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Designation of a neotype for *Myxicola infundibulum* (Montagu, 1808) (Annelida: Sabellidae) and a new species from the UK

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Abstract. The historical context of *Myxicola* species identification, around the UK and Europe, is reviewed and confusion surrounding the type species for the genus, *Myxicola infundibulum* (Montagu, 1808), discussed. *Myxicola infundibulum* is re-described and a neotype designated. A new species, *M. polychroma* sp. nov., is also described from the UK and is discussed, along with *M. infundibulum*, in relation to historical synonymised species from the region as well as current species known worldwide. Genetic and morphological details are provided for both species to aid in distinguishing them and determining the validity of other taxa in the future. *Myxicola polychroma* sp. nov. is distinguished through a combination of non-differentially coloured radiole tips, long, fine pinnulae that terminate below the lower margin of the basal membrane, large, fleshy, triangular radiolar appendages that arise centrally, interramal eyespots, dense, fine notochaetae and uncini with upper teeth $0.6–0.8 \times$ length of the main fang. The type specimens of *Myxicola steenstrupi* Krøyer, 1856 and the status of that species are also discussed.

Keywords. Taxonomy, *polychroma*, *sarsii*, *steenstrupi*, Sabellidae.

Introduction

Myxicola Koch in Renier, 1847 is a small genus of medium to large-sized sabellid fan worms with, up to now, seven valid taxa. The majority of those taxa have limited distributions, but *Myxicola infundibulum* (Montagu, 1808) is currently recorded worldwide from both sides of the Atlantic, the Pacific and Australia, mostly due to the synonymy of many other taxa under that name. *Myxicola infundibulum* is the type taxon for the genus and was first described from the Kingsbridge estuary in the south of England. Several other species were erected in the mid–late1800s, the vast majority with superficial descriptions that did not adequately distinguish them from their congeners. McIntosh (1923) comprehensively synonymised most of these European names and records with *M. infundibulum* and more worldwide taxa were synonymised by Fauvel (1927, 1936) and Hartman (1938, 1942, 1959). In total, 17 taxa are now synonymised under this single name across the world, including taxa described from the west coast

of USA (Johnson 1901; Bush 1905; Chamberlin 1919), Japan (Marenzeller 1884) and southern Africa (Augener 1918). In recent years, other authors have agreed that there are more species of *Myxicola* present than currently recognised, and that the genus is in need of revision with, particularly, a redescription of *M. infundibulum* (Giangrande *et al.* 2012; Tovar-Hernández *et al.* 2017), against which other taxa could then be compared and described. In Australia, *M. infundibulum* is a suspected non-native species and was the subject of an undergraduate thesis (Dane 2008) that undertook extensive morphological and molecular analyses of specimens from Australia, Europe and USA to investigate this hypothesis. The results of that work concluded that more taxa were represented within the analyses than could be attributed to just *M. infundibulum* and that records of *M. infundibulum* from around the world required re-evaluation, but also that Australian specimens could not be distinguished from the European ones used in the study and so should be considered as having been introduced anthropogenically. A more detailed description of *M. infundibulum* from the type locality, along with molecular markers, would therefore enable the establishment of its true native range, potentially facilitating the confirmed recognition of it as a non-native species in other regions, as well as enabling the identification of undescribed taxa or, potentially, the re-validation of synonymised taxa.

In 2019, Amgueddfa Cymru received requests from citizen-science divers in the UK to clarify the taxonomic situation surrounding the 'black-tipped' and 'white-tipped' varieties of *Myxicola* that were being recorded and what names could be used for them. The poor description of *M. infundibulum,* and the lack of other valid names, meant that we were unable to provide clarity on the situation without undertaking a more detailed investigation. A project was developed, in conjunction with the volunteer recording society SeaSearch, to support the collection of 'black-tipped' and 'white-tipped' specimens from several different populations around the UK, using methods that would enable both morphological and molecular investigation. Photographs of in situ *Myxicola* were requested from divers through social media channels in order to create a distribution map of the different forms (Fig. 1) and permission was sought to collect specimens of *M. infundibulum* from Montagu's type locality in the Kingsbridge estuary which is now a protected conservation area. In order to understand *Myxicola* around the UK though, the tangled history of *M. infundibulum* itself first had to be unravelled.

A history of *Myxicola* in Europe

The history of *Myxicola*, and *M. infundibulum* in particular, is confusing and convoluted. The first names erected were by Renier [1804a, 1804b] who provided the name *Sabella gelatinosa* for a tube, stating "It is the home of my *Terebella infundibulum*" [Renier 1804b], but no description was provided. In another manuscript, also attributed the date 1804, the Italian name Terebella trombetta and the Latin name *Terebella buccina* were given for an animal whose description points toward the same animal as in the previous manuscript, although this is not explicitly stated [Renier 1804a]. No mention was made, in either work, of the colour of the radioles or their tips. Another manuscript, produced several years later [Renier 1807], was not obtainable; however, Meneghini (in Renier 1847) provided a review of Renier's words from all three manuscripts and of the latter he reported that Renier established a new genus for the same animal, naming it *Tuba divisa* (or Trombetta divisa in the Italian). Meneghini then stated that the same animal only received incidental mentions in any of Renier's later works.

Renier's 1804 and 1807 works were the subject of a series of submissions to the International Code for Zoological Nomenclature in the 1950s, arguing that they should be rejected for nomenclatural purposes as having never been officially published. It was consequently ruled that this was the case and that the names included therein were considered invalid (ICZN 1954, 1956, 1957a). Although a small minority of the affected names were later campaigned for and validated (ICZN 1957b, 1957c, 1988, 2012), all of those relating to *Myxicola* as we now know it, and as detailed above, remain invalid. Muir & Petersen (2013), accepting that there was no clear description of *M. infundibulum* but that there were undoubtedly more species than that present, and that species in the Mediterranean and the UK were likely to be

Fig. 1. Map showing the distribution of *Myxicola infundibulum* (Montagu, 1808) (closed circles) and *M. polychroma* sp. nov. (open circles) around the British Isles, based on validated specimens and photographs. Grey circles indicate an undetermined species of *Myxicola* in northeast England. Type locality of *Myxicola infundibulum* indicated by black arrow.

different, argued that the name *M. infundibulum* should be retained for the Adriatic form on the basis of common reference. However, this does not make sense when Montagu (1808), only shortly after Renier's work and before all other references to the taxon, provided a clear figure showing dark tips to the radioles in reference to specimens from a defined locality, the first time that this diagnostic character was detailed. The majority of the early descriptions and records of species of *Myxicola* did not report the colour of the radioles, or whether or not dark tips were observed on them, and many publications were also without illustrations which might have shown such colour. Where illustrations were provided, radiole tips were not dark. In this publication it is shown that specimens without dark tips on the radioles are distinct from those with, and that there are likely to be multiple such taxa. It is therefore unlikely to be possible to determine which taxa might have been being discussed in any historic literature that does not mention radiole tip colour, with Montagu providing the first means to do so.

Of those other taxa of *Myxicola* recorded historically around the UK, the earliest was *Amphitrite floscula* Dalyell, 1853 (Scotland, exact location unknown). The animal was figured with dark tips to the radioles and synonymised with *M. infundibulum* early on (McIntosh 1923). *Myxicola steenstrupi* Krøyer, 1856, described from Faroe Islands and Greenland, was recorded from the east coast of Scotland (Cunningham & Ramage 1888) as well as further east into the North Sea (Hofsommer 1913), with the Scottish record detailing the form as 'greenish' with purple tips to the radioles. This description is the only one for *M. steenstrupi* indicating pigmented radiolar tips and most likely should be referred to *M. infundibulum.* Other records of *M. steenstrupi* come from Denmark (Eliason 1920), Norway (Bidenkap 1894), the Bay of Fundy, Canada (Bush 1905; Linkletter *et al.* 1977) and Maine, USA (Webster & Benedict 1887) and, in the few descriptions where radiolar colour is mentioned, it is described as white (Malmgren 1865; Soulier 1903; Hofsommer 1913). Of all the synonymised *Myxicola* taxa described around Europe, *M. steenstrupi* was referred to most often and widely, possibly as it had one of the most detailed descriptions of those early species. Not only did Krøyer provide a more detailed description for that species than for any of his other taxa in *Myxicola*, but *M. steenstrupi* was also further described in some detail by Soulier (1903). The species was synonymised with *M. infundibulum* by McIntosh (1923), although it was listed in Hartman's *Catalogue of the Polychaeta* as valid (Hartman 1959). Type material of *M. steenstrupi* was obtained from Natural History Museum of Denmark and examined with respect to the redescription of both *M. infundibulum* and the new species herein described, *M. polychroma* sp. nov.

Myxicola sarsii, described from Norway by Krøyer (1856) in the same publication as *M. steenstrupi*, was Krøyer's name for *Sabella infundibulum*, briefly described by Sars (1851). Krøyer based his name on Sars' brief description, not on specimens, with only the briefest of descriptions himself at only 13 words in length. Sars (1862) provided a slightly more detailed description, but the species was synonymised with *M. steenstrupi* by Malmgren (1865) (also by Cunningham & Ramage 1888, although this latter paper probably followed the lead of Malmgren, whose description the authors quote)*,* possibly due to the fact that, although described in the same paper, Krøyer's description of *M. sarsii* was so weak in comparison. *Myxicola sarsii* was, however, considered by Phyllis Knight-Jones as being the species observed from northern parts of the UK and maintained it as valid in an identification chapter on annelids, published in a widely-used British textbook on marine fauna (Hayward & Ryland 1990, 2017), despite it having been synonymised many years earlier. This subsequently led to much confusion, particularly among British recorders, with many using the name, not realising it was invalid, for animals observed without dark tips to the radioles. Type material of *M. sarsii* was sought from museums in Denmark and Norway, but none was found.

Finally, McIntosh (1874) gave the name *Sabella viridis* to an animal recorded from the east coast of Scotland, the same name given by Quatrefages (1866) for the *Sabelle à sang vert* published by Milne-Edwards in Cuvier (1836–1849); it was then placed under *Myxicola* by McIntosh (1923), although the description and figures by both McIntosh and Milne-Edwards clearly place it outside of the genus, with

banded radioles not connected by a basal membrane. The taxon was then synonymised with *Myxicola infundibulum* by Fauvel (1927), although it was later synonymised with *Sabella spallanzanii* (Gmelin, 1791) by Hartman (1959).

Further afield, in the Mediterranean, *Myxicola grubii* Krøyer, 1856 (from the same publication as *M. sarsii* and *M. steenstrupi*) appears to have been a re-naming of *Eriographis borealis* Grube, 1850 from Trieste, which Grube himself had already referred to *M. infundibulum* sensu Montagu, 1808 (Grube 1855). Comments made by Krøyer in his own 1856 publication and by Claparède (1869), although not explicit, refer to Krøyer's description in that context, as well as to *M. grubii* having dark tips to the radioles. No publication, other than Montagu (1808), mentions dark radiole tips in reference to Mediterranean specimens prior to Krøyer (1856) and his description of *M. grubii*.

Although other authors mention *Myxicola* species from the Mediterranean (e.g., Forbes 1841 – Greece; Claparède 1869 – Naples; Panceri 1875 – Naples, Trieste, Cherso, Privlaka), these were generally referred to *M. infundibulum*, or occasionally *M. steenstrupi*, and only one other *Myxicola* was described from the region after *M. grubii*. Quatrefages (1866) described two species of *Myxicola*, *M. modesta* from Normandy, in northern France, and *M. parasites* from Sicily. Both taxa were later synonymised with *M. infundibulum*, *M. modesta* by McIntosh (1923) and *M. parasites* by Fauvel (1927). Type localities of valid and invalid European species of *Myxicola* are provided in Fig. 2.

Designation of a neotype

Unfortunately, although some of Montagu's polychaete taxa have associated type material, some do not, such as *Marphysa sanguinea* (Montagu, 1813), for which a neotype was designated more recently (Hutchings & Karageorgopoulos 2003). There are, in fact, two 'syntypes' listed on the Natural History Museum London catalogue, as NHMUK1980.390 and NHMUK1980.391. On the record cards connected to the specimens, collection of specimen NHMUK1980.391 (currently missing) is actually attributed to J. Cranch and not Montagu. John Cranch, a known associate of both Montagu and Leach (who employed Cranch as his collector at the British Museum) actually came from Kingsbridge itself. He was known for his large personal collection of specimens and to have travelled extensively around the southwest coast of England collecting specimens (Smith & Harrison 2008). The other specimen, NHMUK1980.390, which was borrowed for examination, has no collector information noted. Both are noted as "Mus. Leach" material on the record cards and in his review of British Museum annelid specimens, Johnston (1865) referred to two Kingsbridge specimens, one from Cranch and another from 'Mus. Leach'; there is no suggestion of them being attributed to Montagu. Earlier in the same publication, for other taxa described by Montagu (*Lumbrineris tricolor* (=*Arabella iricolor* (Montagu, 1804)), *Cirratulus tentaculatus* (=*Cirriformia tentaculata* (Montagu, 1804)), *Lepidonotus clava* (Montagu, 1804)), Montagu is specifically noted as the collector of the specimens examined. McIntosh, in his description of *M. infundibulum* (McIntosh 1923: 313), also stated: "Leach, in his collections in the British Museum, termed it *Amphitrite infundibulum*, and in his specimens from the coast of Devon the branchiae were of a rich purplish brown". This also suggests that the specimens held by the British Museum were not originally sourced from Montagu but from another collection. On the record cards of other Montagu type specimens held there (e.g., for *Lepidonotus clava* and *Bispira volutacornis* (Montagu, 1804)), the collector is again specified as 'Colonel G.T. Montagu'. The 'syntypes' in the Natural History Museum are therefore deemed, at best, topotypes, collected around the same time as Montagu was working, but not syntypes, which must be from the author's original specimen series used in the description. The available 'syntype' was examined but the outer dermis was in a very poor state and observations on the chaetae were difficult. The specimen has around 140 chaetigers, less than that indicated by Montagu in his description (he stated 150–160), another reason to suspect the type designation. A neotype is therefore designated according to Article 75 of the International Code for Zoological Nomenclature (ICZN 1999), in order to clarify the taxonomic status of *M. infundibulum* and enable the recognition

and description of other taxa in the genus. As required by Article 75.3.4, the reasons for believing the original type material to be missing are set out above.

Results from the UK project here provide a more detailed description of *M. infundibulum*, a newly-designated neotype and barcoding information that should facilitate the investigation of all other '*infundibulum*' taxa around the world. The 'white-tipped' form in the UK, herein named *Myxicola polychroma* sp. nov., is confirmed as a distinct taxon, characterised by non-differentially coloured radiole tips, pinnulae more than half the length of the radioles terminating below the lower margin of the basal membrane and large, triangular dorsal lips arising centrally from the ventral lips and oriented on a dorsal-ventral axis.

