Nemathelminthes

■ **Autapomorphies (Fig. 1 → 1)**

– Two-layered cuticle.
  Composed of a trilamellar epicuticle and a uniform basal layer (Fig. 2).
  The epicuticle covers the entire body; it encloses locomotory and sen-
  sory cilia of the body surface.

– Locomotory cilia limited to the ventral side.
  The complete coverage of the body with cilia in the ground pattern of
  the Bilateria (Vol. 1, p. 112) has developed in the stem lineage of the Ne-
  mathelminthes into a ventral "ciliary creeping sole." The cilia are re-
  duced dorsally and laterally.

– Terminal oral aperture.
  Displacement of the intestinal opening from subventral to the anterior
  body pole.

– Cuticle in the pharynx.
  The cuticle of the body surface is taken internally by the pharyngeal
  epithelium and used to cover the lumen of the pharynx (Fig. 2).
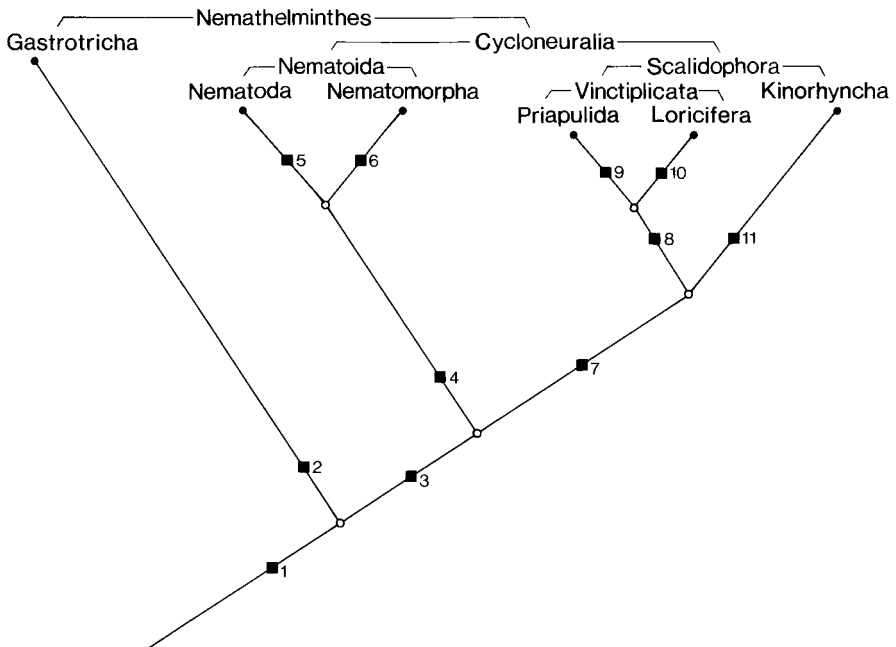

