

New and Little Known Orthopteroid Insects (Polyneoptera) from Fossil Resins: Communication 1

A. V. Gorochov

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia

e-mail: orthopt@zin.ru

Received September 22, 2005

Abstract—New taxa of uncertain position within the infraclass Polyneoptera (Gryllomantidae fam. nov.: *Gryllomantis* gen. nov., Lower Cretaceous; Mantoblattidae fam. nov.: *Mantoblatta mira* gen. et sp. nov., Upper Cretaceous) and within the order Dictyoptera (*Pseudojantaropterix* gen. nov., Lower Cretaceous) are described. The superfamily Umenocoleoidea of uncertain position within the latter order is discussed on the basis of new information on Jantarimantidae and some other Cretaceous Dictyoptera.

DOI: 10.1134/S0031030106060074

Key words: new taxa, orthopteroid insects, Polyneoptera, Cretaceous, fossil resins.

INTRODUCTION

Orthopteroid insects are represented in fossil resins mainly by small nymphs; adults, especially those of large species, are rarely preserved in amber. However, the preservation of amber specimens is usually much better than that of impressions on rocks. Therefore, the taxonomic information provided by amber nymphs is no less rich than that coming from impressions of adults, represented mostly by wing fragments. Although taxonomic treatment of nymphs is difficult and their systematic position cannot always be reliably determined, it is quite possible and even may be quite useful for reconstruction of the late stages of polyneopteran evolution.

The results of the study of the small but interesting material of orthopteroid insects from fossil resins (Late Cretaceous Burmese and Taimyr ambers, Eocene Baltic amber, Miocene Dominican amber, Pleistocene African copal), along with analysis of some of the newest publications allow to add several important additions to the picture of Late Mesozoic and Cenozoic evolution of this infraclass.

MATERIAL

The materials studied are housed at the Natural History Museum, London (NHM), National Museum of Natural History, Washington (NMNH), Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), and Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

In this first communication of a series of papers, representatives of the infraclass Polyneoptera with uncertain ordinal position and members of the order Dictyoptera with unclear subordinal position are considered.

SYSTEMATIC PALEONTOLOGY

POLYNEOPTERA INCERTAE SEDIS

After the whole-bodied fossils of Triassic predatory mantis-like Polyneoptera were discovered and placed into the order Titanoptera (Sharov, 1968), several papers appeared to demonstrate that these insects apparently also occurred in the Permian (Gorochov, 2004) and were quite common in the Triassic (Gorochov, 2003). Moreover, the ambush predator life form existed among Polyneoptera even earlier, e.g., Carboniferous Cnemidolestidae and, possibly, some of their close relatives in the order Eoblattida (Gorochov, 2001a, 2004).

These insects probably occupied the same adaptive zone as modern praying mantises. However, the latter group, constituting the suborder Mantina in the order Dictyoptera, entered the record no earlier than in the Early Cretaceous (Gratshev and Zherikhin, 1993; Grimaldi, 2003). They were also reported from the Late Jurassic (Vršanský, 2002a) based on a single wing fragment the assignment of which to mantises has been questioned (Grimaldi, 2003).

Polyneopterans with obvious adaptations as ambush predators are unknown in the Jurassic. Their absence is hardly possible, because the Jurassic biota is more similar in the array of life forms and taxonomic composition to the Triassic and Early Cretaceous ones, than these latter to the Permian and Late Cretaceous ones, respectively. One may suppose that in the first half of the Jurassic, Titanoptera still existed, whereas in the second half mantises had already appeared. However, these groups apparently did not constitute an essential component of the Jurassic biota, as their remains are absent even from the richest Jurassic assemblages.

It is more logical to assume that in the Jurassic other mantis-like predators were common; however, they pass unrecognized only because they are known from their isolated wings. Predatory orthopterans of the superfamily Hagloidea (suborder Ensifera) may turn out to be such predators. But predatory Ensifera also existed in the Paleozoic (many Oedischidae), Triassic (some Haglidae), and post-Jurassic time (predatory Prophalangopsidae, Tettigonioidea, and Stenopelmatoidea), but they never totally replaced more specialized predators.

The latter circumstance implies that in the Jurassic, after complete or partial extinction of titanopterans and prior to advent of mantises, some other polyneopteran groups tried to occupy these vacated niches. Unexpected finds of recent years in Cretaceous and Paleogene ambers may serve as retrospective indications of possible candidates for Jurassic analogues of mantises.

However, these finds are very difficult to interpret, because they are represented by apterous forms; therefore, their position in the system of infraclass Polyneoptera is insufficiently understood. The most important of these is the recently discovered predatory family Mantophasmatidae Klass, Zompro, Kristensen et Adis, 2002. It was first found in the Baltic amber, and then also in the modern African fauna (Arillo et al., 1997; Zompro, 2001; Zompro et al., 2002; Klass et al., 2002, 2003). This family was placed into a separate order Mantophasmatodea (Klass et al., 2002), which was split into several families (Klass et al., 2003; according to the descriptions, these “families” are so similar to each other that they only merit tribal or subfamilial rank). According to published opinions, these insects may stand close to Titanoptera (Gorochoy, 2001b, 2004) or Grylloblattida (Engel and Grimaldi, 2004), but it is still completely unclear what their real ancestors were.

Other finds were first described by Grimaldi (2003) in his interesting paper on Cretaceous mantises. Along with true mantises, he described three enigmatic forms from Cretaceous ambers, based on nymphs: *Burmantis lebanensis* Grimaldi, 2003 (Lebanon; Lower Cretaceous); *B. asiatica* Grimaldi, 2003; and *Jersimantis burmitica* Grimaldi, 2003 (Myanmar; Upper Cretaceous). These forms obviously cannot belong either to the suborder Mantina or even to the order Dictyoptera.

