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Early Devonian scolecodonts from Podolia, Ukraine

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One of the most fossiliferous and thickest sections of the marine Lower Devonian deposits was, for the first time investigated for the content of polychaete jaws (= scolecodonts). They are represented by elements of five genera and at least nine species but are not abundant and mostly fractured. Only a fraction of the specimens are sufficiently well preserved to allow genus and species-level identification. However, in some of them even the microstructure of the jaw wall can be observed. Over 90% of the determinable specimens are represented by the jaws of paulinitids which mostly belong to three species known from the Silurian of the Baltic region. Additionally, mochtyellids, atraktoprionids, skalenoprionids and, in the lower part of the sequence, polychaetaspids have been recorded. Two new species are established—*Polychaetaspis kozlowskii* sp. nov. and *Atraktoprion podolicus* sp. nov. Status of the genera *Oenonites* Hinde, 1879 and *Kettnerites* is discussed. Lectotype of the first is not determinable to the species level, while holotype of the type species of the second is probably missing and not determinable after the original illustration.

Key words: Polychaeta, scolecodonts, taxonomy, Lochkovian, Pragian, Silurian, Devonian, Podolia.

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Introduction

Scolecodonts (= fossil elements of the polychaete jaw apparatuses) are quite common in Paleozoic marine sediments and very useful for studies of polychaete evolution (Kielan-Jaworowska 1966; Wolf 1980; Szaniawski 1996; Beeslay et al. 2000). They are also suitable for paleogeography, facies recognition and to some extent for biostratigraphy (Bergman 1989; Eriksson 1997; Hints 1998, 2000; Hints and Eriksson 2007; Tonarova et al. 2012). However, the scolecodonts from Silurian–Devonian sequence of Podolia were hitherto completely unknown, despite the fact that deposits of the sequence are well exposed in many outcrops, possess great thickness and have been intensively studied since the 19th century (see Kozłowski 1929; Nikiforova et al.1972; Małkowski et al. 2009 for history of research).

The main aim of this study was recognition of the scolecodont abundance, preservation, distribution and taxonomic diversification in the whole Lower Devonian sequence of Podolia, which represents one of the thickest and best exposed successions of that age in the world. A few Silurian specimens found in one sample, just below the Silurian–Devonian boundary are also described. Present knowledge of the Devonian scolecodonts is limited mainly to old-fashioned publications in which taxonomy has been based upon individual elements only, although some articulated jaw apparatuses are also known (Lange 1949; Szaniawski and Wrona 1973). The comparatively poor knowledge of the Lower Devonian scolecodonts is partly due to the dominance of terrigenous sedimentation during that time interval, and the technical problems of their extraction from clastic rocks. Because of that the scolecodonts described here are compared mainly with the much better known Silurian forms, especially with the collections from the Baltic region described in many modern publications (see e.g., Eriksson et al. 2004).

Institutional abbreviations.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland; Sc.8, collection number; ZPAL Sc.8/14.5; the last two numerals indicate the number of the SEM stub and the specimen number on the stub. The sample numbers are preceded by the first letters of the section name, e.g., S.Dn.1 means: sample one from section Dnistrove.

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Historical background

A review of studies on the Devonian scolecodonts has been recently published by Eriksson et al. (2011). Most of the reported papers concern the Middle and Late Devonian collections while those describing the Early Devonian forms are rare. The first of papers devoted to Early Devonian polychaetes was published by one of the pioneers of the "apparatus based" taxonomy Frederico W. Lange (1947, English translation 1949) and possessed great importance for the further development of scolecodont studies. In that paper numerous articulated jaw apparatuses and natural assemblages of their elements preserved on the bedding planes of shale, were described from the Ponta Grossa Formation in Brazil. This well known, long studied (see Kozłowski 1913) and quite fossiliferous formation is presently recognized as Pragian–Emsian in age (Grahn 2011). Unfortunately almost all of the well preserved specimens of the collection belong to a single species—*Paulinites paranaensis* Lange, 1947. Based on this species a new genus *Paulinites* Lange, 1947 and the family Paulinitidae Lange, 1947 were also established. The author described later other species from the same formation—*P. caniuensis* Lange, 1950, but it differs from *P. paranaensis* mainly by its larger size, what according to Eriksson et al. (2011) is probably a result of intraspecific variability. Different elements of the jaw apparatuses of paulinitids were later identified in many collections. They belong to the most common scolecodonts in the Silurian and Devonian deposits.

Some years after the publication of the first paper by Lange (1947), three Lower Devonian taxa have been reported by Šnajdr (1951), in his important paper on the Lower Paleozoic scolecodonts from Bohemia, Czech Republic. However, no scolecodonts were reported from the "Lochkov Limestones". Magloire (1967) illustrated three well preserved polychaete jaws found in the Early Devonian borehole cores from Algerian Sahara. Two of them represent the first maxilla of paulinitids and are Lochkovian in age, and one, most probably element of atraktoprionids, is "Siegenian". In the same year Taugordeau (1967) described Silurian–Devonian scolecodonts from the Cotentin Peninsula in France; however, only one species of the collection, *Paulinites paranaensis* Lange, 1947, has been found in Lower Devonian deposits. Next year the same author published a paper about numerous Silurian–Devonian and Carboniferous scolecodonts from the borehole cores in the Sahara (Taugordeau 1968). Eighteen form species of the described collection were found in the Lower Devonian sediments. They represent mostly paulinitids and atraktoprionids. Unfortunately their detailed stratigraphic age is not known and some illustrations of the specimens are not sufficient for specific determination. Taugordeau and Gouget (1982) reported twelve Lower Devonian (Siegenian) form taxa from Viré-en-Champagne in France, which were represented mostly by the jaws of paulinitid apparatuses. Xiao-Rong (1994) in a paper on Upper Silurian and Devonian scolecodonts from West Qinling Mountains in China described some isolated jaws of Early Devonian

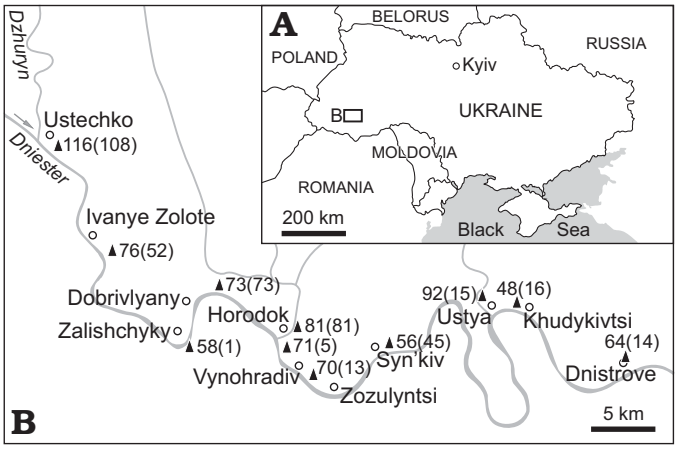


Fig. 1. **A**. General location of the study area. **B**. Locations of the sampled sections (triangles). Numbers of the sections after Nikiforova et al. (1972); in parenthesis numbers used by Drygant and Szaniawski (2012).

age. The elements belong to paulinitids and most probably to mochtyellids; however, they are not well preserved. Suttner and Hints (2010) reported the occurrence of the Late Emsian to Eifelian scolecodonts from the Graz region in Austria. Poor preservation of the material did not allow for certain determinations, but the fauna seems to be dominated by paulinitids.

Geological setting

The Lochkovian deposits in Podolia belong to the continuous Silurian–Devonian marine sedimentary sequence of the Dniester Basin. In the Lochkovian time the basin has been already in regression phase—gradually shrinking and shallowing (see Nikiforova et al. 1972; Małkowski et al. 2009; Drygant and Szaniawski 2012). The deposits have total thickness of about 530 m and are composed of interbedding layers of mudstone, argillite, siltstone, and limestone. They are exposed in the escarpments of Dniester River and its tributaries, beginning from the Silurian–Devonian boundary beds in outcrop 64 (Fig. 1) in the village Dnistrove (former name Volkovtsy) on the southeast and ending on the transitional beds from the open marine sediments to the Old Red type facies in the section 116 near the village Ustechko, in the northwest. The Lochkovian deposits are biostratigrapically subdivided into the Borshchiv, Chortkiv, and Ivanye horizons (Fig. 2), while lithostratigraphically into Khudykivtsi, Mytkiv, Chortkiv, and Ivanye formations (see Drygant 2010; Drygant and Szaniawski 2012). The first two formations belong to the Borshchiv Horizon. The limestone layers are most frequent and thickest in the lower part of the section (Khudykivtsi Formation), while in the upper part the terrigenous deposits are dominant and the limestone layers are thin. Generally the whole Lochkovian sequence is very fossiliferous and the fossils have been described in many publications (see Nikiforova et al. 1972). Nevertheless, the thick and well exposed Silurian–Devonian succession in Podolia requires

