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## A RECONSTRUCTION OF THREE JURASSIC POLYCHAETE JAW APPARATUSES

*Abstract.*—From isolated scolecodonts three new species of jaw apparatuses of Jurassic polychaetes are reconstructed and described: *Schistomeringos expectatus* sp.n., *Arabella diversimaxillata* sp.n. and *Notocirrus compositus* sp.n. The reconstruction criteria are briefly discussed. The ultrastructures preserved on attachment surfaces of soft tissues of scolecodonts are described and shown to be very useful for the reconstruction of jaw apparatuses. Micromorphological comparison showed a striking similarity in structure between Jurassic and Recent jaws of the *Schistomeringos* Jumars.

## INTRODUCTION

Scolecodonts are much rarer in Mesozoic rocks than in the Paleozoic and until recently they were known from only a few reports which mainly dealt with the discoveries of imprints of the whole polychaetes (see: Ehlers 1868, 1869; Eisenack 1939; Roger 1946; Wetzel 1948). The intense study of Mesozoic scolecodonts in recent years (Kozur 1967, 1970, 1971, 1972; Gall and Grauvogel 1967; Wilczewski 1967; Corradini and Serpagli 1968; Deflandre and Taugordeau 1969; Zawidzka 1971, 1975; Charletta and Boyer 1974; Szaniawski 1974; Mierzejewska and Mierzejewski 1977), has mainly dealt with isolated scolecodonts since joined jaw apparatuses are extremely rare in rocks of that age. Up to the present only three apparatuses have been described: two from the Middle Triassic (Zawidzka 1971, 1975) and one from the Middle Jurassic (Szaniawski 1974) of Poland. However, there have also been described by Kozur (1967, 1970) and Zawidzka (1975) some joined jaws from the Middle Triassic. Wetzel (1948) and Corradini and Serpagli (1968) illustrated single Late Cretaceous jaw apparatuses without describing them. It follows that the knowledge of joined apparatuses is still very poor and it is unlikely that there will be any rapid improvement of the situation.

The natural systematics of isolated jaws of Eunicoidea is impossible without the knowledge of the apparatuses to which they belonged. In order to establish the appropriate systematics of isolated elements it is therefore necessary to reconstruct the apparatuses. This is greatly facilitated by the high similarity of Mesozoic jaw apparatuses to the recent ones, as well as usually relatively low specific differentiation of the apparatuses in a given locality. Moreover, the ultrastructural studies appeared to be very useful for such reconstructions.

The paper presents reconstruction of three jaw apparatuses of Jurassic polychaetes belonging to the recent genera of the superfamily Eunicoidea.<sup>1)</sup> The whole of the studied material was extracted using acetic acid from Upper Jurassic limestones, which were penetrated by the borehole Tłuszcz IG-1 (figs 1—2). Numerous scolecodonts were found in white

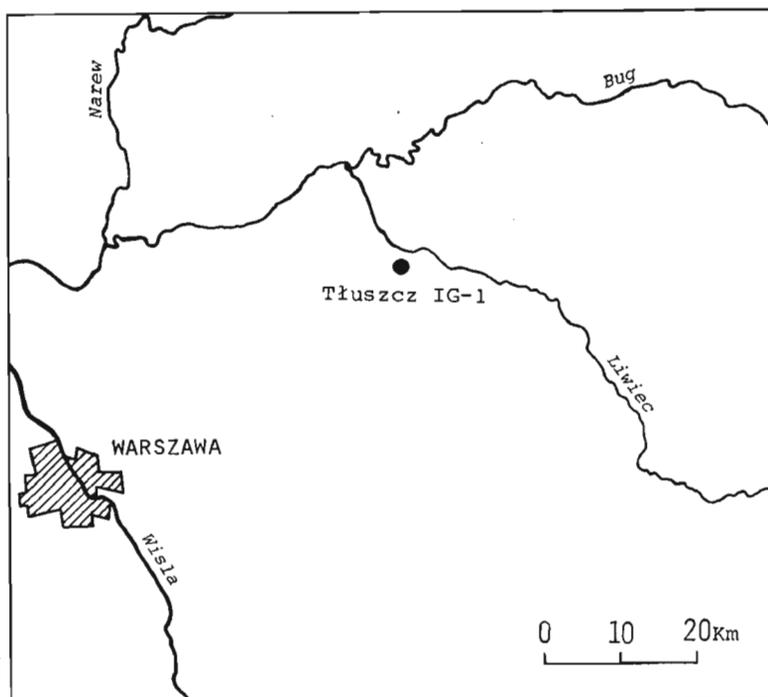


Fig. 1. Location map of the borehole Tłuszcz IG-I.

chalky limestones yielding fairly rich assemblage of corals, gastropods and pelecypods as well as numerous internal linings of foraminifers of the family Nodosariidae, Discorbidae and Epistominidae (see also Gaździcki in preparation), from the depth interval 845—871 m. About 60 kg sample of core material of limestones derived from the depth interval was dissolved. It yielded about 281 well preserved scolecodonts, 254 of

<sup>1)</sup> According to the systematics of Recent polychaetes of Banse and Hobson (1974).

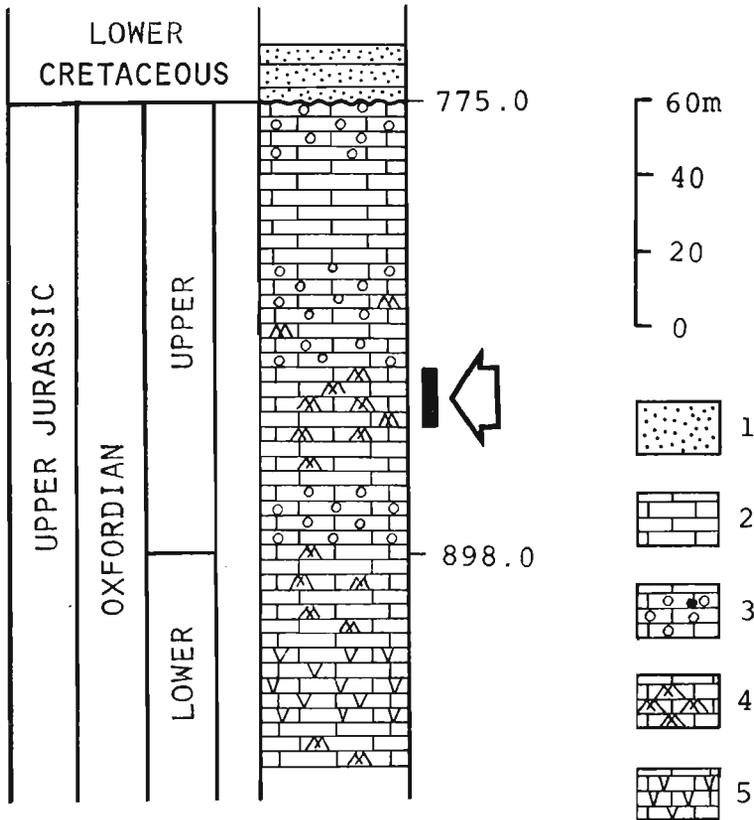


Fig. 2. Detailed profile of the Upper Jurassic deposits from the borehole Tłuszcz IG-I. 1 sandstones, 2 limestones, 3 oolitic limestones, 4 coral limestones, 5 spongy limestones. Arrow head indicates scolecodont-bearing horizon.

which were assigned to the reconstructed apparatuses. The majority of the remaining scolecodonts belong to polychaetes of the superfamily Glyceroidea, which are devoid of composite jaw apparatuses.

Scolecodonts were also found in other Middle and Upper Jurassic horizons, in the profile of the borehole Tłuszcz IG-1 but in numbers insufficient for the analysis.

The material studied is housed in the Institute of Paleobiology of the Polish Academy of Sciences (abbr. ZPAL) in Warsaw.

All the SEM micrographs were made in the Laboratory of the Elektron Microscopy of the Institute of Experimental Biology of the Polish Academy of Sciences in Warsaw.

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## THE PRINCIPLES OF RECONSTRUCTION OF APPARATUSES

Up to the present only three of fossil polychaete jaw apparatuses have been reconstructed on the basis of their isolated elements (Szaniawski 1968, Kozur 1972, Corradini and Olivieri 1974). However, it is fairly possible that the improving knowledge of scolecodonts will help making such reconstruction on much greater scale.

The reconstructions are very important as they markedly contribute to unification of the systematics of fossil polychaetes. However, much caution is necessary as erroneous reconstructions may lead to chaos in the systematics. The reconstructions should be carried out using rich and well-preserved material, as well as several criteria briefly discussed here:

1. The similarity of structural plan to that of already known of either the recent or the joined fossil apparatuses. Of course, the existence of fossil apparatuses markedly different from all the apparatuses hitherto known cannot be excluded but such apparatuses, if they existed, were rare and therefore a special caution is necessary in their eventual reconstruction.

2. All the elements of reconstructed apparatus should fit to each other in the reconstruction. For example right MII of the apparatus *Arabella diversimaxillata* sp.n. displays a longitudinal wide furrow on dorsal side which corresponds to hook of right MI whilst, at the same time, the shank of the same MII is sufficiently long to embrace MI.

3. The similarity of some morphological details from different elements. A detailed morphological analysis of apparatuses usually shows that despite differences in shape all the elements or at least jaws of particular pairs have some characteristic morphological details in common. Shape and relative length of denticles may serve as an example. In the case of the above mentioned apparatus of *Arabella diversimaxillata* sp.n. an example of such characteristic features is seen in the sharp ridges on the apical portion of hooks of both MI and on the biggest denticles of all the remaining jaws.

4. Statistical data. Quantitative ratios of co-occurring elements of a given type of apparatus are usually approximately constant. Larger and stronger built elements are as a rule more numerous.

The jaws MI and MII are usually most numerous but may be highly variable in number. In the apparatus of *Arabella diversimaxillata* sp.n. right MI are markedly less numerous than the left ones as the former are more slender and, therefore, easier to be broken than the latter. In turn, in the apparatus of *Notocirrus compositus* sp.n. the right MII are most numerous and at the same time the largest. The quantitative predominance of large elements may be related to selection during transportation and their greater strength. To a some degree it may also result

from overlooking of smaller elements during picking the scolecodonts from residue.

5. The ultrastructural studies appear to be very useful in the reconstructions. The present studies were limited to structures seen on the surface of pulp cavities of jaws and on the ventral surface of carriers, the analysis of which does not require complex preparation nor destruction of specimens. The studies revealed the presence of structures of the same type on surfaces of pulp cavities of all the jaws and on ventral surfaces of carriers belonging to apparatuses of a single species. Thus these studies confirmed the validity of reconstructions made using other criteria. The ultrastructural studies may be useful for reconstructions only in the case of well-preserved material.

None of these criteria can be considered as sufficient when used separately. The reconstructions are most reliable when a scolecodont assemblage from a given locality is rich in individuals but poor in species. Elements of apparatuses described in the present paper represent 98% of all eunicid scolecodonts from the collection and 85% of them belong to apparatuses of *Arabella diversimaxillata* sp.n.

#### ULTRASTRUCTURES

The results of a few studies on ultrastructure of polychaete jaw apparatuses have been recently published (Strauch 1973; Corradini, Russo and Serpagli 1974; Mierzejewska and Mierzejewski 1975, 1977). This paper presents the first attempt to use these studies for taxonomic purposes in reconstructing jaw apparatuses on the basis of isolated elements.

Corradini, Russo and Serpagli (1974: 127) found that in jaws of Eunicoidea "the ventral side, inside the pulp cavity always shows a granular aspect given by numerous perforations intersecting the whole inner surface". Pulp cavities of some specimens also display a "polygonal network pattern" representing the surface structure at the sites of muscle attachment. Corradini et al. (in preparation) stated that the ultrastructure of pulp cavity surface in scolecodonts is highly variable and may be of certain importance for the taxonomy. The studies carried out by the present authors with the use of SEM included the ultrastructure of the surfaces of soft tissue attachment (pulp cavities of jaws and ventral surfaces of carriers) in several specimens of elements of the apparatuses *Arabella diversimaxillata* sp.n. and *Notocirrus compositus* sp.n. It appeared that the image of these surfaces makes it possible to discriminate elements belonging to different apparatuses. The image particularly depends on the preservation of the specimens but, the majority of specimens display characteristic structures for the species.

