* sp. 14 HC-2011” (Roscoff [France] and Asturias [Spain]) has “Pinkish-yellow to orange body. A bright spot (sometimes two lateral spots can be distinguished) of orange pigment near the tip of the head” (S.A. Maslakova in Chen *et al.* 2010), which resembles *C. rufifrons*, but it turned out to be a sister species of the latter (Figure 4); the sequence may represent *C. bioculata*, *Cephalothrix hymenaeus* Bürger, 1892, or *C. ocellata*. “*Cephalothrix* sp. 8 HC-2011” (Spain) is whitish (S.A. Maslakova in Chen *et al.* 2010), appeared as sister to *C. rufifrons* + “*Cephalothrix* sp. 14 HC-2011”, and possibly represented *C. longissima*. Sequences and colour photographs of specimens from the type localities of the 36 nominal species (Table in Appendix 2) will undoubtedly facilitate future *Cephalothrix* systematics.

Diesing (1850) renamed a number of then-existing helminth taxa (ranging from unicellular organisms, platyhelminths, nemerteans, nematodes, to annelids), with he himself being the naming authority. In this paper I mentioned only four of such ‘new names’ that should be deemed to be unavailable according to Article 11.6 of the Code (ICZN 1999). However, Diesing (1850) created many other such unavailable names in different taxa. For instance, the acotylean polyclad *Stylochus mertensi* Diesing, 1850 was established as a junior synonym of *Planaria sargassicola* Mertens, 1833 (Diesing 1850: 216), and the former appears to be regarded as if it were an available name (Tyler *et al.* 2006–2018). Pointing out all such names in the entire volumes of *Systema Helminthum* is beyond my capacity. On the other hand, there are two points I should mention in favour of Diesing (1850). One is that he seems to be consistent in regarding that a taxonomic naming authority should attribute to the author who creates a new combination of a binomen (just like in the botanical code), rather than to a new specific epithet (as we see in the current zoological code). The second is, in the year 1850 when his first volume of *Systema Helminthum* was published, the Stricklandian Code (Strickland *et al.* 1843), and thus the Principle of Priority, was not in effect in German-speaking countries (Dayrat 2010), including Austria

where this great helminthologist lived (Carus 1877); the *Règles internationales* (Blanchard *et al.* 1905) came into force much later. These would be why Diesing (1850) produced so many unavailable names.

In the COI phylogeny, *Cephalothrix* was basally trichotomous, with each branch represented by *i*) *C. bipunctata*, *C. linearis*, *C. major*, “*Cephalothrix* cf. *spiralis* TCH-2016”, and “*Cephalothrix* sp. 5 HC-2011”; *ii*) “*Cephalothrix* sp. 2 TCH-2015”; and *iii*) the rest of the species included in the analysis. If the name *Procephalothrix* were to be ‘resurrected’, it could be applied to the last clade, since it contains the type species *Planaria filiformis* Johnston, 1828. In that case, *Cephalothrix* could be restricted to the first clade. Two of the uncommon anatomical features found in *C. linearis* (Type-C vessel and lack of longitudinal muscles lateral to lateral nerve) may be shared by the members in the first clade. If so, *C. germanica* and *C. paragermanica* also would be nested within this clade, because they lack such longitudinal muscles in that position (Gerner 1969: 82–87, Figures 9A, 11C; Senz 1993), although the absence might be the result of miniaturization and adaptation to interstitial environments, as these authors argued. Also, members in the first clade may possess only one type of pseudocnidae in the proboscis epithelium (Figure 10E), as opposed to two types in the members belonging to the third clade (Magarlamov *et al.* 2018).

As of writing in 2018, there are 10 GenBank entries of COI gene sequence attributed to putative *C. linearis*. Eight of them are from Norwegian waters (KP697715–KP69771521 and KU840290, M. Strand, unpubl.), all represent a single species, which, however, is not nested within other *Cephalothrix*, but appeared among the outgroup tubulanids in the COI phylogeny (Figure 5). Five images of this taxon are available at a website of the Norwegian Biodiversity Information Centre (<https://www.biodiversity.no>). One of the images depicts an epidermal band, which is unique to Tubulanidae. In tubulanids, the composition of epidermal glandular cells abruptly changes antero-posteriorly from a certain portion in the foregut or anterior intestinal region of the body. In *Callinera emiliae* Kajihara, 2007b, for instance, acidofuchsin-staining cells are predominant anterior to the border, which are posteriorly replaced by Orange-G-staining cells behind the border (Kajihara 2007b). This transition often manifests itself after fixation; Ritger & Norenburg (2006) referred to it as fixation band for *Tubulanus riceae* Ritger & Norenburg, 2006. In light of the epidermal band and the position in the COI phylogeny, ‘*C. linearis*’ sensu Strand should belong to Tubulanidae, rather than Cephalotrichidae. Unfortunately, COI alone cannot place it in a genus with certainty. Besides, *Tubulanus* (and possibly some other tubulanid genera) is not likely monophyletic. However, analyses with slow-evolving markers such as the 16S rRNA and 28S rRNA genes may tell its proper genus affiliation.

