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Variability and symmetry of a Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae)

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ABSTRACT

Cockroaches are as of yet the only animal group with a fossil record complete enough to reveal the quantitative changes of individual intraspecific variability over a considerable interval of time (320 Ma). Ninety three individuals of the first known nocturnal and/or crepuscular carnivorous cockroach Divocina noci gen. et sp. nov. of the family Raphidiomimidae (Middle Jurassic Jiulongshan Formation; Daohugou, Inner Mongolia Province, China) now reveal the comparison of variability and symmetry of right and left wings separately. The sole significant difference is the more pronounced variability of the anterior part (involved in flight) of the left forewings, which may be the consequence of the superposition of the left wing and its protective function associated with vein reorganizations.

The overall variability coefficient of the number of veins in the distal forewing margin and total number of veins at the margin (CVtotal = 7.65; hindwing CVtotal = 7.54) was low when compared with the wing centre, which together with wing symmetry suggest comparatively good flight. The total number of veins is in perfect congruence with the variability of Fortiblatta cuspicolor Liang, Vršanský and Ren, 2009—another raphidiomimid from the same locality (CVtotal = 7.70; hind wing CVtotal = 7.33). In spite of nearly identical overall variability, data for respective veins vary up to 30%. Different also is the mean asymmetry expressed as the difference in the number of veins meeting at the margin between the respective sides (4.7% of Divocina vs 7.0% of Fortiblatta cuspicolor). It follows that the general variability is to a large extent independent of variability of respective characters as well as of symmetry values.

Key words: insects, fossil cockroaches, Bathonian, Middle Jurassic, nocturnal, Raphidiomimidae, predators.

RESUMEN

Las cucarachas son, hasta el momento, el único grupo animal con un registro fósil suficientemente completo para revelar los cambios cuantitativos de la variabilidad intraespecífica individual, a lo largo de un considerable intervalo de tiempo (320 Ma). Noventa y tres individuos de la primera cucaracha nocturna carnívora y/o crepuscular, Divocina noci gen. et sp. nov. de la familia Raphidiomimidae (Formación Jiulongshan del Jurásico Medio; Daohugou, Provincia de Mongolia Interna, China), revelan ahora la...
INTRODUCTION

Carnivorous cockroaches, as one of the most aberrant insects, were recognized based on the few complete individuals originating from the Upper Jurassic sediments of Karatay in Kazakhstan (Vishniakova, 1973). Cosmopolitan Jurassic-Cretaceous representatives of the genus *Liadoblattina* Handlirsch, 1906 were also categorized within this family and these insects appeared as to be common during the whole Jurassic (Vršanský and Ansorge, 2007; Liang et al., 2009) except at the locality of Mintaja in Australia (Martin, 2010), where they were apparently absent or extremely rare. The single published Cretaceous record from Myanmar (Grimaldi and Ross, 2004) is obscure (Vršanský, 2009).

Representatives of the family, first of all, are unique in the morphology of the head, which is, unlike in all other cockroaches, directed forewards (prognathous). This position of the head resulted in the consequent complete head reorganization, with the occurrence of unique structures. The eyes are modified, being divided by a supporting longitudinal ridge (apodema) into two joined parts. Another significant modification is the nearly complete internalization of external ovipositor, which led Anisyutkin and Gorochov (2004a) to a designation of a separate suborder Raphidiomimidae Vishniakova, 1973. Unique also are the legs, the fore ones somewhat adapted for catching food, although not obliquely raptorial, i.e., with retained curvoral function.

Carnivorous cockroaches were common during the Middle Jurassic and, as abundant large top insect predators they significantly influenced trophic interaction within the ancient ecosystem of Daohugou (P. Vršanský, J-H. Liang, D. Ren, C. Labandeira, in preparation).

The perfectly preserved present species is the first documented occurrence of a crepuscular and/or nocturnal predator among cockroaches.

This taxon has become more interesting because for the very first time is possible to conduct the analysis of the variability in right and left wings separately and thus quantitatively access its symmetry – providing a base for the future studies, unlimited to insects.

