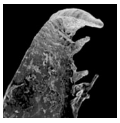
A jawed polychaete fauna from the late Ludlow Kozlowskii event interval in the Prague Basin (Czech Republic)

PETRA TONAROVÁ, MATS E. ERIKSSON & OLLE HINTS



This paper deals with a diverse fauna of polychaetes possessing jaws (= scolecodonts) from the late Silurian Kopanina Formation of the Prague Basin (Czech Republic). The most common genera are *Kettnerites*, *Oenonites* and *Pistoprion*; the entire collection contains at least 16 genera. This is in stark contrast to the four genera recorded from this region by previous authors. The fauna described shows great similarities with coeval ones reported from the Baltic area (Gotland and Estonia), Siberia, Arctic Canada and the British Isles. These new data thus extend the palaeobiogeographical and palaeolatitudinal distribution of several taxa, particularly at the genus but also the species level. The sampled interval embraces the Kozlowskii event and its effects on the polychaetes are briefly discussed. Although the collections are relatively small, particularly from post-event strata, a faunal reorganisation is apparent. The studied collection enabled the stratigraphical ranges of some taxa, including tretoprionids and possibly polychaeturids, to be extended into the late Ludlow. One new species, "*Mochtyella*" *pragensis*, is described. • Key words: scolecodonts, palaeobiogeography, Kozlowskii/Lau event, Silurian, Ludlow, Kopanina Formation, Prague Basin.

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Petra Tonarová, Institute of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic; Czech Geological Survey, Geologická 6, 152 00 Prague 5, petra.tonarova@geology.cz • Mats E. Eriksson, Department of Earth and Ecosystem Sciences, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden; Mats.Eriksson@geol.lu.se • Olle Hints, Institute of Geology at Tallinn University of Technology, Ehitajate 5, 19086 Tallinn, Estonia; Olle.Hints@gi.ee

Polychaete worms represent one of the most common components of benthic invertebrate faunas in the recent oceans and they have a world-wide distribution (*e.g.* Hutchings & Fauchald 2000). Except for their jaws (= scolecodonts), chaetae and their associated tubes and burrows, polychaetes do not fossilize well as they are composed of soft tissue that generally decomposes rapidly. The fossil record of polychaetes dates back to the middle Cambrian (Conway Morris 1979, 1985), but the oldest undoubted scolecodonts are recorded from the latest Cambrian strata (Williams *et al.* 1999). Similarly as in modern-day oceans most Palaeozoic jaw-bearing polychaetes belong to the order Eunicida, representatives of which today live as infaunal burrowers, epifaunal crawlers, tube builders or inhabit reefs and reef-like structures (*e.g.* Paxton 2000). Just as their mode of life is variable, eunicidan feeding strategies are also diverse: carnivorous, herbivorous, omnivorous scavengers; some taxa use their jaws to excavate into coral frameworks and are thus efficient bioeroders (Paxton 2000). Similar modes of life and feeding strategies are expected also in deep time and their inferred behaviour may aid in reconstructing and understanding palaeoenvironments.

The complex eunicidan jaw apparatuses consist of a pair of ventral mandibles and a multi-element dorsal maxillary apparatus (*e.g.* Kielan-Jaworowska 1966, Szaniawski 1996). The maxillae are by convention numbered from posterior to anterior with an "M" and successive Roman numerals: MI–MVI. The paired maxillae are referred to left and right when viewed from the dorsal side. Their composition of resistant organic matter (scleroproteins) and hardening by various metals or other minerals (Michel & DeVillez 1978) add to their fossilization potential.

Only a few reports have been published on Silurian scolecodonts from the Prague Basin (Žebera 1935, Bouček 1941, Šnajdr 1951, Tonarová 2008). One aim of the present paper is to compare results from historical collections, based on specimens preserved on bedding plane surfaces, with new samples from which scolecodonts were recovered

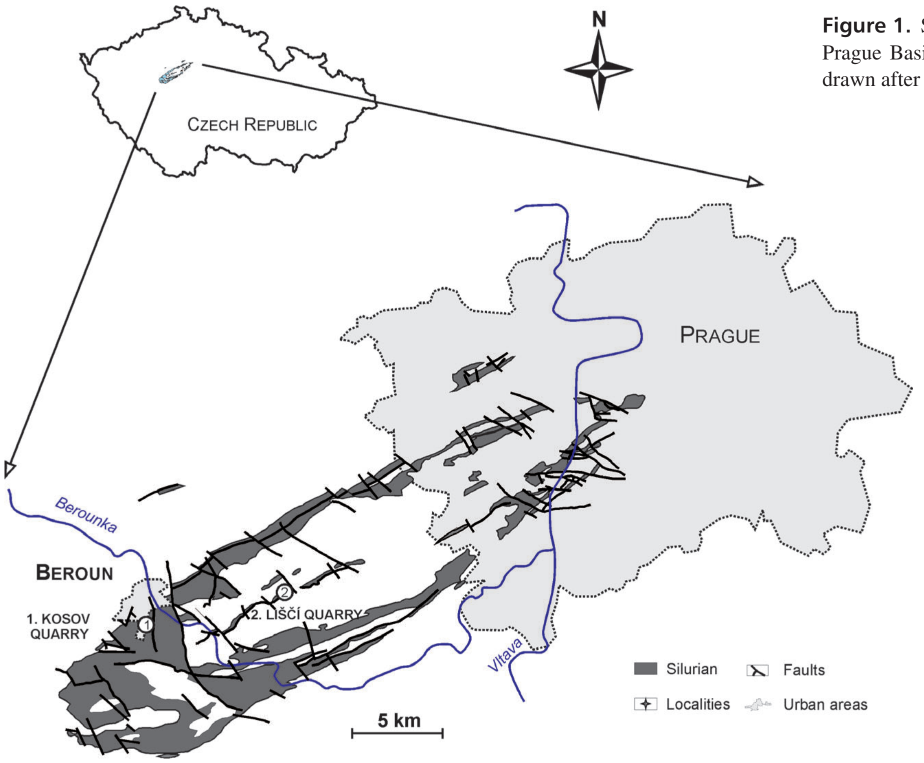


Figure 1. Simplified map of the Silurian rocks of the Prague Basin with localities of interest indicated (redrawn after Havlíček & Štorch 1990).

through acid digestion. As in the previous studies, the Ludfordian Kopanina Formation of the Liščí and Kosov quarries, Prague Basin, Czech Republic, was sampled. The stratigraphical interval spans the *Neocucullograptus kozlowskii* and *Pseudomonoclimacis latilobus–Slovinograptus balticus* graptolite biozones, thus also embracing the Kozlowskii event. Being the first account of a diverse scolecodont assemblage from Perunica, this work provides important information on the distribution, taxonomic composition and biogeography of Silurian polychaetes.

Geological background

The Prague Basin was defined by Havlíček (1981, 1982) for the Ordovician to Middle Devonian deposits situated between Prague and Pilsen. The study of these commonly richly fossiliferous rocks commenced more than 150 years ago (for summary see Chlupáč *et al.* 1998), which makes it one of the best studied early Palaeozoic basins. The entire Silurian succession is non-metamorphosed, with rich and diverse benthic and pelagic fossil faunas. It is confined, together with Devonian deposits, to the central part of the present synclinorium of the Prague Basin (Fig. 1). The gradual synsedimentary deformation accompanied by the strong submarine volcanism that culminated during the late Wenlock and early Ludlow, formed the character of the basin (Kříž 1991). The volcaniclastic accumulations gave rise to submarine elevations and also to an emergent island surrounded by shallow-water bioclastic limestone (Horný 1955, 1962; Kříž 1991). In general, the Silurian deposits originated in a relatively shallow, warm-water environment within the subtropical climatic zone (Kříž 1991, Štorch *et al.* 2006).

The present study is focused on a succession of the Kopanina Formation (late Ludlow) that is composed of cephalopod and brachiopod-rich limestones, dark platy micritic and biomicritic limestone, calcareous shale, tuffaceous limestones, and calcareous tuffs (Horný 1955; Kukal 1955a, b; Kříž 1991, 1992; Ferretti & Kříž 1995; Čáp 2002; Čáp *et al.* 2003). This succession has recently been investigated for graptolite biostratigraphy (Štorch 1995) and the Kozlowskii event (Manda & Kříž 2006, Lehnert *et al.* 2007, Manda *et al.* 2012).

The Kosov and Liščí quarries were chosen for this study on the basis of previous reports on scolecodonts by Žebera (1935) and Šnajdr (1951). The latter author described the Liščí Quarry as the richest locality for scolecodonts in the Prague Basin, even though he dealt only with shales from the upper part of the Kopanina Formation. The localities and regional history of scolecodont research are briefly described below.

The Kosov Quarry

The Kosov Quarry is situated in the western segment of the Prague Basin (*sensu* Kříž 1991) approximately 1.5 km southwest of the city of Beroun (see Fig. 1), on the north-western slope of the Kosov Hill (= "Dlouhá hora"). The sequence of Silurian rocks exposed in this quarry starts with the Motol Formation (Wenlock Series, middle Sheinwoodian) and reaches the middle part of the Přídolí Formation (Přídolí Series) (Horný 1955, Kříž 1992).

The studied section (49° 56´ 22.0˝ N, 14° 03´ 16.2˝ E, Fig. 2A) is situated on the second level of the southern part of the Kosov Quarry area. Detailed information on this exposure is provided by Kříž (1992), Štorch (1995) and Lehnert *et al.* (2007, p. 233, figs 4–6), who documented fossil groups such as graptolites and conodonts, facies architecture and the stable isotope ($\delta^{18}O$, $\delta^{13}C$) record. The studied scolecodont samples derive from beds 2 to 19 *sensu* Lehnert *et al.* (2007). The upper part of the Kopanina Formation (Ludfordian Stage) exposed in this section corresponds to the *N. kozlowskii* and *P. latilobus–S. balticus* graptolite biozones. By comparison, Šnajdr's (1951) scolecodont samples were collected from several shale beds within the *P. latilobus–S. balticus* and *Pristiograptus fragmentalis* biozones.

