

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 ($CV_{total} = 7.65$; hindwing $CV_{total} = 7.54$) 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 cuspidata* Liang, Vršanský and Ren, 2009— another raphidiomimid from the same locality ($CV_{total} = 7.70$; hind wing $CV_{total} = 7.33$). 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 cuspidata*). 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

comparación de la variabilidad y de las alas derecha e izquierda, por separado. La única diferencia significativa es la más pronunciada variabilidad de la porción anterior (involucrada en el vuelo) de las alas anteriores izquierdas, lo cual puede ser consecuencia de la superposición del ala izquierda y su función protectora, asociada a la reorganización de las venas.

El coeficiente general de variabilidad del número de venas en el margen distal del ala anterior y el número total de venas en el margen ($CV_{total} = 7.65$; ala posterior $CV_{total} = 7.54$) fue bajo en comparación con el centro del ala lo que, aunado a la simetría del ala, sugiere, comparativamente, una adecuada capacidad de vuelo. El número total de venas es perfectamente congruente con la variabilidad de *Fortiblatia cuspidata* Liang, Vršanský y Ren, 2009— otro rafidiomímido de la misma localidad ($CV_{total} = 7.70$; ala posterior $CV_{total} = 7.33$). A pesar de la casi idéntica variabilidad general, los datos para las venas respectivas varían hasta en el 30%. También hay variación en la asimetría media, expresada como la diferencia en el número de venas que llegan al margen entre los lados respectivos (4.7% de *Divocina* vs 7.0% de *Fortiblatia cuspidata*). Se concluye que la variabilidad general es en gran medida, independiente de la variabilidad de los caracteres respectivos, así como de los valores de simetría.

Palabras clave: insectos, cucarachas fósiles, Bathoniano, Jurásico Medio, nocturnas, Raphidiomimidae, depredadoras.

INTRODUCTION

Carnivorous cockroaches, as one of most aberrant insects, were recognized based on the few complete individuals originating from the Upper Jurassic sediments of Karatau 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 Ansoerge, 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 forwards (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 Anisytukin and Gorochov (2004a) to a designation of a separate suborder Raphidiomimoidea Vishniakova, 1973. Unique also are the legs, the fore ones somewhat adapted for catching food, although not obliquely raptorial, i.e., with retained cursorial 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).

SYSTEMATIC PALEOENTOMOLOGY

Order Blattida Latreille, 1810

Family Raphidiomimidae Vishniakova, 1973

Genus *Divocina* Liang, Vršanský et Ren, gen. nov.**Type species.** *D. noci* sp. nov., by monotypy.**Differential diagnosis.** Differing from *Liadoblattina*, *Rhipidoblattina* Vishniakova, 1973 and *Cameloblatta* Vishniakova, 1973 in having semiglobular head, facets large, terga sharply cut, and all wings monochromatically colored to a great extent.**Description.** As for species.**Derivation of name.** after *divočina* (Slavic for wilderness, means also miraculous China).*Divocina noci* Liang, Vršanský et Ren, sp. nov.

Figures 1-4

Holotype. CNU-B-NN-2006 067±. A complete female. Deposited in the Capital Normal University, Beijing.**Type horizon.** Bathonian Middle Jurassic Jiulongshan Formation.**Type locality.** Daohugou, Inner Mongolia Province, China.**Additional material.** CNU-B-NN-2006 014, 024, 033, 037, 050, 052 - 066, 068, 069, 081, 086, 090, 094, 097, 099, 104, 105, 107, 117, 120, 121, 160, 166 - 170, 199, 203, 204, 207 - 209, 236, 244, 246, 247, 254, 255, 262, 312, 484 - 489, 605, 659, 683, 686-1-2, 687-1-2, 689, 690 - 695, 698 - 704, 705-1-2 - 715. Locality and horizon the same as for the type.**Description.** Prognathous head semiglobular (Figures 1c, 2c), with strong supporting ridge on the ventral side; eyes divided by longitudinal ridge into two joined parts. Additional ridges separating clypeus are present. Mandibles strong 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 Caloblattinidae. 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.

