Late Viruan (Caradoc) polychaete jaws from North Estonia and the St. Petersburg region

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An abundant, diverse and well-preserved fauna of jaw-bearing polychaetes (Annelida, Polychaeta, Eunicida) was recovered from the late Viruan (Caradoc) of eight borehole sections in North Estonia and the St. Petersburg region. Altogether 46 species are encountered. Two new genera, *Incisiprion* with type species *I. incisus* (Kielan-Jaworowska, 1966) and *Estonioprion* with type species *E. maennili* sp. n., and five new species (*Incisiprion edentulus*, *Polychaetura kielanae*, *Ramphoprion bialatus*, *Ramphoprion peterburgensis*, *Estonioprion maennili*) are introduced. In addition 17 new species are described under open nomenclature. The taxonomy is based on jaw apparatuses, fused or reconstructed ones. Many species found in Estonia have been previously described from the erratic boulders of Poland. The studied polychaete fauna was confined to the North Estonian Confacies, a shallow-water carbonate shelf, which constituted favourable habitats for Ordovician polychaete worms. The stratigraphical ranges of many prevalent polychaete species exceed the interval studied. However, a few species seem to be restricted to particular horizons and may be useful for stratigraphy. Polychaete assemblages of certain time intervals, characterized by very steady species composition and relative frequencies of different taxa, were spatially widespread within the North Estonian Confacies. Based on the changes in the assemblages, some stratigraphical levels, like the boundary beds of the Idavere and Jõhvi stages, can be traced within the study area. The jawed polychaete faunas of Baltica and Laurentia probably had several species in common during the Caradoc.

K e y w o r d s : Polychaetes, scolecodonts, North Estonia, St. Petersburg region, Ordovician, Caradoc, late Viruan.

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Introduction

Early Palaeozoic eunicid polychaetes (Annelida, Polychaeta, Eunicida) are known almost exclusively by their jaw apparatuses. Disjunct elements of these apparatuses, the scolecodonts, are among the most common acid-resistant microfossils, suggesting a high abundance and diversity of jawed polychaete worms since the Early Ordovician.

The first scolecodonts were discovered in the 1850s (Eichwald 1854; Pander 1856). Subsequently their wide geographical and stratigraphical occurrence was recorded, but as in case of conodonts, separate jaws were classified under unnatural, element-based taxonomy in the early stage of the study. In the 1940-60s, biologically founded taxonomy, based on jaw apparatuses was established (Lange 1949; Šnajdr 1951; Kozłowski 1956; Kielan-Jaworowska 1961, 1962, 1966). Up to the present, various aspects of scolecodonts and fossil polychaetes have been studied by different students: ultrastructures (Strauch 1973; Corradini *et al.* 1974; Mierzejewska & Mierzejewski 1974; Szaniawski & Gaździcki 1978), composition (Schwab 1966; Olive 1980; Boyer 1981; Colbath & Larson 1980; Colbath 1986), molting (Olive 1980; Mierzejewski 1978b; Colbath 1987), functional morphology (Wolf 1980), and palaeoecology of polychaete worms (Laufeld 1975; Bergman 1979, 1989, 1991b, 1995; Eriksson 1997). For detailed reviews of the study history see Kielan-Jaworowska (1966), Bergman (1989) and Szaniawski (1996).

Large numbers of Ordovician scolecodonts were recorded from North America by Stauffer (1933) and Eller (1942, 1945, 1969). Polychaete jaws from the Ordovician of Baltoscandia have mostly been described from erratic boulders, whose age and source locality are often unknown (e.g., Kozłowski 1956; Kielan-Jaworowska 1961, 1962, 1966; Mierzejewski 1978a; Mierzejewski & Mierzejewska 1975). Only the material studied by Szaniawski (1970) was obtained from a borehole section and thus has a great importance with regard to stratigraphical distribution. The occurrence of scolecodonts in the Ordovician of Sweden was noted by Grahn (in Bergman 1989: p. 6). A few specimens in the collections of Öpik (1927) and Eisenack (1975) were derived from the outcrop area in Estonia.

This paper aims to give a preliminary review of the taxonomic composition and distribution of jawed polychaetes in North Estonia and the St. Petersburg region. The studied late Viruan sequence corresponds to the main part of the Caradoc, approximately to *Dicranograptus multidens* and *Didymograptus clingani* graptolite zones, and yielded abundant polychaete jaws. Excellent preservation and finds of numerous fused apparatuses greatly facilitated the study. Drill core material and detailed stratigraphical background combined with quantitative study methods allowed an analysis of the distribution and development of polychaete assemblages, and an evaluation of the stratigraphical usefulness of scolecodonts.

Geology

The Baltoscandian Palaeobasin occupied the northwestern part of the East European Platform during the Ordovician. According to the large-scale zonation of this basin, the study area belongs to the relatively shallow-water part, namely the North Estonian Confacies (Fig. 1, see also Männil 1966 and Jaanusson 1976), which was characterized by discontinuous carbonate deposition, high content of clastic material and rich biotas.

The studied stratigraphical interval of the Viru Series, from the Idavere to Rakvere stages (Fig. 2), is mostly represented by marly limestones (Tatruse and Vasavere Formations and Kahula Group), marls (Hirmuse Formation) and cryptocrystalline limestones (Rägavere Formation) in North Estonia. Marly limestones and marls (Gry-

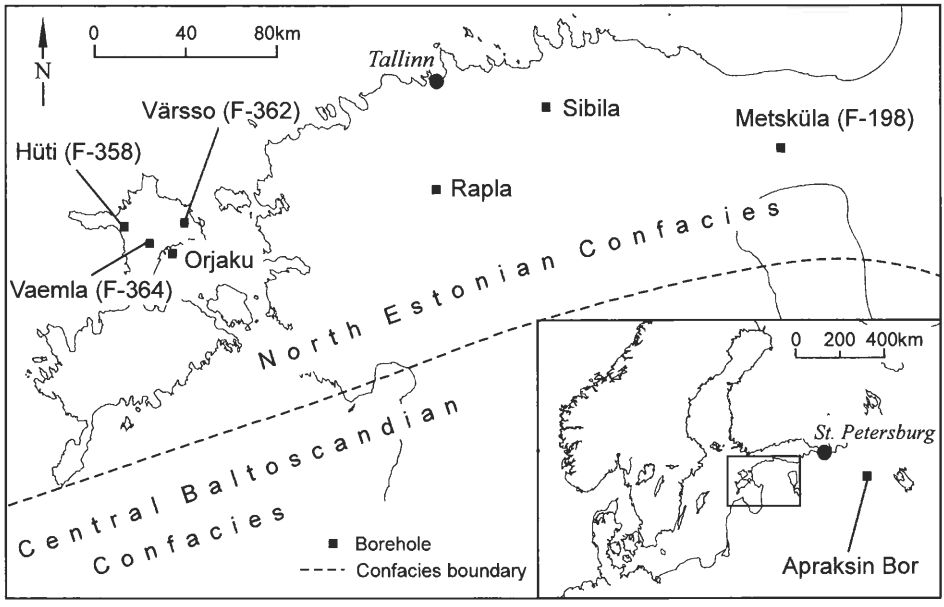


Fig. 1. Sketch map of the study area. Boundary between North Estonian and Central Baltoscandian Confacies is given after Jaanusson 1976. Numbers of boreholes as used by the Geological Survey of Estonia are given in brackets.

azno, Shundorovo, Khrevitsa Formations and lower part of the Jelizavetino Formation) and dolomitized limestones (upper part of the Jelizavetino Formation and overlying strata) occur in the studied section of the St. Petersburg region. The thickness of the late Viruan sequence varies widely, ranging from 40 to 100 m in the studied localities.

An important change in the palaeobasin occurred at the end of the Keila time (see Männil 1966; Põlma 1982; Hints *et al.* 1989; Meidla 1996). It is expressed by the turnover in many common fossil groups, increase in litho- and biofacial zonality and sedimentation rates, and by the first deposition of pure lime muds and formation of carbonate buildups. A change in the taxonomic composition and decrease in abundance of polychaete jaws can be distinguished in this stratigraphical level.

Intense volcanic activity in the Iapetus region during the Idavere, Jõhvi and Keila times caused the formation of a series of K-bentonite beds, each of which marks an isochronous surface. Some of these beds, for instance, the Kinnekulle bed, are traceable over wide areas, providing extremely precise correlation of distant sections (Bergström *et al.* 1995). On this basis, several nearly contemporaneous polychaete assemblages from different localities are compared in the present paper.

Material and methods

The collection studied contains more than 10 000 detached jaws and nearly 70 more or less complete jaw apparatuses. The material is derived from the following boreholes

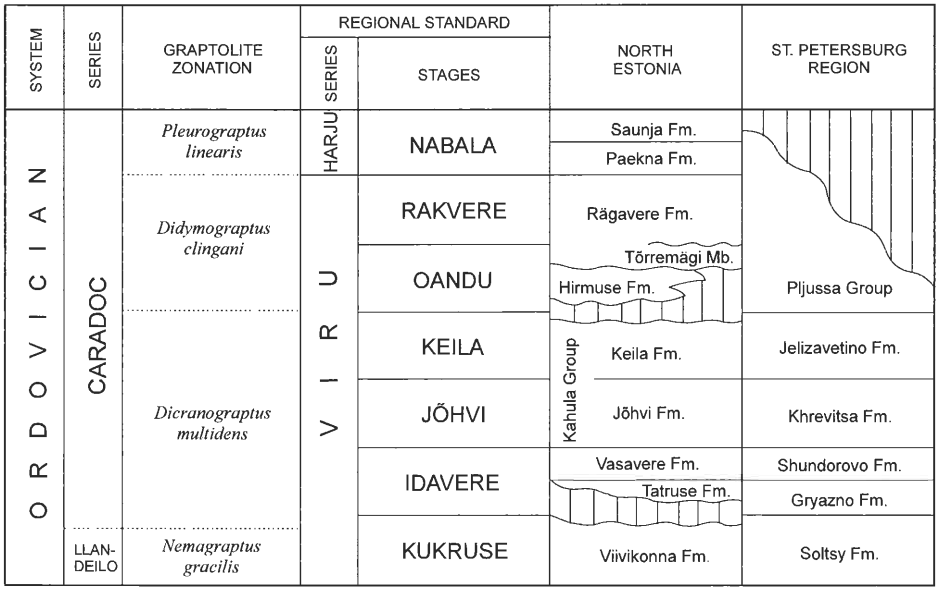


Fig. 2. Stratigraphy of the late Viruan sequence of the study area (after Männil & Meidla 1994 and Nõlvak 1997).

(numbers of boreholes according to the Geological Survey of Estonia) of North Estonia and St. Petersburg region (Fig. 1):

1) Metsküla (F-198) – 24 samples, 300–800 g each, ranging from the Idavere to Rakvere stages.

2) Hüti (F-358) – 4 samples, ca 500 g each, ranging from the Idavere to Keila stages.

3) Värsso (F-362) – 5 samples, ca 500 g each, ranging from the Idavere to Keila stages.

4) Vaemla (F-364) – 5 samples, ca 500 g each, ranging from the Idavere to Keila stages.

5) Apraksin Bor – 17 samples, ca 500 g each, ranging from the Idavere to Keila stages.

6) Rapla – 52 samples, 10–800 g each, ranging from the Kukruse to Nabala stages.

7) Orjaku – 55 samples, usually 50–500 g each, ranging from the Keila to Oandu stages.

8) Sibila – 14 samples, 100–300 g each, ranging from the Keila to Oandu stages.

The samples from the first five boreholes were collected and processed by the author, whereas the scolecodonts and the data from the Rapla, Orjaku and Sibila boreholes were obtained from the microfaunal collection of the Institute of Geology at Tallinn Technical University. Since the latter material had been treated somewhat differently, the emphasis here is on author's own samples to which the following methods refer.

Samples, 200–800 g in weight, were crushed into 10–100 cm^3 pieces. The material was prepared in 3–8 l vessels, mainly by means of dilute acetic acid (10–15%). Occasionally also hydrochloric acid was used to quicken the process. Insoluble residues were washed in the running water through a 34 or 63 μm sieve to remove clay.

Scolecodonts and other organic microfossils were picked up from Petri-dishes with a fine glass pipette. The fossils are stored in glycerin in translucent plastic boxes (2×1 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 ethanol and distilled water and 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 and coated with gold. A scanning electron microscope Tesla BS-300 was used at 19 kV (magnifications × 120–1400). All photos published in this paper are SEM micrographs.

Abbreviations used: GIT – Institute of Geology at Tallinn Technical University, ZPAL – Institute of Paleobiology of the Polish Academy of Sciences, Warsaw; bp – basal plate; Fm – Formation; L – jaw length, Lt – lateral teeth, MI – MV first (or posterior) to fifth maxillae, W – jaw width.

Stratigraphical distribution

The stratigraphic distribution of late Viruan jawed polychaetes is illustrated by faunal logs in Figs 3–5. Apparently many of the forty-six species are long-ranging ones and range beyond the studied interval, appearing below and disappearing above it (Fig. 6). *Mochtyella cristata*, *'Mochtyella' fragilis*, *Xanioprion* sp. B, *Tetraprion pozaryskae*, *Polychaetura gracilis*, *Polychaetaspis varsoviensis, Ramphoprion* sp. A and *Lunoprionella symmetrica*, some of which being found from the Llanvirn to Llandovery, are good examples of that. Such a distribution pattern confirms the relatively low evolutionary rate of many polychaete species as discussed by, e.g., Kielan-Jaworowska (1966), Bergman (1989, 1991b) and Szaniawski & Imajima (1996).

Many species described herein are poorly represented in the collection, the study area is limited to North-Estonian Confacies and faunas of under- and overlying strata are not consistently studied. The effect of these shortcomings can be well illustrated by distribution of *Polychaetaspis latus* Kielan-Jaworowska, 1966. In the studied sections, this species appears below the Idavere and is not found above the Keila Stage. It is a rather common species, and forms a considerable part of the assemblage. However, Kielan-Jaworowska (1966) noted that *P. latus* is found together with some Ashgillian or Llandoverian macrofossils. Recently Eriksson (1997) reported *Oenonites latus* (Kielan-Jaworowska 1966, regarded here as belonging to *Polychaetaspis*) from the Lower Silurian of Gotland, Sweden, and thus the range of *P. latus* is apparently much longer than it appeared on the basis of current material. Consequently ranges of some taxa presented herein cannot be considered as complete but are likely to be extended when more material is studied. However, some trends of the development of polychaete faunas in successive regional stages (see Fig. 2) in North Estonia and St. Petersburg region can be given.

Idavere Stage. — Twenty-three species of jawed polychaetes have been discovered from the Idavere Stage. The most abundant species are *Polychaetaspis gadomskae, P. latus, P.*

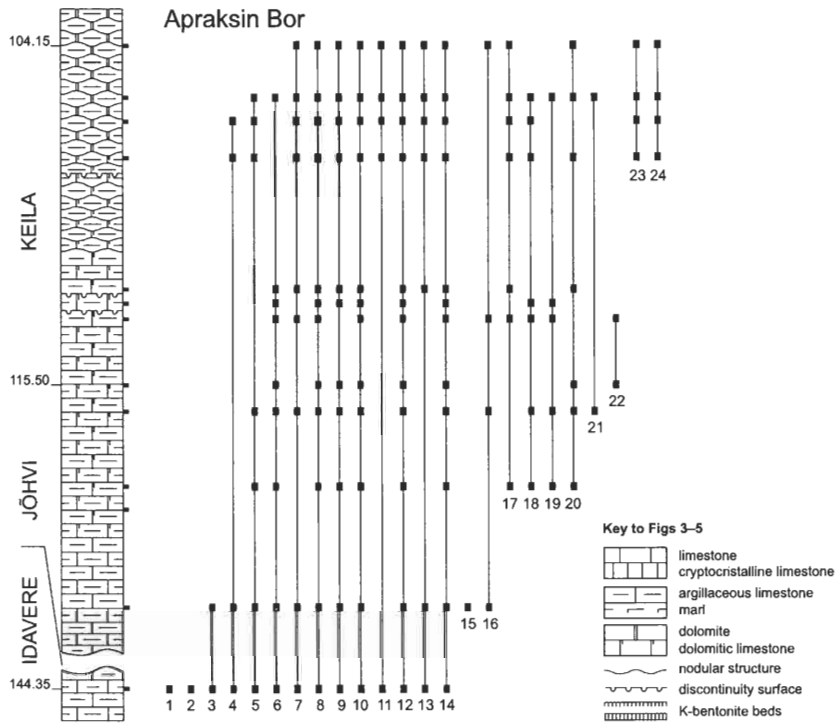


Fig. 3. Distribution of polychaete jaws in the Apraksin Bor borehole. 1 – *Polychaetura kielanae*, 2 – *Pararamphoprion*? sp. B, 3 – *Polychaetaspis latus*, 4 – *Polychaetaspis gadomskae*, 5 – *Atraktoprion cornutus*, 6 – *Tetraprion pozaryskae*, 7 – *Polychaetura gracilis*, 8 – *Polychaetaspis tuberculatus*, 9 – *Mochtyella polonica*, 10 – *Incisiprion incisus*, 11 – *Polychaetaspis* sp. A, 12 – *Mochtyella cristata*, 13 – *Lunoprionella symmetrica*, 14 – *Ramphoprion* sp. A, 15 – *Ramphoprion peterburgensis*, 16 – '*Mochtyella*' *duplicidentata*, 17 – *Kalloprion triangularis*, 18 – *Incisiprion edentulus*, 19 – *Polychaetaspis* sp. B, 20 – *Kozlowskiprion brevialatus*, 21 – *Ramphoprion* sp. C, 22 – *Pararamphoprion urbaneki*, 23 – Gen. et sp. indet. C, 24 – *Polychaetaspis* cf. *wyszogrodensis*.

tuberculatus, P. varsoviensis, Polychaetura gracilis and *Ramphoprion* sp. A, but *Mochtyella cristata, Ramphoprion bialatus, Incisiprion incisus* and *Atraktoprion cornutus* are also common. The relative abundance of scolecodonts is rather low (about 10/100 g) in the lower part of the stage (Vasavere Fm.), but notably higher (up to 50/100 g) in the upper part (Tatruse Fm.). A very low proportion of placognaths (less than 20% of all specimens) and a high diversity of the assemblage (each more abundant species forms less than 10–20% of the whole assemblage) are characteristic of the Idavere Stage.

