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A New Fossil Orchid Bee in Colombian Copal (Hymenoptera: Apidae)

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ABSTRACT

A new fossil orchid bee, *Euglossa (Euglossa) cotylisca* Hinojosa-Díaz and Engel, new species (Anthophila: Apidae: Apinae: Euglossini), is described and figured from a male preserved in Quaternary copal from Santander, Colombia. The bee is the third fossil orchid bee and the first fossil bee formally described from South America. Remarks are made on the distinguishing features of the species as well as its affinity to modern species. Given the young age of the fossil and the fact that this species is not known among the modern fauna, it must be presumed that this species has become relatively recently extinct.

RESUMEN

Se presenta la descripción e ilustración de una especie fósil nueva de abeja de las orquídeas, *Euglossa (Euglossa) cotylisca* Hinojosa-Díaz y Engel, especie nueva (Anthophila: Apidae: Apinae: Euglossini), a partir de un macho preservado en copal cuaternario proveniente de Santander, Colombia. Este es el tercer espécimen fósil de abejas de este grupo y el primero formalmente descrito de América del Sur. Se presentan y discuten las características distintivas de la especie, así como su afinidad con especies modernas. A juzgar por la edad del fósil y la presumible ausencia de la especie en la fauna moderna, se presume que la especie se ha extinguido de manera relativamente reciente.

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INTRODUCTION

Orchid bees (Euglossini), with their frequently bright metallic coloration, perhaps most stunningly symbolize the most wonderful aspects of bees; that is, their tight association with flowering plants. The approximately 125 species of euglossines are the most important floral visitors of Neotropical orchids. Males visit orchid flowers at which they dutifully collect fragrant oils that are stored and processed in unique and characteristic metatibial organs (Cruz-Landim et al., 1965; Cruz-Landim and Franco, 2001) (a structure mimicked in design by the metafemoral organs of some *Eoanthidium*: see Engel, 2004a). By contrast, females are infrequently found at orchids and instead visit a diversity of flowers for nectar and pollen. The specialization of several species of orchids to a narrow number of euglossine species (not uncommonly to just one) makes them dependent on the pollination services of these bees (Roubik and Ackerman, 1987). This specificity also renders the male bees susceptible to the devious acts of unscrupulous entomologists who use a variety of fragrant compounds to lure and trap individuals (e.g., Dodson, 1970), a system that is famous among melittologists for its effectiveness.

The orchid bees are one of four modern tribes of corbiculate Apinae and are, according to morphological, behavioral, and paleontological evidence, as well as combined analyses with DNA sequences, crown-group representatives of the first surviving lineage to have branched from the ancestral corbiculate stock (e.g., Schultz et al., 1999, 2001; Engel, 2001a, 2001b; Noll, 2002). The tribe consists of five genera, all of which have been revised at one time or another (e.g., Kimsey, 1979, 1982; Moure, 2000; Oliveira, 2006; Anjos-Silva and Rebêlo, 2006), except for the most diverse and complicated genus, *Euglossa*. While all euglossines are associated with orchids, species of *Aglae* and *Exaerete* are cleptoparasitic on other orchid bees.

Unlike most other corbiculate tribes, the euglossines have a meager fossil record presently consisting of only two extinct species described in Early Miocene amber from the Dominican Republic (Engel, 1999). Another record, however, does exist and has been

briefly alluded to in the literature (i.e., Ross, 1998; Engel, 2001a). In 1996, Dr. A.J. Ross drew to the attention of the junior author the existence of a male orchid bee in Colombian copal in the collection of the Natural History Museum, London (NHML), which was identified by Engel as a male *Euglossa* superficially resembling *Euglossa cordata* (Linnaeus). The specimen was studied at that time and notes were prepared but work was not completed until the senior author visited the NHML in 2006 to finish work on the fossil. Herein we finally provide an account of this interesting and stunningly beautiful fossil bee (fig. 1). Morphological terminology follows that of Engel (1999, 2001a), with the abbreviation OD used for ocellar diameter (based on the median ocellus), while the general geological history of the Anthophila was summarized by Engel (2004b), Grimaldi and Engel (2005), and Ohl and Engel (2007).

