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Vybrané aspekty z etológie a taxonómie švábov (Blattaria)

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Prehlásenie

Prehlasujem, že som prácu napísal sám s použitím patričných literárnych zdrojov, ktoré sú v práci všetky riadne citované.

V Bratislave, 20.11.2015 Ľubomír Vidlička

Poďakovanie

Na tomto mieste si dovoľujem poďakovať sa všetkým, ktorí ma na mojej dlhej ceste za poznaním švábov sprevádzali alebo správnym spôsobom ovplyvnili. V prvom rade je to RNDr. Milan Kozánek, CSc., u ktorého som ako mladý ašpirant začínal a po prvýkrát som prišiel do styku s masovo chovanými švábmi (*Nauphoeta cinerea*) na vedecké účely. Od tohto okamihu som už šváby nikdy neopustil i keď môj záujem o ne sa vyvíjal rôznymi smermi.

Ďalej musím na tomto mieste poďakovať všetkým bývalým kolegom z Ústavu experimentálnej fytopatológie a entomológie SAV v Ivanke pri Dunaji a taktiež súčasným kolegom z Ústavu zoológie SAV v Bratislave za ich trpezlivosť s mojimi obľúbenými chovancami, ktorí sa viac-menej pravidelne vydávali v nočných hodinách na prieskum ústavu a ráno spôsobovali u nežnejšieho pohlavia zdesenie.

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V neposlednom rade patrí moje poďakovanie mojej manželke, že mala pre moju záľubu pochopenie pri mojich neskorých príchodoch z práce, pri mimoeurópskych expedíciách, ako aj počas dovoleniek venovaných zberom švábov.

Abstrakt

Predložená práca pojednáva o niektorých aspektoch etológie a taxonómie zástupcov radu švábov (Blattaria). Je založená na súbore 17 vedeckých článkov (väčšina z nich je zahrnutá v databáze WOS) a dvoch monografiách, ktoré majú vzťah k riešenej problematike.

Obsah práce je rozdelený do 4 sekcií. Prvá sekcia „Etológia švábov" pojednáva o sexuálnom správaní švábov druhu *Nauphoeta cinerea* počas dvorenia a párenia. Párenie je veľmi zložitý proces pozostávajúci zo 4 fáz. V každej fáze prebiehajú iné deje: i) vytvorenie pevného genitálneho spojenia, ii) kompletizácia a presun spermatofóru v tele samčeka, iii) prenos spermatofóru do burzy copulatrix samičky, iv) ukončenie párenia a rozpojenie genitálií. Jednotlivé fázy sú presne riadené nervovou sústavou, sprostredkované aj zmenami koncentrácie histamínu; počas dvorenia sú riadené hlavne mozgom (nadhltanové ganglium) a vo fáze kopulácie najmä posledným (šiestym) abdominálnym gangliom.

Druhá sekcia „Rozšírenie a taxonómia švábov v Európe a na Slovensku" sa skladá z troch častí. Prvá časť pojednáva o šváboch z rodu *Ectobius*, ktorý je v Európe zastúpený 35 druhmi. Tie sú však rozšírené veľmi nerovnomerne. Väčšinu tvoria endemitné druhy s veľmi malými areálmi rozšírenia, hlavne v južnej Európe. V podmienkach strednej Európy a Slovenska majú širšie zastúpenie iba druhy *E. lapponicus, E. sylvestris* a *E. erythronotus*. V posledných rokoch môžeme pozorovať prenikanie druhu *E. vittiventris* z južného Švajčiarska do oblasti strednej Európy a aj na územie Slovenska. Druh má podobné nároky ako naše natívne druhy. Ťažko si hľadá v prírode voľnú niku a tak často preniká do ľudských príbytkov. Druhá časť tejto sekcie sa zaoberá skupinou *maculata* z rodu *Phyllodromica*. Rod *Phyllodromica* je najväčší európsky rod s množstvom endemitných druhov v centrálnej Európe, vrátane územia Slovenska, Maďarska a Rumunska.

Posledná časť v tejto sekcii hovorí o šváboch zo skupiny *megerlei* z rodu *Phyllodromica*. Túto skupinu tvoria zatiaľ iba tri druhy, z ktorých iba *Ph. megerlei* má širšie rozšírenie. Ďalšie druhy z tejto skupiny sa dajú očakávať hlavne v štátoch východného Stredomoria (Chorvátsko, Albánsko, Macedónsko, Čierna Hora, Srbsko) a západne od Čierneho mora (Bulharsko, Rumunsko).

Tretia sekcia „Šváby juhovýchodnej Ázie a Južnej Ameriky" je zameraná na vybrané endemitné rody žijúce v oblastiach s najväčšou druhovou bohatosťou švábov na svete. V časti o JV Ázii sú detailne spracované informácie o šváboch z rodov *Caeparia*, *Chorisoserrata* a *Spelaeoblatta*. Južnú Ameriku reprezentuje rod *Macrophyllodromia*, ktorý v súčasnosti združuje 12 druhov. Táto časť poukazuje na potrebu urýchleného výskumu v oblastiach tropických pralesov, ktoré sú veľmi rýchlo devastované a miznú.

Posledná sekcia „Fosílne šváby" je pohľadom do života švábov za posledných 300 miliónov rokov. Paleontológovia prinášajú takmer denne nové informácie o fosílnych druhoch, ktoré menia náš pohľad na evolúciu tejto skupiny. Výrazné zmeny nastali aj v paleoetológii švábov. Pozornosť v poslednej dobe vzbudili hlavne dva objavy: šváby ako čističi po dinosauroch a objav švába z „európskeho" rodu *Ectobius* v amerických eocénnych usadeninách.

Abstract

The present habilitation thesis deals with some aspects of ethology and taxonomy focusing on representatives of the order cockroaches (Blattaria). The thesis is based on the collection of 17 scientific papers (most of them included in the Web of Sciences) and 2 monographs, which are related to the thesis main topic.

The content of thesis is divided into four sections. The first section "Ethology of cockroaches" deals with a sexual behaviour of cockroach species *Nauphoeta cinerea* during courtship and copulation. Mating is a very complex process comprising 4 phases. In each phase, different actions are involved: i) forming stable genital connection, ii) assembling and movement of spermatophore in the male body, iii) transferring of spermatophore into female bursa copulatrix and iv) finishing of copulation and disconnection of genitalia.

All phases are exactly controlled by nervous system mediated by the changes of histamine concentration; during courtship is controlled mainly by brain (supraesophageal ganglion) and in the phase of copulation controlled mainly by the last (sixth) abdominal ganglion.

The second section "Distribution and taxonomy of cockroaches in Europe and Slovakia" has three parts. First part deals with cockroach genus *Ectobius* that is represented by 35 species. These species are unequal distributed. The most of them are endemic species with small distribution areas mainly in South Europe. In central Europe including Slovakia, the species *E. lapponicus, E. sylvestris* and *E. erythronotus* are wide distributed. In the last years, we observe infiltration of species *E. vittiventris* from South Switzerland into the area of central Europe including Slovakia. This species has the same food request as our native species. It often occupies human habitats due to non-existing free niche. The second part deals with *maculata*-group of genus *Phyllodromica*. *Phyllodromica* is the most dominant European genus with numbers of endemic species in central Europe including Slovakia, Hungary and Romania.

The last part deals with cockroaches from *megerlei*-group of *Phyllodromica*. This group consists of three species of which only *Ph. megerlei* is wide distributed. Other species from this group are expected to be distributed mainly in the states of east Mediterranean (Croatia, Albania, Macedonia, Monte Negro and Serbia) and westward from Black sea (Bulgaria and Romania).

The third section "The cockroaches of south-east Asia and South America" focuses on selected endemic genera living in the area with the highest species richness worldwide. In the part of south-east Asia, detailed information about cockroaches from the genera *Caeparia*, *Chorisoserrata* and *Spelaeoblatta* can be found. South American cockroaches are represented by genus *Macrophyllodromia* consisting of 12 species. This section highlights the urgent needs of taxonomic research in the area of tropical forest which are nowadays massively devastated.

The last section "Fossil cockroaches" is view to the life of cockroaches over the past 300 million years. The paleontologists bring daily new information about fossil species that are changing are view on the evolution of this group. Significant changes are also described in paleoethology of cockroaches. In last days, more attention is paid on two observations: cockroaches as a cleaner after dinosaurs and cockroaches from "European" genus *Ectobius* found in American Eocene sediments

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1. Úvod

Predložená habilitačná práca sa zaoberá etológiou, taxonómiou a fylogenézou radu švábov (Blattaria), ktorý tvorí spolu s modlivkami (Mantodea), koníkmi, kobylkami, svrčkami (Orthoptera), ucholakmi (Dermaptera), pakobylkami (Phasmatodea), svrčkovcami (Grylloblattodea) a nedávno opísaným radom Mantophasmatodea (KLASS et al. 2002) skupinu ortopteroidného hmyzu.

Šváby ako rad sú tak u nás, ako aj vo svete, pomerne zanedbávaná skupina, čo je zrejme dané malým počtom druhov, ktoré tento rad zahŕňa. Na druhej strane však sú šváby ideálnymi laboratórnymi živočíchmi. Rýchlo a bezproblémovo sa množia, na malom priestore je ich možné dochovať stovky. Preto sa stali laboratórnou „myšou“ pri výskume bezstavovcov. Keď som koncom 80-tych rokov minulého storočia začínal svoju kariéru, bol to práve výskum fyziológie bezstavovcov, zhodou okolností švábov. Príprava pokusov si vyžadovala dôkladné poznanie ich pohlavného správania (pozri časť 3). Táto prvá skúsenosť spojená s výskumom švábov predurčila moju celoživotnú dráhu.

Od etológie tropických laboratórnych druhov sa časom záujem presunul aj na naše autochtónne druhy švábov. V tej dobe bolo zo Slovenska známych len 5 druhov (MAŘAN & ČEJCHAN 1977) a z celej Európy asi 80 druhov švábov. O ich rozšírení či sezónnej dynamike sa vedelo veľmi málo a nakoniec sa aj existujúce determinačné kľúče ukázali ako nespoľahlivé. Vedomosti o švábLoch bolo treba získavať takmer od začiatku. Na Slovensku sa faunistikou či taxonómiou švábov nezaoberal žiadny špecialista a v Českej republike sa im v tej dobe venovali iba dvaja odborníci, obaja však iba popri koníkoch a kobylkách. Štúdium začalo spracovaním muzeálnych zbierok v slovenských a českých múzeách (VIDLIČKA & MAJZLAN 1992, VIDLIČKA & HOLUŠA 1999). Dôkladné zoznámenie sa s literatúrou a všetkými dostupnými dátami vyústilo v spolupráci s vtedy tiež mladými kolegami z Čiech do publikovania nového zoznamu druhov (KOČÁREK et al 1999) ako aj bibliografie ortopteroidného hmyzu (HOLUŠA et al. 1999). Okruh záujmu sa postupne rozšíril aj na územie Maďarska a Rumunska. Spracované boli šváby celej Karpatskej kotliny (VIDLIČKA & SZIRÁKY 1997), Švajčiarska (VIDLIČKA & REZBÁNYAI-RESER 2005), čiastočne Chorvátska (VIDLIČKA & OZIMEC 2011). Popri tom boli objavené a opísané aj pre vedu nové druhy z Maďarska, Rumunska, Bulharska (pozri časť 4). Nazhromaždené údaje vyústili do monografického spracovania Fauny švábov Slovenska (VIDLIČKA 2001) a vďaka možnosti ponúknutej kolegami z Českej republiky aj ilustrovaného kľúča pre Českú Republika a Slovensko (KOČÁREK et al. 2005).

Záujem o taxonómiu švábov zákonite viedol k rozšíreniu záujmového územia na teritóriá bohatšie na faunu švábov – juhovýchodnú Áziu a Južnú Ameriku (pozri časť 5). V týchto dvoch oblastiach žijú tri štvrtiny všetkých známych druhov švábov. Na rozdiel od Európy sú tu početné malé endemické rody. Ich identifikácia je pomerne náročná, odborníkov na šváby je na svete iba pár. Zároveň sú to oblasti postihnuté rýchle vzrastajúcim počtom obyvateľstva a v ruka v ruke s tým aj devastáciou prírody nebývalých rozmerov.

Úzka spolupráca s paleontológom, ktorý sa veľmi úspešne etabloval pri výskume fosílnych švábov, vyústila okrem taxonomickej problematiky aj do výskumu ich paleoetológie (pozri časť 6), čím sa kruh záujmov akoby uzavrel a znovu sa vrátil tam kde začal.

2. Štruktúra práce a jej zameranie

Habilitačná práca pozostáva z úvodnej časti, v ktorej sú stručne načrtnuté štyri záujmové okruhy, ktoré autor rieši alebo v minulosti riešil a zo súboru 17 vedeckých článkov publikovaných v impaktovaných (12) ako aj neimpaktovaných recenzovaných (5) časopisoch a dvoch monografií, ktoré majú vzťah k problematike vybraných tematických okruhov. Pripojené publikované práce sú iba výberom prác autora, keďže autor sa venuje okrem švábov (Blattaria) aj sieťokrídlovcom (Neuroptera) a príležitostne aj iným radom hmyzu (Insecta). Pripojené práce sú zároveň aj reprezentatívnym výberom z prác autora venovaných výskumu švábov z rokov 1993-2015.

Úvodná časť práce slúžia na zoznámenie sa s tým, čo bolo v danej problematike známe do doby autorovho príspevku, s výsledkami autora a prípadne aj s tým, čo sa v tejto oblasti zistilo odvtedy dodnes.

2.1. Tematické okruhy práce

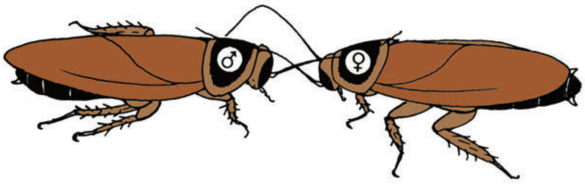
a) Etológia švábov – dvorenie a párenie
b) Rozšírenie a taxonómia švábov v strednej Európe a na Slovensku
    b1) Rod *Ectobius* – rozšírenie a biológia
    b2) Rod *Phyllodromica* – skupina druhov *maculata*
    b3) Rod *Phyllodromica* – skupina druhov *megerlei*
c) Šváby v juhovýchodnej Ázii a Južnej Amerike
    c1) Šváby z rodu *Caeparia* Stål, 1877 (Blaberidae: Panesthiinae)
    c2) Šváby z rodu *Chorisoserra* (Blattellidae: Pseudophyllodromidae)
    c3) Šváby z rodu *Spelaeoblatta* Bolívar, 1897 (Noticolidae)
    c4) Šváby z rodu *Macrophyllodromia* Saussure & Zehnter, 1893 (Blattellidae)
d) Fosílne šváby (Blaberidae, Blattellidae, Ectobiidae)

3. Etológia švábov

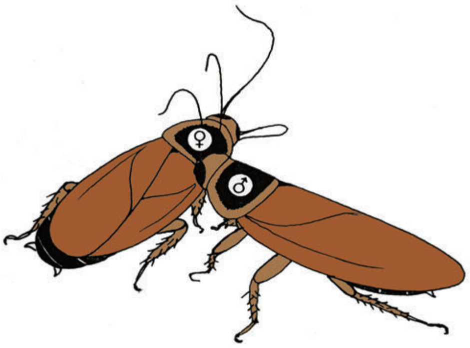
3.1. Dvorenie a párenie

Záujem o detailný priebeh správania sa švábov počas dvorenia a párenia možno datovať do 50-tych rokov minulého storočia. Prelomovou bola práca dvojice amerických švábológov Louisa M. Rotha a Edwina R. Willisa o reprodukčnej biológii švábov (Roth & Willis 1954).

Predkopulačné správanie švábov vykazuje u celej skupiny určité známky uniformity (Roth & Willis 1954, Roth & Dateo 1966; Roth & Barth 1967, Roth 1969, Simon & Barth 1977a,b). Priebeh párenia sa však môže v určitých detailoch líšiť v závislosti od umiestnenia tergálnych žliaz samčeka. V tergálnych žľazách sa tvorí sexuálny (afrodiziakálny) feromón. Podľa spôsobu akým samček láka samičku a zahajuje kopuláciu rozlišujeme tri typy páriaceho správania (A, B a C) (Sreng 1993). Párenie je najlepšie preskúmané na laboratórne chovaných druhoch švábov. Jedným z najčastejšie chovaných druhov je cirkumtropicky rozšírený druh *Nauphoeta cinerea* (Blaberidae: Oxyhaloinae). Z viacerých príčin práve on plní úlohu „laboratórnej myši“ pri výskume bezstavovcov. Spôsobom dvorenia a párenia je šváb *Nauphoeta cinerea* typickým predstaviteľom základného typu A.



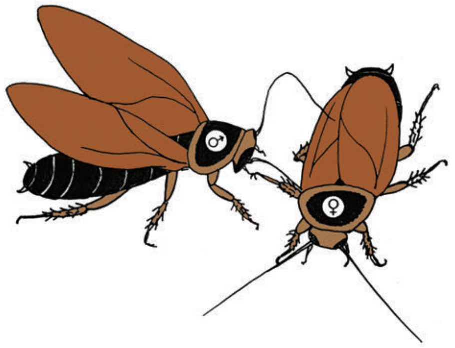
Obr. 1. Stretnutie jedincov rôzneho pohlavia.



Obr. 2. Tykadlový kontakt.

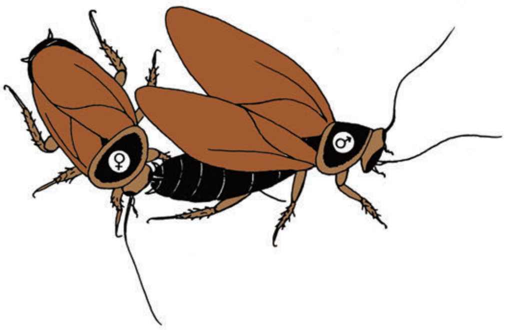
Keď sa k sebe priblížia samček a samička švába *N. cinerea* (obr. 1), ktorí sú pripravení na párenie, začne samček vylučovať prchavé látky krátkeho dosahu a na povrchu samičky sa objavia kontaktné feromóny, ktoré umožňujú druhovú identifikáciu, rozpoznanie pohlavia a zároveň, v prípade stretnutia správneho druhu a páru, uľahčujú aj koordináciu dvorenia samčeka samičke. Využívaniu pohlavných feromónov švábmi sa dlhodobo venoval Coby Schal (Schal 1982, Schal & Bell 1984, 1985, Schal et al. 1990, 1991) a tému prednedávnom komplexne spracoval (Gemeno & Schal 2004). Feromóny neslúžia len pri výbere partnera a na spustenie samčieho dvorenia, ale zároveň môžu regulovať aj viaceré fyziologické procesy. U *N. cinerea* môžu samčie feromóny ovplyvniť dĺžku života samičky, počet potomkov, pomer ich pohlavia a rýchlosť ich vývinu v plodovom vaku (Moore et al. 2001, 2002, 2003).

Pri krátkom tykadlovom kontakte overí samček fyziologickú pripravenosť samičky na párenie (obr. 2). V prípade samičkinej fertility zahajuje samček fázu dvorenia. Dvihne tegminy a krídla do takmer kolmej polohy k telu, čím odokryje tergity na svojom chrbte (obr. 3) a zároveň umožní lepšie pôsobenie



Obr. 3. Dvorenie samčeka samičke.

feromónu produkovaného tergálnymi žľazami. Následne sa ku samičke natočí tak, aby mohla zozadu vyliezť na jeho chrbát. Ak samička nereaguje na takúto ponuku snaží sa samček podsunúť bruško pod jej hlavu čo najtesnejšie.

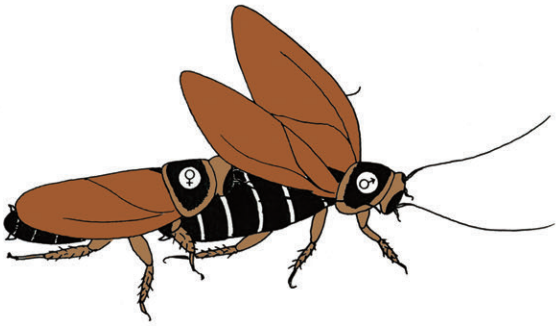


Obr. 4. Vyliezanie samičky na chrbát dvoriaceho samčeka.

Fertilná samička zvyčajne reaguje na ponuku samčeka postupným vyliezaním na jeho chrbát (obr. 4). Súčasne ústnymi orgánmi „olizuje“ produkt samčích tergálnych žliaz (obr. 5). Vyliezanie zvyčajne končí dotykom samičkinej hlavy o dvihnuté krídla samčeka.

Doba, ktorú strávi samička olizovaním sekrétov stačí samčekovi na to, aby vystrčil genitálny hák (ľavá faloméra), zasunul ho pomedzi samičie genitálie, a tak vytvoril dostatočne pevné spojenie so samičkou (obr. 6).

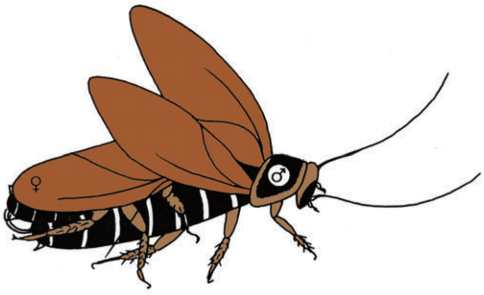
Hákom spoľahlivo pripojený samček sa začne pohybovať dopredu a skladať krídla a tegminy na bruško, čím prinúti samičku zliezť bokom z jeho chrbta (obr. 7) a otočiť sa o 180 stupňov (obr. 8). Tým sa koniec samčieho bruška pretočí a následne ho samček musí dostať do prirodzenej polohy bez toho, aby bolo prerušené ukotvenie pomocou háku. Až po tomto pomerne náročnom úkone sa obaja v páre dostávajú do správnej kopulačne pozície a môže začať vlastná kopulácia (obr. 9). Zaujatú polohu nemení pár až do skončenia kopulácie (Vidlička 2001, Bell et al. 2007).



Obr. 5. Olizovanie samčích sekrétov.

Proces kopulácie môže trvať rôzne dlho. Dĺžka kopulácie je samozrejme medzi druhmi variabilná, ale mení sa aj v rámci druhu. Jej dĺžku ovplyvňuje viacero faktorov. V prvom rade je to vek samčeka, ale vplyv má aj doba uplynutá od jeho posledného párenie a jeho sociálny status. Reálna dĺžka párenia sa dá zistiť iba odstránením vplyvu všetkých týchto faktorov. To znamená, že pozorovania z prírody sú ťažko interpretovateľné. Najdlhšie párenia pozorované v prírodných podmienkach sa týkajú juhoamerického druhu *Xestoblatta hamata* (Blattellidae), kde párenie v dažďovom pralese trvalo až 5 hodín (Schal & Bell 1982) a austrálskeho druhu *Polyzosteria limbata* (Blattidae, Polyzosterinae), kde párenie prebiehalo za denného svetla a páry niekedy zostávali spojené viac ako 24 hodín (Mackerras 1965).

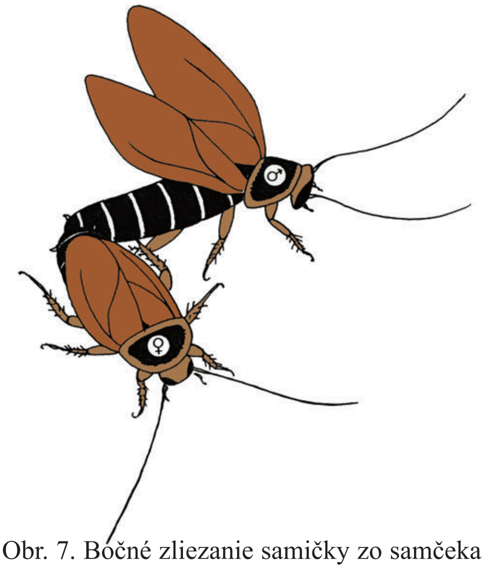
Zhodou okolností sa *Nauphoeta cinerea* pári najkratšie z doteraz študovaných druhov. Za dodržania štandardných podmienok (použitie 14 dní starých panenských samčekov chovaných už od posledného nymfálneho instaru v kolektíve nýmf rovnakého pohlavia pri teplote 25±1°C) je doba jeho párenia prekvapivo stabilná – 12,5 minúty (N=100, SE=0,9 – Vidlička & Hučková 1993).



Obr. 6. Prichytenie samičky hákom.

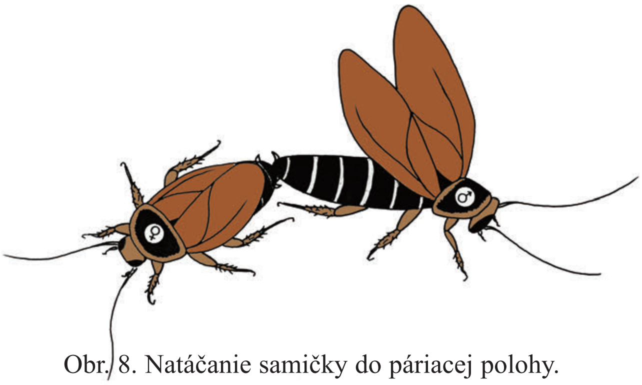
Pri pozmenených podmienkach môže prvé párenie trvať aj 17 minút (ROTH 1964). Druhé párenie s nedostatočným odstupom môže trvať podstatne dlhšie (100 8 min.) a pri treťom párení v rade až 141±2 minúty (ROTH 1964).

Pozornosť bola zvyčajne venovaná dĺžke párenia a jeho úspešnosti, prípadne vlastnostiam potomstva, ale už menej vlastnému priebehu kopulácie. Telo samčekov počas kopulácie pulzuje v nepravidelných intervaloch. U *Nauphoeta cinerea* pulzuje telo samčeka prvé 4 minúty kopulácie približne 15x za minútu, ďalšie 4 minúty frekvencia klesá pod 10 pulzov za minútu, v 9. minúte sa počet pulzov prudko zväčšuje až na 20 za minútu, potom frekvencia pulzov bruška samčeka prudko klesá pod 10 pulzov za minútu (obr. 10) a v poslednej minúte párenia sa fakticky takmer úplne zastavuje (VIDLIČKA & HUČKOVÁ 1993).



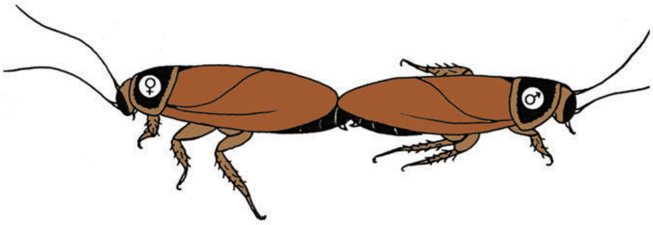
Obr. 7. Bočné zliezanie samičky zo samčeka.

Experimentálne prerušovanie kopulácie v pravidelných intervaloch (po 4, 6, 8, 10 minútach od zaujatia páriacej polohy) prispelo k pochopeniu dejov v priebehu kopulácie. Vo väčšine prípadov mal samček po 4 minútach párenia penis vysunutý, podobne to bolo aj po 8 minútach párenia. V oboch prípadoch došlo v deviatej minúte k vysunutiu spermatoforu a jeho upevneniu k podkladu. Pri prerušení kopulácie po 10. minúte bol penis tiež vysunutý a zostal tak až do 13. minúty (podobne to bolo aj v predchádzajúcich dvoch prípadoch), a potom bol zatiahnutý. Na základe zistených zmien v rýchlosti pulzácie a tiež na základe výsledkov z prerušovania kopulácie bol priebeh kopulácie rozdelený do štyroch fáz: i. tvorba genitálneho kontaktu, vysunutie penisu (1.-4. minúta), ii. tvorba, kompletizácia a presun spermatoforu v tele samčeka (5.-8. minúta), iii. prenos spermatoforu do kopulačnej komôrky (bursa copulatrix) samičky (9. minúta), iv. prerušenie genitálneho kontaktu, zasunutie penisu a uvoľnenie upevňovacieho háku z tela samičky (10.-13. minúta) (VIDLIČKA & HUČKOVÁ 1993).



Obr. 8. Natáčanie samičky do páriacej polohy.

Spermie po skončení párenia nemigrujú zo samčieho spermatoforu umiestneného v kopulačnej komôrke do samičej spermatéky okamžite. Spermatofor obsahuje nepohyblivé, stočené spermie, ktoré sa vystierajú a začínajú sa aktívne pohybovať až asi po 2 hodinách (VIDLIČKA & HUČKOVÁ 1993). Spermie sú aktivované výlučkami spermatéky (KHALIFA 1950).

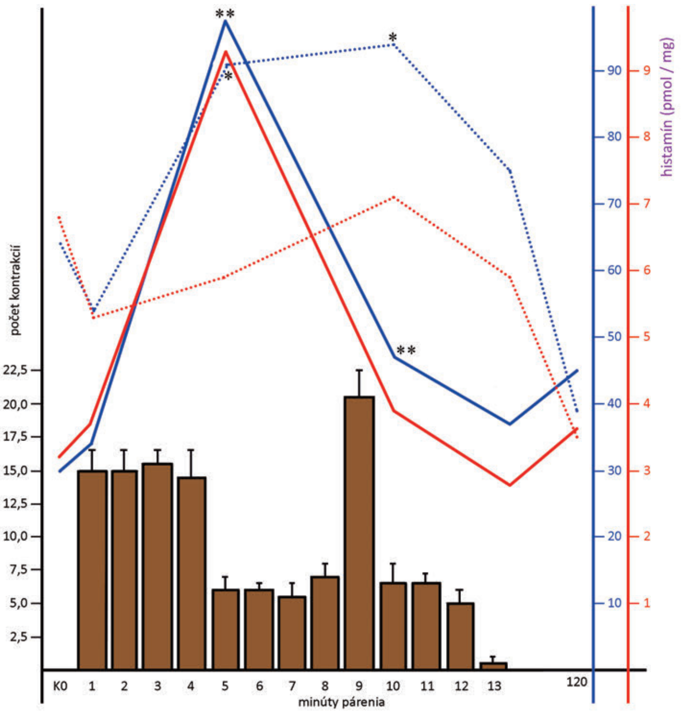


Obr. 9. Kopulácia v lineárnej polohe.

Keďže niektoré výskumy ukázali, že úroveň histamínu ako neurotransmiteru v hmyzích CNS sa mení v odozve na rôzne stresové podnety (Kozánek et al. 1985, Takáč et al. 1990), zvažovala sa aj jeho úloha v reprodukcii švábov *Nauphoeta cinerea* (Hučková et al. 1992).

Priebeh koncentračných zmien histamínu v mozgu (supraoesofageálnom gangliu) *Nauphoeta cinerea* počas párenia bol u samčekov a samičiek veľmi podobný (obr. 10). V čase dvorenia, keď samička vylezie na bruško samčeka a na začiatku kopulácie sa úroveň histamínu zvýšila len mierne. Tento nárast bol trochu prudší v mozgu samičiek oproti mozgu samčekov. V 5. minúte kopulácie sa koncentrácie histamínu u oboch pohlaví výrazne zvýšili a dosiahli asi 3-krát vyššie hodnoty, než boli pozorované u kontrolných nepárených skupín. V 10. minúte kopulácie sa znížila hladina histamínu a bola približne na rovnakej úrovni ako na začiatku kopulácie, avšak u samčekov bola signifikantne vyššia v porovnaní s kontrolnou skupinou. Po 2 hodinách bola hladina histamínu u oboch pohlaví takmer rovnaká ako v kontrolných skupinách alebo na začiatku kopulácie.

V 6. abdominálnom gangliu boli zmeny koncentrácie histamínu výrazne odlišné u samčekov a samičiek (obr. 10). Na začiatku kopulácie bola síce u oboch pohlaví takmer rovnaká ako u kontrolnej skupiny, ale potom (v 5. a 10. minúte párenia) bol u samčekov zaznamenaný prudký nárast koncentrácie. U samičiek zostala koncentrácia histamínu porovnateľná s kontrolnou skupinou. Dve hodiny po ukončení kopulácie boli hodnoty histamínu nižšie ako u kontrolných skupín. To naznačuje úlohu 6. brušného ganglia a histamínu práve pri dotvorení spermatoforu v brušku samčeka a pri jeho presune a upevnení v kopulačnej komôrke samičky (Kozánek et al. 1992, Hučková et al. 1994). Hintze-Podufal & Vetter (1996) poukázali na funkciu juvenilného hormónu pri párení švába *Blaptica dubia*. Významnú úlohu hral hlavne v prvej fáze dvorenia – tykadlový kontakt.



Obr. 10. Priebeh kontrakcií bruška u samčeka a zmeny hladiny histamínu v mozgu (plná čiara) a v 6. abdominálnom gangliu (bodkovaná čiara) u samčekov (modrá čiara) a samičiek (červená čiara) *Nauphoeta cinerea* počas 1. kopulácie.

Ako už bolo naznačené, samčekovi po párení trvá príprava nového spermatoforu (hlavne jeho naplnenie spermiami) značnú dobu. Preto trvajú opakované párenia výrazne dlhšie. Samčekovia švába *N. cinerea*, ktorí sa opätovne párili skôr ako za 24 hodín, mali obmedzený počet spermií a produkovali menej potomkov než panenskí samčekovia a tiež samčekovia, ktorí mali päťdňovú dobu na zotavenie medzi dvoma kopuláciami (MONTROSE et al. 2004). Ukázalo sa, že samičky *Nauphoeta cinerea* sú schopné rozlíšiť samčekov, ktorí sa ešte nepárili od takých, ktorí sa už párili. Ak majú možnosť, vyberajú si panenských samčekov radšej ako samčekov s nedostatkom spermií (HARRIS & MOORE 2005).

U druhu *Schultesia nitor* (Blaberidae: Zetoborinae) bolo pozorované, že samčekovia sa stávajú pohlavne receptívnymi až pár dní po imaginálnom zvlečení. Pred týmto časom nie sú schopní párenia. Samičky sa stávajú fertilnými takmer okamžite po imaginálnom zvlečení, skôr ako sú plne zafarbené a sklerotizované (tenerálne samičky). U tohto druhu je larválny vývoj u samčekov kratší ako u samičiek, čiže tento druh je protandrický. Samičky sa správajú monandricky (pária sa iba raz), zatiaľ čo samčekovia sú polygynní (ak majú príležitosť pária sa viackrát). Samičky u tohto druhu produkujú iba jednu znášku a krátko po vyliahnutí potomstva hynú. Aj u tohto druhu sa ukázalo, že ak majú samičky možnosť voľby, uprednostňujú panenských samčekov pred už skúsenejšími samčekmi (MONCEAU & VAN BAAREN 2012).

Samičky ovoviviparného druhu *Nauphoeta cinerea* vynosia v priemere 6 ooték. Po oplodnení strácajú fertilitu. Keď porodia potomstvo chránia nymfy počas prvého instaru (MOORE & MOORE 2001). Až potom nadobúdajú opäť fertilitu a sú ochotné sa znova páriť (ROTH 1964).

3.2. Prehľad príspevkov autora k poznaniu etológie švábov

(hnedou farbou sú uvedené príspevky, ktoré sú súčasťou habilitačnej práce)

KOZÁNEK, M., TAKÁČ, P., VIDLIČKA, Ľ. 1990. Concentration changes of some monoamines and steroids during courtship and copulation of cockroach Nauphoeta cinerea. *Invertebrate Reproduction & Development* 18(1-2): 120.

TAKÁČ, P., KOZÁNEK, M., VIDLIČKA, Ľ. 1990. Circadian changes of some vertebrate-type hormones in cockroach Nauphoeta cinerea. *Invertebrate Reproduction & Development* 18(1-2): 130.

HUČKOVÁ, A., KOZÁNEK, M., VIDLIČKA, Ľ., TAKÁČ, P. 1992. Histamine distribution in the nervous system of the cockroach Nauphoeta cinerea (Blattodea, Panchloridae) and its changes during development, pp. 129-134. In: *Advances in regulation of insect reproduction*. Institute of Entomology Czech Academy Sciences, České Budějovice. ISBN 80-901250-0-X

VIDLIČKA, Ľ., HUČKOVÁ, A. 1993. Mating of the cockroach Nauphoeta cinerea (Blattodea: Blaberidae): I. Copulatory behaviour. *Entomological Problems* 24(2): 69-73. (Príloha č. 1)

HUČKOVÁ, A., VIDLIČKA, Ľ., KOZÁNEK, M. 1994. Mating of the cockroach Nauphoeta cinerea (Blattodea: Blaberidae): II. Histamine changes during courtship and copulation. *Biologia* 49(5): 691-695. (Príloha č. 2)

VIDLIČKA, Ľ. 2001. *Blattaria – šváby; Mantodea – modlivky (Insecta: Orthopteroidea)*. Veda, Bratislava, 169 pp. (Fauna Slovenska) ISBN 80-224-0640-6 (Príloha č. 18)

4. Rozšírenie a taxonómia švábov v Európe a na Slovensku

Šváby (Blattaria) sú prevažne tropickou skupinou zahŕňajúcou okolo 5000 druhov. Z tohto množstva sa v Európe vyskytuje len okolo 120 druhov čo znamená, že v Európe je najmenšia druhová pestrosť švábov zo všetkých svetadielov (samozrejme okrem Antarktídy).

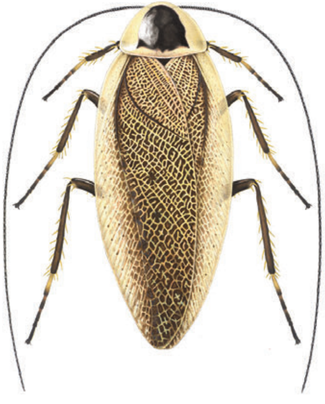
Napriek pomerne malému množstvu druhov je švábologická literatúra zaoberajúca sa územím Európy nepomerne bohatšia ako na iných svetadieloch. Viaceré Európske druhy majú dosť široké rozšírenie a sú značne variabilné, čo spôsobilo, že boli opísané aj niekoľkokrát. Majú množstvo synoným, niektoré druhy aj viac ako desať. Situácia sa preto stala krajne neprehľadnou a paradoxne, určenie niektorých európskych druhov (hlavne balkánskych) je takmer nemožné.

Z územia Európy je známych z natívnych druhov iba 6 rodov švábov – *Ectobius*, *Phyllodromica*, *Loboptera*, *Planuncus*, *Capraiellus*, *Polyphaga* a *Hemelytroblatta*. Z rodu *Polyphaga* zasahuje do Európy iba 1 druh – *P. aegyptiaca*. Rod *Hemelytroblatta* je zastúpený 5 druhmi zasahujúcimi okrajovo do juhovýchodnej Európy. Celý rod sa vyskytuje prevažne v severnej Afrike a na Blízkom Východe. Podobne rod *Loboptera*, ktorý zahŕňa 32 druhov, je z Európy známy iba 6 druhmi, z ktorých iba jeden je širšie rozšírený v Stredomorí – *Loboptera decipiens*. Ostatných 5 druhov je známych iba zo Španielska a boli opísané pomerne nedávno (BOHN 1990) odčlenením od druhu *Loboptera decipiens*. Zvyšok druhov je endemických na Kanárskych ostrovoch, Azorách, Madeire a v Maroku. Výnimku predstavujú dva druhy vyskytujúce sa v Kamerune (*L. loboptera* Princis, 1962) a v Saudskej Arábii (*L. isolata* Grandcolas, 1994).

Rody *Ectobius* a *Phyllodromica* majú európske až eurázijské (palearktické) rozšírenie. Viaceré druhy zasahujú aj do Afriky. V rode *Ectobius* evidujeme v súčasnosti 67 druhov, z ktorých 35 je rozšírených v Európe, pri rode *Phyllodromica* je to 60 z 99 známych druhov. Rod *Capraiellus* vznikol odčlenením troch druhov z rodu *Ectobius* do samostatného podrodu (HARZ 1976), ktorý bol prednedávnom povýšený na samostatný rod (BOHN et al. 2013). Všetky tri druhy rodu *Capraiellus* sa vyskytujú v Európe. Rod *Planuncus* bol tiež zriadený iba pred dvomi rokmi (BOHN et al. 2013) a boli sem preradené 4 druhy z rodu *Ectobius* a 9 druhov z rodu *Phyllodromica*. Až 11 z nich žije v Európe. Oba tieto prípady naznačujú dosť neprehľadnú situáciu v rozlišovaní rodov *Ectobius* a *Phyllodromica*, kde bola donedávna hlavným kritériom dĺžka tegmín.

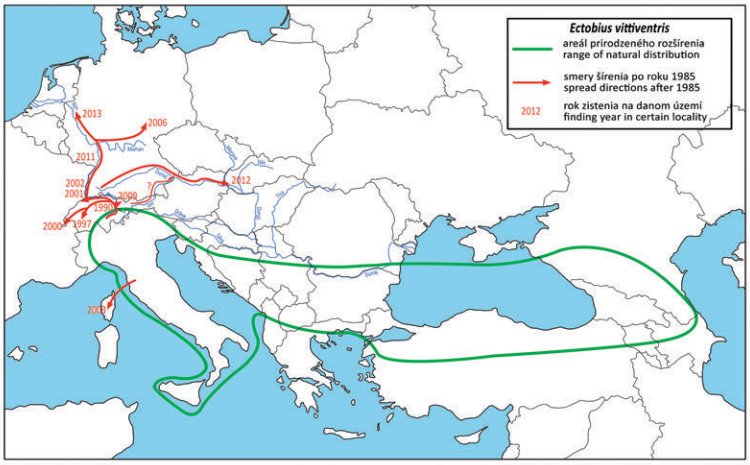
4.1. Rod *Ectobius* – rozšírenie a biológia

Zo spomínaných 35 európskych druhov rodu Ectobius žije 27 na Apeninskom polostrove a na blízkych ostrovoch. Mnoho z nich je tam endemických, hlavne na Sicílii, Sardínii a ďalších menších ostrovoch. Hlbšie do kontinentálnej Európy preniká iba pár druhov. Na území Slovenska boli dlho známe iba 3 druhy – *E. sylvestris* (obr. 11), *E. lapponicus* a *E. erythronotus*. Status a tiež rozšírenie štvrtého druhu *E. lucidus* sú nejasné (BOHN 1989).



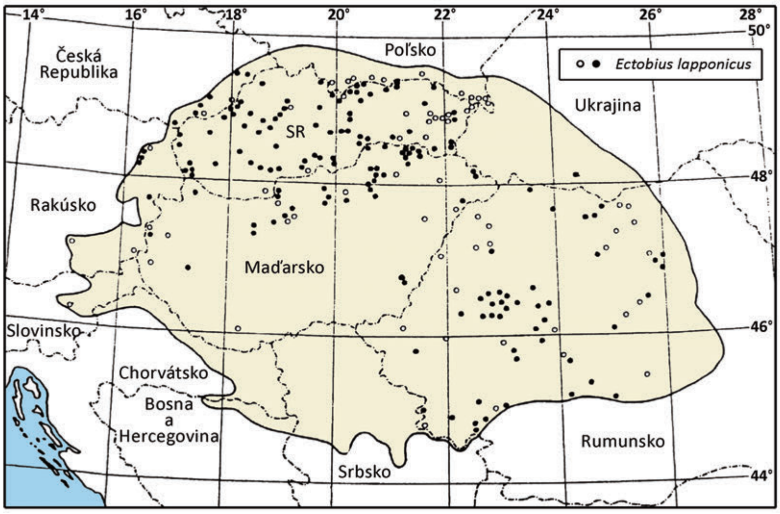
Obr. 11. *Ectobius sylvestris* (VIDLIČKA 2001).

Vďaka otepľovaniu klímy pribudol na našom území približne od roku 2010 nový druh švába pôvodom z južnej (podalpskej) časti Švajčiarska – *Ectobius vittiventris*. Keďže je teplomilnejší ako naše druhy a má podobné teritoriálne nároky, udomácniť sa mu darí iba vo väčších mestách, zvyčajne v trávnikoch, parkoch a záhradách pri domoch. Na Slovensku bol zatiaľ zistený iba v Bratislave, jeho prenikanie do ľudských príbytkov bolo iba sporadické (VIDLIČKA 2014). V roku 2015 však začal do príbytkov prenikať masovo, hlavne na jeseň. Svojim správaním (na rozdiel od synantropného druhu *Blattella germanica* sa neskrýva cez deň pred svetlom) vyvolal v postihnutých domácnostiach zdesenie a u dezinsekčných firiem zmätok (nepubl. údaje). Šírenie tohto druhu do roku 2014 je zobrazené na obrázku 12.



Obr. 12. Mapa pôvodného rozšírenia švábika *Ectobius vittiventris* a smery jeho šírenia po roku 1985. Podľa VIDLIČKU (2014).

Výskyt a rozšírenie švábikov z rodu *Ectobius* ako aj blízko príbuzného rodu *Phyllodromica* v Poľsku spracoval BAZYLUK (1977). V tom istom roku bol spracovaný aj zoznam Československých druhov švábov (MAŘAN & ČEJCHAN 1977). V tej dobe však neboli zo Slovenska ešte známe žiadne endemické druhy. Na Slovensku spracovali zoznam druhov švábov ako aj ich rozšírenie VIDLIČKA a MAJZLAN (1992). Následne bola spracovaná bibliografia literatúry o šváboch v Českej Republike a na Slovensku (HOLUŠA et al. 1999) a na jej základe aj zoznam druhov pre Čechy, Moravu a Slovensko (KOČÁREK et al. 1999). Priebežne boli spracované doplnkové informácie o výskyte švábov v rôznych oblastiach Slovenska: Muránska planina (VIDLIČKA 1997), Devínska Kobyla (VIDLIČKA 2005), ostrov Kopáč (VIDLIČKA 2007), Jurský Šúr (FEDOR et al. 2010), Východné Slovensko (TOMKO et al. 2013).



Obr. 13. Rozšírenie druhu *Ectobius lapponicus* v Karpatskej kotline. Podľa VIDLIČKU & SZIRÁKIHO (1997) – upravené.

Detailné poznanie rozšírenia švábov v celej Karpatskej kotline (zahrnuté boli aj celé Karpaty) (obr. 13) je založené na štúdiu bohatých muzeálnych materiálov z viacerých múzeí. Pre každý druh bola vypracovaná aj distribučná mapa (VIDLIČKA & SZIRÁKI 1997).

Neskôr bolo podobne spracovaných takmer 800 exemplárov švábov z 25 rokov trvajúcich zberov (1975-2000) zo Švajčiarska. Zistených bolo 10 druhov z rodu *Ectobius* (VIDLIČKA & REZBANYAI-RESER 2005). Počas spracovávania bol zistený aj výskyt nového druhu švába (*Ectobius supramontanus* Bohn, 2004). Preto bola práca publikovaná až po zverejnení jeho opisu (BOHN 2004).

Začaté bolo aj pomerne náročné spracovávanie balkánskej fauny švábov. Existuje zoznam švábov bývalej Juhoslávie (US & MATVEJEV 1967), tento však treba inovovať pre jednotlivé nástupnícke štáty a hlavne podľa najnovších zmien v taxonómii. Spracovanie balkánskeho komplexu druhov *Ectobius erythronotus* (KARAMAN & KARAMAN 1987) do danej problematiky väčšiu prehľadnosť neprinieslo, skôr naopak. Najnovší výskum sa začal v oblasti pohoria Biokovo (Chorvátsko), kde bolo v rozmedzí 900-1650 m n.m. zistených predbežne 5 druhov švábov (VIDLIČKA & OZIMEC 2011). Ďalší balkánsky materiál však zatiaľ čaká na komplexnú revíziu.

O biológii švábov z rodu *Ectobius* sa zatiaľ toho veľa nevie. *Ectobius sylvestris* sa v južných Alpách dá zastihnúť až vo výškach okolo 2400 m (BEIER 1974). U nás bol pozorovaný v Belianskych Tatrách do 1700 m (CHLÁDEK 1986). Druhy tohto rodu sa živia hlavne organickým detritom. Cez deň môžeme samčekov často zastihnúť na kvetoch rastlín, najmä na sedmokráskach (*Bellis* sp.) a omanoch (*Inula* sp.), kde sa kŕmia peľom rastlín (VIDLIČKA 2001). Nymfy a samičky sú aktívne hlavne v noci (DREISIG 1971).

V prírode (na Slovensku) sa švábiky hôrne (*Ectobius sylvestris*) vyskytujú od apríla do októbra (VIDLIČKA 1993, 2012) s vrcholom výskytu imág v polovici apríla až začiatkom mája (VIDLIČKA 1993, 2013). V Nemecku v jelšovom lese bola u toho istého druhu zaznamenaná najväčšia migrácia po kmeňoch stromov v druhej polovici mája (GHARAGJEDAGHI 1994). Imága švábika tmavoštíteho (*Ectobius lapponicus*) na východe Čiech dosiahli maximum v druhej polovici júna, respektíve až v júli (HOLUŠA & KOČÁREK 2000). Vrcholy výskytu imág korešpondujú aj s obdobiami znášok ooték (VIDLIČKA 1993) a zároveň aj s výskytom parazitoida *Brachygaster minutus* (VIDLIČKA 1998). Nymfy sa liahnu počas júla a zimujú ako štvrtý nymfálny instar (BROWN 1973a, b, VIDLIČKA 2012), zriedkavo ako druhý alebo tretí instar (BROWN 1983). Zimovanie prebieha najčastejšie v zemi, v trsoch tráv, ale aj v opustených hniezdach vtákov (VIDLIČKA 1999).

4.2. Rod *Phyllodromica* – skupina druhov *maculata*

Je zaujímavé, že tak ako v južnej Európe majú sklony vytvárať množstvo endemitov zástupcovia z rodu *Ectobius*, tak v strednej Európe, kde je rod *Ectobius* zastúpený veľmi chudobne, plnia túto funkciu druhy rodu *Phyllodromica*, hlavne zo skupiny *maculata*. Typový druh *Phyllodromica maculata* (obr. 14) má veľmi široké rozšírenie od Nemecka po JZ Ukrajinu a od stredného Poľska až po severné Chorvátsko a Rumunsko. Jeho sfarbenie je veľmi variabilné a preto vznikli v minulosti problémy pri delení tohto druhu na variety, poddruhy resp. druhy. Novo opisované druhy majú spravidla malé areály rozšírenia a sú endemitmi na daných územiach.

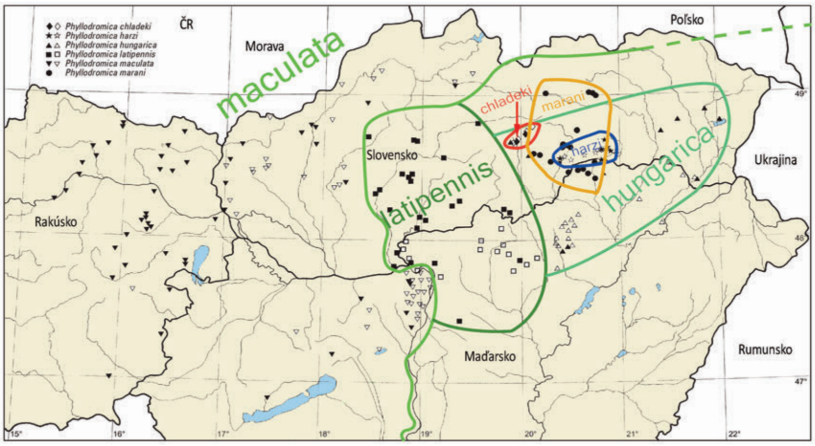
Obr. 14. *Phyllodromica maculata* (VIDLIČKA 2001).

Viaceré endemické druhy boli opísané priamo zo Slovenska alebo susedného Maďarska. Prvými boli *Phyllodromica harzi* Chládek, 1977 zo Slovenského krasu a *Phyllodromica chladeki* Harz, 1977 z Muránskej planiny (CHLÁDEK & HARZ 1977). Druh *Phyllodromica hungarica* Vidlička, 1993 bol pôvodne opísaný z pohoria Bükk na severe Maďarska (VIDLIČKA 1993), ale neskôr bol zistený aj na južnom Slovensku (VIDLIČKA 2001, BOHN & CHLÁDEK 2011, TOMKO et al. 2013). Ďalší nový druh *Phyllodromica dobsiki* (*dobšiki*) Chládek, 1996 bol opísaný z Muránskej planiny, z rezervácie Suché doly pri Tisovci (CHLÁDEK 1996). Neskôr bol tento druh synonymizovaný s druhom *Ph. hungarica* (BOHN & CHLÁDEK 2011).

Zo Slovenska bol opísaný aj poddruh *Phyllodromica maculata marani* (*mařani*) Chládek & Harz, 1980 s výskytom na strednom a východnom Slovensku, v Poľsku a Rumunsku. Od nominálneho poddruhu sa odlišoval morfológiou ootéky (CHLÁDEK & HARZ 1980). Zobrazená ootéka pochádzala zo Slovenského krasu. Ako vyzerajú imága švába sa v práci neuvádza, ale autor tvrdil, že sú zhodné s exemplármi z Brašova (Rumunsko) spomínanými v práci RAMMEHO (1951) ako poddruh *Hololampra maculata schäfferi*. Aj keď Ramme vyslovene hovorí o poddruhu, Chládek ich hodnotí ako melanickú formu *schaefferi* s tým, že medzi formami existujú prechody. To bol dôvod vytvorenia nového mena pre tento poddruh. Zo Slovenska známe jedince daného poddruhu a literatúru k nim sa vzťahujúcu neuvádza. VIDLIČKA a SZIRÁKI (1997) poukázali na to, že tento poddruh je iba synonymom *Ph. maculata schaefferi* známeho zo Slovenského krasu už 150 rokov (FRIVALDSZKY 1867) a z Maďarska 120 rokov (CHYZER 1897). Následne CHLÁDEK (1998) povýšil nový poddruh bez udania dôvodu na nový druh (a omylom uviedol opačné poradie autorov ako v pôvodnej práci – Harz et Chládek, 1980). Druh bol opätovne synonymizovaný s *Ph. maculata schaefferi* (VIDLIČKA 2001). Ak by bol uznaný jeho druhový status, meno by malo byť *Phyllodromica schaefferi*. Status tohto druhu (resp. poddruhu) je značne komplikovaný a zaslúži si krátke vysvetlenie.

Druh bol (ako *Blatta qvarta*) pôvodne „opísaný“ (zobrazený na ilustrácii) v diele prírodovedca **Jacoba Chritiana Schaeffera** (*1718-†1790) pojednávajúcom o hmyze z okolia nemeckého mesta Regensburg (SCHAEFFER 1769). Pôvodný názov bol uznaný za neplatný z dôvodu, že meno bolo vlastne poradovým číslom a šváb samotný bol iba zobrazený na obrázku. Na Schaefferovu počesť dostal od **Johanna Augusta Ephraima Goezeho** (*1731-†1793) druh nové meno *Blatta Schaefferi*. GOEZE (1778) sa odvolal na Schaefferov obrázok a stručne druh charakterizoval. O typovej lokalite sa nezmienil. Neskôr **Johann Friedrich Gmelin** (*1748-†1804) publikoval podobný stručný opis v lipskom vydaní Linného „Systema Naturae“ (GMELIN 1789), ktoré sa stalo veľmi populárne. V práci neuviedol, že použil meno vytvorené Goezem. Vlastný problém vznikol, keď **Johann Christian Daniel von Schreber** (*1739-†1810) opísal z Nemecka druh *Blatta maculata* (teraz *Ph. maculata*) (SCHREBER 1781). Druh bol veľmi podobný druhu *Blatta Schaefferi* len mal svetlejšie tegminy s menšími čiernymi škvrnami. **Gottlieb August Wilhelm Herrich-Schäffer** (*1799-†1874) zaradil Gmelinom použité meno medzi synonymá druhu *Blatta maculata*, čo bolo z hľadiska princípu priority opodstatnené (HERRICH-SCHÄFFER 1840). **Leopold Heinrich Fischer** (*1817-†1886) vo svojom diele „Orthoptera Europaea“ s odvolaním sa na Gmelinom použité meno „*Blatta Schaefferi*“ zaradil tmavé exempláre ako varietu druhu *Blatta maculata* (FISCHER 1853). Keďže sa odvolal na Gmelinov opis bolo to z hľadiska časovej priority mien opäť logické riešenie. Pridal obsiahly opis, avšak nevyriešil rozšírenie, keďže spomína iba jedince z Nemecka a Rakúska. Keď uhorský entomológ **Ján Frivaldský** (*1822 Rajec-†1895 Budapešť) našiel v Zádielskej doline tmavé exempláre z rodu *Phyllodromica* zhodné s Gmelinovým aj Fischerovým opisom, začal pre ne používať meno *Aphlebia maculata* var. *Schäfferi* (FRIVALDSKY 1867). Rod *Aphlebia* Brunner von Wattenwyl, 1865 je synonymom staršieho rodového mena *Phyllodromica* Fieber, 1853. Varietu na poddruh povýšil Richard Ebner, keď použil pre tmavé jedince z Brašova (Rumunsko) názov *Hololampra maculata schaefferi* (EBNER 1930). Rod *Hololampra* Saussure, 1864 je tiež synonymom rodu *Phyllodromica*. Obaja (Frivaldský aj Ebner) použili názov „*schaefferi*“ v podradenom postavení k menu „*maculata*“, čo znamená, že ho považovali za mladší. Vychádzali teda z Gmelinovho opisu, ktorý je mladší ako Schäfferov opis druhu *Blatta maculata*. Pôvodný Goezeho starší opis nepoznali. Nanešťastie sa ukázalo, že takáto tmavá varieta resp. poddruh druhu *Ph. maculata* nežije ani v okolí Regensburgu ani v Nemecku vôbec. Z Nemecka sú známe iba klasicky svetlo sfarbené jedince zodpovedajúce opisu druhu *Phyllodromica maculata*.

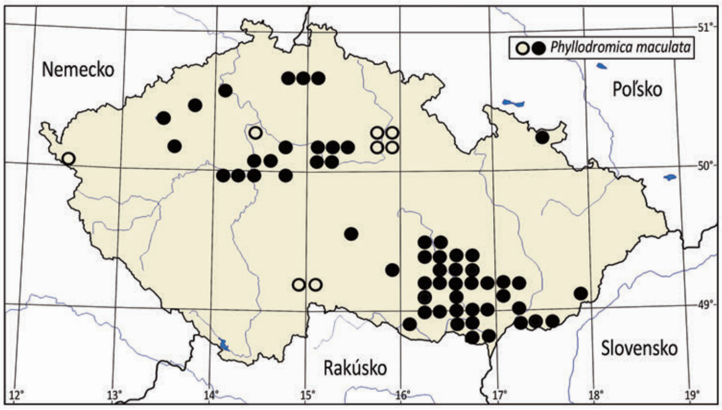
Lokalita Regensburg v Nemecku evidentne nemohla byť typovou lokalitou tmavých jedincov zodpovedajúcich Goezeho, Gmelinovmu či Fischerovmu opisu. Prvou publikovanou lokalitou zodpovedajúcou spomínaným opisom bola Zádielská dolina na Slovensku (FRIVALDSKÝ 1867). Preto bola Zádielská dolina dodatočne určená ako terra typica pre *Phyllodromica maculata schaefferi* v zmysle Gmelinovho opisu (VIDLIČKA 2001). Profesor Bohn z Nemecka chcel riešiť vzniknutú situáciu synonymizovaním názvu „*schaefferi*“ s druhom *Ph. maculata* (pers. comm.). Po upozornení, že meno „*shaefferi*“ je staršie ako „*maculata*“ bolo meno *Blatta schaefferi* klasifikované ako „nomen dubium“ a ponechaný bol iba názov *Ph. maculata* (BOHN & CHLÁDEK 2011). Avšak okolnosť, že druh *Ph. schaefferi* sa nevyskytuje na lokalite, ktorá mu bola pôvodne určená, nie je dôvod na zrušenie mena. Okrem toho sa Goeze ani Gmelin na lokalitu neodvolávali, takže Regensburg nebol oficiálnou typovou lokalitou. Napriek tomu zostalo pre tmavé jedince z okolia Zádielu meno *Ph. marani*, pre časť ďalších tmavo sfarbených jedincov zo stredného Slovenska a severného Maďarska bol vytvorený druh *Phyllodromica latipennis* Bohn & Chládek, 2011 (obr. 15) a pre tmavé exempláre zo Sedmohradska bol tiež vytvorený nový druh *Phyllodromica variabilis* Bohn, 2011 in BOHN & CHLÁDEK 2011). Tento stav je oficiálne doteraz platný, i keď praktické rozlišovanie medzi novo opísanými druhmi je vďaka ich variabilite dosť náročné a neisté. Vzhľadovo podobná *Phyllodromica hungarica* je od ostatných spomenutých druhov ľahko odlíšiteľná kvôli výrazne zahnutým krídlam (VIDLIČKA 1993).



Obr. 15. Rozšírenie švábov zo skupiny *maculata* rodu *Phyllodromica* na Slovensku, v Maďarsku a Rakúsku.

V práci BOHNA a CHLÁDKA (2011) je podrobne spracované rozšírenie všetkých druhov zo skupiny *maculata* v oblastiach ich výskytu. V práci chýba spracovanie rozšírenia *Ph. maculata* na Morave a v Čechách. Viaceré údaje sa nachádzajú v Chládkových starších i novších prácach (CHLÁDEK 1965, 1998, 2006).

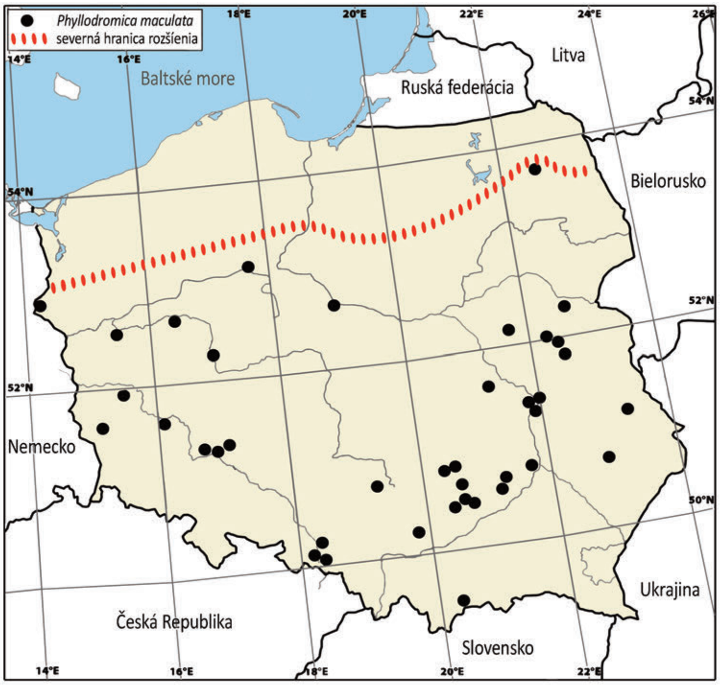
Podrobne bolo spracované rozšírenie tohto druhu v Českej republike v práci VIDLIČKU a HOLUŠU (1999). Druh sa pravdepodobne vyskytuje na vhodných lokalitách po celej republike (KOČÁREK et al. 2005), ani jedným smerom tu nedosahuje hranicu rozšírenia (obr. 16). Je známy aj zo všetkých okolitých štátov.



Obr. 16. Rozšírenie švába *Phyllodromica maculata* v Českej Republike. Podľa VIDLIČKU a HOLUŠU (1999) - doplnené.

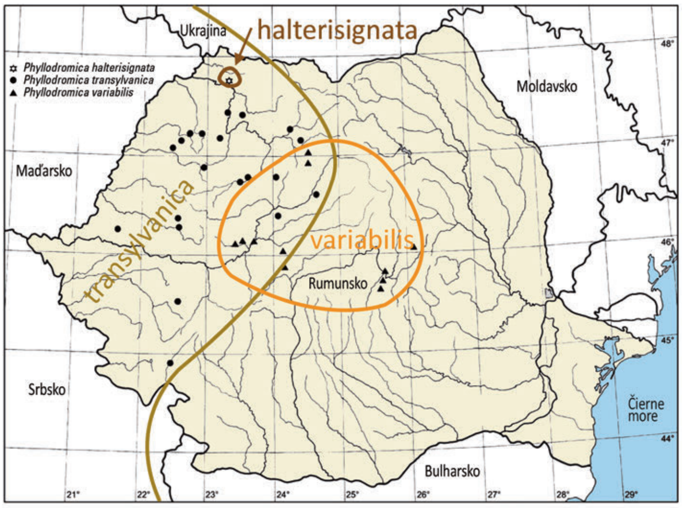
O rozšírení druhu *Phyllodromica maculata* v Poľsku pojednávajú staršie práce BAZYLUKA (1976, 1977). V Poľsku, podobne ako aj v susednom Nemecku, prebieha severná hranica rozšírenia druhu približne na 53° severnej zemepisnej šírky (obr. 17).

Prvé zmienky o šváboch zo skupiny maculata z Rumunska publikoval prírodovedec a entomológ slovenského pôvodu **Oto Herman** (*1835-†1914). Zmienil sa o výskyte druhu *Phyllodromica maculata* z okolia Kluža (Cluj, SZ Rumunsko), ale či sa jednalo o tmavú formu neuvádza (HERMAN 1871). Prvý kto konkrétne písal o tmavej forme (*Aphlebia maculata* var. *Schäfferi*) bol entomológ **Karl Brunner von Wattenwyl** (*1823-†1914) (BRUNNER v. W. 1882). Určiť v súčasnosti o ktorý konkrétny druh išlo sa naisto nedá, keďže v súčasnosti je z Rumunska známych viacej druhov zo skupiny *maculata*.



Obr. 17. Rozšírenie švába Phyllodromica maculata v Poľsku. Podľa BAZYLUKA (1977) – upravené.

Okrem už spomenutého Bohnom opísaného druhu *Phyllodromica variabilis*, rozšíreného v centrálnej časti Rumunska, tu žijú aj ďalšie dva endemické druhy zo skupiny *maculata*. Prvým je už dávnejšie opísaná *Phyllodromica transylvanica* Vidlička, 1994 s pomerne širokým rozšírením v Sedmohradskej oblasti (Transylvánia). Momentálne je areál jeho výskytu ohraničený Karpatmi (Vidlička 1994, Bohn & Chládek 2011). Tento druh nebol zatiaľ nájdený v Maďarsku, ale jeho výskyt na východe Maďarska je pravdepodobný, podobne ako aj na severe Srbska. Ďalším druhom je *Phyllodromica halterisignata* Bohn, 2011 (in Bohn & Chládek 2011). Zatiaľ je známy iba z jednej lokality na SZ Rumunska (obr. 18).



Obr. 18. Rozšírenie švábov zo skupiny *maculata* rodu *Phyllodromica* v Rumunsku.
Podľa Bohna & Chládka (2011) – upravené.

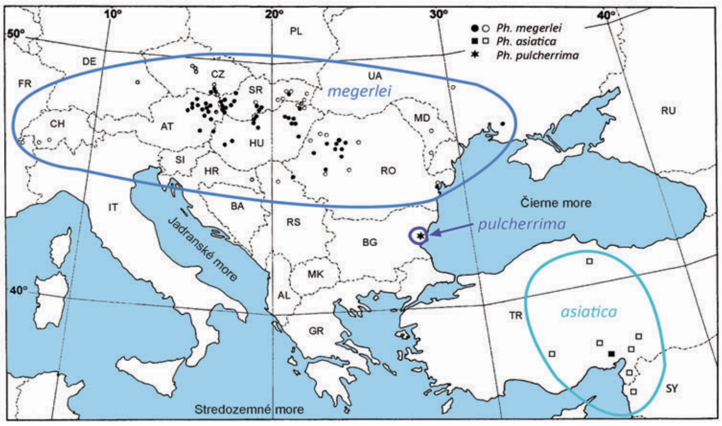
4.3. Rod *Phyllodromica* – skupina druhov *megerlei*

Okrem skupiny druhov maculata z rodu Phyllodromica, je veľmi dobre definovanou aj skupina druhov *megerlei*. Skupina je charakteristická veľmi komplikovaným sieťovaným vzorom na tegminách a zároveň silne skrátenými tegminami u samičiek. Typovým druhom je *Phyllodromica megerlei* (obr. 19). Ani opis tohto druhu sa nezaobišiel bez problémov.

Obr. 19. *Phyllodromica megerlei* (Vidlička 2001).

Druh pôvodne opísal **Toussaint de Charpentier** (*1779-†1847). Charpentier bol nemecký geológ. V rokoch 1811-1828 zastával funkciu Sliezskeho vrchného banského odborníka vo Wroclawe (Wratislaviae). Amatérsky sa na pomerne slušnej úrovni venoval aj entomológii. V roku 1825 mu vo Wroclawe vyšlo dielo „Horae entomologicae“ o európskom hmyze, v ktorom najväčšiu pozornosť venoval ortopteroidnému hmyzu (Dermaptera, Blattaria, Mantodea, Orthoptera). V práci spomína 14 druhov švábov (vtedy všetky v rode *Blatta*), z ktorých dva sú novo opísané (Charpentier 1825). Prvým je *Blatta limbata* z Lusitanie (oblasť zaberajúca časť Portugalska a Španielska), ktorý bol neskôr synonymizovaný s druhom *Loboptera decipiens* (Germar, 1817). Tento druh sa dokonca v práci tiež spomína (ako *Blatta decipiens*). Druhým opísaným druhom bola *Blatta punctata* z Rakúska. Opis druhu je v Charpentierovej práci prisúdený rakúskemu entomológovi **Johannovi Carlovi Megerle von Mühlfeld** (*1775-†1840). Až o 28 rokov si český entomológ (nemeckého pôvodu) **Franz Xaver Fieber** (*1807-†1872) všimol, že meno *Blatta punctata* použil **Johann Friedrich Gustav von Eschscholtz** (*1793-†1831) už v roku 1822 pri opise iného druhu švába (terajšia *Diploptera punctata*) (Eschscholtz 1822). Preto na počesť objaviteľa premenoval druh z Rakúska na *Phyllodromica megerlei*. Keďže Fieber zaradil tento druh do ním novo opísaného rodu, stal sa druh zároveň typovým druhom rodu *Phyllodromica* (Fieber 1853).

Phyllodromica megerlei je síce druh s pomerne širokým areálom výskytu (obr. 20), ale na lokalitách sa vyskytuje vždy iba v neveľkých počtoch. Svojim výzorom (husto škvrnitými tegminami) je dosť odlišný od väčšiny druhov, ktoré boli neskôr do tohto rodu zaradené.



Obr. 20. Rozšírenie švábov zo skupiny *megerlei* rodu *Phyllodromica* v Európe a Ázii.
Podľa VIDLIČKU & MAJZLANA (1997) – upravené.

Rakúsky ortopterológ **Richard Ebner** (*1885-†1961), ktorý sa venoval ortopteroidnému hmyzu Malej Ázie si všimol, že exempláre *Ph. megerlei* vyskytujúce sa v Turecku sú odlišné od jedincov z Európy, takže ich spomenul ako varietu, ale meno jej nepridelil (EBNER 1919). Významný ruský entomológ **Grigorij Jakovlevič Bej-Bienko** (*1903-†1971) v rámci edície „Fauna SSSR“ spracoval skupinu švábov (Blattaria). Aj on si uvedomil odlišnosť ázijských (Tureckých a Sýrskych) exemplárov. Na základe žlto-oranžovej škvrny na štíte (na rozdiel od čiernej škvrny u typickej formy) opísal nový poddruh *Phyllodromica megerlei asiatica* (BEY-BIENKO 1950). Pri opise mal k dispozícii 7 exemplárov zo 6 lokalít, ale všetko to boli samičky, takže opísal iba samičku. Keď nemecký ortopterológ **Willy Adolf Theodor Ramme** (*1887-†1953) spracovával ortopteroidný hmyz južnej Európy a Malej Ázie nemal ešte k dispozícii Bej-Bienkovu „Faunu“. Mal však k dispozícii samčeka švába z Adany (Turecko) s oranžovou škvrnou na štíte a tak ho opísal ako *Hololampra punctata* f. *erythronota* (RAMME 1951). Táto forma bola o pár rokov synonymizovaná s Bej-Bienkovým poddruhom (KARABAG 1958). Až takmer po 50-tich rokoch bol na základe odlišností v tvare tergálnej žľazy, stilusu a genitálneho háku povýšený tento poddruh na samostatný druh *Phyllodromica asiatica* (VIDLIČKA & MAJZLAN 1997). Zároveň bol na základe viacerých exemplárov pochádzajúcich z Bulharska, z lokality Vlas neďaleko Nesebaru opísaný druh podobný *Ph. megerlei*, len výrazne menší. Druh dostal meno Phyllodromica pulcherrima (VIDLIČKA & MAJZLAN 1997). Neskôr bol tento druh zberaný na viacerých lokalitách v Bulharsku (G. Hristov, pers. comm.). V súčasnosti sú tieto tri druhy – *Ph. megerlei, Ph. asiatica* a *Ph. pulcherrima* (obr. 21), jedinými zástupcami skupiny druhov megerlei v rode Phyllodromica. Rozšírenie *Ph. megerlei* bolo spracované v rámci Karpatskej kotliny (VIDLIČKA & SZIRÁKI 1997). Najnovšie údaje o výskyte na východnom Slovensku sú uvedené v práci TOMKU et al. (2013).

Obr. 21. *Phyllodromica pulcherrima* ♂ a ♀
(VIDLIČKA & MAJZLAN 1997).

4.4. Prehľad príspevkov autora k poznaniu švábov na Slovensku a v Európe

(hnedou farbou sú uvedené príspevky, ktoré sú súčasťou habilitačnej práce)

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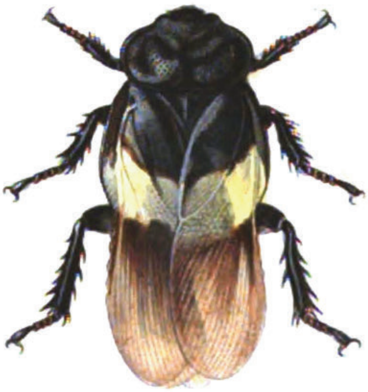
5. Šváby juhovýchodnej Ázie a Južnej Ameriky

Juhovýchodná Ázia (orientálna faunistická oblasť) a Južná Amerika (neotropická faunistická oblasť) sú dve na šváby najbohatšie oblasti s množstvom endemických druhov a rodov. Štyri z nich si bližšie spomenieme.

5.1. Šváby z rodu *Caeparia* Stål, 1877 (Blaberidae: Panesthiinae)

1. *C. saussurii* (Wood-Mason, 1876) – India, Bután, Bangladéš
2. *C. crenulata* (Bruijning, 1948) – Indonézia (Sumatra), Malajzia
3. *C. donskoffi* Roth, 1979 – Vietnam, Laos, Thajsko
4. *C. kaltenbachi* Roth, 1979 – Thajsko, Laos
5. *C. sausai* Vidlička, 1999 – Laos

Všetky druhy rodu *Caeparia* sú pomerne veľké šváby, ktoré majú dobre vyvinuté tegminy aj krídla. Nebolo u nich pozorované ohryzenie tegmín typické pre príslušníkov príbuzného rodu *Panesthia*, ako aj iných príslušníkov podčeľade Panesthiinae. Všetky druhy rodu *Caeparia* majú dvojfarebné tegminy, čo je tiež v rámci podčeľade nezvyklé.



Obr. 24. *Panesthia mandarinea* (SAUSSURE 1863).

História rodu *Caeparia* sa začala odvíjať od omylu. Svetoznámy švajčiarsky ortopterológ **Henri Louis Frederic de Saussure** (*1829-†1905) opísal v roku 1863 z Číny švába *Panesthia mandarinea* (obr. 24). Pohlavie švába neuviedol, lebo opisovanému jedincovi chýbalo bruško (SAUSSURE 1863). O pár rokov neskôr sa mu dostala do rúk samička švába z východnej Indie. Priradil ju k tomu istému druhu, urobil jej pomerne obsiahly opis a v úvode doplnil poznámku, že v predchádzajúcom článku opísal samčeka (SAUSSURE 1869).

Anglický zoológ **James Wood-Mason** (*1846-†1893) po skončení štúdia v Oxforde odišiel v roku 1869 do Indie a získal zamestnanie v Indickom múzeu v Kalkate. Dostal obsiahlu zbierku hmyzu zo štátu Johor v Malajzii s početnou sériou exemplárov *Panesthia mandarinea*. Pri ich štúdiu si všimol, že oba jedince z tohto druhu, ktoré opísal Saussure sú samičky, ale nepatria k tomu istému druhu. Samičke z Indie, ktorá bola opísaná neskôr, vytvoril v roku 1876 nové meno *Panesthia Saussurii*. Do tohto druhu zaradil aj exemplár práve sa zvliekajúceho samčeka zo štátu Sikkim ležiaceho v Himalájach na severovýchode Indie (WOOD-MASON 1876).

O rok neskôr publikoval švédsky ortopterológ **Carl Stål** (*1833-†1878) prácu s opisom viacerých druhov švábov z Filipín a medzi nimi bol aj druh *Panesthia saussurii* (iný ako bol druh rovnako pomenovaný Wood-Masonom). Zároveň v rode *Panesthia* stanovil nový podrod *Caeparia* a zaradil do neho druh *Panesthia mandarinea* opísaný Saussurem. Nenapísal z ktorej Saussureho práce vychádzal, ale na základe diagnostických znakov podrodu je evidentné, že sa jednalo o samičku z Indie opísanú v roku 1869 (STÅL 1877).

V sérii omylov pokračoval aj **Karl Brunner von Wattenwyl** (*1823-†1914). V obsiahlej revízii ortopteroidného hmyzu, ktorú v roku 1893 vydal v Ženeve, povýšil Stålom vytvorený podrod *Caeparia* na samostatný rod s typovým druhom *Caeparia mandarinea* Saussure z lokality Teinzò (BRUNNER DE WATTENWYL 1893). Ktorý druh v skutočnosti myslel nie je isté, ale keďže sa odvoláva na Stålov opis supraanálnej platničky, tak pravdepodobne sa tiež jednalo o exemplár z Indie. Udávaná lokalita Teinzò (asi Teinzô) sa nachádza na severe Mjanmarska, neďaleko od Indie. Brunner uvádza v zozname použitých prác 6 Wood-Masonových článkov (3 o Phasmatodea a 3 o Mantodea), ale jeho prácu o *Panesthia mandarinea* a *P. saussurii* nepoznal (alebo prinajmenšom nepoužil).

Približne v tom istom čase SAUSSURE (1895) spracovával revíziu Panesthinov. Na rozdiel od svojich predchodcov inkriminovaný článok Wood-Masona poznal a poznal aj práce Ståla a Brunnera von Wattenwyl o rode *Caeparia*. Preto poopravil Brunnerov údaj a za typový druh rodu určil *Caeparia saussurei* (upravil chybne vytvorené meno *Saussurii* na *Saussurei*, omylom však uviedol, že pôvodné meno bolo *Sausseuri*) (SAUSSURE 1895). Takže meno *Panesthia mandarinea* zostalo pre druh opísaný v roku 1863. **William Forsell Kirby** (*1844-†1912) vo svojom synonymickom katalógu ortopteroidného hmyzu uvádza v rode *Caeparia* len druh *C. Saussurii* Wood-Mason a pri rode *Panesthia* aj druh *P. Saussurii* Stål (KIRBY 1904).

Situáciu opäť skomplikoval americký ortopterológ **Andrew Nelson Caudell** (*1872-†1936). Domnieval sa, že typom rodu *Caeparia* je druh *Panesthia mandarinea* opísaná Saussurem v roku 1863 (a nie tá z roku 1869). Preto pre druh *Panesthia Saussurii* stanovený Wood-Masonom v roku 1876 vytvoril nový rod *Neocaeparia* (CAUDELL 1924).

Vzniknutý problém sa podujal vyriešiť najvýznamnejší americký švábológ **Louis Marcus Roth** (*1918-†2003). Na základe článku 70(a) pravidiel medzinárodnej zoologickej nomenklatúry sa obrátil na Medzinárodnú komisiu. Keďže Stål zle identifikoval druh „*mandarinea*“ ako typový druh rodu *Caeparia*, navrhol Roth komisii akceptovať možnosť (i) článku 70(a) a designovať za typový druh rodu *Caeparia* druh *Panesthia saussurii* Wood-Mason (ROTH & GURNEY 1983). Toto riešenie bolo prijaté, keďže korešpondovalo aj s prácami SAUSSUREHO (1895) a KIRBYHO (1904). ROTH (1979) na základe tohto rozhodnutia pri revízii rodu *Caeparia* opätovne stanovil za typový druh rodu *Panestia sausurii* Wood-Mason [=*Panesthia mandarinea* Saussure, 1869 (nec 1863)]. Zároveň v zhode s PRINCISOM (1950) synonymizoval rod *Neocaeparia* Caudell, 1924 s rodom *Caeparia*.

Zaujímavý je aj osud druhu *Panesthia mandarinea* Saussure, 1863. V roku 1932 sa nemecký ortopterológ **Karl Richard Hanitsch** (*1860-†1940) zaoberal zbierkami švábov Dr. Odoarda Beccariho a Dr. Elia Modiglianiho zo Sumatry (HANITSCH 1932). Na základe Modiglianim chytených exemplárov druhu *Panesthia transversa* zistil, že tento druh je totožný s jedincom opísaným Saussurem v roku 1863 pod menom *Panesthia mandarinea*. Druh *Panesthia transversa* opísal Burmeister už v roku 1838. Preto Hanitsch názov *Panesthia mandarinea* synonymizoval s názvom *Panesthia transversa*. Z názvu *Panesthia mandarinae*, ktorý bol použitý dvakrát pre dva rôzne druhy tak nezostal nakoniec platný ani jeden.

Všetky doteraz uvedené údaje sa týkali len jediného druhu rodu *Caeparia*, typového druhu *C. saussurii*. Až v roku 1948 opísal holandský entomológ **Conrad Friedrich Albert Bruijning** (*1919-†2004) druh *Neoceparia crenulata* podľa samčeka chyteného na Mount Kerinci (v orig. Mount Indrapura) v pohorí Barisan na západe ostrova Sumatra (Indonézia). ROTH (1979a) revidoval aj samčeka tohto druhu z pevninskej časti Malajzie, z lokality Tapah Perak. BRUIJNING (1948) sa pri zaradení do rodu *Neocaeparia* pridŕžal Caudellovej práce z roku 1924. Do rodu *Caeparia* tento druh presunul až PRINCIS (1965).

Na opis ďalších druhov z rodu *Caeparia* bolo treba počkať ďalších 31 rokov. Roth začal v roku 1977 vydávať rozsiahlu celosvetovú revíziu podčeľade Panesthinae. Celkovo vydal 4 monografické práce (ROTH 1977, 1979a, b, 1982). V druhom diele spracoval aj rod *Caeparia*. Tu pri druhu *Caeparia saussurii* dôkladne charakterizoval obe pohlavia a tiež pridal ďalšie lokality výskytu z Indie, Bangladéša, Bhutánu a Laosu. SAUSSUREM (1895) spomenutý výskyt tohto druhu na lokalite Malacca (JZ Malajzia) Roth spochybnil (podobne ako pred ním aj PRINCIS (1965)), lebo z okolia tejto lokality determinoval len druh *Caeparia crenulata*, ktorý však v dobe vyjdenia Saussureho práce nebol ešte opísaný.

Obr. 25. Samička druhu *Caeparia donskoffi* (VIDLIČKA 1999).

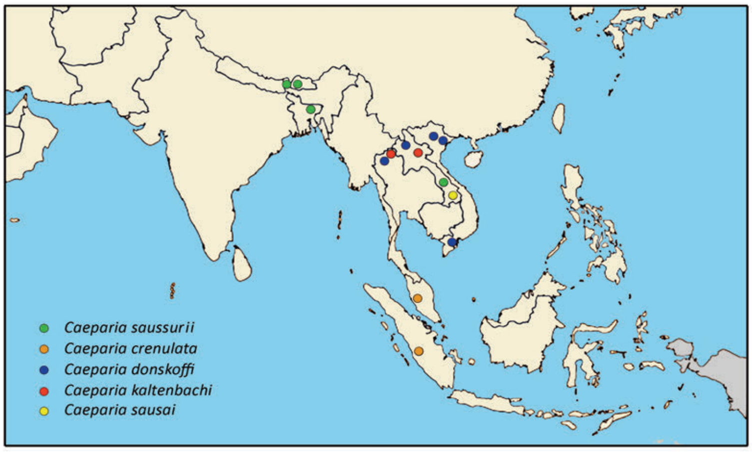
V práci, v ktorej ROTH (1979a) revidoval rod *Caeparia*, zároveň opísal aj dva nové druhy z tohto rodu: *C. donskoffi* (pomenovaný podľa odborníka na Orthoptera Michela Donskoffa z Muséum national d'Histoire naturelle v Paríži) a *C. kaltenbachi* (pomenovaný podľa Dr. Alfreda Kaltenbacha (*1920-†2005) z Naturhistorisches Museum vo Viedni). U druhu *Caeparia donskoffi* bola pôvodne opísaná iba samička (holotyp z Ko-Tichi z Južného Vietnamu, paratypy z Tonkinu zo severného Vietnamu) (ROTH 1979a). Samček bol opísaný až dodatočne zo severného Vietnamu a zo severného Laosu (VIDLIČKA 1999) a samička bola zistená aj v Thajsku (VIDLIČKA 1999).

Druh *Caeparia kaltenbachi* bol opísaný tiež iba na základe samičiek. Holotyp pochádza zo severu Thajska (pohorie Khun Tan) a paratyp zo severného Laosu (Muong Pek) (ROTH 1979a). Samček nie je doteraz známy.

ROTH (1982) uverejnil opis nepomenovanej nymfy z Thajska, ktorá by mohla patriť k jednému z ním opísaných druhov z rodu *Caeparia*. Farebným vzorom sa síce odlišuje od imág *C. donskoffi* (obr. 25) aj *C. kaltenbachi*, ale zadný okraj supraanálnej platničky (dôležitý pri determinácii) je podobný ako u *C. donskoffi*.

Obr. 26. *Caeparia sausai* ♀ (VIDLIČKA 1999).

Zatiaľ posledný, piaty druh z rodu *Caeparia* bol opísaný v roku 1999 na základe samičky zo severného Laosu (provincia Attapu, Bolaven Plateau, 15 km JV od Ban Houaykong). Pomenovaný bol *Caeparia sausai* (obr. 26) na počesť slovenského amatérskeho entomológa **Ondreja Šaušu**, ktorý tento druh objavil (VIDLIČKA 1999). Rozšírenie druhov rodu *Caeparia* ukazuje obrázok 27.



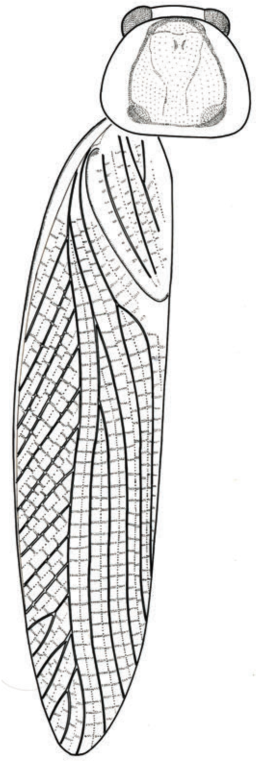
Obr. 27. Rozšírenie švábov z rodu *Caeparia* v juhovýchodnej Ázii.

5.2. Šváby z rodu *Chorisoserra* (Blattellidae: Pseudophyllodrominae)

1. *Ch. sagitaria* (Hanitsch, 1927) – Vietnam
2. *Ch. apicalis* (Hanitsch, 1929) – Indonézia (Sumatra), východné Borneo
3. *Ch. jendeki* Vidlička, 2002 – Laos
4. *Ch. biceps* Wang, Zhang, Feng, 2006 – Čína
5. *Ch. brevicaudata* Wu, Wang, 2011 - Čína

V roku 1927 Hanitsch spracoval zbierku švábov z južného Annamu (terajší stredný Vietnam). Jedným z 19 opísaných nových druhov bol aj druh *Chorisoneura sagitaria*. Opis urobil na základe samčeka z Langbian Peak (provincia Lam Dong) (HANITSCH 1927). Rod *Chorisoneura* vytvoril Brunner von Wattewyl v roku 1865. Je to veľký rod, v súčasnosti s 90 druhmi. V čase keď Hanitsch publikoval opis druhu *Chorisoneura sagitaria* obsahoval tento rod už 55 druhov. Na novoopísanom druhu bolo zaujímavé, že bol nájdený v orientálnej oblasti. Takmer všetky ostatné druhy tohto rodu pochádzali z neotropickej oblasti. Výnimkou boli vtedy 3 druhy z Tajvanu, Číny a Kambodže.

Ďalší druh z orientálnej oblasti opísal Hanitsch zo zbierky švábov švédskeho zoológa **Erica Georga Mjöberga** (*1882-†1938). Zbierku nazhromaždil Mjöberg počas expedície na Sumatre v rokoch 1919-1922. Hanitschom opísaný druh *Chorisoneura apicalis* pochádzal z lokalít Medan a Boeloe-Tjina (HANITSCH 1929). Jedince z rodu *Chorisoneura* majú dosť charakteristický vzhľad a tak správnosť zaradenia týchto dvoch Hanitschom opísaných druhov, svojim rozšírením anomálnych, nikto dlhú dobu nespochybňoval. Dokonca ani jeden z najväčších švábológov sveta Lotiš **Kārlis Aleksandrs Princis** (*1893-†1978), autor zatiaľ neprekonaného 8 dielneho celosvetového katalógu švábov z rokov 1965-1972. V roku 1950 Princis spracovával zbierku švábov z orientálnej oblasti uloženú v entomologickom múzeu Univerzity v Lunde (Švédsko). V zbierke našiel aj druh, ktorý určil ako *Chorisoneura apicalis*. Jedinec pochádzal z východného Bornea (PRINCIS 1950). Na zaradení sa nič nezmenilo ani pri vydaní prvého dielu spomínaného katalógu švábov (PRINCIS 1965).



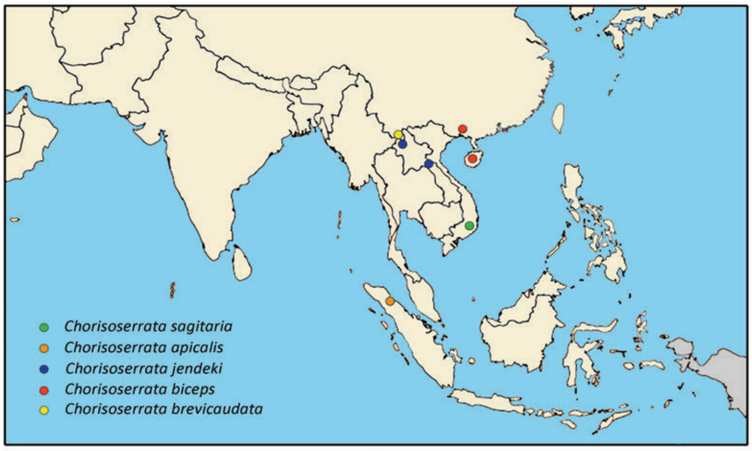
Obr. 28. *Chorisoserrata jendeki* - štít a tegmina (VIDLIČKA 2002).

