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# Nematodes in aquatic environments: adaptations and survival strategies

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**ABSTRACT** Nematodes are found in all substrata and sediment types with fairly large number of species that are of considerable ecological importance. Despite their simple body organization, they are the most complex forms with many metabolic and developmental processes comparable to higher taxa. Phylum Nematoda represents a diverse array of taxa present in subterranean environment. It is due to the formative constraints to which these individuals are exposed in the interstitial system of medium and coarse sediments that they show pertinent characteristic features to survive successfully in aquatic environments. They represent great degree of morphological adaptations including those associated with cuticle, sensilla, pseudocoelomic inclusions, stoma, pharynx and tail. Their life cycles as well as development seem to be entrained to the environment type. Besides exhibiting feeding adaptations according to the substrata and sediment type and the kind of food available, the aquatic nematodes tend to withstand various stresses by undergoing cryobiosis, osmobiosis, anoxybiosis as well as thiobiosis involving sulphide detoxification mechanism.

**KEY WORDS** Adaptations; fresh water nematodes; marine nematodes; morphology; ecology; development.

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## INTRODUCTION

The diversity of animal life is not distributed uniformly across the world and its diversification is not an automated process but requires some characteristics of form and function that allow successful exploitation of new habitats. Such species are, therefore, considered "plastic" or "malleable" that with modifiable genetic material can change or adapt when subjected to evolutionary selective pressures. Nematodes, the most numerous of all Metazoa in number of individuals, exist in all habitats that can support life.

Being ubiquitous, they can be as dynamic as the habitat types and can change through time. With a deceptively simple anatomical design, they are referred as typical representatives of Metazoa (Nelson et al., 1982). However, they are the most complex forms with many metabolic and developmental processes comparable to higher taxa; they demonstrate remarkable abilities to withstand stress and adverse conditions. The nematode *Caenorhabditis elegans* (Maupas, 1900) survived the crash of space shuttl, Columbia that hit the ground with an impact 2,295 times the force of Earth's gravity (Cosgrove-Mather, 2003).

Many species survive the unfavourable conditions by demonstrating anhydrobiosis, cryptobiosis, osmobiosis or cryobiosis. The key to their success in all types of ecosystems and biotopes is their morphological plasticity, physiological adaptability and ecological diversity.

Nematodes are basically aquatic animals that require a film of water to move. They may exist as free-living, commensals or parasites in all types of aquatic habitats viz., freshwater, brackish, marine systems; in extreme environments including sea-ice to hydrothermal vents. They may be found in clay, gravel, epiphytes, on sea grasses and algae. Their vermiform, soft and flexible bodies are well suited to allow bending in the interstitial system of sand grains/particles (Heip et al., 1985; Strayer, 1985; Traunspurger, 1996 a, b).

A number of factors affect their distribution viz., seasons, latitude, water depth, geochemical properties of the sediment, temperature, salinity, water movement, oxygen content, species interaction, resource partitioning and predation (Jensen, 1981; 1987a; Joint et al., 1982; Bouwman et al., 1984; Platt & Lambshead, 1985; Ólafsson, 1992; Giere, 1993; Hendelberg & Jensen, 1993; Soetaert et al., 1994; Modig & Ólafsson, 1998; Steyaert et al., 1999; Wetzel et al., 2002; Armenteros et al., 2009).

The present article highlights the habitat-specific features of aquatic nematodes, their adaptations and compatibility to the environmental conditions.

## Major aquatic groups

Phylum Nematoda includes a diverse array of taxa specific to a variety of aquatic habitats. The typical composition of the freshwater meiofauna differs much from that in marine realm with nematodes more numerous in sediments than in the water columns (Bell & Sherman, 1980; Sibert, 1981). Most species of *Chromadorea* are found in fresh water ecosystems with the exception of few tylenchids, aphelenchids and rhabditids whereas only few species are reported from polar freshwaters (Maslen, 1979).

The species of Araeolaimida, Monhysterida as well as Chromadorida inhabit both fresh water as well as marine environments (De Ley et al., 2005). In Enoplea, the fresh water representatives mainly belong to Triplonchida, Mononchida, Dorylaimida and Mermithida and to a lesser extent Enoplida. The taxa Enoplida, Desmoscolecida, Chromadorida and Monhysterida are predominantly marine. About 4000 species of free-living marine forms have been accounted through various faunal surveys (Jensen, 1981; Sharma & Webster, 1983; Vanreusel et al., 1992). Estuarine nematodes show greater taxonomic affinities to freshwater nematodes and can tolerate significant changes in salinity (Forster, 1998; Warwick, 1981a).

The nematode species with fresh water affiliations are most abundant at the upper edge of the intertidal zone where the marine influence is often weak (Nicholas et al., 1992).

## Morphological characteristics

The aquatic nematodes are quite varied morphologically and no single species can be considered a true representative. However, the similarity in fresh water as well as marine forms on account of their aquatic habitats reflects convergent evolution. Most aquatic nematodes have elongated cylindrical bodies of about one to several millimeters length except ~9 m long whale parasite *Placentonema gigantissima* (Gubanov, 1951). The dark subterranean environment has led to loss or reduction in body pigmentation, hence, the nematodes appear whitish-semi transparent or transparent.

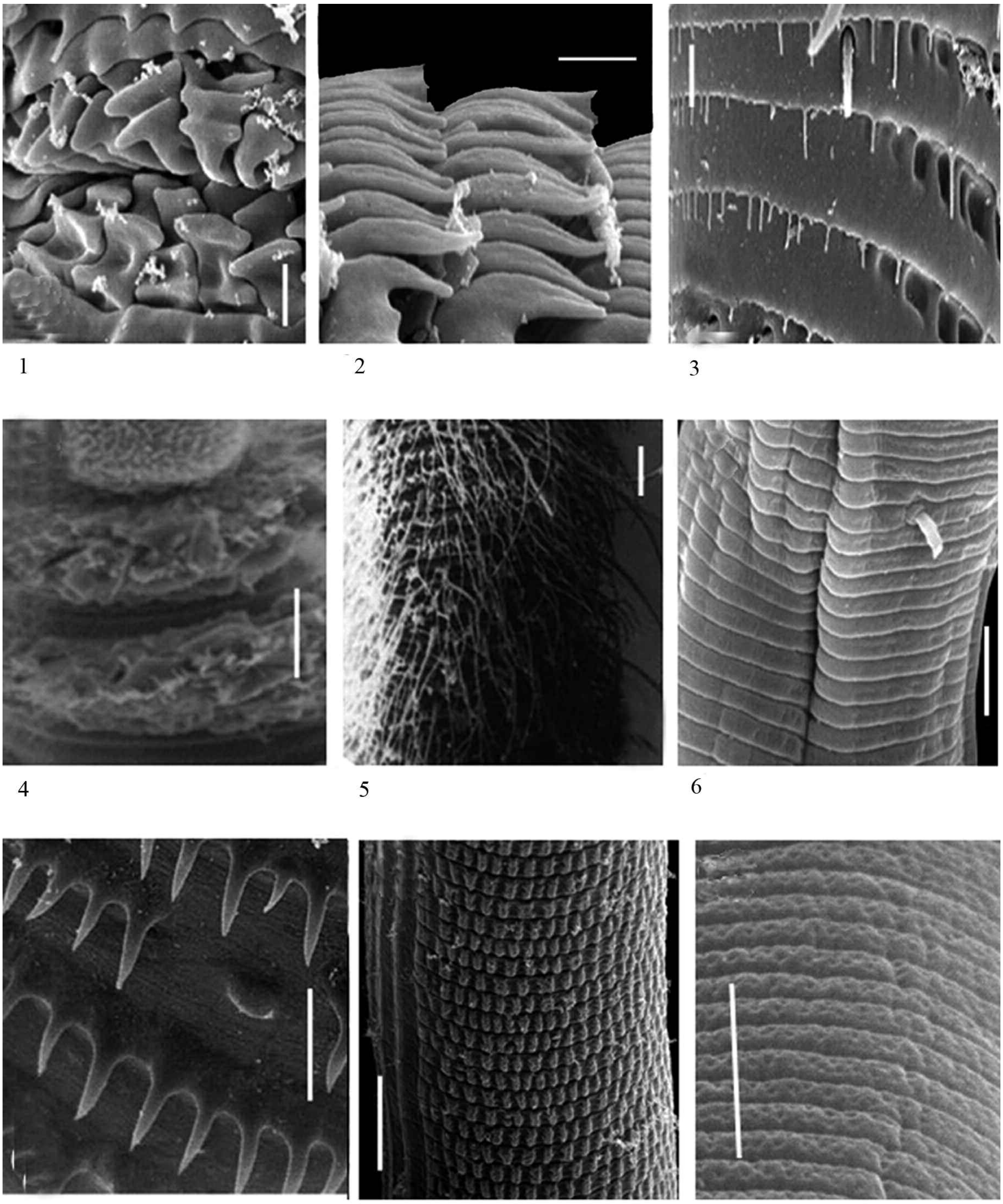
They are characterized by slender, spindle-shaped bodies with enhanced swimming abilities. Wriggling or undulatory propulsion by alternate pushing and bending, is typically found due to presence of only longitudinal musculature. However, some aquatic species can "jump" by bending of their bodies followed by a sudden relaxation (e.g. *Theristus*).

The members of Epsilonematidae and Draconematidae move by "looping" with an alternate adhesion and detachment of their anterior and posterior body ends whereas the desmoscolecids move by contractive waves.

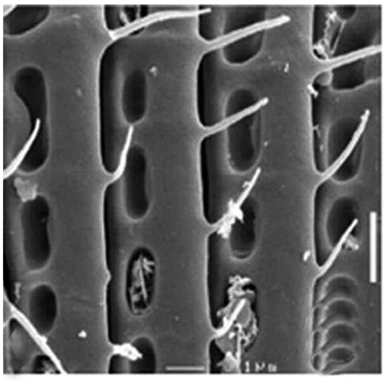
The cuticle of aquatic nematodes may be smooth (most Enoplidae), annulated (Desmodoridae, Desmoscolecidae, most Monhysteridae), punctated (Cyatholaimidae, many Chromadoridae, Comesomatidae), or provided with complicated and compact structures (many Chromadoridae).

There may be diverse types of cuticular modifications (Figs. 1-3, 5, 9, 10). Some nematodes may have longitudinal ridges or alae (Figs. 11-13, 15, 16, 18) aiding in swimming. Punctations in the form of dots (punctation) or pores arranged irregularly or in rows, are also common in many aquatic taxa (Figs. 8, 9, 14). The punctations may fuse into compact structures in many chromadorids (e.g., *Spilophorella paradoxa* de Man, 1888; *Chromadorella* spp.). Often the cuticular surface is covered with a dense “fur” of ectosymbiotic sulfur-oxidizing bacteria to thrive in sulfur-rich marine sediments (Nussbaumer et al., 2004; Ott et al., 2008).

