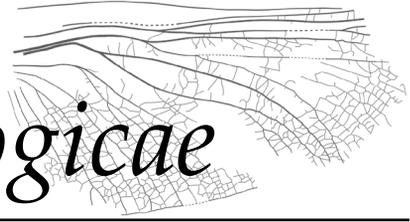


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An orchid bee of the genus *Eulaema* in Early Miocene Mexican amber (Hymenoptera: Apidae)

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Abstract. The first fossil orchid bee from Early Miocene Mexican amber is described and figured. *Eulaema (Apeulaema) zigrasi* Engel, new species, represents the first non-meliponine bee fossil documented from Mexican amber as well as the first fossil of its genus. The new species is distinguished from its congeners and comments are briefly made regarding the geological history of Euglossini.

INTRODUCTION

The fossiliferous amber of southern Mexico comprises a series of deposits that are roughly contemporaneous with the more extensively-studied resin of the Dominican Republic (Engel, 2004a; Solórzano-Kraemer, 2007). Together these ambers provide a window into a wet tropical fauna of continental and Caribbean North America prior to the permanent closure of the Central American Seaway in the Pliocene. Although the faunas of both deposits are relatively modern in character, they do shed considerable light onto the historical biogeography and paleobiology of the region. It is not uncommon for similar species of the same or closely-related genera to occur in both Dominican and Mexican ambers [e.g., termites of the genera *Mastotermes* Froggatt, *Dolichorhinotermes* Snyder & Emerson, and *Incisitermes* Krishna (Emerson, 1969; Krishna & Emerson, 1983; Krishna & Grimaldi, 1991; Schlemmermeyer & Canello, 2000; Engel & Krishna, 2007a, 2007b), bees of the genus *Proplebeia* Michener (Camargo *et al.*, 2000),

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bugs of the genera *Leptosalda* Cobben and *Termitaradus* Myers (Cobben, 1971; Poinar & Doyen, 1992; Grimaldi & Engel, 2008; Engel, 2009a; Poinar & Heiss, 2011; Grimaldi *et al.*, 2013)]. The bee fauna of Dominican amber is remarkably diverse, with a seemingly steady accumulation of taxa every couple of years (*e.g.*, Michez *et al.*, 2012; Engel *et al.*, 2012; Engel & Breitzkreuz, 2013). In contrast, the number of described species of bees in Mexican amber has remained constant for 55 years. *Trigona* (*Nogueirapis*) *silacea* Wille (1959) was described from a small series of workers and, much like *Proplebeia dominicana* (Wille & Chandler) in Dominican amber (Camargo *et al.*, 2000), the species is now known from hundreds of individuals from these deposits (Engel & Michener, 2013a). With the elevation of *Nogueirapis* to generic rank, the species was long known as *Nogueirapis silacea* and compared with those species of this genus with similar facial patterns and occurring in Mesoamerica and Central America (*e.g.*, Wille, 1964). Camargo *et al.* (2000) discussed the relationship of Wille's species relative to *Proplebeia* and considered them to belong to a single lineage, and Camargo & Pedro (2007) subsequently formally transferred the species to *Proplebeia*. Given that there is quite a bit of variation among the large series of specimens now available from various amber localities in Mexico, it was initially thought that there were more than one species in the fauna. However, for virtually every difference discernible there are variants that intergrade between the size classes and no strong evidence any longer exists for the recognition of multiple species (*pers. obs.*). There is considerable inherent interest in *P. silacea* but in the absence of additional bee lineages in the fauna, Mexican amber has not inspired as much interest among melittologists as has that of the Dominican Republic. This long stagnation has finally been broken with the recent discovery of a large orchid bee (Euglossini) in Mexican amber (Fig. 1). A single female of a species of *Eulaema* Lepeletier de Saint Fargeau has been discovered and this new species is described herein. Admittedly, this find leaves the diversity of Mexican amber bees still confined to the corbiculate Apinae, but the discovery of any additional lineages outside of the Meliponini are of considerable interest. Hopefully the present contribution will spark a steady stream of new species from other bee tribes, subfamilies, and families much in the same way the discovery of *Neocorynura electra* Engel broke more than a quarter century of silence after *P. dominicana* for the Dominican fauna (Wille & Chandler, 1964; Engel, 1995), and ushered in a nearly 20 year span in which the number and diversity of Dominican amber bees has continually grown (*e.g.*, Rozen, 1996; Michener & Poinar, 1996; Engel, 1996, 1997, 1999a, 1999b, 1999c, 2000a, 2009b; Engel & Rightmyer, 2000; Camargo *et al.*, 2000; Greco *et al.*, 2011; Engel *et al.*, 2012; Engel & Breitzkreuz, 2013).

