Biologia, Bratislava, **62**/5: 588—592, 2007
Section Zoology
DOI: 10.2478/s11756-007-0116-2

Jumping cockroaches (Blattaria, Skokidae fam. n.) from the Late Jurassic of Karatau in Kazakhstan

Peter Vršanský[1,2]

[1] *Geological Institute, Slovak Academy of Sciences, Dúbravská cesta 9, P.O. BOX 106, SK-84005 Bratislava 45, Slovakia; e-mail: geolvrsa@savba.sk*
[2] *Arthropoda Laboratory, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117868 Moscow, Russia*

Abstract: The jumping cockroach *Skok svaba* gen. et sp. n., characteristic of modern reproduction, is described from the Upper Jurassic Karabastau Formation in Kazakhstan, and attributed to a new family Skokidae. The finding demonstrates the immense plasticity of stem cockroaches from which eusocial termites and predatory mantises evolved.

Key words: fossil insects; new family; phylogeny; Blattaria (=Blattodea); Kimmeridgian

Introduction

Cockroaches comprise diverse life forms such as semisocial insects (Schal et al. 1984), predatory and beetle-like forms (Vishniakova 1973; Vršanský 2002, 2003), exclusive pollinators (Nagamitsu & Inoue 1997), somatically translucent and blind inhabitants of caves (Vidlička et al. 2003), aquatic (Shelford 1909; Takahashi 1926) and bioluminiscent (Zompro & Fritzsche 1999) species, robust wingless desert dwellers, active fliers resembling butterflies, whereas most cockroaches have customary habitus and habits. The decomposition of organic matter provided by cockroaches and related termites is important for structuring modern tropical and subtropical ecosystems. In addition, cockroaches have evolved immense resistance to environmental stress, e.g., radiation (Koval 1983), and they are often used in experiments, including those conducted in space.

Fossil cockroaches address some general evolutionary problems such as the evidence of mass mutations during boundary events, observations of the decreased variability through time and demonstration of fine structure of the oldest insect sense organs (Vršanský 2000, 2005; Vršanský et al. 2001).

Of 6,000–8,000 expected living (Roth 2003) and 2,000 fossil (unpublished) cockroach species, only one taxon was apparently capable of locomotion by jumping, similarly as grasshoppers. It was discovered in the Upper Jurassic strata of Karatau in southern Kazakhstan and is described here. *Skok svaba* sp. n. is attributed to a new, 22nd (14th extinct – sensu Vršanský 2002) family of Skokidae. This peculiar fossil demonstrates the immense plasticity of stem group cockroaches from which eusocial termites, predatory mantises and modern cockroaches derived.

Material and methods

The material originates from the Mikhailovka village of South Karatau in Kazakhstan (Gekker 1948). It represents the Late Jurassic Karabastau Formation, ca. 160 million years old. The rough estimation of age is based on dating of the Daohugou Formation, which is slightly older – Bathonian (168 Myr according to Gao & Ren 2006) and the Shar-Teg Formation, which is significantly younger – Tithonian (150–145 Myr according to Gubin & Sinitza 1996). The collection is deposited in the Paleontological Institute of the Russian Academy of Sciences (PIN, Moscow).

Blattaria Latreille, 1810
Polyphagoidea Walker, 1868
Skokidae fam. n.

Composition. Type genus *Skok* gen. n. described below.

Diagnosis. Minute species (body length ca. 10 mm) with body soft and partially laterally compressed, head very small (not prognathous) and with long palpae; pronotum with paranotalia reduced; legs with reduced spines and carination, fore- and midlegs reduced in size, hindlegs saltatorial, 1.5× longer than whole body, with supporting ridge; ovipositor reduced. Forewings symmetrical, elongated, with long branched Sc, simple R branches, M overlapping apex, simplified CuA and very narrow clavus. Hindwing with simplified venation, but rich M.

