

# Phasmomimidae: Are They Orthoptera or Phasmatoptera?

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Received December 8, 1998

**Abstract**—The family Phasmomimidae (Orthoptera) is restricted to the genera *Phasmomima* Sharov, 1968 and *Jurophasmomima* Gorochov, 1988 from the Upper Jurassic of Kazakhstan. Other genera previously assigned to this family (except for the genus *Paraphasmomima* Zherichin, 1985 from the Jurassic of Siberia whose affinities are obscure) are transferred to Phasmatoptera as the family Susumaniidae Gorochov, 1988, stat. nov. (Susumaniioidea Gorochov, 1988, stat. nov.). The latter family comprises two subfamilies, Susumaniinae Gorochov, 1988 (= Kolymopterinae Gorochov, 1988, syn. nov. = Hagiphasmatidae Ren, 1997, syn. nov.) known from the Cretaceous and Paleocene of Eurasia and North America, and the monobasic Phasmomimoidinae Gorochov, 1988 (including *Phasmomimoides minutus* sp. nov.) from the Upper Jurassic of Kazakhstan.

## INTRODUCTION

The family Phasmomimidae was established by Sharov (1968) to include three species of the genera *Phasmomima* and *Phasmomimoides* with the forewing venation resembling that of fossil stick insects. He attributed this family to Orthoptera, because some body structures (4-segmented tarsus without arolium, carnivorous mandibles) possibly belonging to a representative of the Upper Jurassic genus *Phasmomima* are incompatible with its assignment to Phasmatoptera. The body is poorly preserved in the Upper Jurassic *Phasmomimoides* species, and another. Lower Cretaceous species ascribed to the same genus by Sharov is known from the forewing only.

Subsequently, several related genera and species described from isolated wings from the Cretaceous and Paleocene were assigned to this family or to other groups of insects (Rice, 1969; Kevan and Wighton, 1981; Kuz'mina, 1985), including one of the modern groups of Phasmatoptera (Birket-Smith, 1981). Among these fossils a quite remarkable wing was referred to the genus *Paraphasmomimella* and originally interpreted (Kuz'mina, 1985) as a forewing of Phasmomimidae with partly reduced venation.