Head prognathous: autapomorphy of the Raphidiomimidae.

Head semiglobular: strong plesiomorphy within Raphidiomimidae.

Eyes compound with two distinct parts separated by apodema: autapomorphy, unknown, but likely absent in *Raphidiomima*.

Mandible strong long with sharp teeth: autapomorphy of the Raphidiomimidae.

Palps (maxillary and labial) extremely elongated: synapomorphic with some advanced (known from the Jurassic sediments) Caloblattinidae, homoplastic with Socialidae Vršanský, 2010 (see Vršanský, 2010).

Antenna with sparse short sensilla chaetica: plesiomorphy (possibly at the level of Phylloblattidae).

Pronotum elongated: autapomorphy of the Raphidiomimidae.

Forewing anterior margin straight: autapomorphy of the Raphidiomimidae,

Rest of the forewing (branched narrow Sc, R nearly straight, RS undifferentiated, CuA long and curved, A branched) and hind wing (Sc short simple, RS differentiated, pterostigma absent, M branched, CuA secondarily branched, posteriormost vein with blind branches, CuP simple, A1 not curved) venation scheme: synapomorphic with the advanced Caloblattinidae (with venation reduced to some extent).

Dark coloration with pale anterior margin of both wings: autapomorphy, homoplastic with an undescribed nocturnal liberiblattinid from the Upper Jurassic of Karatau.

Terga sharply cut: autapomorphy of the present species.

Ovipositor with internalized valvae: autapomorphic, homoplastic with advanced cockroaches, mantodeans and termites.

Character of preservation. Ninety-three more or less complete specimens.**Derivation of name.** after *noc* or *nox* (different languages for night).**Remarks.** The present species can be safely categorized within the family Raphidiomimidae. This placement is based on prognathous head with extremely long palps, elongated pronotum, narrow costal space (and general venation scheme, which is not diagnostic because of being synapomorphic with the Caloblattinidae) and short external ovipositor. Its forelegs were covered with numerous sensilla as in unrelated predatory cockroaches of the families Liberiblattinidae and Eadiidae (Vršanský, 2009) and also in

