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Remarks on palaeoenviromental changes based on reviewed Tertiary insect associations from the Krušné hory piedmont basins and the České středohoří Mts in northwestern Bohemia (Czech Republic)

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Abstract. Cenozoic insect fauna of northwestern Bohemia is preserved in fluvio-lacustrine deposits of the Krušné hory piedmont basins and the České středohoří Mts. The fossil insect assemblages are correlated with palaeobotanical results. The local palaeoenvironmental conditions such as the distance from the shoreline or water depth are interpreted. A reflection of changes in distribution of fossil entomofaunas is compared with relevant world localities of different palaeoenvironments. The sparse fossil insect taphocoenoses fill a gap in record of significant diverse non-marine invertebrate communities and serve for reconstruction of terrestrial palaeoecosystems. The selected fossil sites demonstrate insect taphocoenoses formed under conditions of the palaeoenvironment of a diatomaceous lake with subtropical forests (Kučlín), lowlands of riparian and mesophytic forests (Kundratice - Seifhennersdorf), warm-temperate swamp to riparian forests (Bílina mine) and lake sedimentation near mixed mesophytic forests (Mokřina). The aim is to compare fossil entomofaunas from several periods within Tertiary in northwestern Bohemia and search for analogous palaeoenvironmental conditions in other areas. The results are correlated with the previously proposed palaeobotanical models.

Key words: Insecta, fossil, Cenozoic, Tertiary, Late Eocene, Early Oligocene, Late Oligocene, Early Miocene, fluvio-lacustrine deposits, palaeoenvironment, Czech Republic.

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I. INTRODUCTION

The Tertiary of the North Bohemian rift represents a classical territory of palaeontological research. The first pioneers in Czech palaeoentomology such as J. V. DEICHMÜLLER or O. NOVÁK described fossil insect faunas from famous localities such as Kučlín (Kutschlin) or Mokřina (Krottensee) in the late 19th century (DEICHMÜLLER 1881; NOVÁK 1877). New sites found during the 20th century, e.g. Bechlejovice, Břeš any, Pochlovice or Bílina mine, were discovered mainly in conjunction with the mining of brown coal, diatomite, etc. (KUKALOVÁ 1962, ŘÍHA 1974, 1977; PROKOP 1997; SAMŠIŇÁK 1967). The age of the sites range from Late Eocene (Priabonian) to Early Miocene (Karpatian). Nearly all localities yielded rich plant mega-fossils, which have been systematically studied by palaeobotanists (BŮ EK et al. 1982, 1992, 1993; KVAČEK 1998; KVAČEK & HURNÍK 2000; KVAČEK & WALTER 1995, 1998, 2001; SAKALA 2000). On certain sites palynological spectra of pollen were analyzed as well (KONZALOVÁ 1976; DAŠKOVÁ 2000). The accompanying invertebrate and vertebrate fauna is also well known from the papers of LAUBE (1901, 1905), FEJFAR (1989), FEJFAR & KVAČEK (1993) and many others.

The present paper deals with the characteristics of insect taphocoenoses based on the previously described or recently found material classified functionally to higher-level taxa.

A c k n o w l e d g e m e n t s. The author is grateful for the loan of the material to the following museums and institutions: Doly Bílina, National Museum Prague, Staatliches Museum für Mineralogie und Geologie in Dresden, Regional Museum in Teplice and to the private collectors: Zdeněk DVOŘÁK, Jiří VEDRAL, Jan VALÍČEK, Miroslav BUBÍK and Miroslav RADOŇ. The part of research from Bílina mine was elaborated in cooperation with Dr. A. NEL (Museum national d'Histoire naturelle) in Paris. I am indebted to Prof. Z. KVAČEK (Charles University) for palaeoenvironmental data that were assumed from his recent palaeobotanical studies and encouragement throughout the years. I also thank the entomologists and palaeontologists: Dr. S. BÍLÝ, Prof. K. HŮRKA, Dr. D. KRÁL, Dr. P. KRAFT, Doc. J. MAREK, J. SAKALA, Prof. P. ŠTYS and Doc. J. VILÍMOVÁ from Charles University and National Museum for their support or improvements of the manuscript. Lastly I am indebted to Dr. E. KRZEMIŃSKA and Dr. J. ANSORGE for useful comments to the manuscript. The research was supported by grant of the Ministry of Schools CEZ: J13/98: 113100004, J13/98: 113100006, GAUK 197/2000 and GAČR 205/01/0639.

II. GEOGRAPHICAL AND GEOLOGICAL SETTING

The North Bohemian rift structure at the foot of the Krušné hory Mts was formed as a reaction of volcano-tectonic subsidence that was originally composed of the subsided Krušné hory piedmont basins and volcanic magmatic chambers underneath of the České středohoří Mts and of the Doupovské hory Mts (SUK et al. 1984).

The Krušné hory piedmont basins originated by differential subsidence as a response to Saxonian orogenesis. The process of sedimentation began in isolated depressions on a narrow area from Late Eocene (Staré Sedlo Formation) and continued up to Late Pliocene with three expressive stages (HAVLENA 1983). The Paleogene peneplane rifted in the Late Eocene when the first phase of surface volcanic activity of the Doupov Mts stratovolcanos and the České středohoří Mts had been initiated (KVAČEK 2002). The accumulated deposits of pyroclastic rocks and effusive neovulcanites of the Střezov Formation (Early Oligocene to Late Oligocene/ Early Miocene) created large lakes in the Cheb, Sokolov and Most basins (Fig. 1). During the second volcanotectonic subsidence phase the Most Formation (Late Egerian – Eggenburgian) filled the Most Basin that was dated at the basement (Prunéřov) to MN 3a zone by mollusc and mammal fauna (FEJFAR 1974; ČTYROKÝ & ELZNIC 1977). The sedimentation in the Most Basin was highly affected by the presence of the so-called deltas near atec and Bílina where rivers emptied into the basin and formed alluvial fans (Fig. 1 – Bílina mine [12]). At the same time, the Sokolov and Cheb basins were separated from the Most Basin by alkaline effusive and pyroclastic rocks. The next stage of accumulation of fluvio-lacustrine sediments (clays, coal clays, sands) was defined as the Nové Sedlo Formation (Early Oligocene: Rupelian to Oligocene/ Early Miocene: Egerian). It was followed by a hiatus representing approximately the equivalent of the Střezov Formation in the Most Basin. The subsequent hiatus was followed by discordance and sedimentation of the Sokolov Formation (Miocene: Eggenburgian to Karpatian). A large lake that interconnected the Cheb and the Sokolov basins originated due to increased subsidence. Clays and claystones filled it by the Cypris Shale (Karpatian) named after the

