Handbook of Zoology
Annelida

Volume 1:
Annelida Basal Groups and Pleistoannelida, Sedentaria I

Handbook of Zoology

Founded by Willy Kükenthal
continued by M. Beier, M. S. Fischer, J.-G. Helmcke, D. Starck, H. Wermuth
Editor-in-chief Andreas Schmidt-Rhaesa

Annelida

Edited by Günter Purschke, Markus Böggemann
and Wilfried Westheide

DE GRUYTER

Annelida

Volume 1:
Annelida Basal Groups and Pleistoannelida, Sedentaria I

Edited by Günter Purschke, Markus Böggemann
and Wilfried Westheide

DE GRUYTER

Scientific Editors
Prof. Dr. Günter Purschke
Universität Osnabrück
FB 5 - Biologie/Chemie
Barbarastr. 11
49076 Osnabrück
purschke@biologie.uni-osnabrueck.de

Prof. Dr. Markus Böggemann
Universität Vechta - Fakultät II
Natur- und Sozialwissenschaften/Biologie
Driverstr. 22
49377 Vechta
Markus.Boeggemann@uni-vechta.de

Prof. Dr. em. Wilfried Westheide
Gerhart-Hauptmann-Str. 3
49134 Wallenhorst
westheide@biologie.uni-osnabrueck.de

ISBN 978-3-11-029146-9
e-ISBN (PDF) 978-3-11-029158-2
e-ISBN (EPUB) 978-3-11-038178-8
ISSN 2193-4231

Library of Congress Control Number: 2018953239

Bibliografic information published by the Deutsche Nationalbibliothek
The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available in the Internet at http://dnb.dnb.de.

Typesetting: Compuscript Ltd. Shannon, Ireland
Printing and Binding: CPI books GmbH, Leck

www.degruyter.com

Preface

Annelida, the segmented worms, comprise one of the most important taxa of invertebrates. The majority of annelid species occur in the marine environment, but they can be found also in fresh water and terrestrial realms. Especially the marine forms, also known as polychaetes, are one of the most widespread, abundant, and diverse elements of the world benthic fauna. Here, they are present from the upper intertidal down to the deep sea and constitute important members of the respective food chains. In contrast, the mainly terrestrial forms or clitellate oligochaetes are structurally more uniform but nevertheless comparatively speciose and important members in terrestrial decomposer communities. Surprisingly enough, one group of these oligochaetes is closely related to parasitic or carnivorous forms, the leeches.

Although at large comprising somewhat only 21,000 described species, annelids show a remarkable diversity comparable, for instance, with that observed in crustaceans. This diversity could be achieved only by the plasticity of their bauplan constituting prostomium, followed by a number of primarily identical modules, the segments, and the pygidium. Species are usually of median size and do not exceed a few centimeters in length. However, their range is much wider; some of the smallest adult metazoans known belong to this group with body dimensions of less than 0.2 µm – the dwarf male of *Dinophilus* – as well as species exceeding body lengths of more than 3 m, such as *Eunice aphroditois*. The number of segments varies accordingly from less than ten to several hundreds. The marine forms often show broadcast spawning, and primarily, their life cycle comprises a planktonic larva, the trochophore, and a benthic adult. However, there are lots of deviations from this pattern, which inter alia are correlated with life style and body size.

The Annelid volume of the first edition of the *Handbook of Zoology* appeared in the years between 1928 and 1934, edited by W. Kükenthal and T. Krumbach. Especially the anatomical part still serves as a valuable resource of knowledge. However, since then, our knowledge has increased broadly. Although several reviews on annelids have been published, they usually cover only special topics in this group of invertebrates. So around the year 2010, the idea was born that a new edition of this very successful work would be urgently needed. Even more than in former times, today, such a task could not be achieved by a single person or just by a few authorities, and so we began looking for authors who could contribute to such a big effort. Very soon, we had to learn that for many annelid groups, specialists did not exist in the scientific zoological community or were not available for various reasons. Therefore, it took much longer than originally planned to compile the manuscripts, and in spite of our efforts, there will remain a few gaps of missing chapters. Since all authors have lots of other duties and writing of handbook chapters is rather time-consuming, it took some time to compile the manuscripts from our authors. It was a great advantage that each chapter ready for publication was published electronically in Zoology Online so that the chapters were available for the scientific community quite soon after acceptance. All contributions were peer reviewed and revised prior to publication. For these reasons, and very sadly, the important taxon Clitellata could not be included in the *Handbook of Zoology*. We still hope that it will be possible to supplement this sometime in the future.

This book is the first out of four volumes in the *Handbook of Zoology* series treating the morphology, anatomy, reproduction, development, ecology, phylogeny, and systematics of polychaetes. Polychaetes are seen here as those annelids that do not possess a clitellum. As written above, they comprise one of the most important groups of invertebrates in the marine food web, where they can be found in almost every habitat, often in high abundances. Generally, polychaetes are dominant members of the epi- and endobenthos, but there are also a few holopelagic species. However, a few species managed to colonize even freshwater and terrestrial realms. Moreover, polychaetes may occur in comparatively extreme environments from hydrothermal vents at the ocean floor spreading centers to the terrestrial ground water.

Recent phylogenetic analyses have confirmed that polychaetes constitute nothing else but a paraphyletic assemblage of the more or less plesiomorphic Annelida. Besides a so-called basal radiation, the majority of Annelida, now termed Pleistoannelida, fall into two large monophyletic taxa, Errantia and Sedentaria. In a highly derived position, the latter also comprise Clitellata, the earthworms and leeches. In addition, some taxa that in the past were regarded to represent separate phyla turned out to be nothing else but true Annelida, although being morphologically highly derived especially with respect to one so-called key character, segmentation. These taxa are Sipuncula, Myzostoma, Pogonophora, and Echiura, which are now placed in different positions in the phylogenetic tree of Annelida. This fact impressively demonstrates the adaptive capacity and potential of the annelid bauplan.

https://doi.org/10.1515/9783110291582-202

This first volume covers members of the so-called basal radiation and the first part of Sedentaria. The chapters are mostly organized treating the families; their arrangement follows the most recent phylogenetic hypotheses. This first volume is supplemented by chapters on the history of annelid research, their fossil record, and an introduction to the phylogeny of annelids and their position in the tree of life. The second volume will be devoted to the remaining Sedentaria, with the exception of Clitellata, and the third volume will treat the Errantia.

All authors that have contributed to the *Handbook of Zoology* have done an excellent job, and we want to thank them sincerely. We also thank the various reviewers of the sometimes voluminous chapters for their helpful suggestions for improvements, helping to keep the scientific standard as high as possible. Last but not the least, the help of the lectors and employees of our publisher DeGruyter is gratefully acknowledged for their endless help during the publishing process.

Günter Purschke, Wilfried Westheide,
and Markus Böggemann
Osnabrück, Wallenhorst, and Vechta, Germany,
October 2018

Contents

Annelida will be continued in:
Volume 2: Annelida, Sedentaria II, ISBN 978-3-11-029147-6
Volume 3: Annelida, Sedentaria III and Errantia I, ISBN 978-3-11-029148-3
Volume 4: Annelida, Errantia II, ISBN 978-3-11-064531-6

List of contributing authors

James A. Blake
Aquatic Research & Consulting
24 Hitty Tom Road, Duxbury, MA 02332-4112 USA
E-mail: jablake9@gmail.com

Christoph Bleidorn
Georg-August-Universität Göttingen
Animal Evolution and Biodiversity
Untere Karspuele 2, D-37073 Göttingen, Germany
E-mail: christoph.bleidorn@gmail.com

Markus Böggemann
University of Vechta
Faculty II Biologie (Room A 116)
Driverstrasse 22, 49377 Vechta, Germany
E-mail: markus.boeggemann@uni-vechta.de

Michael J. Boyle
Smithonian Marine Station at Fort Pierce
701 Seaway Drive, Fort Pierce, FL 34949, USA
E-mail: BoyleM@si.edu

Temir A. Britayev
Laboratory for Ecology and Morphology of Marine Invertebrates
A.N. Severtzov Institute of Ecology & Evolution RAS
Leninsky pr. 33, 119071 Moscow, Russia
E-mail: britayev@yandex.ru

María Capa
Department of Biology
University of the Balearic Islands
Cra. de Valldemossa, km 7.5.
Palma, Illes Balears, Spain E-07122
E-mail: maria.capa@uib.es

Harlan K. Dean
University of Massachusetts
Biology Department
100 William T. Morrissey Blvd., Boston, MA 02125-3393, USA
E-mail: Harlan.Dean@umb.edu

Brigitte Ebbe
Alfred Wegener Institute
Division Biosciences and Functional Ecology (Room Co-30)
Am Handelshafen 12, 27570 Bremerhaven, Germany
E-mail: Brigitte.Ebbe@awi.de

Mats E. Eriksson
Lund University
Department of Geology
Sölvegatan 12, SE-223 62 Lund, Sweden
E-mail: mats.eriksson@geol.lu.se

Dieter Fiege
Senckenberg Research Institute and Natural History Museum
Frankfurt
Marine Zoology – Marine Invertebrates II
Senckenberganlage 25, 60325 Frankfurt am Main, Germany
E-mail: dieter.fiege@senckenberg.de

Conrad Helm
Georg-August-Universität Göttingen
Johann-Friedrich-Blumenbach Institute for Zoology & Anthropology,
Animal Evolution and Biodiversity
Untere Karspuele 2, D-37073 Göttingen, Germany
E-mail: chelm@gwdg.de

Pat Hutchings
Australian Museum
Australian Museum Research Institute
1 William Street, Sydney, NSW 2010, Australia
E-mail: Pat.Hutchings@austmus.gov.au

Gisele Y. Kawauchi
University of Minas Gerais
Department of Zoology – Biology and Systematics of Annelida
Av. Antônio Carlos, 6627 CEP: 31270-901, Belo Horizonte, MG, Brazil
E-mail: gykawa@gmail.com

Alexandra Kerbl
Universiy of Copenhagen
Department of Biology – Marine Biological Section
Universitetsparken 4, Copenhagen 2100, Denmark
E-mail: alexandra.kerbl@bio.ku.dk

Nancy J. Maciolek
Aquatic Research & Consulting
24 Hitty Tom Road, Duxbury, MA 02332-4112 USA
E-mail: NJMaciolek@gmail.com

Andrew S.Y. Mackie
Amgueddfa Cymru – National Museum Wales
Department of Natural Sciences
Cathays Park, Cardiff, CF10 3NP, UK
E-mail: Andy.Mackie@museumwales.ac.uk

Wagner Magalhães
University of Hawai'i at Mānoa
Water Resources Research Center
2500 Campus Road, Honolulu, HI 96822, USA
E-mail: wagnerfm@hawaii.edu

Daniel Martin
University of Barcelona
Spanish National Research Council (CSIC) – Centre for Advanced
Studies of Blanes (CEAB)
Catalunya 17300, Spain
E-mail: dani@ceab.csic.es

Alejandro Martínez
Department of Zoology
University of Laguna
Avenida Astrofísico Francisco Sánchez, s/n. Campus de Anchieta, Apartado de correos 456, CP 38200, La Laguna, Spain
E-mail: amartinez.ull@gmail.com

Kate Mortimer
Amgueddfa Cymru – National Museum Wales
Department of Natural Sciences
Cathays Park, Cardiff CF10 3NP, UK
E-mail: Katie.Mortimer-Jones@museumwales.ac.uk

Jorge A. Núñez Fraga
Department of Zoology
University of Laguna
Avenida Astrofísico Francisco Sánchez, s/n.
Campus de Anchieta, Apartado de correos 456, CP 38200, La Laguna, Spain
E-mail: janunez@ull.es

Julio Parapar
University of A Coruña
Department of Biology
Rua da Fraga 10, 15008 A Coruña, Spain
E-mail: julio.parapar@udc.es

Luke A. Parry
Yale University
Department of Geology and Geophysics
210 Whitney Av., New Haven, CT 06511, USA
E-mail: luke.parry@yale.edu

Mônica A.V. Petti
University of São Paulo
Instituto Oceanográfico – Biological Oceanography
Praça do Oceanográfico, 191 – Cidade Universitária,
CEP 05508-120 – São Paulo, Brazil
E-mail: mavpetti@gmail.com

Günter Purschke
Osnabrück University
Faculty of Biology/Chemistry – Zoology (Room 35/239)
Barbarastraße 11, 49076 Osnabrück, Germany
E-mail: purschke@biologie.uni-osnabrueck.de

Geoffrey B. Read
NIWA
41 Market Place Viaduct Harbour, 1010 Auckland
Private Bag 99940, Newmarket, Auckland 1149, New Zealand
E-mail: Geoffrey.Read@niwa.co.nz

Sergio I. Salazar-Vallejo
El Colegio de la Frontera Sur
Department of Marine Ecology
Apartado Postal 424, Chetumal, Quintana Roo 77000, Mexico
E-mail: savs551216@hotmail.com

Anja Schulze
Texas A&M University at Galveston
Department of Marine Biology
200 Seawolf Parkway, Galveston, TX 77553, USA
E-mail: schulzea@tamug.edu

Torsten H. Struck
University of Oslo
Natural History Museum (Room 209)
Sars gate 1, Colletts hus, Oslo 0318, Norway
E-mail: t.h.struck@nhm.uio.no

Jakob Vinther
University of Bristol
School of Earth Sciences
Office Life Sciences
117, Wills Memorial Building, Queens Road, Clifton, BS8 1RJ, UK
E-mail: jakob.vinther@bristol.ac.uk

Wilfried Westheide
Osnabrück University
Faculty of Biology/Chemistry – Zoology
Barbarastraße 11, 49069 Osnabrück, Germany
Gerhart-Hauptmann-Str. 3, 49134 Wallenhorst
E-mail: westheide@biologie.uni-osnabrueck.de

Katrine Worsaae
Universiy of Copenhagen
Department of Biology – Marine Biological Section
Universitetsparken 4, Copenhagen 2100, Denmark
E-mail: kworsaae@bio.ku.dk

Anna E. Zhadan
Moscow State University
Department of Biology – White Sea Biological Station
Leninskie Gory, 1–12, Moscow 119234
E-mail: azhadan@wsbs-msu.ru

Part 1: **Introduction**

Geoffrey B. Read

1 A History of Annelida Research

1.1 Introduction

> Now turn to the annelids! What do they lack when compared with the most splendid inhabitants of earth or air? Yet they shun the light, they withdraw themselves from our view, but with no design to attract; and the naturalist alone knows where to seek the strange wonders, which are hidden within the recesses of the rock and beneath the sandy beds of the ocean. (Armand de Quatrefages 1857)

> The Annelids, as a class, are animals of very obscure habits, living principally under stones, in mud, or, as the common earth worm and its congeners, in garden and other soil. Their forms and appearances are, generally speaking, not very attractive, except to the enthusiastic naturalist, who is determined on investigating the various forms of life. (Edward Parfitt 1867)

Annelids have indeed been of interest to many enthusiastic investigators over hundreds of years, despite their usual retiring nature as suggested by Quatrefages and Parfitt, because annelids are an integral and diverse part of many aquatic and terrestrial environments. They can be plain in shape, but many are intricately structured, and we can endorse Parfitt's further comment that terebellid polychaetes "when seen alive in a glass of sea water...are some of the most elegant creatures inhabiting the great deep." Today, more than at any previous time, larger numbers of researchers are believed to be studying some aspect of annelid biology, with "annelid" mentioned in the title of over 220 research articles published in 2017.

A historical review of a more inclusive Annelida, containing former phyla Echiura, Sipuncula, Pogonophora, and Vestimentifera, as established by phylogenetic analysis of molecular and morphological data, has enough scope to be worthy of a book. This is a first attempt at the topic in article length and only selectively covers some of the history of interest to annelid workers. General histories of annelid research include Quatrefages (1866b: 154–173), Ashworth (1912: 1–25), and Fauchald and Rouse (1997: 73–76 and appendices). Later, for polychaetes, there are succinct summaries of the topic by Hutchings and Glasby (2000: 3,7) and Rouse and Pleijel (2001: 1), with both works also including group-specific histories. The history of myzostome worm research is separately covered by Grygier (2000). Next, for sipunculans and echiurans, Stephen and Edmonds (1972) have some history information, as does Cutler (1994) for sipunculans. Ivanov (1963: 3–6) has a historical review for the former phylum Pogonophora (now Siboglinidae), with Rouse (2001) covering the history since Ivanov's monograph, and for oligochaetes, there are contributions by Vejdovsky (1884: 12–14), Reynolds and Cook (1976: 1–4), Brinkhurst (1999), and Rota (2011). Also, for biogeographic history, Stephenson's (1930) oligochaete monograph (Chapter 18) covers some of the early tendency to invoke land bridges preplate tectonics to explain "palaeogeographical problems" with terrestrial worms. There is less analysis of research history available for the leeches, but see Moquin-Tandon (1846: 7–17).

This chapter is focused on a general history of studies on the taxonomy, classification, and biology of Annelida, particularly in relation to technological change. There is an emphasis toward taxonomy, early history, and the traditional polychaete groups. Time and space did not permit inclusion of more world and regionally significant monographies, of major early species-level biology studies, and more on the history of traditional non-polychaetes and clitellates especially, but also the echiurans and sipunculans. Elsewhere in the handbook, in the other general chapters, there are in-depth reviews of annelid phylogeny, and fossil record, as well as chapters by specialists on each taxon group, with more on morphology, reproduction, development, biogeography, phylogeny, plus taxonomic histories. The history of research on fossil annelids is not covered here, as this topic is dealt with in a separate chapter on annelid fossils (see Parry, Eriksson, and Vinther).

The science and the understanding of Annelida began with names created to label and communicate about what was in the environment. Ever since Aristotle, the use of taxonomy for recording and extending knowledge has been important, and it still is. In the 2017 calendar year, there were 155 new species of polychaetes published, and currently, 21,126 species have been described, of which 56% or 11,758 names are valid (Read and Fauchald 2018), with in one estimate, over 6,000 further polychaetes remain undescribed, and a possible upper range of more than twice that number of undescribed oligochaetes may exist (Appeltans *et al.* 2012), based on a likelihood of many cryptic species in that group (e.g., Taheri *et al.* 2018).

1.2 In the beginning – annelids and humans

> One does not see these worms all year round, but only on the 2nd, 3rd, and 4th night after a full moon, which takes place

https://doi.org/10.1515/9783110291582-001

> when the sun is in Pisces, in February and March; one should look for them at that time after the sun has set by the light of torches… (Rumphius 1705, Beekman (1999) translation)

> …they are on every bush and tree, from which they frequently drop on the head and neck of the passer-by, while they always creep up his legs; nay, they can even spring to reach their victim. (Haeckel 1883, on land-leeches)

For thousands of years, each generation of humans must have been aware of the variety of annelids in their environment. Annelid worms are easily visible to the unaided eye, unlike many invertebrates. In warmer, wetter places, unwelcome blood-seeking leeches would have intruded on passers-by and would have been as much a nuisance to early humans as they were to Haeckel in Sri Lanka, whereas in more benign encounters, worms would have been seen whenever hunger or human curiosity led to fossicking for hidden life on the shore, in forest plant-litter, and in diggings. Annelids are welcome food for many animals, but skilled early human gatherers might have preferred tastier, more inviting items to consume, except when starving at times of famine, so it is hard to know what extent of folk knowledge about annelid ecology, habits, and uses was linked to local names for them and passed on to the next generation. There were likely earlier uses in folk medicine preceding those recorded in CE 50–70 by Greek physician Pedanius Dioscorides (*fide* Ashworth 1912). Earthworms, as easily collected, obvious, and harmless, continued to be used as medicinal ingredients through to the 1700s in Europe (Rota 2011) and into the twentieth century in China, Japan, and Burma (Stephenson 1930: Chapter 17). Collection for fish bait was probably common in many prehistoric cultures and is still popular and widely commercialized today (Watson *et al*. 2017). New Zealand postcontact Maori still both ate earthworms and used them as bait (Benham 1904, Miller 1952), with one bioluminescent species said to be used as a lure (Springett *et al*. 1998). Blakemore (2009) reviews work done on the likely translocation of earthworms as humans migrated in the neolithic, carrying soil with their crop plants, possibly important in relation to island or trans-oceanic colonization, and states that 120 (of about 6000) earthworm species have become widely distributed in association with humans.

Consumption of great quantities of marine annelids, spawning ripe and packed with nutritious gametes, occurred in the western Pacific islands and Indonesia, where there is a tradition of collecting and eating worms named "Palolo" (also "Wawo"; local names vary), which are mass-swarming reproductive morphs, mostly of Eunicidae, but also Nereididae. In other places, this harvesting also involved a degree of predicting the times when the Palolo/Wawo swarms will appear based on past observations (Rumphius 1705, as translated in Beekman and Rumpf 1999, Stair 1897, Burrows 1955; Herdrich and Armstrong 2008). Rumphius also gives recipes for cooking Wawo. Echiurans (*Urechis* spp.) are now eaten in Japan and adjacent countries, but whether this is a traditional food rather than for gourmet adventures is uncertain. Swarming Japanese nereidid worms may also have been eaten in the past (so-called Japanese palolo).

In general, annelids, apart from leeches and amphinomid marine fireworms, are harmless, indeed beneficial to human interests (e.g., soil-conditioning by earthworms). Leeches also had a supposed useful role in medicine, with vast numbers once harvested, but it is doubtful if blood-letting through application of hungry leeches was often beneficial, although the practice continued for at least 2000 years (Brookes 1763: 295, Johnson 1816), and still does; leeches have a useful minor role in medical practice today for increasing blood flow and in pharmacology as a source of bioactive compounds (Siddall *et al*. 2007). Today, marine annelids as a commercial product are used for aquaculture food, for waste processing, as well as for fish bait, while freshwater annelids are also used to process sewage sludge (*Lumbriculus* and other genera) and grown as aquarium fish food (*Tubifex*). *Eisenia* "tiger" earthworms are present almost everywhere humans have settlements and are used to process organic waste, both industrially and domestically (vermicomposting). As mentioned, *Hirudo* leeches are cultured for biomedical research. In the recent past, there was a market for earthworms, lugworms, nereidids, and serpulids for educational dissection and as robust animals for respiration and fertilization experiments (Moore 2012).

1.3 The written record

> From the time of Pliny onwards for more than a thousand years little real advance was made in regard to the knowledge of worms. (Ashworth 1912)

> These works are still occasionally consulted, though they afford little useful information, and might without any loss to science be consigned to oblivion. (MacGillivray 1834)

The written record of annelid observation begins in the Mediterranean with Aristotle (384–322 BCE[1]) and Pliny (CE

1 Calendar-year epoch abbreviations BCE "before common era" and CE "common era" are used here as neutral terms for indicating the year count of before and following CE year 1 of historic convenience, with BCE placed *after* the date and CE placed *before* the date.

23–79) (Tab. 1.1). Aristotle reported his own marine discoveries, often very accurately from what we know today, and is much the more reliable of the two. In contrast, Pliny's biota information includes a mixture of secondhand fables, and he was less scientific and more credulous. Pliny's *Historia Naturalis* is a wide-ranging encyclopedia of all knowledge, which is mainly why it was so influential for over 1,500 years and is still analyzed today – this is not so much because part of it concerned "natural history" as we use the term now. However, as eventually published in typeset print for the first time (Pliny 1469), it is said to be the first "printed" natural history book. It may not be widely known that there were no biota illustrations in the original scrolls, nor in the many later medieval copies and derivative extracts, nor in the printed complete editions of Pliny in the fifteenth century, although these were "illuminated" (with elaborate color paintings for enlarged first letters of chapters). This lack did not deter Cuvier from suggesting in 1827 identifications for the *Historia Naturalis* animals (comments repeated as footnotes in Bostock and Riley 1855: vol. 2, 117, etc.).

Aristotle has the earliest recorded observation of Mediterranean Sea sea-scolopendra (sea 'centipedes') as transcribed in the following.

> The so-called "sea-scolopendra," after swallowing the hook, turns itself inside out [proboscis everts?] until it ejects it, and then it again turns itself outside in. The sea-scolopendra...will come to a savoury bait; the creature does not bite with its teeth, but stings by contact with its entire body... (Aristotle ~335 BCE, in English translation by Thompson 1910: 621a)

That account fits an amphinomid fireworm. It is interesting to compare the subsequent Pliny version of the observation, in which the event has become more cataclysmic for the worm but is clearly derivative from Aristotle.

> The scolopendra...if it chances to swallow a hook, will vomit forth all its intestines, until it has disengaged itself, after which it will suck them in again. (Pliny CE ~78, in English translation by Bostock and Riley 1855: vol. 2 Chapter 67, p. 453)

Carrion-feeding amphinomids are known to swim to bait and to swallow baited hooks (Glasby and Bailey-Brock 2001). According to those authors "this bait-taking behaviour appears not to have been previously documented...," but it seems likely Aristotle did that over 2000 years earlier.