V roku 1998 Roth revidoval zástupcov rodu *Chorisoneura*. Všimol si určité odlišnosti dvoch orientálnych druhov z rodu *Chorisoneura* od neotropických druhov, ale tiež aj odlišnosti druhov z Číny, Tajvanu a Kamerunu. Preto pre Hanitschom opísané druhy vytvoril nový rod *Chorisoserrata* a pre ostatné odlišné druhy vytvoril rody *Chorisoneurodes* a *Sorineuchora* (ROTH 1998).

Tretí druh do rodu *Chorisoserrata*, *Ch. jendeki* (obr. 28), pribudol až v roku 2002. Opísaný bol na základe dvoch samčekov a jednej samičky z Laosu (provincie Bolikhamxai a Luang Namtha). Od predchádzajúcich druhov sa okrem iného líšil aj prítomnosťou nezreteľnej tergálnej žľazy na siedmom abdominálnom tergu (VIDLIČKA 2002). Druh dostal meno podľa slovenského entomológa **Eduarda Jendeka**, nálezcu holotypu.

Čínsky entomológovia **Zong-Qing Wang**, **Yan-Ning Zhang** a **Ping-Zhang Feng** z Čínskej akadémie poľnohospodárskych vied opísali na základe 6 jedincov (4 ♂♂, 2 ♀♀) pochádzajúcich z provincie Hainan (ostrov Chaj-nan) a z autonómnej oblasti Guangxi Zhuang (Kuang-si, JV Čína) nový druh *Chorisoserrata biceps*. Od ostatných príslušníkov rodu sa odlišuje dlhou, zakrútenou mediánnou falomérou a zúbkami na konci prídavnej mediánnej faloméry (WANG et al 2006).

Ke-Liang Wu a **Zong-Qing Wang** objavili v južnej Číne, v provincii Yunnan (Jün-nan) samčeka a samičku z rodu *Chorisoserrata*. Samčie genitálie obsahovali dlhú, úzku, na konci guľovito zhrubnutú mediánnu falomérou a prídavnú mediánnu faloméru zakončenú v tvare chĺpkov štetca. Druh pomenovali *Chorisoserrata brevicaudata* (WU & WANG 2011). Oba čínske druhy sú bez špecializácie na 7 abdominálnom tergite.



Obr. 29. Rozšírenie švábov z rodu *Chorisoserrata* v juhovýchodnej Ázii.

5.3. Šváby z rodu *Spelaeoblatta* Bolívar, 1897 (Noticolidae)

1. *S. gestroi* Bolívar, 1897 – Mjanmarsko (Barma)
2. *S. thamfaranga* Roth, 1994 – Thajsko
3. *S. myugei* Vidlička, Vršanský & Shcherbakov, 2003 – Thajsko
4. *S. thailandica* Vidlička, Vršanský & Shcherbakov, 2003 – Thajsko

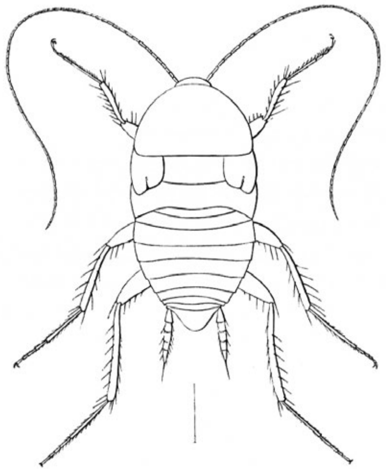
V roku 1892 spracovával španielsky ortopterológ **Ignacio Bolívar y Urrutia** (*1850-†1944) zbierku švábov, ktoré nazberal v marci a apríli 1890 francúzsky arachnológ **Eugène Simon** (*1848-†1924) v jaskyniach na ostrove Luzon (Filipíny). Materiál pochádzal z dvoch provincií – provincia Manila a provincia Morong. Boli to prvé naozaj jaskynné šváby prispôsobené plne životu v tomto netypickom prostredí – malé, dlhonohé, depigmentované, so silne redukovanými očami resp. bez očí (BOLÍVAR 1892). Bolívar opísal na ich základe nový rod *Nocticola*, ktorý zaradil do čeľade Blattidae. Zároveň v rode opísal dva druhy - *Nocticola simoni* (na počesť zberateľa, na základe samčeka a samičky z jaskyne San Mateo, prov. Manila) a *Nocticola caeca* (na základe samičky z jaskyne Antipodo, prov. Morong). Samičky nemali vyvinuté tegminy ani krídla.

Známy taliansky cestovateľ, zoológ, maliar a zberateľ prírodnín **Leonardo Fea** (*1852-†1903) sa v roku 1871 stal asistentom na oddelení entomológie v Museo Civico di Storia Naturele di Genova v Janove. V roku 1885 sa vydal na cestu do Barmy, kde zotrval 4 roky (1885-1889). Nachytané živočíchy pravidelne odosielal do svojho domovského múzea. V decembri 1887 sa dostal do oblasti vrchu Carin medzi riekami Sittang a Saluin. Tu sa mu podarilo v januári 1888 v jaskyni Jaddò (Ya-dò) uloviť samičku jaskynného švába a tiež ho odoslal do múzea v Janove. Riaditeľom múzea bol v tej dobe **Raffaello Gestro** (*1845-†1936). Ten spracoval skupinu Coleoptera a zistenia publikoval v muzeálnom časopise (GESTRO 1888, 1891). Zvyšok materiálu distribuoval na určenie špecialistom na dané skupiny.

Šnába zaslal na determináciu Bolívarovi. Na prvý pohľad bola zaslaná samička dosť podobná jedincom z rodu *Nocticola*, ale bola väčšia a hlavne mala vyvinuté, aj keď silne redukované, tegminy. Na základe tejto samičky opísal Bolívar nový rod jaskynných švábov *Spelaeoblatta*. Nový druh nazval *Spelaeoblatta Gestroi* (na počesť Raffaella Gestroa) (obr. 30) (BOLÍVAR 1897).

Rod *Spelaeoblatta* zostal dlhú dobu monotypický.

George C. McGavin[1] sa špecializuje na výskum suchozemských článkonožcov v tropických lesoch a jaskyniach. V apríli až máji 1992 sa zúčastnil expedície usporiadanej CSCA (Combined Services Caving Association) nazvanej „Exercise Tham Farang“ do



Obr. 30. *Spelaeoblatta gestroi* ♀ (BOLÍVAR 1897).

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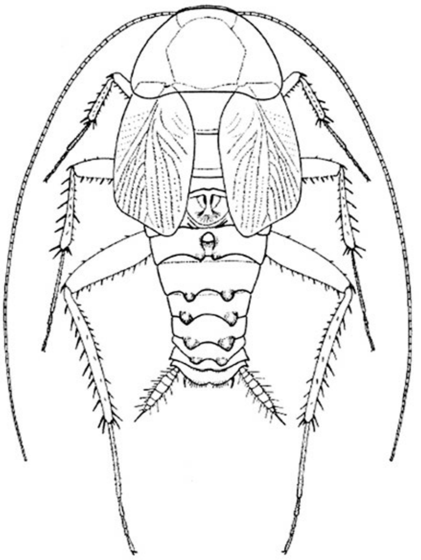
[1] McGavin nie je špecialistom na šváby, zaoberá sa viac popularizačnou činnosťou. Má vlastnú reláciu v BBC a napísal viacero populárnych knižiek o hmyze. Jednu z nich – „Insects, spiders and other terrestrial arthropods“ (MCGAVIN 2000) som mal česť v roku 2000 preložiť pre vydavateľstvo IKAR do slovenčiny (spolu s L. Rollerom).

Thajska. Cieľom expedície bolo zhromaždiť a identifikovať kavernikolné živočíchy jaskynných systémov v provincii Kanchanaburi. V jaskynnom systéme Tham Nam Farang bolo nájdené aj väčšie množstvo samčekov, samičiek aj nýmf jaskynných švábov neznámeho druhu. Preto McGavin požiadal o pomoc s identifikáciou amerického experta na šváby Louisa M. Rotha. Šváby boli identifikované ako nový druh z rodu *Spelaeoblatta*. Roth pomenoval tento druh *Spelaeoblatta thamfaranga* na počesť expedície. Thajské slová „Tham Farang“ znamenajú „jaskynný cudzinec“. Na základe tohto materiálu bol po prvýkrát charakterizovaný aj samček z tohto rodu. Na abdomene majú samčekovia vyvinutú pohlavnú tergálnu žľazu. Prítomnosť tergálnej žľazy na 2 a 3 tergite samčekov je dosť vzácny úkaz medzi švábmi. V práci bola tiež podrobnejšie opísaná aj samička. U tohto druhu na rozdiel od *S. gestroi* mali samičky vyvinuté facetové oči (ROTH & MCGAVIN 1993).

Ruská expedícia skúmajúca jaskyne severného Thajska nazbierala v marci 1997 okrem iného aj neveľký materiál jaskynných švábov. Slovenská expedícia na Ďaleký východ do Primorského (Ussurijského) kraja (Vidlička, Vršanský, Roller – jún 1997) prevzala nazberané šváby na determináciu. Ako sa ukázalo materiál obsahoval minimálne tri druhy jaskynných švábov, z ktorých dva druhy boli zaradené do rodu *Spelaeoblatta*. Opisy oboch vyšli v roku 2003. Prvý dostal meno *Spelaeoblatta myugei* (obr. 31) po svojom zberateľovi N. Myugem (H. Мюге), ktorý zbieral šváby v jaskyni Tham Pha Mon (provincia Mae Hong Son, región Nam Lang). Druhý bol pomenovaný *Spelaeoblatta thailandica* podľa krajiny pôvodu a opísaný bol z jaskyne Red Cliff (provincia Mae Hong Son, región Nam Lang). Oba druhy sa veľmi nápadnými a v rade švábov úplne unikátnymi výbežkami na tergitoch bruška výrazne líšili od predchádzajúcich dvoch druhov a preto bola pre nich vytvorená samostatná skupina druhov *myugei* (VIDLIČKA et al. 2003).



Obr. 31. *Spelaeoblatta myugei* ♂ (VIDLIČKA et al. 2003).

5.4. Šváby z rodu *Macrophyllodromia* Saussure & Zehnter, 1893 (Blattellidae)

1. *M. maximiliani* (Saussure, 1873) – Mexiko, Guatemala, Honduras, Kostarika, Panama
2. *M. splendida* Hebard, 1920 – Panama
3. *M. nigrigena* Hebard, 1926 – Francúzska Guiana, Guyana, Bolívia (?)
4. *M. ecuadorana* Rocha e Silva, 1962 – Ekvádor, Honduras (?)
5. *M. panamae* Rocha e Silva, 1962 – Panama
6. *M. lanceolata* Lopes & Oliveira, 2006 – Brazília
7. *M. multipunctata* Lopes & Oliveira, 2006 – Brazília
8. *M. amabile* Anisyutkin, 2007 – Ekvádor
9. *M. nobile* Anisyutkin, 2007 – Ekvádor
10. *M. beccalonii* Anisyutkin, 2012 – Ekvádor
11. *M. rufidula* Anisyutkin, 2012 – Mexiko
12. *M. onorei* Vidlička, 2013 – Ekvádor

Švajčiarsky ortopterológ **Henri Louis Frederic de Saussure** (*1829-†1905) sa výskumu ortopterofauny strednej Ameriky venoval dlhodobo. Už v roku 1854 podnikol spolu s ďalším švajčiarskym prírodovedcom **Adrienom Jeanom Louisom Françoiscom de Sumichrast** (*1828-†1882) expedíciu do „Západnej Indie“ (Karibské ostrovy) a do Mexika. Chytali hmyz a posielali ho do ženevského múzea. Saussure sa v roku 1856 z Mexika vrátil do Ženevy a začal nazberaný materiál spracovávať.

V roku 1873 spracoval Saussure rozsiahlu zbierku švábov a modliviek, medzi ktorým bolo aj niekoľko exemplárov z Mexika. O ich pôvode sa bližšie nezmieňuje, ale nie všetky pochádzali z jeho vlastných zberov. Jedného zo švábov, charakteristického dvomi nápadnými čiernymi pozdĺžnymi pruhmi na pronóte, pomenoval *Pseudophyllodromia Maximiliani* (obr. 32). Holotyp bol poškodený, chýbalo mu bruško, takže pohlavie neuvádza (SAUSSURE 1873). Dá sa predpokladať, že druh dostal meno po Ferdinandovi Maximiliánovi Jozefovi Habsburskom (*1832-†1867), ktorý bol ako Maximilián I. v rokoch 1861-1867 mexickým panovníkom.


Obr. 32. *Macrophyllodromia maximiliani* (SAUSSURE 1873).

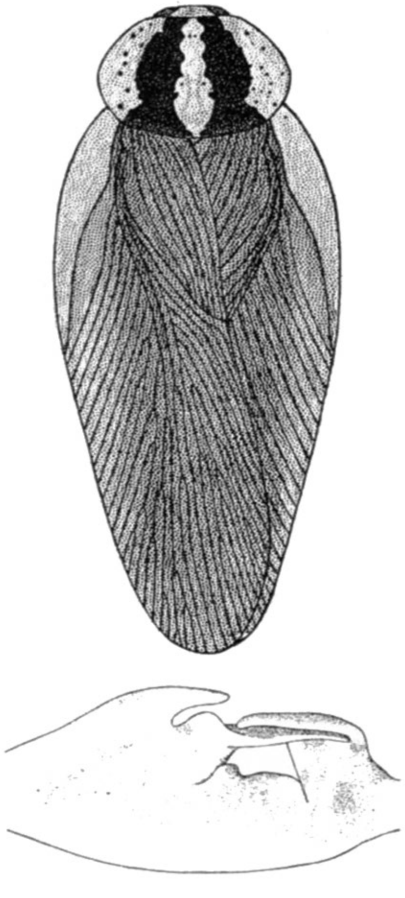
Saussure a jeho spolupracovník **Leo Zehntner** (*1864-†1961), asistent v Natural History Museum v Ženeve, vydali v roku 1893 v rámci edície „Biologia Centrali Americana“ rozsiahle dielo o šváboch a modlivkách Strednej Ameriky. V rámci rodu *Pseudophyllodromia* uvádzajú dva druhy – *P. venosa* a *P. maximiliani*, oba z Mexika. Vzhľadom na odlišnú žilnatinu na tegminách a krídlach týchto druhov ako aj odlišné otŕnenie stehien zaradili druh *P. venosa* (=*Euphyllodromia angustata* (Latreille, 1811)) do nominátneho podrodu *Pseudophyllodromia* a druh *P. maximiliani* do novo vytvoreného podrodu *Macrophyllodromia* (SAUSSURE & ZEHNTNER 1893).

Robert Walter Campbel Shelford (*1850-†1944) zistil, že príslušníci rodu *Pseudophyllodromia* Brunner von Wattenwyl, 1865, ktoré sú rozšírené v indomalajskej (orientálnej) oblasti sa odlišujú od druhov pochádzajúcich z juhoamerickej oblasti, preto vytvoril pre druhy z tohto rodu z juhoamerickej oblasti nový podrod *Euphyllodromia*. Do podrodu *Euphyllodromia* bol zaradený aj druh *P. venosa* a zároveň bol synonymizovaný so starším druhom *Euphyllodromia angustata* (SHELFORD 1908). Saussurem a Zehntnerom stanovený podrod *Macrophyllodromia* bol následne povýšený na rod s jediným druhom *M. maximiliani* (SHELFORD 1908).

Rodák z poľskej časti Sliezska **Eugene Amandus Schwarz** (*1844-†928) emigroval v roku 1872 do USA. Tu prešiel viacerými zamestnaniami až sa stal kurátorom pre chrobáky (Coleoptera) v United States National Museum vo Washingtone D.C. (súčasť Smithsonian Institution). Odtiaľ podnikol viacero dlhších expedícií do Panamy, Guatemaly, Mexika a na Kubu. Šváby, ktoré počas expedícií nazbieral, spracoval americký ortopterológ **Morgan Hebard** (*1887-†1946). Hebard sa tiež zúčastnil v roku 1913 kratšej expedície do oblasti Panamského prieplavu a zberal hmyz. V roku 1920 spracoval Hebard šváby Panamy v monografickom diele (HEBARD 1920). Medzi švábmi sa nachádzal aj samček zo zberov E. A. Schwarza z roku 1911, ktorý bol veľmi podobný jedincovi, ktorého opísal Saussure z Mexika. Hebard ho opísal pod názvom *Macrophyllodromia splendida*. Keďže mal k dispozícii celého jedinca, opísal rod aj druh obšírne, vrátane genitálií (HEBARD 1920).

V ďalších rokoch sa Hebard pustil aj do spracovania švábov z Francúzskej Guiany. Mal vlastnú kolekciu a zároveň spracoval aj materiál od iných Amerických prírodovedcov a zberateľov. Tentoraz natrafil na väčšiu sadu (3 ♂♂, 3 ♀♀ a 2 nymfy) jedincov z rodu *Macrophyllodromia*. Ich genitálie sa značne líšili od predchádzajúceho druhu, takže opísal nový druh *Macrophyllodromia nigrigena* (obr. 33). Jeden samček a dve samičky pochádzali z Hebardovej zbierky z osady a francúzskeho trestaneckého tábora Saint Laurent du Maroni (Francúzska Guiana) a zvyšok jedincov nazberal v roku 1922 americký prírodovedec a entomológ **Charles William Beebe** (*1877-†1962) na lokalite Kartabo (oblasť Bartica, Britská Guyana). Samčekovia mali veľmi komplikovaným spôsobom utvárané výbežky na subgenitálnej platničke (HEBARD 1926). Práve tieto výbežky sú dobrým determinačným znakom.

Isolda Rocha e Silva Albuquerque (*1935) začala už vo svojich 15-tich rokoch pracovať ako praktikantka v Národnom múzeu Brazílskej univerzity, kde v roku 1952 začala budovať zbierku neotropických švábov, ktorá existuje dodnes. V roku 1960 sa stala praktikantkou v United States National



Obr. 33. *Macrophyllodromia nigrigena* ♂, habitus a subgenitálna platnička (HEBARD 1926).

Museum u Dr. Gurneyho a pokračovala u Dr. Rehna v Academy of Natural Sciences vo Filadelfii. Počas pobytu v USA preštudovala zbierky neotropických švábov z viacerých múzeí. Po návrate z USA sa zamestnala v Museu Nacional v Rio de Janeiro. Tu publikovala prácu revidujúcu rod *Macrophylloromia*. Preštudovala 5 ♂♂ a 4♀♀ z druhu *M. maximiliani* z Hondurasu, Guatemaly, Kostariky a Panamy. V zbierke USNM objavila aj samčeka z Panamy, ktorý mal odlišne tvarovanú subgenitálnu platničku ako *M. maximiliani*. Opísala ho pod menom *M. panamae*. Holotyp pochádzal z ostrova Barro Colorado v Panamskom prieplave (ROCHA E SILVA 1962). Uloviť sa ho podarilo **Jamesovi Zetekovi** (*1886-1†959), synovi českých emigrantov v USA. V roku 1911 odcestoval Zetek do Panamy, kde sa ako entomológ stal základňovým riaditeľom Canal Zone Biological Area (CZBA). Základňa bola umiestnená na ostrova Barro Colorado. Zetek sa tu venoval hlavne výskumu termitov, ale zberal aj iné druhy hmyzu, okrem iného aj šváby.

Pri štúdiu švábov v U.S. National Museum sa Rocha e Silva dostala aj ku švábom, ktoré boli do USA dovezené so zásielkami banánov z Hondurasu (?) a Ekvádoru. Na ich základe opísala druh *Macrophyllodromia ecuadorana*. Holotyp (♂) chytený v San Diegu pochádzal z Guayaquilu a allotyp (♀) chytený v Kalifornii pochádzal tiež z Ekvádoru. Okrem toho preštudovala ďalších 7 paratypov chytených na banánoch pochádzajúcich z Ekvádoru a v jednom prípade možno z Hondurasu (ROCHA E SILVA 1962). Na priložených obrázkoch zrejme zobrazila holotyp a allotyp. Je však možné (a vzhľadom na rôzny pôvod aj veľmi pravdepodobné), že všetky jedince označené ako paratypy nepatrili k rovnakému druhu. Z druhu *Macrophyllodromia nigrigena* preštudovala samičku chytenú na lokalite Tumupasa (Bolívia), čo tiež nie je (vzhľadom na umiestnenie lokality) pravdepodobne úplne spoľahlivá determinácia.

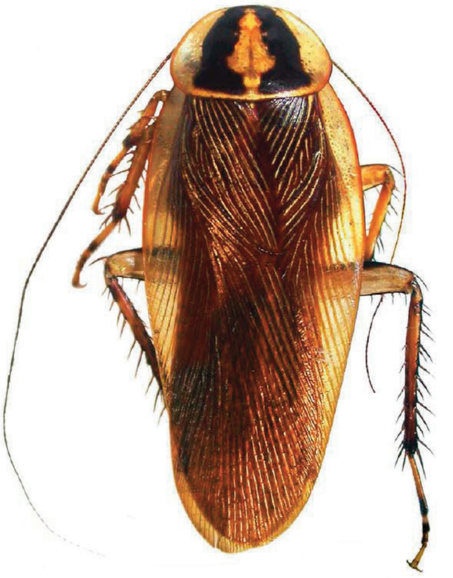
Skôr ako v roku 1988 odišla Rocha e Silva na dôchodok, vychovala si niekoľko následníkov. Jej študentmi boli aj **Sonia Maria Lopes** a **Edivar Heeren de Oliveira**, ktorí momentálne tiež pracujú v Museu Nacional, Universisade do Rio de Janeiro v Brazílii a zaoberajú sa taxonómiou švábov. Zo zbierok múzea opísali dva druhy (oba druhy podľa samčekov) z rodu *Macrophyllodromia*: *M. lanceolata* a *M. multipunctata* zo štátu Acre ležiaceho na západe Brazílie (LOPES & OLIVEIRA 2006).

Zo zvyšných 5 doteraz opísaných druhov z rodu *Macrophyllodromia* pochádzajú 4 z Ekvádoru. Väčšinu opísal ruský entomológ **Leonid Anisyutkin** podľa jedincov nazberaných jeho kolegami: *M. amabile* (1♂ a 1♀) z okolia vodopádu San

Obr. 34. Rozšírenie rodu *Macrophyllodromia*. Podľa VIDLIČKU (2013a) – upravené a doplnené.

Rafael na Rio Coca a *M. nobile* (1♂) z okolia jazera Lago Grande na Rio Cuyabeno, oba druhy z Ekvádoru (ANISYUTKIN 2007) a druhy *M. beccalonii* (1♂) z provincie Napo (Ekvádor) a *M. rufidula* (1♂) z Veracruz (Mexiko) (ANISYUTKIN 2012). Anisyutkin mal k dispozícii aj paratyp druhu *M. ecuadorana*, avšak podľa opisu sa zdá, že v tomto prípade sa jedná o iný druh. Výskyt jednotlivých druhov zobrazuje obrázok 34.

Posledná spomínaná Anisyutkinova práca má síce vročenie 2012, ale vyšla s oneskorením až v roku 2013. Preto nemohla byť zohľadnená v revízii rodu *Macrophyllodromia* (VIDLIČKA 2013a). V rámci tejto revízie bol opísaný nový druh *M. onorei* podľa samčeka (obr. 35) z rezervácie Otongachi (okolie Santo Domingo de los Colorados) (VIDLIČKA 2013a). Paratyp *M. ecuadorana* študovaný Anisyutkinom za zdá byť práve z tohto novo opísaného druhu. Novo opísaný druh nebol zahrnutý do check-listu ekvádorských druhov švábov, ktorý vyšiel súbežne s opisom (VIDLIČKA 2013b).



Obr. 35. *Macrophyllodromia onorei* ♂ (VIDLIČKA 2013a).

5.5. Prehľad príspevkov autora k poznaniu švábov juhovýchodnej Ázie a Južnej Ameriky

(hnedou farbou sú uvedené príspevky, ktoré sú súčasťou habilitačnej práce)

VIDLIČKA, Ľ. 1999. Caeparia sausai sp.nov. from Laos, and description of the male Caeparia donskoffi (Blattaria: Blaberidae: Panesthiinae). *Entomological Problems* 30(2): 1-5. (Príloha č. 7)

VIDLIČKA, Ľ. 2002. The new cockroach species from the genus Chorisoserrata from Laos (Blattaria: Blattellidae: Pseudophyllodromiinae). *Entomological Problems* 32(2): 145-147. (Príloha č. 8)

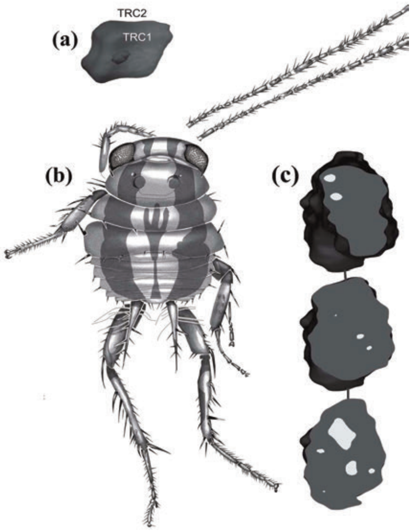
VIDLIČKA, Ľ., VRŠANSKÝ, P., SHCHERBAKOV, D.E. 2003. Two new troglobitic cockroach species of the genus Spelaeoblatta (Blattaria: Nocticolidae) from North Thailand. *Journal of Natural History* 37(1): 107-114. (Príloha č. 9)

VIDLIČKA, Ľ. 2013a. New species of Macrophyllodromia (Blattaria, Blattellidae) from Ecuador and a key to males of the genus. *Zootaxa* 3635(2): 185-193. (Príloha č. 10)

VIDLIČKA, Ľ. 2013b. Cockroaches (Blattaria) of Ecuador—checklist and history of research. *Zootaxa* 3599(5): 401-445. (Príloha č. 11)

6. Fosílne šváby (Blaberidae, Blattellidae, Ectobiidae)

Šváby (Blattaria) vznikli v karbóne v stupni Bashkirian (pred 323,2±0,4 až 315,2±0,2 miliónmi rokov). Najstaršie nálezy pochádzajú z Quilianshan v Číne (ZHANG et al. 2012, GUO et al. 2012). Typické mezozoické čeľade boli odvodené z Phyloblattidae pri P/T hranici a kmeň recentných čeľadí (a tiež všetkých modliviek a termitov) možno vysledovať z druhohornej čeľade Liberiblattinidae (VRŠANSKÝ 2010, VRŠANSKÝ et al. 2012a). Najstarším fosílnym záznamom o druhoch švábov recentnej čeľade je ectobiid (blattellid) *Piniblattella vitimica* (VISHNIAKOVA 1964) z neskorej kriedy (VRŠANSKÝ 1997). Súčasné rody boli známe až od skorého eocénu (ARCHIBALD & MATHEWES 2000) a moderná fauna švábov pochádza z obdobia okolo paleocénno-eocénneho teplotného maxima (PETM; VRŠANSKÝ et al. 2011, 2012b).

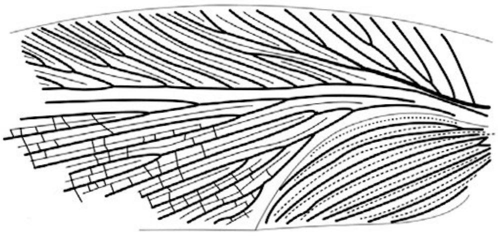


Obr. 36. Nymfa švába z čeľade Blattulidae (VRŠANSKÝ et al. 2013a).

V triase, jure a kriede (druhohory; pred 251±0,4 až 65,5±0,3 miliónmi rokov) žili na Zemi obrovské terestrické plazy – dinosaury. Predpokladá sa, že tieto obrie plazy živiace sa rastlinnou potravou produkovali úmerne veľké množstvo exkrementov. V súčasnosti sú exkrementy odstraňované (rozkladané) hlavne koprofágnym hmyzom. V dobe dinosaurov však bol takýto hmyz zriedkavý. Pri štúdiu švábov z libanonského jantáru vznikla hypotéza, či by tými chýbajúcimi „čističmi po dinosauroch“ nemohli byť šváby. Libanonský jantár spred 125 miliónov rokov uchoval aj nymfu švába zatiaľ neznámeho druhu z vyhynutej čeľade Blattulidae. Nymfa je dokonale zachovaná (obr. 36) a zachovali sa aj jej skamenené exkrementy – koprolity. V týchto koprolitoch boli objavené synchrotrónovou mikrotomografiou zvyšky dreva s hladkými hranami, ktorých zdrojom by mohli byť práve výkaly bylinožravcov. Takže šváby sa pravdepodobne živili exkrementami (obr. 37) dinosaurov a napomáhali ich biodegradácii (VRŠANSKÝ et al. 2013a). Šváby živiace sa exkrementami poznáme aj zo súčasnosti, najčastejšie je to guáno po netopieroch (ROTH & WILLIS 1960, BELL et al. 2007, CHRISTOFFERSEN & DE ASSIS 2013).

Obr. 37. Koprofágne šváby v druhohorách (HTTPS://WWW.PHACTUAL.COM/9-CREEPY-COCKROACH-FACTS-YOU-DIDNT-WANT-TO-KNOW/).

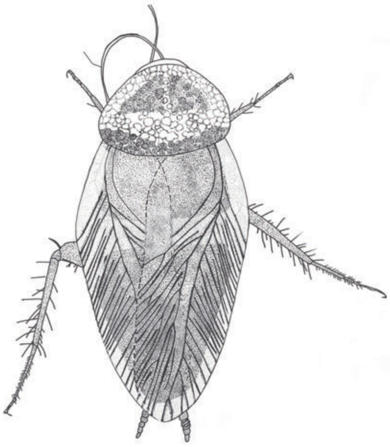
Podľa databázy fosílneho hmyzu (EDNA) je známych z paleocénu (pred 65,5±0,3 až 55,8±0,2 miliónmi rokov) 177 druhov hmyzu. Najviac sú to chrobáky (44), dvojkrídlovce a hemipterný hmyz (po 28 druhov). Šváby sa v tejto databáze donedávna vôbec nevyskytovali. Prvé dva druhy švábov z tohto obdobia boli opísané z danianských (paleocénnych) sedimentov pochádzajúcich z ruského Ďalekého východu (VRŠANSKÝ et al. 2013b). Orientálny (indomalajský) rod *Morphna* zahŕňa 12



Obr. 38. Tegmina švába *Morphna paleo* (VRŠANSKÝ et al. 2013b).

recentných druhov. *Morphna paleo* (obr. 38) bola opísaná na základe zachovanej fosílnej tegminy (VRŠANSKÝ et al. 2013b). Rod *Ergaula* obsahuje 7 recentných druhov, až na jednu výnimku tiež s rozšírením v orientálnej oblasti. Jeden druh (*Ergaula atica*) je známy z eocénu Izraela (ANISYUTKIN et al. 2008) a novoopísaná *Ergaula stonebut* je paleocénneho veku (VRŠANSKÝ et al 2013b).

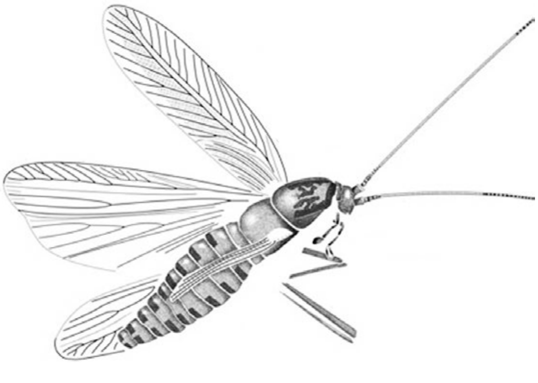
Chiapas, štát na najjužnejšom výbežku Mexika, je známy výskytom jantáru, pre ktorý je príznačné, že pomerne často obsahuje zvyšky rastlín, príležitostne huby, vzácne ulitníky, pavúky, kôrovce, pomerne hojný je hmyz a dajú sa objaviť aj obojživelníky, plazy, vtáčie perie a srsť cicavcov (POINAR 2003, ENGEL 2004, SOLORZANO KRAEMER 2007, VEGA et al. 2009a, b).



Obr. 39. *Supella miocenica* (VRŠANSKÝ et al. 2011).

Chiapaský jantár vznikol v dolnom miocéne (pred 23,03±0,05 až 15,97±0,05 miliónmi rokov). Z hmyzu zachovaného v tomto jantári bolo doteraz opísaných 235 druhov. Druhy, ktoré sa v tomto jantári vyskytujú, patria často do recentných rodov. To je aj prípad švába nájdeného v tomto jantári. Patrí do rodu *Supella*, kde patrí 10 recentných druhov. Súčasné druhy sú výskytom obmedzené na africký kontinent. *Supella miocenica* (obr. 39) z chiapaského jantáru je sesterským druhom ku druhu *S. mirabilis*, ktorý je široko rozšírený v štátoch rovníkovej Afriky. Rozdiel je iba v tvare stredovej škvrny na pronóte a vo veľkosti tela (VRŠANSKÝ et al. 2011). Výskyt rodu *Supella* v miocénnej Amerike naznačuje niekdajší kozmopolitný výskyt tohto rodu, ktorý sa zachoval len v Afrike.

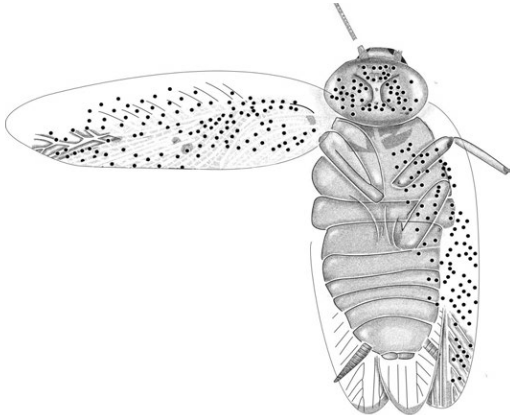
Eocénne (pred 55,8±0,2 až 33,9±0,1 miliónmi rokov) sedimenty rieky Green River v americkom Colorade sú bohaté na fosílie švábov. Z 11 tu zistených rodov švábov (17 druhov), až 9 rodov patrí aj k recentnej faune. Rod *Blattella* môžeme považovať za historicky starší, bol zaznamenaný už v druhohornej kriede (VRŠANSKÝ 2008). Ostatné recentné rody švábov sa objavujú až na začiatku eocénu a majú moderný charakter. K rodom, ktoré sa vyvinuli počas eocénu alebo tesne pred, patrí aj rod *Cariblattoides*. Rod v súčasnosti zahŕňa 13 recentných druhov rozšírených v Strednej a Južnej Amerike. *Cariblattoides labandeirai* (obr. 40) bol v skorom eocéne pri Green River bežným druhom. Našlo sa až 13 fosílií patriacich tomuto druhu.



Obr. 39. *Supella miocenica* (VRŠANSKÝ et al. 2011).

Prekvapivý bol objav švába z rodu *Ectobius* v eocénnych sedimentoch rieky Green River spred 49 miliónov rokov. Šváby rodu *Ectobius* sú v súčasnosti obmedzené výskytom na Euráziu a Afriku (palearktická oblasť). Opísaný bol druh *Ectobius kohlsi* (obr. 41). Jeho nález v Severnej Amerike (nearktická oblasť) indikuje kozmopolitné rozšírenie tohto rodu počas stredného paleogénu a jeho neskoršie vyhynutie (VRŠANSKÝ et al. 2014). Zástupcovia rodu sa reintrodukovali na Americký kontinent v 20. storočí (CHANDLER 1985, 1992, HOEBEKE & NICKLE 1981, HOEBEKE & CARTER 2010).

Zo stredného eocénu (pred 47,8 až 38 miliónmi rokov) pochádzajú fosílie zberané pri Flathead River v Montane (USA). Našiel sa medzi nimi aj šváb z rodu *Latiblattella*. Recentné druhy rodu *Latiblattella* (18 druhov) sú rozšírené v Strednej Amerike a v Karibiku. *Latiblattella avita* predstavuje prvý fosílny nález druhu z tohto rodu (GREENWALT & VIDLIČKA 2015).



Obr. 41. *Ectobius kohlsi* (VRŠANSKÝ et al. 2014).

6.1. Prehľad príspevkov autora k poznaniu fosílnych švábov (Blaberidae, Blattellidae, Ectobiidae)

(hnedou farbou sú uvedené príspevky, ktoré sú súčasťou habilitačnej práce)

VRŠANSKÝ, P., CIFUENTES-RUIZ, P., VIDLIČKA, Ľ., ČIAMPOR, F., VEGA, F.J. 2011. Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. *Geologica Carpathica* 62: 463-475. (Príloha č. 12)

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Prehľad príloh
(Publikácie autora, ktoré tvoria súčasť habilitačnej práce.)

Tematický okruh 1: Etológia švábov

Príloha 1: VIDLIČKA, Ľ., HUČKOVÁ, A. 1993. Mating of the cockroach Nauphoeta cinerea (Blattodea: Blaberidae): I. Copulatory behaviour. *Entomological Problems* 24(2): 69-73.

Príloha 2: HUČKOVÁ, A., VIDLIČKA, Ľ., KOZÁNEK, M. 1994. Mating of the cockroach Nauphoeta cinerea (Blattodea: Blaberidae): II. Histamine changes during courtship and copulation. *Biologia* 49(5): 691-695.

Tematický okruh 2: Rozšírenie a taxonómia švábov v strednej Európe a na Slovensku

Príloha 3: VIDLIČKA, Ľ. 1993. Seasonal dynamycs of vertical migration and distribution of cockroach Ectobius sylvestris (Blattaria: Blattellidae: Ectobiinae) in oak forest. *Biologia* 48(2): 163-166.

Príloha 4: VIDLIČKA, Ľ. 1993. Phyllodromica hungarica sp.nov., a new cockroach species from Hungary (Insecta: Blattodea: Blattellidae: Ectobiinae). *Entomological Problems* 24(1): 63-68.

Príloha 5: VIDLIČKA, Ľ. 1994. Phyllodromica transylvanica sp. nov., a new cockroach species from Romania and key of the maculata-group of Phyllodromica in central Europe. *Entomological Problems* 25(2): 55-62.

Príloha 6: VIDLIČKA, Ľ., MAJZLAN, O. 1997. Revision of the megerlei - group of the cockroach genus Phyllodromica Fieber (Blattaria: Blattellidae, Ectobiinae). *Entomologica Scandinavica* 28: 163-173.

Tematický okruh 3: Šváby juhovýchodnej Ázie a Južnej Ameriky

Príloha 7: VIDLIČKA, Ľ. 1999. Caeparia sausai sp.nov. from Laos, and description of the male Caeparia donskoffi (Blattaria: Blaberidae: Panesthiinae). *Entomological Problems* 30(2): 1-5.

Príloha 8: VIDLIČKA, Ľ. 2002. The new cockroach species from the genus Chorisoserrata from Laos (Blattaria: Blattellidae: Pseudophyllodromiinae). *Entomological Problems* 32(2): 145-147.

Príloha 9: VIDLIČKA, Ľ., VRŠANSKÝ, P., SHCHERBAKOV, D.E. 2003. Two new troglobitic cockroach species of the genus Spelaeoblatta (Blattaria: Nocticolidae) from North Thailand. *Journal of Natural History* 37(1): 107-114.

Príloha 10: VIDLIČKA, Ľ. 2013a. New species of Macrophyllodromia (Blattaria, Blattellidae) from Ecuador and a key to males of the genus. *Zootaxa* 3635(2): 185-193.

Príloha 11: VIDLIČKA, Ľ. 2013b. Cockroaches (Blattaria) of Ecuador—checklist and history of research. *Zootaxa* 3599(5): 401-445.

Tematický okruh 4: Fosílne šváby (Blaberidae, Blattellidae, Ectobiidae)

Príloha 12: VRŠANSKÝ, P., CIFUENTES-RUIZ, P., VIDLIČKA, Ľ., ČIAMPOR, F., VEGA, F.J. 2011. Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. *Geologica Carpathica* 62: 463-475.

Príloha 13: VRŠANSKÝ, P., VIDLIČKA, Ľ., ČIAMPOR, F., MARSH, F. 2012b. Derived, still living cockroach genus Cariblattoides (Blattida: Blattellidae) from the Eocene sediments of Green River in Colorado, USA. *Insect Science* 19: 143–152.

Príloha 14: VRŠANSKÝ, P., VAN DE KAMP, T., AZAR, D., PROKIN, A., VIDLIČKA, Ľ., VAGOVIČ, P. 2013a. Cockroaches Probably Cleaned Up after Dinosaurs. *PLoS ONE* 8(12): e80560. doi:10.1371/journal. pone.0080560

Príloha 15: VRŠANSKÝ, P., VIDLIČKA, Ľ., BARNA, P., BUGDAEVA, E., MARKEVICH, V. 2013b. Paleocene origin of the cockroach families Blaberidae and Corydiidae: Evidence from Amur River region of Russia. *Zootaxa* 3635(2): 117-126.

Príloha 16: VRŠANSKÝ, P., ORUŽINSKÝ, R., BARNA, P., VIDLIČKA, Ľ. & LABANDEIRA, C.C. 2014. Native Ectobius (Blattaria: Ectobiidae) from the Early Eocene Green River Formation of Colorado and Its Reintroduction to North America 49 Million Years Later. *Annals of the Entomological Society of America* 107(1): 28-36.

Príloha 17: GREENWALT, D.E., VIDLIČKA, Ľ. 2015. Latiblattella avita sp. nov. (Blattaria: Ectobiidae) from the Eocene Kishenehn Formation, Montana, USA. *Palaeontologia Electronica* 18.1.16A: 1-9.

Monografie

Príloha 18: VIDLIČKA, Ľ. 2001. *Blattaria – šváby; Mantodea – modlivky: (Insecta: Orthopteroidea).* 1. vyd., Veda, Bratislava, 169 pp. (Fauna Slovenska) ISBN 80-224-0640-6

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Príloha č. 1

VIDLIČKA, Ľ., HUČKOVÁ, A. 1993.
Mating of the cockroach Nauphoeta cinerea (Blattodea: Blaberidae):
I. Copulatory behaviour.
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Mating of the cockroach Nauphoeta cinerea (Blattodea: Blaberidae)

I. Copulatory behaviour

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Abstract. The copulatory behaviour of cockroaches *Nauphoeta cinerea* was observed in details. Four phases of copulation were identified. The durations of copulation and the duration of other copulatory events are under defined environmental conditions relatively fixed. Cockroach, copulatory behaviour, *Nauphoeta*, Blattodea, etology.

Introduction and overview

Sexual and especially mating behaviour of the cockroach *Nauphoeta cinerea* have been observed by many authors (ROTH & WILLIS, 1954; ROTH, 1964; ROTH & BARTH, 1964; ROTH & DATEO, 1966; FUKUI & TAKAHASHI, 1980; 1983 a,b; TAKAHASHI & FUKUI, 1980; 1983; 1991; SRENG, 1979, 1984, 1985, 1990, 1992, 1993). A distinct characteristic of *N. cinerea* males is their calling behaviour. Raising the flattened and elongated abdomen the males expose their sternal glands. From them a volatile sex pheromone, seducin (SRENG, 1990), attracting receptive females from a long distance is emitted. This calling posture is identical to the aggressive one, described by EWING (1967). However, SRENG (1990) suggest that the calling posture resembles the posture occupied by dominant males after winning a combat. That is why dominant males copulate more frequently than subordinate ones (SCHAL & BELL, 1983; MOORE, 1989; BREED, SMITH & GALL, 1980).

Males recognize the difference between sexes by contact chemoreception, particularly via antennal contact with the antennae and body of the other individuals. Intermale contact usually results in agonistic behaviour and characteristic antennal fencing. Aggressive or subordinate status of cockroach male can by identified on the basis of the antennal fencing pattern (EWING, 1967). Mature males are producing a male pheromone (nauphoetin) in the cuticular wax. This pheromone suppresses the wing–raising activity caused by hydrocarbons (FUKUI & TAKAHASHI, 1983a; TAKAHASHI & FUKUI, 1983), but it does not cause aggressive behaviour (SIRUGUE et al., 1992). SIRUGUE et al. (1992) suggested the existence of another contact pheromone that triggers the male agonistic behaviour via antennal contact.

Males in presence of mature females normally display courtship behaviour. During courtship the male raises his wings and tegmina. The chemical factor (wing–raising pheromone) responsible for the wing–raising is present mainly in the hydrocarbon fraction of the cuticular wax of both sexes (FUKUI & TAKAHASHI, 1983). The receptive female is attracted to the male's back. She mounts and feeds (licks) on the male's tergal glands secretion – aphrodisiac sex pheromone (SRENG, 1990), or seducin (ROTH & DATEO, 1966; HARTMAN & ROTH, 1967). The feeding behaviour keeps the female in a proper position for a period sufficient for bringing her genitalia into the contact with those of the male. [Type A pattern of mating behaviour – female in upper position (SRENG, 1993)]. The sex pheromone serves as an attractant as well as arrestant (Roth & Dateo, 1966). As long as the female feeds on the tergal glands secretion, the male moves backward, pushes his abdomen telescopically under the female's abdomen and grasps her abdominal tip with a retractable hook, i.e. right phallomere (R2) (McKittrick, 1964). If the female is willing to mate she allows the contact with the hook. In case of rejecting the copulation attempt she dismounts from the male and prevents the genital contact (Moore & Breed, 1986). Following several unsuccessful mating attempts the male lowers his tegmina and wings. Standing in a distance of about 2 cm from the female he pumps and elongates his abdomen and emits a faint but audible sound (Hartman & Roth,1967). On the other hand, Sirugue at al. (1992) observed that if the female did not respond to the wing-raising of the male, the male resumed the calling posture again, followed by wing-raising. The females generally cease to respond to the male sex pheromone about 2 days after mating.

When the genital contact with the receptive female was successful, the pair resumes in the typical false-linear position (end-to-end position) (Sreng, 1990; Fukui & Takahashi, 1983b; Roth & Dateo, 1966) and the copulation starts. During copulation a spermatophore with non-motile sperm is transferred and firmly cemented into the genital chamber. Its presence inhibits the receptivity of females. Two to three days after mating the spermathecae (receptaculum seminis) are densely filled with motile spermatozoa. The empty spermatophore is extruded by the female several days after mating (Roth, 1964).

This paper reports the results of a study of the behaviour of cockroaches during copulation with special reference to the copulatory behaviour of males.

Material and methods

Observations were made on the cockroach *Nauphoeta cinerea*. Animals were reared at 29±1°C, 45±1% RH and a 12L:12D light:dark cycle. Food (turkey "grower" diet) and water were provided ad libitum. Cockroaches were selected from stock colonies maintained at the Institute of Experimental Phytopathology & Entomology of the Slovak Academy of Sciences. Individuals of both sexes were selected at the last-instar nymph stage and kept in unisexual groups to last ecdysis. The time of adult ecdysis was recorded. About 10 adults were placed together in a 13 × 8 × 6 cm plexiglas container with a plexiglas cover (the same container was used for the observation of mating).

Ethological observations were carried out during the light period. The mature cockroaches mated 14±1 days after the last moult. In the mating container only one male and one female were placed. The durations of different events of the copulatory behaviour were recorded. Direct observations were used in most cases. Some mating interactions (10% of observations) were recorded on a videotape using a Sony HVC-4000 P camera and Sony SL-C9E video cassette recorder and analysed at low speed.

For the mating interruption experiment *N. cinerea* females were manually separated from their partners after being in copula for various times.

Results

The mean duration of the mating [the time from the resuming the end-to-end position to the release of the right phallomere (R2) from the female's body] was 12.5 min (N=100, SE=0.9).

On the basis of the above mentioned results we interrupted the copulation manually in minute 4, 6, 8 and 10. When the copulation was interrupted in minute 4 (N=15), the male's right phallomere stayed pushed out from the male genital chamber and in minute 9 the spermatophore was extruded. After interrupting the copulation the male sometimes retracted the right phallomere into the body but in minute 9 the phallomere was pushed out again and the spermathophore was extruded. In minute 13 the phallomere was retracted into the male genital chamber.

When the copulation was interrupted in minute 6 (N = 15) or 8 (N = 15) the events were the same as mentioned above.

In case the copulation was interrupted in minute 10 (N = 15), the phallomere stayed pushed out to minute 13 and then it was retracted. The spermatophore was not extruded.

The spermatophore contained non–motile and twisted sperm. The diameter of spirals was 15 – 16 µm. 2 hours later the sperm began to be active and was about 250 – 350 µm in length. The frequency of male abdomen contractions and corresponding movement of tegmina and wings during mating were analysed from videorecordings using slow motion. The mean frequency of the abdomen contractions was 132 (N=10, SE= 9.1). The strength and frequency of contractions varied throughout mating (fig. 1).

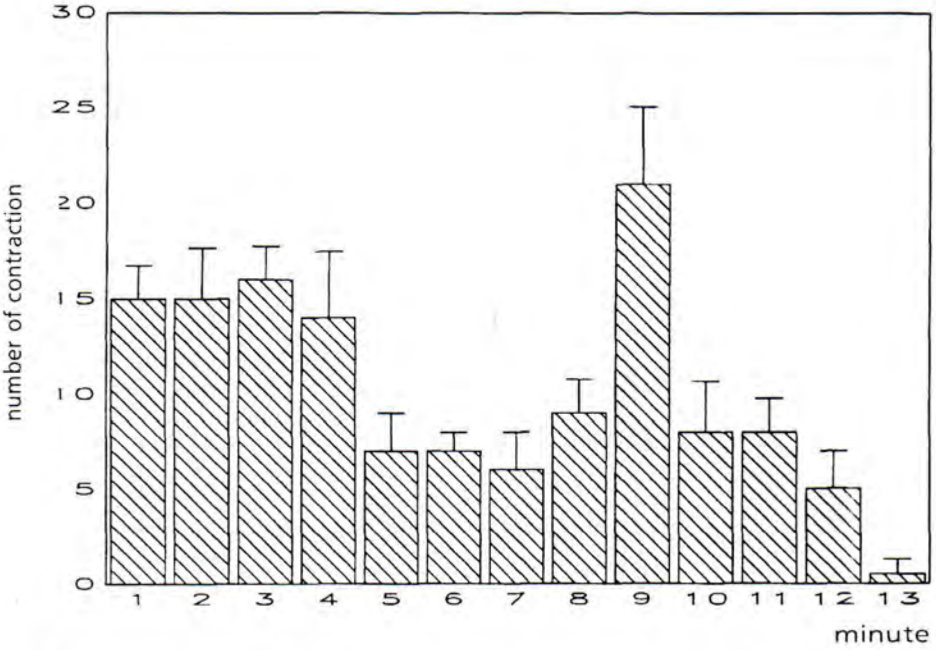

Fig. 1. Mean number (±SE) of male abdomen contractions during copulation, N=10.

On the basis of our results and previous data the following 4 phases of copulation can by identified:

Phase 1	Minute 1 to 4	– establishment of the genital contact;
Phase 2	Minute 5 to 8	– completion of the spermatophore, preparation of the spermatophore transfer;
Phase 3	Minute 9 to 10	– transferring the spermatophore into the female's bursa;
Phase 4	Minute 11 to 13	– spermatophore firmly inserted and cemented in female's bursa.

Discussion

Different durations of copulation in cockroaches have been reported by different authors. ROTH (1964) has found mean duration of copulation 17±1 min at 28±2°C, while MOORE & BREED (1986) 9.5 min at 25–27°C. The closest results to the data reported here have been found by MOORE (1990 a,b) (11 to 11.9 min). All above mentioned data were determined for the initial mating. When males mated 2 or 3 times consecutively, the average time spent in copula was 100±8 min and 141±2 min, respectively (ROTH, 1964). Dominant males copulated significantly longer than subordinate ones (MOORE & BREED, 1986; MOORE, 1990). The presence of dominant males inhibited the calling posture in subordinate individuals (SIRUGUE et al., 1992). Despite of variability in the duration of copulation in various experiments it is very important to note that this value is very constant under the same conditions. The durations of copulation and copulatory events are fixed. It was not possible to influence the copulatory events by manual separation of the mating pair. Timing of spermatophore release and phallomere retraction was the same as if the female was present.

In the subfamily Oxyhaloinae (Blaberidae) male genitalia are uniform. The hook (R2) is on the right side (McKITTRICK, 1964; ROTH, 1971). In the family Blattidae (*Blatta orientalis*, *Periplaneta americana*) the hooked titillator of the left phallomere is the first phallic organ which fastens to the ovipositor to achieve the connection (BAO & ROBINSON, 1990). GUPTA (1947) on the basis of the observation of *P. americana* mating behaviour suggested that the titillator was important to keep the female's vestibulum open and the right phallomere was the main clasping organ to hold the valvae of the female genitalia during copulation. According to BAO & ROBINSON (1990) the right phallomere in *B. orientalis* keeps the first pair of valvae opened, so that the genital chamber is exposed. The male gonopore projects into the female genital chamber where the spermathecal sac and the female gonopore are located. This mechanism probable explains the fact that phallomere is always extended during the spermatophore release even in absence of female.

ROTH (1964) was the first who interrupted the copulation of the cockroach *N. cinerea* manually and observed the mechanism of the loss of female's receptivity. He separated females from their partners after having been in copula for 10–12 min (the average time of copulation was 17 min). In this phase, three different stages of spermatophore transfer could be identified. In the first case the spermatophores were not transfered, in the second case the spermatophores were transfered but not cemented and in the third case they were transfered and firmly cemented. As the duration of copulation in our experiments was 12.5 min, the events recorded in minutes 7.5–9 could correspond to those observed by ROTH (1964) in minutes 10–12 (at the duration of copulation 17 min). The timing of behavioural events in phases 2 and 3 explains variability in termination of spermatophore transfer described by ROTH (1964).

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Príloha č. 2

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II. Histamine changes during courtship and copulation.
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Mating of the cockroach *Nauphoeta cinerea* (Blattodea: Blaberidae)
II. Histamine changes during courtship and copulation

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HUČKOVÁ, A., VIDLIČKA, Ľ., KOZÁNEK, M., Mating of the cockroach *Nauphoeta cinerea* (Blattodea: Blaberidae) II. Histamine changes during courtship and copulation.– Biologia, Bratislava, **49:** 691–695, 1994; ISSN 0006–3088.

The concentrations of biogenic amine histamine were measured in the supraoesophageal and the 6th abdominal ganglia of the cockroach *Nauphoeta cinerea* during courtship and copulation. In both sexes the highest concentration of histamine in their brains was found in the 5th minute of copulation. In the last abdominal ganglion of males a sharp increase in histamine level was recorded in the 5th and 10th minutes, at the time of spermatophore transfer into the female's bursa copulatrix. It suggests the direct involvement of histamine in the regulation of this process during copulation.

Key words: Cockroach *Nauphoeta cinerea*, mating behaviour, histamine, central nervous system, radioenzymatic assay.

Introduction

Biogenic amines are distributed throughout the nervous systems of both vertebrates and invertebrates and are generally considered to function as transmitters, neuromodulators and neurohormones (GERSCHENFELD, 1973; KLEMM, 1976; EVANS, 1980; ORCHARD, 1982). There is good evidence that these compounds play a key role in modulating behaviour and autonomic neural functions (MURDOCK, 1971; DAVID, VERRON, 1982; MERCER, MENZEL, 1982; MERCER, ERBER, 1983), they control the circadian rhytmus (MUSZYNSKA-PYTEL, CYMBOROWSKI, 1978; PRÉÉ, RUTSCHKE, 1983) and are involved in the insect's reaction to various stress stimuli (DAVENPORT, EVANS, 1984; KOZÁNEK et al., 1986).

Histamine (HA) has been increasingly implicated as a putative neurotransmitter in insect visual systems (HARDIE, 1988; NÄSSEL et al., 1988; SIMMONS, HARDIE, 1988). However, some other investigations have also shown that the HA level in insect CNS changes in response to various stress stimuli (KOZÁNEK et al., 1985; HUČKOVÁ et al., 1992) and in addition, possible role for HA in reproduction of cockroach *Nauphoeta cinerea* has also been suggested (HUČKOVÁ et al., 1992).

In a previous study we described the ethological aspect of the mating behaviour of *N. cinerea* (VIDLIČKA, HUČKOVÁ, 1993). The copulatory act alone was divided in 4 phases with strict duration according to the main internal physiological events e.g. spermatophore completion and its transfer into the female's bursa.

In this paper we report the changes in HA concentrations in the brain and the 6th abdominal ganglion of *N. cinerea* in relation to the main copulatory events.

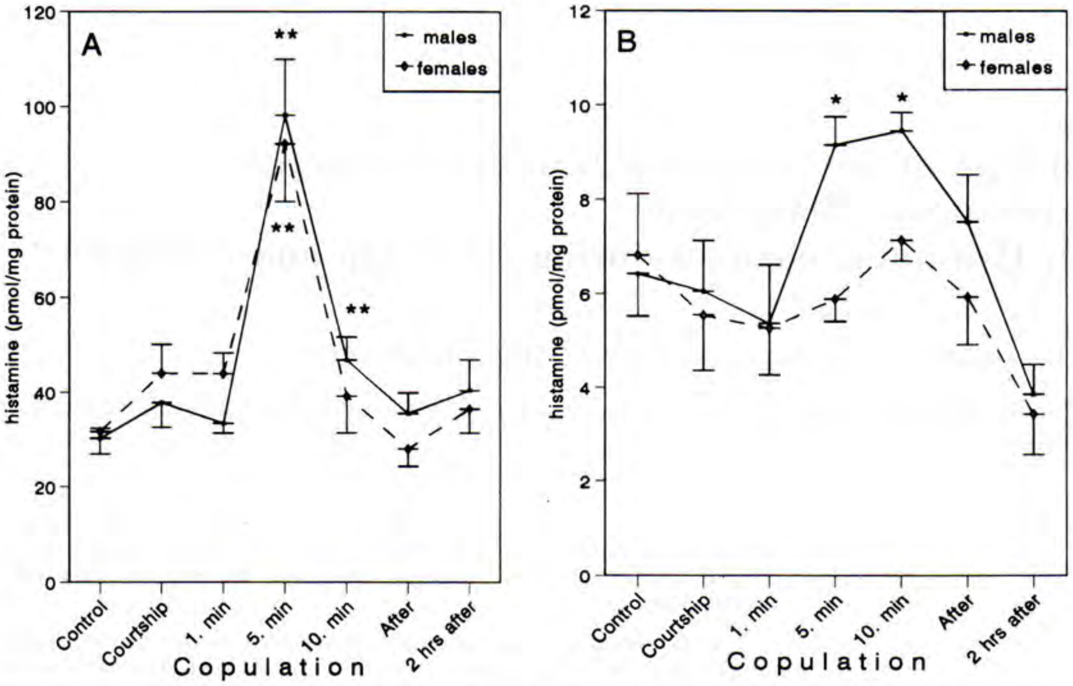

Fig. 1. Histamine concentration changes in the brain (A) and last abdominal ganglion (B) of the cockroach *Nauphoeta cinerea* during courtship and copulation. Each point represents the mean of 6 animals ± S.E.M. * ($P < 0.05$), ** ($P < 0.01$).

Material and methods

Cockroaches were reared at temperature 29 ± 1°C, relative humidity 50 ± 10% and 12 hours reversible light/dark cycle. A semisyntetic food for young turkeys and water were provided ad lib.

Experimental animals were chosen from the stock colony just after the last eclosion and separated into the unisexual groups. For courtship and copulation experiments ten-day-old males and females divided in 7 groups were used: 1 – control unmated individuals, 2 – females and males during courtship, 3, 4, 5 – couples in the 1st, 5th and 10th minutes of copulation, 6 – cockroaches just after copulation, 7 – individuals 2 hours after copulation. For courtship and copulation experiments each couple was placed in a plastic box 8 × 12 × 6 cm. Couples were killed by quick freezing in a mixture of dry ice and ethanol. Supraoesohpageal and the 6th abdominal ganglia were dissected on cooled Petri dish and homogenized in 60–150 μl of solution A (0.2 mol.l^{-1} sodium phosphate buffer pH 7.9:1 mol.l^{-1} sodium hydroxide). The homogenates were centrifuged at 5,000 g for 20 minutes at 4°C. 10 μl of the supernatant was transferred into cooled conical vials and the histamine content was determined radioenzymatically according to BROWNSTEIN et al. (1974). In all experiments 0.5 ng of histamine-dihydrochloride in 10 μl of 0.1 M HCl was used as an internal standard. The radioactivity of samples was measured by means of a Packard scintillation counter.

Protein content was measured in 10 μl of homogenate according to LOWRY et al. (1951) using bovine serum albumine as a standard. The data were analyzed using Student's *t*-test.

Results

The pattern of the concentration changes of histamine (HA) in the supraoesophageal ganglion of *N. cinerea* males and females during mating was very similar (Fig. 1A). In the time of courtship, when the female climbs the male's abdomen, and in the beginning of copulation HA level rose only slightly, this increase was a bit sharper in the female's than in the male's brain. In the 5th minute of copulation HA concentration increased significantly in both sexes ($P < 0.01$), reaching about 3-times higher amounts than were observed in control unmated groups. In the 10th minute of copulation the HA level decreased and was approximately at the same level as at the beginning of copulation, however, in the males it was still significantly higher in comparison with the control group. A slight fall in HA concentration was also found just after copulation, i.e. in the 13th minute. After 2 hours the HA level in both sexes was almost the same as in the control groups or at the beginning of copulation.

In the last abdominal ganglion (AG) the concentration of HA during courtship and at the beginning of copulation was about the same as in the control groups (Fig. 1B). Then a sharp rise in concentration was observed in the 5th and 10th minutes of copulation in the male's 6th AG ($P < 0.05$). In terminal ganglion of females the level of HA also increased reaching the highest value in the 10th minute, but this rise was not so distinct as in males. Then a continual decrease of HA concentration was found in both sexes, and 2 hours after copulation the values were lower than in the control groups.

Discussion

The critical age for *N. cinerea* female receptivity is 3–4 days (ROTH, 1962). According to SCHAL et al. (1984) the preoviposition period for this cockroach is about 13 days. A virgin females that has oviposited will not mate as long as an ootheca is present in uterus. Males may begin to mate and produce spermatophre when 2–3 days old. In respect to this, the ten-day-old individuals we used in our experiment were at the suitable age.

In cockroaches the neurosecretory system in the brain serves to release directly copulatory behaviour (ROTH, BARTH, 1964). Biogenic amines were investigated in relation to several aspects of reproductive cycle, e.g. oviposition (HENTSCHEL, 1972, 1975), ootheca production and juvenile hormone secretion (THOMPSON et al., 1990; PASTOR et al., 1991). A great number of investigations concerning insect reproduction were focused on the effect of biogenic amines and other active substances on the musculature of insect reproductory organs (SOBEK et al., 1986; ORCHARD, LANGE, 1987; STOYA, PENZLIN, 1988). It has been shown that the biogenic amine octopamine (OA) plays a physiological role in the control of locust oviducts, which receive innervation from two octopaminergic dorsal unpaired median neurones located in the 7th abdominal ganglion (LANGE, ORCHARD, 1984; ORCHARD, LANGE, 1985). OA reversibly reduced the amplitude of neurally-evoked contractions in a dose-dependent manner and caused a relaxation in basal tonus (ORCHARD, LANGE, 1986).

Up to now few investigations have been carried out on the relationship between biogenic amine levels and mating behaviour. HODSON and WRIGHT (1963) reported that application of monoamines to *Periplaneta americana* females resulted in contraction in the abdomen, wing rising and behaviour similar to that during oviposition. KOZÁNEK et al. (1990) investigated OA changes in the brain of *Nauphoeta cinerea* during copulation. They found that the level of this amine increased during courtship, but during copulation and in resting cockroaches it decreased.

In our previous research we found significant cyclic changes in histamine concentration in the brain and 6th AG of *N. cinerea* during its adult life (HUČKOVÁ et al., 1992). A possible involvement of HA in the regulation of the reproductive cycle in this cockroach was suggested. In this work we present a relationship between physiological events during mating of *N. cinerea* and HA concentration in their CNS.

The male in the presence of a receptive female showed characteristic mating behaviour. During the courtship he palpated with his antennae the back of the female who then climbed the male's abdomen and fed on the tergal gland secretes. At that time the concentration of HA in the brain increased in both sexes. In the 5th minute of copulation, i.e. in the 2nd phase, which is characterised by completion of spermatophore and its transfer (VIDLIČKA, HUČKOVÁ, 1993), we found a sharp increase of the HA level in the males' as well as the females' brain. Interestingly, at the same time a significant increase of HA was also observed in the males' terminal ganglion. According to our previous ethological observations, the frequency and strength of the male's abdominal contractions, which varied throughout mating, was highest in the 9th minute (VIDLIČKA, HUČKOVÁ, 1993). By manual interruption of copulating pairs it was revealed that just in this phase (9th and 10th min) spermatophore transfer into the female's bursa took place. In resting couples HA concentration in the brain stayed approximately at the same level, while in the 6th AG continually decreased. Thus, our findings of synchronised HA changes in the nervous tissue of copulating cockroaches (at first increase in the brain then in the 6th AG) supported by ethological observations, allow us to suppose that this monoamine is probably involved in regulation of the copulatory process.

To define the precise role of HA in mating behaviour a complex of electrophysiological, immunocytochemical and neurophysiological investigations is needed.

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Príloha č. 3

VIDLIČKA, Ľ. 1993.
Seasonal dynamycs of vertical migration and distribution of cockroach
Ectobius sylvestris (Blattaria: Blattellidae: Ectobiinae) in oak forest.
Biologia 48(2): 163-166.

Biológia, Bratislava, 48/2: 163 – 166, 1993

Seasonal dynamycs of vertical migration and distribution of cockroach *Ectobius sylvestris* (*Blattaria: Blattellidae: Ectobiinae*) in oak forest

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VIDLIČKA, Ľ., Seasonal dynamics of vertical migration and distribution of cockroach *Ectobius sylvestris* (*Blattaria: Blattellidae: Ectobiinae*) in oak forest. Biológia, Bratislava, **48**: 163–166, 1993.

In 1985–1986 the seasonal dynamics of vertical migration and distribution of cokroaches on oak stems in the State Nature Reseve Lindava (Western Slovakia) was studied. Distribution of apterous larvae, brachypterous females and winged males of *Ectobius sylvestris* was observed by means of traps placed in the height of 0.75 m and 4.20–5.20 m. Migration of *Ectobius sylvestris* towards tree tops was recorded from May to October.

Key words: *Ectobius sylvestris*, seasonal dynamics, migration, vertical distribution.

Species of the genus *Ectobius* are typical representatives of cockroaches in temperate climate. They are abundant in European forests and moorlands (MORVAN, 1972). Resting sites are situated under dead leaves in the litter, under loose bark or at the foot of grass. Litter, bushes ferns und grasses are used as foraging sites (GAUTIER, DELEPORTE, RIVAULT, 1988).

BEY-BIENKO (1969) investigated the biological cycle and population density of *Ectobius duskei* in grassland on Russian steppe. Seasonality of *Ectobius panzeri* has been studied by BROWN (1952). BROWN (1973) provided information on overwintering stages of *Ectobius lapponicus* and developmental strategies in *Ectobius pallidus* (BROWN, 1980). MORVAN'S (1972) study of four species of *Ectobius* (*E. lapponicus, lividus, panzeri* and *sylvestris*) dealt with their biological cycle. DREISIG (1971) informed about diurnal migration and vertical distribution of *Ectobius lapponicus*. PATOČKA et al. (1962) recorded the occurrence of *Ectobius lapponicus* in tree tops.

Ectobius sylvestris (PODA, 1761) (*Blattaria: Blattellidae*) occurs according to MORVAN (1972) along the borders between forest and mesophilous heathlands, dry heathlands and edges of peat bogs. It is a semivoltine, solitary and oviparous species. This species has a bisannual development and 5 larval instars. It overwinters in the 3rd to 4th larval stage.

The aim of this work is to supplement the knowledge about larval and adult vertical distribution and upward migration of *Ectobius sylvestris* on oak tree stems.

Material and methods

1. Study area

Our study area was situated in Lindava State Nature Reserve, Lindava Forest (altitude 199–225 m, 80–100 yrs, canopy cover 85 %) near the village Budmerice, map square code 7670, Western Slovakia. The stand was evaluated as

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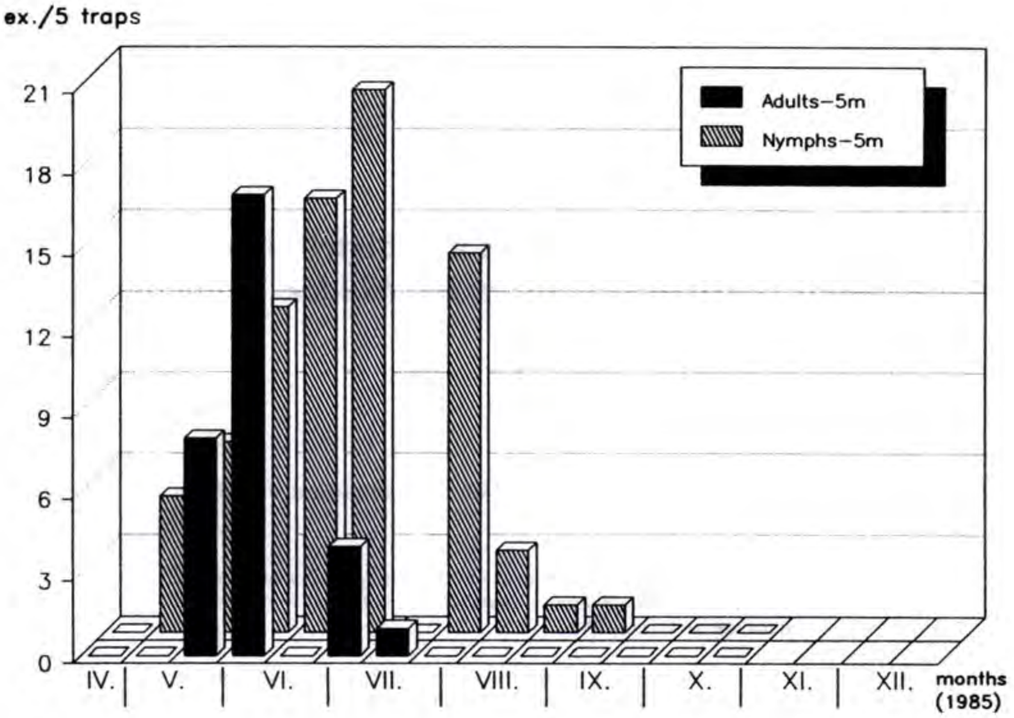

Fig. 1. Seasonal dynamics of migration of larval and adult cockroach *Ectobius sylvestris* on oak tree stems in 1985. The traps were placed in the height of about 5 m.

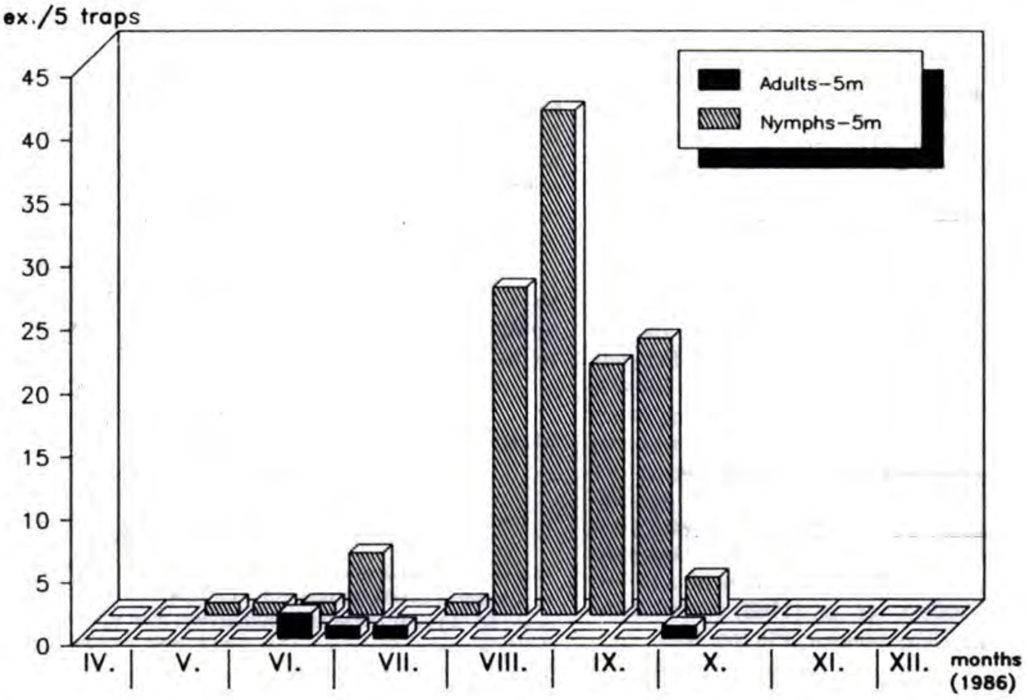

Fig. 2. Seasonal dynamics of migration of larval and adult cockroach *Ectobius sylvestris* on oak tree stems in 1986. The traps were placed in the height of about 5 m.

a variant with *Impatiens parviflora* into the association *Poa nemoralis – Quercetum dalechampii* (MAJZLAN,1986).

2. Sampling design and methods

Cockroaches were collected by means of tree stem traps described by FUNKE (1971) and modified by VIDLIČKA (1989). The function of the traps is based on the principle of positive phototaxis, negative geotropism and silhouette orientation of insects. Insects were entrapping to the trap automatically and continuously. The traps were placed on the stems of oak trees, *Quercus dalechampi.*

The investigations were performed during 1985 and 1986. In 1985 five traps were installed on the trunks, placed in the height of 4.20 – 5.20 m. In 1986 we used the same five traps as in 1985 plus an additional sixth one placed in the height of 0.75 m.

Traps were operating continuously from April to October 1985 and from April to December 1986. The traps were emptied in regular 2-week intervals, 14 catches in 1985 and 18 catches in 1986. The insects collected in the traps were killed and fixed in a mixture of 9 mmol^{-1} picric acid and 68 mmol^{-1} nitric acid and stored in 75 % ethanol.

Material of cockroaches was collected within the framework solution of the research work VI–4–2/10 at Department of Zoology.

Results and disccussion

1. Seasonal dynamics of migration

Our observations in 1985 and 1986 showed that the larvae of *Ectobius sylvestris* migrated on oak tree stems from the beginning of May to the middle of September (Fig. 1) and from the middle of May to the biginning of October (Fig. 2), respectively. We recorded the maximum of upward migration of larvae in the end of June and in the beginning of August 1985 and in the end of August 1986. In June 1986 the increase of migration was less expressive than in 1985. MORVAN (1972) observed larval occurrence in natural habitat from the middle of March to November.It is interresting that we did not record the migration of larvae in October and November. According to MORVAN (1972) 3rd and 4th instar larvae were abundant in the nature in these months. This may have resulted from unsuitable microclimatic conditions and from the shortage of food on tree stems in these months. PATOČKA et al. (1962) found out that cockroaches found their food in tops of trees.

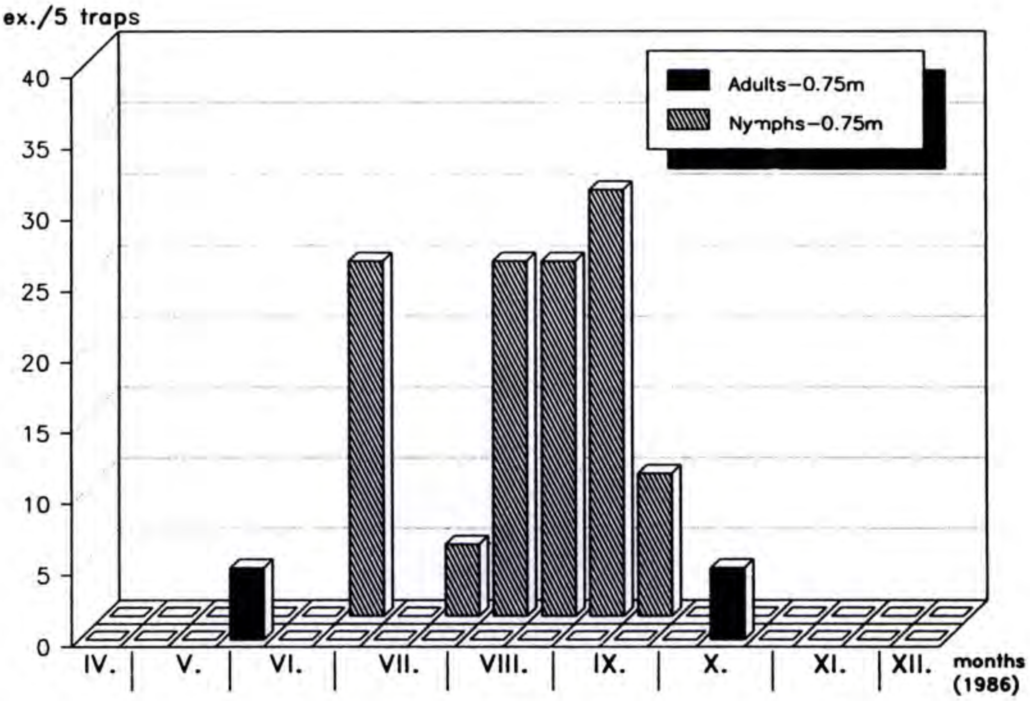

Fig. 3. Seasonal dynamics of migration of larval and adult cockroach *Ectobius sylvestris* on oak tree stems in 1986. The trap was placed in the height 0.75 m.

We recorded the adult cockroaches migration from the middle of May to the middle of July (males and females) and in October (only females). In May and June 1985 the migration of adults was very high. All these data suggest that the dynamics of migration is evidently connected with the dynamics of occurrence, microclimatic conditions and presence/absence of food.

2. Vertical distribution

We found out the first time that larval stages and brachypterous females of the cockroach *Ectobius sylvestris* migrate on the stems into the tops of trees. In both years we observed a much higher migration of apterous larvae (1985–63 %, 1986–95 %) than that of brachypterous females and winged males.

We have not found differences between migration up to the height 0.75 m and up to the height of 5 m (per 1 trap) (fig. 2,3). It is evident that apterous larvae, adult females and partly males use the stems of trees to migrate into the tree tops. This data differ from data about brachypterous females of *Parcoblatta* (Gorton, 1980). Males of this genus are good fliers and are active in tree tops and bushes, however most brachypterous females remain on or near the ground.

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Príloha č. 4

VIDLIČKA, Ľ. 1993.
Phyllodromica hungarica sp.nov., a new cockroach species from Hungary
(Insecta: Blattodea: Blattellidae: Ectobiinae).
Entomological Problems 24(1): 63-68.

Phyllodromica hungarica sp.nov., a new cockroach species from Hungary (Insecta: Blattodea: Blattellidae: Ectobiinae)

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Abstract: Phyllodromica hungarica sp. nov., a new cockroach species from Hungary (Insecta: Blattodea:Blattellidae: Ectobiinae). *Entomol. Probl.*, 24(1):63 - 68, Bratislava, 1993. ISSN 0071-0792.

A new cockroach species, *Phyllodromica hungarica* **sp. nov.** (Blattellidae) is described. It has been found only on the territory of northern Hungary (Bükk mountains).

Key words: cockroach, *Phyllodromica*, Hungary, systematics, taxonomy.

Introduction

The genus *Phyllodromica* FIEBER covers about 80 species which are distributed in Europe (about 40 species), West Asia, North Africa, the Azores, the Canary Islands and Madeira (HARZ, 1976).

Studying the material of cockroaches from Hungary deposited in the Zoological Department of the Hungarian Natural History Museum in Budapest (HNHMB) some males and females of a new *Phyllodromica* species were found and described.

This new species is distributed practically on the same zoogeographical area as *Phyllodromica harzi* CHLÁDEK, 1977 and *Phyllodromica maculata marani* CHLÁDEK, HARZ, 1980, which were described from SE-Slovakia.

Description of the species

Phyllodromica hungarica sp. nov.

(Figs. 1-11,14,15)

Material examined: **Holotype:** Male, Hungary: Bükk National Park, Szarvaskö, Tardos-hegy* - 350m above sea-level, 25.IX.1981, Ádám, HNHMB.
Paratypes: 5f, Bükk N.P., Szarvaskö, Tardos-hegy* - 350m above sea - level, 25.IX.1981, Ádám, HNHMB; 1f, Hungary: Bükk National Park, Szilvásvárad, Bacsó-völgy*, 4.VI.1986, Steinmann, H., HNHMB; 1m, Hungary: Bükk N.P., Felsötarkany, Lök-völgy*, 6.VI.1984, Steinmann, H., HNHMB.

hegy = mountain; völgy = valley

Description: **Male**: Head (Fig.1) with few setae, interocular width larger than the ocular width (IW/OW index = 1.7-1.8). [The interocular width (IW) and ocular width (OW) were measured at the top of the head.] Pronotum with short, thin setae, widest near the hind margin (Fig.2). Front femur Type B (Princis, 1965); tarsal claws asymmetrical, arolia well developed. Tegmina (Fig.3), fully developed but reaching only the end of the seventh abdominal tergum; veins reduced but radial vein distinct. Hind wings (Fig.4) strongly reduced, distal ends bent to the middle at a 135° angle. Seventh abdominal tergum strongly modified, separated into two lobes which are directed towards each other. Glandular pit of tergum 7 (Fig. 11) is hollowed beyond the margins of the opening. The hollows form a large, bilobed pouch. The footprint-like lobes are joined in the middle with a narrow strip. The anterior parts of lobes are evidently wider than the posterior parts. Unlike the species of the *beatica* group of *Phyllodromica*, the pouch of *Ph. hungarica* **sp. nov.** lacks bristles (BOHN, 1992). Subgenital plate asymmetrical (Fig. 9). A single short stylus with few erect bristles is present only on the left side. Endophallic apodeme (L2vm) at the anterior end broadened. Near the posterior end of the endophallic apodeme there is the 'helmet sclerite' covered with small scales which was also found in the species of the *sylvestris* group of *Ectobius* STEPHENS (BOHN, 1989). Extensible and retractable hook (left phallomere; L3 of MCKITTRICK, 1964; Fig. 10) on the left side. Cleft sclerite (R2) and small R3 apodeme on the right side. Cerci composed of 9 segments, ventral side thin and dorsal side thick pubescent.

Coloration. Head black or dark brown except for pale labrum. Antennae with dark brown pedicel, the remaining segments pale. Disk of pronotum broad, in the front angularly rounded, brown, sharply set off from the transparent lateral and anterior borders. Tegmina brownish-black with yellowish spots (Fig.3). Abdominal terga dark brown, sterna entirely black. Legs brown with yellow bristles.

Measurements (mm). Body lenght 6.2 - 8.7; pronotum lenght x width 2.3 x 3.5; tegmina lenght x width 6.0 x 2.5; wing lenght 1.7.

Female. Head with few setae, interocular width greater than ocular width (IW/OW index = 1.6-1.7). Pronotum as in male. Tegmina (Fig.5) shortened, slightly apically truncated. Hind wings (Fig.6) reduced, distal end straight or slightly bent to the middle. Genital structures as in figs. 14,15.

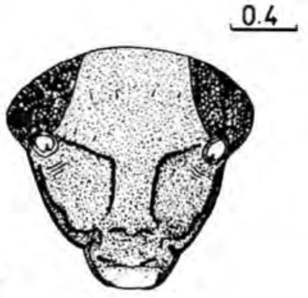
Coloration. Head dark brown except for the pale labrum and the lower part of the clypeus. Antennae pale brown. Pronotum translucent white, the disk of pronotum dark brown. Tegmina yellow with big black spots (Fig.5). Hind wings translucent, apex of wings dark. Abdominal terga and sterna black with white lateral and hind margins. Legs and bristles yellow.

Measurements (mm). Body lenght 5.7-8.4; pronotum lenght x width 2.3 x 3.5; tegmina lenght x width 3.3 x 2.4; wings lenght 1.6.

Etymology: Named after the country, where the type locality is situated.

Geografical distribution: This species is found in the northern part of Hungary.

Systematical remarks: Phyllodromica hungarica **sp. nov.** ranks among the species with the phallomeric "helmet sclerite" and one small stylus. Into this group belong *Phyllodromica carpentana* and relatives, *Ph. chopardi*, *Ph. llorentae*, *Ph. maculata*, *Ph. pallida* and relatives, *Ph. panteli*, *Ph. subaptera* and the Sylvestris Group of *Ectobius* (BOHN, 1989). It is possible to include here also *Ph. harzi* CHLÁDEK and *Ph. chladeki* HARZ.



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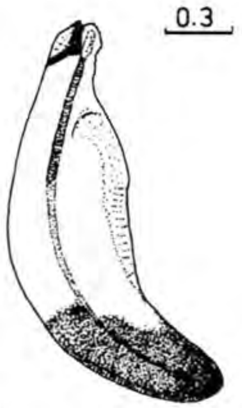

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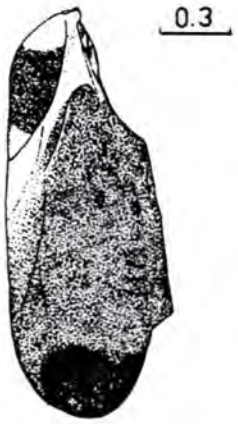

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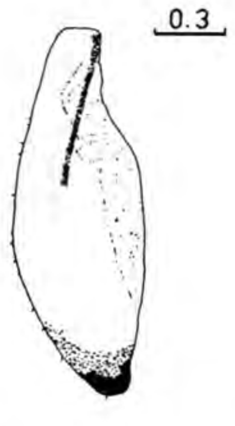

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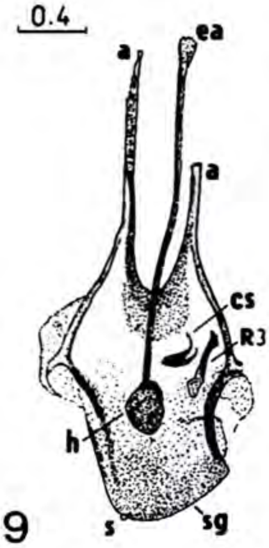
Figs. 1-4. *Phyllodromica hungarica* **sp. nov.** - male: (**1**) Head. (**2**) Pronotum. (**3**) Tegmina. (**4**) Hind wing.
Figs. 5-6. *Phyllodromica hungarica* **sp. nov.** - female: (**5**) Tegmina. (**6**) Hind wing.
Figs. 7-8. *Phyllodrimica maculata marani*: (**7**) Male hind wing. (**8**) Female hind wing. Scale in mm.



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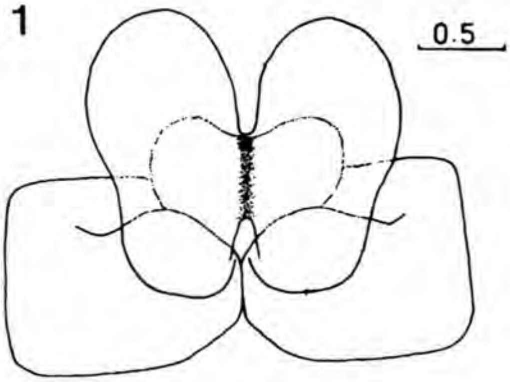

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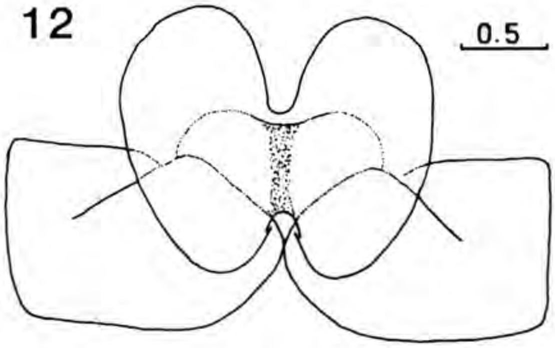

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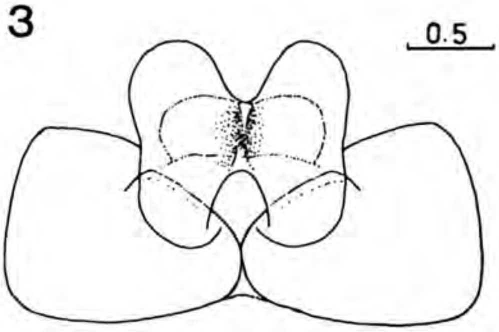
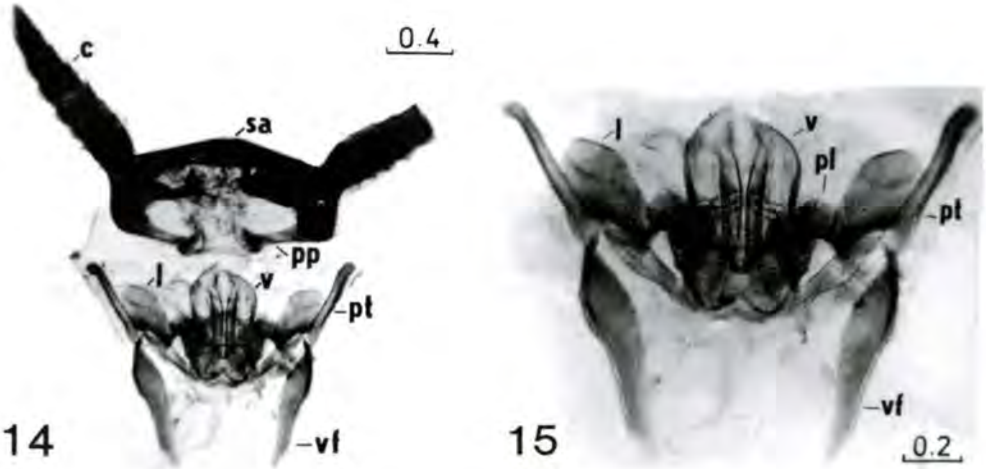


Figs. 9-10. *Phyllodromica hungarica* **sp. nov.** - male: (**9**) Subgenital plate (sg; dorsal view) with 2 anterior apophyses (a), endophallic apodeme of left phallomere (ea), helmet sclerite (h), cleft sclerite (cs), apodeme of right phallomere (R3; hook removed) and stylus (s). (**10**) Hook (posterior end).

Figs. 11-13. Male tergite 7 with gland: (**11**) *Ph. hungarica* **sp. nov.** (**12**) *Ph. maculata marani.* (**13**) *Ph. harzi.* Scale in mm.



