Native *Ectobius* (Blattaria: Ectobiidae) From the Early Eocene Green River Formation of Colorado and Its Reintroduction to North America 49 Million Years Later

P. VRŠANSKÝ,[1,2] R. ORUŽINSKÝ,[3] P. BARNA,[1] L'. VIDLIČKA,[4] AND C. C. LABANDEIRA[5,6,7]

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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.

[1] Geological Institute, Slovak Academy of Sciences, Dúbravska c. 9, P.O. Box 106, 840 05 Bratislava, Slovakia.
[2] Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117868, Moscow, Russia.
[3] Geological Institute, Slovak Academy of Sciences, Ďumbierska 1, 974 01 Banská Bystrica, Slovakia.
[4] Institute of Zoology, Slovak Academy of Sciences, Dúbravska c. 9, 845 06 Bratislava, Slovakia.
[5] Department of Paleobiology, MRC-121, P.O. Box 37012, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012.
[6] Department of Entomology and BEES Program, University of Maryland, College Park, MD 20742.
[7] Corresponding author, e-mail: labandec@si.edu.

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.

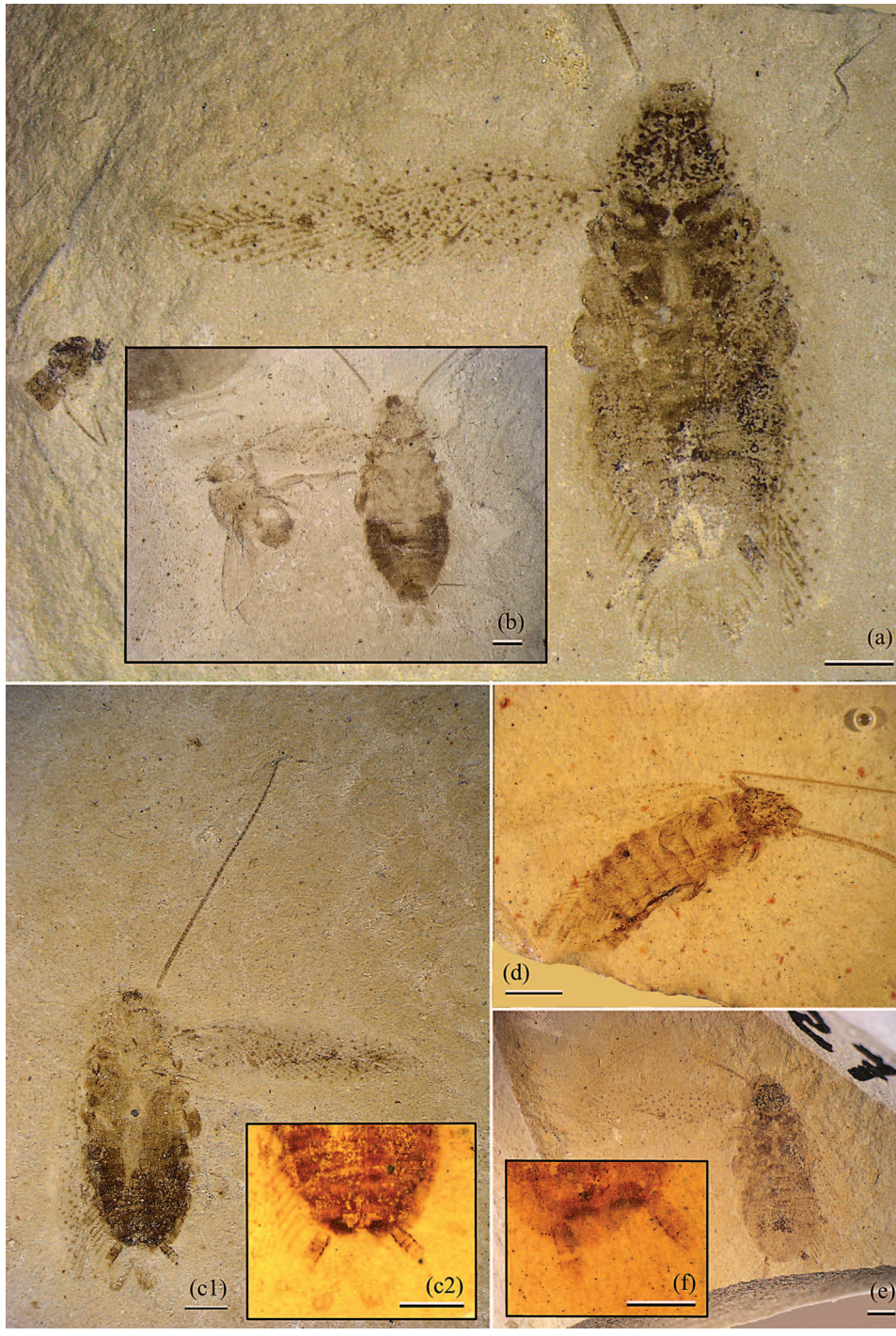

Fig. 1. *E. kohlsi* Vršanský, Vidlička et Labandeira sp. n. (a) **HOLOTYPE.** 41679/53274; negative relief; complete female specimen. (b) 41142/57545; positive relief; complete male specimen. (c1–2) 41142/57239; positive relief, complete female specimen and detail of terminalia. (d) 41075/27701 (negative, 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.

