

ORIGINAL ARTICLE

Derived, still living cockroach genus *Cariblattoides* (Blattida: Blattellidae) from the Eocene sediments of Green River in Colorado, USA

Peter Vršanský^{1,2}, L'ubomír Vidlička^{3,4}, Fedor Čiampor Jr³ and Finnegan Marsh⁵

¹Geological Institute, Slovak Academy of Sciences, Bratislava, Slovakia, ²Paleontological Institute, Russian Academy of Sciences, Moscow, Russia, ³Institute of Zoology, Slovak Academy of Sciences, ⁴Department of Biology, Faculty of Education, Comenius University, Bratislava, Slovakia, ⁵Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

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.

Correspondence: Peter Vršanský, Geological Institute, Slovak Academy of Sciences, Dúbravská cesta 9, P.O. Box 106, 840 05 Bratislava, Slovakia. Tel: +421 2 59203620; email: geolvrsa@savba.sk

This work was generated during the stay of the author in the NMNH, Washington, DC, USA.

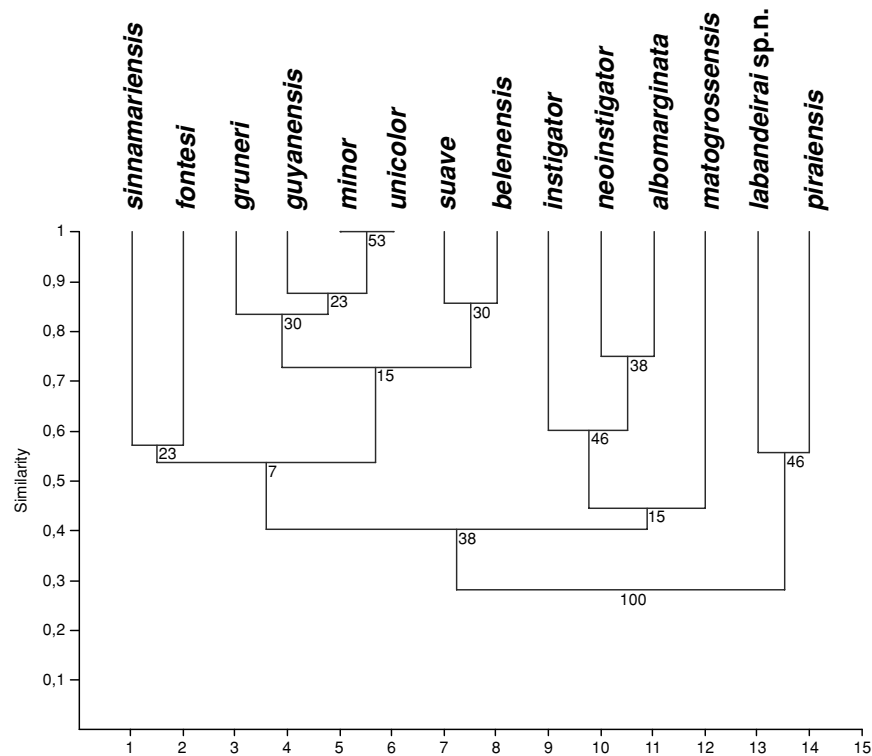


Fig. 1 Cluster analysis of *Cariblattoides* species. Jaccard similarity measure, paired group algorithm, with cophenetic correlation coefficient 0.838 9.

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 – ple-

siomorphic, 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, homoplasi- cally present also in some others, basal blattellid 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**

