GEOLOGICA CARPATHICA, APRIL 2015, 66, 2, xx–yy doi: 10.1515/geoca-2015-0015

New predatory cockroaches (Insecta: Blattaria: Manipulatoridae fam.n.) from the Upper Cretaceous Myanmar amber

PETER VRŠANSKÝ[1] and GÜNTER BECHLY[2]

[1]Geological Institute SAS, Dúbravská cesta 9, P.O.Box 106, SK-840 05 Bratislava, Slovak Republic; geolvrsa@savba.sk
[2]Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany; guenter.bechly@smns-bw.de

(Manuscript received January 9, 2015; accepted in revised form March 12, 2015)

Abstract: We describe a new extinct lineage Manipulatoridae (new family) of cockroaches from the Upper Cretaceous (Cenomanian) amber of Myanmar. *Manipulator modificaputis* gen. et sp. n. is a morphologically unique extinct cockroach that represents the first (of a total of 29 known worldwide) cockroach family reported exclusively from the Myanmar amber. This family represents an early side branch of the stem group of Mantodea (most probably a sister group of Eadiidae within Blattaria/Corydioidea) because it has some synapomorphies with the Mantodea (including the stem group and Eadiidae). This family also retains symplesiomorphies that exclude a position in the crown group, and furthermore has unique autapomorphies that exclude a position as a direct ancestor of Mantodea. The unique adaptations such as strongly elongated extremities and freely movable head on a long neck suggest that these animals were pursuit predators. Four additional specimens (including an immature) reported from the Myanmar amber suggest that this group was relatively rare but belonged to the indigenous and autochthonous inhabitants of the ancient amber forest of the Myanmar region.

Key words: fossil insect, new cockroach family, Mantodea, Blattodea, Upper Cretaceous Mesozoic amber, Myanmar.

Introduction

Big predatory dictyopterans are represented mostly by praying mantises (Mantodea), which can be derived from extinct cockroaches, as recently summarized by Hörnig et al. (2013) and Lee (2014), namely from the family Liberiblattinidae (Vršanský 2002). Nevertheless, some other Mesozoic lineages of cockroaches that are well studied also possessed predatory lifestyles (e.g. on the basis of their gut-content). These include representatives of the families Raphidiomimidae and Eadiidae, both occurring in the Jurassic sediments and Cretaceous ambers, although they are missing in some of the richest fossiliferous Cretaceous sediments (Vishniakova 1973; Vršanský 2003, 2009; Grimaldi 2003; Liang et al. 2009, 2012). The amber record includes *Raphidiomimula burmitica* (herein categorized within Eadiidae) from Myanmar (Grimaldi & Ross 2004), but also many more unstudied species of both families. Here, we describe the holotype specimen of a new species belonging to a morphologically-deviant new family. This species was probably a pursuit predator, filling a niche previously not exploited by extinct cockroaches, differing from pursuit predatory behaviour of the significantly larger and more robust (with extremities of standard length) and phylogenetically different Raphidiomimidae (Caloblattinoidea) that differ in their prognathous head and short neck.

Methods

The specimen was collected in a quarry in the Hukawng valley (26°15′N; 96°33′E; fig. 1A — Cruickshank & Ko 2003). The rock matrix containing amber of the earliest Cenomanian age (Shi et al. 2012) is represented by a greyish to bluish-green volcanoclastic mudstone (Cruickshank & Ko 2003), located in the fine-grained facies of sedimentary rocks at Noije Bum. The host rock is poorly consolidated, such that it can be readily broken with bare hands and petrologically varies between fine-grained sandstones and shales. The amber discs lie parallel to the bedding planes of fine-grained sediment (see Shi et al. 2012 for petrological details). These sediments were deposited in a nearshore environment, with the amber resin being derived from a tropical forest with Araucaria trees.