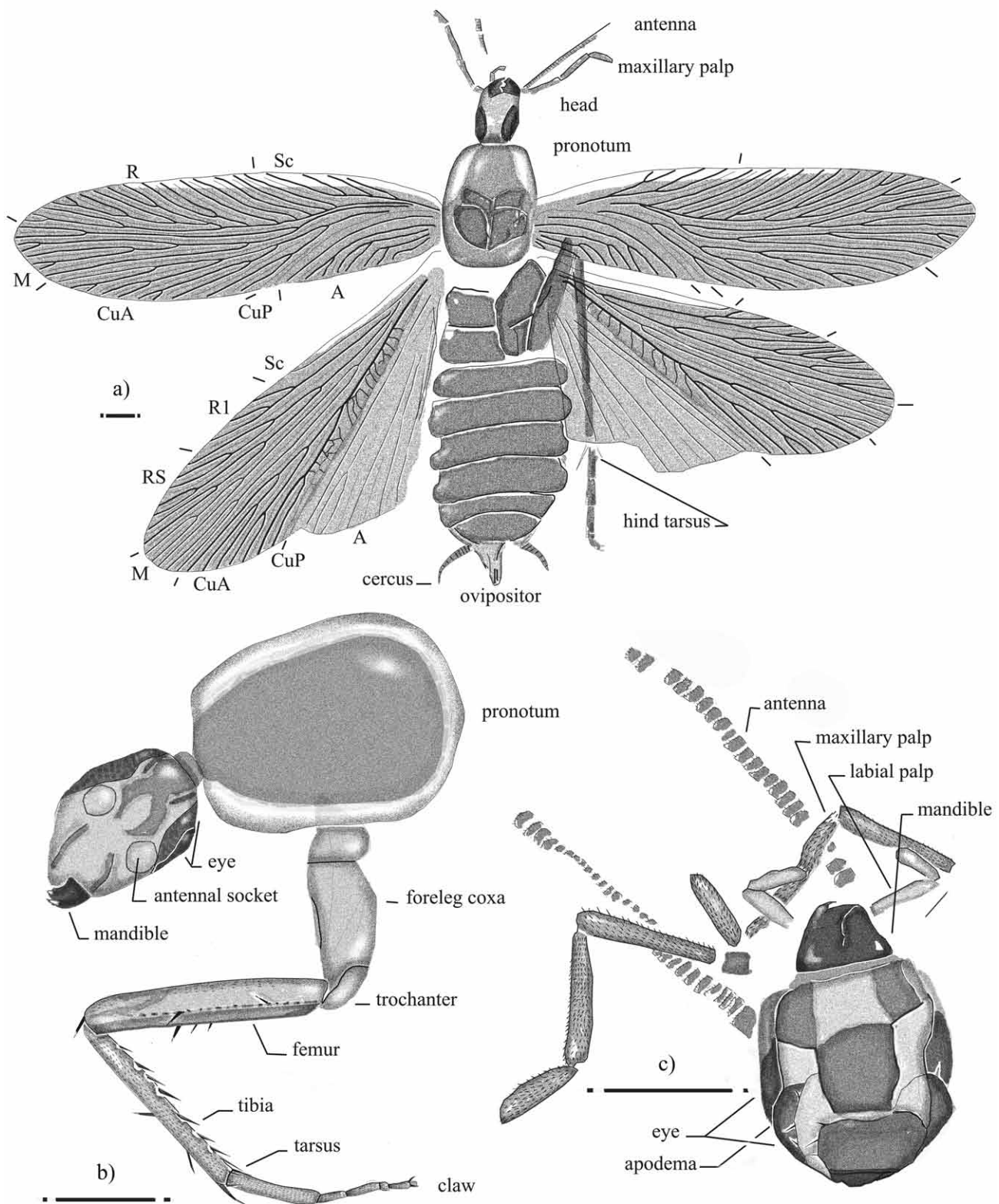


Figure 1. Crepuscular and/or nocturnal carnivorous cockroach *Divocina noci* gen. et sp. nov. (Raphidiomimidae) from the Middle Jurassic of the Jiulongshan Formation, Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University. a: holotype CNU-B-NN-2006-067; b: detail of head and fore 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).

