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MOLTING OF THE JAWS OF THE EARLY PALEOZOIC EUNICIDA (ANNELIDA, POLYCHAETA)

Abstract. — Pharate jaws of the Ordovician and Silurian Eunicida have been studied under a scanning electron microscope and the conjecture has been formed that the molting of jaws in the Early-Paleozoic Eunicida took place many times in the process of their ontogeny and was not necessarily connected with their growth. The cases of jaw replacement, observed so far in the fossil Polychaeta, were of the nature of a cyclic physiological regeneration, whereas the replacement of jaws in Recent forms is a reparative regeneration. The specific name *Mochtyella multilamellata* Szaniawski 1970 is a simultaneously published synonyme of the name *Mochtyella fragilis* Szaniawski 1970, accepted as a valid.

INTRODUCTION

The jaws of the Polychaeta of the order Eunicida are among the most frequent microfossils in the Early-Paleozoic deposits. Assemblages of morphologically identical jaws, inserted into each other according to the "jaw-in-jaw" principle are, however, extremely rare. Such assemblages, which I call pharate jaws, were first described (separately) by Kielan-Jaworowska (1966) and Schwab (1966). In both instances, these were maxillae I of the placognath apparatus having one secondary jaw each in their myocoeles. One of Kielan-Jaworowska's (1966) specimens, now missing, was made up of MIr and MIl of *Mochtyella cristata* Kielan-Jaw. connected with each other. Another, MIl of *Vistulella* sp., was mistakenly (as indicated by an original label enclosed with the specimen) described as *Mochtyella* sp. Schwab's (1966) both specimens, identified as *Staurocephalites* sp., probably also represent the Mochtyellidae. Jaws, having numerous secondary jaws in their myocoeles, were described by Szaniawski (1970) as *Mochtyella multilamellata* Szan. and morphologically identical jaws, but devoid of secondary jaws — as a separate species *Mochtyella fragilis* Szan. All pharate jaws of the Eunicida, described so far, came from the Ordovician and Silurian deposits.

As a result of several years' work of chemical etching of carbonate rocks varying in geological age, I succeeded in obtaining a relatively numerous collection of pharate jaws of the early-Paleozoic Eunicida. The aim of the present paper is to describe this collection, to redescribe H. Szaniawski's material mentioned above and to discuss some physiological aspects of the existence of pharates jaws.

The material described are housed at the Museum of the Earth and at the Paleobiological Institute of the Polish Academy of Sciences in Warsaw.

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TERMINOLOGY

The terminology used so far (cf. Kielan-Jaworowska 1966; Jansonius and Craig 1971) is insufficient for the descriptions of the Eunicida's jaw given below. In this connection, I have introduced or adapted several new terms.

By the term pharate [1] I mean each assemblage of morphologically identical jaws composed according to the "jaw-in-jaw" principle. A pharate jaw consisting of two jaws I call a single pharate (monopharate) jaw, while I apply the term polypharate jaw to a pharate jaw consisting of at

[1] I have borrowed the term pharate (Greek *pharos* = cloak) from the physiology of the arthropods' molting, first made use of by Hinton (1946).

least three jaws. After Schwab (1966), I apply the term primary jaw to designate the outermost jaw of a pharate jaw. Secondary jaw, another term of Schwab, is extended in this paper to include all the remaining elements of a pharate jaw. A pharate jaw with two secondary jaws is termed a double pharate jaw, that with three secondary jaws — a triple pharate jaw, etc. The numeration of secondary jaws within a polypharate jaw starts with the oldest of them, that is, directly underlying the primary jaw.

The terms primary and secondary jaws are purely descriptive in character.

MATERIAL AND METHODS

The material described comprises detached jaws of the Eunicida, etched out by means of acetic or hydrochloric acid from Ordovician and Silurian calcareous erratic boulders. Thus obtained jaws, were subsequently cleaned of mineral impurities by a 48-hour bath in a 20 per cent solution of the hydrofluoric acid. Then, the material, discolored by the Meyer method, was observed under the Zeiss Nf PK light microscope, with a magnification of 525 times. Subsequently, after coating it with coal and gold, I studied the material under the JSM S-1 scanning electron microscope (with an accelerating voltage of 10 kV) at the Laboratory of Electron Microscopy of the Polish Academy of Sciences M. Nencki Institute of Experimental Biology.

Detailed data concerning the material are presented in Table 1.

DESCRIPTIONS

Order **Eunicida** Dales, 1962
Family **Mochtyellidae** Kielan-Jaworowska, 1966
Genus *Mochtyella* Kielan-Jaworowska, 1961
Type species: Mochtyella cristata Kielan-Jaworowska, 1961

Mochtyella fragilis Szaniawski, 1970, emend.

(pl. 16; pl. 18: 7; pl. 19: 3—5)

1970. *Mochtyella fragilis* Szaniawski: 453: pl. 2: 5—7.
1970. *Mochtyella multilamellata* Szaniawski: 454: pl. 2: 1—4.

Revised diagnosis. — Left and right compound jaws flat, composed of very thin walls, with the main ridges anteriorly turning outwards. The laeobasal ridge denticulated, directed posteriorly, considerably longer than a half of the length of the entire jaw, with the first denticle much larger than the remaining ones. The basal ridge very finely denticulated, equalling about one third of the right compound jaw.

