ISSN 0031-0301, Paleontological Journal, 2016, Vol. 50, No. 2, pp. 202–208. © Pleiades Publishing, Ltd., 2016.
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Phytopathology in Fossil Plants: New Data, Questions of Classification

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Received October 7, 2015

Abstract—Examples of damages in fossil plants revealed using electron microscopy are considered. The formal classification of these damages is discussed.

Keywords: fossil plants, phytopathology, classification

DOI: 10.1134/S0031030116020040

INTRODUCTION

In gaining insight into the laws of ecosystem functioning in the geological past, an essential role is played by the study of probable interaction of plants and some groups of animals, fungi, and microorganisms. In particular, such relationships can be revealed based on the presence of the damages of different plant organs. Most of presently available data on damages on fossil plants caused by different agents are leaf damages (mines, galls, feeding traces) visible to the unaided eye (Opler, 1973; Straus, 1977; Labandeira et al., 2002a, 2002b, 2007; Krassilov et al., 2008; Wappler et al., 2009; Donovan et al., 2014; etc.). The data on damages on other organs (reproductive structures, wood, roots) are considerably less abundant (e.g., Stone et al., 2008; Labandeira, 2013; Maslova et al., 2014; Klymiuk et al., 2015).

To date, ichnological studies have reached great success. Although new materials are still very actively described, researchers turn from the initial task of accumulation of isolated facts of interaction between plants and basically arthropods to the analysis of available materials with reference to the taxonomic, coevolutionary, paleogeographical, paleoclimatic, and other aspects.

Effectiveness of these studies depends on the extent of readiness of available data to this analysis. A large part of descriptions of pathological conditions of fossil plants were casual, restricted to brief notes on the presence of certain type of damages connected with a particular agent causing it (most frequently insects). In addition, until recently, the main purpose of the study of biodamages on plants has been revelation of organisms that caused them. Fossil galls, mines, and some feeding traces (e.g., bites) were frequently described as species and genera within the framework of natural taxa of presumable herbivorous insects (see, e.g., Kozlov, 1988). This practice may be justified in some cases for Cenozoic biodamages, although it is hardly applicable to earlier objects. Even presuming the validity of interpretation and assignment of damage to a certain herbivorous taxon, this will give only some expansion of the paleontological characteristics of deposits. At the same time, consideration of damages of a particular type in the historical aspect as independent objects can provide a more interesting result.

The use of isolated and diverse data for wider analysis is difficult; therefore, the classification of fossil phytopathological conditions is brought to the forefront.

The biotic events at the Cretaceous–Paleogene boundary are of particular interest for researchers. While floras from the Cretaceous–Paleogene boundary beds of North America are rather thoroughly investigated in relation to phytopathology, where traces of interactions between plants and other groups of organisms (insects, mites, fungi, and microorganisms) have been recorded (Labandeira et al., 2002a, 2002b, 2007; Ellis et al., 2003; Wilf et al., 2007; Donovan et al., 2014; etc.), similar data on these floras in Asia are rather scarce and poor. We are intended to collect and analyze such facts for Asian Cretaceous–Paleogene floras; this is undoubtedly important for gaining an insight into the coevolution of organisms and restoration of the biota at this boundary.

DAMAGES ON FOSSIL PLANTS REVEALED USING SCANNING ELECTRON MICROSCOPY

Most of the presently known damages caused by various agents on fossil plants are visible to the unaided