Material and methods

Fresh specimens of both 'black-tipped' and 'white-tipped' *Myxicola* were collected subtidally and/or intertidally. In most cases, photographs were taken of each individual before collection to record colour
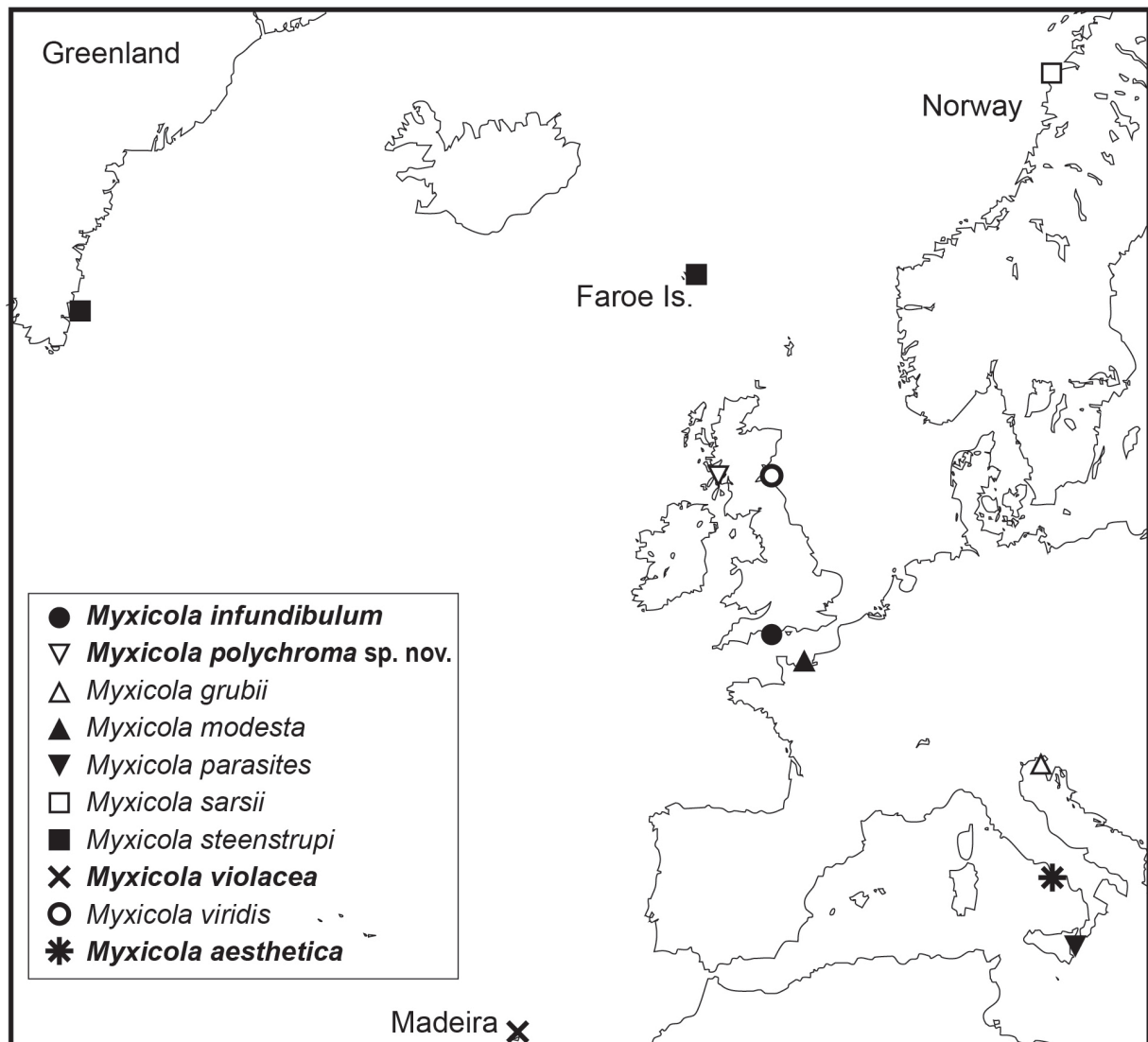

Fig. 2. Map showing the type localities of both valid (bold type) and invalid species of *Myxicola* in Europe.

and appearance while alive. Subtidal collection was undertaken by diver, using a standard garden trowel. The animal and tube retrieved were placed into a pre-labelled, sealable bag and a photo was taken of the bag and specimen to record the label as well as the diver's diving computer, so as to match up the specimen with the correct photographs and locality details post-fixation. Intertidal collections were made at low water using a garden fork. In most cases, the tubes were also retained. Animals that were incomplete following collection, as well as some whole animals, had a small piece of tissue, or a radiole, removed and placed in 100% ethanol, and then the remainder of the animal was fixed immediately in 4% formaldehyde or 4% dekafald (DMDM Hydantoin). Animals retrieved whole by the author were relaxed using 7% magnesium chloride before fixation as previously described. Further photographs were taken of some live animals in the laboratory. Fixed animals were washed in freshwater after 2–3 days and placed in 70–80% ethanol with 2% propylene glycol for long term preservation.

Divers around the UK were also asked to submit photographs of *Myxicola* seen during dives, at as high a resolution as possible, along with details of the locality in which they were taken. Details of crown colour, radiolar tip colour, number of radioles and surrounding sediment type were all possible to record from most photographs and locality data was used to draw up a distribution map of the different forms (Fig. 1).

Morphological examinations and measurements were made using a Nikon Eclipse E400 binocular microscope and a Nikon Labophot-2 compound microscope. Microscope photographs were compiled and stacked using a Leica Wild microscope and Helicon Focus™ software. Specimens used for scanning electron microscopy (SEM) were prepared using a Quorum K850 critical point drier and an Agar sputter coater AGB7341 with subsequent imaging undertaken on a JEOL Neoscope JCM-7000 benchtop SEM.

In the following descriptions, eyespots are described as either 'interramal' or 'lateral'. Interramal eyespots are thoracic and occur centrally on the posterior border of each notopodium. On the abdomen, lateral eyespots occur dorsal (to varying degrees on each segment) to the neuropodia.

The 'syntype' of *Myxicola infundibulum* was obtained from the Natural History Museum, London (NHMUK) for comparative observation along with the syntypes of *Myxicola steenstrupi* from the Natural History Museum of Denmark (NHMD). All specimens identified as *Myxicola* in the Amgueddfa Cymru-Museum Wales collections were analysed and newly collected specimens were accessioned into the same collections (NMW.Z). The holotype and paratypes of *Myxicola polychroma* sp. nov. are accessioned in the zoological collections of NMW.Z. Genetic information was provided by Museum Victoria and GenBank. Voucher specimens for the Museum Victoria sequences and one from the Australian Museum are registered under the respective acronyms F and AM (see Table 1).

Institutional acronyms

AM   =   Australian Museum
F   =   Museum Victoria
NHMD   =   Natural History Museum of Denmark
NHMUK =   Natural History Museum, London
NMW.Z   =   Amgueddfa Cymru-Museum Wales

DNA extraction and sequencing

Universal cytochrome oxidase subunit I (COI) primers (Folmer *et al.* 1994) were used to amplify a 625 bp region of the COI 'barcoding' gene of 16 *Myxicola* specimens (9 *Myxicola infundibulum* and 7 *Myxicola polychroma* sp. nov.). In addition to COI, an approx. 475 bp region of the 16S large subunit mitochondrial ribosomal DNA was also sequenced for the same specimens using the Palumbi (1996) primers 16SarL and 16SbrH.

Table 1 (continued on next page). Taxa used for sequencing in the present study with associated voucher and GenBank accession numbers where available. Colour morphs of specimens, if known, are detailed in brackets after the name in each case.

Species	Voucher	Locality	Accession number / Source	
			16S	**COI**
Nereididae				
Gymnonereis tenera Darbyshire, 2014	NMW.Z.2011.039	–	–	ǂ
Sabellariidae				
Sabellaria spinulosa (Leuckart, 1849)	NMW.Z.2010.039.10	–	ǂ	ǂ
Sabellaria alveolata (Linnaeus, 1767)	NMW.Z.2010.006.1	–	ǂ	–
Fabriciidae				
Fabrisabella vasculosa Hartman, 1969	–	GenBank	HM800969	–
Sabellidae				
Myxicola aesthetica (Claparède, 1870)	–	GenBank (Canada)	–	HQ932577
Myxicola aesthetica (Claparède, 1870)	–	GenBank (Canada)	–	HQ932482
Myxicola aesthetica (Claparède, 1870)	–	GenBank (Canada)	–	HQ932495
Myxicola aesthetica (Claparède, 1870)	–	GenBank (Canada)	–	HQ932483
Myxicola infundibulum (white)	NMW.Z.2019.023.1	Saltstone, Kingsbridge estuary, Eng.	OQ343676	OQ341617
Myxicola infundibulum (white)	NMW.Z.2019.023.2	Saltstone, Kingsbridge estuary, Eng.	OQ343674	OQ341615
Myxicola infundibulum (white)	NMW.Z.2019.023.3	Saltstone, Kingsbridge estuary, Eng.	OQ343675	OQ341616
Myxicola infundibulum (white)	NMW.Z.2019.023.4	Saltstone, Kingsbridge estuary, Eng.	OQ343673	OQ341614
Myxicola infundibulum (white)	NMW.Z.2019.023.5	Gann Flats, Wales	OQ343670	OQ341611
Myxicola infundibulum (white)	NMW.Z.2019.023.6	Gann Flats, Wales	OQ343671	OQ341612
Myxicola infundibulum (white)	NMW.Z.2019.023.7	Gann Flats, Wales	OQ343672	OQ341613
Myxicola infundibulum (pink)	NMW.Z.2019.023.13	Portland Harbour, England	OQ343677	OQ341618
Myxicola infundibulum (red)	NMW.Z.2019.023.14	Portland Harbour, England	OQ343678	OQ341619
Myxicola infundibulum	F111030	Maine, USA	*	*
Myxicola infundibulum	F111031	Maine, USA	*	*
Myxicola infundibulum	F111032	Maine, USA	*	*
Myxicola infundibulum	F111033	Maine, USA	*	*
Myxicola infundibulum	F107007	Port Arlington, Australia	*	–
Myxicola infundibulum	F107009	Port Arlington, Australia	*	*
Myxicola infundibulum	F107012	Port Arlington, Australia	*	–
Myxicola infundibulum	F107014	Port Arlington, Australia	*	–
Myxicola infundibulum	F107015	Port Arlington, Australia	*	*
Myxicola infundibulum	F107020	Rye, Australia	*	*
Myxicola infundibulum	F107021	Rye, Australia	*	–
Myxicola infundibulum	F107022	Rye, Australia	*	–
Myxicola infundibulum	F107023	Rye, Australia	*	*
Myxicola infundibulum	F107024_L3	St Leonards, Australia	–	*
Myxicola infundibulum	–	Adelaide, Australia	*	*
Myxicola infundibulum	F107027	Croatia, Adriatic	*	–
Myxicola infundibulum	–	GenBank (Canada)	–	HQ024104
Myxicola infundibulum	–	GenBank (Canada)	–	HQ024105
Myxicola infundibulum	–	GenBank (Canada)	–	HQ024106
Myxicola infundibulum	–	GenBank (Canada)	–	HQ024107

[a] Capa et al. 2011; [b] Rousset et al. 2007; [c] Lobo et al. 2016; * Unpublished thesis Dane 2008; ǂ Unpublished sequence from author's collection.

Table 1 (continued). Taxa used for sequencing in the present study with associated voucher and GenBank accession numbers where available. Colour morphs of specimens, if known, are detailed in brackets after the name in each case.

Species	Voucher	Locality	Accession number / Source	
			16S	**COI**
Sabellidae				
Myxicola polychroma sp. nov. (orange)	NMW.Z.2019.023.17	Loch Sunart, Scotland	OQ343682	OQ341622
Myxicola polychroma sp. nov.	NMW.Z.2019.023.18	Loch Sunart, Scotland	OQ343684	OQ341623
Myxicola polychroma sp. nov. (white)	NMW.Z.2019.023.20	Loch Duich, Scotland	OQ343679	OQ341620
Myxicola polychroma sp. nov. (green)	NMW.Z.2019.023.21	Loch Duich, Scotland	OQ343680	OQ341621
Myxicola polychroma sp. nov. (white)	NMW.Z.2019.023.23	Martins Haven, Wales	OQ343683	OQ341624
Myxicola polychroma sp. nov. (white)	NMW.Z.2019.023.24	Martins Haven, Wales	OQ343685	OQ341625
Myxicola polychroma sp. nov. (orange)	NMW.Z.2019.023.25	Martins Haven, Wales	OQ343681	OQ341626
Myxicola sp.	AM W30503	Australia	HM800977[a]	–
Myxicola sp.	–	Washington, USA	–	MH242858
Myxicola sp.	–	Washington, USA	–	MH242857
Myxicola sp.	–	Alaska, USA	–	MF121539
Myxicola sp.	–	GenBank (BC, Canada)	–	HM473472
Myxicola sp.	–	GenBank (BC, Canada)	–	HM473471
Sabella pavonina Savigny, 1822	–	GenBank	AY340482[b]	KR916924[c]
Spionidae				
Spiophanes kroyeri Grube, 1860	NMW.Z.2008.059.197	–	‡	–

[a] Capa et al. 2011; [b] Rousset et al. 2007; [c] Lobo et al. 2016; * Unpublished thesis Dane 2008; ‡ Unpublished sequence from author's collection.

For both genes, DNA was extracted using a Bioline Isolate II genomic DNA kit. One µl of extract was used as a template in PCRs using GE Healthcare Illustra PuReTaq PCR beads with 0.25 µl of each primer (10 µM). Each reaction was then made up to 25 µl using ultra-pure water. Cycling conditions (Bioer Little Genius thermal cycler) were as follows: 94°C for 150 s, 35 cycles of 94°C for 45 s, 51°C for 45 s, 72°C for 45 s and finally 72°C for 10 min. For COI, 1–3 µl of extract was used with 0.25 µl of each primer (10 µM). For COI, PCR reactions were undertaken using the same PCR beads and thermal cycler as for 16S and using the following program: 95°C for 120 s, 35 cycles of 95°C for 40 s, 45°C for 45 s and 72°C for 90 s, and finally 72°C for 7 min. All PCR products were cleaned using a Sigma Aldrich GenElute PCR clean up kit, quantified on agarose gels and sequenced by the Medical Sciences Institute, Dundee University. Sequences were edited and compiled in ApE ver. 2.0.38 and all identified haplotypes were submitted to GenBank (Table 1). Edited and aligned sequences were 625 bp and 475 bp in length for COI and 16S respectively.