Aquatic nematodes usually possess long, hair-like sensilla called setae, relatively more developed in marine forms, compared to slightly-raised or mammellate sensilla of terrestrial nematodes. Body (somatic) sensilla (commonly found in Monhysterida,



Figures 1-9. Cuticular modifications.
Figs. 1-3: *Epsilonema pustulatum* after Karssen et al. 2000. Fig. 4: *Desmoscolex* sp. Fig. 5: *Glochinema* sp. Fig. 6: *Plectus* sp. Fig. 7: *Goezia leporini* after Martins and Yoshitoshi, 2003. Fig. 8: *Cruznema* sp. Fig. 9: *Achromadora* sp. (Scale bar: 1-3, 7 =1 µm; 4-6, 8, 9 = 10 µm).



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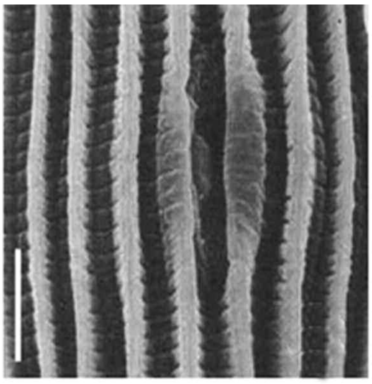

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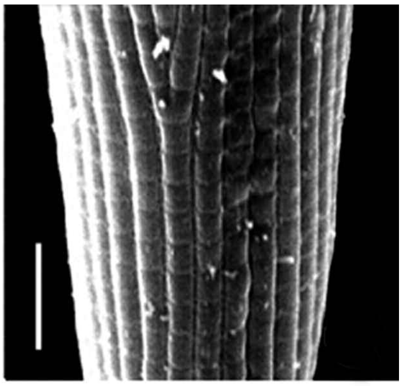

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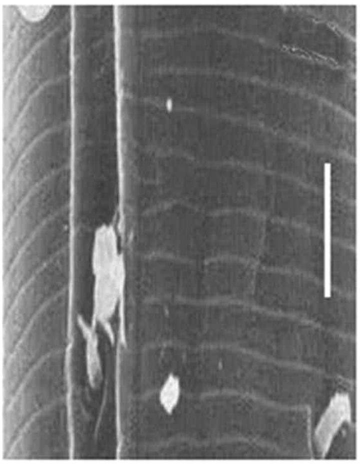

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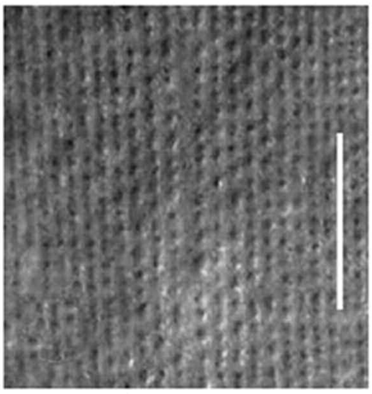

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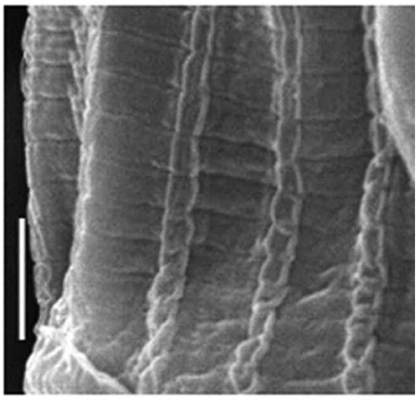

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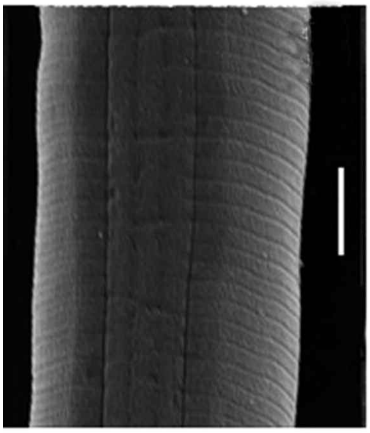

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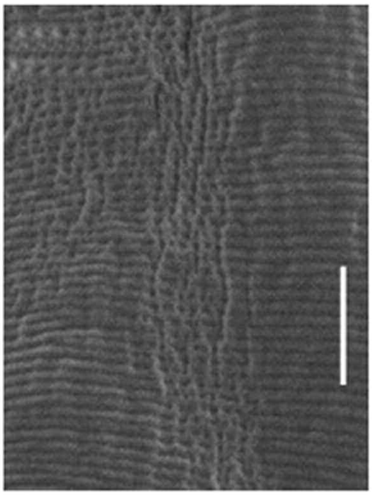

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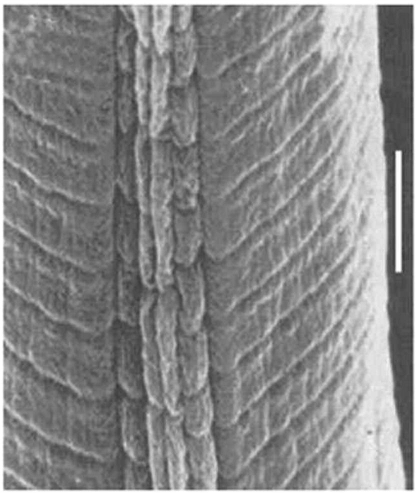

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Figures 10-18. Cuticular modifications.
Fig. 10: *Epsilonema pustulatum* after Karssen et al., 2000. Fig. 11: *Mononchoides* sp. Fig. 12: *Fictor* sp. Fig. 13: *Plectus zelli*. Fig. 14: *Pelodera teres*. Fig. 15: *Diplogastrellus* sp. Fig. 16: *Panagrellus* sp. Fig. 17: *Dorylaimus* sp. Fig. 18: *Chiloplacus* sp. (Scale bar: 10 = 1 µm; 11-18 = 10 µm).

Araeolaimida, Chromadorida and Enoplida) may be arranged in rows or distributed randomly; in absence of eyes, the symmetry of the tactile sensilla and the flexible body serve to guide the crawling worm between sand grains, debris etc. In aquatic habitats the nematode setae of 5 to 10 µm length dominate with shortest setae mostly found in nematodes of littoral zone. Other types of sensilla include caudal setae (Figs. 110, 111) and terminal setae (Figs. 102, 111, 113, 114, 117).

The terrestrial nematodes usually have the primitive arrangement (Fig. 32) of labial sensilla (6 inner labials + 6 outer labials + 4 cephalics) contrary to the configuration in many aquatic nematodes (6 + 10) where outer labials are situated at the level of cephalic sensilla (Fig. 23) or there may be additional setae (Figs. 24, 28). The jointed setae (Fig. 23) found in some aquatic nematodes are comparable to jointed appendages of arthropods indicating some relationship among these ecdysozoans.

Amphids, the bilaterally symmetrical sensory structures demonstrating the first evidence of cilia, are involved in many behavioural functions and are comparable to olfactory organs. Coomans (1979) suggested a mechanoreceptive, secretory as well as photoreceptive function to amphids.

In aquatic nematodes, the amphids are relatively complex, conspicuous and post-labial and mainly circular (Figs. 20, 22, 28), loop-shaped (Figs. 72, 73), spiral, (Figs. 64, 65, 78), shepherd's crook, pocket-like and rarely pore-like compared to the amphids of land-dwelling nematodes that are usually pore-like or slit-like (Figs. 25, 31, 32) and occasionally round or spiral-shaped. Although there is little physiological evidence for photosensitivity in nematodes, ocelli have been defined as discrete photoreceptors (Croll, 1970) and commonly found in marine genera viz., *Thoracostoma* Marion, 1870, *Phanoderma* Bastian, 1865, *Eurystomina* Filipjev, 1921, *Calyptronema* Filipjev, 1921 etc.

Species may be provided with compact conglomerations of pigments (Figs. 81, 94, 95) viz., *Enoplus* spp., *Pseudocella trichodes* (Leuckart, 1849), with diffuse pigments in the cervical region inside pharynx (*Deontostoma* Filipjev, 1925; *Oncholaimus* Dujardin, 1845 and *Chromadorina* Filipjev, 1918) or outside pharynx in epidermis/pseudocoelom (*Araeolaimus* de Man, 1888). Eye spots are often provided with a hyaline "lens" or comparable structure (Fig. 93) e.g., *Symplocostoma* Bastian, 1865 and *Araeolaimus*.

The utility of ocelli in aquatic habitats with particular reference to marine environment, is the negative phototaxis to move to deeper layers/strata, as observed in *Chromadorina bioculata* (Schultze in Carus, 1857); *Oncholaimus vesicarius* (Wieser, 1959); *Enoplus anisospiculus* Nelson et al., 1972 (Croll, 1966; Croll et al., 1972; Bollerup & Burr, 1979; Burr & Burr, 1975; Burr, 1979; Burr, 1984). It probably explains the absence of ocelli in nematodes inhabiting littoral sand. Few nematodes use photosensitivity to determine the photoperiod for successful completion of life cycle. Haemoglobin instead of melanin, in some nematodes including mermithids, serves an optical and light-shadowing function (Ellenby, 1964; Ellenby & Smith, 1966; Croll & Smith, 1975; Burr et al., 2000).

The metanemes (Fig. 92) are spindle-shaped/filamentous proprioceptors (Hope & Gardiner, 1982) or stretch receptors (Lorenzen, 1978, 1981), found in the lateral hypodermal chords of marine enoplids (e.g., *Enoplus* Dujardin, 1845; *Deontostoma* and *Oxyonchus* Filipjev, 1927) lying parallel or at an angle of 10-30° to the main body axis. Metanemes are sensitive to the dorsoventral bending of nematode body thus controlling the body volume.

Some marine enoplids especially Thoracostomopsidae possess a pair of sense organs known as cephalic slits (de Man, 1886) or cephalic organs (Filipjev, 1927), latero-ventrally placed between the circlets of the labial sensilla (Fig. 96). The cephalic organs may possess club-shaped cirri (chemosensory/mechanosensory) in species having powerful buccal armature (Wieser, 1953) e.g., *Oxyonchus dentatus* (Ditlevsen, 1918) Filipjev, 1927.

