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A case of mistaken identification of an amber fossil male strepsipteran (Insecta: Strepsiptera).

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A well preserved specimen of amber Strepsiptera was erroneously described as *Stylops neotropicallis* Kogan and Poinar, 2010. The taxonomic position of the species was based on a count of 6 antennomeres (typical of the Stylopidae), however, further observations showed that there are actually 7 antennomeres, which places the fossil in the family Myrmecolacidae, and it is herein re-described in the genus *Palaeomyrmecolax* Kulicka, 2001. Furthermore, nuclear magnetic resonance spectroscopy analysis of a sample of the amber piece containing the fossil revealed that it was Baltic rather than Dominican amber as originally thought. The fossil was compared to another specimen from Baltic amber in the Poinar collection, which shows close affinity to *P. succineus* Kulicka, 2001, the type species of the genus. *P. neotropicallis* (n.comb.) differs from that specimen and seems to differ also from the other 4 species in the genus *Palaeomyrmecolax*.

Key words: *Stylops neotropicallis*, Myrmecolacidae, *Palaeomyrmecolax*, *Palaeomyrmecolax succineus*, Baltic amber

Introduction

The number of antennal segments is a key male character in the definition of Strepsiptera families. Antennae of the Myrmecolacidae are consistently 7-segmented, with only the 3rd segment bearing a long lateral flabellum. The antennae generally are long and slender, except for those Palearctic species found in Baltic amber (Kinzelbach and Pohl 1994; Pohl and Kinzelbach 1995; Kulicka 2001; Pohl and Beutel 2005; Kathirithamby and Henderickx 2008). In most of those species, antennal segments are short and stout.

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Most fossil Strepsipterans in the Poinar collection are myrmecolacids of Dominican amber origin. They are identified in the collection by a capital 'D' followed by 'St' (for

Strepsiptera) and a sequential number. Among these myrmecolacids are representatives of all four recognized extant genera (*Caenocolax*, *Myrmecolax*, *Stichotrema*, and *Lychnocolax*). One specimen (BSt-1-3a) is of Baltic origin (identified by the capital 'B') and belongs to the fossil genus *Palaeomyrmecolax* Kulicka, 2001. A well preserved specimen, embedded in a flat, sub-oval amber piece that was coded DSt-1-11 had striking characters that seemed to differ substantially from all other specimens in the collection and it was studied separately in 2007-2008. Among those characters were the frontally extended, anteriorly rounded post-frons, the large number (ca. 30) of small eyelets on the posteriorly extended eyes, and, above all, what we assumed based on our best optical assessment and imaging capabilities at the time, was a 6-segmented antenna. The specimen was reluctantly placed in the genus *Stylops*, because this genus, parasitic of solitary bees of the genus *Andrena* (Hymenoptera: Andrenidae), had been known only from temperate zones of the Nearctic and Palearctic regions. There are no records of extant Neotropical *Stylops*. The species was described as *Stylops neotropicallis* Kogan and Poinar, 2010.

The similarity of *S. neotropicallis* to the specimen coded in the collection as BSt1-3a and an inquiry (email from J. Cook to G. Poinar, Feb. 19, 2013) prompted us to re-examine the specimen. Equipped at present with a more advanced imaging system, it was possible to discern the presence of a small pedicellus (antennal segment II) that in our original study appeared fused with the scapus (segment I) (Figures 1(a), (b)). Consequently we had miscounted the number of segments; the antenna is indeed 7-segmented and *S. neotropicallis* belongs in the family Myrmecolacidae, not Stylopidae. Still, the species is atypical of both fossil and extant species of Neotropical myrmecolacids which led us to question whether there had been an added mistake in the origin of the amber piece. Upon NMR analysis of an amber sample from the original piece, it was confirmed that DSt-1-11 was Baltic, not Dominican, amber (J.B. Lambert, 2013, personal communication to G. Poinar; see also Lambert & Poinar 2002; Lambert et al. 1985) (Figure 6). The origin of the piece had been mistaken by the amber collector/dealer who provided it.

Despite some minor discrepant features that are pointed out below, it seems that *neotropicallis* belongs in the genus *Palaeomyrmecolax* Kulicka, 2001, as further defined by Pohl and Beutel (2005). Confirmation of the Baltic origin of the amber makes placement of *neotropicallis* in the genus *Palaeomyrmecolax* congruent with the known geographic distribution of the genus. The epithet – *neotropicallis* – however, remains inevitably incongruent.

The following is a partial re-description of the species. Description of the BSt1-3a specimen that seems to be very similar, if not conspecific, to *Palaeomyrmecolax succineus* Kulicka, 2001, is offered for comparative purposes. An assessment of the status of the 6 species currently included in the genus is made in the discussion section.

Fossil Myrmecolacidae

Males of the family Myrmecolacidae are characterized by 7-segmented antennae with only the 3rd segment extended into a slender and rounded flabellum (except *Palaeomyrmecolax* in which the flabellum is flattened); 4-segmented, clawless tarsi; blade-like long and narrow mandibles; and elongated, stout maxillary palps. Fifteen species of fossil myrmecolacids have been reported to date (Table 1).

Table 1. Fossil Myrmecolacidae

Species	Amber Origin	Reference
<i>Caenocholax dominicensis</i>	Dominican	Kathirithamby and Grimaldi, 1993
<i>Caenocholax brodzinskyi</i>	Dominican	Kathirithamby and Grimaldi, 1993
<i>Caenocholax</i> aff. <i>fenyesi</i>	Dominican	Poinar and Poinar, 1999
<i>Caenocholax groehni</i>	Baltic	Kathirithambi and Henderickx, 2008
<i>Myrmecolax glaesi</i>	Dominican	Kinzelbach, 1983; Kinzelbach and Pohl, 1994;
<i>Palaeomyrmecolax triangulum</i>	Baltic	Pohl and Kinzelbach, 1995; Pohl and Beutel, 2005
<i>Palaeomyrmecolax weitschati</i>	Baltic	Kinzelbach and Pohl, 1994; Pohl and Kinzelbach, 1995; Pohl and Beutel, 2005
<i>Palaeomyrmecolax gracilis</i>	Baltic	Kulicka, 2001; Pohl and Beutel, 2005
<i>Palaeomyrmecolax giecewiczi</i>	Baltic	Kulicka, 2001; Pohl and Beutel, 2005
<i>Palaeomyrmecolax succineus</i>	Baltic	Kulicka, 2001; Pohl and Beutel, 2005
<i>Palaeomyrmecolax neotropicallis</i>	Baltic	Kogan and Poinar, 2010 (as <i>Stylops neotropicallis</i>)
<i>Stichotrema beckeri</i> (Oliveira and Kogan, 1959)	Dominican	Kinzelbach and Pohl, 1994
<i>Stichotrema dominicanum</i>	Dominican	Kinzelbach and Pohl, 1994
<i>Stichotrema</i> sp.	Messel oil slate	Kinzelbach and Pohl, 1994
<i>Stichotrema eocaenicum</i> (Haupt, 1950)*	Brown coal-Halle-an-der-Salle	Kinzelbach and Lutz, 1985
Myrmecolacidae (?) gen. sp.	Baltic	Pohl and Kinzelbach, 2001