MATERIAL AND METHODS

Ninety-three individuals, many of them complete, were collected from the ?Bathonian (Ren et al., 2002; Chen et al., 2004; Liu et al., 2004; Rasnitsyn and Zhang, 2004; Gao and Ren, 2006) Middle Jurassic sediments of the Jiulongshan Formation (Ren et al., 2002), at the Daohugou locality in Inner Mongolia Province, China. The Daohugou fossil beds consist of a set of intercalated, fine-grained lacustrine deposits and fine volcanic ash that unconformably overlie Precambrian rocks (Ren et al., 2002). They are peculiar in their unusual fossil content of insects, bivalves, plants, conchostracans, gastropods, proto-feathered dinosaurs and Eutherian mammals (Ji et al., 2006), and more recently studied pterosaurs and their ectoparasites (Vršanský et al., 2010).

We studied the material using a Leica MZ12.5 dissecting microscope and illustrated samples with an attached drawing tube. Corel-Draw figures were improved digitally using Adobe Photoshop 6.0. Fossil photographs were taken using Leica DC 300 photographic equipment. The rich material allowed discrimination of dozens of new characters unknown for the family and order.

Material is deposited in the Capital Normal University, Beijing (CNU) and in Tianjin Museum of Natural History (TNP).

Abbreviations: Sc– subcosta; R– radial vein; RS– radius sector; M– media; CuA– cubitus anterior; CuP– cubitus posterior; A– anal veins. CV– coefficient of variability, measured in % (deviation/average); ± – positive and negative imprint of the same sample; “687–2” labels the second specimen preserved at the same sample (687).
A Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae) with reticulations. CuP and A1 simple, A2 branched. Apex; M and CuA rich; A branched. Hind wing with simple Sc, R slightly curved, undifferentiated RS does not reach symmetrical styli is present in males (Figure 2f). Externally protruding valves. Pair of short, unsegmented, extremely wide while short, but apparently with distinctly (Figure 1a). Ovipositor (Figure 2g) is unique in being in females placed close to each other near the ovipositor cut tergal margins, cerci very short (under 2 mm) and thin, hairs (Figure 1b). Body wide (3.2 – 4.7 mm), with sharply carinated, except for coxa covered with numerous sensilla chaetica. Lengths: 0.3 mm, 1.4 mm, 1.2 mm, 0.9 mm. Antenna with double teeth. Length/width: 2.0–2.7/ 1.0–1.5. First palpomere unknown, 2nd-5th palpomere with the following lengths: 0.3 mm, 1.4 mm, 1.2 mm, 0.9 mm. Antenna with at least 50 very short segments with a single apical row of ca. 10 very short sensilla chaetica (Figure 2e). Pronotum longitudinal L/W: 2.5 – 3.5/ 2.5 – 3.0 mm. Fore legs raptorial (only complete preserved ones figured – Figures 1b, 2d), strongly carinated, except for coxa covered with numerous hairs (Figure 1b). Body wide (3.2 – 4.7 mm), with sharply cut tergal margins, cerci very short (under 2 mm) and thin, in females placed close to each other near the ovipositor (Figure 1a). Ovipositor (Figure 2g) is unique in being extremely wide while short, but apparently with distinctly externally protruding valves. Pair of short, unsegmented, symmetrical styli is present in males (Figure 2f).

Forewing colored (Figures 2b, 3a-3f), with branched Sc, R slightly curved, undifferentiated RS does not reach apex; M and CuA rich; A branched. Hind wing with simple Sc, RS differentiated, M rich; CuA with quarterly branching veins. Stem and posteriormost CuA branch meeting CuP with reticulations. CuP and A1 simple, A2 branched. Ovipositor is poorly preserved, but was apparently external, rather long, but of a different type than that of the Caloblattiniidae. Its wide base suggests a short-type characteristic of the rest of Raphidiomimidae.

Both wings are dark, with a narrow (10-25%) pale line at fore margin. Forewing length/width: 12.3 – 16/3.2 – 4.8 mm; Sc 2-6; R 8-17; M 5-16; CuA 4-11; A 5-10. Hind wing 10.3–14 mm long; with simple Sc; R1 3-7; RS 5–9; M 2-8; CuA 5-9 (all ranges in this section refer to number of veins at margin).

Character list.


Dark coloration with pale anterior margin of both wings: autapomorphy, homoplasic with an undescribed nocturnal liberiblattinid from the Upper Jurassic of Karatau. Terga sharply cut: autapomorphy of the present species. Ovipositor with internalized valvae: autapomorphic, homoplasic with advanced cockroaches, mantodeans and termites.