Crystalloids (Figs. 82, 83), the crystal-like inclusions or irregular electron dense deposits (Fig. 84) occurring subcutaneously or in pseudocoelom, have been observed in many fresh water (e.g., *Monhystera* Bastian, 1865; *Ironus* Bastian, 1865; *Tobrilus* Andrássy, 1959; *Tripyla* Bastian, 1865) sensu Alekseyev and Dizendorf, 1981; Andrássy 1958, 1981, 1984; Juget, 1969; Micoletzky, 1922, 1925; Riemann, 1970; Jacobs & Heyns, 1990) and marine nematodes e.g., *Sabatieria* Rouville, 1903; *Sphaerolaimus* Bastian, 1865; *Terschellingia* de Man, 1888 (Nicholas et al., 1987). The ultrastructural, ecophysiological and physical microanalysis further revealed high sulphur content of the osmiophilic and homogeneous crystalloids (Nuss & Trimkowski, 1984). Other reports suggested their role in detoxification or preventing harmful accumulation of metal sulphides in the tissues (Nuss, 1984; Nicholas et al., 1987) or in storing food during adverse conditions (Bird et al., 1991).

Body pores (Figs. 85, 86) are common among many *Enoplea*. Generally a body pore leads through a canal to a unicellular, merocrine hypodermal gland (Fig. 87) and an associated bipolar neurocyte e.g., *Chromadorina germanica* (Butschli, 1874). However, Electron Microscopy revealed multivesicular complexes similar to Golgi bodies (Lippens, 1974). Some marine worms e.g., *Ptycholaimellus ponticus* (Filipjev, 1922) Gerlach, 1955 with a system of body pores and hypodermal glands modify the sedimentary microenvironments by building tubes (Hope & Murphy, 1969).

The diversity in nematodes revolves mostly around the evolution of stoma and one or more pharyngeal bulbs. The stoma or buccal cavity, usually a triradiate structure bounded by three or six lips, exhibits variations reflecting the different feeding modes (Wieser, 1953; Jensen, 1987b; Moens & Vincx, 1997; Traunspurger, 1997.

The buccal cavity may be absent or minute (Figs. 48-51) to spacious, unarmed type (Figs. 33, 34) in non selective deposit feeder species. The nematodes feeding on diatoms possess a buccal cavity armed with small to moderate-sized teeth (Jensen, 1982; Romeyn & Bouwman, 1983; Romeyn et al., 1983; Moens & Vincx, 1997). The buccal cavities of powerful predators may further be armed with immoveable armature/teeth (Figs. 37-40, 52-59), rows of small denticles or moveable structures termed mandibles or jaws (Figs. 60, 63).

Pharynx, the anterior muscular part of the gut with a tri-radiate lumen does not show habitat-wise specificity but largely varies according to the feeding modes. In marine nematodes the pharynx is largely cylindrical with posterior part gradually expanding, occasionally forming a muscular bulb. The dorsal gland orifice usually opens through the stegostom while pharyngeal gland nuclei are located in basal part. The pharyngeo-intestinal junction (cardia) and intestine do not show aquatic adaptations.

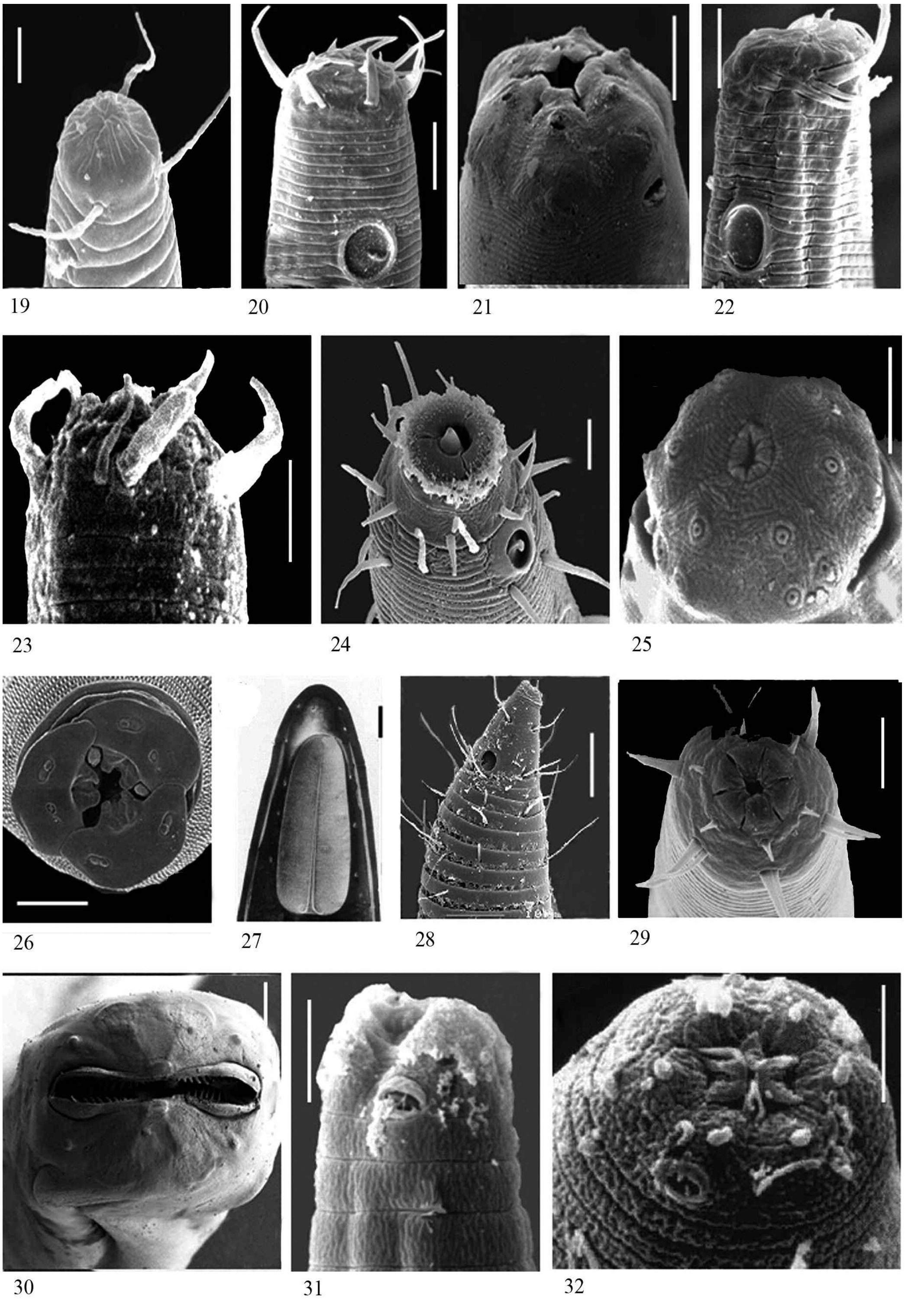
The secretory-excretory cell (renette cell = ventral gland, cervical gland or excretory cell) opens through a ventral pore between mid pharynx to anterior intestine (Bird & Bird, 1991) except *Monhystera disjuncta* Bastian, 1865 and some Ironidae having a labial location (Van de Velde & Coomans, 1987). In marine nematodes, the well developed renette cell has secretory role in tube-building e.g., *Ptycholaimellus* Cobb, 1920 (Jensen, 1988). The secretory role has been also verified in *Sphaerolaimus gracilis* de Man, 1876 (Turpeenniemi & Hyvärinen, 1996) and *Monhystera disjuncta* (Van De Velde & Coomans, 1987).

The number and structure of ovaries along with other genital components though taxonomically important, do not show much difference from those of terrestrial nematodes and are largely specific of higher taxa (Lorenzen, 1981, 1994). Ovaries in aquatic nematodes generally tend to be long and well developed reflecting high fecundity. Likewise the position of vulva usually varies from middle (e.g., members of Tobrilidae, Plectidae etc.) to posterior (e.g., monhysterids) in aquatic nematodes.

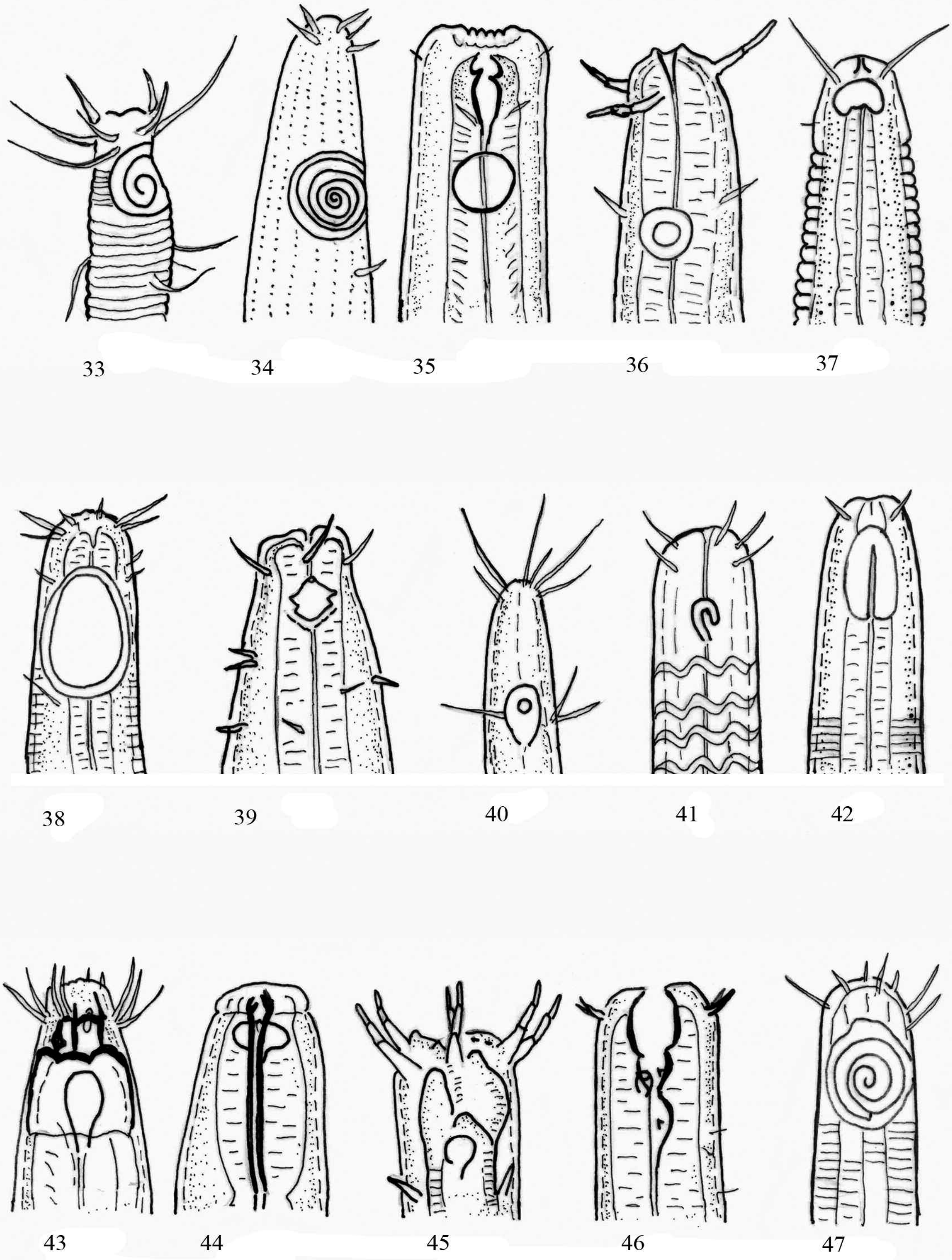
The females are usually didelphic-amphidelphic with antidromously reflexed (outstretched in *Cytolaimium exile* Cobb, 1920) ovaries. However, monhysterids represent mono-prodelphic females while the gonad can be mono-opisthodelphic in most species of Alaimidae. There is a connection between the reproductive and digestive systems in some Oncholaimidae through demanian system (Figs. 97-101), which varies from simple (e.g., *Viscosia* de Man, 1890) to highly-developed one (e.g., *Adoncholaimus* Filipjev, 1918 and *Oncholaimus*).