DNA datasets and analysis

For 16S only one additional sequence, from Australia, was available from GenBank for inclusion. Additional outgroup sequences from Sabellidae were downloaded from GenBank and included along with further sequences from the author's datasets (Table 1). For COI, sequences for *Myxicola aesthetica* (Claparède, 1870)*, M.* 'infundibulum' and *Myxicola* sp. were all obtained from GenBank along with additional outgroup sequences for other Sabellidae and some non-Sabellidae from the author's datasets (Table 1). Sequences of both 16S and COI, from *Myxicola* collected in Australia, Europe and USA, from Dane (2008), were also kindly provided for use by Robin Wilson from Museum Victoria.

Inter- and intraspecific distances (p-distances and K2P distances) were calculated for each population. For the phylogenetic analyses, sequences were aligned by CLUSTALW in MEGA X (Kumar *et al.* 2018) using the default parameters and uncorrected pairwise differences (p-distances) were calculated. Maximum parsimony (MP) analysis with tree-bisection-reconnection search was carried out in MEGA X with clade support assessed via bootstrap values (1000 replicates). Maximum likelihood (ML) analyses were carried out using MEGA X. Bootstrap values were calculated from 1000 replicates to provide a measure of clade support. Bayesian Inference (BI) was conducted using MrBayes ver. 3.2 (Ronquist *et al.* 2012). FindModel ver. 2 (www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html; Posada & Crandall 1998) was used to estimate the appropriate model of sequence evolution in each case (16S: GTR+Γ ; COI: Tamura-Nei+Γ). Two parallel runs of 1 000 000 generations, sampling trees every 1000 generations with the first 25% of trees discarded as burn-in, were implemented for both datasets. Convergence was reached for both analyses before the burn-in period. The majority-rule consensus tree with posterior probabilities was determined from 751 trees.

Results

Taxonomy

<div align="center">

Class Polychaeta Grube, 1850
Order Sabellida Levinsen, 1883
Family Sabellidae Latreille, 1825

Genus **Myxicola** Koch in Renier, 1847

</div>

Type species

Amphitrite infundibulum Montagu, 1808.

Diagnosis (modified from Capa *et al.* 2019)

Medium- to large-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent; radiolar eyes *present or absent*. Dorsal lips with radiolar appendages, pinnular appendages absent; ventral radiolar appendages *present or absent*, ventral lips developed, extending dorso-ventrally along inner surface of base of radiolar lobes; parallel lamellae and ventral sacs absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar absent. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with up to eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 present. Ventral shields absent. Interramal eyespots may be present. Thoracic notochaetae and abdominal neurochaetae in irregular bundles, arranged in low, circular tori, groups within fascicles not differentiated. Thoracic uncini acicular, with similarly sized teeth above main fang on transverse rows, hood absent, long handle; neuropodial companion chaetae absent. Abdominal notopodial tori forming almost complete cinctures around body (feature unique among sabellids); uncini avicular, handle absent, breast developed and several rows of shorter teeth above main fang. Abdominal neurochaetae elongate, narrowly hooded. Pygidial eyespots *present or absent*. Pygidial cirrus absent.

<div align="center">

Myxicola infundibulum (Montagu, 1808)
Figs 1–6, 11, Table 1

</div>

Terebella buccina [Renier, 1804a]: 19.
Sabella gelatinosa [Renier, 1804b]: xiii.
Terebella infundibulum [Renier, 1804b]: 13.
Tuba divisa [Renier, 1807]: tab. vi.

Amphitrite infundibulum Montagu, 1808: 109–110, pl. viii.
Sabella villosa Cuvier, 1830: 192.
Myxicola villosa Koch in Renier, 1847: 52.
Eriographis borealis Grube, 1850: 88, 140.
Leiobranchus modestus Quatrefages, 1850: 371.
Amphitrite floscula Dalyell, 1853: 245, pl. xxxi fig. 9.
Myxicola grubii Krøyer, 1856: 9.
Myxicola sarsii Krøyer, 1856: 9.
Myxicola steenstrupi Krøyer, 1856: 35–36.
Myxicola parasites Quatrefages, 1866: 480.
Myxicola platychaeta Marenzeller, 1884: 213–214, pl. iii fig. 6.
Sabella viridis McIntosh, 1874: 206.
Myxicola pacifica Johnson, 1901: 431–432, pl. 19 figs 193–198.
Myxicola affinis Bush, 1905: 218, pl. xxxviii figs 17–20.
Myxicola conjuncta Bush, 1905: 217–218, pl. xxvi figs 1, 4, pl. xxxviii figs 1–11.
Myxicola michaelseni Augener, 1918: 589–593, pl. vii figs 263–264, textfig. cv.
Myxicola monacis Chamberlin, 1919: 20.

Sabella infundibulum – Delle Chiaje 1841: 72, fig. 5.
Tuba infundibulum – Renier 1847: pl. 9 figs 1–22.
Terebella infundibulum – Renier 1847: 51–54, figs 1–2.
Myxicola infundibulum – Grube 1855: 122. — Claparède 1870: 141, pl. xiv fig. 2. — de Saint-Joseph 1898: 433, pl. xxiii figs 241–247. — Soulier 1902: 20–25, fig. 5. — Rioja 1917: 71.
Arippasa infundibulum – Johnston 1865: 252, 346.
Myxicola modesta – Quatrefages 1866: 480.
Mixicola infundibulum – Panceri 1875: 533. — Cosmovici 1880: 325, pl. xxvii fig. 1.
Leptochone parasites – Langerhans 1884: 272–273.
Myxicola steenstrupi – Cunningham & Ramage 1888: 672. — Bidenkap 1894: 137. — Hofsommer 1913: 348, pl. i figs 23–24. — Eliason 1920: 79.
Myxicola viridis – McIntosh 1923: 319, pl. cxvi fig. 1, pl. cxxi fig. 4, pl. cxxx fig. 6.

Material examined

Neotype
ENGLAND • Kingsbridge estuary, Saltstone; 50.2540° N, 3.7588° W; low shore; 1 Oct. 2019; T. Darbyshire leg.; mud; GenBank: OQ343676 (16S), OQ341617 (COI); NMW.Z.2019.023.0001.

Topotypes
ENGLAND • 3 spec.; same collection data as for neotype; GenBank: OQ343673–5 (16S), OQ341614–6 (COI); NMW.Z.2019.023.0002–0004.

Other material
WALES – **Pembrokeshire** • 4 specs; Gann Flats; 51.7124° N, 5.1661° W; low shore; 27 Nov. 2019; T. Darbyshire leg.; muddy sand; GenBank: OQ343670–2 (16S), OQ341611–3 (COI); NMW.Z.2019.023.0005 to 0008 • 7 specs; same collection data as for preceding; NMW.Z.2019.023.0009 to 0012 • 1 spec.; Milford Haven; 51.6861° N, 4.9769° W; depth 9.9 m; 15 Oct. 1996; S.J. May leg.; medium silt; NMW.Z.2011.045.0037 • 7 specs; Gann Flats; 51.7124° N, 5.1661° W; low shore; P. Knight-Jones leg.; muddy sand; NMW.Z.2009.038.0671.

ENGLAND – **Dorset** • 2 specs; Portland Harbour; 50.5817° N, 2.4663° W; depth 1.9 m; 29 Jul. 2019; T. Darbyshire leg.; sandy mud; GenBank: OQ343677–8 (16S), OQ341618–9 (COI);

NMW.Z.2019.023.0013 to 0014 • 1 spec.; Kingsbridge estuary; 50.2540° N, 3.7588° W; low shore; mud; NHMUK1980.390 – **Cornwall** • 2 specs; Helford estuary; 50.0983° N, 5.1178° W; depth 9 m; 16 Sep. 2012; T. Darbyshire leg.; maerl; NMW.Z.2012.058.0065 to 0066 • 3 specs; St Anthony; low shore; P. Knight-Jones; mud and sand; NMW.Z.2009.038.0675.

IRELAND – **County Galway** • 2 specs; Ballynakill Harbour, Fahy Bay; 53.5604° N, 10.0157° W; low shore; 21 Mar. 1988; A.S.Y. Mackie leg.; muddy gravel; NMW.Z.1988.069.

Description

Neotype complete with 123 chaetigers, 8 thoracic and 115 abdominal; body length 58 mm, crown length 20 mm. Topotypes with 130–149 chaetigers, body length 58–65 mm, crown length 19–22 mm. Preserved colour pale brown over body, darker on chaetigers 1–10 except around parapodia. Dark brown pigmentation present on basal ¼ of radiolar crown, internal side of ventral lobe, radiolar appendages and on radiolar tips, cream elsewhere. Colour when alive with pale orange-brown body, white, pink or purple radioles and dark brown radiolar tips (Fig. 3A–E). Body flattened dorso-ventrally, widest around chaetiger 4, then tapering posteriorly to a blunt pygidium (Fig. 3D).

Radiolar crown with semicircular radiolar lobes bearing 26 pairs of radioles (Fig. 4A, B). Radioles connected by basal membrane along ⅘ of their length (measured from base to lower margin of membrane between radioles) with broad radiolar flanges (Fig. 4C); with long tapered tips (measured from end of pinnulae to tip of radiole), ⅓ of the total radiole length. Dark brown pigmentation occurs over last ¼ of radiole, from just below start of radiolar tip, spreading outward to where basal membrane connects to rachis, then continuing to tip, creating a lanceolate appearance (Figs 3–E, 4A–C, E, 6A); radiolar tip triangular, elongating evenly to tip (Fig. 4E). Radioles supported by two rows of vacuolated cells (Fig. 6B); radiolar eyes absent. Pinnulae slender, with blunt ends in basal region, becoming finer, tapered and
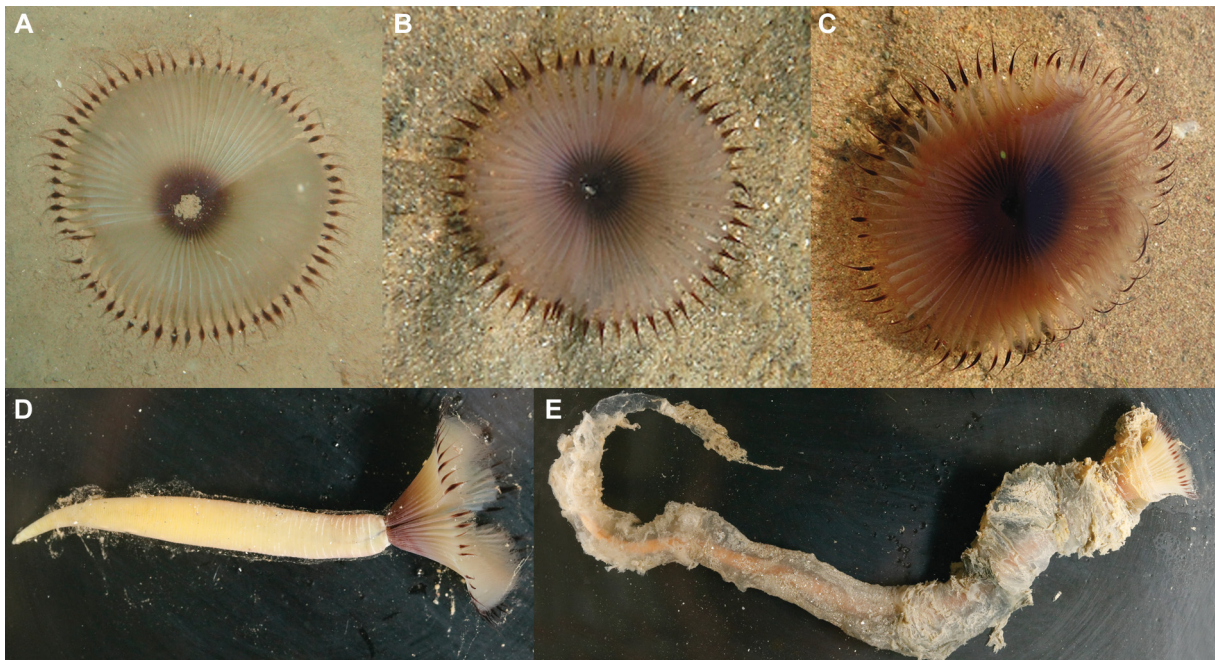

Fig. 3. Images of live *Myxicola infundibulum* (Montagu, 1808) demonstrating different colour morphs. **A**. White crown, Portland Harbour, England. **B**. Pink crown, Portland Harbour, England. **C**. Red crown, Gann Flats, Wales. **D**. Cream-yellow body, Kingsbridge estuary, England. **E**. Orange body, Kingsbridge estuary, England.

longest in distal part of radiole (Fig. 4A), 0.25 × total length of radiole, then rapidly decreasing in length to start of radiolar tip; pinnulae terminate at or just above lower margin of basal membrane.

