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Source: Acta Palaeontologica Polonica, 53(1) : 129-136

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2008.0109>

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New blattarians and a review of dictyopteran assemblages from the Lower Cretaceous of Mongolia

PETER VRŠANSKÝ



Vršanský, P. 2008. New blattarians and a review of dictyopteran assemblages from the Lower Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 53 (1): 129–136.

Dictyopteran assemblages (cockroaches, mantises and termites) from Mongolia were uniform, being composed of the same genera throughout the Early Cretaceous (more than 30 million years), corresponding to the “dry and warm Baissa type” assemblages from Siberia. The assemblage from Shin-Khuduk is exceptional, consisting of a single identifiable blattulid species, *Vrtula sama* gen. et sp. nov. Assemblages from Eastern Erdenyi-Ula, Khurilt, Kholbotu-Gol, and Shar-Tologoy are composed of species already known from the richest Lower Cretaceous locality Bon Tsagaan, but species representation in the various assemblages differs considerably. *Nuurcala srneci* sp. nov. from Khurilt Bed 210/24, with a forewing length under 12 mm, is the smallest and best-studied example of the cosmopolitan Mesozoic family Caloblattinidae. The last occurrence of the predominantly Palaeozoic family Phylloblattidae is reported from Bon Tsagaan.

Key words: Blattaria, Mantodea, Isoptera, cockroaches, Cretaceous, Mongolia.

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Introduction

Winged insects are among the most diverse organisms on our planet (Torsvik et al. 2002), with a fossil record extending back to the Mississippian (ca. 350 Ma). The cockroaches, with about 4300 known living (Roth 2003) and 1500 fossil species [some 500 more species than the estimate of Vršanský et al. (2002)], are among the least diverse of insect groups, but in terms of numbers of individuals they are often dominant (Vršanský et al. 2002). Together with their descendants, termites, they are important at the basic level of the decomposition chain in advanced ecosystems such as rainforests (Zherikhin 1993).

The Mesozoic era was an important period in dictyopteran insect evolution, with the origination of both eusocial termites (Vršanský et al. 2002) and predatory mantises (Vršanský 2002) from a cockroach stem-group (Vršanský et al. 2002) and the diversification of major living cockroach lineages. Mesozoic cockroaches are a monophyletic group characterised by regular venation of the wings with intercalary veins and by the presence of a derived, often shortened ovipositor. They belong to the following families: (1) the stem family Caloblattinidae (ca. 500 known species distributed among ca. 100 genera) which was derived from the Phylloblattidae; (2) the Blattulidae, small cockroaches with simplified venation and a short external ovipositor (14 genera with ca. 300 species); (3) the carnivorous Raphidiomimidae (2 genera with described 3 species); (4) the beetle-like Umenocoleidae (7 genera with 12 species); the oldest representatives of the Blatto-

idea, (5) the Mesoblattinidae (16 genera with 22 species); (6) the minute (5–6 mm) Vitisminae of obscure origin (5 genera with 8 species); and (7) Liberiblattinidae, the stem family for all living families, including termites and mantises (12 genera with 12 species). The oldest living families with a Mesozoic origin are the Cretaceous Blattellidae (a single Mesozoic genus with 5 species) and the Polyphagidae (a single species).

Cretaceous dictyopterans are best described from the Dzun-Bain (Dzuunbayan) Formation in Mongolia where they are quite abundant, very diverse and include one described termite species (Ponomarenko 1988), 3 mantodean species (Gratshev and Zherikhin 1993; Vršanský 2002), and 20 described species of cockroaches (Vršanský 1997, 1999, 2003). The aim of the current paper is to compare the taxonomic composition of cockroach faunas from several localities within a single geographical region but from different environments and, possibly, of slightly different ages. This may shed some new light on the pattern of spatial and temporal distribution of Cretaceous cockroaches.

Material and methods

Fifty-four new specimens of cockroaches (six complete; Table 1), one mantis and two termites from Bon Tsagaan, Eastern Erdenyi-Ula, Khurilt, Kholbotu-Gol, Shar-Tologoy, and Shin-Khuduk have been studied and compared with nearly 700 dictyopteran specimens (21 mantodeans of the family Chateessidae; 3 termites of the family Hodotermitidae; and

Table 1. Distribution of dictyopterans in the Early Cretaceous of Mongolia. Distributions of 9 specimens from the Gurvan Ereny Nuur, 673 specimens from the Bon Tsagaan-Nuur and 34 specimens from the Sharin-Gol are given elsewhere (Vishniakova 1986, Vrřanský 2003, 2005b). Abbreviations: B, body; comp, complete specimen; FW, forewing; HW, hindwing; P, pronotum.