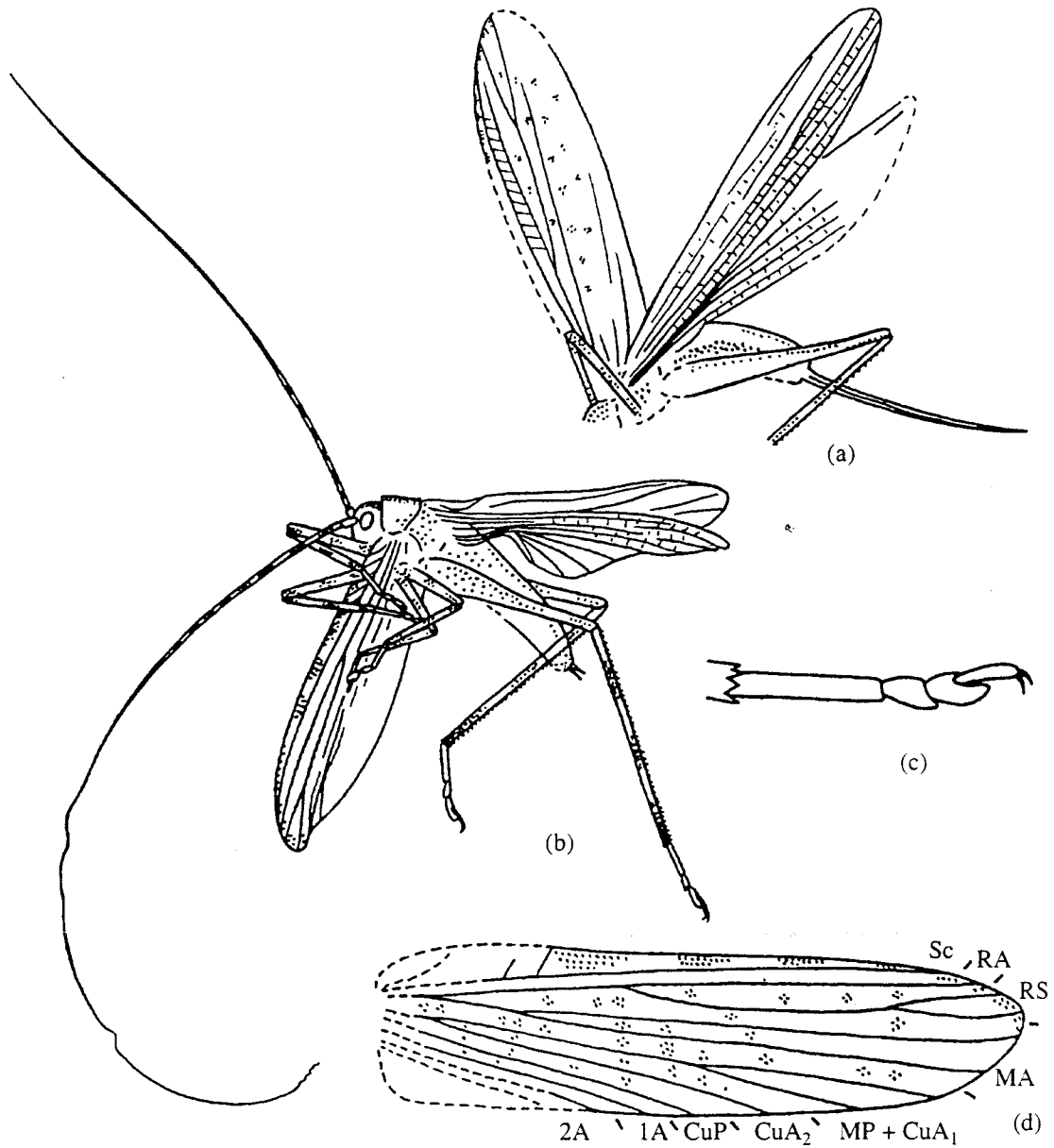
Later the family was retained in the same volume and divided into four subfamilies: Phasmomiminae, Phasmomimoidinae, Susumaniinae and Kolymopterinae (Gorochov, 1988). The first one included the Upper Jurassic *Phasmomima* and *Jurophasmomima*, closely related genera undoubtedly belonging to Orthoptera, so far as the well preserved bodies of Phasmomiminae were found (Figs. 1a–1c). The second subfamily was restricted to the genus *Phasmomimoides* with the only Upper Jurassic species included. Most of the Cretaceous genera and one from the Paleocene were placed in the third subfamily. For three Cretaceous genera with supposedly somewhat reduced forewing venation

(*Paraphasmomimella*, *Palaeopteron* and *Kolymoptera*) the subfamily Kolymopterinae was established.

The same classification of Phasmomimidae was adopted in the book on the system and evolution of the suborder Ensifera (Gorochov, 1995). The body fossils of Phasmomimoidinae, Susumaniinae and Kolymopterinae were virtually absent, but it is noteworthy that in the paper on Jurassic and Cretaceous Phasmatoptera (Gorochov, 1993) a drawing and a photograph were published of a whole insect with barely traceable venation from the Upper Jurassic (Fig. 2), provisionally assigned to the Aerophasmatidae incertae sedis, then the only superfamily of stick insects more or less reliably known from the post-Triassic Mesozoic.

Recently one more family of stick insects, the Hagiphasmatidae, was described from the Upper Jurassic or Lower Cretaceous, and the drawings and photographs of several complete, finely preserved specimens with the wings fully expanded were published (Ren, 1997). This amazing discovery allows us to resolve the question on the systematic position of the Susumaniinae and Kolymopterinae unequivocally. They belong to the same taxon as the Hagiphasmatidae, but the first subfamily was described on the basis of the forewings whereas the second was based on the isolated costal lobes of the hindwings, interpreted as the forewings. There were several reasons for such an error: first, these costal lobes are obviously broken off easily; second, they bear near the base (posterior to 1A) an area with irregular reticulate venation resembling the forewing anal lobe, a condition not found in the hindwings of any other orthopteroids (Figs. 3f, 3g); third, in the best preserved hindwing known prior to the last finds, this area is poorly preserved (Fig. 4b).