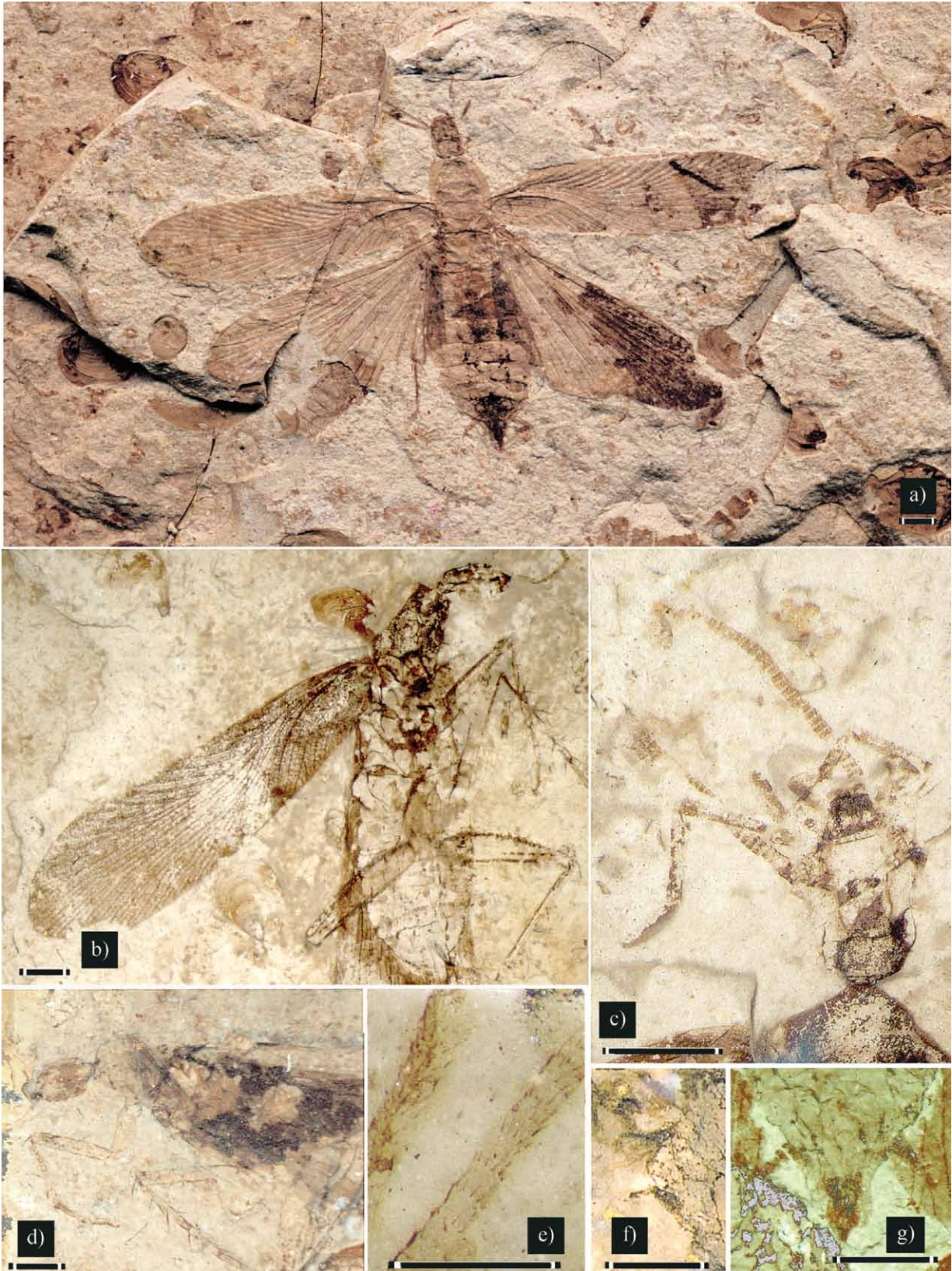


Figure 2. Crepuscular and/or nocturnal carnivorous cockroach *Divocina noci* gen. et sp. nov. (Raphidiomimidae) from the Middle Jurassic of the Jiulongshan Formation, Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University. a: holotype CNU-B-NN-2006-067; b: detail of legs and forewing 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 antenna CNU-B-NN-2006-090; f: detail of male genitalic appendages CNU-B-NN-2006-066; g: detail of female ovipositor CNU-B-NN-2006-051. Scales 1mm (inner black bar).

