



## Variability of *Habroblattula drepanoides* gen. et. sp. nov. (Insecta: Blattaria: Blattulidae) from the Yixian Formation in Liaoning, China

TIAN-TIAN WANG<sup>1</sup>, JUN-HUI LIANG<sup>1,2</sup> & DONG REN<sup>1,\*</sup>

<sup>1</sup>College of Life Sciences, Capital Normal University, Beijing 100037, China

<sup>2</sup>Tianjing Museum of Natural History, Tianjing 300074, China

\*Corresponding author. E-mail: rendong@mail.cnu.edu.cn

### Abstract

*Habroblattula drepanoides* gen. et sp. nov. (Blattulidae) is described from the Late Jurassic or Early Cretaceous sediments of the Yixian Formation in Western Liaoning, China. Wing venation of *Habroblattula drepanoides* reveals low coefficient of variation (CV) for total number of the forewing veins (CV=5.72) which indicates active flight capability. The higher hindwing variability (CV=14.43) might suggest *Habroblattula* was an advanced genus, may be caused by the regulation of the vein. The asymmetry between the left and right forewing in the same individual indicates the flight was limited when comparing with the CV of the left and right forewings.

**Key words:** Blattulidae, new genus, new species, coefficient of variation, Late Jurassic, Early Cretaceous, Yixian Formation, China

### Introduction

Cockroaches have existed since the Carboniferous until now (Carpenter 1953, Tan 1980). At least 19 different families are represented in the fossil record (Vršanský 2002b, Liang 2006).

Representatives of the family Blattulidae were placed in the Mesoblattinidae, until Vishniakova (1983) established the new family and commented on its relation with Polyphagoidea. This relation, namely with the family Liberiblattinidae, was supported by Vršanský (1999, 2002a). The significance of studying on Blattulidae was proved in displaying decreasing variability of the families (Vršanský 2000, Vršanský & Ansoerge 2006), in reconstructing ecosystems of the Mesozoic, but also curious in findings of hindwings from drilling core samples (Vršanský 2005a).

The Blattulidae is a family of cosmopolitan Mesozoic cockroaches. Nevertheless, their diversity at the generic level is poor—only 13 genera are known in their greater than 100 million years history (Vršanský 2005a, Cifuentes *et al.* 2006). It is significant that well-preserved and sophisticatedly coloured complete fossil specimens, belonging to a new genus *Habroblattula* gen. nov., have been recovered from Yixian Formation.

### Material and methods

Twenty eight specimens, housed in the fossil insect collection of the key lab of Insect Evolution and Environment Change, Capital Normal University, Beijing, China, were examined using LEICA MZ12.5 dissecting microscope and illustrated with a drawing tube attached to the microscope. Fossil photographs were made using LEICA DC 300 photographic equipment.

Morphological terminology and the systematics follow Vršanský (1998, 2003).

The strata of the Yixian Formation represent mainly lacustrine sediments intercalated with volcanoclastics (Ren *et al.* 1995). They contain a great deal of Jehol Biota fossils, including dinosaurs, primitive birds, early mammals, angiosperms, and diverse insects (Sun *et al.* 1998, Hou *et al.* 1999, Ding *et al.* 2001). Paleobotanical data (including fossil spores, pollen and plants) from Yixian Formation were interpreted as indicating a warm and moist climate (Ding *et al.* 2001).

They are at least four large sections of sedimentary interlayers bearing fossils of Yixian formation, among them the Jianshangou Bed located at the lower part of Yixian Formation, near Chaomidian Village of Shangyuan Town, Beipiao City of Liaoning Province. Three typical sections of the Jianshangou Bed are considered as follows: Libalanggou-Sihetun, Jianshangou and Huangbanjigou (Chen *et al.* 2004). The materials in this study came from the latter two sections.

The age of Yixian Formation remains contentious. It had been proposed as Late Jurassic (Zheng *et al.* 2003, Ren *et al.* 1997), Late Jurassic to Early Cretaceous (Wang *et al.* 2004, Chen *et al.* 2004, Wang *et al.* 2005), Early Cretaceous (Swisher 1999, Li *et al.* 2001, Pang *et al.* 2002, Zhou *et al.* 2003).

Abbreviations used: A; Cu; M; R; Sc when used with figures mean number of Anal, Cubital, Medial, Cubital, Medial, Radial and Subcostal veins.

## Systematic paleontology

### Order Blattaria Latreille, 1810

### Family Blattulidae Vishniakova, 1983

### Genus *Habroblattula* gen. nov.

#### **Type species.** *Habroblattula drepanoides* sp. nov.

**Diagnosis.** Wings, pronotum and legs with bright and dark colour. Forewing Sc terminally branched, CuP strongly curved, all branches strong and dark, intercalaries and cross-veins distinct. Hindwing with pterostigma (dark macula in the R1), R1 and RS differentiated, CuA with abundant secondary branches.

**Description.** Forewings with more or less parallel margins and characteristic forewing coloration (with falciform dapple of the R and M area and with macula along with the basal part of the posterior margin). Costal space very short and narrow; Sc terminally branched; R slightly curved, multiple simple branches, ending before wing apex; apically descending M simplified; CuA with branches long, running parallel to margin; CuP strongly curved; Anal veins simple and with thick cross-veins (visible even in poorly preserved specimens). Hindwing with pterostigma (dark macula in the R1). Sc simple; R1 and RS differentiated; M without tertiary branchings; CuA with abundant secondary branches; CuP simple. Apex distinctly colored. Pronotum with anomalous dapple, wider than long. Legs long with bright dark macula, femur shorter than tibia; all tibiae very short, with numerous spurs. Body soft, terminal segments with multisegmented cerci and styli.