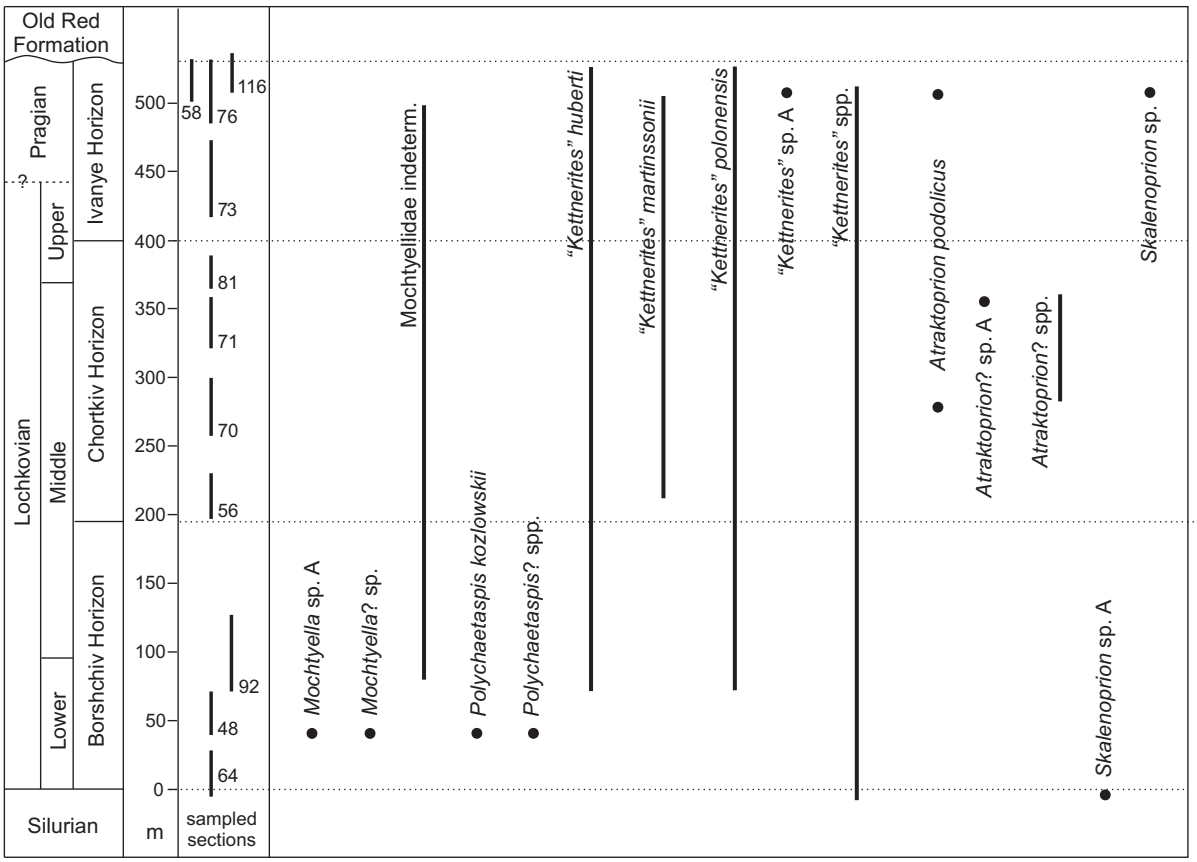


Fig. 2. Stratigraphic ranges of the described scolecodonts. Section numbers as in Fig. 1.

a modern and thorough investigation. Because of the political and economic problems of the country such studies were very limited for many years. In recent years a Polish-Ukrainian team of geologists and paleontologists have conducted extensive biostratigraphic, chemostratigraphic, and paleobiological investigations in Podolia. Many of the results have already been published (Małkowski et al. 2009; Baliński 2010, 2012; Drygant and Szaniawski 2012; Filipiak et al. 2012; Olempska et al. 2012; Olempska 2012; Racki et al. 2012; Voichyshyn and Szaniawski 2012). Independently important results of the Estonian-Ukrainian and exclusively Ukrainian investigations have been also published (Kaljo et al. 2007, 2012; Drygant 2010; Voichyshyn 2011).

Material and methods

The scolecodonts described herein were mainly collected during the search for conodonts described in our previous publication (Drygant and Szaniawski 2012). It does not mean, however, that all the samples processed for scolecodonts and conodonts were the same. Eleven sections representing the nearly whole marine Devonian sequence in Podolia have been sampled (Fig. 1). The lowermost sample was taken from the Silurian–Devonian transitional beds, and the uppermost from transitional beds to the Old Red facies (Fig. 2). The samples were collected only from the layers containing sufficient amount of calcium carbonate for processing in acetic acid. As a result the sampling density has been uneven. All microfossils preserved in the residues of dissolved samples were hand-picked. The commonly used methods in search for conodonts by selecting them from the residuum by its treatment with heavy liquids or separation of fossils by magnetic separator were not followed. In total 212 samples of 0.5–1.5 kg were processed, of which 71 contained determinable scolecodonts (SOM: fig. 1, Supplementary Online Material available at http://app.pan.pl/SOM/app59-Szaniawski_Drygant_SOM.pdf). However, despite very delicate processing, in many of the samples mainly fractured specimens were found. Such preservation is probably caused by turbulent depositional environment. Some of the scolecodonts were also cracked or partly covered with siliceous material. However, the inner structure of the scolecodonts has not been much altered and in some of the specimens their internal microstructure remained well preserved. Structures similar to that visible on the weathered surface of "*Kettnerites*" sp. (Fig. 3) have been observed earlier by Strauch (1973: pl. 1: 1) on the surface of the Triassic *Delosites raridentatus* Kozur, 1967, but studies of the internal microstructures are beyond the scope of the present paper.

In total about 350 comparatively well preserved scolecodonts were found, though, unfortunately they are exclusively isolated elements. They represent mostly the first, second and third maxillae, but some anterior jaws and mandibles

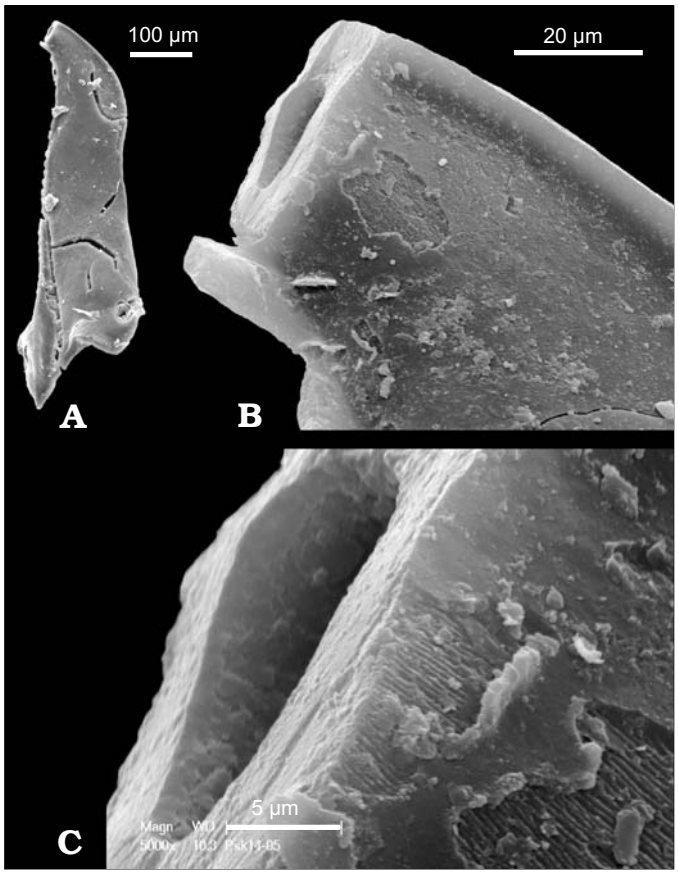


Fig. 3. Internal structure preserved on the weathered surface of the right MI of "*Kettnerites*" sp., ZPAL Sc.8/14.5, sample S.IZ.4 from Ivanye Horizon, Lower Pragian, Podolia.

are also preserved. Much more abundant are undeterminable fragments of different elements. The possibility for reconstruction of the jaw apparatuses based on the numerical data is limited because of the insufficient number of elements in individual samples, as well as their quite strong intraspecific differentiation. Presented reconstructions are based mainly on the morphological comparisons with the previously described Silurian apparatuses and their elements.

Terminology after Kielan-Jaworowska (1966) except for Paulinitidae, where Bergman (1989) is followed.

Systematic palaeontology

Class Polychaeta Grube, 1850

Family Mochtyellidae Kielan-Jaworowska, 1961

Genus *Mochtyella* Kielan-Jaworowska, 1961

Type species: *Mochtyella cristata* Kielan-Jaworowska, 1961, erratic boulder, Poland; Ordovician.

Remarks.—Isolated jaws of similar shape to MI of the genus *Mochtyella* were, in older literature, often assigned to *Staurocephallites* Hinde, 1879. However, in the type species of the genus—*S. niagarensis* Hinde, 1879 only one ridge of denticles is visible, while both MI of *Mochtyella* have two or three denticulated ridges. The difference is of generic rank (see Kielan Jaworowska 1961, 1966).

Mochtyella sp. A

Fig. 4A–C.

Material.—Three isolated right MI and one left (MI ZPAL Sc.8/2.1–3), sample S.Kh.1 from lower part of the Borshchiv Horizon, section 48, Lower Lochkovian, Podolia.

Description.—Right MI about 1.3 mm long, slightly compressed laterally, of about the same width in dorsal as in lateral view. The main ridge has 13 to 15 denticles, gradually decreasing in size posteriorly. The basal ridge extends for about one third of the jaw length, bears about nine small denticles which decrease in size posteriorly. Second ridge lacking. In right lateral view the basal ridge is directed postero-basally, not parallel to the main ridge. In the posterior margin of the inner wall a small, half circular incision occurs. Left MI, known from one incomplete specimen, has very similar denticulation of the main ridge to that present in the right MI.

Remarks.—Right MI of *Mochtyella* sp. A is similar to the *Mochtyella* sp. C of Kielan-Jaworowska (1966) but differs from it by lack of the secondary ridge.

Mochtyella? sp.

Fig. 4D.

Material.—One specimen (ZPAL Sc.8/2.2), sample S.Kh.1 from lower part of the Borshchiv Horizon, section 48, Lower Lochkovian, Podolia.

Remarks.—One specimen representing single tooth of the anterior teeth chain has been found in the same sample as all specimens of *Mochtyella* sp. A and possibly is conspecific with it. In all other samples the anterior teeth of mochtyellids were not found. The specimen has similar shape to the anterior teeth of the mochtyellids hitherto known (see Kielan-Jaworowska 1966: fig. 5), but differ from them in denticulation. Those illustrated in the cited paper are denticulated either on both margins, like *Mochtyella cristata* Kielan-Jaworowska, 1961 and *Vistulella kozlowskii* Kielan-Jaworowska, 1961 or lack the denticulation at all, like *Pistoprion transitans* Kielan-Jaworowska, 1966. The tooth found in Podolia is comparatively large and belonged probably to the posterior teeth of the left chain. It has a shape of wide, slightly curved spine with the upper margin outwardly arched and denticulated while the lower margin is inwardly arched and smooth. Somewhat similar detached teeth were assigned by Eller (1945) to the genus *Eunicites* Ehlers, 1868.

Gen. et sp. indet.

Fig. 4E, F.

Material.—3 specimens (ZPAL Sc.8/6.1, 8.18, 11.5), sample S.I.Z.13, section 76, Lower Pragian, Podolia.

