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REVISION OF *KETTNERITES* ŽEBERA, 1935 (SCOLECODONTA, SILURIAN OF THE BARRANDIAN AREA, CZECH REPUBLIC): PRELIMINARY RESULTS

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Abstract. A revision of the large scolecodont collections of Žebera (1935) and Šnajdr (1951) has been accomplished using among other techniques, electron microscopy. The preliminary results showed a high level of morphological variability in the first and second maxillae of *Kettnerites kosoviensis* ŽEBERA, 1935 which represents the type species of the genus *Kettnerites* ŽEBERA, 1935.

■ Silurian, Prague Basin, Barrandian area, scolecodonts, *Kettnerites.*

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Introduction

Although the research on scolecodonts (= jaws of polychaeteous annelids) started in the 19th century (e. g., Pander 1856) there still remain numerous questions to be answered. Scolecodonts are quite abundant in Ordovician to Devonian sedimentary rocks all over the world (Colbath 1988; Szaniawski 1974), including the Prague Basin (Barrandian area). Silurian rocks have been selected as a starting point for the revision of scolecodonts in the Czech Republic. The type species of the genus *Kettnerites* ŽEBERA, 1935 - *Kettnerites kosoviensis* ŽEBERA, 1935 has been revised. The basis for this study is the collection of K. Žebera housed in the Institute of Geology and Palaeontology, Faculty of Science, Charles University and the collection of M. Šnajdr stored in the National Museum in Prague. These two authors also published two major papers on Bohemian scolecodonts (Žebera 1935; Šnajdr 1951) that are discussed in detail.

Silurian in the Prague Basin

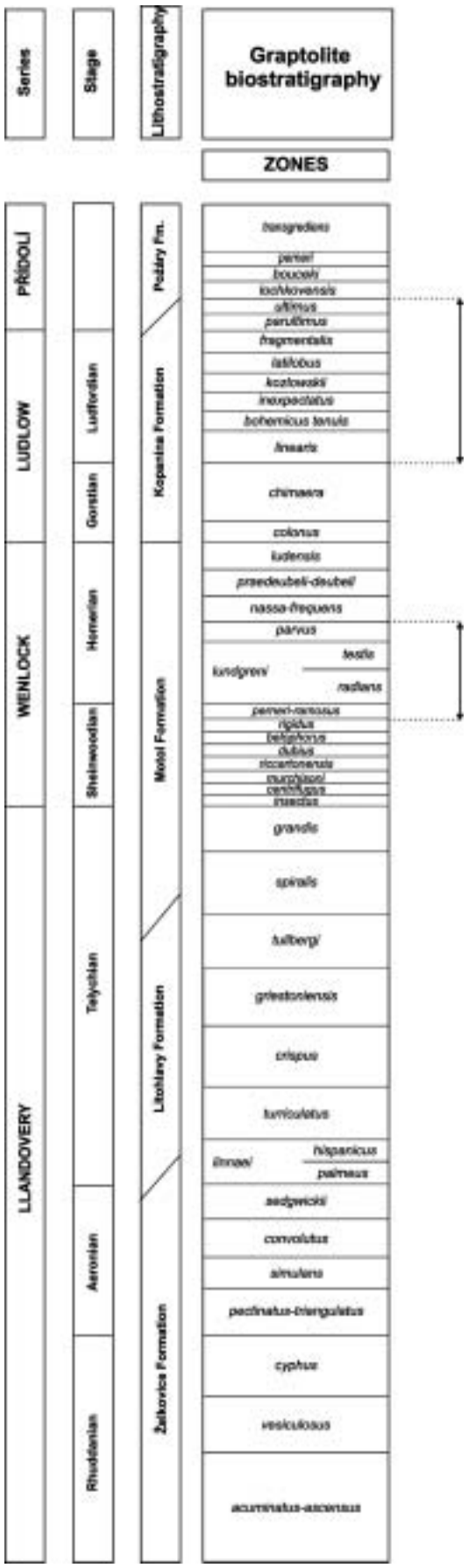
The Prague Basin is a classical geological area with lower Palaeozoic rocks that has been studied for nearly two hundred years (for summaries see: Horný 1955; Havlíček and Štorch 1990; Havlíček 1995, etc.). The research focused mainly on the lithology, faunal benthic communities and the origin and conditions of sedimentation of this palaeobasin. Recently, more complex studies of the fossil environment combined with palaeontological data and with other information such as facial analysis or stable isotopic data has begun (e.g. Kříž 1991; Lehnert et al. 2007).