The most salient feature of these forms immediately distinguishing them from all Dictyoptera is the shortened coxae of all legs, including fore legs (Fig. 1a). It is necessary to note that even in Paleozoic-Mesozoic Mylacridina (the oldest and most primitive suborder of the order Dictyoptera), coxae of all legs are markedly enlarged (Fig. 1b)—one of the key synapomorphies of dictyopterans that formed with the acquisition of “swimming” in the Carboniferous forest litter, characteristic of the ancestors of dictyopterans (Gorochoy, 2004). This peculiarity of the coxae was inherited by descendants of ancient dictyopterans: mantises (Fig. 1c), termites (Fig. 1d), and modern cockroaches

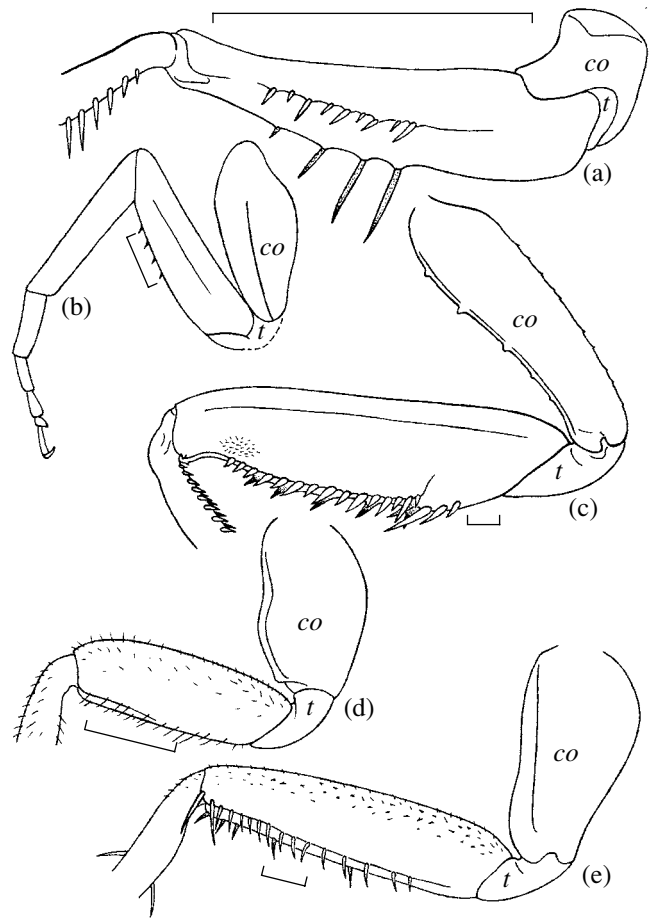


Fig. 1. Fore leg of Gryllomantidae nymph (a) and adults of Dictyoptera (b–e) from inner side: (a) *Gryllomantis lebanensis* (Grimaldi), holotype AMNH L26 (American Museum of Natural History, New York, after Grimaldi, 2003), Lower Cretaceous of Lebanon; (b) *Rhipidoblatta brevivalvata* Vishniakova (Mylacridina), holotype PIN, no. 2239/359 (after Vishnyakova, 1968), Upper Jurassic of Kazakhstan; (c) *Hierodula transcaucasica* Br.-W. (Mantina), modern Afghanistan; (d) *Mastotermes darwiniensis* Froggatt (Termitina), modern Australia; (e) *Periplaneta americana* (Linnaeus) (Blattina), modern Vietnam. Symbols: co, coxa; t, trochanter. Scale bar 1 mm.

(Fig. 1e). In predatory forms such a useful peculiarity, elongating raptorial legs and increasing their mobility, should never be lost, and, therefore, Dictyoptera can not be ancestral to the above-mentioned enigmatic forms.

Another difference from mantises (and Dictyoptera) is the presence of only a median ocellus in some of the specimens described by Grimaldi. Mantises have this ocellus less developed than the lateral ones, possibly owing to loss of the median ocellus in the common ancestors of mantises, cockroaches, and termites, with its subsequent reemergence in mantises alone (Gorochoy, 2001a; Vršanský, 2002a). One more important difference is the presence of very long setae on the cerci, uncharacteristic of all Dictyoptera, including mantises.

The characters listed easily distinguish these Cretaceous forms from Dictyoptera, but do not allow them to be included reliably in any extinct or extant orders. Therefore, they are separated herein into a family *incertae ordinis*.

Family Gryllomantidae Gorochov, fam. nov.

Type genus. *Gryllomantis* gen. nov.

Diagnosis (based on data from Grimaldi, 2003). Head more or less similar to that of mantises: hypognathous, with very large, rounded eyes and long setaceous antennae, with most antennomeres short (like in most Polyneoptera) except for rather long third segment (characteristic of modern Grylloblattida rather than Dictyoptera); if ocelli present, then median ocellus better developed (opposite in mantises). Prothorax without obvious paranotal lobes (pronotum more or less similar to that of modern Grylloblattida). Fore legs raptorial with comparatively short coxa and very short trochanter, these are much shorter than in all known Dictyoptera (Fig. 1); femora long (more than twice as long as coxae) and somewhat broadened, provided with few long spines or (in young nymphs) spiny setae at lower outer margin and usually more numerous short spines at lower inner margin (Fig. 1a); tibiae much shorter than femora, with two rows of more or less long and numerous lower spines, but without stout, curved apical spine (or hook) characteristic of most mantises; tarsus five-segmented, long (longer than tibia), with very long basitarsus devoid of conspicuous spines, but without developed arolium. Mid and hind legs without raptorial spines (cursorial or climbing), with longer femur and tibia (especially hind ones); hind femora somewhat narrower than fore and mid ones; tarsi as in fore legs. Abdomen elongate, in general outline more or less similar to that of mantises and grylloblattids; cerci clearly segmented, with very long setae, distinct from those of Dictyoptera.

