

# Cosmopolitan polychaetes – fact or fiction? Personal and historical perspectives

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**Abstract.** In the biogeographical and taxonomical literature before the 1980s there was a wide perception that widespread, often referred to as ‘cosmopolitan’, species were very common among polychaetes. Here we discuss the origins of this perception, how it became challenged, and our current understanding of marine annelid distributions today. We comment on the presence of widely distributed species in the deep sea and on artificially extended ranges of invasive species that have been dispersed by anthropogenic means. We also suggest the measures needed to revolve the status of species with reported cosmopolitan distributions and stress the value of museum collections and vouchers to be associated with DNA sequences in resolving species distributions.

**Additional keywords:** deep sea, *Hydroides elegans*, *Hydroides norvegica*, invasive species, marine annelids, *Marphysa sanguinea*, *Owenia fusiformis*, *Serpula vermicularis*, species distribution, *Terebellides stroemii*.

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## Introduction

In biogeography, cosmopolitan taxa are defined as those distributed across all biogeographic areas. Clearly, no species is truly cosmopolitan (i.e. found worldwide in all habitats and at all depths) but the term, as it is used in marine biogeography, usually assumes a very wide distribution, at least occurring in both major oceans basins (i.e. Pacific and Atlantic). The idea that polychaetes are different from other invertebrates in showing unusually wide geographic distributions was dominant from the mid-19th century (e.g. Grube 1850; Quatrefages 1865) until the late 1970s. Fauvel (1927, 1953) stressed the wide dispersal of many species and Fauvel (1959) explicitly stated that polychaete species had a high degree of morphological variation and consequently had wide geographic distribution. Knox (1957) suggested that up to 40% of the polychaete fauna of the Indo-Pacific represented cosmopolitan species. Ekman (1953), based on views prevailing in polychaete taxonomy, remarked that polychaetes do not show the same biogeographical patterns as other organisms. Similar statements are found in Day (1967) and Briggs (1974). The aim of this paper is to examine how the concept of large numbers of cosmopolitan species in polychaetes evolved and its current status.

We refer to ‘polychaetes’ here because the term was widely used in the historical literature. However, because recent phylogenetic studies (e.g. Struck *et al.* 2007, 2011; Andrade *et al.* 2015) have shown that Echiura, Siboglinidae and Clitellata are derived annelids and that Sipuncula should be included within annelids, the group should be correctly referred to as ‘marine annelids’.

## Why were so many cosmopolitan polychaete species reported?

Part of the explanation is historical as most supposedly ‘cosmopolitan’ polychaete species have a lot in common. They were described in the 19th and even the 18th century from Europe. For example, the serpulids *Serpula vermicularis* Linnaeus, 1767 from the UK and *Hydroides norvegica* Gunnerus, 1768 from Norway were some of the earliest polychaete species described. Other examples of reportedly cosmopolitan species are *Marphysa sanguinea* (Montagu, 1813) from the UK, *Terebellides stroemii* Sars, 1835 from Norway, and *Owenia fusiformis* Delle Chiaje, 1842 from Naples, Italy, to name just a few. These species are abundant in shallow-water benthic communities and/or large and colourful, the reasons why they were immediately noticed by early researchers. They also may have a distinctive morphological character that made them recognisable and ‘easy to identify’, such as the large branchial structure of *Terebellides stroemii* (see Parapar and Hutchings 2015, fig. 2).

The standards of early descriptions were very different, and sometimes only a name was given (e.g. *Amphitrite cirrata* Müller, 1771). Not only were early descriptions often very brief (Kinberg 1867; Claparède 1870; Verrill 1900) but also the illustrations, if any, were few and often of poor quality, while type material was rarely deposited. Characters now regarded as critical for species definitions, such as the structure and distribution of chaetae, were rarely examined, and often poorly illustrated (e.g. Montagu 1813). No comparisons with congeners were provided because the early species were the types of initially monotypic genera. Later, original brief descriptions were gradually expanded on the

basis of material collected far away from the type locality, becoming composite generic descriptions. For example, the description and figures of *Marphysa sanguinea* from South Africa in Day (1967) bear no resemblance to those in the original description of Montagu (1813).

Because the earliest zoologists were based in Europe and initially focussed on discovering European fauna, there is a clear 'European taxonomic bias' in reported cosmopolitan polychaetes. Even when European researchers examined material collected during expeditions to remote places like Australia, they routinely identified polychaetes using existing names of European species (McIntosh 1885; Augener 1914, 1922; Fauvel 1917; Rullier 1965; Hartmann-Schröder 1979, 1982) and so later did the ecologists undertaking benthic surveys in Australia simply because no other names were available (e.g. Stephenson *et al.* 1970, 1974).

Interestingly, all the points above were the same for taxonomists working on other marine taxa (e.g. crustaceans, echinoderms, fish, and molluscs), so they do not completely explain why polychaetes were perceived as unusual. We speculate that the workers on these groups were faster to start to unpick the widespread view of cosmopolitanism because there were more taxonomists working on these groups and the taxonomic effort in those groups was fuelled by their commercial importance. In contrast, the small field of polychaete taxonomy was dominated by several influential and highly productive scientists who attempted to handle all polychaete families and also happened to have rather conservative views on species concepts assuming very wide variation in characters within a species. They largely worked with a large amount of fixed material in their laboratories, not being able to examine their animals alive, so details of habitat types, ecology and reproductive biology were almost always missing. Thus, early polychaete taxonomists out of necessity used morphological characters to delimit species, and implicitly used the morphological species concept, which defines species as 'the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means' (Cronquist 1978).

Three key polychaete taxonomists and their important monographs should be specifically mentioned. Early well illustrated books on errant and sedentary polychaetes in the *Faune de France* series by Fauvel (1923, 1927) for decades were the most widely used taxonomic guides. His later book on polychaetes of India (Fauvel 1953) reprints many of the illustrations from Fauvel (1923, 1927) and uses the same species names as the author firmly believed in cosmopolitan polychaete distributions. He also used the same name when identifying material collected from remote geographic areas. For example, he records (Fauvel 1922) the opheliid *Polyopthalmus pictus* (Dujardin, 1839), described from France, and *Arenicola cristata* Stimpson, 1856, described from South Carolina, USA, from the Abrohlos Islands, Western Australia, with no comments about these range extensions. There are many similar examples in his publications (Fauvel 1917, 1922) across several families and numerous species were synonymised without even an indication that any material was examined to substantiate these decisions. A monograph on polychaetes of South Africa by Day (1967) with its abundant illustrations has also been widely used outside of southern Africa. John Day, who had undertaken

extensive field surveys in South Africa and spent a year before the publication of the monograph at the Natural History Museum in London examining the collections, still included many European 'cosmopolitan' species, such as the above-mentioned *Marphysa sanguinea*, *Owenia fusiformis*, *Terebellides stroemii*, *Serpula vermicularis* and *Hydroides norvegica*, in his monograph of South African polychaetes. The first attempt to summarise the information on polychaetes was made by Olga Hartman, another prominent supporter of the cosmopolitan polychaete species concept. In her *Catalogues of World Polychaetes* (Hartman 1959, 1965) she synonymised many species without any explanation, as Fauvel and Day did. For example, she suggests that of 66 species of *Marphysa*, 11 should be regarded as *M. sanguinea* and of 22 species of *Terebellides* eight of these should be synonymised with *T. stroemii*.

