ISSN 0031-0301, Paleontological Journal, 2020, Vol. 54, No. 4, pp. 371–374. © Pleiades Publishing, Ltd., 2020.
Russian Text © The Author(s), 2020, published in Paleontologicheskii Zhurnal, 2020, No. 4, pp. 50–53.

First Report of Insect Endophytic Oviposition from the Upper Permian of the Pechora Basin, on a Leaf of *Phylladoderma* (Peltaspermopsida: Cardiolepidaceae)

D. V. Vasilenko[a, b, *] and E. V. Karasev[a, c, **]

[a] *Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia*
[b] *Cherepovets State University, Cherepovets, Russia*
[c] *Kazan Federal University, Kazan, Russia*
**e-mail: vasilenko@paleo.ru*
***e-mail: karasev@paleo.ru*

Received December 25, 2019; revised January 21, 2020; accepted January 21, 2020

Abstract—The first endophytic oviposition from the Upper Permian of the Pechora Basin (Talbeyskaya Formation, Severodvinian–Vyatkian) is described in a formal system. *Paleoovoidus krassilovi* sp. nov. is a linear oviposition arranged in two oppositely directed rows on a leaf of *Phylladoderma arberi* Zalessky, 1913; it was probably produced by an odonatan insect. Cuticle punctures that probably represent traces of feeding by small and/or young palaeodictyopteroid nymphs were previously described from *Phylladoderma* leaves found in the same deposits. Fossil insects remain unknown from the Talbeyskaya Formation, but fossil records of plant–insect interactions enable the reconstruction of a well-balanced insect community that included sucking phytophages (palaeodictyopteroids) and predators (odonatans).

Keywords: evidence of plant-insect interactions, endophytic oviposition, Permian, Pechora basin, new species

DOI: 10.1134/S0031030120040140

INTRODUCTION

The oldest known endophytic ovipositions produced by insects are from the Upper Carboniferous, but there are very few such findings (Bethoux et al., 2004; Laaß and Hoff, 2014). Somewhat more forms are described from Permian deposits, but these paleontological objects are still quite rare in the Permian. The majority of endophytic ovipositions on plant leaves result from the reproductive activity of odonatan insects (Vasilenko and Rasnitsyn, 2007). Paleozoic endophytic ovipositions from the territory of Russia have so far only been described from the Isady locality (Severodvinian of the Upper Permian, Vologda oblast), where they are represented by one oviposition of an arcuate shape (Vasilenko, 2011; Aristov et al., 2013).

The endophytic ovipositions described in this work originate from the Adzva locality. Punctures of the leaf cuticle of *Phylladoderma arberi* Zalessky, 1913, that are probably traces of feeding by small and/or young palaeodictyopteroid nymphs on the mesophyll, were described earlier from the same beds (Vasilenko et al., 2014). These punctures are adjacent to the ovipositions on some leaves, but there is no reason so far to assume that they were connected in any way.

MATERIALS AND METHODS

The materials were collected by M.S. Ignatov, I.A. Ignatiev, and Yu.V. Moseichik in 2011 from outcrop 29A (Chernov, 1932) from the phylladoderm stratum in the upper Talbeyskaya Formation (Pechora series) along the right bank in the middle reaches of the Adzva River (Pechora basin). Well-preserved phytoleimmas of whole leaves were studied without pretreatment, and some of them were macerated by sequential immersion in nitric acid and potassium hydroxide solutions according to a standard procedure. The material was examined using Leica M165C and Zeiss Axioplan 2 light stereomicroscopes. Images were produced using a Leica DFC-420 camera and a Vega Tescan SEM with a BSE detector.

We followed previously published principles and approaches (Vasilenko, 2005, 2008, 2011; Maslova et al., 2016) for our taxonomic description of endophytic ovipositions.