| Locality | Shin-Khuduk | E. Erdenyi-Ula | Khurilt | Khurilt | Kholbotu-Gol | Shar- Tologoy | | | | Total |
|--|-----------------|----------------|---------|---------|--------------|---------------|---------|-----------|------|-----------------|
| Bed | | 388/1 | 207/ 15 | 210/ 24 | 283/11 | 368/4-5 | 381/5-6 | 382/5 | ? | |
| <i>Nuurcala srneci</i> sp. nov. | | | | 1-comp. | | | | | | 1 |
| <i>Liadoblattina mongolica</i> Vrřanský, 2003 | | | | | | | | 2-FW-(1P) | | 2 |
| <i>Archimesoblatta altera</i> (Vrřanský, 1997) | | | | | | 1-FW | 2-FW | | 2-FW | 5 |
| <i>Elisama tsaganica</i> (Vrřanský, 1999) | | 1-FW | 2-FW | | | | | | | 3 |
| <i>Elisama parallela</i> Vrřanský, 2003 | | | 2-HW | | 3-HW | 3-FW | | | | 8 |
| <i>Vrtula sama</i> sp. nov. | 24- 9HW 5-comp. | | | | | | | | | 24 |
| <i>Praeblattella dichotoma</i> Vrřanský, 2003 | | | | | | 3-FW | | | 1-FW | 4 |
| <i>Cretophotina mongolica</i> Gratshev and Zherikhin, 1993 | | | | | | | | 1-FW | | 1 |
| <i>Valditermes acutipennis</i> Ponomarenko, 1988 | | | | | | | | | 1-FW | 1 |
| Unidentified | 4 | | | | | | | 1P | | 5 |
| Total | 28(9HW) | 1-FW | 4-(2HW) | 1-comp. | 3-HW | 7-FW | 2-FW | 4-(2P) | 4-FW | 54- 14HW 7P, 6B |

representatives of the cockroach families Caloblattinidae, Blattulidae, Liberiblattinidae, Mesoblattinidae, Vitisminae, and Blattellidae) from different Mongolian localities (see Sinitza 1993 for details on localities).

In contrast to living cockroaches, where some individuals can have wings half the length of other individuals of the same species (Schneider 1977, 1978), species of Mesozoic cockroaches can easily be recognised based on their discrete forewing size (Vrřanský 2000) and on the range in the total number of veins in the forewing. The occurrences of cockroaches in specific beds are given in Table 1.

Institutional abbreviation.—PIN, Paleontological Institute, Russian Academy of Sciences, Moscow.

Other abbreviations.—A, anal; B, body; comp., complete specimen; FW, forewing; HW, hindwing; P, pronotum. Wing venation: CuA, cubitus anterior; CuP, cubitus posterior; M, media; R, radius; RS, radial sector; Sc, subcosta; ±, part and counterpart of a specimen.

Geological setting

The best preserved dictyopteran assemblages come from deposits in the lower part of the Shar-Teg palaeolake (ca. 100 km²), characterised by a high water level with drifts of material from temporary floods. The shoal stage, interrupted by a short-term increase in lake area, was characterised by the appearance of vast silty plains overgrown with horsetails, and by small lakes with oxyphilous conditions. The final stage resulted in the lake silting-up and becoming infilled, and the formation of fern marshes (for details see Gubin and Sinitza 1996; and the lithological profile at Fig. 1 herein).

This paper deals with fossils from three partially time-

overlapping formations, the Dzun-Bain, Shin-Khuduk, and Sharin-Gol formations, each of which includes several members represented at several localities.

The Dzun-Bain Formation is exposed at the localities Bon Tsagaan, Eastern Erdenyi-Ula, Khurilt, Kholbotu-Gol, and Shar-Tologoy (Vrřanský 2003; see also Fig. 1 and Table 1 herein). It begins with sediments of an intermittent lake deposited in an arid climate (Khurilt Member), sourced by erosion of volcanic Palaeozoic bedrock. The lacustrine sediments are composed of clastic material containing easily re-worked fragments of plagioclase andesitic-basalts, numerous clear acute tables of plagioclase, potassium feldspars, and abundant quartz. Clastic material was transported into the lake by temporary floods and also by sheet wash, as is evident from the presence of angular material in the sandstones and marls. A clay fraction transported from the land was common (Sinitza 1993). Later, but still stratigraphically within the Khurilt Member, the lake deepened and its sediments are characterised by cyanophytes, gastropods, and ostracods, while bivalves were apparently absent. The fauna of the entire Khurilt Member is characterised by the presence of the beetle *Coptoclava longipoda* Ping, 1928 (Coleoptera: Coptoclavidae) and the dragonfly *Hemeroscopus baissicus* Pritykina, 1977 (Odonata: Hemeroscopidae), both indicating a Barremian–Aptian age. Characteristic for this unit is also the presence of plant remains (e.g., *Baissia*) and lycoperid fishes. Absent is the mayfly genus *Ephemeropsis* which is characteristic of the Shin-Khuduk Formation (see below). The insect assemblages from the Khurilt Member are characterised by an abundance of cases and imagos of caddisflies (Trichoptera). Higher in the section at Kholbotu-Gol sediments indicate that the lake became intermittent again but, in contrast to the Khurilt Member, deposition occurred in humid climatic conditions (Sinitza 1993).