Elements of the apparatus *Arabella diversimaxillata* sp.n. display three systems of canals perpendicular to one another. The canals are regularly and densely spaced and about  $0,16\ \mu\text{m}$  in diameter. Two canal systems are parallel to the surface and are represented by narrow and shallow grooves in the surface (pl. 8: 2, 3b). The canals are often poorly visible on the surface and certain intersections may result in apparent deviations from the perpendicular arrangement of canals of the two systems. The third canal system is perpendicular to the surface and there can be noticed on it in a form of regular network of circular pores (pl. 8: 1, 2; pl. 9: 1b, 1c). The spacing of these canals only slightly exceeds their diameter. The three canal systems correspond to the  $\alpha$ ,  $\beta$  and  $\gamma$  canals in the terminology proposed by Corradini, Russo and Serpagli (1974) and are typical of the layer  $C_1$ , that is the fourth layer of wall (counting from the dorsal side). It means that the two latest layers,  $C_2$  and D, are not present in the region of the pulp cavity in jaws of *Arabella diversimaxillata* sp.n. The  $\alpha$ ,  $\beta$ , and  $\gamma$  canals most probably served for increasing the elasticity and strength of jaws. According to Mierzejewska and Mierzejewski (1975, 1977) they originated as a result of a breakdown of collagen fibrils.

The form of the above described surface structures is different for particular specimens or even parts of a single pulp cavity. All the canal systems or some of them may be obliterated. However, the structures may be found on a majority of the specimens and they are similar everywhere. A single left MII (pl. 9: 3) is here an exception as it displays entirely different structures, similar to the structures from pulp cavities of jaws *Notocirrus compositus* sp.n. described below. Independently of the canals, the pulp cavities in the majority of specimens of all the jaws and the ventral surfaces of carriers of the apparatus *Arabella diversimaxillata* sp.n. display a well-preserved polygonal network (pl. 8; pl. 9: 1, 2). The polygons represent depressions delimited by hexagonal raised boundaries, and are about  $7.0\ \mu\text{m}$  in length and  $4.0\ \mu\text{m}$  in width. According to Strauch (1973) and Corradini, Russo and Serpagli (1974) they are related to the configuration of the epithelial cells. The polygons are best preserved in the marginal parts of pulp cavities and, sometimes, almost throughout the pulp cavities.

Structures on the surface of pulp cavities of jaws from the apparatus *Notocirrus compositus* sp.n. are more differentiated. The canal systems described above are also marked here (pl. 10: 2; pl. 11: 1b, 1d), but they are not always visible. The characteristic structure of this apparatus, noted on almost all the jaws, is represented by irregularly distributed pores  $0.3\text{--}1.0\ \mu\text{m}$  in diameter, then markedly wider than the pores of  $\gamma$  canals. The pores represent openings of the canals described by Corradini, Russo and Serpagli (1974) as  $\phi$  canals. According to these authors they occur in the innermost layer of the wall, i.e. layer D and most probably contained nerves. The  $\alpha$ ,  $\beta$  and  $\gamma$  canals are lacking in the layer

D whilst these and the  $\varphi$  canals were found on several jaws of *Notocirrus compositus* sp.n. This means that the  $\varphi$  canals extend up to the layer  $C_1$  in jaws of the latter species. The layer  $C_2$  is not present at all in pulp cavity areas of jaws of that species and the layer D, when present, is greatly reduced and preserved on specimens on which  $\alpha$ ,  $\beta$ , and  $\gamma$  canals are not visible (pl. 10: 1). The openings of the  $\varphi$  canals occur here singly (pl. 10: 1, 3; pl. 11: 1b, 2) or in groups (pl. 10: 4; pl. 11: 1c). Within a single pulp cavity may occur both single openings and groups of openings. The former are more irregularly distributed. The distance between single openings or centres of groups of openings ranges from 3 to 7  $\mu\text{m}$ . The openings are circular in the marginal and central parts of pulp cavities, becoming elongate in the internal part close to pits of denticles (pl. 10: 4b; pl. 11: 1a). This results from the fact that the  $\varphi$  canals are perpendicular to the surface of the faces of the jaws and parallel to it in denticles, so they must be oriented oblique to it in the transitional zone, i.e. close to the denticle pits. The pores of the  $\varphi$  canals are equally well preserved in specimens where the systems  $\alpha$ ,  $\beta$  and  $\gamma$  are visible as well as when they are not visible. The polygon network on the pulp cavity surfaces in the jaws of *Notocirrus compositus* sp.n. is less strongly developed than on jaws of *Arabella diversimaxillata* sp.n. and visible only in the marginal parts of pulp cavities if at all (pl. 11: 1a).

It is still not entirely clear why pores similar to  $\varphi$  canals openings from the jaws of *Notocirrus compositus* sp.n. are marked on one left jaw MII from the apparatus *Arabella diversimaxillata* (pl. 9: 3). This may be explained in two ways: 1. this is the only specimen in which the layer D with its  $\varphi$  canals is preserved whilst the layer was eroded in all the remaining studied specimens or 2. this jaw does not belong to the apparatus *Arabella diversimaxillata* sp.n. in spite of the morphology which is identical to that of the remaining jaws MII of the apparatus. It should be noted here that the left MII from the apparatuses *Arabella diversimaxillata* sp.n. and *Notocirrus compositus* sp.n. are very similar to one another and, therefore, difficult to separate.

The ultrastructural studies also covered the pulp cavity surface of one jaw MII of the *Delosites* sp. (pl. 11: 3). The structures found there are different from those found in the representatives of the genera *Arabella* and *Notocirrus*. On the pulp cavity surface of *Delosites* there are mainly visible the openings of the  $\gamma$  canals characterized by their large diameter (0.15—0.35  $\mu\text{m}$ ) in relation to the distance between them (0.08—0.25  $\mu\text{m}$ ). The openings are apparently irregularly arranged except for the lower left corner in pl. 11: 3, where they are arranged in rows. The  $\alpha$  and  $\beta$  canals are very poorly visible on the studied specimen. The analysis of a single specimen is, however, insufficient for characterizing ultrastructures of a species.

The diagnostic value of ultrastructures from the surfaces of the soft

tissues attachments in scolecodonts cannot be estimated yet as the structures described above may repeatedly occur in several species. It is possible, however, to state that the ultrastructures are helpful in reconstructing apparatuses from isolated elements which is of a remarkable importance for the taxonomy.

#### SYSTEMATIC DESCRIPTIONS

##### Family **Arabellidae** Hartmann, 1944

*Remarks.*—The family Arabellidae is represented by recent forms allocated to about 65 species belonging to 8 genera (Fauchald 1970) and, up to the present, by a few species introduced for fossil isolated jaws from the Upper Cretaceous of the German Democratic Republic (Kozur 1970, 1972) and Middle Triassic of Poland (Zawidzka 1975). To that family may also belong isolated MI described from the Upper Cretaceous of the USA under the generic names *Arabellites* Hinde and *Drilonereisites* Eller by Charletta and Boyer (1974).

Attention should be paid to the marked similarity of jaw apparatuses of the family Arabellidae and those of the family Atraktoprionidae Kielan-Jaworowska, which is represented by 3 genera fairly common in the Paleozoic and Triassic rocks. The genus *Atraktoprion* Kielan-Jaworowska, which is best known of the latter, differs from apparatuses of the family Arabellidae by the presence of the basal plate and the lack of right MIII. The genus *Skalenoprion* Kielan-Jaworowska differs from Arabellidae by the presence of relic basal plate. Anterior jaws of apparatuses of this genus are not known and the jaws MI and MII are very similar to those of the recent genus *Drilonereis* Claparède in shape. The third genus of Atraktoprionidae, *Xanthoprion* Kielan-Jaworowska, is poorly known but it may be said that it resembles apparatuses of the family Arabellidae in paired MIII. A more detailed reconstruction of phylogeny of the families Arabellidae and Atraktoprionidae requires a much richer collection of fossil and especially Mesozoic apparatuses.

##### Genus *Arabella* Grube, 1850

##### *Arabella diversimaxillata* sp.n.

(pls 1—3, 8—9; fig. 4)

*Holotype:* Right MI figured on pl. 1: 3, ZPAL Sc. IV/3.

*Paratypes:* Left MI figured on pl. 1: 12, ZPAL Sc. IV/12 and right MII figured on pl. 2: 6, ZPAL Sc. IV/18.

*Type horizon and locality:* Jurassic, Upper Oxfordian, Central Poland, borehole Tłuszcz IG-1, depth 845—871 m.

*Derivation of the name:* Lat. *diversus* = different, *maxilla* = a jaw; alludes to the strong asymmetry of posterior jaws.

*Diagnosis.*—Posterior jaws of the apparatus strongly asymmetrical. Right MI with slender hook, longer than half of the jaw. Hook of MI left much shorter and wider. Right MII plate-like, much bigger than the left one, differs from it in shape and denticulation. MIII and MIV paired, subtriangular, denticulated. Paired carriers wide in anterior part, strongly narrowing posteriorly. MV and unpaired carrier unknown.

## Denticle formula:

MI	8—12	8—10
MII	8—12	12—14
MIII	6—7	7—8
MIV	6—7	5—7

*Material.*—34 of MI right, 56 of MI left, 39 of MII right, 33 of MII left, 26 of MIII and MIV right, 23 of MIII and MIV left, 4 incomplete carriers and 3 incomplete mandibles.

*Description.*—Length of MI right varies from 0.30 to 0.85 mm, MI left from 0.30 to 1.00 mm, MII right from 0.30 to 0.85 mm, MII left from 0.24 to 0.53 mm.

*Right MI* is an elongate jaw nearly 3 times longer than wide. Very long, narrow hook is equal about 0.60 of the jaw length. In dorsal view a series of denticles slightly increasing in size towards the middle and then more strongly decreasing posteriorly runs along the inner margin from the base of hook to the posterior end of the jaw. The posteriorly directed denticle row in its most posterior part is slightly curved postero-medially. The outer margin is directed postero-laterally along the hook, then posteriorly and in its last distance postero-medially. Inner wing equal in length to about half of the dentary visible in the most posterior part of the jaw. Anterior part of the hook semicircularly curved and strongly bent dorsally. Along the dorsal and ventral sides of the apical portion of the hook run faintly marked sharp ridges. The surface delimited by these ridges is slightly flattened. In left lateral view tip of the hook and denticles directed to the right, almost perpendicularly to the dorsal surface. In ventral view length of the opening of pulp cavity varies around 0.40 of the jaw length.

*Left MI* is in dorsal view about 2.5 times as long as wide. The hook is much shorter and wider than in the right MI, extending for 0.48 of the jaw length. The hook is stout, semicircularly curved and bent dorsally. Sharp ridges on the both sides of the anterior part of the hook are similar to those on the right jaw. A row of denticles vertically inclined and directed backwards form inner margin from the base of hook to posterior end of the jaw. Some of the first denticles increase in size towards the middle, the remainder decrease posteriorly. Usually the biggest are denticles 3—6. On the right side of anterior part of the dentary there is a narrow inner wing tapering posteriorly. Left of the dentary there is a longitudinal furrow gradually disappearing anteriorly, but extending for whole or almost whole the dentary length. The outer margin is at first arched, directed postero-laterally, then almost straight, directed postero-medially, nearly posteriorly. The posterior margin is straight, directed nearly transversally. In right lateral view the dentary is slightly arched. Tip of the hook and denticles directed to the left, almost perpendicularly to the jaw surface. The jaw is widest in the posterior part. In ventral view the opening of pulp cavity extends for 0.60 of the jaw length.

*Right MII* is a comparatively large, plate-like jaw, most probably extending in the articulated apparatus to the inner wing of right MI. Without a shank the jaw is nearly twice as long as wide and is widest in the middle part. Inner margin is to half of the jaw length directed postero-medially, then posteriorly. Along the posterior margin extends a large bight for about half of the jaw length. Anterior margin forms an arch together with the outer margin which is directed postero-laterally, and produced into a comparatively slender shank surrounding the bight laterally. A series of 12—14 denticles extends along the whole length of the inner margin and half of the anterior margin. The first denticle is of medium size, the second is always much bigger than all the rest and remainder denticles increase in size towards the middle and decrease again posteriorly. First two denticles possess faintly marked sharp ridges similar to those on the hook of MI. Left slope is narrow and steep in the posterior part and entirely hidden under the dentary in the anterior

part. Along the outer part of the dorsal surface, from the base of the first denticle to the posterior bight, extends a large furrow. In left lateral view the dentary slightly sigmoidally curved, denticles directed to the right. Along the posterior part of jaw runs a rounded ridge. In ventral view small, crescent-like cover extends for 0.14 of the jaw length.

