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Ultrastructure of the body cuticle of free-living marine nematodes

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Summary. The ultrastructure was studied of the body cuticle of 21 species of free-living marine nematodes belonging to 15 families in the Enoplida, Chromadorida, Desmodorida, Monhysterida and Araeolaimida. Most species had cuticles with osmiophilic epicuticle, striated exocuticle in the cortical position, fibrous mesocuticle and basally positioned endocuticle. The mesocuticle in enoplids, chromadorids, monhysterids and araeolaimids usually is multilayered and frequently has cavities crossed by intra-cuticular radial columns. Strongly sclerotized cuticles of nematode species belonging to the family Chromadoridae are comprised of mesocuticular transversal rings. The cuticle of desmodorids has a more specialized ultrastructure which may be considered as being modified. Punctuations of the cuticle of free-living marine nematodes appear to have evolved independently between orders.
Key words: marine nematodes, cuticle, ultrastructure.

The ultrastructure of the cuticle in parasitic and soil nematodes has been extensively reviewed (Bird, 1971, 1984) but relatively little is known about the ultrastructure of the body cuticle of free-living marine nematodes. However, separate papers published suggest that considerable diversity and complexity occur with cuticle features and that these differences are important for the taxonomy and phylogeny (Inglis, 1964; Watson, 1965; Wright & Hope, 1968; Siddiqui & Viglierchio, 1977; Iken, 1978). Here we present brief descriptions of the body cuticle ultrastructure of 21 nematode species belonging to 15 families of the five main orders of free-living marine nematodes: Enoplida, Chromadorida, Desmodorida, Monhysterida and Araeolaimida. Detailed descriptions of the cuticle structure of several of these species were previously published in several papers (Yushin, 1986, 1988; Malakhov & Yushin, 1987; Yushin et al., 1988; Yushin & Malakhov, 1991, 1992). Here we present new data on the structure of the cuticle of five species and discuss the body cuticle structure of free-living marine nematodes in relation to their taxonomy and phylogeny.

MATERIALS AND METHODS

The species studied, according to the classification of Malakhov (1986), were:

Order Enoplida

1. *Anticoma* aff. *pontica* Filipjev, 1918 (Enoplina, Anticomidae).

2. *Halalaimus leptoderma* Platonova, 1971 (Enoplina, Oxystominidae).

3. *Enoplus demani* Galtsova, 1976 (Enoplina, Enoplidae).

4. *Pseudoncholaimus vesicarius* (Wieser, 1959) Belogurov, 1975 (Oncholaimina, Oncholaimidae).

5. *Bathyeurystomina* sp. (undescribed species) (Oncholaimina, Enchelidiidae).

Order Chromadorida

6. *Paracanthonchus macrodon* Ditlevsen, 1910 (Cyatholaimina, Cyatholaimidae).

7. *Halichoanolaimus sonorus* Belogurov & Fadeeva, 1980 (Cyatholaimina, Selachinematidae).

8. *Euchromadora ezoensis* Kito, 1977 (Chromadorina, Chromadoridae).

9. *Neochromadora poecilosoma* (de Man, 1893) Schuurmans-Stekhoven, 1935 (Chromadorina, Chromadoridae).

Order Desmodorida

10. *Desmodora* sp. (undescribed species) (Desmodorina, Desmodoridae).

11. *Metachromadora itoi* Kito, 1978 (Desmodorina, Desmodoridae).

12. *Monoposthia costata* (Bastian, 1865) (Desmodorina, Monoposthiidae).

Order Monhysterida

13. *Steineria marsiana* Alekseev & Belogurov, 1973 (Monhysterina, Xyalidae).

14. *Sphaerolaimus balticus* Schneider, 1906 (Monhysterina, Sphaerolaimidae).

15. *Siphonolaimus* sp. (undescribed species) (Siphonolaimina, Siphonolaimidae).

16. *Terschellingia glabricutis* Platonova, 1971. (Linhomoeina, Linhomoeidae).

17. *Megadesmolaimus rhodinus* Tchesunov & Yushin, 1991 (Linhomoeina, Linhomoeidae).

18. *Anticyathus plicibucca* Tchesunov & Yushin, 1991 (Linhomoeina, Linhomoeidae).

Order Araeolaimida

19. *Parodontophora marisjaponici* Platonova, 1971 (Axonolaimidae).

20. *Sabatieria* sp. (undescribed species) (Comesomatidae).

21. *Dorylaimopsis peculiaris* Platonova, 1971 (Comesomatidae).

Data on the ultrastructure of the body cuticle of the nematode species enumerated as 1, 5, 8, 9 and 19 are original whereas the data for the other species have been published previously: species 2-4 (Malakhov & Yushin, 1987); species 6 and 20 (Yushin, 1986); species 7 (Yushin & Malakhov, 1992); species 10-12 (Yushin & Malakhov, 1991); species 13-18 (Yushin et al., 1988) and species 21 (Yushin, 1988).

Species 3, 6 and 14 were recovered from silty sand collected in the intertidal zone in Kandalaksha bay, White Sea, in the vicinity of the White Sea Biological Station of Moscow State University. Other species were collected in the Peter the Great Bay, Sea of Japan, in the vicinity of the Marine Biological Station «Vostok» of the Institute of Marine Biology (Vladivostok). Species 2, 5, 12, 16-21 were recovered from silty sediments collected at 10 m depth. Species 7, 9, 15 were collected in the druses of the bivalve *Crenomytilus grayanus*.

Species 10 and 13 were collected in the estuary of a small river, 0.5 m deep. *Pseudoncholaimus vesicarius* (4) was collected from sand at 1 m depth and *Euchromadora ezoensis* (8) was obtained from the tallome of the alga *Cystoseira* sp.

Specimens were fixed for transmission electron microscopy with 2.5% glutaraldehyde solution in 0.05 M sodium cacodylate buffer (pH=7.2) and then post-fixed with 2% osmium tetroxide solution in the same buffer. After post-fixation specimens were dehydrated in an ethanol and acetone series and embedded in Araldite. Ultrathin sections, cut with a Reichert Ultracut E ultratome, were stained with uranyl acetate and lead citrate. Stained sections were observed with a JEOL-JEM 100B electron microscope.

The structure of the cuticle depends on the area of the body region from which it is obtained therefore only short pieces of the nematode were used from the level of the hind part of the oesophagus. The micrographs and diagrams demonstrate the median cuticles and for some specimens the structure of the lateral cuticle also was studied. The nomenclature used to describe the cuticle structure is that of Maggenti (1979) who recognized four principal cuticular layers ("strata"): epicuticle, exocuticle, mesocuticle and endocuticle. Each stratum may be composed of several sublayers.

RESULTS

The main morphometrics obtained from several components of the cuticles studied are presented in Table 1.