Jõhvi Stage. — The Jõhvian fauna is represented by at least 28 species of jawed polychaetes; the most common ones are *Polychaetaspis gadomskae, P. latus, Polychaetura gracilis, Mochtyella cristata* and *Pistoprion transitans*. The latter species becomes abundant somewhat above the lower boundary of the stage. Close to that boundary, the abundance of *Ramphoprion* sp. A decreases and this species becomes notably less frequent than in the underlying strata. The relative abundance of scolecodonts is commonly between 20–30/100 g, but may reach 40/100 g. The placognaths

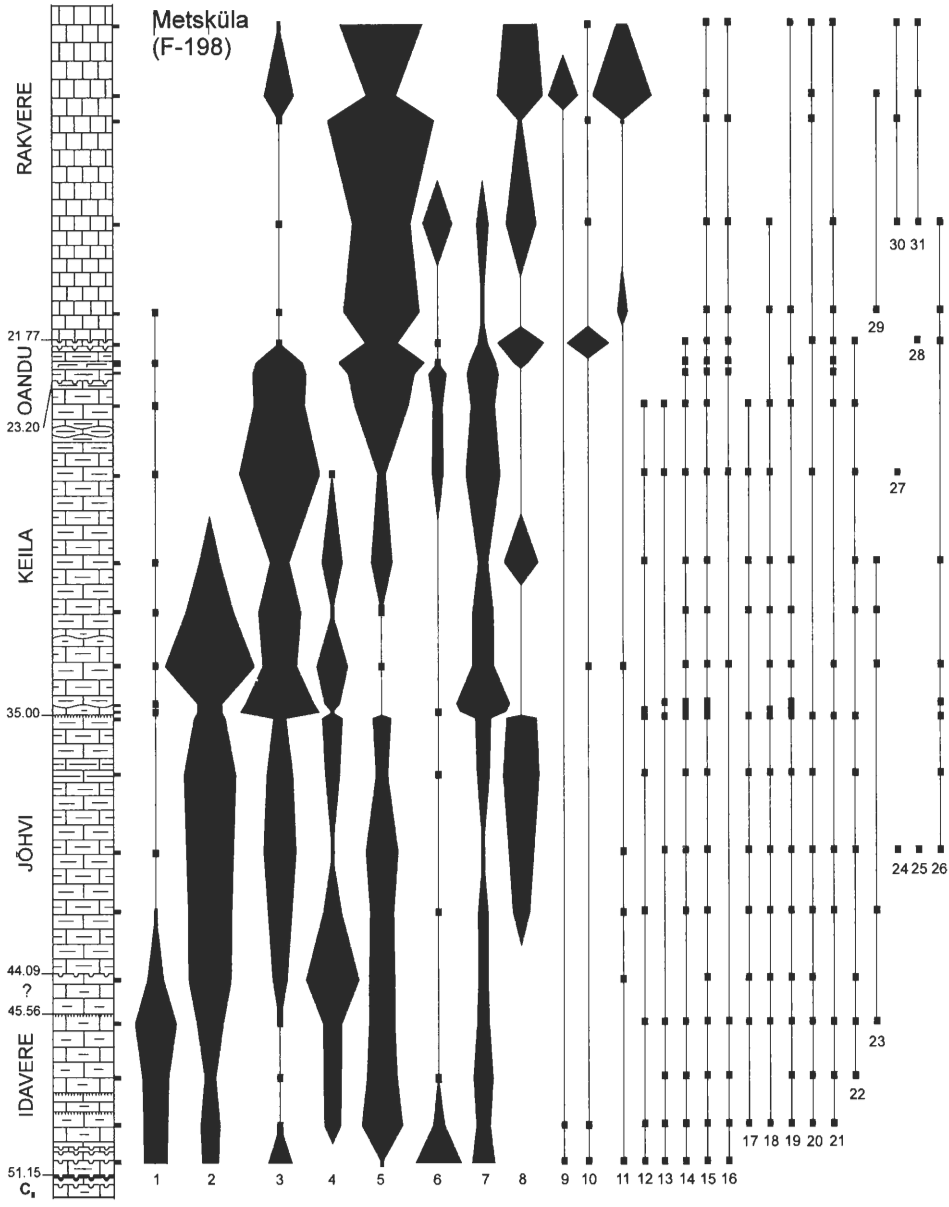


Fig. 4. Distribution of polychaete jaws in the Metsküla (F-198) borehole. 1 – *Ramphoprion* sp. A, 2 – *Polychaetaspis gadomskae*, 3 – *Mochtyella cristata*, 4 – *Polychaetaspis latus*, 5 – *Polychaetura gracilis*, 6 – *Polychaetaspis* sp. A, 7 – *Polychaetaspis tuberculatus*, 8 – *Pistoprion transitans*, 9 – *Mochtyella polonica*, 10 – *Polychaetaspis* cf. *wyszogrodensis*, 11 – *Vistulella kozlowskii*, 12 – *Ramphoprion bialatus*, 13 – *Incisiprion incisus*, 14 – *Atraktoprion cornutus*, 15 – *Kalloprion triangularis*, 16 – *Xanioprion* sp. B, 17 – *Polychaetura kielanae*, 18 – *Lunoprionella symmetrica*, 19 – *Tetraprion pozaryskae*, 20 – '*Mochtyella*' *fragilis*, 21 – *Leptoprion artus?*, 22 – *Kozlowskiprion brevialatus*, 23 – *Polychaetaspis* sp. B, 24 – *Estonioprion maennili*, 25 – *Rhytprion magnus*, 26 – '*Mochtyella*' *duplicidentata*, 27 – *Ramphoprion* sp. B, 28 – *Mochtyella* sp. A, 29 – '*Lunoprionella*' sp. A, 30 – *Atraktoprion major*, 31 – *Xanioprion* sp. A. C_{II} – Kukruse Stage. For lithological legend refer to Fig. 3.

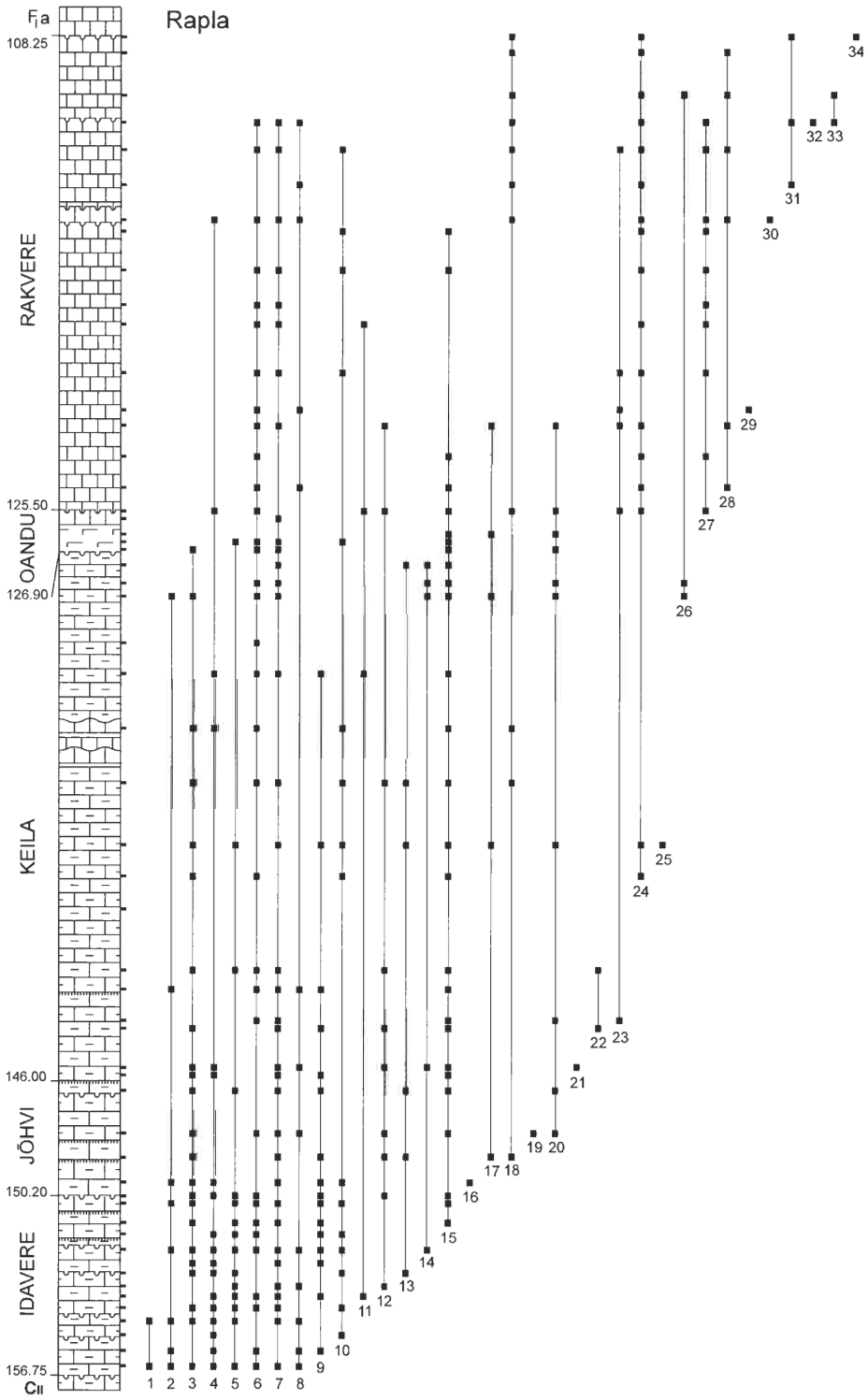
form 20–40% of specimens in the Jõhvi Stage. The diversity of the assemblage, as compared to that of the Idavere Stage, is somewhat lower and one species may form up to 40% of all specimens. Several very rare species such as *Estonioprion maennili*, and *Pararamphoprion* sp. A are only found in the Jõhvi Stage.

Keila Stage. — Over 34 species of jawed polychaetes have been indentified and the faunal composition is rather similar to that of the Jõhvi Stage. The abundance of scolecodonts ranges from 10/100g to 40/100g; with 20/100g as an averge. Jaws of the placognaths form 20 to 50% of all specimens. The most common species are *Polychaetaspis tuberculatus*, *P. gadomskae* and *P. latus, Mochtyella cristata* and *Polychaetura gracilis*. The high abundance of *Polychaetaspis gadomskae* and *P. latus* decreases in the upper part of the stage. From the overlaying strata only a few specimens have been found that with some doubt could be identified as *Polychaetaspis gadomskae* and *P. latus*. *Ramphoprion bialatus* and *Polychaetura kielanae* probably do not cross the upper boundary of the Keila Stage. Many very rare species, such as *Leptoprion* sp. A, *Kalloprion* sp. A, *Ramphoprion* sp. B and Gen. et sp. indet. A are found only in the Keila Stage. Some species, including Gen. et sp. indet. C and *Incisiprion edentulus* are restricted to the St. Petersburg region.

The polychaete assemblage changes significantly just above the Kinnekulle K-bentonite bed at the lower boundary of the Keila Stage. In the Metsküla drill core, *Polychaetaspis gadomskae, Polychaetura gracilis* and *Pistoprion transitans* decrease in numbers notably, whereas *Polychaetaspis tuberculatus* and *Mochtyella cristata* increase (Fig. 4). Similar changes in the frequency of the mentioned taxa were observed in the Hüti, Värsso and Vaemla borehole sections and also in the Pääsküla outcrop (Hints *et al.* 1997). Since there is no evidence of any hiatus below or above the K-bentonite, that widely traceable shift in the scolecodont assemblage may reflect some reorganization of polychaete faunas due to the fall of volcanic ash.

Oandu Stage. — At least 23 species of jawed polychaetes occur in the Oandu Stage. The abundance of scolecodonts reaches 25/100 g in the Hirmuse Formation and only 10/100 g in the Tõrremägi Member. About 30 percent of specimens in the Oandu Stage are placognaths. The most abundant species are *Polychaetura gracilis* and *Mochtyella cristata. Pistoprion transitans* and *Polychaetaspis tuberculatus* are slightly less common. According to present data, *Atraktoprion major* appears and *Incisiprion incisus* disappears in the Oandu Stage. *Polychaetaspis* cf. *wyszogrodensis* becomes abundant in the Tõrremägi Member. The polychaete fauna of the

Fig. 5. Distribution of polychaete jaws in the Rapla borehole. 1 – *Ramphoprion bialatus*, 2 – *Incisiprion incisus*, 3 – *Polychaetaspis gadomskae*, 4 – *Atraktoprion cornutus*, 5 – *Ramphoprion* sp. A, 6 – *Polychaetura gracilis*, 7 – *Mochtyella cristata*, 8 – *Kalloprion triangularis*, 9 – *Polychaetaspis latus*, 10 – *Polychaetaspis* sp. A, 11 – *'Mochtyella' fragilis*, 12 – *Tetraprion pozaryskae*, 13 – *Polychaetura kielanae*, 14 – *Leptoprion artus*?, 15 – *Polychaetaspis tuberculatus*, 16 – *Polychaetaspis varsoviensis*, 17 – *Lunoprionella symmetrica*, 18 – *Pistoprion transitans*, 19 – *Polychaetaspis* sp. B, 20 – *Kozlowskiprion brevialatus*, 21 – *Leptoprion* sp. A, 22 – *Xanioprion* sp. B, 23 – *'Mochtyella' duplicidentata*, 24 – *Polychaetaspis* cf. *wyszogrodensis*, 25 – Gen. et sp. indet. A, 26 – *Vistulella kozlowskii*, 27 – *Xanioprion* sp. A, 28 – *Atraktoprion major*, 29 – *Mochtyella polonica*, 30 – Gen. et sp. indet. B, 31 – *Ramphoprion elongatus*, 32 – *Polychaetura* sp. A, 33 – *Rhytiprion magnus*, 34 – *Atraktoprion mirabilis*. C_{II} – Kukruse Stage, F_{Ia} – Nabala Stage. For lithological legend refer to Fig. 3.


Rapla
F1a
108.25
RAKVERE
125.50
OANDU
126.90
KEILA
146.00
JÕHVI
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IDAVERE
156.75
CII
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34

Tõrremägi Member is very similar to that in the remaining part of the Rägavere Formation (i.e., Rakvere Stage).

Rakvere Stage. — Twenty-eight species of jawed polychaetes were recovered from the Rakvere Stage. A very low relative abundance of scolecodonts (about 10/100 g) is characteristic of the stage. The placognaths are generally more abundant than in the underlying strata and may reach to 80% of the total specimens. The most common species are *Polychaetura gracilis*, *Polychaetaspis* cf. *wyszogrodensis, P.* sp. A, *Pistoprion transitans, Mochtyella cristata* and *Xanioprion* sp. B, but also *Mochtyella polonica* and *Vistulella kozlowskii* are fairly common. Species like *Atraktoprion major, A. mirabilis*, *Xanioprion* sp. A, *Ramphoprion elongatus* and *Polychaetura* sp. A are restricted to the Rakvere Stage or Rägavere Formation (i.e., including the upper part of the Oandu Stage) only.

The usefulness of polychaete jaws in stratigraphy is discussed in several papers (e.g., Taugourdeau 1976; Szaniawski 1970, 1996; Kielan-Jaworowska 1966; Jansonius & Craig 1971; Zawidzka 1975; Shimer & Shrock 1955), but no correlation problems have been solved on the basis of scolecodonts so far. Although scolecodonts are rather frequent in different types of rock and their confused systematics is improving, it is likely that they will never obtain stratigraphical value comparable with that of several other fossil groups.

However, among the 46 species studied herein, appearances or disappearances of seven common species discussed below seem to fall into the late Viruan sequence, at least within the study area. *Polychaetaspis gadomskae, Polychaetura kielanae* and *Ramphoprion bialatus* appear below the Idavere Stage and extend to the top of the Keila Stage. *Inciciprion incisus* also appears below the Idavere but reaches the Oandu Stage. The earliest account of *Pistoprion transitans* come from the topmost Idavere Stage and the species extends into the Silurian. At least in some localities, the range of *Pistoprion transitans* is not continuous and includes several barren intervals (see Fig. 4). *Xanioprion* sp. A and *Atraktoprion major* seemingly appear in the Oandu Stage and extend at least to the Nabala Stage (lowermost Harju Series).

In addition, some characteristics of the assemblages, like diversity and the role of particular species, genera or families may appear useful for stratigraphy, when faunas of the same or similar facies and limited study area are considered.

The Ordovician polychaete jaws described by Kozłowski (1956) and Kielan-Jaworowska (1961, 1962, 1966) were derived mostly from erratic boulders, the ages of which are often unclear (cited as Ordovician or Silurian) or doubtful (cited like ?Middle Ordovician, ?Kukruse Stage). These boulders and their polychaete fauna have been characterized by Kielan-Jawrowska (1966). Assuming that these erratic boulders originated not far from the study area of the present paper, ages of some boulders may be specified.

Boulders No. O.140, O.147, O.213, O.279, O.349 reported as of unknown age may be of Jõhvian age or younger as indicated by the occurrence of *Pistoprion transitans.*

Boulders No. O.366 and O.400 were previously reported as of Kukrusean or Idaverean age. Occurrence of *Polychaetaspis gadomskae* may indicate the Keilan age or older. The insignificant role of the ramphoprionids, on the other hand, is not typical

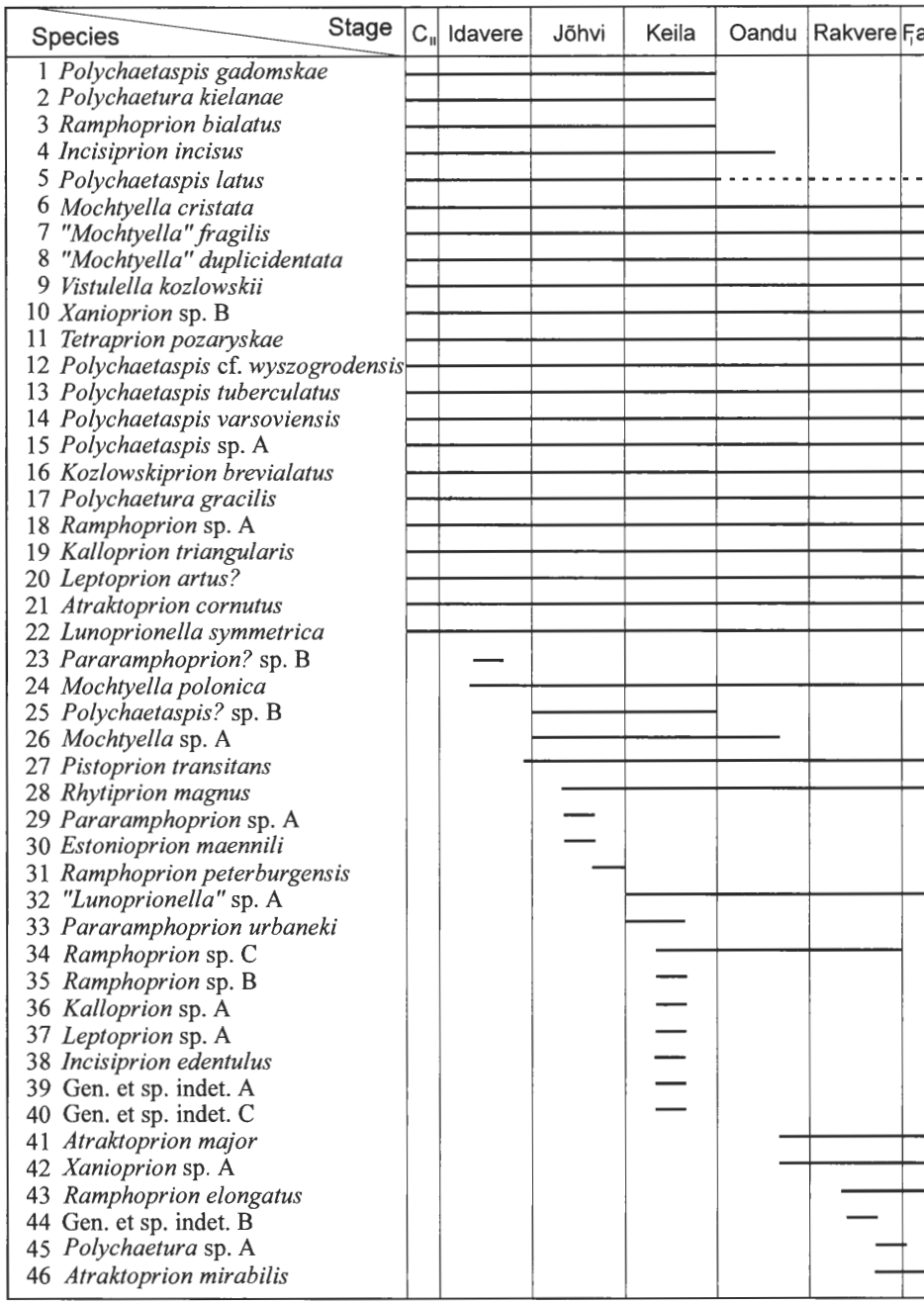


Fig. 6. Summarized distribution of polychaete jaws in the late Viruan of North Estonia and St. Petersburg region. C_{II} – Kukruse Stage, F_1a – Nabala Stage.

of the Kukruse and Idavere stages. Therefore the boulder is probably of Jõhvian or Keilan age. Certain macrofossils (*Clinambon anomalus*) support that opinion.