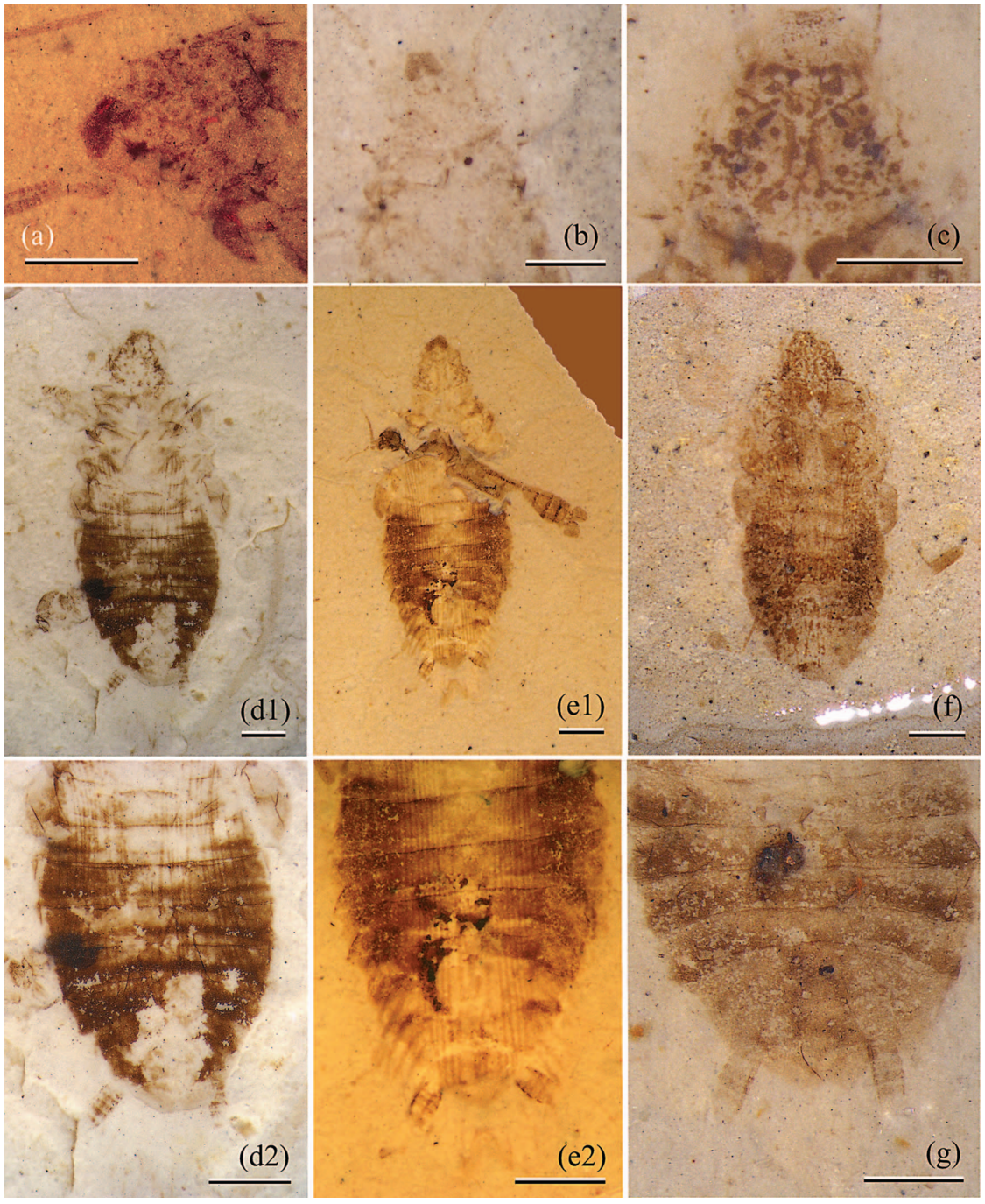

Fig. 2. a–g, *E. kohlsi* Vršanský, Vidlička et Labandeira sp. nov. (a) 41075/27701; positive relief; detail of head and pronotum. (b) 41142/57545; positive relief; male specimen with pronotum. (c) HOLOTYPE. 41679/53274; negative relief, female specimen with pronotum. (d1–2) 41093/75726; positive relief; 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-*