Order Enoplida

A. aff. *pontica* (Figs. 1 & 22.A). The outer cuticle layer is a thin epicuticle composed of two electron-

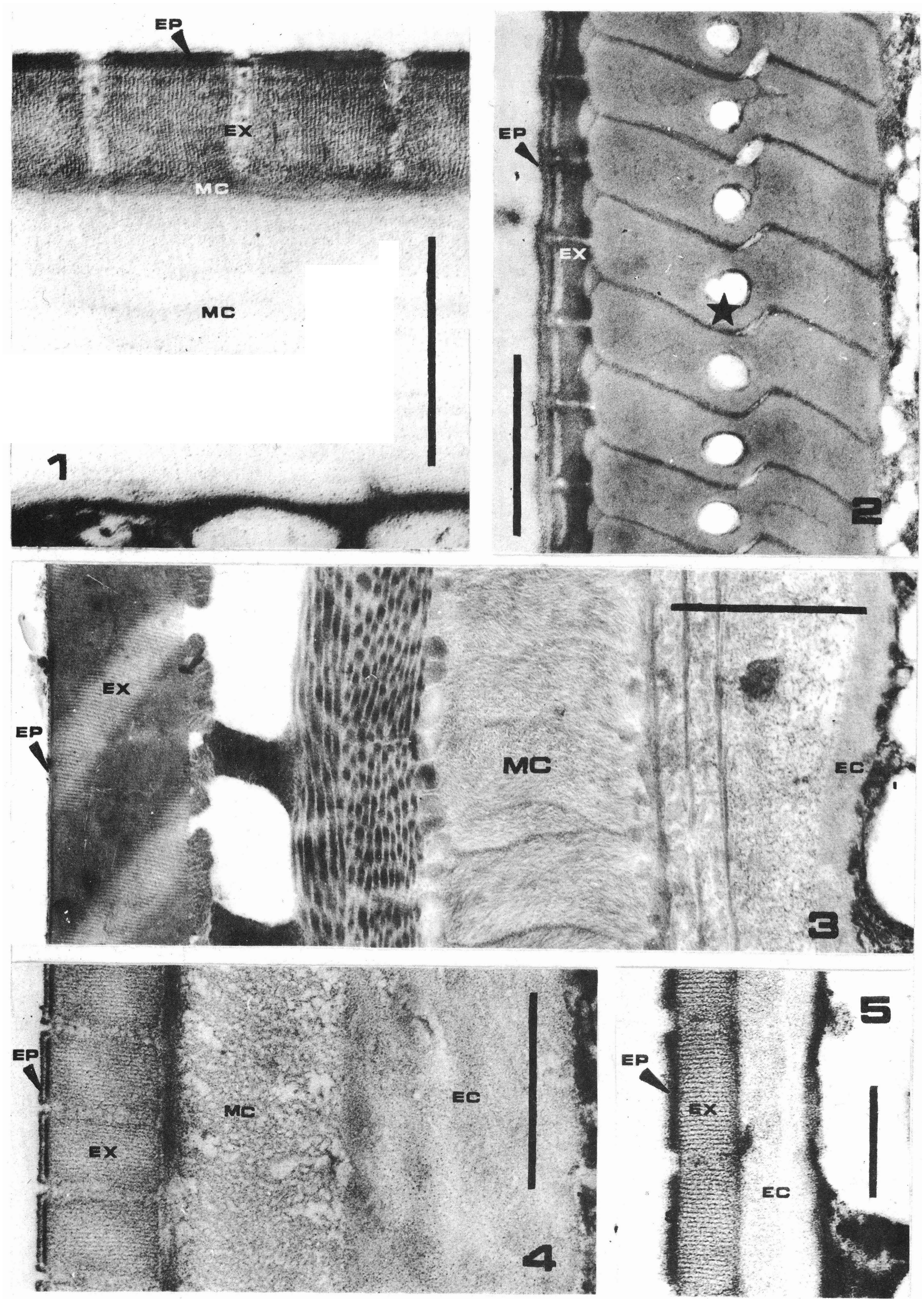
Table 1. Mean morphometrics of several components of the body cuticles in free-living marine nematodes.

Species	Width of annulation (μm)	Thickness (μm)		
		total	exocuticle	endocuticle
Anticoma aff. pontica	0.33	1.0	0.24	0.7
Halalaimus leptoderma	0.22	1.1	—	—
Enoplus demani	0.25	3.6	0.77	1.0-1.4
Pseudoncholaimus vesicarius	0.2	1.4	0.3	
Bathyeurystomina sp.	0.33	0.3-0.4	0.13	0.2
Paracanthonchus macrodon	2.0	2.3	0.4	0.3-0.4
Halichoanolaimus sonorus	1.0	2.4	0.5	0.4
Euchromadora ezoensis	1.8	2.1	0.07	0.05
Neochromadora poecilosoma	2.0	1.6	—	0.09
Desmodora sp.	1.0	1.4	0.07	0.4
Metachromadora itoi	0.55	1.6	0.08	—
Monoposthia costata	3.0	2.2	—	0.2
Steineria marsiana	0.7	1.2	0.15	0.6
Sphaerolaimus balticus	0.9	3.5	0.35	0.3
Siphonolaimus sp.	1.1	0.5	0.16	0.2
Terschellingia glabricutis	0.75	0.7	0.15	0.3
Megadesmolaimus rhodinus	1.2	0.4	0.12	0.1-0.2
Anticyathus plicibucca	2.0	0.3	0.11	0.08
Parodontophora marisjaponici	2.0	1.0	0.37	0.3-0.4
Sabatieria sp.	0.85	0.8	0.22	0.2
Dorylaimopsis peculiaris	0.6	0.9	0.3	0.08

