Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Information Technology and Electrical Engineering
Department of Natural History

Marthe Ree Dille

Lugworms (Arenicolidae, Annelida) in Norwegian waters - species diversity and habitat preferences

Master's thesis in Natural Science with Teacher Education
Supervisor: Torkild Bakken
Co-supervisor: Jon Anders Kongsrud
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Abstract

Arenicola marina Linnaeus, 1758, is a well-known species along the Norwegian coast. Recently a new species was described, which had earlier been identified as *A. marina*. This new species, *Arenicola defodiens*, Cadman & Nelson-Smith 1993, has not yet been confirmed from Norwegian waters. A less known species of the same family, *Arenicolides ecaudata* Johnston, 1835, has fewer reports than *A. marina* along the coast of Norway. The few records primarily result from being overlooked and undersampled because of its less conspicuous presence in the littoral zone than *A. marina*.

This study aimed to use morphology to distinguish these three species of lugworm in the family Arenicolidae, focusing on characters to distinguish post-larva individuals of *A. ecaudata* and *A. marina*. Neuropodia was discovered to be a very efficient way of distinguishing the post-larva *A. ecaudata* from *A. marina*. Descriptions of the two species were made from examination of 296 specimens. Post-larva specimens of *A. ecaudata* and *A. marina* were examined for the development of branchia, when they appeared, and how the development of branchia looked at different development stages. The branchia of *A. ecaudata* appears when the specimen is measuring between 7-13 mm, while *A. marina* measures between 3-5 mm. Depth distribution of both small and large specimens of *A. ecaudata* and *A. marina* were examined and systematized graphically. The adult *A. ecaudata* dominates the deep, while the small specimen is mostly found in the shallows. In *A. marina* the distribution is opposite, with most adults in the shallows and the small specimen in the deep.

Four specimens from museum material in Trondheim were first suspected to be *A. defodiens*. Further examination resulted in these specimens being identified as *A. marina* and *Arenicola* sp. The reported finding of *A. defodiens* from the Norwegian Biodiversity Information Centre (NBIC) were revised, and by this the existence of *A. defodiens* in Norwegian fauna were disproved.

Sammendrag

Arenicola marina Linnaeus, 1758 er en godt kjent art langs norskekysten. Nylig ble en ny art beskrevet som tidligere ble identifisert som *A. marina*. Denne nye arten, *Arenicola defodiens* Cadman & Nelson-Smith, 1993 har ikke enda blitt rapportert i norske farvann. En mindre kjent art fra samme familie, *Arenicolides ecaudata* Johnston, 1835 har færre rapporterte funn enn *A. marina* langs norskekysten. Færre rapporterte funn er hovedsakelig et resultat av at arten oversees og dermed ikke samles inn på grunn av sin mindre tydelige tilstedeværelse i littoralsonen, i motsetning til *A. marina*.

Denne studien hadde som mål å bruke morfologi til å skille disse tre artene av fjæremark i familien Arenicolidae, med spesielt fokus på karakterer som skiller små individ av *A. ecaudata* og *A. marina*. Neuropodier ble oppdaget å være en veldig effektiv måte å skille små *A. ecaudata* fra *A. marina*. Beskrivelser av de to artene ble lagd på grunnlag av observasjon av 296 eksemplarer. Post-larve eksemplar av *A. ecaudata* og *A. marina* ble studert for utvikling av gjeller, når de kommer til syne, og hvordan utviklingen av gjeller ser ut på ulike utviklingsstadier. Gjellene på *A. ecaudata* ser ut til å dukke opp når individene måler mellom 7-13 mm, mens *A. marina* måler mellom 3-5 mm. Dybdedistribusjon av både små og store individ av *A. ecaudata* og *A. marina* ble studert og systematisert grafisk. De voksne *A. ecaudata* dominerer i dypet, mens små individ finnes for det meste i tidevannssonen. Hos *A. marina* er distribusjonen motsatt, med flest voksne i tidevannssonen og de små i dypet.

Fire individ fra museumsmaterialet i Trondheim ble først mistenkt for å være *A. defodiens.* Nærmere studering resulterte i at disse ble identifisert som *A. marina* og *Arenicola* sp. Det rapporterte funnet av *A. defodiens* fra Artsdatabanken (NBIC) ble undersøkt på nytt og med dette ble eksistensen av *A. defodiens* i norsk fauna avkreftet.

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Key concepts and abbreviations

Abranchial	Without branchiae.
Achaetous	Without chaeta.
Apodous	Without parapodia.
BOLD	Barcode of Life Database.
Hinge line	Line which splits the chaetigerous annulus in two.
NTNU-VM	NTNU University Museum.
NBIC	Norwegian Biodiversity Information Centre.
Sp.	Species, used when the species name cannot be specified.
WoRMS	World Register of Marine Species.
ZMBN	University Museum of Bergen.

1. Introduction

Polychaetes show considerable variation in morphology, which reflects their diverse lifestyles (Glasby et al., 2000). This extreme variation in morphology was earlier explained by a wide variation within species, which led to a belief among respected taxonomic authorities that cosmopolitan species were common among polychaetes. These beliefs were not challenged until the 1970s, when new taxonomists examined species again. New observations of morphology led to the description of new species, and one moved away from the old beliefs of cosmopolitan species. As technology improved, sharing ideas and findings among researchers became easier and less time consuming (Hutchings & Kupriyanova, 2018). Newer research has discovered that the number of species is severely underestimated when identification is based on morphology alone. Because of these findings, it is not sufficient to only use morphology when assessing biological diversity (Nygren, 2014). Improvements in instruments and the use of molecular data to distinguish between species has moved researchers from an entire morphological based identification to a combination of both morphology and molecular data (Hutchings & Kupriyanova, 2018). DNA barcoding is an important method for the identification of biological diversity. The method compares specific DNA segments from an unknown organism with a known species DNA present in a DNA library. The same species will have less genetic variation in DNA segments than different species. If the variation is great enough, it can be used to identify unknown organisms. The Barcode of Life Database (BOLD) is such a DNA library with over 9 million sequences from more than 700 000 species (NorBOL, n.d.).

Arenicolidae Johnston, 1835 is a relatively small family of polychaetes that has been well studied because of its important ecological role (Darbyshire, 2020). Polychaetes are not only important prey to other marine species but plays an important role in the ecology otherwise. By living in the sediments, the arenicolid species contribute to supplying the sediment with more oxygen making it habitable for other organisms. In some countries, even humans consume polychaetes. They are an important protein source in the oceans and are in many countries used as bait in fishing as it is prey of fish (Nygren, 2017).

Bait diggers have for many years distinguished between two varieties of the lugworm *Arenicola marina* Linnaeus, 1758. Early research on *A. marina* referred to the two varieties as “laminarian” and “littoral.” The “laminarian” variety was later found to be *Arenicola defodiens* Cadman & Nelson-Smith, 1993, while the “littoral” variety was *A. marina* (Cadman and

Nelson-Smith (1990). They did both genetic and morphological examinations which concluded it was two different species.

The family Arenicolidae consists of four genera: *Abarenicola* Wells 1959, *Arenicola* Lamarck 1801, *Arenicolides* Mesnil 1898, and *Branchiomaldane* Langerhans 1881, containing 10, 6, 3, and 4 species, respectively (Read & Fauchald, 2022). The first two genera contains worms which can be divided into three parts, head, body and tail, while the last two does not have a distinct tail (Cadman & Nelson-Smith, 1993).

Three species of this family are reported along the Norwegian coast. This being *Arenicola marina, Arenicola defodiens* and *Arenicolides ecaudata* (Artskart.artsdatabanken.no, 06.05.2022). By examining the map retrieved from the Norwegian Biodiversity Information Centre (Fig. 1), one can see that there are many more reported findings of *A. marina* (590 records) than *A. defodiens* (1) along the Norwegian coast. These findings include both human observations and preserved specimens but may not coincide with reported distribution in literature as not all habitats or places are examined by NBIC. *Arenicola marina* is a common species along the Norwegian coast and may be undersampled as one sees it and recognizes it immediately. Only one finding of *A. defodiens* can possibly be explained by the fact that the species is relatively newly described as a distinct species from *A. marina*. There are not many findings of *Arenicolides ecaudata* Johnston, 1835 (42 records) either. Records of *A. ecaudata* from a study by Ringvold et al. (2000) suggest that previous studies might have overlooked the species. This could be caused by this being a difficult habitat for shovel use or that the right tools have not been used when sampling these habitats. Another contributing factor may be that *A. ecaudata* lives in coarser gravel than *A. marina* and will therefore have more trouble creating distinct faecal casts in the sand, as the coarse material will fall apart (Ashworth, 1912). However, it is essential to remember that this map is made of reported findings. Much of the coast is possibly not examined, and especially not with the focus of finding neither *A. defodiens* nor *A. ecaudata*.

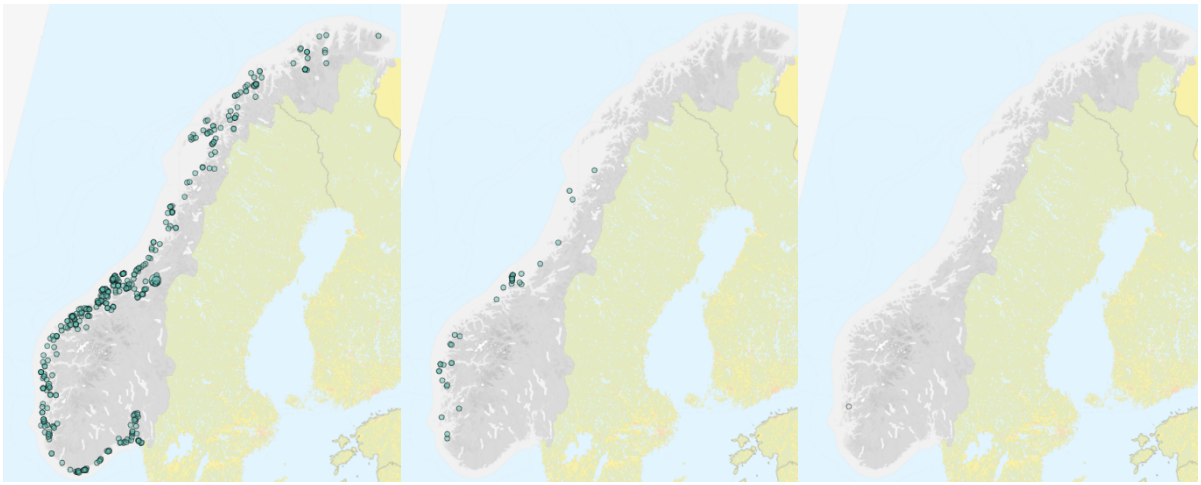

Figure 1: Reported distribution of Arenicolidae along the Norwegian coast. From left to right: *Arenicola marina* (590 records), *Arenicolides ecaudata* (42) and *Arenicola defodiens* (1). Maps retrieved from (Artskart.artsdatabanken.no, 06.05.2022).

1.1 Distribution

According to Wells (1964), temperature plays a direct or indirect role in lugworm distribution. The distribution of *Arenicola* and *Abarenicola* species corresponds roughly with summer surface-water isotherms of 20°C. *Arenicola* is confined to the cold northern waters, though some are found in tropical areas. *Abarenicola* mainly remains in the cold waters of the southern hemisphere, except some species found in the northern Pacific. *Branchiomaldane* is found worldwide (Ashworth, 1912), while *Arenicolides* only have records from Europe (Wells, 1950).

From the *Arenicola* genus, the following three species are known to exist along European coasts: *A. marina, A. defodiens,* and *Arenicola cristata* (Pires et al., 2015). *Arenicola marina* is widely distributed from Portugal to the Arctic (Hartmann-Schröder, 1996; Pires et al., 2015). *Arenicola defodiens* is recorded from the North Sea, England, Wales, Ireland, Skagerrak, and the Iberian Peninsula (Brind & Darbyshire, 2015; Cadman & Nelson-Smith, 1993; Luttikhuizen & Dekker, 2010; Pires et al., 2015). *Arenicola marina* habits the northern cold-waters, while *A. cristata* inhabits the warm-waters (Wells, 1963), with Woods Hole in Massachusetts as a boundary to their distributions (Wells, 1961). *Arenicola cristata* have reports from American waters and are found from Naples to Western Australia (Wells, 1962). From the *Arenicolides* genus, both *A. ecaudata* and *Arenicolides branchialis* are known from European waters, but the latter are mentioned to have a more southern distribution. Around Plymouth, Britain, *A. branchialis* is reaching its northern limit, while *A. ecaudata* is reaching its southern limit (Eve & Southward, 1958). *Arenicolides ecaudata* are known from eastern North-Atlantic to western

Mediterranean. *Arenicolides branchialis* are reported from Iberian waters (Pires et al., 2015), the Mediterranean, the Black Sea, west Scotland to Morocco (Eve & Southward, 1958).

1.2 Morphology in the family Arenicolidae

The family Arenicolidae have some differences in morphology but the traits are generally similar to each other. The worm is either divided into three or two distinct regions (Fig. 2), *Abarenicola* Wells 1959 and *Arenicola* Lamarck 1801, and *Arenicolides* Mesnil 1899 and *Branchiomaldane* Langerhans 1861, respectively. The head is without appendages(Rouse, 2001). Segments in the trunk are divided into five annulations, where the first bearing chaetae, called chaetiger, is somewhat enlarged. In the anterior region these number is reduced and varies between species (Wells, 1950). Notopodium (Fig. 2C,D), dorsal parapodium, are small extensions of the body wall carrying simple capillary chaeta on the end (Rouse, 2001). Neuropodium (Fig. 2), ventral parapodium, can form long (*Arenicola* and *Arenicolides*) or short (*Abarenicola* and *Branchiomaldane*) single rows of long-handled dentate hooks. The hooks consist of a main fang with many small series of teeth over it (Fig. 5). *Branchiomaldane* has rather large teeth in the hooks (Rouse, 2001).

The branchiae are specialized respiratory structures developed from the body wall (Darbyshire, 2020). They are distinct for all species and first appear on different chaetigers within different species, this being on the middle or last part of the worm (Fig. 2A,B). The branchiae lie adjacent or dorsal to the notopodium (Fig. 3A). Branchiae appear on chaetiger 7-8 (*Abarenicola* and *Arenicola*), 12-17 (*Arenicolides*) or 14-20 (*Branchiomaldane*). In *Abarenicola* and *Arenicola* (Fig. 2A) the worm has an achaetous, abranchial tail with small papillae. *Arenicolides* (Fig. 2B) and *Branchiomaldane* lacks this distinct tail (Rouse, 2001). According to Wells (1950) there is some differentiation in the annulations in the trunk of *A. ecaudata* which corresponds to the tail of *Arenicola*, although less profound. All Arenicolidae has a simple structure of the pygidium (Fig. 2A,B) (Rouse, 2001).

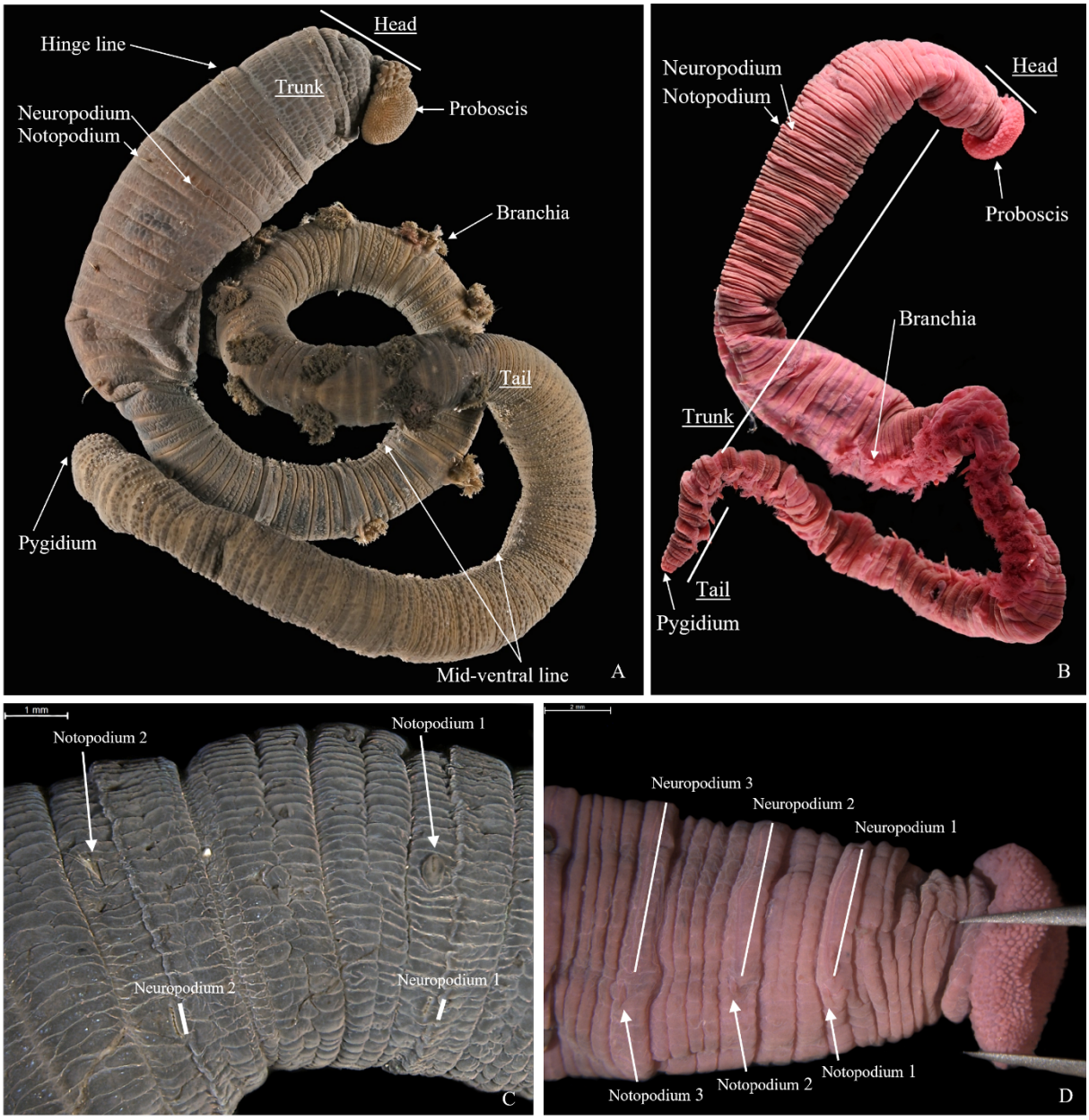

Figure 2: Adult specimen of *Arenicola marina* and *Arenicolides ecaudata*. The three body regions are underlined and marked with lines (B) or marks the start of the region (A). A: *Arenicola marina*, measuring 246 mm (NTNU-VM 83980). B: *Arenicolides ecaudata*, measuring 146 mm (NTNU-VM 83935). C: The two first notopodium and neuropodium, including marks of the length of the neuropodium on a 160 mm long *Arenicola marina* (NTNU-VM 83930). D: The three first notopodium and neuropodium, including marks of the length of the neuropodium on a 146 mm long *Arenicolides ecaudata* (NTNU-VM 83935). Photo: Marthe Ree Dille.