*Left MII* is a bevelled square shaped jaw, much smaller than right MII. In dorsal view the longitudinal branch is comparatively narrow. In dorsal-left lateral view it appears wider, triangular in shape, tapering posteriorly. Maximal width of the jaw in this position, without a shank, is about half of the length. Shank of the transversal branch spine-like directed postero-laterally. A series of 8—11 denticles extends the full length of the slightly arched inner margin. The first denticle is always bigger than all the rest and possesses faintly marked sharp ridges. Remainder denticles increase in size towards the middle and decrease again posteriorly. Inner slope vertical, almost completely hidden under the dentary. In ventral view a comparatively wide belt extends along the full length of the inner margin. In the anterior part it is prolonged into a small cover which occupies only the antero-medial corner of the jaw. In some of the jaws there is preserved an attachment lamella which forms a prolongation of the anterior part of inner slope. Its shape can be different.

*Right MIII* is similar to the mirror image of the left MII but smaller and comparatively wider. Its shank is also wider than in left MII, situated more posteriorly, triangular in shape and directed laterally. Comparatively big denticles are similarly distributed as in left MII but are fewer in number. First denticle is much bigger than all the rest and twisted postero-laterally. In left lateral view the jaw is comparatively wide, triangular, tapering posteriorly. In ventral view the opening of the pulp cavity is almost gaping. In some of the jaws there is preserved comparatively big attachment lamella.

*Left MIII* is almost a mirror image of the right MIII, only its shank is a little wider and situated more posteriorly. As a result of this maximal width of the jaw is behind of its mid-length.

*Right and left MIV* are small, comparatively wide subtriangular jaws with a row of 5—7 big denticles along the inner margin. First denticle is much bigger than the remaining ones. Poorly differentiated shank is situated in posterior part of the jaws. Slightly concave posterior margin forms a shallow and wide bight.

*Carriers.* Anterior part flat, plate-like, wide. In our specimens the width is equal 0.20 to 0.28 mm. Posterior part narrow, filiform, dorsally flat, ventrally convex. Anterior margin nearly straight, rounded on lateral corner. Outer margin, in its anterior part slightly convex, directed postero-medially, then straight directed nearly posteriorly. Inner margin straight. Most posterior part of the carriers unknown.

*Mandibles.* In the collection there are 3 incomplete mandibles, all of the same morphological type. It is not completely certain if these mandibles belong to *Arabella diversimaxillata*, but judging from the fact that this species is much more abundant in the collection than all other scolecodonts together it is most probable that the mandibles also belong to it. Their length is 0.64 to 0.88 mm. Maximal width about 0.2 of the length. Anterior plate length about half that of the whole, 2 times wider than posterior shaft, narrowing posteriorly. On the central side the anterior plate is flat and possesses rings parallel to the outer margin. Shaft beam-like, tapering posteriorly, convex from ventral side.

*Ultrastructure.*— At high magnification a well-developed polygonal network pattern may be noted on surface of pulp cavities of well preserved jaws (pl. 8; pl. 9: 1—2). A threefold system of canals of the internal structure is visible inside the polygons. The canals are regularly spaced and run in three directions normal

to one another. Two canal systems ( $\alpha$  and  $\beta$ ) are represented on the surface of pulp cavities by fine grooves perpendicular to one another and at the same time parallel to the surface (pl. 8: 2, 3b). The third system ( $\gamma$  canals) is represented by micropores normal to the surface (pl. 8: 1—2; pl. 9: 1c). The canals range from 0.08 to 0.30  $\mu\text{m}$  in diameter. The polygons and structural canals were noted on the left and right MI and MII and ventral side of carriers. The ultrastructure of the MIII and MIV has not been studied. The preservation of these structures varies from one specimen to another and from one portion of pulp cavity to another. In pulp cavity of one left jaw MII (see pl. 9: 3) corresponding to the jaw of the new species in shape there appear somewhat larger (0.3—1.5  $\mu\text{m}$  in diameter) and irregularly distributed pores. Similar pores are noted in pulp cavities of jaws of *Notocirrus compositus* sp.n. (see also pp. 9, 16).

*Remarks.*—The apparatus *Arabella diversimaxillata* sp.n. is reconstructed taking into account its similarity to the apparatus of recent species *Arabella tricolor*

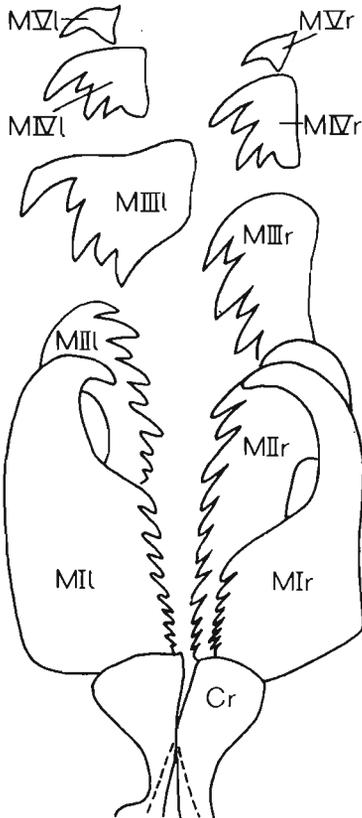


Fig. 3. Diagram of jaw apparatus of *Arabella tricolor* (Montagu), Recent (from Fauchald 1974, original numbering of the jaws). Abbreviations for figs 3—9: *AtIl*—*AtIil* anterior teeth of the left maxillae I—II; *AtIr*—*AtIir* anterior teeth of the right maxillae I—II; *Cr* carriers; *MIl*—*MVl* left maxillae I—V; *MIr*—*MVr* right maxillae I—V.

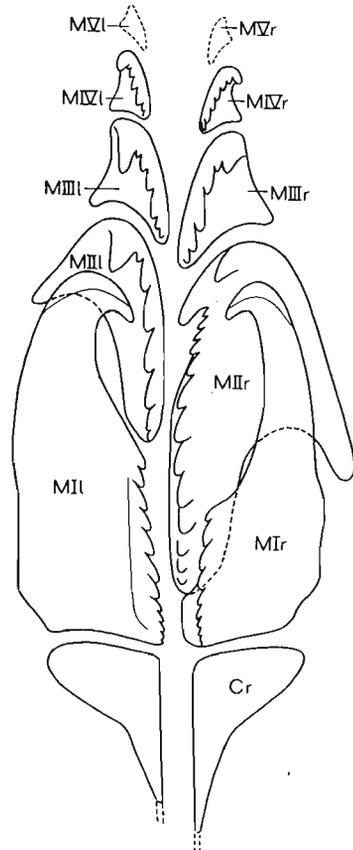


Fig. 4. Reconstruction of jaw apparatus of *Arabella diversimaxillata* sp.n., MV and posterior parts of the carriers are unknown, Tluszcz IG-I borehole, Upper Oxfordian. For abbreviations see fig. 3.

(Montagu) (figs 3—4), detailed morphological analysis of various elements, ultra-structural studies and statistical data.

Fossil jaw apparatuses of the genus *Arabella* are not yet known and only one species of isolated scolecodonts was assigned to that genus (*A. kielanae* Kozur). The species was represented by isolated right and left MI from the Upper Cretaceous of the German Democratic Republic (Kozur 1971). The MI of the newly described species differ from them in having the shape of the left jaws different from that of the right jaws. Moreover right MI of the apparatus of *Arabella diversimaxillata* sp.n. is characterized by a markedly longer hook in relation to their posterior part, markedly smaller opening of pulp cavity and well-developed inner wing. Left MI of the newly described apparatus have somewhat shorter hook than the left MI of *Arabella kielanae* and also differ from the latter in straight posterior margin and less convex inner margin and, thus, somewhat in different shape of their posterior part.

The joined jaws MI and MII, described from the Middle Triassic of the German Democratic Republic as *Notocirrus triassicus* Kozur by Kozur (1971) presumably also belong to the genus *Arabella* (see also remarks to the genus *Notocirrus*).

Kielan-Jaworowska (1966) stated that jaw apparatuses of the Recent species *Arabella iricolor* are characterized by symmetry variation as the jaws MII are strongly asymmetric in some apparatuses and symmetric in others. In the newly described species all the right MII are markedly larger and differently built than the left, and there are no right jaws in the studied material which could be interpreted as mirror image of the left MII. It would follow that the symmetry variation presumably does not occur or is extremely rare in the species in question.

### Genus *Notocirrus* Schmarda, 1861

#### *Notocirrus compositus* sp.n.

(pls. 4, 5, 10, 11; fig. 6)

*Holotype*: Right MII illustrated on pl. 4: 10, ZPAL Sc. IV/230.

*Paratype*: Right MI illustrated on pl. 4: 1, ZPAL Sc. IV/221.

*Type horizon and locality*: Jurassic, Upper Oxfordian, Central Poland, borehole Łuszczy IG-1, depth 845—871 m.

*Derivation of the name*: Lat. *compositus* = composite, the apparatus is a compound of isolated elements.

*Diagnosis*.—MI subtriangular with short hook and long opening of the pulp cavity. MII with bight extending for nearly half of the jaw length. Right MII much longer than left, with very narrow posterior part and with second or third denticle much bigger than the remaining. Right MIII similar in shape to left MII but smaller. Carriers, left MIII and anterior jaws unknown.

Denticle formula:

MI	9—12	10—11
MII	7— 8	11—13
MIII	—	8

*Material*.—3 right MI, 7 left MI, 14 right MII, 8 left MII, 1 right MIII.

*Description*.—Length of jaws: MI right 0.17—0.40 mm, MI left 0.24—0.36 mm, MII right 0.35—0.53 mm, MII left 0.20—0.26 mm, MIII right 0.18 mm.

*Right MI* is a subtriangular jaw with short hook extending for 0.23 of the jaw length. The hook is bent upwards and directed postero-medially. The outer margin in its anterior part is slightly arched, directed postero-laterally, then it turns outwards and runs around a large wing extending to the postero-lateral corner of the jaw. This wing can be different in shape and is usually partly broken. It is

thinner than the rest of the jaw similar to attachment lamella of the other jaws. Outer part of the wing is bent downwards. Posterior margin of the jaw directed postero-medially. Inner part of the hook strongly concave. Behind the hook inner margin straight, denticulated on the full length. First 2—3 denticles increase in size towards the middle and remaining decrease again posteriorly. In left lateral view hook and denticles directed to the right, posterior part of the dorsal surface convex. In ventral view the pulp cavity opening occupies outer part of the jaw and extends for 0.60 of the jaw length. Inner part of the jaw is covered by wide belt which widens anteriorly passing into the cover.

*Left MI* is similar in shape to the mirror image of the right MI but differs from it in some details. Postero-lateral wing is usually smaller than in the right MI and in some jaws completely broken off. In these jaws posterior part of the outer margin exposes postero-medial direction and the jaw appears to be much narrower. On the dorsal surface along posterior part of the dentary runs a longitudinal, flat furrow, disappearing anteriorly. Opening of the pulp cavity on the ventral side extends for 0.70 of the jaw length. The belt is narrower than in the right MI and bent upwards. In right lateral view along the full length of the belt runs a furrow. In some of the jaws there is preserved an inner wing which forms a fragile prolongation of the belt. It is as long as the dentary, wide in the anterior part, tapering posteriorly.

*Right MII* is a long jaw most probably extending in the articulated apparatuses to the posterior end of the MI. Its width is equal 0.43 of the length and it is widest at about 0.6 of the length from the front. Outer margin directed postero-laterally, slightly concave in the middle part. Its posterior part surrounds a large shank. Posterior margin forms a long bight extending for 0.46 of the jaw length. Inner margin of the bight straight, directed posteriorly, nearly parallel to the posterior part of the inner margin. Inner margin denticulated on the full length, directed at first postero-medially, then straight posteriorly. Inner and outer margin converge on the anterior end where the first denticle is placed. The second denticle (in some jaws the third) is much bigger than all the rest, some next denticles increase in size towards the middle and the remaining decrease again posteriorly. Posterior part of the jaw, equal about 0.40 of the jaw length, is very narrow, shaft-like, slightly widening anteriorly. Left slope narrow in posterior part of the jaw and completely hidden under the dentary in anterior part. In left lateral view the jaw is narrow, tapering posteriorly. The denticles are directed to the right and inclined posteriorly. In many jaws there is preserved a small, trapezoidal attachment lamella, forming a prolongation of the inner slope at about 0.3 of the jaw length from its front. In ventral view the cover extends for 0.17 of the jaw length. Along the inner border the cover prolongs into a narrow belt. The remaining part of the ventral side is occupied by opening of the pulp cavity.

