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Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna

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Abstract: Cockroach genera with synanthropic species (*Blattella*, *Ectobius*, *Supella*, *Periplaneta*, *Diploptera* and ?*Blatta*), as well as other insects such as honeybees, although natively limited to certain continents nowadays, had circumtropic distribution in the past. The ease of their reintroduction into their former range suggests a post-Early Miocene environmental stress which led to the extinction of cosmopolitan Tertiary entomofauna in the Americas, whilst in Eurasia, Africa and Australia this fauna survived. This phenomenon is demonstrated here on a low diversity (10 spp.) living cockroach genus *Supella*, which is peculiar for the circumtropical synanthropic brownbanded cockroach *S. longipalpa* and also for its exclusively free-living cavicolous species restricted to Africa. *S. (Nemosupella) miocenica* sp. nov. from the Miocene amber of Chiapas in Mexico is a sister species to the living *S. mirabilis* from the Lower Guinea forests and adjacent savannas. The difference is restricted to the shape of the central macula on the pronotum, and size, which may indicate the around-Miocene origin of the living, extremely polymorphic *Supella* species and possibly also the isochronic invasion into the Americas. The species also has a number of characteristics of the Asian (and possibly also Australian) uniform genus *Allacta* (falling within the generic variability of *Supella*) suggesting *Supella* is a direct ancestor of the former. The present species is the first significant evidence for incomplete hiati between well defined cockroach genera — a result of the extensive fossil record of the group. The reported specimen is covered by a mycelium of a parasitic fungus *Cordyceps* or *Entomophthora*.

Key words: Mexico, synanthropic, fossil insects, parasitic fungi, *Allacta*, *Supella miocenica* sp. nov.

Introduction

Chiapas amber is peculiar for its content of plant remains, occasional fungi, scarce pulmonate gastropods, arachnids, crustaceans, relatively abundant insects, amphibians, reptiles, bird feathers and mammal hair (Poinar 2003; Engel 2004; Solórzano-Kraemer 2007; Vega et al. 2009a,b). Insects are represented by 235 species all of which belong to 146 living families and the living or closely related ($n=3$) genera. The termite *Kalotermes nigritus* Snyder, 1946 (Isoptera, Kalotermitidae), which still lives in South America today (Zherikhin 1970) is famous.

It is worth mentioning that the earliest living insect species are much older, originating from Eocene Baltic amber. These species are *Tetracha carolina* (Linnaeus, 1766) (Coleoptera, Cicindelidae), *Colasposoma metallicum* Clark, 1865; *Palaeomymar anomalum* (Blood & Kryger, 1922) (Hymenoptera, Mymaridae), *Cupes tesselatus* (Motschulsky, 1856) (Coleoptera, Cupedidae) and *Setodes picescens* Ulmer, 1912 (Trichoptera, Leptoceridae). *Drosophila rubrostriata* Becker, 1908 is known from the Oligocene of Fontainebleau.

The specimen reported here was collected from the Los Pocitos locality (Fig. 1) of the amber-bearing Mazantic Shale, overlain by the Balumtum Sandstone (Fig. 1). Both lithostratigraphic bodies are regarded as informal units. The age of the Chiapas amber has been a matter of debate. A Late Oligocene to Early Miocene age has been proposed by Langenheim (1966), Tomasini-Ortíz & Martínez-Hernández (1984), Santiago-Blay & Poinar (1993), Bousfield & Poinar (1994), Poinar & Brown (2002), Poinar (2003), Engel (2004), Castañeda-Posadas & Cevallos-Ferriz (2007). Ferrusquía-Villafranca (2006) described an artiodactyl from the Los Pocitos locality, and considered a Late Oligocene age for these sediments, based on previous biostratigraphic interpretations of Frost & Langenheim (1974) and unreferenced paleomagnetic studies. He suggested that the age of the Los Pocitos strata falls within the 28–26 Ma (Ferrusquía-Villafranca 2006, p. 993). Other authors suggest that the amber-bearing stratigraphic units are of Middle Miocene age, and thus correlatives with the units that produce amber in the Dominican Republic (Meneses-Rocha 2001; Solórzano-Kraemer 2007; Solórzano-Kraemer & Mohrig 2007; Perrilliat et al. 2010). At the Los Pocitos locality (Fig. 1), dark grey shales of the Mazantic Shale contain amber, benthic foraminifera, gastropods, bivalves and crustaceans. Based on $^{87}Sr/^{86}Sr$ measurements taken from a well-preserved shell of *Turbinella maya* from Los Pocitos,

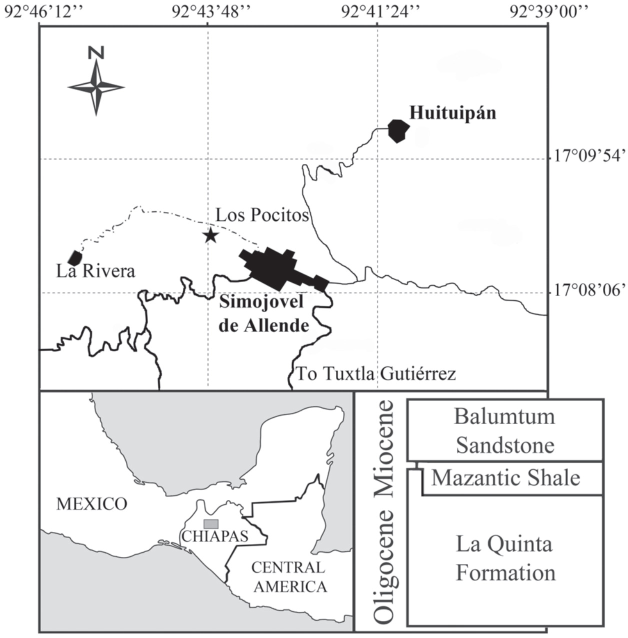


Fig. 1. Location and stratigraphic column of the Los Pocitos locality of the Chiapas amber, Mexico.

Vega et al. (2009a, p. 53) obtained an absolute age of 23 Ma for the Mazantic Shale, placing it right on the boundary between the Oligocene and Miocene. The Mexican amber has been interpreted as the resinous exudates of *Hymenaea* sp., a leguminose tree whose communities developed near the ancient coast, in estuarine environments, very similar to mangroves (Poinar 1992). It is worth mentioning, that the closest relative of amber producing *H. mexicana* is the relictuous *H. verrucosa* from East Africa (Poinar & Brown 2002). Another amber species, *H. allendis* is a relative to *H. courbaril* of Americas (Calvillo-Canadell et al. 2009). The amber was consequently transported to a shallow marine environment (Langenheim 1995; García-Villafuerte 2008).

The native representatives of the genus *Supella* are recently limited to Africa and are considered to have diverged early in the phylogeny of the family, with the genus being the second basalmost offshoot (after *Nahublattella*) of the Blattellidae (Klass 1997). Nevertheless, their position is obscure in some other analyses (see Ware et al. 2008), and there is a single plesiomorphy recorded in respect to most *Symploce* Hebard, 1916 (M and CuA longitudinal), which is considered to be the most primitive blattellid in our previous studies (Vršanský 1997). Thus *Supella* is most likely derived from this genus (Vršanský et al. 2011) or its predecessors.

Thanks to the synanthropic *Supella longipalpa* Fabricius, 1798 (circumtropic — introduced by commerce), the morphology of the present genus is well studied at the microstructural level (Roonwal & Rathore 1983). For example, olfactory, gustatory, and mechanosensory receptors with a density of 73.700 sensilla/mm^2 were found on the most distal segments of maxillary as well as labial palps (Prakash et al. 1995).

The ecology of the genus is much less known. *S. longipalpa* reproduces in temperatures between 25–33 °C (Tsai & Chi 2007). It can be a carrier of human intestinal parasites (Kinfu & Erko 2008), *Salmonella* (Fathpour et al. 2003), perhaps a cryptic species related to *Gregarina blattarum* von Siebold, 1839 (Clopton & Gold 1996) and an allergen source (Tungtrongchitr et al. 2004). Its ootheca may often be parasitized (over 19 %) by host-specific hymenopterans *Comperia merceti* (Compere, 1938) (Encyrtidae) and *Anastatus tenuipes* Bolivar & Pieltain, 1925 (Eupelmidae) (for details see Narasimham 1992). Individuals infected by archiacanthocephalan *Moniliformis moniliformis* (Bremser in Rudolphi 1819) spend more time in the shade (Moore & Gottelli 1992).