Boulder No. O.423 reported as of ?Middle Ordovician age may be of Keilan age or older as indicated by the occurrence of *Polychaetaspis gadomskae* and *Incisiprion incisus.*

Boulder No. O.469 reported as of ?Middle Ordovician age may be of Keilan age or older as indicated by the occurrence of *Incisiprion incisus* and *Polychaetura kielanae.*

Geographical distribution

The global distribution of Palaeozoic jawed polychaetes is not known in any great detail, in spite of the fact that the scolecodonts have been found from various parts of the world (Europe, Asia, North and South America, Africa, Australia). It was noted by Kielan-Jaworowska (1966) that many or even most of the Ordovician species occurring in North America are congeneric with the Baltoscandian fauna. Such genera as *Mochtyella, Polychaetaspis, Ramphoprion, Kalloprion, Leptoprion* and *Atraktoprion* are represented by numerous species on both continents. The first and so far the only positive species-level intercontinental correlation of polychaete jaws is presented by Bergman (1991b).

Concerning the stratigraphic interval of the present study, the North American material is copious, including several hundred element-species most of which have been described by Stauffer (1933) and Eller (1945). The species-level comparison of these faunas is tentative without studying the original collections. However, *Protarabellites fidelis, P. delectus, P. dubius* and *Lumbriconereites cognitus* of Stauffer (1933) and *Lumbriconereites langae* of Eller (1945) show great similarity to *Ramphoprion* sp. A of the present study; some specimens of *Lumbriconereites cameratus* by Stauffer (1933) resemble *Polychaetaspis gadomskae* from Baltoscandia; '*Grubia bifurca*' described by Gries (1944) is supposedly conspecific with *Pararamphoprion* sp. A, and '*Grubia nodosa*' of the same author is very similar and possibly conspecific with *Polychaetaspis tuberculatus*. Consequently, besides many common genera, there seem to have occurred some common species of Ordovician polychaetes in North America and Baltoscandia.

The spatial distribution of jawed polychaetes can be described within North Estonia and the St. Petersburg region. Although the material from the latter area is scanty, it is evident that the polychaete faunas of the Idavere Stage were very similar in North Estonia and the St. Petersburg region. The four most abundant species in Estonian sections (*Polychaetaspis gadomskae, P. latus, Polychaetura gracilis, Ramphoprion* sp. A) were prevailing in the Apraksin Bor drill core too. In addition, the composition of the less common species was rather similar in both areas.

The generally similar Jõhvian faunas of the two areas differ somewhat from each other in assemblage composition. *Polychaetaspis tuberculatus* was the most abundant species in the Apraksin Bor drill core, whereas *Polychaetaspis gadomskae,* which flourished in North Estonia was not found from the Apraksin Bor drill core.

Since the mid Keila time, however, the differences between polychaete faunas of both areas increased. That may reflect distinctive basin development in the St. Petersburg region as noted by, e.g., Dmitrovskaya (1989). The frequency of placognaths was relatively lower in the St. Petersburg region. *Polychaetaspis latus* was not found, *Polychaetaspis gadomskae* and *Mochtyella cristata* were relatively rare in the St.

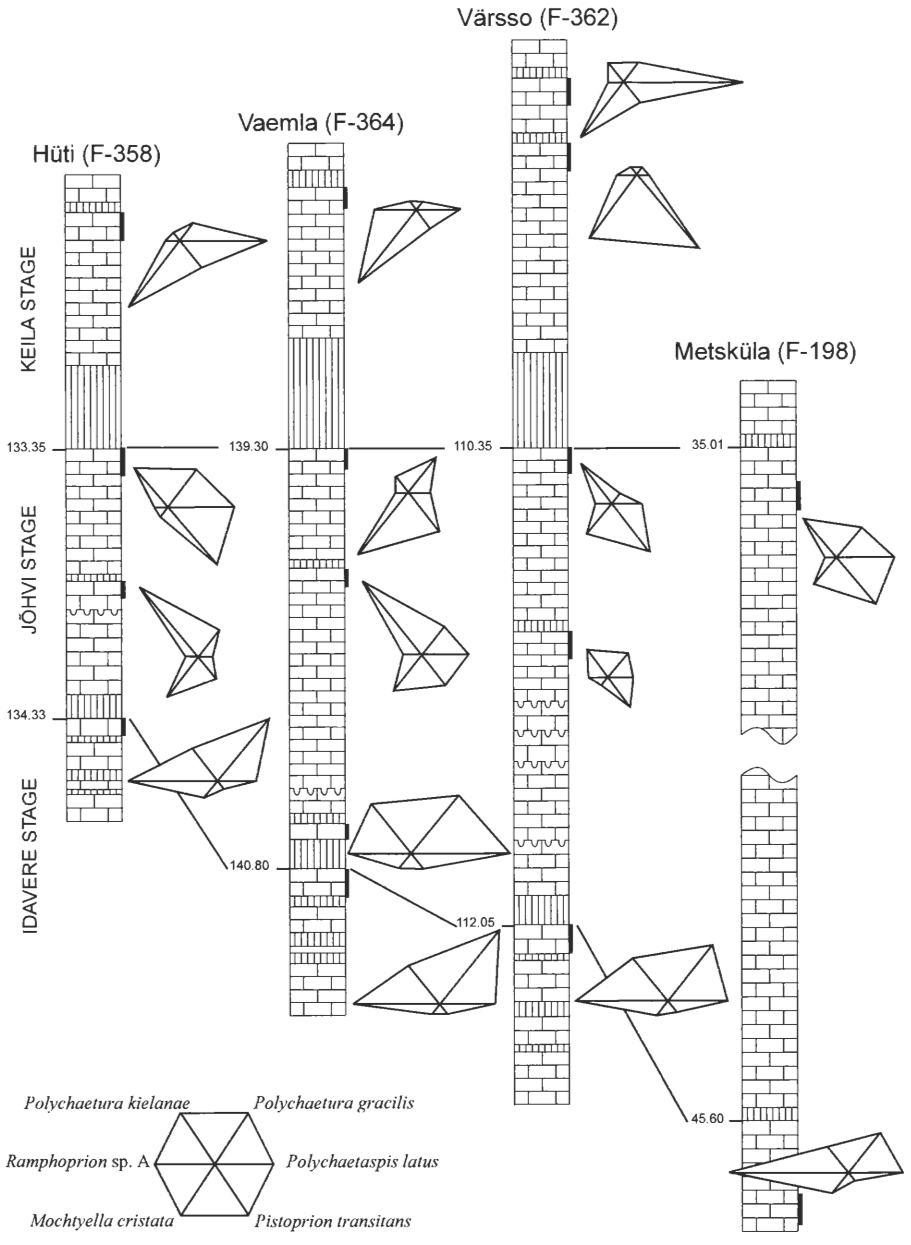


Fig. 7. Star symbol plot showing dynamics of selected species in the samples below K-bentonite beds of four drill core sections. Percents of the six species are represented by the relative lengths of individual rays in each star, the smallest value for each species is plotted on the shortest ray. See additional comments in text. For lithological legend refer to Fig. 3.

Petersburg region in comparison to North Estonia, where they formed an important part of an assemblage. The relative abundance of *Incisiprion incisus, Polychaetaspis tuberculatus, P.* cf. *wyszogrodensis*, *P.* sp. A, and *Kozlowskiprion brevialatus* was

notably higher in the St. Petersburg region. Two species quite common in the Apraksin Bor drill core, *Incisiprion edentulus* and Gen. et sp. indet. C, were not encountered in North Estonia. In spite of these differences, faunas of jawed polychaetes in North Estonia and the St. Petersburg region are rather similar to each other.

The most detailed data on geographical distribution of scolecodonts can be demonstrated by boreholes in North Estonia, where extremely precise correlation of sections was based on K-bentonite layers. Topmost Idaverean, Jõhvian and lower Keilan beds of four borehole sections (Hüti, Värsso, Vaemla and Metsküla) were sampled just below K-bentonites (see Figs 1 and 7). Fig. 7 presents a star symbol plot illustrating dynamics of six common species in 16 samples. The images representing assemblages nearly of the same age are rather similar to each other. This is better expressed in the topmost Idavere Stage (the lowermost samples) where the corresponding stars are almost of the same shape. In addition to the six species, other characteristics of the assemblages tend to be relatively invariable in the Idavere Stage of distant localities. For instance, abundance of scolecodonts in four sections varied from 29/100g to 33/100g, the diversity expressed as a number of species in a sample was 20 or 21, and the assemblages predominated by labidognaths constituted 8 to 11% of placognaths. Furthermore, the Idaverean assemblage in the St. Petersburg region was rather similar to that in North Estonia. It follows that an invariable association of jawed polychaetes, characterized by a particular species composition, prevailing forms and, perhaps population density, was spread over wide areas within the North Estonian Confacies during some periods of the Ordovician. Bergman (1989, 1995) concluded that the occurrence of some Silurian jawed polychaetes was strongly dependent on facies distribution. Accordingly, the distribution of the Idaverean polychaetes seems to reflect a very uniform sedimentary environment, which is in agreement with, e.g., Männil (1966), Põlma (1982), and Hints *et al.* (1989).

Nearly contemporaneous assemblages from the Jõhvi and Keila stages of four sections do also show great similarity, with some exceptions. For example, *Polychaetaspis gadomskae* was not found in the uppermost sample from the Vaemla borehole, whereas in the corresponding samples from other sections this species makes up, on average, a quarter of all specimens. Such anomalies are likely caused by small-scale differences in microfacies distribution and thereby, by some environmental factors. The nature of these factors remains unclear without detailed sedimentological study. Moreover, the fauna may be more sensitive to environmental changes than the deposition regime (Jaanusson 1995). Therefore, the factors controlling the distribution of fauna may not be distinctly reflected in the composition of the sediment, and hence not directly detectable.

Systematic palaeontology

The problems concerning taxonomy of polychaete jaws are discussed in detail by Kielan-Jaworowska (1966, 1968), Jansonius & Craig (1971), Szaniawski & Wrona (1973), Bergman (1989), Szaniawski (1996), Eriksson & Bergman (1997). In brief, the systematics of polychaete jaws, particularly Palaeozoic ones, is in many respects, disordered. The main reason for this is the existence of two basically different classi-

fication concepts. First, the morphological classification which deals with isolated jaws and does not intend to identify species in any biological meaning (in the sense of expressing natural relationships). The second, a more or less natural taxonomy is based on fused or reconstructed jaw apparatuses.

Such dual classification combined with other obstacles has resulted in a great number of synonyms, homonyms, *nomina dubia* and *nomina nuda* making the systematics rather complicated to follow. The great work to merge element- and apparatus-based systematics of Palaeozoic polychaetes into a single taxonomy being in accordance with nomenclature rules (ICZN) is in progress (see Bergman 1989, 1991a; Eriksson & Bergman 1997; Eriksson 1997). In this study, however, some results of these revisions (e.g., replacement of the generic name *Polychaetaspis* Kozłowski, 1956 with the probable older synonym *Oenonites* Hinde, 1879 as proposed by Eriksson 1997) are not followed due to insufficient knowledge of the type species and holotypes.

Further, in some other cases the priority rule of ICZN cannot be applied as that would require detailed revision of several taxa and preferably resampling of type localities, which was not the aim of this study. Consequently it is likely that some generic and specific names used by the present author will prove to be junior synonyms in the future.

Many species described below are referred to under an open nomenclature due to the insufficient material or possible conspecificity with unrevised element-based taxa. Descriptions are only provided for new taxa. In cases of well-known species, the occurrence is documented and material, localities and remarks, including length and width measurements of posterior jaws are presented.

The terminology used in the descriptions is adopted from Kielan-Jaworowska (1966) and Jansonius & Craig (1971). The term 'shank' is used herein for the posteriormost parts (from posterior to maximum longitudinal extension of bight) of labidognathid and prionognathid right MI.

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

Fig. 8A, B.

Mochtyella cristata n. sp.; Kielan-Jaworowska 1961: pp. 248–253, pls 5–7.
Mochtyella cristata Kielan-Jaworowska; Kielan-Jaworowska 1966: p. 54, pl. 1: 1, text-fig. 5A.
Mochtyella cristata Kielan-Jaworowska; Szaniawski 1970: pp. 448, 449, pl. 1: 4.
Mochtyella cf. *cristata* Kielan-Jaworowska; Männil & Zaslavskaja 1985: p. 105, pl. 14: 1a–d, 2a–b.

Material. — More than 600 detached left and right compound jaws.

Localities. — Boreholes: Apraksin Bor 105.2–122.15 m, Metsküla 10.8–50.8 m, Rapla 111.3–156.47 m, Kuusiku 11.8–16.4 m, Kautla 92.77–94.43 m, Rooküla 40.02–41.4 m, Sibila 94.1–95.7 m, Orjaku 131.5–141.75 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

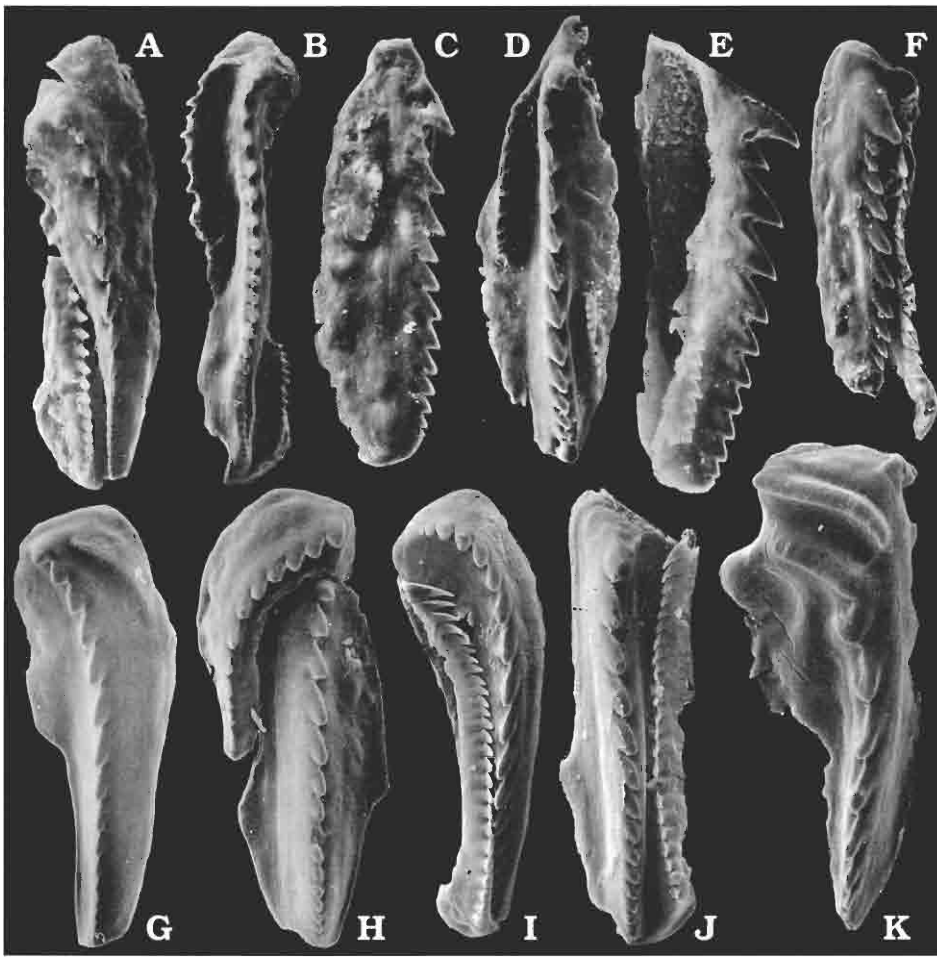


Fig. 8. Mochtyellidae, Rhytiprionidae, Tetraprionidae. **A**, **B**. *Mochtyella cristata*. **A**. Left MI, GIT Sc 2, dorsal view, × 125, Värsso (F-362), 109.02 m, Keila Stage. **B**. Right MI, GIT Sc 1, dorsal view, × 110, Värsso (F-362), 109.02 m, Keila Stage. **C**. *Mochtyella polonica*. Right MI, GIT Sc 3, dorsal view, × 150, Rapla, 121.8 m, Rakvere Stage. **D**. *Mochtyella* sp. A. Right MI, GIT Sc 4, dorsal view, × 125, Metsküla (F-198), 22.0 m, Oandu Stage. **E**. '*Mochtyella*' *duplicidentata*. Left MI, GIT Sc 5, outer-lateral view, × 125, Hüti (F-358), 132.49 m, Keila Stage. **F**. *Tetraprion pozaryskae*. Right MI+bp, GIT Sc 14, dorsal view, × 150, Metsküla (F-198), 37.5 m, Jõhvi Stage. **G**, **H**. *Pistoprion transitans*. **G**. Left MI, GIT Sc 6, dorsal view, × 100, Metsküla (F-198), 39.91 m, Jõhvi Stage. **H**. Right MI+right MII, GIT Sc 7, dorsal view, × 100, Metsküla (F-198), 39.91 m, Jõhvi Stage. **I**, **J**. *Vistulella kozlowskii*. **I**. Left MI+lbp, GIT Sc 9, dorsal view, × 140, Metsküla (F-198), 20.8 m, Rakvere Stage. **J**. Right MI+bp, GIT Sc 8, dorsal view, × 60, Rapla, 110.3 m, Rakvere Stage. **K**. *Rhytiprion magnus*. Left MI, GIT Sc 10, dorsal view, Metsküla (F-198), 39.91 m, Jõhvi Stage.

Dimensions. — Right MI: L = 0.23–1.0 mm, L/W = 2.5–4.5; Left MI: L = 0.25–1.10 mm, L/W = 2.5–4.2.

Occurrence — Idavere to Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia, Ordovician erratic boulders found in Poland, Llandovery and Wenlock of Severnaya Zemlya.

Mochtyella polonica Kielan-Jaworowska, 1966

Fig. 8C.

Mochtyella polonica sp. n.; Kielan-Jaworowska 1966: pp. 54–56, pl. 3: 1, text-fig. 1A.

Material. — Over 20 isolated posterior maxillae.

Localities. — Boreholes: Metsküla 13.25–49.49 m, Rapla 121.8 m, Hüti 133.25 m, Värsso 109.02 m, Vaemla 139.31–139.72 m.

Dimensions. — Right MI: L = 0.3–0.85 mm, L/W = 3–3.5; Left MI: L = 0.34–0.51 mm, L/W = 3.2–3.5.

Occurrence. — Ordovician or Silurian erratic boulders found in Poland, Idavere to Rakvere stages of North Estonia.

Mochtyella sp. A

Fig. 8D.

Material. — More than 10 detached maxillae.

Localities. — Boreholes: Metsküla 22.0 m, Hüti 132.49 m, Värsso 109.25 m, Vaemla 139.31 m.

Description. — Right MI: L = 0.3–0.6 mm, L/W = 2.9. Jaw pointed anteriorly. Main ridge has 12–14 denticles. Second ridge straight with 6–7 denticles, 0.3–0.5 of jaw length, extending to 0.5–0.6 of jaw from anterior. Basal ridge with about 9 denticles, straight and extends to 0.2–0.33 of jaw length.

Left MI: L = 0.76–0.90 mm, L/W = 3. Jaw rounded anteriorly. Main ridge with 14–18 denticles, slightly curved. Cusp indistinct, followed by one intermediate denticle. Laeobasal ridge with 11 denticles laterally compressed, high and separated posteriorly from other part of jaw. Laeobasal ridge about half of jaw length, without reaching the posterior end of main ridge.

