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Revision of existing classification of fossil insect feeding traces and description of new ichnotaxa from Middle Jurassic sediments of Eastern Siberia (Russia)

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Abstract

This paper revises the existing system of formal classification by Vialov and Vasilenko for fossil plants involving insect feeding and oviposition. The classification of these fossil traces has been amended and supplemented in accordance with the requirements of the International Code of Zoological Nomenclature. The following nomenclatural combinations are made: Insectophagichnata (Vialov) Enushchenko and Frolov, comb. et stat. (classis) nov., Phagolignichnidina (Vialov) Enushchenko and Frolov, comb. et stat. (subordo) nov., Phagophytichnidina (Vialov) Enushchenko and Frolov, comb. et stat. (subordo) nov. Fossil traces of these interactions were found and illustrated for Mesozoic insects and leafes of *Ginkgo* tapkensis from Middle Jurassic sediments of the Irkutsk Coal Basin in Eastern Siberia, Russia. The examined traces consist of ovipositions (traces of insect egg laying), galls (traces of insect caused teratologies) and epidermal punctures (traces of piercing and sucking). The following ichnotaxa are described and illustrated: Paleoovidinae Enushchenko and A. Frolov, ichnosubfam. nov., Paleoexoovoidinae Enushchenko and Frolov, ichnosubfam. nov., Sugophytichninae Enushchenko and A. Frolov, ichnosubfam. nov., Sugophytichnida pertusura Enushchenko and Frolov, ichnogen. et ichnospec. nov., Paleoovidus vasilenkoi Enushchenko and A. Frolov, ichnospec. nov., Paleoexoovoida ovoidea Enushchenko and A. Frolov, ichnogen. et ichnosp. nov., Paleogallus vialovi Enushchenko and Frolov, ichnospec. nov. Punctures of the leaf epidermis probably belong Mesozoic cicadas of the Palaeontini, which dominate the adjacent strata of the studied location. The extremely low occurrence of interaction between insects and plants in these Jurassic deposits of Eastern Siberia have ichnotaxonomic importance for understanding the functioning of Jurassic terrestrial paleoecosystems.

Key words: galls, oviposition, punctures, Palaeotinidae, Sugophytichninae, Ginkgo tapkensis, Irkutsk Coal Basin, Zoological nomenclature

Introduction

Higher plants almost from their first appearance were and continue to be closely interconnected with various arthropods, particularly insects. During their evolutionary history, interactions with plants and phytophagous insects solved different ecological and evolutionary problems aimed at achieving a single result – survival. Plants have served as food for phytophagous insects, while improving their physical and biochemical defense mechanisms. As a result of co-association, plants and phytophages have achieved amazing specialization in their interactions through time.

Fossil evidence indicating interactions between insects and higher plants are known in the fossil record commencing during the Late Paleozoic (Naugolnykh & Ponomarenko 2010a, b, Vasilenko & Shcherbakov 2013, Naugolnykh 2017). The first studies on galls and insect-mediated damage on various parts of fossil plants began to appear at the end of the Nineteenth Century. At that time, the study of fossilina damage on plants consisted of establishing the type of herbivore that caused a trace (Weiss 1876, Zeiler 1888, Frić 1901). The growth of interest in fossil traces involving the life histories of herbivores occurred during the middle of the 20th century against the background of the development of ichnology. (Ichnology derives from the Greek $i\chi vo\varsigma$, meaning "trace" and $\lambda \delta \gamma o\varsigma$, meaning "concept"). Since the 1950s injuries and teratologies on plants have been considered an independent phenomena requiring a separate classification (Seilacher 1953, Vialov 1968, 1975, Rozefelds and Sobbe 1987, Wilf and Labandeira 1999, Labandeira 1998, 2000, 2002, Labandeira et al. 2002). To date, information on injuries or teratologies on the vegetative organs of Jurassic and Early Cretaceous plants has been minimal (Ponomarenko 1998a, b, Labandeira 1998, 2002) with most of the recent contributions coming from Northeastern China (Ding et al. 2015, Meng et al. 2017, Lin et al. 2018). New reports of Jurassic plants from Eastern Siberia damaged by insects are of great scientific value for understanding the interactions and processes between plants and insects in past ecosystems. However, a generally accepted classification system of fossil traces for plant-insect interactions that fully meets the requirements of the International Code of Zoological Nomenclature (ICZN 1999, Mezhdunarodnyi Codeks... 2004) currently is lacking. Therefore, before proceeding with the description of new ichnotaxa, we consider it necessary to adjust the existing classification in accordance with the rules of the International Code of Zoological Nomenclature (2004).