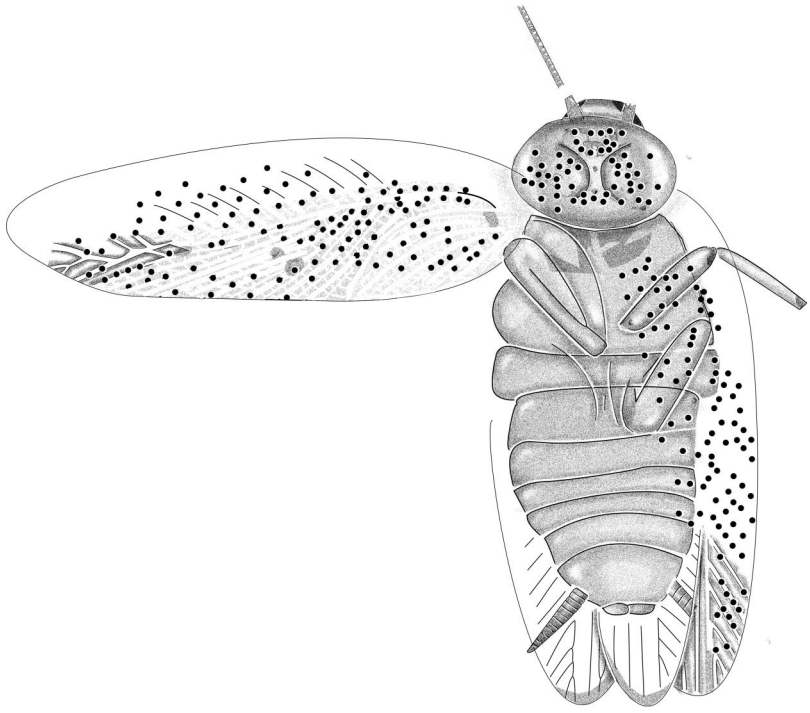

Fig. 3. *E. kohlsi* Vršanský, Vidlička et Labandeira n. sp. HOLOTYPE. 41679/53274; A complete female. The repository is the NMNH, Washington, DC, Green River Formation, latest early Eocene, Piceance Creek Basin, northwestern Colorado. Dots correspond to dorsal sensilla. Negative compression; the right 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-