*The species was removed from the Myrmecolacidae; it was re-established as *Pseudococcites eocaenicum* Haupt, 1950, and placed under *incertae sedis* in Stylopodia (Pohl, 2009)

Genus *Palaeomyrmecolax* Kulicka, 2001: 7

Palaeomyrmecolax Pohl and Beutel, 2005: 366

This genus was erected to include three species found in Baltic amber: *P. succineus* Kulicka, 2001: 7, the genus type species; *P. giecewiczi* Kulicka, 2001: 9; and *P. gracilis* Kulicka, 2001: 10. Pohl and Beutel (2005) added *P. (Stichotrema) triangulum* (Pohl and Kinzelbach, 1995: 199) and *P. (Stichotrema) weitschati* (Kinzelbach and Pohl, 1994: 61) also from Baltic amber. The following diagnostic characters were included in the original description of the genus: mandible lanceolate; maxilla with a short, cylindrical base and long, somewhat flattened palp pointed at tip; antennal segment 7 three or more times longer than 6; lateral flabellum of segment 3 reaching at least half the length of segment 7; hind wing with R₂ vein distally thickened, R₃ and R₄ separated, R₄ longer than R₃, Ma₁ absent; aedeagus hook-shaped. Pohl and Beutel (2005) added short antennae (length less than half that of the hind wing), flabellum of antennal segment 3 wide and flattened and segment 5 slightly arched (as in *P. triangulum* and *P. weitschati*).

***Palaeomyrmecolax neotropicallis* (Kogan and Poinar, 2010)**

***Stylops neotropicallis* Kogan and Poinar, 2010: 228**

Minor discrepancies from the genus description are found in *P. neotropicallis*: lateral flabellum of antennal segment 3 reaches less than half the length of segment 7 (Figures 1(a), (b), 4(a)). Hind wing (Figure 5(a)) with R₄ and R₅ either fused or too close together to be distinguished; Ma₁, Ma₂, CuA₁ and CuA₂ present, CuP possibly present but obscured by edge of abdomen. Aedeagus not visible in the specimen. The rounded post-frons; relative proportions of antennal segments (Table 2, Figure 7), particularly the very short pedicellus and the long segment VI, and wing venation, particularly lack of separation between R₄ and R₅, distinguishes *P. neotropicallis* from the congeneric Palearctic species. The wider mandible (Figure 4(g)) and more rounded tip of the maxillary palp (Figure 4(d)) further distinguish it from *P. succineus*. Table 2 compares relative lengths of antennal segments of *P. neotropicallis* with those of *P. succineus* (after Kulicka, 2001: 8), and *P. aff. succineus* (BSt1-3a). Additional comparative analysis to the other four species of the genus is included in the 'Discussion' section.

***Palaeomyrmecolax aff. succineus* (BSt1-3a)**

Studied material. Male specimen designated BSt1-3a in the George Poinar Collection (Corvallis, Oregon, USA). The specimen is set in an irregular rectangular prism amber piece ca. 3.6 mm X 4.9 mm in cross section and ca. 5.0 mm in height (Figure 3(b)). The specimen is set near the corner of the amber piece, with most anatomical features apparent, except for the tip of the abdomen that required re-positioning of the amber piece to be barely visualized; on dorsal view the specimen suffers from a prism effect that causes duplication of images. The strepsipteran specimen is ca. 1.96 mm long, and the expanded left wing is 1.95 mm long from the axilla to the edge (Figure 5(c)).

Description

Head – Eyes protruding from narrow occipital lateral plates, with at least 22 discernible small eyelets (Figure 6). Width at edges of eyes 0.57 mm. Post-frons rounded anteriorly. Antennae 7-segmented (Figure 4(c)); length of antennal segments in mm (see Table 2): I = 0.05; II = 0.03; III (base) = 0.05; flabellum of segment III = 0.41 tip reaching close to middle of segment VII; IV = 0.03; V = 0.20; VI = 0.70 VII = 0.24; width of flabellum greater than that of segment VII. Mandible (Figure 4(h)) hardly discernible, but clearly lanceolate, very long and narrow, ca. 0.30 mm long, pointed at tip, attached to small, round base near frontal margin of head. Maxillary palp (Figure 4(f)) robust, arched, with linear length = 0.34 mm, arising from short, round basal segment.

Thorax. Prothorax extending frontally between bases of eyes. Mesothorax short; front wing narrow at base, club-shaped at tip. Metathorax (Figure 2(b), 3(a)) with prescutum about as long as scutellum; scutum angularly expanded laterally; postlumbium wide in center, only slightly rounded posteriorly. Postnotum measured along the sagittal line slightly shorter than praescutum+scutellum combined. Sternal features of thorax not clearly discernible. Hind wings (Figures 3(a), 5(c)) 2.15 mm from tip of wing to axillary region; wing venation consisting of C+Sc running along 2/3 of front wing margin; R₁ reaching about as far as tip of C+Sc; R₂ slightly curved, as long as R₃, both veins apparently shorter than those of *P. succineus*; R₄ running for about 1/3 of wing's width; base of R₅ overlapping with tip of R₄ but less so than in *P. succineus*; MA₁ and MA₂ seem present (not in *P. succineus*) but short; CuA₁ and CuA₂ present, not reaching wing margin; CuP present, short (venation nomenclature following Kinzelbach 1971). Legs (Figure 4(i)): coxa of fore- and mid-legs as long as the stout

trochanterofemur and tibia; tarsomere I slightly longer than the 3 distal tarsomeres that are subequal in length and width, appearing ventrally clad with short hairs.