1.2.1 Differences between Arenicola marina and Arenicola defodiens

The annulations between second and third chaetiger is an important characteristic for distinguishing between *A. marina* and *A. defodiens* (Fig. 4). The notation of the annulation pattern for *A. marina* is i2 ii3 iii4, which means that between the first and second chaetiger there are two annulations (i2), while there are three annulations between the second and third chaetiger (ii3), and so forth (Wells, 1957). Later the literature has begun to use the notation

2-3-4, instead of the original notation (Brind & Darbyshire, 2015). The annulation pattern in *A. marina* is 2-3-4, while *A. defodiens* has 2-2-4 (Fig. 4). According to a study by Cadman and Nelson-Smith (1993), this annulation pattern can be incomplete or absent in some cases. This happened in respectively 4.4%, and 2.2% of the 209 worms studied. This is supported by Luttikhuizen and Dekker (2010), who found that 2.3% of the individuals of *A. marina* lack the third annulus and therefore have formula 2-2-4.

Because of this deviation in the annulation pattern, it is essential to rely on several traits for identifying the two species. Mentioned differences by Pires et al. (2015), includes differences in branchia structure and the differences in worm casts between the two species. However, some of the branchia description done by Cadman and Nelson-Smith (1993) regarding the presence of a palmar membrane on *A. defodiens* not present in *A. marina*, has later been falsified by Brind and Darbyshire (2015). They state that both species possess the palmar membrane. The branchia of *A. marina* is described to have 8-12 branchia stems (Fig. 3A) with 3-6 lateral branches (Fig. 3B), while *A. defodiens* have 11-14 stems with 8-14 lateral branches (Cadman & Nelson-Smith, 1993).

DNA sequencing resulted in no genetic difference between populations of the same species. However, it showed that *A. marina* and *A. defodiens* from British waters were more closely related to each other than they were to other *Arenicola* species with available sequences (Brind & Darbyshire, 2015). This being *Arenicola cristata* and *Arenicola loveni.*

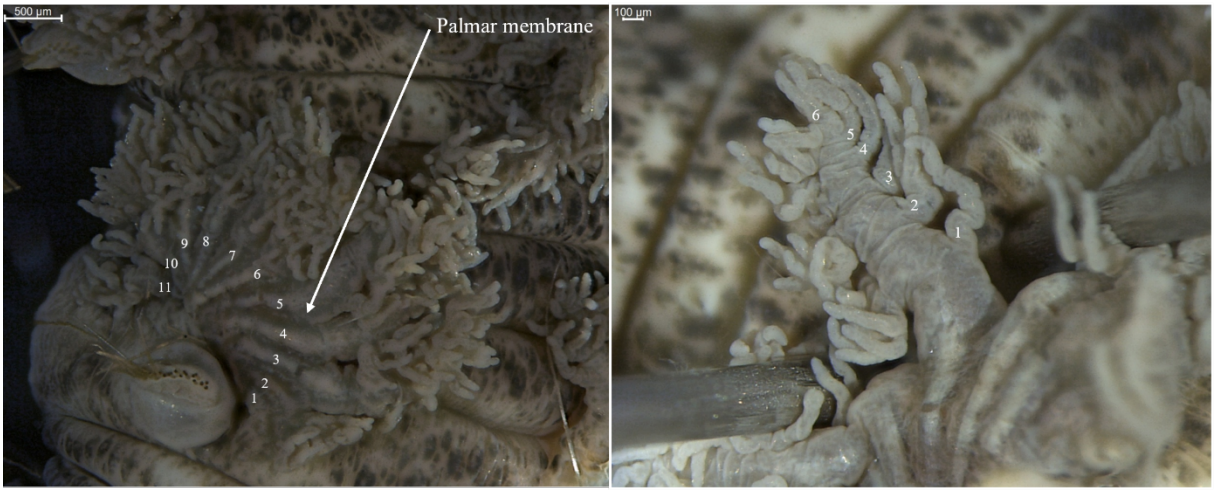

Figure 3: Illustrations of the 11th branchia of *Arenicola marina,* showing how branchia is examined to distinguish between *Arenicola marina* and *Arenicola defodiens*. A: How branchia stems are counted. In this case 11 stems. B: How to count lateral stems. In this case 6 lateral branches. (A, B: NTNU-VM 83987). Photo: Marthe Ree Dille.

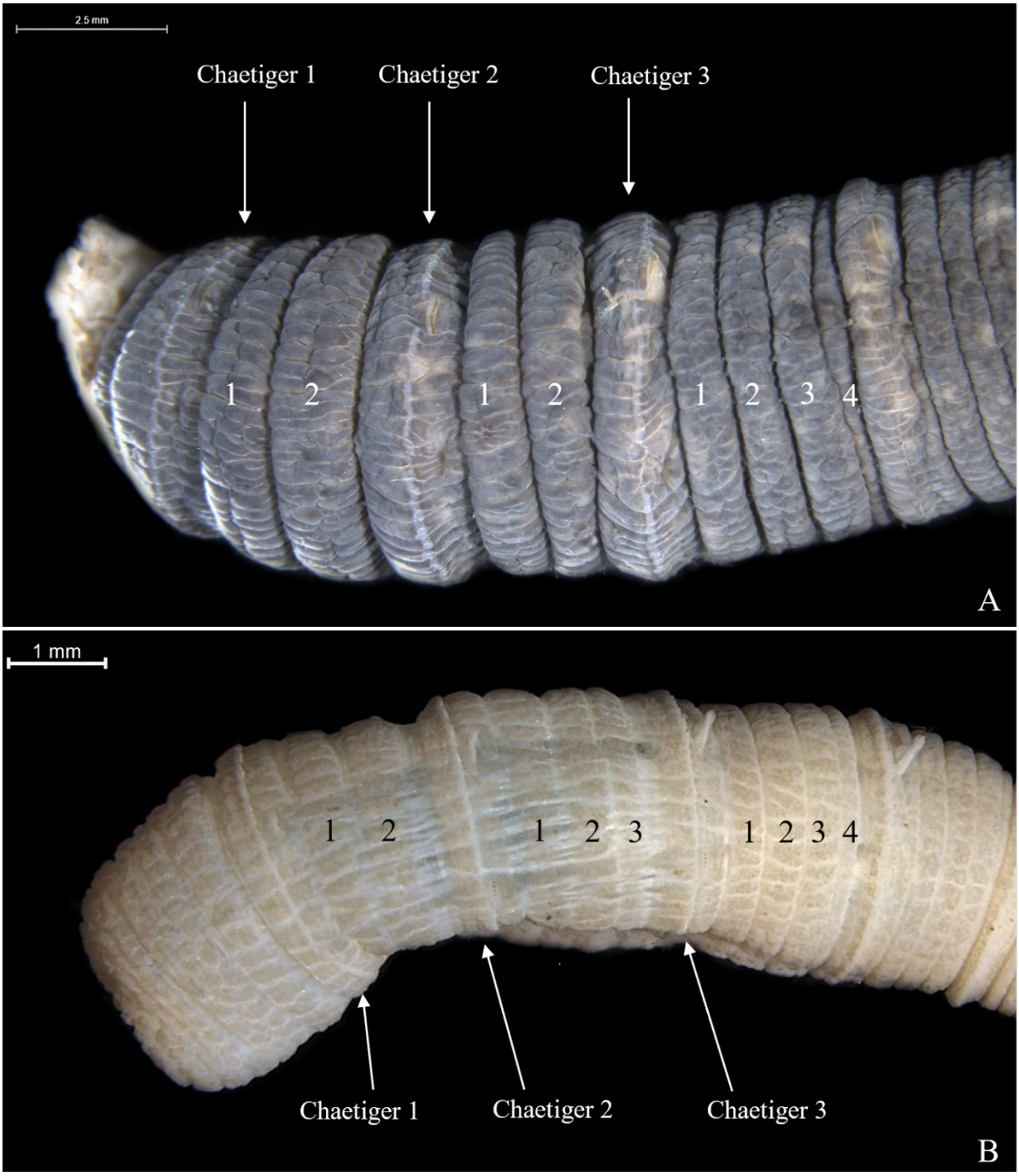

Figure 4: Illustration of how the ring annulation formula looks like in *Arenicola defodiens* and *Arenicola marina*. A: *Arenicola defodiens*, notation: 2-2-4 (NTNU-VM 14905). B: *Arenicola marina*, notation: 2-3-4 (NTNU-VM 75207). Photo: Marthe Ree Dille.

1.2.2 Morphology and habitat of post-larval *Arenicola marina* and *Arenicolides ecaudata*

The expression post-larva is used to refer to the stage where the worm has attained its complete number of chaetigerous segments, but the branchiae are not yet fully developed or even has not appeared yet (Ashworth, 1912). This expression is used because of the uncertainty concerning

size relative to age in *A. marina* (Ashworth, 1912). Assumably the same goes for *A. ecaudata*. In this study, the expression is also used for *A. ecaudata* before it has attained the complete number of chaetigerous segments, as branchia can appear before all these present. During development, both the morphology and the habitat of both *A. marina* and *A. ecaudata* changes (Ashworth, 1912).

Shortly after hatching, the larvae migrate from their burrow and are carried away by the tidal currents (Farke & Berghuis, 1979b). Kirkegaard (1996) describes the small Arenicolidae to be able to swim but do not live a pelagic life as they live between stones on the bottom of the ocean. Already the next summer after hatching the larvae begin their life in the sediment in burrows.

Kirkegaard (1996) describes *A. marina* to be 200-400 μm when hatched. They have then two small eyes and two ciliary bands. The body of the post-larval *A. marina* consists of 19 segments with parapodia. The body is divided into three parts and all segments into five rings, except from the first three segments. The prostomium is apodous, while chaetiger 2-19 is bearing parapodium. The tail is apodous and abranchial. Chaetiger 7-19 is supposed to be branchial. However, they do not appear until the complete number of chaetigerous segments, and about 30 tail-segments, has developed. It may take some time before all the branchial segments, chaetiger 7-19, of the worm is covered with branchia. The first sign of branchia is a slight elevation of the body-wall directly behind the notopodium. Ashworth (1912) describes the development of the branchia in *A. marina* as first conical, then digitiform, and finally branched. According to Gamble and Ashworth (1900) the branchia appear in the centre of the branchial area of an *A. marina* and will from there spread both forwards and backwards. The branchia varies in their time of appearing, and how well developed they are.

Ashworth (1912) mentions that *A. marina* settles into its littoral life before the development of branchia or after some branchia has started to appear. However, he found two individuals swimming in the water column with the complete number of branchia. This is also mentioned by Thorson (1946), which describes post-larvae at 3.9-6.5 mm long floating in the plankton. At this point, the larvae were divided into three sections but were abranchiate. According to (Farke & Berghuis, 1979a), they never found a swimming *A. marina* smaller than about 6 mm. They also state that *A. marina* started showing borrowing behaviour at length 6 mm, and at length 8 mm this behaviour was common.

The following spring after hatching the *Arenicola* measures 8 mm and digs down into the sediment at high places in the littoral zone. The adult digs burrows at lower water (Ashworth, 1912). According to Farke et al. (1979), juvenile *A. marina* tends to inhabit areas of the intertidal zone where there is little adult *A. marina*. Somewhere they seem to be coexisting, but in other areas there seems to be a pattern in which the juveniles settle higher on the intertidal zone. The small *Arenicola* wanders to deeper water in the winter, where they swim horizontally through the water (Kirkegaard, 1996).

Newly hatched *A. ecaudata* has two circular cilia bands and two eyes. When the larvae reach 6-chaetigers, it feeds actively and begins displaying behaviour consistent with the adult. The larvae of *A. ecaudata* grow slowly compared to *A. marina* and *A. branchialis*, but are in other ways very similar (Eve & Southward, 1958). Ashworth (1912) found that small abranchial *A. ecaudata* lives among algae in a gelatinous tube. First when branchia have developed, the animal adapts to the adult way of life. He found that small *A. ecaudata* left the sand at night to wander at the surface or swim freely in the water masses. When exposed to light, the worm buried into the sand again.

According to Wells (1959), the *Arenicolides* larval worm grows backward by means of a growth zone situated in front of the pygidium. Almost the total number of segments must develop in *A. ecaudata*, before any branchia appears (Ashworth, 1912). *Arenicolides ecaudata* attains their complete number of segments during their post-larval stage and could be as high as 64, according to Ashworth (1912). The maximum number of branchia seen in *A. ecaudata* by him is 47 pairs. His findings conclude with that the branchia never appears on individuals less than 8 mm. When the branchiae are bifid or trifid, the worms change their habitat. From living among holdfasts of algae to bury within gravel and sand. The worms without a distinct tail seem to choose coarser sediment than those with a tail. *Arenicolides ecaudata* is most likely to be found between pebbles or rougher sediment than other species which often inhabit sandy beaches (Eve & Southward, 1958).

The different stages of larval development display different of notochaeta and neurochaeta, hooks (Fig. 5). However, this changes rapidly during the development and cannot be used as a trait to distinguish between species. When the worm has obtained its littoral way of life, the crotches attain their characteristic form (Ashworth, 1912).

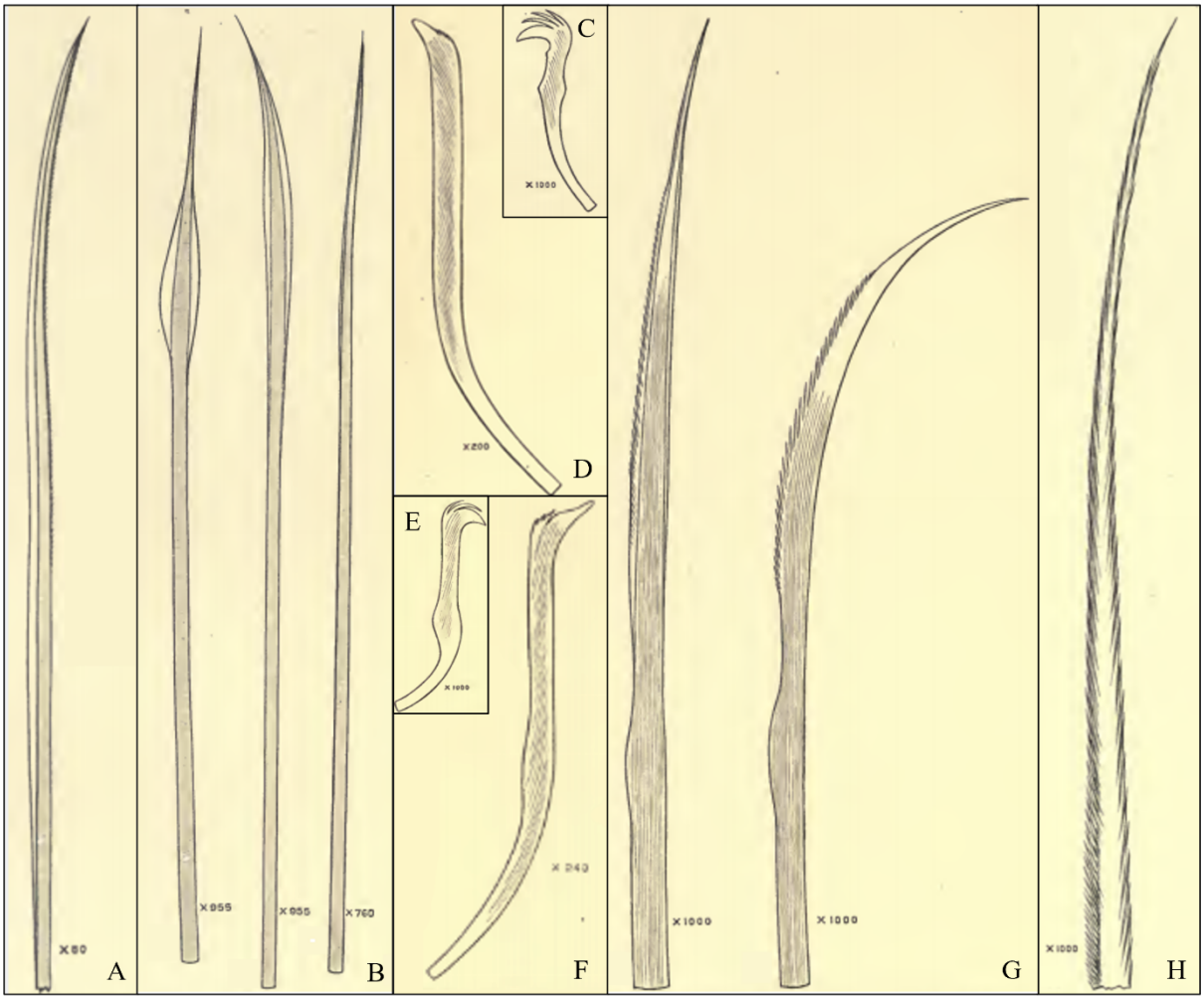

Figure 5: Neuro- and notochaetae of *Arenicola marina* (A-D) and *Arenicolides ecaudata* (E-I). A: Notochaeta of an adult *A. marina*. B: Three notochaetae of a post-larval *A. marina* specimen measuring 4,3 mm long. C: Neurochaeta of post-larval *A. marina* measuring 5 mm. D: Neurochaeta of an adult *A. marina*. E: Neurochaeta of post-larval *A. ecaudata* measuring 8 mm. F: Neurochaeta of adult *A. ecaudata*. G: Two notochaetae from post-larval *A. ecaudata* measuring 7 mm. H: Notochaeta from adult *A. ecaudata*. Figures retrieved from (Ashworth, 1912).