## NOTE ADDED IN PROOF

After the manuscript of this paper was accepted for publication, Dr. Malin Strand (Swedish University of Agricultural Sciences), upon being contacted by the author, corrected the species identity of the ‘*Cephalothrix linearis*’ at the Norwegian Biodiversity Information Centre website, the relevant page of which has been eliminated and is currently not available anymore. In the public nucleotide databases, however, the accession numbers KP697715–KP69771521 and KU840290 are still anchored to the name ‘*Cephalothrix linearis*’ as of March 2019. Based on these sequences, the associated name *Cephalothrix linearis* has been used ‘improperly’—in the light of the present work, though—in Sagorny *et al.* (2019). Although Sagorny *et al.* (2019) sampled *Cephalothrix* specimens in Bergen (Norway), all they obtained in this place turned out to be either *C. filiformis* (MH681957, MH681958, MH681960) or *C. rufifrons* (MH681896). Indeed, *C. linearis* s.str. was not included in the 78 *Cephalothrix* specimens that Sagorny *et al.* (2019) collected at six localities in Europe: Norway (Bergen), Sweden (Kristineberg), France (Roscoff, Concarneau), Italy (Giglio), and Spain (Blanes), suggesting the rarity of the species.

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**Appendix 1.** List of public database accession numbers of COI sequences used for the Bayesian phylogenetic inference and PTP species delimitation analysis performed in the present study, with the locality and species names that are *i)* originally registered in DDBJ/EMBL/GenBank and *ii)* used in this paper. Boldface entries in the latter column denote discordance between the original name in the database.