SYSTEMATIC PALEONTOLOGY

GENUS *EUGLOSSA* LATREILLE

Euglossa (*Euglossa*) *cotylica*, new species figures 1, 2

Euglossinae; Ross, 1998: 63.

Euglossa sp.; Engel, 2001a: 176.

DIAGNOSIS: Integument uniformly brilliant metallic green (fig. 1), with golden highlights; ivory white paraocular marks well developed; labrum, mandibles (although apices are likely brown but cannot be discerned in the fossil), and malar space ivory white. Metatibiae with a deep central, integumental depression on outer surface (fig. 2), following the widest area of the metatibial organ slit's outer section.

DESCRIPTION: *Male*. Body length about 10 mm, head width about 4.5 mm. Malar space length not exceeding flagellar diameter. Labral windows oval, occupying about two-thirds of labral length, closer to clypeus; midlabral ridge well developed and sharp, lateral ridges well developed on upper two-thirds of labrum. Clypeus moderately protruded (i.e., face not flattened), middle ridge sharp, lateral ridges well developed on upper part. Surface of mesocutellum even, not bigibbous, posterior border straight. Metatibia with anterior border (the one abutting



Fig. 1. Photomicrograph of *Euglossa* (*Euglossa*) *cotylisca* Hinojosa-Díaz and Engel, new species (NHML Pal. PI II 670 [1]) in Colombian copal; **above**, a view of the entire piece encapsulating the bee; **below**, dorsal aspect of the bee in detail. [Upper image by I.A.H.-D., 2006; lower image by P.V. York, reproduced with permission of the NHML, © The Natural History Museum, London].

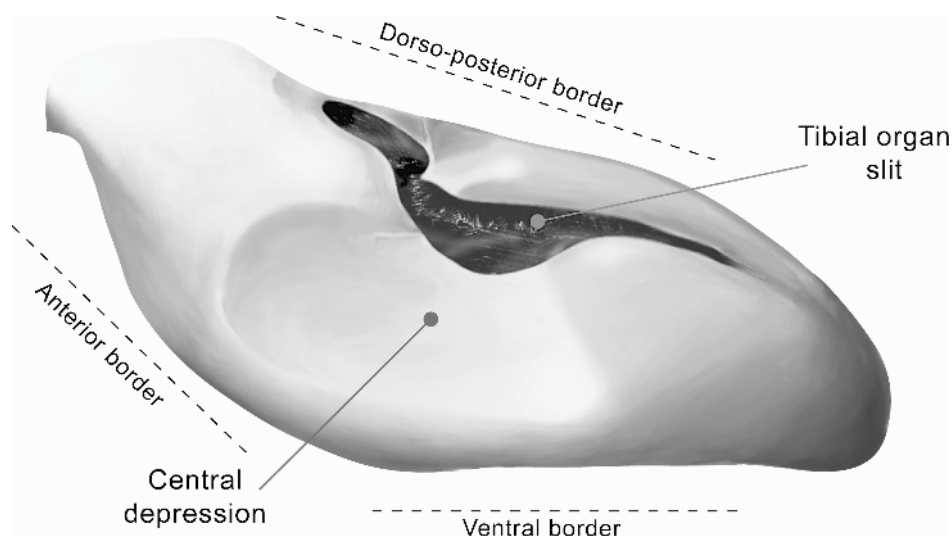


Fig. 2. Metatibia of *Euglossa* (*Euglossa*) *cotylisca* Hinojosa-Díaz and Engel, new species (NHML Pal. PI II 670 [1]) in Colombian copal; setae and punctuation omitted; drawn as viewed from a very slightly oblique aspect.

metafemur when contracted) as long as, or slightly shorter than, ventral border (the opposing border); dorsoposterior border (the diagonal edge) divided in two sections by deep notch on area where dorsal section of metatibial organ slit is present (fig. 2); metatibial organ slit dorsal and outer sections well defined with a junction narrower than the contiguous width of dorsal section; apex of dorsal section acute; outer section spur-shaped; outer surface of metatibia with a large, deeply impressed central depression following the widest area of the metatibial organ slit's outer section (such a depression is present in some modern species, but only faintly so and never to the degree seen in the fossil; this is not an artifact of preservation as there is no compression anywhere on the specimen and the same feature is identical on both metatibiae).

