Biotic Changes Around the Radioisotopically Constrained Carboniferous-Permian Boundary in the Boskovice Basin (Czech Republic)

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Biotic changes around the radioisotopically constrained Carboniferous-Permian boundary in the Boskovice Basin (Czech Republic)

Presented is an analysis of vegetation patterns across the Carboniferous-Permian boundary in continental setting constrained for the first time in Europe and North America by high-precision U-Pb radioisotopic dating. The analysis is performed on the fossil record of the Boskovice Basin (Czech Republic), a Late Palaeozoic half-graben having ~5 km of cumulative thickness. It is dominantly a red bed succession containing numerous grey, mostly lacustrine horizons bearing fairly rich fossil floras and faunas of Late Pennsylvanian to Cisuralian age. U-Pb geochronology on single zircon crystals separated from a volcanic tuff near the top of the Rosice-Oslavany Formation, in the lower part of the basin succession, provided an age of 298.88 ± 0.09 Ma, that nearly exactly corresponds to the Carboniferous-Permian boundary as currently accepted in the International Chronostratigraphic Chart v2016/04. The upper part of the basin fill is correlated via fish faunas with the Intra-Sudetic and Krkonoše-Piedmont basins, where embedded volcanic rocks provided late Asselian ages. The succession of the Boskovice Basin records a well-known aridification trend demonstrated by the transition from Gzhelian coal-bearing sediments of the Rosice-Oslavany Formation to Asselian red beds. This trend is interrupted by grey lacustrine horizons, which represent major windows of preservation formed during more humid intervals. Vegetation patterns show the transition from assemblages dominated by free-sporing plants, mostly tree ferns, typical of Late Pennsylvanian wetlands, to peltasperm–walchian conifers dominated assemblages of the Cisuralian. Similar transition has been observed also in coeval succession of the Intra-Sudetic Basin and elsewhere in the former central and western equatorial Pangea. • Key words: Boskovice Basin, Carboniferous, Permian, flora, fauna, radioisotopic age, climate.

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Increasing aridification at the end of the Pennsylvanian and beginning of the Permian led to the nearly complete disappearance of peat-forming wetlands in central and western tropical Pangea. This change in turn affected the composition of flora and resulted in complex changes from typical wetland vegetation composed of cryptogams (free-sporing plants) and early gymnosperms, to more water-deficiency-tolerant vegetation dominated by gymnosperms, mostly peltasperms and conifers (e.g. Gothan 1912, DiMichele et al. 2008). Climatic changes on several time scales (Cecil 1990, Driese & Ober 2005, Roscher & Schneider 2006, Tabor & Poulsen 2008, Cecil et al. 2014, DiMichele 2014) and the overall low potential of preservation of organic matter, especially that of plants, results in a spatio-temporally discontinuous fossil record concentrated mostly in windows of preservation, and thus makes the precise recognition of the Carboniferous-Permian boundary even more complicated (Brouin et al. 1986, 1990; DiMichele et al. 2008). This is further amplified by absence of any typical guide plant fossil(s) marking the boundary. For a long time, the onset of the “callipteris” flora was taken as a base of the Permian Stage, as well as the boundary between the Palaeophyticum and Mesophyticum (e.g. Göppert 1858, Geinitz 1865, Gothan 1912, Havlena 1964), until callipterids were found in the Stephanian stratotype in the French Massif Central (Bourouz & Döubinger 1977).
Callipterids have subsequently been discovered in evidently Late Pennsylvanian strata at a number of localities in Europe, North America and North Africa (Broutin et al. 1986, 1990; Kerp 1988, 1996; Lyons & Darrah 1989; DiMichele & Aronson 1992; Hmich et al. 2006; DiMichele et al. 2008, 2013; Wagner & Álvarez-Vázquez 2010; Pšenička et al. 2011; DiMichele 2014). In contrast, the Carboniferous-Permian boundary in purely continental settings could be better constrained by insect and conchostracan biostratigraphy, which are in places directly linked by conodont biostratigraphy to the Global Marine Standard Scale (e.g. diMichele et al. 2013, Lucas et al. 2016, Schneider & Scholze 2016).

The onset of aridification (or tectonically improved basin drainage and, in turn, substrate dryness – see Cleal et al. 2010, 2011 for details) becomes obvious at around the Middle-Late Pennsylvanian transition and is marked by intrabiomic changes in dominancy patterns of wetland floras, specifically a drastic decrease in dominancy and diversity of arborescent lycopsids and their replacement by maratillaean ferns (Pfefferkorn & Thomson 1982, Phillips et al. 1985, Cleal et al. 2010). Throughout the Late Pennsylvanian, the climate became more seasonal and formerly widespread wetlands were spatially restricted, and in basinal lowlands flora adapted to water deficiency (e.g. walchian conifers and later also callipterids) appeared for the first time. Around the Carboniferous-Permian boundary the climatic aridification resulted in the further decline of remaining peat-forming wetlands in most of central and western tropical Pangea. Climatic and related environmental changes resulted in more profound vegetational reorganization, characterised by interbiomic transition (e.g. DiMichele et al. 2006, DiMichele 2014) recognized already by Gothan (1912) and again by Kerp (1996) as a transition from the Palaeophyticum to the Mesoophyticum. Due to local differences in climate and environments and high-frequency climatic oscillations superimposed on an overall aridification trend (Roscher & Schneider 2006, Tabor & Poulsen 2008), this transition is spatially and temporarily complex, and in the continental setting led to problems of precise location of the Carboniferous-Permian boundary by macrofloral biostratigraphy (for overview see DiMichele et al. 2006, 2008; DiMichele 2014). Detailed studies of floras from particular basins are therefore required to better understand spatio-temporal variability of these changes across the former tropical Pangea. In the Boskovice Basin, which is one of Late Palaeozoic continental basins in the Czech Republic, a new high precision radioisotopic datum constrains the position of the Carboniferous-Permian boundary, and thus for the first time allows us to characterize in detail vegetational changes across this critical time interval in this basin as a good example of the Central European basins in general.

Geology and lithostratigraphy of the Boskovice Basin

The Boskovice Basin is nearly a 100 km long and 3 to 10 km wide, NNE-SSW striking half-graben situated in the eastern part of the Bohemian Massif at the boundary between Lugo-Danubicum and Moravo-Silesicum (Fig. 1). Its purely continental deposition started in the late Gzhelian (late Stephanian) in southern part of the basin, and without any detected interruption continued in northern part until Cisuralian times (Pešek et al. 2001). The basin depocentre is divided into southern and northern sub-basins, separated by a zone of reduced thickness called the Tišnov–Kuřím Elevation (Havlena 1964, Malý in Pešek et al. 2001). In the older southern Rosice-Oslavany Sub-basin sedimentation started in the late Stephanian and lasted till the “Autunian”. The northern Letovice Sub-basin was established in the early “Autunian” and deposition here continued probably up to the early “Saxonian” (Kozur 1980). After Schneider and Werneburg (2012) and Schneider et al. (2014) the depositional history of the basin lasted from the latest Kasimovian to the earliest Kungurian. The composite sedimentary record in both depocentres is estimated by Jaroš (1962) to about 5000 to 6000 m, although seismic data show that the maximum thickness of the sub-basins does not exceed ~2000 m (Malý 1993). Deposition during most of the sedimentary history was triggered by the Main Fault of the Boskovice Basin situated along its eastern margin (Fig. 2), generating diachronous coarse-grained facies of the Rokytňa Conglomerate interpreted as an alluvial fan system (e.g. Jaroš 1962, Melichar 1995).

Sedimentary fill of the basin is divided into four formations (Fig. 3). The two oldest formations, the Rosice-Oslavany and Padochov, fill the southern sub-basin whereas the remaining two younger formations, the Veveršká Bítyška and Letovice, are present only in the northern Letovice Sub-basin (Pešek et al. 2001, Pešek 2004).