S. longipalpa nymphs may be more capable of producing and utilizing extra metabolic water from food than *Blattella germanica* (Linnaeus, 1767) nymphs (Melton 1995) and its average motility and dispersion ability is also significantly higher than those of *B. germanica* (Khrustalyova 1993).

The average life cycle takes 161 days.

The extremely close relation of the species described here with the exclusively African *S. mirabilis* (Shelford, 1908) may also be an indication of the possibility of living (at least morpho-) species of cockroaches occurring in the Miocene. Living cockroach species are still unknown in the fossil record, possibly because of rapid phylogeny at their species level (Vršanský 2008). Living genera of cockroaches (both primitive and advanced) are known since the Eocene (Vršanský et al. 2011).

What is notable is the identity of the pronotum colouration with numerous representatives of another unrelated genus that includes synanthropic species, the genus *Periplaneta* of the Blattidae, for example, circumtropical *P. australasiae* (Fabricius, 1775). Additionally, *Periplaneta* such as *P. indica* Karny, 1908 from China can be smaller (forewing length 16 mm) (Karny 1908) and superficially could be easily confused with *Nemosupella* Rehn, 1947. *Periplaneta* is known from Eurasia, starting from the Middle Eocene — *P. eocaenica* Meunier, 1921, *P. relicta* Meunier, 1921 and possibly others occur in Messel sediments (Schmied 2009). Miocene representatives are *P. hylecoeta* Zhang, 1989 and *P. lacera* Zhang, 1989 from the Shanwang and *P. sphodra* Zhang, Sun & Zhou, 1994 from Shandong in China. *P. houlberti* Piton, 1940 is reported from the Late Oligocene of Menat in France. The living genus and even some species have a cosmopolitan distribution. The origin of the synanthropic *P. americana* is currently anticipated to have shifted to South, Central and south of North America with the slave ships from tropical Africa (Rehn 1945). Notably, both *P. americana* and *P. australasiae* live both synanthropically and free (Vidlička 2001). *Supella* can be easily discriminated from all *Periplaneta* by the characteristic pale "band" and simplified venation. The identical, but homoplastic habitus of cockroaches significantly differing in size (ca. 10 mm in amber specimen; up to 30 mm in living *Nemosupella* and up to 60 mm in living *Periplaneta*) is obscure.

Another similar and related genus *Allacta* Saussure & Zehntner, 1895 is really problematic, because the only significant difference of species placed in this genus is the geographical distribution which is limited to Asia, shape and colouration of the pronotum and shape of subgenital plate. The vast majority of characters are overlapping between *Supella* and *Allacta* and most likely these two genera represent

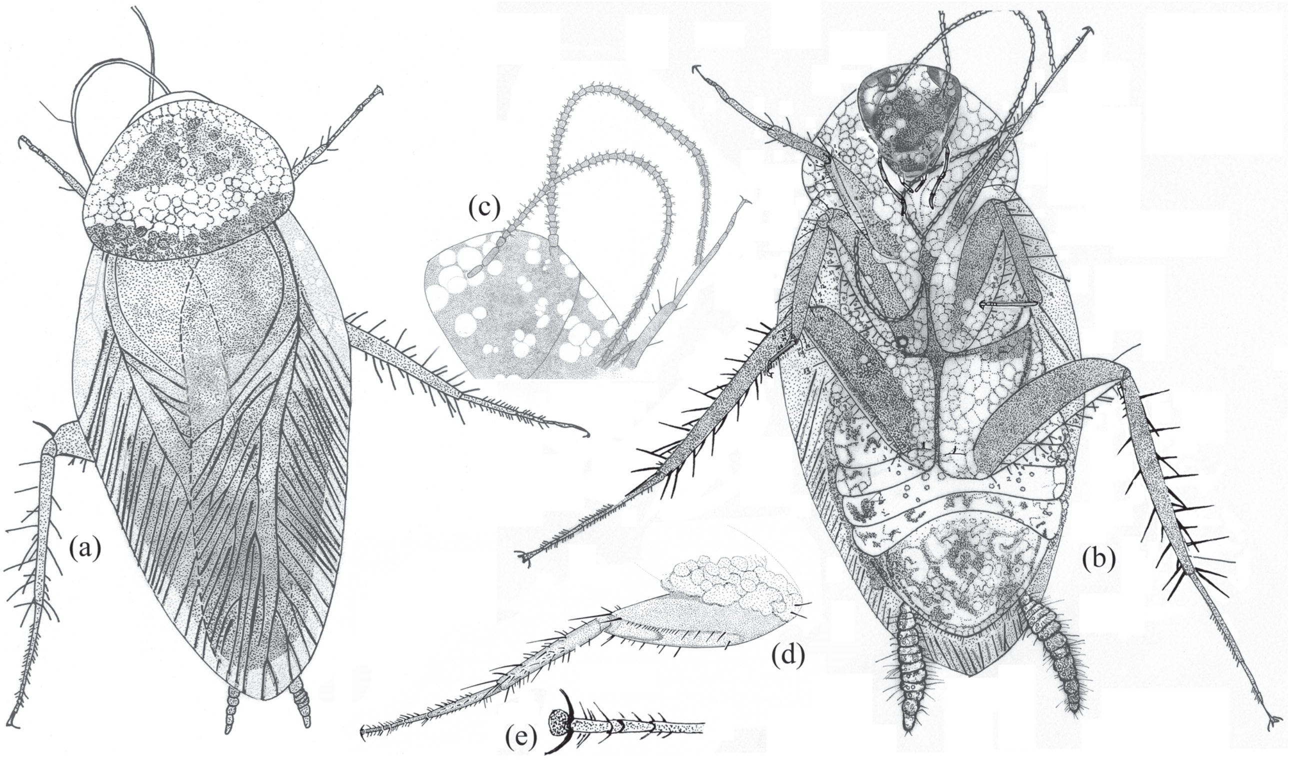


Fig. 2. *Supella miocenica* sp. nov. from the Miocene Chiapas amber of Mexico. Holotype MUCAS-001. **a** — Dorsal view; **b** — Ventral view; **c** — Head; **d** — Fore leg; **e** — Fore tarsus. Original by PC and FV. Total specimen length (from the head to the end of wings) 10 mm.

a single holophyletic taxon. Roth (1993) noticed the extreme similarity of *S. longipalpa* and *A. diluta*. Nevertheless, although we have studied all *Allacta* and *Supella* species, it is not the aim of the present publication to revise both taxa. Because both, and especially *Supella* is extremely polymorphic, we retain the determination of the present species within *Supella* and its subgenus *Nemosupella*, but it is evident *Supella* is a direct ancestor of *Allacta*.

The taxon is evidence of the rich cosmopolitan Tertiary entomofauna, which went extinct in the Americas, but still survives on other continents, in this case in Africa. The African taxa apparently also gave birth to the rich but uniform genus *Allacta*, radiated in the whole of Asia, and comparatively recently also in Australia. *Allacta* itself was also present in America during the Eocene.

It follows that the horse was not the only group which went extinct in the Americas, but could easily be reintroduced there by humans.

Material and methods

A single completely preserved specimen was collected by Luis Zúñiga Miganjos in the Los Pocitos locality and is deposited in Museo Comuntario del Ambar, Simojovel, Chiapas (MUCAS, supported by Instituto Nacional de Antropología e Historia — INAH). It was photographed using a Canon EOS Mark II and drawn with a camera lucida from an Olympus SZH10. Wing terminology follows Vršanský (1997). The living undescribed *Allacta* or *Supella* sp. provided in Fig. 3 was collected in Central Laos, Bolikhamsai province, Ban Nape-Kaew Nua Pass [N 18°22.3′ / E 105°09.1′], by Ondrej Šauša and Eduard Jendek (deposited in IZ SAS Bratislava).