Unfortunately, conodonts are represented mainly by long-ranging coniform taxa, with the exception of bed 10, in which the index species *Polygnathoides siluricus* is present (Lehnert *et al.* 2007; L. Slavík, Prague, personal communication 2010). The lower part of the section represents relatively deeper-water settings of the transition from the lower slope of the Kosov volcanic complex to the basin. It is composed of deep-water shales, tuffitic shales and black spiculitic mud- to wackestone. Upwards through the section the shale content decreases and the environment becomes relatively shallower with strata represented by bioclastic wackestone and packestone (Lehnert *et al.* 2007). The trends in changes of the environment are supported also by previous macrofaunal studies (*e.g.* Kříž 1992).

The Liščí Quarry

The Liščí Quarry (Fig. 1) is situated in the central segment of the Silurian sedimentary area of the Barrandian (*sensu* Kříž 1991) and it is a component of the "Amerika anticline" (Svoboda & Prantl 1954). The quarry is situated approximately 2 km northwest of Karlštejn Castle and about 2 km west of the Mořina village. The quarry and its surroundings have been studied since the first half of 20th century (for details see Horný 1955; Kříž 1986, 2008, and references therein). This locality is one of the richest in terms of Silurian fossils from the Prague Basin with more than 200 species hitherto reported (Kříž 2008). The Kopanina Formation exposed in the quarry comprises several lithotypes varying in the amount of tuffite material, colour and proportion of bioclasts (Kukal 1955b, Mikuláš *et al.* 2003).

The studied section (49° 57´ 18˝ N, 14° 10´ 23˝ E) is located in the north-western part of the quarry. The scolecodont samples derive from eight levels representing the upper part of the *P. siluricus* conodont Zone (L. Slavík, Prague, personal communication 2010), corresponding to the *Acanthalomina minuta* Community (Horný 1955). The rocks are predominantly bioclastic light to dark grey wackestone and packestone with intercalations of grey tuffitic shale (see simplified profile in Fig. 2B).

Material and methods

Twenty-six samples were processed in the palynological laboratory of the Faculty of Science, Charles University in Prague. All samples yielded scolecodonts, sometimes accompanied also by chitinozoans, sponge spicules, brachiopods, graptolites and unidentifiable organic fragments. The weight of the initial bulk samples varied from 200 to 1000 g. Generally only up to 200 g was dissolved using a methodology similar to that described in detail by Kielan-Jaworowska (1966), but with an acetic acid concentration of 5%. Sample processing took approximately one month, including changing of acid and sieving the samples every week. Particularly resistant samples were subsequently treated with 20% hydrochloric and 30% hydrofluoric acid. After digestion the residue was gently rinsed through a 50 μm sieve. Finally, the wet samples were hand-picked from Petri dishes under a stereomicroscope, using a micropipette or an eyelash. Some specimens still had to be cleaned in hydrogen peroxide or hydrofluoric acid depending on the character of adherent particles. The specimens are stored in small plastic containers filled with glycerine and a drop of formaldehyde to prevent mould growth.

The specimens were photographed using a Scanning Electron Microscope (SEM): a JEOL JSM-6380 at the Institute of Geology and Palaeontology (Charles University in Prague), Hitachi S-3400N at the Department of Earth and Ecosystem Sciences (Lund University) and Zeiss EVO MA15 at the Institute of Geology (Tallinn University of Technology). Additional photographs were taken with a digital camera attached to a Nikon AZ100 light microscope in Tallinn. All samples are stored in the collections of the Czech Geological Survey under numbers PT1 to PT27. Scolecodont descriptive terminology follows that of Kielan-Jaworowska (1966).

Scolecodonts from the Prague Basin

Previous records

The first, but also the most disputable, remark on the occurrence of scolecodonts in the Prague Basin is that by Perner

(1894). He found a "conodont", *Prioniodus barrandei* Perner, 1894, in the Silurian rocks of the "Lapworth Colony", subsequently correlated with the Telychian *Streptograptus crispus* graptolite Biozone by Štorch (1994). Perner supposed that his specimen was of polychaete affinity and noted its resemblance to the extant genus *Staurocephalus* Grube, 1855. He used the designation "conodont" merely because the term scolecodont was not coined until considerably later, by Croneis & Scott (1933). Žebera (1935) who probably had this material at his disposal, later interpreted the specimen as a conodont and compared it to his species *Prioniodus perneri* Žebera, 1935. Although this interpretation most probably was correct the type material of *P. barrandei* cannot be located at present, thus further re-evaluation is not possible.

The first detailed study of scolecodonts was by Žebera (1935), who sampled three Silurian localities exposing strata of the *P. latilobus–S. balticus* and *N. ultimus* graptolite biozones. Žebera recovered more than 150 specimens and established nine new species: *Arabellites perneri*, *A. angustidens*, *A. innaequidens*, *A. kettneri*, *Ebetallites ancoraeformis*, *Kettnerites kosoviensis*, *K. depressus*, *Pernerites giganteus* and *Pronereites naviculiformis*. The most common species in the collection is the one he assigned to *A. perneri*, followed by *Pernerites amplus* (the latter was, however, not mentioned in his published paper). The labels in the collection seem to have been prepared for further work that was never completed. Some of the specimens from the Amerika quarries (Liščí Quarry, Mořina area) are closely similar to *A. perneri* but were designated *K. kosoviensis*, indicating that Žebera intended such a reassignment. The collection of Žebera (1935) is housed in the Institute of Geology and Palaeontology, Charles University in Prague under the numbers IGP coll. Žebera 1–154 (not all specimens are present) and at the National Museum in Prague under the number 28368.

Šnajdr (1951) reassigned most of Žebera's taxa to *Kettnerites kosoviensis* Žebera, 1935. The main reason for this was that Šnajdr considered their differences to reflect intraspecific variability. Using the approach of Bergman (1989), the Šnajdr collection would consist of two or three species of *Kettnerites* but the preservation of the specimens does not allow more detailed assessment. The two remaining species of Žebera, *Ebetallites ancoraeformis* and *Pernerites giganteus*, together with *Ildraites*? *budňanensis* Šnajdr, 1951, are of non-paulinitid affinity and need taxonomic revision. Šnajdr obviously was aware that additional species occurred in the samples but left them in open nomenclature or undescribed until it would be possible to match them to apparatus-based species. He worked mainly with specimens that were preserved in associated clusters on the bedding plane surfaces, in order to determine what different types of elements were included in one species. Šnajdr (1951) also emended the diagnosis of *Kettnerites* Žebera, 1935. Unfortunately his study did not include examination of Žebera's original collection but instead he supported the results on his own extensive collections, which consist of several thousand bedding plane specimens from the same stratigraphical interval. Less than one hundred of these specimens belong to genera other than *Kettnerites*, but their proper determination is complicated due to their poor preservation.

The collection of Šnajdr (1951) is presently housed at the National Museum in Prague under collection numbers 32921, 32984 and 32983. For additional information on the historical collections, see Tonarová (2008).

Žebera (1935) and Šnajdr (1951) did not dissolve rocks from the Prague Basin for the recovery of isolated jaws, which generally are essential for accurate taxonomic determination. Despite the remarkable amount of material gathered, the bedding plane specimens are commonly compacted and/or cracked which obviously hampers identification. An attempt by the present authors at dissolving slabs with visible scolecodonts yielded residues with only poorly preserved, usually fragmentary, specimens of little taxonomic value. Therefore, different lithologies and stratigraphical intervals were chosen for this study.

The lower diversity recorded from shale levels in the Prague Basin compared to most of the limestone digested in this study (see below) most likely result from differences in environmental, depositional and/or taphonomical factors, however, the precise interrelationship of which remains to be addressed more closely in the future.

The polychaete fauna of the Kopanina Formation

The new collection comes mainly from the *N. kozlowskii* and *P. latilobus-S. balticus* graptolite biozones. Unlike the previous shale samples of Žebera and Šnajdr, we have focused on limestones in order to recover more three-dimensionally preserved specimens. Altogether the studied collection contains several thousand scolecodonts, including approximately 1100 first and second maxillae. In addition, eight fused jaws and/or semi-articulated tiny maxillary apparatuses (some possibly juveniles) were recovered. Twenty-five different species were identified, not including several unknown jaws that at the present time cannot be reconstructed into apparatuses due to their insufficient number and/or poor preservation. This particularly concerns forms with placognath type apparatuses. The apparatus reconstructions of placognaths are often complicated since different taxa may have certain elements in the apparatus that are virtually indistinguishable. Thus, the actual number of species is estimated to exceed 25.

