

Dissertationes Geologicae Universitatis Tartuensis

Olle Hints

Harju (Late Ordovician) eunicid polychaetes of Estonia

M.Sc. thesis

supervised by Dr. Tõnu Meidla

Tartu 1998

Contents

Abstract	
Kokkuvõte	
Introduction.....	8
Geological setting and stratigraphy	10
Material and methods.....	12
Historical review.....	13
Nature of polychaete jaws	15
Arrangement of jaw apparatuses and morphology of scolecodonts.....	16
Terminology	17
Taxonomy	21
Reconstruction of jaw apparatuses	21
Problems of the “element-based taxonomy”	22
Systematic palaeontology	24
Mochtyellidae Kielan-Jaworowska, 1966	24
<i>Mochtyella</i> Kielan-Jaworowska, 1961.....	24
<i>Mochtyella cristata</i> Kielan-Jaworowska, 1961.....	24
<i>Mochtyella polonica</i> Kielan-Jaworowska, 1966	24
<i>Mochtyella duplicidentata</i> Szaniawski, 1970	24
<i>Mochtyella</i> sp. A.....	25
“ <i>Mochtyella</i> ” ex gr. <i>trapezoidea</i> Kielan-Jaworowska, 1966.....	25
<i>Paramochtyella</i> gen. nov.....	25
<i>Paramochtyella fragilis</i> (Szaniawski, 1970).....	26
<i>Pistoprion</i> Kielan-Jaworowska, 1966	26
<i>Pistoprion transitans</i> Kielan-Jaworowska, 1966	26
<i>Vistulella</i> Kielan-Jaworowska, 1961	27
<i>Vistulella kozlowskii</i> Kielan-Jaworowska, 1961.....	27
<i>Rakvereprion</i> Mierzejewski, 1978	27
<i>Rakvereprion balticus</i> (Eisenack, 1975).....	27
Rhytiprionidae Kielan-Jaworowska, 1966	27
<i>Rhytiprion</i> Kielan-Jaworowska, 1966.....	27
<i>Rhytiprion magnus</i> Kielan-Jaworowska, 1966	27
Xanioprionidae Kielan-Jaworowska, 1966.....	28
<i>Xanioprion</i> Kielan-Jaworowska, 1962.....	28
<i>Xanioprion tenuidentatus</i> sp. nov.....	28
<i>Xanioprion</i> sp. A	28
<i>Xanioprion</i> sp. B	29
Tetraprionidae Kielan-Jaworowska, 1966	29
<i>Tetraprion</i> Kielan-Jaworowska, 1966.....	29
<i>Tetraprion pozaryskae</i> Kielan-Jaworowska, 1966.....	29
<i>Valgaprion</i> gen. nov.	30
<i>Valgaprion huberti</i> sp. nov.....	30
Conjungaspidae fam. nov.....	30
<i>Conjungaspis</i> gen. nov.....	31
<i>Conjungaspis minutus</i> sp. nov.....	32
Symmetroprionidae Kielan-Jaworowska, 1966.....	33
<i>Symmetroprion</i> Kielan-Jaworowska, 1996.....	33
<i>Symmetroprion spatiosus</i> (Hinde, 1882).....	33
Polychaetaspidae Kielan-Jaworowska, 1966	33
<i>Polychaetaspis</i> Kozłowski, 1956.....	33
<i>Polychaetaspis</i> cf. <i>gadomskae</i> Kielan-Jaworowska, 1966	33
<i>Polychaetaspis inclinatus</i> sp. nov.	34
<i>Polychaetaspis kuldigaensis</i> sp. nov.	35

<i>Polychaetaspis latoides</i> sp. nov.	36
<i>Polychaetaspis minutus</i> sp. nov.	36
<i>Polychaetaspis pirguensis</i> sp. nov.	38
<i>Polychaetaspis varsoviensis</i> Kielan-Jaworowska, 1966.	38
<i>Polychaetaspis</i> cf. <i>wyszogrodensis</i> Kozłowski, 1956.	39
<i>Polychaetaspis?</i> <i>multidentatus</i> sp. nov.	39
<i>Kozłowskioprion</i> Kielan-Jaworowska, 1966.	40
<i>Kozłowskioprion angustus</i> sp. nov.	40
<i>Kozłowskioprion brevialetatus</i> Kielan-Jaworowska, 1966.	41
Polychaeturidae Kielan-Jaworowska, 1966.	41
<i>Polychaetura</i> Kozłowski, 1956.	41
<i>Polychaetura gracilis</i> Kozłowski, 1956.	41
<i>Polychaetura harjuensis</i> sp. nov.	41
<i>Laevaprion</i> gen. nov.	43
<i>Laevaprion jaaki</i> sp. nov.	43
Ramphoprionidae Kielan-Jaworowska, 1966.	44
<i>Ramphoprion</i> Kielan-Jaworowska, 1962.	44
<i>Ramphoprion elongatus</i> Kielan-Jaworowska, 1962.	44
<i>Ramphoprion</i> cf. <i>deflexus</i> (Eller, 1942).	45
<i>Ramphoprion</i> sp. A.	46
Paulinitidae Lange, 1947.	47
<i>Kettnerites</i> Zebera, 1935.	47
<i>Kettnerites</i> ssp.	47
Kallopriionidae Kielan-Jaworowska, 1966.	47
<i>Kallopriion</i> Kielan-Jaworowska, 1962.	47
<i>Kallopriion</i> ssp.	47
<i>Kallopriion robustus</i> sp. nov.	47
<i>Leptoprion</i> Kielan-Jaworowska, 1966.	48
<i>Leptoprion</i> ssp.	48
Atraktoprionidae Kielan-Jaworowska, 1966.	48
<i>Atraktoprion</i> Kielan-Jaworowska, 1962.	48
<i>Atraktoprion cornutus</i> Kielan-Jaworowska, 1962.	48
<i>Atraktoprion major</i> Kielan-Jaworowska, 1966.	49
<i>Atraktoprion mirabilis</i> Kielan-Jaworowska, 1966.	49
Skalenoprionidae Kielan-Jaworowska, 1966.	49
<i>Skalenoprion</i> Kielan-Jaworowska, 1962.	49
<i>Skalenoprion alatus</i> Kielan-Jaworowska, 1962.	49
Incertae familiae.	49
<i>Tretoprion</i> gen. nov.	49
<i>Tretoprion astae</i> sp. nov.	50
<i>Lunoprionella</i> Eisenack, 1975.	51
<i>Lunoprionella symmetrica</i> Eisenack, 1975.	51
“ <i>Lunoprionella</i> ” sp. A.	51
Gen. et sp. indet. A.	52
Stratigraphic distribution.	53
The Ordovician–Silurian boundary.	62
Eunicids along the onshore–offshore profile.	66
Conclusions.	79
Acknowledgements.	80
References.	81
Plates.	89

Abstract

Succession of the Harjuan (Late Ordovician) eunicid polychaetes in Estonia is represented by abundant, varied and well-preserved scolecodonts (elements of jaw apparatuses). The material of this study derives from three drill core sections (Orjaku, Laeva-18 and Valga-10), which characterise different facies belts along the onshore – offshore profile of the Baltoscandian Palaeobasin. According to the apparatus-based, biological taxonomy, the number of species in the Harju Series of Estonia apparently exceeds 50. Due to limitations of the material, only 46 species are described herein, including 14 new species (*Xanioprion tenuidentatus*, *Valgaprion huberti*, *Conjungaspis minutus*, *Polychaetaspis inclinatus*, *Polychaetaspis kuldigaensis*, *Polychaetaspis latoides*, *Polychaetaspis minutus*, *Polychaetaspis pirguensis*, *Polychaetaspis? multidentatus*, *Kozlowskiprion angustus*, *Polychaetura harjuensis*, *Laevaprion jaaki*, *Kalloprion robustus* and *Tretoprion astae*). In addition, a new family Conjungaspidae and five new genera (*Paramochtyella*, *Valgaprion*, *Conjungaspis*, *Laevaprion* and *Tretoprion*) are introduced. The monotypic family Conjungaspidae fam. nov. is distinct in having long-horned carriers merged with large basal- and laeobasal plates; it is likely a rather primitive group displaying common features with xanioprionids and some labidognaths. *Paramochtyella* gen. nov. (type species *P. fragilis* Szaniawski) differs from *Mochtyella* in having larger denticles in posterior maxillae and denticulated anterior jaws. *Valgaprion* gen. nov. has closest relationship with *Tetraprion* Kielan-Jaworowska, but its anterior and lateral teeth are smaller and the posterior maxillae developed somewhat differently. *Laevaprion* gen. nov. is distinct in having posterior maxillae provided with long transverse ridges. Its similarity with *Rhytiprion* seems to be superficial, and the genus likely is related to polychaeturids. Systematic position of a labidognath *Tretoprion* gen. nov. with transversally prolonged denticles and specific anterior jaws remains unclear.

Most of the jawed polychaetes common in the Harju Series are long ranging species, occurring in the underlying Viruan deposits as well as in the lowermost Silurian. Therefore the Ordovician-Silurian boundary is not as distinct in the distribution of polychaetes as previously suggested. The elements earlier considered as typical of the Silurian of the Baltic region, like skalenoprionids, paulinitids and symmetropionids appear already in the Harju Series. The possible stratigraphic value of some relatively short-ranged taxa needs further approval. Despite, polychaete assemblages characterised by certain species composition, predominating taxa, diversity and abundance may prove helpful in making stratigraphical consequences.

Harjuan jawed polychaete faunas appeared to be well differentiated along the onshore-offshore profile. Several species may be regarded as characteristic of a particular environment. For example, *Polychaetura gracilis* and *Pistoprion transitans* seem to have favoured relatively shallow-water conditions, *Polychaetura harjuensis* and *Polychaetaspis varsoviensis* were most common in the transitional area between onshore and offshore part of the palaeobasin, and *Rakvereprion balticus* composed low abundance – low diversity assemblages in relatively deeper water environments. Decrease in abundance and diversity towards the offshore part of the palaeobasin is documented, indicating that the more shallow-water part of the palaeobasin offered optimal habitats for the majority of Harjuan jawed polychaetes. The lateral differentiation of polychaete assemblages notably increased in the Pirgu age, compared to the Rakvere and Nabala ages. This is probably due to general increase in the facies differentiation in the Baltoscandian Palaeobasin during the late Harjuan. Cluster- and

factor analyses proved invaluable in generalising and visualising the quantitative distribution data.

Key words: scolecodonts, jawed polychaetes, taxonomy, distribution, Harju Series, Estonia.

EESTI ÜLEMORDOVIITSIUMI (HARJU LADESTIK) LÕUGSED POLÜHEEDID

K o k k u v õ t e

Lõugsed polüheedid (Polychaeta, Eunicida) on Harju ladestiku kivimites esindatud arvukate, mitmekesiste ning hästi säilinud skolekodontidega (lõuaaparaadi osised). Käesoleva töö aluseks olev materjal pärineb kolmest puursüdamikust (Orjaku, Laeva-18 ja Valga-10), mis iseloomustavad Baltoskandia Paleobasseini erinevaid fatsiaalseid vööndeid. Töös kasutatud polüheetide taksonoomia tugineb tervikuna säilinud või rekonstrueeritud lõuaaparaatidel. Uuritud materjali põhjal oli võimalik identifitseerida ja kirjeldada 46 liiki, sealhulgas 14 uut liiki (*Xanioprion tenuidentatus*, *Valgaprion huberti*, *Conjungaspis minutus*, *Polychaetaspis inclinatus*, *Polychaetaspis kuldigaensis*, *Polychaetaspis latoides*, *Polychaetaspis minutus*, *Polychaetaspis pirguensis*, *Polychaetaspis? multidentatus*, *Kozlowskiprion angustus*, *Polychaetura harjuensis*, *Laevaprion jaaki*, *Kalloprion robustus* and *Tretoprion astae*). Töös on püstitatud uus sugukond *Conjungaspidae* ning viis uut perekonda (*Paramochtyella*, *Valgaprion*, *Conjungaspis*, *Laevaprion* and *Tretoprion*). *Conjungaspiididele* iseloomulikuks tunnuseks on pikkade külgjätketega tugiplaadi liitumine basaal- ja laeobasaalplaadiga. Tõenäoliselt on tegu võrdlemisi primitiivse rühmaga, mis omab teatud ühiseid tunnuseid nii mõnede plakognaatide kui ka labidognaatidega. *Paramochtyella*, tüüpiliigiga *P. fragilis* Szaniawski erineb perekonnast *Mochtyella* oma suhteliselt suuremate dentiiklite poolest tagamaksillidel ning selge hammastu esinemise poolest eeslõugadel. *Valgaprion* on küllalt sarnane perekonnale *Tetraprion* erinedes tollest väiksemate ees- ja külghammaste ning eesmiselt ümardunud tagamaksillide poolest. *Laevaprion*'i iseloomulikuks tunnuseks on põiksete dentikuleerimata harjade esinemine tagamaksillide esiosas. Selle perekonna sarnasus *Rhytiprion*'iga on pigem adaptiivse iseloomuga kui fülogeneetilist sugulust näitav. *Laevaprion*'ile lähimad vormid kuuluvad tõenäoliselt polühaeturiidide hulka. Perekonda *Tretoprion*, mida iseloomustavad külgsuunas laienenud dentiiklid tagamaksillidel, ning nõrgalt liitunud hambakestest koosnevad esimaksillid, ei ole olemasoleva materjali alusel võimalik liigitada ühtegi tuntud sugukonda.

Paljud Harju ladestikus esinevad liigid osutusid ulatusliku stratigraafilise levikuga vormideks, mis esinevad nii lamavates kui lasuvates kihtides. Seetõttu on ordoviitsiumi-siluri piir polüheetide levikupildis väljendunud nõrgemalt kui siiani arvatud. Mitmed Baltoskandia silurile tüüpiliseks peetud grupid nagu skalenoprioniidid, paulinitiidid ja sümmetroprioniidid ilmuvad ordoviitsiumi ülemises osas. Mõnede suhteliselt lühikese stratigraafilise levikuga liikide võimalik väärtus indeksfossiilidena nõuab täiendavaid andmeid. Stratigraafilise liigestuse aspektis võivad kasulikuks osutada kindla liigilise koosseisu, teatud domineerivate vormide, mitmekesisuse ning arvukusega iseloomustatud lõugsete polüheetide kooslused.

Uuritud ülemordoviitsiumi polüheetide levik viitab nende stenotoopsusele ning mitmeid liike võib käsitleda kui iseloomulikke teatud keskonnale. Näiteks *Polychaetura gracilis* ja *Pistoprion transitans* eelistasid tõenäoliselt suhteliselt rannalähedasemaid tingimusi, *Polychaetura harjuensis* ja *Polychaetaspis varsoviensis* esinesid kõige arvukamalt üleminekuvööndi faatsiestes ning *Rakvereprion balticus* moodustas madala arvukuse ja mitmekesisusega kooslusi suhteliselt sügavamaveelistes tingimustes. Paleobasseini keskosa faatsieste suunas kahanev arvukus ja mitmekesisus viitab sellele, et suhteliselt rannalähedasemad faatsiesed pakkusid valdavale osale ülemordoviitsiumi polüheetidest kõige optimaalsemaid tingimusi. Pirgu eal, võrrelduna Rakvere ja Nabala eaga, polüheedikoosluste pindalaline differentseeritus kasvas. Tõenäoliselt peegeldab see paleobasseini üldise fatsiaalse differentseerituse suurenemist hilisordoviitsiumi lõpus. Klaster- ja faktoranalüüs osutusid kasulikuks

vahendiks kvantitatiivse levikuandmestiku üldistamisel ja visualiseerimisel võimaldades suhteliselt hästi esile tuua basseini gradiendi suunal kooslustes toimuvaid muutusi.

Märksõnad: skolekodondid, lõugsed polüheedid, taksonoomia, levik, Harju ladestik, Eesti.

INTRODUCTION

Polychaetous annelids are, and have been since the Early Palaeozoic, an important component of various marine ecosystems. However, the geological record of these soft-bodied worms is extremely scarce — except for few tube-dwelling (Order Sabellida), and many jaw-bearing forms (Order Eunicida). In addition, polychaetes may have produced a number of tracks and burrows, preserved as trace fossils, but there is almost no chance to ascribe traces to the particular taxa (Nara 1995).

The jaw apparatuses of eunicid polychaetes are composed of organic material, which is very resistant to chemical and biochemical attack. Isolated elements of such apparatuses, the scolecodonts, are among the most common microfossils in the Palaeozoic marine sediments and provide a good basis for taxonomic work (Kielan-Jaworowska 1966; see discussion below). In spite of that, eunicids have not been a very popular object of study and there is a couple of reasons for that. First, the systematics based on multi-elements jaw apparatuses is rather complicated and confused, partly due to different concepts applied by investigators. Second, the polychaetes are a relatively slowly evolving (Szaniawski & Irajima 1996) and facies dependent group, which considerably reduces their biostratigraphic value. However, as shown in several recent works, it is possible to solve the taxonomic and nomenclature problems more easily as previously supposed (e.g., Bergman 1989, 1991a, 1995; Eriksson 1997). Moreover, stratigraphic usefulness of scolecodonts has been reconsidered (Szaniawski 1970, 1996; Hints 1996 and in press) and their usefulness in palaeoenvironmental studies has been demonstrated (Courtinat & Howlett 1990).

The oldest scolecodonts have been found in the Tremadoc of Canada (Underhay & Williams 1995) and China (R. Brocke *pers. comm.* 1996). The comb-like microfossils reported from the Vendian (Sokolov 1985) and interpreted as scolecodonts apparently belong to some other organism but not to a polychaete worm. Throughout the Phanerozoic, over 25 families of eunicid polychaetes left evidences into the paleontological record. The majority of fossil taxa comes from the Palaeozoic strata, as this stratigraphic interval is most extensively investigated.

In the area concerned in this study (Fig. 1), the oldest polychaete jaws have been discovered from the topmost Arenig. They constitute notable part of acid resistant microfossils in various types of the Ordovician and Silurian sediments. Estonia is a particularly good place for studying Ordovician polychaete jaws for several reasons:

- (1) Scolecodont research has a comparatively long history in the Baltic region, beginning from the works by Kozłowski (1956) and Kielan-Jaworowska (1961, 1962, 1966). A number of taxa referred to herein are described on the basis of complete jaw apparatuses in course of former investigation.
- (2) Due to specific geological history of the area, various fossils, scolecodonts inclusive, are mostly of excellent preservation in Estonian sections, and fused jaw apparatuses,

especially valuable for higher-rank taxonomy of eunicids, are quite frequently found in acid-treated samples.

(3) The Ordovician (and Silurian) sequence is fairly complete representing various environments.

(4) The stratigraphic background is remarkably well elaborated, and various other groups of fauna are extensively studied. That allows tracing of spatial and temporal distribution of polychaetes in detail and facilitates the comparison with other fossil groups.

(5) The material is available both from outcrop area and from drill core sections of subsurface area.

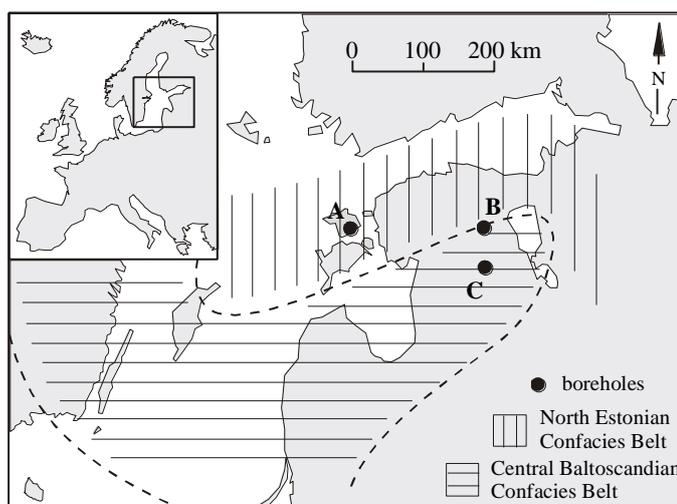


Figure 1. Sketch map of the study area. Approximate boundary between North Estonian and Central Baltoscandian Confacies belts is given in accordance with Jaanusson (1976). Boreholes: A – Orjaku; B – Laeva-18; C – Valga-10

This study is a continuation of my previous work which concerned stratigraphically older, Caradocian scolecodonts from North Estonia (Hints in press; Hints et al. 1997). Herein, however, the subject is somewhat wider as the material is included from the Central and South Estonia, which, in comparison with northern part of the area, constituted offshore part of the Ordovician basin. The main emphasis of the present study is on the taxonomic composition, stratigraphic distribution of Harjuan eunicid polychaetes and their relationship to particular facies.

GEOLOGICAL SETTING AND STRATIGRAPHY

The Harju Regional Series (Nabala, Vormsi, Pirgu and Porkuni Regional Stages) corresponds to the upper part of the Upper Ordovician, embracing the topmost Caradoc and Ashgill. The position of the Caradoc–Ashgill boundary in the study area can be regarded as tentative only (e.g., Männil 1966, 1990; Jaanusson 1982; Põlma 1982; Nõlvak 1997). The lower boundary of Harju Series coincides approximately with the *Pleurograptus linearis* graptolite zone (Jaanusson 1960; Männil 1976). The generalised stratigraphic chart of the Harju after Nõlvak (1997) is given in Fig. 2. Further details are available in Männil & Meidla (1994) and Hints & Meidla (1997).

The epicontinental Baltoscandian Palaeobasin covered extensive marginal areas on the Baltica continent (East European Platform), being situated in the zone of a warm climate in the southern hemisphere during the Harju (Scotese & Mckerrow 1991). Preponderance of carbonate sedimentation associated with rich biotas was typical for this basin.

Männil (1966) was the first to recognise the large-scale configuration of the Ordovician Baltoscandian Palaeobasin. Subsequently his ideas evolved into concept of 'confacies belts' (Jaanusson 1976). In recent works (e.g., Nestor & Einasto 1997), North Estonian Confacies Belt (or marginal, or Estonian-Lithuanian Confacies Belt) is distinguished in northern part of Estonia and Central Baltoscandian Confacies Belt (or central or Swedish-Lithuanian) in South Estonia (see Fig. 1).

In brief, North Estonian Confacies Belt was characterised by rather shallow-water (onshore) environments and discontinuous deposition, resulting in formation of grey-coloured calcareous deposits and occasionally reef limestones. This confacies belt offered excellent habitats for various groups of fauna (echinoderms, bryozoans, algae, brachiopods, trilobites, corals etc.).

Southern part of Estonia, as well as Latvia and Sweden, on the other hand, was characterised by deeper-water (offshore) environments, where fine-grained terrigenous or clayey calcareous deposits, red-coloured in particular horizons, were developed. Central Baltoscandian Confacies Belt represented transitional area between the onshore facies and the deepest area of the palaeobasin, the Scania Confacies Belt, where almost exclusively fine-grained graptolitic muds were formed. It has been shown, that faunal associations of the Central Baltoscandian Confacies were fundamentally different from those in the onshore part of the palaeobasin, being less diverse and usually represented by different taxa (Hints & Rõõmusoks 1997; Hints & Stukalina 1997; Meidla 1996; Põlma 1982; Rõõmusoks 1997). The boundary between the two confacies belts was not sharp nor was its geographical position stable in time. Some authors have distinguished a transitional area between the North Estonian and Central Baltoscandian Confacies Belt (Põlma 1982; Meidla 1996). The general configuration of the confacies belts, regarding the study area during the Harju is given in Fig. 1.

System	Series	Scanian graptolite zonation	Regional standard			
			Series	Stages	North Estonia	South Estonia
O R D O V I C I A N	S			Juuru	VARBOLA Fm.	ÕHNE Fm.
	A S H G I L L	<i>persculptus</i>	H A R J U	Porkuni		SALDUS Fm.
		?			ÄRINA Fm.	KULDIGA Fm.
		<i>complanatus</i>		Pirgu	ADILA Fm.	JELGAVA Fm.
	C a r a d o c	<i>linearis</i>		Vormsi	KÖRGESSAARE Fm.	FJÄCKA Fm.
		<i>clingani</i>		Nabala	SAUNJA Fm.	SAUNJA Fm.
					PAEKNA Fm.	MÕNTU Fm.
				Viru	Rakvere	RÄGAVERE Fm.

Figure 2. Stratigraphy of the Harju Regional Series (after Nölvak 1997).

Männil (1966) distinguished two main phases of development of the Baltoscandian Palaeobasin during Harjuan — the so-called late Caradoc and the Ashgill developmental phases. The first phase, beginning from the Oandu time and continuing to the end of the Vormsi time, was characterised by heightened supply of fine-grained terrigenous material, wide distribution of graptolitic muds and light-coloured lime muds. Differently from the preceding stages, the relatively well-expressed facial zonation was a significant feature of the late Caradocian phase. The Ashgillian phase (Pirgu and Porkuni time) was characterised by the absence of graptolitic muds in the Central Baltoscandian Confacies Belt, development of red-coloured deposits in the Pirgu time, a development of reef facies and bioclastic sediments. The regression occurring in the Porkuni time was interpreted as a result of active tectonic movements by Männil (1966). More recent studies have revealed the crucial importance of the glaciation, which caused an eustatic sea-level fall at the end of the Ordovician (see Brenchley *et al.* 1997 for reference). The sedimentation retreated to South Estonia and Latvia in the late Porkuni time. Therefore, the typically deeper-water area in South Estonia is characterised by shallow-water deposits in the topmost Ordovician.

MATERIAL AND METHODS

Majority of the collection studied comes from three drill core sections in Estonia (see Fig. 1). 20 samples from the Orjaku core represent the North-Estonian Confacies Belt; 40 samples from the Laeva-18 borehole characterise the transitional area between two widely recognised confacies; and 38 samples from the Valga-10 drill core exemplify offshore Central Baltoscandian Confacies. The total number of samples yielding polychaete jaws is smaller because the red-coloured and strongly dolomitised intervals and reef limestones lacked organic-walled microfossils. The total number of isolated elements recovered exceeds 10 000, being derived from more than 5500 specimens (see the explanation of the counting method below). The number of eunicid species obviously exceeds 50 in the Harju Series of Estonia; however, as due to insufficient material on some taxa, only 46 are described or referred to in this study.

The samples from the Orjaku and Laeva-18 cores were collected and processed by myself, those from the Valga-10 drill core were collected by P. Männik. Some additional information was obtained from the microfaunal collection of the Institute of Geology (selected samples from the Kaugatuma-509, Rapla, Butkunai and Remte drill cores). As the latter material has not been collected and processed especially for polychaete jaws, the emphasis here is on the samples from Orjaku, Laeva-18 and Valga-10 sections, to which the following methods refer.

Samples, 400-1600 g in weight, were prepared in 3-8 l vessels, mainly by means of dilute acetic or hydrochloric acid. Insoluble residues were washed in the running water through a 34 or 63 μm screens to remove clay. Scolecodonts and other organic microfossils were picked up from Petri-beakers with a fine glass pipette. The fossils are stored in glycerine in translucent plastic boxes (2x1 cm). The counts of individual scolecodont taxa were derived from the number of the most abundant element in the sample (usually posterior maxillae, but sometimes second maxillae and basal plates).

The material selected for scanning electron microscopy (SEM) was washed in alcohol and distilled water and subsequently dried. Sometimes hydrofluoric acid was used for final cleaning of smaller specimens. Scolecodonts and apparatuses were mounted on SEM stubs with water-soluble tragacanth glue or double-adhesive tape and coated with gold. Scanning electron microscopes Philips XL20 (at the Institute of Paleobiology, Polish Academy of Sciences) and JEOL ISM-840A (at Centre for Materials Research at Tallinn Technical University) have been used.

The present collection is housed at the Institute of Geology at Tallinn Technical University, Estonia for which the abbreviation GIT has been used.

HISTORICAL REVIEW

The first accounts of polychaete jaws date back to 1850s. Eichwald (1854) and Pander (1856), working on the Lower Palaeozoic of the Baltic area, regarded scolecodonts recovered from bedding planes of limestones as fish denticles. Massalongo (1855) found body impressions of worms, associated with poorly preserved jaws, from the Tertiary strata of Italy, and thus understood the real nature of scolecodonts. Similar material was discovered by Ehlers (1968a, 1968b) from the Jurassic lithographic shales of Solnhofen.

The four contributions by Hinde (1879, 1880, 1882, 1896) can be regarded as the initial point of scolecodontology. His material, derived from various Palaeozoic strata of North America and Europe, provided large numbers of new element-based genera and species (for discussion see chapter Taxonomy below). Excluding some incidental reports, since Hinde's work until 1930s no papers was published on polychaete jaw. In 1933, Croneis & Scott used the word "scolecodonts" for the first time, and this term became widely accepted. Stauffer (1933, 1939) described many new scolecodonts from the Ordovician and Devonian of North America. He was probably the first to apply dissolution method to obtain polychaete jaws from the carbonate rocks. In 1933, Eller published his first paper on Palaeozoic scolecodonts of North America (Eller 1933), which was followed by numerous others until 1969. Eller is the most "productive" scolecodontologist being enriched the literature with more than twenty publications and more than four hundreds of new names. In Europe, Eisenack (1939) and Zebera (1935) have described several Palaeozoic scolecodonts during the 1930s.

Lange (1947, 1949) described many articulated jaw apparatuses and isolated jaws of a species from the Devonian of Brazil. He noticed that many of his specimens display a great similarity with taxa described earlier. He introduced a set of new names for his material, actually creating the basis of a new taxonomic concept and a different (multi-element) classification. In subsequent years, Šnaidr (1951), Martinsson (1960) and Kozłowski (1956) published papers on other jaw apparatuses. Kozłowski got the first large collection of well-preserved jaw apparatuses, using improved methods of sample processing. His research has been continued by Kielan-Jaworowska (1961, 1962, 1966) who described a great number of apparatus-based genera and species. For the comparison with Palaeozoic material, Kielan-Jaworowska (1966) studied several apparatuses of recent polychaetes. In this paper, the principles of the family-level classification and a preliminary scheme of phylogeny of extinct forms. This monograph has remained the most important reference on fossil polychaetes. Important contributions have been issued also by Szaniawski (1968, 1970, 1974), Szaniawski & Wrona (1973, 1987), Zawidzka (1971, 1975), Mierzejewska & Mierzejewski (1974), Mierzejewski (1978a, 1978b), Mierzejewski & Mierzejewska (1975, 1977).

In the 1970s, numerous Mesozoic dispersed jaws and apparatuses were described (e.g., Kozur, 1971, 1972; Charletta & Boyer 1974; Szaniawski & Gazdzicki 1978). It

became apparent that eunicids passed a severe crises in latest Palaeozoic, when most taxa became extinct.

The next profound monograph after Kielan-Jaworowska's was that by Bergman (1989), which concerned Silurian paulinitids from Gotland, Sweden. Studies by Bergman (1989, 1991a, 1995), Eriksson & Bergman (1997) and Eriksson (1997) have greatly contributed for merging element- and apparatus based classifications and describing isolated elements with respect to apparatus concept.

Late Ordovician eunicid polychaetes of Baltic region are relatively well know. That is mostly on account of Kielan-Jaworowska's (1966) monograph and a subsequent paper by Szaniawski (1970). In addition, some of the specimens of Eisenack's (1975) collection are derived from the Harjuan of Estonia. North American material has been described mostly by Eller (1942, 1969). Almost nothing is known about the taxonomic composition and distribution of Late Ordovician polychaetes in the other regions of the world.

NATURE OF POLYCHAETE JAWS

Polychaete annelids of four orders may have their proboscides (eversible pharynx) armed with jaws, teeth or hard protuberances. Some representatives of nerillids, phyllodocids and terebellids have one or more pairs of simple needle-shaped or curved jaws, or rows of teeth. Jaws of the representative of these orders are unknown in fossil state and have no, or little taxonomic value below the family level. Only the representatives of the order Eunicida are equipped with complicated jaw apparatus, which may be reduced only in few endoparasitic and interstitial forms. Jaws of three firstly mentioned orders are unknown in fossil state and have no, or little taxonomic value below the family level.