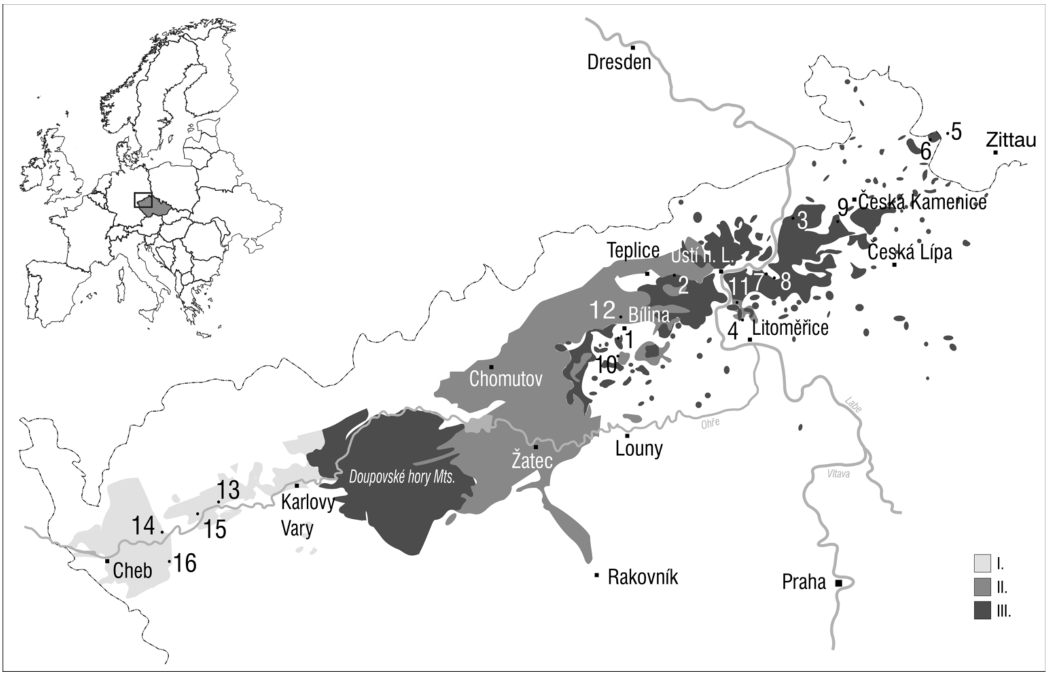

Fig. 1. Map of the Tertiary insect sites in the Krušné hory piedmont basins and volcanic areas. I. – Cheb and Sokolov basins; II. – Most Basin; III. – České středohoří Mts and Doupovské hory Mts; 1 – Kučlín (Kutschlin); 2 – Roudníky; 3 – Bechlejovice u Děčína; 4 – Kundratice u Litoměřic; 5 – Seifhennersdorf; 6 – Varnsdorf; 7 – Holý Kluk u Litoměřic; 8 – Suletice (Sulloditz); 9 – Veselíčko (Freudenshaim); 10 – ichov (Lu ice - Luschitze); 11 – Matrý vrch; 12 – Bílina mine; 13 – Jehličná u Sokolova (Grasseth); 14 – Pochlovice u Kynšperka n. Ohří; 15 – Sokolov (Falkenau); 16 – Mokřina (Krottensee).

ostracod *Cypris angusta* (Reuss 1852). Finally, a process of sedimentation had finished during the third phase by the Vildštejn Formation (Pliocene: Romanian) in the Cheb Basin only.

III. MATERIAL AND METHODS

All studied material was lent from following institutional and museum collections: National Museum Pragae (NM), Staatliches Museum für Mineralogie und Geologie zu Dresden (SMMG), Faculty of Science at Charles University (UK), Regionální Museum v Teplicích (RMT) and private collections of the following owners: Jaroslav Dolejš (JD), Zdeněk Dvořák – doly Bílina (ZD), Jiří Vedral (JV), Jan Valíček (JVK) and Miroslav Bubík (MB) or collected by the author. Ponomarenko and Schultz (1988) previously summarized the material housed in the National History Museum Vienna (MHMV).

The fossil specimens were kept in dry state, without any special conservation methods. The preparation technique uses classical methods (e.g. preparation needle). The material was studied under the binocular microscope; camera lucida drawings were made of major specimens and 96% alcohol was exceptionally used for better clarity.

The classification of insect families follows in general CSIRO (1991) and fossil record was checked by the web updated Carpenter (1992) and Labandeira (1994). Insect specimens are classified mostly on the order or family levels, less often to genera and species, according to the state of preservation. Descriptions of newly found specimens will be published separately in detailed systematic studies elsewhere. Clays or claystones provide in general a better state of preservation of the less sclerotized parts of skeleton than various types of the lacustrine diatom shale or the diatomite (seasonal accumulation of siliceous algal skeletons). The wing venation is distinctively better preserved in clays (e.g., material from Bílina mine [LCH, DCH]). Almost all fossils were compressed with the exception of some three-dimensionally preserved and strongly sclerotized elytra (Coleoptera: Hydrophilidae).

IV. CHARACTERISTICS OF FOSSIL ENTOMOFAUNAS FROM FOUR CHRONOLOGICAL PERIODS

1. Kučlín, Trupelník Hill

(Figs 1, 2; No. 1)

Locality characteristics. The site Kučlín (Kutschlin in German) represents a relict of the volcanogenic complex of the České středohoří Mts situated at the Trupelník Hill near Bílina. Insect fauna is preserved in various types of the diatomite, palynologically dated to Late Eocene (Priabonian); KONZALOVÁ (1981). The Eocene age was also confirmed by radiometrical methods of the overlying tephritic flow (38.3±1.5 Ma; BELLON et al. 1998). Palaeobotanical objects were first described by ETTINGSHAUSEN (1866, 1868, 1869) and revised by a number of authors (see KVAČEK 2002 and references therein). The other palaeontological material is also well known, especially fish fauna that elucidate the draining system of the České středohoří Mts towards the North Sea (MICKLICH & BÖHME 1997).