Deposition of this up to 300 m thick unit took place only in the southern Rosice-Oslavany Sub-basin. Its thickness is affected by basement palaeotopography, further amplified by syndepositional activity of faults (Malý 1993). Its basal part is dominantly represented by coarse-grained facies of the Balinka Conglomerate of local provenance, the thickness of which depends on pre-sedimentary palaeotopography and varies from a few to as much as 75 m (Jaroš 1962). Higher in the section the proportion of conglomerate significantly decreases in favour of red-brown sandstone and mudstone. This “red” part of the formation grades upward into a 120 m thick complex of mostly grey strata, which bear three economically important coals of the Rosice-Oslavany group numbered from top to bottom as the coals Nos I, II and III; 1.5–6.5 m, 0.8–2.4 m and 0.8–1.4 m thick, respectively (Fig. 3). Accompanying clastic sediments include mudstones and sandstones alternating with subordinate conglomerates. Locally present between coals, especially between the Coal I and Coal II are red clastic sedimentary rocks. Their areal extent corresponds to increasing ash content in the Coal I (Malý 1993). About 20 m above the Coal I is the few metres thick lacustrine Helmhacker Horizon, which has provided allochthonous flora (Helmhacker 1866, Rieger 1965). The remaining about 40 m thick uppermost part of the Rosice-Oslavany Formation consists of alternating mudstones and sandstones locally with thin non-workable coals near the top of the formation.

The Rosice-Oslavany Formation (late Gzhelian–early Asselian)

This early “Autunian” lithostratigraphic unit is restricted to the Rosice-Oslavany Sub-basin, where its deposition continued without an interruption from the Rosice-Oslavany Formation (Figs 3, 4). It is a ~ 1200 m thick red bed succession composed of alternating sandstones (locally feldspathic) and mudstones, in which are embedded two few to tens of metres thick grey lacustrine horizons bearing a rich fossil record. Stratigraphically older is the Zbyšov Horizon, situated ~ 50 m above the base of the formation. It is a ~ 60 m thick complex of grey sandstones, mudstones and claystone with a 3-to-4-m-thick horizon of bituminous carbonate. About 900 m higher, near top of the formation is the Říčany Horizon, composed of grey mudstones, claystones and a bed of lacustrine carbonate. Different sedimentation characterised the eastern basin margin, where intensive subsidence along an active fault resulted in deposition of the coarse-grained Rokytná Conglomerate composed of cobbles derived from an eastward-located source area (Pešek et al. 2001).

Veverská Bítýška Formation (Asselian)

This unit is a ~ 1500 m thick complex of dominantly red sandstones and mudstones. Locally present grey strata consist of lacustrine mudstones, claystones, and embedded thin intercalations of clayey limestones. The most prominent grey interval is the Chudčice Horizon near the top of the formation. Unfortunately, no fossils have been found in
this formation. Its deposition is concentrated in the northern Letovice Sub-basin.

Letovice Formation (Asselian)

Deposition of this up to 3000 m unit (Pešek et al. 2001) took place only in the northern Letovice Sub-basin (Figs 3, 4). The age of unit is not satisfactorily resolved and differs by author and study. Kozur (1980) and Pešek et al. (2001) suggested a late Autunnian to early Saxonian age whereas Šimůnek & Martinek (2009) and Schneider & Werneburg (2012) interpreted a Sakmarian to Artinskian age for the formation. In contrast Štamberg (2014), based on duration of fish zones, believes that the upper part of the formation is still of Asselian age. The formation consists of red and grey clastics, the latter ones mostly represented by lacustrine sediments concentrated into nine horizons (Pešek et al. 2001). Some of them provide an important fossil record including fish, amphibians, insects, and plant fossils. In the central and western part of the basin the formation consists of red fluvial sediments including sandstone (locally feldspathic) and mudstones; conglomerates are subordinate. Sediments alternate in a cyclic pattern except in the eastern part, where the formation is represented by the Rokytňa Conglomerate deposited along the eastern tectonic margin of the basin.

Volcanic rocks of the Boskovice Basin

Volcanic rocks in the Boskovice Basin were described as keratophyres by Gartner (1924), Zapletal (1925), Zapletal & Locker (1930) and Malý (1968, 1972). These were interpreted mostly as dykes that cut sediments of the Rosice-Oslavany Formation and stratigraphically adjacent part of red “Permian” sandstones. Přichystal (1993, 1994) used the TAS classification to describe some of them as basic andesites, trachyandesites, and subalkaline dacites. Most are very fine-grained rocks with pale colours, forming both concordant and discordant veins up to 1.5 m thick. They consist mostly of feldspars with oligoclase to albite composition and show typical alterations such as calcitization, chloritization of biotite, and epidotization of plagioclase. Volcaniclastic rocks were described by Králík & Malý (1987) from the Jindřich Mine in Zbyšov. Tuffs or more possibly tuffites form horizons of 10 to 50 cm thickness in sediments surrounding Coal III, and possibly also Coal I.

Figure 3. Lithostratigraphic subdivision of the Boskovice Basin succession. According to Jaroš (1962) and Pešek et al. (2001). Abbreviation: R-O F. – Rosice-Oslavany Formation.
History of stratigraphic research in the Boskovice Basin

The beginning of systematic research dates back to the first half of the 19th century when coal exploitation in the southern part of the basin was established. Besides data from coal mines, important information has been obtained from outcrops, including the section along the Oslava River near Oslavany. It exposes the transition of late Gzhelian to early Asselian strata and has been a matter of several detailed studies (e.g. Jaroš 1962, Šimůnek & Martíněk 2009).

Since the early research in the Boskovice Basin, a fairly large number of authors have contributed to our current knowledge on basin geology and stratigraphy. Detailed overviews of the history of the basin research are provided in the papers of Augusta (1933a, 1937a), Havlena (1955), Šimůnek & Martíněk (2009) and partly also in Pešek (2004). Here we only briefly summarize the opinions on the precise position of the C-P boundary at the base of the Coal I. However, he did not suggest any precise boundary between Carboniferous and Permian. In contrast Havlena (1964) for the same reason located the C-P boundary at the base of the Coal I. This argument was, however, questioned, when Bouroz & Doubinger (1977), and also other authors, described *Autunia conferta* from the Stephanian stratotype and from Stephanian strata elsewhere (Wagner & Álvarez-Vázquez 2010). Later Rieger (1965) collected flora from the shaft Jindřich in Zbyšov across the assumed C-P boundary and found several Callipterid species in the level of the Helmhacker Horizon about 22 m above the Coal I, but no such species in close proximity above that coal, as did Němecj (1951) and Štělik (1951) in coal mine Ferdinand near Babice. However, no precise position of the C-P boundary was suggested. Currently the C-P boundary was placed by Šimůnek (2003) into the roof of the Helmhacker Horizon. Šimůnek in Pešek et al. (2001) provided the first list of plant fossils identified in the Boskovice Basin, which was later updated and extended by newly collected material (Šimůnek & Martíněk 2009).

Apart from the intensive palaeobotanical research in the Boskovice Basin nearly no palynological data exist from this basin due to its high coal rank (Pešek et al. 2001). The only exception is a miospore assemblage from the Řičany Horizon in the upper part of the Padochov Formation of early Permian (“Autunian”) age (Zajíč et al. 1996). The assemblage in the lower part of this horizon is dominated by trilete spores (~ 90%), especially of *Crassispora plicata*, C. sp. and *Lycospora pulsilla*, *Reistrickia saetosa*, *Leiotriletes minutus*, *L. sphaeroangularis* and *Calamospora brevirostrata*. In the upper part of the same horizon, however, ~ 80% of the spores are of monosaccate pollen genera *Potoniesporites* and *Florinites*. Common are also *Illinites*, *Gardanaisporites*, *Alisporites*, *Protohaploxyinus*. Subordinate are *Crassispora*, *Calamospora* spp., *Laevigatosporites minutus* and *L. medius*.

