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TRANSITIONAL JURASSIC/CRETACEOUS COCKROACH ASSEMBLAGE (INSECTA, BLATTARIA) FROM THE SHAR-TEG IN MONGOLIA

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Abstract: A unique Upper Jurassic assemblage of cockroaches with 7 new and one unidentified species occurs in the Shar-Teg in Mongolia (*Shartegoblattina elongata* gen. et sp. nov., *Elisamoides mantiformis* gen. et sp. nov., *Breviblattina minor* gen. et sp. nov., *Mongolblatta accurata* gen. et sp. nov., *Blattula mongolica* sp. nov., *Blattula vidlickai* sp. nov., *Elisama pterostigmata* sp. nov.). The assemblage is the most progressive among Jurassic sites worldwide and displays taxa characteristic for the warm and dry Lower Cretaceous assemblages: a mantid species, two species of Blattulidae represented by *Blattula–Elisama* complex (in the Cretaceous replaced by two sister and additional species of *Elisama*) including small representatives which probably occupied the niche of the Cretaceous Holocompsidae–Vitisminae, and diverse Mesoblattinidae. Additional aberrant species preliminarily placed in the Liberiblattinidae display strong synapomorphies with the mantises. Mesoblattinidae are also known from the Lower Jurassic of Europe and Upper Jurassic of Asia and Africa (generally less diverse assemblages). These assemblages are characterized by the diverse Caloblattinidae and also the Blattulidae, which are also present in Shar-Teg. The assemblage contains a similar ratio of fore- and hindwings probably resulting from an active decomposition. The presence of frequent malformations — vein fusions in different independent taxa, which indicates some ecological stress factors in the paleoenvironment — is unusual.

Key words: Jurassic, Mongolia, systematics, taxonomy, taphonomy, phylogeny, new genera, new species, Blattaria, Mantodea.

Introduction

Fossil plants, gastropods, pelecypods, ostracods, conchostracans, insects, chelycerates, fishes, labyrintodont amphibians, turtles, crocodiles, dinosaurs and mammals have been found at the locality, indicating the uppermost Jurassic age of the locality. Over 5000 specimens of insects (under 1000 species) have been collected so far (Gubin & Sinitza 1996).

The uppermost Jurassic fossil site Shar-Teg has yielded some one hundred and fifty mostly fragmentary specimens of Blattaria, which are of high significance, since they include some transitional taxa leading to contemporary cockroaches and praying mantises (Vršanský 2002). In addition some characters are reported, which are new for the fossil Blattaria. The assemblage itself is important in providing a picture of the Jurassic–Cretaceous transitional taxa. The Cretaceous warm and dry assemblage of Blattaria (Vršanský 1999b) is found already formed, with the niches of the Cretaceous species already formed and filled with their ancestral taxa.

The complete assemblage allows its comparison with the world's most significant sites known in Kazakhstan (Vishniakova 1968), Europe (Vršanský & Ansorge in print) and Africa.

Material and methods

About a hundred and fifty specimens of Blattaria housed in the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia (PIN) are studied. The material comes from the Shar-Teg locality in Mongolia. Shar-Teg is a diverse Late Jurassic insect assemblage (some 5000 fossils of more than 200 families with more than 300 genera and 1000 species) collected in mudstone of the Shar-Teg Beds at the Shar-Teg Ula Mt SW of Adzh-Bogdo Mt, Gobi-Altai Aymag of Mongolia (Gubin & Sinitza 1996; Ponomarenko 1998) (Fig. 1).

The photographs were taken using a NIKON camera and line drawings were made using ROTRING 0.18–0.5 mm pens.

Abbreviations used: B — body; P — pronotum; Veins: Sc — Subcosta, R — Radius, RS — Radius Sector, M — Media, Cu — Cubitus (A — anterior, P — posterior), A — Anal; c — clavus; * — specimen with teratologic fusion of wing veins.

Results

Phyloblattoidea Schneider, 1983
Caloblattinidae Vršanský et Ansorge in Vršanský, 2000

Shartegoblattina gen. nov.

Type species: *S. elongata* sp. nov.
Composition: Type species.
Diagnosis: Sc richly branched, R slightly curved with as much as 17 veins at margin, M and Cu both richly branched (5+). Clavus as much as three times as long as wide with extraordinary branchings of A (Fig. 6.5). Hindwing with differ-

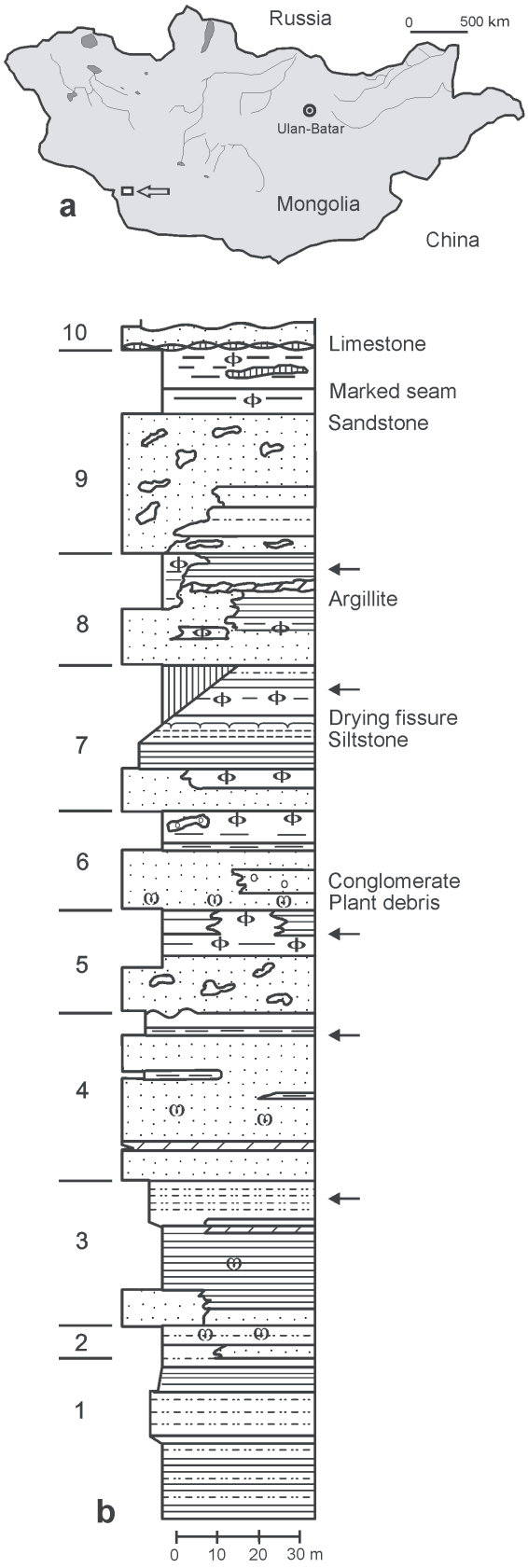

Fig. 1. a — Localization of the Shar-Teg locality (white rectangle) in the framework of Mongolia. **b** — Schematic lithological log of the Shar-Teg profile. Arrows denote the presence of insect horizons.

entiated RS, M weakly branched, CuA with secondary branched veins, and additional blind branches. A_1 branched near the basis.