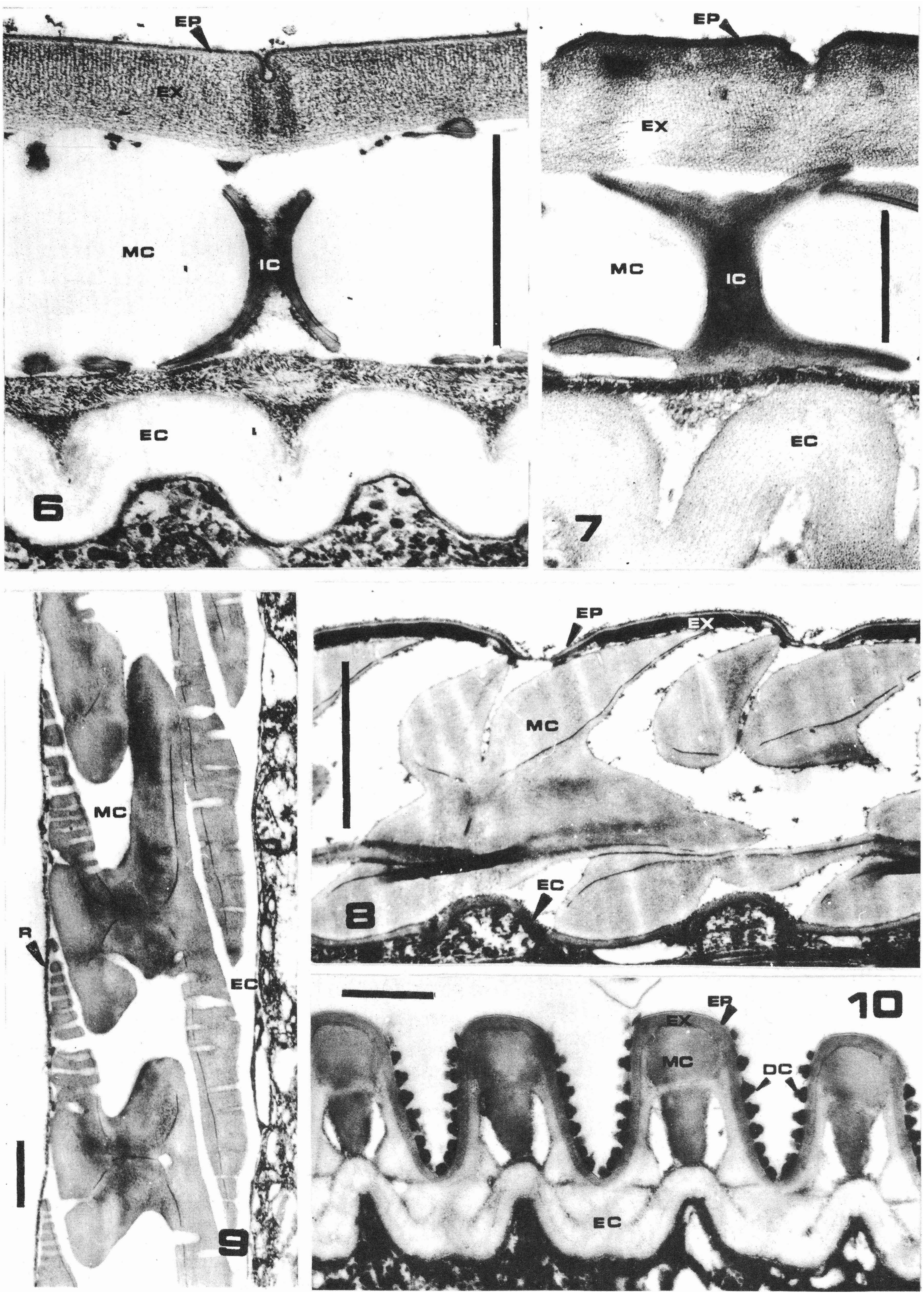
dense layers separated by an electron-transparent zone. The exocuticle is comprised of a striated layer. This layer has been described for several nematode species and typically has a crystalloid ultrastructure with fine osmiophilic radial rods inter-spaced by electron-light material (Bird, 1971; Popham & Webster, 1978). Regular transversal furrows divide the epicuticle and exocuticle into annular segments. Under the exocuticle a thin, fibrous layer (40 nm), stretched longitudinally, may be referred to as the mesocuticle. A thick, basal, electron-light, layer comprising 3/4 of the total thickness of the cuticle may be considered as the endocuticle.

H. leptoderma (Figs. 2 & 22.B). The epicuticle consists of three sublayers. The exocuticle lacks striations and includes two homogeneous sublayers: a translucent layer 25-30 nm thick and a darker layer 80-100 nm thick. Transversal furrows separate the epicuticle and exocuticle into annular segments. It is not possible to subdivide the thick sclerotized zone located under the exocuticle into mesocuticle and endocuticle, therefore this layer may be considered as the meso-endocuticle. In longitudinal sections it appears to be composed of annular segments with zigzag orientation. Each zigzag contains a round foramen corresponding to the annular canal inside the segment of the meso-endocuticle.

E. demani (Figs. 3 & 22.C). The external tri-laminated stratum and underlying layer of thin transversal fibers may be referred to as being the epicuticle. The exocuticle is distinctly striated. Transverse furrows separate the epicuticle and exocuticle into annular segments. The mesocuticle is composed of several sublayers with the outermost



Figs. 1-5. Ultrastructure of the free-living marine nematodes, longitudinal sections. 1: *Anticoma* aff. *pontica*; 2: *Halalaimus leptoderma*, meso-endocuticle indicated by an asterisk; 3: *Enoplus demani*; 4: *Pseudoncholaimus vesicarius*; 5: *Bathyeurystomina* sp. EC - endocuticle, EP - epicuticle, EX - exocuticle, MC - mesocuticle. Scales: 1, 2, 4 – 0.5 μm; 3 - 1.0 μm; 5 - 0.25 μm.



Figs. 6-10. Ultrastructure of the free-living marine nematodes, longitudinal sections. 6: *Paracanthonchus macrodon*; 7: *Halichoanolaimus sonora*; 8: *Euchromadora ezoensis*; 9: *Neochromadora poecilosoma*; 10: *Desmodora* sp. DC - electron-dense caps on the cuticle surface, IC - intra-cuticular columns, R - thin layer of epicuticle and reduced exocuticle; for other abbreviations see legend for Figs. 1-5. Scales - 0. 5 μm.

consisting of thick, longitudinal fibers. The underlying intra-cuticular cavity is crossed by osmiophilic radial columns which meet the outermost of the two subsequent layers of oblique fibers. Several underlying layers of longitudinal and transversal fibers constitute the remaining mesocuticle. Thus, there are total of 12 mesocuticle layers. The electron-light endocuticle is of uniform thickness and slightly undulating.

P. vesicarius (Figs. 4 & 22.D). The epicuticle is distinctly tri-laminated and the exocuticle is striated. Both layers are divided by transverse furrows into annular segments. Thin longitudinal fibers and a loose fibrous layer may be referred to as being the mesocuticle. The endocuticle is a relatively thick, electron-light, homogeneous layer. There is no distinct boundary between the mesocuticle and endocuticle.

Bathyeurystomina sp. (Figs. 5 & 22.E). The cuticle is extremely thin and simple. The striated exocuticle is covered by an osmiophilic epicuticle. The epicuticle and exocuticle are each divided into annular segments. A thin, electron-dense, layer underlying the exocuticle may be considered as being the mesocuticle. A relatively thick homogeneous, electron-light, basal layer may be referred to as being the endocuticle.

Order Chromadorida

Suborder Cyatholaimina

P. macrodon (Figs. 6 & 22.F). A striated exocuticle is located under the tri-laminated epicuticle. Transversal grooves covered with epicuticle form the superficial annulation of the exocuticle. Most of the mesocuticle is occupied by an electron-transparent cavity crossed by radial osmiophilic columns branched at each end. The transversal rows of the columns are distinctly visible with the light microscope as being the transversal annulate punctations. The columns meet the loose fibrous layer which may be referred also to the mesocuticle. From longitudinal sections the electron-light and homogeneous endocuticle looks regularly sinuous.

H. sonorus (Fig. 7). Ultrastructure of the cuticle in this species is almost identical to that of the previous species, however, the exocuticle is subdivided into an external homogeneous layer and an internal striated layer.

Suborder Chromadorina

The body cuticle in the family Chromadoridae is described as being strongly sclerotized and distinctly annulated with numerous sculpture types as revealed by light microscopy (Inglis, 1964, 1969). Only the principal layers constituting chromadorids cuticles are described here.

