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First evidence of plant – arthropod interaction at the Permian – Triassic boundary in the Volga Basin, European Russia

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ABSTRACT

Arthropod traces are found on fossil leaves from the recently discovered in the Volga River Basin trans-boundary end-Permian – earliest Triassic sequence at the base of the Vetlugian Series conformable on the Vyatkian Horizon of the Tatarian Stage. The flora of this interval consists principally of Permian survivors with a few derived forms of peculiar leaf morphology, assigned to the Peltaspermales. A variety of arthropod feeding marks is found on one of such forms, *Vjaznikopteris rigida* Naug. The most remarkable among them are the histoid galls of mites, as well as the curvilinear mine, apparently the geologically oldest hitherto known. The mine track is associated with U-shaped incisions, presumably for cocoon case construction. This association contributes to our knowledge of plant – insect interaction during critical periods of geological history.

KEY WORDS: Plant – insect co-evolution. Fossil galls. Fossil mines. Paleoecology. Permian – Triassic boundary. Russia.

INTRODUCTION

Despite the recently increasing interest in the Permian – Triassic boundary (PTB) events, the terrestrial biota of this interval remains poorly studied, partly because continuous transboundary sequences are rare worldwide. In the Volga River Basin, the historical stratotypic area of the Upper Permian, a widespread hiatus occurs at the base of the Lower Triassic (the Vetlugian Series) producing an impression of abrupt extinction of the Late Permian Tatarinian flora (Gomankov & Meyen 1986). A transitional Permian – Triassic sequence has been first described at Nedubrovo on the Kitchmenga River (Krassilov *et al.* 1999). Here the Nedubrovo Member of the Vetlugian Series is conformable on the Vyatkin Horizon of the Tatarian Stage, containing a plant mesofossil and palynological assemblage with a number of typical Tatarian – Zechsteinian forms, such as *Tatarina* spp., *Quadrocladus* spp., *Ullmannia* cf. *bronnii* Goepp, and a palynomorph *Klausipollenites schaubergii* (Potonié et Klaus) Jansonius. These forms co-occur with a widely recognized megaspore marker of the lowermost Triassic, *Otynisporites eotriassicus* Fugl. and the mass occurrence of *Tympaniicysta stoschiana.* The latter microfossil has been previously considered as indicating the PTB "fungal spike", but re-interpreted as a green alga marking eutrophication of estuarine waters and marine shallows at the PTB (Krasislov *et al.* 1999, Afonin *et al.* 2001, Krassilov 2003). *Lystrosaurus*, a vertebrate Lower Triassic marker, is found above the floristic horizon. On paleontological and magnetostratigraphic evidence, the Nedubrovo Member is correlated with the interval of mixed occurrences of Permian and Triassic forms in the *Clarkinia meishanensis – Hindeodus praeparvus* zone, the uppermost Changxingian of the stratotypic Meishan Section of South China (Lozovsky *et al.* 2001).

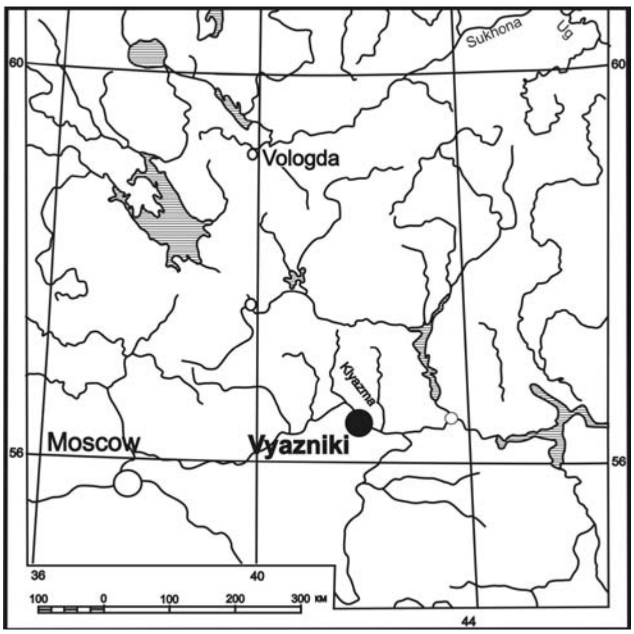

Figure 1. Map of the upper Volga River Basin showing the Vyazniki Locality.