Thus, only the systematic position of Upper Jurassic Phasmomimoidinae still remained unclear. In the three-branched RS in both wing pairs they resemble the Phasmomiminae (RS bears two or three branches in the lat-

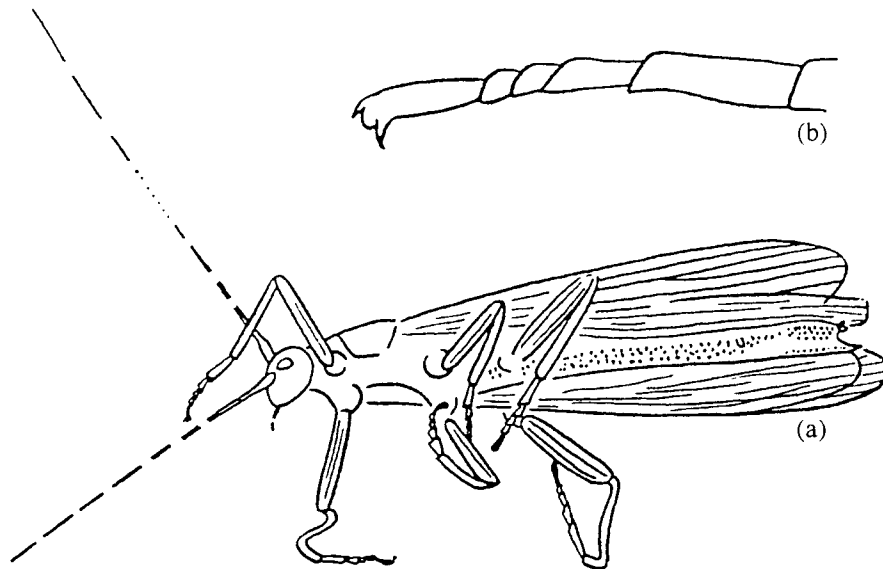


**Fig. 1.** Members of Phasmomimidae from the Upper Jurassic of Kazakhstan: (a) specimen PIN, no. 2784/7, female lacking the head and several legs (gen. et sp. indet.); (b, c) specimen PIN, no. 2904/1976, complete male and its hind tarsus (gen. et sp. indet.); (d) forewing of *Jurophasmomima punctata* Gorochov, 1988, holotype PIN, no. 2784/9. After Gorochov (1988).