Accession number	Locality	Species name registered in DDBJ/EMBL/GenBank	Species name used in this study	Source
AJ436944	Akkeshi, Japan	<i>Procephalothrix filiformis</i>	<b>“<i>Procephalothrix filiformis</i>” sensu Iwata (1954)</b>	Thollesson & Norenburg (2003)
AJ436945	Akkeshi, Japan	<i>Procephalothrix simulus</i>	<b>“<i>Cephalothrix</i> sp. 3 HC-2011”</b>	Thollesson & Norenburg (2003)
AJ436946	WA, USA	<i>Procephalothrix spiralis</i>	<b>“<i>Cephalothrix cf. spiralis</i> THC-2016”</b>	Thollesson & Norenburg (2003)
EFI40788	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Turbeville & Smith (2007)
EU489494	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg <i>et al.</i> (2009)
EU489496	Sweden	<i>Procephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Sundberg <i>et al.</i> (2009)
FJ594739	China	<i>Cephalothrix simula</i>	<b><i>Cephalothrix hongkongensis</i></b>	Chen <i>et al.</i> (2009)
GU227123	Ross Sea, Antarctica	<i>Procephalothrix</i> sp. DH-2009?	“ <i>Cephalothrix</i> sp. DH-2009?”	Heineier <i>et al.</i> (2010)
GU564482	China	<i>Cephalothrix</i> sp. SCS-2010	<i>Cephalothrix</i> sp. SCS-2010	Chen <i>et al.</i> (2011)
GU7726590	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726591	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726592	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726593	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726594	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726595	Koster, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726596	Grötholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726597	Grötholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726598	Vattenholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726599	Vattenholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726601	Wembury/Salcombe, Devon, UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726602	Wembury/Salcombe, Devon, UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726603	Wembury/Salcombe, Devon, UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726604	Wembury/Salcombe, Devon, UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726605	Humlésäcken, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726606	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU7726607	Sakhalin, Russia	<i>Cephalothrix simula</i>	<b>“<i>Cephalothrix</i> sp. SCS-2010”</b>	Chen <i>et al.</i> (2010)
GU7726608	Russia	<i>Cephalothrix</i> sp. 3 HC-2011	<b>“<i>Cephalothrix</i> sp. SCS-2010”</b>	Chen <i>et al.</i> (2010)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
GU726609	Russia	<i>Cephalothrix simula</i>	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726610	Shenzhen, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726611	Hong Kong, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726612	Hong Kong, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726613	Hong Kong, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726614	Hong Kong, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726615	Changdao, China	<i>Cephalothrix</i> sp. 16 HC-2011	“ <i>Cephalothrix hongkongiensis</i> ”	Chen et al. (2010)
GU726616	Changdao, China	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726617	Spain	<i>Cephalothrix</i> sp. 8 HC-2011	“ <i>Cephalothrix</i> sp. 8 HC-2011”	Chen et al. (2010)
GU726618	Zhenjiang, China	<i>Cephalothrix</i> sp. 16 HC-2011	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726619	Changdao, China	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. SCS-2010”	Chen et al. (2010)
GU726620	Oshoro, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726621	Shimoda, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726622	Vietnam	<i>Cephalothrix</i> sp. 13 HC-2011	“ <i>Cephalothrix</i> sp. 13 HC-2011”	Chen et al. (2010)
GU726623	Fukue, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726624	Fukue, Japan	<i>Cephalothrix fasciatus</i>	<i>Cephalothrix fasciatus</i>	Chen et al. (2010)
GU726625	Qingdao, China	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. SCS-2010”	Chen et al. (2010)
GU726626	Qingdao, China	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. SCS-2010”	Chen et al. (2010)
GU726627	Qingdao, China	<i>Cephalothrix simula</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726628	Qingdao, China	<i>Cephalothrix simula</i>	<i>Cephalothrix hongkongiensis</i>	Chen et al. (2010)
GU726629	Qingdao, China	<i>Cephalothrix</i> sp. 5 HC-2011	“ <i>Cephalothrix</i> sp. 5 HC-2011”	Chen et al. (2010)
GU726630	Qingdao, China	<i>Cephalothrix</i> sp. 5 HC-2011	“ <i>Cephalothrix</i> sp. 5 HC-2011”	Chen et al. (2010)
GU726631	Qingdao, China	<i>Cephalothrix</i> sp. 5 HC-2011	“ <i>Cephalothrix</i> sp. 5 HC-2011”	Chen et al. (2010)
GU726632	Wales, UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726633	HI, USA	<i>Cephalothrix</i> sp. 2 HC-2011	“ <i>Cephalothrix</i> sp. 2 HC-2011”	Chen et al. (2010)
GU726634	HI, USA	<i>Cephalothrix</i> sp. 2 HC-2011	“ <i>Cephalothrix</i> sp. 2 HC-2011”	Chen et al. (2010)
GU726635	Akkeshi, Japan	<i>Cephalothrix filiformis</i>	“ <i>Procephalothrix filiformis</i> ” sensu Iwata (1954)	Chen et al. (2010)
GU726636	Akkeshi, Japan	<i>Cephalothrix filiformis</i>	“ <i>Procephalothrix filiformis</i> ” sensu Iwata (1954)	Chen et al. (2010)
GU726637	Oshoro, Japan	<i>Cephalothrix filiformis</i>	“ <i>Procephalothrix filiformis</i> ” sensu Iwata (1954)	Chen et al. (2010)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/EMBL/GenBank	Species name used in this study	Source
GU726639	CA, USA	<i>Cephalothrix</i> sp. 6 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726640	CA, USA	<i>Cephalothrix</i> sp. 6 HC-2011	“ <i>Cephalothrix</i> sp. 6 HC-2011”	Chen et al. (2010)
GU726641	Japan Sea, Russia	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726642	Japan Sea, Russia	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726643	Japan Sea, Russia	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726644	South Korea	<i>Cephalothrix</i> sp. 16 HC-2011	<i>Cephalothrix hongtongensis</i>	Chen et al. (2010)
GU726645	Akkeshi, Japan	<i>Cephalothrix filiformis</i>	“ <i>Procephalothrix filiformis</i> ” sensu Iwata (1954)	Chen et al. (2010)
GU726646	South Korea	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726648	WA, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726649	White Sea, Russia	<i>Cephalothrix spiralis</i>	<i>Cephalothrix filiformis</i>	Chen et al. (2010)
GU726650	White Sea, Russia	<i>Cephalothrix spiralis</i>	<i>Cephalothrix filiformis</i>	Chen et al. (2010)
GU726651	White Sea, Russia	<i>Cephalothrix spiralis</i>	<i>Cephalothrix filiformis</i>	Chen et al. (2010)
GU726652	White Sea, Russia	<i>Cephalothrix spiralis</i>	<i>Cephalothrix filiformis</i>	Chen et al. (2010)
GU726653	White Sea, Russia	<i>Cephalothrix linearis</i>	<i>Cephalothrix filiformis</i>	Chen et al. (2010)
GU726661	Shirahama, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726662	Shirahama, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726663	Shirahama, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726664	Shirahama, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	<i>Cephalothrix simula</i>	Chen et al. (2010)
GU726665	Shirahama, Japan	<i>Cephalothrix</i> sp. 3 HC-2011	“ <i>Cephalothrix</i> sp. 3 HC-2011”	Chen et al. (2010)
GU726666	Shirahama, Japan	<i>Cephalothrix</i> sp. 12 HC-2011	“ <i>Cephalothrix</i> sp. A”	Chen et al. (2010)
GU726667	Shirahama, Japan	<i>Cephalothrix</i> sp. 11 HC-2011	“ <i>Cephalothrix</i> sp. 11 HC-2011”	Chen et al. (2010)
GU726668	FL, USA	<i>Cephalothrix</i> sp. 6 HC-2011	“ <i>Cephalothrix</i> sp. 6 HC-2011”	Chen et al. (2010)
GU726669	FL, USA	<i>Cephalothrix</i> sp. 6 HC-2011	“ <i>Cephalothrix</i> sp. 6 HC-2011”	Chen et al. (2010)
GU726670	Roscoff, France	<i>Cephalothrix</i> sp. 4 HC-2011	“ <i>Cephalothrix</i> sp. 4 HC-2011”	Chen et al. (2010)
GU726671	Roscoff, France	<i>Cephalothrix</i> sp. 4 HC-2011	“ <i>Cephalothrix</i> sp. 4 HC-2011”	Chen et al. (2010)
GU726672	Roscoff, France	<i>Cephalothrix</i> sp. 4 HC-2011	“ <i>Cephalothrix</i> sp. 4 HC-2011”	Chen et al. (2010)
GU726673	Roscoff, France	<i>Cephalothrix</i> sp. 14 HC-2011	“ <i>Cephalothrix</i> sp. 14 HC-2011”	Chen et al. (2010)
GU726674	Roscoff, France	<i>Cephalothrix</i> sp. 14 HC-2011	“ <i>Cephalothrix</i> sp. 14 HC-2011”	Chen et al. (2010)
GU726675	Roscoff, France	<i>Cephalothrix</i> sp. 14 HC-2011	“ <i>Cephalothrix</i> sp. 14 HC-2011”	Chen et al. (2010)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
GU726676	Roscoff, France	<i>Cephalothrix</i> sp. 14 HC-2011	“ <i>Cephalothrix</i> sp. 14 HC-2011”	Chen et al. (2010)
GU726677	Panama	<i>Cephalothrix</i> sp. 15 HC-2011	“ <i>Cephalothrichella</i> sp. B”	Chen et al. (2010)
GU726678	Panama	<i>Cephalothrix</i> sp. 15 HC-2011	“ <i>Cephalothrix</i> sp. 15 HC-2011”A	Chen et al. (2010)
GU726679	Panama	<i>Cephalothrix</i> sp. 15 HC-2011	“ <i>Cephalothrix</i> sp. 15 HC-2011”A	Chen et al. (2010)
GU726680	Panama	<i>Cephalothrix</i> sp. 9 HC-2011	“ <i>Cephalothrix</i> sp. 9 HC-2011”	Chen et al. (2010)
GU726681	Panama	<i>Cephalothrix</i> sp. 10 HC-2011	“ <i>Cephalothrix</i> sp. 10 HC-2011”	Chen et al. (2010)
GU726682	Carrie Bow Cay, Belize	<i>Cephalothrix</i> sp. 15 HC-2011	“ <i>Cephalothrichella</i> sp. C”	Chen et al. (2010)
GU726688	Grötholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726689	OR, USA	<i>Cephalothrix major</i>	<i>Cephalothrix major</i>	Chen et al. (2010)
GU726690	OR, USA	<i>Cephalothrix major</i>	<i>Cephalothrix major</i>	Chen et al. (2010)
GU726691	OR, USA	<i>Cephalothrix major</i>	<i>Cephalothrix major</i>	Chen et al. (2010)
GU726692	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726693	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726694	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726695	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726696	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726697	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726698	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726699	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726700	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726701	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726702	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726703	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726704	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726705	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726706	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726707	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726708	ME, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726709	AK, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
GU726710	AK, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726711	AK, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726712	AK, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Chen et al. (2010)
GU726713	Boden, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726714	Boden, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726715	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726716	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726717	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726718	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726719	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726720	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726721	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726722	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726723	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726724	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726725	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726726	Boden, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726727	Boden, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726728	Skeppsholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726729	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726730	Vattenholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726731	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726732	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726733	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726734	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726735	Grötholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726736	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726737	Stångholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)
GU726738	Koster, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen et al. (2010)