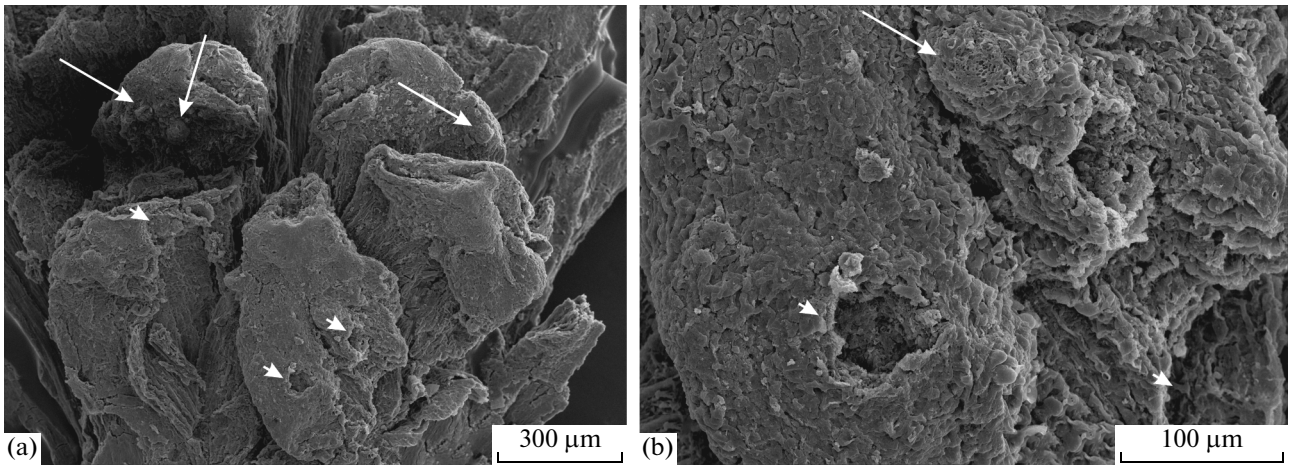

Fig. 1. Damages on infructescences of *Friisicarpus sarbaensis* N. Maslova et Tekleva, specimen PIN, no. 417/10; western Kazakhstan, Sarbai locality; Cenomanian–Turonian; SEM: (a) fruit of five carpels; round galls (long arrows) and holes left as they dropped off (short arrows) are seen; (b) gall (long arrow) and hole seen as a gall has been lost (short arrows).

eye. Some fine details were revealed using a light microscopy. During the study of anatomical features of fossil leaves and reproductive structures using a scanning electron microscope (SEM), we recognized previously unknown types of damages, which have not been recorded earlier without adequate technical equipment because of microscopic size. Several examples of this kind are provided below.

1. Damages on infructescences of *Friisicarpus sarbaensis* N. Maslova et Tekleva (Platanaceae, Cenomanian–Turonian, western Kazakhstan, presently under study). The structure of preserved capitate infructescences of *F. sarbaensis* are described from Cenomanian–Turonian gray clays of the Sarbai quarry near the town of Rudnyi, western Kazakhstan (Maslova and Tekleva, 2012). Along with normally developed fruits, the heads contained fruits with damaged carpels (Fig. 1). The damages are basically accumulated on the apical parts of carpels, but they also occur on their walls. The character of damages in the shape of tissues expansion, which are subsequently torn away by the plant with the formation of round pits, suggests that they are gall-like structures. The presence on the damaged carpels of clusters of microorganisms is probably evidence that they participate in the development of galls. It is not improbable that insects contribute to the invasion of microorganisms, playing a role of carriers of bacteria and, thus, promoting infection of fruit. The secretion produced by trichomes of carpels probably attracted insects.

2. Damages on shoots of *Mesocyparis* McIver et Basinger (Cupressaceae, Paleogene, central Kazakhstan, presently under study). Using SEM, we recognized microscopic damages about 100 mm in size on leaves of the genus *Mesocyparis* from the Paleogene Nizhnii Ashut locality, central Kazakhstan (Fig. 2a). The damages are expansion of tissues forming round plaques with a star-shaped break in the epidermis on the leaf surface (Fig. 2b). In morphological characters, these damages can be regarded as galls; however, very small size of these structures makes them invisible to the naked eye. Microorganisms as well as abundant fungal hyphae and spores were revealed on shoots of *Mesocyparis*, suggesting that they are involved in the formation of galls. As in the case of galls on infructescences of *Friisicarpus*, insects may participate in the transportation of gall-forming organisms.