Another locality of the same or slightly older stratigraphic level has been recently discovered at Vyazniki on the Klyaz'ma River (Sennikov & Golubev 2005). Here the dominant floristic elements are *Permophyllocladus* Karasev et Krassilov and *Vjaznikopteris* Naugonykh, both closely related to the Permian peltasperms, but of a peculiar polymorphic vegetative morphology (Karasev & Krassilov 2007). *Permophyllocladus* is a phylloclade (planated leaf-like shoot with connate leaves) first appearing in the fossil record. *Vjaznikopteris* is an irregularly dissected leaf of unusual shape deserving special attention as a major target of mining and gall induction. In the light of these findings, the transitional PTB flora was a mixture of Permian survivors and the short-lived derived forms of a high morphological plasticity peculiar for this time interval. The first finds of arthropod traces on the foliar structures of such short-lived plant genera open new perspectives for functional analysis of the floristic changes at the PTB.

MATERIAL AND METHODS

The material came from Sokovka Locality, an outcrop of sandstones and variegated clays on the steep right slope of the Klyaz'ma River Valley in the northern outskirts of Vyazniki (Fig. 1). The locality also contains faunistic remains of bivalves, ostracods, conchostracans, insects and vertebrates (Sennikov & Golubev 2005).

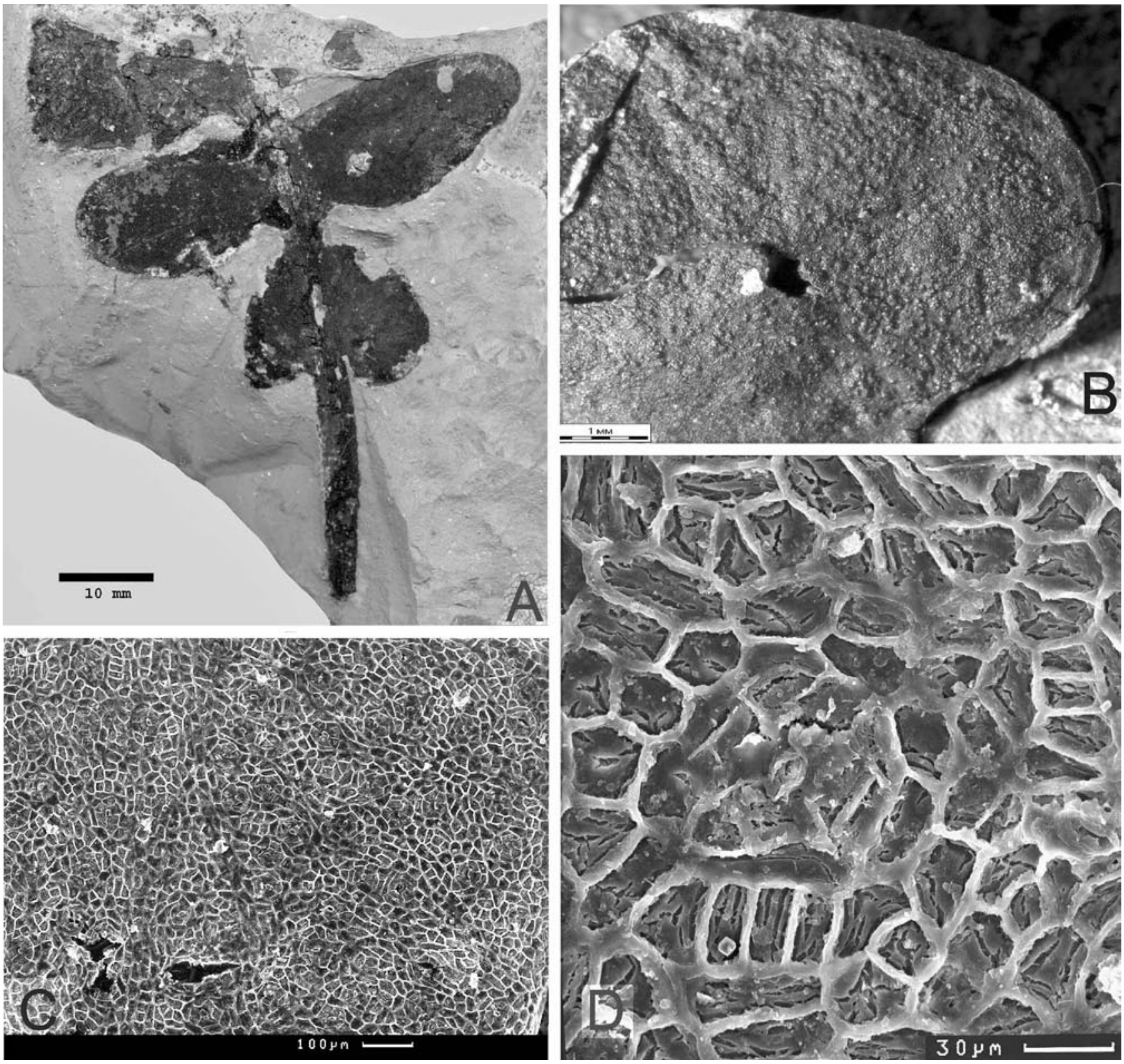

Figure 2. A, *Vjaznikopteris rigida* Naugolnykh, PIN 5139/9; B, leaf lobe of the same plant, PIN 5139/72, bearing eriophyid microgalls; C, epidermal structure of the affected area showing a non-functioning stoma and the strains of hyperplastic cell division (D).

Plant macrofossils are mainly shoot and leaf compressions of pteridosperms and conifers. Common among the latter are the lobed leaves of *Vjaznikopteris rigida* (Fig. 2A) represented by 43 specimens in our collection. Arthropod traces are inconspicuous on intact compressions, but become fairly distinct on cuticular preparations showing microscopic details of histoid galls.

The plant remains were studied under the stereomicroscope and the compressions were subsequently removed from the rock, macerated, and studied under an Axioplan 2 light microscope and CAMSCAN scanning electron microscope. Microphotographs were obtained with Nikon Coolpix 4500 and Leica DFC420 digital cameras.