Ashworth (1912) has an excellent review of many of the early works mentioning annelids and of how successive authors built on from their predecessors or simply repeated previous content (a common failing according to historians of this period of natural history). The authors and names are summarized here (Tab. 1.1). These were convenient Latin descriptive names for referring to various kinds of worms, but sometimes, we can guess what species they might have been. Rondelet is the most reliable of these authors.

The higher classification was still in flux before Linnaeus (and after), and a lot of small biota were "insects" (e.g., annelids as *insectis marinus* in Gessner). Ashworth points out that, following Aldrovandus' (1602) book on "insects" ("classifying" by *aquatica/terrestria* and by *pedata/apoda* so that terrestrial *lumbricus* was far divorced from aquatic *lumbricus*), for a period, several writers, oddly from our evolutionary viewpoint now, split annelids between a very-inclusive "insects" group (which included some marine worms) and a more terrestrial *vermes* group, which included parasitic worms, leeches, and earthworms. However, it should be obvious that these strange early "classifications" are for tracking groupings that are strictly practical (aquatic/land, legs/no legs, etc.) rather than being intended as relationship groupings. Later, Linnaeus (1758) had the second group in his *Vermes Intestina*, with *Nereis* in *Vermes Mollusca*, with *Scolopendra marina* now a synonym in *Nereis*, and with *Serpula* in *Vermes Testacea* (shelled organisms, including today's molluscs). This was still puzzling to Shaw by 1802, who got partly in line with today's usage with the comment: "The genus *Serpula* is inhabited by a very different race of animals from the rest of the testaceous tribe, and which seem to bear some analogy to the Amphitritae and Nereides among the Mollusca, and to the Scolopendrae among Insects." ("naturalist's miscellany", Shaw and Nodder 1789–1813, vol. 14 of 1802: 177)

1.4 Linnaeus and the first annelid genera – the dawn of available names

Although some ancient names are still in use, the original descriptions and usages of all names prior to the 10th edition of Linnaeus, a work assigned the date of 1 January 1758, are excluded from nomenclatorial priority (ICZN 1999). It is important to realize that Linnaeus adopted previous names or newly created his names in relation to name usages by others, cited by him in short synonymies, and for animals he had not seen. The second Strickland Code ended the priority of all names earlier than Linnaeus, including the ancient ones. The authors (Strickland 1878) caustically commented "The nomenclature of [John]

Tab. 1.1: Some early works and name usages on annelids, up to the 10th edition of Linnaeus, adapted and extended from Ashworth (1912).

Author	Date	Taxa names	Title	Figures/of worms	Country/area/occupation
Aristotle (Aristoteles)	~335 BCE	*scolopendra marina*	*Historia Animalium*	No/no	Greece/Athens/teacher
Pliny the Elder (Gaius Plinius Secundus)	CE 78	*scolopendrae, hirudo, lumbricus, sanguisuga* (leech)	*Historia Naturalis*	No/no	Italy/Naples/soldier-scholar
Claudius Aelianus (Aelian)	~220	*scolopendrae*	*De Natura Animalium*	No/no	Italy/Rome/teacher
Isidore (Isodorus) of Seville[1]	~600	*sanguisuga, lumbricus* (=a parasitic worm)	*Etymologiae Book XII De Animalibus*	No/no	Spain/Seville/bishop
Jacob van Maerlant	~1266	*sanguisuga, vermis* (=earthworm)	*Der Naturen Bloeme* (in Dutch rhyme, not Latin)	Yes/yes	Netherlands/Utrecht or Flanders/scholar-poet
Pierre Belon (Petrii Belonii)	1553	*lumbricus marinus* (=first lugworm), *eruca marina* (=indet. marine "caterpillar")	*De Aquatilibus*	Yes/no	France/Paris/physician
Guillaume Rondelet (Rondeletius)	1555	*scolopendrae marinae, hirudo, vermis macrorinchoteros, v. microrinchoteros* (=sipunculids), *penicillo marino* (=marine "paint-brush" = first sabellid), *physsalo* (=aphroditiform), *vermibus in tubulis* (=serpulids)	*Libri de Piscibus Marinis…*	Yes/yes (Rondelet worm figures much copied)	France/Montpellier/ physician-teacher
Conrad Gessner[2] (Conradi Gesneri)	1558	*Hirudo/sanguisuga*, *eruca marina* (=Rondelet's aphroditiform. Figures copies other Rondelet marine annelids)	*Historiae Animalium* (also as *Icones Animalium*)	Yes/yes	Switzerland/Zurich/ physician-teacher
Adriaen Coenen	1578	(Figures copy Rondelet) *scolopendra marina, lumbricus marinus, vermis in tubulis, vermis* spp, *eruca marina, hirudo marina*	*Visboeck* (in Dutch)	Yes/yes	the Netherlands/ Scheveningen/ fisherman-merchant
Ulysses Aldrovandi/o[3] (Ulisse Aldrovandus)	1602	*lumbricus terrestris, l. marinus, scolopendra marina, vermes in tubulis* (serpulids), *hirudo paludosa, h. marina, vermis* spp (figures after Rondelet)	*De Animalibus Insectis libri septem*	Yes/yes	Italy/Bologne/ teacher-naturalist
Thomas Willis	1672	*lumbricus terrestris* anatomy	*De Anima Brutorum*	No/no	England/Oxford and London/ physician-anatomist
Francesco Redi	1684	*lumbricus terrestris* (as not a helminth), *scolopendra marina* (nereidid), *hystrix marina* (marine "porcupine" = Aphrodita)	*De Animalculis Vivis…*	Yes/yes	Italy/Florence/physician-biologist
John Ray[4] (Joanne Raio)	1710	*lumbricus terrestris*, *hirudo*, lugs, *scolopendra marina*	*Historia Insectorum*	No/no	England/Essex/parson-naturalist
Frederik Ruysch (Fredericii Ruischii)	1710, 1725	*eruca marina* (marine "caterpillar" =Aphrodita)	*Thesaurus Animalium primus…*	Yes/no	the Netherlands/Amsterdam/ physician-botanist-collector
Hans Sloane	1725	*teredo or scolopendra maxima* (perhaps *Amphinome rostrata*)	*A voyage to the islands… Jamaica*	Yes/yes	Britain/London/physician-naturalist
Albertus Seba	1734 v1 1758 v3	*eruca marina* (=Aphrodita), *millepeda marina* (amphinomid), *penicillum marinum* (here a serpulid, not sabellid)	*Locupletissimi Rerum Naturalium Thesauri…*	Yes/yes	Netherlands/Amsterdam/ pharmacist-collector
Carl Linnaeus	1735	*Lumbricus, Hirudo, Scolopendra marina*	*Systema Naturae* (1st)	No/no	Sweden and the Netherlands/ Leiden/biologist-teacher

Tab. 1.1: (continued)

Author	Date	Taxa names	Title	Figures/of worms	Country/area/occupation
Carl Linnaeus	1748	*Lumbricus, Hirudo, Amphitrite, Nereis, Aphrodita*	*Systema Naturae* (6th)	No/no	Sweden/Stockholm/ biologist-teacher
Carl Linnaeus	1758	*Lumbricus terrestris, L. marinus* (lugworm), *Hirudo, Aphrodita*, *Nereis, Serpula* (total >40 species)	*Systema Naturae* (10th)	No/no	Sweden/Stockholm/ biologist-teacher

These early titles are well known, mostly encyclopedic, and not included in the references list unless cited in the text. Early biota names in Latin are not capitalized to avoid confusion with post-1735 Linnaean Latin binominals.

[1] The *Etymologiae* of Isidore (c. 560–636), scholar and archbishop of Seville, is a compendium that Isidore gleaned from other sources and was much copied and later printed in many editions, and the text was used in medieval bestiaries. However, annelids barely register; under a subheading of "*De Vermibus,*" Isidore briefly characterizes a *sanguisuga* as a leech, but the *lumbricus* mentioned seems to be intestinal, not a terrestrial annelid. *Lumbricus* was simply the Latin for either an intestinal worm or earthworm; likewise, *sanguisuga* was a leech.

[2] The *Historiae Animalium* of Gessner (1516–1565) is a vast compendium of over 3,500 folio pages in four volumes, with editions in Latin and in German, and a pioneer in zoology publishing for the copious illustrations, also printed separately as *Icones Animalium* (1560) with marine annelids grouped in *insectis marinis,* and with the whole work produced in color in just a few copies (Kusukawa 2010). Gessner freely acknowledged the sources he copied from, notably citing Rondelet for marine annelids – an admirable practice but perhaps also intended to add authority.

[3] The *De Animalibus Insectis* of Aldrovandi (1522–1605) is another compendium, notable for an early example of a bifurcating "classification" diagram at the beginning, which includes his worms. The diagram appears intended as a key for identification rather than for showing hierarchical relationships, but there is no caption. Aldrovandi met Rondelet when both were in Rome and was then inspired by his example to take up natural history. In his other works, there are splendid copperplates, but the in-text worm figures in this work appear to be mostly adaptations from Rondelet, and amusingly, Aldrovandi's artist has added little faces with eyes to Rondelet's realistic sipunculans.

[4] Parson-naturalist John Ray (1628–1705) has a preliminary layout following the worm arrangement of Aldrovandi so that his earthworms were in "Apoda" but "lugs" (text Latin, but a few words are written in English) = lugworms(?) were in "Polypoda aquatica." Again, the layout is for practical identification rather than for indication of relatedness. His name was commemorated some 60 years later in the founding of The Ray Society in 1844 by George Johnston (1797–1855). Johnston was a marine naturalist who published (posthumously) the significant British Museum book (Johnston 1865) *A Catalogue of the British Non-Parasitical Worms*. A later John Ray connection with annelids is that the Society subsequently published McIntosh's British Annelids monographs.

Ray [1627–1705] is chiefly derived from that of Gesner [1516–565] and Aldrovandus [1522–1605], and from these authors we might proceed backward to…Pliny, and Aristotle, till our zoological studies would be frittered away amid the refinements of classical learning.” However, this is an exaggeration; in the case of most early annelid names, there is not much of a problem, as the Latin words applied were in everyday use (*eruca*, *hirudo*, *lumbricus*, *scolopendra*, *vermis*), may even have been used in Greek earlier (*skolopendra*), and may be simply descriptive (*penicillus*, *sanguisuga*, *lumbricus marinus*, *scolopendra marina*). Greek *skolopendra* was the name for multipeds, land or marine, but Greek *skolekos* was a worm, with the Latinized combining-form “scoleco” later giving us a variety of still-used genus names, notably *Scolecolepides* and variant names in Spionidae, and the higher rank names Scoleciformia in Benham (1896) and Scolecida in Rouse and Fauchald (1997). Also, fossilized scolecodonts, which are annelid jaw elements, especially of Eunicida, are the most common form in which annelids occur in the fossil record (see fossils chapter).

Linnaeus combined the two early Latin leech names for his *Hirudo sanguisuga* (now *Haemopsis*). It is more difficult to resolve the new names created by contemporaries of Linnaeus just prior to 1758. No one has compiled them (except perhaps McIntosh (q.v.) as dispersed in his monograph synonymies), but Knight-Jones and Perkins (1998) show how, based on the good figure in Ellis (1755: plate 34), the *corallina tubularia melitensis* of Ellis became named *Serpula penicillus* Linnaeus, 1758 and now corresponds to the well-known *Sabella spallanzanii* (Gmelin 1791). The striking figure of a *penicillo marino* printed much earlier in Rondelet (1555: 111) is probably this species also (Fig. 1.1 A, B, and see later for history of illustrations).

The Linnaeus 10th edition (1758), as the start of nomenclature, established polychaete genera *Aphrodita*, *Nereis*, and *Serpula* (which included names later moved into *Sabella* and into phylum Mollusca [vermetids

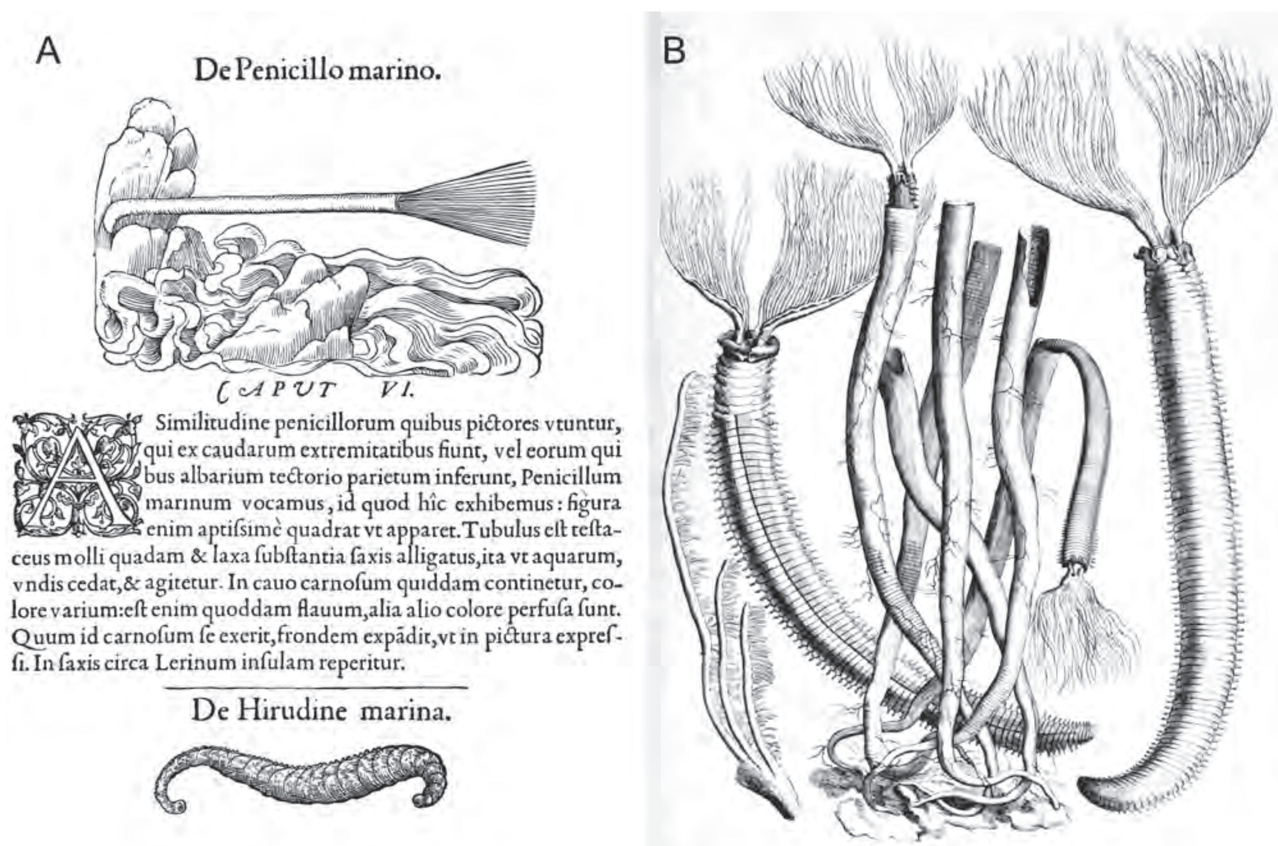

Fig. 1.1: Early representations of *Sabella spallanzanii* from the Mediterranean Sea in Rondelet (1555) and Ellis (1755). A, Rondelet penicillo marino figure and description (with a marine leech below), collected from Lérins Islands near Cannes (immersed tubes can be remarkably straight as in the Rondelet miniature). B, Ellis plate 34, corallina tubularia melitensis from Malta (=Melita) (Ellis’s specimens were not alive when examined; the description is clearly of *S. spallanzanii*). Scale: an adult *S. spallanzanii* is more than 300 mm in body length. Originals at https://biodiversitylibrary.org/page/41733271 and https://biodiversitylibrary.org/page/10676353

and pholads]), oligochaete genus *Lumbricus*, and leech genus *Hirudo*. Later, in the 12th edition (1767), *Sabella*, *Terebella*, and *Sipunculus* were added. No new annelid genera appeared in the 13th edition in 1791, but *Amphitrite* Müller, 1771 appears again there, after a long gap following a dubious listing in the Linnaeus 6th edition (1748). The *Systema naturae* appears not to have been popularized in English until Turton (Linné and Turton 1806) translated the 13th edition (edition inferred from Turton's inclusion of Gmelin on the title page), but by then, it had long been an influential work among scientists. The *Systema naturae* had no illustrations, but (as in the *Sabella* case) sometimes, illustrations can be found in the works Linnaeus cited.

As mentioned, ancient *scolopendra* was long also used for centipede-like marine annelids as well as for multiped land arthropods, starting from before Aristotle, and mostly, those illustrated seem to have been large amphinomids. The grey *Teredo* (a mistaken name usage) or *Scolopendra maxima* worm found with ship-worm-bored driftwood by Sloane (1725: v. 2 plate 234) might have been an *Amphinome rostrata* (Pallas, 1766). Likewise, the Indonesian marine "millipede" "*millepeda marina*, *amboinensis*" of Seba (1734) was suggested to have been a *Hermodice*. Seba's plate (Fig. 1.2) is of an amphinomid, identity uncertain. The Linnaeus *Systema* first edition (1735) still included a dubious *S. marina*, but ultimately, the genus *Scolopendra* was lost to the Arthropoda: Myriapoda: Chilopoda, which are indeed the centipedes, and genus *Nereis* soon replaced it for a while as a parking lot for a diversity of errant and sedentary marine worms (e.g., *Nereis norvegica*, Linnaeus, 1767, a *Eunice*).

The year after the 10th *Systema* was published, the Royal Society *Transactions* printed an article by Jean André Peyssonnel (1759), as "Observations upon the Sea Scolopendre or Sea Millepes," in which Peyssonnel described the external features and the action of the pharynx of what Ashworth placed as a nereidiform

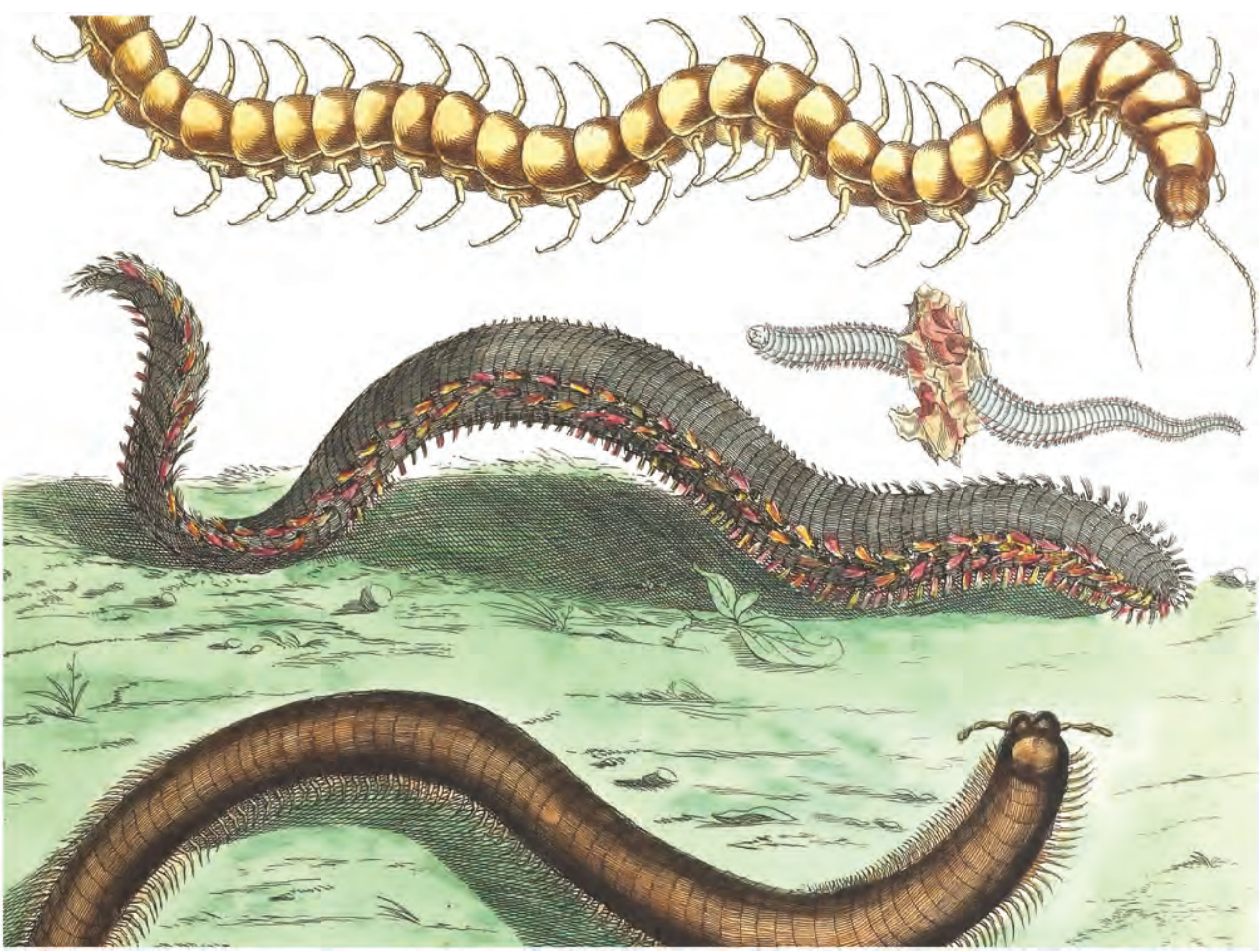

Fig. 1.2: Albertus Seba (1734) unidentifiable amphinomid (as millepeda marina) from Amboina, figure from plate 81, sandwiched between two terrestrial multipedes. No scale. Original at https://biodiversitylibrary.org/page/41047664

worm, but Thompson (1910: 621a) doubted it was a *Nereis*. The description, especially of the prickles penetrating Peyssonnel's fingers, indicates this scolopendre (probably from Guadeloupe), although an elongate "nereidiform" worm was again (as in Aristotle) likely to be a large amphinomid like a *Eurythoe*, *Hermodice*, or *Amphinome*. He wrote: "it was like fire upon the part. It was in vain that I rubbed and washed the part; and tho' the prickles were broken, yet the parts that stuck in the flesh, produced their effect, and caused the pain I felt for some hours."

Finally, it is worth mentioning because of some surrounding taxonomic confusion that Slabber (1781), in a strange late usage, applied the name *S. marina* to two very different forms of marine worms, looking nothing like the *Scolopendra* concept. The first was to a *Polydora*-like spionid that he stated to be closer to *Nereis*, also by Linnaeus, than to *Scolopendra* (Slabber 1781: 25–29, plate VII, Figs. 1–2), and the second was to an indeterminable autolytine syllid (Slabber 1781: 44–46, plate X, Figs. 3–5). These could not be either the same species or an amphinomid-like *Scolopendra*.

1.5 Discoveries and major changes in understanding in Annelida

Interesting changes in the perception of annelid taxa at various levels, began early in the nineteenth century at the top level with the name annelid itself. Jean-Baptiste Lamarck (1802), in his annual major speech at the Paris museum, addressed the assembled *citoyens* of the French Republic to introduce and define "Annelides" (no é accent initially) as the French name of an additional new main "classe" of the animal kingdom, slotting between molluscs and crustaceans and separate from another "vers" group. Mammals were the top group in Lamarck's table, with the groups following in his table supposedly showing a "degradation" of specialized organs. His further representation of groups within the Annelides did not solidify until Lamarck (1818: 286), where he separated Annelides antennées, Annelides sédentaires, and Annelides apodes (echiurans and leeches) within his classe Annelides.

As an alternative to Annelides, Blainville (1816) introduced the French Sétipodes in a formal classification layout, later morphing it to Chétopodes in his *Dictionnaire* entries, and eventually, it was Latinized as Chaetopoda. Fischer von Waldheim (1808) appears to be the first to use "Annulata" for the group when, in a classification summary, he used the informal French Annélides (with é accent) matched with formal Annulata, a name he attributes to Cuvier. Later, Örsted (1842), then notably Grube (1850), used and kept using Annulata as the formal name for Annélides, a practice followed subsequently by a few, notably Kinberg and Malmgren. Grube (1850) also introduced Polychaeta and Oligochaeta for the first time, while finally, Hatschek (1893) Latinized Annélides as class Annelida, which included as subclasses Archiannelida (named in Hatschek 1878 as Archiannelides), Chaetopoda, Hirudinea, and Echiurida, with associated groups Sipunculacea and Chaetognatha.

