

Odontopleurid trilobites of the Katian/Hirnantian boundary interval in the Prague Basin (Bohemia)

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A new association of odontopleurid trilobites is described from calcareous claystone to marlstone, the so-called “Perník Bed”, of the topmost part of the Králův Dvůr Formation. The association includes *Diacanthaspis krizi* sp. nov., associated with *Bojokoralaspis peregrina* (Barrande, 1872) and other rare and poorly known odontopleurids preliminary referred to *Chlustinia* Přibyl & Vaněk, 1965, *Proceratocephala* Prantl & Přibyl, 1949 and *Eoleonaspis* Sheng, 1974. This association indicates a closer relationship to the late Katian and early Hirnantian odontopleurid faunas of Baltica and Avalonia than to those of Armorica (Spain, Sardinia), where the genera *Calipernurus* Whittington, 1956a, *Diacanthaspis* Whittington, 1941, *Dicranurus* Conrad, 1841, *Hispaniaspis* Hammann, 1992, *Radiaspis* Richter & Richter, 1917, and *Whittingtonia* Prantl & Přibyl, 1949 are present in carbonatic buildups of the late Katian age. It is assumed that the deposition of “Perník Bed” is a result of the early Hirnantian sea level lowering and not of the warming related to the Boda event. • Key word: *Diacanthaspis*, odontopleurids, Ordovician, Katian, Hirnantian, Prague Basin.

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The Králův Dvůr Formation is a lithostratigraphical unit probably representing the Upper Katian interval (called also Kralodvorian Regional Stage) in the Prague Basin of the Czech Republic (Havlíček & Vaněk 1966, Havlíček 1982, Havlíček *et al.* 1994, Fatka & Mergl 2009, Budil *et al.* 2011b). Diverse, mainly deep-water faunal associations include common cyclopygid and remopleurid trilobites (see Shaw 2000; Budil *et al.* 2011a, b; Mergl 2011c), moderately diverse small-sized deep-water brachiopods (see Havlíček 1967, 1977), ostracods, gastropods, hyolithids, nuculoid bivalves and cephalopods. The rather deeper-water character of the fauna is emphasized by the absence of large strophomenate brachiopods, bryozoans and pelmatozoans which are characteristic for the rich Katian (Ashgillian) faunas in the SW Europe (Iberian Chains, Central-Iberian zone, Asturias, Montagne Noire, Carnic Alps, Sardinia, Morocco) (Havlíček 1981; Villas 1985, 1995; Leone *et al.* 1991; Venin *et al.* 1998; Villas *et al.* 2002, 2006; Jiménez-Sánchez *et al.* 2007; Colmenar *et al.* 2013 and others).

Unlike the underlying sequence, the topmost part of the Králův Dvůr Formation yields a distinctive fauna, with diverse trilobites, ostracods, medium-sized strophomenate brachiopods, large gastropods, machaeridians, bryozoans, cystoids, blastoids and other fossils (Havlíček & Vaněk 1966, Havlíček & Mergl 1982, Štorch & Mergl 1989). This fauna occurs in a thin bed of carbonate claystone to

marlstone (so-called “Perník Bed”), which is immediately followed by a carbonate claystone bearing the unambiguous Hirnantian shelly fauna (Mergl 2011a). The fauna of the “Perník Bed” is distinctive in containing several species of odontopleurid trilobites, among which presence of *Diacanthaspis* is significant.

Geological setting

The “Perník Bed” (perník = gingerbread) is a slang name for the unusually rich fossiliferous but thin carbonate claystone to marlstone occurring in the top part of the Králův Dvůr Formation (Štorch & Mergl 1989, pl. 1). This bed has been interpreted as being the result of climatic and glacioeustatic changes near the Katian/Hirnantian boundary (Brenchley & Štorch 1989). The bed thickness and its fossil content, although generally uniform, gently differ at particular localities. Shelly fossils are largely allochthonous in all localities. Bioclasts are fragmented, deformed, and are randomly oriented in the sediment. Graded sorting of fossils is present in individual layers and smaller bioclasts are concentrated in paved layers. The fine-grained sediment and presence of minute sorted fossils suggest a deeper shelf environment reached by recurrent suspension streams. Trace fossils penetrate the top of the claystone level, with dragged out bioclasts

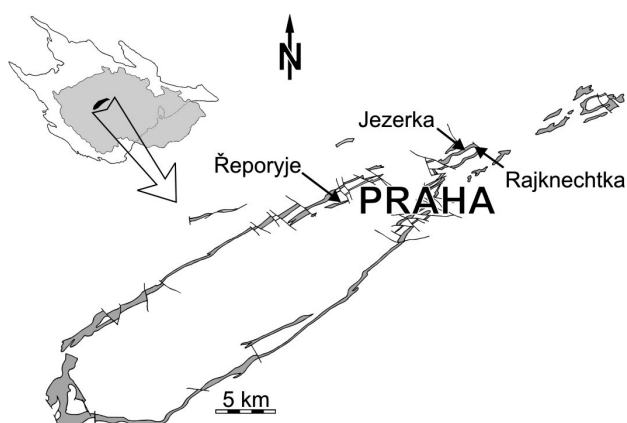


Figure 1. Distribution of the Králův Dvůr Formation (Upper Katian) in the Prague Basin with the location of referred localities.

but leaving the deeper part of claystone intact. The taxonomy of fossils from the “Perník Bed” is well known (Marek 1952, 1964, 1989; Havlíček 1967, 1977; Havlíček & Mergl 1982; Frýda 1989; Shaw 1995, 2000; Ferretti 1998; Mergl 2011b, 2012). The general importance of this fauna has been reviewed by Havlíček & Vaněk (1966), Havlíček (1982, 1989), and Štorch & Mergl (1989).