Abdomen. Eight tergites visible dorsally, segments 3-5 with narrow sclerotized band in middle. Terminalia not visible.

Discussion

Adult males of Myrmecolacidae and Stylopidae (*sensu lato*, after Kinzelbach, 1990) share several important morphological characters. In both families only antennomere III is extended laterally into a long flabellum; antennomere IV is short; the maxillae are long and slender, many are blade shaped; maxillary palps usually are large and stout; in some myrmecolacids and in many stylopids eyes have large numbers of small eyelets; the aedeagus in both families is anchor or hook shaped. Hosts of both families are, at least for the males, hymenopterans. Male Myrmecolacidae are parasites of ants (Hymenoptera: Formicidae), but the family displays heterotrophic heteronomy (Kathirithamby et al. 2010), i.e., each sex parasitizes a different taxon, in this case the hosts of female myrmecolacids are orthopteroids in the orders Orthoptera and Mantodea. All Stylopidae and Xenidae, on the other hand, are parasites of wasps and bees (aculeate hymenopterans, including the families: Andrenidae, Colletidae, Halictidae, Melittidae, Sphecidae, and Vespidae). In most phylogenetic studies the Myrmecolacidae are placed under the super-order Stylopoidea. Kinzelbach (1990) considers Stylopidae a sister group of the clade Elenchidae-Myrmecolacidae, whereas Pohl and Beutel (2005) places Myrmecolacidae as a sister group of the clade Callipharixenidae-Stylopidae (including Xenidae). A fundamental difference between the families then rests in the number of antennal segments: always 7 in Myrmecolacidae, 6 or fewer in Stylopidae, and the antennae of all Neotropical myrmecolacids are long, often exceeding the span of the hind wings, and the antennomeres are cylindrical, not flattened.

The comments above suggest the occurrence of several synapomorphic character states in myrmecolacids and in many *Stylops* species. With the mistaken count of 6 apparent antennomeres we opted to include the fossil in the Stylopidae despite several discrepancies from the typical *Stylops*. For instance, in most *Stylops* the flabellum of the 3rd antennomere is greatly flattened and expanded laterally and the maxillary palps are more complex than those of *P. neotropicalis*. We attributed those discrepancies to species specific differential characters resulting from the geographic isolation of the species then assumed to be of Neotropical origin. With the new evidence presented above, revealing the correct family and Baltic origin of the fossil, both issues are now corrected.

With the corrected genus status of *P. neotropicalis* the Baltic amber fossil genus *Palaeomyrmecolax* includes at present 6 species. Four of these species are known from single specimens; one, *P. weitschati* (Kinzelbach and Pohl, 1994) from 3 specimens; and *P. succineus* Kulicka, 2001, may have a second specimen referred here above as *P. aff. succineus*. In view of this limited representation it is impossible to evaluate the limits of intraspecific variability in body size, relative length of antennal segments, length and width of the maxillary palps, and shape and width of the mandibles. The shape of the aedeagus is only known for *P. triangulum* and *P. weitschati*. So, there is, within the genus, a dearth of singular diagnostic characters for the unambiguous definition of species. Except for *P. triangulum* (Pohl and Kinzelbach, 1995) with a unique triangular 6th antennomere, all other species are very similar to each other.

The study of small specimens imbedded in amber pieces of many different geometric shapes, often obscured by crystallization imperfections and impurities, and altered by dehydration, presents obvious difficulties for precise quantitative measurements or qualitative

observations. Thus antennae often are seen at angles that may distort linear measurements; mandibles may be very thin on lateral view but flat and wide if viewed frontally, hind wings often are twisted and curled in ways that hide or falsify the wing venation. To these potential sources of error, are added various patterns of wing venation which, according to Kinzelbach and Pohl (1994: 63), present considerable individual variation in Strepsiptera so that the importance of observations made on a single individual should not be overstated.

Validity of the *Palaeomyrmecolax* species beyond *P. weitschati* and *P. triangulum*, which is unquestionable for reasons of priority, deserves further scrutiny as additional specimens are eventually discovered. We attempted to assess the level of similarity of the relative length of antennal segments by computing the ratio of the length of segment VII, and flabellum of segment III, to the length of antennomeres IV-VII. Scapus and pedicellus and the base of segment III are very small (usually <0.05mm) and often difficult to measure with precision, so these were excluded. Measurements were taken in mm from Kulicka (2001) for *P. succineus*, *P. giecewizci*, and *P. gracillis*; and from the new image of *P. neotropicalis* (Figure 1(a)). Illustrations of the antennae of *P. weitschati* and *P. triangulum* were scanned and the relative length of segments was estimated by the number of linear pixels measured with the aid of the SPOT® software. Figure 7 shows the ratio of the lengths of the flabellum and segment VII to the sum of the lengths of segments IV-VII. We highlight similarities between *P. gracillis* with *P. weitschati*. There are certain similarities among antennomere proportions of *P. giecewizci*, *P. triangulum*, and *P. neotropicalis* but both latter species do not have a ‘triangular’ segment VI. *P. neotropicalis* has similarities to *P. giecewizci* but the proportion of the flabellum relative to that of segment VII is shorter, and veins R4 and R5 in the hind wing are apparently fused. These relative proportions of antennal segments, together with similarities in wing venation of the species described by Kulicka (2001) with that of *P. weitschati* suggest that a critical review of the genus is warranted as it seems odd that 9 relatively sympatric amber samples would yield 6 different species.