*Left MII* is a bevel square shaped jaw much shorter and comparatively wider than the right MII. In dorsal view its width including the shank is about 0.56 of the length. The bight extends for nearly half of the jaw length. The shank is triangular in shape, narrow and long. Distribution of denticles is similar as in right MII, but they are fewer and comparatively bigger. The second denticle is usually only a little bigger than the remaining. Posterior part of the jaw is not so very narrow as in right MII. In right lateral view the jaw is comparatively wide. Attachment lamella often preserved situated similarly as in MII right, but bigger. In ventral view the belt is wide, narrowing posteriorly.

*Right MIII* is similar to the mirror image of the left MII but smaller and different in some details. Its first denticle is the biggest. In left lateral view the jaw is very wide, triangular in shape, tapering posteriorly. Attachment lamella is much bigger than in left MII and placed more posteriorly.

*Ultrastructure.*—Circular pores 0.3–1.0  $\mu\text{m}$  in diameter are marked on the surface of pulp cavities in the majority of jaws (pl. 10: 1, 3; pl. 11: 1–2). The pores representing openings of  $\varphi$  canals occur singly or in small groups more or less irregularly distributed throughout the surface of pulp cavities. Some jaws display both these pores and the threefold system of structural canals ( $\alpha$ ,  $\beta$  and  $\gamma$ ) perpendicular to one another and much narrower (about 0.12  $\mu\text{m}$  in diameter) similar to those of *Arabella diversimaxillata* sp.n. (pl. 11: 1b, 1d, 2). Some others also display polygonal network pattern, but usually poorly preserved. The preservation of all the structures from various parts of pulp cavity of a single jaw is highly variable (see also p. 8).

*Remarks.*—The newly described jaw apparatus was reconstructed taking into account its similarity to that of the recent species *Notocirrus lorum* Ehlers (figs 5, 6), the results of detailed morphological analysis, ultrastructural studies and, to a some degree, statistical data (see also pp. 6, 7). The amount of particular elements and especially jaws MI in the collection is, unfortunately, too small for detailed reconstruction of size ratios of these elements in the apparatus on the basis of statistical data.

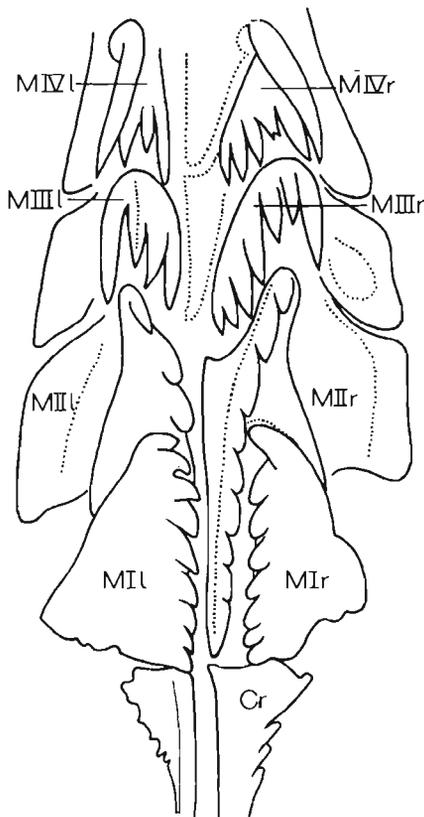


Fig. 5. Diagram of jaw apparatus of *Notocirrus lorum* Ehlers, Recent (after Ehlers, 1897, original numbering of the jaws). For abbreviations see fig. 3.

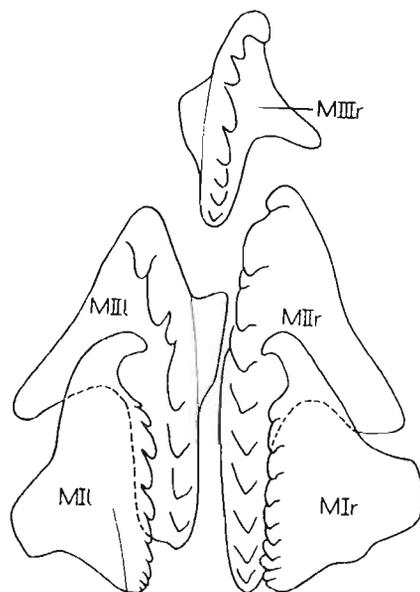


Fig. 6. Reconstruction of jaw apparatus of *Notocirrus compositus* sp.n., carriers, left MIII and anterior jaws are unknown. Tłuszcz IG-I borehole, Upper Oxfordian. For abbreviations see fig. 3.

The fossil polychaete jaws assigned to the genus *Notocirrus* include only two species known from the Triassic of the German Democratic Republic (Kozur, 1971). It should be mentioned here that one of these species, *Notocirrus triassicus* Kozur is very similar to the recent *Arabella iricolor* (Montagu) and, therefore, most probably belongs to the genus *Arabella*. The second Triassic species, *Notocirrus? pulcher* Kozur, is known from isolated left MI and right MII and differs from *N. compositus* sp.n. in the shape of left MI which is more slender, without inner wing and somewhat longer hook in the latter. Moreover, to the genus *Notocirrus* were assigned some scolecodonts reported from the Middle Triassic of Poland by Zawadzka (1975) but they were neither described nor specifically identified.

### Family Dorvilleidae Chamberlain, 1919

*Remarks.*—According to a new systematic revision (Jumars 1974) the family Dorvilleidae is represented by 8 genera. Jaw apparatuses of polychaetes of that family differ markedly from all the remaining Eunicoidea and are the most primitive of them (figs 7—8). Kielan-Jaworowska (1966) termed this type of structure of apparatus as ctenognatha and she also assigned the Paleozoic family Tetraprionidae Kielan-Jaworowska to it. The fossil apparatuses assigned by Kielan-Jaworowska (1966) to the placognatha type are also structurally similar to the above mentioned. The phylogenetic relationships between Paleozoic polychaetes with ctenognatha and placognatha apparatuses and those of the Recent family Dorvilleidae are still not clear because of the inadequate knowledge of Mesozoic polychaetes characterized by a similar structure of apparatuses. The fossil forms which undoubtedly belong to the family Dorvilleidae include Jurassic and Cretaceous representatives of the family, *Ophryotrocha* Claparède and Metschnikov only (Corradini and Serpagli 1968; Szaniawski 1974), and most probably scolecodonts described from the Eocene flysch of France and assigned to parataxonomic genera *Anisocerasites* Eller and *Staurocephalites* Hinde by Jan Du Chêne and Gorin (1974). Moreover, one Cretaceous scolecodont species was assigned to the genus *Dorvillea* Parfitt by Kozur (1971) but its affinity with the genus or even with the family Dorvilleidae is debatable (see remarks to the species *Schistomerings exspectatus* sp.n.).

### Genus ? *Schistomerings* Jumars, 1974

*Remarks.*—The generic status of the scolecodonts described below is debatable at the present state of knowledge of the jaw apparatuses of Dorvilleidae. The jaws seem to be most similar to first jaws of Recent polychaetes of the genera *Schistomerings* Jumars and *Dorvillea* Parfitt (figs 7—9). According to Jumars (1974) jaw apparatuses of these genera mainly differ in length of MII<sup>2)</sup>, whereas the available

<sup>2)</sup> The terminology used here is consistent with that proposed for the fossil apparatuses of the placo- and ctenognatha types by Kielan-Jaworowska (1966). The only differences are connected with introduced subdivision of anterior teeth into maxilla I (AtI) and maxilla II (AtII) anterior teeth and their further subdivision into left and right ones (see figs 7—8). Moreover, the term "carrier" is here accepted after Fauchald (1970) for element heretofore unknown in fossil apparatuses of this type.

A somewhat different terminology is used in the zoological nomenclature of recent Dorvilleidea. According to Fauchald (1970) maxillae are composed of "basal plates" (corresponding to the whole maxillae as interpreted in the present paper), which "are continued anteriorly in rows of denticles" (= anterior teeth).

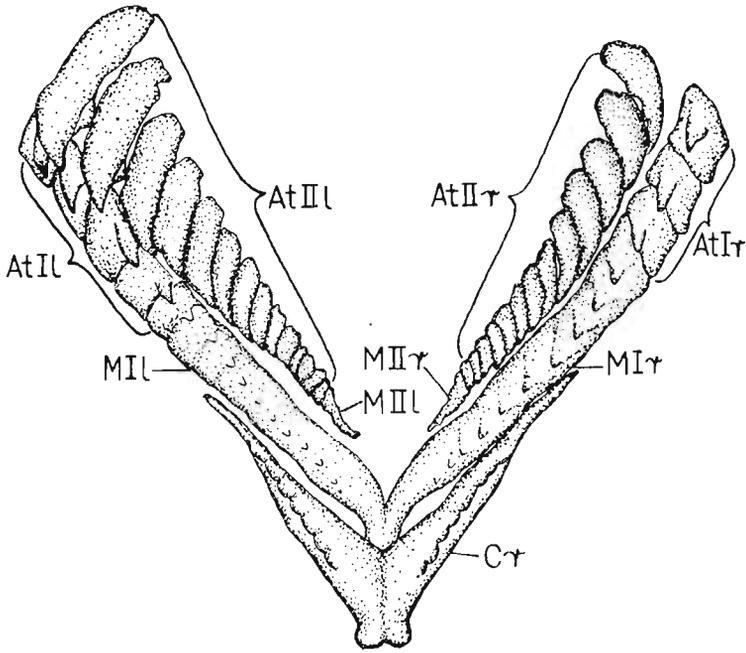


Fig. 7. Jaw apparatus of *Dorvillea gardineri* (Crossland). Recent (from Jumars 1974, original numbering of the elements). For abbreviations see fig. 3.

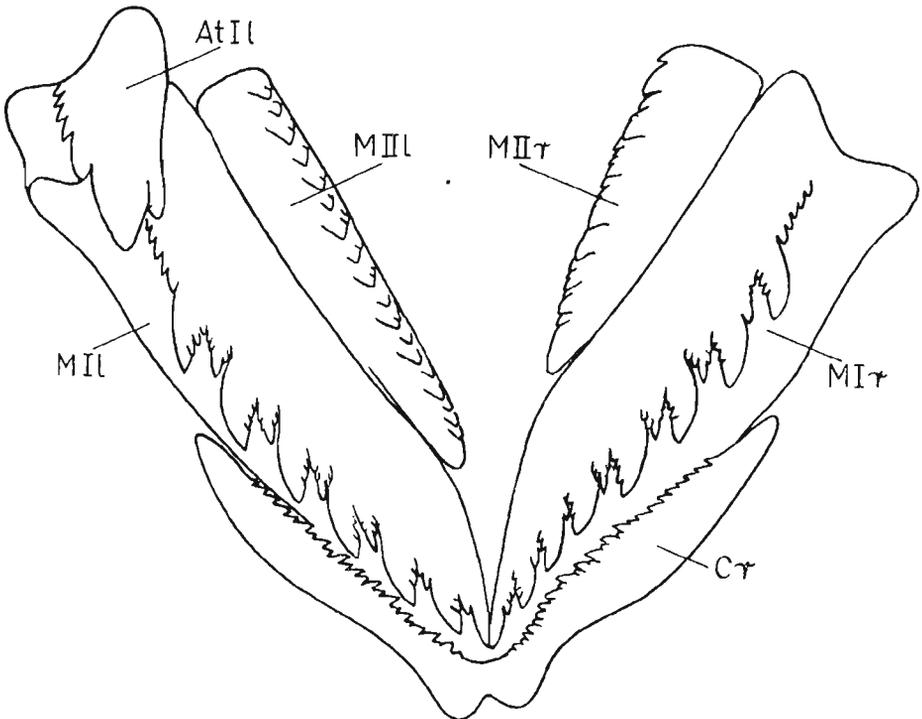


Fig. 8. *Schistomeringos rudolphi* (delle Chiaje). Diagram of posterior part of the jaw apparatus. Recent, Gulf of Naples (original). For abbreviations see fig. 3.

fossil material is composed of MI only. The microstructural studies carried out by the authors showed that the Jurassic jaws and first jaws of the Recent apparatuses belonging to *Schistomeringos rudolphi* (delle Chiaje) and *S. sp.* (pl. 7 and fig. 8) are very similar in structure and denticulation. Both the fossil and recent jaws display small secondary denticles developed on large denticles as well as some minute denticles separating the larger. As it follows from the illustrations given by Jumars (1974: fig. 3) this mode of denticulation is also typical of other species of the genus *Schistomeringos* whilst all the hitherto figured apparatuses of the genus *Dorvillea sensu* Jumars, 1974, are characterized by the jaws MI with only one type of denticles which are devoid of the secondary denticles. That is why the newly found Jurassic jaws are assigned to the genus *Schistomeringos*. However, reservation is made because of some doubts whether or not all the remaining elements of the fossil apparatus were developed as in that genus. The finding of the whole fossil apparatus to which these newly described jaws belonged may show that it is closer to *Dorvillea* or represents a new genus.

