Journal of Natural Science Collections

Title: 100 years of deep-sea tube worms in the collections of the Natural History Museum, London

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Source: Sherlock, E., Neal, L. & Glover, A. (2014). 100 years of deep-sea tube worms in the collections of the Natural History Museum, London. *Journal of Natural Science Collections*, *Volume 2*, 47 - 53.

URL: http://www.natsca.org/article/2079

100 years of deep-sea tubeworms in the collections of the Natural History Museum, London

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Received: 14th Sept 2014
Accepted: 18th Dec 2014

Abstract

Despite having being discovered relatively recently, the Siboglinidae family of polychaetes have a controversial taxonomic history. They are predominantly deep sea tube-dwelling worms, often referred to simply as 'tubeworms' that include the magnificent metre-long *Riftia pachyptila* from hydrothermal vents, the recently discovered 'bone-eating' *Osedax* and a diverse range of other thin, tube-dwelling species. For a long time they were considered to be in a completely separate Phylum, the Pogonophora, but with the discovery of a segmented posterior and then conclusive DNA evidence, they were restored to the Phylum Annelida. In this project curation and research teams have combined to enhance the Museum's collection. This has been facilitated through targeted donation requests, comprehensive digitisation, a location move to the rightful taxonomic place and teaming up with global database initiatives to promote the collection.

Keywords: Siboglinidae; Polychaeta; Annelida; Pognophora; Digitisation; Systematics; Curation

A brief taxonomic summary of the Siboglinidae

The taxonomic group currently known as the polychaete family Siboglinidae (Fig. 1) was discovered 100 years ago (Caullery, 1914). In a small laboratory in France, Maurice Caullery erected a new genus for a long thin worm, notably without any obvious mouth or gut, discovered from material collected on the Dutch Siboga expedition of 1900 from Indonesia (Caullery, 1914). The author did not place the new species in any higher taxon, but did compare it to deuterosomes such as pterobranchs and enteropneusts (Pleijel, *et al*., 2009). 100 years of argument has since ensued as to the true evolutionary placement of these enigmatic animals, and their discovery at deep-sea hydrothermal vents in the late 1970s has questioned the very nature of where complex life might exist in our solar system and beyond (Van Dover, 2000).

Scientific discussion as to the placement of these worms started when another similar gutless worm *Lamellisabella zachsi* was placed within the polychaete family Sabellidae (the feather-duster worms) (Uschakov, 1933). This placement of these worms in the correct phylum and class (if not family) was short-lived however. By the 1970s workers such as Ivanov (Ivanov, 1963) had made a good start on an almost lifetimes work of describing new species of these gutless worms within a new Phylum: Pogonophora. These workers were absolutely convinced that the worms were not related to annelids, had a dorsal nerve cord and radial cleavage during development, thus placing them within the deuterostome group advocated by Caullery back in 1914.

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For a mud-dwelling marine worm from the bottom of the ocean, siboglinids have a good history of making newsprint headlines. In 1955, the Natural History Museum in London (NHM) became involved in the debate when the museum Director Sir Gavin Rylands de Beer published a short paper in the journal *Nature*, clarifying 'reports in the Daily Press…' as to the discovery of a new phylum of animals (the Pogonophora) in Russia (de Beer, 1955). In 1958, British Zoologists Alan and Eve Southward published the first report of *Siboglinum* from the continental slope off the British Isles, again in the prestigious journal *Nature* (Southward & Southward, 1958). Then in 1964, a series of studies showed that the pogonophore worms had a unique feature that nobody had found before – a posterior segmented section, anchored in the tube with small hook-like chaetae (Webb, 1964). This was the beginning of the end for Pogonophora as a phylum, but it took a wealth of developmental, anatomical and genetic studies to finally place these animals back where they had started.