Parsimony analysis was performed using PAUP* software version 4.0b10 (Swofford 2002), with a TBR heuristic search of 1,000,000 replicates and the option ‘save multiple trees’ activated. All characters were treated as unordered (0 — plesiomorphic, 1, 2, 3 — apomorphic states). MaxTrees option was set to 1000. Characters were weighted regarding their evolutionary relevance (characters 9, 12 — weight = 10, character 13 — weigh = 1, remaining characters — weight = 5). Details of the procedure of each character are explicitely stated in the character analysis below. A heuristic search produced 1000 equally parsimonious trees with length 368 (consistency index CI = 0.29, retention index RI = 0.77). Majority consensus tree was constructed and post-edited (coloured) in MESQUITE software version 2.6. Only clades with frequency > 50 % were retained.

Results

Systematic entomology

Order: **Blattida** Latreille, 1810 (= Blattaria Latreille,
1810 = Blattodea Brunner von Wattenwyl, 1882)
Family: **Blattellidae** Karny, 1908
Subfamily: **Pseudophyllodromiinae** Hebard, 1929

Supella Shelford, 1911

Type: *Blatta longipalpa* Fabricius, 1798 (circumtropical, native in Africa).

= *Blatta supellectilium* (Serville, 1839)
= *Blatta incisa* (Walker, 1868)
= *Ischnoptera quadriplaga* (Walker, 1868)
= *Blatta extenuata* (Walker, 1868)
and numerous other synonyms of diverse specimens from the West Indies (see Rehn 1947).

Composition: Besides the type; *S. vicina* Chopard, 1958 [Comores islands]; *S. abbotti* Rehn, 1947 [Kenya, Tanzania, Malawi]; *S. dimidiata* Gerstaecker, 1869 [Kenya, Congo, Angola, Rhodesia, Malawi, Mosambique, Botswana, Natal, Transvaal]; *S. orientalis* Grandcolas, 1994 [Saudi Arabia]; *S.* (*Mombutia*) *chapini* Rehn, 1947 [Congo]; *S.* (*Nemosupella*) *gemma* Rehn, 1947 [Ghana]; *S.* (*Nemosupella*) *mirabilis* [Cameroon, Gabon, Congo, Uganda, Kenya, Tanzania]; *S.* (*Nemosupella*) *occidentalis* Princis, 1963 [Guinea]; *S.* (*Nemosupella*) *tchadiana* Roth, 1987 [Chad]. All extant in Africa.

Diagnosis (Rehn 1947, in part): "Pronotum ovate subtrapezoideal in outline. Tegmina of female varying in length from covering but half the abdomen to surpassing the abdominal apex by a distance equal to the pronotal length, in outline ranging from 1.5 times as long as broad. Apex well-rounded. Costal veins numerous, straight oblique, several of the more distal ones usually ramose, reduced in number in the abbreviated tegmined forms; discoidal sectors oblique, tending toward sublongitudinal in males of *S. abbotti* and *S. mirabilis*. Anal field pyriform, anal veins five or more, regular; discoidal sectors similarly developed, anal field always fully indicated.

Cephalic femora with ventro-cephalic margin bearing a regular series of spines, evenly reducing in length and strength distad (sometimes replaced by setae (e.g. in one limb) — e.g. in *S. mirabilis*), apical spines of same margin two-three in number, the terminal one much the longer; median and caudal femora with ventral margins spined; caudal tarsi with metatarsus in length surpassing the other articles combined. Arolia well developed; tarsal claw of equal length, their margins unarmed, simple."

Subgenus: *Nemosupella* Rehn, 1947

Type: *Phyllodromia mirabilis* Shelford, 1908.

Composition: *Supella mirabilis, S. gemma*, *S. tchadiana*, *S. occidentalis.*

Diagnosis (ex Rehn 1947 in part — only relevant characters): "Females more robust with tegmina and wings broader and in length less markedly surpassing the apex of the abdomen, apex well rounded. Head pyriform in outline, transverse facial ridge nearly straight transverse; palpi with penultimate and antepenultimate articles elongate. Caudal tarsi moderately slender, metatarsus in length somewhat exceeding that of the remaining tarsal articles combined".

Supella (*Nemosupella*) *miocenica* sp. nov.
(Figs. 2a–c, 3a–c)

Holotype: MUCAS-001. A complete female.

Type locality: Los Pocitos, Simojovel de Allende, Chiapas amber.

Type horizon: Lower Miocene, Mazantic Shale, Tertiary.

Differential diagnosis: The present species differs from its consubgeners, *S. mirabilis* in being smaller (total body length with wings ca. 10 mm vs. 16–25.5 mm in *S. mirabilis*), in having discoidal sectors oblique (oblique to sublongitudinal in *S. mirabilis*), and in having the central dark pronotal macula divided into two parts; from *S. gemma* in size (similar as *S. mirabilis*), in having wings more coloured and pronotal central macula smaller; from *S. tchadiana* of a comparable size (12 mm), in having pronotum without markings; and from *S. occidentalis* in colouration and size.

Description: Very small species (overall body length without wings about 9 mm). Head small (length to width: 1.6/1.3 mm) with very fine antenna covered by a row (basal segments) or up to four rows with four short (roughly corresponding to segments' width) sensilla chaetica in each. Pronotum ovate subtrapezoidal in outline, significantly vaulted (1.7/2.9 mm), pale, with dark macula covering the whole posterior margin and central macula, divided into two separate parts.

Body slender, sterna (especially the posteriormost ones) widely carved, cerci with up to 16 segments, very long (1.8 mm) with dense fine sensilla chaetica of diverse length (0.2–2 times as long as the width of the median cercal segment). Legs slender, long (including fore legs), cursorial. Fore legs terminated with claw and arolium; femora (1.7/0.1 mm) with dense chaetica, tibia (0.9/0.07 mm) with at least 5 fine spurs (arrangement of spines along the tibiae in 3 rows), tarsi 5-segmented (0.7, 0.2, 0.1, 0.05, 0.2 mm). Front femur Type B2, with four proximal stout spines succeeded by a row of uniform piliform spinules, terminating in two large spines; pulvilli present only on the fourth tarsomere, tarsal claws symmetrical and unspecialized (simple), simple arolia present.

Mid femora wide and with numerous sensilla (about 26 spines in two rows) (2.1/0.6 mm), tibia also robust (1.6/0.2 mm), with long fine spurs (10 or more); tarsi curious, extremely short (0.7/0.1 mm), with an indistinct claw and arolium. Hind legs long, femora robust (2.6/0.8 mm), with two rows with numerous (about 19×2) fine spurs and terminal two fine spurs; tibia long (2.9/0.2 mm), with numerous (up to 30) fine spines; tarsi long (1.3, 0.3, 0.1, 0.1, 0.3 mm), densely haired, with distinct claw and arolium. First third of the first

Fig. 3. a–d — *Supella miocenica* sp. nov. from the Miocene Chiapas amber of Mexico. Holotype MUCAS-001. Ventral view. a — Complete specimen with curculionid beetle; b — detail on head with mycelia of parasitic fungus *Cordyceps* or *Entomophthora* (white "bubbles"); c — detail on cercus; d — dorsal view, total specimen length (from the head to the end of wings) 10 mm. **e** — Undescribed male of *Allacta* or *Supella* sp. from Central Laos. Total length ca. 12 mm. *Nemosupella* is even more similar in having the nearly identical pronotal shape and colouration (the central macula is divided into 2 parts only in *S. miocenica*). Photograph of the sister species, *S.* (*Nemosupella*) *mirabilis* is available free on the web (FOW).