The specimen was studied with a Leica M80 stereo microscope. Photographs were taken with a Leica DFC490 digital macro camera on a Leica Z16-Apo Macroscope and processed with Leica Application Suite 3.8.0 for focus stacking. Photos were enhanced with Adobe Photoshop™ CS6 image processing software to merge photographs and to reveal the natural colour of the inclusion(s) without the orange tint from amber (selective colour mode and white balance adjustment). Drawing consists of 34 separate photographs (each of them composed of up to 300 shots) redrawn (using stereomicroscope) with Corel Draw X3. Shadows were added using Adobe Photoshop™ CS6.

The concept of "roachoids" is rejected here on the basis of studies of the extinct family Fuziidae (Vršanský et al. 2009). Instead, we use the common name "cockroaches" for all insects that belong to the crown group of Dictyoptera and are similar in habitus to living cockroaches, even if they are basal stem group representatives of Mantodea and/or Isoptera.

Results

Systematic paleontology

Order **Blattaria** Latreille, 1810
Superfamily **Corydioidea** Saussure, 1864
Family **Manipulatoridae** Vršanský et Bechly, fam.n.

Genotype: *Manipulator* Vršanský et Bechly, gen.n.

Composition: Monotypic, only including *Manipulator modificaputis* Vršanský et Bechly sp.n. from the Upper Cretaceous Myanmar amber.

Differential diagnosis: This family differs from all known fossil and living cockroaches by a set of unique autapomorphies, comprising extremely elongated extremities, including semi-raptorial forelegs and extremely long leg-like maxillary palps, modified three basal antennal segments, extremely elongated neck, ocelli with roof-like covering sheaths; elongated saddle-like pronotum; and numerous minute trichoid sensilla (minute hairs). Elongated forewing is unique in having short simply dichotomized at base SC and in dense venation with long A branches within clavus.

Description: As for genus and species.

Manipulator Vršanský et Bechly gen.n.

Type species: *Manipulator modificaputis* Vršanský et Bechly sp.n.

Etymology: Alluding to the extremely long extremities for manipulation of prey.

Diagnosis: As for monotypic family.

Description: As for species.

Manipulator modificaputis Vršanský et Bechly sp.n.

Material: Holotype specimen no. SMNS Bu-116 at State Museum of Natural History Stuttgart, Germany.

Type locality: Hukawng Valley, Kachin State, Myanmar.

Type horizon: Myanmar amber (Burmite), Upper Cretaceous, earliest Cenomanian, ca. 99 Ma (Shi et al. 2012).

Etymology: Combined from *modificare* (Latin for regulate) and *caput* (Latin for head), alluding to the derived head.

Diagnosis: As for monotypic family.

Description: A complete male cockroach with detached right mid and hind femora.

Head elongated, 1.7 mm long, 1.5 mm wide, orthognathous posed on extremely long (1.9 mm) prothorax (alternative positions can be excluded based on the central attachment on the neck, contrary to the basal one in prognathous Raphidiomimidae). Eyes large, protruding beyond the head outline. Ommatidia large (roughly 12 per 0.01 mm^2), amounting to about 310 for each compound eye. Lateral ocelli extremely well developed, protruding above cuticular surface, rounded. Both are covered with distinct, dark black covering roof-like sheath. Central ocellus invisible (its position is visible, covered with normal head pigment, so its presence below transparent cuticle such as those of *Eadia aidae* Vršanský, 2009 is excluded). Antenna black, with at least 55 comparatively wide segments (width 0.14 mm). Segments 1–3 modified (elongated, widened, curved and carved as in Fig. 1C,D, the 1st and 2nd segments are 0.6 mm long each), segments 4–10 not specially short. Segment 11 modified (on both sides), short, other segments consequently elongating towards apex. Maxillary palp black, extremely elongated (1.3/2.4/?/?/0.7 mm; 1.1/1.3/2.4/2.0/0.7 mm) with spatulate terminal segment. Labial palps slightly elongated, transversely pale/dark coloured (with stripes).