The complete non-metamorphosed Silurian succession (lowermost Llandovery to uppermost Přídolí) is exposed in the Prague Basin. Silurian rocks represent only a central part of the former sedimentary basin. The marginal parts are not preserved because of the Variscan deformation and erosion. Synsedimentary deformation of the area was accompanied by a strong submarine volcanism that significantly influenced the character of the environment. The volcanoclastic accumulations gave rise to elevations that provided a shallow-water, favourable environment for rich benthic communities (e. g. Havlíček and Štorch 1990; Kříž 1992).

In the Early Silurian the sedimentation of black graptolitic shale prevailed. Towards the Late Silurian, limestones with a dominating biodetrital component, substituted these sediments. In general, Silurian deposits originated in a quite shallow warm-water environment within the temperate to subtropical climatic zone (Havlíček and Štorch 1990). The four Silurian series, Llandovery, Wenlock, Ludlow and Přídolí, are represented in the Prague Basin by five formations: Želkovice Formation, Litohlavy Formation, Motol Formation, Kopanina Formation and Přídolí Formation. Scolecodonts are documented from the Wenlock, Ludlow and part of the Přídolí series (see Text-fig. 1).

Material and methods

The specimens collected and studied by Šnajdr (1951) are housed in the National Museum in Prague under the following numbers: 32921 (locality Amerika), 32984 (locality Kosov) and 32983 (locality Koledník). From several thousands of mostly discrete scolecodont elements, about 700 specimens were selected for study. The materials studied by Žebera (1935) are housed in collections of the Institute of Geology and Palaeontology, Faculty of Science, Charles



Text-fig. 1. Graptolite biostratigraphy of the Silurian showing the up to present documented occurrences of scolecodonts in the Prague Basin. The graptolite zones are shown proportionally to the supposed relative time length (chart after Kříž 1992; Štorch 2001).

University under the numbers 1-133. The majority of specimens come from the locality "pod Koledníkem" = Koledník and a few elements originate from the Mořina area (Liščí Quarry). An optical microscope Olympus SZX-ILL B200 and Electron Microscope JEOL JSM-6380 in the Institute of Geology and Palaeontology (Charles University) were used during this study.

Polychaete annelids and their classification

Polychaete annelids represent a diverse group encompassing more than 8 000 extant species (Ruppert et al. 2004). Their role in the recent benthic food chain is quite important and it is supposed to have been similar in the past. The importance for palaeontology is connected with their ability to live and prosper even in unfavourable environments (such as the depletion of oxygen, etc.). This attribute has resulted in scolecodonts becoming one of the indicative fossil groups, especially in facies where other fossils are rare or absent.

The taxonomy of polychaetes is quite complicated. They had been divided according to their mode of life into: "Errantia" (motile forms) and "Sedentaria" (sessile forms). The recent cladistic analysis of annelids resulted in a new classification with two main clades: Scolecida and Palpata (see Rouse and Fauchald 1997). The Palpata comprises the majority of polychaete annelids and are divided into Aciculata and Canalipalpata. The Aciculata encompasses practically all the former group Errantia and includes major groups such as Phyllodocida and Eunicida (Rouse et al. 2002). The latter group is the most important in the fossil record primarily because of its resistant jaws (= scolecodonts). The majority of them are mobile animals provided with parapodia which serve for rapid locomotion and with well-developed eyes. Their life style is usually connected with predation.

The first appearance of polychaetes is dated from the "Middle" Cambrian (Conway-Morris 1979; Fauchald and Rouse 1997), while representatives of the order Eunicida occurred in the latest Cambrian. However, the major diversification of this group proceeded during Early and Middle Ordovician (Hints and Eriksson 2004); by the Silurian this group was already diversified (Bergman 1989).