Thus, there was a vicious cycle: poorly developed polychaete taxonomy and conservative views of the most prolific and respected taxonomic authorities resulted in reported cosmopolitan species, and these reports by very influential taxonomists resulted in a lack of taxonomic studies of such species by other workers. It was not until the generation of polychaete taxonomists changed that this view started to change, so the paradigm shift really coincided with the generation shift.

### Demise of the cosmopolitan polychaete distributions concept

In the late 1970s the concept of cosmopolitan polychaete species began to be challenged. This paradigm shift started in the taxonomic literature due to increased taxonomic effort by new workers in the field. Predominantly, the morphological species concept was still used, but morphology was examined in much greater detail. For example, when the senior author became the first polychaete taxonomist in Australia, her early publication (Day and Hutchings 1979) listed 17 genera and 32 species of terebellids, and most of these were records of widely distributed or so-called cosmopolitan species present in Australian waters. By the early 1990s all of these species, except for *Amaeana trilobata* Sars, 1863 were shown to be misidentifications (Hutchings and Glasby 1991) and were recognised as new species restricted in their distribution to Australia. Not surprisingly, the remaining 'European' species *Amaeana trilobata* was most recently shown by Nogueira *et al.* (2015) to be a mixture of two new species (*A. angulus* and *A. ellobophora*), and *A. trilobata* does not occur in Australia. Nogueira *et al.* (2015) undertook a worldwide revision of the genus and provided a range of useful morphological characters to distinguish among the 14 currently accepted species. When later Glasby and Alvarez (1999) examined biogeographic patterns within a group of austral polychaete families, they concluded that an earlier perception of a high proportion of cosmopolitan species (e.g. Knox 1957) reflected the poor state of taxonomic knowledge in the region at the time.

Kristian Fauchald, the former Ph.D. student of Olga Hartman, was one of the prominent workers of the new generation who directly challenged the biogeographical paradigm of predominantly cosmopolitan polychaetes. His famous "pink book" (Fauchald 1977) listed all families and genera based on the Hartman (1959) catalogue but, most importantly, included

the first comprehensive keys to all families and genera as well as a glossary of terms used in polychaete systematics, thus ensuring his status of an authority in polychaete taxonomy. With the help of his research assistant Linda Ward, Kristian Fauchald continued to update this publication, which subsequently evolved into the *World Database of Polychaetes* (Read and Fauchald 2017), a part of the *World Register of Marine Species* (WoRMS Editorial Board 2017). Fauchald (1984) was the first to state that taxonomic problems are the main obstacle to the understanding of polychaete distribution patterns and suggested that, like other organisms, polychaetes can show interesting biogeographical patterns when properly identified. This paper was the plenary at the 1st International Polychaete Conference in 1983.

Arguably, a part of this shift was also due to societal changes: as the world became gradually more globalised and taxonomic studies became internationally collaborative, globally distributed species appeared less likely. Prior to the 1980s the world was a very different place. Finding early literature was time-consuming as the holdings were restricted to the major institutions with extensive libraries. Scientific communication was largely by letters, which could take weeks to arrive, and paper reprints were mailed. While some researchers travelled to other institutions to examine material, face to face meetings were rare. The First International Polychaete Conference held in Sydney in 1983 was for many people the first opportunity to meet their polychaete colleagues in person. Before planning the conference, the senior author travelled to the USA and Europe to confirm that people would fly half way around the world to spend a week talking about polychaetes. Relative decrease of travel costs encouraged people to participate in these conferences, which have continued every three years since that first one and this community has widely embraced the concept of marine annelids but has retained the name of polychaetes in its title. The arrival of electronic mail in the early 1990s and the availability of digital reprints changed the scientific communication by making it easier to access literature, to check species identifications, and to request type material. The mailing list Annelida has been helping connect researchers since 1995. The availability of online databases of museum collections has simplified the task of locating types. The decision by major institutions to digitise their library collections (e.g. Biodiversity Heritage Library) and make them available online, has facilitated checking early descriptions critical for taxonomic studies. The advances in technology, such as the availability of scanning electron microscopy and digital photography, resulted in improved quality of illustrations and helped to identify new characters useful for species recognition. Another advance was the increasing availability of molecular data to help in distinguishing species and this has continued to the present day as the relative costs have declined.

Below, we examine how our understanding of supposedly cosmopolitan distributions has changed using the species mentioned in the beginning of this paper as examples: none of them are now regarded as widely distributed taxa.

Williams (1984) was the first to compare specimens of *Terebellides stroemii* from the type locality (Norway) with specimens collected in several geographic areas and she discovered a suite of morphologically distinct species all

having the typical '*stroemii*' branchial structure. Subsequently, Hutchings and Peart (2000) confirmed that the Australian morphotypes recognised by Williams (1984) indeed represented distinct species. More recently, Parapar and Hutchings (2015) designated a neotype of *T. stroemii* using a specimen collected from the type locality and suggested that this species has a very restricted distribution even in Norway (Nygren, pers. comm.). Parapar *et al.* (2016) provide a summary of studies on the genus *Terebellides*, the former 'cosmopolitan' *Terebellides stroemii*.

Kupriyanova and Rzhavsky (1993) compared specimens of reportedly 'cosmopolitan' *Serpula vermicularis* from the Norwegian Sea and Sea of Japan and suggested that, because these specimens belong to two clearly morphologically different species, *Serpula columbiana* Johnson, 1901 from the Sea of Japan was erroneously synonymised with *S. vermicularis* and needed to be reinstated. The situation became even more complicated when later Kupriyanova (1999) compared specimens of *S. columbiana* from the type locality (Puget Sound, WA, USA) with the specimens from the Sea of Japan and described a new species, *S. uschakovi* Kupriyanova, 1999, from the latter locality. While the cosmopolitan status of *S. vermicularis* that was indiscriminately reported from tropical, subtropical, Arctic and Antarctic waters (reviewed by Kupriyanova 1999) is not justified, the number of species within this species complex remains to be resolved and a much needed neotype needs to be designated.

Another serpulid, *Hydroides norvegica* from Norway, the most cold-tolerant species of the genus (it occurs at its highest latitude at 63.4°N) was for years confused with a morphologically similar congener, *H. elegans* (Haswell, 1883). Ironically, the latter subtropical species described from Port Jackson, Australia, was synonymised with temperate *H. norvegica* by Fauvel (1911) and early reports of *H. elegans* from Australia (e.g. Allen 1953; Wisely 1958; Dew 1959; Straughan 1967) are as *H. norvegica*. The undeserved cosmopolitan status of *Hydroides norvegica* was questioned by Zibrowius (1971) and ten Hove (1974), who rejected this synonymy.

Hutchings and Karageorgopoulos (2003) compared material of *Marphysa* from the type locality of *M. sanguinea* (Cornwall, UK) with material traditionally identified as *M. sanguinea* in Queensland, Australia. They found significant morphological, ecological (very different habitats) and reproductive (bred when water temperatures were very different) differences. They designated a neotype of *M. sanguinea* and described the species from Moreton Bay as a new species, *M. mullawa* Hutchings & Karageorgopoulos, 2003. This study facilitated the most recent discovery of other Australian species of *Marphysa*, all of which had previously been identified as *M. sanguinea* (see Zanol *et al.* 2016 and Zanol *et al.* 2017). Other studies showed that material in South Africa identified as *M. sanguinea* also represents another species (Lewis and Karageorgopoulos 2008).