Composition. *Gryllomantis* gen. nov. (Lower Cretaceous of Lebanon) and *Burmantis* Grimaldi, 2003 (Upper Cretaceous of Myanmar). I provisionally place in *Burmantis* two species that are characterized by comparatively long, not thickened cerci with more or less elongate segments: *B. asiatica* Grimaldi, 2003 and *B. burmitica* (Grimaldi, 2003), comb. nov. (the latter species was originally placed in the genus *Jersimantis* Grimaldi, 1997, belonging to mantises). Besides that, this family possibly includes an undescribed mantis-like nymph from Dominican amber (Miocene of Haiti; photograph see Grimaldi, 1996, p. 88); this form differs in the cerci being even longer and more "grylloblattid-like" than in *Burmantis*.

Comparison. In the presence of a femoral brush of small spinules or short setae at the inner side of fore femora, reduction of arolium and several peculiarities of cerci (elongate segments in later forms and long setae), the new family resembles modern Grylloblattidae (the above-mentioned brush is developed at least in

some species of the genus *Galloisiana* Caud.), but easily differs from them in the greater development of predatory adaptations: large eyes and long raptorial spines on fore legs. It differs from Mantophasmatidae in the absence of the arolium and in having segmented cerci. Differences from Dictyoptera see above. It shows no specific similarities to other Polyneoptera.

Remarks. The similarity between Gryllomantidae and modern grylloblattids mentioned above seems more significant than between the latter and Mantophasmatidae, noted by Engel and Grimaldi (2004). First, Grylloblattidae (like Gryllomantidae) lack the arolium, which is very large in Mantophasmatidae. Second, grylloblattids bear segmented cerci similar to those of later Gryllomantidae, whereas those of Mantophasmatidae are short and unsegmented. Third, abdominal spiracles of grylloblattids resemble short tubes and are situated posteriorly on abdominal segments, while in Mantophasmatidae (according to one of the published illustrations: Klass et al., 2002, text-fig. 2D), they look like in most polyneopterans and are situated at the base of the segments. The structure and position of these spiracles in Gryllomantidae are unknown, but if they are similar to those of modern Grylloblattidae, one cannot exclude that the latter family may be found to be a direct descendant of fairly derived Gryllomantidae that lost their salient predatory adaptations.

Genus *Gryllomantis* Gorochov, gen. nov.

Etymology. From the genera *Gryllus* and *Mantis*.

Type species. *Burmantis lebanensis* Grimaldi, 2003; Lower Cretaceous, Lebanese amber.

Diagnosis (based on data from Grimaldi, 2003). Proximal spines at lower side of fore tibia set at the very base of tibia (Fig. 1a). Cerci short, thickened (especially at base), with short, nearly annulate segments (Grimaldi, 2003, text-fig. 9f).

Composition. Type species.

Comparison. The new genus is easily distinguishable from *Burmantis* in the arrangement of lower proximal spines on fore tibia (in the latter genus the most proximal of these spines are situated at considerable distance from the base of tibia) and the structure of cerci: in *Gryllomantis* they are much thicker and shorter and consist of shorter segments. It should be noted that such a difference in cercal structure in congeneric species is not known in either in mantises or in grylloblattids; only in some modern cockroaches are sexual differences in the structure of cerci found, because the males and females of the same species may belong to different life forms.

Another enigmatic insect from Burmese amber is similar in the structure of the cerci to some Gryllomantidae and partly even Grylloblattidae in the structure of antennae to Mantophasmatidae and in the structure of coxae and general habitus to gracile cockroaches, but differs significantly from all these in the tarsal struc-

ture. This insect clearly belongs to Polyneoptera and is here placed into a separate family, which at present cannot be placed in either of the known orders.

Family Mantoblattidae Gorochov, fam. nov.

Type genus. *Mantoblatta* gen. nov.

Diagnosis (only early instar nymph known). Body slender, with numerous setae. Head opisthognathous, subtriangular, with large eyes containing numerous facets, and antennae of characteristic structure: antennae slightly longer than body, scape moderately long, somewhat thickened; pedicel short; flagellomeres long and slender. Pronotum slightly wider than head, nearly round, with lamellate sides (paranota). Legs long and slender, with conspicuously elongate coxae, without spines, except for unpaired spine at the apex of fore tibia (Fig. 2c); fore tibia slightly shorter than fore femur; mid legs slightly longer than fore legs, and conspicuously shorter than hind legs; all tarsi distinctly three-segmented, without arolium (Figs. 2c, 2d). Abdomen short, with small but distinct paranota (Figs. 2a, 2b); cerci consist of more than one segment, basal segment longest (Fig. 2e).

Composition. *Mantoblatta* gen. nov., Upper Cretaceous of Myanmar.

Comparison. The new family differs from Dictyoptera in the long antennomeres, three-segmented tarsi, and structure of cerci (in all known dictyopterans the relative length of basal cercal segment is much smaller; possibly, the number of cercal segments in Mantoblattidae increased with instar and their cerci became very similar to those of modern Grylloblattida). It differs from Grylloblattidae and Gryllomantidae in the opisthognathous head, presence of conspicuous paranota, long antennomeres, larger coxae and three-segmented tarsi. No similarities to other Polyneoptera are noted, excluding the antennomeres similarly elongated in Mantophasmatidae, which differ from Mantoblattidae in the head position, absence of developed paranota, size of coxae, and especially in the tarsal and cercal structure. It should be noted also that no increase in the number of tarsomeres during postembryonic development has been reported in any member of the infraclass Polyneoptera, with the possible exception of some of the most primitive forms of the Paleozoic order Eoblattida (Gorochov, 2004).

Genus *Mantoblatta* Gorochov, gen. nov.

Etymology. From the genera *Mantis* and *Blatta*.

Type species. *M. mira* sp. nov.