Concerning the evolutionary origin of polychaete jaws, it is presumed that the jaws were first developed in pre-Ordovician eunicids as thickenings of pharyngeal cuticle. Later on, thin plates become thicker and subsequently folds and ridges developed into denticulated ridges. The common viewpoint that the polychaete jaws are composed of chitinous material has proved to be incorrect. According to Voss-Foucart et al. (1973), the jaws of recent eunicids are composed mainly of scleroprotein. Olive (1980) has shown much mixed composition, including tanned protein, amino-acids, glycerine, histidine and some metals. Jaws of several taxa have reinforcement of calcium carbonate (Colbath 1986; Colbath & Larson 1980). Calcite and fluorapatite have been traced in fossil jaws (Schwab 1966; Boyer 1981), but it is not entirely certain whether these minerals have been present in the original composition of jaws. There is no doubt, however, that the primary chemical composition is crucial for preservation of jaws (Brenchley 1979). It is possible also that the species of extinct families may have had somewhat different composition of jaws.

Development of the jaw apparatuses during the ontogeny of eunicids has been discussed in several papers (e.g., Kielan-Jaworowska 1966; Åkesson 1973; Mierzejewski 1978b; Colbath 1987; Paxton 1980). The basic question is whether they grew continuously or were replaced time after time by moulting. In several recent eunicids, moulting of the jaws has been observed, and the ontogenetic dimorphism may occur. Some evidences of shedding of maxillae in some primitive eunicids is present in the fossil record (Schwab 1966; Kielan-Jaworowska 1966; Mierzejewski 1978b). On the other hand, the mandibles of all taxa display growth lines and have likely grew continuously. It has been proposed that palaeontologists should tentatively assume that moulting occurred among the fossil polychaetes (Colbath 1987; Bergman 1989), although the reasons of the process and number of shedding times are not yet entirely certain.

ARRANGEMENT OF JAW APPARATUSES AND MORPHOLOGY OF SCOLECODONTS

The buccal armature of most eunicids is composed of one pair of ventral mandibles, and a multi-element, dorsal maxillary apparatus. Different elements are named by analogy with crustacean mouth parts. Most jaw elements of eunicids are paired, but usually the pairs are not perfectly symmetrical. Many apparatuses also possess some unpaired elements, like basal plates and left MIII. The maxillary apparatus, elements of which are most common, is usually composed of one to five plate-like maxillae; numerous teeth of simple morphology, and some other elements (basal plates and carriers). Dorsal sides of the maxillae are provided with denticulated ridges, usually arranged perpendicular to longitudinal axis of the apparatus (and worms body).

On the basis of shape, number and arrangement of different elements, five types of jaw apparatuses have been generally recognised (see Fig. 3). The **labidognath** type is characterised by maxillae arranged, when retracted, in two semicircles, and by relatively short and broad carriers. The **prionognath** type has maxillae arranged in two

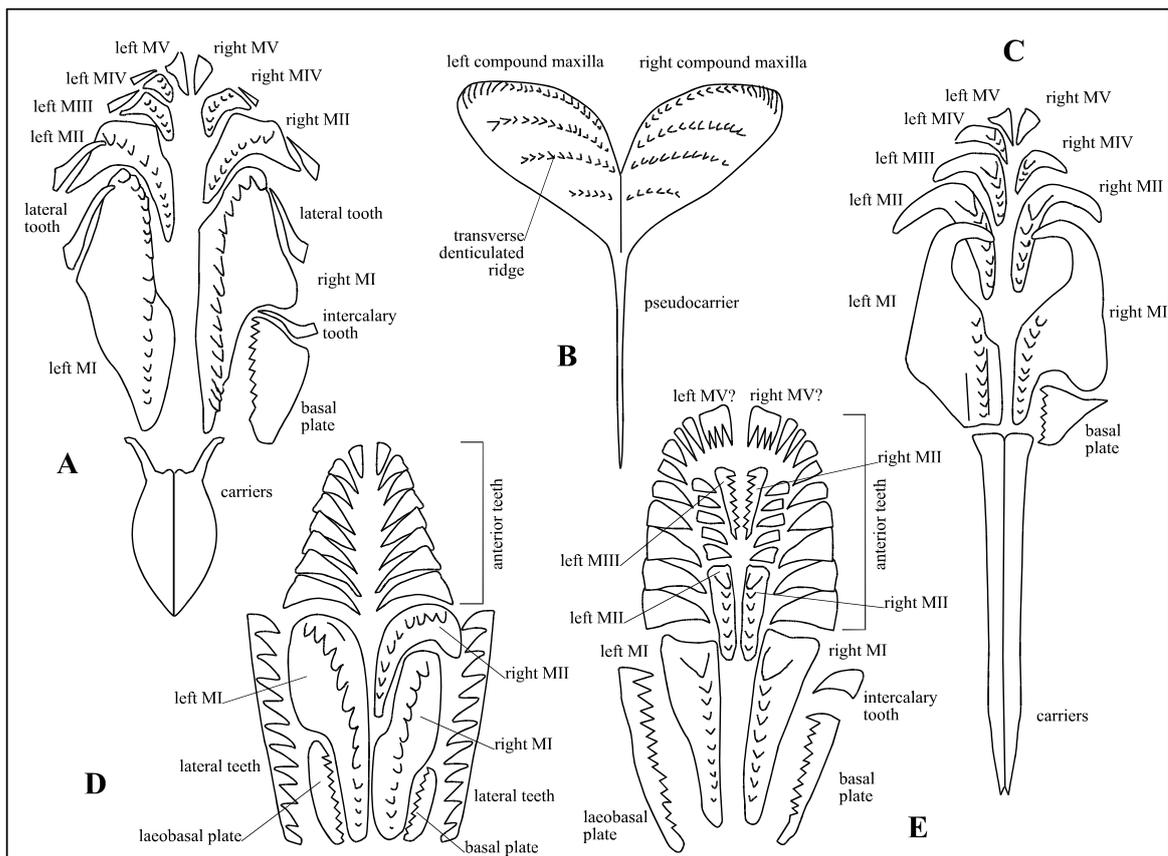


Figure 3. Five main types of polychaete jaw apparatuses (after Kielan-Jaworowska 1966 and Mierzejewski & Mierzejewska 1975; see explanation in text). Maxillary apparatuses, all in dorsal view: **A** – Labidognatha (Polychaetaspidae); **B** – Xenognatha (Archaeoprionidae); **C** – Prionognatha (Atraktoprionidae); **D** – Placognatha (Mochtyellidae); **E** – Ctenognatha (Tetraprionidae).

parallel rows, and very long carriers. The **placognath** type possesses plate-like maxillae with one or more denticulated ridges in the posterior part complemented by rows of teeth in the lateral sides and anterior part of the apparatus. The **ctenognath** type has several symmetrically arranged maxillae and numerous rows of teeth. The **xenognath** type is characterised by two symmetrical plates provided with four sub-transversal denticulated ridges and a single pseudocarrier.

Some authors have proposed to use dental formulae for the descriptions of polychaete jaws (Taugourdeau 1968, 1976; Jansonius & Craig 1971). However, they were constructed with regard to the element-based classification and, as mentioned by Germraad (1980) and Bergman (1989), are typographically complicated, difficult to read and compare. Concerning corresponding jaws within a genus, the use of a dental formula may prove practical if it is sufficiently simple and the dentaries are relatively complex. For the purpose of present investigation, it proved to be useful and rather simple to distinguish denticles of different size classes using operators “greater than” and “smaller than” (< and >). For instance, if a particular jaw is provided with one precuspidal denticle, single cusp, two or three intermediate denticles, one large denticle and six to ten normal, continuously decreasing denticles, the formula would be $1<1>2-3<1>6-10$ (see also Fig. 4G).

Terminology

The basic terminology used in the descriptions of polychaete jaw apparatuses and their elements was introduced by Kielan-Jaworowska (1966). Some additions and modifications were proposed by Jansonius and Craig (1971), Taugourdeau (1976) and Wolf (1980). Since some terms have been differently understood, a glossary of the most important terms used in this study is given below. Figure 4 illustrates morphology and terminology of most common types of Ordovician polychaete jaw elements.

anterior margin – mostly in basal plates: anteriormost margin which is nearly perpendicular to apparatus axis.

anterior teeth – in placognatha and ctenognatha: simple or complex single teeth in front of the maxillae.

antero-lateral margin – the margin from anterior to maximum lateral extension of the jaw.

basal plate – right-hand jaw closely fitting into a posterior bight of right posterior maxillae, if fused with maxilla it is called basal ridge.

basal ridge – in right posterior jaws of placognatha and some prionognatha: a ridge (denticulated or smooth), homologous to the basal plate.

bight – in prionognatha and labidognatha maxillae: concavity of outer postero-lateral margin.

carriers – paired elements, occurring behind the maxillae and serving as support for their posterior ends.

cover – part of jaw wall enclosing myocoele opening in the ventral side. Present in labidognaths and placognaths.

dentary – denticulated ridge, series of denticles most often arranged (sub)parallel to apparatus axis.

denticle – single conical teeth in the dentary.

hook – mostly in prionognatha: sickle-shaped extension of the anterior part of posterior maxillae.

inner face – the inner lateral side of the jaw.

inner margin – the margin, which is closest to the axis of the apparatus and nearly parallel to it.

inner wing – mostly in the posterior maxillae: lateral flat extension of the jaw from dentary to inner margin.

intercalary tooth – a single slender denticle inserted in front of the basal plate.

laeobasal plate – uncommon paired element of basal plate.

laeobasal ridge – in placognatha: a ridge, homologous to laeobasal plate.

laeointercalary tooth – element paired with intercalary tooth.

lateral teeth – in placognatha: rows of teeth in the outer lateral part of maxillae; in labidognatha and prionognatha: single teeth associated with maxillae.

length (abbr. L) – largest dimension of a jaw parallel to apparatus axis, measured from anterior part.

ligament scar – in labidognaths and prionognaths: small, dull roughened area behind in the posteriormost part of lateral side of shank marking an area of muscle attachment.

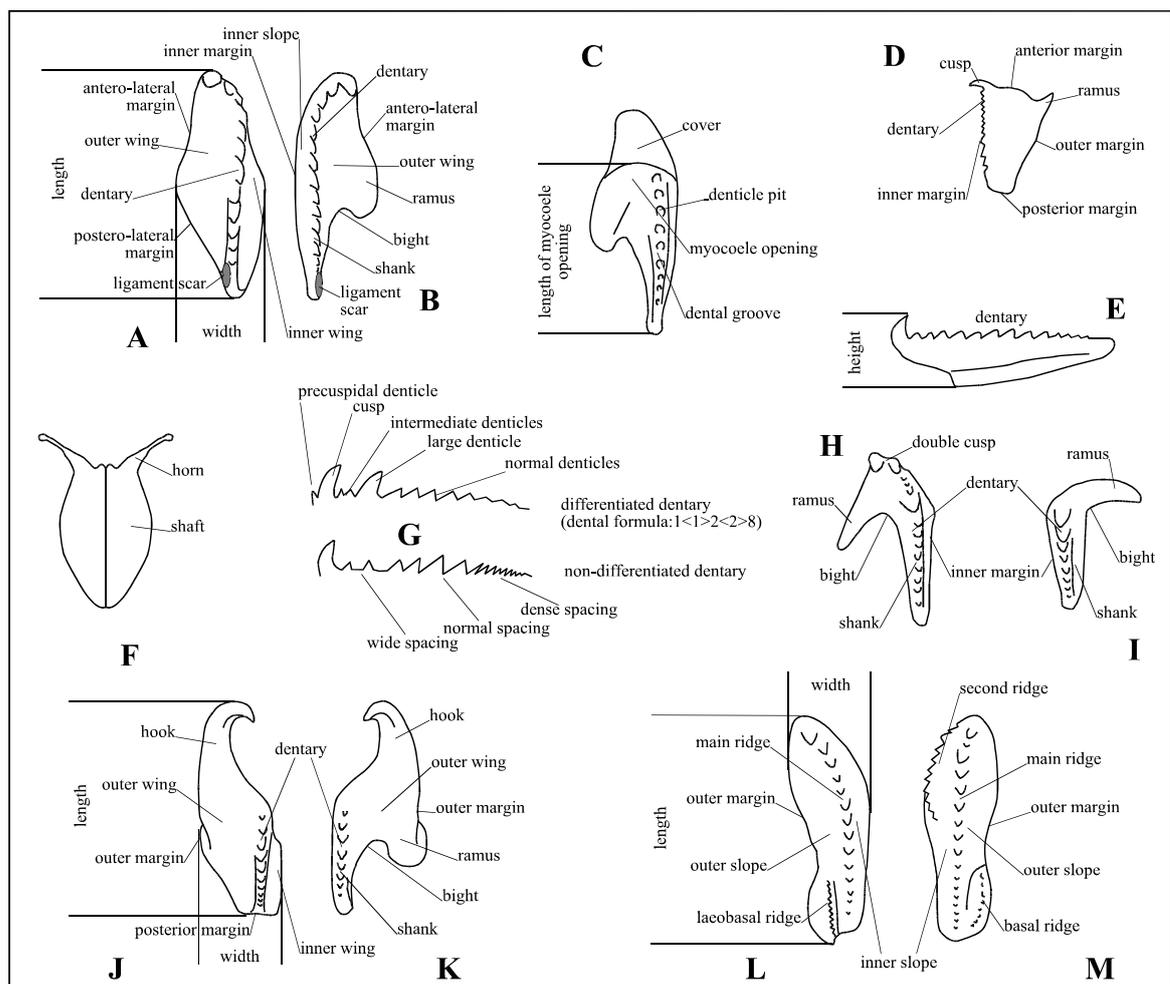


Figure 4. Morphology and descriptive terminology of different elements of polychaete jaw apparatuses: **A** – left MI of a polychaetaspid; **B** – right MI of a polychaetaspid; **C** – the same, in ventral view; **D** – basal plate of a polychaetaspid; **E** – right MI of a polychaetaspid, in left-lateral view; **F** – carriers of a polychaetaspid; **G** – dentaries of different type (see explanation of dental formula in text); **H** – left MII of a ramphoprionid; **I** – right MI of an atraktoprionid; **J** – left MI of an atraktoprionid; **K** – right MI of an atraktoprionid; **L** – left compound maxilla of a mochtyellid; – right compound maxilla of a mochtyellid.

main ridge – in placognaths: main (longest) row of denticles.

maxilla – major, usually denticulated elements of an apparatus. Up to five maxillae in both sides of apparatus may be present, numbered from posterior to anterior (abbr. MI-MV).

myocoele – space inside the jaw; may be partially closed by the cover (in labidognaths and prionognaths).

outer face – the outer lateral slope of the jaw.

outer margin – the margin, which is most distant from the axis of the apparatus and nearly parallel to it.

outer wing – extension of the jaw from dentary to the outer margin.

posterior margin – in some labidognatha and prionognatha: the posteriormost margin of the jaw, which is sub-perpendicular to apparatus axis.

Postero-lateral margin – the margin from maximum lateral extension to posterior of the jaw.

ramus – mostly in labidognaths and prionognaths: arm-like lateral extension of the outer wing; in maxillae directed posteriorly, in basal plates anteriorly.

ridge – denticulated or smooth narrow dorsal or lateral extension of jaw.

second ridge – in placognatha: a short ridge in the anterior part of right MI, left to main ridge.

shank – mostly in labidognatha and prionognatha: backward extension of the posterior part of the jaw from posterior to the anteriormost part of the bight.

width (W) – largest dimension of a jaw, perpendicular to apparatus axis.

TAXONOMY

Classification of recent eunicids is based mostly on soft parts and chetae (George & Hartman-Schröder 1985). Such parts of polychaetes are extremely rare in fossil state and only rare examples are known so far (in Cenozoic material by Massalongo 1855, from the Jurassic by Ehlers 1868a, 1868b, from the Carboniferous by Thompson 1977 [and from the Silurian by Briggs et al. 1996]). However, jaws of eunicid polychaetes (scolecodonts) are common microfossils throughout the Palaeozoic, though somewhat less frequent in younger strata. The taxonomic value of polychaete jaws has been under debate. The early students of fossil scolecodonts, first of all Hinde (1879, 1880, 1882, 1896), being aware of their origin considered classification of scolecodonts tentative. The explanation of this treatment is found in a paper of Claparede (1870), who stated that it was impossible to use polychaete jaws for any taxonomic study. The same opinion prevailed until 1940s, before the introduction of the multi-element species concept in papers by Lange (1947), Šnaidr (1951), Kozłowski (1956), Martinsson (1960) and especially Kielan-Jaworowska (1961, 1962, 1966). Kielan-Jaworowska (1966) noted that the subgeneric taxa based on jaw apparatuses may represent systematic units somewhat smaller or larger than the recent species, but that would not affect the study in general.

For forty years since the apparatus based systematics was introduced, the opinion that the natural systematic units can be recognised only on the basis of fused jaw apparatuses prevailed. Latest studies by Bergman (1987, 1989) and Eriksson (1997) have shown that a “good” species and subspecies may be introduced solely on the basis of isolated elements grouped into hypothetical apparatuses. This approach is supported by the availability of rich material of detached jaws, enabling better understanding of variability of the species. Moreover, it should be noted also that some modern works on recent polychaetes have pointed taxonomic value of jaws and shown their applicability both at species- and higher taxonomic levels (George & Hartmann-Schröder 1985).

In consequence, the species of fossil eunicids based on jaws, as understood also in this study, may not have one-to-one correspondence to particular biological entities. However, this possible shift concerns most animal groups recorded as fossils and since the jaws are the best documentation we ever will have of extinct eunicids, taxonomy of these worms should be based on the jaws.

Reconstruction of jaw apparatuses

The most common detached elements often cannot be referred to higher taxa. Fused jaw apparatuses are relatively rare and until the “wet” technique of the etching method was employed, only rare specimens were known. In early Caradocian material of Estonia (Hints in press) mainly one jaw apparatus per several hundreds of isolated jaws has been found, with rare exceptions. However, it is usually possible to reconstruct the

apparatus from detached elements, even if no fused jaws are recovered. There are several examples of such attempts made by different contributors (e.g., Sylvester 1959; Kielan-Jaworowska 1966; Szaniawski 1968, Corradini & Olivieri 1974; Männil & Zaslavskaya 1985a, 1985b; Bergman 1989, 1991; Eriksson 1997; Eriksson & Bergman 1997; Hints 1998, in press). The main criteria to refer separately found elements to an apparatus (and species) are co-occurrence of different elements and morphological criteria. Co-occurrence has been widely used also by conodontologists. Under morphological criteria, arrangement of the dentaries (e.g., size and shape, and size ratios of denticles); size and colour of the jaws; ultrastructures; the general appearance (often very similar in paired jaws) and some specific features (for instance, presence of small concave lateral extensions in right and left jaws) may be good reasons assigning them to one and the same species.

Reconstructions based on isolated elements have some advantages over fused apparatuses. They allow more accurate estimation of the range of variability and provide more detailed information of morphology of individual elements, which in fused apparatuses are usually rather small and partly cover each other. The main disadvantage of such reconstructions is that only certain part of the apparatuses can be reconstructed. For instance, right and left posterior maxillae of polychaetaspids can be quite easily (and correctly) assigned to a species, even if several species co-occur. Minor parts, especially various single teeth can hardly be successfully assigned to a reconstruction. Some groups having numerous elements of simple morphology can never be reconstructed from detached material. Thus, it remains necessary to seek for fused apparatuses besides just producing reconstructions.

Problems of the “element-based taxonomy”

In the earlier publications, every single jaw plate or teeth was given a name. A few genera were defined on the basis of superficial similarity with living forms (*Eunicites* Ehlers, *Lumbriconereites* Ehlers, *Arabellites* Hinde, *Oeononites* Hinde) and scolecodonts of very different morphology assigned to them. Most genera, were established to group elements of specific morphology. This approach led to a great number of form taxa, actually grouping certain elements of the apparatuses, e.g. right posterior maxillae, basal plates, carriers. Majority of names were based on very few specimens, ignoring the variability of the material.

When the apparatus-taxonomy was established, new taxa were kept separate from element-classification for several reasons (Lange 1947; Kielan-Jaworowska 1966, 1968; Szaniawski & Wrona 1973). The situation appeared to be in conflict with ICZN rules, stating that the names based on parts of organisms or less complete specimens (that is element-taxa in this case) are valid having a priority over younger names based on more complete material (apparatus-taxa; ICZN Article 23). As a result, many names of “biological” classification would turn younger synonyms when the two classification would be combined. It should be mentioned that this mainly concerns Palaeozoic forms,

as majority of the material described under element-based taxonomy derives from the Palaeozoic rocks (mainly Ordovician to Devonian).

Several attempts have been made to merge two classifications, following the nomenclature rules. The first and so far the largest revision was that by Kozur (1970). In that study, element- and apparatus based classifications were combined at the genus level. However, this attempt failed in its object, mostly because the type collections were not inspected by this author. Many of Kozur's proposals were later considered as inaccurate or premature (Szaniawski & Wrona 1973). More beneficial was the work by Jansonius & Craig (1971), who did not try to combine the two sets of names but started to sort out scolecodont systematics. Their revision resulted in election of several lectotypes and type species, whereas some genera have been regarded as nomina dubia and several new genera have been erected for the other (identifiable) taxa.

It is obvious that revision of the genera should be the first step amending the systematic disorder. In other words, all type species, holotypes (or other types) of which are distinguishable at species level, will convey the generic name following the priority rule, and the generic diagnosis should be emended according to apparatus concept. In consequence, the idea of natural classification will remain working and some names will change. The second stage is revision at species level, so that species, types of which are potentially identifiable are included to the corrected set of genera. The names based on material insufficient for species level determination should be regarded as nomina dubia. In practice, however, this is more complicated, mostly as due to insufficient number, and poorly preserved or -exposed type material. In many cases re-sampling of type localities would be essential prerequisite for success and the only mean to reveal other elements of particular apparatuses. Concerning many tens of element-genera and hundreds of -species, this would be enormous work to do at once, and is likely beyond one student's reach.

However, step by step revisions would lead to desirable results. Recent works by Bergman (1989, 1991a, 1995) and Eriksson & Bergman (1997) are good examples of detailed works based on apparatus concept, while considering the material from earlier studies as well. Still, the replacement of the generic name *Polychaetaspis* Kozłowski with *Oenonites* Hinde as proposed by Eriksson (1997) is, in my opinion, premature. The type specimen of the type species of *Oenonites*, being the only specimen of this species, is rather poorly preserved right MI. It likely belongs to the same genus as the type of *Polychaetaspis*, but the material and the state of preservation do not allow confident identification of the species. Further, the emended generic diagnosis of *Oenonites* given by Eriksson (1997) regards only the one element of an apparatus and hence not following the multi-element concept. For these reasons I have not accepted this emendation in the present study.

SYSTEMATIC PALAEOONTOLOGY

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Order Eunicida Dales, 1963

Mochtyellidae Kielan-Jaworowska, 1966

***Mochtyella* Kielan-Jaworowska, 1961**

Type species: *Mochtyella cristata* Kielan-Jaworowska, 1961

***Mochtyella cristata* Kielan-Jaworowska, 1961**

Plate 1, figs 1–2.

1961. *Mochtyella cristata* nov. sp. Kielan-Jaworowska, pp. 248-253, pls 5-7.

1966. *Mochtyella cristata* Kielan-Jaworowska, p. 54, pl. 1 fig. 1, text-fig. 5A.

1970. *Mochtyella cristata* Kielan-Jaworowska, Szaniawski, pp. 448, 449, pl. 1 fig. 4.

1985. *Mochtyella* cf. *cristata* Kielan-Jaworowska, Männil & Zaslavskaja, p. 105, pl. 14 figs 1a-d, 2a-b

Holotype: apparatus ZPAL O.188/1 figured by Kielan-Jaworowska 1961, pl. 7C.

Type locality: erratic boulder No. O.188 found in Poland

Type stratum: ?Middle Ordovician.

Material: approximately 670 posterior maxillae. Orjaku drill core, 33.10-124.43 m; Laeva-18 drill core, 175.64-228.81 m; Valga drill core, 319.4-321.85 m.

Occurrence: Idavere to Juuru stages (Caradoc-Llandovery) of Baltoscandia, Llandovery and Wenlock of Severnaya Zemlya.

***Mochtyella polonica* Kielan-Jaworowska, 1966**

1966. *Mochtyella polonica* sp. nov. Kielan-Jaworowska, pp. 54-56, pl. 3, fig. 1, text-fig. 1A.

Holotype: apparatus ZPAL O.344/1, figured by Kielan-Jaworowska 1966, pl. 3 fig. 1.

Type locality: erratic boulder No. O.344 found in Poland.

Type stratum: unknown (Ordovician or Silurian).

Material: approximately 60 posterior maxillae. Orjaku drill core, 33.10-101.10 m; Laeva-18 drill core, 178.64-228.81 m; Valga drill core, 368.90 m.

Occurrence: Ordovician or Silurian erratic boulders from Poland, Idavere to Juuru stages (Caradoc - Llandovery) of Estonia.

***Mochtyella duplicidentata* Szaniawski, 1970**

1970. *Mochtyella duplicidentata* sp. nov., Szaniawski, pp. 451-453, pl. 1 fig. 3.

Holotype: apparatus ZPAL Sc. I/9, figured by Szaniawski 1970, pl. 1 fig. 3.

Type locality: Mielnik borehole, depth 1120-1154 m.

Type stratum: ?Upper Ordovician.

Material: about 140 posterior maxillae. Orjaku drill core, 47.62-124.43 m; Laeva-18 drill core, 174.63-181.91 m.

Occurrence: ?Upper Ordovician of Poland, Idavere to Juuru stages (Caradoc-Llandovery) of Estonia.

Remarks. – Systematic position of *Mochtyella duplicidentata* was questioned by Mierzejewski (1978a) as this species commonly lacks the second ridge and the basal ridge. The present collection contains some rather large specimens which have extremely minute second ridge developed in the middle portion of the inner face in right MI. Concerning other features, these specimens are identical to those lacking the second ridge. Although the basal ridge is weakly fused to the main jaw and most often

disintegrated, Mierzejewski's opinion about separateness of this species cannot be supported and *Mochtyella duplicidentata* must be regarded as a typical representative of the genus *Mochtyella*. On the other hand, it reveals that presence or absence of a second ridge, if very small, may not be a good characteristic distinguishing species, not to mention genera.

***Mochtyella* sp. A**

M a t e r i a l : about 40 posterior maxillae. Orjaku drill core, 47.62-92.40 m; Laeva-18 drill core, 170.93-174.63 m; Valga drill core, 381.40 m.

O c c u r r e n c e : Caradoc and Ashgill of Estonia

Description. – Right MI: L=0.3-0.6 mm, L/W=2.9. Jaw is anteriorly pointed. Main ridge has 12-14 denticles. Second ridge is straight, comprising 6-7 denticles and corresponding to 0.3-0.5 of jaw length. It extends to 0.5-0.6 of jaw length from anterior. Basal ridge with about 9 denticles is straight having 0.20-0.33 of jaw length.

Left MI: L=0.76-0.90 mm, L/W=3.0. Jaw is anteriorly nearly rounded. Main ridge comprising 14-18 denticles is slightly curved. Cusp is indistinct, followed by one intermediate denticle. Laeobasal ridge with 11 denticles is laterally compressed, high and separated from the other part of the jaw posteriorly. It has length about half of jaw length and does not reach the end of the main ridge posteriorly.

Remarks. – *Mochtyella* sp. A is closely related to *M. polonica*. The left jaws are hardly distinguishable when the species occur together, although the laeobasal ridge is relatively longer and the jaw is anteriorly less pointed in left MI of *Mochtyella* sp. A. Right MI of *Mochtyella* sp. A differs from *M. polonica* in having longer denticulated second ridge and more distinct and stronger basal ridge.

Insufficient knowledge of anterior part of the apparatus does not allow naming of this species at the time being.

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

M a t e r i a l : about 22 posterior maxillae. Orjaku drill core, 54.00-107.40 m; Laeva-18 drill core, 175.64-181.91 m; Valga drill core, 313.45-321.85 m.

Remarks. – Kielan-Jaworowska (1966) distinguished two subdivisions within the genus *Mochtyella* — the *Mochtyella cristata* and *M. trapezoidea* groups. Representatives of the last mentioned group, characterised by very high jaws, long laeobasal plate and lack of the second ridge are typical of the Silurian fauna rather than the Ordovician one. Possibly *M. trapezoidea* and the related forms, including *M. angelini* Mierzejewski, 1978, represent a separate genus of mochtyellids, which due to insufficient material cannot be introduced at the time being.

The scolecodonts similar to the jaws of *M. trapezoidea* are very rare in the present collection and cannot be referred to any particular species of this group.

***Paramochtyella* gen. nov.**

D e r i v a t i o n o f n a m e : Lat. *para* – untrue, referring to previous systematic position of the type species.

T y p e s p e c i e s : *Paramochtyella fragilis* (Szaniawski, 1970)

Stratigraphical and geographical range: Ordovician and Silurian of Baltoscandia.

Species included:

Paramochtyella fragilis (Szaniawski, 1970)

Paramochtyella grazynae (Mierzejewski, 1978)

Diagnosis. – *Paramochtyella* differs from *Mochtyella* in having posterior jaws wider, curved anteriorly, provided with large and blunt denticles in the main ridge. The laeobasal ridge of *Paramochtyella* is longer than typically in *Mochtyella* having a distinctly large and blunt anteriormost denticle. *Paramochtyella* differs from *Pistoprion* and *Vistulella* in having one compound maxilla in the right side of apparatus instead of two or three jaw plates like in *Pistoprion* and *Vistulella*, respectively. The posteriormost anterior teeth of *Paramochtyella* are developed as denticulated plates resembling those of *Multiprion* and *Oxyprion*. *Paramochtyella* differs from the last mentioned genera in having wider posterior jaws with notably larger denticles.

Remarks. – An incomplete apparatus recovered from the Middle Ordovician of Estonia suggests genus-level distinctness of *Paramochtyella fragilis*. Particular feature for that is the form of posteriormost anterior teeth, which look much alike elements considered as anterior maxillae by Szaniawski (1968) and Szaniawski & Wrona (1973). The present collection contains no fused apparatuses, but in addition to posterior maxillae, several detached elements, the posteriormost anterior teeth of *Paramochtyella fragilis* have been found.

Paramochtyella grazynae is assigned to this genus on the basis of outline of jaws and morphology of denticles. Some specimens similar to, but apparently not conspecific with *Paramochtyella fragilis* have been recorded from the lowermost Silurian of the Orjaku core.

***Paramochtyella fragilis* (Szaniawski, 1970)**

Plate 1, fig. 3.

1970. *Mochtyella fragilis* nov. sp. Szaniawski, pp. 453-454, pl. 2 figs 5-7.

1970. *Mochtyella multilamellata* nov. sp. Szaniawski, pp. 454-456, pl. 2 figs 1-4.

1978. *Mochtyella fragilis* Szaniawski; Mierzejewski, pp. 75-80, pl. 16.

H o l o t y p e : Left MI ZPAL Sc I/13, figured by Szaniawski 1970, pl. 2 fig. 6.

T y p e l o c a l i t y : Mielnik borehole 1120-1154 m.

T y p e s t r a t u m : ?Upper Ordovician.

M a t e r i a l : about 240 isolated posterior maxillae. Orjaku drill core, 47.62-112.5 m; Laeva-18 drill core, 178.64-228.81 m; Valga-10 drill core, 368.9-381.4 m.

O c c u r r e n c e : ?Upper Ordovician of Poland, Kunda to Juuru stages (Llanvirn-Llandovery) of Estonia.

***Pistoprion* Kielan-Jaworowska, 1966**

T y p e s p e c i e s : *Pistoprion transitans* Kielan-Jaworowska, 1966

***Pistoprion transitans* Kielan-Jaworowska, 1966**

Plate 1, fig. 4.

1966. *Pistoprion transitans* nov. sp. Kielan-Jaworowska, pp. 60-62, pl. 3 fig. 2, pl. 4 fig. 2, pl. 7, text-fig. 5B.

1970. *Pistoprion transitans* Kielan-Jaworowska; H. Szaniawski, pp. 457-458; pl. 3 figs 5-7.

