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Biodamage on *Phylladoderma* Leaves from the Upper Permian of the Pechora Basin

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Abstract—A new insect damage type on leaves *Phylladoderma arberi* Zalessky, 1913 from the Upper Permian of the Pechora Basin (Adz'va River, Russia) is described. These are punctures about 120 μm in diameter surrounded by circular spots with a dark rim. We suppose that these feeding traces were made by palaeodictyopteroid nymphs.

Keywords: biodamage, *Phylladoderma* leaves, Upper Permian, Pechora Basin

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INTRODUCTION

Traces of feeding on plant juices associated with punctures of the leaf cuticle are much rarer in the fossil record compared to the other damage types, such as marginal and window chewing marks (traces of feeding on the leaf tissues), galls, and perforations on fruits and seeds. First of all, this is due to microscopic size of such traces and the difficulty of identifying them, which is often possible only in the cuticle preparations. In some cases, when punctures of the epidermis are complicated by additional pathological manifestations, these latter may draw attention, greatly simplifying identification of the punctures. So, Neuburg (1960) when describing the leaf morphology of *Phylladoderma* noted "round or elongated-oval spots, tubercles and depressions, sometimes apparently transformed into the through-holes of undoubtedly pathological origin" occurring on the surface of impressions. After making the cuticle preparation it became apparent that many of these spots and tubercles are confined to the microscopic punctures of the epidermis having constant shape and size.

The genus *Phylladoderma* was described by Zalessky (1913) based on leaves from the Permian of Adz'va River. For a long time it was known only from the Kazanian and Tatarian of the Pechora Basin. Meyen found this genus in the Kazanian and Tatarian of the Russian Platform and assigned it to Cardiolepidaceae (Meyen and Gomankov, 1971; Meyen, 1977). *Phylladoderma* was used for stratigraphy on the Russian Platform (Esaulova, 1998) and in the Pechora Basin (Pukhonto, 1998). Phylladodermas are also described from the Permian of Primorye and Kazakhstan and the Ufimian, Vyaznikovian, and Nedubrovian strata of the Russian Platform (Bogov, 1985; Krassilov et al., 1999; Karasev, 2009). Thus, distribution of *Phylladoderma* is restricted to the Permian of Eurasia.

MATERIAL AND METHODS

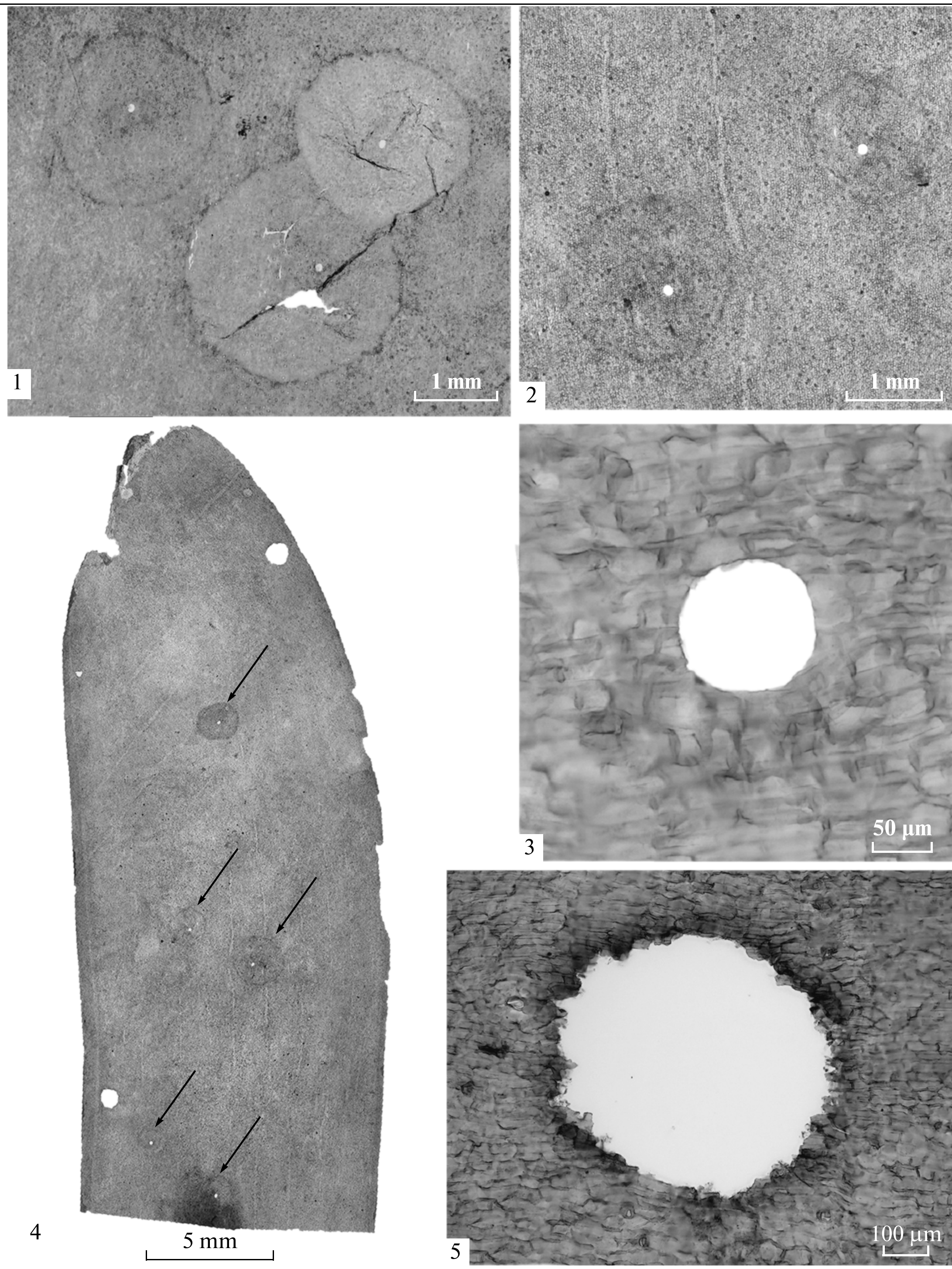
The material originates from outcrop 29-A (Chernov, 1932) of Phylladoderma Beds in the upper part of the Talbei Formation (Pechora Group) that is exposed on the right bank in the middle reaches of the Adz'va River. The material was collected by M.S. Ignatov, I.A. Ignatiev, and Y.V. Mosseichik in 2011. The fossils are well-preserved phytoleims of whole leaves.

