A review of the family Ceramonematidae (marine free-living nematodes), with descriptions of nine species from the White Sea

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Tchesunov, A.V. & Miljutina, M.A. 2002. A review of the family Ceramonematidae (marine free-living nematodes), with descriptions of nine species from the White Sea. *Zoosystematica Rossica*, **11**(1): 3-39.

Morphology, biology and taxonomy of the nematode family Ceramonematidae Cobb, 1933 are summarised and reviewed. Plesiomorph-apomorph polarities of cuticle sculpture, cephalic sensilla pattern, amphid shape are revealed with use of the out-group comparison and ontogenetic observations. The genera *Ceramonema* and *Pselionema* are distinguished by the most apomorph character states; both genera combined comprise the greatest number of species, of the widest overall ecological range. The other ceramonematid genera display more plesiomorph character states and contain much less species; these are strictly confined to coarse sands. Ceramonematidae are related to the families Diplopeltoididae sensu Tchesunov (1990) and Tarvaiidae. The family Ceramonematidae consists of two subfamilies: Ceramonematinae with the genera *Ceramonema* (= *Ceramonemoides*, = *Cyttaronema*), *Dasynemella* (= *Leptodasynemella*), *Dasynemoides* (= *Dasynemelloides*), *Metadasynemella* (= *Dictyonemella*), and *Metadasynemoides*, and Pselionematinae with the genera *Pterygonema* and *Pselionema* (= *Pselionemoides*). Modified diagnoses of the family, subfamilies and genera are given. Separation of higher ceramonematid taxa is based largely on features of body cuticle annulation as well as on anterior sensilla pattern, while cephalic ratio and finer details of body annulation are important for species discrimination. Annotated lists of species are given for each genus. The genus *Ceramonema* is subdivided into two subgenera, *Ceramonema* s. str. (body cuticular annules with zygapophyses) and *Proceramonema* subg. n. (body annules devoid of zygapophyses). New species from the White Sea (*Ceramonema fluctuosum* sp. n., *C. marisalbi* sp. n., *C. mokievskii* sp. n., *Dasynemoides crassus* sp. n., *Metadasynemoides labiatus* sp. n., *Pselionema concinnum* sp. n., and *P. mirabile* sp. n.) are described. *Dasynemella riemanni* Haspeslagh is recorded for the first time from the White Sea. The description of *Pselionema simplex* De Coninck from the White Sea is supplemented with notes on juveniles.

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INTRODUCTION

Members of the family Ceramonematidae have somewhat unusual or even oddly appearance among other marine nematodes. Their cuticle is composed of broad and thick annules, which make together an impression of a strong sculptured armour. Anteriorly, the cuticular annules are fused together in a bullet-shaped cephalic capsule. Because of the light-refractive cuticle, the internal organs of ceramonematids are hardly visible and, hence, poorly studied. The family includes only marine species, mostly confined to coarse sands of sea shallows. The ceramonematids may be very conspicuous in some places attaining even about 5-10% of the species composition. A peculiar feature of the ceramonematid biology is brood care.

Below we propose an essay on the family Ceramonematidae basing on some White Sea species here described.

HISTORY

The first ceramonematid nematodes were described by Cobb (1920). He placed the central genus *Ceramonema* Cobb, 1920 in a newly created order Cytolaimia, which is not retained in the modern nematode classification. Filipjev (1922) is the only other author, who described a ceramonematid species in 1920's. Later, Cobb (1933) established the family Ceramonematidae. Chitwood (1936) published brief descriptions of several further ceramonematid species.

Close and extensive study of ceramonematids was undertaken by Belgian nematologists De

Coninck (1942) and Haspeslagh (1973, 1979). De Coninck established a new standard of detailed species descriptions and modified the classification with amphid shape as a key character. Haspeslagh understood the cuticle construction at the optic level using some new terms (e.g. zygapophyses) and performed an analysis of the family in terms of comparative morphology. Besides that, she complicated considerably the family classification by accommodating new characters (e.g. cuticle vacuolisation) and described a number of minor new genera. However, her classification was not, on the whole, accepted by some nematologists.

In 1950-1960s, many new ceramonematid species were described, especially by Gerlach (see References) during his extensive exploration of the tropical and world faunas of marine nematodes. Contributions to knowledge of the diversity of ceramonematid nematodes were made also by Andrássy, Chitwood, Furstenberg & Vincx, Hopper, Platt, Timm, Vitiello, Ward, Warwick, Wieser, and Zhang (see References). Platt & Zhang (1982) published a pictorial key for species of *Ceramonema*. Hopper (1973) discovered the phenomenon of egg carrying by ceramonematid females.

Lorenzen (1981) anew reduced and thus simplified after Haspeslagh the classification of Ceramonematidae reducing the number of genera. The position of the family within the nematode classification represents a particular problem. Long time, the ceramonematids were considered to be related to desmodorid or even monoposthiid nematodes and respectively were placed together or within those families. This idea was fixed by inclusion of Ceramonematidae in the order Desmodorida by De Coninck (1965) and then by Gerlach & Riemann (1973). Lorenzen (1981) did not found any synapomorphies shared by Ceramonematidae and desmodorid families and therefore included the family Ceramonematidae in the paraphyletic suborder Leptolaimina of the order Chromadorida. However earlier, Gerlach (1950) already assumed for Ceramonematidae a tentative relation to diplopeltid nematodes. Lorenzen (1981) considered Ceramonematidae possibly to be related to Tubolaimoididae basing on the similarity between *Dasynemella* and *Tubolaimoides* in the labial region, buccal cavity, amphids, and shape and pattern of the anterior setae.

In 1990s, first studies on ceramonematid ultrastructure appeared. Australian nematologists Nicholas and Stewart undertook TEM-investigations of cuticles in *Metadasynemoides cristatus* and *Ceramonema carinatum* (Nicholas & Stewart, 1990; Stewart & Nicholas, 1992) and of anterior body in *C. carinatum* (Stewart & Nicholas, 1994). Cuticle as well as some details of cephalic end, pharynx and hindgut in *Pselionema simplex* were studied by Tchesunov (1995).

Only two ceramonematid species were hitherto recorded from Russian seas: *Pselionema annulatum* from the Black Sea (Filipjev, 1922) and *P. simplex* from the White Sea (Tchesunov, 1995).

MATERIAL AND METHODS

The specimens were collected either in the Kandalaksha Bay of the White Sea (*Dasynemella riemanni* and *Pselionema simplex*) or in the Gorlo Strait of the White Sea (all the rest species). Sediment sampling from the depths up to 30 m in the Kandalaksha Bay was done by scuba divers, the samples in the Gorlo Strait as well as the samples from deeper sites in the Kandalaksha Bay were taken using a grab. Nematodes are mounted in glycerine slides.

The following abbreviations are used in the text: a: body length divided by maximum body diameter; a.b.d.: anal body diameter; b: body length divided by oesophageal length; c: body length divided by tail length; c.b.d.: corresponding body diameter; L: body length; V: distance of vulva from anterior end as a percentage of body length.

MORPHOLOGY AND BIOLOGY

Appearance

Body of the ceramonematid nematodes is usually cylindrical, short or thread-like, often wide anteriorly and slightly tapering toward the tail. More seldom, the body shape may be close to fusiform. Body length varies from 400 to 3000 µm. A curious image of the worms is created by the peculiar armoured cuticle. The cuticle consists of broad and thick annules connecting by flexible membranes. Furthermore, the annules are sculpturally complicated by longitudinal ridges and thin undulating peaks overlapping the adjacent annules (Fig. 1). The peaks were termed by Haspeslagh (1973) as zygapophyses. They may enhance rigidity of the cuticle and diminish flexibility of the body. Anteriorly, the cuticle forms a solid bullet-shaped cephalic capsule. Posteriorly, the annules are fused into a solid terminal tail cone. Transverse sutures may be retained anteriorly at the base of the terminal cone. Some ceramonematids provide numerous (up to seven hundred) cuticle annules equally narrow throughout the body length. Other species are characterised by smaller and rather stable (90-100) number of annules. In latter case,

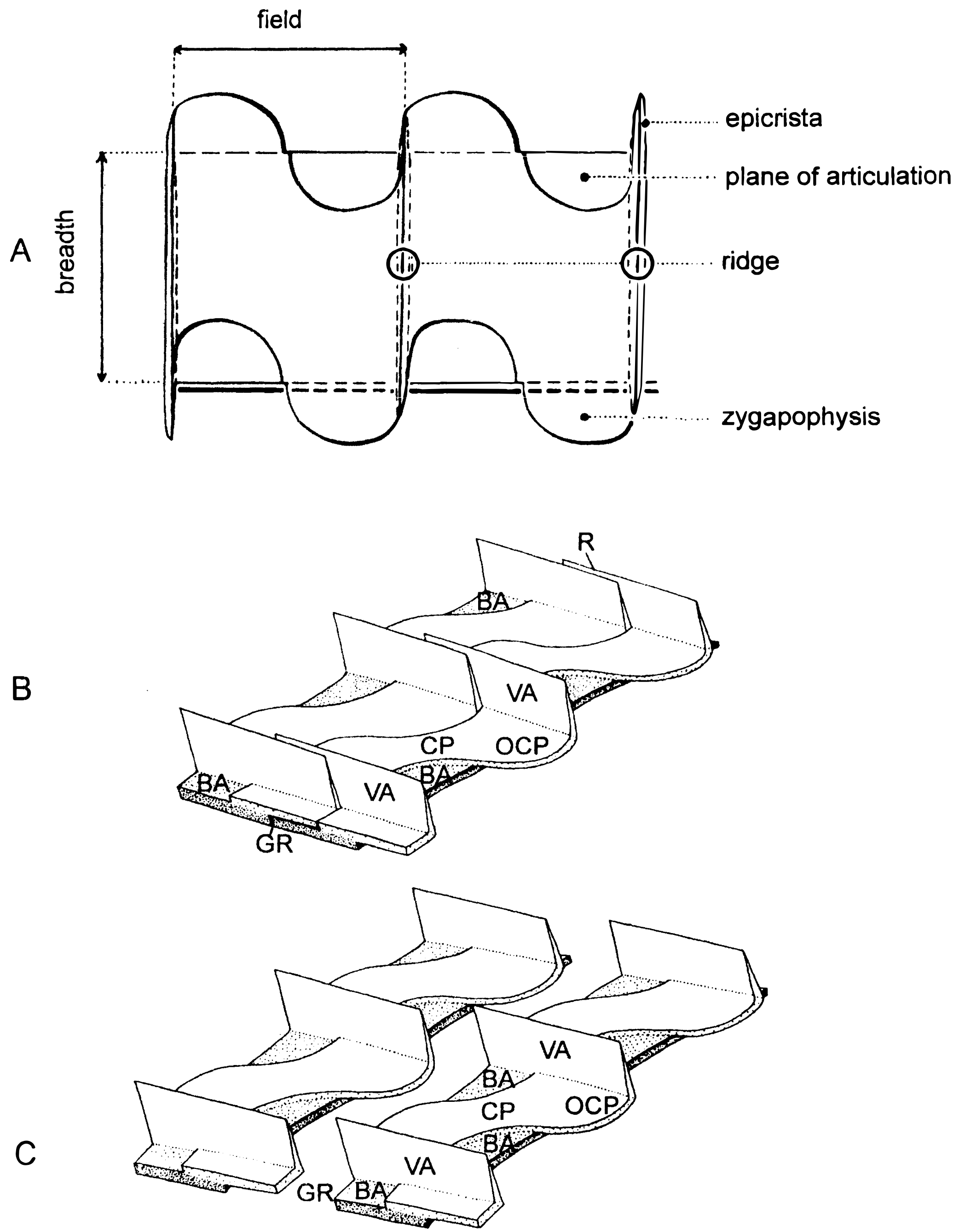

Fig. 1. Structure of ceramonematide cuticle. **A,** structural pattern of an annule; **B, C,** perspective sketches of the cuticle of *Ceramonema carinatum*. Abbreviations for B and C: *BA*, basal platform of cortical plate; *CP*, cortical plate; *GR*, groove between annules; *OCP*, overlapping projection; *R*, ridge; *VA*, vane. Modified after Haspeslagh, 1973 (A) and Stewart & Nicholas, 1992 (B, C).

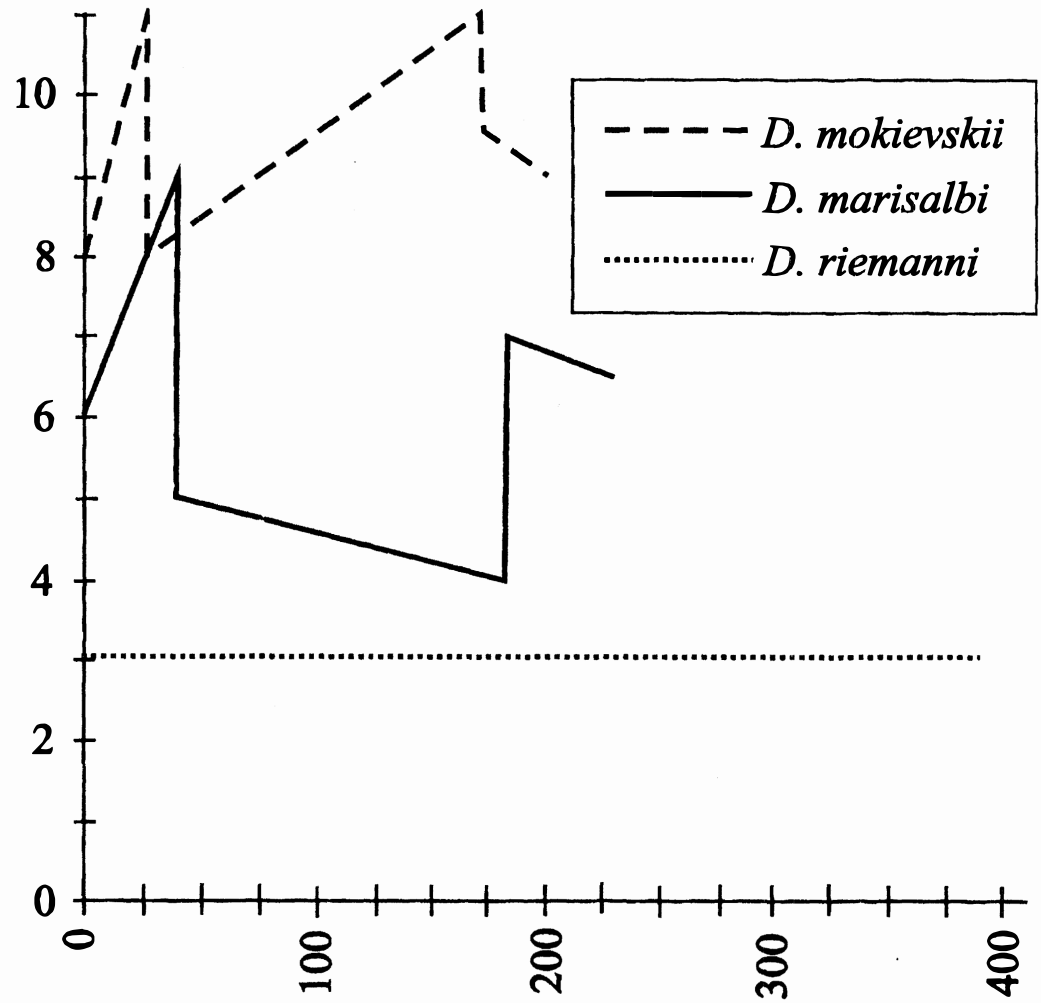

Fig. 2. Change of annule breadth throughout the body length in three ceramonematide species. Vertical axis: annule breadth in ìm; horizontal axis: number of annules.

the annules are broad and unequal. Generally, the annules enlarge gradually from the anterior-most annule to the maximum breadth at the level of the anterior midgut; the next annule is very narrow; then the annules again enlarge gradually in breadth to the maximum anal annule; and then for the third time the annules enlarge gradually in breadth from the first postanal narrow annule to the terminal cone (Figs 2, 3).

Vacuolisation may be developed within the annule cuticle. Tiny vacuoles or vesicles may be distributed around the whole annule or concentrated in small areas underneath the longitudinal ridges. Presence/absence and degree of development of these vacuolisations were treated as key characters for species and genera (Haspeslagh, 1973). Another sculptural complication of the body cuticle is a lateral membrane occurring in some ceramonematids.

Ultrastructure of the cuticle

Ceramonematid cuticle deviates considerably from a general pattern of the nematode cuticle (Maggenti, 1979) consisting of four layers: epi-, exo-, meso- and endocuticle. The ceramonematid cuticle is distinguished, first, by lesser number of layers, and second, by sharp difference between annules and interconnecting membranes.

The cuticle of *Metadasynemoides cristatus*

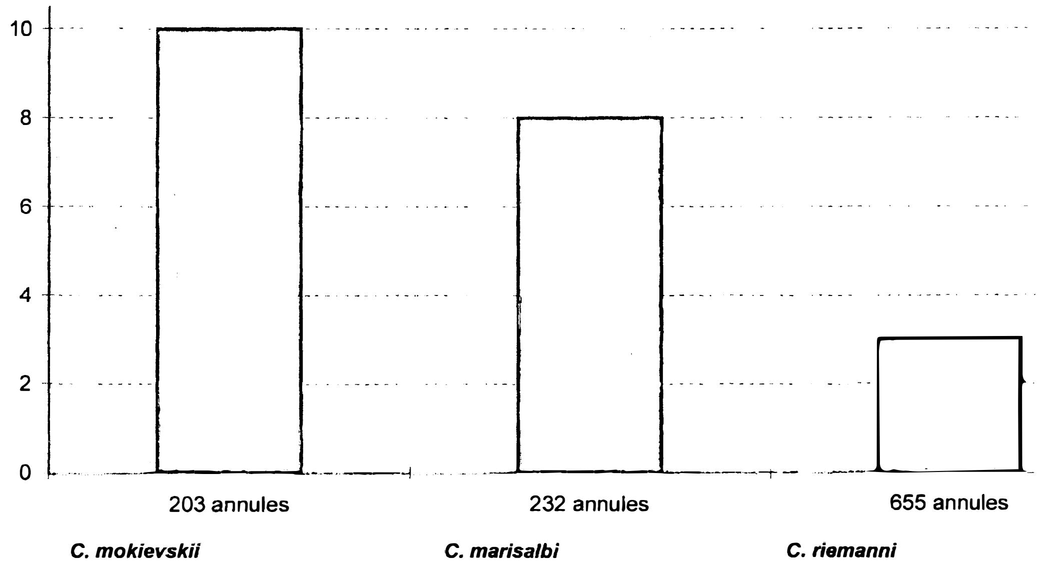

Fig. 3. Average breadth of body annules (vertical axis, µm) and number of the annules (horizontal axis) in three specimens of three ceramonematide species.

consists of many equally narrow annules. Annules are covered by a thin osmiophilic epicuticle. The bulk of the annules is not homogen, but looks as a meshwork of irregular honeycomb-like substructure. A continuous basal layer underlies the annules and simultaneously forms interconnections between the annules (Nicholas & Stewart, 1990) (Fig. 4A).

Unlike that of *Metadasynemoides cristatus*, the cuticle of *Pselionema simplex* is compounded of broad unequal annules. The annules of *P. simplex* are covered by a thin osmiophilic epicuticle, whereas the bulk of the annule is presented by an electron-light homogen material. The annules are connected by flexible multilayered membranes not underlying the homogen material (Fig. 4B). The latter is considered as exocuticle whilst the multilayered flexible interconnections as discontinuous endocuticle (Tchesunov, 1995; Tchesunov et al., 1996). A similar cuticle type was first revealed in another species with broad annules, *Ceramonema carinatum* (Stewart & Nicholas, 1992).

In the somatic cuticle of *Pselionema simplex*, the solid annules alternate with thin flexible interconnections, thus resembling superficially the cuticles of such segmented animals as kinorhynch worms (Tchesunov, 1995).