Diagnosis (early instar nymph). Distance between antennal bases subequal to scape length; scape at least twice as long as pedicel; scape somewhat shorter, and almost twice as wide as flagellomere; maximal eye diameter slightly greater than scape length; maxillary and labial palps rather long (former some-

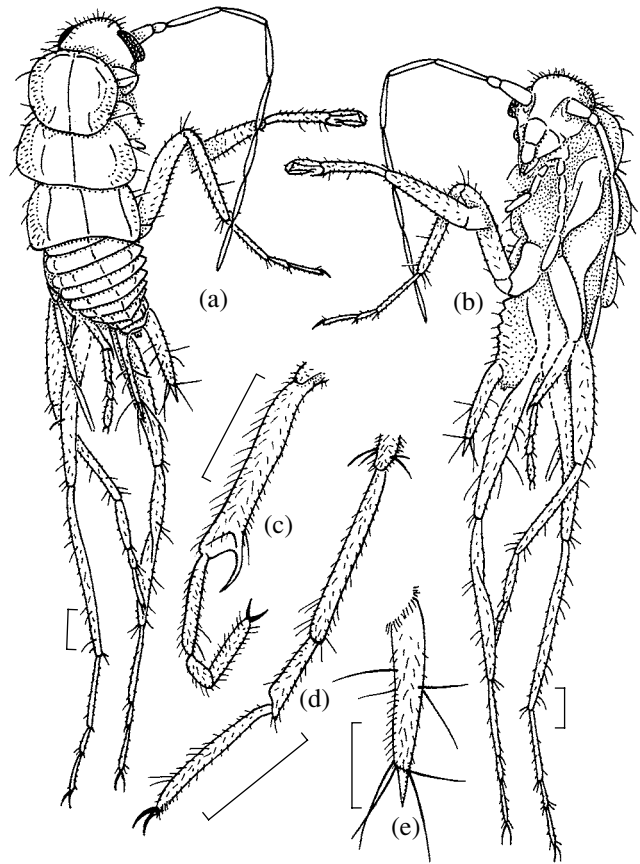


Fig. 2. Nymph of *Mantoblatta mira* sp. nov. (Mantoblattidae), holotype NHM, In. 19132-2: (a) body from above; (b) body from below; (c) tibia and tarsus of right fore leg, lateral; (d) right fore tarsus, lateral; (e) right cercus from above. Scale bar 0.2 mm.

what longer than half head length, latter distinctly longer than head; Fig. 2b). Width of pronotum slightly greater than its length; low and narrow longitudinal carina along midline of pterothoracic and abdominal tergites; weak carinae also on sides of these tergites (at base of paranota, on abdominal tergites additional carinae between these and medial carina; Fig. 2a). Apical spine of fore tibia long, characteristically curved (Fig. 2c); tarsi without widened pulvilli (Figs. 2c, 2d). Cerci with two groups of setae at the basal segment and short, conical terminal segment (Fig. 2e) (possibly, such structure of cerci is characteristic of only young nymphs of this genus).

Composition. Type species.

***Mantoblatta mira* Gorochov, sp. nov.**

Plate 5, figs. 1a and 1b

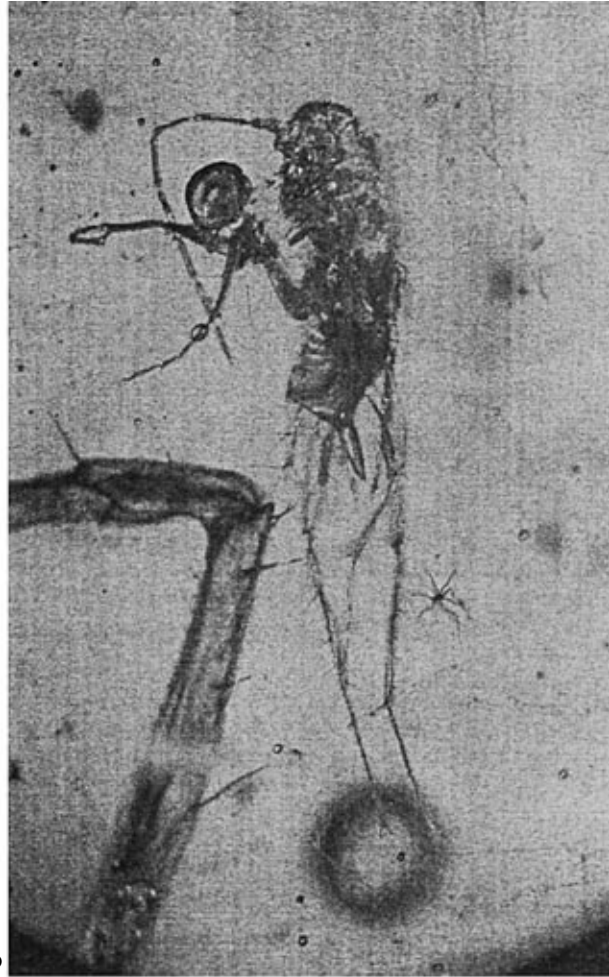
Etymology. Latin *mira* (wonderful).

Holotype. NHM, In. 19132-2, complete early instar nymph (one of fore legs detached and preserved near the body); Burmese amber; Upper Cretaceous.