? *Schistomeringos expectatus* sp.n.

(pl. 6; fig. 9)

*Holotype*: Left MI illustrated on pl. 6: 1a—c, ZPAL Sc. IV/255.

*Type horizon and locality*: Jurassic, Upper Oxfordian, Central Poland, borehole Tłuszcz IG-1.

*Derivation of the name*: *Lat. expectatus* = expected — as the find of Mesozoic apparatuses of ctenognatha type was expected.

*Diagnosis*.—Right and left MI are pointed posteriorly jaws about 4 times longer than wide and of about the same width in dorsal and lateral views. Anterior margin concave. Along the high ridge extends a series of 8—10 big denticles each of which possesses some tiny secondary denticles. In the spaces between big denticles there are groups of fused smaller denticles. In the anterior prolongation of the denticulated ridge there is a series of 6—8 small denticles decreasing in size anteriorly. Along gaping pulp cavity extends deep furrow with two parallel series of bigger and smaller denticle pits. Carriers, maxillae II and anterior teeth are unknown.

*Material*.—2 MI right and 1 MI left.

*Description*.—Length of the possessed specimens: MI left 0.31 mm (holotype), MI right 0.28 and 0.15 mm.

*Left MI* is a strongly elongated jaw about four times longer than wide and with pointed posterior end. Its maximal width in dorsal view is in the mid-length. Anteriorly the jaw is narrowing only a little, much less than posteriorly. Anterior margin curved inwards is wide, V-shaped. Inner part of the margin is prolonged anteriorly, forming together with the inner margin a triangular process. Outer margin slightly convex, directed posteriorly and posteromedially in the posterior part. Inner margin almost straight, directed posteriorly. Outer and inner margins converge at the posterior end. Along the mid-line of the jaw runs very high denticulated ridge with very steep slopes. A series of 8—10 big spine-like denticles (first order denticles) begins at one-fifth of the jaw length from the anterior margin and extends to the almost posterior end of the jaw. First denticle is slightly smaller than the second while all the next are gradually decreasing in size

posteriorly. From the lower-inner side of each of these denticles grow out some (usually 4) very small and slender secondary denticles. In all the inter-denticle spaces occur groups of 4—7 much smaller, partly fused, second order denticles. In the anterior part of jaw the second order denticles are more separate, in the posterior part each of the groups is fused into one unit in form of a wide triangular denticle (second order denticle) with slender secondary denticles on its upper and lower margin. The central secondary denticle is the longest and the remaining ones are decreasing in size posteriorly and anteriorly. In front of the first big denticle (first order denticle) there is an area directed obliquely downwards. Along the mid-line of it extends a series of 6—8 small, slender denticles forming a prolongation of the main denticulated ridge. These denticles are generally increas-

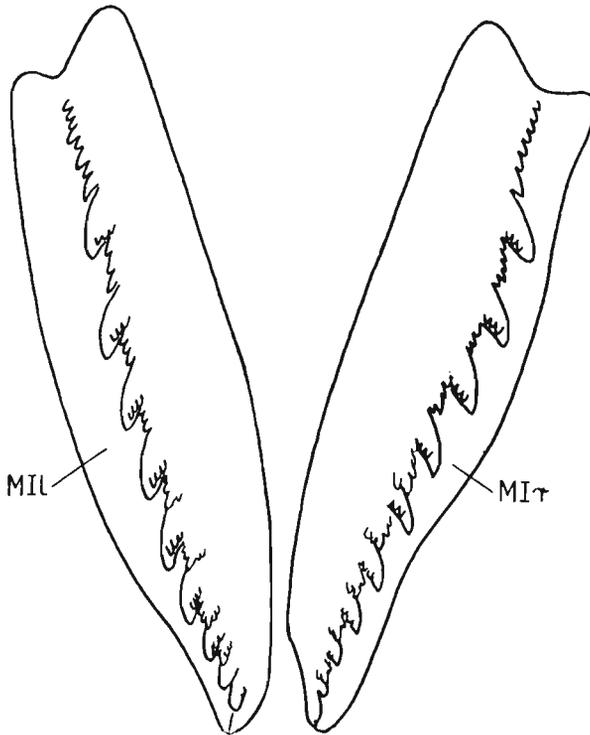


Fig. 9. Diagram of the left and right MI of *Schistomeringos expectatus* sp.n., Tłuszcz IG-1 borehole, Upper Oxfordian. For abbreviations see fig. 3.

ing in size posteriorly but bigger denticles may be separated by smaller. In lateral view the jaw is almost equally wide as in dorsal view. Its maximal width is at one-fifth of the length from the anterior. Anteriorly, the jaw is sharply tapering. The anterior margin is directed obliquely, posteromedially. Denticulated margin converges posteriorly with the inner margin. Whole ventral side is occupied by the gaping pulp cavity. Deep furrow with two parallel series of denticle pits extends along its mid-line. One of the series consists of bigger pits corresponding to the first order denticles and the other, situated a little outwardly of the first, consists of smaller pits corresponding to the groups of fused second order denticles. Between each two bigger pits there is only one smaller.

*Right MI* seems to be a mirror image of the *left MI* but it is not known if they are of the same size.

*Remarks.*—The jaws of newly described species are very similar to *MI* of the recent *Schistomeringos* Jumars (pl. 7 and fig. 8). The similarity concerns not only the shape but also the details of denticulation. The only difference in denticulation is connected with the groups of fused second order denticles marked between first order denticles in the anterior part of the former, whereas each of these groups is fused into one triangular denticle (second order denticle) with secondary denticles on its margins in the latter.

Besides already mentioned *Ophryotrocha* (p. 17) only one species of fossil polychaetes—*Dorvillea jansonii* Kozur—was assigned to the family Dorvilleidae but it is doubtful whether it really belongs to this family. *MI* of all recent dorvilleids are tapering posteriorly close to their attachment to the carriers, whereas they are widening posteriorly in *Dorvillea jansonii*. On the other hand, *D. jansonii* is similar to *MII* of fossil *Skalenoprion* Kielan-Jaworowska and recent *Drilonereis* Claparède.

### Not described Scolecodonts

Besides the above described elements of the three reconstructed apparatuses the collection also comprises some other elements, which are not described here. Some of them represent also eunicoid jaw apparatuses. This is the case of the jaws *MI* and *MII* (pl. 5: 5—6) resembling those described from the Upper Cretaceous of the German Democratic Republic under the generic names of *Lysaretides* Kozur (*MI*) and *Palurites* Kozur (*MII*) by Kozur (1971). Subsequently, Zawadzka (1971) has shown that similar Triassic scolecodonts previously placed in parataxonomic genera *Delosites* Kozur (*MI*) and *Palurites* Kozur (*MII*), actually represent elements of the same apparatus, for which she chose the name *Delosites*. Later Kozur (1972) emended the diagnosis of the genus *Lysaretides* in such a way that it comprised both the *MI* and Cretaceous scolecodonts *MII* previously described under the name of *Palurites*. At present the Triassic scolecodonts previously described under the name *Palurites* are assigned to the genus *Delosites* and the Cretaceous ones—to *Lysaretides*. This once more points out great difficulties connected with unification of the parataxonomical and natural systematics. According to the present authors all these scolecodonts should be allocated in a single genus as the differences in structure of *MI* in *Delosites* and *Lysaretides* are not large and in the case of *MII* are almost none. *MI* figured on pl. 5: 5 seems intermediate between the Triassic *Delosites raridentatus* Kozur and Cretaceous *Lysaretides hartmannae* Kozur. Analysis of pulp cavity surface of the jaw *MII* (pl. 5: 6 and pl. 11: 3) carried out with the use of SEM showed that its ultrastructure differs from those of jaws of both *Arabella diversimaxillata* sp.n. and *Notocirrus compositus* sp.n. The material available, including 3 jaws *MII* and a single *MI*, is unfortunately insufficient for reconstruction of the apparatus.

The collection also contains 23 jaws of polychaetes not belonging to the superfamily Eunicoidea. The most common of the latter (17 specimens) are the representatives of the genus *Glycera* Savigny (pl. 5: 7) belonging to at least 2 species. At high magnification it is possible to note numerous small pores leading to venom canal on several specimens (pl. 5: 7b). This further emphasizes the striking similarity between these jaws and the Late Cretaceous and Recent species (Charletta and Boyer 1974; Szaniawski 1974). The genus *Goniada* is represented by 5 speci-

mens from the species *G. szaniawskii* Kozur which are almost identical as conspecific forms reported from the Upper Cretaceous of the German Democratic Republic (Kozur 1971) and Bathonian of Poland (Szaniawski 1974).

In the collection there is also a single incomplete scolecodont somewhat close to jaws of some representatives of the family Nereidae, e.g. those of the genus *Micronereis* Claparède. Only the anterior part of the jaw is preserved which may be explained by the fact that posterior part of jaws of polychaetes in the family Nereidae is markedly less sclerotized than the anterior part. However, it is debatable whether or not this scolecodont belongs to that family. SEM analysis of its surface showed a characteristic fish scale-like ornament.

Moreover there are in the collection 5 unidentified scolecodonts which are most probably elements of eunicoid jaw apparatuses.

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REKONSTRUKCJA TRZECH JURAJSKICH APARATÓW SZCZĘKOWYCH  
WIELOSZCZETÓW*Streszczenie*

W wapieniach górnego oksfordu wiercienia Tłuszcz IG-1 (figs 1—2) znaleziono stosunkowo liczne i dobrze zachowane szczęki wieloszczetów (skolekodonty). Zebrana kolekcja, składająca się z 281 izolowanych skolekodontów, pozwoliła na dokonanie rekonstrukcji trzech aparatów szczękowych wieloszczetów z nadrodziny Eunicoidea. Dla aparatów tych ustanowiono nowe gatunki i zaliczono je do współczesnych rodzajów: *Arabella diversimaxillata* sp.n., *Notocirrus compositus* sp.n. i ?*Schistomeringos expectatus* sp.n. Rekonstrukcje przeprowadzono w oparciu o analogię do aparatów współczesnych (figs 3—9), szczegółową analizę morfologiczną, dane statystyczne oraz wykorzystane po raz pierwszy w praktyce systematycznej badania ultrastrukturalne. Wszystkie kryteria rekonstrukcji zostały w pracy przedyskutowane. Badania ultrastrukturalne ograniczono do obserwacji przy pomocy SEM powierzchni przyrostu tkanek miękkich (jamy mięksiszowe szczęk, powierzchnie wentralne podpór) co nie wymaga skomplikowanego przygotowania materiału i niszczenia okazów. Stwierdzono, że na powierzchniach tych w różnych elementach jednego aparatu widoczne są podobne struktury. Są one wprawdzie różnie zachowane, lecz w większości okazów można je rozpoznać. Pozwala to na odróżnienie elementów różnych aparatów.

Wobec tego, że poprawna systematyka zoologiczna izolowanych skolekodontów jest niemożliwa bez znajomości aparatów szczękowych, do których skolekodonty te należały, możliwość dokonywania rekonstrukcji aparatów z izolowanych elementów ma duże znaczenie dla systematyki. Połączone aparaty szczękowe spotyka się w utworach mezozoiku niezwykle rzadko; z jury znany był dotychczas tylko jeden niekompletny aparat (Szaniawski 1974).