It is possible to conclude from comparison of various ceramonematid cuticles that the cuticle of *M. cristatus* with continuous basal layer (endocuticle) is closer to the general pattern and thus more plesiomorph, while the cuticles of *P. simplex* and *C. carinatum* with their discontinuous endocuticles represent a derived state.

Cephalic end

Anteriorly, the cuticle is not subdivided into annules, thus forming a solid cephalic capsule. Cuticle of the cephalic capsule, however, does not differ from the body cuticle in thickness or internal ultrastructural stratification. Longitudinal ridges exceed onto the cephalic capsule to some extent. The cephalic capsule does not fuse with pharyngeal tissue, in contrast to certain enoplid nematodes (Fig. 4C).

Overall shape of the cephalic capsule formulated as cephalic ratio (length to basal width of the cephalic capsule) has a great importance for identification at the species level.

The cephalic capsule bears three circles of anterior sensilla (six inner labial papillae, six outer setae or papillae, four cephalic setae), and lateral amphids. Second and third circles are usually more or less widely separated. However, in other species, the cephalic setae may be shifted anteriad, close to the outer labial setae, thus forming a joint crown of ten setae. Cephalic pores are the other structures of supposed sensory nature. Their presence and disposition on lateral and median sides of the cephalic capsule may have some importance for species identification.

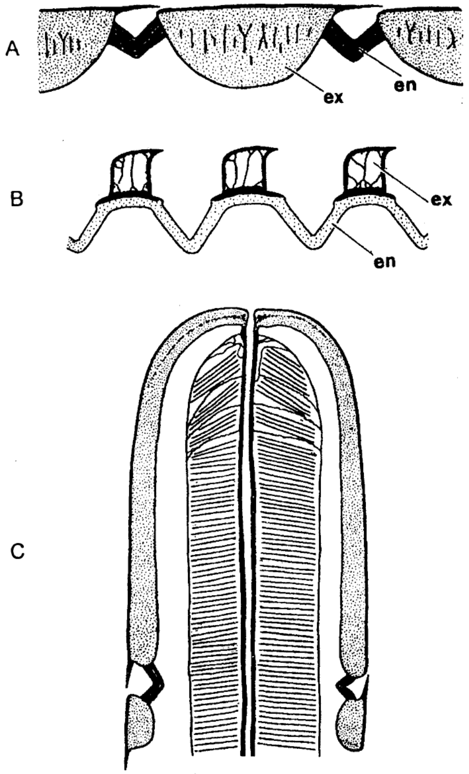

Fig. 4. Schematic representations of cuticular structures in longitudinal sections. **A**, body cuticle of *Metadasynemoides cristatus*; **B**, body cuticle of *Pselionema simplex*; **C**, cephalic end of *Pselionema simplex*. Abbreviations: *ex*, exocuticle; *en*, endocuticle. After Tchesunov, 1995 (A, C) and Nicholas & Stewart, 1990 (B).

Pharynx

Pharynx of most ceramonematid nematodes is poorly discernible under optical microscope because of the thick refractive cuticle. In *Pselionema simplex,* the pharynx distinctly consists of three portions: (1) anterior cylindrical, evenly muscular corpus; (2) middle narrow, elongate isthmus with a nerve ring; (3) posterior pear-shaped inflation formed of pharyngeal gland cell bodies. This type was revealed for *P. simplex* in a TEM study (Tchesunov, 1995). However, according to light microscope observations (Lorenzen, 1981: 216), this type of pharynx is shared by many ceramonematid species. However, other species, particularly those with greater number of equal cuticular annules, may possess a generalised cylindrical pharynx with muscular elements evenly distributed throughout its length (personal observations).

Midgut

There are very scarce published data on the intestine structure. Midgut of *Pselionema simplex* consists of a few cells on cross-section. The cells contain amorphous osmiophilic inclusions, mitochondria, rough endoplasmatic reticulum and very short apical microvilli (Tchesunov, 1995).

Hindgut

Rectum of many ceramonematids is rather long. Cells of the recto-intestinal valve in *Pselionema simplex* provide long cytoplasmic microvilli directed caudad into the hindgut lumen. There is no cuticular layer covering the microvillar zone (Tchesunov, 1995). Cytoplasmic microvilli generally denote active transportation of some dissolved substances through plasmalemma. But the cytoplasm of the recto-intestinal valve cells in *P. simplex* scarcely contains such organelles as mitochondria, dictyosomes and elements of endoplasmatic reticulum, whose abundance is usually associated with metabolic activity.

Ventral gland

Ventral pore is situated usually anterior to the cardia, at the level of posterior thickening of the pharynx, either between annules or within an annule. Ventral gland or renette is rather short and slightly differentiated into ampulla, neck and body. The gland may be up to 150 µm long and occupy a body portion of 10-15 annules (in species with fewer number of annules) and 50 and more (in species with greater number of annules).

Reproductive organs

Ovaries are paired and antidromously reflexed. Eggs ripe alternately in the anterior and posterior ovaries. The ripe eggs are elongate and may attain one-fourth body length. Anterior and posterior ovaries are usually situated at opposite sides of the intestine. However, such observations are seldom cited because these details are often hardly discernible through the refractive cuticle.

Testes are paired and opposed. Anterior (straight) and posterior (reflexed) testes are situated at opposite sides of the intestine (Lorenzen, 1981). The anterior testis is larger than the posterior one. Spicules are usually weak, slightly arched, with distal ends acute and proximal ends narrowed. The shape of spicules is rather stable within the family and hence rarely used for species discrimination (Haspeslagh, 1979). Gubernaculum is normally present, but may be reduced. Usually, the gubernaculum has an appearance of a weak narrow plate parallel to the spicule and not exceeding half length of the latter.

Nurture

Females care own offspring, at least in *Pselionema* species. Hopper (1973) first discovered the phenomenon of nurture for *Pselionema beauforti*. Brood usually consists of two to three simultaneous eggs each in an individual capsule attached with a stalk to the vulvar area on the body (Fig. 23A). Apart ceramonematids, a similar nurture habit is known for Desmoscolecidae as well as for a few species of Desmodoridae. However, all these species use various manners of egg attachments to the mother body. Desmoscolecid female holds a rather large egg pressing it to the ventral side of the body with specialised elongate setae, while desmodorid females either stick the eggs along the ventral body side or in similar way hold eggs on belly with elongate setae.

Postembryonal development

The number of annules increases during the larval ontogenesis in the intestinal body region, but remains constant in the pharyngeal and tail regions during the entire postembryonic life of the nematode (Haspeslagh, 1979).

Whereas the adult amphids are normally elongate loop-shaped, the amphids of the earlier juveniles are rounded, single-loop spirals (Hopper, 1973; personal observations, Fig. 23D).

Nutrition

Until recently, no observations were made on nutrition of the ceramonematids. In all specimens examined, we could not discern any content in their guts. According to morphology of the buccal apparatus, the ceramonematid nematodes belong to the feeding type 1A (selective deposit feeders) in the classification of Wieser (Wieser, 1959b; Heip et al., 1985).

ASPECTS OF MORPHOLOGICAL EVOLUTION AND PHYLOGENY

Ceramonematidae represents one of a few nematode families where it is possible to construct transformatory sequences of character states. First of all, this concerns cuticular structures.

Cuticle

As the plesiomorph state within Ceramonematidae, we assume a body cuticle consisting of great and variable number (from 200 to 700) of equally narrow (2-5 μm) annules devoid of distinct zygapophyses. A similar type of annulation is distributed among the majority of nematode families (e.g. in Monoposthiidae, with sharp annulation and longitudinal alae) (out-group comparison). Among ceramonematids, a great number of equally narrow cuticular annules is shared by the genera *Dasynemoides*, *Metadasynemoides*, *Dasynemella* and *Pterygonema*. Thus, species of *Dasynemella* were documented to possess the maximum number of body annules (up to 691), with average annule breadth about 2.3 μm. However, the number of annules is often not indicated in species descriptions, especially for multiannulated ceramonematids.

Other genera demonstrate two parallel evolutionary trends for diminishing and stabilising the numbers of annules. In *Metadasynemella*, the number of annules diminishes to 90-175 without increase of their breadth. Species of the genus *Metadasynemella* have short bodies (440-492 μm) divided into equal cuticular annules. On the other hand, *Pselionema* and *Ceramonema* tend to have limited numbers of annules varying in breadth (5-14 μm). The annule breadth in these genera varies in several periods along the body (see above). Annules of *Pselionema* are distinguished by more or less prominent zygapophyses. In *Ceramonema*, the zygapophyses become very strong and prominent. However, other ceramonematid genera also may have vestigial zygapophyses. We consider the low number of annuli of unequal breadth and with developed zygapophyses as derived or apomorph state (Fig. 5A).

Cephalic end

In spite of the external image, the ceramonematid nematodes demonstrate some clear plesiomorph states. Mouth opening is triangular and may have three lips. Malakhov (1994) believes the triangular (or three-lipped) mouth represents an initial state, while the hexangular (or six-lipped) mouth is treated as a derived state in nematodes. As ground, he cited a consideration that the triangular configuration corresponds to the symmetry of the internal lumen of the nematode pharynx, and an observation that the triangular mouth opening precedes the hexangular mouth in the ontogenesis in one oncholaimid species, namely *Pontonema vulgare*.

The cuticle around the mouth is neither enlarged nor ultrastructurally modified in two examined species, *Ceramonema carinatum* and

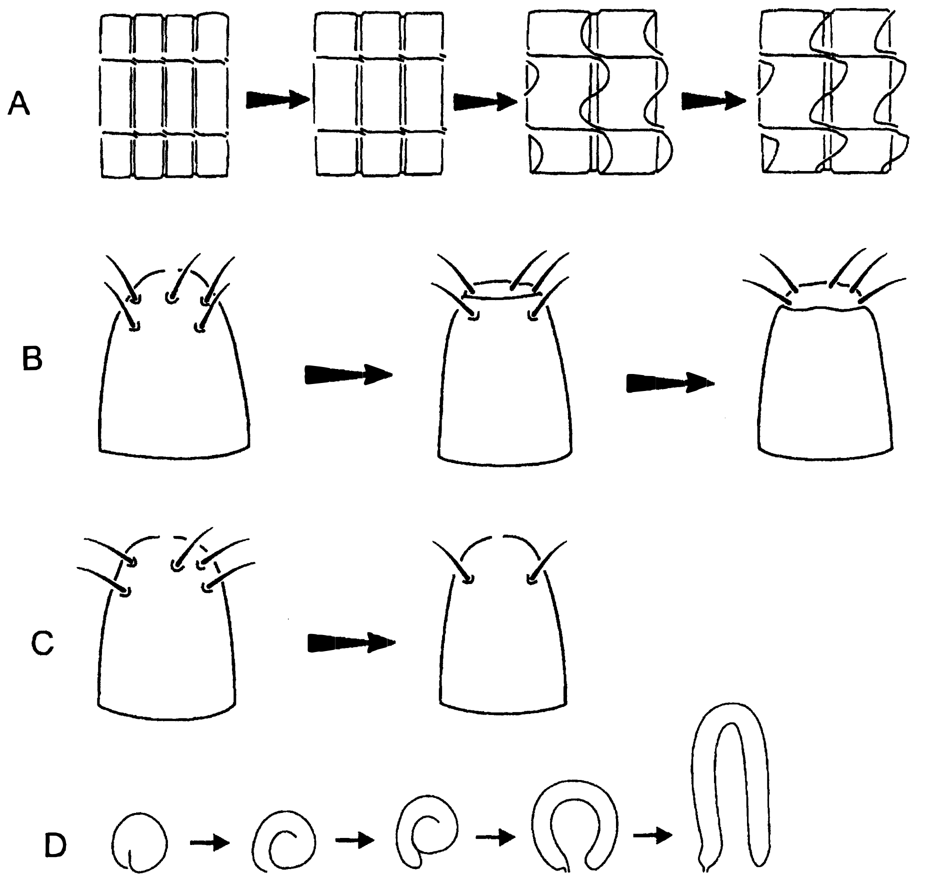

Fig. 5. Assumed sequences of evolutionary structural transformations of: **A**, cuticular annulation from equally narrow numerous rings to unequal broad rings with zygapophyses; **B**, **C**, shifting of outer labial setae and cephalic setae anteriad, together with differentiation of labial region; **D**, amphidial fovea from rounded (plesiomorph) to spiral and further to loop-shaped (apomorph) form.

Pselionema simplex (Stewart & Nicholas, 1994; Tchesunov, 1995), in contrast to many other aquatic nematodes. Buccal cavity or stoma is not developed as a compartment differing from the pharyngeal lumen. In several descriptions, e.g. of "*Dasynema sexalineatum*" by Cobb (1920: fig. 34) and *Ceramonema filipjevi* by De Coninck (1942: figs 11-15), some buccal cavities were figured, but they are evidently artefacts created by fixation of nematodes at the moment of contraction of their radial pharyngeal muscles.

Stomatorhabdions (stoma walls) are not distinguished ultrastructurally from the internal cuticular lining of the pharynx. These fine morphological features may be also considered as plesiomorph on the ground of their structural simplicity.

Anterior sensilla

Ceramonematid species provide a considerable variety of anterior sensilla patterns within one family. Lorenzen (1981, 2000) and Malakhov (1994) considered an arrangement of the anterior sensilla in three separate circles 6+6+4 as plesiomorph, while an alternative arrangement in two circles 6+10 as apomorph. They based on some observations of nematode postembryonic developments where second and third circles are separated in the first juvenile stage and fuse together in the further course of ontogeneses.

The plesiomorph pattern 6+6+4 is shared by the genera *Dasynemella* and *Ceramonema*. Their cephalic capsules are sclerotised entirely including the apical surface, without a distinct labial region. Dendritic processes of the anterior setae pass through well visible "holes" in the cephalic capsule. In *Dasynemoides*, the second and third circles are close together at some extent; cephalic capsule looks truncate anteriorly because of the distinct labial region with seemingly soft cuticle. Outer labial setae in *Dasynemoides* are rooted in the labial region, while the cephalic setae are inserted in the cephalic capsule, with respective "holes". In *Metadasynemoides* and *Metadasynemella*, both second and third setae circles are drawn together, thus forming a joint circle of ten setae, frequently equal in length (Fig. 5B). Such a state is argued by Lorenzen (1981, 2000) to be the most apomorph.

Sensilla of the second circle are presented by minute papillae in *Pselionema* and *Pterygonema*. We evaluate this state as apomorph also basing on observations of some species, where difference in length between second and third sensilla increases during the postembryonic ontogenesis (Fig. 5C).

Amphid shape

Amphid foveae in adult ceramonematids are mostly elongate loop-shaped, but also may be rounded or spirally coiled in one or two turns. According to our observations on *Pselionema simplex*, the fovea changes its shape from rounded to elongated loop during the juvenile development (Fig. 23D). In many other nematodes of various families, the amphid transforms in similar way during the ontogenesis (cases of *Synodontium monhystera*, *Pararaeolaimus nudus*, *Desmodora minuta*, *Dracograllus chiloensis* summarised by Lorenzen, 2000; case of *Chitwoodia tenuipharyngealis* recorded by Tchesunov, 1993). Therefore we assume the round amphid as plesiomorph and elongate loop-shaped amphid as apomorph within Ceramonematidae (Fig. 5D).

Pharynx

As plesiomorph state, we assume evenly muscular pharynx, without either muscular or glandular narrowings or thickenings (according to Tchesunov, 1990). However pharynx features are often hardly discernible through the thick refractive cuticle and hence seldom reported in species descriptions. At least *Metadasynemoides* and some species of *Dasynemella* have a cylindroid and evenly muscular pharynx. Pharynx of *Pselionema*, *Ceramonema* and *Metadasynemella* is differentiated more or less distinctly into three portions: anterior muscular corpus, middle narrowed isthmus, and posterior pear-shaped glandular thickening (Lorenzen, 1981; Tchesunov, 1995; personal observations). We evaluate this pharynx type as an apomorph state.

Phylogenetic reflections and distribution of the ceramonematid diversity in the marine environment

Plesiomorph and apomorph states of characters are distributed among the ceramonematid genera with some degree of congruence. Thus, *Metadasynemoides* shows a set of only plesiomorph character states, whereas *Pselionema* and *Ceramonema* show mainly apomorph features. Other genera display various combinations of plesiomorph and apomorph character states.

Ceramonematid nematodes dwell mostly in the seas with normal oceanic salinity, although a few species occur in the areas of lower salinity, such as *Pselionema annulata* in the Black Sea (S = 1.8%) and *Pselionema simplex* as well as other local species in the White Sea (S = 2.4-3.0%). However, no true brackish or even euryhaline species are known among the ceramonematids.

Most genera and species are associated with coarse sediments such as pure sands and broken shells, where they may compose even up to 5-10% of the total nematofauna. Fine sediments, i.e. silts, may be populated by only species of *Ceramonema* and especially *Pselionema*. The ceramonematid species never occur in periphyton. Most species are known from shallow waters in tidal and upper subtidal zones, although some species of *Metadasynemella* and *Pselionema* were registered at much greater depths.

Among ceramonematids, the most eurytopic taxa are again *Ceramonema* and *Pselionema* occurring in wider ranges of deposits and depths. Other genera are mostly confined to coarse sands and shallow depths (Fig. 6). It may be meaningful that those highly apomorph genera display simultaneously the highest species diversity and widest milieu range.

POSITION IN THE NEMATODE CLASSIFICATION

For a long time, the family Ceramonematidae was assigned to Chromadorida and namely to Monoposthiidae (Filipjev, 1934) or Desmodoridae (Chitwood & Chitwood, 1950) within the order. Indeed, the ceramonematids have some superficial resemblance with those families in the sharp, light-refractive cuticular annulation. De Coninck (1965) and then Haspeslagh (1973), Gerlach & Riemann (1973) and Andrássy (1976) placed the Ceramonematidae within Desmodorida, the order erected by De Coninck (1965).

Lorenzen (1981) considered that since Ceramonematidae do not have twelve folds or rugae in the cheilostoma and possess two testes, the family does not correspond to Desmodorida. He included Ceramonematidae into the Lepto-

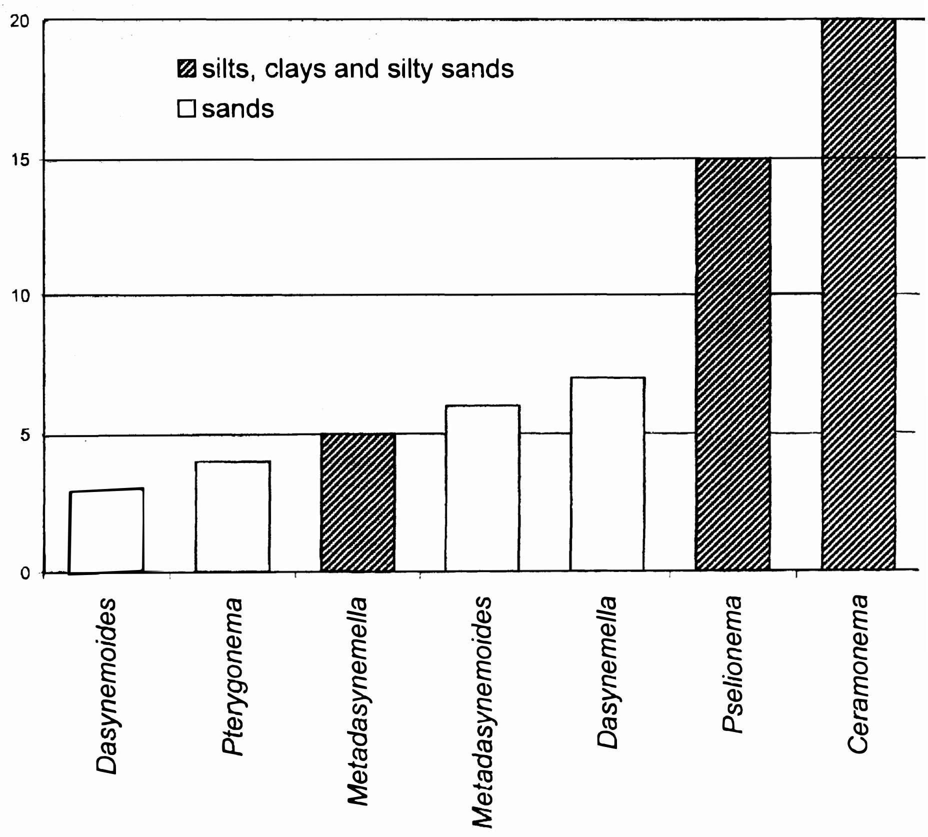

Fig. 6. Number of species and inhabited sediments in ceramonematide genera.

laimina, a paraphyletic subtaxon of Chromadorida. Lorenzen (1981) suggested the ceramonematids are closely related to Tubolaimoididae. Both families share triangular or three-lipped mouth opening, three separate circles of the anterior sensilla and loop-shaped amphid. Inglis (1983) agreed that the Ceramonematidae should not belong to Desmodorida, and placed the ceramonematids in Araeolaimida as a separate suborder with unclear relationships. Recently, first molecular data were revealed for the ceramonematide *Pselionema* sp., along with some other adenophorean taxa (Litvaitis et al., 2000). Comparison of nucleotide sequences of the D3 expansion segment of the 28S rDNA also denies the possibility of close relationships between the Ceramonematidae and Desmodoridae.

