

New data on the Blattogryllidae-Plesioblattogryllidae-Grylloblattidae complex (Insecta: Grylloblattida: Blattogrylloptera tax.n.)

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> Abstract

The taxon Blattogrylloptera tax.n., whose distinctive character is ‘in forewing, M + CuA splitting into MA and MP + CuA’ (as opposed to ‘into M and CuA’), is erected to make possible a taxonomic assignment of isolated grylloblattidan wings which cannot be conclusively assigned either to the Blattogryllidae or the Plesioblattogryllidae. Material of two blattogryllopteridan species collected from the Daohugou locality (Middle Jurassic; Northeast China) is described. The limited available data on the species *Plesioblattogryllus minor* Ren & Aristov, 2011 are complemented by descriptions of four well-preserved specimens, some exhibiting variation in wing venation. *Duoduo qianae* gen.n. et sp.n. is erected on the basis of an isolated wing. Characters useful for the identification of members of the families Blattogryllidae and Plesioblattogryllidae as well as characters possibly linking these taxa with the extant Grylloblattidae are discussed.

> Key words

Grylloblattodea, Blattogrylloptera tax.n., *Duoduo qianae* gen.n. et sp.n., Grylloblattidae, tarsus, postabdomen, familial classification.

1. Introduction

The Middle Jurassic Daohugou locality yielded abundant material of fossil insects, including hundreds of Grylloblattida, i.e. putative relatives of extant Grylloblattidae. As currently understood, the diversity of Grylloblattida varied significantly through time (STOROZHENKO 2002). The earliest representative is from the early Late Carboniferous (CUI et al. 2011), a period during which the group is rare (BÉTHOUX & NEL 2010). In contrast, it is very speciose and abundant during the following period, the Permian (see BECKEMEYER & HALL 2007; among others). The Mesozoic shows a decline in the diversity of Grylloblattida, with no fossil record later than the Early Cretaceous. This shortage is possibly a consequence of the loss of wings (these are the most commonly preserved body parts in rock imprints) in subgroups having gained dominance then, and/or of a modification of ecological preferences making fossilization unlikely. As for the higher systematics, Grylloblattida was divided into three subor-

ders by STOROZHENKO (1998, 2002), but some ‘family shuffling’ (within suborders) between Storozhenko’s 1998 and 2002 contributions suggests that the robustness of the current classification could be improved.

In recent years material from the Daohugou locality received renewed attention. To date several grylloblattidan families have been sampled. The Geinitziidae is comparatively common (especially if compared with its low diversity during the Permian; CUI et al. 2012; HUANG & NEL 2008; STOROZHENKO 1998). Abundant material of another family (Neleidae?) remains to be described (in prep.). Representatives of the Juraperlidae are rare, represented by two species only (CUI et al. 2010; HUANG & NEL 2007). Finally, the family Plesioblattogryllidae was erected by HUANG et al. (2008) based on a single complete female individual, assigned to *Plesioblattogryllus magnificus* Huang, Nel & Petrusevičius, 2008, and preserving details of the head, legs, and eggs. In addition, *Plesioblattogryl-*

lus minor Ren & Aristov, 2011, a smaller species presumably related to *Pl. magnificus* and also occurring at Daohugou, has been documented based on a single forewing only (REN & ARISTOV 2011).

Provided that Plesioblattogryllidae is mostly defined based on body characters (viz. tarsomeres 1–4 with a pair of comparatively large euplantulae; pretarsi with strong claws and no arolia), further evidence for the familial assignment of *Pl. minor* is necessary. Furthermore, based on data available to date, it is not excluded that *Pl. minor* could be the male of *Pl. magnificus*. Additionally, REN & ARISTOV (2011) challenged the view that the Plesioblattogryllidae represent a family on their own, and suggested that the name could be a junior synonym of Blattogryllidae, a family known from many localities (STOROZHENKO 1998). Finally, Blattogryllidae and Plesioblattogryllidae are of particular importance, as these families have been considered as the closest relatives of extant Grylloblattidae (HUANG et al. 2008; RASNITSYN 1976; STOROZHENKO 2002).

In the following I describe additional material from the Daohugou locality belonging to *Pl. minor* and to a new, related species, which complements the available information. The new data prompted me to erect a new taxon encompassing Blattogryllidae, Plesioblattogryllidae, and more tentatively Grylloblattidae, and to reconsider some characters of these families.

2. Material and methods

The material was collected from the Daohugou locality (Chifeng City, Inner Mongolia, Northeast of China; Middle Jurassic; LIU et al. 2004; REN et al. 2002). Specimens were examined using a Leica M165C stereo-microscope and illustrated with the aid of a drawing tube. The drawings were processed by hand and scanned. Photographs were taken using a digital camera Canon EOS 550D coupled to a Canon 50 mm macro lens and a Canon MP-E 65 mm macro lens, and processed using an image editing software. The material referred to as CNU is housed at the Key Lab of Insect Evolution and Environmental Changes, College of Life Science, Capital Normal University (CNU, Ren Dong Curator; Beijing, China). The specimen referred to as PIN is housed at the Paleontological Institute, Russian Academy of Sciences (Moscow, Russia). I follow the wing venation terminology of KUKALOVÁ-PECK (1991), itself derived from the serial wing venation pattern (LAMEERE 1923). Under this scheme each vein system (such as the Cubitus – Cu) is divided into

two sectors, anterior (CuA) and posterior (CuP). Anterior sectors usually are convex (i.e. elevated), and posterior sectors concave (i.e. in a depression). For elements of the postabdomen, including genitalia, the terminology of KLASS (2005, 2008) is followed.

3. Abbreviations

Institutes

CNU – Capital Normal University, Beijing, China; NIGP – Nanjing Institute of Geology and Palaeontology, Nanjing, China; PIN – Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

Wings and their venation

LFW – left forewing; LHW – left hind wing; RFW – right forewing; RHW – right hind wing. — R – Radius; RA – anterior Radius; RP – posterior Radius; M – Media; MA – anterior Media; MP – posterior Media; Cu – Cubitus; CuA – anterior Cubitus; CuA1 – anterior branch of anterior Cubitus; CuA2 – posterior branch of anterior Cubitus; CuP – posterior Cubitus; AA – anterior Analis; AA1 – first branch of anterior Analis; AA2 – second branch of anterior Analis.

Other morphological elements

an – antenna; mp – maxillary palp; af – antennal foramen; ce – compound eye; md – mandible; la – lacinia; lp – labial palp; fl – foreleg; oc – ocellus; eps – epistomal sulcus; ecl – ecdysial line; frs – frontal suture; ps – parietal sulcus; pn – pronotum; ti – tibia; cl – claw; T9 – tergite IX (9th abdominal segment); T10 – tergite X; LS8 – laterocoxosternum VIII (female subgenital plate); CX8 – coxite VIII; LC9 – laterocoxa IX (“gonangulum”); gp8 – gonapophysis VIII; gl9 – gonoplac IX; gp9 – gonapophysis IX; gc9 – male gonocoxite IX; sl9 – male stylus IX.

