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[REVIEW]

Thirty-five Years of Nemertean (Nemertea) Research—Past, Present, and Future

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Developments in nemertean research over the last 35+ years are reviewed from a systematist's perspective. Nemertean systematics and classification, until fairly recently, was not based on explicit phylogenetic hypotheses, but rather on subjective assessment of "important characters". The first cladistic analyses appeared in the 1980s and were criticized at the time by leading researchers in nemertean systematics for not taking into account convergent evolution in ribbon worm morphology. The first molecular study involving the phylum Nemertea appeared in 1992, followed by reports later in the 1990s and early 2000s. Molecular information is now commonplace in nemertean research, and has changed our understanding of evolutionary relationships within the phylum, as well as our view on species and intraspecific variation. Challenges in nemertean systematics and taxonomy are discussed, with special emphasis on future species descriptions, and how to deal with a number of species names that in all likelihood never will be encountered again. Suggestions for how to deal with these challenges are discussed.

Key words: Nemertea, systematics, taxonomy, phylogeny, history

INTRODUCTION

Zoological (and botanical) taxonomy and systematics has a long history, and can be traced back to Aristotle (born 384 B.C.), while naming and grouping of animals has an even longer history still. For a long time, biology (or more correctly, natural history, since the term "biology" was first used in the modern sense by Lamarck in 1802) equalled taxonomy, classification, and descriptions. When I undertook my undergraduate studies in zoology in the beginning of the 1970s, biology was still very much about classification and morphology, while ecology had just recently been introduced in the curriculum. Ecology teaching in those days (at least in Sweden) was about classifying nature into various "communities", and in that sense resembled systematics as it was, and had been, carried out. If nemerteans were mentioned in ecological papers at that time, it was as part of a species list from sampling sites. Nemertean research was in those days, with few exceptions (e.g. physiology, toxins), about taxonomy and systematics. Early papers on nemertean ecology include authors such as McDermott, Nordhausen, Roe, Thiel, and others (e.g. McDermott, 1976; Roe, 1976; Nordhausen, 1988; Thiel and Reise, 1993). These were in the area of community ecology, but papers on evolutionary ecology also appeared, including two on aposematic coloration by Sundberg (1980, 1987).

Here, however, I will focus on the developments and trends in nemertean systematics and taxonomy, and what has happened during the 35 years I have been active in nemertean research. Much of the discussion will reflect my personal views, and is influenced by my own experience. However, the trends seen in nemertean systematics follow a general pattern in systematic research, although there are parts a little more specific to nemerteans, and possibly to the people who have been involved in this process. I will end with a section on challenges for the future, and what is needed to solve some major (as I see it) problems with nemertean systematics and taxonomy.

NEMERTEAN SPECIES DESCRIPTIONS

Every taxonomic group has its own standard and culture when it comes to how species should be described—some of these standards are consequences of the animals themselves (obviously external characters are more problematic for nematodes compared to polychaetes), but much is also due to a culture developed in the groups by active researchers. Species descriptions have not, to the same extent, changed due to technological advances, as for example phylogeny estimates by the advent of molecular techniques. Species descriptions from late 18th and early 19th centuries are commonly short and concerned only with external characters. But advances in microscopy, and microtomes and sectioning techniques, made internal characters more accessible. As a result, we see more detailed descriptions appearing in mid 19th century with plenty of internal features illustrated, described, and used in discussions about classification and phylogeny (e.g. McIntosh, 1873–1874;

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Hubrecht, 1887; Bürger, 1895). Still, their descriptions had not yet taken the shape and format we see in current taxonomic literature. The early 20th century nemertean taxonomy was dominated by the work of W.R. Coe (USA). Coe published over 60 articles on nemertean biology, and described many new species, but still did not fully describe internal characters to the extent that the European taxonomists H. Friedrich and G. Stiasny-Wijnhoff did later in the century. The standard for species descriptions in the latter part of the 20th century was set by R. Gibson from the U.K. Gibson started his career in morphology and physiology rather than taxonomy and systematics, but beginning in the early 1970s he increasingly focused on taxonomy. His (and co-authors) approach took a standardized format with descriptions of external characters followed by descriptions of organ systems. One early paper by Gibson (Gibson, 1973) describing a new littoral hoplonemertean from Brazil is a good example of how many of these descriptions would look like. The papers then ended with a discussion of the systematic position of the species (see below). This format was followed by many fellow nemertean researchers, and is still considered the standard in nemertean taxonomy for a description to be accepted when naming a new species.