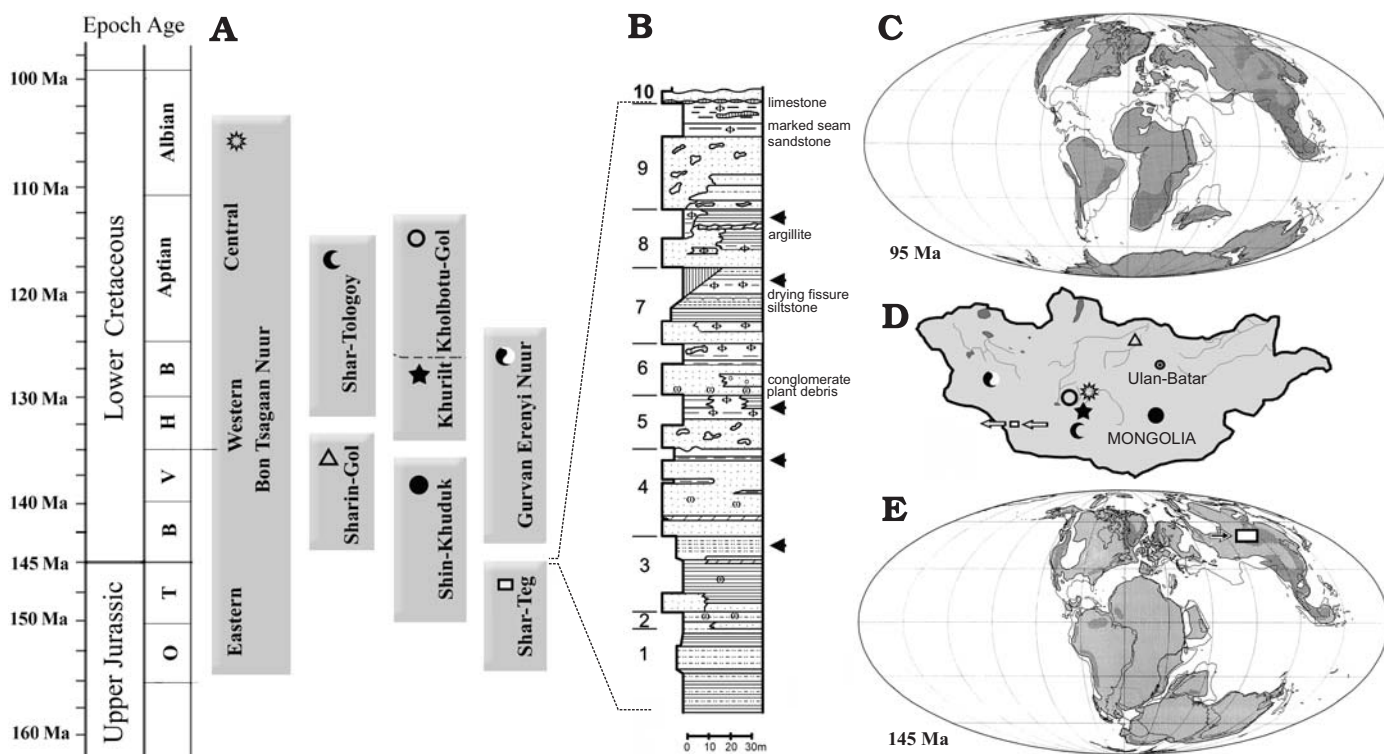


Fig. 1. Sketch map of Mongolia showing the localities discussed in the text. The localities Bon Tsagaan, Eastern Erdenyi-Ula, Khurilt and Kholbotu-Gol, and Shar-Tologoy (A, D) correspond to respective stratigraphical members, all within the Dzund-Bain Formation. The Shar-Teg locality and section (grey column) corresponds to both Shar-Teg Formation, the lithological profile (B), modified after Gubin and Sinitza (1996) shows the subordinated unit, while the numbers correspond to sedimentary, orbital and/or solar driven sedimentary cycles. Arrows show the occurrence of insects in respective beds (layers are the smallest recognisable units within respective beds, which in non-marine aquatic environments were usually deposited in a time scale of one to thousands of years). Ages of sediments are abbreviated as follows: K, Kimmeridgian; T, Tithonian; B, Berriasian; V, Valanginian; H, Hauterivian; B, Barremian. Palaeogeographic maps (C, E), after Smith et al. (1994). Locality symbols: sun, Bon Tsagaan Nuur; moon, Shar Tologoy; triangle, Sharin-Gol; star, Khurilt; ring, Kholbotu-Gol; circle, Shin-Khuduk; jingjang, Gurvan Erenyi Nuur; rectangle, Shar-Teg.

The Shin-Khuduk Formation is composed of dark grey, red and brown, whitish, sandy, cemented conglomerates with sandstones and marls of lacustrine origin. The formation crops out at Shin-Khuduk where the diverse terrestrial biota comprises 12 orders with ca. 40 families (estimate based on ca. 500 collected specimens), dominated by beetles, bugs and cockroaches. The most characteristic fossils in this formation are mayflies (*Ephemeropsis*), chaoborid and chironomid midges, notonectid and enicocorid bugs (*Clypostemma* and *Enicocoris* respectively), and coptocladid and ?hydrophilid beetles (*Coptoclava* and *Cretataenia* respectively).

The Sharin-Gol Formation crops out at Sharin-Gol and is characterised by the presence of coal layers at the base of the section. These layers yield fossil plants including the taxacean *Cephalotaxopsis*, podozamitacean *Podozamites*, ginkgoacean *Ginkgo*, and *Pityophyllum* and *Pityospermum* of uncertain affinities, as well as bivalves and fishes. Very common are terrestrial insects (e.g., 11 families of Coleoptera and 7 families of Hymenoptera), whereas aquatic insects are rather rare. The Gurvan Eren Formation crops out at Gurvan Erenyi Nuur. The formation occurs in a NW-SE oriented graben-synclinal structure and is composed of red and varicoloured Jurassic sediments followed by grey finely laminated Cretaceous sedi-

ments, yellow sandstones and red beds representing two different sedimentary cycles of a single waterbody, with arid intervals of enhanced salinity. For details see Sinitza (1986).