4. Systematics

In the following I use the traditional, ICZN-governed procedure. However I erect a new taxon and associate the name with a definition, as under the cladotypic nomenclatural procedure (BÉTHOUX 2007a,b, 2010). Note that under this procedure all taxon names are written in italics, with a capital letter, just as names of genera

under the traditional procedure. Therefore, in order to prevent confusion, the cladotypic section is provided in an Appendix, and only genus and species names will be italicized in the following.

Order Grylloblattida Walker, 1914

Taxon Blattogryllopterida tax.n.

Distinctive character. In forewing (if present), MP and CuA fused for some distance.

Composition. Species currently assigned to the extinct families Blattogryllidae Rasnitsyn, 1976 and Plesioblattogryllidae Huang et al., 2008, and to the extant Grylloblattidae Walker, 1914, excluding species assigned to the genera *Megablattogryllus* Storozhenko, 1990 and *Protoblattogryllus* Storozhenko, 1990 (see below).

Derivatio nominis. Name derived from ‘Blattogryllidae’ and ‘-pterida’, the latter derived from ‘-pteron’, ‘wing’ in Ancient Greek.

Remarks. No specific rank is assigned to the new taxon, but it is intended to be of a rank superior to those of the family group. Erection of this new taxon was prompted by the difficulty to assign isolated wings at the familial level, viz. either to the Blattogryllidae or to the Plesioblattogryllidae (or to Grylloblattidae, considering the probable presence of winged stem-group representatives): indeed the diagnostic characters of these families are from body parts other than wings. Yet, all species currently assigned to Blattogryllidae or Plesioblattogryllidae have the distinctive character state mentioned above (except for *Megablattogryllus* spp. and *Protoblattogryllus* spp., in which CuA fuses with M but diverges from M+CuA basal to the MA/MP fork). The erection of the new taxon allows isolated wings to be assigned conclusively between the ordinal and the familial ranks. According to this purpose, I list a single character state only (supposedly relevant) rather than a traditional diagnosis. The previously published diagnoses of the included families are to be considered for further identification.

The distinctive character state is well documented in the several winged species, including *Blattogryllus karatavius* Rasnitsyn, 1976 (Fig. 1), *Pl. magnificus* (Huang et al. 2008: fig. 2; REN & ARISTOV 2011: fig. 1a; observation of photographs provided by D. Huang confirmed that the defining character state occurs in the corresponding specimen), and *Pl. minor* (REN & ARISTOV 2011: fig. 1b,c; Fig. 2).

Phylogenetic considerations. It is necessary to address the question of the evolutionary origin of the distinctive character state to determine its polarity. According to STOROZHENKO (1998, 2002; both prior to the erection of Plesioblattogryllidae), the closest relative of Blattogryllidae and Grylloblattidae is the family Megakhosaridae Sharov, 1961. Representatives of this family do not possess a fusion of M+CuA. From this condition, there are two possible antonyms to the distinctive character state, corresponding to two plausible scenarios on its evolutionary origin. The first scenario would involve an early evolutionary stage where CuA is fused with M near wing base, the resulting common stem splitting into M and CuA; and a later stage where the fusion of CuA extends to the basal part of MP. The second scenario would involve a translocation of CuA onto M and the base of MP, with a distal origin of CuA from a MP+CuA common stem. In other words, there would be no intermediate condition with CuA fused with M but diverging from it basal to the MA/MP fork. In both cases the distinctive character state as formulated applies. However, under the first scenario, the antonym of the distinctive character state would be ‘in forewing, CuA diverges from M+CuA basal to the MA/MP fork’. A prerequisite to this condition is the presence of a fusion of CuA with M near the wing base, which is well documented in Blattogryllopterida (e.g. Fig. 6C). Indeed the occurrence of such a free basal portion of CuA fusing with M contradicts a ‘translocation scenario’, under which CuA would have no free part at all (by definition translocation is a full fusion, from the wing base). Additionally, *Megablattogryllus* spp. and *Protoblattogryllus* spp. precisely exhibit the early evolutionary stage (i.e. antonymic state) as hypothesized above, suggesting that the first scenario is more plausible. Note that under the second ‘translocation’ scenario, the antonym of the distinctive character state would be ‘M and CuA fully separated’.

In the absence of additional data on taxa which are the most closely related to Blattogryllopterida (in particular from characters other than from wing venation), analogous cases can be considered. The grylloblattidan family Euryptilonidae, assigned by STOROZHENKO (2002) to the suborder Lemmatophorina (while Blattogryllopterida would belong to the suborder Grylloblattina) is a suitable case: its representatives have a fusion of M with CuA, and the first fork of this composite stem yields an M stem (then splitting into MA and MP) and a CuA stem (see STOROZHENKO 1998). In other words, MP is separated from CuA.

The stem-orthopteran taxon Pantcholmanvissiida represents another relevant analogous case. Its representatives possess an M+CuA basal stem (according to homologies proposed by BÉTHOUX & NEL 2001, 2002). The first fork yields an M stem and a CuA stem, except in the derived Gigatitanidae, in which the same

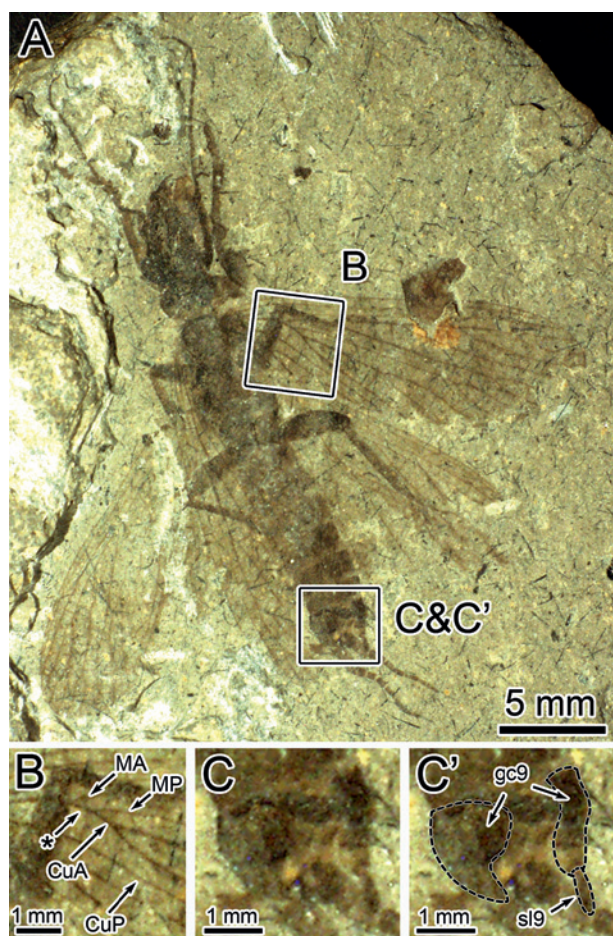


Fig. 1. *Blattogryllus karatavicus* Rasnitsyn, 1976, specimen PIN 2066/795, male. A: Photograph, habitus (positive imprint). B: Photograph of right forewing basal middle area, detail as located on A. C, C': Photograph of end of abdomen, C' with gonocoxites IX outlined by dashed lines.

condition as in Blattogryllopterida occurs (BÉTHOUX 2007c; SHAROV 1968, 1971). Again, a split of M+CuA into M (= MA+MP) and CuA predated a split into MA and MP+CuA.