The Boskovice Basin is also well-known for its faunal remains (see Štamberk & Zajíc 2008 for an overview), both vertebrates (fish, amphibians, and exceptionally also reptiles) and invertebrates (mainly insects). Systematic research of fauna started in the first half of the 20th century and continues through the present (Augusta 1926, 1931c, 1933b, Špinar 1951, 1952a, b, 1959; Kukalová 1955, 1963, 1964, 1965; Schneider 1980, 1984; Klembara 1997; Klembara & Meszaros 1992; Klembara & Bartík 1999; Zajíc 2000; Zajíc & Štamberk 2004; Štamberk 2007, 2013a, b, 2014; Schneider & Wernerburg 2012). Most of the faunal remains occur in the Permian part of the basin succession. Therefore, the role of fauna in stratigraphic re-
search on the position of C-P boundary has played so far a less important role.

**Biostratigraphy of the Boskovice Basin**

Fossil remains in the sedimentary fill of the Boskovice Basin, concerning its quantity and quality of preservation, are spatially and temporarily unevenly distributed, mainly as a consequence of changes in fossilization potential triggered by variations in ground-water table. The major windows of preservation in the Carboniferous part of the basin succession are grey strata of the Rosice-Oslavany coal group, especially roof shales and some clastic partings embedded in coals. In the Permian part of the succession the major fossil-bearing intervals are grey, usually several

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**Figure 4.** The N–S schematic section of the Boskovice Basin with correlation of the grey mostly lacustrine horizons as suggested by Jaroš (1962). Note the depocentre migration to the north. Modified after Pešek et al. (2001).
metres to a few tens of metres thick lacustrine horizons embedded in fluvial red beds (Šimůnek & Martínek 2009). The hundreds of metres thick red beds bear mostly only poorly preserved impressions of walchian conifers or cordaites (Rieger 1965). Although subordinate in volume and irregular in stratigraphic distribution, the fossiliferous horizons cover nearly the whole range of the basin stratigraphy and thus provide valuable information about the floral and faunal dynamics and compositional changes throughout the late Gzhelian to Cisuralian times.

Of key importance for the older part of the basin fill is macroflora, the character of which allows for its assignment to the existing floral zones (Wagner 1984, Wagner & Álvarez-Vázquez 2010). In the Permian part of the basin succession, however, the floral zones become less reliable, whereas the importance of fauna for biostratigraphy significantly increases (e.g. Zajíc 2000; Schneider & Werneburg 2012; Štamberg 2013a, 2014).

**Macroflora**

The oldest flora of the Boskovice Basin is that of the Rosice-Oslavany Formation, where it has been collected mostly from mudstones accompanying coals and from the Helmhacker Horizon about 20 m above the Coal I. All three coals of the Rosice-Oslavany group are accompanied by peat-forming flora (summarised in Fig. 5) with only minor differences between individual seams (Šimůnek in Pešek et al. 2001, Šimůnek & Martínek 2009). The assemblage is typically dominated by pectopterids and pteridosperms (Šimůnek & Martínek 2009). Stratigraphically important species include Sphenophyllum angustifolium (Germar) Goeppert, Sphenopteris mathieli Zeiller, Pseudomariopteris busquetii (Zeiller) Danze-Corsin, P. densifolia Goeppert (Weiss), Alethopteris zeilleri (Ragot) Wagner, Odontopteris schlotheimii Brongniart and Neurocallipteris neuropteroides (Goeppert) Cleal, Shute et Zodrow.

‘Callipteris’ zbejsovensis Augusta, Sphenopteris germanica Weiss, Calmitzschia speciosa (Florin) Clement-Westerhof, Ernestiodendron filiciforme (Schlotheim) Florin, Walchia goeppertiана (Florin) Clement-Westerhof and W. pini-formis Sternberg. Remains of these species were found in discrete layers mostly separately from hygrophilous floras, although stratigraphically in their very close proximity (Němejc 1951, Rieger 1965, Šimůnek & Martínek 2009). Their fragmentary nature led the authors to the conclusion that these species were also transported into the depocentre from habitats situated above the basin lowland. A similar but poorer assemblage is also known from the Helmhacker Horizon (Helmhacker 1866, Rieger 1965), where identified were Odontopteris schlotheimii, Sphenopteris germanica, Autunia conferta, A. naumannii, Dichophyllum flabelliferum, Ernestiodendron filiciforme and Walchia sp. According to Šimůnek in Pešek et al. (2001) and Šimůnek & Martínek (2009) the lower part of the formation up to the Coal II belongs to the Sphenophyllum angustifolium Zone, whereas the remaining part of the formation represents Autunia conferta Zone.

The flora of the following Padochov Formation is known mainly from the lacustrine Zbýšov and Ričany horizons. The former horizon provided diverse (Fig. 5) pteridosperm–conifer dominated plant assemblage (Šimůnek & Martínek 2009). The newly appearing species are Arnhardtia scheibei (Gothan) Hauboldt et Kerp, Rhachiphyllum curretiensis (Zeiller) Kerp, R. lyratifolia (Goeppert) Kerp, Taeniopteris abnormis Gubther, Otovicia hypnoides (Brongniart) Kerp, Carpentaria marocana Němejc et Augusta, Pterophyllum sp., Zamites sp. whereas Dichophyllum flabelliferum, Lodevia nicklesi and “Callipteris” zbejsovensis have their last occurrence in this horizon. Flora of the Ričany Horizon in the upper part of the formation is similar but less diverse than that of the Zbýšov Horizon (Fig. 5). Overlying the Padochov Formation is the Veverská Bítůška Formation containing the Chudčice Horizon of lacustrine origin that provided only poor conifer-dominated assemblage (Šimůnek & Martínek 2009).

In the youngest Letovice Formation up to nine grey lacustrine horizons have been distinguished by Jaros (in Pešek et al. 2001). Flora has been found in the Zbraslav, Zboněk-Svitávka, Lubě, Kochov, Michov and Bačov horizons. The Zbraslav Horizon provided only a low diversity assemblage (Fig. 5) with predominance of pteridosperms and conifers. Relatively diverse assemblage is known also from the Zboněk-Svitávka Horizon where Calmitzschia frondosa (Renault) Clement-Westerhof and C. hirmeri (Florin) Clement-Westerhof occur for the first time (Fig. 5). Fossil record of the horizon is dominated by remains of walchian conifers and of peltasperms of the genus Autunia (Šimůnek & Martínek 2009; Schneider personal communication). Floras of the youngest lacustrine horizons, the Kochov, Michov and Bačov, are very similar (Fig. 5) including dominancy of walchian conifers and peltasperms (Šimůnek & Martínek 2009), which is in agreement with their position within a narrow stratigraphic interval. Among species that newly appear at this level
Figure 5. Stratigraphic ranges of plant taxa identified in the Boskovice Basin. Based on data from Simůnek & Martinek (2009) and Pešek et al. (2001). Abbreviations: R-O F. – Rosice-Oslavany Formation, g. c. – group of coals, D.f. – Dichophyllum flabelliferum, A.c. – Autunia conferta, S.a. – Sphenophyllum angustifolium.
mentioned should be *Supaia moravica* Němejc et Augusta, *Sphenophyllum thonii* Mahr and several species of the conifer genus *Hermitia* (Fig. 5).

**Fauna**

Only sporadic fauna have been found in the Rosice-Oslavany Formation in grey mudstones surrounding coals (Fig. 6). Invertebrates are represented by insect wings of *Anthracoblattina* sp. (Schneider 1983). Vertebrates are represented by small fragment of a pelycosaur reptile *Edaphosaurus* sp. (Prantl 1943) and actinopterygian scales including *Elonichthys krejci* (Opluštil et al. 2013), indicating the local bio/ecozone Sphaerolepis-Elonichthys and consequently a late Stephanian (Gzhelian) age (Zajíc 2000, 2004, 2005).