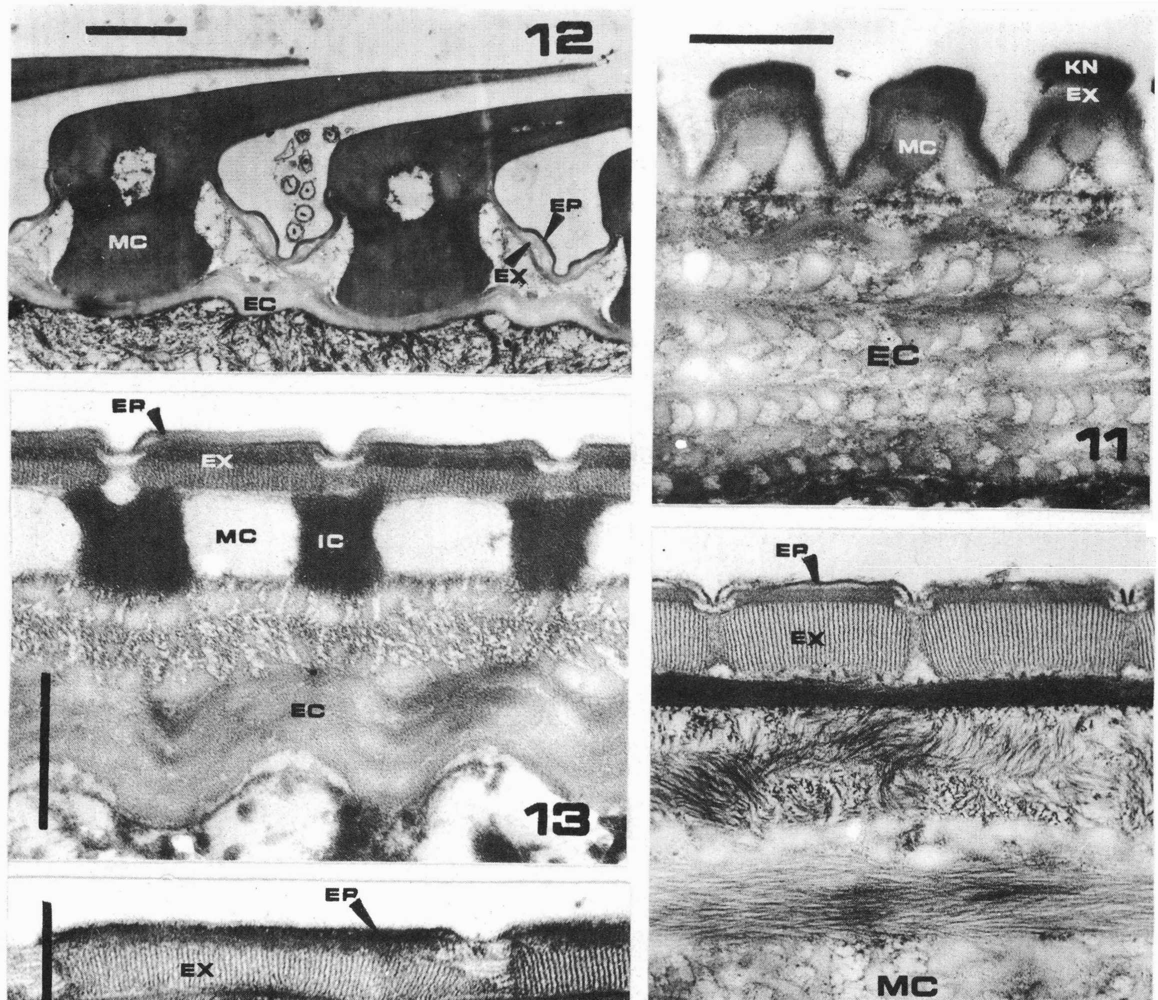
Eu. ezoensis (Figs. 8 & 22.G). Species of the genus *Euchromadora* are characterized by structural differences between the median and lateral cuticles. The ultrastructure of the median cuticle was studied in the closely related species *Eu. vulgaris* (Watson, 1965) and here we report on the lateral cuticle. The outermost layer (epicuticle) is distinctly tri-laminated. The stratum corresponding to the exocuticle is composed of a finely granulated substance. Most of the cuticle is formed by strongly sclerotized transversal rings situated in the intra-cuticular cavity. These rings may be referred to as being the mesocuticle. Each ring is composed of two external and a single internal ring joined by radially oriented bridges. Long processes originating from the bridges go forward and penetrate into the space between the bridges of the next ring and this is repeated in turn. Narrow radial canals run through the sclerotized substance of the intra-cuticular rings. The endocuticle is a thin but distinct electron-light layer of uniform thickness which underlies the mesocuticular rings and delimits the mesocuticular cavity and hypodermis.

N. poecilosoma (Figs. 9 & 23.A). The ultrastructure of the cuticle of this species is similar to that of the former species but differs in the strong reduction of epicuticle and exocuticle. Both layers in *N. poecilosoma* are present only as thin electron dense layers that cover the sclerotized mesocuticular rings and separate the intra-cuticular cavity from the surroundings.