The demanian system serves the functions of maintaining viability of spermatozoa, releasing a sex attractant, facilitating egg deposition and transfer of sperm to the intestine, and elimination of excess sperms deposited in females through the digestive system (Eyualem et al., 2006). The aquatic male nematodes may possess one (monorchic) or two (diorchic) testes largely depending on the taxonomic group they belong to. Typically, the cuticularised spicules and gubernaculum and the genital supplements/papillae are also not habitat-specific.

Most aquatic nematodes possess long filamentous tails and propel themselves faster by its whipping action (Gerlach, 1953, 1971; Wieser, 1959; Warwick, 1971; Riemann, 1974). Nevertheless, the tail shape can be variable from round, conical, cylindroid-clavate to elongated-filiform (Figs. 102-112). In most marine nematodes it may be provided with caudal setae, specifically confined to terminus as terminal setae (Fig. 111). Often the bluntly-rounded tail terminus bears a spinneret- the outlet for caudal glands' (Figs. 113-117) sticky secretion (Distem) that helps in anchorage to an object or substratum. This phenomenon of nictation is a foraging adaptation in aquatic nematodes.



Figures 19-32. Modifications in anterior sensilla.
Fig. 19: *Chronogaster* sp. Fig. 20: *Monhystera* sp. Fig. 21: *Mononchus aquaticus*. Fig. 22: *Hoffmanneria* sp. Fig. 23: *Prismatolaimus* sp. Fig. 24: *Sabatieria lyonessa*. Fig. 25: *Xiphinema* sp. Fig. 26: *Goezia leporini* after Martins & Yoshitoshi, 2003. Fig. 27: *Rhaptothyreus* sp. Fig. 28: *Epsilonema pustulatum* after Karssen et al., 2000. Fig. 29: *Theristus* sp. www.nem.wur.nl/UK/In+the+picture/Gallery/. Fig. 30: *Camallanus tridentatus* after Santos & Moravec, 2009. Fig. 31: *Cephalobus* sp. Fig. 32: *Myctolaimus kishtwarensis* Hussain, Tahseen, Khan & Jairajpuri, 2004(Scale bar = 10 µm).



Figures 33-47. Modifications in anterior sensilla.
Fig. 33: *Paramesonchium* sp. Fig. 34: *Cervonema* sp. Fig. 35: *Prodesmodora* sp. Fig. 36: *Rhabdocoma* sp. Fig. 37: *Aphanolaimus* sp. Fig. 38: *Amphimonhystera* sp. Fig. 39: *Platycoma* sp. Fig. 40: *Wieseria* sp. Fig. 41: *Ceramonema* sp.; Fig. 42: *Diplopeltoides* sp. Fig. 43: *Paramesacanthion* sp. Fig. 44: *Pheronous* sp. Fig. 45: *Cyatholaimium* sp. Fig. 46: *Tobrilus* sp. Fig. 47: *Coninckia* sp.

## Reproduction and development

Reproductive mechanisms do differ among nematodes in different habitats. Mostly marine nematodes are dioecious and amphimictic with obligate bisexuality thus enhancing the chances of fertilization and promoting high genetic variation. However, sex ratio is significantly influenced by temperature in *Pellioditis marina* Bastian, 1865 (Rhabditidae) and *Diplolaimelloides meyli* Timm, 1961 (Monhysteridae), with more males at higher temperatures (dos Santos et al., 2008).

Amictic reproduction is mostly common in the spatially and temporally variable environments (Townsend et al., 2003) thus conforming well to the large proportions of species without males in variable marine habitats or in occasionally stressed habitats (Nicholas, 1975). The sex ratio in some marine forms lean towards femaleness to reproduce more in order to sustain in the unstable environment. The changes in growth rate as well as the duration of life cycle are further indicative of the volatility of environment (Palacin et al., 1993).

The fresh water species inhabiting shallow water bodies or those subject to repeated drying and wetting, tend to be without males (Grootaert, 1976; Wharton, 1986; Ocaña, 1991a) thus opting for parthenogenesis e.g., *Eumonhystera* Andrássy, 1981; *Plectus* Bastian, 1865; *Rhabdolaimus* de Man, 1880. Organisms living in isolated and unstable habitats have evolved cryptobiosis, self-fertilization, and passive dispersal, benefiting them in the challenging conditions.

Life cycle stages often provide a means of surviving changes in the environment. The laid eggs, with their sticky/complex rugose/spinose shell (Figs. 90, 91) surface, adhere to sediment particles. The eggs may further be provided with entangling devices such as byssi or polar filaments to resist water current in fresh water habitats. Experimentally a 5°C increase in temperature produces up to a six-fold increase in the number of eggs laid (Warwick, 1981c). The sperms of some aquatic nematodes may possess a pseudoflagellum (a protoplasmic hair) unlike the typically round or amoeboid (crawling) sperms of terrestrial forms. Retention of the nuclear envelope in mature spermatozoa has also been reported (Lee, 2002). One unique feature found in some marine species is traumatic insemination (Maertens & Coomans, 1979; Chabaud et al., 1983; Coomans et al., 1988), a type of copulation not occurring through vulva, but through puncturing of the cuticle followed by the formation of terminal ducts as a part of the demanian system. The excess sperms are thus discharged into the intestine (Coomans et al., 1988).

The aquatic habitats with high wave action also led to conditions of ovoviviparity in nematodes. *Monhystera paludicola* de Man, 1880 shows intrauterine hatching thus avoiding the risk of loosing the eggs in fast-flowing waters (Hofmanner, 1913; Hofmanner & Menzel, 1915; Juget, 1967). Although facultative ovoviviparity has been also observed in the shallow water populations, this characteristic was frequently expressed in toxic environments (Van Gaever et al., 2006). Some species of *Monhystera* are characterised by a specialized uterus with associated cells and glands (Figs. 88, 89) and a spermatheca.

The uterus is elongated and its length increases with age (Jacobs & Heyns, 1990) so as to hold and protect greater number of developing juveniles in stressed conditions (Otto, 1936; Schiemer et al., 1969; Otto & Schiemer et al., 1973). The highly indeterminate mode of cell division (Justine, 2002) in some aquatic enoplids contrary to normal determinate/ mosaic cell division tends to regulate the development in stressed environments.

In some marine nematodes, such as *Pellioditis marina* the cell lineage with polyclonal cell fate distribution allows a faster embryonic development by reducing the need for cell migrations (Houthoofd et al., 2003) resulting in extremely short generation time (Moens et al., 1996). Many small species have short generation times of usually about one month or less (Gerlach, 1971; Heip et al., 1985). However, the period of development varies from 3 days in Rhabditidae to 12 months in some Chromadoridae and Enoplidae (Houthoofd et al., 2003). Faster development shortens the vulnerable period of embryo to disturbances thus preventing embryonic deformities and/or arrest. Nevertheless, the generation time and fecundity are markedly temperature dependent.

Another aquatic bacterivore *Rhabdolaimus* is stated to survive as dauer stage in warm dry and acidic soils (Dmowska, 2000; Beier & Traunspurger, 2001). It has been reported that marine nematodes from oligotrophic regions of ocean are smaller in size than those from sites showing higher level of organic matter flux (Udalov et al., 2005). Such smaller nematodes produce fewer eggs than larger nematodes.

This leads to the lower rate of reproduction and therefore, to the lower proportion of juveniles. The "male: female" ratio tends to be 0.7 while a ratio of 0.4–0.6 has been found in nematode communities from deep-sea hydrothermal vents (Zekely et al., 2006).

## Ecological adaptations

Light reaches only in the upper layers of the water column; hence photosynthesis is limited to a few 100 meters water depth. The main energy source for deep bottom dwellers, therefore, comes from the primary production at the surface. The organisms inhabiting this niche are mostly extremophiles, tolerant of extremely low temperatures (<0°C) and have an adaptation to high pressure as well. Aquatic nematodes, like their terrestrial counterparts, serve as food for small invertebrates or fungi and can be categorized as herbivores, carnivores, omnivores, predators, bacterivores and fungivores with a range of food sources viz., algae, diatoms, aquatic vegetation, bacteria, fungi, other small invertebrates including nematodes.

Littoral macrophytes, their associated periphytons and free-floating biofilms also provide limited in situ resources for nematodes (Peters & Traunspurger, 2005). The nature of the organic substrate in the environment changes with time. Different food supplies influence species compositions and their succession (Ferris & Matute, 2003; Ruess, 2003; Ruess & Ferris, 2004; Michiels & Traunspurger, 2005; Ferris & Bongers, 2006) directly as well as indirectly.

During the settling of food resources from surface to deep floor, much of the photosynthetic derived material is mineralized. Larval forms of soft-bodied marine invertebrates including nematodes are adapted to take advantage (Manahan, 1990) of the organic carbon as dissolved organic material (DOM). In marine environments, the meiofauna builds the trophic linkage between bacteria and macrobenthos (Kuipers et al., 1981) and constitute an energy sink (McIntyre, 1969).