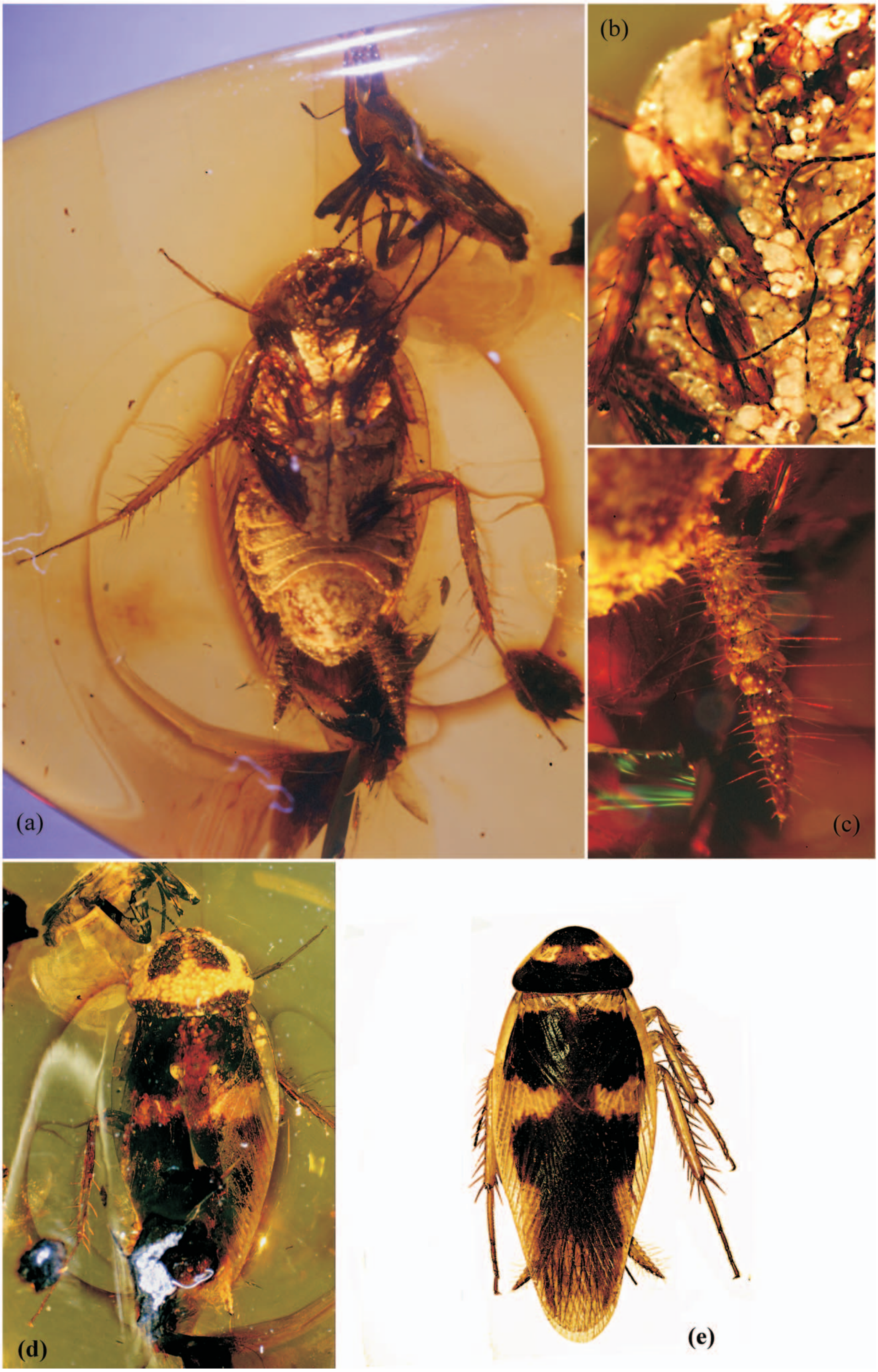


Fig. 3.

tarsal segment sparsely (5) haired, the rest with at least 33 sensilla; second segment with 9, third with two, fourth with six and terminal one with at least two sensilla.

Forewing dark, with characteristic pale anterior margins and central stripe making the illusion of the body being separated into two halves. Apex rounded. Venation simple, with minimum deformities. Total number of veins meeting the margin (without A) ca. 30. Sc simple, short, R nearly straight, R branches simple except for the few terminal branches (18 R veins meet margin). RS not clearly differentiated. Discoidal sectors oblique. M secondarily branched, with about 10 branches at the margin. CuA is fused with M and perhaps consists of a single terminally dichotomized branch. Anal field pyriform, fully indicated, anal veins simple, regular, apparently five or more. Intercalaries locally distinct (in basal R and CuA) and probably common.

Remarks: For comparison and details see Discussion.

Derivation of name: *miocenica* is after the Miocene epoch.

Character analysis: (0 — plesiomorphy; 1–3 — apomorphies relative to other species within genera *Supella* and *Allacta*, and/or *Cariblattoides* Rehn & Hebard, 1927 and *Symploce* (and fossil *Piniblattella* Vršanský, 1997), which were chosen as outgroups based on high similarity, and based on retension of all original states of characters due to standard habitus (not derived like in *Supella* and *Allacta*):

1. Head with interocular (IO) space roughly identical with the distance between antennal sockets: apomorphy; plesiomorphic is partially reduced IO space (as in *Symploce* and most regular cockroaches); IO space nearly absent is a strong apomorphy (2), eyes very small and remote (3).

2. Pronotum large ovate subtrapezoidal in outline, significantly vaulted: plesiomorphic (as in most cockroaches including *Symploce* and *Piniblattella*); apomorphic states are 1) small and round; 2) subelliptical with margins parallel.

3. Pronotal colouration with basal dark stripe and two central maculas: plesiomorphic (central maculas are present in most primitive blattellids such as *Piniblattella*), derived states are alternative colourations (dark with cental pale macula).

4. Subgenital plate long: apomorphy (plate is plesiomorphically of normal length in *Symploce*, *Piniblattella* and most other blattellids).

5. Forewing with apex of radial area reduced to mostly simple branches (RS indistinct): apomorphy (RS distinct in primitive *Symploce* and *Piniblattella*).

6. Forewing M and CuA branched and curved: plesiomorphy (as in Mesozoic cockroaches); these branches are apomorphically longitudinal even in some *Symploce*; serrate (2).

7. Forewing colouration with characteristic transversal stripes: apomorphy at level of common ancestor of *Supella* and *Allacta*. Plesiomorphic state is colouration uniform but not strong as in *Cariblattoides*, and other primitive blattellids (*Nahublattella*, *Neoblattella* etc.).

8. Colouration of wings soft: plesiomorphy; pronotum strongly dark, with sophistic pale stripes on forewing is apomorphic (*funebris* spp. group).

9. Colouration of wings and pronotum with continuous colouration: plesiomorphy; derived apomorphic state is colouration in dark dots, lines and blotches. *This character was found as a global irreversive reorganization of morphology and colouration and thus has been given higher weight in the cladistic analysis.*

10. Hindwing R1 distinct: plesiomorhy (as in most primitive blattellids including *Symploce* and *Piniblattella*); R1 is apomorphically reduced to a single vein.

11. Fore tarsi of B-type: apomorphy (tarsi are plesiomorphically A-type in most primitive blattelids including most *Symploce*).

12. Pulvilli exclusively on 4th tarsomere: apomorphy (pulvilli are plesiomorphically on 4 tarsomeres in primitive blattellids including *Symploce*). *In addition to diagnosis of* Allacta (*Saussure & Zehntner, 1895*)*, this character was found unique, never occurring homoplastically in any other group* (*additionally unrelated with respect to size changes*) *and thus has been given higher weight in the cladistic analysis.*

13. 1 or 2 terminal fore femoral spurs: apomorphy (plesiomorphic state is with 3 spines in both A- and B-types of *Symploce*). *This character was found polymorphic within species and even on one specimen* (*L/R sides — Roth 1991, 1993, 1996 and our observation*) *and thus has been given lower weight in the cladistic analysis.*

14. Habitus robust: plesiomorphy (as in *Piniblattella*), derived apomorphic states are slender (1), extremely fragile (2) and extremely elongated (3).

Allacta Saussure & Zehntner, 1895

= *Abrodiaeta* Brunner von Wattenwyl, 1893
= *Pseudochorisoblatta* Bruijning, 1948
= *Arublatta* Bruijning, 1947

Type: *Abrodiaeta modesta* Brunner de Wattenwyl, 1893 from Carin Ghecu in Burma, by selection.

Composition: ***Funebris* species group** (sensu Roth 1993): *basivittata* (Bruijning, 1947) [New Guinea, Aroe and Aru Islands], *bipunctata* (Walker, 1869) [Celebes, Aru Islands, New Guinea], *funebris* (Walker, 1868) [Borneo] (Roth 1993); *grandcolasi* Roth, 1995 [Irian-Jaya], *megamaculata* Roth, 1995 [Papua New Guinea], *straatmani* Roth, 1995 [Papua New Guinea] (Roth 1995), *diagrammatica* (Hanitsch, 1923) [Malacca, Singapore, Mentawai islands, Sumatra, Java].