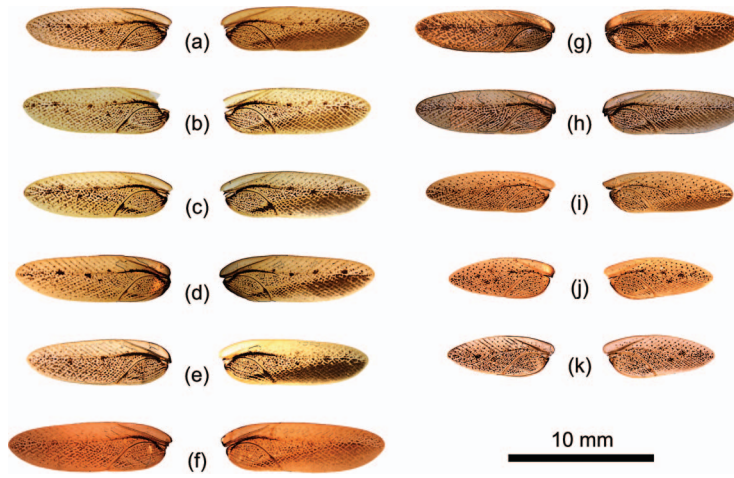

Fig. 4. (a–k) Modern forewings of one population of males of *E. sylvestris* males, occurring at Jur, near Bratislava, Slovakia. Collection of the Zoological Institute SAS, Bratislava. Specimens Es01/1–26/2.

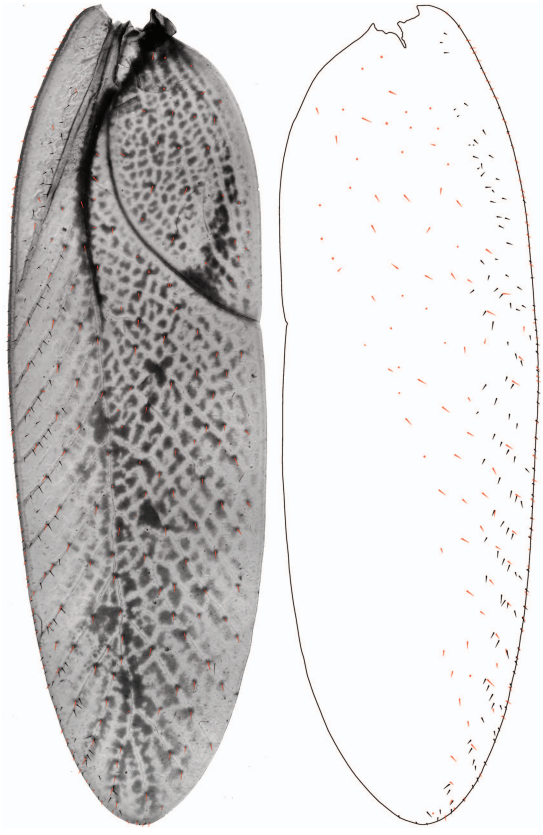

Fig. 5. Left and right forewing of the sensillar system of a modern male of *E. sylvestris*, from Jur, near Bratislava, Slovakia. The collection is from the Zoological Institute SAS, Bratislava. Specimen Es1–2. Black dots represent ventral sensillae; red dots are dorsal structures providing for the presence 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).