Remarks: The new genus is most closely related to *Rhipidoblattina* Handlirsch, 1908. *Shartegoblattina* differs only in that clavus is narrow and R more curved (plesiomorphy).

Etymology: The name is after Shar-Teg. Gender: feminine.

Shartegoblattina elongata sp. nov.
(Figs. 3.4–5, ?5.8, 6.5–6, 7.5–6)

Holotype: PIN 4270/1846±. Forewing.

Additional material: Forewings: PIN 4270/20c, 1785±, 1800c, 1818c, 1875, 1907, 1913; Hindwings: PIN 4270/1803±, 1804±, 1807±, 1814±, 1853±, 1865, 1889, 7194. Body: PIN 4270/1863±.

Description: Forewing elongate, length about 14 mm, width 3.7 mm. Sc 3–4 branched, R, M, and Cu all richly branched (16+, 6+, 5). Clavus 4.2–4.4 mm long with peculiarly branched anal veins.

Hindwing length ca. 14–15 mm. Intercalaries and cross-veins both apparent. A_1 straight but branched near the basis (3); R differentiated into R_1 (5) and RS (7+); M branched (3+); Cu with about 7 veins plus descending additional blind branches.

Etymology: The name refers to the elongate wing form.

Character of preservation: Forewing 8 (clavus 3); hindwing 8; complete specimen 1.

Polyphagoidea Walker, 1868
?Liberiblattinidae Vršanský, 2002

Elisamoides gen. nov.

Type species: *E. mantiformis* sp. nov.

Composition: Type species.

Diagnosis: R, M (simplified) and Cu (rich) all sharply curved, intercalaries not straight but joined with cross-veins. Reticulation abundant, mostly in area of joining M, Cu and R. In this area, dark macula present. Hindwing pterostigma reaching intercalary vein between R_1 and RS.

Remarks: Curved main veins present a plesiomorphic character. The presence of characteristic macula in the forewing is similar to that of Blattulidae. Character of hindwing venation (intercalaries joined with cross-veins) resemble that of early mantises. The species most probably represent the Liberiblattinidae (Vršanský 2002), the abberant Blattulidae or a new family.

If placed in the Caloblattinoidae, *Elisamoides* would be unique there in the wing form, in having forewing macula and in simplified hindwing venation. Therefore it is placed within the Polyphagoidea.

The new genus can be placed within the Liberiblattinidae with reservations, because of the poor state of preservation of the material (Sc and A are not visible). The hindwing is similar to that of *Liberiblattina* Vršanský, 2002, but the pterostigma of *Elisamoides* reaches, but does not overlap the RS. The characters indicating trends leading to mantises support the member-

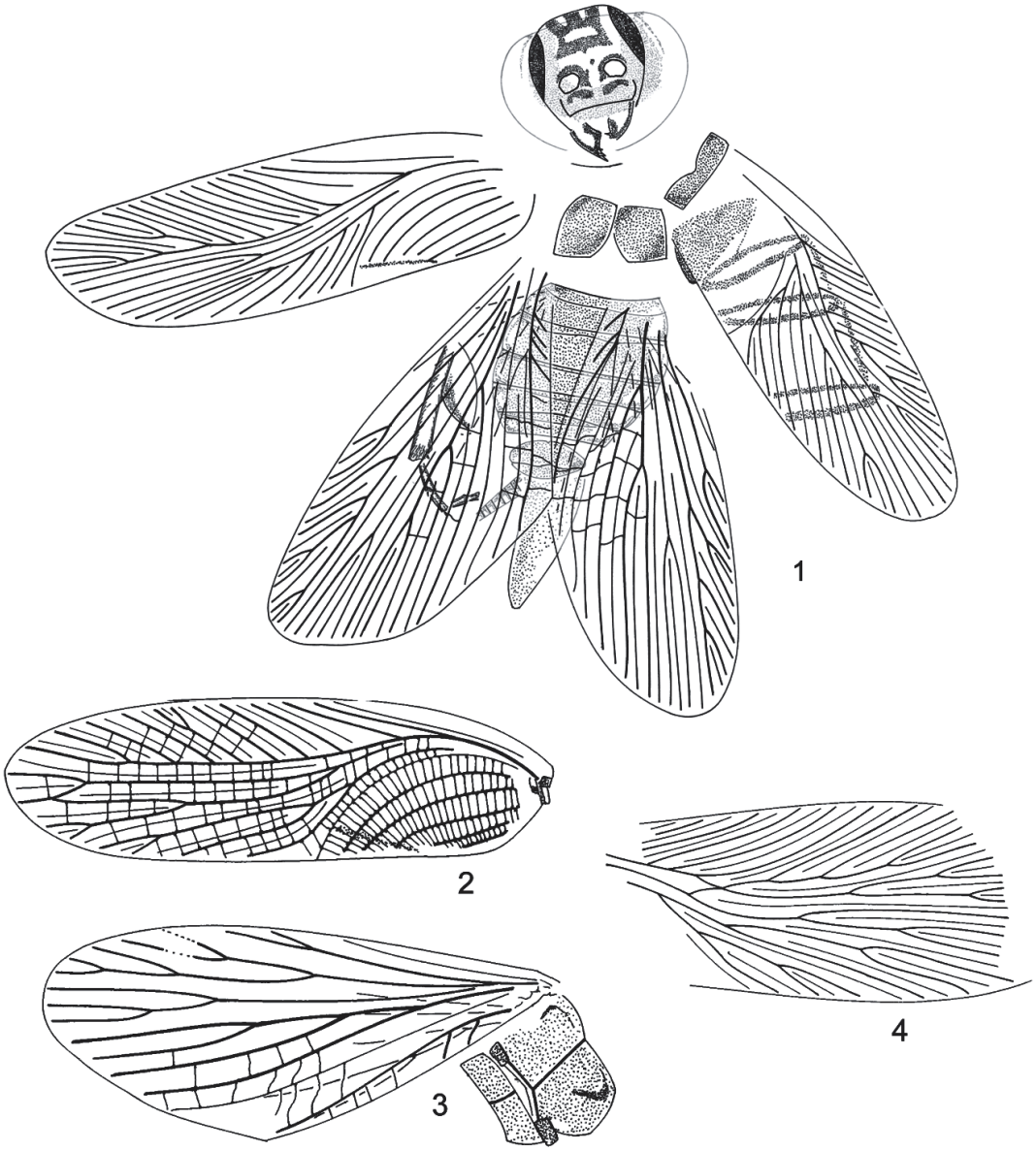

Fig. 2. 1 — *Blattula vidlickai* sp. nov. Reconstruction based on specimens 4270/1850 (complete specimen), 1815 (hindwings), 1919 (forewing on the left), 1834 (hind leg) and 1837 (head-slightly enlarged to display the colouration); **2–3** — *Elisama pterostigmata* sp. nov. 2 — Forewing (4270/1916). 3 — Hindwing (4270/1948); **4** — *Blattula mongolica* sp. nov. Forewing (4270/1798).

ship of the genus in the Liberiblattinidae. *Liberiblattina* differs in having an extensively coloured forewing (but without dark macula). It probably represents a sister taxon to *Elisamoides* (synapomorphies of *Elisamoides* and *Liberiblattina* include simplified forewing M, colouration and hindwing pterostigma). The forewing of *Gurvanoblatta* Vishniakova, 1986 is without reticulations (apomorphy), and has rich M. *Aktassoblatta* Vishniakova, 1971 has rich hindwing branches (plesiomorphy). *Kazachiblattina* Vršanský, 2002 lacks the forewing colouration and differs in having almost straight Cu branches (apomorphy). Hindwing of *Kazachiblattina* is without pterostigma, M is rich (plesiomorphies).