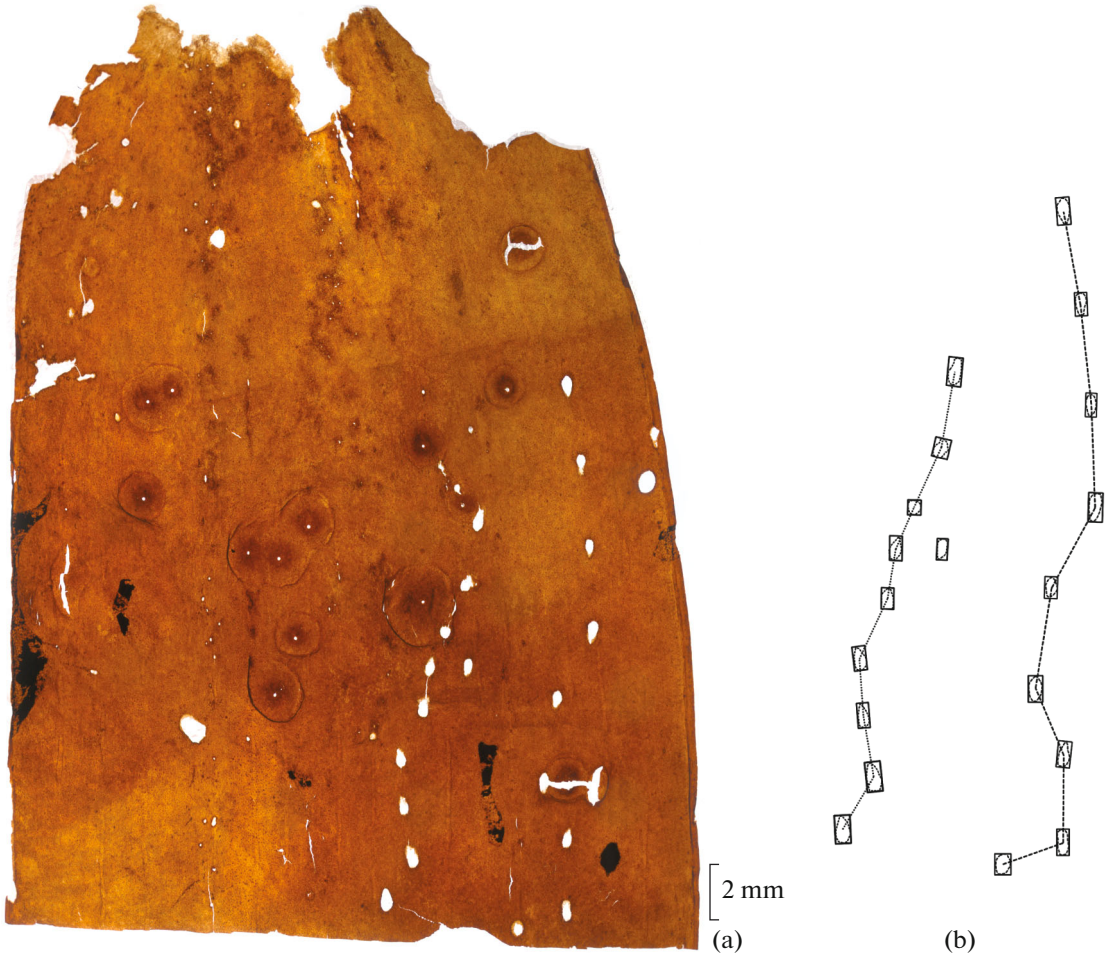

Fig. 1. Endophytic oviposition of *Paleoovoidus krassilovi* sp. nov. on a *Phylladoderma* leaf from Adzva locality (Severodvinian–Vyatkian, Permian of Pechora basin), holotype PIN no. 5483/4: overview of leaf with oviposition (a) and schematic representation of two oviposition chains (b).

Collection no. 5483 is preserved at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN RAS).

SYSTEMATIC PALEONTOLOGY

Family Paleoovoididae Vasilenko, 2005

Genus *Paleoovoidus* Vasilenko, 2005

***Paleoovoidus krassilovi* Vasilenko et Karasev, sp. nov.**

Etymology. The name is in honor of the paleontologist V.A. Krassilov.

Holotype. PIN no. 5483/4, two chains of endophytic ovipositions on a leaf of *Phylladoderma arberi* (Zalessky) Neuburg, 1960; Pechora basin, Chernyshev Ridge, right bank of the Adzva River in its middle reaches, outcrop 29A; Severodvinian–Vyatkian stages of the Permian; phylladoderm stratum in the upper part of the Talbeyskaya Formation.

Description (Fig. 1a). Oviposition of a linear shape, composed of medium-sized oval elements, located near the edge of the leaf blade on the underside of the leaf, oriented along the long axis of the leaf. The chain is slightly sinuous. The arrangement of oviposition elements is not dense. The sparseness is more pronounced in the right chain and less in the left. The elements of an individual chain are located approximately at the same distance from each other, with slight variations (Fig. 2). Some elements of the oviposition are distinctly egg-shaped.