The story is well documented elsewhere (Pleijel *et al*., 2009, Hilario *et al*., 2011), but relevant to the Natural History Museum story is the work of David George in the early 1970s who made the first SCUBA observations (Fig. 2) on populations of *Siboglinum fiordicum* that had been discovered in remarkably shallow depths (35m) near Bergen, Norway (George, 1975, 1977). The observations of the larval behaviour from these studies were suggestive of polychaete (protostome) rather than deuterostome ancestry.

The discovery of the giant hydrothermal vent tubeworm *Riftia pachyptila* in the late 1970s and their description within the Vestimentifera class of the Phylum pogonophora, threw the group again into the newspaper headlines. At the same time, it seemed to reinforce their 'unique' position, given the discovery of their unique method of feeding – via chemoautotrophic bacteria housed inside their bodies gaining energy from the vent chemicals. But eventually, a wealth of DNA studies in the late 20th century (reviewed in Pleijel, *et al.*, 2009 and Hilario, *et al.,* 2011) have convinced the doubters what many had long suspected – the entire pogonophoran and vestimentiferan group were in fact highly-derived deep-sea polychaete worms in the family Siboglinidae.

The most recent twist, and news headlines, in the story of siboglinids has been the discovery of a third group of siboglinids, *Osedax*, found living on the bones of decaying whales at the deep seafloor (Rouse et al. 2004, Glover et al., 2005). These animals, thought to be closely related to the frenulate-type tubeworms (the original long thin worms described by Caullery) also lack a gut, but are able to utilise bacteria in a root structure to extract energy from rotting whale-bones, a remarkable and hitherto undocumented type of microbial association.