**Remarks.** *Habroblattula* is assigned to the family Blattulidae, because the forewing has long Sc, regular venation with distinct intercalaries and hindwing has simple CuP, branched A1. (Vishniakova 1983)

*Habroblattula* gen. nov. is closely related to *Svabula* Vršanský, 2005b from the Berriasian Lower Cretaceous sediments of Sharin-gol in Mongolia. Synapomorphies include wider forewing with margins parallel, branches strong, straight and dark, clavus with cross-veins. *Svabula* differs in small forewing size, different coloured pattern, having less apparent intercalaries and thick cross-veins.

Hindwing of the new genus resembles *Kridla* Vršanský, 2005a from the Albian or Cenomanian Upper Cretaceous sediments of the Kyndalskaya Formation in having distinct pterostigma and distinct apex coloration, but differs from the latter by secondarily branched R1, and A2, simple M and more abundant cross-veins.

The new genus differs from genus *Tarakanula* Vršanský, 2003 by prominently coloured wings, pronotum and legs of new genus, with more dense veins and with apparent thick cross-veins.

*Habroblattula* gen. nov. is easily differentiated from *Elisama* Giebel, 1856 and *Blattula* Handlirsch, 1906–1908 by having coloured wings, pronotum and legs, the forewing with strong, dark branches and apparent cross-veins in clavus and Cu area.

*Xonpepetla* Cifuentes-Ruiz et Vršanský, 2006 from the Campanian of Mexico differ in being robust body with very short and very wide forewings.

**Etymology:** The name is derived from the Greek prefix *habr* (meaning “elegancy”) and the type genus *Blattula* ( the type genus of this family).

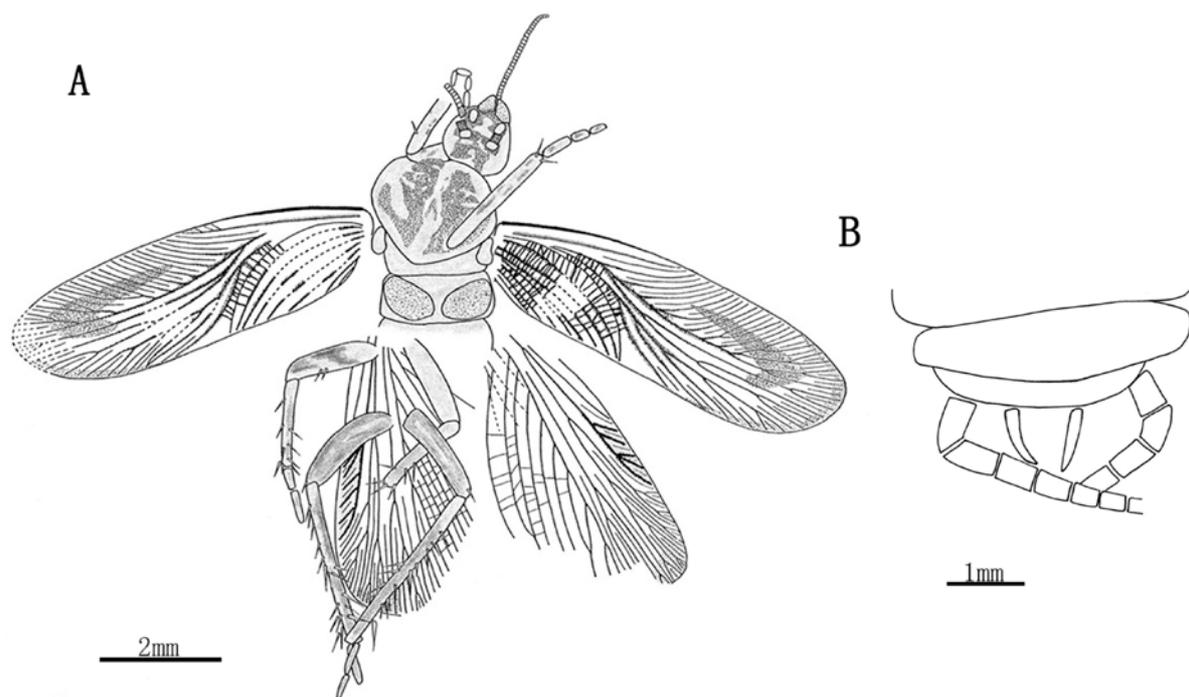
***Habroblattula drepanoides* gen. et sp. nov.**