The fauna of the Padochov Formation is concentrated in the Zbýšov and Říčany lacustrine horizons. Common for both horizons is *Acanthodes gracilis*, which indicates a position in the local bio/ecozone of the same name and is thus equivalent to the Rudnik Horizon in the Krkoňo-Piedmont Basin (Zajíc 2000, 2004; Opluštil et al. 2013). An important representative of this biozone is the shark *Bohemiacanthus carinatus*. In the Zbýšov Horizon present also are amphibians *Moraverpeton remesi*, *Branchiosaurus* sp., and *Pelosaurus* sp. (Štamberg & Zajíc 2008, Opluštil et al. 2013). Invertebrates are represented by pelecypods *Carbonicola thuringensis*, *C. remesi*, *Palaeanodonta sophiae*, *P. compressa*, *P. verneuili* and *P. castor* (Opluštil et al. 2013). Conchostracan remains probably belong to the family Lioestheriidae (Opluštil et al. 2013). The insect fauna is diverse and includes *Moraviptera reticulata*, *Opsiomylacris* cf. *procera*, *Phyloblatta flabellata*, *Phyloblatta moravica*, *Phyloblatta* sp., *Kashmiroblatta* sp., and *Blattinopsis antoniana* (Schneider 1980, 1983, 1984). In the Říčany Horizon no pelecypods have been found yet; however conchostracans of Lioestheriidae indet. occur. The remarkably diversified entomofauna is represented by *Sysciophlebia* cf. *curvata*, *P. dyadica*, *Spiloblattina homigtalensis*, *Poroblattina rotundata*, *Blattinopsis angustai*, *B. lattissimai*, *B. campestris*, *B. martynovae*, *Blattinopsis* sp., and *Pseudomerope gallei* and others (Kukalová 1959, 1965; Schneider 1980, 1984; Schneider & Werneburg 2012). Vertebrates are represented by *Acanthodes* sp., and by actinopterygian fish *Neslovicella rzehaki* and *Actinopterygii* indet. (Fig. 6; Štamberg & Zajíc 2008).

So far no fauna has been found in the Veverská Bítýška Formation. However, rich fauna is known from the lacustrine horizons of the youngest Letovice Formation. In its lower part there are the Zbraslavec, Zboněk-Svitávka and Lubě horizons, the fish fauna of which is uniform for all these horizons and indicate their position within the local *Acanthodes gracilis* Zone. Present also are two actinopterygian species *Letovicthys tuberculatus* and *L. multidentatus* (Štamberg 2007). Insects are common and include stratigraphically important taxa *Sysciophlebia*.

Faunas are relative uniform in the remaining Kochov, Michov and Bačov lacustrine horizons in the middle and upper parts of the Letovice Formation. Besides conchostracans, invertebrates are represented by diversified entomofauna. World-famous is the Obora locality in the Bačov Horizon, from where Kukalová (1963, 1964) and Schneider (1980, 1984) described about 100 insect species. Vertebrates are represented by the index biozone shark taxon *Xenacanthus decheni*. Actinopterygians include common *Paramblypterus* “type B” accompanied in the Kochov Horizon by rare *Bourbonnella hirsuta* (Štamberg 2014). Amphibians are represented by genera *Discosauriscus* and *Letoverpeton* (Špinar 1952a).

### Material and methods

The sample of the radioisotopically dated volcaniclastic rock was taken from a small natural outcrop (GPS: N 49° 08.053' E 016° 20.484') situated along southern slope of the Balinka Creek valley about 1200 m ENE of the town of Oslavany and 700 m WSW of the village of Padochov (Figs 7, 8).

Separation of zircons and their radiometric dating was done in the Isotope Geology Laboratory of the Boise State University, Idaho. A heavy mineral separate containing abundant moderate to highly elongated, prismatic zircon crystals was separated by conventional density and magnetic methods. The bulk zircon separate was annealed in a muffle furnace at 900 °C for 60 hours in quartz beakers prepare the crystals for subsequent chemical abrasion (Mattinson 2005). Individual crystals were hand-picked and chemically abraded using a single aggressive abrasion step in concentrated HF at 190 °C for 12 hours, and the residual crystals processed for isotope dilution thermal ionization mass spectrometry (ID-TIMS). Single crystals were spiked with the ETS35 mixed U-Pb spike, with internal U fractionation correction and Pb fractionation corrected using an externally-derived mass bias derived from the average Pb fractionation of ET2535-spiked samples analysed over the same experimental interval. The details of ID-TIMS analysis are described by Davydov et al. (2010) and Schmitz & Davydov (2012). U-Pb dates and uncertainties for each analysis were calculated using the algorithms of Schmitz & Schoene (2007), the U decay constants of Jaffey et al. (1971), and the ETS35 spike composition of Condon et al. (2007). The quoted uncertainties in Table 1 are based on non-systematic analytical errors, including counting statistics, instrumental fractionation, tracer subtraction, and blank subtraction. These error estimates should be considered when comparing our 206Pb/238U dates with those from other laboratories that used tracer solutions calibrated against the EARTHTIME gravimetric standards. When comparing our dates with those derived from other decay schemes (e.g. 40Ar/39Ar, 187Re-187Os), the uncertainties in tracer calibration (0.03%; McLean et al. 2015) and U decay constants (0.108%; Jaffey et al. 1971) should be added to the internal error in quadrature. Interpreted sample ages are thus reported as ± X (Y) [Z] Ma.
where X is the internal error, Y is the internal plus tracer calibration error, and Z is the internal plus tracer plus decay constant uncertainty.

In addition to the radioisotopic age measurements, the volcanite was studied also petrographically and mineralogically using microscopic methods, X-ray diffraction, and bulk chemical analyses. Microscopic investigation and EDX microanalysis of the tuff components were carried out on an electron microscope (model FEI Quanta 650 FEG) equipped with various detectors (EDX-EDAX Galaxy, WDA-EDAX LEXSY, and CL-Gatan Mono 4 CL). Analyses were made using polished thin sections that were coated with a 10 nm thin film of carbon under the following conditions: 15 kV beam voltage (30 kV in some cases for emission line Sr Kα), 8–10 nA current, 6 or 4.5 μm beam diameter, and a high vacuum exceeding 10⁻³ Pa. Identification and quantification of spectral lines was performed using the decomposition method by means of halographic peak deconvolution (EDAX 2003).

Powder X-ray diffraction analyzes were carried out using a Bruker-AXS D8 Advance instrument with a 2θ/θ measurement geometry and the positionally sensitive detector LynxEye under the following conditions: radiation CoKα/Fe filter, current 40 kV, 40 mA voltage, step mode with a step of 0.014° 2θ, and a total time of 25 seconds per step. Qualitative analysis of diffraction patterns was performed using the EVA software (Bruker-AXS) and the database PDF-2, release 2011 (International Centre for Diffraction Data). The Rietveld method using the TOPAS software, version 4.2 (Bruker) was applied to verify the qualitative analyses and to quantify the mineral phases present.

For bulk chemical analyses, we selected a representative rock sample collected in 2016 weighing approximately 100 g. The chemical analyses were performed at the Bureau Veritas Mineral Laboratories in Vancouver, Canada. The sample was crushed, pulverised to 200 mesh and reduced in weight by quartering. Aliquots for analyses of the standard oxides were dissolved in hot (95 °C) aque regia and analysed using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES).

Analysis of vegetation diversity and pattern is based on data published by Šimůnek in Pešek et al. (2001) and by Šimůnek & Martínek (2009), where nomenclatorically and taxonomically upgraded lists of plant species identified so far in the basin were published. Individual taxa were plotted against the stratigraphic chart. Ranges of taxa are inferred from their presence/absence in particular stratigraphic levels. If a taxon is missing from any level and has been found below and above that level, it is accepted as occurring here (Cleal 2005).

This approach allows for more meaningful recognition of plant diversity throughout the basin succession. This analysis, in turn, also requires the minimum number of organs approach, based on estimation of number of biological species from organ types that best characterize individual plant groups. As an example, diversity of pteridosperms or ferns in compression state of preservation is best expressed by their foliage. This method avoids the inflation of diversity and is commonly used in similar palaeobotanical studies (e.g. Cleal 2005, Cleal et al. 2012). Data were further used for constrained cluster analysis using a Raup-Crick coefficient and the PAST software (Hammer et al. 2001).