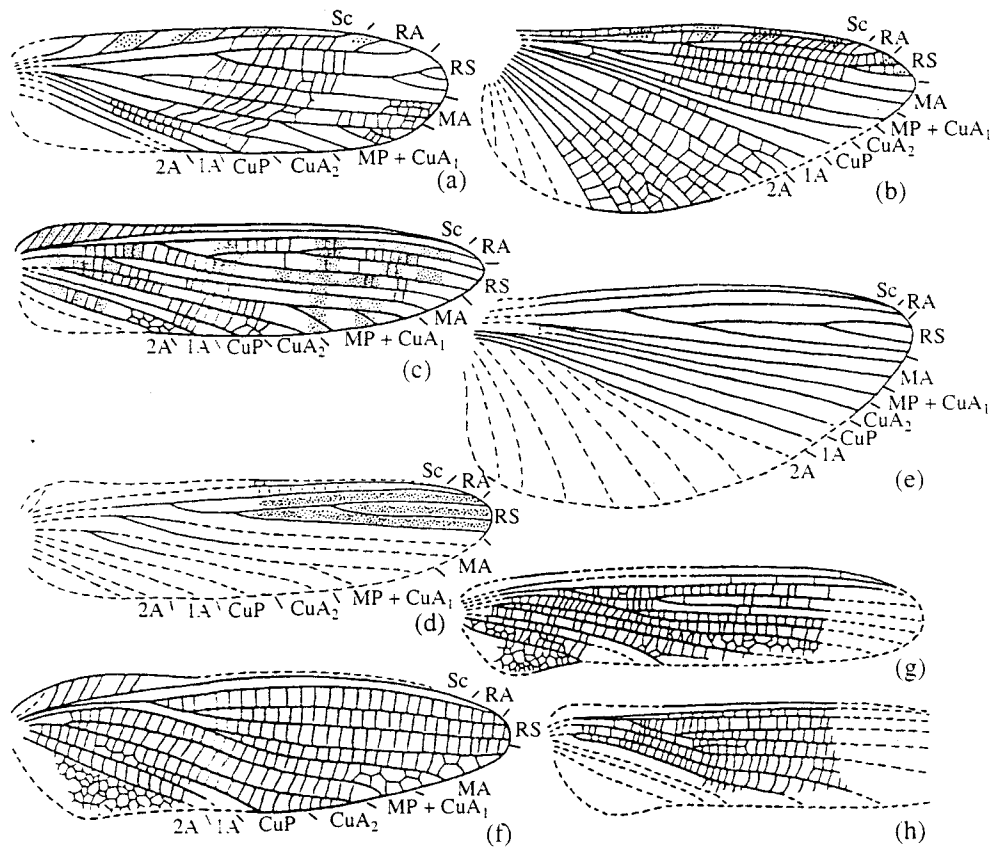
ter, and always two in the Susumaniinae), but in the proximal displacement of both RS bifurcation and RS base and in the widened area between 1A and 2A in the forewings, the Phasmomimoidinae are similar rather to the Susumaniinae (Sharov interpreted this similarity as synapomorphic and included the members of the two latter subfamilies in one genus) (Figs. 1d, 3, and 4). Re-examination of the above-mentioned specimen of Upper Jurassic stick insect shows that it should be assigned to the Phasmomimoidinae (to the genus *Phasmomimoides*), and confirms allocation of this subfamily to Phasmatoptera and probably to the same family as Susumaniinae.

An additional indirect evidence for the assignment of the superfamily Susumaniioidea to stick insects is the paleontologically documented feeding on plant leaves of at least some of their oldest, Late Jurassic representatives (Rasnitsyn and Krassilov, 2000). Such a diet is characteristic of all living stick insects, but possibly not of Jurassic and older orthopterans.

Below the systematic position of orthopteroids, formerly assigned to the Phasmomimidae, is reconsidered. The material (including types) is deposited in the Paleontological Institute, Russian Academy of Sciences (PIN).



**Fig. 2.** *Phasmomimoides minutus* sp. nov., holotype PIN, no. 2384/261, Upper Jurassic of Kazakhstan: (a) complete female; (b) fore tarsus of female. After Gorochov (1993).



**Fig. 3.** The wings of Orthoptera and Phasmatoptera: (a, b) *Phasmomima maculomarginata* Sharov, 1968, Upper Jurassic of Kazakhstan: (a) forewing, holotype PIN, no. 2239/484 (with additions from specimen PIN, no. 2066/935); (b) hindwing, specimen PIN, no. 2066/935; (c–e) *Phasmomimoides* spp., Upper Jurassic of Kazakhstan: (c) forewing of *Ph. lineatus* Sharov, 1968, holotype PIN, no. 2554/318; (d) forewing of *Ph. minutus* sp. nov., holotype PIN, no. 2384/261; (e) specimen PIN, no. 2997/1819, hindwing (sp. indet.); (f–h) forewings: (f) *Presusumania semenica* Gorochov, 1988, holotype PIN, no. 2385/450, Lower Cretaceous of Siberia; (g) *Cretophasmomima vitimica* Kuzmina, 1985, holotype PIN, no. 3064/8392, Lower Cretaceous of Siberia; (h) *Cretophasmomimoides reductus* Gorochov, 1988, holotype PIN, no. 3145/1146, Lower Cretaceous of Mongolia. After Sharov (1968), Kuz'mina (1985) and Gorochov (1988).

## SYSTEMATIC PALEONTOLOGY

Order Orthoptera

Suborder Ensifera

Superfamily Phasmomimoidea Sharov, 1968

## Family Phasmomimidae Sharov, 1968

Composition. *Phasmomima* Sharov, 1968; *Jurophasmomima* Gorochov, 1988 from the Upper Jurassic of Kazakhstan.