Elisamoides also might represent a taxon close to the stem group of Blattulidae, but the more arcuated character of enbranchements would be unique within the family. In that case, also the presence of hindwing reticulations would be enigmatic (both plesiomorphies). Nevertheless, the Blattulidae probably evolved from taxa like *Elisamoides*.

Until more complete specimens are collected, *Elisamoides* is preliminarily placed within the Liberiblattinidae.

Etymology: The name refers to resemblence with *Elisama* in the presence of macula.

Elisamoides mantiformis sp. nov.
(Figs. 3.6–7, 6.3–4)

Holotype: PIN 4270/1828. Forewing.
Additional material: Hindwings: PIN 4270/1844±, 1865.

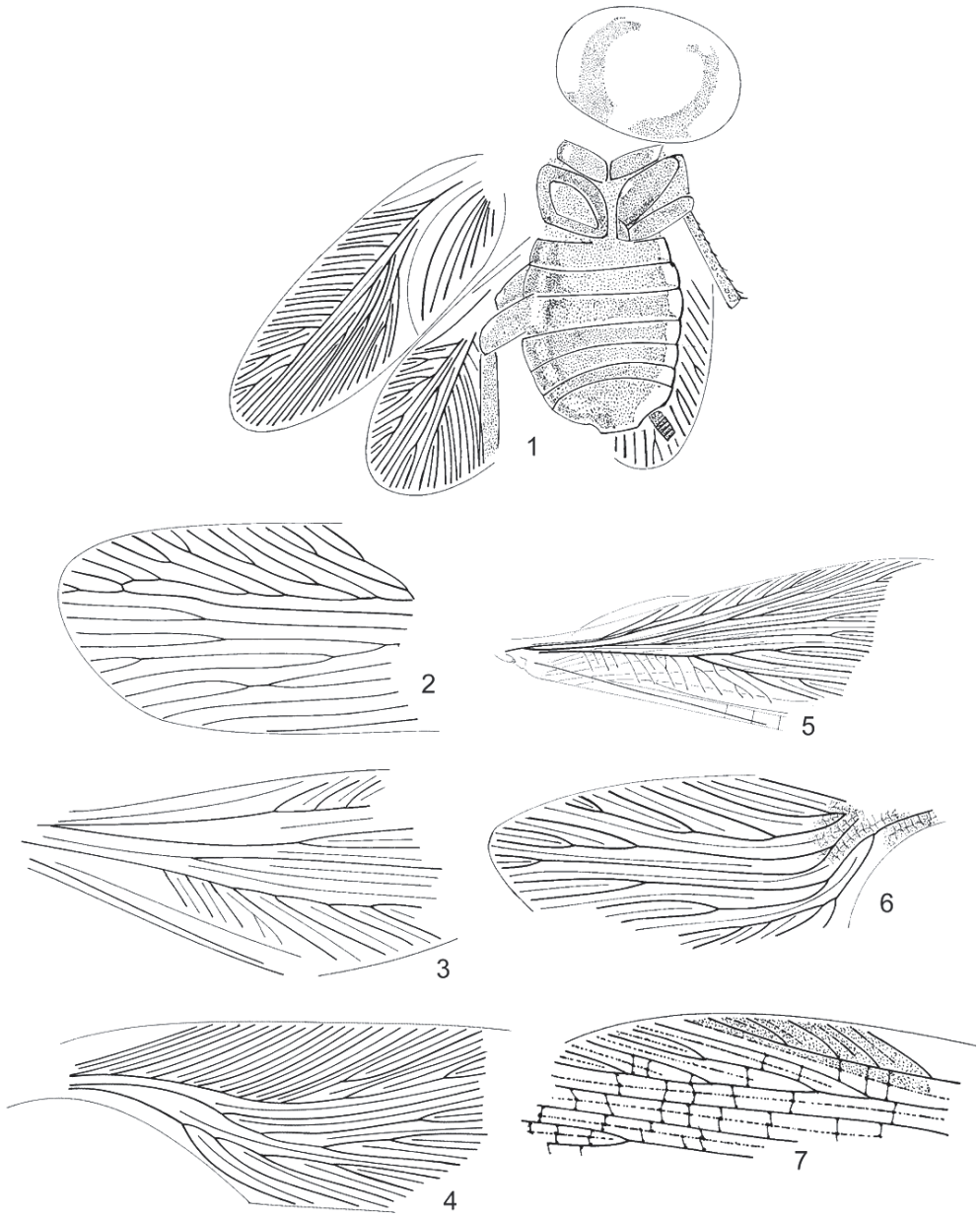

Fig. 3. 1 — *Breviblattina minor* sp. nov. (4270/1843); **2–3** — *Mongolblatta accurata* sp. nov. 2 — Forewing (4270/1856). 3 — Hindwing (4270/1857); **4–5** — *Shartegoblattina elongata* sp. nov. 4 — Forewing (4270/1846). 5 — Hindwing (4270/1807); **6–7** — *Elisamoides mantiformis* sp. nov. 6 — Forewing (4270/1828), 7 — Hindwing (4270/1838).

Description: Forewing length about 8 mm (fragment length 7 mm), width 2.75 mm. Reticulations most abundant in front of clavus. R richly branched with about 10 branches, M with few (about 5) veins, reaching before apex, Cu richly branched (about 9 veins).

Hindwing with differentiated R and RS (5+6–8), branched M (3–4) and incipient pterostigma covering intercalary between R_1 and RS.

Etymology: The name indicates that the species apparently shows a tendency that is realized in the Mantodea.

Character of preservation: Forewing 1, hindwing 2.

Blattulidae Vishniakova, 1983
Blattula Handlirsch, 1906

Blattula mongolica sp. nov. (Figs. 2.4, ?5.2, 6.2)

Holotype: PIN 4270/1798±*. Forewing.

Additional material: Forewings: PIN 4270/28, 1767±, 1826c, 1866.