Pronotum significantly concavely curved, corrugated, saddle-shaped, and slightly elongated (length/width: 1.9/1.4 mm), with black and white stripes (Figs. 1C,D, 2A,B).

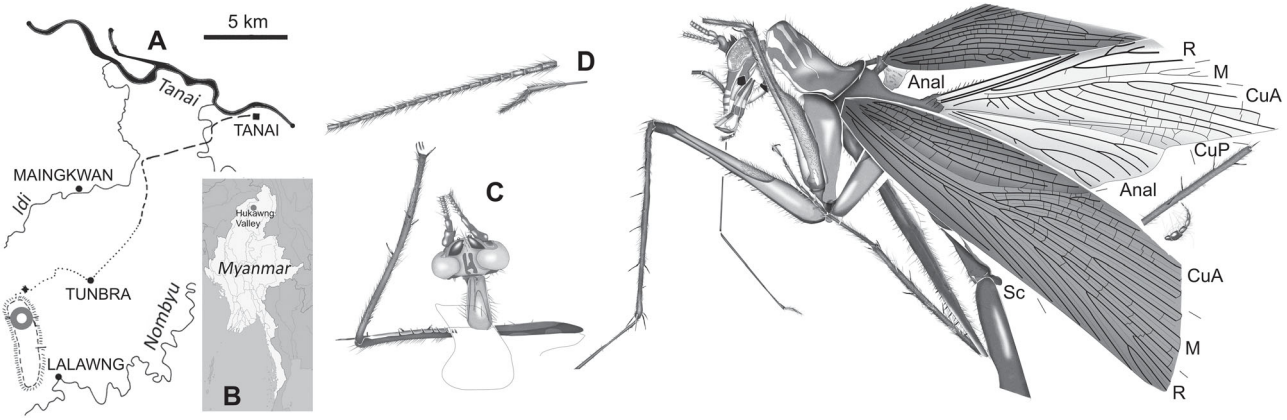
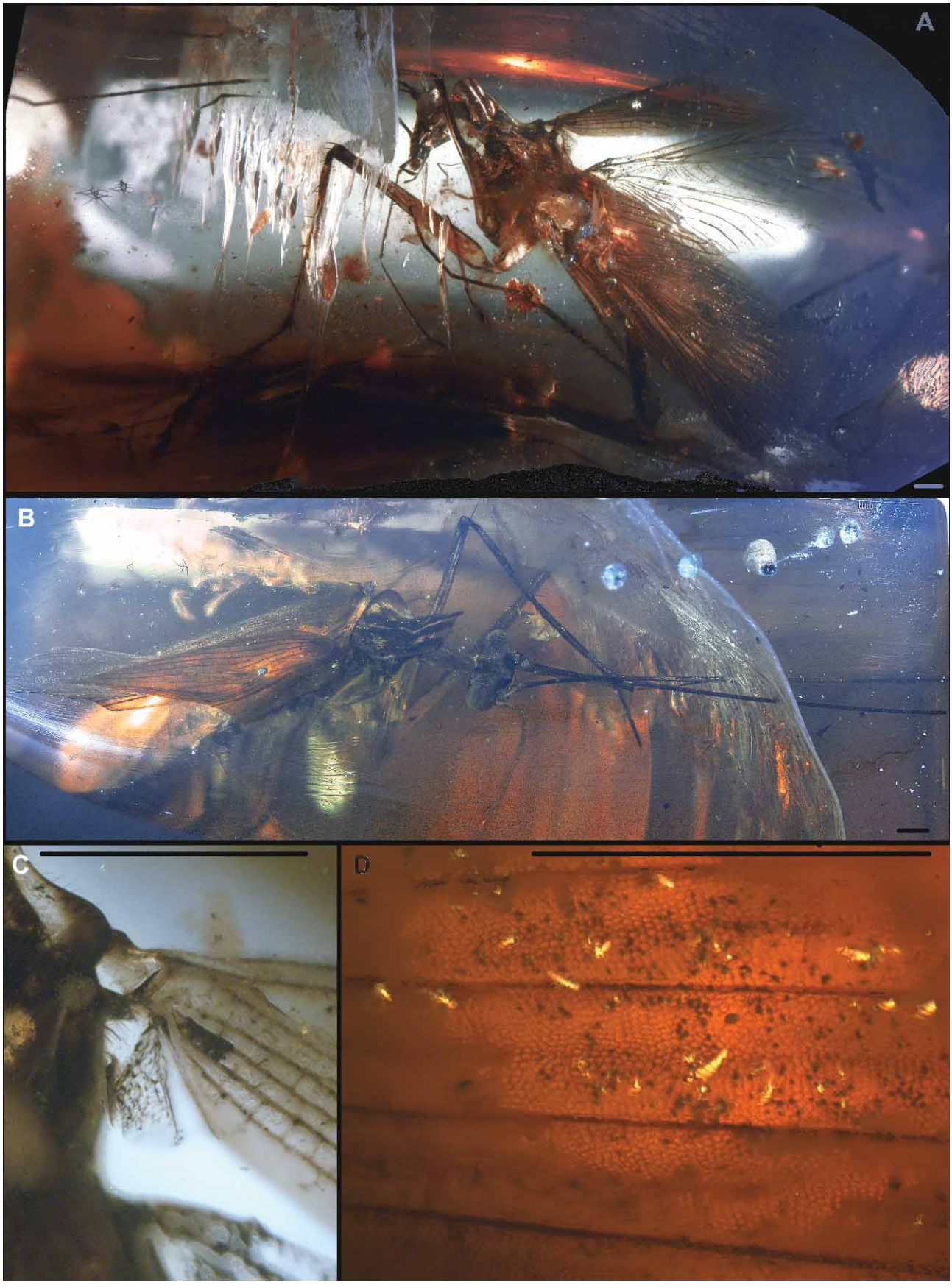