The cosmopolitan status of the Mediterranean *Owenia fusiformis* was initially questioned by Dauvin and Thiebaut (1994). Studies of *Owenia* by Koh and Bhaud (2001) in China and Koh *et al.* (2003) in the North Atlantic Ocean found several species within this supposedly cosmopolitan species. A detailed morphological study of *Owenia fusiformis* in Australia by Ford and Hutchings (2005) resulted in a description of three new

species, confirming that *O. fusiformis sensu stricto* does not occur in Australia. Most recently, Parapar and Moreira (2015) have described another two species from northern Australia.

As already mentioned, the molecular revolution in taxonomy significantly contributed to our understanding of polychaete species distributions, but by that time the paradigm shift had already happened as a result of morphologically based studies. Wide application of molecular methods in taxonomy and phylogeny also facilitated a shift from the purely morphological species concept in polychaetes. The concept of phylogenetic (*sensu* Cracraft 1989) species based on recognition of monophyletic groups (clades) and the genetic species (*sensu* Baker and Bradley 2006) concept that uses levels of sequence variation for determination of genetic isolation as indications of species boundaries, became commonly used. The observed genetic differences are often assumed to indicate the reproductive isolation (see biological species *sensu* Mayr 1942) in both sympatry (e.g. Styan *et al.* 2017) and allopatry (e.g. Manchenko and Radashevsky 1994) but, in some cases, evidence of reproductive incompatibility was used to support species established on the basis of DNA sequence data alone (Styan *et al.* 2008, Halt *et al.* 2009).

A recent review by Nygren (2014) demonstrates that morphology alone seriously underestimates the number of species and that cryptic (morphologically similar species incorrectly classified as a single one) species are common among polychaete families, making up a significant portion of their biodiversity. Thus, real species distribution ranges are actually even more restricted than morphological studies have revealed.

A very similar story could be told about the sipunculans where the active research community is even smaller. A monograph by Stephen and Edmonds (1972) recognised 320 sipunculan species. Over the next two decades Cutler and colleagues nearly halved the number of species (summarised by Cutler 1994). Of these ~150 species, many have been regarded as ‘cosmopolitan’, defined by Schulze *et al.* (2012) as having ranges spanning at least the width of an ocean basin. However, when Schulze *et al.* (2012) investigated three species reported from both the north-east Pacific and the Sea of Japan in terms of egg size, developmental mode and timing, they found that these ‘cosmopolitan’ species are complexes of cryptic species. Subsequently, Johnson and Schulze (2016) found that *Phascolosoma agassizii* Keferstein, 1866, one of the above three species, is restricted to the eastern Pacific and another currently undescribed species occurs in the western Pacific. Similarly, the widely reported *Sipunculus nudus* Linnaeus, 1766 has also been shown to represent a complex of morphologically similar species that can be separated by both morphological and molecular characters (Kawauchi and Giribet 2013).

### Do cosmopolitan polychaete species exist?

Some studies suggest that cosmopolitan polychaetes do exist, but are rare. For example, Schmidt and Westheide (2000) claim that the cosmopolitan nature of *Hesionides arenaria* Friedrich, 1937 has been confirmed by DNA data and Westheide *et al.* (2003) suggest that *Ctenodrilus serratus* (Schmidt, 1857) provides

‘another example of a truly cosmopolitan distribution in an interstitial meiofaunal polychaete’. Morphological and molecular data suggest a cosmopolitan distribution of the polychaete *Proscoloplos cygnochaetus* Day, 1954 (see Meyer *et al.* 2008). There are also two general exceptions to the rule of restricted distribution ranges in polychaetes.

#### Deep-sea species

The traditional view that deep-sea species generally tend to have broader distributional ranges than those of shallow-water species is supported by most recent studies (e.g. McClain and Schlacher 2015; Higgs and Attrill 2015). Polychaetes follow this rule and genetic evidence for cosmopolitan polychaetes indeed can be found. For example, wide distributions of trichobranchids (genus *Terebellides*) have been confirmed by molecular studies (Schüller and Hutchings 2012), which suggest that deep ocean currents are responsible for moving larvae between ocean basins. The vestimentiferan *Sclerolinum contortum* Smirnov, 2000 has shown genetic consistency in the COI gene among specimens collected from both polar regions and the Gulf of Mexico (Georgieva *et al.* 2015). Most recently, Böggemann (2016) has confirmed widespread distributions of some abyssal glycerids using morphological characters and DNA sequence data.

#### Invasive species

Natural restricted distributions of polychaetes can be significantly enhanced by anthropogenic means and it appears that highly invasive species tend to attain nearly cosmopolitan distribution ranges. The classical example is the truly cosmopolitan above-mentioned invasive serpulid *Hydroides elegans*. For this species, biofouling of ship hulls is suggested as a major mode of dispersal (Pettengill *et al.* 2007) and it is considered to be introduced on both sides of the Atlantic, the Mediterranean Sea, the east coast of the USA (Florida), the west coast of North America (California and Mexico), Hawaii, Japan, Russia and New Zealand. Another example includes a large sabellid, *Sabella spallanzanii* (Gmelin, 1791), introduced by ship hull fouling from its native range in the Mediterranean to Australia and New Zealand (e.g. Ah Yong *et al.* 2017). Transport of larvae in ballast water became an important means of the range expansion for marine organisms since the late 1980s with the increased volume of shipping and the advent of container shipping (see Hutchings 2007). Some polychaetes are translocated with aquaculture movement, for example, *Hydroides ezoensis* Okuda, 1934, which was introduced to the Atlantic coast of France with imported oyster spat from Japan (Gruet *et al.* 1976; Zibrowius 1978). Spionids of the genus *Polydora* are often moved with oyster stocks as they are relocated during oyster cultivation (Sato-Okoshi *et al.* 2012).

Unfortunately, the fact that a taxon is easily translocated to new localities and tends to become invasive does not guarantee that it constitutes a single species. As a result of a dedicated study a widely distributed invasive species may still dissolve into a complex of morphologically distinct species, several cryptic genetically distinct species, or a combination of both. A good example is the important fouling serpulid *Hydroides dianthus* (Verrill, 1873), described from New England and distributed

along the east coast of the USA, that has been widely introduced to, and established in, Europe, Brazil, China and Japan. A recent molecular study (Sun *et al.* 2017) showed that this species is made up of two genetically distinct cryptic species within its range. Even more complicated is the story of another fouler, *Hydroides brachyacantha* Rioja, 1941, described from Mexico and reported from many localities. It is a complex of an unknown number of species that in Australia includes two species, both morphologically and genetically distinct from *H. brachyacantha sensu stricto* (Sun *et al.* 2016). Another notable example is *Ficopomatus enigmaticus* (Fauvel, 1923), a cryptogenic reef-building estuarine species reported from many localities worldwide and known as the ‘Australian tubeworm’. The study by Styan *et al.* (2017) revealed the presence in Australia of three genetic groups (not formally described as species yet) with overlapping ranges, one of which is morphologically distinct from the other two.

