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ULTRASTRUCTURE OF THE JAWS OF THE FOSSIL AND RECENT  
EUNICIDA (POLYCHAETA)

*Abstract.*—The ultrastructure of the jaws of Ordovician, Silurian, Permian and Recent Eunicida (Polychaeta) have been studied by transmission and scanning electron microscopy. Primary and secondary zones have been distinguished in the ultrastructure of the jaws. The primary zone is formed of the pharyngeal cuticle containing an orthogonal network of collagen fibrils, while the secondary zone, underlying the primary one, is developed of inner part of the pharyngeal cuticle devoid of a regular network of collagen fibrils. The two zones are pierced by microvilli. The jaws of placognath Eunicida are structured of the primary zone only. The Eunicida with highly organized jaw apparatus have a strongly developed secondary zone underlying the primary one. A preliminary correlation of evolutionary changes in the anatomy and ultrastructure of the jaws of Eunicida has been conducted. It has also been shown that the ultrastructural studies of the scolecodonts were not very useful for taxonomic purposes.

## INTRODUCTION

Studies on the structure of the polychaete jaws were initiated by Tasch and Shaffer (1961), who, observing them with the light microscope, found that they were composed of a fibrous matrix pierced by canals. Schwab (1966), who was the first to apply microtomy to the scolecodonts, maintained that the fibrousness of matrix is an artifact and that the alleged fibres turned out to be systems of fine canals. Detailed studies on the microstructure and histochemistry of the jaws of a Recent representative of the Polychaeta of the order Phyllodocida were conducted by Michel (1971b). The result of studies conducted by electron microscopy were published independently by Michel *et al.* (1973) and Strauch (1973). The ultrastructure of scolecodonts was also studied by Corradini *et al.* (1974), while single electron micrographs of the internal structure of the jaws of fossil Eunicida and Phyllocida were presented in several taxonomic papers (Charletta and Boyer 1974, Jansonius and Craig 1974, Mierzejewski and Mierzejewska 1975).

The present paper is to a considerable extent the result of our investigations of the ultrastructure of the jaws of eunicid polychaetes, conducted under the guidance of Professor Adam Urbanek. It contains a description and interpretation of the internal structure of jaws on the anatomical and ultrastructural level of their organization. Some of the observations and conclusions here presented were previously indicated in abstracts (Mierzejewska and Mierzejewski 1974, 1975). In addition, we published the results of our comparative studies on the structure of jaws of the Jurassic and Recent polychaetes from the genus *Glycera* Savigny (order Phyllodocida) (Mierzejewska and Mierzejewski 1977) and preliminary results of studies on what is known as pharate jaws of the Eunicida (Mierzejewski and Mierzejewska 1977).

#### CHEMICAL COMPOSITION AND FOSSILIZATION OF THE POLYCHAETA JAWS

Of about a dozen orders of the Recent Polychaeta, some occur as early as the Precambrian and Cambrian (Glaessner 1976). As follows from the morphology of the earliest Polychaeta known so far, this class reached its typical level of organization prior to the Cambrian. Striking is, however, the fact that the forms with stomodeal proboscides armed with jaws have only been known since the Lower Ordovician and probably were represented by the order Eunicida only (the taxonomic position of the enigmatic Paleoscolecidae is ambiguous). The toothed Phyllodocida have only been known since the Triassic (Kozur 1970, 1971; Zawidzka 1975), although some data are indicative of the existence of this order as early as the Ediacaran (Glaessner 1976).

The earliest finds of the Eunicida and Phyllodocida jaws known so far, probably mark in the phylogeny of these orders not the moment of appearances of toothed forms, but that at which their jaws acquired resistance to diagenetic factors. This hypothesis is confirmed by the fact that bristles of the Polychaeta, very similar in physical properties and, to a considerable extent also in their ultrastructure, to jaws as a rule do not occur in fossil state (an only, uncertain find has so far been described by Eisenack 1975), although their distinct impressions were more than once described in literature.

The problem of the dependence of the preservation of jaws in fossil state on their chemical composition has already been discussed by Ehlers (1867—1870) and Hinde (1882).

Calling attention to the lack of fossilized jaws of the Nephtyidae and Nereidae families which are common in the Recent seas, Szaniawski (1974) expressed the view that this may result from their specific chemical composition. This supposition is confirmed by our observations of the preservation state of polychaete jaws which occur in Recent North Sea

deposits. They are as a rule poorly preserved and frequently reduced to fragments, while jaws of the Glyceridae and various Eunicida give the impression as if they have recently been separated from the pharynx of polychaetes.

Differences in the chemical composition of the jaws are distinctly indicated by the results of studies published so far. It has primarily been proven that ascribing a chitinous character to all Polychaeta jaws is an error. The Phyllodocida jaws, studied within Glyceridae, Nephtyidae and Nereidae are devoid of chitin (Jeuniaux 1963, Desière and Jeuniaux 1968, Michel 1971b, Voss-Foucart *et al.* 1973), while those of the Eunicida contain only trace amounts of chitin (0.13% of dry weight) of an unknown crystallographic type (Desière and Jeuniaux 1968). The possibility that the presence of chitin might be decisive for the jaw resistance to diagenetic factors is, therefore, out of the question. This is the more obvious as the bristles of polychaetes containing 20% to 38% chitin of dry weight (Jeuniaux 1971) have been preserved in fossil state very rarely only.

Their strong lifetime mineralization was probably among the factors which contributed to the preservation of jaws in fossil state. As follows from the studies of Voss-Foucart *et al.* (1973), mineral salts (mostly carbonates), which make up 83.6% to 88.47% of dry weight of mandibles and 79.64% to 83.57% of dry weight of maxillae, are a fundamental component of the Eunicida jaws. Those of the Aphroditidae, Nereidae and Nephtyidae, that is, families in which jaws are unknown in fossil state, are mostly composed of proteins (45% to 62% of dry weight) with trace amounts of carbonates. There also occur distinct differences in the amino acidic composition of proteins forming the jaws: the proteins of the Eunicida contain twice as much threonine, arginine and glutamic acid, but much less histidine than those of the families of Phyllodocida mentioned above. The jaws of the Glyceridae are mineralized by iron and calcium salts (Michel *et al.* 1973), which is probably the reason why they are strongly resistant to the diagenetic factors. The chemical composition of the Goniadidae jaws has not been studied but, concluding from their close relationship with the Glyceridae, they should also contain considerable amounts of iron and copper (a correlation between the chemical composition of jaws and their systematic position has already been indicated by Voss-Foucart *et al.* 1973 and Jeuniaux 1975).