Fig. 1. Location map within (North) Myanmar (**A, B**) Hukawng Valley, Kachin state (Copyright of map: Uwe Dedering, Wikimedia Commons, under free GNU/CC licence; and modified after Cruickshank & Ko 2003) and *Manipulator modificaputis* gen. et sp. n. (Manipulatoridae fam.n.) holotype SMNS Bu-116 (deposited in the Stuttgart Museum of Natural History) from the Cretaceous Myanmar amber (**C, D**). All hairs are drawn in their proper places. Forewing length 8.3 mm as preserved.

Fig. 2. *Manipulator modificaputis* gen. et sp. n. (Manipulatoridae fam.n.) holotype SMNS Bu-116 (deposited in the Stuttgart Museum of Natural History) from the Cretaceous Myanmar amber. **A** — left view, **B** — dorsal view, **C** — detail on the forewing articulation, **D** — forewing surface hexagonal structure. Scales 0.5 mm.


A
B
C
D

Legs. All leg segments extremely elongated and covered with dense setation (short trichoid hairs — sensilla chaetica). Forecoxa 2.5 mm long, of characteristic shape, and differently coloured on both sides (see Figs. 1D, 2A), forefemur 4.0 mm long, with ventral strong but very short spurs, pale/dark striped; foretibia black, 4.8 mm long. Tarsomere1 of foreleg black and very long (2 mm) long. Mid leg incapable of total bending. Length of segments as follows: Coxa 2.1 mm, femur 4.3 mm, tibia 4.8 mm, tarsomeres 1–5 1.7/0.8/0.3/0.1/0.3 mm. Hind femur 2.7 mm long, tibia 3.2/0.12 mm (length/width).

Forewing 8.3 mm long (as preserved) and 2.8 mm wide, with distinct long clavus; whole sparsely covered with hexagonal surface microstructure and long sensilla chaetica (Fig. 2D). Distance between fore and hind wing extremely elongated (about 2 mm).

