TRILOBITE BIOSTRATIGRAPHY OF THE KRÁLŮV DVŮR FORMATION (UPPER KATIAN, PRAGUE BASIN, CZECH REPUBLIC): GLOBAL FAUNAL CHANGES OR FACIES-RELATED DISTRIBUTION?

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Key words: Teplá-Barrandian Unit, Katian, Prague Basin, trilobite associations

Abstract

Eight trilobite associations and sub-associations have been distinguished in the late Katian Králův Dvůr Formation. Spatial distribution of these associations reflects lithology but their succession was dictated also by global climatic changes and palaeogeographical positioning. Locally developed "Podolí Ore Horizon" trilobite association contains low-diversity but specific forms showing survivals from the underlying Bohdalec Formation combined with the late Katian taxa (Chlustinia, Duftonia, Onnia, etc.). The Amphitryon - Kloucekia Association is newly established for the lower two thirds of the formation. It is characterized by abundant benthic scavenger-predators accompanied by filter feeders and common pelagic/nektic predators. Within Amphitryon –Kloucekia Association can be distinguished four sub-Association 1) the newly established Onnia ultima sub-Association is characterized by a dominance of Onnia and Flexicalymene; it is developed at the lowermost levels of the formation, 2) the deeper-water Nankinolithus granulatus sub-Association (originally established as horizon), 3) rather shallow-water, brachiopod-dominated Dedzetina-Tretaspis sub-Association with rare trilobites and 4) the trilobite-dominated Tretaspis and erssonni sub-Association (originally horizon). Last three sub-associations are considered as rather facies-related, with limited stratigraphical applicability only. Impure bioclastic limestone below top of the formation contains a rich shallow- and temperate-water Marekolithus kosoviensis Association, which better corresponds with the original horizon concept. This association is dominated by small benthic scavenger-predator trilobites, which are associated by the filter feeder Marekolithus. The Mucronaspis Association of medium-sized scavenger-predators is characteristic for the uppermost portion of formation and persisted till the early onset of the glaciation at the base of Hirnantian. Minute detritus feeders are rare but present in all the above-discussed associations excluding the last one.

Introduction

Trilobites of the Králův Dvůr Formation (see fig. 1) belong to the most diversified within the Ordovician of the Prague Basin; they have been investigated since first half of the 19th century (see Barrande 1846, 1852, 1872, Hawle -Corda 1847, Novák 1883; for review of the older data see Havlíček – Vaněk 1966, Shaw 2000, Chlupáč 2002). They share many elements with the temperate-water trilobite assemblages of Baltica (see Kielan 1960, Bruton - Owen 1979, Owen 1981), Avalonia (Ingham 1970, Owen - Romano 2010), Kazakhstania (Apollonov 1974) and also with the European peri-Gondwana - nowadays Sardinia and Iberia (e.g. Hammann 1974, Hammann - Leone 1997). The spatial distribution of fauna of the Králův Dvůr Formation was studied by Havlíček - Vaněk (1966), they proposed the first zonation based mostly on trilobites and on brachiopods. This concept has been further developed by Havlíček -Vaněk (1990) and by Havlíček (1998). Shaw (2000) critically discussed their approach but he accepted the horizon concept in general. The upper part of the Králův Dvůr Formation was studied in detail by Štorch - Mergl (1989). The first occurrence of the Hirnantian fauna in the upper part of Králův Dvůr Formation recently discussed Mergl (2011) and the distribution of the agnostid Arthrorhachis is analyzed by Budil et al. (in press). Recently, Budil et al. (2009a-c, 2010) provided partially re-defined concept of Havlíček - Vaněk (their communities are considered to

represent associations considering them as facies related). However, this revised approach was not properly published.

The association versus assemblage and horizon approach

The concept of trilobite associations of Budil et al. (2007a, b), Mergl et al. (2008) and Fatka – Mergl (2009) is followed here, instead of the traditional horizon and community concept of Havlíček (1998). One of important problems is the autochtonity of fossils. Similarly, the designation "trilobite horizon" as applied in the Králův Dvůr Formation by Havlíček – Vaněk (1966) is considered as inaccurate, especially for lower and middle levels of the unit. The occurrence of key species is rather facies related and/or or locality related (e. g. *Nankinolithus granulatus* occurs only sporadically outside the locality Lejškov). In addition, several tens to hundred meters thick sedimentary successions represent such trilobite horizons. The non-genetic, descriptive designation "Trilobite Association" is appropriate see Turvey – Zhou (2002, 2004).