Phylum as a formal taxonomic rank name was not a term familiar to Lamarck, Cuvier, Blainville, and their contemporaries in the early nineteenth century, at least not as a top-rank label, but previous reviews may not make this clear. Phylum (from Greek *phylon*, a tribe) was the term that gradually became universally accepted following the introduction and use of it by Haeckel (1866) for each main branch of the genealogical tree (Lankester 1890). Before that, the concept was understood, but a phylum-level category could have various early names such as type, branch (embranchment), subkingdom, and class (Lamarck used classe).

Cuvier (1817 (vol. 2): 508) introduced a new concept of a group above the phylum-level annelids of today when he named *Les Animaux Articulés* as his *Troisième grande divivision du Règne animal*. He included in it the annelids, crustaceans, arachnids, and insects, purely on the common structural feature of segmentation. This was the first suggestion that an Articulata grouping (mostly arthropods) should also include annelids as their sister group, and the idea proved to be enduring, although long debated since. While cladistic analysis was dependent on morphological data, an argument could still be made into the late 1990s for the Articulata concept to have an annelidan component (Rouse and Fauchald 1995, 1997, and see the "Phylogeny of Annelida" chapter). With the aid of compelling molecular data, beginning with the first evidence for a split between major clades becoming known as the Ecdysozoa and Lophotrophozoa (Aguinaldo *et al*. 1997), plus better data on embryonic cleavage, we now know that Articulata *sensu* Cuvier is not a natural lineage and that the arthropoda are an Ecdysozoa group, while annelids are in Lophotrophozoa along with the unsegmented molluscs, etc. (e.g., Bourlat *et al*. 2008).

It is not necessary here to further work through all the many progressive changes and substitutions in names for the subgroups of annelids and allies since Lamarck, or over the 260 years since the 10th edition of Linnaeus (for some of these, see Fauchald and Rouse 1997, particularly Appendices A and B, and the "Phylogeny of Annelida" chapter), nor to create a chain of synonyms and variant spellings of names of higher ranks, but there are some other significant ones to look at briefly. By the second edition of *Traité de Zoologie* (Claus and Moquin-Tandon 1884), the standard classification of annelids was starting to emerge in a form we would recognize today. In that treatise, Vermes (still included platyhelminths, nemerteans, and nematodes) had a class Annelides, with subclasses of Hirudinei [sic] and Chaetopoda, the latter with orders of Oligochaeta and Polychaeta, the latter with suborders Sedentaria and Errantia. Myzostomes, as single genus *Myzostoma*, were questionably an adjunct to Polychaeta, and a further class of Vermes was the Gephyrei [sic] (or Sipunculacea), including *Echiura*, *Sipunculus*, *Phoronis*, and *Priapulus*.

Vermes continued to be used for a grouping of miscellaneous "minor" worm-like "phyla" plus Annelida, and even as late as the 1930s, "Vermes Polymera" was the annelids category in the Kükenthal and Krumbach edited *Handbuch der Zoologie*. Remarkably, Vermes was still used by *Zoological Record* into the 1970s as a convenient shorthand title for an all worm-like groups part-issue, with or without a group named Annelida inside it, although the first volume in 1864 had used only Annelida. In 1900, the *Zoological Record* Vermes even included Hemichordata, and in 1924 and earlier, it included the Gephyrea, a concept dealt with next.

Gephyrea was proposed by Quatrefages (1847: 340), from Greek *Gephyra*, meaning a bridge, for a supposed link to holothurian echinoderms, as a sister class to his concept of class Annelida (part of his "Vers" mixture), and just for some hard-to-place worm-like genera of general sac-like form. Later, these genera were believed, except for *Sternaspis*, which was added to the Sedentaria in Annelida, to each belong in the separate phyla of Echiura, Sipuncula, and Priapulida, with the first two remaining in Spiralia and the priapulids becoming much more distant as one of the Ecdysozoa groups. Quatrefages' creation of Gephyrea appears not to be overtly influenced by Rolando's (1822) earlier belief that his new *Bonellia viridis* (Fig. 1.3), now in Echiura, was a new type of echinoderm, but he does comment that it probably belongs in his Gephyrea. Quatrefages (1866b: v.2 563) elaborated on the grouping, and the name was present in titles of taxonomic works up to the 1930s and beyond (Wesenberg-Lund 1934), perhaps in later times just for convenience, and even used later as a phylum (Monro 1931). Although Stephen and Edmonds (1972) state that the name "has no standing in zoological nomenclature" (they meant not valid), they and others also continued to find it appropriate to treat at least sipunculans and echiurans together. Currently, molecular analyses place sipunculans as a basal group within annelids and place the echiurans within the Sedentaria annelids (Andrade *et al*. 2015).

Hatschek (1878) created Archiannelides for *Polygordius*/Polygordiidae, also Archichaetopodes for *Saccocirrus*/Saccocirridae. Then, Hatschek (1893) had Polygordiidae and *Dinophilus*/Dinophilidae in Archiannelida with a new name of Protochaeta (soon forgotten) as the group for Saccocirridae. Further genera for which families were created were found, all meiofaunal and microscopic and not seemingly related, but "archiannelids" remained a convenient holding place for them, so much so that Archiannelida became presented as a class firmly outside Polychaeta to the generations of students who used the editions of Dales (1963, 2nd Ed. 1967) as a university text, despite skepticism (Hermans 1969) or disregard (Pettibone 1982), and despite the perceptive comments of Goodrich (1901) that the Haplodrili (a name of Lankester's for archiannelids) were specialized taxa rather than ancestral. However, an archiannelid group is polyphyletic and not taken seriously for some time due to a lack of support from molecular analyses, with Andrade *et al*. (2015) placing *Polygordius* and two other meiofaunal genera among representatives from the major errant families, and especially with regard to the analysis of Struck *et al*. (2015), which placed representatives of Polygordiidae, Saccocirridae, and three other meiofaunal families as a sister group to errant groups Eunicida and Phyllodocida, split from Nerillidae and three other meiofaunal families grouped

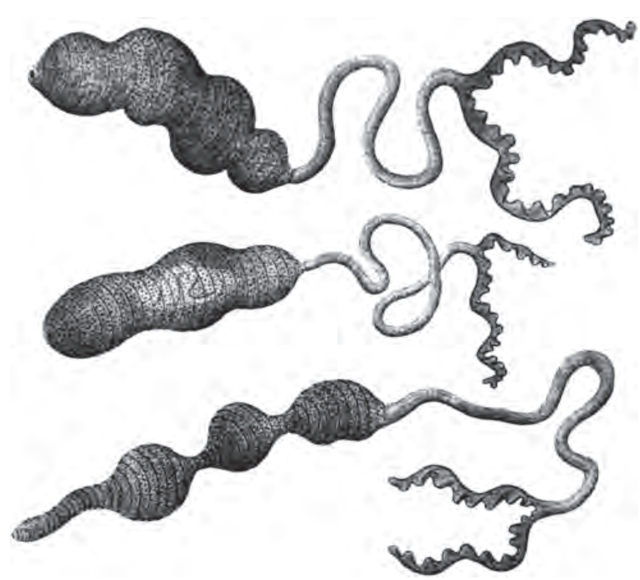

Fig. 1.3: The first Bonelliidae echiuran species, *Bonellia viridis* Rolando, which Rolando (1822) thought was a new type of echinoderm. No scale. Original at https://biodiversitylibrary.org/page/7654161

with Sedentaria Orbiniidae. Struck *et al* (2015) concluded, "inhabiting the interstitial realm and possessing a simple body organization are not ancestral traits of Annelida. The 'Archiannelida' concept has to be rejected…."

The enigmatic and interesting disc-like myzostomes, obligate parasites and commensals of echinoderms, especially crinoids, have been slotted variously within and outside the annelids, and were placed in the helminths when a *Myzostoma* was first found (by Leuckart 1827, but see World Register of Marine Species [WoRMS] for the validity of early names). The biodiversity within the myzostomes is proving to be considerable (>150 species, eight families, *fide* Grygier 2000; Summers and Rouse 2014), so they are not the usual minor group that specialist parasitic annelids tend to be, with some possible taxonomic rank inflation creeping into classifications. Although a molecularly supported platyhelminth link has earlier been put forward (Eeckhaut *et al*. 2000, and others), most annelid specialists have long been comfortable with morphological and other data that myzostomes are annelids, probably a sister group to Errantia (e.g., Summers and Rouse 2014, Weigert *et al*. 2014, but see also Wang and Xie 2014), despite molecular analysis problems with myzostome long-branch attraction to outgroups.

An article title of nearly 20 years ago included the assertion that "Pogonophora is not a phylum" (Boore and Brown 2000). How did we get to have the pogonophorans ("beard-bearer" worms) anyway? They were discovered late, overlooked as being a form of animal life. Researchers on deepwater benthos may sheepishly relate to the possibly apocryphal story, told by the translator in the preface to Ivanov's monograph, that on an Antarctic voyage of *Discovery II* in the 1920s, masses of thread-like fibrous material from abyssal depths were repeatedly simply shoveled back overboard, not recognized as living. The first such extraordinarily slender siboglinid found, *Siboglinum weberi*, collected on its genus namesake vessel, the *Siboga* (derived by Caullery as *Sibog* – plus *linum* "thread"); had no gut, no chaetae, a single tentacle; and was thought to have a dorsal nervecord (Caullery 1914, 1944). In a very brief outline of the further history, more similar forms were discovered, and eventually, there were about 100 species that Ivanov (1960, translated 1963) included in Pogonophora, which he declared to be an independent deuterostome phylum, dismissing Hartman's (1954) polychaete-relative placement, and the earlier detection of posterior chaetal platelets by Caullery (1944). However, a protostome-placement faction developed, which led on to the placement of pogonophorans as annelids or annelid allies (van der Land and Nørrevang 1977). Later, Jones (1985) escalated the vent- and seep-associated Vestimentifera group (first named by Webb 1969) of pogonophorans with much larger body size (*Riftia*, *Lamellibrachia*, etc.) to their own phylum. However, molecular evidence began to support an annelid placement, and Rouse and Fauchald (1997), using morphology, concluded that both groups belonged with the Sabellida annelids at family level. Finally, Rouse (2001) suggested that "all taxa within Siboglinidae that are not genera or species are redundant…." This simple reduction to Siboglinidae of the detailed hierarchies of phyla Pogonophora and Vestimentifera by Rouse (2001, q.v. for a more detailed historic account), and Rouse and Fauchald earlier, based on morphological cladistics, not molecular work, and its acceptance by almost all other scientists interested in the topic, must qualify as one of the most emphatic deflations of superfluous higher taxonomic ranks in the history of biology.

When our knowledge of the variety of animal forms was still poor, a hitherto-unknown major alteration between life stages, a "metamorphosis," could lead to some surplus genera names being created, which subsequently might be useful as the general name for the life stage. This has occurred in annelids, just as it has in other phyla. The best-known is the heteronereid, a gravid member of Nereididae, modified for swimming, after *Heteronereis* Örsted, 1843, erected for two Greenland nereidids. Ehlers (1868) and Malmgren (1869) soon sunk the genus into *Nereis*, but a heteronereis (Fig. 1.4) became the name of the morphology (e.g., review of Clark 1961), although the less family-specific "epitoke" is the term used more today. Similarly, in the Autolytinae syllids, the genera names *Polybostrichus* Örsted, 1843 and *Sacconereis* Müller, 1853 became the technical names, respectively, for the fast-swimming male stolons with their enlarged trailing head appendages and the egg-sac carrying female stolons.

For small planktonic forms, it is understandable that some get named before they were first realized to be only larvae and then later matched to adults. For annelids, *Mitraria* Müller, 1851, figured in Müller (1854), and *Rostraria* Häcker, 1898 are unusual planktonic larval forms in Oweniidae and Amphinomidae, respectively, with the names continuing to be used today for plankton with similar morphologies, although their affinities are now known. Häcker (1898) also came up with the name *Chaetosphaera*, but that was clearly for a spionid larva. The *Mitraria* name of Müller is from the Greek for headdress, presumably because of the miter-shaped head and apparent lack of body (Fig. 1.5). The *Rostraria* name is

Fig. 1.4: Heteronereis-morphology anterior body of a New Zealand *Platynereis australis* live female, first described as *Heteronereis australis* Schmarda, 1861 (©G.B. Read).

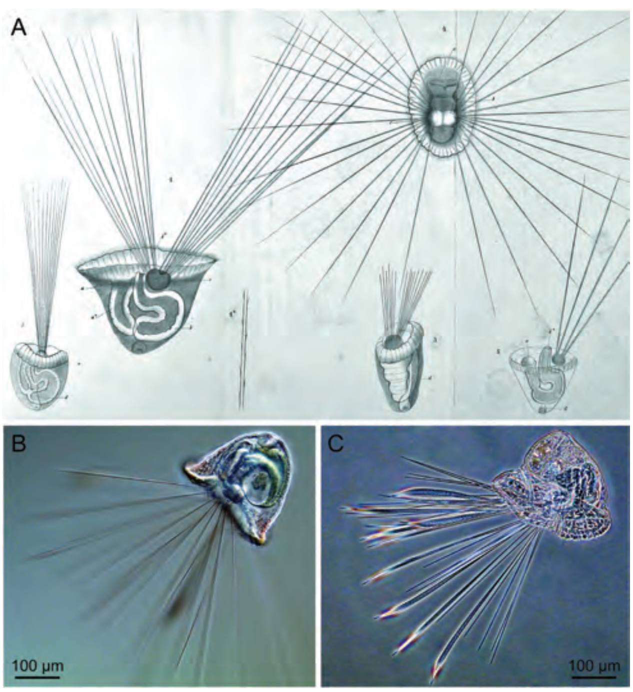

Fig. 1.5: *Mitraria planktonic* larvae that do not resemble the Oweniidae adult. A, *Mitraria* larvae first published figures in Müller (1854, plate 5), original at https://biodiversitylibrary.org/page/14341920; B and C, differential interference contrast and phase-contrast *Mitraria* larva photomicrographs, probably of a *Myriochele* species, Bay of Santander Spain (©R. Martin-Ledo).

analogously formed but does not refer to the main identifying rostraria-larva character of a pair of thick ciliated head tentacles of disproportionate size, particularly noticeable in young larvae. The history of the eventual matching of *Mitraria* to Oweniidae and *Rostraria* to Amphinomidae is given by Wilson (1932) and Bhaud (1972), respectively.

1.6 Use of journals – the path from natural history to model organisms

Preparing and publishing a book in the eighteenth century was a major commitment, and for its readers with a serious interest in natural history, the investment in a useful set of supporting works was also considerable, as books remained expensive during the period of relatively unmechanized printing (Allen 1993). The new avenues for both publication of annelid discoveries and for learning about them were the scientific society and subscriber journals devoted to all sciences or exclusively to various biological sciences, not first appearing until 1665 in France and England with *Philosophical Transactions* (of the Royal Society of London, volume 1, subtitled "giving some account of the present undertakings, studies, and labours of the ingenious in many considerable parts of the world"). The *Transactions*' first definite polychaete seems to be an aphroditid found in a codfish stomach (Molyneux 1695), but in that 1665 first volume, there is a dubious description of "shining worms in oysters" (Anon 1665), reprinting in paraphrase a letter published elsewhere (in the then new French publication *Journal des Sçavans*). Authentication of content was at first up to the editor's judgment, while peer review by Society members was introduced only decades later in 1752 (Spier 2002).

Probably the most important nineteenth and twentieth century English-language journal for annelid biology was the *Annals and Magazine of Natural History* (1841–1967), which was the survivor from a pack of hopeful competitors (Allen 1996), beginning in 1828 under an earlier name and continuing today as *Journal of Natural History*. In such journals, the early natural science reports on annelids, whether morphological, experimental, or taxonomic, were relatively short, unstructured, discursive, and sometimes verbose, but rarely uninteresting. Early titles often indicated the observational content ("An account of...," "Observations on...," "Remarks on...," or simply "On the...," which is still a favorite today). The *Annals* also usefully printed translations of significant work from other countries for its subscribers. Thus, Quatrefages' then new annelid classification in *Annales des Sciences Naturelle* was reprinted in English (Quatrefages 1866a).

The tireless William McIntosh (or as M'Intosh) (1838–1931), in an early career article in the *Annals* (McIntosh 1868), writing on the boring of *Leucodore ciliata* (now *Polydora*), has an example of the loose style. McIntosh is usually very polite, but as a 30-year-old includes sly jabs at fellow scientists ("the want of scientific accuracy in the figures...

renders identification difficult”). A look at McIntosh’s style of nearly 20 years onward in the *Challenger Report* (McIntosh 1885) shows no improvement in conciseness, but as an expedition report, it is effectively a book. By how much would an editor of today reduce its nearly 1,000 pages (including plates)? Over time, the book has remained the ultimate publication for science prestige compared to journal articles, the latter always regarded as having a somewhat fleeting impact, but few individuals of earlier periods or today have the resources to publish a specialist book of limited potential readership. The enormous *Challenger* publications were presumably government subsidized, and McIntosh’s Ray Society monographs (e.g., McIntosh 1923) were supported by society subscribers. The other obvious avenue was to be backed by a for-profit publisher for a work with many illustrations intended for the general public (see later sections), but that (then and now) is an unlikely path in the case of annelids.

Annelid researchers seem to have been in no hurry to adopt the present required arrangement for science journal articles of an introduction, methods, results, and discussion (known as IMRaD), although helpful use of some headings including a “methods” appeared in annelid experimental articles as early as the 1900s (e.g., Allen 1904, Hargitt 1906). Indeed, strict IMRaD first became widespread in science only in the 1950s and was not a formal standard until 1972 (Day 1989). The first annelid experimental article might be Bonnet (1742) on worm regeneration, and the first article with “experiment” in the title is Vaney and Conte (1898), who reported work on the regeneration of *Sabella spallanzanii*. The first journal article predominantly on the ecology of annelids is hard to determine, given that ecology is often a multiphylum community study, but was likely well before the word Ökologie itself was first used by Haeckel (1866). Darwin’s (1840) early examination of earthworm formation of vegetable “mould” (soil-like castings) is ecology. Much later, his further research formed his last book (Darwin 1881), and he described how mosaic floors of ruined Roman Britain buildings had been buried under layers of earthworm castings at Silchester. However, the first article on a named polychaete with ecology in the title (i.e., autecological) is Flattely (1916) on *Cirratulus tentaculata* (now *Cirriformia*).

At the other end of the timeline for journals, indicative of new research avenues and the application of increasing technological power, the development of adequate computer power and software code was required first for Hennigian cladistic analysis to replace the creation of subjective taxa groupings by intuition and experience, at first with morphological character data (e.g., Fauchald 1992, Rouse and Fauchald 1997), then with molecular data. The specialist journals *Molecular Biology and Evolution* and *Molecular Phylogenetics and Evolution* began in 1983 and 1992, respectively, with the first annelid sequence data of the latter journal presented by Dick and Buss (1994), and in the former journal, annelid, vestimentiferan, pogonophoran, sipunculan, echiuran (then all separate) nuclear 18S rRNA sequences were used for phylogeny by Winnepenninckx *et al.* (1995). Siddall and Burreson (1998), Dahlgren *et al.* (2000), and others subsequently used mitochondrial cytochrome oxidase I (CO I or CO1) for higher annelid phylogeny, with Apakupakul *et al.* (1999) also using nuclear 18S rDNA data. The first polychaete-group annelids “barcoded” may have been the *Escarpia* Siboglinidae species studied by Kojima *et al.* (2002). Barcoding in molecular biology is obtaining CO I DNA sequences as used for species delimitation (reviewed in Taylor and Harris 2012), even before CO I was chosen as a standard convenient surrogate for any animal whole genome in 2003.

The first annelid mitochondrial genome was completed for *Lumbricus terrestris* L. by Boore and Brown (1995) and for *Platynereis dumerilii* (Audouin & Milne Edwards, 1833) by Boore (2001). Eventually, randomly sequenced clones of mRNA transcripts became a way to assemble large datasets of annelid species for phylogenetic analyses, beginning with Struck *et al.* (2011), which included 29 annelid species (see also Weigert *et al.* 2014, Weigert and Bleidorn 2016). By 2015, so-called next-generation sequencing techniques more readily enabled the first mitochondrial genome of a syllid to be sequenced (Aguado *et al.* 2015), which was of the remarkable branching annelid *Ramisyllis multicaudata* Glasby, Schroeder & Aguado, 2012. A transcriptome (set of all RNA molecules) has recently been completed for the echiuran *Urechis unicinctus* (von Drasche, 1880) by Park *et al.* (2018). Elucidation of a whole draft genome have been completed (Simakov *et al.* 2013) for model organisms *Helobdella robusta* Shankland, Bissen & Weisblat, 1992 (but see identity comments later) and *Capitella teleta* Blake, Grassle & Eckelbarger, 2009, both annelids with comparatively small genomes. Furthermore, whole genomes for other annelid species must surely be imminent.

So far, at least four annelid species have become regarded as so-called model organisms maintained in laboratory culture, mostly for examining developmental and evolutionary biology (evo-devo) with advanced techniques, including gene expression mapping. These are *P. dumerilii*, *C. teleta*, *Hirudo medicinalis* L., and *H. robusta*. A setback for the reliability and reproducibility of data from research on cultured *Helobdella robusta* occurred when it was discovered to be two species at the original type locality, and a further possible model species was named from a different culture (Kutschera *et al.* 2013). Kutschera and Weisblat (2015) have discussed how to move on to take advantage of the biological and genetic complexity now evident within the group of similar *Helobdella*. Similarly, past biomedical research results on *H. medicinalis* are compromised as the usual commercial supply was found to be of another leech, *Hirudo verbana* Carena, 1820 (Siddall *et al.* 2007). The same danger for the unwary laboratory biologist from the presence of cryptic species exists for the other two model taxa (*C. teleta* is a member of the *Capitella capitata* complex), suggesting that cultures should be molecularly verified. Prospective additional model-organism species have been discussed by Weigert and Bleidorn (2016).

As a last comment on journals, a specialist journal for annelid science has not yet been established (noting *Polychaete Research* ISSN 0961-320X had two issues around 1995–1998, with a brief presence online), although the idea has been talked about at meetings. At times, certain journals (e.g., *Proceedings of the Biological Society of Washington*) have been more favored with frequent annelid taxonomy submissions, and currently, the sheer volume of articles flowing from *Zootaxa*, with its daily online publication, makes it a favored journal for publishing new worm taxa, although most articles in it are not open access.

1.7 The expeditions, explorers, and travelers

How did early naturalists/scientists get to collect worms outside the countries of Europe? It was by vessel, as not just the only way to travel across oceans but also the easiest way to live while travelling and to transport back the volume and weight of samples collected, even if the locations visited were connected by land. Ships were still favored for personal travel for traveling the world, rather than by aircraft, right up until the 1960s, and of course are still used for major scientific voyages today, especially for the higher polar latitudes, still to dredge, trawl, and net as in the nineteenth century, but also to map and explore the deep-sea bottom with high-technology multibeam sonar and unmanned remotely operated underwater vehicles (ROVs) and landers. Early voyages did not always go smoothly, either for the ship or the crew, with shipwreck, illness, and possible death quite likely, nor did the collected material always survive. Naturalists allowed on board, especially on navy ships, likely had other primary duties, such as ship's surgeon (e.g., Quoy and Gaimard, as discussed later).

Some of the prominent scientific exploration ships that were used on voyages resulting in annelid works published in the expeditions' own monographs were *Eugenie* (1851–1853; Kinberg as monograph author and onboard naturalist), *Challenger* (1873–1876; monographs by McIntosh, Selenka, von Graff), *Ingolf* (1895–1896; Ditlevsen, Wesenberg-Lund), *Belgica* (1897–1899; Fauvel), *Valdivia* (1898–1899, Ehlers, Michaelsen), *Siboga* (1899–1900; Caullery, Horst, Mesnil, Pettibone, Sluiter, Southward), *Discovery I* (1901–1904; Ehlers, Lanchester, Stummer-Traunfels), *Discovery I* and *II* (*I*, 1924–1931, and *II*, 1929–1951; Harris, Monro, Stephen, Tebble), *Terra Nova* (1910–1913; Benham, Boulenger, Harding), and *Galathea* 2nd expedition (1950–1952; Kirkegaard, plus brief reports by Hutchings and Holthe). See Hartman (1951), Read and Fauchald (2018), or WoRMS for monograph author references. There were many other lesser-known expedition vessels and particularly many Antarctic expedition voyages named for the sponsoring nation rather than the support vessel. There is even a vessel, the *Michael Sars*, named after an annelid biologist, with a 1910 North Sea expedition (polychaetes by Støp-Bowitz).