Entire individual brilliant metallic green (fig. 1), with golden hue particularly on mesoscutum, mesoscutellum, and metatibia. Ivory paraocular marks well developed running from at least (as much as can be seen) area of antennal insertion to clypeus; marks slightly wider at lower extreme, not exceeding 1.5 times the width at the level of antennal insertion, and occupying about 0.2 of the eye-clypeus disc distance. Labrum and mandibles

ivory, mandibular coloration apparently typical for most *Euglossa* (i.e., ivory with borders and teeth brown). Malar space completely ivory. Major podites of legs brilliant metallic green; tarsomeres (except basitarsi) brown as typical for most *Euglossa*.

Frontal fringe moderately dense, formed of dark, erect, simple setae about as long as 1 OD. Vertex with longer (about 1.5 OD), scattered setae like those of frontal fringe, concentrated on intra-ocular area, lateral depressions (formed between the border of compound eyes and ocellar monticule), and forming a sparse occipital fringe. Supralateral areas surrounding clypeus with some setae as those on vertex; clypeus covered with scattered setae of the same nature but about one-half length of those on frontal fringe. Antennal depressions with moderately dense, whitish, plumose setae; scape with some scarce short setae; pedicel with two dark, erect, small apical setae, otherwise bare; flagellum with fulvous, very short, simple setae scattered over surface; flagellar articles 3 through 11 with usual frontal sensillae. Lower gena with long, whitish, plumose setae. Pronotal lobe with dense setae, darker, thicker, and longer than those on notum, intermixed with some short, fine, whitish, plumose (finely branched) setae that continue to cover pleural and ventral

areas of mesosoma, similar setae on ventral-facing surface of mesoscutellum. Mesoscutum and mesoscutellum with even layer of moderately dense, dark, erect, simple setae, as long as those on frontal fringe; posterior border of mesoscutum with row of scattered, slightly longer setae. Legs covered with moderately dense, light, short setae. Protarsal podites with dense, long, yellowish setae forming chemical-gathering brushes; tibiae with long, whitish setae on posterior areas, especially on median section of dorsoposterior border of metatibia (right after slit notch); dense, dark, sturdy setae on inner surface of meso- and metabasitarsi; metatibial organ slit closed with dark setae. Metasomal terga covered with light, short setae.

Female. Unknown.

HOLOTYPE: Male, Quaternary Colombian copal, Santander, Colombia, BMNH Pal. PI II 670 (1), M. Caycedo, 24 March 1995 (fig. 1). The specimen resides in the Department of Palaeontology, the Natural History Museum, London.

ETYMOLOGY: The specific epithet is derived from the Latin term *cotyliscus* (meaning “cup-shaped cavity or hollow”) and is a reference to the deep depression of the metatibiae.

PRESERVATION: The piece of copal entombing the bee is the size of a small fist. The sole *Euglossa* individual is close to the straight cut, which offers the best view of the numerous insects encapsulated in the resin. The view of the bee through this surface shows the dorsal and left sides with excellent detail; however, owing to the distortion caused by the resin flows, numerous fractures, and the opacity of the resin on the remaining surfaces, no other areas of the bee can be seen with clarity, except for a small portion of right metatibia and the right side of the head. The head is rotated about 90° to the right, allowing the vertex to be seen perfectly. The labiomaxillary complex is extended, although the maxillae are not entirely protruded. The apices of the mandibles cannot be seen. The legs are all held against the body and oriented in a way that renders it impossible to see the modified setose areas of the left mesotibia. The seventh metasomal tergum and sixth metasomal sternum are not completely closed so that the extreme apex of the genital capsule can be observed.