The collection is deposited in the Paleontological Institute, Russian Academy of Sciences, PIN no. 5139.

OBSERVATIONS

The arthropod trace assemblage on *Vjaznikopteris rigida* includes external feeding holes, minute pock microgalls, lenticular galls, and leaf mines. The most frequently occurring microgalls are conical emergences patchily distributed over the micropapillate leaf surface (Fig. 2B). Externally they resemble pock galls of eriophyid mites (Meyer 1987), and the epidermal structure of the affected leaf area reveals cecidogenic histological features, such as the aborted stomata and hyperplasy of surrounding cells (Figs 2C, D). The stomatal apertures are very small or obliterated. The stomatal primordia with radial subsidiary cells around an undivided stomatal initial are discernible in the areas of hyperplastic cell division producing conspicuous strains of linearly aligned, compressed, rectanguloid cells (Fig. 2D). The cuticle of such areas is striate and irregularly crevassed as a result of erosive gall impact.

The lobing of *Vjaznicopteris* leaf blades is extremely irregular and the sinuses between the lobes are angular or slit-like (Fig. 2A). In a small leaf shown in Fig. 3A, the half blade is dissected into three lobes with the sinuses extending nearly to the midrib. The margin is mined by a linear track with minute incisions, marked by a prominent black ridge of callus. Segmentation of the leaf blade in *Vjaznikopteris* might have been initiated by marginal incisions that, with leaf growth, expanded into slit-like, and then wedge-shaped sinuses. Two lower lobes are separated by a winding slit ("c" in Figure 3A), on one side of which a sinuous track is preserved (Figs 3E, F). The track coils show a solid median ridge evidently representing a continuous frass line that is locally punctuated by minute clumps of frass pellets (arrow in Fig. 3F). On the upper lobes, the mine track delineates two U-shaped contours about 1 mm wide, oriented with their broad end toward the margin (Figs 3A, B). They are, marked by a thick slightly crenulate cutting line. One of them is somewhat angular, underlain by the lower leaf cuticle, while the upper cuticle is missing ("b" in Fig. 3A, magnified in Fig. 3B), the other is smoothly curved, perforated in the middle, with remnants of yellowish cuticle over the periphery ("a" in Fig. 3A, magnified in Fig. 3C).