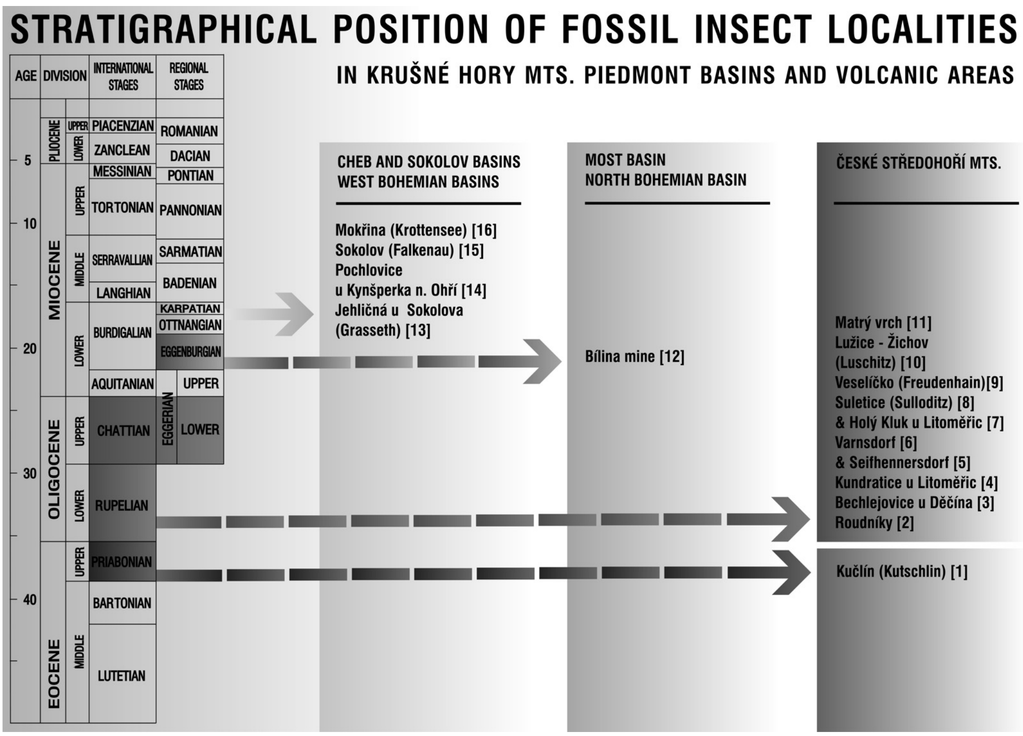

Fig. 2. Stratigraphical position of fossil insect localities in Krušné hory piedmont basins and volcanic areas.

M a t e r i a l. DEICHMÜLLER's collection housed in SMMG contains 66 specimens classified in 7 families of 3 orders (including type series). New material of more than 100 specimens, found by private collectors (JD, ZD, JV, and JVK), complements the previously described records of the following families: Trogositidae (Fig. 6C), Buprestidae (Fig. 6B), Scarabaeidae and Dascillidae.

R e m a r k s o n i n s e c t t a p h o c o e n o s i s. A general feature of the Kučlín insect taphocoenosis is a prevalence of terrestrial insects mostly belonging to Coleoptera families, especially with abundant weevils (Coleoptera, Curculionidae) that widely occur in Eocene deposits worldwide. The relatively common occurrence of Buprestidae and Elateridae supports the view stressing a more significant role in Eocene ecosystems in comparison with the recent fauna (PONOMARENKO 1995). Presence of recent members of Dascillidae living on foliage near water reflects a probable shoreline palaeoenvironment. Only one aquatic element, a specimen of *Anisops heydenii* (DEICHMÜLLER 1881), (Heteroptera: Notonectidae) known only from a single specimen has been found so far.

The comparison with other Eocene localities in Europe indicated an affinity to the Eckfelder Maar and Messel (Middle Eocene) in Germany. These sites have a similar fauna composition dominated by Coleoptera (89%), especially Curculionoidea (Fig. 3A). Insect thanatocoenoses in oil-shale at Messel (49 Ma) are dominated by Coleoptera (63%), followed by Hymenoptera (17%) and Heteroptera (12%). Other orders are represented by less than 2% of total abundance. The order Coleoptera is predominantly represented by Elateridae (30%), Curculionoidea (24%), Buprestidae

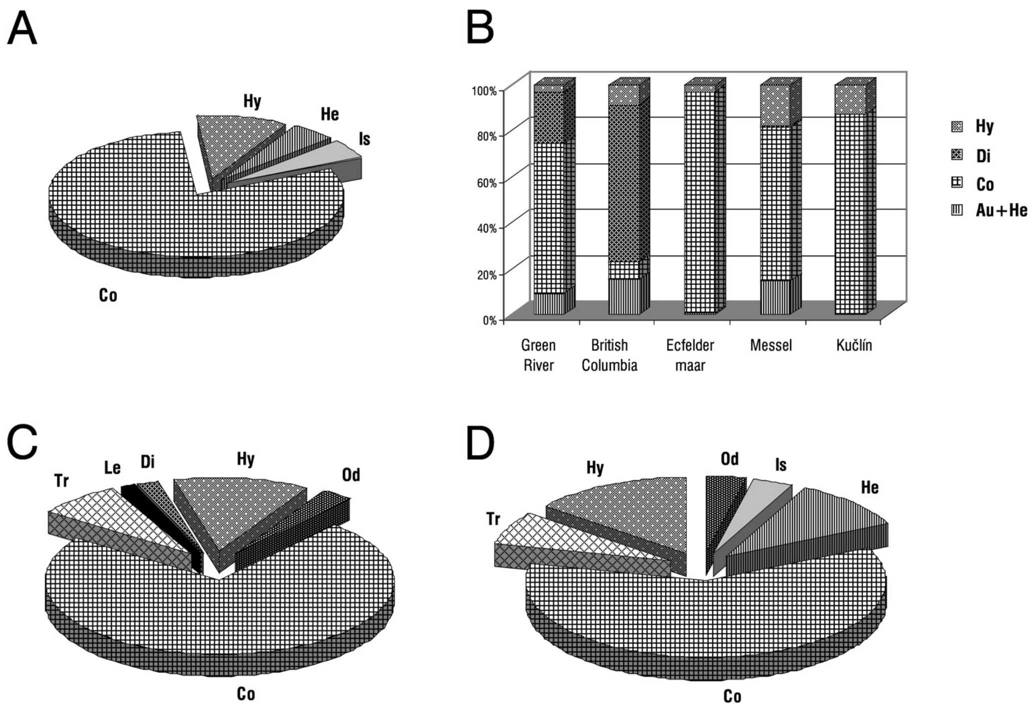

Fig. 3 Relative abundance of insect orders in Late Eocene and Early Oligocene of the Krušné hory piedmont basins and volcanic areas. A – Kučlín (Kutschlin); B – comparison of taphocoenoses from Green River (USA), British Columbia (Canada), Messel (Germany), Ecfelder maar (Germany) and Kučlín; C – Kundratice near Litoměřice; D – Seifhennersdorf (Germany). Data sets were excerpted from DEICHMÜLLER (1881), LUTZ (1988, 1990), ŘÍHA (1979), SCUDDER (1890); TIEZ et al. (1998) and WILSON (1988). Abbreviations: Au – Auchenorrhyncha, Co – Coleoptera, Di – Diptera, He – Heteroptera, Hy – Hymenoptera, Is – Isoptera, Le – Lepidoptera, Od – Odonata, Tr – Trichoptera.