The carbonate claystone grades upward into claystone beds with more abundant coarse siliciclastic detritus. These layers contain a different low-diversity fauna, dominated by ostracods, machaeridians, few orthid brachiopods, and especially the trilobite *Mucronaspis grandis* (Barrande, 1852). The presence of brachiopods *Kinnella kielanae* (Temple, 1965) and *Hirnantia sagittifera* (M’Coy, 1851) and graptolite *Metabolograptus ojsuensis* (Koren & Mikhaylova, 1980) confirms the Hirnantian age of this claystone (Štorch 2006, Mergl 2011a).

Newly described species of *Diacanthaspis* was sampled in the “Perník Bed” in three artificial outcrops. The two sampling sites, the Jezerka and Rajtknechtka localities on territory of Prague have been investigated by Vladimír Havlíček in 1979 and 1982, respectively. Both were described in detail by Štorch & Mergl (1989) with their fauna commented by Havlíček & Mergl (1982). The third locality, a temporary outcrop in Praha-Řeporyje has been discovered by Jiří Kříž and subsequently sampled by Petr Budil and the author in 2007. Its fauna has been preliminarily described by Mergl (2011b, 2012).

The supposed inner shelves of the Prague Basin were possibly narrow in Sandbian time and were continuously supplied by siliciclastic detritus, with confined carbonate deposition. The Katian-aged shallow margins of the basin are not preserved and deep outer shelf environment dominated over now preserved part of the Prague Basin. Shoals on summits of tectonically controlled submarine elevations existed in the Sandbian and early Katian, but these shoals were probably strongly affected by submarine storm-gen-

erated erosion (Havlíček 1982, Havlíček & Štorch 1990). This, temporary available shallow environment inhabited the brachiopod-bryozoan-pelmatozoan (BBP) associations but the carbonate buildups never started to develop there. It is very probable that these elevations were developed and destroyed already before onset of the supposed Boda warming event (*sensu* Fortey & Cocks 2005, for alternative interpretation of this event as a global cooling, see Cherns & Wheelley 2007).

Specimens of the newly described species of *Diacanthaspis* were sampled in the “Perník Bed” in three excavated outcrops. The two sampling sites, the Jezerka and Rajtknechtka localities on territory of Prague have been investigated by Vladimír Havlíček in 1979 and 1982, respectively. Both localities were described in detail by Štorch & Mergl (1989) and discussed by Havlíček & Mergl (1982). The third locality, a temporary outcrop in Praha-Řeporyje was discovered by Jiří Kříž and subsequently sampled by Jiří Vaněk, Petr Budil, Jan Valíček, and the author in 2007. The fauna has been preliminarily described by Mergl (2011b, 2012).

Material and methods

Figured specimens are stored in the palaeontological collections of the University of West Bohemia in Plzeň, Plzeň (PCZCU). Due to their minute size, most of the specimens were photographed with utilization of Quick Photo Deep Focus software and Olympus SX51 binocular lens. Latex casts were only made in a few cases because of the softness of the mudstone and possible damage of specimens. Morphological terminology used follows Whittington *et al.* (1997).

Systematic palaeontology

Family Odontopleuridae Burmeister, 1843

Remarks. – Five species of odontopleurid trilobites have been sampled from the “Perník Bed”, but only one is described as a new species. In addition to the often-cited *Acantholoma mirka* Marek, 1952 (Kielan 1960, Bruton 1968, Šnajdr 1984, Shaw 2000), three other species have since been recognised. However, they are represented by rare and poorly preserved specimens. Therefore, they are only briefly commented and illustrated.

Subfamily Odontopleurinae Burmeister, 1843

Genus *Bojokoralaspis* Šnajdr, 1984

Type species. – *Bojokoralaspis koral* Šnajdr, 1984. Upper Ordovician, Sandbian, Zahořany Formation, Prague Basin, Bohemia.

Discussion. – Pek & Vaněk (1989), and especially Ramsköld & Chatterton (1991, p. 357) and Vaněk (2001, p. 66) intimated that *Bojokoralaspis* Šnajdr 1984 may be a junior subjective synonym of *Eoleonaspis* Sheng, 1974. This opinion was not discussed by Shaw (2000) but was shared by Vaněk & Valíček (2001) and Jell & Adrain (2002). A solution of this quite complicated question is still lacking (but see Vaněk 2001) and is not discussed herein. Provisionally, I propose to retain the name *Bojokoralaspis* for the three species occurring in the Prague Basin and to several species referred to *Primaspis* outside Bohemia. Unlike two early Sandbian *Primaspis* species known from the Prague Basin of Bohemia, *Primaspis ascitus* (Whittington, 1956a) from Virginia, *P. multispinosa* Bruton, 1965 from Norway, *P. evoluta* (Törnquist, 1884) from Norway, Sweden, Latvia (Bruton 1965, 1966, 1968; Suzuki *et al.* 2009), and *Primaspis* sp. from Belgium (Lespérance & Sheehan 1987) and Kazakhstan (Apollonov 1980) lack paired occipital spines. These species should be referred to *Bojokoralaspis* (*sensu* Šnajdr 1984) because, unlike *Primaspis*, all cranidia lack occipital spines.

***Bojokoralaspis peregrina* (Barrande, 1872)**

Figure 4A–D

- 1872 *Acidaspis peregrina* Barrande; Barrande, p. 79, pl. 12, figs 30, 31.
- 1949 *Primaspis peregrina* (Barrande). – Prantl & Přibyl, p. 148.
- 1952 *Acantholoma mirka* Marek; Marek, p. 436, pl. 2, fig. 3.
- 1966 *Primaspis* (*Primaspis?*) *peregrina* (Barrande, 1872). – Přibyl & Vaněk, pl. 5, fig. 4.
- 1968 *Primaspis peregrina* Barrande. – Bruton, p. 13, pl. 2, fig. 5.
- 1984 *Primaspis* (*Bojokoralaspis*) *musca* (Barrande, 1846). – Šnajdr, p. 55, pl. 10, figs 8, 9.
- 2000 *Bojokoralaspis peregrina* (Barrande, 1872). – Shaw, p. 379, pl. 2, figs 2–8.
- 2001 *Eoleonaspis peregrina* (Barrande, 1872). – Vaněk, p. 66.
- 2001 *Eoleonaspis peregrina* (Barrande, 1872). – Vaněk & Valíček, p. 36.