Phytoleims of leaves were macerated by the standard procedure by successive placing first in nitric acid, followed by potassium hydroxide solution. The obtained preparations were studied using light microscope Zeiss Axioplan 2. The collection no. 5483 is deposited in the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN).

STRUCTURE OF TRACES

The feeding traces on *Phylladoderma* leaves are regular round perforations about 120 μm in diameter. They have smooth edges without any thickening or necrotic manifestations at perimeter. In the cuticle preparation a slight change in the cell arrangement at the edge of the puncture is only in places noticeable (Pl. 12, fig. 3). The perforations (punctures) are located in the central part of round spots about 1.5–3.0 mm in diameter (strictly central or slightly offset, but not at the edge of the spot; Pl. 12, figs. 1, 2). The spots differ in color from the surrounding intact areas of the leaf surface (Pl. 12, figs. 1, 2), but are clearly visible only when studying the cuticle preparation in transmitted light. Each spot is traced on both sides of the leaf blade, but the holes are present on only one side. We interpret this as the lower side, since there are clearly visible traces of the veins. The feeding traces are located rather chaotically, but tend towards the central part of lamina, while the punctures are distant

Plate 12



Explanation of Plate 12

Feeding traces on the leaf *Phylladoderma arberi arberi* Zalessky, emend. Neuburg, 1960, specimen PIN, no. 5483/2. Phylladoderma Beds, upper part of Talbei Formation, Severodvinian–Vyatkian, Permian, Pechora Basin.
Figs. 1 and 2. General view of the punctures and their surrounding pathological spots.
Fig. 3. Structure of a puncture.
Fig. 4. Distribution of the feeding traces (marked with arrows) on a fragment of the leaf blade.
Fig. 5. A lysogenic hole unrelated to the feeding traces on leaves.

from the vein traces (Pl. 12, fig. 4). Sometimes they are grouped in 2–3 and in some cases, closely spaced spots partially overlap each other so that the rim of one of the spots in the spot overlap disappears (Pl. 12, fig. 1). The "tubercles and depressions" as well as "through-holes" that were noted by Neuburg may be associated with destruction of the leaf parenchyma during formation of the spots. Thin walls of the epidermis (similar to insect mines) will eventually become brittle and may partially or completely collapse, as deformed cuticle on the lower of the three spots (Pl. 12, fig. 1).

It should be noted that along with punctures on the surface of *Phylladoderma* leaves occur "lysogenic holes that can be regarded as secretory organs that are so common in gymnosperms, including Ginkgoales" (Neuburg, 1960). These holes (Pl. 12, fig. 5) have uneven edge with necrotic manifestations at perimeter and several times larger sizes that allows reliably distinguish them from the punctures.