The larger U-shaped contour on leaf compression in Figure 3D is bordered by a thick callus ridge with a strain of ferruginous specks that may correspond to frass pellets (magnified in Fig. 3E). Inside the contour, the upper leaf cuticle is removed, leaving an irregularly cut margin. The lower leaf cuticle is exposed the interior surface up, showing stomata.

In another specimen (Fig. 4A), a leaf lobe is delineated by a mine track that coils into a tight spiral at the base of it on acroscopic side (arrow in Fig. 4A). The track shows a row of yellowish ferruginous grains, that are more dense in the coils of the spiral part of the mine (Fig. 4C). An elliptical body inside the spiral track may represent a pupation cocoon, but it is insufficiently preserved for a confident interpretation.

DISCUSSION

The fossil record of terrestrial vegetation shows that long periods of relative stability are interrupted by the shorter periods of rapid change (reviewed in Krassilov 2003). Plant – arthropod interactions might have contributed to the high rate evolutionary changes at the critical boundaries (Labandeira *et al.* 1994, 2002a, b). Here we report on arthropod traces on leaves of the recently discovered transitional end-Permian – basal Triassic flora of the Volga River Basin, most of them occurring on *Vjaznikopteris rigida* a highly polymorphous leaf morphotype peculiar to the transitional interval. Among them, the pock structures and associated histological features indicate an eriophyid mite gall of the type common on the leaves of Tertiary and extant angiosperms. This gall occurrence is evidence of the great antiquity of mites as a major group of cecidogenous arthropods.

The mine tracks on the leaves of the same plant are perhaps the oldest presently known. Those extending along the margin and spirally coiled on end are certainly the earliest records of ophioheliconomes. Irregular segmentation of leaf blade characteristic of *Vjaznikopteris*, might have developed from marginal incisions that expanded into the wedge-shaped gaps with leaf growth. Such false lobes are known to be inflicted by marginal mines on growing leaves, in which the mine track itself is marked by a callus ridge or obliterated (Needham *et al.* 1928, Hering 1951).

The peculiar U-shaped structures with the upper epidermis, or occasionally the entire leaf blade, missing are here interpreted as cut-outs for cocoon case construction. Modern miners make cocoons for hibernation of the larva or pupation. Detached cocoons are sometimes preserved as body fossils, but their location in the mine is marked by conspicuous prominences on the fossil mine tracks. Some insects cut their cocoons out with a piece of leaf (or epidermis only) wrapping it as a cocoon case. Marginal holes