Chemical transformations in the organic and inorganic matter of the jaws, which might occur in the process of their fossilization, are unknown. Eisenack's (1968) studies on the percentage of three elements (carbon, hydrogen, nitrogen) contained in a heterogenous sample of the Silurian scolecodonts did not in principle contribute to the solution of this problem. In 1966, the results of studies on the Ordovician and Devonian Polychaeta jaws were presented by Schwab, who applied the methods of the diffraction of X-rays and of spectrography. He proved that the

scolecodonts he studied were mostly composed of fluorapatite with small admixtures of calcium, copper, silica and magnesium. In the course of our transmission electron microscope studies, we conducted staining of fossil and Recent jaws (see below). Their negative outcome undoubtedly resulted from a low degree of the specificity of this method, as well as from a presumable chemical homogeneity of the matrix.

Noteworthy is the fact that the scolecodonts from the Lower Paleozoic carbonate rocks are among the most common organic microfossils. This was probably caused not only by an abundant occurrence of Polycheta in the then seas, but also by the lack of reducing agents capable of decomposing their jaws. Scolecodonts separated from limestones are usually marked by an excellent state of preservation (disregarding some mechanical damage). Traces of bacterial decomposition (Mierzejewska and Mierzejewski 1978) may be observed on their surface only very rarely.

The character of sediment is, in addition to the chemical structure, another factor enabling preservation of jaws in fossil state. Interesting observations concerning the fossilization of scolecodonts dependent on facies were presented by Kozur (1972).

The effects of ultrastructure on the fossil preservation of the jaws seem rather doubtful. As follows from the studies conducted so far, most Eunicida and Phyllodocida jaws are fairly similar to each other in the structural pattern (a network of canals or, less frequently, of fibers embedded in an amorphous ground substance).

#### MATERIAL

Our studies included the maxillae and mandibles of the following fossil and Recent species of Eunicida:

Mochtyellidae: *Mochtyella cristata* Kielan-Jaworowska (Middle Ordovician, erratic boulder 0.400), *Mochtyella fragilis* Szaniawski (Llanvirnian, erratic boulder MZ/42), *Vistulella kozlowskii* Kielan-Jaworowska (Caradocian, erratic boulder MZ/25) — their maxillae I were studied.

Tetraprionidae: *Tetraprion* sp. (Caradocian, erratic boulder MZ/25) — mandible.

Archaeoprionidae: *Archaeoprion quadricristatus* Mierzejewski and Mierzejewska (Caradocian, erratic boulder MZ/25) — compound jaws and pseudocarriers.

Polychaetaspidae: *Polychaetaspis tuberculatus* Kielan-Jaworowska (Middle Ordovician, erratic boulder 0.400) — MI.

Ramphoprionidae: *Ramphoprion elongatus* Kielan-Jaworowska (Ordovician, erratic boulder MZ/15) — MI.

Paulinitidae: *Paulinites polonensis* Kielan-Jaworowska (Silurian, erratic boulder MZ/17) — MI.

Muelleriprionidae: *Kielanoprion pomoranensis* Szaniawski<sup>1)</sup> (Permian, Wejherowo borehole IG-1) — MI.

Lysaretidae: *Halla parthenopeia* Delle Chiaje (Recent, Mediterranean Sea) — MI and carriers.

Uncertain families: "*Nothrites*" sp. (Caradocian, erratic boulder MZ/25), "*Palaeosigma*" sp. (Silurian, erratic boulder MZ/17) — mandibles.

The material studied comes from the collections of scolecodonts of the Polish Academy of Sciences' Museum of the Earth and Institute of Paleobiology.

#### METHODS

The jaws of fossil forms were etched from carbonate rocks by means of hydrochloric or acetic acid. To purify them from mineral impurities, they were kept for 48 hours in hydrofluoric and nitric acids. The jaws of Recent forms came from formalin preparations made several years ago.

The specimens intended for studies by transmission electron microscopy were dehydrated by passing them through a series of 50%, 60%, 75%, 80%, 90% and 96% aqueous solutions of acetone (or ethanol) and through two consecutive portions of propylene oxide. Such dehydrated jaws were embedded in the Durcupan or Epon 812 epoxide resins accordingly to the procedure recommended by the manufacturers or by prolonging several times the time of infiltration. Ultrathin sections were cut of the embedded jaws by means of the Dupont diamond knife and L.K.B.-I, L.K.B.-III and Tesla BS 490 A ultramicrotomes. The sections were collected on 100- or 200-mesh grids or on those with an oval aperture and covered with a formvar film. The staining tests of the sections were conducted by Reynolds' method with the use of a 2% uranyl acetate, 2% potassium permanganate and lead citrate. The studies were conducted in the JEM 7A, JEM 100B and Tesla BS 500 transmission electron microscope, with an accelerating voltage of 60 kV or 80 kV.

The jaws intended for SEM studies were examined by means of a JSM S-1 scanning electron microscope with an accelerating voltage of 10 kV and after coating the jaws with carbon and gold (or with a gold-palladium or palladium).

For the purposes of microscopy, serial sections to 1  $\mu\text{m}$  thin were cut by means of L.K.B. Pyramitome.

The studies were conducted at the Laboratory of Electron Microscopy of the M. Nencki Institute of Experimental Biology and the Polish Academy of Sciences' Center of Experimental Medicine.

<sup>1)</sup> According to Kozur (1972), this name is a junior synonym of *Eunicides oblongus* (Seidel, 1959).

## ULTRASTRUCTURE OF XENOGNATH AND PLACOGNATH JAWS

Kielan-Jaworowska (1961, 1966) maintained that the jaws of polychaetes were formed of a locally transformed pharyngeal cuticle as a result of its hardening, denticulation and thickening. According to this author, the most primitive stage of the morphological evolution of the jaws is represented by compound jaws, that is, those having at least two rows of teeth, which, in the course of the phylogenetic development, divided to form simple jaws. Developing consistently this hypothesis, one might expect that the largest similarity to the structure of cuticle should be preserved by compound jaws, in particular flat and thin ones, such as those in *Archaeoprion* or *Mochtyella*. The genera mentioned above represent, at the same time, jaw apparatuses of the types unknown in the Recent Eunicida (the xenognath and placognath types).