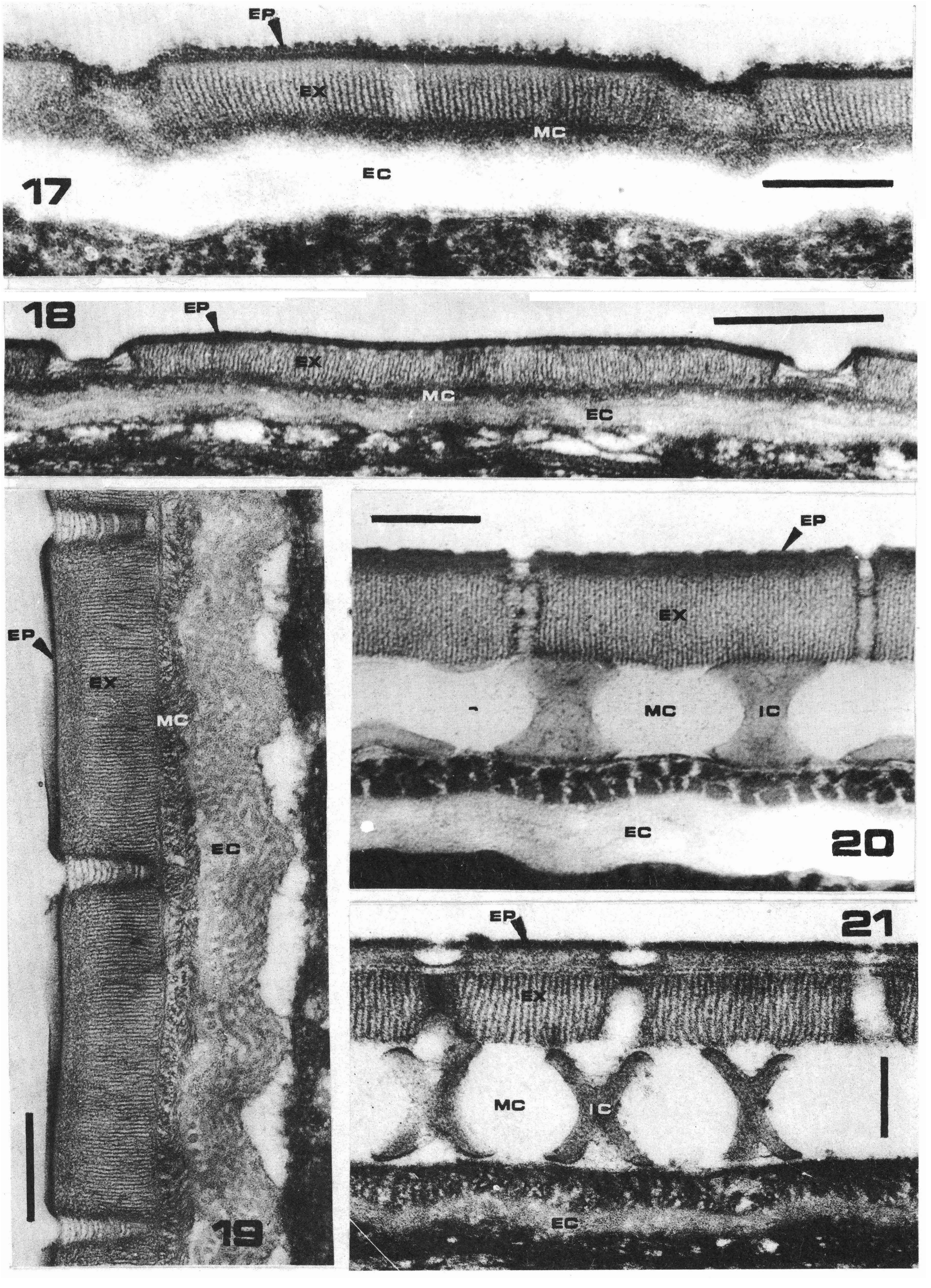
Order Desmodorida

Desmodorids cuticle ultrastructure appears peculiar, therefore application of Maggenti's (1979) nomenclature should be considered tentative.

Desmodora sp. (Figs. 10 & 23.B). Rows of small, electron-dense, caps cover the surface of a thin osmiophilic epicuticle. A homogeneous layer of



Figs. 11-16. Ultrastructure of the free-living marine nematodes, longitudinal sections. 11: *Metachromadora itoi*; 12: *Monoposthia costata*; 13: *Steineria marsiana*; 14: *Sphaerolaimus balticus*; 15: *Siphonolaimus* sp.; 16. *Terschellingia glabricutis*. IC - intra-cuticular columns, KN - disk-like knobs on the surface of the epicuticle; for other abbrevations see legend for Figs. 1-5. Scales: 11, 13, 15, 16 - 0.5 μm; 12, 14 - 1.0 μm.



Figs. 17-21. Ultrastructure of the free-living marine nematodes, longitudinal sections. 17: *Megadesmolaimus rhodinus*; 18: *Anticyathus plicibucca*; 19: *Parodontophora marisjaponici*; 20: *Sabatieria* sp.; 21: *Dorylaimopsis peculiaris*. For abbreviations see legends for Figs 1-10. Scales: 17, 20, 21 - 0.25 μm; 18, 19 - 0.5 μm.

uniform thickness located below the epicuticle may be referred to as being the exocuticle. Sclerotized mesocuticular rings, having «skittle-like» profiles, form the internal skeleton of the cuticle annulations. Two narrow canals of intra-cuticular cavity run along the basal part of each sclerotized ring. The electron-light bilayered endocuticle is sinuous corresponding with the annulations.

M. itoi (Figs. 11 & 23.C). The cuticle bears osmiophilic disk-like knobs on the tops of the cuticle rings. These knobs are readily visible by light microscopy as being the transversal punctations. The epicuticle and exocuticle are similar to those of the former species. Sclerotized rings of the mesocuticle support the annulations of the epicuticle and exocuticle. The intra-cuticular cavity is filled with loose material and contains thick, longitudinal, sinuous, fibers and also may be referred to as being the mesocuticle. The endocuticle is very thick and consists of several layers of longitudinal and transversal fibers.

M. costata (Figs. 12 & 23.D). The cuticle is composed of scales oriented anteriorly. The trunk of the scale consists of mesocuticular sclerotization containing an internal canal. Neighbouring scales are joined by a flexible ligament composed of two electron-light fibrous layers divided by an electron-transparent cavity. The external fibrous layer is covered by the osmiophilic epicuticle and may be referred to as being the exocuticle. The internal layer delimits the base of the scale and the hypoderm and may be referred to as the endocuticle.

Order Monhysterida

S. marsiana (Figs. 13 & 23.E). The exocuticle is subdivided into an external homogeneous layer, covered by the epicuticle, and an internal striated layer. There are longitudinal ribs on the surface of the cuticle. The epicuticle and exocuticle are each subdivided into annular segments by transversal furrows. The mesocuticle consists of three layers with the external layer composed of electron-dense longitudinal fibers and the middle layer having the intra-cuticular cavity crossed by radial osmiophilic columns, which appear like short cylinders. These columns are arranged as transversal rows which are visible by light microscope as annular punctations. Each row of columns corresponds to the overlying transversal furrow in the exocuticle. The columns meet the loosely packed fibrous internal layer of the mesocuticle. The electron-light endocuticle appears to be subdivided into several indistinct sublayers.

S. balticus (Figs. 14 & 24.A). The epicuticle is distinctly tri-laminated. The exocuticle is subdivided into an external homogeneous and an internal striated layer. Transversal grooves form the annulations of the epicuticle and exocuticle. The very thick mesocuticle is composed of six layers. Longitudinal fibers are located immediately below the striated layer. The adjacent internal layer consists of thin oblique fibers followed by two spongy layers delimited by the distinct layer of thin longitudinal fibers. The deepest layer of mesocuticle consists of the loose osmiophilic net. The endocuticle is an electron-light layer of uniform thickness.

Siphonolaimus sp. (Figs. 15 & 24.B). Longitudinal ribs are present on the surface of the cuticle. The exocuticle is subdivided into an external homogeneous and an internal striated layer covered by the osmiophilic epicuticle. The epicuticle and exocuticle are each divided into annular segments. The mesocuticle is composed of two layers with the external layer having electron-dense longitudinal fibers and the internal layer is composed of thin oblique fibers. The electron-light endocuticle appears as a sinusoidal band, as observed from longitudinal sections. The periodicity of this sinusoid coincides with that of the annulations of the epicuticle and exocuticle. The distinct sinuosity of the endocuticle is readily discerned in whole-mount specimens as fine annulations of the body cuticle.