Figs. 14-15. *Phyllodromica hungarica* **sp. nov.** - female: Genital structures of female. Dorsal complex - supraanal plate (sa), cerci (c), paraprocts (pp), paratergites (pt), valves (v), arm of first valvifer (vf), posterior lobes of valvifer II (pl), laterosternite (l). Scale in mm.

Taxonomical remarks and distinctive characteristics: The present new species is similar to *Ph. maculata marani* (CHLÁDEK & HARZ, 1980) and *Ph. harzi* (CHLÁDEK & HARZ, 1977). It can be distinguished from *Ph. maculata marani* especially by the form and coloration of the rudimentary hind wings (see figs. 4 and 7, 6 and 8) and by the form of the tergal gland (see figs. 11 and 12). *Ph. hungarica* **sp. nov.** differs from *Ph. harzi* by tegmina coloration (Figs. 3,4; see also CHLÁDEK & HARZ, 1977) and also by the form of the tergal gland (see figs. 11 and 13) and the hook.

Acknowledgements

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Súhrn: Phyllodromica hungarica sp. nov., nový druh švába z Maďarska (Insecta: Blattodea: Blattellidae: Ectobiinae).

V práci je popísaný nový druh švába, *Phyllodromica hungarica* **sp.nov.** z územia severného Maďarska. Druh bol popísaný na základe exemplárov uložených v Zoologickom oddelení Maďarského prírodovedného múzea v Budapešti.

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Príloha č. 5

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Phyllodromica transylvanica sp. nov., a new cockroach species from Romania and key of the *maculata*-group of *Phyllodromica* in central Europe (Blattaria: Blattellidae: Ectobiinae)

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Abstract. A new cockroach species from Romania, *Phyllodromica transylvanica*. **sp.nov.** (Blattellidae) belonging to the *maculata*-group of the *Phyllodromica*, is described. This group includes also some others species from central Europe, i.e. *Ph. maculata* (SCHREBER), *Ph. chladeki* HARZ, *Ph. harzi* CHLÁDEK and *Ph. hungarica* VIDLIČKA. A key to the *maculata*-group in central Europe is given.

Key words. Cockroach, *Phyllodromica*, Romania, systematic, taxonomy.

Introduction

BEY-BIENKO (1950) divided the species of the genus *Phyllodromica* into 4 subgenera and subgenus *Phyllodromica* into 5 groups (1. *marginata*, 2. *megerlei*, 3. *maculata*, 4. *brevipennis*, 5. *turanica*). He presented some characteristic features for the *maculata*-group: forewings of males fully developed; females with shortened forewings; the costo-radial area of forewings with distinct, more or less regular oblique veins; abdomen of the males strongly specialised; 6th abdominal tergite strongly depressed; 7th tergite elongated; anterior part of the 7th tergite with big angled elevation; furrow at the posterior part dividing the tergite into two lobes; hypandrium with extraordinarily small stylus.

BEY-BIENKO (1950) includes in this group apart from one central European species (*Ph. maculata* SCHREBER, 1781) 6 other species come from Crimea and Caucasus – *Ph. adusta* (FISCHER DE WALDHEIM, 1846), *Ph. polita* KRAUSS, 1888, *Ph. retowskii* (KRAUSS, 1888), *Ph. schelkovnikovi* BURR, 1913, *Ph. kiritschenkoi* BEY-BIENKO, 1948 and *Ph. euxina* BEY-BIENKO, 1950.

CHLÁDEK & HARZ (1977) described two other species (*Ph. harzi* CHLÁDEK, 1977 and *Ph. chladeki* HARZ, 1977) from Slovakia classified within the *maculata*-group. The species *Ph. hungarica* VIDLIČKA, 1993, which also belongs to this group, was found in north-eastern Hungary (VIDLIČKA, 1993). In this paper a representative of the *maculata*-group, *Ph. transylvanica* sp.nov. from Romania is described. Till now, the species found in Hungary and Romania have probably been confused with *Ph. maculata*.

CHLÁDEK & HARZ (1980) divided *Ph. maculata* into two subspecies – *Ph. maculata maculata* (SCHREBER, 1781) and *Ph. maculata marani* CHLÁDEK & HARZ, 1980. It is possible, however, that the species *Ph. maculata* included a complex of closely related species. In this paper a key to the identification of the central European species of the *maculata*-group is given.

Description of the species

Phyllodromica transylvanica sp. nov.

(Figs 1A–C, 3E–H, 5C–D)

Material examined. Holotype, ♂, Romania, Cluj, 1.7.1966, leg. B. Kis, (terminalia on slide, Hungarian Natural History Museum, Budapest, Hungary).

Paratype: ♀, Romania, Cluj, 1.7.1966, leg. B.Kis.

Description: Male: Head with few thin setae, interocular width larger than the ocular width (IW/OW index = 1.9–2.0). Pronotum with short, thin setae, widest near the hind margin. Front femur of type B (Bey-Bienko, 1950); tarsal claws weakly asymmetrical, arolia well developed. Forewings fully developed, distal end rounded, radial vein and veins in costo-radial area well developed (Fig. 3E). Hindwings strongly reduced, distal end pointed (Fig. 3F). Posterior part of 6th tergite in the centre strongly depressed (Figs 1A, B). Posterior border of 7th abdominal tergite with deep angular excision, anterior part connected with rounded rampart (Figs 1A, 5C) in the centre. Hollows of tergal gland form a large, bilobed pouch (Fig. 5D). Subgenital plate asymmetrical. Small hill-like stylus with a few erected bristles well developed on the left side of the subgenital plate. Right stylus strongly reduced (Fig. 1C). Endophallic apodeme (L2vm) broadened at the end. Helmet sclerite, cleft sclerite (R2) and R3 apodeme present on the right side, retractable hook (L3; Fig. 1D) on the left side. Cerci composed of 9 segments.

Colouration. Head dark brown or black except pale labrum. Antennae brown. Pronotum with broad, dark brown or black disk, lateral and anterior margins transparent. Forewings brown with yellowish anterior margin (Fig. 3E). Hindwings pale. Abdominal tergites dark brown, sternites black. Legs brown with yellow spines.

Size (mm). Body length 8; pronotum length × width 1.9 × 3.3; forewing length × width 6 × 2.25; hindwing length 1.5.

Female. Head with few setae, interocular width larger than ocular width (IW\OW index = 1.8–1.9). Pronotum as in male. Forewings (Fig. 3G) shortened, not reaching the end of the 3rd tergite. Hindwings reduced, narrow, pointed (Fig. 3H). Front femur of type B.

Colouration. Head dark brown except pale labrum. Antennae yellowish brown to brown. Disk of pronotum dark brown, margins of the pronotum white, translucent. Legs yellowish brown to brown. Forewings yellow with large dark spot. Hindwings pale. Abdominal tergites and sternites dark with white lateral and hind margins.

Size (mm). Body length 5.8–8.2; pronotum length × width 1.9 × 3.6; forewings length × width 3.2 × 2.4; hindwings length 1.5.

Etymology. Named after the part of Romania where the new species has been found.

Geographical distribution. Found only in the surroundings of Cluj in Romania.

Systematical remarks. The *maculata*-group is best characterised by the morphology of tergal gland and bilobed pouch of the male (Figs 4, 5). The shape of the tergal gland and the bilobed pouch is very similar in *Ph. maculata maculata*, *Ph. maculata marani* and *Ph. hungarica*. The structure of the tergal gland of *Ph. chladeki* and *Ph. transylvanica* is somewhat different. In these species the 7th tergite is not fully divided into two lobes. The anterior parts of the tergite 7 remain connected. *Ph. harzi* is a transition between the two groups – 7th tergite is divided into two lobes, but in the anterior and posterior parts there is a connection between the lobes.

Key for the identification of males of the central European species of the *maculata* – group

1. Apex of the hindwings clearly bent to the middle (Figs 2J, 3J) 2
– Hindwings more or less straight, the apex not bent 3

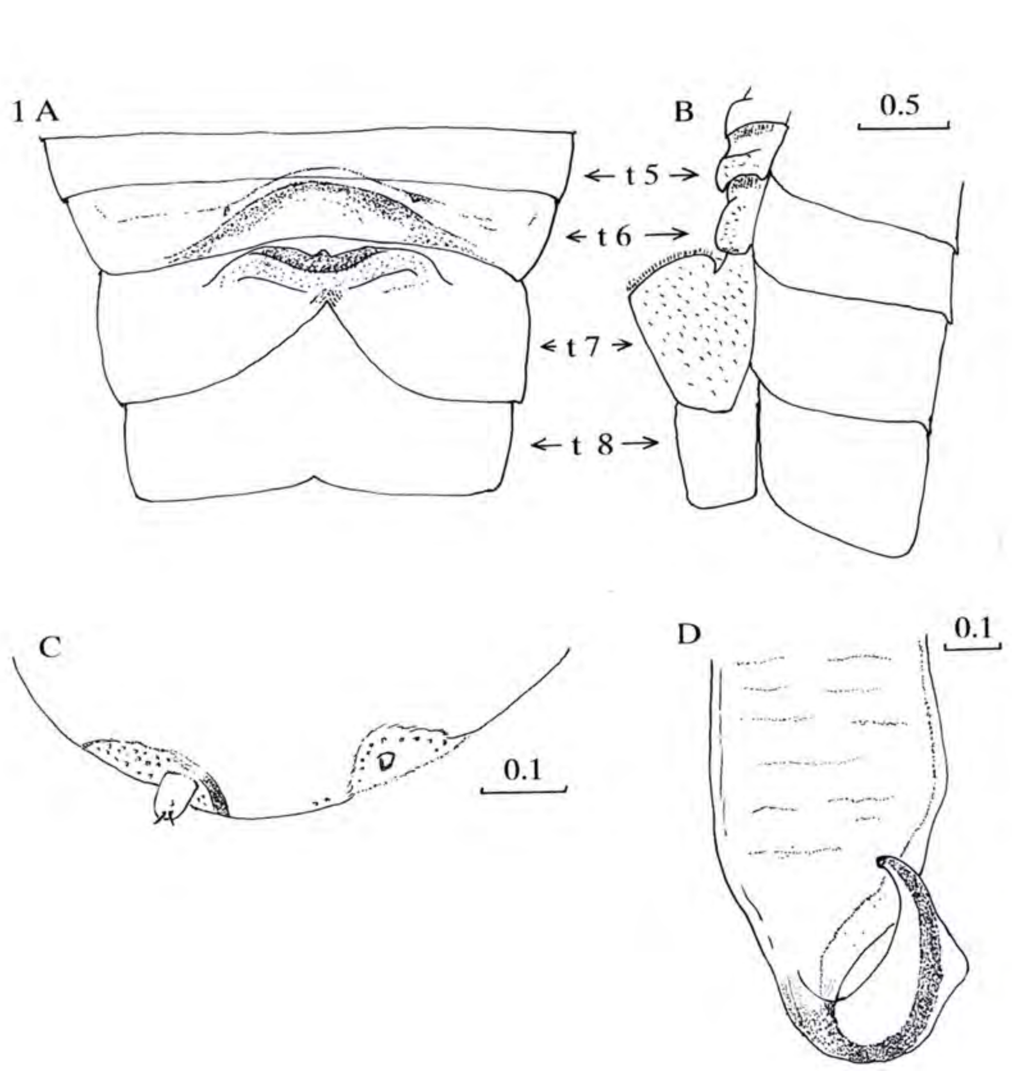

Fig. 1. *Ph. transylvanica*, male. (A, B) abdomen with gland opening, (A) dorsal view, (B) ventral view, (t5–t8) tergites 5–8; (C) subgenital plate with stylus (s); (D) hook – posterior end. Scale in mm.

2. Dark spot in the apical third of the forewings (Fig. 3I); hindwings suddenly narrow in the apical third, black only at the tip (Fig. 3J); tergal gland as in Figs 5E, F. Occurrence: Slovakia – Slovenský Kras mountains .... *Ph. harzi* Chládek, 1977
– Dark spot nearly extending over the whole length of the forewings (Fig. 2I); hindwings not suddenly narrowed, apical third dark (Fig. 2J); tergal gland as in Figs 4E, F. Occurrence: Hungary – Bükk mountains and surroundings .... *Ph. hungarica* Vidlička, 1993
3. Tergite 7 in the middle of the anterior border not divided into two lobes 4
– Tergite 7 separated into two lobes 5
4. Narrow dark spot, at most slightly surpassing the apical half of the forewings (Fig. 3A), forewings tricoloured (yellow-brown-black); the hindwings almost entirely dark (Fig. 3B); tergal gland as in Figs 5A, B. Occurrence: Slovakia – Muránska planina plateau .... *Ph. chladeki* Harz, 1977

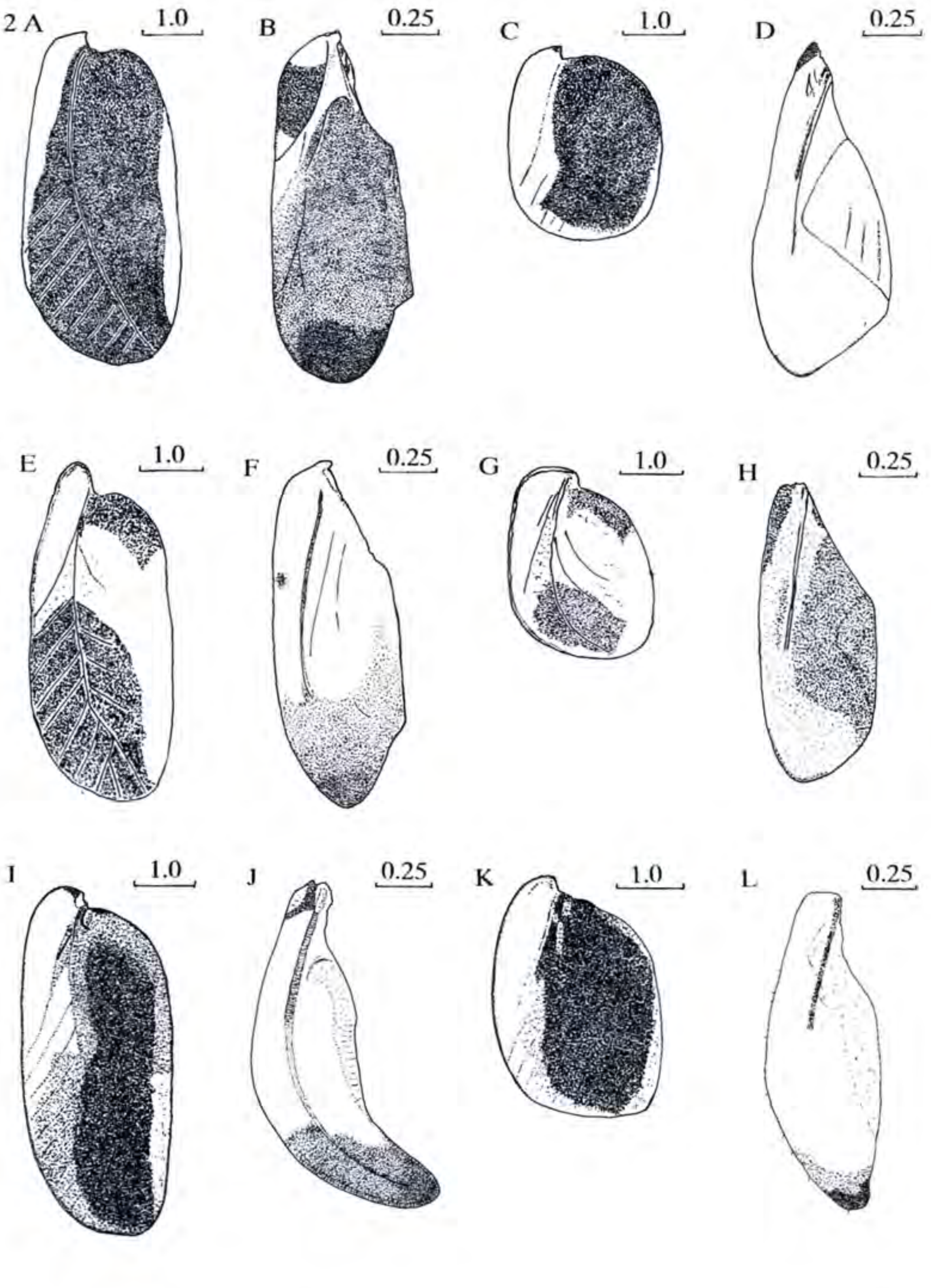

Fig. 2. Forewings (A, C, E, G, I, K) and hindwings (B, D, F, H, J, L) of the *Phyllodromica* species. (A–D) *Ph. maculata marani*, (A, B) male, (C, D) female; (E–H) *Ph. maculata maculata*, (E, F) male, (G, H) female; (I–L) *Ph. hungarica*, (I, J) male, (K, L) female. Scale in mm.

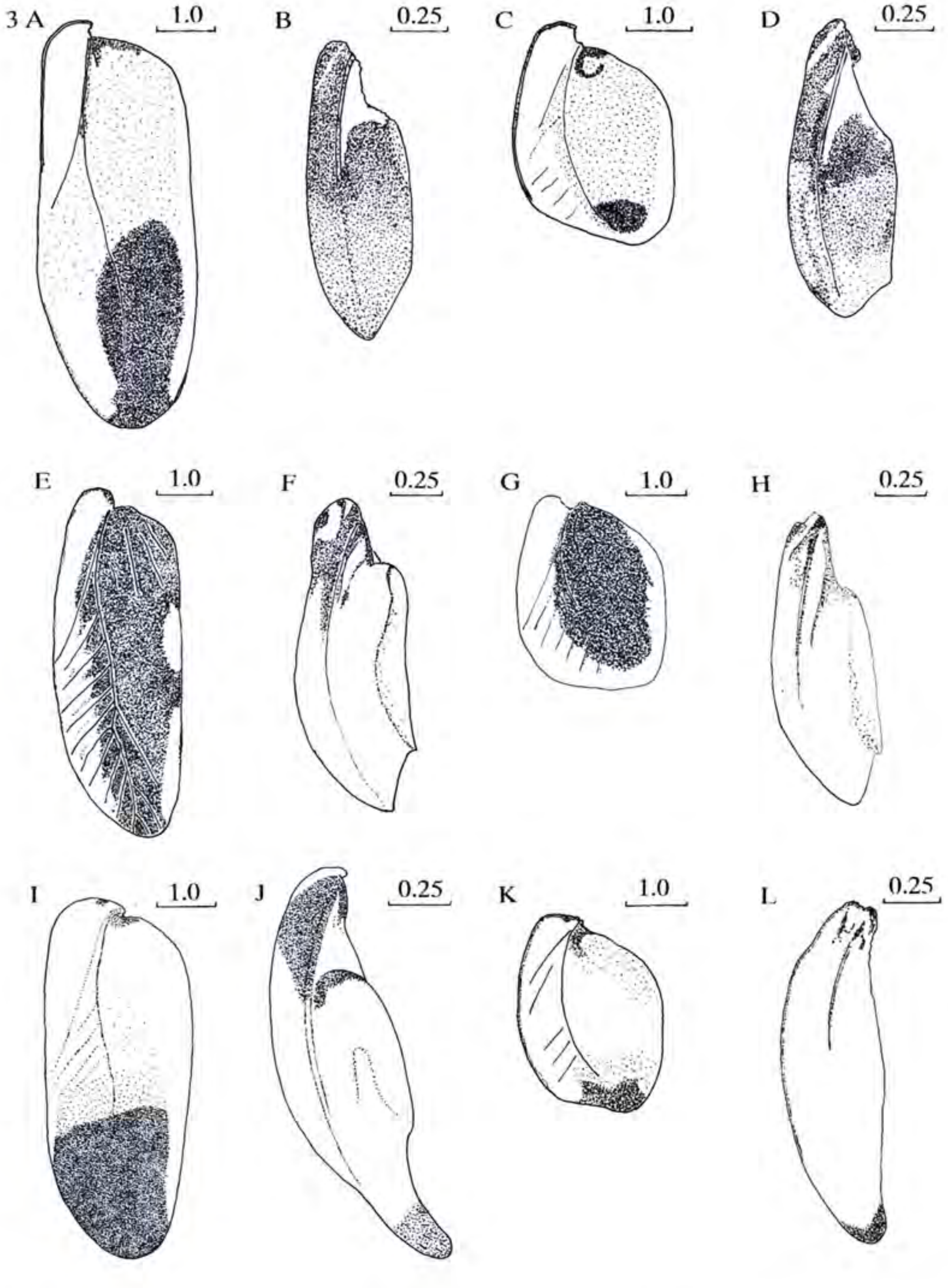

Fig. 3. Forewings (A, C, E, G, I, K) and hindwings (B, D, F, H, J, L) of the *Phyllodromica* species. (A–D) *Ph. chladeki*, (A, B) male, (C, D) female; (E–H) *Ph. transylvanica*, (E, F) mele, (G, H) female; (I–L) *Ph. harzi*, (I, J) male, (K, L) female. Scale in mm.

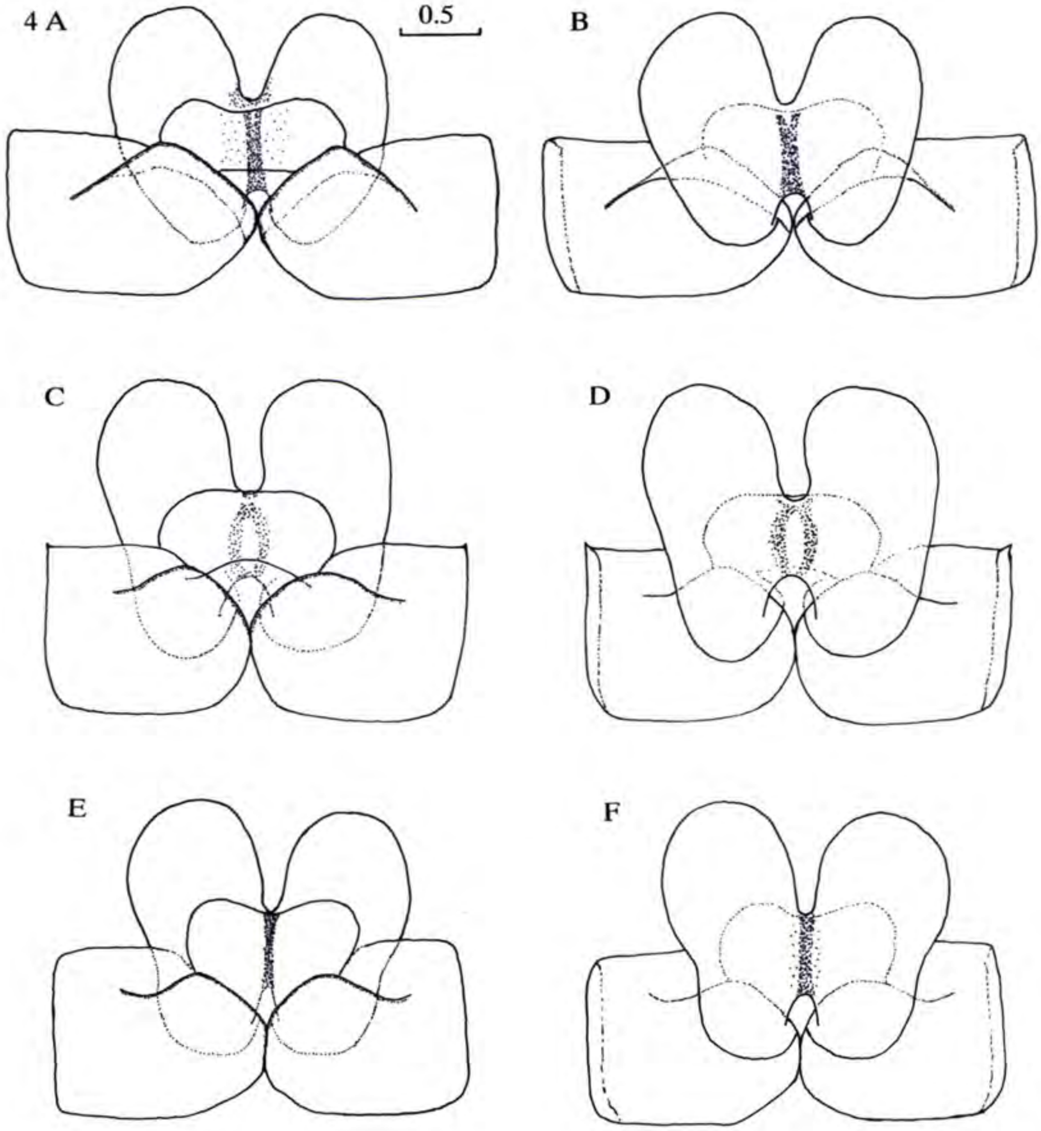

Fig. 4. Tergites 7 of males with tergal glands. (A, C, E) dorsal view, (B, D, F) ventral view; (A, B) *Ph. maculata marani*; (C, D) *Ph. maculata maculata*; (E, F) *Ph. hungarica*. Same scale (in mm) for (A–F).

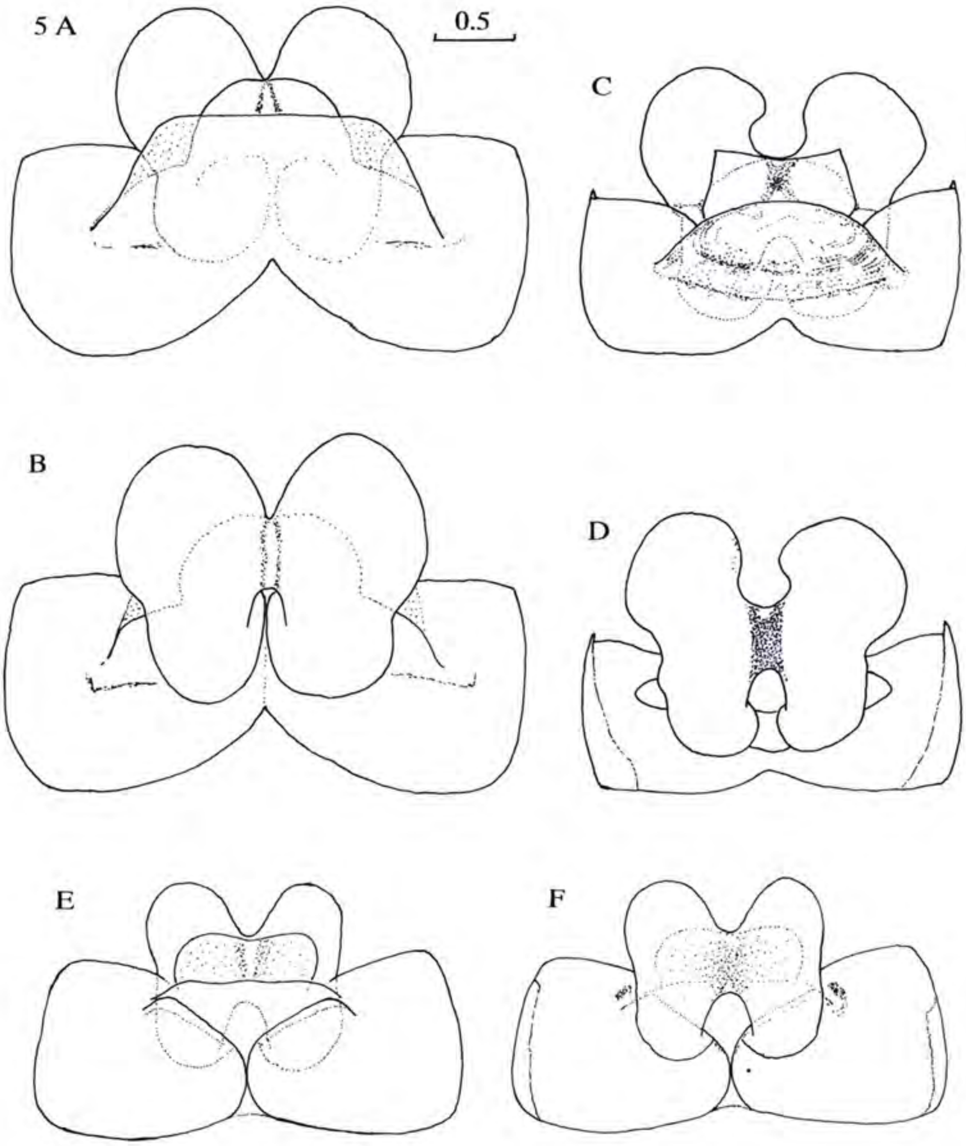

Fig. 5. Tergites 7 of males with tergal glands. (A, C, E) dorsal view, (B, D, F) ventral view; (A, B) *Ph. chladeki*; (C, D) *Ph. transylvanica*; (E, F) *Ph. harzi*. Scale same (in mm) for (A–F).

– Dark spot as long as the forewings (Fig. 3E); the hindwings almost entirely pale, transparent (Fig. 3F); tergal gland at the posterior border of the opening with bent rampart (Figs 5C, D). Occurrence: Romania – Transylvania .... *Ph. transylvanica* sp. nov.

5\. Forewings black with narrow whitish lateromarginal bands (Fig. 2A); hindwings dark with widely rounded apex (Fig. 2B); tergal gland as in Figs 4A, B. Occurrence: middle and eastern Slovakia, north-eastern Hungary, Poland .... *Ph. maculata marani* CHLÁDEK & HARZ, 1980

– Pale forewings with two clearly separated dark spots (Fig. 2E)(light-coloured individuals with inconspicuous spots); hindwings only in the apical third dark, apex narrowly rounded (Fig. 2F); tergal gland as in Figs 4C, D. Occurrence: western Slovakia, Austria, north-western Hungary, Bohemia, Germany, Poland, Romania .... *Ph. maculata maculata* (SCHREBER, 1781)

Key for the identification of females of the central European species of the *maculata* – group

1\. Forewings with one large spot (Figs 2C, K, 3E) 2

– Forewings with 2 (exceptionally one) small spots 4

2\. Apex of the hindwings black, wings narrow (Fig. 2L); forewings as in Fig. 2K. Occurrence: Hungary – Bükk mountains and surroundings .... *Ph. hungarica* VIDLIČKA, 1993

– Apex of the hindwings without black spot 3

3\. Hindwings narrow, pointed (Fig. 3H); forewings subtruncate, dark spot less extended, yellow stripe along posterior and apical margin broader (Fig. 3G). Occurrence: Romania – Transylvania .... *Ph. transylvanica* **sp. nov.**

– Hindwings broad (Fig. 2D); forewings broadly rounded with a large dark spot leaving only a narrow yellow stripe along the posterior and apical margin (Fig. 2C). Occurrence: middle and eastern Slovakia, north-eastern Hungary, Poland .... *Ph. maculata marani* CHLÁDEK & HARZ, 1980

4\. Apex of the hindwings black (Fig. 3L), forewings with two small spots at the anterior and posterior end (Fig. 3K). Occurrence: Slovakia – Slovenský Kras mountains .... *Ph. harzi* CHLÁDEK, 1977

– Apex of hindwings not darker than remaining part 5

5\. Forewings obliquely truncated, tricoloured (Fig. 3C); hindwings with pale spots at the base (Fig. 3D). Occurrence: Slovakia – Muránska planina plateau .... *Ph. chladeki* HARZ, 1977

– Forewings obliquely rounded with 2 larger or smaller spots (light-coloured individuals sometimes wholly without spots) (Fig. 2G); hindwings without pale spots at the base (Fig. 2H). Occurrence: western Slovakia, north-western Hungary, Austria, Bohemia, Germany, Poland, Romania .... *Ph. maculata maculata* (SCHREBER, 1781)

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VIDLIČKA, Ľ, 1993: Phyllodromica hungarica sp. nov., a new cockroach species from Hungary (Insecta: Blattodea: Blattellidae: Ectobiinae). *Entomol. Probl*., 24(1): 63–68.

Manuscript received: 28. 9. 1994

Príloha č. 6

VIDLIČKA, Ľ., MAJZLAN, O. 1997.
Revision of the megerlei - group of the cockroach genus Phyllodromica Fieber
(Blattaria: Blattellidae, Ectobiinae).
Entomologica Scandinavica 28: 163-173.

Revision of the *megerlei*-group of the cockroach genus *Phyllodromica* Fieber (Blattaria: Blattellidae, Ectobiinae)

L'UBOMÍR VIDLIČKA and OTO MAJZLAN

Ent. scand.

Vidlička, L'. & Majzlan, O.: Revision of the *megerlei*-group of the cockroach genus *Phyllodromica* Fieber (Blattaria: Blattellidae, Ectobiinae). *Ent. scand.* 28: 163-173. Copenhagen, Denmark. August 1997. ISSN 0013-8711.

The species of the *megerlei*-group are characterised by shortened wings with typical scattered dark spots and large simple glands on tergite 7 without inner structures. Two of the species are widely distributed from south-eastern Germany to Romania and Ukraine (*P. megerlei* Fieber) or from Turkey to Syria (*P. asiatica* Bey-Bienko), the third is endemic for eastern Bulgaria (*P. pulcherrima* sp. n.). The characteristics of the *megerlei*-group are described and the relationships with the *tyrrhenica*-group are discussed.

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Introduction

Phyllodromica megerlei (Fieber, 1853) was originally described by Charpentier (1825) as *Blatta punctata.* Since Eschsholz (1822) applied same name to another cockroach species (now *Diploptera punctata*) Charpentier's name is a homonym and the name suggested by Fieber is commonly used at the present time. Princis (1971) discerned five subgenera within the genus *Phyllodromica*. *P. megerlei* is the type species of the genus *Phyllodromica* and the subgenus *Phyllodromica.* Bey-Bienko (1950) divided the subgenus *Phyllodromica* into 5 groups. The *megerlei* group included only one species – *P. megerlei.* The second one was described by Bey-Bienko (1950) as a subspecies *P. megerlei asiatica.* Ramme (1951) described the same species as *P. megerlei* f. *erythronota.*

Collections made by the second author in Bulgaria have revealed one new species (*P. pulcherrima*) in this group.

Specimens used in this study are deposited in the following collections:

BN – Collection of Dr Barnabás Nagy, Budapest, Hungary.
L'V – Collection of first author.
HNHM – Magyar Természettudományi Múzeum, Budapest, Hungary; Dr György Sziráky.
MMG – Mátra Múzeum, Gyöngyös, Hungary; Dr Tibor Kovács.
MNB – Museum für Naturkunde, Berlin, Germany; Dr Kurt K. Günther.
NMP – Národní muzeum v Praze, Prague, Bohemia; Dr Ivo Kovář.
NMW – Naturhistorisches Museum zu Wien, Vienna, Austria; Dr Ulrike Aspöck.
OM – Collection of second author.
PFUK – Prírodovedecká fakulta Univerzity Komenského, Bratislava, Slovakia; coll. Dr Ján Gulička.
SNMB – Slovenské národné múzeum – Prírodovedné múzeum, Bratislava, Slovakia; Dr Ilja Okáli.
SSMB – Stredoslovenské múzeum, Banská Bystrica, Slovakia; Dr Tomáš Kizek.

Characteristics of the *megerlei*-group

Bey-Bienko (1950) was the first to attempt a classification of *Phyllodromica* species living in the former Soviet Union and adjacent territories. His classification is based on differences in the degree of tegminal development, on different venation and on the structure of the male tergal gland. The last character is most important also for the division of the closely related genus *Ectobius* into various groups (Failla & Messina 1978).

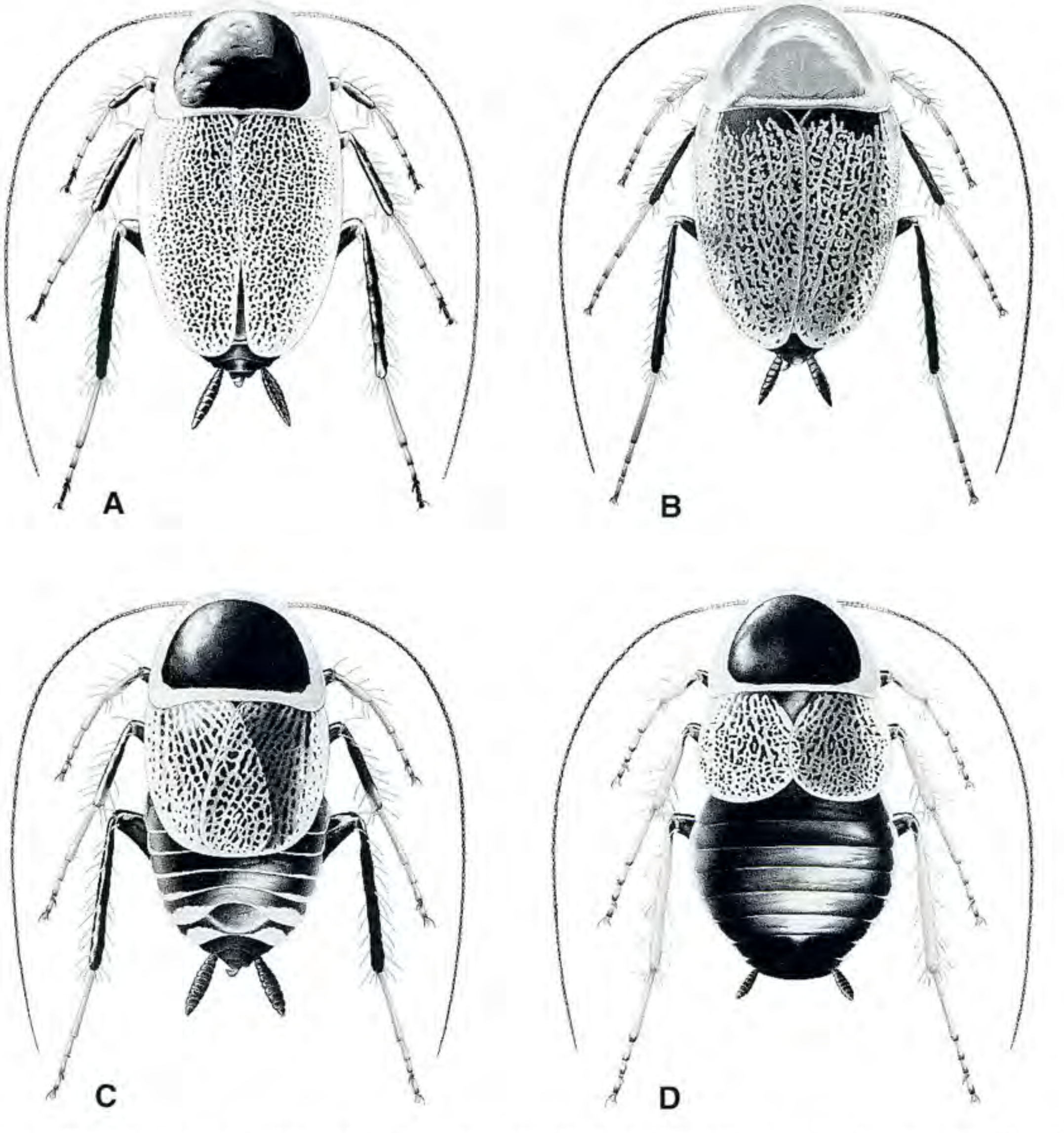

Plate 1. *Phyllodromica* spp., habitus: (A) *P. megerlei*, male; (B) *P. asiatica,* male; (C) *P. pulcherrima*, male; (D) *P. pulcherrima*, female (orig. P. Kuliffay).

Description. – Wings: Forewings in males reaching to the middle of the fourth abdominal tergite or at most to the end of abdomen, in females more strongly shortened, reaching to the second abdominal tergite, with typical irregular net venation, the costo-radial area without oblique veins; hindwings rudimentary. Coloration: Whitish to transparent with different small black or brown spots, subcostal area sparsely or not at all spotted. Legs: Front femur Type B_2; pulvilli present on the 1-4 proximal tarsomeres of all legs, tarsal claws asymmetrical (the posterior claw is longer than the anterior), arolia well developed.

Males. Tergite structures: Posterior margin of sixth abdominal tergite medially deeply excavated, elevated dorso-medially, in its normal position overlapping part of the glandular pit. The glandular pit on tergite 7 simple, transversely oval, inner structures absent. Surface of the pit with sparsely dispersed long bristles with curved tips, the bristles in the center are more densely distributed. Genitalia: Visible part of subgenital plate slightly asymmetrical, broadly triangular, apex rounded, with a single style located to the left of the midline. Stylus well developed, relatively large. The end of the stylus curved and covered with dense short microtrichae (Figs 1G, 3J, 4E). Right stylus only indicated. Retractable hook (L3) slender (Figs 1H, 3K, 4D), endophallic apodeme at the anterior end broadened, cleft sclerite (R2) present.

Females. Genitalia (Fig. 3L): The valves narrow, bent; posterior lobes of valvifer conical with tip on the posterior end; paratergites short. Coloration: The pronotum with yellowish white to transparent borders and with black disk. Sternites black or with narrow whitish lateral borders, tergites black with narrow light posterior borders. On the lateral margins of tergites 5-7 bigger whitish spots. Legs in male brown to black with yellow regions at the coxa-trochanter joint and at the tarsi, tibial spines and sometimes posterior end of tibia yellow. Legs in female brown to yellow, tibial spines yellow.

Systematic relationships

The *megerlei*-group is very closely related to the *tyrrhenica*-group (*P. tyrrhenica, P. clavata, P. pavani*). Similar characters are: the simple form of the glandular pit; a well developed stylus on the left side with dense short bristles, and the coloration of the forewings. The distinguishing character is the venation of the costo-radial area: in the *megerlei*-group oblique veins are absent. The floor of the glandular pit is covered only with a small number of bristles and the absence of other structures in the glandular pit in both *megerlei*- and *tyrrhenica*-groups suggest their partial separation from the remaining groups of the subgenus *Phyllodromica*.

Key to males of the *megerlei*-group

1. Forewings strongly reduced, reaching at most to the middle of the fourth abdominal tergite .... *P. pulcherrima* sp. n.
– Forewings reaching to the end of abdomen 2
2. Disk of the pronotum black; sixth tergite with small, elongated whitish to transparent spots on the posterior lateral margins .. *P. megerlei* Fieber
– Disk of the pronotum orange-yellow (central part) to yellowish (posterior part and corners); sixth tergite dark, without whitish to transparent spots on the posterior lateral margins .... *P. asiatica* Bey-Bienko

1. ***Phyllodromica megerlei*** (Fieber, 1853)

(Plate 1: A; Figs 1A-H, 2, 4G, 5)

Blatta punctata Charpentier, 1825: 77 (nec Eschscholtz, 1822).
Blatta (Phyllodromica) megerlei Fieber, 1853: 94.
Aphlebia punctata (Charpentier): Brunner v. W. 1865: 71; 1882: 41; Jakobson & Bianki 1905: 126.
Hololampra megerlei (Fieber): Bazyluk 1956: 28.
Phyllodromica megerlei Fieber: Rehn 1903: 266; Bey-Bienko 1938: 26; 1950: 232; Princis 1971: 1094; Harz 1976: 276; Bazyluk 1977: 103.
Hololampra punctata (Charpentier): Kirby 1904: 69; Shelford 1907: 11; Harz 1957: 34; 1960: 17.
Phyllodromica punctata (Charpentier): Us & Matvejev 1967: 8.

Type material. – Missing.

Material studied. – SLOVAKIA: Bučany, 150 m, 1 ♂, 22.v.1994, L'. Vidlička (L'V); Piešt'any, 160 m, 2 ♂, 2 ♀, 16.v.1992, L'.Vidlička (L'V); Nová Bošáca, 350 m, 1 ♂, 1 ♀, 30.v.1993, O. Majzlan (L'V); Jakubov, 140 m, 1 ♂, 22.iv.1994, L'. Vidlička (L'V); Horné Plachtince, 1 ♀, 30.v.1990, O. Majzlan (OM); Modrý Kameň, 1 ♀, 13.vi.1990, Bitušík (SSMB); Plavecké Podhradie, 190 m, 1 ♀, 15.v.1959, I. Löbl (SNMB), 1 ♂, 23.v.1994, L'. Vidlička (L'V); Devín, Mt. Devínska Kobyla, 250 m, 2 ♂, 24.iv.1994, L'. Vidlička (L'V); Bratislava, Vlčie hrdlo, 130 m, 1 ♂, 16.v.1992, O. Majzlan (OM); Bratislava, 1 ♂, 14.vi.1992, O. Majzlan (OM); Ivanka pri Dunaji, 130 m, 1 ♂, 18.v.1992, L'. Vidlička, 1 ♀, 30.vi.1992, K. Šmidáková, 3 ♀, 19.v.1993, 1 ♀, 21.v.1993, L'.Vidlička (L'V); Kalinkovo, 130 m, 1 ♀, 11.vi.1975, I. Okáli (SNMB); Oremov Laz – Lešt', 1 ♀, 27.vi.1958, J.Gulička (PFUK); Malacky, 1 ♀, 15.vi.1958, J.Gulička (PFUK); Jur – Šúr, panónsky háj, 1 ♀, 8.ix.1957, J.Gulička (PFUK); Studienka, 5 ♂, 10 ♀, 10.vi.1996, L'. Vidlička (L'V); Vel'ké Leváre, 1 ♂, 10.vi.1996, L'.Vidlička (L'V); Tisovec, 1 ♀, 15.vi.1996, V. Janský (L'V); Záhorie, Rohožník, Obora, 1 ♀, 4.vi.1969, L.Pospíšilová (MMB); Čajkov, 1 ♀, 5.vi.1971, I.Okáli (SNMB); CZECH REPUBLIC (part MORAVIA): Pavlovské kopce, 1 ♀, 21.vii.1957, 10 ♂, 37 ♀, 25.vi.1962 (NMP); Pouzdřany, 1 ♂, 2 ♀, 26.vi.1962 (NMP); AUSTRIA: Mödling, 2 ♂, 2 ♀, H. Türk, 2 ♀, 1862 (NMW); Eichkogl bei Mödling, 1 ♂, 30.v.1909, 1 ♀, vii.1912, 1 ♀, 22.vii.1921, 2 ♀, 7.vi.1950, R. Ebner (NMW); Guntramsdorf, 1 ♀, R. Ebner (NMW); Gurhofgraben bei Aggsbach, Wachau, Holdhaus, 1 ♀, 30.v.1909 (NMW); Hackelsberg, Burgenland, 1 ♀, Koisi (NMW); Hermannskogel, 1 ♀, 28.vii.1907, Karny (NMW); Herzogenburg, 1 ♂, before 1930, L. Mader (NMW); Mauer, 2 ♂, 6 ♀, Brunner v. W., 1 ♂, 1870, Türk (NMW); Plank am Kamp, 1 ♀, vii.65, 1 ♀, 12.v.1948 (NMW); Purgstall, 1 ♀, 17.vii.1955, Sandbruch (NMW); Sulzer Berg bei Wien, 1 nymph, 25.v.1949 (NMW); surroundings Vorau, 1 ♂, before 1952, H. Franz (NMW); St. Veit bei Wien, 2 ♂, 4 ♀ (one with ootheca), Brunner v. W. (NMW); Wien, Weidling, 1 ♂, 1 ♀, before 1946, L. Mader (NMW); Wien, Lainzer Tiergarden, 500 m, 2 ♂, 1 ♀, 26.v.1951, 2 nymphs, 20.v.1950, 1 nymph, 4.x.1951, R. Ebner (NMW); Eichkogl, 1 ♀ with ootheca, 18.vi.1908 (MNB); Austria, Kat.-Nr.3724, coll. Schaum, 1 ♀ (MNB); HUNGARY: Nagybörzsöny, Hosszú-völgy, 1 ♀, 27-31.vii.1975, J. Jablonkay & A. Varga (MMG); Szokolya, Szénpatak-völgy., 300 m, 1 ♂, 3 ♀, 27.vi. 1965, B. Nagy (BN); Szokolya, Szénpatak-völgy, 300m, 1 ♀ (HNHM); Budapest, Csúcs-hegy, 1 ♀, 26.vi.1983, B. Nagy (BN); Cserépfalu, Alsó-Csakány, 1 ♀, 11.vi.1984, Merkl, Korsós (HNHM); Balatonszepezd, 150 m, 1 ♂, 24.v.1990, B. Nagy (BN); Pilisszentkereszt, Dobogokö, 680m, 1 ♀, 16.vii.1961, B. Nagy (BN); Hegyhátszentmárton, 1 ♀, 2.vii.1982, B. Nagy (BN); Hortobágy, Újszentmargita, 1 ♂, 9.iv.-8.v.1974, Kaszáb, 6 ♂, 4 ♀, 9.v.-11.vi.1974, Kaszáb (BN); Keszthely, Koponár-tetö, 1 ♀, 28.vi.1994, B. Nagy (BN); Körösujfalu, 1 ♀, 10.viii.1980, B. Nagy (BN); Köszeg, Alsó-erdö, 1 ♀, 13.vii.1937, Visnya (HNHM); Hortobágy, Ohati-erdö, 1 ♂, 3 ♀, 1 nymph, 15.v.1947, B. Nagy (BN); Tard, Bába-völgy, 1 ♀, 1.vi.1959, S. Tóth (HNHM); Háromhuta, István-kút, 1 ♀, 6-12.vi. 1955, Kaszab, Székessy (HNHM); Pomáz, 1 ♀, 2.vii. 1978, B.Nagy (BN); Szentendre, 2 ♀, 8.vii.1962, B. Nagy (BN); Újszentmargita, 3 ♂, 1 ♀, 26.v.1966, B. Nagy (BN); ROMANIA: Aiud, 1 ♀, 30.v.1909, 2 nymphs, 4.iii.1910, I. Nagy (HNHM), 2 ♀, 25.vi.1961, B. Kis (HNHM); Arcalia, 1♂, 1 ♀ with ootheca, 16.vi. 1976, B. Kis (HNHM); Baisoara, 1 ♀, 16.vii.1962, B. Kis (HNHM); Caraorman, 2 ♀, 27.vii.1967, B. Kis (HNHM); Cluj, Mt. Szaf, 1 ♀, 22.vi.1943, Kolosváry (HNHM); Cluj, Bácsie, 1 ♀, 22.vi.1943, Kolosváry (HNHM); Cluj, 1 ♀, 10.vii.1962, 2 ♀, 28.v.1964, 1 ♀, 10.vii.1969, 2 ♀, 5.vi.1977, B. Kis (HNHM); Cluj, Manastur, 1 ♂, 12.v.1963, B. Kis (HNHM); Ciurtuci, 1 ♀, 5.vii.1972, B. Kis, (HNHM); Giurcuta de Jos, 2 ♀, 4.vii.1972, 2 ♀, 8.vii.1972, B. Kis (HNHM); Deva, 3 ♂, 7 ♀, 25.v.1959, B. Kis (HNHM); Dezmir, 1 ♂, 1 ♀, 18.vi.1977, B. Kis (HNHM); Foeni, 1 ♀, 9.vii.1983, B. Kis (HNHM); Cheile Turzii, 1 ♂, 24.v.1964, B. Kis (HNHM); Mociu, 1 ♂, 1 ♀, 7.v.1976, B. Kis (HNHM); Mraconia, 2 ♂, 1 ♀, 12.vi.1968, B. Kis (HNHM); Tălagiu, 1 ♀; Transilvania, 1 ♂, 1 ♀, Pungar, 2 ♂, 1 ♀ (NMW); Heltau, 1 ♀, 15.vi.1924, A. Müller (MNB); Hammersdorf, 1♀, 10.v.1923, A. Müller (MNB); Reghin, 1♀, 23.vii.1917, A. Müller (MNB); UKRAINE: Cherson, 1♀, 10.v.1903, Ewert (MNB).

Literature records. – SLOVAKIA: Banská Štiavnica (Petricskó 1892); Streda nad Bodrogom (Chládek 1965); Vinné (Gulička 1967), Plešivecká planina (Chládek 1988); Muránska planina Mts: Tesná skala, Kľak (Čejchan 1992); Silická planina, Koniarska planina (Chládek 1994); CZECH REPUBLIC: Choťovice, Třemošnice, Pařížov (Čejchan, 1959); Havlíčkův Brod, Lednice, Želešice (Chládek 1965); HUNGARY: Budaihegység (Frivaldszky 1867); Sárospatak, Sátoraljaujhely, Budapest (Chyzer 1897, Pungur 1900); Köszegihegység (Pongrácz 1940); Egyek, Újszentmargita (Nagy 1983); ROMANIA: Oradea – Jud. Crişana (Frivaldszky 1867); Cluj, Zsul de Cîmcie, Baita, Marpod (Herman 1871); Băile 1 Mai (Mocsáry 1871); Nuşfalău, Zalău, Fetindia, Făgetul, Girceiu, Jac (Pungur 1891); Transilvania (Redtenbacher 1900); Babadag (Jaquet 1903); Marpod, Cluj, Zsul de Cîmpie, Baita, Zalău, Nuşfalău, Hunedoara, Reghin, Ocna Sibiului (Müller 1924); Zalău, Reghin, Nuşfalău, Sibiu, Clui (Knechtel & Popovici-Biznosanu 1959); AUSTRIA: Pitten (Handlirsch 1889); Kalksburg, Mauer, Mödling, Hainbach, Bruck a.d. Leitha (Redtenbacher 1900); Wien (Brunner v. W. 1885; Tümpel 1901); Neusiedler See (Ebner 1951); GERMANY*: SAXONY, BAVARIA: Regensburg (Ramme 1927; Harz 1957; Harz 1960); SWITZERLAND*: Saléve, Siders, Martigny (Fruhstorfer 1921; Harz 1957); MOLDAVIA: Chisinău-Kišinev, Baurci (Bey-Bienko 1938, 1950); UKRAINE: Kirovogradska oblast – Nerubajka (Bey-Bienko 1938, 1950); YUGOSLAVIA: Srem [Szerém] (Pungur 1900); CROATIA: Vinkovci [Nuštar] (Graber 1870); SLOVENIA, BOSNIA-HERCEGOVINA (Us & Matvejev 1967).

Description. – Size (mm): Body length: ♂ 5.8-6.5, ♀ 6.2-7.4; pronotum length x width, ♂ 1.9-2.1 x 3-3.2, ♀ 2.0-2.2 x 3.3-3.6; forewing length, ♂ 4-4.8, ♀ 2.5-3.2.

Male (Plate 1: A). Head with few short setae, interocular width larger than the ocular length (IW/OL index = 1.6). Pronotum semicircular (Fig. 1C), widest near the hind margin, surface sparsely setose. Forewings partly shortened (Fig. 1D), reaching at most to the end of abdomen, distal end narrowly rounded, veins in costo-radial area lost. Posterior margin of the tergite 6 strongly concave (Fig. 1E). Tergite 7 is divided by two longitudinal furrows into three parts, middle part covered by the tergal gland (Fig. 1F). Glandular pit large, trapezoid-oval, reaching to the posterior margin of tergite. Hind margin of supraanal plate rounded, right and left paraprocts are dissimilar, right paraproct is much broader than the left. Cerci long, with 8-9 segments, very often at least one abbreviated. Genitalia: The curved hook portion long, slender, pointed (Fig. 1H); cleft sclerite (R2) present on the right side. Coloration: Head black except for pale labrum, lower part of the clypeus and ocellar spots, proximal region of antennae yellowish (about 13 segments), distal part brownish to black. The maxillary palpomeres brown to black, labial palps brownish. Pronotum black except for narrow, yellowish, anterior and posterior borders and broad, yellowish to transparent, lateral margins. Forewings white to transparent with a great number of small spots, hindwings dark. Abdominal tergites black, sixth to eighth

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*The findings in Germany and Switzerland are very doubtful.

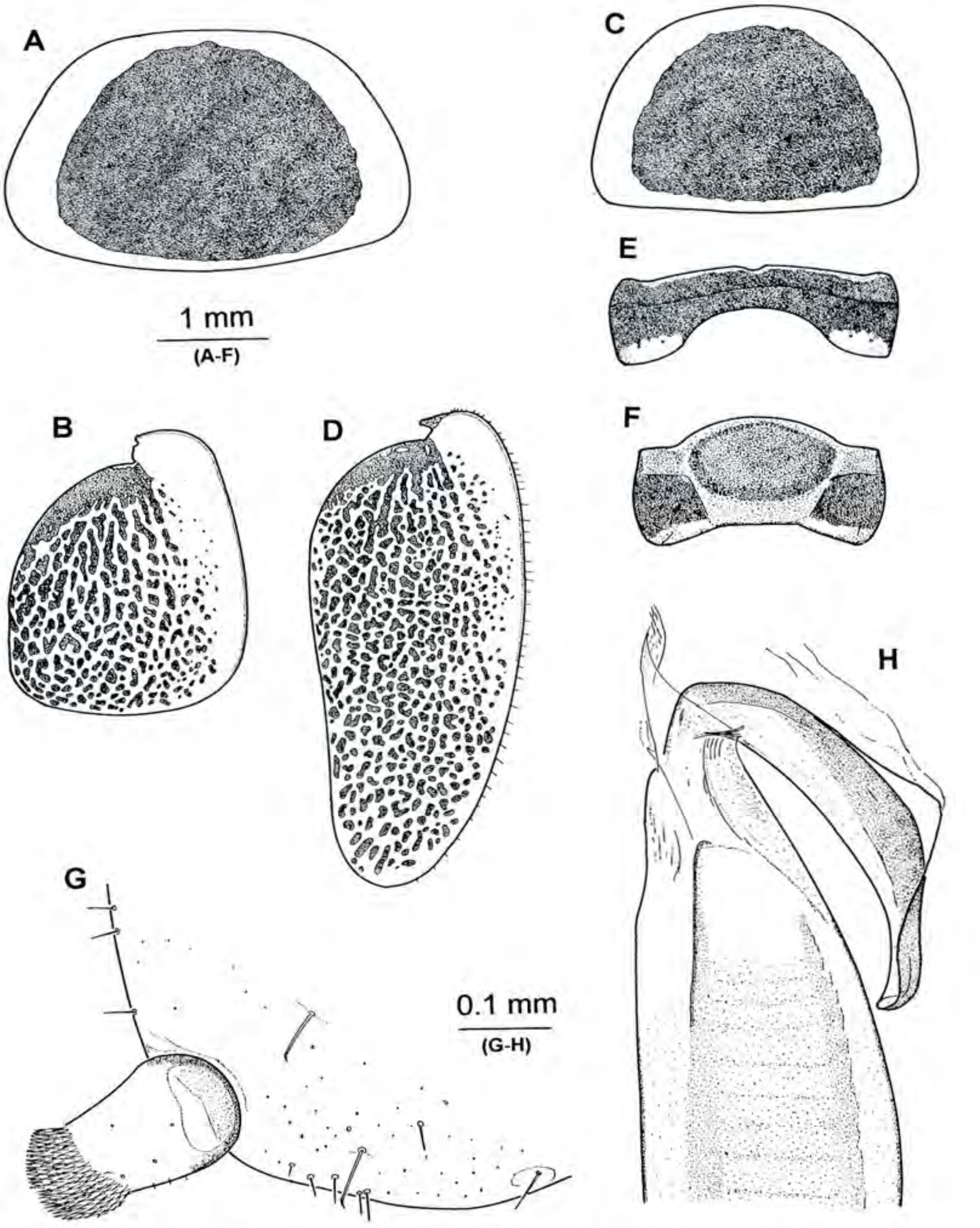

Fig. 1. *Phyllodromica megerlei*, (A-B) female, (C-H) male: Pronotum (A, C), right tegmen (B, D), tergite 6 (E), tergite 7 with glandular pit (F), part of subgenital plate with stylus (G), hook (H).

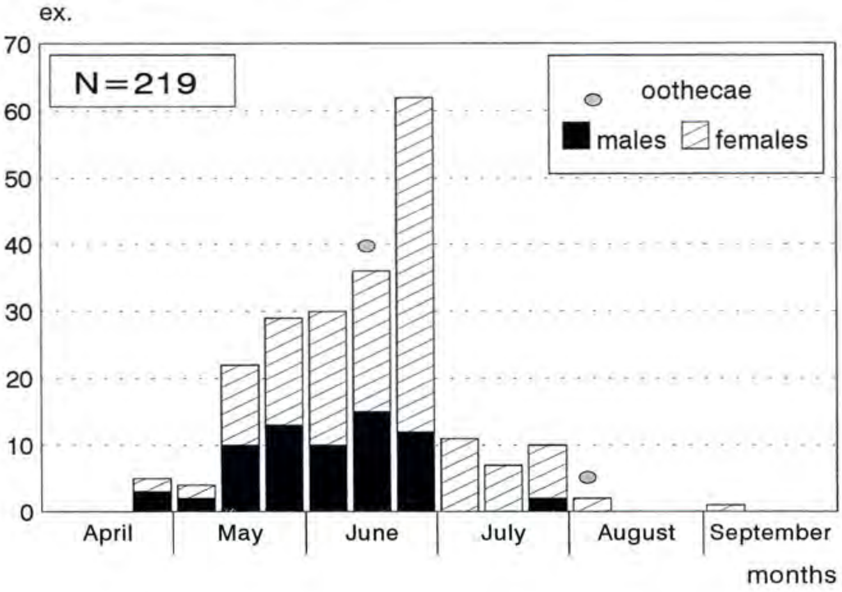

Fig. 2. Seasonal dynamics of *Phyllodromica megerlei*.

tergites with small, elongated whitish to transparent spots on the posterior lateral margins. Abdominal sternites black. Subgenital plate pale to dark brown. Cerci dark brown to black. Femur and tibia black, tarsal segments (tarsomeres) yellow with brown posterior ends, at the coxa-trochanter joint white regions.

Female. Head sparsely setose, interocular space distinctly wider than the ocular length (IW/OL index = 1.6-1.7). Forewings short, transversally truncated (Fig. 1B). Genitalia very similar to *P. pulcherrima*. Coloration: Head black, interocular space brown. Antennae, pronotum and forewings as in male. Abdominal tergites and sternites black, tergites and sternites 2-7 with triangular white lateral margins and often with narrow pale posterior margins. Subgenital plate black with pale lateral margins. Legs brown, tarsal segments yellow with brown posterior ends, tibial bristles yellow. Trochanter and adjacent part of coxa and anteroventral margins of all coxae whitish. Ootheca: Length 2.8 mm, width 2 mm. Surface brown, with 10-12 strong, longitudinal ridges on each side, the keel is serrated, the teeth are small (Fig. 4G).

Geographical distribution. – (Fig. 5) *Phyllodromica megerlei* is widely distributed: SE Germany (Bavaria, Saxony – old, doubtful records only), Czech Republic, Slovakia, Austria, Switzerland (old records only), Hungary, Romania, nordeastern Italy, Slovenia, Croatia (Istria, Dalmatia), Yugoslavia (Serbia – Vojvodina), Bosnia-Hercegovina (Hercegovina), Moldavia, Ukraine (Kirovogradská oblast), but everywhere it is rare. On the territory of Slovakia and Czech Republic it reaches the northern border of its distribution.

Biology. – *Phyllodromica megerlei* occurs at altitudes between sea level and about 700 m. The animals live most frequently in tussocks of grass on xerotherm and mesohygrophilous meadows with bushes and trees, banks of rivers, brooks overgrown with grass, and clearings. Adults occur from April to August and are most abundant at the end of May and at the end of June (Fig. 2).

2. ***Phyllodromica asiatica*** Bey-Bienko, 1950 **stat. n.**

(Plate 1: B; Figs 3A-E, 5)

Phyllodromica megerlei asiatica Bey-Bienko, 1950: 233.

Aphlebia pallida (Brunner v. W.): Brunner v. W. 1882: 42, partim; Jakobson & Bianki, 1905: 127, partim. Misidentifications.

Aphlebia punctata (Charpentier): Bolivar 1899: 585. Misidentification.

Hololampra punctata (Charpentier) var.: Ebner 1919: 152.

Hololampra punctata f. *erythronota* Ramme, 1951: 324 (syn. Karabag 1958).

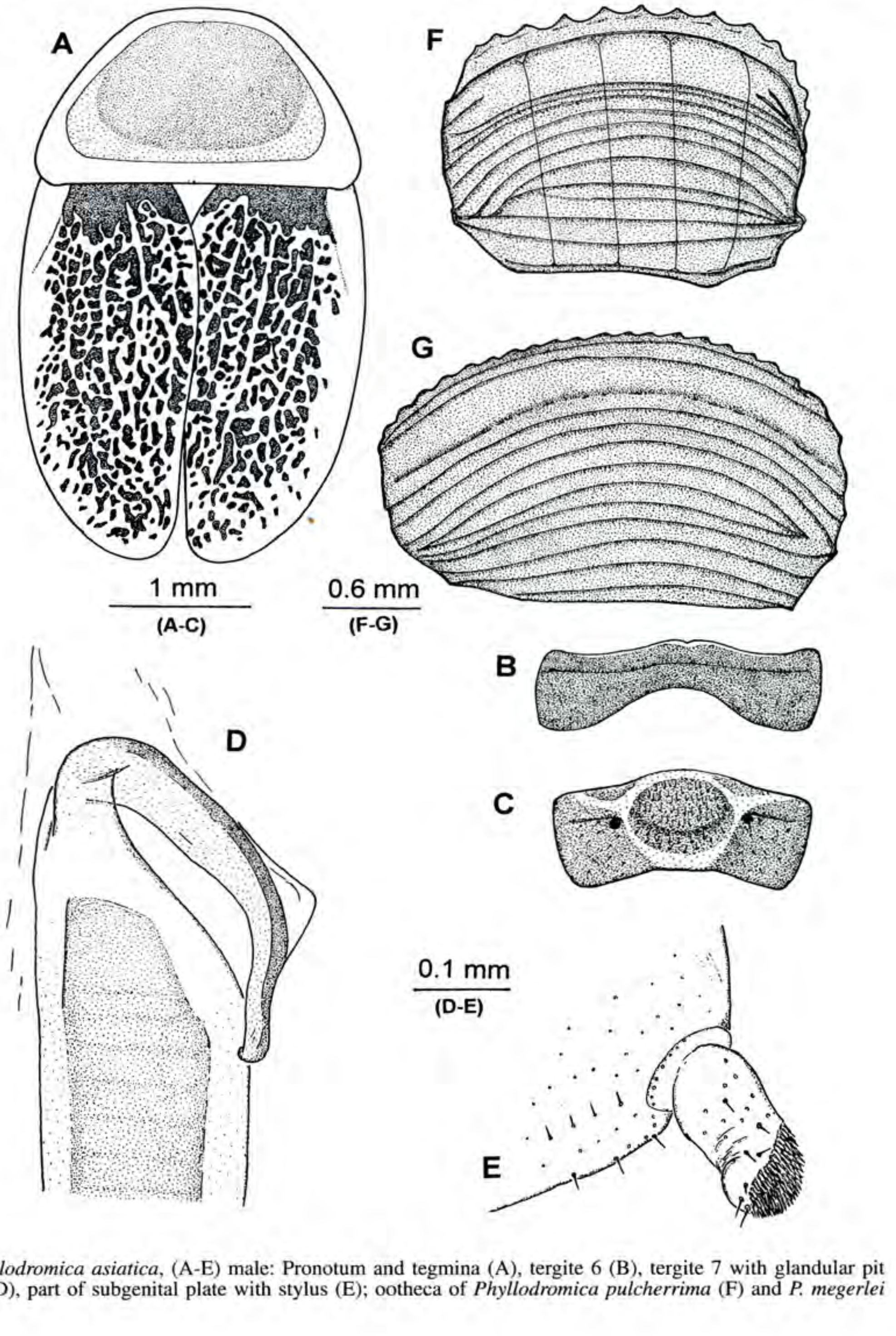

Fig. 3. *Phyllodromica asiatica*, (A-E) male: Pronotum and tegmina (A), tergite 6 (B), tergite 7 with glandular pit (C), hook (D), part of subgenital plate with stylus (E); ootheca of *Phyllodromica pulcherrima* (F) and *P. megerlei* (G).

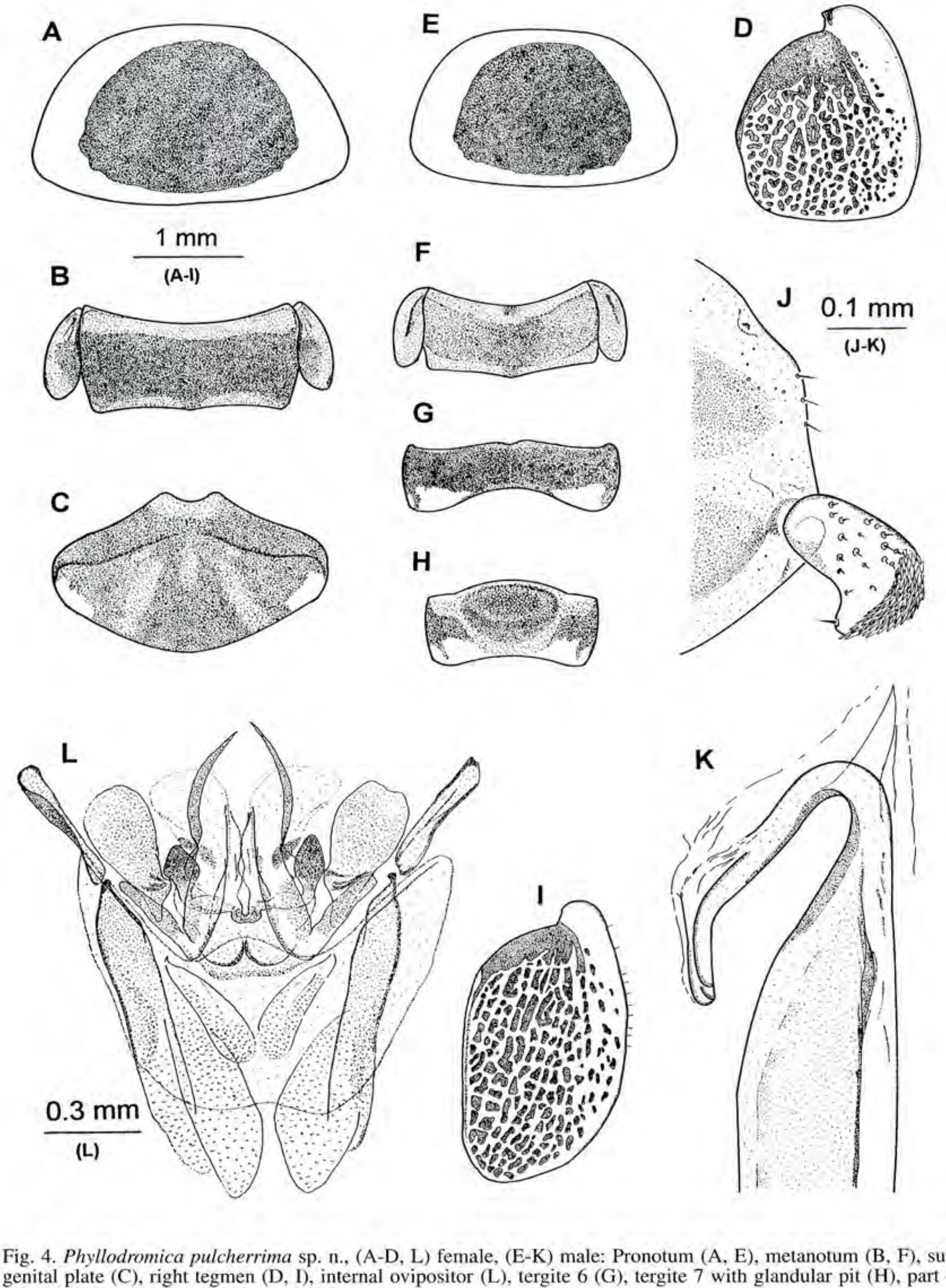

Fig. 4. *Phyllodromica pulcherrima* sp. n., (A-D, L) female, (E-K) male: Pronotum (A, E), metanotum (B, F), subgenital plate (C), right tegmen (D, I), internal ovipositor (L), tergite 6 (G), tergite 7 with glandular pit (H), part of subgenital plate with stylus (J), hook (K).

Material studied. – Holotype ♂ of *Hololampra punctata* f. *erythronota*: Adana, Kleinasien, Rolle leg. (MNB).

Literature records. – TURKEY: Amasya (Brunner v. W. 1882); Akbes, Kahramanmaraş (Bolivar 1899); Bahçe, Amanos Mts (Ebner 1919); Gülek (Bey-Bienko 1950); Adana (Ramme 1951; Karabag 1958); SYRIA: El Lâdhaqiye – Lattakia (Bey-Bienko, 1950).

Description. – Size (mm). Body length: ♂ 5.47; pronotum length x width, ♂ 1.5 x 2.88; forewing length, ♂ 3.97.

Male (Plate 1: B). Head with few short setae, interocular width larger than the ocular length (IW/OL index = 1.8). Pronotum trapeziform, surface sparsely setose. Forewings reaching to the end of abdomen, distal end narrowly rounded, veins in costo-radial area only indicated. Radial, medial and cubital veins can by discriminated. Posterior margin of tergite 6 concave (Fig. 3B). The middle part of tergite 7 covered with the tergal gland (Fig. 3C). Glandular pit large, trapezoid-oval, reaching to the posterior margin of tergite. Hind margin of supraanal plate rounded. Cerci long, with 8-9 segments. Coloration: Head brown, ocellar spots yellowish-white, antennal region pale. Proximal region of antennae yellowish-brown, distal part brown. First and second segments of maxillary palpomeres yellow, thirth black, labial palps brownish. Disk of the pronotum orange-yellow (central part) to yellowish (posterior part and corners). Anterior and posterior borders of pronotum white to transparent. Forewings white to transparent with a great number of small dark spots, basal part with big brownish-black spot (Fig. 3A). Costal field and outer margin of forewings without spots. Hindwings dark to transparent. Abdominal tergites black. Abdominal sternites black, lateral margins of sternite 2.-7. with yellow border. Subgenital plate pale-brown, in the middle white. Femur black, tibia brown-black, tarsal segments (tarsomeres) yellow with brown posterior ends. Cerci black, stylus brown with yellow tip.

Female (not examined, description from Bey-Bienko 1950). Very like as a *P. megerlei*, but usually the disk of pronotum yellowish-orange, rarely blackish-brown. Posterior border of pronotum pale, equally wide as anterior border. Abdomen with pale lateral border equally wide as pale posterior border of pronotum. Ootheca: As in *P. megerlei*, but with 18-19 longitudinal ridges on each side.

Geographical distribution (Fig. 5). – Known only from Asia Minor – Turkey and Syria.

3. *Phyllodromica pulcherrima* sp. n.

(Plate 1: C, D; Figs 3F, 4A-L, 5)

Type material. – Holotype ♂, Bulgaria: Enime plane, Vlas (near Nesebar), 150 m, 30.v.1995, Majzlan (SNMB). Paratypes: 6 ♂, 8 ♀, same locality as holotype, 30.v.1995 and 26.v.1996, Majzlan (SNMB and authors collection).

Etymology. – The species name refers to its very decorative appearance (from latin pulcherrimus = nicelooking, magnificent).

Description. – Size (mm): Body length: ♂ 5.2-5.7, ♀ 6.2-6.6; pronotum length x width, ♂ 1.5 x 2.4, ♀ 1.8 x 2.8; forewing length, ♂ 2.3-2.5, ♀ 2.2-2.3.

Male (Plate 1: C). Head with few short setae, interocular space slightly greater than distance between ocellar spots, interocular width larger than the ocular length (IW/OL index = 1.7). Forewings strongly reduced, reaching at most to the middle of the fourth abdominal tergite, distal end widely rounded, veins in costo radial area absent (Fig. 4I). Hindwings strongly reduced, nearly reach to posterior border of the metanotum (Fig. 4F). Posterior margin of the tergite 6 slightly concave (Fig. 4G). Seventh tergite with wide oblique lateral margins reaching to the tergal gland (Fig. 4H). Glandular pit large, oval. Genitalia: The curved end of hook is very narrow, the tip strongly bent (Fig. 4K), cleft sclerite present. Coloration: Head with clypeus, labrum and ocellar spots whitish, remainder shiny blackish. First, second and fifth maxillary palpomeres brown, third and fourth yellow. Labial palps blackish-brown. First ten segments of antennae yellow, remainder segments gradually brown to black. Pronotum (Fig. 4E) with black disc and yellow to transparent margins, anterior and posterior margins narrower than lateral margins. Forewings white to transparent with a great number of small spots, hindwings dark. Abdominal tergites black, tergites 2-5 with narrow, whitish posterior and lateral borders; tergites 6-8 with large, whitish to transparent spots in the posterior corners. Abdominal sternites black. Subgenital plate pale to dark brown. Femur and tibia dark brown to black, tarsomeres yellow with brown posterior ends, at the coxa-trochanter joint white regions.

Female (Plate 1: D). Head sparsely setose,

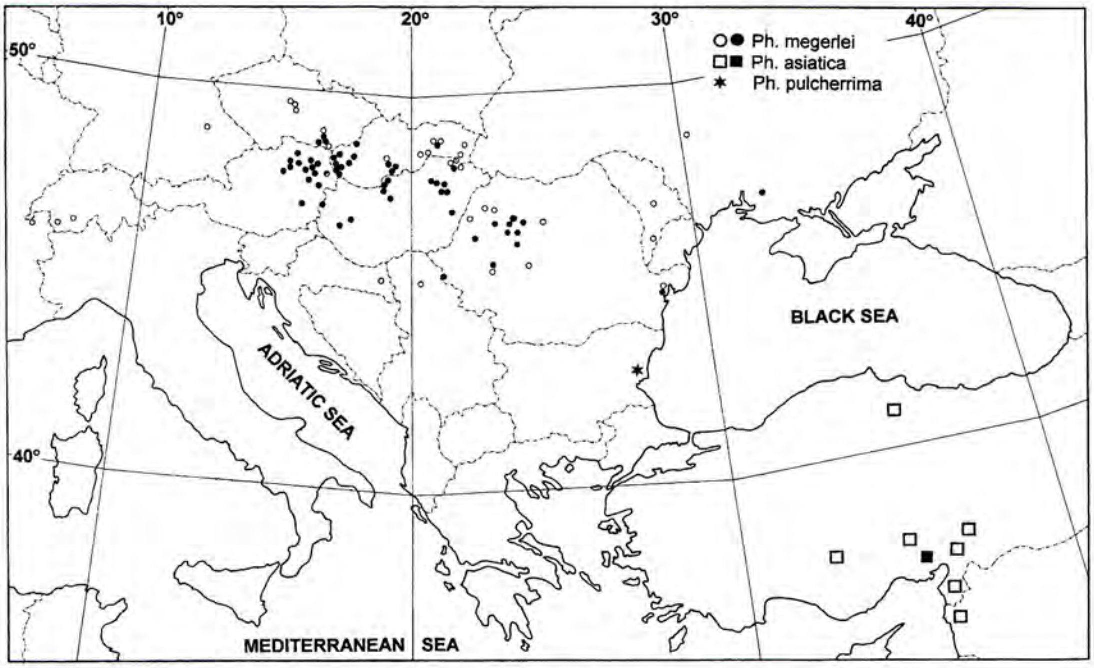

Fig. 5. Geographical distribution of *megerlei*-group of cockroach genus *Phyllodromica* (data from literature – open marks, material studied – filled marks).

interocular space distinctly wider than the ocular length (IW/OL index = 1.6). Forewings short, transversally truncated, their interior margins contacted (Fig. 4D). Genitalia as in Fig. 4L. Coloration: Head black, interocular space orange-brown. Labrum, lower part of clypeus and ocellar spots whitish. Antennae, pronotum (Fig. 4A) and forewings as in male. Abdominal tergites and sternites black, tergites and sternites 2-7 with white lateral margins and often with narrow pale posterior margins. Subgenital plate black with pale lateral margins. Femora yellow-brown, longitudinally striped Tibiae and tibial bristles yellow. Tarsal segments yellow with brown posterior ends. All trochanters, adjacent parts of coxae and their anteroventral margins whitish, remaining parts of coxae brownish. Ootheca: Length 2.3±0.2 mm, width 1.8±0.1 mm. Surface brown, with 11-12 strong, longitudinal ridges on each side. The keel is serrated, with 12-13 small teeth (Fig. 3F).

Biology. – The Bulgarian species *P. pulcherrima* sp. n. lives at an altitude of about 150 m. It occurs in submediterranean, xero-termophilous oak woods (the alliance Quercion pubescenti-petraeae). The specimens were found in grass during May.

Geographical distribution (Fig. 5). – Known only from the type locality in Bulgaria.

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Príloha č. 7

VIDLIČKA, Ľ. 1999.
Caeparia sausai sp.nov. from Laos, and description of the male Caeparia donskoffi
(Blattaria: Blaberidae: Panesthiinae).
Entomological Problems 30(2): 1-5.

Entomological Problems, 30 (2): 1-5, December 1999

Caeparia sausai sp.nov. from Laos, and description of the male *Caeparia donskoffi* (Blattaria: Blaberidae: Panesthiinae)

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VIDLIČKA, Ľ. 1999. Caeparia sausai sp.nov. from Laos, and description of the male Caeparia donskoffi (Blattaria: Blaberidae: Panesthiinae). *Entomol. Probl.* 30(2): 1-5. - The female of a new cockroach species of Panesthiinae, *Caeparia sausai* is described from Laos. The male of *Caeparia donskoffi* ROTH is described. Its habitus is similar to that of the female: pronotum bicolored with dense long hairs; hind margin of supraanal plate entire; genital phallomere L2d strongly toothed. The species is found in North and South Vietnam, Laos, and Thailand.

Key words: *Caeparia sausai*, *Caeparia donskoffi*, cockroaches, Blattaria, southeast Asia, Laos.

Introduction

Four species of *Caeparia* STÅL, 1877, from mainland southeast Asia, are known. Both sexes are known for 2 species, namely *C. saussurii* (WOOD-MASON, 1876) and *C. crenulata* (BRUIJNING, 1948). The males of *C. donskoffi* ROTH and *C. kaltenbachi* ROTH are unknown (ROTH 1979). ROTH (1982) described an unnamed nymph from Thailand which may prove to be either of these last 2 species; the colour pattern of this nymph differs from that of the adults of *C. donskoffi* or *C. kaltenbachi*, but the hind margin of its supraanal plate is similar to that of *C. donskoffi*.

In this paper the female of new species of *Caeparia* (*C. sausai*) from Laos and the male of *C. donskoffi* are described.

Fig. 1: *Caeparia sausai* sp.nov. – habitus.

Caeparia sausai sp.nov.

Holotype ♀ (SNM, Bratislava): Laos south, Attapu prov., Bolaven Plateau, 18-30.IV.1999, 15 km SE of Ban Houaykong, NONG LOM (lake) env., N 15°02', E 106°35', alt. 800 m, E. Jendek & O. Šauša leg.

Description of female (Figs 1 - 3). Head sparsely punctate, ocelli very obvious. Antennae short, thick, widest in the centre, consisting of 35 segments.

Pronotum transverse, widest near the hind margin, the surface of pronotum hairless, sparsely covered with large pits, on the anterior parts crescent-like groove. Lateral margins broadly rounded. Mesonotum between tegmina densely foveolate. Tegmina reaching the hind margin of the 6th tergite, basal half enlarged, the apex rounded. Anterior parts of coxae wrinkled, densely hairy. Femora smooth, anterior and posterior margins with hairs; tibia armed. Euplatulae (pulvilli) present on tarsal segments 1 to 4; tarsal claws smooth, symmetrical, arolia absent.

Abdominal tergites pitted, the hind margins of tergites 3-7 with tubercles, which become gradually longer in posterior tergites. Surface of tergites with large, round impressions. On T7 two very large sublateral tubercles, the lateral angles of T7 deflexed. Supraanal plate with round punctations, hind margin with lateral angles, the area between them subentire. Abdominal sternites narrow, surface medially punctate, laterally with larger pits. S2 in the middle with longitudinal keel. Cerci short, conical, dorsal surface non-setose, ventrally with long setae. Styli not present.

Measurements [mm]. Total length 29; pronotum length x width 5.5 × 9; tegmen length 22.

Coloration. Vertex black, the longitudinal black band between ocelli continued over the clypeus and labrum, remaining parts of head yellow (Fig. 2). Eyes reddish brown, ocelli bright red. Maxillary and labialy palps yellow, apical segments black. First 15 antennomeres shiny black, the succeeding 15 segments dull black, 4 segments yellow and the last one dull black.

Pronotum yellow, in the centre with big lyre-like black spot reaching to the hind margin.

Fig. 2: *Caeparia sausai* sp.nov. – color pattern of head.

Base of left tegmen black, central part with yellow triangular spot and black band, preapical part membranous, yellowish and apex black. Anterior half of right tegmen near to the left one, posterior half dark with yellowish spot (Fig. 3). Legs black, apical parts of coxae and femora, and basal parts of tibiae yellow, spines black with reddish brown apex, tarsi and claws black.

Abdominal tergites black, with small irregular reddish-yellow spots sublaterally. Supraanal plate black, the hind margin brownish red. Abdominal sternites brownish black. Cerci brownish black.

Fig. 3: *Caeparia sausai* sp.nov. – tegmina.

Comments. The head colour of *Caeparia sausai* is similar to that of *C. crenulata*, and its pronotal colour pattern resembles those of *C. donskoffi* and *C. kaltenbachi*. The same colour combination is found in a male nymph from Thailand (*Caeparia* sp. - ROTH 1982), but probably it is not the same species.

The species is named in honour of O. Šauša, who caught this specimen.

***Caeparia donskoffi* ROTH**

Caeparia donskoffi ROTH, 1979: 101, Figs. 84A - F, 85A - F, 89G.

Male (Figs 4a - c, 5, 6a - c, 7a - c). Head sparsely punctate, vertex not foveolate, largely exposed. Clypeus with scattered, slender, long hairs; eyes large, protruded; ocelli well developed; antennae short, consisting about 40 mostly broad, short segments.

Pronotum transverse, anterior margin slightly concave, posterior margin slightly excised medially, lateral margins broadly rounded; anterior half of pronotum with a pair of oblique grooves; surface of pronotum densely covered with long hairs, some black-coloured areas hairless, lateroposterior angles thinly punctate. Mesonotum region between tegmina with long hairs. Tegmina constricted, surpassing the end of the abdomen, their apices rounded. Thoracic sternites and coxae with long hairs. Euplantulae (pulvilli) present on tarsal segments 1 to 4 on all legs; tarsal claws simple, symmetrical, arolia absent.

Abdominal tergites pitted, the hind margins with some tubercles laterally, lateral margins of abdominal segment 7 with 2 bluntly rounded teeth on the anterior half, the lateral angle large, directed caudal. Posterior margin of the supraanal plate with collar-like elevation; medial part of hind margin weakly convex, entire. Cerci small, dorsal surface non-setose, ventrally with long setae. Second sternite narrow, medially with a longitudinal keel. Hind margin of second sternite incised medially.

Fig. 4 *Caeparia donskoffi*: a) habitus of male from Vietnam, b - c) pronotum of males from Laos (a – leg. Kubáò, b – leg. Jendek & Šauša).

The surfaces of abdominal sternites thinly punctate, the lateral punctures denser; sternite 7 punctate on apical half. Subgenital plate small, almost hidden, non punctate. Styli absent. Antero-ventral margin of front femur unarmed except for slender hairs.

Genital phallomere L2d well developed, darkly sclerotized with many large spines along the posterior margin; L2vm long, narrow, strongly sclerotized; L1 small, only lightly sclerotized; R2 lightly sclerotized, markedly reduced, the curved part of the hook absent (Fig. 5).

Right paraproct with two strongly sclerotized apical processes, left paraproct smaller, without apical processes.

Measurements [mm]. Total length 26 - 29.5; pronotum length x width 4 - 5 × 7.5 - 8.5; tegmen length 21 - 23.

Coloration. Head yellow, labrum black, an incomplete or narrow complete black band on the clypeus, a broader transverse black band between the antennae (split around ocelli); 4 broad black vertical bands extend from between the eyes over the vertex to the hind margin of the head, with a black spot behind the eyes (Fig. 6a - c). Eyes reddish brown, ocelli bright red. Maxillary palps yellow, apical segments black. First 10 antennomeres shiny black, the succeeding 20 segments dull blackish grey and about 10 apical segments brownish to reddish-yellow.

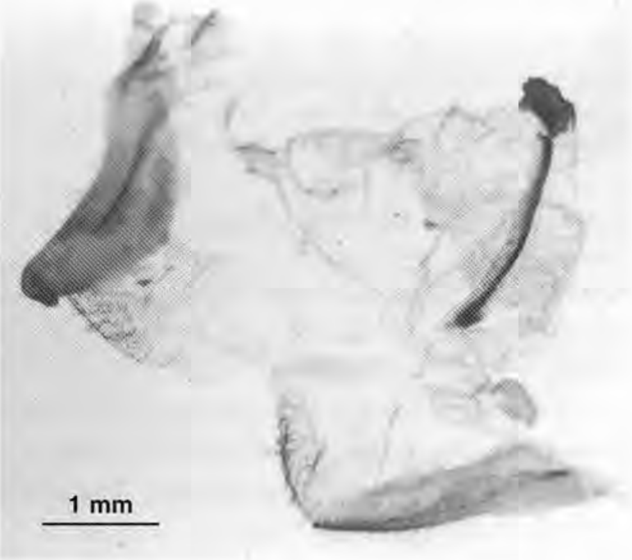

Fig. 5: *Caeparia donskoffi* – genitalia of male from Vietnam.

Pronotum yellow with black anterior and lateral margins, central part with two symmetrical L-shaped black spots, hind angles with black spots, the middle of the hind margins with a black spot; hairs on the pronotum yellow. Left tegmen with a large black basal spot followed by a testaceous area, then

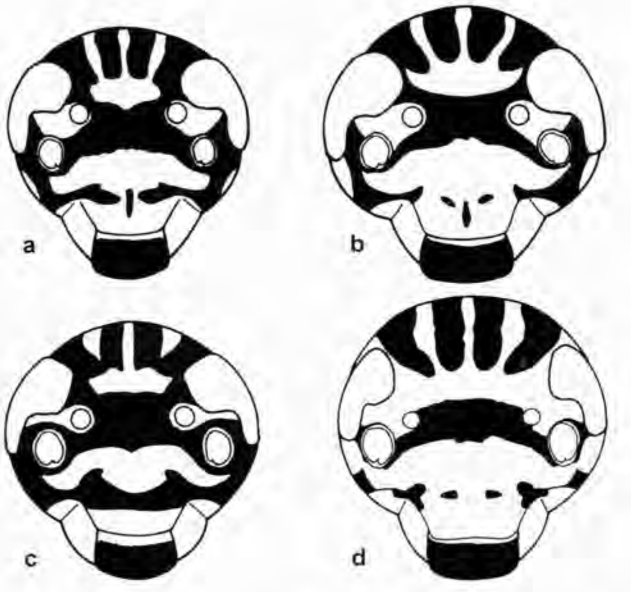

Fig. 6 *Caeparia donskoffi* – colour pattern of head: a) male from Laos (leg. Kubáň); b) male from Laos (leg. Jendek & Šauša); c) male from Vietnam; d) female from Thai-land.