Table 1
(see p. 75)

Species	Type and number of jaws	Age	Lithology	Locality	Collection number
M. fragilis Szan., emend.	13 MIl (6 polypharate) 7 MIr (3 polypharate)	U.? Ordovician (see Szaniawski 1970)	see Szaniawski 1970	borehole Mielnik IG 1	ZPAL No.Sc.I/13-20
„	MIl	Silurian (Chitinozoa)	dark grey, marly limestone	erratic boulder (Orzechowo, prov. of Słupsk)	MZ VIII.0(19p)1
„	7 MIl (1 double pharate) 2 MIr	U. Ordovician (*Discograptus schmidti* Wim.)	similar to Baltic limestone	„	MZ VIII.0(24p)1-3
„	27 MIl (1 double and 3 single pharate) 13 MIr (1 double and 1 single pharate)	Llanvirnian, Kunda St., Aluoja Subst. (conodonts)	light grey, compact limestone	„	MZ VIII.0(42p)1-8
„	MIl	Llanvirnian, Lasnamägi St. (condonts)	light grey coarse grained limestone	„	MZ VIII.0(63p)2
„	MIl	U.? Llanvirnian (conodonts)	dark grey, organogenic limestone	„	MZ VIII.0(105p)1
„	MIl	Ordovician (*Parachitina curvata* Eis.)	similar to Baltic limestone	„	MZ VIII.0(110p)1
„	MIl	Ordovician (*Rhabdohydra tridens* Kozł)	„	„	MZ VIII.0(116p)1
„	MIr	Ordovician or Silurian	dark grey, coarse grained limestone	„	MZ VIII.0(117p)1
„	MIl	Ordovician? (*Pistoprion* sp.)	similar to Baltic limestone	„	MZ VIII.0(120p)1

Species	Type and number of jaws	Age	Lithology	Locality	Collection number
M. ex gr. *trapezoidea* Kielan-Jaworowska	single pharate: MIr, 3 ant. teeth, 1 lat.? tooth	Silurian? (numerous paulinitid jaws)	dark grey, middle grained limestone	erratic boulder (Warszawa)	MZ VIII.0(17p)1
Gen. et sp. indet. 1	single pharate ?ant. tooth, double pharate ?ant. tooth	Llanvirnian, Kunda St., Aluoja Subst. (conodonts)	light grey, compact limestone	erratic boulder (Orzechowo, prov. of Słupsk)	MZ VIII.0(42p)31-32
Gen. et sp. indet. 2	single pharate jaw	Caradocian (conodonts)	similar to Baltic limestone	,,	MZ VIII.0(65p)2
Gen. et sp. indet. 3	single pharate tooth	Ordovician?	,,	,,	MZ VIII.0(50p)1
Gen. et sp. indet. 4	quadruple pharate tooth	Ordovician (*Desmochitina minor ovulum* E.)	dark grey, organogenic limestone	,,	MZ VIII.0(102p)1
Gen. et sp. indet. 5	,,	Ordovician (*Parachitina curvata* Eis.)	similar to Baltic limestone	,,	MZ VIII.0(120p)2
Gen. et sp. indet. 6	double pharate jaw	U. Ordovician (*Discograptus schmidti* Wim.)	,,	,,	MZ VIII.0(24p)4

The second ridge arcuate, situated in the anteroinner corner of jaw, directed posteromedially, very fine denticulated. Lateral? teeth shaped like thin claws. Anterior part of the apparatus unknown.

Denticle formula:

Left compound jaw		Right compound jaw	
laeobasal ridge	15—18	basal ridge	16—23
main ridge	13—17	main ridge	15—20
		second ridge	10—14

Revised description. — Jaws very thin and transparent, 0.48 to 1.78 mm in length. Teeth of main ridges and some anterior teeth of laeobasal ridges darker and opaque. Due to their fragile structure jaws frequently preserved incomplete.

Left compound jaw flat, with a fairly strongly elevated main ridge and long laeobasal ridge parallel to it. Anterior margin of the jaw very wide and rounded. Posterior margin narrow, but also rounded. Inner margin straight, only in its anterior and posterior sections deflected outwards. Outer margin, rarely preserved, usually running irregularly as a result of a gradual turning of the jaw into a non-hardened pharyngeal cuticle. Jaw proportions variable: its width-to-legnth ratio fluctuates from 1:2.4 to 1:3.4. Jaw is the widest near the anterior margin and more or less conspicuously tapering posteriorly.

Main ridge denticulated over the entire length, in its anterior part strongly deflected outwards. This deflection may be so distinct that, in extreme cases, the anterior section of the main ridge happens to be nearly perpendicular to the remaining part of the ridge. Some anterior teeth very large and obtusely terminating, the remaining ones distinctly smaller, sharply terminating and gradually diminishing posteriorly. Teeth slightly deflected posteriorly and, except for those in the anterior section of the main ridge, outwards. A small cusp is frequently situated before the first tooth or, strictly speaking, on its slope.

Laeobasal ridge long, parallel to the main ridge, making up 0.65 to 0.72 of the entire length of jaw. The first tooth very large, conical, frequently equaling in size the largest teeth of the main ridge. The remaining teeth distinctly smaller, gradually diminishing posteriorly. The base of laeobasal ridge situated at the same level as that of the main ridge. Frequently, the first tooth and, now and then, also some subsequent teeth are not connected ventrally by a common groove, which connects the cavities of teeth in the remaining section of the laeobasal ridge.

Right compound jaw is, like the left one, fairly flat and, in addition to the main ridge, has not very high second and basal ridges. The track of the margin and proportions approximately the same as in the left compound jaw.

Main ridge makes up a sort of a mirror image of that in the left jaw.

Second ridge in the form of an arch situated off the place in which the inner margin of the jaw, deflecting outwards, turns into an arcuate anterior margin. The groove, connecting ventrally the cavities of teeth, is poorly developed and gradually disappears posteriorly. Its length constitutes about 0.25 to 0.30 of the length of the entire jaw.

Basal ridge delicate, parallel to main ridge, making up about 0.33 to 0.35 of the length of the entire jaw.

Two long lateral (?) teeth (ZPAL No. Sc. I/18; Szaniawski 1970: pl. 2: 4*a*) have been preserved in one of the left compound jaws from Mielnik.

