

Journal of Melittology

Bee Biology, Ecology, Evolution, & Systematics

The latest buzz in bee biology

No. 16, pp. 1–9

4 September 2013

A male of the bee genus *Agapostemon* in Dominican amber (Hymenoptera: Halictidae)

Michael S. Engel¹ & Laura C.V. Breitkreuz¹

Abstract. The first fossil species of the caenohalictine bee genus *Agapostemon* Guérin-Méneville (Halictinae: Caenohalictini: Agapostemonina) is described and figured from a single male preserved in Early Miocene (Burdigalian) amber from the Dominican Republic. *Agapostemon* (*Notagapostemon*) *luzzii* Engel & Breitkreuz, new species, is compared with modern species and is noteworthy for the absence of metafemoral modifications [in this regard plesiomorphically resembling the West Indian *A. kohliellus* (Vachal) and *A. centratus* (Vachal)], form of the head and protibial antennal cleaner, integumental sculpturing, and male terminalia, the latter of which are fortunately exposed and cleared. Brief comments are made on the affinity of the species to others in the West Indies and surrounding regions as well as possible biogeographic implications.

INTRODUCTION

The genus *Agapostemon* Guérin-Méneville comprises 42 species of typically bright metallic green and often yellow-banded halictine bees (Roberts, 1972; Genaro & Franz, 2008). The only formal revision of the genus is that of Roberts (1972), and although subsequent taxonomic issues have been addressed (e.g., Engel, 2004; Genaro & Franz, 2008), it remains the main source of information regarding the included species. Based on a cladistic analysis, Janjic & Packer (2003) recognized two principal clades within the genus and proposed each as a distinct subgenus. Keys to species from various regions have been provided by Roberts (1972, 1973), Mitchell (1960), Dreisbach (1945), Lovell (1942), and Sandhouse (1936), while Fischer (1950) provided a brief account of the Kansas fauna. Particularly important biological accounts include Roberts (1969, 1973), Eickwort & Eickwort (1969), Eickwort (1981, 1988), Abrams & Eickwort (1980, 1981), Berger *et al.* (1985, 1988), and Ramírez-Freire *et al.* (2012).

Herein we provide the description of the first fossil species of the genus *Agapostemon*, based on one of the few halictine males recovered from the Early Miocene

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deposits of the Dominican Republic (Figs. 1–2). Halictine bees are diverse in Dominican amber (Engel, 1995, 1996, 1997, 2000, 2009; Engel & Rightmyer, 2000), albeit individuals remain noticeably rare in comparison to inclusions of workers of the stingless bee *Proplebeia dominicana* (Wille & Chandler) which are downright common (e.g., Wille & Chandler, 1964; Michener, 1982; Camargo *et al.*, 2000; Greco *et al.*, 2011; Engel & Michener, 2013). Other lineages of bees present in the fauna include panurgines (Rozen, 1996); euglossines (Engel, 1999a), megachilines (Engel, 1999b), xeromelissines (Michener & Poinar, 1996; Engel, 1999c), and exomalopsines (Engel *et al.*, 2012). Although bees have been known in Dominican amber for a long while, much of the fauna was not elucidated until the last 20 years. It is hoped that the present account will spur continued exploration of the fossil bee fauna of the Dominican Republic.

MATERIAL AND METHODS

The age (17–20 Ma), origin, and faunal composition of Dominican amber have been discussed by Iturralde-Vinent & MacPhee (1996, 1999) and Grimaldi & Engel (2005). A summary of the known bee species from Dominican amber was most recently provided by Engel *et al.* (2012), while general accounts of the fossil record of bees have been provided by Engel (2004b, 2011), Ohl & Engel (2007) and Michez *et al.* (2012). The classification of *Agapostemon* that is followed herein is that of Janjic & Packer (2003). Morphological terminology for the description follows that employed by Engel (2001) and Michener (2007), although some terminology (identified in the description) is used from Roberts (1972) to ease comparisons between the present fossil and species accounts in his monograph. Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens. Measurements were taken with an ocular micrometer on an Olympus SZX-12 stereomicroscope and should be considered approximate given that the optimal angle for taking a given metric was not always achievable.