Study of trilobite associations of the Králův Dvůr Formation is complicated by the absence of thick continuous sections, especially in lower and middle levels of the unit. The situation is comparatively better in upper part of the formation (see Štorch – Mergl 1989). The soft shale and claystones forming major part of the formation are often tectonically affected. This tectonics involves usually



intensive folding. In addition, the belts of the Králův Dvůr Formation are commonly represented by tectonically limited blocks. There is also relative lack of exposures because of heavy weathering of the clayey shale (but great help sometimes represent the temporary exposures originated during diverse building activities). These all above-discussed aspects obscure the analysis.

Review of trilobite associations of the Králův Dvůr Formation

More than 60 trilobite species established from the Králův Dvůr Formation are grouped into eight trilobite associations and sub-associations (see tab. 1, fig. 2).

Their spatial distribution reflects rather lithology, especially in lower and middle levels of the formation, while the succession in upper part was directly influenced by the onset of global climatic changes induced by the Boda Event (see Fortey – Cocks 2005), and the subsequent onset of the Hirnantian glaciation in the uppermost portion of the sequence (see also Mergl 2011).

1. The "Podolí Ore Horizon" Trilobite Association (newly defined) locally present at the base of the formation is characterized by very scarce and poorly known trilobite fauna with apparent mixing of species known from the underlying Bohdalec and the Králův Dvůr formations: Onnia cf. ultima, Chlustinia mikulasi (= keyserlingi fide Vaněk - Valíček 2001), Selenopeltis sp., Octillaenus? sp., Actinopeltis cf. gryphus, Duftonia juspa konika (nomen nudum, MS Šnajdr) and Kloucekia sp.

2. The Amphitryon-Kloucekia Trilobite Associa-

Fig. 1: A – A map of the distribution of the Ordovician rocks in the Barrandian area. The asterisks show the position of the major localities of the Králův Dvůr Formation. Modified after Manda (2008). B – The stratigraphical position of the Králův Dvůr Formation.

species/(sub)associations	Podolí Ore Horizon	Onnia ultima	Nankinolithus	Dedzetina - Tretaspis	Tretaspis	Marekolithus	Mucronaspis	podolí Ore Horizon Nankinolithus Dedezetina Tretaspis Tretaspis	Marekolithus	Mucronaspis
<i>"Encrinurus"</i> sp.						R		Chlustinia keyserlingi R R R		
Actinopeltis barrandei					R			Illaenus hospes R		
Actinopeltis carolialexandri			С		R	R?		Kloucekia ruderalis ? R C C	?	
Actinopeltis insocialis						С		Lonchodomas portlocki C R R		
Actinopeltis cf. gryphus	R							Marekolithus kosoviensis	С	
Alceste latissima					R	R		Microparia speciosa C C C	С	
Amphitryon radians		С	С		С			Miraspis sp.	R	
Areia bohemica			R		R			Mucronaspis ganabina	С	
Arthrorachis tarda			R	R	R			Mucronaspis grandis ? ?	С	С
Birmanites kielanae			R		R			Nankinolithus granulatus C ?		
Brongniatella platynota			R					Octillaenus hisingeri ? R	R	
<i>Bumastus</i> sp.						R		Onnia ultima?CR??		
Carmon mutilus			С		R			Phillipsinella parabola R R	R	
Cerampyx gratus			R					Platylichas milosi R		
Cyclopyge marginata			R		R			Pseudosphaerexochus pectinifer R		
Decoroproetus solus					R	R		Raphiophorus tenellus C R	R	
Degamella gigantea					R	R		Selenopeltis vultuosa ? C R		
Dindymene frídericiaugusti			R		R	R		Sphaerexochus latens R		
Dionide speciosa			С		С	R		Staurocephalus cf. clavifrons	R	
Dreyfussina ? simaki					R			Stenopareia oblita	С	
Duftonia morrisiana					?	С	?	Stubblefieldia neglecta R		
Duftonia juspa konika (MS)	R							Symphysops armatus R ?	R	
Dysplanus wahlenbergianus			R		С			Telephina fracta ? R		
Eoleonaspis cf. olini (=mirka)						R		Thorslundops? sp.	R	
Eoleonaspis koral					R	R		Tretaspis anderssoni ? R C		
Eoleonaspis musca					R			Trochurus sp.	R	
Eoleonaspis peregrina			R		R	R		Trochurus toernquisti	R	
Flexicalymene declinata		С	С		С			Xenocybe michle	R	
<i>Girvanopyge</i> sp.					R			Zazvorkaspis neutra R		
Gravicalymene asperula					С	C		Zdicella (=Delgadoa) zeidlerí C R		
Hadromeros fortis					R			Zdicella? sola R	R	
Harpidella cf. kielanae					R					