Material. – Six cranidia, three librigenae, and four pygidia.

Discussion. – New sampling from the “Perník Bed” has yielded numerous specimens of *Bojokoralaspis* (Fig. 4A–D) which in size are much larger compared to the new species of *Diacanthaspis*. If this material belongs to *B. peregrina* (Barrande, 1872) as suggested by Shaw (2000) or whether it is a synonym of *B. mirka* (Marek, 1952) is uncertain and other authors have recently considered it to be a junior subjective synonym of *Eoleonaspis*

olini (Troedsson, 1918) *fide* Ramsköld & Chatterton (1991, p. 366), Vaněk (2001, p. 66) and Vaněk & Valíček (2001, p. 36). This possible synonymy was already suspected by Kielan (1960) and Bruton (1966). In addition, the relation of *Bojokoralaspis* specimens from the “Perník Bed” to *B. vondraceki* Šnajdr, 1987 from the uppermost part of the Kosov Formation (late Hirnantian) is unclear. This species, informally reported already by Marek (1951) and formally described by Šnajdr (1987), most likely belongs to another genus.

Occurrence. – Upper Katian, the top of the Králův Dvůr Formation (“Perník Bed”); localities Králův Dvůr (Kosov), Levín, Praha-Řeporyje, and Vráž.

Genus *Chlustinia* Přibyl & Vaněk, 1965

Type species. – *Odontopleura keyserlingi* Barrande, 1846. Upper Ordovician, Sandbian, Zahořany Formation, Prague Basin, Bohemia.

***Chlustinia?* sp.**

Figure 4F

Discussion. – *Chlustinia* is suggested as an endemic Bohemian genus (Šnajdr 1984), with the first report from the Zahořany Formation (late Sandbian or early Katian). Its latest occurrence is reported in the middle to early late Katian (Podolí ore horizon at the base of the Králův Dvůr Formation; Šnajdr 1982). The single pygidium of *Chlustinia?* sp. coming from the “Perník Bed” (Fig. 4 F) is very probably related to poorly known *C. mikulasi* Šnajdr, 1982 from the Podolí ore Horizon. The shape of principal spines in the newly collected pygidium differs from those of *C. keyserlingi* (Barrande, 1846) present in the Zahořany Formation (late Sandbian to earliest Katian) and from *C. detecha* Šnajdr, 1984 present in the Bohdalec Formation (early to middle Katian). *Chlustinia?* sp. is remarkably similar to *Primaspis* sp. indet. described by Price (1980) from the Ashgillian (Katian) of Wales.

Genus *Diacanthaspis* Whittington, 1941

Type species. – *Diacanthaspis cooperi* Whittington, 1941; Upper Ordovician, Sandbian, Lower Martinsburg Formation, Virginia, USA.

Material. – One pygidium.

Remarks. – The presence of *Diacanthaspis* sp. in the “Perník Bed” has been discussed by Mergl (2011a). Another odontopleurid from the same stratigraphic level referred by

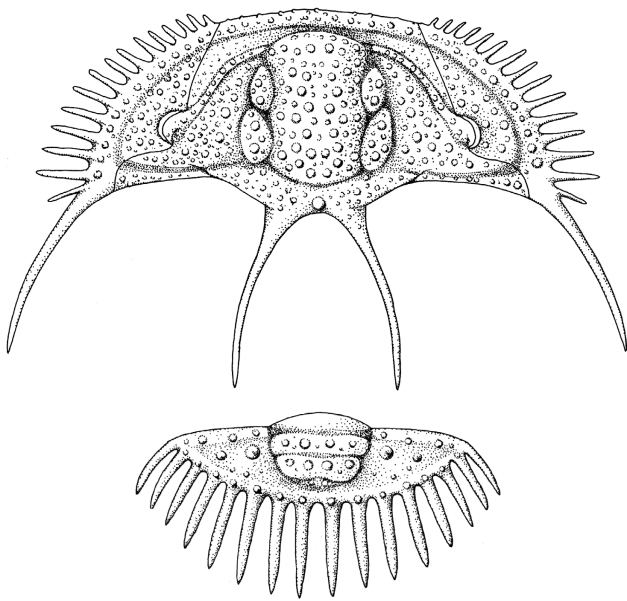


Figure 2. *Diacanthaspis krizi* sp. nov. Reconstruction of cephalon and pygidium; approximately $\times 15$.

Šnajdr (1984), Štorch & Mergl (1989) and by Shaw (2000), belongs to the genus *Bojokoralaspis* and has been also reported by Marek (1952).

Occurrence. – Upper Katian, the top of the Králův Dvůr Formation (“Perník Bed”); locality Praha-Řeporyje.

***Diacanthaspis (D.) krizi* sp. nov.**

Figures 2, 3

Holotype. – Pygidium, internal and external mould figured on Fig. 3O, W (PCZCU 1874).

Type horizon. – Upper Katian, the top of the Králův Dvůr Formation (“Perník Bed”).

Type locality. – Praha-Řeporyje, temporary excavation done in 2007.