The current state of ichnotaxa classification

All fossil traces of insect nutrition with plants indicated by Vialov (1975) and followed by Vasilenko (2005) are combined under the name 'Insectophagichnacea'. Following the rules of nomenclature established to date, it is difficult to establish which taxonomic rank the author wanted to assign to the group he proposed. Inside 'Insectophagichnacea', two groups stand out. The first – 'Coprinisphaeridea' – includes traces of manure from representatives of the family Scarabaeidae. The second – 'Phagophytichnidea' – the principal, especially widespread group of feeding traces made by phytophagous insects, including traces of nutrition of wood feeders (Phagolignichnida) and traces of folivory (Phagophytichnida). The taxonomic rank of these units is unclear. Based on content of 'Coprinisphaeridea' and 'Phagophytichnida', and if we assume that these names were listed as misprints – these groups should be assigned a rank of ordo. Judging by the ending (-a), groups 'Phagolignichnida' and 'Phagophytichnida' should be ordos. However, according to the understanding of Vialov, these groups has a lower rank. Accordingly, group 'Insectophagichnacea' can be considered at a rank not lower than the classis (ending -ata).

The 'Coprinisphaeridea' group is represented only by the family Coprinisphaeridae with the nominative genus *Coprinisphaera* Sauer 1955 (*C. ecuadoriensis* Sauer). The 'Phagolignichnidea' group includes one family, Phagolignichnidae Vialov 1975. Among the fossil traces of leaf feeding, Vialov distinguishes margin eating (family Phagophytichnidae), galls (family Paleogallidae Vialov 1975) and mines (family Paleominidae Vialov 1975). Later, a similar classification of fossil insect feeding traces on plants was proposed by Wilf and Labandeira (1999). They identified traces of external feeding (margin eating), mines, galls, as well as traces of punctures and sucking. However, for their groups, the authors did not offer any formal names, and accordingly did not indicate their taxonomic rank. More than fifty types of damages were identified within these groups according to morphological and topological characteristics (Wilf and Labandeira 1999, Labandeira et al. 2002). This system remains outside of the scope of ICZN and represents an ecological classification of damage not taxonomic in nature (Wilf and Labandeira 1999).

In conformity with rule of priority, Vasilenko (2005a, b, 2006a, b, 2007a, b) took the Vialov system as a basis and expanded its usage. However, Vasilenko also used groups and subgroups as the highest ichnotaxonomic levels. Fossil egg clutches on plants are considered by him within the Paleoovoidida group, represented by one family (Paleoovoididae). Vasilenko (2005a, b) noted that it is necessary to distinguish between endophytic and exophytic egg clutches. At that time, Vasilenko had not yet provided endophytic egg culture a taxonomic rank. The family he described was represented by a typified ichnogenus, including one endophytic ichnospecies: *Paleoovidus rectus* Vasilenko 2005a: 56, 2005b: 631. Later, in his thesis Vasilenko (2007c) distinguishes the Paleoovoidiea group (fossil egg clutches of invertebrates) with the subgroup Paleoovoididae. Here (Vasilenko 2007c) describes several of ichnotaxa, which, like Paleoovoididae and Paleoexovididae, cannot be considered valid, since they do not satisfy the provisions of Art. 11.1. and 8.1. International Code of Zoological Nomenclature (ICZN 1999, Mezhdunarodnyi Codeks... 2004).

As part of Phagophytichnidae, Vasilenko distinguishes the subfamily Folifenistrinae Vasilenko 2007, which includes damage in the form of closed structures ("window" feeding) on one or both sides of the leaf and, as a rule, not extending to the edge of the leaf blade (Vasilenko 2007a, b). Further division of the groups into subfamilies, genera and species is carried out below, based on topological and morphological features.