Description. Small species. Body soft, dorsoventrally flattened, but also at least partially laterally compressed. Head hypo- or orthognathous, comparatively small, with extremely long palpae. Pronotum almost ovoid, with paranotalia reduced. Fore- and midlegs very

Springer

thin and narrow, of medium length. Hindlegs saltatorial, robust and long (1.5× of the total body length). Female with slightly asymmetrical valvifers and reduced ovipositor. Forewing transparent, elongated with sharp tip. Venation simplified, intercalaries fine, cross-veins not apparent. Sc long and branched; R and M simplified, each with about 10 veins at the margin; CuA extremely reduced; clavus extremely narrow, with A reduced but branched.

Hindwing transparent, partially coloured, with simple Sc, R1 with simple branches, RS simplified and reduced (3); M richly branched (6).

Remarks. The new family can be attributed to the Polyphagoidea, based on the character of forewing venation with strong and curved veins, long palps, small pronotum, hindwing morphology and composition of terminalia. Though, the presence of rudiment of external ovipositor, unique saltatory adaptations such as partial reduction of midlegs, and plesiomorphic morphology of wings allow to recognise it as a separate family.

Comparatively short forewing with long branched Sc; hindwing with rich M; pronotum with reduced paranota and reduced ovipositor are synapomorphies with the advanced Liberiblattinidae. Apparently early representatives of that family represent a stem group of Skokidae. The unusual character of forewing coloration with light stripes might indicate relations to the genus *Elisamoides* Vršanský, 2004. Body coloration with pale macula on the lateral sides (visible due to partial compression) is rare. Wings of the new taxon resemble those of the Mesozoic family Caloblattinidae and related families within superfamilies Caloblattinoidea and Raphidiomimoidea, but can be recognised by small size, reduced venation, forewing with sharp apex and narrow clavus.

***Skok* gen. n.**

Composition. Type species *Skok svaba* sp. n. described below.

Description. Minute cockroaches with semi-transparent forewings and transparent hindwings. Head round, with distinct outline coloration and large eyes. Antennae filiform, multi-segmented (over 100 segments). Pronotum coloured, with pale margin. Body tender, dark, with pale spots in lateral part of sterna. Terminalia asymmetrical (see Fig. 1). Cerci with few (less than 20 and most probably under 15) segments, pale with dark margin. All legs with reduced spines. Wing characteristics as for the family.

Etymology. After "skok" (Slovak word for "jump").

***Skok svaba* sp. n.** (Fig. 1)

Description. In adult head comparatively small, oval, with large eyes and extremely long 4–segmented maxillary palps: 1st segment shortest (about 0.37 mm), 2nd about 1.01 mm, 3rd 1.20 mm, 4th 0.55 mm. Antennae filiform, thin and very long (about 1.5× longer than body), with at least 130 segments.

Pronotum suboval, with largely reduced paranotalia, dark with pale margin.

Terminalia asymmetrical, ovipositor reduced; cerci with 8 or more segments, pale with submarginal dark striata. Body soft, pictured, with pale spots in lateral part of sterna. Immature with pale stria. The digestive tract is apparent in the holotype.

As a result of extremely long and free coxae (not preserved, their length is assumed based on their position), the hindlegs and midlegs are particularly shifted backward. Forelegs very thin with all femora and tibiae unusually pale with dark margin, with femora extremely short (about 0.92 mm), tibiae about 1.66 mm long, massive when compared with mid-tibiae, and with long tarsi (segments 1–5 ca. 0.64 mm; 0.28 mm; 0.28 mm; 0.28 mm and 0.37 mm respectively, total length about 1.75 mm). Midlegs long and slender, with femora and tibiae each about 2.48 mm long, femora only about 0.37 mm wide. Femora with up to 12 very fine and short setae, tibiae with 6–8 fine setae. Hindlegs saltatorial, with femora very long in respect to body (3.2 mm) and wide (0.9 mm). Mid- and hindlegs apparently without strong spurs. In immature, slender spines concentrated in apical part of hind tibia, forming 3 rows with 6–8 spines each. Hind femora with single thin seta in the knee area. Tarsi apparently short, with tarsomere 4 the shortest. Arolium probably reduced. Mid and hind femora and tibia pale, with dark, most probably dark gray margin.