Fig 1. A–B , Fig 2. A–H

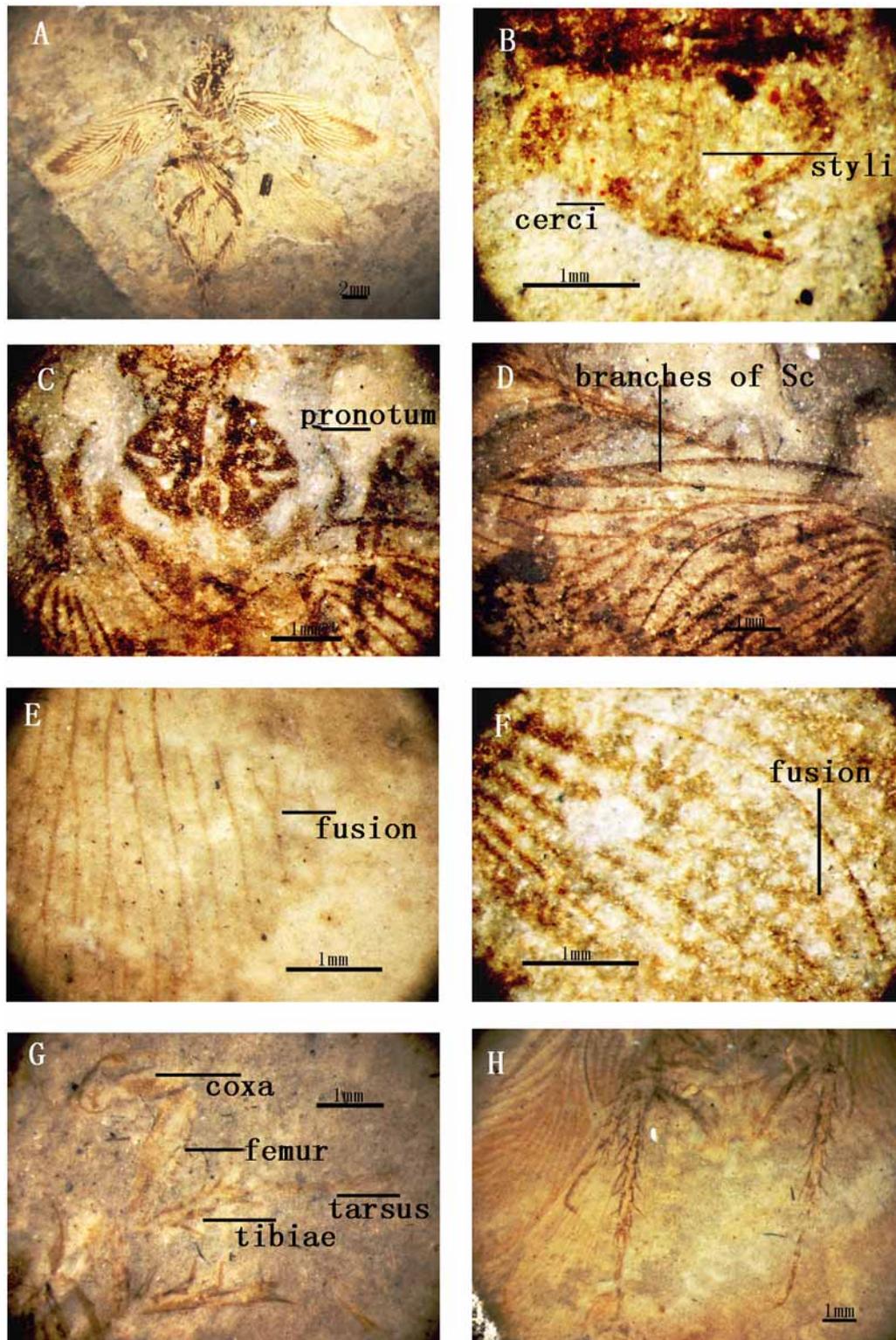
**Holotype.** A complete specimen, No. CNU-B-LB-2006369-1.

**Locality and horizon.** Yixian Formation, Upper Jurassic or Lower Cretaceous, Huangbanjiegou, Chaomidian Village, Beipiao City, Liaoning Province, China.

**Additional Material.** CNU-B-LB-2006305, CNU-B-LB-2006378, CNU-B-LB-2006386, CNU-B-LB-2006389, CNU-B-LB-2006392 (Forewings); CNU-B-LB-2006301, CNU-B-LB-2006302, CNU-B-LB-2006303, CNU-B-LB-2006304, CNU-B-LB-2006369-2, CNU-B-LB-2006390-1, CNU-B-LB-2006390-2, CNU-B-LB-2006306, CNU-B-LB-2006391 (Complete specimens); Yixian Formation, Upper Jurassic or Lower Cretaceous, Huangbanjiegou, Chaomidian Village, BeiPiao City, Liaoning Province, China. CNU-B-LB-2006387, CNU-B-LB-2006380, CNU-B-LB-2006384 (Forewings); CNU-B-LB-2006372, CNU-B-LB-2006383, CNU-B-LB-2006377, CNU-B-L-B-2006320, CNU-B-LB-2006373, CNU-B-LB-2006375, CNU-B-LB-2006381, CNU-B-LB-2006382, CNU-B-LB-385, CNU-B-LB-2006376 (Complete specimens); Yixian Formation, Upper Jurassic or Lower Cretaceous, Jianshangou, Chaomidian Village, Beipiao City, Liaoning Province, China.



**FIGURE 1.** *Habroblattula drepanoides* gen. et sp. nov., A, holotype ,CNU-B-LB-2006369-1 ; B, male terminalia, CNU-B-LB-2006382.