Acknowledgments

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FIGURES

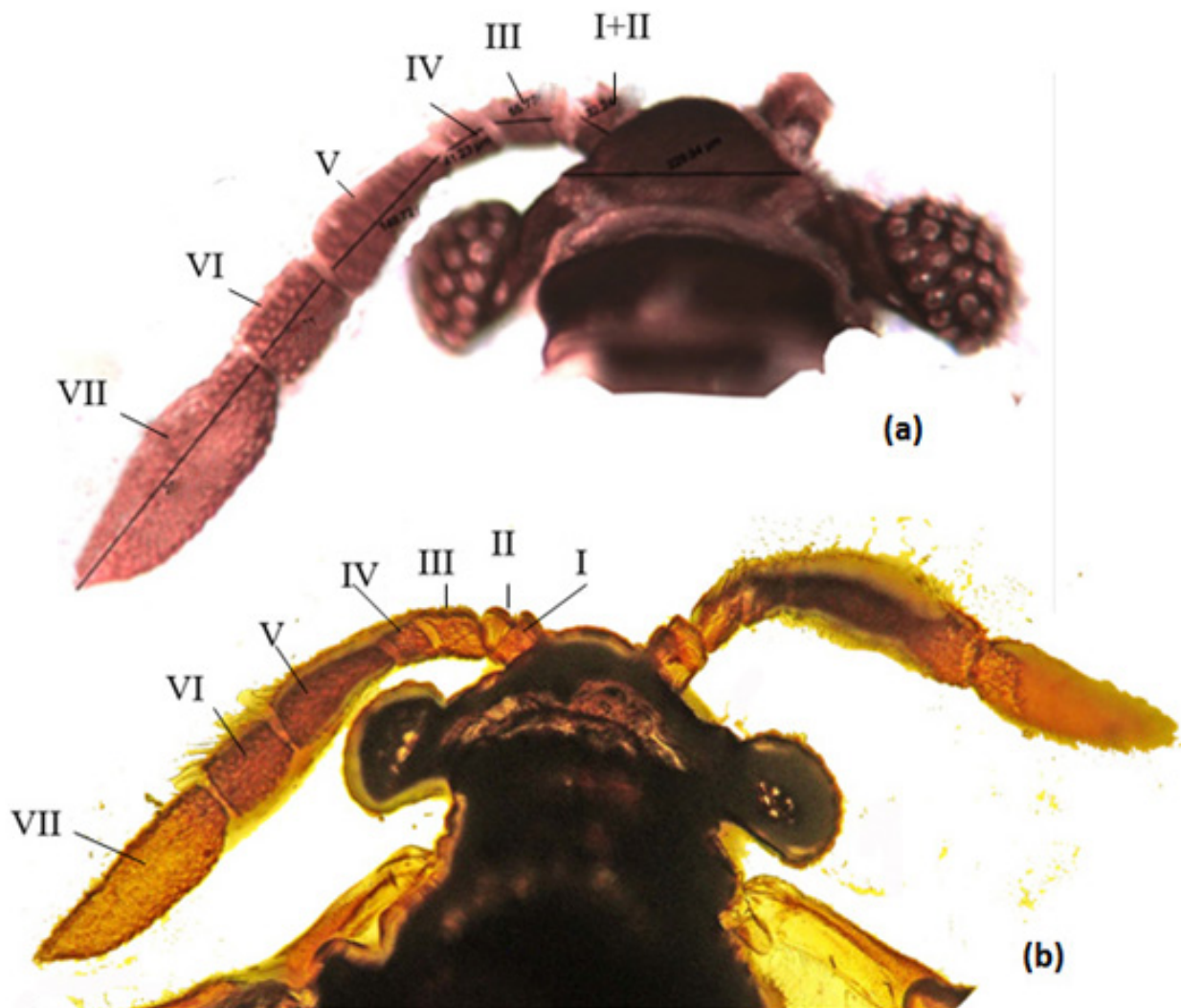


Figure 1. *Palaeomyrmecolax neotropicalis*: (a) Head, dorsal, as originally viewed in Kogan and Poinar (2010) with antennomeres I and II appearing fused (2008 photo). (b) Head dorsal showing extremely reduced antennomere II clearly separated from I (2013 photo).