We also consider Ceramonematidae to be related to such taxa of Leptolaimina as Diplopeltoididae sensu Tchesunov (1990) and Tarvaiidae. Within Leptolaimina, all these families are characterised by loop-shaped amphids, undifferentiated buccal cavity, shape of the ventral gland and position of the ventral pore, absence of tul supplementary organs and trends to formati cephalic capsules and glandular ending o pharynx. However, Diplopeltoididae and Ta idae are strictly characterised by papillose labial sensilla, while in Ceramonematida sensilla of the second anterior circle may t ther setose or papillose.

TAXONOMY

Outstanding contributions to the systen of Ceramonematidae were made by De Co (1942, 1965) and Haspeslagh (1973, 1979). ever, Lorenzen (1981) considered that thes thors had created too many superspecies basing upon insignificant details of cuticle ture. Lorenzen (1981) abolished all subfan synonymised six of the twelve genera diag as valid by Haspeslagh (1973) and pointed possibility of further synonymisation.

Here, two of the four subfamilies of Ha lagh (1973) are restored. These two subfar can be reliably separated from each other in the presence of ten or four anterior setae. The latter character has no intermediate states unlike cuticle structures.

Lorenzen (1981) did not diagnose those ceramonematid genera, which he retained as valid. However, he listed all species for every genus. We fail to diagnose these genera because of their heterogeneity. Therefore, retaining all nominal genera ascertained by Lorenzen, we change their species composition basing on anterior sensilla patterns, cephalic capsule and body cuticle structures (Fig. 7).

Family **CERAMONEMATIDAE** Cobb, 1933

= Dasynemellidae De Coninck, 1965.

Type genus *Ceramonema* Cobb, 1920.

Diagnosis. Body cuticle consists of rigid and often broad and thick annules interconnected by thin flexible membranes. The annules supplied with longitudinal ribs building together alae or ridges along the body. Cuticles of cephalic end and tail tip not subdivided into annules, thus forming, respectively, solid cephalic capsule and terminal cone. Anterior sensilla 6+6+4, where first circle presented by inner labial papillae, second by outer labial papillae or setae, and third by cephalic setae, respectively. Second and third circles may be separated or drawn together. Amphids usually loop-shaped, seldom rounded or oligospiral, sometimes of obscure elongate shape. Cephalic capsule may carry additional setae and pores. Postcephalic body usually supplied with somatic papillae or setae. Buccal cavity and stomatal armature not developed, with one or two possible exceptions. Pharynx slender, often muscular in prenevral portion and less muscular or obscure in postneural portion. Midgut oligocytose. Rectum elongate. Ovaries paired and antidromously reflexed. Testes paired and opposed. Spicules short, weak, slightly bent. Gubernaculum usually as a short indistinct plate, rarely with short dorso-caudal apophysis. Marine.

The family is subdivided into two subfamilies. A key for their determination is presented below:

1(2) Both outer labial and cephalic sensilla setose .... **Ceramonematinae**
2(1) Outer labial sensilla papillose, while posterior cephalic sensilla setose .... **Pselionematinae**

Subfamily CERAMONEMATINAE Cobb, 1933

= Dasynemellinae De Coninck, 1933; = Leptodasynemellinae Haspeslagh, 1973; = Metadasynemellinae De Coninck, 1965; opinion of Lorenzen, 1981.

Type genus *Ceramonema* Cobb, 1920.

Diagnosis. Both outer labial sensilla and cephalic sensilla setose.

Key to genera of Ceramonematinae

1(6) Labial region distinctly separated off the cephalic capsule by a circular suture.
2(3) Body relatively short (less than 1000 µm) and nearly fusiform. Body annules broad and unequal, less than 250 in number.................. **Metadasynemella**
3(2) Body usually longer, slender and cylindrical. Body annules more than 300 in number, narrow and equal.
4(5) Outer labial and cephalic setae arranged in two distinctly separated circles. Outer labial setae situated on the labial region in front of the margin of the cephalic capsule, while cephalic setae inserted on the cephalic capsule anteriorly.......... **Dasynemoides**
5(4) Outer labial and cephalic setae close to one another and rooted on the labial region anterior to the margin of the cephalic capsule......... **Metadasynemoides**
6(1) Labial region not separated from the cephalic capsule.
7(8) Body cuticle consists of numerous (more than 350) equally narrow annules............... **Dasynemella**
8(7) Body cuticle consists of less numerous (less than 350) annules. The annules usually more or less broad and unequal........................ **Ceramonema**

Genus **Ceramonema** Cobb, 1920

= *Ceramonemoides* Haspeslagh, 1973; = *Cyttaronema* Haspeslagh, 1973.

Type species *Ceramonema attenuatum* Cobb, 1920.

Diagnosis. Body cuticle consists of 70-320 broad and thick annules. Annules equal or unequal in breadth. If unequal, their breadth increases gradually from the first subcephalic annule to those near the cardia; then annule width drops sharply and again increases gradually to the broad anal annule; the following annules on the tail narrow gradually to the terminal cone. Intracuticular vacuolisation in the annules may be present. Annule zygapophyses present or absent. Six or eight longitudinal crests extended along the body. Labial region not set off. Outer labial and cephalic setae arranged in two separate circles. Amphids loop-shaped, elongate or rounded.

We propose to arrange the *Ceramonema* species into subgenera *Ceramonema* s. str. and *Proceramonema* differing from each other in the body cuticular annulation. Two dubious species are not placed in subgenera and listed at the end of the genus review.

Subgenus **Ceramonema** Cobb, 1920

Type species *Ceramonema attenuatum* Cobb, 1920.

Diagnosis. There are distinct zygapophyses in body cuticular annules.

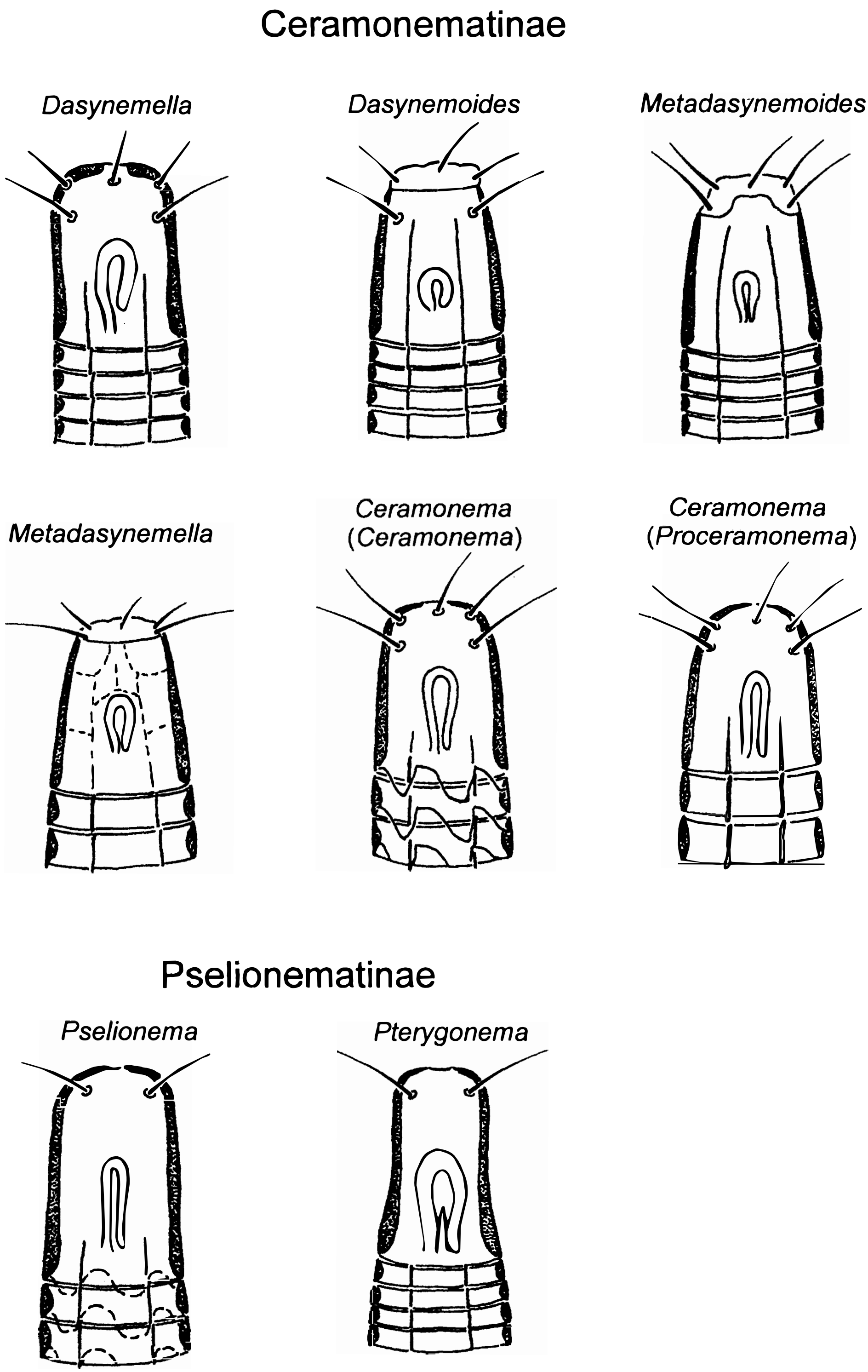

Fig. 7. Cephalic ends of ceramonematide genera and subgenera.

Annotated list of species

1. *C.* (*Ceramonema*) *africanum* Furstenberg & Vincx, 1993: 144-147, Figs 3A-E, 4A-G; South Africa.
2. *C.* (*Ceramonema*) *algoense* Furstenberg & Vincx, 1993: 140-144, Figs 1A-E, 2A-H; South Africa.
3. *C.* (*Ceramonema*) *attenuatum* Cobb, 1920: 264, Fig. 48; Jamaica.
4. *C.* (*Ceramonema*) *carinatum* Wieser, 1959a: 45, Figs 45a-c; Puget Sound, Pacific Coast of North America. An Australian ceramonematid species studied by Stewart & Nicholas (1992, 1994) was identified by them as *Ceramonema carinatum*. However, some figures by Stewart & Nicholas (1994, Fig. 1) do not match altogether the description of Wieser (1959a) and hence the conspecifity of the Australian and North American specimens may be doubted. As it was pointed out by Wieser (1959a), the cuticular longitudinal rows extend into the head as rows of dots, while in the Australian specimens, the longitudinal rows continue into the head as prominent non-interrupted ridges. Another feature is that, according to the original diagnosis (Wieser, 1959a, Figs 45a and 45c), the cephalic setae are situated well in front of the amphid of males, while in the figure of Stewart & Nicholas (1994, fig. 1) they are inserted at the level distinctly posterior to anterior margin of the amphids. This species may be marked by variability of zygapophyses (cf. Wieser, 1959a, Figs 45a and 45b).
5. *C.* (*Ceramonema*) *chitwoodi* De Coninck, 1942: 11-15, Figs 8-10; Mediterranean. Vitiello & Haspeslagh, 1972: 2-4, Pl. 1, Figs 1-2. Haspeslagh, 1973: 247 (*Ceramonemoides*).
6. *C.* (*Ceramonema*) *fluctuosum* sp. n.
7. *C.* (*Ceramonema*) *kromense* Furstenberg & Vincx, 1993: 147-150, Figs 5A-C; South Africa.
8. *C.* (*Ceramonema*) *pisanum* Gerlach, 1953: 565-567, Figs 22 a-d; Mediterranean.
9. *C.* (*Ceramonema*) *racovitzai* Andrássy, 1973: 254-256, Figs 7 E-G; Cuba.
10. *C.* (*Ceramonema*) *reticulatum* Chitwood, 1936: 3, Figs 1 H-J; North Carolina, Atlantic coast of North America. Gerlach, 1952: 363, Figs 27 a-c (*Ceramonema* aff. *reticulatum*); Mediterranean. Haspeslagh, 1973: 247 (*Cyttaronema*). Other records without descriptions were made from Mediterranean, Bermuda, and Bay of Bengal (Gerlach & Riemann, 1973: 254).
11. *C.* (*Ceramonema*) *salsicum* Gerlach, 1956b: 433, Fig. 5; Bay of Biscay.
12. *C.* (*Ceramonema*) *undulatum* De Coninck, 1942: 16-18, Figs 16-21; Mediterranean.
13. *C.* (*Ceramonema*) *yunfengi* Platt & Zhang, 1982: 236-237, Figs 5 a-d; Scotland.

Key to species of the subgenus *Ceramonema*

1(2) Body less than 700 μm long. Cuticular annules less than 90 in number. Amphid small, about 8 μm long and 4 μm wide, or less .... **C. undulatum**
2(1) Body longer than 700 μm.
3(6) Body very slender ("a" about 80, or more).
4(5) Lip region cap-like elevated. Number of cuticular annules from 300-307 (males) to 315 (female) .... **C. algoense**
5(4) Lip region not elevated. Number of cuticular annules very different in male (287) and females (184-186). . ... **C. yunfengi**
6(3) Body relatively thick ("a" about 70, or less).
7(8) Cephalic ratio less than 1 .... **C. racovitzai**
8(7) Cephalic ratio about 1, or greater.
9(20) Intracuticular vacuolisation present in body annules and/or in cephalic capsule.
10(15) Pores in cephalic capsule absent.
11(12) Cephalic capsule widened basally. Cephalic ratio about 1. Cephalic setae 6-9 μm .... **C. chitwoodi**
12(11) Cephalic capsule elongate and evenly wide throughout its length. Cephalic ratio 1.5, or greater. Cephalic setae about 12 μm.
13(14) Amphid near 26 μm long or more than 65% of cephalic capsule length. Cephalic ratio more than 2 . ... **C. fluctuosum** sp. n.
14(13) Amphid about 16 μm long or less than 45% of cephalic capsule length. Cephalic ratio about 1.5 ... . **C. carinatum**
15(10) Pores in cephalic capsule present.
16(17) Cephalic ratio about 1. Length of the cephalic setae exceeds 0.5 length of the cephalic capsule .... **C. reticulatum**
17(16) Cephalic ratio more than 1. Cephalic setae shorter than 0.3 length of the cephalic capsule.
18(19) Amphid elongate, loop-shaped, 21 μm long, situated in the middle of the cephalic capsule. Terminal tail cone elongate, 21 μm long .... **C. salsicum**
19(18) Amphid drop-shaped, 13 μm long, situated in posterior region of the cephalic capsule. Terminal tail cone shorter, about 15 μm long .... **C. africanum**
20(9) Intracuticular vacuolisation absent.
21(24) Cephalic ratio about 1.5.
22(23) Amphid loop-shaped, with equal branches, its length less than 0.3 length of the cephalic capsule. Labial region protruded. Body length about 1600 μm .... **C. pisanum**
23(22) Amphid loop-shaped, with unequal branches, its length exceeds 0.5 length of the cephalic capsule. Labial region not protruded. Body length about 1100 μm .... **C. attenatum**
24(21) Cephalic ratio about 1. Cephalic capsule small and evenly wide. Amphid small (9.5 μm long), its anterior margin just at the level of the posterior cephalic setae. 213 cuticular annules (male) .... **C. kromense**

Ceramonema (Ceramonema) fluctuosum sp. n. (Fig. 8)

Holotype. ♂, **Russia**, White Sea, Gorlo Strait, 66°4.3′N, 39°3.5′E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University.

Paratypes. 5 ♀, same data and deposition.

Description. Body slender, cylindrical. Male: L = 1161 μm; a = 68; b = 8; c = 7. Females: L = 949-1135 μm; a = 47.5-62.5; b = 6-7.5; c = 5-6.5; V = 41-45%. In male, the body diameter is at the level of: cephalic setae 18 μm, nerve ring 18 μm, cardia 18 μm, midbody 16 μm, anus 16 μm. In females, the body diameters are respectively 17-23 μm, 18-23.5 μm, 17-22 μm, 18-24 μm, 12-15 μm.

Body cuticle composed of sharp and thick annules between the cephalic capsule and terminal tail cone. In male, body cuticle consists of 169 annules: 15 annules in pharyngeal region, 115 in intestinal region, and 39 in tail. These numbers in females are 162-172, 17-20, 105-112, and 33-41, respectively. Each annule bears eight short longitudinal ridges forming eight crests

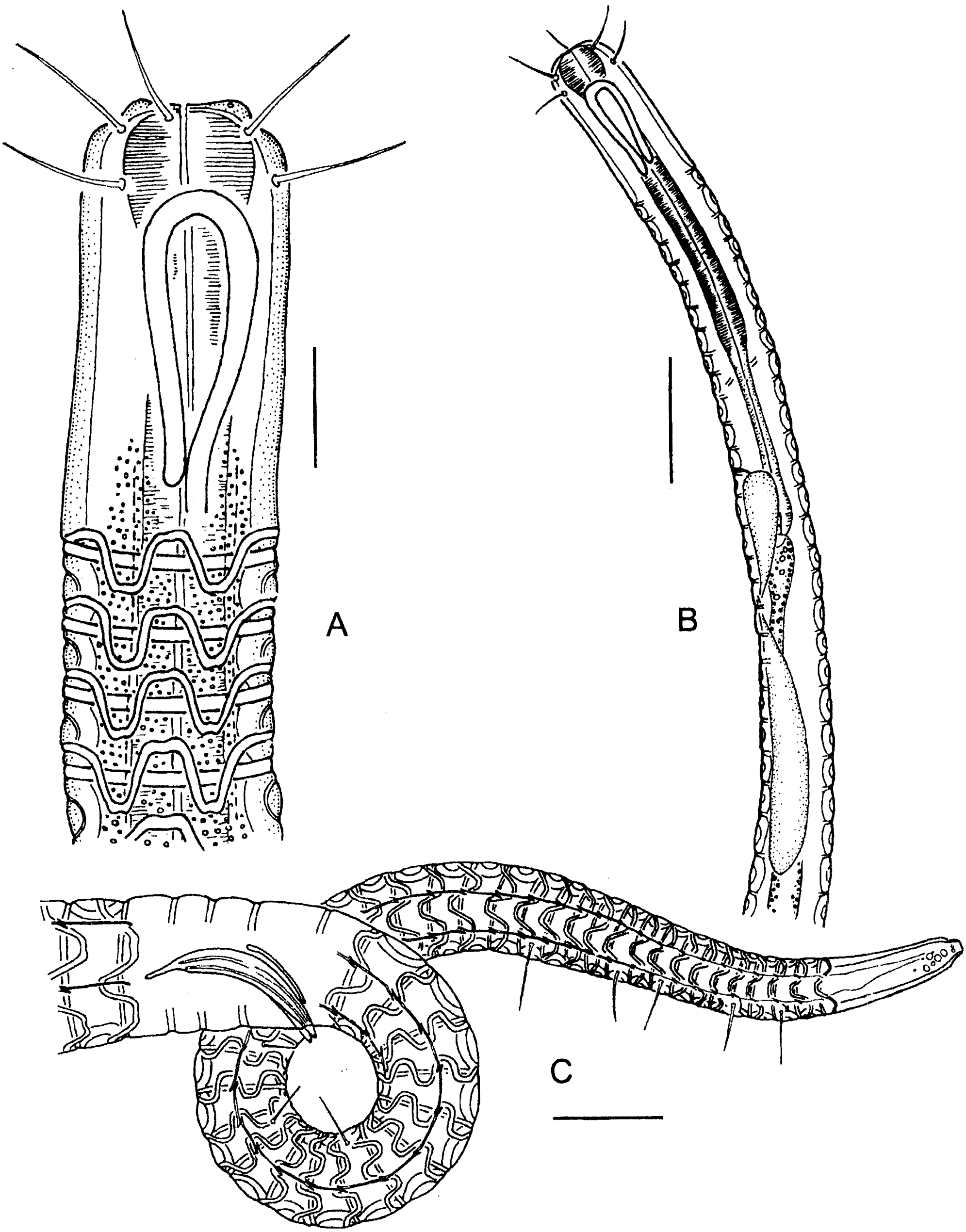

Fig. 8. *Ceramonema fluctuosum* sp. n., holotype male. **A**, cephalic end; **B**, anterior body; **C**, posterior body. Scale bar: A – 10 µm, B – 30 µm, C – 10 µm.

running along the entire body from posterior third of cephalic capsule to terminal cone. Annules vary regularly in width ranging from 6 µm to 10 µm in male and from 5 µm to 10 µm in females. In male, annules increase in width gradually from 1st to 28th annule; the 29th annule is narrow then annules gradually increase in width fror 29th to 131st (anal) ring; tail annules narrow u to terminal cone. In female, annules increase i width from 1st (6 µm) to 40th (8 µm) annule; th

41st annule is narrow (5 μm); further annules increase very slightly in width from 41st to 152nd (to 7 μm); 153rd and 154th are very narrow (3.5 μm); 155th annule is broad (6 μm); following annules to the tail cone are narrow (to 2 μm). Zygapophyses well developed. Intracuticular granularity or tiny vacuolisation present around each annule.