Eulaema presently includes 33 nominal species ranging from northern Mexico to northern Chile and Argentina (*e.g.*, Moure *et al.*, 2007; Nemésio & Rasmussen, 2011; Nemésio & Ferrari, 2012), with these segregated into two subgenera – *Eulaema s.str.* and *Apeulaema* Moure (Moure, 1950, 1963, 2000; Oliveira, 2006, 2007). There are four species presently documented from Mexico – *Eulaema* (*Eulaema*) *meriana* (Olivier), *E. (E.) luteola* Moure, *E. (Apeulaema) polychroma* (Mocsáry), and *E. (A.) cingulata* (Fabricius) [the latter species is polytypic and perhaps represents multiple taxa (Oliveira, 2006), and the form present in Mexico has at times gone by the name *E. marcii* Nemésio: Nemésio (2009)] – and all of these are taxa with broad distributions (*e.g.*, Moure *et al.*, 2007; Hinojosa-Díaz *et al.*, 2009; Hinojosa-Díaz & Engel, 2012a). Several of these widespread species pose taxonomic challenges and are in need of revision, likely with as of yet unrecognized cryptic taxa (*pers. obs.*). Indeed, critical and comprehensive revisions of these species are needed, as is true for many groups of native bees where

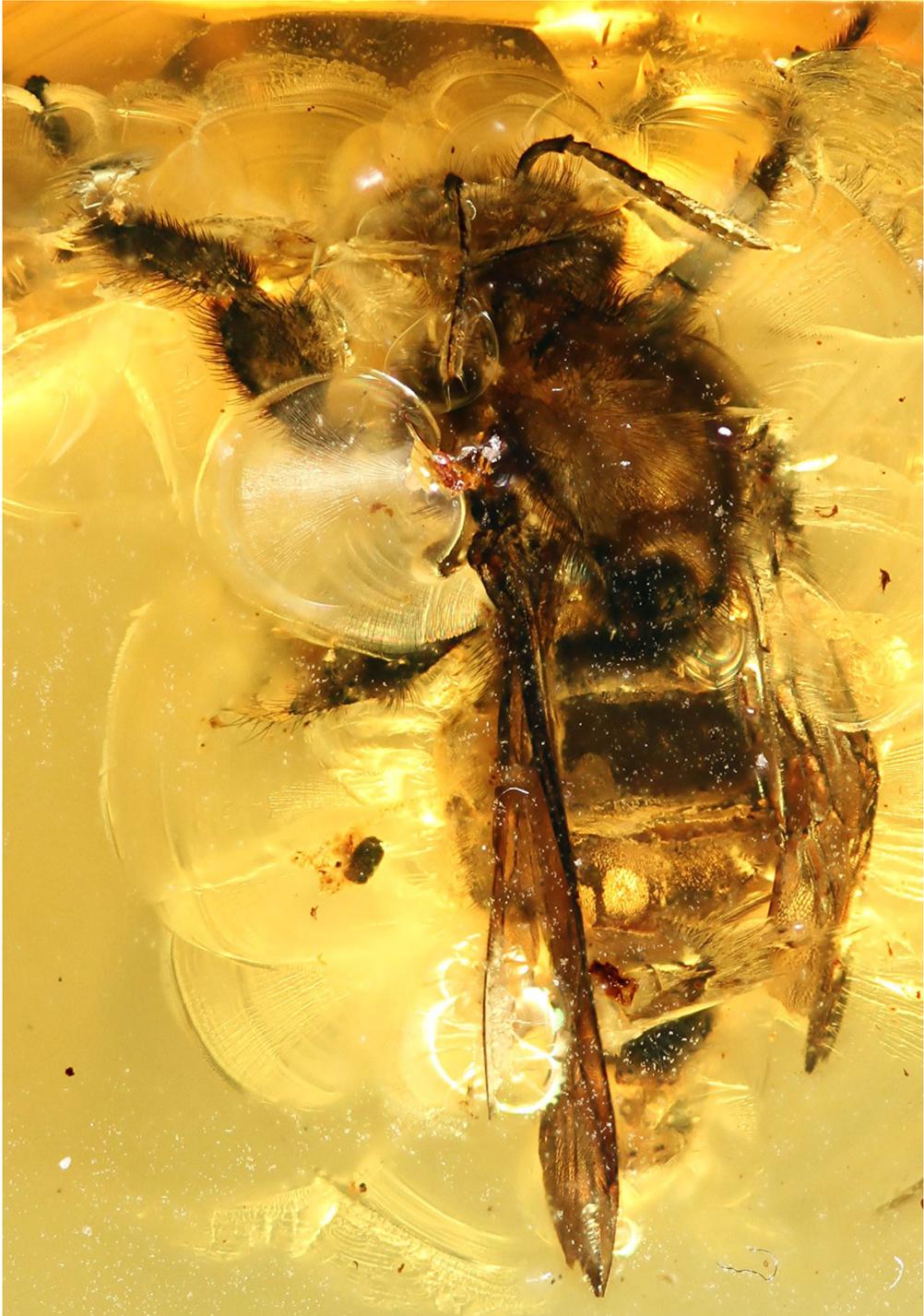


Figure 1. Photograph of dorsal habitus of holotype female (JZC-MX-0023B) of *Eulaema (Apeulaema) zigراسi*, new species, as preserved in Early Miocene Mexican amber.

the circumscription of taxa has not been considered in a modern context (Engel, 2011; Gonzalez *et al.*, 2013). Given the tectonic changes in this region since the Early Miocene