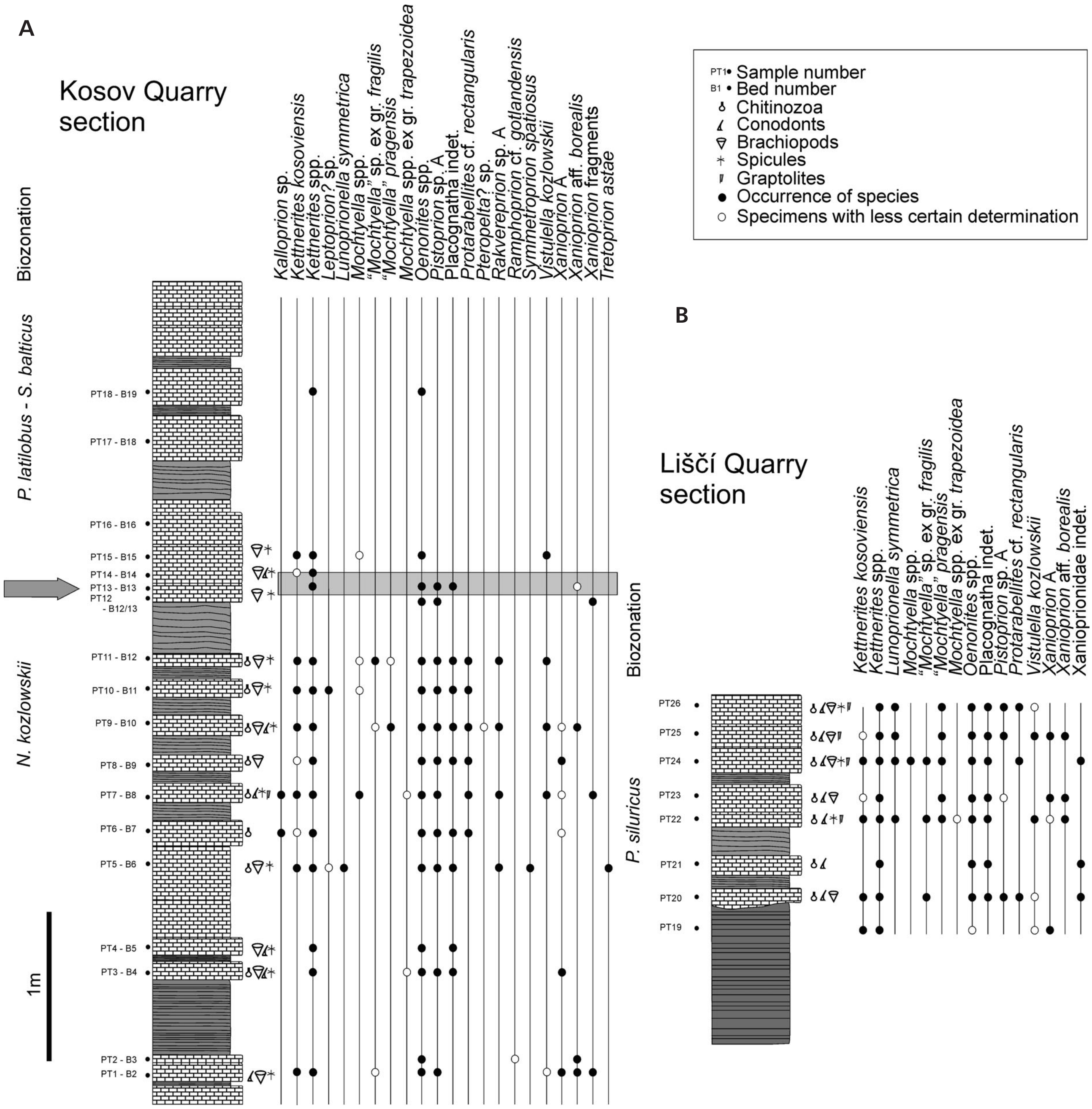


Figure 2. Distribution of scolecodonts in the Kosov and Liščí quarries. • A – the Kosov Quarry section; the lithological column, including bed numbers (B2, etc.), follows Lehnert *et al.* (2007). Arrow pointing to the Kozlowskii event and beginning of the $\delta^{13}C$ excursion. • B – the Liščí Quarry section.

The yield reaches approximately 800 posterior maxillae per kg of rock in the richest sample (PT7), and ranges from 10 to 400 per kg in other productive samples. These are similar or slightly lower numbers than generally reported from the Silurian of Baltica (*e.g.*, Eriksson *et al.* 2004, Hints *et al.* 2006).

The fauna is dominated by polychaetaspids and paulinitids, followed by mochtyellids and xanioprionids. Ramphoprionids are less common, and only rare specimens of tetraprionids, kalloprionids, symmetroprionids and tretoprionids have been found. The polychaete fauna of both quarries is, with few exceptions, closely similar. In the Kosov Quarry the diversity is slightly higher and includes representatives of *Kalloprion* Kielan-Jaworowska, 1962, *Leptoprion* Kielan-Jaworowska, 1966, *Rakvereprion* Mierzejewski, 1978 and *Symmetroprion* Kielan-Jaworowska, 1966 that were not recorded in the Liščí Quarry. This could, however, be attributed also to the greater stratigraphical extent of sampled strata (and more samples) in the former section. The uppermost part of the Kosov Quarry section is composed of gravity flow sediments that yielded only fragmentary scolecodonts, of which only *Kettnerites* Žebera, 1935 and *Oenonites* Hinde, 1879 could be identified. The preservation in general is better in Liščí Quarry due to lithologies and/or post-depositional conditions that apparently did not cause flattening and deformation of the specimens. Similarly, conodonts including both platform and coniform forms are better preserved and more abundant in Liščí Quarry. The distribution of taxa is shown in Fig. 2 and selected characteristic forms are illustrated in Figs 3–6. Individual taxa are discussed further below.

The Kozlowskii/Lau event and its influence on the polychaete faunas

The Ludfordian (late Silurian) environmental and biological crisis known as Lau and/or Kozlowskii event (for Lau and Kozlowskii event correlation problems, see Manda *et al.* 2012 and references therein) has received increasing attention since the introduction of the Lau event by Jeppsson (1993) and Kozlowskii event by Urbanek (1993). This is not surprising considering that the event is associated with the largest positive carbon isotope excursion of the Phanerozoic (Lehnert *et al.* 2003, Munnecke *et al.* 2003), dramatic faunal turnovers (see summary in Jeppsson & Aldridge 2000, Calner 2008) and a collapse of the marine ecosystem (Calner 2005). Profound biotic changes have been recorded, *e.g.*, among conodonts (Jeppsson & Aldridge 2000), acritarchs (Stricanne *et al.* 2006), graptolites (Urbanek 1993, Štorch 1995, Melchin *et al.* 1998, Manda *et al.* 2012), cephalopods (Manda 2008) and fish (Eriksson *et al.* 2009). Barrick *et al.* (2010, p. 32), on the other hand, recorded "normal ecological adjustments to environmental changes" rather than major extinctions and ecosystem collapse, although, as noted by those authors, based on limited faunal data. Similarly Slavík *et al.* (2010) recorded moderate changes in the conodont fauna of the Prague Basin, incomparable to those changes recorded in Gotland, Sweden, or Australia. According to Manda & Kříž (2006) also pelagic orthocerids and the nektonic *Ceratiocaris* passed unaffected through the critical interval.

Jeppsson & Aldridge (2000, p. 1144), referring to Bergman (1989), were the first ones to interpret changes in polychaete faunas as a response to Lau event. Bergman (1989) recorded gradual faunal changes in the Hemse-Eke interval on Gotland. Later, Eriksson *et al.* (2004) concluded that approximately one-third of the polychaete taxa on Gotland went extinct during the event and also reported some lineages with Lazarus gaps. Eriksson & Frisk (2011) noted that the environmental changes linked to the Lau event did not seem to have affected polychaetes as profoundly as planktic and nektic organisms such as graptolites, fish and conodonts.

In this study only the Kosov Quarry section records the event interval (Fig. 2, Manda *et al.* 2012). With the beginning of the carbon isotope excursion (based on $\delta^{13}C$ data of Lehnert *et al.* 2007) the number of polychaete genera decreases from 15 to 4, and only *Kettnerites* spp., *Oenonites* spp. and *Vistulella kozlowskii* Kielan-Jaworowska, 1961 were recorded in the beds above the LAD of *N. kozlowskii* in bed No. 15. In overlying strata only *Kettnerites* spp. and *Oenonites* spp. occur (Fig. 2A), which indicates a dramatic decrease in polychaete diversity across the event. However, it should be kept in mind that the studied succession is stratigraphically restricted and only a limited number of samples represent post-event strata (including the graptolite recovery interval of the Kozlowskii event *sensu* Manda *et al.* 2012). Moreover, those latter few samples come from gravity flow deposits (turbidites or tempestites according to Lehnert *et al.* 2007), where only fragmentary scolecodonts (*Kettnerites* spp. and *Oenonites* spp.) were found. Thus, it cannot be excluded that the lack or rarity of scolecodonts in these beds represents a taphonomical bias.

Nonetheless, *K. kosoviensis* re-appears at least in the shale above this interval, indicating an uninterrupted range through the entire succession, or a reintroduction once environmental conditions stabilized. In addition, some species (*e.g.*, *Protarabellites rectangularis* Eriksson, 2001, *Kettnerites sisyphi* Bergman, 1989, various species of *Oenonites*) have been reported from stratigraphically younger beds elsewhere (Hints 1998, Eriksson 2001), showing that they did not become extinct. On the other hand, *Pistoprion* Kielan-Jaworowska, 1966, which is very common in pre-event strata, has not been reported from the latest Silurian or Devonian (except for a questionable identification by Jansonius & Craig 1972). Although our data suggest a faunal reorganisation, it is obvious that detailed, high resolution studies, preferably also from different regions, are needed in order to resolve precisely how the Kozlowskii/Lau event affected polychaetes.

Palaeobiogeographical significance

Several new reports on Silurian scolecodonts have been published over the last few decades: for an overview, see Eriksson *et al.* (2004). More recently, Hints & Eriksson (2007a, b) and Eriksson *et al.* (in press) discussed the biogeographical patterns of Silurian (and Ordovician) polychaete genera, stressing a strong sampling bias: the majority of the material comes from Baltica, especially Sweden and Estonia, as well as from erratic boulders found in Poland. Some data derive also from Avalonia and Laurentia, whereas the Gondwanan realm is scarcely studied. Therefore the collection from the Prague Basin described herein, representing a part of the peri-Gondwanan microcontinent Perunica (Havlíček *et al.* 1994), is important for understanding the global biogeographical patterns of polychaetes during the Silurian.

The previously known Silurian polychaete assemblages (Eriksson *et al.* 2004; Hints & Eriksson 2007a, b; Eriksson *et al.* in press) are generally similar to those of the Late Ordovician. They are commonly dominated by polychaetaspids, paulinitids and mochtyellids (*e.g.*, *Oenonites*; *Kettnerites*; *Mochtyella* Kielan-Jaworowska, 1961; *Pistoprion*; *Vistulella* Kielan-Jaworowska, 1961), whereas ramphoprionids, atraktoprionids, kalloprionids, symmetroprionids and others may also be present, albeit generally considerably less abundantly. Some genera, for instance *Symmetroprion*, *Skalenoprion* Kielan-Jaworowska, 1966, *Langeites* Kielan-Jaworowska, 1966 and *Lanceolatites* Bergman, 1987 occur primarily in the Silurian, and only a few taxa typical of the Ordovician, such as polychaeturids in the Baltic faunas, are rare or missing in the Silurian. Previous reports on the palaeobiogeography of polychaetes have shown that they, like most other groups of fossils (*e.g.* Armstrong & Owen 2002), display a decrease in endemism from the Ordovician to the Silurian (Hints & Eriksson 2007a, b; Eriksson *et al.* in press).