DISCUSSION

Traditionally the taxonomy of *Euglossa* has relied on the generally sharp differences of external sexual features of males. These characters include the setose outer surface of the mesotibiae, the various modifications of the second metasomal sternum, and the shape of the metatibiae. Some other important characters involve the mesoscutellar shape and the length of the labiomaxillary complex, the latter of which is also related to the degree of clypeal expansion and protrusion. It is, therefore, quite fortunate that the sole individual preserved is a male, thereby permitting a more thorough comparison with modern taxa and a closer approximation of its affinities to other species.

Unfortunately, despite the excellent exposure of several features such as body pilosity and integumental sculpturing, none of the mesotibiae or the sterna can be seen in the specimen owing to the shape and physical characteristics of the copal piece. However, the remainder of those important characters, such as the metatibiae, can be clearly seen and used to determine the taxonomic position of this individual. According to the subgeneric divisions of *Euglossa* by Dressler (1978), this species belongs to *Euglossa* s.str., which, following the same author, embraces five species groups, united by the “rhomboidal” shape of the metatibia. By comparing the fossil with most of the extant species in *Euglossa* s.str., and using those discriminating characters of coloration, presence of paraocular marks, and shape of the metatibial organ slit (the last character not employed by Dressler [1978]), the new species most closely resembles species such as *E. avicula* Dressler, *E. heterosticta* Moure, *E. mourei* Dressler, and *E. townsendi* Cockerell, all placed by Dressler (1978, 1982) in the *purpurea* species group. Following the same set of attributes, the fossil is also somewhat similar to *E. despecta* Moure, *E. gairanii* Dressler, and *E. hemichlora* Cockerell of the *cordata* species group (Dressler, 1978, 1982). Owing to the impossibility of accessing that character most heavily used to define these groups and separating species between and within them, namely the unseen mesotibia, a definitive conclusion regarding the phylogenetic relationship of the fossil could not be made. Moreover,

the monophyly of these groups is exceedingly tenuous. Currently, phylogenetic analyses are being carried out utilizing both morphological (Hinojosa-Díaz, in prep.) as well as molecular data (S. Ramírez, in prep.). These preliminary studies indicate rampant paraphyly and in some instances polyphyly for groups within *Euglossa* proper. It is ultimately hoped that these studies will provide a stronger foundation for the reclassification of species groups within *Euglossa*. At that time, it may be possible to more fully reevaluate the position of the fossil relative to the modern fauna.

The remarkable depression on the outer surface of the metatibiae of *E. cotylisca*, a feature that is clearly observed on both metatibiae (the right one not figured here), is not present in any extant species of the genus. Some specimens of *E. avicula* have a weak depression situated in a similar position, but never as deep and as well defined as in the fossil. The only other species with a depression seemingly like this is *E. dodsoni*, which assuredly belongs to a different group of species, perhaps subgenus, owing to the shape of the metatibia. However, *E. dodsoni* does exhibit a weak depression on the metatibial outer surface, but it is more similar to *E. avicula* than to the state observed in the fossil.

While the fossil is far too young to provide insights into the phylogeny of Euglossini or even *Euglossa* as a whole, the new species is certainly of interest for understanding localized and recent extinctions in the orchid bee fauna of South America. If the depression on the metatibia can be taken as some indication of affinity to *E. avicula*, which is dispersed across Amazonian Brazil, then it is possible that a common ancestor of the fossil and *E. avicula* was more widespread in northern South America, eventually having diverged into different species in at least two regions, with one eventually becoming extinct (i.e., *E. cotylisca*). The unusual depression on the metatibia may have enhanced the absorption of chemicals collected by the bee. Once the substances were transferred from the prothoracic legs, the chemicals may have pooled in the depression as a receptacle and been gradually drawn, in a manner analogous to that of a funnel, into the widest area of the metatibial organ slit (fig. 2).