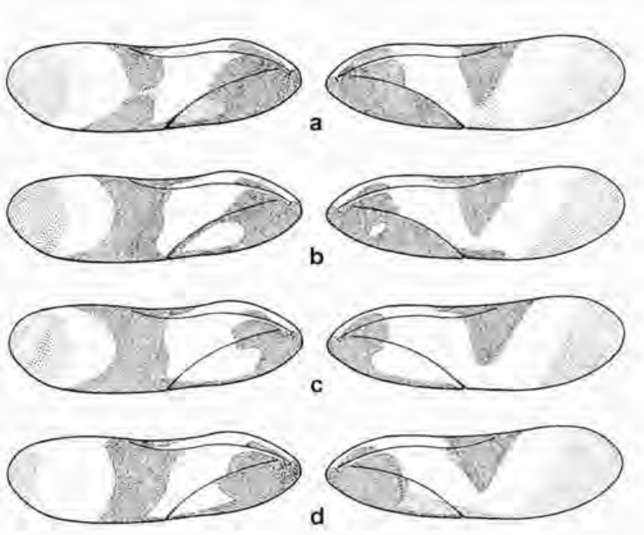

Fig. 7 *Caeparia donskoffi* – colour pattern of tegmina: a) male from Vietnam; b) male from Laos (leg. Jendek & Šauša); c) male from Laos (leg. Kubáň); d) female from Thailand.

a wide blackish to brownish band followed by a transparent zone which reaches the apex of the tegmen. Right tegmen with a large black basal spot followed by a testaceous area, then a triangular spot followed by a wide brownish area (Fig. 7a - c).

Abdominal tergites brownish black with large irregular reddish yellow spots laterally and medially. Supraanal plate brown to brownish red. Abdominal sternites brown, laterally with or without large yellow spots. Cerci dorsally brownish black, ventrally yellowish brown. Legs blackish with transverse yellowish bands, tarsi blackish brown; spines dark brown.

Material examined: **1 ♂: Laos** north, 24-30.V.1997, 20 km NW Louang Namtha, N 21°09.2, E 101°18.7, al. 900±100 m, E. Jendek & O. Šauša leg.; **1 ♂: Laos**, Louang Namtha pr., 21°09' N, 101°19' E, Namtha→Muang Sing, 5-31.V.1997, 900-1200 m, Vít Kubáň leg.; **1 ♂: Vietnam** north, 15.V.-16.VI.1991, Tam Dao nat. park, 75 km NW from Hanoi, E. Jendek leg.

Addition to description of female (Figs 6d, 7d, 8). Ocelli present, flat, less distinct than in male. Antennae 39 segmented; first 15 antennal segments shiny black, the succeeding 15 segments dull blackish grey and 9 apical segments brownish to yellow.

Pronotum nearly hairless, but the coloration was typical for *C. donskoffi*.

Coloration of tegmina is very similar to male with left-right colour asymmetry (Fig. 7 d).

Measurements [mm]. Total length 33; pronotum length x width 6.5 × 10.5; tegmen length 24.

Material examined: 1 ♀: Thailand, Chiang Mai prov., 18°49' N, 98°54' E, 1600 m, Doi Pui Mt., 2-6.V.1996, Vít Kubáň leg.

Comments. The male genital phallomeres are very similar to those of known males of *Caeparia*.

Previously, *C. donskoffi* was known only from North and South Vietnam. The present specimens come from North Vietnam, Laos and Thailand. This species is widely distributed in southeast Asia.

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I am grateful to Dr Ondrej Šauša, Dr Eduard Jendek and Ing. Vít Kubáň who gave me the cockroach material from their own collections from South East Asia and Dr Ján Kodada (Comenius University) for photos.

I would like to thank Dr Louis M. Roth (Harvard University) for valuable comments and linguistic help with the English text.

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Fig. 8: *Caeparia donskoffi* - habitus female

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The new cockroach species from the genus Chorisoserrata from Laos
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Entomological Problems 32(2): 145-147.

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The new cockroach species from the genus *Chorisoserrata* from Laos (Blattaria: Blattellidae: Pseudophyllodromiinae)

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Vidlička, Ľ. 2002. The new cockroach species from the genus Chorisoserrata from Laos (Blattaria: Blattellidae: Pseudophyllodromiinae). ***Entomol. Probl.*** **32(2): 145–147.** – The genus *Chorisoserrata* Roth, 1998 contained up to now only two species, *Ch. apicalis* Hanitsch from Sumatra and *Ch. sagittaria* Hanitsch (only ♂ known) from Vietnam and East Borneo. The male and female of third species *Chorisoserrata jendeki* from Laos are described here. Unlike *Ch. sagittaria* the male of *Ch. jendeki* have developed tergal gland on abdominal tergum 7. The key of the genus *Chorisoserrata* is presented.

Key words: Blattaria, *Chorisoserrata*, Laos

Introduction

The genus *Chorisoserrata* described Roth (1998). Symmetrical serrated tarsal claws, truncate vertex, maxillary palpomere fourth longer that the fifth and unspecialised seventh abdominal tergum were used for separation of this genus from the genus *Chorisoneura* Brunner de Wattenwyl, 1865. Roth (1998) added into the genus *Chorisoserrata* two species: *Ch. sagittaria* described by Hanitsch (1927) from Vietnam and *Ch. apicalis* described by Hanitsch (1929) from Sumatra. Princis (1950) recorded the second species from East Borneo. Both species were previously inserted in *Chorisoneura*. Species that remained in the genus *Chorisoneura* are distributed only in New Word (South, Central and North America).

Key to males of *Chorisoserrata*

1 Hind margin of supraanal plate with a distinct u-shaped excavation; apex of interstylar margin rounded (Fig. 2I) **2**

– Hind margin of supraanal plate without excavation; apex of interstylar margin more or less even. (Vietnam) .... ***Ch. sagittaria***

2 Rounded apex of interstylar margin with deep u-shaped excavation; pronotum semicircular (Figs. 2C, D, I). (Laos) .... ***Ch. jendeki***

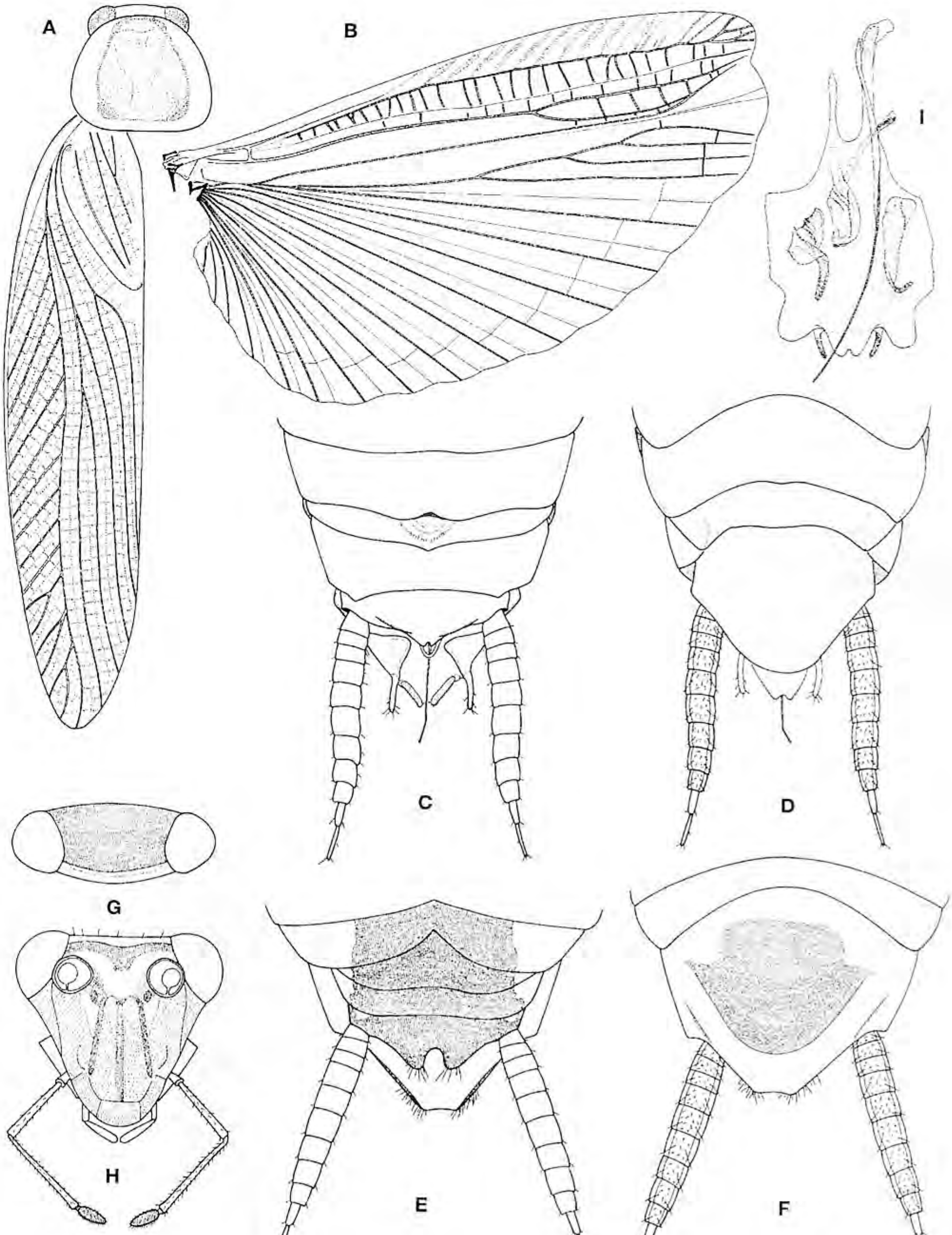
– Rounded apex of interstylar margin without excavation; pronotum suboval. (Sumatra, East Borneo) ... ***Ch. apicalis***

Chorisoserrata jendeki, sp. nov.

(Figs. 1, 2A–I)

Male: Head exposed, markedly triangular, compound eyes relatively small, interocular space wide, vertex flat, maxillary palpomere 2 short, palpomeres 3 and 4 very long and slender, palpomere 5 bulbous, more as 2 time shorter that previous, densely hairy (Figs. 2G, H); antennae longer as the body, scapus 2 time longer as wide, pedicel short, first segment of flagellum about thrice the length as following segments, the segments are lengthen in the direct of apex; pronotum semicircular, posterior margin nearly straight; tegmina narrow, lanceolate, exceeding beyond the end of the abdomen, venation distinct, between veins and branches of costal field obvious screens created spatial cell pattern (Fig. 2A); hind wings well developed, costal field narrow with indistinct visible veins, radial vein simple, in the apex branched, median vein indistinct, visible only near the apex, cubital vein in last fourth Y-bifurcate, on the apex bent upwards, intercalary apical triangle small but distinct


Fig. 1. *Chorisoserrata jendeki* sp. nov. – habitus, male.



Figs. 2A–I. *Chorisoserrata jendeki* sp. nov.: A, pronotum and left tegmen; B, right hind wing; C, D, end of male abdomen, dorsal and ventral view; E, F, end of female abdomen (dorsal and ventral view); G, H, head, vertex and frontal view; I, male subgenital plate, dorsal.

(Fig. 2B); hind wings jetty out tegmen at rest. Front coxae narrow and enlarge. Anteroventral margin of the front femur with 6 small spines near the middle succeeded by several slender setae and terminating in one large spine; puvilli developed on 4 proximal tarsomeres, enlarged, especially fourth; tarsal claws symmetrical, distinctly serrated, arolia well developed. Abdominal tergum 7 narrow, with indistinct but visible tergal gland in the middle; supra-anal plate symmetrical, hind margin with a distinct u-shaped excavation (Figs. 2C, D). Cerci elongated, 11-segmented, ventral surface with a few setae, segments 10–11 very narrow, elongated und cylindrical. Exposed portion of subgenital plate symmetrical, lateral corners produced, turned inside; styles small, slim, placed at the deep indentation, the interstylar region produced, apex with shallow u-shaped excavation. Hook on the right side, apex narrowed, widely rounded; median phallomere with pointed apex; left phallomere with finger-like protrusion; long tapering filament stick up out of body (Fig. 2I).

Female: Head triangular, truncated vertex and compound eyes visible, not overlapped by pronotum, interocular space broad; antennae long; maxillary palpus long and slim, same as male; pronotum semicircular; tegmina lanceolate, reached beyond the abdomen; hind wings well developed, long. Anteroventral margin of front femur with 9 small spines, several setae and terminal large spine, tarsal claws symmetrical, serrated; posterior margin of supraanal plate with deep u-shaped excavation (Fig. 2E); apex of subgenital plate truncated, with long setae (Figs. 2E, F); cerci elongated, slim.

Coloration: Vertex and frons dark brown with white strip between eyes; first ten segments of antennal flagellum dark brown, remains flagellomere yellow; the lateral margins of pronotum hyaline, disc yellow to brown with dark brown margins; tegmina hyaline, subbasaly with shoe-like dark brown macula (Fig. 1); hind wings smoked, costal area yellowish; legs and spines yellow, posterior parts of tarsal segments dark; dorsal part of abdomen yellowish brown with broad longitudinal dark band in the middle; ventral part of abdomen yellow.

Measurements (mm) (♀ in parentheses): Length, 12.75 (12.75); pronotum length × width, 1.9–2.0 × 2.3–2.5 (2.2 × 2.7); tegmen length, 10.4 (10.3); interocular width, 0.8 (0.9).

Holotype: ♂, LAOS: Bolikhamxai prov.: Ban Nok env., N 18°08.7' E 104°28.1', 220 m, 9.-14.v.1998, Coll. O. Šauša & E. Jendek; (Slovak National Museum – Natural History Museum, Bratislava).

Paratypes: LAOS: Same data as holotype, 1♀; Luang Namtha prov.: Namtha → Muang Sing, 21°09'N 101°19'E, 900-1200 m, 1 ♂, 5.-31.v.1997, Coll. V. Kubáň; (Institute of Zoology SAS, Bratislava).

Etymology: The species is dedicated to Dr. E. Jendek (Institute of Zoology), entomologist who collected specimens of this new species.

Remarks: Roth (1998) mentioned, that seventh abdomimal tergum of the males from genus *Chorisoserrata* is unspecialised, without tergal gland. He had available one male of *Ch. sagittaria* and destroyed male of *Ch. apicalis* (from abdomen only with terminalia on slide). Seventh abdominal tergum of here described males *Ch. jendeki* is specialized although the tergal gland is small and indistinct. Other characters of the genus are identical, and suggest close relationship of all three species of *Chorisoserrata*.

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Two new troglobitic cockroach species of the genus Spelaeoblatta
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Journal of Natural History 37(1): 107-114.

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Two new troglobitic cockroach species of the genus *Spelaeoblatta* (Blattaria: Nocticolidae) from North Thailand

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We describe two new troglobitic cockroach species *Spelaeoblatta myugei* n. sp. and *S. thailandica* n. sp. (Blattaria: Nocticolidae) mountain caves of North Thailand. We divided the genus *Spelaeoblatta* into two species groups. The *Myugei* group includes both newly described species, which contain unique large tubercles or elevations on abdominal terga. Using scanning electron microscopy we show details of these special tubercles. The *Thamfaranga* group includes only *S. thamfaranga* Roth is lacking these structures. The entire genus is further characterized by the location of a tergal gland on abdominal segments three and four. A key to identify the males is given. We also describe two specimens of female nymphs, which possibly represent a new genus of cavernicolous cockroaches. Elongated and narrow pronotum as well as very long front legs of these nymphs resemble mantids.

KEYWORDS: Blattaria, Nocticolidae, cockroaches, *Spelaeoblatta myugei* n. sp., *Spelaeoblatta thailandica* n. sp., Thailand.

Introduction

Only two species were included in the genus *Spelaeoblatta* Bolivar, 1897. First, *S. gestroi* was described by Bolivar (1897: 32) based on a single female from Burma (Myanmar). Second, *S. thamfaranga* was described by Roth (Roth and McGavin, 1994: 1321) based on several males and females from Thailand. Here we describe two species, *S. myugei* and *S. thailandica*, from caves in the Nam Lang region (Mae Hong Son province), North Thailand. Specimens of both cockroach species were captured in caves located near the well-known cave Tham Pha Mon about 15 km SE and Red Cliff Cave about 20 km SW from Tham Nam Lang (figure 1).

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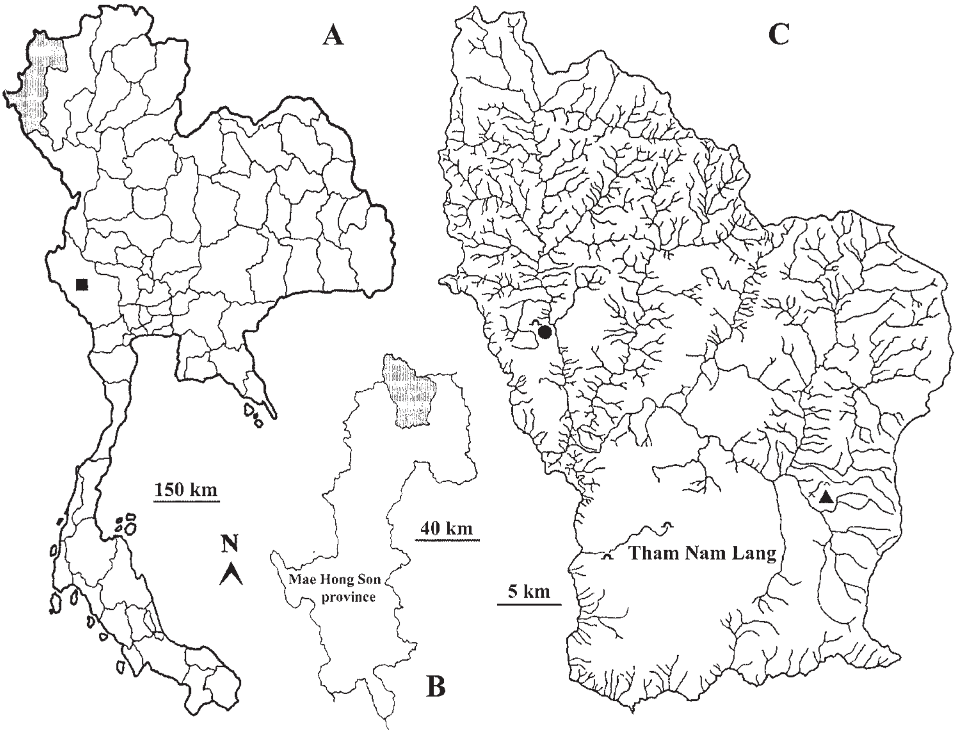

FIG. 1. Distribution of *Spelaeoblatta* species in Thailand. (A) Thailand (grey—Mae Hong Son province); (B) Mae Hong Son province (grey—Nam Lang region); (C) Nam Lang region. (▲) *S. myugei*, (●) *S. thailandica*, (■) *S. thamfaranga.*

Spelaeoblatta myugei n. sp.
(figures 2–4)

Type material. HOLOTYPE: ♂, north-west Thailand: cave Tham Pha Mon (Mae Hong Son Province, Nam Lang region, 19°28′N, 98°14′E), 20 March 1997, N. Myuge (H. Miore) leg., coll. Slovak National Museum–Natural History Museum Bratislava (SNM-NHMB). PARATYPES: 1♂, 3♀, same data as holotype (Vidlička collection).

Etymology. The species is named in honour of N. Myuge, who collected this species.

Description

Size (mm). Body length: ♂ 10.0–10.75, ♀ 9.9–11.8; pronotum length × width, ♂ 2.5 × 3.9, ♀ 2.4–2.75 × 3.5–4.1; forewing length, ♂ 4.5–5.0, ♀ 1.75–2.0.

Male (figures 2A, C, D, E, F, 3A–H, 4A–H). Head longitudinal, oval, partly visible from above; faceted eyes small, strongly reduced, facetes indistinct; ocelli absent; fifth maxillary palpomere shorter than the fourth, apex rounded. Antennae long, slender, about 55 segments, scapus long, pedicel short, third segment as long as scapus, other segments shorter. Pronotum parabolic, lateral hind corner slightly oblong. Tegmina reaching to the base of fourth tergite, obliquely truncate, surface covered by rather sparse trichia. Trichia are present mostly apically on the reduced intercalary veins. Sc is highly expanded and supported by series of branches, clavus is strongly reduced, radial field covers almost the half of the wing's width, media is

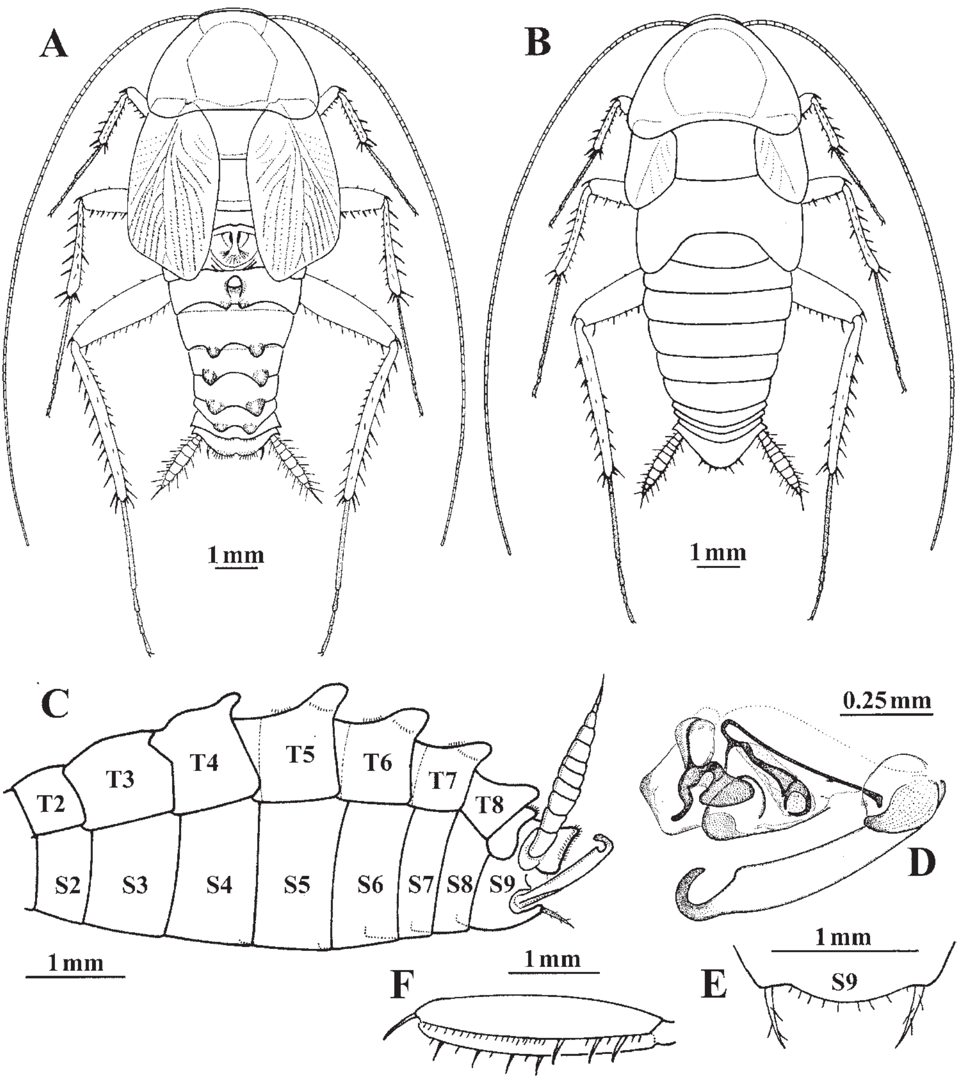

FIG. 2. *Spelaeoblatta myugei*. (A) Male habitus; (B) female habitus; (C) male abdomen (lateral view); (D) male genitalia (ventral view); (E) male subgenital plate (dorsal view); (F) male front femur (anteroventral view).

four branched. Hind wings reduced, lobate (figure 3F), slightly shorter than metanotum. Anteroventral margin of front femur with three large proximal spines succeeded by a row of piliform spinules terminating in a large distal spine (type B_1) (figures 2F, 4C); anterior margin of front tibia with several small spines, followed by three large spines near the centre and terminating in two large spines, posterior margin with many piliform spinules, two large spines at the distal end; tarsal claws simple, symmetrical, pulvilli and arolia absent (figure 4D). Ten terga (T1–T10) are visible on the abdomen (figures 2A, 3A, 4B). Abdominal terga (T2–T8) are strongly specialized: the posterior margin of T2 is medially strongly concave, T3 contains medially large round glandular pit with longitudinal elevated part in the middle, T4 has a large deep fossa, a pair of large tubercles at each posterior border of T5–T8

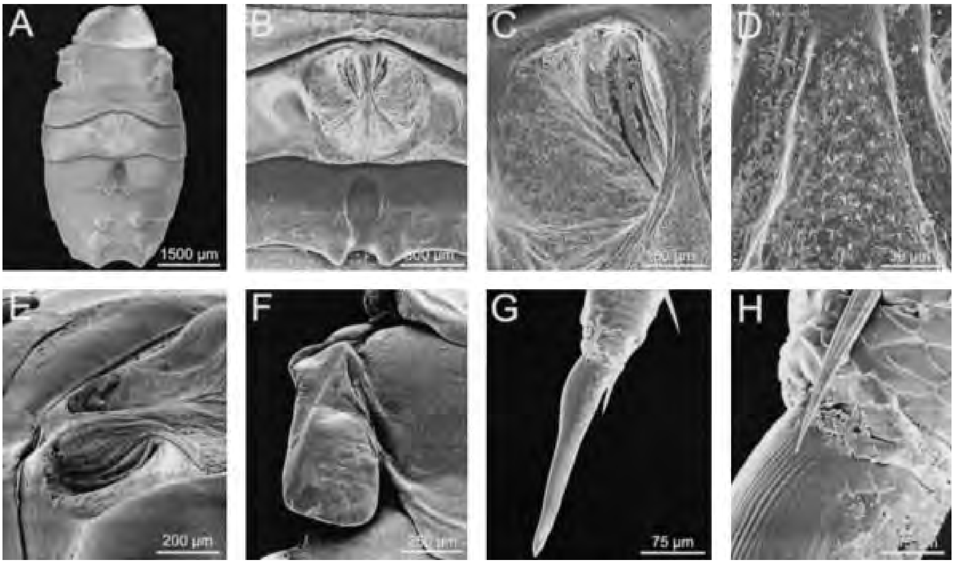

FIG. 3. *Spelaeoblatta myugei*, male. (A) Thorax and abdomen; (B) tergal gland—T3 + T4 (dorsal view); (C, D) tergal gland—detail (dorsal view); (E) tergal gland (dorsolateral view); (F) reduced hind wing; (G, H) apex of left cercus.

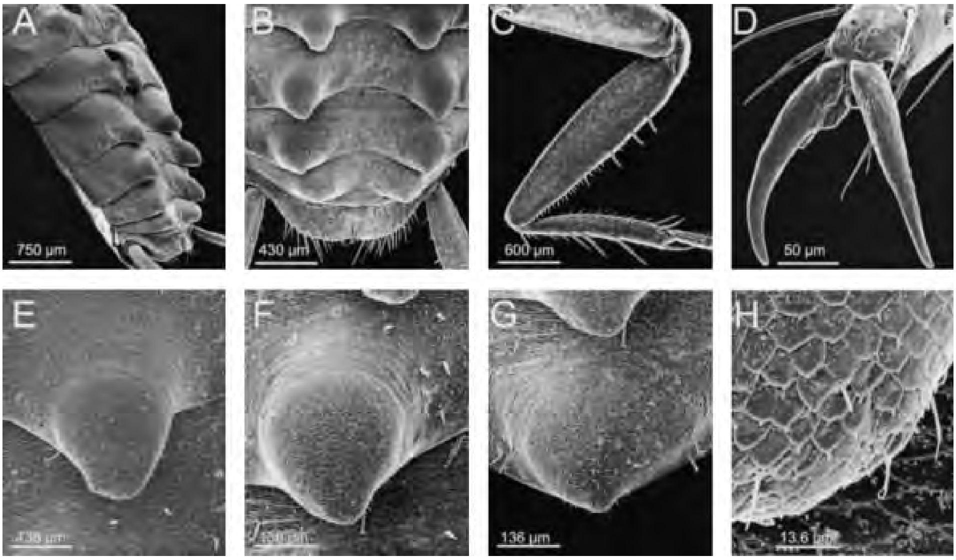

FIG. 4. *Spelaeoblatta myugei*, male. (A) Abdomen (dorsolateral view); (B) abdomen—T5–T10 (dorsal view); (C) front femur and tibia (ventral view); (D) tarsal claws; (E) left tubercle on T5; (F) left tubercle on T6; (G) left tubercle on T7; (H) left tubercle on T5—detail of structure.

(unique in Blattaria; figure 4A, B, E–H). Hind margin of supraanal plate rounded with a shallow medial depression. Cerci 9–10 segmented, surface dorsally smooth, ventrally with long setae, long sensilla on the apex (figure 3G, H). Subgenital plate is symmetrical with two similar setose styles, interstylar margin convexly rounded (figure 2E). Genitalia are shown in figure 2D: genital hook projects on the left side, the apex strongly narrow, curved; right phallomere strongly sclerotized, curved to S shape.

Colour: the specimens are pale brownish yellow, nearly translucent. Only maxillae and tubercles on abdomen are darker.

Female (figure 2B). Head exposed, faceted eyes reduced, but present. Pronotum parabolic, lateral hind corner slightly oblong. Tegmina strongly reduced to lateral pads slightly overlapping mesomotum, veins indistinct. Metanotum laterally distinct elongated. Hind margin of supraanal plate convexly rounded with long setae. Subgenital plate with distinct valves. Pattern of front femur same as in the male.

Colour: the specimens are pale brownish yellow, nearly translucent.

Remarks

This species differs from *S. thamfaranga* described by Roth principally by the presence of large tubercles on the hind margins of abdominal terga 5–8. Roth claimed that the tergal glands were present on the second and third segments, but our observations suggest that he may have missed the narrow first segment. His drawing (figure 2H in Roth and McGavin, 1994: 1322) is very similar to our figure 2A, except for the apparent absence of segment 1.

Spelaeoblatta thailandica n. sp.

(figure 5A–C)

Type material. HOLOTYPE: ♂, north-west Thailand: Red Cliff Cave (Mae Hong Son Province, Nam Lang region, 19°36′N, 98°04′E), 24 March 1997, N. Myuge (H. Miore) leg., coll. SNM-NHMB.

Etymology. The specific name refers to the country of origin.

Description

Size (mm). Body length: ♂ 8.75; pronotum length × width, ♂ 2.4 × 3.4; forewing length, ♂ 5.0.

Male (figure 5A–C). Head longitudinal, oval, partly visible from above; compound eyes strongly reduced but present; ocelli absent; apex of fifth maxillary palpomere rounded. Antennae long, slender, about 60 segments, scapus and third segment long, other segments markedly shorter. Pronotum unicoloured, parabolic, the middle of hind margin straight, lateral corners obliquely truncated. Tegmina reaching to the end of fifth tergite, obliquely truncate, surface covered by rather sparse trichia, especially on apical part of venation. Hind wings reduced, only lobate, reaching to a half of the metanotum length. Ten abdominal terga visible. The posterior margin of T2 medially concave. T3 has a medial, inverted Y-like glandular fossa, with hind margin medially elongated and elevated. T4 with a small medial indentation, and T4–T7 with collar-like elevations on the hind margins. Hind margin of supraanal plate is oval with medial shallow depression. Cerci are composed of 10 segments, surface dorsally smooth, ventrally with long setae, apically with long sensilla. Subgenital plate symmetrical with two similar setose styles, interstylar margin plane contains small medial elevation (figure 5C). The genital hook on the left side, the apex strongly curved.

Colour: the specimen is pale brownish yellow, nearly translucent.

Male nymph. Size (mm): body length: 6.9; pronotum length × width, 1.9 × 2.5;

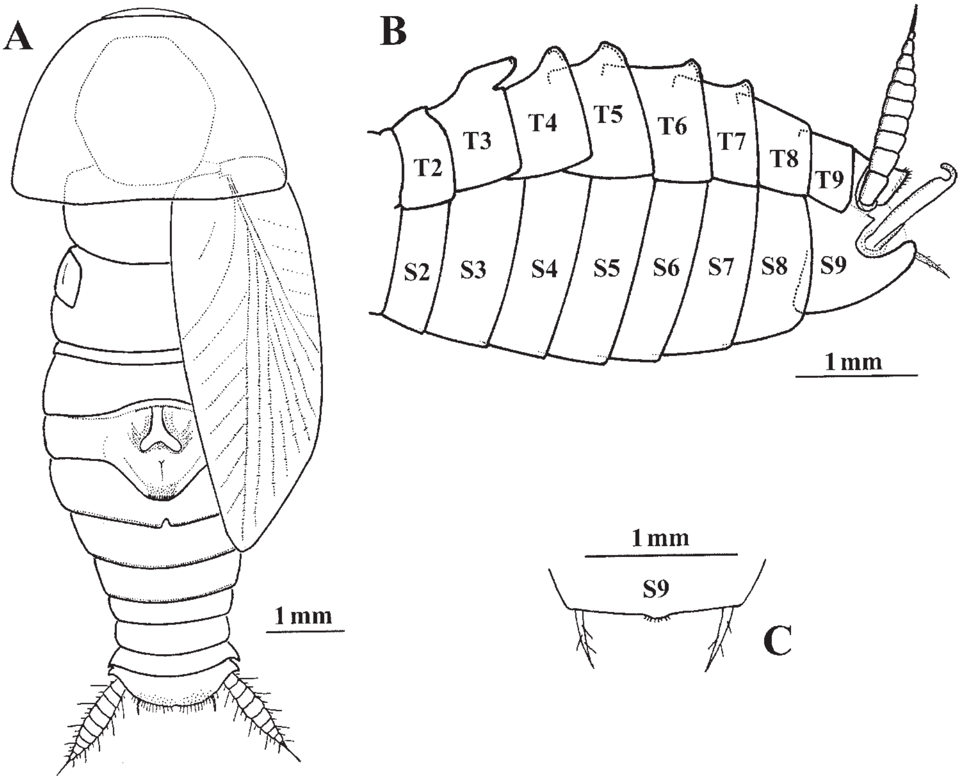

FIG. 5. *Spelaeoblatta thailandica*, male. (A) Habitus; (B) abdomen (lateral view); (C) subgenital plate (dorsal view).

front femur length, 1.9. Head with compound eyes having approximately 100 separated ommatidia that become smaller towards the antennae. Wing pads on meso- and metanotum markedly long. Anteroventral margin of front femur with three large proximal spines followed by a row of piliform spinules (type B_1); tarsal claws simple, symmetrical, pulvilli and arolia absent. T3 medially elongated as in the adult male. Subgenital plate with two small styles.

Remarks

The species *S. thailandica* and *S. gestroi* were only described from a single male and a single female, respectively. So far, their opposite sexes are not known. Until the male of *S. gestroi* is found, we cannot exclude a possibility that *S. thailandica* is a male of *S. gestroi*. However, *S. gestroi* was captured about 170 km SW from the locality inhabited by *S. thailandica*. Known cave-dwelling cockroaches have only very limited areas of distribution (Vandel, 1965; Izquierdo and Oromi, 1994), thus we believe that both described sexes are very probably different species.

Species groups

(1) *Thamfaranga* species-group: Hind margin of male abdominal tergites without elevations or paired tubercles. Species: *S. thamfaranga* Roth.

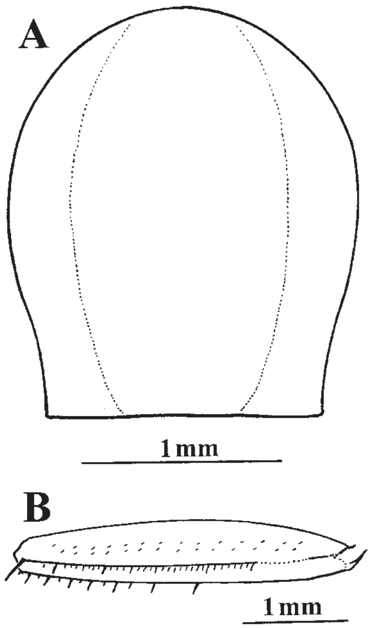

FIG. 6. Female nymph from Red Cliff Cave. (A) Pronotum; (B) front femur (anteroventral view).

(2) *Myugei* species-group: The hind margin of several male abdominal tergites with elevations or paired tubercles. Species: *S. myugei* n. sp., *S. thailandica* n. sp.

Key to males of *Spelaeoblatta* from Thailand

(The male of *S. gestroi* Bolivar from Burma is unknown.)

1 Hind margins of the abdominal tergites without elevations or paired tubercles (see Roth and McGavin, 1994: figure 2F) . . . . *S. thamfaranga*
– Hind margins of several abdominal tergites with elevations or paired tubercles . . 2

2 Paired lateral tubercles on hind margins of segments 5–8 . . . . *S. myugei*
– Elevations on hind margins of segments 4–7 . . . . *S. thailandica*

Note

Together with caged adult males and nymphs of *S. thailandica* were found two female nymphs, possibly of a new genus of cavernicolous cockroach. Nymphs are markedly different from all known species of Nocticolidae. They are completely blind, very slender, yellowish white nearly translucent. The head is sparsely but distinctly setose. Pronotum is long and narrow (figure 6A) similar to that of mantids. Wing pads are indistinct. Front legs are very long, front femur of type C (figure 6B). Subgenital plate without styles. Size of smaller nymph (mm): body length: 6.9; pronotum length × width, 2.13 × 1.75; front femur length, 3.1. Size of larger nymphs (mm): body length: 8.25; pronotum length × width, 2.25 × 1.85; front femur length, 3.4.

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New species of *Macrophyllodromia* (Blattaria, Blattellidae) from Ecuador and a key to males of the genus

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Abstract

Representatives of the cockroach genus *Macrophyllodromia* are widely distributed in Central and South Americas. The genus involves 10 species, including one new species described here, that are divided into 3 species groups—*splendida*, *amabile* and *maximiliani*. *Macrophyllodromia onorei* **sp. n.** is described as the fourth species of this genus from Ecuador. A key is provided for males of all known species of *Macrophyllodromia* and a species distribution map is presented.

Key words: *Macrophyllodromia*, cockroach, distribution, Central and South America, taxonomy

Introduction

The Neotropical zone is known for very rich biodiversity. The cockroach fauna (Blattaria) of this region comprises about 2,000 species belonging to approximately 180 genera. The Ecuadorean cockroach fauna includes 115 species belonging to 45 genera (Vidlička 2013, Vršanský *et al.* 2012). However, descriptions of many new species from this area are expected in close future.

The Neotropical cockroach genus *Macrophyllodromia* is widespread in Central America and the northern half of South America. The genus was first described by Saussure and Zehnter (1893) and *M. maximiliani* was defined as its type species by monotypy. This species was originally described as *Pseudophyllodromia maximiliani* by Saussure (1873) from Mexico. It is widely distributed in Central America (Mexico, Guatemala, Honduras, Costa Rica and Panama). The second species of the genus, *M. splendida* Hebard, 1920 and *M. panamae* Rocha e Silva Albuquerque, 1962, the most recently described Central American species, have been found only in Panama.

Six species are known from South America. Almost all species are poorly represented in insect collections; only *M. nigrigena* has been recorded from more than one country—in Guyana, French Guiana (Hebard 1926) and Suriname (Bruijning 1959). This species also was listed from Bolivia (Rocha e Silva Albuquerque 1962), but the data need reexamination. Evidence on this species in Bolivia is based only on 1 female, the identification of which is problematic. Descriptions of most representatives of *Macrophyllodromia* are based on males and females are unknown. The record from Bolivia indicates a disjunct distribution area of *M. nigrigena*.

Until now, only 2 species (*M. lanceolata* and *M. multipunctata*) have been described from Brazil, both from the same locality, but they look markedly different (Lopes & Oliveira 2006). All other known species (including the species described herein) come from diverse areas of Ecuador. The holotype of *M. ecuadorana* is probably a native from Guayaquil, Ecuador, but it was intercepted at San Diego, California, USA, on bananas. All other examined material from this species derivable from Ecuador was also intercepted in USA. One specimen of this species came from Honduras but its occurrence there is controversial (Rocha e Silva Albuquerque 1962).

Two other species (*M. amabile* and *M. nobile*) were collected in NE Ecuador in 2005 (Anisyutkin 2007). Here I describe a new species from the highland region in central Ecuador. Interpretation of protrusions on the subgenital plate follows Anisyutkin (2007).

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Systematic entomology

Order Blattaria Latreille, 1810

Family Blattellidae Karny, 1908

Subfamily Pseudophyllodromiinae Hebard, 1929

Genus *Macrophyllodromia* Saussure and Zehnter, 1893

Type of genus: *Pseudophyllodromia maximiliani* Saussure, 1873.

Diagnosis. The genus *Macrophyllodromia* consisting of relatively large cockroaches (about 20 mm length) with a broad, dark longitudinal band on the head stretching from interocular field to labrum (absent in *M. nigrigena* Hebard and *M. nobile* Anisyutkin) and a pair of dark longitudinal bands on the pronotum (very modified in *M. multimaculata* Lopes & Oliveira). Males without pheromonal tergal gland on abdomen, subgenital plate asymmetrical with obvious protrusions. Tegmina and wings in both sexes fully developed.

Distribution: Central and South America.

The genus *Macrophyllodromia* shows close relationship to *Latiblattella* Hebard, 1917, *Antitheton* Hebard, 1919, and *Eurylestes* Hebard, 1940 (after Rocha e Silva Albuquerque 1962).

Macrophyllodromia onorei Vidlička, sp. n.

Figs. 1a–e, 2a

Type material. Holotype male, Ecuador, Otongachi reserve, 00°19'15"S; 78°57'06"W, near the village of La Union del Toachi, 33 km E of Santo Domingo de los Colorados, elev. ca 850 m, piedmont evergreen woodland, 19–25 September 2009, Ľ. Vidlička & M. Kozánek leg., deposited at the Institute of Zoology SAS, Bratislava, Slovakia.

Description. General colour of body yellowish brown (Fig. 1a).

Head with occiput pale, epicranium and vertex mostly black, but vertex over the ocelli with narrow irregular transverse yellow strip. Face yellow with broad longitudinal black band continued to labral suture. On clypeus band brown, but distinct. Genae black. Eyes and ocellar spots (fenestrae) yellowish. Maxillary palps yellowish, last joint brownish (Fig. 1b). Antennae brownish, tenuous, longer than whole body.

Pronotum widest in caudal third. Two black longitudinal bands (widest caudally) beginning on front margin, not reaching hind margin of pronotum. Sides of pronotum yellowish translucent, with scattered fine but visible dark dots (Fig. 2a). Tegmina and wings fully developed, folded and overlapping apex of abdomen. Veins reddish brown. Anal fields of forewings with eight anal veins, first vein with four rami. Interveinal areas in anal fields of forewings with narrow yellow stripes. Legs yellow, apical part of tibiae and tarsal segments on all legs black (Fig. 1c). Tarsal joints with large distal pulvilli. Tarsal claws simple, unspecialized, between them well developed arolia with bilobed distal end. Antero-ventral margin of front femur armed with 18 heavy spines of type A (*sensu* Bey-Bienko 1950, Roth 2003).

Abdominal dorsal surface unspecialised. Supra-anal plate short, triangular, bilobed at apex (Fig. 1d). Cerci elongated, composed of 15 distinctly separated segments (Figs. 1d, e). Subgenital plate strongly asymmetrical and of complicated design (Fig. 1e). Apical part divided into three protrusions. Protrusion on left side (LP) forming two large projections, the first extending straight back as a large, sharp horn with finely bifurcate apex (LP1), the second extending to the right as a very long, narrow rod-like sclerite (LP2), partly enclosed by small central growth (CG), and ending just right in deep groove of mitten-like right protrusion (RP) (Figs 1e, 3a). Styli completely absent, protrusions apparently only representing projections of the subgenital plate.

Measurements. Holotype (mm): length of body 20.7, length of pronotum 4.4, width of pronotum 7, length of tegmen 21.4, width of tegmen 6.4.

Etymology. This new cockroach species named in honour of Professor Giovanni Onore, missionary, entomologist and President of the Otonga Foundation in Ecuador.

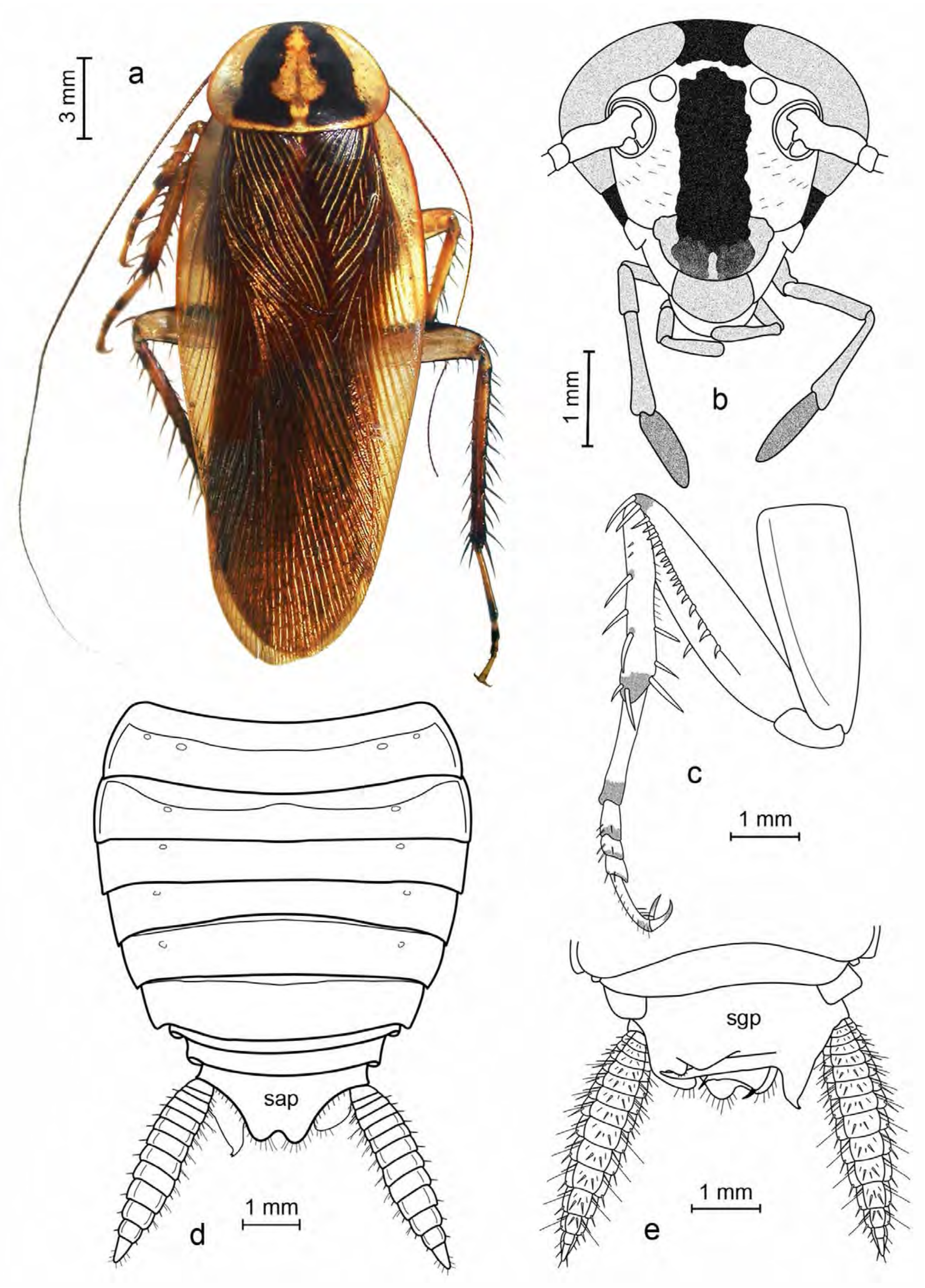

FIGURE 1. ***Macrophyllodromia onorei*** **sp. n.**, male: (a) habitus, (b) head with appendages, (c) right front leg (ventral view), (d) abdomen with cerci (sap: supra-anal plate) (dorsal view), (e) the tip of abdomen (sgp: subgenital plate) (ventral view).

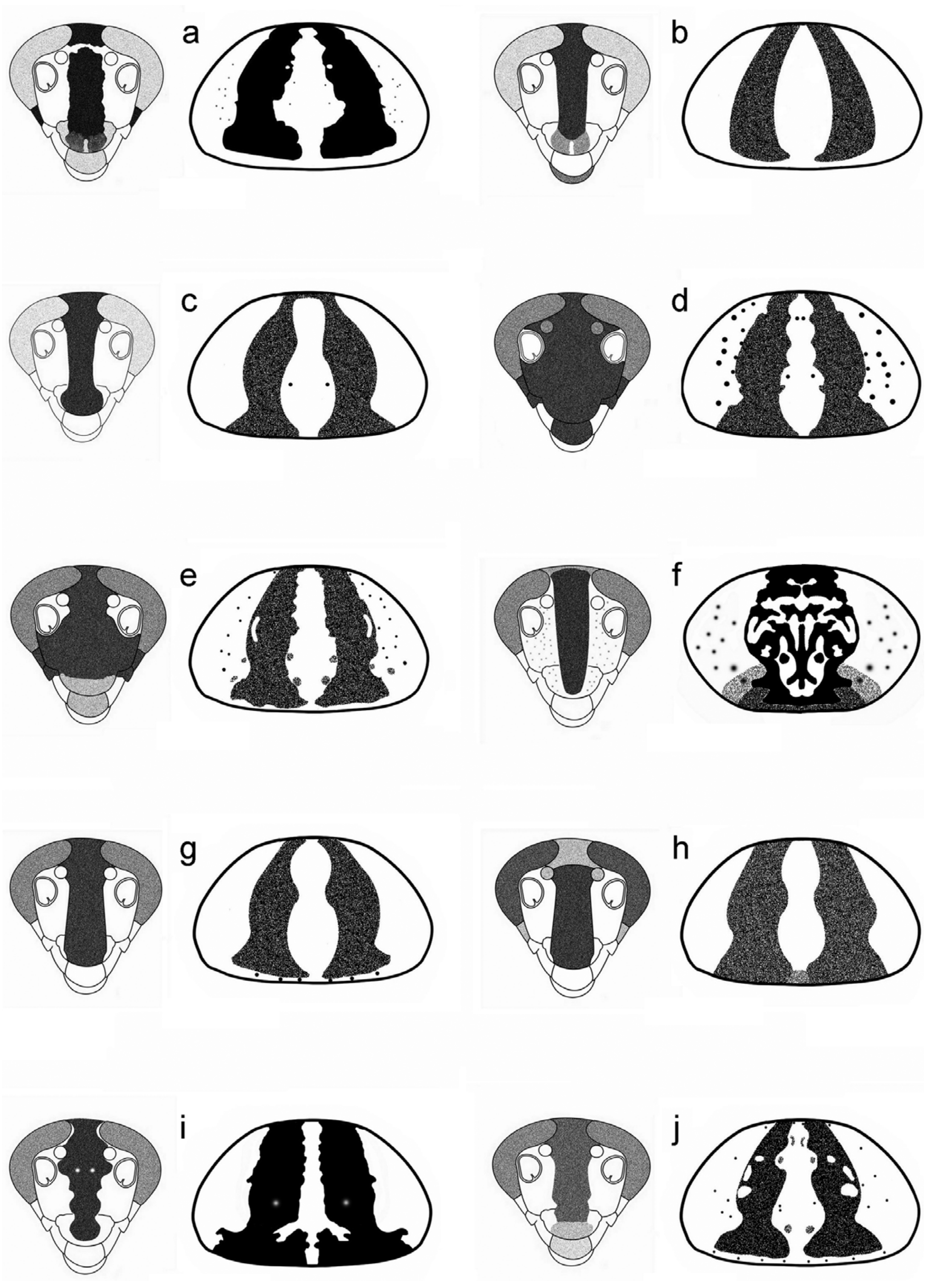

FIGURE 2. Male heads and pronotal shields of *Macrophyllodromia* spp. (a) *M. onorei* **sp. n.**, (b) *M. panamae*, (c) *M. ecuadorana*, (d) *M. nigrigena*, (e) *M. nobile*, (f) *M. multipunctata*, (g) *M. maximiliani*, (h) *M. splendida*, (i) *M. lanceolata*, (j) *M. amabile*. Figures 2b–2j are modified from drawings, descriptions and photos in Hebard (1920, 1926), Rocha e Silva Albuquerque (1962), Lopes & Oliveira (2006) and Anisyutkin (2007).

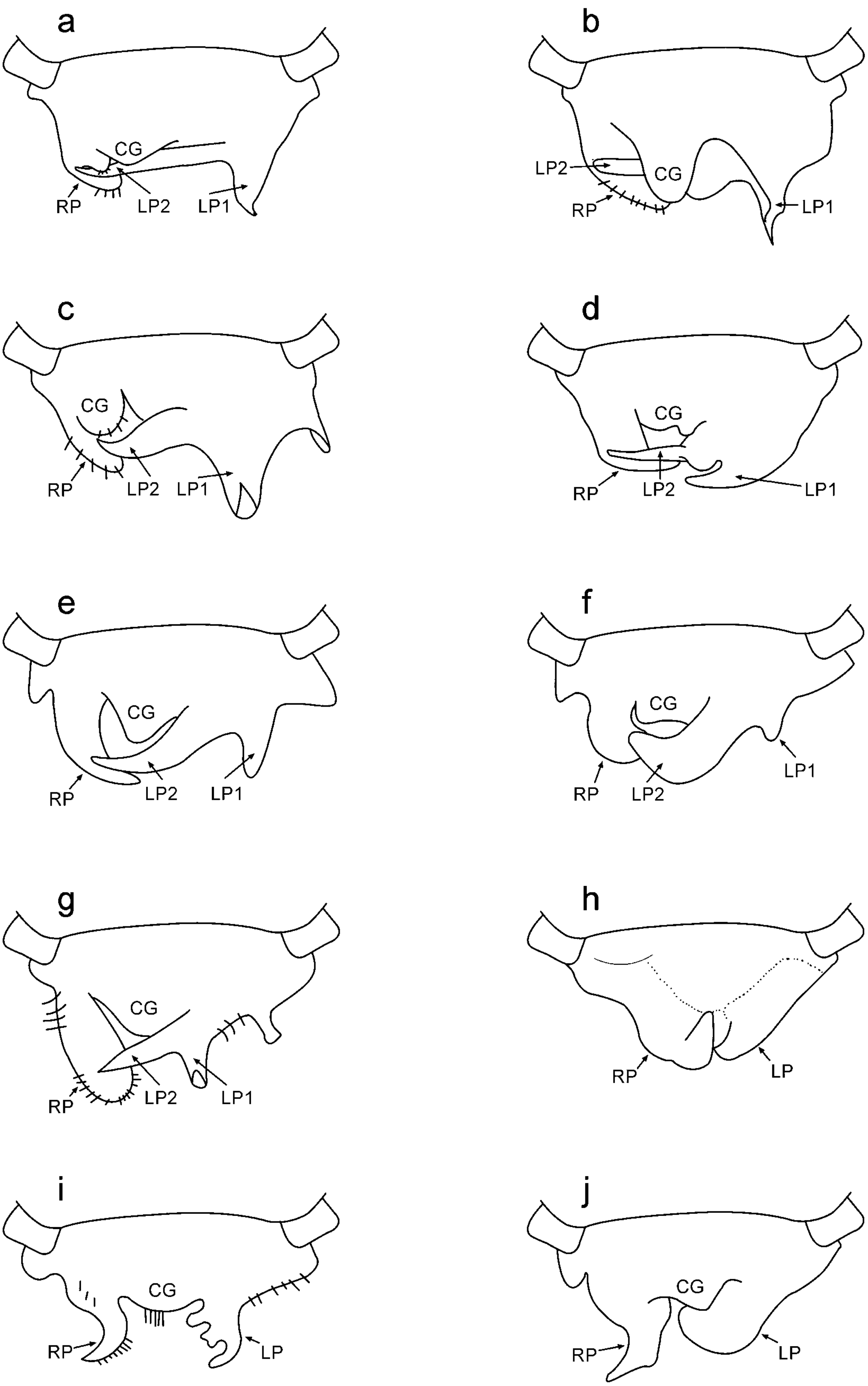

FIGURE 3. Subgenital plate of *Macrophyllodromia* spp. (ventral view). (a) *M. onorei* **sp. n.**, (b) *M. panamae*, (c) *M. ecuadorana*, (d) *M. nigrigena*, (e) *M. nobile*, (f) *M. multipunctata*, (g) *M. maximiliani*, (h) *M. splendida*, (i) *M. lanceolata*, (j) *M. amabile*. RP: right protrusion, LP: left protrusion, LP1, LP2: projections of left protrusion, CG: central growth. Figures 3b–j are modified from descriptions and illustrations in Hebard (1920, 1926), Rocha e Silva Albuquerque (1962), Lopes & Oliveira (2006) and Anisyutkin (2007).

Differential diagnosis. *Macrophyllodromia onorei* **sp. n.** is similar to *M. panamae* in the length of the dark longitudinal bands of the pronotum (bands not reaching posterior margin of pronotum) but not in their form (Figs. 2a, 2b). Structure of the subgenital plate is also similar in both species, but the central growth (CG) is markedly shorter in *M. onorei* (Figs. 3a, 3b). The new species is similar to *M. ecuadorana, M. nigrigena, M. nobile* and *M. amabile* in the coloration of the pronotum (Figs. 2c, 2d, 2e, 2j), but it is easily distinguishable from all those species in the presence and form of the dark longitudinal band on the face (*nigrigena* and *nobile* have the whole face dark; see Figs. 2d, 2e) interrupted with a narrow pale transversal strip over the ocelli. In *M. ecuadorana* and *M. amabile* this band is without interruption (Figs. 2c, 2j).

Survey and distribution of *Macrophyllodromia* species (Fig. 4)

1. *Macrophyllodromia maximiliani* (Saussure, 1873)

Mexico, 1 male (Saussure 1873); Guatemala, 1 male, Dept. Petén, near Lake Eckibix (=Laguna Oquevix, located on the savanna about 40 km south of town Flores) (Rocha e Silva Albuquerque 1962); Honduras, 1 male, 3 females, Guaimas Dist., Tela (Rocha e Silva Albuquerque 1962); Costa Rica, 1 male, intercepted at San Francisco, USA (Rocha e Silva Albuquerque 1962); Panama, 1 female, Barro Colorado Island (Hebard 1933); 1 male, Barro Colorado Island; 1 male, 1 female, intercepted at San Francisco, USA (Rocha e Silva Albuquerque 1962); 1 male, Barro Colorado Island (Roth & Naskrecki 2001).

2. *Macrophyllodromia splendida* Hebard, 1920

Panama, 2 males, Porto Bello (=Portobelo) (Hebard 1920); 1 female, Barro Colorado Island (Hebard 1933).

3. *Macrophyllodromia nigrigena* Hebard, 1926

French Guiana, 1 male, 1 female, St Jean du Maroni; 1 female, St. Laurent du Maroni (Hebard 1926); Guyana, 2 males, 1 juv. male, 1 female, Distr. Bartica, Kartabo (Hebard 1926); Suriname, 1 male, Coppename (Bruijning 1959); Bolivia, 1 female, Tumupasa (Rocha e Silva Albuquerque 1962)

4. *Macrophyllodromia ecuadorana* Rocha e Silva Albuquerque, 1962.

Ecuador, 1 male, Guayaquil, intercepted at San Diego, USA; 2 males, 4 females, 1 nymph, intercepted in USA (Rocha e Silva Albuquerque 1962); Honduras ?, 1 male, intercepted at New Orleans, USA (Rocha e Silva Albuquerque 1962).

5. *Macrophyllodromia panamae* Rocha e Silva Albuquerque, 1962

Panama, 1 male, Barro Colorado Island (Rocha e Silva Albuquerque 1962); 1 male, Barro Colorado Island (Roth & Naskrecki 2001).

6. *Macrophyllodromia lanceolata* Lopes & Oliveira, 2006

Brazil, 8 males, Acre, Senador Guiomard, Reserva Catuaba (Lopes & Oliveira 2006).

7. *Macrophyllodromia multipunctata* Lopes & Oliveira, 2006

Brazil, 1 male, Acre, Senador Guiomard, Reserva Catuaba (Lopes & Oliveira 2006).

8. *Macrophyllodromia amabile* Anisyutkin, 2007

Ecuador, 1 male, 1 female, env. of waterfall San Rafael on Rio Coca, forest, 95 km E of city Quito (Anisyutkin 2007).

9. *Macrophyllodromia nobile* Anisyutkin, 2007

Ecuador, 1 male, 80–85 km E of town Lago Agrio, env. of lake Lago Grande, Rio Cuyabeno (Anisyutkin 2007).

10. *Macrophyllodromia onorei* Vidlička, sp. n.

Ecuador, 1 male, Otongachi reserve, near the village of La Union del Toachi, 33 km E of Santo Domingo de los Colorados.

FIGURE 4. *Macrophyllodromia* species distribution map (Central and South America). (1) *M. maximiliani*, (2) *M. splendida*, (3) *M. nigrigena*, (4) *M. ecuadorana*, (5) *M. panamae*, (6) *M. lanceolata*, (7) *M. multipunctata*, (8) *M. amabile*, (9) *M. nobile*, (10) *M. onorei* **sp. n.**

Key to males of *Macrophyllodromia* (species groups and species).

1. Caudal end of subgenital plate with two distinctly separated protrusions 2
- Left and right protrusions on the caudal end of subgenital plate slightly asymmetrical, separated only with narrow groove (Fig. 3h); two pronotal bands fused at the caudal margin (Fig. 2h) (*splendida* group) . . . . *M. splendida*
2. Right protrusion outward rotated (Figs. 3i, 3j) (*amabile* group) 3
- Right protrusion inward rotated (Figs. 3a–3g) (*maximiliani* group) 4
3. Left protrusion comb-like (Fig. 3i), two black longitudinal bands on pronotum parallel, on posterior margin markedly expanded (Fig. 2i) . . . . *M. lanceolata*
- Left protrusion compact (Fig. 3j), black longitudinal bands on pronotum convergent towards anterior margin of pronotum (Fig. 2j) . . . . *M. amabile*
4. Right protrusion straight, on left stylus a small leftward protrusion (Fig. 3g); tegmen with row of dark, obvious spots. . . . . *M. maximiliani*
- Right protrusion moderately but visibly curved (Figs. 3a–3f); tegmen without spots 5
5. Interior part of left protrusion (LP2) curved toward right stylus, marginal part (LP1) short and straight (Figs. 3e, 3f). 6
- Interior part of left protrusion (LP2) narrow, transverse; marginal part (LP1) obviously curved inward or its tip cuspidate and bent (Figs. 3a–3d) 7
6. Protrusions RP and LP2 equally tapering (Fig. 3e); dark bands on pronotum obvious (Fig. 2e); most of facial part of head dark (Fig. 2e) . . . . *M. nobile*
- Protrusions RP and LP2 thick, tapered only on last third (Fig. 3f); pronotum with intricate dark mosaic not in band-like form (Fig. 2f) . . . . *M. multipunctata*
7. Protrusion LP1 wholly curved inward (Fig. 3d); facial part of head dark (Fig. 2d); two pronotal longitudinal bands briefly separated at the caudal margin (Fig. 2d). . . . . *M. nigrigena*
- Protrusion LP1 pointed, straight or the tip distinctly curved, facial part of head with longitudinal dark band; pronotal longitudinal bands widely separated at the caudal end 8
8. Central growth (CG) not at all overlapping protrusion LP2 (Fig. 3c); extended caudal end of pronotal dark bands reaching posterior margin of pronotom (Fig. 2c) . . . . *M. ecuadorana*
- Central growth (CG) overlapping protrusion LP2 at least partially; caudal end of pronotal dark bands not reaching posterior margin of pronotum. 9
9. Central growth (CG) very long, completely overlapping central part of LP2 (Fig. 3b); pronotal longitudinal bands relatively narrow with smooth margins (Fig. 2b); facial part of head with uninterrupted longitudinal dark band (Fig. 2b) . . *M. panamae*
- Central growth (CG) only slightly protuberant, partially overlapping central part of LP2 (Fig. 3a); pronotal longitudinal bands wide with indented margins (Fig. 2a); facial part of head with longitudinal dark band on facial part of head with transverse light stripe over ocellar spots (Fig. 2a) . . . . *M. onorei* **sp. n.**

Notes. In only five of *Macrophyllodromia* species have females been described. Several unnamed females also have been reported. Anisyutkin (2007) mentioned 4 females from 3 various localities in Ecuador. They probably represent at least two different species, but their assignment to the known species was not possible at that time. Roth & Naskrecki (2001) also mentioned an unknown female (probably a new species) from Costa Rica.

The transverse light stripe over the ocellar spots is characteristic for females of *M. amabile* and also some unnamed females from Rio Aguarico, Ecuador (Anisyutkin 2007). *Macrophyllodromia onorei* is the first species found in which the male has a strong transverse stripe over the ocellar spots.

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Cockroaches (Blattaria) of Ecuador—checklist and history of research

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Abstract

Cockroaches are an understudied group and the total number of described taxa increases every year. The last checklist of Ecuador species was published in 1926. The main aim of this study was to complete a new checklist of cockroach species recorded in Ecuador supplemented with a research history of cockroaches (Blattaria) on the territory of continental Ecuador. In addition, the checklist contains comments on Ecuadorian faunistic records, including the Galápagos Islands. A total of 114 species (105 in continental Ecuador and 18 in Galápagos Islands) belonging to 6 families and 44 genera are listed. Forty species (38.1 %) occur solely in continental Ecuador and five (27.8 %) are endemic on Galápagos Islands.

The results indicate that further research on the cockroach fauna of Ecuador as well as determination of museum collections from this territory is needed.

Key words: cockroach distribution, catalogue, South America, faunistic record

Introduction

Cockroaches (Blattaria) are a mainly tropical and subtropical order of insects. The Neotropical zone (South and Central America, including the Caribbean Islands) have, in comparison with other zoogeographic regions, the richest fauna of cockroaches. About 2,000 of approximately 5,500 known recent species are native to South America. Cockroaches are an understudied group and the total number of described taxa increases every year, especially from the Neotropical region. In the last decade checklists of cockroaches from several South American countries have been published. The greatest number of species was recorded from Brazil, probably due to its great size and diverse biotopes. In 2008, 647 species were listed from Brazil (Pellens & Grandcolas 2008), an increase of almost 70% over the 383 species listed in 1964 (Rocha e Silva Albuquerque 1964a). Recent regional faunal lists in the Neotropics have been published for Colombia (133 species; Vélez 2008), Argentina (89 species; Crespo *et al.* 2010), Venezuela (87 species; Bonfils 1987; Perez 1988), Nicaragua (97 species; Maes 1992a,b,c), Puerto Rico (48 species; Gutiérrez 1999) and Cuba (85 species; Gutiérrez 1995).

Cockroaches of Ecuador are insufficiently explored. The last summaries were compiled by Campos (1923, 1926). Additional data on occurrence of cockroaches are scattered in various publications. The Galápagos Islands are the best studied Ecuadorian region, but a number of species is very low (18 species; Peck & Herrera 2011). An annotated list of Galápagos Blattaria is given in the paper of Peck & Roth (1992).

This study is based on a critical evaluation of the published data on Ecuadorian cockroaches. The base sources were the checklists of Campos (1923, 1926) and the catalogues of Princis (1962, 1963, 1964, 1965, 1966, 1967, 1969, 1971). The classification is based on McKittrick (1964) and Roth (1970d, 2003a), and also takes into account the works of Grandcolas (1996) and Djernaes et al. (2012).

Determination and revision of cockroach material deposited in many museums will be carried out in following years.

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Cockroaches of continental Ecuador—history of research

The oldest reference about cockroaches in the territory of Ecuador was listed in a book from Italian Jesuit **Mario María Cicala** (19 January 1718, Fiume di Nisi–after 1785, Viterbo). Cicala was a missionary in Ecuador and he stayed there for 23 years (1743–1767). He described his experiences in two books, but only the manuscript of the second part from the year 1771 (Cicala 1994, 2004) has been preserved. He divided cockroaches into three groups, but he did not mention any particular species. At the end he wrote, “All houses and apartments are full of cockroaches at all times.” (Cicala 2004:189).

The first cockroach species known and described from Ecuador was *Paratropes aequatorialis* (Saussure, 1864). Swiss orthopterologist **Henri Louis Frédéric de Saussure** (27 September 1829, Geneva–20 February 1905, Geneva) only indicated that this species was from the locality “Respublica Equator” and did not give the name of the collector or more accurate locality data. Saussure visited the West Indies, Mexico and the United States in period of time from 1854 to 1856, where he collected insects (Bedot 1906a, b). He traveled with another Swiss naturalist, **Adrien Jean Louis François de Sumichrast** (15 October 1828, Yvonne, Canton de Vaud, Switzerland–26 September 1882, Tonalá, Chiapas, Mexico). Their valuable collections were taken to Geneva by Saussure in 1856, while Sumichrast decided to stay in Mexico (Papavero & Ibáñez-Bernal 2001). Orthopteroid specimens (now in the Natural History Museum of Geneva) were described by Saussure in a long series of papers (Saussure 1859, 1861, 1862, 1864. 1868, 1869, 1893–1899). These works contained descriptions of orthopterans not only from Central America but also from northern South America countries (Brazil, Guyana, French Guiana, Suriname, Peru, Bolivia, Chile, Venezuela and Ecuador). These specimens may have been obtained during his travel. The aforementioned specimen of *P. aequatorialis* is deposited in the Geneva Museum and has slightly more detailed labeling than the published record: “Quito, Andes, M. H. de Saussure” (J. Hollier, personal communication). One grasshopper species (*Chromactis ictera* (Pictet & Saussure, 1887)) is labelled as “Quito, M. H. de Saussure” (Hollier 2011). These two cases suggest that Saussure was the collector of this cockroach species.

Subsequent data on Ecuadorian cockroaches were published by English entomologist **Francis Walker** (31 July 1809, Southgate–5 October 1874, Wanstead). Between 1844 and 1873 Walker was employed as a curator in the British Museum Natural History where he worked on collections of orthopterous insects. His catalogue of cockroaches (Walker 1868) includes five species from the territory of Ecuador. All five species were described as new to science, but two of them were later synonymized. Two of these species (*Blaberus parabolicus* and *Paratropes lanceolatus* (syn. of *P. aequatorialis*)) originated from the Fraser’s collection. **Louis Fraser** (1819, England–1884, USA) was an excellent British naturalist, zoologist and collector. He was curator at the Museum of the Zoological Society in Brewer Street, Golden Square (London). Fraser participated in a number of expeditions and collected vertebrates and insects in Ecuador in 1857–1859. His first collecting place was Cuenca, the capital city of the Azuay Province (formerly Cuenca) (October–November 1857, March–May 1858). In this locality both species (each of one specimen) were collected. From December 1857 through February 1858 he was at Gualaquiza (Morona Santiago Province) and Zamora (Zamora Province). Afterwards, from June to August 1858 he was at Riobamba (Chimborazo Province) and its sourroundings (Guana, Pinipi, Matos, Titiacun, Punin). He spent four months (August–November 1858) at Pallatanga, a pueblo southeast of Riobamba. In the middle of January 1859 he returned to Riobamba and then made an excursion to Panza (southern slope of Chimborazo), returned to Riobamba, and then moved to Quito. During period of February–April 1859 Fraser visited various places in the surroundings of Quito. From July to September 1859 he visited the environs of Guayaquil, then left for Esmeraldas. During October–December 1859 Fraser paused at Esmeraldas, on the coast of Ecuador and on his route from Guayaquil to Panama by sea (Sclater 1858a, b, 1859, 1860a–e; Sharpe 1906; Moore 2004).

Two other roaches described by Walker (*Megaloblatta longipennis* and *Polyzosteria crassipes* (syn. of *Pycnoscelus surinamensis*)) came from Stevens’ collection. **Samuel Stevens** (11 March 1817, St Martin-in-the-Fields, Middlesex–29 September 1899, Beulah Hill, Croydon, Surrey) was a Fellow of the Linnean and Entomological Societies of London and Entomological Club and a familiar figure at meetings of naturalists. In 1848 he established the Natural History Agency in Bloomsbury Street (London), where bought and sold insects from all over the world. He supported various explorers and collectors, the best known of whom were Alfred Russel Wallace and Henry Walter Bates, who collected natural history specimens in South America, too. Stevens acted as their agent in the distribution of the animals and insects that they obtained. Many specimens were bought from Stevens by the British Museum of Natural History. After Stevens’ death his collections of insects were sold at the auction (Anonymous 1899a, 1899b; Sharpe 1906; Baker 2001).

The last of Walker's cockroach species (*Panchlora nigricornis*) was donated to the British Museum by French naturalist and collector **Jules Bourcier** (1797, Cuisery, Saône-et-Loire–9 March 1873, Batignolles, Paris), who acted as French Consul in Ecuador from 1849 to 1850. All of Walker's specimens are deposited in the Natural History Museum, London.

Further cockroach species from Ecuador were described by the American orthopterologist **Samuel Scudder** (13 April 1837, Boston–17 May 1911, Cambridge, Massachusetts) in 1869. Four of nine species mentioned in his study (Scudder 1869) were newly described, but three of them were later synonymized: *Blabera armigera* (syn. of *Blaberus parabolicus*), *Blabera cubensis* (syn. of *Blaberus discoidalis*), *Blabera femorata* (syn. of *Eublaberus posticus*). Only *Ischnoptera pallipes* is a valid species. The other five species (*Panchlora exoleta*, *Lanxoblatta rudis* (?), *Periplaneta americana*, *Periplaneta australasiae* and *Ischnoptera melasa* [as *I. melana*]) were new records for Ecuador.

Cockroaches determined by Scudder came from the collection of the first expedition of the well-known American theologian, naturalist and collector **James H. Orton** (21 April 1830, Seneca Falls, New York–25 September 1877, shore of Lake Titicaca, Peru) in South America. His expedition team was composed mostly of students from Williams College, and the expedition was made under the auspices of the Smithsonian Institution. The expedition sailed from New York on 1 July 1867, crossed the Isthmus of Panama and reached Paita (NW coast of Peru). Exploration started on 19 July 1867, in the coastal tropical forest of Guayaquil (Ecuador). The first "huge cockroach" (*Blaberus discoidalis*) was caught in the city of Guayaquil (Orton 1870). The general route was from Guayaquil up the Rio Guayas, over the western Cordillera near Chimborazo into the valley of Quito; thence over the eastern Cordillera to the Rio Napo and down that river to the Marañón. Orton's second expedition into South America was in 1873 and the third in 1876. Orton died during the third expedition (Treadwell 1934; Miller 1982).

Additional faunistic records of Ecuadorian cockroaches were made by English entomologist and professor at Oxford University **John Obadiah Westwood** (22 December 1805, Sheffield, Yorkshire–2 January 1893, Oxford) in 1876. In an orchid bulb from Ecuador, he found nine living specimens of cockroaches comprising six different species (*Rhyparobia maderae*, *Nauphoeta cinerea*, *Blatta orientalis*, *Periplaneta americana* and two unknown species). The bulb was purchased by British naturalist **William Chapman Hewitson** (9 January 1806, Newcastle-upon-Tyne-28 May 1878 Oatlands Park) with a collection of roots from Ecuador. Hewitson was wealthy collector who purchased insects (especially Lepidoptera and Coleoptera), bird's eggs and other products of nature from travellers throughout the world (Evans 1908).

The excellent Spanish orthopterologist **Ignacio Bolívar y Urrutia** (9 November 1850, Madrid–20 November 1944, Mexico City) described four Ecuadorian cockroach species: *Blabera aequatoriana* (syn. of *Blaberus parabolicus*), *Zetobora martinezi* (now *Lanxoblatta martinezi*), *Anaplecta pallida*, *Blatta nigrita* (incertae sedis) and provided new Ecuadorian records of six species: *Panchlora pulchella*, *Anaplecta lateralis*, *Ischnoptera consobrina* (syn. of *Ischnoptera rufa*), *Chorisoneura pellucida* (syn. of *Chorisoneura diaphana*), *Chorisoneura minuta*, and *Blatta adspersicolis* (now *Neoblattella adspersicollis*) (Bolivar 1881). Two species new for Ecudorian fauna (*Panchlora viridis* [probably *Panchlora nivea*] and *Blattella germanica*) were published by Bolivar (1884). Quote specimens comes from two collectors:

The first group of specimens was collected during an important Spanish scientific expedition, "The Pacific Scientific Commision", by the Spanish entomologist **Francisco de Paula Martínez y Sáez** (30 March 1835, Madrid–26 February 1908, Madrid). The members of this expedition began its survey of South America in San Salvador (Brazil) on 9 September 1862. On 31 August 1864 they arrived at Guayaquil (Ecuador). They proceeded to Quito (8 October 1864), then travelled across the Andes to River Napo. They also visited Cotopaxi Volcano and on 24 August 1865 reached River Marañón near the Brazilian boundary. Collections were placed in Madrid on 18 January 1866, of which the insect collection contained 19,522 specimens, 10,427 of them caught by Martínez y Sáez. The cockroach species *Lanxoblatta martinezi* was named by Ignacio Bolívar in his honour (Almagro 1866; Martínez y Sáez 1994; López-Ocón 2003).

The second collection was assembled by Polish zoologist **Jean Stanislaus Stolzmann** (or Jan Sztolcman; 19 November 1854, Warsaw–28 April 1928, Warsaw), Director of the Zoological Museum of Branicki at Warsaw from 1887 and Vice Director of the Polish Museum of Natural History from 1919. Stolzmann's zoological expeditions in Peru (1875–1881) and Ecuador (1882–1884) were financially covered by the Branicki brothers. Stolzmann himself focused mainly on birds and mammals, but also collected insects. All cockroaches collected by Stolzmann were caught at the locality "Palmal". Identification of this locality is difficult. Palmal is a humid rainforest in the southern area of the western coast of Ecuador, near the city of Tumbes and the Tumbes River (Taczanowski 1877; Taczanowski & Berlepsch 1885), and probably is identical with "Palmales", situated 10 km from the Peruvian border near the city of Arenillas. Tumbes is located on the northwest coast of Peru, 40 km from Palmales.

The English mountaineer, explorer and illustrator **Edward Whymper** (27 April 1840, London–16 September 1911, Chamonix, France) organized a climbing expedition in Ecuador from 9 December 1879 to 27 July 1880. During this expedition he also collected insects. Regarding his unique orthopteroid collection from high elevations of Chimborazo Volcano, he wrote: "The whole of this collection remains undescribed. Leaping Orthoptera were found very numerous up to the height of 12–13,000 feet, and upon Chimborazo were obtained in the Vallon de Carrel at 16,000 feet" (4,877 m; Whymper 1892). Cockroaches specifically were mentioned from environs of Altar Volcano near Riobamba, upon river Collane: "*Blatta*–Not identified–Valley of Collanes, Altar 12,500 feet" (3,810 m), where Whymper camped on 17–19 June 1880. At the end of expedition, when he was lodged in Guayaquil (16–27 July 1880), he "collected fifty species of vermin in a single room". One of this "vermin" was a big cockroach of the genus *Blaberus*, displayed very faithfully in a table in Whymper (1892).

Swiss entomologist **Henri Louis Frederic de Saussure** and his collaborator **Leo Zehntner** (19 December 1864, Reigoldswil—3 April 1961 Liestal), assistant at the Natural History Museum in Geneva, described in 1895 one new cockroach species, *Hormetica strumosa*, from Ecuador but without detailed faunistic data.

The first comprehensive work on orthopteroid insects from Ecuador was published by the Italian entomologist **Ermanno Giglio-Tos** (25 March 1865, Chiaverano, Turin–18 August 1926, Turin) (Giglio-Tos 1898). Among 30 listed cockroach species were 14 new records for Ecuador and 10 species new to science (*Epilampra stigmosa, Epilampra josephi, Panchlora festae, Zetobora aberrans, Ischnoptera josephina, Xestoblatta hamata, Xestoblatta sancta, Neoblattella festae, Pelmatosilpha cothurnata, Lamproblatta zamorensis*). Specimens studied by Giglio-Tos are deposited in the Turin Museum of Natural History. This extensive collection was gathered by the Italian naturalist **Enrico Luigi Festa** (11 August 1868, da Corrado e da Teodora Vola–30 September 1939, Moncalieri) during an expedition in South America in May 1895–April 1898. He journeyed in Ecuador during 1896 and1897, beginning in Guayaquil. He then travelled to Cuenca and afterwards to the headwaters of the Rio Santiago of the Marañón system, and northwards by Quito to Julian, near the Colombian border (Festa 1909). During this expedition Mr. Festa collected about 150,000 invertebrates.

English orthopterologist **Robert Walter Campbell Shelford** (3 August 1872, Singapore–22 June 1912, Margate) started work in the Department of Zoology, Oxford University Museum as Assistant Curator in 1905, studying Orthoptera and particularly Blattaria. During 1906 and 1907 he described eight new cockroach species from Ecuador (*Anaplecta fusca, Anaplecta pavida, Anaplecta varipennis, Pseudomops albostriatus, Pseudomops bicolor, Pseudomops burri, Pseudomops magnus* and *Chorisoneura morosa*) which originated from the collection of **William Frederick Henry Rosenberg** (1868, Paddington, Hampstead-1957, Hendon, Middlesex). Rosenberg was professional collector and dealer of exotic animals (including insects). His first expedition in 1894 explored Colombia, where he remained about a year; and the second was conducted in western Ecuador from 2 November 1896 to September 1897. Collections of insects (chiefly butterflies, moths and beetles) from this expedition were acquired by the Oxford Museum in 1899 and 1903 (Smith 1986). Rosenberg's cockroach collection originated from two localities: Cabaché – a small village near the river of that name (NW Coast, Prov. Esmeraldas), and Paramba – a farm on the west bank of the River Mira (Prov. Imbabura) (Boulenger 1898).

The type specimen of the cockroach species from Ecuador described by Shelford in 1912 (*Melyroidea magnifica*) came from the Saunders collection deposited in the Oxford Museum. **William Wilson Saunders** (4 June 1809, Little London near Wendover, Buckinghamshire–13 September 1879 Worthing, West Sussex) was a British insurance broker, entomologist and botanist. He was an original member of the Entomological Society and its President from 1841 to 1842 and again from 1856 to 1857. He was also Treasurer of the Linnean Society of London (1861–1873) and a Fellow of several societies including the Royal Society and the Zoological Society. Saunders himself probably never collected insects in Ecuador or in South America, but his collection contained insects collected by other collectors. Orthopteroid insects (including Blattaria) were collected by the English naturalist and explorer **Henry Walter Bates** (8 February 1825, Leicester–16 February 1892, London) during his legendary 11-year expedition to the Amazon (1848–1859). Saunders sold his collection of cockroaches (467 specimens, containing Bates types) to the University Museum, Oxford, in 1873 (Smith 1986). The collector of these Ecuadorian specimens is not clear.

Shelford (1913) described three new species of cockroaches from Ecuador (*Ceratinoptera alticola*, *Eurycotis riveti* and *Zetha rufescens* (syn. of *Zetha vestita*)) and four species recorded for the first time in Ecuador. The collector of these specimens was a French ethnologist, **Paul Adolph Rivet** (7 May 1876, Wasigny, Ardennes–25 March 1958, Paris). In the role of physician, he took part in the Second French Geodesic Mission and scientific expedition (1899–1906), which arrived in Ecuador in 1901. He had spent six years in South America and had worked on an ethnographic study of the Huaorani (Jívaro) people of the Ecuadorian Amazon. In addition, he collected insects throughout Ecuador. When Rivet returned to France (1906), he donated his collections to the Muséum National d'Histoire Naturelle in Paris. One new cockroach species (*Eurycotis riveti*) was dedicated to the collector by Shelford.

The first checklist of Ecuadorian cockroaches was published by Ecuadorian scientist (entomologist), researcher and educator **Francisco Campos Ribadeneira** (11 January 1879, Guayaquil–5 May 1962, Guayaquil) in 1923. On the base of literature data and own collection he included 54 species in the checklist. Several cockroaches collected by Campos were sent to Morgan Hebard for identification. Campos, as professor of medical zoology at the University of Guayaquil, created the first entomological collection in Ecuador (Barragán *et al.* 2009).

American orthopterologist **Morgan Hebard** (23 February 1887 Cleveland, Ohio–28 December 1946, Philadelphia, Pennsylvania) determined not only material from the Campos collection but also cockroaches deposited in the American Museum of Natural History (AMNH). The museum's collection of South American cockroaches consists mostly of specimens acquired by American mammalogist **George Henry Hamilton Tate** (30 April 1894, Strout Green, London–24 December 1953, Morristown, New Jersey, USA), assistant and later curator of the Department of Mammals in AMNH. During 1921–1929 he participated in several collecting expeditions to various South American countries, including Ecuador (1922), Bolivia, Brazil, Venezuela, and British Guyana. Tate assembled a large collection, especially mammals (Dorst 1954). Hebard (1924) published an extensive work on Ecuadorian cockroaches, describing two species new to science (*Panchlora irrorata* and *Anaplecta falcifer*) and providing eight new records for the country. Campos (1926) added these and other species to the checklist to give a total of 67 cockroach species in Ecuador.

Another Ecuadorian cockroach was described about 15 years later. American entomologist **Ashley Buell Gurney** (16 May 1911, Cummington, Massachusetts–10 March 1988, Montgomery, Maryland) began his career at the United States Department of Agriculture in 1935, focusing on cockroaches. He started by processing museum collections of cockroaches from North, South and Central America, including the West Indies. In a 1939 paper he analysed the genus *Xestoblata* and described *Xestoblatta ecuadorana* from Ecuador. All 3 specimens of this species (1 male and 2 females) were collected by a young American collector, **Edward Jackson Brundage Jr.** (20 October 1915, Chicago, Illinois). These cockroach specimens were part of his large collection of South American insects, which was sold to the United States National Museum in Washington, D.C., in 1938 (Wetmore & Abbot 1939). Mr. Brundage previously (January 1938) donated almost 500 arthropods from United States, Panama and Colombia to the Field Museum of Natural History in Chicago (Anonymous 1938). Gurney also donated 400 Ecuadorian cockroaches to the United States National Museum in Washington, D.C., in 1938 (Wetmore & Abbot 1939).

Since 1960 a number of new species have been described from Ecuador: *Macrophyllodromia ecuadorana*, *Nahublattella ecuadorana*, *Xestoblatta bananae* (Rocha e Silva Albuquerque 1962a, b, c); *Xestoblatta amedegnatae* (Grandcolas 1992); *Litopeltis compleptera* (Roth & Gutiérrez 1998); *Macrophyllodromia amabile*, *Macrophyllodromia nobile* (Anisyutkin 2007); *Nahublattella alexandri*, *Nahublattella cuyabeno*, *Nahublattella incurvata*, *Nahublattella reticulata*, *Nahublattella ultima* (Anisyutkin 2009); *Euphyllodromia propinqua*, *Euphyllodromia rasnitsyni* (Anisyutkin 2011).

The current checklist comes nearly 90 years after that of Campos (1926) and includes 105 species from continental Ecuador and 18 species from Galápagos Islands.

Checklist of cockroaches (Blattaria) from Ecuador

Structure of checklist

An italicized name of country means "terra typica"; i.e, the country from which the type specimens originate. A question mark before the species name indicates the occurrence of the species in Ecuador is uncertain. A question mark after the species name indicates that determination of the species is questionable. A question mark after the name of a country suggests uncertain or problematic occurrence.

Family Blaberidae Brunner de Wattenwyl, 1865

Blaberus atropos (Stoll, 1813)

Synonymy:
Blatta atropos Stoll, 1813
Blabera fusca Brunner de Wattenwyl, 1865
Blabera laticollis Walker, 1868

Distribution: Trinidad, Guyana, Ecuador, Chile (terra typica was not defined).
Comments to faunistic records in Ecuador:
Bonsall (1995:33): Misahualli, Jatun Sacha (eventual confusion with *Blaberus discoidalis*).

Blaberus boliviensis **Princis, 1946**

Distribution: *Bolivia*, Ecuador.
Comments to faunistic records in Ecuador:
Princis (1952:6): 1 male, 3.IX.1948, Ecuador, Guayaquil (in a shipment of bananas from near Puna).
Roth & Willis (1960:147): the same data as mentioned by Princis (1952).
Roth (1969:220, 221, 241, 248): 1 male, Guayaquil (det. Princis).
Roth (1970b:310): the same data as mentioned by Roth (1969).

Blaberus craniifer **(Burmeister, 1838)**

Synonymy:
Blabera craniifer Burmeister, 1838
Blabera limbata Burmeister, 1838
Blabera trapezoidea Burmeister, 1838
Blabera varians Serville, 1838
Blabera luctuosa Stål, 1855
Blatta (Blabera) atropos Guérin-Méneville, 1857 non Stoll, 1813
Blabera ferruginea Saussure, 1864
Libisoca aequalis Walker, 1868
Blabera quadrifera Walker, 1868

Distribution: *Mexico*, Costa Rica, Guatemala, Honduras, Panama, Venezuela, Ecuador.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:15) (*Blabera trapezoidea*): San José, Valle del Santiago, Gualaquiza.
Campos (1923:10 and 1926:55) (*Blabera trapezoidea*): the same locality as mentioned by Giglio-Tos (1898).
Maes (1992a:23): Ecuador.
Note: According to Roth (1969) *Blaberus trapezoideus* Burmeister, 1838 is synonym of *Blaberus craniifer* Burmeister, 1838.

Blaberus discoidalis (Serville, 1839)

Synonymy:
Blabera discoidalis Serville, 1839
Blabera varians Serville, 1839
Blabera cubensis Saussure, 1864
Blabera subspurgata Walker, 1868
Blabera rufescens Saussure & Zehntner, 1894

Distribution: *Cuba*, Haiti, Jamaica, Costa Rica, Dominican Republic, Puerto Rico, Vieques Island, Panama, Colombia, Venezuela, Trinidad, Nicaragua, Ecuador.

Comments to faunistic records in Ecuador:

Scudder (1869:342) (*Blabera cubensis*): 2 specimens, Guayaquil.
Giglio-Tos (1898:15) (*Blabera rufescens*): 1 specimen, La Concepción, Valle del Mira.
Campos (1923:11 and 1926:55) (*Blabera rufescens*): the same locality as mentioned by Giglio-Tos (1898); (*Blabera discoidalis*): Guayaquil, Durán, Naranjito, Barraganetal, Posorja, El Morro, Daule, Bucay, Vinces (leg. F. Campos R.) and the same locality as mentioned by Hebard (1924).
Hebard (1924:130): 2 males, 1 female, Guayaquil, Guayas (leg. F. Campos R.), 1 male, Machala, El Oro (leg. Capt. Moirel) and 1 female, Riobamba, Chimborazo (leg. R. Bourgeois).
Roth & Willis (1960:75): Ecuador.
Princis (1963:127): Ecuador ?.
Roth (1969:240, 248): 1 specimen, Ecuador.
Maes (1992a:23): Ecuador.
Note: Princis (1963:128) marked data of Giglio-Tos and Campos with “?” but Scudder’s and Hebard’s data (with same localities) were not questioned.