The late Silurian Prague Basin fauna is characterized by an overall dominance of paulinitids, polychaetaspids and mochtyellids, which is consistent with the most abundant and diverse families in Baltica (Eriksson *et al.* 2004, Eriksson 2006). It is noteworthy that none of the genera identified appears to be endemic to the Prague Basin. However, several taxa that are common elsewhere, particularly in Baltica, were not recorded in the studied collection. For instance, paulinitids are represented only by *Kettnerites*, whereas additional genera are reported from approximately coeval strata from other regions (Bergman 1989, Eriksson *et al.* 2004). Similarly, *Kozlowskiprion* Kielan-Jaworowska, 1966 and other polychaetaspid genera (except for *Oenonites*) known from Gotland (Eriksson 1997, 1998) have not been recorded in the Prague Basin thus far. A particular feature of the present collections is also the scarcity of atraktoprionids and skalenoprionids, both of which are sometimes abundant in the Baltic region (*e.g.*, Eriksson 2006; note, however, that a few atraktoprionid jaws were recorded in Šnajdr's bedding plane collections). The relatively lower diversity, compared to Baltic faunas, can probably be attributed to the limited size and restricted stratigraphical and environmental range of the Bohemian collections. Additional genera, also in common with other regions, will most likely be recorded when more material becomes available.

Notwithstanding this, the present collection represents the most diverse Silurian polychaete fauna from Gondwana/peri-Gondwana and several families (and genera) are identified from this area for the first time. These include symmetroprionids, tetraprionids, tretoprionids and ramphoprionids. Eriksson (2002) noted that ramphoprionids were not recorded from Gondwana and peripheral areas and that their known occurrences indicated that they were confined to near equatorial latitudes during the Silurian. The new Prague Basin findings of *Protarabellites* Stauffer, 1933 and *Ramphoprion* Kielan-Jaworowska, 1962 extend the distribution of ramphoprionids and reveal additional faunal similarities with Baltica.

Similarities of the Bohemian faunas with those known from Baltica, Laurentia and Siberia are noted also at the species level. Findings of *Pistoprion* sp. A, *Vistulella kozlowskii*, *Symmetroprion spatiosus* (Hinde, 1882), *Ramphoprion* cf. *gotlandensis* Eriksson, 2001, *Protarabellites* cf. *rectangularis* Eriksson, 2001 and *Kettnerites* cf. *sisyphi* suggest a wide, possibly cosmopolitan, distribution of these species in the late Silurian. Other species recorded previously from the Baltic region only (*e.g.*, *Tretoprion astae* Hints, 1999) appear now to have had a wider distribution.

In most palaeogeographical reconstructions there is an agreement that Baltica and Laurentia (Laurussia) were located close to the palaeoequator during the late Silurian and represented by tropical to subtropical environments (*e.g.* Torsvik *et al*. 1992, Cocks & Torsvik 2002). The position of Perunica is less well constrained, but according to Tait *et al*. (1997), Cocks & Torsvik (2002) and Fatka & Mergl (2009) it was situated in more temperate climates in the peri-Gondwanan area at *ca* 30° S. Havlíček (1999) argued, based on benthic faunas (brachiopods, trilobites and other fossils), that Perunica was much closer to Baltica than any other region of Gondwana, specifying its position to the northeastern corner of peri-Gondwana. A similar palaeogeographic scenario is suggested from the faunal distribution of nautiloid cephalopods (Stridsberg 1985; Stridsberg & Turek 1997; Manda 2007, 2008; Turek & Manda 2011) and particularly shallow water bivalves (Kříž 1999, 2008). This study also supports close faunal links between Perunica and Baltica and, at least for jawed polychaetes, there seem to have been few climatic or other palaeobiogeographical barriers between these palaeocontinents. Moreover, the new Bohemian collection corroborates the idea of most polychaete genera and many species being geographically wide spread during the Silurian (Hints & Eriksson 2007a, b; Eriksson *et al*. in press).

Systematic palaeontology

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Order Eunicida Dales, 1963
Superfamily Eunicea Grube, 1852
Family Mochtyellidae Kielan-Jaworowska, 1966

Genus *Mochtyella* Kielan-Jaworowska, 1961

Type species. – *Mochtyella cristata* Kielan-Jaworowska, 1961.

“*Mochtyella*” *pragensis* sp. nov.
Figure 3A–S

Holotype. – Right MI (Fig. 3C, D), from sample PT23, specimen number PT27.1, Liščí Quarry.

Type horizon and locality. – Liščí Quarry, Prague Basin, Kopanina Formation, Ludfordian (upper Silurian).

Material. – 12 right MI, 13 left MI.

Etymology. – The specific name refers to the Prague Basin, the location of the species.

Diagnosis. – “*Mochtyella*” *pragensis* is tentatively assigned to *Mochtyella* but differs from the typical species of the genus by its characteristically fragile maxillae, which are similar to those of *M. fragilis* and *M. grazynae*. It differs from *M. fragilis* in having longer, more prominent and more anteriorly placed second ridge in right MI, and posteriorly protruding laeobasal ridge in left MI. *“M.” pragensis* differs from *M. grazynae* also in having anteriorly curved main ridges instead of straight ones.

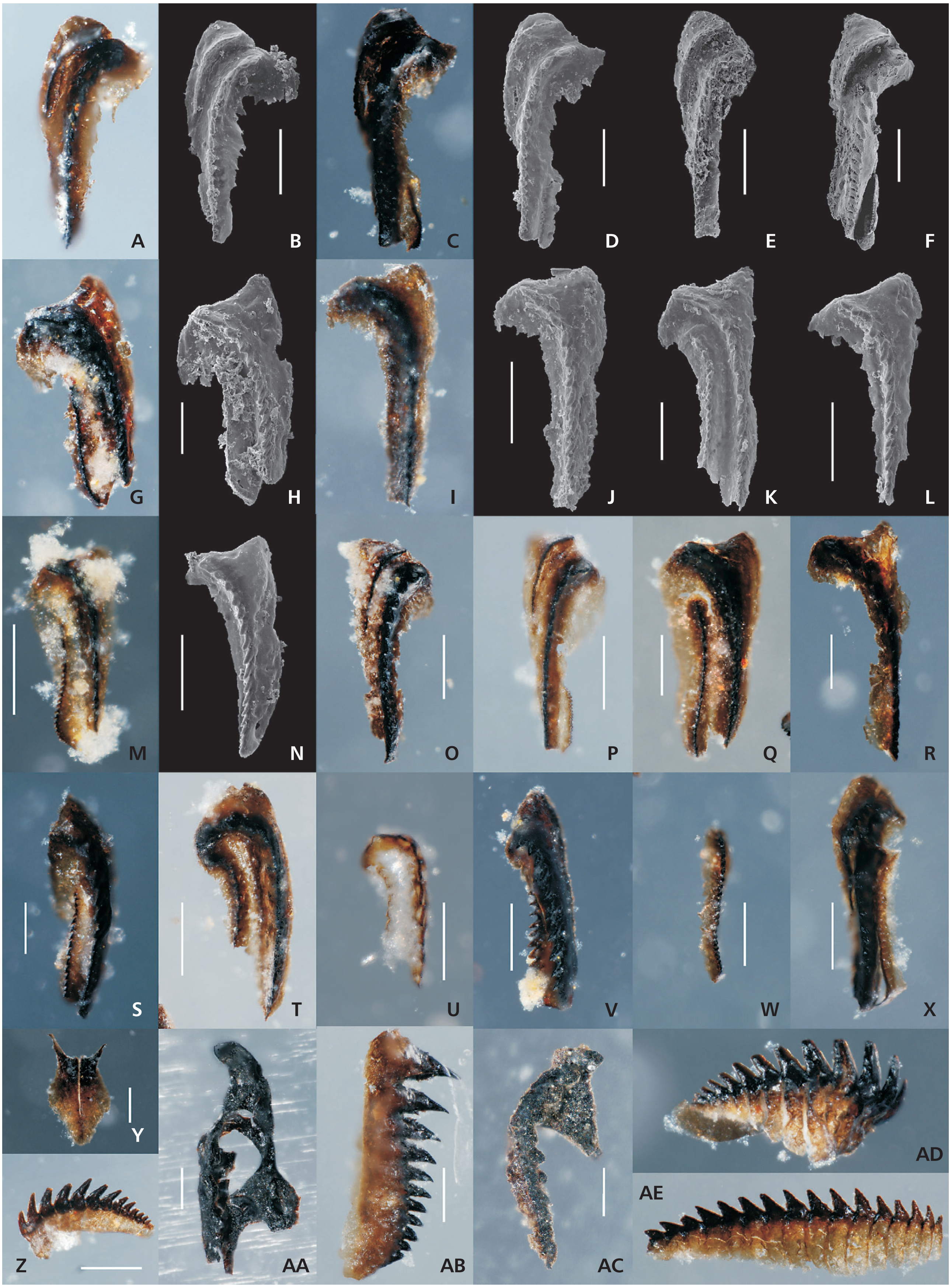
Description. – Both first maxillae are compound jaws of approximately the same length. Except for the black or dark brown denticulated ridges the jaws are almost translucent, composed of yellowish-brown thin membrane.

Right MI is longitudinally elongated and provided with three denticulated ridges, with a typically cordate anterior part. The length is 280–410 μm, the width 110–150 μm (0.3–0.5 of jaw length). In dorsal view the anterior part of the main ridge is almost right-angled. It is composed of 15 to 18 denticles, gradually decreasing in size posteriorly. The second ridge encompasses the left anterior part of the main ridge, forming a semi-arch, ending almost in the middle of the jaw. Its length is 80–220 μm (0.4–0.6 of jaw length). The denticulated basal ridge is situated on the right side of the main ridge but is quite commonly broken off. It is straight, parallel with the posterior part of the main ridge. Its length is 80–115 μm (0.3 of jaw length). In ventral view there is a gaping pulp cavity with three ridges that are distinctly separated.

Left MI is longitudinally elongated with two denticulated ridges, sometimes accompanied by a secondary ridge. The overall shape is suboval, in the anterior part almost rectangular. The length is 285–450 μm, the width 110–225 μm (0.3–0.5 of jaw length). The main ridge is composed of 14 to 17 denticles, decreasing in size posteriorly. In dorsal view the main ridge is in the anterior part almost right-angled. The laeobasal ridge is attached to the left side of the main ridge. It is straight, parallel to the posterior part of the main ridge, filling the space delimited by the flexure, and ending a little beyond the main ridge. The length of the laeobasal ridge is 154–290 μm (0.4–0.6 of jaw length). The length of the second ridge, if present, is 123–154 μm (0.35–0.4 of jaw length). In ventral view there is a gaping pulp cavity, noticeably subdivided into two parts (main and laeobasal ridge).