Materials and methods

The present work is based on the formal classification of damage and neoplasms on the leaves of fossil plants, proposed by Vialov (1975) and supplemented by Vasilenko (2005a, b, 2006a, b, 2007a, b). We have made significant changes and clarifications to the proposed system, in accordance with the rules of the International Code of Zoological Nomenclature (ICZN 1999, Mezhdunarodnyi Codeks... 2004). The new ichnotaxa described in this paper are placed within this transformed system.

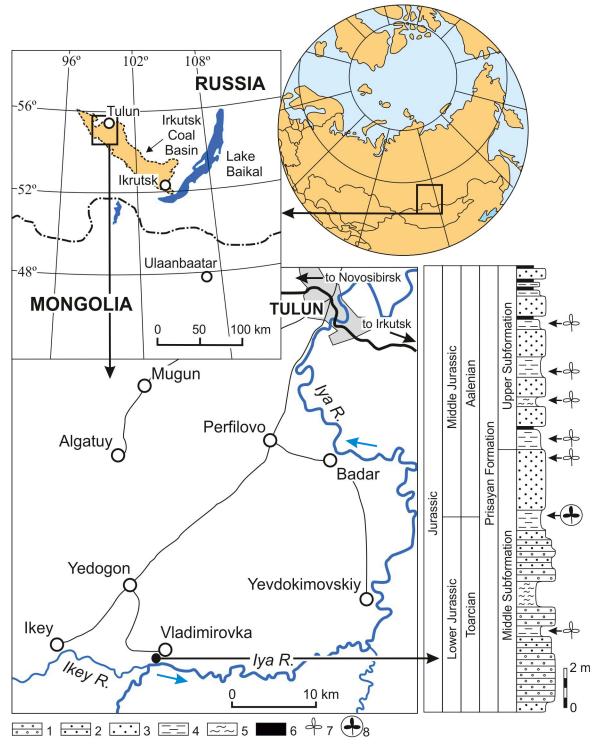


FIGURE 1. Geographical position and lithological structure of the samples locality with traces of the interaction of Mesozoic insects and plants **1.** Coarse sandstones. **2.** Medium grained sandstones, **3.** Fine sandstones. **4.** Siltstones. **5.** Mudstones. **6.** Coals. **7.** Fossil plants. **8.** Fossil plants with traces of insect life activity.

The studied fossil material comes from a natural outcrop located on the left bank of the Iya River (Fig. 1) near the Vladimirovka village (Irkutsk Coal Basin, Eastern Siberia, Russia) (N54°10'31", E100°17'26"). In this outcrop, the Prisayan Formation was founded, represented by the rhythmic alternation of sandstones, siltstones and mudstones with thin intercalated layers of coal (Fig. 1). Remains of horsetails: *Phyllotheca sibirica* Heer, ferns: *Lobifolia* sp., *Coniopteris maakiana* (Heer) Pryn. emend. Kiritch. et Trav., *Cladophlebis haiburnensis* (L. et H.) Sew., *Cl. williamsonii* Brongn., *Cl. williamsonii* (Brongn.) var. *punctata* Brick, *Cladophlebis* sp., *Raphaelia diamensis* Sew., Bennettites: *Anomozamites* sp., Ginkgoales: *Ginkgo* ex gr. *sibirica* Heer, *Ginkgo tapkensis* Dolud. et Rasskaz., Leptostrobales: *Czekanowskia baikalica* Kiritch. et Samyl., *Cz. obiensis* Kiritch. et Samyl., *Cz. irkutensis* Kiritch. et Samyl., *Cz. rigida* Heer, *Phoenicopsis cognata* Kiritch., conifers: *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nath., *Schizolepis mashchukae* A. Frol. and plants of unclear systematic position, such as *Stenorachis* sp., *Carpolithes heeri* Tur.-Ket., *C. minor* Pryn., *Carpolithes* sp. and *Samaropsis rotundata* Heer were found in siltstones and mudstones. Species of *Coniopteris maakiana* (Heer) Pryn. emend. Kiritch. et Trav., *Raphaelia diamensis* Sew., *Phoenicopsis cognata* Kiritch., are the dominant taxa for the Prisayan fossil plant assemblage, characterizing the upper member of the Prisayan Formation, and indicate its Middle Jurassic age, provisionally assignated to the Aalenian Stage (Mikheeva et al. 2017, Demonterova et al. 2017, Frolov et al. 2017, Frolov & Mashchuk 2018).