Blaberus parabolicus (Walker, 1868)

Synonymy:
Blabera parabolica Walker, 1868
Blabera armigera Scudder, 1869
Blabera aequatoriana Bolívar, 1881

Distribution: *Ecuador* (+Galápagos Islands), Bolivia, Brazil, Colombia, Peru, Suriname.

Comments to faunistic records in Ecuador:

Walker (1868:8) (*Blabera parabolica*): 1 male, Cuenca (from Mr. Fraser’s collection).
Scudder (1869:343) (*Blabera armigera*): 1 male, Napo or Marañón (Ecuador or Peru).
Finot (1897:210) (*Blabera parabolica*): the same locality as mentioned by Walker (1868).
Bolivar (1881:479) (*Blabera aequatoriana*): Archidona and Coca, Ecuador (leg. Martínez y Saez).
Bolivar (1884:24) (*Blabera aequatoriana*): the same data as mentioned by Bolivar (1881).
Kirby (1904:164) (*Blabera parabolica*): Ecuador; (*Blabera armigera*): Napo?.
Campos (1923:10 and 1926:55, 56) (*Blabera aequatoriana*): the same localities as mentioned by Bolivar (1881); (*Blabera parabolica*): the same locality as mentioned Walker (1868).
Rehn (1933a:58): Cuenca, Gualaquiza and valley of Santiago, Ecuador.
Princis (1958:74): the same locality as mentioned by Walker (1868); the study identifies as a female the holotype described by Walker (1868).
Bruijning (1959:8): the same localities as mentioned by Rehn (1932).
Princis (1963:129): Ecuador.
Roth (1969:220, 221, 236, 248): Ecuador and the same locality as mentioned by Scudder (1869).
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2214): Isla San Cristóbal.
Peck (1996:1502): the same locality as mentioned by Peck & Roth (1992).
Peck *et al.* (1998:223): Isla San Cristóbal, Isla Santa Cruz.

Eublaberus immaculus (Saussure & Zehntner, 1894)

Distribution: *Brazil*, Ecuador.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:106) (*Blabera immacula*): 1 male, Vinces.
Campos (1923:11 and 1926:55) (*Blabera immacula*): the same locality as mentioned by Giglio-Tos (1898).
Princis (1963:135): Ecuador.

Eublaberus posticus (Erichson, 1848)

Synonymy:
Blabera postica Erichson, 1848
Blatta ferruginea Stoll, 1813 [primary homonym]
Blabera femorata Scudder, 1869
Blabera thoracica Saussure & Zehntner, 1894
Blabera lindmani Shelford, 1911

Distribution: *Guyana*, Suriname, French Guiana, Brazil, Peru, Ecuador, Costa Rica, Nicaragua, Panama, Colombia, Trinidad.
Comments to faunistic records in Ecuador:
Scudder (1869:342) (*Blabera femorata*): 1 male, Napo or Marañón.
Giglio-Tos (1898:15) (*Blabera thoracica*): Valle del Santiago.
Kirby (1904:165) (*Blabera femorata*): Napo.
Campos (1923:11 and 1926:55) (*Blabera thoracica*): the same locality as mentioned by Giglio-Tos (1898).
Princis (1963:134): Ecuador.

Hormetica strumosa Saussure & Zehntner, 1895

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Saussure & Zehntner (1895:56): 1 male, Ecuador (Equator).
Note: The syntype of *Hormetica strumosa* is deposited in Muséum d’Histoire Naturelle de la Ville de Genève, Genève, Switzerland with the data label “[male] Ecuador” (J. Hollier, personal communication 2012).
Kirby (1904:197): Ecuador.
Hebard (1924:130): 1 juv. female, Cuenca, Azuay (leg. F. Campos R.).
Campos (1926:56): the same locality as mentioned by Hebard (1924).
Princis (1963:116): Ecuador.

Phoetalia circumvagans (Burmeister, 1838)

Synonymy:
Nauphoeta circumvagans Burmeister, 1838
Blatta marginicollis Stål, 1860

Distribution: *Brazil*, Ecuador, Colombia (Circumtropical).
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:13) (*Nauphoeta circumvagans*): La Concepción, Valle del Mira, Ibara.
Campos (1923:10 and 1926:54) (*Nauphoeta circumvagans*): the same locality as mentioned by Giglio-Tos (1898).

Phoetalia pallida (Brunner de Wattenwyl, 1865)

Synonymy:
Nauphoeta pallida Brunner de Wattenwyl, 1865
Blatta laevigata Serville, 1839 non Palisot de Beauvois, 1805
Nauphoeta marginalis Walker, 1868

Distribution: *Cuba*, Ecuador (+Galápagos Islands), Colombia, Brazil (Circumtropical).

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:13) (*Nauphoeta laevigata* Pal. de Beauv.): Gualaquiza.

Campos (1923:6, 10 and 1926:50, 54) (*Leurolestes pallidus*): Guayaquil, Durán (leg. F. Campos R.), (*Nauphoeta laevigata* Pal. de Beauv.): the same locality as mentioned by Giglio-Tos (1898).

Hebard (1924:128) (*Leurolestes pallidus*): 1 female, Guayaquil, Guayas (leg. F. Campos R.).

Bonsall (1995:33): Misahualli, Puerto Lopez.

Comments to faunistic records in Galápagos:

Howard (1889:194) (*Nauphoeta laevigata* ? (Pal.)): Galápagos Islands, 3 immature specimens (det. L. Bruner), (according Hebard (1920b:317) these juveniles belong to *Nauphoeta cinerea*; Princis (1967:654) stated it as *Phoetalia circumvagans*).

Scudder (1893:7) (*Nauphoeta circumvagans*): Galápagos Islands: Charles Island, 3 immature females (the same specimens as studied by Howard (1889); according to Hebard (1920b:317) these juveniles belong to *Nauphoeta cinerea*; Princis (1967:653) stated it as *Phoetalia circumvagans*).

McNeill (1901:489) (*Nauphoeta circumvagans*): Galápagos Islands: the same locality as mentioned by Scudder (1893).

Hebard (1920b:316) (*Leurolestes pallidus*): Galápagos Islands: Chatham Island, 1 female, January 1906 (leg. F.X. Williams).

Linsley & Usinger (1966:125) (*Leurolestes pallidus*): Galápagos Islands: San Cristóbal.

Peck & Roth (1992:2214): Galápagos Islands: Isla San Cristóbal (=Chatham), January (the same specimens as studied by Howard (1889) and by Scudder (1893)), but they stated a different locality than Scudder (1893).

Peck (1996:1502) & Peck *et al.* (1998:223): Galápagos Islands: the same locality as mentioned by Peck & Roth (1992).

Epilampra azteca Saussure, 1868

Distribution: *Mexico*, Cuba, Panama, Colombia, Ecuador, Venezuela, Trinidad, French Guiana, Costa Rica, Suriname, Brazil.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:7): males and female, Valle dello Zamora.

Shelford (1910a:16): Ecuador.

Campos (1923:7 and 1926:50): the same locality as mentioned by Giglio-Tos (1898).

Princis (1967:694): Ecuador.

Roth (1970c:470): 1 male, Napo, Santa Cecilia, Rio Aguarico, Ecuador (det. Roth).

Epilampra conferta Walker, 1868

Synonymy:
Epilampra stigmosa Giglio-Tos, 1898

Distribution: *Brazil*, Bolivia, Colombia, Ecuador, Peru, Costa Rica, Panama.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:8) (*Epilampra stigmosa* sp.n.): 4 males, Valle del Santiago.

Kirby (1904:127) (*Epilampra stigmosa*): Ecuador.

Shelford (1910a:16) (*Epilampra stigmosa*): Ecuador.

Campos (1923:7 and 1926:50) (*Epilampra stigmosa*): the same locality as mentioned by Giglio-Tos (1898).

Hebard (1924:128) (*Epilampra stigmosa*): 1 female, 2 juveniles, Allpa-yuca, Rio Pastaza, Tunguragua (from Rosenberg).

Rehn (1933a:54) (*Epilampra stigmosa*): the same locality as mentioned by Giglio-Tos (1898) and Hebard (1924).

Princis (1948:10) (*Epilampra stigmosa*): the same locality as mentioned by Giglio-Tos (1898) and Hebard (1924).

Princis (1967:689): Ecuador.

Roth (1970c:441): 1 male, Napo, Santa Cecilia, Rio Aguarico (det. Roth), and the same data as mentioned by Giglio-Tos (1898).

Note: Hebard (1926:201) states: "This species (*E. opaca*) may prove to be a synonym of the Brazilian *E. maculicollis* (Serville), and the Ecuadorian *E. stigmosa* Giglio-Tos may fall in the same synonymy." Princis (1958:63) synonymized *E. stigmosa* with *E. conferta*. According to Roth (1970c) *Epilampra stigmosa* is probably a different species from *E. conferta*.

Epilampra josephi Giglio-Tos, 1898

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:9): 2 males, San José.

Shelford (1910a:16): Ecuador.

Campos (1923:7 and 1926:50): the same locality as mentioned by Giglio-Tos (1898).

Princis (1967:688): Ecuador.

Roth (1970c): the same data as mentioned by Giglio-Tos (1898).

Epilampra mexicana Saussure, 1862

Distribution: *Mexico*, Panama, Guatemala, Ecuador.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:7): 1 female, Valle del Santiago.

Shelford (1910a:16): Ecuador.

Campos (1923:7 and 1926:50): the same locality as mentioned by Giglio-Tos (1898).

Princis (1946:153): Ecuador.

Princis (1967:689): Ecuador.

Roth (1970c:442) (*Epilampra* sp.): 1 male, Rio Blanco or Ecuador; this specimen was originally determined by Rocha e Silva Albuquerque as *Epilampra mexicana*. Roth (1970c) stated that this male has genitalia very different from *E. mexicana*.

Epilampra opaca Walker, 1868

Distribution: *Guyana*, Brazil, French Guiana, Suriname, Ecuador, Bolivia, Venezuela.

Comments to faunistic records in Ecuador:

Roth (1970c:460): 3 males, Napo, Santa Cecilia, Rio Aguarico, Ecuador.

Note: According to Princis (1958:62) *E. opaca* Walker is a synomym of *E. substrigata* Walker. Roth (1970c:465, 471) indicated, that *E. opaca* and *E. substrigata* are distinct species. Both species belong to subgroup B of the *Burmeisteri* Group.

Epilampra substrigata Walker, 1868

Distribution: Brazil, Venezuela, Ecuador, Colombia (terra typica was not defined).

Comments to faunistic records in Ecuador:

Roth (1970c:461): 2 males, Napo, Santa Cecilia, Rio Aguarico, Ecuador (det. Roth and det. Princis).

Homalopteryx laminata Brunner von Wattenwyl, 1892

Distribution: *St. Vincent*, Grenada, Trinidad, Venezuela, Colombia, Ecuador.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:10): Valle del Santiago.
Campos (1923:8 and 1926:50): the same locality as mentioned by Giglio-Tos (1898).
Princis (1967:658): Ecuador ?.
Note: Princis (1967:658) mentioned the data of Giglio-Tos with "?".

Litopeltis compleptera Roth & Gutiérrez, 1998

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Roth & Gutiérrez (1998:199): 4 females, Gualea, Ecuador (leg. F. Campos).
Note: It is the first record of the genus *Litopeltis* in South America. All other species are known from Central America.

Rhyparobia maderae (Fabricius, 1781)

Synonymy:
Blatta maderae Fabricius, 1781
Blatta major Palisot de Beauvois, 1805
Blatta tuberculata Thunberg, 1810
Blatta maderensia Jones, 1859
Proscratea illepida Walker, 1868
Nauphoeta kukenthali Shelford, 1910

Distribution: *Island Madeira*, Ecuador (+Galápagos Islands), Colombia (Circumtropical).
Comments to faunistic records in Ecuador:
Westwood (1876:xxxii) (*Blatta Maderae*): in bulb of orchid from Ecuador.
Giglio-Tos (1898:11): La Concepción, Valle del Mira.
Shelford (1913:59): Santo Domingo de los Colorados.
Campos (1923:9 and 1926:52): Guayaquil, Durán, Naranjito, Bucay, Posorja, El Morro, Daule, Quito (leg. F. Campos R.), Tambillo (leg. R.P. Luis Mille, S. J.) and the same locality as mentioned by Giglio-Tos (1898) and Shelford (1913); vertical distribution in Ecuador: 0–2850 m.
Hebard (1924:128) (*Leucophaea maderae*): 2 males, 1 female, Guayaquil, Guayas (leg. F. Campos R.); 1 juv. female, Tambillo, Pichincha (leg. F. Campos R.).
Gurney (1953:49) (*Leucophaea maderae*): Ecuador.
Roth & Willis (1960:151, 162): the same data as mentioned by Westwood (1876).
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2214): Isla San Cristóbal, Baquerizo Morena, 11–23.II.1989, 1 male (leg. S.B. Peck).
Peck (1996:1502) & Peck *et al.* (1998:223): the same locality as mentioned by Peck & Roth (1992).

Nauphoeta cinerea (Olivier, 1789)

Synonymy:
Blatta cinerea Olivier, 1789
Blatta gallica Fabricius, 1793
Blatta elegans Eschscholtz, 1822
Nauphoeta bivittata Burmeister, 1838
Nauphoeta grisea Burmeister, 1838

Distribution: *Mauritius*, Ecuador (+Galápagos Islands), Brazil (Circumtropical).

Comments to faunistic records in Ecuador:

Westwood (1876:xxxii) (*Blatta cinerea*): in bulb of orchid from Ecuador.

Giglio-Tos (1898:106): 1 female, Vinces, 1 female, Guayaquil.

Campos (1923:10 and 1926:54): Guayaquil, Durán, Naranjito, Daule (leg. F. Campos R.) and the same locality as mentioned by Giglio-Tos (1898).

Hebard (1924:130): 1 male, Guayaquil, Guayas (leg. F. Campos R.).

Roth & Willis (1960:151, 162): the same data as mentioned by Westwood (1876).

Comments to faunistic records in Galápagos:

Howard (1889:194) (*Nauphoeta bivittata*): 3 specimens, Chatham Island (det. L. Bruner).

Scudder (1893:6): the same exemplars as mentioned by Howard (1889).

Hebard (1920b:317): Chatham Island, 3 males, 4 females, 3 juv., October 1905; Charles Island, 6 males, 8 females, 3 juv., October 1905 (leg. F.X. Williams).

Linsley & Usinger (1966:125): San Cristóbal, Floreana.

Peck & Roth (1992:2214); Peck (1996:1502); Peck *et al.* (1998:223): the same locality as mentioned by Linsley & Usinger (1966).

Achroblatta luteola (Blanchard, 1843)

Synonymy:
Blatta luteola Blanchard, 1843
Paratropes histrio Saussure, 1862
Pseudomops lituriceps Walker, 1868
Zetobora sigillata Walker, 1868
Panchlora tripartita Walker, 1868

Distribution: *Bolivia*, Mexico, Honduras, Costa Rica, Colombia, Brazil, French Guiana, Suriname, Ecuador, Venezuela.

Comments to faunistic records in Ecuador:

Bruijning (1959:15): distribution from Mexico to Bolivia and French Guiana.

Gurney & Roth (1972:525): Ecuador, Guayaquil, intercepted at San Diego, Calif., with bananas, 1 female, 30 March 1953.

Panchlora exoleta Burmeister, 1838

Synonymy:
Panchlora punctum Saussure & Zehntner, 1893

Distribution: *Brazil*, Costa Rica, Panama, Colombia, Ecuador, Peru, Paraguay, Argentina, Venezuela, Suriname, Jamaica, Mexico.

Comments to faunistic records in Ecuador:

Scudder (1869:342): 1 specimen, Napo or Marañón.

Hebard (1920a:106): 1 male, Alpayacu, eastern Ecuador.

Princis (1964:177): Ecuador.

Panchlora festae Giglio-Tos, 1898

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:12): 1 female, Valle del Santiago.

Kirby (1904: 154): Ecuador.

Campos (1923:9) and (1926:53): the same locality as mentioned by Giglio-Tos (1898).

Princis (1964:187): Ecuador.

Panchlora irrorata Hebard, 1924

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Hebard (1924:129): 1 female, Bucay, Guayas, 1922 (leg. G.H.H. Tate).
Campos (1926:53): the same locality as mentioned by Hebard (1924).
Princis (1964:188): Ecuador.

Panchlora nigricornis Walker, 1868

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Walker (1868:28): Quito (M. Bourcier).
Finot (1897:203): Quito.
Hebard (1924:129): Ecuador.
Campos (1926:53): the same data as mentioned by Hebard (1924).
Princis (1964:188): Ecuador.

Panchlora nivea (Linnaeus, 1758)

Synonymy:
Blatta nivea Linnaeus, 1758
Blatta chlorotica Pallas, 1772
Blatta alba Strøm, 1783
Blatta hyalina Stoll, 1813
Blatta virescens Thunberg, 1826
Panchlora cubensis Saussure, 1862
Panchlora poeyi Saussure, 1862
Panchlora luteola Saussure, 1864
Ischnoptera lucida Walker, 1868
Pycnosceloides aporus Hebard, 1919

Distribution: Central and South *America*; Ecuador.
Comments to faunistic records in Ecuador:
Bolivar (1884:17) (*Panchlora viridis* Burmeister [sic]): Baeza, Ecuador (leg. Martínez y Saez)
Giglio-Tos (1898:12) (*Panchlora virescens*): Gualaquiza.
Campos (1923:9) and (1926:53) (*Panchlora virescens*): the same locality as mentioned by Giglio-Tos (1898); (*Panchlora cubensis*): the same locality as mentioned by Hebard (1924).
Hebard (1924:128) (*Panchlora cubensis*): 1 male, 1 female, Ventura, Chimborazo, 12 April 1922 (leg. G.H.H. Tate).

Panchlora peruana Saussure, 1864

Distribution: *Peru*, Ecuador, Brazil.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:12): S. José, Gualaquiza, Valle del Santiago.
Campos (1923:9) and (1926:53): the same locality as mentioned by Giglio-Tos (1898).
Princis (1964:186): Ecuador.

Panchlora pulchella Burmeister, 1838

Distribution: *Brazil*, Ecuador.
Comments to faunistic records in Ecuador:
Bolivar (1881:469): Palmal (leg. Stolzmann).
Campos (1923:10) and (1926:53): the same locality as mentioned by Bolivar (1881).

Pycnoscelus surinamensis (Linnaeus, 1758)

Synonymy:
Blatta surinamensis Linnaeus, 1758
Blatta indica Fabricius, 1775
Blatta melanocephala Stoll, 1813
Blatta corticum Serville, 1839
Perispherus laevis Le Guillou, 1841
Pycnoscelus obscurus Scudder, 1862
Panchlora celebesa Walker, 1868
Polyzosteria latipes Walker, 1868
Polyzosteria crassipes Walker, 1868
Panchlora occipitalis Walker, 1871
Epilampra tatei Tepper, 1894
Epilampra dimorpha Shiraki, 1906
Pycnoscelus surinamensis major Roeser, 1940
Pycnoscelus surinamensis minor Roeser, 1940

Distribution: *Suriname*; Ecuador (+Galápagos Islands) (Circumtropical).
Comments to faunistic records in Ecuador:
Walker (1868:166) (*Polyzosteria crassipes*): Napo River, South America (Mr. Stevens' collection).
Finot (1897:197) (*Polyzosteria crassipes*): Napo River.
Giglio-Tos (1898:12) (*Leucophaea surinamensis*): La Concepcion, Valle del Mira.
Kirby (1904:196) (*Parasphaeria* ? *crassipes*): the same locality as mentioned by Walker (1868).
Campos (1923:10) and (1926:54): the same locality as mentioned by Giglio-Tos (1898).
Bonsall (1995:33): Misahualli.
Comments to faunistic records in Galápagos:
Butler (1877:87) (*Panchlora surinamensis*): Charles Island, 2 adult, 2 immature, June 1875 (leg. W. E. Cookson).
Howard (1889:194) (*Leucophaea surinamensis*): 8 specimens (adults and juv.), 1887–88 (det. L. Bruner).
Scudder (1893:7) (*Leucophaea surinamensis*): Chatham Island, 2 immature specimens obtained by Dr. Baur, and specimens determined by Bruner (Howard 1889) from Charles and Chatham Islands.
McNeill (1901:494) (*Leucophaea surinamensis*): Chatham, 2 juv. females, and older data from 3 previous expeditions: Charles Island and Chatham.
Hebard (1920b:317): Albemarle Island, Villamil, 1 female; Chatham Island, 3 males, 3 juv. females, October 1905; Charles Island, 1 juv. female, October 1905 (leg. F.X. Williams).
Hebard (1934:280): Chatham Island, 1 female, 2 juveniles, 28 December 1925.
Linsley & Usinger (1966:125): Isabela, San Cristóbal, Floreana.
Parkin *et al.* (1972:102): 1 specimen, Floreana, 31 August 1968; 2 juveniles, Santa Cruz, 8 September 1968 (det. D.R. Ragge).
Linsley (1977:4): Floreana, Isabela, Santa Cruz.
Peck & Roth (1992:2214): Isla Floreana, San Cristóbal, Santa Cruz, Islas Campéon, Fernandina, Gardner (at Floreana), Isabela, Santiago.
Peck (1996:1502) & Peck (1998:223): the same locality as mentioned by Peck & Roth (1992).
Peck *et al.* (2001:152): Campéon, Española, Ferdinandina, Gardner at Floreana, Isabela, San Cristóbal, Santa Cruz, Santiago (only older data).

Lanxoblatta emarginata (Burmeister, 1838)

Synonymy:
Zetobora emarginata Burmeister, 1838
Zetobora cicatricosa Burmeister, 1838
Zetobora perspicua Walker, 1868

Distribution: *Brazil*, Guyana, French Guiana, Suriname, Ecuador, Colombia.
Comments to faunistic records in Ecuador:
Roth (1970a:228): 1 male, Ecuador.

Lanxoblatta martinezi (Bolivar, 1881)

Synonymy:
Zetobora martnezii Bolivar, 1881

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Bolivar (1881:478) (*Zetobora martinezii*): 1 female, Archidona, Ecuador (leg. Martínez y Saez).
Bolivar (1884:20) (*Zetobora martinezii*): the same data as mentioned by Bolivar (1881).
Giglio-Tos (1898:13) (*Zetobora martinezii*): 1 female, Valle del Santiago.
Kirby (1904:158) (*Zetobora martinezi*): Ecuador.
Campos (1923:10 and 1926:54) (*Zetobora martinezii*): the same locality as mentioned by Bolivar (1881) and by Giglio-Tos (1898).
Princis (1964:259): Ecuador.

Lanxoblatta rudis (Walker, 1868)

Synonymy:
Zetobora rudis Walker, 1868

Distribution: *Brazil*, Ecuador.
Comments to faunistic records in Ecuador:
Scudder (1869:342) (*Zetobora rudis*): 1 specimen, unlabelled, on either side of the Andes of equatorial South America (James Orton coll.).

? *Parasphaeria ovata* (Blanchard, 1851)

Synonymy:
Blatta ovata Blanchard, 1851
Hormetica chilensis Saussure, 1862
Polyzosteria geissei Philippi, 1863
Polyzosteria valdiviana Philippi, 1863

Distribution: *Chile*, Ecuador ?.
Comments to faunistic records in Ecuador:
Shelford (1913:58): 1 male, Santo Domingo de los Colorados, 510 m.
Campos (1923:6 and 1926:56): the same locality as mentioned by Shelford (1913).
Princis (1964:240): Ecuador.
Note: According to Rehn (1933b:189) *Parasphaeria ovata* is limited in distribution to the southern half of Chile. The unique male specimen examined by Shelford probably belongs to one of the other superficially similar genera of Perisphaerinae.

Zetobora aberrans Giglio-Tos, 1898

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:13): 1 male, San José.
Kirby (1904:158) (*Tribonidium aberrans*): Ecuador.
Campos (1923:10 and 1926:54): the same locality as mentioned by Giglio-Tos (1898).
Princis (1964:256): Ecuador.

Family: Anaplectidae Walker, 1868

Anaplecta alaris Saussure & Zehntner, 1893

Distribution: *Peru*, Ecuador, Brazil.
Comments to faunistic records in Ecuador:
Hebard (1924:121): 1 male, Ventura, Chimborazo, 12 April 1922 (leg. G.H.H. Tate).
Campos (1926:45): the same locality as mentioned by Hebard (1924).

? *Anaplecta brunneri* Shelford, 1906

Distribution: *Brazil*, Ecuador ?
Note: Princis (1965:369) listed this species as recorded in Ecuador, but detailed distribution data are available only from Brazil.

Anaplecta cabimae Hebard, 1920

Distribution: *Panama*, Ecuador.
Comments to faunistic records in Ecuador:
Hebard (1924:122): 1 male, Ventura, Chimborazo, 12 April 1922 (leg. G.H.H. Tate).
Campos (1926:45): the same locality as mentioned by Hebard (1924).
Princis (1965:373): Ecuador.

Anaplecta falcifer Hebard, 1924

Distribution: *Ecuador*, Brazil.
Comments to faunistic records in Ecuador:
Hebard (1924:119): 11 males, 2 females, Ventura, Chimborazo, 1400 feet, 12 April 1922 (leg. G.H.H. Tate).
Campos (1926:45): the same locality as mentioned by Hebard (1924).
Rehn (1933a:11): western Ecuador.
Princis (1965:371): Ecuador.

Anaplecta fusca Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:246): Cachabi, December 1896, 1 female (W.F.H. Rosenberg coll., Oxford Museum).
Shelford (1907a:10): Ecuador.
Hebard (1921:222): the same locality as mentioned by Shelford (1906).
Hebard (1924:122): Ecuador.

Campos (1926:45): the same locality as mentioned by Hebard (1924).
Princis (1965:368): Ecuador.

Anaplecta lateralis Burmeister, 1838

Distribution: *Colombia*, Panama, Venezuela, Brazil, Ecuador (+Galápagos Islands), Argentina.
Comments to faunistic records in Ecuador:
Bolivar (1881:463): Palmal, Ecuador (leg. Stolzmann).
Campos (1923:5 and 1926:44): the same locality as mentioned by Bolivar (1881).
Princis (1965:372): Ecuador.
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2206): Isla Santa Cruz, Puerto Ayora, Charles Darwin Research Station, 3 males, 3–7 March 1992; 5 km N Puerto Ayora, 1 male, 1–30 May 1991; 1.7 km N Santa Rosa, 3 males, 1 female, 1–30 May 1991.
Peck (1996:1502) & Peck *et al.* (1998:223): the same locality as mentioned by Peck & Roth (1992).

Anaplecta mexicana Saussure, 1868

Synonymy:
Anaplecta gemma Hebard, 1920

Distribution: *Mexico*, Costa Rica, Panama, Ecuador.
Comments to faunistic records in Ecuador:
Hebard (1924:119): 1 female, Rio Pescado, Guayas, 1600 feet, 15 May 1922 (leg. G.H.H. Tate).
Campos (1926:45): the same locality as mentioned by Hebard (1924).
Princis (1965:367): Ecuador.

Anaplecta pallida Bolivar, 1881

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Bolivar (1881:463): Palmal (leg. Stolzmann).
Kirby (1904:67): Ecuador.
Shelford (1907a:10): Ecuador.
Campos (1923:5 and 1926:45): the same locality as mentioned by Bolivar (1881).
Princis (1965:369): Ecuador.

Anaplecta pavida Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:245): Cachabi, December 1896, 1 female (W.F.H. Rosenberg coll., Oxford Museum).
Shelford (1907a:10): Ecuador.
Princis (1965:368): Ecuador.

Anaplecta varipennis Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:246): 5 females, Paramba, 3500 feet, May 1897 (W.F.H. Rosenberg coll., Oxford Museum).

Shelford (1907a:10): Ecuador.
Princis (1965:368): Ecuador.

Maraca fossata Hebard, 1926

Distribution: *French Guiana*, Venezuela, Brazil, Ecuador, Suriname.
Comments to faunistic records in Ecuador:
Rocha e Silva Albuquerque (1965:2): Ecuador.

Family: Blattellidae Karny, 1908

Blattella germanica (Linnaeus, 1767)

Synonymy:
Blatta germanica Linnaeus, 1767
Blatta transfuga Brünnich, 1763
Blatta daurica Laxmann, 1769
Blatta asiatica Pallas, 1773
Blatta obliquata Daldorf, 1794
Blatta bivittata Serville, 1839
Ischnoptera paralella Tepper, 1893
Phyllodromia magna Tepper, 1895
Blattella germanica shuguroffi Karny, 1908
Phyllodromia niitakana Shiraki, 1931
Phyllodromia cunei-vittata Hanitsch, 1925
Blattella stylifera Chopard, 1938 (in part)

Distribution: *Danmark*, Ecuador (+Galápagos Islands) (Cosmopolitan).
Comments to faunistic records in Ecuador:
Bolivar (1884:12) (*Blatta germanica*): Baeza, Ecuador (leg. Martínez y Saez).
Giglio-Tos (1898:3) (*Blatta germanica*): Sig-sig (nec Sis-sig), Cuenca, La Concepción, Valle del Mira.
Shelford (1913:57) (*Phyllodromia germanica*): males and juv. females, Tulcan, Balsabamba, Riobamba.
Campos (1923:5 and 1926:46): Quito (leg. F. Campos R.); Tambillo, Cotocollao (leg. R.P. Luis Mille, S. J.); Azógues, Biblián (Dr. Leoncio A. Cordero); Loja (Clodoveo Carrión); vertical distribution in Ecuador: 0–2980 m.
Hebard (1924:123): 1 female, Durán, Guayas, 25 June 1914 (leg. Herbert S. Parish); 1 male, Azogues, Cañar (leg. F. Campos R.).
Bonsall (1995:33): Misahualli, Puerto Lopez, Jatun Sacha, Tena.
Comments to faunistic records in Galápagos:
Hebard (1920b:315): Hood Island (=Isla Española), 1 female, 1 June 1906 (leg. F.X. Williams).
Hebard (1929:358): Charles Island, 1 male, August 1924 (leg. Miss Cheesman).
Linsley & Usinger (1966:124): Hood (=Isla Española).
Peck & Roth (1992:2205): Isla Española (old data) and new records (1990–1992) only from boats based on San Cristóbal and Santa Cruz.
Peck (1996:1502): Española, Santa Cruz.
Peck *et al.* (1998:223): the same locality as mentioned by Peck (1996).

Ischnoptera josephina Giglio-Tos, 1898

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:6): 4 specimens, San José.
Kirby (1904: 83): Ecuador.

Shelford (1908a:8): Ecuador.
Campos (1923:6 and 1926:47): the same data as mentioned by Giglio-Tos (1898).
Princis (1969:746): Ecuador.

? *Ischnoptera melasa* Walker, 1868

Distribution: *Brazil*, Ecuador ?.
Comments to faunistic records in Ecuador:
Scudder (1869:342) (*Ischnoptera melana*): 1 specimen, Napo River.
Note: Species is presented by Scudder with "?", because the specimen from Napo does not entirely agree with Walker's description. Scudder used an incorrect name, *Ischnoptera melana*, but his species description clearly indicates *Ischnoptera melasa* and not *Pseudomops melana* (=*melanus*) as presented by Princis (1969:949).

Ischnoptera pallipes (Scudder, 1869)

Synonymy:
Phyllodromia pallipes Scudder, 1869

Distribution: *Ecuador*, Brazil, Peru.
Comments to faunistic records in Ecuador:
Scudder (1869:342) (*Phyllodromia pallipes*): 1 male, Napo or Marañón.
Kirby (1904:96) (*Phyllodromia pallipes*): the same locality as mentioned by Scudder (1869).

Ischnoptera peckorum Roth, 1988

Distribution: Ecuador–*Galápagos Islands* (endemic).
Comments to faunistic records in Galápagos:
Roth (1988:307): St. Cruz, 1 km east of Bellavista, 210 m, Bellavista Cave No. 2, 14 July 1985, S. & J. Peck leg.
Peck (1990:371); Peck & Roth (1992:2210); Peck (1996:1502) & Peck (2001:151): the same locality as mentioned by Roth (1988).

Ischnoptera rufa (De Geer, 1773)

Synonymy:
Blatta rufa De Geer, 1773
Blatta rufescens Palisot de Beauvois, 1805
Ischnoptera fumata Burmeister, 1838
Ischnoptera consobrina Saussure, 1862
Ischnoptera rubiginosa Walker, 1868
Ischnoptera terminalis Walker, 1868
Ischnoptera conformis Saussure & Zehntner, 1893

Distribution: *Suriname*, Caribbean, Costa Rica, Jamaica, Nicaragua, Panama, Colombia, Guyana, Trinidad, Ecuador, Brazil.
Comments to faunistic records in Ecuador:
Bolivar (1881:463) (*Ischnoptera consobrina*): Palmal (leg. Stolzmann).
Bolivar (1884:14) (*Ischnoptera consobrina*): Pichincha (leg. Martínez y Saez).
Campos (1923:6 and 1926:48) (*Ischnoptera consobrina*): the same data as mentioned by Bolivar (1881).

Ischnoptera santacruzensis Roth, 1992

Distribution: Ecuador–*Galápagos Islands* (endemic).
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2210): Isla Santa Cruz: Puntudo, Cerro Crocker, Los Gemelos, many males and females.
Peck (1996:1502) & Peck (2001:151): the same locality as mentioned by Peck & Roth (1992).

Ischnoptera snodgrassi (McNeill, 1901)

Synonymy:
Temnopteryx snodgrassii McNeill, 1901

Distribution: Ecuador—*Galápagos Islands* (endemic).
Comments to faunistic records in Galápagos:
McNeill (1901:493) (*Temnopteryx snodgrassii*): Albemarle Island (=Isabela), Iguana Cove Mountain, 2000 feet, 1 male, 3 nymphs.
Hebard (1920b:315) (*Anisopygia snodgrassii*): Albemarle Island (=Isabela), 1 male, 1 female, 3 nymphs, 9 June 1899 (the same exemplars as mentioned by McNeill (1901)).
Linsley & Usinger (1966:124) (*Anisopygia snodgrasii*): The same locality as mentioned by McNeill (1901).
Princis (1969:774) (*Anisopygia snodgrasii*): Galápagos Islands.
Peck & Roth (1992:2006–2210): Isla Isabela (Cerro Azul volcano, Sierra Negra, Volcano Chico on Sierra Negra, Volcano Alcedo).
Peck (1996:1502): the same locality as mentioned by Peck & Roth (1992).
Peck (2001:151): Isabela (Cerro Azul, Sierra Negra, Volcano Alcedo, Volcano Wolf).

Ischnoptera taczanowskii Bolivar, 1881

Distribution: *Peru*, Ecuador.
Comments to faunistic records in Ecuador:
Hebard (1924:123): 1 male, Bucay, Guayas, 1922 (leg. G.H.H. Tate); 1 male, 1 female, Milagro, Guayas, December 1922 (leg. G.H.H. Tate); 1 male, Ventura, Chimborazo, 12 April 1922 (leg. G.H.H. Tate); 1 female, Chaguarpata, Chimborazo, 5 April 1922 (leg. G.H.H. Tate)
Campos (1926:48): the same locality as mentioned by Hebard (1924).
Princis (1969:745): Ecuador.

Pseudomops albostriatus Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:259) (*Pseudomops albostriata*): 1 female, Cachabi, November 1896 (W.F.H. Rosenberg coll., Oxford Museum).
Shelford (1908a:4) (*Pseudomops albostriata*): Ecuador.
Princis (1969:947): Ecuador.

Pseudomops bicolor Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:260): 1 male, Paramba, March 1897 (W.F.H. Rosenberg coll., Oxford Museum).
Shelford (1908a:4): Ecuador.

Rehn (1933a:50): the same locality as mentioned by Shelford (1906).
Princis (1969:947): Ecuador.

Pseudomops burri Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:257): 3 females, Cachabi, December 1896 (W.F.H. Rosenberg coll., Oxford Museum).
Shelford (1908a:4): Ecuador.
Princis (1969:952): Ecuador.

Pseudomops magnus Shelford, 1906

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1906:259) (*Pseudomops magna*): Paramba, 1 male, 2 females, February and May 1897 (W.F.H. Rosenberg coll., Oxford Museum).
Shelford (1908a:4) (*Pseudomops magna*): Ecuador.
Princis (1969:947): Ecuador.

Symploce pallens (Stephens, 1835)

Synonymy:
Ectobius pallens Stephens, 1835
Blatta capitata Saussure, 1862
Blatta deprivata Walker, 1868
Phyllodromia hospes Perkins, 1899
Symploce lita Hebard, 1916
Ischnoptera platystyla Chopard, 1938
Symploce benzoni Princis, 1951
Symploce kevani Chopard, 1954
Symploce vicentina Princis, 1959
Cahita gracilis Rocha e Silva, 1965

Distribution: *Cuba*, Ecuador—Galápagos Islands (Circumtropical).
Comments to faunistic records in Galápagos:
Hebard (1920b:316) (*Symploce lita*): Chatham Island (= Floreana), 1 male, October 1905 (leg. F.X. Williams).
Hebard (1934:279) (*Symploce hospes*): Charles Island (= Floreana), Postoffice Bay, 16 males, 2 females, 12 juveniles, 2 oothecae, 20 August –15 September 1925.
Linsley & Usinger (1966:125) (*Symploce lita*): San Cristóbal.
Roth (1984:51): Charles Island, 1 male, 1 September 1925, 1 male, 10–14 September 1925, 1 male, 20–30 August 1925, 1 female, 1–15 September 1925, Wollebaeks (all determined by Hebard as *S. hospes*); Santa Cruz I., 0–100 m, 2 males, September 1970 (J. & M. Sedlacek)
Peck & Roth (1992:2206): Islas Floreana, San Cristóbal, Santa Cruz, Bartolomé, Campeón, Fernandina, Genovesa, Isabela, Marchena, Pinta, Santa Fe, Santiago.
Peck (1996:1502) & Peck *et al.* (1998:223): the same locality as mentioned by Peck & Roth (1992).

Xestoblatta amedegnatae Grandcolas, 1992

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Grandcolas (1992b:163): Napo, Tena, Misahualli, Jatun Sacha, 25 March 1990 and 30 March 1990 (leg. S. Poulain).

Xestoblatta bananae Rocha e Silva Albuquerque, 1962

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Rocha e Silva Albuquerque (1962c:244): 1 male, intercepted in plant quarantine from Ecuador, at San Diego, Calif., 14 April 1953, with bananas, through R. F. Wilkey; 1 female, intercepted in plant quarantine from Ecuador, in California, 30 March 1953.

Princis (1969:896): Ecuador ?.

Xestoblatta ecuadorana Gurney, 1939

Distribution: *Ecuador*, Bolivia.

Comments to faunistic records in Ecuador:

Gurney (1939:106): 1 male, 1 female, Baños–Mera Trail, Rio Pastaza watershed, Ecuador, 22 September 1937, at an altitude of 1200 m (leg. E.J. Brundage Jr.); 1 female, Puyo, Oriente, Ecuador, 900 m, 14 October 1937 (leg. E.J. Brundage, Jr.).

Princis (1948:14): the same locality as mentioned by Gurney (1939).

Princis (1969:896): Ecuador.

Xestoblatta hamata (Giglio-Tos, 1898)

Synonymy:
Ischnoptera hamata Giglio-Tos, 1898

Distribution: *Ecuador*, Colombia, Panama, Brazil.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:4) (*Ischnoptera hamata*): 2 females, Valle del Santiago, Ecuador; 1 male, Gualaquiza, Ecuador.

Shelford (1908a:8) (*Ischnoptera hamata*): Ecuador.

Hebard (1916:371): the same data as mentioned by Giglio-Tos (1898).

Campos (1923:6 and 1926:47) (*Ischnoptera hamata*): the same data as mentioned by Giglio-Tos (1898).

Rehn (1933a:31): eastern Ecuador.

Princis (1969:899): Ecuador.

Xestoblatta sancta (Giglio-Tos, 1898)

Synonymy:
Ischnoptera sancta Giglio-Tos, 1898

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:5) (*Ischnoptera sancta*): 5 females, San José, Ecuador.

Kirby (1904: 83) (*Ischnoptera sancta*): Ecuador.

Shelford (1908a:8) (*Ischnoptera sancta*): Ecuador.

Hebard (1916:371): the same data as mentioned by Giglio-Tos (1898).

Campos (1923:6 and 1926:47) (*Ischnoptera sancta*): the same data as mentioned by Giglio-Tos (1898) and Hebard (1924).

Hebard (1924:124): 1 female, Pasaje, Del Oro (leg. F. Campos R.); 1 female, Chaguarpata, Chimborazo, 5 April 1922 (leg. G.H.H. Tate).
Gurney (1939:117): the same data as mentioned by Hebard (1924).
Rehn (1933a:31): eastern Ecuador.
Princis (1969:899): Ecuador.

Eushelfordia pica (Walker, 1868)

Synonymy:
Paratropes pica Walker, 1868

Distribution: *Brazil*, Ecuador, Peru.
Comments to faunistic records in Ecuador:
Campos (1923:8 and 1926:49) (*Paratropa/Paratropes pica*): Baños (leg. F. Campos R.).
Hebard (1924:126): 1 female, Baños, Tunguragua (leg. F. Campos R.).
Princis (1967:633): Ecuador.

Megaloblatta blaberoides (Walker, 1871)

Synonymy:
Epilampra blaberoides Walker, 1871
Megaloblatta rufipes Dohrn, 1887

Distribution: *Nicaragua*, Costa Rica, Panama, Ecuador.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:6) (*Megaloblatta rufipes*): 1 male, 1 female, Valle del Santiago; 1 male, San José; 1 nymph, Gualaquiza.
Campos (1923:7 and 1926:49) (*Megaloblatta rufipes*): Bucay, Chimbo, Baños (leg. F. Campos R.) and the same data as mentioned by Giglio-Tos (1898).
Princis (1967:632): Ecuador ?.

Megaloblatta longipennis (Walker, 1868)

Synonymy:
Blabera longipennis Walker, 1868
Megaloblatta peruviana Dohrn, 1887

Distribution: *Ecuador*, Panama, Peru.
Comments to faunistic records in Ecuador:
Walker (1868:8) (*Blabera longipennis*): 1 male, Guayaquil (Mr. Stevens' collection).
Finot (1897:210) (*Blabera longipennis*): the same locality as mentioned by Walker (1868).
Kirby (1904:109): the same locality as mentioned by Walker (1868).
Shelford (1908b:4): Ecuador.
Hebard (1920a:92): 1 female, Ecuador.
Campos (1923:41): Bucay (leg. F. Campos R.).
Hebard (1924:127): 1 female, San Domingo de los Colorados, Pichincha (leg. F. Campos R.).
Campos (1926:49): the same data as mentioned by Hebard (1924).
Princis (1967:631): Ecuador.

Megaloblatta regina (Saussure, 1870)

Synonymy:
Blabera regina Saussure, 1870

Distribution: *Brazil*, Ecuador.
Comments to faunistic records in Ecuador:
Hebard (1924:127): 1 female, 1 juv. male, ootheca, Allpa-yacu, Rio Pastaza, Tunguragua, 3600 feet (Rosenberg).
Campos (1926:49): the same locality as mentioned by Hebard (1924).
Gurney (1959:133): 1 female, Banos, Ecuador.
Princis (1967:631): Ecuador.
Bell *et al.* (2007:6): 1 ootheca, Ecuador.

Nyctibora glabra Giglio-Tos, 1897

Distribution: *Bolivia*, *Peru*, Brazil, Ecuador, Argentina.
Comments to faunistic records in Ecuador:
Shelford (1913:58): 1 female, 1 larve, Santo Domingo de los Colorados.
Campos (1923:7 and 1926:48): the same data as mentioned by Shelford (1913).
Princis (1967:626): Ecuador.
Note: Giglio-Tos (1897:9) listed only localities from Peru (La Masa) and Bolivia. Hebard (1921:271) mentioned the same localities as Giglio-Tos (1897): San Francisco and Caiza (San Francisco Solano in Gran Chaco, Bolivia and Caiza, Yacuíba, Bolivia), but both were incorrectly placed in Ecuador.

? *Nyctibora humeralis* Dohrn, 1888

Distribution: *Brazil*, Ecuador ?, Bolivia ?.
Note: Princis (1967:624) reported the occurrence of this species in Brazil, Ecuador and Bolivia, but published data are available only from Brazil: Fonte Boa (Brazil, Alto Amazonas). Literature data: Dohrn (1888:129): Alto Amazonas, Fonteboa; Kirby (1904:107): Upper Amazonas; Shelford (1908b:2): Upper Amazonas; Rocha e Silva Albuquerque (1964a:18): Amazonas.

Nyctibora noctivaga Rehn, 1902

Distribution: *Nicaragua*, Panama, Jamaica, Virgin-Islands, Colombia, Ecuador.
Comments to faunistic records in Ecuador:
Campos (1923:41): San Remo (leg. F. Campos R.).
Hebard (1924:126): 1 male, San Xavier [A. N. S. P.]; 1 female, San Remo, Los Rios (leg. F. Campos R.).
Campos (1926: 48): Bucay and the same data as mentioned by Hebard (1924).
Princis (1967:628): Ecuador ?.
Note: Princis (1967:628) used “?” in the case of Ecuador and in the Campos papers, but not in the case of Hebard paper, athough the same Ecuadorian locality is mentioned.

Nyctibora obscura Saussure, 1864

Distribution: *Brazil*, Colombia, Trinidad, Ecuador, Peru.
Comments to faunistic records in Ecuador:
Hebard (1924:125): 1 female, Chaguarpata, Chimborazo, 5 April 1922 (leg. G.H.H. Tate).
Campos (1926:48): the same data as mentioned by Hebard (1924).
Princis (1967:626): Ecuador.

Paratropes aequatorialis Saussure, 1864

Synonymy:
Paratropa lanceolatus Walker, 1868

Distribution: *Ecuador*, Bolivia, Brazil, Peru.
Comments to faunistic records in Ecuador:
Saussure (1864:309): 1 female, Ecuador (Respublica Equator).
Note: The syntype of *Paratropes aequatorialis* is deposited in Muséum d'Histoire Naturelle, Genève, Switzerland with the data label "Quito, Andes, [female] M. H. de Saussure" (J. Hollier, personal communication 2012).
Walker (1868:150) (*Paratropes lanceolatus*): 1 female, Cuenca (Mr. Fraser's collection).
Finot (1897:190) (*Paratropa aequatorialis*): Ecuador (République de l'Équateur).
Kirby (1904:109): Ecuador.
Shelford (1908b:3): Ecuador.
Princis (1958:72): the same locality as mentioned by Walker (1868).
Princis (1967:619): Ecuador.

Family: Pseudophyllodromiidae Hebard, 1929

? *Amazonina conspersa* (Brunner de Wattenwyl, 1865)

Synonymy:
Phyllodromia conspersa Brunner de Wanttenwyl, 1865
Neoblattella sooretamensis Rocha e Silva Albuquerque, 1958

Distribution: *Brazil*, Venezuela, Trinidad, Guyana, Suriname, French Guiana, Brazil, Peru, Paraguay, Argentina, Ecuador ?.
Comments to faunistic records in Ecuador:
Rocha e Silva Albuquerque (1974:57): Ecuador, Rio Branco (2,000 m alt.).
Note: In other Rocha papers, the locality Rio Branco is mentioned in Amazonas (Brazil) – Rocha e Silva Albuquerque (1964a, 1972).

Ceratinoptera alticola Shelford, 1913

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1913:57): 2 males and 5 larves, Borma (3,100 m), Loja.
Campos (1923:7 and 1926:48): Loja (Clodoveo Carrión) and same data as Shelford (1913).
Princis (1969:762): Ecuador.

Ceratinoptera picta Brunner de Wattenwyl, 1865

Synonymy:
Phyllodromia conspersa Brunner de Wanttenwyl, 1865
Phyllodromia binotata Bruner, 1906

Distribution: *Brazil*, Guatemala, Panama, Colombia, Trinidad, Suriname, French Guiana, Ecuador, Peru.
Comments to faunistic records in Ecuador:
Hebard (1924:122): 1 female, Rio Pescado, Azuay, 1600 feet, 15 May 1922 (leg. G.H.H. Tate).
Campos (1926:48): the same data as mentioned by Hebard (1924).
Princis (1969:760): Ecuador.

Chorisoneura carpenteri Roth, 1992

Distribution: Ecuador–*Galápagos Islands* (endemic).
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2210): Isla Isabela: Santo Tomas, Siera Negro, Volcan Siera Negro, Volcan Alcedo, Volcan Cerro Azul; Isla Santa Cruz: Academy Bay, Los Gemelos, Media Luna, Puntudo, Santa Rosa; Isla Floreana: Black Beach; Isla Santiago: Aguacate Camp.
Peck (1996:1502): the same locality as mentioned by Peck & Roth (1992).

Chorisoneura cristobalensis Roth, 1992

Distribution: Ecuador–*Galápagos Islands* (endemic).
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2213): Isla San Cristóbal – El Junco.
Peck (1996:1502): the same locality as mentioned by Peck & Roth (1992).

Chorisoneura diaphana Princis, 1965

Synonymy:
Blatta pellucida Saussure, 1864

Distribution: *Mexico*, Ecuador, Colombia ?.
Comments to faunistic records in Ecuador:
Bolivar (1881:468) (*Chorisoneura pellucida*): Palmal (leg. Stolzmann).
Campos (1923:9 and 1926:52) (*Chorisoneura pellucida*): the same locality as mentioned by Bolivar (1881).

Chorisoneura minuta Saussure, 1869

Distribution: *Argentina*, Ecuador.
Comments to faunistic records in Ecuador:
Bolivar (1881:469): Palmal (leg. Stolzmann).
Campos (1923:9 and 1926:52): the same locality as mentioned by Bolivar (1881).
Princis (1965:339): Ecuador.

Chorisoneura morosa Shelford, 1907

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1907b:44): 1 specimen, Cachabi, December 1896 (W.F.H. Rosenberg coll., Oxford Museum).
Princis (1965:340): Ecuador.

Chorisoneura translucida (Saussure, 1864)

Synonymy:
Blatta translucida Saussure, 1864

Distribution: *Mexico*, Guatemala, Costa Rica, Panama, Colombia, Ecuador.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:11): 1 specimen, Valle del Santiago.

Campos (1923:9 and 1926:52): the same locality as mentioned by Giglio-Tos (1898).

Princis (1965:340): Ecuador ?.

Euphyllodromia erythromelas Rehn, 1932

Distribution: *Peru*, Colombia, Brazil, Ecuador.

Comments to faunistic records in Ecuador:

Anisyutkin (2011:383): 7 males, 5 females, prov. Sucumbíos, E of town Lago Agrio, November 2005 (coll. A. Gorochov, A. Ovtshinnikov).

Euphyllodromia hystrix (Saussure, 1869)

Synonymy:
Pseudophyllodromia hystrix Saussure, 1869
Pseudophyllodromia histrio Saussure, 1870

Distribution: *Venezuela*, Colombia, Ecuador, Peru, Costa Rica.

Comments to faunistic records in Ecuador:

Hebard (1924:124): 10 females, Rio Pescado, Azuay, 1600 feet, 15 May 1922 (leg. G.H.H. Tate).

Hebard (1929:360) (*Euphyllodromia histrio*): 1 female, Ecuador.

Campos (1926:47): the same locatity as mentioned by Hebard (1924).

Princis (1969:937): Ecuador.

Anisyutkin (2011:383): 1 male, prov. Sucumbíos, E of town Lago Agrio, November 2005 (coll. A. Gorochov, A. Ovtshinnikov).

Euphyllodromia nigrochlamys Rehn, 1928

Distribution: *Peru*, Ecuador.

Comments to faunistic records in Ecuador:

Anisyutkin (2011:394): 9 males, 3 females, prov. Sucumbíos, SE of town Lago Agrio, November 2005 (coll. A. Gorochov, A. Ovtshinnikov); 1 male, prov. Morona Santiago, bank of Rio Morona, January 2010 (coll. A. Gorochov).

Euphyllodromia peruana (Saussure, 1864)

Synonymy:
Blatta peruana Saussure, 1864

Distribution: *Peru*, Brazil, Ecuador.

Comments to faunistic records in Ecuador:

Anisyutkin (2011:378): 2 males, 1 female, prov. Sucumbíos, E of town Lago Agrio, November 2005 (coll. A. Gorochov, A. Ovtshinnikov); 1 male, 1 female, prov. Morona Santiago, bank of Rio Morona, January 2010 (coll. A. Gorochov).

Euphyllodromia propinqua Anisyutkin, 2011

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2011:390): 5 males, 5 females, prov. Sucumbíos, SE (or E) of town Lago Agrio, November 2005 (coll. A. Gorochov, A. Ovtshinnikov).

Euphyllodromia rasnitsyni Anisyutkin, 2011

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2011:391): 1 male, 2 females, 95 km E of city Quito, November 2005 (coll. A. Gorochov, A. Ovtshinnikov).

Euphyllodromia venezuelica Princis, 1951

Distribution: *Venezuela*, Ecuador.

Comments to faunistic records in Ecuador:

Anisyutkin (2011:380): 1 male, prov. Sucumbíos, SE of town Lago Agrio, November 2005 (coll. A. Gorochov, A. Ovtshinnikov).

? *Imblattella albida* (Saussure, 1869)

Synonymy:
Blatta albida Saussure, 1869

Distribution: *Colombia*, Ecuador ?.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:2) (*Blatta albida*): 1 female, San José (determination is questionable).

Campos (1923:5 and 1926:45) (*Blatta albida*): the same locality as mentioned by Giglio-Tos (1898).

Princis (1969:797): Ecuador.

? *Latiblattella vitrea* (Brunner de Wattenwyl, 1865)

Synonymy:
Phyllodromia vitrea Brunner de Wattenwyl, 1865
Blatta latimargo Walker, 1868
Blatta alaris Saussure & Zehntner, 1893
Blatta maya Saussure & Zehntner, 1893

Distribution: *Mexico*, Honduras, Costa Rica, Ecuador ?.

Comments to faunistic records in Ecuador:

Campos (1923:6) (*Phyllodromia vitrea* ?) (determination is questionable) and (1926:47) (*Phyllodromia vitrea* ?): Bucay (leg. F. Campos R.).

Lophoblatta brevis Rehn, 1937

Distribution: *Guyana*, Venezuela, Suriname, Ecuador, Brazil.

Comments to faunistic records in Ecuador:

Rocha e Silva Albuquerque (1964b:4): Ecuador, Puyo, 900m, 16 males, 9 females, 14 October 1937 (Clarke, Macintyre, Brundage coll.).

Princis (1969:785): Ecuador.

Lopes & Oliveira (2003:346): Ecuador, Pastaza: Puyo, 900m, 2 males, 1 female, 14 October 1937 (Clarke, Macintyre, Brundage col., Museu Nacional, Universidade Federal do Rio de Janeiro).
Lopes (2004:345): Ecuador (on the map of South America).

Lophoblatta speerae Roch e Silva Albuquerque & Gurney, 1963

Distribution: *Brazil*, Ecuador.
Comments to faunistic records in Ecuador:
Rocha e Silva Albuquerque (1964b:6): Ecuador, Puyo, 900m, 1 male, 14 October 1937 (Clarke, Macintyre, Brundage coll.).
Princis (1969:786): Ecuador.
Lopes & Oliveira (2003b:352): Ecuador.
Lopes (2004:345): Ecuador (on the map of South America).

Macrophyllodromia amabile Anisyutkin, 2007

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Anisyutkin (2007:29): 1 male, 1 female, E. Ecuador, env. of waterfall San Rafael on Rio Coca, 95 km E of city Quito, forest, 1300 m (leg. A. Gorochov, A. Ovitshinnikov).

Macrophyllodromia ecuadorana Rocha e Silva Albuquerque, 1962

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Rocha e Silva Albuquerque (1962a:425): 1 male, Guayaquil, Ecuador, intercepted at San Diego, California, in bananas, 14 April 1953 (leg. R. Wilkey); 1 female, Ecuador, intercepted in California, 16 April 1953, in bananas (leg. R. Wilkey).
Princis (1969:773): Ecuador.

Macrophyllodromia nobile Anisyutkin, 2007

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Anisyutkin (2007:32): 1 male, E. Ecuador, 80–85 km E of town Lago Agrio, env. of lake Lago Grande, Rio Cuyabeno (leg. A. Gorochov, A. Ovitshinnikov).

Melyroidea magnifica Shelford, 1912

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1912:375): 1 female, Ecuador (Saunders collection, Oxford museum).
Princis (1965:357): Ecuador.

Nahublattella alexandri Anisyutkin, 2009

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2009:611): 7 males, E. Ecuador, 80–85 km E of Lago Agrio, near lake Lago Grande (Rio Cuyabeno), 2–9 November 2005 (leg. A. Gorochov, A. Ovchinnikov).

Nahublattella cuyabeno Anisyutkin, 2009

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2009:610): 1 male, E. Ecuador, 80–85 km E of Lago Agrio, near lake Lago Grande (Rio Cuyabeno), 2–9 November 2005 (leg. A. Gorochov, A. Ovchinnikov).

Nahublattella ecuadorana Rocha e Silva Albuquerque, 1962

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Rocha e Silva Albaquerque (1962b:114): 1 male, Ecuador, on bananas, in cargo at San Pedro, CA, USA, 22 August 1959; 1 female, Ecuador, on bananas at New Orleans, LA, USA, 20 February 1953.

Princis (1969:795): Ecuador.

Nahublattella incurvata Anisyutkin, 2009

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2009:611): 1female, W Ecuador, 10 km E of Aqua Blanca, env. of Puerto Lopez, 26–29 October 2005 (leg. A. Gorochov, A. Ovchinnikov).

Nahublattella reticulata Anisyutkin, 2009

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2009:621): 1 male, 2 females, E. Ecuador, 80–85 km E of Lago Agrio, near lake Lago Grande (Rio Cuyabeno), 2–9 November 2005 (leg. A. Gorochov, A. Ovchinnikov).

Nahublattella ultima Anisyutkin, 2009

Distribution: *Ecuador.*

Comments to faunistic records in Ecuador:

Anisyutkin (2009:616): 2 males, E. Ecuador, 70 km NE of Lago Agrio, near S. Pablo de Kantesiya Vill., on Rio Aguarico, 10–17 November 2005 (leg. A. Gorochov, A. Ovchinnikov); 1 male, 80–85 km E of Lago Agrio, near lake Lago Grande (Rio Cuyabeno), 2–9 November 2005 (leg. A. Gorochov, A. Ovchinnikov).

Neoblattella adspersicollis (Stål, 1860)

Synonymy:
Blatta adspersicollis Stål, 1860

Distribution: *Brazil*, Ecuador.

Comments to faunistic records in Ecuador:

Bolivar (1881:466) (*Blatta adspersicolis*): Palmal (leg. Stolzmann).
Campos (1923:5 and 1926:46) (*Blatta adspersicolis*): the same locality as mentioned by Bolivar (1881).

Neoblattella festae (Giglio-Tos, 1898)

Synonymy:
Blatta festae Giglio-Tos, 1898

Distribution: *Ecuador*, Venezuela ?.

Comments to faunistic records in Ecuador:

Giglio-Tos (1898:2) (*Blatta Festae*): 1 male, 1 female, Gualaquiza, Ecuador.
Kirby (1904: 94) (*Phyllodromia festae*): Ecuador.
Shelford (1908a:14) (*Phyllodromia festae*): Ecuador.
Campos (1923:5 and 1926:46) (*Blatta Festae*): the same data as mentioned by Giglio-Tos (1898).
Rehn (1903:268) (*Blattella festae*): the same data as mentioned by Giglio-Tos (1898).
Rehn (1949:12) (*Blattella festae*): the same data as mentioned by Giglio-Tos (1898).
Princis (1969:794): Ecuador.
Note: Based on the Campos papers Princis (1969:898) listed by mistake Ecuador as the country of distribution for *Xestoblatta festae* (Griffini, 1896). Campos evidently referred to *Neoblattella festae* (Giglio-Tos, 1898).

Supella longipalpa (Fabricius, 1798)

Synonymy:
Blatta longipalpa Fabricius, 1798
Blatta (*Phyllodromia*) *supellectilium* Serville, 1839
Blatta cubensis Saussure, 1862
Blatta phalerata Saussure, 1863
Blatta extenuata Walker, 1868
Blatta incisa Walker, 1868
Ischnoptera quadriplaga Walker, 1868
Ischnoptera vacillans Walker, 1868
Blatta subfasciata Walker, 1871
Blatta transversalis Walker, 1871

Distribution: *Southern America* (“India orientali”), Ecuador (Circumtropical).

Comments to faunistic records in Ecuador:

Campos (1923:6 and 1926:47) (*Supella supellectilium*): Guayaquil, Durán, Yaguachi, Milagro, Naranjito, San Rafael, Bucay, Posorja, El Morro (leg. F. Campos R.).
Hebard (1924:122) (*Supella supellectilium*): 2 males, 3 females, Guayaquil, Guayas (leg. F. Campos R.).
Hebard (1929:358) (*Supella supellectilium*): 1 male, Ecuador (leg. G. Hammond).

Family: Blattidae Stephens, 1835

Blatta orientalis Linnaeus, 1758

Synonymy:
Blatta lucifuga Poda, 1761
La Blatte des cuisines Geoffroy, 1762
Blatta secunda Schaeffer, 1769
Blatta tertia Schaeffer, 1769
Blatta culinaris De Geer, 1773
Blatta ferruginea Thunberg, 1810

Blatta europaea Bartsch, 1846
Blatta castanea Blanchard, 1851
Blatta hemialata Gistel, 1856
Pulex imperator Westwood, 1858
Blatta badia Saussure, 1863
Kakerlac pallipes Philippi, 1863
Kakerlac platystetho Philippi, 1863
Stylopyga orientalis gracilis Adelung, 1903
Stylopyga orientalis spontanea Semenov-Tian-Shansky, 1909

Distribution: *America*, *Oriente*; Ecuador (Cosmopolitan).
Comments to faunistic records in Ecuador:
Westwood (1876:xxxii): in bulb of orchid from Ecuador.
Roth & Willis (1960:151, 162): the same data as mentioned by Westwood (1876).

Pelmatosilpha cothurnata (Giglio-Tos, 1898)

Synonymy:
Eurycotis cothurnata Poda, 1761

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:11) (*Eurycotis cothurnata*): Guajaquil (sic), Canar, S. José, Cuenca.
Kirby (1904:144) (*Eurycotis cothurnata*): Ecuador.
Shelford (1910b:12) (*Eurycotis cothurnata*): Ecuador.
Shelford (1913:58) (*Eurycotis cothurnata*): 1 female, Cuenca.
Campos (1923:8 and 1926:51) (*Eurycotis cothurnata*): the same locality as mentioned by Giglio-Tos (1898) and by Hebard (1924).
Hebard (1924:125) (*Eurycotis cothurnata*): 1 male, Cuenca, Azuay, (Captain Noirel); 1 male, 1 female, 7800 feet, 12 July 1922 (leg. G.H.H. Tate); 1 female, Mount Chimborazo, 12467 feet (leg. Captain Noirel).
Gurney (1965:7): Ecuador.
Princis (1966:462): Ecuador.

Pelmatosilpha praestans Dohrn, 1887

Synonymy:
Periplaneta aterrima Walker, 1869

Distribution: *Peru*, Brazil, Ecuador.
Comments to faunistic records in Ecuador:
Shelford (1913:58) (*Pelmatosilpha aterrima*): 1 male, Santo Domingo de los Colorados.
Campos (1923:9 and 1926:52) (*Pelmatosilpha aterrima*): the same locality as mentioned by Shelford (1913) and by Hebard (1924).
Hebard (1924:125): 1 male, Canelos, Rio Bobonaza, Oriente (leg. Rosenberg).
Gurney (1965:7): Ecuador.
Princis (1966:461): Ecuador.

Periplaneta americana (Linnaeus, 1758)

Synonymy:
Blatta americana Linnaeus, 1758
Blatta ferrugineo-fusca Gronovius, 1764
Blatta kakerlac De Geer, 1773

Blatta orientalis Sulzer, 1776 non Linnaeus, 1758
Blatta aurelianensis Fourcroy, 1785
Blatta siccifolia Stoll, 1813
Blatta heros Eschscholtz, 1822
Periplaneta stolida Walker, 1868
Periplaneta americana colorata Rehn, 1902

Distribution: *America*, Ecuador (+ Galápagos Islands) (Cosmopolitan).

Comments to faunistic records in Ecuador:

Scudder (1869:342): 1 specimen, Napo or Marañón.
Westwood (1876:xxxii) (*Blatta Americana*): in a bulb of orchid from Ecuador.
Giglio-Tos (1898:106): 1 male, Vinces
Campos (1923:8 and 1926:51): Guayaquil, Durán, Naranjito, Posorja (leg. F. Campos R.) and same locality as Giglio-Tos (1898).
Roth & Willis (1960): the same information as mentioned by Westwood (1879).
Bonsall (1995:33): Misahualli, Puerto Lopez, Jatun Sacha, Tena.
Comments to faunistic records in Galápagos:
Butler (1877:87): Charles Island, 2 adult specimens, June 1875 (leg. W.E. Cookson).
Howard (1889:193): Chatham Island, 10 specimens, 1887–88 (det. L. Bruner).
Scudder (1893:6): only the same exemplars as stated by Butler (1877) and by Howard (1889).
Hebard (1934:279): Charles Island, (= Floreana), Postoffice Bay, 1 female, 1 juv., 15–19 November 1925.
Linsley & Usinger (1966:125): San Cristóbal, Floreana.
Peck & Roth (1992:2205): Islas Floreana, San Cristóbal, Genovesa, Isabela, Santa Cruz (Bellavista, El Chato).
Peck (1996:1051); Peck *et al.* (1998:223) & Peck (2001:149): the same data as mentioned by Peck & Roth (1992).

Periplaneta australasiae (Fabricius, 1775)

Synonymy:
Blatta aurantiaca Stoll, 1813
Periplaneta zonata Haan, 1842
Periplaneta inclusa Walker, 1868
Periplaneta rapenda Walker, 1868
Periplaneta subcincta Walker, 1868
Periplaneta emittens Walker, 1871
Polyzosteria subornata Walker, 1871

Distribution: Ecuador (+ Galápagos Islands) (Circumtropical); (terra typica was not defined).

Comments to faunistic records in Ecuador:

Scudder (1869:342): 2 specimens, Napo or Marañón.
Bolivar (1884:16): Coca, Ecuador (leg. Martínez y Saez).
Giglio-Tos (1898:10): Gualaquiza, Valle dello Zamora, La Concepcion nella valle del Mira – Ecuador.
Shelford (1913:59): Santo Domingo de los Colorados, Riobamba, Balsabamba.
Campos (1923:8): Guayaquil, Durán, Naranjito, San Rafael, Bucay, Posorja, El Morro (leg. F. Campos R.) and the same locality as mentioned by Giglio-Tos (1898).
Hebard (1924:125): 1 male, Guayaquil, Guayas, (leg. F. Campos R.); 1 female, Rio Zamora, Loja (leg. F. Campos R.).
Campos (1926:50): Daule (leg. F. Campos R.), Portoviejo (leg. Justino Cornejo V.) and the same locality as mentioned by Giglio-Tos (1898), Shelford (1913) and Campos (1923).
Roth & Willis (1960:80): Ecuador (according Campos (1926)).
Bonsall (1995:33): Misahualli, Puerto Lopez, Jatun Sacha, Tena.
Comments to faunistic records in Galápagos:
Howard (1889:194): Charles Island, 3 images and 3 nymphs, 1887–88 (det. L. Bruner).
Scudder (1893:6): only the same exemplars as mentioned by Howard (1889).
McNeill (1901:494): Chatham, 1 male, and the same locality as mentioned by Howard (1889).
Hebard (1920b:316): Chatham Island, 1 female, October 1905–January 1906; Charles Island, 3 males, 6 females, October 1905 (leg. F.X. Williams).

Hebard (1929:364): Charles Island, 1 juv. female, August 1924 (leg. Miss Cheesman).
Hebard (1934:279): Charles Island, (= Floreana), Postoffice Bay, 2 males, 3 females, 1 juv., 5 August–25 November 1925.
Linsley & Usinger (1966:125): San Cristóbal, Floreana.
Parkin *et al.* (1972:102): 1 specimen, Floreana, 31 August 1968 (det. D.R. Ragge).
Maes (1992b:3): Galápagos.
Peck & Roth (1992:2205): Islas Floreana, San Cristóbal, Isabela, Santa Cruz.
Peck (1996:1501); Peck (1998:223) & Peck (2001:149): the same data as mentioned by Peck & Roth (1992).

Periplaneta brunnea Burmeister, 1838

Synonymy:
Periplaneta patens Walker, 1868
Periplaneta concolor Walker, 1868
Periplaneta truncata Krauss, 1892
Periplaneta ignota Shaw, 1925

Distribution: *Chile* and Demerary, Ecuador (+ Galápagos Islands) (Circumtropical).
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:106) (*Periplaneta truncata*): Guayaquil.
Campos (1923:8 and 1926:51) (*Periplaneta truncata*): Guayaquil, Durán (leg. F. Campos R.).
Bonsall (1995:33): Misahualli, Puerto Lopez, Jatun Sacha, Tena.
Comments to faunistic records in Galápagos:
Hebard (1920b:316): Chatham Island, 1 female, January 1906 (leg. F.X. Williams).
Linsley & Usinger (1966:125): San Cristóbal.
Peck & Roth (1992:2205): Isla San Cristóbal (according Hebard (1920b)).
Peck (1996:1501); Peck *et al.* (1998:223) & Peck (2001:149): the same data as metioned by Peck & Roth (1992).

Lamproblatta zamorensis (Giglio-Tos, 1898)

Synonymy:
Stylopyga zamorensis Giglio-Tos, 1898

Distribution: *Ecuador*, Peru.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:10) (*Stylopyga zamorensis*): 1 female, Valle del Zamora.
Kirby (1904: 139) (*Blatta zamorensis*): Ecuador.
Shelford (1910b:15) (*Stylopyga zamorensis*): Ecuador.
Campos (1923:8 and 1926:51) (*Stylopyga zamorensis*): the same locality as mentioned by Giglio-Tos (1898).
Princis (1966:546): Ecuador.
Roth (2003a:286): Ecuador.

Eurycotis riveti Shelford, 1913

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Shelford (1913:58) (*Eurycoti Riveti*): 3 females, 1 nymph, Loja.
Campos (1923:8 and 1926:52): the same locality as mentioned by Shelford (1913).
Princis (1966:555): Ecuador.

Family: Polyphagidae Walker, 1868

Compsodes mexicanus (Saussure, 1868)

Synonymy:
Latindia mexicana Saussure, 1868
Latindia tolteca Saussure & Zehntner, 1894

Distribution: *Mexico*, Ecuador.
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:15) (*Latindia mexicana*): 1 specimen, Gualaquiza.
Campos (1923:10 and 1926:54) (*Latindia mexicana*): the same locality as mentioned by Giglio-Tos (1898).
Princis (1963:104): Ecuador ?.

Holocompsa nitidula (Fabricius, 1781)

Synonymy:
Blatta nitidula Fabricius, 1781
Holocompsa capsoides Shelford, 1911
Corydia collaris Burmeister, 1838

Distribution: *Suriname,* Brazil, Ecuador–Galápagos Islands (Circumtropical).
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2205): Isla Isabela, 4 males, 3 females, 9 March 1989.
Peck (1996:1501); Peck (2001:149): the same locality as mentioned by Peck & Roth (1992).

Holocompsa sp.

Distribution: Ecuador—Galápagos Islands.
Comments to faunistic records in Galápagos:
Peck & Roth (1992:2205): Isla Santa Cruz (Academia Bay, 15 March 1970; Mirador, 10 July 1970), 3 males different from *H. nitidula*.
Peck (1996:1501): the same locality as mentioned by Peck & Roth (1992).

Zetha simonyi (Krauss, 1892)

Synonymy:
Holocompsa simonyi Krauss, 1892
Blatta vestita Brullé, 1838 [primary homonym]
Holocompsa chavesi Bolívar, 1894
Zetha freyi Chopard, 1942
Zetha rufescens Shelford, 1913

Distribution: *Canary Islands*, Azores Islands, Kapeverde, Peru, Ecuador, Guatemala, Hawai.
Comments to faunistic records in Ecuador:
Shelford (1913:59) (*Zetha rufescens* sp.n.): 1 female, Loja.
Campos (1923:10 and 1926:55) (*Zetha rufescens*): the same locality as mentioned by Shelford (1913).
Princis (1963:89): Ecuador.

Species incertae sedis

Blatta (?) *nigrita* Bolivar, 1881

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Bolivar (1881:477(31)) (*Blatta nigrita*): Baeza, Ecuador (leg. Martínez y Saez).
Bolivar (1884:12) (*Phyllodromia nigrita*): the same locality as mentioned by Bolivar (1881).
Kirby (1904:96) (*Phyllodromia nigrita*): Ecuador.
Shelford (1908a:14) (*Phyllodromia nigrita*): Ecuador.
Campos (1923:5 and 1926:46) (*Blatta nigrita*): the same locality as mentioned Bolivar (1881).
Princis (1969:1010): Ecuador.
Note: More accurate classification is not possible in this species. The type material is not preserved.

Theganopteryx (?) sp. (Anaplectinae)

Distribution: *Ecuador.*
Comments to faunistic records in Ecuador:
Giglio-Tos (1898:2): 1 specimen, Valle del Zamora.
Campos (1923:4 and 1926:44): the same locality as mentioned by Giglio-Tos (1898).
Note: All known species from the genus *Theganopteryx* occur only in Africa and Madagascar. The determination was evidently erroneous.

In conclusion, records of 114 cockroach species (Blattaria) in the territory of Ecuador 105 in continental Ecuador and 18 in Galápagos Islands) are summarized. These species belong to 6 families and 42 genera (Table 1). Occurrence of another 8 species is questionable. Forty species (38.5 %) were recorded exclusively from the territory of continental Ecuador. Five of 18 species living on the Galápagos Islands (27.8 %) are endemic. Currently, the continental Ecuadorian cockroach fauna shares the highest number of species with the Brazilian (43.3%) and Colombian faunas (28.8 %) (Table 2). However, further studies on Ecuadorian as well as other Neotropical cocroaches are needed.

TABLE 1. Number of genera and species of cockroaches in continental Ecuador and in Galápagos Islands. Species of questionable occurrence are not included.

Family	Ecuador (continental)		Galápagos Island		Ecuador + Galápagos	
	Genera	Species	Genera	Species	Genera	Species
Blaberidae	14	33	5	5	14	33
Anaplectidae	2	10	1	1	2	10
Blattellidae	8	22	3	5	9	27
Pseudophyllodromiidae	9	28	1	2	9	30
Blattidae	5	8	1	3	5	8
Polyphagidae	2	2	1	2	3	4
Species incertae sedis	2	2	0	0	2	2
Total	**42**	**105**	**12**	**18**	**44**	**114**

TABLE 2. Distribution of Ecuadorian cockroach species in surrounding countries.

Species / Country	Ec	GI	Br	Co	Pe	Ve	GS	Ar	Bo	Ch
Blaberidae										
Blaberus atropos (Stoll, 1813)	X						X			X
Blaberus boliviensis Princis, 1946	X								X	
Blaberus craniifer (Burmeister, 1838)	X					X				
Blaberus discoidalis (Serville, 1839)	X			X		X				
Blaberus parabolicus (Walker, 1868)	X	X	X	X	X		X		X	
Eublaberus immaculus (Saussure & Zehntner, 1894)	X		X							
Eublaberus posticus (Erichson, 1848)	X		X	X	X	X	X			
Hormetica strumosa Saussure & Zehntner, 1895	X									
Phoetalia circumvagans (Burmeister, 1838)	X		X	X	x	x	x		x	
Phoetalia pallida (Brunner von W., 1865)	X	X	X	X	x	x	x		x	
Epilampra azteca Saussure, 1868	X		X	X		X	X			
Epilampra conferta Walker, 1868	X		X	X	X				X	
Epilampra josephi Giglio-Tos, 1898	X									
Epilampra mexicana Saussure, 1862	X									
Epilampra opaca (Walker, 1868)	X		X			X	X		X	
Epilampra substrigata Walker, 1868	X		X	X		X				
Homalopteryx laminata Brunner von W., 1892	X			X		X				
Litopeltis compleptera Roth & Gutiérrez, 1998	X									
Rhyparobia maderae (Fabricius, 1781)	X	X	x	X	x	X	x		x	
Nauphoeta cinerea (Olivier, 1789)	X	X	X	x	x	x	x		x	
Achroblatta luteola (Blanchard, 1843)	X		X	X	X	X	X		X	X
Panchlora exoleta Burmeister, 1838	X		X	X	X	X	X	X		
Panchlora festae Giglio-Tos, 1898	X									
Panchlora irrorata Hebard, 1924	X									
Panchlora nigricornis Walker, 1868	X									
Panchlora nivea (Linnaeus, 1758)	X		X	X	x	X	x		x	
Panchlora peruana Saussure, 1864	X		X		X					
Panchlora pulchella Burmeister, 1838	X		X							
Pycnoscelus surinamensis (Linnaeus, 1758)	X	X	X	X	x	X	X	X	x	x
Lanxoblatta emarginata (Burmeister, 1838)	X		X	X			X			
Lanxoblatta martinezi (Bolivar, 1881)	X									
Lanxoblatta rudis (Walker, 1868)	X		X							
Parasphaeria ovata (Blanchard, 1851)	?									X
Zetobora aberrans Giglio-Tos, 1898	X									
Anaplectidae										
Anaplecta alaris Saussure & Zehntner, 1893	X		X		X					
Anaplecta brunneri Shelford, 1906	?		X							
Anaplecta cabimae Hebard, 1920	X									

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TABLE 2. (continued)

Species / Country	**Ec**	**GI**	**Br**	**Co**	**Pe**	**Ve**	**GS**	**Ar**	**Bo**	**Ch**
Anaplecta falcifer Hebard, 1924	X		X							
Anaplecta fusca Shelford, 1906	X									
Anaplecta lateralis Burmeister, 1838	X	X	X	X		X		X		
Anaplecta mexicana Saussure, 1868	X									
Anaplecta pallida Bolivar, 1881	X									
Anaplecta pavida Shelford, 1906	X									
Anaplecta varipennis Shelford, 1906	X									
Maraca fossata Hebard, 1926	X		X			X	X			
Blattellidae										
Blattella germanica (Linnaeus, 1767)	X	X	X	X	x	X	x	X	x	X
Ischnoptera josephina Giglio-Tos, 1898	X									
Ischnoptera melasa Walker, 1868	?		X							
Ischnoptera pallipes (Scudder, 1869)	X		X		X					
Ischnoptera peckorum Roth, 1988		X								
Ischnoptera rufa (De Geer, 1773)	X		X	X			X			
Ischnoptera santacruzensis Roth, 1992		X								
Ischnoptera snodgrassi (McNeill, 1901)		X								
Ischnoptera taczanowskii Bolivar, 1881	X				X					
Pseudomops albostriatus Shelford, 1906	X									
Pseudomops bicolor Shelford, 1906	X									
Pseudomops burri Shelford, 1906	X									
Pseudomops magnus Shelford, 1906	X									
Symploce pallens (Stephens, 1835)	x	X	X	x	x	x	x		x	
Xestoblatta amedegnatae Grandcolas, 1992	X									
Xestoblatta bananae Rocha e Silva, 1962	X									
Xestoblatta ecuadorana Gurney, 1939	X								X	
Xestoblatta hamata (Giglio-Tos, 1898)	X		X	X						
Xestoblatta sancta (Giglio-Tos, 1898)	X									
Eushelfordia pica (Walker, 1868)	X		X		X					
Megaloblatta blaberoides (Walker, 1871)	X									
Megaloblatta longipennis (Walker, 1868)	X				X					
Megaloblatta regina (Saussure, 1870)	X		X							
Nyctibora glabra Giglio-Tos, 1897	X		X		X			X	X	
Nyctibora humeralis Dohrn, 1888	?		X						?	
Nyctibora noctivaga Rehn, 1902	X			X						
Nyctibora obscura Saussure, 1864	X		X	X	X					
Paratropes aequatorialis Saussure, 1864	X		X		X				X	
Pseudophyllodromiidae										
Amazonina conspersa (Brunner v. Wattenwyl, 1865)	?		X		X	X	X	X		

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TABLE 2. (continued)

Species / Country	**Ec**	**GI**	**Br**	**Co**	**Pe**	**Ve**	**GS**	**Ar**	**Bo**	**Ch**
Ceratinoptera alticola Shelford, 1913	X									
Ceratinoptera picta Brunner von W., 1865	X		X	X	X		X			
Chorisoneura carpenteri Roth, 1992		X								
Chorisoneura cristobalensis Roth, 1992		X								
Chorisoneura diaphana Princis, 1965	X			?						
Chorisoneura minuta Saussure, 1869	X							X		
Chorisoneura morosa Shelford, 1907	X									
Chorisoneura translucida (Saussure, 1864)	X			X	X					
Euphyllodromia erythromelas Rehn, 1932	X		X	X	X					
Euphyllodromia hystrix (Saussure, 1869)	X			X	X	X				
Euphyllodromia nigrochlamys Rehn, 1928	X				X					
Euphyllodromia peruana (Saussure, 1864)	X		X		X					
Euphyllodromia propinqua Anisyutkin, 2011	X									
Euphyllodromia rasnitsyni Anisyutkin, 2011	X									
Euphyllodromia venezuelica Princis 1951	X					X				
Imblattella albida (Saussure, 1869)	?			X						
Latiblattella vitrea (Brunner von W., 1865)	?									
Lophoblatta brevis Rehn, 1937	X		X			X	X			
Lophoblatta speerae Rocha e Silva & Gurney, 1963	X		X							
Macrophyllodromia amabile Anisyutkin, 2007	X									
Macrophyllodromia ecuadorana Rocha e Silva, 1962	X									
Macrophyllodromia nobile Anisyutkin, 2007	X									
Melyroidea magnifica Shelford, 1912	X									
Nahublattella alexandri Anisyutkin, 2009	X									
Nahublattella cuyabeno Anisyutkin, 2009	X									
Nahublattella ecuadorana Rocha e Silva, 1962	X									
Nahublattella incurvata Anisyutkin, 2009	X									
Nahublattella reticulata Anisyutkin, 2009	X									
Nahublattella ultima Anisyutkin, 2009	X									
Neoblattella adspersicollis (Stål, 1860)	X		X							
Neoblattella festae (Giglio-Tos, 1898)	X					?				
Supella longipalpa (Fabricius, 1798)	X		X	X	x	X	x	X	x	x
Blattidae										
Blatta orientalis Linnaeus, 1758	X		X	x		X		X		X
Pelmatosilpha cothurnata (Giglio-Tos, 1898)	X									
Pelmatosilpha praestans Dohrn, 1887	X		X		X					
Periplaneta americana (Linnaeus, 1758)	X	X	x	X	x	X	x	X	x	X
Periplaneta australasiae (Fabricius, 1775)	X	X	X	X	X	X	X	x	x	x
Periplaneta brunnea Burmeister, 1838	X	X	X	X	x	X	X	X	x	X

......to be continued on the next page

TABLE 2. (continued)

Species / Country	**Ec**	**GI**	**Br**	**Co**	**Pe**	**Ve**	**GS**	**Ar**	**Bo**	**Ch**
Lamproblatta zamorensis (Giglio-Tos, 1898)	X				X					
Eurycotis riveti Shelford, 1913	X									
Polyphagidae										
Compsodes mexicanus (Saussure, 1868)	X									
Holocompsa nitidula (Fabricius, 1781)	x	X	X	x	x	x	x		x	
Holocompsa sp.		X								
Zetha simonyi (Krauss, 1892)	X				X					
Species incertae sedis										
Blatta (?) *nigrita* Bolivar, 1881	X									
Theganopterix (?) sp.	X									
Number	105	18	48	30	25	24	16	11	8	7

Abbreviations: Ec—Ecuador, GI—Galápagos Islands, Br—Brazil, Co—Colombia, Pe—Peru, Ve—Venezuela, GS—Guyana, Suriname and French Guiana, Ar—Argentina, Bo—Bolivia, Ch—Chile; X—occurrence based on published data, ?—questionable occurrence, (?)—questionable status in classification, x—expected occurrence of circumtropical and synantropic species

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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,

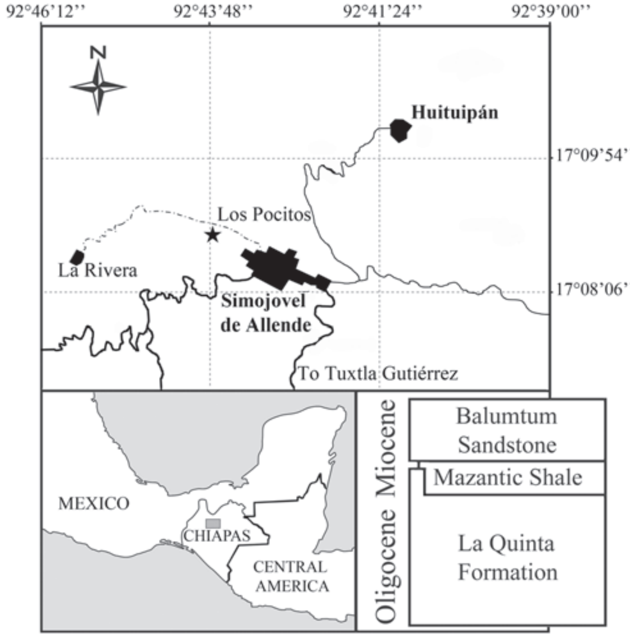


Fig. 1. Location and stratigraphic column of the Los Pocitos locality of the Chiapas amber, Mexico.

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

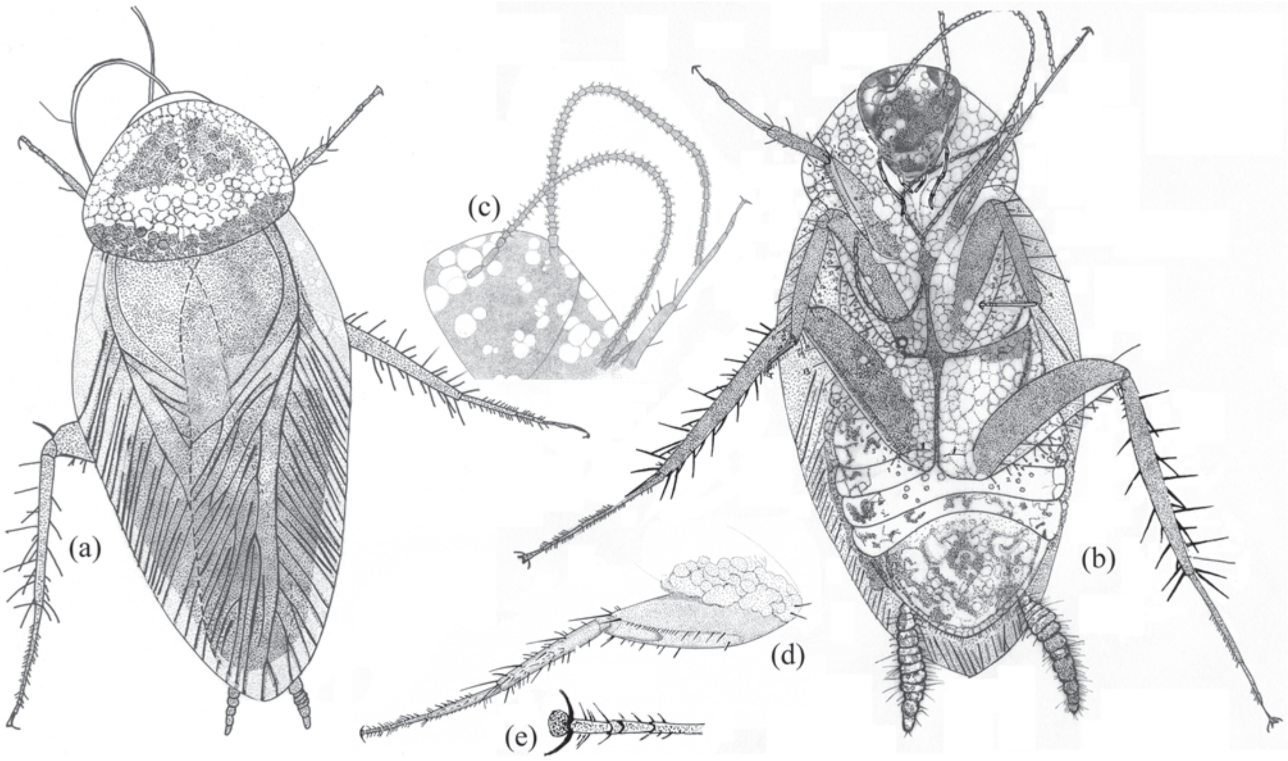


Fig. 2. *Supella miocenica* sp. nov. from the Miocene Chiapas amber of Mexico. Holotype MUCAS-001. **a** — Dorsal view; **b** — Ventral view; **c** — Head; **d** — Fore leg; **e** — Fore tarsus. Original by PC and FV. Total specimen length (from the head to the end of wings) 10 mm.

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).