(e.g., Iturralde-Vinent & MacPhee, 1999), it is unlikely that the fossil species discussed herein is a close relative of any of the aforementioned living taxa today occurring in the Chiapas region. Fossil orchid bees have been previously discovered in copal and Dominican amber, the latter comprising species of *Eufriesea* Cockerell and *Euglossa* Latreille (Engel, 1999a; Hinojosa-Díaz & Engel, 2007). The new species from Mexican amber is described, figured, and compared with its living congeners.

MATERIAL AND METHODS

Morphological terminology used follows that of Engel (1999a, 2001a) and Michener (2007), while the format for the description is loosely based on previous works pertaining to Euglossini (e.g., Kimsey, 1982; Moure, 2000; Oliveira, 2006; Ayala & Engel, 2008; Hinojosa-Díaz & Engel, 2007, 2011a, 2011b, 2012b; Hinojosa-Díaz *et al.*, 2011). Photography was done using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens and illuminated by a Xenon flash, while an ocular micrometer on an Olympus SZX-12 stereomicroscope was employed for measurements. Measured values should be considered somewhat approximate since an optimal angle was not always possible. The age, origin, and paleobiota of Mexican amber have been recently summarized by Engel (2004a) and Solórzano-Kraemer (2007), while general accounts of the fossil history of bees have most recently been provided by Engel (2004b), Ohl & Engel (2007), and Michez *et al.* (2012), with sundry updates by Wappler *et al.* (2012), Engel *et al.* (2012, 2013, 2014), Engel & Breitkreuz (2013), Engel & Michener (2013a, 2013b), Kotthoff *et al.* (2013), and Dewulf *et al.* (2014).