Fig. 1. Diagram of phylogenetic relationships within the Nemathelminthes. (Ahlrichs 1995;
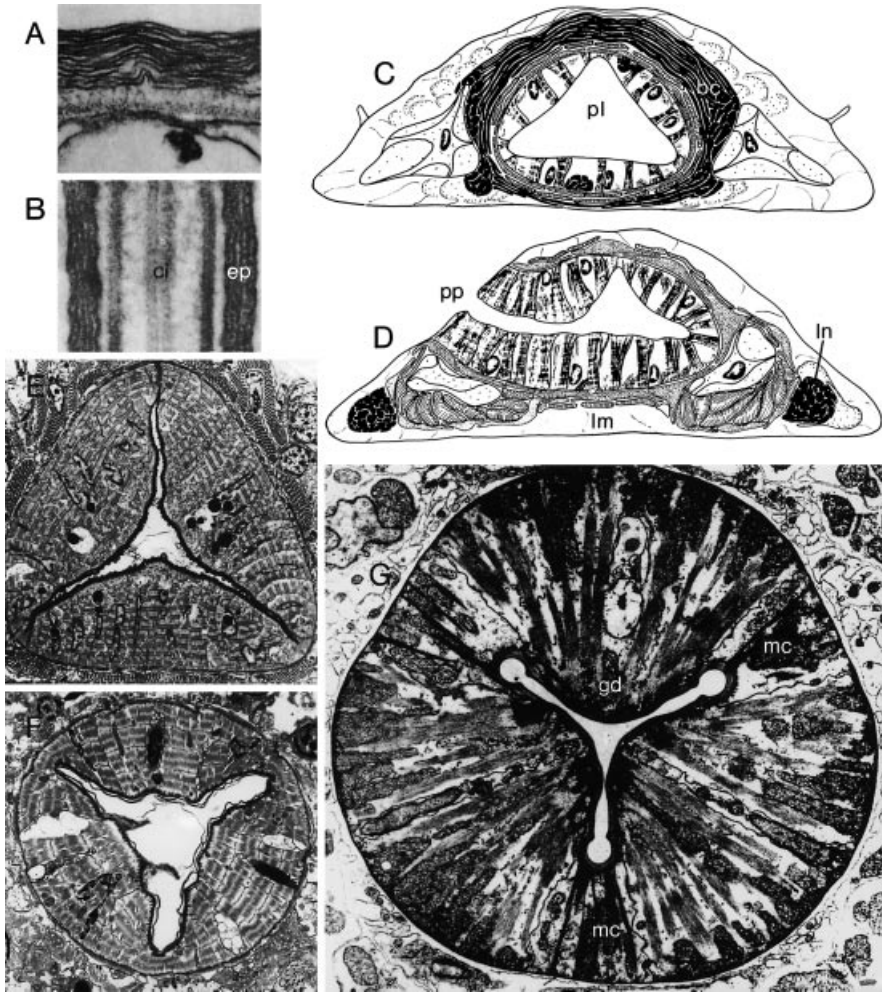Ehlers et al. 1996; Schmidt-Rhaesa 1996a; Lemburg 1999)

Fig. 2. Nemathelminthes. Cuticle in Gastrotricha. Pharynx in Gastrotricha and Nematoda. **A** Turbanella ocellata (Gastrotricha, Macrodasyida). Section through the dorsal cuticle. Epicuticle consisting of several layers of trilamellar units over a uniform basal layer. **B** *Macrodasys* (Gastrotricha, Macrodasyida). Longitudinal section of locomotory cilium with surrounding epicuticle. **C** and **D** *Turbanella cornuta* (Gastrotricha, Macrodasyida). Body cross sections in the pharynx region. **C** At the level of the brain commissure. Wide, triradiate lumen, with a surface to the ventral side. **D** At the level of the pharyngeal pores. The pharynx lumen with two passages to the outside. Passage and pore in the body wall only to be seen on one side. **E** *Paraturbanella* (Gastrotricha, Macrodasyida). Cross section of the pharynx. Myoepithelial cells with 12 sarcomeres. **F** *Halichaetonotus* (Gastrotricha, Chaetonotida). Cross section of the pharynx. One edge of the triradiate lumen in ventral direction. Myoepithelial cells with four sarcomeres. **G** *Caenorhabditis elegans* (Nematoda). Cross section of the pharynx. Configuration of the lumen as in the Gastrotricha Chaetonotida. Monosarcomeric myoepithelial cells at the surfaces, muscle-free marginal cells at the edges of the lumen. *bc* Brain commissure; *ci* cilium; *ep* epicuticle; *gd* glandular duct; *lm* longitudinal muscle; *ln* longitudinal nerve; *mc* marginal cell; *pl* pharynx lumen; *pp* pharyngeal pore. (**A,B** Rieger & Rieger 1977; **C,D** Teuchert 1977; **E,F** Ruppert 1982; **G** Bird & Bird 1991)

– Cuticularized oesophagus.
  The oesophagus joins the pharynx as a short, straight tube with cuticle. Epithelial cells protruding into the lumen form the boundary to the midgut.

With the first item I have taken new ideas about the evolution of the **cuticle** of Nemathelminthes and the value for kinship research into account (LEMBURG 1999). In the ground pattern of the Nemathelminthes, the trilaminar epicuticle consists of two electron-dense laminae with a lighter, less electron-dense lamina in between them. Moving inwards, there is a uniform, protein-containing basal layer. This cuticle probably evolved from a simple glycocalyx (RIEGER 1984).

In the ground pattern of the Gastrotricha, several trilamellar layers are combined to a multilamellar epicuticle. This may be an autapomorphy of the Gastrotricha; however, I will also discuss the possibility of a much earlier evolution in the stem lineage of the Nemathelminthes later (p. 7). In any case, the basal layer at first remains unchanged.