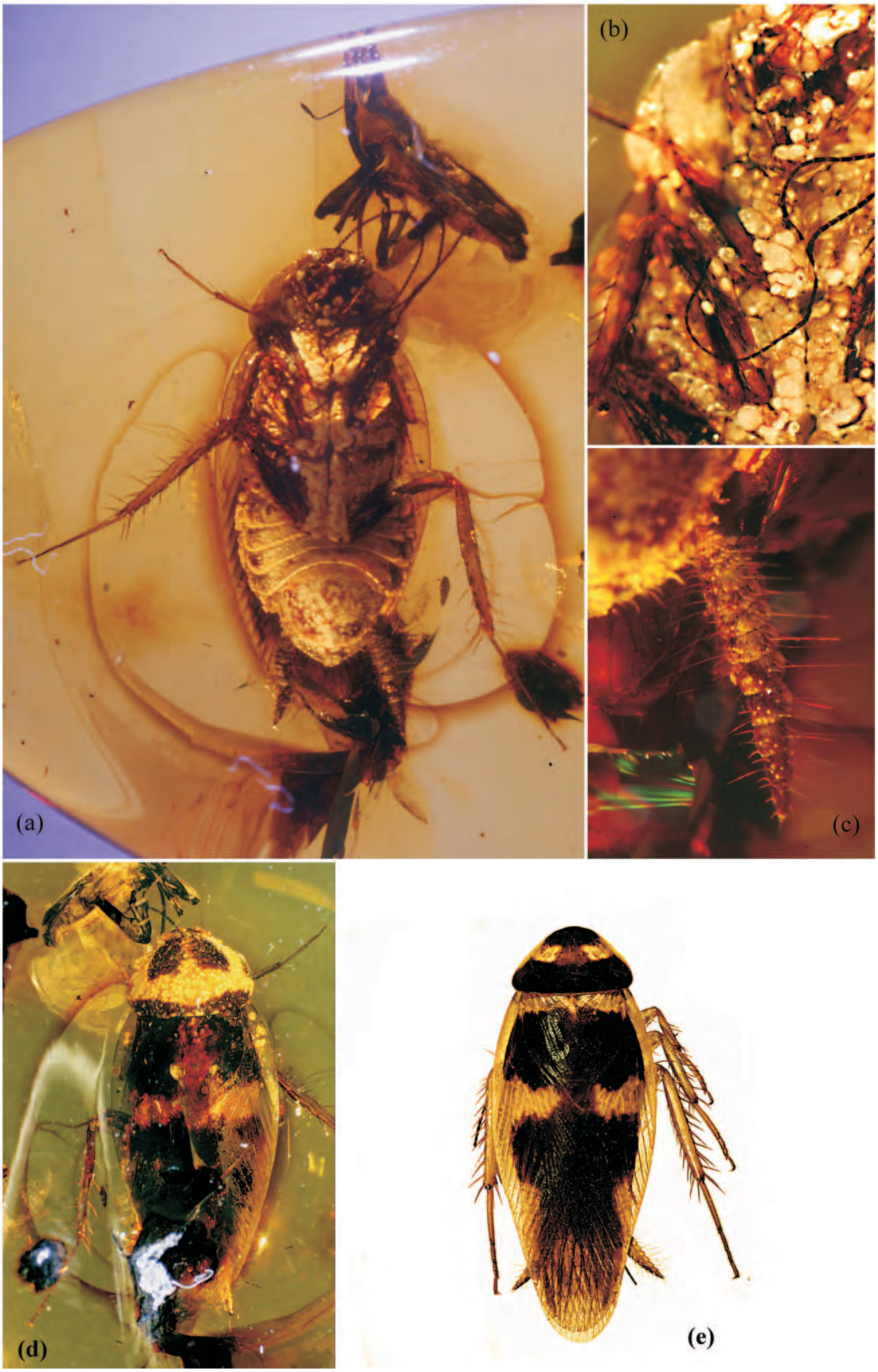


Fig. 3.

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.

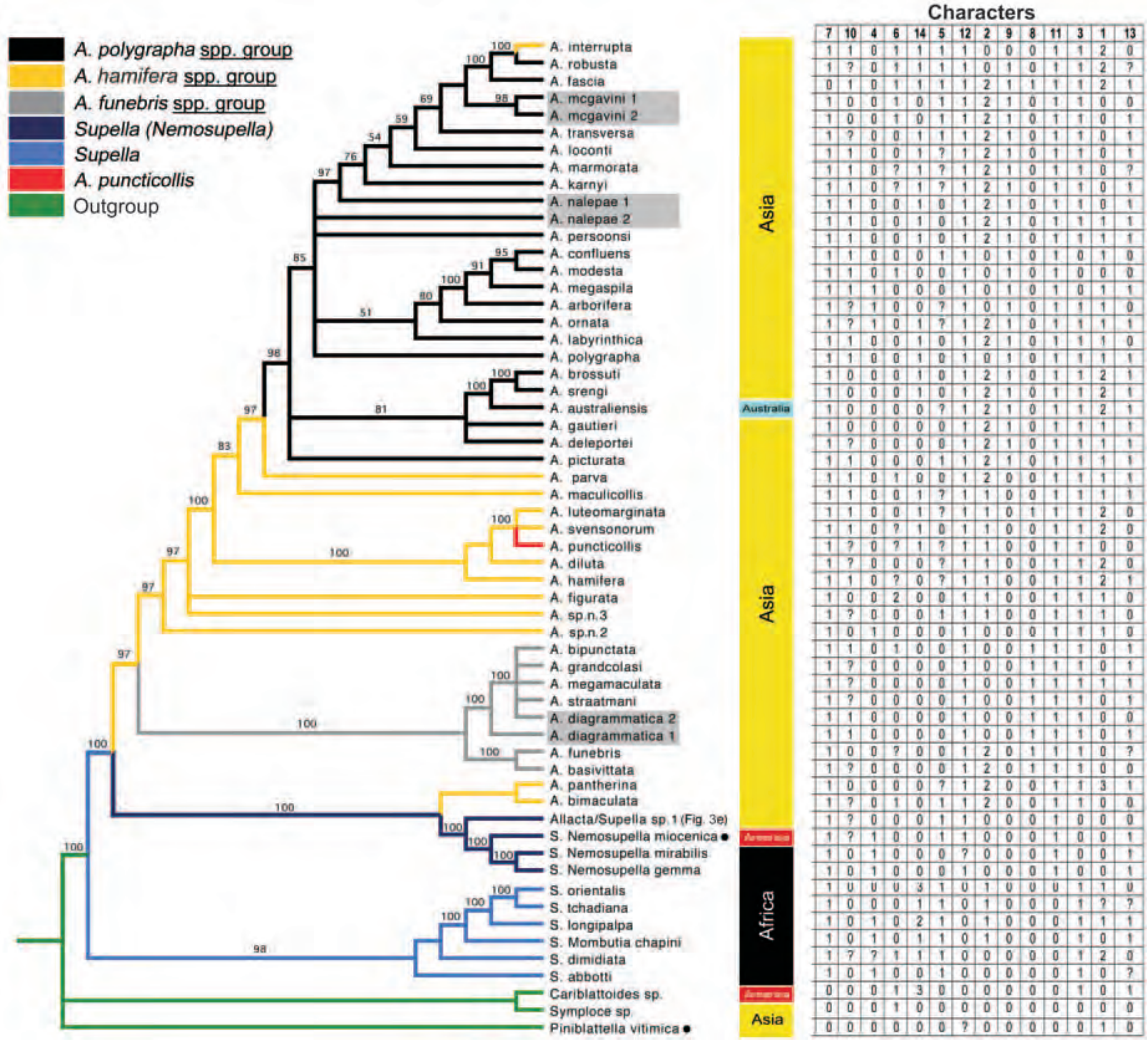
The colouration and general appearance is hardly recognizable from females of *S. mirabilis*, its sister species, although the shape of the pronotum is somewhat transitional between its males and females. Except for the significantly smaller size of the present new species, the sole difference between 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



	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 Philippines) — 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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ORIGINAL ARTICLE

Derived, still living cockroach genus *Cariblattoides* (Blattida: Blattellidae) from the Eocene sediments of Green River in Colorado, USA

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Abstract *Cariblattoides labandeirai* sp.n. from the Eocene sediments of Green River in Colorado, USA bear only two plesiomorphies, but also several significant autapomorphies within the advanced and highly derived living cockroach genus. Thus, *Cariblattoides* with extant occurrence in the Caribbean and South America was historically common in the Nearctic, and represents important evidence for the occurrence of derived living genera of cockroaches ∼50 Ma ago. Generally, the vast majority of living genera were absent during the Palaeocene, thus the diversification of most living cockroach lineages near the Palaeocene/Eocene boundary must have been extremely rapid. Females of living *C. suave*, the type species, have identical (sophisticated) coloration of pronotum, but the most related living taxa are *C. piraiensis* and *C. fontesi* from Brazil (supported by phylogenetical analysis).

Key words Blattida = Blattaria = Blattodea, *Cariblattoides*, Eocene, fossil insects, Green River, Tertiary cockroaches

Introduction

Among 11 cockroach genera (17 species) found in the Green River locality, Colorado, USA, nine represent still living recognised taxa (genera). Only the genus *Blattella*, although advanced in behavior (female bearing ootheca until nymphs emerge), can be considered historically primitive, because it is recorded from the Albian Cretaceous Mesozoic (Vršanský, 2008). All other living genera of cockroaches are recorded only starting from the Eocene, and as with *Ectobius* among those found in Green River, are modern. Nevertheless, one of two genera with derived morphology, the *Cariblattoides*, suggests that even derived cockroach genera evolved during or before the Eocene. Taking into consideration absence of any living genera except *Blattella* before the Eocene, and presence of relic Mesozoic taxa in the Eocene, it seems that the living cockroach fauna evolved extremely rapidly near the Palaeocene/Eocene boundary. This is supported by several thousands cockroaches known from the terminal Mesozoic, with occurrences of exclusively Mesozoic cockroach families except the primitive Blattellidae related to *Symploce* and *Blattella*. It is very unlikely that such a rich record would not reveal some other representatives of this, starting from the earliest Cretaceous, dominant cockroach family.

The genus *Cariblattoides* is contemporary in Cuba, Puerto Rico, Guadaloupe, French Guiana and Brazil, and in the past was apparently distributed more widely, at least in North America, and was present in different remote localities at Green River.

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This work was generated during the stay of the author in the NMNH, Washington, DC, USA.

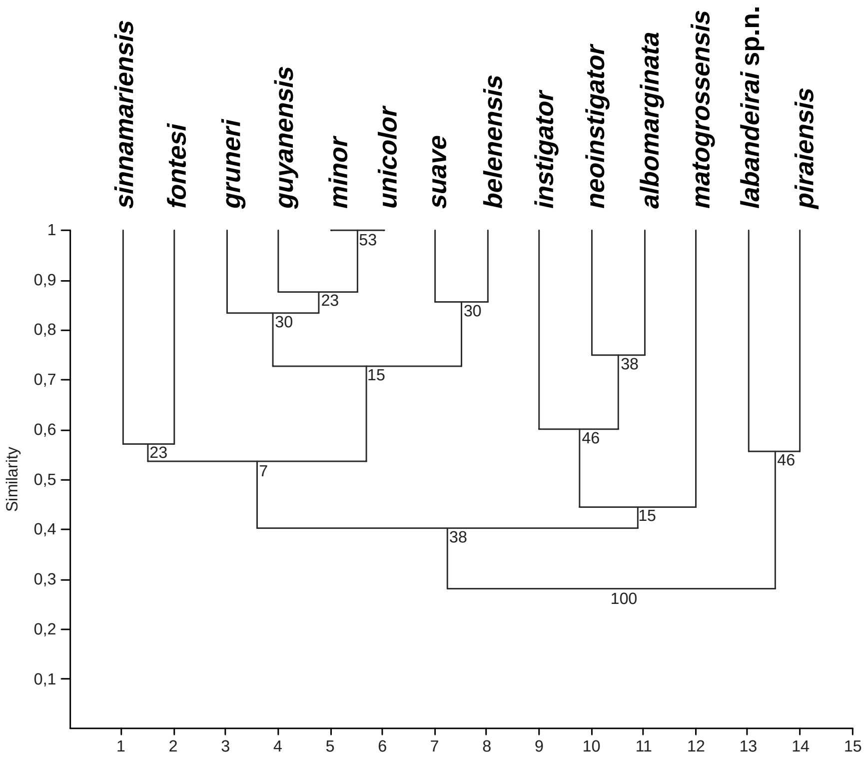

Fig. 1 Cluster analysis of *Cariblattoides* species. Jaccard similarity measure, paired group algorithm, with cophenetic correlation coefficient 0.838 9.

Material and methods

The material was collected by David Kohls and Louis Pribyl in the Anvil Points (AP) – Labandeira Site (LS); Denson Site (DS) and Parachute Creek (PC) of the Green River Locality in Colorado, USA. All the 13 specimens of the present taxon are deposited in the National Museum of Natural History (NMNH), Washington, DC. The numbers represent official NMNH numbers, site number (40193 – Anvil Points; 41088, 41678 – Anvil Points – Labandeira Site; 41619 – Denson Site; 41142 – Denson Site 3, 4, 5; 40190 – Paleoburn; 41139 – Parachute Creek – Gunderson)/ official USNM catalogue number (these do not correspond with the numbers on the rocks).

The photographs were made using an Olympus SZX12 stereozoom microscope and the figure represents redrawn photographs with Corel Draw 13 and Adobe Photoshop 6.0.

Cluster analysis (Fig. 1) was made using PAST 1.43 (Hammer *et al.*, 2001); parsimony analysis was performed using PAUP* software version 4.0b10 (Swofford, 2002), with a tree bisection reconnection (TBR) heuristic search of 10 000 replicates and the option ‘save multiple trees’ activated. All characters were treated as ordered (0 – plesiomorphic, 1 – apomorphic state). MaxTrees option was set to 500. All 13 morphological characters were set as ordered and equally weighted except character no. 10. As simple CuA (present in most living *Cariblattoides*, but not in *C. labandeirai*) is a strong apomorphy, homoplasically present also in some others, basal blattelid genera (e.g., in the primitive *Supella* this character is polymorphic), we set it at a higher (5) weight (branched CuA is a very strong plesiomorphy within *Cariblattoides*). Heuristic search produced 46 equally parsimonious trees with length 30 (consistency index [CI] = 0.5, retention index [RI] = 0.643). Majority rule consensus revealed most of the nodes resolved in more than 50% of the trees produced by heuristic search (Fig. 2). Terminology of wings follows Vršanský (1997).

Results

Systematic paleoentomology

Blattida Latreille, 1810
Blattellidae Karny, 1908
***Cariblattoides* Rehn et Hebard, 1927**

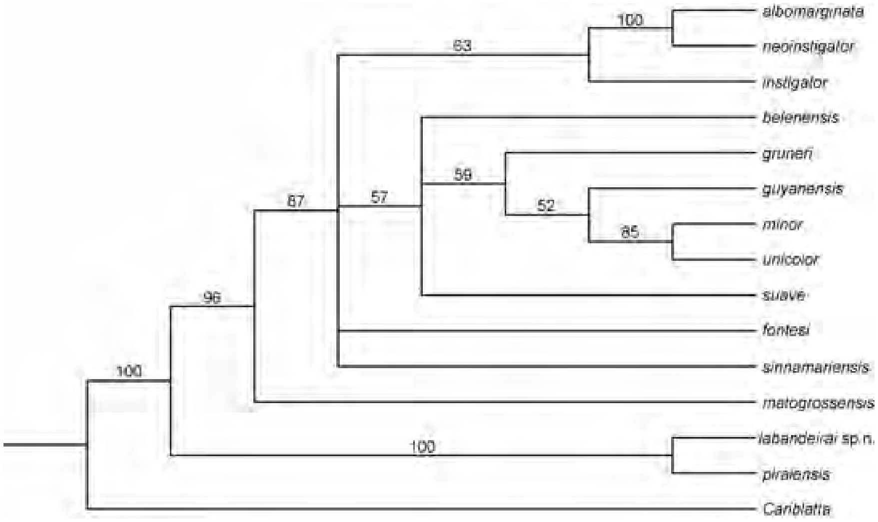

Fig. 2 Majority consensus tree of the parsimony analysis (46 equally parsimonious trees with length 30 [for details see Material and Methods]) of *Cariblattoides* species with *Cariblatta* used as outgroup. Numbers above branches show group frequencies (in %).

Type species *Cariblattoides suave* Rehn et Hebard, 1927. Extant, Puerto Rico.

Composition – Princis (1969) and additions In addition to the type species, *C. albomarginata* Rocha e Silva Albuquerque, 1967 (Brazil), *C. belenensis* Rocha e Silva Albuquerque, 1964a (Brazil); *C. fontesi* Rocha e Silva Albuquerque, 1954 (Brazil); *C. gruneri* Bonfils, 1975 (French Guiana); *C. guyanensis* Bonfils, 1975 (French Guiana); *C. instigator* Rehn et Hebard, 1927 (Cuba); *C. matogrossensis* Rocha e Silva Albuquerque, 1958 (Brazil); *C. minor* Rocha e Silva Albuquerque, 1964b (Brazil); *C. neoinstigator* Rocha e Silva Albuquerque, 1958 (Brazil); *C. piraiensis* Rocha e Silva Albuquerque, 1955 (Brazil); *C. sinnamariensis* Bonfils, 1975 (French Guiana); *C. unicolor* Rocha e Silva Albuquerque, 1964b (Brazil). All extant.

Diagnosis – Rehn and Hebard (1927): "Size small, form depressed, females slightly broader and heavier than males, size approximately similar. Head subdepressed, distinctly and broadly visible cephalad of pronotum; interocular space wide . . . , . . . maxillary palpi with third palpomere (joint in the original text) elongate, slender; fourth palpomere shorter than third palpomere; first palpomere slightly shorter or slightly longer than fourth palpomere. . . . Tegmina elongate lanceolate, considerably surpassing the abdomen in both sexes. Costal margin moderately arcuate (proximad), sutural margin almost straight: radial (scapular in the original) field broad: mediocubital veins (discoidal sectors in the original) longitudinal, six to seven in number (including the media (median in the original) and cubital (CuA – ulnar in the original) and rami of the median veins); anal groove (sulcus in the original) strongly arcuate proximad, straight oblique in greater portion of length; anal field elongate pyriform; diagonal channel of right tegmen well indicated. Wings elongate, relatively narrow, moderately iridescent: subcosta (mediastine in the original) and a number of costal veins clavate; ulnar vein quadriramose; axillary vein with three rami in distal two-thirds; intercalated triangle small but distinctly and clearly defined . . . "

Character analysis (0 – plesiomorphy; 1 – apomorphy relative to other species within genus and/or *Cariblatta*, which was chosen as an outgroup based on high similarity, but retention of all original states of characters due to standard habitus (not derived like in *Cariblattoides*):

1. *Head significantly elongated:* apomorphy; plesiomorphic state is elongated, but more or less of normal cockroach appearance, i.e., less than 1.2 times longer than wide (head more or less standard in both *Cariblatta* Hebard, 1916 and *Neoblattella* Shelford, 1911)
2. *Pronotum with coloration concentrated in cervical structures:* apomorphy; plesiomorphic state is coloration simple or dark stripes are more primitive in the Blattellidae
3. *Terminal palpomere short:* apomorphy; plesiomorphic state is the terminal palpomere long (also in *Cariblatta* and *Neoblattella*)
4. *Terminal palpomere cup-like:* apomorphy; plesiomorphic state is normal shape of the terminal palpomere such as in *Cariblatta* and *Neoblattella*

(even when the terminal palpomere is homoplasically cup-like in several unrelated Blattellidae)

5. *Forewing elongated more than 3.5:1:* apomorphy (elongation itself is an autapomorphy of the genus); plesiomorhic state is the forewing normal, as in majority of cockroaches including the outgroup, *Cariblatta*
6. *Forewing with distinct costal margin:* apomorphy (plesiomorphically absent in *Cariblatta*, *Neoblattela* and most *Cariblattoides* species)
7. *Forewing monochromatically colored:* apomorphy (plesiomorphic coloration of forewing is medial (with more dark central stripe) in some *Cariblatta* and *Neoblattella*; the coloration in the later two genera vary, except for the coloration mentioned, the coloration is different from those appearing in *Cariblattoides*)
8. *Forewing colored monochromatically medially, with more dark central stripe:* plesiomorphy (see above), monochromatic median coloration without the central stripe is an apomorphy
9. *Forewing RS indistinct, terminal R(+RS) branches not dichotomized:* apomorphy (plesiomorphically is RS distinct and/or terminally branched like in all studied *Cariblatta* and *Neoblattella* – the eventual reduction is homoplasic)
10. *Forewing M+Cu with over 10 branches:* plesiomorphy (also in *Neoblattella*); apomorphy is reduced number
11. *Forewing CuA branched:* strong plesiomorphy in primitive Blattellidae (homoplasically simple in *Cariblatta*)
12. *Hindwing with simplified RS:* apomorphy (branched in otgroup *Cariblatta* and rest Blattellidae)
13. *Hindwing monochromatic, pale:* plesiomorphy (state in *Neoblattella* and *Cariblatta*); apomorphic is any other derived coloration pattern.

Cariblattoides labandeirai sp. n.

Holotype. 41619/542284-AB. Part and counterpart of a complete ?male (Figs. 3a, 4, 5).

Type locality. Denson Site 1998, Green River, Colorado, USA.

Type horizon. Green River Formation, Eocene, Tertiary.

Paratypes: 40190/542285; 40193/542288 (AP), 542286, 542287, 542289; 41088/542290, 542291 (AP LS 95); 41139/542292 (PC) (Diptera collection databasis); 41142/542293, 542294 (DS 4); 41678/542295(8)9, 542297 (LS 99). All the same locality and horizon as the type (for sublocalities see M&M).

Differential diagnosis The present species can be differentiated from all living *Cariblattoides* species by branched forewing median vein M, terminally branched CuA and strong, distinct and black, overlapping apex costa, and by differentiated hindwing R1. All other characters are present in some of the living species, but in different combinations (see discussion for remarks and comparison).

Description Head free, often preserved in upright position; palps long, the last segment short and cup-like. Antennae very soft and long, with at least 90 segments. Pronotum coloration as in Fig. 3A. Both wings strongly elongated, with reduced venation. Forewing extremely elongated (length/width 9–10 mm/2.5 mm), with sharpened apex, with extremely short simple Sc. Radial field very narrow (not reaching half of the wing's width) with main stem of R nearly straight; rich simple R (15 in holotype) ascending parallel, without secondary branches; M rich (10 in holotype), but short, with parallel branches descending directly from the main branch in angle comparable to ascendance of R, a single M is dichotomised, rest are simple; CuA reduced to a single branch dichotomised near margin (2 veins meet margin); few simple A present (4 or 5 in holotype), except for A1 all meet posterior margin. Dark forewing coloration restricted to longitudinal stripe along the clavus and central part of the medial and cubital areas, reaching to the apical part of the radial area. Hindwing Sc simple, very short – end before the wings halve; RS differentiated, mostly simple – a single branch is dichotomised (9 veins meet margin in the holotype). R1 consists of one richly branched (6 veins at the margin in the holotype) branch vein, with dense secondarily branched veins; M simple, slightly curved; CuA reduced to 2 (possibly 3 branches, with 3–4 veins at margin), CuP simple, copying the posterior-most CuA; A1 widely branched (4). Vannus pleating veer-like. Body soft and thin. Sterna and terga colored posteriorly. Legs long with margins colored, hindleg femur very long.

Remarks and comparison See discussion.

Derivation of name After Conrad C. Labandeira, a superb teacher, scientist and one of the collectors of the Green River material.

Character of preservation 13 complete specimens.

Discussion

In addition to characteristic unconfuseable elongated habitus and size with extremely long legs, strong autapomorphies such as elongated head, hindwing with widely branched A1 or A2, maxillary palps with characteristic ratio of respective palpomeres (?:1:0.9:1:0.8 – see Figs. 3A, 4D) with

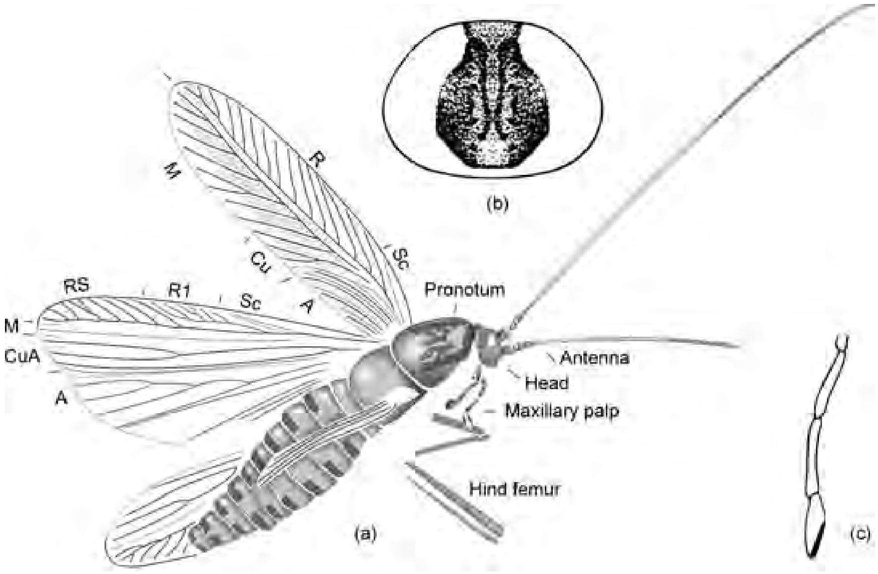

Fig. 3 *Cariblattoides labandeirai* sp.n. Holotype. NMNH 41619/542284-A. (A) A complete ?male. Eocene. Green River, Colorado, USA. Forewing length 10 mm. (B) pronotum of the female allotype (Aibonito, Guayama, Puerto Rico, July 14–17, 1914; HG Barber; AMNH New York) of the type species, *C. suave* Rehn et Hebard, 1927, identical to that of the *C. labandeirai* sp.n. holotype. (C) palp of *C. guayanensis* Bonfils, 1975.

terminal segment cup-like (homoplasically in *Supella abotti* Rehn, 1947) allow the cathegorization within the genus *Cariblattoides*. Large, deplanate pronotum, slender and narrow body, pale and widely arcuate base of forewing makes this genus with 13 living species a good monophylectic group originating from *Supella* or its precursors (retaining the original blattellid bauplan of both wings and the lack of autapomorphies characteristic for other genera of the Blattellidae, and synapomorphic reduction of forewing RS and CuA, differentiate this genus from the rest of Blattellidae). Alternatively, both genera can had a shared history during the Green River times.

The present new fossil species share all the apomorphies with living representatives of the genus, except the simple CuA and branched hindwing R1. It additionally has some secondary characters limited to *Cariblattoides*, namely the sophisticated coloration of pronotum identical with *C. suave*, and the coloration of forewings with indistinct basal-most R, identical with *C. fontesi*. Thus it can be safely catherorized within the genus.

On the other hand, there are some differences, which need clarification. While the general habitus, details of head and pronotum and wing coloration are characteristic for *Cariblattoides*, the wing venation pattern is identical with related *Supella longipalpa* (Fabficius, 1789) as figured by Rehn (1951) (as *Supella supellectilium*). Thus it is necessary to analyse the differences in detail. The forewing radial area is identical with *Supella* and closely related to (*Supella*) *Namablatta* Rehn, 1937 in having R simple and in undifferentiated RS. Nevertheless, some extinct as well as extant species of *Supella* (whole subgenus *Nemosupella* Rehn, 1947) have RS differentiated and venation expanded (Rehn, 1947) and this character is polymorphic even within species of *Supella* and could not be treated as diagnostic. Moreover, this character is polymorphic even within *Cariblattoides* and thus represents no contradiction of placing the present fossil within this genus. R branches are homoplastically simple in diverse other more or less related living cockroaches such as in *Eustegasta*, *Pseudomops*, *Ectobius*, *Chorisoneura*, *Euphyllodromia* and others, mostly with reduced venation and/or size.

The more unusual is the character of branching of M and CuA, descending in an angle opposite to bifurcations of R. This character is different to that of the living *Cariblattoides* and is present exclusively in *Supella* and *Ectobius*. But again, in these genera this character of dichotomisation is polymorphic (Rehn, 1947), apparently due to reduction of venation in smaller species (e.g., in *Supella longipalpa*) and as such is without phylogenetic and/or taxonomic relevance.

The most significant difference with phylogenetical information is the branched forewing CuA, suggesting that *Cariblattoides* (based on the present species) diverged before the divergence of *Cariblatta* and *Neoblattella* spp. Within the lineage, this character is significantly plesiomorphic (branched) only in the very basal *Symploce* (Rehn, 1951), but polymorphic also in derived *Supella* (Rehn, 1947). Due to the terminal dichotomisation, and not a fully expressed branch, this can also eventually be a unique character reversal or deformity of the holotype.

The clear separation of branched hindwing R1 is also different. In contrast to other characters, this one is plesiomorphic and polymorphic (polymorphic also in *Supella*), with R1 indicated (although not richly branched) in some living *Cariblattoides* species (see character 9), but reduced in the closest relative of *Supella*, the *Namablatta* (Rehn, 1937). R1 tends to reduce even within Polyphagidae and Blattidae – see Rehn (1951).

Thus, *Supella* is similar in venation and palp, but not in general habitus, even when *S. longipalpa*, the most departured from the standard morphotype of the genus has also a slender habitus, and *S. orientalis* Grandcolas, 1994 has general habitus identical with the *Cariblattoides* (including the form of forewing, but head is not elongated, and coloration with characteristic central stripe, see Grandcolas, 1994). Thus it is possible that the precursors of *Supella* were direct ancestors of *Cariblattoides*. All this taken together does not contradict the placement within *Cariblattoides*, although eventually would allow us to erect a new subgenus, which we would not consider oblique.

Additionally, *Cariblattoides* has flattened pronotum larger than the most related *Cariblatta* and *Neoblattella*, longer narrow tegmina, with subparallel margins (see Hebard, 1916 for *Cariblatta*). It can be further distinguished from *Neoblattella* by fewer discoidal sectors of the tegmina and strongly deplanate pronotum (Rehn & Hebard, 1927). Thus the sister genus is *Cariblatta* with *Neoblattella* a sister taxon to them (Rehn & Hebard, 1927). Both *Neoblattella* and *Cariblatta* are known from the Eocene sediments of Europe (Schmied, 2009, unpublished observation), with the whole group apparently derived from precursors of *Supella* (synapomorphic in elongated forewing with numerous parallel M branches descending directly from the main M branch in an angle comparable to descention of R, weakly separated RS; A except A1 ending in posterior margin; simple CuA (in advanced *Supella*); and in reduced hindwing CuA and general venation scheme of the hindwing with separation of basal-most RS, which is plesiomorphy of basal living *Supella* – subgenus *Nemosupella*.

Cariblattoides labandeirai sp.n. resembles *C. suave* from Puerto Rico in maxillary palp fourth joint significantly longer than fifth, unlike in *C. instigator* from Cuba where both segments are of subequal length. Nevertheless, *C. labandeirai* has apical segment even shorter and much more oval. Females of *C. suave* also have identical coloration of pronotum, similar to some representatives of the genus *Cariblatta*, supporting indication about their relation (Rehn & Hebard, 1927). (Nevertheless, it must be noted that both *Cariblattoides* and *Cariblatta* contain species with pronota with two dark stripes as well as species with characteristic cervical coloration.) On the other hand, *C. suave* has coloured hindwing, which was apparently pale in *C. labandeirai* sp.n., and more expanded coloration of forewing, which reaches the posterior margin in *C. suave*.

It is notable that in *C. suave* females have shorter and broader wings than in males, but the holotype of *C. labandeirai* has wings significantly elongate and thus is unlikely to represent a female (thus this specific coloration pattern appears plesiomorphic for both sexes). In seven collected individuals of *C. suave*, the forewing measurements (9.5–11.5/2.9–3.5 mm) of *C. labandeirai* were more elongate, similar to *C. instigator* (−9.6/−2.7 mm). The number of veins of *C. suave* and *C. labandeirai* in the radial area is approximately the same (14–19), but *C. labandeirai* apparently has less reduced venation in the medial and cubital area (12 M + CuA) compared to *C. suave* (6–7 discoidal veins – M + CuA), *C. instigator* (7 discoidal veins in holotype), *C. minor* (8), *C. unicolor* (7), *C. guyanensis* (6), *C. fontesi* (7) and *C. sinnamariensis* (9 discoidal veins in holotype) (for others, see below). The single extant species with expanded M is *C. piraiensis* (11 including one CuA). There are conservatively 5 anal veins present in all species of *Cariblattoides*.

C. gruneri Bonfils, 1975 – a larger species (forewing length/width 11.7/3.2 mm) also has simple hindwing M, and 4 CuA branches (3 in *C. labandeirai*). Another larger species is *C. guyanensis* (forewing length/width 11.6–12.5/2.9–3.1 mm), which has even more expanded venation in the radial area (±20), and reduced venation of Media (6). The process of reduction of CuA, characteristic for the genus, is nearly complete in this species (and also in *C. sinnamariensis*) – a single CuA fuses with the radial stem. Palp of *C. guyanensis* is very similar to *C. labandeirai* (perhaps a synapomorphy). Hindwing of *C. guyanensis* has apomorphically widened apexes of radial branches (even more expressed in *C. sinnamariensis*), present cross-veins (most likely an autapomorphy), but branched M (plesiomorphic even in respect to *C. labandeirai*). *C. sinnamariensis* has plesiomorphically (in respect to all the known species) branched hindwing CuA (7).

C. minor is another comparatively large species, with less prolonged tegmina (12/3.5 mm) and pronotum coloration similar to *C. labandeirai*, but with finer dark pattern.

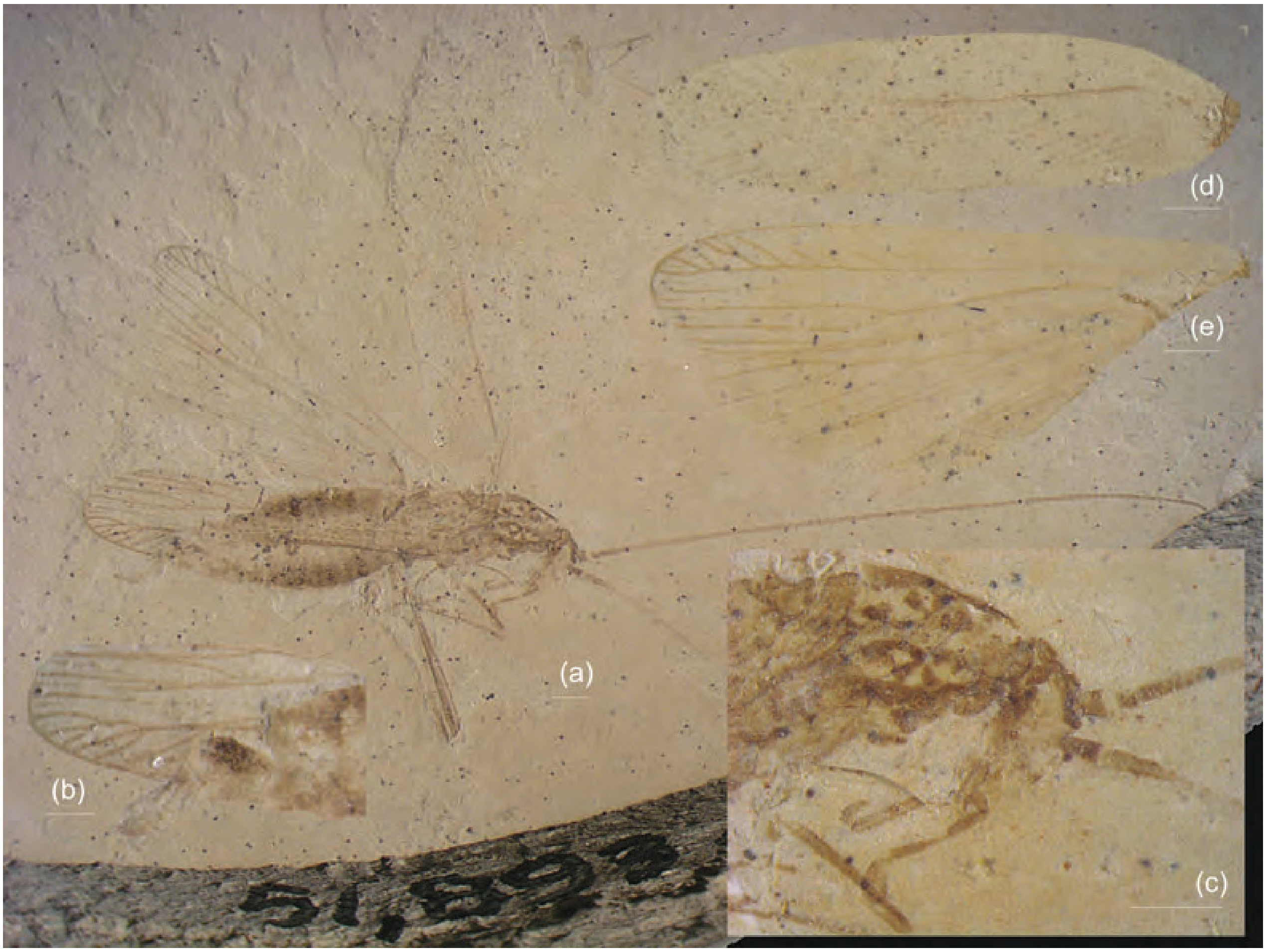

Fig. 4 *Cariblattoides labandeirai* sp.n. Holotype. NMNH 41619/542284. A complete ?male. Eocene. Green River, Colorado, USA. (A) general habitus; (B) forewing; (C) hindwing; (D) pronotum and head; (E) terminalia and hindwing. Forewing length 10 mm. Scales = 1 mm.

C. unicolor differs in having uniform coloration of significantly elongated forewing (12/3 mm).

C. fontesi has comparatively robust forewing (10/3 mm), but coloration similar to *C. labandeirai*. Similar lengths are present also in the palps, but the apical palpomere is not oval as in *C. labandeirai* and *C. piraiensis*. Hindwing of *C. fontesi* has more expanded venation in the RS area (plesiomorphy).

C. piraiensis has palp entirely identical with *C. labandeirai*, with oval cup-like terminal segment and also identical forewing coloration (in some specimens – this character varies). It is also a single species with expanded forewing M (10). Pronotum coloration is also similar. Nevertheless, this species differs in having less elongated forewings (under 4:1) – a plesiomorphy and expanded hindwing RS (plesiomorphy).

C. mattogrossensis and *C. neoinstigator* have pronotum with two dark stripes and expanded forewing RS. Their tegmina are less elongated (under 3.5:1).

C. albomarginata with the forewing length 11 mm is likely the taxon with the most primitive characters, as it has shortest head, widest wing, rich R (20), and standard dichotomisation of M (with both branches descending at the same angle) resembling *Neoblattella* (in *Cariblattoides* posterior branches tend to descent from the straight stem). On the other hand, it has simplified M (6) and simple CuA (both synapomorphies of living representatives of the genus; expanded M is characteristic also for *C. piraiensis*) and uniformly colored center of the pronotum.

C. belenensis with the most simplified M (5), simple CuA and (as with all known species) 5 anal veins, and simplified hindwing CuA (3), appears to be the most

Fig. 5 *Cariblattoides labandeirai* sp.n. (A) Holotype NMNH 41619/542284-B; (B) NMNH 41139/542292 (PC) (Diptera collection databasis); (C) NMNH 40193/542286 (AP); (D) NMNH 41142/542293 (DS 4). Eocene. Green River, Colorado, USA. Scales = 10 mm.

Table 1 *Cariblattoides* character matrix of 13 extant and the present extinct species of *Cariblattoides*, and *Cariblatta* spp. as outgroup (OG) (the same dataset is provided for related *Neoblattella* and *Supella* as well as the rest of Blattellidae).

sp/character	1	2	3	4	5	6	7	8	9	10	11	12	13
Cariblatta (OG)	0	0	0	0	0	0	0	0	0	0	?	0	0
albomarginata	0	0	0	0	0	0	0	0	0	1	1	?	1
belenensis	1	1	1	0	1	0	0	0	?	1	1	?	0
fontesi	1	0	1	0	0	0	0	1	1	1	1	1	0
gruneri	1	?	0	0	1	0	1	?	?	1	1	?	0
guyanensis	1	1	1	0	1	0	1	?	0	1	1	0	0
instigator	1	0	0	0	1	0	0	0	?	1	1	?	1
labandeirai sp.n.	0	1	1	1	1	1	0	1	1	0	0	1	0
matogrossensis	0	0	1	0	0	0	0	0	0	1	1	0	0
minor	1	1	1	0	1	0	1	?	1	1	1	?	0
neoinstigator	0	0	?	?	0	0	0	0	1	1	1	?	1
piraiensis	0	1	1	1	1	0	0	0	0	0	1	1	0
sinnamariensis	1	0	0	0	0	0	1	?	0	1	1	1	0
suave	1	1	1	0	1	0	0	0	0	1	1	1	1
unicolor	1	1	1	0	1	0	1	?	1	1	1	?	0

0 – plesiomorphy; 1 – apomorphy; ? unknown character. Data were obtained basing on the present study, unpublished observations and the following references: Hebard (1916), Rehn and Hebard (1927), Rocha e Silva Albuquerque (1954, 1955, 1958, 1964ab, 1967) and Bonfils (1975).

derived species (in spite of its large size with forewing length 12 mm).

To summarise, *C. labandeirai* has palp identical with *C. piraiensis* (synapomorphy) (nearly identical with *C. fontesi*), pronotum identical with females of *C. suave* (plesiomorphy) and forewing coloration identical with *C. fontesi* and similar to *C. piraiensis* (synapomorphies). Thus, the most related living taxon appears *C. piraiensis* from Brazil.

The cluster analysis (Fig. 1) and the consensus tree of the parsimony analysis (Fig. 2) reveal results comparable with the empiric observation, but the relation of *C. suave* and *C. belenensis* appears artificial.

Generally, variation within the genus includes diverse variations in the combinations of all studied characters (see Table 1) except for hindwing (with an exception of coloration, hindwing venation is principally identical in all living representatives – variable only in the number of veins in RS area), CuA (simple in all extant species) and colored costa of *C. labandeirai*. The conservative pattern of hindwing (with unmodified radial area [most significantly involved in flight], and more similar to that of *Supella* and primitive *Symploce*) in the earliest *C. labandeirai* infers the strong selection due to active flight (and elongated habits) in all living *Cariblattoides*. It is notable that extinct *C. labandeirai* has the hindwing radial area (most significantly involved in flight) unmodified, and is more similar to that of *Supella* and primitive *Symploce*.

The present species can be more easily identified than other undescribed species – it is very distinct morphologically and as such is easily determinable (in contrast to most other species at the locality, which can be confused according to the preservation of body only, and as such belong to indetermined specimens). Otherwise the preservation is standard (with an exception of the holotype which is the only specimen at the locality with both wings visible), and even in these completely preserved specimens, venation is indistinct due to overlap with body structures.

All specimens have size and coloration within normal intraspecific variability range as the type species and thus very probably belong to a single biological species. Nevertheless, a closely related taxon due to eventually belonging to slightly different layers cannot be excluded. This is a general problem of palaeoentomology and authors are not aware of any larger type series which would not face this problem. Thus the material is included in the type series, clearly representing the same morphospecies, but eventually not the biological species.

The presence of a derived living genus in the Eocene suggests the radiation of newly evolved living genera after the Paleocene/Eocene boundary must have been extremely rapid (it indicates that nearly all living genera – even such advanced ones as *Cariblattoides* – evolved, speciated and radiated within 5 Ma at most). The earliest representative of such a derived genus, the present *C. labandeirai* cannot be considered more primitive than most of the living species. Radiation but also origination of modern genera of cockroaches thus could be associated with the thermal maximum (PETM) and massive invasions of tropical elements polewards – into unoccupied habitats.

Conclusions

- *Cariblattoides labandeirai* sp.n. was a common species in the Eocene assemblage of the Green River. Nevertheless, according to taphonomic advantages, 13 of 289 identified cockroaches may be a little overestimated figure compared to other species.
- It was a rather advanced taxon within the genus, apomorphic in 8 of 13 characters, with only two significant plesiomorphies (dichotomized forewing CuA and branched hindwing R1).
- Most closely related living species is C. *piraiensis* from Brazil.
- The presence of this derived blattelid genus during the Eocene indicates the radiation of most living cockroach genera must have taken place in a short time interval near the Palaeocene/Eocene boundary.

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Cockroaches Probably Cleaned Up after Dinosaurs.
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Cockroaches Probably Cleaned Up after Dinosaurs

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Abstract

Dinosaurs undoubtedly produced huge quantities of excrements. But who cleaned up after them? Dung beetles and flies with rapid development were rare during most of the Mesozoic. Candidates for these duties are extinct cockroaches (Blattulidae), whose temporal range is associated with herbivorous dinosaurs. An opportunity to test this hypothesis arises from coprolites to some extent extruded from an immature cockroach preserved in the amber of Lebanon, studied using synchrotron X-ray microtomography. 1.06% of their volume is filled by particles of wood with smooth edges, in which size distribution directly supports their external pre-digestion. Because fungal pre-processing can be excluded based on the presence of large particles (combined with small total amount of wood) and absence of damages on wood, the likely source of wood are herbivore feces. Smaller particles were broken down biochemically in the cockroach hind gut, which indicates that the recent lignin-decomposing termite and cockroach endosymbionts might have been transferred to the cockroach gut upon feeding on dinosaur feces.

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Introduction

The Triassic, Jurassic and Early Cretaceous terrestrial ecosystems differed from extant ecosystems for various reasons, one of them being the presence of gigantic reptiles. The energy flow was principally less efficient (more rapid) and also the general appearance of the landscape was dissimilar [1,2]. Grasses, flowers with their fruits, large butterflies, and before the latest Jurassic, all eusocial insects (cockroaches, termites, ants, bees) were absent [3,4]. Discerning between dinosaur feces decomposers (which were not identified until now) is also essential as it changes the general appearance of our assemblage reconstructions. Moreover, the problem is of a principal, systemic importance. If nothing fulfilled this role, a large amount of dung would prevent soil regeneration just as it suffocated the pasture systems and prevented grass regeneration in present-day Australia [5]. Grasses were absent before the Early Cretaceous, but such influence will definitely alter extinct cenoses similar to some extent to the variety of living fern groups or perhaps taxa such as *Gnetum* and *Ephedra*. On the other hand, bird droppings are known to significantly (often positively) influence vegetation composition of ombrotrophic bogs [6]. Late Cretaceous biomes actually contain grasses and silicified plant tissues (phytoliths) preserved in the Maastrichtian coprolites (presumably from titanosaurid dinosaurs) from the Lameta Formation in India show that at least five taxa from extant grass (Poaceae) subclades were present during the latest Cretaceous [7].

Was the Mesozoic world full of sterile dinosaur dung, clean as a modern forest, or transitional between these two extremes? Circumstantial evidence of dinosaur (probably hadrosaur) coprolites [8,9] suggests that feces were used. The absence of dung-beetles during the Triassic and near-absence during most of the Jurassic [10] (roughly half of the age of dinosaurs) and their radiation associated only with the spread of modern grasslands [1] is still under discussion [2].

Feces have a greater capacity to retain moisture than the parent plant tissue [11] and coprophages exploit the microbial consortia concentrated on these recycled cellulose-based foodstuffs; the microorganisms serve not only as a source of nutrients and gut mutualists, but they also pre-digest recalcitrant substrates [12]. Microbial dominance is so pronounced that fecal pellets may be considered as living organisms [12]. They consist largely of living cells, they consume and release nutrients and organic matter, and they serve as food for animals higher on the food chain [13].

Any excrement is a valuable source of nitrogen, and its amount must have been huge [14] at least seasonally [15], during the age of dinosaurs. Each single separate dung might have had a volume of 7 liters [8]. Probably an important feature of dinosaur and pterosaur excrements (as in birds and reptiles when compared with mammals) was the large proportion of nitrogen compared with phosphorus [16]. The association with urine and thus with a high concentration of phosphoric acid, oxalic and carbonic acids and salts, primarily sodium chloride, leads to the recent conclusion about the association of dung-beetles and coprophagy with mammals (not with dinosaurs) since the very beginning [17]. On the other hand, some common (11 of the 15 deposits) fossilised dinosaur coprolites contain 13–85% of rotting conifer wood with only 0.20–0.30% of nitrogen (conifers are utilized by the living cockroach *Cryptocercus* – the most important wood-decomposing cockroach) with its attendant microbial and detritivore fauna and thus augmented the resource options of Cretaceous ecosystems that lacked fodder provided by grasses and other derived angiosperms [8,18]. The consistency of the coprolites during the deposition varied from fairly cohesive to viscous liquid and fluid to some extent – those containing a significant amount of wood are most easily recognizable as their high wood content prevented degradation [8].

In addition to dung, it has recently been proposed that the density of sauropods was high enough to produce the amounts of methane necessary for sustaining the warm climate during the Mesozoic [19].

The cockroach family Blattulidae, described by Vishniakova [20] originated in the Late Triassic and constitutes a (co-)dominant group of insects (~1%) throughout the whole Jurassic and Cretaceous [21]. They are often completely preserved [22–24] and contributed to knowledge of some general patterns such as the decreasing variability of species over time, and mass mutations [25,26]. The Blattulidae constitute the sole cockroach fossils preserved in several Cretaceous localities such as Shin Khudukh and some others in Mongolia and Verchnebureinskaja Vpadina in Russia, and are the dominant insect fossils in diverse Mesozoic ambers [27,28]. The hypothesis tested and supported in the course of the present research was the heterogeneous character of the diet of these Mesozoic cockroaches (in contrast to homogeneous one of all the studied Cenozoic and present ones). There are numerous Tertiary (Cenozoic) cockroaches preserved with the gut-content, but all of them have a homogeneous diet. The same holds for the studied living cockroaches. The occurrence of any wood (digested twice, a second time by cockroaches, after it was previously digested by herbivores; Figs. 1E, S1) was entirely unexpected.

Protozoan cysts and helminth eggs preserved in the Early Cretaceous *Iguanodon* coprolite represent the only reported case of dinosaur parasites [29], but the discovered trophic relation of dinosaur-age vertebrate herbivore and insects might appear important also due to the structuring of the extinct ecosystems via parasites (and pathogens) transferred. Trophic association of Mesozoic vertebrates and insects suggest endoparasite transfer as well.

A similar transfer is known from numerous living species, e.g., from *Blatta orientalis* and *Periplaneta americana* feeding on human excrement that contained cysts of *Chilomastix mesnili* and rats eating food that had been contaminated with feces from these cockroaches became infected with this protozoan [30].

Materials and Methods

The material studied herein is from Mdeirij-Hammana, Baabda District Governorate Mount Lebanon, Central Lebanon - detailed coordinates for the localities of completely studied specimens (mostly immatures: (59, 76A, 623i-m, 778AB, 799, 800, 810CD, 845AB, 934AB, 1062, 1274B,D, FAL -3C (Falougha), 133.C, JEZ.F-14 (Wadi Jezzine, Jezzine District, Governorate Southern Lebanon), 1669-B, RIH-33 (Rihane outcrop, Jezzine District, Governorate Southern Lebanon), (deposited at the Lebanese University); AMNH Lebaneese amber 22, 77, 84, 91 (Bcharreh District, Governorate North of Lebanon; Jouar Ess-Souss, Bkassine, Jezzine District, Governorate Southern Lebanon, all deposited in the American Museum of Natural History), *J. lebani* holotype (Jouar Ess-Souss, Bkassine, Jezzine District, Governorate Southern Lebanon, Acra collection) can not be revealed due to site protection [31], in a Lower Cretaceous (ca. 120 Ma) amber-bearing deposit. An enicocephalid assassin bug, three ceratopogonid biting midges, and two male coccids occur as syninclusions. Examined specimen (1094A-I) was not embedded in epoxy resin due to ST examination, but for photography a drop of maple sirup and a coverslip glass was attached to see inside. It is deposited at the Lebanese University, Faculty of Sciences II, Lebanon. We performed a microtomographic scan of the amber piece (0.185 g, well transparent dark yellow-red sample) at the full-field X-ray imaging station TopoTomo beamline of the ANKA light source. The scan covered 180 angular degrees with 2,800 radiographic projections measured. We used a filtered white beam radiation with a spectrum peak at ~20 keV. A sample-to-detector distance of 35 cm resulted in both absorption contrast and edge enhancing phase contrast in the projection images. These were recorded by an indirect detector system based on a scintillator coupled to an optical microscope and a CCD detector [32]. The magnification factor of the optical microscope was 22.4 which led to an effective pixel size of 0.4 μm with attached CCD camera pco.4000 with 4008×2672 pixels. We processed each radiographic projection using a single distance phase retrieval algorithm [33] integrated in ANKA phase plugin [34] for ImageJ and reconstructed the volume by PyHST reconstruction software [35]. The triangle algorithm is unknown, but the original surfaces contain so many polygons that the details lost to a reduction to 10% are negligible.

For segmentation of the coprolites we used software Amira 5.4. After loading the volume data as an image stack of virtual slices, we labelled the whole coprolites and the dense particles with the segmentation editor of the program. We exported and reassembled the surface models from the labels with the software Cinema 4D R12. Volumes were calculated from the polygon meshes using the GeoTools2010 plug-in.

Before creating the interactive 3D graphics, we reduced the surface polygons once more to 10%. The objects were saved as Collada files and opened with the software Right Hemisphere® Deep Exploration 6. After creating the object hierarchy, we saved the data as Universal 3D files, opened with Adobe® Acrobat® 9 Pro Extended, and integrated into PDF files.

Results

Distribution of the Blattulidae is associated with the abundance of dinosaurs (fig. 2F). In the Lebanese amber, the Blattulidae constitute 8 of the 15 identified (21 studied) cockroach samples including *Ocelloblattula ponomarenkoi* Anisyutkin et Gorochov, 2007 [36], in addition to the Umenocoleidae (n = 1), Caloblattinidae (n = 2), Raphidiomimidae (n = 1), Liberiblattinidae (n = 1), Blattellidae (n = 2), and Mesoblattinidae (n = 2; *Nymphoblatta azari*) [37].

The present fossil (Fig. 1) can be categorized as belonging to Blattulidae on the basis of small size, chaetotaxy and a significant comparative specimens of amber which include both immatures and adults [28,38]. Its characteristics are a small size, large head, antennae with corrugated surfaces, and with 2–3 rows of long sensilla (Fig. 1BC), pronotum and abdomen with two longitudinal stripes, cerci with long spurs and extremely long sensilla, legs short. Especially notable are round elevated pronotal structures of the present nymph (see Fig. 2B), somewhat resembling lanterns (A lantern is a specialised light-producing organ of cockroaches.) of the luminescent cockroaches of the genus *Lucihormetica* [39,40].

The diet of the Blattulidae is revealed for the first time. Five coprolites (the last one still protruding from the abdomen) that are

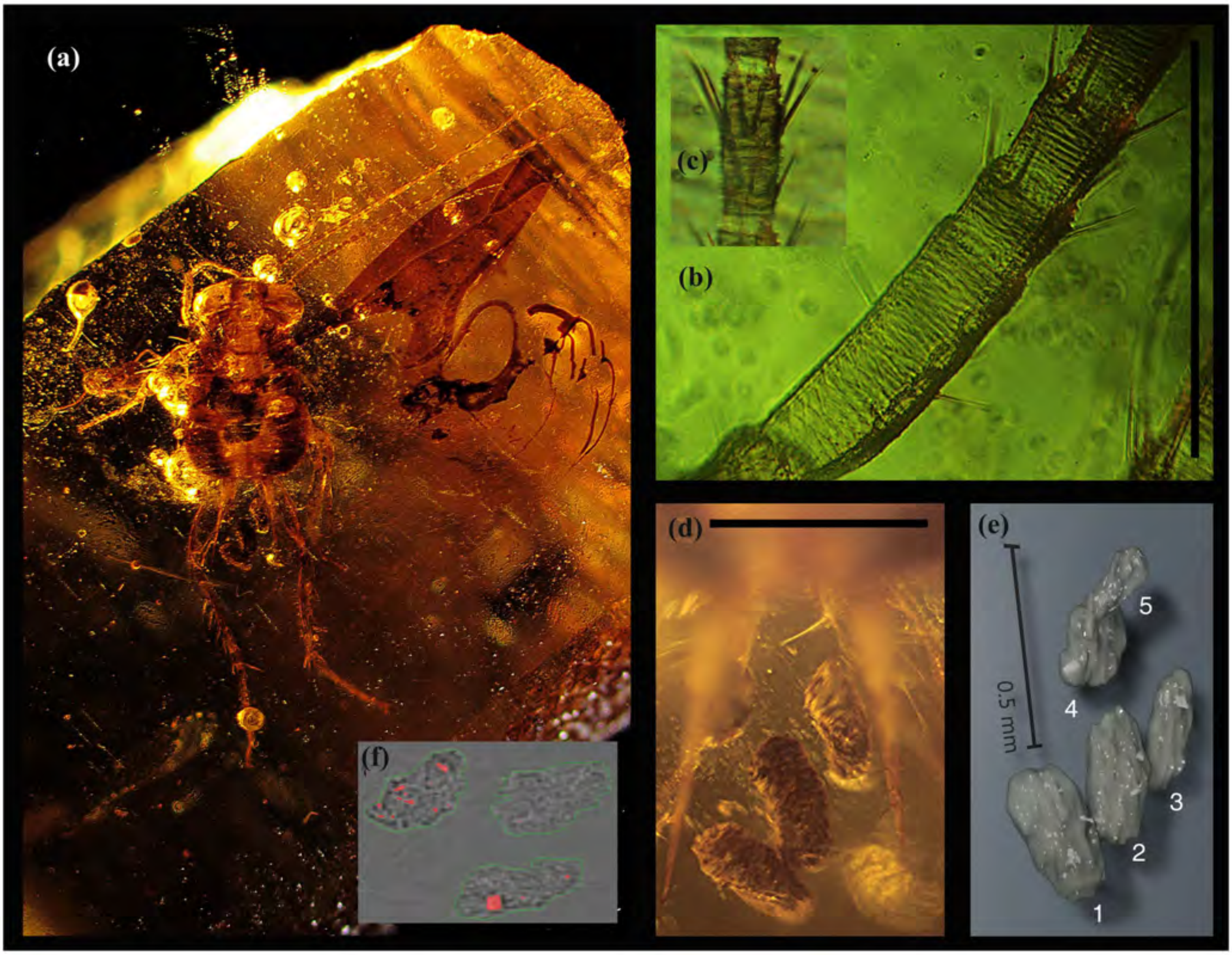

Figure 1. Dinosaur-age cockroach of the extinct family Blattulidae. (A – head to leg end length: 3.8 mm) with antennal sensory system (B, C) and five preserved coprolites (D – optical, E – surface rendering of numbered coprolites and dense particles based on the image stack from synchrotron X-ray microtomography; F – ST orthoslice with labelled boundaries and fragments). Lebanon amber 1094A-I. Scales 0,5 mm.
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elliptical in shape and circular in cross section (volumes 847,381 μm^3, 2080,512 μm^3, 2401,192 μm^3, 3435,904 μm^3, 4597807 μm^3) (Fig. 1E, S1) amounting to a total volume of 13362,796 μm^3, and about 0.35 mm long contain heterogeneous material. They are preserved in a single piece of amber, adjacent to a fossil of the Early Cretaceous cockroach, and represent a new type of trace fossil (coprolite adjacent to a preserved dead organism) that will be designated elsewhere. 1.06% (141,081 μm^3) is filled by partially digested particles of wood. The structure of the wood is revealed on the largest particles and the lignin bilayer (part of the numerous parenchymatous tangential ray cells) is apparent on Fig. 2a and S1. The distance among parenchymatous tangential cells is roughly 10 μm.

The surfaces are smooth and the edges of the particles are rounded even in the largest particles (and also inside of cavities). The size of them (ca. 30,000 μm^3) is still very small when compared to the mouthpart and mouthful size (e.g., particles of the cockroaches of this size often reach 0.4 mm at the widest point).

Wood within the present coprolites has a characteristic, possibly power law distribution of particles larger than 100 μm^3 (distribution curve at Fig. 2F can be characterised with the equation $y = -1.964x + 10.695$; y = log (size); x = log (number of debris)), but the frequency of smaller particles decreases (Fig. 2D) at 100 μm^3, which is far enough to be recorded by the present technique (effective pixel sizes below 0.5 μm are common for the present synchrotron (ST)). The wood particles are not distributed concentrically and/or in an otherwise ordered way.

Additionally, this wood is apparently decayed in the hind gut (intestine and/or rectum - as in termites - not in mid gut or stomach) as the last incompletely formed coprolite (caused by stress-defecation and still extruding from the body) contains numerous larger wood particles (S1). This enhanced gut activity is documented by the amorphous structure of the coprolite apparent in the sections (Fig. 2C).

The distribution curve of the wood particles is ambiguous. The gut-processed particles are diminished below 100 μm^3, which is the rough limit for the smooth edges caused by the cockroach gut-processing. On the other hand, the linear (in log scale) distribution of particles, combined with rounded edges in larger scale (up to 10,000 μm^3) and the absence of small particles and isolated tracheae (only 3 linear particles are present, and they probably do

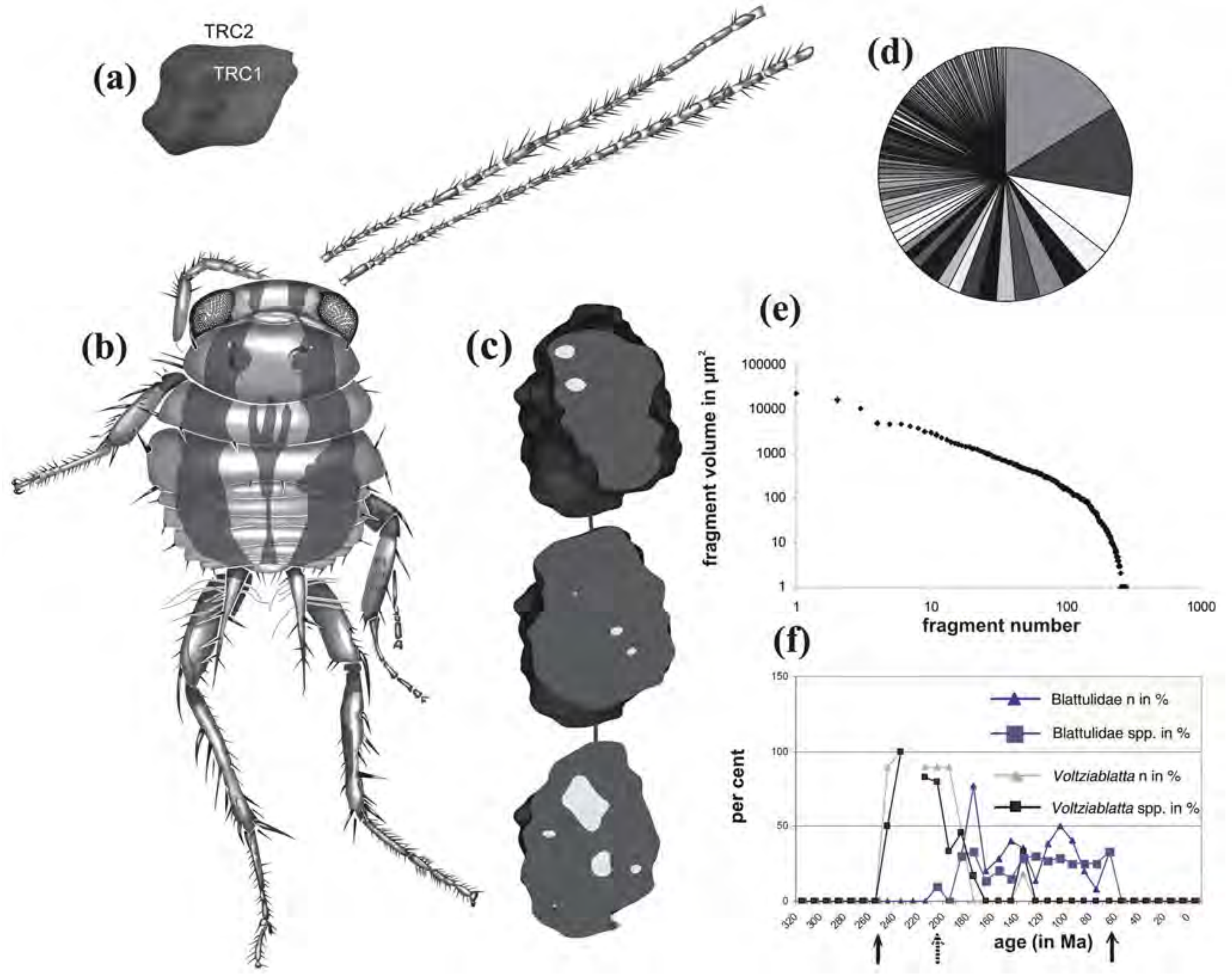

Figure 2. Dinosaur-age wood decomposing cockroach with coprolite and its ecological context. A) wood fragment no. 123 (coprolite no. 3), volume 23077 μm^3 (TRC- parenchymatous tangential ray cells); **B)** Lebanese amber (Blattulidae 1094A-I), length (head to leg end): 3.8 mm; **C)** a virtual synchrotron section (~1.2 mm) through coprolite no. 3, wood particles are pale; **D)** percentual representation of volume of the respective wood particles; **E)** distribution analysis of simple particle count of 280 wood fragments present in all five coprolites plotted over the fragment size; **F)** Ratios of the Blattulidae and "*Voltziablatta*"- group – families that replaced each other during the Triassic (interrupted arrow) – to all cockroaches, plotted over the timescale (in Ma). The origin and extinction of dinosaurs are pointed with arrows. "N in %" means percentual representation of number of specimens, "spp in %" is a percentual representation of species. Original data.
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not represent tracheae) in the present coprolite suggests external pre-digestion.

Dinosaurs apparently had consumed leaves along with the twigs, but the soft parts of leafs are unrecognizable in the ST signal. Only the hard and dense wood particles are distinct.

Discussion

The most effective exploiters of nitrogen in animals are cockroaches, often capable of nitrogen extraction and symbiont transfer even from their own feces or from feces of vertebrates including the popular guano of diverse vertebrates. Its storage and transfer to conspecifics is thought to be used as currency in mating and parental investment strategies [12]. Cockroaches feed on the droppings of frugivorous, insectivorous, and haematophagous bats, but not carnivorous bats [41]. Insect communities on the dung of crocodiles, varanid lizards and big turtles are virtually unstudied, and bird dung is generally too small to be utilized by a specialized dung cohort [17]. Nevertheless, several living cockroaches are associated with bird nests and presumed to feed on bird dung [12,42–46]. The only large volume bird dung of the oil bird *Steatornis caripensis* or guacharo (see Tab. 1) is processed by cockroaches [47], which is another (indirect) support for the present inferences as birds are direct descendants of dinosaurs (often systematically cathegorized directly inside them). Numerous authors [48] note explicitly but without specification direct utilisation of reptile dung. Christoffersen & De Assis [49]summarise pentastomid parasites transferred to cockroaches via feeding on reptile and amphibian feces (see Tab. 1). Although appearing trivial, cockroaches, one of the dominant insect orders during the Mesozoic were never examined as representing top candidates for partial processors of dinosaur dung.

The present specimen represents a derived secondary trace within a trace (traces of microorganisms on wood preserved in a coprolite–a trace of a cockroach within amber–a trace of a tree).

Table 1. Distribuition of living dung-feeding cockroaches supporting their common and cosmopolitan distribution [41], exclusively in dark (nocturnal, cave or under dung) environments.

Species	Family	Locality	Country	Dung	Host	Habitat	Continent	Reference
Arenivaga grata	Corydiidae	Tucson Mountains,	USA, Arizona	guano	Bat	Bat cave	North America	[83]
Blabverus discoidalis	Blaberidae	Bogor, Java	Indonesia	feces	Flat-tailed gecko	Outdoors	Asia	[84]
Blatta orientalis	Blattidae	Johannesburg Hospital	South Africa	dung	Human	Hospital	Africa	[30]
Blattella germanica	Ectobiidae	?	Egypt	feces	Human	Villages	Africa	[85,86]
Ergaula scarabaeoides	Corydiidae	Selangor	Malaysia	guano	Bat	Bat cave	Asia	[87,88]
Eublaberus distanti	Blaberidae	Guanapo Cave	Trinidad and Tobago	dry guano	Fruit bat	Bat cave	South America	[4]
Eublaberus posticus	Blaberidae	Trinidad island	Trinidad and Tobago	feces	Bat	Indoors	South America	[89]
Eublaberus posticus	Blaberidae	Tamana cave	Trinidad and Tobago	guano	Oilbird	Bird cave	South America	[52]
Euthyrrhapha nigra	Corydiidae	Antsinomy grotto	Madagascar	guano	Bat	Bat cave	Africa	[90]
Gyna kazungulana	Blaberidae	?	East Africa	guano	Bat	Bat cave	Africa	[91]
Gyna maculipennis	Blaberidae	Lualaba	Dem Rep Congo	guano	Bat	Bat cave	Africa	[92]
Opisthoplatia maculata	Blaberidae	Formosa	Formosa (=Taiwan)	dung	Human	Outside	Asia	Shikano in [93]
Paratemnopteryx kookabinnensis	Ectobiidae	Kookabinna George	Western Australia	guano	Bat	Cave	Australia	[94]
Paratemnopteryx rufa	Ectobiidae	Nullarbor Plain	Australia	guano	Bird	Cave	Australia	[95]
Paratemnopteryx weinsteini	Ectobiidae	Rope Ladder Cave	Queensland	guano	Bat	Cave	Australia	[94]
Parcoblatta bolliana	Ectobiidae	Texas	USA	dry dung	Cow	Pine woods	North America	[96]
Parcoblatta fulvescens	Ectobiidae	Florida	USA	dry dung	Cow	Pine woods	North America	[97]
Periplaneta australasiae	Blattidae	Sarawak Mt. Jibong	Malaysia	guano	Bird	Cave	Asia	[98]
Periplaneta australasiae	Blattidae		Malaysia	feces	Small reptiles	Outdoors	Asia	[99]
Periplaneta australasiae	Blattidae	Punta Gorda, Florida	South Africa	dung	Goat	Outside; vacant house	North America	[100]
Periplaneta americana	Blattidae	Formosa	Formosa (=Taiwan)	feces	*Macaca cyclopis*	Indoors	Asia	[101]
Periplaneta americana	Blattidae	Vengurla	India	guano	Bat	Bat cave	Asia	[102]
Periplaneta americana	Blattidae	Sumatra Sawah Lunto	Indonesia	feces	Human	Coal mine	Asia	[103]
Periplaneta americana	Blattidae	western Bengal	India	feces	Human	Coal mine	Asia	[104,105]
Periplaneta americana	Blattidae	Johannesburg Hospital	South Africa	dung	Human	Hospital	Africa	[30]
Periplaneta americana	Blattidae	?	Egypt	feces	Human	Villages	Africa	[85,86]
Periplaneta americana	Blattidae	Accra – laboratory	Ghana (Gold Coast)	feces	*Erythrocebus patas*	Indoor (glass jars)	Africa	[106]
Periplaneta americana	Blattidae	Araripe	Brazil	feces	Worm lizard	Outdoors	South America	[107]
Perisphaerus sp.	Blaberidae	Jalor caves	Malaysia	guano	Bat	Cave	Asia	[108]
Pycnoscelus surinamensis	Blaberidae	St. Croix	USA, Virgin Islands	feces	Chicken	Chicken roosts	CentralAmerica	[109]
Pycnoscelus surinamensis	Blaberidae	Puerto Rico Mona Island	USA	dry dung	Cow	Pine woods	CentralAmerica	[43]

Table 1. Cont.

Species	Family	Locality	Country	Dung	Host	Habitat	Continent	Reference
Pycnoscelus striatus	Blaberidae	Selangor	Malaysia	guano	Bat	Cave	Asia	[87,88]
Simandoa conserfariam	Blaberidae	Simandou Mts.	Guinea	guano	Fruit bat	Cave	Africa	[110]
Symploce cavernicola	Ectobiidae	Sarawak Mt. Jibong	Malaysia	guano	Bird	Cave	Asia	[98]
Tivia macracantha	Corydiidae	Katanga Province	Dem Rep Congo	guano	?	Cave	Africa	[92]
Tivia sp.	Corydiidae	Antsinomy grotto	Madagascar	guano	?	Cave	Africa	[90]
Trogloblattella nullarborensis	Ectobiidae	Nullarbor Plain	Australia	guano	Bird	Cave	Australia	[95]
Xestoblatta hamata	Ectobiidae	La Selva	Costa Rica	dung	Bird	?	Cental America	[4]
Xestoblatta immaculata	Ectobiidae	Chilibrillo	Panama	guano	Bat	Cave	Cental America	[111]
unidentified	?	?	?	dung	Horse, Cow	Desert	?	[112]
unidentified	Corydiidae	?	Ecuador	dung	Bird	Outdoors	South America	[12]
unidentified	?	?	Malaysia	feces	House gecko	Indoors	Asia	[113]
unidentified	?	Hawai	USA	feces	Giant toad	Outdoors	North America	[114]

Feeding of diverse cockroaches on bird excrements and also facultative feeding on reptile and amphibian dungs is apparent. Based on Bell et al. [12], Christoffersen & De Assis [49] and Roth & Willis [115].
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Although it represents a unique find in respect to both quality of preservation in amber as well as the incidental character of the preserved "act", coprolite feedings of Mesozoic cockroaches from other families can be excluded based on the positive evidence in the form of preserved gut contents. Several dozen species from the sedimentary record of diverse families (Mesoblattinidae, Caloblattinidae, Ectobiidae, Liberiblattindiae, Umenocoleidae) were found with the gut content. All of them contain unprocessed heterogenous organic debris, but no wood (unpublished observation), which is irreconcilable with coprophagy. Thus the only family adept for such duties is the family Blattulidae–the last ecologically significant family with unstudied gut content. The generic diversity of this family was significantly low, namely only 12 genera are present in their 80 million years of ecological dominance. This low diversity is also represented in the fossil inventory of the Lagerstätten and is direct evidence for very uniform, constant niches and probably also for a more or less uniform diet. This phenomenon is also visible in the unusually minor differences between genera of the sedimentary and amber records. This minimal diversity is highlighted to a greater extent by the sparse disparity. With the exception of two rare species, all Blattulidae are very similar. Uniformity is especially shown by the transversally striated extremities. This coloration dominates in the whole Mesozoic, but was lost at the K/Pg boundary along with the extinction of dinosaurs, although this colouration occurs in extant, nocturnal and arboreal *Allacta australiensis* under different body colors.

Just a lack of diversity could mean it had a limited niche, one that could be seen in modern roaches, but combined with the longest lasting ecological dominance within cockroaches and unique morphology (such as corrugated surface of antennae–Fig. 2B,C), indicating the niche of the Blattulidae was different from that of living cockroaches.

Generally, during the Mesozoic representatives of the family Blattulidae usually comprise ~1% of all insects and over 30% of cockroaches (Fig. 2F), and thus were probably associated with a dominant group of vertebrates–probably sauropod dinosaurs. Special features of the present specimen such as extremely short and wide body with very long cerci suggest it is closely related to *Grandocularis kurnubinsi* from Jordanian amber (described based on a nymph [50] of a similar stage and size). It apparently represents a closely related species, but differs in the form of the pronotum, eye size, coloration and chaetotaxy. In adults, bioluminescent "lanterns" were apparently absent–adults of at least several species of the Blattulidae were documented as crepuscular or diurnal, not nocturnal–on the basis of the eye morphology and common occurrence together with diurnal species within a single pterosaur and/or dinosaur coprolites and/or regurgites [51]. Cockroach nymphs occurring in dung would signal to adult ovipositing females by a lantern system. But the detection of luminescence of lanterns embedded in amber would be difficult. Unfortunately, the ST signal in a large piece of amber is too weak even to reveal morphological details and thus the presence of these morphofunctional units cannot be validated.

One can imagine the distinct contrast coloration characterized by distinct alternating light-and-dark stripes would be advantageous (for communication) in an open and confined habitat of dung surfaces. On the other hand, neither cockroach guano dwellers nor recent "external" coprophages have any conspicuous coloration. Additionally, all living coprophagous cockroaches live concealed within and/or under dung. In nocturnal conditions of caves, nymphs also burrow in the surface of loose guano. They may be completely concealed, or may rest with their heads on the surface with their antennae extended up into the air; if the guano is compacted, the cockroaches remain on its surface and are attracted to irregularities such as the edge of a wall, a rock, or even a footprint [52]. In these dark conditions, guano cockroaches are also present on dung and mostly are absent from cave zones of dry soil, stones, or pebbles [53,54].

The low diversity may be a consequence of a heterogenous diet and/or low specialization of herbivorous animals of which dinosaurs were the most abundant (suggesting there was relatively little nutritional variability in their excrement and thus less need for specialized roaches). Low specialization of at least some dinosaurs is confirmed by phytoliths extracted from the Upper Cretaceous coprolites (from dicotyledons, conifers, and palms) from India, suggesting that the suspected dung producers (titanosaur sauropods) fed indiscriminately on a wide range of plants, including grasses [7]. With the diversification of mammals [55], diverse specialized dung-beetles co-evolved [2] and these cockroaches, possible with low specialization in their feeding behaviors became extinct.

Generally, before the massive radiation of the Blattulidae at the beginning of the Jurassic, their niche was occupied by the superficially similar "*Voltziablatta*" group of cockroaches, which became extremely rare along with the radiation of the Blattulidae. In all Mesozoic sites, "*Voltziablatta*" and the Blattulidae occur in congeneric species pairs, discretely differing in size, but not in general appearance, thus doubtfully representing nocturnal and diurnal cohorts (occurrence of both sexes in both groups was validated earlier [51]). This enigmatic observation is unexplained and needs further investigation. The *Voltziablatta* group phylogenetically connects its descendants, the herein studied Blattulidae and living cockroaches which bear endosymbionts; namely termites, *Sociala* and *Cryptocercus* all descended from Liberiblattinidae. If this mutualism had a single origin, it must have been in the *Voltziablatta* group (fixed to flora and wood of *Voltzia* plants), where the lignin consumption must have originally evolved. In the opposite case, we would need to consider three independent origins of endosymbionts, which molecular data do not support [56].

Coprolite and Dung Decomposition

Presence of related endosymbionts in termites and cockroaches of the family Cryptocercidae was postulated to be an evidence for their direct relation. Nevertheless, the probable presence of endosymbionts in the Mesozoic clade which diverged from stem of higher cockroaches explains the monophyletic origin of these symbionts in both groups also in the phylogenetic reconstructions where they are not directly related [3]. The question is why was this capability lost in most regular cockroaches?

The hypothesis that lignin-decomposing insect and their endosymbionts originated via the consumption of wood pre-digested by herbivore animal needs explanation. Feeding on lignified wood and also foliage-eating became more widespread in both dinosaurs and insects only with the radiation of angiosperms at the Early Cretaceous/Late Cretaceous boundary [1]. Dung consumption by Mesozoic termites, assisting in decomposition of processed plant matter was already proposed [14].

Even the wood decay is preserved in a single sample, it is clear that these cockroaches might have employed at least a semisocial way of life to provide the horizontal endosymbiont transfer (thus supporting the view that it evolved just once, as confirmed by the phylogenetical scheme). In recent tropics, where food is available for bats throughout the year, guano deposition is predictable and also supports very large, persistent groups of cockroaches–guanobies [57].

To summarize the arguments supporting dung processing, this single sample is decisive in showing a coprolite still extruding from the body (and thus belonging to the body fossil as a producer, excluding incidental preservation) and containing modified wood fibres with typical parenchymatous tangential ray cells. Lignin can not be processed this way without endosymbionts and even in the case it has been modified to some extent by some fungi, it must have been pre-processed externally. The wood was apparently processed before it entered the cockroach digestive tract as indicated by the large extent of digestion apparent in cavities (which definitely exclude the mechanical processing) and the fragment preservation plotting fragment volume over the fragment number–Fig. 2e; additional indirect support comes from dung-processing of living cockroaches, Tab. 1. It must be stressed, that the extent of smoothing of large particles including large cavities excludes the exclusively within insect processing and is evidence for external pre-digestion. In this respect, a source of the wood directly from the environment can be excluded. There are only three possibilities for the pre-digestion, namely the fungal (excluded below based on selective disadvantage of preference of large indigestible particles and absence of wood damages before the Late Cretaceous contrasting with plethora of coprolites containing wood) and vertebrate pre-processing or their combination. Large particles are numerous indicating that they were not selectively avoided during consumption. Underrepresentation of smaller particles was apparently due to biochemical digestion of wood lignin as do their eusocial (extinct cockroaches of the family Socialidae and termites) and semisocial (Cryptcercidae) descendants. Although it is very probable that dinosaurs preferred wood processed by fungi, fungi-only pre-digestion and feeding of these cockroaches can be excluded based on the presence of large fragments combined with low partition of wood. Such a small amount would suggest selective feeding on fungi-modified wood, in which circumstances large particles are contradictive; on the contrary, unselective feeding on coprolites would contain the expected spectrum of particles of diverse size. The only possible explanation is that these were caused by herbivorous vertebrates. Due to the dominance of these cockroaches for the same 200 million years as dinosaurs, no other vertebrate group is as promising for this candidature. It can not be excluded that cockroaches also cleaned up after some small, unknown vertebrate herbivores, but these can be excluded from the present study as small vertebrates can not digest wood.

Certainly, in such a case, in any solitary taxa the capability of symbiont transfer and thus utilizing lignin was necessarily lost. Termites did not exist before the Middle Jurassic, but their precursors under study were apparently pre-adapted for wood decomposition – and thus possessed one of the necessary conditions for the origin of a eusocial way of life. Nevertheless, termites were diversified in the very beginning of the Cretaceous as evidence from the presently studied locality in Lebanon also indicates [3,58,59].

Transfer of microflora within dinosaurs was proposed via juvenile coprophagy [60], which facilitates microflora but also endoparasite transfer with cockroaches. It is actually the intestinal bacteria and metabolic by-products [61,62] of the herbivore gut (perhaps dinosaurs), which likely allowed for lignin digestion in Blattulidae (by protozoans). The small proportion of wood content ($\sim 1\%$ is of only partially processed wood remnants and up to 5% of completely processed wood, not recognized in the ST) in the cockroach coprolite indicates that wood was not the primary constituent of the diet of the present individual, and rather supports the derived source. This is also indicated by the Late Cretaceous dung of herbivorous reptiles [63], probably dinosaurs (entirely of comminuted plant tissue with the predominance of secondary conifer xylem tissues of Cupressaceae). The unmodified state of the cells and the absence of gymnospermous wood in dung [64] is still problematic, but the small size of the plant fragments infilling the fossil burrows suggests comminution or sorting by invertebrates [63]. Also several gymnosperms remains (Cheirolepidiacae and Araucariacae) were found in the unstudied coprolite (larger than the present ones) from the same deposit in Lebanese amber.

The distance among parenchymatous tangential cells of the wood in the present coprolite is roughly 10 µm, which is comparable to the structure of wood of fossil *Taxodioxylon vanderburghii* or *Metasequoia glyptostroboides* (20–30 µm [65]). Even more similar parenchymatous tangential cells (10–20 µm) are found in unidentified conifer wood from dinosaur coprolites (as indicated in Fig. 5B, upper part of [8]). Interestingly, this wood originates from trees growing in warm and semiarid Late Cretaceous environments preserved in the sediments of the Two Medicine Formation [8], which is in contrast to the warm and humid amber-producing Early Cretaceous forest of Lebanon. Anyway the specific determination of fossil conifer woods is very difficult and requires comparisons of many features that do not seem to be present in the small particles of wood in the fecal pellets.

The wood (the length of the largest fragment was 13 cm) preserved in dinosaur coprolites is characterized by absence of cylindrical wood stems (no terminal twigs were digested); damage to lignin such as the presence of pliant tracheids, uneven cell walls and deformed and missing cells is also characteristic [8]. This, along with the fact that the vertebrate gut cannot hold complex lignolytic organisms, because these protists are anaerobic suggests fungal decay prior to consumption [8]. On the contrary, the small amount of small wood particles in these coprolites indicates they were processed within dinosaurs and support decomposition of the smallest particles both in dinosaur and cockroach coprolites.

Coprolite and Dung Decomposition-defecation

In spite of the diversity of behaviors reported from amber, a review by Arillo [66] contains a single defecation, reported from a Dominican amber termite [67]. Nevertheless, there is a rich Cretaceous termite record of distinctive fecal pellets with diagnostic hexagonal cross-sections that commence during the Hauterivian or Barremian [68] and continue to occur in various woods to the end of the Cretaceous. Some of these pellets may have originated from individuals belonging to taxa such as the eusocial cockroach *Sociala* that occurs in Mesozoic amber [3]. Fecal pellets from wood are known [69], and most amber coprolites contain wood remains and are assigned to wood borers among termites, beetles or some other insects [70,71]. Additional pellets are known from the Dominican amber [72] and frass containing fungi are known from Archingeay amber [73]. Defecation was probably often associated with escaping behaviour, because more than 60 samples of Lebanese amber (coprolites are often separated) contain coprolite of diverse size and shape (large elongate, oval). Lots of them were preserved with wood fibers. In the same piece there are insects like ceratopogonids, chironomids, archizelmerids (extinct flies) and wasps, but these coprolites are not associated with insects and are mentioned here to demonstrate the common defecation behaviour, not the wood processing. No trace fossils documenting specialized dung provisioning are known before the Late Cretaceous [2].

General Ecology of Dung Provisioning

Detritic food chains strongly predominated in the Mesozoic [2] and the dominance of the Blattulidae among cockroaches seems to be associated with dung being the most valuable source of nitrogen. It is improbable that there were specialized guilds of dung feeders in the Mesozoic comparable with modern regarding structural complexity and ecological efficiency: Sciaridae and Scatopsidae (flies) with rapid larval development were remarkably rare [74], as well as dung beetles, although both are present in the Lebanese amber [75] along with decomposer flies of the families Psychodidae and Sciaridae. However, they were absent before the Jurassic and extremely rare during the entire Jurassic [10,64,75].

Alternative opportunistic exploiters of dinosaur dung were snails. Multiple associations of 132 (with 0–66 specimens each) fossils (*Megomphix*, *Polygyrella*, *Hendersonia*, *Prograngerella*, and three aquatic taxa) have also been observed on or within 6 of the 15 herbivorous dinosaur coprolite deposits [15].

Despite the great diversity and quantity of scarabeid beetles in the Mesozoic ([10] especially in the Middle Jurassic locality Daohugou in Inner Mongolia, China), only a few species can be considered as possibly coprophagous. Only 3 dung ball-makers from the subfamily Scarabaeinae are known: *Prionocephale deplanate* (Upper Cretaceous Lanxi formation, Zhejiang, China [76]), *Cretonitis copripes* (Early Cretaceous Zaza Formation, Baissa, Russia) and an undescribed species [72,77] of the living coprophagous genus *Trypocopris*. Representatives of the Geotrupidae were probably coprophagous: *Parageotrupes incanus* from the Yixian Formation [78], and *Cretogeotrupes convexus* and *Aphodius* (s.l.) (Aphodiinae) from Baissa [77,79].

An alternative hypothesis claiming mainly aquatic plant diet of dinosaurs [80] and thus water defecation does not explain at least some damage to terrestrial plants.

The dung of known Mesozoic herbivores is composed mainly of undigested fern and gymnosperm tissues and was utilized by opportunistic detritivores together with other plant litter [2].

The specialized coprophagy by beetles is recorded as late as the Late Cretaceous when the diet of grazing dinosaurs apparently contained angiosperms other than grasses and ecosystems were based on biomes similar to grasslands [1]. Based on our investigations, pollen and angiosperms in the Lebanon amber are indicated by at least 5–6 different taxa.

The decay of wood pre-digested in dinosaur gastrointestinal tracts explains and predicts the single origin of lignin consumption in the common ancestor of termites, eusocial cockroaches (*Sociala*), and semisocial cockroaches of the family Cryptocercidae. It would also explain a huge number of termite-like fecal pellets (containing wood) in Mesozoic ambers with parallel absence of any termite damage to wood [68]. The fact that termites were a major lineage responsible for the degradation of plant tissues (when compared with cockroaches) is irrelevant in this respect as they originated not earlier than in the Middle Jurassic when their ancestors, certain Liberiblattinidae appear in the fossil record [4] and thus can not play any role in the decomposition of early sauropod dung. In contrast, blattulid cockroaches and their ecological equivalents originated as early as the Permian–Triassic boundary.

The contemporary robust appearance of Cryptocercidae does not require a major morphological shift from anticipated dung-beetle-habits. It is likely that dung processors will also lose wings like Cryptocercidae, but in caves, wing loss and associated morphological changes occur more frequently in organisms that rely on plant debris than those that rely on guano [81]. Under all circumstances it is apparent, that termite and cryptocercid ancestors were pre-adapted for lignin decay and, likely, provided a limited sanitation to herbivorous reptiles. Based on the correlation of distribution of reptiles and the dominance of the blattulid cockroaches in Mesozoic ecosystems, and their coeval occurrence in the present amber-bearing strata [82], these herbivorous reptiles were most likely the dominant sauropod dinosaurs.

Supporting Information

Figure S1 Synchrotron imaging of 5 coprolites of dinosaur-age immature cockroach from the Lebanese amber (Blattulidae 1094A-I). Select transparent mode for 3D visualization and rotation.
(PDF)

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Author Contributions

Conceived and designed the experiments: P. Vršanský TV P. Vagovič. Performed the experiments: P. Vršanský TV P. Vagovič. Analyzed the data: P. Vršanský TV LV P. Vagovič. Contributed reagents/materials/analysis tools: P. Vršanský TV DA AP P. Vagovič. Wrote the paper: P. Vršanský TV DA AP LV P. Vagovič. Initiated the research, identified and drew the immature cockroach with coprolite, and erected and validated the present hypotheses: P. Vršanský. Provided the material and dinosaur information from the locality: DA. Provided and designed the µST experiment, and provided particle measurements and volume segmentation of reconstructed µST data and edited the text: TV P. Vagovič. Provided information on dung beetles and ecology: AP.

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Paleocene origin of the cockroach families Blaberidae and Corydiidae: Evidence from Amur River region of Russia

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Abstract

Morphna paleo **sp. n.,** the earliest winged representative of any living cockroach genus and the earliest representative of the family Blaberidae, is described from the Danian Arkhara-Boguchan coal mine in the Amur River region (Russian Far East). The branched Sc and A suggest Ectobiidae (=Blattellidae) probably is not the ancestral family because Blaberidae were derived directly from the extinct family Mesoblattindae. The associated Danian locality Belaya Gora yielded *Ergaula stonebut* **sp. n.**, the earliest record of the family Corydiidae. Both species belong to genera codominant in the Messel locality, thus validating their dominance in early Cenozoic assemblages.

Key words: fossil insects, fossil cockroaches, Tertiary, Blaberidae, Corydiidae, *Morphna*, *Ergaula*

Introduction

The Paleocene epoch, with 177 known extinct insect species: 44 coleopterans, 28 dipterans, 28 hemipterans, 27 hymenopterans, 15 odonates, 10 orthopterans, 8 neuropterans, 6 trichopterans, 5 mecopterans, 2 dermapterans, and 1 lepidopteran (EDNA fossil insect database; http://edna.palass-hosting.org; active 2.5. 2012) is the least known Tertiary period in terms of insect diversity. No cockroaches, only two related termite species and a single mantodean *Arvernineura insignis* have been described from Menat (Piton 1940). In contrast, 6124 Eocene, 2663 Miocene and 2550 Oligocene species have been recorded. Pliocene and Pleistocene species are also numerous, but in EDNA underrepresented due to the presence of living species in these Epochs (EDNA catalogise only original designations of species).