DISCUSSION

Structural features of the punctures (smooth edge and geometrically regular shape) indicate that these traces were left by insects that fed on plant juices. In the Pechora Basin insects are known mainly from the Lek-Vorkuta and Inta Formations that occur stratigraphically much lower than the Talbei Formation. The Pechora Group comprises the Upper Ufimian, Kazanian, and Tatarian strata, the Phylladoderma Beds containing a plant assemblage characteristic of the Upper Tatarian (Pukhonto, 1998), i.e., the Upper Permian (Severodvinian and Vyatkian) in the now-accepted tripartite division of the Permian (Kotlyar, 2006). Only few insects were found in the Pechora Group, so for reconstructing insect-plant trophic associations we can use the richest Severodvinian entomofauna of the Isady locality, Sukhona River. This fauna includes no less than 25 orders and 69 families (Aristov et al., 2013) and possibly reflects the actual insect diversity in the Late Permian ecosystems most completely.

In the Permian, Mesozoic and Cenozoic piercing-and-sucking insect phytophages are represented with the orders Thysanoptera (thrips) and Hemiptera (diverse homopterans including Psyllomorpha and Auchenorrhyncha, and also true bugs unknown before the Triassic), and in the Permian and Carboniferous also with the superorder Palaeodictyopteroidea.

According to the puncture size (about 120 μm in diameter) they were made by rather large insects, so one may exclude thysanopterans. Many homopterans produce around the stylet bundle (mandibles and maxillae) inserted into plant tissue so-called salivary sheath, tubular formation of hardened salivary secretions, which marks the puncture site and is sometimes preserved in the fossil state (Krassilov et al., 2004). There are no traces of salivary sheaths in our material, but even if they were not preserved in the cuticle preparations, the stylet bundle diameter still could not be less than 80–100 μm. Among modern homopterans so thick stylets are found in Auchenorrhyncha no less than 15–20 mm in length. Homoptera, first of all Auchenorrhyncha, constitute one of numerically dominating groups in the Middle and Late Permian entomofaunas (Shcherbakov, 2008). In the Isady fauna are fairly common large hoppers of the Permian family Pereboriidae, which is known also from rare finds in the Pechora Basin, including the Pechora Group.

Most groups of modern Homoptera feed on phloem sap, and some groups (singing cicadas, spittlebugs, and some Cicadellidae) on xylem sap. Contained in these juices excess water (and sugars in the phloem) is shunted through the contact of remote areas of the intestine, the filter chamber that evolved in the ancestors of all Homoptera (Emeljanov, 1987). Feeding on vascular bundle does not cause death of plant tissues around the puncture. Feeding on phloem and plant reproductive organs is considered initial for Hemiptera (Shcherbakov, 2000). Among Homoptera only one Cenozoic subfamily of Cicadellidae (Typhlocybinae) passed to feeding on the content of mesophyll cells; these leafhoppers are particularly small and cause appearance on the leaves of irregularly shaped spots without clear boundaries; their filter chamber is secondarily simplified.

Unlike feeding traces of the modern Hemiptera, the punctures on *Phylladoderma* leaves having comparatively large diameter are remote from the leaf veins and surrounded by circular spots with a rim. Perhaps spots around the punctures were not formed during the prolonged feeding of insects in one place, and caused by subsequently developed phytopathogens. But even in this case, lack of association between the punctures of considerable diameter and vascular bundles of the plant casts doubt on the attribution of these feeding traces to Homoptera. Pereboriidae belong to the primitive Cicadomorpha, and there is no reason to assume for them a feeding mechanism largely different from modern Homoptera. Can these punctures belong to Palaeodictyopteroidea?

Many Palaeodictyoptera were very large; punctures made by them on the seeds of Paleozoic plants are 0.5–1.1 mm in diameter, corresponding to the thickness of their stylet bundle (Sharov, 1973). It was assumed that most Palaeodictyopteroidea were adapted to feeding on seeds (Zherikhin, 2002), but at least some of them fed on vegetative organs: punctures 0.45 mm in diameter are described in the Carboniferous fern rachis, reaching phloem and xylem and surrounded by salivary sheath (Labandeira and Phillips, 1996). Small palaeodictyopteroids are known as well, especially in the Permian. Nymphs of this group had flattened body and sucking proboscis and probably led rather sedentary life on their food plants. The described punctures may well belong to small and/or young palaeodictyopteroid nymphs that fed on mesophyll of fleshy leaves of phylladodermas.

In the Middle and especially Late Permian palaeodictyopteroids have become extremely rare and locally distributed, although in some refugia with favorable climate they apparently survived until the end of the Permian and went extinct by the beginning of the Triassic (Shcherbakov, 2008, 2011). Could they survive until the Late Permian in the Pechora basin as well? Yes, because it is there in the Vorkuta Group (late Early Permian) they were more numerous (8–19% of the total insect specimens; Rasnitsyn et al., 2005) than anywhere else in the Permian, which could be due to the paleoclimate more mild than in the neighboring regions of the Russian Platform (Shcherbakov, 2008).

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