In summary, although independent data is lacking, it is likely that a split of M+CuA into M (= MA+MP) and CuA historically predated the 'Blattogryllopterida split' into MA and MP+CuA. If so, the exclusion of *Megablattogryllus* and *Protoblattogryllus* from Blattogryllopterida is granted. This is linked with favouring the first scenario, although the chosen formulation of the distinctive character state is designed to accommodate the second 'translocation' scenario.

Representatives of the included extant family Grylloblattidae do not possess wings, but close relationships with Blattogryllidae and Plesioblattogryllidae have been assumed by RASNITSYN (1976), STOROZHENKO (2002), and HUANG et al. (2008). As for the latter contribution, no support is evident from the character states listed when considering character polarity. For example, these authors list '5-segmented

tarsus', which clearly is a plesiomorphy (BEUTEL & GORB 2006). Characters listed by STOROZHENKO (2002; see also fig. 393 therein) and supporting a monophyletic clade containing Blattogryllidae and Grylloblattidae are: (1) head as broad as pronotum, and (2) male gonocoxites asymmetrical. The second character state is the most useful and is a solid apomorphy present in extant species. STOROZHENKO's (2002) account basically rests on RASNITSYN's (1976), who described and listed male specimens of the fossil Blattogryllidae species *B. karatavicus*, and reported "male genitalia less asymmetrical [than in Grylloblattidae]", implying some level of asymmetry. However, based on observations of various photographs (provided by O. Béthoux and D.S. Aristov), it turns out that the abdomen apex of the specimen PIN 2384/205, which is illustrated by RASNITSYN (1976: fig. 1.III), is viewed somewhat laterally, making asymmetry of gonocoxites (or the lack thereof) difficult to appreciate. The specimen PIN 2066/795 was also listed by RASNITSYN (1976) as a male of *B. karatavicus*, but not illustrated. Observation of a photograph of this specimen (provided by O. Béthoux; Fig. 1) is suggestive of gonocoxite asymmetry (Fig. 1C,C'). However the resolution of the photograph is limited, and the location of the corresponding specimen is currently unknown (D.S. Aristov & A.P. Rasnitsyn, pers. comm. 2012), impeding further investigation.

A few points should be noted. First, the separation of the left and right gonocoxites IX can be considered as plesiomorphic within Insecta. It agrees with conditions in e.g. Archaeognatha (BITSCH 1974), while in many other Polyneoptera the two are fused into a subgenital lobe (e.g. Dictyoptera in KLASS 1997, Mantophasmatodea in KLASS et al. 2003). Asymmetry between the left and right gonocoxites IX is apomorphic, contrasting symmetry in Archaeognatha as well as most Polyneoptera (including Mantophasmatodea and many Dictyoptera). However, apomorphic asymmetry also occurs in the fused male subgenital lobes in some other polyneopteran taxa (e.g. some Dictyoptera, KLASS 1997). Second, the condition of the gonocoxites IX is unknown for all other fossil Grylloblattida. It is therefore unclear whether asymmetry only supports Blattogryllidae + Grylloblattidae or any more inclusive subgroup of Grylloblattida.

I also note that the female genitalic region of *Pl. minor*, as far as it is visible in the specimen CNU-GRY-NN-2011002, shows considerable resemblance with that of Grylloblattidae (compare the tentative interpretation in Fig. 3E' with WALKER 1943: figs. 5, 7 and KLASS 2005: fig. 9.3). However, this structural pattern does not include any apomorphies shared specifically by these taxa.

In summary the proposition that Blattogryllidae and Grylloblattidae are close relatives is to be con-

sidered as a working hypothesis which would require additional evidence. As far as the composition of Blattogrylloptera is concerned, the inclusion of Grylloblattidae is to be considered provisional. In any case, the taxon Blattogrylloptera is based on its distinctive character state, not its composition. In other words, as herein conceptualized, the Blattogrylloptera would be unaffected, should the Grylloblattidae prove to belong to another taxon.

Family Plesioblattogryllidae Huang, Nel & Petrulevičius, 2008

Type genus. *Plesioblattogryllus* Huang, Nel & Petrulevičius, 2008.

Revised diagnosis. Body: Mandibles very strong with a sharp pointed apical tooth, and a few marginal teeth with a broad base; compound eyes and ocelli present; antenna slightly longer than head, with antennomeres 4–6 (??) shorter than others; tarsomeres 1–4 with a pair of rather large euplantulae (not well documented in *Pl. minor*); pretarsi with strong claws and no arolia; eggs olive-shaped; cerci segmented. **Forewings:** ScP ending on the anterior wing margin; area between anterior margin and ScP narrow; RA simple, nearly parallel to ScP; RP posteriorly pectinate, with several branches; M fused with CuA in basal part; MA usually simple; MP with 1–3 branches; CuA1 with two branches. **Hind wings:** ScP ending on the anterior wing margin; RA parallel to ScP, simple; RP posteriorly pectinate, with four branches; MA simple; MP forked; CuA with three branches.

Discussion. The revised diagnosis is based on data from HUANG et al. (2008), and new data herein. Notably, leg morphology is better documented in HUANG et al. (2008).

Genus *Plesioblattogryllus* Huang, Nel & Petrulevičius, 2008

Type species. *Plesioblattogryllus magnificus* Huang, Nel & Petrulevičius, 2008.

Plesioblattogryllus minor Ren & Aristov, 2011 Figs. 2–5

Revised diagnosis. Small species (forewing about 20 mm long, hind wing 15 mm long); pronotum rectangu-

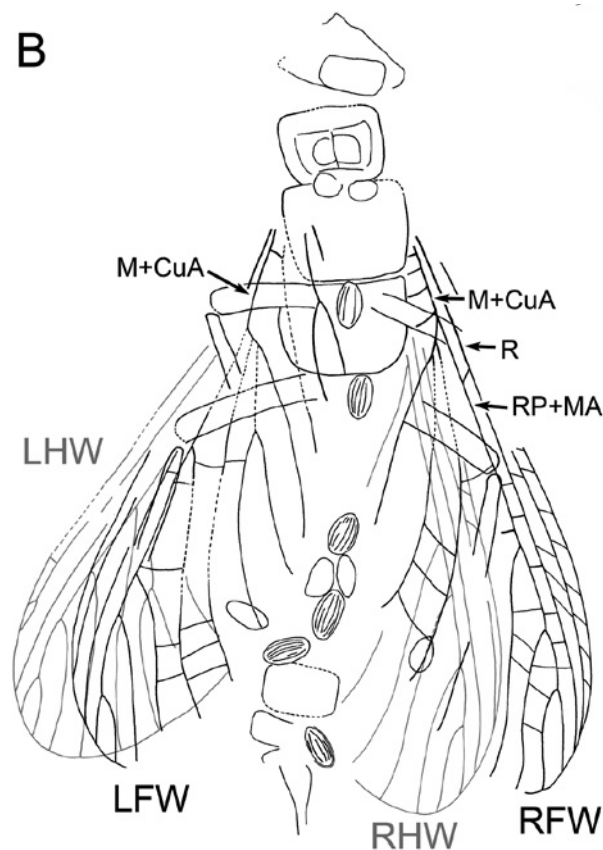


Fig. 2. *Plesioblattogryllus minor* Ren & Aristov, 2011, specimen CNU-GRY-NN-2011001, female. **A:** Photograph, habitus (positive imprint). **B:** Reconstruction of body and wings.