Dorsal lips with fleshy, large, triangular radiolar appendages, oriented transversely and arising from ventral internal border of ventral lips; surrounded by enlarged ventral lips connected to radiolar lobes dorsally (Figs 4D, 6C); pinnular appendages absent; ventral radiolar appendages absent; parallel lamellae and ventral sacs both absent.
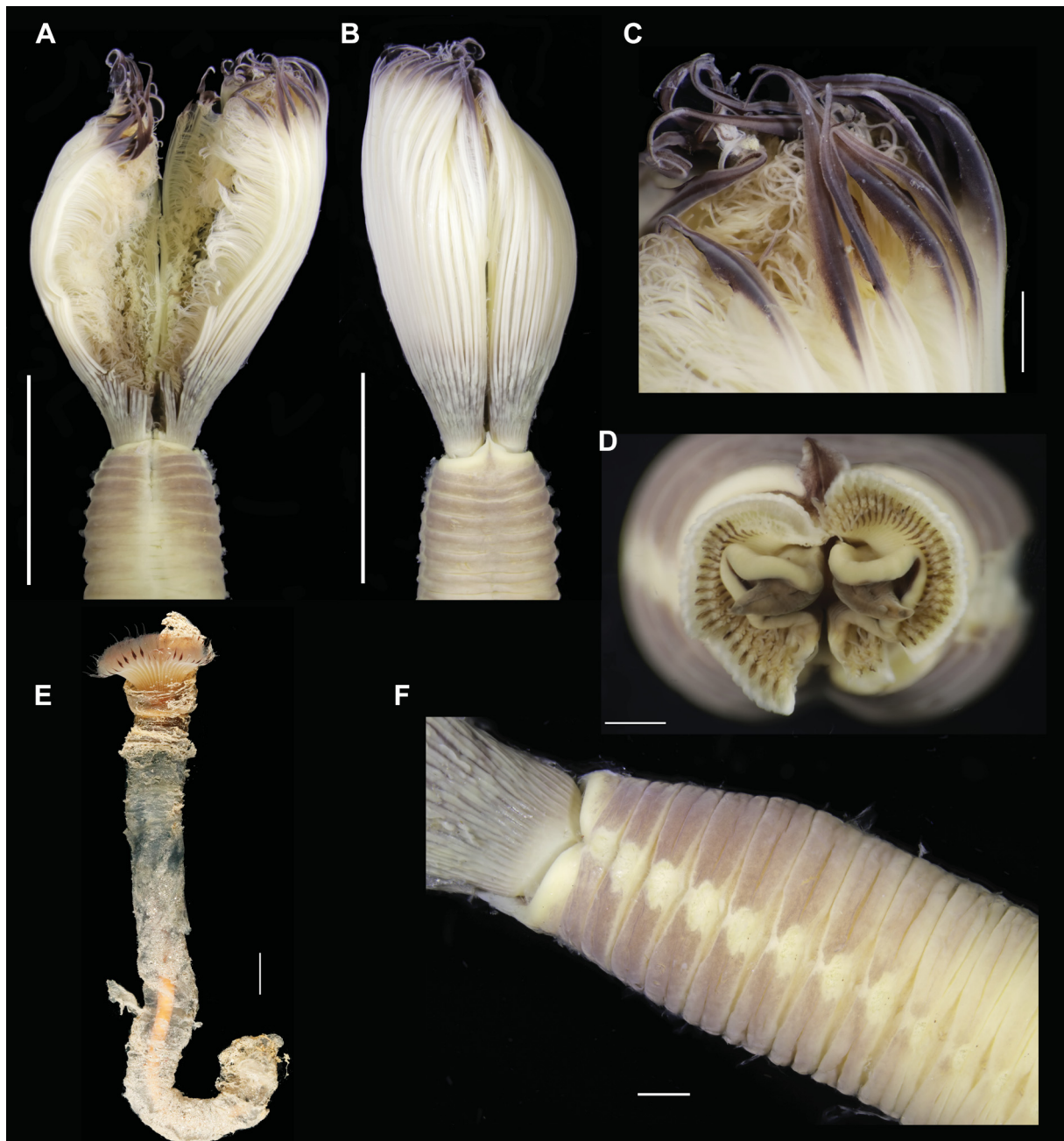
Fig. 4. *Myxicola infundibulum* (Montagu, 1808). **A–D**. Neotype (NMW.Z.2019.023.0001). **A**. Antero-dorsal view. **B**. Anteroventral view. **C**. Radiolar tips. **D**. Dorsal and ventral lips, anterior view. **E**. NMW.Z.2019.023.0003. Live specimen in tube, entire. **F**. Neotype (NMW.Z.2019.023.0001). Anterolateral view. Scale bars: A–B, E–F = 10 mm; C–D = 1 mm.

Posterior peristomial ring collar absent. Anterior peristomial ring with ventral, triangular lobe, high with concave indentation (Fig. 4B). Lateral notches present, deep, impacting chaetiger 1 (Fig. 4F). Glandular girdle present, toward posterior boundary of chaetiger 2 (Figs 3D, 4A–C). Ventral shields inconspicuous. Interramal eyespots present, one or two, from chaetiger 3 to chaetiger 8; lateral eyespots present in abdominal region to end of body, minute, 1–2 per segment (Fig. 4F).

First notopodia as oval cushions with dense, fine, narrow-hooded notochaetae (Fig. 5A), up to 150. Second notopodia twice the size of the first, then reducing in size gradually along thorax (Fig. 4F); notochaetae
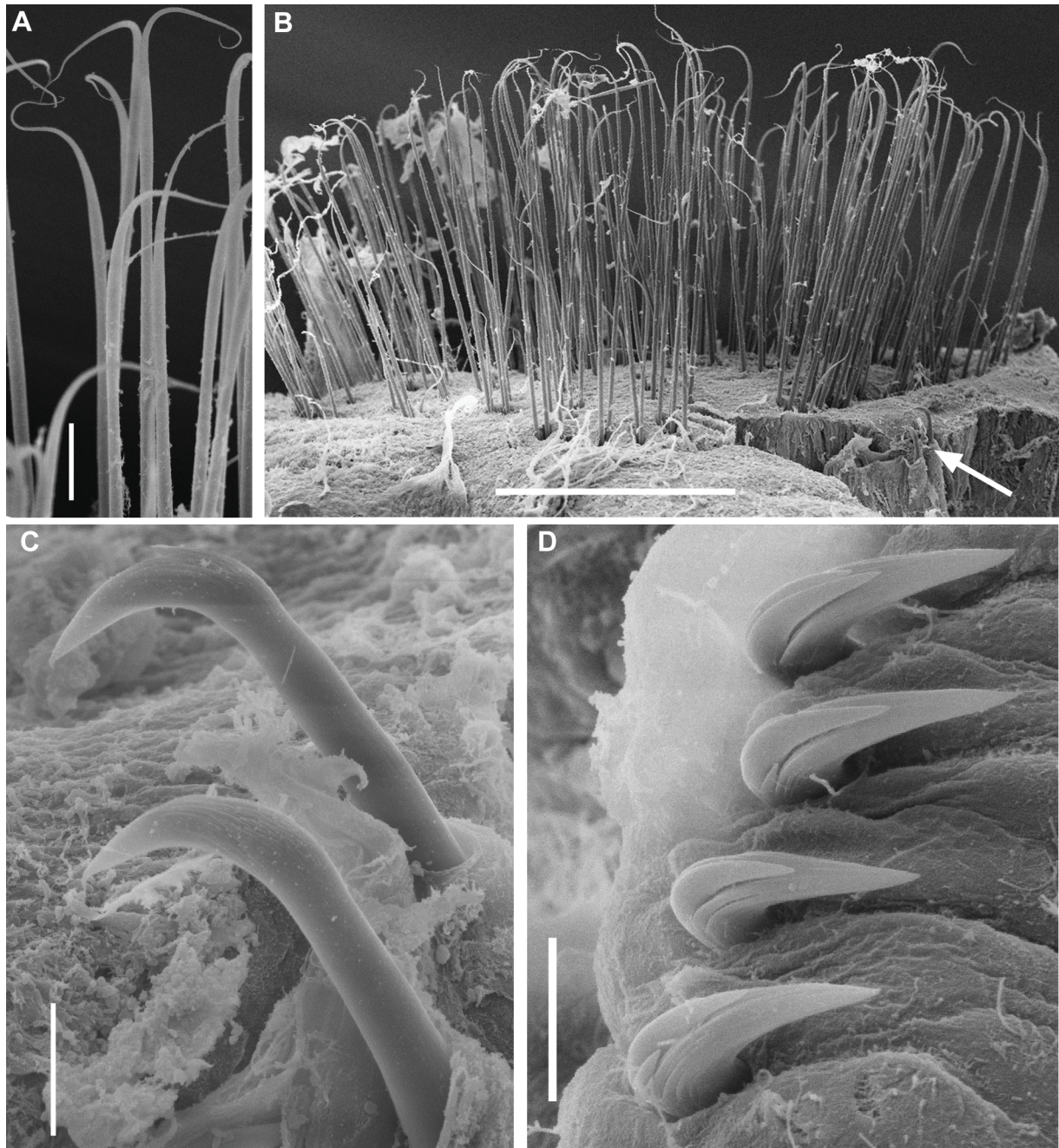

Fig. 5. *Myxicola infundibulum* (Montagu, 1808), NMW.Z.2019.023.0002. **A**. Thoracic chaetae, chaetiger 1. **B**. Thoracic chaetae, chaetiger 4, white arrow indicates thoracic uncini. **C**. Thoracic uncini, chaetiger 4. **D**. Abdominal uncini, chaetiger 9. Scale bars: A = 200 µm; B = 20 µm; C–D = 10 µm.

of same form as on first notopodium (Figs 5B, 6D), 150–200 per fascicle. Thoracic neurochaetae acicular uncini with long handles, mostly non-emergent; long elongate fang, not greatly hooked, with several minute teeth above and a slight constriction at top of shaft (Figs 5C, 6E). Companion chaetae absent. Neuropodia small, oval with narrow-hooded neurochaetae. Abdominal notopodial tori forming almost complete cinctures around body, with avicular uncini with 1–2 large teeth and 1–3 smaller teeth over main fang; upper teeth 0.5–0.65 × length of main fang (Figs 5D, 6F); breast rounded, equal to or slightly longer than main fang, handle absent (Fig. 6F).

Pygidium rounded, eyespots present in a transverse line across tip. Pygidial cirrus absent. Tube semi-transparent, gelatinous, with light covering of fine sand grains, some pale brown colouration toward proximal end (Figs 3E, 4E).

Methyl green staining pattern
Peristomial ring and ventral lobe with solid staining followed by complete rings on the posterior border of each segment.

Variation
Radiolar pinnulae 0.13–0.25 × total length of radioles. Interramal eyespots present on thorax from chaetiger 3 or 4; lateral eyespots present or absent on abdomen for a variable number of chaetigers, minute and easily missed. Pygidial eyespots present or absent (usually present). Data from photos submitted by divers or taken by the author, along with the examination of museum specimens confirmed as *M. infundibulum*, show a range in the number of radioles from 13 to 37 pairs. The tube has a slightly firmer feel to it than that of *M. polychroma* sp. nov., which is softer.

Remarks
Myxicola infundibulum and *M. violacea* (Langerhans, 1884) (the latter described from Madeira) are the only current taxa in the genus described with dark coloured tips to the radioles of the crown. Records of *M. infundibulum* are only verified here (through genetics and morphology) for the UK, Adriatic and Australia although darkly-tipped *Myxicola* are reported from elsewhere in the Mediterranean (see Discussion). *Myxicola violacea* is only recorded from Madeira and no other records of the species have been found. Langerhans' description and figures bear strong resemblance to those of *M. infundibulum*, particular those of the radiole tip and thoracic chaetae (Langerhans 1884). However, Langerhans also described and figured two sets of peristomial eyes for *M. violacea*, as well as abdominal uncini that
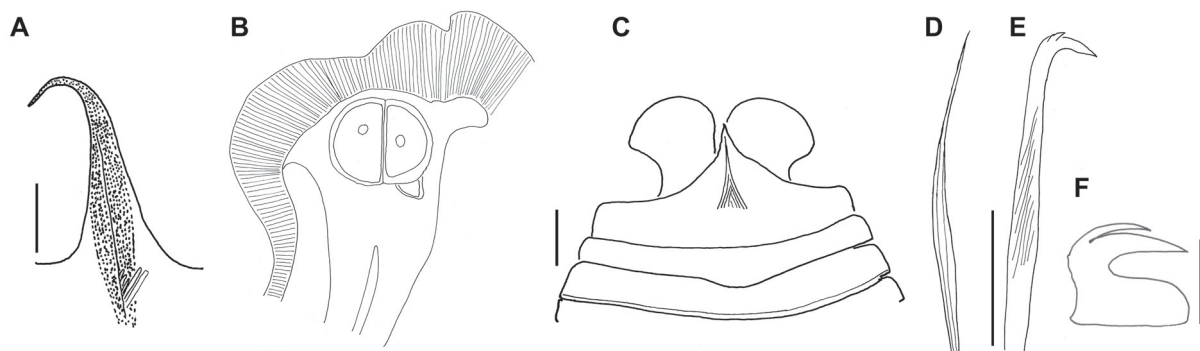

Fig. 6. *Myxicola infundibulum* (Montagu, 1808). **A–C**. Neotype (NMW.Z.2019.023.0001). **A**. Radiole tip illustrating basal membrane, pigmentation pattern and extent of pinnulae. **B**. Cross-section of radiole. **C**. Ventral and radiolar lobes, anteroventral view. **D–F**. NMW.Z.2019.023.0002. **D**. Thoracic chaeta, chaetiger 5. **E**. Thoracic uncinus, chaetiger 5. **F**. Abdominal uncinus, chaetiger 12. Scale bars: A, C = 1 mm; B = 100 μm; D–E = 50 μm; F = 20 μm.

are alternately large or small in each cincture; these features are not reflected in *M. infundibulum* as described here and are the main distinctions available between the two taxa at this time. It should be noted that Langerhans described his specimens as immature; all were small, no more than 15 mm in length or with no more than 11 pairs of radioles, and some radioles were not darkly-tipped, giving rise to the potential that Langerhans may have been looking at more than one species at the time as well as juveniles that might exhibit modified characters, although juvenile *M. infundibulum* observed during this study did not exhibit peristomial eyes or more than one type of uncinus and all had dark radiole tips. Type material for *M. violacea* was enquired of from museums in Germany but was not found, and so further investigation needs to be done to determine whether the taxa that exist around the island are, or include, true *M. infundibulum*. If they do, then *M. violacea* would become a junior synonym of *M. infundibulum*. For now, both names are retained until their relationship can be resolved and morphological characters confirmed.

The pigment present in the tips does not break down easily as in some taxa and can still be identified in specimens over 200 years old, as was evident in the specimens from NHMUK. The presence or absence of darkly pigmented radiole tips can therefore be used as a diagnostic character for this taxon, although other characters should be taken into account as well. Other pigment features such as the abdominal (lateral) eyespots and pygidial eyespots are not so consistent and are unreliable as characters. Thoracic (interramal) eyespots were consistent in their presence across all body sizes.

In addition to the dark radiole tips, *Myxicola infundibulum* can be distinguished from all other current members of the genus using a range of other characters. *Myxicola aesthetica*, with which it overlaps in distribution, and *M. nana* Capa & Murray, 2015 (described from Australia) are both smaller, with fewer thoracic chaetigers (*M. infundibulum*: 8; *M. aesthetica*: 3–4; *M. nana*: 6) and fewer pairs of radioles (*M. infundibulum*: 13–33; *M. aesthetica*: 7–10; *M. nana*: 6). Around the UK, *M. infundibulum* is distinct from the newly described *M. polychroma* sp. nov. by the radiolar pinnulae which, in *M. infundibulum*, are 0.13–0.25 × the length of the radiole and terminate around the lower margin of the basal membrane, whereas in *M. polychroma* sp. nov. pinnulae are 0.22–0.3 × the length of the radiole, at their longest, and terminate below the lower margin of the basal membrane. Additionally, the dorsal lips of *M. infundibulum* are oriented transversely and arise from the ventral internal border of the ventral lips, whereas in *M. polychroma* sp. nov. the dorsal lips are oriented dorsal-ventral and arise centrally. Finally, the abdominal uncini in *M. infundibulum* have a rounded breast, whereas those of *M. polychroma* sp. nov. show a more angled profile. Of the remaining larger species, which are more geographically removed, *M. sulcata* Ehlers, 1912 (Antarctica) has only 10–20 thoracic chaetae, on inconspicuous notopodia, on each segment (Tovar-Hernández *et al.* 2017), in comparison to over 100 for *M. infundibulum* on large notopodial pads, *M. ommatophora* Grube, 1878 (Philippines) has a clay tube (not gelatinous) and paired subdistal radiolar eyes (absent in *M. infundibulum*), and *M. fauveli* Potts, 1928 (Suez Canal) has only around 12 pairs of radioles and a sharply delineated filiform radiolar tip (triangular tip, not sharply delineated in *M. infundibulum*).