Hind wing (5.4 mm length of pleating area) pleating except for base without trichiae. Left hind wing at least with one fusion (sensu Vršanský 2005 — R1 dichotomized improperly, see Wei & Ren 2013 for the same deformity type in another Mesozoic cockroach; smaller insects such as cockroach parasites reveal such theratologies rarely — Li et al. 2014). Characters of wing venation are listed in detail in the character analysis section.

Body dorsoventrally flattened, wide. The preserved body length is about 4.5 mm, width is difficult to measure, but the body is very wide as in standard cockroaches (over 2 mm), a little narrower basally, pale, with black lateral maculas. Cerci 0.3 mm wide, extremely elongated, with 20 segments and diverse sensilla including extremely long and thin filaments and a terminal spine (both trichoid sensilla chaetica). Terminal hook (*hla*- sclerite according to Klass & Meier 2006) very strongly chitinized and black. Setation present throughout the specimen as short fine trichoid sensilla chaetica. Characteristic for cockroaches long sensilla (hairs and spines) are restricted to certain regions such as foreleg and pronotum. Typical spurs including the femoral terminal spur are significantly shortened (a trend further expressed in mantodeans).

Phylogenetically annotated list of characters of the species

Character polarization was established by outgroup comparison with Paleozoic cockroach-like stem Dictyoptera as well as modern cockroaches and mantodeans:

- Head connection extremely mobile — autapomorphy;
- Eyes extremely large, protruding beyond head outline — synapomorphy with Eadiidae (in mantodeans and Raphidiomimidae, eyes are constructed differently, in predatory Liberiblattinidae eyes are unkown; large eyes are also present homoplastically as a jumping adaptation in Skokidae and *Saltoblattella montistabularis* — see Bohn et al. 2010 and Picker et al. 2012);
- Ocular facets comparatively large — symplesiomorphy at level of order Blattaria;
- Lateral ocelli extremely well-developed — autapomorphy;
- Central ocellus missing — apomorphy (homplastic loss in numerous cockroach lineages, but not mantodeans);
- Superocular lateral ocelli-overing roof-like shield — synapomorphy with some mantodeans;
- Antennal segments 1–3 extremely modified (elongated, widened, curved and carved) — autapomorphy;
- Antennal trichoid sensilla comparatively short, in 3–6 rows — synapomorphy of Corydioidea (including Blattulidae, Liberiblattinidae, Mantodea and likely (unproved) also "*Voltziablatta*-group");
- Antennal segment 11 extremely short and modified: this character can represent a theratologic — like deformity (in both antennae). However, the character is autapomorphic and is presented here due to its very unusual character (antennal segment 3rd and more apical is extremely rarely modified in Dictyoptera);
- Antenna segments 4–13 short — plesiomorphy at level of earliest Dictyoptera (including earliest mantodeans and termites);
- Mandibles large and partially uncovered — symplesiomorphy for the order Blattaria;
- Maxillary palps extremely elongate — autapomorphy;
- Terminal palpomere extremely small, but elongated with ventral cavity — autapomorphy;
- Neck present as a very narrow and extremely elongated connection to the prothorax — autapomorphy;
- Pronotum saddle-like, elongated — autapomorphy;
- Forewing elongated (1:4) — autapomorphy within Corydioidea (occurs by multiple convergence in mantodeans, Mutoviidae, and Raphidiomimidae);
- Forewing SC short, only reaching level of clavus — plesiomorphy at the level of Blattaria (SC elongates in certain Liberiblattinidae and their direct descendants including earliest Mantodea);
- Forewing SC consisting of two near base separated simple branches — autapomorphy;
- Forewing R reduced to less than 10 branches at margin — autapomorphy;
- Forewing A branched — symplesiomorphy at level of order Blattaria;
- Forewing A dense with long branches — synapomorphy with mantodeans (homplastic in some Paleozoic and living taxa);
- Forewing pseudovein missing — symplesiomorphy at level of order Blattaria (pseudovein present in earliest mantodeans);
- Forewing clavus extremely long — autapomorphy;
- Forewing intercalaries distinct, wide, cross-veins sporadical — synapomorphy of Corydioidea;
- Fore and hind wing extremely distant (about 2 mm) — synapomorphy with predatory Liberiblattinidae (including certain mantodeans);
- Hind wing lacking fan-like pleating — synapomorphy of Corydioidea;
- Hind wing with sigmoidally curved SC — synapomorphy of Corydioidea;
- Hind wing with sporadically branched R — synapomorphy of Corydioidea;
- Hind wing with branched M — symplesiomorphy at level of Dictyoptera;