Systematic palaeontology

Order Blattaria Latreille, 1810

Superfamily Caloblattinoidea Vršanský and Ansoerge in Vršanský (2000)

Family Caloblattinidae Vršanský and Ansoerge in Vršanský (2000)

Genus *Nuurcala* Vršanský, 2003

Type species: *Nuurcala popovi* Vršanský, 2003. Bon Tsagaan Nuur, Bed 87/8, Mongolia; Barremian or Aptian.

Nuurcala srneci sp. nov.

Fig. 2.

Derivation of the name: After my friend Ivan Srnec (former employee of the Slovak Embassy in the Russian Federation) and his family, who offered kind assistance during my research.

Holotype: PIN 3790/6. A complete female.

Type locality: Khurilt, Mongolia.

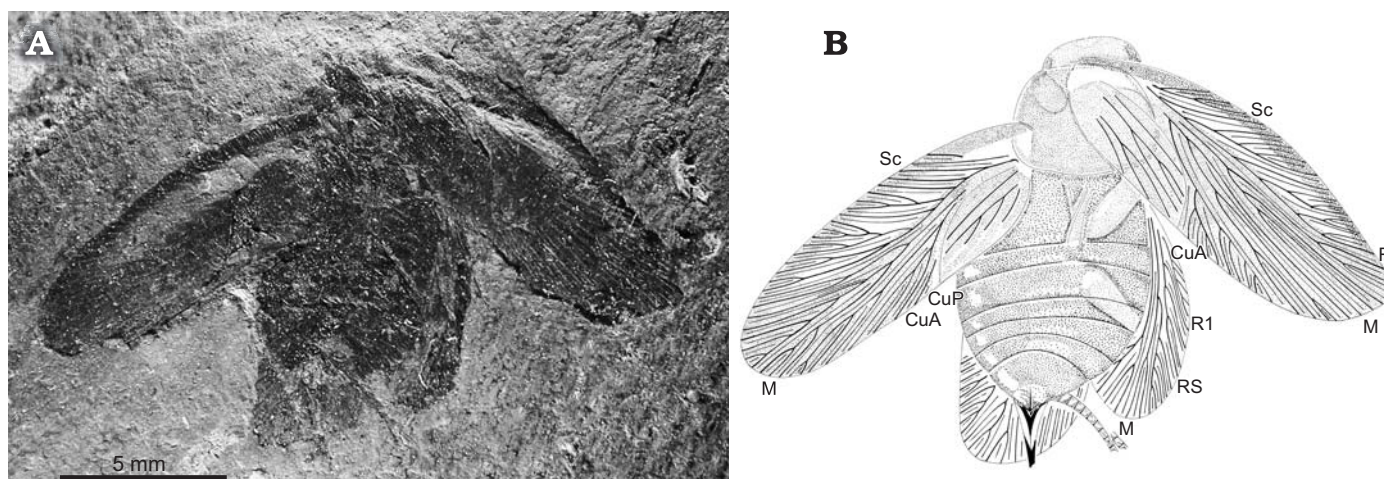


Fig. 2. Caloblattinid cockroach *Nuurcala srneci* sp. nov. Holotype, female, PIN 3790/6. Bed 210/24, Khurilt, Mongolia, Barremian or Aptian.. Photograph (A) and explanatory drawing (B). Abbreviations: CuA, cubitus anterior; CuP, cubitus posterior; M, media; R, radius; R1, radius anterior; RS, radial sector; Sc, subcosta.

Type horizon: Bed 210/24, Khurilt Member, Dzund-Bain Formation, Barremian or Aptian, Early Cretaceous.

Material.—Holotype only.

Diagnosis.—The genus *Nuurcala* is characterized by its small size and by having both pairs of wings shortened, a large head and characteristic colouration. *N. srneci* differs from its only known congener, *N. popovi* Vršanský, 2003, by the lack of terminal dichotomies on the major veins, and reduced venation in all vein systems. The total number of veins meeting the wing margin before the anal veins is about 35 (max. 37), whereas it is more than 50 in *N. popovi*. *Nuurcala srneci* has short forewings (length/width = 11.5–12.1/3.6–4.1 mm), while the forewings of *N. popovi* are much longer (length/width = 17.0–26.0/4.7–7.3 mm). The head of *N. srneci* is of roughly the same size as that of *N. popovi*, i.e., comparatively large (width 3.4 mm, or $0.7 \times$ versus $0.5 \times$ pronotal width in *N. popovi*), and the pronotum (as in Fig. 2) (3.4/4.6 mm or $0.37 \times$ versus $0.3 \times$ wing length in *N. popovi*) is more derived in form, i.e., transversely asymmetrical, with respect to *N. popovi* (Vršanský 2003: 121, fig.1).

Description.—Head large, 2.9 mm wide. Pronotum almost quadrate in outline (width/length: 4.4/3.4 mm), all margins slightly convex. Forewings asymmetrical (not as a result of deformation, but due to the number of veins in respective vein systems and their branching pattern), left wing without branched posterior CuA branch, narrow with rounded apex; right wing comparatively wide, with apex subacute and richly terminally branched CuA veins. Characteristics: Left wing Sc: 3±; R 16; M 11; Cu 8; Right wing Sc: 3±; R 13; M 6; Cu 14. Colouration as in Fig. 2A, B. Hindwings with reduced venation (Sc 5+; R 4–5+ [hardly visible]; RS 5+; M 2–5+ [right wing]; Cu 7+). Body wide (6.0 mm), terminal abdominal segments with strongly curved posterior and anterior margins. Female with long (2.1 mm or more) external ovipositor and cerci at least 3.9 mm long, with up to 13 or more subequal cercomeres.