***Hamifera* species group** (sensu Roth 1993): *bimaculata* Bey-Bienko, 1969 [China], *diluta* (Saussure, 1863) [Ceylon, India], *figurata* (Walker, 1871) [Ceylon, India], *hamifera* (Walker, 1868) [Malacca, Java, Borneo, Philippinen], *interrupta* (Hanitsch, 1925) [Borneo], *luteomarginata* (Hanitsch, 1923) [Singapore], *maculicollis* (Hanitsch, 1927) [Vietnam], *parva* Shelford, 1906 [Borneo], *pantherina* (Hanitsch, 1933) [Borneo] (Roth 1993); *svensonorum* Roth, 1995 [Malaysia, Borneo] (Roth 1995).

***Polygrapha* species group** (sensu Roth 1993): *fascia* Roth, 1993 [Indonesia], *immunda* (Brunner von Wattenwyl, 1893) [Burma, Malacca], *polygrapha* (Walker, 1868) [Thailand, Malacca, Singapore, Sumatra, Borneo], *picturata* (Shelford, 1907) [Singapore, Sumatra, Thailand, Malaysia, Borneo], *marmorata* Walker, 1869 [Burma, Sumatra, Malaysia], *mcgavini* Roth, 1991b [Indonesia], *robusta* Bey-Bienko, 1969 [China], *transversa* Bey-Bienko, 1969 [Vietnam]; *arborifera* (Walker, 1868) [Malaysia, Java, Borneo, Mentawai Islands], *australiensis* Roth, 1991 [Queensland], *confluens* (Hanitsch, 1925) [Borneo], *labyrinthica* (Hanitsch, 1927) [Vietnam], *loconti* Roth, 1993 [Indonesia], *megaspila* (Walker, 1868) [Malacca, Mentawai Islands, Java, Borneo], *ornata* Bey-Bienko, 1969 [China], *modesta* (Brunner von Wattenwyl, 1893) [Burma; type], *karnyi* (Hanitsch, 1928) [Mentawai Islands, Sumatra] (Roth 1993), *brossuti* Roth, 1995 [Irian-Jaya], *deleportei* Roth, 1995 [Papua New Guinea], *gautieri* Roth, 1995 [Papua New Guinea], *nalepae* Roth, 1995 [Papua New Guinea], *persoonsi* Roth, 1995 [Papua New Guinea], *srengi* Roth, 1995 [Papua New Guinea] (Roth 1995).

A. puncticollis (Brunner von Wattenwyl, 1898) [Borneo] (not placed sensu Roth 1993) and *A. crassivenosa* Bolívar, 1897 [India] (incertae sedis sensu Roth 1993). Except for problematic *A. australiensis*, all are extant in Asia.

Diagnosis: Front femur Type B [B2 or B3 according to Roth 1993, or C (right and left femur can differ in type (B2-B3 or even B-C) according to Roth (1991, 1996))]; pulvilli present on fourth tarsomere only, tarsal claws simple, symmetrical, arolia present (Roth 1995).

Discussion

Supella-Allacta *complex*

Because there is an immense similarity and relation between the genera *Supella* and *Allacta*, it is necessary to provide arguments for the categorization of the present fossil within *Supella*.

These genera are clearly distinguished among other blattellids by autapomorphies including the characteristic colouration with a pale stripe appearing to divide the body into two (or, in combination with the pronotal colouration into 3) separate parts; M and CuA descending in an obtuse angle; mostly simple R branches with indistinct RS (homoplastic with *Pseudomops* Serville, 1831 and *Ectobius* Stephens, 1835); and in other characters unseen in the present fossil (see Rehn 1947). *Supella* restricted to Africa is much more diverse and polymorphic (including forms identical with *Allacta*) which suggests its direct ancestral position in respect to Asian and Australian *Allacta* (the latter is restricted to a single species *A. australiensis* from Queensland, which has an indicated hindwing R1 as in *Supella*, but is very different from both *Supella* and *Allacta* in having eyes nearly connected, and in subelliptical — with anterior and posterior margins parallel — form of pronotum; thus it can simply represent *Supella* or a different genus).

The present amber species has fore legs of B type identical (!including the number of proximal spines and terminal spurs) with *Allacta*, dissimilar to most *Supella* (A-type), but these types can be polymorphic (L/R) in a single specimen of *Allacta* (B2/B3 or even B/C — see above), and the *Supella* subgenus *Nemosupella* can have this B-type pattern too. The most primitive living blattellid, *Symploce* has mostly A3 type, but ocassionally B3, thus it is likely A is the original type, but the above-mentioned polymorphisms are evidence for a convergent nature of this character changes. Closely related and perhaps derived from *Supella* is also the genus *Cariblattoides* with A-type and pulvilli on 4 tarsomeres, supporting this state as ancestral.

Phylogenetically obscure is also the distribution of knee spines at the distal end of the femora — 2 in present species and some *Allacta* (see character matrix) and *Supella*, but more often 3 (also in figured most closely related *Allacta* sp.).

The present amber species clearly differs from representatives of the *A. funebris* species group, which are very dark including the pronotum (eventually with a narrow pale margin only) and with basal narrow pale stripes. *A. polygrapha* spp. group differs in having a large symmetrical pronotal pattern of dark dots, lines and blotches and forewings chequered with dark cells between veinlets and with larger blotches (*A. confluens* placed here is somewhat different from other representatives of this species group, it has more coherent colouration and pronotum colouration most similar to the amber specimen. Nevertheless, the shape of the pronotum of *S. miocenica* is different: dissimilar to any described *Allacta* spp.). *A. puncticollis* is also completely different, with a subparabolic reddish brown pronotum with small yellowish spots, but has pulvilli limited to the 4th tarsomere. *A. crassivenosa* is categorized as incertae sedis and most likely belongs to another genus. The most related to the present amber species within *Allacta* is the *A. hamifera* spp. group, which differs in having smaller pronota with a different colouration pattern and in the shape of the subgenital plate which is never as long in *Allacta*. Even more similar, and hardly recognizable from the *Nemosupella* spp. is an undescribed representative putatively attributed to *Allacta* on the basis of identical legs (pulvilli limited to the 4th tarsomere — Figure 2b). Alternatively it can mean that this species belongs to *Supella* and is its only Asian representative, but more likely it is a transitional taxon leading to *Allacta*. The figured undescribed species (Fig. 3e) cannot be placed into any spp. groups of *Allacta*, but is most closely related to the *A. hamifera* spp. group in the shape of the head and underived colouration. It is apparent that *A. funebris* and *A. polygrapha* spp. groups were derived much later, the latter apparently derived via *A. confluens*, which has similar pronotum colouration and underived forewing colouration.

It is clear, that there is no strict hiatus between these two genera, but this cannot be used as a reason for their synonymization or for the erection of additional genera. The problem is that there are known “missing link” taxa in all cockroach families and we also know a half-cockroach–half termite (Vršanský 2010) and also half-cockroach–half mantodean. All studied living cockroach genera with fossil records have these transitional stages too, and the present taxon is no exception. This is a half-*Supella*–half-*Allacta*, but better *Supella* than *Allacta*. So splitting or erecting does not have a proper place here just because the group is well studied. Paraphyletic taxa and incomplete hiati are present in the vast majority of studied cockroaches, which is a result of the extensive fossil record with ca. 100,000 specimens. So our specimen has synapomorphies of *Allacta*+*Supella* (colouration, venation), autapomorphies of *Allacta* (extremities), but major autapomorphies of *Supella* (pronotum, subgenital plate).