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Accession number	Locality	Species name registered in DDBJ/EMBL/GenBank	Species name used in this study	Source
GU726739	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726740	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726741	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726742	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726743	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726744	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726745	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726746	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726747	Vattenholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU726748	Vattenholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU733829	Gröholmen, Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Chen <i>et al.</i> (2010)
GU733830	Trieste, Italy	<i>Cephalothrix simula</i>	<i>Cephalothrix simula</i>	Kajihara <i>et al.</i> (2013)
GU807436	Hiroshima, Japan	<i>Cephalothrix simula</i>	<i>Cephalothrix simula</i>	Andrade <i>et al.</i> (2012)
HQ848604	Rhos-on-Sea, Wales, UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Andrade <i>et al.</i> (2012)
HQ848614	Qingdao, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Andrade <i>et al.</i> (2012)
HQ848615	Qingdao, China	<i>Cephalothrix hongkongiensis</i>	<i>Cephalothrix hongkongiensis</i>	Andrade <i>et al.</i> (2012)
HQ848616	Rhos-on-Sea, Wales, UK	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Andrade <i>et al.</i> (2012)
HQ848617	Sylt, Germany	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Andrade <i>et al.</i> (2012)
JX453463	Galicia, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453464	Galicia, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453465	Asturias, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453466	Asturias, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453467	Cantabria, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453468	Cantabria, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453469	Cantabria, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453470	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453471	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453472	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453473	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
JX453474	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453475	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453476	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453477	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453478	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453479	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453480	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453481	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453482	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453483	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453484	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453485	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453486	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453487	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453488	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453489	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453490	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453491	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453492	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453493	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
JX453494	Catalunya, Spain	<i>Cephalothrix cf. simula</i>	<i>Cephalothrix simula</i>	Fernández-Álvarez & Machordom (2013)
KF955501	Spain	<i>Cephalothrix bipunctata</i>	<i>Cephalothrix bipunctata</i>	Kvist <i>et al.</i> (2014)
KM083809	Bocas del Toro, Panama	<i>Cephalothrix</i> sp. 1 FL-2014	“ <i>Cephalothrix</i> sp. 9 HC-2011”	Leasi & Norenburg (2014)
KM083811	Bocas del Toro, Panama	<i>Cephalothrix</i> sp. 1 FL-2014	“ <i>Cephalothrix</i> sp. 1 FL-2014”	Leasi & Norenburg (2014)
KM083812	Bocas del Toro, Panama	<i>Cephalothrix</i> sp. 3 FL-2014	“ <i>Cephalothrix</i> sp. 3 FL-2014”	Leasi & Norenburg (2014)
KM083814	Belize	<i>Cephalothrix fasciatus</i>	“ <i>Cephalothrix fasciatus</i> ”	Leasi & Norenburg (2014)
KM083815	Belize	<i>Cephalothrix</i> sp. 5 FL-2014	“ <i>Cephalothrix</i> sp. 5 FL-2014”	Leasi & Norenburg (2014)
KM083818	Belize	<i>Cephalothrix alba</i>	“ <i>Cephalotrichella</i> sp. D”	Leasi & Norenburg (2014)
KM083819	Panama	<i>Cephalothrix alba</i>	“ <i>Cephalotrichella</i> sp. E”	Leasi & Norenburg (2014)