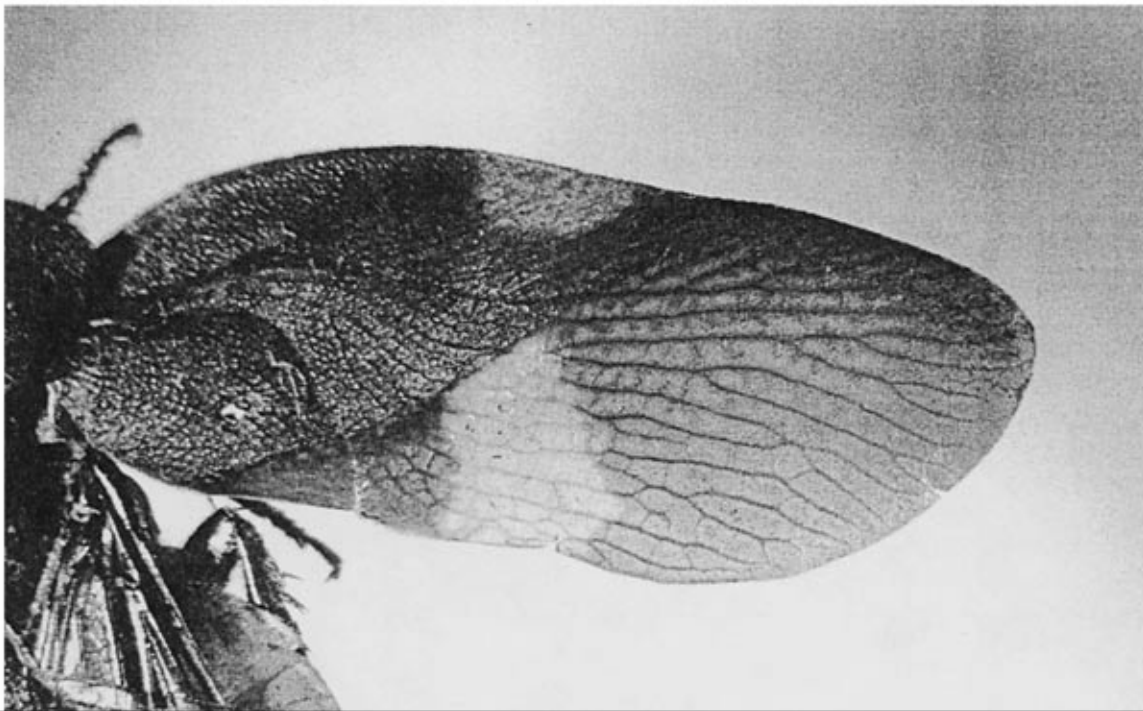
Description (Fig. 2). The coloration is uniformly light brown; thoracic paranota with fine darker



1a



1b



2

streaks. Segments of mid tarsi are clearly longer than those of fore tarsi, and somewhat shorter than those of hind legs. The cerci of the young nymph are subequal to the fore femur in length and width.

M e a s u r e m e n t s (length in mm): body, 1.6; pronotum, 0.38; hind femur, 0.7; hind tibia, 0.73; and hind basitarsus, 0.33.

M a t e r i a l. Holotype.

DICTYOPTERA *INCERTAE SEDIS*

One of main difficulties in the systematics of fossil dictyopterans is the problem of separating some higher taxa of this order. Moreover, comparison of morphological and paleontological data accumulated by many authors for long years with results of modern karyological and molecular studies revealed a close relationship between the three former “orders” of orthopteroid insects: cockroaches, termites, and praying mantises. Their proximity and comparatively late divergence from each other (apparently, in the second half of the Jurassic) preclude giving these taxa the same rank as other well-studied orders of Polyneoptera, which diverged from each other no later than at the beginning of the Permian. In this connection a preliminary scenario of dictyopteran evolution was proposed, along with associated modifications of their classification elucidating the boundaries between higher taxa of this order (Gorochov, 2001a).

However, the above-mentioned paper, published in the Brazilian journal *Acta geologica leopoldensia* was edited in such a way that made a mockery of the author’s text (no proofs were sent to the author). Let us to mention only few distortions and only from the part devoted to Dictyoptera: to characterize the suborder Mantina, it was written in the manuscript that the mantid ootheca is formed “out of the female genital chamber,” whereas the published text states that it is formed “within the female genital chamber”; the manuscript states in the diagnosis of Blattoidea that their ootheca is formed within the female genital chamber and this passage is omitted in the publication; I also wrote in the manuscript that modern cockroaches and mantises might have been descendants of unspecialized representatives of the superfamily Raphidiomimoidea, possibly, belonging to the family Blattulidae, but in the publication it was stated that Raphidiomimoidea descended from Blattulidae; and at last, it was noted in the manuscript that key adaptations of the order possibly originated in association with “swimming” in loose forest litter, but it appeared in the publication that the first dictyopterans “swam” in loose soil.

These and other distortions force me to review here briefly the ideas put forward in that paper. It was sug-

gested to divide the order Dictyoptera into four suborders: Mylacridina (extinct Paleozoic–Mesozoic suborder characterized by retention of long ovipositor, oviposition into the soil or another substrate, coxopodites of the ninth male abdominal segment probably still separated from its sternite, and possibly segmented male styli), Blattina (cockroaches), Mantina (mantises), and Termitina (termites).

The last three of these suborders separated from Mylacridina apparently only in the Mesozoic; their common ancestor possessed a significantly shortened ovipositor (not suitable for ovipositing deep into the substrate) and possibly a very primitive ootheca, representing two compact egg rows deposited onto some surface and concealed with secretion of accessory glands. The origin of such an ootheca formed outside the female genital chamber could be a consequence of this ancestor’s turn to obligatory phytophilous mode of life (an open egg batch is also found in some modern phytophilous katydids with a markedly shortened ovipositor).

It was proposed to include the above common ancestor in Raphidiomimoidea, the most primitive superfamily of the suborder Blattina, along with the Mesozoic families Raphidiomimidae and, possibly, Blattulidae, which were hypothesized to possess the above primitive ootheca. The second superfamily of this suborder (Blattoidea) was derived from Raphidiomimoidea, not from specialized Raphidiomimidae, but from Blattulidae or similar forms. Blattoidea were considered as embracing all modern cockroach families and distinguished from Raphidiomimoidea mainly in the acquisition of the characteristic cockroach ootheca formed within the female genital chamber and in the resulting concealment of ovipositor rudiments deep in this chamber.

The suborder Mantina was likewise hypothesized to have evolved from some Jurassic Raphidiomimoidea similar to the ancestor of Blattoidea (and it was noted that mantises apparently inherited from these Raphidiomimoidea a primitive ootheca formed outside the female genital chamber), and the suborder Termitina from Jurassic representatives of the suborder Blattina. Later on (Gorochov, 2004; Anisyutkin and Gorochov, 2005) several corrections and additions were published: a scenario of the origin of this order and a hypothesis on its possible relationships were put forward; the superfamilies Raphidiomimoidea and Blattoidea were raised to infraordinal rank (Raphidiomimidea and Blattidea); ancestors of Termitina were specified as some members of the infraorder Blattidea that already possessed the cockroach ootheca formed within the female genital chamber (these groups were shown to be synapomorphic in the structure of ootheca by Nalepa and Lenz (2000)).