Discussion.—The genus is characterised by several apomorphies for the family, such as the short forewings and hindwings, small pronotum and large head (the oldest and presumed most primitive representatives of the family as well as their precursors in Phylloblattidae have large pronotums and small heads), sophisticated colouration similar to taxa close to *Rhipidoblattina* (Caloblattinidae), and richly branched CuA veins in the right wing only (this asymmetry is apparently derived).

The long external ovipositor and long cerci are plesiomorphic characters, typical of primitive and early cockroaches. The small size of this new species might indicate a more derived and specialised habitat, or a free-living and active life-style when compared with its congener; however, the stronger asymmetry of the forewings of *N. srneci* does not support this conclusion. Generally, asymmetry increases with decrease in flying abilities, as shown in several cockroach families. In this respect the members of this family were perhaps weak fliers. Notably in the present genus, the asymmetry of wings is expressed as terminal branches of CuA in the right forewing. Reduced venation and smaller size are strong apomorphies and thus *N. srneci* is interpreted as the sister taxon or a descendant of *N. popovi*.

Superfamily Blattuloidea Vishniakova, 1982

Family Blattulidae Vishniakova, 1982

Genus *Vrtula* nov.

Derivation of the name: From the Slovakian *vrt*, a drill, and the genus name *Blattula*. *Vrtula* in Slovakian also means propeller, alluding to its improved flight abilities.

Type species: *Vrtula sama* sp. nov.

Diagnosis.—Differs from all other representatives of the family in having extremely elongated wings, the forewing being $3.3\text{--}4.0 \times$ longer than wide, with the clavus reaching the basal third of the wing and anal veins densely distributed (autapomorphies). The dark macula in CuA is synapomor-

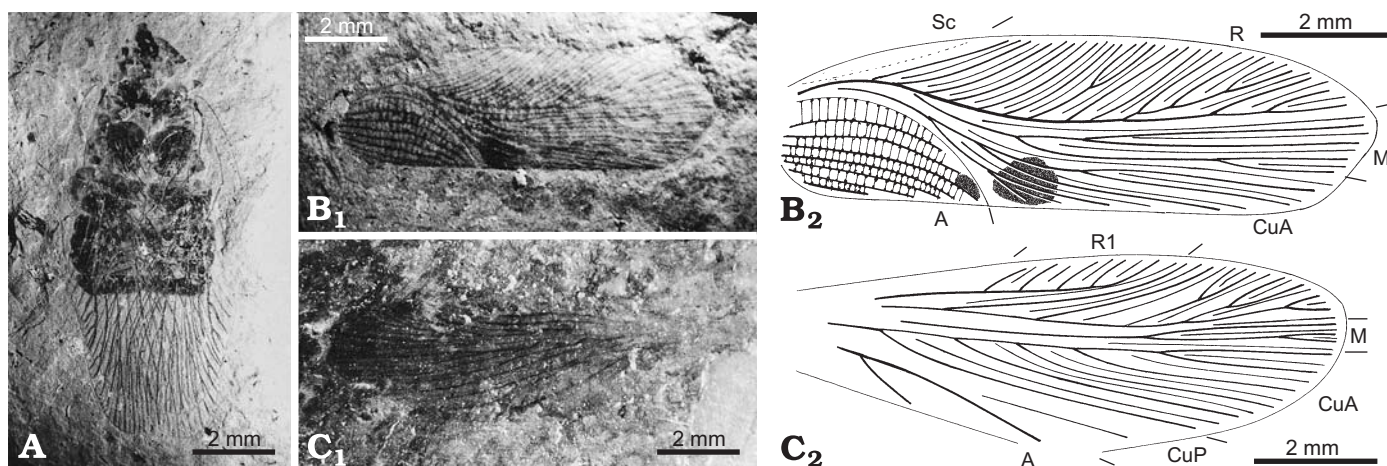


Fig. 3. Blattulid cockroach *Vrtula sama* gen. et sp. nov. A. PIN 3664/2201, a complete specimen. B. Holotype, PIN 3664/2216; photograph (B₁) and explanatory drawing (B₂). C. PIN 3664/2220, a hindwing: 9 mm; photograph (C₁) and explanatory drawing (mirrored) (C₂). All from Shin-Khuduk, Mongolia. Early Cretaceous. Abbreviations: A, anal; CuA, cubitus anterior; CuP, cubitus posterior; M, media; R, radius; R1, radius anterior; Sc, subcosta.

phic with *Elisama* Giebel, 1856, which lacks any autapomorphies and may be directly derived from *Blattula* Handlirsch, 1906; *Vrtula* is thus probably derived from *Elisama*, which is paraphyletic with respect to *Vrtula*.

Description.—Head large, body wider than forewing width. Forewing elongated, on average $3.5 \times$ longer than wide. Sc simple and very short. R with most veins simple, RS not differentiated; M reduced to a few long straight branches; CuA reaching the apical narrow space of the wing. A numerous, simple. Cross-veins distinct in the clavus. Dark spot present at the base of the CuA area. Hindwing Sc simple; R1 and RS differentiated—i.e., stem of the anterior branches of R widely separated; M compressed; CuA with simple branches; CuP simple; A1 branched.