Results

Stratigraphic position of the volcanic body

The dated sample of volcanoclastic rock was taken from a ~ 2 m thick volcanic body that is embedded in a succession of irregularly alternating green-grey mudstones silt-

Figure 8. Dated volcanic rocks embedded in sediments in top of the Rosice-Oslavany Formation.
stones and fine-grained sandstones, possibly of fluvial in origin, dipping south-east (120°/30°). Because of vegetation cover the body is laterally traceable only for a few metres but scree fragments suggest its lateral extent further south for at least hundred metres. Gilíková in Buriánek et al. (2011) interpreted the stratigraphic position of the volcanic body within green-grey sediments in upper part of the Rosice-Oslavany Formation. To obtain more precise location we calculated vertical distance above the Coal I from data derived from the geological map and our field observations. Assuming the surface distance between outcrops of the Coal I and the volcanic bed at the 248 m a.s.l. is about 115 m and average dip of strata of 30°, the stratigraphic distance between the Coal I and the dated volcanite is 57 m. This suggests the position of the volcano less than 40 m above the Helmhacker Horizon. Although the volcanite has not been found in the well-studied Oslava River Section (Jaroš 1962, Pešek et al. 2001, Šimůnek & Martínek 2009) located along the bank about 1 km further south (Fig. 7) its approximate position can be constrained from dip and strike of strata to below the top of the Rosice-Oslavany Formation (Fig. 9).

Table 1. U-Pb Isotopic Data of the Oslavany tuffite. Abbreviations: (a) z1, z2, etc. are labels for single zircon grains or fragments chemically abraded at 190°C; analyses in bold used in the weighted mean calculations. (b) Model Th/U ratio calculated from radiogenic 206Pb/207Pb ratio and 207Pb/235U date. (c) Pb* and Pbc are radiogenic and common Pb, respectively. mol% 206Pb* is with respect to radiogenic and blank Pb. (d) Measured ratio corrected for spike and fractionation only. Samples were spiked with the ETS535 tracer, with an external Pb fractionation correction of 0.20 ± 0.03 (1-σ)/amu (atomic mass unit), based on analysis of NBS-981 and NBS-982. (e) Corrected for fractionation, spike, common Pb, and initial disequilibrium in 230Th/238U. Up to 0.5 pg of common Pb is assigned to procedural blank with composition of 206Pb/204Pb = 18.042 ± 0.61; 207Pb/235U = 15.537 ± 0.52; 208Pb/204Pb = 37.686 ± 0.63 (1-σ). Excess over blank was assigned to initial common Pb, using the Stacey & Kramers (1975) two-stage Pb isotope evolution model at 300 Ma. (f) Errors are 2-σ, propagated using algorithms of Schmitz & Schoene (2007). (g) Calculations based on the decay constants of Jaffe et al. 1971. 206Pb/238U and 207Pb/206Pb ratios and dates corrected for initial disequilibrium in 230Th/238U using Th/U [magma] = 3.

| Grain | Th/U x10^−13 | 206Pb* | mol% | Pb* | Pbbc | 206Pb | 207Pb | % err | 207Pb/206Pb | % err | 208Pb/206Pb | % err | 206Pb* | 207Pb | 208Pb | 206Pb | 207Pb | 208Pb | 207Pb/206Pb | % err | 207Pb/235U | % err | 208Pb/238U | % err | cor. coef. | 206Pb | 207Pb | 208Pb | 206Pb | 207Pb | 208Pb | 207Pb/235U | % err | 207Pb/235U | % err | 208Pb/238U | % err | 208Pb/238U |
|-------|--------------|--------|------|-----|------|--------|--------|-------|--------------|-------|--------------|--------|--------|--------|-------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| z4    | 0.519        | 0.5417 | 99.16%| 36   | 0.36  | 2149   | 0.164  | 0.052397 | 0.236  | 0.343260 | 0.279  | 0.047514 | 0.071  | 0.687  | 302.8  | 5.4   | 299.64 | 0.72   | 299.24 | 0.21   |
| z3    | 0.278        | 0.4410 | 98.90%| 25   | 0.41  | 1640   | 0.088  | 0.052362 | 0.286  | 0.343222 | 0.329  | 0.047466 | 0.078  | 0.652  | 298.8  | 6.5   | 298.93 | 0.85   | 298.95 | 0.23   |
| z5    | 0.329        | 0.5030 | 98.88%| 25   | 0.47  | 1604   | 0.104  | 0.052348 | 0.261  | 0.343257 | 0.306  | 0.047465 | 0.071  | 0.699  | 300.6  | 6.0   | 299.13 | 0.79   | 298.94 | 0.21   |
| z2    | 0.161        | 0.3703 | 99.24%| 36   | 0.23  | 2381   | 0.051  | 0.052442 | 0.208  | 0.343195 | 0.255  | 0.047464 | 0.083  | 0.684  | 304.7  | 4.7   | 299.59 | 0.66   | 298.93 | 0.24   |
| z1    | 0.215        | 0.5281 | 99.48%| 53   | 0.23  | 3457   | 0.068  | 0.052519 | 0.150  | 0.343667 | 0.199  | 0.047459 | 0.073  | 0.774  | 308.1  | 3.4   | 299.95 | 0.52   | 299.90 | 0.21   |
| z6    | 0.253        | 0.6041 | 97.85%| 13   | 1.10  | 843    | 0.080  | 0.052308 | 0.278  | 0.342232 | 0.325  | 0.047452 | 0.074  | 0.707  | 298.9  | 6.3   | 298.86 | 0.84   | 298.86 | 0.22   |
| z8    | 0.421        | 0.6489 | 99.22%| 37   | 0.43  | 2302   | 0.133  | 0.052192 | 0.232  | 0.341344 | 0.275  | 0.047433 | 0.071  | 0.684  | 298.4  | 5.3   | 299.19 | 0.71   | 298.75 | 0.21   |
| z5    | 0.189        | 0.7163 | 98.89%| 25   | 0.67  | 1634   | 0.060  | 0.052408 | 0.221  | 0.341855 | 0.267  | 0.047309 | 0.073  | 0.715  | 303.3  | 5.0   | 298.58 | 0.69   | 297.98 | 0.21   |
Macroscopically the dated volcanite is a green to grey fine-grained massive rock. In the basal part this greenish rock consists of volcanic ash with lapilli up to few centimetres in diameter. In the direct overburden of massive volcanic rock are tuffites with similar composition, i.e., albite prevailing over quartz, and mica mineral and mineral from the chlorite group. Microscopically the sample is a massive volcanic rock composed of very fine-grained matrix consisting solely of plagioclase and splinters of quartz. RTG data indicate albite as a dominant mineral (69%), subdominant quartz (29%), and subordinate muscovite (1%) and hematite (1%). SEM observations show presence of accessory crystals of zircon, apatite, baryte, and TiO₂ minerals and possibly minerals of the monazite, xenotime, and rhabdophane groups (Fig. 10).

Chemical composition of the dated sample falls within a field of rhyolites (SiO₂ = 76.0 wt% and Na₂O + K₂O = 6.6 wt%) in the TAS classification (Le Maitre 2002). The content of K₂O (0.5 wt%) is very low whereas high concentration of Na suggests albitionization of feldspar, which is seen also from spatial distribution of these elements done by element mapping. More details concerning mineralogy, petrology, and geochemistry of volcanioclastic complex are given in Jirásek et al. (unpublished data).

Radioisotopic age of the volcanite

The sample of the Oslavany volcanite (lower tuff part) contained a homogeneous population of prismatic zircon crystals with a variety of aspect ratios from near equant (1:1) to highly elongate (10:1). No rounded zircon crystals or other minerals suggestive of detrital input were recognized. From the most elongate prismatic crystals, eight crystals were selected for chemical abrasion, dissolution and isotope dilution analysis. Six of those eight crystals yielded concordant and equivalent U-Pb isotope ratios, with a weighted mean ²⁰⁶Pb/²³⁸U date of 298.88 ± 0.09(0.17)[0.36] Ma (MSWD = 0.52; n = 6 of 8). This date is interpreted as the age of rapid, immediately pre-eruptive zircon crystallization, and thus approximates the age of eruption and deposition of the tuff. Two additional crystals yielded slightly older or younger dates, which are interpreted as biased by crystal inheritance from earlier magmatic episodes or Pb loss, respectively.

