

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3272, 14 pp., 7 figures, 3 tables

August 10, 1999

The First Fossil *Euglossa* and Phylogeny of the Orchid Bees (Hymenoptera: Apidae; Euglossini)

MICHAEL S. ENGEL¹

ABSTRACT

The first fossil *Euglossa* (tribe Euglossini) is described and figured from Miocene Dominican amber as *Euglossa moronei* new species. The species is differentiated from extant euglossines, and its apparent lack of close affinity to any extant subgenus or species group is discussed. The existing data pertinent to the internal phylogeny of Euglossini are reconsidered, and a new hypothesis of relationships among the genera is proposed. The distribution of the euglossines, particularly in the West Indies, and their associations with orchids is briefly considered.

INTRODUCTION

All the past these mountains saw
All the years of toil and strife
Lives unknown that went before
They gave us this: Our present life.

—Theodore D. A. Cockerell (1927)

The orchid bees are among the most spectacular of the Apoidea owing to their frequently robust body size and brilliant metallic coloration or banding on the metasoma. The group is sometimes known as the golden bees; however, this is a misnomer since few species exhibit golden coloration and most

are brilliant metallic green or blue. Far more notable than their coloration is the extreme modification of the mouthparts. The proboscis of the orchid bees is elongated such that in many species the end of the glossa extends beyond the metasoma when in repose. Orchid bees are the most important pollinators of tropical orchids in the Western Hemisphere (Dodson, 1967, 1975; Dodson and Frymire, 1961; Dressler, 1982b). Males are the most common visitors of orchid inflorescences while females are rarely found there. Males collect various fragrant compounds from the flowers using modified tufts of setae on their tarsi; these fragrances are in turn transferred to distinctive foveae on the hind tibiae where they are absorbed. The exact

¹ Research Scientist, Department of Entomology, American Museum of Natural History.

TABLE 1

Hierarchical Classification of Tribe Euglossini

Tribe Euglossini Latreille
Genus <i>Aglae</i> ^a Lepeletier de Saint Fargeau & Serville
Genus <i>Eufriesea</i> Cockerell
Genus <i>Euglossa</i> Latreille ^b
subgenus <i>Dasystilbe</i> Dressler
subgenus <i>Euglossa</i> Latreille
subgenus <i>Euglossella</i> Moure
subgenus <i>Glossura</i> Cockerell
subgenus <i>Glossurella</i> Dressler
subgenus <i>Glossuropoda</i> Moure
Genus <i>Eulaema</i> Lepeletier de Saint Fargeau
Genus <i>Exaerete</i> ^a Hoffmannsegg

^a Genus is parasitic.

^b The subgenera of *Euglossa* are at present poorly defined and much work remains to be done on the characterization of natural groups within this genus.

function of these fragrances is not entirely understood, but they possibly play a role as pheromones (Vogel, 1966). Females are not attracted to the raw substances on the flowers while males are, and thus the compounds, as they are constituted by the flowers, must be precursors of the final chemical presumably used by males for attracting females (Michener, 1974; Dressler, 1982b). Differing chemicals and blends attract different bee species (Dodson et al., 1969; Dodson, 1970), and they are believed to play an important role in reinforcing reproductive isolation among floral species (Michener, 1974; Dodson, 1975; Ackerman, 1983).

The orchid bees are segregated into five genera and together form the tribe Euglossini (see table 1). Of the 150+ known species, most euglossines are classified in the nominate genus, *Euglossa* Latreille (1802), six in the parasitic genera *Aglae* Lepeletier de Saint Fargeau and Serville (1825) and *Exaerete* Hoffmannsegg (1817), and the remainder in the genera *Eulaema* Lepeletier de Saint Fargeau (1841) and *Eufriesea*² Cockerell (1908). The genus *Euglossa* has been split into several subgenera and species groups (see table 1; also Dressler, 1978, 1982a; Moure, 1989); however, these are poorly defined and often

² The fossil recently proposed by Poinar (1998a) as *Paleoeuglossa*, although poorly described, is best placed as an enigmatic species of *Eufriesea* (new synonymy) and thus results in the new combination *Eufriesea melissiflora* (Poinar).