The position of Phasmomimoidea in the system of the suborder Ensifera was analyzed in an earlier monograph (Gorochov, 1995). All the suprageneric taxa of the Phasmomimoidea were described in that paper; the

superfamily diagnosis needs no revision, and the diagnosis of the family Phasmomimidae is identical to that of the former subfamily Phasmomiminae (the genus *Paraphasmomima* Zherichin, 1985 is herein excluded from the Phasmomimoidea, and its relationships remain unknown).

Order Phasmatoptera

Superfamily Susumaniioidea Gorochov, 1988, stat. nov.

*Susumaniinae*: Gorochov, 1988, p. 37.

Diagnosis (Figs. 2; 3c–3h; 4). Distinct from Permian and Triassic Prochresmodoidea Vishniakova,

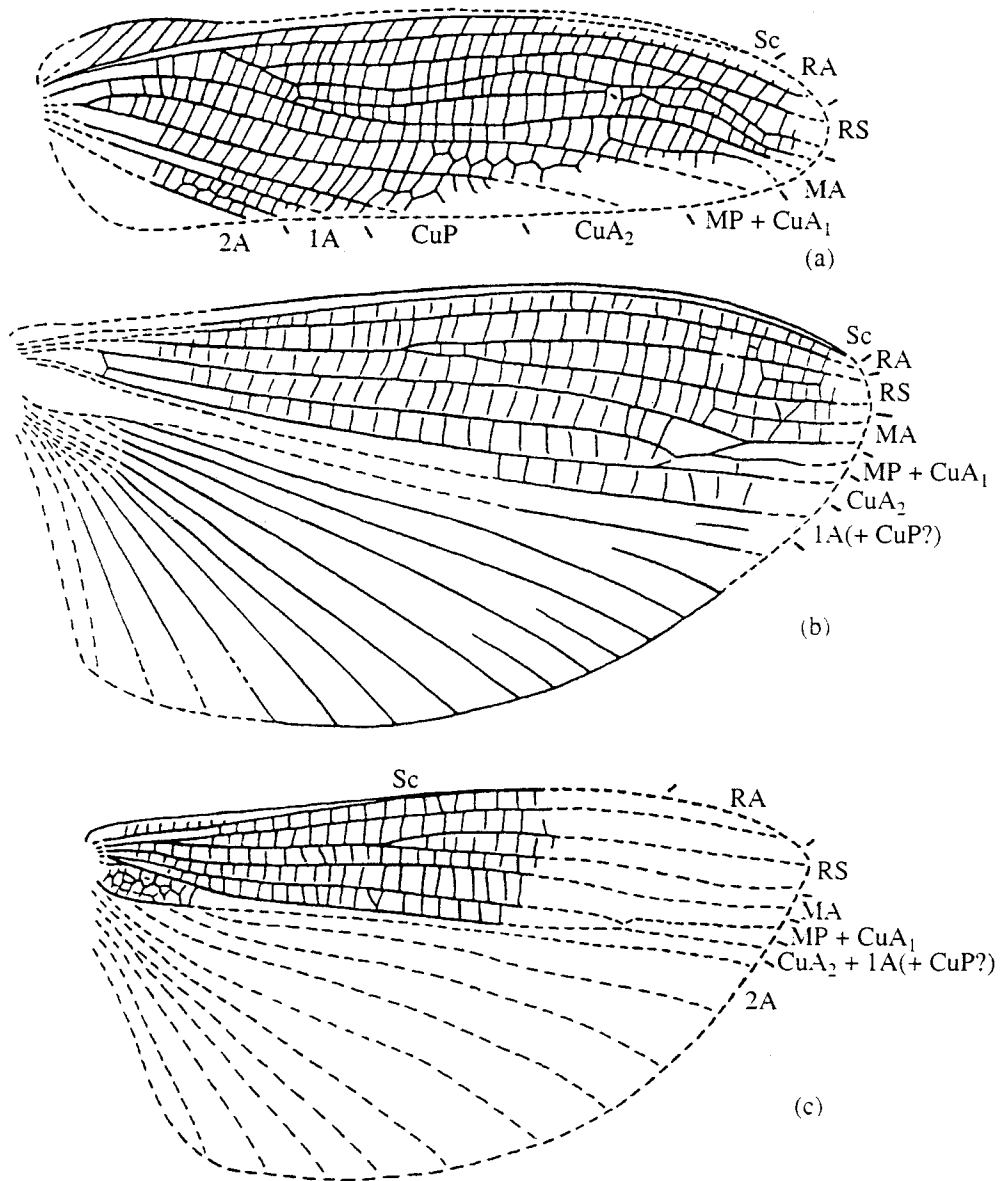


Fig. 4. The wings of Susumaniinae: (a) forewing of *Susumania flexuosa* Gorochov, 1988, holotype PIN. no. 1832/130, Upper Cretaceous of Siberia; (b) specimen PIN. no. 1832/4, Upper Cretaceous of Siberia, hindwing (gen. et sp. indet.); (c) hindwing of *Paraphasmomimella chetanica* Gorochov, 1988, holotype PIN. no. 3800/1715b, Lower Cretaceous of Siberia. After Gorochov (1988), interpretation altered.

1980 and Triassic Xiphopteroidea Sharov, 1968 (the latter are possibly not stick insects) in reduction of secondary C in forewings and in proximal RS origin in both wing pairs. Distinct from Aeroplanoidea Tillyard, 1918 in less parallelized forewing venation and in RS starting to branch in proximal (or at least middle) parts of both wing pairs. Distinct from Cenozoic Phasmatoidea Leach, 1815 in forewings not shortened, almost entirely covering hindwings in repose, and in retention of external ovipositor.

In the body shape Susumanoidea resemble the generalized modern stick insects, their tarsi are primitive, with the arolium, the antennae are likewise primitive, long and setiform, and the forewings are not abbreviated. These characters indicate that Susumanoidea are more primitive than Phasmatoidea (probably comprising all living stick insects). Taking into account that both forewing and hindwing venation of Phasmatoidea are derivable from that of the Susumanoidea, the latter could be