H o l o t y p e : apparatus ZPAL O.213/1, figured by Kielan-Jaworowska 1966, pl. 6 fig. 2.
T y p e l o c a l i t y : erratic boulder No. O.213 found in Poland.
T y p e s t r a t u m : unknown (Ordovician or Silurian).
M a t e r i a l : about 950 posterior maxillae. Orjaku drill core, 33.10-122.55 m; Laeva-18 drill core, 170.93-228.81 m; Valga drill core, 316.4-321.85 m.
O c c u r r e n c e : Ordovician or Silurian erratic boulders from Poland, Idavere to Juuru stages (Cardoc - Llandoverly) Estonia.

***Vistulella* Kielan-Jaworowska, 1961**

T y p e s p e c i e s : *Vistulella kozlowskii* Kielan-Jaworowska, 1961

***Vistulella kozlowskii* Kielan-Jaworowska, 1961**

Plate 1, figs 9–11.

1961. *Vistulella kozlowskii* nov. sp., Kielan-Jaworowska, pp. 243-248, pl. 1-4, text-fig. 2.

1966. *Vistulella kozlowskii* Kielan-Jaworowska, Kielan-Jaworowska, p. 64, text-fig. 5c.

1978. *Vistulella kozlowskii* Kielan-Jaworowska, Mierzejewski, p. 2278, fig. 1.

H o l o t y p e : apparatus ZPAL O.245/6, figured by Kielan-Jaworowska 1961, pl. 1.

T y p e l o c a l i t y : erratic boulder No. O.245 found in Poland.

T y p e s t r a t u m : ?Silurian.

M a t e r i a l : about 150 detached jaws. Orjaku drill core, 33.10-112.50 m; Laeva-18 drill core, 175.64-176.75 m.

O c c u r r e n c e : Ordovician and Silurian Erratic boulders from Poland, Jõhvi to Juuru stages (Caradoc - Llandoverly) North Estonia.

***Rakvereprion* Mierzejewski, 1978**

T y p e s p e c i e s : *Rakvereprion balticus* (Eisenack, 1975).

***Rakvereprion balticus* (Eisenack, 1975)**

Plate 1, figs 13, 15; Plate 2, fig. 17.

1975. *Staurocephalites? balticus* sp. nov. Eisenack, fig. 45-46.

1978a. *Rakvereprion balticus* (Eisenack); Mierzejewski, p. 280, pl. 2 fig. 2.

M a t e r i a l : approximately 270 posterior maxillae. Orjaku drill core, 76.65 m; Laeva-18 drill core, 178.64-228.08 m; Valga drill core, 327.30-369.67 m.

Rhytiprionidae Kielan-Jaworowska, 1966

***Rhytiprion* Kielan-Jaworowska, 1966**

T y p e s p e c i e s : *Rhytiprion magnus* Kielan-Jaworowska, 1966

***Rhytiprion magnus* Kielan-Jaworowska, 1966**

Plate 2, figs 1–4.

1966. *Rhytiprion magnus* nov. sp., Kielan-Jaworowska, pp. 66-68, pl. 8, text-fig. 5D.

1966. *Rhytiprion* sp. a, Kielan-Jaworowska, p. 68, pl. 9, fig. 1.

1970. *Rhytiprion magnus* Kielan-Jaworowska, Szaniawski, pp. 459-460, pl. 4 figs 5-6.

H o l o t y p e : incomplete apparatus ZPAL O.256/12, figured by Kielan-Jaworowska 1966, pl. 8 fig. 5.

T y p e l o c a l i t y : erratic boulder No. O.256 found in Poland

T y p e s t r a t u m : ?Ordovician.

M a t e r i a l : about 90 posterior maxillae. Orjaku drill core, 76.65-107.40 m; Laeva-18 drill core, 180.44-228.81 m; Valga drill core, 373.35-381.40 m.

O c c u r r e n c e : ?Ordovician erratic boulders from Poland, Jõhvi and Rakvere stages of North Estonia.

Xanioprionidae Kielan-Jaworowska, 1966

Xanioprion Kielan-Jaworowska, 1962

Type species: *Xanioprion borealis* Kielan-Jaworowska, 1962

Xanioprion tenuidentatus sp. nov.

Plate 1, figs 7–8.

Derivation of name: Lat. *tenuis* – fine, slender; *dentatus* – toothed, referring to small and densely spaced denticles in MII.

Holotype: Left MII GIT Sc 107; Plate 1, fig. 8.

Type locality: Laeva-18 borehole, depth 225.15 m.

Type stratum: Mõntu Formation, Nabala Regional Stage (top Caradoc).

Material: six MII. Laeva-18 drill core, 197.51–225.15 m; Orjaku drill core, 87.11–92.4 m.

Occurrence: Nabala to Pirgu regional stages (top Caradoc - Ashgill).

Diagnosis. – *Xanioprion tenuidentatus* differs from other xanioprionids in having very slender and densely spaced denticles in MII.

Description. – Apparatus consists of probably elongated right and left MI (not yet recovered), and arcuate right and left MII.

Right MI: Jaw is arcuate, its length along the dentary is 0.22–0.41 mm. Inner face relatively wide. Ramus distinct, usually a drop-like, arranged to the main part of jaw by right angle. Dentary comprises about 16 slender, densely spaced and slanting denticles in the main part of the ridge, and numerous very small, somewhat irregularly arranged denticles in the ridge on the ramus. Number of these small denticles may reach to about 15.

Left MI is mirror image of right MI.

Variability. – Outline of MII seems to vary widely, whereas the type of denticulation is rather consistent in all specimens recovered.

Xanioprion sp. A

Plate 1, fig. 6.

Material: about 70 left and right MII. Orjaku drill core, 33.10–127.45 m; Laeva-18 drill core, 172.45–186.64 m; Valga drill core, 368.90–378.10 m.

Description. – Posterior part of the apparatus of *Xanioprion* sp. A consists of elongated MI fitting into cavity of posterior margin of arcuate MII in both sides, and basal and laeobasal plates.

Left MII: L=1.3 mm, L/W=1. Jaw is arcuate, without clear ramus and shank. Curved dentary has 11 sharp denticles, size of which decrease distally. Inner wing has postero-laterally directed rounded extension and prominent concavity left to it. Jaw wall is fragile in the lowermost part and thus the jaw margin is somewhat irregular. Borders between denticles are prolonged into the jaw wall in form of grooves in the anterior and inner side.

Right MII is a mirror image of the right MII.

Remarks. – *Xanioprion* sp. A is similar to *X. borealis* but differs from it in absence of pointed ramus, in having rounded postero-lateral extension and cavity in the posterior part of the jaws.

***Xanioprion* sp. B**

Plate 1, fig. 5.

Material: About 360 posterior maxillae. Orjaku drill core, 47.62-127.45 m; Laeva-18 drill core, 170.93-227.57 m; Valga drill core, 321.85-367.26 m.

Description. – Jaw apparatus consists of two symmetrical elongated MI and elongated basal and laeobasal plates.

Right MI: L=0.46 mm, L/W=3.6. In the first 0.15 of jaw length it has laterally directed pointed ramus, which has length less than one-fifth of the jaw length. The main portion of jaw is narrow, nearly straight and composed of row of 16 posteriorly and anteriorly decreasing denticles. Antermost part of the ridge in the ramus is undenticulated. In the mid-third of jaw, the borders between denticles, especially in the proximal jaw wall, are developed in form of upward narrowing rifts. Denticles are weakly fused to each other in the upper part of jaw only (see Fig. 9 C, E). Therefore the anterior and posterior parts of jaws being more compact, are, in most cases, found disintegrated.

Basal plate is almost as long as right MI. It consists of a row of denticles, from which at least three first ones are long and sharp, weakly fused teeth.

Remarks. – *Xanioprion* sp. B differs from other xanioprionids described so far in having one pair of main jaws (MI) instead of two (MI and MII).

Material described herein is probably conspecific with that mentioned by Kielan-Jaworowska (1966, p. 65) as a new species with one jaw (MI) instead of two jaws (MI and MII). Mierzejewski's (1978a) opinion that these undescribed apparatuses of *Xanioprion* may be congeneric with *Rakverepriion* Mierzejewski seem to be unfounded. The specimens assigned to *X. borealis* and figured by Kielan-Jaworowska (1962, pl. 12-13) and Szaniawski (1970) are similar to broken specimen of *Xanioprion* sp. B rather than to type specimen of *X. borealis* (Kielan-Jaworowska, 1962, pl. 11).

Tetraprionidae Kielan-Jaworowska, 1966

***Tetraprion* Kielan-Jaworowska, 1966**

Type species: *Tetraprion pozaryskae* Kielan-Jaworowska, 1966

***Tetraprion pozaryskae* Kielan-Jaworowska, 1966**

1966. *Tetraprion pozaryskae* nov. sp. Kielan-Jaworowska 1966, pp. 76-77, pl. 6, text-fig. 4B.

Holotype: apparatus ZPAL O.400/62, figured by Kielan-Jaworowska 1966, pl. 10 fig. 2.

Type locality: erratic boulder No. O.400 found in Poland.

Type stratum: ?Middle Ordovician.

Material: about 150 posterior maxillae. Orjaku drill core, 47.62-127.45 m; Laeva-18 drill core, 178.64-200.50 m; Valga drill core, 367.26 m.

Occurrence: ?Middle Ordovician erratic boulders from Poland, Idavere to Pirgu stages (Caradoc - Ashgill) of Estonia.

***Valgaprion* gen. nov.**

Derivation of name: named after the Type locality of the type species of this genus.

Type species: *Valgaprion huberti* sp. nov.

Stratigraphical and geographical range: Late Ordovician of Estonia.

Diagnosis. – *Valgaprion* differs from *Tetraprion* in having anterior portions of the posterior maxillae rounded instead of being provided with straight or concave anterior margin like in *Tetraprion*, and in lacking a distinct cusp in posterior maxillae. In addition, the mandibles are relatively much larger in *Valgaprion*.

***Valgaprion huberti* sp. nov.**

Plate 2, figs 5–16.

Derivation of name: named in honour of Professor Hubert Szaniawski.

Holotype: Incomplete apparatus GIT Sc 123, Plate 2, figs 12–16.

Type locality: Valga borehole, depth 321.85 m.

Type horizon: Kuldiga Formation, Porkuni Regional Stage (Late Ashgill)

Material: three incomplete apparatuses, more than 220 posterior maxillae, some MII, MIII, basal and laeobasal plates. Valga borehole, depth 313.45–368.9m; Orjaku borehole, depth 47.62–127.45 m.

Occurrence: Rakvere to Porkuni Regional Stages (Late Caradoc and Ashgill) of Estonia.

Diagnosis. – As for the genus.

Description. – Apparatus consists of left and right MI, MII, MIII, MIV, basal plate, laeobasal plate and number of lateral and anterior teeth.

Right MI: L = 0.21–0.80 mm, L/W = 2.2–4.5. Outline of the elongated jaw is sub-oval or bow-, or drop-like, wider anteriorly. Inner and outer margins are sometimes irregular as the edge of the jaw wall is thin and fragile. There are usually narrow inner and outer wings surrounding the jaw or part of it. The dentary consists of 10–17 denticles which most often are arranged so that the one or two larger ones are preceded by up to three small denticles. The myocoele is gaping.

Left MI: L = 0.3–0.76 mm, L/W = 2.3–6.6. The jaw is almost identical to the mirror reflection of the right MI, except being very slightly shorter while arranged in an apparatus. Besides its dentary has 10–15 denticles.

Right MII: Jaw is similar to right MI, comprising about 0.6 of length of right MI.

Conjungaspidae fam. nov.

Diagnosis. – Jaw apparatus of Conjungaspidae is similar to those of labidognaths as it is similarly composed of posteriorly rounded carriers, several pairs of maxillae, basal- and laeobasal plates, intercalary- and laeointercalary teeth and lateral teeth. Apparatus of Conjungaspidae differs from those of other labidognathid polychaetes described so far in having very long basal and laeobasal plates which are posteriorly merged together by the carriers. The carriers have small rounded shaft and long and wide antero-lateral processes.

Remarks. – Almost symmetrical Palaeozoic jaw apparatuses are known in a single labidognathid, *Symmetropirion spatiosus* (Hinde), in some placognaths, and in all ctenognaths and xenognaths (for review see Kielan-Jaworowska 1966, Mierzejewski & Mierzejewska 1975). Jaw apparatus of conjungaspid is very different in composition

from those of ctenognaths and xenognaths. Concerning the shape and arrangement of jaws, it differs also from *Symmetroprion spatiosus*. However, posterior maxillae of conjungaspids have very long shanks like in some xanioprionid placognaths, in which first and second maxillae are fused forming long posterior jaws (Kielan-Jaworowska 1966, Hints 1998). In addition, presence of sub-symmetrical basal and laeobasal plates, although not the shape of these jaws, remind xanioprionids. The carriers are not recorded in xanioprionids so far, but their outer slopes of basal- and laeobasal plates sometimes have a thin posteriorly extending appendages. Antero-lateral processes of basal plates of conjungaspids may correspond to posterior appendages in xanioprionids.

Anterior parts of posterior maxillae of conjungaspids have no distinct ramus but fit tightly to posterior lateral teeth, which are postero-laterally prolonged. Some polychaetaspids like *Polychaetaspis inconstans* Kielan-Jaworowska, have similarly developed second maxillae. Thus, one possibility to interpret the nature of posterior jaws of conjungaspids is to consider posterior maxillae as homologous to second maxillae of other taxa. In that case, basal- and laeobasal plates of conjungaspids would be homologous to posterior maxillae and the “real” basal- and laeobasal plates are not present. This, however, seem to be very unlikely because of the shape of basal- and laeobasal plates and presence of teeth interpreted as intercalary and laeointercalary teeth.

In consequence, the features discussed above may not reflect the actual phylogenetic relationships of conjungaspids. Several characteristics of the jaw apparatus, such as presence of laeobasal plate, intercalary and laeointercalary teeth, relatively large size of basal and laeobasal plates and almost gaping myocoeles suggest that conjungaspids are a rather primitive group displaying similarity with labidognaths and some placognaths. It seems that conjungaspids represent a separate lineage, which has originated perhaps early in the Ordovician, and survived among more advanced taxa at least to the end of the Ordovician.

***Conjungaspis* gen. nov.**

Derivation of name: Lat. *conjungo* - join, referring to basal and laeobasal plates which are joined by the carriers.

Type species: *Conjugaspis minutus* sp. nov.

Stratigraphical and geographical range: Middle and Late Ordovician of Estonia.

Diagnosis. – As for the family.

Remarks. – Two minute jaw apparatuses belonging to this genus are found from the Uhaku Regional Stage (Llanvirn-Llandeilo) of North Estonia. They are not described in the present paper but are used as the source of additional information on the apparatus composition and structure in conjungaspids. They might be conspecific with *Conjungaspis minutus* but additional material is needed for a conclusion.

***Conjungaspis minutus* sp. nov.**

Plate 3, figs 1–10, 14.

Derivation of name: *minutus* - small, referring to small size of jaws of this species.

Holotype: Carriers merged with basal- and laeobasal plates GIT Sc 130, Plate 3, fig. 6.

Type locality: Valga-10 borehole, depth 321.9 m.

Type horizon: Porkuni Regional Stage, Kuldiga Formation (Late Ashgill).

Material: one incomplete apparatus, 76 right MI, 60 left MI, 54 basal- and laeobasal plates some of which joined with the carriers, some separated carriers. Valga-10 borehole, depth 316.4–321.9 m, Orjaku borehole, depth 76.65–92.4.

Occurrence: Vormsi, Pirgu and Porkuni Regional Stage (Ashgill) of Estonia.

Diagnosis. – As for the genus.

Description. – Apparatus consists of posterior maxillae, basal and laeobasal plates which are joined together with the carriers, intercalary and laeointercalary teeth, lateral teeth attached to posteriormost parts of the maxillae. Right MI: L = 0.2–0.4 mm, L/W = 1.5–3.3. Anterior 0.2–0.4 of the jaw is in most specimens strongly curved distally, forming approximately a 45° angle with the posterior part of the jaw. Sometimes, however, the jaw is nearly straight. Minute triangular ramus reaches to 0.2–0.3 of jaw length, there is no distinct bight. Inner slope is considerably higher than the outer and thus the jaw is inclined distally. There is a small irregular extension in the inner margin at about anterior 0.3 of jaw length. The dentary consists of 15–21 denticles. In the anterior part of the jaw, the denticles are usually smaller than those located posteriorly, being sometimes developed as poorly distinguishable protuberances. There is no distinct cusp or fang. The myocoele is almost gaping.

Left MI: L = 0.18–0.35 mm, L/W = 1.3–4.8. The jaw is almost mirror image of the right jaw. Its dentary consists of 14–18 denticles similar to those in the right jaw.

Basal plate is long and sub-triangular, slightly shorter than MI. Its dentary has about 25 denticles, those in the anterior 0.2–0.5 of jaw length are long, very slender and sharp and relatively widely spaced. Posterior denticles are triangular, rather small, often poorly distinguishable. Right horn of the carriers is merged to the outer margin, slightly posterior from the mid-length of the jaw. If the carriers are separated from the basal plate, the joining area is marked by irregular incision.

Laeobasal plate is similar to basal plate, but its dentary has less denticles, anteriormost of which being relatively smaller. Besides the ridge is twisted almost vertical and the incision for the left horn of basal plate is more distinct and longer than in basal plate.

Carriers are somewhat shorter than basal and laeobasal plates. They are V-shaped with relatively small shaft and long and wide horns being merged with basal and laeobasal plates. Posteriormost part of carriers has small rounded lateral extensions in both sides.

Posteriormost lateral teeth are triangular teeth which fit tightly to the outer-lateral margin of left and right MI forming ramus-like supplement for MI. Its myocoele is a continuation of that of MI.

Symmetroprionidae Kielan-Jaworowska, 1966

Symmetroprion Kielan-Jaworowska, 1996

Type species: *Symmetroprion spatiosus* (Hinde, 1882).

Symmetroprion spatiosus (Hinde, 1882)

Plate 3, figs 11–13.

1882. *Lumbriconereites spatiosus* sp. nov. Hinde, pp. 23-24, pl. 3 figs 23-24, pl. 3 fig. 72.

1882. *Lumbriconereites laeospatiosus* sp. nov. Hinde, pp. 23-24, pl. 3 fig. 73.

1882. *Oeononites securis* sp. nov. Hinde, p. 16, pl. 2 fig. 37.

1966. *Symmetroprion reduplicatus* sp. nov. Kielan-Jaworowska, pp. 72-73, pl. 12 figs 9-11.

1966. *Symmetroprion* sp. a; Kielan-Jaworowska, pp. 73-74, pl. 12 figs 1-8.

1995. *Symmetroprion spatiosus* (Hinde); Bergman, pp. 147-149, fig. 5.

Material: two basal and one laeobasal plate. Valga-10 drill core, 313.45 m.

Occurrence: topmost Ordovician of South Estonia, Silurian of Baltoscandia.

Remarks. – The oldest occurrence of this species was previously regarded as of early Wenlockian (Bergman 1995). In the present collection, few specimens of *Symmetroprion spatiosus* are recorded in the topmost Ordovician Saldus Formation. Further, *S. spatiosus* appeared to be rather common in the Puikule Formation of lowermost Silurian.

Polychaetaspidae Kielan-Jaworowska, 1966

Polychaetaspis Kozłowski, 1956

Type species: *Polychaetaspis wyszogrodensis* Kozłowski, 1956

Remarks. – The emendation to replace the generic name *Polychaetaspis* with possible senior synonym *Oeononites* Hinde, 1879 as proposed by Eriksson (1997) has not been adopted in this study. See further discussion of this problem **Error! Bookmark not defined.**

Jaws of polychaetaspids, in first order those of the genus *Polychaetaspis*, are among the most common and varied scolecodonts in the present collection. The number of species of *Polychaetaspis* definitely exceeds a dozen. However, the present state of knowledge and amount of material available do not enable to describe them all. Therefore, several apparently independent species are referred herein to as *Polychaetaspis* ssp.

Polychaetaspis cf. *gadomskae* Kielan-Jaworowska, 1966

Plate 4, figs 15–16.

cf. 1966. *Polychaetaspis gadomskae* nov. sp. Kielan-Jaworowska, pp. 81-83, pl. 15, text-fig. 8C.

Material: About 90 posterior maxillae. Orjaku drill core, 98.6-112.5 m; Laeva-18 drill core, 179.70-227.57 m; Valga-10 drill core, 381.4 m.

Occurrence: Late Ordovician of Estonia.

Remarks. – Most specimens of *Polychaetaspis* cf. *gadomskae* differ from the type material of *Polychaetaspis gadomskae* in having less “angular” posterior jaws.

***Polychaetaspis inclinatus* sp. nov.**

Plate 5, figs 4, 10.

Derivation of name: Lat. *inclinatus* – inclined, referring to the shape of posterior maxillae.

Holotype: right MI GIT Sc 160, Plate 5, fig. 4.

Type locality: Orjaku borehole, depth 47.86 m.

Type stratum: Adila Formation of the Pirgu Regional Stage (mid Ashgill).

Material: six left MI, three left MI, a pair of carriers, one left MII probably belonging to this species. Orjaku drill core, 47.68 m; Kaugatuma-509 drill core, 343.45 m.

Occurrence: Pirgu Regional Stage (mid Ashgill) of Estonia.

Diagnosis. – *Polychaetaspis inclinatus* differs from other representatives of the genus *Polychaetaspis* in having narrow shank; distinct sub-rectangular, distally directed ramus; anteriorly strongly curved ridges; usually very large denticles (especially the anteriormost one or two); and very distinct ligament scar which extends to dorsal side of the ridge.

Description. – Right MI: L=1.7-2.2 mm, L/W=2.2-2.4. Antero-lateral margin strongly concave. Ramus is distinct, sub-rectangular, directed distally, extending to 0.43-0.50 of jaw length from anterior. Outer margin of ramus is almost straight, sub-parallel to ridge. Shank is narrow. Ligament scar distinct, extending to dorsal side of ridge and having approximately 0.14 of jaw length. Dentary comprises 13-15 relatively large denticles, the anteriormost one the largest, sometimes hook-like. The ridge is often somewhat inclined proximally, especially in the anterior portion of the jaw. Cover extends to about 0.16 of jaw length.

Left MI: L=0.5-1.8 mm. Antero-lateral margin somewhat concave, greatest width of outer wing is located at anterior 0.4 of jaw length, outer margin of distal part of outer wing may have short portion sub-parallel to ridge (corresponding to shape of ramus in right MI). Smoothly convex inner wing is relatively narrow, its length comprises about 0.6 of jaw length. Ligament scar distinct, comprising 0.14 of jaw length and extending to dorsal side of ridge. Dentary consists of 15-19 denticles (1>1>2-3<9-14). The ridge is somewhat inclined proximally. Cover extends to about 0.18 of jaw length.

Basal plate is sub-triangular, 1.75 times longer than wide, its length corresponds to 0.6 of length of right MI. Dentary comprises 11 denticles (1>3<7).

Carriers oval, 1.6 times longer than wide (excluding horns), corresponding to about 0.7 of length of MI. Antero-laterally directed horns comprise approximately 0.25 of shaft's length.

Variability. – Variability of posterior maxillae of *Polychaetaspis inclinatus* concerns the extension of ramus and the denticulation, which in smaller specimens seems to be less clearly differentiated.

Remarks. – The shape and denticulation of posterior maxillae of *Polychaetaspis inclinatus* is somewhat different from that of typical representatives of the genus *Polychaetaspis*. However, the shape of carriers corresponds exactly to that of other species of *Polychaetaspis* and therefore *P. inclinatus* can be assigned to this genus.

***Polychaetaspis kuldigaensis* sp. nov.**

Plate 4, figs 4–10, 14.

Derivation of name: named after the Kuldiga Formation where the species is found.

Holotype: right MI GIT Sc 143, Plate 4, fig. 6.

Type locality: Valga-10 borehole, depth 319.4 m.

Type stratum: Porkuni Regional Stage, Kuldiga Formation (Late Ashgill).

Material: one apparatus, some joined jaws, 40 right MI, 36 left MI, 14 basal plates, eight carriers and some anterior jaws and lateral teeth. Valga-10 borehole, depth 316.4–321.9 m.

Occurrence: Porkuni Regional Stage (Late Ashgill) of South Estonia.

Diagnosis. – Jaw apparatus of *Polychaetaspis kuldigaensis* differs from those of other species of *Polychaetaspis* in having very long inner wing in left MI and more elongated basal plate. In addition, left and right MI of *P. kuldigaensis* are provided with small furrows in the lateral side of outer wings anterior from mid-length. These furrows make the antero-lateral margins of MI sinusoidal in dorsal view. Regarding the latter feature and more closed myocoeles, *P. kuldigaensis* differs also from the species of *Kozlowskiprion*.

Description. – Jaw apparatus consists of posterior maxillae, from which the right one is a little longer than the left one; anterior maxillae (the MIII occurs only in the left side); basal plate; carriers and lateral teeth. Intercalary teeth is apparently not present.

Right MI: $L = 0.12\text{--}1.05$ mm, $L/W = 2.2\text{--}3.2$. Ramus extends to slightly less than mid-length from anterior. Antero-lateral margin before the tip of ramus is sinusoidal with two convexities. In right lateral view, there is a short longitudinal furrow which supports the distal part of posteriormost lateral tooth. Outer wing along the shank is usually slightly convex. Dentary consists of 9–11 large posteriorly decreasing triangular denticles. Triangular ligament scar is fairly large and distinct. The cover extends to 0.15–0.23 of jaw length.

Left MI: $L = 0.11\text{--}1.00$ mm, $L/W = 2.2\text{--}3.2$. Outer wing is sub-triangular or slightly trapezoidal, its maximum lateral extension is located at about 0.4 of jaw length from anterior. Antero-lateral side is, like in right MI, sinusoidal with two small convexities having longitudinal furrow for better connection with lateral tooth. Inner wing is long extending to 0.65–0.8 of jaw length from posterior. Dentary consists of 8–11 large denticles. Ligament scar is large and relatively distinct. The cover reaches to 0.21–0.27 of jaw length.

Basal plate has 0.55–0.60 of length of right MI. It is elongated, 1.8–2.5 times longer than wide. Inner margin is somewhat longer than outer margin. Anterior margin sinusoidal, posterior end rounded. Dentary consists of 7–10 denticles. Distal part of basal plate has usually longitudinal groove. In ventral view, myocoele is observable only in anterior half of jaw as widely as one third of jaw width.

Right MII is arcuate jaw with high inner wall, its length is about 0.35–0.40 of right MI. Shank is almost as long as ramus. The dentary has 7–9 denticles.

Left MII is similar to right MII, but relatively longer extending to 0.5 of length of left MI. The dentary consists of 6–9 denticles.

Right MIV is high, bow-like jaw without clear ramus, its dentary has some 6 denticles.

Lateral teeth are relatively short conical teeth, the posteriormost ones have wide anteriorly directed base.

Carriers are sub-oval with antero-laterally directed horns forming 0.30-0.36 of their length. Carriers form approximately 0.3 of length of MI.

Variability. – The shape of posterior maxillae and denticulation of *Polychaetaspis kuldigaensis* is rather consistent although the length/width ratio varies quite widely as due to different deformation. Besides, the size ratios of different jaws like MI and MII and MI and basal plates vary quite widely.

***Polychaetaspis latoides* sp. nov.**

Plate 4, fig. 20; Plate 5, figs 7–8.

Derivation of name: Lat. *latus* – broad, *-oides* – similar to, referring to similarity with *Polychaetaspis latus* Kielan-Jaworowska.

Holotype: right MI GIT Sc 156, Plate 4, fig. 20.

Type locality: Orjaku borehole, depth 112.5 m.

Type stratum: Rägavere Formation, Rakvere Regional Stage (upper Caradoc).

Material: approximately 120 right and left MI. Orjaku drill core, 98.6-127.45 m; Laeva-18 drill core, 178.64-191.3 m.

Occurrence: Rakvere to Põrgu regional stages (upper Caradoc-mid Ashgill) of Estonia.

Diagnosis. – *Polychaetaspis latoides* is most similar to *P. latus* differing in a smaller size and more slender form of posterior maxillae and much longer shank in right MI. *Polychaetaspis latoides* differs from other species of *Polychaetaspis* in having long shank and sub-rectangular ramus with outer margin sub-parallel to dentary. Posterior maxillae of *P. latoides* resemble also those of *Kozłowskiiprion* but differ in having less higher jaws, sub-triangular rather than sub-trapezoidal outer wing in left MI and sub-rectangular ramus.

Description. – Right MI: L=0.25-0.43 mm, L/W=2.3-2.9. Antero-lateral margin straight. Ramus extending to 0.4-0.5 of jaw length from anterior, its outer margin is straight and sub-parallel to dentary. Shank is slender. Dentary comprises approximately 12 posteriorly decreasing denticles from which anteriormost one or two are relatively more slender. Cover extends to about 0.1 of jaw length.

Left MI: L=0.25-0.34, L/W=2.4-3.1. Antero-lateral margin straight, postero-lateral margin straight or slightly convex. Greatest width of outer wing is located at about anterior 0.3 of jaw length. Inner wing wider anteriorly extending to about half of jaw length. Dentary comprises about 15 denticles, the anteriormost two sometimes followed by two or three intermediate denticles. Cover extends to about 0.15 of jaw length.

Variability. – The length of shank and the shape of ramus, as well as the denticulation (especially in left MI) may vary widely.

***Polychaetaspis minutus* sp. nov.**

Plate 4, figs 17–19.

Derivation of name: Lat. *minutus* – small, referring to relatively small size of jaws.

H o l o t y p e : right MI GIT Sc 154, Plate 4, fig. 18.

T y p e l o c a l i t y : Laeva-18 borehole, depth 228.08 m.

T y p e s t r a t u m : Mõntu Formation, Nabala Regional Stage (top Caradoc).

M a t e r i a l : approximately 95 right and left posterior maxillae, one incomplete apparatus. Laeva-18 drill core, 176.75-228.08 m; Orjaku drill core, 51.0-92.4 m.

O c c u r r e n c e : Lasnamägi to Juuru stages of Estonia.

Diagnosis. – *Polychaetaspis minutus* differs from other species of *Polychaetaspis* in having distinct, very narrow, distally tapering ramus, relatively long and slender shank and rather high inner face in right MI. Left MI is distinct in that the inner and outer wings usually meet the ridge beyond the posteriormost point of the jaw. In addition relatively small size of jaws is typical of *Polychaetaspis minutus*.

Description. – Right MI: $L=0.16-0.32$, $L/W=1.4-2.3$. Antero-lateral margin concave, distinct ramus is narrow, distally tapering, extending to 0.32-0.50 of jaw length from anterior. Shank is slender. Inner face is usually wide and high, inner margin sharply curved towards dentary at anterior 0.2-0.25 of jaw length. Dentary comprises approximately 12 denticles, decreasing in size posteriorly. Cover extends to about 0.15 of jaw length.

Left MI: $L=0.17-0.33$, $L/W=2.0-2.6$. Antero-lateral and postero-lateral margins concave, the greatest width of outer wing is located at about 0.37 of jaw length from anterior. Outer wing usually meets the ridge beyond posteriormost point of the jaw. Sub-rectangular inner wing is relatively wide, extending to nearly half of jaw length. Posteriorly it meets the ridge beyond the termination of the jaw. Dentary comprises 10-14 denticles, the largest in the middle portion of ridge. Cover extends to about 0.24 of jaw length.

Basal plate is rather large in relation to right MI, sub-triangular, approximately two times longer than wide. Anterior and outer margins are almost of the same length. Dentary is composed of about 10 denticles which are more slender anteriorly.

Variability. – The variability of posterior maxillae of *Polychaetaspis minutus* is relatively wide, concerning the length/width ratio, extension of ramus, and the shape of inner face in right MI. The shape of ramus and arrangement of wings in left MI are very stable throughout the recovered stratigraphic range of this species.

***Polychaetaspis pirguensis* sp. nov.**

Plate 4, figs 1–3, 13.

Derivation of name: named after the Pirgu Regional Stage where the species is most abundantly found.

Holotype: apparatus GIT Sc 140, Plate 4, figs 1–3, 13.

Type locality: Butkunai borehole, depth 554.6 m.

Type stratum: Taučionys Formation, upper Ashgill.