Cephalic capsule elongate, nearly cylindrical and slightly narrowed apically, its length, basal diameter, and cephalic ratio are 38.5 μm, 17 μm, and 2.26, respectively, in male and 36-52.5 μm, 17-23 μm, and 1.98-2.27 in females. Cuticle gradually thinned to mouth.

Inner labial papillae not seen. Outer labial and cephalic setae situated in two separate circles 6+4. Setae of both circles thin, hair-like. In male, outer labial setae 11 μm and cephalic setae 9 μm long; in females, these lengths are 11-13 μm and 11-12 μm, respectively. No other setae along the body until the anus.

Amphids ventrally bent and loop-shaped, occupying posterior 2/3 to 3/4 of cephalic capsule. In male amphid, dorsal branch 24 μm and ventral branch 27 μm long, amphid width 6.5 μm, distance from anterior end to amphid 9.5 μm. In female amphids, these measurements are 16.5-21 μm, 22.5-27 μm, 5.5-7.5 μm, 12-21 μm, respectively. No cephalic pores.

Buccal cavity not developed. Pharynx widened anteriorly. Anterior muscular region of pharynx extending until 8th annule, 94 μm long in male and 86-116.5 μm long in females. Middle region of pharynx is a narrow isthmus. Posteriorly, pharynx forms a muscular bulb. Nerve ring at anterior end of the isthmus.

Excretory pore situated at 12th annule (152 μm from anterior end) in male and at 11-16th annules (111-130 μm from anterior end) in females. Renette cell thick and long, extended for 14 annules in male.

Testes not discernible. Spicules equal and arched, their distal ends tapered and proximal ends narrowed. Gubernaculum as a thin plate along the spicule. Spicules 19 μm (chord) or 21 μm (arch) long. Tail 10.5 anal diameters long in male and 13-17 anal diameters long in females. Male tail with subventral setae. Terminal tail cone 12 μm long in male and 12-17 μm in females.

Comparison. *C. fluctuosum* sp. n. resembles *C. carinatum* and especially *C. salsicum*. The new species differs from *C. carinatum* in the more elongate cephalic capsule (cephalic ratio 2.25 *versus* 1.6), longer body (1161 μm *versus* 860 μm), and longer amphid (26 μm *versus* 16 μm). *C. fluctuosum* sp. n. is clearly related to *C. salsicum*, but differs in the index "a" (68 *versus* 38), position of the amphid in the posterior portion of the cephalic capsule (in *C. salsicum*, in the middle of the cephalic capsule), and shorter terminal cone (12 μm *versus* 21 μm).

Etymology. The name "*fluctuosum*" (Latin "wavy") reflects an impression of undulation created by protruded zygapophyses of this species.

Subgenus **Proceramonema** subg. n.

Type species *C.* (*Proceramonema*) *marisalbi* sp. n.

Diagnosis. Zygapophyses are lacking or indistinct.

Annotated list of species

1. *C.* (*Proceramonema*) *filipjevi* De Coninck, 1942: 15-16, Figs 11-15; Mediterranean.
2. *C.* (*Proceramonema*) *marisalbi* sp. n.
3. *C.* (*Proceramonema*) *mokievskii* sp. n.
4. *C.* (*Proceramonema*) *rectum* Gerlach, 1957: 447, Figs 12 i-m; Brazil.
5. *C.* (*Proceramonema*) *rhombus* Andrássy, 1973: 256-257, Figs 7 A-D; Cuba.

Key to species of the subgenus *Proceramonema*

1(6) Length of the outer labial setae 5 μm or less. Body relatively short (L < 1000 μm). a < 40.

2(3) Body small (L < 600 μm) and consists of less than 100 narrow (2-6.5 μm) annules. Cephalic ratio 1.64 . ... **C. filipjevi**

3(2) Body longer (700-900 μm). Cuticular annules broad, 8-10 μm wide.

4(5) Cephalic ratio > 1 .... **C. rectum**

5(6) Cephalic ratio = 1. 187-195 cuticular annules .... **C. rhombus**

6(1) Outer labial setae 10-11 μm long. Body longer (> 1000 μm) and slender (a > 60). About 200 cuticular annules.

7(8) Cephalic capsule elongate, cephalic ratio > 2. Outer labial setae longer than cephalic setae .... **C. mokievskii** sp. n.

8(7) Cephalic capsule stout, cephalic ratio 1.2-1.5. Outer labial setae shorter than cephalic setae .... **C. marisalbi** sp. n.

Ceramonema (Proceramonema) marisalbi sp. n. (Fig. 9)

Holotype. ♀, **Russia**, White Sea, Gorlo Strait, 66°4.3´N, 39°3.5´E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University.

Paratype. ♂, same data, lost.

Description. Body slender, cylindrical, not narrowed anteriorly and very slightly narrowed to anus. Male: L = 1452 μm; a = 73; b = 7.6; c = 6.4. Female: L = 1155 μm; a = 42.8; b = 6.72; c = 6.24; V = 46.8%. In male, body diameter is at the level of: cephalic setae 23.5 μm; nerve ring 21 μm; cardia 21 μm; midbody 20 μm; anus 21 μm. These measurements in female are 24 μm, 27 μm, 26.5 μm, 27 μm, and 20 μm, respectively.

Cuticle brownish, seems evenly granular

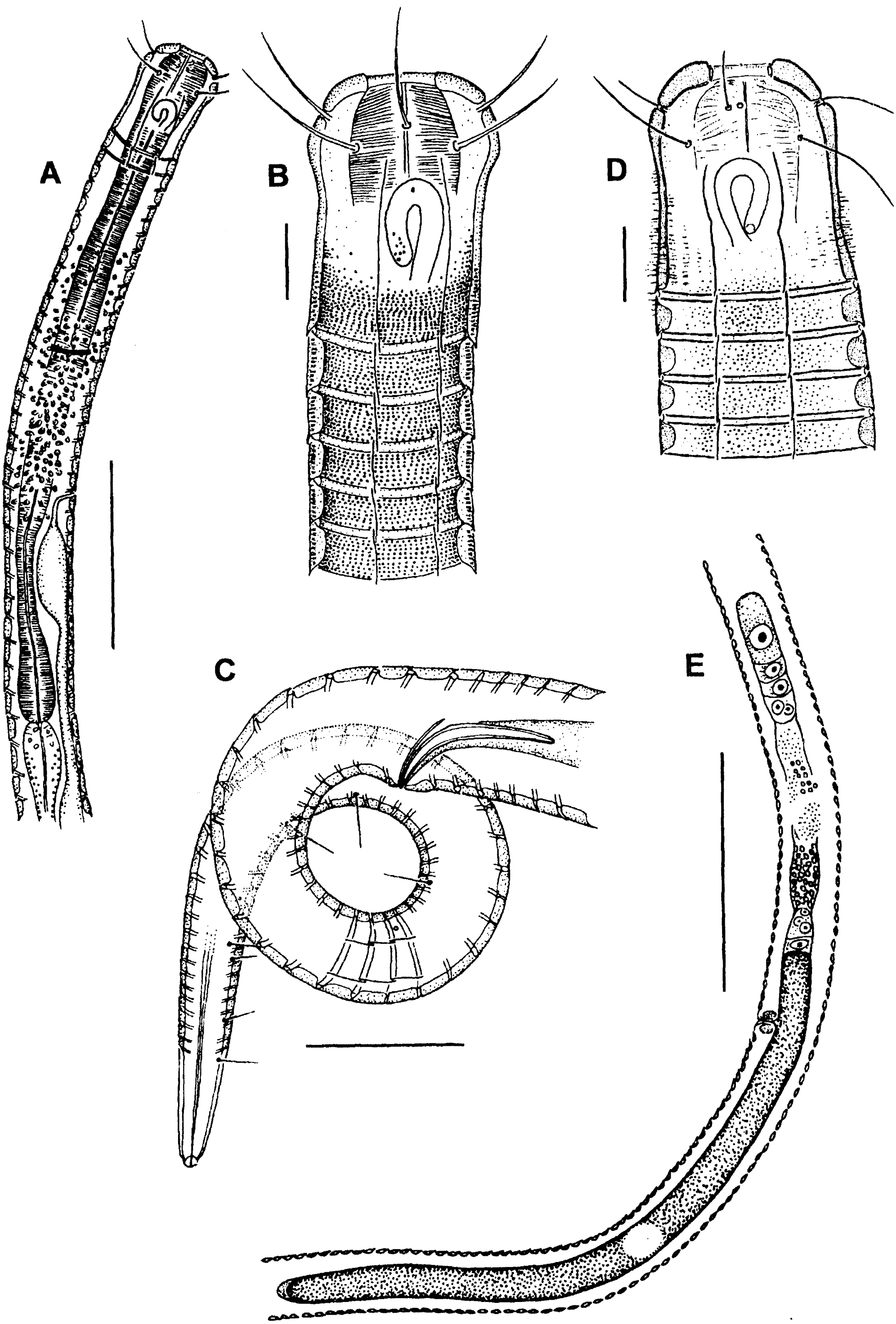

Fig. 9. *Ceramonema marisalbi* sp. n. (A-C, paratype male; B and D, holotype female). **A**, cephalic end; **B**, ante body; **C**, posterior body; **D**, cephalic end; **E**, reproductive system. Scale bars: A, D – 20 µm; B – 50 µm, C – 30 µ

throughout the body length because of fine internal vacuolisation. Body cuticle consists of 232 (male) and 249 (female) free annules between the cephalic cuticle and terminal cone. In male, 31 annules in pharyngeal region, 153 in intestinal region, and 48 in tail; annules gradually increase in width from the first subcephalic (6 μm) to 40th (9 μm), then again from the narrow 41st annule (5 μm) to the anal 184th annule (7 μm wide). In female, 31 annules in pharyngeal region, 174 in intestinal region (79 prevulvar and 95 postvulvar), and 44 in tail; all postcephalic annules are subequal in width (4-5 μm). Cuticle varies in thickness throughout the body reaching 3 μm in pharyngeal region and about 1.5-2 μm in other body regions. Cuticular crests (apparently eight in number) extend along the body from cephalic capsule to terminal cone. Crests consist of short ridges on every annule. Ridges of each annule overlap slightly at anterior and posterior ends those of adjacent anterior and posterior annules. Zygapophyses not developed.

Cephalic capsule slightly elongated and apically widened, its length, basal diameter and cephalic ratio are 31 μm, 21 μm, and 1.48, respectively, in male and 30.5 μm, 25.5 μm, and 1.20 in female. Cuticle thickened around mouth and thinned to middle of cephalic capsule, homogeneous and devoid of vacuolisation in anterior half of capsule and with intracuticular vacuolisation transitting posteriad to the body cuticle in posterior half of capsule. Longitudinal crests start at anterior third of cephalic capsule. Inner labial sensilla not seen. Outer labial and cephalic setae thin, hairlike, arranged in two separate circles 6+4. In male, outer labial setae 11 μm, cephalic setae 16 μm long; in female, 8.5 μm and 15.5 μm, respectively. No other setae throughout the body. Amphid loop-shaped, situated at middle of cephalic capsule. In male, amphid dorsal branch 9 μm, ventral branch 13 μm long; distance from anterior end to amphid 15 μm. In female, these measurements are, respectively, 9.5 μm, 11 μm and 13.5 μm. No pores on the cephalic capsule.

Buccal cavity not developed. Pharynx obscure because of the nerve cell bodies, especially in intermediate region; anterior prenevral pharynx muscular, posterior ending is weakly widened.

Nerve ring situated at the level of 13th (male) or 15-16th (female) body annule. Excretory pore located at 22th (male) or 25th (female) annule.

Anterior ovary situated to the right from intestine; position of posterior ovary obscure. Anterior ovary contains a large oocyte 257 μm (26% of body length). Anterior germinative zone shifted by the oocyte posteriad to the vulva.

Spicules thin, slightly arched, tapered at both ends, 34 μm (arch) or 30.5 μm (chord) in length. Gubernaculum as a thin plate.

Rectum 12.5 preanal cuticular annules (male) or 9 annules (female) long. Tail conical, 11 anal diameters long (male). Terminal cone 21 μm (male) or 26.5 μm (female) long. Eight lateroventral setae 8-9 μm long on each side of tail.

Comparison. C. marisalbi sp. n. is characterised by the absence of zygapophyses and relatively long body with rather large number of annules. This species resembles *C. mokievskii* sp. n., but differs from the latter in the size and shape of the cephalic capsule (31 μm long with cephalic ratio 1.2-1.5 *versus* 45 μm and 2.4) and the cephalic setae longer than outer labial setae (in *C. mokievskii*, cephalic setae shorter than outer labial setae).

Etymology. Marisalbi (Latin) means "of the White Sea".

Ceramonema (Proceramonema) mokievskii sp. n. (Figs 10, 11)

Holotype. ♂, **Russia**, White Sea, Gorlo Strait, 66°4.3'N, 39°3.5'E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University.

Description. Body slender, cylindrical, threadlike. Male: L = 1750 μm; a = 97; b = 7.2; c = 9.7. Body diameter at the level of: cephalic setae 21 μm, nerve ring 20 μm, cardia 18 μm, midbody 18 μm, anus 19 μm.

Cuticle seems granular because of fine vacuolisation evenly distributed around annules and along the body. Body cuticle consists of 203 annules between cephalic capsule and terminal cone: 22 annules in pharyngeal region, 149 in intestinal region, and 32 in tail. Annule width varies from 7 to 11 μm; it increases gradually from first subcephalic annule (8 μm) to 28th annule (11 μm); 29th annule is narrow (8 μm), the subsequent annules widen gradually posteriad up to the middle of the tail (14-15th tail annules are the broadest, 8 μm wide). Eight longitudinal cuticular crests extend from cephalic capsule to base of terminal cone. Crests consist of short ridges slightly overlapping by ends with anterior and posterior ridges. Zygapophyses not evident. No lateral membrane.

Cephalic capsule elongated, bullet-like; its length 45 μm, basal diameter 19 μm (cephalic ratio 2.37). Fine vacuolisation present along the entire cephalic capsule except a narrow longitudinal stripe anterior to the amphid on each side. Longitudinal crests start at a distance of 1/3 cephalic capsule length from anterior end, just at the level of cephalic setae. No cephalic pores discernible. Lips and inner labial sensilla not seen. Outer labial setae and cephalic setae thin, hair-like, arranged in two separate circles 6+4; outer labial setae 11 μm and cephalic setae

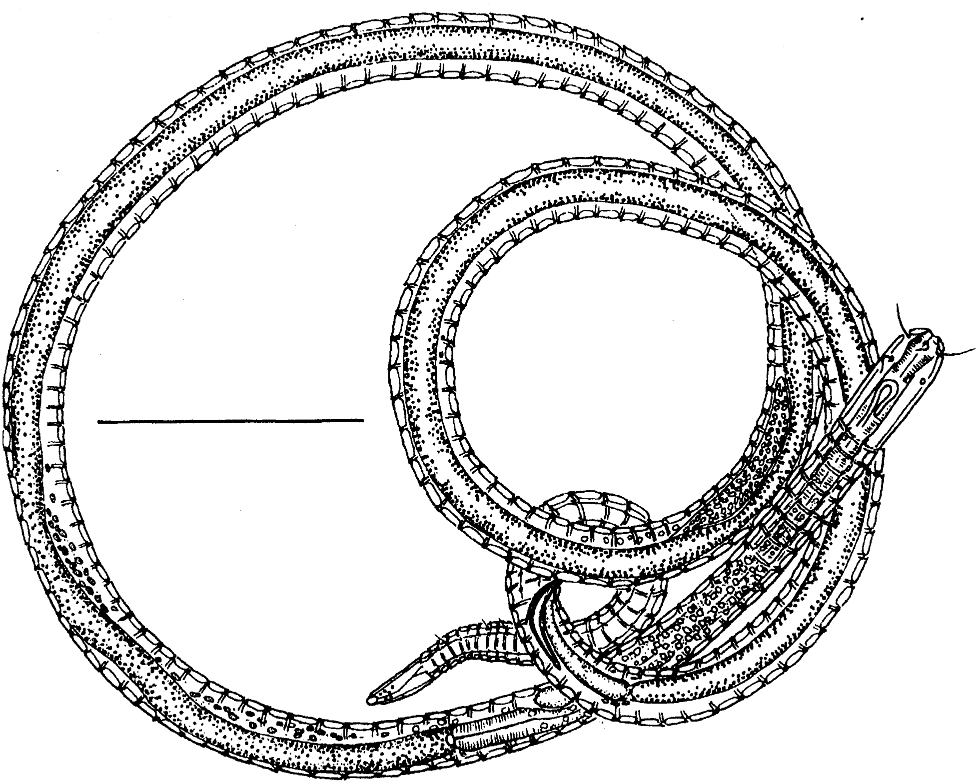

Fig. 10. *Ceramonema mokievskii* sp. n., holotype male, habitus. Scale bar: 100 μm.

7.5 μm long. No other setae along the body until the tail. Amphid loop-shaped, occupying posterior half of cephalic capsule. Amphid dorsal branch 15 μm, ventral branch 19 μm long, amphid width 6.6 μm (32% of corresponding body diameter), distance from anterior end to amphid 23.5 μm.

Buccal cavity not developed. Pharynx hardly visible because of covering cell bodies. Posteriorly, the pharynx is swollen in a small bulb. Rectum long, extending for eleven cuticular annules.

Ventral gland cell anteriorly with an ampulla and a ventral pore situated on the 17th annule.