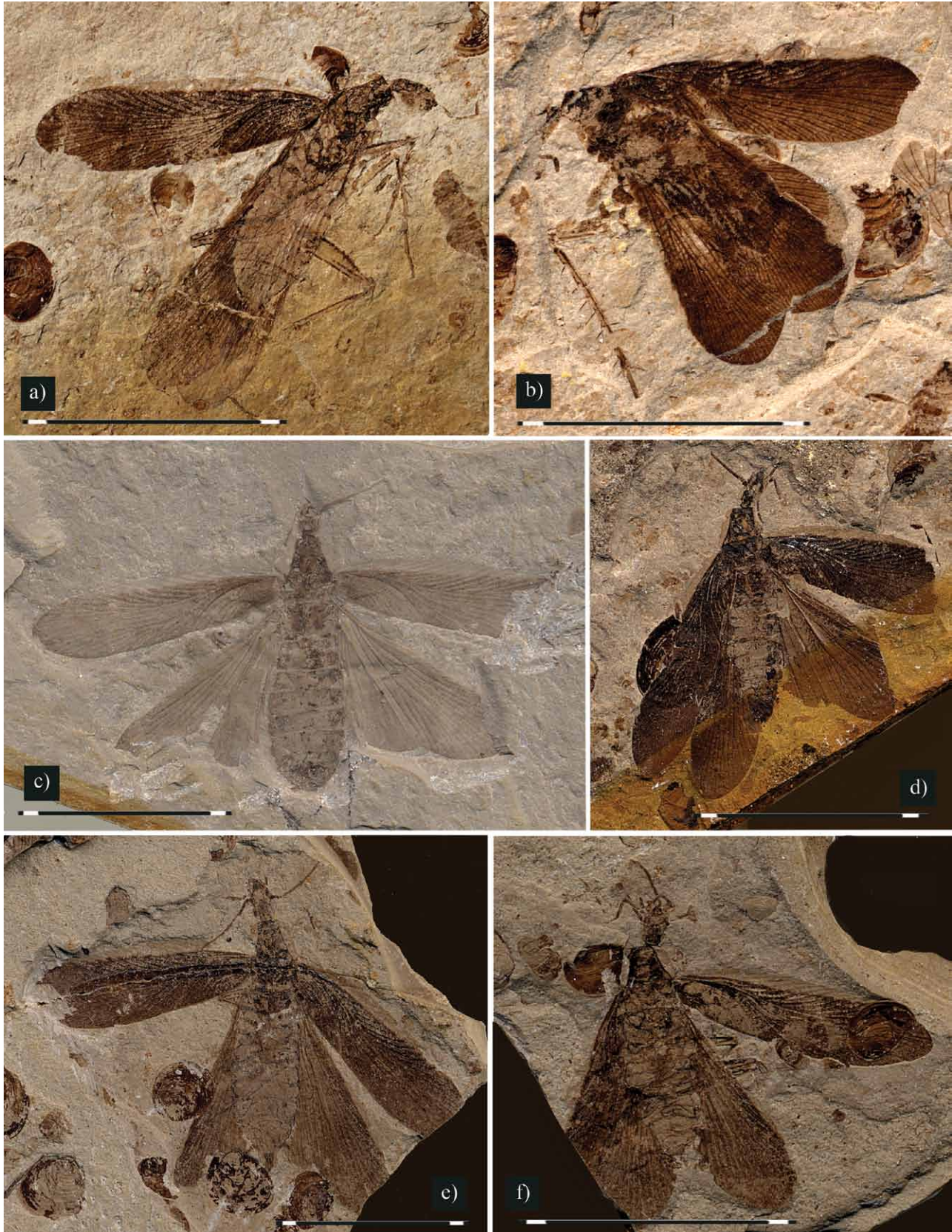


Figure 3. Crepuscular and/or nocturnal carnivorous cockroach *Divocina noci* gen. et sp. nov. (Raphidiomimidae) from the Middle Jurassic of the Jiulongshan Formation. Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University. a: CNU-B-NN-2006-065; b: CNU-B-NN-2006-037; c: CNU-B-NN-2006-069 - 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).

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 mechanoreceptors 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 *Raphidiomima*. 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 4AA-BH) was comparatively low, perfectly fitting the variability of the sole studied representative of the family, *Fortiblatia 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 ($CV_M=30.15$) 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

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; TNP42412-1LFW (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.

