



***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* Vršanský 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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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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TABLE 1. The Cenozoic fossils of Ectobiidae.

Subfamily*	Genus	Species	Epoch	Location	Reference
Anaplectinae	<i>Anaplecta</i>	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Blattellinae	<i>Ischnoptera</i>	sp.	Miocene	Chiapas amber (Mexico)	Solórzano Kraemer, 2007
Blattellinae	? <i>Symploce</i>	<i>rete</i>	Pleistocene	African copal	Gorochov, 2007
Ectobiinae	<i>Agrabtoblatta</i>	<i>symmetrica</i>	Pleistocene	African copal	Gorochov, 2007
Ectobiinae	<i>Ectobius</i>	<i>arvernensis</i>	Paleocene	Menat (France)	Piton, 1940
Ectobiinae	<i>Ectobius</i>	<i>balticus</i>	Eocene	Baltic amber	Germer and Berendt, 1856
Ectobiinae	<i>Ectobius</i>	<i>menatensis</i>	Paleocene	Menat (France)	Piton, 1940
Ectobiinae	<i>Ectobius</i>	<i>glabellus</i>	Late Oligocene	Rott (Germany)	Statz, 1939
Ectobiinae	<i>Ectobius</i>	<i>kohlsi</i>	Early Eocene	Green River (USA)	Vršanský et al., 2014
Ectobiinae	<i>Ectobius</i>	spp. (3)	Early Eocene	Green River (USA)	Vršanský et al., 2011
Ectobiinae	<i>Isoplates</i>	<i>longipennis</i>	Middle Eocene	Gieseltal (Germany)	Haupt, 1956
Ectobiinae	<i>Telmablatta</i>	<i>impar</i>	Middle Eocene	Gieseltal (Germany)	Haupt, 1956
Nyctoborinae	<i>Nyctibora</i>	<i>elongata</i>	Late Oligocene	Rott (Germany)	Statz, 1939
Pseudophyllodromiinae	<i>Cariblatta</i>	spp. (2)	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiina	<i>Cariblattoides</i>	<i>labandeirae</i>	Early Eocene	Green River (USA)	Vršanský et al., 2012
Pseudophyllodromiina	<i>Euthlastoblatta</i>	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiinae	<i>Latiblattella</i>	<i>Avita</i> sp. nov.	Middle Eocene	Kishenehn Formation (USA)	Vidlička and Greenwalt (This study)
Pseudophyllodromiinae	<i>Plectoptera</i>	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiinae	<i>Plectoptera</i>	<i>electrina</i>	Miocene	Haitian amber	Gorochov, 2007
Pseudophyllodromiinae	<i>Pseudosymploce</i>	sp.	Miocene	Dominican amber	Gutiérrez and Pérez-Gelabert, 2000
Pseudophyllodromiinae	<i>Supella</i>	<i>miocenica</i>	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 sub-

family Ectobiinae, provide most of the extant cockroach diversity in the Palaearctic (Bohn et al., 2013). Ectobiidae, which originated from the family Mesoblattellidae, 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 $^{40}\text{Ar}/^{39}\text{Ar}$ 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)

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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

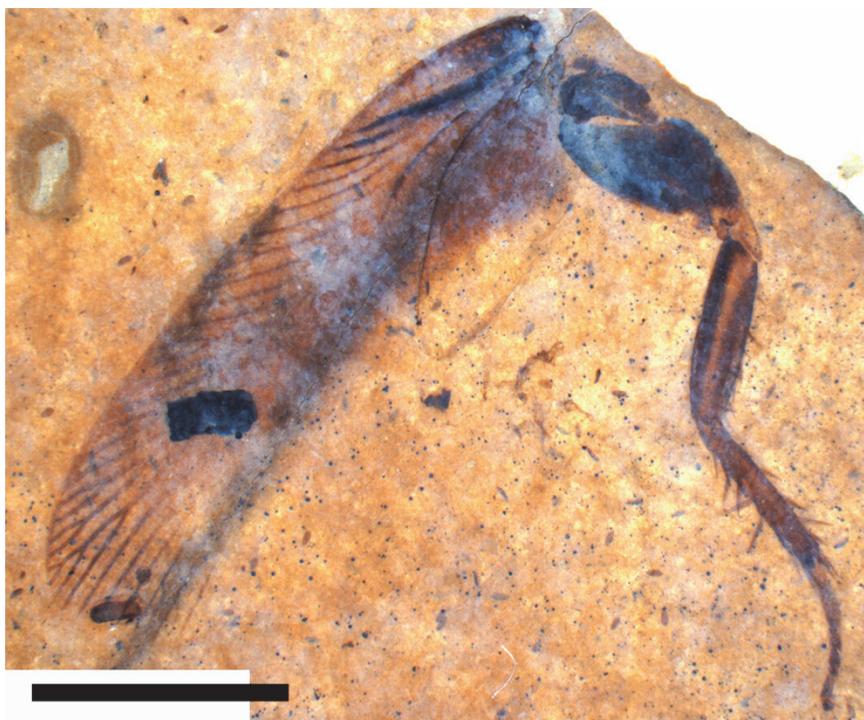


FIGURE 1. *Latiblattella avita* sp. nov. (USNM 595139). Tegmen attached (?) to an intact middle leg. Scale bar equals 5 mm.