The ships that did not produce, but should have or could have produced, annelid work include the first *Endeavour* voyage (1768–1771) of Cook, the *Erebus & Terror* voyage (1839–1843) of James Clark Ross, and possibly the *Beagle* voyage (1831–1836) of Fitzroy with Darwin. In all of those, part of the material was lost or neglected when back in England. The Joseph Banks team on board the famous first *Endeavour* expedition to the "South Seas", commanded by James Cook, evidently paid much lesser attention to marine invertebrates outside of crabs and molluscs, overwhelmed as they were with new discoveries of vertebrates and plants. Additionally, a unified publication of the zoology of the voyage never happened (Whitehead 1969, Carter *et al.* 1981). A first passage around New Zealand was a significant part of the voyage, but disappointingly, no polychaetes are known, although at least a collection of serpulid tubes was likely (Glasby and Read 1998).

Charles Darwin was a gentleman naturalist on the *Beagle*; there was also a ship's physician-naturalist, but Darwin has the subsequent fame for obvious reasons. It is notable that Darwin makes almost no mention of annelids in his zoology notes (Keynes 2000). The surviving labeled annelid material, at least that known about at Oxford, is only four jars (Chancellor *et al.* 1988).

Jean Quoy and Joseph Gaimard have their names forever linked as the surgeon-naturalist collectors on voyages through the Pacific, on both Freycinet's *Uranie* (1817–1820) and d'Urville's *Astrolabe* (1826–29). On the first voyage, *Uranie* was wrecked early in 1820 with loss of some collections, but the crew survived and reached home by buying a replacement, the *Physicienne*, which is why there are two ships in the title of the expedition results (Freycinet *et al*. 1824). While they published almost no annelid work themselves (one species in Tomopteridae), their annelid material was received into the Paris museum, and they are thus recorded as joint collectors for about 40 taxa just in Quatrefages' (1866b) *Histoire naturelle* alone.

Baird's (1865, 1869) subsequent description of a few worms from the James Clark Ross *Erebus* and *Terror* Southern Seas Expedition has created one enduring mystery. Where is elusive Narcon Island? Baird named a subantarctic serpulid *Serpula narconensis* Baird, 1865, later found to be widespread and reef-forming, and he named a not-yet-seen-again eunicid *Eunice narconi* Baird, 1869. This island is embedded in the literature and in the London Natural History Museum specimen catalogues, yet no support for it can be found in the voyage narrative or anywhere, and the most favored explanation is that it was created by Baird's misreadings of a cursive script "Marion Island" on a label (Helmut Zibrowius and GBR unpublished).

Later, as shipping routes established, it was not always necessary to be on a dedicated expedition ship. Notable scientist/collectors who collected annelids worldwide by "hitchhiking" on passenger ships or government-operated vessels include the Austrian Ludwig Schmarda in mid-nineteenth century and the German Hugo Schauinsland and Dane Theodor Mortensen in late nineteenth to early twentieth century, all visitors to the still remote and relatively unknown New Zealand main islands. Schmarda was the pioneer and annelid taxonomist of the three. He travelled around the world (1853–1857), collected intertidally, and wrote a book about it (Schmarda 1861a, typeset in difficult-to-read cursive German). On the way homeward, Schmarda lost his luggage to thieves while crossing the Panama Isthmus, with the loss of a large part of his documents and specimens from his work in New Zealand and Australia (Schmarda 1859), but at least some of his New Zealand type specimens made it back to the Naturhistorisches Museum in Vienna (Glasby and Read 1998). Schmarda contributed 21 annelid names for New Zealand and 223 mostly for the southern hemisphere, including 17 oligochaetes and 3 leeches (Schmarda 1861b). Although he had color plates and some in-text figures in his monograph books, these were inadequately detailed and descriptions were brief; consequently, annelid workers view Schmarda's work with some ambivalence.

Schauinsland and his wife travelled (1896–1897) through Pacific Coast North America, Australia, Ceylon, and Egypt, and to some remote places in the Pacific, and later did more trips. He spent time on Laysan in the Hawaiian chain and the Chatham Islands off New Zealand, with his diaries and letters home later written up as an around-the-world travel book (Dünzelmann *et al*. 1999). Mortensen, an echinoid expert, travelled remarkably widely and produced a prodigious output on his speciality. His trip to Japan, the Philippines, Australia, New Zealand, Hawaii, California, and Panama was in 1914–1916, with many researchers later publishing on his collections as part of the series "Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16." In New Zealand, Mortensen managed to get himself onto government scientific vessels, and in summer 1914–1915, he travelled to the subantarctic Auckland and Campbell Islands. Schauinsland and Mortensen collected a variety of marine taxa; their polychaetes were written up by European-based Ehlers and Augener, respectively, who both made major contributions to knowledge of polychaetes in New Zealand (Glasby and Read 1998). Michaelsen (1899) wrote up Schauinsland's oligochaetes.

1.8 Tracking specimens – museums, nomenclature, and taxonomy

> Our unrivalled store of scientific wealth, [...] available for the instruction and amusement of the people... (Jeffreys 1863: 237)

> There appears to be an optimum period during which the observations from a biological expedition have to be completed... The stores of museums, laboratories and universities all over the world are cluttered with collections which are "going to be worked up." (Wheeler 1984, Endeavour collections)

> Where I found it I do not remember. (Hans Sloane 1725: v. 2 p. 194)

Until institutional museums were founded, naturalist's hard-won specimens were in personal "cabinets of curiosities" and were traded between wealthy private collectors. This did not bode well for long-term preservation, for continuity, or for tracking provenance, even though collections from foreign lands had real monetary value, notably the one founding the British Museum (physician-naturalist Hans Sloane's priceless lifetime acquisitions), acquired in 1753 by the state for a nominal £20,000 (de Beer 1953). The Paris museum began in 1718 as Jardin du Roi, reorganized in 1793 during the revolution as Muséum national d'Histoire naturelle, and the British Museum, London, began in 1759, a year after the 10th edition of *Systema Naturae*. Even after museums were well established, specimens

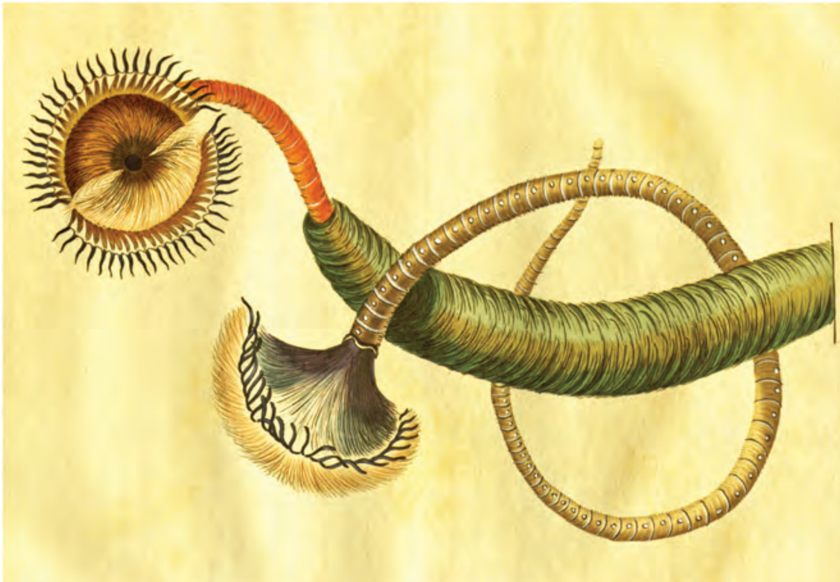

Fig. 1.6: *Amphitrite infundibulum* Montagu, 1808 (now *Myxicola*), painted by Liza Dorville. No scale. Original at https://biodiversitylibrary.org/page/757878

could be lost through neglect or mischance (Sloane's zoological specimens in the British Museum later rotted or were ruined by vermin). It is an imperfect world. Although Joseph Banks and the participants in the first James Cook "South Seas" voyage of 1768–1771 have been admired and celebrated ever since, much of the material they gathered ultimately decayed unlooked at or lost provenance as it was dispersed (Whitehead 1969), with, for example, Linnaeus eventually receiving "Cookian" first-voyage molluscs via one or more intermediaries (Dance 1967). In another example in the next century, the hard-won dredged samples from the James Clark Ross, *Erebus* and *Terror* Southern Seas Expedition (1839–1843), in a bad state, were discovered by Hooker in Ross's back garden after Ross died in 1862 (Rainbow 2005).

Part of the collection of Devon naturalist George Montagu did make it to the British Museum, purchased for the then substantial sum of £1,100 according to Oliver *et al*. (2017: 363), but by 1863, it was almost annihilated. "Nearly the whole of his priceless collection of British shells [...] has unluckily been lost to science; and [for] the few specimens that are still preserved [no care was taken] in the course of rearrangement to retain the names affixed by the donor to his types" (Jeffreys 1863: 237). It seems that some of Montagu's polychaetes in spirits (i.e., diluted alcohol) did rather better as the important Montagu specimens of *Amphitrite volutacornis* (type species of *Bispira*), *Aphrodita clava* (type species of *Lepidonotus*), and *Amphitrite infundibulum* (Fig. 1.6) (the probable type of *Myxicola*) are all in The Natural History Museum, London. However, usually, alcohol-stored specimens are more vulnerable to permanent destruction through evaporation of the liquid. As assessed in 2008, the London Museum contained about 288,000 specimen lots of annelids, the vast majority of which would be in spirits, and 4,500 annelid types (Rainbow 2008). Maintaining good condition in such a large collection is not a trivial task. Preservation in spirits, rather than dry, was done from the mid-seventeenth century. Wet preservation is essential for annelids, and polychaete worker George Johnston is said to be one of the two early nineteenth century naturalists to adopt spirit-filled corked glass tubes for keeping individual specimens, when glass became cheaper (Allen 1976).

The specimens from Linnaeus's collection were purchased privately in 1784 and transferred to London and eventually to the Linnean Society (Dance 1967). Linnaeus named 65 annelids (WoRMS data) that remain valid species, including at least eight species now in other phyla. Types of four *Serpula* species (actually molluscs) survive, but it is uncertain what else. Dance (1967) lists 17 Linnaean annelids, all *Serpula* or *Sabella*, that are *not* in the Linnean Society collection. There is some possibility that the Museum Adolphi Friderici collection within the Swedish Museum of Natural History also has some annelids examined by Linnaeus. Types have also got destroyed through mischance, such as the wartime damage to European museums, but occasionally, rediscoveries are made. Types of some significant Langerhans species from Madeira, at least those on slides, were rediscovered at Naturhistorisches Museum Wien by the late Phyllis Knight-Jones in 1994, along with Langerhans' inventory of manuscript names (personal communication).

Another problem with collections was lack of documentation. Early labeling was inadequate for proper tracking and, coupled with mistaken matching by post hoc curatorial guessing of provenances for specimens, is fraught with danger of error. We can laugh at the stark honesty of the Hans Sloane "I do not remember" quote earlier, but the historic literature shows that loss of memory by the collector might not be the real problem, as keen describers looking through specimens with minimal-associated information did not let that get in the way of creating a new name, perhaps with a bad description. There is the heretical idea of whether we would be better off without some of these early names and the confusion of unwinding exactly what they named. Glasby and Read (1998) commented on the problems regarding polychaetes extracted from New Zealand by early collectors.

The type specimen concept in zoological taxonomy is of quite recent origin, or at least the formal rules surrounding it are, so we must accept that an early annelid taxonomist cannot be castigated for lack of type material for his/her names. A type species concept for a genus was introduced by the Strickland code (1878), the product of a committee including Charles Darwin. The type specimen concept was present in the "*Règles internationales*...," the first truly international code (Blanchard *et al*. 1905), but only in an appendix as a recommendation. However, in the first edition true ICZN code (1961), the importance of holotype specimens is very clear and entrenched. Type specimens are highly significant today, yet the type collections of translocated native life from colonized countries as held in major natural history museums are alienated from the country of origin where they are now most needed for active research (the biotic equivalents of the "Elgin" marbles). New techniques of displaying images of type specimens are likely to help to some extent, but annelids are very difficult to identify just from whole-body photographs.

Contemporaries Edouard Claparède and Armand de Quatrefages in the nineteenth century had different approaches to types, or at least to the use of preserved specimens. The two, both excellent annelid biologists, were in open conflict after publication of a preliminary outline of Quatrefages' *Histoire Naturelle des Anneles* and Claparède's (1866) adverse comments on many mistaken classifications in it. Their different work practices were an additional matter, and Claparède (1868) wrote (in translation),

> "Why did M. de Quatrefages, who so admirably knows the annelids, let himself be led to describe so many genera and species according to individuals preserved in alcohol at the Paris Museum? He knows, better than anyone, that this kind of work is profoundly useless, that annelids can only be studied at the seaside, using live individuals. Describe, as he does, so many alcohol varieties [variétés alcooliques], is to embarrass the science of a *caput mortuum* [useless residue] which will take long years to get rid of."

The disapproving terminology "variétés alcooliques" appears to be unique to Claparède. Fauchald (1989) has commented that "Claparède, true to his principle, deposited no specimens in any museum [gbr – maybe some reached museums], making many of his new taxa difficult to define accurately" and "The most important aspect of Claparède's work was that he demonstrated that a remarkable amount of information could be gained by looking at live organisms." No one would disagree with Claparède and Fauchald on that, but it is not always possible, and the Paris Museum specimens came from many distant locations and are still available (Solís-Weiss *et al*. 2004).

1.9 Cataloguers

An enduring problem for annelid researchers in the nineteenth and twentieth centuries, especially those in more remote places, was how to learn of new research and new species and then how to get hold of the publications in timely fashion. This was a once fundamental limitation on keeping up with contemporary research activity if you were not at one of the upper-echelon of universities and museums and were as yet without a network of personal contacts with your peers who would send you their papers. It is a problem now vanished with the universality of access to the Internet. There is now free access to older literature scans via the Biological Heritage Library Consortium (BHL), a major advance scarcely believable to those who, not many decades ago, once waited weeks for journal loans and spent hours making blurry copies at primitive photocopy machines. Once there was no possibility for most biologists to see the quite rare and expensive Ray Society monographs of McIntosh (eight monographs between 1874 and 1923), but now, they are all online except the last (McIntosh 1923), because it was published past the BHL public-domain cutoff date of pre-1923. We also learn of new work via casual publicity pushed out to the world on open social media networks (e.g., Twitter, starting from 2006) and via free e-mail journal publisher alerts and special-interest mailing lists (e.g., "Annelida" run by one Geoff Read from 1995 to present) and can learn of forthcoming research via conferences for taxa groups, with the first international polychaete conference held in 1983.

One of the venerable commercial print alerting services for annelids is *Zoological Record* (yearly issues, began 1864, developing complex subject analysis), important as an authority for tracking name changes and publication dates. It included abstracts and subjective commentary on major works only up to 1906 (Bridson 1968). The related, much more frequent, *Biological Abstracts* began in 1926 for all life sciences, and both are now accessed mainly online in integrated form. In Germany, other nineteenth century journals ran literature-recording/commentating sections for periods, with the extracted or paraphrased content sometimes mistaken for a new publication by the unwary. These were *Archiv für Naturgeschichte* 1835–1923, *Zoologischer Anzeiger* (later *Bibliographia Zoologica*) 1878–1934, and *Zoologischer Jahresbericht* 1879–1913.

Early cataloguers of zoological species and genera names include Sherborn with *Index Animalium* (Sherborn 1902–1933) and Neave with *Nomenclator Zoologicus* (Neave 1939–1945, genera only), both now as online databases, and Hartman (1951) has a list of other bibliographic sources. William McIntosh could be considered among the cataloguers as an earlier compiler of comprehensive polychaete synonymies. His coverage in the monographs on British annelids (e.g., McIntosh 1923) is exhaustive, including pre-Linnaean names, and was later used by Hartman (1959, 1965) for her catalogues. His knowledge of the literature of his time and the historic polychaete literature is impressive given his many non-annelid commitments and duties.

We know nothing of how McIntosh recorded information but to compile their seminal works (Hartman 1959, 1965; Fauchald 1977) Olga Hartman (1900–1974) and Kristian Fauchald (1935–2015) used index cards, a standard precomputer technique, which developed from the practice of Linnaeus and others to keep organized paper slips in a “file,” a term derived from the woven thread (Latin *filum*) first used to bundle loose papers (Charmantier and Müller-Wille 2014). Sherborn reportedly created over a million slips/cards (Shindler 2016). For a time, Hartman aimed only to cover the Western Hemisphere polychaetes fully (Hartman 1951: vi). Hartman’s sources checked for names are not fully known, although undoubtedly were extensive – she lists some in Hartman (1951: v, 284), including *Zoological Records* and museum catalogues. She does not mention Sherborn, but she does mention Neave’s *Nomenclator Zoologicus*. Hartman took all her index cards with her on her travels to museums, a somewhat risky practice as at least once, at the outbreak of WWII when travelling alone, she was separated from them in Europe for a period, and there were no duplicates. A contemporary letter in 1939 from Waldo Schmitt, Invertebrate Curator at the Smithsonian, indicates his concern at this situation (unpublished letters held at Smithsonian National Museum of Natural History and Natural History Museum of Los Angeles County (LACM)). At a later stage of preparation of the Catalogue (Hartman 1959, 1965), the index cards were transcribed from cards onto larger loose sheets typed and hand annotated and filed in a series of binders (Leslie Harris personal communication). These binders of annotated sheets are still held at LACM, but the content is from a later time; the index cards and sheets of 1959–1965 can no longer be found.

Overall, Hartman’s cataloguing work rightly should be regarded with awe. The World Catalogue (Hartman 1959, 1965) was an amazing achievement and remarkably accurate given its ad hoc construction from original handwriting. A particularly useful feature today when much of the old literature can quickly be found online is that she included page numbers for original descriptions coupled to an item number in the 1951 bibliography. WoRMS editors are still using these page numbers and are including them in species records. However, Hartman’s World Catalogue has several idiosyncrasies that are sometimes misunderstood because people have such faith in her work. For instance, she included at least 42 pre- and post-Linnaean names from McIntosh’s synonymies in the form “*aus bus* X in McIntosh,” which, if taken literally, seems to be saying McIntosh had published and made them valid, when all she meant was a personal shorthand to record a name attributed to X and harvested by her while she was reading McIntosh. One example is the unavailable William Leach museum label name “*Alveolaria arenosa*.” There is no such genus. There are numerous similar examples relating to authors besides McIntosh. Another oddity was her practice as a convenient shorthand to cite the name then thought to be the valid senior synonym name to a type species of a genus as the “genotype” rather than the actual logical type species by date. The entry for *Dorvillea* is an example. Researchers have occasionally incorrectly interpreted this as if she had wrongly newly Code-designated an ineligible name as a type species.

Hartman’s sources or rationale for her innumerable synonymies are very likely to be the prior literature (Hartman 1959: 1), but while she may have recorded them originally, she did not cite these sources, probably due to space limitations. In retrospect, from our point of view, this was a mistake, and they would have been so useful now. Researchers often assume Hartman miraculously made these synonymies de novo out of her head and cite her as the first recombiner or synonymizer. Sometimes, this will be true, but it is likely to be most usually untrue. The Hartman catalogue has also been influential in determining by subsequent designation which candidate original species was type species of a genus. Hartman consistently used page order priority, which seems reasonable and was part of the code applicable to her time, known as the *Règles* (Blanchard *et al*. 1905); page priority was possible then if no other factor applied.

Fauchald (1977) produced what became known as the "pink book", an invaluable set of polychaete genera keys and listings. He later transferred Hartman's catalogue data to his personal computer database, also adding new literature. He worked on it alone, including during his evenings, for many years, keeping it private, but finally donating it in 2007, together with linked sources, to what became the WoRMS database (Horton *et al*. 2017; Vandepitte *et al*. 2018). The WoRMS database coverage of Annelida continues today, contributed to by several editors via direct editing online (Read and Fauchald 2018). Earlier, a database continuation of Hartman's (1951) bibliography had been made available for public download (Ward and Fauchald 1997, assisted by GBR).

Oligochaeta were catalogued by Michaelsen (1900), with a then worldwide species total of 1,200, and subsequently in *Nomenclatura Oligochaetologica* (Reynolds and Cook (1976, with printed supplements in 1981, 1989, 1993), and now online as *N. O. – Editio Secunda* (Reynolds and Wetzel 2013–2018), and also with its data being added to WoRMS. Brinkhurst and Jamieson (1971) had earlier catalogued the aquatic oligochaetes. Other divisions of the current Annelida have also been presented in various monographic books, notably Stephen and Edmonds (1972) for Echiura and Sipuncula and Ivanov (1963) for Pogonophora (=siboglinids), and the online WoRMS catalogue is in the process of extending from a predominantly marine annelid content to also covering freshwater and terrestrial annelids.

1.10 Prolific species describers

Gesa Hartmann-Schröder is the (first-author) taxonomist with the most polychaete species still valid. From 1758 to 2016, 835 individuals were first authors, with Hartmann-Schröder (517 species), Olga Hartman (473), and Adolf-Eduard Grube (472) the top three most prolific first authors, and along with another 22 prolific authors, these individuals have provided descriptions of almost 5,250 species, or nearly 46% of total polychaete species (unpublished WoRMS data analysis by Joko Pamungkas). Hartmann-Schröder was active from 1956 to 1998 (last article finalized by another author) and had mostly worked alone. Hartman was active from 1936 to 1971 and did have collaborators later in her career. Grube was active from 1840 (17 still-valid names) to 1881 and almost invariably worked alone. He would take top honors for the most very short descriptions, so his unusual productivity may be a consequence of brevity both of examination and description, a tactic probably not endearing him to his peers and certainly not to later taxonomists.

In the decade 2007 to 2017, the most prolific authors or co-authors with more than 50 polychaete species were Hutchings (99), Nogueira (94), San Martin (81), Salazar-Vallejo (77), Blake (75), Rouse (53), and Carrerette (52) (data from Read and Fauchald 2018). These authors mostly worked collaboratively, with Hutchings solo for just 3 species and Nogueira for 2, whereas Salazar-Vallejo and Blake were the most prolific solo authors at 47 and 45 species, respectively.

1.11 Illustration and early photography

Annelid art has evolved somewhat patchily over the centuries, until now when we regard quality illustration as an essential adjunct to annelid research and to communication with the public. Drawings of animals had first appeared thousands of years ago, first as cave art, then in early Egyptian culture as decoration and story-telling on walls, household objects, and papyrus scrolls. Wall art is more durable than papyrus, and we know that by c.1600 BCE, the first marine organisms (swimming fish) had been depicted by Mycenaeans on Cretan walls. Also, we know that food-item marine invertebrates have been skillfully recorded for over 2000 years because mosaics created at Pompeii c.100 BCE showed realistic octopuses and lobsters (Dance 1989). However, it is not surprising that we can only speculate on the first depiction, if ever to be discovered, of the less edible, less obvious annelids. Perhaps, an Egyptian artist might have included common sights such as a bird with an earthworm or ragworm in its beak, or fishermen using worms for bait.

Papyrus scrolls with illustrations have been found in tombs of Old Kingdom Egypt, 3000 BCE, and the library of Alexandria held 700,000 scrolls, many of which would have been illustrated (Weitzmann 1971). Aristotle and Pliny were not illustrated, but it was quite possible to include small figures on scrolls in Pliny's time, except that Pliny did not approve of the practice and comments disparagingly about the colored figures in certain Greek herbals (Pliny book 25, Chapter 4). The biota illustrations that might have accompanied text on scrolls of papyrus or parchment before CE 300 are largely unknown now. Around that time, codices (singular codex), which were bound, handwritten, hand-illustrated books, and easier to handle, were taking over from scrolls.

Fig. 1.7: Miniature painted scenes in Van Maerlant (~1266, copy of ~1350) of a leech (sanguisuga) and of land worms (vermis), where the artist has rendered them like fat eels with faces. A, river leech leaving bloody cuts on a human foot. (B) Two earthworms (in translation "With these [earth]worms it is that one fools the fish hook and the fish"). Original work at https://www.kb.nl/en/themes/middle-ages/der-naturen-bloeme-jacob-van-maerlant

Bestiaries were a feature of codex manuscripts of the European medieval period (about CE 400 to 1500). They were didactic religious works in Latin with moral tales based around an illustrated animal, realistic or imagined, mainly vertebrates, sometimes interacting with people, and including the unicorn and phoenix. Various worm-like biota might be mentioned briefly in the text, including leeches correctly described by Isidore as "*vermis aquatilis*, *dicta quod sanguinem sugit*" (water worm that drinks blood). The Flemish religious poet Jacob van Maerlant (~1230 to ~1291) produced the first bestiary around 1266, that was in Dutch (rather than Latin) and in rhyme, but it was a derivative codex condensed from contemporary works in Latin. The art is crudely drawn, but he has lively miniature watercolor scenes of a leech (*sanguisuga*) in action and of land worms (*vermis*) waving their bodies (Fig. 1.7 A, B, from van Maerlant ~1350, original lost, copy dates from ~1350).