	Length	Width	Sc	R	M	CuA	A	R+M	R+Cu	M+Cu	SUM	Total
n	36 19; 14	36 19; 16	44 21; 22	44 21; 22	44 21; 22	44 21; 22	43 21; 21	44 21; 22	44 21; 22	44 21; 22	43 21; 22	43 (21; 21)
Min	12.3 12.3; 13	3.2 3.2; 3.5	2 2; 2	8 8; 11	5 5; 5	4 5; 4	5 5; 5	18 19; 18	17 17; 18	13 (14; 13)	28 28; 29	35 (35; 36)
Max	16 14; 16	4.8 4.3; 4	6 6; 4	17 17; 16	16 16; 14	11 10; 11	10 9; 10	29 26; 29	28 28; 28	25 25; 24	39 39; 39	48 48; 47
Median	13.6 13.2; 14	4 4; 3.95	3 3; 3	13 14; 13	9 10; 8	8 8; 8	7 7; 8	22.5 23; 22	22 23; 22	18.5 19; 17	35 36; 33	42 42; 41
Mode	15 13.2; 13.9	4 4; 4	3 3; 3	13 15; 13	8 (11; 8)	8 7; 9	6 6; 8	22 24; 22	22 23; 22	19 19; 19	32 32; 32	44 44; 41
Average	13.894 13.8; 14.07	3.892 3.9; 3.83	3.136 3.09; 3.18	13.591 13.86; 13.36	8.977 9.33; 8.59	7.864 8; 7.73	7.209 6.91; 7.48	22.568 23.19; 21.96	22.455 22.86; 22.1	17.841 18.33; 17.32	34.545 32.19; 33.76	41.744 42.19; 41
Deviation	0.961 1.00; 14.06	0.279 0.25; 0.21	0.852 1.00; 0.73	1.796 2.10; 1.50	2.707 2.78; 2.70	1.579 1.45; 1.75	1.206 1.14; 1.25	2.463 2.18; 2.66	2.556 2.94; 2.20	2.702 2.71; 2.71	2.8971 3.09; 2.66	3.193 3.50; 3.07
CV in%	6.92 7.17; 6.57	7.17 6.45; 5.61	27.17 32.16; 23.03	13.21 15.19; 11.21	30.15 29.80; 31.46	20.07 18.11; 22.66	16.73 16.45; 17.42	10.91 9.41; 12.13	11.38 12.85; 9.97	15.14 14.77; 15.68	8.39 9.58; 7.89	7.65 8.30; 7.49