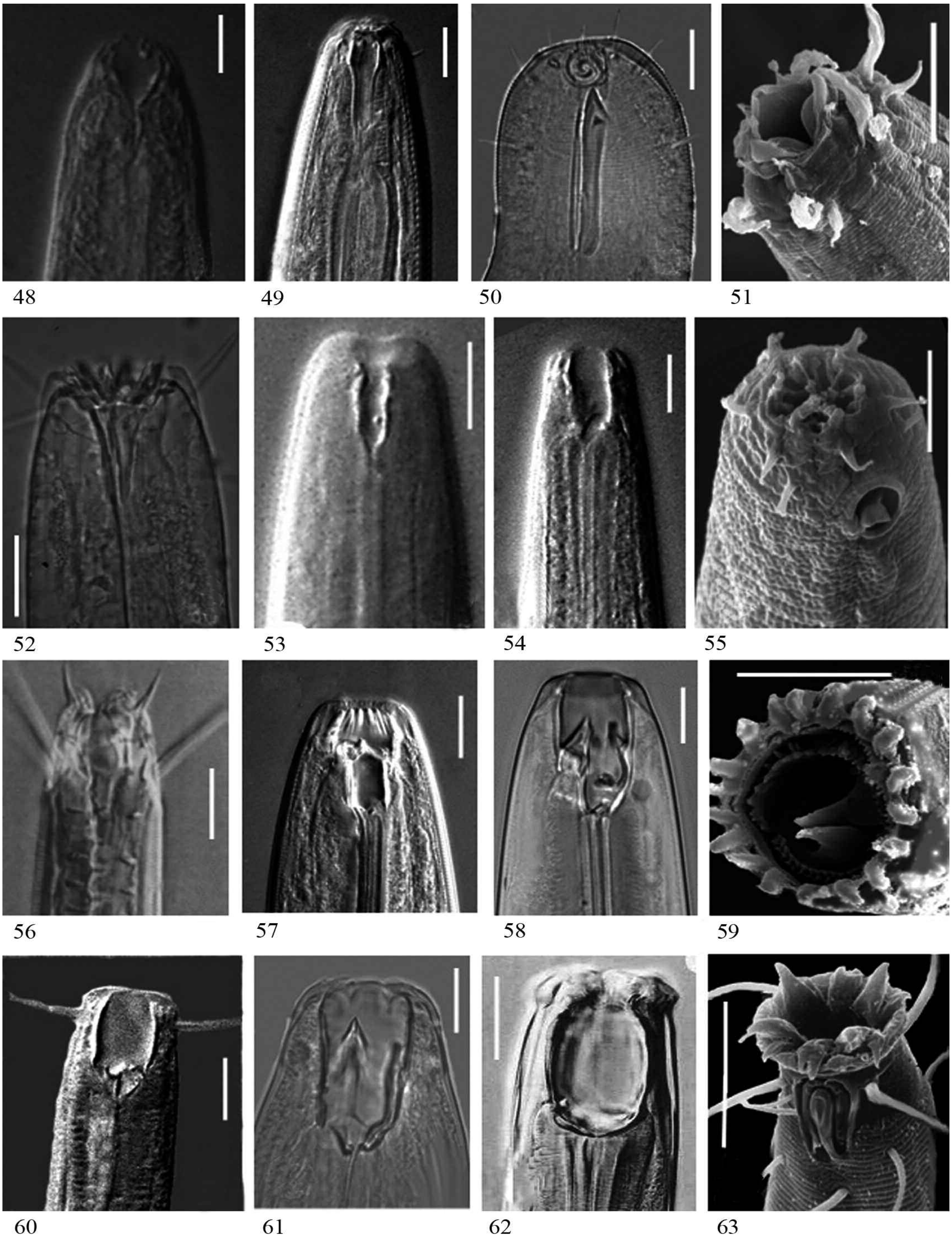
Besides the direct consumption of detritus, nematodes carry out double remineralization and cycle in carbon twenty times their mass annually (Platt & Warwick, 1980). Thus nematodes facilitate the detrital conversion by mechanical breakdown of the detritus, excretion of limiting nutrients to bacteria, producing films conducive to bacterial growth and by bioturbating sediments around detritus (Riemann & Schrage, 1978; Meadows & Tufail, 1986) hence increasing porosity and light penetration. Thus the meiofaunal nematodes affect mat communities through bioturbation and grazing (Höckelmann et al., 2004).

The habitat preference has been observed in some marine nematode families (Tietjen, 1977) e.g., muds: Comesomatidae, Linhomoeidae; muddy sands: Comesomatidae, Monhysteridae, Desmodoridae, Linhomoeidae; fine sands: Monhysteridae, Comesomatidae, Desmodoridae, Axonolaimidae; medium-coarse sands: Monhysteridae, Desmodoridae, Chromadoridae; clean, coarse sands: Epsilonematidae and families of Draconematoidea. Current transport apparently plays a significant role in the dispersal of certain meiobenthic nematodes.

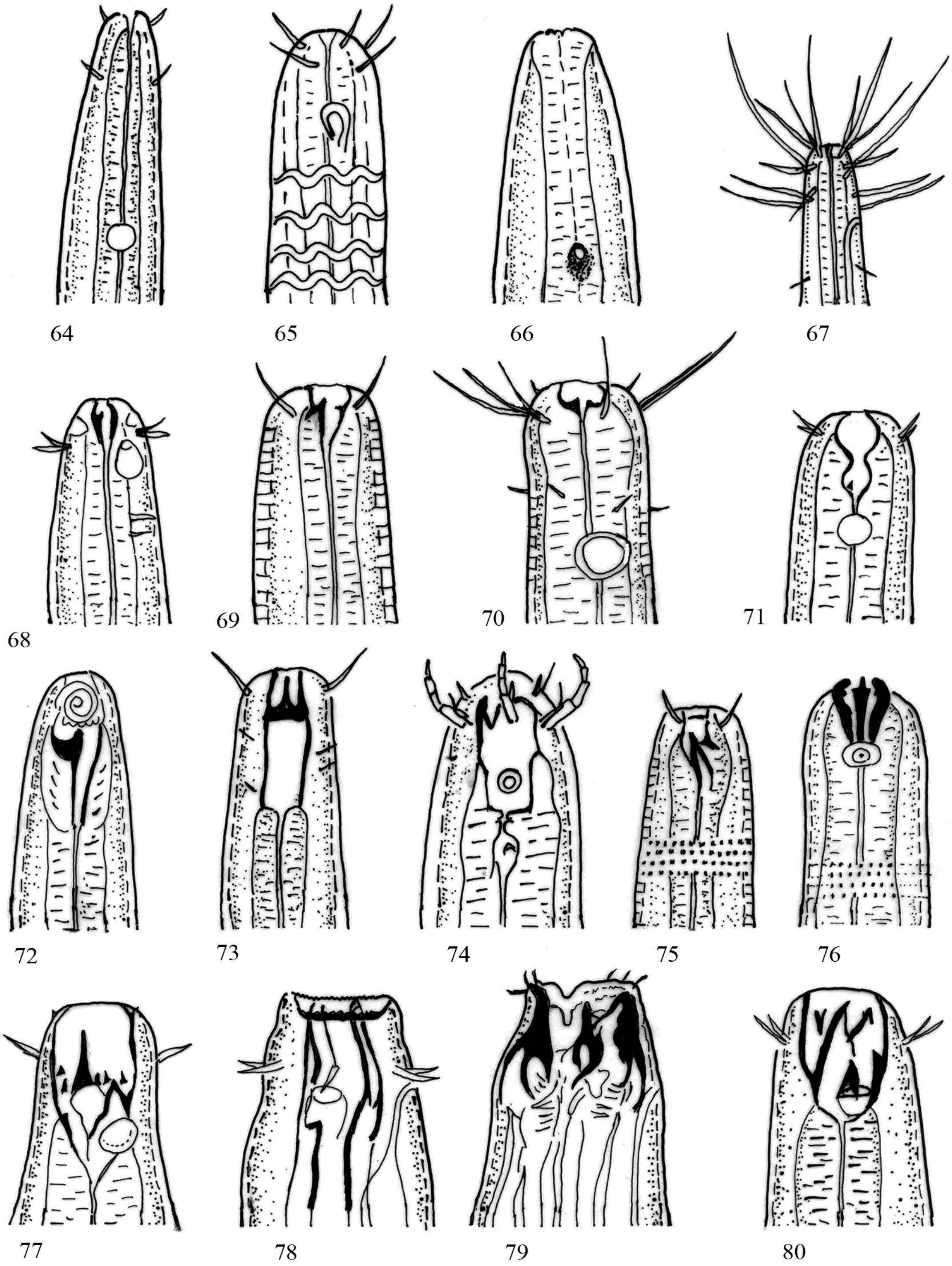
However, the nematodes occurring in the surfacial layers of the sediments seem to be the most affected (Witthöft-Mühlmann et al., 2007). Some species like *Sabatieria pukhra* (Schneider, 1906) and *Odontophora setosa* (Allgen, 1929) found in the deeper sediment layers are rarely suspended (Eskin & Palmer, 1985). The species diversity and the occurrence of the nematodes are influenced mainly by wind speed and river discharge. In calm weather and low discharge, species diversity is reduced and deposit feeders dominate.

The feeding habits can be inferred from the physiognomic characters of buccal cavities (Wieser, 1960; Wieser & Kanwisher, 1961; Boucher, 1973; Platt, 1977; Romeyn & Bouwman, 1983; Jensen, 1987b) and associated structures (Bouwman et al., 1984) in aquatic species. The epistrate feeders e.g., *Eudiplogaster paramatus* (Schneider, 1938); *Chromadorita tenuis* (Schneider, 1906) etc. are toothless or possess a small tooth in buccal cavity to break open cell membranes and suck out the cell contents (juice feeders); deposit feeders (particulate feeders) with or without tooth, swallow the whole food item and prevent its escape e.g., *Daptonema biggi* (Gerlach, 1965) Lorenzen, 1977 (swallowing diatoms), *Linhomoeus gittingsi* Jensen, 1986 (engulfing sulphide-oxidising bacteria.

Sediments with high silt content generally show abundance of deposit-feeders (Heip et al., 1985) usually scoring 2 or 3 on the coloniser-persister scale (Bongers et al., 1991, 1995), characterised by short life cycles and a high colonisation ability (Schratzberger et al., 2007). Predators with buccal cavities armed with movable/protrusible mandibles



Figures 48-63. Modifications in stoma.
Fig. 48: *Bujaurdia* sp. Fig. 49: *Plectus* sp. Fig. 50: *Onyx* sp. Fig. 51: *Tripylina* sp. Fig. 52: *Odontophora* sp. Fig. 53: *Udonchus* sp. Fig. 54: *Diplogastrellus* sp. Fig. 55: *Achromadora* sp. Fig. 56: *Enoplolaimus* sp. Fig. 57: *Mononchoides* sp. Fig. 58: *Odontopharynx* sp. Fig. 59: *Fictor* sp. Fig. 60: *Prismatolaimus* sp.; Fig. 61: *Onchulus* sp. Fig. 62: *Iotonchus* sp. Fig. 63: *Odontophora* sp. www.nem.wur.nl/UK/In+the+picture/Gallery/ (Scale bar = 10 µm).