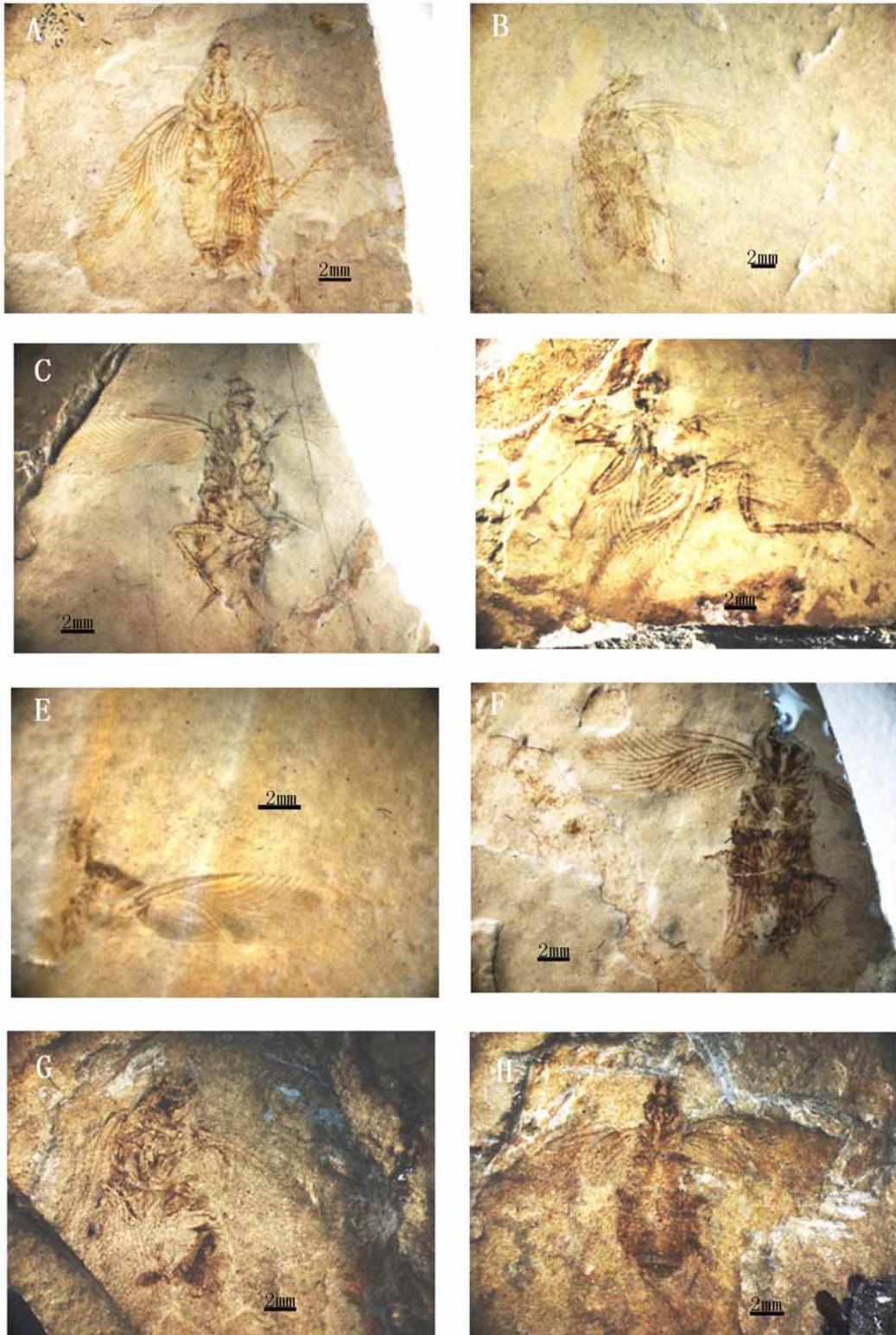


**FIGURE 2.** *Habroblattula drepanoides* gen. et sp. nov. A, holotype, CNU-B-LB-2006369-1; B, male terminalia, CNU-B-LB-2006382; C, pronotum with anomalous dapple, CNU-B-LB-381; D, forewing Sc terminally branched, CNU-B-LB-2006381; E, unusual fusion of the veins, CNU-B-LB-2006384 (left hindwing); F, unusual fusion of the veins, CNU-B-LB-2006377 (left forewing). G, Fore legs, CNU-B-LB-2006301; H, middle legs and hind legs, CNU-B-LB-2006391.

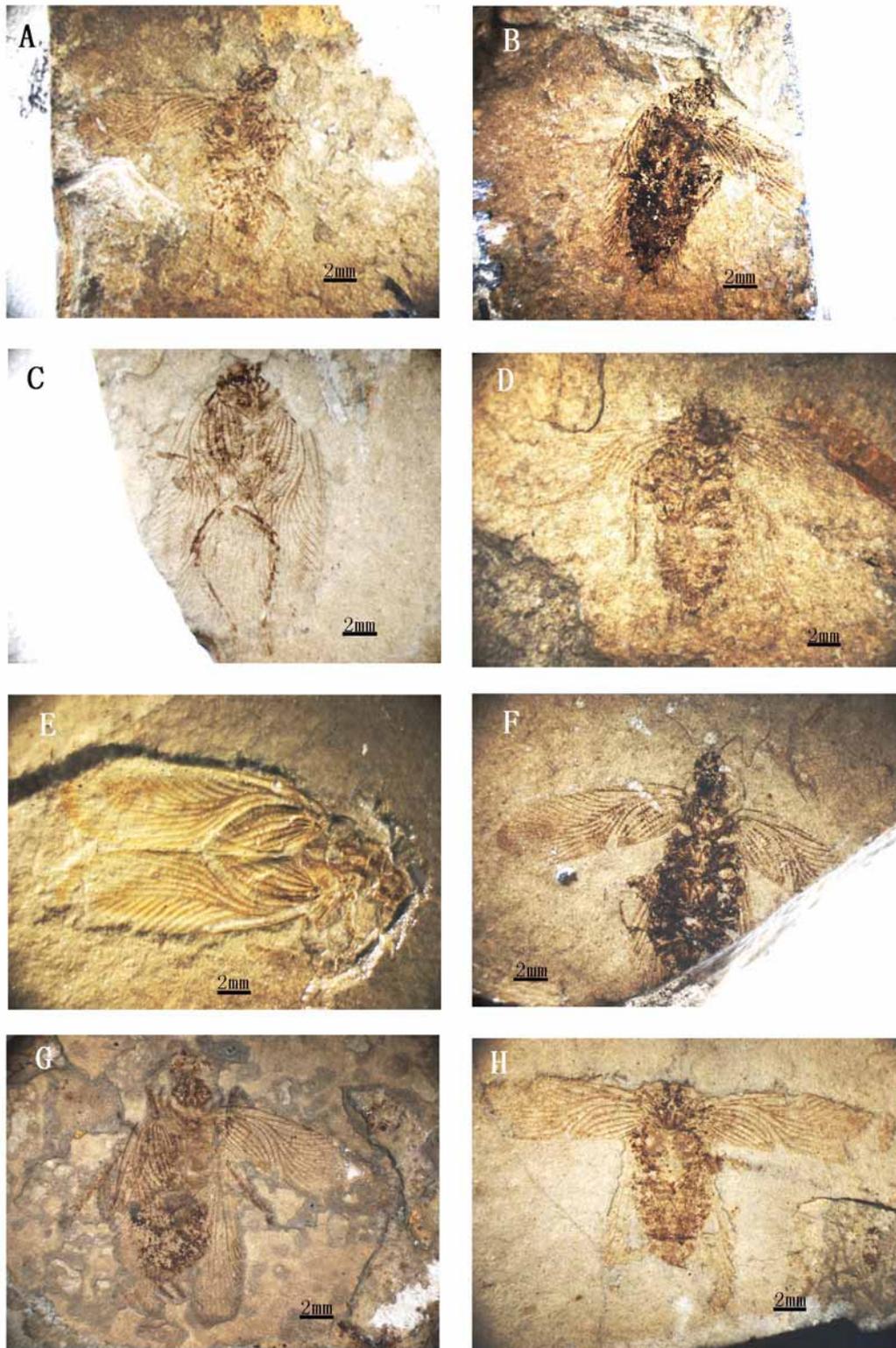
**Description.** (Figs 1–6) Large species. Head length/width: 2.0–2.7/2.0–2.2mm, more or less globular; antennae filiform, shorter than body length; mandibles strong with sharp dentition; maxillary palps 5-seg-

mented, 2nd and 3rd segments being the longest.