Around 1578 to 1585, Adriaen Coenen, who lived in the Dutch fishing port of Scheveningen, produced the unique handcrafted, handwritten *Visboeck* (fish book) and *Walvisboeck* (whale book), both including his marine animal watercolors, which he exhibited to the public for a fee. The presentation is rather naïve and scrapbook-like, but there were recognizable named annelids (Tab. 1.1), including a *vermis*, which appears to be a sipunculan; an *eruca* aphroditiform; and a *hirudo marina* marine leech (Coenen 1578). The works were not circulated as copies at the time, but both survive and are an insight into the nonscholarly knowledge of marine annelids of the time, even if some figures are replicated from a copy of Rondelet (1555) printed earlier, as they appear to be.

When considering early printing-press illustrated books, a relevant example would be *Das Buch der Natur* (*Book of Nature*), a late medieval manuscript credited to the German scholar-priest Konrad von Megenberg (1309–1374), but not first print published until 1475. It also has some plates of purely fanciful life forms in the style of the time, but there is one plate, interesting because it is a farming-related, semi-ecological mixture of animals showing bees at bee hives, a large snail, butterflies, flies, grasshoppers, and lastly indeed what seem to be earthworms exposed from a digging into the soil (Megenberg 1475: in online pdf, p. 245]). Dance (1989) claims that it is the "first illustrated book which attempted to inform its readers about animals," and this included worms.

Rondelet's *Libri de piscibus marinis* is an impressive achievement both for the text and woodcut figures (Rondelet 1555). The cluster of serpulids clearly shows their stalked opercula. Gesner's *Icones animalium* serpulid figure of 1558 is a mirror-image direct copy and credited to Rondelet.

In the seventeenth century, pioneer conchologist Martin Lister (1639–1712) produced the first illustrated books for the public on molluscs, and shells books have been popular ever since, but not worm books! It seems that an annelid-only illustrated popular book has yet to make it into print, perhaps because of worms lacking the reliable eye-appeal of shells, not being enduring structural objects, and lacking the same ease of classification. Nevertheless, excellent marine annelid color images have appeared in monographs and more recently as photographs in field-guide sections and in more technical works such as Rouse and Pleijel's *Polychaetes* (2001).

Fig. 1.8: Sowerby's (1806, plate 51) colored pectinariid and its cone tube, as *Nereis pectinata*, watercolor, with ship in distance. Original at https://biodiversitylibrary.org/page/28913891

The natural history collector Seba's 1734 *Locupletissimi rerum naturalium thesauri* is noteworthy for the increased quality of the printed art, with the originals contributed by 12 artists. According to Holthuis (1969), "Seba's text [in both Latin and French] is very poor and non-binomial, [but the good] plates make Seba's work one of the more important of its time, also for purposes of zoological nomenclature, as Linnaeus and many subsequent authors based new species upon figures from Seba's work." Seba's annelids are not new forms or many, but he has a natural-looking presumed amphinomid (Fig. 1.2) among arthropod *scolopendra*, perhaps the first color *Aphrodita*, and his *penicillum marina* appears to be a serpulid bare of its tube.

A major illustrated popular work of the 1790s, George Shaw's "The Naturalists' miscellany" (Shaw and Nodder 1789–1813), contains dual Latin/English text by Shaw introducing over 1,000 hand-colored plates from the global fauna, haphazardly ordered, and drawn by the Nodder family. This commercial venture is notable for introducing numerous new species names, including for echidna and platypus. As it was issued as a monthly part-work of a few plates each, sold for one shilling and sixpence, and to be bound later as volumes were completed, there was much dating uncertainty in taxonomy later (Dickinson *et al.* 2006). How did the annelids rate among the vibrant exotic birds and strange quadrupeds? Their appearances could not have enthused the English public for the group – a leech plate, some uninteresting serpulid tubes, an *Amphitrite* (here a limp-looking Mediterranean sabellid), and a more life-like amphinomid as *Terebella rostrata* from Indian seas, perhaps *A. rostrata* (Pallas, 1766).

Around the same time as Shaw's series, James Sowerby (1806: plate 51) published a splendid hand-colored figure of a realistic pectinariid and its cone tube as *Nereis pectinata* (Fig. 1.8). George Brettingham Sowerby II (1812–1884) illustrated later editions of Kingsley's *Glaucus*… (Kingsley 1873) with colorful marine biota scenes. There are *Sabella*, *Serpula*, and a "*Terebella*" (=*Lanice*), but most interesting is the "*Siphunculus Bernhardus* in shell of *Turritella*," an observation of a sipunculan using a shell in a hermit-crab-like manner – as they do. About three decades later, Ernst Haeckel (1904) published his "Kunstformen der Natur" (art forms of nature), a much-admired and influential work of 100 plates, including one for various Chaetopoda. Altogether, Haeckel's art is spectacular and stylish, with overriding themes of symmetry and organization. It should be successful for the metameric form of annelids, but those familiar with the live worms of his color plate 96 might think that his depictions look more like prototypes for plastic toys—not real, but we know approximately what they are supposed to be.

Those, other than authors, who did the technical plates of annelids are largely anonymous to readers, unless they check the exhaustive compendium of Nissen (1969). Due recognition is not helped by the usual practice of signing plates with initials only. Artist Pierre Lackerbauer in the mid-nineteenth century is one exception, as he signed his name in full and is known to have illustrated many taxa. In Moquin-Tandon and Lackerbauer (1866: 380, plate 21), he has a magnificent color plate of a multispecies group of worms on the sea bottom (Fig. 1.9). The worms, including a swimming nereidid epitoke, are in vivid natural pose, albeit somewhat diagrammatic in finer detail. His next plate is a convincing *S. spallanzanii* shown in situ (as "Sabelle unispirale" plate 22), drawn from a live aquarium specimen at Concarneau. Around the same time Quatrefages (1866b) had produced figures with superior anatomical detail (Fig. 1.10) and initialed his own monograph color plates (as ADe Q del.). It looks very much like Lackerbauer had used certain of those as models;

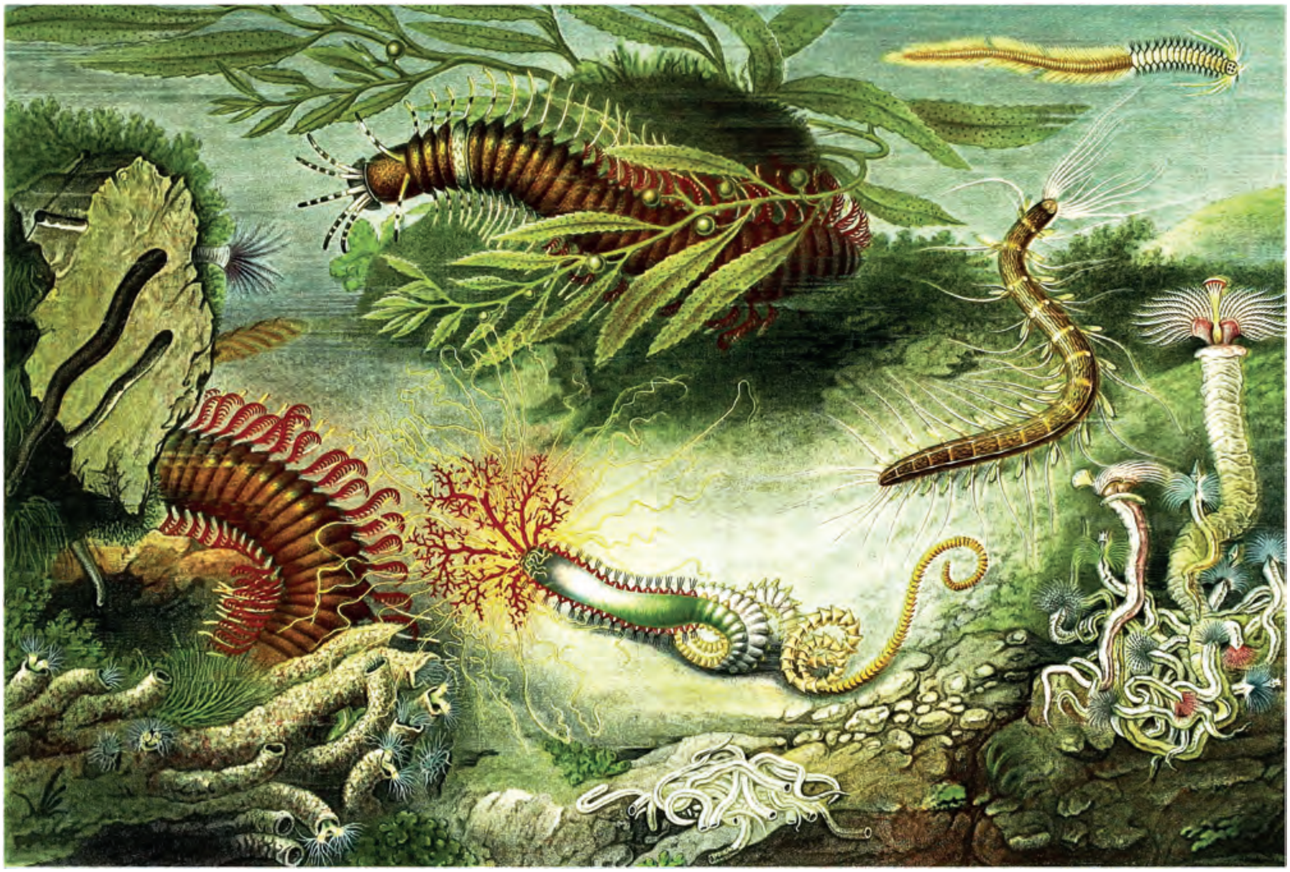

Fig. 1.9: Moquin-Tandon and Lackerbauer (1866 plate 21) plate by artist Pierre Lackerbauer of a multispecies group of worms on the sea bottom. Original at https://www.biodiversitylibrary.org/page/2073453

notably, the *Terebella* of his plate 21 matches plate 14 in Quatrefages.

Three family-associated and strictly amateur artists are Liza Dorville (1760s–1844), illustrating for her partner George Montagu; Catherine Johnston (1794–1871), artist for her husband George Johnston; and Roberta McIntosh (1842–1869), artist for her brother William McIntosh. William was also a skilled artist but was very proud of his young sister's work and arranged for exhibitions of her annelid paintings (Gunther 1977). Liza Dorville, who inspired genus *Dorvillea*, is said to have learned on the job, getting more skilled later (Cleevely 1978). Liza did a spectacular first illustration of what became *Myxicola infundibulum* (Fig. 1.6), although the worm tube she shows as free is in nature embedded in mud. Gosse (1853) wrote of Catherine: "The skilful pencil of Mrs. Johnston, employed in the delineation of the interesting forms that stand on the verge of animal life, has succeeded in presenting them to us with peculiar truth and beauty." He named *Johnstonella catharina* for her [sic for Catherine]. Roberta's most famous and popular worm painting is of a green sinuous *Alitta virens*, which has been widely reproduced in books (e.g., as an uncredited full-page plate in *Traité de Zoologie*, Avel *et al*, 1959) and once appeared on the front page of a leading journal of science. Sadly, Roberta died young. McIntosh dedicated the first *British Annelids* monograph of 1874 to her, and much later, Ada Hill Walker (1879–1955) did the figures for McIntosh. Unfortunately, little can be found on Ada and her connection to McIntosh, although her art features in nearly 60 plates of the monographs. She was inter alia a St. Andrews art teacher and painted local scenes. McIntosh (1923: xi), in the final *British Annelids*, noted that "for many years [she] has, with rare ability, drawn the annelids from life and represented the typical structures under the microscope."

A demonstration of the variation in skill of representation, and particularly the increase in detail possible as decades pass and printing quality improves, is given in Parapar and Hutchings (2015: figs. 2 and 3), who show the successively more realistic drawings of the no-longer "cosmopolitan" *Terebellides stroemii* Sars, 1835 published by authors, beginning with the very basic first attempt by Sars, with the suggestion that the recent ones might reveal more than one species.

Fig. 1.10: Terebellidae painted by Quatrefages (1866b plate 19): main painting *Terebella edwardsii* Quatrefages, 1866 (now *Neoamphitrite*); at the bottom right, an unidentified terebellid; other objects visible are not terebellid related. No scale (scan by GBR from original).

Photography had become available after 1839, but at first, there were severe technical limitations on what live fauna could be illustrated from life, so early photographs were of rigidly dead taxa (Bridson 1989). Use in microscopy was found to be easier and is covered in the next section. In some non-microscope-based early appearances, Darwin (1881) presents earthworm cast piles as engravings taken from photographs. Half-tones, allowing integrated machine printing of photographs with text, did not come into regular use until the early 1880s (Bridson 1989). By the early twentieth century, Enders (1909) had photos of *Chaetopterus* bodies, tubes, and beach occurrences in *Journal of Morphology*, and Walcott (1911) presented numerous Burgess-shale Cambrian fossil photos, including of the *Canadia* polychaetes (plate 23) and other fossils then misinterpreted as annelids. Malaquin and Carin (1914, war-delayed to 1922) had body photographs of *Tomopteris*, and Caullery (1915) presented, in a use for demonstrating an unusual interaction, a photograph of a *Polycirrus* with two large copepod parasites attached on the body. Thus, publication of photographs for annelid research was becoming more commonplace, but it is likely that in journals, there were restrictions or special costs for authors including photographic figures in articles, as there still are today for some, whereas for photos in monographs and books, the cost was proportionately less.

1.12 Microscopy and photomicrography

> …my microscope and lenses revealed an infinite world to my eyes, my pencils and brushes enabled me to secure rough illustrations of these treasures to be filled up at some future time with more care and exactitude… (Quatrefages 1857: vol. 1: 57)

> …the figures of such minute objects highly magnified under a microscope; the eye which examines, and the pencil which delineates them, will occasionally vary… (Montagu 1803: 190)

What optical aids did annelid researchers have before the twentieth century? Also, might occasional misinterpretations occur with early poor optics, like the imaginary canals on Mars seen through a telescope by straining eyes? Specimen detail better-than naked-eye from use of low-power magnifying hand lenses and spectacles was available around CE 1300 before the early microscopes were developed from the early 1600s onward (Carpenter and Dallinger 1901). There were early low-power compound microscopes as used by Hooke of *Micrographia* fame, but at first, a much higher magnifying power could be achieved with just a single bead-like lens attached to a specimen-support that could be focused. By 1690, an improved microscope design with rack and pinion and a substage condenser had been created (Blackham 1882). By the early nineteenth century, microscope usage was widespread, but good instruments, each carefully handmade, were evidently expensive and still scarce until the 1840s, at least in Britain (Allen 1976, Cleevely 1978). Nevertheless, Devon naturalist Montagu became a keen microscopist, with its aid referred to many times in his writings of 1808 and before, especially in *Testacea Britannica* (Montagu 1803), which includes many polychaetes. He was occasionally unfairly criticized for seeing things that were not there (*fide* Cleevely 1978), but his comment quoted earlier appears in context to be a not-too-subtle jab at another worker.

By 1831, young Charles Darwin was well set up for microscopy as he had purchased a Bancks single-lens unenclosed microscope to take on the *Beagle* voyage (Keynes 2000). It was a remarkably versatile simple system, with a set of several lenses, and could be used for reflected light dissecting as well as transmitted light (Ford 2009). However, by the 1840s Quatrefages (1857: 5) was travelling with a more sophisticated compound Oberhäuser drum microscope which he thought was excellent. Correction of compound microscopes for chromatic aberration (multicolored edge artifacts) via achromatic lenses had first appeared around the later 1820s from a design by Lister (Blackham 1882). By the 1880s, Langerhans is known to have preserved his small polychaetes from Madeira on microscope slides, which still exist today (see "Tracking Specimens" section). Also, by the 1880s, researchers were producing excellent histological figures by using compound microscopes (e.g., Vejdovsky 1878 on *Tomopteris*, 1884 on Oligochaeta). Also, indicative of the increased public interest, there was a "Postal Microscopical Society" established in the 1870s (and still going) that circulated parcels of interesting slides. It had a short-lived journal which inter alia published an article on *Tubifex* (Hammond 1882).

Annelid researchers need good "dissecting" microscopes as well as compound microscopes. Several optical designs of twin-eyepiece microscopes with prisms splitting light from a single objective were tried from the mid-1800s, including that of Nachet, but twin-objective stereo-binocular dissecting microscopes, image not reversed (which is the popular Greenough system as still used today), were not manufactured until the 1890s, and the addition of a further common main objective and continuous zoom did not appear until the late 1950s (Wise 1950, Sander 1994, Chambers 2014). Viguier (1886: 350) used a Nachet microscope for studies on live *Alciope* and *Iospilus*. Pierantoni (1908: 125), searching samples for live *Protodrilus*, was an early adopter of the Zeiss Greenough microscope. Meyer's (1887) microscope technique is not explained, but he produced brilliant figures of dissected *S. spallanzanii* internal anatomy (Fig. 1.11).

The camera lucida, an optical drawing tool for artists, was invented by Wollaston, who published a design in 1806 (Usselman 2015). Naturalists and taxonomists, with their need for accurate illustration, soon tried out the instrument and have been keen users ever since. Quatrefages (1857: 59) took his on his travels but confessed that the mirror became ruined by a flood of seawater. There is no indication that he used it attached to his microscope, but Mörch (1863: 483) might have done so for his camera lucida operculum figures, and Allen (1904: 148) certainly did use one later to draw his microtomed and stained sections of *Poecilochaetus*. The microtome itself, an important histological tool for cutting serial tissue slices for microscopy, much finer than could be cut by hand, has an unclear history, but its development had begun in the late 1700s, and a century later, Allen (1904: 85) tells us his was made by Jung, evidently by then a standard design.

It has long been the custom for respected biologists to be photographed for a portrait sitting alongside their microscope, although sometimes it might be an obsolete ornament included to add ambience, so there was no guide to what technology was in use at the time. A nice example of this ambivalence is a 1928 photograph of an elderly Professor McIntosh, obviously posing for the camera, not using the antique monocular microscope alongside him but instead peering through a magnifying glass (Gunther 1977). In contrast, the Japanese polychaete worker Minoru Imajima (1930–2016), noted for his fine illustrations, is photographed with what are clearly his working microscopes (Sato-Okoshi 2017).

Photomicrography, demonstrated by Delves (1853) only 14 years after photography was possible, was an early successful application for reaching "beyond the limits of human vision" (Bridson 1989). Viguier (1886: 349) implies that photomicrography was common at the time he wrote. He took photomicrographs of alive, but likely anesthetized, pelagic polychaetes, but his figures are drawings from the photographs, and likewise, Whitelegge's (1890) *Polydora* larva drawings are "from a photomicrograph." Half-tone printing of "real" photographs (see previous section) was still recent technology, but by 1914, Malaquin and Carin (publication delayed until 1922) had prepared plates of multiple *Tomopteris* photomicrographs.

While ordinary light microscopy is still the basic tool for annelid biologists, scanning electron microscopy (SEM), with its great depth of field removing the ambiguity of interpreting narrow focal planes, is also particularly useful for annelid chaetal structure and body micro-ornamentation, and its use has been commonplace since the 1970s. The first use for annelids has not been determined, but Holborow (1971) and Gustus and Cloney (1973) are early users for trochophores of *Harmothoe imbricata* and chaetae of *Nereis vexillosa*, respectively, and by 1984, the *Proceedings of the First International Polychaete Conference* has four articles using SEM images, mostly for chaetal structure. Like computers, SEM size has reduced, and now, instead of a large, dedicated room, desktop models can be of similar dimensions to an optical microscope. Specialist high-resolution SEM machines, usually equipped with field emission illuminating systems, are still large and expensive but allow observations of very delicate structures.

Whereas SEM techniques are primarily applied for clarifying taxonomical questions and enabling sophisticated species descriptions, transmission electron microscopy has greatly increased knowledge of ultrastructural annelid morphology and anatomy since the 1960s. The first structures to be studied in annelids were integument (epidermis and cuticle), chaetae, musculature, and sense organs, especially eyes (e.g., Eakin and Westfall 1964,

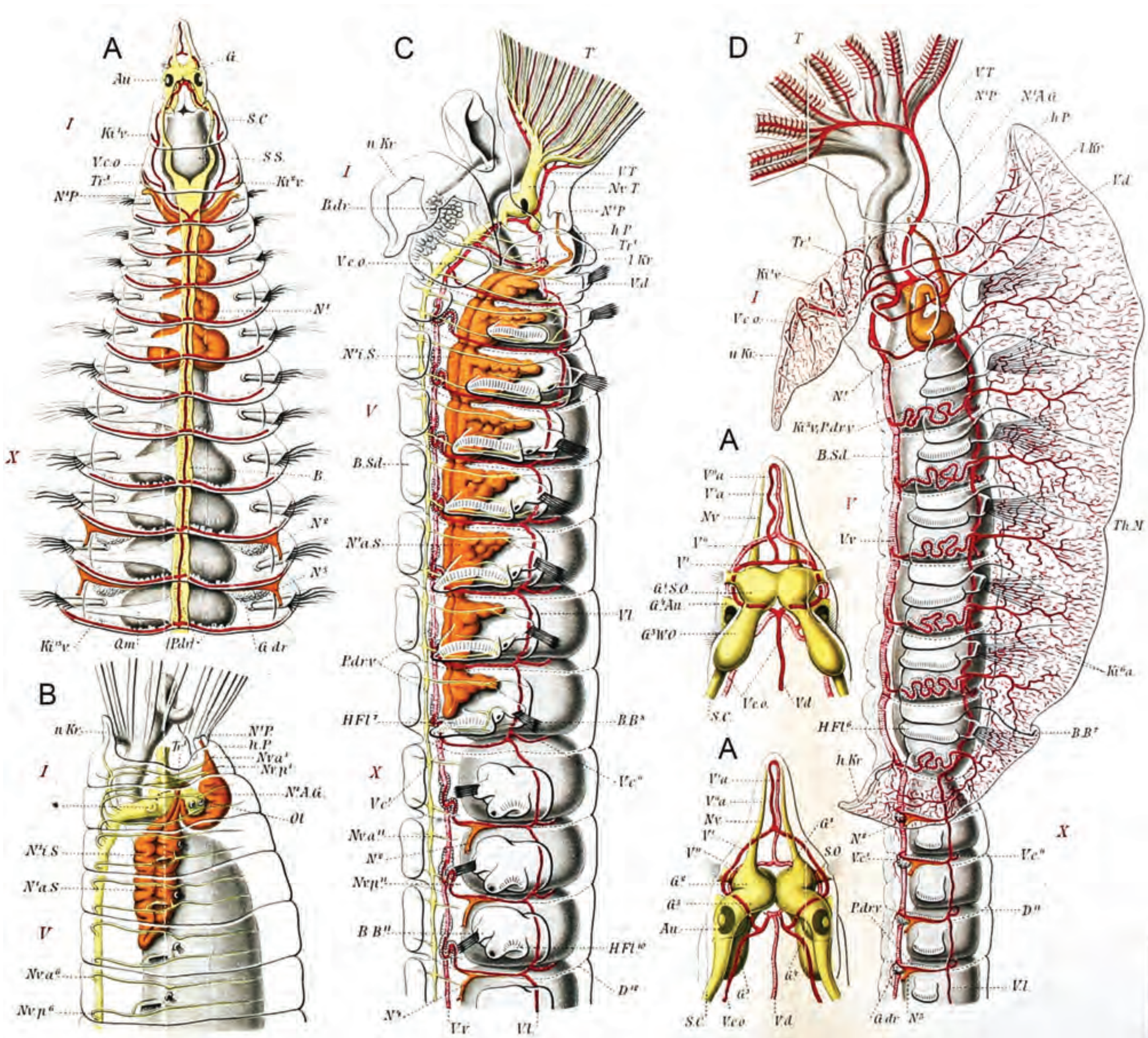

Fig. 1.11: Annelid internal anatomy reconstructed by Meyer (1887: plate 23) from serial sections with orange, red, and yellow as nephridial, circulatory, and nerve structures, respectively, no scale. Figures (plate right side) relabeled here. A, Cirratulid *Chaetozone setosa* (three figures); B, sabellid *Myxicola infundibulum*; C, sabellid *Sabella spallanzanii* (as *Spirographis*); D, serpulid *Protula tubularia* (as *Psygmobranchus protensus*). Original at https://biodiversitylibrary.org/page/47101780

Röhlich and Török 1964, Krasne & Lawrence, 1966). Bartolomaeus and Purschke (2005) and Purschke *et al.* (2014) have reviewed the many studies of annelid ultrastructure since published.