Figures 64-80. Modifications in stoma.
Fig. 64: *Oxystomina* sp. Fig. 65: *Ceramonema* sp. Fig. 66: *Pseudocella* sp. Fig. 67: *Barbonema* sp. Fig. 68: *Odontanticoma* sp. Fig. 69: *Neochromadora* sp. Fig. 70: *Cobbia* sp. Fig. 71: *Gammarinema* sp. Fig. 72: *Gomphionema* sp. Fig. 73: *Parodontophora* sp. Fig. 74: *Bathylaimus* sp. Fig. 75: *Ptycholaimellus* sp. Fig. 76: *Synonchium* sp. Fig. 77: *Octonchus* sp. Fig. 78: *Calyptronema* sp. Fig. 79: *Filipjevia* sp. Fig. 80: *Ditlevsenella* sp.

for swallowing the whole prey (e.g., members of Thoracostomopsidae, Enoplidae, Selachinematidae) can be largely classified as persisters; and the scavengers with buccal cavity provided with a lumened onchium (tooth-like structure) to feed on dead animals or suck the cell contents of injured animals e.g., oncholaimids and enchelidiids.

Bonger's (1990) colonizer-persister classification of nematodes holds good for terrestrial and freshwater habitats, however, it has less application in marine habitat (Bongers et al., 1991; Fraschetti et al., 2006), partly due to a lack of empirical support for the classification of some marine genera and the absence of extreme colonisers and persisters in most marine habitats. Nevertheless, *Sabatieria* has been found to be a good colonizer showing dominance in anthropogenically disturbed sediments (Tietjen, 1980).

The individuals have evolved life-history characteristics (e.g. rapid growth rate, ability to adapt to a wide range of environmental conditions) that allow them to quickly establish in newly exposed habitats or disturbed sediments in high densities (Thistle, 1981; Moore & Bett, 1989; Somerfield et al., 1995). The environmental constraints restrict species establishment and mediate interactions between successful colonists (Schratzberger et al., 2008) *Leptolaimus* de Man, 1876 found at physically disturbed sites, is not classified as truly opportunistic species (Modig & Ólafsson, 1998).

Ullberg & Ólafsson (2003) hypothesised that the agility of such small, surface-dwelling nematode species with high dispersal potential (Lee et al., 2001; Commito & Tita, 2002) might be an evolutionary response towards higher levels of competence for coping with disturbance (Schratzberger et al., 2009).

## Adaptations to stress

Many aquatic nematodes can adapt physiologically to environmental challenges (Samoiloff et al., 1980, 1983; Mutwakil et al., 1997; Doroszuk et al., 2006). Fresh water as well as deep sea environments offer much hostile and extreme conditions compared to other aquatic habitat types. Therefore, the physiological challenges faced by nematodes are greater in these ecosystems.

A variety of environmental stresses may trigger quiescence viz., desiccation or high temperature (anhydrobiosis), low temperature (cryobiosis), osmotic stress (osmobiosis) and low oxygen (anoxybiosis); in extreme cases of prolonged quiescence, the metabolic rate may fall below detectable levels and appear to cease. This extreme dormant condition is referred to as anabiosis (Wharton, 1986) or alternatively as cryptobiosis (Cooper & van Gundy, 1971). Unlike diapause, the dormant state ends when the environmental stress is relieved.

***Temperature***. Many biological structures, such as enzymes and lipid bilayer membranes may show molecular instability or fluidity due to temperature extremes. Increasing temperatures can increase reaction rates and can cause protein denaturation, resulting in complete and often irreversible loss of function (Hochachka & Somero, 1984). In fresh water ecosystems such as springs, nematodes generally tend to avoid high temperatures above 43°C and high ionic concentrations (Ocana, 1991a, b) except *Rhabditis terrestris* (Stephenson, 1942). At hydrothermal vents, however, temperature can range from 2°C to 400°C and animals may have occasional brief contact with temperature difference of 100°C (Chevaldonné et al., 1992; Delaney et al., 1992; Cary et al., 1998; Desbruyères et al., 1998).

The deep sea is a relatively inhospitable environment for metazoans with constantly low (~2 °C) ambient temperature, high pressure, absence of light and scarce organic carbon. Adaptation to the deep sea includes presence of more "fluid" proteins and lipids to counter the high pressure and low temperature (Hochachka & Somero, 1984). Low temperatures may slow or impede many biochemical reactions and decrease the fluidity of lipids, a factor of primary importance to cell membrane function (McMullin et al., 2000).

Most of the adaptations that enable polar intertidal invertebrates to survive freezing, are associated with their ability to withstand aerial exposure. Nematodes surviving the freezing, exhibit low metabolic rate and slow growth rate and the inability to survive at temperatures above 3-8°C. The bacterial-feeder, *Plectus murrayi* Yeates, 1970 (Timm, 1971) inhabiting semi-aquatic and terrestrial biotopes in the Antarctic McMurdo Dry Valleys, has its distribution limited by organic carbon and soil moisture and survives extreme desiccation, freezing conditions, and other types of stresses (Adhikari et al., 2010).

The Antarctic nematode, *Panagrolaimus davidi* Timm, 1971 shows both freeze-avoidance and freeze-tolerance strategies thus experiencing freezing temperatures over nine months of the year and facing regular cycles of freezing and thawing in spring; the nematode thus undergoes cryoprotective dehydration instead of freezing when held at its nucleation temperature for a longer period, or when cooled at a slower rate (Wharton et al., 2003).

*P. davidi* is the only animal known to survive ice crystallization within its cells (Wharton et al., 2005). With slower cooling rates, the water inside the worm is super cooled, thereby creating a vapor pressure difference between the ice in the medium and the nematode. Besides synthesizing trehalose, *P. davidi* produces a protein that inhibits the activity of organic ice nucleators though the sequence of this protein has no homology with any other anti-freeze or ice-nucleating proteins (Wharton et al., 2005).

***Oxygen***. Many meiobenthic species persist over extensive periods under hypoxic and anoxic conditions (Wetzel et al., 2002). Nematodes are the most tolerant organisms as their species richness does not change in hypoxic-anoxic conditions though their species composition and trophic structure display significant changes (Gambi et al., 2009).

Jensen (1987a) found that species, living in deeper sediment layers were significantly more slender than their oxybiotic, surface-dwelling congeners, however, nematodes of the genera *Desmoscolex* Claparède, 1863; *Tricoma* Cobb, 1894 and *Cobbionema* Filipjev, 1922 have been reported mostly from the anoxic depths (> 300 m) of the Black Sea (Zaitsev et al., 1987). At some places even *Desmoscolex* and *Bolbolaimus* Cobb, 1920 are replaced by the species (*Chromadorella* Filipjev, 1918, *Sabatiera* Rouville 1903 and *Polysigma* Cobb 1920) more tolerant to the extreme conditions (Gambi et al., 2009).

Oxygen stress is successfully tackled by the fresh water genera of Monhysteridae and Tobrilidae (Triplonchida) having prevalence in the habitats with limited or no oxygen (Nuss, 1984; Jacobs, 1987). Low oxygen concentrations are tolerated well by most *Rhabditida* (Ocana, 1993). Such species survive anaerobic sediments by anaerobic metabolism, facultative anaerobic metabolism or quiescence (Bryant et al., 1983). Few species can cope with changing oxygen levels by alternating between aerobic and anaerobic metabolism similar to the mechanism found in the insect parasite *Steinernema carpocapsae* Weiser, 1955 (Shih et al., 1996).

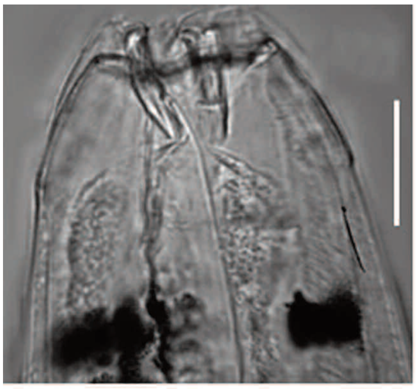
Likewise a species *Allodorylaimus andrassyi* (Meyl, 1955) Andrássy, 1986 (Dorylaimida) found to survive in oxygen-free sediments of Lake Tiberias (Israel) for 8 months of a year (Por & Masry, 1968). High salinity and high temperature are less common physiological stresses for aquatic nematodes than low oxygen. In springs, *Udonchus* Cobb, 1913 and *Rhabdolaimus* have been reported to tolerate high salinity and temperature (Ocaña, 1991a, b). However, the genus *Mesodorylaimus macrospiculum* Zullini, 1988 seems to withstand stress (Tudorancea & Zullini, 1989) in intermittent lakes that are subject to high salinity and temperature.

The ability to survive under anaerobic conditions may thus be quite widespread among nematodes, although different mechanisms may be involved (Schiemer & Duncan, 1974; Bryant et al., 1983). The presence of *Theristus anoxybioticus* Jensen, 1995 at the oxygenated sediment surface of muddy sediment suggested that even this facultative anaerobe nematode needs to reach oxygen for its reproduction (Jensen, 1995).

Thus, survival under anoxia would be possible only under critical conditions. For reproduction on the other hand, especially for the development of eggs, there must be another more efficient pathway of energy production (Riess et al., 1999) although nitrate respiration has never been reported in nematodes so far.

In shallow beaches drifting macroalgal mats in the summer months induce anoxic and sulfidic conditions with devastating effects on members of the benthic fauna. Other disturbances like eutrophication in conjunction with density-stratified water masses frequently results in severe oxygen depletion of bottom waters, especially during the summer months, leading to hypoxic (dissolved oxygen concentration <2 mg $l^{-1}$) or even anoxic (dissolved oxygen concentration of 0 mg $l^{-1}$) conditions (Rosenberg et al., 1992). While most hypoxic events affect the fauna in deeper sublittoral regions below a thermo- or halocline; eutrophication has also been attributed to the increase in benthic macroalgae (Rosenberg, 1985; Hull, 1987; Raffaelli et al., 1991; Kolbe et al., 1995).