The bee is preserved in a large, relatively clear piece of light yellowish-orange amber from the mines of Chiapas, Mexico. Originally a large, polished, spherical piece clearly meant as an objet d'art, it was cut with a water-fed trimming saw and then several flat surfaces were polished, particularly from above, behind, and lateral to the bee. Given the bee's proximity to other surfaces, only smaller windows could be prepared from below and near the face. These cuts afforded critically important views of the bee, particularly the integument. Despite these necessary preparations, observation of the specimen remains somewhat hampered owing to the presence of several large, reflective fracture planes within the amber piece and around the bee (Figs. 1–4).

SYSTEMATIC PALEONTOLOGY

Genus *Eulaema* Lepeletier de Saint Fargeau

Subgenus *Apeulaema* Moure

Eulaema (Apeulaema) zigrasi Engel, new species

ZooBank: urn:lsid:zoobank.org:act:DD572414-5F21-41DF-8E28-13EA2E888731

(Figs. 1–5)

DIAGNOSIS: The new species is characterized by the overall dark brown to black coloration of the integument, which is lacking metallic highlights, its dark fuscous pubescence (ochraceous or reddish pubescence not present anywhere), and the form of the clypeal ridges as described below.

DESCRIPTION: ♀: Total body length 14.5 mm; forewing length 10.5 mm; hind wing length 7.9 mm. Head wider than long, length 2.93 mm, width 4.36 mm. Labrum length 1.12 mm, width 1.06 mm. Clypeus moderately protuberant, ridges weak, medial ridge extending from base about two-thirds clypeal length and then disappearing, weak

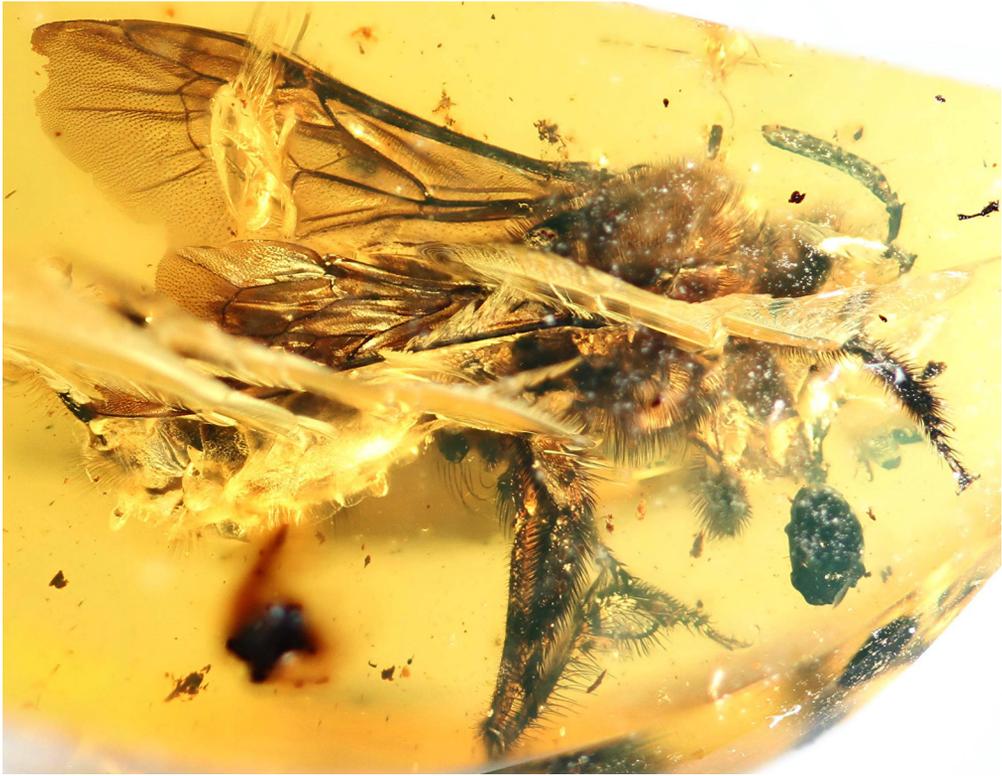


Figure 2. Photograph of right lateral habitus of holotype female (JZC-MX-0023B) of *Eulaema* (*Apeulaema*) *zigrasi*, new species.