Scolecodonts in the Prague Basin

There are only a few reports on the presence of scolecodonts in the Prague Basin. Because of the insufficient laboratory equipment, this group of microfossils has been omitted from research for quite a long time. One of the first authors dealing with different groups of microfossils was Perner (1894), who found a "conodont" *Prioniodus barrandei* in the Ordovician. Perner mentioned the resemblance of this form with the jaws of the extant annelid *Staurocephalus* Grubbe, 1855, it suggests that this microfossil should be classified as "scolecodont" according to the present point of view. Its grey translucent appearance shifts this microfossil nearer to conodonts as it was considered by Žebera (1935). Unfortunately, the original material was not found and thus the assignment could not be confirmed. Later, Kodym et al. (1931) reported a similarly controversial finding from the

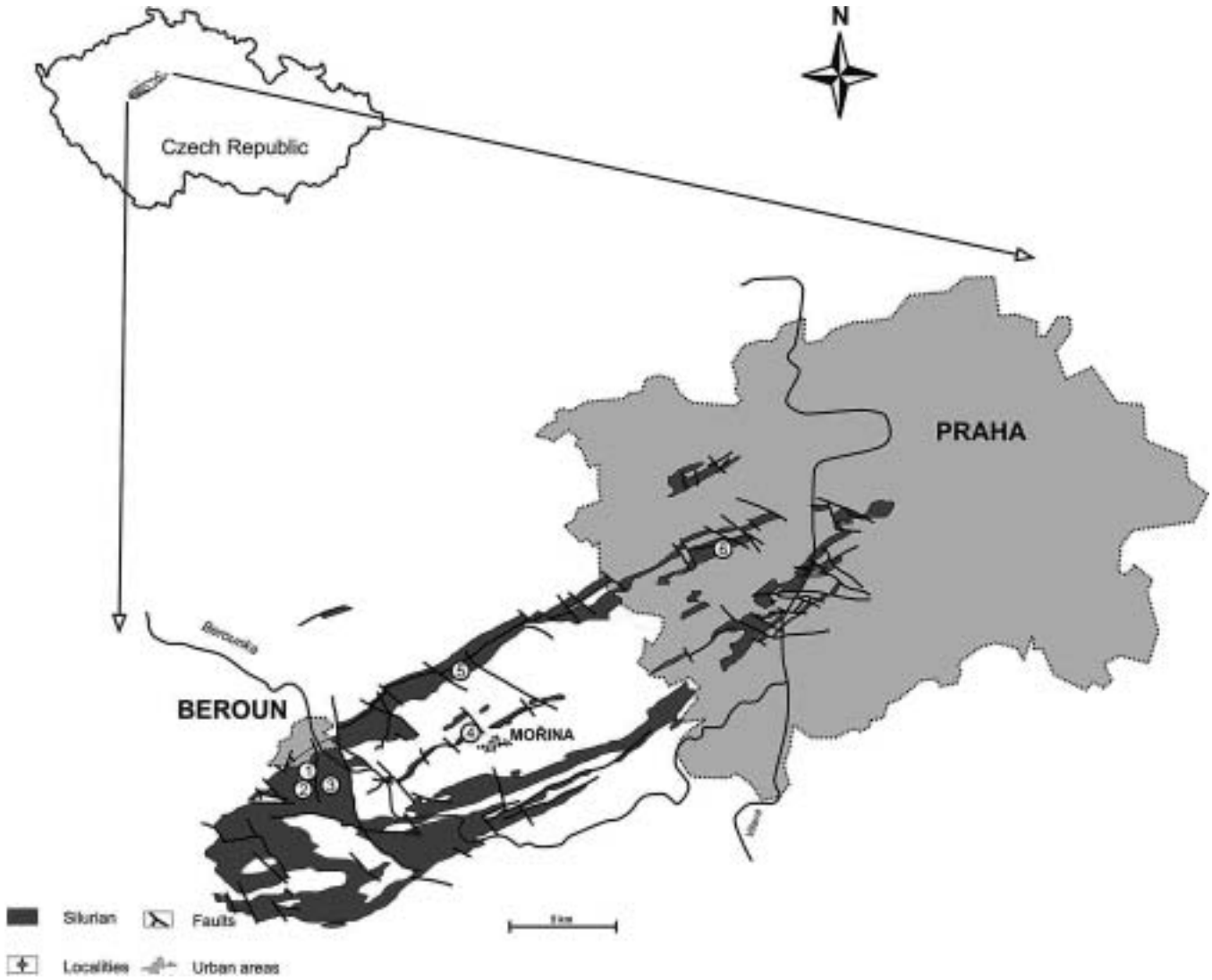
quarry "pod Koledníkem", that was later classified by Žebera (1935) as scolecodont. Further sampling was also carried out by Bouček and Šulc whose findings together with the continued initiative of Perner, provided an impulse for consequent research, especially that of Žebera.