Remarks. – This species belongs to the same group of taxa as *M. fragilis* Szaniawski, 1970 and *M. grazynae* Mierzejewski, 1978. The outline of their jaws, characteristic laeobasal ridges, and the “fragile” form of the jaws differ from those of typical *Mochtyella* (including the type species *M. cristata* and also *M. polonica*), suggesting that they may represent a separate mochtyellid genus. Since the latter still awaits formal description, we assign the new species to “*Mochtyella*”.

Figure 3. Light microscopy images of selected scolecodonts showing the colours and thin membranes, to be compared with SEM micrographs. All specimens are in dorsal view, except possibly Z, AB, AD and AE, that may be in lateral view. Scale bars correspond to 100 μm. • A–S – “*Mochtyella*” *pragensis* n. sp. A, B – right MI No. PT27.2 from sample PT23, Liščí Quarry. C, D – right MI No. PT27.1 (holotype) from sample PT23, Liščí Q. E – right MI No. PT23E.1 from sample PT23, Liščí Q. F – right MI No. PT22H.1 from sample PT22, Liščí Q. G, H – same specimen, left MI No. PT27.3 from sample PT22, Liščí Q. I, J – left MI with broken laeobasal ridge (=lb ridge) No. PT27.4 from sample PT22, Liščí Q. K – left MI No. PT27.5 from sample PT22, Liščí Q. L – left MI with broken lb ridge No. PT27.6 from sample PT22, Liščí Q. M – left MI No. PT26D.1 from sample PT26, Liščí Q. N – left MI with broken lb ridge No. PT27.7 from sample PT22, Liščí Q. O – right MI No. PT24D.1 from sample PT24, Liščí Q. P – right MI No. PT25G.1 from sample PT25, Liščí Q. Q – left MI No. PT25G.2 from sample PT25, Liščí Q. R – left MI with broken lb ridge No. PT24D.2 from sample PT24, Liščí Q. S – left MI No. PT22F.1 from sample PT22, Liščí Q. • T, U – *Mochtyella* sp. ex gr. *fragilis* Szaniawski, 1970. T – left MI No. PT25G.5 from sample PT25, Liščí Q. U – left MI No. PT24D.3 from sample PT24, Liščí Q. • V – *Mochtyella* sp. ex gr. *trapezoidea* Kielan-Jaworowska, 1966, left MI No. PT22F.2 from sample PT22, Liščí Q. • W, X – *Vistulella kozlowskii* Kielan-Jaworowska, 1961. W – broken piece No. PT22F.3 from sample PT22, Liščí Q. X – part of an apparatus No. PT25G.3 from sample PT25, Liščí Q. • Y – carriers of a polychaetaspid No. PT26A.1 from sample PT26, Liščí Q. • Z – *Lunoprionella symmetrica* Eisenack, 1975, No. PT24D.4 from sample PT24, Liščí Q. • AA – *Leptoprion*? sp., right MI No. PT10B.1 from sample PT10, Kosov Q. • AB – *Rakvereprion* sp. A?, basal plate No. PT25G.4 from sample PT25, Liščí Q. • AC – *Tretoprion astae* Hints, 1999, right MI No. PT5D.1 from sample PT5, Kosov Q. • AD, AE – *Lunoprionella symmetrica* Eisenack, 1975. AD – No. PT26D.2 from sample PT26, Liščí Q. AE – No. PT25G.6 from sample PT25, Liščí Q.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"Mochtyella" pragensis is most similar to *"Mochtyella"* sp. D of Hints *et al.* (2006, pl. 2:3) from the uppermost Llandovery of Estonia. It differs from the latter in having a longer second ridge and laeobasal ridge. Eller (1963, p. 175, pl. 1, figs 15–17) described a similar form from the Devonian Dundee limestone of the Sibley and Dundee quarries (Michigan) under the name *Starocephalites ejectus*. It possesses a similar second ridge but the laeobasal ridge seems to be broken. There are some additional species of Eller assigned to *Staurocephalites* Hinde, 1879, that are quite similar to "*M.*" *pragensis* but type collection studies are necessary for more detailed assessments.

Occurrence. – Liščí and Kosov quarries, late Ludfordian, Silurian.

Annotated list of taxa

In the following list, selected characteristic taxa are briefly discussed. Some specimens could be determined only to genus level or higher, because of their poor preservation.

Family Mochtyellidae Kielan-Jaworowska, 1966

Discussion. – Mochtyellids generally are abundant in Silurian strata (Eriksson *et al.* 2004). In the Prague Basin *Pistoprion* Kielan-Jaworowska, 1966 dominates, but *Vistulella* Kielan-Jaworowska, 1961 is also relatively common. The genus *Mochtyella sensu lato* is represented mainly by specimens of the *M. fragilis* group; only a few specimens of *M. polonica* group and questionable specimens of *M. trapezoidea* group are present. The identification of mochtyellids has, to some extent, been hampered by preservation. Thus many fragmented specimens were classified merely as Placognatha indet. (Figs 2, 4V, Y).

Genus *Mochtyella* Kielan-Jaworowska, 1961

***Mochtyella* sp. ex gr. *fragilis* Szaniawski, 1970** (Figs 3T, U, 4E) occurs in several samples from both sections studied, and sometimes together with "*M.*" *pragensis* (see above). It has a thin and translucent jaw wall, darker large denticles on the main ridges of both MI, and a long laeobasal ridge. It is most similar to *M. fragilis*, but differs in lacking the second ridge on the right MI. Both this species and *M. fragilis* differ considerably from the type species of *Mochtyella* and therefore the present generic assignment is tentative. Mierzejewski (1978, p. 275) argued that mochtyellids possessing no second ridge cannot be assigned to *Mochtyella*. Here, however, we consider that the presence/absence of secondary ridge may be a species rather than genus level character within some groups of taxa.

***Mochtyella* sp. ex gr. *polonica* Kielan-Jaworowska, 1966** (Fig. 4C). This species or group of species is quite rare but some specimens might have been missed because of their poor preservation.

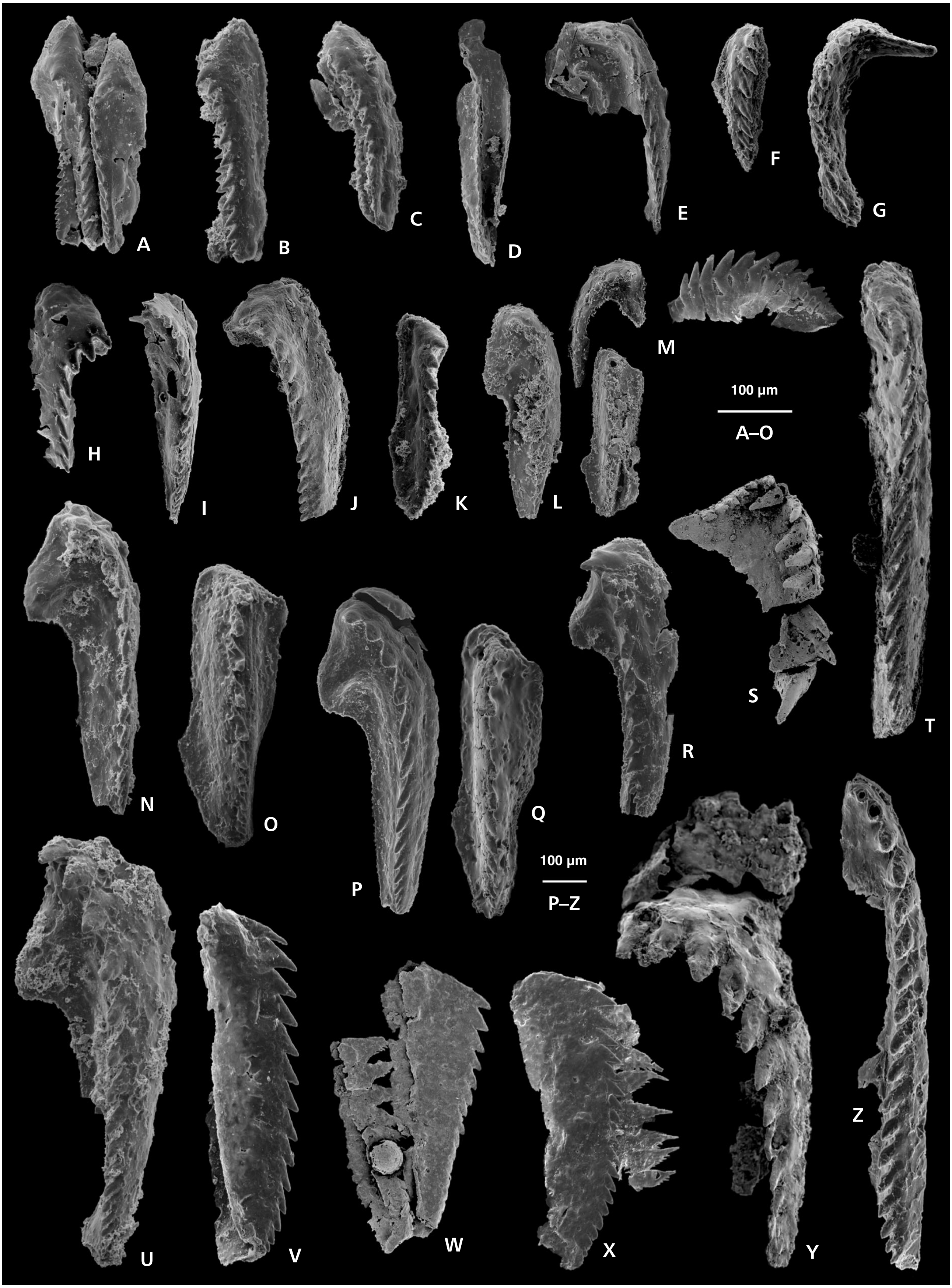
"*Mochtyella*" *pragensis* sp. nov. (Fig. 3A–S) occurs in both the Liščí and Kosov quarries. See the systematic description and further discussion above.

***Mochtyella* sp. ex gr. *trapezoidea* Kielan-Jaworowska, 1966** (Figs 3V, 4B). Only a few questionable specimens are present in samples PT3, PT7 and PT22. Even though specimens are recorded from both the Kosov and Liščí quarries, more precise determination is not possible due to their preservation.