Biostratigraphy

The rich fossil record of floras and faunas in the Boskovice Basin has resulted in establishment of independent biostrati-graphies based on macrofloras, fish, amphibians and blattoid insects (e.g. Havlena 1964, Šimůnek in Pešek et al. 2001, Schneider & Werneburg 2012, Zajíc 2000, Štamberg 2014). Unfortunately, there is no clear agreement among individual biostratigraphies and several contrasting opinions on chronostratigraphy exist. “Classical” is a floral biostratigraphy, formerly affected by the opinion that the first appearance of callipteris species indicates base of the Permian (e.g. Goeppert 1858, Geinitz 1865, Gothan 1912, Havlena 1964). This opinion was questioned by Němejc (1951) and later abandoned in agreement with findings of callipterids in the stratotype area of the Stephanian stage in French Massif Central and elsewhere in Europe (Bourouz & Doubinger 1977, Kerp 1988, Brouin et al. 1990, Wagner & Álvarez-Vázquez 2010), North America (DiMichele et al. 2013, DiMichele 2014) and north Africa (Hmich et al. 2006). Consequently Wagner & Álvarez-Vázquez (2010) assigned their Autunia conferta zone to a Stephanian C–lower Autunian age, which is now considered to represent part of the Gzhelian (Gradstein et al. 2012; International Chrono-stratigraphic Chart v2016/v4). It should be mentioned that floral zonation, as suggested by these authors, is widely used in European basins, however, its two youngest zones,
Autunia conferta and Annularia spicata, are rather poorly defined. Poor definition in comparison to older zones results from limited availability of fossiliferous successions, in which these biozones are completely preserved in context with the under/overlying ones and thus allowing much wider and reliable correlations among European basins. In addition, the fossil record across the Carboniferous-Permian transition is concentrated mainly into discrete, usually lacustrine horizons (Opluštil et al. 2016b), and is thus less continuous compared to the Early to Middle Pennsylvanian coal-bearing strata. Except for Kozur’s (1980) zonation based on the succession of callipteris flora, that has not been widely accepted (Kerp 1988), no other reliable macrofloral biozones exist above the youngest and poorly constrained Annularia spicata Zone of Wagner & Álvarez-Vázquez (2010). For that reason, mostly faunas are used for the stratigraphic subdivision of Permian successions in the Boskovice and other basins elsewhere in Europe.

Macrofloral zones were first applied in the Boskovice Basin by Wagner (1984) and Šimůnek (in Pešek et al. 2001). They assigned the lower part of the Rosice-Oslavany Formation up to the level of the Coal II to the Sphenophyllum angustifolium Zone, whereas the interval between the Coal I and the Ričany Horizon in the upper part of the Padlochov Formation was attributed to the Autunia conferta Zone (Fig. 5). The youngest Annularia spicata Zone was not defined yet in that time. The position of these zones in the Boskovice Basin is established on the presence of Sphenophyllum angustifolium in the coals II and III, the first occurrence of Neurocallipteris neuropteroides in the level of the Coal II, and of Autunia conferta, Ernestiodendron filiciforme and Walchia piniformis in the Coal I. Worth noting is Němejc’s (1951) observation, that callipterids occur in close proximity to the Coal I, however, as drifted allochtonous remains together with walchian conifers in discrete beds separate from the hygrophyllous flora in the roof of the Coal I, dominated by typically late Stephanian species including Alethopteris zeilleri (= A. bohemia according to Němejc 1951). Slightly higher, in the Zbýšov Horizon, Annularia spicata occurs for the first time. Its first appearance marks the base of the middle to upper Autunian A. spicata Zone in western Europe (Wagner & Álvarez-Vázquez 2010) and is thus in contradiction with the previous assignment of this interval to the A. conferta Zone by Šimůnek (in Pešek et al. 2001). This zone is characterised by increased diversity of peltasperms and conifers; however, its upper boundary is not clearly constrained because of generally poor fossil record due to low preservation potential.

Recently Opluštil et al. (2016a, b) provided high-precision radioisotopic ages and for the first time calibrated floral zones based on their ranges in the basins of central and western Bohemia and Sudetic area. There the upper boundary of the S. angustifolium Zone is estimated to be ~ 300.5 Ma, whereas its position in the Boskovice Basin between the coals I and II (Šimůnek in Pešek et al. 2001) is probably slightly younger taking into account the new radioisotopic age 298.88 ± 0.09 Ma of the volcanic body above the Helmhacker Horizon.

This simple comparison suggests that top of the S. angustifolium or base of the A. conferta zones in the
Boskovice Basin should be rather situated around the base of the Rosice-Oslavany group of coals (Fig. 5). The top of the A. conferta or base of the A. spicata Zone is rather poorly constrained in the basins of central and western Bohemia and the Sudetic basins (Opluštil et al. 2016a, b), but seems to be located approximately between 298.5 and 298.0 Ma. This interval is in the Boskovice basin situated most probably in the lower part of the Padocoh Forma-

tion. Indeed, in the Zbyšov Horizon in lower part of the for-
mation there is the first occurrence of A. spicata, thus
marking the approximate position of base of the zone. Al-
though Kozur’s (1980) calliperis zones are not widely
used, they can be constrained in the Boskovice Basin and
demonstrate changes in caliperis flora throughout the sec-
tion (Fig. 5).

The faunal record is concentrated into discrete lacu-

trine horizons and includes stratigraphically important amphibian, fish and blattoid insect species (Fig. 6). Am-

phibians and blattoid insect zonations are based on evolu-
tionary lineages where disappearance of one key-taxon is
replaced by another species of the same lineage (for details see Schneider & Werneburg 2012). The chrono-

stratigraphy of amphibians and insect zones is based on their correlation to marine biozones in basins where both terrestrial and marine sediments alternate, as well as on some radioisotopic dates by different methods of various precision (Schneider et al. 2014). These zonations, how-
ever, suggest different ages comparing to those based on
fish faunas or floras. It is currently beyond the scope of ex-
isting data to resolve this disagreement. Instead, we explain our preferred chronostratigraphic interpretation based on fish fauna as suggested by Zajíc (2000) and Štamberg (2014). Sphaerolepis–Elonichthys, Acanthodes gracilis and Xenacanthus decheni zones have been identified in the Boskovice Basin as well as in the Krkonoše-Piedmont and Intra-Sudetic basins. Their identification is based on the occurrence of key-taxa (Fig. 6) and follows an as-
sumption that since late Stephanian (Gzhelian) times all
our preferred chronostratigraphic interpretation based on
fish fauna as suggested by Zajíc (2000) and Štamberg (2014). Sphaerolepis–Elonichthys, Acanthodes gracilis and Xenacanthus decheni zones have been identified in the Boskovice Basin as well as in the Krkonoše-Piedmont and Intra-Sudetic basins. Their identification is based on the occurrence of key-taxa (Fig. 6) and follows an as-
sumption that since late Stephanian (Gzhelian) times all

Plant diversity and vegetation patterns

About 94 whole-plant taxa have been identified so far in the Boskovice Basin (Fig. 5). Except for a few mostly poorly
preserved gymnosperm remains found in the fluvial red
beds, the entire plant fossil record is concentrated to usu-
gally grey to green-grey lacustrine strata and to the mudstones in the vicinity of coals, mostly in their roof (Augusta 1951, Němejc 1951, Šetlík 1951, Rieger 1965). These fossilifer-
ous strata represent major windows of preservation and provide insight into the plant diversity of the basin land-
scape. Significant differences in stratigraphic ranges of in-
dividual taxa result in prominent changes in diversity as
well as vegetation patterns throughout the fossiliferous part of the basin sequence (Figs 12, 13). There is an initial rise
in diversity, which doubles from base to top of the Rosice-Oslavany group of coals and reaches 54 species in the
level of the Coal I. This significant diversification fully corresponds to increasing economic importance of individ-
ual coals and thus may partly reflect a sampling artefact at
the lower edge of the taphonomic window. Above the Coal
I diversity drops to 43 species in the Helmhacker Horizon and again rises to the maximum 55 species in the Zbyšov Horizon in the lower part of the Padocoh Formation (Figs 5, 12, 13). The changes in diversity are accompanied by the disappearance of a suite of wetland species typical of the Rosice-Oslavany group of coals, and the onset of new taxa in the Zbyšov Horizon. A diversity level of ~ 50 spec-
ies is typical for the entire Padocoh Formation, above
which there is a drop between the Říčany and Chudčice ho-
rizons from 50 to 39 species respectively. Diversity then
becomes stable (38–41 species) throughout the ~ 3000 m
thick succession represented by the upper Veverská Bi-
týška and entire Letovice formations.