Pronotum vaulted, slightly transverse, often wider than long, with many bright anomalous dapple coloration. length/ width =3.0–4.0/3.0–4.0mm (Fig 2. C).



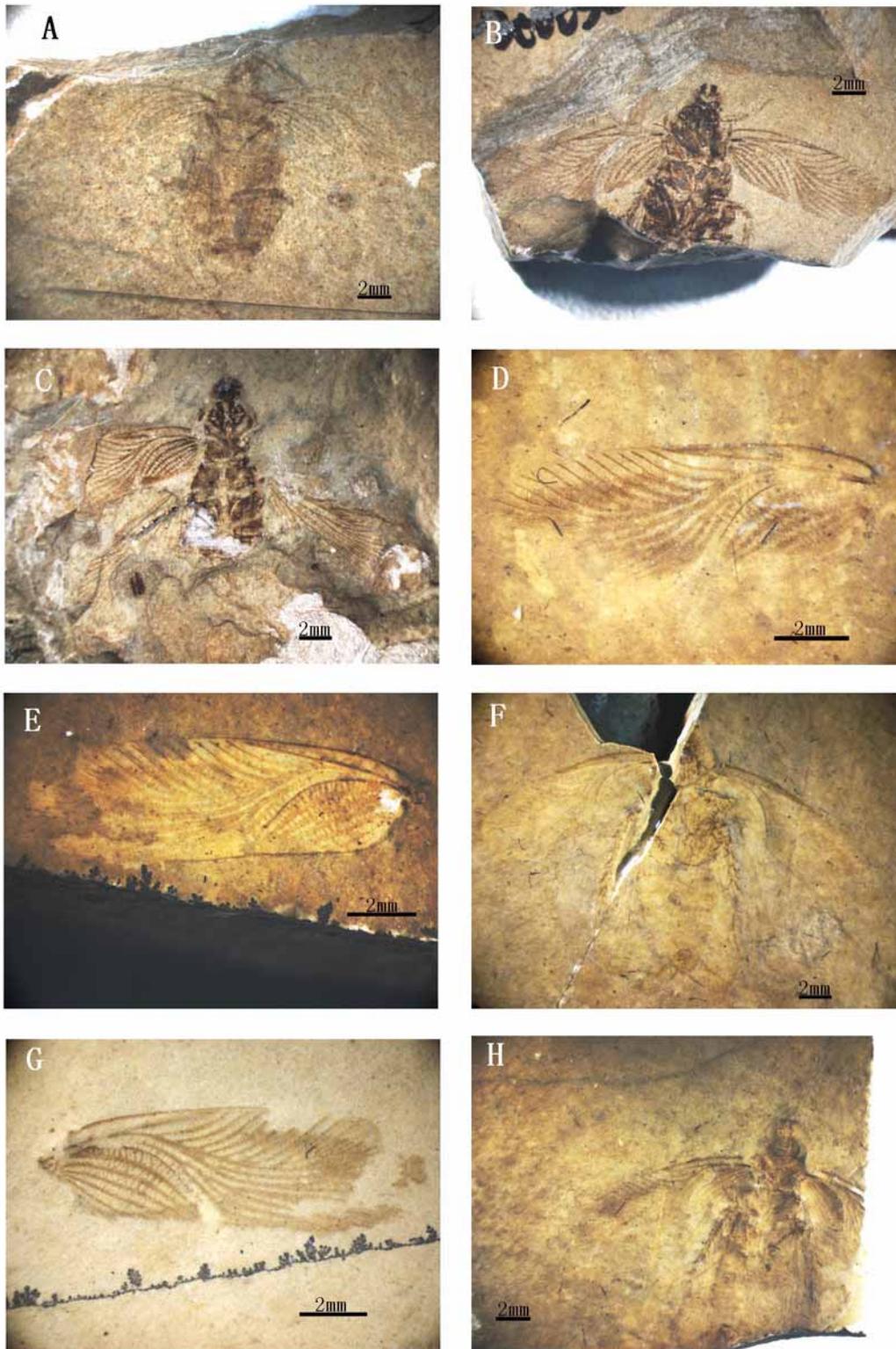
**FIGURE 3.** *Habroblattula drepanoides* gen. et sp. nov. Additional material: A, CNU-B-LB-2006301; B, CNU-B-LB-2006302; C, CNU-B-LB-2006303; D, CNU-B-LB-2006304; E, CNU-B-LB-2006305; F, CNU-B-LB-2006306; G, CNU-B-LB-2006320; H, CNU-B-LB-2006372.