only are confidently recognized in the males. The euglossines are the most basal tribe of the corbiculate Apinae (Roig-Alsina and Michener, 1993; Chavarría and Carpenter, 1994; Schultz et al., 1999). The corbiculate apines are the most recognized group of bees throughout the world and were, until recently, treated as a single family (Apidae sensu Michener, 1990). The group is most readily identified by the presence of a broad, slightly concave area bordered by long hairs on the hind tibia of females (except in queens and parasitic species). This distinctive morphological structure is known as the corbicula; hence the vernacular name for this clade. This monophyletic complex of four tribes contains the familiar honey bees (tribe Apini), the bumble bees (tribe Bombini), and the stingless bees (tribe Meliponini) in addition to the orchid bees. Two of these groups, the honey bees and stingless bees, have played significant roles in human culture, agriculture, and religion for centuries (particularly the Apini) and, owing to their conspicuous, large, eusocial colonies, have been the focus of most biological work in bees. Both apiculture and meliponiculture are profitable enterprises in today's economy. Similarly, the eusocial lifestyle of the bumble bees, although not as elaborate as that of the Apini and Meliponini, along with their large, noticeable body size has historically brought them the attention of many biologists. Like their cousins, the economic value of bombines in agriculture (bombiculture?) is already becoming quite significant. Unlike other corbiculate tribes that are eusocial to varying degrees, the euglossines lack eusocial societies altogether and are the least known of the tribes. Most euglossines are completely solitary except for a few species of *Euglossa* and *Eulaema*, which are communal (Dodson, 1966; Zucchi et al., 1969; Garófalo, 1985, 1991; Garófalo et al., 1998; Roberts and Dodson, 1967). Euglossines, *Euglossa* in particular, frequently collect plant resins for use in the construction of their nests. The resins are used to line the walls of cells that are later provisioned with pollen from a variety of angiosperm families (Dodson, 1966; Roberts and Dodson, 1967; Sakagami et al., 1967; Zucchi et al., 1969; Garófalo, 1991). Flowers of the families visited by orchid bees for pollen possess poricidal an-

thers and euglossines therefore use “buzz” mechanisms to free the pollen (Michener, 1962), although some other floral types are utilized (Dressler, 1982b).

The tribe is restricted to the Western Hemisphere, presumably having arisen sometime after the separation of the African and South American continents. The genera are further restricted to the more tropical regions of the New World, reaching only as far north as the southernmost boundaries of Texas and as far south as northern Argentina. Of the recognized genera, only *Euglossa* occurs in the West Indies today but once again in a restricted distribution. Two species occur on the island of Jamaica, these being the endemic *Euglossa (Euglossa) jamaicensis* Moure (1968) and *E. (Glossura) ignita* Smith (1874), which is more widely distributed on the mainland from Panama to Peru and northern Brazil. Trinidad and Tobago, which are considered to be largely continental areas and faunas, are the only other Caribbean islands to host species of this tribe. These include *E. (E.) townsendi* Cockerell (1904), the type species for the genus, *E. (E.) cordata* (Linnaeus, 1758), and the widely distributed *E. (G.) ignita*. On the mainland, *E. townsendi* ranges from southern Mexico to northern Brazil, while *E. cordata* occurs only in northern South America.

General reviews of euglossine biology have been presented by Zucchi et al. (1969), Dressler (1982b), Kimsey (1980, 1984, 1987), and Michener (1974, 1990); the parasitic euglossines have been reviewed by Moure (1964) and Kimsey (1979). The most recent catalog of the Euglossini was produced by Kimsey and Dressler (1986)³; however, several species have been described since then, and a new general catalog is needed. The internal phylogeny of the Euglossini has been investigated by Kimsey (1982, 1987) and Michener (1990) presented a critique and modification of her data. A modern, detailed study of the tribe, including the relationships among the subgenera of *Euglossa*, remains to be undertaken, and at

present there is no strong evidence for any of the proposed topologies. An attempt is made to reevaluate the current evidence for relationships among the genera and to present a new hypothesis of tribal phylogeny.