1.3 Aims

The overall aim of this project is to describe *A. ecaudata,* both regarding morphological differences between life stages, how this is related to habitats, and morphological differences from *A. marina* and *A. defodiens. Arenicola marina* is considerably reported along the Norwegian coast. *Arenicola defodiens* has one finding, although not officially confirmed. *Arenicolides ecaudata* is poorly known, and the difference to the other two species is little described. Findings suggest that this species has particular habitat demands during different life stages.

Specific objectives:

- Describe morphological differences between small and large individuals of *A. ecaudata*.
- Explain habitat change within *A. ecaudata* by using morphological differences between small and large individuals.
- Confirm the existence of *A. defodiens* in Norwegian fauna.
- Describe the morphological difference between individuals of *A. ecaudata* compared to *A. marina* and *A. defodiens*.
- Contribute to molecular confirmation on the species through the work of the *Invertebrate fauna of marine rocky shallow-water habitats* project.

2. Method

2.1 Fieldwork

Fieldwork was done on rocky bottom and sandy beaches in the littoral zone (Fig. 6). Samples were collected using a shovel in the littoral zone at low tide. At one station, some snorkelling was conducted. This way, some samples from the sublittoral zone were collected as well. A handheld scrape was used from a dock. These samples were roughly separated in the field and put on 96% ethanol. Coordinates and habitat observations were noted for all the stations during the fieldwork.

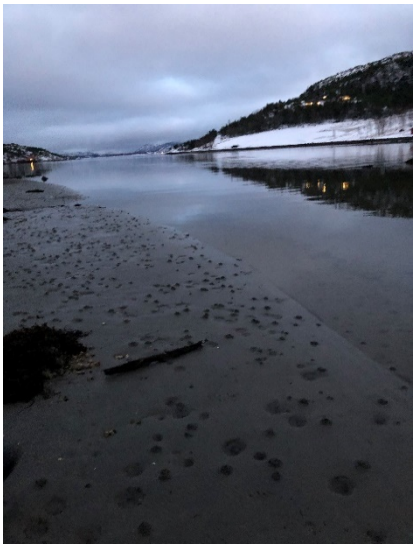

Figure 6: Fieldwork conducted on sandy beach in Leite, Jøa. Photo: Marthe Ree Dille.

2.2 Material

Most of the material examined is from the museum material of NTNU University Museum in Trondheim (Bakken et al., 2022) and the University Museum in Bergen. This material was used for the description of *A. marina* and *A. ecaudata.* The material from Bergen was especially important for the study of small specimens of Arenicolidae. Some material were received from Åkerblå and NIVA. Åkerblå sometimes stains material with rose Bengal, making it easier to distinguish animals from the sediment. Therefore, some of the pictures included are of pink specimen. Both *A. ecaudata* and *A. marina* were found in this material. All details regarding the examined material are found in Appendix I.

2.3 Laboratory analysis

Identification of the material was done by using the following literature: *Investigations of the Black Lugworm (Arenicola defodiens) in South Wales* (Brind & Darbyshire, 2015) and *New records of Arenicolides ecaudata (Johnston, 1865) (Polychaeta, Arenicolidae) from Norwegian waters* (Ringvold et al., 2000). Literature with identification keys includes *Handbook of the Marine Fauna of North-west Europe* (Knight-Jones et al., 2017). Identification follows the nomenclature of World Register of Marine Species (WoRMS) (WoRMS Editorial Board, 2022).

The analysis of Arenicolidae was done by observation of external morphology. The proboscis was also observed in cases where the specimen had an everted proboscis. In literature the

proboscis is referred to as an internal morphological structure but is included in this master thesis regardless.

Individuals of both *A. ecaudata* and *A. marina* were studied for morphological traits in Leica Wild M3B, Leica MZ AP0 and Leica M165 C stereo microscopes. Pictures were taken using Leica LAS X Software using cameras, Leica MC170HD and Leica DMC5400, attached to stereo microscopes Leica M165C and Leica MZ16A, respectively. The photos and illustrations were edited using Gimp version 2.10.30 and Microsoft Word version 2108.

The length of individuals was measured after fixation on ethanol or formalin. These measurements may be inaccurate as the worms can contract when fixated directly on ethanol. According to Cadman and Nelson-Smith (1993) length of relaxed worms was 1.5-2.0 times the length of contracted specimens. Branchia may also contract, making the examination of these structures difficult. The specimen measurements in this study are done by stretching the worms and making an as accurate as possible observation of the actual length. Since this is done by hand, there is some uncertainty on accuracy regarding length. However, it gives an approximate indication sufficient to recognize and distinguish when different morphological traits appear or disappear. Measurements of the smallest material were done with a Leica M165 C with a millimetre scale paper (Fig. 7). The length measurements are somewhat approximately read as there is a limit to how much one can stretch a worm before it breaks. The tweezers break the water, making the lines on the millimetre scale paper bend somewhat (Fig. 7). The adult specimens were measured using millimetre scale paper without stereo microscope.

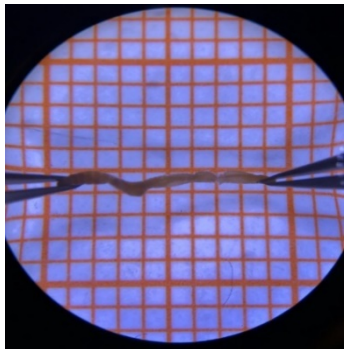

Figure 7: Photo of how length was measured on the smallest material, here an *Arenicolides ecaudata* (NTNU-VM 83954). Photo: Marthe Ree Dille.

Methyl blue was applied to some of the Arenicolidae to see if it could help identify the assumed *A. defodiens*. It did not seem to be any difference in the appearance of the worms. Therefore, this was not further used.

2.4 DNA barcoding

Some of the material from mentioned fieldwork was sent to DNA barcoding in Canada to expand the BOLD systems records of Arenicolidae. This also included some available material from earlier fieldwork fixated on ethanol, existing in storage of NTNU University Museum in Trondheim. Samples for DNA barcoding were collected from the individuals by using a scalpel and a pincer. The scalpel and pincer were put in 96% ethanol to sterilize them. These were used to cut out a small part of the body wall of large specimens, while the posterior part of small specimens was taken. The tests were placed in Eppendorf tubes with 96% ethanol and appurtenant museum number.

3. Results

3.1 Species description

3.1.1 Arenicola marina Linnaeus, 1758

Material examined

NTNU-VM 14800 (1), NTNU-VM 14801 (1), NTNU-VM 14802 (1), NTNU-VM 14804 (1), NTNU-VM 14805 (1), NTNU-VM 14806 (1), NTNU-VM 14807 (1), NTNU-VM 14823 (6), NTNU-VM 14824 (1), NTNU-VM 14825 (1), NTNU-VM 14846 (1), NTNU-VM 14847 (1), NTNU-VM 14899 (3), NTNU-VM 14901 (2), NTNU-VM 14903 (2), NTNU-VM 14905 (5), NTNU-VM 14906 (3), NTNU-VM 14907 (1), NTNU-VM 14909 (1), NTNU-VM 65076 (1), NTNU-VM 65077 (2), NTNU-VM 69440 (3), NTNU-VM 70330 (1), NTNU-VM 70331 (1), NTNU-VM 70332 (1), NTNU-VM 70333 (1), NTNU-VM 70334 (1), NTNU-VM 72280 (3), NTNU-VM 72281 (2), NTNU-VM 72282 (1), NTNU-VM 72283 (1), NTNU-VM 73647 (1), NTNU-VM 75207 (2), NTNU-VM 76495 (2), NTNU-VM 83920 (2), NTNU-VM 83921 (1), NTNU-VM 83922 (1), NTNU-VM 83923 (1), NTNU-VM 83924 (2), NTNU-VM 83927 (5), NTNU-VM 83928 (1), NTNU-VM 83929 (1), NTNU-VM 83930 (1), NTNU-VM 83931 (1), NTNU-VM 83936 (1), NTNU-VM 83939 (5), NTNU-VM 83944 (2), NTNU-VM 83945 (1), NTNU-VM 83958 (1), NTNU-VM 83960 (9), NTNU-VM 83961 (1), NTNU-VM 83962 (1), NTNU-VM 83963 (1), NTNU-VM 83964 (1), NTNU-VM 83967 (1), NTNU-VM 83970 (1), NTNU-VM 83973 (4), NTNU-VM 83974 (3), NTNU-VM 83978 (1), NTNU-VM 83979 (3), NTNU-VM 83980 (4), NTNU-VM 83986 (1), NTNU-VM 83987 (1), ZMBN 47667 (2), ZMBN 147152 (1).

Description

Body regions. The body of *A. marina* has 19 chaetigerous segments and can be divided into three regions. Anterior on the worm is an apodous “head” without palps, cirri, or other appendages. Middle region, or “body”, with parapodia and branchia. Posterior is a tail without branchia and parapodia (Fig. 8A).

Prostomium and peristomium. Head is achaetous. Consists of prostomium, peristomium with proboscis, and the following achaetous segments (Fig. 8A).

Proboscis. This sac-like structure can be everted and has many small papillae in circular arrangement (Fig. 8A,D). Proximal on the proboscis, the papillae are large, while distally, small.

Trunk region. Trunk region with distinct annulations, divided into five rings per segment (Fig. 8C). Chaetigers are somewhat thicker than the annulations between chaetigers throughout the entire specimen. The annulation formula is 2-3-4. On the 7th chaetiger, the branchia appears, the first pair often reduced in size. Chaetiger 7-20 is branchial, equal to 13 pairs of branchia in total.

Parapodia. Notopodia is a flap-like structure extended from the body wall (Fig. 8B). Proximal to the body wall, the notopodia looks like a volcano-shaped skin flap, which distally ends in a rounded flap divided into two lateral sections. Between these two sections, the hair-like chaetae emerge. Neuropodia is a long line of hook-like chaetae which may give a shiny glance in the stereo microscope (Fig. 8C).

Chaetae. Hair-like when emerging from the notopodium (Fig. 8B). They are emerging through the body wall, and when pulling them off the animal, they seem much longer than first assumed. Chaetae in the neuropodium are much shorter and may seem like short hooks in a long line (Fig. 8C).

Branchia. Branchia is attached to the body wall inferior to the notopodia (Fig. 8B). The stem is as broad as the notopodium. The stem of the branchia continues to be this broad for 1/3 of the length. It then gets broader and continues into a fan-like structure. After about ½ of the total length, the branchia starts to ramify. First it ramifies in thick stems, which gets thinner during subsequent ramification. A palmar membrane is present (Fig. 8B).

Tail region. The tail is achaetous and abranchial but has many small papillae in transverse rows throughout the entire length (Fig. 8A). It mostly appears to be thinner than the previous section. Ring annulations are not apparent in the tail. At the end of the tail is the pygidium, without any appendages.

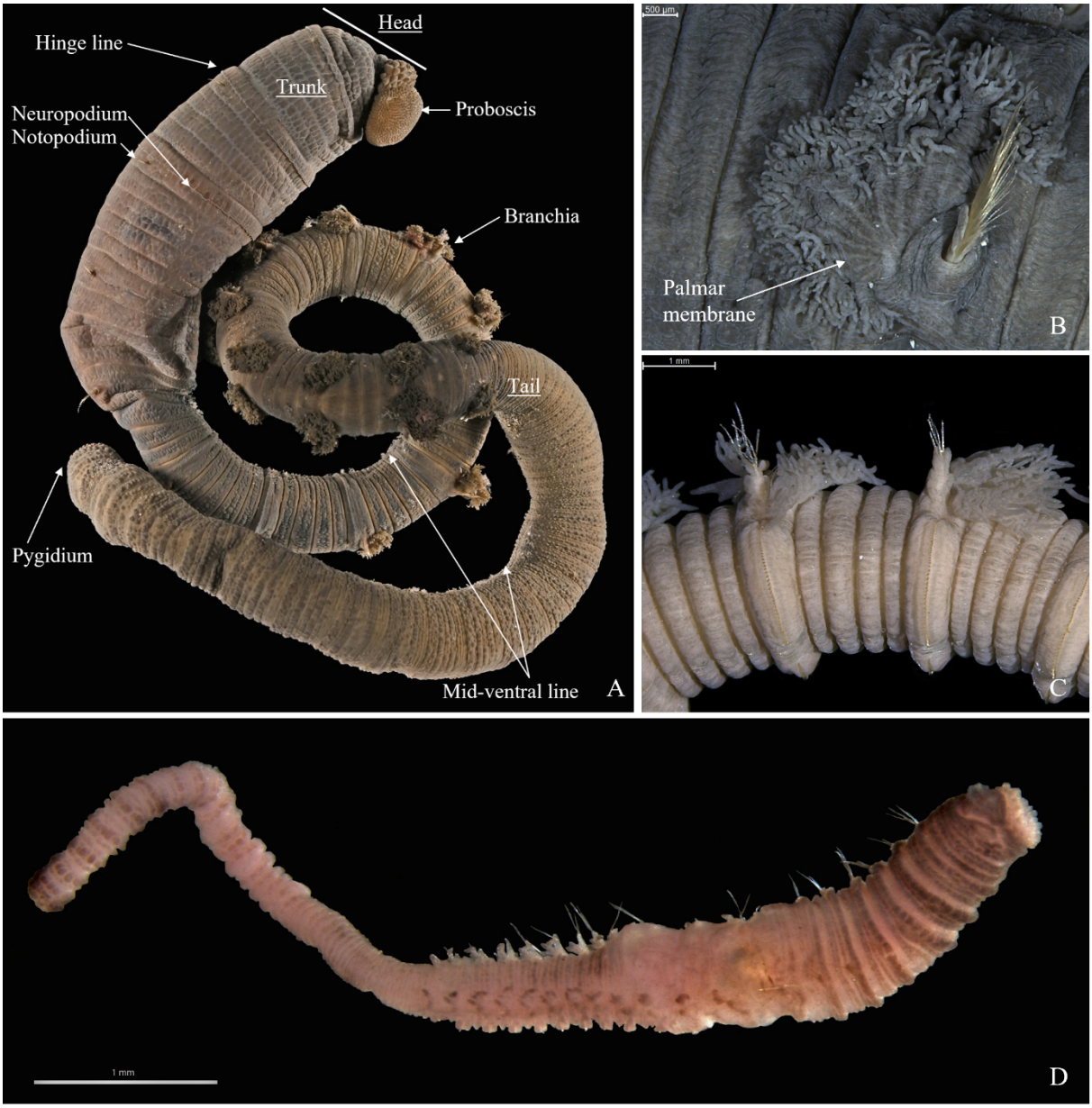

Figure 8: *Arenicola marina.* A: the three body parts are marked with underscored writing at the start of the region. The specimen measures 246 mm (NTNU-VM 83980). B: 9th branchiae with palmar membrane (NTNU-VM 83986). C: Chaetiger 11 and 12 with notopodium, neuropodium and branchia (NTNU-VM 14807). D: Post-larval specimen of *Arenicola* sp. measuring 6 mm showing tripartition (NTNU-VM 83938). Photo: Marthe Ree Dille.

Variation

The material examined ranges from 3-246 mm in length. Reported length from literature includes 25-109 mm (Brind & Darbyshire, 2015) and an average length of 180-230 mm, with larger obtained specimens measuring 360 mm in length (Ashworth, 1912).

On small individuals, the branchia first appears as a small outpouching of the body wall, like a wart. Then it elongates to a slender digitate branchia. Next follows the appearance of more digitate branches (Fig. 8D). The branches become numerous before they grow and resemble the

adult branchiae in the end. The development of branchia is not proportional to the length of the worm. Some individuals may be equally long but have very different branchiae structure. While some worms measuring 5 mm have branchia, others also measuring 5 mm are abranchiate (see Fig. 19 below).

Two of the individuals, NTNU-VM 83931 (125 mm) and NTNU-VM 83987 (165 mm), has on one side 14 branchiae. The first specimen (Fig. 9) has one extra notopodium behind this 14th branchia, which has developed on the tail. Both specimens lack neuropodium on this segment. The latter specimen has a neuropodium on the opposite side of the 14th branchia. Both specimens have the first branchia appearing on the 7th chaetiger, which is reduced as usual. The fourteenth branchia on the 20th chaetiger seems fully developed. It is known that sometimes the branchia may appear on the 6th chaetiger, and occasionally there are 14 pairs of branchia (Brind & Darbyshire, 2015).

Remarks

Between chaetigers, there are small annulations that vary in size and clearness among individuals. Some large specimens seem to have stretched annulations and chaetigers, while smaller specimens seem to have more distinct protruding annulations and chaetigers. In some cases, the chaetigers can be so bloated that it is challenging to count ring annulations between them, which is an important character in distinguishing between *A. marina* and *A. defodiens.* In the case of *A. marina,* the ring formula is 2-3-4, while *A. defodiens* has 2-2-4. This last ring on the second chaetiger can sometimes hide under the third chaetiger and trick the examiner into thinking it is an *A. defodiens*. The annulations can be difficult to count as the animal can be contracted because of rhythmic contractions of the body (Cadman & Nelson-Smith, 1993). Also, one must be aware that the chaetiger has a hinge line, which can be distinct and resemble the end of the chaetiger. A good indication is to examine the notopodium as they are situated posterior of the hinge line on a chaetiger.

One of the study's aims was to contribute to the DNA library regarding the family Arenicolidae. The material sent to DNA barcoding contained eight specimens. Morphological examination identified six of these as *A. marina,* and two as *A. ecaudata*. No results are available at this moment.