The cladogram (Fig. 4) supports all the above-mentioned inferences, with nearly ideal separation of all spp. groups, but it was weak in the position of *A. interrupta* (well nested within *hamifera* **group** by intuition (Roth 1993), very closely related to *A. hamifera*) within the *polygrapha* **group**. The second problem is the terminal position of *A. confluens* which is expected to be the basalmost *polygrapha* **group** stem (it has a very basal position when all characters were equally weighted). Third, *A. bimaculata*+*A. pantherina* (*hamifera* **spp. group**) appear nested within *Supella*. Notably, all three problems are absent in the cladogram with the normal weight of character 13 (weight 1 in contrast to weight 5 of all other characters except weight 10 of characters 9 and 12), which is polymorphic (and thus has been given a lower weight), *A. bimaculata*+*A. pantherina* (*hamifera* **spp. group**) are nested (as basalmost offshots) within *hamifera* **spp. group** using the same weights but using different (500) number of maximal search trees. *A. puncticollis* (out of any spp. group) appears to be a sister taxon to *A. svensonorum* and *A. luteomarginata* (trichotomy at cladogram). When all characters were weighted normally and in many other options tried, *S. dimidiata* were often nested within *Allacta*. *S. dimidiata* is a good *Supella*, and this placement is evidence for numerous homoplasies within the group. Generally, the homoplasies wihin cockroaches are enormous.

Paleogeographically, the basalmost blattellids were preserved in Asia, but their ancestors within the Mesoblattinidae were also common in Europe (Vršanský & Ansorge 2007). The basalmost *Supella* is up to recently clearly nested within Africa, but the present American species is clear evidence for the past circumtropic distribution. *Allacta* was possibly derived in Africa but radiation was apparently not limited to Asia (except for the mentioned synanthrope, *Allacta* is present in sediments of the Green River in Colorado). According to this cladogram *A. australiensis* was derived quite recently from one of the species in the *polygrapha* **spp. group**.

From the most primitive blattellids, *Nahublattella* and *Symploce* (for position of these genera within Blattellidae see also Klass & Meyer (2006)), there is a significant reduction and simplification of venation, which is evidence of the very early divergence of the whole complex from the main blattellid stem. Another eventual conclusion considers the small size of the present species, which may be a plesiomorphic character, which would explain the significant simplification of venation even in large living species. Notably, in the derived genus *Allacta*, terminal radial veins are simplified only in the smallest species (*A. parva*).

Notwithstanding, some living *Supella* and *Nemosupella* in particular have more primitive traits and likely diverged before the speciation of *S. miocenica*. Its single insignificant deformity (not clearly visible, insignificantly changing the wing geometry) supports the fact that Eocene and Miocene species have few accumulated wing deformities and their occurrence in living species represents support for them being inheritable mutations (see Vršanský 2005).

Extinct American Supella

In spite of the close relation of its 3 known subgenera, the general habitus of the respective taxa in *Supella* is very diverse. *S. longipalpa* is a slender, fine cockroach, while *S. orientalis* has extremely elongated wings (~1:4.5), and the subgenus *Nemosupella* is clearly differentiated by robust habitus with a robust unplain pronotum and more or less normal longitudinal veins. The present species share all the autapomorhies of the genus and subgenus *Nemosupella* and can be safely categorized within this taxon.

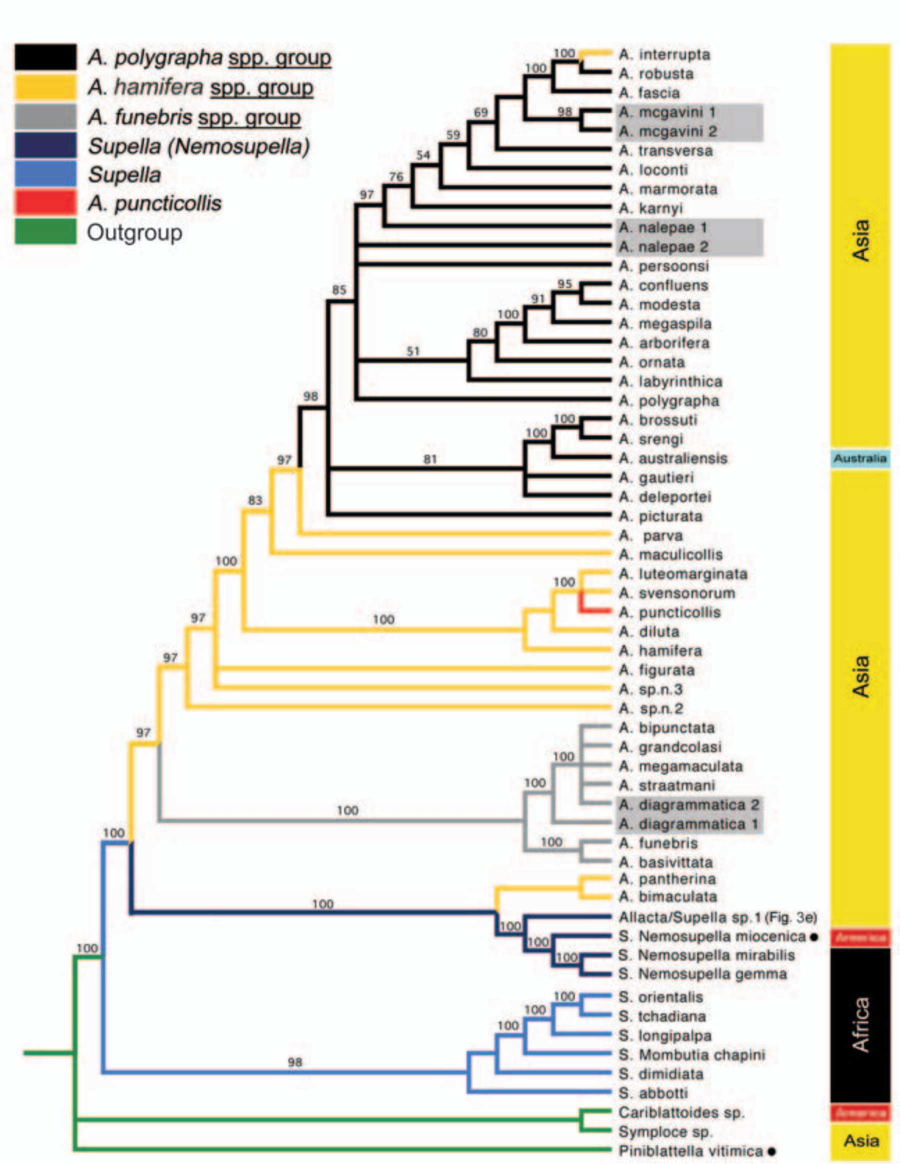
The colouration and general appearance is hardly recognizable from females of *S. mirabilis*, its sister species, although the shape of the pronotum is somewhat transitional between its males and females. Except for the significantly smaller size of the present new species, the sole difference between the two taxa is the divided central pronotal macula. There are no additional plesiomorphies, which indicate the present as well as the living species of *Nemosupella* diverged near the Mid-Miocene. The other three representatives of the subgenus are closely related to *S. mirabilis*, but are dissimilar to the present fossil due to different colouration.

On the other hand, other representatives of the genus such as *S. longipalpa* reveal significant divergence from the main morphological standard and suggest rapid phylogeny at the subgeneric level.

The similarity with the undescribed representatives of the genus *Allacta* (Fig. 3e) is so striking (and involves size — *Nemosupella* are much larger), that it is apparent *Allacta* is derived from *Nemosupella* via the predecessors of this undescribed taxon and also via predecessors of *Supella miocenica*. Its direct ancestry can be excluded based on the derived pronotum of *S. miocenica*. While there is a standard *Allacta* placed within a living **spp. group** (*polygrapha*) present in much older Eocene Green River sediments, the Chiapas is apparently another case of the presence of primitive species in amber, when compared to isochronous sedimentary record. Relic character of amber cockroach (and all insect to some extent) assemblages is characteristic also for the only two studied Mesozoic ambers (Lebanon and Archingeay, but also in Baltic amber), which might either be caused by different methods of dating, or by the more humid, dark and colder source microclimates of amber forests. This is in contrast to Cretaceous ecosystems, where primitive cockroach forms of the Jurassic type are restricted to younger, but dry to semiarid ecosystems (Vršanský et al. 2002).

