

THE SECOND ANNUAL RISER LECTURE: ECLECTICISM AND THE STUDY OF POLYCHAETES

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Abstract.—The study of polychaetes has involved two very different research programs: the morphological and systematic descriptions on one hand and the biological and physiological traditions on the other hand. The two traditions each represent two systems of two different approaches to the study of nature: on one hand structural versus procedural studies and on the other hand process-oriented versus taxon-oriented studies. None of the paradigmatic approaches common in biology (e.g., ecological, physiological, genetic or evolutionary) can solve their own problems by using only one of the four approaches. Understanding the biology of the group can only come from a carefully managed eclectic approach to the study of the group.

During the early part of my career the theory of science always appeared to exist totally independent of what I was doing as a biologist: Biology was something to be done, not thought about. A paper published about 25 years ago (Platt 1964) demonstrated that I had been very wrong; the quality of a study depends crucially on the manner in which it is planned and performed.

Since then I have examined my own and my fellow workers output for signs of an awareness of theoretical issues associated with the study of biology. I have concentrated on the polychaete literature with which I am most familiar. By now more than 200 years worth of papers on polychaete morphology, systematics, phylogeny, physiology and ecology have accumu-

lated, representing more than 10,000 individual papers and books.

In this paper I will review, very briefly, the development of the study of polychaetes. I will then attempt to put this overview into a minimal theoretical context. The results are some rather trivial admonitions. I believe these recommendations to be worthwhile because most of my colleagues still behave as if their activities were theory-independent. If I can set them thinking about these issues, then the purpose of this paper will have been fulfilled.

Early Studies of Polychaetes

Aristoteles reported what might be interpreted as scaleworms in the ocean; Pliny the Older gave a much more convincing description of "marine scolopenders" (Gillet 1988) and this latter report was expanded on by both Rondelet and Gesner (Williams 1851); these "scolopenders" have traditionally been identified as nereidid polychaetes. For all practical purposes polychaetes were first described in 1758 in the 10th edition of Linnaeus *Systema Naturae*. These early reports and the transition into a scientific

The Riser Lecture Series.—In 1985 the annual Riser Lecture was initiated by members, alumni and friends of the Marine Science Center, Northeastern University at Nahant, Massachusetts. The occasion was the official retirement of Professor Nathan W. Riser. As teacher, biologist and founder of the facility, "Pete" Riser endowed the laboratory with a legacy—the importance of considering the whole organism regardless of one's special focus. We dedicate these annual lectures to that principle.

study of the polychaetes is described by Gillet (1988).

Names and descriptions.—The Linnean nomenclature separated names as labels from descriptions and definitions of the organisms studied. For the first time logical procedures known since antiquity could be applied to the description of the living world. One could name an organism and define that label by descriptive terms, independent of the names themselves. The process has been taught as part of introductory classes in logic for a long time, nevertheless, the importance of this first application to biology was overwhelming. The new nomenclatural system made possible intelligible discourse about Nature in a way that no other device, before or after, has done. The practices of the scientists of the period reflected an awareness of the different language levels involved in descriptive processes (Popper 1979). For example, I believe that the use of names of gods and goddesses for genera of various organisms reflects an awareness of the importance of the separation of names from definitions and descriptions. The trivial names, what we now call the species names, often were simple mnemonics: *Nereis virens* for example: the green nereid. *Nereis diversicolor* is another example of this naming tradition.

The descriptions and definitions included morphological features. Microscopes were so primitive that not much more than gross morphological features could be distinguished. However, early illustrations may be remarkably accurate and detailed. Written descriptions uniformly are far less detailed. The early zoologists did exactly what we do: Include sufficient detail to distinguish new taxa from previously known ones. One can hardly blame Linnaeus and his contemporaries for not appreciating how many different kinds of worms would eventually be found, or for not developing the complete terminology for describing their wealth of morphological detail. The first major describers of polychaetes were Danes,

Otto Friedrich Müller (Müller 1776) and Otto Fabricius (Fabricius 1780), Russians, such as Peter Paul Pallas (Pallas 1766) and by the turn of the century the famous French scientists Cuvier, Lamarck, and Savigny.