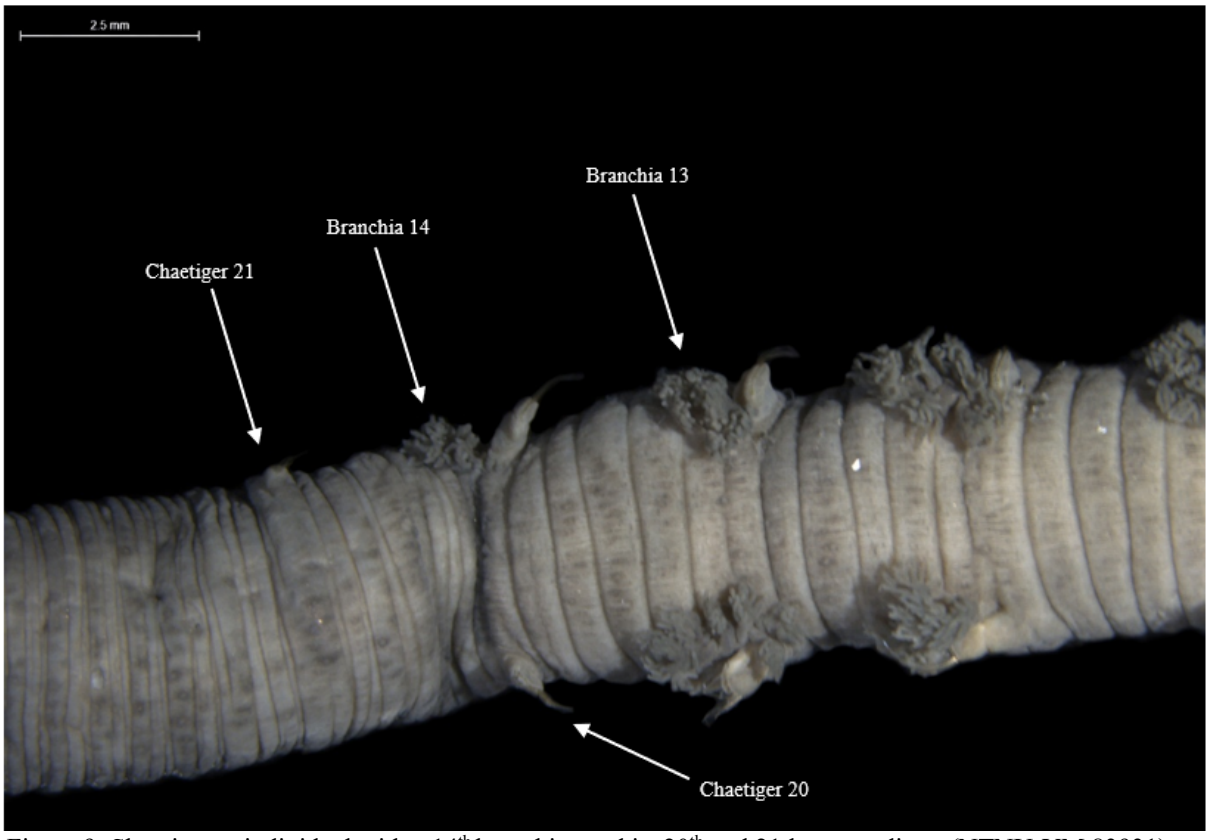

Figure 9: Showing an individual with a 14th branchiae and its 20th and 21th parapodium. (NTNU-VM 83931). Photo: Marthe Ree Dille.

Distribution

The material studied is from the Norwegian coastline, with records from Sandnessjøen in Nordland south to Sandefjord in Vestfold and Telemark. Nordland: Nye skorpa in Sandefjord. Trøndelag: Gjerdinga, Grandefjæra, Hopavågen, Indreøypollen, Leite, Lorvik, Mannbruholmen, Prestvågen, Ramsøyvika, Rataren, Rakkavika, Slettvik, Storfosna, Sund, Tindvika, Øyamelen and Øysand. Møre og Romsdal: Bjørnslykkestranda. Rogaland: Bøvågen, Hinna and Karmsundet. Vestfold og Telemark: Sandefjord. Vestland: Inderøypollen; os. Viken: Hvaler and Træla.

Arenicola marina is distributed in the North Atlantic Ocean north of 41° N latitude, the northern part of the western Mediterranean, and southern parts of the Arctic Ocean (Ashworth, 1912). It is widely distributed around the UK (Brind & Darbyshire, 2015). With findings in Spain and Portugal (Pires et al., 2015), Dutch Wadden Sea (Beukema & De Vlas, 1979), Arctic, North Pacific, North Atlantic to the Mediterranean, the Adriatic Sea and the Black Sea, to the English Channel, entire North Sea, Kattegat, western and central Baltic Sea to Rügen (Hartmann-Schröder, 1996).

The examined material ranges from depths of 0-140 m (Fig. 10). Not all material has depth reported and is therefore not included in Figure 10. Most adult individuals are found in the littoral zone, while some measuring 165 mm and 74 mm are found at depths of 10 m and 51 m, respectively. One specimen measuring over 115 mm are found at 107 m depth. Most of the smallest individuals are sampled at 22-140 m, while one measuring over 5 mm is found in the littoral zone.

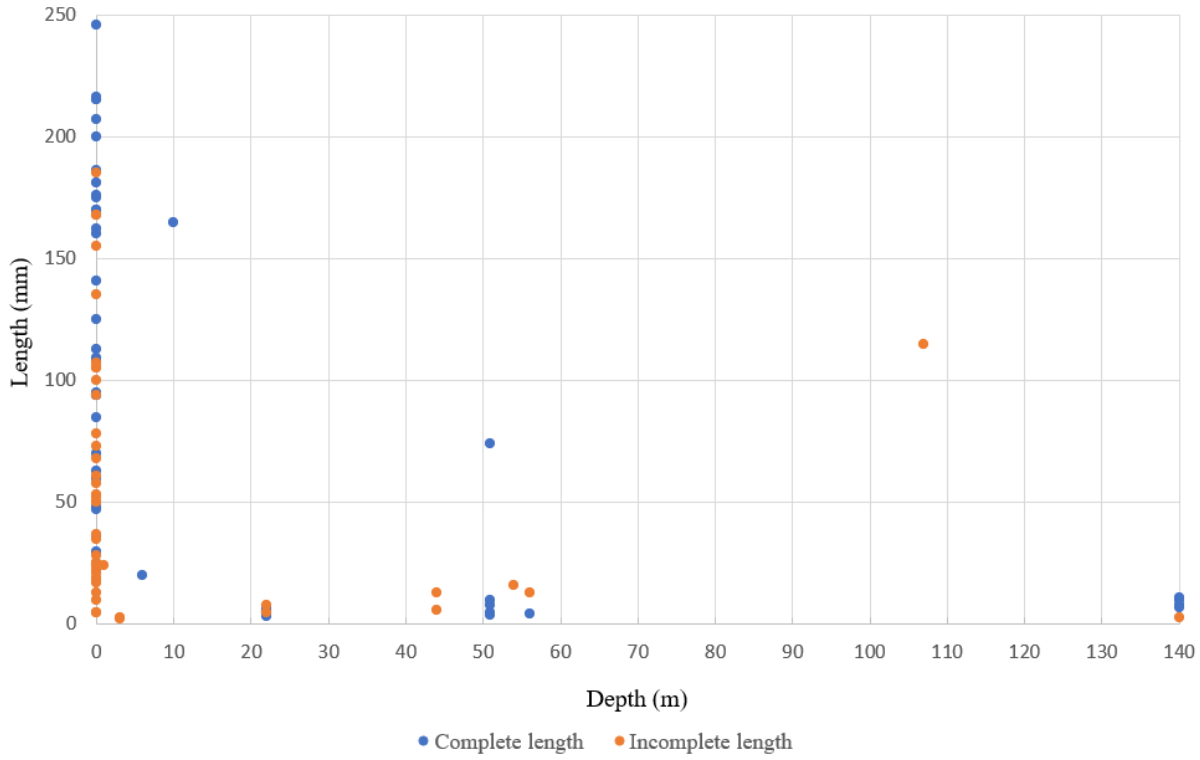

Figure 10: Depth distribution of 102 individuals of *Arenicola marina* at different body lengths. The blue circles are complete worms, while the orange circles are incomplete worms, e.g., lacking the tail or head. Not all worms from examined material have reported depth and are therefore not included in the figure.

Habitat

The material collected during the fieldwork was all found on soft bottom substrate on sandy beaches and were all adult *A. marina*. Remaining adult *A. marina* material is reported to be collected from soft bottom, shell sand, and sand. The small *A. marina* is reported from shell sand, sand, and gravel. Most of the material on *A. marina* has not reported habitat descriptions.

Arenicola marina bury in a U-shaped burrow down to 20-30 cm. They are to be found between the feeding depression (Cadman & Nelson-Smith, 1990) and the surface cast, which is quite messy (Brind & Darbyshire, 2015) (Fig. 11).

Figure 11: Surface cast and feeding depression of *Arenicola marina*. Photo: Marthe Ree Dille.

3.1.2 *Arenicola defodiens* Cadman & Nelson-Smith, 1993

This species description for *A. defodiens* is exclusively based on literature (Brind & Darbyshire, 2015; Cadman & Nelson-Smith, 1993), as the material for this study does not include *A. defodiens*.

Description

Body regions. The body of *A. defodiens* has 19 chaetigerous segments and can be divided into three regions. Anterior on the worm is a "head." Middle region, or "body," with parapodia and branchia. Posterior is an abranchial and apodous tail.

Prostomium and peristomium. Head is achaetous. Consists of prostomium, peristomium, and the following achaetous segments.

Proboscis. Eversible structure with many papillae, proximally large and distally small. The large papillae are chitinous-looking with black tips.

Trunk region. Segments are divided into distinct annulations, where one of them is somewhat thicker and bears the parapodia. The annulation formula is 2-2-4. On the 7th chaetiger, sometimes 6th, the branchia appear. Chaetiger 7-19 is branchial, equal to 13 pairs of branchia in total, occasionally 14 pairs.

Parapodia. Notopodia is a button-like structure from which long hair-like chaeta protrudes. There is dark shading around the outer edge of the anterior face of the notopodium. Neuropodia is a long line of hook-like chaeta.

Chaeta. Projections from the parapodia. Hair-like when emerging from the notopodium, hook-like when emerging from the neuropodium.

Branchia. Branchia is attached to the body wall dorsal and posterior to the notopodium. A palmar membrane is present. The branchia has 11-14 stems with 8-14 lateral branches.

Tail region. The tail is achaetous and abranchial.

Remarks

The reported length includes 122-232 mm (Brind & Darbyshire, 2015) and 80-270 mm (Cadman & Nelson-Smith, 1993).

Both type of chaetae and the shape of lobes in parapodia is described to be similar between *A. defodiens* and *A. marina* (Brind & Darbyshire, 2015).

During the examination of the museum material, four worms stood out, seemingly having the annulation formula characteristic of *A. defodiens* (Fig. 12). However, this is not enough to identify them as *A. defodiens* because of the mentioned deviation in annulation formula in *A. marina* (Cadman & Nelson-Smith, 1993). According to a study by Cadman and Nelson-Smith (1993) the annulation pattern characteristic for *A. marina* is in 4.4% cases incomplete or, in 2.2% cases absent altogether. This is supported by Luttikhuizen and Dekker (2010), who found 2.3% of *A. marina* in their study with annulation formula 2-2-4. Because of rhythmic contractions of the body and the branchia, the worms studied must be relaxed prior to measurement of their length and observation generally. When describing branchia, Ashworth (1912) also mentions that when specimens are thrown directly into strong alcohol, the branchia may contract to such an extent that their branching can be challenging to describe. Additional features used to distinguish the two species include branchia structure and faecal cast structure (Cadman & Nelson-Smith, 1993).

When examining the branchiae of one of the suspected *A. defodiens* it became clear that it was *A. marina* (Fig. 12B), as the specimen had branchiae corresponding to the number of stems and lateral branches of *A. marina.* The remaining three (Fig. 12A,C,D) were identified as *Arenicola* sp. because of reduced branchiae, lack of branchiae as it was torn off after the 6th chaetiger, and underdeveloped branchiae, respectively.

The consulting company Rådgivende biologer reported a finding of *A. defodiens* in Norway, which is the one finding in the map retrieved from NBIC (Fig. 1). This material was examined and identified as one *A. marina* (NTNU-VM 83978) and three *Arenicola* sp. (NTNU-VM 83977). The former was identified as *A. marina* because the annulation formula was 2-3-4, which was underdeveloped in the other three. Because of this, the branchiae were examined. Also, them being underdeveloped. Not unexpected as these specimens measured somewhere around 6-8 mm, as all were incomplete. The largest individual measured 17 mm and was identified as *A. marina*.

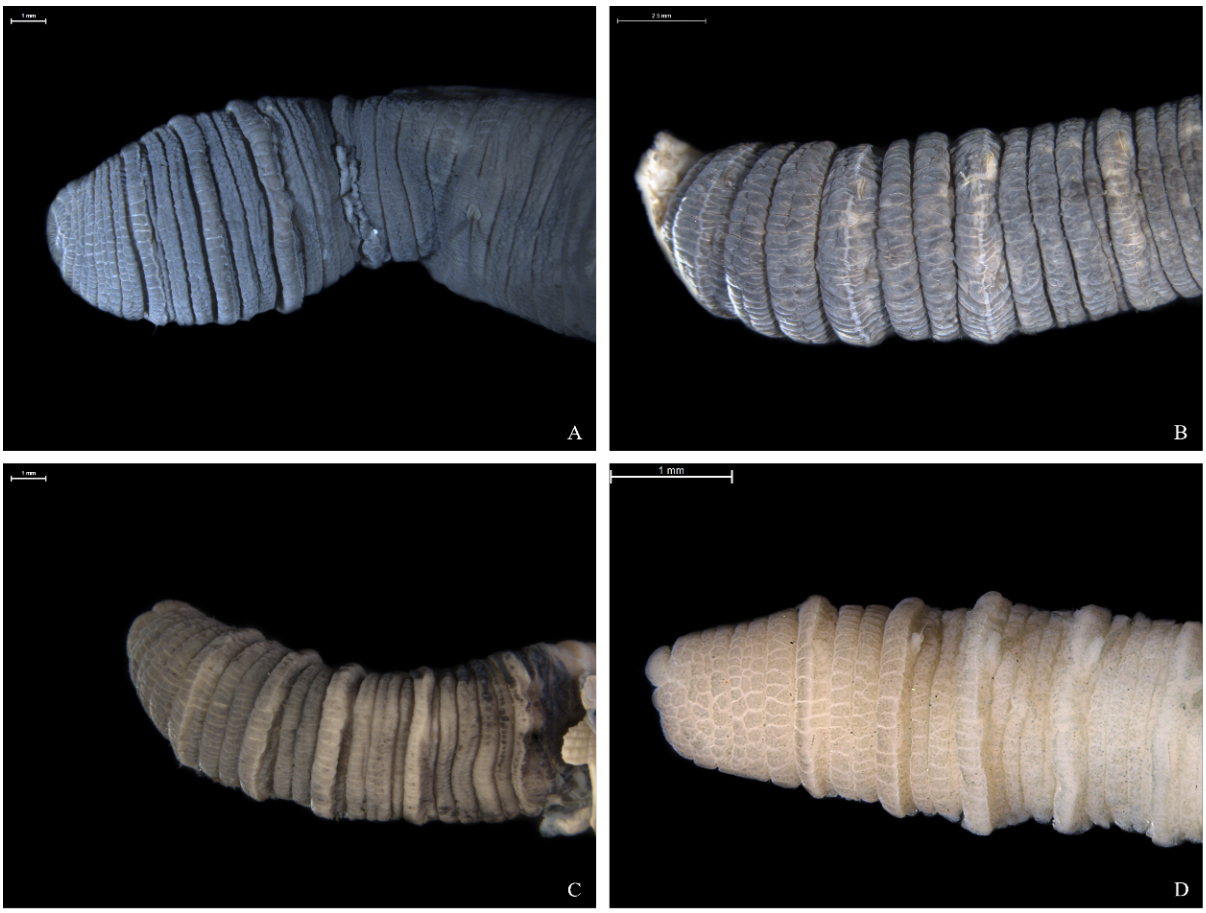

Figure 12: The material examined with annulation formula 2-2-4, consistent with *Arenicola defodiens*. A, C, D: *Arenicola* sp. (NTNU-VM 83982, NTNU-VM 83984, NTNU-VM 83985). B: *Arenicola marina* (NTNU-VM 83983). Photo: Marthe Ree Dille.

Distribution

Arenicola defodiens have records from Skagerrak, the North Sea, and western Wadden Sea (Luttikhuizen & Dekker, 2010), as well as localities around south-west Wales and south Wales (Brind & Darbyshire, 2015; Cadman & Nelson-Smith, 1993), England and Ireland (Brind & Darbyshire, 2015). It is also reported from the Iberian Peninsula in the Ria de Aveiro lagoon

(Pires et al., 2015). The report from Skagerrak is from Koster Island in Sweden (Luttikhuizen & Dekker, 2010).

Habitat

Arenicola defodiens inhabits moderately exposed sandy beaches but not in estuaries in contrast to *A. marina*. It is found at mid-tide level or below but reaches maximum abundance at spring tides low water, where it extends sub-tidally to an unknown extent. When co-existing with *A. marina* it appears lower on the beach (Cadman & Nelson-Smith, 1993).

Figure 13: Surface cast and feeding depression of *Arenicola defodiens*. Photo: A.S.Y. Mackie. From: (Darbyshire, 2020).

Arenicola defodiens bury almost vertically down in a J-shape below a neatly coiled cast, with a feeding depression in the middle (Fig. 13) (Brind & Darbyshire, 2015). The feeding depression may be hard to spot (Pires et al., 2015), as it may be more inconspicuous than Figure 13 shows. The worm lays with its head downwards and can extend to depths of 50-100 cm (Cadman & Nelson-Smith, 1990).

3.1.3 *Arenicola* sp. Lamarck, 1801

Material examined

NTNU-VM 75885 (1), NTNU-VM 83938 (6), NTNU-VM 83948 (1), NTNU-VM 83953 (2), NTNU-VM 83959 (6), NTNU-VM 83965 (1), NTNU-VM 83968 (1), NTNU-VM 83969 (1), NTNU-VM 83971 (1), NTNU-VM 83972 (1), NTNU-VM 83975 (3), NTNU-VM 83976 (2), NTNU-VM 83977 (3), NTNU-VM 83981 (1), NTNU-VM 83982 (1), NTNU-VM 83984 (1), NTNU-VM 83985 (1).