Material: about 50 posterior maxillae, two incomplete apparatuses. Kaugatuma drill core, 343.45 m; Orjaku drill core, 47.62–80.75 m, Butkunai drill core 554.6 m.

Occurrence: Vormsi to Porkuni regional stages (Ashgill) of East Baltic.

Diagnosis. – Posterior maxillae of *Polychaetaspis pirguensis* are most similar to those of *Polychaetaspis kuldigaensis*, the differences concern the shank which is markedly longer in *P. pirguensis*, the shape of ramus which is more rounded in *P. pirguensis* and shape of antero-lateral margins which in *P. pirguensis* are not distinctly sinusoidal as in *P. kuldigaensis*. *Polychaetaspis pirguensis* differs from other species of *Polychaetaspis* in having a long sub-rectangular inner wing in left MI, rounded ramus and rather great size and small number of denticles in posterior maxillae. *Polychaetaspis pirguensis* differs from species of *Kozlowskiprion* in having wider posterior maxillae and greatest width of apparatus located across MI instead of MII like in *Kozlowskiprion*.

Description. – Right MI slightly longer than left MI, intercalary tooth present.

Right MI: L=0.30–1.00 mm, L/W= \sim 2.4. Antero-lateral margin slightly concave or straight. Ramus is rounded extending to 0.35–0.43 of jaw length from anterior. Ligament scar distinct. Dentary comprises about 11–12 fairly large posteriorly decreasing denticles. Cover extends to less than 0.1 of jaw length.

Left MI: L=0.38–0.95 mm, L/W= \sim 2.4. Antero-lateral and postero-lateral margins nearly straight, greatest width of outer wing located at about anterior 0.42 of jaw length. Sub-rectangular inner wing is wide (up to 0.4 of jaw width) and long, comprising about 0.7 of jaw length. Dentary consists of 9–12 fairly large denticles (2>0-3<7-9). Ligament scar large and distinct. Cover extends to about 0.13 of jaw length.

Basal plate: Length of jaw is 0.6 of right MI, approximately 2.3 times longer than wide. Dentary comprising some 12 denticles.

Right MII: Length of jaw is about 0.43 of right MI. Shank and ramus arranged at right angle. Shank 1.4 times longer than narrow ramus. Inner face wide and fragile. Dentary consists of 9 denticles.

Left MII: Almost a mirror image of right MI

Variability. – The most remarkable variability concerns the length of inner wing in left MI and extension of shank. The number of intermediate denticles in left MI may vary from zero to three.

***Polychaetaspis varsoviensis* Kielan-Jaworowska, 1966**

Plate 4, figs 11–12.

1966. *Polychaetaspis varsoviensis* sp. nov. Kielan-Jaworowska, pp. 93–95, pl. 19 figs. 1–3, text-fig. 8H.

Holotype: apparatus, ZPAL No. O.400/239, figured by Kielan-Jaworowska 1966, pl. 19 fig. 1.

Type locality : erratic boulder No. O.400 found in Poland

Type stratum : Middle Ordovician.

Material : about 150 right and left posterior maxillae. Orjaku drill core, 33.1-122.55 m; Laeva-18 drill core, 170.93-227.57 m; Valga-10 drill core, 373.35-381.40 m.

Occurrence : Ordovician and lowermost Silurian of Baltoscandia.

***Polychaetaspis cf. wyszogrodensis* Kozłowski, 1956**

Plate

cf. 1956. *Polychaetaspis wyszogrodensis* nov. sp. Kozłowski, pp. 175-176, figs 3-4.

cf. 1966. *Polychaetaspis wyszogrodensis* Kozłowski; Kielan-Jaworowska, pp. 76-78, pl. 13 figs 1-3, pl. 19 fig. 4.

cf. 1970. *Polychaetaspis wyszogrodensis* Kozłowski; Szaniawski, p. 463, pl. 4 fig. 1.

cf. 1997. *Oenonites cf. wyszogrodensis* (Kozłowski); Eriksson, p. 226-227, fig. 15.

Material : About 330 posterior maxillae, one incomplete apparatus. Orjaku drill core, 47.62-127.45 m; Laeva-18 drill core, 175.64-181.91 m, Rapla drill core, 107.1-125.4 m.

Occurrence : Ordovician and Silurian of Baltoscandia.

Remarks. – The specimens very similar to the type material of *P. wyszogrodensis* are rather widespread, both in geographical and stratigraphical sense. It is not certain whether all specimens assigned to *P. wyszogrodensis* by different authors are actually conspecific or represent several closely related forms. The morphology of posterior maxillae of herein considered material shows relatively wide range of variability, even within a sample. Some specimens are almost identical with the type specimen of *P. wyszogrodensis*, whereas the others have less elongated maxillae, longer inner wing in left MI and shorter shank.

***Polychaetaspis? multidentatus* sp. nov.**

Plate 5, figs 1–2.

Derivation of name : Lat. *multi* – many, *dentatus* – toothed, referring to large number of denticles in posterior maxillae.

Holotype : right MI GIT Sc 158, Plate 5, figs 1–2.

Type locality : Laeva-18 borehole, depth 227.57 m.

Type stratum : Mõntu Formation, Nabala Regional Stage (top Caradoc)

Material : four right MI, one left MI. Laeva-18 drill core, 226.78-227.57 m; Orjaku drill core, 54.0-98.6 m.

Occurrence : Nabala to Pirgu regional stages (top Caradoc - mid Ashgill) of Estonia.

Diagnosis. – *Polychaetaspis? multidentatus* differs from other species of *Polychaetaspis* in having relatively short shank, large ligament scar and large number and small size of denticles in posterior maxillae.

Description. – Right MI: L=0.60-0.86 mm, L/W=2.8-3.1. Jaw elongated, antero-lateral margin slightly concave or straight. Ramus extends to 0.60-0.65 of jaw length from anterior. Posterior termination of shank is stout, provided with large ligament scar extending to dorsal side of the shank. Ligament scar may be as long as 0.15 of jaw length. Dentary comprises 20-22 very small and almost equal sized denticles. Cover extends to 0.15-0.25 of jaw length.

Left MI: L=0.40 mm, L/W=2.7. Jaw elongated, antero-lateral margin slightly concave, postero-lateral margin convex, the greatest width of outer wing located at about 0.37 of jaw length from anterior. Inner wing extends to 0.55 of jaw length from posterior, its inner margin is somewhat concave. Ligament scar is large and distinct, the ridge

extends posteriorly farther than inner wing. Dentary comprises about 21 undifferentiated denticles, which are very small and almost of equal size. Cover reaches to 0.3 of jaw length.

Variability. – Variability concerns the length/width ratio, extension of ramus, size of the ligament scar and length of cover, still being rather slight in the few specimens described.

Remarks. – A particular type of denticulation, as well as relatively short shank in posterior maxillae of *Polychaetaspis? multidentatus* may point at its distinct taxonomic position. However, due to scanty material the species is tentatively assigned to *Polychaetaspis*.

***Kozlowskiprion* Kielan-Jaworowska, 1966**

Type species: *Kozlowskiprion brevialetus* Kielan-Jaworowska, 1966

***Kozlowskiprion angustus* sp. nov.**

Plate 5, figs 13–15.

Derivation of name: Lat. *angustus* – narrow, referring to shape of posterior maxillae.

Holotype: right MI GIT Sc 171, Plate 5, fig. 15.

Type locality: Orjaku borehole, depth 54.0 m.

Type stratum: Adila Formation, Pirgu Regional Stage (mid Ashgill).

Material: about 15 right and left posterior maxillae, one basal plate, one left MII. Orjaku drill core, 47.62–80.75 m.

Occurrence: Vormsi and Pirgu regional stages of North Estonia.

Diagnosis. – *Kozlowskiprion angustus* differs from *Kozlowskiprion brevialetus* and *K. longicavernosus* in having maxillae more slender and higher, longer shank and smaller, sharply pointed ramus.

Description. – Right MI: L=0.25–0.50 mm, L/W=2.5–3.0. Jaw is high, antero-lateral margin convex, short. Ramus minute but distinct, distally pointed, extending to about 0.26 of jaw length from anterior. Bight absent. Shank is very slender. Inner face is high along posterior 0.8 of jaw length. Dentary comprises 11–15 slender, laterally flattened denticles (1>1–2<9–12). Anterior edge of fang is sharp. Cover absent.

Left MI: L=0.28–0.53 mm, L/W=~3.4. Jaw is narrow and high. Outer wing sub-trapezoidal, antero-lateral margin convex extending to anterior 0.15–0.20 of jaw length, postero-lateral margin convex reaching to 0.2–0.3 of jaw length from posterior, middle portion of outer margin sub-parallel to dentary. Inner wing sub-rectangular extending to 0.55–0.60 of jaw length from posterior. Dentary comprises 11–14 slender, laterally flattened denticles, two or three after fang relatively small. Anterior edge of fang sharp. Cover absent.

Basal plate is club-like, 2.2 times longer than wide. Dentary comprising about 13 slender denticles is directed dorsally rather than laterally.

Left MII is relatively high, 1.2 times longer than wide. Ramus very narrow, three times shorter than shank. Inner face is wide along posterior two thirds of jaw length. Dentary comprises some ten slender denticles, the anteriormost the largest.

Variability. – The variability of specimens described herein is rather low, concerning mostly the number of denticles, length/width ratio and shape of outer wings in left and right MI.

Remarks. – All jaws assigned to *Kozlowskiprion angustus* were found in disintegrated form in the samples. The reconstruction of the apparatus is based on morphological characteristics common to all jaws (e.g., very high jaws, slender and similarly differentiated dentaries), and on co-occurrence of different elements.

***Kozlowskiprion brevialetus* Kielan-Jaworowska, 1966**

1966. *Kozlowskiprion brevialetus* sp. nov. Kielan-Jaworowska, pp. 101-102, pl. 21, text-fig. 8J.

H o l o t y p e : apparatus ZPAL O.469/32, figured by Kielan-Jaworowska 1966, pl. 21 fig. 5.

T y p e l o c a l i t y : erratic boulder No. O.469 found in Poland.

T y p e s t r a t u m : ?Middle Ordovician.

M a t e r i a l : about 25 posterior maxillae. Laeva-18 drill core 179.7-200.5 m.

O c c u r r e n c e : Ordovician erratic boulders found in Poland, Idavere to Pirgu regional stages (Caradoc-Ashgill) of East Baltic.

Polychaeturidae Kielan-Jaworowska, 1966

***Polychaetura* Kozłowski, 1956**

T y p e s p e c i e s : *Polychaetura gracilis* Kozłowski, 1956

***Polychaetura gracilis* Kozłowski, 1956**

Plate 5, fig. 9; Plate 8, fig. 7.

1956. *Polychaetura gracilis* sp. nov. Kozłowski, pp. 192-195; figs 17-18.

1966. *Polychaetura gracilis* Kozłowski; Kielan-Jaworowska, pp. 103-105, pl. 22, pl. 23 figs 3-7, text-fig. 8L.

H o l o t y p e : Apparatus figured by Kozłowski 1956, Fig. 17.

T y p e l o c a l i t y : Erratic boulder O.116 found in Poland.

T y p e s t r a t u m : ?Middle Ordovician.

M a t e r i a l : approximately 340 posterior jaws.

O c c u r r e n c e : ?Middle Ordovician erratic boulders from Poland, Idavere to Keila stages of St. Petersburg region, Kunda to Rakvere stages of North Estonia.

***Polychaetura harjuensis* sp. nov.**

Plate 5, figs 5–6, 11–12, 16, 18; Plate 6, figs 1–5.

D e r i v a t i o n o f n a m e : named after Harju Series where the species is found.

H o l o t y p e : right MI GIT Sc 162, Plate 5, fig. 6.

T y p e l o c a l i t y : Laeva-18 borehole, depth 225.15 m.

T y p e s t r a t u m : Nabala Regional Stage (top Caradoc).

M a t e r i a l : seven pairs of carriers, more than 130 right MI, 135 left MI and 50 basal plates. Valga-10 drill core, 373.4 m; Laeva-18 drill core, 221.4-228.8 m; Rapla drill core, 111.3 m; Orjaku drill core, 92.4-107.4 m.

O c c u r r e n c e : Rakvere to Vormsi Regional Stages (upper Caradoc - lower Ashgill) of Baltoscandia.

Diagnosis. – Posterior maxillae of *Polychaetura harjuensis* are most similar to *P. kielanae*, the main difference concerns outline of the shank, which is sub-triangular in *P. harjuensis*, but sub-rectangular in *P. kielanae*. Left MI of *P. harjuensis* has narrower posterior margin and differently shaped outer wing. *P. harjuensis* differs from *P. gracilis* in having posterior margin of left MI and anterior margin of carriers straight instead of

incised like in *P. gracilis*. Besides, sub-transversally prolonged anteriormost denticles in MI are characteristic to *P. harjuensis* only.

Description. – Right MI: L = 0.3-1.1 mm, L/W = 2.0-2.9. Outer-lateral margin is almost straight or with a little incurvature in the middle. Ramus extends to 0.43-0.55 of jaw length from anterior. Outer margin along the shank is directed posteriorly in the first half of the shank, then it bends continuously and is directed towards the end of the dentary. Posterior termination has a small tubercle. Dentary comprises 11-17 denticles, first three of which are prolonged transversally reminding short ridges. Myocoele is very slightly closed, the cover extends to 0.05-0.07 of jaw length.

Left MI: L=0.4 mm, L/W=2.4. Outer margin runs most often postero-laterally at 0.4-0.5 of jaw length, then turns towards the ridge, then continues sub-parallel to dentary until it meets the posterior margin. Sometimes a little bight, similar in extension to that in right MI, can be found. Inner wing is long reaching to 0.70-0.75 of jaw length from posterior. Posterior margin forms 0.35-0.50 of jaw width. Dentary consists of 10-15 denticles, three first ones are prolonged transversally like in right MI. Myocoele is very slightly closed, cover extends to about 0.05 of jaw length.

Basal plate is about half as long as right MI. Length/width ratio varies from 2.0-3.3. Inner margin of sub-trapezoidal jaw is longer than the outer margin. In dorsal view, posterior termination has usually posteriorly directed narrow blunt extension. Dentary has 10-18 denticles. Cover reaches to 0.35-0.50 of jaw width.

Fused carriers are about 2.2 times longer than wide. The shaft of a single carrier has two posteriorly directed branches, the proximal being 3 times longer than the distal one. Anterior margins of carriers are nearly straight.

Variability. – The outline, especially the length/width ratio varies widely. In basal plates, two types of denticulation occur: (1) all denticles are large having nearly equal size and shape, and (2) anteriormost denticles are smaller and/or more slender.

Remarks. – As based on morphology of posterior maxillae and basal plates, *P. harjuensis* is regarded to be a successor of *P. kielanae* Hints. Latter species is known from somewhat older strata in the same region (Hints in press). Carriers, which are assumed to be of great taxonomic value above the species level (Kielan-Jaworowska 1966, Edgar 1984) have not been found in *P. kielanae*, but above described material suggest that both mentioned species are closely related to *P. gracilis*. Since *P. gracilis* is the so far stratigraphically oldest polychaeturid, it likely gave rise to *P. kielanae*.

P. harjuensis has been most abundantly found in the Vormsi Stage of Laeva-18 drill core, where it makes up about one third of all specimens. At the same time, interval of Vormsi age contained only seldom specimens of *P. harjuensis* in Orjaku borehole, the locality characterised by more shallow-water deposits. It is interesting to note that a single sample (depth 1120-1126 m, courtesy to Prof. H. Szaniawski) from the Mielnik drill core, eastern Poland, was characterised by similarly high abundance of *P. harjuensis*. According to Modlinski (1970), the rather long interval of the mentioned sample corresponds to the Nabala and Vormsi Regional Stages. This seems to indicate

that *P. harjuensis* has relatively short stratigraphic range with almost isochronous acme, and a wide regional distribution in Baltoscandian palaeobasin.

***Laevaprion* gen. nov.**

Derivation of name: after Laeva-18 borehole, the type locality of the type species of this genus.

Type species: *Laevaprion jaaki* sp. nov.

Stratigraphical and geographical range: late Caradoc of Estonia.

Diagnosis. – Morphology of posterior and second maxillae of *Laevaprion* suggest that it belongs to labidognath subdivision. This genus differs from other labidognaths known so far in having dentaries in MI and MII provided with one (MII) or two (MI) long and smooth transverse ridges. In this respect, *Laevaprion* reminds a placognath *Rhytiprion* Kielan-Jaworowska, but differs in having prominent inner wing in left MI, distinct ramus in right MI, slightly closed myocoeles in MI and more slender MII provided with clear, usually denticulated shank. There seem to occur intermediate forms between some polychaeturids and *Laevaprion*, the latter however differs from them in lack of transverse posterior margin in left MI, and occurrence of smooth transverse ridges.

Remarks. – Jaw apparatus of *Laevaprion jaaki* is considered to be of labidognath type according to the following criteria: (1) similarly developed right and left MII, (2) presence of inner wing in left MI, (3) left MI provided with sub-triangular outer wing, whereas the right MI has a ramus and bight which suggest the presence of yet unknown basal plate, (4) very slightly closed myocoeles.

A great similarity of the first and second maxillae of *L. jaaki* and a placognath *Rhytiprion magnus* Kielan-Jaworowska is regarded to exemplify convergence. Presumably both species were adopted to a common mode of feeding.

There is a single right MI (Plate 5, fig. 17.), which is, in many aspects intermediate between *Laevaprion jaaki* and a polychaeturid *Polychaetura harjuensis*. The latter species has some anteriormost denticles in MI slightly prolonged in transversal direction and could be taken as an example between “normally” developed dentaries and those with plain transverse ridges. Despite the single specimen which seems to relate *Laevaprion* to polychaeturids there are several notable differences between *L. jaaki* and *P. harjuensis*. For instance, lack of the posterior margin in the left MI in *L. jaaki*. The basal plates, which are frequently preserved in *P. harjuensis* have not been recorded in *L. jaaki*, whereas the MII being common in *L. jaaki* are not yet known in *P. harjuensis*; that suggests some differences also in these jaws.

However, as due to insufficient material, *Laevaprion* can be only tentatively included to polychaeturids.

***Laevaprion jaaki* sp. nov.**

Plate 6, figs 6–14.

Derivation of name: named in honour of Mr. Jaak Nõlvak who recovered the first specimens of this species.

H o l o t y p e : right MI GIT Sc 184, Plate 6, fig. 10.

T y p e l o c a l i t y : Laeva-18 borehole, depth 225.15 m.

Type horizon: Mõntu Formation, Nabala Regional Stage (topmost Caradoc).

M a t e r i a l : approximately 15 right and 20 left MI and 10 left and right MII. Laeva-18 borehole, depth 224.0-226.8 m.

O c c u r r e n c e : Nabala Regional Stage (top Caradoc) of Central Estonia.

Diagnosis. – As for the genus.

Description. – Right MI: L = 0.42-0.65 mm, L/W = 1.8-2.6. Outer margin is directed postero-laterally at anterior 0.3-0.4 of jaw length, then it bends steeply and runs postero-laterally towards the tip of ramus. Ramus extends to 0.50-0.56 of jaw length. Shank is relatively slender. The dentary is provided with two smooth transversal ridges, the first being approximately two times longer (transversely) than the second. In some specimens, there is a small conical denticle in the distal end of the first ridge, rarely something similar may occur in the second ridge. The first denticle behind the ridges is slightly prolonged transversely or is large and blunt. The remaining ones are “normal”, posteriorly decreasing denticles. The number of denticles excluding the transversal ridges is 8-10. Myocoele is very slightly enclosed, cover extends to 0.1 of jaw length or less.

Left MI: L = 0.30-0.86 mm, L/W = 1.8-2.4. Outer wing is sub-triangular, its maximum lateral extension is located at 0.3-0.4 of jaw length from anterior. Postero-lateral margin is very slightly sinusoidal. Inner wing is long reaching to about 0.7 of jaw length from posterior, its inner and anterior margins are usually straight. Dentary is provided with two transverse ridges in the anterior part and is very similar to that in right MI though the number of denticles reaches 12 (except the ridges). Cover extends to 0.1 of jaw length or less.

Right MII: Jaw is Π-shaped, ramus being more slender and slightly longer than shank. Anterior part of the jaw has long transverse ridge similar to those in the MI. Ramus has up to 11 small denticles, which sometimes may almost be worn off and indistinct.

Left MII: Jaw is mirror image of right MII.

Variability. – The morphology of jaws of *Laevaprion jaaki* varies quite widely in length/width ratio and extension of the ramus. More interesting is the variability of the dentaries: although the number of smooth transverse ridges remains constant, sometimes a small conical teeth may occur in the distal parts of the ridges, and rarely such ridges seem to be composed of several transversely prolonged denticles.

Ramphoprionidae Kielan-Jaworowska, 1966

***Ramphoprion* Kielan-Jaworowska, 1962**

T y p e s p e c i e s : *Ramphoprion elongatus* Kielan-Jaworowska, 1962

***Ramphoprion elongatus* Kielan-Jaworowska, 1962**

Plate 7, figs 8–9, 13.

1962. *Ramphoprion elongatus* nov. sp. Kielan-Jaworowska, pp. 315-318; pls 8-10.

1966. *Ramphoprion elongatus* Kielan-Jaworowska; Kielan-Jaworowska, pp. 108-109, pl. 25 fig. 3.

H o l o t y p e : apparatus ZPAL O.398/1, figured by Kielan-Jaworowska 1962, pl. 8; 1966, pl. 25 fig. 3

T y p e l o c a l i t y : erratic boulder O.398, found in Poland.

T y p e s t r a t u m : Middle Ordovician.

M a t e r i a l : about 25 posterior maxillae. Orjaku drill core, 107.40-112.50 m, Laeva drill core, 221.35-228.81 m, Rapla drill core, 108.15 m.

O c c u r r e n c e : Ordovician erratic boulders found in Poland, Rakvere and Nabala stages (upper Ashgill) of Estonia.

Remarks. – Some of the specimens referred to herein differ from the type specimen of *Ramphoprion elongatus* in being slightly less elongated. They are however almost identical to the specimens figured by Kielan-Jaworowska (1962, pl. 9) and Szaniawski (1996, pl. 2, figs 7b, 7c).

***Ramphoprion cf. deflexus* (Eller, 1942)**

Plate 7, figs 1–7.

cf. 1942. *Lumbriconereites deflexus* sp. nov. Eller, pl. 1 figs 5-6.

cf. 1942. *Lumbriconereites copiosus* sp. nov. Eller, pl. 1 figs 7-12.

cf. 1979. Gen. et sp. indet. a; Bergman, fig. 28-11B, *non* fig. 28-11A.

M a t e r i a l : six differently preserved apparatuses, nine right MI, 11 left MI, some basal plates and anterior jaws. Valga-10 borehole, depth 335.2-344.9 m.

O c c u r r e n c e : Pirgu Regional Stage (Ashgill) of Estonia, Late Ordovician of Ontario, Wenlock of Gotland.

Description. – Right MI: L = 0.25-1.10 mm, L/W = 2.4-2.8. Outer margin runs posteriorly to about mid-length of jaw where it bends steeply outwards and forms ramus with sub-rectangular outline. Ramus extends to 0.65-0.75 of jaw length from anterior. Inner margin is convex. Ridge is often somewhat inclined proximally. Dentary consists of 13-18 denticles, 2-4 of them after the fang are very small and crenulation-like, the following ones increase in size to about mid-length and then decrease posteriorly. Cover reaches to 0.37-0.45 of jaw length.

Left MI: L = 0.36-1.95 mm, L/W = 2.5-3.0. Outer wing has its maximum lateral extension at 0.54-0.58 of jaw length from anterior. Short inner wing is sub-triangular or sinusoidal extending to 0.25-0.33 of jaw length. Posterior margin forms about 0.5 of jaw width. Dentary consisting of 14-20 denticles is similar to that in right MI, except the number of small, crenulation-like denticles after the fang. The number of these small denticles may reach to eight. Cover extends to 0.50-0.55 of jaw length.

Basal plate has 0.30-0.35 of length of right MI. Anterior margin is strongly concave, more than twice longer than posterior margin. Ramus is relatively wide and pointed. Dentary consists of 8-10 denticles, about four anterior denticles are smaller than the following ones. Cover reaches to 0.4 of jaw width.

Right MII has 0.52-0.60 of length of right MI, its shank is about twice as long as ramus. Undifferentiated dentary consists of 9-13 denticles, first of which being slightly larger than the following ones.

Left MII is elongated jaw forming 0.60-0.65 of length of left MI. Shank is about twice as long as ramus. Dentary has 9-14 denticles from which one or two after the first and biggest denticle are very small.

Left MIII forms 0.33 of length of left MI. It is similar to left MII but its shank is relatively shorter and dentary with about 10 denticles is undifferentiated.

Right MIV is small arcuate jaw with about eight minute denticles. Its length equals to approximately 0.25 that of right MI.

Left MIV is similar to right MIV but has about seven denticles and is a little shorter in relation to posterior maxillae.

Posteriormost lateral teeth are long and slender, fitting tightly to distal margins of posterior maxillae.

Carriers are about as long as 0.37 of posterior maxillae, 1.2 times longer than wide, with slightly convex anterior margin.

Remarks. – It is noteworthy that there was about one jaw apparatus of *Ramphoprion* cf. *deflexus* per four single elements of this species in two samples. Usually one jaw apparatus per several hundreds of isolated elements can be found in the Ordovician rocks of Estonia. Further, as noted by Kielan-Jaworowska (1966), and confirmed by myself, jaw apparatuses of ramphoprionids are particularly rare though the isolated elements may be rather frequent. High abundance of apparatuses of *Ramphoprion* cf. *deflexus* seems to be a result of exceptional preservation in carbonate rock with high clay content. Such type of rock did not dissolve completely in acetic acid and the jaws in apparatuses were kept together by insoluble sediment particles. This unique case implies that polychaete jaw apparatuses being preserved in the rock in clusters may be rather frequent, but most usually, even if the samples and residues are treated with extra care, most of them have no chances to preserve in fused state.

***Ramphoprion* sp. A**

M a t e r i a l : about 30 posterior maxillae. Orjaku drill core, 47.62-127.45 m; Valga-10 drill core, 371.10 m.

Description. –Right MI: L=0.14-0.70, L/W=1.6 - 2.9. Antero-lateral margin almost straight. Ramus extends to 0.7-0.8 of jaw length. Inner margin is convex or sub-trapezoidal. In left-lateral view, commonly some longitudinally oriented shallow pits or grooves occur in middle of jaw length. Dentary comprises 10-14 denticles decreasing in size posteriorly. Rarely two first denticles distinctively larger than following ones. Cover extends to about 0.4 of jaw length.

Left MI: L=0.16-0.58, L/W=1.8-3.0. Outer wing sub-triangular, maximum width located at 0.55-0.6 behind posteriormost point of jaw. Posterior margin wide, 0.55-0.65 of jaw width. Sub-rectangular or sub-triangular inner wing extends to about mid-length with maximum width in first quarter of its length. Cover extends to 0.35-0.55 of jaw length.

Remarks. – *Ramphoprion* sp. A is different from other species in having relatively stout posterior maxillae, very short shank and basal plate lacking distinct posterior margin. The right MI of *Ramphoprion* sp. A is most similar to the jaws described from North America as *Protarabellites fidelis* Stauffer, 1933; *P. dubius* Stauffer, 1933; *P. delectus* Stauffer, 1933; *Lumbriconereites langae* Eller, 1945; and perhaps *L. irregularis*

Eller, 1945. The exact relations, and possible conspecificity, however, cannot be resolved without studying the type collections. *Ramphoprion* sp. A is also similar to *Pararamphoprion? nordicus* Männil & Zaslavskaya, 1985 but differs from the latter in having shorter shank and more closed myocoeles and sub-rectangular or sub-triangular inner wing instead of a crest-like in left MI.

Paulinitidae Lange, 1947

***Kettnerites* Zebera, 1935**

Type species: *Kettnerites kozoviensis* Zebera, 1935

***Kettnerites* ssp.**

Plate 3, fig. 15.

Material: about 12 MI and MII. Orjaku drill core, 47.62 m; Laeva-18 drill core, 195.69 m; Valga-10 drill core, 313.45-369.7 m.

Remarks. – Insufficient number of specimens does not allow species level identification of the specimens referred herein as *Kettnerites* ssp.

Kalloprionidae Kielan-Jaworowska, 1966

***Kalloprion* Kielan-Jaworowska, 1962**

Type species: *Kalloprion ovalis* Kielan-Jaworowska, 1962

***Kalloprion* ssp.**

Material: approximately 100 posterior maxillae. Orjaku drill core, 33.10-112.50 m; Laeva-18 drill core, 174.63-228.08 m; Valga-10 drill core, 319.40-381.40 m.

Remarks. – The present collection likely yields several species of *Kalloprion* in addition to *K. robustus* described below. Because of wide range of variability and insufficient knowledge of apparatuses these species are referred to as *Kalloprion* ssp. in this study.

***Kalloprion robustus* sp. nov.**

Plate 7, figs 11–12, 16–17.

Derivation of name: Lat. *robustus* – robust, strong; referring to morphology of maxillae and basal plate.

Holotype: right MI fused with basal plate GIT Sc 203, Plate 7, fig. 17.

Type locality: Laeva-18 borehole, 225.15 m.

Type stratum: Mõntu Formation, Nabala Rregional Stage (top Caradoc).

Material: about 15 MI, one right MI fused with basal plate, some left and right MII. Orjaku drill core, 87.11-98.60 m; Laeva-18 drill core, 225.15 m.

Occurrence: Nabala and Vormsi Stages of (top Caradoc-base Ashgill) of Estonia and East Poland.

Diagnosis. – *Kalloprion robustus* differs from *Kalloprion ovalis* and *K. triangularis* in having stouter jaws, smaller number and greater size of denticles in maxillae. In addition, it differs from *K. triangularis* in having relatively shorter basal plate, and from *K. ovalis* in having antero-lateral margins in MII concave instead of convex like in *K. ovalis*.

Description. – Right MI: L= \sim 0.84 mm, L/W= \sim 2.0. Jaw is stout, antero-lateral margin concave. Ramus extends to about 0.6 of jaw length from anterior. Dentary comprises approximately 11 denticles, the two after the anteriormost denticles are smaller than the following ones.

Left MI: L= \sim 0.8 mm, L/W= \sim 2.0. Jaw is stout. Outer wing sub-triangular with its greatest width located at about anterior 0.65 of jaw length. Inner wing is relatively wide, extending to half of jaw length. Dentary is composed of about 14 denticles, the largest (except the anteriormost one) in the middle part of the ridge.

Basal plate is sub-triangular, slightly longer than wide, corresponding to 0.43 of length of right MI. Antero-lateral margin somewhat longer than postero-lateral margin. Dentary consists of about 10 relatively small, almost equal sized denticles.

Left MII: Antero-lateral margin concave. Ramus is relatively slender, distally pointed, corresponding to half of length of shank. Dentary comprises 6 very large and blunt denticles, the second smaller than adjacent ones.

Right MII: Almost mirror image of left MI.

***Leptoprion* Kielan-Jaworowska, 1966**

Type species: *Leptoprion polonicus* Kielan-Jaworowska, 1966

***Leptoprion* ssp.**

Plate 6, fig. 15; Plate 7, figs 14–15.

Material: about 130 posterior maxillae, some fused jaws. Orjaku drill core, 33.10-124.43 m; Laeva-18 drill core, 172.45-227.57 m; Valga-10 drill core, 313.45-367.26 m.

Remarks. – Specimens referred to herein show a wide range of variability and likely represent several species. The features of *Leptoprion*, which are considered of great diagnostic value by Kielan-Jaworowska (1966) seem to vary widely. The present material, particularly the lack of fused apparatuses is insufficient to allow meaningful distinction of the species of *Leptoprion*.

Atraktoprionidae Kielan-Jaworowska, 1966

***Atraktoprion* Kielan-Jaworowska, 1962**

Type species: *Atraktoprion cornutus* Kielan-Jaworowska, 1962

***Atraktoprion cornutus* Kielan-Jaworowska, 1962**

1962. *Atraktoprion cornutus* sp. nov. Kielan-Jaworowska, pp. 304-306, pl. 1, text-fig. 3B.