In the 1930`s Žebera and Augusta sampled the localities "Pod Koledníkem", "Pod lanovkou" and Mořina (= Liščí quarry) and found more than 150 specimens of scolecodonts and one conodont specimen. Žebera (1935) summarized the results of the fieldwork and classified the majority of jaws as *Arabellites perneri* ŽEBERA, 1935 (all established taxa are summarized in Tab. 1). This species was relocated by Šnajdr (1951) to the genus *Kettnerites* ŽEBERA, 1935 in the family Paulinitidae Lange, 1947.

Bouček (1941) was the next author who mentioned Silurian scolecodonts, while describing new Wenlockian and Ludlowian sections exposed in the road cut from Loděnice to Bubovice. Later, Bouček (1947) reported a few specimens of the complete polychaetous worm *Palaeochaeta kettneri* from the same exposure. Unfortunately, these samples are also lost.

The paper published by Šnajdr (1951) comprised the most significant revision of scolecodonts in the Prague Basin. He elaborated on material coming from the following localities: Kosov Quarry, Jarov near Beroun (= Koledník), Arethusina Gorge and the Liščí Quarry (quarries Amerika near Mořina) (see Text-fig. 2). The latter quarry is the richest in scolecodonts; Šnajdr collected several thousands discrete jaw elements and even several composite jaw apparatuses. The most common species is *Kettnerites kosoviensis* ŽEBERA, 1935, assigned by Šnajdr (1951) to a family of "errant" predatory polychaetes called Paulinitidae Lange, 1947. Furthermore, Šnajdr (1951) described specimens of *Pernerites* cf. *giganteus* ŽEBERA, 1935 and *Ildraites* (?) *budňanensis* ŠNAJDR, 1951 (the established taxa are summarized in the Tab. 1). The same species was also found by Horný (1955) in the Srbsko-Mořina area (Liščí quarry) in the *Phacops fecundus communis* Horizon and in the Kosov quarry in the *Scutellum haidingeri* Horizon.

The goal of the present research is to put together all the published data on Silurian scolecodonts from the Barrandian area and to revise in detail the type species of the genus *Kettnerites*.



Text-fig. 2. The Prague Basin and localities of the documented scolecodont occurrences (map after Havlíček and Štorch 1990) 1. Kosov Quarry, 2. Pod lanovkou, 3. Koledník, 4. Liščí Quarry, 5. cut of the road from Loděnice to Bubovice, 6. Arethusina Gorge.

Systematic part

Terminology is based on Bergman (1989) and Kielan-Jaworowska (1966).

Phyllum **Annelida** Lamarck, 1809

Class **Polychaeta** Grube, 1850

Order **Eunicida** Dales, 1963

Superfamily **Eunicea** Grube, 1852

Family **Paulinitidae** Lange, 1947

Genus ***Kettnerites*** Žebera, 1935 emend. Šnajdr 1951

1964 *Kettnerites* Žebera; Tasch and Stude, p. 649, 651
1971 *Kettnerites* Žebera; Jansonius and Craig, p. 280, pl. 1
1973 *Kettnerites* Žebera; Tasch, p. 459
1985 *Kettnerites* Žebera; Männil and Zaslavskaya, p. 117-118
1991 *Kettnerites* Žebera; Bergman, p. 249, 253
1999 *Kettnerites* Žebera; Eriksson, p. 403
2004 *Kettnerites* Žebera; Eriksson et al., p. 269, 278, 281, 283, 284, tab. 1
2008 *Kettnerites* Žebera; Eriksson, p. 629, 631, 632

Type species: *Kettnerites kosoviensis* Žebera, 1935.

Locus typicus: Prague Basin, Teplá-Barrandian Region, Czech Republic.

Stratum typicum: "Budňany Limestone" after the original designation of Žebera (1935), Požáry Formation, Přídolí, Silurian.

Diagnosis (Žebera 1935, p. 95, translation of the Czech and French versions):

Specimens with a sharply terminated posterior base that is largely elongated (= shank). Middle part of the lower margin is thickenned or with a mound that compose a spur. The anterior part of the base merges into one prominent full tooth (= fang) that is followed by smaller denticles. The fang (first and largest denticle) of the genus *Kettnerites* resembles that of the genus *Arabellites* (maxillae I) but they differ in the sharply terminated posterior part of the base.