There is induction of Hb synthesis in many invertebrates under stressful conditions (hypoxia, temperature increase and CO poisoning). The mud-dwelling nematode *Enoplus brevis* Bastian, 1865 with a pharyngeal haemoglobin (Hb) shows feeding rates under hypoxia than the related, *E. communis* Bastian, 1865 that lacks Hb (Atkinson, 1977). Hb may be associated with vital functions in euryhaline invertebrates living in widely different salinities and pH and lacking significant osmotic, ionic, and acid-base regulatory capacities (Weber & Vinogradov, 2001).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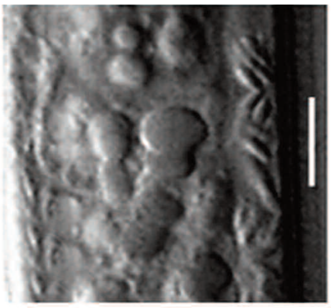
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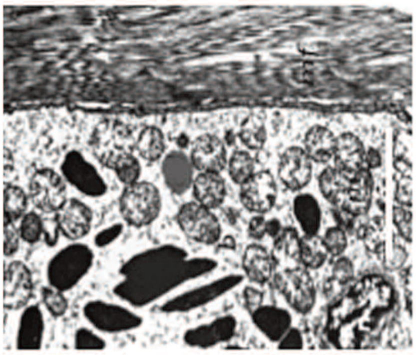
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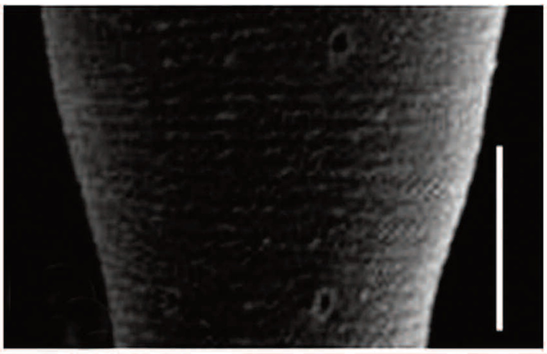
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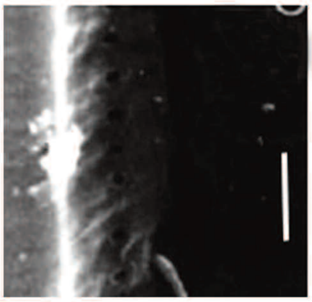
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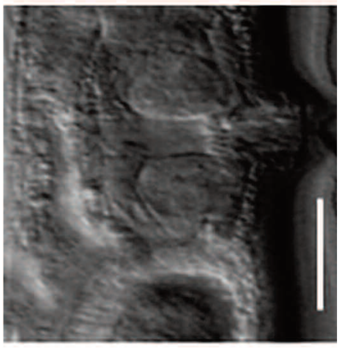
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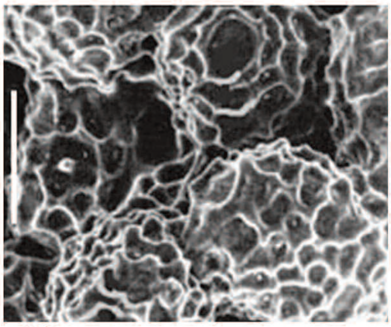
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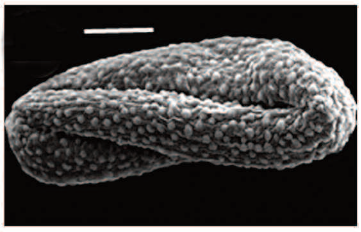
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Figures 81-91. Fig. 81: Pigment spot in *Enoplus* sp. Fig. 82, 83: Crystalloids in pseudocoelom of *Tobrilus* sp. and *Ironus* sp. Fig. 84: Ultra structure showing longitudinal section of muscle fibres with crystalloids and electron-dense bodies. Fig. 85, 86: Body pores in *Cryptonchus* sp. and *Ptycholaimellus* sp. Fig. 87: Hypodermal gland openings. Fig. 88, 89: glands associated with uterus and vagina. Fig. 90, 91: Egg shells with rugose or spinose surface [Scale bar: 81-83, 85-89, 90, 91 = 10 µm; 84 = 1 µm).

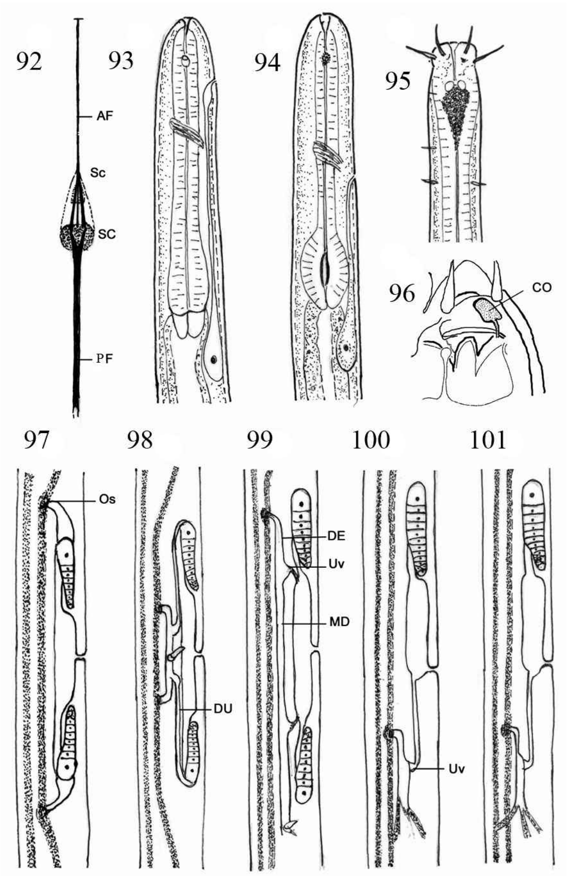


Figure 92: Metaneme (AF: anterior filament, PF: posterior filament, Sc: Scapulus, SC: sensory cell). Fig. 93: pigment spot. Fig. 94: Ocellus. Fig. 95: Ocellus surrounded by pigments. Fig. 96: Anterior end of nematode with cephalic organ (CO). Figures 97-101: Demanian system (Os: Osmosium; Uv: Uvette; MD: Main duct; DE: Ductus entericus; DU: Ductus uterinus).

***Water.*** The aquatic nematodes face two basic problems of water gain or water loss depending upon the type of surrounding environment.

Marine nematodes the osmoconformers, often live in water that has a very stable composition and, hence, they have a very constant internal osmolarity. Many invertebrates that osmoconform achieve tissue tolerance by increasing intracellular osmolarity by mobilization of amino acids, thereby balancing extracellular fluid.

This reduces the osmotic gradient across cell membranes and maintains constant cell volume (Schmidt-Nielsen, 1997; Kirk et al., 2002). *Panagrolaimus davidi*, an Antarctic nematode, is associated with ornithogenic soils (Porazinska et al., 2002) in coastal areas that are ice-free during spring and summer with sufficient meltwater from adjacent snowbanks. The water content of these sites varies from saturated to completely dry (Wharton, 1998) and the nematode faces changes in external osmotic concentration (Wharton, 2003). *Panagrolaimus davidi* maintains its internal osmotic concentration above that of the external medium and is thus an hyperosmotic regulator.

The nematode achieves regulation under hyposmotic stress more rapidly than under hyperosmotic stress (Wharton, 2010). The nematodes found in coastal zones are exposed to conditions of rapid de- and rehydration similar to the mosses and lichens. Drying initially decreases rates of anaerobic microbial processes in sediments due to reduced oxygen penetration (Baldwin & Mitchell, 2000). Differences among aquatic and terrestrial species in resistance to desiccation and inundation cause shifts in community composition along hydro-period gradients (Larned et al., 2007).

The ability to enter anhydrobiosis may be one of the most important and widespread adaptations in evolutionary terms amongst nematodes but not expressed in species of stable habitats. Freshwater nematodes of temporary ponds commonly enter quiescence in response to water stress (Wharton, 1986; Womersley & Ching, 1989). The phenomenon is also common in nematodes of polar regions (Pickup & Rothery, 1991; Wharton & Barclay, 1993; Wharton, 2004). Important information on anhydrobiosis has been provided by several workers (Cooper & van Gundy, 1971; Demeure & Freckman, 1981; Wharton, 1986; Womersley, 1987; Barrett, 1991; McSorley, 2003).

The onset of anhydrobiosis marks a gradual water loss from 75-80% to 2-5% in anhydrobiotic forms (Demeure & Freckman, 1981). The fresh water nematodes *Actinolaimus hintoni* Lee 1961 and *Dorylaimus keilini* Lee, 1961 were revived from cryptobiotic (anabiotic) stage in dried mud (Lee, 1961).

Anhydrobiotic nematodes contain large amounts of sugars, especially the disaccharide trehalose, a dimer of glucose that protects cells by replacing water associated with membranes and proteins.

However, most species are killed if drying occurs too quickly whereas repeated events of drying and rehydration decrease viability of nematodes (Demeure & Freckman, 1981; Barrett, 1991). Anhydrobiotic nematodes rehydrate in water, but there is an average lag time (from less than an hour to several days) between immersion and their return to normal activity (Cooper & Van Gundy, 1971; Wharton, 1986; Barrett, 1991). Recovery is improved if rehydration is slow, and nematodes are exposed to high relative humidity before being immersed in water. Anhydrobiosis involves decreased cuticular permeability and the condensation or packing together of tissues with increased levels of trehalose or glycerol (Demeure & Freckman, 1981; Wharton, 1986; Womersley, 1987; Barrett, 1991). Coiling is a typical behavioral response observed in anhydrobiotic nematodes.

***Pollutants.*** Environmental pollution is an important cause of stress in natural populations. Besides affecting the population dynamics, it can also lead to genetic changes (mutations) and adaptations. The nematode bioassays lead to detection of a wide range of chemical concentrations with distinct toxic effects of lethality, developmental inhibition and mutagenicity. Most studies have been undertaken using the continental species *Panagrellus redivivus* Goodey, 1945 against few studies carried out on aquatic nematodes to determine pollution and toxicity in marine environments (Warwick, 1981b; Samoiloff & Wells, 1984; Bogaert et al., 1984; Vranken et al., 1991).

Aller & Aller (1992) showed that meiofauna activity stimulated solute fluxes and reaction rates, particularly aerobic decomposition and associated processes such as nitrification in the oxic zone of the marine sediments. Among toxicants, sulfide is perhaps the most abundant with its impacts on biological systems well documented (Somero et al., 1989; Grieshaber & Völkel, 1998).

Sulfide, in just micromolar amounts, is capable of impairing biological processes and may severely inhibit aerobic metabolism by interfering with cellular respiration and oxygen transport in different metazoan (Somero et al., 1989; Vismann, 1991; Grieshaber & Völkel, 1998; Szabó, 2007). In the mitochondria, sulfide may poison the respiratory enzyme cytochrome c oxidase, thus inhibiting ATP production by the electron transport chain and is capable of inhibiting muscular contraction independent of its effects on aerobic metabolism (Julian et al., 1998).

Thus an organism adopts the strategies to avoid sulfide, switch to anaerobic metabolism (Grieshaber & Völkel, 1998), exclude sulfide from sensitive tissues, or oxidize sulfide to less toxic forms. Most inhabitants of vent and seep environments do not realistically have the option of avoiding sulfide altogether. Some marine nematodes e.g., *Oncholaimus campylocercoides* De Coninck & Stekhoven, 1933; *Sabatieria wieseri* Platt, 1985; *Terschellingia longicaudata* de Man, 1907; *Sphaerolaimus papillatus* Kreis, 1929; *Siphonolaimus ewensis* Warwick & Platt, 1973; *Pontonema vulgare* Bastian, 1865, while living in sulphidic transition zones convert hydrogen sulphide to elemental sulphur which temporarily reduces the concentration and toxic effect of $H_2S$ and also provides an energetic 'deposit' for latter oxidation to thiosulphate, sulphite or sulphate under oxic conditions (Thiermann et al., 2000).