1966. *Atraktoprion cornutus* Kielan-Jaworowska; Kielan-Jaworowska, pp. 133-134, pl. 31, text-figs 5 P, 12 B.

1966. *Atraktoprion robustus* sp. nov. Kielan-Jaworowska, pp. 134-135, pl. 36 figs 1-2, text-fig. 12 A.

Holotype: apparatus ZPAL O.400/1, figured by Kielan-Jaworowska 1962, pl. 1.

Type locality: erratic boulder No. O.400 found in Poland.

Type stratum: ?Keila Regional Stage (mid Caradoc).

Material: about 12 posterior maxillae. Orjaku drill core, 107.40-112.50 m.

Occurrence: Middle and Late Ordovician of Baltoscandia.

Remarks. – Due to similar morphology of *Atraktoprion cornutus* and *A. robustus*, and wide range of variability, *A. robustus* is considered herein as younger synonym of *A. cornutus*.

***Atraktoprion major* Kielan-Jaworowska, 1966**

Plate 8, figs 13–14.

1966. *Atraktoprion major* sp. nov. Kielan-Jaworowska, pp. 139-140, pl. 34, text-fig. 12D.

H o l o t y p e : apparatus ZPAL O.319/7, figured by Kielan-Jaworowska 1966, pl. 34 fig. 4.

T y p e l o c a l i t y : erratic boulder No. O.319 found in Poland.

T y p e s t r a t u m : unknown (Ordovician or Silurian).

M a t e r i a l : about 45 posterior maxillae. Orjaku drill core, 101.10-127.45; Laeva-18 drill core, 189.6-228.08; Valga-10 drill core, 319.4-378.10 m.

O c c u r r e n c e : Ordovician or Silurian erratic boulders from Poland, Oandu to Porkuni stages of Estonia.

***Atraktoprion mirabilis* Kielan-Jaworowska, 1966**

Plate 8, figs 11–12.

1966. *Atraktoprion mirabilis* sp. nov., Kielan-Jaworowska, pp. 137-138, pl. 32 fig. 3-4, pl. 33, text-fig. 12C.

H o l o t y p e : Apparatus ZPAL O.398/8, figured by Kielan-Jaworowska 1966, pl. 33 fig. 2.

T y p e l o c a l i t y : Erratic boulder No. O.398 found in Poland.

T y p e s t r a t u m : ?Middle Ordovician.

M a t e r i a l : 11 posterior maxillae. Orjaku drill core, 87.11 m; Laeva-18 drill core, 186.64-197.51; Rapla drill core, 108.15 m.

O c c u r r e n c e : Ordovician erratic boulders from Poland, Rakvere to Pirgu stages of Estonia.

Skalenoprionidae Kielan-Jaworowska, 1966

***Skalenoprion* Kielan-Jaworowska, 1962**

T y p e s p e c i e s : *Skalenoprion alatus* Kielan-Jaworowska, 1962

***Skalenoprion alatus* Kielan-Jaworowska, 1962**

Plate 8, fig. 15.

1962. *Skalenoprion alatus* sp. nov. Kielan-Jaworowska, pp. 308-310, pl. 3-4.

H o l o t y p e : incomplete apparatus, ZPAL O.59/1, figured in Kielan-Jaworowska, 1966, pl. 3.

T y p e l o c a l i t y : erratic boulder No. O.59 found in Poland.

T y p e s t r a t u m : unknown (Ordovician or Silurian).

M a t e r i a l : six posterior maxillae. Orjaku drill core, 47.62-70.20 m; Laeva-18 drill core, 178.64-187.45 m.

O c c u r r e n c e : Nabala to Juuru stages of Estonia, Ordovician and/or Silurian erratic boulders found in Poland.

Incertae familiae

***Tretoprion* gen. nov.**

D e r i v a t i o n o f n a m e : Gr. *treto* - with a hole, *prion* - a saw, referring to the shape of outer wing of left posterior maxilla.

T y p e s p e c i e s : *Tretoprion astae* sp. nov.

S t r a t i g r a p h i c a l a n d g e o g r a p h i c a l r a n g e : Ashgill of Estonia.

Diagnosis. – *Tretoprion* differs from other eunicid polychaetes known so far in having posterior maxillae provided with three very high, transversely prolonged, ridge-

like denticles and in having second maxillae composed of weakly merged denticles, which dorsally resemble those in anterior part of posterior maxillae.

Remarks. – The morphological distinctiveness of the apparatus construction as well as the shape of individual jaws of *Tretoprion* suggest that, in light of the present suprageneric subdivision of Palaeozoic eunicids, it likely represents a new family. Nevertheless, the carriers, which may reveal its relationships with other groups are unknown so far, and thus I preferred not to establish a new family on the basis of current material. There is no doubt, however, that *Tretoprion* should be assigned to labidognaths.

***Tretoprion astae* sp. nov.**

Plate 8, figs 1–6, 8–10.

Derivation of name: named in honour of Dr. Asta Oraspõld, who has been working on the sedimentology of the strata, which contain abundant jaws of this species.

Holotype: right MI fused with basal plate GIT Sc 205, Plate 8, fig. 2.

Type locality: Orjaku borehole, depth 58.57 m.

Type stratum: Pirgu Regional Stage (Ashgill).

Material: two apparatuses, two right MI fused with basal plate, one right MI together with basal plate and right MII, approximately 35 right and 25 left MI, some broken MII, one basal plate. Orjaku drill core, 54.0–92.4 m; Laeva-18 drill core 222.4m.

Occurrence: Vormsi and Pirgu Regional Stages (Ashgill) of Estonia.

Diagnosis. – As for the genus.

Description. – The apparatus consists of posterior maxillae, basal plate, lateral teeth,

Right MI: $L = 0.23\text{--}0.78$ mm, $L/W = 2.2\text{--}3.0$. Outer-lateral margin is nearly straight, ramus extends to 0.32–0.40 of jaw length, its tip is narrow. Shank is long and very slender. The ridge is curved distally at first 0.3 of jaw. The dentary consists of 12–21 denticles, first three of which (especially the first one) are rather high and prolonged transversally into short ridges. The following denticles are small and laterally triangular increasing towards the posterior third of the ridge. The cover reaches to approximately 0.15 of jaw length.

Left MI: $L = 0.25\text{--}0.45$ mm, $L/W = 1.7\text{--}3.3$. Jaw is mostly rhomboidal in outline, inner margin and the ridge are curved distally at about mid-length of the jaw. Outer wing has its maximum lateral extension slightly before the mid-length of the jaw, posterior from that the outer wing is rather fragile and often broken. Outer wing is perforated in its central portion. The dentary is very similar to that in right MI, although the number of denticles is slightly smaller (13–16). The cover extends to 0.15–0.25 of jaw length.

Basal plate: Length of a triangular jaw reaches two thirds of length of the right MI. Its inner margin is 1.25 times longer than the outer margin. Anterior margin is almost straight, slightly curved anteriorly in the distal end. Dentary consists of about 14 posteriorly decreasing denticles, those in the anterior half of the jaw are somewhat more slender. The cover extends to one third of jaw width.

Right MII is an arcuate jaw being composed of about four transversally prolonged denticles which are loosely fused to each other in the distal part. The first denticle is the

largest, its posterior termination forms a ramus. Such “ramuses” are often found separately from other particles of the jaw. The proximal portion of the jaw, the shank, is sub-triangular plate without distinct denticles.

Left MII has not been found in well preserved state, but some loose “ramuses” display a great similarity with those of the right MII.

Posteriormost lateral teeth are conical, relatively slender elements, approximately as long as antero-lateral margins of MI.

Variability. – Variability of posterior maxillae of *Tretoprion astae* concerns most remarkably the outline of left MI, which due to fragile jaw wall may have rather different shape. Besides, the degree of curvature of the ridges, and the length/width ratios vary quite remarkably. The arrangement of dentary, except for the number of denticles, seems to be rather invariable.

***Lunoprionella* Eisenack, 1975**

Type species: *Lunoprionella symmetrica* Eisenack, 1975.

Remarks. – Eisenack (1975) established the new genus with four new species. He used the outline of the dentary (in lateral view) as the main diagnostic feature. Because of the variability of the shape, the present author regards three of Eisenack’s species conspecific.

The apparatus arrangement of *Lunoprionella* is unknown. Mierzejewski (1978a) notes that this genus belongs to placognath eunicids and may be synonymous with an older genus of this group. However, jaws of *Lunoprionella* apparently do not constitute minor elements of some well-know species. Further, abundant jaws of *Lunoprionella* are found from samples lacking other scolecodonts of unknown affinity. Thus, they probably do not represent also minor elements of some unknown apparatus type, but make up the main part of an placognath jaw apparatus, which cannot be reconstructed so far.

***Lunoprionella symmetrica* Eisenack, 1975**

Plate 1, fig. 14.

1975. *Lunoprionella symmetrica* sp. nov. Eisenack, p. 247, figs 38-40.

1975. *Lunoprionella asymmetrica* sp. nov. Eisenack, p. 247, figs 42-43.

1975. *Lunoprionella* sp. Eisenack, p. 247, fig. 44.

H o l o t y p e : S.G. 126 No. 2, figured by Eisenack 1975, fig. 40.

T y p e l o c a l i t y : erratic boulder found in Germany.

T y p e s t r a t u m : Caradoc.

M a t e r i a l : about 80 jaws. Orjaku drill core, 47.62-112.50 m; Laeva-18 drill core, 178.64-228.08 m; Valga drill core, 368.90 m.

O c c u r r e n c e : Lasnamägi to Juuru stages (Llanvirn - Llandovery) of Baltoscandia.

“*Lunoprionella*” sp. A

M a t e r i a l : about 40 posterior maxillae. Orjaku drill core, 37-35-92.40 m; Laeva-18 drill core, 174.63-187.45 m; Valga drill core, 316.40-321.85 m.

Description. – Jaws are very high constituting one denticulated ridge with up to 40 small and slanting denticles. Borders between denticles are prolonged to the jaw wall.

Therefore inner and outer face consist of numerous parallel lamellae. In the outer(?) face these lamellae are separated from each other. The ventralmost part of the inner(?) face is flat and fragile.

Remarks. – Jaws of “*Lunoprionella*” sp. A differ from those of *L. symmetrica* in having jaw faces composed of discrete lamellae, and in greater number and smaller size of denticles. Relationships of “*Lunoprionella*” sp. A with type species are, however, not entirely certain and thus it is only tentatively assigned to this genus.

Gen. et sp. indet. A

M a t e r i a l : three right MI. Orjaku drill core, 63.8-70.20 m.

Description. – Right MI: L=0.17-0.23 mm, L/W=3.4-4.7. Outer wing triangular, lacking distinct ramus and bight. Jaw has greatest width at anterior 0.35-0.50 of jaw length. Straight dentary comprises 9-13 denticles. Anteriormost denticle only slightly larger than the following ones. Anterior end, and sometimes also posterior end, more or less pointed. Height of jaw is approximately equal to width. Dental groove straight and deep, cover absent.

Remarks. – The construction of the apparatus of Gen. et sp. indet. A may be notably different from that of well-known species. For instance, lack of a bight probably excludes occurrence of the basal plate.

STRATIGRAPHIC DISTRIBUTION

Applicability of scolecodonts in stratigraphy has often been debated and completely opposing viewpoints do exist. For example, Kielan-Jaworowska (1968), Szaniawski (1970, 1996), Jansonius & Craig (1971), Shimer & Shrock (1955) and Hints (1996, in press) consider scolecodonts as possibly useful guide fossils, the main shortage on it being insufficient knowledge. Tougeourdeau (1976) and Underhay & Williams (1995), on the other hand, regard scolecodonts as of little, if any stratigraphic value.

The majority of species referred to herein are long-ranging ones. Only a few of the recovered species are confined to a narrow stratigraphic interval. For instance, *Polychaetura harjuensis* occurs in the Rakvere, Nabala and Vormsi stages; *Polychaetaspis kuldigaensis* in the Porkuni Stage; *Tretoprion astae* in the Vormsi and Pirgu stages; *Polychaetaspis pirguensis* in the Vormsi and Pirgu stages; *Ramphoprion elongatus* in the Rakvere, Nabala and Vormsi stages; *Laevaprion jaaki* in the Nabala Stage; *Kalloprion robustus* in the Nabala and Vormsi stages. However, the stratigraphic value of these species is difficult to estimate on the basis of data from a limited number of localities. At best, the ranges of taxa revealed in this study may be considered as local ranges. Although the ranges of the individual eunicid taxa may not be directly applicable for distinguishing a particular stratigraphic interval, the assemblages prove to be more useful for this purpose. The faunal logs showing distribution of scolecodonts and indicating relative abundance of selected species in the three cores are presented in Figs 5-7. Fig. 8 summarises the data on all species and localities. The assemblages of jawed polychaetes in the stages and formations of the Harju Series, represented in the studied sections, can be characterised as follows.

Nabala Stage is represented by argillaceous limestones and marls of the **Paekna** and **Mõntu** formations and cryptocrystalline limestones of the **Saunja** Formation. There are no basic differences between the polychaete assemblages of these formations. The abundance of scolecodonts is, on average, higher than in underlying beds, being still very low in the Mõntu Formation of the Valga-10 core (up to eight, but usually less than one specimen per 100 g of sample). However, in the marls of the Mõntu formation of Laeva-18 core, as many as 23 specimens were recorded per 100 g of rock. 9-25 specimens per 100 g of rock have been recorded in the Nabala Stage of Orjaku core. Altogether more than 35 species occur in the Nabala Stage. Most often, the assemblage is predominated by *Polychaetura gracilis*, *Paramochtyella fragilis*, *Polychaetaspis latoides*, *Pistoprion transitans*, *Polychaetaspis* cf. *wyszogrodensis*, *Polychaetaspis* cf. *gadomskae*, *Rhytiprion magnus*, and rarely *Laevaprion jaaki*. The last mentioned species with very distinct morphology is confined to the Nabala Stage and up to now recovered only from Laeva-18 drill core. In the Valga-10 core, *Polychaetaspis varsoviensis* accounts for significant part of specimens in the lower part of the stage. In addition to mentioned taxa, species like *Ramphoprion elongatus*, *Atraktoprion major*, *Polychaetura harjuensis*, *Kalloprion robustus*, *Polychaetaspis* cf. *gadomskae*, *P.* cf.

wyszogrodensis, *P. minutus*, *Xanioprion* sp. A, *Leptoprion* ssp., *Xanioprion* sp. B,
Mochtyella cristata and *Mochtyella polonica*

are fairly common in the Nabala Stage. *Rakvereprion balticus* becomes abundant in the upper part of the Nabala Stage in the Valga-10 core. The same species has been recorded much less abundantly in the Laeva-18 core. Some very rare species like *Polychaetaspis multidentatus*, *Xanioprion tenuidentatus* appear in the Nabala Stage. In addition, the oldest occurrence of skalenoprionids (*Skalenoprion alatus*) and paulinitids (*Kettnerites* ssp.) in the Baltic region is recorded from the Nabala Stage. In general, the assemblage of the Nabala Stage is rather similar to that of the Rakvere Stage.

Vormsi Stage. Argillaceous limestones of the **Kõrgessaare** Formation (in Orjaku drill core) are characterised by relatively rich assemblage of polychaete jaws. Abundance of scolecodonts ranges from 18 to 36 per 100 g of rock, the total number of species is at least 27 in the Kõrgessaare Formation. The most common species are *Pistoprion transitans*, *Polychaetaspis* cf. *wyszogrodensis*, *Polychaetura gracilis*, *Xanioprion* sp. B, *Rhytiprion magus*, *Polychaetaspis* ssp., *Tetraprion pozaryskae*, *Mochtyella duplicidentata*, and *Mochtyella cristata*. The oldest specimens of *Conjungaspis minutus*, *Polychaetaspis pirguensis* and *Kozlowskiprion angustus* have been recorded from the top of the Kõrgessaare Formation.

The **Tudulinna** Formation (in the Laeva-18 drill core) is represented mostly by marls. The jawed polychaete fauna is of low diversity being represented by some 16 species. The abundance of scolecodonts is 15-20 per 100 g of sample. The most remarkable feature of the assemblage is strong dominance of *Polychaetura harjuensis*, which accounts for 30-35 per cents of all specimens. *Paramochtyella fragilis*, *Rhytiprion magnus*, *Polychaetaspis* ssp. *Pistoprion transitans* and *Xanioprion* sp. B are among the most common species. The oldest occurrence of *Tretoprion astae* is recorded in the Tudulinna Formation.

The dark argillite of the **Fjäckä** Formation (in the Valga-10 drill core) could not be studied due to core loss.

Eunicid assemblages of the Vormsi Stage differ from those in underlying strata by somewhat increased abundance and higher content of labidognath forms (that is, polychaetaspids and polychaeturids).

Pirgu Stage. The **Moe** and **Adila** Formations (in the Orjaku drill core) comprising various limestones are characterised by rather high abundance of scolecodonts (15-28/100 g of rock). The taxonomic composition of polychaete faunas is rather similar in both formations. At least 31 species occur and most often the assemblage is predominated by *Pistoprion transitans*, *Vistulella kozlowskii*, *Mochtyella duplicidentata*, *Xanioprion* sp. B, *Polychaetura gracilis*, *Polychaetaspis* ssp. In addition, species like *Tetraprion pozaryskae*, *Mochtyella fragilis*, *Mochtyella* sp. A, *Kalloprion* sp., *Polychaetaspis* cf. *wyszogrodensis* are rather frequent. *Kozlowskiprion angustus* and *Polychaetaspis pirguensis* seem to be a characteristic element of polychaete fauna of the Moe and Adila formations. Rare specimens of *Skalenoprion alatus*, *Kettnerites* ssp. and Gen. et sp. indet. A have been found in the Adila Formation.

The **Halliku** Formation (in Laeva-18 drill core) is represented by marls and argillaceous limestones. Rather low abundance of scolecodonts is typical of this formation (up to 12 per 100 g of sample). Altogether some 28 species are found. The most abundant species are *Polychaetaspis varsoviensis*, *Polychaetaspis* ssp., *Kozlowskiprion brevialetus*, *Tetraprion pozaryskae*,

Kalloprion ssp. and *Leptoprion* ssp. *Rakvereprion balticus*, which is typical species of the Jelgava Formation is also rather common in the Halliku Formation. A ramphoprionid resembling *Ramphoprion* cf. *deflexus* and rare specimens of *Skalenoprion alatus* have been recorded from the Halliku Formation.

The **Jelgava** Formation (in Valga-10 drill core) represented mostly by marls is characterised by polychaete assemblage of very low abundance (up to 8 per 100 g of rock) and strong predomination of *Rakvereprion balticus*. Significant is the occurrence of *Ramphoprion* cf. *deflexus* in the middle part of the formation. This form is possibly conspecific with North American species found from the Upper Ordovician of Ontario. In addition to the mentioned species, *Kalloprion* sp., *Valgaprion huberti*, *Xanioprion* sp. B, *Atraktoprion* sp. *Leptoprion* sp. *Polychaetaspis* sp. and *Lunoprionella* sp. have been recovered from the Jelgava Formation.

Lowermost part of the Pirgu Stage in Central- and South Estonia (**Jonstorp** Formation), and the topmost part in South Estonia (**Kuili** Member of the Jelgava Formation) are represented by red-coloured sediments, which contain no organic-walled microfossils. However, seemingly the conditions resulting in the red colour did not affect the faunas of eunicids but only the preservation potential of organic material. A good reason to assume this is the distribution pattern of *Rakvereprion balticus* in Valga-10 drill core (see Fig. 7). The species forms considerable part of the assemblages in the upper part of the Nabala Stage and continues with the same relative abundance in the Jelgava Formation (upper Pirgu Stage), whereas the red-coloured interval of the lower Pirgu Stage of the section is “cut out”.

Porkuni Stage. In North Estonia, the Porkuni Stage is represented by various shallow-water deposits like reefs and lagoonal deposits (**Ärina** Formation), most of which are unfavourable for preservation of organic microfossils. Thus no scolecodonts have been recovered from the Porkuni Stage of Orjaku core.

Bioclastic limestones and marls of the **Kuldiga** Formation (in Valga-10 drill core), often somewhat dolomitised, are characterised by almost complete absence of fossils of planktonic biotas (like chitinozoans, graptolites and acritarchs) and quantity of those of benthic origin (like melanoscleritoids and scolecodonts). At least 17 species occur in the Kuldiga Formation; *Pistoprion transitans*, *Mochtyella* aff. *cristata*, *Conjungaspis minutus*, *Valgaspis huberti* and *Polychaetaspis kuldigaensis* form the principal part of the assemblage. The abundance of scolecodonts is very high in the lowermost part (nearly 50/100 g of rock) but decreases considerably towards the upper part of the formation (to only 3/100 g of rock). In some respects polychaete association of the Kuldiga formation reminds that of the lowermost Silurian Puikule Member of the Õhne Formation. The common features include similar abundance, which is relatively high in the lower part of both units and decreases upwards. An assemblage predominated by *Pistoprion transitans* in the lower part is succeeded by abundance peak of species of *Mochtyella* and several polychaetaspids. In addition, a small percentage of planktonic component is typical of the Kuldiga as well as the Puikule formation. Possibly both rock

units, or at least certain parts of them, have been formed in rather similar facies conditions.

Well-laminated limestones and dolomites and sandy limestones of the **Saldus** Formation (in Laeva-18 and Valga-10 cores) represent the youngest sediments of the Ordovician in the study area. The Formation is unfossiliferous in the Laeva-18 core but contains rare and rather poorly preserved scolecodonts of at least eight species in the Valga-10 core. Most remarkable is the find of *Symmetroprion spatiosus*, which so far was thought to be restricted only to the Silurian. In addition, *Mochtyella* ex gr. *trapezoidea*, *Kettnerites* sp., *Polychaetura gracilis*, *Valgaprion huberti*, *Polychaetaspis* sp., *Atraktoprion* sp. and *Leptoprion* sp. have been recorded from the Saldus Formation.

The Ordovician–Silurian boundary

The Ordovician–Silurian boundary interval has been recognised as one of the most important crises in the history of life (Donovan 1989). The so-called Late Ordovician extinction event was controlled by the growth and decay of the Gondwanan ice sheet following a sustained period of environmental stability associated with high sea level. As a result of mostly this event, there are only few species common in the Ordovician and Silurian (e.g., Brenchley 1989; Robertson et al. 1991; Sheehan 1982). According to data on main fossil groups in the East Baltic region, on average less than 10 per cent of species and 40 per cent of genera of main fossil groups survived the latest Ordovician extinction event (Nestor et al. 1991; Kaljo & Hints 1996).

There is not much information available how the end Ordovician event influenced eunicid polychaetes. Kielan-Jaworowska (1966) distinguished Ashgillian and Silurian polychaete associations, but her material derived from erratic boulders, most of them without precise age determinations. Szaniawski's (1970) study confirmed Kielan-Jaworowska's conclusions about distinctness of Ordovician and Silurian polychaete faunas, both at the species and genus level. Both authors regarded genera like *Polychaetura*, *Kalloprion*, *Leptoprion*, *Pistoprion* and *Rhytiprion* as being restricted to the Ordovician. Further, the ramphoprionids were supposed to lack in the Silurian and symmetroprionids and skalenoprionids regarded as being characteristic of the Silurian.

Recent studies have extended the stratigraphic ranges of several mentioned taxa. For example, ramphoprionids are spread throughout the Silurian (Hints 1998), *Rhytiprion* has been recorded from the Silurian of Gotland and Indiana, North America (Bergman 1991b).

The Ordovician–Silurian boundary has not been the main object of this study and the Silurian material is not described, but several new aspects can still be emphasised. Many species are common between the Ordovician and Silurian in the present collection (Fig. 8). Among them several long-ranging taxa like *Pistoprion transitans* and *Polychaetura gracilis* appearing in the uppermost Arenig and lower Caradoc, respectively. This shows a considerably wider stratigraphic range of the genera *Pistoprion* and *Polychaetura* than proposed earlier (Szaniawski 1970). Also *Polychaetaspis varsoviensis*, *Archaeoprion quadricristatus*, *Mochtyella polonica*, *Mochtyella cristata*, *Vistulella kozłowskii*, *Lunoprionella symmetrica*, *Xanioprion* sp. B,

Xanioprion sp. A are recorded in the Silurian. The Ordovician genera *Kallopriion* and *Leptoprion* are represented at least in the lowermost part of the Silurian, being represented by new species.

Although skalenoprionids and symmetropionids are obviously a characteristic element of the Silurian fauna, they are recorded from the upper Ordovician also: the oldest species of *Skalenoprion* derives from the Nabala Stage, occasional specimens of the same genus are found in the Pirgu and Porkuni stages also. Few specimens of *Symmetropion spatiosus* are discovered from well-laminated, probably lagoonal part of the Saldus Formation. This agrees well with Bergman (1995), who found that *S. spatiosus* occurs preferably in lagoonal and inter-reefal environments in Gotland. Possibly, appearance of this species in study area is determined by availability of particular environmental conditions rather than by evolution of a new species.

Despite there are many species crossing the Ordovician–Silurian boundary, appearance of a number of taxa is confined to the lowermost Silurian, including several new species of polychaetaspids and mochttyellids, but likely some new genera as well. A characteristic feature of the Silurian fauna in the study area is a notable increase in abundance of paulinitids, although the first specimens of *Kettnerites* sp. are found already in the Nabala Stage. An increase of relative abundance of scolecodonts can be recorded in the lowermost Silurian as compared to average for the Harju. Some of the richest samples in the present collection derive from the Puikule Member of the Õhne Formation, yielding up to 120 specimens per 100 g of rock. Often a very small number of species is responsible for great abundance, actually meaning a remarkably lower diversity than in most Ordovician samples.

In consequence, eunicid polychaetes were probably less strongly influenced by the late Ordovician event than representatives of many other groups of fauna. In the Estonian sequence, the Ordovician–Silurian boundary is expressed in the polychaete faunas by appearance of some new taxa as well as by increased abundance, decreased diversity and changed structure of assemblages. However, this change seems to be resulted mostly in rearrangement of environments and only partly due to evolution of eunicids.

EUNICIDS ALONG THE ONSHORE – OFFSHORE PROFILE

Majority of the recent eunicid polychaetes are bottom-dwellers confined to a narrow spectrum of environmental conditions. The most important agents determining distribution of eunicids are thus the type of bottom, content of nutrients, oxygen and light availability, salinity and water energy. Apparently the Palaeozoic forms, which are regarded quite close to modern taxa, were influenced by the same properties of ancient environments. These conditions change more rapidly along an onshore-offshore profile than parallel to the shoreline. Accordingly, lateral changes in polychaete faunas are expected to be more distinct along the basin gradient. A degree of facies relationship of extinct jawed polychaetes, being a subject of this section, is therefore most easily detected along the onshore-offshore profile.

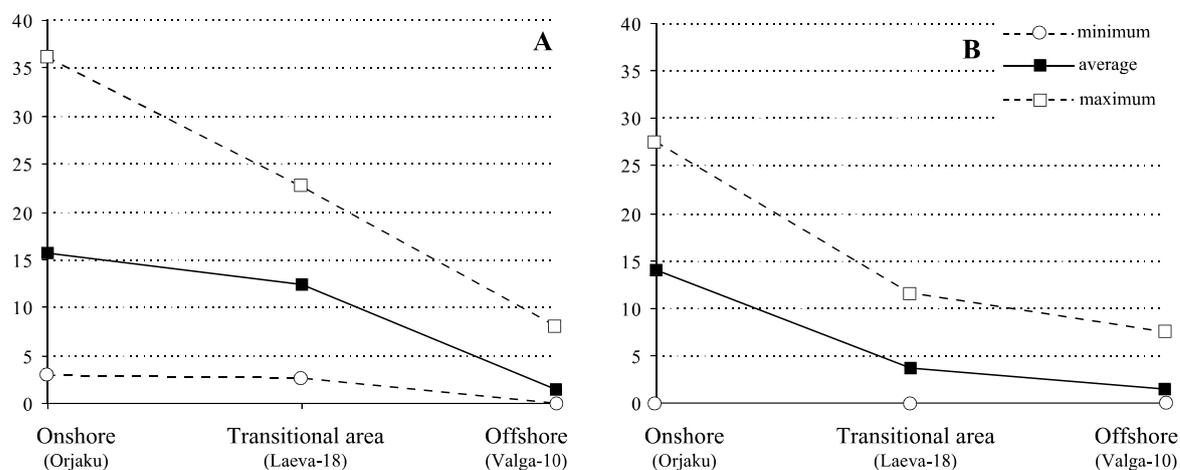
The distribution pattern of scolecodonts, described in this study, comprises the temporal and spatial element. To interpret the lateral changes of fauna, the temporal component must be eliminated or minimised. Although Harjuan eunicids evolved rather slowly, the temporal succession would obscure the faunal changes along the onshore-offshore profile. Probably the analysis of faunas of each regional stages would retrieve most accurate results, but due to several empty intervals and relatively low sampling density this was unattainable. For these reasons the studied sequence was split into two parts, the first corresponding to the Rakvere, Nabala and Vormsi stages, and the second to the Pirgu Stage. The Porkuni Stage could not be included as it contained no scolecodonts in the Orjaku and Laeva-18 cores. The Kuldiga Formation of the Porkuni Stage (in Valga-10 core) is rich in scolecodonts, but it represents the deposits formed in conditions of sea-level lowering and has no contemporaneous equivalents in the onshore part of the basin.

The main characteristics of an assemblage, whether living or fossil one, are the abundance, diversity and taxonomic composition. The latter may be described in different ways, from simple list of taxa (most often species) to frequency ratios of e.g., different families.

Figure 9 illustrates the maximum, minimum and average **abundance** of scolecodonts (specimens per 100 g of sample; see chapter of methods above) in the studied sections. Decrease of abundance towards the off-shore part of the palaeobasin is clearly visible for the whole sequence. The difference between the average abundance of Orjaku and Valga-10 cores is about ten times in both older and younger part of the sequence. The average abundance in Laeva-18 core is changed in time, being rather similar to that in the Orjaku core for the Nabala and Vormsi stages, and more like that in the Valga-10 core for the Pirgu Stage.

The abundance of scolecodonts, like any fossils, in the rock is a function of actual density of individuals in a once lived community, degree of post-mortem transportation and accumulation, the rate of deposition and preservation. In regard to eunicid polychaetes, the process of shedding of jaws may have also been involved. However, in

the present case, there is no sedimentological features, nor evidence of other fossils that suggest large-scale re-deposition or selective preservation of scolecodonts. The probable shedding would likely not affect recognition of main trends of distribution but



multiply the actual number of individuals lived. Consequently the abundance in samples may be simplified to a combination of actual abundance and the deposition rate.

Thickness of the Harju Series is comparable in three studied sections (50–70 m). The sequence in the southern part of the study area is thought to be more continuous. Thus, in a broad scale, the deposition rates in Central Baltoscandian Confacies belt unlikely exceeded those in the North Estonian Confacies belt. The decreased abundance of scolecodonts in the samples from the Valga-10 section probably reflects the primarily lower density of the eunicids, compared to other sections. In other words, the density of specimens inhabiting a particular environment was higher in onshore part of the palaeobasin.

Figure 9. Abundance of polychaete jaws in three drill core sections (specimens per 100 g of sample, see p. 9 for explanation of counting method). **A** – Rakvere, Nabala and Vormsi stages; **B** – Pirgu Stage.

The **diversity** change along the onshore-offshore profile is shown in Figure 10. Index of the diversity of assemblage is calculated by Simpson's formula (Simpson 1949),

$$D = N(N-1) / \sum n(n-1),$$

where N – number of specimens in a sample, n – number of specimens within a species. The higher is dominance of few species, the smaller is value of the index. The assemblage containing great number of species, thus having high taxonomic diversity, does not necessarily have a high value of the diversity index.

