

The First Documented Occurrence of Phyllophagy in Pre-Cretaceous Insects: Leaf Tissues in the Gut of Upper Jurassic Insects from Southern Kazakhstan

A. P. Rasnitsyn and V. A. Krassilov

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117868 Russia

Received December 8, 1998

Abstract—*Brachyphyllophagus phasma* A. Rasnitsyn, gen. et sp. nov. and *B. phantassus* A. Rasnitsyn, sp. nov. are described from the Upper Jurassic of Kazakhstan. They are insects of uncertain systematic position, possibly belonging to the same order as embiids. The gut contents of these specimens, as well as of the stick insect *Phasmomimoides minutus* Gorochoy, 2000 from the family Susumaniidae, is represented by the leaf fragments of *Brachyphyllum* or *Pagiophyllum* with cuticular characters of the Hirmerellaceae, accompanied by the pollen grains of *Classopollis*.

INTRODUCTION

The earliest chewing marks on the leaves of terrestrial plants, made by organisms of the insect size class, are known since the Late Carboniferous, but were rare until the Late Cretaceous (except for leaf mines, i.e. selective chewing out of the leaf parenchyma, common in the Late Cretaceous; Zherikhin, 1980). However, attribution of these feeding traces to insects and not to, say, myriapods or terrestrial crustaceans, remains conjectural. It is also uncertain whether the marks were left on alive, rather than on fallen leaves. Some insect groups now characterized by chewing phyllophagy already had appeared in the Paleozoic (the oldest stick insects in the terminal Early Permian; Gorochoy, 1994) but remained uncommon at least until the Cretaceous (Zherikhin, 1980). However, these data are not very reliable because the changes in life history are not always closely correlated with morphological evolution and its taxonomic interpretations. Therefore, the question concerning the time of origin of such important and characteristic peculiarities of insects as chewing upon ample parts of leaves is still open.

During recent studies of the gut contents of fossil insects by the present authors, chewing palynophagy was found to have been widespread at least in the Permian and Jurassic (Rasnitsyn and Krassilov, 1996a, 1996b; Krassilov and Rasnitsyn, 1997; Krassilov *et al.*, 1997a, b) and to have occurred in the Cretaceous (data from this period are still limited; Krassilov and Rasnitsyn, 1982). Previously, this phenomenon was predicted from indirect evidence (Sharov, 1966, 1968; Rasnitsyn, 1969, 1980). Pollen overwhelmingly dominates in gut contents in dozens of the studied specimens, belonging to various orders. The leaf fragments are revealed only in three instances described below, being not an admixture with the pollen but the only rec-

ognizable element of the gut contents, excluding the few isolated pollen grains which occasionally adhered to the leaves. The leaf fragments are discovered in two insect groups that were not closely related; and indicate rare cases of specialization for the Jurassic. It is of interest and possibly not mere coincidence that the host plant was the same in both cases, and possibly even more important that it belongs to a group of conifer-like proangiosperms, i.e., precursors and possibly even ancestors of the angiosperms (Krassilov, 1997). The leaves of *Brachyphyllum*-type had a loose, succulent mesophyll, which made them especially attractive to chewing insect phyllophages. Jurassic insects fed on the pollen of these plants as well (Krassilov *et al.*, 1997b). Hence, active influence from insects possibly favored the evolution of these plants towards angiospermy.

The part of this paper with the description of the Brachyphyllophagidae is by A.P. Rasnitsyn, using some of the ideas of A.V. Gorochoy. The plant material is described by V.A. Krassilov. The material studied (including the types) is deposited in the collection of the Paleontological Institute, Russian Academy of Sciences (PIN).

SYSTEMATIC PALEONTOLOGY

Phyllophagous Stick Insect

A food mass consisting of leaf fragments of *Brachyphyllum* or *Pagiophyllum* (see below) is found in the gut of the insect (Fig. 1; Pl. 9, fig. 1) described as a stick insect *Phasmomimoides minutus* Gorochoy, 2000, assigned to the family Susumaniidae and subfamily Phasmomimoidinae (concerning the complicated taxonomical history of this group of insects and its present position in the system see Gorochoy, 2000). The fossil