There are some obvious problems with morphological descriptions, besides purely technical like how to avoid sectioning contracted animals. One is how characters are defined; do two authors mean the same with a term such as "elaborate cerebral organs"? This problem became evident when Sundberg (1989a, b) presented the first cladistic analyses of nemerteans, coding characters from papers by Moore and Gibson (1972, 1973, 1981, 1985, 1988) as the basis for phylogenetic analyses. Moore and Gibson (1993) criticized the resulting trees, one criticism being my misinterpretation of characters. For example, when Moore and Gibson had described the cerebral organs in two *Pantinonemertes* species, and *Geonemertes* species as "elaborated" (and coded by Sundberg as such in the cladistic analyses), they were in fact "elaborated in completely different ways" (Moore and Gibson, 1993: 94). This is just one example showing the need for standardized descriptions of nemerteans, where morphological characters and character states are clearly illustrated and defined. Another reason for standard descriptions is to eliminate the problem of knowing whether a particular character, or character state, is missing, if it has not been checked for, or just not mentioned in the description. The need for a standardized approach to nemertean descriptions was already discussed in Gibson (1985) and presented at the first international nemertean meeting. The issue was also discussed at later meetings, and Hylbom (1993) suggested and defined characters and their states to be included in palaeonemertean descriptions. Sundberg et al. (2009a) took the concept of standardized descriptions further, with an extended list of characters, and attempted to clearly define the characters and their states. This matrix of characters was also used in the same paper to describe two new species, thus without the need to describe each organ system in detail in the running text, but instead referring to a table. The underlying idea with this matrix was also to make it easier to extract characters for phylogenetic analyses. Furthermore, it was also meant as a checklist for future description, thus clearly stating if a character/character state is missing if not mentioned, or if it is a matter of not having been able to observe it. This paper was meant to act as a guide for future taxonomists when describing new species. This character matrix has been used in subsequent descriptions (e.g. Taboada et al., 2013; Strand et al., 2014) and appears to be gaining acceptance although critical voices were raised during the publication procedure of Sundberg et al. (2009a). One of the reviewer's main concerns was that such a character matrix should be web-based and allow everyone to add and refine the matrix. A paper-based approach has (according to the reviewer) "very significant ontological and mechanical shortcomings (…) especially as it is not built on a community consensus—hence, no stability can be assumed." I agree that it would have been better if we had been able to reach this consensus, but efforts in this direction during some of the first nemertean international meetings were unfortunately not followed up.

PRE-CLADISTIC NEMERTEAN SYSTEMATICS

There had been a few papers discussing the intraphylum systematics and phylogeny in the 19th and early 20th century, but in the late 1970s nemertean systematics was mainly concerned with taxonomy and describing new species. Wijnhoff (1912) published a paper on nemertean systematics and classification where she argued that the current classification (from Bürger) was not phylogenetic, but just a description of the evolution of the nervous system. Stiasny-Wijnhoff (1936) later suggested the classification of "higher" taxa that is still in use but with renamed ranks in some cases (Sundberg, 1991), to make them consistent with current systematic practice, and with some additional changes (Thollesson and Norenburg, 2003; Andrade et al., 2012). Iwata (1960) introduced Archinemertea, a third taxon within the Anopla, but later studies have shown this to be equivalent to Cephalotrichidae, making Palaeonemertea, a paraphyletic group, and the name is no longer in use.

When it comes to less inclusive taxa, such as genera and families, nemertean systematics is clearly problematic for taxa constructed on non-phylogenetic grounds. All classification efforts until the end of the 1980s were based on subjective assessments of the "importance" (in a supposedly phylogenetic sense) of certain characters. At that time, it was common to discuss (not just in nemertean systematics) characters to be at the "family level", or "genus level", thus defining these taxon levels. The "importance" of characters was in general an issue in the nemertean literature up to the beginning of the 1990s. A few citations from Crandall (1993) are representative of the systematic practice of some of the leading nemertean taxonomists of the time period. "It is with those characters significant at the generic and higher levels that this discussion is primarily concerned. However, a number of features given in older descriptions, now regarded as minor characters, are still valuable in distinguishing between species within genera" (Crandall, 1993: 115). In that paper, Crandall evaluates different organ systems and then makes conclusions such as: "Seems well established as a character at the generic level, and in some cases, perhaps is applicable at the family level. I think the conclusion must be that the details of the septum, while very useful at the specific level, should be used with caution at higher levels" (Crandall, 1993: 125). Gibson (1985: 12) is also an example of the kind of

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systematic thinking in those days. Gibson concluded that, "the only character which can presently be used to reassess the groupings of heteronemertean genera into families is the arrangement of the proboscis muscle layers." In addition, he also speculates which is the primitive arrangement and from there he classifies genera into a number of families. Gibson (1985) is based on a presentation at the first international meeting on nemerteans in Philadelphia 1983. In the same volume, Iwata (1985) proposed a suggestion for the higher classification of Nemertea based on embryology. This paper is also an example of the view of evolution as moving from "primitive" to "advanced", and how this is used as basis for classification and systematization.