Cockroaches originated in the Bashkirian Carboniferous, with the oldest record originating from the Quilianshan in China (Zhang *et al.* 2012, Guo *et al.* 2012). Typical Mesozoic families were derived from the Phyloblattidae near the P/T boundary and the stem of the living families (but also the stem for all mantodeans and termites) can be traced from the Mesozoic family Liberiblattinidae (Vršanský 2002, 2010, 2012). The earliest record of any living family is the ectobiid (blattellid) *Piniblattella vitimica* (Vishniakova, 1964) from the earliest Cretaceous (Vršanský 1997). Before this study, living cockroach genera, including highly advanced forms, were known starting from the early Eocene (Archibald & Mathewes 2000) and the modern fauna is considered to originate around the Paleocene-Eocene Thermal Maximum (PETM—Vršanský *et al.* 2011, 2012b). (The amber fossil *?Blattella lengleti*, is a nymph and may represent a separate genus.) The present study provides evidence for the occurrence of at least some extant genera before the Palaeocene side of the PETM, and in parallel provides earlier evidence for the two living families Corydiidae and Blaberidae.

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Material and methods

Two joined forewings were collected by Yu.L. Bolotsky in the stratotype section of the Tsagayan Formation (Belaya Gora locality). This specimen is deposited in the Amur Natural History Museum of the Institute of Geology and Nature Management, Far Eastern Branch Russian Academy of Sciences (ANHM IGNM FEB RAS), Blagoveshchensk, Russia. One isolated wing was collected by E.V. Bugdaeva in the upper plant-bearing bed in the Arkhara-Boguchan coal mine. This specimen is deposited in Paleontological Institute of Russian Academy of Sciences, Moscow, Russia. Comparative living material provided in the photograph originates from the collection of Vít Kubáň (Thailand, Mae Hong Son Province, Soppong, 7–12.V.1996) deposited in collection of the second author (ĽV) in the Institute of Zoology, SAS, Bratislava.

Geological background

The Zeya-Bureya Basin is located in the middle course of the Amur (Heilongjiang) River (Fig. 1B–D). Development of its sedimentary cover began in the Late Cretaceous with accumulation of the Kundur Formation (Santonian-Campanian). This stratigraphic unit is represented by sandstones, siltstones, and mudstones containing abundant freshwater fauna. These sediments in some structures are oil-and-gas bearing. Over them is the Tsagayan Formation, which is divided into three subformations. The lower Tsagayan Formation consists of conglomerates, mainly clays with sandstone interbeds; its geological age is the early-middle Maastrichtian (Bugdaeva 2001; Markevich 1994, 1995; Markevich *et al.* 2004, 2010, 2011). The late Maastrichtian part of the middle Tsagayan Formation includes conglomerates, sandstones siltstone, and lenses with plant remains. The Danian upper part of the Tsagayan Formation is represented by conglomerates, sandstones, clays and coal seams. The plant-bearing beds occur here. The fossil plants have been studied since the 19th century (Heer 1878; Kryshtofovich & Baikovskaya 1966; Krassilov 1976). This flora was named Tsagayan flora.

The stratotype section of Tsagayan Fm is outcropped in the mouth of the Darmakan River, along the northern and north-eastern slopes of Belaya Gora Mount. It is represented by conglomerates, sandstones, siltstones, and mudstones. We obtained from each bed abundant fossil spores and pollen that allowed us to define the Maastrichtian and Danian age of deposits and the position of the K-T boundary (Bugdaeva 2001). The clay with bedded plant remains lies 37 m above that boundary (Fig. 1C); the thickness of this bed is 3 m. The following fossil plants were collected: *Podocarpus tsagajanicus* Krassil., *Taxodium olrikii* (Heer) Brown, *Metasequoia disticha* (Heer) Miki, *Androvettia catenulata* Bell, *Potamageton* cf. *nordenskioldii* Heer, *Hydrocharis* sp., *Limnobiophyllum scutatum* (Dawson) Krassil., *Trochodendroides arctica* (Heer) Berry, *Carinalaspermum bureicum* Krassil. and *Nyssa bureica* Krassil. The burial is dominated by leaves of *Limnobiophyllum* and shoots and leaves of *Taxodium*. Other remains occur rarely. Remains of fossil insects have been found in this locality, including Buprestidae, Chironomidae, as well as caddisworm cases of *Folindusia* cf. *communita* Cockerell, 1925 and *Terrindusia minuta* Vialov et Sukacheva, 1976. The upper part of the upper Tsagayan Fm contains productive coal seams and several coal mines. One of the mines (Arkhara-Boguchan coal mine) is located near Arkhara settlement. It has three plant-bearing beds with abundant fossil plants; the cockroach wing was found in the upper plant-bearing bed (Figs. 1B–C).

The family name Ectobiidae is used instead of Blattellidae and Corydiidae is substituted for Polyphagidae, based on ICZN Ruling (see Beccaloni & Eggleton 2011; but with reservations of inclusion of termites within order of cockroches).

Systematic palaeoentomology

Blattaria Latreille, 1810 (= Blattodea Brunner von Wattenwyl, 1882)

Blaberidae Brunner von Wattenwyl, 1865

Epilamprinae Princis, 1960

Epilamprini Handlirsch, 1925

Morphna Shelford, 1910

= *Morphnina* Princis, 1958

Diagnosis (after Shelford 1910): Form rather dorsoventrally flattened. Vertex of head covered or almost covered by pronotum, which is trapezoidal, sub-cucullate and posteriorly produced obtusely. Tegmina and wings fully developed, exceeding the apex of the abdomen. Supra-anal lamina of typical Epilamprine shape. Cerci moderately long. Femora moderately armed with spines beneath. Posterior metatarsus equal in length to succeeding joints; all the joints entirely unarmed beneath, their pulvilli large, pulvillus of metatarsus apical but produced towards the base of the joint.

Type species. *Morphna maculata* (Brunner von Wattenwyl, 1865).

Composition (updated from Princis 1967, 1971).

Morphna amplipennis (Walker, 1868) (India)
  = *Epilampra amplipennis* Walker, 1868
Morphna auriculata (Brunner von Wattenwyl, 1865) (India)
  = *Epilampra auriculata* Brunner von Wattenwyl, 1865
Morphna badia (Brunner von Wattenwyl, 1865) (Thailand, Malaysia, Sumatra, Java, Borneo)
  = *Epilampra badia* Brunner von Wattenwyl, 1865
  = *Epilampra ramifera* Walker, 1869
Morphna clypeata Anisyutkin & Gorochov, 2001 (Vietnam)
Morphna decolyi (Bolívar, 1897) (India)
  = *Molytria decolyi* Bolívar, 1897
Morphna dotata (Walker, 1869) (Thailand, Malaysia, Borneo)
  = *Epilampra dotata* Walker, 1869
Morphna humeralis Bruijning, 1948 (Sumatra)
Morphna imperatoria (Stål, 1877) (Philippines)
  = *Epilampra imperatoria* Stål, 1877
Morphna maculata (Brunner von Wattenwyl, 1865) (Malaysia, Sumatra, Java, Borneo)
  = *Epilampra maculata* Brunner von Wattenwyl, 1865
  = *Epilampra polyspila* Walker, 1868
  = *Molytria shelfordi* Kirby, 1903
Morphna moloch (Rehn, 1904) (Thailand)
  = *Epilampra moloch* Rehn, 1904
Morphna plana (Brunner von Wattenwyl, 1865) (India, Sri Lanka)
  = *Epilampra plana* Brunner von Wattenwyl, 1865
  = *Homalopteryx biplagiata* Bolívar, 1897
  = *Epilampra punctifera* Walker, 1868
  = *Homalopteryx templetoni* Kirby, 1903
Morphna pustulata Hanitsch, 1930 (Sumatra)
Morphna sp. (Germany) extinct, Eocene (MES 10188)

Morphna paleo sp. n.
(Figs. 1A, 2C)

Holotype. PIN 5142/12. Right forewing fragment; type locality, Archara-Boguchan, Far East, Russia; type horizon, Tsagayan Formation, Danian Paleocene.

Diagnosis. Forewing with length about 23 mm, width 9 mm. Numerous cross-veins present in M and CuA. Anal intercalaries punctuated.

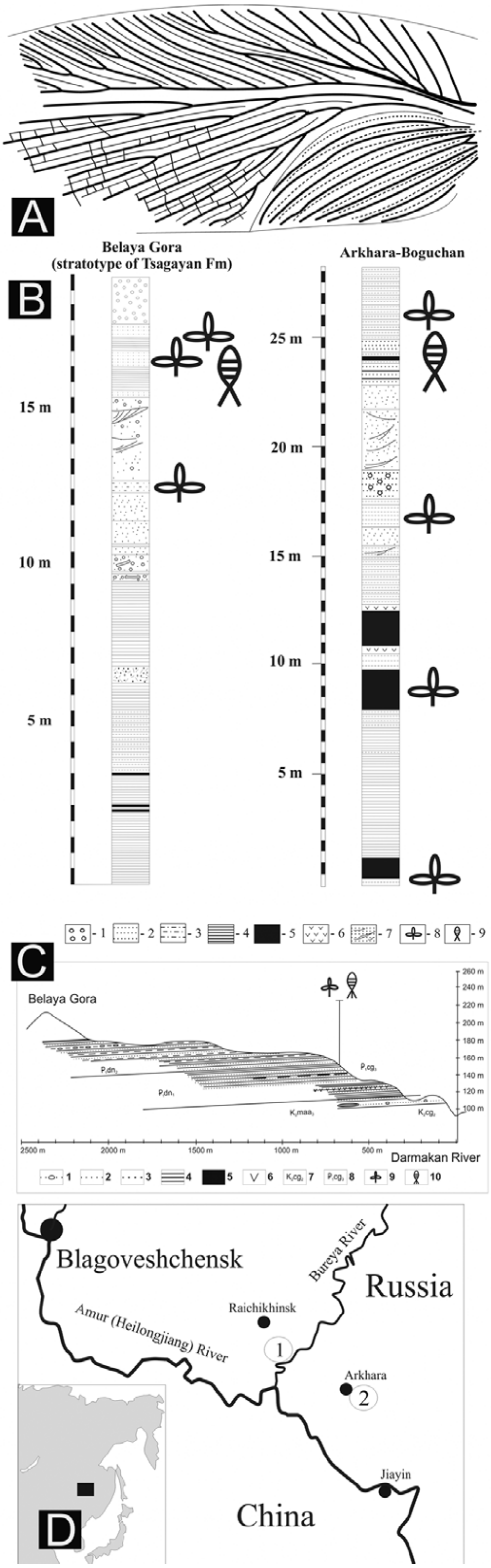

FIGURE 1. **A**) *Morphna palaeo* **sp. n.**, holotype PIN 5142/12; Danian sediments (or Paleocene sediments) of Archara-Bogučan in the Far East of Russia. Forewing length 23 mm; **B)** sections of Danian localities Belye Gory: Belaya Gora (**1**) and Arkhara-Boguchan (**2**) (1—conglomerate; 2—sandstone; 3—siltstone; 4—claystone; 5—coal; 6—acid tuff; 7—strata with cross-bedding; 8—locality of fossil flora; 10—locality of fossil insects); **C)** Profiles of Belaya Gora locality, the stratotype section of Tsagayan Formation (1—conglomerate; 2—sandstone; 3—siltstone; 4—claystone; 5—coal; 6—acid tuff; 7—deposits of the Maastrichtian middle Tsagayan Formation; 8—deposits of the Danian upper Tsagayan Formation; 9—locality of fossil flora; 10—locality of fossil insects; **D)** Localization (Japan to the Right).

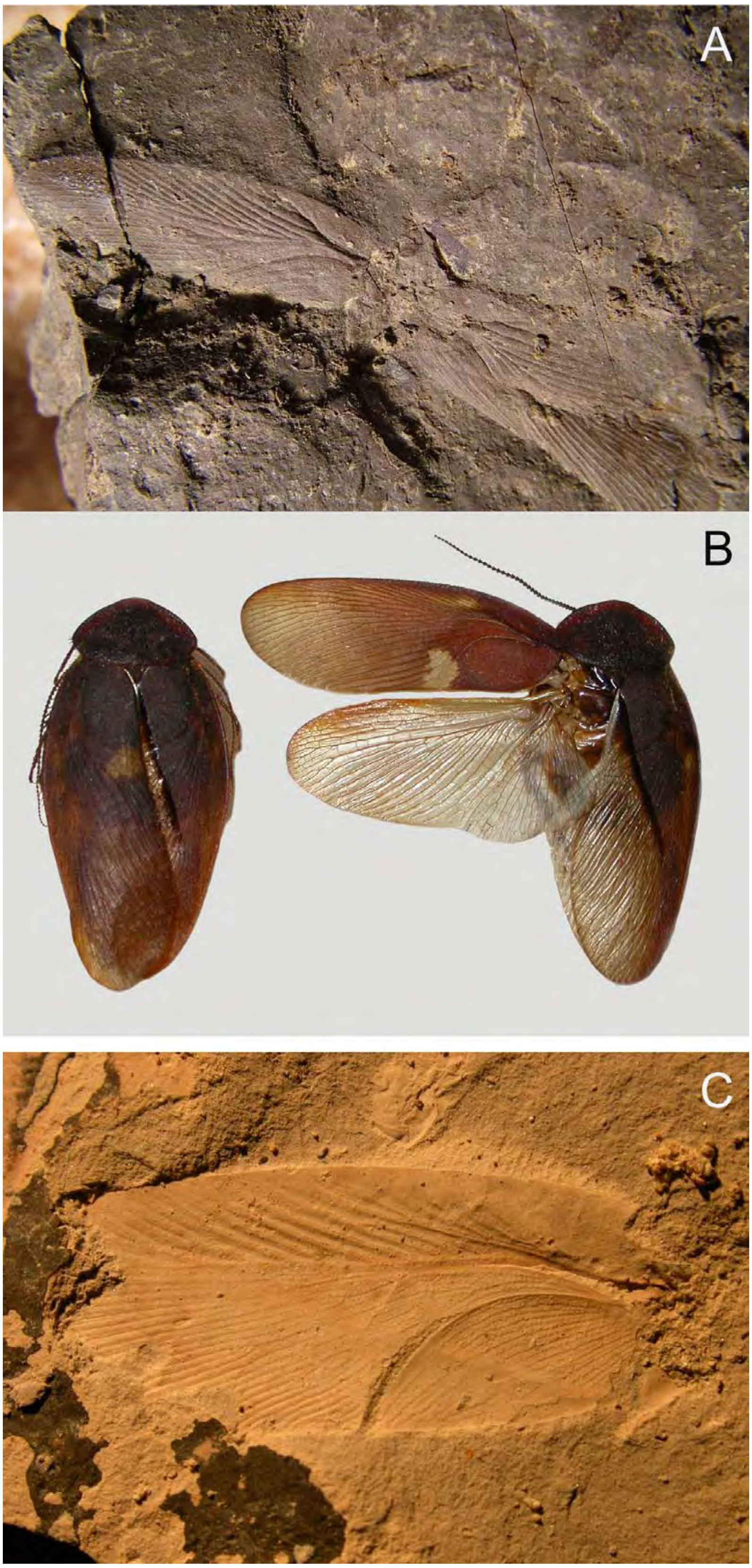

FIGURE 2. A) *Ergaula stonebut* **sp. n.** Holotype ANHM 4/7; Danian sediments (or Paleocene sediments) of Belaya Gora, Far East, Russia. Left forewing 31mm long. **B**) Males of *Ergaula capucina*, Thailand (Mae Hong Son prov., Soppong, 7.–12.V.1996, Vít Kubáň leg., coll. Ľ. Vidlička, ZIN SAS). Note significant folding line on right forewingand strong fold along Sc, apparent also in fossil. **C)** *Morphna palaeo* **sp. n.** Holotype PIN 5142/12; Danian sediments (or Paleocene sediments) of Archara-Bogučan in the Far East of Russia. Forewing length 23 mm.

Description. Forewing without coloration. Venation distinct with apparent intercalaries and rich cross-veins in M and CuA. Subcostal area wide, with Sc richly branched (secondarily). R regular, parallel; M (5) slightly curved, running close to R (apomorphy), fusing to CuA. CuA rich (8). Anal veins simple with punctuated intercalaries.

Remarks. The combination of parallel forewing margins, wide and branched Sc, fusion of M with CuA running close to R, basalmost branches of CuA running parallel to CuP and simple A place this taxon in *Morphna*.

Morphna has been considered to be a comparatively terminal taxon of Epilamprinae (Rehn 1951). Nevertheless, the new species points to a very initial stage of the evolution of Blaberidae, since compared with Ectobiidae (=Blattellidae) fusion of M with CuA running close to R and wide, branched Sc are apomorphies. In the living fauna, *Morphna* is restricted to southeast Asia (India, Sri Lanka, Malaysia, Sumatra, Java, Borneo, Philippines and Thailand). The genus is quite diverse in species and some seem to have little in common (e.g., *M. pustulata* is elongated, with curved forewing posterior margin). On the other hand, the most closely related living species, *M. plana* (Brunner von Wattenwyll, 1865) from Sri Lanka, differs only in possessing numerous cross-veins (plesiomorphy) and in size. All the living representatives of the genus are considerably larger than *M. paleo* **sp. n.** (apomorphy), with forewing lengths of 41–50 mm.

Two basal branches of R have teratological fusion of veins (see Vršanský 2005: this particular parallel fusion of two ascending R branches is unknown in fossils), but this character is without systematic value. Irregularity between R and M is interpreted as an apomorphy based on the absence of this character in Cretaceous cockroaches.

Etymology. From Greek *palaios*: ancient or primitive.

Corydiidae Saussure, 1864 (= Polyphagidae Walker, 1868)

Corydiinae Saussure, 1864 (= Polyphaginae Walker, 1868)
Corydiini *sensu* Rehn, 1951

Diagnosis (after Rehn 1951). Both sexes with at least tegmina present, wings usually present, but sometimes considerably reduced. Tegmina varying from normal to somewhat reduced, obovate and densely coriaceous (mostly in females). Humeral area more developed than in Polyphagini, if coriaceous then broadly expanded. Sc rami regular, not crowded. R without posterior branches, most branches terminating anteriorly, some apically, instead of curving posteriorly. M with free base, its branching regular and direct. Cu not curving distinctly away from plical furrow, CuP not joining cubitus.

Diagnosis (after Walker 1868). Female: Body short-elliptical, convex, dull, very thickly and minutely punctured. Head shining, impressed between the eyes, with a transverse furrow near the mouth. Eyes not far apart. Second joint of the palpi subclavate; third slightly securiform, very much longer than the second. Antennae setaceous, submoniliform, not more than half the length of the body; first, second and third joints short; following joints very short. Prothorax extending somewhat beyond the head and over the basal part of the fore wings when they are expanded, rounded in front and on each side, slightly furrowed along each side; its breadth along the hind border more than twice its length; hind border hardly rounded; hind angles slightly falcate; a lyre-shaped mark in the disk. Mesothorax, metathorax, pectus and abdomen shining, mostly smooth. Abdomen with the segments above and beneath near the tip retracted in the middle towards the disk; sides fringed, with bristles; subanal lamina small, bilobed. Cerci lanceolate, submoniliform, setose. Legs stout; tibiae armed with some strong spines; first joint of the tarsi twice the length of the fifth, which is very much longer than the second. Fore wings coriaceous, membranous towards the border; costa much rounded; tips conical; principal veins distinct in the coriaceous part; transverse sectors numerous, irregular. Hind wings membranous, strongly and thickly reticulated; transverse sectors numerous, irregular.

Type species. *Ergaula carunculigera* (Gerstaecker, 1861)

Composition (updated from Princis 1963).

Ergaula Walker, 1868
= *Dyscologamia* Saussure, 1893 (type is *cesticulata* = *pilosa*)
= *Parapolyphaga* Chopard, 1929 (type is *erectipilis* = *pilosa*)
?= *Netherea* Vršanský et Anisyutkin, 2004 (type is *haatica*)

Ergaula capensis (Saussure, 1893) (Nigeria, Cameroon, Democratic Republic of the Congo, Congo, Uganda, Kenya, Tanzania, Zambia, Zimbabwe, Angola)
=*Dyscologamia capensis* Saussure, 1893
=*Dyscologamia wollastoni* Kirby, 1909
Ergaula capucina (Brunner von Wattenwyl, 1893) (Myanmar)
=*Homoeogamia capucina* Brunner von Wattenwyl, 1893
Ergaula carunculigera (Gerstaecker, 1861) (Philippines (Luzon))
=*Corydia carunculigera* Gerstaecker, 1861
=*Ergaula scaraboides* Walker, 1868
Ergaula funebris (Hanitsch, 1933) (Borneo)
=*Dyscologamia funebris* Hanitsch, 1933
Ergaula nepalensis (Saussure, 1893) (Nepal, Myanmar)
=*Dyscologamia nepalensis* Saussure, 1893
Ergaula pilosa (Walker, 1868) (Sumatra, Malaysia, Java, Borneo)
=*Zetobora pilosa* Walker, 1868
=*Dyscologamia cesticulata* Saussure, 1893
=*Dyscologamia chopardi* Hanitsch, 1923
=*Parapolyphaga erectipilis* Chopard, 1929
=*Polyphaga sumatrensis* Shelford, 1908
Ergaula silphoides (Walker, 1868) (Cambodia)
=*Polyphaga silphoides* Walker, 1868
Ergaula atica Vršanský et Anisyutkin, 2008 (Israel) extinct, ?Eocene (based on male)
?= *Netherea haatica* Vršanský et Anisyutkin, 2008 (Israel) extinct, ?Eocene (based on female)
Ergaula spp. (Germany) extinct, Eocene (common in Messel, based on both sexes)

Ergaula stonebut **sp. n.**

Holotype. IGNM FEB RAS ANHM 4/7. Both forewings; type locality, Archara-Boguchan, Belaya Gora locality, stratotype of the Tsagayan Formation, Far East, Russia; type horizon, Tsagayan Formation, Danian.

Diagnosis. Forewing narrow, length/width: 31/11 mm, its venation reduced to approximately 50 veins at margin. Sc branched broadly. Intercalaries distinct, coloration indistinct.

Description. Forewing fore margin slightly arcuate. Sc with both anterior (3 on left forewing, 1 on right forewing) and posterior (4, 4) branches. R more or less regularly branched, with venation more dense towards apex; veins secondarily branched (19, 16). M with secondary branches, curved posteriorly (11, 12). CuA largely simplified, reduced to 3 branches at most. Anal veins sparse (6, 7).

Remarks. *E. stonebut* **sp. n.** differs from *Therea* Bilberg, 1820 (India) (the same tribe) in having costal space comparatively narrow and Sc less expanded and with branches running more longitudinally, M and R reduced to some extent and fused. *Eucorydia* Hebard, 1929 (SE Asia) and *Miroblatta* Shelford, 1906 (Borneo) have exclusively straight stem of R (without any posterior branches), the latter comprises deviant forms with extremely wide forewings, sometimes reduced to some extent. *Homoeogamia* Burmeiser, 1838 is limited to America (Mexico and South America) today.

Ergaula stonebut **sp. n.** can be placed within *Ergaula* by simple exclusion and differs from its congeners only in minor characters. It is generally very similar to *E. atica* from the sediments of Israel (presumably Eocene in age), including the narrowness of forewings with distinct intercalaries and wide space between respective Sc branches (3 symplesiomorphies). *E. atica* also is very large, (forewing length 35 mm). The single preserved individual is distinctly coloured and posses numerous deformations. Undescribed specimens from the Messel, Germany are also very similar (H. Schmied, in preparation).

The *E. stonebut* **sp. n.** forewing is without deformities; it is narrower than in any living species. The type species *E. carunculigera* differs in having a considerably smaller forewing (21–27 / 13.5 mm) (Gerstaecker 1861). *Ergaula. capucina* differs in having all Sc venation dense; *E. pilosa* has dense Sc venation in the anterior region only (Rehn 1951). Males of *E. capensis* are much larger (55–57 mm in total body length) (Hanitsch 1938).

The much smaller forewing of *E. funebris* (forewing length 22 mm: (Hanitsch 1933)) is monochromatic a character likely shared by *E. stonebut* **sp. n.** However, the wing of *E. funebris* is much wider. *Ergaula nepalensis* is unique in having discoidal veins straight and longitudinal (Saussure 1893), and *E. silphoides*, like most living species, has a rounded fore-margin of the forewing (Walker 1868).

Some distinct characters revealed in the course of study of living *E. capucina* are seen in forewing of the present fossil. The most distinct among them are asymmetrical sclerotisation (due to folding of wings over each other) and invagination in the base of R, which represents the huge ventral ridge serving for folding of the hind wing. Visible are also reticulations caused by sclerotisation in the costal area.

Etymology. *stonebut* is derived from some Slavic languages (means something).

Discussion

Based on study of terminal Mesozoic as well as Eocene cockroaches, it follows that most living cockroach genera originated directly at or around PETM (Vršanský *et al.* 2011, 2012b). Warming not only expanded the geographical range and the thermic optimum in more northern latitudes, but also produced conditions different from those present in the original source area. Changes on land resulted in a higher evolutionary tempo as evidenced by cockroaches (Vršanský 2011, 2012ab). Nevertheless, the present observations are direct evidence for the pre-PETM origin of some of cockroach genera, which was unexpected. It is notable that both of the species described herein belong to genera present (as codominants) in the Eocene Messel (47Ma) assemblage of Germany (Schmied 2009, unpublished observation), suggesting the characteristic Eurasian assemblage was already formed before the Paleocene side of the PETM.

Ergaula occurs also in the presumably Eocene or Oligocene mangals of Israel (Anisyutkin *et al.* 2008) and a leathery wing described as *Netherea haatica* Vršanský & Anisyutkin, 2008 seems to represent the smaller female of living *Ergaula*—a common sexual dimorphism of this genus. This associations are likely very similar unless identical in respect to generic content and support the Eocene stage for obscure (originally presumed to be Mesozoic) locality in Israel.

Different were some Eocene North American localities, where predominantly smaller species were preserved (Vršanský *et al.* 2011a, 2012).

Very little can be learned from the geography of the two specimens. *Ergaula* currently is widely distributed in Africa and Asia, but apparently was also present also in Europe in PETM, but absent in the Americas during the Eocene. *Morphna* has a similar wide pattern in Asia (absent in Africa), with occurrence in Europe during PETM.
The important aspect of deformed wings is ambiguous in this respect. While no wing deformation (developmental change modifying wing geometry, most often fusion of veins or irregularity), is reported in hundreds of Eocene individuals from the Green River in Colorado, very few are present in Early Miocene localities. Deformations are common and abundant in more recent fossils and in living cockroaches. The single specimen of *Morphna* from the Paleocene possesses at least one such deformity, which may be stochastic.

Morphna is peculiar also in another respect in that it is not only the earliest occurrence of any living genus, but also the first occurrence of the family Blaberidae. It is possible that the original blaberid genera, representing the most advanced cockroaches of the time, survived with minor modifications to the present. In any case, the traces of plesiomorphies are valuable: branched A, branched Sc and punctuated intercalaries are all characteristics of Mesoblattinidae, and were lost in the initial stage of the evolution of the family Ectobiidae (=Blattellidae). Therefore, it seems likely that Blaberidae originated directly from the extinct Mesoblattinidae, and not from Blattellidae as has been generally accepted (see Djernaes *et al.* 2012). These results do not contradict with living material-based analyses, as Blattellidae are direct descendants of the Mesoblattinidae.

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Native *Ectobius* (Blattaria: Ectobiidae) From the Early Eocene Green River Formation of Colorado and Its Reintroduction to North America 49 Million Years Later

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ABSTRACT *Ectobius kohlsi* sp. n. and three undetermined species of the common Eurasian cockroach genus *Ectobius* Stephens, 1835 are reported from the lower middle Eocene of North America. This species indicates a cosmopolitan distribution of the genus during the mid Paleogene, and supports its current relict distribution in modern north-temperate and African ecosystems. When compared with the living species, *E. kohlsi* was either neutral or plesiomorphic in all characters, but exhibited a close relationship to the extant *Ectobius kraussianus* Ramme, 1923 Species Group in the identical structure of the pronotum. *E. kohlsi* also was similar to extant *Ectobius ticinus* Bohn, 2004, in the character of its wing venation (see Bohn 2004), in particular the forewing vein M, and to extant *Ectobius vittiventris* (Costa 1847) in details of forewing coloration. These latter two species are members of the *Ectobius sylvestris* Species Group (Bohn 1989). *Ectobius balticus* Germar et Berendt, 1856—a conspicuously dominant cockroach from mid-Eocene Baltic amber—also appears plesiomorphic in all characters despite being a few million years younger than *E. kohlsi*. One reason for the complete disappearance of this dominant genus from North America is the peculiar consequence that, after 49 million years, a cool-adapted *Ectobius lapponicus* (L.) was capable of being reintroduced to a significantly cooler North America than that its antecedents which inhabited North America during a warmer European Eocene. Modern *E. lapponicus* is synanthropic in North America, even though no synanthropism is recorded for this species in its native habitat throughout Europe.

KEY WORDS cockroach, Europe, fossil insect, paleoclimate, relict distribution

The global cockroach fauna can be differentiated historically into three distinct phases that collectively form deep and varied evolutionary trajectories. These phases are the late Paleozoic, the Mesozoic, and the Cenozoic; the latter, or modern fauna, is overwhelmingly composed of extant taxa. The late Paleozoic and Mesozoic faunas are characterized by oviposition of isolated eggs through use of an external ovipositor, which was long and prominent in Paleozoic forms and comparatively short to blunt in Mesozoic taxa, with eggs deposited in a conglomeratic fashion. By contrast, the Ectobiidae (=Blattellidae), originating near Jurassic−Cretaceous boundary, and possibly some of their predecessors, the Mesoblattinidae (Vršanský 1997, Wei and Ren 2013), in addition to the entire modern cockroach fauna, are characterized by taxa that lay their eggs within a hardened egg-case, the oötheca. Most Mesozoic families, such as the dominant Blattulidae and Caloblattinidae, disappeared before the K−Pg boundary at the end of the Cretaceous, which responded to a major ecological crisis, at least in North America (Labandeira et al. 2002).

Extant genera of the modern cockroach fauna evolved during the beginning of the Paleogene Period (Vršanský 2002; Vršanský et al. 2002, 2011, 2012, 2013), and after the K−Pg event. The early Paleogene fauna consisted of transitional taxa, predating the origin of most exclusively modern families, but also consisting of uniquely ancestral, extinct, and primitive genera. During the mid-Eocene, rare Mesozoic relicts such as the Mesoblattinidae and Skokidae persisted, although at that time most other taxa were affiliated modern families and genera. It was during the latest early Eocene that the genus *Ectobius* appears in the Palearctic fossil record of Baltic amber (Statz 1939) as a dominant species. As it now turns out, this also is the time interval of the earliest record of the genus in the Nearctic.

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Materials and Methods

Our study accessed specimens from the Parachute Creek Member of the Green River Formation, in the Piceance Creek Basin, in Garfield County, northwestern Colorado, ≈20 km west of Rifle, and in cliffs overlooking the Colorado River. The material originates from the upper portion of the Parachute Creek Member, a regionally ponded lacustrine deposit characterized by a distinctive organic-rich "mahogany zone" that is 20–60 m thick, which extends throughout the Basin and serves as a stratigraphic reference datum at ≈48.8 million years old (Ma), to which insect-bearing subjacent localities can be compared (Smith et al. 2010). The Parachute Creek Member consists of evaporates and especially laminated, organic-rich, often kerogenous, shales, and fine-grained siltstones (Hail 1992). A recent study (Smith et al. 2010) analyzing the "Curly tuff" immediately below the mahogany zone yielded a ^{40}Ar/^{39}Ar age date with a weighted mean value of 49.02 ± 0.30 Ma with a ± 2σ error margin (Smith et al. 2010). These results suggest a date of 49 Ma for the collective insect deposits mentioned herein, which would vary minimally, attributable to their subtle variation in stratigraphic position from the 49 Ma data. This date is equivalent to the latest Ypresian Stage of the early Eocene Epoch (Gradstein et al. 2012).

Although insect fossils were frequently revealed along splits in the bedding planes, additional preparation of occluding matrix by thin needle-like picks was necessary in most instances for further preparation. Prepared specimens were photographed with an Olympus SZH stereomicroscope attached to an Olympus 5060 camedia camera with 5.1 megapixel storage capability. Lighting was provided by a fiber-optic illuminator with plane polarized light and a fluorescent-style ring light to occasionally capture cuticular details. Images of specimens were taken with and without ethanol immersion, the latter to enhance specimen contrast with the surrounding rock matrix. Characters were polarized based on the genus *Symploce* Hebard, 1916, which is one of the basalmost and primitive living representatives of the family Ectobiidae (Vršanský 1997, Klass 1997, Vršanský et al. 2011). Venational nomenclature follows Comstock and Needham (1898); Vršanský (1997); Rasnitsyn (2002); and Vršanský et al. (2012, 2013).

Results

Blattaria Latreille, 1810 (=Blattida Latreille, 1810 = Blattodea Brunner von Wattenwyl, 1882)

Ectobiidae Brunner von Wattenwyl, 1865

Ectobius Stephens, 1835

Type Species. *Blatta lapponica* L., 1758 (=*Blatta lapponicus lapponica*).

Ectobius kohlsi Vršanský, Vidlička et Labandeira, sp. nov.

(Figs. 1–3)

HOLOTYPE. 41679/53274; a complete female. Deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC.

Type Horizon. Green River Formation, lower middle Eocene, equivalent to the latest early Eocene (Gradstein et al. 2012).

Type Locality. Piceance Creek Basin, ≈20 km west of Rifle, northwestern Colorado.

Additional Material. 41075/27701; 25971+-, 31499; 41228; 41087/105061+-; 41088/25457; 41093/75726; 41142/55491; 57239; 57545; 58123; 41222/27865; 41225/30376; 41227/137007+-; 41236/139337; 41237/147735; 41679/53476, 52833; 41822/53843; SAV97/147911. The general locality for the additional material is the same as the type, although specimens were taken from several stratigraphically adjacent horizons.

Differential Diagnosis. A new species most closely resembling *Ectobius bruneri* Seoane, 1879, superficially with partially punctate pronotum, identical coloration, and three, characteristically large maculae (a plesiomorphy). It differs in M fused with the R (an apomorphy). Same venation in *E. kohlsi* occurs in *Ectobius ticinus* Bohn, 2004, possessing a separate and distinct M vein (a plesiomorphy).

Description. Head coloration as in Figs. 1 and 2. Antennae delicate; long, at least 6.5 mm; and 0.7 mm wide. Pronotum transverse; width 1.3 mm, length 1.9 mm, nearly ovoid; distinctively colored (Fig. 2). Forewing (length 5.9–6.0 in females, and 6.5 in males), with R vein expanded, reaching the proximal part of apex. M vein separated from R apically; reduced to a simple vein. CuA vein expanded and fused directly to main R branch. Coloration with characteristic dark dots and four, large, dark maculae; apex veins pale, with dark margins. Hindwing angulate, tip somewhat rounded and colored in posterior aspect. Body width 2.5–3.0 mm.

Comparisons. The present species is assigned to the extant, exclusively Eurasian and African genus, *Ectobius*, based on characteristic forewing venation, including coloration (Figs. 1–3). The specimen significantly differs from the extant subgenus *Ectobiola*, such as *Ectobius duskei* Adelung, 1904, which has numerous dark spots on the forewing, the absence of punctae on the pronotum, and possession of a characteristic horseshoe-like pattern of coloration on the forewing. Females bear reduced wings. Owing to a zone of distinct coloration, *Ectobiola* is linked to the *Ectobius lapponicus* (L.) Species Group by an autapomorphy consisting of a sharp, pronotal posterior margin; dark maculae investing the R vein; and slender punctation expanded to the entire surface of the wing. We suggest that *Ectobiola* is distantly related to the extant species, *Ectobius tuscus* Galvagni, 1978, which has a pronotum with sparse punctation, short forewings, and an odd, reduced venation with large, numerous maculae, perhaps indicating that this latter taxon should be referred to a separate derived species group not closely related to the present species.

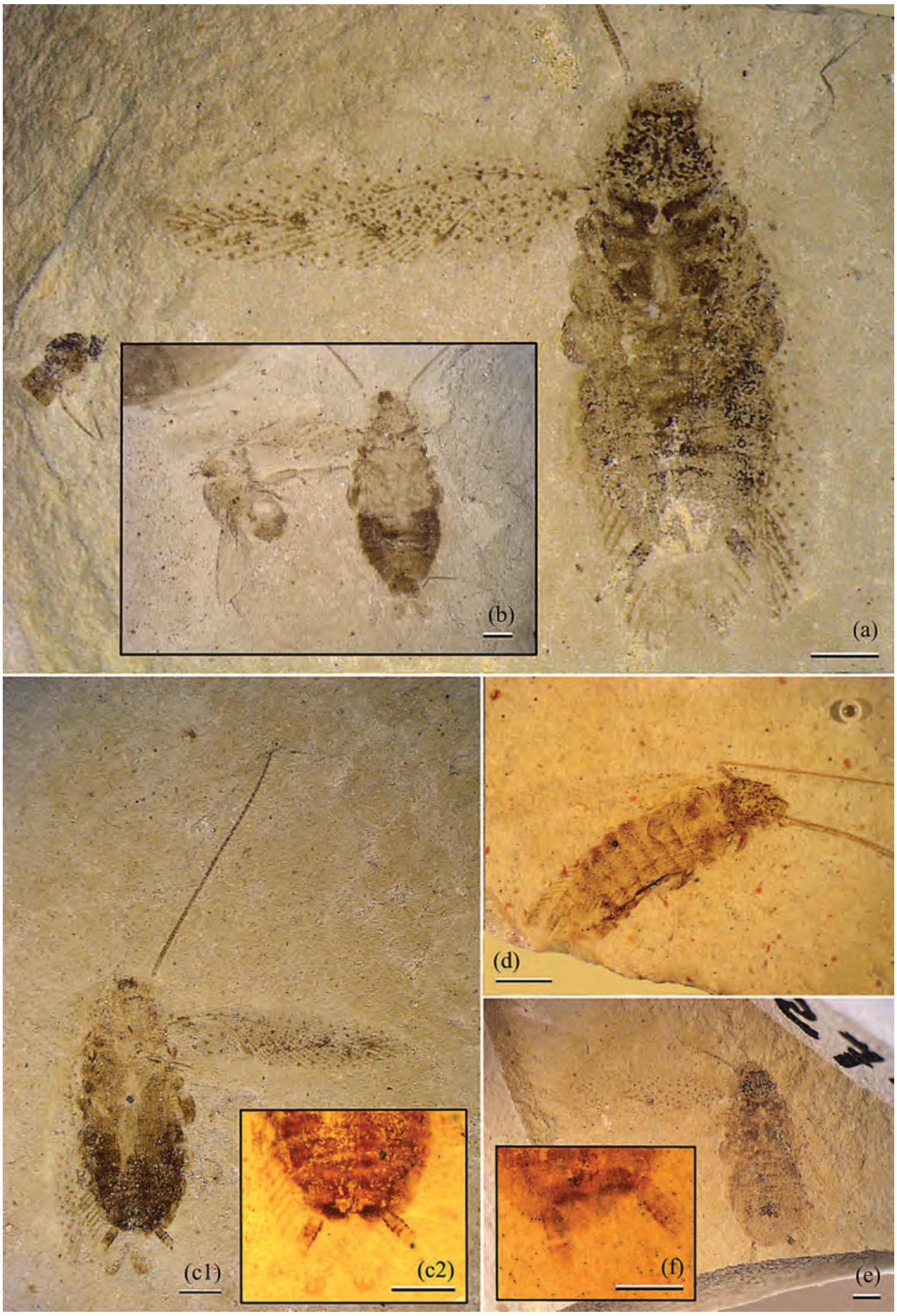

Fig. 1. *E. kohlsi* Vršanský, Vidlička et Labandeira sp. n. (a) HOLOTYPE. 41679/53274; negative relief; complete female specimen. (b) 41142/57545; positive relief; complete male specimen. (c1–2) 41142/57239; positive relief, complete female specimen and detail of terminalia. (d) 41075/27701 (negative, sex unknown). (e) 41679/53274; ?positive relief, probable female. (f) 41142/58123; detail of female terminalia. All specimens are deposited at the National Museum of Natural History (NMNH), Washington, DC. C2, d, and f photographed under alcohol immersion. The material is from the Green River Formation, of latest early Eocene age; Piceance Creek Basin, Northwestern Colorado. Scale bars represent 1 mm.

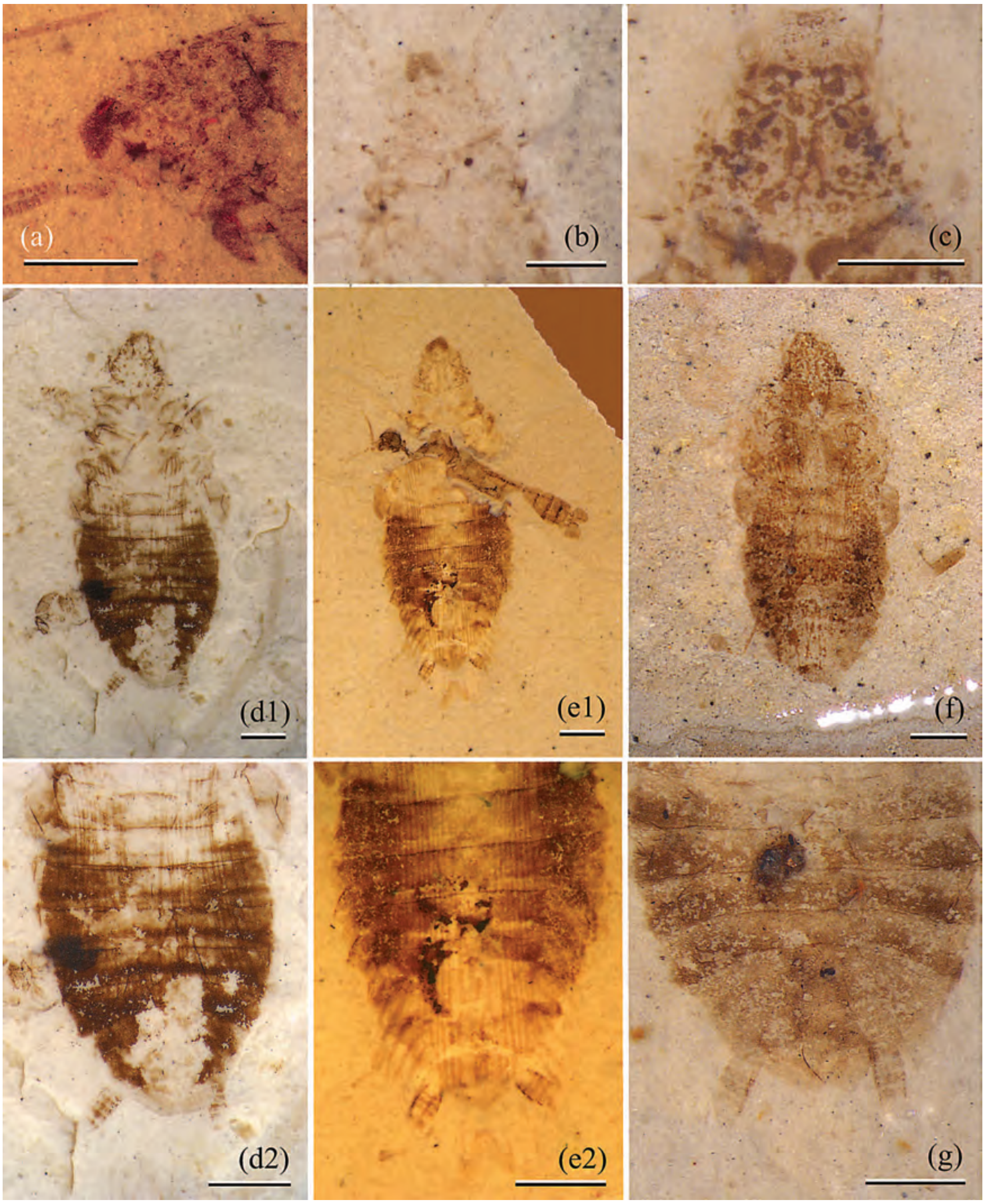

Fig. 2. a–g, *E. kohlsi* Vršanský, Vidlička et Labandeira sp. nov. (a) 41075/27701; positive relief; detail of head and pronotum. (b) 41142/57545; positive relief; male specimen with pronotum. (c) HOLOTYPE. 41679/53274; negative relief, female specimen with pronotum. (d1–2) 41093/75726; positive relief; female specimen. (e1–2) 41087/105061; positive relief; male specimen. (f) 41075/25971; positive relief; female specimen. (g) 41088/25457; negative relief, female specimen, with detail of terminalia. All specimens deposited in the NMNH, Washington, DC, Green River Formation, latest early Eocene. All specimens photographed while immersed under alcohol, and originate from Green River Formation, northwestern Colorado. Scale bars represent 1 mm.

Another extant apomorphic species is *Ectobius semenovi* Bei-Benko, 1935, bearing an extremely enlarged pronotum without punctuation and monochromatic forewings. Another aberrant species is *Ectobius tadzhicus* Bei-Bienko, 1935, with pronotal coloration and extremely shortened wings similar to that of *Ec-*

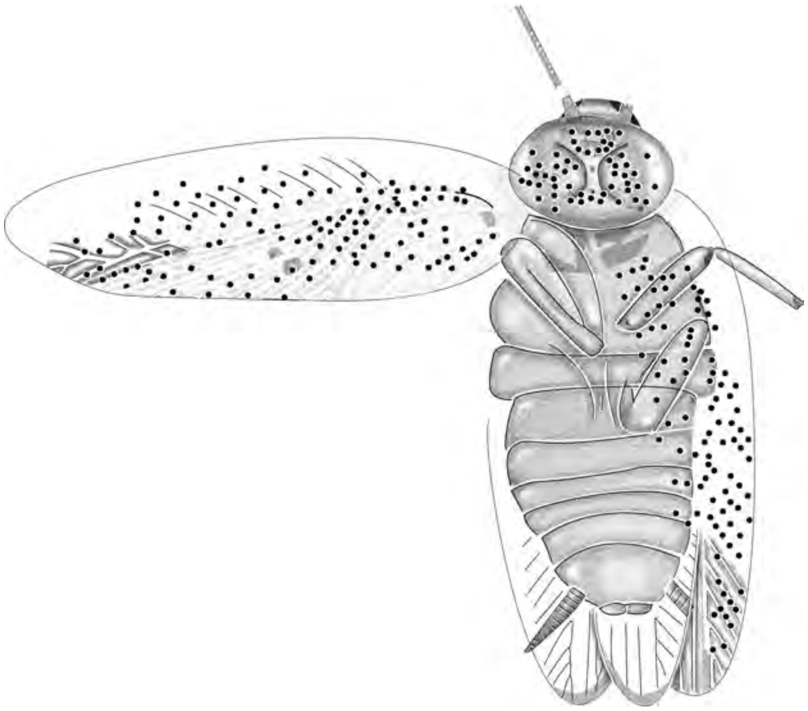

Fig. 3. *E. kohlsi* Vršanský, Vidlička et Labandeira n. sp. HOLOTYPE. 41679/53274; A complete female. The repository is the NMNH, Washington, DC, Green River Formation, latest early Eocene, Piceance Creek Basin, northwestern Colorado. Dots correspond to dorsal sensilla. Negative compression; the right forewing is outstretched; length 5.9 mm.

tobiola duskei. The Subgenus *Capraiellus* of the *Ectobius panzeri* Stephens 1835 Species Group is similar to the present species, possessing punctae, pronotal darkening, a horseshoe-like pattern of coloration and short female forewings, similar to *Ectobiola.* The *Ectobius corsorum* Ramme, 1923 Species Group, is a more derived lineage that has a punctate pronotum with a sharply curved posterior margin, and spots on forewings that are placed more basally than other taxa. The *Ectobius minutus* Failla et Messina, 1977, Species Group is related to *Ectobius montanus* (Costa 1866), the *Ectobius sylvestris* Species Group (Bohn 1989) and *Ectobius friesanus* Princis, 1963, all of which have similar glands, but differ in sensillar distribution, the shape of the cerci and the presence of a boss at the center of glandular pits. *E. friesanus* may deserve placement in a separate species group but is not directly related to the present species.

Instead, *E. kohlsi* possesses a combination of characters that occur in two lineages. The first lineage is the *Ectobius kraussianus* Ramme 1923 Species Group, such as *Ectobius lagrecai* Failla et Messina, 1981, and *Ectobius aetneus* Ramme, 1927, whose venation differs in having a punctate forewing radial area. The pronotum in this species group has characteristically dense punctae, and two, symmetrical, arcuate ridges identical in some individuals to those found in the present species. The second lineage is the *E. sylvestris* (Poda 1761) Species Group that lacks pronotal punctae, although the forewing venation (Fig. 4) is nearly identical with the new species (Fig. 1). *E. sylvestris* females differ in having shortened wings, and in the form and coloration of the pronotum. The most similar character to the present species is venation, also occurring in *E. ticinus*, with a separate and distinct M vein (a plesiomorphy). *E. sylvestris* also is similar in pronotal ridge features, but strongly differs by having brachypterous females (an apomorphy; Fig. 4). *E. bruneri* has a partially punctate pronotum, but the M is fused with the R (an apomorphy). Coloration is identical to the present species, bearing three, characteristically large maculae (a plesiomorphy), but with an unseparated M (an apomorphy). In *E. vittiventris* (Costa 1847, Baur et al. 2004), the females have distinct, long wings (a plesiomorphy; Figs. 4 and 5). By contrast, extinct *E. glabelus* Statz, 1939, from the Oligocene of Rott-am-Siebengebirge, differs in having rather angulate forewings. *Ectobius balticus* Germar et Berendt, 1856, from middle Eocene Baltic amber, possesses all characters, including pronotal morphology and coloration, which resembles the most basal Ectobiidae (Fig. 6) (Germar and Berendt 1856).

Undescribed species, presumably assignable to *Ectobius*, also are present in middle Eocene strata of Messel, in central Germany (Schmied 2009), of age slightly younger than *Ectobius* mentioned in this report.

Remarks. An investigation of a single population of living males of *E. sylvestris* in Slovakia revealed female brachyptery (Fig. 4), a broad variability of forewing area (Coefficient of Variation = 13.36%, $n = 41$), a distinctive venational pattern (Fig. 4), and a distinc-

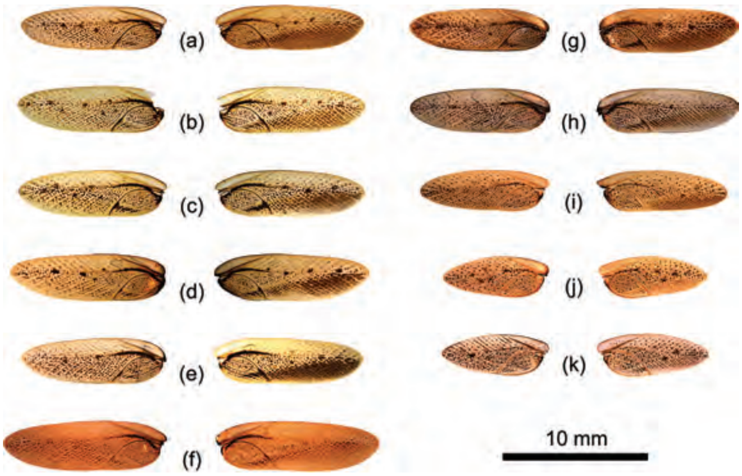

Fig. 4. (a–k) Modern forewings of one population of males of *E. sylvestris* males, occurring at Jur, near Bratislava, Slovakia. Collection of the Zoological Institute SAS, Bratislava. Specimens Es01/1–26/2.

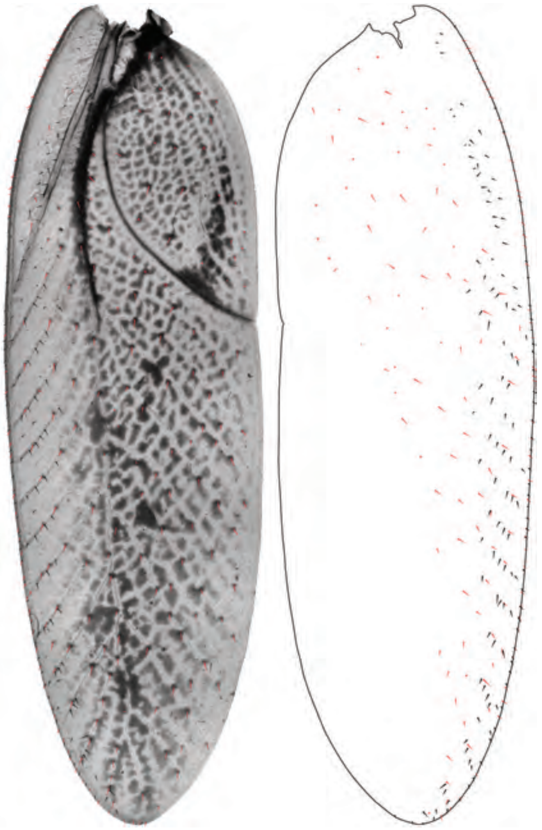

Fig. 5. Left and right forewing of the sensillar system of a modern male of *E. sylvestris*, from Jur, near Bratislava, Slovakia. The collection is from the Zoological Institute SAS, Bratislava. Specimen Es1–2. Black dots represent ventral sensillae; red dots are dorsal structures providing for the presence of dorsal sensilla exclusively on dark dots. The right wing is missing dorsal sensilla in area overlapped by the left wing.

tive pattern of sensillar distribution on both surfaces of fore- and hind wings (Fig. 4) (Quercetum Mtns. of Jur, Slovakia, collected in 2008 by O. Majzlan and L'. Vidlička). Another analysis revealed the presence of dorsal mechanoreceptors on minute dark maculae, which correspond to dark dots preserved on the forewing surface of the new species (Fig. 3). Surprisingly, except for microscopic openings (punctae) on the ventral side, there are no macroscopic sensilla on posterior three-quarters of the wings.

Etymology. The species designation honors David Kohls, a collector of considerable Green River fossil insect material deposited at the National Museum of Natural History, in Washington, DC.

Character of Preservation. Twenty-one complete specimens; five with wings, and one laterally preserved.

Discussion

Living species of the genus *Ectobius* appear as relicts of a richer, ancient fauna that are closely related to European Oligocene species. Currently, only *E. sylvestris* and *E. lapponicus* are widely distributed throughout the forested Palearctic Region (Zherikhin 1970). However, during the Eocene, the genus *Ectobius* apparently was widely distributed in the Palearctic as well as in the Nearctic. In North America, it became extinct and typically was not replaced by other cockroach taxa. Within the United States, similar cool-temperate habitats were colonized within the past several decades by *Parcoblata* cockroaches (12 species), preferring forests under bark. Other *Ectobius* species have been found in association with herbaceous vegetation, such as tansy, *Tanacetum vulgare* L. (Asteraceae), in coastal New Hampshire, with males predominating in a sex ratio of ≈2:1. Adults of this species were seen at or near the crowns of various plants and on flowers or leaves, but when disturbed, quickly dropped to the ground (Chandler 1992).

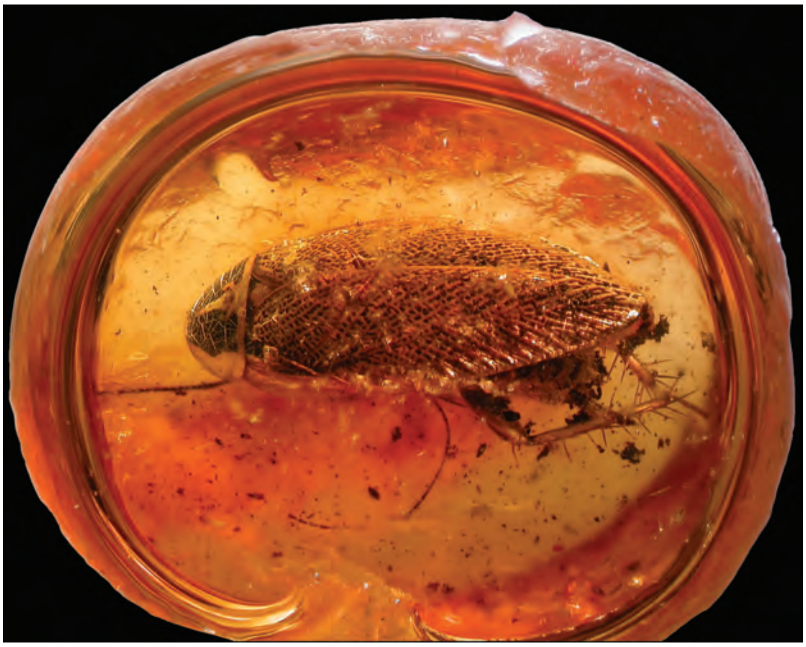

Fig. 6. *E. balticus* Germar et Berendt, 1856, from the early middle Eocene Baltic amber. Gusakov collection no. VI-008. Original image courtesy of D. S. Shcherbakov.

Nielsen (1987) found individuals on flowers of wild raspberries, *Rubus idaeus* L. (Rosaceae). By contrast, in Europe, nymphs and adult males of the "dusky cockroach" are found on low lying vegetation, with adult females commonly found on the ground in leaf litter (Roth and Willis 1960).

The reintroduction of *Ectobius* into the United States after 49 million years is peculiar. *E. sylvestris* was established in the northeast United States (Hoebeke and Nickle 1981); *E. pallidus* also was established in the Northeast and, in addition, the Midwest; and *E. lapponicus* as well became a denizen of the Northeast (Atkinson et al. 1991, Chandler 1985, 1992). In particular, *E. pallidus* appears to have been established in Massachusetts sometime in 1951, and it occurs in houses and other domestic effects surrounding human habitation (Helfer 1987). In 1984 the "dusky cockroach," *E. lapponicus,* was found in southeastern New Hampshire by Chandler (1985), the first North American record of this European immigrant. A subsequent collection in eastern Vermont was noted by Nielsen (1987), and this species has now been collected repeatedly in coastal and central New Hampshire (Chandler 1992). *Ectobius lucidus* was reported recently from the eastern United States (Hoebeke and Carter 2010). Interestingly, these reintroduced species in the United States are associated with human habitation and thus possess synanthropic behaviors. By contrast, no synanthropism was recorded for the same species throughout their native European habitats, and only rare cases of building infestation are known from Europe (Mielke 2000).

During the latest middle Eocene, at least four distinct species that significantly differed in size were present at the various Green River localities of Colorado. Of these species, three were poorly preserved and larger than *E. kohlsi*, but remain undescribed. (These specimens are represented by preliminary specimen numbers 41088/26584, 41221(2)/27865, and 41221/87663.) However, it is impossible to conclude whether these additional species occurred contemporaneously with *E. kohlsi* or otherwise were allopatric. The reasons for the disappearance of *Ectobius* from the North American continent remain obscure. A temperature change is known to be responsible for a similar pattern of extinction and after human-based reintroduction in some aquatic organisms (Strasser 1998). Cooling could be responsible for the extinctions of diverse *Ectobius* taxa in North and Central America, as the thermophilic representatives of the genus have specialist associations and have a high degree of endemism in contrast to more northerly, widely distributed European generalists (Vidlička and Sziráki 1997, Bohn 2004, Scholczová 2013). Nevertheless, the current distribution of *Ectobius* from northernmost Europe extends southward to the southernmost Africa, with a latitudinal biogeographical discontinuity along an equatorial belt (Bei-Benko 1950), suggesting that a warming temperature change would enable survival of the genus in the southern North and Central America in the near future.

In the late early Eocene Green River ecosystem, *E. kohlsi* had a similar wing size for both sexes (a plesiomorphy), with females of slightly smaller size than males, the difference being <1 mm. Representation of both sexes is roughly equal in the fossil population, indicating similar flight activity. This condition contrasts to living representatives of the genus, wherein the sex ratio is variable but different from equality. Such a nonequilibrial sex ratio perhaps is associated with conspecific males involved in active flight.

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Latiblattella avita sp. nov. (Blattaria: Ectobiidae) from the Eocene Kishenehn Formation, Montana, USA

Dale E. Greenwalt and Ľubomír Vidlička

ABSTRACT

Latiblattella avita Greenwalt and Vidlička, 2015, sp. nov., and the first fossil of the genus, is described. The discovery of a fossil representative of this genus suggests that *Latiblattella* was more widely distributed in the Eocene. The Eocene American cockroach fauna is mostly comprised of what are today, cosmopolitan genera while the extant genus *Latiblattella* Hebard, 1917 is restricted in its geographical distribution to Central America, Mexico, Florida and Arizona. The discovery of *Latiblattella avita*, in combination with the recent description of *Cariblattoides labandeirai* Vršansky et al., 2012, also documents the presence of rather derived representatives of the family Ectobiidae as early as the Middle Eocene.

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Keywords: Fossil insect; Cenozoic cockroaches; Pseudophyllodromiinae; new species

INTRODUCTION

Cockroaches form one of the taxonomically smaller insect orders with only about 5,000 living species, the majority of which are found in tropical forests (Vidlička, 2001; Vršanský et al*.*, 2002; Roth, 2003; Grimaldi and Engel, 2005; Beccaloni and Eggleton, 2013). This contrasts with the high diversity of ecological and behavioral niches occupied by this clade, as exemplified by the recent discoveries of eusocial, jumping, aquatic, extinct predatory, pollinating, troglobitic and luminescent species (Vishniakova, 1973; Zompro and Fritzsche, 1999; Bohn et al., 2010; Vršanský, 2007; 2010; Vršanský and Chorvat, 2013 – but see Greven and Zwanzig, 2013). Extinct species number over 1,000 but nearly 80% of these are Paleozoic "roachoids" (Mitchell, 2013). The modern cockroach fauna is thought to have evolved immediately after the Cretaceous-Paleogene boundary (Vršanský et al., 2002, 2011, 2012, 2013) although only 53 fossil species have been described from the Cenozoic era (Mitchell, 2013; Arillo and Ortuño,

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palaeo-electronica.org/content/2015/1118-new-eocene-cockroach

TABLE 1. The Cenozoic fossils of Ectobiidae.

Subfamily*	Genus	Species	Epoch	Location	Reference
Anaplectinae	*Anaplecta*	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Blattellinae	*Ischnoptera*	sp.	Miocene	Chiapas amber (Mexico)	Solórzano Kraemer, 2007
Blattellinae	*?Symploce*	*rete*	Pleistocene	African copal	Gorochov, 2007
Ectobiinae	*Agrabtoblatta*	*symmetrica*	Pleistocene	African copal	Gorochov, 2007
Ectobiinae	*Ectobius*	*arverniensis*	Paleocene	Menat (France)	Piton, 1940
Ectobiinae	*Ectobius*	*balticus*	Eocene	Baltic amber	Germar and Berendt, 1856
Ectobiinae	*Ectobius*	*menatensis*	Paleocene	Menat (France)	Piton, 1940
Ectobiinae	*Ectobius*	*glabellus*	Late Oligocene	Rott (Germany)	Statz, 1939
Ectobiinae	*Ectobius*	*kohlsi*	Early Eocene	Green River (USA)	Vršanský et al., 2014
Ectobiinae	*Ectobius*	spp. (3)	Early Eocene	Green River (USA)	Vršanský et al., 2011
Ectobiinae	*Isoplates*	*longipennis*	Middle Eocene	Gieseltal (Germany)	Haupt, 1956
Ectobiinae	*Telmablatta*	*impar*	Middle Eocene	Gieseltal (Germany)	Haupt, 1956
Nyctoborinae	*Nyctibora*	*elongata*	Late Oligocene	Rott (Germany)	Statz, 1939
Pseudophyllodromiinae	*Cariblatta*	spp. (2)	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiina	*Cariblattoides*	*labandeirae*	Early Eocene	Green River (USA)	Vršanský et al., 2012
Pseudophyllodromiina	*Euthlastoblatta*	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiinae	*Latiblattella*	*Avita* sp. nov.	Middle Eocene	Kishenehn Formation (USA)	Vidlička and Greenwalt (This study)
Pseudophyllodromiinae	*Plectoptera*	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiinae	*Plectoptera*	*electrina*	Miocene	Haitian amber	Gorochov, 2007
Pseudophyllodromiinae	*Pseudosymploce*	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiinae	*Supella*	*miocenica*	Miocene	Chiapas amber (Mexico)	Vršanský et al., 2011
*Subfamily assignments based on Beccaloni (2014)					

2005; Solórzano Kraemer, 2007; Gorochov, 2007). Undescribed material includes that presently studied from the Green River (e.g., the genera *Blattella* Caudell, 1903, *Namablatta* Rehn, 1937, *Diploptera* Saussure, 1864, *Sigmella* Hebard, 1940 and *Symploce* Hebard, 1916) in Colorado (Vršanský et al., 2011, 2012).

The most speciose family within Blattaria is Ectobiidae (= Blattellidae) with approximately 2,400 species in about 220 genera (Beccaloni and Eggleton, 2013). *Ectobius* Stephens, 1835 and *Phyllodromica* Fieber, 1853, two genera in the subfamily Ectobiinae, provide most of the extant cockroach diversity in the Palaearctic (Bohn et al., 2013). Ectobiidae, which originated from the family Mesoblattindae, first appeared in the Early Cretaceous and became dominant during the Cenozoic (Vršanský, 1997; 1999; 2002; Anisyutkin et al., 2008; Wei and Ren, 2013). Fifteen different genera and 13 described and a number of undescribed species representing all five subfamilies of Ectobiidae have been reported in the Cenozoic record (Table 1). Of these, 10 genera have been reported from the New World with the majority, seven, in

Miocene amber from either Mexico or Hispaniola. Only *Cariblattoides labandeirae* Vršanský et al., 2012 and *Ectobius kohlsi* Vršanský et al*., 2014* from the Green River Formation in Colorado*,* and *Latiblattella avita* Greenwalt and Vidlicka, 2015 sp. nov. from the Kishenehn Formation in Montana, are from North American Eocene deposits.

Dates of the Coal Creek Member of the Kishenehn Formation of northwestern Montana have been estimated to be 46.2 ± 0.4 Ma (middle Eocene) by ^{40}Ar/^{39}Ar analysis and 43.5 ± 4.9 Ma by fission-track analysis (Constenius, 1996). Deposition of the fossiliferous deposits of the middle sequence of the Coal Creek Member occurred in a shallow near-shore setting that exhibited little or no water flow in a seasonal subtropical/tropical environment (reviewed in Greenwalt et al., 2015, in press). The Kishenehn fossil insect fauna is quite diverse with 15 different orders identified to date although only a single specimen (USNM 595139) out of 6,558 is from the order Blattaria (Greenwalt et al., 2015, in press).

MATERIALS AND METHODS

Specimen USNM 595139 was collected at the Dakin site on the Middle Fork of the Flathead River near Pinnacle, Montana in 2013 in accordance with USFS Authorization HUN281. The piece of oil shale that contained the fossil also contained a fossil notonectid (Heteroptera) and a leg of a tipulid (Diptera). The specimen was photographed with an Olympus SZX12 microscope equipped with a Q-Color5 Olympus camera. Image-Pro Plus 7.0 software (Media Cybernetics, Inc., Bethesda, MD) was used to capture and record the images. The specimen was immersed in 95% ethanol for examination and photography. Measurements were made with the Image-Pro Plus 7.0 software. All measurements are in millimeters (mm). Venational terminology is from Vršanský (1997) as originally developed by Comstock and Needham (1898).

SYSTEMATIC PALEONTOLOGY

Order BLATTARIA Burmeister, 1829 (= Blattariae
Latreille, 1810; = Blattodea Brunner von
Wattenwyl, 1882)
Family ECTOBIIDAE Brunner von Wattenwyl, 1865
Genus LATIBLATTELLA Hebard, 1917

Type Species. *Latiblattella rehni* Hebard, 1917

Diagnosis of the genus (after Hebard, 1917), relevant material only. Size moderately large to medium, form moderately broad to very broad, for the group. Tegmina (in fully developed condition, found in numerous species only in the male) delicate, moderately broad, with costal and sutural margins straight and subparallel in greater part, scapular field very broad; discoidal (radial) sectors numerous (usually, including their branches, eight to ten), moderately oblique. Ventral margins of median and caudal femora supplied with elongate, moderately stout spines. First three tarsal joints supplied distad with small pulvilli, brief ventral surface of fourth joint occupied by a pulvillus. Moderately large arolia present.

Latiblattella avita sp. nov.
(Figures 1-3)

zoobank.org/7225896D-EC71-4088-8B05-008C85F3A7B6

Etymology. The new species name is derived from the latin avitus meaning ancient or ancestral.

Holotype. USNM 595139; a fragment containing an intact tegmen attached (?) to an intact middle leg. Deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia.

Type Horizon. Kishenehn Formation, middle Eocene (Lutetian).

Type Locality. Dakin site, Middle Fork of the Flathead River, near Pinnacle, Montana.

Differential Diagnosis. The significantly less oblique radial sectors of the tegmen of *Latiblattella avita* sp. nov. distinguish it from species in the closely related genera *Neoblattella,* Shelford, 1911 and *Lupparia* Walker, 1868. Species of the genus *Balta* Tepper, 1893 differ from *Latiblattella* in having a protruded clavus. In addition, the marginal and scapular fields of the tegmina are narrower in *Latiblattella* than those in *Eoblatta* Shelford, 1911 (=*Balta* Tepper, 1893; synonymized by Roth, 1990)*. L. avita* differs from most living representatives of the genus *Latiblattella* in having a basally forked, wide and darkly pigmented *Sc* vein as well as a more pronounced coloration.

Description. Tegmen (forewing) elongated, 15.1 mm long and 4.4 mm wide (width measured at the distal terminus of the anal field) with a length/width ratio = 3.40. *Sc* wide and heavily pigmented, arcuate basally with a slight inflection near the anterior margin of the tegmen (Figure 1). Basal of *Sc*, the tegmen is mottled with black pigmentation (Figures 2, 3.1). *Sc* itself is 4.75 mm long and 0.45 mm in width at the point where it diverges from *R*, and extends to a point about 66% of the length of the anal field. *Sc* has no anterior branches. The humeral field is 4.79 mm long, arcuate basally and without anterior branches. *Sc* has a single posterior branch which diverges from *Sc* at a point

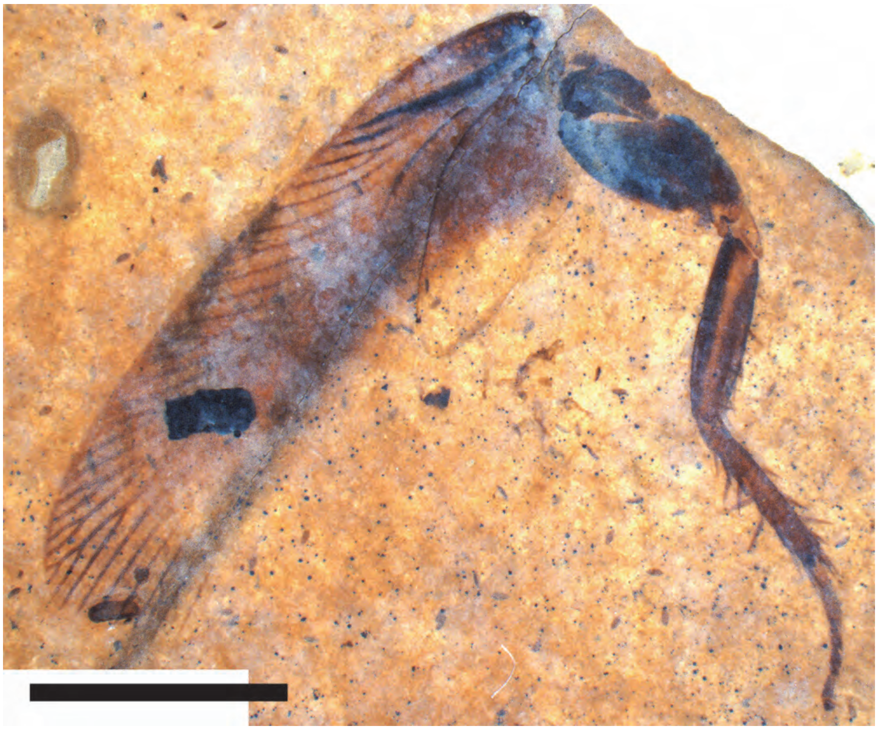

FIGURE 1. *Latiblattella avita* sp. nov. (USNM 595139). Tegmen attached (?) to an intact middle leg. Scale bar equals 5 mm.

approximately 1/2 the distance from its origin; this vein is heavily pigmented and is 2.18 mm long and 0.12 mm wide. Both *Sc* and its single branch reach the wing's margin. The basal portion of the radius is distinctly curved and is pigmented to a point 4.5 mm from the wing's base. There are 10-12 apical branches of the radius – the origins of these branches are not preserved. These branches are oblique, evenly spaced and approximately half of them are branched. The apical radial branches are complexly branched and, with the anterior branches of *M,* parallel to subparallel to the anterior margin of the tegmen. Overall number of *R* branches meeting margin is 26. Posterior branches of *M* and those of *Cu* subparallel to the tegmen's longitudinal margin. The radial field is 8.5 mm long. The apex of the tegmen is evenly curved. Intercalated veins and crossveins are invisible throughout the membrane. The anal field is 6.58 mm long and 2.51 mm wide at its widest point and contains at least 10 near parallel simple longitudinal veins. The plical furrow is subangulate and pigmented basally. The plical notch is distinct although the posterior margin of the tegmen is poorly preserved. The tegmen is brown in coloration, more darkly brown within a wide longitudinal stripe along the central part of the wing with the margins of the wing lighter in color. The anal field is dark brown except for the postero-apical third which is essentially the same color as the shale matrix. Given the poor preservation of the posterior tegminal margin, the distribution of color may have been affected by taphonomic processes. Given the length of the tegmen of this specimen, the insect may have been a male (see Discussion).

In cockroaches, the dorsal aspect of the base of the coxa is very closely apposed to the base of the forewing and, given its size and association with the forewing, the leg of this fossil may be a mesothoracic appendage (Figure 1). It is 13 mm in total length. The coxa, which is attached to the preserved thoracal-coxal joint, is 4.05 mm long, 2.14 mm wide and black/dark brown in color. The basal portion of the coxa and the trochanter are light brown. The trochanter is triangular in shape, 1.13 mm long, 0.80 mm wide and overlaps the basal femur by about 0.5 mm. Its shape resembles that of Ectobiinae [vs. species in Blattellinae (Bazyluk, 1977)]. The femur is brown in color, slightly fusiform in shape, 3.76 mm long and 1.0 mm wide. Its posterior margin contains seven or eight relatively short spines approximately 0.4 mm long and 0.04 mm wide, mostly on the apical half of the femur. The tibia, also brown in color, is 3.3 mm long and slightly wider apically (0.49 mm vs. 0.56 mm). The tibia contains 14 visible spines, evenly distributed

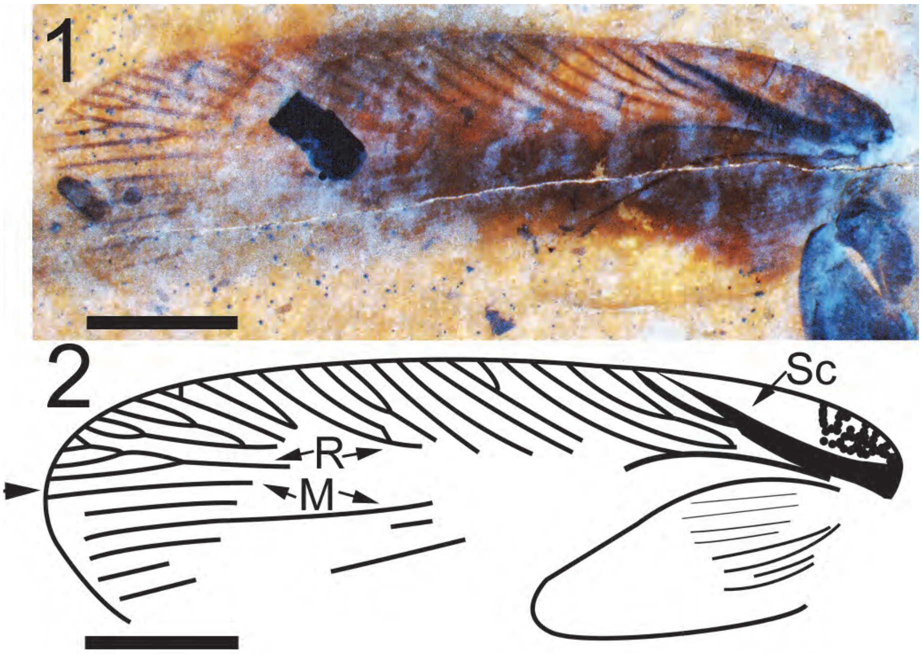

FIGURE 2. *Latiblattella avita* sp. nov. (USNM 595139). 2.1. A photograph of the tegmen. 2.2. A line drawing of the forewing venation. The arrow denotes the boundary between the radial and medial fields. M, medial veins; R, radial veins; Sc, subcostal vein. Scale bar equals 3 mm.

over its length, 0.8 mm long and 0.08 mm wide. Four of the tibial spines originate at the terminus of the tibia and lie parallel to the first tarsal segment (Figure 3.2). The dimensions of the five tarsal segments are 1.3 mm x 0.31 mm, 0.5 mm x 0.2mm, 0.35 mm x 0.22 mm, 0.2 mm x 0.2 mm and 0.46 x 0.17 mm increasing distally to 0.24 mm wide. T1, T2 and T3 have triangular distal extensions, which may contain remnants of tarsal pads (pulvilli). T4 is bilobed basally, as in Ectobiinae [vs. species in Blattellinae in which the apical and basal margins are parallel (Bazyluk, 1977)]. The single asymmetrical claw that is preserved/visible is approximately 0.36 mm long. The arolium is about 0.2 mm in length and black/dark brown.

DISCUSSION

Assignment of the New Species to the Genus *Latiblattella*

The present specimen is categorized within the genus *Latiblattella* based on the generally unspecialized appearance of the comparatively robust leg, including an asymmetrical claw, nearly identical venation of tegmen with branched *Sc*, short, pigmented and distinctly curved *R*, more or less straight *M* and *CuA*, very distinct and arcuate boundary between clavus and rest of the tegmen. It differs from the related genera *Eoblatta* and *Supella* Shelford, 1911 in the decidedly less strongly oblique radial sectors of the tegmen. In addition, the marginal and scapular fields are narrower in *Latiblattella* than those in *Eoblatta*. It differs from the related genera *Neoblattella* and *Lupparia* in the degree of the obliqueness of the radial sectors of the tegmen; those of *Latiblattella* are decidedly less oblique. The closely related genus *Balta* is characterized by a protruded clavus, a morphological character absent in *Latiblattella*. Nevertheless it is necessary to note that the present specimen has coloration and general appearance somewhat similar to *Lupparia adimonialis* Walker, 1868 (see plate 1, figure 12 in Shelford, 1908) suggesting a close relationship to the colored representatives of *Latiblattell*a such as the present species. The present specimen is, in contrast to living representatives of the genus, somewhat coloured, but coloration varies greatly within the related cockroach genera. For example, *Balta* varies from completely colorless to strongly coloured species. The number of veins falls within the variation of the genus (see Rehn, 1951; Brunner von Wattenwyl, 1865). Branching of *Sc* occurs within the genus, although the basal branching is considered to be a plesiomorphy (i.e., present in ancestral Mesoblattinidae) (Vrsansky et al., 2002).

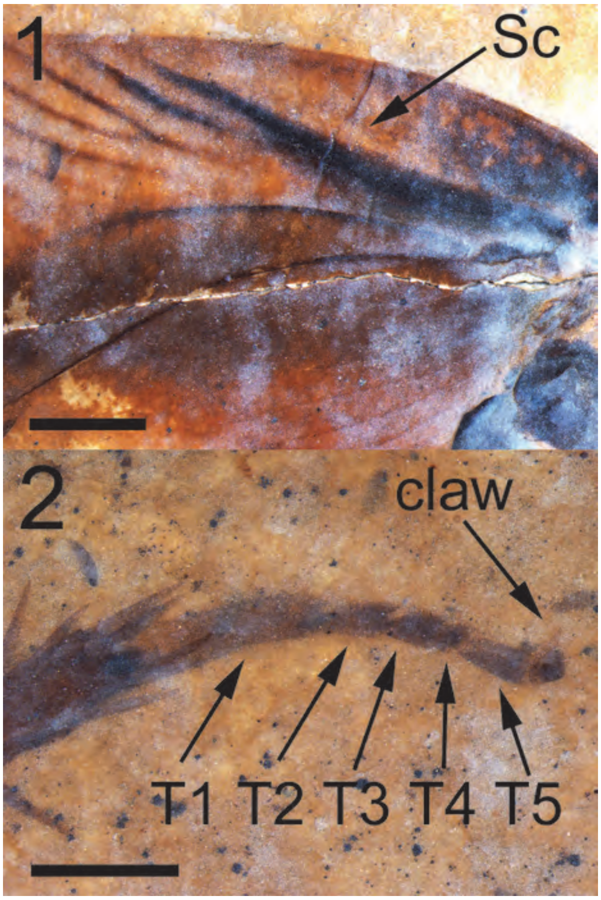

FIGURE 3. *Latiblattella avita* sp. nov. (USNM 595139). 3.1. The subcostal field of tegmen showing the wide and darkly pigmented Sc vein. 3.2. The five segmented tarsus. The arrows denote tarsal segments 1 – 5 and the end of the single visible claw. Scale bars equal 1 mm.

L. avita sp.n. has venation almost identical with *L. rehni*. Unfortunately, the data do not reveal enough information for a phylogenetic analysis. While the *Sc* vein is often simple in extant species of *Latiblattella*, it exhibits a single posterior branch in both *L. avita* and *L. vitrea* Brunner von Wattenwyl, 1865. The posterior branch originates closer to the forewing margin than the origin of *Sc* in both species. Similarly, in both species, both *Sc* and the distinctly curved basal portion of the radius are heavily pigmented. Dark pigmentation of the single posterior branch of *Sc* is however unique to *L. avita*.

Extant species of *Latiblattella*, in addition to exhibiting sexual dimorphism relative to body and wing length such that females often have significantly reduced wings, vary significantly in size (Hebard, 1917, 1921, 1922, 1932). The holotype of *Latiblattella vitrea* (♂) was reported to have a tegmina length of 10 mm while that of *L. mexicana* Saussure, 1864 is 16 mm (Brunner von Wattenwyl, 1865; Saussure, 1864). *L avita* sp. n. is 15.1 mm in length and therefore amongst the largest of the species of this genus. The tegmina length/width ratio of extant species ranges from 3.0 (*L. pavida* Rehn, 1903) to 4.53 (*L. azteca* Saussure and Zehntner, 1893) although this latter species is unusual in that most species exhibit a ratio between 3.0 and 3.5 (Rehn, 1903); the tegmina of *L. avita* sp. n. fits comfortably within this range. The length of the humeral field, defined as the distance, on a line parallel to the wing's anterior margin, from the tegmina's base to the fusion of the primary *Sc* vein with the wing's margin, relative to that of the anal field, is another potentially valuable morphometric measurement. Unfortunately, most holotypes and paratypes have not been figured in the literature and, as a result, the data is limited. This ratio is equal to 0.92-0.94 (*L. rehni*), 0.92 (*L. lucifrons* Hebard, 1917), 0.79 (*L. vitrea*) and 0.66 (*L. avita* sp. n.) (Hebard, 1917; Rehn, 1951; Brunner von Wattenwyl, 1865). Given this limited available data and the single fossil specimen, the significance of *L. avita*'s smaller ratio is unknown.

Latiblattella avita **sp. nov. and the Fossil Record**

Different extant species of *Latiblattella* have extraordinarily diverse habitats given their small number. *L. rehni* is found under cracks in the bark of *Pinus caribea* and within strands of *Dendropogon usneoides* (Spanish moss), *L. chichimeca* Saussure and Zehntner, 1893 is found on bromelias, *L. lucifrons* feeds on pollen and detritus on the flowers of *Yucca elata* and *L. zapoteca* Saussure, 1862 is found under stones along the margins of rivers (Rehn, 1906; Hebard, 1917; Ball et al., 1942; Blatchley, 1920; Picado, 1913). The conserved fragment of *L. avita* appears to be a remnant that could have been dropped from a predator or washed into the margins of the lake via a small stream and it is impossible to know the niche occupied by the insect. Although pine leaves - yet to be identified - are found in the shales and siltstones of the Kishenehn Formation, none are known from the Dakin site although a single pine seed has been collected there.

Most Cretaceous cockroach clades (e.g., Blattulidae, Caloblattinidae and nearly all of the Mesoblattinidae and Skokidae) are not present in the fossil record of the Cenozoic; only the single extant genus *Blattella* has a fossil record in the Cretaceous (Vršanský, 2008). On the other hand, nearly all (9/11) cockroach genera from the Green River

Formation and all genera from Dominican Republic and Mexican amber are extant. The marked differences in the composition of the Cenozoic and Cretaceous entomofauna suggest a very rapid evolution and radiation of the cockroach biota in the Paleocene and early Eocene (Vršanský et al., 2011; 2012; 2013; Gorochov, 2007). Interestingly, *Namablatta, Diploptera, Ectobius, Allacta* Saussure and Zehntner, 1895*, Blattella* and *Supella* are all extant genera that were present in the North and Central American Paleogene that are now, except for recent reintroduction, extinct in those areas (Vršanský et al., 2011). Their absence, in combination with the highly advanced nature and restricted geographical distribution of the Dominican fauna (Central and South America), led Vršanský et al. (2011) to suggest that an environmentally/biologically-mediated extinction event precipitated extinction of Paleogene fauna and set the stage for the evolution of a distinctly American fauna. On the other hand, *Cariblattoides labandeira*, present in the lacustrine sediments of the early Eocene Green River Formation, is an extant species with a present-day distribution in South America and the Caribbean (Vršanský et al., 2012). *Latiblattella avita* sp.n. is a species from yet another genus that was able to persist from the middle Eocene to present-day in Central America (An alternative explanation would be the migration of *L. avita* from its Eocene territory to its present day location sometime over the last 46 million years due to the cooling temperatures of the latter half of the Cenozoic.). Extant species of *Latiblattella*, restricted to Central America, Cuba, Mexico, the Bahamas, Florida and Arizona (Princis, 1969), may be restricted in distribution relative to that of the Eocene. So too, *Cariblattoides* Rehn and Hebard, 1927, which is presently restricted to Cuba, Puerto Rico and Brazil (Bonfils, 1975). Given their preference for the tropics and the near universal subtropical/ tropical environments of the Eocene (Wolfe, 1995; Zachos et al., 2001), the presence of these genera in Eocene North America is not unexpected. Although recent molecular phylogenetic data has indicated a close relationship between Latiblattella and the oriental genus *Balta* (Inward et al., 2007), there is no fossil record for the latter genus and a paleobiogeographical link between the two has yet to be established.

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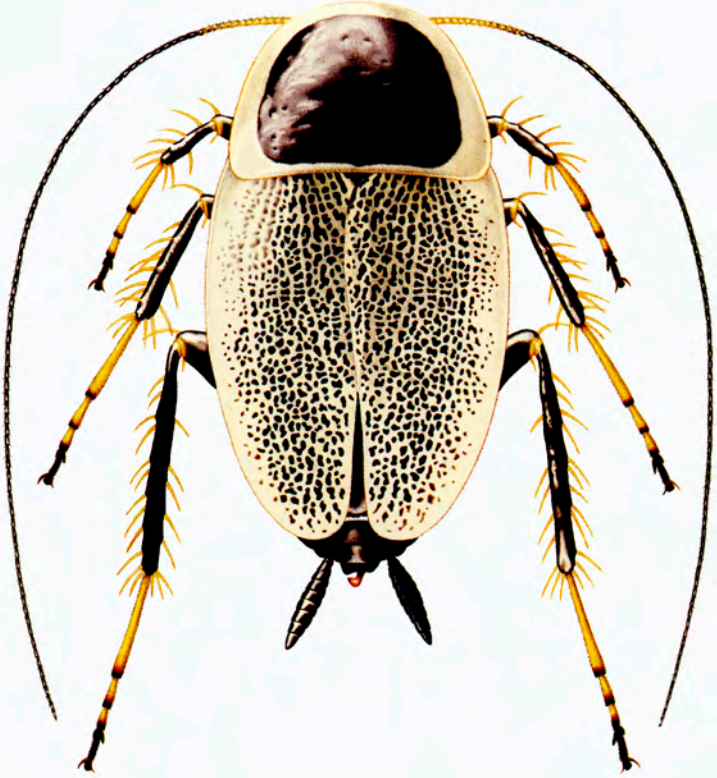
Mantodea – modlivky
(Insecta: Orthopteroidea)

ĽUBOMÍR VIDLIČKA



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Blattaria – šváby
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(Insecta: Orthopteroidea)

Ľubomír Vidlička

VEDA, vydavateľstvo Slovenskej akadémie vied
Bratislava 2001

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Rad: BLATTARIA Burmeister, 1829 – šváby

Úvod

Šváb, rus, tarakán – kto by nepoznal aspoň jeden z týchto názvov označujúcich malé zvieratko, ktoré sa cíti dobre práve v ľudských príbytkoch a sprevádza človeka už niekoľko storočí (či možno tisícročí) na jeho cestách. Tieto synantropné druhy majú často kozmopolitné rozšírenie, ale ich bližšiemu poznaniu bráni skrytý nočný spôsob života a veľká rýchlosť, akou unikajú pred svetlom. Iba nepatrné percento ľudí, zväčša iba tí, ktorí sa zaoberajú biológiou, vedia, že prevažná väčšina druhov švábov žije voľne v prírode a viacero druhov dokonca aj u nás. Napriek tomu, že sú blízkymi príbuznými už spomínaných synantropných druhov, ich pôsobenie v prírode môžeme hodnotiť kladne. Všežravosť švábov je v prirodzených podmienkach, najmä v trópoch a subtrópoch, kde má prevažná väčšina druhov svoj domov, ideálnou vlastnosťou z hľadiska rozkladu organických látok.

Šváby sú jednou z najstarších hmyzích skupín. Ich prví prapredkovia sa objavili na Zemi pred viac ako 300 miliónmi rokov v karbóne (prvohory) a zanedlho sa stali jedným z najväčších hmyzích radov. V súčasnosti žijúce šváby (4 500 – 5 000 druhov z asi 460 rodov) sú v porovnaní s inými radmi hmyzu iba malou skupinou, ale ich zástupcovia sú rozšírení takmer po celej Zemi.