The bee fauna of the Dominican amber was, until recently, known only on the basis of the common stingless bee, *Proplebeia dominicana* (Wille and Chandler, 1964: as *Trigona dominicana*). Since then, the number of species recognized from the Oligocene-Miocene of the West Indies has grown both in number and taxonomic diversity (recently summarized by Michener and Poinar, 1996; with some additions by Engel, 1997; Poinar, 1998; Camargo et al., in prep.). At present there are ten Dominican amber species reported in the literature, representing four families, four subfamilies, and seven tribes of bees, although other unstudied species exist (Engel, personal obs.; D. A. Grimaldi, personal commun.). Like most of the Dominican amber insect fauna, these species are closely aligned to present-day taxa, in contrast to some older amber deposits where the species are often difficult to place into recent higher categories (e.g., for bees see Engel, 1998a). The age of Dominican amber is approximately 15–20 Ma, placing it within the Miocene. Grimaldi (1995) argued that Dominican amber must be younger than the Oligocene and Eocene dates that have been stated, while Iturralde-Vinent and MacPhee (1996) provided a sound stratigraphic basis for the Miocene age of these deposits. The orchid bee presented herein is not just the first representative of its genus in amber, but the first *Euglossa* ever recorded from the geological record. The use of plant resins by orchid bees for the construction of nests makes them suitable for entrapment and preservation in amber. For this reason it is somewhat remarkable that until recently the tribe has been completely unknown from the fossil record. As will be noted below, the bee described herein is easily recognizable as a species of the genus *Euglossa* but some features suggest that it represents a lineage of these bees that is no longer extant and therefore cannot be assigned as to subgenus. Because of the imperfect nature of the specimen and the present difficulties with the infrageneric classification of *Euglossa*, I have cho-

³ It should be noted that the name they list as *E. stilbonata* Dressler (Kimsey and Dressler, 1986: 233) is an incorrect subsequent spelling for what should have been *E. stilbonota* Dressler (1982a: 138).

sen not to erect a new subgenus for it but have provided an epithet for the species.

ACKNOWLEDGMENTS

I am indebted to the graciousness of Dott. Ettore Morone of Turin, Italy, for allowing me to study this magnificent inclusion from his amber collection. To him I extend my most sincere gratitude. I am also grateful to David A. Grimaldi who acted as courier for the specimens between Morone and myself, for providing the photograph depicted here as figure 1, and for many delightful discussions about this study and amber in general. My work is further supported by the generosity of Robert G. Goelet, Chairman Emeritus of the American Museum of Natural History Board of Trustees, and by Jerome G. Rozen, Jr., both to whom I express my deepest appreciation. The manuscript received significant improvements through critical reviews from James M. Carpenter, Gabriela Chavarría, David A. Grimaldi, Charles D. Michener, Molly G. Rightmyer, and Jerome G. Rozen, Jr. I thank each of them for their time and kind assistance.

TERMINOLOGY

The morphological terminology generally follows that proposed by Michener (1944) with additions for mandibular structure provided by Michener and Fraser (1978). Others have used the term "lorum" for the submentum because of the difficulty in determining the homology between this structure and the true submentum of other Hymenoptera or insects (e.g., Plant and Paulus, 1987; Michener, 1990). Similarly, the small subapical projection on the submental arms has been termed the "loral splinter" (Plant and Paulus, *op. cit.*). I prefer to retain the terminology originally used by Michener (1944) and use submentum in place of lorum until the homology—rather, the lack thereof—has been shown conclusively. Michener (1944), however, did not refer to the structure corresponding to the "loral splinter" and so I have provided the term *submental spine* for this character. Roig-Alsina and Michener (1993) referred to the cleft which demarcates the submental spine as the "longitudinal fissure." Because the upper paraocular region

separating the lateral ocellus from the compound eye is important in apine systematics (e.g., Bombini in particular), I prefer to use a separate term for this area: *the ocellorbital area*. This small region has been given various names in apine studies such as the parocular area (Sakagami, 1975) and ocellocular area (Sakagami, 1972), but I prefer the term ocellorbital as it was used by Moure and Sakagami (1962). I employ the term *interocellar furrow* as defined by Engel (1998b), the term *jugal comb* for the series of bristles orchid bees possess in place of the membranous region forming the jugal lobe (Kimsey, 1982), and the term *anal vein* in place of vannal vein.