Remarks

Examined material measures from 3 mm to over 87 mm. Some of the material could not be identified as either *A. marina* or *A. defodiens*. This is both because some of the individuals were very small, so the ring formula could not be seen, and the branchia was underdeveloped, while others missed the first segments. In the latter case, one only had the branchia to examine. Some of these specimens were identified to genus because of underdeveloped branchiae, while others had reduced branchiae.

Depth distribution for the material identified as *Arenicola* sp. ranges from 0-97 m and measures 3 mm to over 87 mm (Fig. 14). Not all material has depth reported and is therefore not included in results about depth. Specimen measuring under 10 mm are found at depths of 22-97 m, with one exception measuring 7 mm found in the littoral zone. One incomplete specimen measuring 9 mm are found at 54 m depth and may be measuring over 10 mm when complete. The largest specimens are found in the littoral zone.

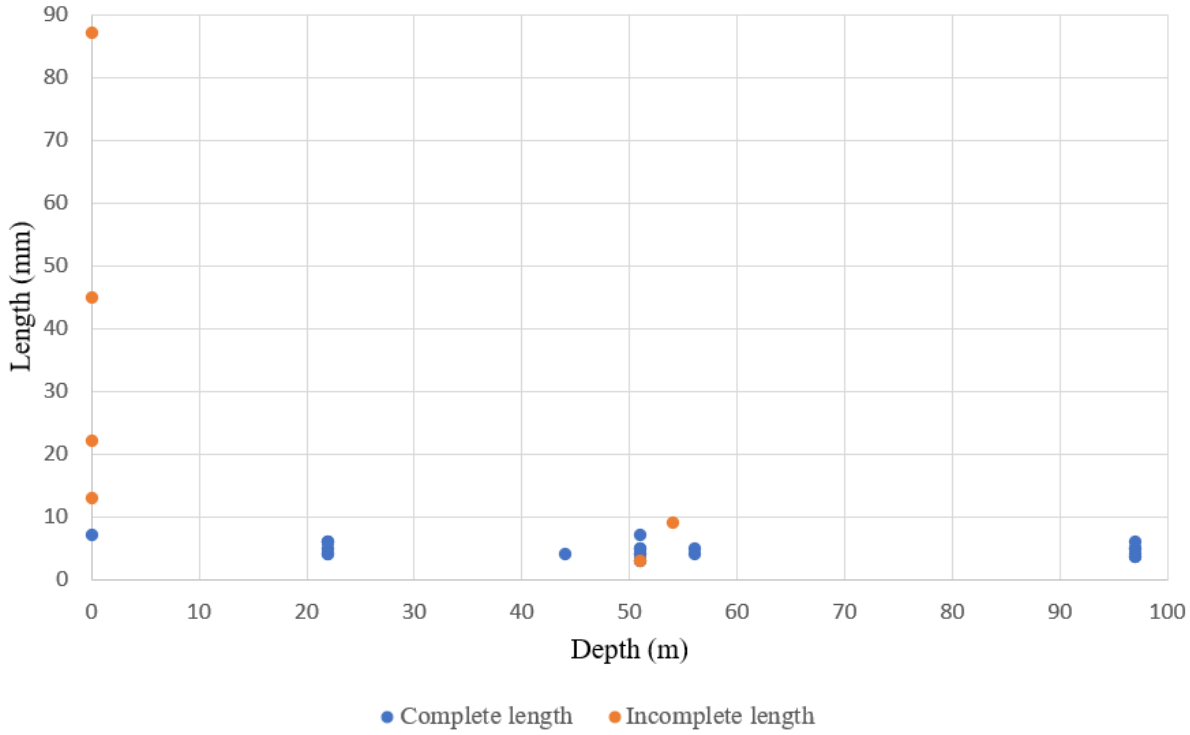

Figure 14: Depth distribution of 29 specimens of *Arenicola* sp. at different lengths. The blue circles are worms at complete length, while the orange circles are worms which are incomplete, e.g., lacking the tail or head. Not all worms examined have reported depth and are therefore not included in the figure.

3.1.4 *Arenicolides ecaudata* Johnston, 1835

Material examined

NTNU-VM 83925 (1), NTNU-VM 83926 (1), NTNU-VM 83932 (2), NTNU-VM 83933 (2), NTNU-VM 83934 (3), NTNU-VM 83935 (2), NTNU-VM 83937 (2), NTNU-VM 83940 (2), NTNU-VM 83941 (1), NTNU-VM 83942 (1), NTNU-VM 83943 (1), NTNU-VM 83946 (1), NTNU-VM 83947 (1), NTNU-VM 83949 (2), NTNU-VM 83949 (2), NTNU-VM 83950 (9), NTNU-VM 83951 (1), NTNU-VM 83952 (6), NTNU-VM 83954 (1), NTNU-VM 83955 (2), NTNU-VM 83956 (1), NTNU-VM 83957 (1), NTNU-VM 83966 (1),
ZMBN 45880 (1), ZMBN 47668 (2), ZMBN 77503 (81), ZMBN 77505 (1),
ZMBN 77506 (2), ZMBN 77507 (8).

Description

Body regions. The body of adult *A. ecaudata* consists of 40-60 chaetigers divided into two regions (Fig. 15A). First 15-16 chaetigers abranchial, then 30-40 pairs of branchia. The anterior region is abranchial but bears parapodia, while the posterior region has parapodia and branchiae.

Prostomium and peristomium. Head is achaetous. Consists of prostomium, peristomium, and the following achaetous segments.

Proboscis. This sac-like structure can be everted and has large papillae proximal to the worm, decreasing in size as they get distal and seemingly absent most distally (Fig. 15A).

Trunk region. Chaetigers are broader and somewhat more bloated than the annulations between chaetigers. On chaetiger 15-16, the branchia appears and lasts for 30-40 segments (Fig. 15A). The last 1-7 chaetigers can be abranchial but can bear parapodium. These last abranchial segment(s) may bear both neuropodium and notopodium, one or none of the two. Pygidium is without any appendages (Fig. 15A).

Parapodia. Notopodium is a flap-like structure extended from the body wall (Fig. 15C,E). Proximal to the body wall, the notopodia looks like a volcano-shaped skin flap, which distally ends in a rounded flap divided into two lateral sections. The chaetae emerge between these two sections (Fig. 15C,E). The notopodia are somewhat reduced from their first appearance on the second segment but increase in size as the branchia appears. Neuropodia is a long line of hairs that may give a shiny glance in the stereo microscope (Fig. 15B,C). They are at extending from

right under corresponding notopodia and down until the body line under the worm from the second segment.

Chaeta. Shiny projections from the parapodium. Hair-like when emerging from the notopodium. They are emerging through the body wall, and when pulling them off the animal, they seem much longer than first assumed. Chaetae in the neuropodium are much shorter and may seem like short hooks in a long line (Fig. 15B,C).

Branchia. Branchia stems are thinner than the notopodium, and start to ramify after ¼ of the total length. Branchia is proximally somewhat fan-like shaped. In total, the branchia is ramified several times.

Variation

Examined material includes specimens ranging from 2-146 mm. The reported length from literature is 130-180 mm on average, and the largest encountered individual measures 255 mm (Ashworth, 1912).

The examined material contained specimens with annulation formula 2-4-4, while some had annulation formula 3-4-4. According to Wells (1950) the latter is correct. He explained the confusion of the former being caused by overlapping chaetigerous annuli so that the last annuli may be inconspicuous.

By examining mentioned material, some of the worms did not have the mentioned pairs of branchiae special for *A. ecaudata* (30-40 pairs, according to Hayward & Ryland). Some individuals in the examined material had 18, 21, 26, and 43 pairs of branchia. One specimen (NTNU-VM 83937) has developed two notopodia on one side of the worm, completely posterior. It only has notopodium on one of the sides and no neuropodium.

On the small specimen, the branchia first appears as a small outpouching of the body wall, like a wart. Then it elongates to a slender digitate branchia (Fig. 15D). Next follows the appearance of more digitate branches. The branches become numerous before they grow and resemble the adult branchiae in the end. The worm's length is not a certain measure of how large or well developed the branchiae are. Some individuals may be equally long but have very different structure of branchiae (Fig. 21). Some worms at 10 mm have branchia while others do not. The branchia may first appear some chaetigers behind their normal start within an adult, being the 15th or 16th chaetiger. The branchia will from there grow both forward and backward.

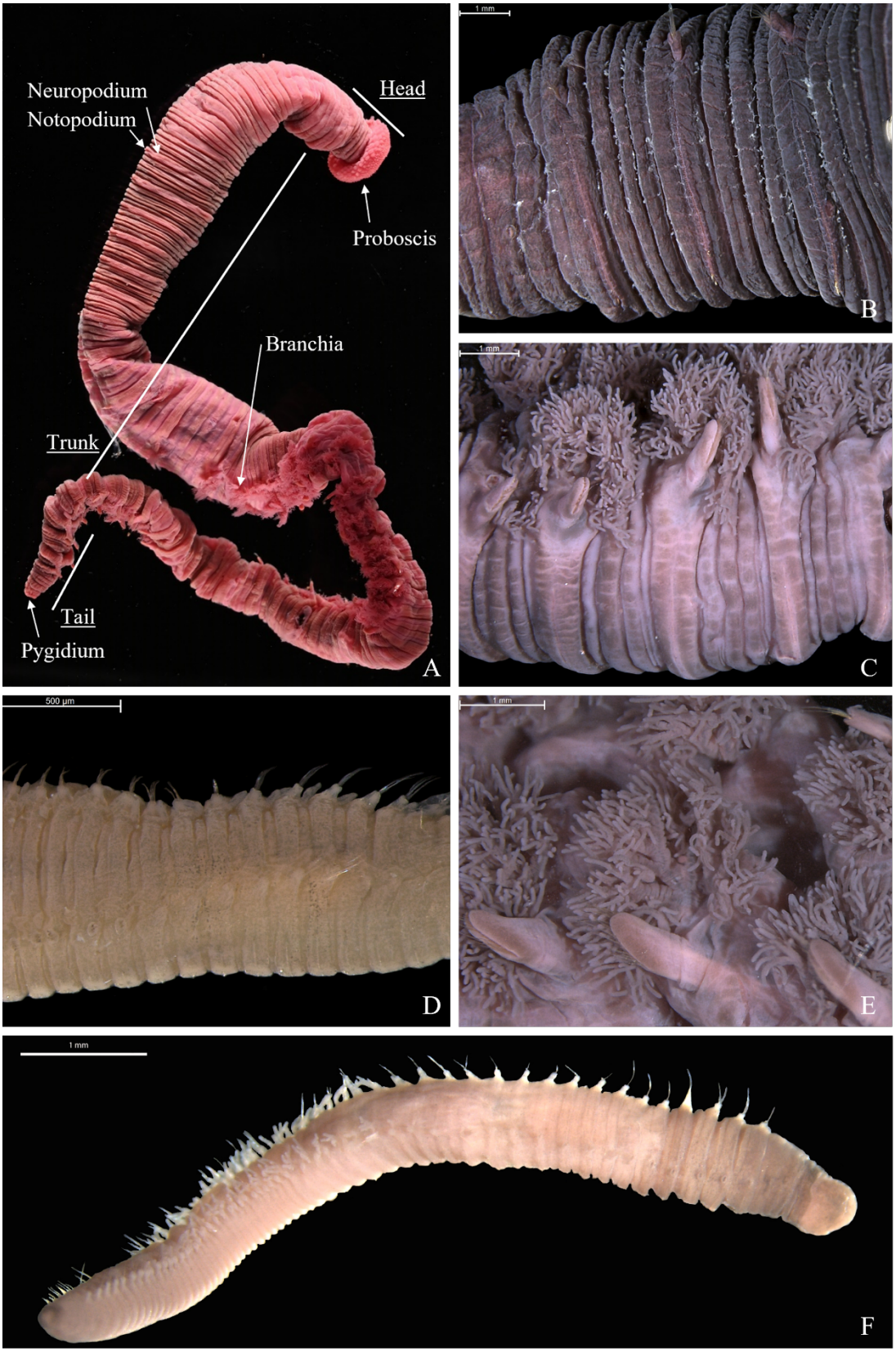

Figure 15: *Arenicolides ecaudata*. A: The three body regions are written in underscore and marked with lines. Specimen measuring 146 mm (NTNU-VM 83935). B: Chaetiger 1 and 2 with parapodium (NTNU-VM 83933). C: Branchiae and parapodia on chaetiger 20-22 (NTNU-VM 83932). D: Individual at 19mm showing typical branchia habitus on the posterior part of small individuals (ZMBN 77503). E: Adult branchiae at chaetiger 26 (NTNU-VM 83932). F: Post-larval individual measuring 7 mm (NTNU-VM 83946). Photo: Marthe Ree Dille.

Remarks

The annulation formula is not an important characteristic to distinguish *A. ecaudata* from *A. marina* since the body is divided into two regions, unlike three in *A. marina.* In addition, the branchia starts at a much later chaetiger (chaetiger 15-16) in *A. ecaudata* than in *A. marina* (chaetiger 7). However, it might be helpful for identification if one only has access to the first six chaetigers of a lugworm. The neuropodium is another useful character to distinguish species when possessing only some of the first chaetigers. In *A. ecaudata* these extend from notopodium and completely to the worm's ventral side throughout the worm's length (Fig. 2D). As opposite to *A. marina* where the neuropodium on the first five chaetigers is much smaller, almost the length of the notopodium (Fig. 2C).

Distribution

From the examined material records of *A. ecaudata* stretches from Gjerdinga in Trøndelag south to Karmsundet in Rogaland. Trøndelag: Gjerdiga, Håbranden, Indre Skjervøy, South end of Kråkøya, dock north of Kommersøya, Nordskag and Rataren. Møre og Romsdal: Brunsvik, Suholmen and Sotra. Vestland: Bekksneset, Inderøypollen; os, Juvika and Kviturdvikspollen biological station. Rogaland: Karmsundet.

Arenicolides ecaudata has records from western Norway (Ringvold et al., 2000), eastern north-Atlantic to west Mediterranean, the English Channel, northern and southern North Sea to Skagerrak (Hartmann-Schröder, 1996; Knight-Jones et al., 2017). It also occurs on the Swedish coast and along the Norwegian coast from Stavanger to Trondheim. To summarize, the distribution is the coasts of north-western and western Europe above the 45° N latitude (Ashworth, 1912).

Large individuals ranging from 98 mm to 135 mm are found at depths around 200 m at several stations, with one as deep as 333 m. Not all material has depth reported and is therefore not included in depth results as visible in Figure 16. Some of the other smaller individuals, ranging from 2.5 mm to 19 mm, are found at 8-10 m depth. One of the smaller individuals, measuring 7 mm, is found at 97 m. Another deep finding is of a 13 mm long worm found at 56 m depth. Most of the small individuals are found at 9 m because of a large sample from this area, containing 81 specimens.

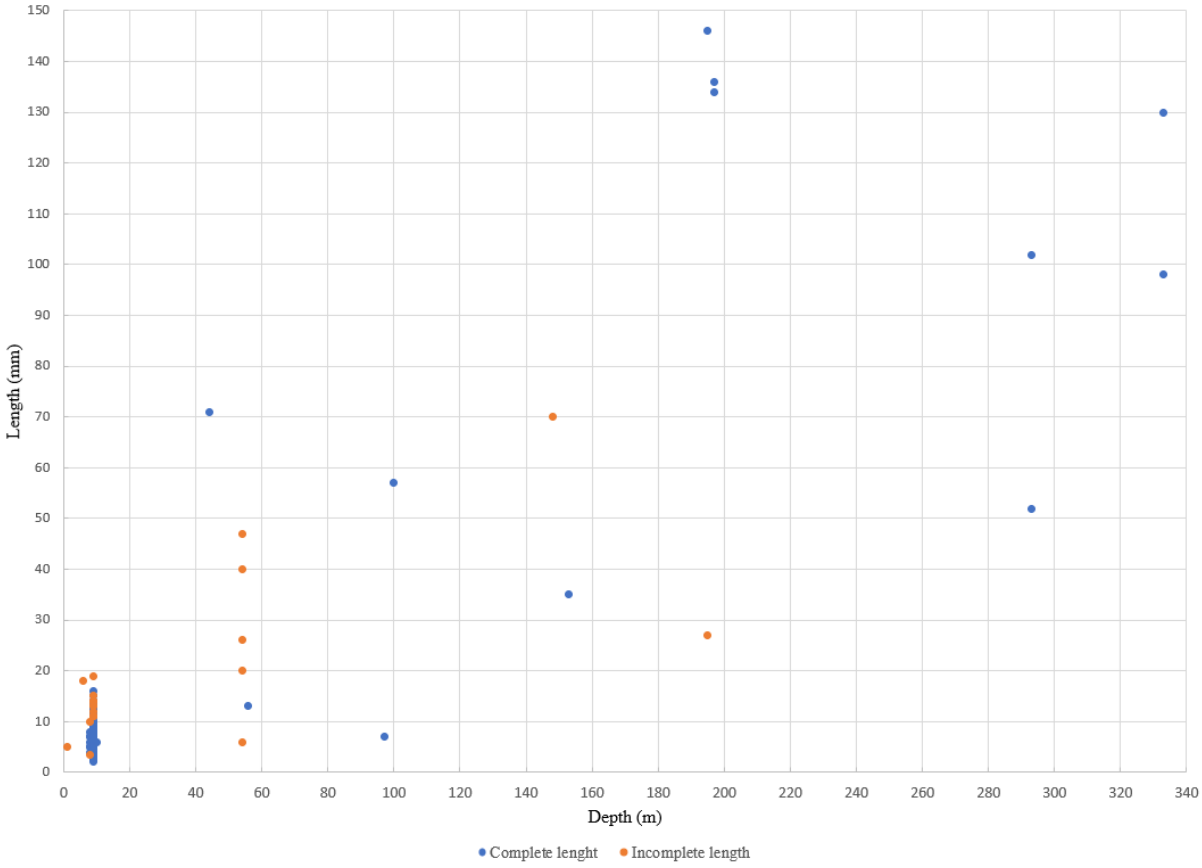

Figure 16: Depth distribution of 113 specimen of *Arenicolides ecaudata* at different lengths. The blue circles are worms at complete length, while the orange ones are worms which are incomplete, e.g., lacking the tail or head. Not all worms examined have reported depth and are therefore not included in the figure.