Remarks.—The illustrated specimens, representing right and left MI of mochtyellids, have been found in one sample

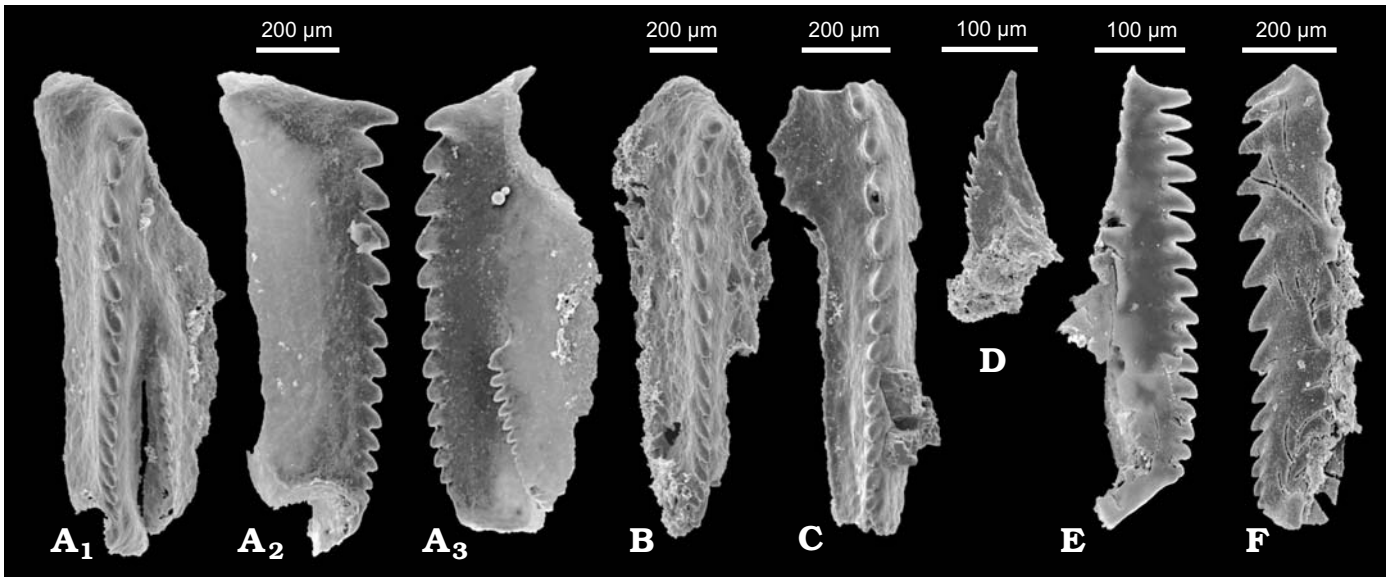


Fig. 4. SEM micrographs of mochtyellid scolecodonts from Podolia. **A**–**C**. *Mochtyella* sp. A, lower part of the Borshchiv Horizon, section 48, Lower Lochkovian, sample S.Kh.1. **A**. ZPAL Sc.8/2.1, right MI in dorsal (A_1), left lateral (A_2), and right lateral (A_3) views. **B**. ZPAL Sc.8/2.2, incomplete right MI in dorsal view. **C**. ZPAL Sc.8/2.3, incomplete left MI in dorsal view. **D**. *Mochtyella*? sp., anterior tooth; lower part of the Borshchiv Horizon, section 48, Lower Lochkovian, sample S.Kh.1, ZPAL Sc.8/2.21. **E**, **F**. Mochtyellidae gen. et sp. indet., undetermined elements MI, upper part of the Ivanye Horizon, section 76, Pragian. **E**. ZPAL Sc.8/11.5, sample S.IZ.13, incomplete right MI in left lateral view. **F**. ZPAL Sc.8/8.18, sample S.IZ.13, left MI in right lateral view.

S.IZ.13, from the upper part of the Ivanye Horizon, in section 76. They possibly belong to the same species. Both the jaws are laterally compressed and their denticulated ridge bear 14–15 denticles decreasing in size in the posterior part. Besides five other MI elements have been found in different levels of the Lochkovian sequence. They are differentiated morphologically and incompletely preserved.

Family Polychaetaspidae Kielan-Jaworowska, 1966

Remarks.—Scolecodonts of the family are very common in the Ordovician and Silurian. They still occur in the Devonion and Carboniferous but are not so abundant. They are well known from joined and reconstructed jaw apparatuses of the genera: *Polychaetaspis* Kozłowski, 1956, *Kozlowskiprion* Kielan-Jaworowska, 1966, *Dubichaetaspis* Eriksson, 1998 and *Incisiprion* Hints, 1998, as well as from many detached jaws described under different generic names. Similar jaw apparatuses to those of polychaetaspids are possessed also by the genus *Polychaetura* Kozłowski, 1956 (according to Hints and Eriksson [2010] younger synonym of *Pteropelta* Eisenack, 1939) but because of their distinct bifurcating carriers Kielan-Jaworowska (1966) established separate family Polychaeturidae. The relationship problem of the two families has been recently discussed by Hints and Eriksson (2010).

Genus *Polychaetaspis* Kozłowski, 1956

Type species: Polychaetaspis wyszogrodensis Kozłowski, 1956, erratic boulder, Poland; Ordovician.

Remarks.—Genus *Polychaetaspis* is known from numerous species which are based on rich material of joined jaw apparatuses (Kozłowski 1956; Kielan-Jaworowska 1966; Szaniawski and Wrona 1973; Hints 1998) as well as their reconstructions of isolated elements (Walliser 1960; Männil and Zaslavskaya 1985; Hints 1998). However, formal status of the genus has been questioned by Eriksson (1997). The author restudied the original collection of Hinde (1879) and came to the conclusion that *Polychaetaspis* should be treated as a junior synonym of *Oenonites* Hinde, 1879. In our opinion this proposition cannot be accepted because the singular specimen of its "lectotype"—*Oenonites curvidens* Hinde, 1879, designated by Jansonius and Craig only in 1971, is not determinable to the species level and should be treated as nomen dubium. The lectotype is "...based upon one right MI of inferior quality..." (Eriksson 1997: 217) which "... rests in a slide glued onto a piece of paper with the ramus facing the observer" (Eriksson 1997: 219). In result it can be seen well only in oblique dorsal view. Despite of its modern illustrations, presented by Eriksson (1997), the observable structural details are not sufficient for determination at the species level.

The genus *Oenonites* was originally established for nine species (Hinde 1879) but each of them is represented by a single specimen. The specimens are morphologically diverse and have been assigned to some different genera in later literature. It seems rather obvious that Hinde's concept of the genus *Oenonites* was completely different from that of *Polychaetaspis* because in his later publication (Hinde 1882) the very well preserved first maxillae of typical polychaetaspids were assigned not to *Oenonites* but to *Lumbriconereites* Ehlers, 1868 (e.g., *Lumbriconereites obliquus* Eichwald, 1854). The latter generic name has been later commonly used for detached MI of polychaetaspids. However, the type species of the genus—*L. deperditius* (Ehlers, 1868) has been

based on a body imprint preserved in Jurassic litographic limestone from Solnhofen and cannot be well compared with scolecodonts (see also Jansonius and Craig 1971).

Polychaetaspis kozlowskii sp. nov.

Fig. 5A–G.

Etymology: In honour of the great paleontologist and teacher Roman Kozłowski (1889–1977), who first described polychaete jaw apparatuses of the genus.

Holotype: Right MI, ZPAL Sc.8/2.6 (Fig. 5A).

Type locality: Section 48, near Khudykivtsi village, Podolia, Ukraine.

Type horizon: Lower part of the Borshchiv Horizon, Lower Lochkovian, Lower Devonian.

Material.—3 right MI, 4 left MI, and 1 basal plate (ZPAL. Sc.8/2.4–2.6, 2.13–2.15, 2.17), sample S.Kh.1. All from the type locality and horizon, from lower part of the section 48 (Fig. 2).

Diagnosis.—Right MI of the length more than two times bigger than width, with bight significantly longer than half of the jaw length and 14–15 denticles on the inner margin. First denticle curved posteriorly, in the direction of the outer margin. Inner slope steep, narrowing posteriorly. Opening of the pulp cavity much longer than half of the jaw length. Left MI widest above the middle length, with dentary line slightly sigmoid and inner wing much longer than half of the jaw length. Basal plate about three times longer than wide gradually narrowing in posterior part, with inner margin nearly straight, bearing about 15 denticles.

Description.—Right MI more than twice longer than wide. Bight longer than half of the jaw length. Shank well differentiated, triangular, directed postero-laterally. Dentary formed of 14–15 denticles. The first one large, in form of a hook curved posteriorly, toward the outer margin. Of the others the biggest are some at the middle part and the smallest those at the most posterior part. Inner slope wide, narrowing posteriorly. Left MI widest above the middle length. Dentary line slightly sigmoid, curved medially in the anterior part and outwardly in the posterior part, bears 13–15 denticles of which those in the middle part are the biggest. First denticle much bigger than all others, directed posteriorly. Shank short, well differentiated, triangular in shape, pointed laterally. Outer margin over the shank slightly concave, beneath the shank straight, directed postero-medially. Inner wing wide, longer than half of the jaw length. Ligament scar in both MI not preserved. Basal plate of the length about three times the width. Its denticulated, inner margin nearly straight, bears 15 denticles of which the first is longest and hooked. Next four are much smaller, narrow and laterally directed. Others gradually increase in width, became triangular and posteriorly directed. The last two are smaller, short and again laterally directed. Outer margin convex in the anterior part and nearly straight, directed postero-medially in the posterior part. Its anterior part is separated from the posterior one by a small incision. Most posterior part of the plate is triangular and pointed.