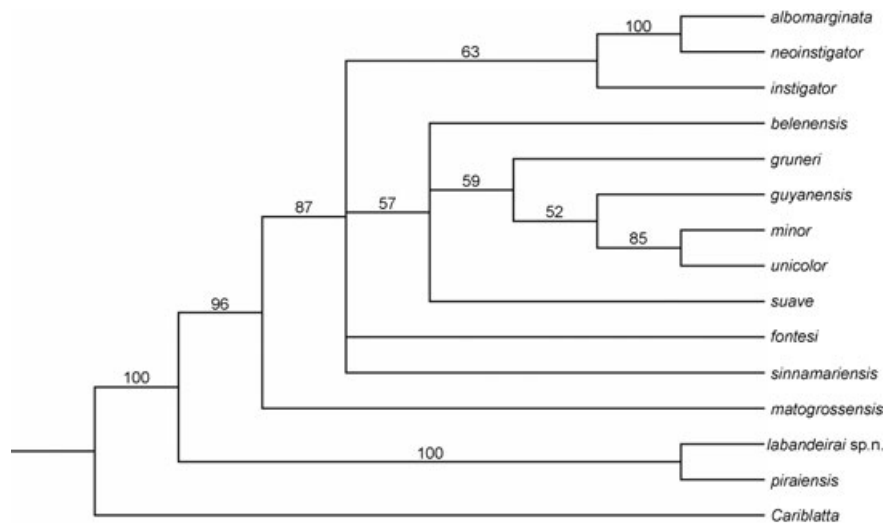


Fig. 2 Majority consensus tree of the parsimony analysis (46 equally parsimonious trees with length 30 [for details see Material and Methods]) of *Cariblattoides* species with *Cariblattea* used as outgroup. Numbers above branches show group frequencies (in %).

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 (discoial 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 quadrimarose; 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 *Cariblattea*, 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 *Cariblattea* 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 *Cariblattea* and *Neoblattella*)
4. *Terminal palpomere cup-like*: apomorphy; plesiomorphic state is normal shape of the terminal palpomere such as in *Cariblattea* 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); plesiomorphic 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*, *Neoblattella* 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 homoplastic)
 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 outgroup *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

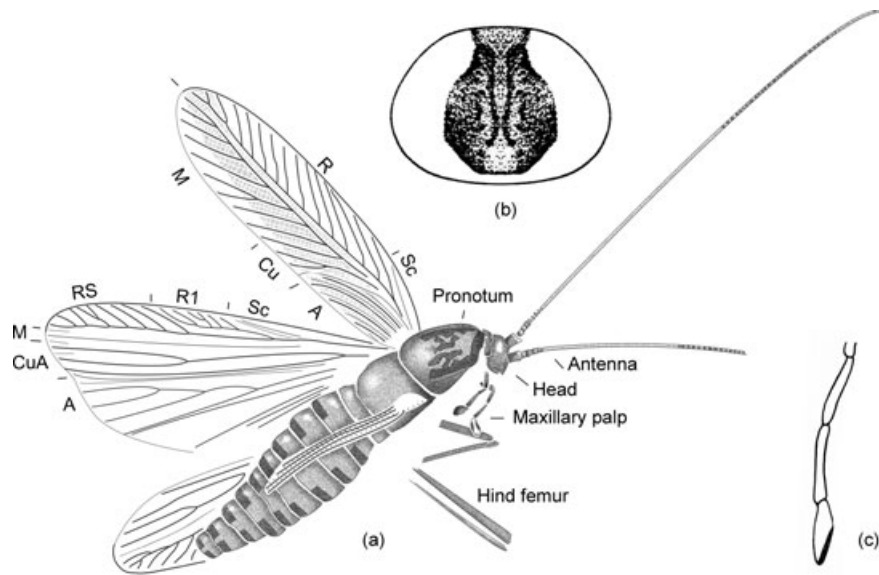


Fig. 3 *Cariblattoides labandeirai* sp.n. Holotype. NMNH 41619/542284-A. (A) A complete ?male. Eocene. Green River, Colorado, USA. Forewing length 10 mm. (B) pronotum of the female allotype (Aibonito, Guayama, Puerto Rico, July 14–17, 1914; HG Barber; AMNH New York) of the type species, *C. suave* Rehn et Hebard, 1927, identical to that of the *C. labandeirai* sp.n. holotype. (C) palpus of *C. guayanensis* Bonfils, 1975.

terminal segment cup-like (homoplasically in *Supella abotti* Rehn, 1947) allow the categorization 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 monophyletic 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 have 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 categorized 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* (Fabricius, 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 homoplasically 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 departed 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 descension 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.