Male gonads paired. Spicules slightly arched, tapered at both ends, 28 μm (arch) long. Gubernaculum as a thin plate at the distal half of the spicule; its length 17.5 μm.

Tail elongated-conical, 9.5 anal body diameters long. Terminal cone 24 μm long, 7.5 μm wide at base. Four setae 7 μm long, situated lateroventrally on each lateral side of tail.

Comparison. *C. mokievskii* sp. n. differs from the majority of *Ceramonema* species in the relatively long body subdivided into many annules. The new species is most close to *C. marisalbi* sp. n., but differs from the latter in the size and shape of the cephalic capsule and in the outer labial setae longer than cephalic setae (shorter than cephalic setae in *C. marisalbi*).

Etymology. The species is named after collector, marine ecologist and nematologist V.O. Mokievski.

Dubious species of *Ceramonema*

C. pselionemoides Gerlach, 1953: 567-568, Fig. 23, Mediterranean. De Coninck, 1965: 628 (*Dasynemella*). Lorenzen, 1981: 218 (*Dasynemoides*). Described from a single juvenile specimen. No further findings are known.

C. sculpturatum Chitwood, 1936: 3, Fig. 1 K; North Carolina, Atlantic coast of North America. Described from a single juvenile. No further findings are known.

Genus **Dasynemella** Cobb, 1933

= *Dasynema* Cobb, 1920 (nom. praeocc.); = *Leptodasynemella* Haspeslagh, 1973.

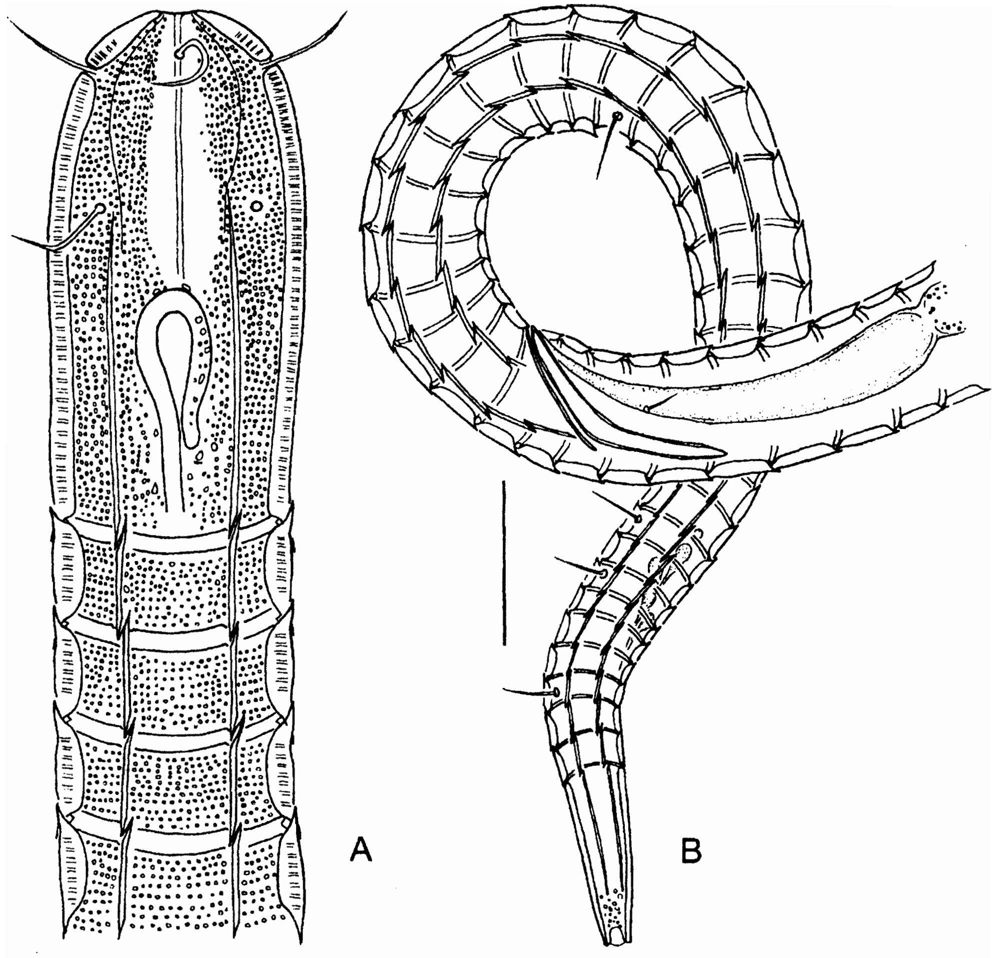

Fig. 11. *Ceramonema mokievskii* sp. n., holotype male. **A**, cephalic end; **B**, posterior body. Scale bars: A – 10 µm; B – 20 µm.

Type species *Dasynema sexalineata* Cobb, 1920.

Diagnosis. Body cuticle consists of many (400-1000) equally narrow annules. Zygapophyses not developed. Labial region not set off. Circles of the outer labial and cephalic setae separated. Amphid spirally coiled in one turn, loop-shaped, or round in outer contour.

Annotated list of species

1. *D. cincta* Gerlach, 1957: 448, Figs 13 e-f; Brazil. Haspeslagh, 1973: 245 (*Leptodasynemella*). Lorenzen, 1981: 218 (*Dasynemoides*).

2. *D. conica* Gerlach, 1956: 101-102, Figs 32 m-n; Kiel Bay of Baltic Sea. Haspeslagh, 1973: 245 (*Leptodasynemella*). Lorenzen, 1981: 218 (*Dasynemoides*).

3. *D. phalangida* Chitwood, 1936: 5, Figs 1 R-S; North Carolina, Atlantic coast of North America.

4. *D. riemanni* (Haspeslagh, 1973), **comb. n.** – *Dasynemella* sp.: Riemann, 1966: 144-145, Figs 37 a-b; North Sea. – *riemanni* Haspeslagh, 1973: 245, Fig. 1a (*Leptodasynemella*). – *albaensis* Warwick & Platt, 1973: 149-150, Figs 9 A-D (*Dasynemella*), **syn. n.**; Scottish coast. Lorenzen, 1981: 218 (*Dasynemoides*); Blome, 1982: 117 (*Leptodasynemella*). North Sea.

Non: Nichols & Musselman, 1979: 454-456, Fig. 4 (*Leptodasynemella riemanni*). Non: Bouwman, 1981: 367, Fig. 18 (*Dasynemella* cf. *albaensis*).

Since comparison of our specimen with descriptions of *Dasynemella albaensis* and *Leptodasynemella riemanni* could not reveal any significant differences, we synonymise both species. As the description of *L. riemanni* was published on January 30, 1973, and that of *D. albaensis* on May 15, 1973, we accept the first name as the valid one.

5. *D. sexalineata* (Cobb, 1920), **comb. n.** Cobb, 1920: 253-254, Figs 34 a-b (*Dasynema sexalineatum*); Massachusetts, Atlantic coast of North America.

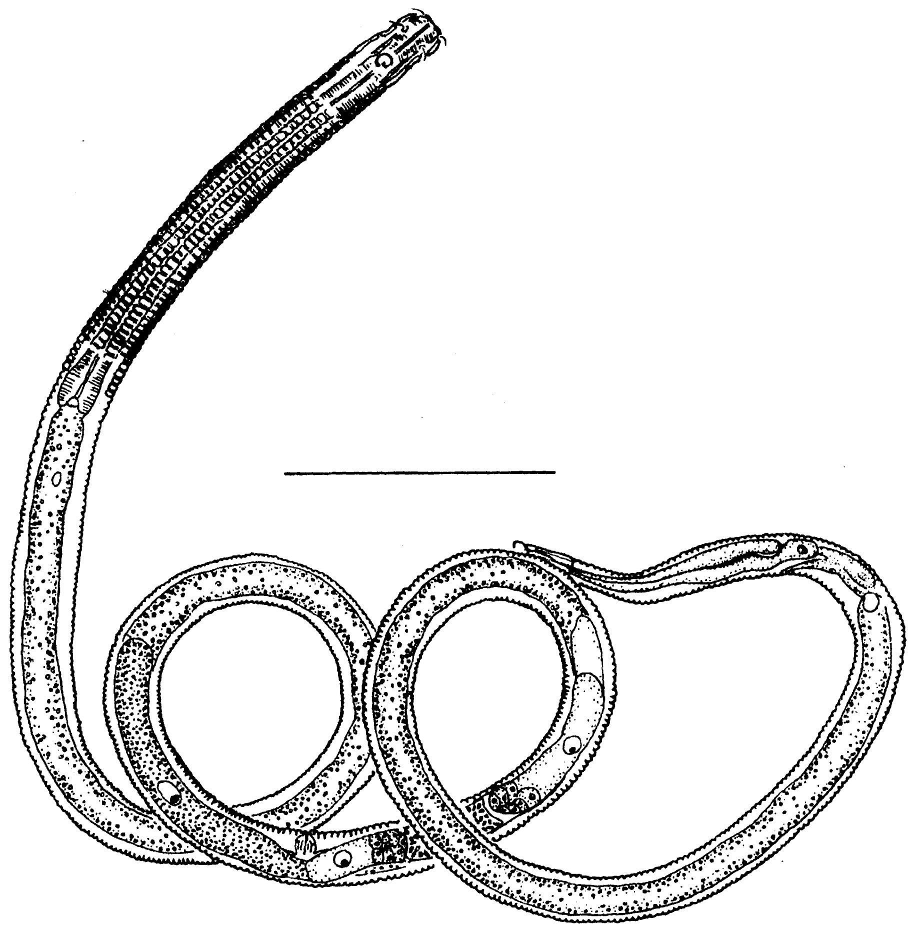

Fig. 12. *Dasynemella riemanni*, female, habitus. Scale bar: 100 μm.

Key to species of *Dasynemella*

1(6) Body length exceeds 1500 μm.
2(5) Length of the cephalic setae equal to 0.66 c.b.d. or more.
3(4) Cephalic ratio about 1. Cephalic capsule evenly wide throughout its length .... **D. phalangida**
4(3) Cephalic ratio greater than 1. Cephalic capsule narrowed anteriorly .... **D. conica**
5(2) Length of the cephalic setae less than 0.5 c.b.d. Amphid in male loop-shaped, in female circular .... **D. riemanni**
6(1) Body length less than 1500 μm.
7(8) Cuticular crests extend onto anterior half of the cephalic capsule. Cephalic ratio about 1. Outer labial and cephalic setae equally long (0.2 c.b. d.) .... **D. sexalineata**
8(7) Cuticular crests extend to only the posterior half of the cephalic capsule. Cephalic capsule narrowed anteriorly. Cephalic setae 0.8 c.b.d. long .... **D. cincta**

Dasynemella riemanni (Haspeslagh, 1973) (Figs 12, 13)

Material examined. 1 ♀, **Russia**, White Sea, Gorlo Strait, 66°4.3′N, 39°3.5′E, depth 20 m, coarse sand with broken shells, 3.VIII.1984.

Description. Body long, cylindrical, thread-like. L = 1884 μm; a = 94; b = 8.4; c = 10; V = 51%. Body diameter at the level of: cephalic setae 17 μm, nerve ring 18 μm, cardia 18 μm, mid-body 20 μm, anus 15.5 μm.

Body cuticle consists of about 655 narrow annules: 60 annules in pharyngeal region, about 550 in intestinal region, and 45 in tail. Annules of nearly equal width (2.5-3 μm) and thickness (1.5-2 μm in the optical section), without any prominent zygapophyses (undulations). Subcuticular vacuolisation absent. Every annule divided by eight longitudinal ridges. Each ridge

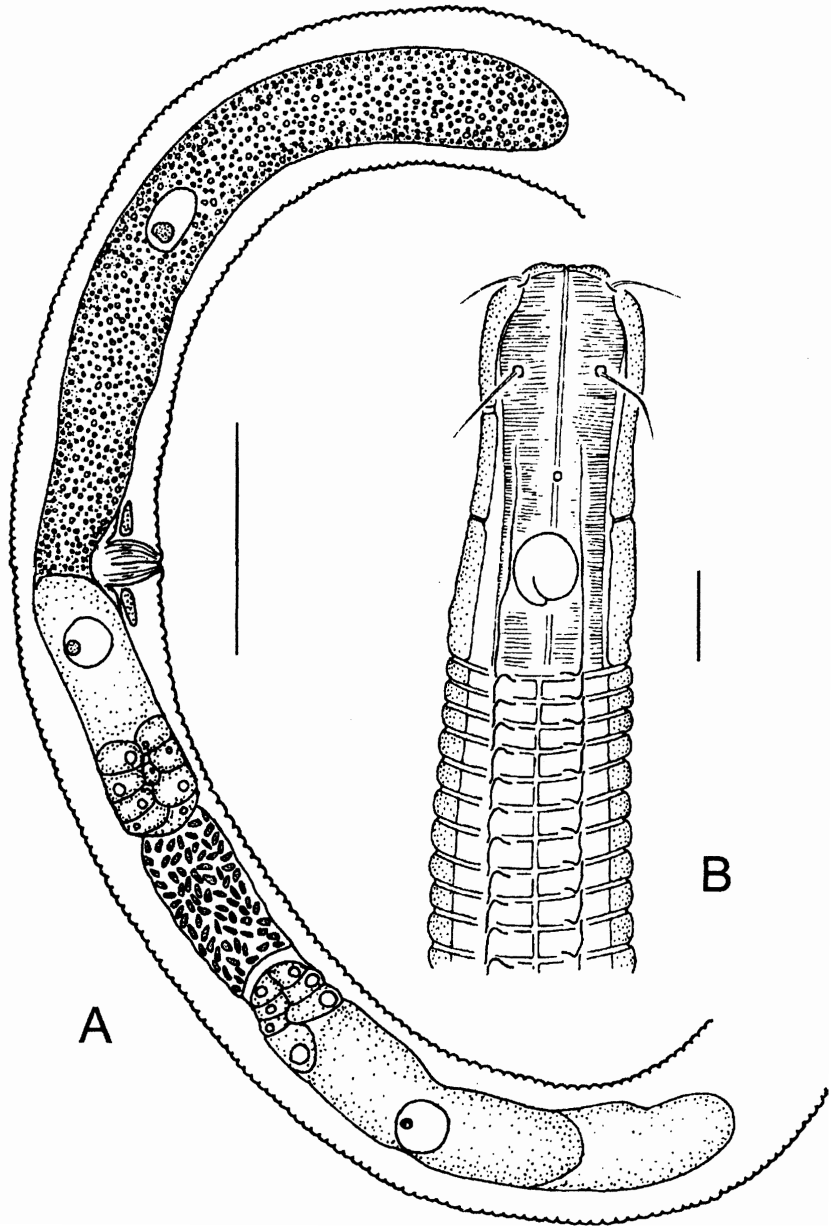

Fig. 13. *Dasynemella riemanni*, female. **A**, cephalic end; **B**, reproductive system. Scale bars: A – 20 µm, B – 50 µm.

overlaps slightly with corresponding ridges of adjacent anterior and posterior annules. Ridges form eight longitudinal crests extending along the body from the middle of cephalic capsule to posterior third of terminal cone. Narrow lateral membrane extends from first annule along the entire body to tail cone.

Cephalic capsule nearly cylindrical, but slightly narrowed in middle; its length 40 µm and basal diameter 20 µm (cephalic ratio 2.00). Cuticle of the capsule apically thin and further posteriad uniformly thick, equal in thickness to body cuticle. Longitudinal crests originate at the middle constriction of cephalic capsule. Inner labial sensilla not visible. Six outer labial setae 7 μm long; four cephalic setae 8 μm long. Both crowns separated from each other by a distance 10 μm. All these setae thin, hair-like. Amphid is a rounded spiral in one turn, situated in the middle of the cephalic capsule. Amphid width 7 μm; distance from apex to amphid 27 μm. Six cephalic pores: one middorsal and one midventral just posterior to cephalic setae, one middorsal and one midventral level with the anterior amphid edging, and two lateral pores, right and left, at the middle of the cephalic capsule, anterior to the amphid.

Buccal cavity not developed. Pharynx poorly discernible, narrow, anteriorly cylindrical, with a slight posterior widening, muscular along its entire length. Nerve ring and renette cell not seen.

Vulva situated in the 330th body annule. Ovaries paired, antidromously reflexed, with spermatheca. Anterior ovary with a long oocyte, 159 × 20 μm.

Tail conical, 9 anal diameters long. Terminal cone 30 μm long.

Remarks. The specimen examined fits well the descriptions cited above in the "Annotated list...". Warwick & Platt (1973) indicated somewhat different number of longitudinal crests changing along the body in sequence 8-10-8-6. The difference may be caused by individual variability.

Specimens sampled off the coast of Peru and identified as "*Leptodasynemella riemanni*" by Nichols & Musselman (1979) certainly do not correspond to the species diagnoses because of their greater body length (2417-3391 μm in females), apparently longer cephalic setae, and very prominent angular projections arranged in the longitudinal cuticular crests. Specimens found in the Ems Estuary (North Sea) and reported under the name *Dasynemella* cf. *albaensis* by Bouwman (1981) scarcely belong to this species because of their twice greater amphids and longer cephalic setae.

Distribution. South-eastern part of the North Sea, 10-26.5 m, fine to medium sand (Riemann, 1966) and medium sand in the intertidal zone of Sylt Island (Blome, 1982). Sandy beach of Western Scotland (Warwick & Platt, 1973). The species is registered from the White Sea for the first time.

Genus **Dasynemoides** Chitwood, 1936

= *Dasynemelloides* Haspeslagh, 1973.

Type species *Dasynemoides setosus* Chitwood, 1936.

Diagnosis. Body cuticle consists of many equally narrow annules devoid of zygapophyses. Labial region distinctly set off the cephalic capsule. Six outer labial setae rooted in labial region, whereas four cephalic setae inserted on cephalic capsule. Amphid loop-shaped or round loop-shaped.

Annotated list of species

1. *D. crassus* sp. n.
2. *D. filum* (Gerlach, 1957). Gerlach, 1957: 447-448, Figs 13 a-d (*Ceramonema*); Brazil. Lorenzen, 1981: 218.
3. *D. setosus* Chitwood, 1936: 5, Figs 1 T-U; Brazil.
4. *D. tenuis* Furstenberg & Vincx, 1993: 148-150, Figs 5 D, E.; South Africa.

Key to species of *Dasynemoides*

1(2) Body very slender (a = 120). L = 1560 μm. Cephalic ratio 1.9 .... **D. tenuis**
2(1) Body relatively thicker (a < 100).
3(6) Cephalic capsule elongate (cephalic ratio > 1).
4(5) Cephalic longitudinal crests extend along the almost entire capsule to the labial region .... **D. setosus**
5(4) Cephalic longitudinal crests extend to only basal part of the cephalic capsule .... **D. filum**
6(3) Cephalic capsule very short and stout (cephalic ratio< 1) .... **D. crassus** sp. n.

Dasynemoides crassus sp. n.
(Fig. 14, 15)

Holotype. ♀, **Russia**, White Sea, Gorlo Strait, 66°4.3′N, 39°3.5′E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University.

Description. Body cylindrical. Female: L = 1687 μm; a = 40; b = 6; c = 10; V = 58%. Body diameter at the level of: cephalic setae 27 μm; nerve ring 37 μm; cardia 36 μm; midbody 42 μm; anus 32 μm.

Cuticle consists of about 685 free annules between cephalic capsule and terminal cone: 88 annules in pharyngeal region, 541 in intestinal region, and 56 in tail. All annules more or less equally narrow, 3-5 μm wide and 1-2 μm thick. A narrow lateral membrane 4-5 μm wide extends from about the 65th annule nearly to the anus. Cuticular crests (about ten in number) run along the entire body from cephalic capsule to terminal cone. Crests are made up of short ridges on each annule. Zygapophyses vestigial. Intracuticular vacuolisation very weak and fine, restricted to narrow areas under the crests.