Genus *Pistoprion* Kielan-Jaworowska, 1966

***Pistoprion* sp. A** (Fig. 4K, L, N–R, U) is the most common taxon after *Kettnerites* and *Oenonites* in both sections

Figure 4. SEM micrographs of selected mochtyellids and xanioprionids. All specimens are in dorsal view, except M, V to X in lateral(?) view. Scale bars correspond to 100 μm, the first one for figures A to O and the second for P to Z. Two scale bars are used because of the big difference in size of the specimens. • A – *Mochtyella* sp., part of an apparatus No. PT26H.3 from sample PT26, Liščí Quarry. • B – *Mochtyella* sp. ex gr. *trapezoidea* Kielan-Jaworowska, 1966, left MI No. PT27.10 from sample PT22, Liščí Q. • C – *Mochtyella* sp. ex gr. *polonica* Kielan-Jaworowska, 1966, left MI No. PT27.11 from sample PT22, Liščí Q. • D – *Vistulella kozlowskii* Kielan-Jaworowska, 1961, incomplete left MI No. PT26H.2 from sample PT26, Liščí Q. • E – *Mochtyella* sp. ex gr. *fragilis* Szaniawski, 1970, incomplete left MI No. PT20A.2 from sample PT20, Liščí Q. • F – *Tetraprion* sp. *sensu* Szaniawski, 1970?, MII? No. PT27.13 from sample PT23, Liščí Q. • G – *Xanioprion* aff. *borealis*, right MII No. PT27.14 from sample PT23, Liščí Q. • H, I – mochtyellids. H – right jaw No. PT9A.5 from sample PT9, Kosov Q. I – left MI No. PT1A.4 from sample PT1, Kosov Q. • J – *Vistulella kozlowskii* Kielan-Jaworowska, 1961, left MI No. PT22H.3 from sample PT22, Liščí Q. • K, L – *Pistoprion* sp. A. K – right MI No. PT27.15 from sample PT23, Liščí Q. L – left and right MI, right MII from the same apparatus Nos. PT11C.2–4 from sample PT11, Kosov Q. • M – *Lunoprionella symmetrica* Eisenack, 1975, No. PT5A.5 from sample PT5, Kosov Q. • N–R – *Pistoprion* sp. A. N – left MI No. PT27.12 from sample PT26, Liščí Q. O – right MI No. PT11A.6 from sample PT11, Kosov Q. P – left MI No. PT11A.7 from sample PT11, Kosov Q. Q – right MI No. PT11B.2 from sample PT11, Kosov Q. R – left MI No. PT11A.8 from sample PT11, Kosov Q. • S – *Xanioprion* sp. A, left MII No. PT5C.7 from sample PT5, Kosov Q. • T – *Xanioprion*? sp. A, left MI No. PT26G.2 from sample PT26, Liščí Q. • U – *Pistoprion* sp. A, left MI No. PT9A.4 from sample PT9, Kosov Q. • V – Placognatha indet., No. PT22G.9 from sample PT22, Liščí Q. • W, X – *Rakvereprion* sp. A. W – flattened MI, No. PT5C.8 from sample PT5, Kosov Q. X – flattened MI No. PT5A.4 from sample PT5, Kosov Q. • Y – Placognatha indet., left jaw No. PT9B.4 from sample PT9, Kosov Q. • Z – *Xanioprion* sp., left MI No. PT7A.7 from sample PT7, Kosov Q.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studied. Despite having an informal name here, this species is well known from several other Silurian regions around the world, including Gotland (Bergman 1979), Estonia (Hints *et al.* 2006, Rubel *et al.* 2007), Siberia (Männil & Zaslavskaya 1985), and Arctic Canada (Hints *et al.* 2000). The latter authors have used the historical name *Eunicites serrula* Hinde, 1880 or *Pistoprion serrula*. However, inspection of Hinde's type material (by MEE and PT) suggests that this may be a misidentification (*cf.* Eriksson *et al.* 2004). Therefore open nomenclature is used here with the aim to describe the species formally based on better preserved material than what is currently available from the Prague Basin. The stratigraphical range of *Pistoprion* sp. A seems to be rather extensive, spanning from at least the upper Llandovery to the Ludlow.

Pistoprion is regarded as being indicative of relatively shallow water facies, typical for nearshore environments and not occurring in the central part of palaeobasins (Hints 2000, Rubel *et al.* 2007). Its presence thus seems to support the interpretation of a relative sea-level fall in the studied stratigraphical interval (Lehnert *et al.* 2003, 2007).

Genus *Rakvereprion* Mierzejewski, 1978

***Rakvereprion* sp. A** (Figs 3AB, 4W, X) has been recorded from the middle part of the sampled interval at Kosov Quarry. *Rakvereprion* Mierzejewski, 1978 possesses simple, symmetrical posterior maxillae and long basal and laeobasal plates that have secondarily denticulated ridges. Compared to the Upper Ordovician *Rakvereprion balticus* (Eisenack, 1975), the MI of the Kosov Quarry specimens are larger and their outline in lateral view is subrectangular rather than subtriangular. These differences may reflect evolutionary changes within the genus from the Late Ordovician to the Ludfordian. Previous Silurian occurrences of *Rakvereprion* are rare and limited to a few specimens recovered from the Llandovery/Wenlock boundary beds of Estonia (OH, unpublished data).

Several authors (Mierzejewski 1978; Hints 2000, 2001; Eriksson & Frisk 2011) have noted that the Late Ordovician *Rakvereprion* is a stenotopic genus preferring deeper shelf settings. Thus the findings of *Rakvereprion* from the lower part of the Kosov Quarry section may reflect slightly different environmental settings than those in the upper part and of the Liščí Quarry section. This agrees with previous interpretations of an upwards shallowing environment (Horný 1955).

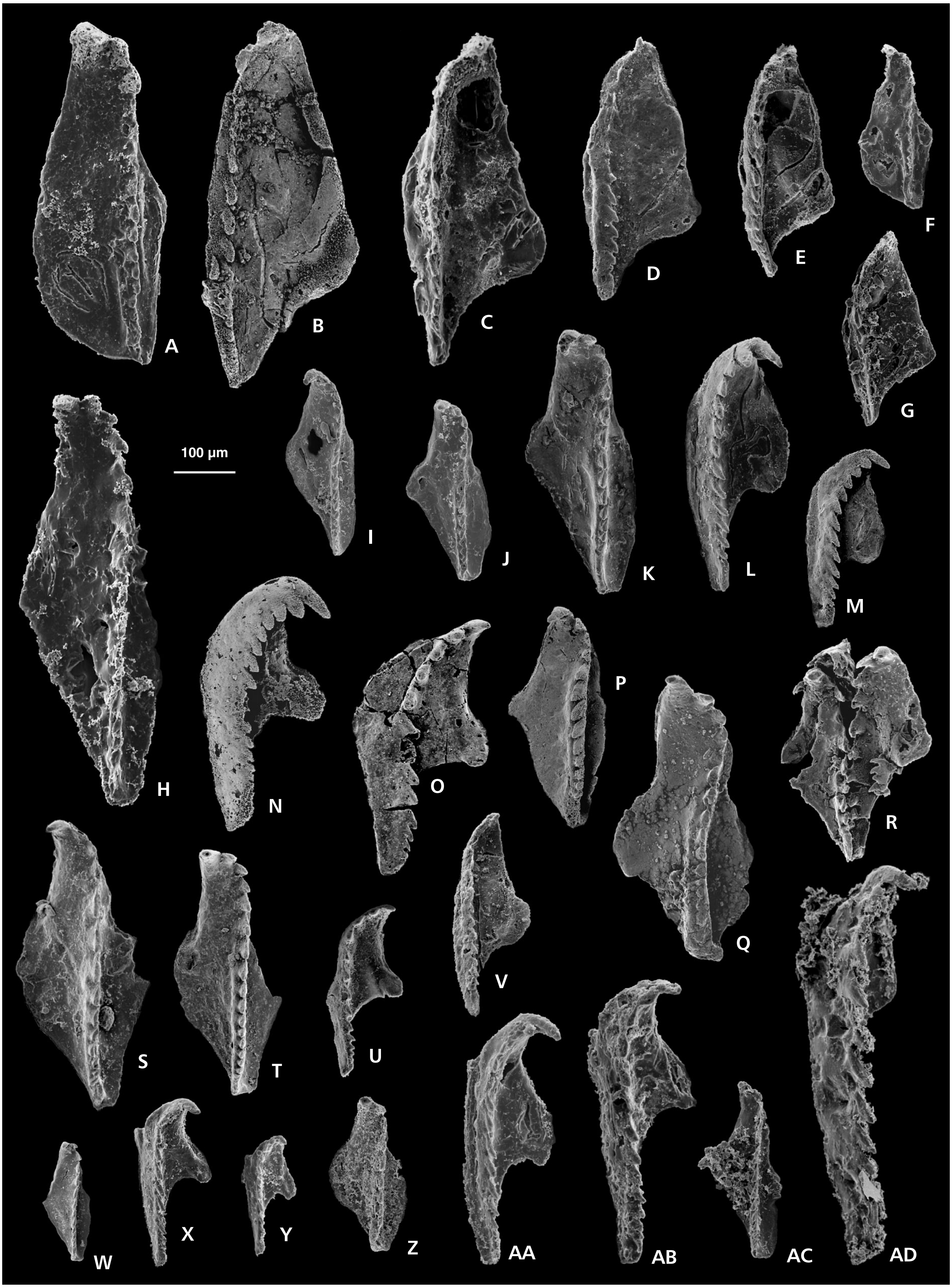
Genus *Vistulella* Kielan-Jaworowska, 1961

***Vistulella kozlowskii* Kielan-Jaworowska, 1961** (Figs 3W, X, 4D, J) is a rather common taxon in the collections studied. The left MI of *Vistulella* may be difficult to identify since similar elements are found also in other placognath taxa. Moreover, the right MI, especially if poorly preserved, are similar to those of *Pistoprion*. Therefore, some occurrences of *Vistulella* may have been overlooked (and placed within the Placognatha indet. category). Based on published records, the stratigraphical range of *V. kozlowskii* is one of the longest among Early Palaeozoic jawed polychaetes, extending from the Darriwilian (Hints & Eriksson 2007a) to the Ludlow (the present collection). It cannot be excluded that this species name actually holds more than one species. However, at present a finer subdivision of individual species seems impossible. Geographically, Silurian *Vistulella* has been reported from Estonia (Hints *et al.* 2006), Gotland (MEE, unpublished data), Arctic Canada (Hints *et al.* 2000) and Severnaya Zemlya (Männil & Zaslavskaya 1985). Adding the herein reported occurrence from Perunica, it can be seen that *Vistulella* was widely distributed in the Silurian.