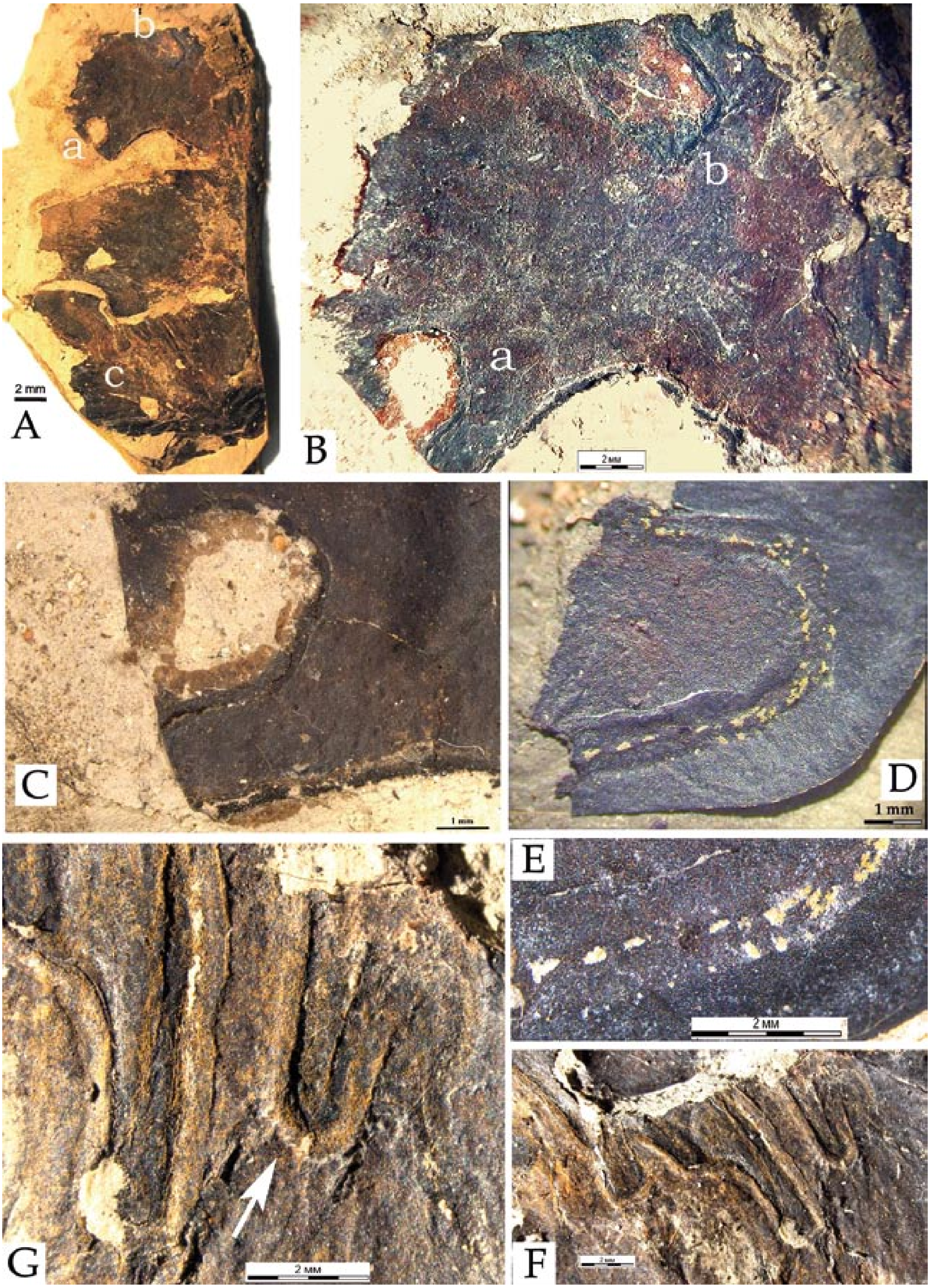

Figure 3. A – C, F, G, *Vjaznikopteris rigida* Naugolnykh, PIN 5139/69, leaf blade dissected by the slit-like and wedge-shaped incisions: letters a, b – U-shaped contours with whole blade or epidermal cut-outs, c – sinuous mine track; B, upper lobe of the same leaf showing a marginal mine track and two U-shaped contours; C, contour with the whole leaf blade cut out leaving narrow cuticle strip along the margin; E, F, a sinuous mine track, arrow on frass pellets; D, E, *Vjaznikopteris rigida* Naugolnykh, PIN 5139/75, U-shaped contour with the upper epidermis removed, the yellow bodies probably representing frass pellets of a bordering track.