As compared with other Mochtyellidae, the left and right compound jaws frequently occur as mono- or polypharate jaws. The packing of secondary in primary jaws is usually fairly compact. The teeth of the main and laeobasal ridges exactly penetrate the interiors of overlying teeth, while those of second and basal ridges do not mesh with each other or do but only to an insignificant extent. The number of secondary jaws in a primary jaw varies from one to eight. There is no relationship between the size of jaw and the presence of secondary jaws in it. The primary and secondary jaws are more or less identical in thickness (pl. 19: 3-5).

Variability. — It is expresse mostly in the number of teeth on jaws, proportions of jaws and extent of the bend of the main ridges. The material, coming from the erratic boulders, is marked by a lower degree of the complexity of structure of pharate jaws. The number of secondary jaws in pharate jaws from erratic boulders MZ/24 and MZ/42 varies within the limits of 1 and 3, whereas in those from the Mielnik borehole — of 3 and 8. These differences are probably of the nature of the interpopulation variability, the more so strongly marked as the populations under study are not only allochthonous, but also allochronic in character. The lack of pharate jaws with 1 to 2 secondary jaws in the materials from Mielnik should be considered as accidental and resulting in part from a poor state of their preservation.

The poor state of preservation may seemingly increase differences between jaws. This usually results from breaking off parts of jaws along the inner and outer margins, which causes an apparent gracilization.

Remarks. — Two new species of the Mochtyellidae were erected by Szaniawski (1970) on the basis of twenty detached jaws, almost all of them poorly preserved coming from the Upper (?) Ordovician of the Mielnik borehole. They were *Mochtyella fragilis* Szaniawski, 1970 and *Mochtyella multilamellata* Szaniawski, 1970. Their original descriptions included remarks on the impossibility of confusing the jaws of these species with those of other taxons, resulting from their specific morphology and the structure of their walls. According to Szaniawski, *Mochtyella fragilis* differed from other species of the genus *Mochtyella* Kielan-Jaw. in its thin walls, considerable length of laeobasal plate (not larger, however, than in *M. trapezoidea* Kielan-Jaw. — my remark, P. M.), strong bend of main ridge and a frontal situation of second ridge. Also in that author's opinion, *M. multilamellata* differed from *M. fragilis* only in a "lamellar" structure of its walls and in a lack of the second ridge.

The materials I collected from the erratic boulders and its comparison with the type material revealed that what was described under the name *M. multilamellata* were actually polypharate jaws of *M. fragilis*. The alleged lack of the second ridge on the jaws of *M. multilamellata* was a result of basing the original description on MIr of this species on three incomplete jaws, only one of which had a basal ridge and a complete main ridge. Two pharate MIr (pl. 16: 1), which I found, correspond morphologically to the original diagnosis of *M. fragilis* given by Szaniawski (1970: 453), but have a "lamellar" structure (that is, secondary jaws) like that in *M. multilamellata*. A diagnostic importance is ascribed by Szaniawski (1970) to a strongly developed first tooth of the laeobasal ridge of *M. fragilis*, but an identically developed tooth I also occurs in the holotype of *M. multilamellata* (cf. Szaniawski 1970: pl. 2: 4*a*), which has not been taken into account either in the diagnosis, or description of this species. The holotype of *M. multilamellata* is a triple polypharate MIl. I found an identically developed MIl, as a triple polypharate jaw, in the materials from erratic boulder MZ/42, which is an additional confirmation of the conspecificity of the materials from the erratic boulders and those from Mielnik.

According to Article 24 of the International Code of Zoological Nomenclature, the specific names *Mochtyella fragilis* Szaniawski, 1970 and *Mochtyella multilamellata* Szaniawski, 1970 should be considered as simultaneously published names. Under these circumstances, I maintain the former name as valid for the taxon discussed.

A conspicuous numerical predominance of MIl over MIr attracts attention in the materials coming from Mielnik and from the erratic boulders.

M. fragilis Szan. differs from the remaining species of the genus *Mochtyella* Kielan-Jaw. in a distinct flattening of jaws, their small thickness, strong bend of the main ridge and a relatively large frequency of its occurrence in the form of pharate jaws.

It is very likely, that the anterior teeth of this species are described below under the name Gen. et sp. indet. 1.

Geographical distribution and stratigraphic range. — Poland, Llanvirnian through Upper Ordovician, Silurian? (erratic boulders), Upper? Ordovician (the borehole at Mielnik on the Bug).

Mochtyella ex gr. *trapezoidea* Kielan-Jaworowska, 1966

(pl. 17)

Description. — The material was etched out in the form of detached jaws, which, however, come almost for certain from one and the same apparatus, as indicated by the facts that they strongly differ in size from the remaining scolecodonts, found in erratic boulder MZ/17, that they fit to each other and that their myocoeles contain identically developed secondary jaws. MIr is a compound jaw, laterally flattened and resembling that of the Silurian *Mochtyella trapezoidea* Kielan-Jaworowska, 1966, from which it differs in a more strongly marked denticulation of the basal ridge. Main ridge formed by 13 teeth, with its posterior section indistinctly denticulated. Basal ridge distinct, having 5 teeth and equaling about 0.2 of the length of the main ridge. Second ridge not developed. MIl incomplete (lacking the laeobasal ridge), also flattened laterally, broken to pieces during preparation. Anterior teeth provided with four tips, the first of them the largest, the second distinctly smaller, while the third and fourth are only marked in the form of small elevations. They resemble the anterior teeth of *M. trapezoidea*. A single tooth, accompanying the elements mentioned above, is in all likelihood a lateral tooth. The secondary jaws, embedded in myocoeles, are distinctly thinner than the primary ones with which they contact only slightly.

Incertae familiae

Gen. et sp. indet. 1

(pl. 18: 1)

Description. — Jaws resembling anterior teeth of *Mochtyella trapezoidea* and the forms described above. One of them is a single, the other a double pharate jaw. Secondary jaws are identical in thickness with primary ones. They are transparent even without discoloration and their contact is fairly close.