Diagnosis: The largest (forewing length almost 12 mm) blattulid of the site. Forewing characteristics: length/width: ≤12 mm/3.5 mm; R 13+; M 3–7; Cu 4–7; A 6+ (simple

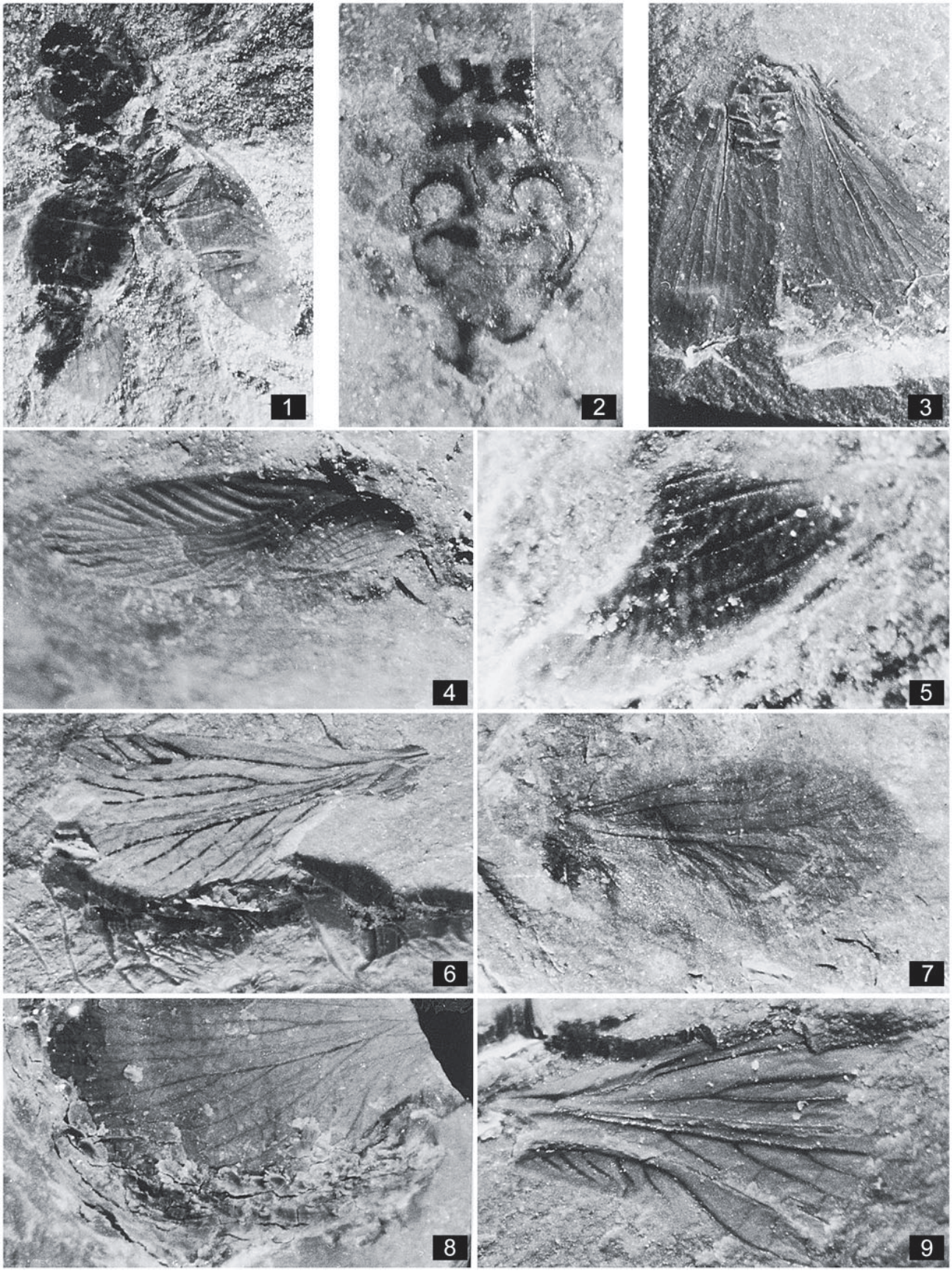

Fig. 4. *Blattula vidlickai* sp. nov. (Figs. 4.1–9: 4270/1850, 1837, 1815, 1919, 1903, 1881, 1847, 1792, 1881).

veins). Total number of veins about 30.

Description: The largest *Blattula* known. Sc probably simple; R richly branched (without secondary branches), curved; M almost straight, comparatively rich; Cu rich, reaching apical quarter of the forewing.

Remarks: Because the single completely preserved wing is generally deformed in shape (in addition to fusion between M and R it has expanded R, which could be a result of the fusion), it is very difficult to appreciate the phylogenetical position of the species within *Blattula.*

The species differs from all the known Jurassic representatives of the genus in being large.

Both *B. mongolica* and *B. vidlickai* described herein are without characteristic dark macula in the forewing and therefore assigned to the genus *Blattula*, and not *Elisama* Giebel, 1856.

Etymology: The species name is after Mongolia.

Character of preservation: Forewing 5 (clavus 1).

Blattula vidlickai sp. nov. (Figs. 2.1, 4.1–9)

Holotype: PIN 4270/1897 = 1919. Forewing.

Additional material: Forewings: PIN 4270/21(+P), 25, 1759±, 1763±, 1764, 1771, 1773, 1777, 1780, 1782, 1783±, 1786, 1788, 1793, 1811±, 1829±, 1834±leg, 1854±, 1858±, 1861±, 1871=1903c, 1873, 1874, 1878±, 1885, 1891, 1893, 1909; Hindwings: PIN 4270/14, 1768, 1769, 1784±, 1792, 1799, 1815±, 1816±, 1819±, 1847±, 1872, 1881; Complete specimens: PIN 4270/1850±, 1905.

Diagnosis: One of the smallest (forewing length under 6 mm) blattulids known. Hindwing with pterostigma indicated, and with richly branched A_1 (unique within Blattaria). Forewing with simplified venation, with the total number of veins about 25 (23–27), with tip sharply curved. Massive sheath covering ovipositor present.

Description: Forewing characteristics: length/width: 4.0–5.7 mm/1.3–1.9 mm; Sc 1; R 10–12; M 2–7; Cu 2–5; A 5–6. Posterior anal vein may be forked.

Hindwing with the simple Sc, R_1 (2–4) + RS (2–6) with 6–8 veins and indicated pterostigma in the region of R_1; M may be occasionally richly branched, usually with 2 veins (2–7); CuA with 3–5 veins; CuP simple; A_1 richly branched (6–7). A_2 up to 4-branched. Cu with numerous cross-veins. Pronotum with two parallel stripes.

Remarks: In spite of the strong autapomorphies discriminating the species among other *Elisama* species (richly branched A_1 and A_2 in the hindwing), the taxon is similar to Vitisminae (Holocompsidae Rehn, 1951) in the general groundplan of the hindwing and sharply curved CuP in the forewing. The extremely small size of some specimens (up to forewing length 4 mm in PIN 4270/1847) is also similar to Vitisminae.