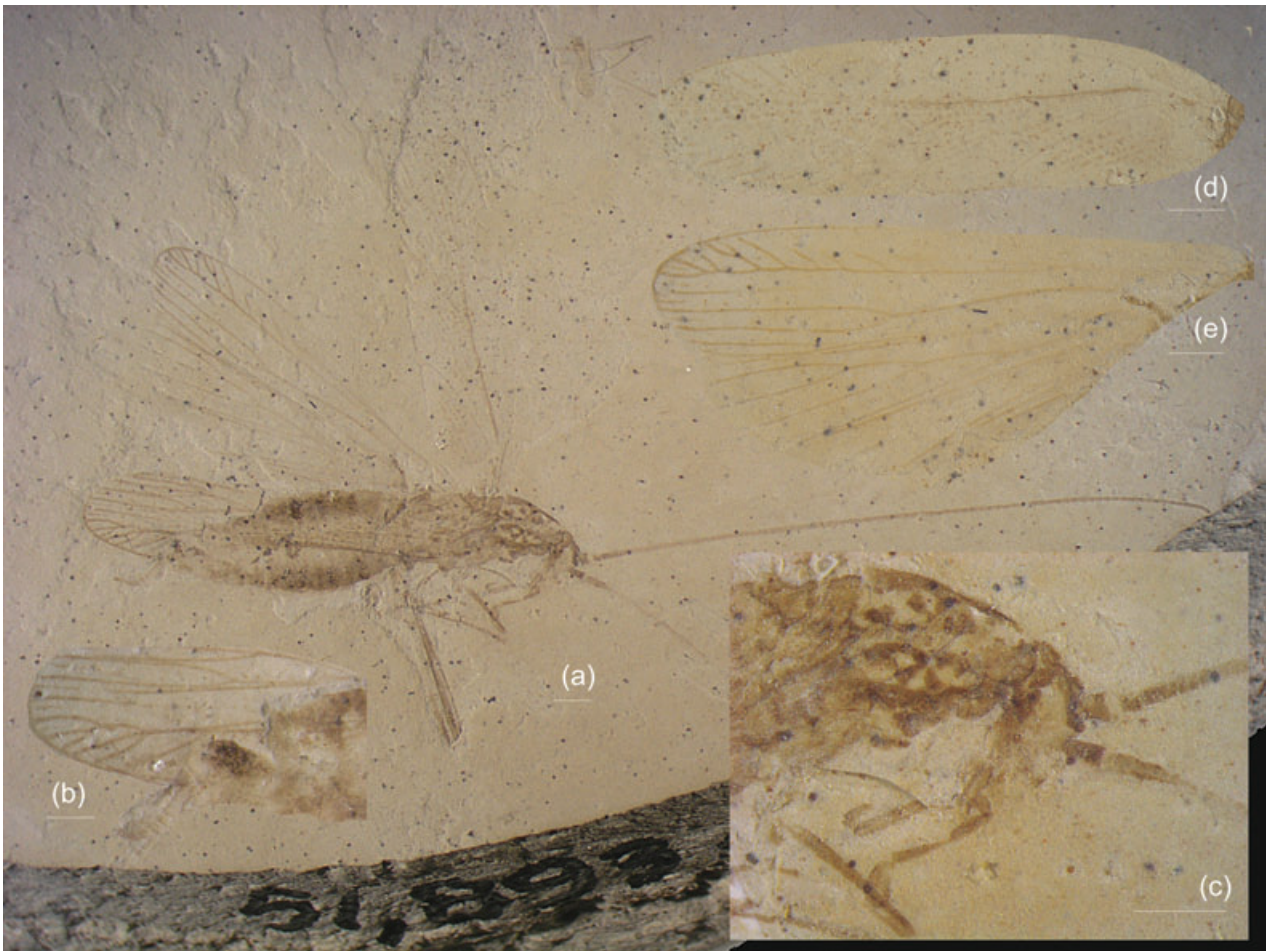


Fig. 4 *Cariblattoides labandeirai* sp.n. Holotype. NMNH 41619/542284. A complete ?male. Eocene. Green River, Colorado, USA. (A) general habitus; (B) forewing; (C) hindwing; (D) pronotum and head; (E) terminalia and hindwing. Forewing length 10 mm. Scales = 1 mm.