SYSTEMATIC PALEONTOLOGY

GENUS *EUGLOSSA* LATREILLE

Euglossa moronei, new species

Figures 1, 2, 4, 5

DIAGNOSIS: This species can be separated from extant West Indian species by the moderately protuberant clypeus, absence of medioclypeal ridge or carina, strongly pubescent labrum, apically narrowed labral ovals, entirely fuscous pubescence, absence of plumose hairs dorsal to antennal sockets, strongly ridged vertex, and interocellar furrow. Many of these same characters differentiate this species from any of the known subgenera or species groups. For instance the complete absence of a clypeal ridge, the only moderately protuberant clypeus, absence of plumose hairs just dorsal to the antennal sockets, and noticeably pubescent labrum are all features not found among other *Euglossa*. The relatively "short" glossa suggests species of the subgenus *Euglossa*, while some species of various *Euglossa* groups have a weakly developed interocellar furrow. Furthermore, the long marginal cell is a peculiarity of this orchid bee alone. All extant euglossines have a relatively short marginal cell that ends well before the wing apex. This might be an enigmatic species of the subgenus *Euglossa* or, more likely, an infrageneric lineage that has since become extinct.

DESCRIPTION: Female (male unknown): Head length 5.1 mm, width 4.1 mm. Mandible tridentate and finely imbricate over

much of its surface, becoming smooth basally, broad along its entire length; imbricate integument most notable on trimmal expansion, exposed area of trimma at base with small punctures separated by puncture width, integument otherwise smooth; acetabular carina and groove strong; outer ridges and grooves faint; outer interspace becoming glabrous; malar space short, much less than basal mandibular width. Mentum and submentum fused; submental arms reaching nearly to apex of mentum; submental spine present; apex of mentum blunt, not emarginate or gently concave, expanded relative to shaft, about three-quarters wider at apex than along shaft, apex about as wide as base of prementum. Stipital comb deeply concave, occupying entire distal half of stipes; maxillary palpus two-segmented, second segment slightly longer than first. Proboscis long, probably having extended to sternum 1 or 2 when in repose. Labrum finely imbricate with small areas of rugulose integument along margins; two large, narrow oval areas bordering median area, such areas black and faintly imbricate; labrum noticeably bends posteriorly at lateral borders. Clypeus not as strongly protuberant as in extant *Euglossa* (figs. 3, 4); lacking median carina (which runs lengthwise in extant species); integument with weak punctures separated by about a puncture width or less; integument otherwise minutely imbricate. Supraclypeal area as on clypeus. Epistomal sulcus forming an approximate right angle, slightly bulging near anterior tentorial pit such that clypeus appears to be gently depressed before joining paraocular area. Frontal line strongly impressed, running from between antennae to midway between antennal sockets and median ocellus, becoming a faint depression from that point on. Integument surrounding antennal sockets distinctive in a ring approximately half of an antennal socket diameter; along inner borders integument of ring with minute punctures separated by 1–2 times puncture width, integument otherwise glabrous; along outer borders glabrous and impunctate, small punctures reappearing near border with compound eye; sockets slightly sunken owing to the weak protrusion of the clypeus, supraclypeal area, and suprantennal area; sockets separated by approximately two

antennal socket diameters, separated from compound eye by slightly less distance. Lower paraocular area with weak, coarse punctures, a few slightly elongate, separated by about a puncture width, integument between minutely imbricate; punctures becoming more well defined and slightly smaller as they near compound eye and in paraocular area at level of antennae, separated by width or less in these areas. Suprantennal area slightly protuberant; punctures along lower margins near antennal sockets and supraclypeal area separated by about a puncture width and more well defined than those of clypeus, supraclypeal area, and lower paraocular area; integument otherwise minutely imbricate; punctures rapidly becoming closer until separated by much less than a puncture width (but not contiguous), such dense punctures covering majority of suprantennal area; punctures becoming slightly smaller and weaker near ocelli and vertex. Small punctures between lateral ocelli separated by approximately 1–2 times puncture width and irregularly scattered, integument between smooth, eventually giving way to the interocellar furrow (impunctate, gentle depression); median ocellus separated from lateral ocellus by just less than one-half ocellar diameter (based on the median ocellus); distance between lateral ocelli approximately one ocellar diameter. Ocellorbital area minutely imbricate and mostly impunctate except for a few irregularly placed, faint, small punctures on area nearest compound eye; area just slightly more than one ocellar diameter wide. Vertex behind interocellar furrow gently ridged, extending just above upper tangent of compound eyes; punctures reappearing on vertex and gena like those on majority of suprantennal area.