paramedial ridges present only in apical half; upper clypeal width 0.90 mm, clypeal medial length 1.22 mm. Upper interorbital distance 2.07 mm, lower interorbital distance 1.76; ocellocular distance 0.42 mm; interocellar distance 0.42 mm. Scape elongate; first flagellomere longer than second flagellomere; second flagellomere as long as third flagellomere; first flagellomere length 0.42 mm; second flagellomere length 0.25 mm; third flagellomere length 0.25 mm (flagellomeres somewhat compressed as preserved, so individual widths were not taken as they are certainly not indicative of the width in life). Mesoscutal length 2.61 mm; intertegular distance 2.92 mm; tegula subtriangular; mesoscutellum long, projecting over metanotum and propodeum, mesoscutellar length 1.65, basal width 1.86 mm. Mesotibia shorter than mesobasitarsus, length 2.02 mm; mesobasitarsal length 2.08 mm, maximum width 0.63 mm; metatibial corbicula as depicted in figure 5, metatibial length 4.38 mm, maximum width 1.92 mm; metabasitarsal length 2.50, width 1.08 mm, metabasitarsus with lateral margins roughly parallel. Forewing with pterostigma small, scarcely longer than wide, tapering slightly along marginal cell, border with marginal cell relatively straight; marginal cell with apex rounded and not appendiculate, offset from anterior wing margin by one vein width; basal vein basad 1cu-a by one vein width; basal vein relatively straight, with weak arch proximally; first submarginal cell not significantly longer than second or third submarginal cells; abscissa of Rs forming apical border of first submarginal cell straight, angled apicad; r-rs shorter than anterior border of second submarginal cell; posterior border of second submarginal cell not bent posteriorly; 1rs-m distad 1m-cu by five times vein width, meeting cell at apical third; anterior border of second



Figure 3. Photograph of left lateral habitus of holotype female (JZC-MX-0023B) of *Eulaema (Apeulaema) zigrasi*, new species.

submarginal cell along Rs slightly shorter than anterior border of third submarginal cell along Rs; 2rs-m arched in anterior half, relatively straight in posterior half, and generally perpendicular to long axis of wing, confluent with 2m-cu; membrane papillate apical to distalmost veins (Fig. 2). Hind wing with 22 distal hamuli arranged in an evenly-spaced series. Maximum metasomal width as preserved 5.1 mm.

Coloration generally dark brown to black (*Nota bene*: coloration is not obvious on all areas of the integument owing to areas of fine froth, taphonomic alteration, or microscopic separation of integument from the amber giving portions of surfaces a silvery metallic sheen common in amber inclusions); head, where evident, dark brown to black (note that large portions of face are taphonomically altered and worn such that surface appears light brown in places, but unaltered integument is also present, including mandible and labrum, and depicts the original black coloration). Mesosoma dark brown, without metallic coloration (fine froth is present over much of integument and between setae but areas of integument can be observed in regions where froth is thin to absent); legs black; wing membranes lightly infumate, veins dark brown to black. Metasomal terga dark brown, without obvious metallic highlights of any kind; sterna brown to dark brown.