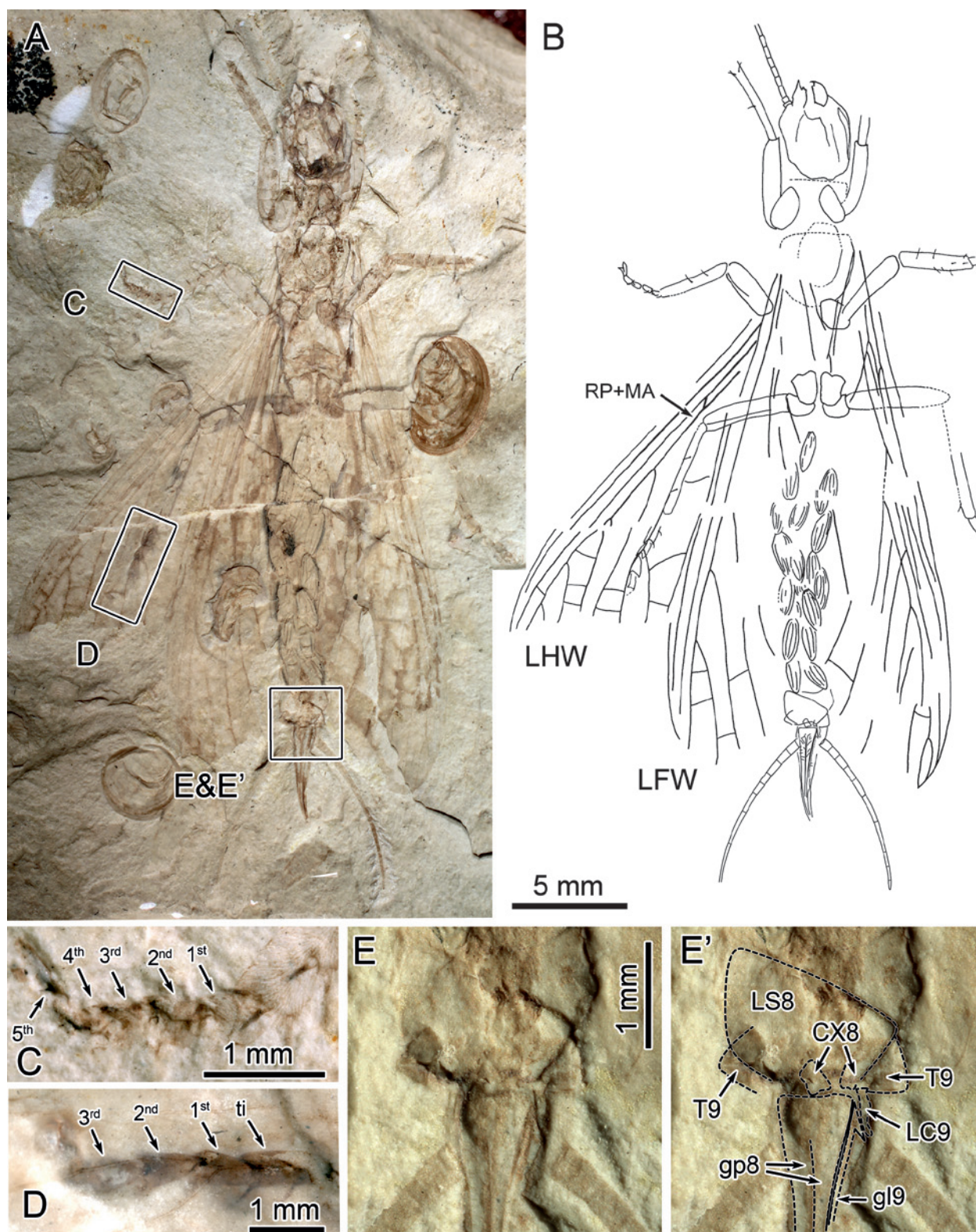


Fig. 3. *Plesioblattogryllus minor* Ren & Aristov, 2011, specimen CNU-GRY-NN-2011002, female. **A:** Photograph, habitus (positive imprint). **B:** Reconstruction of body and wings. **C:** Photograph of right midleg, detail as located on A (numbers indicate tarsomeres). **D:** Photograph of right hind leg, detail as located on A (numbers indicate tarsomeres). **E, E':** Photograph of end of abdomen (dorsal view), as located on A, E' with some elements outlined by dashed lines (E and E' same scale).

lar, nearly same width as head, or narrower; MA fused with RP slightly distal to the origin of RP; MP simple or 2-branched, rarely 3-branched.

Referred material. CNU-GRY-NN-2011001, CNU-GRY-NN-2011002, CNU-GRY-NN-2011003, CNU-GRY-NN-2011004.

