

apparatuses are close set, their subsidiary cells being contiguous or narrowly separated. The density of stomata is about six per 0.5 mm<sup>2</sup>. The structure of stomatal apparatus is incomplete-amphicyclic, with markedly thickened ring of five subsidiary cells and virtually unthickened coronary cells forming an irregularly shaped, usually incomplete outer ring. The longer axis of the subsidiary cell ring is ca. 80 μm; the stomatal aperture is 28–30 μm long.

The periclinal walls of the subsidiary cells are unevenly cutinized, without distinct papillae. The periclinal walls of ordinary and coronary cells bear a small hollow papilla, their anticlinal walls being developed as the thick ribs of uneven height. The coronary cells are of quite variable size, mostly being as large as the ordinary cells or smaller and rounded. However, a few of them stand in a markedly greater size, almost twice surpassing the average ordinary cell. The trichomes are developed chiefly in the marginal zone. The trichome base developed as a small thickened cell of rhomboidal shape is surrounded by six or seven radially arranged peritrichome cells and by an incomplete ring of the outer cells. The opposite (upper) cuticle is considerably thinner, without stomata, with the contours of epidermal cells and the trichome bases obscured.

Some pollen grains of *Classopollis*-type having are preserved adhering to the cuticle: they are rounded elliptical, with a distinct rimula and the distal pseudopore is of irregular shape. The longer axis of the pollen grain is ca. 20 μm. The equatorial rim is of uneven width (4–9 μm).

Shoots with the scale-like leaves of this type (brachyphylls) are placed in the morphological genera *Brachyphyllum* and *Pagiophyllum*, formally differing in the size ratio of the cushion and the free part of the leaf (Harris, 1979). This ratio, in fact having no serious taxonomic significance, cannot be estimated from our material. The cuticle structure is characteristic of the family Hirmerellaceae, such assignment being confirmed by the *Classopollis* pollen grains having adhered to the cuticle, which are typical for the family.

Among six brachyphyll species described from the Jurassic flora of Karatau, our material shows maximal similarity in the cuticular characters with *Pagiophyllum peregrinum* Lindl. et Hutt. (Doludenko and Orlovskaya, 1976). The size and shape of to cells are virtually identical, and the structure of the stomatal apparatus is quite similar as well. However, in the leaves figured by Doludenko and Orlovskaya the stomata are arranged in longer, regular rows, preventing the identification of the fragments from the insect gut with this presumably collective species (known from the Lower and Middle Jurassic as well). Among the Jurassic species from other localities it is note worthy that there is a close similarity in the arrangement of stomata and configuration of the subsidiary cells with that of *P. maculosum* Kendall and shoots of *Hirmerella kendalliae* Harris (Harris, 1979).

*Unexpected Relatives of Embiids,  
or One More "John out of Kin?"*

Embiids, or web-spinners, constitute a small group of insects characteristic of warm climatic zones. They dwell in colonies, in the silken galleries made by all the colony members (both immature and adult numbers of either sex) by the secretion from the glands in the modified foreleg basitarsus. The females are always wingless and the males sometimes so. The adults are small to medium-sized, rarely above 2 cm. The wing structure is unique among insects. In their galleries, web-spinners run equally fast headwards and tailwards, the winged males being just as good as the wingless females and immatures, so far as their wings are soft and during backward motion merely bend over the head. As for the wing rigidity necessary for flight, it is achieved by forcing the hemolymph into the sinuses surrounding the radial and other veins (Ross, 1991), i.e., by erection. Embiids are rare in the fossil record (the earliest undoubted find is from the Late Cretaceous or Paleogene Burmese amber; Zherikhin, 1978) and considered to be descendants of Grylloblattida (Storozhenko, 1997). All these features make embiids quite unexpected candidates for a close relationship with the large, phyllophagous insects, that had become extinct long ago (and had winged females and unmodified fore tarsi lacking a reservoir of the large silk gland). Nevertheless some, although not indisputable arguments exist for such an assumption.

**Family Brachyphyllophagidae A. Rasnitsyn, fam. nov.**

Type genus. *Brachyphyllophagus* gen. nov.