Explanation of Plate 5

Fig. 1. *Mantoblatta mira* sp. nov. (Mantoblattidae), holotype NHM, In. 19132-2: body viewed from (1a) above and (1b) below; Upper Cretaceous Burmese amber.

Fig. 2. *Eucorydia purpuralis* (Kirby) (Corydiidae), modern China; lower elytron.

Superfamily Umenocoleoidea Chen et Tian, 1973

In the recent paper by Vršanský (2002a) a new species, genus, and family of mantises (*Archimantis zherikhini*, Archimantidae) were described from the Late Cretaceous amber of New Jersey, the United States. Because of homonymy, the genus and family were soon renamed *Jantarimantis* and Jantarimantidae (Vršanský, 2002b). Somewhat later it was claimed that the holotype of *J. zherikhini* is in fact not a mantis but a cockroach of the family Umenocoleidae (Grimaldi, 2003, pp. 11–12). This enigmatic Early Cretaceous family was originally described in Coleoptera (Chen and Tian, 1973), later transferred to Protelytroptera (Carpenter, 1992), and then included in Blattaria as a separate superfamily Umenocoleoidea (Vršanský, 1999). Assignment of this superfamily to the order Dictyoptera appears correct (Blattaria *sensu* Vršanský = Mylacridina + Blattina), but its subordinal position is not so clear.

According to the first description of *J. zherikhini* and photographs of the holotype (Vršanský, 2002a, text-figs. 1, 28), this species, contrary to Grimaldi's opinion, unquestionably belongs to the suborder Mantina, as it possesses features characteristic of this group such as hemispherical eyes and development of all three ocelli. It should be noted that in the remaining dictyopterans, except for termites and some blind or nearly blind cockroaches, the eyes are reniform or horseshoe-shaped, and the median ocellus is absent in all Dictyoptera, except for mantises (see the previous section). The median ocellus is clearly seen on the first mentioned photograph of the *J. zherikhini* holotype.

The absence of distinct raptorial spines on fore legs of this species may be a consequence of incomplete specialization to predatory life (the life mode is already predatory, but noticeable adaptations to the capture of prey have not yet formed, e.g., in some predatory katydids of the subfamily Tettigoniinae) or, conversely, retreat from obvious predation (or shift from hunting on large and mobile prey to feeding on small and/or sluggish invertebrates).

Therefore, if Grimaldi's opinion about the proximity of *J. zherikhini* to Umenocoleidae is true, then the superfamily Umenocoleoidea should be transferred into the suborder Mantina. There are additional reasons for this opinion presented in the same paper by Grimaldi. So, the Early Cretaceous genus *Santanmantis* Grimaldi, 2003 shows, on the one hand, undoubted affinity to mantises (general habitus and wing structure, especially presence of the oblique pseudovein in both fore wings), and, on the other hand, similarity to true Umenocoleidae (shape of head and pronotum, especially presence of arcuate transverse fold separating the narrow posterior part of disc from its anterior part (Vršanský, 2003, text-figs. 10, 11, 13, 15, 65; Grimaldi, 2003, text-figs. 16a, 16b)).

The most interesting is a certain similarity in fore wing venation of *Santanmantis* and Umenocoleidae. Compared to primitive dictyopterans and mantises, the number of longitudinal vein branches decreased significantly in both taxa. Their venation is easily derivable from that of the hypothetical ancestral form, which started to acquire specialization to four-winged flight, namely some costalization of forewings and lightening their weight by partial reduction of longitudinal veins.

It is also important that the structure of pseudovein in the forewings of *Santanmantis* seems the most primitive among other undoubted mantises with the wing venation known. This structure appears in many modern cockroaches, but on the lower elytron only. It represents a weak longitudinal depression with sclerotized integument, situated along the line of the overlap of the medial (anal) margin of the upper elytron in repose. Sometimes the part of lower elytron concealed by the upper elytron in repose is also more or less membranized (modern genus *Eucorydia* Heb., Corydiidae; Pl. 5, fig. 2). Adaptation of elytra to flapping flight in hypothetical descendants of *Eucorydia* could result in similar membranization (hemipterization) of the upper elytron (as took place in the modern genus *Holocompsa* Burm.), and then in transformation of both elytra into almost entirely membranous flight organs (as in the modern genus *Hypercompsa* Sauss.). In contrast to these two genera, constituting a separate evolutionary lineage within Corydiidae, these descendants of *Eucorydia* could most probably have retained traces of the boundary between sclerotized and membranized parts of fore wing as an oblique pseudovein crossing the clavus. An analogous process might occur at the origin of such primitive mantises as *Santanmantis*.

Assigning two other dictyopterans from Cretaceous ambers (apart from the rather enigmatic *Jantarimantis*) to Umenocoleidae and treating some modern cockroaches as closely related to this family (Vršanský, 2003) seems incorrect. Moderate sclerotization of forewings in ancient dictyopterans followed nearly the same pattern; namely, an increase in the number of longitudinal vein branches and their approximation to each other. But further sclerotization of these wings proceeded along different ways. The straightest way was adopted by dictyopterans that acquired almost beetle-like elytra via thickening numerous longitudinal branches and narrowing the spaces between them (among these, the modern genus identified by Vršanský as *Prosoplecta* Sauss.; Vršanský, 2003, text-figs. 125–127). It was apparently associated with partial fusion of these branches in places where crossveins (or their traces) were retained. The resulting, strongly sclerotized elytron usually bears traces of numerous close-set longitudinal veins interspersed by longitudinal rows of small pits (punctures), each row being a remnant of a single row of former cells between these approximated veins.