Examples of oviposition, galls and punctures on the epidermis of leaves inflicted by insects were found on leaf cuticle preparations of *G. tapkensis*, which were prepared after maceration of compression matrix, based on the standard method of a Schulze mixture (Kreisel 1932). The study of this material was carried out using a Micromed 3 Led M light microscope equipped with a ToupCam 8.0 MP digital video eyepiece. The studied material is stored at the Institute of the Earth's Crust of the Siberian Brunch of Russian Academy of Sciences (Coll. Iya-2011; Irkutsk, Russia), and the Paleontological Institute of the RAS (Coll. No. 5140; St. Petersburg, Russia). We also used the illustrations of Vasilenko (Fig. 3), cited in his thesis (Vasilenko, 2007c).

Results

The general paleoichnological classification is based on the same principle as natural zoological classification; consequently, all the rules of zoological systematics apply to it (Vialov 1993). The same subordinate taxonomic units are distinguished above the genus – families, superfamilies and orders, for example. In the natural system of zoology, there are no such taxonomic units above the family as the group and subgroup, which were established by Vialov (1975) and Vasilenko (2005, 2006, 2007a, b). Therefore, there is a need to assign these units to a generally accepted taxonomic rank. In this regard, the classification of fossil traces of insect feeding proposed by Vialov and Vasilenko should be the following.

Classis INSECTOPHAGICHNATA (Vialov) Enushchenko and Frolov, comb. et stat. nov. = gr. Insectophagichnacea Vialov 1975: 152.

Fossil Insect Feeding Traces

I Ordo Coprinisphaerida Vialov 1975: 152 [recorded with misprint – "Coprinisphaeridea"]

1. Familia Coprinisphaeridae Vialov 1975: 152 (*Coprinisphaera ecuadoriensis* Sauer 1955: 123)

II Ordo Phagophytichnida Vialov 1975: 152 [recorded with misprint – "Phagophytichnidea"]; Vasilenko, 2007a: 88.

Fossil Plant Feeding Traces

1. Subordo **Phagolignichnidina** (Vialov) Enushchenko and Frolov, **comb**. **et stat**. **nov**. = gr. Phagolignichnida Vialov 1975: 152.

Traces of bark and wood feeding (borings, engravings or tunnels).

1.1. Familia Phagolignichnidae Vialov 1975: 153 [recorded with misprint – "Family Phagolignichnidae"] (*Phagolignichnus arboreus* Vialov 1975: 153)

Subordo Phagophytichnidina (Vialov) Enushchenko and Frolov, comb. et stat. nov. = gr. Phagophytichnidea Vialov 1975: 152, 153; Vasilenko 2005a: 55; Vasilenko 2005b: 629; 2007a: 88. = subgr. Phagophytichnida Vialov 1975: 152, 153; Vasilenko 2005a: 55; Vasilenko 2005b: 631; Vasilenko 2007a: 88; Vasilenko 2007b: 208. Traces of feeding on leaves and stems.

2.1. Familia Phagophytichnidae Vialov, 1975: 152, 153; Vasilenko 2005a: 55; Vasilenko 2005b: 629; Vasilenko 2006a: 54; Vasilenko 2006b: 288; Vasilenko 2007a: 88; Vasilenko 2007b: 208.

External traces of green tissues feeding (hole feeding, marginal eating, skeletonization and surface feeding). (*Phagophytichnus ekowskii* Amerom 1966: 182)

2.2. Familia Paleoovoididae Vasilenko 2005a: 55, 2005b: 629 Fossil formations on various parts of plants interpreted as clutches of invertebrates.

Subfamilia Paleoovidinae Enushchenko and Frolov, ichnosubfam. nov.

Fossil damage on various parts of plants partially or completely immersed in its tissue (endophytic oviposition) and interpreted as egg clutches of arthropods invertebrates. They are single eggs introduced by animals using an ovipositor. If, at the same time, a gall formation process occurred, such neoplasms should be considered within the family Paleogallidae Vialov, 1975.