The evolution of chitin is then an important evolutionary step in the stem lineage of the Cycloneuralia (Fig. 1). The cuticle can now by divided into three layers. The trilamellar epicuticle is followed be a protein-containing exocuticle (middle layer) and a fibrillary endocuticle (basal layer) with chitin.

Adult Nematoda and Nematomorpha, however, do not have chitin in their body covering. When they are taken together as Nematoida forming with the Scalidophora, the two sister groups of the Cycloneuralia, the result is surprising: the chitin "just" evolved in the stem lineage of the Cycloneuralia has already been lost again in the Nematoida. We have no other possible interpretation for this. The lack of chitin in the integument of adult Nematoida must be a secondary condition. The reason is simple. The larvae and young stages of the Nematoida have the three-layered cuticle with chitin in the endocuticle from the ground pattern of the Cycloneuralia (SCHMIDT-RHAESA 1996 a; NEUHAUS et al. 1995). Furthermore, chitin has recently been detected in the pharyngeal cuticle of adult Nematoda.

"For the Scalidophora no unambiguous autapomorphy concerning the cuticle can be given" (LEMBURG 1998, p. 156). The integument consisting of trilamellar epicuticle, exocuticle and endocuticle with chitin has been taken over by the Scalidophora and continued in the stem lineage of the Vinctiplicata (Priapulida + Loricifera). In contrast, an evolutionary change has occurred in the stem lineage of the Kinorhyncha. Chitin is present in the homogeneous middle layer, whereas the basal layer is free of chitin.

The **pharynx** of the Nemathelminthes with its numerous divergent forms presents further problems. At a first approximation, two states can be distinguished.

1. The Gastrotricha, Nematoda and Loricifera each have a pharynx with epithelial muscle cells in which the myofibrils are arranged radially. The myoepithelium encloses a triradiate lumen (Fig. 2).
2. The Kinorhyncha and Priapulida, on the other hand, possess muscle-free pharyngeal epithelia and a subepithelial pharyngeal musculature. The pharynx has a round lumen in both taxa (Fig. 12).

Myoepithelia have frequently been suggested as a primitive contractile tissue in the Bilateria. Thus, among the Nemathelminthes, the myoepithelially organized pharynx is generally considered as a plesiomorphous state. This assumption is now vigorously rejected (LEMBURG 1999).

When a myoepithelial pharynx is postulated for the stem species of the Nemathelminthes, then the pharyngeal bulbs of the Priapulida and Kinorhyncha with muscle-free epithelia must have arisen secondarily within the Nemathelminthes. This is unlikely. The arrangement and innervation of the circular and longitudinal musculature of the Priapulida are identical to those of the body musculature from which the pharyngeal musculature has developed.

In cases of a myoepithelial pharynx, there are also considerable differences in the structure and distribution of the myofilaments. In the Gastrotricha there are always multisarcomeric myoepithelial cells. In the Nematoda there are monosarcomeric myoepithelial cells on the plains of the pharynx lumen and myofilament-free cells on the apical edges. In the Loricifera (*Nanaloricus mysticus*) there are alternating apical cells with monosarcomeric myofilaments and interapical cells with disarcomeric myofilaments.

For the rest, there is no continuous alternative in the subepithelial pharyngeal musculature. It is absent only in the Nematoda. In the Gastrotricha, there is a network of circular and longitudinal muscles around the myoepithelial cells of the pharynx that continues around the subsequent midgut. The Loricifera also possess circular muscle bundles around the myoepithelial pharynx.

This briefly described situation leads to the following considerations. A pharynx of muscle-free epithelial cells with a round lumen and a weak subepithelial musculature belongs to the ground pattern of the Nemathelminthes (LEMBURG 1999). The evolution of myoepithelial radial muscle cells must have occurred convergently in the Gastrotricha, Nematoda, and Loricifera. The same holds for the triradiate pharynx lumen through which a sucking pharynx with the ability to expand strongly is reached. There are even good arguments to propose a double evolution of the triradiate pharynx within the Gastrotricha (p. 10).

Since the sister group of the Nemathelminthes cannot be determined satisfactorily (see below), the question of the extent to which the outlined features of the ground pattern of the pharynx – muscle-free epithelium, round lumen, subepithelial musculature – are plesiomorphies or autapomorphies of the Nemathelminthes remains open.

