

Damages on Mesozoic Plants from the Transbaikalian Locality Chernovskie Kopi

D. V. Vasilenko

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117997 Russia

e-mail: lab@palaeoentomolog.ru

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Abstract—Plant remains with traces of damages are known mainly from the Paleozoic and Cenozoic. Structures on coniferous and ginkgoaceous leaves, galls and egg batches, are here described from the Jurassic–Cretaceous locality of Chernovskie Kopi. The classification of damages proposed by Vjalov is revised. For the locality Chernovskie Kopi, damages are statistically analyzed, their distribution on different plants and in various burial types is considered.

Key words: ichnofossils, traces, galls, Mesozoic, Transbaikalia.

INTRODUCTION

Recently, interest in various kinds of traces of vital activity of organisms, and especially in indications of animal–plant interactions, has increased (Krassilov *et al.*, 2004; Labandeira, 1997, 2002; Wilf, Labandeira, 1999; etc.). Such traces often indicate the presence of organisms that are absent from burials and provide unique information about ecological links between representatives of extinct faunas and floras. Fossil evidence of plant–animal (most often terrestrial arthropod) interactions is represented by various plant damages.

Let us define damages as structures of various shape on different parts of plants that are not linked to processes of the plants' vital activity or appeared as results of external manipulation; i.e., galls, mines, traces of chewing, punctures of the cuticle, as well as traces of animal reproduction like ovipositions on leaf and stem surfaces. Most often, such damages result from vital activity of insects that utilize plant tissues as food or as a substrate necessary for oviposition or feeding and protection of larvae developing in a gall or a mine. Similar damages may also be caused by other organisms, such as mites, phytonematodes, some fungi, and viruses.

Plant damages are most abundant at the end of the Paleozoic–beginning of the Mesozoic, especially in the Permian and Triassic, and in the Cenozoic, where their diversity becomes closer to its present level. Data about Jurassic and Cretaceous damages are much scarcer. Such data would be interesting in the light of the transition from the Mesophytic to the Cenophytic and the global turnover of insect assemblages in the mid-Cretaceous, which is thought to be associated with this transition.

Regrettably, many authors do not consider fossil plant damages within a single, even if formal, system, thus making it difficult to analyze and interpret different types of damage, the number of known specimens of which increases progressively. Wilf and Labandeira suggested a classification of plant damages that incorporates four main types of damages, i.e., traces of external feeding, galls, mines, and traces of piercing and sucking. Over 50 types of damages are recognized within these groups on the basis of morphological and topological features (Wilf and Labandeira, 1999; Labandeira *et al.*, 2002). Such an approach to the classification of damages is most convenient at the present state of knowledge.

In 1975, Vjalov proposed a formal classification of damages. According to this classification, traces of insect feeding on plants are brought together in the group Phagophytichnidea. This group comprises traces of feeding on bark and wood (Phagolignichnida) and traces of feeding on leaves and stems (Phagophytichnida). The latter division includes traces of gnawing leaf margins (family Phagophytichnidae), galls (family Paleogallidae), and mines (family Paleominidae) (Vjalov, 1975). We adhere to the classification proposed by Vjalov for several reasons. First, due to the principle of priority; second, since this system utilizes the whole hierarchical tree of formal taxonomic categories, it seems to be able to classify plant damages in the most detail, which, with accumulation of material, will facilitate its interpretation.

However, since galls and mines are used by organisms both for feeding and protection, and since it is impossible to assign unambiguously certain damage to insects (and not to mites or, for example, pathogenic viruses), we suggest considering all types of plant damages within the taxon Phagophytichnidea. The histori-

cal name Phagophytichnida is proposed to be kept for leaf and stem damages, but this taxon is to be considered as a group of leaf and stem damages, not only as traces of feeding on them, and is to include traces of oviposition and piercing of the cuticle that do not lead to expansion of plant tissues. We retain the names of the formal families proposed by Vjalov but attribute new values to the taxa, considering specific damages of any origin within them.