considered among possible ancestors of Phasmatoidea, along with Aeroplanoidea and Prochresmodoidea. Derivation of Phasmatoidea from Prochresmodoidea is obstructed by the absence of post-Triassic prochresmodoids and pre-Cenozoic phasmatooids. On the contrary, the latest Aeroplanoidea now seem more probable ancestors of Phasmatoidea than even Susumanoidea, because their hindwing venation is more similar to that of the primitive living forms (proximal CuA section prior to CuA<sub>2</sub> separation reduced, CuA<sub>2</sub> looking like the posterior branch of MP + CuA<sub>1</sub>). Presumed ancestors of Susumanoidea are either Prochresmodoidea (more generalized than Triassic Prochresmodidae with unbranched RS and MP + CuA<sub>1</sub>) or enigmatic Xiphopteroidea. From the venation of these latter the venation patterns of all extinct stick insect superfamilies are easily derivable. Aeroplanoidea are not likely to be ancestral to Susumanoidea because the forewing venation is more parallel.

The position of Susumanoidea in the system of Phasmatoptera merits special discussion. All the suprageneric taxa need redescription and genera, a revision. Such study is beyond the scope of this paper and is planned for the future (an exception is made for the genus *Phasmomimoides* because of the newly discovered species), but the other questions are only briefly considered below.

#### Family Susumaniidae Gorochov, 1988, stat. nov.

*Susumaniinae*: Gorochov, 1988, p. 37.

**Diagnosis** (Figs. 2; 3c–3h; and 4). Forewings with costal area very narrow (except for small proximal part) and area between 1A and 2A widened; both wing pairs with RS 2–3-branched, their apices near end of abdomen. Tarsus 5-segmented. External ovipositor quite short.

#### Subfamily Susumaniinae Gorochov, 1988

*Kolymopterinae*: Gorochov, 1988, p. 41 (syn. nov.).

*Hagiphasmatidae*: Ren, 1997, p. 269 (syn. nov.).

**Diagnosis** (Figs. 3f–3h and 4). Forewings with RS two-branched, bifurcating in proximal wing part. Hindwings with anterior MA branch reduced or displaced into distal wing part, and with small irregularly reticulate area posterior to 1A base.