- Hind wing with concavely curved main stem of CuA — autapomorphy;
- Hind wing CuA branches simple — autapomorphy (convergent to Blattulidae);
- Hind wing with blind CuA rami — symplesiomorphy at level of Phylloblattoidea (stem Paleozoic superfamily for all modern Dictyoptera);
- Hind wing with CuP weak and simple — autapomorphy;
- Hind wing with simple A1 (reduced) — autapomorphy;
- Body wide, dorsoventrally flattened — symplesiomorphy at the level of order;
- Legs extremely elongated (including coxae) — autapomorphy (convergent to Raphidiomimidae, but not to that extent);
- Terminal femoral spur nearly reduced (synapomorphy with mantodean lineage);
- Leg spines largely reduced — autapomorphy;
- Foreleg with extremely long tibia — autapomorphy, convergent to Raphidiomimidae;
- Forefemur with tibia filling shifted ventrally, with few strong, but very short spurs — autapomorphy (different from both mantodeans and all raptorial cockroaches);
- Terminal claw symmetrical, large — autapomorphy;
- Arolium present —symplesiomorphy at the level of Dictyoptera;
- Arolium nearly reduced — synapomorphy with some primitive fossil stem mantodeans;
- Leg sensilla chaetica — hairs, numerous and short, often defragmented — synapomorphy with mantodeans (present also in some Umenocoleidae=Ponopterygidae and Nocticolidae);
- Cerci elongated: synapomorphy with lineage leading to Mantodea (including predatory cockroaches Liberiblattinidae and Eadiidae);
- Cerci with extremely long filaments — synapomorphy of Corydioidea;
- Styli short with few segments — synapomorphy for Corydoidea except Blattulidae and "*Voltziablatta*-group".

Discussion

On the basis of fossil evidence and wing venation characters, we endorse a reclassification of Dictyoptera, in which the order Mantodea is phylogenetically subordinate within the Corydioidea (=Polyphagoidea) — a superfamily that includes diverse extant but also extinct cockroaches sometimes placed within Dictyoptera but outside the standard order of cockroaches (Blattida, Blattaria or Blattodea — see Vršanský 2002). This interpretation of phylogeny contradicts some other morphological and molecular studies (see Djernaes et al. 2012, 2014 for summarization), which rather support a holophyletic Blattodea (only recent cockroaches+termites) as a sister group of Mantodea. Nevertheless, the short forewing SC vein and the reduced central ocellus of Manipulatoridae implies that this family belongs to Blattaria (=Blattodea) in the traditional sense, and could be interpreted as evidence against an attribution to the stem group of Mantodea. However, the following discussion is based on the new classification described above.

The new family Manipulatoridae can be attributed to Dictyoptera on the basis of multisegmented cerci, dorsoventrally flattened body, and forewing with clavus. The plesiomorphic well-developed clavus excludes a position at least in the crown group of Isoptera. A position in the crown group of Mantodea can be excluded on the basis of the missing forewing pseudovein, missing central ocellus, undifferentiated mouthparts, cockroach-like hind wing venation, and only partly differentiated forelegs.