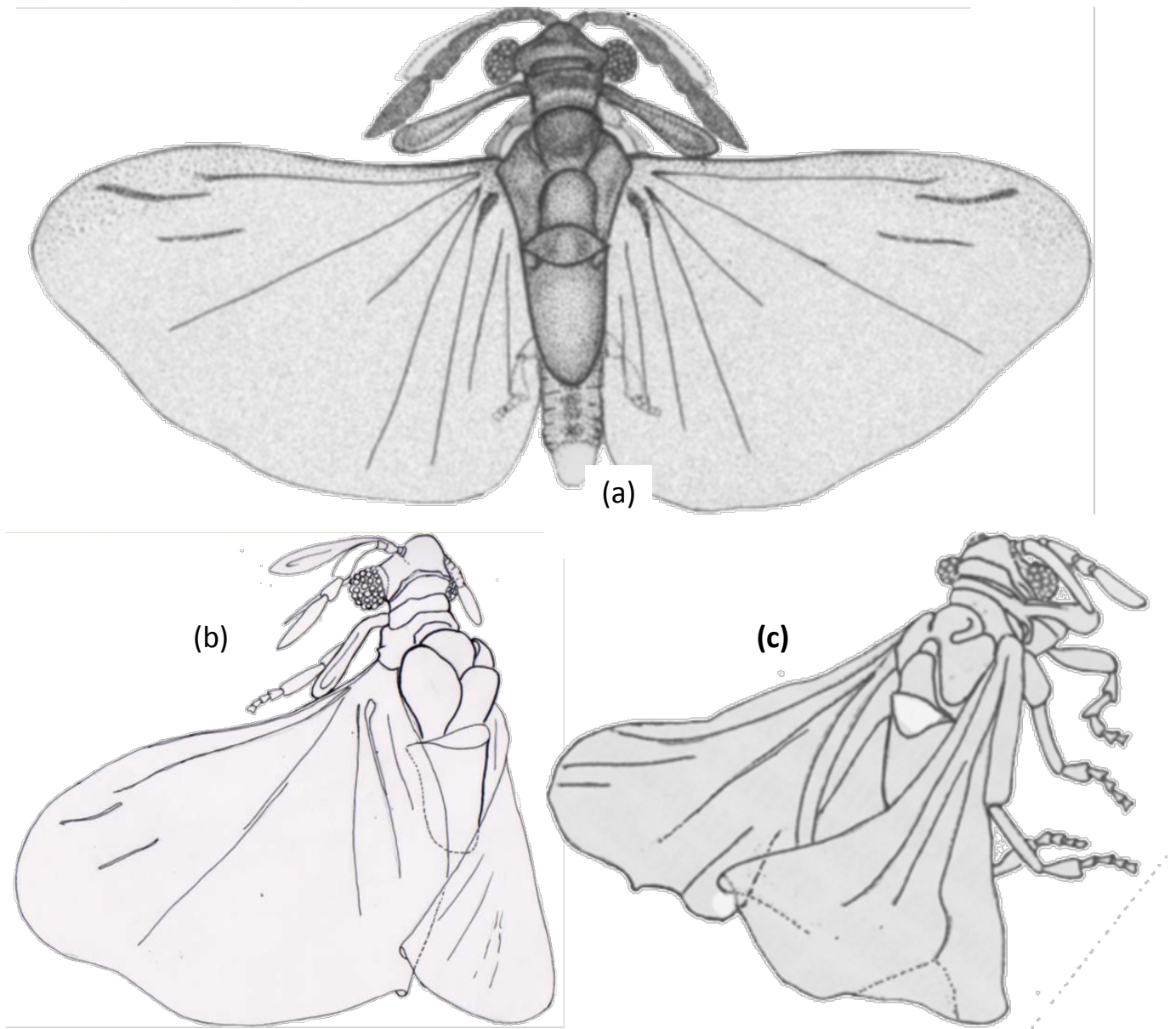
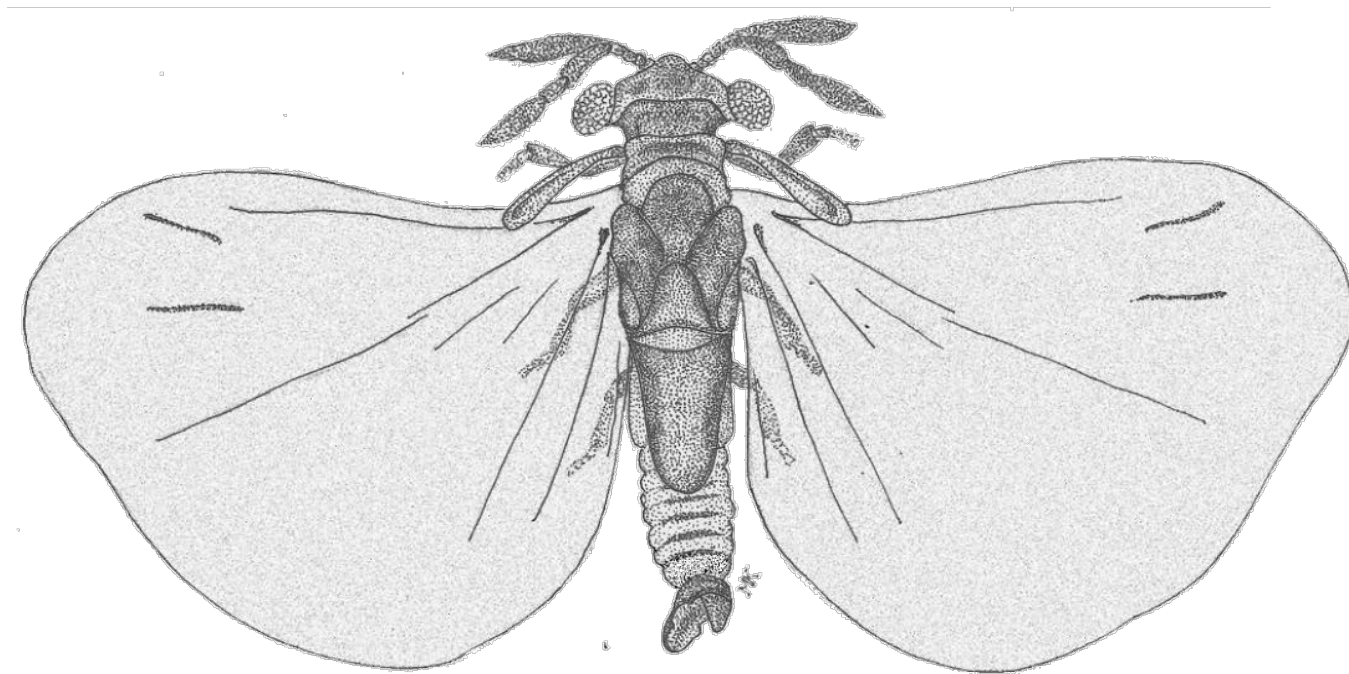


Figure 2. (a) *Palaeomyrmecolax neotropicalis* reconstructed from the original in amber. (b) *P. aff. succineus* (coded BSt-1-3A in the G. Poinar Collection). (c) *P. succineus* redrawn after Kulicka (2001: figure 10).



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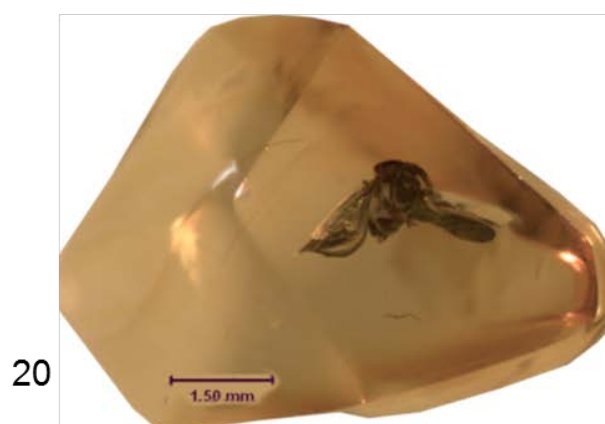


Figure 3. *Palaeomyrmecolax* aff. *succineus*: (a) Dorsal view of reconstructed amber imbedded specimen. (b) Amber piece showing imbedded specimen.