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Accession number	Locality	Species name registered in DDBJ/EMBL/GenBank	Species name used in this study	Source
KM083820	Bocas del Toro, Panama	<i>Cephalothrix</i> sp. 1 FL-2014	“ <i>Cephalothrix</i> sp. 1 FL-2014”	Leasi & Norenburg (2014)
KM1230034	Galicia, Spain	<i>Cephalothrix</i> sp.	<i>Cephalothrix hermaphroditica</i>	Fernández-Álvarez <i>et al.</i> (unpublished)
KM1230035	Asturias, Spain	<i>Cephalothrix</i> sp. 2 AM-2014	“ <i>Cephalothrix</i> sp. 14 HC-2011”	Fernández-Álvarez <i>et al.</i> (unpublished)
KM1230036	Asturias, Spain	<i>Cephalothrix</i> sp. 2 AM-2014	“ <i>Cephalothrix</i> sp. 14 HC-2011”	Fernández-Álvarez <i>et al.</i> (unpublished)
KM1230037	Camarones Bay, Argentina	<i>Cephalothrix</i> sp.	<i>Cephalothrix hermaphroditica</i>	Fernández-Álvarez <i>et al.</i> (unpublished)
KP270866	Vietnam	<i>Balionemertes</i> sp.	“ <i>Balionemertes</i> sp.”	Kvist <i>et al.</i> (2015)
KP270867	Vietnam	<i>Cephalothrix cf. alba</i>	“ <i>Cephalotrichella</i> sp. F cf. <i>alba</i> ”	Kvist <i>et al.</i> (2015)
KP270873	Russia	<i>Cephalothrix iwatai</i>	<i>Cephalothrix iwatai</i>	Kvist <i>et al.</i> (2015)
KP411243	Zierikzee, Netherlands	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Faasse & Turbeville (2015)
KP411244	Zierikzee, Netherlands	<i>Cephalothrix simula</i>	<i>Cephalothrix simula</i>	Faasse & Turbeville (2015)
KP411245	Sint Annaland, Netherlands	<i>Cephalothrix simula</i>	<i>Cephalothrix simula</i>	Faasse & Turbeville (2015)
KP411246	Sint Annaland, Netherlands	<i>Cephalothrix simula</i>	<i>Cephalothrix simula</i>	Faasse & Turbeville (2015)
KP411247	Sint Annaland, Netherlands	<i>Cephalothrix simula</i>	<i>Cephalothrix simula</i>	Faasse & Turbeville (2015)
KU197677	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Hiebert & Maslakova (unpublished)
KU197678	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Hiebert & Maslakova (unpublished)
KU197679	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Hiebert & Maslakova (unpublished)
KU197680	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Hiebert & Maslakova (unpublished)
KU197681	OR, USA	<i>Cephalothrix</i> sp. 4 TCH-2015	“ <i>Cephalothrix</i> sp. 4 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197682	OR, USA	<i>Cephalothrix</i> sp. 4 TCH-2015	“ <i>Cephalothrix</i> sp. 4 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197683	OR, USA	<i>Cephalothrix</i> sp. 4 TCH-2015	“ <i>Cephalothrix</i> sp. 4 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197684	OR, USA	<i>Cephalothrix</i> sp. 4 TCH-2015	“ <i>Cephalothrix</i> sp. 4 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197685	OR, USA	<i>Cephalothrix</i> sp. 4 TCH-2015	“ <i>Cephalothrix</i> sp. 4 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197686	OR, USA	<i>Cephalothrix spiralis</i>	<i>Cephalothrix spiralis</i>	Hiebert & Maslakova (unpublished)
KU197687	OR, USA	<i>Cephalothrix major</i>	<i>Cephalothrix major</i>	Hiebert & Maslakova (unpublished)
KU197688	OR, USA	<i>Cephalothrix</i> sp. 1 TCH-2015	“ <i>Cephalothrix</i> sp. 1 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197689	OR, USA	<i>Cephalothrix</i> sp. 1 TCH-2015	“ <i>Cephalothrix</i> sp. 1 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197690	OR, USA	<i>Cephalothrix</i> sp. 1 TCH-2015	“ <i>Cephalothrix</i> sp. 1 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197691	OR, USA	<i>Cephalothrix</i> sp. 1 TCH-2015	“ <i>Cephalothrix</i> sp. 1 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197692	OR, USA	<i>Cephalothrix</i> sp. 1 TCH-2015	“ <i>Cephalothrix</i> sp. 1 TCH-2015”	Hiebert & Maslakova (unpublished)