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

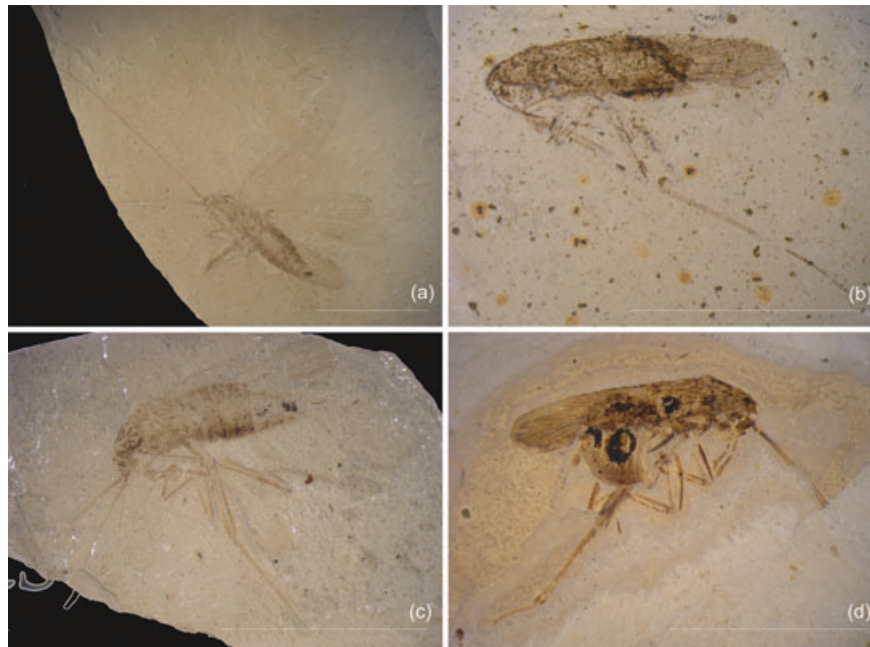


Fig. 5 *Cariblattooides labandeirai* sp.n. (A) Holotype NMNH 41619/542284-B; (B) NMNH 41139/542292 (PC) (Diptera collection databasis); (C) NMNH 40193/542286 (AP); (D) NMNH 41142/542293 (DS 4). Eocene. Green River, Colorado, USA. Scales = 10 mm.

Table 1 *Cariblattooides* character matrix of 13 extant and the present extinct species of *Cariblattooides*, 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
<i>Cariblatta</i> (OG)	0	0	0	0	0	0	0	0	0	0	?	0	0
<i>albomarginata</i>	0	0	0	0	0	0	0	0	0	1	1	?	1
<i>belenensis</i>	1	1	1	0	1	0	0	0	?	1	1	?	0
<i>fontesi</i>	1	0	1	0	0	0	0	1	1	1	1	1	0
<i>gruneri</i>	1	?	0	0	1	0	1	?	?	1	1	?	0
<i>guyanensis</i>	1	1	1	0	1	0	1	?	0	1	1	0	0
<i>instigator</i>	1	0	0	0	1	0	0	0	?	1	1	?	1
<i>labandeirai</i> sp.n.	0	1	1	1	1	1	0	1	1	0	0	1	0
<i>matogrossensis</i>	0	0	1	0	0	0	0	0	0	1	1	0	0
<i>minor</i>	1	1	1	0	1	0	1	?	1	1	1	?	0
<i>neoinstigator</i>	0	0	?	?	0	0	0	0	1	1	1	?	1
<i>piraiensis</i>	0	1	1	1	1	0	0	0	0	0	1	1	0
<i>sinnamariensis</i>	1	0	0	0	0	0	1	?	0	1	1	1	0
<i>suave</i>	1	1	1	0	1	0	0	0	0	1	1	1	1
<i>unicolor</i>	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 ex-

tremely 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.

Acknowledgments

We thank David Kohls and Louis Pribyl (NMNH Washington DC) for collecting the material, and Conrad Labandeira for organising the study; Alexandr P. Rasnitsyn (PIN Moscow), Sonia M. Lopés (MN/UFRJ), Pavel Štys (CU Prague) and Heiko Schmied (SI Bonn) for fruitful advice and revision of the manuscript, and Ladislav Roller (ZI Bratislava) for literature supply. Supported by the UNESCO, Amba, National Museum of Natural History, Washington D.C. award, VEGA 6002, 2/0125/09, 2/0167/09, MVTS and the Literary Fund.

References

- Bonfils, J. (1975) Blattopera (Orthopteroidea) récoltés en Guyane Française par la mission du Muséum national d'Histoire naturelle. *Annales de la Societe Entomologique de France (N.S.)*, 11(1), 29–63.
- Grandcolas, P. (1994) Blattaria (Insecta: Dictyoptera) of Saudi Arabia: a preliminary report. *Fauna of Saudi Arabia* 14 (eds.