Tab. 1: The occurrence of the trilobites in the Králův Dvůr Formation. Modified after Shaw (2000).

tion (newly defined) is confined to the lower two thirds of the formation (see also fig. 4). It is characterized by the dominance of benthic scavenger-predatory forms associated with filter feeders and common pelagic/nektic predators. The association includes two previously defined trilobite "horizons" (*Tretaspis granulatus* and *Tretaspis seticornis sensu* Havlíček – Vaněk 1966) and one newly defined sub-association.

2.1. The Onnia ultima Trilobite sub-Association (newly defined) is known near the base of the formation at the locality Lejškov, Velká Chuchle and several other outcrops. It is poorly diversified, with dominant Onnia ultima, Flexicalymene declinata, Amphitryon radians, Microparia speciosa and only rare Kloucekia ruderalis.

2.2. The rather deeper-water Nankinolithus granulatus Trilobite sub-Association (horizon sensu Havlíček – Vaněk 1966) contains 29 trilobite species ranged to the following genera: Nankinolithus, Onnia, Amphitryon, Kloucekia, Actinopeltis, Microparia, Flexicalymene, Octillaenus, Selenopeltis, Nobiliasaphus, Lonchodomas, Phillipsinella etc. and the agnostoid Arthrorhachis. 2.3. Rather shallow-water *Dedzetina-Tretaspis* brachiopod-dominated sub-Association (= compact shales with *Foliomena* and *Dedzetina sensu* Havlíček and Vaněk 1966) locally occurs in middle levels of the formation. Three species of rare, minute trilobites are known from this sub-association: *Lonchodomas portlocki, Arthrorhachis tarda*, and *Tretaspis anderssoni*.

2.4. *Tretaspis anderssoni* Trilobite sub-Association (horizon *sensu* Havlíček – Vaněk 1966) is characteristic by highly diversified trilobites (44 species known); it shows proportional presence of the main feeding strategies (see fig. 3). It also shares many species with the older *Nankinolithus granulatus* sub-Association (see tab. 1, fig. 2). However, it is distinguished from the later sub-association by the presence of *Tretaspis anderssoni* as well as by somewhat higher position in the sequence. However, both index species are often mismatched in older collections. Both sub-associations characterized by dominance of benthic scavengers and planktonic or nektonic forms. The typical genera of the *T. anderssoni* sub-association are *Tretaspis, Amphitryon, Kloucekia, Microparia, Actionopeltis, Flexica*



Fig. 2: A – The classical (Havlíček – Vaněk 1966 and Havlíček in Chlupáč et al. 1998) concept of trilobite horizons in the Králův Dvůr Formation. B – A new proposal of trilobite associations (see text).

lymene, Octillaenus, Selenopeltis, Nobiliasaphus, Lonchodomas; rare but typical are Arthrorhachis, Phillipsinella etc.

The richly fossiliferous, dark grey to almost black claystones are traditionally called the "Lejškov facies" of the Králův Dvůr Formation (Havlíček – Vaněk 1966, Havlíček 1998). It was supposed to be restricted to the lower part of the formation. However, the occurrence of index *Nankinolithus granulatus* together with *Normallograptus angustus* and *Dicellograptus* cf. *laticeps* (determination by P. Štorch; see Budil et al. in press) combined with the questionable co-occurrence of *N. granulatus* and *T. anderssonni* (see Vonka – Kolář 2006) approves the comparatively wider stratigraphical range of *N. granulatus*.