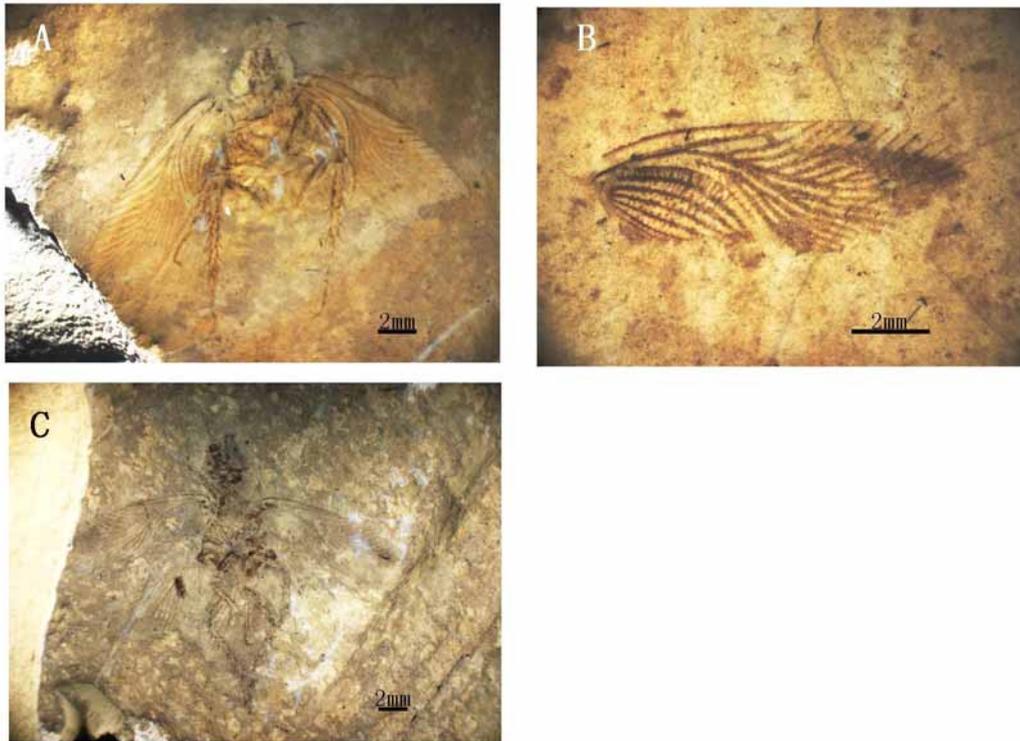
**FIGURE 4.** *Habroblattula drepanoides* gen. et sp. nov. Additional material: A, CNU-B-LB-2006373; B, CNU-B-LB-2006375; C, CNU-B-LB-2006376; D, CNU-B-LB-2006377; E, CNU-B-LB-2006378; F, CNU-B-LB-2006380; G, CNU-B-LB-2006381; H, CNU-B-LB-2006382.

Forewing elongate, elliptical, length/width=11.0–12.0mm/3.2–4mm, with more or less parallel margins and characteristic coloration (dark macula apically of the R and M, look like “falcate” and in the basal part of the posterior margin); Cross-veins distinct, mainly in clavus and Cu area; intercalaries pale; apex oval; costal

space narrow, occupies 1/3 of the wing length; Sc straight and somewhat thickened, simple or with several simple branches (1–4) (Fig 2. D); R space taking 43.0% of wing width, R slightly curved, terminated prior to the apex, forming 12–17 branches; M reaching apex, with 3–8 veins; CuA gently curved, with 3–6 branches; CuP simple; Clavus occupies 1/3 the length of the posterior margin of the wing, anal veins numerous (6–8).



**FIGURE 5.** *Habroblattula drepanoides* gen. et sp. nov. Additional material: A, CNU-B-LB-2006383; B, CNU-B-LB-2006384; C, CNU-B-LB-2006385; D, CNU-B-LB-2006386; E, CNU-B-LB-2006387; F, CNU-B-LB-2006390-2; G, CNU-B-LB-2006389; H, CNU-B-LB-2006390-1.



**FIGURE 6.** *Habroblattula drepanoides* gen. et sp. nov. Additional material: A, CNU-B-LB-2006391; B, CNU-B-LB-2006392; C, CNU-B-LB-2006369-2.

Hindwing length 10.0–11.0mm. Simple weak Sc reach 1/3 the wing length; Pterostigma present in the R1 (5–6), RS (9–11), diverged from R basally; M with 2–5 simple branches, reaching the apex; CuA with 6–9 veins; thin CuP simple straight; A1 forked; Intercalaries and cross-veins apparent, apex distinctly coloured.

Legs cursorial, colored (Figs 2. G. H). Fore legs thin compare with mid and hind legs, femora narrow, as wide (0.35mm) as tibiae; Mid legs longer than fore legs, femora (3.0 mm) shorter than tibiae (3.5 mm); tarsus (2.5mm) longer than 1/2 length of tibia; Hind legs longer than fore legs and mid legs, tibiae (5.0mm) gracile and 1.4 times as long as femora (3.5mm), tarsus (3.0mm) longer than half length of tibia. Fourth tarsal segment shorter than total length of other four segments; both femora and tibiae with long spines bearing very smooth helical ridges.

Body elongate; Cerci short, with 9 and more segments (Fig 2. B).

**Remarks.** Forewing venation fusion (Fig 2. F) is present in 4 of 28 specimens, mainly in different Cu and A branches. Hindwing venation fusion (Fig 2. E) is present in Cu area (2 of 28 specimens). Fusions might have been caused by some environmental factors (Vršanský 2005a).

The hindwing pterostigma and the branched SC in forewing probably represent plesiomorphic characters within the Blattulidae (Vršanský 2002a).

**Variability.** (Tables 1–4) The total number of the forewing veins (23–27, exclude Sc and A) meeting the forewing margin has the lowest CV (5.72). Comparatively, low CV value (8.22) is observed in R+M system (17–22). M (3–8) seems to be the most variable (CV=30.99) vein. Limited variation in the anterior part of the wing suggests enhanced flight capabilities when compared with the representatives of the Spiloblattinidae, Poroblattinidae, Mylacrididae, Caloblattinidae, Mesoblattinidae, supporting the hypothesis that the Blattulidae were active flyers (Vršanský 2000).

Variability is lower than that found in *Blattula langfeldi* and *Elisama tsaganica* possibly due to relatively small sample size (Vršanský 2003).

**TABLE 1.** *Habroblattula drepanoides* sp. nov. Forewing venation variability. Sc and A are excluded in the sum. CV: coefficient of variation.