Remarks. — It seems quite likely that the jaws described are so far unknown anterior teeth of *Mochtyella fragilis*. They occur in a considerable number in the residue after boulder MZ/42, which abounded in jaws of this species. They are similar to each other in a small thickness of walls and fairly close packing of secondary jaws.

Gen. et sp. indet. 2

(pl. 18: 2; pl. 19: 2)

Description. — A fragment of an arcuate jaw with a widely open myocoele. Secondary jaw nearly twice as thick as the primary one. They contact each other fairly closely.

Remarks. — The fragmentary state of preservation precludes any discussion of its situation in the jaw apparatus and even an approximate identification of its taxonomic position.

Gen. et sp. indet. 3

(pl. 18: 3; pl. 19: 6)

Description. — Tooth, flat, subtriangular in outline, with a wide base and strongly bent tip. Secondary and primary teeth equal in thickness, closely packed, damaged as a result of the burrowing activity of saprophytic microorganisms.

Remarks. — A specimen deceptively resembling in shape the lateral teeth of *Mochtyella* Kielan-Jaw. and *Pistoprion* Kielan-Jaw., as well as some anterior teeth of *Tetraprion* Kielan-Jaw.

Gen. et sp. indet. 4

(pl. 18: 4)

Description. — Quadruple pharate tooth, triangular in outline and in transverse section, devoid of base. Four secondary tooth, embedded in primary tooth are approximately identical in thickness and very closely packed.

Remarks. — The location of the tooth within the apparatus and even approximate identification of the systematic position are impossible.

Gen. et sp. indet. 5

(pl. 18: 5; pl. 19: 1)

Description. — Quadruple pharate tooth slightly bent, oval in transverse section, devoid of base. Primary tooth distinctly thinner than the secondary ones. Contact very close.

Remarks. — Cf. remarks on Gen. et sp. indet. 1.

Gen. et sp. indet. 6

(pl. 18: 6)

Description. — Double pharate jaw of the cheiridogenys type. Myocoele open, attachment lamella distinctly marked. The first, so-called precuspidate, tooth distinctly smaller than the rest of them and situated somewhat laterally. The remaining four teeth large, bluntly terminating, gradually diminishing posteriorly. Contact between the secondary jaws and primary one fairly close, walls equal in thickness, slightly transparent.

Remarks. — A jaw resembling MIVr of *Polychaetaspis wyszogrodensis* Kozł., illustrated by Szaniawski (1970: pl. 4: 1*f*), from which it differs only in a smaller number of teeth (five not six). A considerable homeomorphy of jaws of this type in the Eunicida precludes the possibility of assigning them to the Polychaetaspidae. It is, however, very likely that this jaw comes from a labidognath apparatus, which seems to be confirmed by studies on it conducted by means of a transmission electron microscope (G. Mierzejewska, oral communication).

DISCUSSION

I agree with Kielan-Jaworowska's (1966) statement that the existence of pharate jaws shows that the jaws of some Lower Paleozoic Eunicida were replaced during ontogeny. Schwab (1966) considered such an interpretation of pharate jaws as hardly acceptable, since the jaws of the Recent Nephtyidae and Glyceridae have fairly distinct growth lines. Such lines were also described on the jaws of the Nephtyidae (Kirkegaard 1970, Retière 1976). However, the families mentioned above represent the order Phyllodocida, whose phylogenetic relationships with the Eunicida are very remote as found by anatomical studies (Dales 1962) and confirmed by biochemical examination of jaws (Voss-Foucart *et al.* 1973, Jeuniaux 1975). The occurrence of growth lines on the jaws of the Nepthyidae, Nereidae and Glyceridae indicates that their growth took place by an increase in base at the expense of the adjacent pharyngeal cuticle. Thus, it is a typical growth by apposition. However, apart from the growth by apposition, the Phyllodocida also display the molting of jaws. It was found by Herpin (1926) in the course of a larval development of *Odontosyllis ctenostoma* Claparède (Syllidae). If the growth of the jaws of the Eunicida took place by apposition, the statement of such a fact would be very easy. The morphology of the eunicid jaws is frequently very complex and a possible increase in their dimensions at the expense of the adjacent pharyngeal cuticle would have considerable effects on changes in their shape. Such differences in the morphology of small and large jaws of specimens belonging to one and the same species have not been observed so far. Theoretically, there is the possibility of an increase in the dimensions of jaws by intussusception, that is, by the deposition of new substances between the existing ones. It is, however, precluded by biochemical changes occurring in jaws after their hardening (Mierzejewska and Mierzejewski, in press). This distinctly implies that any possible increase in the dimensions of jaws during ontogeny may occur in the Eunicida only by molting, that is, similarly as in the case of the arthropod cuticular organs.

The possibility of forming new jaws during the eunicid ontogeny was proved by the instance of Recent forms with a ctenognath (= polygnath) apparatus, that is, in the Dorvilleidae (Heider 1922, 1924; Jumars 1974). A certain difference occurs, however, between the replacement of jaws in the Dorvilleidae and the known cases of such a replacement in the fossil Eunicida. In the former, the appearance of new jaws underlying the old ones is a response to a mechanical damage of the old jaw apparatus (Jumars 1974). It is, therefore, a phenomenon of the nature of a reparative regeneration, probably stimulated in its first stage by what is known as "traumatic hormones". The reproduction of jaw apparatus in the Dorvilleidae's ontogeny has hitherto been described in four species, but in none of them the jaws were embedded in the myocoeles of old jaws. As follows from Heider's (1922) and Jumars' (1974) observations, new jaws are entirely sunken in the soft tissue underlying old ones. The only exception in this respect is the genus *Ophryotrocha* Claparède and Metschnikov, in which, as follows from Bonnier's (1893) observations, new jaws are formed next to old ones. A similar manner of developing new jaws might of course also occur in the early Paleozoic Eunicida, but the "double" jaw apparatus of this type had a slim chance to be preserved in fossil state. On the other hand, we may conclude from the known fossil materials that the jaw replacement of quite a different type, so far unknown in the Recent Polychaeta, occurred in the Paleozoic Eunicida, that is, new jaws were formed in the myocoeles of old ones. The existence of the polypharate jaws precludes the possibility of interpreting this replacement as a reparative regeneration and induces us to explain it as a cyclic physiological regeneration, probably controlled by the hormones of the central nervous system.