The systematics of Nemertea was, and still is, problematic with taxa "above" a specific level not being identified by synapomorphies, and many (most?) names do not refer to monophyletic groups. Certain genera really are "catch-all" names (like *Lineus* and *Tetrastemma*) where clearly unrelated species have been placed in for convenience (Strand and Sundberg, 2005). To avoid this, the current trend is to form monotypic genera to avoid mistakes caused by vague generic diagnoses. According to Strand et al. (2014) more than 60% of nemertean genera are monotypic, while there are a few that include hundreds of species. The situation is no better at family level, and family diagnoses are equally vague and undefined in a strict phylogenetic sense. The intraphylum classification at these levels is essentially still a matter of a one-dimensional placement of species in boxes based on their resemblances and lacks the second dimension of a time axis, i.e., the phylogeny.

Gibson and collaborators (especially J. Moore) developed an approach used to place new species in genera; I have referred to this as the "unique combination-of-characters" (Sundberg, 1993) fallacy. It followed a reasoning and procedure that can be described as follows: The species in question was thoroughly described from a number of characters. A systematic discussion followed at the end of the paper, accompanied with a table including a selected number of characters listed for supposedly related species. Based on this table, a systematic conclusion was drawn which typically can be exemplified by this citation "Table 1 shows that this combination of characters enables the present form to be excluded from all the known taxa (…) and is accordingly placed in the new genus, *Alaxinus*" (Gibson et al., 1990: 196). Besides the logical problem of getting an increasing number of unique combinations with increasing numbers of characters included, thus leaving us with more taxa—and indeed eventually every specimen could be placed in a separate taxon with a large number of characters (e.g. DNA sequences)—there are also problems from a phylogenetic point of view. This was pointed out, and argued, in Sundberg (1993) and I will not reiterate the arguments in detail here. I will just emphasize that this approach is essentially non-phylogenetic, is logically flawed, and should be abandoned if we wish to put names to monophyletic groups, and not just any arbitrary grouping of nemerteans.

Gibson (1988) is probably the first attempt to base a classification of nemerteans in a more explicit phylogenetic (in the modern sense) framework. However, this is still based on single characters in the tradition of a subjective assessment of what characters are primitive/derived, and educated guesses about homologous character states. It has repeatedly been argued that mere similarity cannot be evidence for homology, but this has to be analysed within a phylogenetic framework, using several characters in concert to hypothesize about possible homologies. Sundberg (1990) later showed that the suggested classification could not be confirmed by a cladistic analysis. Gibson's classification did not gain acceptance, and is not used in current nemertean systematics.

CLADISTIC ANALYSES OF NEMERTEAN RELATIONSHIPS

The papers of Sundberg (1989a, b) were the first to apply cladistic principles to the classification and systematics of nemerteans. The two analyses were based on characters in papers by Moore and Gibson (1972, 1973, 1981, 1985, 1988), the main reason being these were very thorough descriptions, and covering essentially the entire groups (as they were known). The revision of *Geonemertes* was also highlighted by Gibson (1985) as having been based on "a standardized approach to descriptions of the species' morphology" (Gibson, 1985: 7), which he considered to be of particular value in this revision. However, these cladistic analyses met a lot of criticism from Moore and Gibson, the main argument being that my interpretation of their characters were incorrect; evidently the "standardised approach" was still open to personal interpretations. This is also one of the underlying reasons for suggesting the character matrix approach in Sundberg et al. (2009a) discussed above.