T. glabricutis (Figs. 16 & 24.C). Loose electron-dense material covers the surface of the osmiophilic epicuticle. The exocuticle is subdivided into very thin external homogeneous, and an internal striated, layers. The epicuticle and exocuticle are each annulated by transversal furrows. The mesocuticle and endocuticle are similar to those of the former species, but, in *T. glabricutis* the endocuticle is

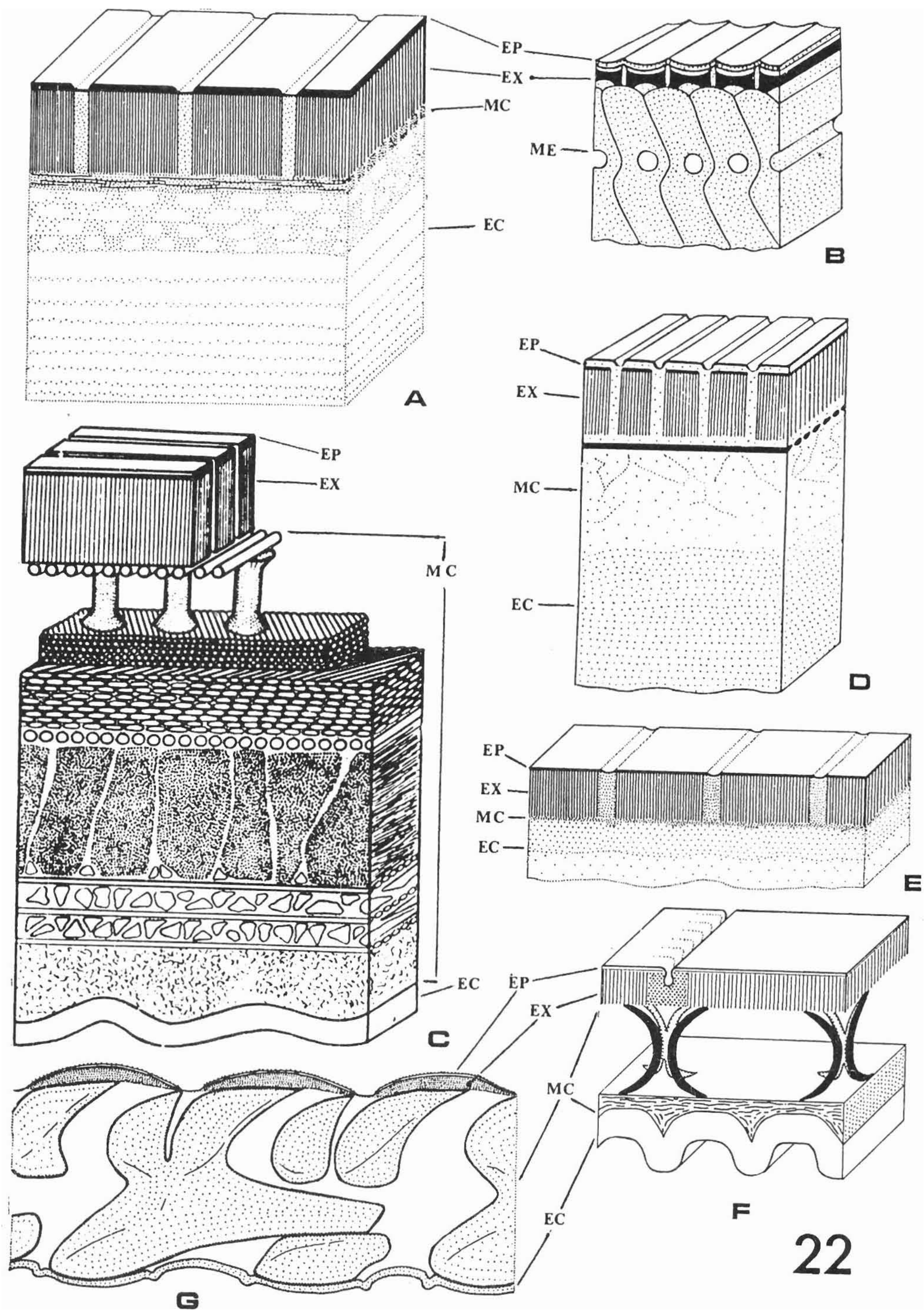


Fig. 22. Diagrammatic representations of the ultrastructure of the cuticle of the free-living marine nematodes. A: *A.* aff. *pontica*; B: *H. leptoderma*; C: *E. demani*; D: *P. vesicarius*; E: *Bathyeurystomina* sp. ; F: *P. macrodon*: G: *Eu. ezoensis*. ME - meso-endocuticle; for other abbreviations see legend for Figs. 1-5.

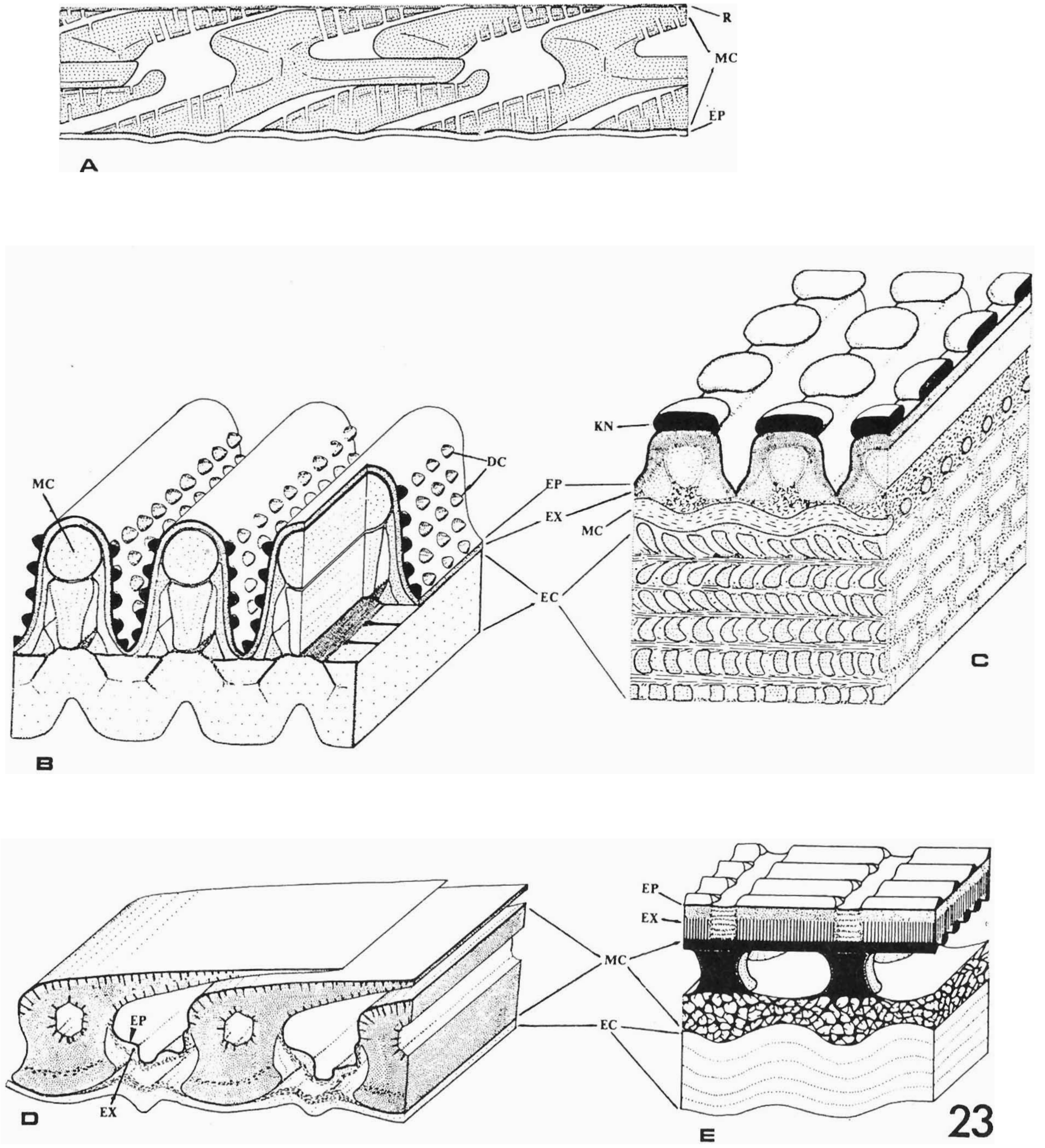


Fig. 23. Diagrammatic representations of the ultrastructure of the cuticle of the free-living marine nematodes. A: *N. poecilosoma*; B: *Desmodora* sp.; C: *M. itoi*; D: *M. costata*; E: *S. marsiana*. For abbreviations see legends for Figs 1-10.

comprised of several layers of closely packed fibers. The endocuticle also is visible in whole-mount specimens as fine annulations of the body cuticle.