For the Rakvere, Nabala and Vormsi stages, an average of the diversity index is almost identical in Orjaku and Laeva-18 cores, slightly exceeding that in the Valga 10 core. The maximum is highest in the Valga-10 core, but this is likely due to small number of specimens encountered. For the Pirgu Stage, a notable decrease in diversity towards

the offshore part of the palaeobasin is recorded, matching the decrease in abundance. The basic reason being generally responsible for the decrease in diversity is an increased environmental stress and the same is suggested for the present case of study. That is, the habitats in the Central Baltoscandian Confacies belt were of higher stress for jawed polychaetes than those in onshore part of the palaeobasin, at least during the Pirgu time. The properties of an environment which account for the most of this stress cannot be recovered on the basis of present data set, however.

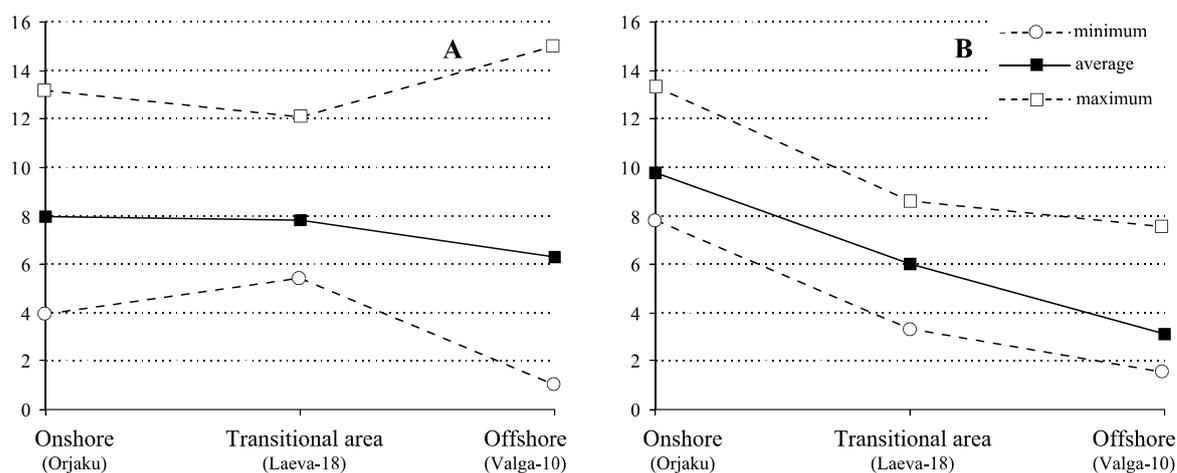


Figure 10. Diversity indices of eunicid assemblages in three drill core sections (calculated by Simpson's formula, see explanation in text). **A** – Rakvere, Nabala and Vormsi stages; **B** – Pirgu Stage.

A significant part of the species recorded occur in all three sections, but the **taxonomic composition** appeared to be variable along the onshore-offshore profile. This is primarily expressed in the list of predominating species. It appeared that many of the prevailing species are abundant in one section only (see Fig. 11). The following species are the best examples of that.

Pistoprion transitans is one of the most common species in the Nabala, Vormsi and Pirgu stages of the Orjaku core. It is common, but markedly less abundant in the Laeva-18 core and absent in contemporaneous rocks of the Valga-10 core. In the latter locality *Pistoprion transitans* appears in the Kuldiga Formation, formed in conditions of a low sea-level. This suggests that *P. transitans* favoured onshore environments rather than the offshore ones.

Rakvereprion balticus predominates in the Nabala and Pirgu Stages of the Valga-10 core. The species is found in several samples of the Laeva-18 core also, but it never prevails over other species there. Only seldom specimens of *Rakvereprion balticus* have been recorded in the samples from the Orjaku core. It is apparent that *Rakvereprion balticus* was adopted to survive better offshore than onshore part of the palaeobasin.

Polychaetaspis varsoviensis is one of the predominating species in the Pirgu Stages of the Laeva-18 core. The same species is found throughout the sequence in the Orjaku core, though it is not abundant. In the Valga-10 core, *Polychaetaspis varsoviensis* occurs

only in the Rakvere and Nabala stages and sometimes forms a significant part of all specimens. In generalised terms, *P. varsoviensis* showed preferences for transitional area and more offshore environments, being eclipsed by other species of the same genus in the onshore part of the palaeobasin.

Polychaetura gracilis is also confined to onshore and transitional facies. It is completely absent in the Harjuan sequence of the Valga-10 core, except for the shallow-water Saldus Formation of the Porkuni Stage where rare specimens have been recorded.

Polychaetura harjuensis is the most abundant species in the Vormsi Stage of the Laeva-18 core. Stratigraphical range of this species is actually wider, beginning from the Rakvere Stage (in Rapla drill core). A single specimen of *P. harjuensis* is found from the Nabala Stage of Valga-10 drill core, and few specimens derive from the Nabala and Vormsi stages of the Orjaku core. Vormsi Stage of the Valga-10 core could not be investigated due to core loss and the relative abundance of *P. harjuensis* in these beds cannot be estimated. However, this species is seemingly confined to a very particular environment. This suggestion is confirmed by a rich assemblage of scolecodonts in the Nabala-Vormsi stages of the Mielnik borehole (East Poland), where the same species is of very high density. Similar facies conditions can be suggested on this basis for Central (and Southern?) Estonia and East Poland during Nabala-Vormsi age.

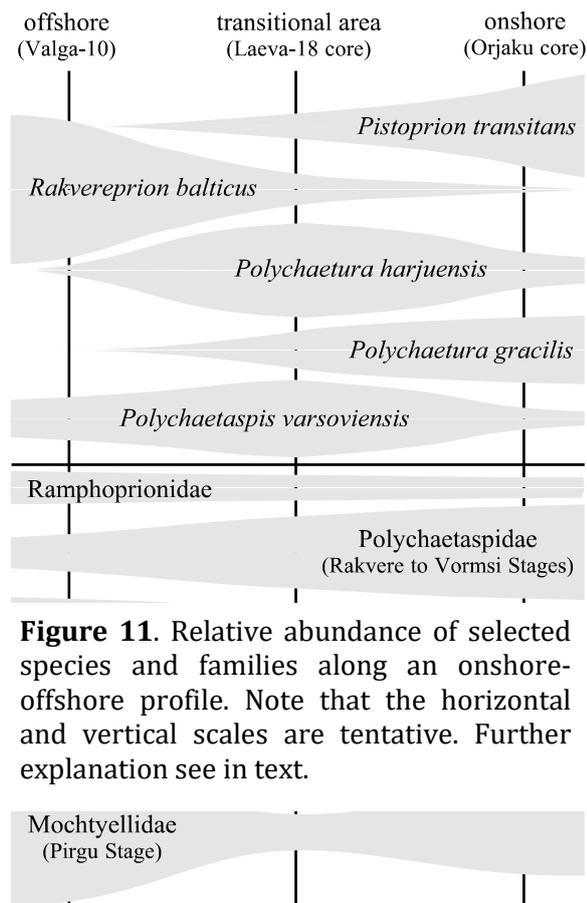


Figure 11. Relative abundance of selected species and families along an onshore-offshore profile. Note that the horizontal and vertical scales are tentative. Further explanation see in text.

In addition to the specific composition of the assemblage, the distribution of higher taxa of jawed polychaetes, like families, can be traced. In the Harju Series of Estonia, majority of the eunicid specimens belong to Polychaetaspidae, Mochtyellidae, Polychaeturidae and Xanioprionidae. In few samples only, ramphoprionids, atraktoprionids, kalloprionids, tertraprionids, rhytiprionids and conjungaspids may also make up a considerable part of an assemblage. On the basis of average percentage of specimens belonging to particular families, it appeared that only the distribution of ramphoprionids shows a distinct trend in the Harju Series – a slight increase towards the offshore part of the palaeobasin (see Fig. 11). For other families, the distribution changed in time. For instance, role of polychaetaspids decrease and that of mochttyellids increase continuously offshore in the Rakvere to Vormsi stages. In the Pirgu Stage, mochttyellids are abundant in the onshore and offshore area whereas polychaetaspids prevail in the transition area.

In order to summarise the information on all species, two types of multivariate analyses were performed on the present data set. Different modifications of cluster and factor analyses are usually relatively simple, still efficient and thus the most frequently used methods. Many examples of applicability of both methods can be found in palaeontological literature too (e.g., Baarli 1987; Hayes 1980; Mello & Buzas 1968; De Keyser 1977; Valentine & Peddicord 1967; Sepkoski & Sheehan 1983). Different similarity coefficients have been employed in palaeontological studies to calculate the matrix on

which the graphical output of the clustering is based (see Cheetam & Hazel 1969 and Fallaw 1979 for reference). The simplest distance measure, the Euclidean distance, coupled with Ward's linkage rule (see Ward 1963 for details) was used in this study.

The principal components method of the factor analyses is based on correlation coefficients. Usually the cluster analysis gives better results regarding differences between particular cases/variables, whereas the factor analyses is relatively more efficient for detecting higher-level groupings within a composite data set. The data matrix used herein was composed of abundance of scolecodonts, and percentage of taxa in samples as variables. The samples (cases) containing no or unidentifiable polychaete jaws, as well as the species having very low abundance were omitted to minimise the statistical noise.

First, an attempt was made to analyse the entire data set at once. The corresponding

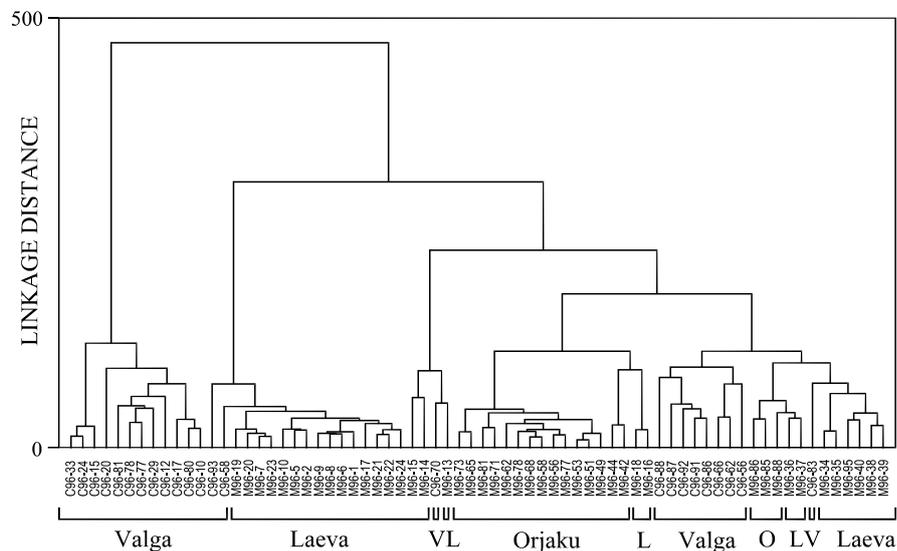


Figure 12. Dendrogram of the cluster analyses, based on data from 66 samples (Rakvere to Juuru stages are included). See explanation in text and Figs 5–7 for positions of the samples in three core sections. V – Valga-10 core, L – Laeva-18 core, O – Orjaku core.

dendrogram of cluster analyses is presented in Figure 12. One may observe a relatively complicated picture, supposedly much influenced by temporal change of the composition of assemblages. The adjacent samples mostly tend to group together, but the grouping is indistinct and apparently does not reflect the lateral distribution of eunicids. However, some interesting aspects can be mentioned. The similarity between the polychaete faunas of the Kuldiga Formation and Puikule Member, discussed in the section of stratigraphical distribution, is well expressed in this chart (samples C96-70, M96-13, M96-14 and M96-15). The Silurian samples from the Orjaku core and some Silurian samples of the Laeva-18 core also group together.

For reducing the effect of the temporal changes, the data was separated into two subsets as explained above. Results of cluster and factor analyses of the Rakvere to Vormsi stages are illustrated in Figs 13-14. In Figure 13, the dendrogram of cluster analysis displays several groupings of samples, which do not match the three localities. Samples from different sections tend to be mixed together, even those from the most distant localities (Orjaku and Valga-10 cores). The similarity between the lowermost samples of the Laeva-18 core (M96-40, M96-39, M96-38) and Valga-10 core (C96-95) should be noted. In first order, this is due to relatively high per cent of *Paramochtyella fragilis* and similar abundance of scolecodonts. The lithological characteristics of the samples of two localities are different: argillaceous marls of the Valga-10 core are replaced by argillaceous limestones in the Laeva-18 core. This may indicate that the clay content of the substrate did notably not affect jawed polychaete faunas. In other words, Harjuan eunicids did not concern whether the mud on or in which they lived was clayey or carbonaceous. This disagrees with data on some other benthic microfossils like ostracodes, distribution of which was supposedly strongly influenced by content of terrigenous argillaceous material (Meidla 1996).

Table 1.

Eigenvalues and per cents of total variance of eight principal components (data from the Rakvere, Nabala and Vormsi stages, see also scatter plot in Fig. 14.)

Principal component	Eigenvalue	% of total variance	Cumulative eigenvalue	Cumulative % of total variance
1	9.01	31.07	9.01	31.07
2	3.62	12.47	12.63	43.54
3	2.80	9.65	15.43	53.19
4	2.38	8.20	17.81	61.40
5	2.16	7.46	19.97	68.85
6	1.47	5.08	21.44	73.93
7	1.32	4.57	22.76	78.50
8	1.15	3.95	23.91	82.45

The scatter plot of the factor analyses for the Rakvere to Vormsi stages (Fig. 14.) demonstrates differentiation of the samples according to the localities. Although the data points of three localities are close to each other in regard to the first two axis, they are not mixed allowing to enclose samples of every locality. During the analyses eight factors (eigenvalues > 1) were extracted (see Table 1). Concerning the first three principal components, the following variables are responsible for higher factor scores: (1) *Polychaetaspis*

ssp., (2) abundance per 100 g, (3) *Paramochtyella fragilis*, (4) *Polychaetura gracilis*, (5) *Pistoprion transitans*, (6) *Rakvereprion balticus*, (7) *Polychaetaspis* cf. *wyszogrodensis*, (8) *Xanioprion* sp. A, (9) *Polychaetaspis latoides* and (10) *Polychaetura harjuensis*.

The picture is completely different for the Pirgu Stage (Figs 15-16). The dendrogram of cluster analyses (Fig. 15) has three discrete branches, each corresponding to a locality and characterising a certain belt on the onshore-offshore profile. Scolecodont assemblages in the samples from the Valga-10 core appear to be more distinctly separated from those of Laeva-18

and Orjaku cores, but the variability within the group is rather high. This may partly be due to small abundance of scolecodonts and correspondingly lower reliability of counting results. The assemblages of the Orjaku and Laeva-18 sections are well distinguished, but more similar to each other as compared to the distance between them and the group of samples from the Valga-10 core.

The result of the factor analysis coincides remarkably well with that of cluster analysis. The scatter plot of two first principal components (Fig. 16) shows a clear distinction of samples of different localities. The data points representing samples from the Valga-10 core show a rather high dispersion and are distant from the Orjaku and Laeva-18 fields. The three factors were extracted (eigenvalues > 1, see Table 2). The variables standing for higher factor scores are (1) *Polychaetaspis* ssp., (2) abundance per 100 g, (3) *Polychaetaspis varsoviensis*, (4) *Rakvereprion balticus*, (5) *Pistoprion transitans*, (6) *Polychaetaspis* cf. *wyszogrodensis*, (7) *Vistulella kozlowskii*, and (8) *Xanioprion* sp. B.

Table 2.

Eigenvalues and per cents of total variance of three principal components (data from the Pirgu Stage, see also scatter plot in Fig. 16.)

Principal component	Eigenvalue	% of total variance	Cumulative eigenvalue	Cumulative % of total variance
1	15.48	55.29	15.48	55.29
2	5.21	18.61	20.69	73.90
3	3.04	10.86	23.73	84.76

As a summary, the results of multivariate methods are invaluable in generalising and visualising the complicated data set, which otherwise could hardly be done.

There are few earlier studies concerning the ecology of fossil polychaetes. Bergman (1989) was able to distinguish eury- and stenotopic species of the family Paulinitidae in the Silurian of Gotland. A symmetroprioid *Symmetropriion spatiosus* was demonstrated to prefer lagoonal and inter-reef habitats (Bergman 1995). Eriksson (1997, 1998) reported facies dependence of some Silurian polychaetaspids. Bergman (1989) and Eriksson (1996) concluded that a rather shallow-water and low-water energy environments likely offered the most varied and optimal conditions for the majority of Palaeozoic eunicids. Furthermore, associations of low abundance and diversity have been found in shales deposited in relatively deep water environments (Courtinat & Howlett 1990; Courtinat *et al.* 1990; Underhay & Williams 1995). Recent

polychaetes are known to range from the intertidal zone to abyssal depths, being most diverse in the shallower part of the continental shelf (George & Hartman-Schröder 1985).

The present work is the first to account all jawed polychaete species (not only particular taxonomic subdivision of eunicids) of different facies. It reveals from the data presented above that jawed polychaete assemblages of three core sections are relatively different. The question

to ask is whether the data express a major trend and can be considered as representative. Lateral changes in the Late Viruan (Caradoc) assemblages of jawed polychaetes within the North Estonian Confacies Belt appeared to be rather minor (Hints in press). Despite a relatively lower facial zonality of the palaeobasin during the Viru epoch (Männil 1966), this suggest that the trends revealed herein may be spatially extrapolated. It is suggested that the Harjuan polychaete assemblages were well differentiated along the onshore-offshore profile. A decrease in abundance and diversity towards the offshore part of the palaeobasin indicates that the onshore facies provided most favourable habitats for the majority of Harjuan jawed polychaetes. This agrees with the earlier studies on ecology of fossil polychaetes mentioned above, as well as with the knowledge on many recent polychaetes.

Losovskaya (1977), studying polychaetes on the shelf of Black sea, reported that the depth ranges of particular species have rather discrete lower-, but transitional upper boundaries. Specimens of the most species have been found above, but not much below their optimal depth interval. This is unlikely due to specific gas regime of the Black Sea, which strongly affects life in greater depths but not much in the shallower part of the shelf. It is possible that some Ordovician eunicids displayed the same tendency in their distribution. That would explain the fact that the species preferring offshore or transitional conditions, like *Rakvereprion balticus*, *Polychaetaspis varsoviensis* and *Polychaetura harjuensis* are found from North Estonian Confacies also, while the species preferring onshore or transitional facies like *Polychaetura gracilis* and *Pistoprion transitans* are completely absent from the Central Baltoscandian Confacies, which is regarded to represent relatively deeper-water environments.

The succession of jawed polychaete assemblages show that the biofacies zonality of polychaetes was relatively less distinct in the Rakvere and Nabala times and increased remarkably in the Pirgu time. This is well seen in the diversity data (Fig. 10.): in the lower part of the sequence the diversity is almost the same in three sections, but clearly differentiated in the Pirgu Stage. Moreover, the lateral changes in the taxonomic composition are differently expressed for the Rakvere to Vormsi and for the Pirgu Stage. A clear indication of this is provided by the multivariate methods (Figs 13-16), where the samples from Rakvere to Vormsi stages are barely distinguished between three localities. In the Pirgu Stage, on the other hand, three distinct groups of samples, corresponding to different localities and hence to different zones in the onshore-offshore profile are present. The present material is not detailed enough to make conclusions for the Porkuni time, but development of the palaeobasin and data on other fossil groups suggest that the Porkuni time was characterised by very high lateral differentiation of jawed polychaete assemblages also. The reasons of increase in

biofacial zonality in the Pirgu and Porkuni stages are likely connected with the development of the palaeobasin which was noted already by Männil (1966).

CONCLUSIONS

1. The eunicid polychaete fauna of the Harju Series comprises more than 50 species. 46 species, including 14 new ones are described in this study. Based on fused and reconstructed jaw apparatuses a new family Conjungaspidae and five new genera (*Paramochtyella*, *Valgaprion*, *Conjungaspis*, *Laevaprion* and *Tretoprion*) are erected.
2. Construction of jaw apparatuses and morphology of first maxillae, basal plates and carriers allows to propose a phylogenetic scheme of the Ordovician polychaeturids. *Polychaetura gracilis* Kozłowski, the oldest known polychaeturid is regarded to have given a rise to Caradocian *Polychaetura kielanae* Hints. Latter species is presumably ancestor of *P. harjuensis* described in this study.
3. The smooth transversal ridges in the first and second maxillae of phylogenetically distant species, *Rhytiprion magnus* Kielan-Jaworowska and *Laevaprion jaaki* gen. et sp. nov. are regarded to express convergence. Both species were likely adapted to a common mode of feeding.
4. Distribution pattern of *Rakvereprion balticus* Eisenck in Valga-10 drill core indicates that the conditions caused red colour of the sediments (Jonstorp Formation) did likely not influenced the polychaete faunas once lived, but only disabled the preservation of organic substance of the jaws as well as other organic-walled microfossils.
5. Many of the abundant eunicid species in the Harju Series are long-ranging, occurring also in under- and/or overlying strata. The possible stratigraphic value of some relatively short-ranged taxa needs further approval.
6. The stratigraphic ranges of several taxa were justified in this study. Skalenoprionids, symmetropionids and paulinitids, earlier considered as typical of the Silurian of the Baltic region, were recorded from the Harju Series. The Ordovician-Silurian boundary is not as distinct in the distribution of polychaetes as previously suggested.
7. Harjuan jawed polychaete faunas were well differentiated along the onshore-offshore profile. Abundance and diversity were the highest in the more shallow-water part of the palaeobasin, which seemingly offered optimal habitats for the majority of Harjuan jawed polychaetes.
8. The lateral differentiation of the assemblages increase in the Pirgu Stage, likely reflecting the general increase of the facies differentiation in the palaeobasin.
9. A multivariate approach proved invaluable in generalising and visualising the complicated data set, which otherwise could hardly be done.

ACKNOWLEDGEMENTS

Dr. Tõnu Meidla showed great interest to my work, providing invaluable suggestions as well as linguistic help, both of which significantly improved the study. Prof. Hubert Szaniawski helped me a lot during my visit to the Institute of Palaeobiology of Polish Academy of Sciences. He offered access to his collection of Harjuan scolecodonts from the Mielnik drill core and discussed several aspects of fossil and recent jawed polychaetes. Dr. Peep Männik kindly put at my disposal his samples from the Valga-10 drill core.

The SEM studies were performed at the Institute of Palaeobiology of Polish Academy of Sciences and the Centre for materials research at Tallinn Technical University. A great assistance in this work was provided by Dr. Cyprian Kulicki and Dr. Valdek Mikli. The prints were made by Gennadi Baranov.

I am deeply grateful to all these persons, without their help this project would not have been possible.

The study is a contribution to IGCP project 410 “The Great Ordovician Biodiversification Event”. Most of the financial support came from the grants No. 1935 and 3516 of the Estonian Science Foundation.

REFERENCES

- Åkesson, B. 1973. Morphology and life history of *Ophryotrocha maculata* sp. n. (Polychaeta, Dorvilleidae). – *Zoologica scripta* **2**, 141–144.
- Baarli, B. G. 1987. Benthic faunal associations in the Lower Silurian Solvik Formation of the Oslo-Asker Districts, Norway. – *Lethaia* **20**, 75–90.
- Bergman, C. F. 1979. Polychaete jaws. – In: Jaanusson, V., Laufeld, S. & Skoglund, R. (eds). *Lower Wenlock faunal and floral dynamics - Vattenfallet Section, Gotland. Sveriges Geologiska Undersökning C762*, 92–102.
- Bergman, C. F. 1989. Silurian paulinitid polychaetes from Gotland. – *Fossils and Strata* **25**, 127 pp.
- Bergman, C. F. 1991a. Revision of some Silurian paulinitid scolecodonts from western New York. – *Journal of Paleontology* **65**, 248–254.
- Bergman, C. F. 1991b. Palaeoecology of two Early Palaeozoic polychaete species. – *Lund Publications in Geology* **2**, 7.
- Bergman, C. F. 1995. *Symmetrion spatiosus* (Hinde), a jawed polychaete showing preference for reef environments in the Silurian of Gotland. – *Geologiska Föreningens i Stockholm Förhandlingar* **117**, 143–150.
- Boyer, P. S. 1981. Calcite in the mandibles of a marine polychaete. – *Review of Paleobotany and Palynology* **34**, 247–250.
- Brenchley, G. A. 1979. Post-mortem transportation and population longevity recorded in scolecodont death assemblages. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **28**, 297–314.
- Brenchley, P. J. 1989. The Late Ordovician Extinction. – In: Donovan, S. K. (ed.). *Mass extinctions: Processes and Evidence*. Columbia University Press, New York. p. 104–132.
- Brenchley, P. J., Marshall, J. D., Hints, L. & Nölvak, J. 1994. Bathymetric and isotopic evidence for a short-lived Late Ordovician glaciation in a greenhouse period. – *Geology* **22**, 295–298.
- Briggs, D. E. G., Siveter, David J. & Siveter, Derek J. 1996. Soft-bodied fossils from a Silurian volcanoclastic deposit. – *Nature* **382**, 248–249.
- Charletta, A. C. & Boyer, P. S. 1974. Scolecodonts from Cretaceous greensand of the New Jersey coastal plane. – *Micropaleontology* **20**, 354–366.
- Cheetam, A. H. & Hazel, J. E. 1969. Binary (presence–absence) similarity coefficients. – *Journal of Paleontology* **43**, 1130–1136.
- Claparede, E. 1870. Annelides chetopodes du golfe de Naples. – *Memoires de la Societe de physique et d'histoire de Geneve* **19-20**.
- Colbath, G. K. 1986. Jaw mineralogy in eunicean polychaetes (Annelida). – *Micropaleontology* **32**, 186–189.
- Colbath, G. K. 1987. Evidence for shedding of maxillary jaws in eunicid polychaetes. – *Journal of Natural History* **21**, 443–447.
- Colbath, G. K. & Larsson, S. K. 1980. On the chemical composition of fossil polychaete jaws. – *Journal of Paleontology* **54**, 485–488.

- Corradini, D. & Olivieri, R. 1974. *Langeites sicilensis* n. sp., a polychaete jaw apparatus from the Permo-Carboniferous of north-western Sicily. – *Bolletino della Societa Paleontologica Italiana* **13**, 156–163.
- Courtinat, B. & Howlett, P. 1990. Dorvilleids and arabellids as indicators of dyusaerobic events in well laminated non-bioturbated deposits of the French Mesozoic. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **80**, 145–151.
- Courtinat, B., Crumiere, J.-P. & Meon, H. 1990. Les organoclastes du Cenomanien superieur du bassin Vocontien (France): Les Scolecodontes. – *Geobios* **23**, 387–397.
- Courtinat, B., Crumiere, J.-P. & Podegrat, A.-M. 1990. Scolocodonts, remains of Annelida Errantida, witnesses of suboxy rather than anoxy in Mesozoic black shales. – *Compte Rendu de l'Academie des Sciences* **2**, 1089–1093.
- Croneis, C. & Scott, H. W. 1933. Scolecodonts. – *Bulletin of the Geological Society of America* **44**, 207.
- De Keyser, T. L. 1977. Late Devonian (Frasnian) Brachiopod community patterns in western Canada and Iowa. – *Journal of Paleontology* **51**, 181–196.
- Donovan, S. K. 1989. Introduction. – In: Donovan, S. K. (ed.). *Mass extinctions: Processes and Evidence*. Columbia University Press, New York. p. 1–19.
- Edgar, D. R. 1984. Polychaetes of the Lower and Middle Paleozoic: A Multi-element analysis and phylogenetic outline. – *Review of Palaeobotany and Palynology* **43**, 225–285.
- Ehlers, E. 1968a. Ueber eine fossile Eunicee aus Solenhofen (*Eunicites avitus*), nebst Bemerkungen über fossile Würmer überhaupt. – *Zeitschrift für wissenschaftliche Zoologie* **18**, 421–443.
- Ehlers, E. 1968b. Ueber fossile würmer aus dem lithographischen Schiefer in Bayern. – *Palaeontographica* **17**, 145–175.
- Eichwald, E. 1854. Die Grauwackenschichten von Liev- und Esthland. – *Bulletin de la Imperiale des Naturalistes de Moscou* **27**, 1–111.
- Eisenack, A. 1939. Einige neue Annelidenreste aus dem Silur und dem Jura des Balticums. – *Zeitschrift für Geschiebeforschung und Flachlandsgeologie* **15**, 153–176.
- Eisenack, A. 1975. Beiträge zur Anneliden - Forschung, I. – *Neues Jahrbuch für Geologie und Paleontologie Abhandlungen* **150**, 227–252.
- Eller, E. R. 1933. An articulated annelid jaw from the Devonian of New York. – *American Midland Naturalist* **14**, 186.
- Eller, E. R. 1942. Scolecodonts from the Erindale, Upper Ordovician, at Streetsville, Ontario. – *Annals of the Carnegie Museum* **29**, 241–270.
- Eller, E. R. 1945. Scolecodonts from the Trenton Series (Ordovician) of Ontario, Quebec, and New York. – *Annals of the Carnegie Museum* **30**, 119–212.
- Eller, E. R. 1969. Scolecodonts from well cores of the Maquoketa Shale, Upper Ordovician, Ellsworth County, Kansas. – *Annals of the Carnegie Museum* **41**, 1–17.
- Eriksson, M. 1996. Taxonomy and palaeoecology of some labidognathid polychaetes from the Lower Silurian of Gotland. – *Geologiska Föreningens i Stockholm Förhandlingar* **118** Jubilee issue, A59.

- Eriksson, M. 1997. Lower Silurian polychaetaspid polychaetes from Gotland, Sweden. – *Geologiska Föreningens i Stockholm Förhandlingar* **119**, 213–230.
- Eriksson, M. 1998. *Dubichaetaspis bergmani* gen. et sp. nov., a facies controlled polychaete from the Silurian of Gotland, Sweden. – *Geologiska Föreningens i Stockholm Förhandlingar* **120**, 21–25.
- Eriksson, M. & Bergman, C. F. 1997. How to cure the scolecodont plague. – *Lund Publications in Geology* **134**, 10.
- Fallaw, W. C. 1979. A Test of the Simpson coefficient and other binary coefficients of faunal similarity. – *Journal of Paleontology* **53**, 1029–1034.
- George, J. D. & Hartman-Schröder, G. 1985. Polychaetes: British Amphinomida, Spintherida & Eunicida. – *Synopses of the British Fauna (New Series)* **32**, 221 pp.
- Germraad, J. H. 1980. Dispersed scolecodonts from the Cainozoic strata of Jamaica. – *Scripta Geologica* **54**, 1–24.
- Hayes, B. J. R. 1980. A cluster analyses interpretation of Middle Ordovician biofacies, southern Mackenzie Mountains. – *Canadian Journal of Earth Sciences* **17**, 1377–1388.
- Hinde, G. J. 1879. On Annelid jaws from the Cambro-Silurian, Silurian and Devonian formations in Canada and from Lower Carboniferous in Scotland. – *The Quarterly Journal of the Geological Society of London* **35**, 370–389.
- Hinde, G. J. 1880. On annelid jaws from the Wenlock and Ludlow Formations of the West of England. – *The Quarterly Journal of the Geological Society of London* **36**, 368–378.
- Hinde, G. J. 1882. On annelid remains from the Silurian stata of the Isle of Gotland. – *Bihang till Kungliga Vetenskapsakademiens Handlingar* **7(5)**, 3–28.
- Hinde, G. J. 1896. On the jaw-apparatus of an annelid (*Eunicites reidiae* sp. nov.) from the Lower Carboniferous of Halkin Mountain, Flintshire. – *The Quarterly Journal of the Geological Society of London* **52**, 438–450.
- Hints, L. & Meidla, T. 1997. Sedimentary cover: Ordovician. Harju Series (Upper Ordovician). – In: Raukas, A. & Teedumäe, A. (eds), *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn. p. 80–85.
- Hints, L. & Rõõmusoks, A. 1997. Formation of the territory: Evolution of life during the Vendian – Devonian. Ordovician articulate brachiopods. – In: Raukas, A. & Teedumäe, A. (eds), *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn. p. 224–225.
- Hints, L. & Stukalina, G. 1997. Formation of the territory: Evolution of life during the Vendian – Devonian. Echinoderms. – In: Raukas, A. & Teedumäe, A. (eds), *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn. p. 238–241.
- Hints, L., Meidla, T., Nõlvak, J. & Sarv, L. 1989. Some specific features of the late evolution in the Baltic Basin. – *Proceedings of the Estonian Academy of Sciences. Geology* **38**, 83–88.
- Hints, O. 1996. Scolecodonts and stratigraphy: an example from upper Middle Ordovician of North Estonia. – In: Meidla, T., Puura, I., Nemliher, J., Raukas, A & Saarse, L. (eds). *The Third Baltic Stratigraphical Conference, Abstracts, Field Guide*. TartuUniversity Press, Tartu. p. 28.