Emended diagnosis (Šnajdr 1951, p. 260-261):

Jaw apparatus composed of one pair of mandibles and of seven asymmetrical maxillary plates with a pair of carriers.

Anteriorly the mandibles have a broad anterior part (frontal plate), which posteriorly terminates as elongated, gradually narrowing basal shafts. On the ventral side, in the anterior part is an oblique, raised plate, from which a carinate rim continues in the direction towards the farthest ends of the shafts.

The carriers are elongated, of conical shape, with an irregularly convex anterior margin, with distinctly bent lateral margins. In the original position they overlap somewhat anteriorly.

The forceps are asymmetrical, carinate, and attached to the carriers; anteriorly they have a characteristic hook, and their inner margin has for almost the whole of its length, minute conical denticles. On the upper side of the jaws, a strong rim runs along the anterior and outer lateral margins. In the posterior part of the right forceps is a curved basal plate of irregular shape, which fills the gap in the basal part of the forceps at the outer lateral margin.

The asymmetrical dental plates are characterised by their characteristic triangular shape and by a shank on the outer lateral margin, approximately at half the length of the jaw. The shape and number of denticles on the inner margin differs greatly.

The unpaired piece is also triangular, with some unequally long denticles on the inner lateral margin.

The paragnaths are also asymmetrical, with an approximately square shape, with a row of minute denticles on the inner margin of the jaw and with a distinctly thinning outer lateral margin.

Remarks

Bergman (1989) published a major revision of the paulinitid polychaetes, including specimens of the genus *Kettnerites* from Gotland (Sweden). In this monograph a detailed synonymy of the genus and documentation of several new species are included. Bergman (1989) distinguished two subgenera: *Kettnerites* (*Kettnerites*) Žebera, 1935 and *Kettnerites* (*Aeolus*) Bergmann, 1987 based on different first and second maxillae – "*K. (Aeolus)* has fairly slender MI`s often with a fairly wide basal portion and on the slender MII`s the pre-cuspidal denticles, if any, are small".

Species ***Kettnerites kosoviensis*** Žebera, 1935

Pl. 1, figs 1-11

1935 ? *Ebetallites ancoraeformis* Žebera, p. 9, pl. II, fig. 10
1935 *Arabellites perneri* Žebera, p. 3, pl. 1, figs. 1, 2
1935 *Arabellites innaequidens* Žebera, p. 5, pl. I, fig. 3
1935 *Arabellites kettneri* Žebera, p. 6, pl. I, fig. 4
1935 *Arabellites angustidens* Žebera, p. 6, pl. I, fig. 5
1935 *Pronereites naviculiformis* Žebera, p. 7, pl. II, fig. 6
1935 *Kettnerites kosoviensis* Žebera, p. 8, pl. II, fig. 7
1935 *Kettnerites depressus* Žebera, p. 8, pl. II, fig. 8
1966 *Paulinites kosoviensis* (Žebera); Kielan-Jaworowska, p. 124, 125
1967 *Kettnerites kosoviensis* Žebera; Taugourdeau, p. 471, pl. XV, figs. 11-13, pl. XVI, figs. 4, 12
1970 *Paulinites kosoviensis* (Žebera); Szaniawski, p. 466
1972 *Kettnerites kosoviensis* Žebera; Taugourdeau, p. 240, tab. 1
1989 *Kettnerites kosoviensis* Žebera; Bergman, p. 49

Holotype: pl. 2, fig. 7 in Žebera (1935) – the specimen was not found

Locus typicus: Kosov, quarry "pod Koledníkem"

Stratum typicum: "Budňany Limestone" after original designation of Žebera (1935) = in actual terminology: Požáry Formation, Přídolí, Silurian

Holotype: (Žebera 1935, p. 95, translation of Czech and French version)

From a carinate basis (with an elliptical cross profile) extends a massive solid hook-like denticle followed by smaller ones. The denticles' length is about ¼ of the hook and they are conical, unpointed and usually sloping posteriorly. The inner margin – denticulated – is separated by a shallow depression from the posterior part of the base. At one third of the posterior part of the outer margin is a mould representing a transition to a spur. A more distinct spur is a typical character of MII of the genus *Arabellites*. Length 1.8 mm.