M. rhodinus (Figs. 17 & 24.D). The cuticle is very thin and simple. The exocuticle is subdivided into an external homogeneous and an internal striated layer and is covered by the osmiophilic epicuticle. Shallow grooves form annulations on the epicuticle and exocuticle. Striations of the exocuticle disappear under the grooves. The electron-light endocuticle stretches below the thin, fibrous, mesocuticle.

A. plicibucca (Fig. 18). The cuticle is extremely thin and resembles the very simple cuticle of the former species. However, the periodicity of the annulation is greater in this species.

Order Araeolaimida

P. marisjaponici (Figs. 19 & 24.E). There are longitudinal ribs on the surface of the cuticle. The exocuticle is subdivided into an external homogeneous and an internal striated layer and is covered by the osmiophilic epicuticle. The epicuticle and endocuticle are each divided, by deep transversal grooves, into annular segments. The mesocuticle is composed of an external layer of thin longitudinal fibers and two underlying layers of thin oblique fibers. The sinuous endocuticle is comprised of several closely packed layers of transversal and longitudinal fibers.

Sabatieria sp. (Figs. 20 & 24.F). The exocuticle is subdivided into an external homogeneous and an internal striated layer and is covered by the osmiophilic epicuticle. Transversal rows of radial canals divide the exocuticle into annular segments. Shallow furrows on the cuticle surface divide the epicuticle with five to six annuli on the epicuticle corresponding to one annule of the exocuticle. The mesocuticle is composed of three layers with the external layer having the intra-cuticular cavity crossed by electron-light, «spool-like», columns arranged in transversal rows which, under light microscopy appear as annular punctuations. The columns meet the two layers of relatively thick oblique fibers. The electron-light endocuticle is slightly sinuous in longitudinal sections.

D. peculiaris (Fig. 21). The cuticle is similar to that of the former species. The epicuticle and exocuticle are each subdivided by the transversal rows of radial canals into annular segments. The mesocuticle consists of an intra-cuticular cavity crossed by electron-light columns which form six branches at their ends and meet the fibrous layer. The thin endocuticle is electron-light and homogeneous.

DISCUSSION

The results presented here provide evidence of the diversity in the ultrastructure of cuticles in free-living marine nematodes. The four strata model proposed by Maggenti (1979) is supported by our results. The strata were obvious in the simple cuticle of some enoplids, e.g. *Anticoma pontica, Pseudoncholaimus vesicarius, Bathyeurystomina* sp. The cuticles of these nematodes consist of osmiophilic epicuticle, striated exocuticle, fibrous mesocuticle and homogeneous endocuticle. This type of cuticle appears to be the most simple, thus may be considered the most primitive form.

The cuticle of adult *Enoplus demani* is characterized by a complicated mesocuticle, unlike the cuticle of the first stage larva which has osmiophilic epicuticle, striated exocuticle, only two fiber layers of mesocuticle and a thick electron-light endocuticle (Yushin & Malakhov, 1989). This larval cuticle is more similar to the simple cuticles of some enoplids, e.g. *A. pontica, P. vesicarius* or *Bathyeurystomina* sp. It appears probable that the post-embryonic development of cuticle layering in *E. demani* provides an example of the evolution of cuticle development in enoplids. The thick, complicated, cuticle of *E. demani* resembles the cuticle of the large enoplid nematode *Deontostoma californicum* which was studied by Siddiqui & Viglierchio (1977). The cuticle of *D. californicum* possesses a very complicated mesocuticle with two thick layers of oblique fibers. *D. californicum* does not have an intra-cuticular cavity, but does have a layer of radially arranged osmiophilic rods stretched under the striated exocuticle. These rods are considered to be homologous to the radially arranged osmiophilic columns which cross the mesocuticular cavity in *E. demani*.