It differs from the most of the Blattulidae in its small size — such small *Blattula* species with the sharp tip of the forewing are known also from the Lower Jurassic deposits of Germany and England (Vršanský & Ansorge, in print), but A_1 in the hindwing is not branched.

The absence of the cases of vein fusion in this most common species is significant. This indicates its ability to resist the stress factors which affected other roach species in the locality.

Etymology: The species is named after Ľubomír Vidlička, the scientist who introduced me into the world of contemporary cockroaches.

Character of preservation: Forewing 29 (clavus 2); hindwing 12 (both hindwings 1); complete specimens 2.

Elisama Giebel, 1856

Elisama pterostigmata sp. nov. (Fig. 5.1,3,5,7)

Holotype: PIN 4270/1916*. Forewing.

Additional material: Forewings: PIN 4270/10, 24, 26, 1758±, 1770c, 1774*, 1775(B), 1801, 1802, 1832±, 1835±*, 1841c, 1845±, 1851±c, 1859±, 1875, 1894c, 1899. Hindwings: PIN 4270/16, 22, 1765±(B), 1781, 1794, 1797±, 1828, 1848±, 1855±, 1920±.

Diagnosis: Pterostigma is slightly indicated in the hindwing. Total forewing length usually 7–8 mm. Macula is shifted more centrally, comparing to the Cretaceous representatives of the genus.

Description: Forewing characteristics: length/width: 6.5–9 mm/2.1–2.6 mm (clavus ca. 3 mm). Sc 1; R 10–13; M 4–7; Cu 2–7, A 5–6 (simple veins).

Hindwing length 7–8 mm. The most stable venation character R 6+4 (3+4 in a single specimen); M 3; Cu 4–5+1.

Remarks: Fusion of veins (fused are different branches of M or of R and M) is present in at least 3 of 19 specimens (most wings collected are incomplete) being an extraordinarily high proportion within the Blattulidae and cockroaches in general.

The hindwing pterostigma probably represents a plesiomorphic character within the Blattulidae. Figure 5.3 shows sharply curved CuP in the forewing, a character typical for Holocompsidae.

It is one of the oldest (Jurassic) species of the genus. It differs from other (even Cretaceous) representatives of the genus in having sharply curved CuP in the forewing and dark macula shifted more centrally.

Etymology: The species name refers to the pterostigma present in the hindwing.

Character of preservation: Forewing 19 (body 1), hindwing 10 (body 1).

Mesoblattinoidea Handlirsch, 1906 (= Blattoidea)
Mesoblattinidae Handlirsch, 1906

Breviblattina gen. nov.

Type species: *B. minor* sp. nov.

Composition: Type species.

Diagnosis: The genus with the smallest known species of the family (wing length 7 mm or less). Pronotum very large, as wide as half of wing length; forewing margins not parallel (in general, small species have margins less parallel), venation simplified, without terminal forks, Sc simple, hindwing R richly branched.

Remarks: The genus differs from *Hispanoblatta* Martínes-Delclóz, 1993 in having non-parallel wing margins (apomorphy depending on the diminished size of the insect).

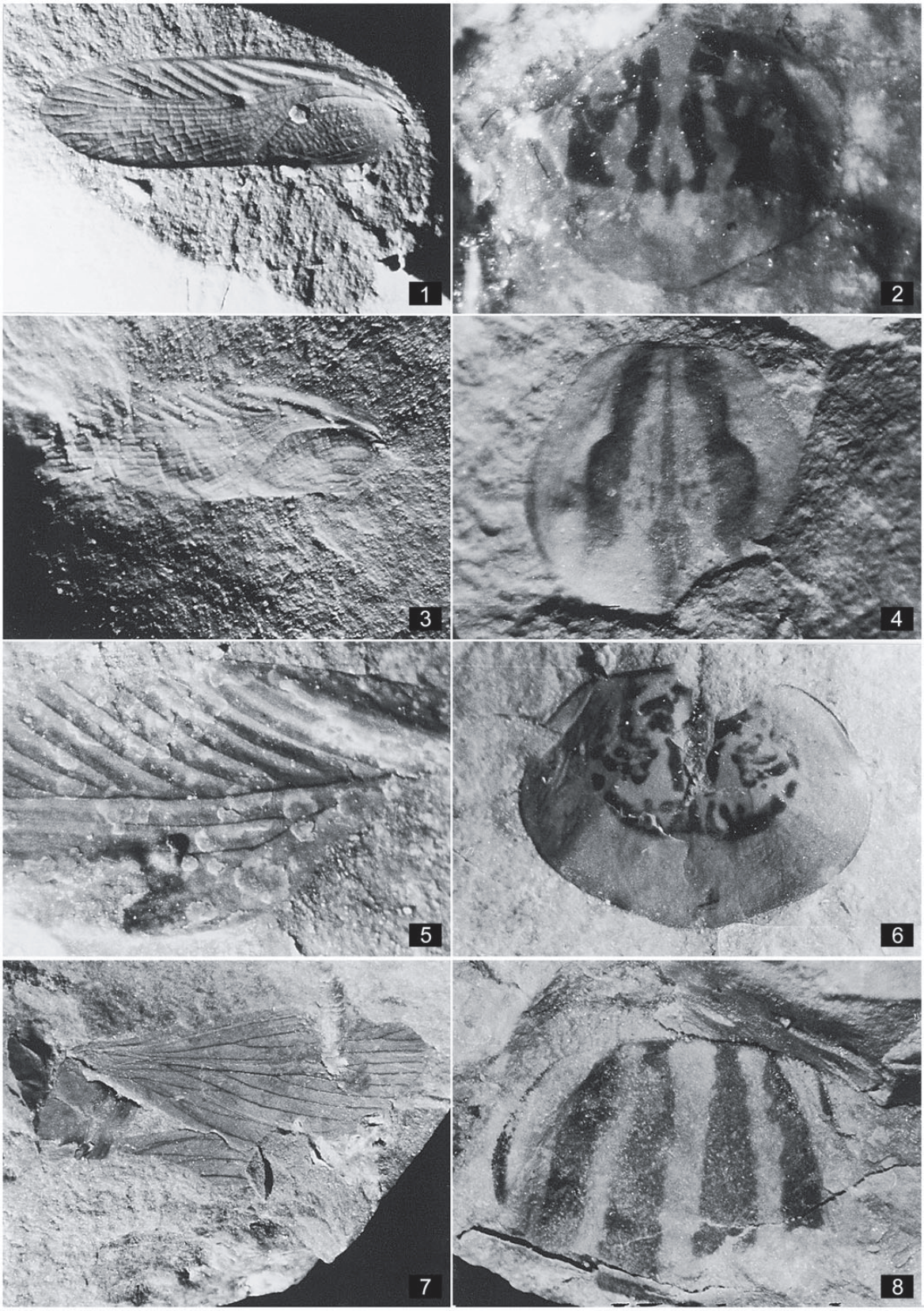

Fig. 5. 1 — *Elisama pterostigmata* sp. nov. Forewing (4270/1916); **2** — ?*Blattula mongolica* sp. nov. Pronotum (4270/1860); **3** — *Elisama pterostigmata* sp. nov. Forewing (4270/1774); **4** —?Pronotum (4270/1760); **5** — *E. pterostigmata* sp. nov. Forewing (4270/1899); **6** — ?Pronotum (4270/1822); **7** — *E. pterostigmata* sp. nov. Hindwing (4270/1848); **8** — *Shartegoblattina elongata* sp. nov. Pronotum (4270/1776).