Reviews and classifications.—Lamarck and Cuvier, independently and in competition, reviewed all polychaetes described, sorted out, and named a whole series of new higher taxa, especially genera and families (Lamarck 1816, Cuvier 1817). Another famous French worker, Savigny, had made most of the new observations and descriptions. He was a careful observer with a fine eye for finding differences among similar forms (Savigny 1820). Lamarck added considerably to our understanding of the relationships among the polychaetes. Also his separation of the polychaetes into two major groups, those with red blood and those with white blood, revealed an interest in physiological properties of the organisms. Nevertheless, more of Cuvier's morphology-based system has been retained than of Lamarck's.

Detailed descriptions of newly discovered polychaetes became divorced from the time in which they were penned. The descriptions have increased in detail and length from one or two lines to several printed pages, but we still use most of the terminology and the overall pattern of descriptions established by Audouin and Milne Edwards in a study of the French fauna in the early 1830's (summarized in Audouin & Milne Edwards 1834).

The system used by Audouin and Milne Edwards closely resembled the Cuvierian system and formed the base for all workers over the next 20 years. By 1850 however, the emphasis of exploration shifted to Germany: Adolph-Eduard Grube (1850) issued a major review of the polychaete families and this paper was the standard for the next 15 years.

Two scientists working in Stockholm made the next major advances in the mid 1860's. Kinberg reported on his worldwide

travels and Malmgren detailed the North Atlantic and Arctic Ocean faunas. These two scientists represent two very different approaches to descriptive science. Kinberg briefly described species collected on the cruise of the *Eugenie* around the globe and added numerous new taxa at all levels (Kinberg 1865, 1910). Malmgren's (1867) studies were intensive; he focussed his attention on a much smaller area and carefully reviewed all previous work before committing himself to describing a new taxon. This difference in approach closely matches a perennial difference among descriptive biologists; among modern systematists Gesa Hartmann-Schröder and Olga Hartman both have used Kinberg's approach, whereas Marian H. Pettibone more closely matches Malmgren. I have done a bit of both.

Kinberg and especially Malmgren did their best to increase the consistency in use of terms and in the amount of detail required for adequate descriptions. Quatrefages (1866) issued a large-scale review of the whole annelid fauna as he knew it. Perhaps more pedestrian a systematist than the others mentioned, he nevertheless became extremely influential, due in part I believe to his location: he was in Paris, and had a long history of publications on polychaetes by the time he issued his magnum opus. Kinberg had published a few earlier papers, but neither he nor Malmgren ever issued any additional major contributions to the study of polychaetes. They both left science shortly after the papers mentioned were published.

Ludwig Schmarda is one of the more colorful persons in the history of polychaete studies. He travelled around the world in the 1850's, not in an exploring vessel, but by hitch-hiking on commercial sailing vessels. His description of his trip from South Africa to Australia is singularly harrowing, including very bad weather, seasickness, scurvy and assorted other diseases. In Chile he lost his collections to a fire on board; in Panama he was robbed by some rather un-

savory characters who made their living by preying on people going from the U.S. east coast to the west coast via the Isthmus. Despite the loss of his collections, he published a large report (Schmarda 1861) that apparently was largely overlooked by his contemporaries. This was probably in part due to the increasing standards of descriptions and illustrations. Schmarda's effort was, however, the earliest worldwide tropical survey of polychaetes. He described a large number of new species for which there are few types available and poor locality information. At that time, there was no requirement that types should be deposited anywhere: Descriptions were considered adequate evidence for the presence of a new taxon. However, the first Nomenclature Code, and perhaps just as importantly, the first volume of Zoological Record, was issued in 1864.