Such an interpretation of the replacement of jaws in the fossil Eunicida irresistibly leads one to compare it with the molting of the Arthropoda. In the arthropods, there occurs a stage called pharate instar (Hinton 1946), in which an individual is yet covered by an old cuticle despite the fact that a new one has already been developed under it. Single pharate jaws of the Eunicida correspond to this stage. Polypharate jaws of the Eunicida constitute a specific instance of molting: in several cases, the apolysis (the loss of direct contact between the jaw and the underlying epithelium) was not followed by the ecdysis (casting-off the old jaw).[2] On the basis of data found in literature, I suppose, that a similar process may also occur in the Onychopora.

The anterior intestine of the Onychophora is also provided with teeth resulting from the transformation of the pharyngeal cuticle. The teeth and the pharyngeal cuticle, together with the cuticle covering the body and claws, molt every other week and are replaced by new forms (Robson 1964). The teeth and claws of the Onychophora marked by an identical structure as that of the polypharate of the Eunicida were also described (Bouvier 1905, Schwab 1966). Since the cuticle of the Onychophora is not multilamellar (Robson 1964) the occurrence of the polypharate jaws and claws in them may only be explained by the suspension of ecdysis for several stages of molting in succession.

The occurrence of an identical abnormality in the molting of the fossil Eunicida and the Recent Onychophora may be of interest from the phylogenetic viewpoint. In view of the occurrence of indubitably close phylogenetic relationships between the Annelida and Onychophora, we may interpret this phenomenon as a specific atavism. On the other hand, we

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[2] Such a manner of molting has hitherto been known only in the ostracods of the suborder Eridostraca and in the Conchostraca (cf. also Adamczak 1961).

cannot, however, preclude the possibility that it was formed independently in the two groups. Unlike the apolysis, the ecdysis in the arthropods is not a process controlled by hormones (Jenkin 1966) and it seems very likely that the pharate jaws in the Onychophora and Eunicida were formed as a result of a mechanical wedging of new in the interior of old forms. Likewise, there is the possibility that in the process of a subsequent molting the accumulated exuvia might be cast off in the form of pharate jaws as follows from my finding, presented above, and according to which the size of the jaws of *Mochtyella fragilis* Szan. is irrelevant to the occurrence in the pharate stage, or number of secondary jaws.

The possibility that forming pharate jaws in the Eunicida was conditioned genetically seems to be well founded. According to so far available data, *Mochtyella fragilis* Szan. formed in the Llanvirnian at most triple pharate jaws, but in the Upper (?) Ordovician — even octuple ones.

It seems very likely that the molting of jaws was in the Eunicida, having jaw apparatus of the placognath type, a typical phenomenon. The fact that the findings of pharate jaws in fossil state are rare should be ascribed to the following conjectural causes:

(1) Similarly as in the Arthropoda and Onychophora, the apolysis and ecolysis could occur so rapidly that the possibility of an organism's death precisely in the pharate state is rather small.

(2) In the few individuals which died before the ecdysis, the pharate jaws might be divided into single jaws during the decomposition of the carcass and as a result of the movement of bottom sediments.

(3) The pharate jaws embedded in rocks may be divided as the rock is etched or as its residue is washed out.

Frequently, the existence of polypharate jaws may have nothing in common with the process of growth of jaw apparatus. A cyclic molting of cuticle not related with the changes in the organization or size of an organism (Wigglesworth 1969: 124) is known in Recent primitive insects of the order Thysanura.

So far, there is no proof that the molting of jaws could occur in other fossil Eunicida besides the placognath forms. However, there are certain indications (cf. p. 100) that also some anterior elements of labidognath apparatus could occur in the form of pharate jaws. The possibility of forming pharate jaws by elements having partly covered myocoeles is rather improbable. If such would be the case, the formation of a new jaw could take place only after casting-off an old one (cf. Heider 1924). This seems to be confirmed by Ehlers' (1864—1868) and Kielan-Jaworowska's (1966) observations of incipiently developed jaw apparatus in adult individuals of Recent Eunicida.

It can be expected that studies on pharate jaws conducted by means of transmission electron microscopes will give essential information on the mechanism of jaw replacement in the fossil Eunicida. As suggested by preliminary results of such observations (Mierzejewski and Mierzejewska, 1978), the molting of jaws was accompanied by a partial resorption of their inner layers.

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PIOTR MIERZEJEWSKI

LINIENIE SZCZĘK WCZESNOPALEOZOICZNYCH EUNICIDA (ANNELIDA, POLYCHAETA)

Streszczenie

Z materiałów pochodzących z głazów narzutowych opisano ordowickie i sylurskie szczęki wieloszczetów (Polychaeta) z rzędu Eunicida, mające w swych myocelach jedną lub kilka szczęk wtórnych. Większość opracowanych skolekodontów reprezentuje najprawdopodobniej Eunicida o plakognatycznym typie aparatów szczękowych. Nie jest jednak wykluczone, iż szczęka opisana jako Gen. et sp. indet. 6 pochodzi z aparatu labidognatycznego. Opisane materiały sugerują, że linienie szczęk, przynajmniej u niektórych wieloszczetów wczesnopaleozoicznych, zachodziło wielokrotnie w toku ontogenezy i niekoniecznie wiązało się z procesami wzrostu. Taki typ linienia, mający charakter cyklicznej regeneracji fizjologicznej, nie został opisany dotąd u wieloszczetów współczesnych (znane przypadki wymiany szczęk u współczesnych Eunicida reprezentują regenerację reparatywną). Brak odrzucania starych szczęk po utworzeniu nowych był prawdopodobnie efektem mechanicznego zaklinowania się jednych elementów w drugich. Na podstawie danych literaturowych wysunięto przypuszczenie, że identyczny proces występuje u współczesnych Onychophora.