Very little can be said about the **ecology of the present species**. Generally the ecosystems of Chiapas were perhaps diverse, ranging from lowland tropical dry forest tending toward open forest and mangroves (Solórzano-Kraemer 2007). The wide range of ecosystems from the rainforest down to savannas, of the closely related *S. mirabilis*, indicate this genus is highly adaptable to diverse conditions. This ecological plasticity could have resulted in invasions of early *Supella (Nemosupella)* into the Americas before the Mid-Miocene (and later into Asia as the genus *Allacta*). Living species of *Supella* are cavicolous (Grandcolas 1994) and the genus most likely also originated in Africa because the most primitive blattellid, *Symploce* Hebard, 1916 is circumtropic, but rare in America. On the other hand, the genus *Nahublattella* Bruijning, 1959 considered to be even more primitive by Klass (1997) is native to Central and South America, which could indicate the opposite.

The parasitic (or predatory) fungus *Entomophthora* or *Cordyceps* is indeterminable, but the mycelium is richest in



Characters

	7	10	4	6	14	5	12	2	9	8	11	3	1	13
A. interrupta	1	1	0	1	1	1	1	0	0	0	1	1	2	0
A. robusta	1	?	0	1	1	1	1	0	1	0	1	1	2	?
A. fascia	0	1	0	1	1	1	1	2	1	1	1	1	2	1
A. mcgavini 1	1	0	0	1	0	1	1	2	1	0	1	1	0	0
A. mcgavini 2	1	0	0	1	0	1	1	2	1	0	1	1	0	1
A. transversa	1	?	0	0	1	1	1	2	1	0	1	1	0	1
A. loconti	1	1	0	0	1	?	1	2	1	0	1	1	0	1
A. marmorata	1	1	0	?	1	?	1	2	1	0	1	1	0	?
A. karnyi	1	1	0	?	1	?	1	2	1	0	1	1	0	1
A. nalepae 1	1	1	0	0	1	0	1	2	1	0	1	1	0	1
A. nalepae 2	1	1	0	0	1	0	1	2	1	0	1	1	1	1
A. persoonsi	1	1	0	0	1	0	1	2	1	0	1	1	1	1
A. confluens	1	1	0	0	0	1	1	0	1	0	1	0	1	0
A. modesta	1	1	0	1	0	0	1	0	1	0	1	0	0	0
A. megaspila	1	1	1	0	0	0	1	0	1	0	1	0	1	1
A. arborifera	1	?	1	0	0	?	1	0	1	0	1	1	1	0
A. ornata	1	?	1	0	1	?	1	2	1	0	1	1	1	1
A. labyrinthica	1	1	0	0	1	0	1	2	1	0	1	1	1	0
A. polygrapha	1	1	0	0	1	0	1	0	1	0	1	1	1	1
A. brossuti	1	0	0	0	1	0	1	2	1	0	1	1	2	1
A. srengi	1	0	0	0	1	0	1	2	1	0	1	1	2	1
A. australiensis	1	0	0	0	0	?	1	2	1	0	1	1	2	1
A. gautieri	1	0	0	0	0	0	1	2	1	0	1	1	1	1
A. deleportei	1	?	0	0	0	0	1	2	1	0	1	1	1	1
A. picturata	1	1	0	0	0	1	1	2	1	0	1	1	1	1
A. parva	1	1	0	1	0	0	1	2	0	0	1	1	1	1
A. maculicollis	1	1	0	0	1	?	1	1	0	0	1	1	1	1
A. luteomarginata	1	1	0	0	1	?	1	1	0	1	1	1	2	0
A. svensonorum	1	1	0	?	1	0	1	1	0	0	1	1	2	0
A. puncticollis	1	?	0	?	1	?	1	1	0	0	1	1	0	0
A. diluta	1	?	0	0	0	?	1	1	0	0	1	1	2	0
A. hamifera	1	1	0	?	0	?	1	1	0	0	1	1	2	1
A. figurata	1	0	0	2	0	0	1	1	0	0	1	1	1	0
A. sp.n.3	1	?	0	0	0	1	1	1	0	0	1	1	1	0
A. sp.n.2	1	0	1	0	0	0	1	0	0	0	1	1	1	0
A. bipunctata	1	1	0	1	0	0	1	0	0	1	1	1	0	1
A. grandcolasi	1	?	0	0	0	0	1	0	0	1	1	1	0	1
A. megamaculata	1	?	0	0	0	0	1	0	0	1	1	1	1	1
A. straatmani	1	?	0	0	0	0	1	0	0	1	1	1	0	1
A. diagrammatica 2	1	1	0	0	0	0	1	0	0	1	1	1	0	0
A. diagrammatica 1	1	1	0	0	0	0	1	0	0	1	1	1	0	1
A. funebris	1	0	0	?	0	0	1	2	0	1	1	1	0	?
A. basivittata	1	?	0	0	0	0	1	2	0	1	1	1	0	0
A. pantherina	1	0	0	0	0	?	1	2	0	0	1	1	3	1
A. bimaculata	1	?	0	1	0	1	1	2	0	0	1	1	0	0
Allacta/Supella sp.1 (Fig. 3e)	1	?	0	0	0	1	1	0	0	0	1	0	0	0
S. Nemosupella miocenica ●	1	?	1	0	0	1	1	0	0	0	1	0	0	1
S. Nemosupella mirabilis	1	0	1	0	0	0	?	0	0	0	1	0	0	1
S. Nemosupella gemma	1	0	1	0	0	0	1	0	0	0	1	0	0	1
S. orientalis	1	0	0	0	3	1	0	1	0	0	0	1	1	0
S. tchadiana	1	0	0	0	1	1	0	1	0	0	0	1	?	?
S. longipalpa	1	0	1	0	2	1	0	1	0	0	0	1	1	1
S. Mombutia chapini	1	0	1	0	1	1	0	1	0	0	0	1	0	1
S. dimidiata	1	?	?	1	1	1	0	0	0	0	0	1	2	0
S. abbotti	1	0	1	0	0	1	0	0	0	0	0	1	0	?
Cariblattoides sp.	0	0	0	1	3	0	0	0	0	0	0	1	0	1
Symploce sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Piniblattella vitimica ●	0	0	0	0	0	0	?	0	0	0	0	0	1	0

Fig. 4. Parsimony analysis of all the known *Supella* and *Allacta* species (excluding obscure *A. crassivenosa*, *S. occidentalis*, *S. vicina*, and including 3 undescribed *Allacta* and/or *Supella* species) with their geographic distribution. *S. miocenica* and *Piniblattella vitimica* are extinct. Position of *A. interrupta* (top) is illusory due to numerous homoplasies with *A. robusta* and other *polygrapha* **spp. group** species, as this species apparently belongs to the *hamifera* **spp. group.** 50% majority consensus tree from 1000 equally parsimonious trees was gained with maximum parsimony search (PAUP). Numbers above branches represent clade frequencies in %.

the junction of head and pronotum and could have its epicentre in the head. This fungus provides a contribution to the poorly known microorganisms of the Chiapas amber. Only a ?*Bacillus*-like cell and two types of budding-bacteria-like microrganisms were reported previously (Veiga-Crespo et al. 2007).

Comments on synanthropism in cockroaches

The fifty species of synanthropic cockroaches comprise only an insignificant fraction of the total of about 5000 (Bell et al. 2007) described species of living cockroaches. Nevertheless, they are important for their number and ecological significance. Most of the species had their genera recently limited to certain continents and only nowadays have become cosmopolitan (or circumtropical). On the contrary, their history on a geological scale is much richer than we would expect and their original distribution was also circumtropical.

The genus *Blattella* was until very recently limited to Africa (26 species), Asia and the Pacific islands (23 species) (Roth 1985), and the synanthropic species *B. germanica* spread to the whole world from east Asia (Roth 1985). The occurrence of this genus in the Mesozoic of Europe as a single nymph (adult could eventually differ) (Vršanský 2008) and in the Eocene of the USA (Green River, Colorado) is thus surprising.

Free *Ectobius* is limited to Europe, but in the Tertiary it was cosmopolitan. The same situation is found with the present *Supella* introduced from North Africa to Central America on slave ships (Rehn 1947). The Miocene of Mexico is quite distant from the recent distribution limited to Africa.

According to Princis (1954), *Blatta* originates from the Near and Middle East — the native place of the closely related *Shelfordella* Adelung, 1910, but the other predicted origin of this genus is North Africa (Rehn 1945; Cornwell 1968), and *Blatta furcata* Bohn, 1985 is known from the Near East and North Africa (Bohn 1985). Their close relative also occurred in the Eocene of the USA (Green River).