(16%); (excluding specimens of uncertain family assignment (LUTZ 1990). The entomofauna at the Eckfelder Maar (45 Ma) contains more than 96% of coleopterans, especially Curculionoidea, Chrysomelidae, Buprestidae and Elateridae (LUTZ 1988). A new material of 4500 specimens from the Eckerfelder Maar comprises about 85% coleopterans with dominating weevils and is being now under study (WAPPLER, pers. comm.). Both previous sites display complete absence of aquatic insects and predominance of large and heavy species, probably due to freight selection, which resulted in fauna composition from Kučlín (Fig. 3B). These characteristics indicate a near shore lake deposition sensu WILSON (1982).

However, palaeoenvironmental conditions were different from those in German sites due to the different type of sedimentation; Kučlín was probably a small and not sunken forest diatomaceous lake in forests (about 1 km^2). The floristic analysis shows a mineral swamp with significantly represented palaeosubtropical elements (KVAČEK pers. comm.) that are in consensus with insect fauna significantly dominated by today diverse subtropical families as Buprestidae or Dascillidae. Finally, the presence of Isoptera and predominance of Curculionoidea living in near shore environments (Barinae) or on trees (Molythinae: *Hylobius* sp.) at present supports this idea (Fig. 6A, 6E).

2. Kundratice near Litoměřice and Seifhennersdorf, example from the České středohoří Mts.

(Figs 1, 2; No. 2-11)

L o c a l i t y c h a r a c t e r i s t i c s. The Early Oligocene localities ranged gradually in the České středohoří Mts such as Roudníky [2] (numbers in square brackets refer to localities in Fig. 1), Bechlejovice [3], Varnsdorf [6], Holý Kluk [7], Suletice [8], Veselíčko (Freudenshain) [9], Lu ice (íchov) [10] Matrý vrch [11] ranged gradually are represented by a sparse insect record. The relatively diverse insect faunas from Kundratice near Litoměřice (Jezuitská rokle) [4] and equivalent site Seifhennersdorf [5] in Germany represent examples of the Lower Oligocene palaeoenvironment described herein. The geographical position of Kundratice (Jezuitská rokle) is a side valley of the Rytina Creek, about halfway from Litoměřice to Ústí nad Labem [4]. Fossil insects are preserved in several interbeds of the brownish diatomite. The position of Seifhennersdorf (Oberlausitz, Germany) is north of Varnsdorf (Czech Republic), about 2 km beyond the Czech-German borderline [5]. Fossil insects are preserved in the greyish diatomite. The age of both sites was dated by radiometrical methods of the overlying basaltoid rock to 32.75±0.82 Ma in Kundratice and to 30.2±1.6 Ma in Seifhennersdorf respectively (KVAČEK & WALTHER 2001). Both localities have yielded a rich palaeobotanical record that has been recently studied (KVAČEK & WALTHER 1998; WALTHER 1996). The palaeozoological material is predominantly represented by ichthyofauna (OBRHELOVÁ 1979).

M a t e r i a l. DEICHMÜLLER's collection housed in SMMG contains 53 specimens from Kundratice, assigned to 7 families of 5 orders and 23 specimens from Seifhennersdorf classified in 9 families of 5 orders (Table I). Recently discovered material of several specimens collected by palaeobotanists is housed in NM, DB and RMT. Insect specimens are quite poorly preserved with a high grade of degradation of organic substance. Finally, several specimens from Seifhennersdorf

Table I

Stratigraphical occurrence of insect families in Tertiary localities of northwestern Czech Republic. Asterisks indicate site presence (I. – Kučlín; II. – Oligocene sites; III. – Bílina mine; IV – Cypris Shale

		Tertiary			
		Eocene	Oligocene	Miocene	
		I.	II.	III.	IV.
Odonata	Aeshnidae		*	*	
	Gomphaeschnidae			*	
	Libellulidae		*		*
Plecoptera	Perlidae			*	
Isoptera	Hodotermitidae			*	
	fam. incertae sedis	*	*		
Dermaptera	Forficulidae		*		
	fam. incertae sedis	*			
Ensifera	Tettigonidae		*	*	
Hemiptera	Cicadidae		*	*	
	Cercopidae				*
	Gerridae		*		
	Belostomatidae		*	*	
	Corixidae				*
	Naucoridae				*
	Notonectidae	*	*		
	Alydidae			*	
	Cydnidae				*
	Pentatomidae			*	*
	Coreidae			*	
	Lygaeidae				*
	Tingidae				*
Coleoptera	Cupedidae			*	*
	Carabidae		*		
	Dytiscidae			*	*
	Hydrophilidae		*	*	
	Silphidae		*		
	Lampyridae		*		
	Elateridae	*		*	
	Buprestidae	*	*	*	
	Trogositidae	*		*	
	Melandryidae		*		
	Apionidae	*	*		
	Curculionidae	*	*	*	
	Dascillidae	*			
	Lucanidae	*			*
	Geotrupidae	*	*		
	Scarabaeidae	*	*	*	*
	Tenebrionidae			*	
	Cerambycidae	*	*	*	
	Chrysomelidae			*	
Diptera	Tipulidae			*	*
	Ptychopteridae				*
	Bibionidae			*	*
	Sciaridae				*
	Syrphidae			*	
Trichoptera	Phryganeidae			*	*
	Limnephilidae		*		
	fam. incertae sedis		*	*	
Lepidoptera	Notodontidae			*	
	fam. incertae sedis		*		
Hymenoptera	Ichneumonidae			*	*
	Vespidae		*	*	
	Formicidae	*	*	*	*
	Apidae		*	*	*

Abbreviations: I. - Kučlín u Bíliny, II. - České středohoří Mts., III. - Bílina mine, IV. - Cypris shale in Cheb and Sokolov basins were previously classified in 6 families of 5 orders. They are housed in the Staatliches Museum für Naturkunde Görlitz and private collections (JEREMIES et al. 1998; TIETZ et al. 1998).