SYSTEMATIC PALEONTOLOGY

Genus *Agapostemon* Guérin-Méneville

Subgenus *Notagapostemon* Janjic & Packer

***Agapostemon (Notagapostemon) luzzii* Engel & Breitkreuz, new species**

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(Figs. 1–6)

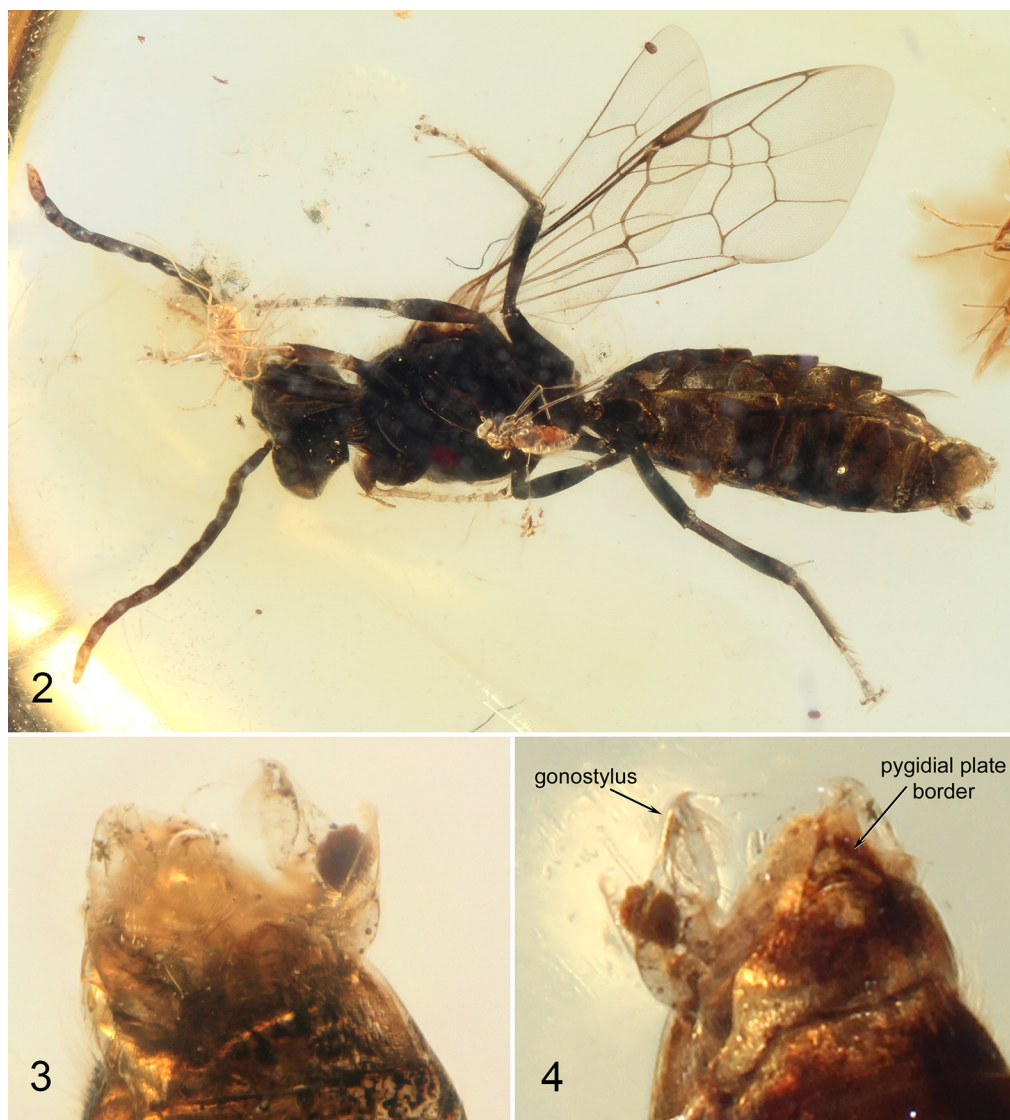
DIAGNOSIS: The new species is similar to the living West Indian species, *A. kohliellus* (Vachal) and *A. centratus* (Vachal) in the absence of a metafemoral tooth and unmodified metafemora and metatibiae but differs from both in the dark brown metasomal integument (rather than amber colored in *A. centratus* and black with yellow bands in *A. kohliellus*) and in the unique shape of the pygidial plate. In addition, the form of the male genitalia differs between the species (Figs. 3–6; *cf.* figures in Roberts, 1972). Like *A. kohliellus* the apical portion of the clypeus is angled and somewhat flattened.

