New evolutionary evidence of Grylloblattida from the Middle Jurassic of Inner Mongolia, north-east China (Insecta, Polyneoptera)

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The small modern insect order Grylloblattida has an abundant fossil record during the Late Palaeozoic and the Mesozoic. The relationships between these fossil taxa and the modern grylloblattids remain unclear because most of them are based on isolated wings or have poorly preserved body features. Modern grylloblattids are wingless insects. The new grylloblattid family *Plesioblattogryllidae* fam. nov. is erected for the new genus and species *Plesioblattogryllus magnificus* gen. nov., sp. nov., from the Middle Jurassic of north-eastern China. The well-preserved specimen provides further evidence that could support its close relationships with the modern grylloblattids: (1) several very similar head structures, e.g. developed laciniae with inner row of setae, maxillary palps segmented into five, labial palps segmented into three, large labrum, and morphology of antenna; (2) paired eoplantulae on tarsomeres 1–4; (3) long ovipositor and large eggs comparable with those of modern taxa. The new genus has strongly developed mandibles with sharp pointed apical teeth and strong marginal teeth, and strong hook-like fore claws with basal teeth, suggesting it was carnivorous. The major differences between the extinct and extant Grylloblattida, such as the lack of wings, the eyes and ocelli either degenerated or absent, and the thorax degenerated in the modern forms, are probably related to their adaptation to their life under rocks and rock-crawler habits. © 2008 The Linnean Society of London, Zoological Journal of the Linnean Society, 2008, 152, 17–24.

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INTRODUCTION

The small order Grylloblattida (rock crawlers), currently considered as ‘living fossils’, comprises 26 living species within four genera (Vrsansky et al., 2001). Its fossil record is distinctly larger with more than 44 families, even extending to the Late Carboniferous (Storozhenko & Vranský, 1995; Storozhenko, 1997). However, many of these taxa are based on isolated wings, with their body features unknown. Extant grylloblattids are wingless insects. The definition of the Grylloblattida *sensu* Storozhenko (1997, 2002: 279) is far from being clear. This author indicated that the synapomorphies of the Grylloblattida are ‘absent because of paraphyletic state of the order in respect to other perlideans’. Storozhenko (1998, 2002) considered that the Embiotoptera are ‘derived’ from the Permian grylloblattid *Sheimia* Martynova, 1958. There is still not consensus on the relationships between Plecoptera, modern Grylloblattidae, Embiotoptera, and Dermaptera. Wheeler et al. (2001) considered that the modern Grylloblattidae are the sister group of the Dermaptera, being together the
sister group of (Phasmida + Orthoptera), and that the (Plecoptera + Embioptera) are not directly related to this clade. Beutel & Gorb (2001) considered that the Grylloblattidae are the sister group of the clade (Phasmatodea + [Mantodea + (Isoptera + Blattodea)]). Grimaldi (2001) supposed that the extant and fossil ‘Grylloblattida’ falls in an unresolved polytomy with the majority of the other ‘polyneopteran’ orders. Terry & Whiting (2005) and Cameron, Barker & Whiting (2006) considered that the Grylloblattida could be the sister group of the recently discovered order Mantophasmatodea, and altogether could be the sister group of the Dictyoptera. Grimaldi & Engel (2005: 223) also supposed that the Palaeozoic and Mesozoic alate ‘grylloblattids’ could ‘represent a stem group of both apterous Grylloblattida and Mantophasmatodea. Lastly, even if Rasnitsyn (1976, 1980) listed several similarities between Blattogryllus and the extant Grylloblattidae, the potential synapomorphies of this last group with the fossil ‘Grylloblattida’ are not clear.

Thus, the present discovery of a new Middle Jurassic fossil insect attributable to the ‘Grylloblattida’, with well-preserved body structures, is potentially of great interest to solve the problem of the relationships between the extant Grylloblattidae and the fossil ‘Grylloblattida’.