(Paleoovidus rectus Vasilenko 2005a: 56, 2005b: 631)

Paleoovidus vasilenkoi Enushchenko and Frolov, ichnospec. nov.

(Fig. 2)

Holotype. Coll. Iya-2011-14/17-16, oviposition on a leaf *Ginkgo tapkensis*. Irkutsk Basin, Iya River near Vladimirovka village; middle member of Prisayan Formation, of Middle Jurassic age. Holotype is stored at the Institute of the Earth's Crust of the SB RAS (Irkutsk, Russia).

Diagnosis. Fragment of laying of two closely spaced, non-touching eggs located on the lower surface of the leaf epidermis. Eggs are spindle-shaped with blunt lower and subacute upper end; length 260 μ m, width in the middle (widest) part 160 μ m. Attached to the vein, pairwise, asymmetrically, close to each other.

Etymology. The species is named after our colleague, paleontologist and entomologist D.M. Vasilenko (Moscow, Russia).

Subfamilia Paleoexoovoidinae Enushchenko and Frolov, **ichnosubfam**. **nov**. = fam. Paleoexovididae Vasilenko 2007c: 74, nom. invalid.

Diagnosis. Fossil formations on various parts of the plant attached to the surface of the plant cuticle and interpreted as egg clutches of invertebrates (exophytic ovipositions). The egg cultches can be clusters of several eggs enclosed within a common shell, or a single, relatively large egg. Traces of the protective mucosa or wedding can remain rarely with fossilization.

(*Paleoexoovoida ovoidea* Enushchenko and Frolov **nom**. **nov**. = *Paleoexoovidus ovoideus* Vasilenko, 2007c: 74, nom. invalid.)

Paleoexoovoida Enushchenko and Frolov, ichnogen. nov.

Diagnosis. Oval formations (eggs) located on the surface of a plant organ in ordered groups. As a rule, the eggs are broadly oval or round and are clustered.



FIGURE 2. Paleoovidus vasilenkoi Enushchenko and A. Frolov, ichnospec. nov.

P. ovoidea Enushchenko and Frolov, ichnosp. nov. (Fig. 3)

Holotype. Amur Region, Arkharinsky District, Udurchukan (vol. 16), egg laying on a sheet of *Quereuxia* sp.; Upper Cretaceous, Campanian, upper Kundur Formation (Paleontological Institute, RAS, No. 5140/11).

Diagnosis. Fragment of set of compactly arranged eggs, in contact with other eggs, forming a slightly arched row. Traces of organic matter are observed around the egg clutch on the slab, indicating that the eggs were enclosed in a protective shell. The eggs are ovoidal. The length of the egg clutch is 2.5 mm, the width is 1.25 mm; the length of the invidual egg is 0.85–0.95 mm and the width in the widest part is 0.5–0.6 mm (Fig. 3).

Notes. In addition to the nominative species, three more taxa were described within the subfamily, which, according to Art. 11.1 and 8.1 (ICZM 1999, Mezhdunarodmyi Codeks..., 2004) cannot be considered valid: *P. amplus* Vasilenko, 2007c: 74, nom. invalid., *P. catenulatus* Vasilenko, 2007c: 76, nom. invalid. and *P. multus* Vasilenko, 2007c: 75, nom. invalid. All of these taxa were also noted on the leaves of *Quereuxia* sp. in deposits of Upper Cretaceous age from the Kundur Formation (Amur Region, Arkharinsky District, Udurchukan River).

2.3. Familia Paleogallidae Vialov, 1975: 152, 153; Vasilenko 2005a: 55, 57, 2005b: 629; Vasilenko 2007a: 88; Vasilenko 2007b: 208.

The family includes taxa established for fossil galls (cecidia) that consist of formations on various parts of plants that look like local pathological neoplasms or other teratologies.