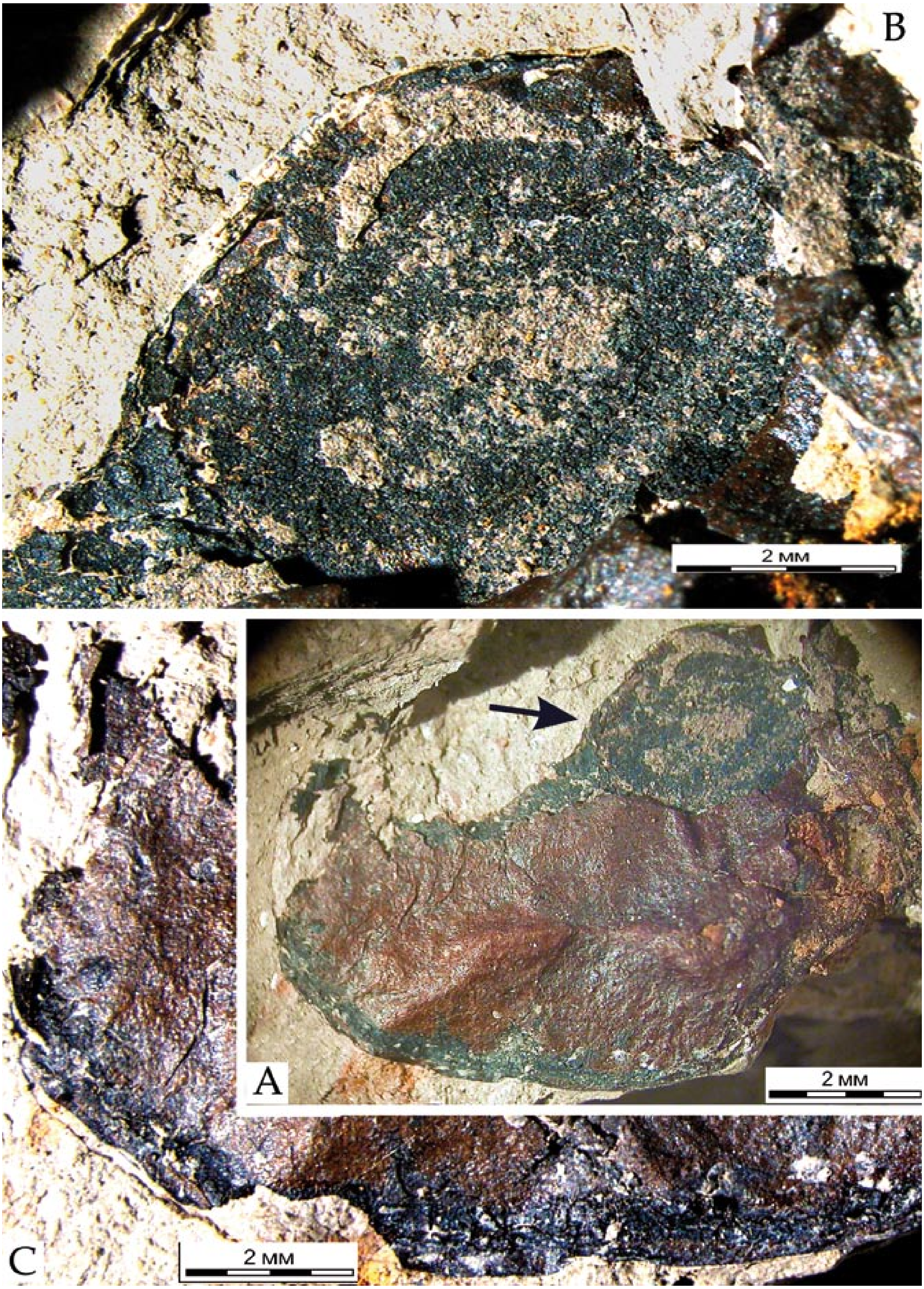

Figure 4. A – C. *Vjaznikopteris rigida* Naugolnykh, PIN 5139/71, leaf lobe mined over the margin and coiled around an elliptical bulge (arrow), B, coiled part of the track magnified; C, part of marginal track with distinct frass pellets.

("cut-outs") for cocoon cases are often preserved on fossil angiosperm leaves.

The habit of cutting leaves for cocoon cases or nest construction occurs among non-folivorous insects, such as megachilid bees known since the Eocene (Brooks 1955). Among the present-day miners, pupation cocoons are cut out and transformed into lenticular pupation cases by sawflies and beetles, as well as by the heliozelid and tischeriid Lepidoptera (Hering 1951). In all the Helozelidae (Lepidoptera), *Rhynchaenus* (Coleoptera: Curuculionidae) and some species of *Phyllotoma* (Hymenoptera: Tenthredinidae), pupation case is made of the whole leaf piece, whereas the habit of cutting out the upper epidermis alone is characteristic of buprestid beetles mainly.

On *Vjaznikopteris*, the U-shaped structures are obviously associated with mining and their contours are delineated by the marginal mine tracks. A piece of upper epidermis or occasionally the whole leaf blade can be removed from within the contour indicating a coleopteran habit of case construction. In addition, the configuration of the erratically winding mine track on *Vjaznicopteris* is characteristic of coleopteronomes in the first place.

U-shaped structures are known also from the roughly contemporaneous trace assemblages on glossopterid leaves from South Africa (observed by one us) and on gigantopterid leaves from North America (Labandeira 2002) presumably representing a widespread parasitic habit of the time.

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