Comparisons.—Basal plate of the new species is somewhat similar to that described by Eller (1938) from the Devonian of Michigan, as *Oenonites orthodentes* Eller, 1938, but is comparatively wider, has more and differently arranged denticles and shorter undenticulated posterior part of the plate. Right MI is similar to the jaw described by Eller (1961) from the well samples of the Devonian of Michigan as *Lumbriconereites cooperi*? Eller, 1938 but differs from it by longer bight and bigger number of denticles. From the *Polychaetaspis* sp. found in the Upper Devonian of Poland (Szaniawski and Wrona 1973) the new species differs significantly by the shape of the basal plate. From the joined jaws described by Jansonius and Craig (1974) as *Polychaetaspis cooperi*? (Eller, 1938) comb. nov. The right MI of the new species differs with slightly longer bight, while the left MI differs by concave anterior part of the outer margin. The new species is very similar to the species described by Männil and Zaslavskaja (1985) as *Polychaetaspis* cf. *aequilateralis* Kielan-Jaworowska, 1966. However, the right MI of the new species differs from the corresponding element of it by concavity in the anterior part of the outer margin and by longer inner wing of the left MI. The right MI of the new species is very similar to corresponding element of *Polychaetaspis* cf. *wyszogrodensis* Kozłowki, 1956 described by Hints (1998). It differs from it only by somewhat narrower posterior part and longer bight. Both MIs of the new species are very close to the corresponding jaws illustrated as *Oenonites* sp. from Silurian of Canadian Arctic (Hints at al. 2000: figs. 7–9) but the left MI of the new species is somewhat wider while the right MI has a longer bight. The right MI of the new species is very close to the corresponding jaw from boring cores of the Wenlockian deposits in Estonia, assigned to *Oenonites* sp. by Hints et al. (2006: pl. 2: 8), but is slightly narrower.

Remarks.—Possessed collection is not rich but contain three most characteristic and well preserved elements of a polychaetaspid apparatus. The elements fit to each other very well and have been found in the same sample. There is no doubt that they belonged to apparatuses of the same species, the more that all other samples did not contain any elements of polychaetaspids. The new species belongs to the group of species similar to *Polychaetaspis wyszogrodensis* Kozłowski, 1956 (sensu Kielan-Jaworowska 1966).

Stratigraphic and geographic range.—Type locality and horizon only.

Polychaetaspis? sp.

Fig. 5H.

Material.— One left MIII? (= unpaired element?) (ZPAL. Sc.8/2.20), sample S.Kh.1., section 48, Lower Lochkovian, Podolia.

Description.—An arch-shaped jaw, narrow in dorsal view but wide in lateral, bearing ten denticles, represents probably the unpaired left MIII of *Polychaetaspis kozlowskii* sp. nov. It has been found in the same sample as all other elements of the species.

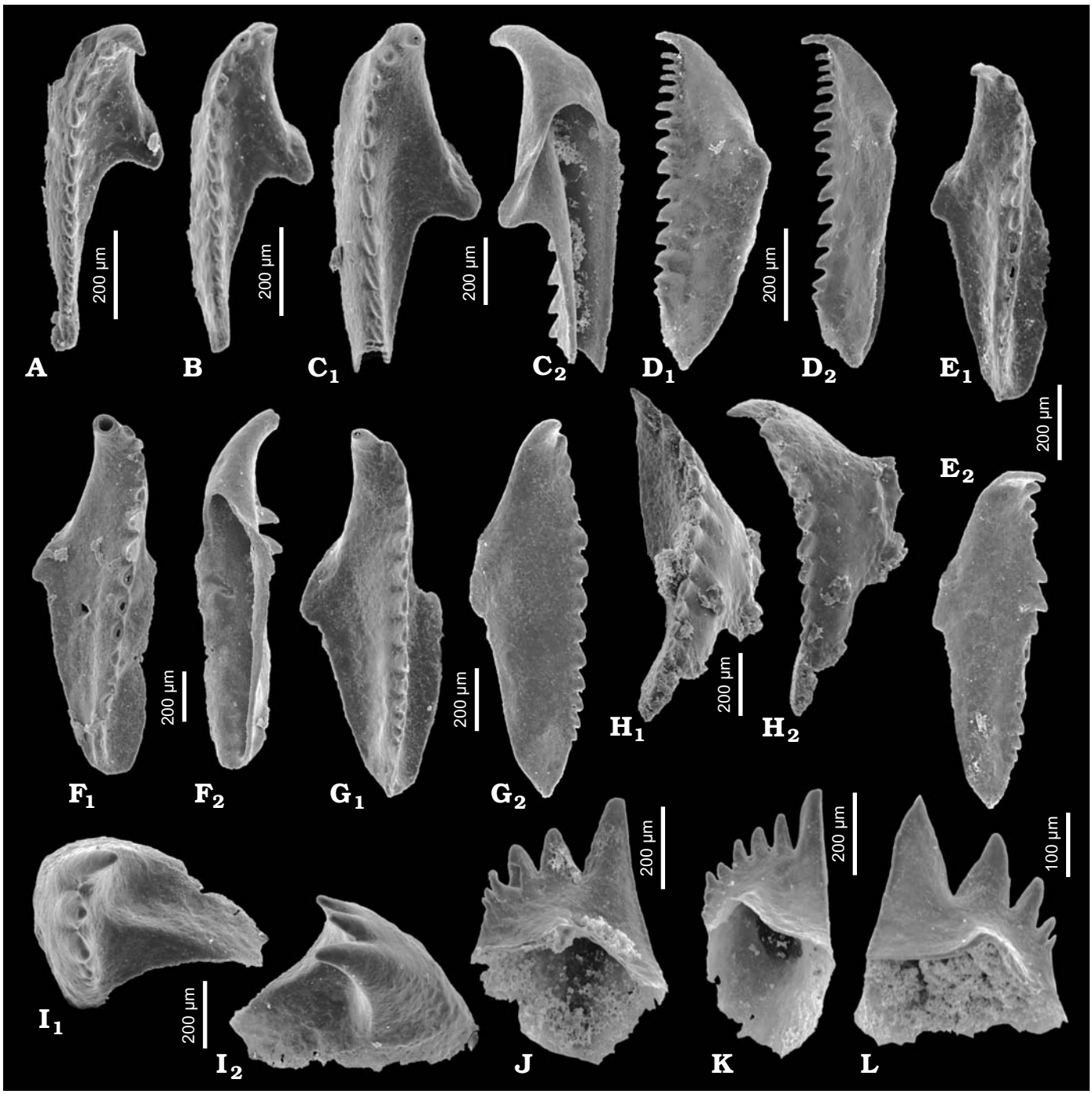


Fig. 5. SEM micrographs of polychaetaspid scolecodonts from Lower Lochkovian of Podolia, lower part of Borshchiv Horizon, section 48, sample S.Kh.1. **A**–**G**. *Polychaetaspis kozlowskii* sp. nov. **A**. ZPAL Sc.8/2.6, holotype, right MI in dorsal view. **B**. ZPAL Sc.8/2.15, right MI in dorsal view. **C**. ZPAL Sc.8/2.14, incomplete right MI in dorsal (C_1) and ventral (C_2) views. **D**. ZPAL Sc.8/2.5, basal plate in dorsal (D_1) and right lateral (D_2) views. **E**. ZPAL Sc8/2.17, left MI in dorsal (E_1) and left lateral (E_2) views. **F**. ZPAL Sc.8/2.13, left MI in dorsal (F_1) and oblique ventral (F_2) views. **G.** ZPAL Sc.8/2.4, left MI in dorsal (G_1) and oblique left lateral (G_2) views. **H**. *Polychaetaspis*? sp., ZPAL Sc.8/2.20, left MIII? in dorsal (H_1) and right lateral (H_2) views. **I**–**L**. *Polychaetaspis*? spp. anterior plates (MIV). **I**. ZPAL Sc8/2.1, right MIV in dorsal (I_1) and dorsal lateral (I_2) views. **J**, **K**. Right MIV in ventral lateral view. **J**. ZPAL Sc8/2.12. **K**. ZPAL Sc.8/2.11. **L**. ZPAL Sc8/2.24, left MIV in ventral lateral view.

Polychaetaspis? spp.

Fig. 5I–L.

Material.—Anterior plates: one left (ZPAL.Sc.8/2.24), sample Sc.8/2.11, and 4 right MIV (ZPAL.Sc.8/2.1, 2.11, 2.12, 2.24), sample S.Kh.1; section 48, Lower Lochkovian , Podolia.

Description.—Five right and one left similar plate-like anterior jaws with five or six teeth of which the first is much bigger than the rest, and with wide opening of the pulp cavity. The jaws have been found in the same sample as all the elements of *P. kozlowskii* sp. nov. and probably represent

MIV of the species. Somewhat similar elements occur also in apparatuses of other eunicids, e.g., in paulinitids (see Fig. 7I–L) or *Kielanoprion* Szaniawski and Wrona, 1973. Jansonius and Craig (1971) based on somewhat similar elements proposed to establish genus *Cheiridogenys* but it can be a junior synonym of *Polychaetaspis*. Certain determination of most of the isolated anterior elements of eunicids is presently not possible. However, the co-occurrence of all illustrated here elements with the jaws of *P. kozlowskii*, as well as total lack of similar elements in all other samples, strongly suggest that they also belong to the same species.

Family Paulinitidae Lange, 1947

Genus "*Kettnerites*" Žebera, 1935

Type species: *Kettnerites kosoviensis* Žebera, 1935, Bohemia; Silurian.

Remarks.—Status of the genus is uncertain. The holotype of its type species *Kettnerites kosoviensis* Žebera, 1935 has been "inaccessible" for Šnajdr (1951: 243, English translation), who gave "a new diagnosis of the genus" (1951: 259) and "was not found" by Tonarova (2008: 188), who published revision of the genus. The only illustration of the holotype published by Žebera (1935: fig. 7) shows a singular, most probably deformed right MI or MII, which based on the illustration is not determinable. Another species assigned by the author to the same genus—*K. depressus* Žebera, 1935 (pl. 2: 8) probably represents a left MII and is somewhat similar to those elements in paulinitids but different from all hitherto known. Moreover the typical MI and MII of *Kettnerites*, sensu Šnajdr (1951), were assigned by Žebera (1935: fig. 2, pl. I: 1–5) not to *Kettnerites*, but to *Arabellites* Hinde, 1879, what means that his concept of the genus *Kettnerites* was different from that of Šnajdr (1951). Also the differences between the genera *Kettnerites* and *Paulinites* Lange, 1947 are not well defined. Kielan-Jaworowska (1966: 125) was in the opinion that they are insignificant and regarded *Kettnerites* as "... a junior subjective synonym of *Paulinites* Lange". Another opinion was expressed by Bergman (1989: 49), who widely used the name *Kettnerites* in his monograph of the Silurian paulinitids from Gotland and stated that "... none of the European species belong to *Paulinites*". However, he did not substantiate this conclusion. In our opinion formal status of the genus *Kettnerites* Žebera, 1935 is uncertain and should be clarified but it is out of the scope of the present paper. Therefore we use the name with quotation marks.