Przeprowadzono szczegółowe porównanie morfologii współczesnych i kopalnych szczęk z rodzaju *Schistomeringos* Jumars (figs 8—9; pls 6—7), które wykazało ich daleko idące analogie dotyczące nawet szczegółów ząbkowania. Aparaty szczękowe o tym typie budowy uważane są za najprymitywniejsze wśród wieloszczetów współczesnych. Podobne im aparaty znane są z dolnego paleozoiku (Kielan-Jaworska 1966), lecz nie były dotychczas znane z okresów późniejszych.

Poza elementami zrekonstruowanych aparatów w kolekcji znajduje się tylko 28 innych skolekodontów. W większości są to szczęki wieloszczetów z współczesnych rodzajów *Glycera* i *Goniada*, które nie posiadają połączonych aparatów szczękowych. Ponadto w kolekcji znajdują się trzy elementy aparatu *Delosites* (Kozur) znanego dotychczas z triasu i z ?kredy.

ХУБЕРТ ШАНЯВСКИ, АНДЖЕЙ ГАЗДЗИЦКИ

РЕКОНСТРУКЦИЯ ТРЁХ ЮРСКИХ ЧЕЛЮСТНЫХ АППАРАТОВ  
МНОГОЩЕТИНКОВЫХ ЧЕРВЕЙ

## Резюме

В известняках верхнего оксфорда скважины Тлуц IG-1 (фиг. 1—2) обнаружены относительно многочисленные и хорошо сохранившиеся челюсти многощетинковых червей (сколекодонты). Собранный коллекция, состоящая из 281 изолированных сколекодонтов, позволила провести реконструкцию трёх челюстных аппаратов многощетинковых червей из надсемейства Eunicoidea. Для этих аппаратов были установлены новые виды и причислены к современным родам: *Arabella diversimaxillata* sp. n., *Notocirrus compositus* sp. n. и ?*Schistomeringos expectatus* sp. n. Реконструкция была произведена на основе сходства их к современным аппаратам (фиг. 3—9), подробного морфологического анализа, статистических данных, а также, впервые в практике систематических исследований, ультраструктуры. В статье обсуждены все критерия реконструкции. Ультраструктурные исследования сводились к наблюдениям с помощью SEM поверхности прироста мягких тканей (мягкитной ямы челюстей, вентральной поверхности подпор), что не требовало сложных приготовлений материалов и разрушения образца. Обнаружено, что на поверхностях этих различных элементов одного аппарата наблюдаются подобные структуры. Хотя они не одинаково сохранились, однако для большинства образцов их можно определить. Это делает возможным выделять элементы различных аппаратов.

Потому что правильная зоологическая систематика изолированных сколекодонтов невозможна без познания челюстных аппаратов, к которым эти сколекодонты принадлежали, то следовательно возможность проведения этой реконструкции аппаратов из изолированных элементов имеет для систематики большое значение. Целые челюстные аппараты встречаются в отложениях мезозоя чрезвычайно редко; до сих пор был известен с юры только один неполный аппарат (Szaniawski 1974).

Проведено детальное сравнение современных и ископаемых челюстей рода *Schistomeringos Jumars* (фиг. 8—9; пл. 6—7), которое показало далеко идущее сходство, касающееся даже деталей зазубренности челюстей. Челюстные аппараты такого ктеногнатического типа строения относят к наиболее примитивным среди современных многощетинковых червей. Подобные аппараты известны из нижнего палеозоя (Kielan-Jaworowska 1966), однако до сего времени они не были известны в более поздних периодах.

Кроме элементов реконструированных аппаратов в коллекции надоятся также только 28 прочих сколекодонтов. В большинстве это челюсти многощетинковых червей родов *Glycera* и *Goniada*, которые не имеют соединённых челюстных аппаратов. В коллекции также находятся 3 элемента аппарата *Delosites* (Kozur), известного до настоящего времени из отложений триаса и мела.

## EXPLANATION OF THE PLATES

All specimens shown in Plates 1—6 and 8—11 are derived from Tuszcz IG-1 borehole, Upper Oxfordian, depth 845—871 m.

## Plate 1

*Arabella diversimaxillata* sp.n.

1—6. Right MI; 1 left lateral view, 2—4 different dorsal views, 3 holotype, 5—6 different ventral views, in 5 inner wing is broken off. ZPAL Sc. IV/1—6.

7—12. Left MI; 7 right lateral view, 8—9 slightly different ventral views, 10—12 dorsal views. ZPAL Sc. IV/7—12.

1×133; 2—4, 6, 7, 11×100; 5, 8—10, 12×66

## Plate 2

*Arabella diversimaxillata* sp.n.

1—3, 5. Left MII; 1 dorso-left lateral view, 2 right lateral view, 3 ventral view, note preservation of attachment lamella, 5 dorsal view. ZPAL Sc. IV/13—16.

4, 6—9. Right MII: 4, 6—7 slightly different dorsal views, 8 ventral view, 9 left lateral view. ZPAL Sc. IV/17—21.

1, 3, 5—7, 9×133; 2, 4×100; 8×66

## Plate 3

*Arabella diversimaxillata* sp.n.

1. Left MIV in dorso-left lateral view. ZPAL Sc. IV/29.

2. Right carrier in ventral view, posterior part is broken off. ZPAL Sc. IV/29.

5—7. Left MIII; 5, 6 dorsal views, 7 dorso-left lateral view. ZPAL Sc. IV/22—24.

8—9. Right MIII; 8 dorsal view, 9 antero-dorsal view. ZPAL Sc. IV/25—26.

10. Right MIV in dorso-left lateral view. ZPAL Sc. IV/28.

? *Arabella diversimaxillata* sp.n.

3. Right mandible in ventral view, posterior and the most anterior parts broken off. ZPAL Sc. IV/30.

4. Left mandible in ventral view, the most anterior part broken off. ZPAL Sc. IV/31.

1, 6—10×200; 5×166; 2×133; 3, 4×100

## Plate 4

*Notocirrus compositus* sp.n.

1—2. Right MI; 1 dorsal view, 2 ventral view, ventral wall in front of pulp cavity broken. ZPAL Sc. IV/221—222.

3—5. Left MI; 3 dorsal view, 4 ventral view, 5 right lateral view, anterior part of hook and posterior part of belt are broken off. ZPAL Sc. IV/223—225.

- 6—10. Right MII; 6—7 ventral views, 8 left lateral view, attachment lamella broken off, 9—10 dorsal views, 10 holotype. ZPAL Sc. IV/226—230.
11. Right MIII in dorsal view. ZPAL Sc. IV/231.  
3, 4, 6, 7×133; 5, 8, 10×166; 1, 2, 9×200; 11×300

## Plate 5

*Notocirrus compositus* sp.n.

- 1—4. Left MII; 1 dorsal view, 2 ventral view, 3 left lateral view, specimen with preserved attachment lamella, 4 dorso-left lateral view. ZPAL Sc. IV/232—235.

*Delosites* sp.

5. Left MI, in dorsal view, anterior part of the jaw partly broken. ZPAL Sc. IV/260.
6. Right MII in right lateral view. ZPAL Sc. IV/261.

*Glycera* sp.

7. Right jaw in ventral view; *a* whole specimen except for the most posterior part of the jaw, which is broken off, *b* enlarged detail of the same specimen as in *a*, slightly different position showing pores leading to venom canal. ZPAL Sc. IV/265.

*Goniada szaniawski* Kozur

8. Macrognath in dorsal view. ZPAL Sc. IV/284.

? *Nereidae*, gen. et sp. indet.

9. Anterior part of the left jaw in dorsal view. ZPAL Sc. IV/290.  
5, 6, 7a×133; 9×166; 1, 3, 4×200; 2, 5×233; 7b×400

## Plate 6

? *Schistomeringos expectatus* sp.n.

1. Left MI; *a* dorsal view, posterior part of right slope is broken off, ×166; *b* the same in dorso-right lateral view, the illustration is composites of two photos taken at slightly different angles, ×400; *c* fragment of the posterior part of the same jaw showing details of denticulation, ×1330. ZPAL Sc. IV/255.
2. Right MI; *a* ventral view, ×400; *b* left lateral view of the same specimen, ×600. ZPAL Sc. IV/256.
3. Right MI; *a* dorso-left lateral view, posterior part of the inner slope is partly broken, ×400; *b* fragment of the same specimen showing details of denticulation, ×1330. ZPAL Sc. IV/257.

## Plate 7

*Schistomeringos rudolphi* (delle Chiaje), Recent, Gulf of Naples

1. *a* slightly deformed complete jaw apparatus in dorsal view, ×100; *b* posterior part of the same apparatus in slightly different position, showing carriers, left

and right MI, left and right MII and most posterior anterior teeth,  $\times 300$ ; *c* enlarged detail of *b* showing anterior part of left MI and MII and first anterior teeth,  $\times 520$ .

*Schistomeringos* sp., Recent, Gulf of Naples

2. *a* left side of the posterior part of jaw apparatus in dorsal view, posterior part of the carrier bent outwards,  $\times 300$ ; *b* fragment of MI and carrier of the same specimen in dorso-right lateral view showing details of denticulation,  $\times 1330$ ; *c* fragment of MI and MII of the same specimen showing details of denticulation,  $\times 1000$ . ZPAL Sc. IV/292.
3. *a* slightly deformed complete jaw apparatus in dorsal view,  $\times 66$ ; *b* posterior part of the same, showing carriers, left and right MI and first anterior teeth of MI, left and right MII hidden under MI and anterior teeth; left carrier partly damaged,  $\times 300$ . ZPAL Sc. IV/293.

Plate 8

*Arabella diversimaxillata* sp.n.

1. Right MI; *a* central part of pulp cavity with polygonal network pattern and numerous pores of  $\gamma$  canals inside the polygons,  $\times 2000$ ; *b* enlarged detail of *a*, showing faintly marked  $\alpha$  and  $\beta$  canal grooves and rows of pores of  $\gamma$  canals,  $\times 6000$ . ZPAL Sc. IV/32.
2. Left MI (the same specimen as on pl. 1: 8); *a* marginal part of pulp cavity surface with polygons, rows of pores of  $\gamma$  canals and  $\alpha$  and  $\beta$  canal grooves (left side of the photo)  $\times 2000$ ; *b* enlarged detail of *a*,  $\times 6000$ .
3. Left MII, pulp cavity surface; *a* polygonal network pattern disappearing towards the inner part of the pulp cavity,  $\times 600$ ; *b* enlarged detail of *a*, with  $\alpha$  and  $\beta$  canal grooves,  $\times 6000$ . ZPAL Sc. IV/33.

Plate 9

*Arabella diversimaxillata* sp.n.

1. Right MII (the same specimen as on pl. 2: 8) central part of pulp cavity; *a* well developed polygonal network pattern,  $\times 450$ ; *b* enlarged detail of *a*, visible raised boundaries of polygonal areas and pores of  $\gamma$  canals inside of them,  $\times 2000$ ; *c* enlarged detail of *b*, showing also  $\alpha$  and  $\beta$  canal grooves,  $\times 6000$ . ZPAL Sc. IV/19.
2. Right carrier with faintly marked polygonal network pattern in ventral view (the same specimen as on pl. 3: 2),  $\times 600$ . ZPAL Sc. IV/29.

? *Arabella diversimaxillata* sp.n.

3. Left MII; *a* pulp cavity surface with irregularly distributed pores of  $\phi$  canals; pores become elongate toward the innermost part of the cavity,  $\times 600$ ; *b* enlarged detail of *a*, some of the pores are closely grouped,  $\times 2000$ . ZPAL Sc. IV/34.

Plate 10

*Notocirrus compositus* sp.n.

1. Right MI, outer part of the pulp cavity surface with irregularly distributed pores of  $\phi$  canals,  $\times 2000$ . ZPAL Sc. IV/236.

2. Right MI (the same specimen as on pl. 4: 2); central part of the pulp cavity with pores of  $\gamma$  canals visible in lower right part of the photo and  $\alpha$  and  $\beta$  canal grooves,  $\times 6000$ .
3. Left MI (the same specimen as on pl. 4: 4); *a* pulp cavity with pores of  $\varphi$  canals,  $\times 750$ ; *b* enlarged detail of *a*,  $\times 2000$ .
4. Left MII (the same specimen as on pl. 5: 2); *a* outer part of the pulp cavity surface with groups of pores of  $\varphi$  canals,  $\times 2000$ ; *b* inner part of the pulp cavity with pores of  $\varphi$  canals regularly grouped; in the innermost part of the cavity (lower margin of the picture) the pores are elongate,  $\times 2000$ .