Vegetation patterns expressed either by numbers of species of major plant groups or by their percentage in the overall diversity in plant assemblage of individual fossiliferous intervals, vary significantly throughout the basin sequence. The most striking is a gradual shift from a gentle predominance in number of species of cryptogamc plants over the seed plants in the basal part of the basin succession to an opposite ratio in its upper part (Fig. 12). Expressed in numbers, about 20 cryptogamic species in the lower part of the basin succession are gradu-
ally reduced to 10 species in the top of the Letovice Forma-

tion, whereas about 10 seed plant taxa increase to 25–30
species in the opposite way. This trend is even more pron-
oced in the case of percentage of these two major plant
groups due to a gradual decrease in overall diversity throughout the section. Thus the proportion of cryptogams decreases in two steps from 60% in the Coal III to only
25% in the Bačov Horizon at the top of the Letovice Forma-
tion (Fig. 12).

The decrease of cryptogamous plants is mainly due to the
disappearance of ferns of all three major groups, zygopteridales, filicales and marattiales (Figs 12, 13), whereas sphenopsid diversity remains fairly unaltered. In the case of seed plants, an increase in number of species up the basin succession is observed among conifers. There are already 6 species just above the Coal I and this number increases to 13–14 species in the upper part of the Letovice Formation. This rise in the role of conifers in the fossil record is even more striking in normalised vegetation pattern (Fig. 12) where the percentage of conifers increases from a few to ~ 35% at the top of the Letovice Formation.

A rather different pattern is displayed by pteridosperms (Figs 12, 13). They reach a maximum diversity of up to 20 species in the Padochov Formation from which their number decreases to 10–12 in the remaining Veverská Bítěška and Letovice formations. Due to a more pronounced decrease in diversity of cryptogamic plants in the same way, however, the percentage of pteridosperms throughout the basin sequence remains nearly constant. Apparent trends exist among particular plant groups within pteridosperms. Concerning species numbers, medullo-saleans reach the maximum diversity in the Rosice-Oslavany group of coals (≤ 11), whereas maximum diversity of peltasperms, up to 9 species, is achieved in the overlying Padochov Formation of early Asselian age (Fig. 13). Plants of uncertain affinity, possibly pteridosperms (Taylor et al.  ...
2009) including genera *Taeniopteris* and *Supaia* appear at a maximum of 4 species in the upper part of the Letovice Formation, whereas only one species is present in the late Gzhelian Rosice-Oslavany Formation. Their increasing role to top of the basin succession (late Asselian) is amplified when expressed as percentage of overall diversity (Fig. 13).

### Similarity of plant assemblages

Plant assemblages of major fossiliferous horizons were statistically evaluated by calculating measure of similarity for the constrained unweighted pairs using the Simpson coefficient (Fig. 14). For each horizon we included species that have been physically found in the particular horizon as well as those whose presence is assumed from their occurrence below and above. Three stratigraphically constrained major clusters represent principal plant assemblages established after major compositional and ecological changes, possibly driven by climate. In other words, each of major clusters represents intervals of relative ecological and compositional stability with only minor changes in plant assemblages between neighbouring lacustrine horizons.

The cluster 1 is characterised by dominance of hygrophilous flora of clastic and peat-forming wetlands that includes sigillarians and even lepidodendroid lycopsids, although dominating are maratialean ferns. Subdivision into two subgroups is due to occasional appearance of conifer and peltasperm remains, typical of the Permian part of the succession, in the vicinity of the Coal I and in the Helmhacker Horizon above it. These are, however, found as drifted allochtonous remains separate from typical hygrophilous flora (Němejc 1951). The cluster 2 includes lacustrine horizons of the Padochov, Veverská Bítýška and lower parts of the Letovice formations, up to the level of the Zboněk-Svitávka Horizon. According to Šimůnek & Martínek (2009) assemblages of these fossiliferous horizons are dominated by pteridosperms with conifers being co-dominant or subdominant. The cluster 3 groups horizons in the upper part of the Letovice Formation, the plant assemblages of which are dominated by conifers, as reflected in their diversity (Figs 12, 13) as well as in predominance of their remains (Šimůnek & Martínek 2009). Worth noting is that these major clusters of similarity of plant assemblages nearly faithfully correspond to the assemblages of fish faunas as suggested by Zajíc (2000) and Štumberg (2014).

### Discussion

The Late Pennsylvanian–Early Permian is a time of the Late Paleozoic Ice Age culmination (see Fielding et al. 2008, Bishop et al. 2009, Isbell et al. 2012, Montañez & Poulsen 2013). Physical environmental data from this interval provide support for a long-term, 10^5-year scale progressive trend of warming and increasing drying in equatorial Pangea (Schneider et al. 2006, Montañez et al. 2007, Tabor & Poulsen 2008). Combined with this trend are shorter 10^4-year scale intervals of global warming and cooling (Birgenheier et al. 2009), recorded in the paleotropics of central and western Pangea as alternation of dry and wet phases (Roscher & Schneider 2006, Opluštil & Cleal 2007), and possibly related to incompletely understood variations in CO2/O2 levels in the atmosphere (Horton et al. 2007), although there is a parallel opinion that substrate dryness, driven at least partly by tectonic processes, may be a more important controlling factor than simple climate (Cleal et al. 2010, 2011).

Further superimposed on these intervals are even shorter climatic oscillations of ~ 10^5 years recorded as glacio-eustatically driven cycles or cyclothems (Tandon & Gibling 1994, Gibling & Rygel 2008, Heckel 2008). This climatic complexity is evident not only from the sedimentary record and paleosols (Driese & Ober 2005; Tabor et al. 2008; Rosenau et al. 2013a, b; Allen et al. 2014; Opluštil et al. 2015; Lojka et al. 2009, 2016), but also from time-coinciding changes of terrestrial biota (e.g. Falcon-Lang et al. 2009, 2011; DiMichele et al. 2006, 2008; DiMichele 2014).

In the Boskovice Basin the overall trend of increasing aridity and drying is recorded as a transition from the upper Gzhelian grey coal-bearing strata of the Rosice-Oslavany Formation to the lower Cisuralian dominantly red bed strata of the Padochov, Veverská Bítýška and Letovice formations. This climatic trend affected also the preservation of organic matter and character of plant fossil-bearing horizons. In the Rosice-Oslavany Formation these were mostly peat and clastic swamps developed on lake shallows (Šimůnek & Martínek 2009). Lake level prevented the wetlands from seasonal water table changes and allowed long-lasting peat accretion. In contrast from the overlying Padochov Formation, coal seams, even thin, are absent. Instead, plant remains are preserved only in nearshore mudstones and siltstones or offshore black shales and organic matter-rich limestones, whereas dessication cracks are observed in lake mudflat sediments of the Chudčice Horizon (Šimůnek & Martínek 2009).