Therefore, while the existence of widely distributed species should not be ruled out, all evidence accumulated to date suggests that polychaete species usually have restricted geographic distributions. Therefore, the null hypothesis should normally assume a narrow rather than wide range.

### What do we do with reported cosmopolitan polychaete species?

Remarkably, some polychaetes are still referred to as cosmopolitan in recent ecological (e.g. Maria *et al.* 2011), toxicological (e.g. Eça *et al.* 2013; Gomes *et al.* 2014) and biodiversity (e.g. Souza and Borzone 2000; Surugiu *et al.* 2010) studies. The concept of cosmopolitan species in polychaetes is still widespread as demonstrated by some presentations at the 12th International Polychaete Conference held in Cardiff, Wales, in August 2016. Therefore, we as taxonomists need to increase awareness among non-taxonomists of the fact that wide distributions in marine annelids are suspicious and have to be proven rather than taken for granted. This has been consistently shown in recent studies using molecular data (e.g., Álvarez-Capos *et al.* 2017a, 2017b; Capa *et al.* 2010, 2013; Nygren and Pleijel, 2011; Sun *et al.* 2016). This is what we suggest needs to be done.

### Integrative taxonomic revisionary studies

Species reported as cosmopolitan should be revised on a global scale using a combination of morphological and molecular data. This is crucial for economically important reportedly invasive species, and being able to distinguish among introduced, known native, and yet undescribed native species ensures that neither unnecessary eradication programs are implemented, nor new introductions are overlooked. International collaborative efforts are essential to understand true diversity and distribution of supposedly cosmopolitan species. While some of the most widely reported species, such as those mentioned here, are recognised as plural taxa and partially revised, many others, e.g. serpulids *Spirobranchus kraussii* (Baird, 1865) and *S. tetraceros* (Schmarda, 1861), terebellids *Pista cristata* (Müller, 1776) and *Thelepus setosus* (Quatrefages, 1865), are suspected of representing suites of both morphologically distinct and cryptic species.

### Need for voucher specimens to be associated with published DNA sequences

While depositing sequences resulting from revisionary studies to public databases such as GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) or in BoLD (Barcode of Life Data System) (<http://www.boldsystems.org/>) is critical, it is equally important that these sequences are associated with voucher specimens so that sequence identifications can be validated. Such vouchers should be deposited in museums, while their precise collecting locality, means of identification, and place of deposition should be listed in resulting publications. While some authors have been doing this routinely, others have not and journals should require voucher specimens to be listed in the tables of material sequenced. This is important because GenBank sequences are already riddled with errors that come from misidentification even by experts and taxonomic changes still not reflected in the databases. We suggest that unreliable sequences (such as lacking sufficient collection locality and voucher deposition information to be validated) should be ignored.

### Sequences associated with type material

Because of the above potential problems, we argue that that not all sequences are created equal. The sequences associated with the types of material of newly described species are inherently more reliable and constitute a golden standard for comparative molecular identifications. However, obtaining sequence data for species described decades ago is usually problematic, so specimens for revisionary sequencing should be topotypical, that is, collected as close as possible to the type locality. If no type material was designated or it was lost, then, as a part of a revisionary study of a questionably cosmopolitan species, a neotype should be designated and sequenced (as, for example, was done by Sun *et al.* 2016).

### Development of regional identification tools

The polychaete fauna of many regions is still largely undescribed. For example, Poore *et al.* (2015) concluded that 72% of the polychaetes off the Western Australian coast were new to science. The same is true for the fauna of most of India, most of Asia, South America, and Africa. Unfortunately, because of the lack of regional identification guides polychaete workers in these regions still use the outdated books by Fauvel (1923, 1927) and Day (1967) and, thus, report cosmopolitan polychaete species. Development of regional guides with illustrated interactive keys accompanied by full descriptions and making these easily available online is important to facilitate the recognition of undescribed species. Wherever possible these guides should include molecular markers for the species. A contribution to this was the development of a CD of interactive keys and illustrated descriptions to all world genera and Australian species by Wilson *et al.* (2003), which complemented the interactive digital key (known as Polikey) to polychaete families by Glasby and Fauchald (2003), which obviously needs updating to reflect the true composition of marine annelids. Such identification tools are critically important to ecologists to ensure they correctly identify their fauna.

### Role of museums in resolving cosmopolitan species complexes

All the above indicates that the value of databased and available online museum collections (including both traditional specimens and frozen tissues) and the need for their continuous growth is increasing in the age of molecular taxonomy. At least in Australia, funding for research in museums is declining leading to loss of taxonomists and associated support staff (e.g. Hutchings 2012). We suggest that taxonomists need to become more proactive and explain the value of correct identifications and develop ways and means of training new generation of taxonomists and ensuring that there is a career path after they graduate. In the recently developed Australian National Marine Science Plan (<http://www.marinescience.net.au/national-marine-science-plan/biodiversity-conservation-and-ecosystem-health/>, accessed 06 July 2017), one of the subtheme white papers discusses the need for documentation, curating and systematics of marine biodiversity. This paper, coordinated by the senior author, discusses the declining taxonomic ability in Australia and suggests that priority should be given over the next five years to document Australia's biodiversity. This should include increasing funding for taxonomic research and a coordination between museums to allocate new appointments across taxonomic groups to minimise duplication of effort. In parallel, support should be given to include species in national databases and increasingly associate keys, distribution maps and illustrations for better integration of biodiversity into industry needs and biodiversity health. While obviously this is an Australian perspective, we would suggest that much of this is relevant elsewhere and could be used to increase our knowledge of marine biodiversity, of which marine annelids make up a major component.

### Conflicts of interest

The authors declare no conflicts of interest.