Character of preservation. Ninety-three more or less complete specimens.

Derivation of name. afterлион (Slavic for wilderness, means also miraculous China).


Description. As for species.

Derivation of name. after дивоцина (Slavic for wilderness).
Figure 1. Crepuscular and/or nocturnal carnivorous cockroach *Divocina noci* gen. et sp. nov. (Raphidiomimidae) from the Middle Jurassic of the Jiulongshan Formation. Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University. a: holotype CNU-B-NN-2006-067; b: detail of head and fore legs CNU-B-NN-2006-024; c—head CNU-B-NN-2006-050. Sc—subcosta, R—radial vein, R1—radius anterior, RS—radius sector; M—media; CuA—cubitus anterior, CuP—cubitus posterior; A—anal veins. Scales 1mm (inner black bar).
A Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae)

Figure 2. Crepuscular and/or nocturnal carnivorous cockroach *Divocina noci* gen. et sp. nov. (Raphidiomimidae) from the Middle Jurassic of the Jiulongshan Formation, Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University. a: holotype CNU-B-NN-2006-067; b: detail of legs and forewing pattern CNU-B-NN-2006-065; c: head CNU-B-NN-2006-050; d: detail of head and fore legs CNU-B-NN-2006-024; e: detail of antennae CNU-B-NN-2006-090; f: detail of male genital appendages CNU-B-NN-2006-066; g: detail of female ovipositor CNU-B-NN-2006-051. Scales 1mm (inner black bar).
Figure 3. Crepuscular and/or nocturnal carnivorous cockroach *Divocina noei* gen. et sp. nov. (Raphidiomimidae) from the Middle Jurassic of the Jiulongshan Formation. Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University. a: CNU-B-NN-2006-065; b: CNU-B-NN-2006-037; c: CNU-B-NN-2006-069; note a very different character of the sediment of this sample (gray color; no conchostracans); d: CNU-B-NN-2006-033; e: CNU-B-NN-2006-051; f: CNU-B-NN-2006-050. Scales 10mm (inner black bar).
A Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae)

earliest mantises (Vršanský, 2002). Very similar (although much shorter) are also thin cerci like in predatory Eadiidae and some earliest Mantodeans.

Head with a typical supporting ridge on ventral side, strong mandibles and long mecanoreceptors approximating eyes resemble some crepuscular and nocturnal ice-crawlers (see Vršanský et al. 2001). Large facets and dark coloration also suggest namely this way of life. The identical coloration of fore and hind wings, which are normally hidden (at least the characteristic pale anterior margin), provide additional evidence of homeotic genes acting in both pair of wings, as explained by one of us (Vršanský and Aristov, 2012).

Lateral ocelli, absent in many living and fossil cockroaches (Vidlička, 2001; Deitz et al., 2003; Vršanský, 2008), are invisible in present specimens, but they are anticipated due to their presence in a more advanced Raphidiomimina. Unique carved tergal margins are obscure, eventually might be a cause for sound production or attachment of males during courtship. Internalized inner valvae suggest laying eggs in conglomerates or even within ootheca.

**DISCUSSION**

The variability of the forewings of the present species (CV total = 7.65 – see Table 1, Figures 4A-AH) was comparatively low, perfectly fitting the variability of the sole studied representative of the family, Fortiblatta cuspicolor, in which the total number of veins meeting the margin has a CV of 7.70 (the same age and locality). This value appears constant in spite of the fact that these related taxa significantly differ in statistics of the competent venial systems and also in different degree of symmetry and were thus significantly differing in life style and in flight abilities. This provides serious support for the constant variability coefficient (of total number of veins) of isochronous related species and thus for grounding of the hypothesis of decreasing variability over time and other variability trends (Vršanský, 2000). This was recently supported also on trends in variability of polymorphisms among trilobites (Webster 2007).

The variability of the forewing anterior margin (CV R = 13.21; CV R+M = 10.91), which is important for flight (Vršanský, 2000), is also very low, and this provides support for the excellent flight of this species. This is also comparable with F. cuspicolor (CV R+M = 8.42). Notable is higher variability of the present species in the center of the wing (CV R+M = 30.15) when compared to that of F. cuspicolor (20.54). It follows herein that the described species had higher variability of these respective branches, but equal variation of the total number of veins, which may be a consequence of regulation of the total number of veins and their different number in both species (39-56, Mean 50.47 of F. cuspicolor vs. 38-48, Mean 41.74 of the present species).