In older literature elements similar to MI of paulinitids were usually assigned to *Nereidavus* Grinnel, 1877, but the genus is not valid because the holotype of its type species *N. varians* Grinnel, 1877 was incompletely preserved and became damaged (Jansonius and Craig 1971). The above cited authors proposed to establish new genus *Nereigenys* Jansonius and Craig, 1971 "to accommodate all forms traditionally assigned to *Nereidavus*" (Jansonius and Craig 1971: 274). However, the type species proposed by them—the *Nereigenys disjunctus* (Eller, 1963) belongs in our opinion to *Paulinites* or *Kettnerites*. For discussion of the problem see also Eriksson (1999).

In the Lower Devonian deposits of Podolia the jaws of "*Kettnerites*" are most abundant and diversified. Over 250 comparatively well preserved elements were found, but because of their wide intraspecific variability and infrequency of individual elements in samples, not all of them can be determined to the species level. The more that in many samples elements of different species occur. All the three recognized here species were hitherto known from the Silurian of the Baltic region only.

"*Kettnerites*" *huberti* Bergman, 1987

Fig. 6A–G.

1970 *Paulinites polonensis* Kielan-Jaworowska, 1966; Szaniawski 1970: 465–466, pl. 1: 5A–D.

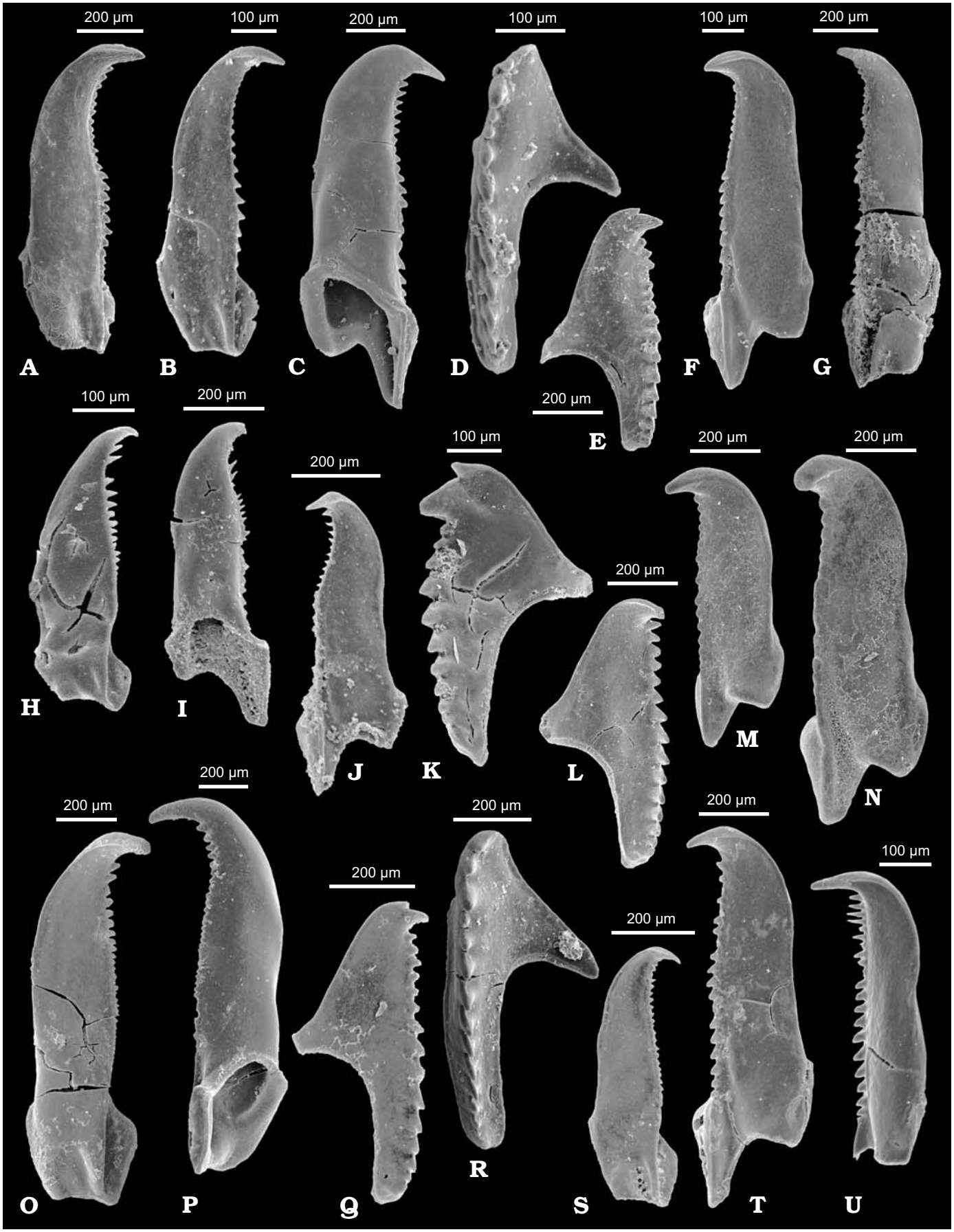
1987 *Kettnerites* (*K.*) *huberti* nov. sp.; Bergman 1987: 59–62, figs. 13R–U, 18, 34–36.

1989 *Kettnerites* (*K.*) *huberti* Bergman, 1987; Bergman 1989: 65–70, figs. 18D, 34–36.

Material.—20 right MI, one of them with preserved basal plate, 22 left MI, 24 right MII, 25 left MII (ZPAL.Sc.8/4.13, 5.8, 7.3, 7.7, 7.10, 9.2, 12.1), samples S.Ust.1, S.Sy.3, S.Vy.3, S.Za.4, S.I.Z.13, 16, 17. Elements of the species occur in the almost whole Lower Devonian sequence of Podolia, except the lower part of the Borshchiv Horizon (Fig. 2).

Remarks.—The Early Devonian specimens do not differ significantly from the hitherto known Silurian forms. Most specimens of both MIs have an inner margin characteristic for the species, which is usually concave in the anterior part and slightly convex in the posterior part. Their denticles are usually much bigger in the posterior part. The fang is comparatively large and has well developed cutting edge. Basal plate is about 8 times shorter than the jaw, is nearly square shaped and only its inner basal portion is extended poste-

Fig. 6. SEM micrographs of paulinitid scolecodonts from Lower Devonian of Podolia: Ivanye Horizon, section 58 (E, L–N, R, T), section 73 (O, P), section 76 (A, C, D, F, H–J, S); Chortkiv Horizon, section 56 (B, K), section 70 (G); upper part of Borshchiv Horizon, section 92 (U, V). **A**–**G**. "*Kettnerites*" *huberti* Bergman, 1987. **A**, **B**. Left M1 in dorsal view. **A**. ZPAL Sc.8/7.3, sample S.IZ.16. **B**. ZPAL Sc.8/4.13, sample S.Bo.3. **C**. ZPAL Sc.8/12/1, sample S.IZ.13, left M1 in ventral view. **D**. ZPAL Sc.8/7.10, sample S.IZ.16, right MII in dorsal view. **E**. ZPAL Sc.8/7.7, sample S.IZ.16, left MII in dorsal view. **F**, **G**. Right MI in dorsal view. **F**. ZPAL Sc.8/9.2, sample S.IZ.17. **G**. ZPAL Sc.8/5.8, sample S.Vy.3. **H**–**L**. "*Kettnerites*" *martinssonii* Bergman, 1987. **H**. ZPAL Sc.8/8.23, sample S.IZ.16, left MI in dorsal view. **I**. ZPAL Sc.8/1.1, sample S.Za.4, right MI in ventral view. **J**. ZPAL Sc8/1.5, sample S.Za.1, right MI in dorsal view. **K.** ZPAL Sc.8/4.16, sample S.Sy.3, right MII in dorsal view. **L**. ZPAL Sc.8/10.9, sample S.Za.12, left MII in dorsal view. **M**, **N**. "*Ketttnerites*" sp. A, right MI in dorsal view. **M**. ZPAL Sc.8/10.10, sample S.Za.11. **N**. ZPAL Sc8/10.15, sample S.Za.11. **O**–**U**. "*Kettnerites*" *polonensis* Kielan-Jaworowska, 1966. **O**. ZPAL Sc.8/6.4, sample S.Do.5, left MI in dorsal view. **P**. ZPAL Sc.8/6.19, sample S.Do.1, right MI in ventral view. **Q**. ZPAL Sc.8/1.10, sample S.Za.1, left MII in dorsal view. **R**. ZPAL Sc.8/7.20, sample S.IZ.18, right MII in dorsal view. **S**. ZPAL Sc.8/1.4; sample S.Za.1, left MI in dorsal view. **T**. ZPAL Sc.8/3.7, sample S.Usty.2, right MI in dorsal view. **U**. ZPAL Sc.8/3.8, sample S.Usty.2, incomplete right MI in right lateral view. →



riorly. Basal plate of the species was hitherto known only from one joined jaw apparatus (Szaniawski 1970). Right MII has two precuspidal denticles, narrow ramus directed postero-laterally, posterior part of the jaw long and bluntly ended. Left MII have one precuspidal denticle. Denticles of the anterior part of inner margin much smaller than those of the posterior part.

Jaws of "*K.*" *huberti*, similarly as elements of other paulinitids, are morphologically variable and only the well preserved specimens can be identified to the species level. The uppermost hitherto known stratigraphic range of the species was Upper Ludlow.

"*Kettnerites*" *martinssonii* Bergman, 1987

Fig. 6H–L.

1960 *Paulinites* sp.; Martinsson 1960: 5–6, fig. 1: 6.
1987 *Kettnerites* (*K.*) *martinssonii* n. sp.; Bergman 1987: 62–66, figs. 12A–G, 18, 37–40.

Material.—3 right MI, 2 left MI, 3 right MII, and 4 left MII (ZPAL Sc.8/1.1, 1.5, 4.16, 8.23, 10.9), samples S.Sy.3, S.I.Z.16, S.Za.1, 4, 12 from the Chortkiv and Ivanye horizons; Middle Lochkovian, Lower Pragian, Podolia.

Remarks.—Shape of both MI and MII correspond to the description of Bergman (1987, 1989). Denticles of both MI slightly spaced in the anterior part. Shank of right MI sharply pointed. Right MII with one large precuspidal denticle and wide ramus. Left MII with wide shank and a series of characteristic, comparatively short and nearly equal in size, anterior denticles.