3. Damages on infructescences of *Kunduricarpus* Kodrul, N. Maslova, Tekleva et Golovneva (Platanaceae, Campanian, Amur Region). A unique damage type of platanoid infructescences of the genus *Kunduricarpus* from the Campanian Kundur locality in the Amur Region has been described previously (Maslova et al., 2014). The influence of microorganisms on carpels is evidenced by the traces of penetration of microorganisms into carpel walls (Fig. 3a), three-dimensional structures (isolated and in chains) rounded in section, which fill the inner space of the carpel (Fig. 3b), and impressions of these structures on the inner surface of the carpel wall cuticle (Fig. 3c).

Carpel walls were probably damaged by bacteriomorphic microorganisms even during the plant's life.

4. Damages on fruit of *Porosia* Hickey (Rutaceae, Paleocene, Amur Region, presently under study). The reproductive structures of *Porosia,* represented by schizocarpic fruits, were described previously (Manchester and Kodrul, 2014) from a number of localities in North America and Asia. On fruits of *Porosia* from the Tsagayan Formation (Belaya Gora locality at the lower reaches of the Bureya River), we recognized a complex of microstructures, which penetrated there during the plant's life or fossilization.

The SEM study of preparations of the cuticle covering the fruit locules of *Porosia* has revealed round structures located chaotically in groups or singularly and varying in size from 5 to 15 mm (Fig. 4a). The nature of

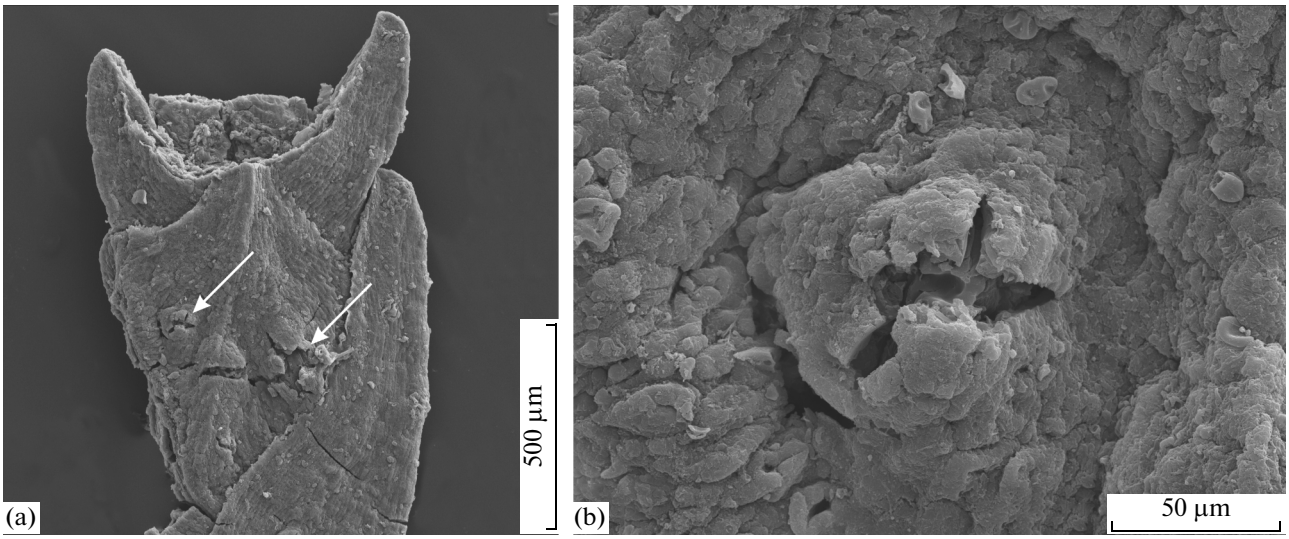

Fig. 2. Damages on shoots of *Mesocyparis* McIver et Basinger, specimen BIN, no. 1585-34; central Kazakhstan, Nizhnii Ashut locality; Paleogene; SEM: (a) damaged shoot fragment, galls are marked by arrows; (b) gall.