Forewing with basal vein straight, basad cu-a by about 1.5 times vein width (difficult to determine because of debris on wing); second submarginal cell about as long as first (but veins demarcating cells are heavily covered with debris and thus hard to determine); 1m-cu entering second submarginal cell along apical quarter of cell; marginal cell reaching nearly to wing apex, cell apex acute, slightly separated from wing margin. Hind wing lacking jugal lobe, instead with a jugal comb composed of long, stiff bristles (fig. 5).



Fig. 1. Photomicrograph of female head of *Euglossa moronei*, n. sp. (Photo by D.A. Grimaldi, AMNH).

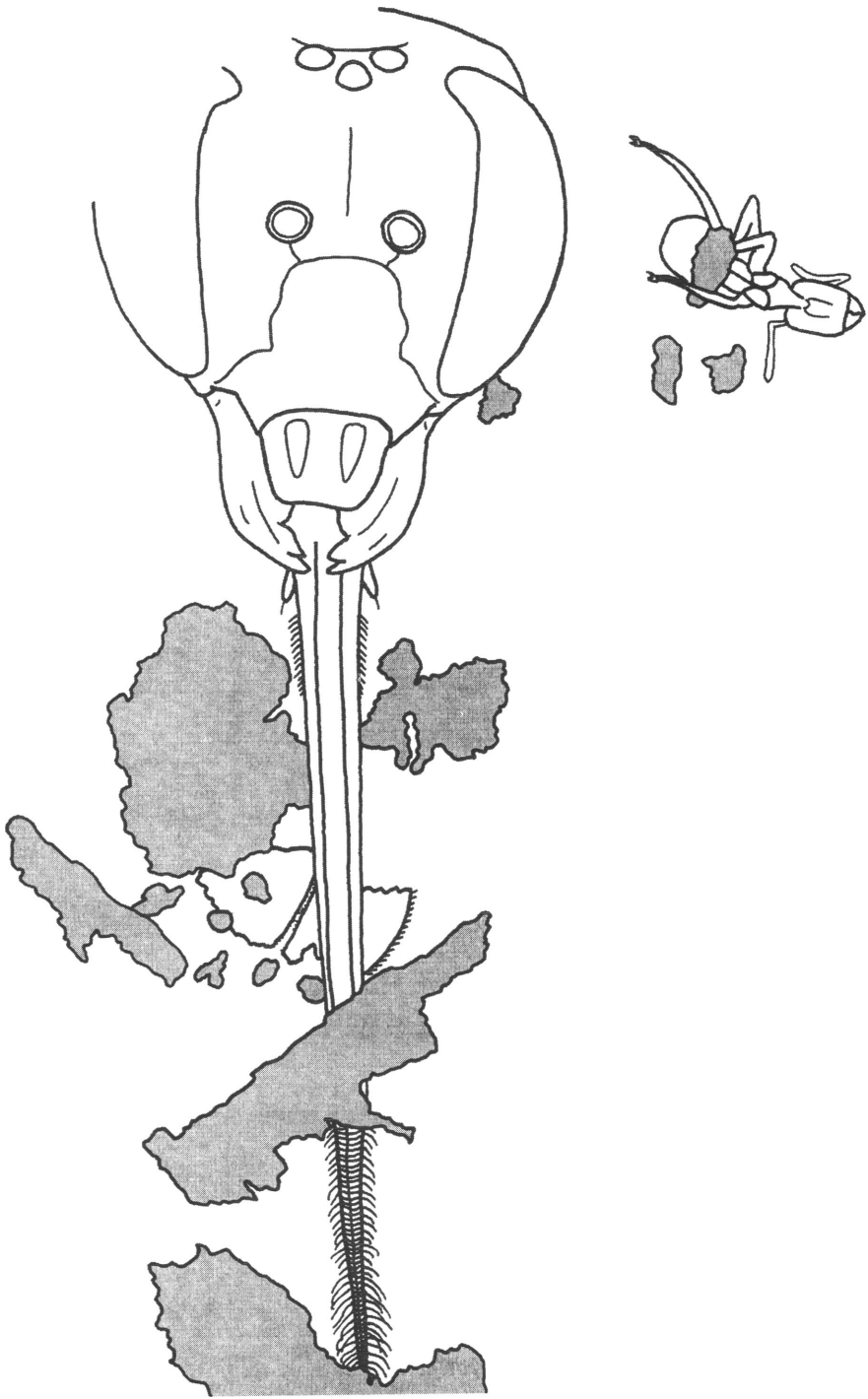
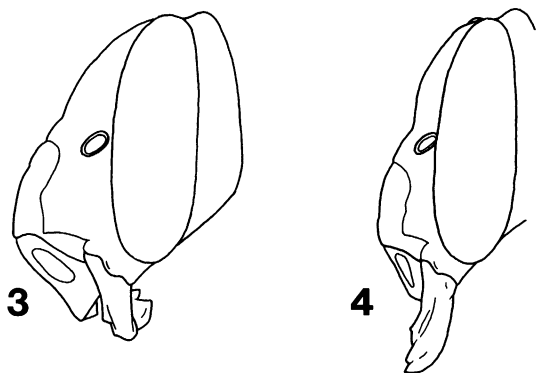