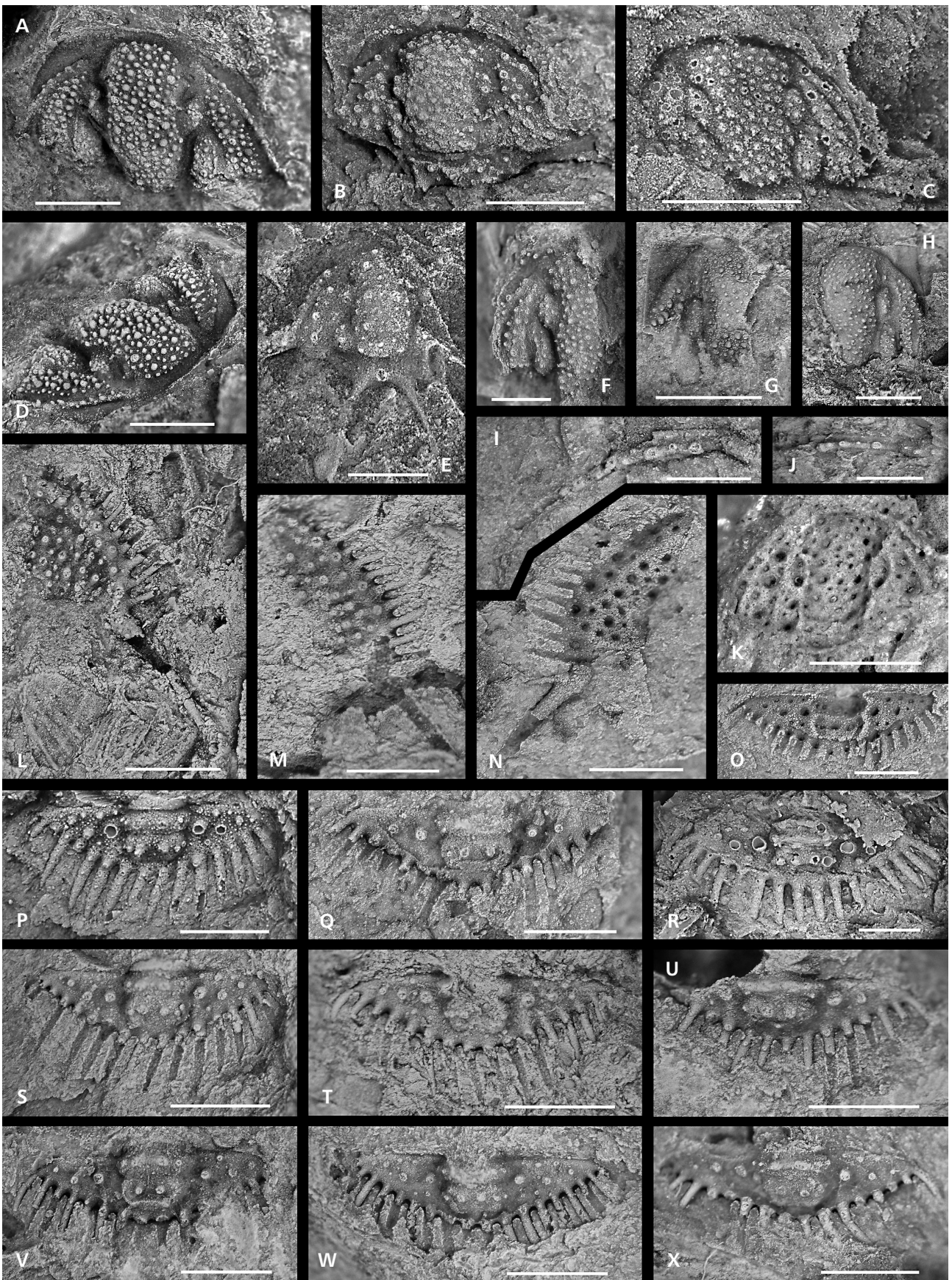
Etymology. – In honour of Jiří Kříž, the prominent Czech palaeontologist.

Material. – Twenty cranidia, ten librigenae, sixteen pygidia, two incomplete segments and incomplete part of the thorax with five segments, all preserved as internal and external moulds in claystone.

Diagnosis. – *Diacanthaspis* with thin and long occipital spines, a long inward curved librigenal spine, twelve long librigenal border spines, a distinct longitudinal row of spines on librigenal border, undivided pleural field in pygidium, and eight long border spines of uniform size in pygidium.

Description. – Species small-sized, maximal estimated sag. length of entire specimen does not exceed 6 mm. Cranidium strongly vaulted (sag. and tr.), semicircular in outline, sag. length including the occipital ring without spines is 2 mm. Glabella inclusive the occipital ring broadly ovoid in outline, with the maximum width across L1. Glabella strongly arched (tr. and sag.), well limited by deep axial furrows. Three glabellar lobes distinct. L1 largest, ovoid, twice as long as wide, strongly arched (sag. and tr.), well separated from the median glabellar lobe by unevenly deep S1. L2 about one-third size of L1, directed anteromesially. S2 distinct and deep. L3 is connected with the frontal lobe, distinct as a small node on anterolateral slope of the frontal lobe. Anterior margin of glabella gently rounded. Median glabellar lobe subrectangular, gently constricted opposite to L1 and L2 and slightly expanding in anterolateral corners. Occipital furrow deep and broad. Occipital ring convex (tr. and sag.), mesially widened (sag.), occupying some 20% of cranidial length. Occipital lobes small. Long tubular paired occipital spines as long as glabella. Spines posterolaterally directed, with gently upward curved proximal and inward curved distal parts. Median occipital organ distinct. Tubercles on the glabella large, circular, showing paired spacing, otherwise without distinct paired or other regular spacing. L1 and L2 with two larger tubercles. Interspaces between large and medium-sized tubercles covered by very fine evenly sized and randomly spaced spines. Fine spines cover also a floor of axial and border furrows. Fixigenae raised,