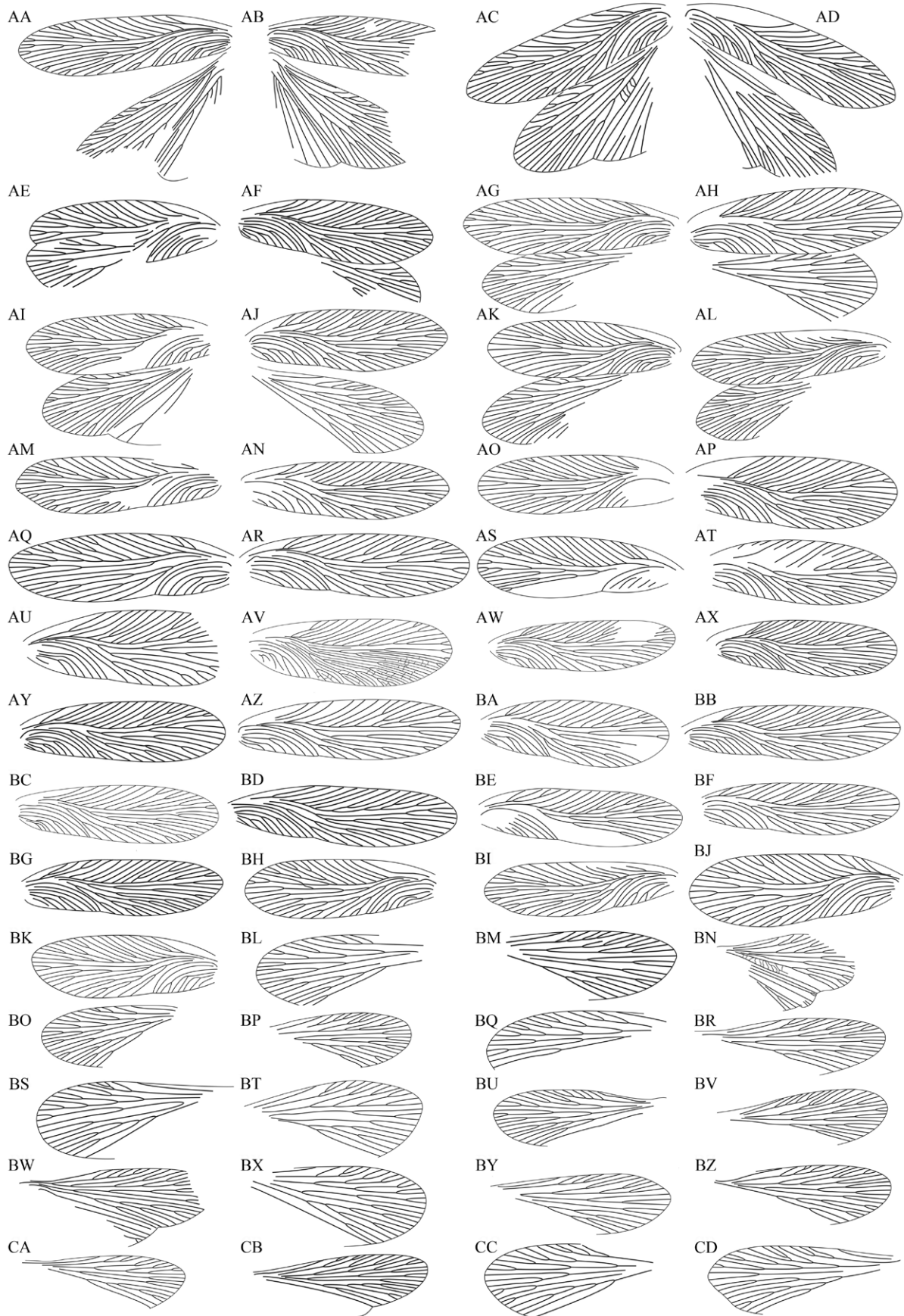


Table 2. Hindwing venation variability of *Divocina noci* sp. nov. Numbers in the second line represent data of left and right forewings separately. Measured individuals: CNU-NN-006-067, 033; 069; 90; 104; 105; 120; TNP42412-1; 486; 488; 686; 687-2; 691 (left forewing); CNU-NN-006-067, 051, 069, 204, 486, 488, 489, 683, 686, 687-2, 690, 691, TNP42412-1RHW (right forewing). Sc- subcosta; R1-radius anterior; RS- radius sector; M- media; Cu- Cubitus anterior + posterior; A- anal; Total- total number of remigial veins at the margin; CV- coefficient of variation.

	Length	Width	Sc	R1	RS	R1+RS	M	CuA	R+M	R+Cu	M+Cu	Total
n	20	19	26	25	26	25	26	26	25	25	26	25
	10; 10	9; 10	13; 13	12; 13	13; 13	12; 13	13; 13	13; 13	12; 13	12; 13	13; 13	12; 13
Min	10.3	3.3	1	3	5	9	2	5	13	16	11	21
	10.3; 11	4; 3.3	1; 1	3; 3	6; 5	10; 9	2; 4	6; 5	13; 13	18; 16	11; 10	22; 21
Max	14	4.8	1	7	9	16	8	9	20	23	16	29
	14; 14	4.5; 4.8	1; 1	7; 6	9; 9	16; 14	7; 8	9; 8	20; 20	23; 23	16; 15	28; 29
Median	10.3	4	1	4	7	11	6	7	17	19	13	26
	13.35; 13.5	4; 4	1; 1	4; 5	7; 7	11; 11	6; 6	7; 6	17; 17	19; 19	14; 13	26; 26
Mode	14	4	1	4	7	11	6	6	17	19	13	26
	14; 14	4; 4	1; 1	4; 5	7; 7	12; 11	6; 6	7; 6	17; 18	19; 19	15; 13	27; 26
Average	12.94	4.14	1	4.36	7.08	11.44	5.62	6.73	17.04	19.16	13.35	25.76
	13.05; 12.83	4.2; 4.09	1; 1	4.25; 4.46	7.23; 6.92	11.5; 11.38	5.62; 5.62	7.08; 6.38	16.78; 17	19.58; 18.69	13.69; 12.92	25.85; 25.31
Deviation	1.053	0.32	0	0.952	0.891	1.387	1.267	0.919	1.814	1.650	1.468	1.943
	1.148; 0.997	0.245; 0.381	0; 0	1.055; 0.877	0.832; 0.954	1.624; 1.193	1.446; 1.121	0.954; 0.768	2.048; 1.915	1.505; 1.843	1.494; 1.552	1.772; 2.428
CV in %	8.14	7.73	0	21.83	12.58	12.12	22.55	13.66	10.65	8.61	11.0	7.54
	8.80; 7.77	5.83; 9.32	0; 0	24.83; 19.66	11.51; 13.79	14.12; 10.48	25.72; 19.94	13.48; 12.04	12.26; 11.26	7.69; 9.86	10.91; 12.02	6.86; 9.59