DESCRIPTION: ♂: Total body length (as preserved) 8.48 mm; forewing length 5.89 mm. Head wider than long, width 1.68 mm (not possible to get direct line of measurement for length owing to curvature of amber surface but length is distinctly shorter than head width); compound eyes emarginate just above tangent of antennal toruli, with inner margins slightly converging below; compound eyes bare; integument of



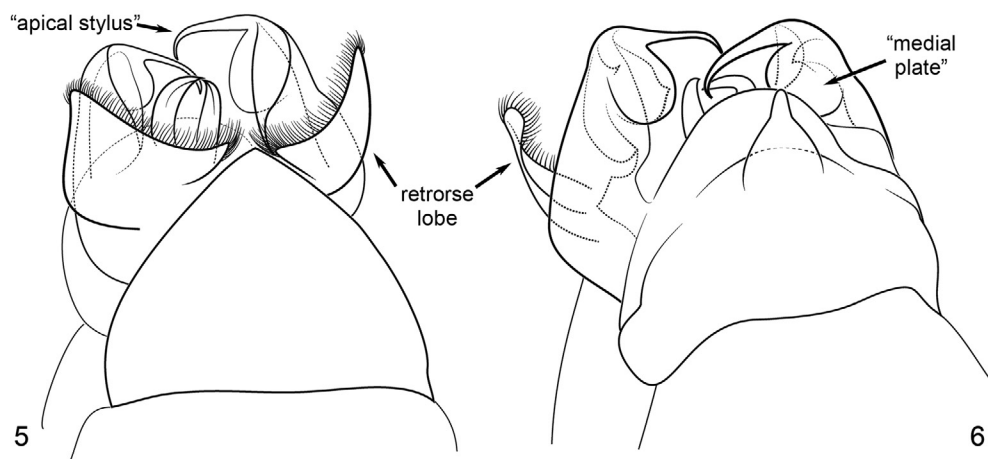
Figure 1. Photomicrograph of dorsal habitus of holotype male (SEMC-F001020) of *Agapostemon luzzii*, new species, in Early Miocene (Burdigalian) amber from the Dominican Republic.

head black or dark brown with weak metallic green highlights, with contiguous, minute punctures giving surface a granular appearance, such punctures apparently larger, more shallow, and more spaced on basal portion of clypeus. Clypeus angled but not



Figures 2–4. Photomicrographs of holotype male (SEMC-F001020) of *Agapostemon luzzii*, new species, in Early Miocene (Burdigalian) amber from the Dominican Republic. **2.** Ventral habitus. **3.** Ventral view detail of metasomal apex showing portions of cleared genitalia. **4.** Dorsal detail of metasomal apex showing pygidial plate and exposed portions of the cleared genital capsule.

greatly produced, with somewhat flattened apical surface giving it a somewhat truncate appearance, apical portion of flattened surface not dark metallic and imbricate and impunctate (apparently had been yellowish in life); supraclypeal area weakly convex; malar space linear, virtually absent; mandible simple, yellowish except apex reddish brown. Labrum yellowish, transverse, basal transverse ridge weak, not interrupted medially, apical margin unmodified. Occipital carina strong, with numerous long, branched setae arising in fringe along it. Antenna dark brown; scape length 0.39 mm, apical width 0.12 mm; pedicel length 0.16 mm, width 0.12 mm; first flagellomere length 0.16 mm, width 0.12 mm; second flagellomere length 0.39 mm, width 0.12 mm;



Figures 5–6. Details of male metasomal apex and genitalia of holotype (SEMC-F001020) of *Agapostemon luzzii*, new species, in Early Miocene (Burdigalian) amber from the Dominican Republic; structures labeled using terminology of Roberts (1972). 5. Ventral view. 6. Dorsal view.

flagellum weakly sinuate owing to more pronounced ventral surface of flagellomeres 4–11 (resembling in this respect some species of *Dinagapostemon* Moure & Hurd but, of course, the fossil differing from that genus by the bare compound eyes and absence of hind leg modifications, among other details).