Diagnosis. Large, slender phyllophagous insects, possibly nocturnal, with head capsule closed between mouth and occipital foramen, with chewing mouthparts, moderately polymerous antennae. Pronotum not elongate, possibly with paranota. Wings folding most probably flat over abdomen in repose; forewings long, narrow, with more or less straight anterior margin and convex posterior one, narrow costal area, simplified parallel venation. Veins possibly weak (in impressions recognizable only as pale streaks interrupting colored areas of membrane, without any traces of convexity or concavity). SC unbranched; RS separating from R in middle wing third, fused with MA near base of the latter; RS + MA regularly pectinate; MP unbranched; CuA with 3–5 branches, at least in one case pectinate. Clavus occupying no less than one third of wing; structure of anal area uncertain. Crossveins simple, parallel, sparse, arranged in transverse rows, or rather dense (at least locally). Hindwing with broad anal fan. Legs short, not jumping, without distinguishable armature; tarsi not shortened, not oligomeric; foreleg basitarsus unmodified. Middle and hind coxae (as judged from position of dark spots marking them in one of the fossils) widely separated from midline, i.e., meso- and metathoracic sterna external, not invaginated. Ovipositor well developed, external.

**Composition.** Type genus.

**Remarks.** The new family is known only from two impressions of an incomplete and rather peculiar preservation: the outline of the body and appendages in both cases are barely noticeable in the rock matrix, and only the dark pattern on some body parts and dark gut contents are clearly visible. Obviously the cuticle was mostly weak and unpigmented.

**Systematic position.** Insufficient preservation and unusual character combinations do not permit inclusion of the new family within any known insect order beyond doubt. The chewing mouthparts, wings folding over the abdomen, broad hindwing anal fan and widely separated pterothoracic coxae indicate that it belongs to the infraclass Gryllones (=Polyneoptera); in other groups the widely separated coxae and free pterothoracic sterna co-occur with foldable wings only rarely and only in markedly flattened insects (which is not the case in the fossils described). Among Gryllones, orthopterans clearly differ from the new family in the characteristic jumping hind legs, earwigs in the elytrized forewings; stoneflies and embiids in the shortened three-segmented tarsi; cockroaches in the broad forewing costal area with either very short or multi-branched SC; termites in the much less regular venation; praying mantids in the raptorial fore legs; Carboniferous Eoblattida in the incomparably richer venation. For the remaining stick insects and Grylloblattida, there are no so evident contra-indications (although retention of the only free M branch is not characteristic of them either), but any specific similarities to the new family could not be found. Hence, it does not seem possible to include the Brachyphyllophagidae in any known insect order without expanding considerably its diagnosis.

Another possible way, a search for at least a few apparent synapomorphies with some other insect order (even though dissimilar in other features), turns out to be a little more productive. Such a character is found viz. the head capsule closed by a continuous cuticular bridge between the mouth and occipital foramen. Among Gryllones this feature is known, apart from in *Brachyphyllophagus*, only in embiids. Most of their specializations (often unique to Gryllones or sometimes to all the insects) are also alien to the fossils in question. These are, life in silken galleries and in particular the silk source (another known example of silk production by the fore tarsi is the true flies of the family Empididae, but their silk is used in a different way), and especially the erection of wings at flight.

The head capsule of embiids is usually described as closed by the gular plate, i.e., the secondary structure independently appears in different insects by way of sclerotization of the cervical membrane. However, the embiid "gula" shows no trace of existence of the membrane between it and the head capsule, characteristic of true gula (DuPorte, 1962; Rasnitsyn, 1969, fig. 143). Moreover, embiid "gula," anteriorly reaching the level of posterior tentorial pits (marking the boundary

between the hypostoma and postocciput), continues posteriorly without any boundary into the ring surrounding the occipital foramen (Rähle, 1970), and therefore represents the postoccipital bridge. This feature makes the embiid head capsule unique. The detailed structure of the bridge between the mouth and occipital foramen is unknown in *Brachyphyllophagus*, but, judging from its rigidity (this area of the head is not depressed at all in the impressions), it can quite possibly be homologous to the bridge in embiids.

There are no such notable (but nevertheless significant) differences of embiids from *Brachyphyllophagus* as their preferential saprophagy (in contrast to feeding on the green parts of the plants, as indicated by the gut contents of the fossils), female aptery, homonomous wings with much poorer venation (but often with MP forked). Unlike the pale veins in our fossils, the embiid veins remain dark pigmented, pale stripes on the suffused membrane appearing as concave intercalars between convex veins (analogous to cockroaches). Furthermore, in embiids the legs are short with the tarsus tri-segmented, the ovipositor is lost, and the cerci are stout, although only di-segmented (in *Brachyphyllophagus* the cerci could be developed only as relatively weakly sclerotized appendages).