Figure 3. A–X – *Diacanthaspis krizi* sp. nov. • A, D – cranidium, internal mould in dorsal and oblique views, PCZCU 1866. • B – cranidium, internal mould, PCZCU 1868. • C – cranidium, latex cast of exterior, PCZCU 1842. • E – cranidium, internal mould, PCZCU 1886. • F – incomplete cranidium, internal mould, PCZCU 1879. • G – incomplete cranidium, internal mould with remains of exoskeleton, PCZCU 1884. • H – incomplete cranidium, internal mould, PCZCU 1863. • I – incomplete segment from the posterior part of thorax, internal mould, PCZCU 1890. • J – fragment of segment, internal mould, PCZCU 1891. • K – incomplete cranidium, external mould, PCZCU 1867. • L – right librigena, internal mould, PCZCU 1882. • M – right librigena, internal and external moulds, PCZCU 1888. • O, W – pygidium, external and internal moulds, PCZCU 1874. • P, S – pygidium, latex cast of exterior and internal mould, PCZCU 1873. • Q – pygidium, internal mould, PCZCU 1872. • R – pygidium, latex cast of exterior, PCZCU 1889. • T – pygidium, internal mould, PCZCU 1876. • U – pygidium, internal mould, PCZCU 1875. • V – pygidium, internal mould, PCZCU 1869. • X – pygidium, internal mould, PCZCU 1870. Stratigraphic and geographic location: The top of the Králův Dvůr Formation, “Perník Bed”. Localities: Praha-Řeporyje (A–D, F, I–X), Praha-Jezerka (G, H), and Praha-Rajtknechtka (E). Bars equal to 1 mm. All photos by the author.



narrow, gently arched (tr.). Posterior border widens laterally. Posterior border furrow deep and narrow (sag.), becoming wider and shallower laterally. Ocular ridge distinct, narrow, obliquely backwards curving and separated from inner field of fixigena by a deep furrow devoid of large tubercles. Inner genal field narrowly triangular, with surface bearing large tubercles in three to five oblique rows. Palpebral lobes weakly developed, small, highly raised above surface of fixigena, situated about opposite midlength of L1. Anterior branches of suture gently subparallel anteriorly, running along the edge of ocular ridge. Anterolateral field of fixigena outside the ocular ridge triangular, highly raised. Anterior border narrow (sag.), highly raised, separated by a deep narrow border furrow.

Librigenae triangular, with flat surface and gently rounded lateral border becoming wider toward the librigenal spine. Eye supported by a low stalked eye socle. Librigenal spine thin and long, swollen at the base, directed outwards, gently curved. Short notch present inside the base of the librigenal spine. Border with at least twelve thin forward to outwards directed border marginal spines. The first anterior border marginal spine short and thin. The size and length of border marginal spines increase backwards. The most posterior border marginal spine shorter than others and situated opposite to the notch of the librigenal spine. Outer surface of the border with single longitudinal row of dorsally directed short spinose tubercles. Cheek surface with larger spinose tubercles, having interspaces with fine spines.

Thoracic segments short (sag.), with significantly vaulted axis and subhorizontal pleurae. Principal pleural ridge with five vertical spines. Axis with short spines. Principal pleural spine short, directed laterally in anteriormost segments. The posterior thoracic segments with long and strongly backward curved pleural spine.

Pygidium of semielliptical outline (border spines included) twice as long (sag.) as wide, with straight anterior margin and gently curved posterior margin. Maximum width including border spines at about anterior third. Pleural area flat, narrowly triangular, without distinct pleural ridge. Axis moderately convex, prominent, bordered by narrow and deep axial furrows. The axis is subquadrate in a plan view, lowering backwards, anteriorly occupying one-fourth of the anterior pygidial margin. Articulation half ring short. Two axial rings present, weakly divided by a shallow and narrow furrow. The first axial ring prominent, strongly arched (sag.), about one third long (sag.) as wide (tr.). The second axial ring slightly narrower (tr.), and slightly longer than the first axial ring, gently arched (tr.). Each axial rings bear a pair of large tubercles. The first ring has three additional pairs of smaller tubercles placed laterally to large tubercles and a median small tubercle in the axial line. Each large tubercle at the second axial ring laterally associated with two smaller tubercles. Pleural field un-

divided, with flat surface bearing symmetrically arranged tubercles. Large upward directed tubercle symmetrically situated opposite to interring furrow on pleural field. Three to four smaller tubercles arranged in a row along the anterior margin of the pygidium. Additional three to four smaller tubercles present on the flat surface of the each pleural field. Short spinose upward directed tubercle is situated near the base of each border spine with the exception of the most lateral spine. Border spines cylindrical in section, long, evenly sized and radially arranged, weakly tapering distally, with acute tips. Distal tips of spines weakly curved downwards. There are usually eight spines along the posterior border but pygidia with seven or nine pairs of spines, respectively, have been observed. Surface of axis and pleural fields between tubercles is covered by minute spines. Very fine spines cover surface of border spines.

Discussion. – Several late Katian species of *Diacanthaspis* similar to the new species are known outside the Prague Basin. Hammann (1992) described *Diacanthaspis conica* Hamman, 1992 and *D. margaritata* Hammann, 1982 from the Rebosilla Member of the Iberian Chains (upper Katian, Spain). *Diacanthaspis conica* differs from *D. krizi* in possessing distinctly shorter border spines at the librigena, a well developed occipital organ, shorter paired occipital spines and by distinctly shorter and fewer marginal spines on the pygidium. *Diacanthaspis krizi* sp. nov. has the marginal spines on pygidium twice longer than those present in *D. conica*. Although one pygidium having seven spines occurs in the type collection of *D. krizi*, the majority of pygidia show eight spines. Librigena of *D. krizi* has a longitudinal row of upwardly directed spinose tubercles on the librigenal border. Librigena of *D. conica* figured by Hammann (Hammann 1992, pl. 34, figs 4, 5) exhibits longer spines than illustrated on the reconstruction (Hammann 1992, text-fig. 32). Figures also show a distinct row of upwardly directed spines on the librigenal border (Hammann 1992, pl. 34, fig. 4) but they are considerably shorter than those on librigena of *D. krizi*. *Diacanthaspis margaritata* has larger tubercles on the cephalon and pygidium than *D. krizi* and they are more closely spaced forming a rosette pattern. Librigenal spine of *D. margaritata* is more robust than that of *D. krizi* and the dorsal surface of librigena is covered by thicker and much larger tubercles. Pygidium of *D. margaritata* is distinct by shorter, more stout and less numerous posterior spines.