11 specimens with both complete wings, left and right sides differ on the average of only 1.9 veins at the margin (respective specimens differ as follows: 0 (identical number of veins at both sides), +1 (+1 vein at left side), +1, +1, +1, -1 (-1 vein at left side), +2, -2, +3, +4, -5), which is 4.6% of the average of 41.22 veins of measured individuals – a very low value when we consider asymmetrical superposition of left wing over the right one. Also it is a much lower value than expected for *Fortiblatia* with a mean difference of 3.55 veins of the average of total 50.95 veins of measured individuals, which is 7% - nearly twice as much (see Liang *et al.* 2009 for specimen details). Other known data are from *Fuzia dadao* Vršanský, Liang et Ren, 2009 (n = 9) of the related family Fuziidae Vršanský, Liang et Ren, 2009 with an average difference of 2.33 (of 39.76) for the wing (0, +1, +1, -1, -1, +3, +4, +7, +7), which is 5.86% and supports a good, although not excellent, flight of that species (Vršanský *et al.*, 2009).

Nevertheless, hind wing differences (see Table 2, Figures 4AA-AP, BL-CD) in *Divocina noci* (n= 7) are similar to its forewings, with a mean difference of 2.0 (0, 0, 0, +1, +2, -5, +6). The hind wing variability, namely variability

of remigial veins (CV= 7.54), is in full concordance with the conclusions based on forewings. Surprising is the high degree of variability of hindwing anterior branches (R1+RS) and thus a possible presence of the same phenomenon as in the Blattulidae – namely the regulation of vein strength in the Cubital area (Vršanský, 1999; Vršanský and Ansoerge, 2001). The presence of such regulation in the present group where veins have more or less constant width would be surprising.

There is apparently no significant preference of one side above the other in terms of prevailing number of veins at one side (forewing and hindwing), which is surprising as the left wing usually fold over the right one, even though exceptions are known (Vršanský, 2009). Also known are cases of mirror symmetry in one taxon (e.g. see Anisyutkin and Gorochoy, 2004b).

Only two wing deformities, namely a fusion joining R and M in a forewing (CNU-B-NN-2006-065 left) and fusion of two Medial veins (037LFW – Figures 3b, 4AI) are present among 44 complete wings, which suggest a stabilized morphotype (see Vršanský 2005).

The coordinated flight may also be a cause of the

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 LFW and LHW; AB – 069 RFW and RHW; AC – TNP42412 LFW and LHW; AD – TNP42412 RFW and RHW; AE – 312 LFW and LHW; AF – 312 RFW and RHW; AG – 700 LFW and LHW; AH – 700 RFW and RHW; AI – 686 LFW and LHW; AJ – 686 RFW and RHW; AK – 033 RFW and RHW; AL – 120 RFW and RHW; AM – 488 LFW; AN – 488 RFW; AO – 489 LFW; AP – 489 RFW; AQ – 687 LFW; AR – 687 RFW; AS – 691 LFW; AT – 691 RFW; AU – 035 RFW; AV – 037 RFW AW – 050 RFW; AX – 051 RFW; AY – 053 RFW; AZ – 054 RFW; BA – 254 RFW; BB – 480 RFW; BC – 484 RFW; BD – 486 RFW; BE – 683 RFW; BF – 690 RFW; BG – 707 RFW; BH – 056LFW; BI – 105 LFW; BJ – 204 LFW; BK – 485 LFW; BL – 486 LHW; BM – 486 RHW; BN – 035RHW; BO – 488 LHW; BP – 489 RHW; BQ – 683 LHW; BR – 683 RHW; BS – 691 LHW; BT – 691 RHW; BU – 687 LHW; BV – 687 RHW; BW – 051 RHW; BX – 090 RHW; BY – 105 RHW; BZ – 204 RHW; CA – 480 RHW; CB – 489 RHW; 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 *Fortiblattea cuspicolor* 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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