On the other hand, there are some other characters in common between *Brachyphyllophagus* and embiids besides the similar head structure, but they are much less conclusive. These are the weak wing veins, narrow costal area, unbranched and not too greatly shortened SC, fusion of MA and RS (although these veins separate from R and M and unite much more proximally, almost near the wing base in embiids). Possibly a nocturnal activity of winged individuals should be added to the list; the very weak sclerotization of the cuticle in *Brachyphyllophagus* may be evidence of this.

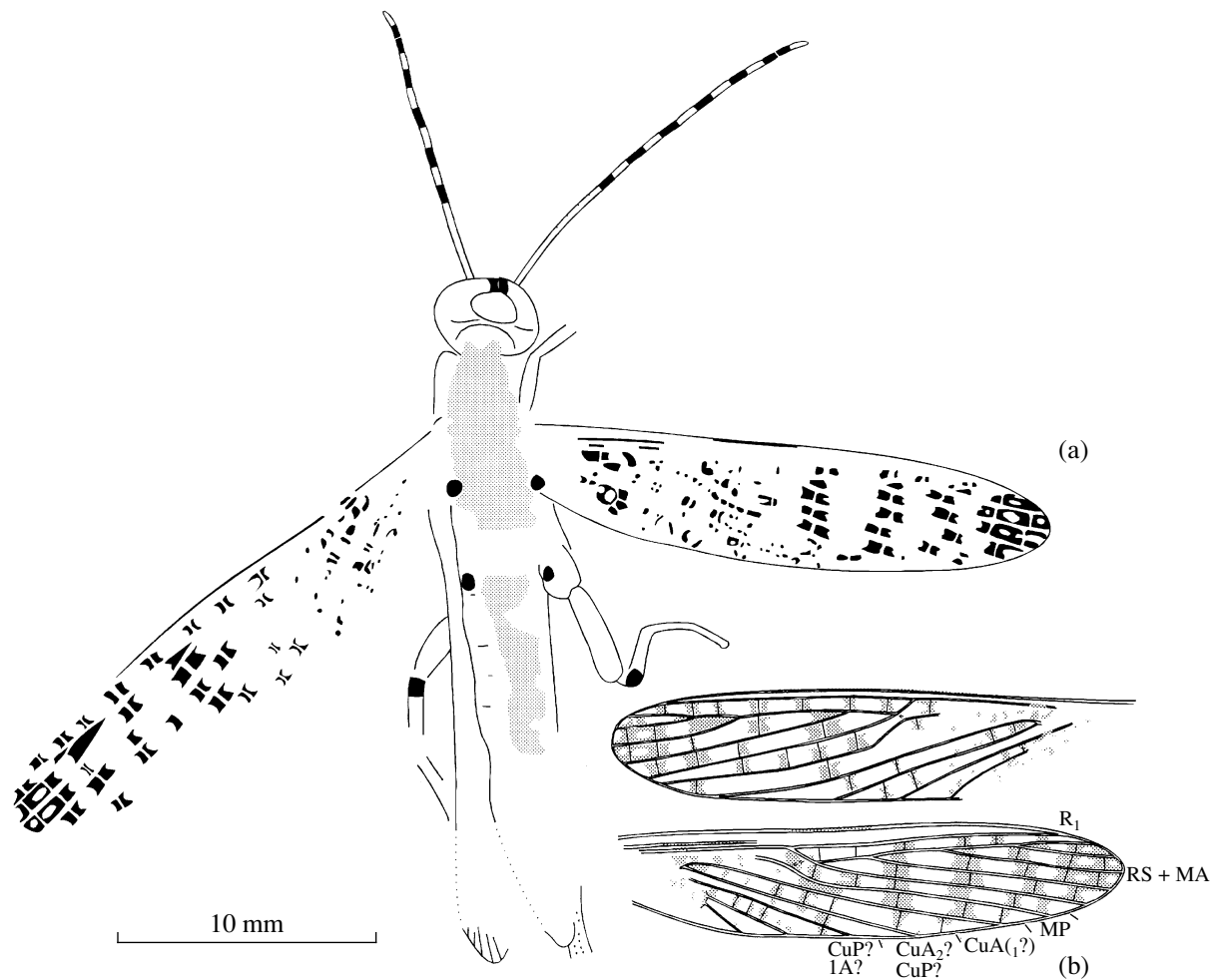
The peculiarities listed are not sufficient to include the described taxon in the order Embioptera as, for example, a separate suborder. However, to create a new order for so incompletely known, though clearly peculiar, insects is premature. Thus it is proposed, until more necessary data is obtained, to treat the Brachyphyllophagidae as a satellite family of Embioptera on the concept of satellite taxon see Meyen (1984).