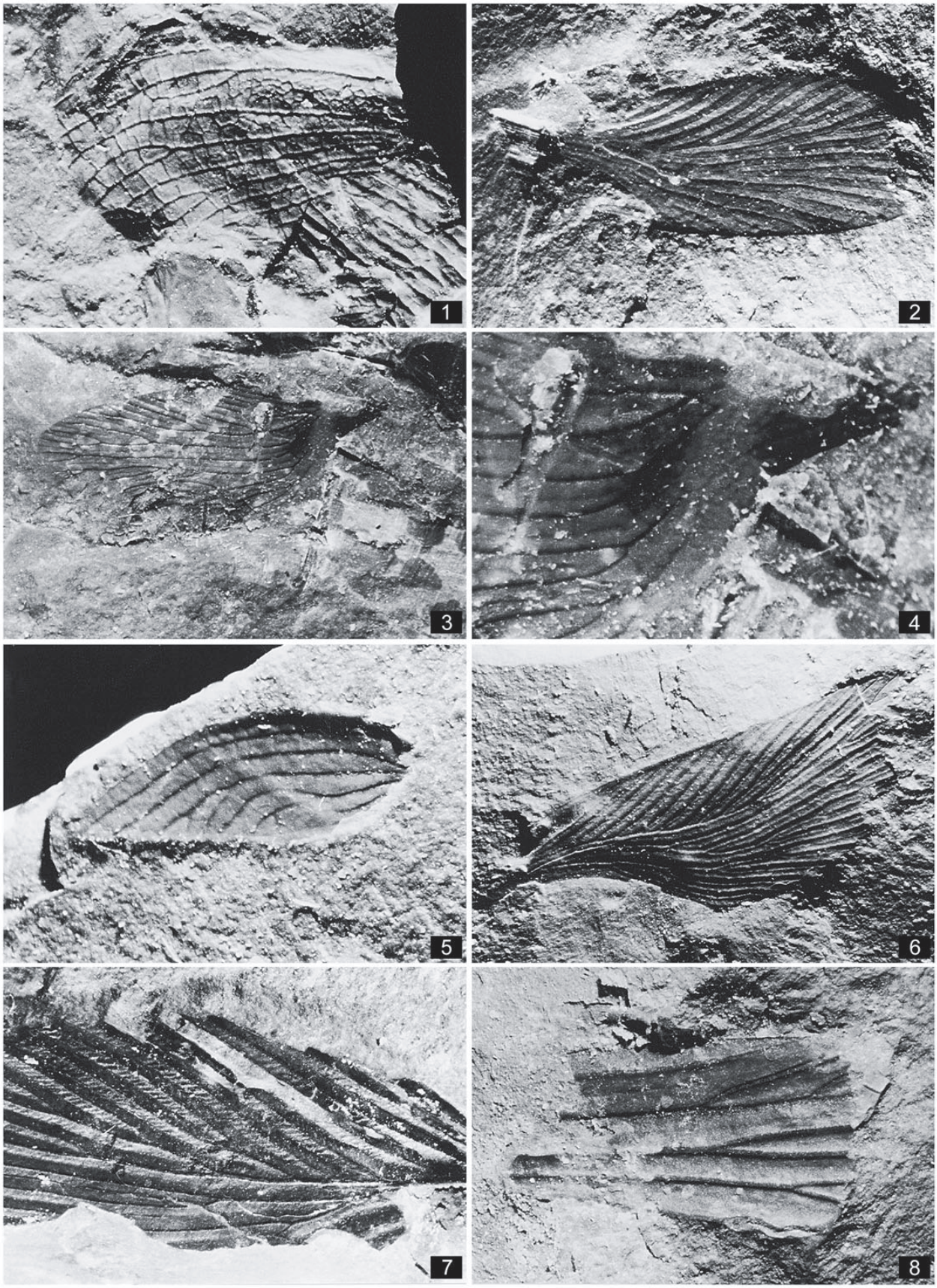

Fig. 6. 1 — *Juramantis initialis* Vršanský, 2002 (4270/1842); **2** — *Elisama mongolica* sp. nov. Forewing (1798); **3–4** — *Elisamoides mantiformis* sp. nov. Forewing (4270/1828); **5** — *Shartegoblattina elongata* sp. nov. Forewing (4270/1818); **6** — *Shartegoblattina elongata* sp. nov. Forewing (4270/1846); **7–8** — gen. et sp. indet. 7 — Forewing (4270/1825). 8 — Hindwing (4270/1795).

Similarly non-parallel wing margins (plesiomorphic — derived from Caloblattinidae which are large in size) are also known in *Archimesoblatta altera* (Vršanský, 1997), "*Artitocoblatta*" *colominasi* (Meunier, 1914), and partially in *Mesoblattina* Geinitz, 1880.

The genera *Archimesoblatta* Vršanský, 2003 and "*Artitocoblatta*" *colominasi* differ from *Breviblattina* in rich venation, large size and terminal branchelets (all plesiomorphies). *Mesoblattina* differs in having partially irregular venation (plesiomorphy).

(According to Vršanský 2000, the above-mentioned are all representatives of the family Mesoblattinidae. Other "Mesoblattinidae" are placed in Caloblattinidae Vršanský et Ansorge, 2000 or belong to other families.)

Etymology: The genus name is after *brevis*, the Latin for short, and genus *Blatta*. Gender: feminine.

Breviblattina minor sp. nov. (Figs. 3.1, 7.4)

Holotype: PIN 4270/1843. Complete specimen.

Additional material: Forewings: PIN 4270/1801, 1868±c, 1906, 1912±.

Description: Wing length/width 5.4–7 mm/ca. 2.7 mm. Sc branched, R expanded, with as much as 14 veins at margin, M with 2–4 branches, Cu with 5 veins. Hindwing with richly branched M.

Etymology: The species name refers to the small size of the insect.

Taphonomy: Forewing 4 (clavus 1), body 1.

Mongolblatta gen. nov.

Type species: *M. accurata* sp. nov.

Composition: Type species.

Diagnosis: Forewing leatherous, venation regular, Sc branched, RS differentiated, M and Cu richly branched, anal veins simple, intercalaries punctuated in anal area.

Remarks: In general appearance the genus resembles *Hispanoblatta* (and also *Piniblattella* Vršanský, 1997 from Blattellidae, which differs in having Sc simple), but the wing is leatherous and anal intercalaries punctuated.