Of particular interest was the possibility of studying the ultrastructure of *Archaeoprion quadricristatus* whose compound jaws represent the most primitive of all stages of morphological evolution of jaw apparatuses known so far (Mierzejewski and Mierzejewska 1975). However, because of very small dimensions of the jaws and a limited amount of the material, we did not succeed in cutting ultrathin sections of the jaws of this species. Studies, conducted by means of the SEM did not contribute any essential information on the ultrastructure of the jaws of *A. quadricristatus*. The ventral surface of the compound jaws of this species is somewhat rough and displays few, irregularly distributed pores (cf. Mierzejewski and Mierzejewska 1975, pl. 23: 1). The surface of the pseudocarrier is similar but devoid of pores. The jaws, whose fracture surfaces were observed, seem to be homogeneous, but it is difficult to draw any conclusions on the ultrastructure based on this observation. For, in some cases the picture viewed in the SEM and implying the homogeneity of a jaw, did not reveal its actual ultrastructure (see below).

Of several species of the genus *Mochtyella* described so far, the flattest and thinnest are the jaws of *M. fragilis*. The outer margins of these jaws are even indistinct in outline, since they gradually turned in a non-hardened pharyngeal cuticle. As revealed by TEM observations, they have the following structure pattern. The jaw forming matrix is a substance marked by a high electron density, with two canal systems running through it (pl. 23: 3). One of them is formed by canals parallel to the surface of jaw and arranged orthogonally in several to some scores of layers depending on the thickness of a jaw. The largest diameters occur in the canals situated in the central part of the section (central subzone), while those located just below the ventral (ventral subzone) or dorsal (dorsal subzone) surface are pronouncedly narrower. The other system is formed by canals perpendicular to the surface of jaw. They become detached from myocoele and usually open on the dorsal surface. Such is the structure pattern

of almost the whole jaw, including its basal (or laeobasal) and second ridges. A distinct departure from this pattern is observed only in the structure of teeth of the main ridge, which are formed at the expense of a very strong hypertrophy of the dorsal and ventral zones, accompanied by a sinuous trace of the canals, while the canals of the second system do not open on the dorsal surface (pl. 24: 1a).

The structure pattern of the jaw of *M. fragilis* described above, if presented in the form of a negative, would deceptively resemble that of

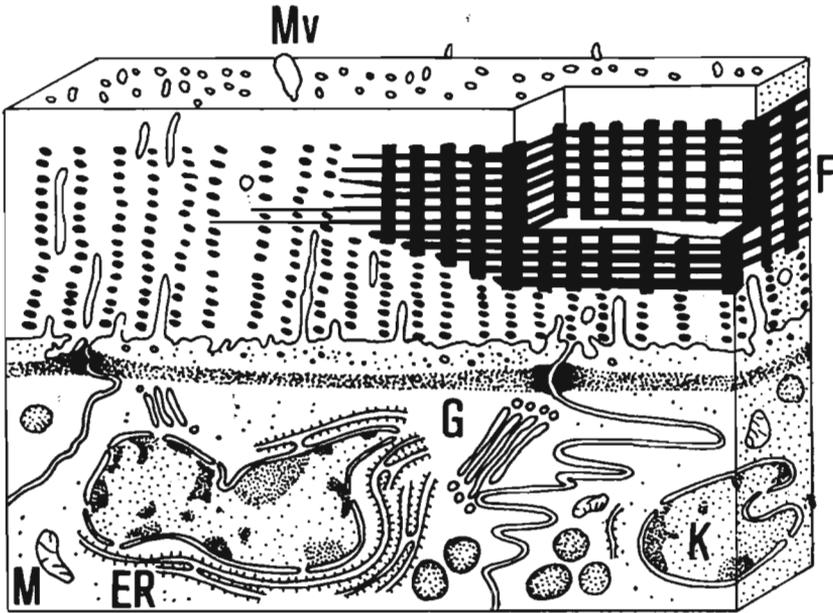


Fig. 1. Ultrastructure of collagenous cuticle of polychaete worm. Abbreviation: ER rough endoplasmatic reticulum, F system of collagenous fibrils of the cuticle, G Golgi complex, K nucleus of the epithelium cell, M mitochondrium, Mv distal bulbous part of microvillus penetrated the cuticle. From Storch by Lavry.

the cuticula of polychaetes, which is composed mostly of collagen fibrils, embedded in a basic mucopolysaccharide substance marked by a low electron density (Brökelmann and Fischer 1966, Michel 1969, 1971a, Storch and Welsch 1970, Misuraca and Nagy 1970, Bantz and Michel 1971). The collagen fibrils are arranged in layers parallel to the surface of epithelium, the fibrils of consecutive layers being more or less orthogonal to each other. The fibrils are perpendicularly interlaced by microvilli (fig. 1). The cuticle of the Oligochaeta (Ruska and Ruska 1961, Coggeshall 1966, Baccetti 1967) and Hirundinea (Storch and Welsch 1970) is composed according to this same pattern. This striking resemblance indicates that the jaw of *M. fragilis* is, in regard to histology, a folded, denticulated cuticle whose matrix was subject to sclerosis and collagen—to degradation. Under such circumstances, the canals running parallel to the surface of

jaw should be interpreted as traces of collagen fibrils and those perpendicular to them as traces of microvilli. The soundness of this interpretation is also confirmed by the following facts:

(1) The identical arrangement pattern of horizontal canals in jaws and collagen fibrils in cuticle. The characteristic contraction of horizontal canal under the ventral and dorsal surface of a jaw is fully reflected in changes occurring in the diameter of collagen fibrils in the cuticle covering in the diameter of collagen fibrils in the cuticle covering the bodies of the Eunicida (Misuraca and Nagy 1970) and Oligochaeta (Coggeshall 1966).