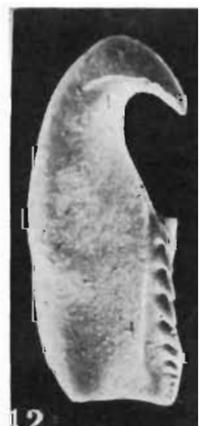
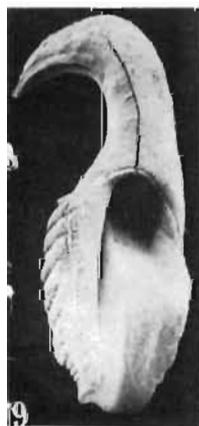
## Plate 11

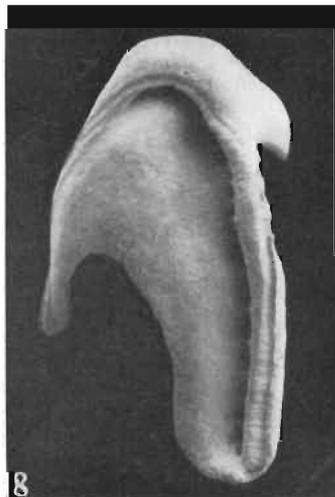
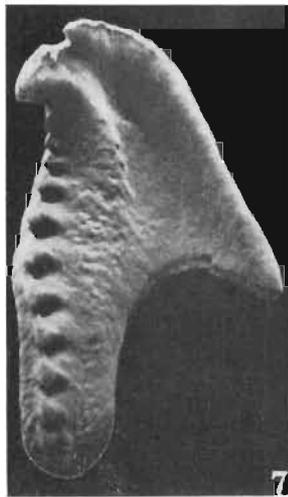
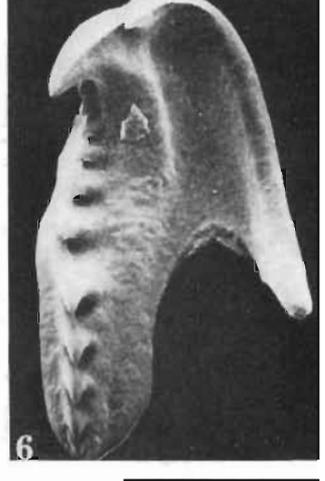
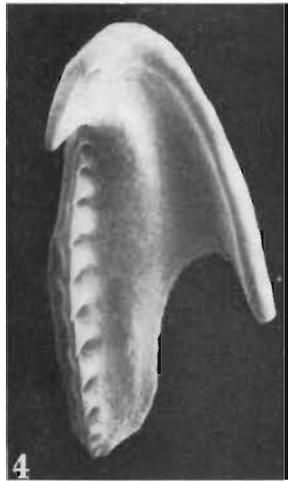
*Notocirrus compositus* sp.n.

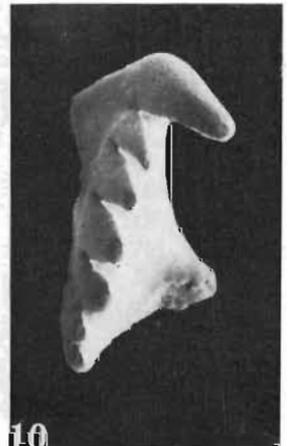
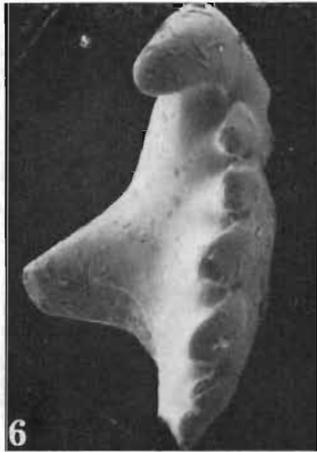
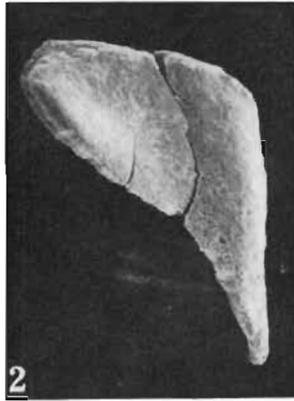
1. Right MII (the same specimens as on pl. 4: 6); *a* pulp cavity with pores of  $\varphi$  canals becoming elongate towards denticle pits and with faintly marked polygons in outer parts of the cavity (lower part of the photo),  $\times 600$ ; *b* enlarged detail of the central part of *a* showing pores of  $\varphi$  canals and rows of small pores of  $\gamma$  canals,  $\times 3000$ ; *c* enlarged detail of the inner part of the pulp cavity with groups of slightly elongate pores of  $\varphi$  canals,  $\times 3000$ ; *d* enlarged detail of the central part of the pulp cavity with pores of  $\varphi$  canals,  $\alpha$  and  $\beta$  canal grooves and pores of  $\gamma$  canals,  $\times 6000$ .
2. Right MII (the same specimen as on pl. 4: 7), central part of the pulp cavity with pores of  $\varphi$  canals and rows of pores of  $\gamma$  canals,  $\times 6000$ .

*Delosites* sp.

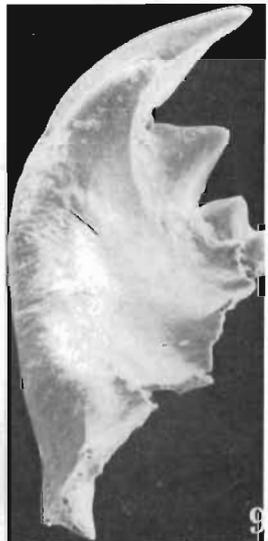
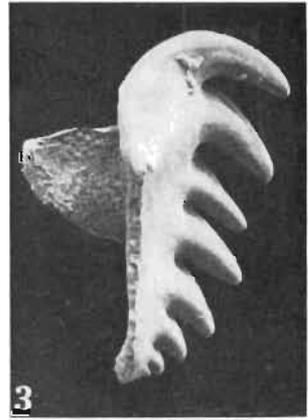
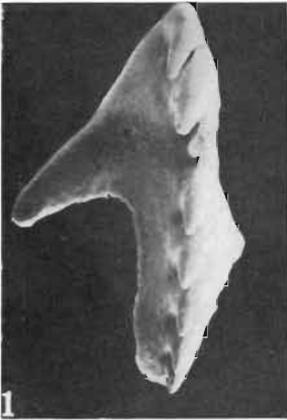
3. Right MII, pulp cavity surface with pores of  $\gamma$  canals,  $\times 6000$ . ZPAL Sc. IV/262.
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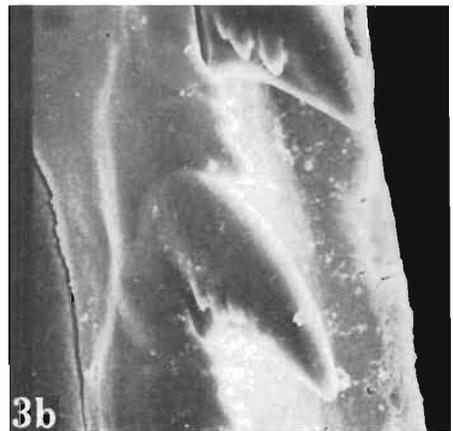
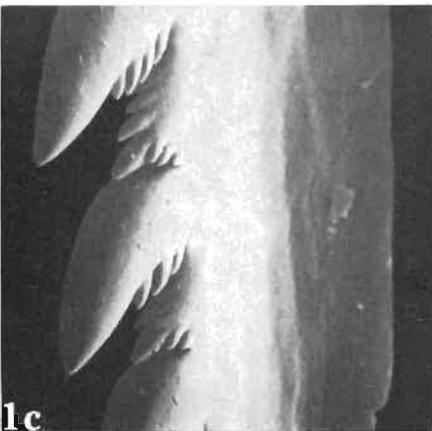




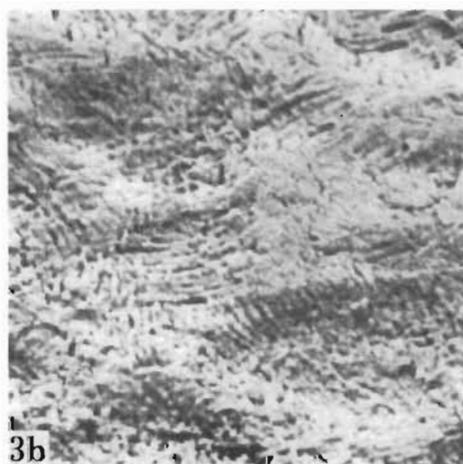
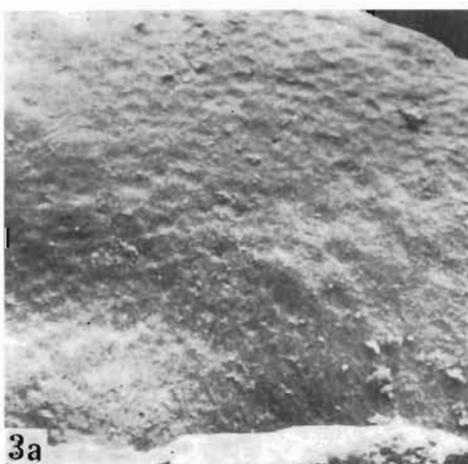
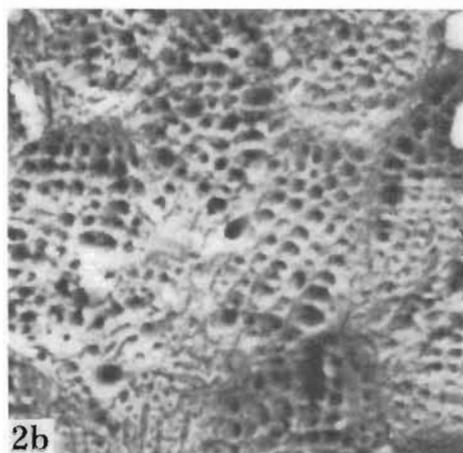
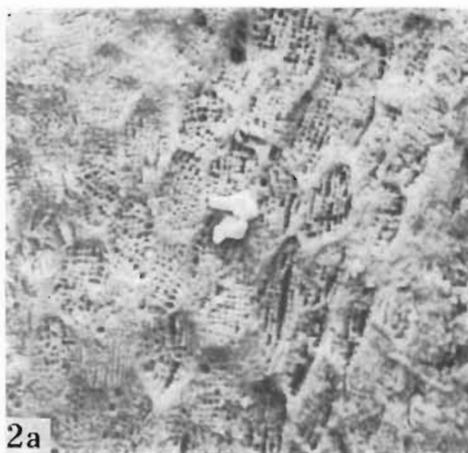
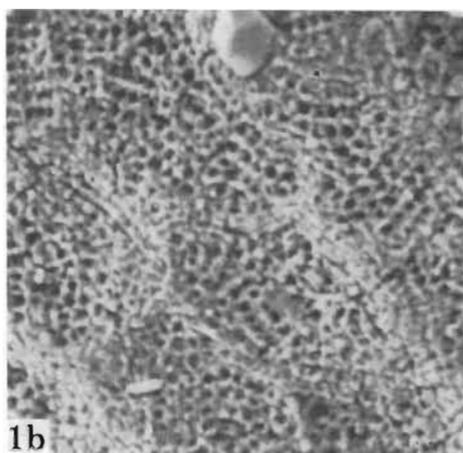
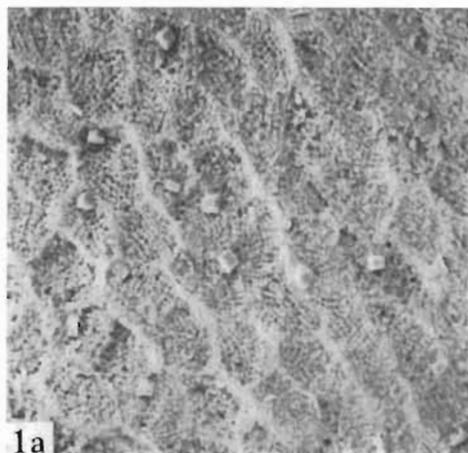