Vrtula sama sp. nov.

Fig. 3.

Derivation of the name: Shortened from *Elisama* meaning alone; also in Slovakian to be in love with, alluding to its unique dominance in the Shin-Khuduk assemblage.

Holotype: PIN 3664/2216. Isolated right forewing.

Type locality: Shin-Khuduk, Central-Gobi aymag, Mongolia.

Type horizon: Shin-Khuduk Formation, Lower Cretaceous.

Additional material: Forewings: PIN 3664/ 2206, 2219, 2216, 2224, 2215, 2218, 2214c, 2225, 2212. Hindwings: PIN 3664/ 2203, 2204, 2205±, 2207= 2210, 2209, 2211, 2213, 2220, 2226. Complete specimens: PIN 3664/ 2201, 2202, 2208, 2217 larva, 2222.

Description.—Body width up to 3.4 mm. Forewing length/width 8.0–14.0/ 2.5–3.3 mm. Sc simple; R slightly curved, with 12–17 branches; M 3–4; CuA 5–8, cubital area with dark spot. Clavus with about 7 simple A. Hindwing Sc 1; R1 4–6; RS 6–8; M 3–5; CuA 6–7, CuP simple. A1 branched (A2 and veins of the vannus not preserved).

Family Phylloblattidae Schneider, 1983

Gen. et sp. indet.

Fig. 4.

Material.—Entire basal half and anterior part of distal half of right forewing (PIN 3559/8013) from Bon Tsagaan Nuur (Barremian or Aptian, Early Cretaceous).

Description.—One of the largest known Mesozoic cockroaches, forewing length up to 50 mm. Forewing venation rich, with a typical connection of main branches with intercalary veins (Fig. 4B, C). R not differentiated into R1 and RS, M moderately rich, CuA dense, extremely expanded with local irregularities in spacing of veins.

Discussion.—The specimen under study can be referred to Phylloblattidae, which is easily distinguishable from all other groups of Mesozoic Dictyoptera, based on the persistence of the following plesiomorphic characters: curved homonomous veins and intercalaries with irregular spacing, and the presence of terminal branchlets in several branches of CuA. The presence of a typical venation pattern with intercalary veins is apomorphic with respect to all Palaeozoic families.

This specimen cannot be formally distinguished from Palaeozoic representatives of the family, although the time difference of more than 110 million years suggests that it could be a new genus and species.

Discussion

The oldest assemblage known to contain Mesozoic dictyopterans of Cretaceous and/or Recent type (mantodeans, Blattellidae and Vitismidae and possibly Umenocoleidae) occurs in the Tithonian (Upper Jurassic) of Shar-Teg in Mongolia, where 8 cockroach and a single mantodean species have been identified (Vršanský 2002, 2004). This transitional assemblage is characterised by the presence of derived taxa such as the earliest known specimen of the mantodean, *Elisama* and some derived Mesoblattinidae. The assemblage is of low diversity and contains numerous specimens with deformities (mutations), typical also of modern destabilised