Measurements, mm: maximal observed oviposition length approximately 20 (the sparse right chain of 8 elements) and approximately 15 (the denser left chain of 9 elements). The lengths of the individual oviposition elements, their width, and the distance between them are shown in Fig. 2.

Remarks. The arrangement of oviposition elements in the new species is most similar to that in *P. rectus* Vasilenko, but the two species are distinguished by the sizes of individual elements and the distances between them. The linear shape of the oviposition distinguishes *P. krassilovi* sp. nov. from the other

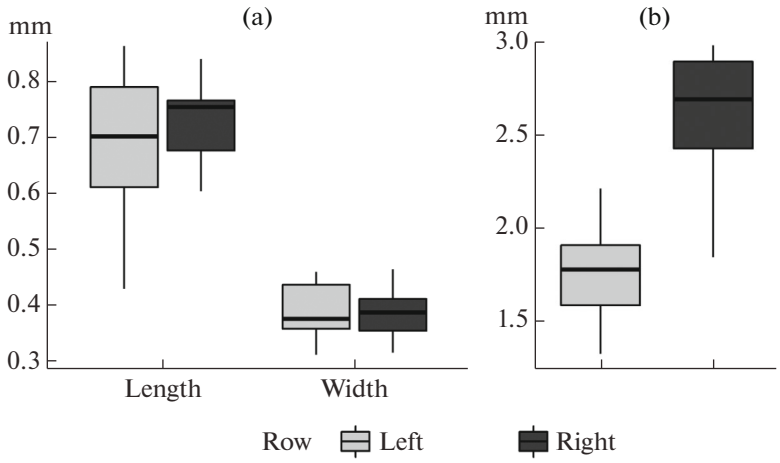

Fig. 2. Dimensions of individual *Paleoovoidus krassilovi* sp. nov. oviposition elements (a) and distance between them (b).

known species. Two parallel ovipositions were found on the leaf. The orientation of the egg-shaped elements shows that the directions of these ovipositions were opposite. It is entirely possible that both ovipositions belonged to the same individual; at least, it is obvious that both chains should be assigned to the same formal species, notwithstanding the small differences in dimensions (in particular, the distance between the elements). The variability of such features as the length and width of individual elements, as well as the distance between them, is shown in Fig. 2. The distance between the oviposition elements was apparently different for the two chains, whereas the length of individual elements was quite stable in both chains and fell within the limits of variability.

M a t e r i a l. Holotype.

DISCUSSION

The diagnosis of the genus *Paleoovoidus* is rather broad and encompasses almost all known structures interpreted as endophytic ovipositions, because the number of formal species described is still relatively small. Most of these structures are linear or arched ovipositions of medium-sized elements on leaves. The division of *Paleoovoidus* into distinct genus-level taxa for ovipositions of different shapes (chaotic, arched, or linear) may become necessary in the future, but such a division is premature at the current stage of research. We accept the overall concept of Sarzetti et al. (2009), especially regarding the refinement of the diagnosis of the genus *Paleoovoidus,* in relation to the material currently available to us.

The degree of preservation of the Adzva material described in this article is unique. The leaves with ovipositions are not represented by imprints in the rock, but rather by virtually intact leaf blades with perfectly preserved cuticles that can be easily separated from the fossil-bearing rock; moreover, all eggs in the ovipositions were likely buried after the egress of the larvae (or the egg shells were not preserved during fossilization), and therefore the oviposition has the appearance of openings arranged in a linear manner and generally corresponding to the size and shape of the eggs. These openings are not filled with rock and do not form casts, as often observed for imprints. However, they cannot be termed scars in the sense of leaf damage; scars have a specific elongated rhombic shape, often with pointed edges along the longer axis, and look like the traces of regeneration of cuts on the leaf tissue. These scars are found on the leaves of Paleozoic plants and sometimes on the leaves of Mesozoic gymnosperms but are rare on angiosperms (probably due to their leaves being relatively soft and thin). Scar sizes are extremely variable, so that it is hardly possible to infer egg size from scar size, but the arrangement of the scars on the leaf, as well as their mutual arrangement, corresponds to the characteristics of the oviposition. Thus, the scars are probably traces of incisions from the ovipositor, rather than remnants of the oviposition itself. The traces described in the present study are of a different type. These openings are assumed to be almost identical to the actual eggs. They are characterized by a fairly stable size and, in some cases, even a noticeable ovoid shape.