"*Kettnerites*" *polonensis* (Kielan-Jaworowska, 1966)

Fig. 6O–U.

1966 *Paulinites polonensis* n. sp.; Kielan-Jaworowska 1966: 126–129, figs. 5L, 11, pl. 29, pl. 30: 7, 8.
1980 *Paulinites polonensis* Kielan-Jaworowska, 1966; Wolf 1980: 86–87, pl. 12: 102–104.
1989 *Kettnerites* (*K.*) *polonensis* (Kielan-Jaworowska, 1966); Bergman 1989: 66–69, pls. 42–44.

Material.—4 right MI, 6 left MI, 7 right MII, 5 left MII (ZPAL Sc.8/1.4, 1.10, 3.7, 3.8, 6.4, 6.19, 7.20), samples S.Usty.2, S.Do.1, S.I.Z.18, S.Za.1, 5. Elements of this species occur in almost whole Lower Devonian sequence in Podolia except of the lower part of the Borshchiv Horizon.

Remarks.—The Lochkovian specimens from Early Devonian do not differ much from those described from the Silurian erratic boulders from Poland (Kielan-Jaworowska 1966) and Silurian of Gotland Island (Bergman 1989). Both MI are very long and have inner and outer margins nearly parallel but the inner one is slightly concave in the anterior part while the outer one in the posterior part. Denticulation of the margins differentiated but in most specimens the denticles are longer in the anterior part. The short spine protruding from the posterior part of outer margins of both MI, characteristic for type material of the species, is not well developed in any of the MIs from Podolia. Right MII has two precuspidal denticles and narrow ramus. Denticles of their inner margin are biggest in the middle part. Left MII have one precuspidal denticle. Denticles of the inner margin are biggest below its middle.

"*Kettnerites*" sp. A

Fig. 6M, N.

Material.—2 right MI (ZPAL Sc.8/10.10, 10.15), sample S.Za.11, section 58, from upper part of Ivanye Horizon, Pragian, Podolia.

Remarks.—Jaws wide and comparatively short. Inner margin nearly straight with denticles short and rounded. Fang thick, directed medially. Inner wing narrow, tapering posteriorly. Shank short. They differ from all other right MI of the collection by bigger width, nearly straight inner margin and rounded denticles.

"*Kettnerites*" spp.

Fig. 7H, M–O.

Material.—42 specimens of left MIII (= unpaired element) (ZPAL Sc.8/6.6, 6.7, 11.5, 11.13), samples S.Do.6, S.I.Z.12 18 from different levels of the whole Lower Devonian sequence of Podolia.

Remarks.—Determination of the detached left MIII to the species level, based on their morphology only, is presently not possible because our knowledge of the elements is still comparatively poor. The unpaired MIII of the genus are known from two joined jaw apparatuses of the "*Kettnerites*" *polonensis*, described by Kielan-Jaworowska as *Paulinites polonensis* (1966: pl. 29: 2, 3) and "*K.*" *huberti* described by Szaniawski (1970: pl. 1: 5) also as *Paulinites polonensis*. Besides they are known as detached elements of *K. bankvaetensis* Bergman, 1987, *K. sisyphi klasaardensis* Bergman, 1987, and *K. siaelsoeensis* Bergman, 1987. However the specimens from Lochkovian of Podolia differ from those of the earlier described species in outline and denticulation. Possessed elements cannot be determined also based on numerical data because of small number of well preserved specimens in individual samples.

All left MIII in our collection have 8 or 9 denticles and in all but one the third denticle is the biggest. The longitudinal branch in lateral view is triangular and tapers posteriorly. The ramus is narrow, sharply pointed, directed nearly perpendicularly to the longitudinal branch. In some specimens the outer margin of the ramus in lateral view is concave. The jaws are somewhat similar to corresponding elements of *Paulinites paranaensis* Lange, 1947 named "unpaired piece" in English translation of the paper (Lange 1949: pl. 11: 1–12).

"*Kettnerites*"? spp.

Fig. 7A–D.

Material.—Mandibles, 6 specimens (ZPAL Sc.8/8.7, 8.19, 10.6, 11.14), samples S.I.Z.2, 13, 16, S.Za.2, 12, all from the Ivanye Horizon, Pragian, Podolia.

Remarks.—Co-occurence of the mandibles with numerous jaws of "*Kettnerites*" strongly suggests that they belonged to apparatuses of the same genus. Their paulinitid origin

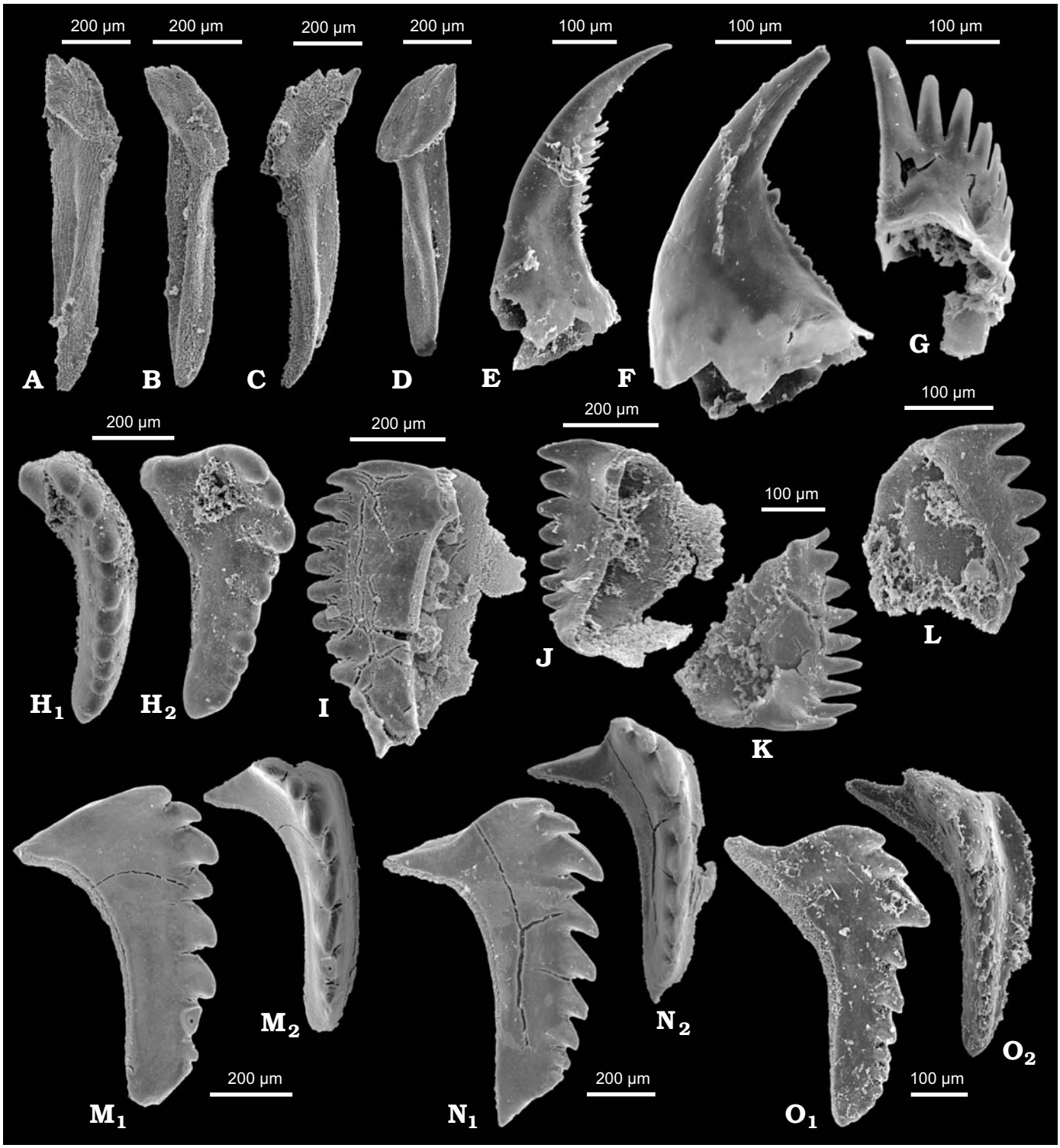


Fig. 7. SEM micrographs of selected elements of paulinitid scolecodonts and undetermined anterior elements from Lower Devonian of Podolia: Ivanye Horizon, section 58 (D, O), section 73 (M, N, K), section 76 (A–C, E, G–J, L); Chortkiv Horizon, section 70 (F). **A–D**. "*Kettnerites*"? spp. **A**, **B**. Left mandibles in dorsal view. **A**. ZPAL Sc.8/8.19, sample S.IZ.13. **B**. ZPAL Sc.8/11.14, sample S.Za.2. **C**, **D**. Right mandibles in dorsal view. **C**. ZPAL Sc.8/7.1, sample S.IZ.16. **D**. ZPAL Sc.8/10.6, sample S.Za.12. **E**. Family uncertain, gen. et sp. indet. A, ZPAL Sc.8/7.9, sample S.IZ.16, in lateral view. **F**. Family uncertain, gen. et sp. indet. B, ZPAL Sc.8/4.22, sample S.Zo.4, in lateral view. **G**. Family uncertain, gen. et sp. indet. C, ZPAL Sc.8/7.18, sample S.IZ.18, in lateral view. **H**, **M–O**. "*Kettnerites*" spp. left MIII. **H**. ZPAL Sc.8/11.5, sample S.I.Z.18, in dorsal (H_1) and left lateral (H_2) views. **M**. ZPAL Sc.8/6.6, sample S.Do.6, in right lateral (M_1) and dorsal (M_2) views. **N**. ZPAL Sc.8/6.7, sample S.Do.6, in left lateral (N_1) and dorsal (N_2) views. **O**. ZPAL Sc.8/11.13, sample S.Za.12, in left lateral (O_1) and dorsal (O_2) views. **I–L**. "*Kettnerites*"? spp. left and right MIV. **I**. ZPAL Sc.8/7.13, sample S.IZ.18, right element in ventral lateral view. **J**. ZPAL Sc.8/8.22, sample S.I.Z.13, right element in ventral lateral view. **K**. ZPAL Sc.8/6.15, sample S.Do.2, left element in dorsal lateral view. **L**. ZPAL Sc, 8/8.8, sample S.IZ.6, left element in ventral lateral view.

is suggested also by their morphological similarity to the mandibles of *Paulinites paranaensis* Lange. In some of them similar denticulation of the anterior margin is preserved also (see Lange 1949: pl. 7: 1, 4, 10).