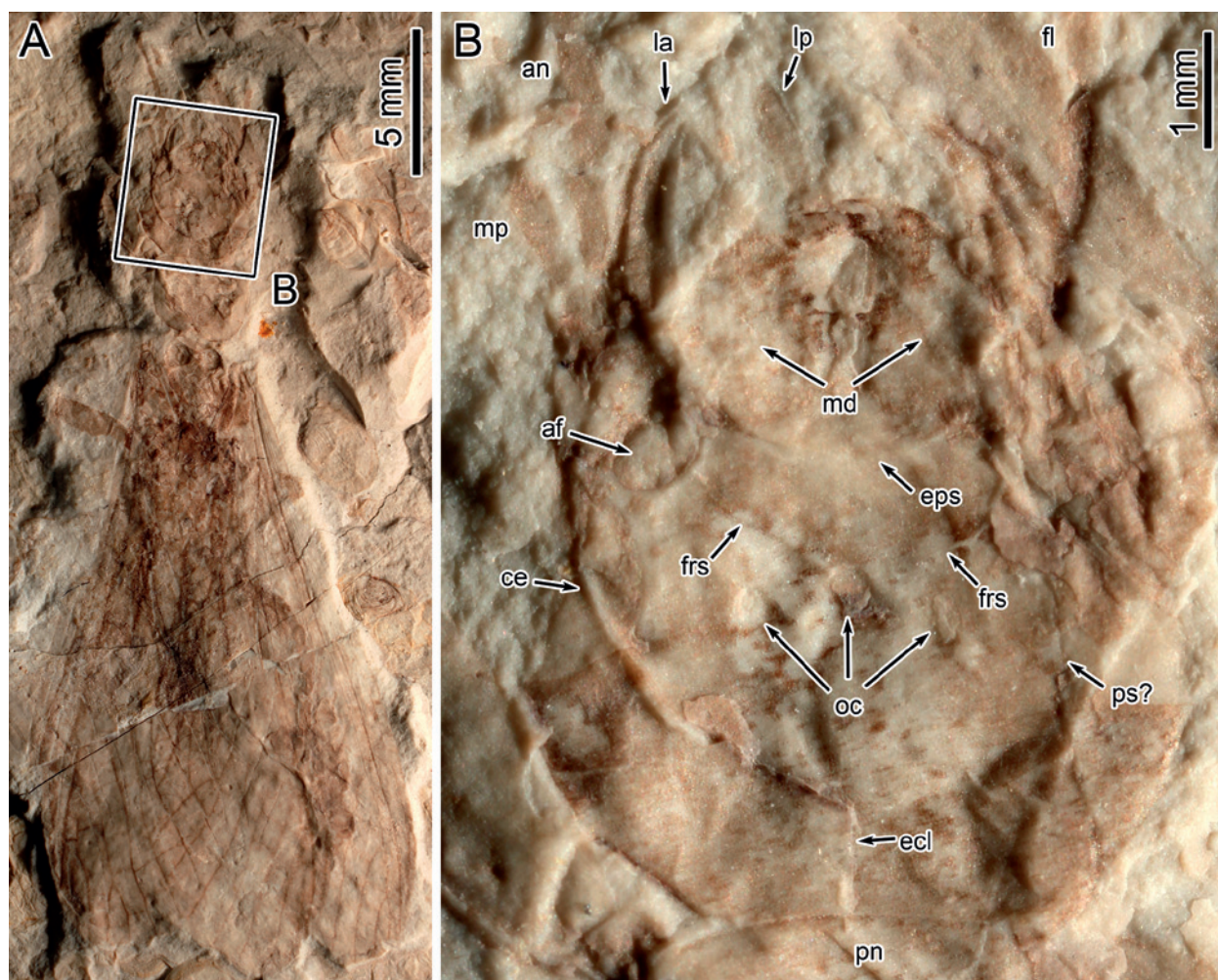


Fig. 4. *Plesioblattogryllus minor* Ren & Aristov, 2011, specimen CNU-GRY-NN-2011003. **A:** Photograph, habitus (positive imprint). **B:** Photograph of head, detail as located on A.

Descriptions. CNU-GRY-NN-2011001 (Fig. 2): Moderately well preserved female specimen, wings partly folded back, positive and negative imprints; head partly preserved, 2.5 mm long, 4.2 mm wide; pronotum 2.6 mm long, 3.4 mm wide; mesothorax 3.3 mm long, 4.1 mm wide; metathorax 3.0 mm long, 4.3 mm wide; middle and hind legs partly preserved; three last segments of abdomen visible, outline of ovipositor visible; at least 10 visible, large, olive-shaped eggs, scattered in the abdomen area, some with strong longitudinal ridges. **Forewings:** 19.4 mm/19.1 mm long, 6.0 mm/6.8 mm wide as preserved (left forewing / right forewing, respectively); stem of M fusing with stem of CuA near wing base; CuA1 with two branches (one preserved in right forewing); left forewing with CuP straight and simple; AA1 forked. **Hind wings:** preserved 14.8 mm/15.7 mm long, 7.2 mm/5.9 mm wide (left hind wing / right hind wing respectively).

CNU-GRY-NN-2011002 (Fig. 3): Well-preserved female specimen, positive imprint; head 4.0 mm long, 2.7 mm wide as preserved; mandibles asymmetrical, each with one apical tooth and one proximal incisive

tooth; antenna 3.8 mm long as preserved, with scape large, 0.26 mm long, 0.35 mm wide; pedicel shortest; segments 4–6 obviously shorter than others. **Left foreleg:** coxa 1.5 mm long, 0.7 mm wide; femur 2.9 mm long, 0.6 mm wide; tibia 0.4 mm wide, with three strong apical spines. **Right foreleg:** coxa 1.7 mm long, 1.0 mm wide as preserved; femur 3.6 mm long, 0.8 mm wide; tibia 0.3 mm wide. **Left midleg** (Fig. 3C): femur 2.5 mm long, 0.9 mm wide; tibia 2.8 mm long, 0.4 mm wide, with five spines visible on the ventral margin; tarsus with five segments visible, segments 1–4 with structures suggestive of poorly preserved euplantulae; fifth segment elongate; pretarsus with a pair of claws without arolii. **Right midleg:** coxa rounded; femur 3.2 mm long, 0.7 mm wide at the broadest; tibia 2.9 mm long, 0.6 mm wide, with several spines. **Left hind leg:** coxa nearly square-shaped, 1.3 mm long, 0.9 mm wide; trochanter 1.0 mm long, 0.8 mm wide; femur 3.6 mm long, 0.7 mm wide; tibia 4.0 mm long, 0.3 mm wide, with two strong spines; three tarsal segments visible, others hidden under the stone. **Right hind leg:** incomplete, identical to left hind leg in preserved parts.

Abdomen: between the hind legs and the last segment of abdomen, at least 16 eggs preserved; LS8 nearly rectangular, 1.0 mm long, 1.6 mm wide in the middle part; T9 partly visible (likely the ventrally bending lateral parts); T10 largely missing, preserved edges suggesting rounded shape, narrower than LS8; cerci complete, 6.9 mm long, densely covered with hairs; left and right cerci with similar and uniform curvature; cercomeres stout, more than seven visible in each cercus, width decreasing from basal to terminal cercomere; first five visible cercomeres similar in length (Fig. 3B); ovipositor well-preserved, 3.9 mm long, 0.7 mm wide at the base; CX8 nearly rectangular, located at the base of GP8; LC9 located immediately behind CX8 (Fig. 3E,E'), anterolaterally in contact with T9, and posteromesally in contact with base of gl9; gl9 longer than gp8, overlying these elements; gl9 taper gradually. **Forewings:** incompletely preserved. **Left hind wing:** 16.2 mm long as preserved, 6.0 mm wide; RP fused with MA for 3.2 mm long, with at least three branches.

CNU-GRY-NN-2011003 (Fig. 4): Complete specimen, wings overlapping, head well preserved, positive imprint. **Forewings:** about 20 mm long. **Head** (Fig. 4B): 3.5 mm wide; three ocelli delimiting an isosceles triangle, located between the eyes; left mandible 1.1 mm long, 0.8 mm wide, right mandible 1.2 mm long, 0.7 mm wide; each mandible with a curved, sharply pointed apical tooth (which is likely followed by a subapical tooth: difficult to see for left side due to mutually overlapping tips of mandibles); a long median cutting edge follows, proximad of which another tooth is present; further proximally median edge of each mandible being convex, slightly tooth-like (especially on right side); lacinia pointed at apex, about 1.2 mm long (as visible); basal part of left antenna and maxillary palp preserved; two basal segments of labial palp preserved; epistomal sulcus arch-shaped, ends anteromesad of the anterior margin of the two antennal foramina; darker spots in this area representing the anterior tentorial pits; outline of clypeolabrum not clear (basal parts possibly represented by feeble lines heading anteromesally from the aforementioned darker spots); ecdysial line Y-shaped, with coronal in the middle, half of head length, forked into two frontal sutures between compound eyes, each frontal suture ending at posterior edge of compound eye; a parietal sulcus is possibly visible in the middle between coronal and the right margin of head.