Forewing 7.7–8.1 mm long, elongate, with taper apex and reduced venation, with faint intercalaries. Subcosta reaching apical third of wing, with 4–5 branches. Radius not reaching wing apex, with 9–11 veins at margin. M comparatively expanded, with (6)7–10 veins at margin. CuA reduced, with only about 4 branches. Anal veins with at most 7 veins at margin. Dark coloration present in the apical half, with light pair of spots separated by intercalaries.

Hindwing except for apex without coloration, with simple long Sc, R1 with 4 branches in both preserved hindwings; RS with 3 branches (both hindwings). M with 6–9 branches (6 in both hindwings of the holotype; 9 in left hindwing of 2554/77), unusually rich even in respect to larger cockroaches with ordinary (not reduced) venation. CuA with secondarily branches (5 or more).

Holotype: adult female, PIN 2554/44, Mikhailovka, South Karatau, Kazakhstan, Karabastau Formation, Late Jurassic. **Additional material:** complete adult (sex unknown), PIN 2554/77; left forewing, PIN 2066/322; immature, PIN 2784/684. All same origin as holotype.

Remarks. The female sex may be determined based on divided subgenital plate, and a presence of rudiments of external ovipositor.

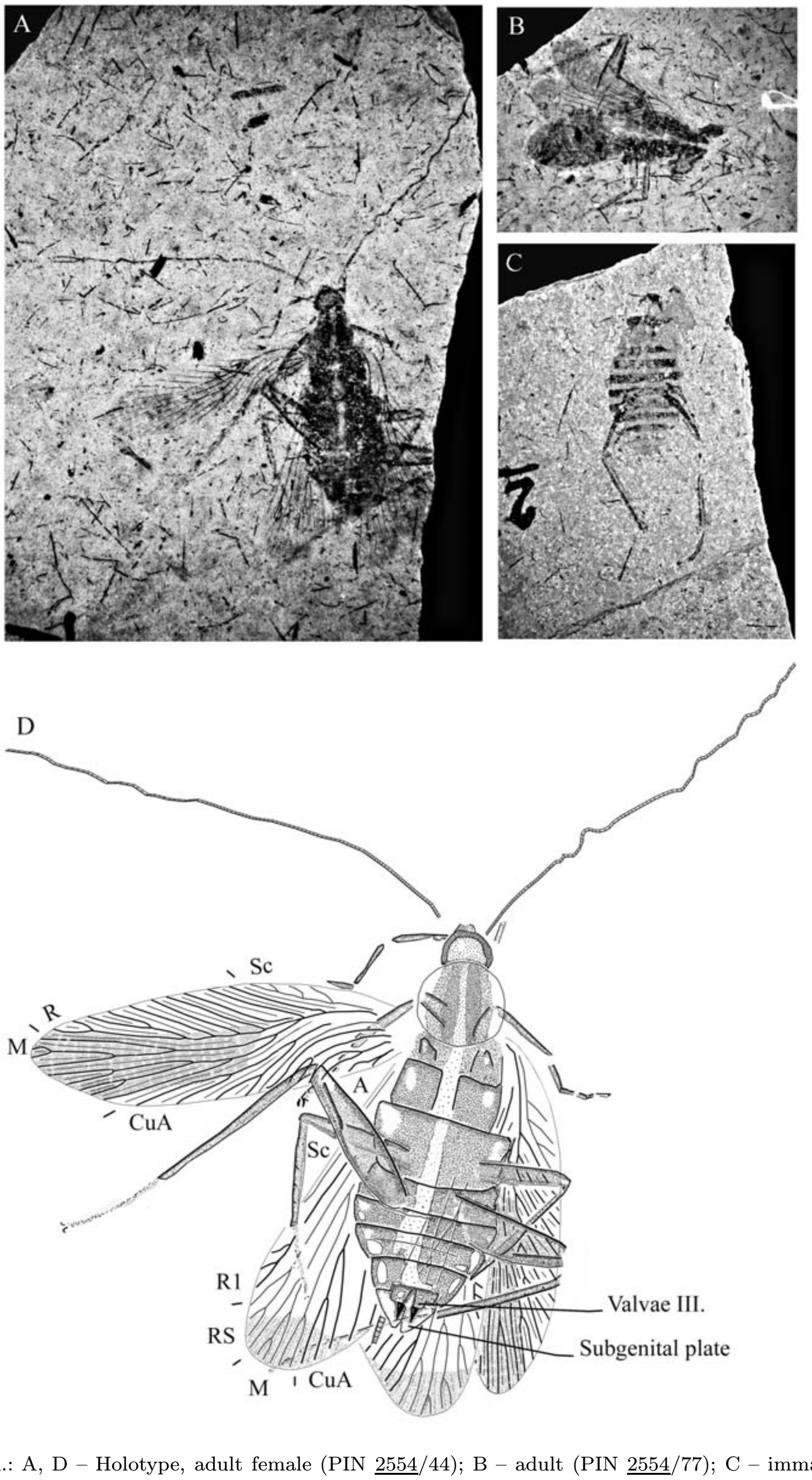

Fig. 1. *Skok svaba* sp. n.: A, D – Holotype, adult female (PIN 2554/44); B – adult (PIN 2554/77); C – immature (PIN 2784/684). Photographed immersed in alcohol with polarizing illumination. Sc – subcosta, R, R1 – radius, RS – radius sector, M – media, CuA – cubitus anterior, A – anal.

Etymology. After "šváb" (Slovak word for "cockroach").

Discussion

Jumping adaptations require general bauplan reorganization as evidenced by frogs, kangaroos, jerboas, and among insects by grasshoppers, fleas, cicadas, beetles and also the present cockroach species.

Jumping adaptation of insects characterise higher taxa such as archaeognathans, orthopterans, cicadas and fleas, but the mechanics of jump vary. Main muscles involved in jump are abdominal in machilis; thoracical in cicadas, fleas, winter scorpion flies (*Boreus)* and diverse flies; femoral in orthopterans, wasps and beetles. Nevertheless, even those insects with femora incrassate, may retain thoracic muscles important in jumping, e.g., some chalcidoid wasps are good jumpers, and only few of them have hind femora incrassate, Encyrtidae and Eupelmidae jump with mid legs which are ordinary in femur form.