SYSTEMATIC PALEONTOLOGY

Thus, the formal classification of plant damages (Vjalov, 1975, updated) looks as follows:

Group Phagophytichnidea (fossil plant damages)

1. Subgroup Phagolignichnida includes damages to bark and wood.

2. Subgroup Phagophytichnida includes structures on leaves and stems (shoots) that are not typical of the vital activity of plants.

2.1. Family Phagophytichnidae Vjalov, 1975 includes damages to leaf tissues (marginal chewing marks, skeletonization, etc.).

2.2. Family Paleominidae Vjalov, 1975 includes fossil mines (burrows in leaf tissue).

2.3. Family Paleogallidae Vjalov, 1975 includes fossil galls (neoplasms on leaves).

2.4. Family Paleovoididae fam. nov. includes fossil egg batches on plant organs.

A separate family within the taxon Phagophytichnida should probably be erected for traces of piercing of the cuticle.

A disadvantage of such a classification is an a priori violation of the systematic approach (separation of taxa of the rank of a formal family on the basis of results of interpretation of damages), which is, however, less painful than classifications in which formal genera and species of damages are described within natural taxa of hypothesized invertebrates that caused the damage, as has happened in some publications.

Three types of damages to leaves of conifers *Pityophyllum* sp. and *Desmiophyllum* sp. and ginkgoaceous *Ginkgoites* sp. not associated with a considerable mechanical influence on plants are found in the Transbaikalian locality of Chernovskie Kopi, the age of which is uncertain within Late Jurassic–Early Cretaceous.

All kinds of damages in the locality of Chernovskie Kopi are rather clearly differentiated morphologically and do not have transitional forms. Furthermore, structures of only one kind are usually present on one leaf.

Damages of the edges of conifer and ginkgoaceous leaves have also been recorded in oryctocenoses of this locality, but they are not considered in this paper. The

type material is housed in the collection of the Paleontological Institution (PIN), Russian Academy of Sciences.

FOSSIL OVIPOSITION ON PLANT ORGANS

This formal family includes fossilized structures on the leaf and stem cuticle of plants that resemble egg batches of various invertebrates. As a rule, individual elements of oviposition (eggs) of one biological species of animals are of the same size and arranged regularly in rows or in groups. Oviposition may occur on living plants as well as dead ones, in terrestrial environments or in water.

In his compendium of plant–animal associations, Labandeira (2002) produced a number of pictures of ovipositions from Permian, Triassic, Paleogene, and Neogene deposits. Cenozoic and, sometimes, Mesozoic structures are interpreted as odonatan ovipositions (Konijnenburg-van Cittert and Schmeißner, 1999). Some authors attribute the ovipositions to the odonatan families Coenagrionidae and Lestidae, according to their size and shape (Hellmund and Hellmund, 1991, 1998, 2002).

Since ovipositions are specific for an animal, and their shapes do not depend much on the plant species, interpretation of fossil oviposition is possible following careful analysis of the paleoentomofauna of a particular locality. Variation of some characters of oviposition on different host plants may apply only to spatial arrangement of the oviposition, e.g., in a chain on narrow leaves and in rows on broad leaves.

It is necessary to distinguish endo- and exophytic ovipositions. Exophytic ovipositions can be represented by aggregation of several eggs under a common mucous or arachnoid coat or by isolated relatively large eggs. Traces of the protective mucous or arachnoid coat can be preserved during fossilization. Endophytic ovipositions are represented by solitary eggs inside plant tissues laid by animals with the aid of ovipositors. If it leads to a gall creation process, such neoplasms should be considered within the family Paleogallidae.

Family Paleovoididae Vasilenko, fam. nov.

Type genus. *Paleovoidus* gen. nov.

Diagnosis. Fossil formations on different parts of plants interpreted as invertebrate egg batches.

Composition. Type genus.