The last significant synanthrop is *Periplaneta*, recently limited to Asia.

The only viviparous cockroach group met the same fate: the Diplopteridae, now restricted to two genera (one African, one Asiatic), were common in America during the Eocene (in Green River). This family is also reported from the Eocene of Quilchena (Archibald & Methewes 2000), but the figured specimen (Q-0040) is very different from all known Diplopteridae (details to be provided elsewhere).

Thus it is apparent that all the synanthropic species belong to cosmopolitan genera (cosmopolitan genera are otherwise rare), very likely with a broad environmental tolerance — and thus pre-adapted for synanthropism.

Lost Tertiary American entomofauna

The occurrence of some cosmopolitan synanthropic species in the Americas and their absence prior to re-introduction, triggered the present discussions about the causes of the extinction of these entomofaunas during the Tertiary.

It was Eocene *Ectobius* from the Green River — a member of an extinct genus, but which was extremely easily reintroduced in North America several times (with 3 species), which concentrated our efforts on the search for this fauna in 2006. It was very rapidly supported by the discovery of a honey bee in the Miocene sediments of Nevada (Engel et al. 2009), a genus extinct in the Americas.

Poinar et al. (1999) also noticed the Early Tertiary North American extinctions of species of living tropical ant genera *Technomyrmex* Mayr, 1872, *Leptothorax* Mayr, 1855 and *Dolichoderus* Lund, 1831, recorded in the Eocene of British Columbia. These records comprise only the species level, which is insignificant on the present time scale, but *Technomyrmex* is now, with the exception of a single Central American species (and its abundance in the Dominican amber), limited to the tropics of the old world; *Leptothorax* is holarctic today; *Dolichoderus* is cosmopolitan.

The Eocene of the Okanagan Highlands reveals a representative of the Myrmeciinae, currently limited to the Australian region (Archibald et al. 2006). The only genus — determined hemipteran from Quilchena, *Megymenum* is today found in only in the Oriental biotic region and Australia (G. Gross, personal communication in Archibald & Mathewes 2000).

The post-Miocene cooling was unlikely to be a reason for this extinction, as both *Ectobius* and *Apis* Linnaeus, 1758 occur in Northern Europe today.

The loss of another taxon from North America is now apparent — *Supella*, in which case cooling could be the reason as nowadays this genus is restricted to Africa. On the other hand it is hardly possible that this taxon went extinct in warm Central and South America. Their historical absence in South America is also difficult to anticipate as other cockroach taxa from the Dominican amber are present in South America (see below).

Thus, of fourteen studied cockroach genera (all still living) from the Eocene–Miocene of North America only two (*Cariblattoides*, *Sigmella*) survive nowadays in (South and Central) America and only *Cariblattoides* is characteristic for Central America (although it occurs in Brazil). It is perhaps not incidental that a representative of *Sigmella* was dominant during the Eocene and also in the present Mexican amber. An additional taxon reported from the Mexican amber is *Ischnoptera* sp., currently distributed in Central and South America, but this determination is obscure (determination may be correct, but no diagnostic characteristics for the genus are provided, and the species (*Ischnoptera* sp. 1 in Solórzano-Kraemer 2007) may well belong to *Supella* or some other blattellid taxon). All things being equal, the diversity of cockroaches in Chiapas amber was certainly high: 7 specimens belong to 7 different genera and species of the family Blattellidae.

Another cockroach genus, exclusively African today, known from the Tertiary of North America is *Namablatta* Rehn, 1937.

The closely related termites are ubiquitous in the present context. While *Kalotermes nigritus* still lives in South America, the whole cosmopolitan family Mastotermitidae (present as *Mastotermes electromexicus* Krishna & Emerson, 1983 and *Mastotermes electrodominicus* Krishna & Grimaldi, 1991 occurring in the Dominican amber according to Solórzano-Kraemer (2007)) went extinct in the Americas and survives only in Australia.

Some other insect groups from the Mexican amber (Solórzano-Kraemer 2007) and Green River (our data) reveal a similar pattern, to be analysed in detail elsewhere.

It is of special consideration that the Dominican amber shows a very different pattern in respect to the distribution of cockroach genera. If the determinations of Arillo & Ortuño (2005) are correct, then there are no shared taxa (even on the generic level) between the Mexican and the Dominican amber, and all Dominican amber cockroach genera are not only highly advanced, but with the exception of the circumtropical *Anaplecta* Burmeister, 1838 all — *Euthlastoblatta* Hebard, 1917, *Pseudosymploce* Rehn & Hebard, 1927, *Plectoptera* Saussure, 1864, *Cariblatta* Hebard, 1916, *Holocompsa* Burmeister, 1838 (a single species (*H. debilis* (Walker, 1868)) also occurs in Ceylon, Java, Sumatra, Borneo and Philipines) — are characteristic of Central and/or South America. Taxa described by Gorochov (2007), including obscure *Agrabtoblatta* Gorochov, 2007 and *Erucoblatta* Gorochov & Anisyutkin, 2007, also appear limited to South America.

Taking all this preliminary information together, it is apparent that sometime after the Mid-Miocene some extensive environmental change influenced North and probably also Central and South America, resulting in the loss of cosmopolitan Early Tertiary entomofaunas. Judging from the modern composition of the Dominican amber, this may (if the abovementioned determinations are correct) mean a recovery occurred during the time between the Early Miocene Mexican amber (23–7.1 Ma) and the Dominican amber times

(20.5–16.4 Ma). The dating of both of ambers is still uncertain (the abovementioned datings are after EDNA database), more counterbalanced by the Late Barstovian (14.5–14 Ma) dating of the Nevada (with honeybee) sediments. Recently, the age of 23 Ma was designated for the basalmost amber bearing strata of Chiapas (Vega et al. 2009a).

As it is very difficult to imagine some geological or ecological process which would be able to trigger such an extensive change (aridization and/or cooling would not influence some of the cockroaches), the change was probably biological — either caused by diversification of cockroach parasites which were consequently reduced (as reintroduction has been easy), or diversification of more progressive insect groups. The parasite hypothesis may be valid in the present case, as *Comperia merceti* eradicated populations of synanthropic cockroaches in Europe, even when its function as a control of *Supella* is still not validated (Goudey-Perriere 1991) and Encyrtidae and Eupelmidae parasitizing ootheca have Tertiary origin (A.P. Rasnitsyn, personal communication 2010), known only from Europe starting with the Eocene Baltic amber (Trjapitzin 1963). (These parasites could also cause extinctions of external ovipositor bearing cockroaches which did not lay eggs in ootheca.)

The occurrence of advanced taxa in the Dominican amber (isochronous with the Mexican amber according to Solórzano-Kraemer (2007), however see above) would favour the diversification and radiation of the modern South-American cockroach taxa hypothesis. Nevertheless, *Diploptera* is the most advanced cockroach that has ever lived, and thus its extinction in the Americas falsifies the latter hypothesis. On the other hand, it is possible that its viviparity evolved only in the common ancestor of Asian and African species.

Plants were perhaps not as influenced as fauna, as Eocene flora of British Columbia in Canada is characteristic of the modern eastern North American deciduous forest zone, principally the mixed mesophytic forest, but also including extinct taxa: taxa known only from eastern Asian mesothermal forests, and a small number of taxa restricted to the present-day North American west coast coniferous biome (Greenwood et al. 2005). Also, according to Solórzano-Kraemer (2007), all plants from the Chiapas amber are currently present in Pacific coastal forest.

Conclusions

The genus *Supella* with *S. miocenica* sp. nov. was native to America during the Miocene time of the Chiapas amber. It represents another case of rich cosmopolitan Early Tertiary entomofauna, which suddenly went extinct in America somewhere around the Miocene (but which still survives in other continents). *Supella/Allacta* complex (*Allacta* was derived from *Supella*) is another case of the genera which now includes synanthropic species, which were natively circumtropic, and can be easily reintroduced in America nowadays. *S.* (*Nemosupella*) *miocenica* sp. nov. is the earliest known cockroach which can be categorized within the living subgenus and also the first published direct evidence of transitional species (and thus incomplete hiatus) at the level of living genera.

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