Many nematodes (Stilbonematinae, Desmodoridae) harbour symbiont chemoautotrophic bacteria (Hentschel et al., 2000; Ott et al., 2008; Bayer et al., 2009) that oxidize sulfide and fix $CO_2$. The Hbs of these organisms bind sulfide without covalent modification of the heme groups and facilitates its transport or diffusion thus protecting the tissues from sulfide poisoning.

These symbionts, in turn, constitute the worms' major food source and are acquired from the environment and shed off at every moult but reacquired from the environment. The mechanisms of symbiont recruitment from the environment (Bulgheresi et al., 2006) have shown that $Ca_2+$-dependent lectin Mermaid mediates symbiont–symbiont and worm–symbiont attachment in *Laxus oneistus* (Ott et al., 1995).

Thick tubes or cuticles reduce or prevent exposure of some external tissues to sulfide with *Ptycholaimellus* serving a good example (Nehring et al., 1990). The effect of mercury contamination was rather confusing as low doses of mercury appeared to have much more drastic effects than the medium and high doses.

Austen and McEvoy (1997) observed that low doses of copper and zinc seem too toxic to kill all the bacteria and meiofauna in the samples so that complete decomposition of nematodes did not occur (Hermi et al., 2009). Schratzberger et al. (2009) found *Araeolaimus bioculatus* (de Man, 1876) to be intolerant to mercury contamination, with effects observed even at the low concentration used (0.084 ppm dw).

*Marylynnia stekhoveni* (Wieser, 1954) was categorized as "opportunistic" at low and medium mercury doses with Hg(L) and Hg(M) concentrations whereas *Prochromadorella neapolitana* (de Man, 1876) Micoletzky, 1924 was found to be a "mercury-resistant" species (Schratzberger et al., 2009).

Pollutants also modify the distribution and abundances of nematodes through indirect ecological interactions (Johnston & Keough, 2003). If pollution decreases abundance of a competitively dominant species, inferior competitors may increase in abundance not as a direct result of the contaminant but due to altered competition. Copper causes decrease in recruitment and abundance of a number of organisms (Johnston & Keough, 2000, 2003; Mayer-Pinto et al., 2010). Thus metazoans largely detoxify absorbed or ingested metals by using metal-binding proteins (metallothioneins) and forming subcellular inclusions.

These mechanisms often act jointly to consolidate and enclose excess metals, which then accumulate within tissues and/or skeletal structures over time (Beeby, 1991; Luoma & Carter, 1991). The metal detoxification strategies used by nematodes are not very different from those used by other organisms (McMullin et al., 2000) for example the existence of phytochelatins, the heavy metal-binding peptides, in nematodes that are synthesized by plants and fungi when exposed to metals (Monserrat et al., 2003).

## Phylogenetic implications

Assuming that all life originated in the sea and that metazoan phyla evolved more than 550 million years ago (mya) during the Precambrian period (Conway, 1993; Valentine et al., 1996, 1999; Fedonkin & Waggoner, 1997; Peterson & Davidson, 2000), it can be assumed that the ancestral nematode was also marine.

Nematodes also lack an informative fossil record (the oldest known fossil, *Cretacimermis libani* Poinar et al., 1994 (Poinar, 2003) dates to around 135 mya). Filipjev (1929, 1934) and Lambshead & Schalk (2001) have accepted the marine ancestry of Nematoda while De Ley & Blaxter (2002, 2004) considered a terrestrial origin for the Nematoda.

As highly productive terrestrial ecosystems existed in the Precambrian there might have been chances of supporting the evolution of a new phylum (Kenny & Knauth, 2001). Nevertheless, a marine origin of the Nematoda can be traced as some terrestrial taxa of current phylogeny have been found nested within marine clades.

The strongest evidence for a marine ancestry of the Nematoda comes from the Chromadorea: the basal clades are all predominantly marine (Microlaimoidea, Chromadorida, Desmodorida, Monhysterida, and Araeolaimida) whereas the almost exclusively non-marine *Rhabditida* are derived from the ancestor of the Monhysterida or Araeolaimida (Meldal et al., 2007).

The similarity in cuticular structure of *Acanthonchus* Cobb, 1920 (Wright & Hope, 1968), *Chromadorina* Filipjev, 1918 (Lippens, 1974), and *Caenorhabditis* (Epstein et al., 1971; Zuckerman et al., 1973) lends circumstantial evidence to the hypothesis that the Secernentea arose from chromadorid-like ancestors. However, a reinterpretation of the cuticular structure by Decraemer et al. (2003) suggested that this is a homoplasic character that has appeared independently in several clades.

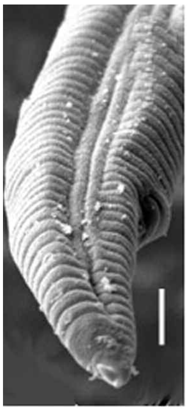
Though aquatic nematodes can not be treated separately as far as the phylogenetic grouping is concerned. Nevertheless, one of these lineages includes marine, freshwater and terrestrial taxa, suggesting that early *Enoplia* were characterised by much greater osmotic tolerance than early *Dorylaimia* (De Ley, 2006).

Most enoplids include large predators with big hooks or teeth in more or less complex arrangements as well as some additional sensory structures such as eyespots and the stretch receptors (metanemes). They are interesting phylogenetically because of possessing some features, presumably ancestral within Nematoda viz., a highly indeterminate mode of development (Justine, 2002) and retention of the nuclear envelope in mature spermatozoa (Lee, 2002).

The ventrally spiral amphid was considered plesiomorhic by Lorenzen (1981), yet the non-spiral form seemed to be a secondary character loss. Likewise, the presence of ocelli is usually considered to be a primitive character though these structures are the most complex photoreceptors that the nematodes possess.

Coomans (1979) suggested that the pigment spots and their associated amphidial photoreceptors are less elaborate and may represent a stage that originated later in the evolution and so have not yet achieved great complexity.

Nevertheless, the occurrence in nematodes with both types of photoreceptors: rhabdomeric and ciliary, supports Vanfleteren & Coomans's (1976) and Sharma et al.'s (2006) conclusion that morphological characters used in the classification are not enough to recognize phyla along the main lines of evolution.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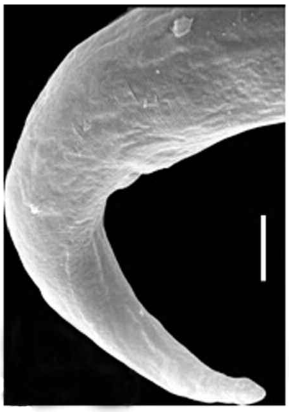
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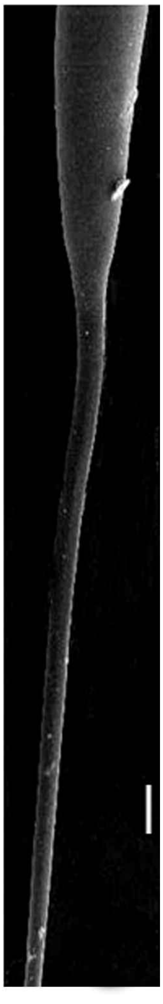


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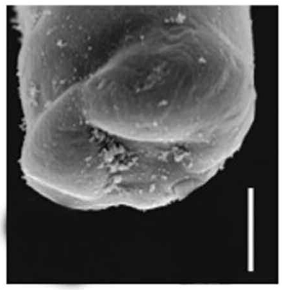
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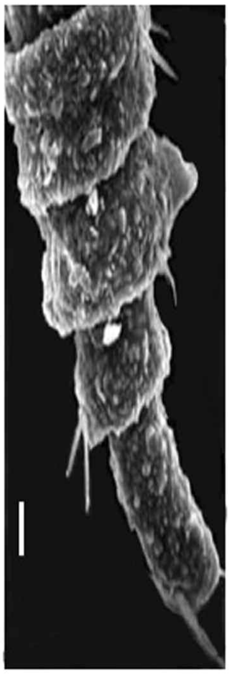
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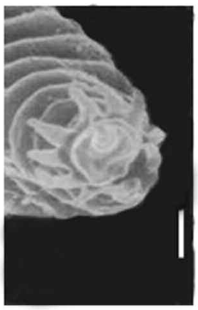
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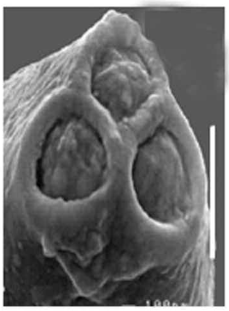
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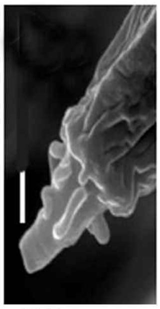
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Figures 102-112. Modifications at posterior body end.
Fig. 102: *Anaplectus* sp. Fig. 103: *Panagrellus* sp. Fig. 104: *Rhabdolaimus* sp. Fig. 105: *Tripylina* sp. Fig. 106: *Chronogaster* sp. Fig. 107: *Plectus* sp.; Fig. 108: *Tobrilus* sp. Fig. 109: *Philometra* sp. Fig. 110: *Epsilonema pustulatum* after Karssen et al., 2000. Fig. 111: *Desmoscolex* sp. Fig. 112: *Cryptonchus* sp. Figures 113-117. Modifications at tail terminus. Fig. 113: *Plectus* sp. Fig. 114: *Chronogaster* sp. Fig. 115: *Epsilonema pustulatum* after Karssen et al., 2000. Fig. 116: *Dorylaimopsis variabilis* Muthumbi et al., 1997. Fig. 117: *Tobrilus* sp. (Scale bar: 102-112 = 10 µm; 113-117 = 1 µm).

## CONCLUSION

Aquatic nematodes are of vital importance as a very significant portion of the energy flow in the benthic system passes through these nematodes. However, one of the main reasons for the aquatic nematodes being ignored is that they are not of direct benefit or nuisance to man. Their role in stimulating bacterial metabolism is now well documented (Tenore et al., 1977; Tietjen, 1980) and they have an important and direct influence on the productivity of shallow waters by enhancing nutrient regeneration in the sediments.

They also affect the texture (Cullen, 1973) and the physical characteristics of sediments by mucous secretion, which are significant for dredging and dumping operations. It can be further said that the story of their adaptations to a particular environment type is far more complex than could be inferred. Despite the recent information gained, studies are required on the plesiomorphous forms, the mutants and the apomorphs to reveal how far deviations exist.

Future researches should further consider the detailed structure and anatomy of the receptors as modification in them are reflected in changes in behaviour. Although the nematode nervous system is considered to be a conservative system with a rather small number of cells, different behavioural patterns exist according to the different environments and ecological niches occupied by the species.

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