CNU-GRY-NN-2011004 (Fig. 5): three wings and part of body preserved, positive imprint. **Right forewing:** nearly complete (distal part missing), 17.0 mm long, 5.7 mm wide; RP originating from R near the basal third wing length, with basal part nearly parallel to RA, then directed posteriorly and fusing with MA, 1.2 mm distal to its origin; MA apparently forked, but an-

terior branch considered as a portion of RP fused with MA (i.e., MA is simple; see discussion on taxon); MP forked distal to wing midlength. **Left forewing:** distal part missing; RP fused with MA in the basal part, fusion 2.9 mm long; MP with three branches. **Left hind wing:** 15.5 mm long, 6.3 mm wide; RP fused with MA for 2.1 mm; RP first branch originating 2.6 mm distal to the divergence of RP and MA. **Left midleg:** coxa trapezoid-shaped, 0.9 mm long, 1.0 mm wide in the middle part; trochanter shaped as equilateral triangle; basal part of femur preserved, 0.7 mm wide. **Left hind leg:** coxa square-shaped, 1.2 mm long, 1.2 mm wide; trochanter shaped as isosceles triangle; femur 4.5 mm long, 0.9 mm wide in the widest part; tibia 5.6 mm long, 0.4 mm wide; inner margin of tibia with three pairs of strong and aligned spines; apical end of tibia with small spines; tarsus five-segmented.

Discussion. The specimens are attributed to the species *Pl. minor* Ren & Aristov, 2011 mainly because of the small size, especially that of evident female specimens (Figs. 2, 3). This discovery excludes the possibility that specimens of *Pl. minor* could be males of *Pl. magnificus* Huang, Nel & Petrusevičius, 2008 (known from a single female). Furthermore, in the forewings of all the specimens, it is observed that RP is fused with MA, a character unknown in *Pl. magnificus* (with some intra-individual variation in *Pl. minor*, as documented in the specimen CNU-GRY-NN-2011004, Fig. 5B). The character 'costal field narrower than subcostal field in the distal third of the [fore]wing', a diagnostic character for *Pl. minor* according to REN & ARISTOV (2011), is documented for all forewings and hind wings of the new specimens I described, except for the left forewing of the specimen CNU-GRY-NN-2011001 (Fig. 2B), which indicates that this character has to be considered with caution. I found no evidence suggesting that some specimens could belong to a different species.

All forewings of this species exhibit a simple MA except for CNU-GRY-NN-2011004 (Fig. 5B). However it is not excluded that in the latter the anterior branch of 'MA' actually belongs to RP, because the first posterior branch diverging from the main RP stem is located in an unusually distal position. If so it can be assumed that the first posterior branch of RP runs fused with MA at the level of the RP+MA connection (Fig. 5B), or 'jumped' from the stem of RP by means of a translocation (such transformation has been documented in several insect groups, such as Recent Mantodea, see BÉTHOUX & WIELAND 2009, and Carboniferous stem-Dictyoptera, see GUO et al. in press; see also BÉTHOUX 2009).

The tentatively identified parietal sulcus (ps? in Fig. 4B) could be another argument for a relationship between Plesioblattogryllidae and Grylloblattidae (and

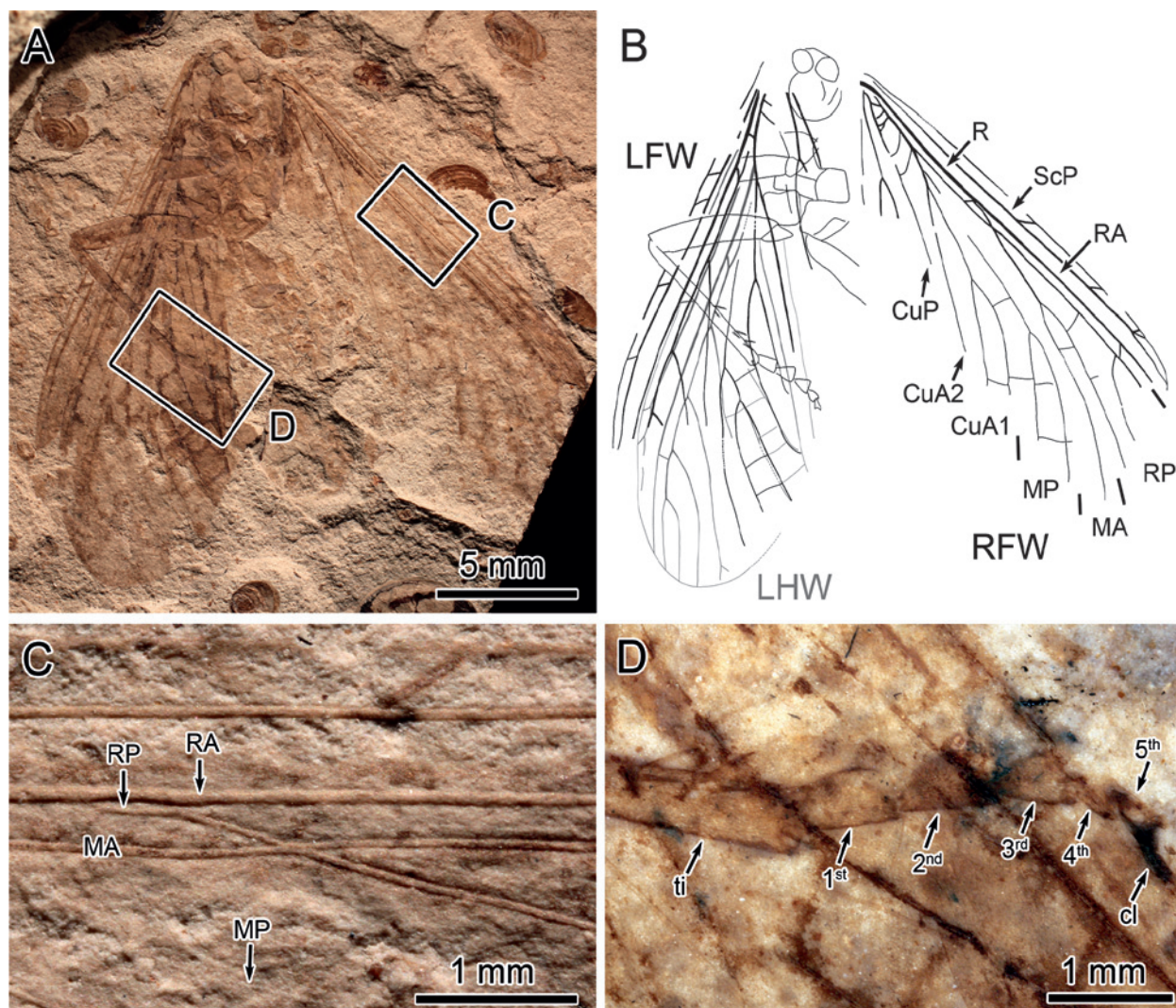


Fig. 5. *Plesioblattogryllus minor* Ren & Aristov, 2011, specimen CNU-GRY-NN-2011004. **A:** Photograph, habitus (positive imprint). **B:** Reconstruction of body and wings. **C:** Photograph of right forewing anterior middle area, detail as located on A. **D:** Photograph of left hind leg, detail as located on A.

perhaps Blattogryllidae; see WALKER 1931: fig. 1), but further evidence is needed.