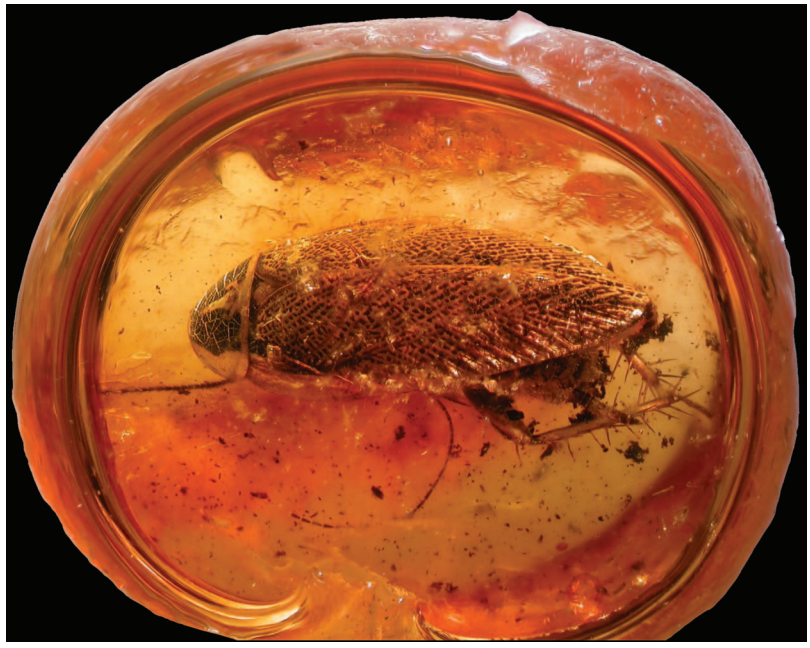

Fig. 6. *E. balticus* Germar et Berendt, 1856, from the early middle Eocene Baltic amber. Gusakov collection no. VI-008. Original image courtesy of D. S. Shcherbakov.

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.

Acknowledgments

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References Cited

Adelung, N. 1904. Eine neue *Ectobia*, *E. duskei* n. sp. (Orthoptera, Blattodea), vom Bogdo, sovie einige Bemerkungen über russischen Varietäten der *E. perspicillaris* Herbst (*livida* Fabr.). Lebensbild Eines großen Russischen Entomologen 37: 127–137.

Atkinson, T. H., P. G. Koehler, and R. S. Patterson. 1991. Catalog and atlas of the cockroaches of North America north of Mexico. Misc. Publ. Entomol. Soc. Am. 78: 1–85.

Baur, H., I. Landau-Lüscher, G. Müller, M. Schidt, and A. Coray. 2004. Taxonomie der Bernstein—Waldschabe *Ectobius vittiventris* (A. Costa, 1847) (Blattodea: Ectobiidae) und ihre Verbreitung in der Schweiz. Revue Suisse de Zoologie 111: 395–424.

Bei-Benko, G. 1935. Description of six new species of Palearctic Blattodea. Konowia 14: 117–134.

Bei-Benko, G. 1950. Insects: cockroaches, pp. 332–336. *In* A. A. Shtackelberg (ed.), Fauna U.S.S.R., New Series. U.S.S.R. Academy of Sciences, Moscow, Russian.

Bohn, H. 1989. Revision of the *Sylvestrys* group of *Ectobius* Stephens in Europe (Blattaria: Ectobiidae). Entomol. Scand. 20: 317–342.

Bohn, H. 2004. The Blattoptera fauna of Switzerland and the adjacent regions of France, Italy and Austria. I. The species of the *sylvestris*-group of *Ectobius* (Ectobiidae, Ectobiinae). Spixiana 27: 253–285.

Brunner von Wattenwyl, W. C. 1865. Noveau système des Blattaires. G. Bramüller, Vienna, Austria.

Brunner von Wattenwyl, W. C. 1882. Prodromus der europäischen Orthopteren. Wilhelm Engelmann, Leipzig, Germany.

Chandler, D. S. 1985. A new introduction of a European cockroach, *Ectobius lapponicus* (Dictyoptera: Blatellidae). Entomol. News 96: 98–100.

Chandler, D. S. 1992. New records of *Ectobius lapponicus* in North America (Dictyoptera: Blatellidae). Entomol. News 103: 139–141.

Comstock J. H., and J. G. Needham. 1898. The wings of insects. Am. Nat. 32, 376: 231–257.