"*Kettnerites*"? spp.

Fig. 7I–L.

Material.—18 specimens of left and right MIV (named also paragnaths) (ZPAL Sc.8/6.15, 7.13, 8.8, 8.22), samples S.Do.2, S.Z.6, 13, 18, from different stratigraphic levels of Upper Lochkovian and Lower Pragian, Podolia.

Remarks.—The anterior elements of fossil jaw apparatuses are rarely described. They are seldom well preserved because of small size and fragility. Of the paulinitids the elements are known only in *P. paranaensis* (Lange, 1947), "*K.*" *polonensis* (Kielan-Jaworowska, 1966) and "*K.*" *sisyphi klasaardensis* (Bergman, 1987). The elements found in Podolia are rather poorly preserved. In lateral view they are plate-like, partly rounded, with inner margin denticulated. Most of them have 6 to 8 denticles which gradually decrease in size posteriorly. They differ from the corresponding elements of polychaetespids (see Fig. 5I–L) mainly by the larger number of denticles and narrower opening of the pulp cavity. Their specific determination is in present state of knowledge not possible.

Family Atraktoprionidae Kielan-Jaworowska, 1966

Genus *Atraktoprion* Kielan-Jaworowska, 1966

Type species: *Atraktoprion cornutus* Kielan-Jaworowska, 1962, erratic boulder; Ordovician, Poland.

Remarks.—Isolated MI of this genus were in older literature usually assigned to *Arabellites* Hinde, 1879. Sylvester (1959) designated *A. hamatus* Hinde, 1879 as the lectotype. However, the status of the genus has been discussed later in several publications (for the summary see Eriksson 2008). The latter author reviewed all preserved specimens assigned by Hinde (1879) to *Arabellites* and presented their modern illustrations. However, he reserved his judgment concerning the important problem of the relationship of *Arabellites* to *Atraktoprion*, Kielan-Jaworowska, 1962 explaining that it "will be discussed in detail elsewhere" (Eriksson 2008: 629). The relationship problem is not easy to solve because the lectotype of *Arabellites* represents the left MI, which is very similar to the corresponding elements of three later established genera *Atraktoprion* Kielan Jaworowska, 1962, *Skalenoprion* Kielan-Jaworowska, 1962, and *Leptoprion* Kielan-Jaworowska, 1966, while some other elements of the three genera are significantly different. Because of this Kielan-Jaworowska (1966) assigned the genera to three different families. This means, that after morphology only, it is difficult to determine their isolated left MI even to the family level. Because of that, in our opinion, all the "species" of *Arabellites* based on singular specimens of the left MI have to remain undetermined in the sense of biological systematics, as long as we do not know other elements of apparatuses to which they belonged. In the case of their co-occurrence with other elements the numerical data can help to solve the problem.

Hinde (1879: 377) establishing the genus *Arabellites* stated: "I propose to include in this genus jaws of widely different forms which have a general resemblance to those of the existing genus *Arabella* Grube". The idea was generally correct because the author did not treat each element of jaw apparatus as a separate taxon, as many later authors did. However, in that time he did not know that many fossil polycheates possessed a very different structure of jaw apparatuses from modern forms. Right MI of Paleozoic apparatuses similar in shape to Recent *Arabella* Grube, 1850 possess usually either bight or basal plate, what means they are significantly different from the MI of Recent *Arabella*. Therefore it is understandable that most of the species of *Arabellites* based by Hinde (1879, 1880, 1882) on the MI are left jaws. Two of the three species based by the author on the right MI, the *Arabellites extensus* Hinde, 1880 and *Arabellites spicatus* Hinde, 1880 possess bight characteristic for MI of Atraktoprionidae, while the third species *Arabellites fastigatus* Hinde, 1882 possess basal ridge and shape characteristic for the right MI of Skalenoprionidae.

Atraktoprion podolicus sp. nov.

Fig. 8A–H, M.

Etymology: In reference to its type region Podolia, Ukraine.

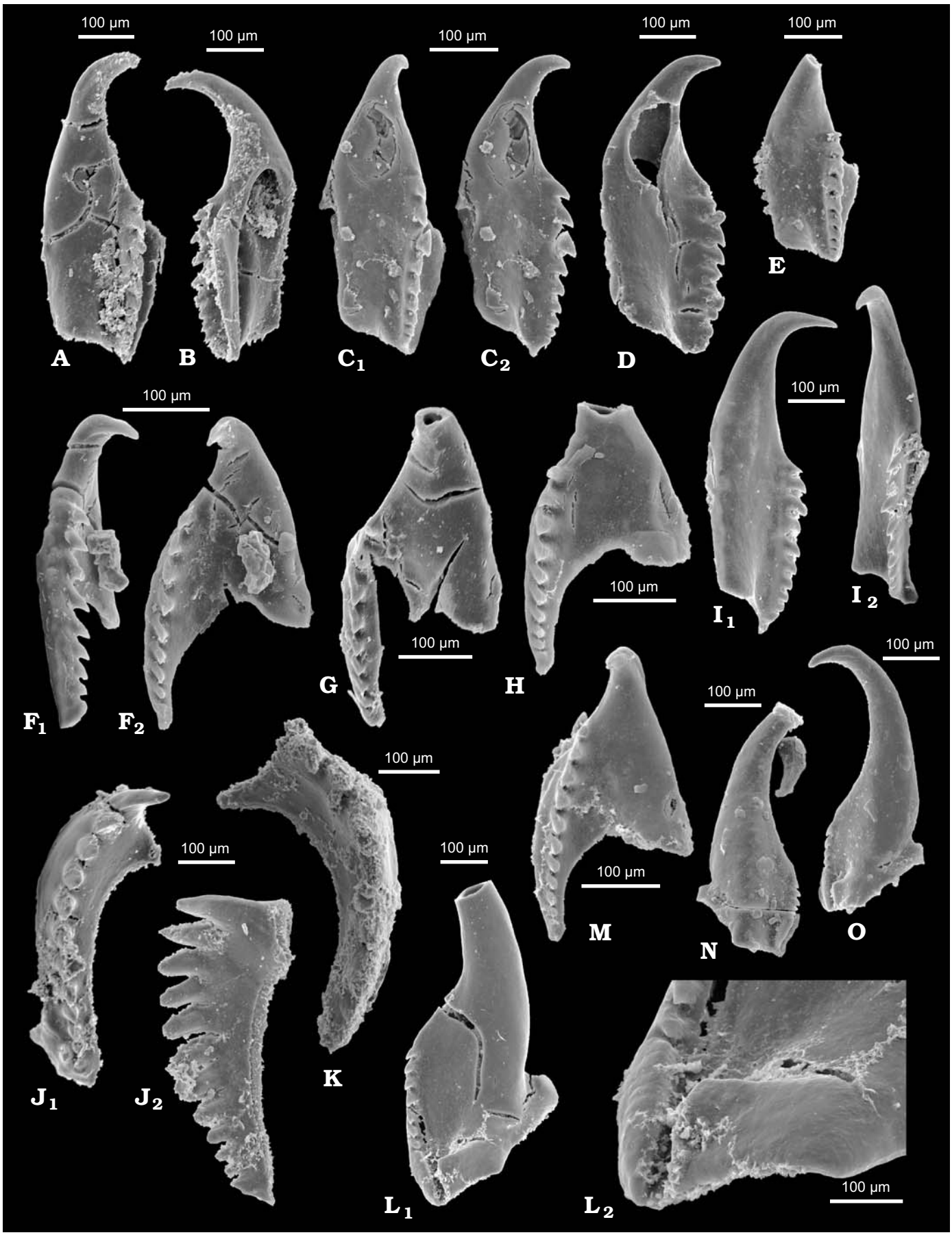
Holotype: Right MI, ZPAL Sc8./14.1 (Fig. 8F).

Type locality: Ivanye Zolote, Podolia, Ukraine.

Type horizon: Upper part of the Ivanye Horizon, middle part of the section 76, Pragian.

Material.—4 right MI (two of them incomplete) and 6 left MI (ZPAL Sc.8/4.18, 4.19, 4.20, 7.15, 8.4, 8.24, 11.1, 14.1, 14.3, 14.4), samples S.Zo.4, S.Vy.3, S.I.Z.4, 10, 16, 18, S.Uste.2,

Fig. 8. SEM micrographs of atraktoprionid and skalenoprionid scolecodonts from Lower Devonian of Podolia: Chortkiv Horizon, section 70 (A, B, G, K), section 71 (J); Ivanye Horizon, section 58 (M), section 76 (C, D, E, F, H, I); Borshchiv Horizon, section 48 (L); Silurian–Devonian transition beds, section 64 (N, O). **A**–**H**, **M**. *Atraktoprion podolicus* sp. nov., Middle Lochkovian–Lower Pragian. **A**–**D**. Left MI. **A**. ZPAL Sc.8/4.19; sample S.Zo.4, in dorsal view. **B**. ZPAL Sc.8/4.20, sample S.Zo.4, in ventral view. **C**. ZPAL Sc8/14.3, sample S.Uste.2, in oblique dorsal (C_1) and dorsal (C_2) views. **D**. ZPAL Sc.8/11.1, sample S.IZ.10, in dorsal view. **E**. ZPAL Sc.8/7.15, sample S.IZ.18, in dorsal view. **F**. ZPAL Sc.8/14.1, holotype, sample S.IZ.4, right MI in lateral (F_1) and dorsal (F_2) views. **G**. ZPAL Sc.8/4.18, sample S.Zo.4, incomplete and deformed right MI in dorsal view. **H**. ZPAL Sc.8/14.4, sample S.IZ.4, incomplete right MI in dorsal view. **M**. ZPAL Sc.8/8.24, sample S.IZ.16, right MI in dorsal view. **I**. *Atraktoprion*? sp. A, Middle Lochkovian, ZPAL Sc.8/5.4, sample S.Vy.3, left MI in dorsal (I_1) and right lateral (I_2) views. **J**, **K**. *Atraktoprion*? spp., Middle Lochkovian. **J**. ZPAL Sc.8/4.17, sample S.Zo.2, right MII in dorsal (J_1) and right lateral (J_2) views. **K**. ZPAL Sc.8/2.3, sample S.Kh.1, left MII in dorsal view. **L**. *Skalenoprion* sp., Lower Pragian, ZPAL Sc.8/10.1, sample S.Za.11, incomplete right MI in dorsal view (L_1) and posterior, inner part (L_2). **N**, **O**. *Skalenoprion* sp. A. **N**. ZPAL Sc8/13.2, sample S.Dn.1, left MI in dorsal view (anterior portion of the hook broken off during preparation). **O**. ZPAL Sc8/13.1, sample S.Dn.1, right MI in dorsal view.



from Chortkiv and Ivanye horizons, Middle Lochkovian–Pragian, Podolia.