Distribution

Present on the west and southwest coasts of the UK only as far north as southern Scotland and the south and west coasts of Ireland; also Adriatic Sea (Croatia) and Australia, confirmed through genetic sequencing. All records from the UK and Ireland of 'black-tipped' *Myxicola* are attributed to *M. infundibulum*. Records of 'black-tipped' *Myxicola* also exist from Penpoull (Brittany, France; De Saint-Joseph 1894) and additional locations in the Mediterranean (Grube 1850; Claparède 1869; Soulier 1902) but need confirmation as to whether they are *M. infundibulum* or another taxon that has dark radiole tips. All records of *Myxicola infundibulum* without black tips on the radioles should be re-evaluated and those with black tips but from outside the northeast Atlantic region should be considered suspect and re-evaluated according to the new description and genetic information available.

Ecology

From intertidal to shallow waters (15–20 m) in mud, muddy sand and muddy gravel.

Myxicola polychroma sp. nov.
urn:lsid:zoobank.org:act:ECEE8088-72FD-4C8F-9F4E-C579193E04A5
Figs 1–2, 7–11, Table 1

Myxicola sarsi – Knight-Jones *et al.* 2017: 226, fig. 6.21b.

Diagnosis

Body with 8 thoracic chaetigers and over 180 abdominal chaetigers; glandular ridge on chaetiger 2. Crown with 17–32 pairs of orange, green or white radioles with non-differentially-coloured tips; pinnulae long, fine, terminating below the lower margin of the basal membrane, 0.22–0.3 × yhr total length of the radiole. Dorsal lips with large, fleshy triangular radiolar appendages. Thoracic notochaetae dense, fine, narrow-hooded, over 100 per notopodium; abdominal neurochaetae similar. Abdominal uncini form almost complete cincture around the body. Interramal eyespots present, lateral eyespots present or absent, pygidial eyespots present or absent. Tube very soft, gelatinous.

Etymology

As the generic name *Myxicola* is derived from Greek stems, the specific epithet is also taken from Greek rather than Latin; a noun in apposition derived from the Greek '*poly*' (= 'many') and '*chromos*' (= 'colour') referring to the three different colour variations, not just shades of a single colour, found within the species.

Material examined

Holotype
SCOTLAND • Loch Fyne; 56.2594° N, 4.9347° W; depth 12 m; 12 Nov. 2022; L. Baldock leg.; sandy mud; NMW.Z.2019.023.0015.

Paratypes
SCOTLAND – **Loch Fyne** • 1 spec.; same collection data as for holotype; NMW.Z.2019.023.0016. – **Loch Sunart** • 1 spec.; 56.6677° N, 5.8910° W; depth 26 m; 23 Oct. 2019; G. Brown leg.; mud; GenBank: OQ343682 (16S), OQ341622 (COI); NMW.Z.2019.023.0017 • 1 spec.; same collection data as for preceding; depth 22 m; L. Baldock leg.; mud; GenBank: OQ343684 (16S), OQ341623 (COI); NMW.Z.2019.023.0018 • 1 spec.; same collection data as for preceding; depth 24 m; 24 Oct. 2019; G. Brown leg.; NMW.Z.2019.023.0019.

WALES – **Pembrokeshire** • Martins Haven; 1 spec.; 51.7376° N, 5.2443° W; depth 14 m; 29 Jun. 2019; T. Darbyshire leg.; sandy mud; GenBank: OQ343683 (16S), OQ341624 (COI); NMW.Z.2019.023.0023 • 1 spec.; same collection data as for preceding; depth 12.7 m; GenBank: OQ343685 (16S), OQ341625 (COI); NMW.Z.2019.023.0024.

Other material
SCOTLAND – **Loch Duich** • 1 spec.; 57.2612° N, 5.5142° W; depth 20 m; 3 May 2019; C. Rickard leg.; GenBank: OQ343679 (16S), OQ341620 (COI); NMW.Z.2019.023.0020 •   1 spec.; same collection data as for preceding; depth 19.5 m; 14 Oct. 2019; sandy mud; GenBank: OQ343680 (16S), OQ341621 (COI); NMW.Z.2019.023.0021 • 1 spec.; same collection data as for preceding; 17 May 2019; NMW.Z.2019.023.0022. – **Shetland** • 2 specs; Sullom Voe; depth 24 m; 1985; fine

sand; NMW.Z.1986.112.0091 to 0092 • 1 spec.; near Sullom Voe; 31 m; Apr. 1984; medium sand; NMW.Z.1986.112.0486.

WALES – **Pembrokeshire** • 1 spec.; Martins Haven; 51.7376° N, 5.2443° W; depth 13.4 m; 29 Jun. 2019; T. Darbyshire leg.; sandy mud; GenBank: OQ343681 (16S), OQ341626 (COI); NMW.Z.2019.023.0025.

ISLE OF MAN – **Irish Sea** • 1 spec.; 7 mi. W of Sloc; 54.1294° N, 4.9156° W; depth 55 m; muddy sand and shell gravel; NMW.Z.2009.038.0678.

Description

Holotype complete with 104 chaetigers, 8 thoracic and 96 abdominal; body length 55 mm, crown length 22.7 mm. Paratypes with 86–191 chaetigers, body length 41–140 mm, crown length 19.7–31 mm. Preserved colour uniformly cream for both crown and body. Colour when alive, cream/pinkish body with white, orange or pale green radioles (Fig. 7A–E). Body flattened dorso-ventrally, widest around chaetiger 4–5 (Fig. 8A–B), then tapering posteriorly to a blunt pygidium (Fig. 7E).

Radiolar crown with semicircular radiolar lobes (Fig. 8A–B, D) bearing 29 pairs of radioles. Radioles connected by basal membrane along 85% of their length (Fig. 8C; measured from base to lower margin of connection between radioles); radioles with broad radiolar flanges and digitiform tips (Figs 8C, 10A; measured from end of pinnulae to tip of radiole), 18% of total radiole length. Radioles supported by two rows of vacuolated cells (Fig. 10B). Radiolar eyes absent. Pinnulae slender with blunt ends in basal region, becoming finer, tapered and longest in distal part of radiole, 0.24× total length of radiole, then rapidly decreasing in length, terminating below lower margin of basal membrane.

Dorsal lips with large, fleshy, triangular radiolar appendages, arising centrally and oriented dorsal-ventrally on a central line, surrounded by enlarged, lobate ventral lips connected to radiolar lobes
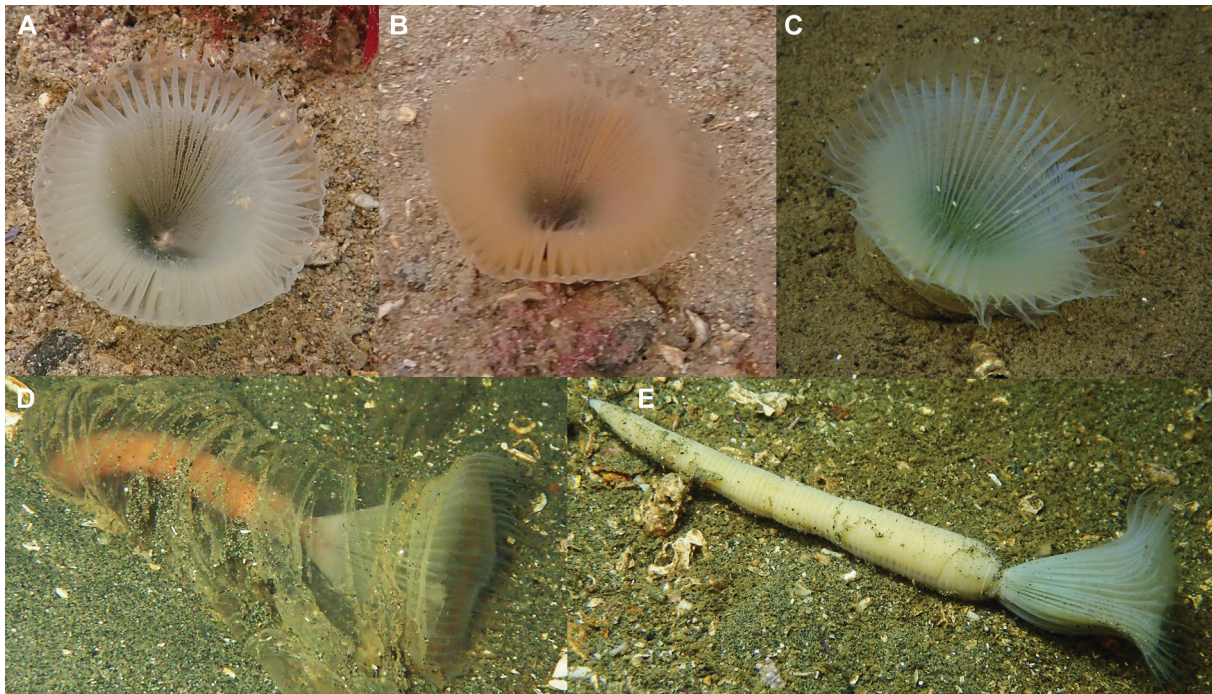

Fig. 7. Images of live *Myxicola polychroma* sp. nov. demonstrating different colour morphs. **A**. White crown, Martin's Haven, Wales. **B**. Orange crown, Martin's Haven, Wales. **C**. Green crown, Loch Duich, Scotland. **D**. Orange body, Loch Duich, Scotland. **E**. White-cream body, Loch Duich, Scotland. Photos courtesy of Rhian Lewis James (A–B) and Chris Rickard (C–E).

dorsally (Figs 8D, 10C–D); pinnular appendages absent; ventral radiolar appendages absent; parallel lamellae and ventral sacs both absent.

Posterior peristomial ring collar absent. Anterior peristomial ring with ventral triangular lobe, high with concave indentation (Fig. 7B). Lateral notches present, shallow, not impacting chaetiger 1 (Fig. 8E). Glandular girdle present, toward posterior boundary of chaetiger 2 (Fig. 8A, E). Ventral shields inconspicuous. Interramal eyespots present, one or two, minute, from chaetiger 3 or 4 to chaetiger 8, absent from abdominal region.

First notopodia as oval cushions with dense, fine, narrow-hooded notochaetae, up to 100. Second notopodia twice the size of the first, then reducing in size gradually down thorax; notochaetae of same
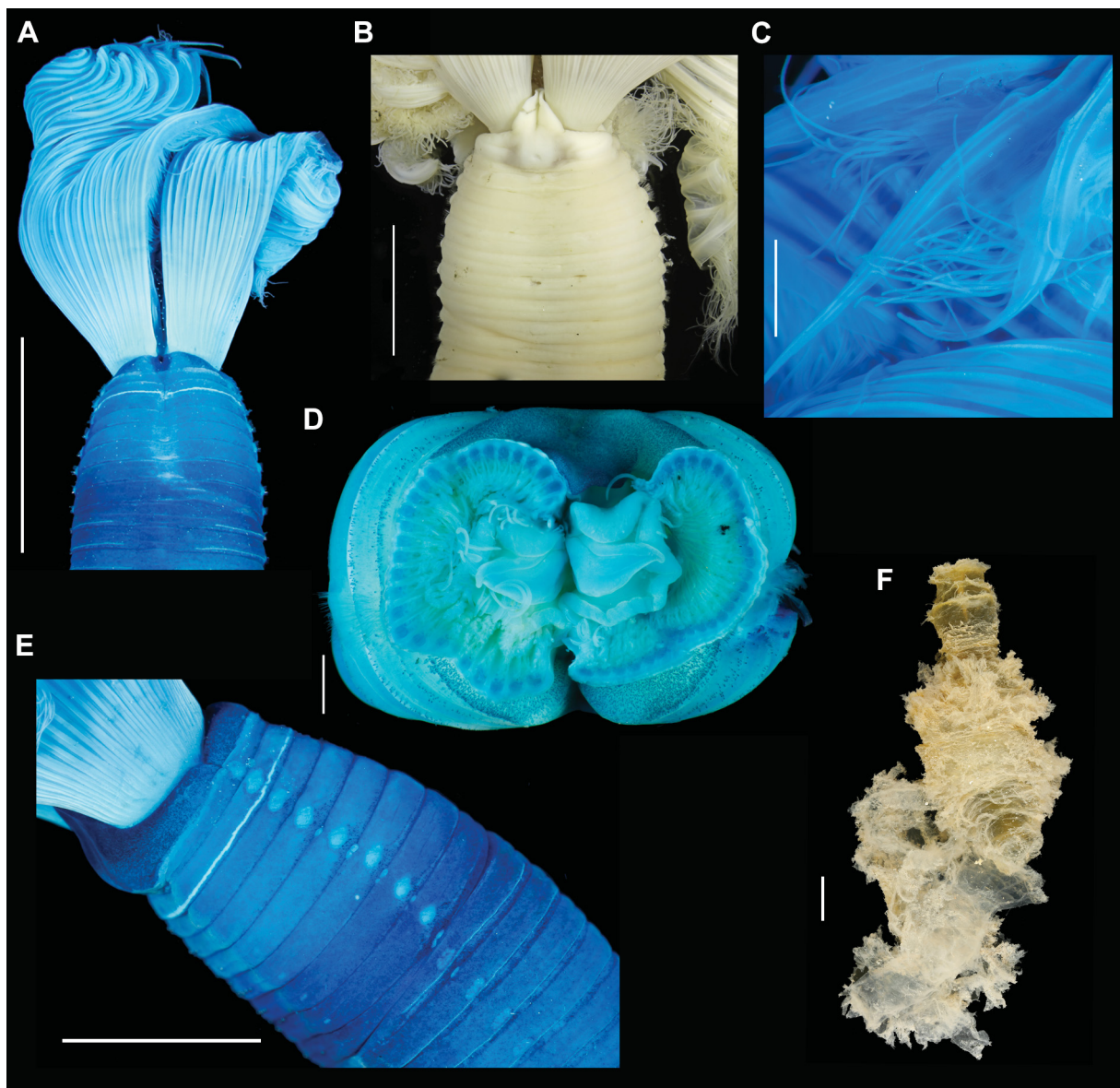

Fig. 8. *Myxicola polychroma* sp. nov. **A**. Anterodorsal view (NMW.Z.2019.023.0023). **B**. Anterodorsal view (holotype, NMW.Z.2019.023.0015). **C**. Radiolar tips (NMW.Z.2019.023.0024). **D**. Dorsal and ventral lips (NMW.Z.2019.023.0023). **E**. Anterolateral view (NMW.Z.2019.023.0023). **F**. Tube. Scale bars: A, F = 10 mm; B–C = 5 mm; D–E = 1 mm.

form as on first notopodium, 100–150 per fascicle (Fig. 8E, 9A, 10E). Thoracic neuropodia situated at posteroventral border of notopodia, with few (up to 5) acicular uncini with long handles, strongly hooked, with long main fang and no clear teeth above (Figs 9B, 10F). Companion chaetae absent. Abdominal neuropodia small, oval, with narrow-hooded neurochaetae (Fig. 9C). Abdominal notopodial tori forming almost complete cinctures around body, with avicular uncini with one large tooth and 0–4 smaller teeth, variable in size, over main fang; upper teeth 0.6–0.8× length of main fang (Figs 9D–E, 10G); breast well-developed, with angled profile, slightly longer than main fang, handle absent (Fig. 10G).