Costa, A. 1847. Memorie entomologiche. Estr. degli Ann. dell' Accad. Degli Aspiranti Naturalisti 2. Ser. (Ortotteri) 1: 80.

Costa, A. 1866. [1860–70]. Fauna del Regno di Napoli ossia enumerazione di tutti gli animali che abitano le diverse regioni di questo Regno e le acque che le bagnano e descrizione de'nuovi o poco esattamente conosciuti con figure ricavate da originale viventi e dipinte al naturale. Nevrotteri. Stamperia di Antonio Cons, Naples, Italy.

Failla, M. C., and A. Messina. 1977. Ectobius minutus, nuova specie di Blattodea delle isole ponziane (Insecta, Blattodea, Ectobiidae). Animalia 4: 217–222.

Failla, M. C., and A. Messina. 1981. Una nuova specie di *Ectobius* di Sicilia e redescrizione de *Ectobius aetneus* Ramme. (Insecta, Blattaria, Ectobiidae). Animalia 8: 43–49.

Galvagni, A. 1978. Ectobius tuscus nuova specie dell'Isola Capraia (Insecta, Blattoptera, Ectobiinae). Atti della Accademia Roveretana degli Agiati 16/17B: 187–192.

Germar, E. F., and G. C. Berendt. 1856. Die im bernstein befindlichen hemipteren und orthopteren der vorwelt, pp. 1–110. *In* G. C. Berendt (ed.), Die im Bernstein Befindlichen Organischen Reste der Vorwelt, vol. 2. Commission der Nicholai Schen Buchhandlung, Berlin, Germany.

Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. Ogg. 2012. The Geologic Time Scale 2012. Elsevier, Boston, MA.

Hail, W. J., Jr. 1992. Geology of the central roan plateau area, northwestern Colorado. U.S. Geol. Surv. Bull. 1787-R: 1–26.

Helfer, J. R. 1987. How to know the grasshoppers, crickets, cockroaches and their allies. Dover, New York, NY.

Hoebeke, E. R., and D. A. Nickle. 1981. The forest cockroach, *Ectobius sylvestris* (Poda), a Eur. species newly discovered in North America (Dictyoptera: Blattodea: Ectobiidae). Proc. Entomol. Soc. Wash. 83: 592–595.

Hoebeke, E. R., and M. E. Carter. 2010. First North American record of *Ectobius lucidus* (Hagenbach) (Blattodea: Ectobiidae: Ectobiinae), with notes on recognition characters and seasonal history, and additional records for other *Ectobius* species in the Northeastern United States. Proc. Entomol. Soc. Wash. 112: 229–238.

Klass K.-D. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. Bonn Zool. Monogr. 42: 1–341.

Labandeira, C. C., K. R. Johnson, and P. Wilf. 2002. Impact of the terminal Cretaceous event on plant-insect associations. Proc. Natl. Acad. Sci. U.S.A. 99: 2061–2066.

Latreille, A. 1810. Considérations générales sur l'orde naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes. Avec un tableau méthodique de leurs genre, disposées en familles. F. Schoell, Paris, France.

Linneaus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentis, synonymis, locis, vol. 1, 10th ed. Holmiae, Sweden.

Mielke, V. U. 2000. Über das auftreten der lapplandschabe (*Ectobius lapponicus* (Linne 1758)) in Gebaeuden. Anz. Schaedlingsk 73: 152–154.

Nielsen, G. R. 1987. [No title given.] Vermont Entomol. Pl. Pathol. News 8: 22–23. 10: 26–27.

Poda, N. 1761. Insecta musei graecensis, quae in ordines, genera et species juxta Systema Naturae Caroli Linnaei. Widmanstadius, Graz, Austria.

Princis, K. 1963. Ergebnisse der Albanien-expedition 1961 des Deutschen Entomologischen Institutes. 9. Beitrag Blattariae. Beitr. Entomol. 13: 65–71.

Ramme, W. 1923. Vorarbeiten zu einer monographie des blattiden genus *Ectobius* Steph. Archiv Naturges 89A: 97–145.