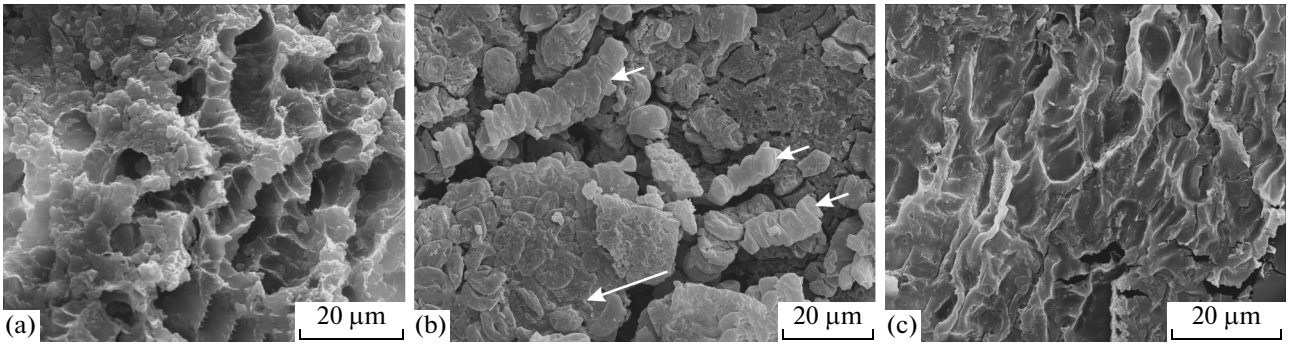

Fig. 3. Damages on infructescences of *Kunduricarpus* Kodrul, N. Maslova, Tekleva et Golovneva, specimen GIN, no. 4867-K16/6-61; Amur Region, Kundur locality; Campanian; SEM: (a) carpel wall after maceration, traces of penetration of microorganisms; (b) microorganisms in chains (short arrows) and single cluster (long arrow); (c) carpel wall cuticle after maceration, with impressions of microorganisms, inner view.

these structures remains uncertain, but their dimensional characteristics and spherical shape suggest that they likely have bacteriomorphic organization.

The study of preparations of exocarp cuticles with the aid of SEM has shown the presence of predominantly round microstructures with a spinate surface on both outer and inner sides of the cuticle (Fig. 4b). These spinate structures are probably of fungal origin. As the microstructures are disrupted, the cuticle surface remains pits with impressions of spines (Fig. 4b); consequently, the fungal invasion occurred during the plant's life or after falling into a pond, where they underwent fossilization.

On the surface and inside fruit of *Porosia*, one more type of the structures were recorded; these are apparently fruit bodies of putrefactive microscopic fungi. They vary in size from 10 to 30 μm and shaped as round or flattened structures with a pedicle and porous surface (Fig. 4c).

5. Damages on leaves of *Platimeliphyllum valentinii* Kodrul et N. Maslova (Angiospermae, Paleocene, Amur Region, presently under study). Leaves of *P. valentinii* have been described from the Tsagayan Formation of the Arkhara–Boguchan brown coal field in the Amur Region (Kodrul and Maslova, 2007). The material is impressions of leaves with phytoleim fragments. The epidermal structure of these leaves was studied in preparations of the cuticle and incrustations. The incrustations, which are thin mineral films formed around vegetative remains during fossilization (Krassilov and Makulbekov, 1996), are preserved on the impression surface and its counterpart after removal of coaly phytoleim. The fine preservation of the material enables the topography of epidermal structures to be