Pygidium rounded, eyespots not seen. Pygidial cirrus absent. Tube semi-transparent, gelatinous, with few fine sand grains attached, slight colouration toward proximal end (Fig. 8F).

Methyl green staining pattern
Peristomial ring and ventral lobe with solid staining (Fig. 8A, E) followed by complete rings on the posterior border of each segment.

Variation
Radiolar pinnulae 0.22–0.3× total length of radioles. Interramal eyespots present from chaetigers 3 or 4 and on rest of thorax; lateral eyespots absent or on first 1–4 segments of abdomen; the larger
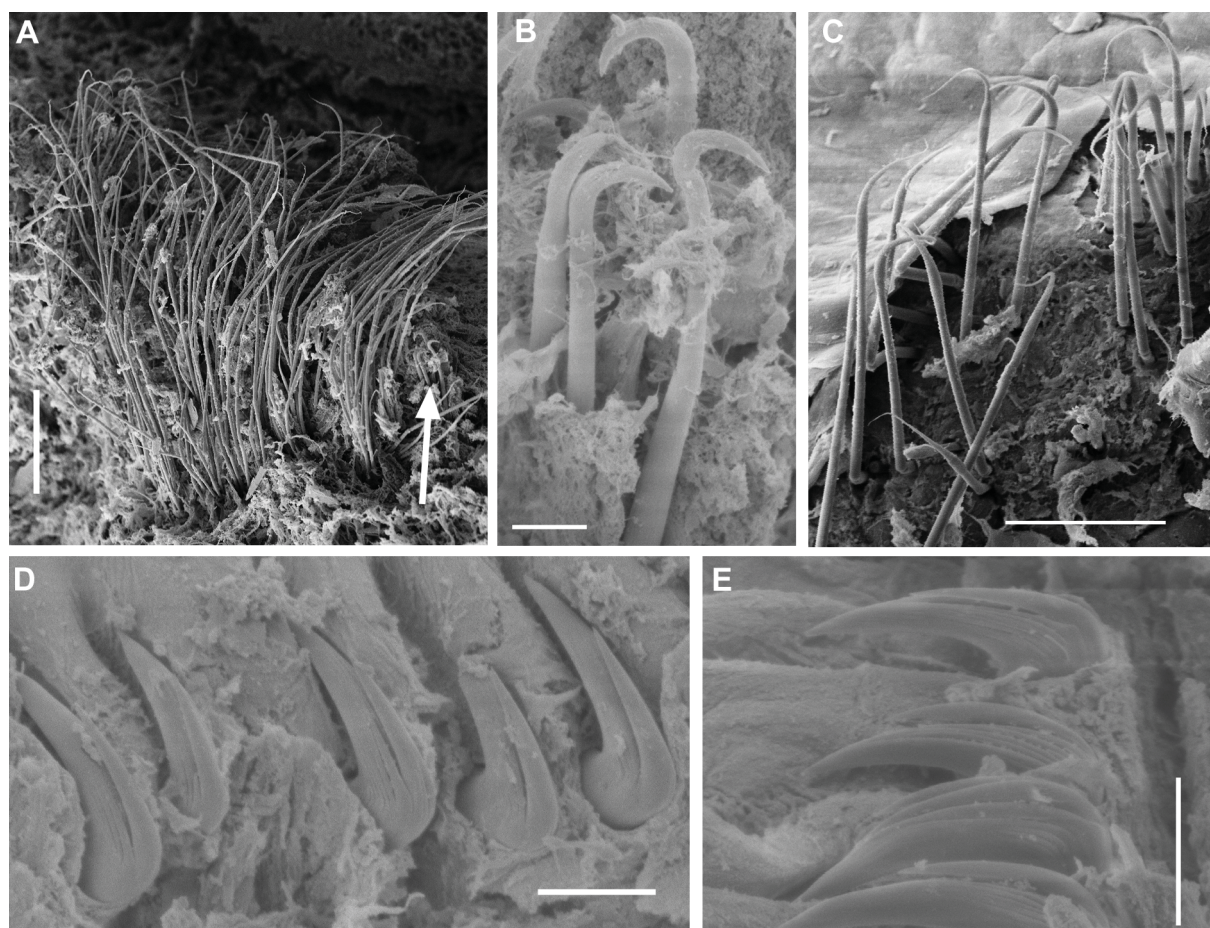

Fig. 9. *Myxicola polychroma* sp. nov., NMW.Z.2019.023.0024. **A**. Thoracic chaetae, chaetiger 4, white arrow indicates thoracic uncini. **B**. Thoracic uncini, chaetiger 4. **C**. Abdominal chaetae, chaetiger 11. **D**. Abdominal uncini, top view. **E**. Abdominal uncini, lateral view. Scale bars: A = 100 μm; B, D–E = 10 μm; C = 50 μm.

the animal the fewer the eyespots. Pygidium generally without eyespots although a row of 7 minute eyespots laterally on either side found on one small specimen. Radiole count 17–32 pairs, determined from a combination of divers' photos and collected specimens.

Remarks

Myxicola polychroma sp. nov. has been recorded around the UK for many years, although it has not been recognised as a separate species. Other names that have previously been recorded from British waters are *M. sarsii*, *M. steenstrupi* and *M. viridis*, all of which were synonymised with *M. infundibulum* many years ago. As it is likely that more species of *Myxicola* will be identified in the future, possibly with the re-validation of previously synonymised names, it is worth making distinctions here from those other, currently invalid, species described from European waters. The original description of *M. sarsii* does not provide any information on which to base a comparison; however, Sars (1862) provided more detail, finding a radiole count only ranging from 12 to 21 pairs, accounting for both juvenile and mature specimens (*Myxicola polychroma* sp. nov. has 17–32 pairs of radioles). *Myxicola steenstrupi*, as detailed later, is represented by type specimens that themselves appear to represent different taxa; however, the type from Greenland has slender, digitiform radiolar appendages (large, triangular radiolar appendages in *M. polychroma* sp. nov.) and the Faroe Island type has short radiolar tips and small, blunt radiolar appendages (*M. polychroma* sp. nov. has long radiolar tips and large, triangular radiolar appendages); all specimens of *M. steenstrupi* also possess only 12–21 pairs of radioles, as opposed to 17–32 pairs in *M. polychroma* sp. nov. *Myxicola grubii* was described with dark tips to the radioles (Krøyer 1856) and *M. viridis* with green banded radioles (McIntosh 1874), and so neither could be potential candidates for the identity of *M. polychroma* sp. nov. The remaining two (invalid) European species *M. modesta* and *M. parasites*, were both clearly very small specimens, with only 9 and 11 pairs of radioles described, respectively (Quatrefages 1866), and it is unknown whether they represented juvenile forms of larger taxa or not. If they were not juveniles, then the small body size and few radioles would distinguish them from *M. polychroma* sp. nov. immediately. In addition to the radioles though, *M. parasites* had only a short basal membrane, in comparison to the long membrane present in *M. polychroma* sp. nov., and *M. modesta* possessed no lateral or interramal eyes. Although it has been stated earlier in this paper that the presence or absence of lateral eyes is an unreliable character, interramal eyes are more consistent; both are always present in small specimens and it is only in larger and preserved specimens that lateral eyes become inconsistent or fade. Quatrefages' specimens were described live, so preservation was
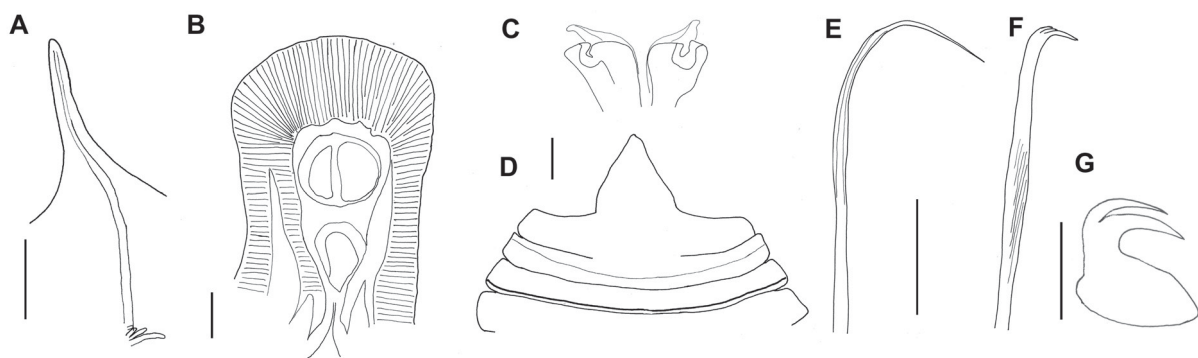

Fig. 10. *Myxicola polychroma* sp. nov. **A**. Radiole tip illustrating basal membrane and extent of pinnulae (NMW.Z.2019.023.0024). **B**. Cross-section of radiole (NMW.Z.2019.023.0018). **C–G**. NMW.Z.2019.023.0024. **C**. Dorsal lips, ventral lips and radiolar lobes. **D**. Anterodorsal view showing ventral lobe and glandular ridge. **E**. Thoracic chaeta, chaetiger 4. **F**. Thoracic uncinus, chaetiger 4. **G**. Abdominal uncinus, chaetiger 12. Scale bars: A, C–D = 1 mm; B = 100 µm; E–F = 50 µm; G = 20 µm.

not a factor, and either juvenile (so eyespots should be present if they were the same as *M. polychroma* sp. nov.) or a naturally small taxon, in which case they could also be discounted.

Myxicola polychroma sp. nov. is distinct from the other valid species of *Myxicola* in the UK, *M. infundibulum* and *Myxicola aesthetica*, by the lack of differential colour on the radiole tips (dark radiole tips in *M. infundibulum*) and by having 8 thoracic chaetigers and 17–32 pairs of radioles, as opposed to 3–4 thoracic chaetigers and 7–10 pairs of radioles in *M. aesthetica* (Soulier 1902). All other known species are far removed geographically, but can be distinguished through a variety of characters: *Myxicola violacea*, the only other European species, has dark tips to the radioles (*M. polychroma* sp. nov. has pale tips), *M. nana* has only 6 thoracic chaetigers (Capa & Murray 2015) (*M. polychroma* sp. nov. has 8), *M. ommatophora* has paired subdistal radiolar eyes and a clay tube (Grube 1878) (*M. polychroma* sp. nov. has no radiolar eyes and a gelatinous tube), *M. fauveli* has only 12 pairs of radioles with longitudinal green bands and sharply delineated filiform tips (Potts 1928) (*M. polychroma* sp. nov. has more than 12 pairs of radioles, without banding or sharply delineated tips) and *M. sulcata* also has only 12–17 pairs of radioles (Tovar-Hernández *et al.* 2017) and few, inconspicuous notochaetae (*M. polychroma* sp. nov. has more than 17 pairs of radioles and more than 100 fine but conspicuous notochaetae per notopodium).

Distribution

Found on the west and southwest coasts of the UK: west coast of Scotland, Isle of Man, west Wales and southwest England. A single record was received from the east coast of Scotland.

Ecology

Subtidal from 5–35 m (occasionally deeper) in sandy mud and muddy, soft sediments.

Myxicola steenstrupi Krøyer, 1856

Material examined

Syntypes
FAROE ISLANDS • 1 spec.; Tórshavn; NHMD 109911.

GREENLAND • 1 spec.; NHMD 109912.

Additional material
FAROE ISLANDS • 1 spec., 1 juv.; head of Kaldbakfjord; depth 1–2 m; P. Knight-Jones leg.; from abandoned *Mytilus* ropes; NMW.Z.2009.038.0673.

Description

Faroese specimens
Faroe Islands syntype complete, in 2 pieces, with 54 chaetigers, 7–8 thoracic (difficult to determine due to condition) and 46 abdominal; body length 26 mm, crown length 11 mm. Other specimens complete, with 46 and 50 chaetigers, of which 8 are thoracic; body lengths 12 and 31 mm, crown lengths 5 and 9 mm. Preserved colour cream (NMW.Z) or pale brown (syntype), no pigment observed. 1–2 minute interramal (thoracic) and lateral (abdominal) eyespots present on NMW.Z specimens only, as well as pygidial eyespots, pygidium tip missing on type.

Radiolar crown with semicircular radiolar lobes bearing 20 pairs of radioles (type) or 12 and 17 pairs, respectively, on juvenile and larger NMW.Z specimens. Connecting basal membrane long (damaged

between most radioles on type). All radiole tips damaged except on juvenile: very high basal membrane with free portion of tip less than 10% total length of radiole, tip tapering to a blunt point; pinnulae long, thin, ca 0.25 × total length of radiole, terminating below lower margin of basal membrane. Radiolar eyes absent. Dorsal lips with small, digitiform radiolar appendages, arising centrally, surrounded by enlarged, lobate ventral lips that overlap centrally, connected to radiolar lobes dorsally; pinnular appendages absent; ventral radiolar appendages absent; parallel lamellae and ventral sacs both absent. Anterior peristomial ring with small ventral, triangular lobe, concave. Lateral notches present. Notopodia as oval cushions with fine notochaetae, number difficult to assess due to damage, but less than 100. Form of notochaetae and uncini not observed. Tube not present.

Greenlandic syntype

Syntype complete with 55 chaetigers, 8 thoracic and 47 abdominal; body length 41 mm, crown length 15 mm. Preserved colour pale brown, no pigment or eyespots observed. Body shape unclear due to extent of dissection, but widest anteriorly, tapering to pygidium, tip missing. Radiolar crown with semicircular radiolar lobes bearing 20–21 pairs of radioles. Radioles with wide radiolar flanges and long, tapered tips, approximately 23% of total radiole length. Pinnulae very fine, dense, longest in distal part of radiole, up to 0.25 × total length of radiole, then rapidly decreasing in length, terminating at or above lower margin of basal membrane. Radiolar eyes absent. Dorsal lips with slender, digitiform radiolar appendages, arising centrally, surrounded by enlarged, lobate ventral lips connected to radiolar lobes dorsally; pinnular appendages absent; ventral radiolar appendages absent; parallel lamellae and ventral sacs both absent. Anterior peristomial ring too damaged and degraded to describe. Notopodia as oval cushions, notochaetae all broken. Uncini not observed. Pygidial tip missing, tube not present.