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 . The right MI of *Mochtyella* sp. A differs from *M. polonica* in having longer denticulated second ridge and a more distinct and robust basal ridge.

Occurrence. — Jõhvi to Oandu stages of North Estonia.

'*Mochtyella*' *fragilis* Szaniawski, 1970

Mochtyella fragilis n. sp.; Szaniawski 1970: pp. 453–454, pl. 2: 5–7.
Mochtyella multilamellata n. sp.; Szaniawski 1970: pp. 454–456, pl. 2: 1–4.
Mochtyella fragilis Szaniawski; Mierzejewski 1978a: pp. 75–80, pl. 16.

Material. — More than 180 isolated posterior maxillae.

Localities. — Boreholes: Metsküla 10.8–49.49 m, Rapla 118.6–153.9 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Remarks. — Right MI: L = 0.23–0.76 mm, L/W = 2.7; Left MI: L = 0.28–1.20 mm, L/W = 2.7. '*Mochtyella*' *fragilis* differs from other species of *Mochtyella* in having relatively flat and fragile jaws, strongly bent main ridges provided with bump-like denticles, and a long laeobasal ridge with a large anteriormost denticle. Supposedly, '*M*'. *fragilis* belongs together with *M. grazynae* Mierzejewski to a different genus of mochtyellids. The insufficient knowledge of apparatuses, however, does not support establishment of a new genus at this time, and thus the species is tentatively assigned to *Mochtyella*.

Occurrence. — ?Upper Ordovician of Poland, Idavere to Rakvere stages of North Estonia.

'*Mochtyella*' *duplicidentata* Szaniawski, 1970

Fig. 8E.

Mochtyella duplicidentata sp. n.; Szaniawski 1970: pp. 451–453, pl. 1: 3.

Material. — More than 60 detached posterior maxillae.

Localities. — Boreholes: Metsküla 14.15–39.91 m, Hüti 132.49–134.33 m, Värsso 109.02–111.01 m, Vaemla 138.36–139.72 m.

Dimensions. — Right MI: L = 0.26–0.64 mm, L/W = 2.5–4.5; Left MI: L = 0.26–0.8 mm, L/W = 3.

Remarks. — '*Mochtyella*' *duplicidentata* is most similar to *M. trapezoidea* and related species although it has a somewhat shorter laeobasal ridge. It lacks a second ridge, and, as pointed out by Szaniawski (1970) and Mierzejewski (1978) possibly also the basal ridge. The present material shows no signs of the presence of a fused basal ridge. This does not exclude the presence of some homologous element, but in that case, it may be a basal plate rather than a basal ridge. *'M'. duplicidentata* presumably belongs to another genus of mochtyellids. Due to the insufficient material, however, the species is tentatively assigned to *Mochtyella* herein.

Occurrence. — ?Upper Ordovician of Poland, Idavere to Rakvere stages of North Estonia.

Pistoprion Kielan-Jaworowska, 1966

Type species: *Pistoprion transitans* Kielan-Jaworowska, 1966.

Pistoprion transitans Kielan-Jaworowska, 1966

Fig. 8G, H.

Pistoprion transitans n. sp.; Kielan-Jaworowska 1966: pp. 60–62, pl. 3: 2, pl. 4: 2, pl. 7, text-fig. 5B.
Pistoprion transitans Kielan-Jaworowska; Szaniawski 1970: pp. 457–458; pl. 3: 5–7.

Material. — More than 400 detached posterior maxillae, some joined elements.

Localities. — Boreholes: Metsküla 10.8–42.0 m, Kuusiku 12.2–15.2 m, Kautla 92.77–93.48 m, Rooküla 68.29–69.0 m, Sibila 94.00–95.45 m, Rapla 108.2–147.8 m, Orjaku 129.5–131.33 m, Hüti 132.49–133.78 m Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right MI: L = 0.20–1.5 mm, L/W = 2.2–3.6; Left MI: L = 0.27–0.80, L/W = 2–3.

Occurrence. — Ordovician or Silurian erratic boulders found in Poland, Idavere to Rakvere stages of North Estonia.

Vistulella Kielan-Jaworowska, 1961

Type species: *Vistulella kozlowskii* Kielan-Jaworowska, 1961.

Vistulella kozlowskii Kielan-Jaworowska, 1961

Fig. 8 I, J.

Vistulella kozlowskii n. sp.; Kielan-Jaworowska 1961: pp. 243–248, pls 1–4, text-fig. 2.
Vistulella kozlowskii Kielan-Jaworowska; Kielan-Jaworowska 1966: p. 64, text-fig. 5c.
Vistulella kozlowskii Kielan-Jaworowska; Mierzejewska & Mierzejewski 1975: p. 99, text-fig. 1.
Vistulella kozlowskii Kielan-Jaworowska; Mierzejewski 1978a: p. 2278, fig. 1.

Material. — More than 40 dispersed jaws, some joined elements and one apparatus.

Localities. — Boreholes: Metsküla 10.8–44.43 m, Rapla 110.8 m.

Dimensions. — Right MIa: L = 0.3–0.4 mm, L/W = 4.5; Left MI: L = 0.3–0.85 mm, L/W = 2.5–4.

Occurrence. — Ordovician and Silurian Erratic boulders found in Poland, Jõhvi to Rakvere stages of North Estonia.

Rhytiprionidae Kielan-Jaworowska, 1966

Rhytiprion Kielan-Jaworowska, 1966

Type species: *Rhytiprion magnus* Kielan-Jaworowska, 1966.

Rhytiprion magnus Kielan-Jaworowska, 1966

Fig. 8K.

Rhytiprion magnus n. sp.; Kielan-Jaworowska 1966: pp. 66–68, pl. 8, text-fig. 5D.

Rhytiprion sp. a; Kielan-Jaworowska 1966: p. 68, pl. 9: 1.
Rhytiprion magnus Kielan-Jaworowska; Szaniawski 1970: pp. 459–460, pl. 4: 5–6.

Material. — Three left MI, one broken right MI.

Localities. — Boreholes: Metsküla 39.91 m, Rapla 110.3–111.3 m.

Dimensions. — Left MI: L = 0.5–0.9, mm L/W = 2.5.

Occurrence. — ?Ordovician erratic boulders found in Poland, Jõhvi and Rakvere stages of North Estonia.

Xanioprionidae Kielan-Jaworowska, 1966
Xanioprion Kielan-Jaworowska, 1962

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

Xanioprion sp. A

Fig. 9A.

Material. — Three left MII, one right MII.

Localities. — Boreholes: Metsküla 10.8–17.75 m, Rapla 123.45 m.

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

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

Left MII is a mirror image of the right MII.

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

Occurrence. — Rakvere Stage of North Estonia.

Xanioprion sp. B

Fig. 9C–E.

Occurrence. — Jõhvi Stage of North Estonia.

Material. — One right MI with broken basal plate.

Locality. — Metsküla borehole, 35.22 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 first 0.15 of jaw length it has laterally directed pointed ramus, less than one-fifth of the jaw length. Main portion of jaw narrow, nearly straight and composed of row of 16 posteriorly and anteriorly decreasing denticles. Anteriormost part of ridge in ramus undenticulated. In mid-third of jaw, borders between denticles, especially in proximal jaw wall, are developed in form of upward narrowing cracks. Denticles weakly fused to each other in dorsal part of jaw only (see Fig. 9C, E). In most cases anterior and posterior parts of jaw, which are more compact, are found separately.

Basal plate almost as long as right MI and consists of a row of denticles. At least three anterior ones are long, sharp and 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) belief that these undescribed apparatuses of *Xanioprion* may be congeneric with *Rakvereprion* Mierzejewski seems to be unfounded. The specimens of *X. borealis* figured by Kielan-Jawo-

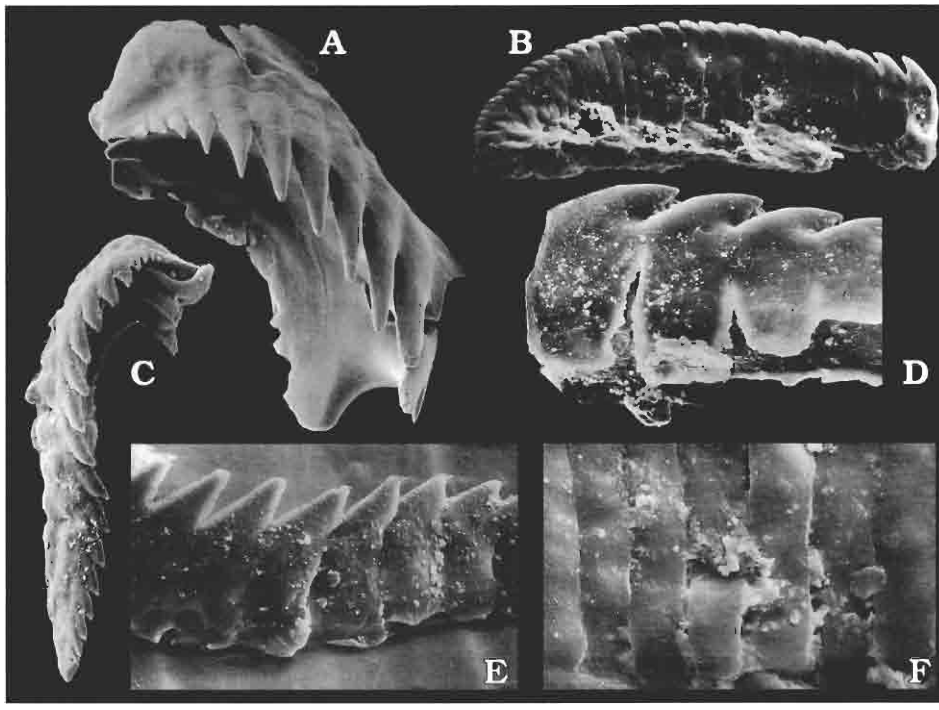


Fig. 9. Xanioprionidae *incertae sedis*. **A**. *Xanioprion* sp. A. Left MII, GIT Sc 11, dorsal view, × 40, Metsküla (F-198), 17.65 m, Rakvere Stage. **B**, **F**. '*Lunoprionella*' sp. A. **B**. MI, GIT Sc 90, lateral view, × 175, Hüti (F-358), 132.49 m, Keila Stage. **F**. Detail of the jaw wall of the same specimen, × 625. **C–E**. *Xanioprion* sp. B. **C**. Right MI, GIT Sc 12, dorsal view, × 125, Metsküla (F-198), 35.12 m, Jõhvi Stage. **D**. Posterior part of broken right MI, GIT Sc 13, left-lateral view, × 160, Metsküla (F-198), 35.12 m, Jõhvi Stage. **E**. Detail of **C**, left- lateral view, × 210.

rowska (1962: pls 12, 13) and by 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

Fig. 8F.

Tetraprion pozaryskae n. sp.; Kielan-Jaworowska 1966: pp. 69–71, pls 9–11, text-fig. 5F.

Material. — More than 400 detached posterior maxillae, several joined jaws.

Localities. — Boreholes: Apraksin Bor 105.2–144.25 m, Metsküla 10.8–49.49 m, Rapla 122.2–153.6 m, Kuusiku 15.25–16.40 m, Orjaku 133.50–133.62-m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right and left MI: L = 0.15–0.45 mm, L/W2.6–4.4.

Occurrence. — ?Middle Ordovician erratic boulders found in Poland, Idavere to Rakvere stages of North Estonia.

Polychaetaspidae Kielan-Jaworowska, 1966

Polychaetaspis Kozłowski, 1956

Type species: *Polychaetaspis wyszogrodensis* Kozłowski, 1956.

Polychaetaspis cf. *wyszogrodensis* Kozlowski, 1956

Fig. 10A–C.

Material. — Over 50 isolated right and left posterior maxillae, some basal plates.

Localities. — Boreholes: Apraksin Bor 105.5–122.15 m, Metsküla 10.8–49.49, Kuusiku 11.8 m, Rapla 108.2–138.6 m.

Dimensions. — Right MI: L = 0.35–1.1 mm, L/W = 2.4–3.2.; Left MI: L = 0.4–0.9 mm, L/W = 2.1–2.9.

Remarks. — The remarkable variability of *P.* cf. *wyszogrodensis* concerns the length of shank in the right MI, which varies between 0.40–0.65 of the length of right MI. In one specimen of *P.* cf. *wyszogrodensis* inverted symmetry has been observed (Fig. 10C).

Occurrence. — Jõhvi and Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia.

Polychaetaspis gadomskae Kielan-Jaworowska, 1966

Fig. 10E–H.

Polychaetaspis gadomskae n. sp.; Kielan-Jaworowska 1966: pp. 81–83, pl. 15, text-fig. 8C.

Material. — More than 1000 dispersed posterior maxillae, some joined jaws and jaw apparatuses.

Localities. — Boreholes: Apraksin Bor 122.5–144.25 m, Metsküla 29.8–50.8 m, Rapla 156.47–129.9 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 139.31–140.81 m.

Dimensions. — Right MI: L = 0.2–0.6 mm, L/W = 2.0–2.8; Left MI: L = 0.20–0.55 mm, L/W = 2.3–2.8.

Occurrence. — ?Middle Ordovician erratic boulders found in Poland, Idavere to Keila stage of the St. Petersburg region, Idavere to Keila stages of North Estonia.

Polychaetaspis tuberculatus Kielan-Jaworowska, 1966

Fig. 10D.

Polychaetaspis sp.; Kozłowski 1956: p. 182, assemblage D, fig. 7.
Polychaetaspis cf. *wyszogrodensis*; Kozłowski 1956: p. 182, figs 9B–F, 11B.
Polychaetaspis tuberculatus n. sp.; Kielan-Jaworowska 1966: pp. 78–81, pl. 13: 4.

Material. — More than 150 isolated posterior maxillae, several tens of basal plates, few joined jaws.

Localities. — Boreholes: Apraksin Bor 105.2–144.25 m, Metsküla 20.9–47.88, Rapla 115.2–150.3 m, Kuusiku 12.8–16.4 m, Kautla 93.48–94.3 m, Rooküla 38.0–41.3 m, Sibila 94.0–95.7-m, Orjaku 129.7–141.75 m , Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right MI: L = 0.25–2.10 mm, L/W = 2.1–3.0; Left MI: L = 0.30–1.65, L/W = 2.6–2.9.

Occurrence. — ?Middle Ordovician erratic boulders found in Poland, Idavere to Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia.

Polychaetaspis varsoviensis Kielan-Jaworowska, 1966

Fig. 10J–L.

Polychaetaspis varsoviensis sp. n.; Kielan-Jaworowska 1966: pp. 93–95, pl. 19: 1–3, text-fig. 8H.

Material. — Over 50 isolated posterior maxillae, one incomplete jaw apparatus.

Localities. — Boreholes: Metsküla 17.75–50.8 m, Hüti 132.49–134.33 m, Värsso 109.12–112.15 m.

Dimensions. — Right MI: L = 0.25–0.80 mm, L/W = 2.5–2.7; Left MI: L = 0.25–0.75, L/W = 2.6–2.9.

Occurrence. — Middle Ordovician erratic boulders found in Poland, Idavere to Rakvere stage of North Estonia.

Polychaetaspis latus Kielan-Jaworowska, 1966

Fig. 10O, P.

Polychaetaspis latus n. sp.; Kielan-Jaworowska 1966: pp. 89–90, pl. 17: 3, 4, text-fig. 8F.
Oenonites latus (Kielan-Jaworowska); Eriksson 1997: pp. 222–223, figs 11, 12.

Material. — More than 450 isolated posterior maxillae, several joined jaws and some jaw apparatuses.

Localities. — Boreholes: Apraksin Bor 115.5–144.25 m, Metsküla 26.62–50.8 m, Rapla 138.25–150.4 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right MI: L = 0.2–0.6 mm, L/W = 2.1–3.0; Left MI: L = 0.2–0.5 mm, L/W = 2.4–3.0.

Occurrence. — Ordovician or Silurian erratic boulders found in Poland, Lower Visby and Högklint Beds of Gotland, Idavere to Keila stages of the St. Petersburg region, Idavere to Keila stages of North Estonia.

Polychaetaspis sp. A

Fig. 10Q, R.

Material. — Over 150 isolated posterior maxillae.

Localities. — Boreholes: Apraksin Bor 144.25–105.2 m, Metsküla 17.75–50.8, Hüti 133.35–133.78 m, Värsso 109.02–111.01 m, Vaemla 138.36 m.

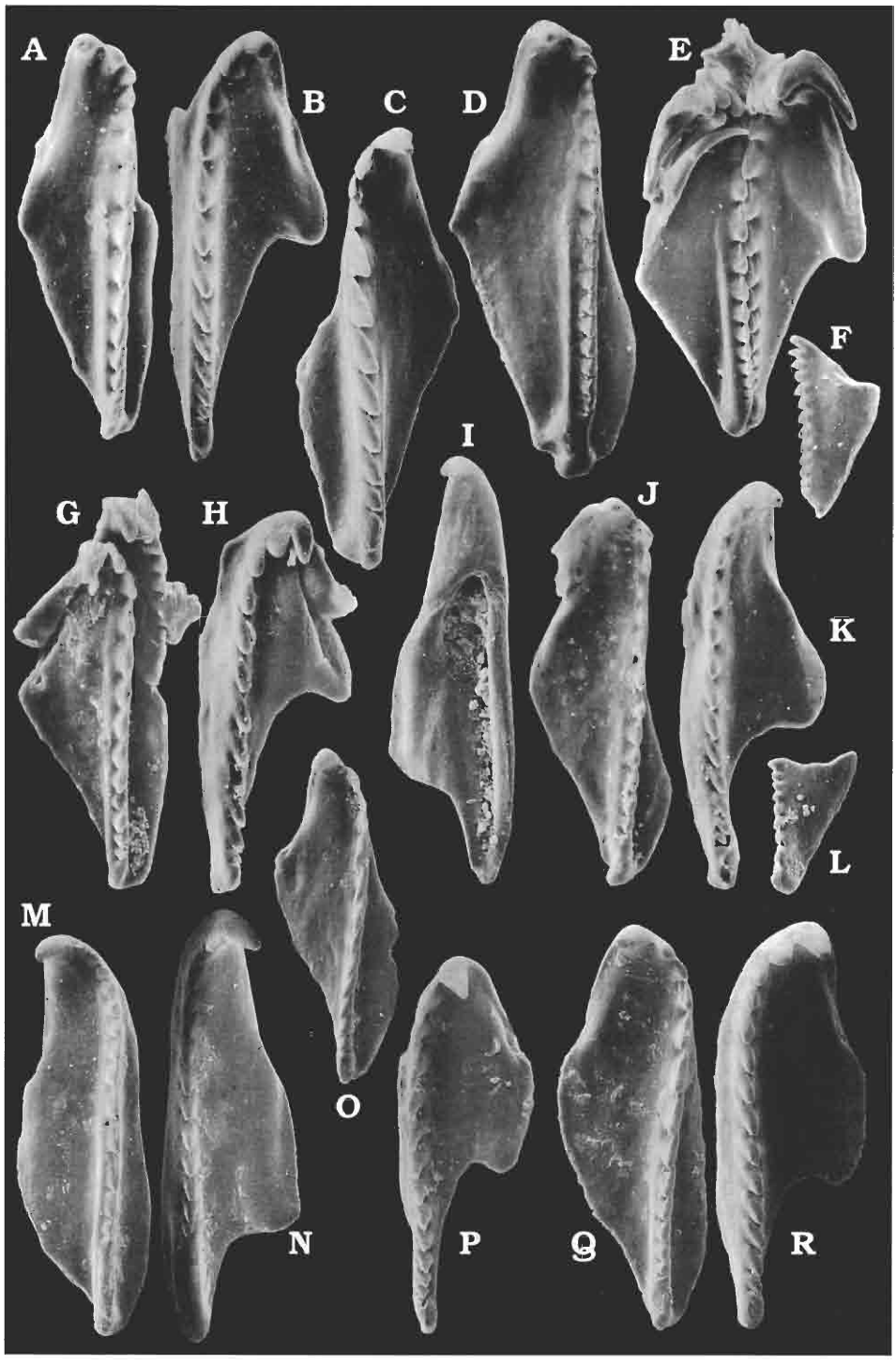
Description. — Right MI: L = 0.25–0.70 mm, L/W = 2.8–3.4. Jaw commonly elongated, outer margin behind the ramus is nearly parallel to the dentary. Ramus extends to 0.60–0.75 of jaw length from posterior. Inner margin runs along the dentary which has 13–16 posteriorly decreasing denticles. Ligament scar on outer side of shank is relatively prominent. Cover extends to about 0.2 of jaw length.