Fig. 2. Illustration depicting scene from figure 1, *Euglossa moronei*, n. sp., with positions of debris and ant indicated.



Figs. 3, 4. Female heads of two *Euglossa* species, profile. 3. *Euglossa (Euglossa) ignita* Smith. 4. *E. moronei*, n. sp., reconstructed profile.

Pubescence entirely fuscous and simple. Mandible with minute hairs along faint outer grooves, extending about $\frac{2}{3}$ to $\frac{3}{4}$ distance to mandible base; those of ventral surface longer and extending the entire length of mandible. Labrum with many long hairs, longest and most dense laterally, somewhat shorter medially. Hairs of face longest just below antennal sockets and on lateral margins of clypeus near epistomal angle; hairs progressively becoming more sparse and shorter on upper half of suprantennal area and around ocelli, once again becoming long on vertex. Upper border of antennal sockets lacking plumose pubescence typical in extant *Euglossa*; outer border of antennal sockets without pubescence. Compound eyes bare.

PRESERVATION: The amber piece is teardrop in shape with the *Euglossa* head positioned at one side of its broadest end. The tongue is extending away from the face towards the broadest border of the amber piece (figs. 1, 2). There is a small ant (worker) positioned near the head (fig. 2) as well as much debris throughout the amber piece. The metasoma is completely lost as is the vast majority of the mesosoma and legs excepting for a few tiny fragments near the forewing which is preserved in about half of total length of the amber piece from the head. The forewing is mostly covered in debris, making it difficult to follow the veins. A fragment of the hind wing, which is mostly torn (fig. 5), is positioned on the opposite side of the piece. The upper left corner of the head is

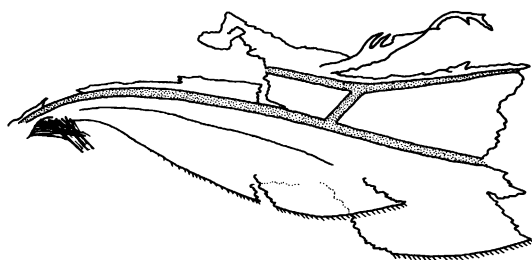


Fig. 5. Hind wing fragment of *Euglossa moronei*, n. sp., depicting the jugal comb at wing base.

difficult to view due to the strong curvature of the amber at this point. The posterior surface of the head is easily viewed and the proboscis, its base in particular, can be examined in quite extraordinary detail.

HOLOTYPE: Female (M-1149), Miocene Dominican amber, Morone Amber Collection, Turin, Italy; specimen incomplete.

ETYMOLOGY: The specific epithet is a patronym honoring Dott. Ettore Morone who graciously allowed the study of this, and many other, fine fossils from his collection.

DISCUSSION

The placement of this species within the Euglossini and *Euglossa* despite the incomplete specimen can be made with remarkable ease and confidence. Among the corbiculate Apinae the orchid bees and bumble bees lack a jugal lobe in the hind wing. The euglossines are further modified with a series of strong bristles in place of the jugal lobe (the jugal comb); a distinctive synapomorphy of the Euglossini. As was mentioned in the description above, a fragment of the hind wing is preserved with the specimen and nicely exhibits this unique structure (fig. 5). Another feature unique to the euglossines among corbiculate bees is the fusion of the mentum and submentum (termed the "lorum" by Plant and Paulus, 1987). The postmentum in most bee groups exists as a single structure with a well-defined mentum and submentum. In the Apini, Bombini, and Meliponini the mentum and submentum become separated, one of several synapomorphies for this grouping. In the fossil, the base of the mouthparts can be plainly seen and, although there is much connective tissue exposed, the entire mentum as well as