Remarks

The two type specimens from the Faroes and Greenland were borrowed from the Natural History Museum of Denmark and examined along with two additional specimens in NMW.Z from the Faroe Islands collected by Phyllis Knight-Jones. Both type specimens were in poor condition and many of those characters that have been detailed above for *M. infundibulum* and *M. polychroma* sp. nov. could not be observed. The larger NMW.Z specimen also had a badly damaged crown, limiting observations on the crown and dorsal lips, and the remaining specimen was a juvenile, although in good condition. No attempt is therefore made here to re-validate the species. Although it is considered that the species is likely to be found to be valid in the future, to do so will require the examination and/or collection of new specimens from the type localities to gather the necessary morphological details and, ideally, tissue samples for comparative genetic work. In the meantime, the details above are noted.

Both syntypes had labels with remarks from Mary Petersen stating that they were specimens of Krøyer's, listed in his unpublished catalogue of worms received by NHMD from the Royal Museum, and in that way they had been identified as syntypes for the described species. The two syntypes are very different in size, the type from Greenland being nearly twice as large as that from Faroe Islands, but for roughly the same number of chaetigers and radioles. The NMW.Z specimens were of a similar size to the Faroe Island type, with similar numbers of chaetigers and radioles. The damage and degradation on both types made some observations on the body and chaetae almost impossible as well as on the crown of the Faroe Islands type. The crown of the Greenland type was in a much better condition. The two types show different characteristics in the radioles and dorsal lips, leading to the conclusion that they represent different taxa, although further observations on the chaetae are also needed. This also presents a dilemma as to which type specimen would be designated for the name. Although it is believed that *Myxicola steenstrupi* is likely to be recognised as a valid species in the future, at the present time it must wait until new specimens are available and a detailed description can be developed in conjunction with one of the available type specimens.

DNA Results

The UK *Myxicola infundibulum* specimens showed no genetic variation within the 16S and COI genes, with only a single haplotype being present for each. The same 16S haplotype was also retrieved from all Australian specimens, except one, and the specimen from Croatia, both of which showed small variations (16S: 0.0042 and 0.0085) from the rest. For COI, fewer Australian sequences were available, and none for the Mediterranean, but of the six that were available, all were identical to the UK specimens except for the one from Adelaide (K2P = 0.0109). Of the United States and Canadian *M.* '*infundibulum*' and *Myxicola* sp. sequences analysed, either from GenBank or from Dane (2008), none returned a K2P distance less than 0.2154 (COI) or 0.0389 (16S) from the 'true' *M. infundibulum*. The COI sequences for *Myxicola aesthetica*, on the other hand, were closer to those for *M.* '*infundibulum*' from the USA and Canada (K2P = 0.1214–0.1768) than they were to any UK or Australian specimens (K2P = 0.2154–0.2559) of *M. infundibulum* or *M. polychroma* sp. nov. *Myxicola polychroma* sp. nov. showed a similar scale of distance from 'true' *M. infundibulum* as it did from United States and Canadian *M.* '*infundibulum*'.

Maximum parsimony returned 7 most parsimonius trees for the 16S dataset (tree length: 477; CI = 0.7862). All trees contained the same major clades (outgroups, 'true' *infundibulum*, USA *Myxicola* and *M. polychroma* sp. nov.), only differing in the relationships within the 'true' *infundibulum* clade, all of which had little support. Two most parsimonius trees were returned for the COI dataset (tree length = 651; CI = 0.6559), the main difference between them being the position of the *M. polychroma* sp. nov. clade with respect to the outgroups and the other taxa of *Myxicola*. Maximum likelihood, Bayesian inference and the maximum parsimony consensus trees for both genes all returned similar tree topologies with the same well-supported overarching clades (Fig. 11A–B).

In both the 16S and COI datasets, those specimens identified as *Myxicola infundibulum* from the UK, including those from the type locality, formed a strongly supported distinct clade along with all specimens from Australia and, for 16S, the specimen from Croatia (16S: 88–95% bootstrap support, 0.7 Bayesian posterior probability; COI: 100% bootstrap support, 1.0 posterior probability). There was no distinction between the populations around the UK or between the UK, Australia and Croatia (Fig. 11A). *Myxicola aesthetica* formed a separate clade, along with one of the *Myxicola* sp. sequences, in the COI tree, indicating a probable identity match (Fig. 11B). The remaining two *Myxicola* sp. sequences formed their own well-supported clade, sister to that of *Myxicola aesthetica*, and it is likely that they represent an as-yet undescribed *M. aesthetica*-like taxon. All USA (16S) and USA and Canadian (COI) *M.* '*infundibulum*' sequences formed a strongly-supported distinct clade for both genes (Fig. 11A–B), confirming their different identity and the restriction of *M. infundibulum*'s native range to the northeast Atlantic, except where anthropogenically introduced.

Myxicola polychroma sp. nov. formed a strongly or fully supported clade in all analyses, although its affinities to the other taxa were not completely resolved, with the COI tree returning it as sister to 'true' *infundibulum* (Fig. 11B), but the 16S analyses finding it to be sister to a combined *M. infundibulum* and USA *Myxicola* clade (Fig. 11A). The latter analyses, however, did not include any *M. aesthetica* or Pacific *Myxicola* sequences that would provide a wider comparison of taxa.

Discussion

Myxicola infundibulum has a tangled history caused partly by confusion over the first author of the species, as well as by a long list of synonymies instigated by a handful of authors (McIntosh 1923; Fauvel 1927; Hartman 1959). The synonymisation itself was caused by the superficial similarity of taxa to each other and the lack of a sufficiently detailed description with which to compare each taxon

properly. Only one new species has been added to the genus since 1928 (*Myxicola nana*: Australia (Capa & Murray 2015)), most likely due to that wide-scale synonymisation, placing most worldwide records under a single name. With the advent of that new species, as well as a detailed redescription of an older one, *Myxicola sulcata* Ehlers, 1912 by Tovar-Hernández *et al.* (2017), greater detail in the morphology began to be recognised and new potential characters highlighted. In the Mediterranean, Giangrande *et al.* (2012) highlighted the likely presence of taxa of *Myxicola* other than *M. infundibulum* in the region and work is currently underway to investigate this (Putignano *et al.* 2023).

Molecular analyses of specimens from several regions around the world (UK, Croatia, Australia, USA, Canada) confirm a more conservative restriction of *M. infundibulum* to the northeast Atlantic, except where anthropogenically introduced. References to dark-tipped *Myxicola* in the Adriatic Sea date back to Grube (1850) and, subsequently, *Myxicola grubii* (Krøyer 1856, Claparède 1869). The confirmed population of *M. infundibulum* in Croatia is considered to be part of the native range of the taxon, due to the combination of past literature and the fact that a different haplotype is present to that found in the UK, rather than it being a more recent introduction. The true native range of the species is therefore considered here to extend from the southern border of Scotland, in the north of the UK, south to the Mediterranean Sea and at least to the Adriatic Sea.

Fig. 11. Bayesian inference trees. **A**. 16S rRNA dataset. **B**. Cytochrome oxidase I gene dataset. The first value at each node represents maximum likelihood bootstrap support, the second the Bayesian posterior probabilities and the third the maximum parsimony bootstrap support.

Further investigation into *Myxicola* with dark-tipped radioles in other parts of Europe, as well as *M. violacea* in Madeira, is needed to confirm whether or not dark tips are indeed a unique character to the taxon, or whether they also occur in other, currently unrecognised species. Dark-tipped specimens were reported from northern France (Brittany – De Saint-Joseph 1894) and the Mediterranean (Naples – Claparède 1869; Golfe du Lion – Soulier 1902), and images of dark-tipped individuals are also recorded by observers on the social media recording site iNaturalist (https://www.inaturalist.org) from the northern coasts of France and Spain, Portugal, Gibraltar, the Mediterranean Sea (France, Corsica, Sardinia), the Adriatic Sea (Croatia) and the Aegean Sea (Greece). Additional images of dark-tipped individuals from the Canary Islands, as well as one from California, show animals that have dark radiolar rachis at the tips but with an unpigmented membrane on either side, which differs from the situation in *M. infundibulum*, where pigmentation on the radiolar tips extends out over the adjoining membrane, creating a lanceolate appearance. This suggests that other taxa may exist with dark radiolar tips, with the extent of the pigmentation possibly being diagnostic, and further investigation is required.

With the designation of a neotype, type locality and native range, the recognition of *M. infundibulum* as a non-native species elsewhere is facilitated. The presence of *M. infundibulum* as a non-native species in Australia was already confirmed by Dane (2008), although there was some doubt as to its origin due to the uncertainty surrounding the taxonomy. The single, same haplotype present for the UK specimens and the majority of the Australian specimens could indicate that the UK was the source of the Australian population. However, a different haplotype present in one Australian specimen suggests a possible secondary introduction as well, although it did not match the only other haplotype available from the Croatian specimen.

The morphological and molecular analyses of UK specimens also confirmed the presence of an additional, previously undescribed, species, *Myxicola polychroma* sp. nov., making a total of three taxa of *Myxicola* now known in the UK. *Myxicola polychroma* sp. nov. exhibits a wider distribution in the UK than *M. infundibulum* which appears to be restricted to more southerly regions. Photographs submitted by British divers, however, also highlighted an additional phenotype present off the northeast coast of England; it exhibits a deep red-purple colouration of the fan without differentially-coloured tips, different from anything seen so far in *M. polychroma* sp. nov., and it appears to be generally smaller in size than both *M. infundibulum* and *M. polychroma* sp. nov. It was not possible to obtain specimens, but it is suspected that it may represent another, as yet unrecognised, taxon. *Myxicola steenstrupi*, described from the Faroes and Greenland, requires re-evaluation with respect to new characters and is likely to be valid, but the type material comes from two different regions and appear to represent different taxa. This additional complication will require further specimens from both regions to help determine identity. An initial examination of the dorsal lips and radioles of both type specimens indicates that they are different from both *M. infundibulum* and *M. polychroma* sp. nov. However, the proximity of the Faroe Islands to northern parts of the UK means that species present there could exist within the UK fauna and this must be considered when identifying *Myxicola* from the UK, particularly from northern regions.

Myxicola aesthetica was described from the Gulf of Naples in the Mediterranean (Claparède 1870) but has been recorded from northern France, the UK, Pacific Canada and Alaska. Sequences used in the analysis of *M. infundibulum*, and identified as *M. aesthetica* on GenBank, were from Pacific Canada and Alaska. In light of the findings from the analyses of *M. infundibulum*, it is considered doubtful that *M. aesthetica* is present in the Pacific, unless it is an introduced species. *Myxicola glacialis* Bush, 1905 has been considered as having been synonymised with *M. aesthetica*, this being attributed to Berkeley (1930) (WoRMS 2023) who herself referred to McIntosh (1923). Neither, in fact, explicitly synonymised the two species, only saying that they are 'possibly' the same; however, Hartman (1959) in her Catalogue did do so. *Myxicola glacialis* should therefore also be re-evaluated as a potentially valid species.

Acknowledgements

References

Augener H. 1918. Polychaeta. *Beitrage zur Kenntnis der Meeresfauna Westafrikas* 2 (2): 67–625. https://doi.org/10.5962/bhl.title.11824

Berkeley E. 1930. Polychaetous annelids from the Nanaimo District. Part 5. Ammocharidae to Myzostomidae: with an appendix on some pelagic forms from the Straits of Georgia and the west coast of Vancouver Island. *Contributions to Canadian Biology and Fisheries* 6 (1): 65–77.

Bidenkap O. 1894. Diagnoser af tre nye Annulata Polychaeta. *Forhandlinger i Videnskabs-Selskabet i Christiania* 1894 (3): 1–6. Available from https://www.biodiversitylibrary.org/page/43710686 [accessed 12 Sep. 2023].

Bush K.J. 1905. Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. *Harriman Alaska Expedition* 12: 169–346. https://doi.org/10.5962/bhl.title.2461

Capa M. & Murray A. 2015. A taxonomic guide to the fanworms (Sabellidae, Annelida) of Lizard Island, Great Barrier Reef, Australia, including new species and new records. *Zootaxa* 4019 (1): 98–167. https://doi.org/10.11646/zootaxa.4019.1.8

Capa M., Hutchings P. Aguado M.T. & Bott N.J. 2011. Phylogeny of Sabellidae (Annelida) and relationships with other taxa inferred from morphology and multiple genes. *Cladistics* 27: 449–469. https://doi.org/10.1111/j.1096-0031.2010.00341.x

Capa M., Giangrande A., Nogueira J.M.M. & Tovar-Hernández M.A. 2019. Sabellidae Latreille, 1825. *In*: Westheide G. & Purschke G. (eds) *Handbook of Zoology: Annelida Vol. 2: Pleistoannelida, Sedentaria II*: 164–212. De Gruyter, Germany.

Chamberlin R.V. 1919. New polychaetous annelids from Laguna Beach, California. *Pomona College Journal of Entomology and Zoology* 11 (1): 1–23.

Claparède É. 1869. Les annélides chétopodes du Golfe de Naples. Seconde partie. Ordre IIme. Annélides sédentaires (Aud. et Edw.). *Mémoires de la Société de Physique et d'Histoire naturelle de Genève* 20 (1): 1–225.

Claparède É. 1870. Les annélides chétopodes du Golfe de Naples. Supplément. *Mémoires de la Société de Physique et d'Histoire naturelle de Genève* 20 (2): 365–542. https://doi.org/10.5962/bhl.title.2142

Cosmovici L.-C. 1880. Glandes génitales et organes segmentaires des annélides polychètes. *Archives de Zoologie expérimentale et générale* 8: 233–372.

Cunningham J.T. & Ramage G.A. 1888. The Polychaeta Sedentaria of the Firth of Forth. *Transactions of the Royal Society of Edinburgh* 33 (3): 635–684.