We follow the terminology of the wing venation of Storozhenko (1998) in order to allow a more simple comparison of our fossil with those already described, even if we reserve our opinion on its real phylogenetic value, especially concerning the problem of the exact nature of the vein ‘M5’ (see Kukalová-Peck, 1991).

**SYSTEMATIC PALAEONTOLOGY**

Order ‘Grylloblattida’ Walker, 1914
(sensu Storozhenko, 2002)

**PLESIOBLATTOGRYLLIDAE FAM. NOV.**

*Type genus: Plesioblattogryllus* gen. nov.

**Diagnosis:** Wing venation nearly identical to that of *Blattogryllus karatavicus* Rasnitsyn, 1976; mandibles very strong with a sharp pointed apical tooth and a few marginal teeth with a broad base; eyes and ocelli present; antenna short with segments 2–7 shorter than others; pronotum with broad lateral expansions; tarsomeres 1–4 with a pair of rather large euplantulae; tarsi with strong claws and no arolia; fore tarsal claw with a large base and strong basal tooth.

**Remark:** Some new material of grylloblattids was discovered in the same locality after recent fieldwork. Two new forms seem to be closely related or attributable to the new family. Thus, a further cladistic analysis of the Plesioblattogryllidae will be possible in the near future.

**PLESIOBLATTOGRYLLUS GEN. NOV.**

**Derivation of the name:** Named after the Greek ‘plesios’ meaning close or near, and *Blattogryllus*.

**Type species:** *Plesioblattogryllus magnificus* sp. nov.

**Diagnosis:** That of the family.

**PLESIOBLATTOGRYLLUS MAGNIFICUS**

*GEN. NOV., SP. NOV.*

**FIGURES 1–3**

**Derivation of the name:** Named after the wonderful state of preservation of the type specimen.

**Material:** Only the holotype included (NIGP 133701). The holotype is an almost complete female specimen with brownish colour, dorsally compressed, and without counterpart. The material is deposited in the Nanjing Institute of Geology and Palaeontology.

**Type locality:** Daohugou Village, Ningcheng County, Inner Mongolia, north-east China; Middle Jurassic, Jiulongshan Formation.

**Description:** Head 10.5-mm long, 7.7-mm wide, rather developed, upper surface covered with small tubercles and tiny setae; eyes 3.4-mm long, 1.9-mm wide (left one), 4.0-mm apart, in lateral position, subelliptic in shape, contracted posteriorly; three ocelli 0.6 mm in diameter at middle, olive shaped, disposed in a triangle but nearly aligned between eyes; left mandible 4.8-mm long (without tip), 2.8-mm wide at base, right mandible 5.2-mm long and 2.6-mm wide at base, both very robust, asymmetrical (problem of preservation?), left mandible with a long, curved, and sharp pointed apical tooth and three marginal teeth, first and second being strong and pointed, and third marginal tooth located near base and very blunt; lacinia c. 4-mm long and very developed, pointed at apex, with a row of dense setae in middle inner margin; preserved part of maxillary palp 4.5-mm long, developed, with five segments of distinctly increasing width forwards, covered with fine setae; labial palp 4.3-mm long, developed, with three elongated segments of nearly the same width, covered with fine setae, second segment being shorter than the other two, the last one distinctly swollen and rounded at apex; clypeus 1.2-mm long, 2.8-mm wide, strong, with the shape of a transverse ellipse; labrum 2.5-mm long, developed, slightly projected in median part of anterior edge, extending to two-thirds of the
mandibles; antenna c. 15-mm long, as long as head + pronotum, its base located close to the mandible; about 24 antennomeres, first one large, second shortest, third rather long, segments 4–7 distinctly shorter than the others, segments 8–24 with a notable decreasing width, last one with rounded end, all antennomeres covered with fine setae; ecdysial distinctly visible, Y-shaped.