	R	M	Cu	A	R+M	M+Cu	R+Cu	SUM
Minimum	12	3	4	6	17	9	17	23
Maximum	17	8	7	9	22	13	24	27
Median	14	5	6	7	19	11	19	26
Mode	14	5	6	6	17	10	18	26
Std. Error of Mean	0.36	0.34	0.20	0.16	0.36	0.24	0.54	0.34
Std. Deviation	1.67	1.52	0.92	0.95	1.56	1.03	2.40	1.43
CV	11.68	30.99	15.47	13.71	8.22	9.37	11.87	5.72

It is notable that the variation in hindwing is higher than that in the forewing, which is also the case for advanced Mesozoic blattulids. The higher variation in the hind wing may be caused by the regulation of the vein strength (Vršanský 2003).

The difference between left and right wings in the same individual in Blattaria is a common phenomenon in Fossil of cockroaches. It was observed in *H. drepanoides*, with the left forewings differing from right ones in the following characters: CV of the total number of the veins meeting the right forewing margin is slightly higher CV (5.82) than the left forewing (CV=5.64) as well as the CV of the R, M, A, R+Cu. The CV of the Cu R+M of the right forewing is a bit lower than the left forewing. It is notable that M+Cu in the right forewing (CV=12.86) is much higher than the left forewing (CV=6.77). The asymmetry between left and right wings in one specimen suggests that the specimen had limited flight capability. An appreciation of the asymmetry of the venation is very important for identifying fossil Blattaria. It clarifies which features of venation are important for identification of fossils.

**TABLE 2.** *Habroblattula harpeodes* gen. et sp. nov. Hind wing venation variability. Sc and A are excluded in the sum.

	R1	RS	R	M	Cu	R+M	M+Cu	Sum
Minimum	4	5	10	2	7	12	10	12
Maximum	7	11	16	5	10	20	14	30
Median	5	8	12	4	8	16	11	23
Mode	4	5	16	4	8	15	10	23
Std. Error of Mean	0.35	0.67	0.80	0.34	0.30	0.97	0.50	1.31
Std. Deviation	1.05	2.11	2.40	1.06	0.83	2.91	1.41	3.46
CV	206	26.35	18.45	32.10	10.27	17.91	12.38	14.43

**TABLE 3.** *Habroblattula drepanoides* sp. nov. Right forewing venation variability. Sc and A are excluded in the sum. CV: coefficient of variation.

	R	M	Cu	A	R+M	M+Cu	R+Cu	SUM
Minimum	12	3	5	6	17	9	17	23
Maximum	17	8	7	9	21	13	24	27
Median	14	5	6	7	19	11	19	26
Mode	13	5	5	6	19	10	18	26
Std. Error of Mean	0.59	0.62	0.28	0.26	0.51	0.50	0.90	0.55
Std. Deviation	1.76	1.75	0.83	1.00	1.35	1.41	2.53	1.46
CV	12.50	33.38	14.42	14.29	7.03	12.86	12.74	5.82

**Etymology:** after Greek for *drepanoides* (falcate), refers to the forewing falcate dapple.

**Character of preservation.** 20 complete specimens and 8 isolated forewings.

**TABLE 4.** *Habroblattula drepanoides* gen. et sp. nov. Left forewing venation variability. Sc and A are excluded in the sum. CV: coefficient of variation.

	R	M	Cu	A	R+M	M+Cu	R+Cu	SUM
Minimum	12	3	4	6	17	10	17	23
Maximum	17	8	7	9	22	12	24	27
Median	14	5	6	7	19	11	20	25
Mode	14	5	7	7	17	11	18	24
Std. Error of Mean	0.49	0.43	0.33	0.25	0.54	0.23	0.71	0.44
Std. Deviation	1.64	1.42	1.05	0.92	1.78	0.74	2.36	1.40
CV	11.64	30.05	17.57	12.97	9.45	6.77	11.69	5.64

## Discussion

Yixian Formation is characterised by a high ratio of *H. drepanoides*, a colored cockroach species, possibly indicating warm and moist climate.

In the wing venation for *H. drepanoides*, the total number of veins (excluding SC and A) reaching the wing margin is found to be the least variable character, suggesting active flight, supported by the asymmetrical difference between left and right forewings. Higher variability of the hind wing might suggest *habroblattula* was an advanced genus, with vein strength control mechanisms.

*Habroblattula* gen. nov. is most closely related to *Svabula* Vršanský, 2005, supporting its near the J/K boundary age.

## Acknowledgements

We sincerely thank Dr. Peter Vršanský (Geological Institute SAS, Bratislava and Paleontological Institute RAS, Moscow) for revision of the manuscript, valuable consultations and practical help. Our research has been supported by grants from the National Nature Science Foundation of China (No. 30025006, 30370184, 30430100), Scientific Research Key Program (KZ200410028013), PHR Project of Beijing Municipal Commission of Education and VEGA 6002 and MVTs.

## Reference

- Carpenter, F.M. (1953) The geological history and evolution of insects. *American Scientist*, 41, 256–270.
- Chen, P.j., Wang, Q.f., Zhang, H.C., Cao, M.Z., Li, W.B., Wu, S.Q. & Shen, Y.B. (2004) Discussion on the stratotype of Jianshangou of Yixian Formation. *Science in China Series, D, Earth Sciences* 34, 883–895. [in Chinese].
- Cifuentes-Ruiz P., Vransk P., Vega F.J., Cevallos-Ferriz S.R.S., Gonzles-Soriano E. & de Jess, C.R.D. (2006) Campanian terrestrial arthropods from the Cerro del Pueblo Formation, Difunta Group in northeastern Mexico. *Geologica Carpathica*, 57, 5, 347–354.
- Ding, D.H., Zhang, L.D., Guo, S.Z., Zhang, C.J., Peng, Y.D., Jia, B., Chen, S. W. & Xing, D.H. (2001) The stratigraphic sequence and fossil bearing horizon of the Yixian Formation in western Liaoning, China. *Geology and Resources*, 10, 193–198.
- Hou, L.H., Martin, L.D. & Zhou, Z.H. (1999) A diapsid skull in a new species of the primitive bird *Confuciusornis*.

