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Research paper

Galls and gall makers on plant leaves from the lower Miocene (Burdigalian) of the Czech Republic: Systematic and palaeoecological implications

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ABSTRACT

A detailed study of more than 4000 plant macrofossils from the lower Miocene of the Most Basin (localities Bílina Mine and Břešťany) in northern Bohemia has been made in order to implement quantitative and taxonomic analyses of gall occurrences. Fourteen distinct arthropods were identified as possible causers of fossil galls. Similarities in the form, size and position on the host-plant leaves allowed identifications at least to the generic level and to discuss their relationships to extant gall-inducing species that cause morphologically similar galls on related host-plant species. The fossil galls were induced by members belonging to the following insect and mite families: Psyllidae (Hemiptera), Cecidomyiidae (Diptera), Cynipidae (Hymenoptera) and Eriophyidae (Acari). Galls on *Taxodium* induced by gall midges of the genus *Taxodiomyia* (Diptera: Cecidomyiidae) are recorded for the first time. All here described galls are the first records of fossil galls from the Neogene of the Central Europe and complement the view plant–insect interactions during the lower Miocene. The Bílina Mine collection comprises material from several fossiliferous layers representing also different ecosystem types. The presence of elevated gall frequency in the Lake Clayey Horizon (LCH) accompanied by the lower diversity of the other damage types implies colder and drier habitat with unevenly distributed rainfall in comparison with Delta Sandy Horizon (DSH).

1. Introduction

Galls are remarkable structures, which may occur on roots, stems, leaves, flower buds and flowers and on fruits of various plants. Most are cause by parasitic insects, but the formation of galls can also be induced by viruses, bacteria, fungi, nematodes, and mites (Price et al., 1987; Stone and Schönrogge, 2003). The ability of organisms to induce galls on plants has evolved independently many times during the evolution of insects as well as of other groups, with over 13,000 described species with this habit (e.g., Shorthouse and Rohfritsch, 1992; Williams, 1994; Crespi et al., 1997; Raman et al., 2005a). Galls are believed to provide the inducer with enhanced nutrition, a favorable microclimate and, in some cases, protection from natural enemies (Stone and Schönrogge, 2003). Insect galls are thus an extended phenotype of their inducers — with the gall exposed to selection pressures related to predation and host resistance (Dawkins, 1982; Stone and Schönrogge, 2003). About 80% of the insect galls are found on leaves, but the first documented occurrence in the fossil record is on plant stems (Labandeira, 1998).

Nearly three thousand extant gall-causing and associated organisms are known from Central and Northern Europe (Buhr, 1964–1965). They belong to various groups of organisms: about one third to bacteria and fungi, two-thirds to animals. Three groups of animals are the species richest causers of galls on various plants: (i) the gall midges (Cecidomyiidae, Diptera) with about 600 species; (ii) eriophyid mites (Eriophyoidea, Acarina) with about 350 species and (iii) aphids (Aphidoidea, Hemiptera) with about 370 species. Since that time many new species of gall-causing organisms have been discovered and described and the number of these organisms is at present much higher. Due to prevailing subtropical climatic conditions in Neogene of Central Europe it can be supposed that there was higher insect diversity including probably some other gall inducing taxa like thrips (Thysanoptera).

In this paper we describe the induced fossil plant galls from the lower Miocene of the Most Basin in the northern Bohemia and implement a quantitative and taxonomic analysis of gall occurrences. These galls are two- or three-dimensional impressions, preserved as remains or traces found on various plant organs, most frequently on leaves. On the basis of the gall similarities in the form, size and their position on the leaves of the fossil host plants it was possible to identify their taxonomical group to at least generic level and to ascribe their relationships to gall-inducing species that currently cause morphologically similar galls on related host plant species. It is likely that some causers of Neogene galls are tightly related to their recent relatives, since the

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insect fauna of that time, shows close similarity with the recent one (Grimaldi and Engel, 2005).