All things being the same, saltatory adaptations have primarily evolved as escaping strategy, consequently being used in many different ways such as flight initiation and capturing prey. The evolutionary meaning of jump is high. The ecological problem of insects with incomplete metamorphosis is that their immature stages lack wings as escaping tools. As a result, holometabolous insects with alternative defending strategies (jumping or smelling) dominate in living ecosystems. Other hemimetabolous insects change environment during ontogenesis (dragonflies, ephemerans, plecopterans), or imagines lack wings as in some dermapterans, ice crawlers, embiopterans, zorapterans, termites, cockroaches, trips, scale insects, lice, stick insects, psocopterans, which is a result of narrow specialisation (Rasnitsyn 1965).

Fossils considered below are morphologically unique and distinctive in being minute, slightly laterally compressed, but most notable in possessing saltatorial hindlegs with reduced spines, while the fore- and midlegs are reduced to some extent (Fig. 1). Saltatory adaptations include robust, wide femora bearing a marked supporting ridge with reduced carination, a significant reduction in the size of tarsi, and free coxae, associated with comparatively terminally positioned legs in respect to other cockroaches. Also significant are the terminalia, representing geochronologically the oldest known cockroach taxon with reduced ovipositor, indicating modern form of reproduction, i.e., eggs were laid within soil substrates or possibly enveloped by leathery oothecae (an egg case of extant cockroaches), unlike the Palaeozoic and Mesozoic cockroaches which possessed an external ovipositor and deposited eggs directly into a substrate. According to designation of the present family within the living Polyphagoidea, this advanced, virtually modern reproduction shifts the origin of the modern cockroaches deeper into the Mesozoic and the origin of modern reproduction might be traced to the ancestors of this taxon, known since the Middle Jurassic. These are apparently represented by advanced Liberiblattinidae as evidenced by the unique morphology of wings, the pronotum and the palpae. An undescribed species of the Liberiblattinidae additionally possess comparatively large legs (unpublished data).