The morphological tradition.—The morphological tradition, outlined above, has continued through the work of McIntosh (1885), Fauvel (1923, 1927), and Augener (1918), and is now followed by most practicing systematists. The total focus of this tradition is very limited in the kind of evidence deemed acceptable. Most systematists will accept only features that can be seen either with the naked eye or with stereo or compound microscopes as valid taxonomic characters. Furthermore, a tradition among polychaete systematists suggests that all reasonably well preserved specimens, especially anterior ends, should be identifiable to species. I have more than once heard complaints from well known systematists that a published description was too difficult to use, or was impractical, because it used information not readily available using minimal technical equipment, or required the presence of complete specimens. This tradition is clearly at odds with, for example, students of isopod crustaceans who for years have accepted limits on the identifiability of all specimens.

The biological tradition.—Another tradition in the study of polychaetes dates back

to about 1850. Thomas Williams (1851) published a major review of the biology and physiology of the polychaetes. This summary is now rarely quoted; it has been superseded by more recent reviews, but it was important historically because Williams reviewed all information available about the life of all worms known to science. Some of the data quoted by Williams date back to Lamarck and are speculative rather than observational in nature and some rather quaint notions were paraded only eight years before the publication of Darwin's *Origin of Species*. Williams made some original physiological observations on various English polychaetes.

The most impressive of the early polychaete biologists was Eduard Claparède, a rather tubercular-looking Swiss, who did most of his work in France and Italy (Claparède 1854). By 1865 he had gotten into a rather virulent quarrel with Quatrefages over all of Quatrefages' new taxa, defined in many cases without access to any material (Quatrefages 1865a, Claparède 1865, Quatrefages 1865b). Claparède emphasized the importance of observations on live organisms; Quatrefages by that time had become very collections-oriented. This difference in approach formed the background for the disagreement. Claparède, true to his principle, deposited no specimens in any museum, making many of his new taxa difficult to define accurately.

The second tradition was biological in nature: studying live organisms and making observations of the live processes, such as reproduction, development and feeding. These kinds of observations were difficult to quantify in an age of poor mechanical recording devices, no photography to speak of, and certainly no electronic recording devices. Additionally, statistics had not yet developed to the point where repeated samples were taken. The studies were therefore often episodic in nature, and observations were only rarely organized into tables or other means of presenting large, easily sur-

veyed data. The kinds of observations attempted by Claparède are still difficult to document for theoretical reasons that I will touch on below.

Claparède combined his studies of live organisms with a detailed study of microanatomical structures. These studies are excellent and are still the best starting point for any anatomical studies in the groups he covered. Claparède's illustrations are among the best ever published on polychaetes. 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. He also demonstrated that detailed anatomical and histological studies yielded systematically distributed information, which could be potentially useful in systematics.

Ehlers tried to combine the two traditions in his massive publication "*Die Borstenwürmer*" issued in two parts (Ehlers 1864–1868). Some of his descriptions of new taxa run 10–15 printed pages, accompanied by one or two full packed plates of illustrations. Consequently, Ehlers succeeded in going through less than $\frac{1}{3}$ of the then known polychaete taxa in roughly 700 pages of text, but for the groups he covered, his volume is absolutely indispensable. Ehlers' research later devolved to thoroughly traditional, morphological descriptions. I can find no evidence in any of his publications that he attempted to complete the massive study he had started.

The study of live polychaetes eventually developed into a tradition of physiological studies, based usually on members of relatively few families with highly characteristic, often unusual physiological patterns. These studies are often performed by process-oriented rather than by comparative scientists. Reproductive studies, while covering in part members of most groups, have been focussed on eunicids, nereidids and syllids (Schroeder & Hermans 1975); studies of respiratory and blood physiology on glycerids, terebellids and scattered other

groups (Dales 1969, Florkin 1969). Studies of regeneration have focussed on sabellids with few glances in other directions (Needham 1969). Genetic studies have been done on dorvilleids and little else (Åkesson 1982). Neurophysiologists have studied the properties of the giant nerve fibers in sabellids of the genus *Myxicola* with very little concern for the biology of the organism at all. There are about 80 families of polychaetes and of these at least 60 are common in shallow water and relatively readily available; nevertheless live studies have focussed on a few popular groups and usually on only one or a few species in each group at that.