#### **Genus *Brachyphyllophagus* A. Rasnitsyn, gen. nov.**

**Etymology.** From *Brachyphyllum* and Greek *phagos* (eater).

**Type species.** *B. phasma* sp. nov.

**Diagnosis.** Large, slender insects with short legs, long, narrow variegated wings (with dark spots and in distal half with transverse bands). Head transverse oval or almost round, apparently somewhat wider than thorax. Antennae thin, of more than 20 elongate segments, shorter than body. Pronotum transverse, nearly parallel-sided. Wings slightly surpassing the abdominal apex; forewing with straight anterior and



**Fig. 2.** *Brachyphyllophagus phasma* A. Rasnitsyn, sp. nov.: (a) holotype PIN, no. 2904/1690; (b) reconstructed venation of holotype. Symbols as in Fig. 1.

slightly convex posterior margin, more than four times as long as wide. RS and MA originating just before wing midlength, fused to each other close to their bases, and giving five branches (first one at their junction). Cubital vein with 3–5 branches (unknown, whether counting CuP or not), diverging chiefly in basal wing third, and arranged pectinate (at least in the case of three-branched Cu). Crossveins simple, all or nearly all vertical, often forming widely separated transverse rows, sometimes more dense (separated by less than half of their length); no crossveins found in costal area. Hindwing with broad anal fan repeatedly folded in repose. Length of fore tibia less than head width. Length of hind femur no more than head width; tibia much shorter than femur, tarsus slightly so. Abdominal segments apparently unmodified. Ovipositor wide, its lateral surface with short thick spinules.

**Composition.** Two new species from the Upper Jurassic of Kazakhstan.

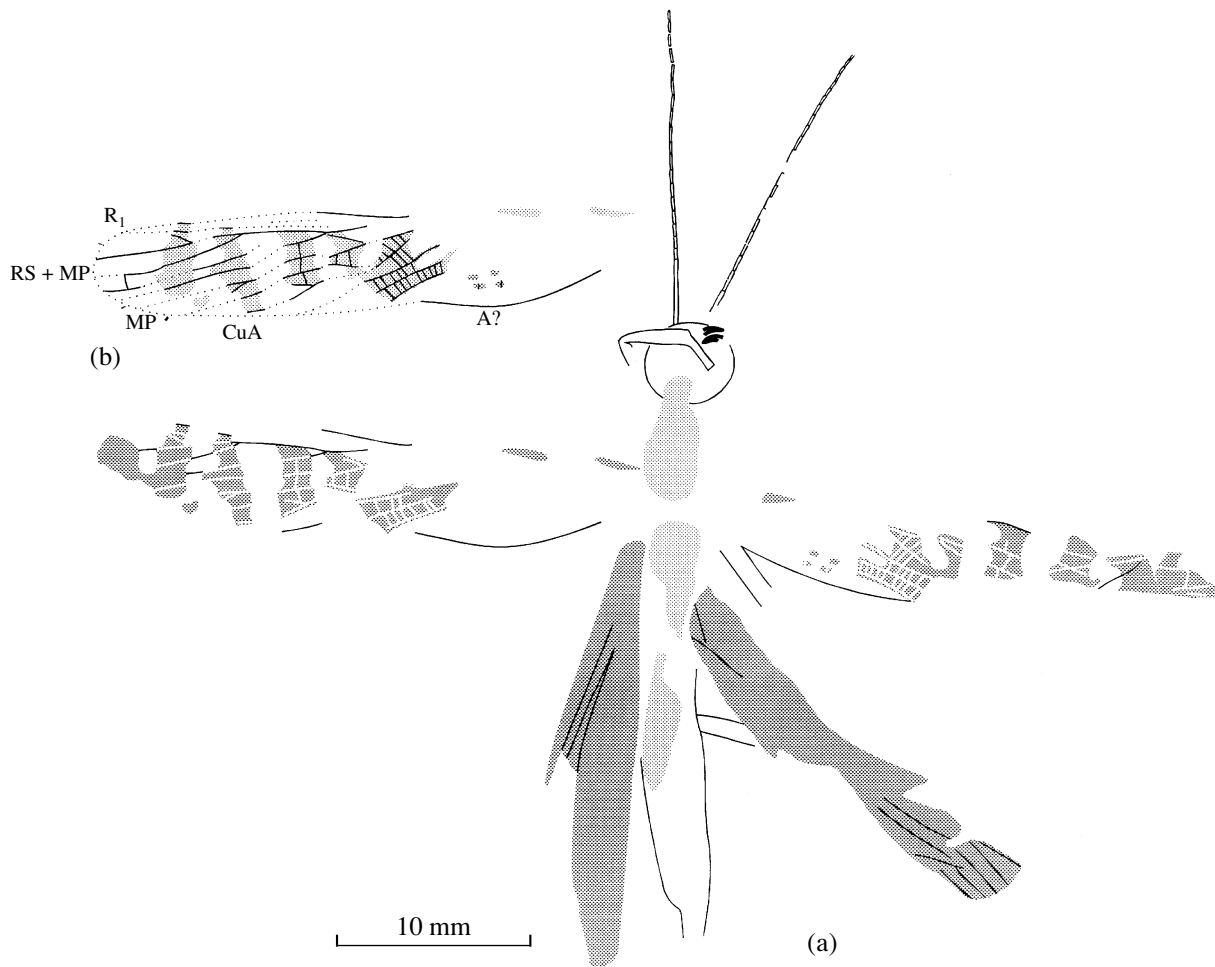
**Remarks.** The hindwing structure (except for presence of broad anal fan), and the length and shape of the ovipositor are unknown.