Habitat

The material containing small *A. ecaudata* is reported collected from rocky bottom, *Saccorhiza polyschides*, *Laminaria hyperborea,* scraping on plastic pontoons, sand, and shell sand. Adult *A. ecaudata* is reported from sand, mud, silt, clay, shell sand, and gravel. Mostly from shell sand and sand or silt.

Burrows are skewed and made in gravel or between stones. The surface cast is often hard to find since the habitat is so coarse that the material will not cohere and therefore easily fall apart. The surface cast is inconspicuous in its surroundings and is therefore easily overlooked (Ashworth, 1912).

3.2 Difference between post-larva specimen of *Arenicola marina* and *Arenicolides ecaudata*

3.2.1 Neuropodia

The neuropodia of *A. marina* and *A. ecaudata* differs in length and placement in relation to the notopodium. Neuropodium in *A. marina* is much shorter in the anterior region than *A. ecaudata*, both in small and adult individuals (Fig. 17). The neuropodia of both small and large specimen of *A. ecaudata* start straight beneath the notopodium and goes down to the mid-ventral line from the first chaetiger. Within *A. marina,* the neuropodium is very small for approximately the first five chaetigers before it gets longer and moves closer to the mid-ventral line. The neuropodium in *A. marina* reaches the mid-ventral line at around 8-10th chaetiger.

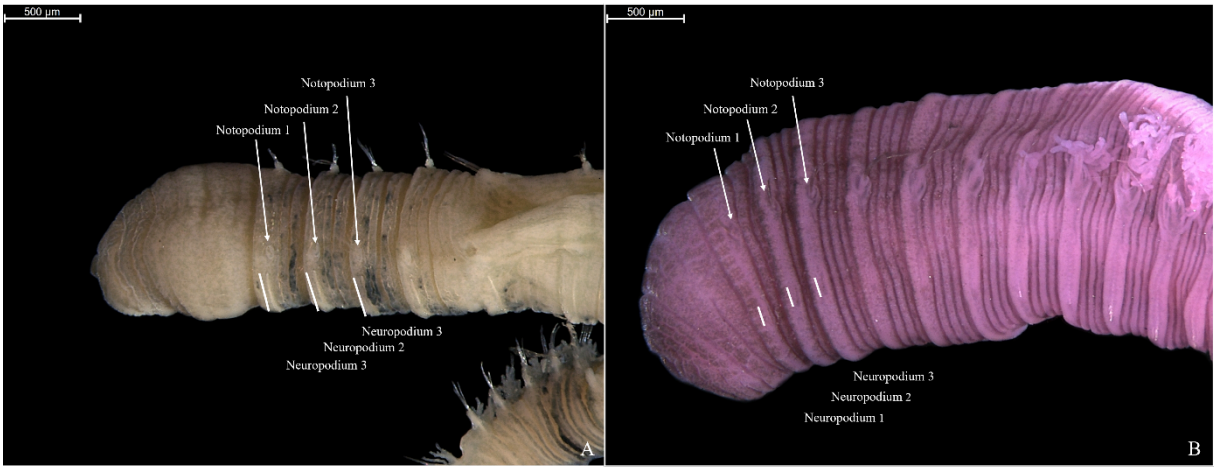

Figure 17: Illustration showing the three first notopodia and neuropodia, including length of the latter, on small specimen of *Arenicola marina* and *Arenicolides ecaudata.* A: *Arenicolides ecaudata* measuring 10 mm (NTNU-VM 83952). B: *Arenicola marina* measuring 11 mm (NTNU-VM 83939). Photo: Marthe Ree Dille.

3.2.2 Branchia as a function of length

The examination of branchia as a function of length is focused on small specimen. This is to illustrate how some of the different stages of branchia development look and to see if there is a certain length where the branchiae appear. Adult branchia is not a focus area in this thesis as they are already well discussed and pictured in literature. They also do not change their appearance when they have attained their adult form. The examination was based on complete specimen, which is a small portion of the material. Because of this, the figures regarding length and presence of branchiae stop at 11 mm length for *A. marina* and 19 mm for *A. ecaudata* (Fig. 19, 20).

The material studied contained 44 individuals of small *A. marina* and *Arenicola* sp. ranging from 2.5-11 mm. The branchia seems to arise when the worms are between 3-5 mm, as visible in Figure 19. There is, however, little material to say anything for certain. It is interesting that a 3 mm *Arenicola* sp. was found with branchia, whereas another at 5 mm was found without branchia. It could be that the branchia are reduced and therefore hard to spot.

Another interesting observation is that one specimen measuring only 3.5 mm has distinct annulations, while another measuring 5 mm does not. This is why some of the points in Figure 19 are at genus level, while others are at species level. An example of how the ring formula may look in small specimen is visible in Figure 18.

The material studied contained 109 small individuals of *A. ecaudata* ranging from 2-19 mm. The worms were examined for branchia especially, number of branchia, and where they start. This was challenging as the worm often twirl once or twice around its own axis. In the material, the worms with branchia range from 7 mm and up, and the specimens without branchia range from 2,5-13 mm. There is an overlap from 7-13 mm in abranchial and branchial worms. But as visible in Figure 20, there is a shift in how many of the worms has branchia or not from 7 mm to 10 mm.

Figure 18: Image showing how in some cases the ring formula may be hard to count as the animal is too small to have distinct rings or be somewhat broken in the area of interest. This individual measuring 4 mm was only identified to genus level, *Arenicola* sp. (NTNU-VM 83959). Photo: Marthe Ree Dille.

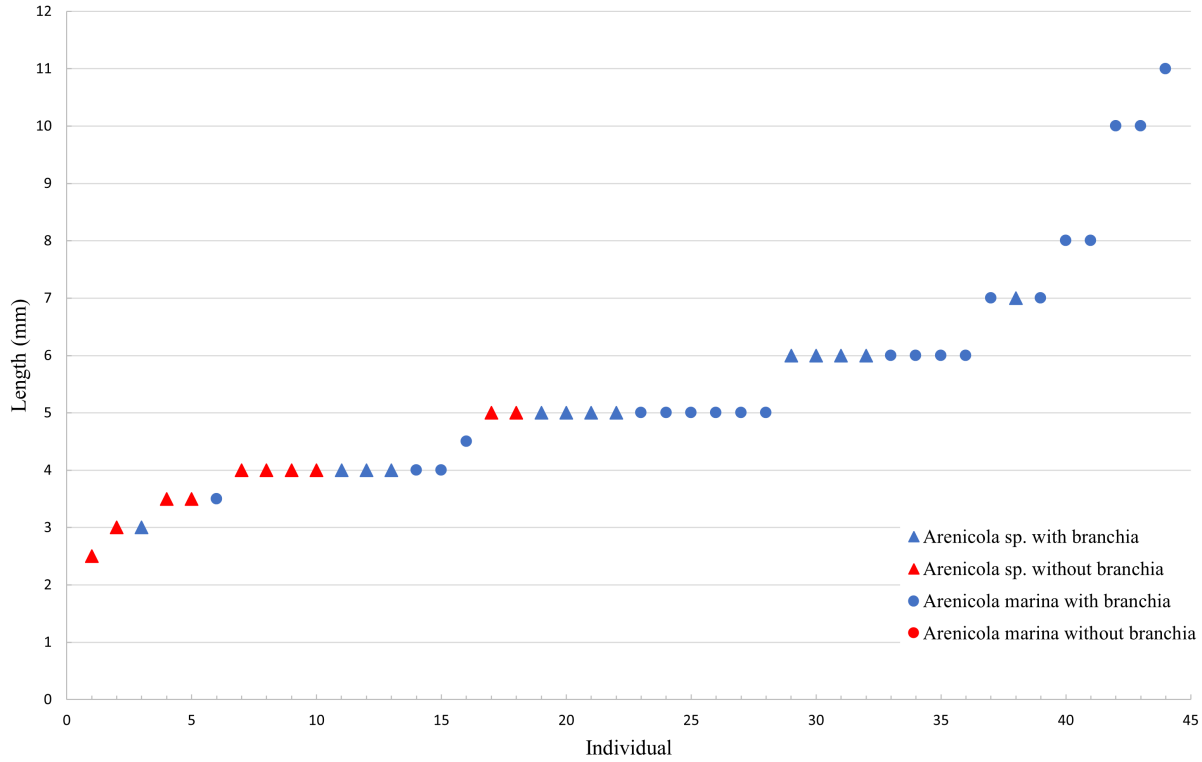

Figure 19: All complete specimens of *Arenicola* examined from the material, the incomplete ones could not give a reliable length measure and are therefore excluded. *Arenicola* sp. is triangles, while *Arenicola marina* is circles. The red triangles and circles mark the material without branchia. Some of the material is only at genus level because the annulation formula is not yet developed or difficult to count.

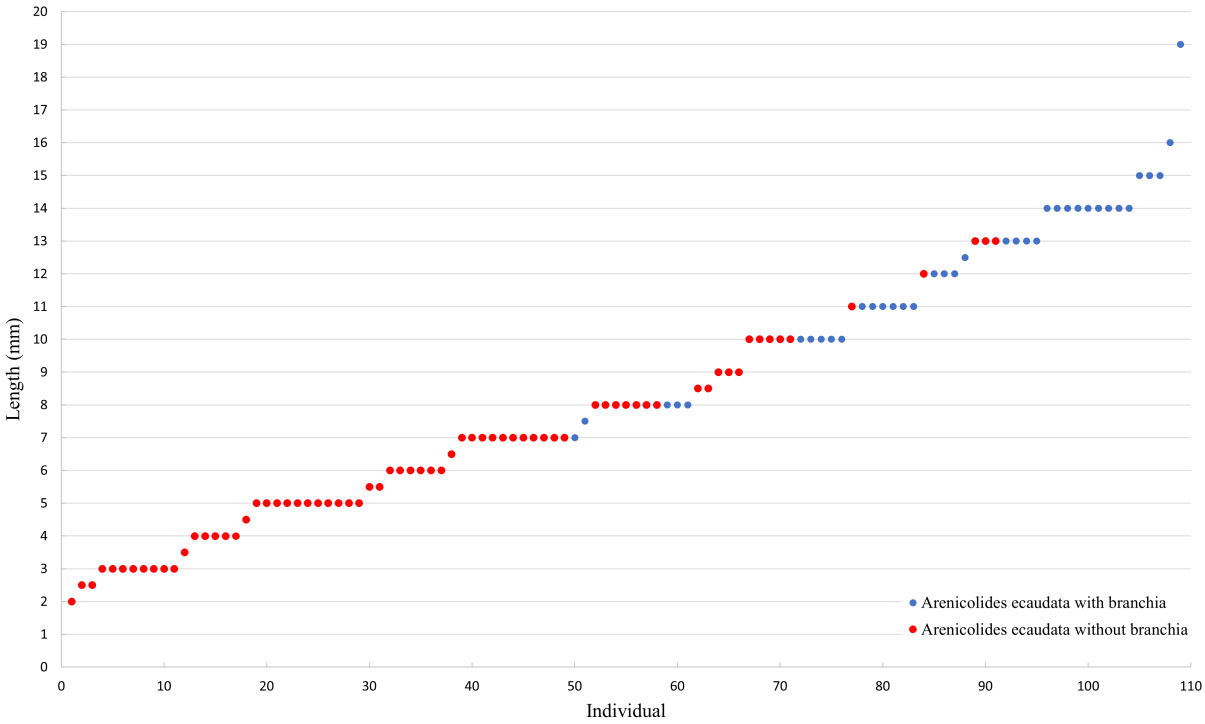

Figure 20: All complete specimens of *Arenicolides ecaudata* examined from the material, the incomplete ones could not give a reliable length measure and are therefore excluded. The red spots marks *A. ecaudata* without branchia.

3.2.3 Development of branchia

The development of branchia does not follow the length of either *A. marina* or *A. ecaudata*. On the small specimen, the branchia first appears as a small outpouching of the body wall, like a wart. Then it elongates to a slender digitate branchia. Next follows the appearance of more digitate branches. The branches become numerous before they grow and resemble the adult branchiae in the end. Figures 21 and 22 show the development described in increasingly developed branchiae for *A. ecaudata* and *A. marina*, respectively.

It is best to spot the neuropodia in silhouette on the smallest specimen. They are often very small and hard to spot without focusing and having a bright background. Often it is helpful to change the light in both direction it is coming from and its strength. When using LEICA M165 C, one can easily switch between different angles of light, and this can often be helpful in spotting neuropodia on the smallest worms. The same goes for branchia. They are easier to spot in silhouette, as visible in Figure 21B.

Figure 21: Branchiae development in *Arenicolides ecaudata*. A: Specimen at 11 mm (ZMBN 77503). B: Specimen at 13 mm (ZMBN 77503). C: Specimen at 19 mm (ZMBN 77503). D: Specimen at 7 mm (NTNU-VM 83946). E: Specimen at 10 mm (NTNU-VM 83952). F: Specimen at 43 mm (ZMBN 47668). Photo: Marthe Ree Dille.

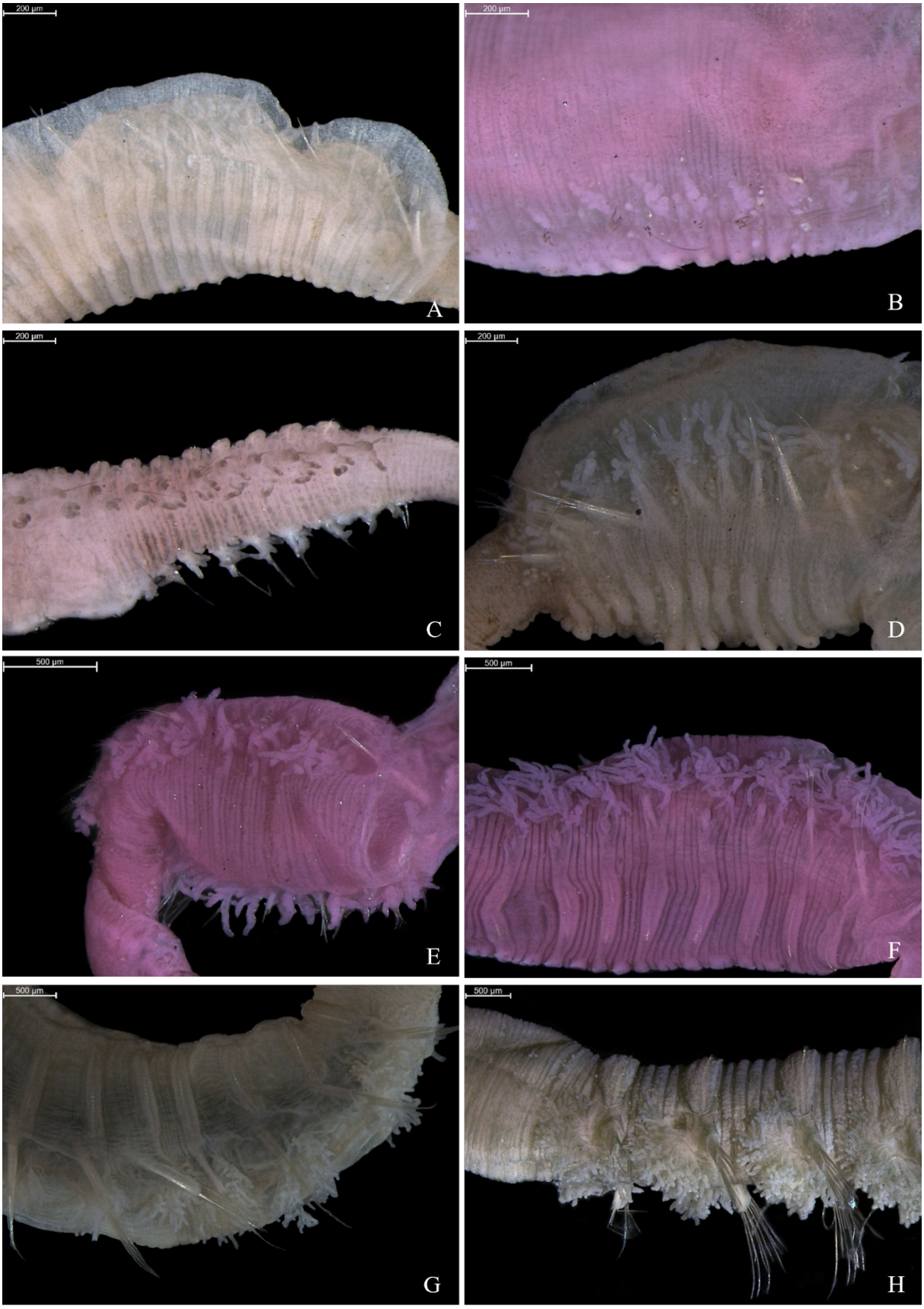

Figure 22: Branchia development in *Arenicola marina*. A: Specimen at 3 mm (NTNU-VM 83959). B: Specimen at 6 mm (NTNU-VM 83960). C: Specimen at 6 mm (NTNU-VM 83938). D: Specimen at 7 mm (NTNU-VM 83959). E: Specimen at 8 mm (NTNU-VM 83939). F: Specimen at 10 mm (NTNU-VM 83939). G: Specimen at 20 mm (NTNU-VM 83962). H: Specimen at 25 mm (NTNU-VM 72283). Photo: Marthe Ree Dille.

3.3 Comparison table

Differences between the examined species in the study are summarized in Table 1. The number of stems and branches in the branchia of *A. ecaudata* is not an important trait for distinguishing it from the other two species. Therefore, it is not investigated, nor included in the table. The depth distribution of *A. defodiens* is not included as there are no records of this.

Table 1: Comparison table of *Arenicola marina, Arenicola defodiens* and *Arenicolides ecaudata* containing some of the differences between the three species. Lengths contained in parentheses are lengths retrieved from literature. Where only one length is written in parentheses, it is the largest individual mentioned in literature. The number of stems and lateral branches in *A. ecaudata* is not investigated as it is not an important character for identification. The depth distribution of *A. defodiens* is not investigated. Burrow depth of *A. ecaudata* is not recorded.