The hind wing venation is of the derived pattern typical of Corydioidea, so that the new family can be assigned to this group. In addition to the characters mentioned above, the supraocular sheaths support an attribution of this family to the stem group of mantodeans within Corydioidea, most probably as a sister taxon to Eadiidae, with which it shares the enlarged and protruding eyes. However, the raptorial forelegs have autapomorphic specializations (short and strong spurs, elongated segments including tibia), which exclude a direct ancestral position relative to Mantodea.

Even though this new taxon exhibits striking convergences to the predatory cockroaches of the family Raphidiomimidae (elongated legs, derived head with narrow neck, modified pronotum), a closer relationship can be excluded on the basis of the corydioid venation of both wings, contrasting with caloblattinoid venation of the Raphidiomimidae. As a result of the unique habitus with numerous autapomorphies along with several plesiomorphies, the erection of a new family is well justified.

The absence of spines on the walking legs suggests that this species was an active runner and pursuit predator, which evolutionarily lost the passive protection of spines. The surface of the holotype is covered with fine hairs — sensilla chaetica, often detached from the insect body (dislocated up to 2 cm). The individual was apparently an old imago, as is documented by the presence of few parasites as well as by numerous broken setae and detached hairs. However, the large piece of amber does not allow the documentation and identification of the globular multicellular parasites attached to the head and body as well as the parasite-like looking cells with dichotomous filaments on the knee articulations (Myanmar amber also yielded a gametocyst of the gregarine protozoan parasite, *Primigregarina burmanica* (Poinar 2014) attached to a cockroach). Some sensilla detachments were apparently not caused by the trapping in amber, but rather happened during life prior to deposition because they are missing or are damaged in numerous small areas of the body (especially on legs) and do not occur in the adjacent parts of amber.

The new species exemplifies the reverse trend to that observed in the mantodeans, namely an elongation of extremities, including palps. This elongation especially applies to the elongation of tibia – a trend validated for both Eadiidae and Raphidiomimidae (Vršanský 2009; Liang et al. 2012).

In addition to the pursuit predatory lifestyle, it can be inferred that these insect were autochthonous inhabitants of the Cretaceous Araucaria amber forest in Myanmar. This inference is mainly based on the fact that four additional specimens of this new taxon (with one early immature specimen) are known to us from traders of Myanmar amber inclusions.

According to data of Grimaldi et al. (2002) and Ross et al. (2010) obtained for Myanmar, it is a fraction of 2/5 resp. 4 % of collected insect represented by cockroaches.

Acknowledgments: We thank four anonymous reviewers for helpful comments and Dr. Sieghard Ellenberger (Kassel, Germany) for discovering this specimen, preparing it, and making it available for science. The first author is grateful to Dr. K. Wolf-Schwenninger (SMNS) for support during his visit to the Stuttgart museum. This work was supported by the Slovak Research and Development Agency under the contract No. APVV-0436-12, and by UNESCO-Amba; VEGA 2/0125/09, 0012-14; MVTS; Literary Fund.

References

Bohn H., Picker M. & Klass K.D. 2010: A Jumping Cockroach from South Africa, *Saltoblattella montistabularis*, gen. nov., spec. nov. (Blattodea: Blattellidae). *Arthropod Systematics & Phylogeny* 68, 1, 53–69.

Cruickshank R.D. & Ko K. 2003: Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *J. Asian Earth Sci.* 21, 441–445.

Djernæs M., Klass K.D. & Eggleton P. 2014: Identifying possible sister groups of Cryptocercidae+Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. *Mol Phylogenet. Evol.* Doi: 10.1016/j.ympev.2014.08.019

Djernæs M., Klass K.D., Picker M.D. & Damgaard J. 2012: Phylogeny of cockroaches (Insecta, Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling. *Sys. Entomology* 37, 1, 65–83.

Grimaldi D. 2003: A revision of Cretaceous Mantises and their relationships, including new taxa (Insecta: Dictyoptera: Mantodea). *Amer. Mus. Novit.* 3412, 1–47.