Phase contrast light microscopy for live transparent cells and semitransparent larvae has been available since the 1930s, but the halo around objects is a drawback, and differential interference contrast (or Nomarski) microscopy, available from the 1950s, may give superior detail, although both are useful (Fig. 1.5). Confocal laser scanning microscopy (CLSM), coupled with immunohistochemistry, can be used to investigate the structure and function of cell types within annelids. Worsaae and Rouse (2010) have an early use on males of *Osedax* bone-worms. Finally, while not strictly microscopy, microcomputed tomography (X-ray microtomography) is being adapted to study three-dimensional structures in annelids that are difficult to visualize by other techniques (Faulwetter *et al.* 2013). Although currently providing less resolution than conventional microscopes and CLSM, the main advantage of this method is that it is nondestructive, allowing investigation of internal structures even in valuable museum types.

1.13 Encyclopedic works and their role

We expect encyclopedias and dictionaries to be distillations of information already published elsewhere, just like *Wikipedia*, today's all-encompassing online encyclopedia, with its "no original research" dictum. However, this was not the policy of early encyclopedists, notably those in France, for their works were good opportunities for advocacy of new ideas and even for presenting original taxonomy, with new classifications, and new species (sometimes deliberate, sometimes unintentional). In France, during the late eighteenth through to the first half of the nineteenth century, there was a drive to show new natural history knowledge to the public via ambitious publishing projects, involving the many eminent scholars associated with the Paris museum and using "collection du museum" specimens for the taxonomy. Today, there are many thousands of pages of French erudition accessible to us in sets of volumes via the BHL digitizations, but the long years of laborious production, the sheer quantity, the often-similar short versions of titles (variations on *Histoire* [or *Dictionnaire*] *Naturelle des*...), and the various editions do make for confusion over the relative timelines and over who were the authors/editors.

The most prominent mid-eighteenth century French true encyclopedia was probably the *Encyclopédie*, *ou dictionnaire raisonné des science*s, edited by Diderot and d'Alembert, but if they put in worm content, then it is hard to find. The pioneer for the field of natural history was their influential contemporary, Comte de Buffon (1707–1788), with an illustrated highly successful series titled *Histoire naturelle*, *générale et particulière avec la description du Cabinet du Roi* of 1749–1788. However, lesser known is that this series, and its later editions and translations, got no further than the vertebrates. Even so, Buffon's name was used in later titles, including invertebrates, notably the various editions of the so-called *Les Suites à Buffon*... (sequels to Buffon, also as *Novelles Suites à Buffon*), a series title inferred but usually missing on title pages. Table 1.2 is an outline of some of the major works published in Paris during several productive decades to 1850, in first-volume date order. The influential authors for annelid taxonomy are Lamarck (1744–1829), with his 1818 *Histoire naturelle*... and over 100 annelid names, and Savigny (1777–1851) in the 1822 *Description de l'Égypte* (36 annelid names, discussed later), whereas Cuvier (1769–1832), with his 1817 *Règne Animal*, although famous worldwide and much translated, was relatively weak on annelids. Quatrefages' (1810–1892) *Histoire Naturelle des Annele*s... of 1866 is more significant than any of the preceding works, and is included in the table as a natural late part of the *Suites à Buffon* series, but was published beyond the half century.

Savigny was one of the adventurous "savants" who travelled to Egypt to study its natural history while the Napoleonic army was there and at 21 years old was a junior biologist of the team. From 1802, he worked in Paris on the collections made, including preparing many plates, but his later career did not go well due to eye disease, and he finally became a near-blind recluse. The use of Savigny (1822) manuscript-derived information, adapted to be included in Lamarck (1818), is contentious regarding present-day "credit" or priority via authorship for names that may have been devised by Savigny but for which the associated species were described by Lamarck first, due to the delayed and spaced-out publication of *Description de l'Égypte* works (see background in Álvarez-Campos *et al*. 2015). Strictly, what is published in Lamarck is text written by Lamarck; species authorities are utilitarian, not hinging on modern notions of fair-play.

In contrast to the enthusiastic French biologist-encyclopedists, the authors of the English-language *Encyclopedia Britannica* first edition 1768–1771 contributed nothing significant on annelids (as Vermes), and even for the 11th edition (1910–1911), the Annelida entry was still very short. However, a somewhat anomalous early nineteenth century entry written by the British Museum's William Elford Leach (5th edition supplement, ~1816) included Vermes in "Annulosa" and had a classification with much information and even introduced new Polychaeta taxa with figures, including the well-known genera *Lepidonotus* and *Cistena* (decreed a synonym of *Pectinaria*). In the twentieth century, after production had moved to the United States, Olga Hartman wrote a long Polychaeta entry in the 14th edition *Britannica* of the 1960s. The main Annelida article, first written in the late 1940s, was by endocrinologist Grace Evelyn Pickford (1902–1986), who had done her doctoral thesis on African earthworms, and the Hirudinea section was by J. Percy Moore (1869–1965), better known for his Polychaeta work.

Also, various late nineteenth to early twentieth century book series, intended as overviews of all biota for an undergraduate to research level of understanding, summarized annelid information, sometimes in vast detail. William Benham (1896) in the *Cambridge Natural History* had his own version of a higher classification for Annelida, created suborder Spioniformia, and proposed a separate family Polydoridae for the *Polydora*-like genera. At around the same time (1900), his mentor Ray Lankester was series editor for an intended eight-volume *A Treatise on Zoology*' but an annelid volume did not appear. The

Tab. 1.2: Overview of French encyclopedia-style works between 1750 and 1850 that are relevant to annelids.

Main editor	Dates	Title and content description
Buffon, Comte de (Georges-Louis Leclerc) and later Lacépède, Étienne de	1749–1788, 1788–1804	*Histoire naturelle, générale et particulière avec la description du Cabinet du Roi*: 36 volumes + 8 under Lacépède; volumes by taxa group and within by informal categories (e.g., Oiseaux de proie. Des aigles) and species by French names (taxonomy as footnotes); discursive style; *vertebrates only*; many editions and translations followed.
Bomare, Valmont de	1764	*Dictionnaire raisonné universel d'histoire naturelle*: five volumes (ultimately 15 v. in the 4th edition of 1800); unbroken flow of encyclopedia-style entries; include Aphrodite, Nereide, etc.; no new annelid taxa; a first successful model for all subsequent dictionnaire. https://doi.org/10.5962/bhl.title.102034
Panckoucke, Charles-Joseph (editor/publisher)	1782–1832 (Vers 1789)	*Encyclopedie methodique, ou par ordre de matières*: 156 volumes; successor to the Diderot Encyclopédie; volumes by topic (otherwise, text alphabetical by genera), with 3 volumes for *Histoire Naturelle des Vers*, vol. 1, first part by Jean Guillaume Bruguière; at least eight new polychaeta names (tagged as nob. = our name), including *Amphinome*; content analyzed by Evenhuis (2003). https://doi.org/10.5962/bhl.title.8638
Lamarck, Jean-Baptiste (author/publisher)	1801	*Systeme des Animaux sans vertebres, ou tableau general des classes…*: one-volume book; phyla chapters with annelids as "vers extérieurs" inside "vers"; at least six new annelid names. http://dx.doi.org/10.5962/bhl.title.14255
Castel (series editor) Bosc, Louis Augustin Guillaume (vers author)	1802	*Histoire naturelles des vers, contenant leur description et leurs moeurs; avec figures dessinées d'après nature*: Imprint Chez Deterville (only on half-title page [may be missing] as in ~62 volume series *Histoire naturelle de Buffon*, or *suites à Buffon*); 3 small format volumes. Bosc also contributed crustacean and mollusca volumes; with 2nd edition 1828; 11 new annelid taxa including *Polydora*. https://doi.org/10.5962/bhl.title.64025
Commission d'Egypte Savigny, Jules-Cesar (*Annelides* author)	1809–1822 (Annelides 1822)	*Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française…*: 23 volumes; *Histoire Naturelle* vol. 1(3), a taxonomic monograph as *Système des annélides* (1822) by Savigny; 36 new annelid names. 2nd Panckoucke edition 1826; https://doi.org/10.5962/bhl.title.62506
Lamarck, Jean-Baptiste (author)	1815–1822 (Annelides 1818)	*Histoire naturelle des Animaux sans Vertèbres, présentant les caractéres généraux et particuliers…*: seven volumes, >4,100 pages; at least 107 new annelid names; with 2nd edition 1838. https://doi.org/10.5962/bhl.title.12712
Cuvier, Baron (Georges Cuvier) (author, except Latreille vol. 3)	1817	*Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux…*: four volumes, 1,809 pages; nine new annelid names, including *Eunice*; 2nd edition 1829–1830. Multiple editions and translations followed. https://doi.org/10.5962/bhl.title.41460 *Iconographie du Règne Animal* is a separate work (1829–1844) of 448 new plates edited by Guérin-Méneville.
Saint-Vincent, Bory de	1822–1831	*Dictionnaire classique d'histoire naturelle*: 17 volumes; encyclopedia-style entries, with author initials; Annelides by Latrielle, *Nereis* by Audouin, etc.; two annelid color plates (using figures prepared for Savigny?); new names in molluscs, but not known for annelids. https://doi.org/10.5962/bhl.title.33901
Levrault, F.G. (not Cuvier)	1828–1845	*Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature*: 61 volumes, encyclopedia-style entries, with author initials, vol. 57 includes *Vers* entry by Henri Marie de Blainville; about 26 new annelid taxa including *Capitella*, *Lumbrineris, Scolelepis*. https://doi.org/10.5962/bhl.title.42219
Audouin, Jean Victoire and Milne Edwards, Henri	1829	*Précis d'Entomologie ou d'Histoire naturelle des animaux articulés. Première Division. Histoire naturelle des annélides, crustacés, arachnides et myriapodes…*: one volume; overview of families and species; seven annelid plates; no new taxa. https://doi.org/10.5962/bhl.title.1857
Guérin-Méneville, Félix Édouard	1833–1839	*Dictionnaire pittoresque d'histoire naturelle et des phénomènes de la nature*: nine volumes; encyclopedia-style entries, with author initials; Annelides topic by Rousseau, with color plate, but other authors likely. Includes species-level annelid taxonomy.
Roret, Nicolas (editor, publisher de Quatrefages, Armand (author *Anneles*)	1834–1890	*Suites à Buffon formant avec les œuvres de cet auteur un cours complet d'histoire naturelle…*: 89 volumes under imprint *Librairie encyclopédique de Roret*; includes Quatrefages' two volume (1866) *Histoire Naturelle des Anneles…* (around 465 new annelid names); Vaillant (1889) authored a clitellates volume.
"Une Réunion de Disciples de Cuvier" (authors)	1836–1849	[Disciples edition of Cuvier, *Le Règne Animal…*] also known as "*Le règne animal illustré*" (short title used by Fauvel and Quatrefages): by Audouin, Blanchard, Deshayes, d'Orbigny, Doyère, Dugès, Duvernoy, Laurillard, Milne Edwards, Roulin et Valenciennes; 22 undated volumes (but see Cowan 1976 for collation), Les Annelides vol. 9; text nearly unchanged from Cuvier 1817, but volumes of plates by Milne Edwards and Quatrefages added nine new annelid names. https://doi.org/10.5962/bhl.title.39612
d'Orbigny, Alcide… Dessalines	1847–1849	*Dictionnaire universel d'histoire naturelle*: (editor) 13 volumes, three atlases of plates; encyclopedia-style entries, with author initials; Annelides and Vers, etc., by Paul Gervais; one annelid color plate, one new annelid name. https://doi.org/10.5962/bhl.title.23115

Biodiversity Heritage Library DOI links are given when available. These works are not included in the references list unless cited elsewhere in the text.

two-volume Parker and Haswell (1910) *A Text-Book of Zoology* was the next standard in English of its day. The authors used Gephyrea as a class in "Annulata" alongside class Chaetopoda for polychaetes and oligochaetes. Later, the *Traité de Zoologie* series third edition for annelids (Avel *et al*. 1959) was a stunning achievement, with over 1,100 pages of high-quality printing (Fauvel wrote the polychaete sections). For zoologists based in Germany, Austria, Switzerland, and the Netherlands, as well as the Scandinavian Countries, some *Handbuch der Zoologie* titles with different lead editors were published that included annelids, of which the 1930s Kükenthal and Krumbach edition has already been mentioned and is the most well known. The massive series *Das Tierreich*, initiated by *Deutschen Zoologischen Gesellschaft*, has a taxonomy scope only, and for annelids, only the Oligochaeta volume was published (Michaelsen 1900).

More recent single-volume works intended for student purchase were the multiple editions (8th in 2009) of *Invertebrate Zoology* by Robert D. Barnes (later with E. Ruppert), from which for decades many English-speaking university students worldwide had their first taste of annelid biology and diversity. The first edition (Barnes 1963) was reviewed by no less than Libbie Hyman, famed American author of the influential six-volume McGraw-Hill *The Invertebrates* series (published 1940–1967). Hyman never managed to do the seventh volume, intended to be annelids and echiurans, but in 1959, McGraw-Hill had published her volume 5, *Smaller Coelomate Groups*, which included the pogonophorans and sipunculans (Hyman 1959). Later, the Brusca and Brusca–initiated *Invertebrates* (1st edition 1990) became a rival to the Barnes work, and Greg Rouse has authored the 2016 3rd edition Annelida chapter, cautiously subtitled *The Segmented (and Some Unsegmented) Worms* (Rouse and Giribet 2016).

1.14 Educators and popularizers

> Worms [...] are out every mild night in the winter, as any person may be convinced that will take the pains to examine his grass-plots with a candle; are hermaphrodites and much addicted to venery, and consequently very prolific. (White 1789)

> "Oh! Papa," cried May, "I do think here is a sea-mouse lying on the shore. Bah! I don't much like to touch it." [...] "I do not think, papa," said Jack, "that it looks much like a worm." (Houghton 1870: 11)

> You are going down, perhaps, by railway, to pass your usual six weeks at some watering-place along the coast, and as you roll along think more than once, and that not over-cheerfully, of what you shall do when you get there... (Kingsley 1855, *Glaucus*..., opening sentence)

There have been many popularizers of nature. Gilbert White (1789), quoted from the classic and much reprinted *Natural History of Selbourne* collection of letters to friends, did not overlook reporting on the local earthworm reproductive activity of his rural setting. At the coast, Houghton's (1870) book of seaside walks used a similar literary device, and if his quotes seem too contrived today, nevertheless, his observation rings true. *Aphrodita* do strand just as he described, do not look like worms, and what follows in Houghton is a page or so of believable detailed information. This conversational or letter-to-a-friend style gradually lost its appeal in favor of a more scientific presentation according to Moore (2014), who reviews the many works of a seaside-visit self-improvement genre, published in the British Isles between the mid-nineteenth and early twentieth century. The best-known early exponents were Philip Gosse, author of *A Naturalist's Rambles*... and *The Aquarium*), and Charles Kingsley, friend of Darwin, author of *Glaucus or, the Wonders of the Shore* (for the annelids, see earlier section on illustration). Such works were knowledge reportage and might describe live behaviors and interactions that were not yet recorded or widely known elsewhere, particularly by taxonomists. Also, in Britain, for a time in the mid-nineteenth century, keeping marine aquaria became a national craze according to Allen (1976: 138–140), with a railway-travelling, more literate public having an appetite for learning about natural history for themselves, although consequently, the accessible coastal stretches "were largely stripped of their attractive inhabitants."

In the twentieth century, local seashore guides of various levels of understanding and readability that included annelids were common enough. At the upper technical end, the "Light's Manual" for Californian shores is a classic, first published 1941 for S.F. Light's summer field course for Berkeley students (attended by Olga Hartman in 1933), and now in the 4th edition (Carlton 2007) as a bulky tome of 1,000 pages, with six Annelida editors, but lacking worm photographs. More typical is Morton and Miller's (1968) local classic *The New Zealand Sea Shore*, structured by habitats, with a conversational style, but science based, using binominals not invented vernaculars, with sets of photographs and color plates, and presenting new information on New Zealand annelid occurrences. Another recent genre containing marine annelids are the diver-generated field guides with an array of miniature color photographs and minimal text, such as the *Reef Creature Identification* series (e.g., Humann 2010), with its identifications checked by experts.

Photograph-based community identification sites where scientists and citizens can interact for mutual benefit to reach "research-grade" identifications (e.g., www.inaturalist.org) are a new tool and a source of useful distribution data for scientists. Also, a stunning feature of science outreach to the public today, with direct viewing replacing written reportage, are the live streamings worldwide of video from ROV deep-sea explorations from ships such as the *Nautilus*, *Falkor*, and *Okeanos Explorer* during voyages in 2016–2017 (reviewed in Bell *et al*. 2017, Raineault *et al*. 2018). Live streaming, with further social media transmission, has been very popular with the public and equally so with scientists, who can see for the first time such unusual annelids as swimming squid worms, live siboglinid colonies around vents and seeps, polynoids and alvinellids feeding millimeters away from dangerously hot hydrothermal fluid, methane-ice hesionids, and caterpillar-crawling *Hyalinoecia* quill worms.

1.15 Acknowledgments

I thank the Biodiversity Heritage Library (BHL), as well as their funders and collaborators, for creating the system allowing my access, while living at an out-of-the-way location in the South Pacific, to over 100,000 digitized freely available historic titles, making possible the writing of this article. Thanks to Leslie Harris, who provided background information on Olga Hartman, to Harry ten Hove, who provided guidance on early Dutch works, and to Joko Pamungkas for WoRMS author statistics. Thanks especially to Handbook editor Günter Purschke for help in the final stages, and a very long leash during composition.

1.16 References

Aguado, M.T., Glasby, C.J., Schroeder, P.C., Weigert, A. & Bleidorn, C. (2015): The making of a branching annelid: an analysis of complete mitochondrial genome and ribosomal data of *Ramisyllis multicaudata*. *Scientific Reports (Nature)* 5.

Aguinaldo, A.M.A., Turbeville, J.M., Linford, L.S., Rivera, M.C., Garey, J.R., Raff, R.A. & Lake, L.A. (1997): Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* 387: 489–493.

Aldrovandi, U. (1602): *De animalibus insectis libri septem, cum singulorum iconibus ad viuum expressis*. Ioannem Baptistam Bellagambam, Bologna.

Allen, D.E. (1976): *The naturalist in Britain: a social history*. 1st Ed. Allen Lane, London.

Allen, D.E. (1993): Natural history in Britain in the eighteenth century. *Archives of Natural History* 20: 333–347.

Allen, D.E. (1996): The struggle for specialist journals: natural history in the British periodicals market in the first half of the nineteenth century. *Archives of Natural History* 23: 107–123.

Allen, E.J. (1904): The anatomy of *Poecilochaetus*, Claparede. *Quarterly Journal of Microscopical Science*, *London* (new series) 48: 79–151.

Álvarez-Campos, P., Gil, J. & San Martín, G. (2015): Unveiling the Rosetta Stone of syllids: redescription and neotype designation of *Syllis monilaris* Savigny in Lamarck, 1818, type species of type genus of family Syllidae Grube, 1850 (Annelida). *Zootaxa* 4040: 317–330.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Anon (1665): Observations about shining worms in oysters. *Philosophical Transactions* 1: 203–206.

Apakupakul, K., Siddall, M.E. & Burreson, E.M. (1999): Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. *Molecular Phylogenetics and Evolution* 12: 350–359.

Appeltans, W., Read, G.B., Appeltans, W., *et al*. (2012): The magnitude of global marine species diversity. *Current Biology* 22: P2189–2202.

Ashworth, J.H. (1912): *Catalogue of the Chaetopoda in the British Museum*. *A. Polychaeta: Part. 1. Arenicolidae*. British Museum, London.

Avel, M., de Beauchamp, P., Brien, P., Dawydoff, M. et al. (1959): Traité de Zoologie. Anatomie, Systématique, Biologique. Tome V(1). Annélides, Myzostomides, Sipunculiens, Echiuriens, Priapuliens, Endoproctes, Phoronidiens. Masson et Cie, Paris.

Baird, W. (1865): Description of several new species and varieties of tubicolous annelides (=Tribe Limivora of Grube), in the collection of the British Museum. *Zoological Journal of the Linnean Society*., 8, 10–22, pls1–2.

Baird, W. (1869): Remarks on several genera of annelides, belonging to the group Eunicea, with a notice of such species as are contained in the collection of the British Museum, and a description of some others hitherto undescribed. *Journal of the Linnean Society of London, Zoology*, 10, 341–361.

Barnes, R.D. (1963): *Invertebrate zoology*. Saunders, Philadelphia.

Bartolomaeus, T. & Purschke, G. (eds.) (2005): Morphology, Molecules, Evolution and Phylogeny in Polychaeta and related taxa. *Developments in Hydrobiology* 179, 1–387.

Beekman, E.M. [translator] & Rumpf, G.E. (1999): *The Ambonese Curiosity Cabinet*. Yale University Press, New Haven, CT; London.

de Beer, G.R.C. (1953): Sir Hans Sloane and the British Museum. *The British Museum Quarterly* 18: 2–4.

Bell, K.L.C., Flanders, J., Bowman, A. & Raineault, N.A. (2017): New frontiers in ocean exploration: The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2016 field season. *Oceanography* 30: 1–94.

Benham, W.B. (1896): Archiannelida, Polychaeta, Myzostomaria. In: Harmer, S.F. & Shipley, A.E. (Eds.) *The Cambridge Natural History*. Macmillan and Co. London: 241–334.

Benham, W.B. (1904): On some edible and other new species of earthworms from the North Island of New Zealand. *Proceedings of the Zoological Society of London* (year 1904): 220–263.

Bhaud, M. (1972): Identification des larves d'Amphinomidae (annélides polychètes) recueillies près de Nosy-Bé (Madagascar) et problèmes biologiques connexes. *Cahiers O.R.S.T.O.M. Série Oceanographie* 10: 203–216.