Left MI: L = 0.25–0.60 mm, L/W = 2.2–2.6. Outer wing nearly convex or slightly sigmoidal with its maximum lateral extension in the middle of the jaw. Convex inner wing is long, extends to 0.75–0.8 of jaw length from posterior. Anterior and posterior parts of the inner wing are smooth, without any strong incurvature. Greatest width of the inner wing is up to one-fifth of jaw width and it in the posterior quarter of jaw. Dentary usually comprises 12–16 posteriorly decreasing denticles. Prominent ligament scar occurs posteriorly on outer side of ridge. Cover extends to 0.25–0.30 of jaw length.

Remarks. — *Polychaetaspis* sp. A is most similar to *P. latus* and *Polychaetaspis* sp. a of Kielan-Jaworowska (1966), but differs from them in having smoother inner and outer margins of both posterior maxillae. In addition, it has a maximum width of the MI around the mid-length whereas *P.*

→

Fig. 10. Polychaetaspidae. **A–C**. *Polychaetaspis* cf. *wyszogrodensis*. **A**. Left MI, GIT Sc 17, dorsal view, × 100, Metsküla (F-198), 10.8 m, Rakvere Stage. **B**. Right MI, GIT Sc 16, dorsal view, × 140, Metsküla (F-198), 10.8 m, Rakvere Stage. **C**. Abnormal right MI, GIT Sc 15, dorsal view, × 125, Rapla, 111.3 m, Rakvere Stage. **D**. *Polychaetaspis tuberculatus*. Left MI, GIT Sc 20, dorsal view, × 65, Apraksin Bor, 105.5 m, Keila Stage. **E–H**. *Polychaetaspis gadomskae*. **E**. Apparatus, GIT Sc 18, dorsal view, × 125, Värsso (F-362), 112.05 m, Idavere Stage. **F**. Basal plate from the same apparatus, dorsal view, × 125. **G**. Left MI+left MII+lt, GIT Sc 19, dorsal view, × 200, Värsso (F-362), 111.0 m, Jõhvi Stage. **H**. Right MI from the same specimen as previous, dorsal view, × 200. **I, M, N**. *Polychaetaspis* sp. B. **I**. Right MI, GIT Sc 25, ventral view, × 65, Apraksin Bor, 113.6 m, Keila Stage. **M**. The same specimen, dorsal view, × 65. **N**. Left MI, GIT Sc 26, dorsal view, × 50, Apraksin Bor, 112.95 m, Keila Stage. **J–L**. *Polychaetaspis varsoviensis*. **J**. Left MI, GIT Sc 22, dorsal view, × 125, Rapla, 149.7 m, Jõhvi Stage. **K**. Right MI from the same specimen, dorsal view, × 125. **L**. Basal plate from the same specimen, dorsal view, × 125. **O, P**. *Polychaetaspis latus*. **O**. Left MI, GIT Sc 21, dorsal view, × 150, Metsküla (F-198), 41.88 m, Jõhvi Stage. **P**. Right MI from the same specimen, dorsal view, × 150. **Q–R**. *Polychaetaspis* sp. A. **Q**. Left MI, GIT Sc 23, dorsal view, × 90, Apraksin Bor, 105.5 m, Keila Stage. **R**. Right MI, GIT Sc 24, dorsal view, × 110, Apraksin Bor, 104.15 m, Keila Stage.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latus has greatest width in front of the mid-length. The shank is shorter than that of *P. latus*. *Polychaetaspis* sp. A differs from *Polychaetaspis* sp. B in having stouter jaws, longer shank and a shorter toothless part of the ridge.

Variation of *Polychaetaspis*. sp. A concerns the L/W ratio of MI and extension of the ramus. The outline of the inner and outer wings is relatively stable.

Occurrence. — Idavere to Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia.

Polychaetaspis? sp. B.

Fig. 10 I, M, N.

Material. — Eight right MI and three left MI.

Localities. — Boreholes: Apraksin Bor, 105.5–115.5 m; Metsküla, 24.24–33.43 m; Rapla 147.9 m; Vaemla, 139.36 m.

Description. — Right MI: L = 0.24–0.97 mm, L/W = 2.7–3.4. Antero-lateral margin forms smooth incurvature at about anterior third of jaw. Ramus extends to 0.70–0.74 of jaw length, shank is short and strong. Dentary has 12–14 denticles, posteriormost part of the ridge is undenticulated along 0.15–0.25 of jaw length. Distinct ligament scar has the same length, or is slightly longer than edentulate ridge. Cover extends to 0.24–0.27 of jaw length. Myocoele opening sub-triangular.

Left MI: L = 0.43–1.17 mm, L/W = 2.7–2.9. Outer wing sigmoidal. Convex inner wing narrow, extending to mid-length of the jaw. Dentary similar to that in the right MI, edentulate ridge extends 0.22–0.28 of jaw length. Cover extends to 0.27–0.37 of jaw length.

Remarks. — The posterior maxillae of *Polychaetaspis*? sp. B. are similar to those of *Polychaetaspis* sp. A, but differ in being more elongated and having longer edentulate ridges. *Polychaetaspis*? sp. B is also similar to the species of *Incisiprion* in having elongated jaws, sub-triangular myocoele openings, and relatively long edentulate ridges and ligament scars. The differences concern the absence of distinct incisions of outer wings, notably shorter shank and convex outer wing in left MI instead of a sub-triangular outer wing as that of *Incisiprion*. In these respects *Polychaetaspis*? sp. B. may be an intermediate form between *Polychaetaspis* and *Incisiprion*.

Occurrence. — Keila Stage of the St. Petersburg region, Jõhvi and Keila stages of North Estonia.

Incisiprion gen. n.

'*Polychaetaspis*' (partim); Kielan-Jaworowska 1966: p. 96–97, pl. 16: 1, 2, text-fig. 8K.

Derivation of name: Lat. *incisus* – cut out, Gr. *prion* – a saw, referring the shape of posterior maxillae.

Type species: *Incisiprion incisus* (Kielan-Jaworowska, 1966) = '*Polychaetaspis*' *incisus* Kielan-Jaworowska, 1966.

Diagnosis. — *Incisiprion* differs from *Polychaetaspis* in having more slender posterior jaws, the outer margins of which are incised at mid-length, and in having more closed and sub-triangular myocoele openings. *Incisiprion* differs from *Kozlowskiprion* in having a shorter shank, incised outer margins and more closed, sub-triangular myocoele openings.

Remarks. — Kielan-Jaworowska (1966) has stated that '*Polychaetaspis*' *incisus* was attributed to genus *Polychaetaspis* provisionally due to the scanty material. Although the present author's material adds no new data on the construction of the jaw apparatus of *I. incisus*, closely related species motivate the erection of a new genus.

Stratigraphical and geographical range. — Caradoc of Baltoscandia.

Incisiprion incisus (Kielan-Jaworowska, 1966)

Fig. 11C, D.

'*Polychaetaspis*' *incisus* sp. n.; Kielan-Jaworowska 1966: pp. 96–97, pl. 16: 1, 2, text-fig. 8K.

Material. — More than 240 isolated posterior jaws.

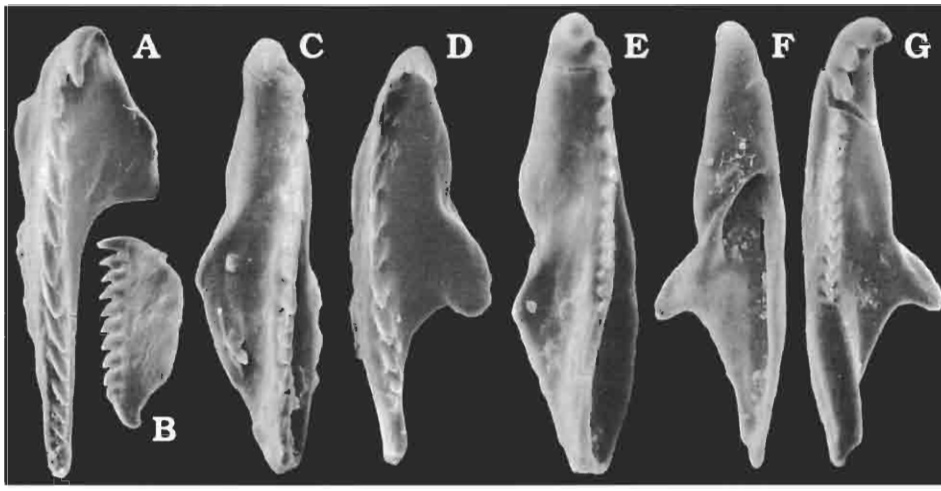


Fig. 11. Polychaetaspidae. **A**, **B**. *Kozlowskiprion brevialatus*. **A**. Right MI, GIT Sc 31, dorsal view, × 125, Apraksin Bor, 105.5 m, Keila Stage. **B**. Basal plate, GIT Sc 32, dorsal view, × 140, Apraksin Bor, 105.5 m, Keila Stage. **C–D**. *Incisiprion incisus*. **C**. Left MI, GIT Sc 27, dorsal view, × 140, Apraksin Bor, 105.5 m, Keila Stage. **D**. Right MI, GIT Sc 28, dorsal view, × 175, Apraksin Bor, 105.5 m, Keila Stage. **E–G**. *Incisiprion edentulus* sp. n. **E**. Left MI, GIT Sc 30, dorsal view, × 200, Apraksin Bor, 104.15 m, Keila Stage. **F**. Right MI, GIT Sc 29 (holotype), ventral view, × 175, Apraksin Bor, 107.05 m, Keila Stage. **G**. The same right MI as previous, dorsal view, × 175.

Localities. — Boreholes: Apraksin Bor 104.15–144.25 m, Metsküla 24.24–50.8 m, Rapla 126.3–156.47 m, Orjaku 129.07–133.0 m, Kuusiku 15.9–12.35 m, Hüti 133.78 m, Värsso 111.01 m, Vaemla 139.31–139.72 m.

Dimensions. — Right MI: L = 0.20–0.61 mm, L/W = 2.5–3.7; Left MI: L = 0.21–0.58 mm, L/W = 2.8–3.8.

Occurrence. — Idavere to Oandu and ?Rakvere stages of North Estonia, Idavere, Jõhvi and Keila stages of the St. Petersburg region, erratic boulders of ?Middle Ordovician and unknown age found in Poland.

Incisiprion edentulus sp. n.

Fig. 11E–G.

Holotype: Right MI, GIT Sc 29 (Fig. 11F, G).

Derivation of name: Lat. *edentulus* – toothless, referring to long undenticulated part of the ridge.

Type locality and type stratum: Apraksin Bor borehole, depth 107.05 m, the St. Petersburg region; Keila Stage, Caradoc.

Material. — Eight right MI, two left MI.

Locality. — Apraksin Bor borehole, 115.5–105.5 m.

Diagnosis. — Posterior maxillae of *Incisiprion edentulus* differ from those of *I. incisus* in having comparatively smaller denticles, more pointed ramus and pointed shank. Toothless parts of the ridges and prominent ligament scars in both MI extend farther than 1/4 of jaw length in *I. edentulus* instead of typically less than 1/5 in *I. incisus*.

Description. — Right MI: L = 0.26–0.47 mm, L/W = 2.5–3.3. Antero-lateral margin incised at two thirds of its length. Ramus distinct, more or less pointed and directed postero-laterally at about 45°, reaching to 0.62–0.70 of jaw length. In right lateral view ramus is bent upwards. Shank triangular with pointed tip, its outer margin straight. Dentary consists of 11–14 comparatively small denticles,

which significantly decrease in size posteriorly. Posterior 0.26–0.39 of ridge undenticulated, thicker and provided with very long ligament scar on outer lateral side. Posterior part of ridge inclined laterally. Cover extends to 0.30–0.39 of jaw length.

Left MI: L = 0.27–0.31 mm, L/W = 2.7–3.2. Outer margin incised around middle part of jaw. Maximum width of outer wing located at anterior 0.63–0.66 of jaw length. Inner margin runs along dentary then curves to inner wing, which reaches to about 0.4 of jaw length from posterior. Width of inner wing up to one third of jaw width. Dentary similar to that in right MI. Posteriormost part of ridge thicker and undenticulated in 0.30–0.35 of jaw length. Ligament scar prominent, as long as toothless part of ridge. Cover extends to 0.45 and 0.48 of jaw length.

Remarks — The variability of *I. edentulus* is expressed in the number and size of denticles, extension of ramus and length of the toothless part of the ridge.

Occurrence. — The Keila Stage of the St. Petersburg region.

Kozlowskiprion Kielan-Jaworowska, 1966

Type species: *Kozlowskiprion brevialatus* Kielan-Jaworowska, 1966.

Kozlowskiprion brevialatus Kielan-Jaworowska, 1966

Fig. 11A, B.

Kozlowskiprion brevialatus sp. n.; Kielan-Jaworowska 1966: pp. 101–102, pl. 21, text-fig. 8J.

Material. — More than 80 isolated posterior maxillae, several basal plates, one strongly compressed jaw apparatus.

Localities. — Boreholes: Apraksin Bor 105.2–111.5 m, Metsküla 22.0–47.88 m, Sibila 95.1–95.3 m, Rapla 126.3–147.9 m, Orjaku 129.5–135.6 m, Hüti 133.78–134.33 m, Värsso 110.35–112.05 m, Vaemla 140.81 m.

Dimensions. — Right MI: L = 0.25–0.75 mm, L/W = 2.7–3.4; Left MI: L = 0.3–0.6 mm, L/W = 2.8–3.6.

Occurrence. — ?Middle Ordovician erratic boulders found in Poland, Keila stage of the St. Petersburg region, Idavere to Oandu stages of North Estonia.

Polychaeturidae Kielan-Jaworowska, 1966
Polychaetura Kozłowski, 1956

Type species: *Polychaetura gracilis* Kozłowski, 1956.

Polychaetura gracilis Kozłowski, 1956

Fig 12A–D.

Polychaetura gracilis n. sp.; Kozłowski 1956: pp. 192–195; figs 17, 18.
Polychaetura gracilis Kozłowski; Kielan-Jaworowska 1966: pp. 103–105, pl. 22, pl. 23: 3–7, text-fig. 8L.

Material. — More than 800 posterior maxillae, 6 more or less complete apparatuses, several fused jaws.

Localities. — Boreholes: Apraksin Bor 144.15–104.15 m, Metsküla 50.8–10.8 m, Rapla 156.47–111.3 m, Orjaku 137.2–129.5 m, Kuusiku 15.8–12.35 m, Kautla 94.4–92.8 m, Rooküla 41.7–38.6 m, Sibila 95.75–94.10 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 139.31–140.81 m.

Dimensions. — Right MI: L = 0.15–0.55 mm, L/W = 2.0–3.1; Left MI: L = 0.20–0.45 mm, L/W = 2.2–2.7.

Occurrence. — ?Middle Ordovician erratic boulders found in Poland, Idavere to Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia.

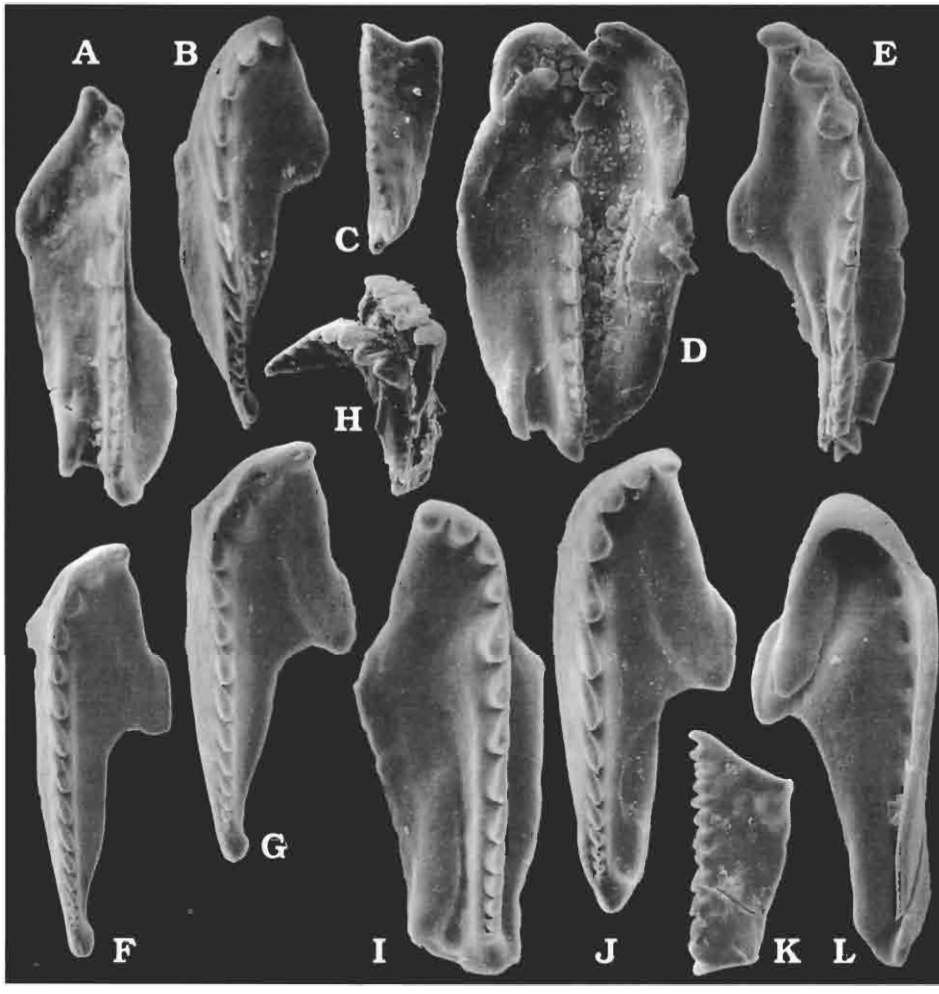


Fig. 12. Polychaeturidae. **A–D**. *Polychaetura gracilis*. **A**. Left MI, GIT Sc 40, dorsal view, × 150, Apraksin Bor, 104.15 m, Keila Stage. **B**. Right MI from the same apparatus, dorsal view, × 150. **C**. Basal plate from the same apparatus, dorsal view, × 150. **D**. Apparatus, GIT Sc 41, dorsal view, × 150, Apraksin Bor, 144.25 m, Idavere Stage. **E–G**. *Polychaetura* sp. A. **E**. Left MI, GIT Sc 39, dorsal view, × 140, Rapla, 111.3 m, Rakvere Stage. **F**. Right MI, GIT Sc 37, dorsal view, × 75, Rapla, 111.3 m, Rakvere Stage. **G**. Right MI, GIT Sc 38, dorsal view, × 175, Rapla, 111.3 m, Rakvere Stage. **H–L**. *Polychaetura kielanae* sp. n. **H**. Right MII+right MIV, GIT Sc 34 (from the same apparatus as I.), dorsal view, × 140. **I**. Left MI, GIT Sc 34, dorsal view, × 140, Metsküla (F-198), 31.35 m, Keila Stage. **J**. Right MI, GIT Sc 33 (holotype), dorsal view, × 100, Vaemla (F-364), 138.36 m, Jõhvi Stage. **K**. Basal plate, GIT Sc 36, dorsal view, × 125, Apraksin Bor, 144.25 m, Idavere Stage. **L**. Right MI, GIT Sc 35, ventral view, × 125, Rapla, 135.15 m.