Specimen CNU-GRY-NN-2011002 is herein considered to be viewed from dorsal, because the wings are clearly located above the legs, the cerci are clearly located above other terminal elements, and the venation is imprinted as dorsal view (for example RA is obviously convex). The fact that eggs and basal parts of legs (such as coxae) can be seen clearly does not contradict this interpretation. The use of ethanol allows observation of structures lying below the specimen surface (such as coxae), by rendering the rock matrix somewhat translucent. Additionally, the splitting plane likely passed through different levels along the specimen axis. Notably, most of the abdominal tergites are missing, revealing eggs. The ‘missing’ tergites probably lie in the counterpart of the specimen (unfortunately missing). The interpretation of the abdominal terminal elements is based on these premises. In par-

ticular, based on the location and elevation of cerci, it is assumed that T10 is mostly missing, revealing bases of gl9. In other words, it is assumed that the ovipositor is split longitudinally.

Family incertae sedis

Genus *Duoduo* gen.n.

Type species. *Duoduo qianae* sp.n.; designated herein.

Derivatio nominis. Derived from ‘duo’ [duō], ‘many’ in Chinese, for ‘many branches of CuA1’ and ‘many branches of AA’.

Diagnosis. As for species.

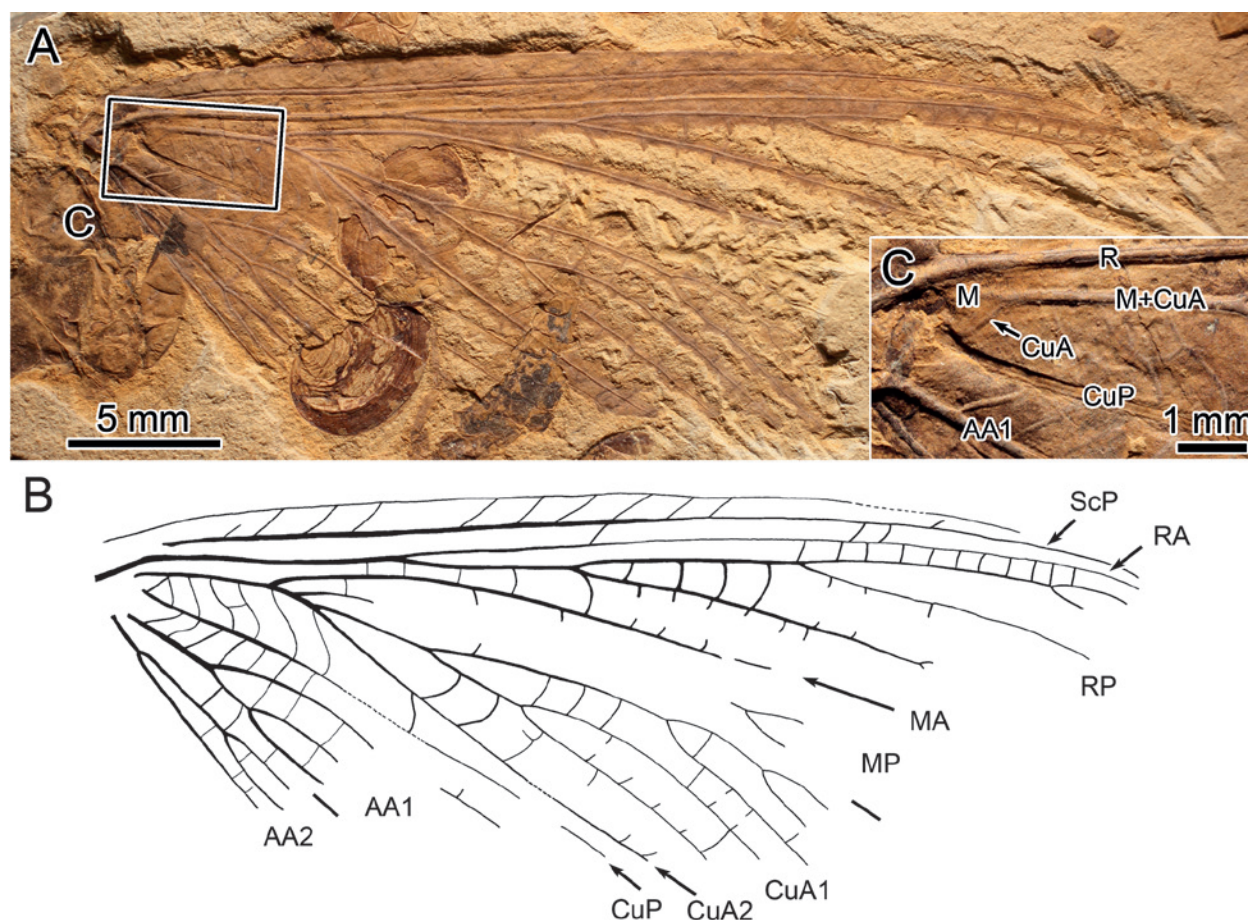


Fig. 6. *Duoduo qianae* gen.n. et sp.n., specimen CNU-GRY-NN-2011005. **A:** Photograph (positive imprint). **B:** Reconstruction. **C:** Photograph of basal area, detail as located on A.

Duoduo qianae sp.n.

(Fig. 6)

Derivatio nominis. In honour of Dr. Y. Qian (Institute of Applied Entomology, Yangzhou University, China), for her help to the author during a visit to the Yangzhou University.

Holotype. CNU-GRY-NN-2011005.

Diagnosis. No fusion between RP and MA; CuA1 with 5 branches; AA1 and AA2 with 3 branches each (at least).

Description. Specimen CNU-GRY-NN-2011005 (Fig. 6): isolated wing incompletely preserved, positive imprint, 34.5 mm long, 12.4 mm wide, as preserved; area between anterior wing margin and ScP narrow, 0.9 mm wide in the broadest part, with at least 9 cross veins; R forked into RA and RP in the basal third, with RA simple and nearly parallel with ScP; RP posteriorly pectinate, with at least 5 branches; CuA emerging from Cu near wing base, short, fused with M (Fig. 6C); M+CuA branching into MA and MP+CuA; MA simple,

emerging 4.2 mm basal to the first fork of R; area between R/RP and MA narrow (0.5 mm opposite to origin of RP); MP originating shortly after MA, not visible for most of its basal part (concave and weak), with at least two branches located distal to wing midlength; CuA with a total of six branches; CuA1 forked 3.9 mm distal to its origin, anterior branch 3-branched, posterior branch forked; CuA2 simple; area between CuA and CuP broad in the basal part, with several sigmoidal cross veins; CuP simple and weak; AA1 and AA2 both with three branches (as preserved), posteriorly and anteriorly pectinate, respectively.

Discussion. Wings are in resting position as in the holotype specimen of *Pl. magnificus* (HUANG et al. 2008: fig. 2), making the interpretation of the wing venation difficult, in particular that of the hind wings. The hind wing venation in *Pl. minor* is also poorly documented. As a consequence it is tricky to determine to which wing pair the specimen CNU-GRY-NN-2011005 belongs.