R e m a r k s o n i n s e c t t a p h o c o e n o s e s. The character of the insect taphocoenosis of Kundratice shows the predominance of terrestrial specimens, mostly represented by Coleoptera (83,6%), especially Curculionoidea (35%). This composition is typical for all Oligocene localities and similar to the taphocoenosis from Kučlín. The reason could be probably assigned to selective abiotic factors as the chemism and particularly higher disposal of elytron for preservation. It is probably also influenced by ecological and morphological aspects of the concerned taxa, particularly beetles (SMITH 1999).

The Hymenoptera are represented by Formicidae and previously described species *Apis petrefacta* (ŘÍHA 1973). Other specimens of Diptera and Lepidoptera are preserved only as fragments of bodies and wings. In contrast to Kučlín, the presence of a few aquatic elements such as fossilized caddis cases is significant for palaeoecological interpretations. The majority of specimens are terrestrial (Lepidoptera, Hymenoptera: Formicidae, Apidae) or living in edges of water as Odonata: Aeshniidae (Fig. 3C).

The fauna of Seifhennersdorf (Fig. 3D) is in general similar to that from Kundratice with the majority of Coleoptera (55%) represented mostly by Curculionidae. There are also accessory aquatic elements present such as fossilized caddis cases or water beetles, e. g., Hydrophilidae. The majority of specimens are terrestrial or living in edges of water as represented by adults of Odonata, similarly as at Kundratice. The presence of genus *Agonum* s. l. (Carabidae) indicates a relatively more humid environment. Data sets from both sites are too small (less than 100 specimens) to be compared with other world sites. Many taxa are represented by single specimen only (e.g., Cerambycidae, Scarabaeidae).

Palaeobotanical data on both sites enabled the definition of floristic assemblages Kundratice - Seifhennersdorf, which reflect two types of vegetation in Early Oligocene of Cetral Europe (KVAČEK & WALTHER 1998). The first type is a riparian forest with deciduous elements in Seifhennersdorf and the second is a mesophytic mixed evergreen and deciduous forest without riparian elements in Kundratice. The local palaeoenvironmental conditions in Kundratice and Seifhennersdorf indicate more champaign in comparison with Kučlín and broader circumlittoral zone accompanied by a characteristic flora (*Alnus* sp.) and lowland insect forest element (Geotrupidae: *Typhaeus* sp.). Increased abundance of aquatic elements (e.g., fossilized caddis cases, Coleoptera: Hydrophilidae) in comparison with Kučlín suggests a lower salinity and thus better living conditions subsequently.

3. Bílina mine

(Figs 1, 2; No. 12)

L o c a l i t y c h a r a c t e r i s t i c s a n d t a p h o n o m y. The locality of the Bílina mine (the former Maxim Gorkij) is a brown coal opencast mine situated in the Most Basin near the town of Bílina. A detailed geological setting has been recently described (BŮ EK et al. 1992, 1993; MACH 2003). Insects are preserved in three fossiliferous horizons (Lake Clayey Horizon [LCH], Delta Sandy Horizon [DSH], Clayey Superseam Horizon [CSH]) of the Most Formation dated to Early Miocene (Eggenburgian/Ottnangian) (Fig. 4). The age of the Most Formation at the base is correlated indirectly with two mammalian sites: MN 3a at Merkur and MN 3b at Tuchořice (FEJFAR 1989; FEJFAR & KVAČEK 1993). The flora includes a wealth of plant mega-fossils and palynospectra that were studied and correlated (DAŠKOVÁ 2000; KVAČEK 1998; SAKALA 2000). Other palaeozoological material such as molluscs, fish, amphibians, reptiles, birds and mammals were also recorded (LAUBE 1901; FEJFAR & KVAČEK 1993).

M a t e r i a l. There are more than 250 insect remains, collected by ZD and by author since 1992, housed in the collection of DB or NM. Material has been classified mostly into family or genera levels of 11 orders (Table I) (PROKOP 1997, 2002; PROKOP & BÍLÝ 1999; PROKOP & BOULARD 2000, PROKOP & NEL 1999, 2000a, 2000b). Insect fauna has a unique state of preservation that al-

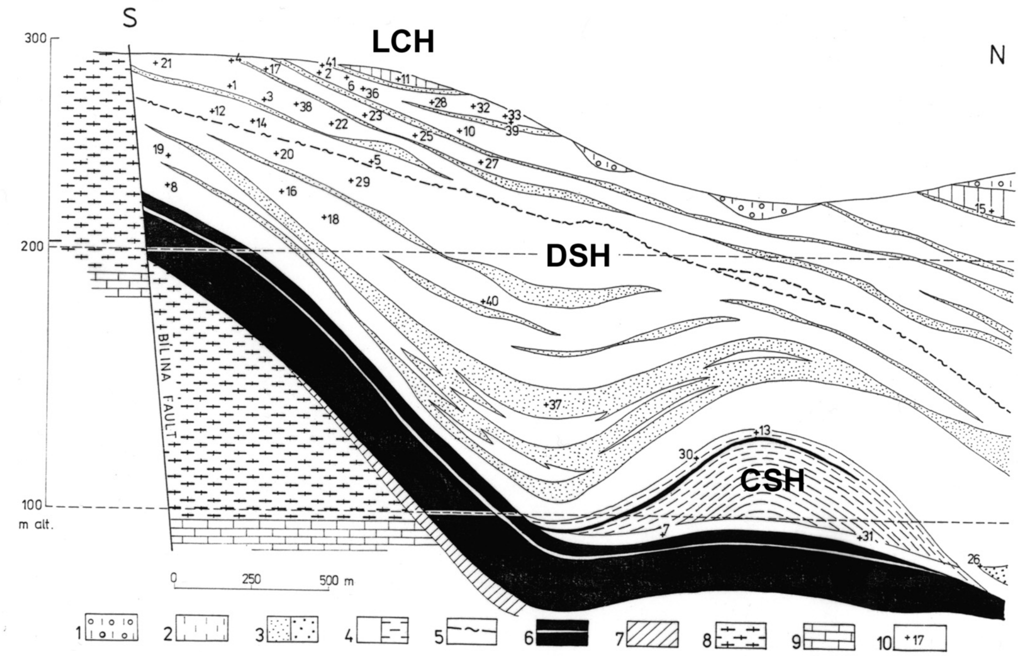

Fig. 4. Geological section of the Bílina mine. 1 – Quaternary; 2 – Lake Clayey Horizon [LCH]; 3 – Delta Sandy Horizon [DSH]; 4 – Clay Superseam Horizon [CSH]; 5 – coal clay; 6 – lignite seam; 7 – clayey coal; 8 – neovulcanite bodies of the Střezov Formation; 9 – Upper Cretaceous; 10 – fossiliferous layers (according to BŮ EK et al. (1992), modified).