Pronotum 5.2-mm long medially, 5.7-mm long laterally, 9.3-mm wide, broader than head, covered with tiny setae, with middle line and large rounded lateral expansions, anterior margin slightly projected, with pronounced angles, posterior margin rounded; mesonotum 4.2-mm long, about 4.7-mm wide, contracted backwards, distinctly narrower than pronotum.

*Figure 1. Plesioblattogryllus magnificus* gen. nov., sp. nov., holotype NIGP 133701. A. Photograph of general habitus (scale bar represents 10 mm). B. Photograph of foreleg (scale bar represents 2 mm). C. Photograph of head (scale bar represents 5 mm). D. Photograph of hind leg (scale bar represents 2 mm). E. Photograph of eggs (scale bar represents 2 mm).
Legs all similar; femora, tibiae, and tarsi densely covered with distinct setae; fore and hind coxae visible, and rather elongate; forelegs rather sturdy, femur 6.8-mm long, 1.8-mm wide, tibia 5.7-mm long, 0.8-mm wide; median legs rather short, femur 9.2-mm long, 1.7-mm wide, tibia 6.5-mm long, 1.1-mm wide; posterior legs slender, femur 9.6-mm long, 1.9-mm wide, tibia 9.7-mm long, 0.8-mm wide, tarsi 5.0-mm long; inner margin of median tibia with three strong aligned spines; inner margin of posterior tibia with four strong aligned spines, apical end with three strong spines; all tarsi with five segments, tarsomeres 1–4 with a pair of rather large euplantulae, fifth segments rather elongate with increased width; no arolia but two claws, hind tarsal claws 0.7-mm long, strong, and rather straight, fore tarsal claws 0.9-mm long, with a large base and a strong basal tooth.

Wings partly overlapping and difficult to interpret, in particular for the anal areas; wings dark infuscate with darker spots in distal halves; preserved parts of fore and hindwings similar, but the possible differences in the anal areas are not preserved; wings hyaline; forewing 43-mm long, about 11-mm wide; costal area between subcosta (Sc) and anterior wing margin narrow, 1.0-mm wide, in all wings, with about 20 more or less sigmoidal cross-veins between Sc and anterior wing margin; costal vein reaching wing apex; vein Sc ending on anterior wing margin 3.7 mm to wing apex; radius (R) ending very close to wing apex; Sc and R closely parallel; several cross-veins in area between Sc and R, the most distal ones being oblique; base of Rs 22 mm from wing base, in basal half of wing; area between R and radial sector (Rs) rather narrow, 1.2-mm wide in its broadest part, with one or two rows of cells; Rs posteriorly pectinate, with five main branches; cubitus apex (CuA) emerging from Cu at wing base and basally fused with common stem R + media (M); R and M + CuA separating about 4 mm from wing base; M + CuA anteriorly pectinate, with first branch media anterior (MA) emerging 7 mm...
from its base; MA posteriorly pectinate, with three branches in its distal fourth; media posterior (MP) emerging 10 mm from base of M + CuA and apparently simple; CuA posteriorly pectinate with three long and simple branches; cubital area between M + CuA and cubitus posterior (CuP) broad, with long sigmoidal cross-veins; CuP simple; anal vein 1 (A1) posteriorly pectinate with three simple branches; A2 forked; hindwing about 40-mm long.

Abdomen 15.8-mm long, segmentation not clearly visible, first visible abdominal segment shorter than half of the second, and other visible segments with distinct lateral lobes; last segment very small with slight lateral angles; two long, parallel-sided, and straight structures corresponding to the ovipositor, c. 8.0-mm long; right cercus (?) with three visible elongate segments, second segment distinctly longer than the first one; at least 11 visible large olive-shaped eggs, c. 3-mm long, 1.5-mm wide, with several strongly developed longitudinal ridges, first egg at level of second abdominal segment, but smaller than the more distal eggs.