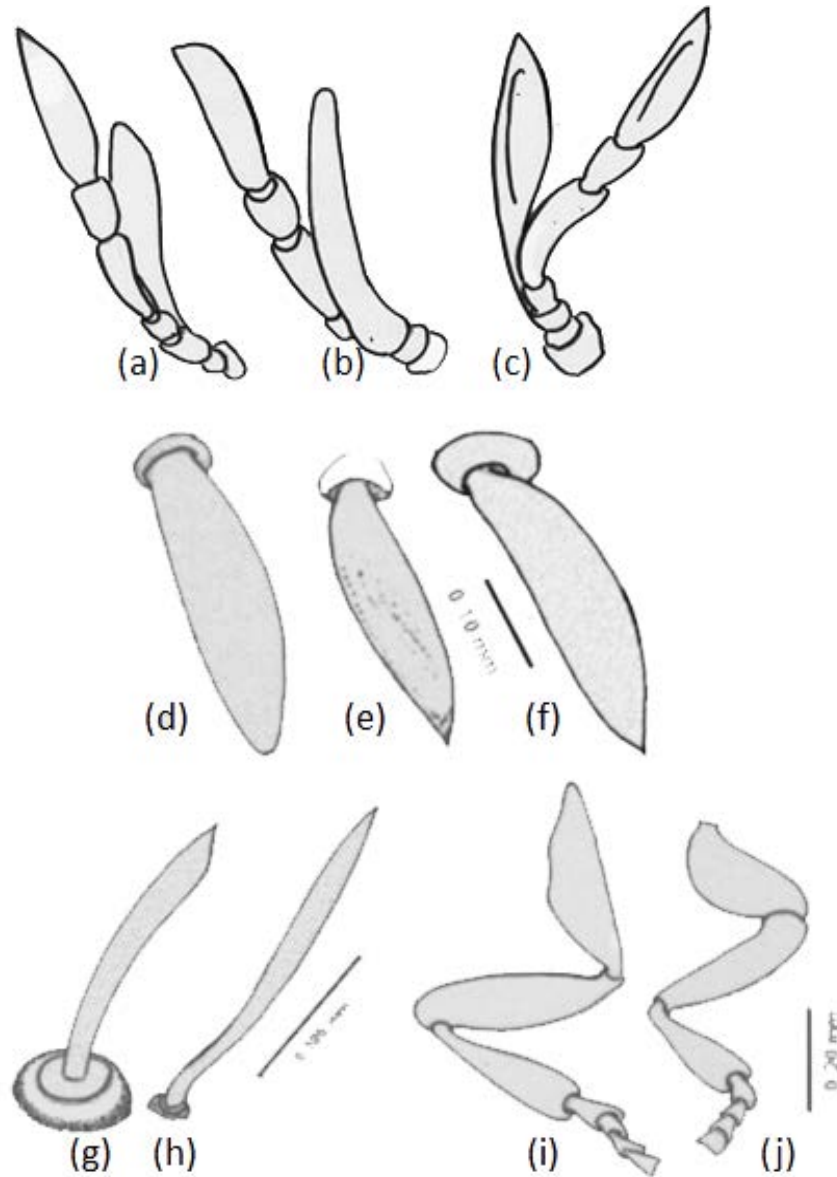


Figure 4. *Palaeomyrmecolax neotropicalis*: (a) Antenna; (d) Maxilla; (g) Mandible; (j) Hind leg. *P. succineus* (redrawn after Kulicka 2001): (b) Antenna; (e) Maxilla. *P. aff. succineus*: (c) Antenna; (f) Maxilla; (h) Mandible; (i) Hind leg.

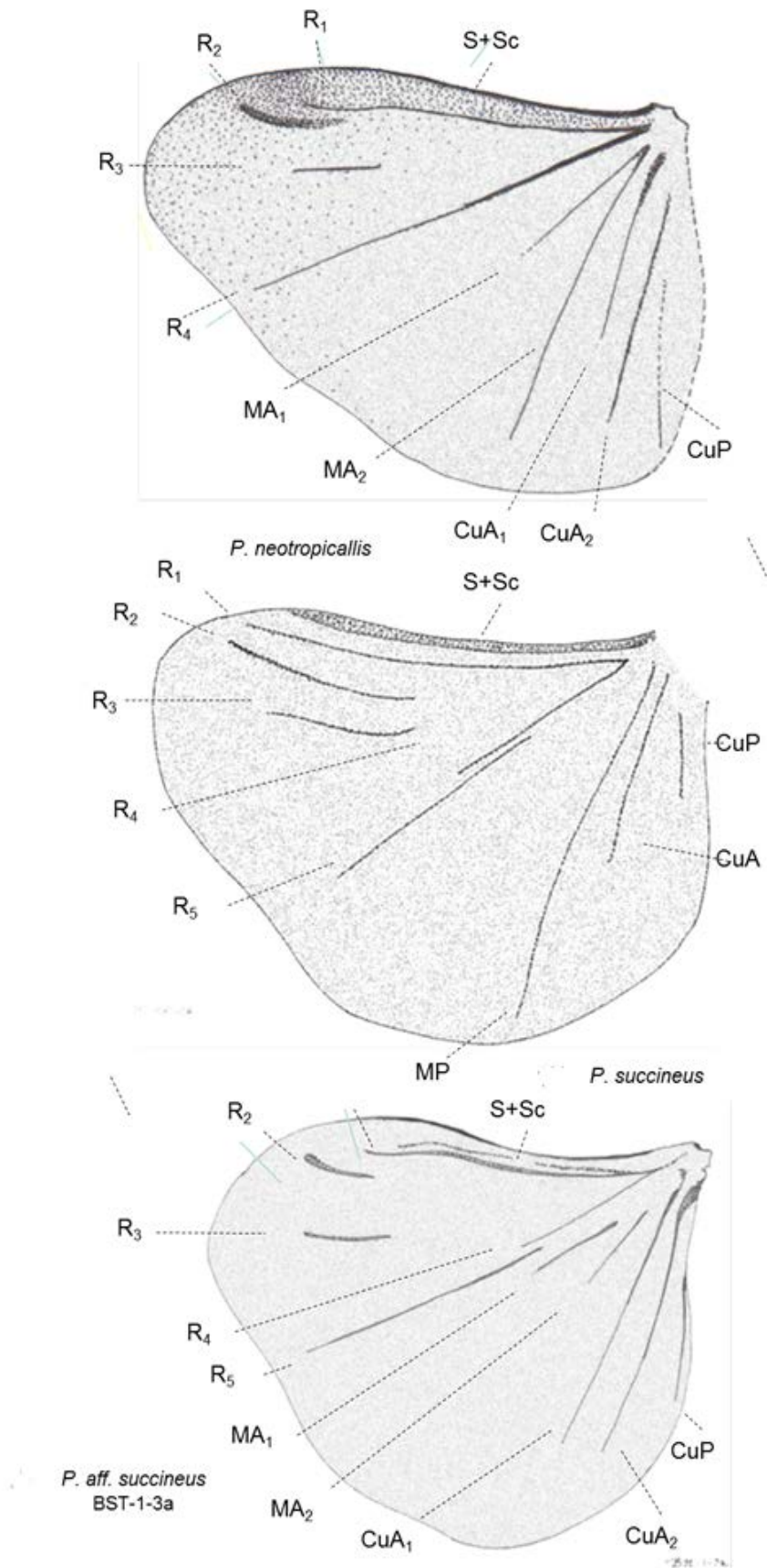


Figure 5. Left wings: (a) *Palaeomyrmecolax neotropicalis*. (b) *P. succineus* (redrawn after Kulicka 2001). (c) *P. aff. succineus*.