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### References

- Ahyong, S. T., Kupriyanova, E., Burghardt, I., Sun, Y., Hutchings, P. A., Capa, M., and Cox, S. L. (2017). Phylogeography of the invasive Mediterranean fan worm, *Sabella spallanzanii* (Gmelin, 1791), in Australia and New Zealand. *Journal of the Marine Biological Association of the United Kingdom*. doi:10.1017/S0025315417000261
- Allen, F. E. (1953). Distribution of marine invertebrates by ships. *Australian Journal of Marine and Freshwater Research* **4**, 307–316. doi:10.1071/MF9530307
- Álvarez-Campos, P., Giribet, G., and Riesgo, A. (2017a). The *Syllis gracilis* species complex: a molecular approach to a difficult taxonomic problem (Annelida, Syllidae). *Molecular Phylogenetics and Evolution* **109**, 138–150.
- Álvarez-Campos, P., Giribet, G., San Martín, G., Rouse, G. W., and Riesgo, (2017b). Straightening the striped chaos: systematics and evolution of *Trypanosyllis* and the case of its pseudo-cryptic type species *Trypanosyllis krohnii* (Annelida, Syllidae). *Zoological Journal of the Linnean Society* **179**, 492–540.
- Andrade, S. C. S., Novo, M., Kawauchi, G. Y., Worsaae, K., Pleijel, F., Giribet, G., and Rouse, G. W. (2015). Articulating “Archiannelids”: phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* **32**, 2860–2875. doi:10.1093/molbev/msv157
- Augener, H. (1914). Polychaeta 11, Sedentaria. In ‘Die Fauna Sudwest Australiens’. (Eds W. Michaelsen and R. Hartmeyer.) pp. 1–700. (Verlag von Gustav Fischer: Jena, Germany).
- Augener, H. (1922). Results of Dr. E. Mjöberg’s Scientific Expedition to Australia 1910–1913. *K. Svenska Vetenskaps akademien. Stockholm Handlingar* **63**, 1–49.
- Baird, W. (1865). Description of several new species and varieties of tubicolous annelides Tribe Limivora of Grube, in the collection of the British Museum. I & II. *Journal of the Linnean Society. London (Zoology)* **8**, 10–22.
- Baker, R. J., and Bradley, R. D. (2006). Speciation in mammals and the genetic species concepts. *Journal of Mammalogy* **87**, 643–662. doi:10.1644/06-MAMM-F-038R2.1
- Böggemann, M. (2016). Glyceriformia (Annelida) of the abyssal SW Atlantic and additional material from the SE Atlantic. *Marine Biodiversity* **46**, 227–241. doi:10.1007/s12526-015-0354-4
- Briggs, J. C. (1974). ‘Marine Zoogeography.’ (MacGraw-Hill: New York.)
- Capa, M., Bybee, D. R., and Bybee, S. M. (2010). Establishing species and species boundaries in *Sabellastarte* Krøyer, 1856 (Annelida: Sabellidae): an integrative approach. *Organisms, Diversity & Evolution* **10**, 351–371. doi:10.1007/s13127-010-0033-z
- Capa, M., Pons, J., and Hutchings, P. (2013). Cryptic diversity, intraspecific phenetic plasticity and recent geographic translocations in *Branchiomma* (Sabellidae, Annelida). *Zoologica Scripta* **42**, 637–655. doi:10.1111/zsc.12028
- Claparède, E. (1870). Les Annélides Chétopodes du Golfe de Naples. Pt. 2. Annélides Sedentaires. *Mémoires de la Société de Physique et d’Histoire Naturelle de Genève* **20**, 51–223.
- Cracraft, J. (1989). Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In ‘Speciation and Its Consequences’. (Eds D. Otte and J. A. Endler.) pp. 28–59. (Sinauer Associates: Sunderland, MA.)
- Cronquist, A. (1978). Once again, what is a species? In ‘BioSystematics in Agriculture’. (Ed. L. V. Knutson.) pp. 3–20. (Alleheld Osmun: Montclair, NJ.)
- Cutler, E. B. (1994). ‘The Sipuncula. Their Systematics, Biology and Evolution.’ (Cornell University Press: Ithaca, NY.)
- Dauvin, J. C., and Thiebaut, E. (1994). Is *Owenia fusiformis* Delle Chiaje a cosmopolitan species? *Mémoires du Muséum national D’histoire naturelle* **162**, 383–404.
- Day, J. H. (1954). The Polychaeta of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938*, 1–35.
- Day, J. H. (1967). A monograph on the Polychaeta of southern Africa. *British Museum of Natural History Publications* **656**, 459–878.
- Day, J. H., and Hutchings, P. A. (1979). An annotated check-list of Australian and New Zealand Polychaeta, Archiannelida and Myzostomida. *Records of the Australian Museum* **32**, 80–161. doi:10.3853/j.0067-1975.32.1979.203
- Delle Chiaje, S. (1842). ‘Descrizione e notomia degli Animali Invertebrati della Sicilia citeriore osservati vivi negli anni 1822–1830’, Napoli 8 vols [1841–1844]
- Dew, B. (1959). Serpulidae (Polychaeta) from Australia. *Records of the Australian Museum* **25**, 19–56. doi:10.3853/j.0067-1975.25.1959.654
- Dujardin, F. (1839). Observations sur quelques Annélides marines. *Annales des sciences naturelles series 2* **11**, 287–294.
- Eça, G. F., Pedreira, R. M. A., and Hatje, V. (2013). Trace and major elements distribution and transfer within a benthic system: polychaete