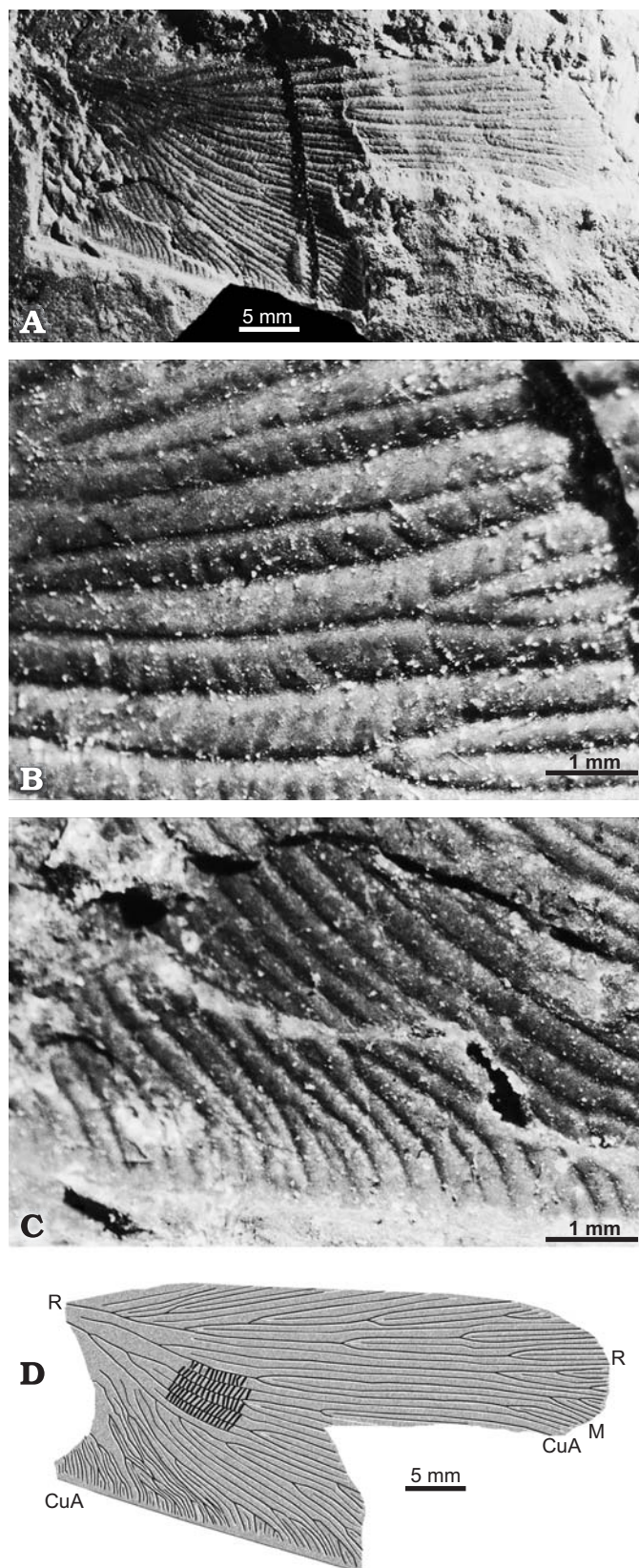


Fig. 4. Right forewing of an unidentified genus and species of the family Phylloblattidae. PIN 3559/8013 from Bon Tsagaan, Mongolia, Barremian or Aptian. Whole specimen (A), details of the cubital area (B, C), and explanatory drawing (D). Abbreviations: CuA, cubitus anterior; M, media; R, radius.

ecosystems (Vršanský 2005a). Apparently similar assemblages of the same age have been described from several localities in the Yixian Formation of northern China (Ren et al. 1995; Wang et al. 2007a, b).

The oldest Cretaceous assemblage in Mongolia occurs in the Sharin-Gol Formation. The following taxa are present: the typically Cretaceous mantodean *Cretophotina selenginensis* Vršanský, 2002 (Chaeteessidae); the smallest and apparently most advanced member of Vitisminae (*Vitisma orientalis* Vršanský, 2005b) with the most reduced venation; and two representatives of Blattulidae, *Svabula vzorkovana* Vršanský, 2005b, a monotypic genus known only from this locality, and the widespread genus *Elisama*. The blattellids are represented by the derived species *Piniblattella sharingolensis* Vršanský, 2005b and caloblatinids by *Shartegoblattina colorata* Vršanský, 2005b, the latter being a species belonging to a genus otherwise known only from the Tithonian.

The assemblage found in the Shin-Khudukh Formation is of roughly the same age (Sinitza 1993). The presence of a single species (*Vrtula sama*) which is abundant (24 specimens) and highly variable is extremely unusual, especially when the quantity of other insects in the Shin-Khudukh Formation is considered. Such a strong dominance is generally characteristic of assemblages exhibiting taphonomic bias but may possibly be natural for some Triassic localities (Papier and Grauvogel-Stamm 1994). The burial of a single generation is rather unlikely because no single species of the family Blattulidae has been documented to show such a high individual variability in a single generation. Neither forewings nor hindwings show any characteristics (e.g., strong incrustation) that might favour their selective preservation. Such a single species-dominated assemblage is especially surprising for the otherwise extremely conservative family Blattulidae, with only 14 identified genera throughout its 100 million year history (Vršanský 2002; Cifuentes et al. 2006; Wang et al. 2007a, b; Anisutkin and Gorochoy 2008). The occurrence of additional species in this assemblage cannot be ruled out, since there are 4 indeterminate fragments.

The assemblage of the Gurvan Ereny Nuur described by Vishniakova (1986) consists of *Elisama tsaganica*, *E. gurvaniensis* (Vishniakova, 1986), and two representatives of the genus *Gurvanoblatta* (*G. mongolica* Vishniakova, 1986 and *G. ichesnurensis* Vishniakova, 1986) within the family Libri-blattinidae. These species are absent from other localities of similar age.

The dictyopteran assemblages from different localities (Eastern Erdenyi-Ula, Khurilt, Kholbotu-Gol, and Shar-Tologoy) in the Dzun Bain Formation are generally of similar taxonomic composition. The exceptions are Khurilt Bed 210/24, yielding a single specimen of *Nuurcala srneci*, and presence at Shar-Tologoy of the termite *Valditermes acutipennis* Ponomarenko, 1988 (Hodotermitidae). Although these assemblages contain similar taxa, the contribution of particular species to the assemblages varies significantly. These differences were most probably caused by ecological factors, especially progressive increase of the humidity.

The composition of dictyopteran assemblages helps in local ecostratigraphical correlation between outcrops in the Lower Cretaceous of Mongolia. Especially useful seems to be the distributional pattern of *Elisama*. The Khurilt Bed 207/15 and the Kholbotu-Gol assemblages may correspond in time to Bon Tsagaan Beds 74 and/or 78, or are slightly older due to the absence of derived taxa. All the Shar-Tologoy assemblages contain archaic taxa compared to the Barremian or Aptian taxa from the Bon Tsagaan. *Elisama tsaganica* and *Elisama parallela* from the Khurilt assemblage have wing characteristics identical to specimens from the type locality (Bon Tsagaan).