- W. Büttiker & F. Krupp), pp. 40–58. National Commission for Wildlife Conservation and Development, Pro Entomologia, Riyadh, Basle.
- Hammer, Ø., Harper, D.A.T. and Ryan, P.D. (2001) PAST: Palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1), 1–9.
- Hebard, M. (1916) A new genus *Cariblatta*, of the group Blattellites (Orthoptera, Blattidae). *Transactions of the American Entomological Society*, 17, 147–186, pl. XI–XIII.
- Karny, H.H. (1908) Die zoologische Reise des Naturwissenschaftlichen Vereins nach Dalmatien im April 1906. B. Spezieller Teil. Bearbeitung des gesammelten Materiales. 6. Orthoptera und Blattaeformia. *Mitteilungen des Naturwissenschaftlichen Vereins an der Universität Wien*, 6, 8, 101–113.
- Latreille, P.A. (1810) *Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides et des Insectes avec un tableau méthodique de leurs genres disposés en familles*. Schoell, Paris. 1–444 pp.
- Princis, K. (1969) Blattariae: Subordo Epilamproidea: Fam.: Blattellidae. *Orthopterorum Catalogus. Pars 13* (ed. M. Beier), pp. 711–1038. Dr. W. Junk N.V., 's-Gravenhage.
- Rehn, J.A.G. (1937) African and Malagasy Blattidae (Orthoptera). Part. III. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 89, 17–123.
- Rehn, J.A.G. (1947) African and Malagasy Blattidae (Orthoptera). Part IV. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 99, 59–92.
- Rehn, J.W.H. (1951) Classification of the Blattaria as indicated by their wings (Orthoptera). *Memoirs of the American Entomological Society*, 14, 1–134.
- Rehn, J.A.G. and Hebard, M. (1927) The Orthoptera of the West Indies: No.1. Blattidae. *Bulletin of the American Museum of Natural History*, 54(1), 1–320.
- Rocha e Silva Albuquerque, I. (1954) Uma espécie de “Cariblattoides” Hebard, 1927 (Blattidae, Pseudomopinae). *Revista Brasileira de Biologia*, 14(4), 355–359.
- Rocha e Silva Albuquerque, I. (1955) Sôbre uma nova espécie de “Cariblattoides” Hebard, 1927 (Blattidae, Pseudomopinae). *Revista Brasileira de Biologia*, 15(1), 79–82.
- Rocha e Silva Albuquerque, I. (1958) Descrição de um alotipo e duas espécies novas de Cariblattoides Rehn & Hebard, 1927 (Blattidae – Pseudomopinae). *Boletim do Museu Nacional, N.S., Zoologia, Rio de Janeiro*, 184, 1–14.
- Rocha e Silva Albuquerque, I. (1964a) Sobre tres espécies novas de Blattaria do Brasil (Epilampridae-Blattellinae). *Boletim do Museu Paraense Emilio Goeldi, (N.S.), Zoologia*, 44, 1–9.
- Rocha e Silva Albuquerque, I. (1964b) Duas espécies de “Cariblattoides” Rehn & Hebard, 1927 (Epilampridae, Blattellinae). *Revista Brasileira de Biologia*, 24(2), 193–196.
- Rocha e Silva Albuquerque, I. (1967) Sobre quatro espécies novas de baratas da Amazônia (Dictioptera: Blattaria). *Boletim do Museu Paraense Emilio Goeldi*, 65, 1–11.
- Serville, J.G.A. (1839) *Histoire Naturelle des Insectes. Orthoptères*. Librairie Encyclopédique de Roret, Paris, 776 pp.
- Shelford, R. (1911) Preliminary diagnoses of some new genera of Blattidae. *The Entomologist's Monthly Magazine, (Second series)*22, 154–156.
- Schmied, H. (2009) Cockroaches (Blattodea) from the middle Eocene of Messel (Germany). Diploma thesis, University of Bonn.
- Swofford, D.L. (2002) *PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods)*, Version 4.0b10. Sinauer, Sunderland, MA.
- Vršanský, P. (1997) *Piniblattella* gen. nov. – the most ancient genus of the family Blattellidae (Blattodea) from the Lower Cretaceous of Siberia. *Entomological Problems*, 28, 67–79.
- Vršanský, P. (2008) Mesozoic relative of the common synanthropic German cockroach (Blattodea). *Deutsche Entomologische Zeitschrift*, 55, 215–221.

Accepted August 30, 2010