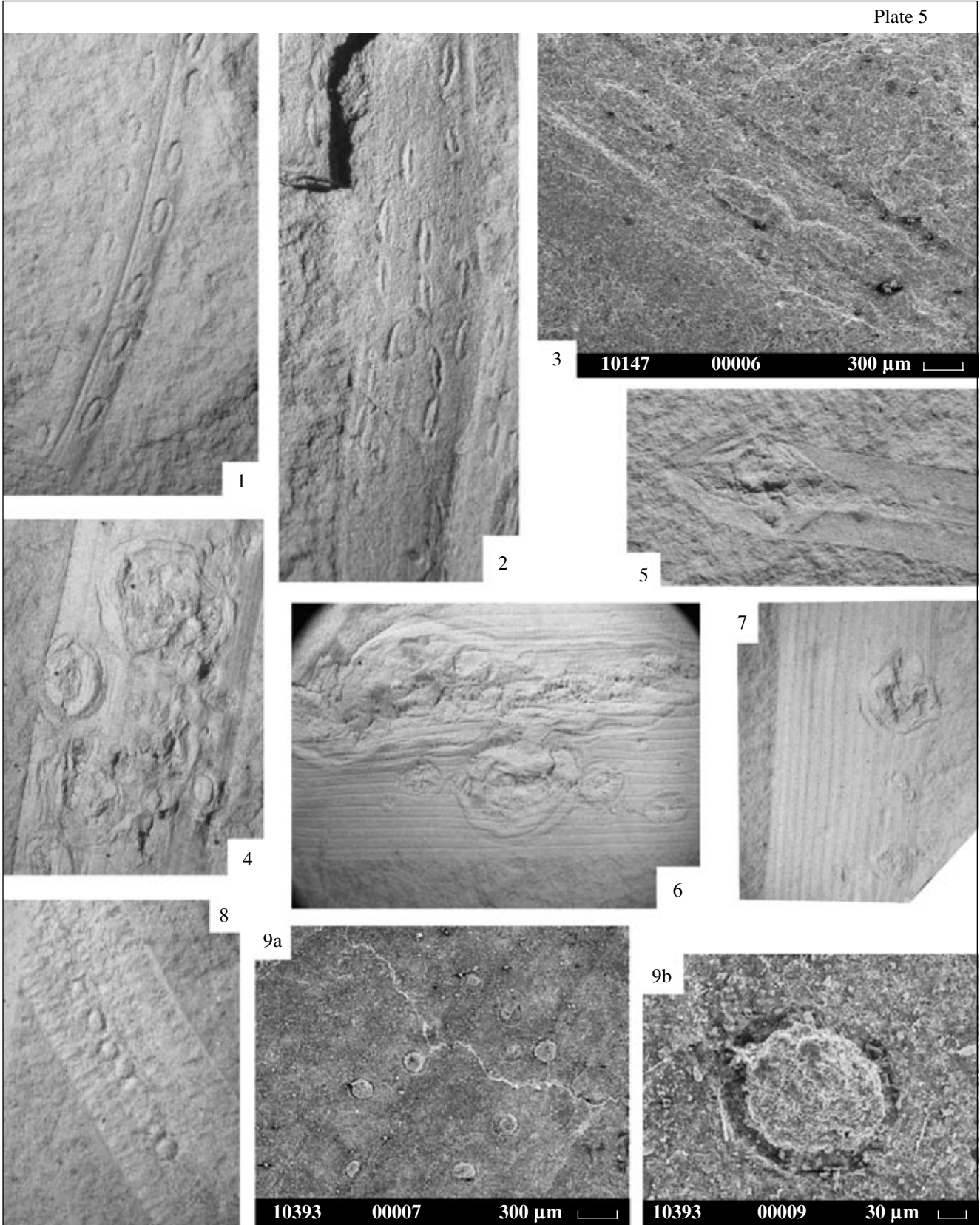
Genus *Paleovoidus* Vasilenko, gen. nov.

Etymology. From the Greek *palaios* (ancient) and the English *ovoid* (egg-shaped). Masculine gender.

Type species. *P. rectus* sp. nov.

Diagnosis. Oval or lentiform structures (eggs) with regular distribution over substrate.

Species composition. Type species.



Paleoovoidus rectus Vasilenko, sp. nov.

Plate 5, figs. 1–3

E t y m o l o g y. From the Latin *rectus* (regular).

H o l o t y p e. PIN, no. 4626/464, damages on a leaf of conifer *Pityophyllum* sp.; Chita Region, Chita district, locality of Chernovskie Kopi; Upper Jurassic–Lower Cretaceous, Doroninskoe Formation, Chernovskaya transitional sequence.