The presence of a few to tens of metres thick grey, mostly lacustrine intervals “interrupting” the overall fluvial red beds succession (Nehyba & Mastalerz 1997, Pešek et al. 2001) suggests the existence of shorter-term climatic oscillations between semi-humid to semi-arid conditions (Šimůnek & Martínek 2009). Similar climatic oscillations may have resulted in alternation of peat and clastic deposition of the Rosice-Oslavany group of coals, the latter being
Figure 13. Vegetation patterns within major plant groups. Abbreviations: V.B. – Veverská Bítýška, Zbon.-Svit. – Zboněk-Sviťávka.
locally red. Assuming the coal-bearing cycles of these continental basins were driven by similar mechanisms to cyclothems of the paralic basins (glacieustacy driven by global climate), their length can be estimated in rank of ky (Heckel 2008, Gastaldo et al. 2009). In contrast, the hygrophilous assemblage from the roof of coals lacks the remains of callippterids and conifers. Callippterids appear for the first time in a close proximity above the roof of the Coal I, but separately from the hygrophilous flora (Augusta 1946, Němejc 1951). Their fragments occur in association with similarly fragmented conifer remains and unidentifiable plant detritus thus indicating an allochthonous origin of the assemblage (Němejc 1951). The onset of callippterids above the Coal I possibly indicates a climatic shift to drier conditions (Šimůnek & Martínek 2009). Floras of lacustrine horizons of the Padochov Formation are generally mixed pteridosperm- and conifer-dominated assemblages as indicated both by diversity patterns (Figs 12, 13) and frequency of their plant remains (Šimůnek & Martínek 2009). In contrast, the Chudčice Horizon in the Veverská Bítýška Formation provided plant assemblages dominated by conifers (Šimůnek & Martínek 2009) and a marked drop of diversity of ferns and pteridosperms including peltasperms (Figs 12, 13). Conifers are considered as one of the most reliable indicators of environments with seasonal moisture stress (DiMichele 2014) and their dominancy in this level indicates further shift to drier climate. A return to pteridosperm-dominated flora is observed in the Zboněk-Svitávka and Lubě lacustrine horizons in the lower part of the Letovice Formation (Šimůnek & Martínek 2009). The pteridosperms are dominated by peltasperms, especially by Autunia conferta, and this assemblage possibly indicates a slight increase of humidity. Flora of the Michov and Bačov lacustrine horizons in the upper part of the Letovice Formation are again conifer-dominated based on frequency of their remains, and therefore interpreted as evidence for increased aridity in comparison with the lower part of the Letovice Formation (Šimůnek & Martínek 2009). This interpretation is in agreement with diversity of plant assemblages of this stratigraphic interval (Figs 12, 13), where conifers attain the highest diversity of all plant-bearing intervals of the Boskovice Basin. In contrast diversity of ferns significantly decreases. Typical for these youngest lacustrine windows are representatives of the genera Taeniopteris and Supaia. The above described assemblages clearly indicate a gradual, although not regular trend of increasing aridity recorded as a transition from the hygrophilous plant assemblage of the Rosice-Oslavany group of coals to peltasperm and especially conifers dominated plant assemblages preserved in the lacustrine horizons of Permian part of the basin succession.
Comparisons

The above-described succession of vegetation patterns and plant assemblages around the Carboniferous-Permian transition is not unique to the Boskovice Basin but has been observed elsewhere in Europe and North America where this transition is preserved (Broutin et al. 1990, 1992; Châteauneuf et al. 1992; DiMichele et al. 2001, 2005, 2007; Barthel & Rößler 2012, Opluštil et al. 2016b). This trend is characterised by a general decline of “Carboniferous-type” wetlands flora and increasing importance of walchian conifer-peltasperm floras (Kerp 1996, 2000; DiMichele et al. 2005, 2008, 2009; DiMichele 2014; Looy et al. 2014). The latter appear sporadically in the basin lowlands during the Late Pennsylvanian and become dominant during the early Permian as a consequence of aridification trend (DiMichele et al. 2008). Spatio-temporal differences in vegetation patterns and their successions, however, exist across central and western tropical Pangea, including the local presence of some “Mesophytic” elements like taeniopterids, supaioids and Podozamites or voltzian conifers (DiMichele et al. 2001). Some of these assemblages have been found in association with evaporites or calcic vertisols suggesting strong seasonality further supported by presence of growth rings (Falcon-Lang et al. 2011, 2014). Detailed comparison is, however, beyond the scope of this study, partly because of absence of precise radioisotopic data to establish high-resolution correlation between individual areas. Currently only the Intra-Sudetic Basin in the northern part of the Czech Republic provides the comparably high stratigraphic resolution and data for comparison (Opluštil et al. 2016b). In the Intra-Sudetic Basin the radioisotopically constrained Carboniferous-Permian transition is recorded in the Chvaleč and Broumov formations, the floras and fish faunas of which are equivalent to the entire Boskovice Basin succession. The apparent difference between these two areas exists in overall floral diversity, which is more than doubled in the Boskovice Basin (up to ~ 50 species comparing to over 20 species maximum in this interval in the Intra-Sudetic Basin). Apart from this difference the vegetation patterns are very similar, showing an increase in diversity of conifers and peltasperms throughout this interval and decrease of “Carboniferous-type” wetlands flora or complete decline of some of its elements (lepidodendroid lycopsids). In the Intra-Sudetic Basin the percentage of conifers in vegetation patterns increases from 12% in the late Gzhelian to about 40–50% in the late Asselian part of the succession. In equivalent strata of the Boskovice Basin the proportion of conifers rises from few to ~ 35% (Fig. 12). Differences of similar rank exist also among most other groups; however, increasing proportion of conifers and peltasperms up the section is obvious in both basins for time equivalent strata.

Summary and conclusions

The Boskovice Basin is a half-graben that preserves about 5 km thick succession of continental red beds interrupted by grey mostly lacustrine horizons bearing rich floras and faunas, and recording biotic changes across the Carboniferous-Permian transition. Our new high-resolution U-Pb CA-IDTIMS dating of single zircon crystals separated from acid volcanic rock embedded below the top of the Rosice-Oslavany Formation in lower part of the basin succession provided an age of 298.88 ± 0.09 Ma. This age nearly exactly corresponds to the Carboniferous-Permian boundary as currently accepted by the International Chronostratigraphic Chart (v2016/4). Physical connection of the Boskovice Basin with the Intra-Sudetic and Krkonoš-Piedmont basins in northern part of the Czech Republic allowed for correlation of their successions based on similarities of their fish faunas. This correlation suggests a late Asselian age for the youngest fish faunas of the Boskovice Basin. This age is confirmed also by radioisotopic ages of volcanites embedded in strata associated with lacustrine horizons bearing very similar fish faunas in the Intra-Sudetic and Krkonoš-Piedmont basins. These radioisotopic ages enable us to better characterise vegetation changes in purely continental settings in a temporal context and to correlate them with global marine stages.

The fill of the Boskovice Basin records a well-known aridification trend marked by the transition from Late Gzhelian grey coal-bearing strata to Asselian fluvial red beds. The red beds succession is interrupted by grey lacustrine horizons suggesting that upon the long-term trend of increasing aridity are superimposed shorter-term oscillations between drier and more humid climates. Possible existence of even shorter climatic variations is indicated by lake level fluctuation and occasional complete dessication.

These climatic changes had a profound effect on biota and affected its preservation. Fossil remains are concentrated into windows of preservation formed under high ground water table or lake level during humid phases. Vegetation patterns of individual windows of preservation, formerly being wetlands and lakes, mimic the major climatic variations. In the broadest view they clearly demonstrate the overall aridification trend between late Gzhelian and late Asselian times. It is characterised by transition from assemblages dominated by free-sporing plants, mostly tree ferns, typical of Late Pennsylvanian wetlands, to peltasperm-walchian conifers-dominating patterns. Similar successions have been observed elsewhere in the former central and western equatorial Pangea including the Intra-Sudetic Basin. Vegetation patterns of equivalent strata of both basins shows strong similarity, although diversity in the Intra-Sudetic basin is only about half of that in the Boskovice Basin.
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