Another reason for the criticism was that cladistics is particularly vulnerable to convergences: "Cladistics (...) rests on the assumption that convergence is a rare event" (Moore and Gibson, 1993: 91). Additionally, since convergence "is widespread amongst marine nemerteans" (Moore and Gibson, 1993: 99) this would render cladistic analyses unsuitable for nemertean systematics according to Moore and Gibson (1993: 100). Moore and Wilmer (1997) took the concept of convergences further, using it to claim that cladistic analyses in general is inferior when it comes to classifying animals into natural groups. Much of the criticism was unfortunately based on several misunderstandings including the Hennigian principles, cladistic analyses in general, and the principle of parsimony in particular. The criticism did not, however, stop nemertean systematists from turning to cladistic and phylogenetic analysis and classifications based on monophyletic groups. Even those nemertean researchers who originally argued quite forcefully against cladistics, later used this approach in their work (e.g. Crandall, 2001). The phylogenetic approach is now standard in nemertean classification and the "traditional" (*sensu* Moore and Gibson, 1993: 100) method is no longer in use. The consensus among active nemertean systematists is that classification should be based on phylogeny and the first step in that process is to estimate the phylogeny. Although there have been attempts to do this based on morphology, the advances in molecular biology have—if not completely superseded it—made morphology less important in phylogeny estimation. This is essentially due to the problems and time involved in obtaining good morphological data, and the limited number of informative morphological characters compared to molecular data.

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CURRENT NEMERTEAN SYSTEMATICS AND THE INTRODUCTION OF MOLECULAR DATA

While technical developments as to descriptions and morphology are few (but see Chernyshev (2010) and use of confocal microscope), the situation is completely different when it comes to phylogeny, and phylogeny estimation. We are essentially still using basic light microscopy in morphology (electron microscopy has not gained any strong position in species descriptions and taxonomy in nemertean taxonomy/systematics), while the image processing is mostly now digital. In phylogeny, however, the situation is different. The first cladistic analyses mentioned above were based on morphological characters and parsimony analysis. Electrophoresis data were the first non-morphological characters used in nemertean taxonomy. Williams et al. (1983) used isoenzymes to analyze closely related *Lineus* species. Sundberg and Janson (1988) analysed the supposedly intraspecific variation in *Oerstedia dorsalis* (a species well known for its extensive polymorphism in external characters) and concluded that one of the forms was in fact a separate species (*Oerstedia striata* Sundberg, 1988). A.D. Rogers has used enzyme electrophoresis in a series of papers (e.g. Rogers et al., 1993) to analyze species delimitations and population genetics in nemerteans. However, no one has used this kind of data for phylogeny estimation. Molecular data, on the other hand, was used straight from the start to analyze phylogenetic relationships. The first study of nemertean relationships using molecular data was that of Turbeville et al. (1992), which analysed the position of nemerteans among metazoans. The first within-phylum study was that of Sundberg and Saur (1998) which inferred relationships among some heteronemertean species, using the mtDNA 16S rRNA gene sequences. Since then, several studies have incorporated molecular data to solve taxonomic (e.g. Chen et al., 2010) as well as systematic questions (e.g. Andrade et al., 2012, 2014). The latter two papers are the result of the first truly international collaboration to resolve the intra-phylum phylogeny and systematics of the taxon.

The advent of molecular data—the evolution of these data is generally considered easier to model—also changed the way phylogeny was reconstructed, and also the terminology. From having been “reconstructed”, phylogenies are now “estimated,” and the analyses are currently considered to be more of a statistical problem. Parsimony analyses appear to be more and more connected to studies based on morphological data, while molecular-based studies use maximum likelihood and/or Bayesian analyses. The same trend is seen in nemertean systematics.

While I am confident that molecular data have given us better tools for reliable phylogenies, and thus classifications, we have not witnessed much progress as to phylogenies at less inclusive levels like families and genera. Nemertean systematics/classification is problematic at these levels. There are many clearly undefined genera and families and, as mentioned above, genera such as *Lineus*, *Cerebratulus* and *Tetrastemma* are really no more than catch-all groups into which species with some superficial similarity have been placed. In this situation of undefined genera, it is tempting to place a new species in a new genus (the zoological code and the naming system requires a genus name) to avoid mistakes. The number of monotypic genera is high in nemertean classifications (like in most phyla) (Strand and Panova, 2015), and this is maybe something to consider for future systematists working on the group. I hope that classifications will be based on increasingly better and more robust phylogenetic hypotheses, and that genera are revised in connection to this. Classification at family level is even worse, and the current definitions are not based on any phylogenies; furthermore, in many cases they are difficult to distinguish from each other when the diagnoses are critically scrutinized.