Cephalic capsule stout, slightly narrowed apically, its length 26 μm, cephalic ratio 0.74. Cuticular crests starting at anterior margin of cephalic capsule, just behind the level of cephalic setae. Intracuticular vacuolisation present under longitudinal crests, not clearly visible in annules posterior to the cephalic capsule. Soft-cuticular labial region well demarcated from hard-cuticular cephalic capsule.

Inner labial sensilla not seen. Six outer labial setae and four cephalic setae united in one crown of ten thin, hair-like setae situated just posterior to anterior margin of cephalic capsule. Outer labial setae 11 μm, cephalic setae 7.5 μm long. A few tiny setae, 1.5-2 μm long, visible in intesti-

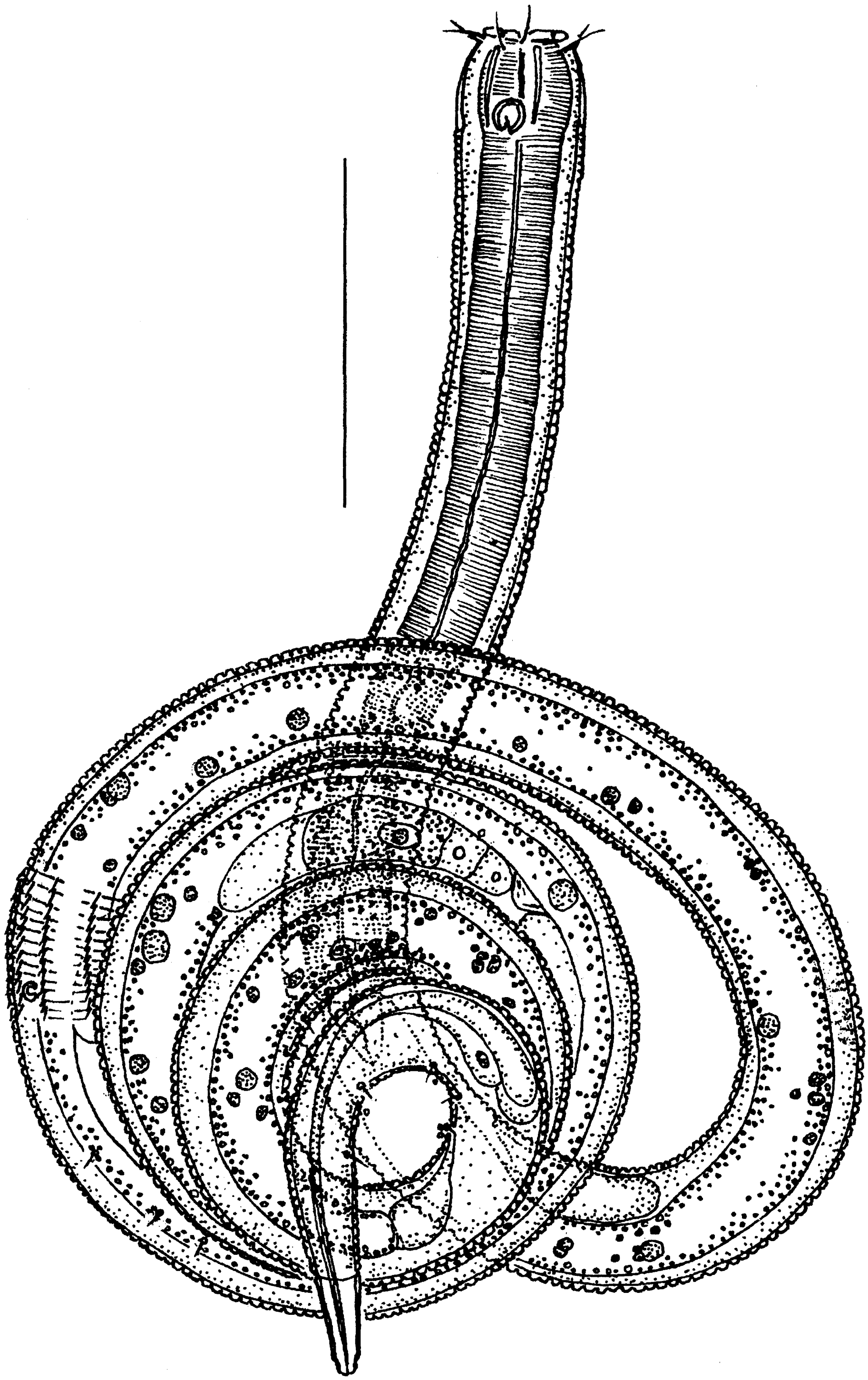

Fig. 14. *Dasynemoides crassus* sp. n., holotype female, habitus. Scale bar: 100 µm.

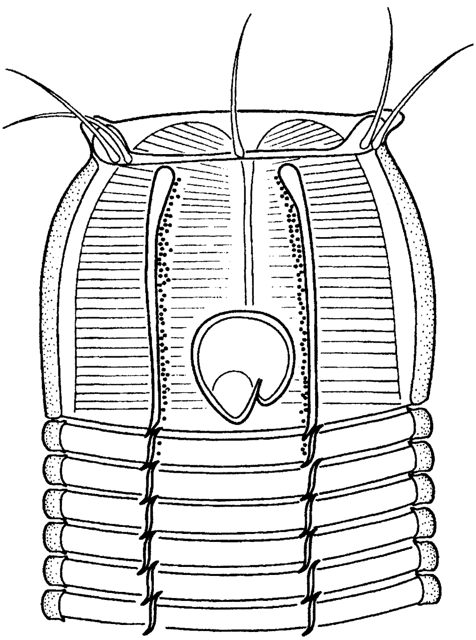

Fig. 15. *Dasynemoides crassus* sp. n., holotype female, cephalic end. Scale bar: 30 μm.

nal body region. Amphid rounded, comma-like, 10 μm in width; distance from anterior end to amphid 19.5 μm.

Buccal cavity not developed. Pharynx evenly muscular along its length, with a weak posterior widening. Midgut contains rounded corpuscles of unknown origin, sized 3-11 μm. Rectum 21 preanal annules long.

Nerve ring at the level of 63th annule. Excretory pore at the 105th annule, at a distance 286 μm from anterior end.

Ovaries paired, antidromously reflexed, both situated to the left of the intestine. The greatest oocyte 43 μm long.

Tail conical, 5 anal diameters long. Four lateroventral setae 2-4 μm long situated on each tail side. Terminal cone 32 μm long. Three caudal glands discernible.

Comparison. The new species is well characterised by the position of outer labial and cephalic setae in one circle situated at the anterior edge of the cephalic capsule. This position distinguishes *D. crassus* sp. n. from other *Dasynemoides* species as well as from species of the related genus *Metadasynemoides*. In the latter genus, at least the outer labial setae are inserted on the labial region in front of the anterior edge of the cephalic setae. Therefore, the new species is placed within the genus *Dasynemoides* tentatively, with possible reconsideration later. In addition, *D. crassus* sp. n. differs from *D. setosus* in the stout cephalic capsule with cephalic ratio 0.74 (in *D. setosus*, the length of the cephalic capsule is sufficiently greater than its basal diameter) and smaller index "b" (6 *versus* 11). *D. crassus* sp. n. differs from *D. tenuis* in the stout cephalic capsule (cephalic ratio 0.74 *versus* 1.90) and thicker body (index "a" 40 *versus* 120).

Etymology. Crassus (Latin): corpulent.

Genus **Metadasynemoides** Haspeslagh, 1973

Type species *Dasynemoides longicollis* Gerlach, 1952.

Diagnosis. Body cuticle consists of many equally narrow annules. Zygapophyses not developed. Cuticular crests extend from near anterior margin of cephalic capsule to terminal cone. Labial region distinctly set off the cephalic capsule. Outer labial and cephalic setae subequal in length and arranged in two separate but close circles both inserted on labial region anterior to the margin of cephalic capsule. Amphid spirally coiled in 1-2 turns, loop-shaped, rounded or of other shape, often differently shaped in males and females.

Annotated list of species

1. *M. cristatus* (Gerlach, 1957). Gerlach, 1957: 448, Figs 13 g-i (*Dasynemoides*); Brazil. Haspeslagh, 1973: 245. Nicholas & Stewart, 1990: 247-261, Figs 1-12; New South Wales, Australia, ultrastructure.
2. *M. labiatus* sp. n.
3. *M. latus* (Gerlach, 1957). Gerlach, 1957: 450, Figs 13 k-m (*Dasynemoides*); Brazil. Haspeslagh, 1973: 245.
4. *M. longicollis* (Gerlach, 1952). Gerlach, 1952: 363-364, Abb. 28 a-c (*Dasynemoides*); Mediterranean. Haspeslagh, 1973: 245.
5. *M. spinosus* (Gerlach, 1963), **comb. n.** Gerlach, 1963: 101-102, Abb. 13 g-i (*Dasynemoides*); Maldive Islands.

Key to species of *Metadasynemoides*

1(8) Body length about 1500 μm or less.
2(7) Cephalic setae 5-12 μm long (up to 70% of c. b.d.).
3(6) Tail about 4.5-5 anal diameters long; index "c" > 11. Amphid rounded, at least in females.
4(5) Cephalic capsule elongate and tapered anteriorly. Cephalic ratio > 1. In male, amphid loop-shaped, its longer ventral branch extends to postcephalic annules. Outer labial setae longer than cephalic setae .... **M. cristatus**
5(4) Cephalic capsule stout and truncated anteriorly. Cephalic ratio near 1. In male, amphid rounded, spirally coiled in two turns. Outer labial and cephalic setae equal in length .... **M. latus**
6(3) Tail about 8-11 anal diameters long; index "c" < 11. Cephalic capsule elongate, tapered anteriorly. Amphid of female loop-shaped, with longer ventral branch extending to the second postcephalic annule .... **M. labiatus** sp. n.
7(2) Cephalic setae 24 μm long (>100% of c.b.d.). Cephalic capsule elongate, tapered anteriorly. Amphid loop-shaped, with longer ventral branch .... **M. spinosus**

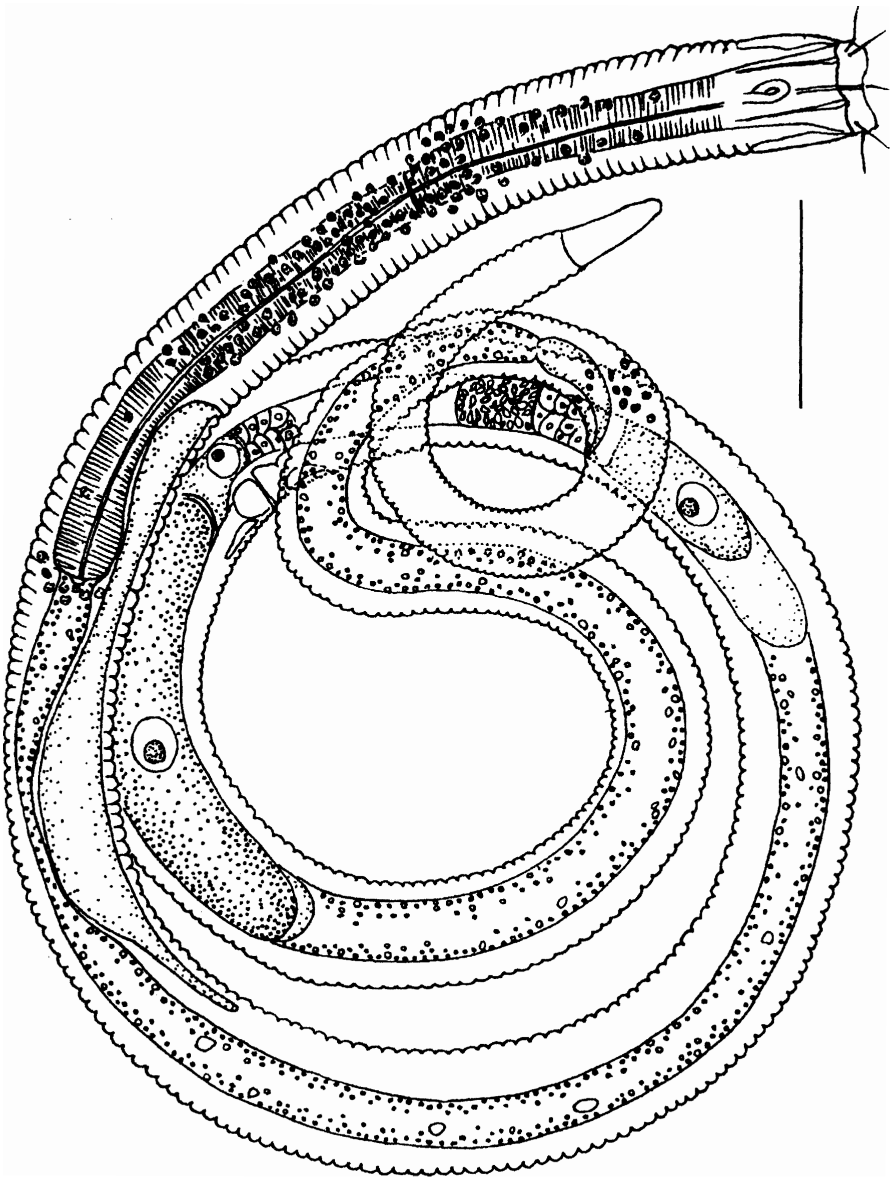

Fig. 16. *Metadasynemoides labiatus* sp. n., paratype female, habitus. Scale bar: 40 µm.

8(1) Body length 2000-3000 µm. Cephalic setae 17 µm long; circles of outer labial and cephalic setae close to each other. Cephalic capsule stout and anteriorly truncated . . . . **M. longicollis**

Metadasynemoides labiatus sp. n.
(Figs 16, 17)

Holotype. ♀, **Russia**, White Sea, Gorlo Strait, 66°4.3´N, 39°3.5´E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University, Moscow.

Paratype. ♀, same data and deposition.

Description. Body long, slender, cylindrical. Females: L = 1040-1217 µm; a = 43.5-52; b = 5.63-6; c = 8-9; V = 52.8-54%. Body diameter at the level of: cephalic setae 15-20.5 µm; nerve ring 19-27 µm; cardia = 18-25.5 µm; midbody 20-28 µm; anus 15.5-27 µm.

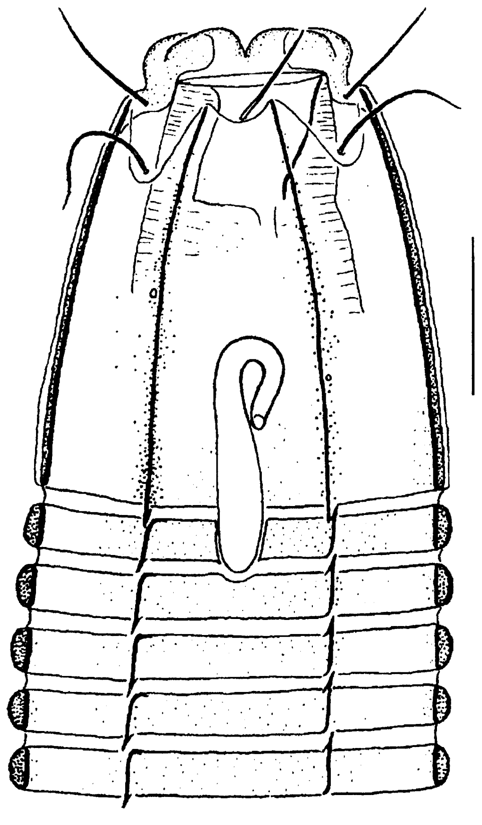

Fig. 17. *Metadasynemoides labiatus* sp. n., holotype female, cephalic end. Scale bar: 20 μm.

Body cuticle consists of 335-433 free annules between cephalic capsule and terminal cone: 55-63 annules in pharyngeal region, 241-306 in intestinal region, and 39-64 in tail. Annules 1-2.5 μm thick, narrow and mostly equal in width (about 2 μm). However, widened annules also occur irregularly; for instance, the 39th annule in paratype is twice as wide as the 40th. Eight cuticular crests extend along body from cephalic capsule to terminal cone. Crests consist of short ridges on each annule slightly overlapping by anterior and posterior ends with corresponding ridges of adjacent anterior and posterior annules. There is a narrow lateral membrane, 1.5-2 μm wide, extending from near the level of excretory pore to middle of tail. Annules devoid of zygapophyses and intracuticular vacuolisation.

Cephalic capsule shortly cylindrical, truncated anteriorly, 19-29 μm long (cephalic ratio 1.1-1.14). Capsule cuticle thick, tapering to anterior margin. Crests start at the very anterior margin of cephalic capsule. Labial region soft-cuticular, sharply demarcated from hard-cuticular cephalic capsule. Anterior margin of cephalic capsule sinuous, with deep emarginations in sites of cephalic setae attachments. Mouth opening surrounded by soft-cuticular lips.

Inner labial sensilla not discernible. Six outer labial and four cephalic sensilla represented by thin, hair-like setae; both circles situated close to each other. Outer labial setae 5-7 μm, cephalic setae 5-7 μm long. Amphid loop-shaped, situated in posterior half of cephalic capsule, with sharply unequal branches; ventral branch protruded to first subcephalic annule. Dorsal branch 6 μm, ventral branch 9.5-13.5 μm long; amphid width 4 μm; distance from anterior end to amphid 13-18 μm. Somatic setae 3-5 μm long, very few in number, sparsely dispersed along the body.

Buccal cavity small, soft-walled, obscure (holotype) or not developed (paratype). Pharynx vaguely discernible, but likely muscular and almost evenly wide throughout its length, with only weak widening at posterior end. Rectum 14 preanal annules long.

Nerve ring situated at the level of 20th (holotype) or 31st-32nd (paratype) annules.

Renette cell long and thick. In holotype, excretory pore located in the 41th annule, at a distance 183 μm from anterior end. In paratype, excretory pore between 50th and 51st annules, at a distance 135 μm from anterior end.

Tail elongate conical, 8-11 anal diameters long. Terminal cone 16-27 μm long.

Comparison. *M. labiatus* sp. n. is related to *M. spinosus* in the shape of the amphid with unequal branches, but differs in the position of the amphid at the posterior portion of the cephalic capsule, cuticular crests extending to the anterior margin of the cephalic capsule, and short cephalic setae (5-7 μm *versus* 24 μm). The new species is similar to *M. cristatus* and *M. latus* in the shape of the cephalic capsule and body measurements. *M. labiatus* sp. n. differs from *M. cristatus* in the shorter outer labial setae (5 μm *versus* 11 μm), shape of amphid (loop-shaped *versus* rounded), and longer tail (8 anal diameters *versus* 5), and from *M. latus* in the shape of amphid (loop-shaped *versus* rounded) and longer tail (8 anal diameters *versus* 4.5).

Etymology. *Labiatus* (Latin): lip-bearing; the name reflects the prominent labial region of the species.

Genus **Metadasynemella** De Coninck, 1942

= *Dictyonemella* Haspeslagh, 1973.

Type species *M. macrophalla* De Coninck, 1942.

Diagnosis. Body short, usually elongate spindle-shaped, rarely cylindrical. Cuticle annules moderate in number (up to 175), broad, unequal along the body; zygapophyses lacking or weakly developed; intracuticular vacuolisation may be present. Labial region set off the cephalic capsule. Cephalic capsule usually with longitudinal and transversal crests. All setae inserted on the labial region. Outer labial setae and cephalic setae arranged in two close circles or united in a joint circle. Amphids loop-shaped.

Annotated list of species

1. *M. cassidiensis* Vitiello & Haspeslagh, 1972: 7-8, Pl. 2, Figs 3-4; Mediterranean.
2. *M. elegans* Vitiello, 1974: 548-550, Figs 1 A-D; Mediterranean.
3. *M. falciphalla* Vitiello & Haspeslagh, 1972: 5-6, Pl. 2, Figs 1-2; Mediterranean.
4. *M. macrophalla* De Coninck, 1942: 7-10, Figs. 1-7; Mediterranean.
5. *M. picrocephala* (Haspeslagh, 1973). Haspeslagh, 1973: 246, Pl. I, Figs 4, 7, pl. II, Fig. 2 (*Dictyonemella*); Lorenzen, 1981: 219.