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

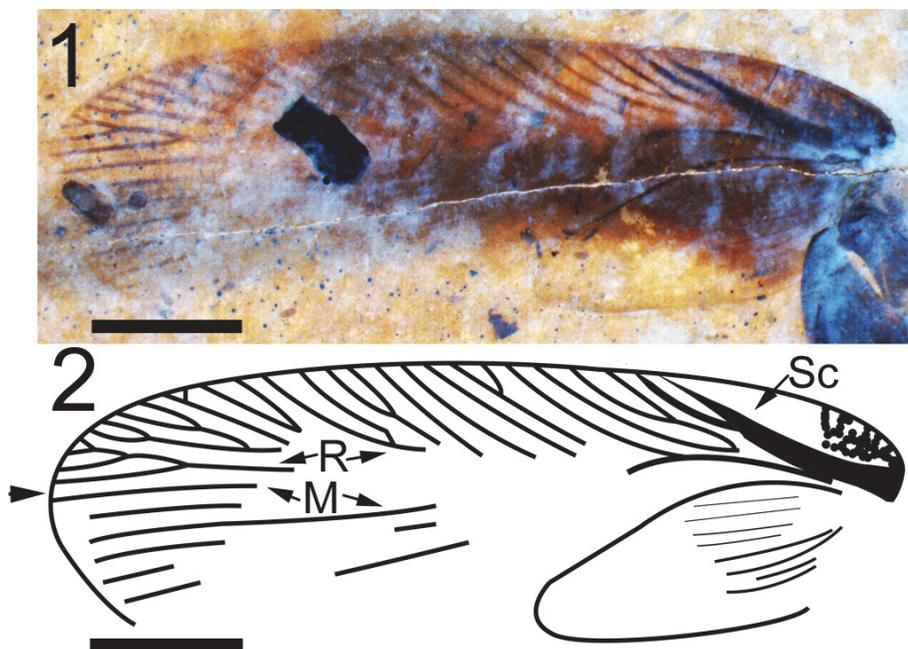


FIGURE 2. *Latiblattella avita* sp. nov. (USNM 595139). 2.1. A photograph of the tegmen. 2.2. A line drawing of the forewing venation. The arrow denotes the boundary between the radial and medial fields. M, medial veins; R, radial veins; Sc, subcostal vein. Scale bar equals 3 mm.

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 0.2 mm, 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 adimoniaalis* Walker, 1868 (see plate 1, figure 12 in Shelford, 1908) suggesting a close relationship to the colored representatives of *Latiblattella* 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).

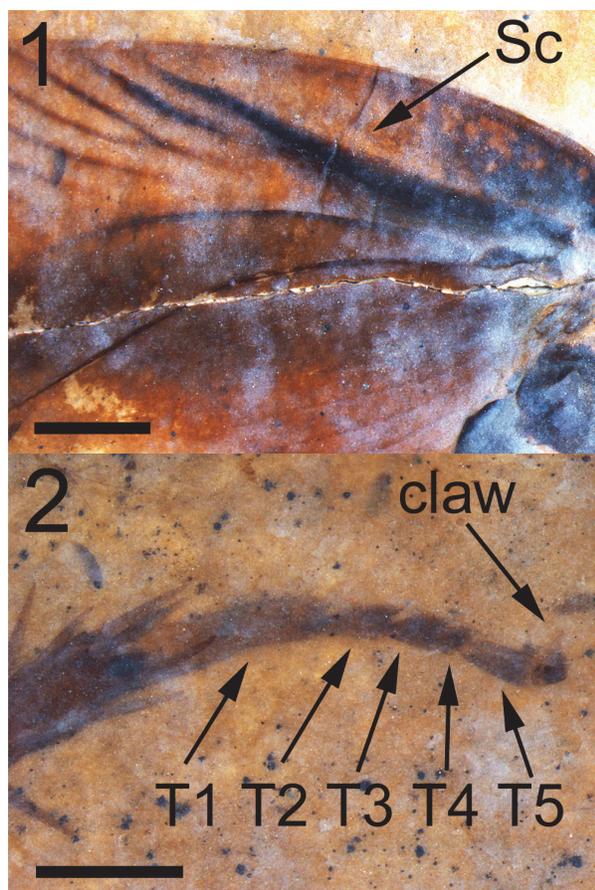


FIGURE 3. *Latiblattella avita* sp. nov. (USNM 595139). 3.1. The subcostal field of tegmen showing the wide and darkly pigmented Sc vein. 3.2. The five segmented tarsus. The arrows denote tarsal segments 1 – 5 and the end of the single visible claw. Scale bars equal 1 mm.

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; Gorochoy, 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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