Grimaldi D.A. & Ross A.J. 2004: *Raphidiomimula*, an enigmatic new cockroach in Cretaceous amber from Myanmar (Burma) (Insecta: Blattodea: Raphidiomimidae). *J. Sys. Palaeontology* 2, 2, 101–104.

Grimaldi D.A., Engel M.S. & Nascimbene P.C. 2002: Fossiliferous cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. *Amer. Mus. Novitates* 3361, 1–72.

Hörnig M.K., Haug J.T. & Haug C. 2013: New details of *Santanmantis axelrodi* and the evolution of the mantodean morphotype. *Palaeodiversity* 6, 157–168.

Klass K.-D. & Meier R. 2006: A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. *Entomol. Abh.* 63, 1–2, 3–50.

Lee S. 2014: New Lower Cretaceous basal mantodean (Insecta) from the Crato Formation (NE Brazil). *Geol. Carpathica* 65, 4, 285–292.

Li L.F., Shih C.C. & Ren D. 2014: Revision of *Anomopterella* Rasnitsyn, 1975 (Insecta, Hymenoptera, Anomopterellidae) with two new Middle Jurassic species from northeastern China. *Geol. Carpathica* 65, 5, 365–374.

Liang J.H., Vršanský P. & Ren D. 2012: Variability and symmetry of a Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae). *RMSG* 29, 2, 411–421.

Liang J.H., Vršanský P., Ren D. & Shih C. 2009: A new Jurassic carnivorous cockroach (Insecta, Blattaria, Raphidiomimidae) from the Inner Mongolia in China. *Zootaxa* 1974, 17–30.

Picker M., Colville J.F. & Burrows M. 2012: A cockroach that jumps. *Biology Letters* 8, 3, 390–392.

Poinar G. Jr. 2014: Evolutionary history of terrestrial pathogens and endoparasites as revealed in fossils and subfossils. *Advances in Biology*, ID 181353, 1–29.

Ross A.J., Mellish C., York P. & Crighton B. 2010: Burmese Amber. In: Penney D. (Ed.): Biodiversity of fossils in amber from the major world deposits. *Siri Scientific Press*, 208-235.

Shi G., Grimaldi D.A., Harlow G.E., Wang J., Wang J., Yang M., Lei W., Li Q. & Li X. 2012: Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163.

Vishniakova V.N. 1973: New cockroaches (Insecta: Blattodea) from the Upper Jurassic of Karatau mountains. In: Narchuk E.P. (Ed.): Problems of the Insect Paleontology Lectures on the XXIV Annual Readings in Memory of NA Kholodkovsky (1–2 April 1971). *Nauka*, Leningrad, 64–77 (in Russian).

Vršanský P. 2002: Origin and the early evolution of Mantises. *AMBA Projekty* 6, 1, 1–16.

Vršanský P. 2003: Unique assemblage of Dictyoptera (Insecta — Blattaria, Mantodea, Isoptera, Mantodea) from the Lower Cretaceous of Bon Tsagaan Nuur in Mongolia. *Entomol. Probl.* 33, 1–2, 119–151.

Vršanský P. 2005: Mass mutations of insects at the Jurassic/Cretaceous boundary? *Geol. Carpathica* 56, 6, 473–781.

Vršanský P. 2009: Albian cockroaches (Insecta, Blattida) from French amber of Archingeay. *Geodiversitas* 31, 1, 73–98.

Vršanský P., Liang J.-L. & Ren D. 2009: Advanced morphology and behaviour of extinct earwig-like cockroaches (Blattida: Fuziidae fam. nov.). *Geol. Carpathica* 60, 6, 449–462.

Wei D. & Ren D. 2013: Completely preserved cockroaches of the family Mesoblattinidae from the Upper Jurassic–Lower Cretaceous Yixian Formation (Liaoning Province, NE China). *Geol. Carpathica* 64, 4, 291–304.