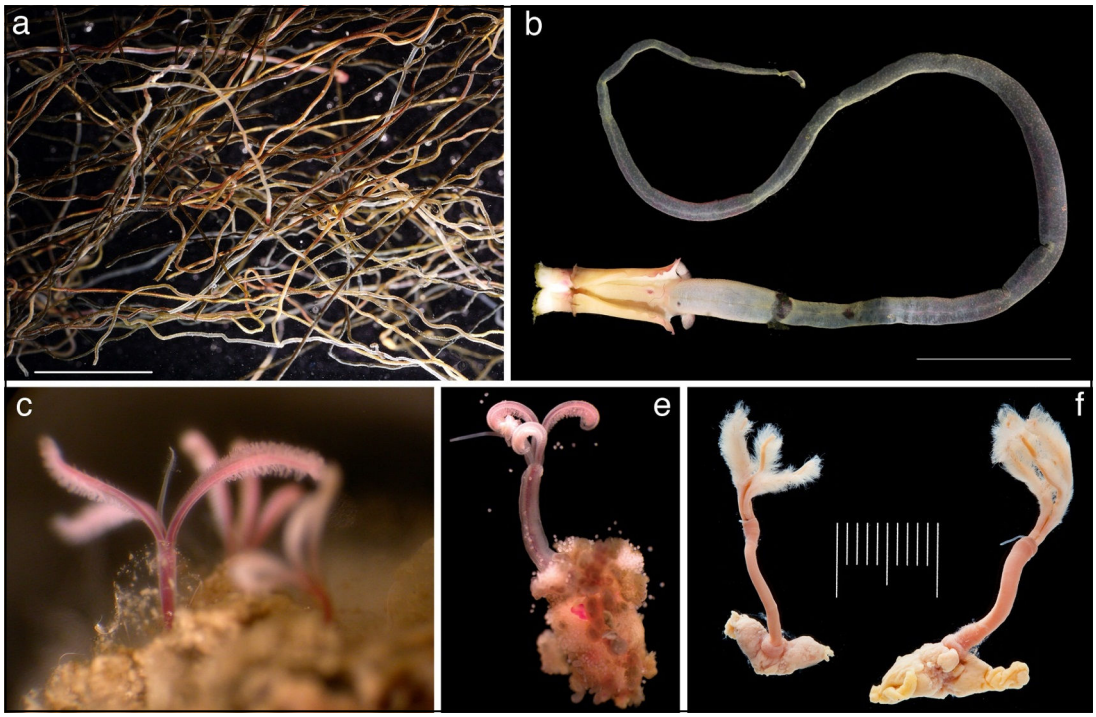

Fig. 1. Siboglinidae (Annelida), formerly within the Phylum 'Pogonophora'. (a) Thin tube-dwelling pogonophore worms recovered from Antarctic sediments (scale bar 1cm), (b) vestimentiferan-type cold-seep tubeworm (scale bar 3cm), (c) *Osedax mucofloris* growing on a whale bone, (e) *Osedax mucofloris* dissected out from whale bone, (f) *Osedax rubiplumus* donation to the NHM from Dr Greg Rouse, Scripps Institution of Oceanography. Images (a -e) by Adrian Glover, (f) by Natural History Museum Photo Unit.

Fig 2. The first Natural History Museum SCUBA dive team was setup in the 1960s, here diving at the 35m *Siboglinum fiordicum* depths in the early 1970s. Early observations of living siboglinids were an important clue in understanding their evolutionary history. Photo by Dr David George.

Introduction to the Natural History Museum polychaete collections

The polychaete collections at the NHM started out life, as did all the earliest of the NHM specimens, as part of the British Museum in Bloomsbury. In 1865, the British Museum produced a 350-page bound catalogue of the British non-parasitical worms, a book containing lengthy descriptions and fine hand-drawn plates, with the majority of the book dedicated to the class Polychaeta within the Phylum Annelida (Johnston, 1865). The polychaetes had been housed with the Mollusca collection under the care of E A Smith (Curator, 1867-1876), but in 1881 the new museum in South Kensington was opened and the polychaetes were moved there now under the care of Francis Bell (Curator, 1876-1912).

In 1912, Arnold Baylis took charge and set up the Annelida section for the first time and the profile of polychaetes within the collection would continue to rise. From 1922-1939 Charles Monro was head of the Annelida section and a polychaete worker himself. During his time in charge the number of depositions to the collection would rise dramatically (in 1920 less than 100 polychaetes were accessioned, in 1926 approximately 300 specimens were accessioned and in 1927 over 400 specimens were accessioned. (Natural History Museum, 1920-1927).

Progress continued with Norman Tebble (Curator, 1950-1961) and then Reginald Sims (an Oligochaete researcher) who was the annelid collections manager from 1961-1985. During this period (in 1968) the annelid section was split with the clitellate annelids (e.g earthworms, leeches) staying with Sims while David George managed the Polychaeta (and Porifera) sections. It was also in this year that David George set up the diving group in the Museum. This again led to a rise in specimen additions to the collection and rise in profile for the polychaete group. By the early 1970s one focus for David George and his diving team was the study of the pogonophores, as they were then known. In 1974 Alex Muir arrived at the Museum and worked on the collections under David George as well as later on a range of polychaete systematic studies (Chambers & Muir, 1997). In recent decades polychaete researcher Gordon Paterson made a large contribution to our understanding of polychaete biodiversity and taxonomy, with particular emphasis on deep-sea habitats (e.g Paterson, *et al.*, 1988; Paterson, *et al.*, 2009). Recent research programs led by one of the authors (AG) have focussed on deep-sea biodiversity, Antarctic biodiversity and in particular studies of whale-fall siboglinids including *Osedax* (e.g Glover, *et al.*, 2005, Glover, *et al.*, 2013).

Introduction to the Siboglinidae research and collections at the Natural History Museum

The pioneering work of Eve and Alan Southward led to the first major deposition of type material at the NHM in the 1950s. The first deposited specimens were syntypes *Siboglinum atlanticum* 1958.8.28.1 and *S. inermis* 1958.8.28.2-3 (Appendix 1). There are now 66 registered specimens in total, representing 33 different species (Appendix 1). An important aspect of the collection is the large proportion of types (51 of the 66, or 77%), particularly the result of the work of the Southwards and later George and now Glover and colleagues. A strength of the collection is the coverage of type material from all types of siboglinid habitat including vent-dwelling large tubeworms, the frenulate (pogonophore) type mud-dwelling worms and most recently the bone-eating *Osedax*.