The results of the biological and physiological studies have been very valuable, but less as a comparative study of polychaetes than as an exploration of various biological and physiological mechanisms.

Theory and the Study of Polychaetes

The rather conservative descriptive tradition continues among polychaete systematists; for each advance in morphological or anatomical technique, traditionalists hang back, not wanting to get involved with new methods or add new features to the descriptions. Often the young turks among polychaetologists are traditionalists in the study of other groups of organisms, especially vertebrates. Very few of the scientists closely associated with the study of polychaetes have demonstrated strong theoretical interests. For example, it is difficult to find any reference to evolution, or to Darwinian or anti-Darwinian thinking anywhere. Ehlers' publication from 1864–1868 gave no indication of a major revolution in biological thinking taking place at the time. McIntosh (1885) mentioned nothing about phylogeny in his treatment of the *Challenger* polychaetes. One outstanding exception is E. Meyer, who in his studies of polychaetes indicated a good, often anticipatory understanding of biological theory (Meyer 1890). This paper is frequently quoted in the literature on phy-

logeny of the invertebrates, but not often by polychaete taxonomists.

Some of the developmental biologists associated with the study of spiral cleavage at Woods Hole Marine Biological Laboratory used polychaetes for their studies. These scientists had deep theoretical interests and showed great skill in using the polychaete material in clarifying theoretical problems (Wilson 1898, Treadwell 1901).

The reason for the lack of theoretical and one might say scholarly interest in the study of polychaetes is relatively easily found. Most scientists published only a single paper on polychaetes and very few made the study of these animals their lifetime occupation (Reish 1958). Through about 1950, the study of polychaetes was a relatively leisurely pursuit. Even in most early benthic ecology studies (Petersen 1911, Blegvad 1930), few polychaetes are mentioned or named, except to family. In morphological studies, the annelids were considered a stepping stone to the arthropods (Hanström 1928, Binard & Jenner 1928, and the discussion of the anterior nervous system of the annelids and arthropods) and thus of interest insofar as they showed the step-wise advance to the conditions present in the arthropods. Parenthetically, papers that treat polychaetes well from a theoretical point of view were, with few exceptions, written by scientists with a limited experience in the group (Hanström 1928, Hatschek 1893). This generalization is far less true today than it was before WWII.

The rapid development of interest in benthic ecology following the publication of Thorson's (1957) review of the topic led to considerable change in attitude. Polychaetes have turned out to be extremely common in the marine benthos; benthos ecologists have changed their attitudes towards the importance of polychaetes with the mesh-size of their screens. Further, modern ecologists are aware that no questions can be answered by studying only a few "representative" organisms, usually se-

lected among "easily identified" organisms, such as some crustaceans, echinoderms and mollusks, as done in the early days of benthic ecology.

Simple thoughts on theory.—Organisms may be studied in four different ways, which may be organized into two systems of two. First, one may either attempt to describe the structural characteristics of an organism, or one may study interactions among structures in time or space. The other system of classifying observations describes the investigational intent. One may study the same process in a variety of organisms; or, alternatively, one may study a variety of processes and structures in the same kinds of organisms.

Structural descriptions historically started with external morphology, and proceeded via internal anatomy to microscopic anatomy in all its phases. Structural descriptions deal with the material presence of anything, including atoms and subatomic particles. In gross morphological descriptions the unaided eye is used; all other descriptions are based on interpretation of images created by various pieces of gear: microscopes of all kinds, meters and dials and color-reactions, spectrophotometers, or small patches of color on a starch gel. The more highly magnified the analysis becomes, the more remote the interpretation of the findings become from normal human experiences, but, at least in theory, no different from observations of gross morphology. In some sense, interpretation becomes easier with increasing magnification, since the higher magnification allows a far more precise use of language in describing limiting conditions than do observations of a morphological or anatomical nature.