"*Artitocoblatta*" *colominasi* and *Archimesoblatta altera* differ in having wing margins not parallel.

The new genus differs from *Mesoblattina* in having fully regular venation.

The taxon appears transitional between Mesoblattinidae and Blattellidae, it is placed in Mesoblattinidae because of the branched hindwing M.

Etymology: The genus is named after Mongolia. Gender: feminine.

Mongolblatta accurata sp. nov. (Figs. 3.2–3, 7.1–3)

Holotype: PIN 4270/1849. Forewing.

Additional material: Forewings: PIN 4270/1796±, 1827±*, 1831±, 1833±, 1856±*, 1864c, 1877, 1898, 1900, 1908c. Hindwings: PIN 4270/11, 1761±, 1766±, 1806, 1838±, 1839±, 1857±.

Description: Forewing leatherous, anal intercalaries with typical punctuation; hindwing with narrow remigium. Forewing length/width: 10 mm/3.9 mm. Forewing Sc 2 branched; R with 13 or more branches (R branches and first branch of M with dark colouration), in the preserved specimens M and Cu with 5 branches each. Clavus ca. 5 mm long. Hindwing R_1 with 5–7, RS with 9–12 veins, M with 4 branches. CuA secondarily branched.

Remarks: It is of interest that the fore- and hindwings collected are almost equal in number, in spite on the fact that forewings are leatherous and stiff, and yet many of them are fragmented indicating a kind of damage. Normally the hindwings, being thin and so more vulnerable to mechanical damage, experience considerable loss before and during the burial process.

Colouration is similar to *Piniblattella vitimica* (Vishniakova, 1964), but with coloured first branch of M.

Etymology: The species name (*accurata* is the Latin for accurate) alludes to the intermediate size of the species.

Character of preservation: Forewing 11; hindwing 7.

Family, genus et species incertae sedis (Fig. 6.7–8)

Material: Forewings: PIN 4270/1808±, 1825; hindwing: 1795±.

Description: Forewing length about 20 mm. Venation is unique in possessing numerous comb-like connections of veins to the apparent intercalaries. Veins more or less straight, R rich.

Systematic remarks: The poor state of preservation disallows identification of the position of the fossil within the current system. The species may well represent a Paleozoic or even a new family. A similar but more sophisticated pattern of the forewing venation is present in Paleozoic Phyloblattidae. Nevertheless, the straight veins and modern character of the branches indicate rather advanced taxon. The character of venation similar to *Archimesoblatta altera* (Vršanský, 1997) (Mesoblattinidae), except for comb-like interconnection of veins.

Character of preservation: Forewing 2; hindwing 1.

Discussion

The cockroach diversity of some Upper Jurassic environments (Karatau as partly described by Vishniakova 1968: 1750 specimens with 25 species of 15 genera) is thought to be comparable to the diversity of contemporary tropical forests (Panfilov 1968) (nevertheless such comparison is not significant because of taphonomical differences). The same diversity is known for the Lower Cretaceous sites (Baissa described by Vršanský 1997, 1998, 1999a,b: 583 specimens with 24 species of 9 genera in 2 diferrent assemblages; Bon Tsagaan according to Vršanský (2003): 651 specimens with 20 species of 12 genera).

Diversity of the Shar-Teg assemblage (171 specimens with 8 or 9 species in 6 genera) is considerably lower, even richer than other Lower Jurassic sites in Europe (120 specimens with 6 species in 4 genera in the Toarcian of Germany and England, as described by Vršanský & Ansorge, in print).

Moderate in diversity, the Shar-Teg fauna is important for the presence of modern family Mesoblattinidae and advanced Blattulidae — with two species — and also Mantids (Fig. 6.1 —

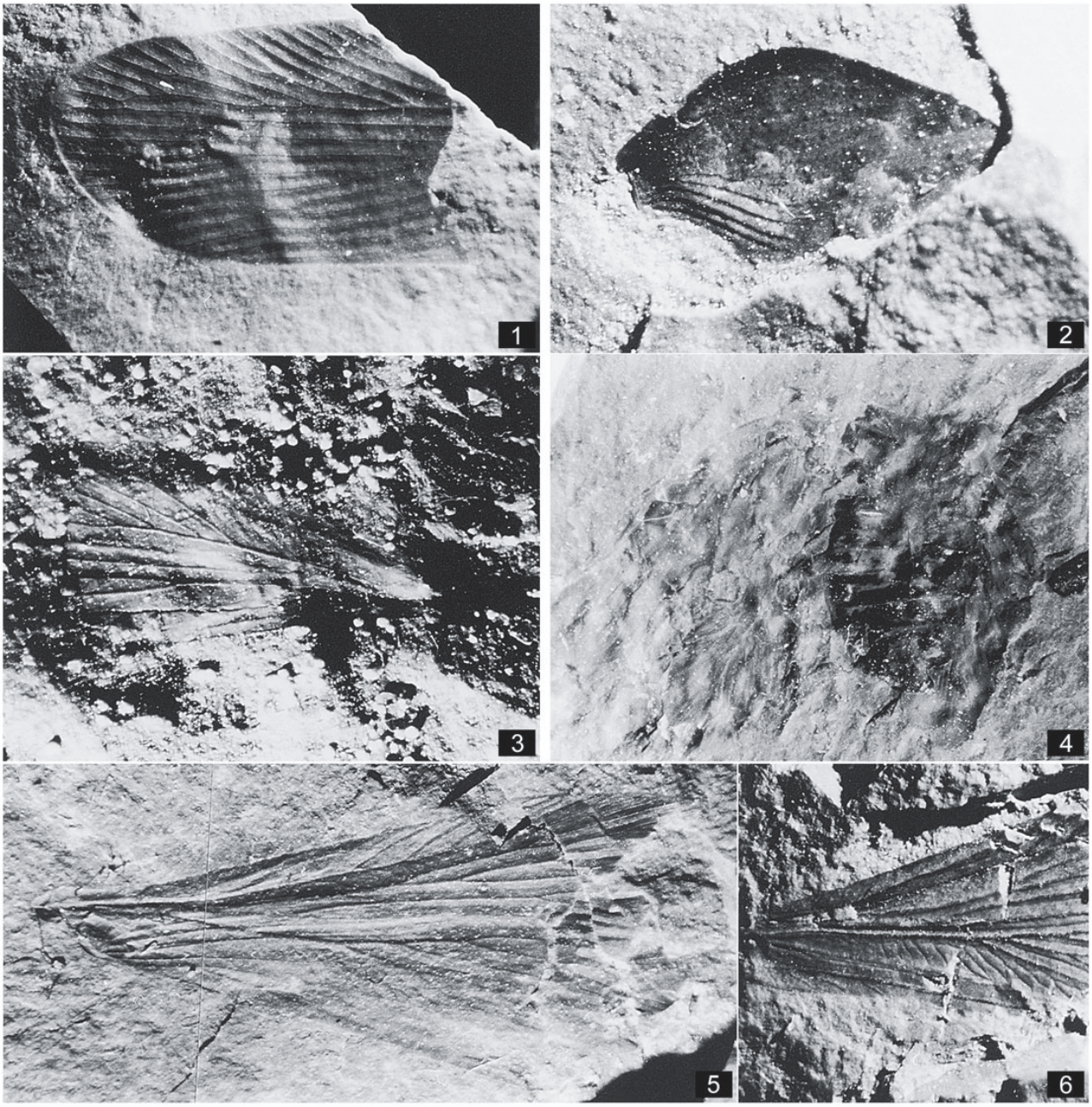

Fig. 7. 1–3 — *Mongolblatta accurata* sp. nov. Forewings (4270/1856, 1864). Hindwing (4270/1857); **4** — *Breviblattina minor* sp. nov. (4270/1843); **5–6** — *Shartegoblattina elongata* sp. nov. Hindwing (4270/1807, 1804).