Clypeus with well-defined small punctures separated by much less than a puncture width, integument between micro-granulose; remainder of face with smaller punctures more widely spaced, integument between such punctures smoother and apparently more polished. Pronotum strongly imbricate with widely scattered, coarse, shallow punctures. Mesoscutum with small punctures separated by less than a puncture width to nearly contiguous, integument otherwise, where evident, strongly im-



Figure 4. Photograph of frontal view of holotype female (JZC-MX-0023B) of *Eulaema* (*Apeulaema*) *zigrasi*, new species.

bricate; tegula imbricate and apparently impunctate; mesoscutellum as on mesoscutum, although punctures slightly larger and shallower. Pleura with small punctures separated by less than puncture width, integument otherwise imbricate. Metasomal terga with minute punctures separated by less than one puncture width, integument otherwise finely imbricate; sterna strongly imbricate with widely scattered, faint, shallow punctures.

Pubescence throughout dark fuscous, no ochraceous setae present anywhere on body; setae generally long and dense, although not obscuring integument; dense mesoscutellar tuft of black setae present (Fig. 1), mesoscutellar tuft large, about two-thirds length and nearly one-half width of mesoscutellum. Metasomal terga with shorter setae than those of mesosoma, setae subappressed and one-third length of mesoscutal setae, intermingling with slightly longer setae on progressively more apical terga; sternal setae generally erect, elongate, long (similar in length to mesoscutal setae), and dark fuscous on basal sterna, becoming progressively lighter (light fuscous), finer, and intermingling with erect and suberect setae on more apical sterna.

♂: Unknown.



Figure 5. Detail of right metatibia and metatarsus of holotype female (JZC-MX-0023B) of *Eulaema (Apeulaema) zigrasi*, new species.

HOLOTYPE: ♀, JZC-MX-0023B, in Early Miocene (Burdigalian) amber from Chiapas, Mexico; specimen in collection of Mr. James Zigras, available for study through the Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet honors Mr. James S. Zigras, collector of this and many excellent amber inclusions. James recognized the significance of the specimen and graciously permitted its preparation and study.

COMMENTS: Placement of the species in *Apeulaema* is evidenced by the lack of metallic coloration on the metasomal terga, particularly the basal three segments. Given that so much of the taxonomy of Euglossini surrounds characters of the male, particularly the structure and shape of the mesotibial and metatibial modifications, as well as coloration, integumental sculpturing, and male terminalia, it is challenging to make comparisons between the fossil and the most obvious traits used to circumscribe living taxa. It is further problematic that euglossine females may be remarkably similar across groups of related species, so much so that keys are often built for males only and females are placed by association. Despite this, among other species of *Apeulaema* s.str. the fossil is certainly somewhat reminiscent of *E. (A.) nigrita* Lepeletier de Saint Fargeau in the overall black coloration, the body being entirely covered with black setae and lacking any ochraceous or reddish bands on the metasoma, the latter of which are more familiar in species such as *E. polychroma* or *E. cingulata*. The species differs notably from *E. nigrita*, however, in the slightly lighter metasomal integument (dark brown to brown), absence of blue-violet metallic highlights on the apicalmost terga, and the form of the clypeal ridges (medial ridge only extending two-thirds of length from base, weak paramedial ridges only present in apical half).

DISCUSSION

Interestingly, with the discovery of the species described herein, all of the non-parasitic genera of Euglossini are now known from the fossil record (Engel, 1999a; Hinojosa-Díaz & Engel, 2007), demonstrating the presence of these groups in the Early Miocene of North America. None of the fossils are obviously stem groups and it is therefore likely that the individual genera are, in fact, much older, particularly as the fossil *Euglossa moronei* Engel is clearly not of the putatively basal subgenera *Euglossella* Moure or *Dasystilbe* Dressler (pers. obs.), demonstrating that considerable cladogenesis had already taken place by the start of the Neogene. This observation should not be surprising, as the orchid bees as a whole form the basal branch of the corbiculate Apinae (Engel, 2001b; Schultz *et al.*, 2001; Noll, 2002; Cardinal & Packer, 2007), and the lineage must be of great antiquity. Naturally, this does not mean that orchid bees are as old as the divergence of their earliest ancestors from the common ancestor with the remainder of the Corbiculata, a group which extends at least into the latest Cretaceous (*e.g.*, Engel, 2000b; Grimaldi & Engel, 2005). If the lineage had a long fuse leading to the origin of the crown group, and thereby bees familiar enough as euglossines, then the Euglossini as we conceive of them based on living taxa could be of Early Tertiary age, even though the clade as a whole deviated from other corbiculates in the Late Cretaceous. Under such a scenario the specialization on orchids, and thereby their suite of unique morphological specializations, may have come millions of years after the basal cladogenesis among corbiculates. Such realities regarding the differences in origin between stem and crown groups and the divergence from their closest living relatives are often ignored in molecular-only estimates of dating – perhaps because such concepts seem to be foreign to many neontologists. Indeed, it is a great fallacy to