(2) The accordance of the diameter of collagen fibrils and corresponding horizontal canals. In *M. fragilis*, the diameter of horizontal canals fluctuates within limits of 0.02 to 0.06  $\mu\text{m}$  in the ventral and dorsal subzones and 0.15  $\mu\text{m}$  in the central subzone. In the cuticle of *Platynereis dumerilli*, the diameter of collagen fibrils amounts to 0.02 to 0.08  $\mu\text{m}$  (Bröckelmann and Fischer 1966) and in *Lumbriscus terrestris* it reaches as much as 0.2  $\mu\text{m}$  (Coggeshall 1966).

(3) The concordance of the diameter of vertical canals and microvilli. In *M. fragilis*, these canals are mostly 0.08 to 0.09  $\mu\text{m}$  in diameter, while the diameter of microvilli in the cuticle of *Platynereis dumerilli* amounts to about 0.08  $\mu\text{m}$  (Bröckelmann and Fischer 1966).

The ultrastructure of the cuticle of the sessile polychaete *Cirrophorus branchiatus* Ehlers, studied by Strelcov (1973), is an additional argument in favor of the direct relationship between the structure of jaw in *M. fragilis* and the collagen cuticle in the Polychaeta. The inner zone of this cuticula is of the nature of a typical collagen cuticle, while its outer zone represents in a way its negative: the canals corresponding in diameter to the underlying fibrils run through the matrix marked by a high electron density.

Lateral parts of jaws in *M. cristata* (pl. 25: 1a; Mierzejewski and Mierzejewska 1975: pl. 1) and *Vistulela kozlowskii* are structured identically with those of *M. fragilis*, although considerable differences are observed in the ultrastructure of the main ridge of teeth. At this point, there occurs a sudden increase in the thickness of jaw and a gradual modification in the spatial distribution of canals. An increase in the thickness appears mostly as a result of the growth of the central subzone and the vertical canals running through it become characteristically bent (pl. 25: 1b). The main canals approximately parallel to the longitudinal axis of the jaw (pl. 26: 1a) are situated at the level of the main ridge of teeth nearer the dorsal surface. Below them, there occurs a part with irregularly distributed canals which is a continuation of the ventral subzone in the thinner parts of jaw (pl. 26: 1b). In *M. cristata*, the diameter of horizontal canals varies from 0.02 to 0.04  $\mu\text{m}$  in the ventral and dorsal and from 0.15 to 0.18  $\mu\text{m}$  in the central subzone.

## ULTRASTRUCTURE OF LABIDOGNATH AND PRIONOGNATH JAWS

The jaws of the labidognath and prionognath forms we studied have a distinctly bizonal structure. The outer zone corresponds in structure to the ultrastructure of the jaws of the placognath forms. For this reason, we introduce for it the name of a primary zone and, for the underlying zone unknown in the placognath Eunicida, the name of a secondary zone.

The primary zone is marked by an approximately orthogonal arrangement of horizontal canals, with vertical canals penetrating between them. Like in the placognath Eunicida, this zone may be divided into dorsal, central and ventral zones.

The occurrence of horizontal canals not directly below the dorsal surface (pl. 25: 1a), as in the *Mochtyella* or *Vistulella*, but somewhat deeper (pl. 26: 2) is typical of the jaws of the labidognath and prionognath apparatus. Due to this feature, the dorsal surface of jaws is covered with a zone of a homogeneous basic substance devoid of canals, called by Strauch (1973) a compacta. The compacta develops mostly at the expense of the disappearing canals of the dorsal subzone, which many cause in extreme cases that the canals of the central zone are situated directly below the compacta (pl. 26: 1c). We did not find any regularities in the disappearance of canals in the dorsal subzone, occurring within the range of the jaws studied and, therefore, they might disappear in various parts of the jaw.

A discordance in the arrangement of horizontal canals within the dorsal subzone was observed sporadically (pl. 28: 1). The canals of the ventral subzone are developed similarly as in the jaws of placognath apparatus (pl. 27: 1b; pl. 28: 1). The lower boundary of the ventral subzone makes up, at the same time, a boundary between the primary and secondary zone.

The proportion of the thickness of the primary and secondary zones is variable even within limits of one and the same jaw. The primary zone may equal in thickness the secondary zone, but it may be also several times narrower or wider than this (pl. 27: 1a; pl. 30: 1a, 1c; pl. 31: 1). The secondary zone is devoid of the orthogonal network of horizontal canals which indicates that it was formed of a zone of cuticula devoid of collagen fibrils. It is penetrated only by vertical canals (microvilli) continued also within the primary zone (pl. 26: 2; pl. 30: 1b). In *Polychaetaspis tuberculatus*, they are accompanied by considerably wider canals, called by Corradini *et al.* (1974) "δ-canals". In all likelihood, these are the traces of lacunae, described by Bröckelmann and Fischer (1966) in the collagen cuticle of *Platynereis dumerilli*. As follows from our observations made so far, the occurrence of lacunae in the jaws is connected with the presence of the secondary zone. It is not unlikely, however, that they were also formed in jaws composed of the primary zone only. Such was pro-

bably the structure of an indeterminate scolecodont whose transverse sections was illustrated by Strauch (1973, pl. 4: 19).

The secondary zones in small and large jaws of specimens of the same species display certain ultrastructural differences. Thus, the secondary zone of a small MI in *P.tuberculatus* is almost completely amorphous, with only microvillous canals occurring on it here and there (pl. 32: 1a). On the other hand, this same zone in large MI displays, besides more numerous canals of microvilli, traces of lacunae and an irregular network of very fine and indeterminate canals (pl. 32: 1b).

In regard to electron density, the basic substance of the secondary zone is identical with the matrix of this zone. This picture cannot be changed even by contrasting tests on the Recent material. An incomplete sclerosis of matrix may sporadically be observed in the two zones (pl. 28: 2; pl. 29: 1).