In the 1970s, David George made a contribution to the debate on pogonophore systematics particularly with collections made with his newly-formed diving team (George & Southward, 1973; George, 1975; George, 1977). During this period he was able to establish that the *Siboglinum* larvae swam with their central nerve cord situated ventrally. This was a real breakthrough in the breaking down perceived barriers between the pognophore and annelid anatomical studies (George, 1975), but it took another 20 years for this theory to be accepted.

In recent years, Adrian Glover has been part of a team which led to the discovery of a number of new *Osedax* species. In 2005 Glover and colleagues described a new species, *Osedax mucofloris* (literally, the 'bone-eating snot flower') from remarkably close to one of the best studied marine

habitats in the world – the Skagerrak of the North Sea on the west coast of Sweden (Glover, *et al.*, 2005). This was the first shallow-water *Osedax* species to be described, following the original description of the genus from almost 3000m in the north-east Pacific in 2004 (Rouse, *et al.*, 2004). Glover has since worked up a number of further species descriptions, including the first Antarctic specimens, expanding the geographic range of the genus (*O. antarcticus*, *O. crouchi*, *O. deceptionensis*, *O. nordenskjoeldi* and *O. rogersi*). Given that the NHM polychaete research group have been at the forefront of recent discoveries of Siboglinidae, the Annelida curator (Emma Sherlock) teamed up with the researchers to bring the collections in line with 21st century discoveries.

Enhancing the collections

The collections at the NHM are large and their coverage very broad. However, to keep collections relevant, useful and current, they need to be not only well maintained but also updated and enhanced. Passively the collections are being enhanced every year through donations from collectors and researchers worldwide. However, to be of maximum benefit to the users certain areas of the collection, either with historical strength or research importance have been targeted as areas for active enhancement, to create areas of excellence within the collection.

The Siboglinidae has been chosen as one of these target groups. In order to make the NHM Siboglinidae collection as comprehensive as possible, deep-sea biologists were approached with a donation request from the museum. In some cases exchanges are being organised, with duplicate material housed within the museum where possible. Not only does this help the research team, but it also encourages visits from other researchers worldwide. A physical move was also required for the material already present, from the Minor Phyla store to its rightful position within the polychaete collections.

The collection needed to be accessible to the international research community, as well as other users of the collection such as exhibitors and educational projects, particularly in this digital age. To facilitate this, a database update needed to be completed. The older specimens in the collection were housed under Minor Phyla in the collections database, whilst the newer acquisitions were under Annelida. This meant some of the collections were 'virtually hidden' from the research community. This has now been updated. The type material has been professionally photographed, with JPEG images available online (Fig. 3 and 4) and high-definition TIFFS are available as a 'virtual loan' to anyone who enquires. Additionally, the NHMs collections are now linked in comprehensive databases such World Register of Marine Species (WoRMS) (Fig. 5), the WoRMS Siboglinidae entries have also been updated through a separate project funded by the WoRMS LifeWatch grants and the International Network for the Scientific Investigation of Deep-sea Ecosystems (INDEEP) coordinated by the WoRMS Annelida Editor, Geoff Read and carried out at the NHM by Lenka Neal.

We hope our short communication celebrating the 100th year since the discovery of the Siboglinidae will help promote research and curation into these extraordinary animals.