Šváby sú z hospodárskeho a medicínskeho hľadiska významnou skupinou. Aj preto sa v 20. storočí stali jedným z najčastejších hmyzích objektov biologického vedeckého výskumu. Značná pozornosť, ktorá im je venovaná, sa prejavuje vo veľkom počte publikovaných prác a samozrejme i v množstve poznatkov o tejto skupine. Celosvetový katalóg švábov zahrnujúci približne 3 800 dovtedy opísaných druhov zostavil švédsky blattológ Karlis Princis (1962, 1963, 1964, 1965, 1966, 1967, 1969, 1971). Komplexnému spracovaniu švábov východného palearktu sa venoval Bey-Bienko (1950). Jeho práca sa stala spolu so staršou Rammeho revíziou rodu *Ectobius* (Ramme 1923) základom pri štúdiu stredoeurópskych druhov švábov. Prvý kľúč stredoeurópskych druhov švábov vypracoval Harz (1957). Následne boli spracované šváby Európy (Princis 1965 a Harz 1976). Od vydania spomínaných prác bolo z Európy opísaných viacero druhov švábov z rodov *Phyllodromica* a *Ectobius*. Revízii niektorých skupín rodu *Phyllodromica* sa v posledných rokoch venovali Bohn (1992, 1993, 1999) a Vidlička a Majzlan (1997). Mnohé z publikovaných prác majú podobu obsiahlych monografií zaoberajúcich sa predovšetkým biológiou švábov a ochranou pred nimi – Roth & Willis (1960), Beier (1961, 1974), Cornwell (1968, 1976), Bell & Adiyodi (1981), Rust et al. (1995) a ďalšie.

Najstaršie údaje o výskyte švábov z územia dnešného Slovenska pochádzajú spred takmer 200 rokov (Bartholomaeides 1806 – 1808). Do súčasnosti sa nahromadilo množstvo najmä faunistických údajov, ktoré bolo potrebné v prvom rade sumarizovať a kriticky zhodnotiť (Vidlička a Majzlan 1992; Vidlička a Sziráky 1997). Až následne mohlo vzniknúť monografické spracovanie švábov.

Predložená práca vzhľadom na svoj rozsah a svoje poslanie zďaleka nie je a ani nemôže byť úplným súhrnom poznatkov o tejto zaujímavej skupine hmyzu. Snahou bolo podať ucelenú a prehľadnú charakteristiku celého radu Blattaria a v systematickej časti zhrnúť a obohatiť doterajšie poznatky o šváboch žijúcich na území Slovenska. Dúfam, že sa to aspoň čiastočne podarilo.

A. Všeobecná časť

1. Morfologická charakteristika imág

Veľkosť. Šváby dosahujú väčšinou stredne veľké až veľmi veľké rozmery, malé druhy sú zriedkavejšie. Najmenšie sú v termitiskách žijúce druhy z rodu *Nocticola* (asi 3 mm) a v mraveniskách žijúce druhy z rodu *Attaphilla* (asi 4 mm). Najväčší známy šváb je *Megaloblatta longipennis* s rozpätím krídiel viac ako 18 cm a šváby z rodu *Blaberus* dlhé okolo 120 mm. Najťažším švábom je bezkrídly austrálsky druh *Macropanesthia rhinoceros*, ktorý dosahuje dĺžku 65 mm a hmotnosť okolo 20 gramov (DAY 1950).

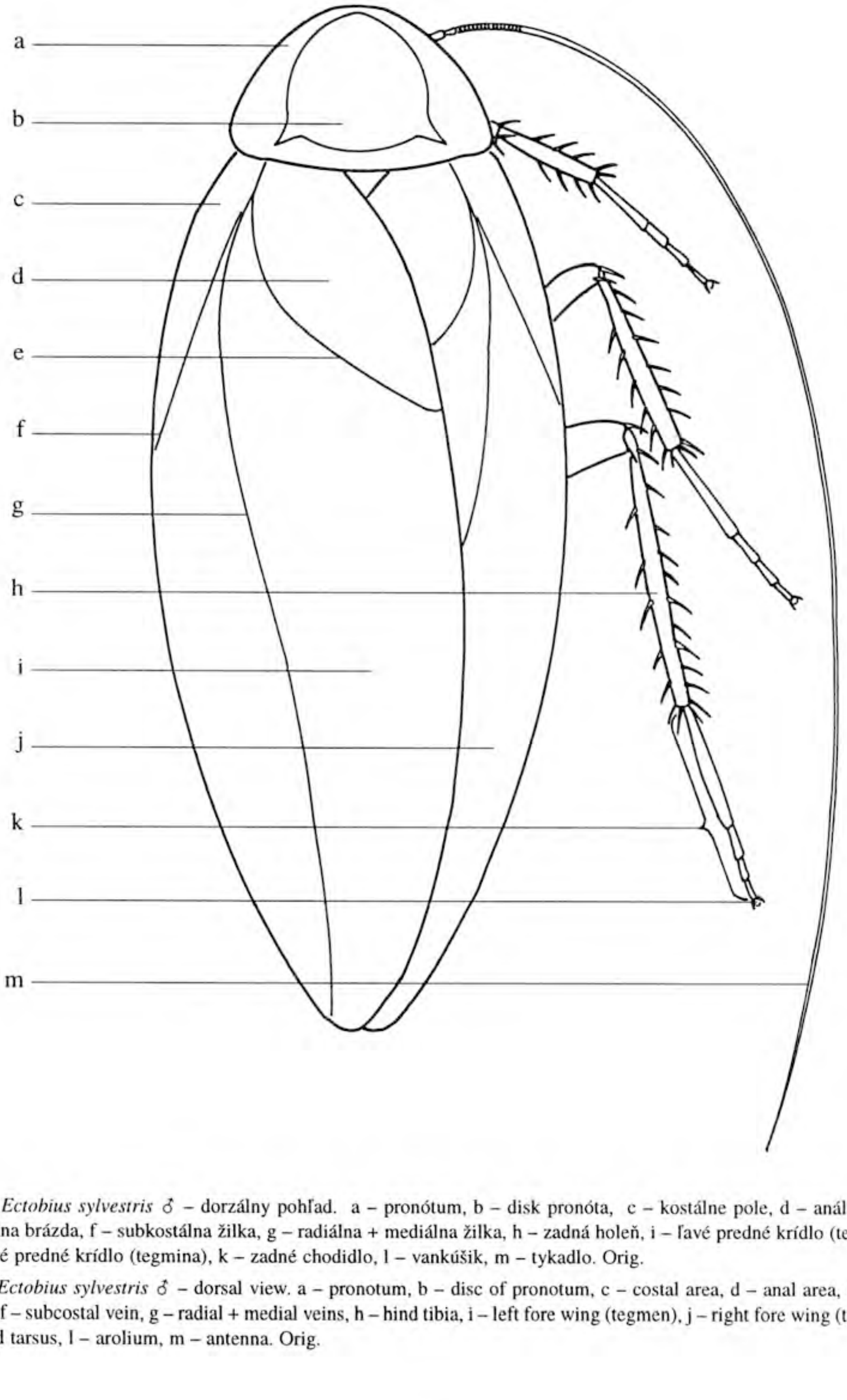
Integument (integumentum). Šváby, ako aj ostatné článkonožce, majú vonkajšiu kostru (exosceletum). Exoskelet je tvorený na povrchu nebunkovou kutikulou, ktorá je vylučovaná vonkajšou (ektodermálnou) vrstvou telových buniek – epidermou. Pod epidermou je tenká bazálna membrána. Epiderma s kutikulou a bazálnou membránou tvoria integument. Aby bola zabezpečená pohyblivosť, kutikula netvorí homogénny celok, ale jednotlivé články sú kryté malými platničkami (skleritmi) navzájom pospájanými mäkkými a pružnými blankami – intersegmentálnymi membránami. Integument je u švábov obyčajne mäkký, ale u niektorých skupín, najmä u bezkrídlych foriem môže dosahovať značnú tvrdosť (napr. Polyphaginae, Panesthinae). Kutikula švábov, tak ako u ostatného hmyzu, sa skladá z troch hlavných vrstiev. *Periplaneta americana* má kutikulu hrubú 40 µm. Jej najvnútornejšia vrstva – endokutikula – je hrubá 20 – 30 µm a skladá sa z vonkajšej a vnútornej vrstvy. Nad ňou je 10 – 20 µm hrubá exokutikula, ktorá obsahuje čierne pigmenty – melaníny. Extrémne tenká vonkajšia vrstva – epikutikula má 2 µm. Skladá sa z dvoch chemicky odlišných vrstiev. Tenká vonkajšia vrstva (0,02 – 0,03 µm) je priehľadná, hygrofobická a odolná voči kyseline. Vnútorná vrstva je jantárovo sfarbená a nie je odolná voči kyseline. Na povrchu epikutikuly je vosková vrstva, ktorá má dôležitú funkciu pri priepustnosti vody. Vosková vrstva u švábov sa obnovuje počas celého ich života. Predpokladá sa, že vosk je u švábov vylučovaný na povrch kutikuly v roztoku, ktorý sa vyparuje len veľmi pomaly. Vosková vrstva u švábov je zložená z nenasýtených uhľohydrátov, mastných kyselín a z rôznych aldehydov. U posledného nymfálneho instaru *Periplaneta americana* je táto vrstva hrubá 0,4 µm a u dospelých 1 – 2 µm. Podobne je to aj u *Blatta orientalis*, kde vosková vrstva dosahuje na brušku hrúbku 0,6 µm (BEAMENT 1945; DENNELL & MALEK 1955a, 1955b, 1956).

Povrch tela švábov je väčšinou hladký a lysý. Hustejšie ochlpenie sa vyskytuje iba zriedkavo, častejšie je iba u púštnych a stepných druhov. Rôzne výrastky a tŕne na kutikule sú veľmi vzácne. Ojedinelá je i zrnitá štruktúra.

Sfarbenie. Šváby majú takmer výlučne pigmentózne sfarbenie. Najbežnejšie je slamovožlté, žltohnedé a tmavohnedé, zriedkavejšie čierne. Väčšina švábov je sfarbená veľmi nenápadne. Kovové sfarbenie je veľmi zriedkavé (napr. *Eustegasta buprestoides* z Kamerunu a Konga alebo niektoré Plectopterinae). Občas sa vyskytuje i mimetické sfarbenie (bližšie pozri časť Obrana).

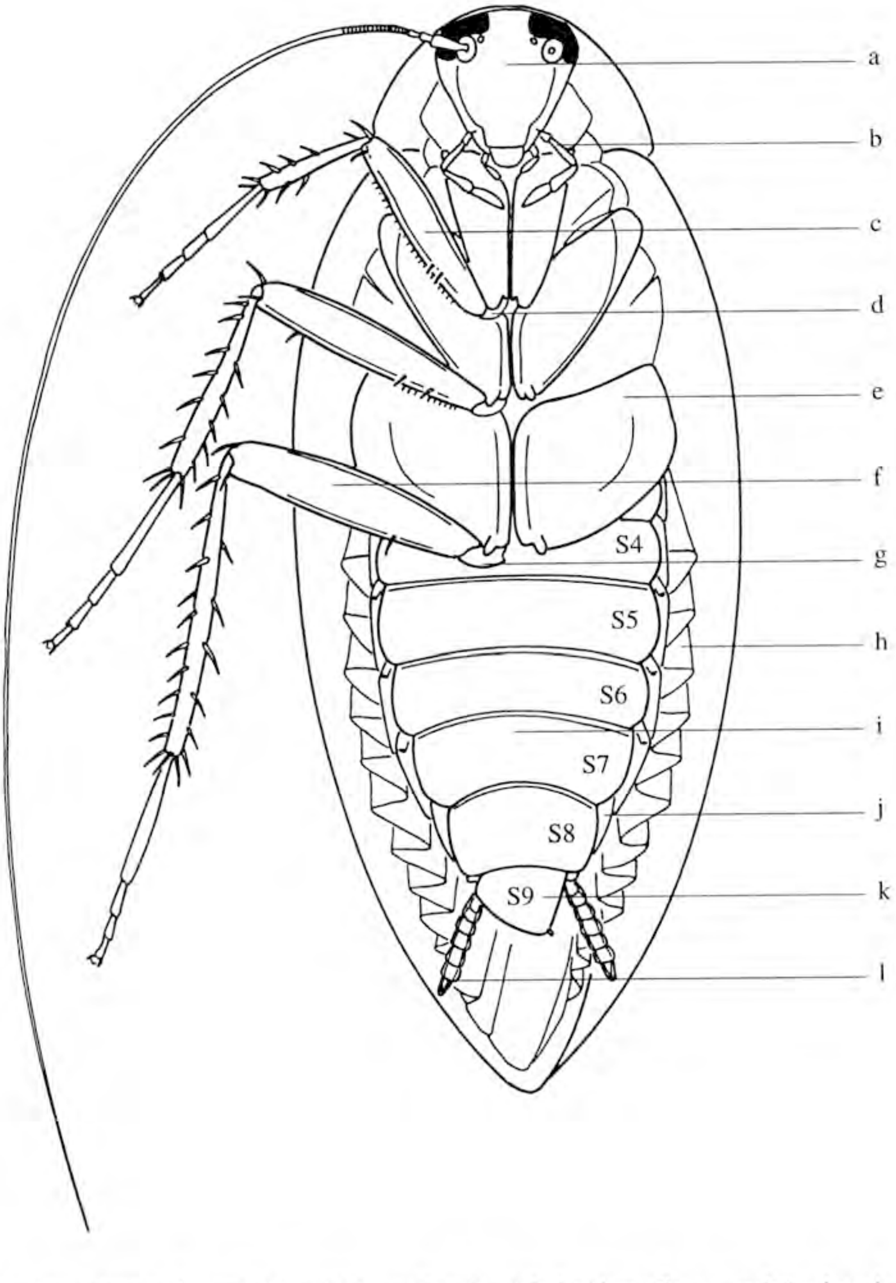
Sfarbenie švábov nie je dobrým diagnostickým znakom, vykazuje vysoký stupeň variability. Bežné je odlišné sfarbenie jedincov toho istého druhu z rôznych lokalít.

Hlava (caput) (obr. 3) je voľná, väčšinou hypognátna (caput hypognathale), priečne stlačená s typickými švami a s dobre vymedzenými skleritmi. Epikraniálny šev (sutura epicranialis) nie je u dospelých vždy prítomný. Čelo (frons) a čelový štítok (clypeus) sú veľké, dobre vyvinuté. Tentórium (vnútorná kostra hlavy) je charakteristické otvorom v stredovej časti (v tele tentória). Zhora je hlava buď úplne zakrytá štítom alebo je predná časť hlavy čiastočne viditeľná. Zložené oči (oculi compositi) sú skoro vždy vyvinuté, veľké sú najmä u krídlatých foriem. Bezkrídle formy majú oči výrazne menšie a medziočný priestor veľmi široký. Zriedkavo môžu byť oči redukované alebo



Obr. 1. *Ectobius sylvestris* ♂ – dorzálny pohľad. a – pronótum, b – disk pronóta, c – kostálne pole, d – análne pole, e – análna brázda, f – subkostálna žilka, g – radiálna + mediálna žilka, h – zadná holeň, i – ľavé predné krídlo (tegmina), j – pravé predné krídlo (tegmina), k – zadné chodidlo, l – vankúšik, m – tykadlo. Orig.

Fig. 1. *Ectobius sylvestris* ♂ – dorsal view. a – pronotum, b – disc of pronotum, c – costal area, d – anal area, e – anal furrow, f – subcostal vein, g – radial + medial veins, h – hind tibia, i – left fore wing (tegmen), j – right fore wing (tegmen), k – hind tarsus, l – arolium, m – antenna. Orig.

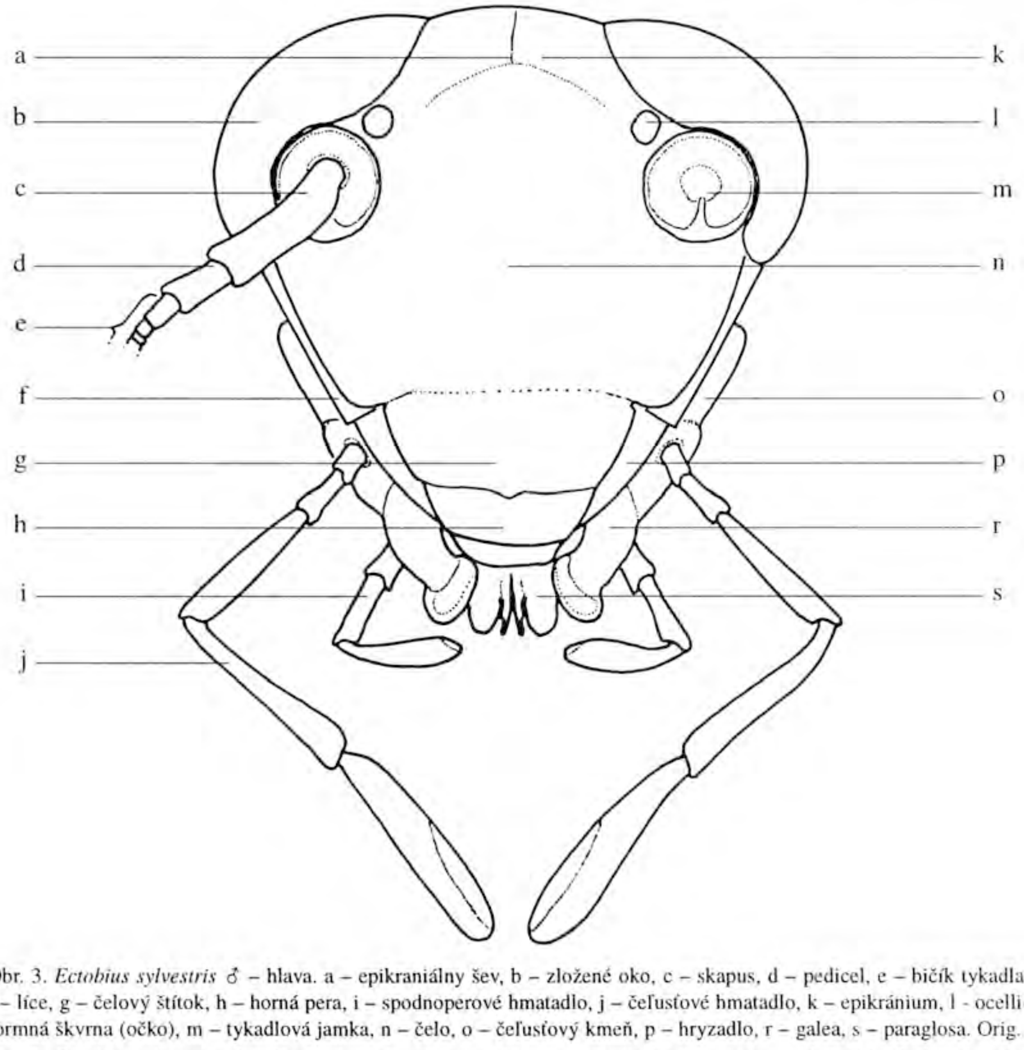


Obr. 2. *Ectobius sylvestris* ♂ – ventrálny pohľad. a – hlava, b – čeľusťové hmatadlo, c – predné stehno, d – predný trochanter, e – zadná panvička, f – zadné stehno, g – zadný trochanter, h – vejárovito zložené zadné krídlo, i – siedme sternum, j – siedme tergum, k – subgenitálna platnička, l – cerkus. Orig.

Fig. 2. *Ectobius sylvestris* ♂ – ventral view. a – head, b – maxillary palp, c – front femur, d – front trochanter, e – hind coxa, f – hind femur, g – hind trochanter, h – folding hind wing, i – sternum 7, j – tergum 7, k – subgenital plate, l – cercus. Orig.

chýbajú, najmä u myrmekofilných a kavernikolných foriem (napr. u zástupcov rodu *Spelaeoblatta* z Barmy a Thajska alebo *Trogloblattella* zo Sarawaku). Zložené oči sú vytvorené z množstva malých omatídií, každé omatídium má bikonvexnú šošovku vytvorenú z priehľadnej kutikuly. U niektorých druhov švábov sú vyvinuté dve jednoduché očká (ocelli), ale častejšie sú na ich mieste iba 2 bledé, na svetlo citlivé, ocelliformné škvrny (fenestrae) pri vnútornom okraji očí. Fenestrae sú nervami spojené s mozgom a ich histologická štruktúra pripomína degenerované očká redukované na pigmentovanú kutikulu. U foriem s plne vyvinutými krídlami sú očká obyčajne dobre vyvinuté, u bezkrídlych (apterných) foriem hrabajúcich v zemi zvyčajne chýbajú.

Tykadlá (antennae) sú mnohočlánkové, veľmi dlhé (často dlhšie ako telo), nitkovité, smerom ku koncu sa zužujú. Zriedkavejšie sú v strede zhrubnuté, vretenovité (napr. u tropického rodu *Pseudothyrsocera*). Ku hlave sa pripájajú približne v strede vnútorného okraja očí. Vyrastajú z okrúhlej tykadlovej jamky ohraničenej tykadlovým švom (sutura antennalis), ktorý má uprostred

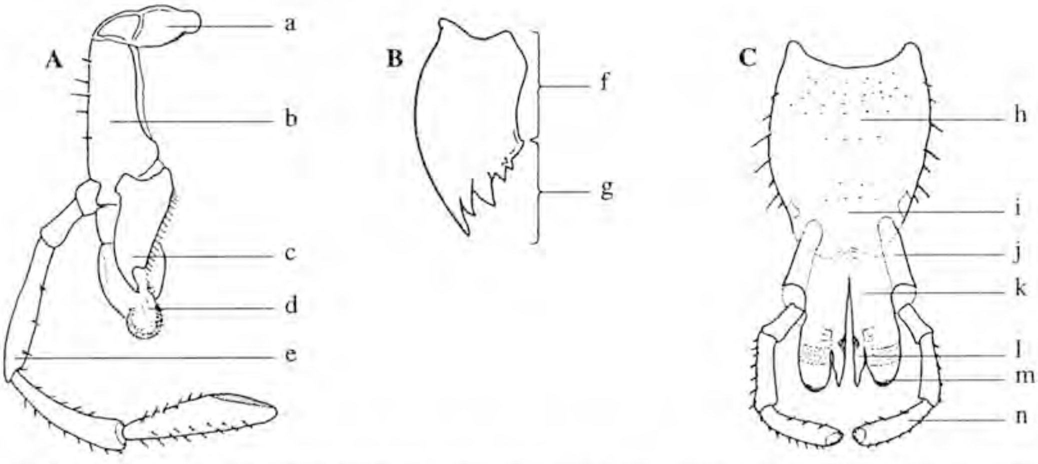


Obr. 3. *Ectobius sylvestris* ♂ – hlava. a – epikraniálny šev, b – zložené oko, c – skapus, d – pedicel, e – bičík tykadla, f – líce, g – čelový štítok, h – horná pera, i – spodnoperové hmatadlo, j – čeľusťové hmatadlo, k – epikránium, l - ocelliformná škvrna (očko), m – tykadlová jamka, n – čelo, o – čeľusťový kmeň, p – hryzadlo, r – galea, s – paraglosa. Orig.

Fig. 3. *Ectobius sylvestris* ♂ – head. a – epicranial suture, b – compound eye, c – scape, d – pedicel, e – antennal flagellum, f – gena, g – clypeus, h – labrum, i – labial palp, j – maxillary palp, k – epicranium, l – fenestra, m – antennal pit, n – frons, o – stipes, p – mandible, r – galea, s – paraglossa. Orig.

vnútorného okraja apofýzu. Prvý tykadlový článok, skapus (scapus) je najdlhší, druhý článok, pedicel (pedicellus) má tvar guličky, ostatné články sú obdĺžnikovité, navzájom podobné. Všetky články sú zvyčajne pokryté jemnými krátkymi chĺpkami. Sfarbené sú spravidla jednofarebne tmavo, ale časté je i biele sfarbenie niekoľkých článkov v strednej časti tykadla. Tykadlá sú orgánom čuchu a hmatu. Sú veľmi pohyblivé.

Ústne orgány (trophi) (obr. 4) smerujú pri odpočinku dozadu a dolu. Sú hryzavého typu (trophi masticatorii). Tvorí ich 5 dobre oddelených častí – horná pera (labrum), hryzadlá (mandibulae), čeľuste (maxillae), jazýčok (hypopharynx) a spodná pera (labium). Hryzadlá sú veľké, nepravidelne štvoruholníkovité, silne sklerotizované, na vnútornej strane ozubené, na báze s dobre vyvinutými žuvacími plochami. Hryzadlá švábov nesú prívesky (prostheca). Na zadnom povrchu každého hryzadla sú pozdĺžne rady štetín. Čeľuste sa skladajú z viacerých častí. Čap (cardo) je krátky, rozdelený. Na predĺženom kmeni (stipes) je sformovaný osobitný sklerit nazývaný subgalea. Na kmeni sú na malých palpiferoch umiestnené 5-článkové čeľusťové hmatadlá (palpi maxillares). Galea je pomerne mäkká, cylindrického tvaru. Lacínia má na vnútornej strane dva dobre vyvinuté do stredu smerujúce zúbky, v strede je na jej povrchu množstvo dlhých štetín. Jazýčok je veľký s bočnými sklerotizovanými výbežkami (suspenzóriami) a stredovou priehlbinou (sitophora). Spodná pera tvorí najväčší diel zadnej časti hlavovej kapsuly. Skladá sa z veľkého, širokého a oválneho podbradku (submentum), malej brady (mentum) a prementa nesúceho na palpigeroch pár 3-článkových spodnoperových hmatadiel (palpi labiales). Na distálnom konci spodnej pery sú dobre vyvinuté párové glosy (glossae) a paraglosy (paraglossae). Na ich vrchole sú rady jemných, k ústnemu otvoru smerujúcich štetín.



Obr. 4. *Ectobius sylvestris* ♂ – ústne orgány. A – čeľusť; B – hryzadlo; C – spodná pera. a – čap, b – kmeň, c – lacínia, d – galea, e – čeľusťové hmatadlo, f – ostrie, g – rezáky, h – podbradok, i – brada, j – palpiger, k – prementum, l – glosa, m – paraglosa, n – spodnoperové hmatadlo. Orig.

Fig. 4. *Ectobius sylvestris* ♂ – mouth parts. A – maxilla; B – mandible; C – labium. a – cardo, b – stipes, c – lacinia, d – galea, e – maxillary palp, f – mola, g – denticles, h – submentum, i – mentum, j – palpiger, k – prementum, l – glossa, m – paraglossa, n – labial palp. Orig.

Krčok (cervix). Hlava je na predohruď pripojená dlhým krčkom. Dorzálna strana krčka je zreteľne kratšia ako ventrálna strana. To umožňuje ohnutie hlavy pod hruď i jej horizontálne vysunutie. Krčok je pokrytý arthrodiálnou membránou. Na spevnenie krčka slúžia dva páry bočných cervikálnych skleritov (cervicalia) ležiace medzi záhlavnými kondylami a latero-anteriornými rohmi predohrudného sterna. Keď je hlava zatiahnutá pod hruď, cervikálna membrána na spodnej strane krčka sa prehne pod predný a zadný okraj ventrálnych cervikálnych skleritov. Tým sa dosahuje skrátenie funkčnej dĺžky ventrálnej strany krčka (POPHAM 1961).

Hruď (thorax). Predohruď (prothorax) nesie dorzálne veľký, silne sklerotizovaný predohrudný štít (pronotum), ktorý väčšinou prekrýva hlavu. Povrch pronóta je slabo klenutý, buď hladký alebo s neveľkými hrbolčekmi v zadnej časti nad základmi prvého páru krídiel. Inokedy môže byť povrch zrnitý alebo jemne ochlpený. Bočné okraje a prípadne i predný okraj pronóta bývajú často jasnejšie sfarbené ako jeho stred (disk) a obyčajne sú priezračné (napr. *Ectobius*). Mezo- a metanótum sú viac alebo menej pravouhlé a navzájom podobné, u krídlatých foriem slabo sklerotizované a úplne zakryté tegminami a krídlami. Obe sú rozdelené na akrotergit (acrotergit), predštít (prescutum), štít (scutum) a obyčajne vypuklý štítok (scutellum). Postnóta nie sú vyvinuté. Na bokoch sú závesné kĺby (kondyly) na uchytenie tegmín a krídiel. U brachypterných a apterných foriem je mezo- a metanótum silne sklerotizované, bez akýchkoľvek štruktúr. Vzhľadom sú podobné na abdominálne tergá za nimi.

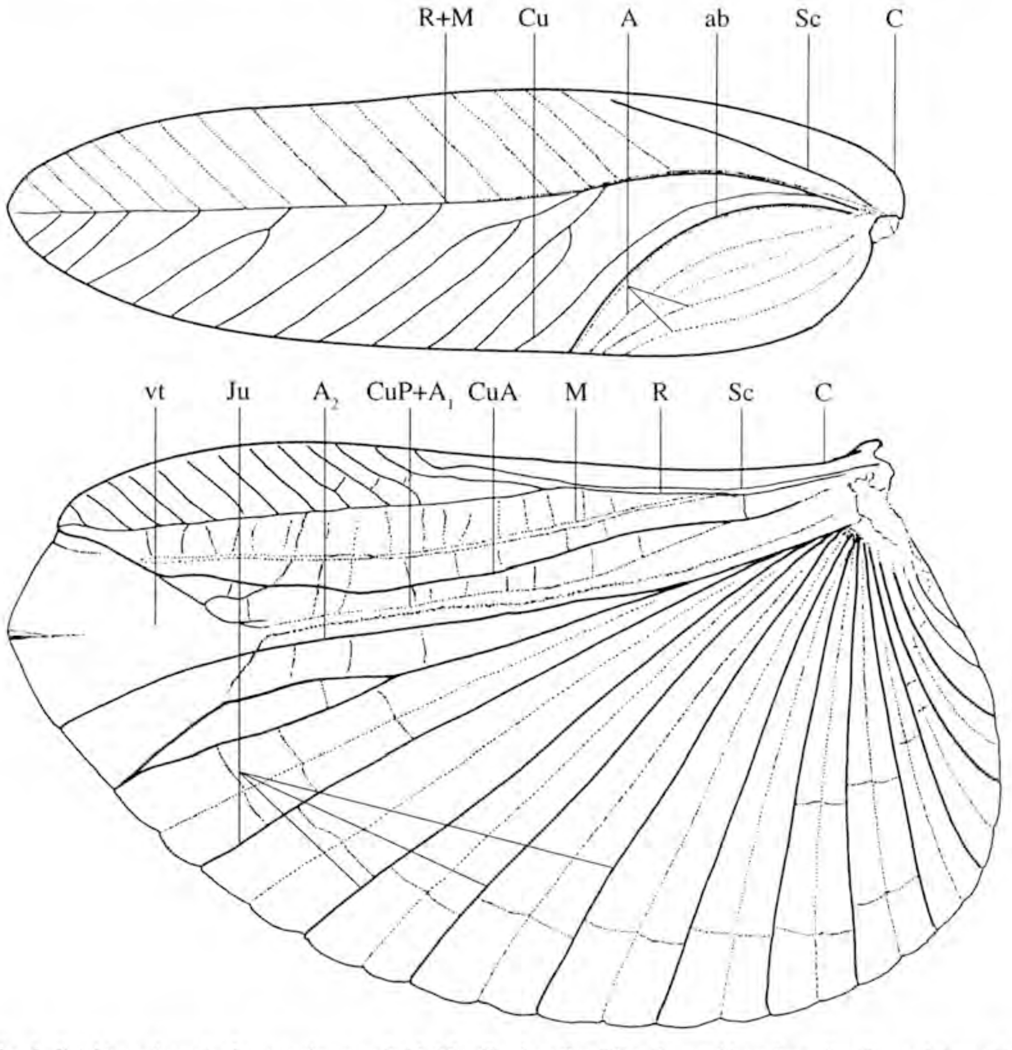
Pleury sú vďaka silne sploštenému telu a mohutnému rozvoju hrudných tergov malé. Episternity sú omnoho väčšie ako epimeróny. Stredo- a zadohrudné spirákulá sú prítomné.

Sterná sú slabo sklerotizované, trochu stlačené, väčšinou zakryté silne vyvinutými panvičkami. Prosternit je tvorený drobnou, úzkou, pretiahnutou platničkou rozdelenou priečnym švom na dve časti – predný eusternit (basisternit) a zadné sternellum (furcasternit). Vzadu je malé prosternellum (spinasternit). U mezo- a metasternitu je bazisternit redukovaný a po dĺžke rozdelený na dve malé platničky, furkasternit (sternellum) je silne redukovaný, vo vnútri má furku v tvare písmena Y. Mezospinasternit je vyvinutý, metaspinasternit chýba.

Nohy (pedes) sú väčšinou behavé (pedes cursorii), nemodifikované, všetky tri páry stavané podobne (homonómne). Zriedkavejšie sú prispôsobené hrabaniu v zemi (pedes fossorii), najmä predný pár (napr. u *Arenivaga*, *Panchlora*, *Nymphytria*). Holene sú v tom prípade vpredu zhrubnuté a vyzbrojené silnými tŕňmi. Panvičky (coxae) sú dlhé, uložené veľmi blízko pri sebe, často sú obrúbené. Trochanter je veľmi malý, pripojený k zadnej časti stehien. Stehná (femora) sú dlhé, po celej dĺžke približne rovnako široké, spodná (ventrálna) strana často s dvomi kýlovitými okrajmi, vyzbrojenými mnohými dlhými tŕňmi. Otŕnenie je charakteristické najmä na spodnom prednom (anteroventrálnom) okraji predného páru stehien. Typ otŕnenia je dôležitý aj taxonomicky. Vzhľadom na charakter otŕnenia sú známe 3 typy predných stehien – pôvodnejší typ A a odvodené typy B a C. Typ A je charakterizovaný radom silných, dlhých tŕňov, ktoré sa postupne mierne skracujú od bázy stehna k jeho vrcholu (napr. *Blatta*, *Periplaneta*, *Supella*). Typ B je charakteristický zmenou väčšiny tŕňov na jemné štetinky, zachovávajú sa iba bazálne tŕne (napr. *Phyllodromica*, *Ectobius*). Pri type C sú všetky tŕne zmenené na štetinky (napr. *Nocticola*). V rámci typov môžeme ďalej rozlišovať rôzne obmeny základného typu (označované A1, A2, A3, B1, B2 atď.). Pri všetkých typoch je distálny vrchol stehna vyzbrojený 2–3 dlhými vrcholovými tŕňmi. Zadný spodný okraj stehna sa nevyznačuje žiadnymi osobitosťami, otŕnenie je rovnakého typu a rovnakej veľkosti. Podobné otŕnenie ako na predných stehnách sa nachádza i na stredných a zadných stehnách. Na distálnom konci stredných a zadných stehien v mieste pripojenia holene sa nachádza veľký kolenný tŕň (chýba len pri niektorých špecializovaných skupinách, napr. podčeľaď Panesthiinae). Kolenný tŕň nie je nikdy na predných stehnách. Holene (tibiae) sú vždy vyzbrojené mnohými tŕňmi. Väčšinou sú dlhé, ale u druhov hrabajúcich v zemi sú krátke a široké. Chodidlá (tarsi) sú vždy 5-článkové. Menší počet chodidlových článkov je výsledkom regenerácie, ak bola noha poškodená alebo prišlo k jej strate počas nymfálneho vývoja. Prvý chodidlový článok býva väčší ako ostatné a označuje sa ako basitarzus alebo metatarzus. Koncový piaty chodidlový článok nesie pár viac alebo menej zahnutých pazúrikov, medzi ktorými je alebo nie je prítomné arólium. Pazúriky (unguiculi) sú buď symetrické – rovnako dlhé alebo asymetrické – jeden je skrátený. Len veľmi zriedkavo pazúriky chýbajú (rod *Nymphytria*) alebo je vyvinutý iba jeden (rod *Mononychoblatta*). Vnútorná strana pazúrikov môže byť hladká alebo so zúbkami. Chodidlové články (tarsomerae)

1 – 4 majú obyčajne na ventrálnej posteriornej strane vankúšikovité orgány – plantulae (u švábov niekedy nesprávne označované aj pulvili). Plantulae a aróliá pomáhajú pri pohybe na hladkých alebo strmých povrchoch. U kavernikolných foriem sú často redukované alebo chýbajú, ale môžu chýbať aj u epigeických foriem.

Krídla (alae) (obr. 5) sú na stredo- a zadohrudi rôzne utvárané (heteronómne). U druhov s plne vyvinutými letovými orgánmi sú krídla prvého páru (tegminy, mezotorakálne krídla, alae anticae) obyčajne viac alebo menej sklerotizované, kožovité. Ich úlohou je predovšetkým chrániť blanité zadné krídla a bruško. Iba u niekoľkých druhov majú oba páry krídiel rovnakú štruktúru (napr. *Cardacus willeyi*). Tvar a rozmery tegmín môžu byť často u rôznych pohlaví odlišné, pričom je badateľná tendencia k ich redukcii. Skrátenie alebo úplnú stratu tegmín (ale aj krídiel) môžeme



Obr. 5. *Ectobius sylvestris* ♂ – tegmina a zadné krídlo. C – kostálna žilka, Sc – subkostálna žilka, R – radiálna žilka, M – mediálna žilka, Cu – kubitálna žilka, CuA – predná kubitálna žilka, CuP – zadná kubitálna žilka, A – análne žilky, A_1 – prvá análna žilka, A_2 – druhá análna žilka, Ju – jugálne žilky, ab – análna brázda, vt – vsunutý trojuholník. Orig.

Fig. 5. *Ectobius sylvestris* ♂ – tegmen and hind wing. C – costa, Sc – subcosta, R – radius, M – media, Cu – cubitus, CuA – cubitus anterior, CuP – cubitus posterior, A – anal veins, A_1 – first anal vein, A_2 – second anal vein, Ju – jugal veins, ab – anal furrow, vt – intercalated triangle. Orig.

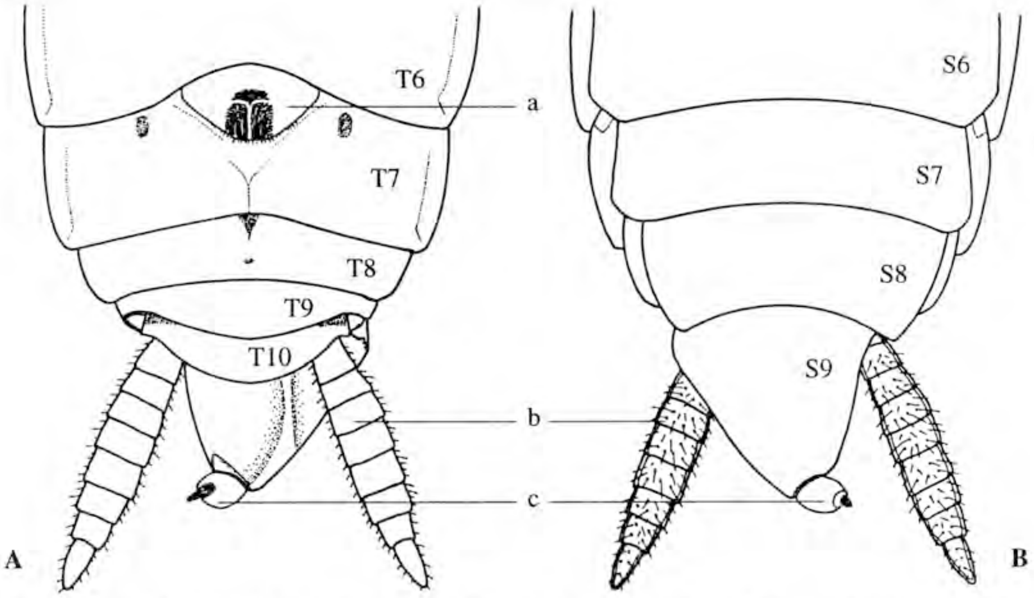
pozorovať najmä u samičiek, vďaka čomu je u švábov bežný veľký pohlavný dimorfizmus (napr. tegminy samičiek rodov *Escala* a *Robshelfordia* (Blattellidae) a *Blatta* (Blattidae) sú redukované na okrajové lalôčiky a zadné krídla chýbajú; u *Laxta granicollis* (Blaberidae) a *Arenivaga bolliana* (Polyphagidae) sú samičky bezkrídle; samčekovia týchto druhov majú úplne vyvinuté tegminy aj krídla). Zriedkavejšie dochádza u oboch pohlaví ku skráteniu (napr. *Loboptera*) alebo úplnému vymiznutiu (napr. *Cryptocercus*, *Gromphadorhina*) tegmín i krídiel. Nie je známy žiadny prípad, že by redukcia tegmín nekorelovala s redukciou krídiel. Tegminy nie sú použiteľné na aktívny let, môžu slúžiť nanajvýš na plachtenie. Žilnatina je zvyčajne veľmi hustá, dobre vyvinutá. Ak sú tegminy kožovité, jednotlivé žilky sú dobre viditeľné (napr. *Ectobius*), ak sú silne sklerotizované, žilnatina sa stáva nezreteľnou alebo sa úplne stráca (napr. *Phyllodromica*). Časť jednej z tegmín, ktorá je pri odpočinku zakrytá, je obyčajne viac blanitá alebo prinajmenšom menej kožovitá ako zvyšok tegminy. V prevažnej väčšine je to pravá tegmina. V niektorých prípadoch môže byť bazálna časť tegmín nepriehľadná, ochlpená, bez viditeľných žiliek a vrcholová časť je priehľadná so zreteľnými žilkami (napr. *Holocompsa nitidula* z tropickej Ameriky).

Kostálna žilka (C) tvorí okraj tegmín, subkosta (Sc) je krátka, radiálna žilka (R) obyčajne s viacerými prednými hrebeňovitými vetvami. Mediálna (M) a kubitálna (Cu) žilka zaberajú veľkú časť tegmín. Krátka, zahnutá postkubitálna žilka (CuP; PCu) oddeľuje zreteľne utvárané análne pole – clavus. Análna brázda (sulcus analis; línia prechodu žiliek CuP + A_1) je na rozdiel od rovnokrídlovcov oblúkovitá. V análnom poli je výrazne vyvinutá iba druhá análna žilka (A_2) a jej vetvy. Jugálne žilky (Ju) sú veľmi slabé a nejasné. (V zátvorkách sú uvedené skratky názvov žiliek.)

Zadné (metatorakálne) krídla (alae posticae) sú väčšinou blanité, prispôsobené lietaniu. Zriedkavo môžu byť zhrubnuté. Podľa ich tvaru rozoznávame 2 hlavné typy. Prvý, polyfagoidný typ má veľké preaxilárne (remígiové) pole a malé análno-jugálne pole. Druhý typ sa vyskytuje u všetkých ostatných švábov a je charakteristický relatívne veľkým preaxilárnym poľom a veľmi veľkým análno-jugálnym poľom. Počas odpočinku je análne pole zložené v mieste medzi CuP a A_1. A_1 (prvá análna žilka) je atrofovaná a zliata s CuP. U niektorých druhov švábov je na konci tejto žilky vyvinutý menší alebo väčší tzv. vsunutý trojuholník (triangulum intercalare). Análno-jugálne pole je od zvyšku krídla oddelené análnym záhybom (plica analis). Z análnych žiliek je dobre vyvinutá iba A_2, aj to nanajvýš len s krátkymi vetvičkami. Jugálne žilky sú usporiadané radiálne. V pokoji je análno-jugálne pole obyčajne naskladané do tvaru vejára a zložené pod predanálnu oblasť krídla. Poskladané zadné krídla sú obyčajne kratšie ako tegminy a sú úplne zakryté. Zriedkavo sú krídla výrazne dlhšie ako tegminy. V tom prípade sú v pokoji buď v strede zložené a celé prekryté tegminami (napr. *Diploptera*), alebo nie sú zložené a vzadu vytŕčajú spod tegmín (napr. *Euthyrrhapha*).

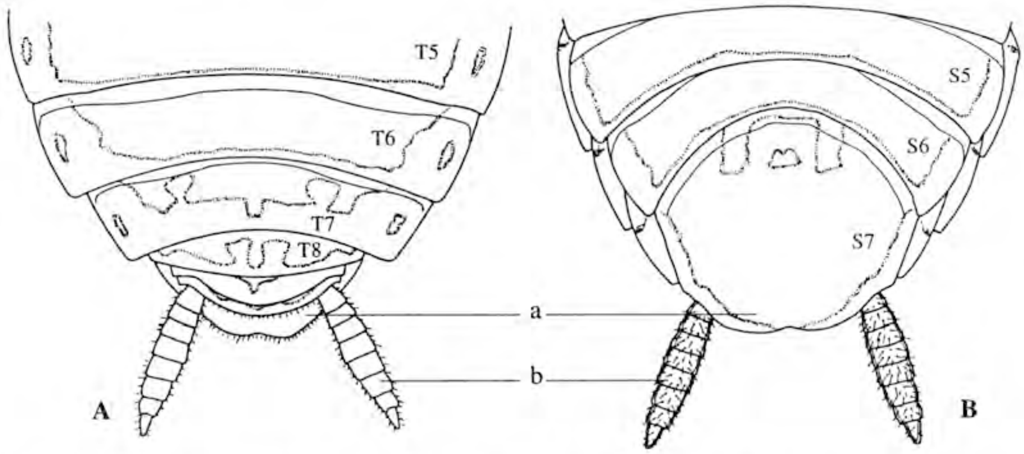
Žilnatina zadných krídiel je taxonomicky dôležitá. Kubitálna žilka je, alebo nie je vetvená. Ak je vetvená, môže mať rôzny počet vetiev, ktoré sú buď úplné (t. j. dosahujú vrchol krídla), alebo neúplné (nedosahujú vrchol). Druh môže mať aj brachypterné aj makropterné formy. Niektorí taxonómovia kladú veľký dôraz na redukciu letových orgánov a považujú ju za základný rodový alebo druhový znak.

Bruško (abdomen) (obr. 6, 7) je silne dorzoventrálne sploštené. Pôvodne sa skladalo z 11 článkov. U súčasných druhov je zreteľných desať tergov (T1 – T10), jedenásty (epiprokt) je splynutý so supraanálnou platničkou (lamina supraanalis = T10). Preto sa lalokovitý výbežok supraanálnej platničky vyskytujúci sa u niektorých švábov niekedy označuje ako epiprokt. Tergá T8 a T9 sú u oboch pohlaví malé a sú skryté pod T7. Samičky mnohých druhov majú vyvinuté rôzne abdominálne žľazy používané pri obrane alebo na prilákanie samčeka (Roth 1969; Roth & Alsop 1978; Brossut & Roth 1977). Tergálne žľazy používané pri sexuálnom správaní sa vyskytujú len u samčekov. Vylučujú feromón atraktívny pre samičky. Ich prítomnosť alebo neprítomnosť a ich umiestnenie a tvar sú taxonomicky dôležité. Tergálne žľazy vytvárajú často preliačeninu v strede terga. U podčeľade Blattellinae sú často na 5. alebo 7. tergu, ale môžu byť na ktoromkoľvek tergu. U samčekov rodu *Ectobius* a *Phyllodromica* je tergálna žľaza vždy na 7. tergu.



Obr. 6. *Ectobius lapponicus* ♂ – bruško. A – dorzálny pohľad; B – ventrálny pohľad. a – vyústenie tergálnej žľazy, b – cerkus, c – stilus. Orig.

Fig. 6. *Ectobius lapponicus* ♂ – terminal segments of abdomen. A – dorsal view; B – ventral view. a – tergal gland, b – cercus, c – stylus. Orig.



Obr. 7. *Ectobius lapponicus* ♀ – bruško. A – dorzálny pohľad; B – ventrálny pohľad. a – subgenitálna platnička (S7), b – cerkus. Orig.

Fig. 7. *Ectobius lapponicus* ♀ – terminal segments of abdomen. A – dorsal view; B – ventral view. a – subgenital plate (S7), b – cercus. Orig.

Prvé sternum je malé alebo chýba, siedme sternum u samičiek a deviate u samčekov je predĺžené a vytvára subgenitálnu platničku (lamina subanalis). Jedenáste sternum je rozdelené na paraprokty, ktoré sú ventrálne kryté subgenitálnou platničkou. Z tohto článku vyrastajú i cerkusy. Cerkusy (cerci) sú väčšinou krátke, niekoľkočlánkové, u rodu *Panesthia* sú jednočlánkové.

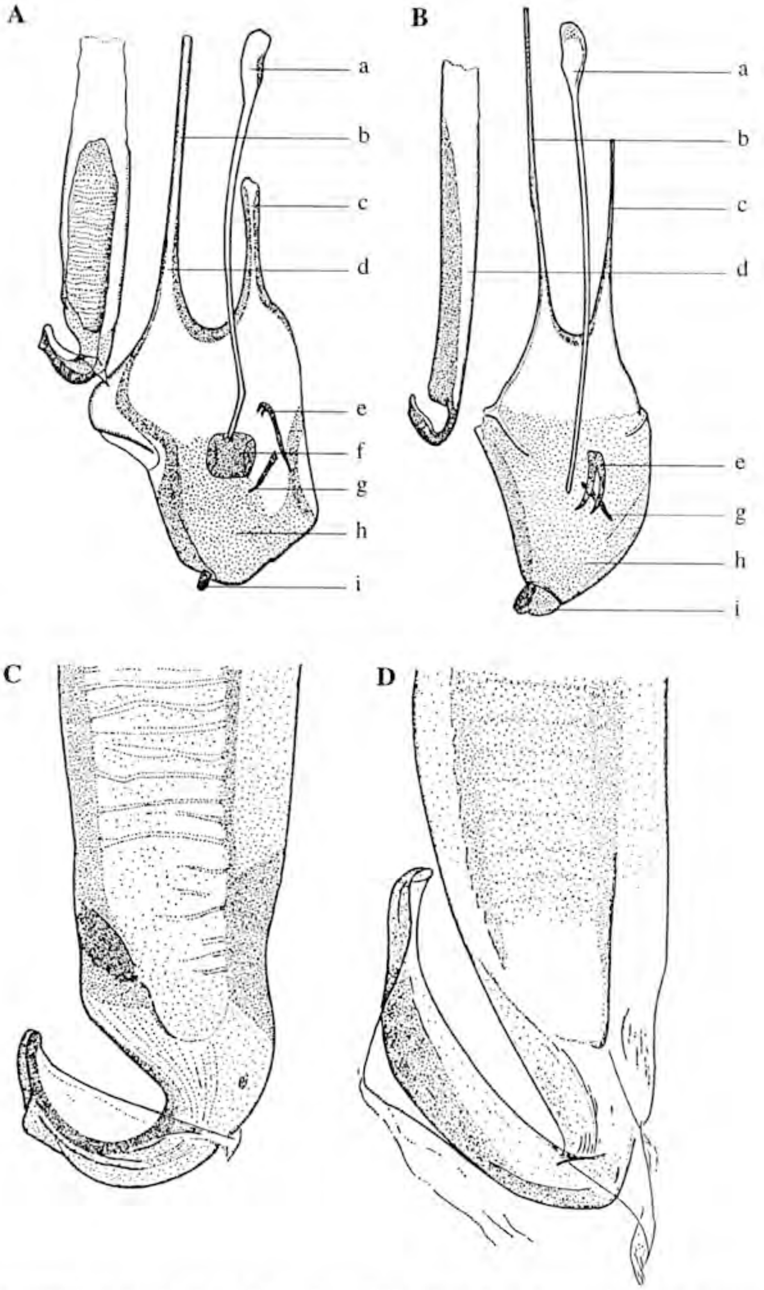
Výnimočne môžu byť úzke a dlhé – u *Periplaneta americana* až viac ako 20-článkové. Zo spodnej strany sú zvyčajne pokryté množstvom rôznych hmatových, čuchových a sluchových senzíl.

Spirákulá 2. – 7. článku sú otvorené na pleurálnej membráne, na 1. a 8. článku sú pripojené k bočnému okraju tergov.

Na samčej subgenitálnej platničke (S9 = hypandrium) sú obyčajne dva stilusy (styli), ktoré môžu byť špecificky rozdielne. Samčekovia rodov *Ectoneura*, *Stenectoneura* a druhu *Richanitschia luteomarginata* (Blattellidae) majú iba jeden stilus. U všetkých zástupcov podčeľade Panesthiinae (Blaberidae) a u viacerých rodov čeľade Blattellidae (*Arawakina*, *Neoloboptera*, *Loboptera*, *Astyloblatta*, *Astylella*, *Caffroblatta*, *Jacobsonina*, *Parascalida*, *Phymatosilpha* a *Pseudoceratinoptera*) nemajú samčekovia stilusy vôbec vyvinuté (Roth 1977, 1989, 1993). Niektoré druhy (napr. *Shelfordina orchidae* a niektoré ďalšie druhy tohto rodu) majú výbežok vznikajúci pri báze každého stilusu, takže sa zdá, akoby mali 4 stilusy (Roth 1990). U dospelých samičiek nie sú stilusy nikdy vyvinuté.

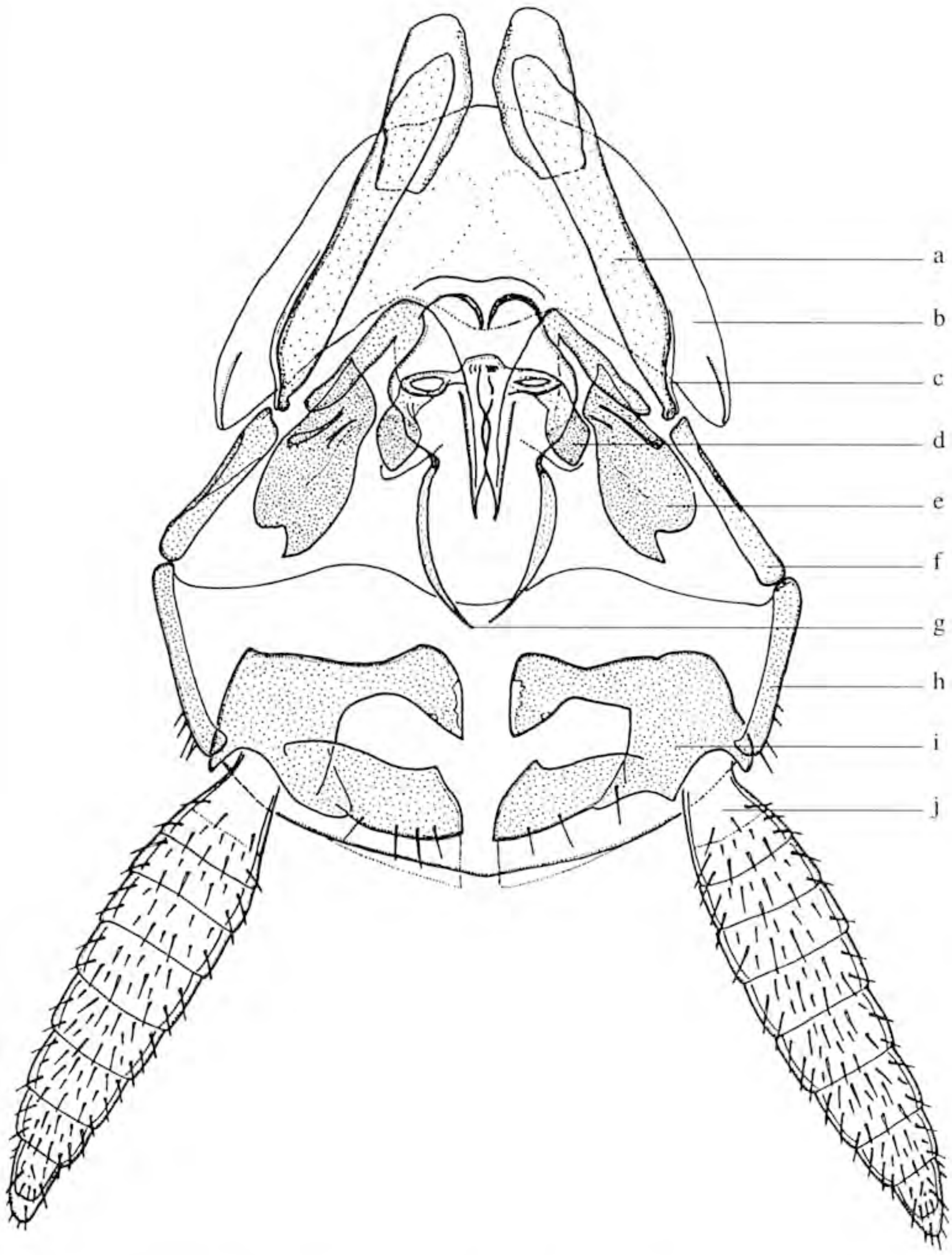
Vonkajšie genitálie (organa genitalia externa). Samčie genitálie (falické orgány) (obr. 8) sa skladajú zo skupiny asymetrických sklerotizovaných falomér, medzi ktorými leží genitálny otvor (gonoporus). Faloméry (phallomerae) sú skryté v blanitom genitálnom vaku ležiacom nad deviatym sternom a pred paraproktami. Často poskytujú vynikajúce druhové znaky. U čeľade Blattidae a Polyphagidae sú faloméry zložité, u čeľade Blattellidae a Blaberidae sú jednoduchšie (McKittrick 1964). Homológiu samčích genitálnych skleritov študovali Mizukubo & Hirashima (1987) a Bohn (1987). Falické orgány druhotne vyrastajú z prednej blanitej steny genitálneho vaku. Vyskytujú sa v niekoľkých odlišných typoch. Primárne sa skladajú z 3 lalokov alebo falomér, ktoré sú rôzne obkľúčené skleritmi, z ktorých niektoré majú tvar tŕňov, hákov a gombíkov. Pravá a ľavá faloméra je prítomná u všetkých švábov. Tretia, ventrálna faloméra, ktorá leží pod otvorom semenometu (ductus ejaculatorius), čiže pod falotrémou (phallotreme), je prítomná len u Blattidae a Polyphagidae. U niektorých Blattellidae je posteriorným pokračovaním semenometu kónický blanitý penis (phallus) medzi pravou a ľavou falomérou. Sklerity sa pre lepšiu orientáciu číslujú v smere od dorzálnych k ventrálnym, na pravej falomére ako R1, R2, R3 a mediálne až laterálne, na ľavej falomére ako L1, L2, L3. Výnimočne u Polyphagidae existuje i prídavný sklerit L4 (Snodgrass 1937; McKittrick 1964). Funkciu gonopod prevzali stilusy.

Samičie vonkajšie genitálie (obr. 9) sú usporiadané symetricky. Subgenitálna platnička (7. sternum – S7) je zväčšená, ohnutá a spolu s redukovanými a čiastočne blanitými S8, S9 a S10 je pohltená do stien veľkého genitálneho átria. Genitálny vak (atrium) je rozdelený do dvoch široko spojených komôrok – veľké posteriorné vestibulum, kde je vytváraná ootéka a menšia anteriorná kopulačná komôrka (bursa copulatrix) s otvorom spoločného vajíčkovodu a otvorom spermatéky. Strecha vestibula je zložená z pomerne pevného rámu skleritov podopierajúcich tri páry ovipozičných valvúl. Podlaha, hoci sa skladá čiastočne zo stredového vestibulárneho skleritu, je väčšinou blanitá. Podlaha kopulačnej komôrky skladajúca sa zo sklerotizovanej laterosternálnej plošiny je trocha vyvýšená nad podlahu vestibula. Strecha kopulačnej komôrky je primárne stavaná z troch zliatych skleritov, ktoré sú anteriorne pripojené k laterosternálnej plošine. Skrytý, vnútorný ovipozitor je zložený z troch párov malých, prstovitých valvúl vo vnútri komôrky. Prvý pár valviferov leží vždy bočne od báz prvého páru valvúl a je s nimi zliaty alebo spojený. Druhý pár valviferov leží hneď za prvým párom valviferov. Je zliaty s kruhovitou štruktúrou, ktorá je zložená z predného oblúka, podporujúceho druhý, vnútorný pár valvúl a z páru zadných lalokov, ktoré podporujú bázy tretieho páru valvúl. Prvý (ventrálny) pár valvúl má ontogenetický pôvod v 8. sterne a druhý a tretí pár (bočné a vnútorné valvuly ovipozitora) sa vytvárajú z deviateho sterna (Nel 1929). Malá vyčnievajúca plošina (centrálna apodéma) vzniká medzi bázami druhého a tretieho páru valvúl. Medzi bázami druhého páru valvúl ústia dve kolateriálne žľazy a malý vestibulárny orgán. Valvuly a valvifery sú držané na mieste pomocou páru dlhých, úzkych apodém, ktoré sú natiahnuté



Obr. 8. Samčie vonkajšie genitálie. A, B – subgenitálna platnička s falomérami, hák je čiastočne odsunutý; C, D – posteriorný koniec háku. A – *Phyllodromica maculata maculata*; B – *Ectobius lapponicus*; C – *Phyllodromica hungarica*; D – *Phyllodromica megerlei*. a – endofalická apodéma ľavej faloméry (L2vm – virga), b – ľavá anteriorná apodéma, c – pravá anteriorná apodéma, d – hák (L3), e – pravá faloméra R2, f – helmet sklerit, g – pravá faloméra R3, h – subgenitálna platnička, i – stilus. Orig.

Fig. 8. Male external genitalia. A, B – subgenital plate with phallomeres, hook is partly displace; C, D – posterior end of hook. A – *Phyllodromica maculata maculata*; B – *Ectobius lapponicus*; C – *Phyllodromica hungarica*; D – *Phyllodromica megerlei*. a – endophalic apodeme of left phallomere (L2vm – virga), b – left anterior apodeme, c – right anterior apodeme, d – hook (L3), e – right phallomere R2, f – helmet sclerite, g – right phallomere R3, h – subgenital plate, i – stylus. Orig.



Obr. 9. Samičie vonkajšie genitálie u švába *Phyllodromica maculata maculata*. a – rameno prvého valviferu, b – ventrálna časť kladielka, c – bazivalvula, d – zadný lalok druhého valviferu, e – laterosternit, f – paratergit, g – valvula, h – siedme sternum (subgenitálna platnička), i – paraprokt, j – cerkus. Orig.

Fig. 9. Female external genitalia of *Phyllodromica maculata maculata*. a – first valvifer arm, b – ventral part of ovipositor, c – basivalvula, d – hind lobus of valvifere II, e – laterosternite, f – paratergite, g – valve, h – sternit 7 (subgenital plate), i – paraproct, j – cercus. Orig.

anteroventrálne z bočných okrajov ôsmeho a deviateho terga. Tieto hrebeňovité apodémy sú zložené zo zliatych predĺžených paratergitov článkov VIII a IX. Paratergity IX sú často dlhšie ako paratergity VIII. Stredné konce paratergitov VIII sú spojené s prvým párom valviferov. Samičie genitálie sú u takmer všetkých švábov trochu asymetrické, stupeň asymetrie varíruje od druhu k druhu (McKittrick 1964).

2. Anatomická charakteristika imág

Dýchacia sústava (systema respiratorium). Vzdušnicová (tracheálna) sústava švábov je holopneustická. S vonkajším prostredím je spojená s desiatimi pármi spirákul – 2 hrudnými a 8 abdominálnymi. Cez spirákulá vstupuje vzduch do vzdušnicovej sústavy švábov. Spirákulá sú pripojené k trom párom veľkých paralelných tracheálnych kmeňov spojených pomocou prekrížených komisúr. Vzdušnice (tracheae) a jemnejšie vzdušničky (tracheolae) respiračného systému švábov tvoria rozvetvenú sieť rúrok ležiacu vo vnútri hemocelu. Rozvetvujú sa po celom tukovom telese, prenikajú tkanivá telových stien a vnútorností a privádzajú kyslík do všetkých častí tela švábov. Keďže na hlave nie sú spirákulá, vzdušnica zásobujúca prednú časť tela švábov je tvorená vetvami pochádzajúcimi z hrude.

Obehová sústava (systema circulatorium). Primárnou funkciou cievnej sústavy je zásobovať vnútorné orgány a tkanivá hemolymfou. Hemolymfa privádza produkty trávenia a odoberá odpadový materiál z metabolizmu do exkrečných orgánov. Hemolymfa tvorí tiež médium pre cirkuláciu hormónov produkovaných neuroendokrinnými orgánmi. U hmyzu je tzv. otvorený systém cirkulácie hemolymfy. Cirkulujúca tekutina sa pohybuje voľne v telovej dutine (haemocoel). Pohyb hemolymfy zabezpečuje pulzujúca chrbtová cieva (vas dorsale), ktorej zadný koniec je uzavretý a predný koniec je otvorený. Chrbtová cieva leží pod dorzálnym povrchom integumentu, jej predná časť (srdcovnica – aorta) je umiestnená v hrudi a zadná časť (srdce – cor) v prvých deviatych abdominálnych článkoch. Upevnená je (u *Periplaneta*) pomocou 12 párov krídlových svalov (musculi alares). Má tvar priamej rúrky, rozdelenej na srdcové komôrky. Hemolymfa z perikardiálneho sinusu vstupuje pri diastole do srdca cez 12 párov otvorov (ústie – ostium). Tri párové laterálne otvory sú v hrudnej časti a deväť v abdominálnej časti. Zo srdca vychádza šesť párov ciev – 2 hrudné (mezo- a metatorakálne) a 4 abdominálne (v článkoch 3. – 6.). Tie vedú hemolymfu zo srdca do okrajových častí tela.

Okrem chrbtovej cievy existujú rôzne prídavné cirkulačné orgány, ktoré zásobujú hemolymfou dlhšie telové výbežky. U švába *Periplaneta americana* je známe tzv. tykadlové srdce umiestnené v hlave pred mozgom. Skladá sa z dvoch pri báze tykadiel ležiacich baniek (ampullae) spojených s rytmicky sa sťahujúcim priečnym svalom. Z baniek vychádzajú tykadlové cievy do tykadiel. Počas relaxácie priečneho svalu tlačia elastické banky hemolymfu do tykadiel (Hertel & Penzlin 1992).

Hemolymfa švábov je číra tekutina s vysokým obsahom aminokyselín a dioxidov. Nemá funkciu nosiča kyslíka, a preto neobsahuje krvné farbivá – pigmenty. Hemolymfu tvorí tekutá plazma a množstvo rôznych typov buniek – hemocytov.

Tráviaca sústava (systema digestorium). Tráviaca rúra (tractus intestinalis) začína ústnou dutinou (cavum oris) a končí konečníkom (rectum). Šváby sú všežravé (omnivorné), a preto nie sú ich ústne ústroje špecializované (podrobnejší opis pozri Morfologická charakteristika). Samotná tráviaca rúra je točitá a asi dvakrát dlhšia ako telo. Zvyčajne rozlišujeme tri dobre odlíšiteľné časti – predné, stredné a zadné črevo. Predné a zadné črevo majú ektodermálny pôvod, stredné črevo má endodermálny pôvod. Črevo je dobre zásobované vzdušnicami, ktoré ho držia v telovej dutine medzi lalokmi tukového telesa. Svalové steny predného čreva sú inervované sympatickým nervovým systémom a zadné črevo nervami z terminálneho abdominálneho ganglia (Cornwell 1968).

Predné črevo (stomodeum) sa začína ústnou dutinou (cavum oris). V jej hornej časti je hypofarynx a epifarynx. Odtiaľ potrava prechádza do dolnej časti – do slinovníka (salivarium) a po premiešaní slinami prechádza do hltanu. Hltan (pharynx) je vybavený rozťahovacími svalmi umožňujúcimi jeho značné zväčšenie (veľká žravosť je pre šváby typická). Ďalej prechádza potrava cez pažerák (oesophagus) a dobre vyvinutý hrvoľ (ingluvies) do puchorčeka (proventriculus). Puchorček sa skladá vpredu z armária a vzadu zo stomodeálnych valvúl. Armárium je charakteristické 12 veľmi komplikovanými, špecializovanými kutikulárnymi záhybmi. Každý záhyb má vpredu sklerotizované zúbkovanie, v strede je vankúšik pokrytý chĺpkami a vzadu chlopnička. Zúbkovanie a vankúšiky sú u švábov druhovo špecifické. S výnimkou druhov čeľade Blaberidae je zúbkovanie veľké alebo stredne veľké, u čeľade Blaberidae je veľmi malé. Prechod medzi puchorčekom a stredným črevom tvorí chlopnička predného čreva (valvula cardiaca). Táto chlopnička je vsunutá do stredného čreva a tvorí prechod medzi ektodermálnou a endodermálnou časťou čreva.

Stredné črevo (mesenteron) tvorí žalúdok (ventriculus). Vpredu má 8 slepých výbežkov (coeca). Na rozdiel od predného a zadného čreva je hemocélový povrch stredného čreva zásobovaný viscerálnymi vzdušnicami idúcimi od všetkých párov abdominálnych spirákul. Stredné črevo nemá kutikulárny lem. Jeho epitelový lem je zložený zo sekrečných a absorbčných buniek. Zadná časť stredného čreva je lemovaná Malpighiho rúrkami (vasa Malpighii; tvoria vylučovaciu sústavu). Je ich okolo 60 – 100 a sú usporiadané v skupinách po 6 (Blattidae), po 4 (Blattellidae) alebo po 3 (Blaberidae) (Leconte et al. 1967). Zúčastňujú sa na regulácii iónovej rovnováhy a obsahu vody v hemolymfe. U švábov z rodu *Periplaneta* rúrky obsahujú intracelulárne enzýmy .

Zadné črevo (proctodeum) má za úlohu odčerpávať vodu zo strávenej potravy. Výsledkom sú suché granule trusu. Zadné črevo je rozdelené na tri časti – tenké črevo (ileum), hrubé črevo (colon) a konečník (rectum). Tenké črevo je najkratšou časťou čreva. Hrubé črevo sa od ostatných častí ľahko rozozná podľa tmavej farby jeho obsahu. Na konečníku je 6 konečníkových papíl (papillae recti) (Cornwell 1968; Oschman & Wale 1969).

Slinné žľazy sú dobre vyvinuté, ležia v hrudi po oboch stranách pažeráka (oesophagus). Majú zvláštne vývody spojené do spoločného vývodu vyúsťujúceho v záhybe medzi hypofaringom a spodnou perou. Na každej strane je jeden veľký rezervoár.

Vylučovacie orgány (organa uropoetica). Vylučovanie je regulačný mechanizmus, pomocou ktorého sa udržuje množstvo dusíkatých látok, anorganických solí a vody v hemolymfe v uspokojivej rovnováhe a takto zabezpečuje stabilnú skladbu iónov a osmotický tlak. Konečným produktom metabolizmu je dusík. Jeho odstránenie v podobe kyseliny močovej je primárnou funkciou hmyzieho vylučovacieho systému. U švábov existujú štyri miesta zabezpečujúce reguláciu vylučovania: 1. Malpighiho rúrky, ktoré v spojení so zadným črevom sú zodpovedné za elimináciu odpadov cez konečník (anus), 2. určité bunky tukového telesa, ktoré sú schopné zadržiavať dusík v procese označovanom ako „vylučovanie skladovaním", 3. močové žľazy, špeciálne rúrky prídavných žliaz samčekov určitých druhov švábov, ktoré odstraňujú uráty (močovinu) v spojení so spermatofórom počas kopulácie a 4. kutikula, do ktorej môže byť odkladaný odpadový materiál, ktorý je následne počas zvliekania eliminovaný. Nie je možné povedať, ktoré z týchto miest vylučovania je u švábov primárne zodpovedné za reguláciu odpadov. Ak uvážime, že v Malpighiho rúrkach švábov nebola zistená kyselina močová ako základný konečný produkt exkrécie hmyzu, tak potom by veľkú úlohu pri regulácii odpadov mohlo hrať tukové teleso.

Tukové teleso (corpus adiposum) je u švábov silne vyvinuté, uložené je predovšetkým v abdominálnej oblasti. Vonkajšiu vrstvu tukového telesa tvoria dva typy buniek – trofocyty (tukové bunky) a urocyty (urátové bunky). Trofocyty sú zapojené do syntézy, skladovania a mobilizácie tukov a bielkovín, zatiaľ čo funkciou urocytov je zhromažďovanie urátov (kyselina močová a jej soli). Samičky švábov inkorporujú počas oogenézy kyselinu močovú do svojich ooték, kde je za pomoci bakteriocytov využitá počas embryogenézy. Bakteriocyty (mycetocyty alebo všeobecne symbiocyty) tvoria vnútornú časť tukového telesa. Obsahujú špeciálne intracelulárne bakteriálne symbionty nazývané bakteroidy (*Blattabacterium cuenoti*), ktoré sú obalené vakuolárnou membránou produkovanou eukaryotickými bunkami hostiteľa (Bigliardi et al. 1989). Bakteroidy sú veľmi dôležitou skupinou mikroorganizmov pravdepodobne všeobecne rozšírenou medzi švábmi. Doteraz boli zistené v desiatkach druhov švábov z mnohých rodov. Švábom poskytujú rôzne výživné látky a tak sa spolupodieľajú na ich normálnej výžive – recyklujú dusíkaté odpadové látky uložené v urátových bunkách. Odstránenie bakteroidov pomocou antibiotík spôsobuje zmeny v správaní, predĺženie vývoja, zvýšenie mortality a neschopnosť reprodukcie. Bakteroidy prenikajú i do vajíčkových buniek a transovariálne sa dostávajú i do embryí švábov.

Nervová sústava (systema nervosum). Nervová sústava švábov zodpovedá typicky hmyziemu vzoru nervovej sústavy. Skladá sa z troch sústav. Najznámejšia je centrálna nervová sústava (somatická sústava), ktorú tvorí mozog, ventrálna nervová páska a jej gangliá (nervové uzly). Ďalšie sú periférna (obvodová) a sympatická (viscerálna) nervová sústava.

Mozog (nadhltanový nervový uzol – ganglion supraoesophagale) leží nad pažerákom. Vznikol splynutím 3 hlavových ganglií a je rozdelený na tri časti. Predný mozog (protocerebrum), reprezentujúci splynutý pár ganglií optického článku (prozocefalónu), je rozdelený do dvoch hemisfér so zrakovými lalôčikmi (lobi optici) po stranách. Stredný mozog (deutocerebrum), reprezentujúci splynuté gangliá tykadlového článku (deutocefalónu), sa skladá z čuchových lalôčikov (lobi olfactori), z ktorých vybiehajú tykadlové nervy. Najmenší je zadný mozog (tritocerebrum). Vznikol z ganglií tretieho hlavového článku (tritocefalónu) a leží bočne od čreva.

Ventrálna nervová páska je u švábov zložená z 10 ganglií pospájaných párovými konektívami. Prvé ganglium (podhltanový nervový uzol – ganglion suboesophagale) vzniklo splynutím ganglií zvyšných troch hlavových článkov a leží pod pažerákom. S mozgom je spojené pomocou párových konektív (cirkumezofageálnych konektív) prechádzajúcich cez otvor v tentóriu. Tri gangliá sú v hrudi (ganglion thoracicum primum, secundum et tertium) a inervujú hrudné svaly (aj svaly nôh a krídiel). Jedno (prípadne až tri) z predných abdominálnych ganglií splýva so zadohrudným gangliom, čo má za následok prítomnosť iba 6 samostatných abdominálnych ganglií (bruškové nervové uzly – ganglia abdominales). Prvých 5 inervuje telové svalstvo. Šieste, terminálne abdominálne ganglium je väčšie ako predchádzajúcich 5 ganglií, lebo vzniklo splynutím ganglií viacerých terminálnych článkov.

Periférna nervová sústava sa skladá z nervov, ktoré vychádzajú z ganglií a inervujú všetky časti tela.

Sympatická nervová sústava vykazuje tak nervovú, ako aj endokrinnú (hormonálnu) aktivitu a skladá sa zo senzorických, motorických a asociačných nervov. Tvoria ju tri časti: a) stomatogastrická sústava obsahujúca gangliá a nervy inervujúce prednú časť čreva, b) ventrálny viscerálny nervový systém – nervy, ktoré vznikli z ventrálnej nervovej pásky, inervujú a spájajú spirákulá a c) kaudálna (proktodeálna) sústava, ktorá sa skladá z nervov vznikajúcich z terminálneho abdominálneho ganglia a inervujúca zadnú časť čreva (Cornwell 1968). Stomatogastrická nervová sústava je u švábov dobre vyvinutá. Skladá sa zo 4 ganglií – čelového ganglia (ganglion frontale), záhlavného ganglia (ganglion hypocerebrale), ingluviálneho ganglia a páru ganglií ležiacich na povrchu pučorčeka, z návratného nervu (nervus recurrens) a pažerákového nervu (nervus oesophagealis).

Vnútorné pohlavné orgány (organa genitalia interna). U samčekov švábov sa párové semenníky (testes) skladajú zo 4 alebo viacerých semenníkových folikulov (folliculi testiculares) obyčajne uzavretých v peritoneálnom obale. Semenovody (vasa deferentia) smerujú dozadu a ústia do semenometu (ductus ejaculatorius). Na prednom konci semenovodu je jeden alebo viac párov semenných váčkov a väčší počet tubulárnych prídavných žliaz (glandulae accesoriae) rôznej dĺžky. Tieto žľazy vylučujú materiál, z ktorého je vytvorený spermatofór. Sú očividne mezodermálneho pôvodu, u nýmf sa vyvíjajú z ampulky na konci každého semenovodu. U samčekov sa nachádza aj nepárová „chumáčová žľaza" rôzneho tvaru, ktorá leží pod prídavnými žľazami a ústi oddelene medzi falomérami.

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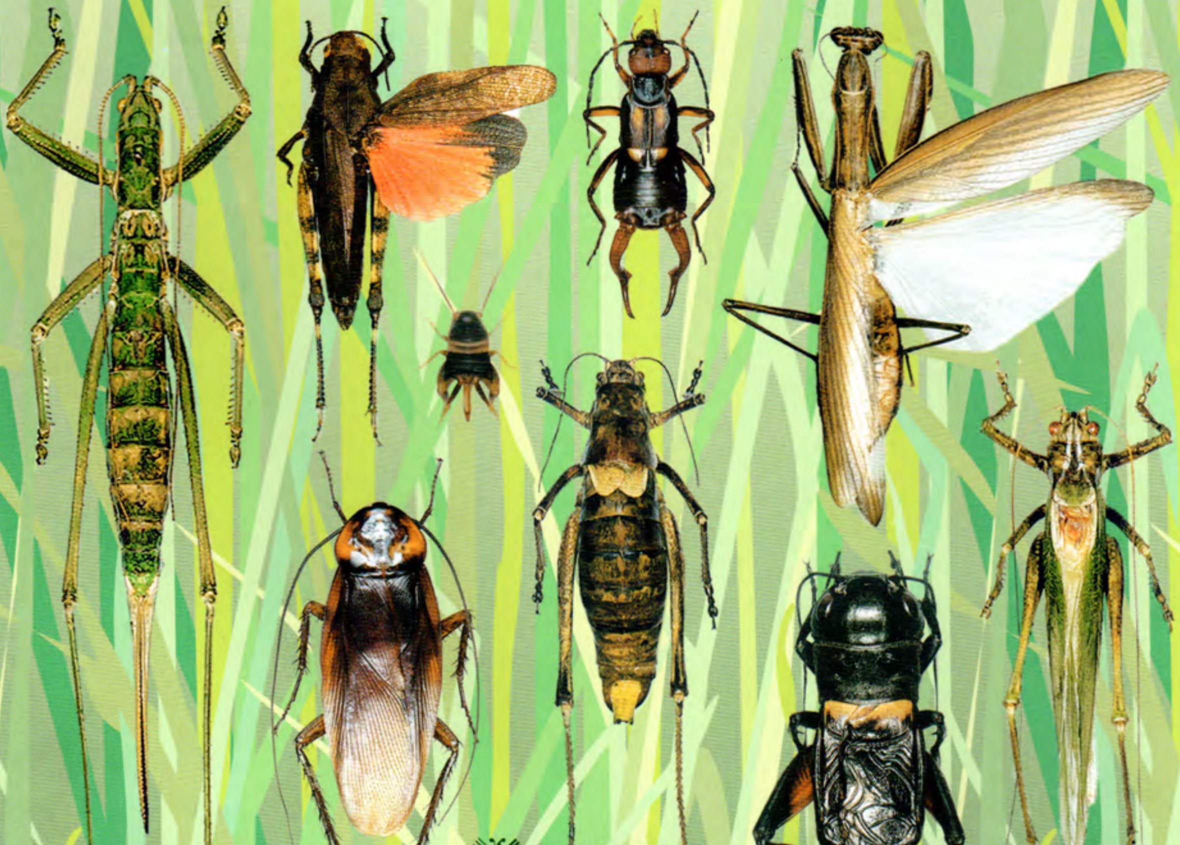

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The order Blattaria

Ľubomír Vidlička

Introduction

Extant cockroaches (Blattaria) are a relatively small insect group encompassing about 4,000-4,500 species described and classified in approximately 460 genera. They belong to the exopterygote Neoptera and, together with the orders Grylloblattodea, Mantodea, Isoptera, Phasmatodea, Orthoptera, Dermaptera, Embioptera and Zoraptera, to the series Polyneoptera.

Most extant cockroaches inhabit warm forests of the tropics and subtropics. Only about 2-3% of the known species inhabit the temperate zone. In Europe, cockroaches only received more attention when the synanthropic species *Blatta orientalis* and *Blattella germanica* entered major European ports with Greek merchant vessels and unstoppably invaded the entire continent. Various forms of the word "kakerlac", apparently derived from the Spanish "cucaracha", have been used as vernacular names for cockroaches. Besides the English name, its equivalents are still used to denote a cockroach in other countries, such as kakerlac in the Netherlands and Denmark, kackerlacka in Sweden, kackerlackor in Finland and cackerlac and cancrelat in France. The Czech and Slovak common name "šváb" comes from the German "Schwab(e)" and "Schabe". The generic name *Blatta*, which is also the stem of the order's name, is derived from the Greek βλαπτω (to harm, be harmful, injure, damage). Any harmful and cryptic domiciliary insects used to be called by that name in old Latin literature.

The systematics of cockroaches is rather disparate, although two approaches are most frequently used at present. The first one developed by Princis (1962-1971) divides cockroaches into 28 families. The other one recognises 6 families: Polyphagidae, Blattellidae, Blaberidae, Blattidae, Cryptocercidae and Nocticolidae (McKittrick, 1964, Roth, 1988). In the Czech and Slovak Republics, one may find only the native representatives of the family Ectobiidae (sometimes included in the family Blattellidae) freely in nature; our domiciliary species belong to the families Blattidae and Blattellidae. Members of the family Polyphagidae inhabit more southern and arid parts of the Palaearctic and Nearctic regions. The family Cryptocercidae has only 5 species distributed in the Palaearctic and Nearctic regions; Grandcolas (1994) included this family in Polyphagidae. The speciose family Blaberidae is distributed mainly in the Neotropical, Indomalayan and Ethiopian regions. Species of a small family Nocticolidae are similarly distributed.

Bey-Bijenko (1950) treated cockroaches of the eastern part of the Palaearctic region, including most central European species in his revision. A key to central European species was published by Harz (1957). Princis (1965) and Harz & Kalten-

Řád Blattaria

Ľubomír Vidlička

Úvod

Švábi (Blattaria) tvoří v současnosti relativně malou skupinu hmyzu zahrnující okolo 4000-4500 popsaných druhů v přibližně 460 rodech. Patří mezi exopterygotní Neoptera. Spolu s řády Grylloblattodea, Mantodea, Isoptera, Phasmatodea, Orthoptera, Dermaptera, Embioptera a Zoraptera náleží do kohorty Polyneoptera.

Pro většinu recentních druhů švábů jsou domovem vlhké a teplé lesy tropické a subtropické zóny. Mírné pásmo obývají jen asi 2-3% známých druhů. V Evropě se švábi dostali do centra pozornosti až tehdy, když synantropní druhy *Blatta orientalis* a *Blattella germanica* pronikly řeckými obchodními loděmi do velkých evropských přístavů a odtud se nezadržitelně šířily po celé Evropě. V minulosti byli švábi označováni různými variantami výrazu „kakerlac“, odvozeného zřejmě od španělského „cucaracha“. I v současnosti se používají varianty tohoto jména na označování švábů v různých zemích – kakerlac (Holandsko a Dánsko), kackerlacka (Švédsko), kackerlackor (Finsko), cackerlac, cancrelat (Francie), cockroach (Anglie). Německé výrazy Schwab(e) a Schabe se staly základem pro slovenské i české pojmenování „šváb“. Rodové jméno *Blatta*, které tvoří i slovní základ názvu celého řádu, je odvozeno z řeckého slova βλαπτω (škodit, rušit, překážet). Ve starších latinských písemnostech se tímto jménem označoval každý škodlivý hmyz žijící skrytě v domácnostech.

Systematika švábů je značně nejednotná. V současnosti jsou nejpoužívanější 2 přístupy. První, vytvořený Princisem (1962-1971), dělí šváby na 28 čeledí. Podle druhého se švábi dělí na 6 čeledí: Polyphagidae, Blattellidae, Blaberidae, Blattidae, Cryptocercidae a Nocticolidae (McKittrick, 1964, Roth, 1988). V přírodě se u nás vyskytují pouze zástupci čeledi Ectobiidae (někdy řazené do čeledi Blattellidae). Naše synantropní druhy jsou z čeledí Blattidae a Blattellidae. Zástupci čeledi Polyhagidae žijí v jižnějších a aridnějších částech palearktického a nearktického regionu. Čeleď Cryptocercidae má pouze 5 druhů rozšířených v palearktické a nearktické oblasti; Grandcolas (1994) řadí tuto čeleď k Polyphagidae. Druhově bohatá čeleď Blaberidae je rozšířená především v neotropické, indomalajské a etiopské oblasti. Podobné rozšíření mají také druhy malé čeledi Nocticolidae.

Šváby východní části palearktické oblasti zpracoval Bey-Bijenko (1950) a jeho práce zahrnuje také většinu středoevropských druhů. Klíč na určování středoevropských druhů vypracoval Harz (1957). Princis (1965) a Harz & Kaltenbach (1976) později zpracovali šváby celé Evropy. Podrobnou revizi rodu *Ectobius* publikoval Ramme (1923, 1951). Nověji se revizemi některých skupin rodu *Phyllodromica* zabývali Bohn (1992, 1993) a Vidlička & Majzlan (1997). Celobach (1976) subsequently treated cockroaches of the entire Europe. A thorough revision of the genus *Ectobius* was published by Ramme (1923, 1951). Recent revisions of some species-groups of the genus *Phyllodromica* have been carried out by Bohn (1992, 1993) and Vidlička & Majzlan (1997). A world catalogue of cockroaches was published by Princis (1962, 1963, 1964, 1965a, 1966, 1967, 1969, 1971). The biology of the cockroaches was studied by Roth & Willis (1960), Beier (1961, 1974), Cornwell (1968) and Rust et al. (1995).

The first faunistic data from the territory of the Czech Republic and Slovakia were reported by Seidl (1836) and Frivaldszky (1868), respectively. Faunistic data from Slovakia, taken from literature and museum collections, have recently been summarised by Vidlička & Majzlan (1992) and those from the Carpathian Basin by Vidlička & Sziráky (1997). The first key to all species of the former Czechoslovakia including the Subcarpathian Ukraine was published by Obenberger (1926a, 1926b). Later on, cockroaches were also treated within the series *Key to the fauna of Czechoslovakia* (Dobšík, 1959b). A key of the genus *Phyllodromica* including the recently described species was published by Vidlička (1994).

Adult morphology

Cockroaches are usually medium-sized to large insects. The smallest species belong to the genus *Nocticola* (about 3 mm), and the largest are in the genus *Blaberus* (up to 120 mm).

The body is dorsoventrally flattened and often oval. The body surface is usually smooth and bare, only seldom (especially in desert and steppe species) with a comparatively dense pubescence. Cuticular projections, spines and a rough surface are rare.

The head is usually hypognathous, partly visible from above or entirely covered by the pronotum; it is transversely flattened with typical sutures. The epicranial suture is not always developed in adults. The frons and the clypeus are large, well developed. An opening in the central part is characteristic for the tentorium. The composed eyes are nearly always developed, and composed of a large number of small ommatidia. They are large, especially in winged species; rarely, they are reduced or entirely absent, especially in myrmecophilous and cavernicolous species. The ocelli are developed in some cockroaches; however, they are more often replaced by two pale, ocelliform spots near the inner eye margins. The antennae are multi-segmented, often longer than the body. They are filiform and tapering towards the apex, less frequently thickened in the median part and spindle-shaped. They are articulated to the head capsule in the middle of the inner eye margin. All antennomeres are usually covered by short fine hairs. The biting mouthparts consist of five well-separated parts – the labrum, mandibles, maxillae, hypopharynx and labium. The mandibles are robust, irregularly quadrangular, strongly sclerotised, and possess a dentate inner part. Each mandible bears an appendage (prostheca). The maxilla is composed of several parts. The cardo is short; the stipes is elongate and its inner face often bears a sclerite

BLATTARIA	page/str.	Figs./obr.
Blattidae		
Periplaneta Burmeister, 1838	→ 42/43	
P. americana (Linné, 1758)	→ 42/43	319
P. australasiae (Fabricius, 1775)	→ 42/43	320-321
P. brunnea Burmeister, 1838	→ 42/43	
Blatta Linné, 1758	→ 42/43	
B. orientalis Linné, 1758	→ 42/43	322-323
Blattellidae		
Blattella Caudel, 1903	→ 44/45	
B. germanica (Linné, 1767)	→ 44/45	324-325
Supella Shelford, 1911	→ 44/45	
S. longipalpa (Fabricius, 1798)	→ 44/45	326-327
= *supellectilium* Serville, 1839		

	page/str.	Figs./obr.
Ectobiidae		
Ectobius Stephens, 1835	→ 46/47	
E. lapponicus (Linné, 1758)	→ 48/49	328-329
E. sylvestris (Poda, 1761)	→ 46/47	330-332
[*E. erythronotus erythronotus* (Burr, 1913)]	→ 48/49	
[*E. erythronotus ater* Bazyluk, 1961]	→ 48/49	
E. erythronotus nigricans Ramme, 1923	→ 48/49	333-334
Phyllodromica Fieber, 1853	→ 50/51	
= *Hololampra* Saussure, 1864		
P. dobsiki Chládek, 1996	→ 54/55	
P. harzi Chládek, 1977	→ 52/53	335-336
P. hungarica Vidlička, 1993	→ 54/55	337-338
P. chladeki Harz, 1977	→ 50/51	339-340
P. maculata maculata (Schreber, 1781)	→ 52/53	341-342
P. maculata schaefferi (Gmelin, 1789)	→ 52/53	343-344
P. megerlei Fieber, 1853	→ 50/51	345-346
= *punctata* Charpentier, 1825		


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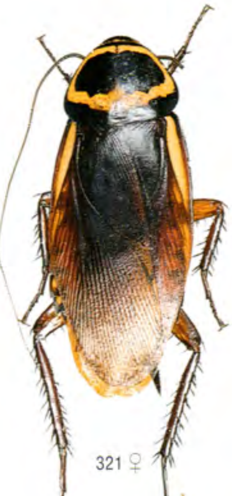
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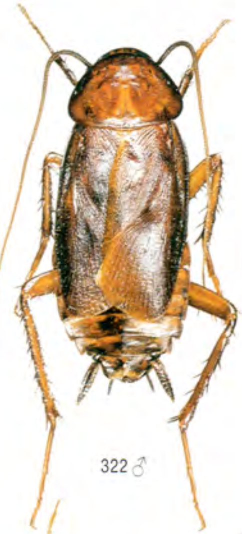
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