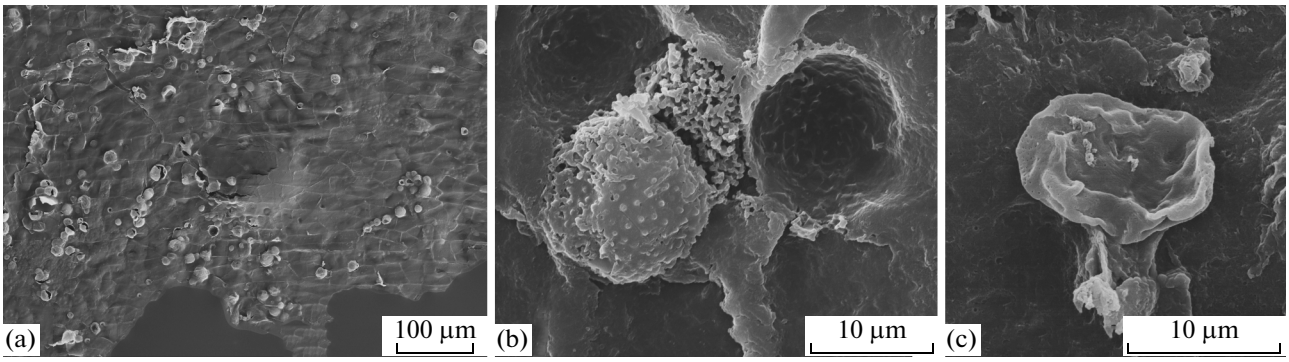

Fig. 4. Damages on fruit of *Porosia* Hickey, specimen GIN, no. 4867-BG-2269; Amur Region, Belaya Gora locality; Paleocene; SEM: (a) fruit locule cuticle; round bacteriomorphic microstructures arranged in groups and singularly are visible; (b) exocarp cuticle; round microstructures disintegrated to varying extent, with spinate surface and also their impressions on the cuticle, showing traces of thorns in the shape of pits are visible; (c) fungal fruit body on the *Porosia* fruit surface, with porous surface.

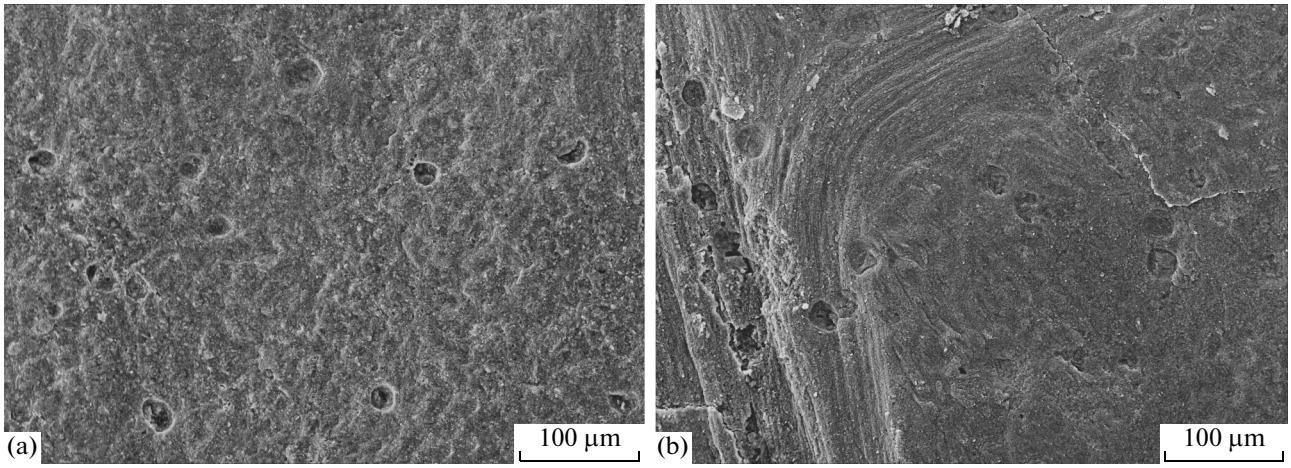

Fig. 5. Damages on leaves of *Platimeliphyllum valentinii* Kodrul et N. Maslova, specimen GIN, no. 4867-AB1-109; Amur Region, Arkhara–Boguchan brown coal field; Paleocene; SEM: (a) incrustation of the upper leaf surface, damages of leaf surface in the shape of small holes; (b) incrustation of the lower leaf surface, damage on the vein and in the intercostal leaf zone.