Mesosoma black with metallic green highlights throughout except tegula translucent light brown and without metallic highlights; intertegular distance 1.17 mm; integumental sculpturing, where evident, apparently granulose; medial surface of mesosoma polished off at amber surface so many details of mesoscutal and mesoscutellar integument impossible to determine; left lateral surface of propodeum obscured by tightly appressed layer of air reflecting darker integument underneath, propodeum in ventrolateral view evidently with posterior surface bordered by low carinae. Forewing membrane hyaline and without pattern of infuscation, venation as depicted in figures 1 and 2, veins brown with paler area in center of pterostigma and Sc+R dark brown, no veins weakened; hind wing with 7 distal hamuli arranged in a single linear series. Legs generally unmodified and dark brown, nearly black, with metallic green highlights on basal podites except tarsi, particularly apical tarsomeres, lighter with basitarsi largely dark brown (except probasitarsus as on other tarsomeres) and medio- and distitarsi yellowish translucent (likely yellow in life); protibial antennal cleaner with malus absent beyond velum (as in *A. kohliellus*); metafemur and metatibia not swollen; metafemur without tooth; spurs simple; metabasitarsus apically fused to second metatarsomere, without other modifications; pretarsal claws strongly curved and with strong inner tooth, arolium unmodified.

Metasoma simple (not petiolate or distinctly slender), dark brown with faint metallic green highlights in some places; terga weakly imbricate with shallow, small punctures separated by a puncture width or less except apparently absent in narrow apical marginal zone where integument is impunctate and imbricate; pygidial plate with broadly curved and strongly ridged outer borders, medioapically with short, acute medial extension; sterna apparently imbricate with scattered faint punctures except in apical marginal zones, sterna unmodified; male genitalia with outer surface of gonocoxa with exceedingly fine longitudinal striations (scarcely evident on cleared integument but evident under high magnification), otherwise integument appears un-

adorned, gonostylus with long and simple apical stylus recurved towards its apex (*sensu* Roberts, 1972), medial plate simple, without transverse folds or protrusions, basal stylus (*sensu* Roberts, 1972) not evident; retrorse lobe large, with numerous short setae along its apical margin (Figs. 3–6).

♀: Unknown.

HOLOTYPE: ♂, SEMC-F001020, Early Miocene amber; Dominican Republic (specific mine unknown); deposited in the fossil insect collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

ETYMOLOGY: The specific epithet is a patronym honoring Michael Luzzi, nephew of Keith Luzzi, collector of this and many other excellent inclusions in amber.

COMMENTS: The new species generally agrees in observable traits with the diagnosis provided by Janjic & Packer (2003) for *Notagapostemon*, and the particular combination of other features not necessarily included in the diagnosis (*e.g.*, absence of the malus, truncate clypeus) but indicative of species within this clade.