Characteristic internal cavities, occurring in the shanks of the *Polychaetaspis* (fig. 2) and *Ramphoprion* (pl. 33: 1) and in the posterior parts of MI of *Kielanoprion* (pl. 33: 2), have so far escaped notice of the investigators of scolecodonts. The cavities, fairly regular in shape, do not display any connection with the myocelle or with the dorsal surface of jaws. Their presence gives the shanks a characteristic convex shape (fig. 2). Concluding from the morphology of jaws in other Eunicida, their presence may also be expected in MI of such genera as *Leptoprion* Kielan-Jaw.,

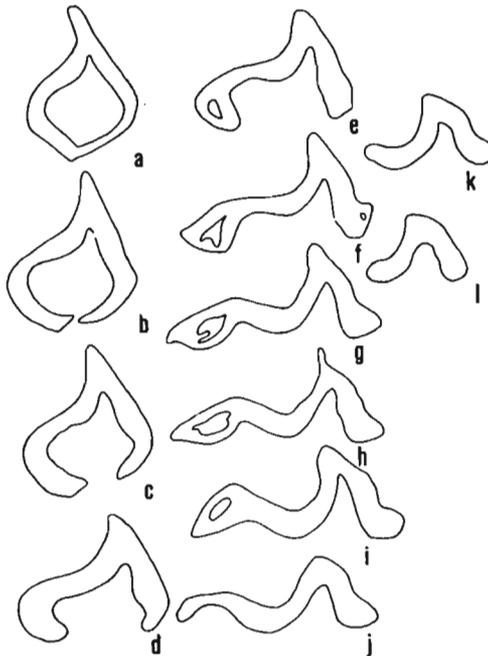


Fig. 2. *Polychaetaspis tuberculatus* Kielan-Jaworowska, 1966. Serial cross sections through left MI; a—d anterior part of the jaw; e—j middle part of the jaw with a shank; k—l posterior part of the jaw.

*Kallopriion* Kielan-Jaw., *Polychaetura* Kozł., etc. The nature and origin of the internal cavities are not clear. They could not be explained only by the lack of sclerosis in the matrix of shanks, since this would not justify the presence of characteristic swellings occurring over these cavities on the surface of the jaws. In the jaws we examined, the internal cavities were situated within secondary zones only. Much smaller cavities could also be observed in inner margins of the jaws (fig. 2).

#### THE ROLE OF CANALS IN JAWS

The role of canals in the jaws of polychaetes was briefly discussed by Strauch (1973) and Corradini *et al.* (1974), who, however, studied the structure of jaws without analyzing the origin of canals. According to Strauch (1973), the canals in jaws enabled a physiological contact with living tissues and increased the elasticity of jaws, while the function of increasing elasticity and resistance and decreasing the mass of jaws was ascribed to horizontal canals by Corradini *et al.* (1974), who believed that wide vertical canals ("φ-canals" as they called them and, in our interpretation, spaces left by the lacunae) were filled by nerves (!). This view is unacceptable, since for both physiological and histological reasons the possibility of the existence of an organ which could, at the same time, perform the functions of a jaw and a sense organ is out of the question. In fact, any sensory role of the jaws in the Polychaeta has never been revealed either by studies on their functions (Beklemishev 1950, Hartmann-Schröder 1967), or by cytological examination (Michel 1971b).

In our opinion, no special function should be ascribed to the horizontal canals in jaws and no functional causes of their formation should be discussed. Instead, their existence should be connected with the specific metabolic activity of collagen and biochemical changes occurring within the hardened basic substance. In the process of ontogeny, collagen is subject to degradation and, afterwards, is formed anew. The biological period of the semi-degradation of collagen is variable and depends, among other things, on the type of tissue and organ. In mammals, this period may fluctuate between 20 and 300 days (no studies have been conducted on the time of renovation of collagen in the polychaetes). As a component of the pharyngeal cuticle, which, in the course of ontogeny, was transformed into jaws, collagen was also subject to gradual degradation. As a result of biochemical changes in the matrix, the reproduction of new collagen fibrils in jaws is impossible, since the soluble precursors of collagen may pass from the cells to the basis substance and polymerize in it provided that it preserves the character of a gelatinous mass marked by a specific biochemical composition. The hardening of matrix as a result of its mineralization and, maybe also, its quinone tanning is tantamount to the loss of these properties. Thus, the presence of horizontal

canals in jaw is only a colateral effect of the natural degradation of collagen.

The biochemical mechanism of the degradation of collagen in the jaws of the Polychaeta is unknown. We have previously made the conjecture that this process results from the activity of collagenase (Mierzejewska and Mierzejewski 1975). It is not unlikely, however, that the breakdown of collagen is a more complex process which occurs as a result of the activities of several collagenolytic proteases. The data we obtained imply that the lysis of collagen fibrils in jaws is a very orderly process. In the jaws of *Halla parthenopeia*, we distinguished layers of collagen fibrils situated alternately to empty canals which were once filled with collagen (Mierzejewska and Mierzejewski 1977; pl. 25: 1). The regularity of this system allows us to presume that the course of the degradation of collagen may, similarly as the arrangement of fibrils itself, be concealed in the mucopolysaccharide matrix. The solution of this problem requires, however, conducting detailed biochemical studies. It should be emphasized that the life-time lysis of collagen by animal bodies has hitherto been known by far insufficiently.

Biochemical transformations in matrix preclude the formation within its limits of new collagen fibrils and, consequently, also preclude the growth of jaws by intusseption.

#### CORRELATION OF EVOLUTIONARY CHANGES IN JAWS CONCERNING THEIR ANATOMY AND ULTRASTRUCTURE

The question to what an extent the anatomical changes in jaws are reflected in the ultrastructure is a very interesting subject concerning the evolution of jaw apparatus in the Eunicida. Kielan-Jaworowska (1961, 1966) pointed out that the most primitive Eunicida had (or have, e.g. the Dorvilleidae) completely open myocells of their MI. On the other hand, forms marked by a higher degree of organization have more or less covered myocytes (this problem was also discussed by Kozur 1970).

Regarding this phenomenon as a symptom of the evolutionary trend in jaws, we can attempt to correlate tentatively the evolutionary anatomical and the evolutionary ultrastructural transformations. Such a tentative correlation is shown below in Table 1.