D e s c r i p t i o n. Oval or lentiform relief structures; individual eggs orientated in chain on leaf blades.

M e a s u r e m e n t s, mm. Length of oviposition elements, 1–1.2; their width, 0.3–0.4.

R e m a r k s. Egg batches are arranged in two chains along the central vein on *Pityophyllum* needles and in up to four subparallel rows between veins on *Ginkgoites*, in the latter case individual elements are elongated lentiform and laterally compressed.

M a t e r i a l. Besides the holotype and paratypes PIN, nos. 4626/472, 4626/473, 30 leaf remains with damages.

FOSSIL GALLS

This family comprises taxa erected for fossil galls (cecidia). A gall, as a biochemical response to chemical agents released by a gall-former, is specific not only to the gall-former, but probably to a greater extent to the plant.

The majority of modern gall-inducers are insects of the orders Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, Hymenoptera, mites and, to a less degree, phytoneumatodes that form root and stem galls. The role of viruses, bacteria, and fungi in forming galls is also important.

Slepian (1973) considers formation of galls from a medical point of view, treating it as a local pathological process. In his opinion, producing galls aims to limit the movement of a pest and the damage caused by it within the plant body, which could otherwise lead to a greater disturbance of the plant's vital functions. In a paper on fossil mangrove assemblages from Cretaceous deposits of Israel, Krassilov *et al.*, 2004 provide data on the significance of cecidogenesis as a factor in plant morphogenesis, reaching conclusions on the explosive nature of coevolutionary processes with regard to the creation of new biotic communities (Krassilov *et al.*, 2004). It is already clear at this stage of studying phytopathological processes that cecidogenesis involves

mechanisms that are not restricted to simple growth of tissues to isolate a parasite, but acts at a deeper, probably genetic, level.

Fossil galls are known from Carboniferous, Triassic and, to a lesser degree, from Jurassic and Cretaceous deposits; however, they reached their maximum diversity in the Cenozoic. Their interpretation is rather conventional. There are cases when a gall appears on a leaf as a result of either an insect attacking the stem, or even without direct contact with a gall-inducer, if the plant had such contact earlier (Monod and Schmitt, 1968).

Classifications of modern galls are based on two main principles, morphotopological and morphogenetic. A more complex and thorough classification was suggested by Slepian (1973), who used a system of coordinated taxa and Latin names for them. However, classification of fossil objects should be based, first of all, on characters available for direct examination; we cannot evaluate by direct observation such important taxonomic characters in Slepian's classification as the number and structure of internal gall cavities.

A single case of galls buried with gall-inducers, mites and dipterans, is known from Cretaceous deposits of Israel (Krassilov *et al.*, 2004).

Thus, we propose establishing formal genera on a topological basis (leaf, stem/shoot, root) within the family Paleogallidae established for fossil galls by Vjalov. Later on, subgeneric categories can be erected after confirmation of specific associations of fossil galls with certain parts of a leaf (e.g., at the leaf edge or on the veins, as in modern galls) or the particular form of galls (flat, "nuts," felt-like, etc., by analogy with modern galls).

A formal redescription of the family and genera of leaf galls, descriptions of new species of galls from the locality of Chernovskie Kopi, as well as descriptions of species established by Vjalov (1975) on the basis of bibliographic reference but left undescribed, are provided below.

Family Paleogallidae Vjalov, 1975

T y p e g e n u s. *Paleogallus* Vjalov, 1975.

D i a g n o s i s. Structures on various parts of plant, appearing as local pathological neoplasms in fossils.

C o m p o s i t i o n. Type genus.

Explanation of Plate 5

Figs. 1–3. *Paleoovoidus rectus* sp. nov.; (1) holotype PIN, no. 4626/464, $\times 4$; (2) paratype PIN, no. 4626/473, $\times 4$; and (3) paratype PIN, no. 4626/472, $\times 23$; Figs. 1 and 3 show egg batches on conifer leaves of *Pityophyllum*, Fig. 2 shows damages on *Ginkgoites* leaves.