- Hints, O. 1998. Revision of the Ordovician and Silurian ramphoprionid polychaetes from Severnaya Zemlya, Russian Arctic. – *Proceedings of the Estonian Academy of Sciences. Geology* **47**, 77-85.
- Hints, O. in press. Late Viruan (Caradoc) polychaete jaws from Estonia and St. Petersburg region. – *Acta Paleontologica Polonica*.
- Hints, O., Kallaste, T. & Kiipli, T. 1997. Mineralogy and micropalaeontology of the Kinnekulle altered volcanic ash bed (Ordovician) at Pääsküla, North Estonia. – *Proceedings of the Estonian Academy of Sciences. Geology* **46**, 107–118.
- Jaanusson, V. 1960. Graptoloids from the Ontikan and Viruan (Ordovician) limestones of Estonia and Sweden. – *Bulletin of the Geological Institutions of the University of Uppsala* **38**, 289–366.
- Jaanusson, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Baltoscandia. In: Bassett, M. G. (ed.). *The Ordovician System. – Proceedings of a Paleontological Association Symposium*. University of Wales Press, Cardiff. p. 301–326.
- Jaanusson, V. 1982. Introduction to the Ordovician of Sweden. – In: Bruton, D. L. & Williams, S. H. (eds). *Field excursion guide. IV International Symposium of the Ordovician System. Palaeontological Contributions of the University of Oslo* **297**, 1–10.
- Jaanusson, V. 1995. Confacies differentiation and upper Middle Ordovician correlation in the Baltoscandian Basin. – *Proceedings of the Estonian Academy of Sciences. Geology* **44**, 73–86.
- Jansonius, J. & Craig, J. H. 1971. Scolecodonts: I – Descriptive terminology and revision of systematic nomenclature; II – Lectotypes, new names for homonymus, index of species. – *Bulletin of Canadian Petroleum Geology* **19**, 251–302.
- Kaljo, D. & Hints, L. 1996. Late Ordovician–Early Silurian Succession of Paleoecosystems in Estonia. – *Paleontological Journal* **30**, 693–700.
- Kielan-Jaworowska, Z. 1961. On two Ordovician polychaete jaw apparatuses. – *Acta Palaeontologica Polonica* **6**, 237–254.
- Kielan-Jaworowska, Z. 1962. New Ordovician genera of polychaete jaw apparatuses. – *Acta Palaeontologica Polonica* **7**, 291–325.
- Kielan-Jaworowska, Z. 1966. Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and comparison with modern forms. – *Paleontologia Polonica* **16**, 152 pp.
- Kielan-Jaworowska, Z. 1968. Scolecodonts versus jaw apparatuses. – *Lethaia* **1**, 39–49.
- Kozłowski, R. 1956. Sur quelques appareils masticateurs des Annelides Polychaetes ordoviens. – *Acta Palaeontologica Polonica* **3**, 165–210.
- Kozur, H. 1970. Zur Klassifikation und phylogenetischen Entwicklung der fossilen Eunicida und Phyllodocida (Polychaeta). – *Freiberger Forschungshefte* **C260**, 35-81.
- Kozur, H. 1971. Die Eunicida und Phyllodocida des Mesozoikums. – *Freiberger Forschungshefte* **C267**, 73-111.
- Kozur, H. 1972. Die Bedeutung der trassischen Scolecodonten insbesondere für die Taxonomie und Phylogenie der fossilen Eunicida. Hat sich die Synthese vom 'ortotaxonomischen' und 'parataxonomischen' System in der Praxis bewährt? – *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten* **21**, 745–776.

- Lange, F. W. 1947. Annelidos poliquetos dos folhelhos devonianos do Parana. – *Arquivos do Museu Paranaense* **6**, 161–230.
- Lange, F. W. 1949. Polychaete annelids from the Devonian of Parana, Brazil. – *Bulletin of American Paleontology* **33**, 5–104.
- Laufeld, S. 1975. Paleocology of Silurian polychaetes and chitinozoans in a reef-controlled sedimentary regime. – *The Geological Society of America. Abstracts with Programs*. p. 804–805.
- Losovskaya, G. V. 1977. *Ecology of polychaetes in Black Sea* [in Russian]. Naukova Dutka, Kiev. 92 pp.
- Martinsson, A. 1960. Two assemblages of polychaete jaws from the Silurian of Gotland. – *Bulletin of the Geological Institutions of the University of Uppsala* **39:2**, 1–8.
- Massalongo, A. 1855. Monografia delle nereidi fossili del Monte Bolca. – *Tipografia G. Antonelli, Verona*, p. 1–55.
- Meidla, T. 1996. *Late Ordovician Ostracodes of Estonia. Fossilia Baltica* **2**. Tartu University Press, Tartu. 222 pp.
- Mello, J. F. & Buzas, M. A. 1968. An application of cluster analyses as a method of determining biofacies. – *Journal of Paleontology* **42**, 747–758.
- Mierzejewska, G. & Mierzejewski, P. 1974. The ultrastructure of some fossil invertebrate skeletons. – *Annals of the Medical Sections of the Polish Academy of Sciences* **19**, 133–135.
- Mierzejewski, P. 1978a. New placognath Eunicida (Polychaeta) from the Ordovician and Silurian of Poland. – *Acta Geologica Polonica* **28**, 273–281.
- Mierzejewski, P. 1978b. Molting of the jaws of the Early Paleozoic Eunicida (Annelida, Polychaeta). – *Acta Palaeontologica Polonica* **23**, 73–88.
- Mierzejewski, P. & Mierzejewska, G. 1975. Xenognath type of polychaete jaw apparatuses. – *Acta Palaeontologica Polonica* **20**, 437–444.
- Mierzejewski, P. & Mierzejewska, G. 1977. Preliminary transmission electron microscopy studies of phaerete jaws of Palaeozoic Eunicida. – *Acta Medicinica Polonica* **18**, 347–348.
- Männil, R. M. 1966. *Evolution of the Baltic Basin during the Ordovician* [in Russian]. Valgus, Tallinn. 200 pp.
- Männil, R. M. 1976. Distribution of graptoloids in the Ordovician carbonate rocks of the East Baltic area [in Russian]. – In: Kaljo, D. & Koren, T. (eds). *Graptolites and stratigraphy*. Estonian Academy of Sciences, Tallinn. p. 105–118.
- Männil, R. 1990. The Ordovician of Estonia. In: Kaljo, D. & Nestor, H. (eds). *Field Meeting, Estonia 1990. An Excursion Guidebook*. Estonian Academy of Sciences, Tallinn. p. 11–20.
- Männil, R. & Meidla, T. 1994. A. The Ordovician System of East European Platform. – *IUGS special Publication* **28**, 1–52.
- Männil, R. M. & Zaslavskaya, N. M. 1985a. Silurian polychaetes from the northern Siberia [in Russian]. – *Trudy Instituta Geologii i Geofiziki SO AN SSSR* **615**, 98–119.
- Männil, R. M. & Zaslavskaya, N. M. 1985b. Finds of Middle Palaeozoic polychaetes in the southeastern part of West Siberian Platform. [in Russian]. – *Trudy Instituta Geologii i Geofiziki SO AN SSSR* **619**, 69–72.

- Nara, M. 1995. *Rosselia socialis*: a dwelling structure of a probable terebellid polychaete. – *Lethaia* **28**, 171–178.
- Nestor, H. & Einasto, R. 1997. Formation of the territory: Ordovician and Silurian carbonate sedimentation basin. – In: Raukas, A. & Teedumäe, A. (eds). *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn. p. 192–204.
- Nestor, H. E., Klaamann, E. R., Meidla, T. R. Männik, P. E., Männil, R. P., Nestor, V. V., Nõlvak, J. R., Rubel, M. P., Sarv, L. J. & Hints, L. M. 1991. Faunal Dynamics on the Boundary between the Ordovician and Silurian in the Baltic Basin [in Russian]. – In: Kaljo, D., Modzalevskaya, T. & Bogdanova, T. (eds). *Major Biological events in Earth History. Transactions of the XXXII Session of All-Union Paleontological Society*. Tallinn. p. 79–86.
- Nõlvak, J. 1997. Sedimentary cover: Ordovician. Introduction. – In: Raukas, A. & Teedumäe, A. (eds). *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn. p. 52–55.
- Olive, P. J. W. 1980. Growth lines in polychaete jaws (teeth). In: Rhoads, D. C. & Lutz, R. A. (eds), *Skeletal Growth of Aquatic Organisms. Biological Records of Environmental Change*. Plenum Press, New York. p. 561–626.
- Pander, C. H. 1856. *Monographie der fossilen Fische des Silurischen Systems der Russisch-Baltischen Gouvernements*. Kaiserliche Akademie Wissenschaften, St. Petersburg. 91 pp.
- Paxton, H. 1980. Jaw growth and replacement in Polychaeta. – *Journal of Natural History* **14**, 543–546.
- Põlma, L. 1982. *Comparative lithology of Ordovician carbonate rocks in North and Central East Baltic* [in Russian]. Valgus, Tallinn. 163 pp.
- Robertson, D. B. R., Brenchley, P. J. & Owen, A.W. 1991. Ecological Disruption Close to the Ordovician–Silurian Boundary. – *Historical Biology* **5**, 131–144.
- Rõõmusoks, A. 1997. Formation of the territory: Evolution of life during the Vendian – Devonian. Ordovician trilobites. – In: Raukas, A. & Teedumäe, A. (eds), *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn. p. 234–238.
- Schwab, K. W. 1966. Microstructure of some fossil and recent scolecodonts. – *Journal of Paleontology* **40**, 416–423.
- Scotise, C. R. & McKerrow, W. S. 1991. Ordovician plate tectonics reconstructions. – In: Barnes, C. R. and Williams, S. H. (eds). *Advances in Ordovician Geology. Geological Survey of Canada, Paper 90-9*. p. 271–282.
- Sepkoski, J. J. & Sheehan, P. M. 1983. Diversification, Faunal Change, and Community replacement during the Ordovician Radiations. – In: Tevesz, M. J. S. & McCall, P. L. (eds). *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum Press, New York. p. 673–717.
- Sheehan, P. M. 1982. Brachiopod Macroevolution at the Ordovician–Silurian Boundary. – *Proceedings of the third North American Paleontological Convention* **2**, 477–481.
- Shimer, H. W. & Shrock, R. R. 1955. *Index fossils of North America. Chapter VI Worms*. p. 228–234.
- Simpson, E. H. 1949. Measurements of diversity. – *Nature* **163**, 688.

- Sokolov, B. S. 1985. Vendskie polihety. – In: Sokolov, B. S. & Ivanovskii, A. B (eds). *Paleontologiya* [in Russian]. Nauka, Moskva. p. 198–200.
- Szaniawski, H. 1968. Three new polychaete jaw apparatuses from the Upper Permian of Poland. – *Acta Palaeontologica Polonica* **13**, 255–281.
- Szaniawski, H. 1970. Jaw apparatuses of the Ordovician and Silurian polychaetes from the Mielnik borehole. – *Acta Palaeontologica Polonica* **15**, 445–472.
- Szaniawski, H. 1974. Some Mesozoic scolecodonts congeneric with recent forms. – *Acta Palaeontologica Polonica* **19**, 179–199.
- Szaniawski, H. 1996. Scolecodonts. – In: Jansonius, J. & McGregor, D. C. (eds), *Palynology: Principles and applications*. American Association of Stratigraphic Palynologists Foundation 1. p. 337–354.
- Szaniawski, H. & Gazdzicki, A. 1978. A reconstruction of three Jurassic polychaete jaw apparatuses. – *Acta Palaeontologica Polonica* **23**, 3–19.
- Szaniawski, H. & Imajima, M. 1996. Hartmaniellidae – living fossils among polychaetes. – *Acta Palaeontologica Polonica* **41**, 111–125.
- Szaniawski, H. & Wrona, R. M. 1973. Polychaete jaw apparatuses and scolecodonts from the Upper Devonian of Poland. – *Acta Palaeontologica Polonica* **18**, 223–267.
- Szaniawski, H. & Wrona, R. 1987. Polychaete jaws from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica. – *Palaeontologia Polonica* **18**, 223–267.
- Stauffer, C. R. 1939. Middle Devonian Polychaeta from the lake Eire district. – *Journal of Paleontology* **13**, 500–511.
- Stauffer, C. R. 1933. Middle Ordovician Polychaeta from Minnesota. – *Bulletin of the Geological Society of America* **44**, 1173–1218.
- Strauch, F. 1973. Die Feinstruktur einiger Scolecodonten. – *Senckenbergiana Lethaea* **54**, 1–19
- Sylvester, R. K. 1959. Scolecodonts from central Missouri. – *Journal of Paleontology* **33**, 33–49.
- Šnajdr, M. 1951. On Errant Polychaeta from the Lower Paleozoic of Bohemia. – *Sbornik of the Geological Survey of Czechoslovakia, Paleontology* **18**, 241–296.
- Zawidzka, K. 1971. A polychaete jaw apparatus and some scolecodonts from the Polish Middle Triassic. – *Acta Palaeontologica Polonica* **21**, 361–377.
- Zawidzka, K. 1975. Polychaete remains and their stratigraphic distribution in the Muschelkalk of Southern Poland. – *Acta Palaeontologica Polonica* **25**, 257–274.
- Zebera, K. 1935. Les Conodontes et Scolecodontes du Barrandien. – *Bulletin international de l'Academie des Sciences de Boheme* **36**, 88–96.
- Taugourdeau, P. 1968. Propositions concernant l'establisement de formules dentaries pour l'etude des Scolecodontes. – *Proceedings IPU, 23 International geological congress*. p. 347–442.
- Taugourdeau, P. 1976. The Scolecodonts. – *Biological memoirs* **1**, 1–40.
- Thompson, I. 1977. Errant polychaetes (Annelida) from the Pennsylvanian Essex Fauna of Northern Illinois. – *Palaeontographica* **A163**, 169–199.
- Underhay, N. K. & Williams, S. H. 1995. Lower Silurian scolecodonts from the Cow Head Group, western Newfoundland. – *Canadian Journal of Earth Sciences* **32**, 895–901.

- Valentine, J. W. & Peddicord, R. G. 1967. Evaluation of fossil assemblages by cluster analyses. – *Journal of Paleontology* **41**, 502–507.
- Voss-Foucart, M. F., Fonce-Vignaux, M. T. & Jeuniaux, C. 1973. Systematic characters of some annelid Polychaetes at the level of the chemical composition of the jaws. – *Biochemical Systematics and Ecology* **1**, 119–122.
- Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. – *Journal of the American Statistical Association* **58**, 236.
- Wolf, G. 1980. Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). – *Senckenbergiana Maritima* **12**, 1–182.

PLATES

PLATE 1

- Figs 1–2.** *Mochtyella cristata* Kielan-Jaworowska. **1** – left MI GIT Sc 101, dorsal view, x80; **2** – right MI GIT Sc 102, dorsal view, x60; Orjaku drill core, depth 112.5 m, Rakvere Stage.
- Fig. 3.** *Paramochtyella fragilis* (Szaniawski). Left MI GIT Sc 103, dorsal view, x180, Orjaku drill core, depth 58.57 m, Pirgu Stage.
- Fig. 4.** *Pistoprion transitans* Kielan-Jaworowska. Left MI GIT Sc 104, dorsal view, x60, Orjaku drill core, depth 70.2 m, Pirgu Stage.
- Fig. 5.** *Xanioprion* sp. B. Apparatus GIT Sc 105, dorsal view, x100, Orjaku drill core, depth 87.11 m, Vormsi Stage.
- Fig. 6.** *Xanioprion* sp. A. Left MII GIT Sc 11, dorsal view, x50, Metsküla (F-198) drill core, depth 17.65 m, Rakvere Stage.
- Figs 7–8.** *Xanioprion tenuidentatus* sp. nov. **7** – right MII GIT Sc 106, dorsal view, x300, Laeva-18 drill core, depth 222.4 m, Vormsi Stage; **8** – left MII GIT Sc 107 (holotype); dorsal view, x180; Laeva-18 drill core, depth 225.15 m, Nabala Stage.
- Figs 9–11.** *Vistulella kozlowskii* Kielan-Jaworowska. **9** – left MI fused with laeobasal plate GIT Sc 9, dorsal view, x140, Metsküla (F-198) drill core, depth 20.8 m, Rakvere Stage; **10** – MIIa GIT Sc 8, dorsal view, x60; **11** – right MI fused with basal plate from the same apparatus as previous; Rapla drill core, depth 110.0 m, Rakvere Stage.
- Fig. 12.** *Lunoprionella* sp. Maxilla GIT Sc 108, dorsal view, x100, Valga-10 drill core, depth 321.85 m, Porkuni Stage.
- Fig. 13.** *Rakvereprion balticus* (Eisenack). Apparatus GIT Sc 109, dorsal view, x280, Valga-10 drill core, depth 368.9 m, Nabala Stage.
- Fig. 14.** *Lunoprionella symmetrica* Eisenack. Maxilla GIT Sc 110, dorsal view, x200, Laeva-18 drill core, depth 226.78 m, Nabala Stage.
- Fig. 15.** *Rakvereprion balticus* (Eisenack). Detail of apparatus GIT Sc 109, dorsal view, x580, Valga-10 drill core, depth 368.9 m, Nabala Stage.

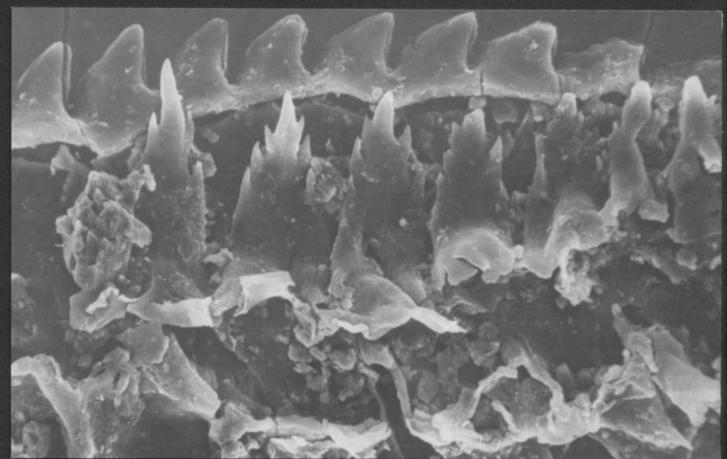
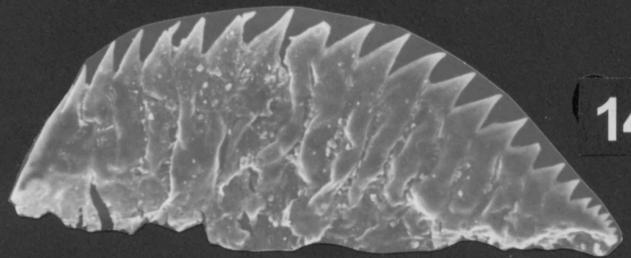
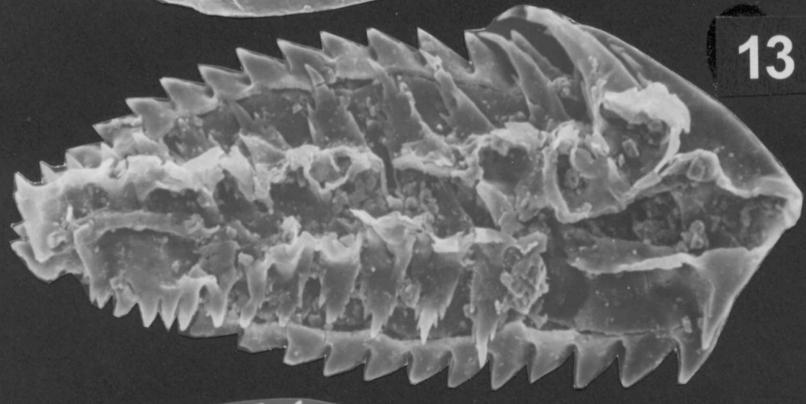
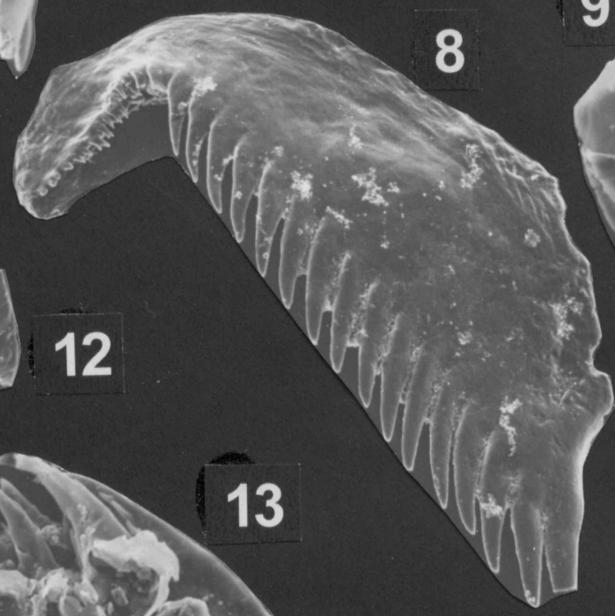
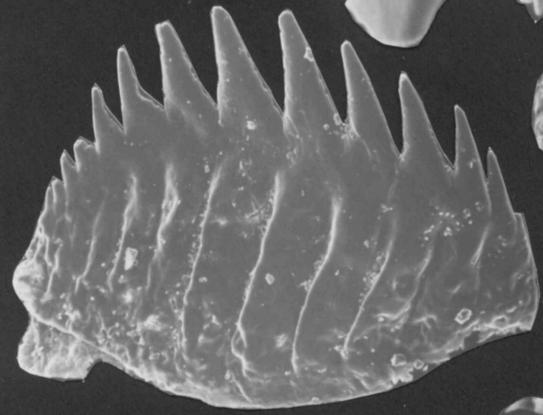
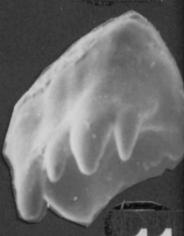
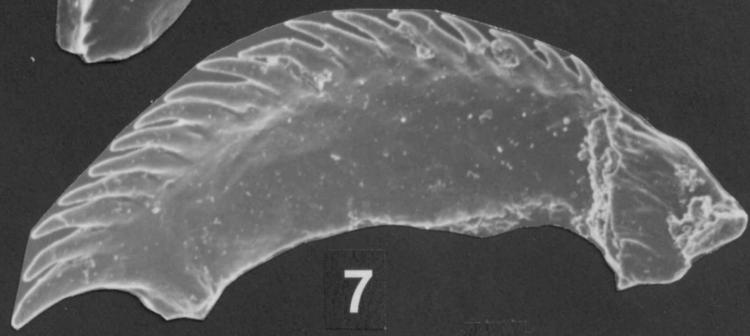
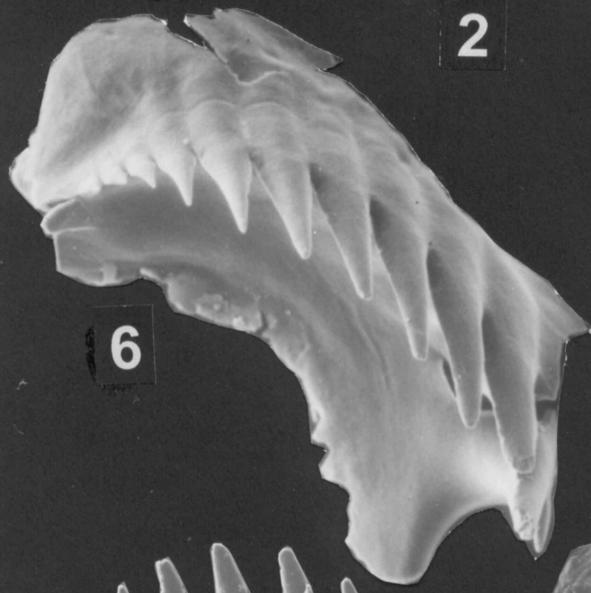
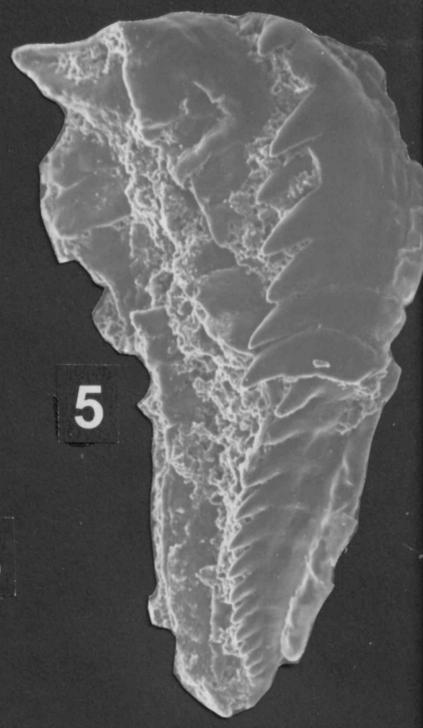
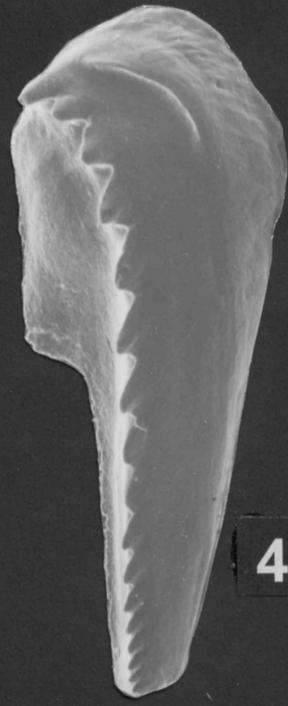
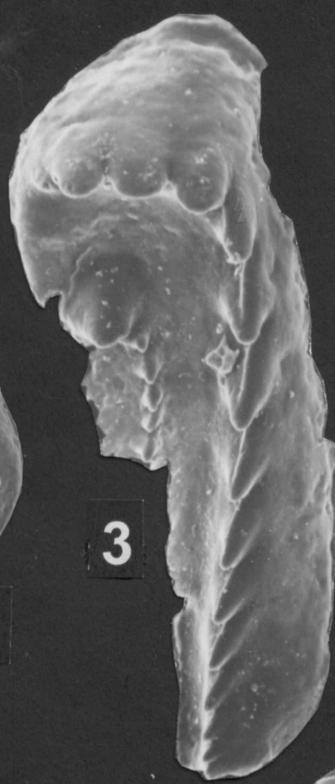


PLATE 2

Figs 1–4. *Rhytiprion magnus* Kielan-Jaworowska. **1** – left MII GIT Sc 112, dorsal view, x100; **2** – right MI GIT Sc 113, dorsal view, x100; **3** – right MII GIT Sc 114, dorsal view, x100; **4** – left MI GIT Sc 115, dorsal view, x140; Laeva-18 drill core, depth 225.15 m, Nabala Stage.

Fig. 5–16. *Valgaprion huberti* gen. et sp. nov. **5** – left MI GIT Sc 116, dorsal view, x100; **6** – left MI GIT Sc 117, dorsal view, x120; **7** – left MII GIT Sc 118, dorsal view, x150; **8** – right MI GIT Sc 119, dorsal view, x100; **9** – right MI GIT Sc 120, dorsal view, x150; **10** – right MI GIT Sc 121, dorsal view, x100; **11** – left MI GIT Sc 122, dorsal view, x150; **12** – left MII GIT Sc 123 (holotype); dorsal view, x180; **13** – anterior teeth GIT Sc 123 (holotype), dorsal view, x180; **14** – right MI GIT Sc 123 (holotype), dorsal view, x180; **15** – basal plate GIT Sc 123 (holotype), dorsal view, x180; **16** – left MI, basal plate and anterior teeth GIT Sc 123 (holotype), dorsal view, x180; Valga-10 drill core, depth 321.85 m, Porkuni Stage.

Fig. 17. *Rakvereprion balticus* (Eiesenack). Right MI fused with basal plate GIT Sc 124, dorsal view, x300; Valga-10 drill core, depth 368.9 m, Nabala Stage.