Family Xanioprionidae Kielan-Jaworowska, 1966

Discussion. – Xanioprionids are common throughout both sections studied, below the Kozlowskii event. Unfortunately the specimens are quite often fragmented which

Figure 5. SEM micrographs of selected polychaetaspids, ramphoprionids and ?polychaeturids, all specimens are in dorsal view. Scale bar corresponds to 100 μm except for Fig. R and AC where it corresponds to 200 μm. • A–G – *Protarabellites* cf. *rectangularis* Eriksson, 2001. A – left MI No. PT11A.3 from sample PT11, Kosov Quarry. B – right MI No. PT5C.2 from sample PT5, Kosov Q. C – right MI No. PT27.9 from sample PT9, Kosov Q. D – right MI No. PT5A.2 from sample PT5, Kosov Q. E – right MI No. PT7A.5 from sample PT7, Kosov Q. F – left MI No. PT9A.3 from sample PT9, Kosov Q. G – right MI No. PT25A.2 from sample PT25, Liščí Q. • H – *Oenonites* sp., left MI No. PT11A.5 from sample PT11, Kosov Q. • I–M – *Oenonites* cf. *olavi* Eriksson, 1997. I – left MI No. PT25A.3 from sample PT25, Liščí Q. J – left MI No. PT25A.4 from sample PT25, Liščí Q. K – left MI No. PT1A.3 from sample PT1, Kosov Q. L – right MI No. PT1A.2 from sample PT1, Kosov Q. M – right MI No. PT5C.6 from sample PT5, Kosov Q. • N–P – *Oenonites* cf. *jennyensis* Eriksson, 1997. N – right MI No. PT5C.5 from sample PT5, Kosov Q. O – right MI No. PT5C.4 from sample PT5, Kosov Q. P – left MI No. PT5C.3 from sample PT5, Kosov Q. • Q–V – *Oenonites* sp. Q – left MI No. PT13A.2 from sample PT13, Kosov Q. R – part of the apparatus No. PT9B.3 from sample PT9, Kosov Q. S – left MI No. PT9B.2 from sample PT9, Kosov Q. T – left MI No. PT26G.1 from sample PT26, Liščí Q. U – right MI No. PT7A.6 from sample PT7, Kosov Q. V – right MI No. PT5A.3 from sample PT5, Kosov Q. • W, X – *Oenonites* cf. *gadomskae* Kielan-Jaworowska, 1966. W – left MI No. PT26H.1 from sample PT26, Liščí Q. X – right MI No. PT23E.2 from sample PT23, Liščí Q. • Y–AB – *Oenonites* sp. Y – right MI No. PT22G.8 from sample PT22, Liščí Q. Z – left MI No. PT11C.1 from sample PT11, Kosov Q. AA – right MI No. PT11A.4 from sample PT11, Kosov Q. AB – right MI No. PT9A.2 from sample PT9, Kosov Q. • AC – *Oenonites* sp., left MI, No. PT23E.3 from sample PT23, Liščí Q. • AD – *Pteropelta*? sp., right MI No. PT9B.1 from sample PT9, Kosov Q.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complicates proper determination and may distort their actual representation in the sections.

Genus *Xanioprion* Kielan-Jaworowska, 1962

***Xanioprion* aff. *borealis* Kielan-Jaworowska, 1962** (Fig. 4G). The second maxillae were found in both sections and are closely similar to those of *X. borealis* but additional elements are needed for unambiguous identification. *Xanioprion borealis* was originally described from Ordovician boulders from Poland (Kielan-Jaworowska 1962) and later the stratigraphical range was extended into the Wenlock (Eriksson *et al.* 2004). This taxon may be conspecific with *Lumbriconereites falciformis* Hinde, 1882, described from Gotland, Sweden.

***Xanioprion* sp. A.** (Fig. 4S, T) is recorded throughout both sections. This species differs from *X.* aff. *borealis* in having wider outer face and concave posterior margins in MII and longer MI, developed as clearly discrete jaws. It resembles *Xanioprion* sp. B *sensu* Hints (2000) reported from the Darriwilian to Wenlock (Eriksson & Hints 2009).

Family Tetraprionidae Kielan-Jaworowska, 1966

Genus *Tetraprion* Kielan-Jaworowska, 1966

?*Tetraprion* sp. *sensu* Szaniawski, 1970 (Fig. 4F). A single maxilla was found in sample PT23. Its identification is based on close similarity to forms discussed by Szaniawski (1970), Hints (2000), Hints & Eriksson (2007a, figs 3G, H, P) and Rubel *et al.* (2007, fig. 6) from the Upper Ordovician to Wenlock of the Baltic region and North America. From the latter regions abundant isolated jaws and several fused apparatuses of the same genus have been recovered. The assignment to *Tetraprion* is, however, tentative; more likely it represents a new tetraprionid genus.

Family Symmetroprionidae Kielan-Jaworowska, 1966

Genus *Symmetroprion* Kielan-Jaworowska, 1966

***Symmetroprion spatiosus* (Hinde, 1882)** (Fig. 6M). A single characteristic right MI was found in sample PT5 from Kosov Quarry. *Symmetroprion* is common in the Wenlock to late Ludlow reef-related environments on Gotland (Bergman 1995) and is known also to occur in shallow-water environments of Estonia (Rubel *et al.* 2007) and Arctic Canada (Hints 2000). Recently, Hints & Eriksson (2007a) found the oldest members of the genus from the middle Upper Ordovician of the USA.

Family Polychaetaspidae Kielan-Jaworowska, 1966

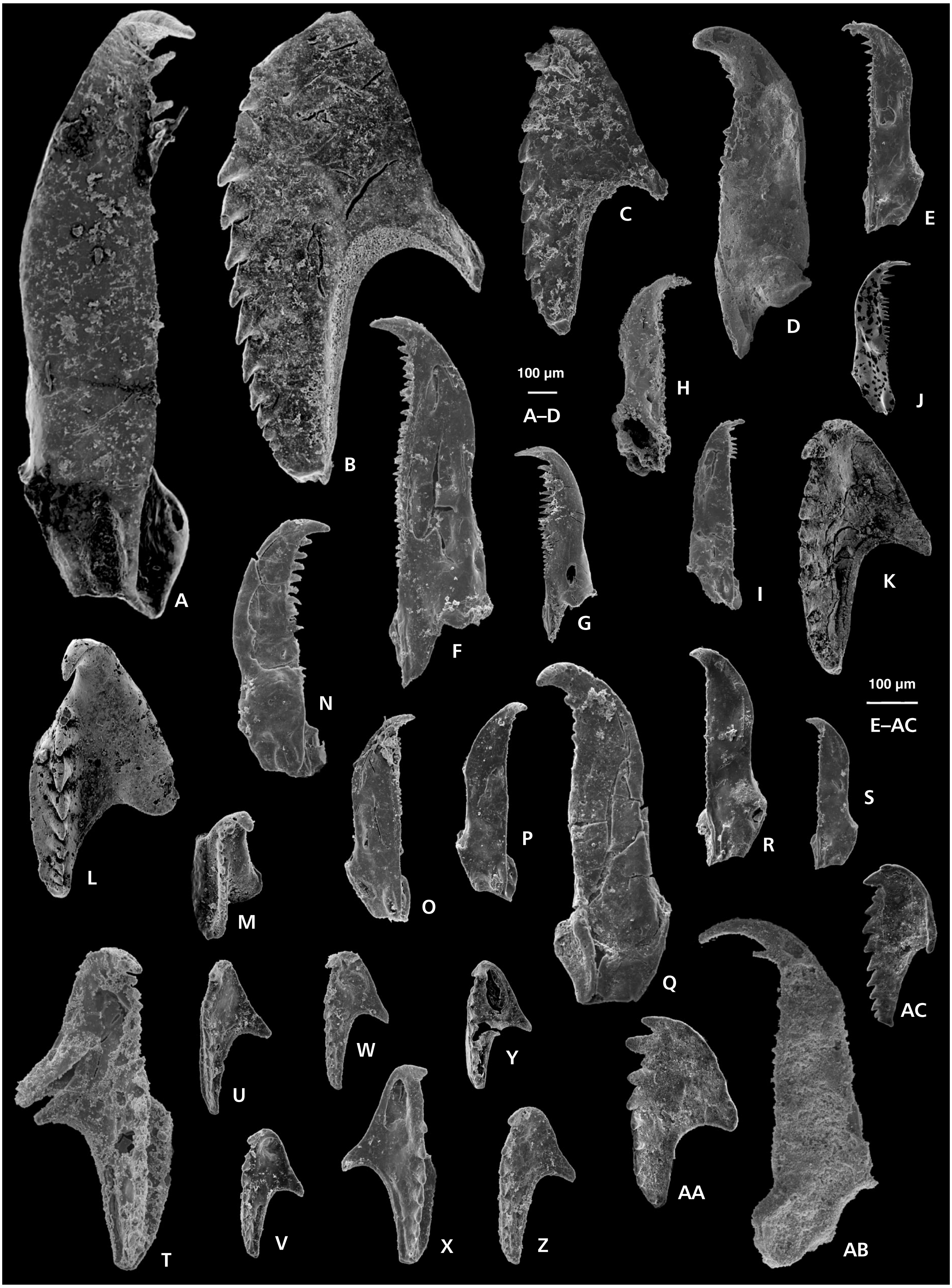
Genus *Oenonites* Hinde, 1879

Discussion. – Oenonites is represented by at least five different species and accounts for more than one third of the scolecodonts in the collection. However, distinguishing individual species has in several samples been difficult (due to inadequate preservation) and thus they are grouped as *Oenonites* spp. in the distribution charts (Fig. 2). Three, more distinctive, species are listed below.

***Oenonites* aff. *olavi* Eriksson, 1997** (Fig. 5I–M) belongs to the *latus* group *sensu* Kielan-Jaworowska. The Prague specimens have more elongated posterior maxillae compared to those of *O. olavi* from Gotland, and resemble also those of Eriksson & Hints (2009, fig. 4M) and Hints (1998, fig. 10R).