recognized. Apart from the proper epidermal features, impressions of both leaf sides display microscopic damages, which are only recognized using SEM (Figs. 5a, 5b). These damages are round holes from 15 to 30 mm in diameter, which are probably sometimes confined to the area of stomata or trichome bases. At present, it is difficult to treat this damage type. They do not look as typical traces of plant–arthropod interactions or lifetime damages of fungal or bacterial nature; however, it is evident that they are damages. As frequently occurs in such cases, repeated finds and new specimens can throw light on their nature.

6. Damages on leaves of *Beringiaphyllum* Manchester, Crane et Golovneva (Cornaceae, Paleocene, Amur Region, presently under study). Leaves of the genus *Beringiaphyllum* from the Tsagayan Formation of the Arkhara–Boguchan brown coal field show visible to the unaided eye damages in the shape of oval or rectangular holes or "windows" located between the secondary veins (Fig. 6a). The holes 6–8 mm long and up to 4 mm wide have a distinct thickened margin. As a specimen with a leaf of *Beringiaphyllum* is examined using SEM in a low vacuum mode without gold spraying, the structures morphologically similar to those visible by the naked eye are recognized. However, these structures are very small, a hole up to 1 mm in diameter, with the rim framing it about 200 μm wide (Fig. 6b). In addition, we have recorded similar structures (with a thickened margin), but even smaller (300 mm in diameter) and without a hole (Fig. 6c). The general morphological characteristics of these damages suggest that all the above structures, both microscopic and visible to the unaided eye, should be regarded as a series showing successive phases of plant response to a pathogen influence.

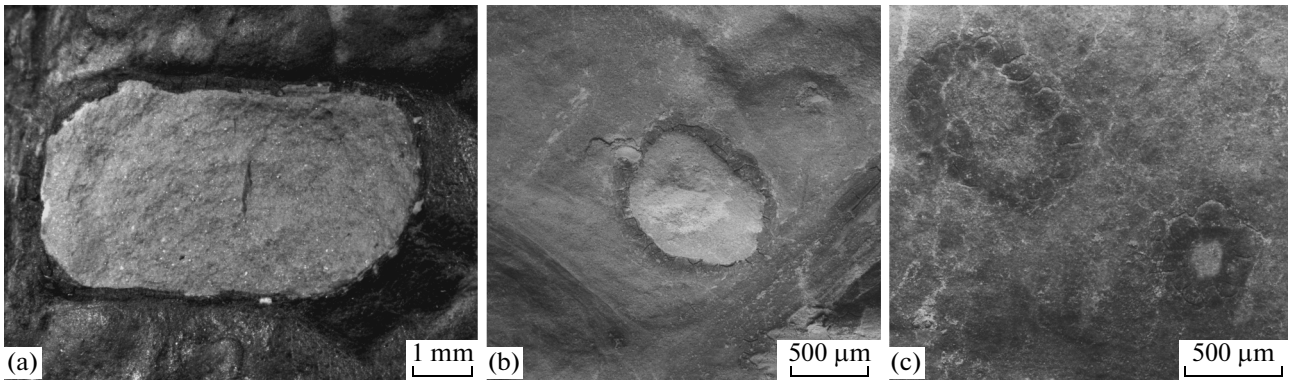

Fig. 6. Damages on leaves of *Beringiaphyllum* Manchester, Crane et Golovneva, specimen GIN, no. 4867-AB1-261; Amur Region, Arkhara–Boguchan brown coal field; Paleocene: (a) hole between two leaf veins bordered by a rim left after the loss of a developed mine; (b) smaller hole, SEM; (c) initial developmental stage of a mine, with leaf tissue preserved inside it.