Diacanthaspis tariccoi Hammann & Leone, 2007 was described from the Portixeddu Formation, at locality Ovile Cannamenda (Can 1c) of Sardinia only (Hammann & Leone 2007). This species is similar to *D. krizi* in having a densely tuberculate ornamentation, distinct longitudinal row of spinose tubercles on librigenal border, long and numerous border spines at librigena, paired occipital spines and by similar outline of the pygidium. *Diacanthaspis*

tariccoi has fourteen posterior border spines on the pygidium while *D. krizi* has sixteen to eighteen spines. However, one pygidium of *D. krizi* is known with fourteen spines but there are always only twelve spines of subequal size in *D. tariccoi*, having the first anterior pair distinctly smaller than other spines. Occipital spines of *D. krizi* are slender and distinctly longer than those of *D. tariccoi*.

Diacanthaspis sladensis (Reed, 1905) from the base of the Haverford Mudstone Formation of Wales (Cocks & Price 1975) and the top of the Keisley Limestone (Temple 1969) is other species similar to *D. krizi*. The pygidium of *D. sladensis* has, as well as the pygidium of *D. krizi*, sixteen posterior spines. *D. krizi* has shorter occipital spines than the lectotype cranidium of *D. sladensis* illustrated by Cocks & Price (1975, pl. 82, fig. 10). *D. krizi* seems to be related to *D. sladensis* but morphology of the latter species is not sufficiently known.

Bruton (1968) described three unassigned species of *Diacanthaspis* from Estonia. The pygidium of *Diacanthaspis* sp. indet. B from the Oandu Stage (early Katian) of Estonia is remarkably similar to the pygidium of *D. krizi*. There is almost the same arrangement of tubercles on the pleural fields and two pairs of large tubercles on each axial rings. The main difference between both species is the presence of only fourteen marginal spines in this taxon (Bruton 1968; Fig. 5B, C) compared to *D. krizi*. Another pygidium and the librigena referred to *Diacanthaspis* sp. indet. C are also similar to *D. krizi*, but it is more rectangular and differs by only fourteen marginal spines. *Diacanthaspis* sp. indet. B and *D. sp. indet. C* are not well preserved and are hardly comparable with the present new species. They are stratigraphically earlier coming from the Sandbian and early to mid-Katian. All species of *Diacanthaspis* described by Whittington (1956a) from the Middle Ordovician of Virginia strikingly differ from *D. krizi*, mainly by distinctly developed major spines in pygidium. The type species *D. cooperi* Whittington, 1941 differs from *D. krizi* mainly by six pairs of marginal spines and by a development of major spine on upper surface of pygidium.

Occurrence. – Upper Katian, the top of the Králův Dvůr Formation (“Perník Bed”); locality Praha-Řeporyje, Praha-Rajtknechtka, Praha-Jezerka.

Genus *Eoleonaspis* Sheng, 1974

Type species. – *Acidaspis shanensis* Reed, 1915. Upper Ordovician, Hirnantian, Pangsha-pye Formation, Burma.

Eoleonaspis? sp.

Figure 4E

Material. – Two cranidia.

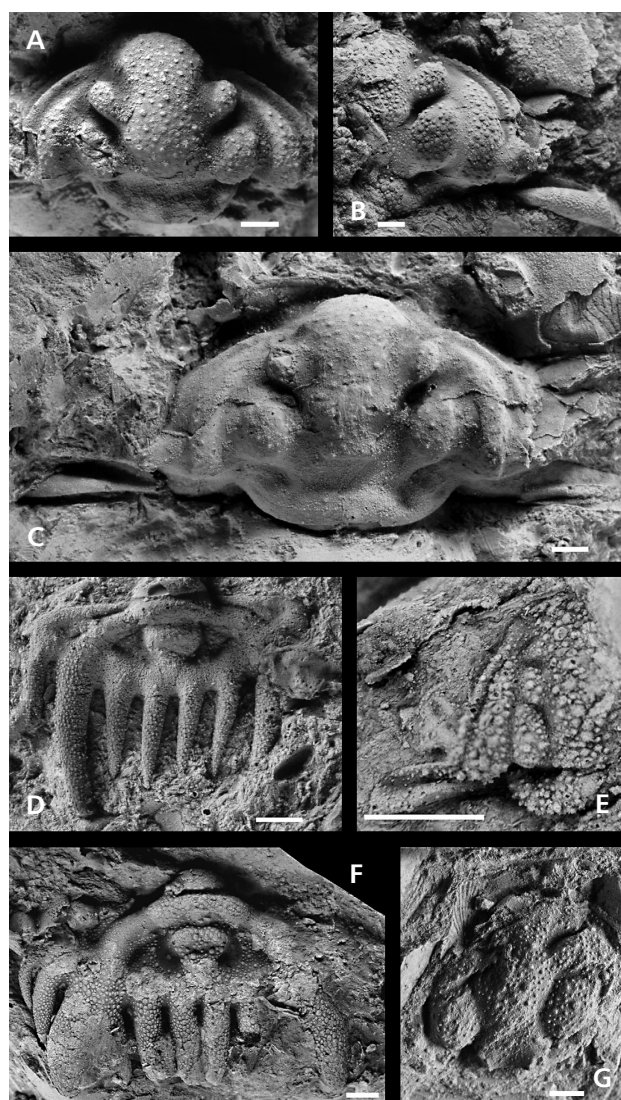


Figure 4. A–D – *Bojokoralaspis peregrina* (Barrande, 1872). • A – cranidium, internal mould, PCZCU 1892. • B, C – cranidium, latex cast of exterior and internal mould, PCZCU 1893. • D – pygidium, latex cast of exterior, PCZCU 1894. • E – *Eoleonaspis* sp., cranidium, latex cast of exterior, PCZCU 1895. • F – *Chlustinia*? sp., pygidium, latex cast of exterior, PCZCU 1896. • G – *Proceratocephala*? sp., incomplete cranidium, internal mould, PCZCU 1987. The top of the Králův Dvůr, “Perník Bed”. Locality: Praha-Řeporyje. Bars equal to 1 mm. All photos by the author.