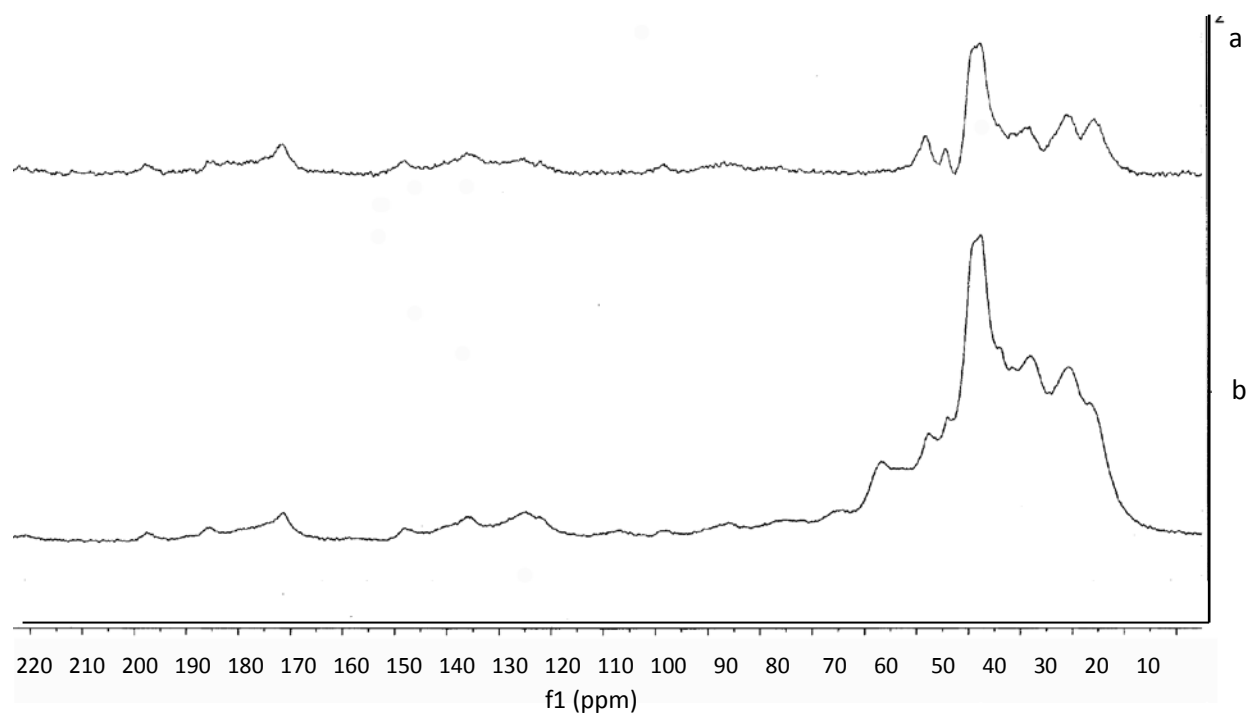
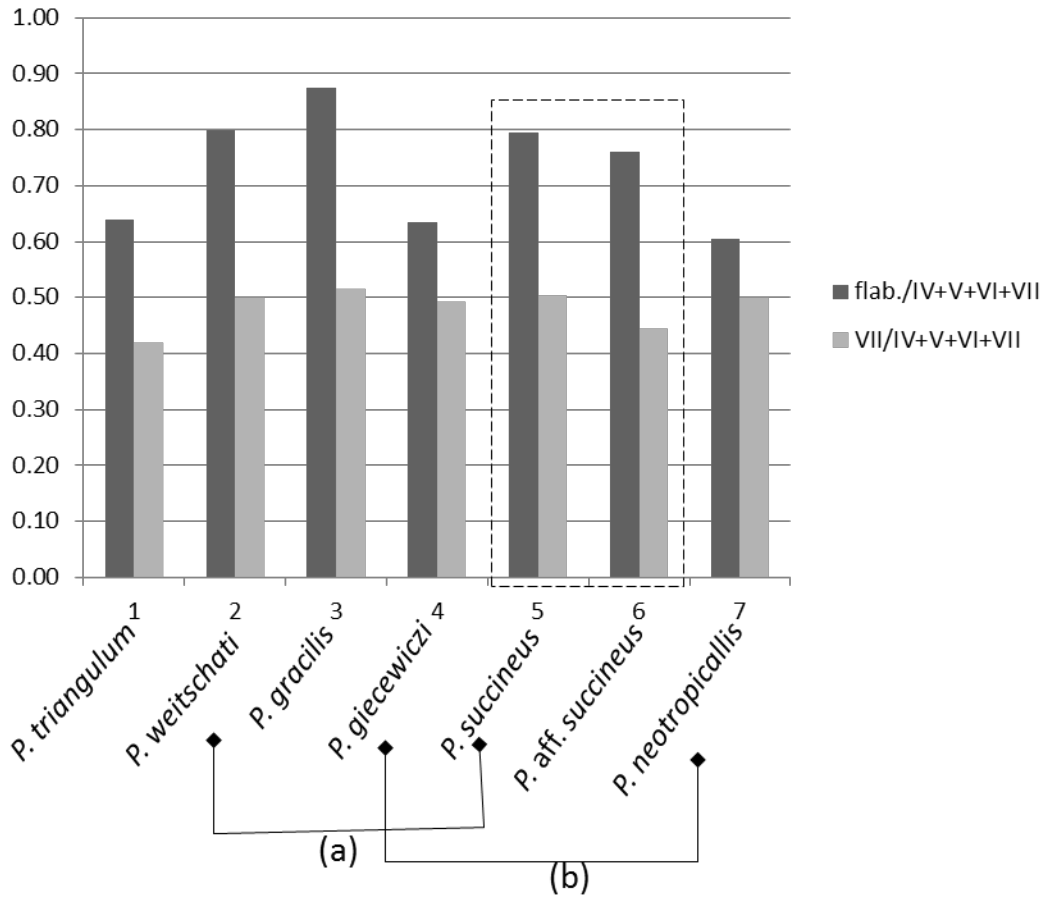