DISCUSSION

Thus, we provided some examples of new damage types on fossil plants, which were recognized during SEM studies. This discovery poses new questions to researchers: determination of the type of microscopic damage, revelation of probable pathogens, establishment of coevolutionary relationships between plants and other organisms, and classification of damage types.

Gall-like structures that have been recognized on infructescences of *Friisicarpus* and shoots of *Mesocyparis* differ from all known fossil galls of the microscopic size class. Although they vary somewhat in morphology and developmental pattern (the structures on *Friisicarpus* probably drop off with time, leaving round pits in the carpel wall, while the galls on shoots of *Mesocyparis* probably remain in the same place), they share presumable participation in their development of microorganisms, which were found on the surface of plant remains with such damages. The major question arising as microorganisms are recognized on fossil plant remains is whether they are true fossils or introduced living forms acquired during storage or treatment of specimens. In the case of *Friisicarpus* and *Mesocyparis,* we undoubtedly deal with fossil microorganisms. First, microorganisms are found exclusively on the affected organs and absent on healthy ones. In the case of *Friisicarpus,* we examined more than ten capitate infructescences, only two of which are damaged. Structurally preserved shoot fragments of *Mesocyparis,* extracted by dissolution of the rock in acid, are strongly affected by galls and their surface displays microorganisms. Other objects under study (in particular, leaves of *Pinus*) extracted similarly from the same sample lack a trace of microorganisms. Consequently, such a selective "infection" with microorganisms of the shoots of *Mesocyparis* did not occur during treatment or storage. Second, the different preservation of microorganisms suggests that they underwent certain changes during fossilization.

Another important aspect is whether the plants were infected and damaged tissues developed during their life or after death during biodestruction. Unfortunately, we have to agree that, in many cases, it is difficult or impossible to resolve this question unequivocally. However, in some cases, certain characters of lifetime development of damages are seen. For the microorganisms morphologically similar to cyanobacteria, found on the carpels of platanoid infructescences of *Kunduricarpus*, the developmental pattern from the structures arranged in chains to individual, stuck in clusters has been reconstructed. In the previous paper we provided arguments for the lifetime infection of plants caused by microorganisms (Maslova et al., 2014).

Earlier, Krassilov (1976) reported on cell papillae in cuticular preparations of *Porosia*. Studies using the modern optical technique and SEM have shown that this cuticle reflects epidermal cells covering fruit locules (Manchester and Kodrul, 2014). We have revealed that the round structures previously taken for papillae of epidermal cells are located chaotically, frequently in groups and do not belong to the cuticular structures. Based on the size and shape of these structures, we propose that they are probably of bacterial nature.

Thus, we provide reliable evidence that bacteriomorphic structures participated in phytopathological processes in extinct plants. It has become possible to recognize these damages of fossil plant organs due to the use of SEM.

The new types of damages on fossil plants reported here are caused by various agents and require consideration of the systematization of available information and classification of damage types.

The basis of the first universal classification of damages on fossil plants have been elaborated by Vyalov (1975). Subsequently, it was supplemented considerably (Vasilenko, 2005, 2006, 2007, 2008; Aristov et al., 2013). The essence of this classification is as follows: the concept of damage taxa is based exclusively on the external structural features of damages

and new formations on plants. The characters of taxa in such a classification are grouped in a manner providing easy diagnostics in the material varying in preservation. In so doing, the purpose of the study does not include identification of agents harmful for plants; these data, even if they are obtained, do not play an important role in the determination of the position of a particular damage type in the formal classification. Information on a plant with a particular damage type is also diagnostically insignificant (at least at the level of genera and families). Such a classification allows systematization of available data, more correct comparison with the data on various time intervals and various geographical points, and also estimation of their changes during the geological time.