The evolution of jaws presented in the above Table is partly hypothetical in character. This reservation concerns the correlation of the stage of contracting the pulp cavity with ultrastructural changes. Examining fossil jaw apparatus and comparing them with Recent ones, one may observe in some cases the occurrence of distinct phylogenetic lines (Kielan-Jaworowska 1966, Kozur 1970, Zawidzka 1975). However, a line which might be traced from stage 1 to stages 4 or 5 of the anatomical level, has so far been unknown. Theoretically, it is possible, therefore,

Table 1

Correlation of evolutionary anatomical and ultrastructural changes in jaws

Anatomy	Ultrastructure
Stage 1. Local hardening of the cuticle	Stage 1. Hardening and mineralization resulting in an increase in the electron density of the matrix and, consequently, in a change in its biochemical properties (the loss of the capability of reconstructing the degraded collagen and the formation of canals). Decrease in the number of microvilli piercing the dorsal surface.
Stage 2. Folding and denticulation of the hardening cuticle, the formation of compound jaws. Differentiation in the height of folds.	Stage 2. Occurrence of the microvilli piercing the dorsal surface and reaching peripheral parts becomes limited by an increase in the density of matrix.
Stage 3. Disintegration of compound jaws into simple jaws	Stage 3. Microvilli do not open on the dorsal surface. An incipient compacta appears.
Stage 4. Incipient contraction of myocytes	Stage 4. Decrease in and disappearance of the hardening and mineralization between the rows of teeth in compound jaws.
Stage 5. Distinct contraction of myocytes.	Stage 5. Strong development of the compacta. Appearance of the secondary zone. Dorsal subzone tends to disappear.

that MI of labidognath and prionognath jaw apparatus were formed of pharyngeal cuticle, which only in its outer part had an orthogonal network of collagen fibrils. This problem should be explained by studies on the pharyngeal cuticle of the contemporary Eunicida, conducted by means of a transmission electron microscope. Due to the lack of properly fixed material, we were unable to conduct such studies.

#### ULTRASTRUCTURE OF MANDIBLES

The mandibles of pharynx in the Eunicida are differently situated than the remaining parts of the jaw apparatus and play specific roles (Hartmann-Schröder 1967). So far, they have not been studied ultrastructurally.

On the surface of mandibles, we observed the occurrence of characteristic polygonal structures, so far known only from maxillae. First described by Tasch and Shaffer (1961) as "growth cells", they were also

illustrated by Schwab (1966), Taugourdeau (1972), Strauch (1973), Corradini *et al.* (1974) and Eisenack (1975). The taxonomic usefulness of these polygonal structures was discussed by Taugourdeau (1972). On a mandible of *Tetraprion* sp.,<sup>2)</sup> we found the polygonal structure on a very limited area, that is, on the place of a ligament connecting both mandibles (pl. 23: 1; pl. 34). The mandibles of *Palaeosigma* sp. have their polygonal structures distributed over a somewhat larger area, but their occurrence is limited to the shaft only.

No information was contributed by SEM studies of the internal structure of mandibles. The mandibles viewed on fracture surfaces seemed to be composed of a homogeneous substance devoid of canals or fibrils. As follows from TEM observations, the mandibles of *Tetraprion* sp. and "*Nothrites*" sp. distinctly differ from each other in ultrastructure. The inside of a mandible of *Tetraprion* sp. displays a network of canals whose trace departs from the orthogonal pattern observed in maxillae. The central part of shaft is occupied by distinctly wider canals (pl. 35). The mandibles of "*Nothrites*" sp. have an almost homogeneous ultrastructure so that only indistinct traces of canals may scarcely be discerned (pl. 23: 2).

#### THE ULTRASTRUCTURE OF SCOLECODONTS AND THE TAXONOMY OF THE POLYCHAETA

Difficulties resulting from the taxonomy of the Polychaeta, based on fossil jaws, are generally known (for references see Zawadzka 1975). Under such circumstances, quite obvious is the interest in the possibilities of making use of ultrastructural studies for the purposes of classification. The importance of the internal structure of jaws to classification is directly connected with biochemical properties of the basis substance. The distribution of canals in jaws is related with that of collagen fibrils in the pharyngeal cuticle. In many organs of various animals, collagen displays a very regular and constant arrangement. In all likelihood, this is connected with the fact that fundamental information on the formation of collagen fibrils, for example, by a temporary sulphate gap, is coded in the basic mucopolysaccharide substance. In some cases, the manner of distributing collagen in a given tissue may be characteristic of a taxon (Bailey 1971). Misuraca and Nagy (1970) proved that the system of collagen in the cuticle of the Eunicida is very typical of this group due to a characteristic gradation of the diameter of fibrils and distinctly differs it from other Polychaeta. As follows from our results presented above, this system is also reflected in that of the canals of the jaws of the Eunicida. Comparing the structure of jaws in various Polychaeta, one can — due to the characteristic gradation of canals — distinguish the jaws of the Euni-

<sup>2)</sup> Single mandibles of the genus *Tetraprion* have been described under the specific name *Monothrites acutus* Eisenack, 1968.

cida from those of such Phyllodocida as Glyceridae, Nepthyidae or Nereidae. The comparisons of this type are of little importance to taxonomy, since the distinction of the jaws of the Eunicida from those of the Phyllodocida mostly does not pose any problems even during a superficial observation.

The jaws of the placognath Eunicida distinctly differ in ultrastructure from those of the prionognath or labidognath forms. On the other hand, the representatives of various prionognath and labidognath families of the Eunicida have, however, jaws whose structural patterns are identical. Within this pattern considerable differences are sometimes observed even within one and the same jaw. These differences occur in the ratio of thickness of the primary and secondary zone, in the degree of development of the dorsal zone and of the compacta, in the direction of the trace of canals and in the structure of secondary zone. Taking into account the time-consuming method of TEM studies and the unreliability of the results of SEM studies (see below), we can be greatly doubtful about the suitability of ultrastructural studies to the taxonomy of the Polychaeta. This concerns the jaws of the Phyllodocida to a much greater degree than those of the Eunicida. As we have already pointed out (Mierzejewska and Mierzejewski 1977), fundamental ultrastructural differences may occur even in the jaws of various species of the same genus. This is in conformity with the results obtained by Storch and Welsch (1970), which are indicative of the absence of relationships between the ultrastructure of cuticle and the systematics of the polychaetes. In this respect, only the Eunicida constitute a certain exception (Misuraca and Nagy 1970), which only confirms the isolated position of this order within the Polychaeta.