Ramme, W. 1927. Die dermapteren und orthopteren Siziliens und Kretas. Mit kritischen Beiträgen und Revision aus den Gattungen *Hololampra Sauss.*, *Acrometopa* Fieb., *Pholidoptera* Br., *Platycleis* Fieb. u. a. Eos. 3: 111–200.

Rasnitsyn, A. P. 2002. Superorder Blattidea Latreille, 1810, pp. 260–270. *In* A. P. Rasnitsyn and D. L. J. Quicke (eds.), History of Insects. Kluwer, Dordrecht, The Netherlands.

Roth, L. M., and E. R. Willis. 1960. The biotic associations of cockroaches. Smithson. Misc. Coll. 141: 1–470.

Schmied, H. 2009. Cockroaches (Blattodea) from the middle Eocene of Messel (Germany). Diploma thesis, University of Bonn, Germany.

Scholczová, L. 2013. Švàby rodu *Ectobius* a ich rozšírenie v Európe. B.A. thesis, Comenius University, Bratislava, Slovakia.

Seoane, V. L. 1879. Description de deux orthoptérès nouveaux d'Éspagne. Mitt. Schweiz. Entomol. Ges. 5: 485–487.

Smith, M. E., A. R. Carroll, and B. S. Singer. 2010. Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, Western United States. Geol. Soc. Am. Bull. 120: 54–84.

Statz, G. 1939. Geradflüger der oligocänen Ablagerungen von Rott. Decheniana 99A: 1–102.

Stephens, J. F. 1835. [1836–1837]. Illustrations of British Entomology; or, a synopsis of indigenous Insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. vol. 6. Mandibulata. Baldwin & Cradock, London, United Kingdom.

Strasser, M. 1998. Mya arenaria: an ancient invader of the North Sea coast. Helgoländer Meeresuntersuchungen. 52: 309–324.

Vidlička, L'., and G. Sziráki. 1997. The native cockroaches (Blattaria) in the Carpathian Basin. Folia Entomol. Hungarica 58: 187–220.

Vršanský, P. 1997. *Piniblattella* gen. nov.: the most ancient genus of the family Blattellidae (Blattodea) from the Lower Cretaceous of Siberia. Entomol. Prob. 28: 67–79.

Vršanský, P. 2002. Origin and the evolution of mantises. AMBA Proj. 6: 1–16.

Vršanský, P., V. N. Vishniakova, and A. P. Rasnitsyn. 2002. Order Blattida Latreille, 1810, pp. 263–270. *In* A. P. Rasnitsyn and D.L.J. Quicke (eds.), History of Insects. Kluwer Academic, Dordrecht, The Netherlands.

Vršanský, P., P. Cifuentes-Ruiz, L'. Vidlička, F. Čiampor Jr., and F. J. Vega. 2011. Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. Geol. Carpath. 62: 463–475.

Vršanský, P., L'. Vidlička, J. R. Čiampor, Jr., and F. Marsh. 2012. Derived, still living cockroach genus *Cariblattoides* (Blattida: Blattellidae) from the Eocene sediments of Green River in Colorado, USA. Ins. Sci. 19: 143–152.

Vršanský, P., L'. Vidlička, P. Barna, E. Bugdaeva, and V. Markevich. 2013. Paleocene origin of the cockroach families Blaberidae and Corydiidae: evidence from Amur River region of Russia. Zootaxa 3635: 117–126.

Wei, D.-D., and D. Ren. 2013. Completely preserved cockroaches of the family Mesoblattinidae from J/K Yixian Formation, China. Geol. Carpath. 64: 291–304.

Zherikhin, V. V. 1970. Zoogeographical relations of Palaeogene insects, pp. 29–88. *In* Lectures on the Twelfth Annual Readings in Memory of N.A. Kholodkovsky, 14 April 1969, Nauka, Leningrad, U.S.S.R. Russian.

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