**Composition**. *Palaeopteron* Rice, 1969 (Upper Cretaceous of Canada), *Coniphasma* Birket-Smith, 1981 (Upper Cretaceous of Europe), *Promastacoides* Kevan et Wighton, 1981, *Phasmomimella* Kevan et Wighton, 1981 (Paleocene of Canada), *Cretophasmomima* Kuzmina, 1985 (Cretaceous of Siberia), *Paraphasmomimella* Kuzmina, 1985, *Eosusumania* Gorochov, 1988, *Prosusumania* Gorochov, 1988, *Cretophasmomimoides* Gorochov, 1988 (Lower Cretaceous of Siberia), *Susumania* Gorochov, 1988, *Kolymoptera* Gorochov, 1988 (Upper Cretaceous of Siberia), *Hagiphasma* Ren, 1997, *Orephasma* Ren, 1997, *Aethephasma* Ren, 1997 (Upper Jurassic or rather Lower Cretaceous of China<sup>1</sup> and possibly *Phasmomimula* Kevan et Wighton, 1981 (Paleocene of Canada).

**Remarks**. This Cretaceous and Paleocene subfamily differs from Phasmomimoidinae only by the autapomorphies and is presumably descended from this latter.

#### Subfamily Phasmomimoidinae Gorochov, 1988

**Diagnosis** (Figs. 2 and 3c–3e). Forewings with RS tri-branched, bifurcating in middle wing part. Hindwings with anterior MA branch well developed, separating in proximal wing part, and without distinct, irregularly reticulate area posterior to 1A base.

**Composition**. Genus *Phasmomimoides* Sharov, 1968 from the Upper Jurassic of Kazakhstan.

**Remarks**. Late Jurassic Phasmomimoidinae differ from Susumaniinae only by plesiomorphous characters and are presumably ancestral to the latter.

#### Genus *Phasmomimoides* Sharov, 1968

**Type species**. *Ph. lineatus* Sharov, 1968; Upper Jurassic of Kazakhstan.

**Diagnosis** (Figs. 2 and 3c–3e). Preserved parts of antennae no shorter than either wings or pterothorax plus abdomen. MP + CuA<sub>1</sub> obviously branched in forewings. Legs not very long; femur clearly longer than pronotum, but slightly shorter than head plus pronotum.

**Composition**. Type species and *Ph. minutus* sp. nov.

<sup>1</sup> Radiometric data indicate the Early Cretaceous age of these beds (Swisher, C.C., Wang, Y.-Q., Wang, X.-L., Xu, X., and Wang, Y., Cretaceous Age for the Feathered Dinosaurs of Liaoning, China. *Nature*, 1999, vol. 400, pp. 58–61).

*Phasmomimoides minutus* Gorochov, sp. nov.

**E t y m o l o g y.** From Latin *minutus* (small).

**H o l o t y p e.** PIN, no. 2384/261, complete female with wings folded (part and counterpart); Aulie near the village of Mikhailovka (the Karatau-Mikhailovka locality), Chayan District, Chimkent Region, Kazakhstan; Upper Jurassic, Karabastau Formation.

**D e s c r i p t i o n** (Figs. 2, 3d). The size is not large. The forewings are quite broadly rounded apically, with characteristic color pattern: dark longitudinal stripes along the medial part of the interradiial areas. The legs lack distinct spines; the fore tibia is considerably longer than the head and slightly longer than the pronotum.

**M e a s u r e m e n t s** (mm): length of the specimen from the rostrum tip to the wing apices, 44; forewing length, 34.

**C o m p a r i s o n.** Distinct from *Ph. lineatus* in the smaller size (forewing length 55 mm in *Ph. lineatus*) and the forewing color pattern of longitudinal stripes (in *Ph. lineatus* the dark spots are more or less grouped into transverse bands: compare Figs. 3c and 3d).

**R e m a r k s.** The gut in the holotype is filled with plant matter consisting of leaf fragments of *Brachyphyllum* or *Pagiophyllum* (for details see Rasnitsyn and Krassilov, 2000).

**M a t e r i a l.** Holotype.

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