Blackham, G.E. (1882): President's address: the evolution of the modern microscope. *Proceedings of the American Society of Microscopists* 4: 25–47.

de Blainville, H. (1816): Prodrome d'une nouvelle distribution du regne animal. *Bulletin des Sciences par la Société Philomatique de Paris* year 1816: 113–124.
Blakemore, R.J. (2009): Cosmopolitan earthworms – a global and historical perspective. In: Shain, D.H. (ed.) *Annelids in Modern Biology*. Wiley-Blackwell, Hoboken, New Jersey: 257–283.
Blanchard, R., Maehrenthal, F.v. & Stiles, C.W. (1905): *Règles internationales de la nomenclature zoologique adoptées par les congrès internationaux de zoologie: International rules of zoological nomenclature. Internationale regeln der zoologischen nomenklatur*. F.R. de Rudeval, Paris.
Bonnet, C. (1742): An abstract of some new observations upon insects: By M. Charles Bonnet of Geneva. Communicated in a letter to Sir Hans Sloane, Bart. Late president of the Royal Society & Translated from the French by P. H. Z. Esq; F. R. S. *Philosophical Transactions* 42: 458–488.
Boore, J.L. (2001): Complete mitochondrial genome sequence of the polychaete Annelid *Platynereis dumerilii* [letters to the editor]. *Molecular Biology and Evolution* 18: 1413–1416.
Boore, J.L. & Brown, W.M. (1995): Complete sequence of the mitochondrial DNA of the annelid worm *Lumbricus terrestris*. *Genetics* 141: 305–319.
Boore, J.L. & Brown, W.M. (2000): Mitochondrial genomes of *Galathealinum*, *Helobdella*, and *Platynereis*: sequence and gene arrangement comparisons indicate that Pogonophora is not a phylum and Annelida and Arthropoda are not sister taxa. *Molecular Biology and Evolution* 17: 87–106.
Bostock, J. & Riley, H.T. (1855): *The Natural History of Pliny [Annotated Translation of Historia Naturalis]*. Vol. 2. Henry G. Bohn, London.
Bourlat, S.J., Nielsen, C., Economou, A.D. & Telford, M.J. (2008): Testing the new animal phylogeny: A phylum level molecular analysis of the animal kingdom. *Molecular Phylogenetics and Evolution* 49: 23–31.
Bridson, G.D.R. (1968): The zoological record – a centenary appraisal. *Journal of the Society for the Bibliography of Natural History* 5: 23–34.
Bridson, G.D.R. (1989): From xylography to holography: five centuries of natural history illustration. *Archives of Natural History* 16: 121–141.
Brinkhurst, R.O. (1999): Retrospect and prospect: reflections on forty years of study of aquatic oligochaetes. *Hydrobiologia* 406: 9–19.
Brinkhurst, R.O. & Jamieson, B.G.M. (1971): *Aquatic Oligochaeta of the world*. Oliver and Boyd, Edinburgh.
Brookes, R. (1763): *A New and Accurate System of Natural History (vol. 4). The Natural History of Insects, With Their Properties and Uses in Medicine*. J. Newbery, London.
Burrows, W. (1955): Palolo. Notes on the periodic appearance of the annelid worm *Eunice viridis* (Gray) in the southwest Pacific Islands. *Journal of the Polynesian Society* 64: 137–154.
Carlton, J.T. (ed.) (2007): *The Light and Smith Manual. Intertidal Invertebrates from Central California to Oregon*. 4th edition (previously as Light's manual.) University of California Press, Berkeley.
Carpenter, W.B. & Dallinger, W.H. (1901): *The Microscope and Its Revelations*. 8th ed. J. & A. Churchill, London.
Carter, H.B., Judith, A.D., Humphries, C.J. & Alwyne, W. (1981): The Banksian natural history collections of the Endeavour voyage and their relevance to modern taxonomy. *Archives of Natural History* 1981 special issue. History in the service of systematics, 61–70.
Caullery, M. (1914): Sur les Siboglinidae, type nouveau d'invertebres receuillis par l'expedition du Siboga. *Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences* 158: 2014–2017.
Caullery, M. (1915): Sur les Térébelliens de la sous-famille Polycirridae [sic] Malmgr. 1. Délimitation des genres. 2. *Polycirrus arenivorus* n. sp. *Bulletin de la Société Zoologique de France* 40: 239–248.
Caullery, M. (1944): *Siboglinum* Caullery, 1914. Type nouveau d'invertebres, d'affinites a preciser. *Siboga-Expeditie, Leiden Monographie* 138 (monograph 25): 1–26.
Chambers, B. (2014): More zoom in stereo microscopy. *Quality Magazine*.
Chancellor, G., DiMauro, A., Ingle, R. & King, G. (1988): Charles Darwin's beagle collections in the Oxford University Museum. *Archives of Natural History* 15: 197–231.
Charmantier, I. & Müller-Wille, S. (2014): Carl Linnaeus's botanical paper slips (1767–1773). *Intellectual History Review* 24: 215–238.
Claparède, E. (1866): Remarks on Quatrefages' notes on the classification of the Annelids [translation]. *Annals and Magazine of Natural History* 17 (series 3): 100–107.
Claparède, E. (1868): *Les Annélides Chétopodes du Golfe de Naples*. Ramboz et Schuchardt, Genève.
Clark, R.B. (1961): The origin and formation of the heteronereis. *Biological Reviews* 36: 199–236.
Claus, C. & Moquin-Tandon, G. (1884): *Traité de zoologie*. 2nd ed. 2. éd. française, traduite de l'allemand sur la 4. éd., entièrement refondu et considérablement augm./par G. Moquin-Tandon. Ed. F. Savy, Paris.
Cleevely, R.J. (1978): Some background to the life and publications of Colonel George Montagu (1753–1815). *Journal of the Society for the Bibliography of Natural History* 8: 445–480.
Coenen, A. (1578): Visboeck (Fish book). In: *Medieval Manuscripts*. Koninklijke Bibliotheek, National Library of the Netherlands, Scheveningen, the Netherlands. p. 410 leaves. With watercolour drawings made by himself.
Cowan, C.F. (1976): On the disciples' edition of Cuvier's Règne Animal. *Journal of the Society for the Bibliography of Natural History* 8: 32–64.
Cutler, E.B. (1994): *The Sipuncula. Their Systematics, Biology, and Evolution*. 1st ed. Cornell University Press, Ithaca.
Cuvier, G. (1817): *Le règne animal distribé d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparee. Volume 2. Contenant les Reptiles, les Poissons, les Mollusques et les Annélides. [Les Annélides. p. 515–532]*. Deterville, Paris.
Dahlgren, T.G., Lundberg, J., Pleijel, F. & Sundberg, P. (2000): Morphological and molecular evidence of the phylogeny of Nereidiform polychaetes (Annelida). *Journal of Zoological Systematics & Evolutionary Research* 38: 249–253.
Dales, R.P. (1963): *Annelids*. 1st ed. (2nd ed. 1967). Hutchinson University Library, London.
Dance, S.P. (1967): Report on the Linnaean shell collection. *Proceedings of the Linnean Society of London* 178: 1–24.
Dance, S.P. (1989): *The Art of Natural History*. 2nd ed. Bracken Books, London.

Darwin, C. (1840 [read 1837]): On the formation of mould. *Transactions of the Geological Society* 5: 505–509.

Darwin, C. (1881): *The Formation of Vegetable Mould, through the Action of Worms: With Observations on their Habits*. J. Murray, London.

Day, R.A. (1989): The origins of the scientific paper: the IMRAD format. *American Medical Writers Association Journal* 4: 16–18.

Delves, J. (1853): On the application of photography to the presentation of microscopic objects. *Transactions of the Microscopical Society of London* 1: 57–58, plate VII.

Dick, M.H. & Buss, L.W. (1994): A PCR-based survey of homeobox genes in *Ctenodrilus serratus* (Annelida: Polychaeta). *Molecular Phylogenetics and Evolution* 3: 146–158.

Dickinson, E.C., Bruce, M.D. & Dowsett, R.J. (2006): Vivarium naturae or the naturalist's miscellany (1789–1813) by George Shaw: an assessment of the dating of the parts and volumes. *Archives of Natural History* 33: 322–343.

Dünzelmann, A.E., König, V. & Lüderwaldt, A. (1999): *Hugo H. Schauinsland. Unterwegs in Uebersee. Aus Reisetagebüchern und Dokumenten de früheren Direktors des Bremer Übersee-Museums*. Verlag Hauschild, Bremen.

Eakin, R.M. & Westfall, J.A. (1964): Further observations on the fine structure of some invertebrate eyes. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, 62, 310–332.

Eeckhaut, I., McHugh, D., Mardulyn, P., *et al.* (2000): Myzostomida: a link between trochozoans and flatworms? *Proceedings of the Royal Society London* 267: 1383–1392.

Ehlers, E. (1868): *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Wilhelm Engelmann, Leipzig.

Ellis, J. (1755): An essay toward a natural history of the corallines and other marine productions of the like kind commonly found on the coast of Great Britain and Ireland. To which is added the description of a large marine polype taken near the North Pole, by the whale fisheries, in the summer 1753. A. Millar in the Strand, London.

Enders, H.E. (1909): A study of the life-history and habits of *Chaetopterus variopedatus* Renier et Claparede. *Journal of Morphology* 20: 479–531.

Evenhuis, N.L. (2003): Dating and publication of the Encyclopédie Méthodique (1782–1832), with special reference to the parts of the Histoire Naturelle and details on the Histoire Naturelle des Insectes. *Zootaxa* 166: 1–48.

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, 1–188.

Fauchald, K. (1992): A review of the genus *Eunice* (Polychaeta: Eunicidae) based upon type material. *Smithsonian Contributions to Zoology*, 523, 1–422.

Fauchald, K. (1989): The second annual Riser lecture: Eclecticism and the study of polychaetes. *Proceedings of the Biological Society of Washington* 102: 742–752.

Fauchald, K. & Rouse, G. (1997): Polychaete systematics: past and present. *Zoologica Scripta* 26: 71–138.

Faulwetter, S., Vasileiadou, A., Kouratoras, M., Dailianis, T. & Arvanitidis, C. (2013): Micro-computed tomography: introducing new dimensions to taxonomy. *ZooKeys* 263: 1–45.

Fischer von Waldheim, G. (1808): *Tableaux synoptiques de zoognosie: publiés à l'usage de ses élèves à l'Université Impériale de Moscou [Synoptic Charts of Zoognosia: Published for the Use of Students at Moscow Imperial University]*. de l'Imprimerie de l'Université Impériale, Moscou.

Flattely, F.W. (1916): Notes on the ecology of *Cirratulus (Audouinia) tentaculata* (Montagu). *Journal of the Marine Biological Association of the United Kingdom* 11: 60–70.

Ford, B.J. (2009): Charles Darwin and Robert Brown – their microscopes and the microscopic image. *Infocus* 15: 19–28.

Freycinet, L.d., Quoy, J. & Gaimard, J. (1824): *Voyage autour du monde: entrepris par ordre du roi…exécuté sur les corvettes de S. M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820*. Imprimerie en taille-douce de Langlois, Paris.

Glasby, C.J. & Bailey-Brock, J. (2001): Bait-taking fireworms (Amphinomidae: Polychaeta) and other polychaetes. *Beagle* 17: 37–41.

Glasby, C.J. & Read, G.B. (1998): A chronological review of polychaete taxonomy in New Zealand. *Journal of the Royal Society of New Zealand* 28: 347–374.

Gmelin, J.F. & [Linnaeus]. (1791): *Caroli a Linné, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. [Linnaeus 13th ed., 1788 [vol. 1(1) & 1791 for Vol. 1(6)]. Vol. tome 1 (6) [vermes etc p. 3021–3910]. G.E. Beer, Lipsiae.

Goodrich, E.S. (1901): On the structure and affinities of *Saccocirrus*. *Quarterly Journal of Microscopical Science London n.s.* 44: 413–428, pls. 27–29.

Gosse, P.H. (1853): *A Naturalists Rambles on the Devonshire Coast*. John van Voorst, London.

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

Grygier, M. (2000): Class Myzostomida. In: Beesley, P.L., Ross, G.B. & Glasby, C.J. (eds.). *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 297–329.

Gunther, A.E. (1977): *William Carmichael M'Intosh, M.D., F.R.S. [aka McIntosh]*. 1st ed. Scottish Academic Press Ltd., St. Andrews.

Gustus, R.M. & Cloney, R.A. (1973): Ultrastructure of the larval compound setae of the polychaete *Nereis vexillosa* Grube. *Journal of Morphology* 140: 355–366.

Häcker, V. (1898): Die pelagischen Polychaeten- und Achaetenlarven der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* 2: 1–50, plates 1–5.

Haeckel, E. (1866): *Generelle Morphologie der Organismen: allgemeine Grundzuge der organischen Formen-Wissenschaft, mechanisch begrundet durch die von Charles Darwin reformirte Descendenz-Theorie*. Georg Reimer, Berlin.

Haeckel, E. (1883): *A visit to Ceylon* [Translated by C. Bell]. Kegan Paul & Co., London.

Haeckel, E. (1904): *Kunstformen der Natur ("Artforms of Nature")*. Verlag des Bibliographischen Instituts, Leipzig und Wien.

Hammond, A. (1882): On *Tubifex rivulorum*. *The Journal of the Postal Microscopical Society* 1: 14–21, plate 1, continued Vol. 2, 165–175.

Hargitt, C.W. (1906): Experiments on the behaviour of tubicolous annelids. *Journal of Experimental Zoology*, 3, 295–320.

Hartman, O. (1951): *Literature of the Polychaetous Annelids. Vol. I. Bibliography*. Edwards Brothers Inc., Ann Arbor, MI.

Hartman, O. (1954): Pogonophora Johansson, 1938. *Systematic Zoology* 3: 183–185.

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. Parts 1 & 2. *Allan Hancock Foundation Occasional Paper* 23: 1–628.

Hartman, O. (1965): Catalogue of the polychaetous annelids of the world. Supplement 1960–1965 and index. *Occasional Papers of the Allan Hancock Foundation* 23: 1–197.

Hatschek, B. (1878): Studien über die Entwicklungsgeschichte der Anneliden. *Arbeiten aus dem Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest* 1: 1–128.

Hatschek, B. (1893): System der Anneliden, ein vorläufiger Bericht. *Sitzungsberichte des Deutschen Naturwissenschaftlich-Medicinischen Vereines für Böhmen "Lotos" in Prag.*, Neue Folge 13: 123–126.

Herdrich, D. & Armstrong, K. (2008): *Final Report. Historic Fishing Methods in American Samoa*. Pacific Islands Fisheries Science Center, National Oceanic and Atmospheric Administration, Honolulu, HI.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Holborow, P.L. (1971): The fine structure of the trochophore of *Harmothoe imbricata*. In: Crisp, D.J. (ed.) *Fourth European Marine Biology Symposium.* Cambridge University Press, Cambridge: 237–246.

Holthuis, L.B. (1969): Albertus Seba's "Locupletissimi rerum naturalium thesauri…" (1734–1765) and the "Planches de Seba" (1827–1831). *Zoologische Mededelingen* 43: 239–252.

Horton, T., Gofas, S., Kroh, A., *et al.* (2017): Improving nomenclatural consistency: a decade of experience in the World Register of Marine Species. *European Journal of Taxonomy* 389: 1–24.

Houghton, W. (1870): *Sea-side Walks of a Naturalist with His Children*. Groombridge and sons, London.

Hudson, W.H. (1919): *The Book of a Naturalist*. 1st ed. George H. Doran Company, New York.

Humann, P.D.N. (2010): *Reef Creature Identification: Tropical Pacific*. 2nd printing 2012. New World Publications, Jacksonville, FL.

Hutchings, P.A. & Glasby, C. J. (2000): History of discovery. In: Beesley, P.L., Ross, G.B., Glasby, C.J. (eds). *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*, CSIRO Publishing, Melbourne: 3–9.

Hyman, L.H. (1959): *The Invertebrates: Smaller coelomate groups. Chaetognatha, Hemichordata, Pogonophora, Phoronida, Ectoprocta, Brachiopoda, Sipunculida, The coelomate Bilateria*. McGraw-Hill Book Co., New York.

International Commission on Zoological Nomenclature (ICZN). (1961): *Code international de nomenclature zoologique adopte par le XVe Congres international de zoologie [International Code of Zoological nomenclature adopted by the XV International Congress of Zoology]*. 1st ed. International Trust for Zoological Nomenclature, London.

International Commission on Zoological Nomenclature (ICZN). (1999): *International Code of Zoological Nomenclature*. 4th ed. The International Trust for Zoological Nomenclature, London.

Ivanov, A.V. (1963): *Pogonophora*. [Translated by D.B. Carlisle] Consultants Bureau, New York.

Jeffreys, J.G. (1863): *British Conchology*. Vol. 2. John van Voorst, London.

Johnson, J.R. (1816): *A Treatise on the Medicinal Leech: Including Its Medical and Natural History, with a Description of its Anatomical Structure: Also, Remarks upon the Diseases, Preservation and Management of Leeches*. Longman, Hurst, Rees, Orme, and Brown, London.

Johnston, G. (1865): *A Catalogue of the British Non-Parasitical Worms in the Collection of the British Museum*. 1st ed. Trustees of the British Museum, London.

Jones, M.L. (1985): On the vestimentifera, new phylum, six new species, and other taxa, from hydrothermal vents and elsewhere. *Bulletin of the Biological Society of Washington* 6: 117–158.

Keynes, R.D. (2000): *Charles Darwin's Zoology Notes & Specimen Lists from H.M.S. "Beagle"*. Cambridge University Press, Cambridge.

Kingsley, C. (1873): *Glaucus, or, The Wonders of the Shore*. 5th ed. Macmillan, London.

Knight-Jones, P. & Perkins, T.H. (1998): A revision of *Sabella*, *Bispira* and *Stylomma* (Polychaeta: Sabellidae). *Zoological Journal of the Linnean Society* 123: 385–467.

Kojima, S., Ohta, S., Yamamoto, T., (2002): Molecular taxonomy of vestimentiferans of the western Pacific and their phylogenetic relationship to species of the eastern Pacific. II. Families Escarpiidae and Arcovestiidae. *Marine Biology (Berlin)* 141: 57–64.

Krasne, F.B. & Lawrence, P.A. (1966): Structure of the photoreceptors in the compound eyespots of *Branchiomma vesiculosum*. *Journal of Cell Science*, 1, 239–248.

Kusukawa, S. (2010): The sources of Gessner's pictures for the *Historia animalium*. *Annals of Science* 67: 303–328.

Kutschera, U., Langguth, H., Kuo, D.H., Weisblat, D.A. & Shankland, M. (2013): Description of a new leech species from North America, *Helobdella austinensis* n. sp (Hirudinea: Glossiphoniidae), with observations on its feeding behaviour. *Zoosystematics and Evolution* 89: 239–246.

Kutschera, U. & Weisblat, D.A. (2015): Leeches of the genus *Helobdella* as model organisms for Evo-Devo studies. *Theory in Biosciences* 134: 93–104.

Lamarck, J.-B.d. (1802 [privately published, reprinted 1906]): Discours d'Ouverture, Prononcé le 27 floréal An 10, au Muséum dHistoire naturelle. Recherches sur l'organisation des corps vivans *Bulletin Scientifique de la France et de la Belgique* (5th series) 40: 483.

Lamarck, J.B.d. (1818): *Histoire Naturelle des animaux sans vertebres, [presentant les caracteres generaux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, etla citation des principales especes qui s'y rapportent; precedes d'une Introduction offrant la determination des caracteres essentiels de l`Animal, sa distinction du vegetal et desautres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie]*. 1 ed. Deterville, Paris.

van der Land, J. & Nørrevang, A. (1977): Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera). *Det Kongelige Danske Videnskbernes Selskab Biologiske Skrifter* 21: 1–102.

Lankester, E.R. (1890): The history and scope of zoology. In: Lankester, E.R. *The Advancement of Science. Occasional Essays & Addresses*. Macmillan, London.

Leach, W.E. (1816): Annulosa. p. 401–453 In: *Supplement to the 4th, 5th, and 6th editions of the Encyclopaedia Britannica*. Vol. 1. Archibald Constable, Edinburgh.

Leuckart, F.S. (1827): *Versuch einer naturgemässen Eintheilung der Helminthen nebst dem Entwurfe einer Verwandschafts- und Stufenfolge der Thiere überhaupt*. Neue Akademische Buchhandlung von Karl Gross, Leipzig.

Linnaeus, C. (1758): *Systema naturae per regne tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis. Editio Decima, Reformata*. Laurentii Salvii, Holmiae [Stockholm].
Linné, C.L. & Turton, W. (1806): *Volume 4. Worms. In a General System of Nature, through the Three Grand Kingdoms of Animals, Vegetables, and Minerals, Systematically Divided into Their Several Classes, Orders, Genera, Species, and Varieties, with Their Habitations, Manners, Economy, Structure and Peculiarities* [7 volumes, 1802–1806] [expanded English translated version of Gmelin's edition of Systema Naturae]. Printed for Lackington, Allen, and Co., Temple of the Muses, Finsbury Square, London.
MacGillivray, W. (1834): *Lives of eminent zoologists, from Aristotle to Linnaeus: with introductory remarks on the study of natural history, and occasional observations on the progress of zoology*. 2nd Ed. Oliver & Boyd, Edinburgh
Maerlant, J.van. (~1350): *Der Naturen Bloeme [The Flower of Nature]*. Utrecht or Flanders. In: *Medieval Manuscripts*. Koninklijke Bibliotheek, National Library of the Netherlands, Scheveningen, the Netherlands.
McIntosh, W.C. (1868): On the boring of certain annelids. *Annals and Magazine of Natural History*, (Series 4) 2, 276–295.
McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. 'Challenger' during the years 1873–76. *Report of the Scientific Results of the Exploring Voyage of H.M.S. Challenger 1873–76*, 12 [part 34 of the reports], 1–554.
McIntosh, W.C. (1923): A monograph of the British marine annelids. Vol. IV - Part II. Polychaeta, Sabellidae to Serpulidae. With additions to the British marine Polychaeta during the publication of the monograph. *Ray Society*, 4, 251–538.
Malaquin, A. & Carin, F. (1922): Tomoptérides provenant des campagnes de l'Hirondelle et la Princesse-Alice (1888–1910). *Resultats des Campagnes Sciencitifiques, Monaco* 61: 1–52.
Malmgren, A.J. (1869): Ueber die Gattung *Heteronereis* (Örst.) und ihr Verhältniss zu den Gattungen *Nereis* (Gr.) und *Nereilepas* (Gr.) *Zeitschrift fur Wissenschaftliche Zoologie* 19: 476–478.
Megenberg, K.von (1475): *Das Buch der Natur*. Johann Bämler, Augsburg.
Meyer, E. (1887): Studien über Körperbau der Anneliden. Mitteilungen der zoologische Station zu Neapel zugleich ein *repertorium für Mittelmeerkunde*, 7, 592–741.
Michaelsen, W. (1899): Oligochaeten von den Inseln des Pacific, nebst Erörterungen zur Systematik der Megascoleciden. (Esgebnisse einer Reise nach dem Pacific. Schauinsland 1896/97). *Zoologische Jahrbücher. Abteilung für Systematik, Okologie und Geographie der Tiere* 12: 211–246.
Michaelsen, W. (1900): Vermes. Oligochaeta. *Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen* 10: 1–575.
Miller, D. (1952): The insect people of the Maori. *Journal of the Polynesian Society* 61: 1–61.
Molyneux, T. (1695): Account of a not yet described Scolopendra marina, by Thomas Molyneux, M.D. S. R. S. communicated by Mr. Locke. *Philosophical Transactions* 19: 405–412.
Monro, C.C.A. (1931): Group Vermes. In: Pycraft, W.P. (ed.) *The Standard Natural History. From Amoeba to Man*. Frederick Warne and Co., London and New York: 41–67.
Montagu, G. (1803, 1804): *Testacea Britannica, or, Natural History of British Shells, Marine, Land, and Fresh-Water, Including the Most Minute: Systematically Arranged and Embellished With Figures. Pt. 1, 2*. J. White, London.
Moore, P.G. (2012): The supply of marine biological specimens (principally animals) for teaching and research in Great Britain from the nineteenth century until today. *Archives of Natural History* 39: 281–301.
Moore, P.G. (2014): Popularizing marine natural history in eighteenth- and nineteenth-century Britain. *Archives of Natural History* 41: 45–62.
Moquin-Tandon, A. (1846): *Monographie de la famille des hirudinées*. 2nd ed. J. B. Baillière, Paris.
Moquin-Tandon, A. [as Frédol, Alfred] & Lackerbauer, P.A. (1866): *Le Monde de la mer*. 2nd ed. Librairie de L. Hachette, Paris.
Mörch, O.A.L. (1863): Rivisio Critica Serpulidarum et Bidrag til Rorormenes Naturhistorie. *Naturhistorisk Tidsskrift, Kobenhavn*, (3rd series) 1, 347–470, plate 11.
Morton, J. & Miller, M. (1968): *The New Zealand Sea Shore*. 1st ed. Collins, London.
Müller, J. (1854): Ueber verschiedene Formen von Seethieren. *Archiv für anatomie physiologie und wissenschaftliche* 1854: 69–98, plates 4–6.
Neave, S.A. (1939–1946): *Nomenclator Zoologicus. A list of the Names of Genera and Subgenera in Zoology from the Tenth Edition of Linnaeus 1758 to the End of 1935*. Zoological Society of London, London.
Nissen, C. (1969 [vol 1], 1978 [vol 2]): *Die Zoologische Buchillustration. Ihre Bibliographie und Geschichte*. Anton Hiersemann, Verlag, Stuttgart.
Oliver, P.G., Morgenroth, H. & Salvador, A. (2017): Type specimens of Mollusca described by Col. George Montagu in the Royal Albert Memorial Museum & Art Gallery, Exeter and The Natural History Museum, London. *Zoosystematics and Evolution* 93: 363–412.
Örsted, A.S. (1842): Udtog af en Breskrivelse af Groenlands Annulata dorsibranchiata. *Naturhistorisk Tidsskrift* (series 1) 4: 109–127.
Parapar, J. & Hutchings, P.A. (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.
Parfitt, E. (1867): The annelids of Devon, with a resume of the natural history of the county. *Devonshire Association for the Advancement of Science, Literature and Art* 2: 203–208.
Park, C., Han, Y.-H., Lee, S.-G., *et al.* (2018): The developmental transcriptome atlas of the spoon worm *Urechis unicinctus* (Echiurida: Annelida). *GigaScience* 7(3): giy007–giy007.
Parker, T.J. & Haswell, W.A. (1910): *A Text-Book of Zoology*. MacMillan, London.
Pettibone, M.H. (1982): Annelida. In: Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill, New York.
Peyssonnel, J.A. (1759): [as John Andrew Peyssonel] Observations upon the sea scolopendre or sea millepes. *Philosophical Transactions of the Royal Society of London* 51: 35–37.
Pierantoni, U. (1908): *Protodrilus. Fauna und Flora des Golfes von Neapel* 31: 1–226.
Pliny the Elder. (1469): *Plinius secundus nouocomensis equestribus militiis industrie functus… [line 12] Libros Naturalis Historiæ nouitiu camenis qritiu tuo opus natu apud me proxima fetura &c. [Ends:--Colophon.] Quem modo tam rarum cupiens uix lector haber&: Quiq etiam fractus pene legendus eram: Restituit Venetis me nuper Spira Ioannes: Exscripsitq libros*