***Brachyphyllophagus phasma* A. Rasnitsyn, sp. nov.**

**Etymology.** Greek *phasma* (ghost).

**Holotype.** PIN, no. 2904/1690, almost complete, moderately preserved female; South Kazakhstan, Chimkent Region, Chayan District, Karatau Range, Aulie near the village of Mikhailovka, Karatau-Mikhailovka locality; Upper Jurassic, Karabastau Formation.

**Description** (Fig. 2). Female. The cuticle is pale, with only few dark areas: some antennal segments (counting from apex, segments 2, 3, 5, 7, 9, 11, and 13), tips of mandibles, supposedly dorsobasal spots on middle and hind coxae, bases of hind tibiae, some forewing cells (in distal two thirds the dark cells are arranged in five transverse bands, including the apical one; near the wing apex and less so about midwing many dark cells have a pale, oval, central spot), and partly the hindwing apex. The antennae supposedly 23–25-segmented, thin, scarcely thickened from about the midlength almost up to the apex; the 1st and 4–12th segments from the apex are about 2–2.5 times, the 2nd one from the apex about 1.5 times, and the other discernible segments about twice as long as wide. In the forewing the bases of RS



**Fig. 3.** *Brachyphyllophagus phantasmus* A. Rasnitsyn, sp. nov.: (a) holotype PIN, no. 2384/260; (b) reconstructed venation of holotype. Symbols as in Fig. 1.

and MA are short, markedly oblique. The Cu vein has three straight branches. Almost all the crossveins are widely separated from each other. The posterior margin of the forewing lacks a discernible emargination at the supposed claval apex.

Measurements (mm): body length up to abdominal apex, 27; length of antenna, no less than 15; forewing length, 21; length of hind femur, 4; of tibia, ca. 2.5; of tarsus, ca. 3.5; head width, 4.2; pronotum width, probably less than 4; forewing width, 4.7; maximal width of abdomen (near the base), 3.3; width of ovipositor at abdominal apex, 0.7.

**Material.** Holotype.

*Brachyphyllophagus phantasmus* A. Rasnitsyn, sp. nov.

**Etymology.** The name of Greek god of sleep.

**Holotype.** PIN, no. 2384/260, almost complete, moderately preserved insect (sex unknown); South Kazakhstan, Chimkent Region, Chayan District, Karatau Range, Aulie near the village of Mikhailovka, Karatau-

Mikhailovka locality; Upper Jurassic, Karabastau Formation.

**Description** (Figs. 3 and 4a). The cuticle is pale, with only few dark areas: apices of antennal segments (except for basal ones), mandibles, five or six transverse bands in the middle and distal thirds of the forewing (small and ocellate spots are rare or absent), and apparently the whole hindwing. The antennae supposedly 25–30-segmented, thin, gradually thickened towards the apex; the segments no less than 4–5 times as long as wide. The head is almost round. The legs (discernible only by their fine pubescence) are rather slender and not long; the length of the fore tibia is less than the head width. In the forewing the longitudinal veins do not seem straight (possibly due to the wing impression being deformed), the bases of RS and MA are comparatively long, gradually converging. The Cu vein has five visible, conspicuously curved branches, only one of them separating distal to the supposed claval apex (marked by a distinct emargination of the posterior wing margin). The dense, parallel crossveins are trace-