Cuvier G. 1830. *Le Règne animal distribué d'après son Organisation, pour servir de Base à l'Histoire naturelle des Animaux et d'Introduction à l'Anatomie comparée. Edition 2, volume 3*. Paris: Déterville & Crochard. https://doi.org/10.5962/bhl.title.49223

Cuvier G. 1836–1849. *Le Règne animal distribué d'après son Organisation, pour servir de Base à l'Histoire naturelle des Animaux, et d'Introduction à l'Anatomie comparée. Edition [3] accompagnée de Planches gravées... par une Réunion de Disciples de Cuvier, MM: Audouin, Blanchard, Deshayes, Alcide d'Orbigny, Doyère, Dugès, Duvernoy, Laurillard, Milne-Edwards, Roulin & Valenciennes*. Fortin, Masson et Cie, Paris. https://doi.org/10.5962/bhl.title.39612

Dalyell J.G. 1853. *The Powers of the Creator Displayed in the Creation: or, Observations on Life Amidst the Various Forms of the Humbler Tribes of Animated Nature with Practical Comments and Illustrations. Volume 2* [Vermes, etc]. John van Voorst, London. https://doi.org/10.5962/bhl.title.21823

Dane L. 2008. *Morphological and Genetic Variation in the Cryptic Species Complex Myxicola infundibulum (Polychaeta, Sabellidae), and its Introduction to Australia*. BSc Thesis, University of Melbourne, Australia.

Delle Chiaje S. 1841. *Descrizione e Notomia degli Animali invertebrati della Sicilia citeriore*. 5 volumes. C. Batelli & Co., Naples. Available from https://www.biodiversitylibrary.org/page/10599187 [accessed 12 Sep. 2023].

de Saint-Joseph A.d'A. 1894. Les annélides polychètes des côtes de Dinard. Troisième Partie. *Annales des Sciences naturelles, Paris, Séries 7* 17: 1–395.

de Saint-Joseph A.d'A. 1898. Annélides polychètes des côtes de France (Manche et Océan). *Annales des Sciences naturelles, Zoologie et Paléontologie, Série 8* 5: 209–464.

Eliason A. 1920. Biologisch-faunistische Untersuchungen aus dem Öresund. V. Polychaeta. *Lunds Universitets Årsskrift* 2 (16): 1–103.

Fauvel P. 1927. Polychètes sédentaires. Addenda aux Errantes, Arachiannélides, Myzostomaires. *Faune de France, Vol. 16.* Paul Lechevalier, Paris.

Fauvel P. 1936. Annélides polychètes du Japon. *Memoirs of the College of Science, Kyoto Imperial University, Ser. B* 12 (1): 41–92.

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Forbes E. 1841. On two remarkable marine Invertebrata inhabiting the Aegean Sea. *Annals and Magazine of Natural History* 8 (51): 244–245.

Giangrande A., Cosentino A., Lo Presti C. & Licciano M. 2012. Sabellidae (Annelida) from the Faro coastal lake (Messina, Ionian Sea), with the first record of the invasive species *Branchiomma bairdi* along the Italian coast. *Mediterranean Marine Science*: 13: 283–293. https://doi.org/10.12681/mms.310

Grube A.E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin* 16 (1): 249–364.

Grube A.E. 1855. Beschreibungen neuer oder wenig bekannter Anneliden. *Archiv für Naturgeschichte, Berlin* 21 (1): 81–136. https://doi.org/10.5962/bhl.part.13989

Grube A.E. 1878. Annulata Semperiana. Beiträge zur Kenntnis der Annelidenfauna der Philippinen. *Memoires de l'Academie imperiales des Sciences de St. Petersbourg, Série 7* 25 (8): 1–300.

Hartman O. 1938. Annotated list of the types of polychaetous annelids in the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology at Harvard College* 85 (1): 3–31.

Hartman O. 1942. A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin of the Bingham Oceanographic Collection, Yale University* 8 (1): 1–98.

Hartman O. 1959. Catalogue of the Polychaetous Annelids of the World. Parts 1 and 2. *Allan Hancock Foundation Occasional Paper* 23: 1–628.

Hayward P.J. & Ryland J.S. (eds) 1990. *The Marine Fauna of the British Isles and Northwest Europe: Introduction and Protozoans to Arthropods, Volume 1*. Clarendon Press, Oxford.

Hayward P.J. & Ryland J.S. (eds) 2017. *Handbook of the Marine Fauna of Northwest Europe. Second edition*. Oxford University Press, Oxford.

Hofsommer A. 1913. Die Sabelliden-Ausbeute der 'Poseidon'-Fahrten und die Sabelliden der Kieler Bucht. *Wissenschaftliche Meeresuntersuchungen, Kiel, Ser. neue Folge* 15: 305–364.

Hutchings P. & Karageorgopoulos P. 2003. Designation of a neotype of *Marphysa sanguinea* (Montagu, 1813) and a description of a new species of *Marphysa* from eastern Australia. *Hydrobiologia* 496 (1–3): 87–94. https://doi.org/10.1023/A:1026124310552

ICZN 1954. International Commission on Zoological Nomenclature. Opinion 316. Rejection for nomenclatorial purposes of the Tavola alfabetica delle Conchiglei Adriatiche and Prospetto delle Classe dei Vermi of S.A. Renier commonly attributed to the year 1804. *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* 9 (5): 91–106.

ICZN 1956. International Commission on Zoological Nomenclature. Opinion 427. Rejection for nomenclatorial purposes of the work by Renier (S.A.) known as Tavole per servire alle classificazione e connescenza degli animali and commonly attributed to the year 1807 and addition to the Official Indexes of Rejected and Invalid Names in Zoology of certain names first used in the foregoing work or in two earlier works by the same author commonly known as the Tavola alfabetica and the Prospetto respectively and both commonly attributed to the year 1804. *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* 14 (11): 281–310.

ICZN 1957a. International Commission on Zoological Nomenclature. Opinion 436. Addition to the Official Indexes of Rejected and Invalid Names in Zoology of certain names attributed to Renier (S.A.) as from 1804 and 1807 respectively (Opinion supplementary to Opinion 427). *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* 15 (1): 1–24.

ICZN 1957b. International Commission on Zoological Nomenclature. Opinion 477. Validation under the plenary powers of the generic name *Cerebratulus* [Renier], [1804], and of the specific name *marginatus* [Renier], [1804], as used by the foregoing author in the combination *Cerebratulus marginatus* (class Nemertea) (Opinion supplementary to Opinion 427). *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* 16 (20): 343–352.

ICZN 1957c. International Commission on Zoological Nomenclature. Opinion 478. Validation under the plenary powers of the generic name *Polycitor* [Renier], [1804], and of the specific name *crystallinus* [Renier], [1804], as used by the foregoing author in the combination *Polycitor crystallinus* (class Urochorda) (Opinion supplementary to Opinion 427). *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* 16 (21): 353–364.

ICZN 1988. International Commission on Zoological Nomenclature. Opinion 1486. *Tubulanus* Renier, [1804] and *T. polymorphus* Renier, [1804] (Nemertea): reinstated and made available. *Bulletin of Zoological Nomenclature* 45 (2): 157–158.

ICZN 1999. International Commission on Zoological Nomenclature. *International Code of Zoological Nomenclature. Fourth edition, adopted by the International Union of Biological Sciences*. The International Trust for Zoological Nomenclature, London.

ICZN 2012. International Commission on Zoological Nomenclature. Opinion 2296 (Case 3525). *Tricoelia variopedata* Renier, [1804] (currently *Chaetopterus variopedatus*; Annelida, Polychaeta): specific name conserved. *Bulletin of Zoological Nomenclature* 69 (2): 143–144.

Johnson H.P. 1901. The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society for Natural History* 29 (18): 381–437.

Johnston G. 1865. *A Catalogue of the British non-Parasitical Worms in the Collection of the British Museum.* 1–365. British Museum. London. https://doi.org/10.5962/bhl.title.12291

Knight-Jones P., Knight-Jones E.W., Mortimer-Jones K., Nelson-Smith A., Schmelz R.M. & Timm T. 2017. Annelids. *In*: Hayward P.J. & Ryland J.S. (eds) *Handbook of the Marine Fauna of Northwest Europe. Second edition*: 165–270. Oxford University Press, Oxford.

Krøyer H. 1856. Meddelelser af en Afhandling om Ormeslaegten *Sabella* Linn., især med Hensyn til dens nordiske Arter [Alternate title: Bidrag til Kundskab af Sabellerne]. *Oversigt over det kongelige danske Videnskabernes Selskabs Forhandlinger* 1856: 1–36.
Available from https://www.biodiversitylibrary.org/page/40359509 [accessed 12 Sep. 2023].

Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35 (6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Langerhans P. 1884. Die Wurmfauna von Madeira. IV. *Zeitschrift für wissenschaftliche Zoologie* 40: 247–285.

Linkletter L.E., Lord E.I. & Dadswell M.J. 1977. *A Checklist of Marine Fauna and Flora of the Bay of Fundy*. Huntsman Marine Laboratory, St. Andrews, NB, Canada.

Lobo J., Teixeira M.A.L., Borges L.M.A., Ferreira M.S.G., Hollatz C., Gomes P.T., Sousa R., Ravara A., Costa M.H. & Costa F.O. 2016. Starting a DNA barcode reference library for shallow water polychates from the southern European Atlantic coast. *Molecular Ecology Resources* 16 (1): 298–313. https://doi.org/10.1111/1755-0998.12441

Malmgren A.J. 1865. Nordiska hafs-annulater. *Öfversigt af kungliga Vetenskaps-Akademiens Förhandlingar, Stockholm* 22 (5): 355–410.

Marenzeller E. von 1884. Südjapanische Anneliden. II. Ampharetea, Terebellacea, Sabellacea, Serpulacea. *Denkschriften der Akademie der Wissenschaften, Wien* 49 (2): 197–224.

McIntosh W.C. 1874. On the invertebrate marine fauna and fishes of St. Andrews. *Annals and Magazine of Natural History* 14: 192–207. https://doi.org/10.1080/00222937408680955

McIntosh W.C. 1923. Polychaeta – Hermellidae to Serpulidae with additions to the British marine Polychaeta during the publication of the monograph. *A Monograph of the British Marine Annelids* 4 (2): 251–538. Ray Society, London. Available from https://www.biodiversitylibrary.org/page/62569284 [accessed 12 Sep. 2023].

Montagu G. 1808. Description of several marine animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London* 9: 81–114. https://doi.org/10.1111/j.1096-3642.1818.tb00327.x

Muir A.I. & Petersen M.E. 2013. Authorship of some polychaete (Annelida) names derived from the works of Renier and Savigny. *Zootaxa* 3717 (3): 383–388. https://doi.org/10.11646/zootaxa.3717.3.8

Palumbi S.R. 1996. Nucleic acids II: the polymerase chain reaction. *In*: Hillis D.M., Moritz C. & Mable B.K. (eds) *Molecular Systematics. Second Edition*: 205–247. Sinauer Associates, Sunderland, MA.

Panceri P. 1875. Catalogo degli Annelidi, Gefirei e Turbellarie d'Italia. *Atti della Società italiana di Scienze naturali* 18: 246–249.

Posada D. & Crandall K. 1998. MODELTEST: Testing the Model of DNA Substitution. *Bioinformatics* 14: 817–818. https://doi.org/10.1093/bioinformatics/14.9.817

Potts F.A. 1928. Zoological results of the Cambridge expedition to the Suez Canal. Report on the annelids (sedentary polychaetes). *Transactions of the Zoological Society of London* 22 (5): 693–705.

Putignano M., Gravili C. & Giangrande A. 2023. The peculiar case of *Myxicola infundibulum* (Polychaeta: Sabellidae): echo from a science 200 years old and description of four new taxa in the Mediterranean Sea. *Zoological Journal of the Linnean Society* 90 (1): 506–546. https://doi.org/10.1080/24750263.2023.2219710

Quatrefages A. de 1850. Études sur les types inférieurs de l'embranchement des annelés. Mémoire sur le système nerveux des annélides proprement dites. *Annales des Sciences naturelles, Paris, Série 3* 14: 329–398.

Quatrefages A. de 1866 (1865). *Histoire naturelle des Annelés marins et d'Eau douce. Annélides et Géphyriens*, vol. 1: 1–588. Librarie Encyclopédique de Roret. Paris.

Renier S.A. [1804a]. [Rejected publication; see ICZN 316] *Prospetto della Classe dei Vermi, nominati ed ordinati secondo il Sistemo de Bosc.* Padua, Italy.

Renier S.A. [1804b]. [Rejected publication; see ICZN 316] *Tavola alfabetica delle Conchiglie adriatiche. Nominate dictro il Sistemo di Linneo, Edizione di Gmelin.* Padua, Italy.

Renier S.A. [1807]. [Rejected publication. See ICZN 427] *Tavole per servire alla Classificazione e Conoscenza degli Animali.* Tipografia del Seminario, Padua.

Renier S.A. 1847. *Osservazioni postume di Zoologia adriatica del Professore Stefano Andrea Renier, Membro effettivo dell'Istituto italiano, pubblicate per cura dell'I.R. Istituto Veneto de Scienze, Lettere ed Arti a studio del membro effettivo Prof. G. Meneghini.* Giovanni Cecchini, Venice.

Rioja E. 1917. Datos para le conocimiento de la fauna de anélidos poliquetos del Cantábrico. *Trabajos del Museo nacional de Ciencias naturales, Serie Zoológica* 29: 1–111.

Ronquist F., Teslenko M., van der Mark P., Ayres D., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rousset V., Pleijel F., Rouse G.W., Erseus C. & Siddall M.E. 2007. A molecular phylogeny of annelids. *Cladistics* 23 (1): 41–63. https://doi.org/10.1111/j.1096-0031.2006.00128.x

Sars M. 1851. Beretning om i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken. *Nyt Magazin for Naturvidenskaberne* 6 (2): 121–211.

Sars M. 1862. Foredrag om de ved Norges Kyster forekommende Arter af den Linnéiske Annelideslægt *Sabella. Forhandliger i Videnskabs Selskabet i Christiania* 1861: 116–133.
Available from https://www.biodiversitylibrary.org/page/60512085 [accessed 12 Sep. 2023].

Smith E. & Harrison K. 2008. *Rifle-Green by Nature. A Regency Naturalist and his Family, William Elford Leach*. Ray Society, London.

Soulier A. 1902. Révision des annélides de la région de Cette. pt.1. *Mémoires de l'Académie des Sciences et Lettres de Montpellier* 3: 109–163.

Soulier A. 1903. Révision des annélides de la région de Cette. pt.2. *Mémoires de l'Académie des Sciences et Lettres de Montpellier* 3: 193–278.

Tovar-Hernández M.A., de León-González J.Á. & Bybee D.R. 2017. Sabellid worms from the Patagonian Shelf and Humboldt Current System (Annelida, Sabellidae): Phyllis Knight-Jones' and José María Orensanz's collections. *Zootaxa* 4283 (1): 1–64. https://doi.org/10.11646/zootaxa.4283.1.1

Webster H.E. & Benedict J.E. 1887. The Annelida Chaetopoda, from Eastport, Maine. U.S. Commission of Fish & Fisheries. *Report of the United States Commissioner of Fisheries. 1885. Pt 13, II. Appendix to Report of Commissioner,* D.22: 707–758.

WoRMS. 2023. *World Register of Marine Species.*
Available from https://www.marinespecies.org [accessed 27 Jan. 2023].