DISCUSSION

It is exciting that the relatively well known fauna of bees in Dominican amber should continue to offer up remarkable surprises. Not long ago two specimens of an exomalopsine were recorded (Engel *et al.*, 2012) and now a new halictine, representing the first fossil of the genus *Agapostemon*. Equally remarkable is that the specimen is a male. Fossils of male bees are exceedingly uncommon, with our perspective of paleomelittology distinctly female-skewed, and it is an added fortune that the genitalia are extended and somewhat cleared (Figs. 3–4) (not uncommon for insect cuticle preserved in amber as this can result from the natural diagenesis the amber and its inclusions undergo). It is perhaps not surprising that a fossil *Agapostemon* from Hispaniola should share a number of features with some of the species today living in the islands, although these similarities are assuredly plesiomorphies and not indicative of an immediate relationship among them. *Agapostemon luzzii* shares with *A. centratus* and *A. kohliellus* the absence of a metafemoral tooth, unique among the West Indian fauna. Despite this, *A. centratus* and *A. kohliellus* are not close relatives, each occupying a basal position in separate clades within the genus – *A. kohliellus* at the base of *Notagapostemon* Janjic & Packer, *A. centratus* at the base of a basal clade within *Agapostemon* s.str. Overall, there are additional similarities between *A. luzzii* and *A. kohliellus*, such as the truncate clypeus, more simplified medial plate of the gonostylus, and absence of the malus beyond the velum of the protibial antennal cleaner, and so it seems more probable that *A. luzzii* also is relatively basal among *Notagapostemon*. Particularly noteworthy is the form of the protibial antennal cleaner between *A. kohliellus* and *A. luzzii*, suggestive of a more close relationship between these two species, although it too could be plesiomorphic, leaving the latter species either basal to the entire subgenus or as a basal stem group to the former. If the species were sister or a stem group to *A. kohliellus*, then this would continue to support a possible interpretation of multiple invasions of *Agapostemon* into the Caribbean. Alternatively, if *A. luzzii* were basal to *Notagapostemon* as a whole, then one could argue for a Caribbean origin of the clade or even a more inclusive group, a scenario generally dismissed by Janjic & Packer (2003). Despite the presence of a putatively primitive fossil *Agapostemon* in the Caribbean, we do not believe that *A. luzzii* reverses the biogeographic position adopted by Janjic & Packer (2003) and their line of reasoning remains solid. It is most likely that *Agapostemon* diverged from its closest relative (which could have been a group now extinct) in

Central America during the latter half of the Oligocene, with species perhaps extending into the Caribbean via the Nicaraguan Rise (Iturralde-Vinent & MacPhee, 1999). These early stem groups, both to the two subgenera and the genus as whole, have assuredly disappeared. Extinction within the genus certainly has been more rampant than the singular loss of *A. luzzii* in the Caribbean, with various species in Central America assuredly having been lost during the numerous tectonic and environmental changes that have occurred over the last 20+ million years (e.g., Iturralde-Vinent & MacPhee, 1999). The exploration of generally contemporaneous ambers in southern Mexico remains in its infancy and it would not be surprising if species of *Agapostemon* were recovered from the Early Miocene of Chiapas. Given our presently limited knowledge of Mexican amber diversity, a current lack of information cannot be equated with biogeographic and temporal absence of a taxon. The origin of the genus and its initial cladogenetic events must predate *A. luzzii*, indicating that the genus is certainly older than the Early Miocene. Interestingly, this predates some molecular estimates of divergence, although these should be reanalyzed in the light of new paleontological material, and this might bring them into alignment with the fossil record. For example, the analysis of Brady *et al.* (2006) considered the *Notagapostemon*-*Agapostemon* s.str. divergence [the subgenera represented by *A. leunculus* (Vachal) and *A. tyleri* Cockerell, respectively] to have been in the Late Miocene. The presence of an *Agapostemon* in the Early Miocene demonstrates that this divergence was much older and perhaps during the latest Oligocene. The same analysis suggested the divergence between *Augochlora* Smith and *Augochlorella* Sandhouse was during the Early Miocene but, similar to the case with *Agapostemon*, the presence of a definitive *Augochlora* in Dominican amber (Engel, 2000) demonstrates that the basal diversifications within this genus predate that time period and thereby an even deeper divergence from *Augochlorella* must be older, perhaps also in the latest Oligocene.

ACKNOWLEDGEMENTS

We are grateful to Keith Luzzi for bringing the present specimen to our attention, and for permitting its study and deposition at the University of Kansas. Additional thanks are provided to two anonymous reviewers who provided constructive criticism on earlier drafts of the manuscript. Support for photomicrography was provided by the Engel Illustration Fund of the College of Liberal Arts & Sciences, University of Kansas, while L.C.V.B. was supported by U.S. National Science Foundation grant DEB-1144162 (to M.S.E.). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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Journal of JM Melittology

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The *Journal of Melittology* was established at the University of Kansas through the efforts of Michael S. Engel, Victor H. Gonzalez, Ismael A. Hinojosa-Díaz, and Charles D. Michener in 2013 and each article is published as its own number, with issues appearing online as soon as they are ready. Papers are composed using Microsoft Word® and Adobe InDesign® in Lawrence, Kansas, USA.

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ISSN 2325-4467