FUTURE CHALLENGES

Biological organisms need names for many reasons. One reason, and this is something that has become increasingly important, is the need to identify and correctly distinguish species in databases. And in that case it does not work to call species Genus sp. 1, sp. 2, etc., which is a common practice in cases where authors, for various reasons, do not want to put names on species they have found. One reason for the reluctance to construct new names is certainly attributable to the current procedure to describe a nemertean species, which has become the “standard” and a necessary requirement by some reviewers. By this procedure, I refer to the detailed descriptions of external and internal characters, the latter only accessible through histological sectioning. Sundberg and Strand (2010) have argued against this, and here I will only point to the main problems. First, histological sectioning is time-consuming, and requires special equipment, competence, and training. Today, it is difficult to attract students to do this kind of work, and detailed morphology has little acceptance in research council applications unless coupled to broader questions. The alternative, the use of technical staff for this kind of routine work, is not a reality with shrinking research budgets in many departments. The kinds of basic funded resources (technical staff and consumables) that once were common in academic departments are now dependent on external grants, and therefore less available in many, if not most, institutions. Secondly, characters are often quite difficult to interpret from sections, and require both very well preserved specimens to be reliable along with the skilled experience of the interpreter. Intraspecific variation furthermore confuses the taxonomic interpretation of the characters, something pointed out by e.g. Sundberg (1979). Strand et al. (2014) also showed that even with good sections and skilled interpreters, morphological characters are not a panacea for good taxonomy, as is often stated in nemertean literature. One of the myths, repeatedly stated, is that nemerteans can only be securely identified from internal characters (see e.g. Gibson (1985)) or as stated by Roe et al. (2007: 221): “Identification of most nemertean species is difficult and time-consuming, usually requiring study of internal anatomy by means of light microscopy on serial sections”. First, I would say that external characters could identify many species. Second, I very much doubt that internal characters will help in difficult situations where there are groups containing species with similar external appearance, or in the cases of cryptic species. It is in many cases difficult to find differences in internal characters even in good valid species (see e.g. Envall and Sundberg, 1993; Strand et al., 2005; Sundberg et

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al., 2009b; Strand et al., 2014). Third, I very much doubt that anyone will bother to section a nemertean in order to identify it to species level when it comes to identification of nemerteans in, for example, marine surveys. Schander and Willassen (2005) showed that only around 5% of the nemerteans in the samples were identified to anything more than "Nemertea sp." in the marine inventories they had surveyed. So, internal characters are not, and will not be, used for identification. Will internal morphology be useful for phylogeny reconstruction—yes, they can add to other data but it will still be a matter of the availability.

Therefore, my suggestion is, that we, as a community of researchers working on the Nemertea, accept species descriptions that do not meet the "standard" of detailed accounts of internal characters as described above. We should allow a species name to refer to a DNA sequence, the holotype, and voucher specimens. The description could just be the external characters in order to simplify identification to a level that in many cases is enough (and probably better than what we see today). To describe external characters (together with habitat and ecology) is more important for the identification process than detailed anatomical accounts. Along with my collaborators, I have encountered outspoken resistance to this approach, especially in the process of getting Strand and Sundberg (2011) published. I am therefore glad to see an increased acceptance of species identification solely using DNA sequences as in e.g. Leasi and Norenburg (2014), even if these authors did not take the full step and describe/name species based on sequences.

Another problem, and challenge, in nemertean systematics (which we share with many other phyla) is the significant number of names that we will never be able to retrace, or assign to a specimen. Gibson (1985) noted that around 50% of known nemertean species had been established by the beginning of the 20th century, and were inadequately described. The number of known species has increased since 1985, but still a major proportion are not described in a way that would allow a specimen to be securely assigned to one of these names. Thus, the descriptions are essentially too vague and indifferent to be useful, but the names are still there and have to be accounted for. It may be that we, nemertean systematists, should work in the direction of forming a list of available names (LAN) as has been done for species-group taxa in phylum Rotifera. In order to get a stable taxonomy in those instances, one should ideally go to the type locality (when known) and collect specimens that resemble the species of interest, then re-describe it, and appoint a neotype to be placed in a proper and acceptable (by the Code) public collection. The neotype is for most of these species not a problem, as no holotype has been deposited. I suggest that we accept re-descriptions of old names based on DNA sequences and external characters in the same way as I suggested above for new species. Furthermore, I suggest we relax the condition that requires neotypes, or voucher specimens, to be from the type locality, even if such is mentioned, and accept specimens from within reasonable vicinity. This would make it easier for systematists to anchor old names to neotypes, DNA sequences, and external characters, thereby making it possible to use these names in a more fruitful way.

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