Problems and perspectives in the systematics of Nematomorpha

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The 10th edition of Carl von Linné’s Systema Naturae (1758) may be regarded as the beginning of biodiversity research, because naming specific entities in a uniform manner represents the basis for describing and understanding biotic diversity. Some 250 years later, it does not seem exaggerated to expect a more or less solid foundation on which estimates of taxonomic diversity could be based. In reality, however, this is not so. The standard of species descriptions has changed dramatically over time, due to the increasing amounts of taxa and information, as well as improved methods of investigation and documentation. These changes cause problems with assigning and comparing species and specimens. They are reviewed here for the Nematomorpha, or horsehair worms.

Nematomorpha is a taxon including about 300 species in 21 genera. Eight of these genera are monotypic and 13 contain more than one species. All Nematomorpha are long and slender worms (Fig. 1A) with average lengths around 10–20 cm (maximal values more than 2 m) and diameters of about 1 mm. They can be found in any type of aquatic habitat, but only four species of the genus Nectonema Verrill, 1879 are marine while all others live in fresh water (taxon Gordiida). The adults have a more or less limited set of taxonomically important characters, the cuticular structure and the male posterior end being the most important.

In practice, it is often very difficult to assign new specimens of Nematomorpha to early species descriptions. New observation techniques, especially the Scanning Electron Microscope (SEM), have proven valuable for species description and have become a standard in nematomorph taxonomy. The traditional method for determination is to cut a superficial section of the cuticle with a razor blade, remove the adjoining tissue (epidermis and musculature) and observe this piece under the light microscope (LM). This method is still important, but it is supplemented by SEM observations which may also reveal characters not observable by LM. For example, in some species of the genus Beatogordius Heinze, 1934, cuticular structures (called areoles) arranged in form of an “H” are characteristic (Fig. 1C), with are arranged parallel to the longitudinal axis of the animal. The horizontal element of the “H” appears as a well defined oval structure with LM (Fig. 1C), but SEM reveals that there is a tree-like structure with a stem (equivalent to the horizontal element) from which there are broad anterior and posterior projections (Fig. 1D). On the other hand, some structures can not be observed with SEM, because they lie below the cuticular surface. This applies to one type of cone-shaped structures that usually occur in pairs, rarely as clusters of four (Fig. 1B). The function and significance of these structures is not yet known, but it is important to note their presence or absence as well as their distribution.

While most species descriptions pronounce the presence or absence of certain structures, patterns such as characteristic clusters or distributions are often neglected. An example is a cluster of two areoles with a central projection between them (Fig. 1E). This pattern has been neglected in species descriptions if the involved areoles are not considerably larger than the surrounding ones. However, it is widely distributed among gordiids, being present at least in Paragordionus Heinze, 1935 (Schmidt-Rhaesa 1997), Pseudochordodes Carvalho, 1942 (Carvalho 1942), Euchordodes Heinze, 1937 (Schmidt-Rhaesa et al. 1998), Chordodes Creplin, 1847 (Villalobos & Miralles 1997), some species assigned to Gordionus Müller, 1927 (Schmidt-Rhaesa in press) and, in a modified way, in Parachordodes Camerano, 1897 (Schmidt-Rhaesa 1997), and is therefore an important character for nematomorph systematics.

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Another pattern character that has escaped most authors consists in distributions of cuticular structures (areoles) differing between body regions. Areoles may vary along the longitudinal axis as well as around the circumference. This is especially important in taxa with a high diversity of areolar types such as in the genus *Chordodes*. If only a small cuticular sample is taken for determination, such distribution patterns likely escape the investigation.

A large portion of nematomorph species descriptions is based on single collections of one or few specimens. Out of 98 species described for Europe, only 43 have been found on more than one occasion (Schmidt-Rhaesa 1997). Of the remaining 55 species descriptions, 34 are each based on a single specimen, while in the remaining 21 cases more than one specimen was collected at one occasion. The species are sometimes distinguished by fine details, which implies that intraspecific variation does not occur. However, were larger collections investigated, polymorphism has been found to be a considerable factor in nematomorphs. An example are recent investigations on larger numbers of *Gordius* specimens from Britain and Ireland as well as from one single stream in Germany, the Breitenbach/Röhn (Schmidt-Rhaesa & Bleidorn 2000, Schmidt-Rhaesa in press).

They have revealed an enormous intra-specific variation in cuticular characters, ranging from a type that has been described as characteristic for *G. violaceus* Baird, 1853 (Fig. 1F) to a type characteristic for *G. wolterstorffi* Camerano, 1888 (Fig. 1G). It is concluded that these specimens represent only one species that also includes further specimens matching still more *Gordius* species descriptions. Therefore, it seems very likely that there are few polymorphic *Gordius* species in Europe rather than many invariant ones.

Up to now, morphological characters have been the only tool for the recognition of species entities within Nematomorpha. Crossbreeding experiments have not been applied because it has not been possible to establish the entire life cycle in the lab. Only recently have the first nematomorphs been successfully kept during their parasitic phase (Hanelt & Janovy 1999). However, crossbreeding experiments would be very time-consuming, because the life cycle of most species takes one full year. Future approaches will certainly try to correlate morphological with genetic differences via methods such as DNA sequencing, RAPDs or RFLPs.

The key to a well-founded systematization of Nematomorpha is the documentation of character states for each species. Therefore, a certain standard needs to be developed and applied. Investigation and documentation should take place using both LM and SEM. Investigation should cover different body areas such as anterior end, midbody and posterior end, as well as regional differences on the circumference, especially in the genus *Chordodes*. If possible, several specimens should be investigated to allow hypotheses about character variation. This applies to new descriptions as well as to redescriptions. For well-founded questions and conclusions concerning the biodiversity of Nematomorpha, the taxonomic basis to date is too weak. On the one hand it is highly probable that numerous undescribed species are housed in museums, or have not yet been collected at all. On the other hand, the detection of intraspecific variation and subsequent synonymizations may reduce the number of species already described.

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References


Fig. 1. A. *Chordodes ferox* Camerano, 1897 (NHM 1947.5.20.195–198). B. Subsurface structures in *Chordodes capensis* Camerano, 1895 (NHM 1927.8.16.5). C. D. Cuticular structure of *Beatagordius rafflesia* Camerano, 1893 (NHM 1938.11.3.8/9) with LM (C) and SEM (D). Anterior and posterior of the animal are to the right and left of the figures. E. Clustering areoles in an undetermined *Gordi nus* species (NHM 1986.3831). F. Areoles typical for *Gordi nus violaceus* (NHM 1975.1921). G. Areoles typical for *Gordi nus wolterstorffi* (NHM 1927.7.22.44). Note that determinations in A and B are preliminary. Scales: A: 5 mm, B–D: 10 µm, E-G: 20 µm.