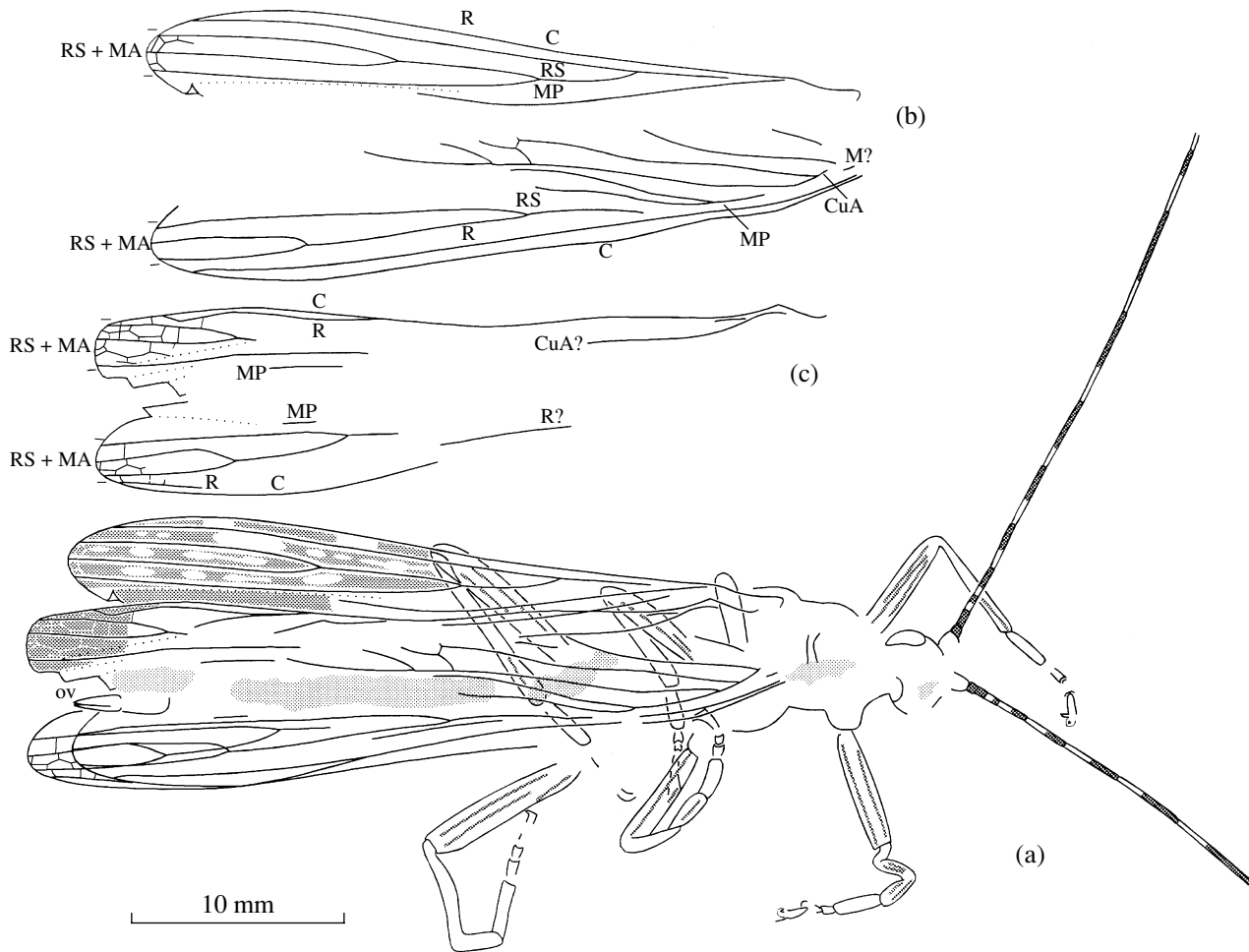


Fig. 1. *Phasmomimoides minutus* Gorochov, 2000, holotype PIN, no. 2384/261: (a) complete female; (b, c) its fore- and hindwing venation as preserved. Symbols: ov, ovipositor; vein symbols as usual; food remains in the mouth cavity and in the gut slightly shaded, preserved elements of color pattern more densely so. Scale 10 mm for all figures.

was collected in the deposits of the Upper Jurassic Karabastau Formation in Aulie, Karatau Range near the village of Mikhailovka (Chayan District, Chimkent Region, South Kazakhstan).

From the plant material filling the gut of *Ph. minutus* the leaf fragments with well preserved cuticles (Pl. 9, figs. 2–5) were extracted using the maceration technique. Their sizes are up to 0.5 mm². The contours of the margin and base of the small, scale-like leaves are discernible in some instances. The cuticle of the supposedly lower leaf surface is thick. It was clearly developed contours of polygonal and irregularly polygonal

cells that are isodiametric with rounded angles, or longitudinally (rarely transversely) elongated and pointed, thick-walled. The isodiametric cells are ca. 25 µm in diameter, the elongate ones up to 40 µm long. The cells chiefly show no regular arrangement or form short longitudinal rows.

The stomata are developed over the whole surface, except for the narrow marginal zones consisting of comparatively small cells. The stomatal apparatuses are sunken, oriented longitudinally, more rarely oblique relative to the leaf long axis, forming short rows of two or three stomata arranged in line. In some instances the

Explanation of Plate 9

Fig. 1. *Phasmomimoides minutus* Gorochov, 2000, holotype PIN, no. 2384/261 (×2).

Figs. 2–5. Epidermal structure of the fragments of scale-like leaves extracted from the gut of *Ph. minutus*: 2, pollen grain of *Clas-sopolis* adhering to the cuticle, SEM (×2500); 3–5, configuration of the cells and stomata, SEM (×800, 330 and 260).

Fig. 6. Cuticle from the gut of *Brachyphyllophagus phantasmus* A. Rasnitsyn, sp. nov., holotype PIN, no. 2384/260, part of stomatal groove visible, SEM (×550).