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Plant–arthropod associations from the Early Miocene of the Most Basin in North Bohemia—Palaeoecological and palaeoclimatological implications

Stanislav Knor [a,*], Jakub Prokop [a], Zlatko Kvaček [b], Zdeněk Janovský [c], Torsten Wappler [d]

[a] Charles University, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44, Praha 2, Czech Republic
[b] Charles University, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, CZ-128 43 Praha 2, Czech Republic
[c] Charles University, Faculty of Science, Department of Botany, Benátská 2, CZ-128 01, Praha 2, Czech Republic
[d] Steinmann Institute for Geology, Mineralogy and Palaeontology, Division Palaeontology, University of Bonn, Nussallee 8, D-53115 Bonn, Germany

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ABSTRACT

Terrestrial plants and insects account for the majority of the Earth's biodiversity today, and herbivorous interactions are dated back more than 400 million yr. However, investigation of their associations remains in its infancy in Europe. The Miocene is characterized by palaeogeographic re-organization due to the collision of the African with the Eurasian plates. Antarctica's enormous impact on global climatic conditions, and thus on European palaeoenvironment, resulted from a series of episodes of minor glaciations in the Early Miocene after the initial cooling and ice sheet formed during the Oligocene.

More than 3500 plant remains showing various kinds of feeding damage were available for the present study. These trace fossils are classified according to their external morphology into damage types (DT) and grouped to functional feeding-groups. The Neogene plant record in Europe is rich and diverse, offering a profound large-scale understanding of the floristic and vegetational development. A database of fossil traces from the Most Basin was compiled and analyzed by various statistical methods in terms of the diversity and intensity of palaeoherbivory. The primary objective is to present results on the development of insect herbivory through the section of the Bílina Mine in North Bohemia, with the aim of understanding the principal factors that caused the observed phenomena. The research was focused on two horizons—Delta Sandy Horizon (DSH) and Lake Clayey Horizon (LCH)—both sufficiently represented to compare their palaeoecological and palaeoclimatological signals on the basis of the presence of damages caused by insects and other herbivorous arthropods. A total sample of 60 different damage types, attributed to eight main functional feeding groups, was examined. Results from analyses of the frequency and diversity of the selected categories of plant arthropod associations within both examined horizons significantly support different environmental conditions. The LCH seems to be affected by the relatively colder and drier climatic conditions as indicated by a four times greater frequency of leaves with galls and lower taxonomic diversity and species equability, whereas DSH indicates warmer and more humid conditions reflecting the higher diversity of the plant species and damage types.

1. Introduction

The ecology of plant–insect associations currently is a significant aspect of modern ecological research. Consequently, studies of insect herbivory on fossil leaves provide crucial information on the ecology of feeding associations and the association of plants and their insect herbivores that cannot otherwise be obtained separately from the record of plant macrofossils and insect body fossils. Because food webs incorporating plants and phytophagous insects account for up to 75% of global diversity, it is essential to examine how factors like global warming and cooling affect insect herbivory.

The Earth's climate was gradually cooling during the Tertiary (the last 65 Ma). This trend was punctuated by three more abrupt cooling steps (e.g., Zachos et al., 2001a). Palaeoclimate indicators suggest that the East Antarctica ice-sheet formation, which initiated in the Late Oligocene (Lyle et al., 2007), resulted in a decrease in global sea level by nearly 70 m during this time (Berggren et al., 1995; Berggren, 2002). Subsequently, in the Miocene important vegetation changes resulted from this altered global climate (Utescher et al., 2011, and references herein). These changes were mainly triggered by fluctuations in and later expansion of the Antarctic continental ice-sheet (Barker and Thomas, 2004; Shevenell et al., 2004). Except at the very beginning of the Early Miocene, the glaciation of Antarctica was ephemeral and unstable compared to the present extent (Naish et al., 2001) and the Northern Hemisphere was largely ice-free at that time (Billups, 2002, and references therein). The Early to Middle Miocene

* Corresponding author. Tel.:+420 221951837; fax: +420 221951840.
E-mail address: knor@natur.cuni.cz (S. Knor).

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glaciation fluctuations, which were probably caused by Milankovitch cycles, came to an end with the final deep-freezing of Antarctica in the mid-Miocene (Zachos et al., 1997, 2001b; Shevenell et al., 2004). Constant decrease of pCO_2 is suspected to be one of the most probable causative factors (Holbourn et al., 2005). All of these events deeply affected terrestrial ecosystems, especially in mid latitudes (Casanovas-Vilar et al., 2005; Böhme et al., 2008; Wappler, 2010).

The study of plant–insect associations during the Early Miocene thus gives an opportunity to test some important predictions with regard to climatic fluctuations of the time. The European Miocene has not been subjected to such a detailed analysis of plant–insect associations and allows significant, new and extended understanding of Miocene regional climate dynamics and how they differ from those of the present day. A fossil assemblage covering this time period coupled with excellent preservation of insects and plants is the Early Miocene deposit at Bílina Mine. The Early Miocene Lagerstätte of Bílina Mine in the Most Basin, Czech Republic provides a unique view into a Neogene freshwater ecosystem and records a time of significant changes in climate, biodiversity, and floral and faunal composition (Kvaček et al., 2004).

Herein we document changes in insect herbivory through the Early Miocene, with the aim of understanding the principal factors involved in the observed variations, combined with a variety of proxies to estimate palaeotemperature, precipitation, and nutrient levels (e.g., Pearson and Palmer, 2000; Utescher et al., 2000, 2011; Mosbrugger et al., 2005; Uhl et al., 2006, 2007).