2. Overview on the history of fossil leaves with galls

The study of galls has a long history. The famous Italian physician and researcher Marcello Malpighi, the founder of microscopic anatomy, is considered to be also the founder of cecidology. Malpighi (1675) published the comprehensive work "Anatome Plantarum", in which he included the chapter called "De Gallis" (in English: About galls). The literature on galls is very extensive. For summaries of our knowledge on galls we refer to: Houard (1908–1909, 1922–1923), Felt (1940), Mani (1964, 2000), Buhr (1964–1965), Ananthakrishnan (1984), Shorthouse and Rohfritsch (1992), Yukawa and Masuda (1996), Redfern et al. (2002), Raman et al. (2005a,b), Ozaki et al. (2006).

There is not too much data on fossil galls induced by various organisms on organs host plants. Nevertheless, galling associations have a long evolutionary history reaching back to the late Palaeozoic. Gall-inducing insects were already present during the Pennsylvanian, ~300 million years ago (Labandeira and Phillips, 1996), but galling types became more common and diverse with the initial adaptive angiosperm radiation at the beginning of Late Cretaceous (Scott et al., 1994; Labandeira, 2006; Krassilov, 2008). Larew (1992) included 63 findings in his summary of fossil galls. One of the richest collections of fossil galls, including 34 impressions, was described by Straus (1977) from the upper Pliocene of Willershausen in the Harz Mountains, Germany. He ascribed them to seven groups of organisms: Fungi (2 impressions), Eriophyidae (12), Eriosomatidae (1), Aphidae (1), Adelgidae (1), Cecidomyiidae (6) and Cynipidae (3). More specimens were reported by Titchener (1999), who studied on all types of plant–insect interactions from this locality. Scott et al. (1994) examined more than 14,000 leaves of angiosperms from Cretaceous, Paleogene and Neogene localities. They described 25 types of galls on leaves of various angiosperms together with rough identifications of the gall-causers and in some cases establishing their recent relatives, particularly of families such as Cecidomyiidae, Cynipidae, Psyllidae and Eriophyidae.

Apart from angiosperms, insect-induced galls have also been described from organs of various gymnosperms. For instance, Möhn (1960) discovered the fossil gall midge species *Sequoiomyia kraeuseli* Möhn, 1960 in the seeds of *Sequoia langsdorfii* (Brongniart) Heer, 1868 (Taxodiaceae) from the Miocene of the Rhineland (Germany) and described larvae and pupae of this gall midge. This is one of the rare cases, where the causer of fossil gall is known. Galls are rather common on broad-leaved angiosperms plants, since this group is much more diverse than gymnosperms.

In the Miocene of Spain Villalta (1957) found fossil galls on leaves of *Quercus drymeja* Unger, 1845 and ascribed them to two species of eriophyid mites. He described fossil galls on leaf of *Fagus castaneaefolia* Unger, 1845 as the species *Mikiola pontiensis* Villalta, 1957. However, these galls were probably caused by another recent gall midge species — *Phegomyia fagicola* Kieffer, 1913 (Skuhravá, 2006). Straus (1977) assumed that impressions on *Betula* L., 1753 leaves were caused by *Contarinia carpini* Kieffer, 1897. The galls on *Betula* leaves were caused by another species because *Contarinia carpini* is specifically associated with *Carpinus* L., 1753.

Diéguez et al. (1996) identified thirteen types of fossil galls on leaves of eleven host plants, belonging to five plant families from the upper Miocene of La Cerdaña in northern Spain. Six of these fossil galls were considered to have been induced by Eriophyidae (Acari), three by Cecidomyiidae (Diptera) and two by Cynipidae (Hymenoptera). Waggoner and Poteet (1996) described unusual elongated galls on the leaf of *Quercus hannibali* Dorf, 1936 from the Miocene of North America, which were attributed to perpetrators of the family Cynipidae (Hymenoptera). In last few years, impressive records have been reported from the Neogene of North America. There are two leaves of *Quercus simulata* Knowlton, 1898 known from the middle Miocene of Oregon (USA), each with another type of gall, belonging to *Antronoides cyanomontana* Erwin et Schick 2007 and *A. oregonensis* Erwin et Schick, 2007 (Erwin and Schick, 2007).