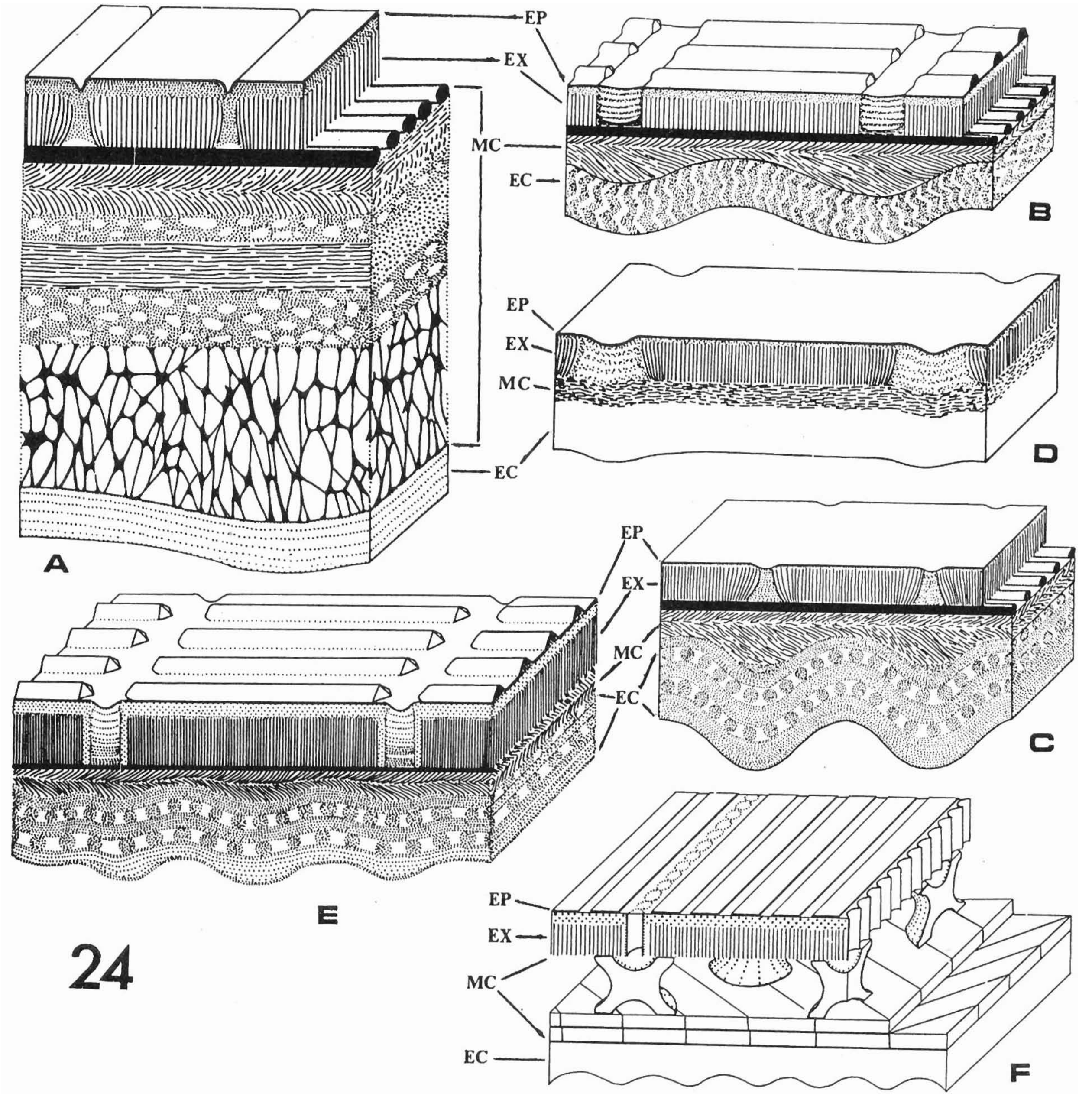


Fig. 24. Diagrammatic representations of the ultrastructure of the cuticle of the free-living marine nematodes. A: *Sph. balticus*; B: *Siphonolaimus* sp.; C: *T. glabricutis*; D: *M. rhodinus*; E: *P. marisjaponici*; F: *Sabatieria* sp. For abbreviations see legend for Figs 1-5.

It is difficult to interpret the cuticle of enoplid *Halalaimus leptoderma* from the position of Maggenti's (1979) model. The mesocuticle and endocuticle are impossible to separate in the cuticular arrangement in this nematode. Perhaps, *H. leptoderma* is an example of a particular line of cuticle evolution which branched at an early stage in phylogenetic development, when the primitive cuticle did not have separate layers of mesocuticle and endocuticle. In the embryonic development of the cuticle of *E. demani* there is a stage, where the cuticle consists of osmiophilic epicuticle, striated exocuticle and undifferentiated meso-endocuticle (Yushin & Malakhov, 1989).

The thin cuticles of linhomoeids [*Terschellingia glabricutis, Megadesmolaimus rhodinus, Anticyathus plicibucca*, see also *Desmolaimus zeelandicus* in Tchesunov, (1991)], siphonolaimids [*Siphonolaimus* sp., see also *Siphonolaimus tubicen* and *Astomonema jenneri* in Ott et al., (1982)], monhysterids (Tchesunov, 1990a) and some xyalids (Tchesunov, 1990a,b; Nicholas, 1984) seem to be similar to that of some enoplids, e.g. *A. pontica* and *Bathyeurystomina* sp. These cuticles have the simple four layer composition including the almost undifferentiated fibrous mesocuticle. The more complicated cuticle of the xyalid nematode *Steineria marsiana* has a distinct intra-cuticular cavity crossed by osmiophilic columns. *Shaerolaimus balticus* (Sphaerolaimidae) appears to be an example of a monhysterid nematode with a very complicated body cuticle, resembling the multilayered cuticle of *Enoplus demani*. Therefore, some parallelism in the cuticle arrangement is apparent between the two nematode orders, Enoplida and Monhysterida.

The simple cuticle of the araeolaimid nematode *Parodontophora marisjaponici* is similar to the cuticle of some monhysterids, especially linhomoeids and siphonolaimids. It would appear that araeolaimids may be closely related to monhysterids, as suggested by Lorenzen (1981).

The cuticle of representatives of the family Cyatholaimidae are characterized by a voluminous mesocuticular cavity crossed by radial columns [*Paracanthonchus macrodon*, see also *Acanthonchus duplicatus* in Wright & Hope, (1968)]. The cuticle of species from the related family Selachinematidae (*Halichoanolaimus sonorus*) appear to be identical with that of cyatholaimids. Radial columns present in the cuticles of these nematodes appear as refringent sclerotizations (called 'punctations') when studied by light microscopy. Similar punctated cuticles are present in nematodes in the family Comesomatidae and they also contain an intra-cuticular cavity with radial columns (Iken, 1978). However, some authors suggest that comesomatids are more closely related to araeolaimids than to chromadorids (Lorenzen, 1981; Malakhov, 1986). Moreover, the recently described new species *Nicascolaimus punctatus*, in the order Araeolaimida, is characterized by having distinct intra-cuticular punctations which broadens the diagnosis of the order (Riemann, 1986). Intra-cuticular cavities with radial columns have been reported for several very divergent taxons of nematodes (Wright & Hope, 1968; Raski & Jones, 1973; Lee, 1977; Iken, 1978; Grotaert & Jaques, 1979; Edgar et al., 1982). It appears probable therefore that cuticular punctations are the result of parallel evolution and also punctations observed by light microscopy may represent different structures.

Nematodes belonging to the family Chromadoridae are characterized by having heavily sclerotized cuticles. This sclerotization is formed by the strong and complicated mesocuticular transversal rings which are dominant as the main cuticular structure (Watson, 1965; Lippens, 1974). However, different members of the family display a gradual reduction in the development exocuticle. The cuticle of *Chromadorina germanica* contains a distinct striated exocuticle (Lippens, 1974), the exocuticles of *Euchromadora ezoensis* and *Eu. vulgaris* (Watson, 1965) lack striations and are significantly reduced and the cuticle of *Neochromadora poecilosoma* is characterized by the absence of a distinct exocuticle with only a thin osmophilic layer covering the strong mesocuticular rings.

It is evident therefore that some taxons of free-living marine nematodes have highly developed cuticle types. However, interpretation of the development of the cuticle layering is not yet possible for the enoplid nematode *Halalaimus leptoderma*, desmodorids (Nebelsick et al., 1992) and the chromadorid nematode *Metadasynemoides cristatus* (Ceramonematidae) (Nicholas & Stewart, 1990).

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Юшин В. В., Малахов В. В. Ультраструктура кутикулы тела свободноживущих морских нематод.

Резюме. Исследована ультраструктура кутикулы тела 21 вида свободноживущих морских нематод, принадлежащих к 15 семействам в отрядах Enoplida, Chromadorida, Desmodorida, Monhysterida и Araeolaimida. Кутикула большинства видов состоит из осмофильной эпикутикулы и исчерченной экзокутикулы, образующих кортикальный слой, волокнистой мезокутикулы и базально расположенной эндокутикулы. Мезокутикула нематод отрядов Enoplida, Chromadorida, Monhysterida и Araeolaimida обычно многослойна и часто содержит полости, пересеченные внутрикутикулярными радиальными балками. Сильно склеротизированная кутикула нематод, принадлежащих к отряду Chromadorida, содержит жесткие мезокутикулярные кольца. Кутикула нематод отряда Desmodorida представляет пример наибольшей специализации среди изученных групп. Кутикулярные специализации, такие, как ряды точек или склероций, появляются в разных отрядах независимо.