2. Materials and methods

The material studied is housed in the National Museum in Prague, the Bílina Mine Enterprise collections, and the Senckenberg Naturhistorische Sammlungen Dresden. The Bílina Mine collection comprises material from 23 fossiliferous layers belonging to three different horizons [Clayey Superseam Horizon (CSH), Delta Sandy Horizon (DSH), Lake Clayey Horizon (LCH) *sensu* Bůžek et al. (1992), see Fig. 1] (see also supplementary material in Appendix 2). The collection from the Břešťany locality consists entirely of the specimens found in Břešťany clayes stratigraphically identical with LCH of the Bílina mine. Both localities are situated in the Most Basin and belong to the Most Formation of Early Miocene age. The sedimentation of Most Formation represents coal-bearing basin fill that can be divided into four basic units: Duchcov ("Underlying"), Holešice ("Main Seam"), Libkovice ("Overlying") and Lom ("Lom Seam") members *sensu* Domácí (1977). The deposits of CSH and DSH consisting of sandy–clayey delta bodies and overlying the main lignite seam are included into the Holešice Member, the LCH deposits are situated at the lowest part of Libkovice Member. Accurate setting of geological age and stratigraphical extend of individual units is unavailable due to the lack of volcanic rocks allowing radioisotope dating. Nevertheless, the rocks underlying the main coal seam of Holešice Member were dated to mammal zone MN3 of Early Burdigalian (~Early Eggenburgian) age—see Fejfar (1989), Fejfar and Kvaček (1993). The Libkovice Member of the Most Basin has been dated by palaeomagnetic study (Bucha et al., 1987). For the lower part of this member, comprising the Břešťany clayes the age of 20 Ma was given. According to the different floral assemblages occurring in specific sedimentary environments, all three horizons represent distinct ecosystems: 1) swamp forest, 2) riparian–levee forest and 3) upland lakeshore forest (Bůžek et al., 1987; Boulter et al., 1993; Kvaček et al., 2004). However, various types of the forest vegetation give only approximate palaeoclimatic data and the ratio of deciduous *vs.* evergreen woody elements does not indicate very precisely the variation of the palaeoclimatic conditions. The palaeoclimatic estimation using CLAMP method was made only for the Břešťany flora and the following values were obtained (Teodoridis and Kvaček, 2006): Mean Annual Temperature (MAT) 15.9 ± 1.2 °C; mean temperature of the warmest month (WMMT) 25 ± 1.6 °C; mean temperature of the coldest month (CMMT) 7 ± 1.9 °C. The age and geological and palaeoclimatic setting of the Most Basin (in preceding literature so-called North Bohemian Brown Coal Basin) has been also briefly summarized by Kvaček (1998) and Prokop et al. (2010).

More than 4300 specimens of plant compression fossils have been examined, most of which are leaves of woody dicotyledonous plants (Table 1). Water plants and gymnosperms were excluded from the statistical analysis due to their rarity of affliction. The resulting 3509 specimens were examined for the presence of insect damage, which was determined to damage types according to Labandeira et al. (2007; and subsequent edition in prep.). Furthermore, the fossils

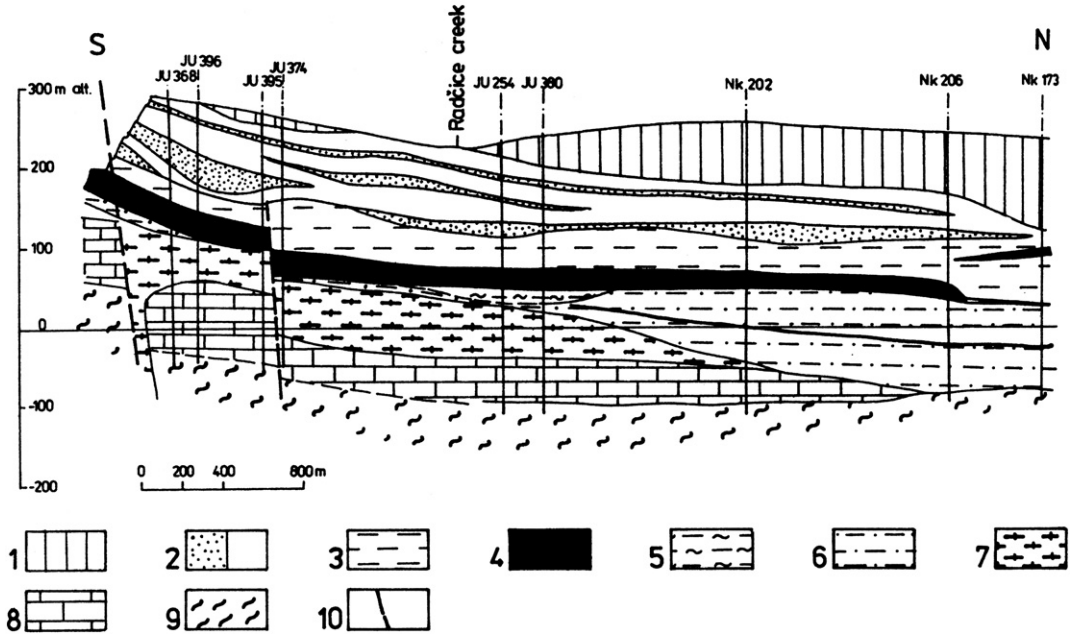

Fig. 1. Geological section of the Bílina Mine. (1) Lake Clayey Horizon; (2) Delta Sandy Horizon (sand, clay); (3) Clayey Superseam Horizon; (4) Coal Seam; (5) coaly clay; (6) Lower Sandy–clayey Member; (7) Neovolcanites; (8) Upper Cretaceous; (9) crystalline basement; (10) fault (adopted from Bůžek et al., 1992).