Figs. 4–7. *Paleogallus zherichini* sp. nov.; (4) paratype PIN, no. 4626/467, $\times 7$; (5) paratype PIN, no. 4626/470, $\times 7$; (6) paratype PIN, no. 4626/468, $\times 8$; and (7) holotype PIN, no. 4626/469, $\times 5$; Figs. 4, 6, and 7 show galls on *Desmiophyllum* leaves, Fig. 5 shows galls on *Pityophyllum* leaves.

Figs. 8 and 9. *Paleogallus porusiformis* sp. nov.; (8) paratype PIN, no. 4626/471, showing galls on *Pityophyllum* leaves, $\times 9$; (9a) and (9b) holotype PIN, no. 4626/472, showing galls on *Ginkgoites* leaves, (9a) $\times 23$, (9b) $\times 167$.

Genus *Paleogallus* Vjalov, 1975

Type species. *P. cynipidaeformis* Vjalov, 1975.

Diagnosis. Structures (galls) on leaf blade or leafstalk in form of local pathological neoplasms.

Species included. Four species.

***Paleogallus zherichini* Vasilenko, sp. nov.**

Plate 5, figs. 4–7

Etymology. In memory of the paleoentomologist V.V. Zherikhin.

Holotype. PIN, no. 4626/469, solitary gall on *Desmiophyllum* sp. leaf; Chita Region, Chita district, locality of Chernovskie Kopi; Upper Jurassic–Lower Cretaceous, Doroninskoe Formation, Chernovskaya transitional sequence.

Description. When fossilized, galls resemble small rounded cankers with irregular edges; they are not associated with veins.

Comparison. The new species differs from *P. neuroteriformis* in its irregularly rounded shape and in the continuous growth of the galls. It differs from *P. cynipidaeformis* in having a more distinct relief and in the absence of an association of galls with leaf veins.

Remarks. In the locality of Chernovskie Kopi, the galls were recorded on *Desmiophyllum* sp., *Pityophyllum* sp. and, to a less degree, on *Ginkgoites* sp. leaves. As galls grow, several of them can merge and cover a large part of a leaf blade (Pl. 5, figs. 4, 6). Sometimes, a gall situated on a *Pityophyllum* vein can grow along the vein (Pl. 5, fig. 5); this is probably connected to peculiarities of the plant reaction.

Measurements, mm. Diameter, 0.5–6.

Material. Besides the holotype and paratypes PIN, nos. 4626/467, 4626/468, 4626/470, 110 leaf remains with damages.

***Paleogallus porusiformis* Vasilenko, sp. nov.**

Plate 5, figs. 8 and 9

Etymology. From the Latin *porusus* (rash).

Holotype. PIN, no. 4626/466, aggregation of small galls on *Ginkgoites* sp. leaf; Chita Region, Chita district, locality of Chernovskie Kopi; Upper Jurassic–Lower Cretaceous, Doroninskoe Formation, Chernovskaya transitional sequence.

Description. Small round relief structures, which are bordered with rings with depressed relief; the central part is elevated. These structures are not associated with leaf veins.

Comparison. This species differs from its congeners in being small and in having a distinct ring around the gall.

Remarks. In the locality of Chernovskie Kopi, such galls occur on *Pityophyllum* sp. and *Ginkgoites* sp. leaves. They quite often form aggregations. Keeping their shape and general appearance, galls are larger on

Pityophyllum sp. leaves and drawn towards the main vein. This can probably be explained by differences in the physiology of these genera.

Measurements, mm. Diameter of galls on *Ginkgoites* sp. leaves, 0.18–0.20; on *Pityophyllum* sp. leaves, up to 0.4.

Material. Besides the holotype and paratype PIN, no. 4626/471, 50 leaf remains with damages.

***Paleogallus cynipidaeformis* Vjalov, 1975**

Holotype. Galls on leaf of oak *Quercus cognatus*, figured in Hoffman's paper (Hoffman, 1932, p. 342, text-fig. D); USA, Washington, Douglas Co.; Upper Miocene.

Description. Galls are rounded and centrally convex; they are associated with leaf veins.

Comparison. This species differs from its congeners in the association of galls with leaf veins and in the nature of their relief.

Measurements, mm. Diameter, 3–4.