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Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
KU197693	OR, USA	<i>Cephalothrix</i> sp. 1 TCH-2015	“ <i>Cephalothrix</i> sp. 1 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197694	OR, USA	<i>Cephalothrix</i> sp. 2 TCH-2015	“ <i>Cephalothrix</i> sp. 2 TCH-2015”	Hiebert & Maslakova (unpublished)
KU197695	OR, USA	<i>Cephalothrix</i> sp. 2 TCH-2015	“ <i>Cephalothrix</i> sp. 2 TCH-2015”	Hiebert & Maslakova (unpublished)
KU517442	OR, USA	<i>Cephalothrix</i> cf. <i>spiralis</i> TCH-2016	“ <i>Cephalothrix</i> cf. <i>spiralis</i> TCH-2016”	Hiebert & Maslakova (unpublished)
KU839795	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839796	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839797	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839827	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839828	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839829	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839830	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839831	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839832	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839833	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839834	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839835	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839836	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839837	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839838	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839839	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839840	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839841	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839842	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839843	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839844	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839845	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839846	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839847	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839848	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
KU839849	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839850	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839851	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839852	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839853	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839874	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839875	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839987	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839988	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU839989	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840001	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840002	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840003	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840004	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840005	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840006	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840007	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840008	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840009	Sweden	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840010	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840099	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840100	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840101	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840102	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840103	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840104	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840105	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840106	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840107	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
KU840108	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840109	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840110	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840111	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840112	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840113	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840114	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840115	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840116	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840117	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840118	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840119	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840120	unknown	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840127	UK	<i>Cephalothrix rufifrons</i>	<i>Cephalothrix rufifrons</i>	Sundberg et al. (2016)
KU840128	UK	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Sundberg et al. (2016)
KU840136	Wales, UK	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Sundberg et al. (2016)
KU840156	Sweden	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Sundberg et al. (2016)
KU840171	Chile	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Sundberg et al. (2016)
KU840181	Chile	<i>Cephalothrix arenaria</i>	<i>Cephalothrix arenaria</i>	Sundberg et al. (2016)
KU840182	Chile	<i>Cephalothrix hermaphroditica</i>	<i>Cephalothrix hermaphroditica</i>	Sundberg et al. (2016)
KU840183	Chile	<i>Cephalothrix hermaphroditica</i>	<i>Cephalothrix hermaphroditica</i>	Sundberg et al. (2016)
KU840213	Chile	<i>Cephalothrix hermaphroditica</i>	<i>Cephalothrix hermaphroditica</i>	Sundberg et al. (2016)
KU840272	Vietnam	<i>Cephalothrix sp.</i>	<i>“Cephalothrix sp. 13 HC-2011”</i>	Sundberg et al. (2016)
KU840273	Vietnam	<i>Cephalothrix cf. alba</i>	<i>“Cephalothrix sp. F cf. alba”</i>	Sundberg et al. (2016)
KU840274	Vietnam	<i>Cephalothrix cf. alba</i>	<i>“Cephalothrix sp. G cf. alba”</i>	Sundberg et al. (2016)
KU840289	unknown	<i>Cephalothrix filiformis</i>	<i>Cephalothrix filiformis</i>	Sundberg et al. (2016)
LC422243	Bergen, Norway	<i>Cephalothrix linearis</i>	<i>Cephalothrix linearis</i>	this study
NC_012821	China	<i>Cephalothrix simula</i>	<i>Cephalothrix honglongiensis</i>	Chen et al. (2009)
NC_014869	China	<i>Cephalothrix sp. SCS-2010</i>	<i>“Cephalothrix sp. SCS-2010”</i>	Chen et al. (2011)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDB/EMBL/GenBank	Species name used in this study	Source
Outgroup				
AJ436947	Russia	<i>Tubulanus punctatus</i>	<i>Tubulanus punctatus</i>	Thollesson & Norenburg (2003)
AJ436948	FL, USA	<i>Tubulanus rhabdotus</i>	<i>Tubulanus rhabdotus</i>	Thollesson & Norenburg (2003)
AJ436949	WA, USA	<i>Tubulanus sexlineatus</i>	<i>Tubulanus sexlineatus</i>	Thollesson & Norenburg (2003)
KP270865	Russia	<i>Callinera kasyanovi</i>	<i>Callinera kasyanovi</i>	Kvist et al. (2015)
KP270868	Russia	<i>Tubulanus</i> sp.	“ <i>Tubulanus</i> sp. B”	Kvist et al. (2015)
KP270869	Russia	<i>Tubulanidae</i> sp.	<i>Parahubrechitia</i> sp.	Kvist et al. (2015)
KP270870	Russia	<i>Tubulanus</i> sp.	“ <i>Tubulanus</i> sp. A”	Kvist et al. (2015)
KP270871	Vietnam	<i>Tubulanidae</i> sp.	<i>Parahubrechitia</i> sp.	Kvist et al. (2015)
KP270872	Russia	<i>Tubulanus punctatus</i>	<i>Tubulanus punctatus</i>	Kvist et al. (2015)
KP697715	Froysjøen, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697716	Froysjøen, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697717	Froysjøen, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697718	Froysjøen, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697719	Hagoeya, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697720	Froysjøen, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697721	Froysjøen, Norway	<i>Cephalothrix linearis</i>	“ <i>Cephalothrix linearis</i> ”	Strand (unpublished)
KP697780	Grottsundet, Norway	<i>Tubulanus ambiguus</i>	<i>Tubulanus ambiguus</i>	Strand (unpublished)
KP697781	Sandsøya, Norway	<i>Tubulanus annulatus</i>	<i>Tubulanus annulatus</i>	Strand (unpublished)
KP697782	Storfosna-Lyngholmen, Norway	<i>Tubulanus linearis</i>	<i>Tubulanus linearis</i>	Strand (unpublished)
KP697783	Droebakksgrunnen, Norway	<i>Tubulanus polymorphus</i>	“ <i>Tubulanus polymorphus</i> ”	Strand (unpublished)
KP697784	Grottsundet, Norway	<i>Tubulanus superbus</i>	“ <i>Tubulanus polymorphus</i> ”	Strand (unpublished)
KU197696	OR, USA	<i>Tubulanus polymorphus</i>	“ <i>Tubulanus polymorphus</i> ”	Hiebert & Maslakova (unpublished)
KU197697	OR, USA	<i>Tubulanus polymorphus</i>	“ <i>Tubulanus polymorphus</i> ”	Hiebert & Maslakova (unpublished)
KU197698	OR, USA	<i>Tubulanus sexlineatus</i>	<i>Tubulanus sexlineatus</i>	Hiebert & Maslakova (unpublished)
KU197699	OR, USA	<i>Tubulanus sexlineatus</i>	<i>Tubulanus sexlineatus</i>	Hiebert & Maslakova (unpublished)
KU197700	OR, USA	<i>Tubulanus sexlineatus</i>	<i>Tubulanus sexlineatus</i>	Hiebert & Maslakova (unpublished)
KU197701	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015A	Hiebert & Maslakova (unpublished)
KU197702	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015B	Hiebert & Maslakova (unpublished)