The existence of this structurally unique taxon demonstrates the extreme plasticity of the stem group Polyphagoidea, which gave rise to termites and mantises (Vršanský 2002), and was ancestral for all living cockroach families.

Convergent changes such as body and wing size reduction, transparency and reduced venation of wings are observable in the mostly diurnal Mesozoic cockroach family Blattulidae (Vršanský 2004). By analogy with those body structures, and with the small facets, the new taxon also represents a diurnal species. Nevertheless, in the Blattulidae these changes are associated with a relative enhancement of head size, a reduced number of antennal segments and a shortening of labial and maxillary palps. The Blattulidae additionally possessed apparently short but robust ovipositor.

The newly discovered, supposedly saltatory cockroach (position of legs under the body (even at least partially laterally compressed) limit the jumping abilities) did not cross the Jurassic/Cretaceous boundary, but during the Karatau (Upper Jurassic) time it might be not rare in spite only three adults and one immature (of about 3,000 cockroaches preserved at the site) are preserved. This may be due to taphonomical reasons – the species is very small, fragile and an excellent flier. Even perfectly preserved specimens are barely visible in rocks, requiring the application of alcohol and/or polarized illumination. The finding of an immature of this taxon, one of only about 50 immature cockroaches collected at Karatau, also contradicts the rarity, but it may also indicate living close to water and question the spatiotemporal abundance (in spite of the eventual confinement of jumping specimens to one layer).

Judging from living species with similar life habits (symmetrical wings, light body and wings, but without jumping adaptations), the act of jumping was not necessary to initiate flight or associated with carnivory. Extant small and light-weight tropical cockroaches are excellent fliers and yet they have no apparent jumping adaptations. The new fossil species was apparently an excellent flier, indicated by symmetry of its wings. The association of jumping with carnivory likewise can be excluded for the present species, attributable to their comparatively small heads, suggesting palynivory. However, considerably long palpae occur in cockroaches such as the predaceous Mesozoic Raphidiomimidae as well as in palynivorous species. The light body disallows the precise direction of jump.

Thus, the most likely hypothesis for the saltatory habits in this cockroach is an escape strategy, retained also for immatures of some species of praying mantises and cockroaches, the latter including *Dorylea* (D. Mann, personal communication) inhabiting early succession communities. The reproductive success of some extant adult male mantids such as *Tenodera sinensis* (Saussure, 1871) is based on the efficacy of a single precise jump directed towards the female – otherwise the male is eaten by his prospective mate (Liske & Davis 1987). Jumping in mantises is retained mostly in smaller species, which may use both mid- and hind legs characterized by femora that are widened proximally (Anisyutkin & Gorochov 2004). Even excluding insects such as immatures of the moth *Cydia saltitans* (Westwood, 1858) responsible for movements of Mexican bean, or the gall wasp *Neuroterus saltatorius* (Edwards, 1874) causing jumping of the Garry oak acorn, jumping as the primary means of locomotion has independently arisen several times in pterygote insects recognized clades such as fleas, grasshoppers, cicadas, true bugs, beetles, dipterans, hymenopterans, scorpion flies, mantises, and, now, also in one taxon of cockroaches.

Acknowledgements

I thank Prof. A.P. Rasnitsyn (Paleoeontological Institute, Moscow), Dr. L. Anisyutkin (Zoological Institute, Petersbourg), Dr. Ľ. Vidlička (Institute of Zoology, Bratislava), Dr. C. Nalepa (North Carolina State University, Raleigh), Dr. G. Beccaloni (Natural History Museum, London), Dr. D. Mann (Hope Entomological Collection, Oxford) and Dr. C. Labandeira (National Museum of Natural History, Washington, D.C.) for revision of the manuscript and for fruitful consultations. The research was supported by the UNESCO-IGCP-458, VEGA No. 2/6002/27, MVTS, and Literárny fond, Bratislava.

References

Anisyutkin L.N. & Gorochov A.V. 2004. *Haania doroshenkoi*, a new species of mantises from Cambodia (Mantina: Mantidae: Thespinae) and a case of mirror symmetry in the structure of the male genitalia of mantises. Rus. Entomol. J. **13 (3):** 119–122.