Polychaetura kielanae sp. n.

Fig. 12H–L.

'*Polychaetura*' sp. a, Kielan-Jaworowska 1966: pp. 105–106, pl. 23: 1, 2.

Holotype: Right MI GIT Sc 33, Fig. 12J.

Derivation of name: Named in honor of Professor Zofia Kielan-Jaworowska, who first described this species.

Type locality and type stratum: Vaemla borehole, depth 139.31 m, North Estonia; Keila Stage, Caradoc.

Material. — One apparatus consisting of left MI, broken right MI, right MII, right MIII; one right MI fused with basal plate, more than 80 isolated posterior maxillae; two isolated basal plates.

Localities. — Boreholes: Apraksin Bor 144.25 m, Metsküla 49.49–24.24 m, Rapla 126.9–153.1 m, Orjaku 133.62–136.59 m, Hüti 133.35–134.33 m, Värsso 109.02–112.05 m, Vaemla 139.31–140.81 m.

Diagnosis. — *Polychaetura kielanae* differs from *P. gracilis* in having a wider posterior maxillae, straight posterior margin (incurved in *P. gracilis*) and longer inner wing in left MI. The shank of the right MI of *P. kielanae* has sub-rectangular outline instead of triangular as in *P. gracilis*.

Description. — Right MI: L = 0.24–0.68 (average 0.45) mm, L/W = 1.8–2.9 (2.3). Outer margin runs at first postero-laterally and has small smooth concavity in the first quarter of jaw length. Ramus extends to 0.46–0.58 (0.52) of total jaw length. Outer margin of ramus has convex extension, where the jaw wall is somewhat thinner. Tip of ramus commonly somewhat pointed. Outer margin of shank almost parallel to dentary, outer wing extends to posterior end of jaw. Posteriormost part of ridge is curved outwards, forming a small concavity. Width of wing on shank is 0.25–0.40 of jaw width. Dentary comprises 11–15 denticles, somewhat larger in middle part of ridge. Cover usually extends to less than 0.1 of jaw length.

Left MI: L = 0.21–1.38 (0.44) mm, L/W = 1.6–2.9. Sub-triangular outer wing has its maximum width at 0.35–0.5 of jaw length from anterior. Sub-rectangular inner wing occupies 0.55–0.75 of jaw length and commonly has smooth concavity in posterior part. Posterior margin straight, directed sub-transversally, length 0.5–0.8 of jaw width. Dentary with 12–15 denticles similar to that of right MI. In inner slope, close to inner wing, the boundaries between denticles are visible and remind rounded hollows. Cover extends to about 0.1 of jaw length.

Basal plate: L = 0.24–0.26 mm, L/W = 2.0–2.4. Length of trapezoidal jaw in apparatus is about half of right MI. Postero-laterally directed anterior margin 1.5–1.6 times longer than posterior margin. Dentary comprises 12 denticles, increasing in size posteriorly. Cover extends to about half of jaw width.

Remarks — The variation of the posterior maxillae includes the size and L/W ratio and the shape of inner and outer wings whereas the denticulation and the shape of posterior ends of both jaws are more stable.

Occurrence. — Idavere Stage of St. Petersburg region, Idavere to Keila stages of North Estonia.

Polychaetura sp. A

Fig. 12E–G.

Material — Three right and one left MI.

Locality. — Rapla borehole 111.3 m.

Description. — Right MI: L = 0.31–0.71 mm, L/W = 1.7–2.9. Antero-lateral margin has concavity at about first quarter of jaw length. Ramus extends to 0.47–0.52 of jaw length. Outer margin along shank directed posteriorly in first half of shank, then bends smoothly and is directed towards the end of the dentary. Small tubercle forms posteriormost part of jaw. Dentary consists of 12–13 denticles, first three oriented sub-transversally to posterior dentary resembling short ridges. Cover extends to 0.06 of jaw length.

Left MI: L = 0.4 mm, L/W = 2.4. Outer margin crest-like, with greatest extension at mid-length. Convex inner wing long (0.73 of jaw length). Posterior margin narrow (0.2 of jaw width). Dentary has 12 denticles, similar to those of right MI. Myocoele very slightly closed.

Remarks. — Posterior maxillae of *Polychaetura* sp. A are generally similar to *P. kielanae*, the main difference concerns the outline of the shank, which is triangular in *Polychaetura* sp. A, but sub-rectangular in *P. kielanae*. In the left MI, the differences include the posterior termination which is

notably narrower in *Polychaetura* sp. A. In addition, the sub-transversally prolonged anteriormost denticles are characteristic only for *Polychaetura* sp. A.

Occurrence. — Rakvere Stage of North Estonia.

Ramphoprionidae Kielan-Jaworowska, 1966

Ramphoprion Kielan-Jaworowska, 1962

Type species: *Ramphoprion elongatus* Kielan-Jaworowska, 1962.

Ramphoprion elongatus Kielan-Jaworowska, 1962

Fig. 13G–K.

Ramphoprion elongatus n. sp.; Kielan-Jaworowska 1962: pp. 315–318; pls 8–10.
Ramphoprion elongatus Kielan-Jaworowska; Kielan-Jaworowska 1966: pp. 108–109, pl. 25: 3.

Material. — Two right MI and two left MI.

Locality. — Rapla borehole 108.2–113.5 m.

Dimensions. — Right MI: L = 0.78–0.85 mm, L/W = 2.8–3.3; left MI: L = 0.82 mm, L/W = 2.9.

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

It is difficult to estimate the range of variability of *Ramphoprion elongatus*, however, there is one abnormal reversed specimen, where typical features of right jaw occur in the left position (Fig. 13K).

Occurrence. — Rakvere and Nabala stages of North Estonia.

Ramphoprion bialatus sp. n.

Fig. 13A–F.

Holotype: Right MI GIT Sc 43, Fig. 13D–E.

Derivation of name: Lat. *bis* – double, *alatus* – winged, referring the presence of additional inner wing in the right MI.

Type locality and type stratum: Metsküla (F-198) borehole, depth 134.33 m, Idavere Stage, Caradoc.

Material. — More than 30 posterior maxillae, 3 left MII.

Localities. — Boreholes: Metsküla 26.62–50.8 m, Hüti 132.49–143.33 m, Värsso 109.02–112.05, Vaemla 138.36–140.81, Rapla 153.47–154.9.

Diagnosis. — *R. bialatus* differs from other ramphoprionids in having a more distinct, triangular inner wing with subtransversal anterior margin in right MI. Posterior maxillae differ from *R. elongatus* also in being comparatively wider.

Description. — Right MI: L = 0.37–0.66 mm, L/W = 2.6–3.5. Antero-lateral margin nearly straight. Ramus extends to 0.65–0.75 of jaw length from anterior. Inner margin runs along dentary until it reaches narrow and short triangular inner wing at 0.5–0.6 behind anteriormost point of jaw, then bends and continues almost straight towards the posterior end. Inner wing supports the right MII, which fits into longitudinal groove in the inner face just above the wing. Dentary consists of 15–21 denticles, anteriormost 3–5 typically more erect, sharper, and higher than following ones. Cover extends to 0.35–0.45 of jaw length.

Left MI: L = 0.19–0.53 mm, L/W = 2.4–2.7. Outer wing sub-triangular, maximum width located at 0.6 of jaw length from anterior. Sub-rectangular inner wing reaches about one-third of jaw length from posterior. Width of inner wing almost one-third of jaw width. Width of posterior termination about 0.6 of jaw width. Dentary with 22–28 denticles is similar to that of right MI. Cover extends to 0.45–0.55 of jaw length.

Left MII: Elongated jaw about two-thirds of length of left MI. Both ramus and shank narrow and pointed, shank being four times longer than ramus. Dentary consists of 11–14 denticles. Anteriormost dentices more slender and sharper than following ones. Compared to corresponding denticles in posterior jaws they are much bigger in MII.

Remarks. — Variation of *R. bialatus* includes the number of denticles, length/width ratio, direction of posterior margin and extension of the ramus.

Occurrence. — Idavere to Keila stages of North Estonia.

Ramphoprion peterburgensis sp. n.

Fig. 13L–S.

Holotype: Apparatus, consisting of right and left posterior maxillae, right MII, right MIV, basal plate and one lateral tooth, GIT Sc 52, Fig. 13L–S.

Derivation of name: After the St. Petersburg region where the species is found.

Type locality and type stratum: Apraksin Bor (17) borehole, 122.15 m, the St. Petersburg region; Jõhvi Stage, Caradoc.

Material. — One apparatus consisting of right and left posterior maxillae, right MII, right MIV, basal plate and one lateral tooth.

Locality. — Apraksin Bor borehole, 122.15 m.

Diagnosis. — *Ramphoprion peterburgensis* differs from other species of this genus in having almost parallel inner and outer margins in the anterior half of left MI. As compared to *R. elongatus* and *R. bialatus*, posterior jaws are wider with fewer denticles and shorter shank.

Description. — Right MI: L = 0.75 L/W = 2.4. Outer margin concave between anterior end and ramus, ramus extends to 0.7 of jaw length. Shank very wide in anteriormost part. Inner margin convex, its maximum width from dentary within first 0.55 of jaw length. Dentary with 13 denticles almost straight. Denticles, excluding fang, increase in size towards the sixth denticle from anterior and posterior. Cover extends to almost 0.45 of jaw length.

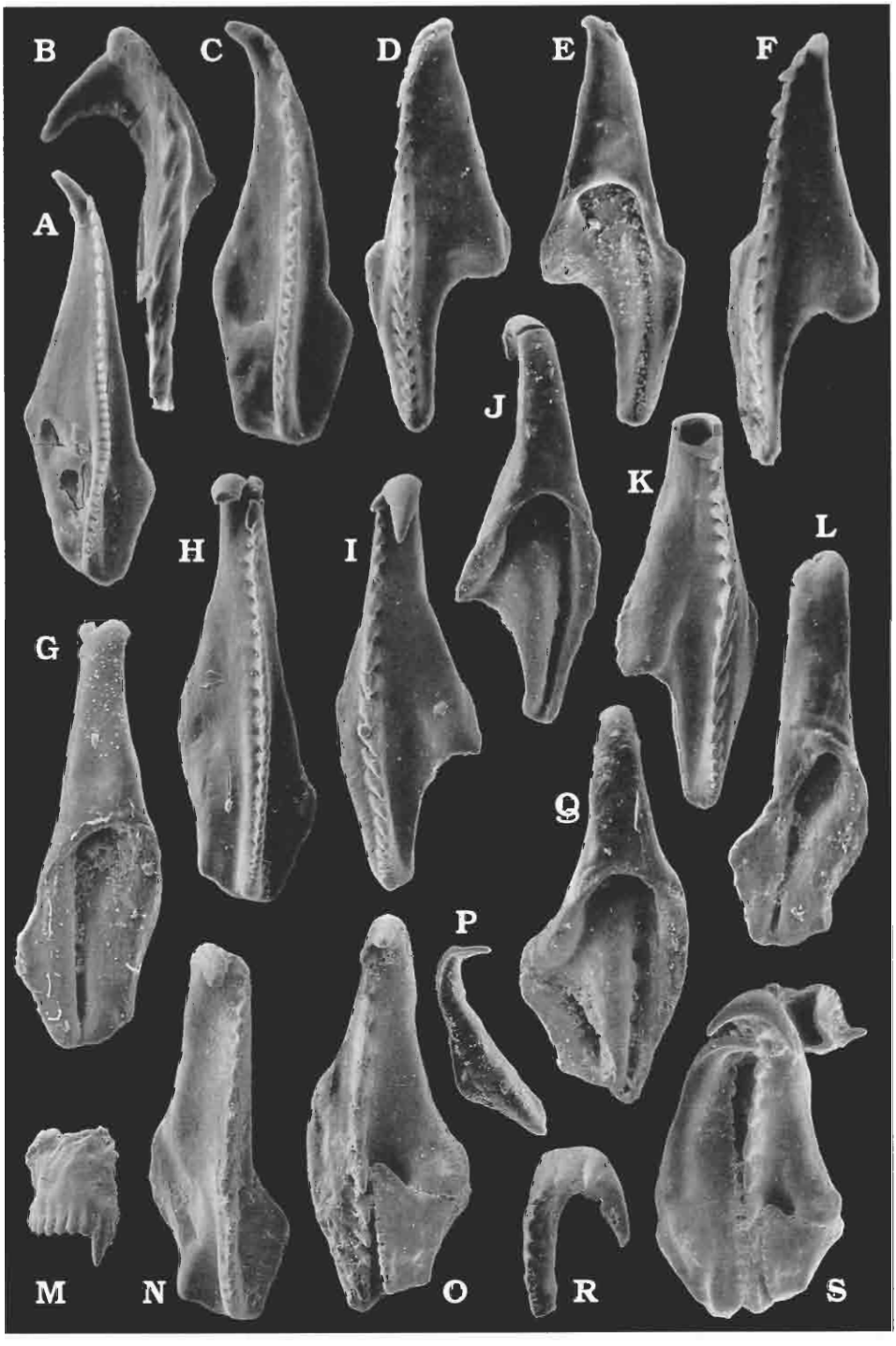
Left MI: L = 0.73 L/W = 2.5. Outer margin directed nearly posteriorly in anterior half of jaw, then forms convexity with maximum width in the 0.6 of jaw length, and runs posteriorly until meeting posterior margin. Inner margin parallel to dentary until it reaches inner wing within anterior two-thirds of jaw length. Inner wing wide (0.4 of jaw width), sub-rectangular with maximum lateral extension in first third of its length. Posterior termination as wide as 0.6 of jaw width. Dentary comprises 18 denticles which reach maximum size in central part. Cover extends to 0.6 of jaw length.

Basal plate: Length of sub-rectangular jaw equals one-third of right MI. Anterior margin two times longer than posterior margin. Anterior and outer margins concave, wide ramus directed antero-laterally. Dentary consists of 10 denticles of almost equal size.

Right MII: Jaw about 2.2 times shorter than right MI. Ramus pointed, shank with narrow outer wing two times longer than ramus and ends bluntly. Dentary comprises 10 denticles, which decrease in size posteriorly.

Right MIV: Jaw very high, with ramus and shank of equal length. Dentary consists of 7 denticles, the anteriormost large and pointed.

Fig. 13. Ramphoprionidae. **A–F.** *Ramphoprion bialatus* sp. n. **A.** Left MI, GIT Sc 47, dorsal view, × 150, Metsküla (F-198), 50.7 m, Idavere Stage. **B.** Left MII, GIT Sc 45, dorsal view, × 175, Hüti (F-358), 134.33 m, Idavere Stage. **C.** Left MI, GIT Sc 46, dorsal view, × 175, Metsküla (F-198), 50.7 m, Idavere Stage. **D.** Right MI, GIT Sc 43 (holotype), dorsal view, × 125, Metsküla, 42.0 m, Jõhvi Stage. **E.** The same right MI, ventral view, × 125. **F.** Right MI, GIT Sc 44, dorsal view, × 140, Hüti (F-358), 134.33 m, Idavere Stage. **G–K.** *Ramphoprion elongatus*. **G.** Left MI, GIT Sc 55, ventral view, × 75, Rapla, 108.2 m, Rakvere Stage. **H.** The same left MI, dorsal view, × 75; × 100. **I.** Right MI, GIT Sc 54, dorsal view, × 70, Rapla, 108.2 m, Rakvere Stage. **J.** The same right MI, ventral view, × 70. **K.** Abnormal left MI, GIT Sc 53, dorsal view, × 30, Rapla, 113.5 m, Rakvere Stage. **L–S.** *Ramphoprion peterburgensis* sp. n. All jaws from apparatus, GIT Sc 52 (holotype), Apraksin Bor, 122.15 m, Jõhvi Stage. **L.** Left MI, ventral view, × 75. **M.** Right MIV, × 75. **N.** Same as L., dorsal view, × 75. **O.** Right MI+bp, dorsal view, × 75. **P.** Right LtI, × 75. **Q.** The same right MI+bp as O., ventral view, × 75. **R.** Right MII, dorsal view, × 75. **S.** Apparatus before disjunction, dorsal view, × 60.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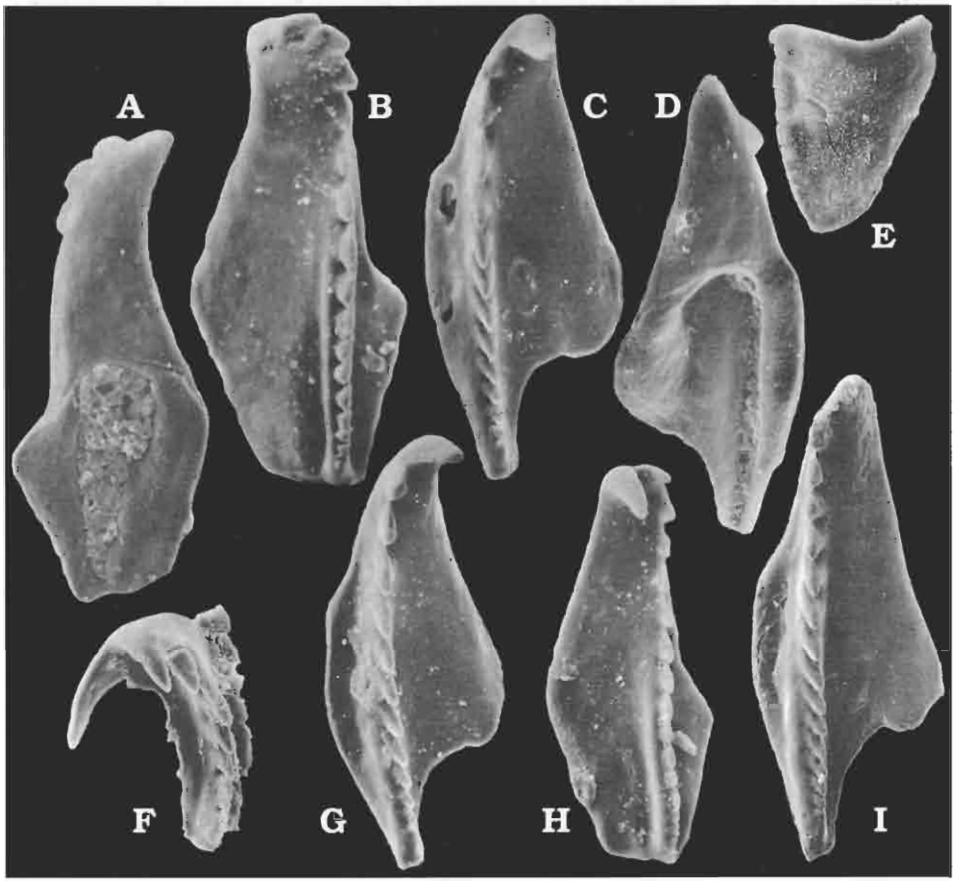


Fig. 14. Ramphoprionidae. **A–I**. *Ramphoprion* sp. A. **A**. Left MI, GIT Sc 65, ventral view, × 125, Metsküla (F-198), 45.8 m, Idavere Stage. **B**. The same left MI, dorsal view, × 125. **C**. Right MI, GIT Sc 64, dorsal view, × 140, Metsküla (F-198), 45.8 m, Idavere Stage. **D**. The same right MI, ventral view, × 140. **E**. Basal plate, GIT Sc 68, dorsal view, × 300, Värsso (F-362), 112.05, Idavere Stage. **F**. Left MII, GIT Sc 70, dorsal view, × 125, Rapla, 154.9 m, Idavere Stage. **G**. Right MI, GIT Sc 66, dorsal view, × 140, Metsküla (F-198), 45.8 m, Idavere Stage. **H**. Left MI, GIT Sc 67, dorsal view, × 175, Metsküla (F-198), 45.8 m, Idavere Stage. **I**. Right MI, GIT Sc 69, dorsal view, × 75, Apraksin Bor, 144.25 m, Idavere Stage.