Diagnosis.—Right MI wide, with wide bight extending for about 0.4 of the jaw length. Hook stout with apical part bent posteriorly. Inner margin beneath the hook slightly convex, denticulated. Outer margin nearly straight, directed postero-laterally. Left MI with outer margin slightly oval, inner margin beneath the hook nearly straight, denticulated, posterior margin directed postero-medially. Inner wing in the anterior part wide, narrowing posteriorly.

Description.—Right MI about two times longer than wide. Length of both complete specimens below 0.5 mm. Hook stout with apical part bent posteriorly. Denticulated inner margin bears 8–10 posteriorly inclined denticles. First 3 to 4 of them slightly increase in size posteriorly and the rest decrease. Outer margin beneath the hook nearly straight, directed postero-laterally. Bight very wide with anterior margin oval shaped. Shank short, nearly triangular. Left MI with hook slightly longer than 1/3 of the jaw length. Inner, denticulated, margin slightly convex, bears 8–9 denticles differentiated in size, similarly as in right MI. Outer margin slightly convex. Posterior margin directed postero-medially, slightly concave in the middle part. Inner wing begins at the level of the second denticle, wide in the anterior part, gradually narrows posteriorly. The posteriormost portion of the jaw sub-triangular, with vertical concavity in the middle. Opening of the pulp cavity long, extends to the basal part of the hook.

Comparisons.—Right MI is most similar to *Leptoprion*? sp. described by Tonarova et al. (2012) from Ludlow of Prague Basin but is narrower from it and has slightly less curved hook. It is also similar to the Middle Devonian jaws described by Stauffer (1939) as *Arabellites anatinus* but differs from them with smaller hook and narrower shank. Left MI is somewhat similar to *Arabellites elegans* Hinde, 1879 (illustrated also by Eriksson 2008: fig 1.11) but differs from it by less curved hook, larger number of denticles and triangular posterior end. Both MI of the new species are somewhat similar to those of *Atraktoprion eudoxus* Szaniawski, 1968 from the Permian of Poland, but right MI of the new species has smaller hook and left MI differ in shape of posterior portion.

Atraktoprion? sp. A

Fig. 8I.

Material.—One left MI (ZPAL Sc.8/5.4), sample S.Vy.3, from the upper part of Chortkiv Horizon, section 71, Middle Lochkovian, Podolia.

Description.—Jaw strongly elongated. Hook extending for about half of the jaw length. Inner margin provided with 10 denticles. Outer margin oval. Posterior margin short, directed postero-medially, slightly concave in the middle part.

Remarks.—The jaw differs from corresponding element of *Atraktoprion podolicus* nov. sp. mainly by being more elongated and having much longer hook. It is not certain if the jaw belong to the genus *Atraktoprion* or to *Skalenoprion*.

Atraktoprion? spp.

Fig. 8J, K.

Material.—One right and one left MII? (ZPAL Sc.8/4.17, 2.3), samples S.Zo.2, S.Kh.1, from sections 70 and 71, Lochkovian, Podolia.

Remarks.—Longitudinal branch of the both, right and left forms arch shaped, long and narrow, bear about 14 comparatively big denticles decreasing in size posteriorly. Transversal branch short, narrow and pointed.

It is not certain if the jaws belong to the same species. It is possible that they are conspecific with the above described *Atraktoprion podolicus* sp. nov. or *Atraktoprion*? sp. A. The right jaw (Fig. 8J) has been found in the same sample as the specimens of *Atraktoprion podolicus* sp. nov. while the left jaw in the same sample as *Atraktoprion*? sp. A.

Family Skalenoprionidae Kielan-Jaworowska, 1966

Genus *Skalenoprion* Kielan-Jaworowska, 1962

Type species: *Skalenoprion alatus* Kielan-Jaworowska, 1962, erratic boulder; Ordovician, Poland.

Skalenoprion sp. A

Fig. 8N, O.

Material.—Two right MI and one left MI (ZPAL Sc.8/13.1, 13.2), partly broken during preparation. Besides, two left MI became completely damaged during preparation. All were found in the same sample S.Dn.1 from the Silurian–Devonian transition beds, section 64, Dnistrove, Podolia.

Description.—Right MI has hook about twice as long as basal part of the jaw. Inner margin of the basal part denticulated only in its upper part, bears 4–5 denticles of nearly equal size. Lower part of the margin in form of the ridge. Fused basal plate short, undenticulated, well separated from the inner margin by a furrow. Inner wing narrow and short, visible only beneath the denticles. Outer margin convex, except of the most posterior part where forms deep incision. Posterior margin nearly straight, directed postero-medially. Left MI close to the mirror image of the right MI but without the basal plate.

Comparisons.—The species is most similar to *Skalenoprion alatus* Kielan-Jaworowska, 1962 but differ from it by longer hook and undenticulated posterior part of the inner margin.

Skalenoprion sp.

Fig. 8I.

Material.—One incomplete right MI (ZPAL Sc.8/10.1), sample S.Za.11, section 58, Pragian, Podolia.

Remarks.—Length of the hook unknown. Inner margin provided with seven denticles in the anterior part, undulated in the posterior part. Outer margin oval with an incision in the posteriormost part. Posterior margin directed postero-medially. Fused basal plate, undenticulated, transversally elongated for half of the jaw width, separated from the jaw by a furrow along the whole inner and anterior side. The jaw is similar to the right MI of the described above *Skalenoprion*

sp. a but has longer denticulated part of the inner margin and more transversally elongated basal plate.

Family uncertain

Gen. et sp. indet. A

Fig. 7E.

Material.—One specimen (ZPAL Sc.8/7.9), sample S.I.Z.16 from the upper part of Ivanye Horizon, section 76, Lower Pragian, Podolia.

Remarks.—Arch shaped spine with numerous thin, spine-like, anteriorly directed denticles along the middle part of inner margin. Similar scolecodonts were hitherto unknown and it is not quite certain if the spine belong to polychaetes but its manner of preservation, as well as the co-occurrence with scolecodonts suggest the affinity.

Gen. et sp. indet. B

Fig. 7F.

Material.—One specimen (ZPAL Sc.8/4.22), sample S.Zo.4 from the middle part of the Chortkiv Horizon, section 70, Middle Lochkovian, Podolia.

Remarks.—Thick spine with very wide basal part and narrow anterior part. The basal part irregularly denticulated along the inner margin. Another ridge of spine-like denticles occur along the anterior part of the left lateral side of the basal part. The denticles increase in size in anterior direction. Similarly as in the case of the specimen described above it is not quite certain if the specimen belong to polychaetes.

Gen. et sp. indet. C

Fig. 7G.

Material.—One specimen (ZPAL Sc.8/7.18), sample S.I.Z.18 from the Ivanye Horizon, section 76, Lower Pragian, Podolia.

Remarks.—Plate-like right MIV? with seven long, comparatively slim teeth, regularly decreasing in size in posterior direction

Concluding remarks

The Lochkovian scolecodonts of Podolia are not abundant and mostly fractured. Their low frequency is probably caused by dispersion in sediments, resulted by very high sedimentation rate and dominance of the terrigenous material in the deposits. The diversified conditions of the shallow water sedimentation caused probably also the mass fracturing of specimens. However, the inner structure of the jaws is not greatly changed and many of them are preserved quite well. In some of the calcareous layers, mainly in the upper part of Ivanye Horizon (Fig. 2; sections 76 and 58), the well preserved jaws are quite numerous and taxonomically diverse.

In the Silurian–Devonian transition beds the well preserved scolecodonts have been found in one sample only, just below the boundary (Fig. 2). They are represented by *Skalenoprion* sp. A and indeterminable fragments of "*Kettnerites*". In the lower part of the Borshchiv Horizon, exposed in the section 64 (= lower part of the Khudykivtsi Formation), only fragments of "*Kettnerites*" MI have been found. Higher up, in one sample from lower part of section 48, belonging also to the Khudykivtsi Formation, the only representatives of Polychaetaspidae, namely *P. kozlowskii* sp. nov. and *P.*? spp. were found. Besides them only a few elements of *Mochtyella* sp. A and *Mochtyella*? sp. occurred within the sample. In all younger strata the paulinitids are dominant. They are represented mainly by three species "*Kettnerites*" *polonensis,* "*K.*" *martinnsonii*, and "*K.*" *huberti,* known until now only from the Silurian of the Baltic region. Their occurrence in the Upper Lochkovian of Podolia significantly extends their hitherto known stratigraphic ranges as well as geographic distribution. The only species of paulinitids unknown in the Silurian "*K.*" sp. A is represented in the collection by two specimens of right MI only. They have been found in the uppermost part of the Lochkovian sequence. In addition, some elements of the same genus remain undetermined. Apart from the paulinitids the elements of mochtyellids, atraktoprionids, and skalenoprionids occur very rarely in the higher parts of the sequence, while elements of polychaetaspids were not found at all. Most probably the substantial change of the scolecodont assemblage in the Early Lochkovian has been caused by changes of the facies conditions as a result of the shallowing of the basin which preceded ingression of the Old Red facies.

The most numerous scolecodonts have been found in the upper part of the Ivanye Horizon, in sections 58 and 76, and because of this, the sections have been sampled twice. However, in the uppermost 5 meters of the sections, as well as in the upper part of the section 116, that means in the sediments representing gradual passage to the Old Red facies, the scolecodonts were not found at all.

The Silurian scolecodonts of Podolia remain still almost completely unknown and their investigations should be undertaken in order to understand the evolutionary trends of jaw-bearing polychaetes across the Silurian–Devonian boundary. However the over 900 m thick continuous sequence of the Silurian and Devonian marine sediments with diverse lithology, exposed in fragments in many localities, needs lot of time for thorough examination. The more that most of the exposures are presently difficult for investigations because of steep slopes or overgrowing by bushes and trees.

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