Character	*Arenicola marina*	*Arenicola defodiens*	*Arenicolides ecaudata*
Body division	Three	Three	Two
Annulation formula	2-3-4	2-2-4	3-4-4
First branchia	7^{th} chaetiger	7^{th} chaetiger	15^{th} or 16^{th} chaetiger
Pairs of branchia	13 or 14	13 or 14	30-40
Branchia	8-12 stems, 3-6 lateral branches	10-14 stems, 9-12 lateral branches	-
First five neuropodia	Does not extend to the mid-ventral line	Does not extend to the mid-ventral line	Extend to the mid-ventral line
Length	3-246 mm (360 mm)	(80-270 mm)	2-146 mm (255 mm)
Habitat	Soft bottom substrate, shell sand, sand, gravel	Moderately exposed sandy beaches	Rocky bottom substrate, shell sand, sand, slit
Worm cast	Chaotic coiled	Neatly coiled	Unsuspicious
Burrow-shape	U-shaped	J-shaped	Skewed
Burrow depth	20-30 cm depth	50-100 cm depth	-
Depth distribution	0-140 m	-	0-333 m

4. Discussion

During this study, one can conclude that there are no reports of *A. defodiens* in Norwegian fauna. However, there is a need for more studies and different tools to prove its existence in Norway. The post-larval *A. marina* and *A. ecaudata* have different depth distributions, and the two species can easily be separated even when very small by examining neuropodia. The adult *A. marina* and *A. ecaudata* have different depth distributions as well. *Arenicolides ecaudata* is probably more common along the Norwegian coast than literature report. Therefore, there is a need for a new sampling of the species to find its true distribution. This study does not include any new identification key, as the one used (Knight-Jones et al., 2017) is sufficient to identify species one may encounter in Norway. The samples sent for DNA barcoding have not yet produced any results, but the contribution is made, as it is one of the study's objectives.

Differences between small and large individuals of *Arenicolides ecaudata*

The post-larva *A. ecaudata* are similar to the adult individuals in their division of the body into two parts and are similar in all other ways, only much smaller. The neuropodia extend from the notopodium to the mid-ventral line, even in small specimens (Fig. 17B). Both the neuropodial hooks and notochaeta are different between post-larval and adult specimens of both *A. ecaudata* (Fig. 5E-I) and *A. marina* (Fig. 5A-D). In post-larvae *A. ecaudata,* the hooks have a beard below the main hook (Fig. 5E), absent in the adult hooks (Fig. 5F). Post-larval notochaeta has a narrow lamina along one side, which beaks up into fine teeth as an adult (Fig. 5G,H) (Ashworth, 1912).

Small specimens of *A. ecaudata* were closely examined for branchia structure and development. Since there is some variation in the number of branchia pairs on the adult *A. ecaudata,* there was an interest in counting these in the small individuals. Also because post-larval specimens may have more pairs of branchiae than the adult, as they often lose some of the branchiae during growth (Ashworth, 1912). Due to the complicated process of counting branchia pairs of *A. ecaudata* depending on the varying quality and completeness of specimens, the results of this examination were not included in this study.

Some of the examined specimens from this study did not have the described number of branchia according to the used classification key (Knight-Jones et al., 2017). One specimen (NTNU-VM 83937) had 26 pairs of branchiae in contrast to the described number of 30-40 pairs. Another species in the genus *Arenicolides, A. branchialis,* is in many ways similar to *A. ecaudata.* In fact, *A. branchialis* is described to have 20-30 pairs of branchiae, which coincides with this deviating specimen. However, the branchia of *A. branchialis* starts on chaetiger 11-12 (Knight-

Jones et al., 2017), which is not the case for this mentioned specimen, where the branchia starts at chaetiger 15. The same specimen has two half-developed parapodia posterior. This may be caused by some segments being lost, which is reported from literature (Ashworth, 1912), and hence also explain the missing pairs of branchiae. Another supporting theory of this specimen not being *A. branchialis* is that this species has a more southern distribution than *A. ecaudata*. The former approaches its northern limit at Plymouth, Britain (Eve & Southward, 1958).

Habitat change within Arenicolidae

During development, both the morphology and the habitat of *A. ecaudata* change (Ashworth, 1912). Most of the small individuals of *A. ecaudata* are in this study found in the shallows, while the adult individuals are found in the deep (Fig. 16). Post-larva *A. ecaudata* are known to live among algae in the shallows (Ashworth, 1912), which is also reported in this study. Some of the specimens are found among *Saccorhiza polyschides* and *Laminaria hyperborean*, and in shell sand, and sand. Only one specimen of *A. ecaudata* was found in as shallow waters as 1 m depth. This was a result of using a scrape on plastic pontoons. This specimen measured somewhere over 5 mm.

The specific aims of this study to explain the habitat change within *A. ecaudata* by using morphological differences between small and large individuals must therefore be explained by the development of branchia. The habitat change happens between post-larval and adult specimen as the branchia are bifid or trifid, according to Ashworth (1912). His findings, however, conclude that branchia never appear on individuals less than 8 mm. In this study, there is a 7 mm long specimen found to have branchia which have been developing for a while (Fig. 21D). All *A.* ecaudata from the study measuring 14 mm or more has branchia, although not all branchia are fully developed (Fig. 21C). Most of the post-larval specimen in this study is found at 9 m depth, with one exception at 97 m depth. There are no findings of large specimens of *A. ecaudata* in the shallows, with the largest individual at 9 m depth measuring somewhere over 19 mm, as this individual is not complete.

There is a shift in vertical distribution between *A. ecaudata* and *A. marina* as well. The shallower grounds are dominated by small *A. ecaudata*, while the small *A. marina* dominates the deep. In this study, the small *A. marina* is found in shell sand, sand, and gravel. The findings in Figure 10 regarding the vertical distribution of *A. marina* are to some extent consistent with Hartmann-Schröder (1996), who stated that the vertical distribution of adult *A. marina* stretches from above the eulittoral to about 20 m depth. In this study, however, some individuals of

relatively large size are found at depths below 20 m. The young animals are described by Hartmann-Schröder (1996) to mostly live in the uppermost eulittoral. In this study, most of the small animals are distributed from the shallows and down to 140 m. To enhance the chance of surviving, the small *A. marina* settle in areas which are not dominated by adults. This could be higher in the intertidal zone (Farke et al., 1979). Therefore, it may be the case that the small *A. marina* are not obtained from the shallows to the same extent as the adult, because they settle in different areas, which may be overseen. This could explain some of the divergence with Hartmann-Schröder (1996) regarding small animals' vertical distribution.

Arenicolides ecaudata has a deeper distribution of adult individuals than *A. marina*, according to the results from this study (Fig. 10 & 16). However, *A. ecaudata* are known to live in coarser sediment than *A. marina* and may therefore be grossly overlooked (Ringvold et al., 2000). They are difficult to find in the littoral zone, since *A. ecaudata* does not make a distinct worm cast as the other worms. On the other hand, environmental monitoring often occurs in areas that *A. ecaudata* does not inhabit as it thrives in coarser sediments. The monitoring is obliged to follow the standard procedures regarding benthic impact from marine fish farms, which is not adapted to sampling from coarse sediments with gravel and pebbles, as this has not been developed yet (Standard Norge, 2016). However, an expansion in aquaculture could lead to facilities placed in areas more exposed to wave action and currents. This way there may be a greater chance of encountering *A. ecaudata* from future samples. Deep water sampling or coarse sediments may require the use of large box-corers, grabs, and dredges. This larger equipment requires larger vessels and can be very time-consuming (NS-EN ISO 16665, 2013). When the substrate shifts to coarser sediment, there is a need for new standards on equipment and procedures so that also these animals will be sampled. An effective sampling device for collecting *A. ecaudata* mentioned by Ringvold et al. (2000) is a lightweight diver-operated airlift suction sampler specified to sample crustaceans from cobble substrate.

Arenicolides ecaudata compared to *Arenicola marina* and *Arenicola defodiens*

The aim to describe the morphological difference between the three species of interest in this study is summarized in Table 1. The most important feature to distinguish *A. ecaudata* from the two other species is the lack of distinct tripartition in the former (Fig. 2). Both branchia and parapodium can extend completely to the pygidium in *A. ecaudata*, while the two other has a distinct apodous tail. Also, the branchia starts a much later chaetiger in *A. ecaudata* than in both *A. marina* and *A. defodiens*, this being 15-16th chaetiger and 6-7th chaetiger, respectively. The

neuropodia is an important way to distinguish *A. ecaudata* from the two other species when one does not have access to more than the first 5th chaetigers. In *A. ecaudata* these extend from the notopodium to the mid-ventral line in all body segments (Fig. 2D). This only occurs in the posterior part of the trunk in *A. marina* and *A. defodiens*, which have short neuropodium in the anterior segments (Fig. 2C).

The worm casts of *A. ecaudata* differs from the two other species by having a less conspicuous cast. This may be a contributing factor for the poor reports of *A. ecaudata*, and why most of the material of this species in this study is from the deep. Both *A. marina* and *A. defodiens* make distinct surface casts in the sand. They can be distinguished from each other since *A. defodiens* makes a neatly coiled cast, with the feeding depression placed in the middle of the cast (Fig. 13). *Arenicola marina* makes a messy cast and has feeding depression nearby the cast (Fig. 11).

Post-larva specimens of *A. ecaudata* and *A. marina* can be distinguished from each other using some of the same characters as in adults. The tripartition of the latter can be evident in the post-larval specimen (Fig. 8D), which is not present in the former (Fig. 15F). *Arenicolides ecaudata* can have parapodia and branchia extending all the way to the pygidium, as the adult. One will never be in doubt of a small individual being an *A. marina* or *A. ecaudata* if branchiae are visible. The annulations can be reduced or not yet developed in the post-larva specimen (Fig. 18). If one only has access to the first six chaetigers of a post-larval specimen, one can use neuropodia to distinguish *A. ecaudata* from *A. marina* (Fig.17). The former has neuropodia extending all the way from notopodia until the mid-ventral line from the first chaetiger (Fig. 17B). In contrast, the latter has short neuropodia attached more ventral on the side from the first chaetiger (Fig. 17A). The anterior neuropodium of *A. marina* may not be easy to spot at all, because of its short length. At chaetiger 8-10, the neuropodia of *A. marina* also extends down to the mid-ventral line.

The findings in this study give the impression that the branchia of *A. marina* appears when the worm is between 3-5 mm. Thorson (1946), on the other hand, found *A. marina* at 3.9-6.5 mm, which was floating among plankton and were abranchiate. Since the material studied in this study is a relatively small sample, it is not possible to say anything for certain. According to Ashworth (1912), the worm measures 8 mm when it digs into the sediment, which is a behaviour done after attaining branchiae. This coincides with the findings in Figure 19, by all specimens measuring over 8 mm having branchia.

Regarding *A. ecaudata* the findings suggest that branchiae start to appear at 7 mm length, and at 10 mm, most of the worms are in development of branchiae. This is not supported by Ashworth (1912), who says that branchiae never appear on individuals measuring less than 8 mm. Perhaps this contradiction is caused by inaccurate measurements. The measurements in this study is prone to human fault and depending on the eye which sees. However, in Figure 21 D, there is a specimen measuring 7 mm with quite distinct and well developed branchiae.

The branchia varies in their time of appearing on *A. marina* and how well developed they are (Gamble & Ashworth, 1900), as shown in Figures 21 and 22 for *A. ecaudata* and *A. marina,* respectively. In the case of *A. ecaudata,* there is one worm measuring 19 mm with less developed branchiae than one at 7 mm, as visible in Figure 21. Interesting is the large difference between the branchiae of specimen A in Figure 21, measuring 11 mm, and specimen E in the same figure, measuring 10 mm. The first has only wart-like branchia, while the latter has elongated branchiae and has ramified into several digitate branches and is beginning to resemble the adult branchia. When examining Figure 22 of *A. marina,* one may get the impression that the development of branchiae follows the length of the specimens. This is, however, not the case as the material contains one specimen of *Arenicola* sp. measuring 5 mm without branchiae while another at 3 mm has branchiae (Fig. 19).

Invalidation of *Arenicola defodiens* in Norwegian fauna

The one reported finding of *A. defodiens* from NBIC (Fig. 1) contained four specimens identified as *A. defodiens.* This material has in this thesis been studied and identified as *Arenicola* sp. and *A. marina.* These worms measured over 6 mm, 7 mm, 8 mm, and 17 mm. Three of the individuals were identified as *Arenicola* sp. because they were too small to count the ring formula, and the branchia were not developed enough to use for identification. The specimen measuring over 17 mm was identified as *A. marina* as the annulation formula was 2-3-4.

While examining the museum material from the University Museum in Trondheim, four specimens stood out with annulation formula 2-2-4 (Fig. 12). First, they were suspected to be *A. defodiens* as the annulation formula indicated, but after closer examination of other characters, one can conclude it is not *A. defodiens.* As mentioned, there is some deviations in the annulation formula recorded by both Cadman and Nelson-Smith (1993) and Luttikhuizen and Dekker (2010), where *A. marina* displays annulation formula 2-2-4. Therefore, it is important to use other characters for identification, such as the structure of branchia (Pires et

al., 2015). The first specimen (NTNU-VM 83982) had very reduced branchia, maybe caused by the preservation method. This made it impossible to count any branchia stems or lateral branches and had to be identified as *Arenicola* sp. The following specimen (NTNU-VM 83983) had branchiae that were good enough to conclude it was *A. marina*. Specimen NTNU-VM 83984 was smothered after the 6th chaetiger, and one could not study the branchia, which led to the identification as *Arenicola* sp. The last specimen (NTNU-VM 83985) measured approximately 22 mm, but examination of the branchia was difficult as the specimen was white and the branchia so closely placed. Therefore, this specimen was identified as *Arenicola* sp. Examinations of branchia might have been easier if the material had been relaxed before preservation, as the branchia and body of the worms may contract when preserved directly on ethanol (Cadman & Nelson-Smith, 1993). This contraction of the body may be the reason why some of the specimen mentioned here has annulation formula characteristic for *A. defodiens* but are identified as *A. marina*.

Though there are no evidence of *A. defodiens* existing in Norwegian fauna, it may exist here. Since the reported findings of *A. defodiens* from Skagerrak is from Koster Island in Sweden (Luttikhuizen & Dekker, 2010), it is likely that it also exists along the Norwegian coast, as this island is situated close to the Norwegian boarder. Adult *A. marina* has been recorded swimming in the water, suggestively when migrating from one burrow to another. Post-larval stages of *A. marina* are recorded in the spring plankton when doing a migration to suitable places for starting the adult way of life (Newell, 1948). This could perhaps be transferable to *A. defodiens* as well. However, as this is not an extended pelagic phase (Newell, 1948), it could perhaps explain why there are no reports of *A. defodiens* along the Norwegian coast yet. It could also be that the lack of material on the species is caused by lack of information. The well-known surface casts along the coast, may not be of interest for sampling, as one believes one knows which species it is and forgets to take a closer look at the structure of the surface cast.

There are in this study, 24 specimens identified as *Arenicola* sp. found at depths of 22-97 m. Perhaps one can explain this abundance of small specimens in the deep by shallower burrow depths than adult specimens. If the small specimen buries shallower in the sediment, these will easier be collected by a grab or box corer. Therefore, there could be of interest using tools that digs deeper into the sediment to see if one also could find more large individuals at such depths. One specimen identified as *A. marina* found at 107 m depth measures over 115 mm. This specimen does not have the first segments intact and could be explained by being torn off due to the grab not penetrating deep enough into the sediment. It is also known that *A. marina*

burrows shallower into the sediment than *A. defodiens*. The former buries 20-30 cm down into the sediment, while the latter buries 50-100 cm down (Cadman & Nelson-Smith, 1990). This could explain why there are no reports of *A. defodiens* in Norway.

The fact that *A. defodiens* buries deeper into the sediment is also relevant in the shallows. Maybe the use of a spade, as one often uses in search of *A. marina,* is not suitable in the search for *A. defodiens.* A useful tool for this is described by Brind and Darbyshire (2015) to be a bait pump. Another contributing factor to the non-existing evidence of *A. defodiens* is that it often buries lower on the beach when co-existing than *A. marina*. It is described to be found at low water of spring tides and extends sub-tidally to an unknown extent (Cadman & Nelson-Smith, 1993).

To validate the existence of *A. defodiens* in Norwegian fauna, new studies must be conducted where one searches specifically for *A. defodiens.* One should look at worm casts and collect specimens for both DNA barcoding and preservation. One could team up with the monitoring companies to create a large quantity of material suitable for barcoding to expand the library on the arenicolid species and perhaps validate the existence of *A. defodiens*. According to an international standard on quantitative sampling and sample processing, samples should be fixated on formalin as soon as possible. If there is no need for long-term storage, storage in ethanol is advised as these can be used for DNA barcoding (NS-EN ISO 16665, 2013). Therefore, much of the material which is identified as *Arenicola* sp. in this study could not be sent to barcoding to be identified any further.

5. Conclusion

This study has provided knowledge of different stages of branchia during the development of post-larval *A. marina* and *A. ecaudata.* Another finding includes neuropodium as a useful character to distinguish the two species even when examining post-larval specimens. Adult and small *A. ecaudata* and *A. marina* show different depth distributions. Small specimens of *A. ecaudata* are numerous in the shallows, while the adult specimens are mostly found in the deep. Within *A. marina*, adult specimens are numerous in the shallows, while small specimens are mostly found in the deep. A comparison table for the three species of interest summarizes the findings regarding the morphological difference between the species. Another important discovery is the invalidation of the reported *A. defodiens* in Norwegian fauna. As the species is reported from Skagerrak, further studies are needed to validate the existence of *A. defodiens* in Norway as well. It is also of importance to study *A. ecaudata* further, as there is reason to believe it is grossly overseen along the coast of Norway.

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Appendix I

Table A1: Overview of all specimens examined in this study. Some of the records are missing different information and is marked with "-". The number of specimen(s) is contained in column marked N. Specimens sent to DNA barcoding is marked in yellow.