Subfamily PSELIONEMATINAE De Coninck, 1965

Type genus *Pselionema* Cobb, 1933.

Diagnosis. Outer labial sensilla as papillae.

Key to genera

1(2) Body cuticle consists of numerous (more than 300), equally narrow annules. Zygapophyses not developed. Often a cuticular thickening present between amphid branches .... **Pterygonema**

2(1) Cuticle annules less numerous (up to 300), more or less broad and usually unequal. Zygapophyses present. No cuticular thickening between amphid branches .... **Pselionema**

Genus **Pselionema** Cobb, 1933

= *Pselionemoides* Haspeslagh, 1973.

Type species *Steineria annulata* Filipjev, 1922.

Diagnosis. Cuticle consists of 70-210 annules. Annules usually thick and broad. Zygapophyses usually more or less developed. Labial region not set off. Amphid loop-shaped, elongate.

Annotated list of species

1. *C. annulatum* (Filipjev, 1922). Filipjev, 1922: 122-123, Figs 13 a-b (*Steineria annulata*); Black Sea. Schulz, 1938: 115 (*Ceramonema*); North Sea. Schuurmans Stekhoven, 1942: 253, Figs 22 A-B; Mediterranean. Gerlach, 1950: 153-154, Figs 9 a-c; Kiel Bay of the Baltic Sea.
2. *P. beauforti* Chitwood, 1936: 3, Fig. 1 L-M (*Pselionema annulatum beauforti*); North Carolina, Atlantic coast of North America. Chitwood, 1951: 641.
3. *P. concinnum* sp. n.
4. *P. deconincki* Vitiello & Haspeslagh, 1972: 8-10, Pl. 3, Figs 1-3; Mediterranean.
5. *P. detriticola* Vitiello, 1974: 552-554, Figs 2 A-E; Mediterranean.
6. *P. dissimile* Vitiello, 1974: 554-556, Figs 3 A-F ("*dissimilis*"); Mediterranean.
7. *P. longissimum* Gerlach, 1953: 568-569, Figs 24 a-b; Mediterranean.
8. *P. minutum* Vitiello & Haspeslagh, 1972: 11-12, Pl. 3, Figs 4-5; Mediterranean.
9. *P. mirabile* sp. n.
10. *P. ornatum* (Timm 1961). Timm, 1961: 58-60, Figs 45 a-d (*Pterygonema*); Bay of Bengal. Haspeslagh, 1973: 242.
11. *P. parasimplex* Vitiello, 1971: 872, Figs 10 a-c; Mediterranean.
12. *P. richardi* De Coninck, 1942: 20-22, Figs 22-25; Mediterranean.
13. *P. rigidum* Chitwood, 1936: 3, Figs 1 P-Q; North Carolina, Atlantic coast of North America.
14. *P. simile* De Coninck, 1942: 23-26, Figs 26-30; Mediterranean.
15. *P. simplex* De Coninck, 1942: 26-30, Figs 31-40; Mediterranean. Tchesunov, 1995: 117-130, Figs 1-6, 7 A,C, 8; White Sea, ultrastructure.

Note. Pselionema longiseta Ward, 1974 differs significantly from all other species of *Pselionema* in the greater number (350) of the equally narrow cuticular annules devoid of zygapophyses, cylindrical pharynx not swollen at the posterior end, and presence of a dorso-caudal apophysis of the gubernaculum. On this ground, we transfer this species from the genus *Pselionema* to *Pterygonema* despite the evident lack of a spine-like structure between the amphid branches, which was considered by Platt & Warwick (1988) a typical character of *Pterygonema*.

Key to species of *Pselionema*

1(4) Body cuticular annules about 200 in number.

2(3) Body annules narrow (2.5-3.5 μm). Body slender ("a" about 70) .... **P. dissimile**

3(2) Body annules broad, from 8 to 11 μm throughout the body. Body stouter ("a" about 40) .... **P. mirabile** sp. n.

4(1) Body annules about 150 or fewer in number.

5(6) Body short, about 400 μm or less, and stout ("a" near 20-30) .... **P. minutum**

6(5) Body length exceeds 400 μm.

7(12) Body length about 1000 μm or more.

8(9) Body relatively stout ("a" 50-60). Cephalic setae shorter than 10 μm .... **P. simile**

9(8) Body slenderer ($a > 70$). Cephalic setae about 15 μm long.

10(11) Gubernaculum present .... **P. longissimum**

11(10) Gubernaculum absent ...... **P. concinnum** sp. n.

12(7) Body length about 900 μm or less.

13(14) Zygapophyses not developed .... **P. ornatum**

14(13) Zygapophyses distinct.

15(18) Pores on the cephalic capsule present.

16(17) Spicules long, about 30 μm .... **P. annulatum**

17(16) Spicules short, less than 20 μm ..... **P. detriticola**

18(15) No pores on the cephalic capsule.

19(20) Number of body annules about 150 or more. Body about 580 μm long. Tail short, $c = 8$. Amphid relatively large, about 12 μm long .... **P. richardi**

20(19) Number of the body annules less than 130. Body short, 500-700 μm long.

21(24) Body very short, about 500 μm.

22(23) Body annules about 70 in number .... **P. simplex**

23(22) Body annules about 120 in number. Cephalic setae very short (about 3 μm) .... **P. deconincki**

24(21) Body longer, 600-700 µm.
25(26) Cephalic capsule large, 32 µm or longer .... **P. rigidum**
26(25) Cephalic capsule short, 20-25 µm long.
27(28) Cephalic setae short, about 4 µm. Ventral pore on 19th body annule. Spicules short, about 20 µm long .... **P. parasimplex**
28(27) Cephalic setae longer, about 8 µm. Ventral pore on 13th body annule. Spicules longer, about 30 µm . ... **P. beauforti**

Pselionema concinnum sp. n.
(Figs 18, 19)

Holotype. ♂, **Russia**, White Sea, Gorlo Strait, 66°4.3' N, 39°3.5' E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University.
Paratypes. 7 ♂, 7 ♀, same data.

Description. Body slender, cylindrical, threadlike. Males: L = 1048-1325 µm; a = 72-91; b = 5.8-6.8; c = 6.9-8.1. Females: L = 1046-1253 µm; a = 62-87; b = 5.6-6; c = 6-7; V = 43.5-48.2%. In males, body diameter at the level of: cephalic setae 10-14.5 µm; nerve ring 13-19 µm; cardia 13-17 µm; midbody 13-16.5 µm; anus 13-16 µm. These measurements in females, respectively: 12-15 µm, 15-18 µm, 14-19 µm, 14-18 µm, 10-13 µm.

In males, body cuticle consists of 127-146 annules: 16-18 in pharyngeal region, 80-96 in intestinal region, and 28-33 in tail. In females, respective numbers are 123-133, 16-19, 81-96, and 23-27. Annule width varies regularly along the body. In holotype male, 1st annule narrow (8 µm), then annules increase in width gradually up to 24th annule (13 µm); the 25th annule narrow (7 µm); the width of subsequent annules increases gradually to 96th annule (9 µm); the 97th, anal annule very broad (17 µm, may be composed of two fused annules); subsequent annules narrow very slowly to the tail cone. A few females show sharply enlarged annules at the end of intestinal region (three-four annules in front of anus) or in the middle of tail (the 10-13th postanal annule) with subsequent annules of nearly the same width. Each annule subdivided by eight(?) longitudinal ridges. Each ridge slightly S-shaped, with ends overlapping slightly with corresponding ridges of adjacent anterior and posterior annules. Ridges form eight longitudinal crests extending along the body from base of cephalic capsule to terminal cone. No subcuticular vacuolisation or lateral membrane in the annules. Zygapophyses well developed as fluent sinusoid undulation.

Cephalic capsule elongate, bullet-shaped, 33-47 µm long (cephalic ratio 2.4-2.7) in males and 36-44 µm long (cephalic ratio 2.2-3) in females. Inner and outer labial sensilla not seen. Four cephalic setae situated apically, 11-13 µm long in males and 12-14 µm in females. Amphid elongate, loop-shaped, situated in posterior half of cephalic capsule. In males, dorsal branch of amphid 12-16 µm and ventral branch 14-20 µm long; amphid width 4.2-5.3 µm; distance from anterior end to amphid 17-20.5 µm. These measurements in females are respectively 14-16 µm and 15-19 µm; 3.2-4.3 µm; 13-19 µm.

Stoma not developed. Pharynx distinctly subdivided into three regions. Anterior region muscular, slightly thickened apically. Middle region narrowed, without visible muscular striation, obscured by cell bodies. Posteriorly, pharynx widened pearlike, with well discernible radial striation. Anterior region of pharynx 85-126 µm long in males and 88-111 µm long in females (ending at the level of 5-8th cuticular annules). In holotype, middle region of pharynx 89 µm long and posterior bulb 11 µm long.

Nerve ring situated at transition from anterior to middle region of pharynx (at the level of 6th cuticular annule in holotype). Ventral pore in holotype located between 13rd and 14th cuticular annules, at a distance 162 µm from anterior end. Ventral gland extending for 9 cuticular annules.

Spicules slightly arcuate, 18.5-33 µm (arc) or 18-26 µm (chord) long. No gubernaculum.

Tail length in males 11-12.5, in females 14-19 anal diameters. Males with several subventral setae about 5.5 µm long on the tail.

Comparison. *P. concinnum* sp. n. is most similar to *P. longissimum* and *P. simile*, which are also characterised by elongate (L > 1000 µm) and slender (a > 50) body with about 130 cuticular annules (the number of annules is not indicated in *P. longissimum*).

The new species differs from *P. simile* in the size and shape of the cephalic capsule (its length 33-47 µm in *P. concinnum, versus* 25-31 µm in *P. simile*; cephalic ratio 2.2-3 *versus* 1.54-1.8, respectively); longer cephalic setae (17.3-18.2 µm *versus* 10.7-13.9 µm); smooth zygapophyses (*versus* rather angular in *P. simile*); and longer amphid branches (ventral branch 12-16 µm long and dorsal branch 14-20 µm long in *P. concinnum, versus*, respectively, 8.8 µm and 11 µm in *P. simile*). *P. concinnum* sp. n. is most similar to *P. longissimum*, but differs in the absence of gubernaculum, presence of tail setae in males, shorter cephalic setae (10.7-13.5 µm long *versus* 15 µm), and unequal amphid branches.

Etymology. The Latin word "*concinnum*" means nice, fine.

Pselionema mirabile sp. n.
(Figs 20, 21)

Holotype. ♂, **Russia**, White Sea, Gorlo Strait, 66°4.3'N, 39°3.5'E, depth 20 m, coarse sand with broken shells, 3.VIII.1984, deposited in Zoological Museum of Moscow State University.

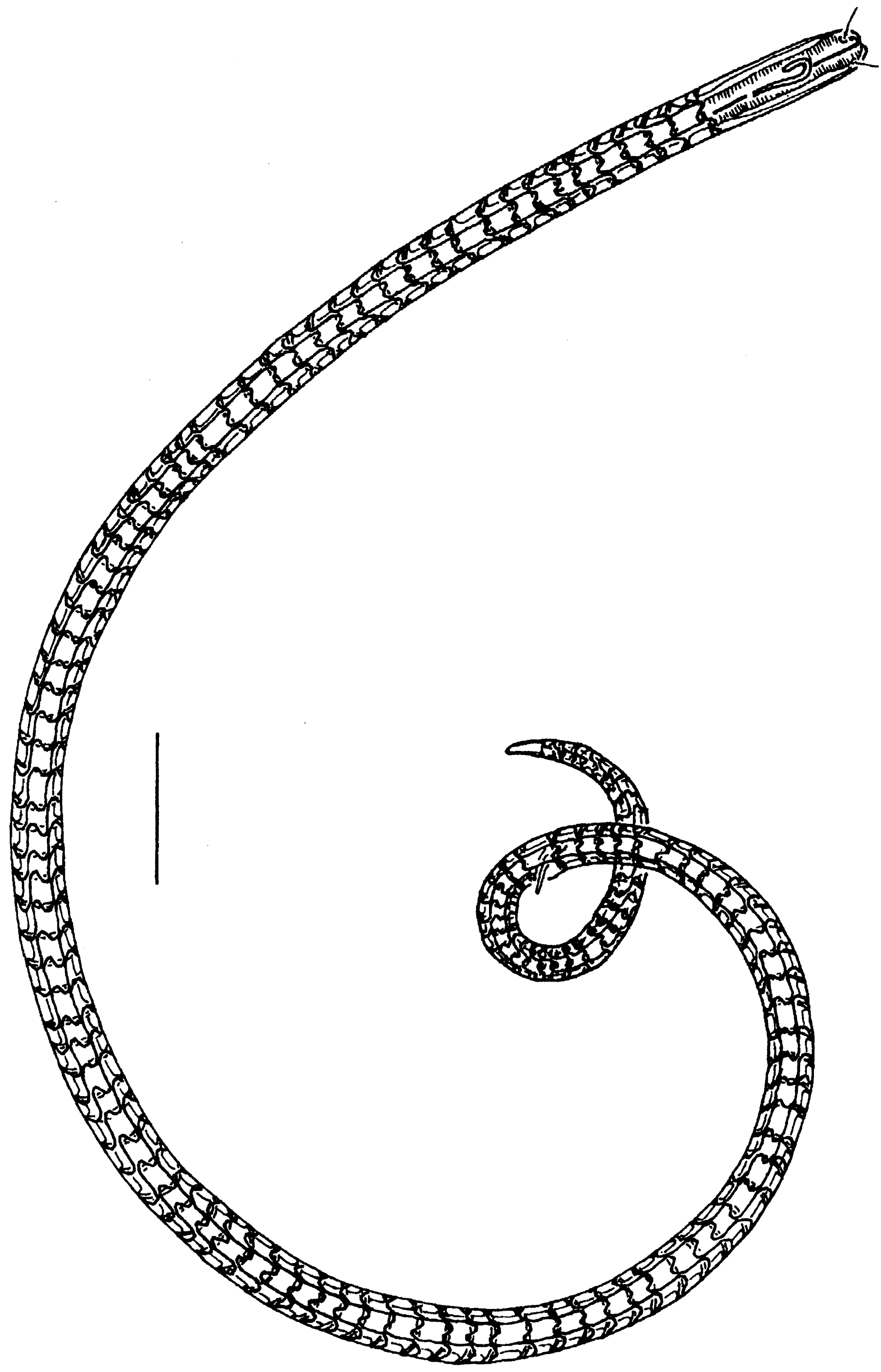

Fig. 18. *Pselionema concinnum* sp. n., holotype male, habitus. Scale bar: 50 µm.

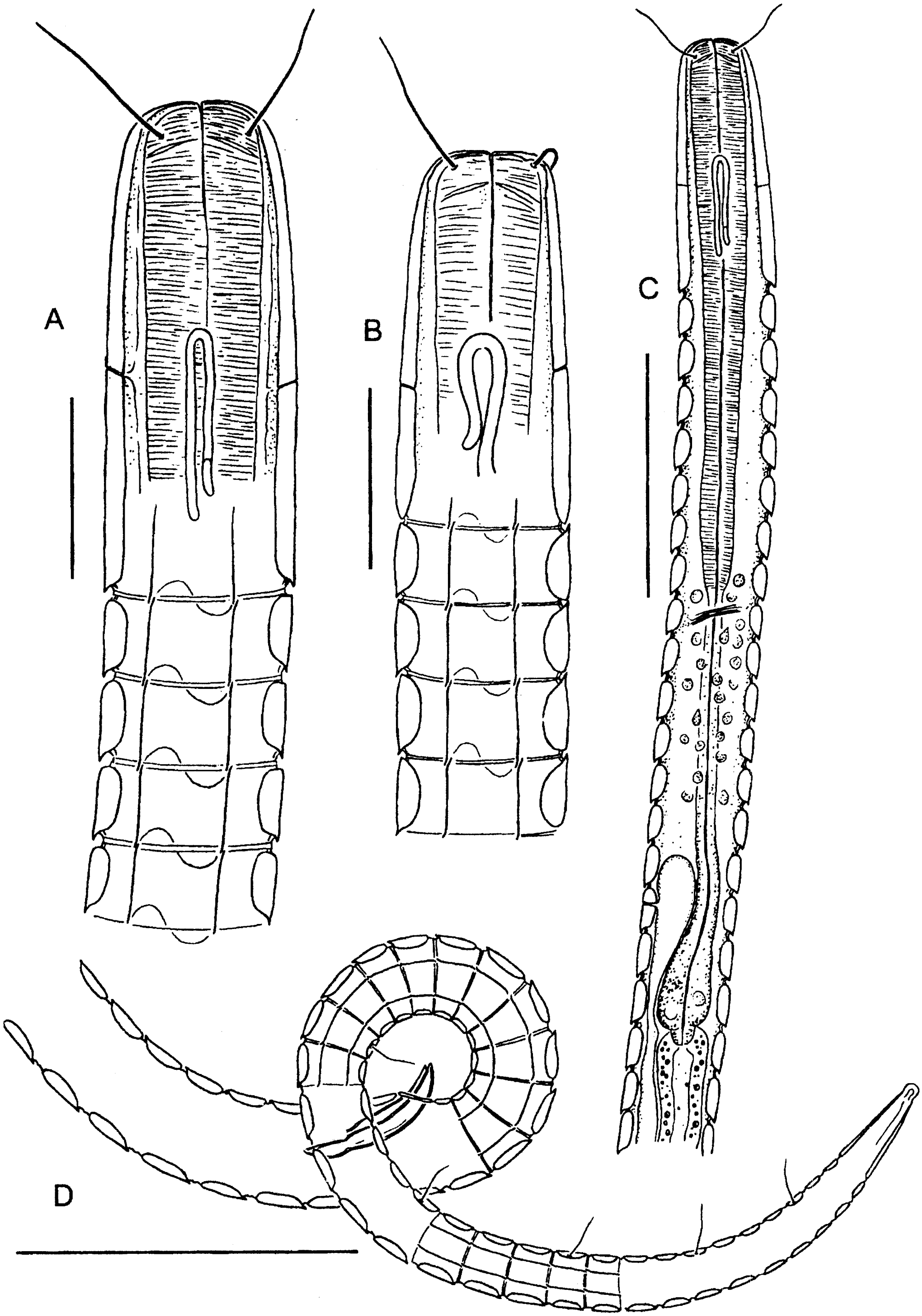

Fig. 19. *Pselionema concinnum* sp. n. (A, C, D, holotype male; B, paratype female). **A, B**, cephalic end; **C**, anterior body; **D**, posterior body. Scale bars: A, B – 10 µm; C – 30 µm; D – 60 µm.