assume for extant sister clades that they are of the same geological age. This assumption is only partly true. Yes, the lineages producing those living clades are of identical ages, but their crown groups may not be, depending on the duration of time between the initial divergence and the origin of the separate crown groups — taxa which experienced their own, independent evolutionary trajectories and times of origin and intracladal radiation. Any attempt to chronicle the history of a group of organisms should be astutely aware of the fossil record, even if fossils are not available for a group, as it is a simple reality that the majority of life is extinct and although stem groups may be long passed and typically forgotten, the impact of their lives shapes the very world in which we live. How one might recognize a stem-group euglossine is not immediately clear, as initial morphological changes in the lineage may not be those external features we associate with the clade today, particularly as many of such traits are associated with their orchid association, and the superficial habitus may have been something similar to a centridine or bombine, leading to misidentification of Paleocene or Eocene compressions. Geometric morphometrics of wing shape offers some tantalizing opportunities to explore such compressions in greater detail (*e.g.*, Wappler *et al.*, 2012; Kotthoff *et al.*, 2011, 2013; Dewulf *et al.*, 2014) [as long as the wings are not distorted or crumpled as preserved — *cf.* wings in Engel (2001c) versus those in Engel (2002, 2006), Engel & Archibald (2003), Wappler & Engel (2003), Engel & Peñalver (2006), and Wappler *et al.* (2012)], and at least one such fossil from the Middle Eocene Parachute Member may represent such a stem group (M. Dehon, D. Michez, A. Nel, M.S. Engel, & T. De Meulemeester, unpubl. data). It would not be unexpected for stem-group Euglossini to potentially reside outside of the area of distribution of modern orchid bees, perhaps even far afield as has been discovered in the pattern of biogeography for other corbiculate tribes (*e.g.*, Engel *et al.*, 2009; Kotthoff *et al.*, 2013). In addition, euglossine fossils have the potential to preserve direct or indirect evidence of paleobiologies and behaviors, illuminating the early evolution of complex behavioral suites (*e.g.*, Engel, 2009c; Chaboo *et al.*, 2009; Wedmann *et al.*, 2009; Davis & Engel, 2010; Wang *et al.*, 2010; Batelka *et al.*, 2011; Knecht *et al.*, 2011; Gu *et al.*, 2012; Pérez-de la Fuente *et al.*, 2012; Huang *et al.*, 2012, 2013; Krogmann *et al.*, 2013; Wappler *et al.*, 2013). Evolving techniques of study and a greater appreciation of fossils will ultimately provide broader avenues for unraveling the origins of the charismatic Euglossini and their intimate relationship with orchids.

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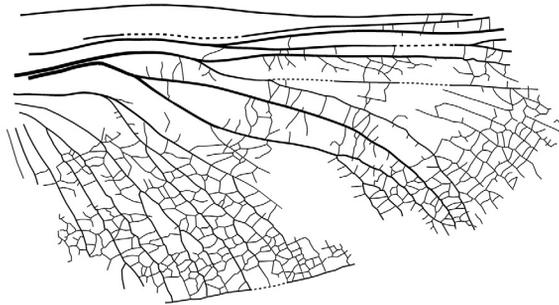
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Pharciphyzelus lacefieldi Beckemeyer & Engel, 2011

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