**COMPARISON WITH FOSSIL GRYLLOBLATTIDA**

After the available phylogenetic analysis of the fossil taxa currently attributed to the Grylloblattida, *P. magnificus* gen. nov., sp. nov., would fall in the Blattogryllidae Rasnitsyn, 1976 because of the following characters, after Storozhenko (1998, 2002): (1) forewing with sigmoidal cross-veins in area between CuP and M + CuA/CuA. Storozhenko (2002) interpreted them as branches of CuA terminating on CuP; (2) costal area of fore and hindwings narrow; (3) cross-veins of forewing area between Sc and C simple, not H- or Y-shaped. Storozhenko (2002: 284) indicated that the Blattogryllidae have ‘Sc veinlets H- or Y-shaped’, which is absolutely not the case in all the taxa currently included in the family; (4) forewing veins CuA and M basally fused (no veinlet ‘M5’ between them); (5) forewing cubital area with a series of branches of CuA directed to posterior wing margin; (6) forewing CuA with a strong anterior flexure at base. In fact, its forewing venation is closely similar to that of *B. karatavicus* Rasnitsyn 1976.

However, Storozhenko (1988a, b, 2002: 284) indicated that both *B. karatavicus* and *Blattogryllulus mongolicus* have tarsi with a large arolia and lacking claws. *Plesioblattogryllus* has strong claws and no arolia. These two characters are sufficient to separate *Plesioblattogryllus* from the Blattogryllidae, as the type species of this last family is *B. karatavicus*.

Another possible difference is the thorax as broad as pronotum in the Blattogryllidae, unlike the thorax with broad lateral expansions of *Plesioblattogryllus*. But it is necessary to be prudent with this character because of the taphonomic deformations of the body structures in these insects with large thoraces and heads. Interestingly, the thorax of *Parakhosara nasuto* Storozhenko, 1993 (Megakhosaridae Sharov, 1961; sister group of Blattogryllidae + Mesoblattinae, after Storozhenko, 2002) is similar to that of *Plesioblattogryllus*.

We also have to compare *Plesioblattogryllus* with the taxa currently attributed to the Blattogryllidae because some of these taxa are based on isolated wings:

(i) *Baharellus* Storozhenko, 1988a (two species: *Baharellus lineatus* Storozhenko, 1988a, Middle Jurassic, and *Baharellus madygensis* Storozhenko, 1992; Triassic). Both have the forewing Rs with only two main branches and with a corresponding area relatively reduced (Storozhenko, 1988a, 1992, 1998).

(ii) *Blattogryllulus* Storozhenko, 1988a (two species: *B. mongolicus* Storozhenko, 1988a, and *Blattogryllulus lucidus* Storozhenko, 1988a, both Upper Jurassic). Both have a forewing MA and CuA simple, and an Rs not pectinate, with a double fork (Storozhenko, 1988a).

(iii) *Parablattogryllus* Storozhenko, 1988a (one species: *Parablattogryllus obscurus* Storozhenko, 1988a, Lower Cretaceous). This taxon is based on a hindwing, even if it was labelled as a forewing in Storozhenko (1988a: fig. 1.i). Thus, it is difficult to compare with our specimen but its Rs is not pectinate.

(iv) *Dorniella* Bode, 1953 (two species: *Dorniella pulchra* Bode, 1953; Lower Jurassic, *Dorniella primitiva* Storozhenko, 1992, Middle or Upper Triassic). Both have Rs with only two branches (Storozhenko, 1988a, 1992). *D. primitiva* is based on a hindwing, which is very difficult to compare with the known forewings of *D. pulchra*. Thus the generic identity of these two species is questionable.

(v) *Costatoviblatta* Storozhenko, 1992 (one species: *Costatoviblatta aenigmatosa* Storozhenko, 1992; Middle or Upper Triassic).

(vi) *Mesoblattogryllus* Storozhenko, 1990 (three species: *Mesoblattogryllus intermedius* Storozhenko, 1990; *Mesoblattogryllus conjunctus* Storozhenko, 1992; both from Middle or Upper Triassic, *Mesoblattogryllus longipennis* Storozhenko, 1992; Lower or Middle Jurassic). These two genera have a short Sc and its first branch of Rs is pectinate, instead of being simple (Storozhenko, 1992, 1998).