Lt (right MI): strong tooth, almost of half length of right MI, myocoele opening occupies 0.45 of tooth's length.

Occurrence — Jõhvi Stage of the St. Petersburg region.

Ramphoprion sp. A

Fig. 14.

Material. — Two poorly preserved apparatuses, more than 500 detached left and right posterior maxillae.

Localities. — Boreholes: Apraksin Bor 105.2–144.25 m, Metsküla 20.9–50.8 m, Rapla 111.3–156.47 m, Orjaku 129.5–140.45 m, Sibila 94.3–95.4 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Description. — Right MI about 1.1 times longer than left jaw of same apparatus. Right MI: L = 0.14–0.70 mm, 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 mm, 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.

Basal plate: Jaw sub-triangular, length about one-third of the right MI. L/W ratio near 1. Anterior margin concave, ramus wide, posterior margin rounded. Dentary comprises 7 minute denticles covering anterior 0.6 of inner margin. Cover extends to 0.5 of jaw width.

Left MII: Length of jaw about half-length of left MI. Shank two times longer than ramus. Ramus slender, pointed and directed posteriorly. Denticles in slightly curved ridge decrease in size posteriorly.

Remarks. — *Ramphoprion* sp. A is different from other species in having relatively stout posterior maxillae, a short shank and a basal plate lacking a 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.

Ramphoprion sp. A is the most abundant ramphoprionid in the studied sections of North Estonia and the St. Petersburg region.

Occurrence. — Idavere to Rakvere stages of North Estonia, Idavere to Keila stages of the St. Petersburg region.

Ramphoprion sp. B

Fig. 15A–C.

Material. — One right MI and one left MI probably from the same apparatus.

Locality. — Metsküla borehole, 26.62 m.

Description. — Right MI: L = 1.5 mm, L/W = 2.9. Outer margin strongly concave in anterior half of jaw. From mid-length outer margin continues subparallel to dentary up to maximum extension of ramus at two-thirds of jaw length. Almost straight dentary consists of 17 denticles. Anteriormost two denticles markedly bigger than following ones. Following denticles increase in size towards the sixth denticle from anterior and posterior. Cover extends to 0.37 of jaw length.

Left MI: L = 1.4 L/W = 2.9. Outer margin concave from anterior to maximum width of outer wing (at about anterior 0.65 jaw length), then bends and runs toward posterior margin. Sinusoidal inner wing long and narrow, representing around quarter of jaw width. Posterior margin subperpendicular to ridge, representing 0.6 of jaw width. Dentary comprises 21 denticles, anteriormost three denticles larger than following ones. Cover extends to 0.5 of jaw length.

Remarks. — Right MI of *Ramphoprion* sp. B is most similar to *Ramphoprion* sp. C, although it lacks a pointed ramus and has a more gently concave outer margin in the first half of jaw. The left jaw is characteristic in having a long and narrow sinusoidal inner wing.

Occurrence. — Keila Stage of North Estonia.

Ramphoprion sp. C

Fig. 15D–H.

Material. — Four right MI and two left MI.

Localities. — Boreholes: Apraksin Bor 105.2–113.6 m, Rapla 111.3–126.3 m.

Description. — Right MI: L = 0.40–1.95 mm, L/W = 2.3–2.8. Outer margin between anterior end and ramus strongly concave. Ramus extends to 0.6–0.7 of jaw length, distal part sub-rectangular or rounded, antero-laterally bent downwards. Bight open or very slightly closed. Shank very broad in its anterior part. Inner margin slightly subtrapezoidal. Dentary consists of 13–14 denticles. Cover extends to about 0.4 of jaw length.

Left MI: L = 1.4–1.5 mm, L/W = 2.5–2.8. Outer margin consists of two concave parts separated by somewhat pointed convexity in first 0.6 of jaw. Sinusoidal inner wing comprises 0.4 of posterior part of jaw with width about 0.35 of jaw width. Length of posterior margin is about 0.6 of jaw width. Dentary consists of 19–21 denticles, anteriormost three distinctly largerthan following ones. Cover extends to 0.5 of jaw length.

Remarks. — *Ramphoprion* sp. C is very similar to *Ramphoprion peterburgensis,* but differs from it in having a sinusoidal inner wing on left MI and subtrapezoidal shape of inner margin in the right MI. *Ramphoprion*. sp. C differs from other species in having a sub-rectangular or rounded ending of the ramus, a more convex posterior part of the outer margin anterior to the ramus, and a strongly convex posterior part of the outer margin of left MI.

Occurrence — Oandu and Rakvere stages of North Estonia, the Keila Stage of the St. Petersburg region.

Pararamphoprion Männil & Zaslavskaja, 1985

Type species: *Pararamphoprion urbaneki* (Kielan-Jaworowska, 1966).

Pararamphoprion urbaneki (Kielan-Jaworowska, 1966)

Fig. 15M–O.

Ramphoprion urbaneki sp. n.; Kielan-Jaworowska 1966: pp. 109–110, pl. 24: 1–3.

Material. — Five right MI and one left MI.

Localities. — Boreholes: Apraksin Bor 111.2–113.6 m, Sibila 95.75 m.

Dimensions. — Right MI: L = 1.35–2.1 mm, L/W = 2.6–2.7; left MI: L = 1.33 mm, L/W = 2.4.

Remarks. — Some of the right MI assigned to *Pararamphoprion urbaneki* herein differ slightly from the type specimen in having more strongly differentiated dentary, deeper bights and somewhat longer shank.

Occurrence. — Keila Stage of North Estonia and the St. Petersburg region, erratic boulders found in Poland.

Pararamphoprion sp. A

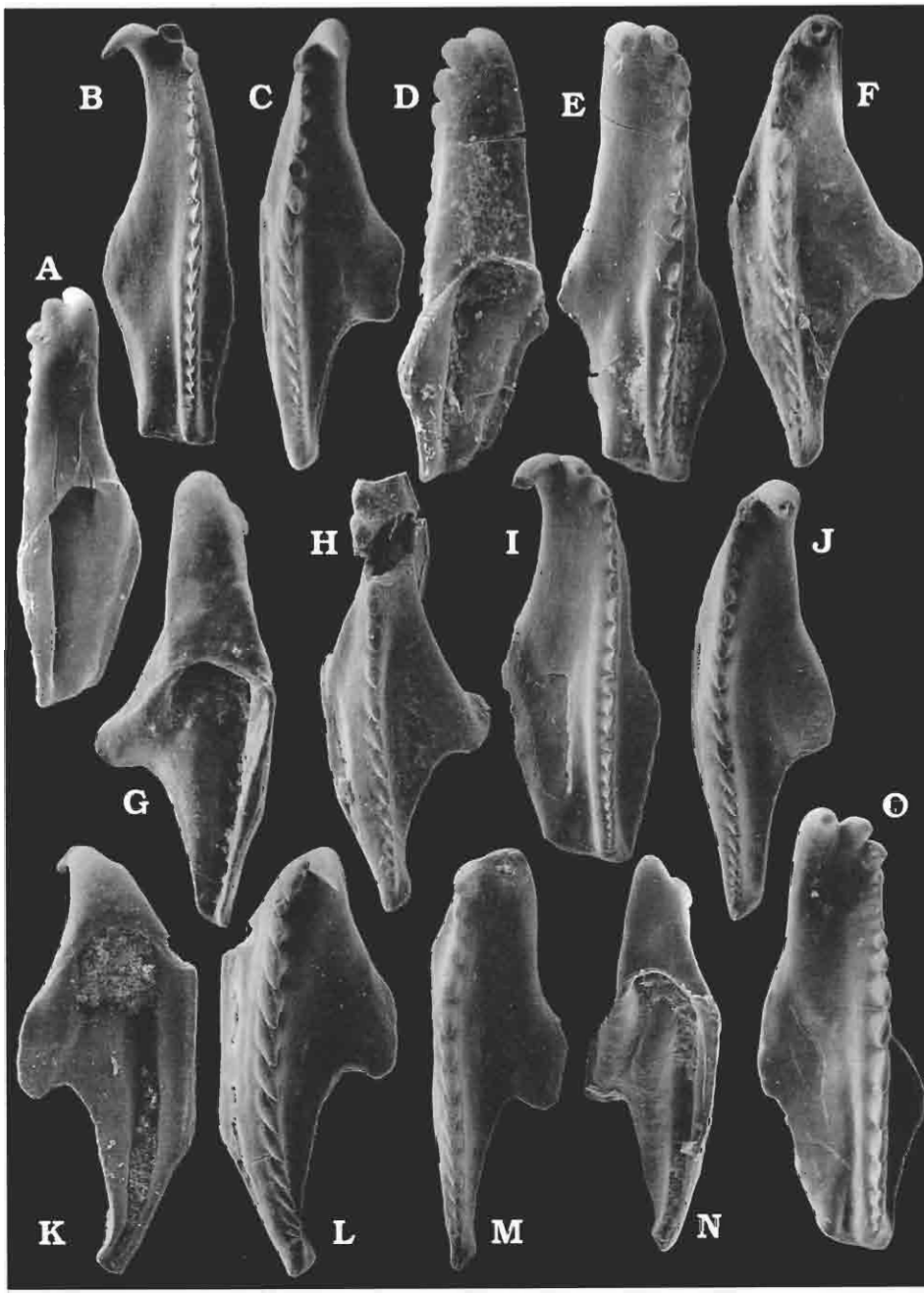
Fig. 15K, L.

Material. — One right MI.

Locality. — Värsso borehole, 110.35 m.

Description. — Right MI: L = 0.93 mm, L/W = 2.2. Outer margin directed postero-laterally in anterior third of jaw length, then turnes posteriorly and runs almost parallel to dentary. Ramus extends to 0.55 of jaw length. Inner face distinctly trapezoidal with distinct angles in anterior third and two thirds of jaw length. Dentary has 14 denticles, anteriormost two largest, followed by one small intermediate denticle and row of posteriorly decreasing denticles. Cover reaches to 0.22 of jaw length.

Fig. 15. Ramphoprionidae. **A–C**. *Ramphoprion* sp. B. All jaws from the same apparatus, GIT Sc 51, Metsküla (F-198), 26.62 m, Keila Stage. **A**. Left MI, dorsal view, × 40. **B**. The same left MI, ventral view, × 40. **C**. Right MI, dorsal view, × 40. **D–H**. *Ramphoprion* sp. C. **D**. Left MI, GIT Sc 58, ventral view, × 40, Apraksin Bor, 113.6 m, Keila Stage. **E**. The same left MI, dorsal view, ×40. **F**. Right MI, GIT Sc 57, dorsal view, × 50, Apraksin Bor, 105.5 m, Keila Stage. **G**. The same right MI, ventral view, × 50. **H**. Right MI, GIT Sc 60, dorsal view, × 40. **I, J**. *Pararamphoprion*? sp. B. **I**. Left MI, GIT Sc 48, dorsal view, × 30, Apraksin Bor, 144.25 m, Idavere Stage. **J**. Right MI from the same apparatus.



K, L. *Pararamphoprion* sp. A. **K.** Right MI, GIT Sc 62, ventral view, × 65, Värsso (F-362), 110.35 m, Jõhvi Stage. **L.** The same right MI, dorsal view, × 65. **M–O.** *Pararamphoprion urbaneki*. **M.** Right MI, GIT Sc 59, dorsal view, × 30, Apraksin Bor, 112.95 m, Keila Stage. **N.** Right MI GIT Sc 63, ventral view, × 40, Apraksin Bor, 112.95 m, Keila Stage. **O.** Left MI, GIT Sc 61, dorsal view, × 45, Apraksin Bor, 111.2 m, Keila Stage.

Remarks. — This specimen is almost identical to '*Grubia bifurca*' figured by Gries (1944: pl. 1: 3, 4). The difference is that *Pararamphoprion* sp. A has one intermediate denticle instead of two, and a somewhat longer shank. It resembles *P. urbaneki* in having similar shape of inner margin, ramus and myocoele. However, the right MI of *Pararamphoprion* sp. A is less elongate and has less denticles.

Occurrence. — Jõhvi Stage of North Estonia, Ordovician of North America.

Pararamphoprion? sp. B

Fig. 15 I, J.

Material. — One right, one left MI and one right MII probably from the same apparatus.

Locality. — Apraksin Bor borehole, 144.25 m.

Description. — Right MI: L = 1.95 mm, L/W = 2.8. Antero-lateral margin concave, maximum width of outer wing located at the middle part of jaw. Ramus indistinct, comprising 0.6 of jaw length from anterior. Dentary has 21 denticles, anteriormost two somewhat larger than following ones. Normal denticles reach maximum size in middle portion of ridge. Cover extends to 0.3 of jaw length.

Left MI: L = 1.8 mm, L/W = 2.4. Outer wing sub-triangular with maximum width in the anterior 0.55 of jaw length. Inner margin follows dentary until the rise to inner wing in mid-length of jaw. Posterior margin represents 0.6 of jaw width. Dentary comprises 23 denticles, three anteriormost denticles larger than following ones, posteriormost denticles very small. Cover extends for 0.4 of jaw length.

Right MII. Shaped as twisted horseshoe with length 0.45 of length of right MI. Relatively wide and pointed ramus half the length of shank. Dentary comprises 10 denticles, second denticle the largest. Size of following denticles decreases evenly toward posterior.

Remarks. — *Pararamphoprion*? sp. B differs from other species of this genus in having a ramus poorly differentiated from the other part of outer wing in the right MI and in having a more triangular inner wing and longer posterior margin of left MI. *Pararamphoprion?* sp. B is assigned to this genus provisionally.

Occurrence. — The Idavere Stage of the St. Petersburg region.

Kalloprionidae Kielan-Jaworowska, 1966

Kalloprion Kielan-Jaworowska, 1962

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

Kalloprion triangularis Kielan-Jaworowska, 1966

Fig. 16A, B.

Kalloprion triangularis sp. n.; Kielan-Jaworowska 1966: pp. 115–118, pl. 26, text-fig. 10D.

Material. — More than 70 isolated posterior maxillae, some joined jaws.

Localities. — Boreholes: Apraksin Bor 105.2–122.15 m, Metsküla 10.8–50.8 m, Rapla 111.3–156.0 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right MI: L = 0.30–0.60 mm L/W = 1.9–3.2; Left MI: L = 0.35–0.80 mm L/W = 2.6–3.

Occurrence. — Middle Ordovician erratic boulders found in Poland, Idavere to Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia.

Kalloprion sp. A

Fig. 16N.

Material. — One left MI.

Locality. — Metsküla borehole, 29.8 m.

Description. — Left MI: L = 0.37 mm L/W = 2.5. Outer wing sub-triangular, antero-lateral margin straight and postero-lateral margin irregular. Maximum width of jaw at anterior 0.6 of jaw length. Inner wing long, reaching to 0.55 of jaw length from posterior. Posterior margin straight and directed

transversely. Dentary comprises 8 denticles, anteriormost one forming hook of almost quarter of jaw length. Remaining 7 denticles more or less of equal size and arranged in straight row.

Remarks. — *Kalloprion* sp. A resembles *Kalloprion* sp. a Kielan-Jaworowska, 1966 but differs from it in having a more slender left MI with a longer hook and narrower inner wing. The left MI of *Kalloprion* sp. A differs from *K. ovalis* and *K. triangularis* in having a longer hook.

Occurrence. — Keila Stage of North Estonia.

Leptoprion Kielan-Jaworowska, 1966

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

Leptoprion artus? Kielan-Jaworowska, 1966

Fig. 16E–G.

Material. — More than 50 detached posterior maxillae, some joined jaws and one incomplete jaw apparatus.

Localities. — Boreholes: Apraksin Bor 105.2–122.15 m, Metsküla 10.8–49.49 m, Kuusiku 13.30 m, Sibila 95.7 m, Rapla 127.4–149.7 m, Orjaku 133.62–137.7 m, Hüti 133.35–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right MI: L = 0.20–2.45 mm, L/W = 2.1–2.5; Left MI: L = 0.30–0.65 mm L/W = 1.75–2.4. Length of the carriers is about 0.7 of MI length, their width is 0.4 of that left MI.

Remarks. — Specimens described herein are with some doubts assigned to *L. artus*.This is due to insufficient material, the unclear species level subdivision of the genus and the variability of the features that Kielan-Jaworowska (1966) considered of great diagnostic value.

Occurrence. — Middle Ordovician erratic boulders found in Poland, Idavere to Keila stages of the St. Petersburg region, Idavere to Rakvere stages of North Estonia.

Leptoprion sp. A

Fig. 16C, D.

Material. — One right MI.

Locality. — Rapla borehole, 145.6 m.

Description. — L = 1.35 mm, L/W = 2.3. Outer margin runs postero-laterally, then posteriorly and forms short ramus reaching 0.6 of jaw length. Inner wing continues in shank, which is comparatively wide but narrowing posteriorly. Inner face along dentary wide with maximum of 0.2 of jaw width. Posterior part of inner face bends below ridge, visible in posterior end like a separate knob. Well-developed hook represents 0.22 of jaw length. Dentary comprises 12 denticles, first denticle posterior to hook very small compared with others, which after the second decrease in size posteriorly. Cover extends for 0.27 of jaw length.

Remarks. — *Leptoprion* sp. A differs from *L. polonicus* and *L. artus* in having longer hook, longer shank and a wider outer face.

Occurrence. — Keila Stage.

Atraktoprionidae Kielan-Jaworowska, 1966

Atraktoprion Kielan-Jaworowska, 1962

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

Atraktoprion cornutus Kielan-Jaworowska, 1962

Fig. 16O, P.

Atraktoprion cornutus sp. n.; Kielan-Jaworowska 1962: pp. 304–306, pl. 1, text-fig. 3B.
Atraktoprion cornutus Kielan-Jaworowska; Kielan-Jaworowska 1966: pp. 133–134, pl. 31, text-figs 5P, 12B.
Atraktoprion robustus sp. n.; Kielan-Jaworowska 1966: pp. 134–135, pl. 36: 1, 2, text-fig. 12A.

Material. — Almost 200 detached posterior maxillae, some joined jaws and incomplete apparatuses.

Localities. — Boreholes: Apraksin Bor 104.15–144.25 m, Metsküla 22.7–50.8 m, Rapla 126.3–156.47 m, Sibila 94.4–94.6 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Dimensions. — Right MI: L = 0.30–0.60 mm, L/W = 2.0–2.5; Left MI: L = 0.35–0.60 mm, L/W = 2.4–2.8.

Remarks. — Due to their similar morphology and the wide range of variability observed, *A. robustus* is regarded as a junior synonym of *A. cornutus*.

Occurrence. — Middle Ordovician erratic boulders found in Poland, Idavere to Keila stages of the St. Petersburg region, Idavere to Oandu stages of North Estonia.

Atraktoprion major Kielan-Jaworowska, 1966

Fig. 16H–K.

Atraktoprion major sp. n.; Kielan-Jaworowska 1966: pp. 139–140, pl. 34, text-fig. 12D.

Material. — Over 20 isolated posterior maxillae, some MII, one basal plate.

Localities. — Boreholes: Metsküla 10.8–22.0 m, Rapla 108.65–124.5 m.

Dimensions. — Right MI: L = 0.65–1.10 mm, L/W = 2.2–2.4; Left MI: L = 0.40–1.25 mm, L/W = 2.3–2.5.