During the past ten years since the modernized Vyalov's system was proposed, colleagues responded to it differently, depending on the type of the objects classified. For example, the principles offered for classification of endophytic ovipositions are widely applied and newly obtaining material is usually described in the previously established formal taxa (Sarzetti et al., 2009; Popa and Zaharia, 2011; Moisan et al., 2012; etc.). At the same time, a similar approach to classification of galls, mines, and bites, with rare exception, has not met with approval. This is evidence of the necessity of further development of classification with a more thorough choice of characters. Successful demonstration of replacement of assemblages of formal biodamage taxa in the geological time and their correlation with the main events in the evolution of individual groups of animals and plants and the biosphere as a whole should become the best proof of correctness of this approach.

A different approach to the systematization of information on fossil plant damages was undertaken by a team of American researchers, who published a handbook intended for identification of damage types (Labandeira et al., 2007). The material of this analysis included Permian, Late Cretaceous, and Early Paleogene floras of North America and also Late Triassic floras of South Africa. The handbook contains brief descriptions of 150 damage types (DT) and their photographs; it allowed addition, which was subsequently performed (in particular, by Donovan et al., 2014; etc.). The size, shape, internal structural features, and position of damages on the organ surface as well as the type and extent of development in response to the damage and the presence of preserved coprolites were taken into account, as the damage type was established. Based on these characters, damages were assigned to the groups: feeding traces in the shape of holes (hole feeding), marginal bites (margin feeding), skeletonization, superficial bites (surface feeding), traces of piercing and sucking agents (piercing-and-sucking), oviposition, mines (mining), galls (galling), bites on seeds (seed predation), fungal damages (fungal), and the group of damages of uncertain nature (incertae sedis). In the catalogue, it is marked that all fossil specimens based on which it was compiled are included in a database containing all necessary information on them. However, this information is not present in the catalogue; thus, to become acquainted with it, one should contact the authors and ask about interesting specimens; certainly, this complicates the analysis of the material.

Such a perfectly illustrated catalogue is undoubtedly useful, it helps to identify particular damages. However, comparisons are frequently complicated, because for the damage types figured in the catalogue, variation of characters in particular types is not taken into account. For example, in the hole feeding group, the types DT01, DT02, and DT04 are only distinguished by dimensional characteristics. If a specimen has holes varying in diameter (a rather frequent case), the description should contain all types, including the entire size range of holes, although size variation of damages is likely caused by the developmental stage of the same type. For example, as follows from our observation of damages on leaves of *Beringiaphyllum* under SEM in a low vacuum mode, the leaf surface has both round or oval holes visible to the naked eye and holes less than 1 mm in diameter and also similar structures of even smaller size (about 300 μm in diameter) and without a hole. The morphological similarity of these damages suggests that they are developmental stages of the same type.

Note that, without taking into account the data provided by the SEM study, the damages on leaves of *Beringiaphyllum* can be assigned to the so-called window feeding, in which the rim framing holes is treated as callosal tissue developing by plant in response to trauma. However, the variation series of conditions of the damages investigated includes structures that retain leaf tissue inside the thickened ring; this excludes interpretation of these damages as hole feeding. We treat this series of damages as various stages of mining from microscopic round structures with distinct circular rims, through similar ones, but with a central hole, to larger round or oval (rarely polygonal) structures that have lost tissues in the central part. We observed such mines, with all listed transitions in extant plant, *Liquidambar styraciflua* (presently under study). This example shows that, without taking into account variations of conditions of the damage type, it is frequently difficult to determine and treat the assignment of a particular type to a certain group and its developmental pattern.

The catalogue provided by Labandeira et al. (2007) puts in order the data on known damage types, but should not be regarded as a thoroughly developed classification. The necessity for classification of plant damages recorded in fossils is caused by the growing number of the investigated types from various time intervals, a need for their comparative analysis. As an independent object of the study rather than an accompanying attribute of descriptions of fossil plants, phytopathological structures deserve special attention of

paleobotanists. The absence of a suitable classification system for the analysis of available data is a great problem of modern studies.

ACKNOWLEDGMENTS

The study was supported by the Russian Foundation for Basic Research, project nos. 14-04-00800, 15-34-20745, 13-04-01839, 15-55-53019-GFEN.

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Translated by G. Rautian