ere notante meos. Fessa manus quondam moneo: Calamusq quiescat. Nanq labor studio cessit studio cessit: & ingenio. M.CCCC.LXVIIII. 1st ed. J. Spira, Venice.
Purschke, G., Bleidorn, C. & Struck, T. (2014): Systematics, evolution and phylogeny of Annelida – a morphological perspective. *Memoirs of Museum Victoria*, 71, 247–269.
de Quatrefages, A. (1847): Etudes sur les types inférieurs de l'embranchement des Annelés. Mémoire sur l'Echiure de Gaertner (*Echiurus gaertnerii* Nob.). *Annales des sciences naturelles, Paris, 3rd Series, Zoologie* 7: 307–343, plate 6.
de Quatrefages, A. (1857): *The rambles of a naturalist on the coasts of France, Spain, and Sicily* [Translated by E. C. Otté]. Longman, Brown, Green, Longmans, & Roberts, London.
de Quatrefages, A. (1866a): On the classification of the annelides [Translated by W. S. Dallas]. *Annals and Magazine of Natural History* 17 (series 3): 1–24.
de Quatrefages, A. (1866b [imprint 1865]): *Histoire naturelle des Anneles marins et d'eau douce. Annelides et Gephyriens. Vol. 1 & 2 (separate pagination)*. Librarie Encyclopedique de Roret, Paris.
Rainbow, P.S. (2005): From natural history to biodiversity: collections of discovery. *Archives of Natural History* 32: 221–230.
Rainbow, P.S. (2008): Marine biological collections in the 21st century. *Zoologica Scripta* 48(s1): 33–40.
Raineault, N.A., Flanders, J. & Bowman, A. (2018): New frontiers in ocean exploration: The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2017 field season. *Oceanography* 31: 1–126.
Read, G.B. & Fauchald, K. (2018): World Polychaeta database. Accessed at http://www.marinespecies.org/polychaeta/aphia.php on 2018-04-27.
Reynolds, J.W. & Cook, D.G. (1976): *Nomenclatura Oligochaetologica. A Catalogue of Names, Descriptions and Type Specimens of the Oligochaeta*. University of New Brunswick, Fredericton, New Brunswick.
Reynolds, J.W. & Wetzel, M.J. (2013–2018): Nomenclatura Oligochaetologica – Editio Secunda. Accessed at http://wwx.inhs.illinois.edu/people/mjwetzel/nomenoligo on 2018-04–27.
Röhlich, P. & Török, L.J. (1964): Elektronenmikroskopische Beobachtungen an den Sehzellen des Blutegels, *Hirudo medicinalis L. Zeitschrift für Zellforschung und Mikroskopische Anatomie*, 63, 618–635.
Rolando, L. (1822 [1821 volume]): Description d'un animal nouveau qui appartient à la classe des Echinodermes. *Memorie della Reale Accademia delle Scienze di Torino* 26: 539–556.
Rondelet, G.R. (1554–1555): *[vol.1 (1554)] Libri de piscibus marinis: in quibus verae piscium effigies expressae sunt: quae in tota piscium historia continentur, indicat elenchus pagina nona et decima: postremo accesserunt indices necessarij. [vol.2 (1555)]… Universae aquatilium historiæ pars altera, cum veris ipsorum imaginibus*. Matthiam Bonhomme, Lyon.
Rota, E. (2011): Early oligochaete science, from Aristotle to Francesco Redi. *Archives of Natural History* 38: 136–163.
Rouse, G.W. (2001): A cladistic analysis of Siboglinidae Caullery, 1914 (Polychaeta, Annelida): formerly the phyla Pogonophora and Vestimentifera. *Zoological Journal of the Linnean Society of London* 132: 55–80.
Rouse, G.W. & Giribet, G.S. (2016): *Phylum Annelida: The Segmented (and Some Unsegmented) Worms* [Chapt 14]. *In*: Brusca, R.C., Moore, W. & Shuster, S.M. (Eds.) *Invertebrates*. Sinauer Associates, Sunderland, Massachusetts.
Rouse, G.W. & Fauchald, K. (1995): The articulation of Annelids. *Zoologica Scripta* 24: 269–301.
Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.
Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, Oxford.
Ruysch, F.F.R. (1710): *Thesaurus animalium primus: cum figuris aeneis = Het eerste cabinet der dieren*. Apud Joannem Wolters, Amsterdam.
Sander, K. (1994): An American in Paris and the origins of the stereomicroscope. *Roux's Archives of Developmental Biology* 203: 235–242.
Sato-Okoshi, W. (2017): Obituary: Minoru Imajima (1930–2016). *Journal of the Marine Biological Association of the United Kingdom* 97: 1203–1203.
Savigny, J.-C. (1822 [official date]): Systeme des annelides, principalement de celles des cotes de l'Egypte et de la Syrie, offrant les caracteres tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Especes. *Description de l'Égypte… Histoire Naturelle, Paris* 1: 3–128, 325–472.
Schmarda, L.K. (1859): *Neue Turbellarien, Rotatorien und Anneliden beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857 von Ludwig K. Schmarda. Erster halfte [Part.I] [New Turbellarien, Rotatorien and Anneliden observed and collected on a journey around the Earth 1853 to 1857. First half [Part.I]*. 1st ed. Wilhelm Engelmann, Leipzig.
Schmarda, L.K. (1861a): *Ludwig K. Schmarda's Reise um die Erde in den Jahren 1853–1857*. G. Westermann, Braunschweig.
Schmarda, L.K. (1861b): *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erdr [sic] 1853 bis 1857 von Ludwig K. Schmarda. Erster Band. Turbellarien, Rotatorien und Anneliden. Zweite Hälfte*. Wilhelm Engelmann, Leipzig.
Seba, A. (1734): *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam:opus, cui, in hoc rerum genere, nullum par exstitit/ex toto terrarum orbe collegit, digessit, descripsit, et depingendum curavit Albertus Seba*. Vol. 1. Apud Janssonio-Waesbergios & J. Wetstenium & Gul. Smith, Amsterdam.
Shaw, G. & Nodder, F.P.a. (1789 [to 1813]): *Vivarium Naturae or The naturalist's Miscellany, or Coloured Figures of Natural Objects*. Nodder & Co., London.
Sherborn, C.D. (1902–1933): *Index animalium sive index nominum quae ab A.D. 1758 generibus et speciebus animalium imposita sunt [covers 1758 to 1850]*. E typographio Academico, Cantabrigiae (= Cambridge).
Shindler, K. (2016): A magpie with a card-index mind – Charles Davies Sherborn 1861–1942. *ZooKeys* 550: 33–56.
Siddall, M.E. & Burreson, E.M. (1998): Phylogeny of leeches (Hirudinea) based on mitochondrial cytochrome c oxidase subunit I. *Molecular Phylogenetics and Evolution* 9: 156–162.
Siddall, M.E., Trontelj, P., Utevsky, S., Nkamany, M. & Macdonald, K. (2007): Diverse molecular data demonstrate that commercially available medicinal leeches are not *Hirudo medicinalis*. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1481–1487.
Simakov, O., Marletaz, F., Cho, S.-J. (2013): Insights into bilaterian evolution from three spiralian genomes. *Nature* 493: 526–531.
Slabber, M. (1781): *Physikalische Belustigungen oder Mikroskopische Wahrnehmungen von drey und vierzig in- und ausländischen Wasser- und Landthierchen durch Martinus Slabber, Mitglied*

der holländischen Societät der Wissenschaften, und der Vlißingischen, wie auch verschiedener deutschen Gesellschaften zur Aufnahme nüzlicher Künste und Wissenschaften. Winterschmidt, Nürnberg.

Sloane, H. (1725): *A voyage to the islands Madera* [sic], *Barbados, Nieves, St Christophers and Jamaica: with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, &c. of the last of those islands*. Printed by B.M. for the author, London.

Solís-Weiss, V., Bertrand, Y., Helléouet, M.-N. & Pleijel, F. (2004): Types of polychaetous annelids at the Muséum national d'Histoire naturelle, Paris. *Zoosystema* 26: 377–384, appendix S1–21.

Sowerby, J. (1806): *The British Miscellany, or, Coloured Figures of New, Rare, or Little Known Animal Subjects: Many Not Before Ascertained to be Inhabitants of the British Isles: and Chiefly in the Possession of the Author, James Sowerby*. Vol. 1–2. R. Taylor & Co., London. Sold by the author, J. Sowerby, by White, Johnson, Symonds, and all other booksellers.

Spier, R. (2002): The history of the peer-review process. *Trends in Biotechnology* 20: 357–358.

Springett, J.A., Gray, R.A.J., Barker, D.J., *et al.* (1998): Population density and distribution of the New Zealand indigenous earthworm *Octochaetus multiporus* (Megascolecidae: Oligochaeta) in hill pastures. *New Zealand Journal of Ecology* 22: 87–93.

Stair, J.B. (1897): Palolo, a sea-worm eaten by the Samoans. *Journal of the Polynesian Society* 6: 141–144.

Stephen, A.C. & Edmonds, S.J. (1972): *The phyla Sipuncula and Echiura*. British Museum, London.

Stephenson, J. (1930 [reprinted 1972]): *The Oligochaeta*. Clarendon Press (reprinted by Verlag Von J. Cramer), Oxford.

Strickland, H.E. (1878): *[Strickland Code. Deceased nominal author] Rules for Zoological Nomenclature*. John Murray, London.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology*, 25, 1993–1999

Struck, T.H., Paul, C., Hill, N., *et al.* (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

Summers, M.M. & Rouse, G.W. (2014): Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Evolutionary Biology* 14: 170.

Taheri, S., James, S., Roy, V., *et al.* (2018): Complex taxonomy of the 'brush tail' peregrine earthworm *Pontoscolex corethrurus*. *Molecular Phylogenetics and Evolution* 124: 60–70.

Taylor, H.R. & Harris, W.E. (2012): An emergent science on the brink of irrelevance: a review of the past 8 years of DNA barcoding. *Molecular Ecology Resources* 12: 377–388.

Thompson, D.W. & Aristotle. (1910): *Historia Animalium*. 1st ed. Clarendon Press, Oxford.

Usselman, M.C. (2015): *Pure Intelligence: The Life of William Hyde Wollaston*. The University of Chicago Press, Chicago.

Vandepitte, L., Vanhoorne, B., Decock, W., *et al.* (2018): A decade of the World Register of Marine Species – general insights and experiences from the Data Management Team: where are we, what have we learned and how can we continue? *PLoS ONE* 13: e0194599.

Vaney, L. & Conte, A. (1898): Recherches experimentales sur la regeneration chez *Spirographis spallanzanii*. *Comptes Rendus de la Societe Biologique, Paris* 1: 973–975.

Vejdovsky, F. (1878): Beiträge zur Kenntnis der Tomopteriden. *Zeitschrift fur Wissenschaftliche Zoologie* 31: 81–100, plates 6–7.

Vejdovsky, F. (1884): *System und Morphologie des Oligochaeten*. Commissimbuchhandlung von Franz Rivnac, Prague.

Viguier, C. (1886): Etudes sur les Animaux inferieurs de la Baie d'Alger. Recherches sur les Annelides pelagiques. *Archives de Zoologie Experimentale et Generale* 4: 347–442, plates 21–27.

Walcott, C.D. (1911): Cambrian geology and paleontology. Middle Cambrian annelids. *Smithsonian Miscellanous Collections* 57: 109–144.

Wang, Y. & Xie, Q. (2014): The molecular Symplesiomorphies shared by the stem groups of Metazoan evolution: can sites as few as 1% have a significant impact on recognizing the phylogenetic position of Myzostomida? *Journal of Molecular Evolution* 79: 63–74.

Ward, L.A. & Fauchald, K. (1997): *Literature on the Polychaeta (Annelida)*. 2nd ed. (database files). Accessed at https://web.archive.org/web/20080602022426/www.annelida.net/bibliog/bibliowf.html on 2018-04-27.

Watson, G.J., Murray, J.M., Schaefer, M. & Bonner, A. (2017): Bait worms: a valuable and important fishery with implications for fisheries and conservation management. *Fish and Fisheries* 18: 374–388.

Webb, M. (1969): *Lamellibrachia barhami*, Gen. Nov. Sp. Nov. (Pogonophora), from the Northeast Pacific. *Bulletin of Marine Science* 19: 18–47.

Weigert, A. & Bleidorn, C. (2016): Current status of annelid phylogeny. *Organisms Diversity & Evolution* 16: 345–362.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Weitzmann, K. (1971): *Studies in Classical and Byzantine Manuscript Illumination*. University of Chicago Press, Chicago; London.

Wesenberg-Lund, E. (1934): Gephyreans and annelids. The Scoresby Sound Committee's 2nd East Greenland expedition in 1932 to King Christian IX's land. *Meddelelser om Groenland* 104: 1–38.

Wheeler, A. (1984): Daniel Solander and the zoology of Cook's voyage. *Archives of Natural History* 11: 505–515.

White, G. (1789): *The Natural History and Antiquities of Selborne, in the County of Southampton*. 1st ed. Printed by T. Bensley, for B. White and Son, at Horace's Head, Fleet Street, London.

Whitehead, P.J.P. (1969): Zoological specimens from Captain Cook's voyages. *The Journal of the Society for the Bibliography of Natural History* 5: 161–201.

Whitelegge, T. (1890): Report on the worm disease affecting the oysters on the coast of New South Wales. *Records of the Australian Museum, Sydney*, 1, 41–54.

Wilson, D.P. (1932): On the *Mitraria* larva of *Owenia fusiformis* delle Chiaje. *Philosophical Transactions of the Royal Society of London*, 221, 231–334.

Winnepenninckx, B., Backeljau, T. & De Wachter, R. (1995): Phylogeny of protostome worms derived from 18S rRNA sequences. *Molecular Biology and Evolution* 12: 641–649.

Wise, F.C. (1950): The development of the binocular microscope. *Monographs of the Quekett Microscopical Club* 5: 5–21.

Worsaae, K. & Rouse, G.W. (2010): The simplicity of males: Dwarf males of four species of *Osedax* (Siboglinidae; Annelida) investigated by confocal laser scanning microscopy. *Journal of Morphology*, 271, 127–142.

Torsten H. Struck

2 Phylogeny

2.1 Phylogenetic position

The phylogenetic position of Annelida within Metazoa was uncontroversial for a long time. Ever since Cuvier (1817), the dominant hypothesis was the Articulata hypothesis, which regarded Annelida as closely related to Arthropoda. This hypothesis was still dominant in textbooks of invertebrate zoology until recently, usually placing Articulata within Spiralia (Westheide and Rieger 1996, Ax 1999, Nielsen 2001, Brusca and Brusca 2003). However, the new placement of Annelida is now also reflected in textbooks (Ruppert *et al.* 2004, Pecheni, 2010, Westheide and Rieger, 2013, Brusca *et al.* 2016, Urry *et al.* 2017). The characters supposed to strongly support the Articulata hypothesis are a segmented body organization including a rope ladder-like nervous system and segment formation by a posterior growth zone, longitudinal muscles of the body wall in distinct bundles, and presence of mushroom bodies in the brain (e.g., Westheide and Rieger 1996, Ax 1999, Scholtz 2003). Articulata was regarded as closely related to other spiralian taxa such as Mollusca based on spiral cleavage (e.g., Ax 1995, Westheide and Rieger 1996, Ax 1999), although Arthropoda show no sign of spiral cleavage in their development (Scholtz 1997, Dearden *et al.* 2002, Alwes and Scholtz 2004, Hejnol and Schnabel 2005, Hertzler 2005). During the first cell divisions of spiral cleavage, the spindle has an alternating oblique orientation in comparison to the previous one and gives rise to differently sized daughter cells in a stereotypic pattern (Nielsen 2010). Furthermore, some of the spiralian taxa (i.e., Mollusca and Entoprocta) and Annelida share a trochophore larva in their life cycle. Even Nemertea and Cycliophora might possess highly modified trochophora larvae (Funch 1996, Maslakova *et al.* 2004a,b).

Surprisingly, early phylogenetic studies based on molecular data (i.e., 18S rRNA) were not able to recover Articulata but still showed a closer relationship of Annelida to Mollusca as well as Brachiopoda, a lophophorate taxon (Field *et al.* 1988, Ghiselin 1988, Field *et al.* 1989, Patterson 1989, Raff *et al.* 1989, Lake 1990). Halanych *et al.* (1995), who included 18S rRNA data of representatives of all lophophorate lineages, confirmed these previous results with strong bootstrap support and coined the name Lophotrochozoa for this group. Lophotrochozoa is defined as including the last common ancestor of lophophorates, molluscs, and annelids, and its descendants. Hence, an apparent conflict was evident between morphological and molecular data regarding the placement of Annelida either as sister to Arthropoda or within Lophotrochozoa, respectively. Based on 18S rRNA data, Arthropoda was later placed as closely related to nematodes and their allies with strong nodal support (Aguinaldo *et al.* 1997); this placement became known as the Ecdysozoa hypothesis. Whereas previous studies (Field *et al.* 1988, Ghiselin 1988, Field *et al.* 1989, Patterson 1989, Raff *et al.* 1989, Lake 1990, Halanych *et al.* 1995) and even a morphological cladistic analysis by Eernisse *et al.* (1992) that placed Annelida as more closely related to other spiralian taxa than to Arthropoda passed more or less "unnoticed," the paper of Aguinaldo *et al.* (1997) initiated a strong controversy about the conflict between morphological and molecular data. The discussion of this conflict and the quality of both the morphological and molecular data concentrated on the topic Articulata versus Ecdysozoa and, thus, the placement of Arthropoda rather than that of Annelida (e.g., Schmidt-Rhaesa *et al.* 1998, Wägele *et al.* 1999, Wägele and Misof 2001, Zrzavy 2001, Scholtz 2002, Giribet 2003, Scholtz 2003, Schmidt-Rhaesa 2006).

Of the characters supporting Articulata, segmentation is regarded as a key character due to its complexity (Scholtz 2002, 2003). Scholtz (2002, 2003) defined a segment as an anteroposteriorly repeated body unit, which can be defined by a set of substructures occurring together. These substructures per body unit are an outer annulus, one pair of coelomic sacs, one pair of metanephridia, one pair of ventral ganglia with commissures, lateral nerves and connectives (i.e., the rope ladder-like ventral nerve cord), one pair of appendages, and a set of muscles. Strictly applied, several annelid and arthropod taxa would not fulfill this definition.

With regard to annelids, some taxa have no appendages or even chaetae (e.g., Capitellidae, Clitellata, Protodrilida, and Dinophilidae). Coelomic sacs are fused to varying degrees (e.g., Arenicolidae and Tomopteridae). The nervous system shows a high degree of variability affecting all elements of the nerve cord, even possessing a medullary nerve cord or an orthogonal-like organization (Bullock and Horridge 1965, Golding 1992, Hessling and Westheide 1999, Orrhage and Müller 2005, Müller 2006, Purschke 2016). Moreover, segmentation is strongly reduced in several interstitial polychaete taxa due to paedomorphosis (for review, see Worsaae and Kristensen

https://doi.org/10.1515/9783110291582-002

2005, Struck 2006). For further review of the variability of morphological characters in Annelida, see Purschke *et al.* (2014). Similar cases can be shown for arthropods with respect to the nervous system, lack of transitory coelomic sacs, or a different development of the nephridial system (Tiegs 1947, Arnaud and Bamber 1987, Klag and Ksiazkiewicz Kapralska 1989, Schwalm 1997, Mayer 2006, Mayer and Harzsch 2007, Bartolomaeus *et al.* 2009). However, it has been argued that this high plasticity in Annelida and Arthropoda reveals the high complexity of the complex segmentation, as substructures are independent from each other (Scholtz 2002).

On the other hand, other protostome taxa also exhibit a repetitive organization in different organ systems. Kinorhyncha possess repeated body units with an outer annulus, one pair of ganglia, and a set of muscles (Schmidt-Rhaesa and Rothe 2006). Monoplacophora (Mollusca) are repetitively arranged in their musculature, excretory organs, gills, and gonads (Friedrich *et al.* 2002, Wanninger and Haszprunar 2002). Serial repetition in one or more tissues or organs occurs also in several other taxa, i.e., eucestodes, other platyhelminths, Polyplacophora, some nematodes and nematomorphs, and a nemertean (e.g., Westheide and Rieger 1996, Schmidt-Rhaesa 2007). Therefore, from a structural point of view, these bilaterian taxa would fulfill the definition of segmentation by Scholtz (2002, 2003), if the definition is not strictly applied. On the other hand, a strict application of the definition would exclude most of the annelid and arthropod taxa as well. In summary, within Protostomia, as well as within both Annelida and Articulata, serial repetition is exhibited with different degrees of complexity ranging from just one or few organs or tissues being affected to more or less the complete body. Hence, a common origin of segmentation of Annelida and Arthropoda cannot be derived with certainty from the structural components and an independent origin in both taxa is as likely.

Other characters supporting Articulata is longitudinal muscles of the body wall in distinct bundles and the presence of mushroom bodies in the brain (e.g., Westheide and Rieger 1996, Ax 1999, Scholtz 2003). However, these characters also exhibit a high variability in Annelida and thus call their presence in the ground pattern of Annelida or the homology to arthropod structures into question (e.g., Tzetlin and Filippova 2005, Loesel and Heuer 2010). For example, mushroom bodies as seen in arthropods can be observed only in Nereididae and Aphroditiformia. Slightly different or less prominent ones are present in Hesionidae, Nephtyidae, and Phyllodocidae, whereas all other taxa investigated to date show no evidence for mushroom bodies (i.e., Syllidae, Tomopteridae, Opheliidae, Eunicidae, Lumbrineridae, Arenicolidae, Terebelliformia, Sabellidae, and Clitellata) (Heuer *et al.* 2010). However, this character is in need of a more comprehensive and detailed reinvestigation (see Purschke 2016). Furthermore, longitudinal muscles are also concentrated in other bilaterian taxa like Nematoda or Kinorhyncha.

While some cladistic analyses of morphological data recovered Articulata (Meglitsch and Schram 1991, Rouse and Fauchald 1995, Sørensen *et al.* 2000, Nielsen 2001, Brusca and Brusca 2003), others reveal a closer relationship of Annelida to spiralian taxa like Mollusca rather than to Arthropoda (Eernisse *et al.* 1992, Zrzavy *et al.* 1998, Giribet *et al.* 2000, Peterson and Eernisse 2001, Zrzavy *et al.* 2001, Zrzavy 2003). This might be indicative of the homoplasious nature of the characters supporting Articulata as well as Lophotrochozoa and Ecdysozoa. However, the practice of character and taxon selection, character coding and scoring, or usage of exemplar or ground pattern characters for terminals in such studies is controversially discussed and strongly contributes to the differences in these studies (e.g., Jenner 2000, Prendini 2001, Jenner 2004a,b). Finally, the assessment if a character is primarily absent or secondarily lost can be problematic in morphological cladistic analyses (e.g., Purschke *et al.* 2000, Jenner 2004c, Struck 2006, Bleidorn 2007).

The suitability of the 18S rRNA data used in the first molecular studies regarding bilaterian relationships has been criticized, and support for Ecdysozoa been attributed to chance similarity only (e.g., Philippe *et al.* 1994, Wägele *et al.* 1999, Wägele and Misof 2001). However, since then, an impressive array of different molecular markers has been used. None supported monophyly of Articulata, but all favored the placement of Annelida close to or within the lophotrochozoans, although not all recovered monophyly of Lophotrochozoa or Ecdysozoa. This array comprises larger 18S rRNA datasets (e.g., Van de Peer *et al.* 2000), 28S rRNA (Mallatt and Winchell 2002, Telford *et al.* 2005, Passamaneck and Halanych 2006, Baguñà *et al.* 2008, Paps *et al.* 2009b), Hox gene data (de Rosa *et al.* 1999, Balavoine *et al.* 2002, Passamaneck and Halanych 2004, Baguñà *et al.* 2008), mitochondrial genomes (e.g., Boore and Brown 2000, Helfenbein and Boore 2004, Podsiadlowski *et al.* 2009), myosin II heavy chain (Ruiz-Trillo *et al.* 2002), Na-K ATPase α-subunit (Anderson *et al.* 2004), aldolase, triosephosphate isomerase, phosphofructokinase, methionine adenosyltransferase, elongation factor 1α, ATP synthase β chain, catalase (Peterson *et al.* 2004, Peterson and Butterfield 2005, Helmkampf *et al.* 2008a, Sperling *et al.* 2009a), glyceraldehyde-3-phosphate dehydrogenase, histone H3, intermediate filaments, tropomyosin, phosphofructokinase (Baguñà *et al.* 2008, Paps *et al.* 2009a) or dyskerin, vacuolar ATP synthase subunit, carnitine palmytoyltransferase, enolase, RNA polymerase II