(vii) *Baharellinus* Storozhenko, 1992 (two species: *Baharellinus dimidiatus* Storozhenko, 1992; *Baharellinus pectinatus* Storozhenko, 1992; both from Middle or Upper Triassic). They have very different wing shapes, rounded in *B. dimidiatus* and very elongate
in *B. pectinatus*. Nevertheless, their Sc is short and Rs has three branches (Storozhenko, 1992, 1998).

(viii) *Protoblattogryllus* Storozhenko, 1990 (three species: *Protoblattogryllus zajsanicus* Storozhenko, 1990; *Protoblattogryllus asiaticus* Storozhenko, 1990; *Protoblattogryllus abruptus* Storozhenko, 1990; Middle or Upper Triassic). They have a short Sc and an Rs with two branches (Storozhenko, 1990).

(ix) *Microblattogryllus* Storozhenko (1990) (one species: *Microblattogryllus variabilis* Storozhenko, 1990; Middle or Upper Triassic). It has a short Sc and a simple Rs.

(x) *Anoblattogryllus* Storozhenko, 1990 (one species: *Anoblattogryllus fundatus* Storozhenko, 1990; Middle or Upper Triassic). Its Sc is short.

(xi) *Gryphopteron* Handlirsch, 1939 (one species: *Gryphopteron molle* Handlirsch, 1939; Lower Jurassic). Its MA is fused with Rs, and its Rs has two distal branches (Ansorge, 1996).

(xii) *Megablattogryllus* Storozhenko, 1990 (two species: *Megablattogryllus magister* Storozhenko, 1990; *Megablattogryllus austerus* Storozhenko, 1990; *Megablattogryllus pinguis* Storozhenko, 1990; Middle or Upper Triassic). The only difference of *Plesioblattogryllus* with *Blattogryllus* in the wing venation is its MP being apparently simple. All other characters are identical (Rasnitsyn, 1976; Storozhenko, 1990).

Remark: All the species currently attributed to the Blattogryllidae based on isolated wings now fall into uncertain position between the Blattogryllidae and the Plesioblattogryllidae because these two families can be separated only on the basis of the body characters.

**EVOlUTIONARY RELATIONSHIP**

The present discovery and characters listed in Rasnitsyn (1976) show that there are numerous structures of at least some fossil *Grylloblattida* (Blattogryllidae and Plesioblattogryllidae) similar to those of extant Grylloblattidae. But these characters have never been polarized in a phylogenetic analysis. Thus, the establishment of a direct phylogenetic relationship between these groups remains questionable. A well-supported phylogenetic analysis of all polyneopterous orders, including the fossil taxa, is necessary. Re-analyses of the characters available in fossils (wing venation) could help to solve this problem, as Béthoux & Nel (2002a, b) already showed for the orthopteroid taxa.

Although more than 44 extinct families have been attributed to Grylloblattida, very few fossils have well-preserved body structures (Storozhenko & Vranský, 1995; Storozhenko, 1997). The new fossil material from the Middle Jurassic of north-east China provides some new similarities with the modern grylloblattids.

1. Some head structures of *P. magnificus* gen. nov., sp. nov. correspond to those of the living grylloblattids, namely: laciniae developed with an inner row of marginal setae; maxillary palp segmented into five; labial palp segmented into three; labrum developed; antenna with a large first segment, smallest second segment, and segments 2–7 distinctly shorter than the others. The structure of the antenomeres, viz. antenomere 2 smaller than 3, and antenomeres 4–7 distinctly shorter than the other distal segments, visible in *Plesioblattogryllus*, is a rather typical feature present in extant grylloblattids, but also in the modern Embiotoptera *Embia major* (Crampton, 1917: fig. 9). The rather developed antenomere 3 and its adjacent segments are especially similar to *Galloisiana yezoensis* (Asahina, 1961), and the third antenomere is even more developed in some other species such as *Galloisiana bryongensis* (Namkung, 1974). The mandibles and eyes in the new genus are remarkably larger than those of the extant forms. Moreover, the large ocelli of our fossil, absent in all modern grylloblattids, is an important difference. In addition, no evidence indicates that theclypeus of *Plesioblattogryllus* is divided into an anteclypeus and a postclypeus, as in extant forms.