3. Diversified fauna of the Marekolithus kosoviensis Trilobite Association (horizon sensu Havlíček - Vaněk 1966) is confined to calcareous claystone in the uppermost levels of the formation. It contains the index filter feeder Marekolithus associated with shallow-water, small benthic scavenger-predators. Thirty trilobite species of the genera Marekolithus, Mucronaspis, Duftonia, Actinopeltis, Stenopareia, Flexicalymene, Decoroproetus and Diacanthaspis are known. The upper part of these claystone yielded slightly different association with Staurocephalus and rare but significant *Eoleonaspis* (= *Bojokoralaspis*). The association is supposed to be allochtonous, representing remains of rather shallow-water origin transported into the deeper part of basin (for different interpretation see Shaw 2000). In our opinion, this interval represents material transported by mudflows produced by the global sea level fall. It could reflect the onset of glaciations. In this association, Mergl (2011) recently described the first elements of the Hirnantian fauna, although this level is traditionally considered as of uppermost Katian in age.

4. The *Mucronaspis* Trilobite Association (horizon *sensu* Havlíček – Vaněk 1966) of medium-sized scavengerpredators is characteristic for the uppermost portion of the formation and persists to the appearance of the first dropstone level at the base of Hirnantian. Only two species of *Mucronaspis – M. grandis* and *M. ganabina* occur in the association, and very rare *Duftonia*? sp. The association clearly shows stress conditions and probably reflects a sudden deterioration of environment, when only a few species survived.

Supposed feeding modes of trilobites of the Králův Dvůr Formation

All supposed feeding strategies defined by Fortey - Owens (1999) were recognized within each of the eight trilobite associations and sub-associations (see also Budil et al. 2009 a, c, 2010) in the Králův Dvůr Formation. Their frequencies, however, strongly vary in separate association (see fig. 3). Numerous small benthic scavenger-predatory strategists (acastoids, calymenids, diversified illaenids, cheirurids, rare lichids) accompanied by rare large scavenger/predatory forms (e. g. Birmanites), common filter-feeders (Nankinolithus, Cerampyx, Lonchodomas, Raphiophorus), minute particle feeders (Phillipsinella, very rare Harpidella), and common pelagic/ nectic? predator-scavengers (Amphitryon, cyclopygids, odontopleurids, rare Telephina) constitute the deeperwater trilobite-dominated Nankinolithus granulatus sub-Association in the gray and green claystones. Minute



Fig. 3: The comparison of possible feeding modes in different associations of trilobites of the Králův Dvůr Formation.

filter feeders (*Tretaspis, Lonchodomas*) and benthic and/ or epi-planctic agnostids (*Arthrorhachis*) prevail in the brachiopod-dominated *Dedzetina – Tretaspis* Association. Trilobite-dominated *Tretaspis anderssoni* sub-associations show a comparable composition with the *Nankinolithus* granulatus sub-Association. The *Marekolithus kosoviensis* Association is restricted to the bed of calcareous claystone to impure bioclastic limestones in the upper levels of the formation. Numerous small and medium-sized benthic scavenger-predatory strategists of this association probably used several different life strategies (dalmanitids, acastoids, calymenids, cheirurids, illaenids, very rare lichids and encrinurids). They are accompanied by filter feeders (common *Marekolithus*, very rare *Thorslundops?*)



Fig. 4: *Amphitryon radians* (Barrande, 1846) and *Kloucekia*? *rude-ralis* (Hawle and Corda, 1847) (= *K. pachypa* Přibyl and Vaněk, 1980) – two typical elements of the newly defined *Amphitryon-Kloucekia* association confined to the lower and middle parts of the Králův Dvůr Formation. The scale bar represents 5 mm.

and rare, minute particle feeders (*Decoroproetus*). Active nectic/pelagic forms are represented by cyclopygids, rare odontopleurids and possibly also by some cheirurids. Only medium-sized scavenger-predatory strategists survived to the youngest, monotypic *Mucronaspis* Association.

Acknowledgements

This study was supported by grants from the Ministry of Education (Project N° MSM0021620855) and the Grant Agency of Czech Academy of Science through the Project No IAA301110908. We would like to express many thanks to the staff of the Palaeontological department of the National Museum, Prague, namely to the Dr. V. Turek and Dr. M. Valent and Dr. J. Cundiff (Museum of Comparative Zoology, Harvard University, Boston, USA) for their generous help with searching and photographing the specimens, far beyond their curatorial responsibilities. We would like to express many thanks also to both reviewers M. Valent and M. Steinová for their critical remarks, which improved the early version of the manuscript.

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