- Chaetopterus variopedatus*, commensal crab *Polyonyx gibbesi*, worm tube, and sediments. *Marine Pollution Bulletin* **74**, 32–41. doi:10.1016/j.marpolbul.2013.07.036
- Ekman, S. (1953). 'Zoogeography of the Sea.' (Sidgwick & Jackson: London.)
- Fauchald, K. (1977). The polychaete worms, definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County, Science Series* **28**, 1–190.
- Fauchald, K. (1984). Polychaete distribution patterns, or: can animals with Palaeozoic cousins show large-scale geographical patterns? In 'Proceedings of the First International Polychaete Conference', July 1983, Sydney, Australia. (Ed. P. Hutchings.) pp. 1–6. (The Linnean Society of New South Wales: Sydney.)
- Fauvel, P. (1911). Annélides polychètes du Golfe Persique recueillies par M. M. Bogoyawlewsky. *Archives de Zoologie Experimentale et Generale series* **5** **6**, 19–21.
- Fauvel, P. (1917). Annélides polychètes de l'Australie méridionale. *Archives de Zoologie Experimentale et Generale* **56**, 159–278.
- Fauvel, P. (1922). Annélides polychètes de l'Archipel Houtman Abrolhos (Australie occidentale) recueillies par M. le Prof. W. J. Dakin, F.L.S. *Journal of the Linnean Society of London* **34**, 487–500.
- Fauvel, P. (1923). Un nouveau serpulien d'eau saumâtre *Mercierella* n. g., *enigmatica* n. sp. *Bulletin de la Société Zoologique de France* **47**, 424–430.
- Fauvel, P. (1927). 'Faune de France. Vol. 16. Polychètes sédentaires. Addenda aux errantes, Arachiannélides, Myzostomaires.' (Librairie de la Faculté des Sciences Paul Lechevalier: Paris.)
- Fauvel, P. (1953). 'Annelida Polychaeta. The Fauna of India, including Pakistan, Ceylon, Burma and Malaya.' (The Indian Press: Allahabad, India.)
- Fauvel, P. (1959). Classes des annélides polychètes. Distribution géographique. *Traité de Zoologie* **5**, 163–165.
- Friedrich, H. (1937). Polychaetenstudien. I-III. 1. *Hesionides arenaria* n. sp. n. gen., ein neuer Polychaet aus der Otoplanenzone der Nordsee. 2. *Polydora ligni* Webster 1880 in der Ostsee. 3. Über einige Klein-Polychaeten von Helgoland. *Kieler Meeresforschungen* **1**, 343–351.
- Ford, E., and Hutchings, P. A. (2005). An analysis of morphological characters of *Owenia* useful to distinguish species: description of three new species of *Owenia* (Oweniidae: Polychaeta) from Australian waters. *Marine Ecology (Berlin)* **26**, 181–196. doi:10.1111/j.1439-0485.2005.00062.x
- Georgieva, M. N., Wiklund, H., Bell, J. B., Eilertsen, M. H., Mills, R. A., Little, C. T. S., and Glover, A. G. (2015). A chemosynthetic weed: the tubeworm *Sclerolinum contortum* is a bipolar, cosmopolitan species. *BMC Evolutionary Biology* **15**, 280. doi:10.1186/s12862-015-0559-y
- Glasby, C. J., and Alvarez, P. (1999). Distribution patterns and biogeographic analysis of austral Polychaeta (Annelida). *Journal of Biogeography* **26**, 507–533. doi:10.1046/j.1365-2699.1999.00297.x
- Glasby, C. J., and Fauchald, K. (2003). 'POLiKEY.' Version 2. Australian Biological Resources Study, Canberra. Available at <http://www.environment.gov.au/biodiversity/abrs/online-resources/polikey/index.html> [accessed 15 March 2016].
- Gmelin, J. F. (1791). Vermes. In 'Caroli a Linnaei Systema Naturae per Regna Tria Naturae'. Ed. 10. Tome 1(6). (Ed. J. F. Gmelin.) pp. 3021–3910. (G. E. Beer: Lipsiae [Leipzig]). Available at: <http://www.biodiversitylibrary.org/item/83098#5>
- Gomes, I. D. L., Lemos, M. F. L., Amadeu, M. V., Soares, M., Barata, C., and Faria, M. (2014). The use of cholinesterase as potential biomarker: *in vitro* characterization in the polychaete *Capitella teleta*. *Marine Pollution Bulletin* **85**, 179–185. doi:10.1016/j.marpolbul.2014.05.053
- Grube, A. E. (1850). Die Familie der Anneliden. *Archiv für Naturgeschichte* **16**, 249–364.
- Gruet, Y., Héral, M., and Robert, J. M. (1976). Premières observations sur l'introduction de la faune associée au naissan d'huîtres japonaises *Crassostrea gigas* (Thunberg), importé sur la côte atlantique Française. *Cahiers de Biologie Marine* **17**, 173–184.
- Gunnerus, J. (1768). Om nogle norske coraller. *Skrifter det Kongliger norske Videnskabselskabet Trondhjem* **4**, 38–73.
- Halt, M. N., Kupriyanova, E. K., Cooper, S. J. B., and Rouse, G. W. (2009). Naming species with no morphological indicators: species status of *Galeolaria caespitosa* (Annelida, Serpulidae) inferred from nuclear and mitochondrial gene sequences and morphology. *Invertebrate Systematics* **23**, 205–222. doi:10.1071/IS09003
- Hartman, O. (1959). Catalogue of the polychaetous annelids of the world. Parts I & II. Allan Hancock Foundation Occasional Paper No. 23. 1–628 {Part I, pp 1–353; Part II pp. 355–628}. University of Southern California Press, Los Angeles, California.
- Hartman, O. (1965). Catalogue of the polychaetous annelids of the world: supplement, 1960–1965, and index. Allan Hancock Foundation Occasional Paper No. 23 supplement and index 197 pp. University of Southern California Press, Los Angeles, California
- Hartmann-Schröder, G. (1979). Teil 2. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). In 'Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden'. (Eds G. Hartmann-Schröder, and G. Hartmann.) *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **76**, 75–218.
- Hartmann-Schröder, G. (1982). Teil 8. Die Polychaeten der subtropisch-antiborealen Westküste Australiens (zwischen Cervantes im Norden und Cape Naturaliste im Süden). In 'Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden'. (Eds G. Hartmann-Schröder, and G. Hartmann.) *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **79**, 51–118.
- Haswell, W. A. (1883). On some new Australian tubicolous annelids. *Proceedings of the Linnean Society of New South Wales* **7**, 633–638.
- Higgs, N. D., and Attrill, M. J. (2015). Biases in biodiversity: wide-ranging species are discovered first in the deep sea. *Frontiers in Marine Science* **2**, doi:10.3389/fmars.2015.00061
- Hutchings, P. (2007). Introduced marine pests – how they get here, how do we get rid of them, and how do we know they are really introduced. In 'Pest or Guest: the Zoology of Overabundance'. (Eds D. Lunney, P. Eby, P. Hutchings, and S. Burgin.) pp. 79–87. (Royal Zoological Society of New South Wales: Sydney.)
- Hutchings, P. A. (2012). The chill winds of climate change freeze funding for biodiversity's critical infrastructure – a personal view. In 'Science under Siege: Zoology under Threat'. (Eds P. Banks, D. Lunney, and C. Dickman.) pp. 9–12. (Royal Zoological Society of New South Wales: Sydney.)
- Hutchings, P. A., and Glasby, C. J. (1991). Phylogenetic implications of the biogeography of Australian Terebellidae. *Ophelia. Supplementum* **5**, 565–572.
- Hutchings, P. A., and Karageorgopoulos, P. (2003). Designation of a neotype of *Marphysa sanguinea* (Montagu, 1813) and a description of a new species of *Marphysa* from eastern Australia. *Hydrobiologia* **496**, 87–94. doi:10.1023/A:1026124310552
- Hutchings, P. A., and Peart, R. (2000). A revision of the Australian Trichobranchidae (Polychaeta). *Invertebrate Taxonomy* **14**, 225–272. doi:10.1071/IT98005
- Johnson, H. P. (1901). The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society for Natural History* **29**, 381–437, plates 1–19. Available at [http://www.archive.org/stream/proceedings\\_bost07unkngoog#page/n436/mode/2up](http://www.archive.org/stream/proceedings_bost07unkngoog#page/n436/mode/2up).