Przeprowadzono rewizję gatunku *Mochtyella fragilis* Szaniawski, 1970. Wykazano, iż szczęki tego gatunku mające w myocelach szczęki wtórne, zostały opisane jako odrębny gatunek pod nazwą *Mochtyella multilamellata* Szaniawski, 1970.

ПИОТР МЕЖЕЙЕВСКИ

ЛИНЬКА ЧЕЛЮСТЕЙ РАННЕПАЛЕОЗОЙСКИХ EUNICIDA (ANNELIDA, POLYCHAETA)

Резюме

Из материалов, найденных в эрратических валунах, были описаны ордовицкие и силурские челюсти многощетинковых (Polychaeta) из отряда Eunicida, имеющих в своих миоцелях одну или несколько вторичных челюстей. Большая часть исследованных сколекодонтов представляет собой, вероятно, Eunicida с плакогнатическим типом челюстного аппарата. Однако не исключено, что челюсть, описанная как Gen. et sp. indet. 6 принадлежит к лабидогнатическому типу. Описанные материалы указывают, что линька челюстей, а по крайней мере, у некоторых многощетинковых раннего палеозоика, происходила многократно во время онтогенеза и необязательно была связана с процессом роста. Такой тип линьки, имеющей характер циклической физиологической регенерации, не был до сего времени описан у современных многощетинковых (известные примеры смены челюстей у современных Eunicida представляют собой репаративную регенерацию). Отсутствие процесса образования новых было вызвано, вероятно, эффектом механического заклинирования одних элментов в другие. Основываясь на литературных данных, была предложена гипотеза, что такой же процес происходит у современных Onychophora.

Была произведена ревизия вида *Mochtyella fragilis* Szaniawski, 1970. Показано, что челюсти этого вида имеют в миоцелях вторичные челюсти, которые были описаны как отдельный вид под названием *Mochtyella multilamellata* Szaniawski, 1970.

EXPLANATION OF THE PLATES

All figures, excluding pl. 19, fig. 3, are SEM micrographs.
Abbreviations: *N* primary jaw, *N+1* first secondary jaw, *N+2* second secondary jaw, etc.

Plate 16

Mochtyella fragilis Szaniawski, 1970, emend.

1. Specimen no. MZ VIII.0/42p/2, double pharate right compound jaw (MIr), *a* left lateral view, ×300, *b* fragments of second ridges of primary (*sr*) and secondary (*s'*, *sr''*) jaws, left lateral view, ×900, Llanvirnian (Kunda Stage, Aluoja Substage), erratic boulder MZ/42 (Orzechowo).
2. Specimen no. MZ VIII.0/42p/3, right compound jaw devoid of second ridge, dorsal view, ×200, Llanvirnian (Kunda Stage, Aluoja Substage), erratic boulder MZ/42 (Orzechowo).

3. Specimen no. MZ VIII.0/42p/1, double pharate left compound jaw (MIl), left lateral view, ×200, Llanvirnian (Kunda Stage, Aluoja Substage), erratic boulder MZ/42 (Orzechowo).
4. Specimen no. MZ VIII/24p/1, single pharate left compound jaw (MIl), ventral view, ×200, Upper Ordovician, erratic boulder MZ/24 (Orzechowo).

Plate 17

Mochtyella ex gr. *trapezoidea* Kielan-Jaworowska, 1966, MZ VIII/17p/1, Silurian, erratic boulder MZ/17 (Warszawa): *1a* single pharate anterior tooth, ×60, *1b* single pharate anterior tooth, ×75, *1c* single pharate anterior tooth, ×100, *1d* single pharate lateral ? tooth, ×150, *1e* single pharate right compound jaw (MIr), right lateral view, ×60.

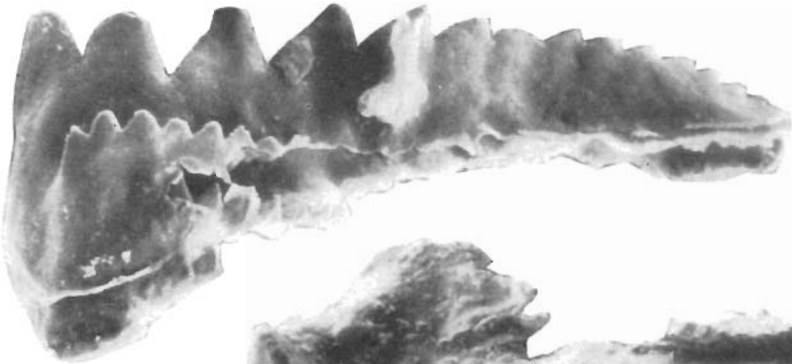
Plate 18

1. Gen. et sp. indet. 1, MZ VIII/42p/31, double pharate jaw (anterior tooth of placognath apparatus ?), ×180, Llanvirnian (Kunda Stage, Aluoja Substage), erratic boulder MZ/42 (Orzechowo).
2. Gen. et sp. indet. 2, MZ VIII/65p/2, fragment of a single pharate jaw, ×100, Caradocian, erratic boulder MZ/65 (Orzechowo).
3. Gen. et sp. indet. 3, MZ VIII/50p/1, single pharate tooth, ×160, Ordovician ?, erratic boulder MZ/50 (Orzechowo).
4. Gen. et sp. indet. 4, MZ VIII/102p/1, quadruple pharate tooth, ×60, Ordovician, erratic boulder MZ/102 (Orzechowo).
5. Gen. et sp. indet. 5, MZ VIII/120p/2, triple pharate tooth, ×60, Ordovician, erratic boulder MZ/120 (Orzechowo).
6. Gen. et sp. indet. 6, MZ VIII/24p/4, double pharate jaw, ×100, Upper Ordovician, erratic boulder MZ/24 (Orzechowo).
7. *Mochtyella fragilis* Szaniawski, 1970, emend., MZ VIII/42p/3, left compound jaw (MIl), dorsal view, ×200, Llanvirnian (Kunda Stage, Aluoja Substage), erratic boulder MZ/42 (Orzechowo).