Studies of fossil insect galls are tightly interconnected with other research of plant–insect associations, which advanced very rapidly in recent years. Current approaches involve many aspects and are based on different case studies, which greatly contribute to our knowledge of ancient environments (Wappler, 2010; Wappler et al., 2012). The palaeoecological, palaeoclimatological and the palaeogeographical implications are of the great importance (Wilf and Labandeira, 1999; Wilf et al., 2005, 2006; Wappler et al., 2009; Currano et al., 2010; Paik et al., 2012). Some of these studies emphasise the long-term evolutionary coexistence of the plant host and arthropod gallers (Erwin and Schick, 2007; Wappler et al., 2010) and miners (Opler, 1982; Winkler et al., 2010).

3. Material and methods

The material studied belongs to the collections of the Bílina Mine enterprise and the National Museum in Prague, comprising almost 4300 specimens of various plant fossils of early Miocene age, collected during the past few decades. We have also examined historical material from the Břešťany Clay, which is housed in the collections of the National Museum in Prague, and in the collection of the Senckenberg Museum for Mineralogy and Geology in Dresden, Germany. Both localities are situated in the Most Basin and belong among the well known Lagerstätten in Central Europe. The overlaying coal seam horizons offer unique state of preservation of fauna and flora together with opportunity to study changes of their assemblages in a short time period of development (e.g., Kvaček et al., 2004). Insect fossils are also well known counting almost 350 specimens within 11 orders (Prokop, 2003). Several species are well linked to other Neogene localities (e.g., Prokop and Nel, 2000; Fikáček et al., 2008). Individual plant tissues and organs are often found together allowing so called "Whole-plant" reconstructions (Kvaček, 2008). Exceptionally preserved parts of the plants, especially leaves, seeds, fruits and even wood, provide also very important information on prevailing climatic conditions at that time (Kvaček, 1998, 2000; Sakala, 2007).

Our research focused on an assemblage of 3509 fossil dicotyledonous leaves and 133 *Taxodium* branchlets. Twenty-three fossiliferous horizons overlying the coal seam of the Bílina Mine, together with the corresponding layers of the Břešťany Clay, are grouped into three main sedimentary environments [Clayey Superseam Horizon (CSH), Delta Sandy Horizon (DSH) and Lake Clayey Horizon (LCH) sensu Bůžek et al. (1992), Fig. 1]. These horizons contain floral assemblages of rather distinct composition and thus probably represent different ecosystems reflecting rapid palaeoenvironmental changes (Kvaček, 1998; Kvaček et al., 2004). The sediments of the Most Formation represent a coal-bearing basin fill that can be divided into four basic units: the Duchcov ("Underlying"), the Holešice ("Main Seam"), the Libkovice ("Overlying") and the Lom ("Lom Seam") members sensu Domácí (1977). The deposits of the CSH and the DSH consisting of sandy–clayey delta bodies and overlying the main lignite seam are included in the Holešice Member; the LCH deposits form the basis of the Libkovice Member. The rocks underlying the main coal seam of the Holešice Member were assigned to mammal zone MN3a, early Burdigalian (~early Eggenburgian) (Fejfar, 1989; Fejfar and Kvaček, 1993). The Libkovice Member of the Most Basin was dated by palaeomagnetically (Bucha et al., 1987); for the lower part of this member, comprising the Břešťany clays an age of 20 Ma was inferred. According to the different floral assemblages occurring in specific sedimentary environments, all three horizons represent distinct ecosystems: 1) a swamp forest, 2) a riparian–levee forest and 3) an upland lakeshore forest (Bůžek et al., 1987; Boulter et al., 1993; Sakala, 2000; Kvaček et al., 2004). However, the various types of the forest vegetation give only approximate palaeoclimatic data and the ratio of deciduous vs. evergreen woody elements do not precisely indicate the variation of the palaeoclimatic conditions. The age and geological and palaeoclimatic setting of the Most Basin (in older literature often called North Bohemian