- Johnson, N. D., and Schulze, A. (2016). Genetic structure in two *Phascolosoma* species in the Pacific Ocean. *Marine Biology Research* **12**, 739–747. doi:10.1080/17451000.2016.1196819
- Kawauchi, G., and Giribet, G. (2013). *Sipunculus nudus* Linnaeus, 1766 (Sipuncula): cosmopolitan or a group of pseudo-cryptic species? An integrated molecular and morphological approach. *Marine Ecology (Berlin)* **35**, 1–14.
- Keferstein, W. (1866). Untersuchungen über einige amerikanischen Sipunculiden. *Nachrichten von der Gesellschaft der Wissenschaften zu Göttingen* **1866**, 215–228.
- Kinberg, J. G. H. (1867). Annelata nova. In 'Öfversigt af Kongl'. *Vetenskaps-Akademiens Förhandlingar. Tjugondredje. Argängen Stockholm* **9**, 337–355.
- Knox, G. A. (1957). The distribution of polychaetes within the Indo-Pacific. *Proceedings of the 8th Pacific Science Congress* **3**, 403–411.
- Koh, B. S., and Bhaud, M. (2001). Description of *Owenia gomsoni* n. sp. (Oweniidae, Annelida Polychaeta) from the Yellow Sea and evidence that *Owenia fusiformis* is not a cosmopolitan species. *Vie et Milieu* **51**, 77–86.
- Koh, B. S., Bhaud, M. R., and Jirkov, I. A. (2003). Two new species of *Owenia* (Annelida: Polychaeta) in the northern part of the North Atlantic Ocean and remarks on previously erected species from the same area. *Sarsia* **88**, 175–188. doi:10.1080/00364820310001318
- Kupriyanova, E. K. (1999). The taxonomic status of *Serpula columbiana* Johnson, 1901 the Asian and American coasts of the North Pacific Ocean. *Ophelia* **50**, 21–34. doi:10.1080/00785326.1999.10409386
- Kupriyanova, E. K., and Rzhavsky, A. V. (1993). *Serpula* and *Crucigera* (Annelida, Polychaeta) of the Russian Far Eastern Seas. *Ophelia* **38**, 47–54. doi:10.1080/00785326.1993.10429923
- Lewis, C., and Karageorgopoulos, P. (2008). A new species of *Marphysa* (Eunicidae) from western Cape of South Africa. *Journal of the Marine Biological Association of the United Kingdom* **88**, 277–287. doi:10.1017/S002531540800009X
- Linnaeus, C. (1766). 'Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.' 12th edn. Vol. I, Part 1, pp. 1–532. (Laurentii Salvii: Holmiae.)
- Linnaeus, C. (1767). 'Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.' 12th edn. Vol. I, Part 2, pp. 533–1327. (Laurentii Salvii: Holmiae.)
- Manchenko, G. P., and Radashevsky, V. I. (1994). Genetic differences between two allopatric sibling species of the genus *Polydora* (Polychaeta: Spionidae) from the West Pacific. *Biochemical Systematics and Ecology* **22**, 767–773. doi:10.1016/0305-1978(94)90079-5
- Maria, T. F., Esteves, A. M., Vanaverbeke, J., and Vanreusel, A. (2011). The effect of the dominant polychaete *Scolecopsis squamata* on nematode colonisation in sandy beach sediments: an experimental approach. *Estuarine, Coastal and Shelf Science* **94**, 272–280. doi:10.1016/j.ecss.2011.07.006
- Mayr, E. (1942). 'Systematics and the Origin of Species: From the Viewpoint of a Zoologist.' (Columbia University Press: New York.)
- McClain, C. R., and Schlacher, T. A. (2015). On some hypotheses of diversity of animal life at great depths on the sea floor. *Marine Ecology (Berlin)* **36**, 849–872. doi:10.1111/maec.12288
- McIntosh, W. C. (1885). Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873–1876. *Challenger Reports* **12** (Zoology), 554 pp.
- Meyer, A., Bleidorn, C., Rouse, G. W., and Hausen, H. (2008). Morphological and molecular data suggest a cosmopolitan distribution of the polychaete *Proscoplos cygnochaetus* Day, 1954 (Annelida, Orbiniidae). *Marine Biology* **153**, 879–889. doi:10.1007/s00227-007-0860-4
- Montagu, G. (1813). An account of some new and rare marine British shells and animals. *Transactions of the Linnean Society of London* **11**, 179–204.
- Müller, O. (1771). 'Von Würmern des süssen und salzigen Wassers.' (Linnaen Society of London: Copenhagen)
- Müller, O. (1776). 'Zoologicae Danicae Prodrum, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium.' (Havniae: Copenhagen) xxxii+282 pp. [Plates published in 1777, Hallagerii, Havniae.]
- Nogueira, J. M. M., Carreretta, O., and Hutchings, P. (2015). Review of *Amaeana* Hartman, 1959 (Annelida, Terebelliformia, Polycirridae) with descriptions of six new species. *Zootaxa* **3994**, 1–2. doi:10.11646/zootaxa.3994.1.1
- Nygren, A. (2014). Cryptic polychaete diversity: a review. *Zoologica Scripta* **43**, 172–183. doi:10.1111/zsc.12044
- Nygren, A., and Pleijel, F. (2011). From one to ten in a single stroke – resolving the European *Eumida sanguinea* (Phyllodocidae, Annelida) species complex. *Molecular Phylogenetics and Evolution* **58**, 132–141.
- Okuda, S. (1934). Some tubicolous annelids from Hokkaido. *Journal of the Faculty of Science, Hokkaido University. Series 6, Zoology* **3**, 233–246.
- Parapar, J., and Hutchings, P. (2015). Redescription of *Terebellides stroemii* (Polychaeta, Trichobranchidae) and designation of a neotype. *Journal of the Marine Biological Association of the United Kingdom* **95**, 323–337. doi:10.1017/S0025315414000903
- Parapar, J., and Moreira, J. (2015). The Oweniidae (Annelida: Polychaeta) from Lizard Island, Great Barrier Reef, Australia with the description of three new species. *Zootaxa* **4019**, 604–620. doi:10.11646/zootaxa.4019.1.20
- Parapar, J., Moreira, J., and Martin, D. (2016). On the diversity of the SE Indo-Pacific species of *Terebellides* (Annelida; Trichobranchidae), with the description of a new species. *PeerJ* **4**, e2313. doi:10.7717/peerj.2313
- Pettengill, J. B., Wendt, D. E., Schug, M. D., and Hadfield, M. G. (2007). Biofouling likely serves as a major mode of dispersal for the polychaete tubeworm *Hydroides elegans* as inferred from microsatellite loci. *Biofouling* **23**, 161–169. doi:10.1080/08927010701218952
- Poore, G. C. B., Avery, L., Błażewicz-Paszkowicz, M., Browne, J., Bruce, N. L., Gerken, S., Glasby, C., Greaves, E., McCallum, A. W., Staples, D., Syme, A., Taylor, J., Walker-Smith, G., Warne, M., Watson, C., Williams, A., Wilson, R. S., and Woolley, S. (2015). Invertebrate diversity of the unexplored marine western margin of Australia: taxonomy and implications for global biodiversity. *Marine Biodiversity* **45**, 271–286. doi:10.1007/s12526-014-0255-y
- Quatrefages, A. de (1865). Note sur la classification des annélides. Academie des Sciences, Paris. *Compte rendu hebdomadaire des seances* **60**, 586–600.
- Read, G., and Fauchald, K. (Ed.) (2017). World Polychaeta Database. Available at <http://www.marinespecies.org/polychaeta> [accessed 18 January 2017].
- Rioja, E. (1941). Estudios anelidológicos, 2. Observaciones de varias especies del género *Hydroides* Gunnerus (*sensu* Fauvel) de las costas mexicanas del Pacífico. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* **12**, 161–175.
- Rullier, F. (1965). Contribution à la faune des Annelides Polychètes de l'Australie. Papers, Department Zoology, University of Queensland **2**, 163–210.
- Sars, M. (1835). 'Beskrivelser og lagttagelser over nogle mærkelige eller nye i Havet ved den Bergenske Kyst levende Dyr av Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes Classer, med en kort Oversigt over de hidtil af Forfatteren sammsteds fundne Arter og deres Forekommen.' (Thorstein Hallagers Forlag: Bergen.)
- Sars, M. (1863). Geologiske og zoologiske lagttagelser, anstillede paa en Reise i en Deel af Trondhjems stift i Sommeren 1862. *Nyt magasin for naturvidenskaberne* **12**, 253–340.
- Sato-Okoshi, W., Okoshi, K., Koh, B. S., Kim, Y. H., and Hong, J. S. (2012). Polydroid species (Polychaeta: Spionidae) associated with commercially