Figure 6. ¹³C NMR spectra of a sample of the amber piece inclosing the *Palaeomyrmecolax neotropicallis* holotype specimen (G. Poinar collection specimen BSt-1-11 (formerly DSt-1-11)). Upper graph (a) interrupted decoupling; lower graph (b) normal decoupling. Analysis performed in the laboratory of Dr. J.B. Lambert, Trinity University, San Antonio, Texas, November 2013.



Tables

Table 1. Fossil Myrmecolacidae

Species	Amber Origin	Reference
<i>Caenocholax dominicensis</i>	Dominican	Kathirithamby and Grimaldi, 1993
<i>Caenocholax brodzinskyi</i>	Dominican	Kathirithamby and Grimaldi, 1993
<i>Caenocholax aff. fenyesi</i>	Dominican	Poinar and Poinar, 1999
<i>Caenocholax groehni</i>	Baltic	Kathirithambi and Henderickx, 2008
<i>Myrmecolax glaesi</i>	Dominican	Kinzelbach, 1983; Kinzelbach and Pohl, 1994;
<i>Palaeomyrmecolax triangulum</i>	Baltic	Pohl and Kinzelbach, 1995; Pohl and Beutel, 2005
<i>Palaeomyrmecolax weitschati</i>	Baltic	Kinzelbach and Pohl, 1994; Pohl and Kinzelbach, 1995; Pohl and Beutel, 2005
<i>Palaeomyrmecolax gracilis</i>	Baltic	Kulicka, 2001; Pohl and Beutel, 2005
<i>Palaeomyrmecolax giecewiczii</i>	Baltic	Kulicka, 2001; Pohl and Beutel, 2005
<i>Palaeomyrmecolax succineus</i>	Baltic	Kulicka, 2001; Pohl and Beutel, 2005
<i>Palaeomyrmecolax neotropicalis</i>	Baltic	Kogan and Poinar, 2010 (as <i>Stylops neotropicalis</i>)
<i>Stichotrema beckeri</i> (Oliveira and	Dominican	Kinzelbach and Pohl, 1994

Kogan, 1959)		
<i>Stichotrema dominicanum</i>	Dominican	Kinzelbach and Pohl, 1994
<i>Stichotrema</i> sp.	Messel oil slate	Kinzelbach and Pohl, 1994
<i>Stichotrema eocaenicum</i> (Haupt, 1950)*	Brown coal-Halle-an-der-Salle	Kinzelbach and Lutz, 1985
Myrmecolacidae (?) gen. sp.	Baltic	Pohl and Kinzelbach, 2001

*The species was removed from the Myrmecolacidae; it was re-established as *Pseudococcites eocaenicum* Haupt, 1950, and placed under *incertae sedis* in Stylopidia (Pohl, 2009)

Table 2: Measurements of antennomeres in mm. A- Revised measurements based on Figure 2;
 B- Measurements based on original Figure 1

Palaeomyrmecolax neotropicallis:

	I	II	III	Flabellum	IV	V	VI	VII
A	0.030	0.024	0.052	0.35	0.039	0.145	0.106	0.289
B	.032		0.056	0.30	0.041	0.148	0.096	0.276

Palaeomyrmecolax aff. succineus (BST1-3a)

0.05	0.03	0.05	0.41	0.03	0.20	0.07	0.24
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Palaeomyrmecolax succineus Kulicka, 2001

0.055	0.038	0.049	0.411	0.035	0.144	0.077	0.261
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Explanation of Figures

Figure 1. *Palaeomyrmecolax neotropicalis*: (a) Head, dorsal, as originally viewed in Kogan and Poinar (2010) with antennomeres I and II appearing fused (2008 photo). (b) Head dorsal showing extremely reduced antennomere II clearly separated from I (2013 photo).

Figure 2. (a) *Palaeomyrmecolax neotropicalis* reconstructed from the original in amber. (b) *P. aff. succineus* (coded BSt-1-3A in the G. Poinar Collection). (c) *P. succineus* redrawn after Kulicka (2001: figure 10).

Figure 3. *Palaeomyrmecolax aff. succineus*: (a) Dorsal view of reconstructed amber imbedded specimen. (b) Amber piece showing imbedded specimen.

Figure 4. *Palaeomyrmecolax neotropicalis*: (a) Antenna; (d) Maxilla; (g) Mandible; (j) Hind leg. *P. succineus* (redrawn after Kulicka 2001): (b) Antenna; (e) Maxilla. *P. aff. succineus*: (c) Antenna; (f) Maxilla; (h) Mandible; (i) Hind leg.

Figure 5. Left wings: (a. *Palaeomyrmecolax neotropicalis*. (b) *P. succineus* (redrawn after Kulicka 2001. (c) *P. aff. succineus*.

Figure 6. C NMR spectra of a sample of the amber piece inclosing the *Palaeomyrmecolax neotropicalis* holotype specimen (G. Poinar collection specimen BSt-1-11 (formerly DSt-1-11)). Upper graph (a) interrupted decoupling; lower graph (b) normal decoupling. Analysis performed in the laboratory of Dr. J.B. Lambert, Trinity University, San Antonio, Texas, November 2013.

Figure 7. Relative proportions of the length of the flabellum and that of VII antennomere to the sum of the lengths of segments IV-VII. Dashed line box highlights similarity of ratios for *P.*

succineus and *P. aff. succineus*. Lines with arrow heads indicate ratio similarities among two pairs of species: (a) *P. weitschati* and *P. succineus*, and (b) *P. neotropicallis* and *P. giecewizci*