Two species of *Elisama* (*E. parallela* and *E. tsaganica*) occur in Khurilt Bed 207/15 where other cockroaches are absent. The Kholbotu-Gol assemblage is represented solely by *E. parallela*. These assemblages may correspond to Beds 74 and 78 of Bon Tsagaan where *E. parallela* dominates and *E. tsaganica* is subdominant while other species of *Elisama* are rare. The absence of advanced *Elisama* species at Khurilt and Kholbotu-Gol may also indicate their older age. Both localities contain an impoverished *Elisama* fauna and were postulated by Sinitza (1993) to differ in age and palaeoclimate. Sinitza (1993) also interpreted the Khurilt assemblage as the older and more arid, and the Kholbotu-Gol assemblage as younger and more humid. It is peculiar that both assemblages are dominated by a single species, *E. parallela* (see Table 1). Only a single forewing of *Elisama tsaganica* has been found in the Eastern Erdenyi-Ula assemblage. In the Bon Tsagaan assemblage, *E. parallela*, *E. tsaganica*, and *Tarakanula shcherbakovi* Vršanský, 2003 are common, while two additional species, *E. incerta* Vršanský, 2003 and *E. grandis* Vršanský, 2003, are rare, limited to one and two beds respectively.

The Shar-Tologoy assemblages come from layers that differ slightly in fossil content. Layer 368/4–5 contains *Archimesoblatta altera*, *Elisama parallela*, and *Praeblattella dichotoma*, layer 381/5–6 contains only *A. altera*, while layer 382/5 contains *Liadoblattina mongolica* and the mantodean *Cretophotina mongolica*. These assemblages differ from any of the 17 beds at Bon Tsagaan. The presence of mostly archaic species at Shar-Tologoy and the absence of derived species such as *Praeblattella ponomarenkoi* Vršanský, 2003 might suggest that this assemblage is slightly older than that from Bon Tsagaan (Barremian or Aptian). *P. ponomarenkoi* dominates Barremian and/or Aptian beds at Bon Tsagaan, except for Bed 78 where this species occurs but is not dominant. This abundance is striking and can hardly be explained by taphonomic reasons. *P. ponomarenkoi* is the most derived mesoblattinid known from the assemblages discussed and therefore it is reasonable to argue that the Bon Tsagaan assemblages represent the youngest fauna, although the basalmost beds (22–23) still contain exclusively more archaic taxa and are possibly much older. *Praeblattella* is absent in the Early Barremian Eurasian assemblage of Montsec in Spain (Ansorge 1993; Martínez-Delclòs 1991; Rasnitsyn and Martínez-Delclòs 2000), although it is present in the Berriasian of England and the Valanginian of Siberia (Vršanský 1999). This raises questions about the narrow stratigraphic ranges of species of *Prae-*

blattella; most probably *Praeblattella* was dependent on the presence of forests (Vršanský 2003). The cockroaches and mantis found in different layers of the Khurilt Member belong to the same species, and differences in the composition of assemblages from particular beds are most probably due to the statistically insignificant numbers of specimens available. Fragmentation of cockroach bodies at burial occurs routinely, producing a dominance of the more rigid forewings except possibly for Kholbotu-Gol where three hindwings but no forewings have been collected.

The discovery of a representative of the predominantly Palaeozoic family Phylloblattidae (Fig. 4), which is characterised by a primitive venation and a long external ovipositor of primitive type (some Mesozoic cockroaches have autapomorphically even longer ovipositors, but of different morphology; see e.g., Laurentiaux-Vieira and Laurentiaux 1979), is surprising since the last occurrence of this family is in Late Permian deposits (Vršanský et al. 2002). This is one of the most relict occurrences in the history of cockroaches. No diagnostic characters could be found to differentiate the Cretaceous specimens from their Permian ancestors. Unfortunately, based on the preserved fragment it is impossible to trace relationships within the family. Phylloblattidae are a paraphyletic stem group from which advanced Dictyoptera were descended through the Phylloblattidae–Caloblattinidae–Liberiblattinidae lineage, which is derived from ancestors of Archimylacrididae (Vršanský 2002).

Conclusions

The composition of Berriasian to Albian dictyopteran assemblages is generally uniform. The oldest typically Cretaceous dictyopterans appeared in the Tithonian (Late Jurassic) of Shar-Teg in Mongolia (Vršanský 2004). This assemblage is relatively destabilised (with occurrences of wing malformations) and less diverse than succeeding assemblages. Nevertheless, the diversity of all these assemblages is paradoxically lower than that of their Middle and Late Jurassic counterparts. The Shin-Khuduk assemblage is unique in containing a single highly variable monotypic species. Assemblages contain different proportions of the same set of cockroach species. The differences in the contributions of particular taxa to the assemblages can be explained by their different ecological conditions and/or slightly different ages (up to 0.1 million years). The assemblage from Khurilt Bed 210/24 contains advanced taxa compared to Bon Tsagaan. The Aptian Shar-Tologoy assemblage is more archaic compared to the Barremian or Aptian deposits at Bon Tsagaan.

Acknowledgements

I thank Alexandr P. Rasnitsyn (Paleontological Institute, Moscow, Russia), Klaus Klass (Staatliche Naturhistorische Sammlungen, Dresden, Germany), Jörg Schneider (Freiberg University of Mining and Technology, Freiberg, Germany), Darren Mann (Oxford University

Museum of Natural History, UK), Silvia Kotuličová (Slovak Academic Information Agency, Bratislava, Slovakia), Paul D. Taylor and Maxwell Barclay (both Natural History Museum, London, UK), and an anonymous referee for reviewing the manuscript, and Alexandr G. Ponomarenko (Paleontological Institute, Moscow, Russia) and Sonia M. Sinitza (Chita State University, Russia) for fruitful advice. This study was supported by UNESCO, HESP, Bratislava, VEGA 6002, MVTs, and by the Literárny Fond, Bratislava.

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