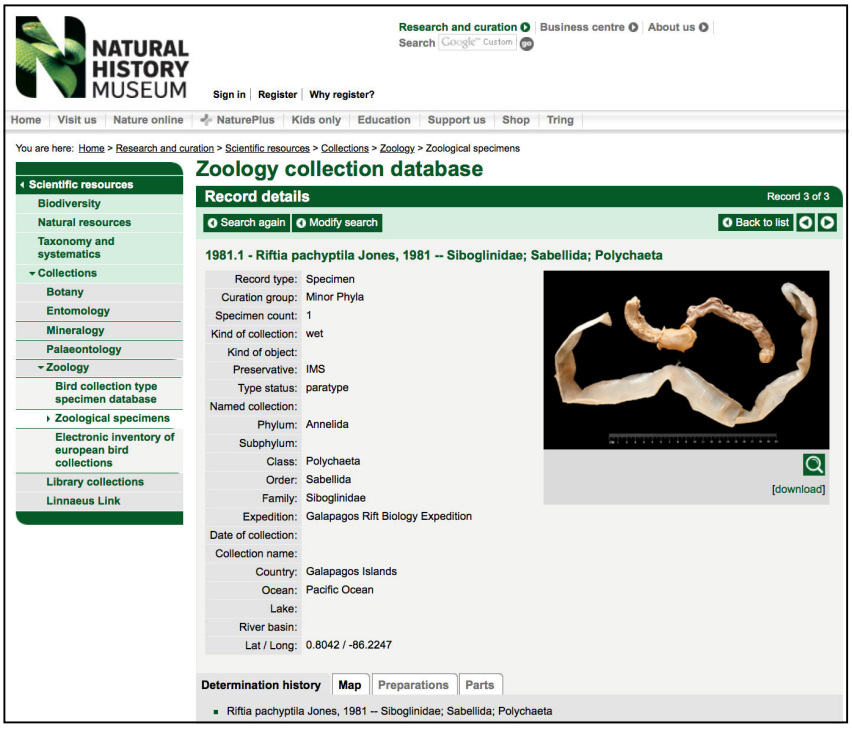

Fig 3. External access to the Natural History Museum collections data through http://www.nhm.ac.uk/research

Fig 5. External access to the Natural History Museum collections data through the World Register of Marine Species: http://www.marinespecies.org/

Acknowledgements

The authors would like to thank Dr. David George very much for his help and the use of the Diving image. Also thanks to the NHM data manager, Tim Conyers. Thank you to the anonymous reviewers.

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APPENDIX 1

Siboglinidae listings at the NHM London

Registration Number	*Genus*	*Species*	*Type Status*
2013.484	*Osedax*	*antarcticus*	non-type
2013.483	*Osedax*	*antarcticus*	non-type
2013.482	*Osedax*	*antarcticus*	Voucher
2013.481	*Osedax*	*nordenskioeldi*	Voucher
2013.479-480	*Osedax*	*nordenskioeldi*	Paratypes
2013.478	*Osedax*	*nordenskioeldi*	Holotype
2013.477	*Osedax*	*rogersi*	Paratype
2013.476	*Osedax*	*rogersi*	Holotype
2013.475	*Osedax*	*crouchi*	Voucher
2013.474	*Osedax*	*crouchi*	Paratype
2013.473	*Osedax*	*crouchi*	Holotype
2013.437	*Osedax*	*antarcticus*	Paratype
2013.436	*Osedax*	*antarcticus*	Paratype
2013.435	*Osedax*	*antarcticus*	Holotype
2013.25	*Riftia*	*pachyptila*	non-type
2012.44-45	*Osedax*	*rubiplumus*	non-type
2012.42-43	*Osedax*	*frankpressi*	non-type
2012.104	*Osedax*	*rubiplumus*	non-type
2011.28	*Riftia*	*sp*	non-type
2010.233	*Lamellibrachia*	*anaximandri*	paratype
2010.232	*Lamellibrachia*	*anaximandri*	paratype
2010.231	*Lamellibrachia*	*anaximandri*	paratype
2010.232	*Lamellibrachia*	*anaximandri*	paratype
2010.233	*Lamellibrachia*	*anaximandri*	paratype
2011.28	*Riftia*	*sp*	non-type
2012.42-43	*Osedax*	*frankpressi*	non-type
2012.44-45	*Osedax*	*rubiplumus*	non-type
1960.10.1.1	*Zenkevitchiana*	*longissima*	non-type
1960.10.1.3	*Polybrachia*	*capillaris*	types
1962.9.24.1	*Siboglinum*	*lacteum*	type
1969.3.3.3	*Siboglinum*	*pusillum*	non-type
1969.3.3.4-5	*Siboglinum*	*pusillum*	non-type
1971.2.1.26	*Lamellibrachia*	*barhami*	paratype
1978.3.21.1	*Lamellisabella*	*denticulata*	paratype
1978.3.21.2	*Lamellisabella*	*denticulata*	paratype
1978.3.21.3	*Lamellisabella*	*denticulata*	non-type
2013.25	*Riftia*	*pachyptila*	non-type
2013.435	*Osedax*	*antarcticus*	holotype
2013.436	*Osedax*	*antarcticus*	paratype
2013.437	*Osedax*	*antarcticus*	paratype