Table II

The fossil insect record as an indicator of shoreline distance *sensu* WILSON (1988)

No.	Distance from shoreline (significant characters of fossil entomofauna)	Palaeoenvironment
I	Near shore zone in DSH (majority of aquatic and shore zone specimens (59%) as water beetles and caddisflies cases together with strictly terrestrial species as termites or buprestid beetle; fewer complete insects)	**shallow pond or oxbow lake with calm water**
II	Off shore zone in LCH (majority of Hymenoptera and Diptera, scarcely any aquatic insects, more rare plant macro fossils)	**deepening lake sedimentation**
III	Alternation of near shore and off shore zones within CSH (alternation of layers with rich aquatic and terrestrial specimens change for layers with abundant Hymenoptera and very few other specimens)	**oligotrophic environment with developing connected mire**

* Correlation partly based on paleobotanical results KVAČEK (pers. comm.)

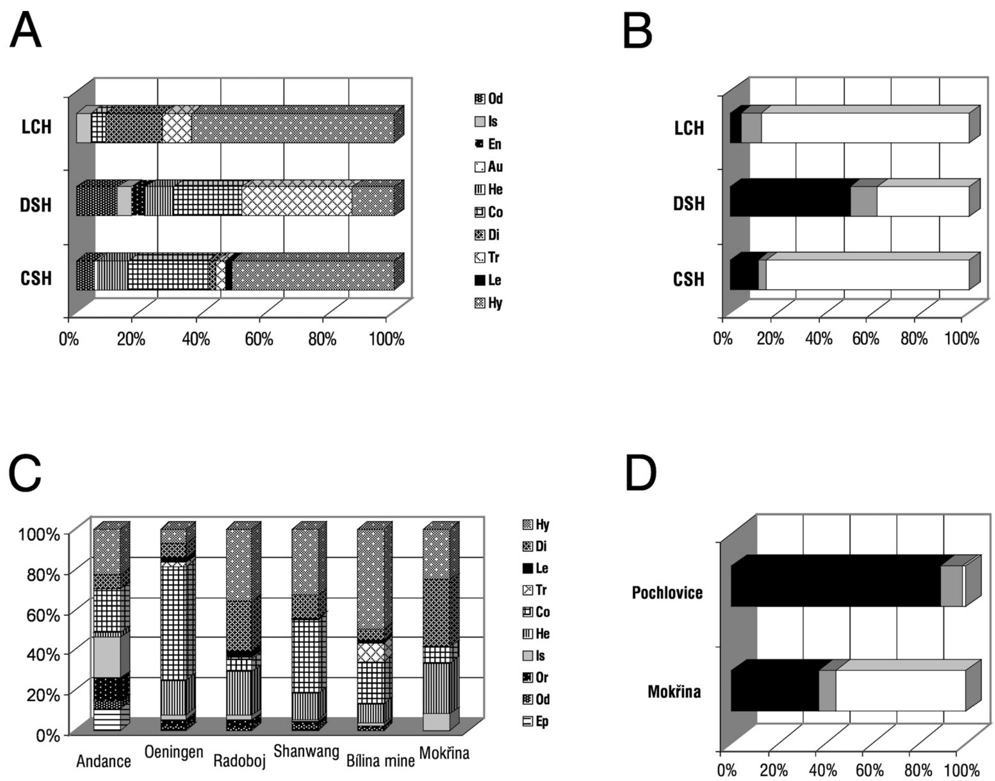

Fig. 5. Relative abundance of insect orders in Early Miocene of the Krušné hory piedmont basins. A – Bílina mine; B – distribution of aquatic [I - black color], shore zone [II - grey] and terrestrial [III - white] specimens within fossiliferous horizons at Bílina mine; C – comparison of taphocoenoses from Andance (France), Öhningen (Germany), Radoboj (Croatia), Shanwang (China), Bílina mine and Mokřina (Krottensee); D – distribution of aquatic [I.], shore zone [II.] and terrestrial [III.] specimens at Pochlovice and Mokřina (Krottensee). Data sets were excerpted from DEICHMÜLLER (1881), NOVÁK (1877), RIOU (1988), ŘÍHA (1979), SCUDDER (1890); WILSON (1988) and ZHANG et al. (1994). Abbreviations: Au – Auchenorrhyncha, Co – Coleoptera, Di – Diptera, En – Ensifera, Ep – Ephemeroptera, He – Heteroptera, Hy – Hymenoptera, Is – Isoptera, Le – Lepidoptera, Od – Odonata, Tr – Trichoptera; CSH – Clay Superseam Horizon, DSH – Delta Sandy Horizon, LCH – Lake Clayey Horizon.

lows the study of fine structures (e.g., Lepidoptera: Notodontidae). The presence of plant-insects interactions as galls, traces on foliage and wood borings has been recorded (Fig. 6H).

Remarks on insect taphocoenoses. General character of insect taphocoenoses differs with respect to the specific fossiliferous horizon, starting from the dual character in CSH sometimes explained by occasional flooding, shallow ponds or oxbow lake with calm water in DSH and finally deepening lake sedimentation in LCH (Table II). Representatives of the family Formicidae are most abundant in LCH (60%) and CSH (52%) whilst DSH display a dominance of water specimens (52%) such as larval caddis cases and water beetles (Dytiscidae, Hydrophilidae); (Figs 6D, 6F, 6I, 6J).

The palaeobotanical record suggests a deep peat swamp occupied by mixed swamp forests in CSH through assemblages connected with the alluvial plain represented by riparian mixed forest in DSH and finally a shallow lake with swamp trees in LCH (KVAČEK 1998). Insect taphocoenoses reflected these changes in relative presence of aquatic, shore zone and terrestrial taxa respectively that vary in evolving fresh-water palaeoenvironment (Figs 5A, 5B).