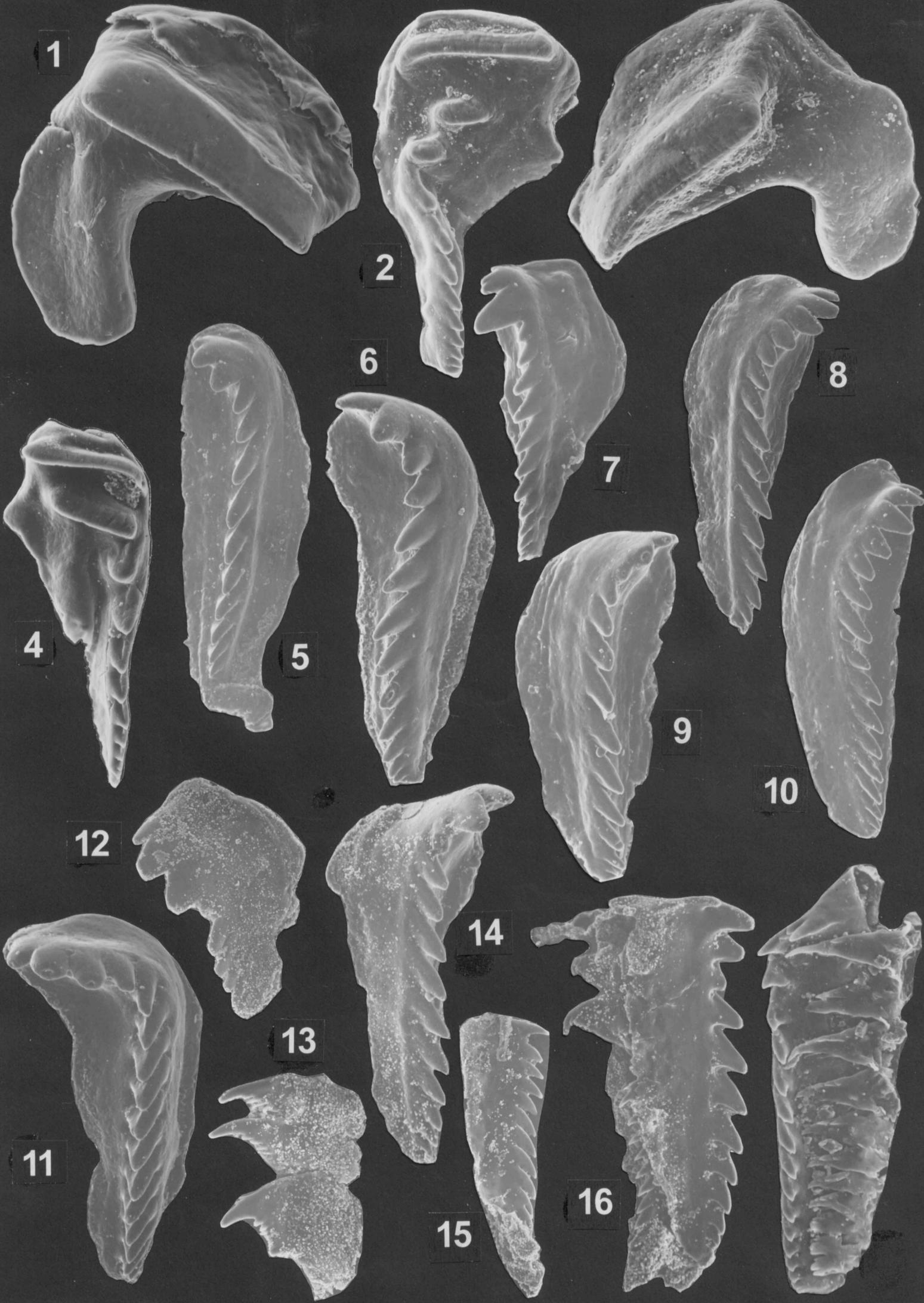


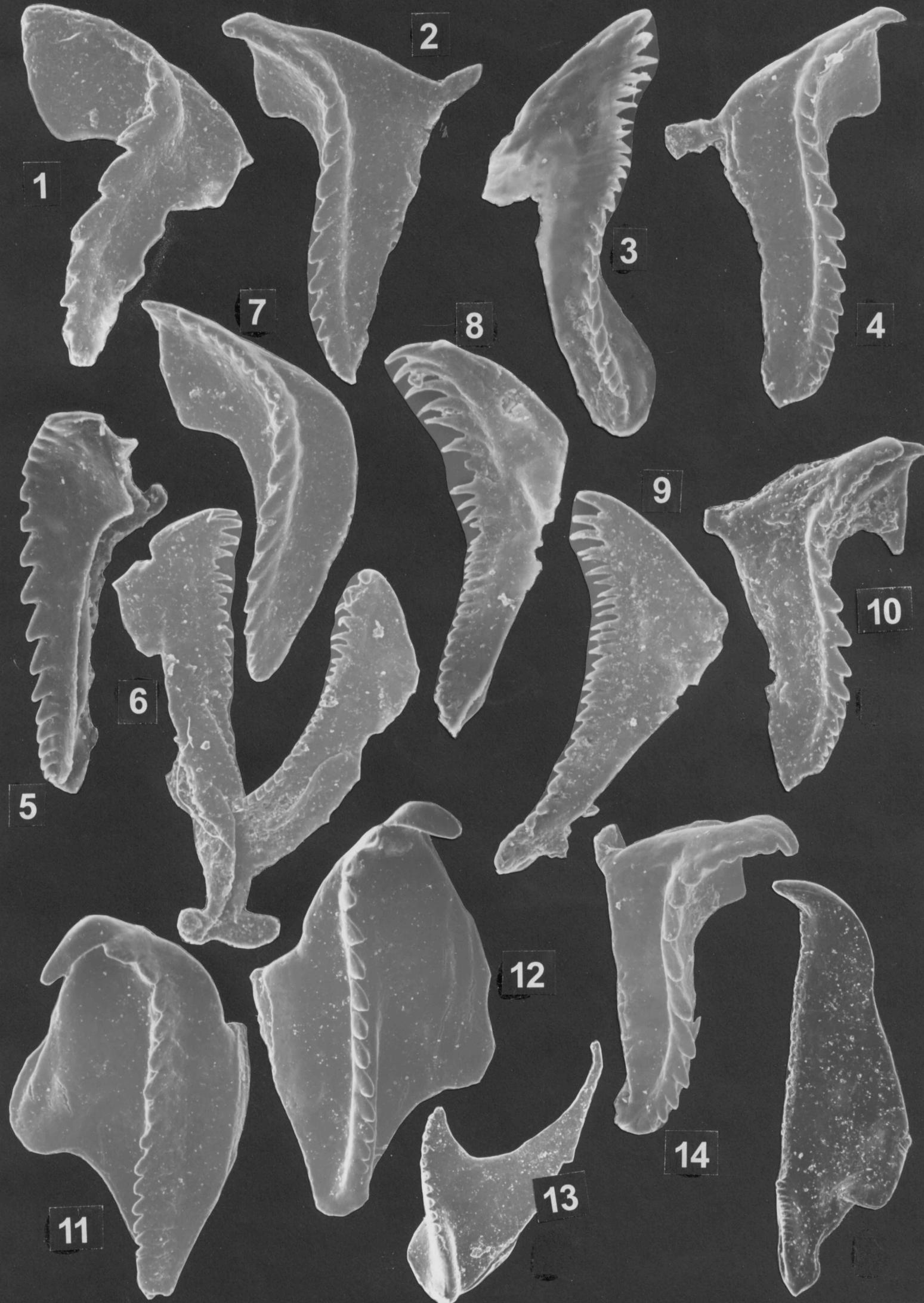
PLATE 3

Figs 1–10. *Conjungaspis minutus* gen. et sp. nov. **1** – left MI GIT Sc 125, dorsal view, x200; **2** – left MI GIT Sc 126, dorsal view, x200; **3** – laeobasal plate GIT Sc 127, dorsal view, x280; **4** – right MI GIT Sc 128, dorsal view, x180; **5** – right MI GIT Sc 129, right lateral view, x300; **6** – joined basal- and laeobasal plates GIT Sc 130 (holotype), dorsal view, x180; **7** – left MI GIT Sc 131, dorsal view, x200; **8** – basal plate GIT Sc 132, dorsal view, x220; **9** – basal plate GIT Sc 133, dorsal view, x220; **10** – right MI fused with lateral tooth GIT Sc 134, dorsal view, x280; Valga-10 drill core, depth 321.85 m, Porkuni Stage.

Figs 11–13. *Symmetropirion spatiosus* (Hinde). **11** – left MI GIT Sc 135, dorsal view, x140; **12** – right MI GIT Sc 136, dorsal view, x140; **13** – basal plate GIT Sc 137, dorsal view, x140; Valga-10 drill core, depth 313.45 m, Porkuni Stage.

Fig. 14. *Conjungaspis minutus* gen. et sp. nov. Right MI GIT Sc 138, dorsal view, x200; Valga-10 drill core, depth 321.85 m, Porkuni Stage.

Fig. 15. *Kettnerites* sp. Right MI GIT Sc 139, dorsal view, x60; Valga-10 drill core, depth 321.85 m, Porkuni Stage.



1

2

3

4

7

8

9

10

6

5

12

14

11

13

PLATE 4

Figs 1–3. *Polychaetaspis pirguensis* sp. nov. **1** – left MII GIT Sc 140 (holotype), dorsal view, x100; **2** – left MI GIT Sc 140 (holotype), dorsal view, x100; **3** – right MI GIT Sc 140 (holotype), dorsal view, x100; Butkunai drill core, depth 554.6 m, Pirgu Stage.

Figs 4–10. *Polychaetaspis kuldigaensis* sp. nov. **4** – left lateral teeth I GIT Sc 141, dorsal view, x100; **5** – left MI GIT Sc 142, dorsal view, x100; **6** – right MI GIT Sc 143 (holotype), dorsal view, x70; **7** – left MII GIT Sc 144, dorsal view, x200; **8** – basal plate GIT Sc 145, dorsal view, x100; **9** – basal plate GIT Sc 146, ventral view, x80; **10** – left MI GIT Sc 147, ventral view, x110; Valga-10 drill core, depth 319.4 m, Porkuni Stage.

Figs 11–12. *Polychaetaspis varsoviensis* Kielan-Jaworowska. **11** – left MI GIT Sc 148, dorsal view, x120; **12** – right MI GIT Sc 149, dorsal view, x120; Orjaku drill core, depth 122.55 m, Rakvere Stage.

Fig. 13. *Polychaetaspis pirguensis* sp. nov. Right MII GIT Sc 140 (holotype), dorsal view, x100; Butkunai drill core, depth 554.6 m, Pirgu Stage.

Fig. 14. *Polychaetaspis kuldigaensis* sp. nov. Right MI GIT Sc 150, dorsal view, x100; Valga-10 drill core, depth 319.4 m, Porkuni Stage.

Figs 15–16. *Polychaetaspis* cf. *gadomskae* Kielan-Jaworowska. **15** – left MI GIT Sc 151, dorsal view, x160; **16** – right MI GIT Sc 152; dorsal view, x160; Laeva-18 drill core, depth 225.15 m, Nabala Stage.

Figs 17–19. *Polychaetaspis minutus* sp. nov. **17** – left MI GIT Sc 153, dorsal view, x250; **18** – right MI GIT Sc 154 (holotype), dorsal view, x250; Orjaku drill core, depth 63.8 m, Pirgu Stage; **19** – basal plate GIT Sc 155, dorsal view, x280; Laeva-18 drill core, depth 228.08 m, Nabala Stage.

Fig. 20. *Polychaetaspis latoides* sp. nov. Right MI GIT Sc 156 (holotype), dorsal view, x160; Orjaku drill core, depth 54 m, Pirgu Stage.

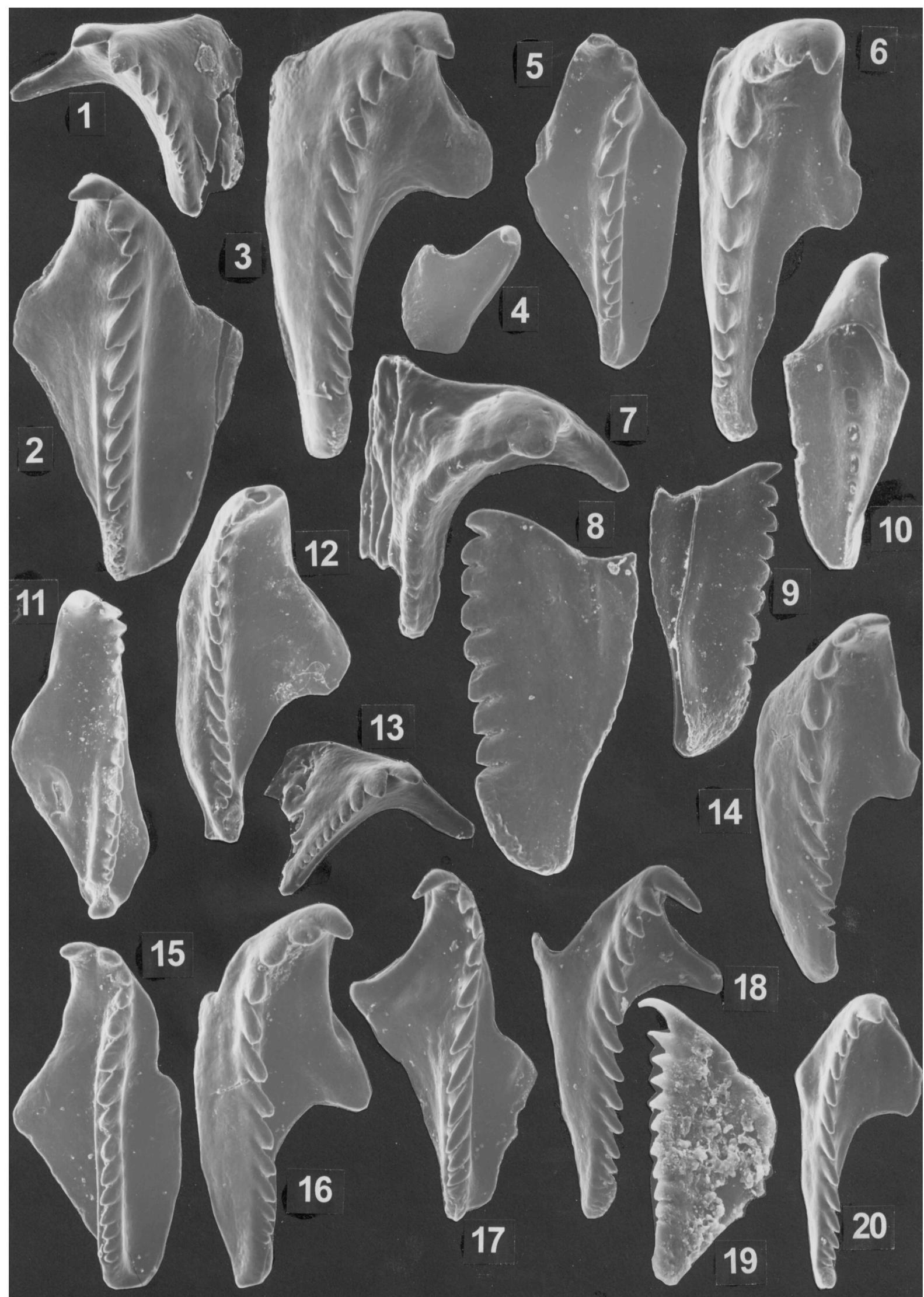
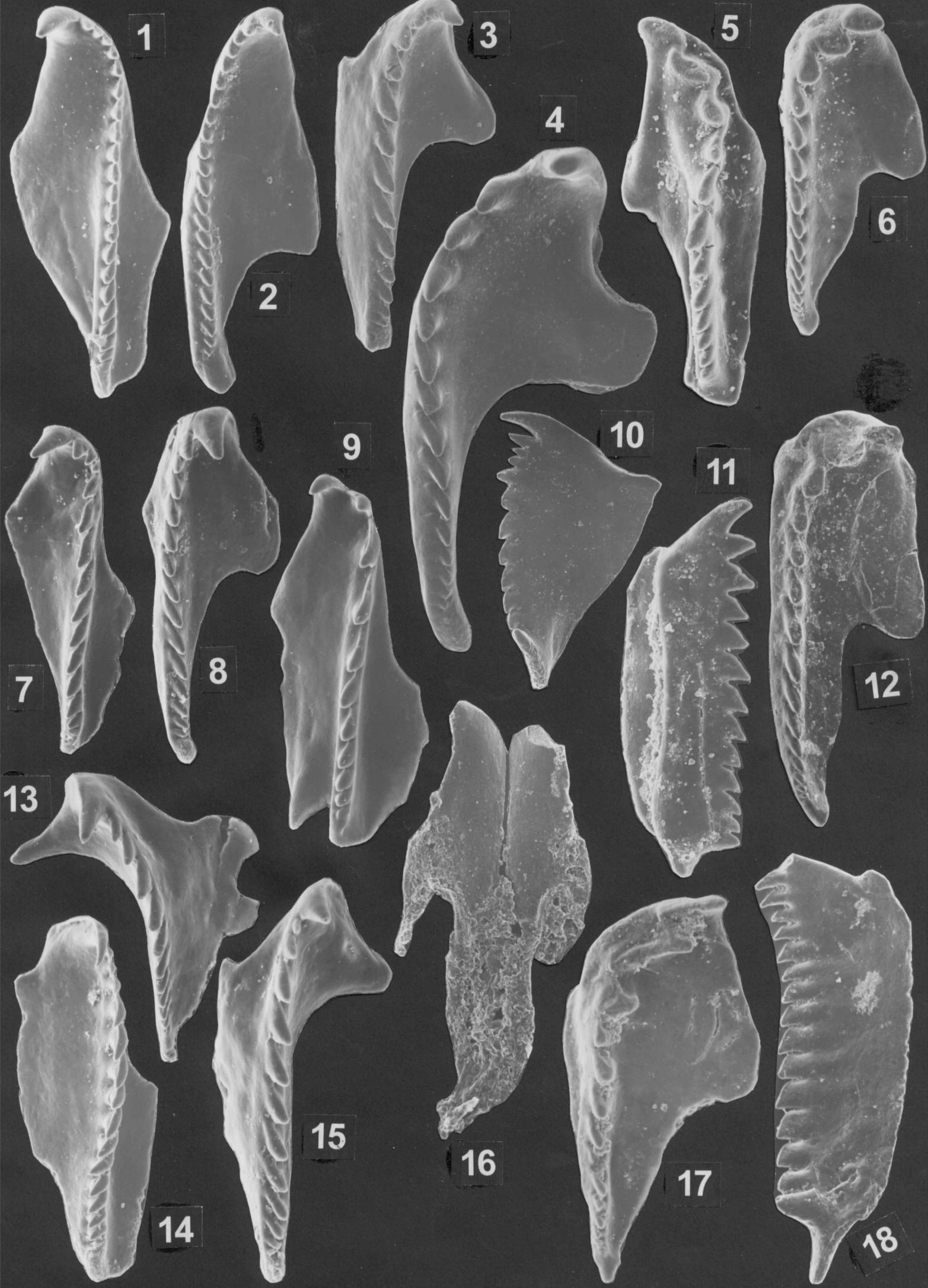


PLATE 5

- Figs 1–2.** *Polychaetaspis? multidentatus* sp. nov. **1** – left MI GIT Sc 157, dorsal view, x180; Orjaku drill core, depth 98.6 m, Nabala Stage; **2** – right MI GIT Sc 158 (holotype), dorsal view, x120; Laeva-18 drill core, depth 227.57 m, Nabala Stage.
- Fig. 3.** *Polychaetaspis* cf. *wyszogrodensis* Kozłowski. Right MI GIT Sc 159, dorsal view, x100; Orjaku drill core, depth 112.5 m, Rakvere Stage.
- Fig. 4.** *Polychaetaspis inclinatus* sp. nov. Right MI GIT Sc 160 (holotype), dorsal view, x45; Orjaku drill core, depth 47.62 m, Pirgu Stage.
- Figs 5–6.** *Polychaetura harjuensis* sp. nov. **5** – left MI GIT Sc 161, dorsal view, x120; Laeva-18 drill core, depth 221.35 m, Vormsi Stage; **6** – right MI GIT Sc 162 (holotype); dorsal view, x100; Laeva-18 drill core, depth 225.15 m, Nabala Stage.
- Figs 7–8.** *Polychaetaspis latoides* sp. nov. **7** – right MI GIT Sc 163, dorsal view, x160; **8** – left MI GIT Sc 164, dorsal view, x160; Orjaku drill core, depth 54.0 m, Pirgu Stage.
- Fig. 9.** *Polychaetura gracilis* Kozłowski. Left MI GIT Sc 165, dorsal view, x280; Orjaku drill core, depth 122.55 m, Rakvere Stage.
- Fig. 10.** *Polychaetaspis inclinatus* sp. nov. Basal plate GIT Sc 166, dorsal view, x45; Orjaku drill core, depth 47.62 m, Pirgu Stage.
- Figs 11–12.** *Polychaetura harjuensis* sp. nov. **11** – basal plate GIT Sc 167, ventral view, x110; Laeva-18 drill core, depth 223.4 m, Vormsi Stage; **12** – right MI GIT Sc 168; dorsal view, x100; Laeva-18 drill core, depth 225.15 m, Nabala Stage.
- Figs 13–15.** *Kozłowskiiprion angustus* sp. nov. **13** – left MII GIT Sc 169, dorsal view, x150; **14** – left MI GIT Sc 170, dorsal view, x150; **15** – right MI GIT Sc 171 (holotype), dorsal view, x280; Orjaku drill core, depth 54.0 m, Pirgu Stage.
- Fig. 16.** *Polychaetura harjuensis* sp. nov. Carriers GIT Sc 172, dorsal view, x160; Laeva-18 drill core, depth 222.4 m, Vormsi Stage.
- Fig. 17.** *Polychaetura?* sp. Right MI GIT Sc 173, dorsal view, x100; Laeva-18 drill core, depth 197.51 m, Pirgu Stage.
- Fig. 18.** *Polychaetura harjuensis* sp. nov. Basal plate GIT Sc 174, dorsal view, x130; Laeva-18 drill core, depth 223.4 m, Vormsi Stage.



1

3

5

6

2

4

7

9

10

11

8

12

13

15

16

17

14

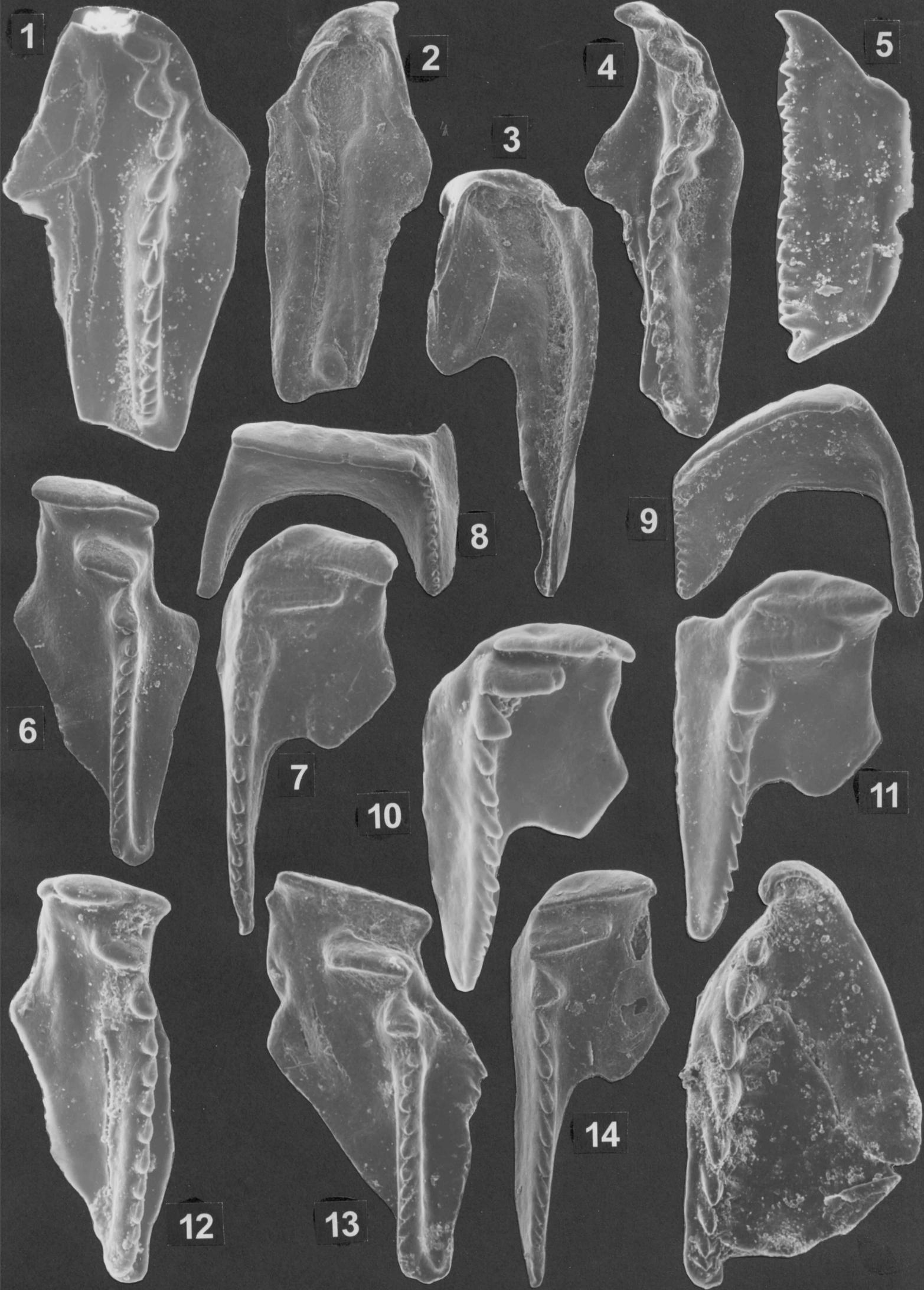
18

PLATE 6

Figs 1–5. *Polychaetura harjuensis* sp. nov. **1** – left MI GIT Sc 175, dorsal view, x100; Laeva-18 drill core, depth 221.35 m, Vormsi Stage; **2** – left MI GIT Sc 176, ventral view, x80; Laeva-18 drill core, depth 223.4 m, Vormsi Stage; **3** – right MI GIT Sc 177, ventral view, x80; Laeva-18 drill core, depth 227.57 m, Nabala Stage; **4** – left MI GIT Sc 178, dorsal view, x100; Laeva-18 drill core, depth 226.78 m, Nabala Stage; **5** – basal plate GIT Sc 179, dorsal view, x120; Laeva-18 drill core, depth 221.35 m, Vormsi Stage.

Figs 6–14. *Laevaprion jaaki* gen. et sp. nov. **6** – left MI GIT Sc 180, dorsal view, x100; Laeva-18 drill core, depth 224.0 m, Nabala Stage; **7** – right MI GIT Sc 181, dorsal view, x130; Laeva-18 drill core, depth 225.15 m, Nabala Stage; **8** – left MII GIT Sc 182, dorsal view, x140; **9** – right MII GIT Sc 183, dorsal view, x170; Laeva-18 drill core, depth 224.0 m, Nabala Stage; **10** – right MI GIT Sc 184 (holotype), dorsal view, x180; **11** – right MI GIT Sc 185, dorsal view, x120; Laeva-18 drill core, depth 225.15 m, Nabala Stage; **12** – left MI GIT Sc 186, dorsal view, x180; Laeva-18 drill core, depth 226.78 m, Nabala Stage; **13** – left MI GIT Sc 187, dorsal view, x130; Laeva-18 drill core, depth 225.15 m, Nabala Stage; **14** – right MI GIT Sc 188, dorsal view, x125; Laeva-18 drill core, depth 224 m, Nabala Stage.

Fig. 15. *Leptoprion* sp. Right MI fused with basal plate GIT Sc 189, dorsal view, x200; Laeva-18 drill core, depth 225.15 m, Nabala Stage.



1

2

4

5

3

6

8

9

7

10

11

12

13

14

PLATE 7

Figs 1–7. *Ramphoprion cf. deflexus* (Eller). **1** – apparatus GIT Sc 190, dorsal view, x80; **2** – right MII GIT Sc 191, dorsal view, x80; **3** – left MII GIT Sc 192, dorsal view, x80; **4** – basal plate GIT Sc 193, dorsal view, x80; **5** – apparatus GIT Sc 194, dorsal view, x200; **6** – left MI GIT Sc 195, dorsal view, x80; **7** – right MI GIT Sc 196, dorsal view, x80; Valga-10 drill core, depth 338.2 m, Pirgu Stage.

Figs 8–9. *Ramphoprion elongatus* Kielan-Jaworowska. **8** – left MI GIT Sc 55, dorsal view, x80; **9** – right MI GIT Sc 54, dorsal view, x80; Rapla drill core, depth 108.0 m, Nabala Stage.

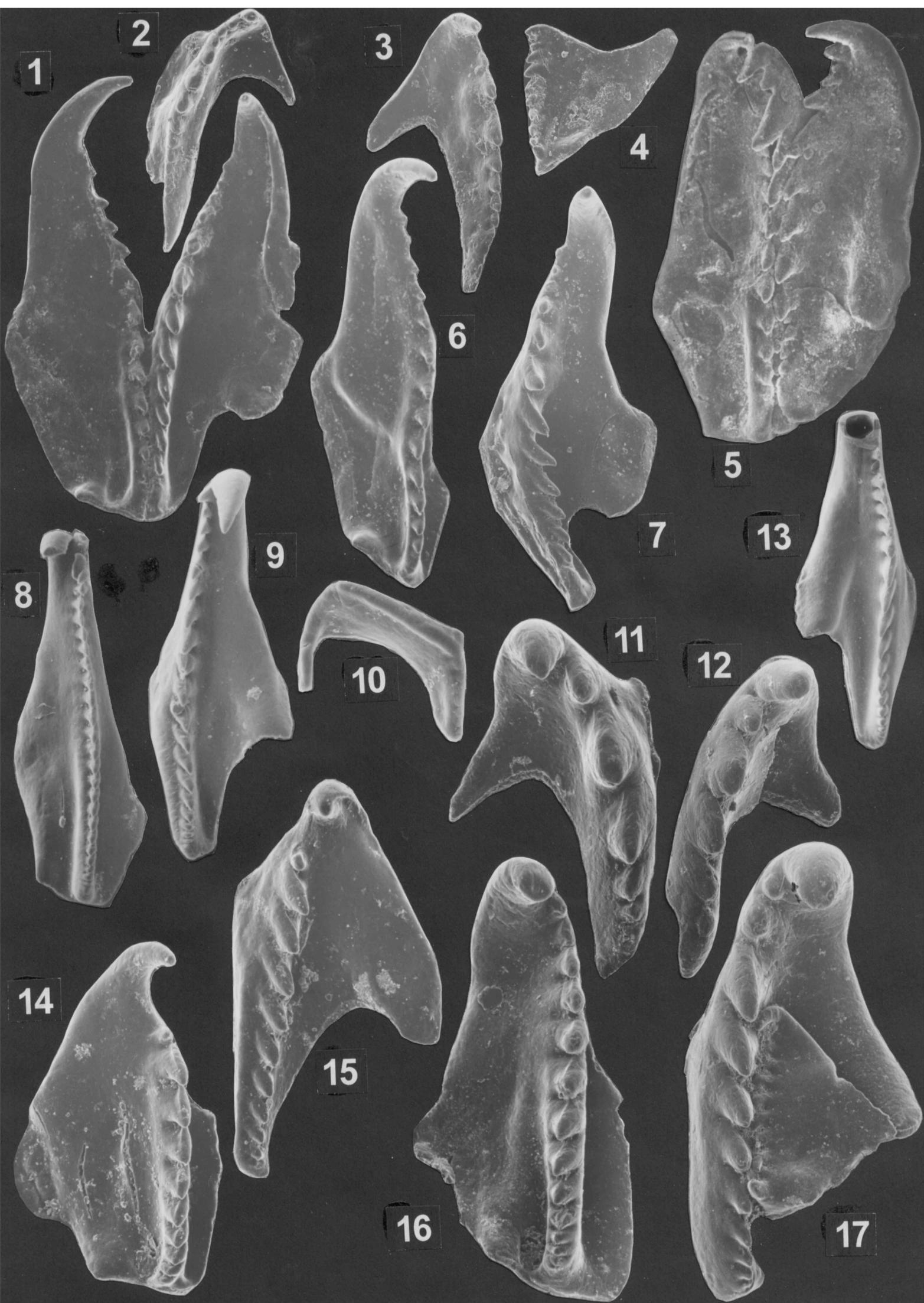
Fig. 10. *Laevaprion jaaki* gen. et sp. nov. Left MII GIT Sc 197; dorsal view, x120; Laeva-18 drill core, depth 225.15 m, Nabala Stage.

Figs 11–12. *Kalloprion robustus* sp. nov. **11** – left MII GIT Sc 198, dorsal view, x100; **12** – right MII GIT Sc 199, dorsal view, x100; Laeva-18 drill core, depth 225.15 m, Nabala Stage.

Fig. 13. *Ramphoprion elongatus* Kielan-Jaworowska. Inverted left MI GIT Sc 53, dorsal view, x30; Rapla drill core, depth 114 m, Rakvere Stage.

Figs 14–15. *Leptoprion* sp. **14** – left MI GIT Sc 200, dorsal view, x200; **15** – right MI GIT Sc 201, dorsal view, x200; Laeva-18 drill core, depth 225.15 m, Nabala Stage.

Figs 16–17. *Kalloprion robustus* sp. nov. **16** – left MI GIT Sc 202, dorsal view, x100; **17** – right MI fused with basal plate GIT Sc 203 (holotype), dorsal view, x100; Laeva-18 drill core, depth 225.15 m, Nabala Stage.



1

2

3

4

5

6

7

13

8

9

10

11

12

14

15

16

17

PLATE 8

Figs 1–6. *Tretoprion astae* gen. et sp. nov. **1** – left MI GIT Sc 204, dorsal view, x180; **2** – right MI fused with basal plate GIT Sc 205 (holotype), dorsal view, x180; Orjaku drill core, depth 58.57 m, Pirgu Stage; **3** – left MI GIT Sc 206, dorsal view, x200; **4** – left MI GIT Sc 207, ventral view, x200; **5** – right MI fused with basal plate GIT Sc 208, dorsal view, x200; **6** – apparatus GIT Sc 209, dorsal view, x210; Laeva-18 drill core, depth 222.4 m, Vormsi Stage.

Fig. 7. *Polychaetura gracilis* Kozłowski. Right MI GIT Sc 210, dorsal view, x200; Orjaku drill core, depth 122.55 m, Rakvere Stage.

Figs 8–10. *Tretoprion astae* gen. et sp. nov. **8** – apparatus GIT Sc 211, dorsal view, x400; **9** – left MI GIT Sc 212, dorsal view, x200; **10** – right MI GIT Sc 213, dorsal view, x200; Laeva-18 drill core, depth 222.4 m, Vormsi Stage.

Figs 11–12. *Atraktoprion mirabilis* Kielan-Jaworowska. **11** – left MI GIT Sc 81, dorsal view, x100; **12** – right MI GIT Sc 82, dorsal view, x100; Rapla drill core, depth 108.0 m, Nabala Stage.

Figs 13–14. *Atraktoprion major* Kielan-Jaworowska. **13** – basal plate GIT Sc 80, dorsal view, x60; **14** – right MI GIT Sc 80, dorsal view, x60; Rapla drill core, depth 124.0 m, Rakvere Stage.

Fig. 15. *Skalenoprion alatus* Kielan-Jaworowska. Right MI GIT Sc 214, dorsal view, x180; Orjaku drill core, depth 47.62 m, Pirgu Stage.