Plate 19

Fragments of pharate jaws in great magnification.

1. Gen. et sp. indet. 5, MZ VIII/120p/2, triple pharate tooth, ×600, Ordovician, erratic boulder MZ/120 (Orzechowo).
2. Gen. et sp. indet. 2, MZ VIII/65p/2, single pharate jaw, ×1250, Caradocian, erratic boulder MZ/65 (Orzechowo).
3. *Mochtyella fragilis* Szaniawski, 1970, emend., posterior part of sixtuple pharate left compound jaw (MIl), ×280, Upper ? Ordovician, Mielnik borehole.
4. *Mochtyella fragilis* Szaniawski, 1970, emend., MZ VIII/42p/1, double pharate left compound jaw (MIl), ×1000, Llanvirnian (Kunda Stage, Aluoja Substage), erratic boulder MZ/42 (Orzechowo).
5. *Mochtyella fragilis* Szaniawski, 1970, emend., MZ VIII/24p/1, single pharate left compound jaw (MIl), ×1000, Upper Ordovician, erratic boulder MZ/24 (Orzechowo).
6. Gen. et sp. indet. 3, MZ/VIII/50p/1, single pharate tooth, surface burrowed by saprophytic microorganisms, ×1000, Ordovician ?, erratic boulder MZ/50 (Orzechowo).



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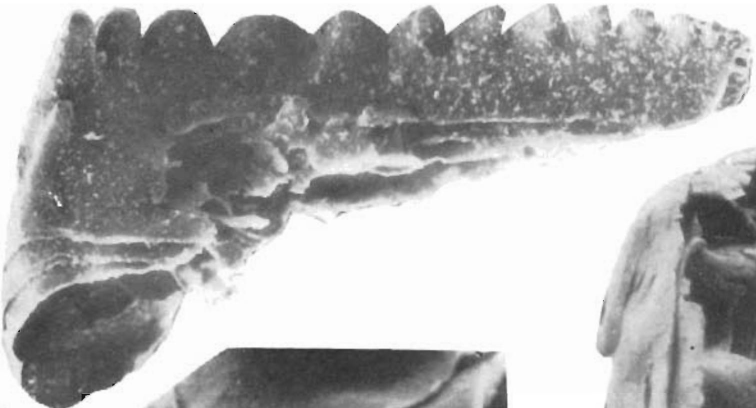

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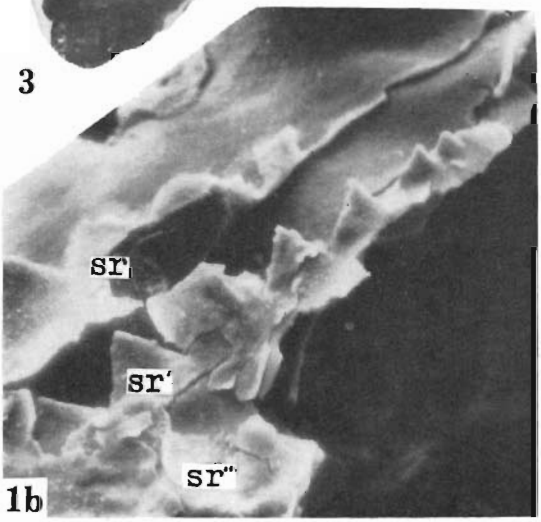

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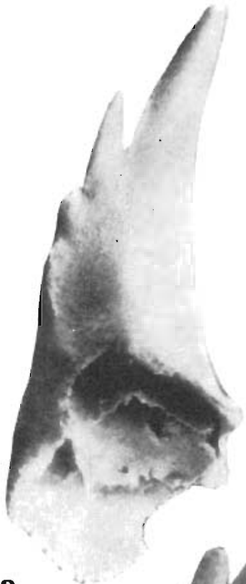

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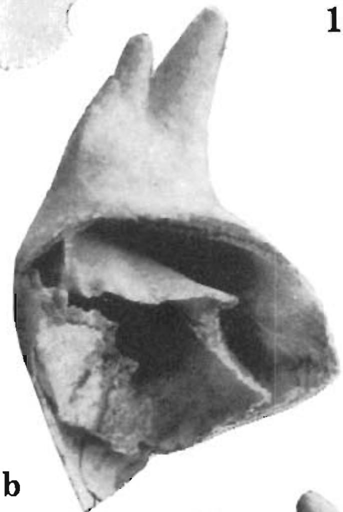

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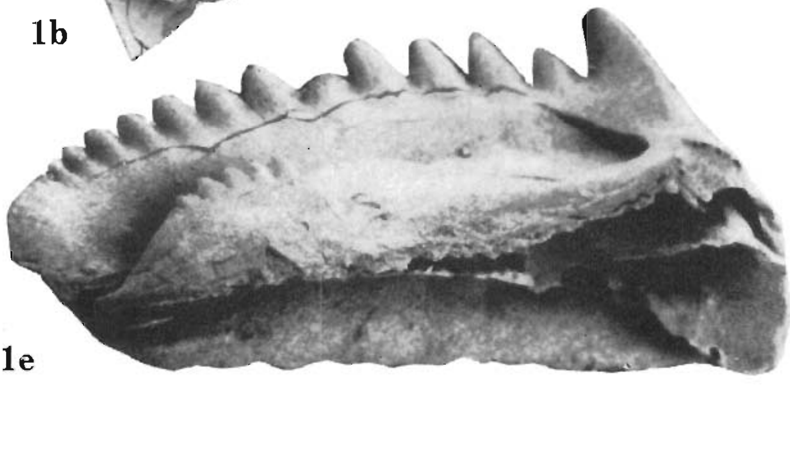