(Paleogallus cynipedaiformis Vialov 1975: 153)

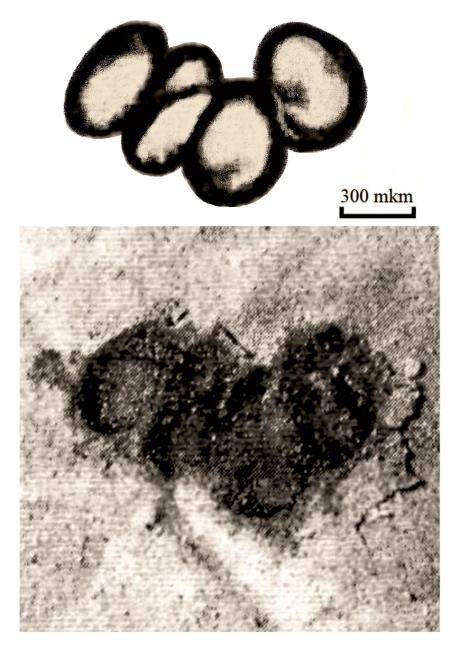


FIGURE 3. Paleoexoovoida ovoidea Enushchenko and A. Frolov, ichnospec. nov.

Paleogallus vialovi Enushchenko and Frolov, ichnospec. nov.

(Figs 4, 5)

Holotype. Coll. Iya-2011-14/17-1b, oviposition on a leaf of *Ginkgo tapkensis*. Irkutsk Basin, Iya River near the Vladimirovka village; middle member of Prisayan Formation, Middle Jurassic. Holotype is stored at the Institute of the Earth's Crust of the SB RAS (Irkutsk, Russia).

Diagnosis. Gall oval, 270.0 μ m long, 120.0 μ m wide; hollow; the edges are even or slightly tuberous; located on the lower surface of the leaf, confined to the vein.

Etymology. The species is named after the outstanding Soviet geologist and paleontologist O.S. Vialov.

Note. The described taxon is on the same *Ginkgo tapkensis* cuticle preparation together with *Paleoovidus vasilenkoi* (Fig. 5).



FIGURE 4. Paleogallus vialovi Enushchenko and A. Frolov, ichnospec. nov.

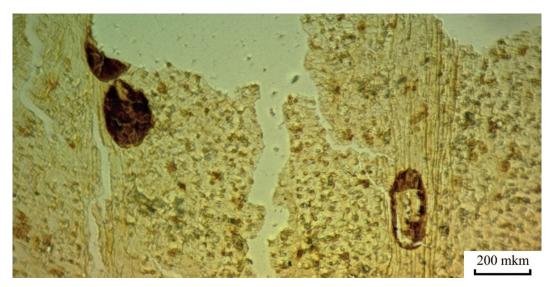


FIGURE 5. *Paleogallus vialovi* Enushchenko and A. Frolov, ichnospec. nov. and *Paleoovidus vasilenkoi* Enushchenko & Frolov, ichnospec. nov. on the leaf of *Ginkgo tapkensis* (specimen No Iya-2011-14/17-1b, Holotype).

2.4. Familia Paleominidae Vialov, 1975: 152, 153; Vasilenko 2005a: 55; Vasilenko 2005b: 629.

Internal traces of feeding – mines within the thicknesses of tissues in various parts of plants (*Paleomina lepidop-terana* Vialov 1975: 153)

2.5. Subfamilia Sugophytichninae Enushchenko and Frolov, ichnosubfam. nov.

Diagnosis. Traces of insect feeding with a style mouthparts apparatus engaged in piercing and sucking. The damage feeding represents the traces of punctures in the epidermis penetrating vegetative organs of plants, followed by the proliferation of surrounding tissues.

Sugophytichnida Enushchenko and Frolov, ichnogen. nov. (Figs 6–9)

Diagnosis. Rounded, rarely slightly elongated, dark-colored sections of 60–80 (100) μ m in diameter with a more or less pronounced puncture site in the center and elongated epidermal cells radially diverging from the edges (Figs 6, 7); located on the reverse side of the leaf blade, along the veins (Fig. 8) less often near them (Fig. 9), singly or in rows.

Etymology. The genus name is formed by a combination of the Latin words *sugo* – "suck" and *phyta* – "plant" with the addition of the ending *-chnidus*, in accordance with the rules of the nomenclature of the genus rank ichnotaxa (Article 20, ICZM).