#### ARTIFACTS

The results of studies, obtained by the methods of electron microscopy, are fundamentally influenced by the types of the investigating techniques applied. The technique of cutting ultrathin sections is of particular importance to TEM studies of the ultrastructure of scolecodonts. At first, we made use for this purpose of glass knives, which, however, as it turned out later, considerably deformed the ultrastructure of jaws (pl. 36: 1, 2). The unawareness of this fact caused our erroneous interpretation (Mierzejewska and Mierzejewski 1974) of the ultrastructure of some scolecodonts.

A misleading picture of the real ultrastructure of scolecodonts may also be caused by the application of a scanning electron microscope. The ultrastructure of scolecodonts was studied by Corradini *et al.* (1974) almost exclusively by SEM methods. This prevented them from noticing a specific gradation in the diameter of horizontal canals ( $\alpha$  and  $\beta$  canals

according to their terminology) and from discovering the subzones which we termed a ventral and dorsal subzone and which are so important to considerations on the genesis of the ultrastructure of vertical canals ( $\gamma$  and  $\delta$  canals) and to the ultrastructure of the secondary zone (the presence of narrow, irregularly running canals). The causes of the incomplete identification of the structure of scolecodonts by Corradini *et al.* (1974) is explained by way of example by a micrograph of the transverse section of an MI of *Polychaetaspis tuberculatus* taken in a transmission electron microscope (pl. 36: 3). It reveals that the terminal sectors of canals left by the microvilli are filled with a substance with the electron density higher than that of the basic substance. In the scanning electron microscope, discernible are only the empty parts of canals, which causes the illusion that they are shorter than their actual length. A similar filling of some other canals explains the fact that Corradini *et al.* (1974) failed to notice the occurrence of the ventral and dorsal zones in jaws and all other details of the secondary zone. It is worth mentioning that, studying the ultrastructure of jaws of the genus *Glycera* Savigny (Mierzejewska and Mierzejewski 1977) or mandibles of the Eunicida (as above), we recognized their actual ultrastructure only in TEM. Viewed in SEM, they seemed to be completely homogeneous. The limited suitability of SEM to studies on the ultrastructure of the graptolites has recently been pointed out by Urbanek (1976). The SEM usefulness for histo- and cytological studies on organic tissue is still of little importance and, therefore, the SEM technique is made use for histostructural identification, rather than ultrastructural studies.

Observing scolecodonts in SEM, Jansonius and Craig (1974) found that they were lamellar in structure, which was allegedly a sufficient evidence of the continuity of the growth of jaws. This interpretation was erroneous, since in fact their micrograph displays not lamellae but canals revealed as a result of the destruction of the compacta. Similar pictures, but correctly interpreted, were formerly described by Strauch (1973).

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GRAZYNA MIERZEJEWSKA I PIOTR MIERZEJEWSKI

ULTRASTRUKTURA SZCZĘK KOPALNYCH I WSPÓŁCZESNYCH EUNICIDA  
(POLYCHAETA)

*Streszczenie*

Praca przedstawia wyniki badań prowadzonych metodami transmisyjnej i skaningowej mikroskopii elektronowej nad ultrastrukturą szczęk kopalnych i współczesnych wieloszczetów z rzędu Eunicida.

Szczęki wieloszczetów powstają z kutikuli gardzielowej wskutek sfałdowania jej, dentykulacji i sklerotyzacji. W ultrastrukturze proces ten zaznacza się silnym wzrostem gęstości elektronowej substancji podstawowej oraz degradacją kolagenu, po którym pozostają puste kanały. Zmiany własności biochemicznych pierwotnie mukopolisacharydowej substancji podstawowej uniemożliwiają polimeryzację w niej nowych włókien kolagenu i wykluczają możliwość wzrostu szczęk przez intususcepcję.

Wyróżniono w ultrastrukturze szczęk zonę pierwotną i zonę wtórną. Zona pierwotna formuje się z kutikuli gardzielowej zawierającej ortogonalną sieć włókien kolagenu. Zona wtórna, leżąca pod zoną pierwotną, tworzy się z wewnętrznej partii kutikuli gardzielowej pozbawionej regularnej sieci włókien kolagenu. Obie zony poprzecinane są przez microvilli. Szczęki plakognatycznych Eunicida zbudowane są wyłącznie z zony pierwotnej. Eunicida o aparatach szczękowych wyżej uorganizowanych mają pod zoną pierwotną silnie rozwiniętą zonę wtórną. Przeprowadzono wstępną korelację zmian ewolucyjnych szczęk Eunicida na stopniach anatomicznych i ultrastrukturalnych. Wskazano na niewielką przydatność badań nad ultrastrukturą skolekodontów dla celów taksonomicznych.

ГРАЖИНА МЕЖЭЙЕВСКА, ПИОТР МЕЖЭЙЕВСКИ

УЛЬТРАСТРУКТУРА ИСКОПАЕМЫХ И СОВРЕМЕННЫХ ЧЕЛЮСТЕЙ  
EUNICIDA (POLYCHAETA)

## Резюме

В работе даны результаты исследований под трансмиссионным и растровым электронными микроскопами ультраструктуры ископаемых и современных челюстей многощетинковых червей отряда Eunicida.

Челюсти многощетинковых образуются из гладкой кутикулы в результате её сморщения, дентикуляции и склеротизации. Этот процесс для ультраструктур обуславливается сильным увеличением электронной плотности матрикса и удалением фибр коллагена, после которого остаются пустые каналы. Изменения биохимических свойств первично мукополисахаридового матрикса делают невозможным полимеризацию новых волокон коллагена и не позволяют челюстям увеличиваться из-за интуссисцепции.

В ультраструктуре челюстей выделены первичная и вторичная зоны. Первичная зона образуется из гладкой кутикулы, содержащей ортогональную сеть фибр коллагена. Вторичная зона, лежащая под первичной зоной образуется из внутренней части гладкой кутикулы, неимеющей правильной сети фибр коллагена. Через обе зоны проходят микровилии (microvilli). Плакоидные челюсти Eunicida построены исключительно из первичной зоны. Eunicida с челюстным аппаратом высшей степени организации имеют под первичной зоной хорошо развитую вторичную зону. Была проведена вступительная корреляция эволюционных изменений челюстей Eunicida относительно анатомии и тонких структур. Указано на небольшую пригодность исследований ультраструктур сколекодонтов для таксономических целей.