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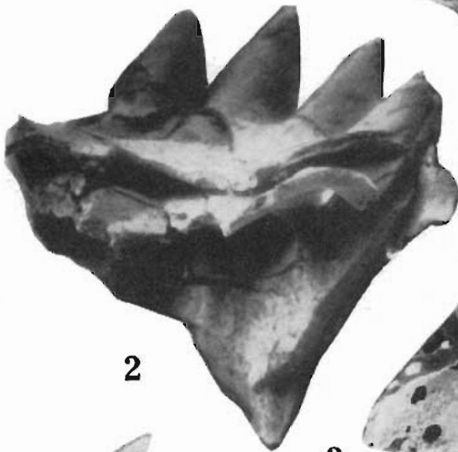
1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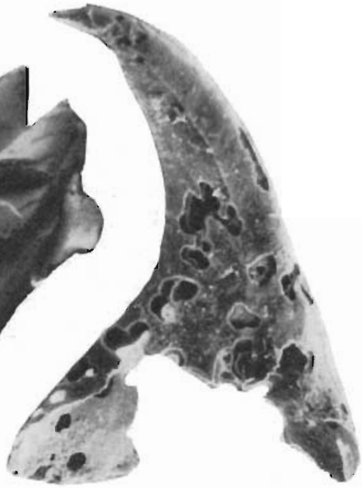
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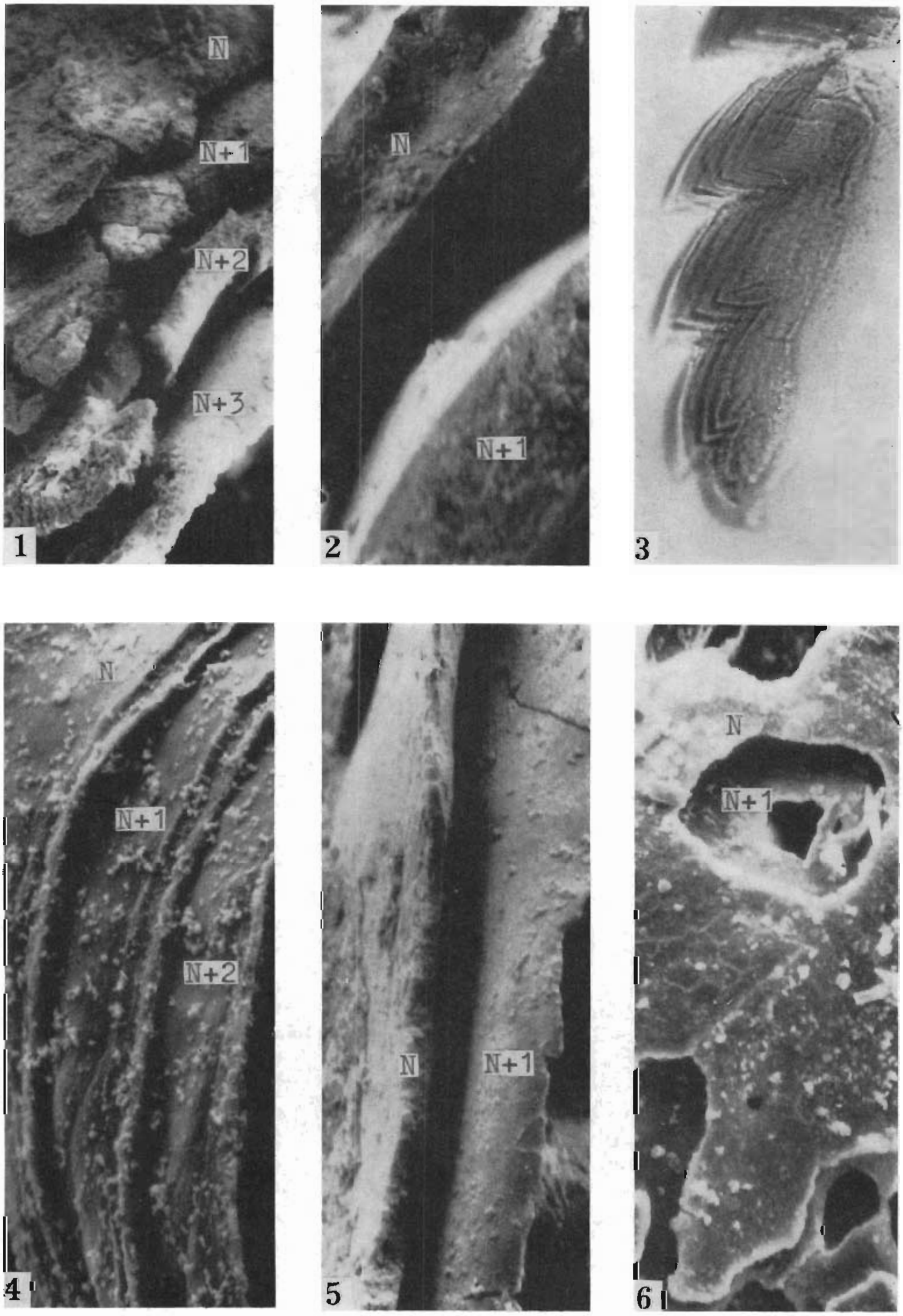
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