These values are somewhat transitional, i.e., not as high as in species characteristic of the earliest stages of the familial phylogeny (Vršanský, 2000; Liang et al., 2009; Schneider, 1977, 1978), but not as low as advanced Palaeozoic taxa (Vršanský, 2000; Schneider, 1980a, b) or advanced Mesozoic taxa (references above). This indirectly suggests Raphidiomimidae evolved slightly before the Middle Jurassic. Nevertheless, when compared to other species, 11 specimens with both analysed wings may decrease the final variability figures to some extent.

Good flight is also supported and stressed by its very high level of symmetry (see Figures 1A, 2A). In

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Table 1. Forewing venation variability of *Divocina noci* sp. nov. Numbers in the second line represent data of left and right forewings separately. Measured individuals: CNU-NN-006-033; 037; 053; 056; 065; 067; 068; 069; 090; 104; 105; 120; 204; 312; 485; 488; 489; 686; 687; 2; 691; TNP42412-LFW (left); CNU-NN-006-035; 050; 051; 052; 054; 067; 068; 069; 105; 312; 480; 484; 486; 488; 489; 683; 686; 687-2; 690; 691; 707; TNP42412-1 (right); 056, 254 (indetermined). Sc- subcosta; R-radius; M-media; Cu- Cubitus anterior (CuA) + Cubitus posterior; A- anal; Total- total number of veins at the margin with A (SUM is without A); CV– coefficient of variation.
Figure 4. Venation of *Divocina noci* gen. et sp. nov. (Raphidiomimidae), Middle Jurassic of Daohugou, Inner Mongolia, China. L- left, R- right, FW- forewing, HW- hind wing. AA – 069 LF and LHW; AB – 069 RF and RW; AC – TNP4212 LF and LHW; AD – TNP42412 RF and RW; AE – 312 LF and LHW; AF – 312 RF and RW; AG – 204 LF and LHW; AH – 486 LF and LHW; AI – 035 LF and LHW; AJ – 486 RF and LHW; AK – 035 RF and RW; AL – 120 RF and RW; AM – 486 LF; AN – 486 RF; AO – 489 LF; AP – 489 RF; AQ – 687 LF; AR – 486 LF; AS – 687 LF; AT – 486 LF; AU – 035 RF; AV – 037 RF AW – 050 RF; AX – 051 RF; AY – 053 RF; AZ – 054 RF; BA – 254 RF; BB – 480 RF; BC – 484 RF; BD – 486 RF; BE – 683 RF; BF – 690 RF; BG – 707 RF; BH – 056LF; BI – 105 LF; BJ – 204 LF; BK – 485 LF; BL – 486 LF; BM – 486 RF; BN – 035RH; BO – 488 LF; BP – 489 RF; BQ – 683 LF; BR – 683 RF; BS – 691 LF; BT – 691 RH; BU – 687 LHW; BW – 687 RF; BX – 051 RH; BY – 090 RH; BZ – 015 RH; CA – 480 RH; CB – 489 RH; CC – 690 LHW; CD – 707 LHW. All to scale, 1mm.
dominance of the species in the nocturnal cohort of the assemblage. Unless caused by imperfect preservation state, or higher activity of males during flight, the sex ratio appears biased towards males – significantly, only four of 19 relevant individuals are females easily recognized based on the presence of distinct external ovipositor.

CONCLUSIONS

*Divocina noci* sp. nov. of the family Raphidiomimidae was a dominant nocturnal cockroach predator. Males were either more active in flight or prevailed over females.

Difference between left and right side (expressed as a different number of forewing veins meeting margin) is estimated as significantly below 5%, which together with low variability of the anterior margin and with the dominance in the assemblage suggest it was a good flyer.

The variability coefficient of the total number of veins can be considered nearly identical (difference 0.65%) to the relative *Fortibiliata cupsicolor* of the same family (and locality), but variation of respective veins and values of symmetry fluctuates up to 30%.

The general variability is independent of variability of respective characters as well as on symmetry values.

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