## EXPLANATIONS OF THE PLATES 23—36

Abbreviations: cs — central subzone, ds — dorsal subzone, PZ — primary zone, SZ — secondary zone, vs — ventral subzone.

## Plate 23

1. *Tetraprion* sp., Caradocian, erratic boulder MZ/25. Part of jaw apparatus composed of a mandible (Mdb), an MII and a laeobasal plate (lbp). Polygonal structures are visible halfway the length of mandible (cf. also pl. 12). SEM,  $\times 250$ .

2. "*Nothrites*" sp., Caradocian, erratic boulder MZ/25. Part of the transverse section of a mandible (artifact: parallel streaks). TEM.
3. *Mochtyella fragilis* Szaniawski, Llanvirian, erratic boulder MZ/42. A transverse section of the lateral part of an MII. TEM.

## Plate 24

*Mochtyella fragilis* Szaniawski, Llanvirian, erratic boulder MZ/42

- 1a. Transverse section of a tooth in the main ridge of an MII. TEM,  $\times 10000$ .
- 1b. Part of a transverse section of the dorsal and, partially, central subzone. TEM.

## Plate 25

*Mochtyella cristata* Kielan-Jaworowska, Middle Ordovician, erratic boulder 0.400

- 1a. Part of a transverse section of an MII near the inner margin. TEM,  $\times 5100$ .
- 1b. Part of a transverse section of an MII near the main ridge. TEM,  $\times 5500$ .

## Plate 26

1. *Mochtyella cristata* Kielan-Jaworowska, Middle Ordovician, erratic boulder 0.400. The ultrastructure of an MII seen in transverse section at the level of the main ridge, 1a—under the dorsal surface, 1b—under the ventral surface. TEM, ca  $\times 10000$ .
2. *Ramphoprion elongatus* Kielan-Jaworowska, Ordovician, erratic boulder MZ/15. Part of a transverse section of the primary and, partially, secondary zone of an MII. TEM,  $\times 6800$ .

## Plate 27

*Kielanoprion pomeranensis* Szaniawski, Permian, Wejherowo IG-1 borehole

- 1a. Transverse section of a tooth in MII. TEM,  $\times 3300$ .
- 1b. A boundary between the primary and secondary zone of an MII. TEM,  $\times 10400$ .
- 1c. Ultrastructure of an MII under the dorsal surface; the dorsal subzone lacking. TEM,  $\times 17300$ .
- 1d. Ultrastructure of an MII under the dorsal surface; the dorsal subzone poorly developed. TEM, ca  $\times 10000$ .

## Plate 28

1. *Kielanoprion pomeranensis* Szaniawski, Permian, Wejherowo IG-1 borehole. A discordance in the arrangement of horizontal canals of the central subzone of an MII. TEM,  $\times 8000$ .
2. *Ramphoprion elongatus* Kielan-Jaworowska, Ordovician, erratic boulder MZ/15. Matrix (o) in an MII not hardened. TEM,  $\times 11500$ .

## Plate 29

*Kielanoprion pomeranensis* Szaniawski, Permian, Wejherowo IG-1 borehole

1. Losses in matrix within the central subzone of an M1r (resulting from an incomplete hardening?). TEM,  $\times 49800$ .
2. Ultrastructure of the central subzone of an M1r. TEM,  $\times 8650$ .

## Plate 30

*Paulinites polonensis* Kielan-Jaworowska, Silurian, erratic boulder MZ/17

- 1a. Transverse section at the level of an MII tooth. SEM,  $\times 3000$ .
- 1b. Ultrastructure of the secondary zone; vertical canals visible (traces left by microvilli). SEM,  $\times 6000$ .
- 1c. Transverse section of the lateral part of an MII. SEM,  $\times 3000$ .
- 1d. Contact point of the primary and secondary zones in an MII. SEM,  $\times 10000$ .

## Plate 31

1. *Halla parthenopeia* Della Chiaje. a — transverse section of a carrier  $\times 4000$ , b — tangential section of the central subzone of an MII  $\times 5000$ . TEM.
2. *Polychaetaspis tuberculatus* Kielan-Jaworowska, Middle Ordovician, erratic boulder 0.400. Transverse section of an M1r. TEM.

## Plate 32

*Polychaetaspis tuberculatus* Kielan-Jaworowska, Middle Ordovician, erratic boulder 0.400

1. Ultrastructure of the secondary zone of a small M1r (x — sample damaged here). TEM.
2. Ultrastructure of the secondary zone of a large M1r. TEM,  $\times 6750$ .

## Plate 33

1. *Ramphoprion elongatus* Kielan-Jaworowska, Ordovician, erratic boulder MZ/15. Internal cavity (c) of an M1r. SEM,  $\times 600$ .
2. *Kielanoprion pomeranensis* Szaniawski, Permian, Wejherowo IG-1 borehole. Internal cavity (c) of an M1r,  $\times 3200$ .

## Plate 34

*Tetraprion* sp., Caradocian, erratic boulder MZ/25

- 1a. Part of a polygonal structure. SEM,  $\times 4000$ .
- 1b. Details of the surface of a polygonal structure. SEM,  $\times 7500$ .

## Plate 35

„*Nothrites* sp.” Caradocian, erratic boulder MZ/25

- 1a. Ultrastructure of the central part of a mandibular shaft. TEM.
- 1b. Ultrastructure of the marginal part of a mandibular shaft. TEM.
- 1c. Transverse section of a mandibular shaft. TEM.

## Plate 36

1. *Kielanoprion pomeranensis* Szaniawski, Permian, Wejherowo IG-1 borehole. Ultrastructure of the primary zone of an MIR deformed by cutting the material with a glass knife. TEM.
  2. *Mochtyella cristata* Kielan-Jaworowska, Middle Ordovician, erratic boulder 0.400. Ultrastructure of the peripheral part of an MIR deformed by cutting the sample with a glass knife. TEM.
  3. *Polychaetaspis tuberculatus* Kielan-Jaworowska, Middle Ordovician, erratic boulder 0.400. Vertical canals (traces left by microvilli) filled with a substance marked by considerable electron density. TEM.
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