2. The five-segmented tarsi and the tarsal euplantulae of *P. magnificus* gen. nov., sp. nov. are strongly similar to those of some modern grylloblattids (Walker, 1938: pl. 10; Caudell & King, 1924: plate 3: 2–3; Namkung, 1974: figs 10, 11; Storozhenko, 1998; Beutel & Gorb, 2006). However, Crampton (1927: 125) indicated that ‘some Mantids have flange-like tarsal pads very suggestive of those occurring in *Galloisiana* and in certain Gryllacrids’ (see also Crampton, 1933). Thus, this type of euplantulae seems to be not uniquely present in Grylloblattida, but also occurs in some Mantodea and Orthoptera. Thus, it is not sufficient alone to attribute *Plesioblattogryllus* to the same clade as the extant Grylloblattidae. Nevertheless, the wing venation and body structures of *Plesioblattogryllus* strongly differ from those of the Mantodea and Orthoptera, suggesting that it belongs to a very different order. The marginal and apical strong spines of posterior tibia in *Plesioblattogryllus* also display similarities with the modern forms.
3. The ovipositor and eggs are similar to those of modern forms. We interpret two long and parallel-sided straight structures as the ovipositor bases. Such structures are not only comparable with the ovipositor of extant female grylloblattids, but also to the similar structures described in some other extinct grylloblattid taxa (Storozhenko & Novokshonov, 1994). The large elliptic eggs are similar to those of modern grylloblattids (Crampton, 1927, 1933). They occupy a broad space in the abdomen, suggesting the adult female of *Plesioblattogryllus* had large ovaries. Similar size and arrangement of eggs in the abdomen are also found in some other Mesozoic grylloblattids (family Tshekardominiidae) (Novokshonov & Aristov, 2002).

In addition, the body of *P. magnificus* is covered with tiny setae as are those of the modern grylloblattids.

The well-developed wings of this large insect suggest it was probably an active flyer. Its fore tarsal claws differ from those of hind legs (the middle claws are not visible) in their hook-like shape with a large base and bearing a strong basal tooth. Moreover, the fore tarsal claws are also distinctly longer than the rather straight hind claws. After preservation, the fore tarsal claws and the most apical tarsomeres were probably movable structures. Such structures could have been associated with the capture of small prey. The very strong mandibles with a sharp pointed apical tooth could help to kill the prey, and the strong marginal teeth would help to destroy it. The developed eyes and ocelli suggest it was an active hunter. *Plesioblattogryllus* was probably a predator.

The fossil evidence indicates that the Permian grylloblattid *Tillyardembia* was probably a pollen eater (Afonin, 2000). Therefore the food habits of the early grylloblattids were very diverse. The modern grylloblattids probably became adapted to live under rocks or hidden in moss liver through the degeneration of their sensitive organs and wings. Even the eyes are absent in some cave-living species (Namkung, 1974). Their large ovaries suggest it was probably a predator. Its fore tarsal claws are more parallel-sided straight structures as the ovipositor bases. Such structures are not only comparable with the ovipositor of extant female grylloblattids, but also to the similar structures described in some other extinct grylloblattid taxa (Storozhenko & Novokshonov, 1994). The large elliptic eggs are similar to those of modern grylloblattids (Crampton, 1927, 1933). They occupy a broad space in the abdomen, suggesting the adult female of *Plesioblattogryllus* had large ovaries. Similar size and arrangement of eggs in the abdomen are also found in some other Mesozoic grylloblattids (family Tshekardominiidae) (Novokshonov & Aristov, 2002).

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