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REFERENCES

- Anjos-Silva, E.J.dos, and J.M.M. Rebêlo. 2006. A new species of *Exaerete* Hoffmannsegg (Hymenoptera: Apidae: Euglossini) from Brazil. *Zootaxa* 1105: 27–35.
- da Cruz-Landim, C., and A.C. Franco. 2001. Light and electron microscopic aspects of glands and pseudoglandular structures in the legs of bees (Hymenoptera, Apinae, Euglossini). *Brazilian Journal of Morphological Sciences* 18(2): 81–90.
- da Cruz-Landim, C., A.C. Stort, M.A.C. Cruz, and E.W. Kitajima. 1965. Órgãos tibial dos machos de Euglossini: estudo ao microscópio óptico e eletrônico. *Revista Brasileira de Biologia* 25: 323–342.
- Dodson, C.H. 1970. The role of chemical attractants in orchid pollination. In: K.L. Chambers (editor), *Biochemical coevolution*: 83–107.

- Corvallis: Oregon State University Press, x + 117 pp.
- Dressler, R.L. 1978. An infrageneric classification of *Euglossa*, with notes on some features of special taxonomic importance (Hymenoptera: Apidae). *Revista de Biología Tropical* 26(1): 187–198.
- Dressler, R.L. 1982. New species of *Euglossa*. 4. The *cordata* and *purpurea* species groups (Hymenoptera: Apidae). *Revista de Biología Tropical* 30(2): 141–150.
- Engel, M.S. 1999. The first fossil *Euglossa* and phylogeny of the orchid bees (Hymenoptera: Apidae; Euglossini). *American Museum Novitates* 3272: 1–14.
- Engel, M.S. 2001a. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.
- Engel, M.S. 2001b. Monophyly and extensive extinction of advanced eusocial bees: insights from an unexpected Eocene diversity. *Proceedings of the National Academy of Sciences USA* 98(4): 1661–1664.
- Engel, M.S. 2004a. A new species of the bee genus *Eoanthidium* with extraordinary male femoral organs from the Arabian Peninsula (Hymenoptera: Megachilidae). *Scientific Papers, Natural History Museum, University of Kansas* 34: 1–6.
- Engel, M.S. 2004b [2005]. Geological history of the bees (Hymenoptera: Apoidea). *Revista de Tecnología e Ambiente* 10(2): 9–33.
- Grimaldi, D., and M.S. Engel. 2005. *Evolution of the insects*. Cambridge: Cambridge University Press, xv + 755 pp.
- Kimsey, L.S. 1979. An illustrated key to the genus *Exaerete* with descriptions of male genitalia and biology (Hymenoptera: Euglossini, Apidae). *Journal of the Kansas Entomological Society* 52(4): 735–746.
- Kimsey, L.S. 1982. Systematics of bees of the genus *Eufriesea* (Hymenoptera, Apidae). *University of California Publications in Entomology* 95: 1–125.
- Moure, J.S. 2000 [2003]. As espécies do gênero *Eulaema* Lepeletier, 1841 (Hymenoptera, Apidae, Euglossinae). *Acta Biologica Paranaense* 29(1–4): 1–70.
- Noll, F.B. 2002. Behavioral phylogeny of corbiculate Apidae (Hymenoptera: Apoidea), with special reference to social behavior. *Cladistics* 18(2): 137–153.
- Ohl, M., and M.S. Engel. 2007. Die Fossilgeschichte der Bienen und ihrer nächsten Verwandten (Hymenoptera: Apoidea). *Denisia* 20: in press.
- Oliveira, M. 2006. Três novas espécies de abelhas da Amazônia pertencentes ao gênero *Eulaema* (Hymenoptera: Apidae: Euglossini). *Acta Amazonica* 36(1): 121–128.
- Ross, A.J. 1998. *Amber: The natural time capsule*. London: Natural History Museum, 73 pp.
- Roubik, D.W., and J.D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. *Oecologia* 73(3): 321–323.
- Schultz, T.R., J.S. Ascher, and M.S. Engel. 2001. Evidence for the origin of eusociality in the corbiculate bees (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 74(1): 10–16.
- Schultz, T.R., M.S. Engel, and M. Prentice. 1999. Resolving conflict between morphological and molecular evidence for the origin of eusociality in the “corbiculate” bees (Hymenoptera: Apidae): a hypothesis-testing approach. *University of Kansas Natural History Museum Special Publication* 24: 125–138.

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