In comparison with certain other Miocene localities such as Radoboj (Croatia), Öhningen (Germany) and Shandong (China) it was concluded (Fig. 5C): the taphocoenosis from the Middle Miocene at Radoboj (Croatia) is dominated by the Hymenoptera with abundant family Formicidae. The order Diptera is similarly represented by families Tipulidae and Bibionidae. In Shandong (China) the Coleoptera (36%) dominated whilst Hymenoptera made 32%, Diptera 11% and Heteroptera

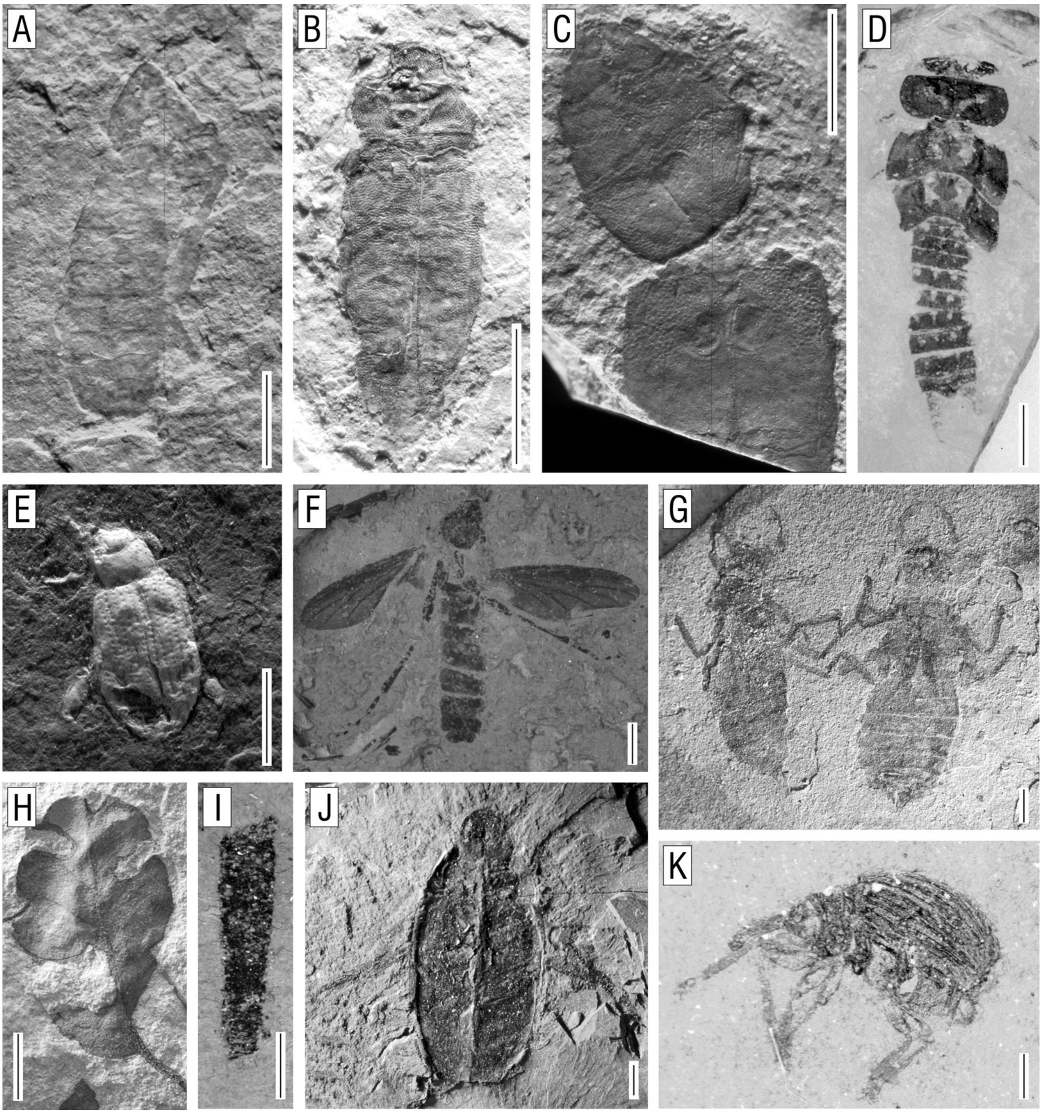

Fig. 6. Photographs of insect specimens from localities in the Krušné hory piedmont basins and the České středohoří Mts. A – Isoptera, fam. indet. (Kučlín, JV2136a, scale 3 mm); B – Coleoptera: Buprestidae: Psilopterini gen. et sp. indet. (Kučlín, JD2101, scale 3 mm); C – Coleoptera: Trogositidae gen. et sp. indet. (Kučlín, JD2098, scale 3 mm); D – Plecoptera: Perlidae: *Perla* cf. *burmeisteriana* CLAASEN (Bílina mine, ZD0185, scale 3 mm); E – Coleoptera: Curculionidae: cf. *Baris* sp. (Kučlín, 2078a, scale 3 mm); F – Diptera: Bibionidae, *Bibio* sp. (Bílina mine, ZD9701a, scale 3 mm); G – Odonata: Libellulidae – larvae (Pochlovice, UK002, scale 3 mm); H – insect marginal trace on *Dicotylophyllum* sp. (Bílina mine, ZDI0033, scale 3 mm); I – Trichoptera: larval case (Bílina mine, ZD0070, scale 3 mm); J – Coleoptera: Hydrophilidae: *Hydrophilus* sp. (Bílina mine, ZD9708, scale 5 mm); K – Coleoptera: Apionidae gen. et species indet. (Kundratice, ZDKj01, scale 1 mm).

10%. Also other characteristics at Bílina mine show similar local palaeoenvironmental conditions as found in Shandong (ZHANG et al. 1994), but these scarce data do not allow for a more precise correlation.

4. Cypris Shale represented by sites at Mokřina, Pochlovice near Kynšperk, Jehličná and Sokolov

(Figs 1, 2; Nos. 13-16)

Locality characteristics. The localities represent a lake sedimentation environment characterized by abundant occurrence of ostracods (*Cypris angusta*) when the Cheb and Sokolov basins were interconnected and constituted as a single stratigraphical unit (Cypris Shale/ Cypris Schiefer), as defined by REUSS (1852). The classical sites as Mokřina (Krottensee) [16] or Jehličná (Grasseth) [13] were originally studied by NOVÁK (1877) and HANDLIRSCH (1906-08). During the coal mining activity in 1950s and 60s further localities (e.g. Pochlovice [14], Sokolov [15]) were mentioned by KUKALOVÁ (1962) and ŘÍHA (1979). Insects are preserved in "cypris" greenish marls belonging to the Sokolov Formation dated by mammals to the MN 4 and MN 5 zones of Early Miocene (Ottnangian/Karpatian). The geological setting and reviewed palaeobotanical data were summarized by BŮ EK et al. (1996). Palaezoological material is well known from the mammalian fauna that has been studied at Dolnice and Františkovy Lázně (FEJFAR & KVAČEK 1993). Four local characteristic biozones based on the fish fauna were defined by OBRHELOVÁ and OBRHEL (1983, 1987).