Remarks. – A small-sized odontopleurid distinguished by absence of the occipital spines and less distinctive L1 and L2 has been sampled in the “Perník Bed” (Fig. 4 E). This material is remarkably similar to the type specimens of *Eoleonaspis shanensis* (Reed, 1915) redescribed also by Cocks & Fortey (2002) from the Hirnantian of Burma. Cranidia from the “Perník Bed” are also strikingly similar to “*Bojokoralaspis*” *vondraceki* of the latest Hirnantian age (Šnajdr 1987). However, “B.” *vondraceki* is not sufficiently known and probably belongs to *Eoleonaspis* Sheng, 1974 (see also discussion of

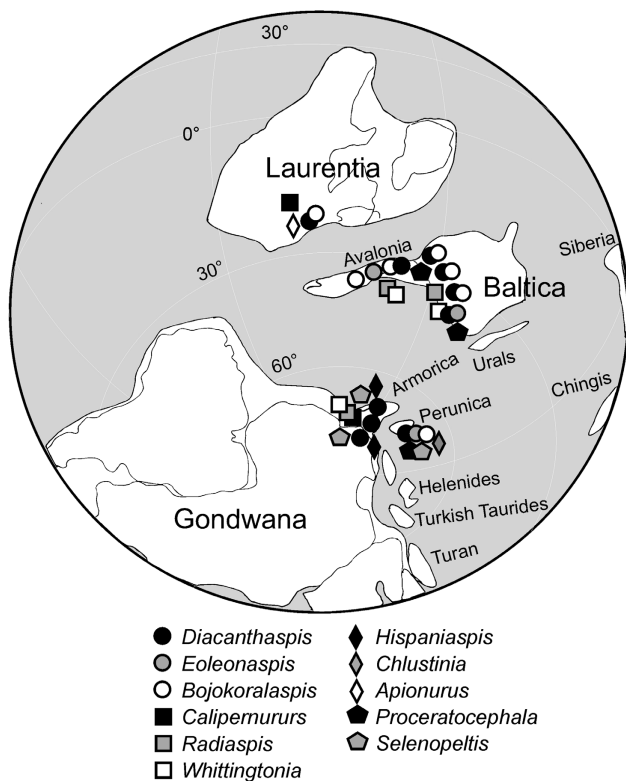


Figure 5. Palaeogeographical reconstruction for the Katian (after Popov *et al.* 2013, modified) showing geographical distribution of the Middle and Late Ordovician odontopleurid trilobites. Data mainly after Bruton (1965, 1966, 1968), Hammann (1992), Hammann & Leone (2007), Kielan (1960), Lesperance & Sheehan (1987), Price (1980), Šnajdr (1984), and Whittington (1956a).

Bojokoralaspis herein). New specimens are similar to specimens referred to *Eoleonaspis olini* (Troedsson, 1918) by Kielan (1960) and Bruton (1966) and to several other species referred to *Eoleonaspis* of the Hirnantian to Llandoveryan age (Reed 1915, Apollonov 1980, Curtis & Lane 1998; see comments of Cocks & Fortey 2002). Taxonomical and phylogenetic problems regarding *Eoleonaspis* and its relation to *Primaspis* have been discussed by Cocks & Fortey (2002), who noted, that the cladistic analysis of Ramsköld & Chatterton (1991) likely requires a reworking.

Occurrence. – Earliest Hirnantian, the top of the Králův Dvůr Formation (“Perník Bed”); locality Praha-Řeporyje.

Subfamily Miraspidinae Richter & Richter, 1917

Genus *Proceratocephala* Prantl & Přibyl, 1949

Type species. – *Acidaspis terribilis* Reed, 1914. Upper Ordovician, Katian, Drummuck Group, Starfish Bed, Scotland.

***Proceratocephala?* sp.**

Figure 4G

Material. – One cranium.

Remarks. – The poorly preserved cranium belongs to medium sized odontopleurid (Fig. 4G). Presence of two robust occipital spines, large L1 and L2, and weak and uneven spinosity may be indicative of Miraspidinae Richter & Richter, 1917. The specimen is provisionally referred to *Proceratocephala* Prantl & Přibyl, 1949, a genus known from the Katian of Scotland (Reed 1914, Whittington 1956b), and Poland (Kielan 1960).

Occurrence. – Upper Katian, the top of the Králův Dvůr Formation (“Perník Bed”); locality Praha-Řeporyje.

Discussion

To compare with previous stage of knowledge (Štorch & Mergl, 1989, Shaw 2000), the odontopleurid association of the Katian/Hirnantian boundary strata is substantially more diversified in the Prague Basin. This association in the “Perník Bed” clearly differs from older (Sandbian to mid-Katian) odontopleurid associations of the Prague Basin by absence of *Selenopeltis* and first occurrence of minute odontopleurid genera (*Diacanthaspis*, *Eoleonaspis*) and a miraspidinae *Proceratocephala*. Sandbian and mid-Katian representatives of the Odontopleuridae Burmeister, 1843 in Bohemia belong to genera *Bojokoralaspis*, *Chlustinia*, *Primaspis*, and *Selenopeltis* Hawle & Corda, 1847. Of these, *Selenopeltis* occurs as early as Darriwilian (Šárka Formation) with the latest possible record from early late Katian (lower to middle parts of the Králův Dvůr Formation: Šnajdr 1984, Shaw 2000, Bruton 2008). *Primaspis* is restricted to the Sandbian–lowermost Katian (Libeň to Zahorany formations; Šnajdr 1984). *Chlustinia* ranges from the late Sandbian to probably early upper Katian. *Bojokoralaspis* is known from the Sandbian to the latest Katian (Šnajdr 1984).