## Appendix I. Continued.

Accession number	Locality	Species name registered in DDBJ/ EMBL/GenBank	Species name used in this study	Source
KU197703	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015B	Hiebert & Maslakova (unpublished)
KU197704	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015B	Hiebert & Maslakova (unpublished)
KU197705	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015B	Hiebert & Maslakova (unpublished)
KU197706	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015B	Hiebert & Maslakova (unpublished)
KU197707	OR, USA	<i>Tubulanus</i> sp. 1 TCH-2015	<i>Tubulanus</i> sp. 1 TCH-2015A	Hiebert & Maslakova (unpublished)
KU197708	OR, USA	<i>Tubulanus</i> sp. 2 TCH-2015	<i>Tubulanus</i> sp. 2 TCH-2015	Hiebert & Maslakova (unpublished)
KU197709	OR, USA	<i>Tubulanus</i> sp. 2 TCH-2015	<i>Tubulanus</i> sp. 2 TCH-2015	Hiebert & Maslakova (unpublished)
KU197710	OR, USA	<i>Tubulanus</i> sp. 2 TCH-2015	<i>Tubulanus</i> sp. 2 TCH-2015	Hiebert & Maslakova (unpublished)
KU197711	OR, USA	<i>Tubulanus</i> sp. 3 TCH-2015	<i>Tubulanus</i> sp. 3 TCH-2015	Hiebert & Maslakova (unpublished)
KUS17445	OR, USA	<i>Tubulanus</i> sp. 3 TCH-2015	<i>Tubulanus</i> sp. 3 TCH-2015	Hiebert & Maslakova (unpublished)
KU840154	Philippines	<i>Callinera emiliae</i>	<i>Callinera emiliae</i>	Sundberg <i>et al.</i> (2016)
KU840288	Sweden	<i>Callinera grandis</i>	<i>Callinera grandis</i>	Sundberg <i>et al.</i> (2016)
KU840290	Norway	<i>Cephalothrix</i> cf. <i>linearis</i>	“ <i>Cephalothrix linearis</i> ”	Sundberg <i>et al.</i> (2016)
KX853119	Roscoff, France	<i>Tubulanus polymorphus</i>	<i>Tubulanus polymorphus</i>	Krämer <i>et al.</i> (unpublished)
KX853120	Roscoff, France	<i>Tubulanus polymorphus</i>	<i>Tubulanus polymorphus</i>	Krämer <i>et al.</i> (unpublished)
KX853121	WA, USA	<i>Tubulanus ruber</i>	<i>Tubulanus ruber</i>	Krämer <i>et al.</i> (unpublished)
KX853122	WA, USA	<i>Tubulanus ruber</i>	<i>Tubulanus ruber</i>	Krämer <i>et al.</i> (unpublished)
KX857632	Roscoff, France	<i>Tubulanus superbus</i>	<i>Tubulanus superbus</i>	Krämer <i>et al.</i> (unpublished)
MH243013	WA, USA	<i>Tubulanus sexlineatus</i>	<i>Tubulanus sexlineatus</i>	Leray & Pauly (unpublished)

Appendix 2. List of nominal species that are likely included in *Cephalothrix*.

Nominal species	Type locality	Representative COI	Remarks
<i>Asteroma longum</i> Örsted, 1843	Denmark	—	Pre-oral region same length as <i>C. rufifrons</i> ; body white; possibly not <i>Cephalothrix</i> at all.
<i>Cephalothrix aliena</i> Punnett, 1903	Maldives Islands	—	Split of body-wall outer circular muscle near lateral nerve not conspicuous.
<i>Cephalothrix arenaria</i> Hylobius, 1957	Sweden	KU840156	Mesopsammion; body translucent with yellow tinge; 10 mm long.
<i>Cephalothrix atlantica</i> Gerner, 1969	France	—	Mesopsammion, intertidal to shallow subtidal; body 10 mm long; ovaries posterior to rhynchocoel; longitudinal muscles present laterally to lateral nerve.
<i>Cephalothrix bicolorata</i> Örsted, 1843	Denmark	—	Body 3 inches long, anteriorly red, medially dark, posteriorly hyaline, with two small, brown eyes at anterior tip of body.
<i>Cephalothrix bipunctata</i> Bürger, 1892	Italy	KF935501	Body up to 10 cm long, ochre yellow in colour; adult with pair of epidermal eyes; in <i>Amphioxus</i> sand.
<i>Cephalothrix buergeri</i> Wijnhoff, 1913	Italy	—	Body yellowish white; 12 cm long; co-occurs with <i>C. bipunctata</i> in sand.
<i>Cephalothrix coeca</i> Örsted, 1843	Denmark	—	Body 3–4 inches long, white.
<i>Cephalothrix galatheae</i> Dieck, 1870	Italy	—	From egg masses of the spiny squat lobster <i>Galathea strigosa</i> ; body 2–7 cm long, bright brick red in colour; pre-cerebrally with a pair of comma-shaped eyes.
<i>Cephalothrix germanica</i> Gerner, 1969	Germany	—	Mesopsammion, up to 4 mm in body length; longitudinal muscles absent between lateral nerve and outer circular muscle layer; horizontal muscle plate absent.
<i>Cephalothrix hongkongensis</i> Sundberg, Gibson & Olsson, 2003	Hong Kong	GU72661, etc.	Body up to 130 mm long, variable in colour ranging from pale translucent yellowish hue to bright orange; tip of head orange; replacement name of <i>Procephalothrix arenaria</i> Gibson, 1990.
<i>Cephalothrix hymeneus</i> Bürger, 1892	Italy	—	Body 3–4 cm long, colourless or whitish; with two red spots on the tip of head; the specific name is a noun in the nominative singular.
<i>Cephalothrix iwatai</i> Chernyshev, 2013	Russia	KP270873	In preserved state, body 8–24 mm long, pale yellowish or whitish in colour; epidermis with numerous brown pigment granules; from 1494–3334 m depth in the Sea of Japan.
<i>Cephalothrix kefersteini</i> Senz, 2000	Arabian Gulf	—	Body up to 4.5 mm long; gonads distributed over the entire foregut region; longitudinal muscles present between lateral nerve and body-wall outer circular muscle layer.
<i>Cephalothrix lactea</i> Senz, 1993	Croatia	—	Mouth just behind brain; possibly hermaphroditic. Generic name incorrectly spelled <i>Cephalotrix</i> in the original description.
<i>Cephalothrix longissima</i> Keferstein, 1862	France	—	Body bright yellowish gray; pre-oral region long, 10 times as long as width at the mouth.