S. pertusura Enushchenko and Frolov, ichnospec. nov.

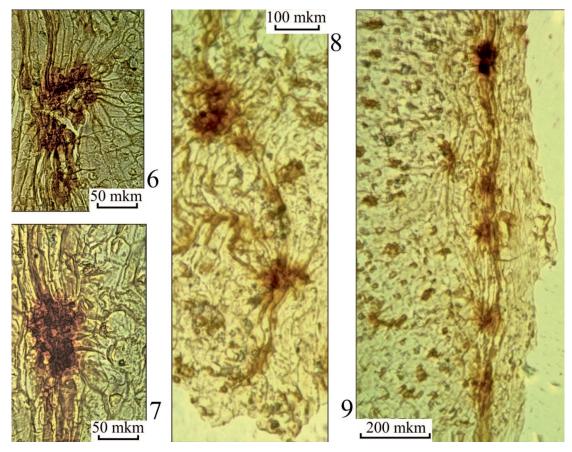
Holotype. Coll. Iya-2011-14 / 17-2, damage on a leaf of *Ginkgo tapkensis*. Irkutsk Basin, Iya River near the Vladimirovka village; middle member of Prisayan Formation, Middle Jurassic. The holotype is stored at the Institute of the Earth's Crust of the SB RAS (Irkutsk, Russia). **Further specimen**: Coll. Iya-2011-14/17-1b.

Diagnosis. Identical to that of genus description

Etymology. Species epithet is derived from the Latin word *pertusura* (-ae, *f*) – "drilling", "puncture".

II Ordo Phagozoonichnida Vialov 1975: 153 [recorded with misprint – "Phagozoonichnidea"].

Traces of animal nutrition (not considered here).



FIGURES 6–9. Sugophytichnida pertusura Enushchenko and A. Frolov, ichnogen., ichnospec. nov. (specimen No Iya -2011-14/17-2, Holotype): 6, 7—common view of *S. pertusura*, 8—*S. pertusura*, confied to the vein of *Ginkgo tapkensis*, 9—*S. pertusura* far from the vein of *G. tapkensis*.

Discussion

Insects during the Jurassic were the most diverse class of animals and were of great importance in terrestrial and freshwater ecosystems. In Eastern Siberia, knowledge of terrestrial insect communities, in comparison with freshwater communities, is consider as rather weak (Zherikhin, 1985). Traces of the interaction of terrestrial insects with plants within the region under consideration here are extremely rare and are described for the first time in this paper.

The studied oviposition, galls, and modified leaf epidermis left behind by insects are confined to the taphofauna of the *Mesoleuctra–Mesoneta* community. This community has important stratigraphic significance for Early Jurassic deposits of Kazakhstan (Karaganda Basin), Siberia (Kuznetsk and Irkutsk Basins) and Western Mongolia (Zherikhin, 1985). One of the richest insect locations of the *Mesoleuctra–Mesoneta* community are outcrops on the Iya River of the Irkutsk Basin. This location contains the remains of terrestrial insects, among which the Palaeotinidae cicadas (Zherikhin, 1985) are numerically dominant and for which trophic relations with Ginkgoales are assumed. This assumption is based on the distribution of the remains of Palaeotinidae cicadas and Ginkgoales leaves co-occuring in the same deposits in Kazakhstan, Siberia, and Western Mongolia (Zherikhin and Kalugina, 1985). Based on these observations, it can be assumed that the numerous punctures observed on the leaves epidermis of *G. tapkensis* were left behind by Palaeotinidae cicadas. At this stage of research it is difficult to establish affiliation of studied oviposition damage and galls to a definitive group of insects.

Conclusion

Paleontological materials acquainted us with only a small part of the true variety of Mesozoic insects. The existing collections from the discussed region, considered here, provide a sense of the taxa of the limnic insect fauna, while indeed the vast majority of insect species during the Jurassic, lived on land. Judging from the taxonomic composition, the terrestrial component of the taphonomic fauna of the study area reflects almost exclusively a fauna of floodplain forests, principally the inhabitants of trees and shrubs. In general, the knowledge of the Jurassic insect of Siberia, especially terrestrial taxa, is recognized as rather weak. Materials documenting the traces of insect feeding on plants can significantly supplement the information based on the contemporary insect fauna and the functioning of terrestrial communities. In the present work, the first steps of this documentation have been taken to contribute to this interesting subject.

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