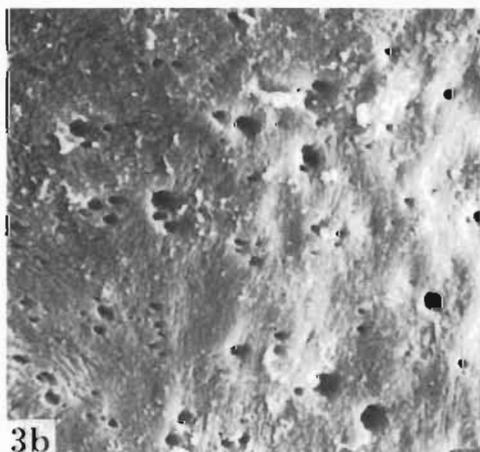
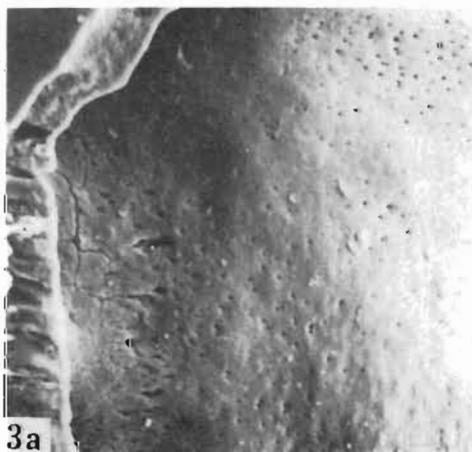
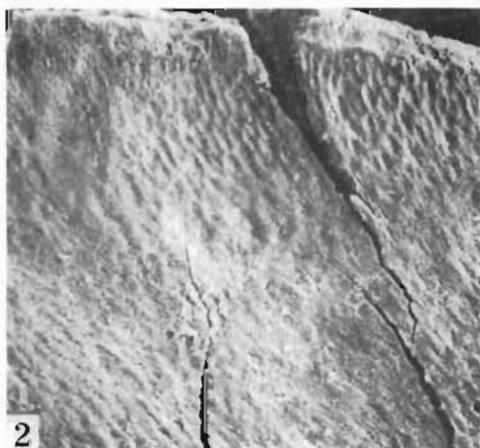
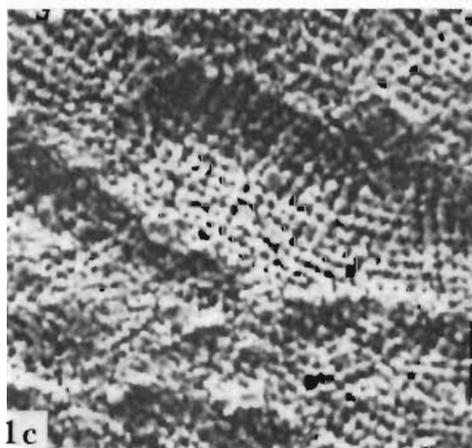
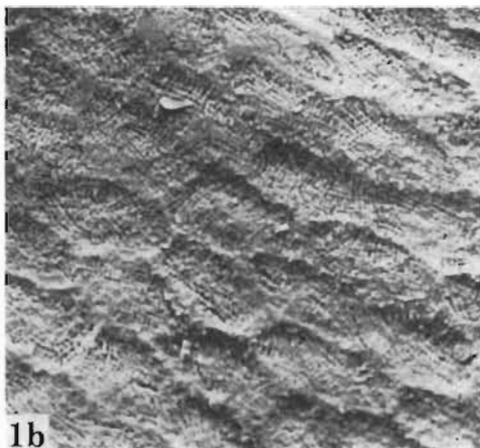
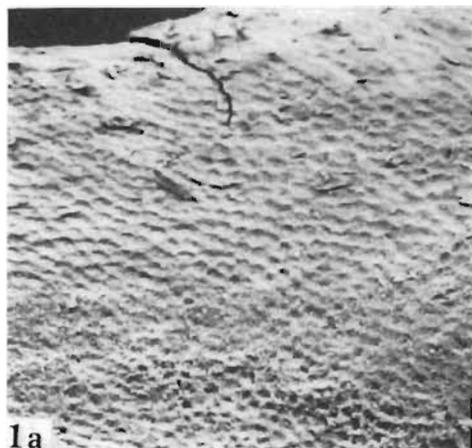


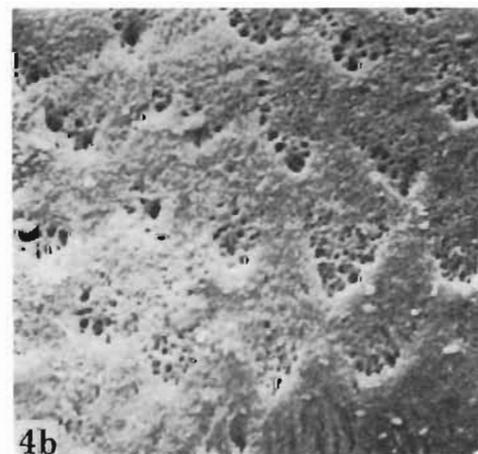
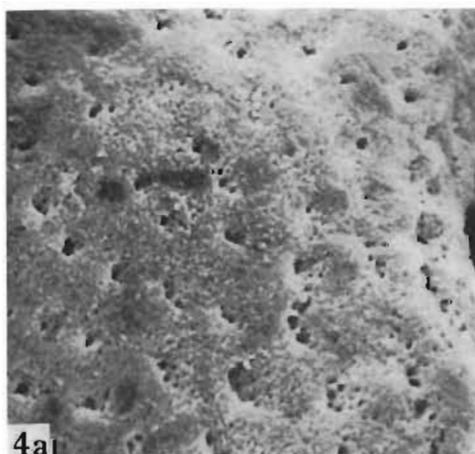
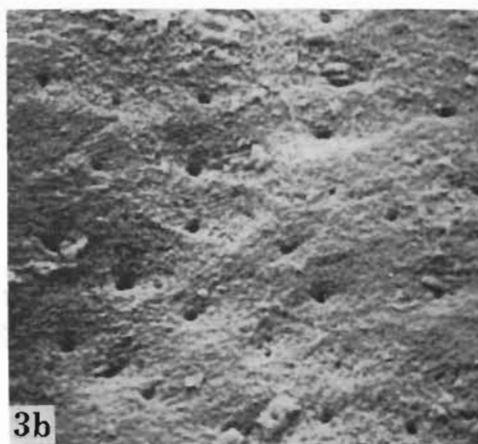
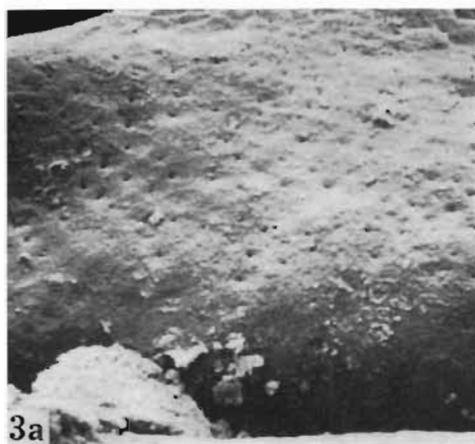
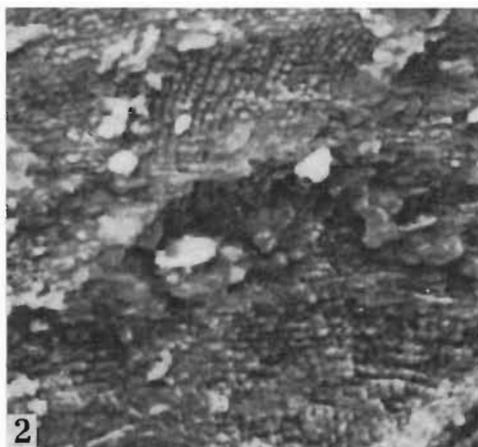
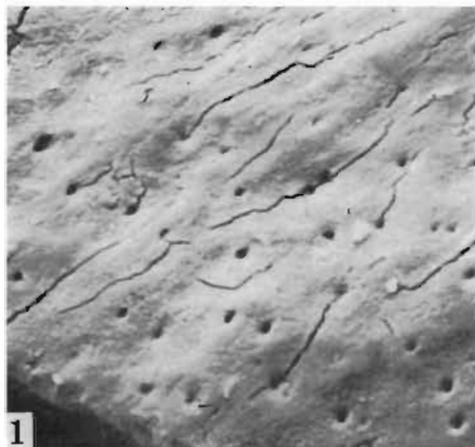






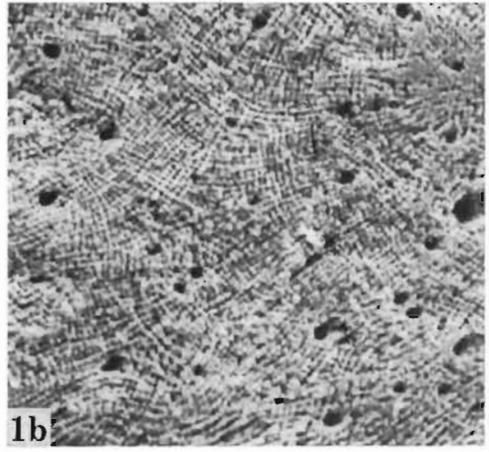




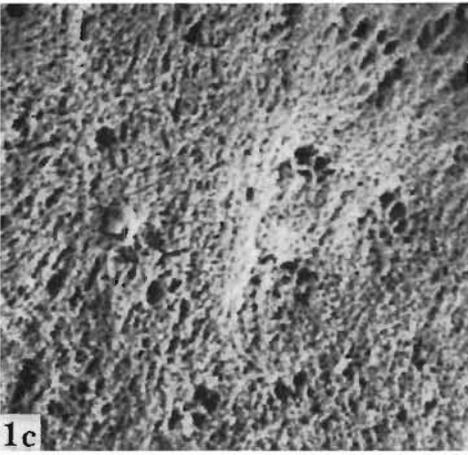




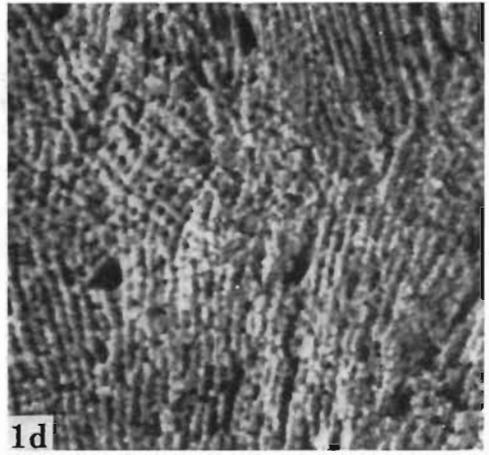
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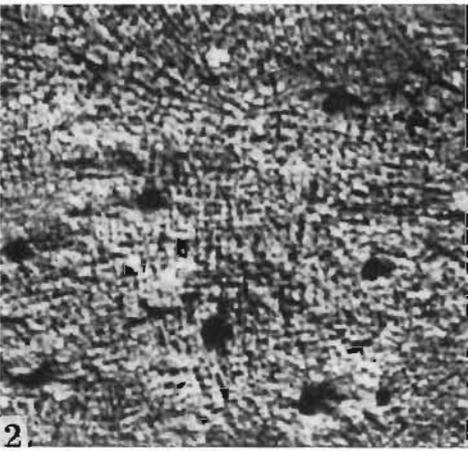
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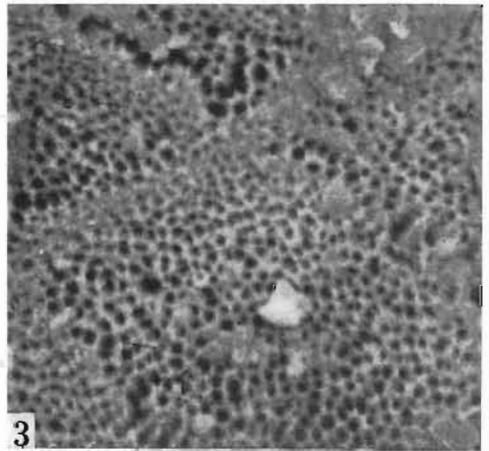
1c



1d



2



3