## Appendix 2. Continued.

Nominal species	Type locality	Representative COI	Remarks
<i>Cephalothrix major</i> Coe, 1930	Pacific coast of North America	GU726689, etc.	Body up to 125 cm long, 1–2 mm wide, pale flesh colour to straw colour; pre-oral region pinkish, 4–6 cm long in a 100-cm-long specimen.
<i>Cephalothrix mediterranea</i> Gerner, 1969	France	—	Mesopsammion; body up to 4 mm long, 0.2 mm wide; rhynchocoel, with septa, extends almost to the hind end of body.
<i>Cephalothrix notabilis</i> Iwata, 1954	Japan	—	Body up to 20 cm in length, opaque white in colour; pre-oral region 5 time as long as width at mouth.
<i>Cephalothrix ocellata</i> Kefefstein, 1862	France	—	Body up to 10 cm long, yellowish gray in colour; tip of head reddish.
<i>Cephalothrix pacifica</i> Gerner, 1969	WA, USA	—	Mesopsammion; body up to 3.5 mm; caudal with adhesive plate; ovaries confined to anterior body.
<i>Cephalothrix paragermanica</i> Senz, 1993	Croatia	—	Longitudinal muscles absent between lateral nerve and body-wall circular muscle layer; gonads distributed in rhynchocoel-region; horizontal longitudinal muscle plate absent. Generic name incorrectly spelled Cephalotrix in the original description.
<i>Cephalothrix spiralis</i> Coe, 1930	Atlantic coast of North America	GU726697	Body 75 mm long, pale yellow, flesh colour or straw colour; rosy or pinkish pre-orally.
<i>Gordius gracilis</i> Dalyell, 1853	Scotland	—	Body 3 inches long, anteriorly reddish (when contracted), fading posteriorly to white.
<i>Nemertes rufifrons</i> Johnston, 1837	Britain	HQ848604, etc.	Body 2 inches long, yellowish in colour, verging on rose-red anteriorly.
<i>Planaria filiformis</i> Johnston, 1828	Britain	HQ848616	Body 6 inches, uniform whitish or yellowish-white in colour.
<i>Planaria linearis</i> Rathke, 1799	Norway	LC422243	Body up to 16 cm long, bright orange in colour; pre-orally reddish.
<i>Procephalothrix adriatica</i> Senz, 1993	Croatia	—	Body 10 mm long in preserved state, uniformly white.
<i>Procephalothrix fasciculus</i> Iwata, 1952	Japan	GU726623	Body 10 cm long, greenish ochre pre-orally, ochre in intestinal region, lateral margins translucent; the specific name is a noun in nominative singular, and does not change its ending irrespective of the genus to which it is combined.
<i>Procephalothrix hermaphroditica</i> Gibson, Sánchez & Méndez, 1990	Chile	KU840171, etc.	Body up to 6 cm long, orange in colour; hermaphrodite; specific name mandatorily changed from <i>hermaphroditicus</i> after Articles 31.2 and 34.2 of the Code (ICZN 1999).
<i>Procephalothrix kiliensis</i> Friedrich, 1935	Germany	—	Body size and colouration unknown; subtidal, mud, silt, sand, 2–15 m depth; external feature in living state unknown.
<i>Procephalothrix mokovskii</i> Korotkevich, 1982	Russia (Sakhalin)	—	Body 42 mm in length, flesh, beige or pale pink in colour (probably in preserved state).

## Appendix 2. Continued.

Nominal species	Type locality	Representative COI	Remarks
<i>Procephalothrix oestrymnica</i> Junoy & Gibson, 1990	Spain	—	Body up to 70 mm in length, pinkish-white in colour, head paler; specific name mandatorily changed from <i>oestrymnicus</i> after Articles 31.2 and 34.2 of the Code (ICZN 1999).
<i>Procephalothrix orientalis</i> Gibson, 1990	Hong Kong	—	Body up to 450 mm in length; anterior end of body pale brown colour on all sides, posteriorly continuing as broad dorsal and narrow ventral stripes, laterally fading to a whitish to very pale brown hue.
<i>Procephalothrix quequensis</i> Moretto, 1974	Argentina	—	Body up to 150 mm in length, dorsally reddish-yellow in colour, ventrally pale or colourless.
<i>Procephalothrix simula</i> Iwata, 1952	Japan	GU726622	Body up to 30 cm in length, yellowishbrown except tip of head, which becomes pinkish; specific name mandatorily changed from <i>simulus</i> after Articles 31.2 and 34.2 of the Code (ICZN 1999).