Registration Number	Genus	Species	Type Status
2013.473	*Osedax*	*crouchi*	Holotype
2013.481	*Osedax*	*nordenskioeldi*	Voucher
2013.479-480	*Osedax*	*nordenskioeldi*	paratypes
2013.478	*Osedax*	*nordenskioeldi*	holotype
2013.476	*Osedax*	*rogersi*	holotype
2013.477	*Osedax*	*rogersi*	paratype
2013.475	*Osedax*	*crouchi*	voucher
2013.474	*Osedax*	*crouchi*	paratype
2013.482	*Osedax*	*antarcticus*	voucher
2013.483	*Osedax*	*antarcticus*	non-type
2013.484	*Osedax*	*antarcticus*	non-type
1978.3.21.3-5	*Lamellisabella*	*denticulata*	non-type
2005.239	*Osedax*	*mucofloris*	holotype
2005.240	*Osedax*	*mucofloris*	paratype
2005.241	*Osedax*	*mucofloris*	paratype
2012.104	*Osedax*	*rubiplumus*	non-type
2007.977	*Spirobrachia*	*tripeira*	holotype
1958.8.28.1	*Siboglinum*	*atlanticum*	syntype
1958.8.28.2-3	*Siboglinum*	*inermis*	syntypes
1960.10.1	*Polybrachia*	*capillaris*	syntype
1962.1.9.1	*Galathealinum*	*arcticum*	holotype
1963.5.2.1	*Siboglinum*	*holmei*	holotype
1963.5.2.2	*Siboglinum*	*holmei*	paratype
1963.5.2.3	*Siboglinum*	*holmei*	paratype
1969.3.3.1	*Siboglinum*	*vancouverensis*	holotype
1969.3.3.2	*Lamellisabella*	*coronata*	holotype
1978.1.13.1	*Unibrachium*	*colombianum*	paratype
1978.1.13.2-3	*Sclerolinum*	*minor*	paratypes
1978.1.13.4-7	*Sclerolinum*	*major*	paratypes
1978.1.13.8-15	*Sclerolinum*	*magdalenae*	paratypes
1978.1.13.16	*Oligobrachia*	*gracilis*	holotype
1978.1.13.17	*Oligobrachia*	*gracilis*	paratype
1978.1.13.18-20	*Oligobrachia*	*gracilis*	paratypes
1978.1.13.21-22	*Oligobrachia*	*gracilis*	paratypes
1978.1.13.23-27	*Oligobrachia*	*gracilis*	paratypes
1980.1-3	*Oligobrachia*	*hawaiiensis*	paratypes
1980.4	*Oligobrachia*	*hawaiiensis*	paratype
1980.5-8	*Siboglinum*	*ordinatum*	paratypes
1981.1	*Riftia*	*pachyptila*	paratype
1991.4	*Lamellibrachia*	*columna*	paratype
1996.1048	*Arcovestia*	*ivanovi*	holotype
1996.1049	*Arcovestia*	*ivanovi*	paratype
2001.6633	*Paraescarpia*	*echinospica*	paratype
1991.1-3	*Siphonobrachia*	*lauensis*	paratypes