- Nature*, 399, 672–682.
- Liang, J.H. (2006) The fossil Blattaria of China—a review of present knowledge In: *Acta Zootaxonomica Sinica* 31, 102–108. [in Chinese].
- Li, P.X., Cheng, Z.W. & Pang, Q.Q. (2001) The horizon and age of Confuciusornis in Beipiao, western Liaoning. *Acta Geologica Sinica*, 75, 1–13. [in Chinese].
- Pang, Q.Q., Li, P.X., Tian, S.G. & Liu, Y.Q. (2002) Discovery of ostracods in the Dabeigou and Dadianzi Formations at Zhangjiagou, Luanping County, northern Hebei Province of China and new progress in the biostratigraphic boundary study. *Geological Bulletin of China*, 21, 329–336. [in Chinese].
- Ren, D., Lu, L.W., Ji, S.A. & Guo, Z.G. (1995) Faunae and Stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas. *Seismic Publishing House*, Beijing, China, 222pp.
- Ren, D., G, Z.G., Lu, L.W., Ji, S.A., T, F., Jin, Y.G., Fang X.S. & Ji, Q. (1997) A further contribution to the knowledge of the Upper Jurassic Yixian Formation in western Liaoning. *Geological Review*, 43, 449–459. [in Chinese].
- Sun, G., Dilcher, D.L., Zheng, S.L. & Zhou, Z.K. (1998) In search of the first flowers: a Jurassic angiosperm, *Archaeofructus*, from Northeast China, *Science*, 282, 1692–1695.
- Swisher, C.C., W, Y.Q., Wang, X.L., Xu, X. & Wang, Y. (1999) Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature*, 400, 58–61.
- Tan, J.J. (1980) Geological history of insects. *Acta Zootaxonomica Sinica*, 5, 1–12. [in Chinese].
- Vishniakova, V.N. (1982) Jurassic cockroaches of the new family Blattulidae from Siberia. *Palaeontological Journal*, 2, 67–77.
- Vršanský, P. (1997) Piniblattella gen.nov.—the most ancient genus of the family Blattellidae(Blattodea) from the Lower Cretaceous of Siberia. *Entomological Problems*, 28(1), 67–79.
- Vršanský, P. (1998) Lower Cretaceous Blattodea. Abstracts of the First International Palaeoentomological conference, Moscow, 44.
- Vršanský, P. (1999a) Two new species of Blattaria (Insect) from the Lower Cretaceous of Asia, with comments on the origin and phylogenetic position of the families Polyphagidae and Blattulidae. *Entomological Problems*, 30, 85–91.
- Vršanský, P. (1999b) Lower Cretaceous Blattaria. In: Vransk, P. (ed.) 1999. *Proceedings of the First International Palaeoentomological Conference*, Moscow 1998. Bratislava, 167–176.
- Vršanský, P. (2000) Decreasing variability—from the Carboniferous to the present! (Validated on Independent Lineages of Blattaria) *Paleontological J. Vol. 34 Suppl. 3*, 374–379.
- Vršanský, P. & Ansoerge, J. (2001) New Lower Cretaceous polyphagid cockroaches from Spain (Blattaria, Polyphagidae, Vitisminae subfam. nov. ) *Cretaceous Research*, 22, 157–163.
- Vršanský, P. (2002a) Origin and the early evolution of mantises. *Amba projekty*, 6, 16PP.
- Vršanský, P., Vishniakova, V.N. & Rasnitsyn, A.P. (2002b) Order Blattida Latreille, 1810. The cockroaches. In: Rasnitsyn, A.P. & Quicke, D.L. J. (eds.). *History of insects. Kluwer Academic Publisher*, Dordrecht, 263–271.
- Vršanský, P. (2003) Unique assemblage of Dictyoptera (Insecta-Blattaria, Mantodea, Isoptera) from the Lower Cretaceous of Bon Tsagaan Nuur in Mongolia. *Entomological Problems*, 1–2, 119–151.
- Vršanský, P. (2004) Transitional Jurassic/Cretaceous cockroach assemblage (Insecta, Blattaria) from the Sharteg in Mongolia *Geologica Carpathica*, 55,6, 457–468.
- Vršanský, P. (2005a) A fossil insect in a drilling core sample-cockroach *Kridla stastia* gen.et sp. nov. (Blattulidae) from the cretaceous of the Verkhne-Bureinskaya Depression in Eastern Russia. *Entomological Problems*, 35, 115–116.
- Vršanský, P. (2005b) Lower Cretaceous cockroaches and mantids (Insecta: Blattaria, Mantodea) from the Sharin-Gol in Mongolia. *Entomological Problems*, 35, 163–167.
- Vršanský, P. & Ansoerge, J. (2006) Lower Jurassic cockroaches (Insecta, Blattaria) from Germany and England. *African Invertebrates*, 47, 27pp.
- Wang, W.L., Zhang, L.J., Zheng, S.L., Zheng, Y.J., Zhang, H., Li, Z.T. & Yang, F.L. (2004) A new study on the stratotype and biostratigraphy of the Yixian stage in Yixian, Beipiao region, Liaoning. Establishment and study of stratotypes of the Yixian Stage. *Acta Geologica Sinica*, 78, 433–447. [in Chinese].
- Wang, W.L., Zhang, L.J., Zh.eng, S.L., Zheng, Y.J., Zhang, H., Li, Z.T. & Yang, F.L. (2005) The age of the Yixian Stage and the boundary of Jurassic-Cretaceous—the establishment and study of stratotypes of the Yixian Stage. *Geological Review*, 51, 234–242. [in Chinese].
- Zheng, S.L., Zheng, Y.J. & Xing, D.H. (2003) Characteristics, age and climate of late Jurassic Yixian flora from western Liaoning. *Journal of Stratigraphy*, 27, 233–241. [in Chinese].
- Zhou, Z.H., Barrett, P. M. & Hilton, J. (2003) An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, 421, 807–814.