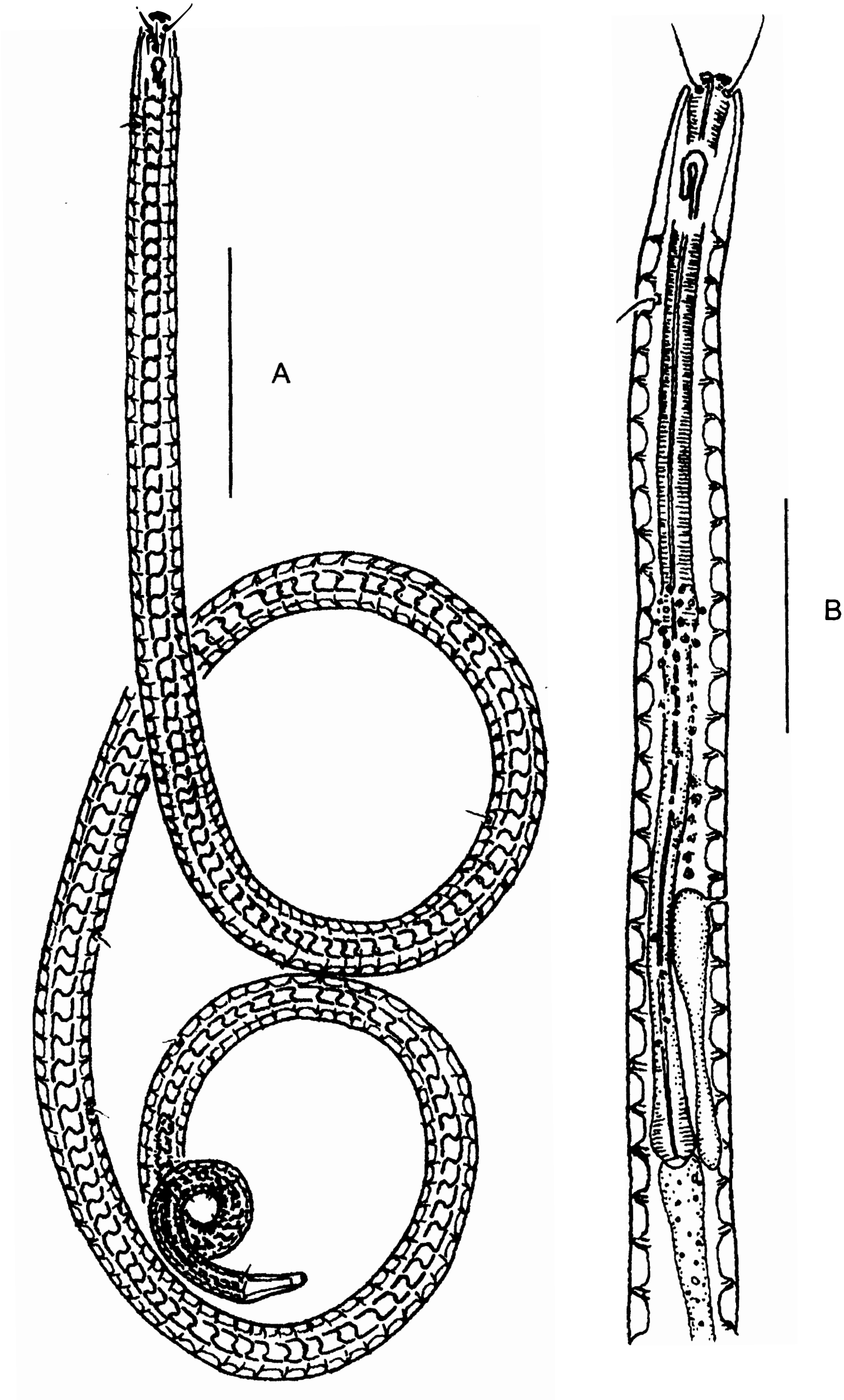

Fig. 20. *Pselionema mirabile* sp. n., holotype male. **A**, habitus; **B**, anterior body. Scale bars: A – 50 µm, B – 100 µm.

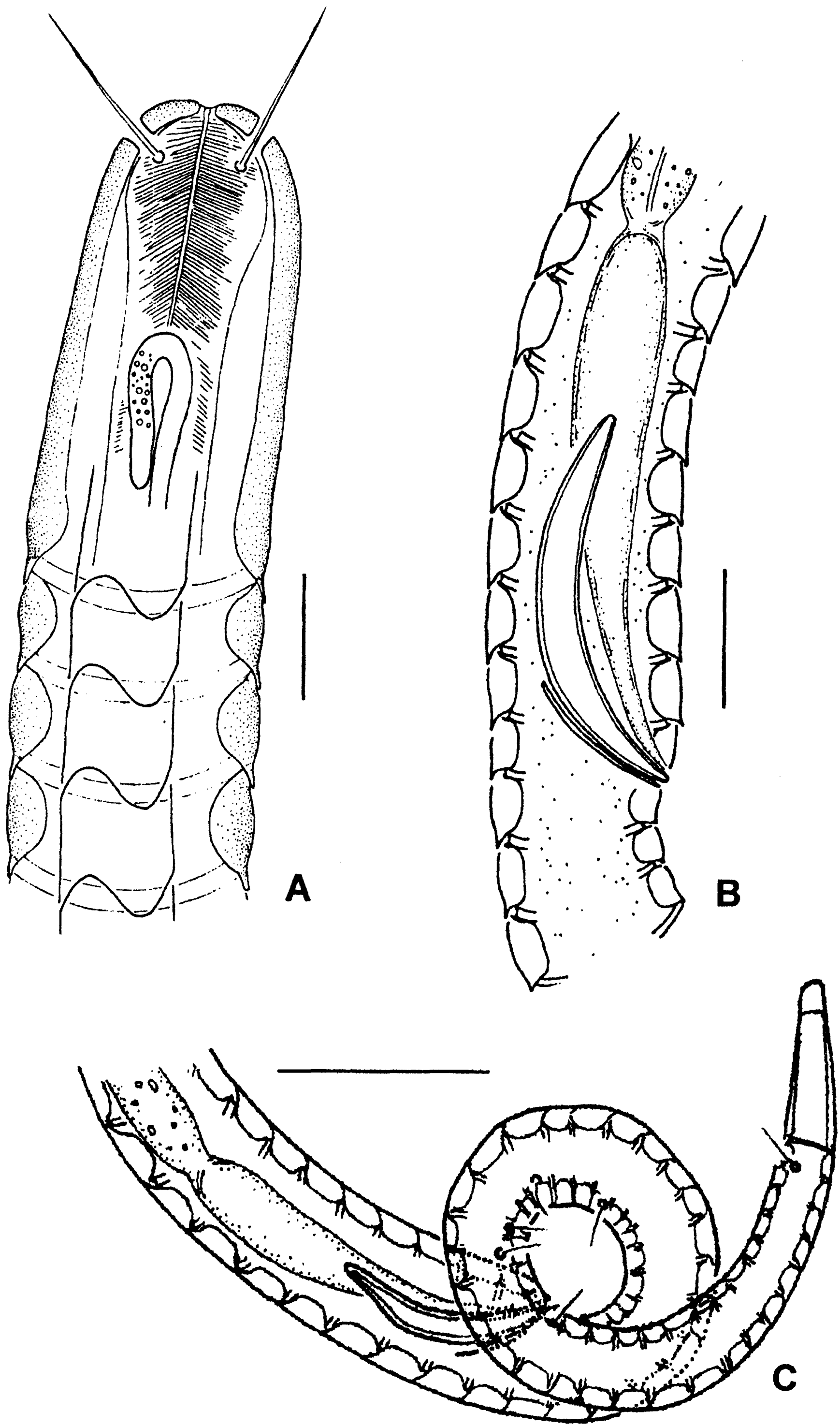

Fig. 21. *Pselionema mirabile* sp. n., holotype male. **A**, cephalic end; **B**, copulatory apparatus; **C**, tail. Scale bars: A, B – 10 μm, C – 20 μm.

Description. Body moderately slender, cylindrical. Male: L = 821 µm; a = 40; b = 3; c = 4.4. Body diameter at the level of: cephalic setae 15 µm; nerve ring 17 µm; cardia 18 µm; midbody 20.5 µm; anus 17 µm.

Body cuticle consists of 206 free annules between cephalic capsule and terminal cone: 23 annules in pharyngeal region, 149 in intestinal region, and 34 in tail. Annules broad and 1.5-2 µm thick. No intracuticular vacuolisation. Annules vary in width from 1st postcephalic annule (8 µm) gradually to 29th annule (11 µm), then again from narrow 30th annule (6 µm) gradually to 105th annule (9 µm), then the annules narrow to the last annule before the tail cone. Six longitudinal cuticular crests extended along the body from posterior region of cephalic capsule to base of terminal cone. Each crest consists of short ridges on every annule; ridges at both ends slightly overlapped with ridges of adjacent anterior and posterior annules. Zygapophyses well developed, sinusoid, smooth.

Cephalic capsule nearly cylindrical, slightly narrowed anteriorly, 38.5 µm long; cephalic ratio 2. Cuticle thickened at base and gradually thinned to mouth region. No pores on cephalic capsule. Longitudinal crests start at the level of posterior end of amphid loop. Inner and outer labial sensilla not seen. Four cephalic setae situated apically, 14 µm long. No other setae on the body, except those on the tail. Amphid loop-shaped, situated on posterior half of cephalic capsule. Amphid dorsal branch 11 µm and ventral branch 15 µm long; distance from anterior end to amphid 17 µm.

Buccal cavity not developed. Pharynx subdivided into three regions. Anterior muscular region 23 µm long, widened anteriorly. Intermediate region narrowed and obscured by neuron cell bodies. Posterior region as a pear-shaped widening with transverse striation.

Nerve ring evidently at anterior end of intermediate region of pharynx, at the level of 10-12th annules. Renette extending from 18th to 24th body annules, with excretory pore situated at 18th annule (distance from anterior end 192 µm). Testes paired; spicules slightly arched, tapered anteriorly and posteriorly, 42.5 µm (arch) or 33.5 µm (chord) long. Gubernaculum as a thin plate 21.3 µm long.

Tail conical, 11 anal diameters long. Terminal cone 23 µm long. There are 6 lateroventral setae 6.5-7.5 µm long on each tail side.

Comparison. *P. mirabile* sp. n. is characterised by the combination of relatively short and thick body (L = 821 µm, a = 40) and large number of cuticular annules (206) that is unusual for the majority of *Pselionema* species. The new species resembles *P. dissimile* in the number of annules, but other characters of both species are quite different.

P. mirabile sp. n. is also related to *P. detriticola* in the body length, indices "a" and "b", and some other features, but differs in the higher number of body annules (206 *versus* 103), size of cephalic capsule (38.5 µm *versus* 26 µm long), length of cephalic setae (14.5 µm *versus* 6.5 µm), and absence of lateral cephalic pores.

Etymology. *Mirabilis* (Latin): wonderful.

Pselionema simplex De Coninck, 1942
(Figs 22, 23)

Material examined. One adult female and six juveniles of various stages, **Russia**, White Sea, Kandalaksha Trench, 66°25.9′N, 34°33.4′E, depth 270 m, silt, 27.VII. 1998.

Notes and discussion. A description of White Sea specimens was published by Tchesunov (1995). Therefore we only mention here some features of juveniles in comparison with those of adults: (1) cuticle annules of juveniles lack zygapophyses in contrast to those of adults; (2) amphids of juveniles are rather rounded, though loop-shaped, while loop-shaped amphids of adults are elongate; (3) cephalic setae of juveniles are significantly shorter.

Distribution. *P. simplex* was described from the Mediterranean Sea (De Coninck, 1942) and thereafter was found only in the White Sea, first at the depth of 20 m (Tchesunov, 1995), and now at the depth of 270 m. All specimens were extracted from silt sediments.

Genus **Pterygonema** Gerlach, 1954

Type species *Pterygonema alatum* Gerlach, 1954.

Diagnosis. Body cuticle consists of many (250-350) narrow, equal annules. Zygapophyses not developed. Labial region not set off the cephalic capsule. Amphid loop-shaped, elongate. Gubernaculum with dorso-caudal apophysis.

Annotated list of species

1. *P. alatum* Gerlach, 1954: 223, Figs. 6 a-c; Mediterranean.
2. *P. cambriense* Ward, 1973: 204-205, Fig. 1; Ireland Sea.
3. *P. longiseta* (Ward, 1974), **comb. n.** Ward, 1974: 93-94, Fig. 1 (*Pselionema*); Ireland Sea. See *Note* to *Pselionema*.
4. *P. papenkuili* Furstenberg & Vincx, 1993: 150-151, Figs 5 F, G; South Africa.
5. *P. platti* Zhang, 1983: 223-225, Fig. 2; West coast of Scotland.

Acknowledgements

The present publication was supported by the Russian Foundation for Basic Research, project No. 00-04-48002. The second author was also granted by the INTAS programme No. YSF 00-247.

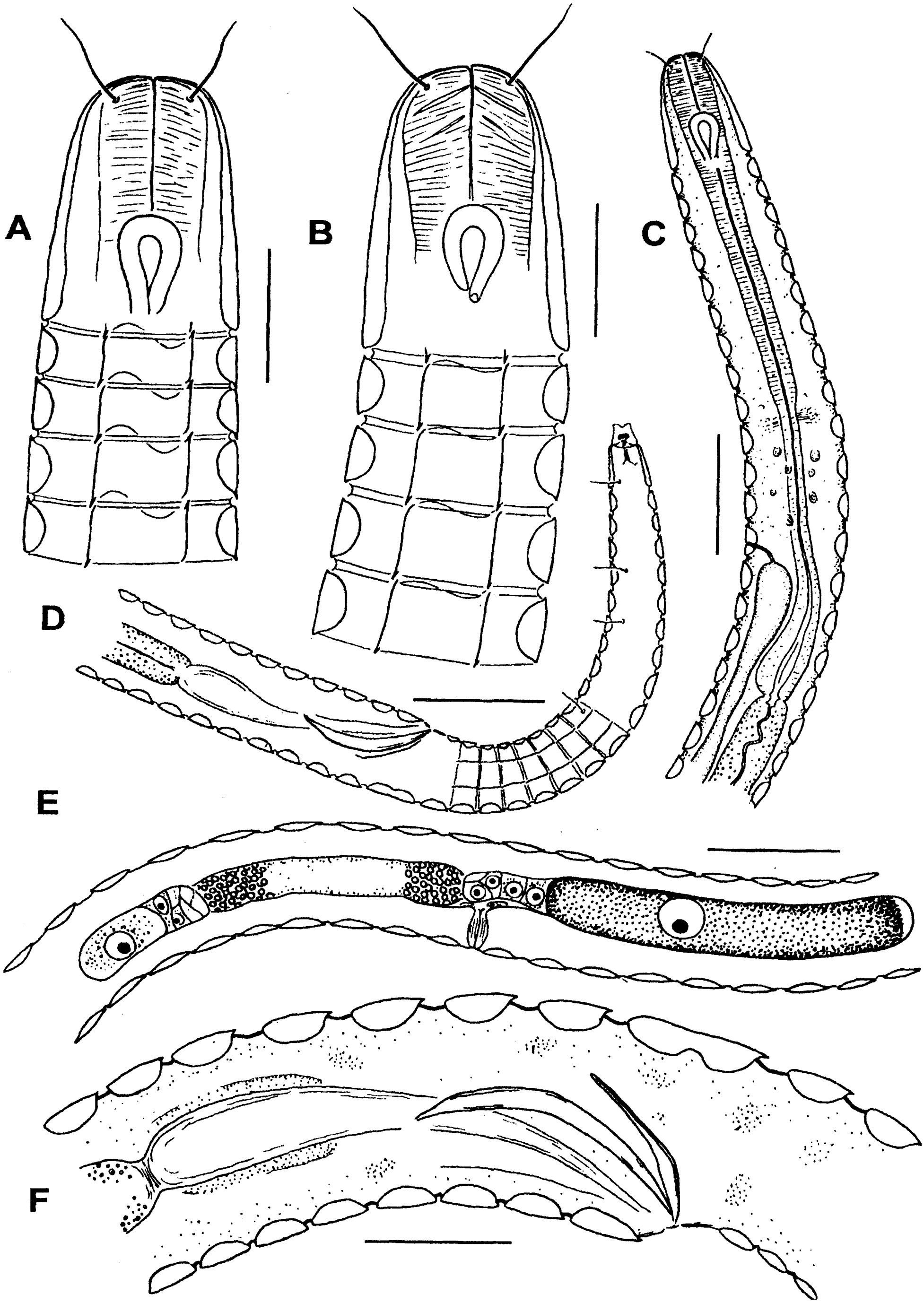

Fig. 22. *Pselionema simplex.* **A**, cephalic end of male; **B**, cephalic end of female; **C**, anterior body of male; **D**, posterior body of male; **E**, female gonads; **F**, hindgut and copulatory apparatus of male. Scale bars: A, B, F – 10 µm, C, D, E – 20 µm. After Tchesunov, 1995.

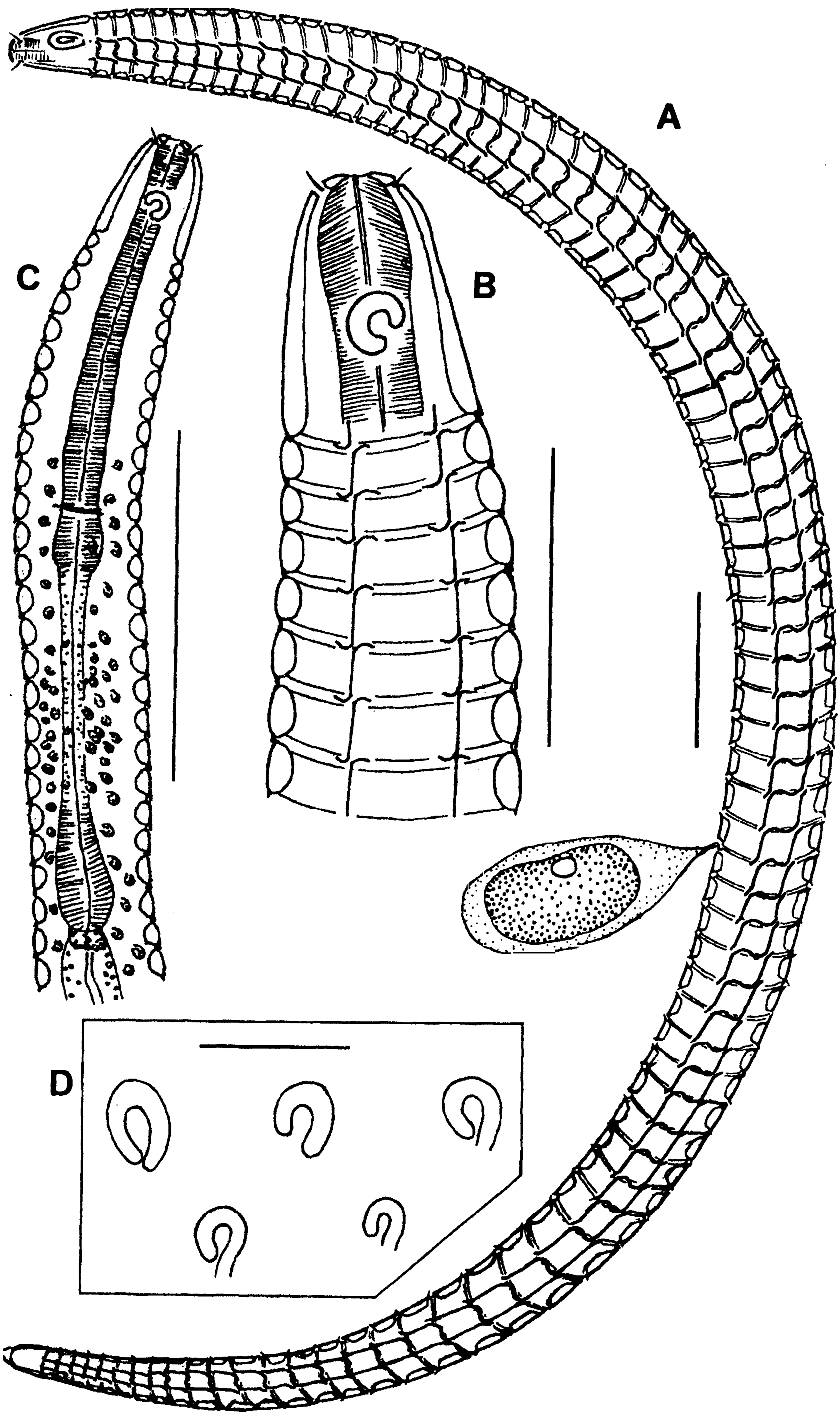

Fig. 23. *Pselionema simplex.* **A**, habitus of an adult female with an egg attached at the vulva; **B**, cephalic end of a juvenile; **C**, anterior body of the same juvenile; **D**, amphids of juvenile stages. Scale bars: A, C – 50 μm, B – 10 μm.

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Received 6 December 2001