It can be assumed that it is a hind wing, because: (1) the area between the anterior branch of CuA1 and CuP is very broad, with a 5-branched CuA1 (usually

not occurring in forewings of Blattogryllidae and Plesioblattogryllidae, except specimen PIN 2554/225, belonging to *B. karatavicus* (RASNITSYN 1976: fig. 1:1); (2) the anal area is broad, with more abundant branches than usually occurring in forewings of Blattogryllidae and Plesioblattogryllidae (STOROZHENKO 1998). It is not excluded that both characters can occur in a forewing, but this would be a very uncommon condition.

In any case it is difficult to be conclusive because, in Blattogrylloptera, the venation of the hind wing is nearly identical to that of the forewing (HUANG et al. 2008; STOROZHENKO 1998; and new data on *Pl. minor*, see above). The character ‘CuA concave in hind wings’, known to occur in most grylloblattidan insects (BÉTHOUX & NEL 2010; STOROZHENKO 2002; among others; but also in stem-Dictyoptera, see BÉTHOUX et al. 2011; as opposed to its convex condition in hind wings of most winged insects, such as Plecoptera, Orthoptera), is not conclusive here, because CuA is convex in hind wings of *Costatoviblatia aenigmatica* Storozhenko, 1992 and *Mesoblattogryllus intermedius* Storozhenko, 1990 (observations based on photographs provided by D.S. Aristov).

Similarly numerous branches of CuA1, or of AA, are documented in forewings of two species of the family Blattogryllidae, namely *B. karatavicus* and *C. aenigmatica*, respectively. These species were considered to exhibit nearly the same wing venation as members of the Plesioblattogryllidae (HUANG et al. 2008). However, according to the published data, there is no case in which both of these traits co-occur.

Thus I cannot conclude on which wing pair the specimen CNU-GRY-NN-2011005 represents. Also, the familial assignment cannot be determined because no body characters are preserved. Regardless of these issues, the erection of the new genus and species is necessary, because the specimen exhibits a combination of character states unknown in other genera in the Blattogrylloptera.

Notice that the wing base of the specimen CNU-GRY-NN-2011005 is well preserved and shows a distinct CuA stem, diverging from Cu, and fusing with M (Fig. 6C).

5. Discussion

Body characters observed in the new specimens of *Plesioblattogryllus minor* reinforce the view that Plesioblattogryllidae differs from Blattogryllidae in tarsus morphology (HUANG et al. 2008), in particular

the strong claws and lack of (or very small) arolia in the former (observed in right mid- and hind legs; Fig. 3C,D). Although the available material is not conclusive, the tarsomeres 1–4 likely have a pair of (large?) euplantulae (right mid- and hind legs in Fig. 3C,D; left hind leg in Fig. 5D).

All observed specimens of *Pl. minor*, have RP fused with MA in both fore- and hind wing pairs. As for the length of this fusion, intra-individual variability was observed in specimen CNU-GRY-NN-2011004 (Fig. 5B): RP and MA are fused for a long distance in left fore- and hind wings, but are only connected for a very short distance, and then separated from each other, in the right forewing (Fig. 5C). Alternatively, if the hypothesis of a RP *partim* + MA stem is accepted (following indications on Fig. 5B), it can be considered that a particularly long RP + MA stem occurs. In any case, the right forewing represents an important variation to the usual morphology.

The diagnosis of the Plesioblattogryllidae by HUANG et al. (2008) includes the character ‘pronotum with broad lateral expansions’. However, in their discussion (p. 21), these authors take a more cautious stand on the importance of this character. Its relevance is also challenged by REN & ARISTOV (2011). In the new specimens of *Pl. minor*, the pronotum is not distinctly wider than the meso- and metathorax (Figs. 2A,B; 3A,B; 4), a condition similar to that in Blattogryllidae (especially in specimens without obvious deformation). It suggests that the width of the pronotum is not a useful character to identify members of the two families.

HUANG et al. (2008) listed the character ‘MP simple’ (in forewing) as diagnostic of *Plesioblattogryllus*, allowing its distinction from *Blattogryllus* Rasnitsyn, 1976, among others. However the new data demonstrate that *Pl. minor* possesses a branched MP, making this trait relevant at the species level only, at best (or the simple condition observed in the holotype of *Pl. magnificus* is an unusual variant).

This study also provides evidence on the phylogenetic relationships between extant Grylloblattidae and the fossil Blattogryllidae and Plesioblattogryllidae. First, the apomorphic asymmetry of gonocoxites (which show a plesiomorphic medially divided condition) is herein confirmed for *Blattogryllus*, which in this character conforms with Grylloblattidae. Features of the female genitalic region which are visible in a specimen of *Plesioblattogryllus minor* show a remarkable similarity with Grylloblattidae, though it is not possible at present to extract shared apomorphies from this character system. The head of *Pl. minor* also bears much resemblance with that in Grylloblattidae. The tentative identification of a parietal sulcus in *Pl. minor* might represent an apomorphy shared with Grylloblattidae. These results on the relationships between

Grylloblattidae and (Plesio)blattogryllidae is highly important as such a link allows for tracing the evolution of the wingless extant representatives back to the early radiation of Neoptera by use of wing venation characters. Yet, more evidence on non-wing characters is needed in order to confirm these relationships.

6. Conclusion

Characters of wing venation previously considered as diagnostic of the Plesioblattogryllidae, as compared to the Blattogryllidae, were found to lack relevance. On the contrary, characters relating to the leg morphology, viz. tarsomeres 1–4 with a pair of euplantulae, and pretarsi with strong claws and no arolia, were found to be useful. Their occurrence in *Pl. minor* is confirmed, at least for the latter character. In this context, the erection of a distinct family for the genus *Plesioblattogryllus* by HUANG et al. (2008) renders the familial assignment of numerous genera and species mostly based on isolated wings and currently assigned to the Blattogryllidae difficult, if not impossible (REN & ARISTOV 2011). This situation prompted me to erect a new taxon, viz. Blattogryllopterida, to accommodate such cases. This taxon is believed to include members of the extant family Grylloblattidae. Further discoveries of material preserving body parts undoubtedly will allow our knowledge of the relationships between fossil and extant Blattogryllopterida species to be refined.

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Appendix

Taxon *Blattogryllopterida* nom.-dis.-typ. n.

Derivatio nominis. See main text.

Definition. Species that evolved from the (segment of the) metapopulation lineage in which the character state ‘in forewing, MP and CuA fused for some distance’, as exhibited by *magnificus* Huang et al., 2008, and *minor* Ren & Aristov, 2011, has been acquired (venation designations as herein).

Cladotypes. Specimen NIGP 133701 (female of *magnificus* Huang et al., 2008, holotype; see HUANG et al. 2008: figs. 1, 2), and specimen CNU-GRY-NN-2011001 (female of *minor* Ren & Aristov, 2011; see Fig. 2).

Discussion. Polarity of the defining character state is discussed in the main text. Cladotypic species were selected based on data availability.

Composition. In the main text, under the Linnaean procedure, it is stated that the taxon is not conceptualized based on its composition, but based on its distinctive character state. Under the cladotypic procedure, it is implicit that composition is by no means defining. In other words, the composition of *Blattogryllopterida* is merely the consequence of its character-state-based definition, not the taxon definition itself. As a consequence, whether grylloblattidaeans belong, or not, to *Blattogryllopterida* is not relevant regarding the taxon validity.