Juramantis initialis described by Vršanský (2002)). This characterizes the Shar-Teg assemblage as Cretaceous in essence. In addition to praying mantises, mesoblattinids and blattulids, the modernization is represented by *Elisamoides* (probably Liberiblattinidae; the family otherwise known from the Middle–Upper Jurassic of Kazakhstan and Mongolia and Lower Cretaceous of Mongolia).

According to the presence of the most of the modern elements in the lowermost Cretaceous of Mongolia and Siberia (where they occur for the first time), it is possible that the advanced Shar-Teg taxa (*Juramantis* sp., *Elisama* spp., *Breviblattina* sp. etc.) are directly ancestral for them.

The evolution of mantids — specialized carnivores — during the latest Jurassic, represents an important phenomenon. The rapid radiation of mantids which are known from all the paleoentomologically well explored Early Cretaceous regions of Laurasia and Gondwana (starting from the Turonian also in North America (New Jersey)) is interesting.

In comparison with Shar-Teg, the less diverse European Lower Jurassic sites as well as the diverse Upper Jurassic of Karatau possess more ancient fauna with archaic lineages dominating.

In the Shar-Teg assemblage, the presence of the two blattulid species complexes, represented by *Blattula vidlickai* and

Elisama pterostigmata is considerable (there is an additional, but rare species of *Blattula* present, which could not play an important role in the ecosystem). The ecological importance of the presence of the two morphologically similar species is not known, but is present in contemporary *Ectobius* Stephens, 1835 (two related species usually inhabit different levels of the vegetation), and in the Cretaceous–Tertiary *Elisama* (closely related to *Blattula*). It is interesting that *Elisama* which is recorded starting from the Jurassic, and during the lowermost Cretaceous spread all over the globe (the close position of continents in the Berriasian did not form barriers) replaced a niche of *Blattula* in the Cretaceous, when the sister species complex is formed exclusively by *Elisama* (*Blattula* is absent).

The presence of dark macula in the forewing presents an interesting phylogenetic problem. The macula is present in *Eublattula* Handlirsch, 1939 — possibly an ancestral taxon with strong plesiomorphies within the family Blattulidae, and also in *Elisamoides*, a genus probably belonging to another family (Liberiblattinidae). Therefore the macula most probably represent a plesiomorphic character within the Blattulidae, which was independently lost in *Blattula, Rithma* Giebel, 1856, *Tarakanula* Vršanský, 2003, etc.

Derived characters such as branched A_1 in the hindwing (probably supporting the wing in flight) and the sheath covering the ovipositor in a blattulid species (*Blattula vidlickai*) appoint to the developed evolutionary stages of some niches.

The taphonomy of the site (Table 1) is notable, since the majority of the specimens are isolated wings with the very low partuition of bodies. Most surprising is low ratio of the preserved fore- and hindwings (ca. 2:1). The usual ratio is much higher as in the Early Cretaceous of Bon Tsagaan in Mongolia with ca. 5:1, and Baissa with ca. 6:1. It is interesting that in the Baissa warmer assemblage, a much lower ratio (2:1, like in the Shar-Teg) is observed (Vršanský 1998). In the warmer water, the wings may be more easily disarticulated from bodies because of decomposition, and thus the partuition of bodies in warmer assemblages of Baissa is also low, like in Shar-Teg. The role of decomposition is additionally confirmed by the high proportion of isolated forewing clavi. Thus the preservation pattern observed in Shar-Teg indicates the predominantly autochthonous preservation with the low mechanical damage, possibly in contrast to assemblages with a higher rate of forewings collected. In these circumstances, the possible explanation of the underrepresentation of roach bodies is the activity of predators such as fish.

The high participation of teratologic vein fusion is also notable. It clearly indicate some stress factor in the paleoenvironment. However, *Blattula vidlickai,* the most common species at the site is free of such fusions, possibly because a kind of adaptation to the stress agents.

Table 1: Taphonomy of the site. Unidentifiable Blattaria are: PIN 4270/15, 27, 1757±*,1787, 1789=1790, 1791, 1810±, 1813, 1869, 1883, 1887, 1888, 1910, 1914, 1921 (forewings); PIN 4270/1812±, 1821±, 1884, 1890, 1892, 1896, 1915, 1923, 1924 (hindwings); PIN 4270/17, 1809±, 1830±, 1876, 1904 (bodies and/or pronota); PIN 4270/12, 13, 23, 1772, 1778, 1779, 1801, 1852±*, 1862, 1867, 1870*, 1882, 1886, 1879, 1895, 1917, 1918 (others); PIN 4270/1824, 1836, 1880, 1911 are found to not belong to Blattaria; PIN 4270/19 is missing in the collection. I assume that at least one additional species is hidden within the unidentified specimens. If numbers are in parentheses, the specimens are included under numbers without parentheses.

Species	Forewings	Hindwings	Bodies	Sum
gen. et sp. indet	2	1	–	**3**
S. elongata	8 (3c)	8	1	**17**
B. minor	4	–	1	**5**
M. accurata	11	7	–	**18**
B. vidlickai	29 (2c)	12	2	**43**
E. pterostigmata	19 (4c)	10	(2)	**29**
B. mongolica	5 (1c)	–	–	**5**
E. mantiformis	1	2	–	**3**
Unidentifiable	15+	9+	5 fragm	**47**
SUM	**91+(10c)**	**49+**	**9 (6)**	**170**

Conclusions

— The cockroach assemblage of Shar-Teg shows moderate taxonomic diversity and is composed of both — archaic (possibly even Paleozoic) as well as advanced (transitional to contemporary) taxa.

— In spite of the Jurassic age and persistence of a possible Paleozoic relict, the Shar-Teg assemblage is of Cretaceous type in essence, as the presence of diverse Mesoblattinidae and Blattulidae (2 abundant and additional infrequent species) show.

— The assemblage probably presents a fragmentary orycto-cenosis which resulted from active decomposition (and possibly predation) rather than from transport by running water.

— Some extraordinary ecological stressing factor was probably operating in the Shar-Teg biocenosis, resulting in malformations (in form of vein fusions) during the development of insects.

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