Museum number	Date	Species	Identifier	Lat/long	N	Depth (m)	Collector	Method
NTNU-VM 14800	20.06.1998	Arenicola marina	Torkild Bakken	63.59111 9.53833	1	0	Anon	-
NTNU-VM 14801	1971	Arenicola marina	Anon	63.8612 11.3094	1	-	Anon	-
NTNU-VM 14802	-	Arenicola marina	Anon	63.9481 11.3738	1	-	Anon	-
NTNU-VM 14804	24.04.1995	Arenicola marina	Torleif Holthe	63.578 10.6115	1	0	Stein Hokstad	Handpicked sample
NTNU-VM 14805	17.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14806	17.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	-
NTNU-VM 14807	17.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	-
NTNU-VM 14823	-	Arenicola marina	Anon	63.622 9.5245	6	-	Anon	-
NTNU-VM 14824	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14825	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14826	16.07.1971	Arenicola sp.	Marthe R. Dille	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14827	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14828	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14829	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14830	16.07.1971	Arenicola sp.	Marthe R. Dille	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14846	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14847	16.07.1971	Arenicola marina	Anon	63.8819 11.362	1	0	Anon	Box corer

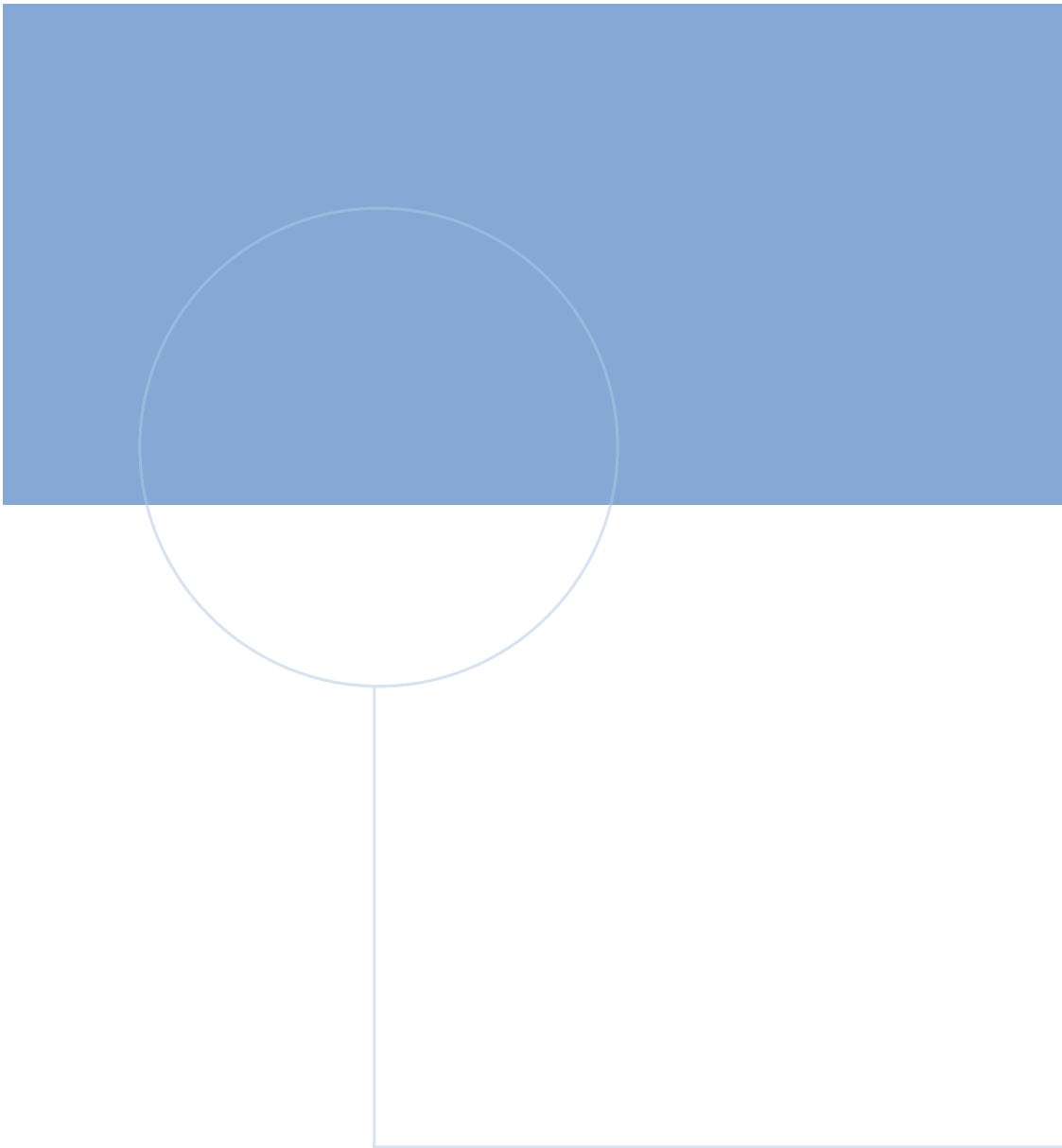
NTNU-VM 14899	01.03.1974	Arenicola marina	Anon	63.3395 10.2185	3	0	Anon	-
NTNU-VM 14901	01.03.1974	Arenicola marina	Anon	63.3395 10.2185	2	0	Anon	-
NTNU-VM 14903	01.03.1974	Arenicola marina	Anon	63.3395 10.2185	2	0	Anon	-
NTNU-VM 14905	16.07.1971	Arenicola marina	Marthe R. Dille	63.8819 11.362	5	0	Anon	Box corer
NTNU-VM 14906	16.07.1971	Arenicola marina	Marthe R. Dille	63.8819 11.362	3	0	Anon	Box corer
NTNU-VM 14907	16.07.1971	Arenicola marina	Marthe R. Dille	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 14909	22.05.1936	Arenicola marina	Marthe R. Dille	63.6673 9.4041	1	0	Carl Dons	-
NTNU-VM 65076	22.05.1936	Arenicola marina	Torkild Bakken	63.6673 9.4041	1	0	Carl Dons	-
NTNU-VM 65077	08.08.1906	Arenicola marina	Torkild Bakken	63.8101 10.645	2	-	Anon	-
NTNU-VM 69440	18.06.2013	Arenicola marina	Torkild Bakken	63.59111 9.53833	3	0	Torkild Bakken	Handpicked sample
NTNU-VM 70330	28.08.2014	Arenicola marina	Grethe S. Haugen	63.68033 9.5646	1	0	Grethe Sundet Haugen	Handpicked sample
NTNU-VM 70331	28.08.2014	Arenicola marina	Grethe S. Haugen	63.68033 9.5646	1	0	Grethe Sundet Haugen	Handpicked sample
NTNU-VM 70332	09.10.2014	Arenicola marina	Grethe S. Haugen	64.32945 1.57536	1	0	Grethe Sundet Haugen	Handpicked sample
NTNU-VM 70333	31.10.2014	Arenicola marina	Grethe S. Haugen	63.33577 10.21567	1	0	Grethe Sundet Haugen	Handpicked sample
NTNU-VM 70334	28.08.2014	Arenicola marina	Grethe S. Haugen	63.70331 9.57267	1	0	Grethe Sundet Haugen	Handpicked sample
NTNU-VM 72280	05.09.2016	Arenicola marina	-	63.59217 9.54043	3	0	Maria Capa	Handpicked sample
NTNU-VM 72281	05.09.2016	Arenicola marina	-	63.59217 9.54043	2	0	Maria Capa	Handpicked sample
NTNU-VM 72282	06.09.2016	Arenicola marina	-	63.59761 9.52782	1	0	Maria Capa	Handpicked sample
NTNU-VM 72283	06.09.2016	Arenicola marina	-	63.59761 9.52782	1	0	Maria Capa	Handpicked sample
NTNU-VM 73647	28.06.2017	Arenicola marina	Jon Arne Sneli	-	1	0	Torkild Bakken	Handpicked sample
NTNU-VM 75207	04.09.2018	Arenicola marina	Torkild Bakken	63.43622 10.49932	2	0	Maria Capa, Tuva B. Munkeby, Torkild Bakken	Handpicked sample

NTNU-VM 75885	04.09.2018	Arenicola sp.	Marthe R. Dille	63.43336 10.51248	1	0-1	Maria Capa, Tuva B. Munkeby, Torkild Bakken	Handpicked sample
NTNU-VM 76495	17.09.2018	Arenicola marina	Torkild Bakken	59.11402 10.23026	2	3	Maria Capa, Tuva B. Munkeby, Torkild Bakken	Grab
NTNU-VM 83920	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	2	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83921	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	1	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83922	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	1	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83923	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	1	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83924	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	2	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83925	02.09.2021	Arenicolides ecaudata	Marthe R. Dille	63.63551, 9.31313	1	2-6	August R. Nymoen	Snorkelling
NTNU-VM 83926	01.09.2021	Arenicolides ecaudata	Marthe R. Dille	63.63825, 9.33040	1	0-1	August R. Nymoen	Scrape
NTNU-VM 83927	09.06.2015	Arenicola marina	Torkild Bakken	-	5	0	Torkild Bakken	Handpicked sample
NTNU-VM 83928	09.06.2015	Arenicola marina	Torkild Bakken	-	1	0	Torkild Bakken	Handpicked sample
NTNU-VM 83929	09.06.2015	Arenicola marina	Torkild Bakken	-	1	0	Torkild Bakken	Handpicked sample
NTNU-VM 83930	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	1	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83931	01.01.2022	Arenicola marina	Marthe R. Dille	64.68012 11.29433	1	0	Marthe R. Dille	Handpicked sample
NTNU-VM 83932	13.01.2021	Arenicolides ecaudata	Marthe R. Dille	61.07633 5.38437	2	333	Åkerblå	Grab
NTNU-VM 83933	14.10.2020	Arenicolides ecaudata	Marthe R. Dille	61.9086 5.29093	2	197	Åkerblå	Grab
NTNU-VM 83934	18.04.2020	Arenicolides ecaudata	Marthe R. Dille	63.71883 8.55075	3	54	Åkerblå	Grab
NTNU-VM 83935	13.02.2020	Arenicolides ecaudata	Marthe R. Dille	61.89703 5.63413	2	195	Åkerblå	Grab
NTNU-VM 83936	20.05.2020	Arenicola marina	Marthe R. Dille	66.03093 12.48148	1	107	Åkerblå	Grab
NTNU-VM 83937	05.03.2019	Arenicolides ecaudata	Marthe R. Dille	61.07633 5.38393	2	293	Åkerblå	Grab

NTNU-VM 83938	03.08.2021	Arenicola sp.	Marthe R. Dille	64.94485 11.46048	6	97	Åkerblå	Grab
NTNU-VM 83939	08.10.2020	Arenicola marina	Marthe R. Dille	62.1677 5.6035	5	140	Åkerblå	Grab
NTNU-VM 83940	18.04.2020	Arenicolides ecaudata	Marthe R. Dille	63.71883 8.55075	2	54	Åkerblå	Grab
NTNU-VM 83941	17.10.2020	Arenicolides ecaudata	Marthe R. Dille	63.9424 9.13198	1	153	Åkerblå	Grab
NTNU-VM 83942	13.10.2021	Arenicolides ecaudata	Nathalie Skahjem	63.49593 8.0285	1	100	Åkerblå	Grab
NTNU-VM 83943	04.05.2020	Arenicolides ecaudata	Nathalie Skahjem	63.78203 8.51655	1	44	Åkerblå	Grab
NTNU-VM 83944	04.05.2020	Arenicola marina	Marthe R. Dille	63.78203 8.51655	2	44	Åkerblå	Grab
NTNU-VM 83945	17.08.2020	Arenicola marina	Marthe R. Dille	63.84603 8.52393	1	54	Åkerblå	Grab
NTNU-VM 83946	03.08.2021	Arenicolides ecaudata	Marthe R. Dille	64.94485 11.46048	1	97	Åkerblå	Grab
NTNU-VM 83947	23.02.2021	Arenicolides ecaudata	Marthe R. Dille	64.28748 10.315	1	148	Åkerblå	Grab
NTNU-VM 83948	04.05.2020	Arenicola sp.	Marthe R. Dille	63.78225 8.52417	1	44	Åkerblå	Grab
NTNU-VM 83949	-	Arenicolides ecaudata	Marthe R. Dille	-	2	-	Åkerblå	-
NTNU-VM 83950	-	Arenicolides ecaudata	Marthe R. Dille	-	9	-	Åkerblå	-
NTNU-VM 83951	-	Arenicolides ecaudata	Marthe R. Dille	-	1	-	Åkerblå	-
NTNU-VM 83952	-	Arenicolides ecaudata	Marthe R. Dille	-	6	-	Åkerblå	-
NTNU-VM 83953	-	Arenicola sp.	Marthe R. Dille	-	2	-	Åkerblå	-
NTNU-VM 83954	-	Arenicolides ecaudata	Marthe R. Dille	-	1	-	Åkerblå	-
NTNU-VM 83955	-	Arenicolides ecaudata	Marthe R. Dille	-	2	-	Åkerblå	-
NTNU-VM 83956	-	Arenicolides ecaudata	Marthe R. Dille	-	1	-	Åkerblå	-
NTNU-VM 83957	-	Arenicolides ecaudata	Marthe R. Dille	-	1	-	Åkerblå	-
NTNU-VM 83958	04.06.2015	Arenicola marina	Marthe R. Dille	59.35042 5.3108	1	51	NIVA	-

NTNU-VM 83959	04.06.2015	Arenicola sp.	Marthe R. Dille	59.35042 5.3108	6	51	NIVA	-
NTNU-VM 83960	04.06.2015	Arenicola marina	Marthe R. Dille	59.36495 5.29001	9	22	NIVA	-
NTNU-VM 83961	03.11.2015	Arenicola marina	Marthe R. Dille	59.26395 10.43212	1	1	NIVA	-
NTNU-VM 83962	05.09.2016	Arenicola marina	Marthe R. Dille	59.10534 10.86463	1	6	NIVA	-
NTNU-VM 83963	04.06.2015	Arenicola marina	Marthe R. Dille	59.35205 5.31412	1	56	NIVA	-
NTNU-VM 83964	04.06.2015	Arenicola marina	Marthe R. Dille	59.35205 5.31412	1	56	NIVA	-
NTNU-VM 83965	04.06.2015	Arenicola sp.	Marthe R. Dille	59.35205 5.31412	1	56	NIVA	-
NTNU-VM 83966	04.06.2015	Arenicolides ecaudata	Marthe R. Dille	59.35205 5.31412	1	56	NIVA	-
NTNU-VM 83967	04.06.2015	Arenicola marina	Marthe R. Dille	59.36495 5.29001	1	22	NIVA	-
NTNU-VM 83968	04.06.2015	Arenicola sp.	Marthe R. Dille	59.35205 5.31412	1	56	NIVA	-
NTNU-VM 83969	04.06.2015	Arenicola sp.	Marthe R. Dille	59.35042 5.3108	1	51	NIVA	-
NTNU-VM 83970	04.06.2015	Arenicola marina	Marthe R. Dille	59.35042 5.3108	1	51	NIVA	-
NTNU-VM 83971	04.06.2015	Arenicola sp.	Marthe R. Dille	59.35042 5.3108	1	51	NIVA	-
NTNU-VM 83972	04.06.2015	Arenicola sp.	Marthe R. Dille	59.36495 5.29001	1	22	NIVA	-
NTNU-VM 83973	04.06.2015	Arenicola marina	Marthe R. Dille	59.36495 5.29001	4	22	NIVA	-
NTNU-VM 83974	04.06.2015	Arenicola marina	Marthe R. Dille	59.35042 5.3108	3	51	NIVA	-
NTNU-VM 83975	04.06.2015	Arenicola sp.	Marthe R. Dille	59.36495 5.29001	3	22	NIVA	-
NTNU-VM 83976	04.06.2015	Arenicola sp.	Marthe R. Dille	59.36495 5.29001	2	22	NIVA	-
NTNU-VM 83977	29.08.2018	Arenicola sp.	Marthe R. Dille	-	3	-	Rådgivende Biologer AS	-
NTNU-VM 83978	29.08.2018	Arenicola marina	Marthe R. Dille	-	1	-	Rådgivende Biologer AS	-
NTNU-VM 83979	15.04.2022	Arenicola marina	Marthe R. Dille	64.65830 11.17407	3	0	Marthe R. Dille	-

NTNU-VM 83980	15.04.2022	Arenicola marina	Marthe R. Dille	64.68059 11.29697	4	0	Marthe R. Dille	-
NTNU-VM 83981	17.08.2020	Arenicola sp.	Marthe R. Dille	63.84603 8.52393	1	54	Åkerblå	Grab
NTNU-VM 83982	05.09.2016	Arenicola sp.	-	63.59217 9.64043	1	0	Maria Capa	Handpicked sample
NTNU-VM 83983	16.07.1971	Arenicola marina	Marthe R. Dille	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 83984	16.07.1971	Arenicola sp.	Marthe R. Dille	63.8819 11.362	1	0	Anon	Box corer
NTNU-VM 83985	04.09.2018	Arenicola sp.	Marthe R. Dille	63.43336 10.51248	1	0-1	Maria Capa, Tuva B. Munkeby, Torkild Bakken	Handpicked sample
NTNU-VM 83986	28.06.2017	Arenicola marina	Jon Arne Sneli	-	1	0	Torkild Bakken	Handpicked sample
NTNU-VM 83987	1995	Arenicola marina	Marthe R. Dille	63.65328 9.33565	1	10	-	Grab
ZMBN 147152	12.11.1966	Arenicola marina	Marthe R. Dille	-	1	-	Tore Nielsen	-
ZMBN 45880	16.07.1954	Arenicolides ecaudata	Fauchald	-	1	-	Biol.st.	-
ZMBN 47667	29.07.1950	Arenicola marina	Fauchald	-	2	-	J. Eckhoff	-
ZMBN 47668	24.09.1950	Arenicolides ecaudata	Fauchald	-	2	-	J. Eckhoff	-
ZMBN 77503	27.07.1997	Arenicolides ecaudata	HI-project	-	81	9	HI-project	-
ZMBN 77505	26.08.1997	Arenicolides ecaudata	HI-project	60.65361 4.7875	1	9	HI-project	-
ZMBN 77506	26.08.1997	Arenicolides ecaudata	HI-project	60.44361 4.92333	2	10	HI-project	-
ZMBN 77507	26.08.1997	Arenicolides ecaudata	HI-project	60.17639 5.00056	8	8	HI-project	-



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