- important mollusk shells in Korean waters. *Aquaculture* **350–353**, 82–90. doi:10.1016/j.aquaculture.2012.04.013
- Schmarda, L. K. (1861). Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. I. Turbellarien. *Rotatorien und Anneliden* **2**, 1–164.
- Schmidt, O. (1857). Zur Kenntnis der Turbellaria, Rhabdocoela und einiger anderer Wuermer des Mittelmeeres. *Sitzungsberichte der Kaiserliche Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Klasse* **23**, 347–366.
- Schmidt, H., and Westheide, W. (2000). Are the meiofaunal polychaetes *Hesionides arenaria* and *Stygocapitella subterranea* true cosmopolitan species? – Results of RAPD-PCR investigations. *Zoologica Scripta* **29**, 17–27. doi:10.1046/j.1463-6409.2000.00026.x
- Schüller, M., and Hutchings, P. A. (2012). New species of *Terebellides* (Polychaeta: Trichobranchidae) indicate long-distance dispersal between western South Atlantic deep-sea basins. *Zootaxa* **2395**, 1–16.
- Schulze, A., Maiorova, A., Timm, L. E., and Rice, M. E. (2012). Sipuncular larvae and ‘cosmopolitan’ species. *Integrative and Comparative Biology* **52**, 497–510. doi:10.1093/icb/ics082
- Smirnov, R. V. (2000). Two new species of Pogonophora from the arctic mud volcano off northwestern Norway. *Sarsia* **85**, 141–150.
- Souza, J. R. R., and Borzone, C. A. (2000). Population dynamics and secondary production of *Scolecopsis squamata* (Polychaeta: Spionidae) in an exposed sandy beach of southern Brazil. *Bulletin of Marine Science* **67**, 221–233.
- Stephen, A. C., and Edmonds, S. J. (1972). ‘The Phyla Sipuncula and Echiura.’ (Trustees of the British Museum of Natural History: London.)
- Stephenson, W., Williams, W. T., and Lance, G. N. (1970). The macrobenthos of Moreton Bay. *Ecological Monographs* **40**, 459–494. doi:10.2307/1942340
- Stephenson, W., Williams, W. T., and Cook, S. D. (1974). The benthic fauna of soft bottoms, southern Moreton Bay. *Memoirs of the Queensland Museum* **17**, 73–123.
- Stimpson, W. (1856). Description of some new marine invertebrates. *Proceedings, Academy of Natural Sciences of Philadelphia* **7**, 385–395.
- Straughan, D. (1967). Marine Serpulidae (Annelida: Polychaeta) of eastern Queensland and New South Wales. *Australian Journal of Zoology* **15**, 201–261. doi:10.1071/ZO9670201
- Struck, T. H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D., and Halanych, K. M. (2007). Echiura, Siboglinidae, and Clitellata are derived annelids with polychaete sister taxa, and that Sipuncula should be included within annelids. *BMC Evolutionary Biology* **7**, 1–11.
- Struck, T. H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G., and Bleidorn, C. (2011). Phylogenomic analyses unravel annelid evolution. *Nature* **471**, 95–98.
- Styan, C. A., Kupriyanova, E. K., and Havenhand, J. N. (2008). Strong barriers to cross-fertilization between populations of a polychaete species are unlikely to have arisen through gametic compatibility arms-races. *Evolution* **62**, 3041–3055. doi:10.1111/j.1558-5646.2008.00521.x
- Styan, C. A., McCluskey, C. F., Sun, Y., and Kupriyanova, E. K. (2017). Cryptic sympatric species across the Australian range of the global estuarine invader *Ficopomatus enigmaticus* (Serpulidae, Annelida). *Aquatic Invasions* **12**, 53–65. doi:10.3391/ai.2017.12.1.06
- Sun, Y., Wong, E., Tovar-Hernandez, M., Williamson, J., and Kupriyanova, E. K. (2016). Is *Hydroides brachyacantha* (Serpulidae, Annelida) a widely-distributed species? *Invertebrate Systematics* **30**, 41–59. doi:10.1071/IS15015
- Sun, Y., Wong, E., Keppel, E., Williamson, J., and Kupriyanova, E. K. (2017). A global invader or a complex of regionally distributed species? Clarifying the status of an invasive calcareous tubeworm *Hydroides dianthus* (Verrill, 1873) using barcoding. *Marine Biology* **164**, 28. doi:10.1007/s00227-016-3058-9
- Surugiu, V., Revkov, N., Todorova, V., Papageorgiou, N., Valavanis, V., and Arvanitidis, C. (2010). Spatial patterns of biodiversity in the Black Sea: an assessment using benthic polychaetes. *Estuarine, Coastal and Shelf Science* **88**, 165–174. doi:10.1016/j.ecss.2010.03.012
- ten Hove, H. A. (1974). Notes on *Hydroides elegans* (Haswell, 1883) and *Mercierella enigmatica* Fauvel, 1923, alien serpulid polychaetes introduced into the Netherlands. *Bulletin of the Zoological Museum, Amsterdam* **4**, 45–51.
- Verrill, A. E. (1873). Results of the recent dredging expeditions on the coast of New England. No. 3. *American Journal of Science New Haven* **6**, 435–441. doi:10.2475/ajs.s3-6.36.435
- Verrill, A. E. (1900). Additions to the Turbellaria, Nemertina and Annelida of the Bermudas, with revisions of some New England genera and species. *Transactions of the Connecticut Academy of Arts and Sciences* **10**, 595–671. doi:10.5962/bhl.part.7035
- Westheide, W., Haß-Cordes, E., Krabusch, M., and Müller, M. (2003). *Ctenodrilus serratus* (Polychaeta: Ctenodrilidae) is a truly amphiatlantic meiofauna species – evidence from molecular data. *Marine Biology* **142**, 637–642. doi:10.1007/s00227-002-0960-0
- Williams, S. J. (1984). The status of *Terebellides stroemii* (Polychaeta, Trichobranchidae) as a cosmopolitan species on a worldwide morphological survey, including description of a new species. In ‘Proceedings of 1st International Polychaete Conference’. (Ed. P. A. Hutchings.) pp. 118–142. (Linnean Society of New South Wales: Sydney.)
- Wilson, R., Hutchings, P. A., and Glasby, C. J. (2003). ‘Polychaetes: An Interactive Identification Guide.’ (CSIRO Publishing: Melbourne.)
- Wisely, B. (1958). The development and setting of a serpulid worm, *Hydroides norvegica* Gunnerus (Polychaeta). *Marine and Freshwater Research* **9**, 351–361. doi:10.1071/MF9580351
- WoRMS Editorial Board (2017). World Register of Marine Species. Available at <http://www.marinespecies.org> [accessed 18 January 2017].
- Zanol, J., Silva, T., and Hutchings, P. (2016). *Marphysa* (Eunicidae, Polychaeta, Annelida) species of the *sanguinea*-group from Australia, with comments on pseudo-cryptic species. *Invertebrate Biology* **135**, 328–344. doi:10.1111/ivb.12146
- Zanol, J., Silva, T., and Hutchings, P. (2017). One new species and two redescription of *Marphysa* (Eunicidae, polychaete, Annelida) species of the *Aenea*-group from Australia. *Zootaxa* **4268**, 411–426.
- Zibrowius, H. (1971). Les espèces Méditerranéennes du genre *Hydroides* (Polychaeta, Serpulidae): remarque sur le prétendu polymorphisme de *Hydroides uncinata*. *Tethys (Cornella de Llobregat)* **2**, 691–746.
- Zibrowius, H. (1978). Introduction du polychète Serpulidae japonaise *Hydroides ezoensis* sur la côte atlantique française et remarques sur la repartition d’autres espèces de Serpulidae. *Tethys (Cornella de Llobregat)* **8**, 141–150.

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