The forms which may be provisionally designated as true Umenocoleoidea (Early Cretaceous *Umenocoleus* Chen et Tian, *Petropterix* Vršanský, *Elytropterix* Vršanský, and *Ponopterix* Vršanský) show another pattern: the number of longitudinal branches is decreased (but they are nevertheless more or less distinct), the spaces between these branches are widened, and the small pits between them are numerous and do not form any regular longitudinal rows. Such structure may evolve if elytrization proceeds via transforming a prolific cross venation between widely spaced longitudinal branches into a fine-celled network. Thickening of such irregularly situated “crossveins” may result in the pattern of elytral sclerotization characteristic of Umenocoleoidea.

It is worth noting that one of the possible genera of Early Cretaceous Umenocoleoidea described by Vršanský (*Blattapterix* Vršanský) is figured as possessing numerous and, in places, even regular crossveins between sparse longitudinal branches (Vršanský, 2003, text-fig. 14). This genus may well represent a more primitive stage of forewing elytrization than the other above-mentioned genera of Umenocoleoidea, if not only nearly complete absence in it of the cockroach clavus, the most characteristic peculiarity of Dictyoptera during almost the entire history of this order (in true Umenocoleoidea the clavus is more similar to that of cockroaches).

One of the possible explanations why the elytral venation of Umenocoleoidea is atypical for dictyopterans lies in an assumption that in ancestors of this superfamily the elytral longitudinal venation was impoverished, say, because of improvement of aerodynamic properties allowing forewings to participate in active flapping flight, as apparently took place at the origins of the mantis suborder. Similar reasoning along with information about the presence in Umenocoleoidea of the markedly shortened external ovipositor (Vršanský, 1999) allowed me to suppose that Umenocoleoidea may be found to be either members of the infraorder Raphidiomimidea or even a side branch from the early Mantina (Gorochoy, 2001a, 2001b).

The latter hypothesis raised objections by Grimaldi (2003) who stated that the hind wing venation, sclerotization of elytra, wide abdomen, and short legs of Umenocoleidae exclude their close relationship to mantises, and that their fore legs are not raptorial at all. The first opinion is difficult to agree with, because mantises descended from primitive cockroaches and hence the wing of their early representatives must resemble those of cockroaches; moreover, a similarity in hind wing venation between Umenocoleoidea, Blattulidae, and mantises was noted not only by me, but by Vršanský (1999, p. 172) as well. Sclerotized elytra constitute an obvious autapomorphy of the group in question. Somewhat widened abdomen and comparatively short legs may well be its symplesiomorphies

with cockroaches. As for information on the presence of almost raptorial legs in *Ponopterix axelrodi*, this was taken from the original description of this species, co-authored by Grimaldi himself (Vršanský et Grimaldi in Vršanský, 1999, p. 172: “Fore legs similar to raptorial legs of early mantises”). Fore legs of possible Umenocoleoidea were discussed in more detail above.

DICTYOPTERA ERRONEOUSLY ASSIGNED TO UMENOCOLEOIDEA

Both dictyopterans from Cretaceous ambers ascribed to the genus *Jantaropterix* Vršanský et Grimaldi, originally assigned to Umenocoleoidea (Vršanský, 2003), have elytral venation virtually indiscernible (a vein separating the clavus is visible in one of them). It is impossible to decide which type of elytrization took place in evolution of these forms, but the absence of the fold or groove on the pronotum (separating its more or less wide posterior zone from the rest of the disc) characteristic of Umenocoleidae forces us to exclude these forms from this family. They most probably belong to some other group within Blattina or even Mylacridina. The latter possibility cannot be excluded, because in one of these dictyopterans the fore femur is almost as long as the tibia (Vršanský, 2003, fig. 81), and in another the structure of fore leg is unknown (Mylacridina and primitive Raphidiomimidea have fore legs similar to that above-mentioned, whereas other Raphidiomimidea and their possible descendants (Mantina, Blattidea, and Termitina) have fore tibiae much shortened); in addition, the structure of abdominal apex is unknown in female and insufficiently known in male.

Other features of these forms (in *J. newjersey* Vršanský et Grimaldi from the Upper Cretaceous of the United States elytra are leathery, translucent rather than stiff and well sclerotized, which is not characteristic of Umenocoleidae; in *J. lebani* Vršanský et Grimaldi from the Lower Cretaceous of Lebanon the pronotum is broad, much wider than the head, a feature that again is not characteristic of Umenocoleidae) not only additionally distinguish them from Umenocoleoidea, but also make them essentially different from each other, enough to be separated into at least different genera.

Genus *Pseudojantaropterix* Gorochoy, gen. nov.

E t y m o l o g y. From the genus *Jantaropterix*.

Type species. *Jantaropterix lebani* Vršanský et Grimaldi, 2003; Lower Cretaceous, Lebanese amber.

Diagnosis (based on data from Vršanský, 2003). Male. Pronotum broad (much wider than head), with subangulate posteromedian projection. Elytra probably rather strong (not translucent), comparatively wide, with markedly convex costal margin, straight anal margin and rather narrow apex; only CuP is dis-

cernible in elytral venation, markedly arched and separating fairly large, but not long, clavus. Hind wings with quite primitive venation (Vršanský, 2003, fig. 79), not folding transversely. Tarsi apparently short, at least length of hind tarsus no more than two-thirds the width of pronotum or elytron.

Composition. Type species.

Comparison. The new genus is easily distinguishable from *Jantaropterix* with the only species from Upper Cretaceous New Jersey amber (*J. newjersey*) in the clearly broader pronotum, its angulate (not rounded) posterior projection, wider, more laterally convex, not translucent elytra with distinct CuP, and much shorter tarsi (in *Jantaropterix* the length of the hind tarsus is no less than the width of the pronotum and distinctly greater than the width of the elytron). This genus differs from the other genera with reduced elytral venation in the shape of elytra and clavus and in the structure of hind wings.