Remarks

There have been several different classification schemes for the *Kettnerites*. Kielan-Jaworowska (1966) transferred its type species *Kettnerites kosoviensis* Žebera, 1935 to the genus *Paulinites* Lange, 1947, while Szaniawski (1970) saw a resemblance of *Paulinites polonensis* Kielan-Jaworowska, 1966 to *Kettnerites kosoviensis* and *P. burgensis* Martinsson, 1960. However, he was not certain because of insufficient preservation of the species. A quite different view was published by Bergman (1989) who considered the species *kosoviensis* as a representative of the genus *Kettnerites* and emphasized its resemblance to the species *Kettnerites* (*K.*) *martinssonii* Bergman, 1987 (originally described by Martinsson (1960) as *Paulinites* sp.). Similarly, Bergman (1989) assigned the species *Paulinites polonensis* (Kielan-Jaworowska, 1966) to the genus *Kettnerites*.

Recently, Bergman's classification has been widely accepted, for example, Jansonius and Craig (1971) classified *Kettnerites* as a valid and relatively common genus occurring in different regions. Although the Šnajdr`s (1951) relocation of the species established by Žebera (see Tab. 1) to *Kettnerites* seems to be correct, a more detailed study is inevitable. Szaniawski (1974, p. 183) partially supported the transfer of the species *Pronereites naviculiformis* Žebera, 1935 by mentioning its assignment to the family Paulinitidae Lange 1947. In the same way, Eriksson (2008) examined the specimens of the genus *Arabellites* Hinde, 1879 and proposed the transfer of some species to the genus *Kettnerites*. However, a future separation of several taxa within the *Kettnerites kosoviensis* from the Prague Basin is highly possible.

Conclusions

A revision of the collections of K. Žebera and M. Šnajdr has been carried out. Recent study of the earlier established scolecodont taxa shows, that their taxonomy is much more complicated than previously supposed. With regard to the present state of preservation of specimens of the type species *Kettnerites kosoviensis* Žebera 1935, a new type specimen should be established. The differences in the first and second maxillae are possibly greater than could fall within the variability of one species (*K. kosoviensis*). That means a more detailed morphological analysis is needed. Moreover, a comparison with newly sampled and isolated specimens is necessary for determination of this species.

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Tab. 1. Scolecodont species described or transferred by different authors from the Silurian of the Prague Basin.

Žebera (1935)	Šnajdr (1951)	Kielan-Jaworowska (1966)	Bergman (1989)	this paper
Ebetallites ancoraeformis	*Kettnerites kosoviensis*	*Paulinites kosoviensis*	*Kettnerites kosoviensis*	*Kettnerites kosoviensis*
Arabellites perneri				
Arabellites innaequidens				
Arabellites kettneri				
Arabellites angustidens				
Pronereites naviculiformis				
Kettnerites kosoviensis				
Kettnerites depressus				
Pernerites giganteus	*Pernerites cf. giganteus*			under revision
	Ildraites (?) budnanensis			under revision

PLATE 1

1–6. *Kettnerites kosoviensis* ŽEBERA, Photographs of Šnajdr's (1951) original specimens.
1'-6': Schematic illustrations for easier recognition. The specimens are housed in the collection of the National Museum in Prague. The scale bar is 500 μm.
1. MIr**,** L33117 (32921-138).
2. MIIr, L33110 (32921-134).
3. MIIr, L33106 (32921-135).
4. MI`s with carriers, L33116 (32921-133).
5. MIl, L33102 (32921-136).
6. carriers, L33122 (32921-130).

7–11.*Kettnerites kosoviensis* ŽEBERA, Photographs of Žebera's (1935) original specimens. **7'-11'** Žebera's (1935) Original illustrations. Specimens are housed in the collection of the Institute of Geology and Palaeontology, Charles University in Prague. The scale bar is 1 mm.
7. *Ebetallites ancoraeformis* ŽEBERA, 1935; Uk-41.
8. *Arabellites kettneri* ŽEBERA, 1935; Uk-27.
9. *Arabellites innaequidens* ŽEBERA, 1935; Uk-43.
10. *Arabellites perneri* ŽEBERA, 1935; Uk-4.
11. *Pronereites naviculiformis* ŽEBERA, 1935; Uk-32.

Explanatory notes:
MIr = right first maxilla (forceps)
MIl = left first maxilla
MII = second maxillae and so on – MIII, MIV

PLATE 1