Material. The NOVÁK's collection from Mokřina in NM contains 73 specimens representing families listed in Table II. The collection from Pochlovice near Kynšperk is housed at UK and NM and comprises in total more than 400 specimens. Insect specimens were classified in 5 orders of the families listed in Table II (PONOMARENKO 1973; ŘÍHA 1961, 1974, 1977, 1979). Several specimens from Jehličná (Grasseth) and Sokolov (Falkenau) are housed in MHMV (BACHMAYER 1952; HANDLIRSCH 1906-08) and a private collection at Sokolov (MB). Other rich material of insect compressions was collected by Pavel ŘÍHA (PR) together with palaeobotanists during the drilling prospection for coal in western Bohemia (eastern part of Cheb Basin and Dukla mine (Sokolov Basin)). The insects were partially identified by ŘIHA (1977) and represent a collection of 94 specimens provisionally housed at the Charles University, Praha.

Remarks on insect taphocoenoses. All localities represent a lake sedimentation yielded remains of the mixed mesophytic forest. After comparison of insect taphocoenoses it is concluded:

At the Pochlovice site (Ottnangian) the insect fauna composition shows dominance of aquatic groups as masses of larvae of Odonata: Libellulidae (Fig. 6G), Aeshniidae; Coleoptera: Dytiscidae that were living in the paleolake, and shore insects as adults of Odonata: Libellulidae or Diptera: Bibionidae living at the edge of water (Fig. 5D). These features support a near shore palaeoenvironment as small drying out ponds or a larger shallow lake sensu WILSON (1988). There is also one explanation of non-presence of terrestrial insects due to far distance of shore line from the nearest vegetation or possible living environments. The original shallow pool was much larger and slope of water decreased with higher amplitude to shore line. Such a lake environment could be found at present, e.g. in temporary pools (billabongs) in Australia (PROKOP, FLECK and NEL in press). Sparse records from Jehličná and Sokolov support similar conditions with a number of anisopteran larvae (Libellulidae) described by HANDLIRSCH (1906-08).

On the other hand, the Mokřina site (Karpatian) shows a different insect composition without any aquatic specimens. There are abundant Hymenoptera and Diptera, especially Tipulidae, Bibionidae and Formicidae that suggest off shore conditions (Fig. 5D) of a large lake sensu WILSON (1988). Coleoptera are relatively in minority and material is relatively weight sorted that indicates a transport, which was not the case in Pochlovice. This view is supported by the palaeobotanical record with rare plant macrofossils (BŮ EK et al. 1996). An analogous composition of insect taphocoenosis within the Late Eocene site with stagnant water regime and probable transport of insects by wind can be found in Florissant, USA (SCUDDER 1890). However, the complete record from Florissant is not isochronous and reflects local site-specific environmental conditions by different relative abundance (SMITH 1999).

V. CONCLUSIONS

In spite of fact that relative abundances of fossil assemblages do not correspond well with the composition of living fauna (as it was demonstrated on Willcox Playa by SMITH, 1999), we can assume some environmental and ecological conclusions based on significant insect species together with palaeobotanical reconstruction of the vegetation. The comparison of relative abundances and insect diversity at palaeontological sites together with the actual approach may help understanding of some aspects of insect preservation and of the palaeoenvironement. Moreover, these quantitative data elucidate depositional environment such as shore line distance *sensu* WILSON (1982). There are several following steps reflecting the local type palaeoenvironment after the comparison of fossil insect taphocoenoses from the localities in the Krušné hory piedmont basins and volcanic areas of the České středohoří Mts.

The Late Eocene insect fauna represented by Kučlín has a significant high abundance of thermophilous elements (Coleoptera: Buprestidae (Psilopterini), Dascillidae, Elateridae: *Campsosternus* sp.). A predominance of Curculionidea living close to water bodies or on trees indicates possible near shore lake depositional conditions with presence of surrounding forests. The palaeoenvironment at Kuclin exemplifies a maar lake without distinctive shoreline vegetation as usual in the Oligocene sites (e. g. , Kundratice) and could be also correlated with German localities at Messel and especially, the Eckerfelder maar (LUTZ 1988, 1997; WAPPLER pers. comm.).

During Early Oligocene the number of subtropical elements decreased due to Antarctic glaciation with consequent global cooling. The insect taphocoenoses are still similar to those of Late Eocene. The dramatically opposite situation concerns aquatic specimens whose number significantly increases toward the end of palaeogene in all studied sites (Heteroptera: Belostomatidae, Gerridae, Notonectidae, Trichoptera larval cases. An expansion of grasslands based on papaeobotanical evidence is suggested by presence of dung beetle (Geotrupidae) in Seifhennersorf. Local palaeoenvironmental conditions at Kundratice and the equivalent site of Seifhennersorf indicate more open landscape with rich near shore vegetation. This is documented by a presence of shoreline elements (Odonata, Coleoptera: *Agonum* sp.) together with a number of aquatic elements (Trichopetra larval cases, Coleoptera: Hydrophilidae).

Rapid changes in sedimentary environment illustrate three fossiliferous horizons at the Bílina mine representing different insect taphocoenoses, which reflect palaeoenvironmental changes in short time period. This locality could be compared with local palaeoenvironmental conditions at Shandong (China) with similar relative abundance of insect specimens. Several insects from the Bílina mine are notably linked to other Miocene localities (e.g. Isoptera: *Ulmeriella* sp.) and extending the spectra of fossil diversity (PROKOP 2002; PROKOP & BÍLÝ 1999; PROKOP & BOULARD 2000; PROKOP & NEL 1999, 2000a, 2000b).

Finally, two localities (Pochlovice and Mokřina) represent different insect taphocoenoses within the same stratigraphical level of Cypris Shale (upper Lower Miocene). At Pochlovice, the majority of aquatic specimens (larvae of Odonata: Libellulidae, Coleoptera: Dytiscidae) reflect an environment that had been episodically flooded or a shallow lake environment rapidly drying out. This environment could resemble, e.g., Australian temporary pools, or Aral Lake as interpreted by OBRHELOVÁ and OBRHEL (1983). On the other hand, Mokřina has a different insect composition represented by wings of Hymenoptera and Diptera indicating off shore conditions where the transport by wind played probable a leading role.

The proposed general conclusions are in consensus with palaeobotanical and palynological models of local palaeoenvironmental conditions for the above mentioned areas.

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