ACKNOWLEDGMENTS

The author is grateful to curators of paleontological collections A. Ross (NHM) and C. Labandeira (NMNH), and to the staff of Arthropoda Lab (PIN) for making possible to study the above material, including types, and to amber collector A. Krylov (Kaliningrad) and E. Sugonyaev (ZIN), who passed some of the inclusions studied to the author. The study was supported by the Program of the Presidium of the Russian Academy of Sciences "Origin and Evolution of the Biosphere" (2004), Russian Foundation for Basic Research (project no. 04-04-48189), and grant of the Smithsonian Institution (Washington, D.C.) for short visit to NMNH (2005).

REFERENCES

1. L. N. Anisyutkin and A. V. Gorochov, "On the Possible Evolutionary Scenario of the Origin of Higher Taxa of Dictyoptera (Dictyoptera)," in *Abstracts of Papers of the Session on the Results of Scientific Research in 2004* (Zool. Inst. Ross. Akad. Nauk, St. Petersburg, 2005), pp. 3–4 [in Russian].
2. A. Arillo, V. M. Ortuno, and A. Nel, "Description of an Enigmatic Insect from Baltic Amber," *Bull. Soc. Entomol. France* **102** (1), 11–14 (1997).
3. F. M. Carpenter, "Superclass Hexapoda," *Treatise on Invertebrate Paleontology: Part R, Arthropoda 4* (Geol. Soc. Am., Boulder; Kansas Univ. Press, Lawrence, 1992), Vols. 3–4.
4. S. Chen and Ch.-ch. Tian, "A New Family of Coleoptera from the Lower Cretaceous of Kansu," *Acta Entomol. Sin.* **16** (2), 169–178 (1973).
5. M. S. Engel and D. A. Grimaldi, "A New Rock Crawler in Baltic Amber, with Comments on the Order (Mantophasmatodea: Mantophasmatidae)," *Am. Mus. Novit.*, No. 3431, 1–11 (2004).
6. A. V. Gorochov, "On the Higher Classification of the Polyneoptera (Short Course)," *Acta Geol. Leopold.* **24** (52/53), 11–56 (2001a).
7. A. V. Gorochov, "The Most Interesting Finds of Orthopteroid Insects at the End of the 20th Century and a New Recent Genus and Species," *J. Orthopt. Res.* **10** (2), 353–367 (2001b).
8. A. V. Gorochov, "New and Little Known Mesotitanidae and Paratitanidae (Titanoptera) from the Triassic of Kyrgyzstan," *Paleontol. Zh.*, No. 4, 62–69 (2003) [*Paleontol. J.* **37** (4), 400–406 (2003)].
9. A. V. Gorochov, "Primitive Titanoptera and the Early Evolution of the Polyneoptera," *Lectures in Memory of N.A. Kholodkovskii*, Issue 57, No. 1, 1–54 (2004).
10. V. G. Gratshev and V. V. Zherikhin, "New Fossil Mantids (Insecta, Mantida [Sic])," *Paleontol. J.* **27** (1A), 148–165 (1993).
11. D. Grimaldi, "Captured in Amber," *Sci. Am.* **274** (4), 84–91 (1996).
12. D. Grimaldi, "A Revision of Cretaceous Mantises and Their Relationships, Including New Taxa (Insecta: Dictyoptera: Mantodea)," *Am. Mus. Novit.*, No. 3412, 1–47 (2003).
13. K.-D. Klass, O. Zompro, N. P. Kristensen, and J. Adis, "Mantophasmatodea: A New Insect Order with Extant Members in the Afrotropics," *Science* **296**, 1456–1459 (2002).
14. K.-D. Klass, M. D. Picker, J. Damgaard, et al., "The Taxonomy, Genitalic Morphology, and Phylogenetic Relationships of Southern African Mantophasmatodea (Insecta)," *Entomol. Abh.* **61** (1), 3–67 (2003).
15. C. A. Nalepa and M. Lenz, "The Ootheca of *Mastoterme darwiniensis* Froggatt (Isoptera: Mastotermitidae): Homology with Cockroach Oothecae," *Proc. R. Soc. Lond. B* **267**, 1809–1813 (2000).
16. A. G. Sharov, "Phylogeny of Orthopteroid Insects," *Tr. Paleontol. Inst. Akad. Nauk SSSR* **118**, 1–217 (1968).
17. V. N. Vishnyakova, "Mesozoic Cockroaches with an External Ovipositor: Distinctive Features of Their Reproduction (Blattodea)," in *Jurassic Insects of the Karatau Mountains* (Nauka, Moscow, 1968), pp. 55–86 [in Russian].
18. P. Vršanský, "Lower Cretaceous Blattaria," in *Proc. First Int. Palaeoentomol. Conf., Moscow, 1998* (AMBA projects AM/PFICM 98/1.99, Bratislava, 1999), pp. 167–176.
19. P. Vršanský, "Origin and Early Evolution of Mantises," *AMBA projekty* **6** (1), 1–16 (2002a).
20. P. Vršanský, "*Jantarimantis* nom. nov. and *Jantarimantidae* nom. nov., New Replacement Names for the Genus *Archimantis* Vršanský, 2002, and the Family Archimantidae Vršanský, 2002 (Insecta, Mantodea)," *AMBA projekty* **6** (2), 1 (2002b).
21. P. Vršanský, "Umenocoleoidea—An Amazing Lineage of Aberrant Insects (Insecta, Blattaria)," *AMBA projekty* **7** (1), 1–32 (2003).
22. O. Zompro, "The Phasmatodea and *Raptophasma* n. gen., Orthoptera incertae sedis, in Baltic Amber (Insecta: Orthoptera)," *Mitt. Geol.-Palaeontol. Inst. Univ. Hamburg* **85**, 229–261 (2001).
23. O. Zompro, J. Adis, and W. Weitschat, "A Review of the Order Mantophasmatodea (Insecta)," *Zool. Anz.* **241**, 269–279 (2002).