Occurrence. — Ordovician or Silurian erratic boulders found in Poland, Oandu and Rakvere stages of North Estonia.

Atraktoprion mirabilis Kielan-Jaworowska, 1966

Fig. 16L, M.

Atraktoprion mirabilis sp. n.; Kielan-Jaworowska 1966: pp. 137–138, pl. 32: 3, 4, pl. 33, text-fig. 12C.

Material. — Two left MI and one right MI.

Locality. — Rapla borehole, 107.25 m.

Dimensions. — Right MI: L = 0.6 mm, L/W = 2.8; Left MI: L = 0.6 mm, L/W = 2.8.

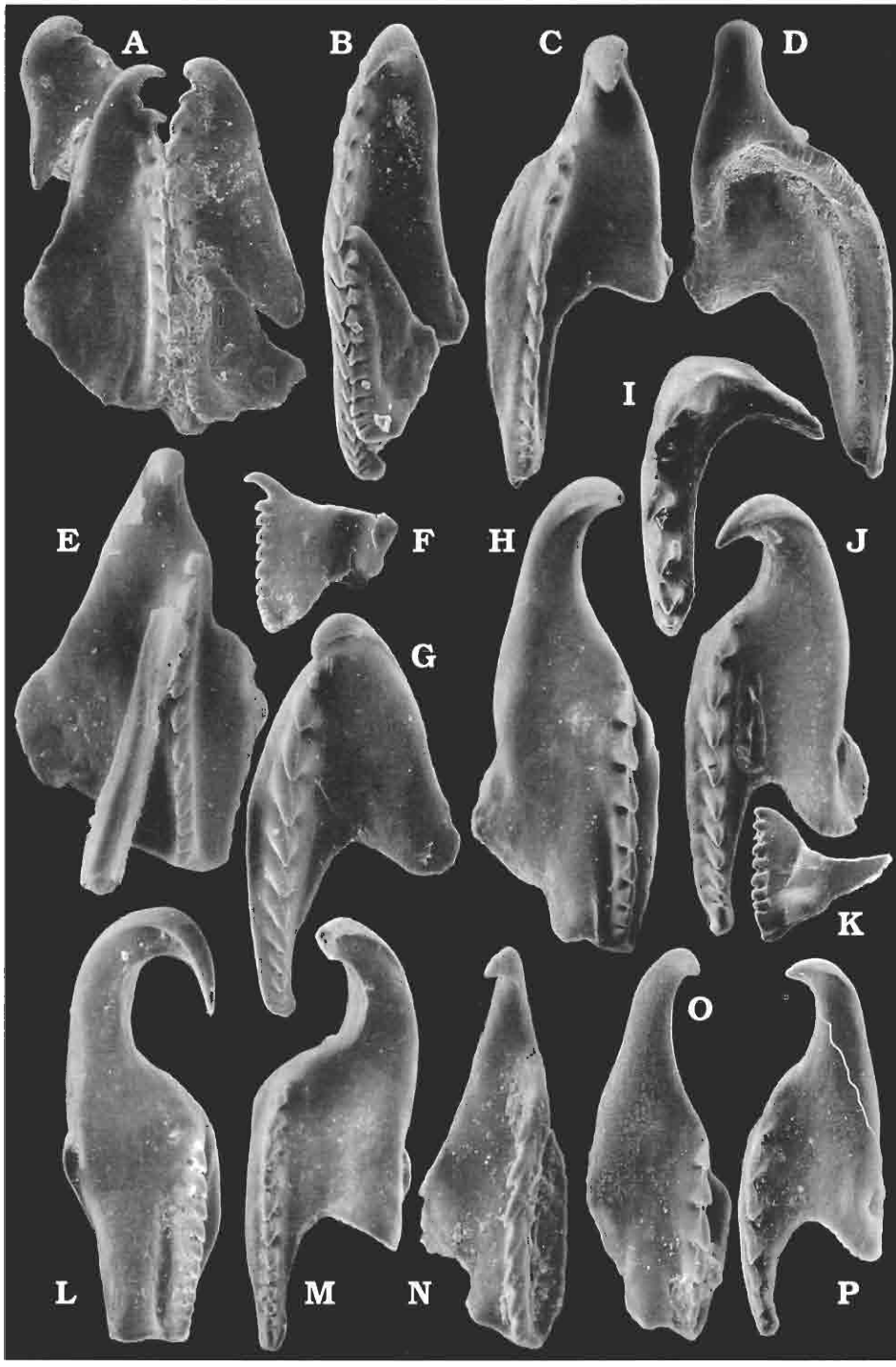
Occurrence. — ?Middle Ordovician erratic boulders found in Poland, Rakvere Stage of North Estonia.

Estonioprion gen. n.

Type species: *Estonioprion maennili* sp. n. herein.

Derivation of name: After Estonia, the study area where the taxon is found and Gr. *prion* – a saw.

Fig. 16. Kalloprionidae, Atraktoprionidae. **A**, **B**. *Kalloprion triangularis*. **A**. Apparatus, GIT Sc 71, dorsal view, × 70, Kuusiku, 11.77 m, Oandu Stage. **B**. Right MI+bp, GIT Sc 72, dorsal view, × 100, Metsküla (F-198), 47.75 m, Idavere Stage. **C**, **D**. *Leptoprion* sp. A. **C**. Right MI, GIT Sc 75, dorsal view, × 50, Rapla, 145.6 m, Keila Stage. **D**. The same right MI, ventral view, × 75. **E–G**. *Leptoprion artus*?. All jaws from the apparatus, GIT Sc 74, Orjaku, 141.8 m, Keila Stage. **E**. Left MI, dorsal view, × 125. **F**. bp, dorsal view, × 125; Right MI, dorsal view, × 125. **H–K**. *Atraktoprion major*. **H**. Left MI, GIT Sc 78, dorsal view, × 125, Rapla, 108.65 m, Rakvere Stage. **I**. Right MII, GIT Sc 79, dorsal view, × 140, Rapla, 120.0 m, Rakvere Stage. **J**. Right MI, GIT Sc 80, dorsal view, × 60, Rapla, 124.5 m, Rakvere Stage. **K**. Basal plate from the same apparatus, dorsal view, × 60. **L**, **M**. *Atraktoprion mirabilis*. **L**. Left MI, GIT Sc 81, dorsal view, × 100, Rapla, 108.2 m, Nabala Stage. **M**. Right MI, GIT Sc 82, dorsal view, × 100, Rapla, 108.2 m, Nabala Stage. **N**. *Kalloprion* sp. A. Left MI, GIT Sc 73, dorsal view, × 150, Metsküla (F-198), 29.8 m, Keila Stage. **O**, **P**. *Atraktoprion cornutus*. **O**. Left MI, GIT Sc 77, dorsal view, × 175, Metsküla (F-198), 45.8 m, Idavere Stage. **P**. Right MI, GIT Sc 76, dorsal view, × 175, Metsküla (F-198), 45.8 m, Idavere Stage.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Diagnosis. — Posterior maxillae of *Estonioprion* are generally similar to those of atraktoprionids, but differ from them in having dentary developed in form of knobs extending to the hook, long edentulate parts of the ridge in the shank, relatively higher ridges, the presence of a long inner wing in the right MI and wider hooks in MI. Posterior parts of the MI of *Estonioprion* also resemble some paulinitids, but the complete jaws differ from them in being less elongated.

Remarks. — In spite of the small number of speciemens of the type species of *Estonioprion* recovered, exceptional morphology of posterior maxillae suggests, at least genus-level distinctness. The relationships of *Estonioprion* with other jawed polychaetes are not known in any great detail. The shape of the posterior maxillae, long hooks and the presence of an unfused basal plate is similar to Atraktoprionidae. However, the above mentioned diagnostic features are not present in any atraktoprionid genera or species known so far. *Estonioprion* is provisionally assigned to Atraktoprionidae until more material is studied.

Stratigraphic and geographic range. — Caradoc of North Estonia.

Estonioprion maennili sp. n.

Fig. 17A–C.

Holotype: Right MI GIT Sc 83, Fig. 17B, C.

Derivation of name: Named in honour of the late Dr. Ralf Männil, who first collected specimens of this species.

Type locality and type stratum: Metsküla (F-198) borehole, depth 39.79 m, North Estonia; Jõhvi Stage, Caradoc.

Material. — Two right MI and one left MI.

Locality. — Metsküla borehole, 39.79 m.

Diagnosis. — As for the genus.

Description. — Right MI: L = 0.5–1.1 mm, L/W = 2.6–2.7. Strong and wide hook comprises 0.45–0.50 of jaw length, directed dorsally. Ramus extends to about anterior 0.75 of jaw, its outer margin sub-rectangular. Inner and outer margins of shank parallel to ridge. Narrow inner wing as wide as ridge. Ridge very high and distinct. Dentary begins on inner lateral side of hook in form of small protuberances, about 10 small knob-like denticles on ridge trend slightly posteriorly. On smaller specimen, denticles on ridge are indistinct. Ridge along shank undenticulated. Cover extends to 0.4–0.5 of jaw length, dental groove posteriorly very narrow and deep.

Left MI: L = 0.7 mm, L/W = 2.1. Strong and wide hook comprises 0.5 of jaw length, directed more or less dorsally. Outer margin evenly convex in anterior 0.8 of jaw length, then bends and runs parallel to dentary in posterior part of jaw. Small triangular, pointed extension occurs in anterior 0.6 of outer margin. Dentary very similar to that of right MI, consisting of 11 distinct denticles, begins in inner lateral side of hook in form of minute protuberances. Ridge high, posterior part smooth along 0.2 of jaw length from posterior. Cover extends for 0.43 of jaw length.

Remarks. — Left and right MI of *Estonioprion maennili* are grouped to one apparatus on the basis of the very similar and uniquely developed dentaries, and the presence of strong and wide hooks.

Occurrence. — Jõhvi Stage of North Estonia

Incertae familiae

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 great variability of the shape, the present author regards three of Eisenack's species as conspecific.

The apparatus arrangement of *Lunoprionella* is not known. Mierzejewski (1978a) includes this genus within the placognath Eunicida, and suggests it may be synonymous with an older genus of this group. However, the jaws of *Lunoprionella* apparently do not constitute minor elements of some

well-know species. Further, abundant jaws of *Lunoprionella* are found in samples lacking other scolecodonts of unknown affinity. Thus, they probably do not represent minor elements of some unknown apparatus type, but make up the main part of placognath jaw apparatus, which cannot be reconstructed so far.

Stratigraphical and geographical range. — Middle Ordovician of North Estonia and the St. Petersburg region, Ordovician erratic boulders found in Finland and Germany, and lower Silurian beds of Gotland.

Lunoprionella symmetrica Eisenack, 1975

Fig. 17F.

Lunoprionella symmetrica n. sp.; Eisenack 1975: p. 247, figs 38–40.
Lunoprionella asymmetrica n. sp.; Eisenack 1975: p. 247, figs 42, 43.
Lunoprionella sp.; Eisenack 1975: p. 247, fig. 44.

Material. — More than 100 detached posterior maxillae.

Localities. — Boreholes: Apraksin Bor 104.15–144.25 m, Metsküla 14.15–49.49 m, Rapla 122.2–48.7 m, Orjaku 131.0–141.8 m, Hüti 132.49–134.33 m, Värsso 109.02–112.05 m, Vaemla 138.36–140.81 m.

Remarks. — The variability of *L. symmetrica* includes the number and height of denticles, the size of the jaw, and the outline of the dentary. The latter feature varies from almost straight to semicircular.

Occurrence. — Lasnamägi to Rakvere stages of North Estonia, Idavere to Keila stages of the St. Petersburg region, Ordovician erratic boulders found in Germany and Finland.

'*Lunoprionella*' sp. A

Fig. 9B, F.

Material. — Four jaws (probably MI).

Localities. — Boreholes: Metsküla 13.25–20.9 m, Hüti 132.49 m.

Description. — Jaws very high forming one denticulated ridge with up to 40 small and slanting denticles. Borders between denticles prolonged to jaw wall, hence inner and outer face consist of numerous parallel lamellae. In outer(?) face these lamellae are separated from each other. 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 denticles of greater number and smaller size.. The relationships of '*Lunoprionella*' sp. A with type species cannot be proved and thus it is only tentatively assigned to this genus.

Occurrence. — Keila to Rakvere stages of North Estonia.

Gen. et sp. indet. A

Fig. 17G.

Material. — One right MI.

Locality. — Rapla borehole, 137.5 m.

Description. — Right MI: L = 0.56 mm, L/W = 2.8. Postero-lateral margin slightly convex. Ramus with wide and thin lateral extension reaches to 0.66 of jaw length from anterior. Width of inner face reaches about 0.2 of jaw width. Ridge almost straight, dentary comprises 21 densely spaced and posteriorly slanting denticles. Anteriormost denticle hook-shaped, being several times larger than following ones. Second denticle very small. Cover extends for 0.36 of jaw length.

Remarks. — Gen. et sp. indet. A shows some similarities with Kalloprionidae and Ramphoprionidae, but differs from former in having a more elongated shape and from Ramphoprionidae in having a small hook.

Occurrence. — Keila Stage of North Estonia.

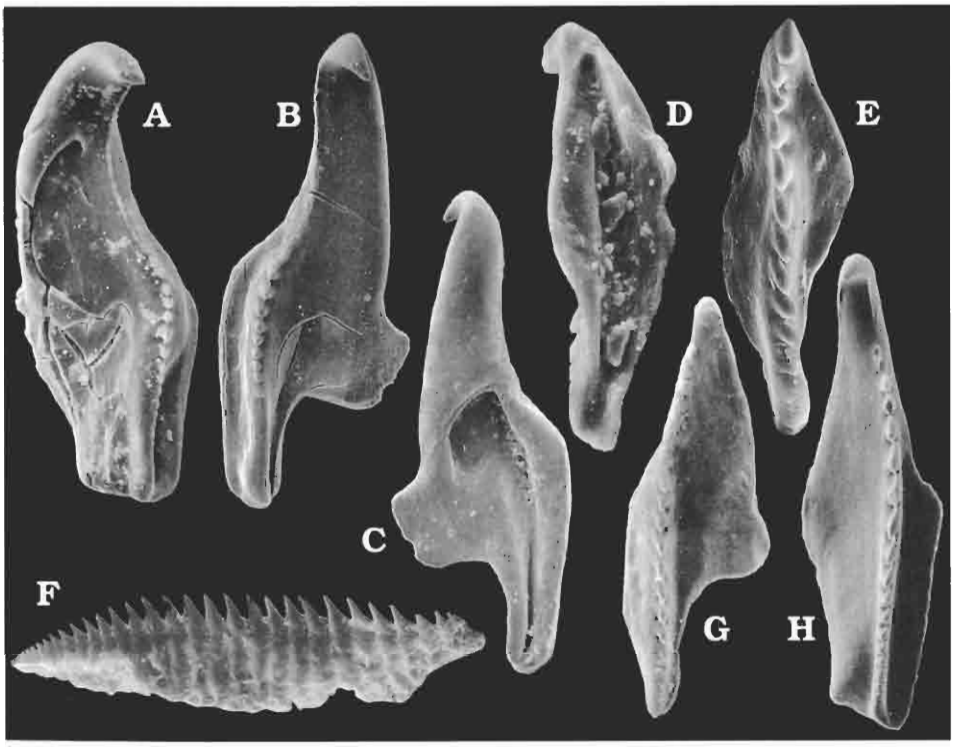

Fig. 17. Atraktoprionidae?, *incertae sedis*. **A–C**. *Estonioprion maennili* sp. n. **A**. Left MI, GIT Sc 84, dorsal view, × 85, Metsküla (F-198), 39.91 m, Jõhvi Stage. **B**. Right MI, GIT Sc 83, dorsal view, × 60, Metsküla (F-198), 39.91 m, Jõhvi Stage. **C**. The same right MI, ventral view, × 60. **D, E**. Gen. et sp. indet. C. **D**. Right MI, GIT Sc 87, ventral view, × 300, Apraksin Bor, 105.2 m, Keila Stage. **E**. Right MI, GIT Sc 88, dorsal view, × 200, Serebryaniki, 985.5 m, Keila Stage. **F**. *Lunoprionella symmetrica*. MI, GIT Sc 89, lateral view, × 80, Kuusiku, 15.94 m, Keila Stage. **G**. Gen. et sp. indet. A. Right MI, GIT Sc 85, dorsal view, × 100, Rapla, 137.5 m, Keila Stage. **H**. Gen. et sp. indet. B. Left MI, GIT Sc 86, dorsal view, × 85, Rapla, 114.8 m, Rakvere Stage.

Gen. et sp. indet. B

Fig. 17H.

Material. — One left MI.

Locality. — Rapla borehole, 114.8 m.

Description. — Left MI: L = 0.74 mm, L/W = 2.7. Outer wing sub-triangular. Inner wing long and rectangular, width about quarter of jaw width. Length of straight posterior margin nearly 0.5 of jaw width. Length of small hook 0.17 of jaw length. Dentary with 18 denticles extends anteriorly somewhat onto hook. Cover extends for 0.37 of jaw length.

Remarks. — Gen. et sp. indet. B resembles kalloprionids and ramphoprionids. It differs from kalloprionids in having a more elongated posterior jaw and from the ramphoprionids in having a small hook. It is possible that Gen. et sp. indet. B constitutes the left MI of Gen. et sp. indet. A, but insufficient material and the long stratigraphical interval between the specimens make such reconstruction uncertain.

Occurrence. — Rakvere Stage of North Estonia.

Gen. et sp. indet. C

Fig. 17D, E.

Material. — More than 20 right MI.

Locality. — Apraksin Bor borehole, 104.15–107.05 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 0.35–0.5 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. C may be notably different from that of well-known species. For instance, lack of bight probably exclude the typical occurrence of the basal plate.

Occurrence. — Keila Stage of the St. Petersburg region.

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Karadockie aparaty szczękowe wieloszczetów z północnej Estonii i regionu Petersburga

OLLE HINTS

Streszczenie

Z osadów późnego wiruanu (karadok) z ośmiu wierceń na obszarze północnej Estonii i z regionu Petersburga wydobyto liczne dobrze zachowane aparaty szczękowe wieloszczetów z rodziny Eunicidae. Ogółem oznaczono 46 gatunków wieloszczetów. Wyróżniono dwa nowe rodzaje: *Incisiprion*, z gatunkiem typowym *I. incisus* (Kielan-Jaworowska, 1966) i *Estonioprion*, z gatunkiem typowym *E. maennili*

sp. n. Opisano też pięć nowych gatunków: *Incisiprion edentulus, Polychaetura kielanae, Ramphoprion bialatus, Ramphoprion peterburgensis* i *Estonioprion maennili*. Ponadto w nomenklaturze otwartej opisano 17 nowych gatunków. Systematykę oparto na aparatach złożonych z kilku szczęk, lub zrekonstruowanych na podstawie izolowanych szczęk. Liczne gatunki znalezione w Estonii były poprzednio opisane z ordowickich głazów narzutowych Polski. Badana fauna wieloszczetów występuje w Estonii na obszarze wapiennego szelfu, na którym w ordowiku panowały korzystne warunki dla rozwoju tej grupy. Zasięgi stratygraficzne wielu badanych gatunków przekraczają interwał, z którego pochodzi badana fauna. Jednakże niektóre gatunki wydają się być ograniczone do określonych poziomów i mogą być użyteczne dla stratygrafii. Na podstawie zmian w zespołach wieloszczetów w poszczególnych poziomach karadoku, w pracy tej wyróżniono pewne poziomy stratygraficzne oparte na wieloszczetach, jak, np. warstwy przejściowe między piętrami Idavere i Jõhvi. Wiele gatunków wieloszczetów w karadoku było zapewne wspólnych dla regionu Bałtyckiego i Kanady.