Natural historians and some physiologists (a subgroup of the comparative and ecological physiologists) seek a completely different kind of information about organisms, information which we have had a great deal of difficulty entering into our structurally derived patterns. All organisms change

with time and all structural landmarks change in relation to each other during ontogenesis, presumably in an organized fashion, but not necessarily in the same pattern even in genetically similar organisms. Information derived from these changes is as much an expression of the genome of the organism as is the structural information. I am aware of the problems including this kind of information in our descriptions will create, but I believe that until we do, we will fall short of understanding the organisms we are studying. Computerized modelling may offer help in creating testable predictions for such studies.

The other system of groupings of study is familiar to most scientists, especially in technically more complex fields. Scientists become experts on the use of a single technique: transmission and scanning electron microscopes, enzyme electrophoresis, DNA hybridization and so forth and will investigate the limits of what the technique can do. The results of this approach have been excellent and have led to major advances in our understanding of microstructures and various processes.

The other major way of looking at the organisms is as a specialist on a single animal group; a taxon-oriented person. Such a person may be eclectic in their use of techniques, but will rarely add to the development of new techniques. These biologists often have a better understanding of the evolutionary significance of differences in processes among the organisms studied than the process-oriented scientists, but are usually rather parochial in their view of the world. A polychaete's-eye view of the globe is limiting in many ways.

These four ways of studying organisms do not agree with the traditional breakdown of specialities among biologists. Taxonomists, while primarily concerned with description of structure, frequently resort to adaptive explanations. Physiologists, while exploring functional issues, base themselves in knowledge of the structures involved in

the particular processes studied. Perhaps most confused are the activities that are now subsumed under the heading of ecology. In part, ecologists describe structure in their case patterns of distribution of organisms in nature, but usually use functional explanations for the patterns demonstrated. The separation of the two modes of thinking is not trivial, but is built into the language. Ideally a language describing structure should use only shape and position words; in practice we use such words as "branchiae" and "notopodial cirri." For trained taxonomists and morphologists the usual meanings of these words have become trivial: they are using both words as shape and position markers. However, notopodial cirri, usually slender, often very long cirri projecting from the dorsolateral sides of the worms, often appear to be as much respiratory as sensory in function.

Eclecticism and the study of polychaetes.—Thus an adequate description of any polychaete would require a rather eclectic collection of pieces of information, both static and dynamic.

Most structural descriptions of polychaetes now include a minimal mention of major morphological features. At least one species of most families have been studied anatomically, at least at the light microscope level. Very few truly comparative studies have been performed within each family. Comparative studies among the families are rather common, but without knowledge of how much variation to expect within each family, the interpretation of such comparative studies will always be difficult. Microanatomical studies are becoming rather more common, but again, with some very salutary exceptions, have focussed more on the relations among the families. Other studies, with both structural and functional components, are mentioned below.

Studies of comparative physiology have given us important information about the interactions among the structures, e.g., studies of mechanisms of respiration among polychaetes. However, most physiological

studies have been focussed more on elucidating process and are for that reason usually not very useful for comparative purposes. Most life history studies published so far include an account of parts of the larval development and metamorphosis into a postlarvae, but little about the rest of the life of the organisms, including longevity (Fauchald 1983). The bits we have are interesting, but are insufficient for all species.

I am advocating eclecticism because I believe that this approach will force us to change our approach to our studies. Currently we learn one, or perhaps a few, techniques and then proceed to apply these to all problems, whether the application can solve the problems posed or not. The investigative technique and the detail sought must depend on the question asked, rather than the other way around. For example, it is not always useful or necessary to identify organisms to the species level in a benthic investigation. The first step in planning a study therefore must be to question the purpose of the investigation. If the purpose is an exploration of the area—a study of which organisms are present in what quantities—then identification to species is not only desirable, but the only way such information should be presented. But if the purpose is to investigate feeding biology or perhaps trophic structure, in addition to giving a listing of taxa present, at the very least as much effort must be put into investigation of gut contents and mechanisms of feeding, as into the identification of the specimens. Most investigators now identify their organisms (more or less accurately) and then quote some authority for the other information needed, e.g., feeding physiology. For the polychaetes, most quote Fauchald & Jumars (1979), an inappropriate source of information for this purpose. The Diet of Worms was written as a summary of what little information was available in the mid 1970's and was intended to spur investigations: It has apparently done so, but sufficient information is still not available for any species to my knowledge.