A new formal species of endophytic ovipositions provides additional unique evidence of the reproductive activity of insects (probably odonatans) in the Late Permian. The ovipositions along with the tissue punctures (traces of sucking) on *Phylladoderma* leaves described earlier from the same locality enable the reconstruction of a fairly balanced and diverse composition of the paleoentomofauna that included (from indirect indications) sucking phytophages (probably paleodictyopteroids) and, possibly, odonatans, active predators that mainly consume other insects (aquatic in the case of larvae, and terrestrial in the case of adults). The presence of insect remains in such an

oryctocenosis is highly likely, but no insect finds from these deposits have been reported yet; this may be for taphonomic reasons or due to insufficient collecting. It should be noted that all insects known so far from the Pechora sequence of the Adzva River Basin belong to the substantially older Rudnitskoe sub-formation of the Lekvorkut Formation, which is attributed to the Kungurian. All insects identified in these beds belonged to the families Geinitziidae (Aristov, 2004) and Lemmatophoridae (D.S. Aristov, personal communication, December 6, 2019) of the order Reculida.

ACKNOWLEDGMENTS

The authors are grateful to M.S. Ignatov (Main Botanical Garden, RAS), for kindly providing the *Phylladoderma* material, in which the ovipositions described were discovered, and to A.P. Rasnitsyn (PIN RAS) for reading the manuscript and providing valuable comments.

FUNDING

This work was supported by the Russian Foundation for Basic Research, projects 19-04-00046 and 18-04-00322.

REFERENCES

Aristov, D.S., The fauna of grylloblattid insects (Grylloblattida) from the end of the Late Permian to the first half of the Triassic, *Paleontol. J.,* 2004, vol. 38, no. 5, pp. 517–521.

Aristov, D.S., Bashkuev, A.S., Golubev, V.K., et al., Fossil insects of the Middle and Upper Permian of European Russia, *Paleontol. J.,* 2013, vol. 47, no. 7, pp. 641–832.

Bethoux, O., Galtier, J., and Nel, A., Earliest evidence of insect endophytic oviposition, *Palaios,* 2004, vol. 19, pp. 408–413.

Chernov, A.A., Stratigraphy and tectonics of the coal basin on the Adzva River in the Pechora region according to investigations carried out in 1929, *Izv. Vses. Geol.-Razv. Ob"ed.,* 1932, vol. 51, no. 70, pp. 1039–1051.

Laaß, M. and Hoff, C., The earliest evidence of damselfly-like endophytic oviposition in the fossil record, *Lethaia,* 2014, vol. 48, no. 1, pp. 115–124.

Maslova, N.P., Vasilenko, D.V., and Kodrul, T.M., Phytopathology in fossil plants: New data, questions of classification, *Paleontol. J.,* 2016, vol. 50, no. 2, pp. 202–208.

Sarzetti, L.C., Labandeira, C.C., Muzon, J., et al., Odonatan endophytic oviposition from the Eocene of Patagonia: The ichnogenus *Paleoovoidus* and implications for behavioral stasis, *J. Paleontol.,* 2009, vol. 83, no. 3, pp. 431–447.

Vasilenko, D.V., Damages on Mesozoic plants from the Transbaikalian locality Chernovskie Kopi, *Paleontol. J.,* 2005, vol. 39, no. 6, pp. 628–633.

Vasilenko, D.V. and Rasnitsyn, A.P., Fossil ovipositions of dragonflies: review and interpretation, *Paleontol. J.,* 2007, vol. 41, no. 11, pp. 1156–1161.

Vasilenko, D.V., Insect ovipositions on aquatic plant leaves *Quereuxia* from the Upper Cretaceous of the Amur Region, *Paleontol. J.,* 2008, vol. 42, no. 5, pp. 514–521.

Vassilenko, D.V., The first record of endophytic insect oviposition from the Tatarian of European Russia, *Paleontol. J.,* 2011, vol. 45, no. 3, pp. 333–334.

Vassilenko, D.V., Shcherbakov, D.E., and Karasev, E.V., Biodamage on *Phylladoderma* leaves from the Upper Permian of the Pechora Basin, *Paleontol. J.,* 2014, vol. 48, no. 4, pp. 447–450.

Translated by S. Semenova