There is no body cavity in the ground pattern of the Nemathelminthes. Primarily, millimeter-sized Nemathelminthes such as the Gastrotricha, Kinorhyncha, Loricifera and free-living Nematoda have a **compact organization** with extracellular matrix (ECM) between the tissue and organs of the body (Figs. 2, 11; Vol. I, Fig. 45). When, as a consequence of increases in body size, liquid-filled cavities occur in parasites, these are primary body cavities – defined as "a cavity between ectoderm and endoderm that is surrounded by extracellular matrix" (Vol. I, p. 113). It could be disputed to what extent a cavity created by the dissolution of a compact organization can be included in the term primary body cavity. However, this is merely a question of the definition of a term. In no case is there a particular cavity that characterizes the Nemathelminthes as an entity and, accordingly, there is no justification for the term pseudocoel. This misleading term as well as the group name Pseudocoelomata derived thereof should be abandoned.

Eutely is the term for cell constancy – for the establishment of the individuals of a species by a specific number of cells in the construction of the body. With the absence of cell divisions in the adult, appreciable regeneration processes are hindered. In attempts to characterize the Nemathelminthes, one often speaks of a tendency or trend for eutely. In place of this loose, indefinite formulation we can today make a clear statement for the monophylum Nemathelminthes within the boundaries given here. Eutely most certainly does not belong the ground pattern (SCHMIDT-RHAESA 1996 a). The ability for regeneration has been demonstrated for Gastrotricha. In *Pontonema vulgaris* (Nematoda, Enoplida), mitosis starts in cells of the intestinal epithelium when the intestinal tube is interrupted by injury (MALAKHOV 1998). In the Nematomorpha and the entire Scalidophora, there are no indications at all for a possible cell constancy.

The question of the primary **cleavage pattern** in the development of the Nemathelminthes cannot yet be answered satisfactorily.

First of all, the frequent attempts to attribute the development of the Gastrotricha and Nematoda to a common, bilaterally symmetrical cleavage pattern is doomed to failure. To be sure, the few studies on Gastrotricha do support an early determination of the body axes at the four-cell stage (TEUCHERT 1968). For the Nematoda, however, the classical idea of a mosaic development with determination of the fate of each blastomere has undergone a radical change (SCHIERENBERG et al. 1997/98). The early cleavage of certain Enoplida (*Enoplus, Pontonema vulgare*) is characterized by

variability in the arrangement of the blastomeres. There is no evidence for a strict determination of blastomeres. Furthermore, the bilateral symmetry only appears later in the embryogenesis at the stage of ca. 500 cells (MA-LAKHOV 1998). "Our studies suggest that a precise cell lineage is not a necessary attribute of nematode development" (VORONOV & PANCHIN 1998, p. 143).

Secondly, our knowledge of the Scalidophora is very poor. No observations on the Loricifera and Kinorhyncha are available. According to LANG (1953), the cleavage of *Priapulus caudatus* follows a radial pattern. VAN DER LAND summarized the few, sometimes contradictory data on the Priapulida as follows: "Cleavage is total and equal (only occasionally are the cells of a markedly different size), of the bilateral type,…" (1975, p. 62).

Systematization

We now come to a consequent, phylogenetic systematization of the Nemathelminthes and bring the subordinated taxa – nearly all of which have already been mentioned – in the appropriate order (Fig. 1).

Nemathelminthes
    Gastrotricha
    Cycloneuralia
        Nematoida
            Nematoda
            Nematomorpha
        Scalidophora
            Vinctiplicata
                Priapulida
                Loricifera
            Kinorhyncha

The highest placed adelphotaxa of the Nemathelminthes are the **Gastrotricha** with numerous primitive features and the **Cycloneuralia** with a circumpharyngeal nerve ring of uniform density and specific distribution of perikarya and neuropil.

Within the Cycloneuralia, the Nematoida and Scalidophora are placed side by side as sister groups.

At this point, the exclusive existence of longitudinal muscles under the skin and the thus resulting, undulatory movements of the body may be mentioned as an outstanding autapomorphy of the **Nematoida**. As presumed sister groups the Nematoida encompasses the array of free-living and parasitic Nematoda as well as the Nematomorpha with their well-known larval and juvenile parasitism.