***Paleogallus neuroteriformis* Vjalov, 1975**

Holotype. Galls on oak leaf figured by Laurentiaux (1953, p. 403, fig. 1); France, Vienne, Lager Berg; Lower Pliocene.

Description. Galls are rounded and regular shaped, having depressed central areas and elevated margins that form rings. The galls are not associated with leaf veins.

Comparison. It differs from *P. porusiformis* sp. nov. in having depressed central areas and elevated margins of galls.

Remarks. Laurentiaux ascribed these damages to the hymenopteran *Neuroterus*.

Measurements, mm. Diameter, 5.

DISCUSSION

The ratio of leaves with damages to undamaged leaves varies in beds with different burial types. Thus, there are three main kinds of burials of plant remain in oryctocenoses of the locality of Chernovskie Kopi (Sinitza, 1995; Sinitza, pers. comm.; author's field observations).

(1) Burials of large fragments of plant debris, occasionally orientated, in siltstones and claystones. *Pityophyllum* needle fragments dominate in these burials. All kinds of leaf damages are approximately equally represented in beds with this burial type, which can be explained by transporting plants from various parts of a biotope.

(2) Abundant burials of intact plant leaves (beddings) in siltstones and sandy siltstones without of transportation disturbance by currents. Remains of *Pityophyllum* sp. bearing damages *Paleogallus porusiformis* (46%), *P. zherichini* (27%), and *Paleoovoidus rectus* (27%) dominate numerically in these burials.

Ginkgoites sp. leaves with rare *P. porusiformis* and even rarer *P. zherichini* are subdominants. *P. rectus* is extremely rare on ginkgoaceous leaves (a single record). Beds with this burial type yield damages on 10% of *Pityophyllum* sp. leaves and on 5% of *Ginkgoites* sp. leaves. Taking into account the type of burial (bedding), it is rather difficult to count the total number of leaf remains examined, but a preliminary estimate gives at least 5000 specimens.

(3) The third type is characterized by the domination of intact leaves of the bush *Desmiophyllum*, buried sparingly, probably after a short transportation. Ginkgoaceous and conifer leaves occur rarely and have traces of their transportation. The composition of this type of beds is characterized by an increased sand content; lithological traces of currents are absent. *Desmiophyllum* sp. leaves are damaged only by *P. zherichini*, *Pityophyllum* sp. needles are damaged mainly by *P. zherichini* and only in isolated cases by *P. porusiformis* and *P. rectus*. *Ginkgoites* sp. leaves are rare; however, there are many leaves with all three kinds of damages among them. The proportions of damaged leaves are as follows: *Desmiophyllum* sp. leaves, 80%; *Pityophyllum* sp., about 60%; *Ginkgoites* sp., about 60%. About 500 leaf remains have been examined.

Plant remains recorded from this locality are not restricted to those damaged. There are ferns *Asplenium*, *Birisia*, *Cladophlebis*, *Coniopteris*, and *Osmunda*; cycadophytes *Nilsonia* and *Ptilophyllum*; ginkgoaceous *Baiera*, *Pseudotorellia*, and *Sphenobaiera*; conifers *Coniferites*, *Podozamites*, *Pseudolarix*, and *Taxocladus*; as well as various fructifications and stems (according to unpublished data by Grigorieva, with additions by Karasev, pers. comm). Remains of the above plants are scarce, and damages or neoplasms have not been recorded on them.

Entomofauna of the locality includes representatives of 15 orders: Orthoptera, Plecoptera, Diptera, Blattodea, Isoptera, Odonata, Neuroptera, Megaloptera, Mecoptera, Trichoptera, Hymenoptera, Coleoptera, Ephemeroptera, Homoptera, and Heteroptera. About 500 insect remains were collected altogether. Orthopterans and beetles dominate among terrestrial insects. Aquatic groups are generally more abundant and are represented by mayflies, caddisflies, and stoneflies (Sinitshenkova, 1998).

Thus, structures on leaves that are not typical of normal vital activity of plants are described from the Upper Mesozoic locality of Chernovskii Kopi, Transbaikalia. Treating these and other similar structures (damages) within the proposed formal classification will greatly facilitate their systematization and analysis.

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