Unlike in Bohemia, *Bojokoralaspis*, *Chlustinia*, *Eoleonaspis* and *Proceratocephala* are absent among the late Katian odontopleurids of European peri-Gondwana and NW Gondwana (= present day SW Europe and NW Africa). Here, the odontopleurid trilobites are represented by particular species of *Diacanthaspis* associated with *Callipernurus* Whittington, 1956a, *Dicranurus* Conrad, 1841, *Radiaspis* Richter & Richter, 1917, *Whittingtonia* Prantl & Přibyl, 1949, and the endemic *Hispaniaspis* Hammann, 1992 (Hammann 1992). The sudden appearance of *Callipernurus*, *Diacanthaspis*, *Dicranurus*, *Radiaspis*, and *Whittingtonia* in the late Katian of Spain (Cystoid Limestone; Hammann 1992) and Sardinia (Portixeddu and

Domusnovas formations; Hammann & Leone 2007) indicates a rapid dispersion of the Laurentian and Baltic warm-water elements onto high-latitude shallow shelves with carbonate buildups (Hammann 1992). Their occurrence preceded an abrupt climatic cooling and sea level lowering in the present day Spain and Sardinia at the beginning of the Hirnantian.

Diacanthaspis and *Calipernurus* are known in the Middle Ordovician of Laurentia (Whittington 1956a). *Diacanthaspis* is a pandemic genus in tropical and temperate belts. It is known, although often poorly understood (Bruton 1965, 1968; Kielan 1960; Apollonov 1980; Suzuki *et al.* 2009) from the Lower to the uppermost Ordovician from all palaeocontinents.

Bojokoralaspis probably originated in the early Middle Ordovician in low-latitude (Laurentia or Baltica). This genus, as the new element, appeared in the Prague Basin during the late Sandbian. It may be assumed, that *Bojokoralaspis* was a new invader into the Prague Basin where *Primaspis* (with occipital spines) already existed since the early Sandbian. Both genera co-occur herein (Šnajdr 1984) in the late Sandbian to early Katian Zahorany Formation.

Diverse Middle and Upper Ordovician odontopleurid faunas are further known from Baltica, some of them being shared with Laurentia: *Acidaspis*, *Apianurus*, *Radiaspis* and *Whittingtonia*. None of these genera is known in Middle and Upper Ordovician of the Prague Basin.

Conclusions

The sudden immigration of *Diacanthaspis*, *Radiaspis* and *Whittingtonia* from Baltica and/or Laurentia and evolution of endemic *Hispaniaspis* certainly indicates warming and expansion of shallow water carbonate facies in NW Gondwana and European peri-Gondwana (= present day NW Africa and SW Europe). Their immigration into the Prague Basin was much restricted and probably happened later, at least in the now preserved part of the basin.

The Katian global warming and expansion of low-latitude fauna with *Heliomera*, *Ovalocephalus*, *Staurocephalus*, proetids, and odontopleurids into high latitudes (Boucot *et al.* 2003, Fortey & Cocks 2005, for alternative interpretation see especially Cherns & Wheeley 2007) influenced the shelves in NW Gondwana and European terranes on periphery of Gondwana. Similar suitable shelves probably did not border the Prague Basin. When the Hirnantian sea-level lowering has started, the restricted ecospace for the BBP association developed along margins of the Prague Basin for a short time. However, this environment became too cool for immigration of *Whittingtonia*, *Calipernurus*, other odontopleurids and majority of other low-latitude trilobite taxa. Only *Diacanthaspis* and a

rare miraspidine *Proceratocephala* immigrated into the Prague Basin, where *Chlustinia* and *Bojokoralaspis* persisted since the Sandbian and/or early Katian, respectively. Despite the short time existence of ecospace suitable for the low-latitude trilobite taxa, also proetids and some other warm to temperate-water elements accompanied the odontopleurid association in the “Perník Bed”. Next progressive cooling terminated the short time existing BBP association, and a poor *Hirnantia* fauna with trilobites *Mucronaspis* and *Eoleonaspis* occupied the Prague Basin. It is noteworthy that “*Primaspis*” *evoluta* is associated with *Mucronaspis mucronata* after the decline of the taxonomically rich, earliest Hirnantian fauna with *Diacanthaspis*, *Whittingtonia* and *Radiaspis* (Suzuki *et al.* 2009) in Dalarna, Sweden. The assumption about cooling in the time and/or immediately before the sedimentation of the “Perník Bed” and its early Hirnantian age is supported by presence of small *Eoleonaspis*, which is a typical element of the *Hirnantia* fauna (Kielan 1960, Cocks & Fortey 2002, see also Mergl 2011a, b, Mitchell *et al.* 2001, Melchin *et al.* 2003).

In summary, the available data concerning odontopleurids from the “Perník Bed” support the interpretation, that there were more sources and not only one immigration wave of odontopleurids present. *Bojokoralaspis* immigrated into the Prague Basin possibly from the Baltica in the late Sandbian or early Katian. *Diacanthaspis* and *Proceratocephala* immigrated from Baltica or nearby Avalonia in the latest Katian, likely at the time of the Boda event and persisted here up to the base of the Hirnantian. The last immigrant *Eoleonaspis* appeared in the Prague Basin in the early Hirnantian together with other elements of the rapidly spreading *Mucronaspis* fauna (Budil 1996). It is supposed, that all immigrants evolved into particular geographic species in the Prague Basin. Only the very rare *Chlustinia?* sp. can be assumed to have been derived from ancestors living in the Prague Basin.

In summary, the fauna preserved in the “Perník Bed” is obviously younger than faunas from Spain and Sardinia, which are pre-Hirnantian in age. It is not excluded, that carbonate platform formed outside the range of now preserved Ordovician sediments of the Prague Basin during the supposed warming of the Boda event. However, the origin of the “Perník Bed” reflects sea level lowering, which moved the biofacies belts basinwards. The short-time immigration of “warm-water” elements in the rich BBP fauna indicates none progressive cooling of surface waters at that time. This is contradictory with ideas of Cherns & Wheeley (2007) but supports well the original concept of Boda event.

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