***Oenonites* aff. *jennyensis* Eriksson, 1997** (Fig. 5N–P) has been found in both quarries. This species has a distinct posterior extension of the ridge in the left MI. Unlike in *O. jennyensis* from Gotland, Sweden, the extension is proximally directed and not "forked" in the Prague specimens.

Figure 6. SEM micrographs of selected paulinitids, kalloprionids and symmetroprionids. All specimens are in dorsal view except H, in ventral view. Scale bar refers to all figures, except for A to D that have separate scale bar. • A, C, E–K – *Kettnerites kosoviensis* Žebera, 1935. A – left MI No. PT15A.1 from sample PT15, Kosov Quarry. C – right MII No. PT9A.1 from sample PT9, Kosov Q. E – right MI No. PT22G.10 from sample PT22, Liščí Q. F – right MI No. PT22G.7 from sample PT22, Liščí Q. G – right MI No. PT20A.1 from sample PT20, Liščí Q. H – right MI No. PT10A.1 from sample PT10, Kosov Q. I – left MI No. PT11A.2 from sample PT11, Kosov Q. J – left MI No. PT11B.1 from sample PT11, Kosov Q. K – right MII No. PT22H.2 from sample PT22, Liščí Q. • B, D, Y–AC – Different morphotypes of *Kettnerites*; deformation or poor preservation hampered species determination. B – right MII No. PT13A.1 from sample PT13, Kosov Q. D – right MI No. PT7A.4 from sample PT7, Kosov Q. Y – right MII No. PT1A.1 from sample PT1, Kosov Q. Z – right MII No. PT22G.1 from sample PT22, Liščí Q. AA – right MII No. PT5A.1 from sample PT5, Kosov Q. AB – right MI No. PT7A.2 from sample PT7, Kosov Q. AC – right MII No. PT7A.1 from sample PT7, Kosov Q. • L – *Leptoprion*? sp., right MI No. PT5C.1from sample PT5, Kosov Q. • M – *Symmetroprion spatiosus* (Hinde, 1882), right MI No. PT5B.1 from sample PT5, Kosov Q. • N–X – *Kettnerites* cf. *sisyphi* Bergman, 1987. N – left MI No. PT7A.3 from sample PT7, Kosov Q. O – left MI No. PT25A.1 from sample PT25, Liščí Q. P – left MI No. PT22G.6 from sample PT22, Liščí Q. Q – right MI No. PT5A.6 from sample PT5, Kosov Q. R – right MI No. PT27.8 from sample PT24, Liščí Q. S – right MI No. PT22G.11 from sample PT22, Liščí Q. T – left MII No. PT11A.1 from sample PT11, Kosov Q. U – right MII No. PT22G.5 from sample PT22, Liščí Q. V – right MII No. PT22G.4 from sample PT22, Liščí Q. W – right MII No. PT22G.3 from sample PT22 Liščí Q. X – left MII No. PT22G.2 from sample PT22, Liščí Q.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***Oenonites* cf. *gadomskae* Kielan-Jaworowska, 1966** (Fig. 5W, X) is virtually indistinguishable from the Ordovician material illustrated by Kielan-Jaworowska (1966), Hints (2000) and Hints & Eriksson (2007a).

Family Polychaeturidae Kielan-Jaworowska, 1966

Genus *Pteropelta* Eisenack, 1939

***Pteropelta*? sp.** (Fig. 5AD). The polychaeturid genus *Pteropelta* is identified in the present collection on the basis of one right MI found in sample PT9 from the Kosov Quarry. The elongated jaw has a very long shank, narrow ramus and missing bight. The dentary has 11 fairly large denticles, of which the three following the fang are smaller than the subsequent ones. In overall shape the specimen resembles the Late Ordovician morphotype of *Pteropelta gladiata* (Eisenack, 1939), illustrated by Hints & Eriksson (2010, figs 1P, Q), but it is considerably narrower and has a differentiated dentary. It may be argued that the morphological trend observed in the long-ranging *P. gladiata* through the Ordovician by Hints & Eriksson (2010) continued into the Silurian. Previously, polychaeturids have only been recorded from the Ordovician and lowermost Silurian and hence the present finding would extend their range to the upper Silurian. However, since the left MI are most diagnostic for polychaeturids, the present identification must be considered as only tentative and additional material is needed for an unambiguous assessment.

Family Ramphoprionidae Kielan-Jaworowska, 1966

Genus *Protarabellites* Stauffer, 1933

***Protarabellites* cf. *rectangularis* Eriksson, 2001** (Fig. 5A–G) is present in both quarries and approximately 20 first maxillae were recovered. The Prague specimens are, similar to those reported from Skåne, southernmost Sweden (Eriksson 2002), intermediate between *P. rectangularis* Eriksson, 2001 and *P. triangularis* Eriksson, 2001. As noted also by Eriksson (2001), these species can be difficult to distinguish from each other, particularly if the specimens are deformed or otherwise poorly preserved.

Genus *Ramphoprion* Kielan-Jaworowska, 1962

***Ramphoprion* cf. *gotlandensis* Eriksson, 2001.** One poorly preserved MI of this species was found in sample PT2 (specimen PT2A.1), the Kosov Quarry.

Family Kalloprionidae Kielan-Jaworowska, 1966

Genus *Kalloprion* Kielan-Jaworowska, 1962

***Kalloprion* sp.** is very rare in the collection studied; poorly preserved first maxillae were recorded in two samples (PT6, PT7) only.

Genus *Leptoprion* Kielan-Jaworowska, 1966

***Leptoprion*? sp.** (Figs 3AA, 6L). Only one maxilla has been found, in sample PT5; another fragmentary specimen was found in sample PT10, both from the Kosov Quarry. Morphologically this species is intermediate between *Leptoprion* and *Atraktoprion* Kielan-Jaworowska, 1962, having a longer fang and larger denticles than those in typical *Leptoprion*. Closely similar, probably conspecific, specimens have been described from Arctic Canada (Hints *et al.* 2000) and are known from Gotland and Estonia (MEE and OH, unpublished data). *Arabellites spicatus* described by Hinde (1882, p. 18, pl. 2, fig. 47, sample No A2216) from Gotland also seems to be closely related.

Family Paulinitidae Lange, 1947

Discussion. – Paulinitids occur abundantly but are represented only by *Kettnerites* Žebera, 1935. Specimens of *Kettnerites* are recorded in all but one of the scolecodont-yielding samples. Based on the morphology of the second maxillae, which according to Bergman (1989) are the most diagnostic elements in paulinitids, at least two different species (listed below) can be distinguished in the studied material. Representatives of this genus also dominate on the bedding plane surfaces of the Kopanina Formation shale intercalations as confirmed by previous studies and the new sampling. Their dominance could be artificially inflated because of their quite easy identification even on fragments and the relatively resistant nature of, particularly, the first and second maxillae. In the Baltic region and the Welsh Borderland of the British Isles contemporaneous strata commonly yield also *Lanceolatites* Bergman, 1987 which is missing in the Prague Basin. The distribution of Silurian paulinitids is discussed in detail by Bergman (1987, 1989) who described more than 20 species from Gotland.

Genus *Kettnerites* Žebera, 1935

***Kettnerites kosoviensis* Žebera, 1935 *sensu* Šnajdr 1951** (Fig. 6A, C, E–K) is distinguished especially by its double-cusped right MII. This species has been recorded with certainty only from the Prague Basin. Taugourdeau

(1967) described *K. kosoviensis* from France and Taugourdeau (1972) and Taugourdeau & Iliescu (1983) recorded *K.* cf. *kosoviensis* from the Sahara and Romania, respectively. However, that material needs restudy.

***Kettnerites* cf. *sisyphi* Bergman, 1987** (Fig. 6N–X). The right MII of this species has one small precuspidal denticle and particularly resembles *K. sisyphi* Bergman, 1987 from Gotland. Similar specimens are known also for example from the Wenlock of the Canadian Arctic (Hints *et al.* 2000) and Estonia (Hints *et al.* 2006).

***Kettnerites* spp.** (Fig. 6B, D, Y–AC). In addition to the above mentioned *Kettnerites* species, other species are present within the collection. However, due to imperfect preservation and insufficient material for apparatus reconstructions, these cannot presently be identified to species level.

Family Tretoprionidae Hints, 1999

Genus *Tretoprion* Hints, 1999

***Tretoprion astae* Hints, 1999** (Fig. 3AC). A single right MI of this enigmatic species was recorded in sample PT5 from the Kosov Quarry. It has a slender shank and ramus and transversally extended denticles in the anterior part of the dentary. This species was first described from the Upper Ordovician of Estonia (Hints 1999), but rare specimens have subsequently also been found from the upper Llandovery and lower Wenlock of the same area (Hints *et al.* 2006) and from the Upper Ordovician of subsurface Gotland, Sweden (Eriksson & Hints 2009). The Kosov Quarry specimen extends the stratigraphical range of the genus into the Ludlow, and shows also its wide geographical distribution.

Family uncertain

Genus *Lunoprionella* Eisenack, 1975

***Lunoprionella symmetrica* Eisenack, 1975** (Figs 3Z, AD, AE, 4M) is represented by approximately 20 specimens from both quarries. The family affinity and apparatus arrangement of this species are unknown. The stratigraphical range of the genus is from the Middle Ordovician to the upper Silurian. For further discussion of *Lunoprionella*, see Hints (1998).

Conclusions

1. The collection of scolecodonts from the Prague Basin represents the most diverse Silurian jawed polychaete fauna hitherto recorded from the peri-Gondwanan region.
2. The Ludfordian polychaete faunas described from the Kosov and Liščí quarries include at least 16 genera, of which *Kettnerites*, *Oenonites* and *Pistoprion* are most common.
3. The faunal composition corresponds well with that of coeval faunas, particularly from Baltica and, to some extent, Avalonia, Laurentia and Siberia. The Prague Basin material extends the palaeolatitudinal and palaeobiogeographical distribution of some genera (*Protarabellites*, *Symmetroprion*, *Kalloprion* and *Tretoprion*). Collectively, this suggests a geographically widespread nature of the Silurian polychaete faunas.
4. The abundance and relatively good preservation of the scolecodonts recovered through acid digestion of rocks, clearly show the limitations of the historical bedding plane collections and suggest good potential for future studies.
5. The Kozlowskii event reorganised the polychaete fauna in the Prague Basin, although additional high-resolution sampling is needed in order to accurately evaluate the precise impact of the event.

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