Gao K.Q. & Ren D. 2006. Radiometric dating of Ignimbrite from inner Mongolia provides no indication of a post-middle Jurassic age for the Daohugou Beds. Acta Geol. Sin. **80:** 42–45.

Gekker R.F. 1948. Karatau – locality of Jurassic fauna and flora. Trudy Paleontol. Inst. AN SSSR **15:** 7–85.

Gubin Y.M. & Sinitza S.M. 1996. Shar-Teg – a unique Mesozoic locality of Asia, pp. 311–318: In Morales M. (ed.), The Continental Jurassic, Mus. South Arisona Bull. **60**.

Koval T.M. 1983. Intrinsic resistance to the lethal effects of x-irradiation in insect and arachnid cells. Proc. Natl. Acad. Sci. U. S. A. **80:** 4752–4755.

Liske J. & Davis W.J. 1987. Courtship and mating behavior of the Chinese praying mantis *Tenodera aridifolia sinensis*. Anim. Behav. **35:** 1524–1537.

Nagamitsu T. & Inoue T. 1997. Cockroach pollination and breeding system of *Uvaria elmeri* (Annonaceae) in a lowland mixed-dipterocarp forest in Sarawak. Am. J. Bot. **84:** 208–213.

Rasnitsyn A.P. 1965. Some aspects of interrelations between morphogenesis and growth in the evolution of insect ontogeny. Entomol. Obozr. **44:** 476–485. [in Russian, English translation in Entomol. Rev. **44:** 279–284].

Roth L.M. 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). Oriental Insects **37:** 1–186.

Schal C., Gautier J.Y & Bell W.J. 1984. Behavioural ecology of cockroahes. Biol. Rev. **59:** 209–254.

Shelford R. 1909. Note on some amphibious cockroaches. Record of the Indian Museum **3:** 125–127.

Takahashi R. 1926. Observations on the aquatic cockroach, *Opistoplatia maculata*. Dobutsugaku Zassi **38:** 89.

Vidlička L., Vršanský P. & Shcherbakov D.E. 2003. Two new troglobitic cockroach species of the genus *Speleoblatta* (Blattaria: Nocticollidae) from North Thailand. J. Nat. Hist. **37:** 107–114.

Vishniakova V.N. 1973. New cockroaches (Insecta: Blattodea) from the Upper Jurassic sediments of the Karatau, pp. 64–77. In: Narchuk E.P. (ed.), Problems of the Insect Palaeontology, Lectures on the XXIV Annual Readings in Memory of N.A. Kholodkovsky (1–2 April, 1971), Nauka, Leningrad.

Vršanský P. 2000. Decreasing variability – from the Carboniferous to the Present! (Validated on Independent Lineages of Blattaria). Paleontol. J. **34,** Suppl. 3: 374–379.

Vršanský P. 2002. Origin and the early evolution of Mantises. Amba Projekty **6 (1),** 16 pp. http://fossilinsects.net/lib.htm

Vršanský P. 2003. Umenocoleoidea – an amazing lineage of aberrant insetcs (Insecta, Blattaria). Amba Projekty **7 (1),** 32 pp. http://fossilinsects.net/lib.htm

Vršanský P. 2004. Transitional Jurassic/Cretaceous cockroach assemblage (Insecta, Blattaria) from the Shar-Teg in Mongolia. Geologica Carpathica **55:** 457–468.

Vršanský, P. 2005. Mass mutations of insects at the Jurassic/Cretaceous boundary? Geologica Carpathica **56:** 473–781.

Vršanský P., Quicke D.L.J., Rasnitsyn A.P., Basibuyuk H., Ross A., Fitton M. & Vidlicka L. 2001. The oldest fossil insect sensilla. Amba Projekty **4 (1),** 8 pp. http://fossilinsects.net/lib.htm

Zompro O. & Fritzsche I. 1999. *Lucihormetica* n. gen. n. sp., the first record of luminescence in an orthopteroid insect (Dictyoptera: Blaberidae: Blaberinae: Brachycolini). Amazoniana **15:** 211–219.

Received April 12, 2006
Accepted July 4, 2007