Polychaetes are valuable for a variety of studies. Polychaetes are ubiquitous and common in all marine environments. The numbers of polychaete taxa is large enough to allow the use of the statistical data reduction, but is not as overwhelming as in some other groups. Most major subgroups have morphologically very strict body plans and can be identified to family by rank tyros.

The group is very old (Fauchald 1984) and the major body plans were laid down a long time ago: We can in the polychaetes investigate current evolution of ancient body plans. For example, the eunicids are very uniform in general morphological appearance; in fact, the jaws have not changed much since Palaeozoic times. Nevertheless, a preliminary numerical study of about 300 individuals of approximately 12 species (Fauchald 1989) demonstrate several different patterns of growth and of control of the body proportions, implying rather different physiological properties, perhaps related to the maximum absolute size of each species.

The consequences of the studies of Grassle & Grassle (1976) and Eckelbarger & Grassle (1987), to mention only two of a series, are fascinating. They have given us a view of a worldwide group of small, ever-changing populations of capitellids becoming isolated, perhaps going extinct locally, perhaps meeting up again before, or after, completing a speciating process—in short, a complex mosaic.

Chromosome studies of various polychaetes indicate that ploidy relations may play a more important part in evolution in polychaetes than previously expected; perhaps leading to a reconsideration of the importance of the various processes in the evolution of animals.

An eclectic approach may thus complete the transformation of the study of polychaetes from an intellectual backwater to the forefront of biology.

Some final notes.—I agree with my alter ego of 25+ years ago that theory of science

exists with little reference to what I do on a day to day basis. I have come to the realization that this is perhaps the way it ought to be. If the theory of science was strictly a description of what scientists do, then one could not expect discussion of normative rules. We all use theoretical constructs in even the simplest observations. The belief in theory-independent observations appears now on the wane. Philosophers of science study and perhaps build into systems the theories behind our observations and make us as working scientists aware of these constructs. Without the precision in thinking and data definition theory enforces, very little advance is possible.

A significant fraction of current papers are routine descriptions of a few new taxa, usually with a review paper as authority for the separate status of the new taxa; the material examined is minimal and comparison with types of previously described species is rare. If current theory and methods were applied to these studies, I am convinced that the deluge of new taxa would slow down. Most of the new taxa are collected during quantitative investigations and the authors do not have the luxury of performing a complete and detailed review of the family or genus of interest before publishing a new taxon or two. Detailed and rigorously performed reviews of previously described taxa are lacking for nearly all polychaete families and very few are now on the horizon. Most of the investigations in which the bulk of new material is collected have poorly, or inappropriately defined, goals; however, one requirement runs through most of them: No matter what the stated purpose of the investigation is, the organisms collected must be identified to species. This requirement forces the researches to make rapid, often incorrect decisions. A careful definition of study goals would leave both ecologists and polychaetologists happier and the few polychaetologists working full time on polychaete taxonomy less overwhelmed.

There is little support for all the other kinds of studies needed to describe and study

polychaetes adequately. The result is that most of the polychaetologists are limping along, without being able to do even the necessary revisory work, and certainly without being able to apply theory or attempt to add truly new information to our descriptions of polychaetes. A rather sad conclusion, but I believe one in which experts on other groups also would concur.

Acknowledgments

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I would like thank the committee, Drs. M. Patricia Morse, Joan Ferraris and Jon Norenburg for giving me the opportunity to give the lecture. Dr. Leonard P. Hirsch read and rejected several versions of the paper, for which I am now very grateful; what makes sense in this paper is due to my friends; what appears hare-brained is my own responsibility.

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