TABLE 2

Character Matrix for Euglossine Genera^a

	1	2	3	4	5	6	7	8	9	10	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	
<i>Aglae</i>	1	1	0	0	2	0	0	0	0	0	1	0	0	0	1	1
<i>Eufriesea</i>	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	1
<i>Euglossa</i>	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1
<i>Eulaema</i>	1	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1
<i>Exaerete^b azteca</i>	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1
<i>Exaerete dentata</i>	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1
<i>Exaerete frontalis</i>	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1
<i>Exaerete smaragdina</i>	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1
<i>Exaerete trochanterica</i>	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	1
<i>Apis</i>	0	0	0	0	0	?	?	0	0	2	0	0	0	0	0	0
<i>Bombus</i>	0	0	0	0	0	?	?	0	0	2	0	0	0	0	0	0
<i>Xylocopa</i>	0	0	0	0	0	?	?	0	0	2	0	0	0	0	0	0

^a Updated and modified from Kimsey (1987) and Michener (1990) with the inclusion of outgroups (*Apis*, *Bombus*, and *Xylocopa*). Character descriptions are provided in table 3.

^b Because of the variability in some generic-level characters, I have coded each species of this genus individually.

submentum can be easily found. As is to be expected for a putative euglossine, there is a clear connection between the base of the mentum and the medial region of the submentum. The mentum among the Apini, Bombini, and Meliponini tends to be fairly short and anywhere from weakly to strongly V-shaped at its apex, while in the fossil and extant Euglossini the mentum is long and narrow with a blunt or only weakly concave apex. Similarly, the euglossines are the only corbiculate bees that possess a submental spine (see Terminology) near the apex of the submental arms and this character can also be clearly distinguished in the fossil. In addition to these characters, the greatly elongate mouthparts and short malar space also attest to the placement of this species in the Euglossini, while its labrum and pubescence position it in *Euglossa* (refer to Description).

The phylogenetic affinities among the genera of Euglossini are difficult to ascertain and thus the overall position of *Euglossa* (and thereby this fossil) is of some uncertainty. In the three phylogenetic analyses that have been undertaken, the genera have undergone considerable rearrangement (fig. 6). As was observed by Michener (1990), many of the characters used in the analyses of Kimsey

TABLE 3

Character Descriptions for Data Matrix Presented in Table 2.

The two multistate characters (5 and 10) are treated as nonadditive.

1. Labial palpus: four-segmented (0); two-segmented (1).
2. Scutellum in profile: convex, depressed medially (0); flat, bladelike (1).
3. Scutellar tuft: absent (0); present (1).
4. Sternal groove: absent (0); present (1).
5. Male mesotibial carina: absent (0); incomplete (1); complete (2).
6. Male metatibial slit: broad, ovoid (0); narrow, curved (1).
7. Male metatibial slit: reaching apex (0); not reaching apex (1).
8. Male metatibial shape: round apical margin (0); pointed apical margin (1).
9. Gonocoxal projection: absent (0); present (1).
10. Volsella: ovoid (0); linear, setose (1); fused (2).
11. Hypoepimeral knob: absent (0); present (1).
12. Male metafemoral dentition: absent (0); present (1).
13. Male mesobasitarsal tooth: absent (0); present (1).
14. Male metatibial slit: absent (0); present (1).
15. Jugal comb: absent (0); present (1).

(1982, 1987) are autapomorphies for particular genera and provide no grouping information. A revised data matrix for the Euglossini is presented in table 2 and descriptions of characters in table 3. In addition to removing the autapomorphic characters, I have made the following modifications of the studies of Kimsey (1982, 1987) and Michener (1990): included three outgroups (*Apis*, *Bombus*, and *Xylocopa*) in place of assumed character polarizations; included three characters as potential synapomorphies for the tribe; broken the genus *Exaerete* into its constituent species because that genus varies; added some characters pertinent to the internal phylogeny of *Exaerete*. The data were manipulated in DADA (Nixon, 1995) and submitted from there to Hennig86 (Farris, 1988) for analysis using the *mh** and *bb** commands. Trees were visualized and printed using CLADOS (Nixon, 1993). Three trees resulted of length 22, CI 0.77, and RI 0.85; the strict consensus (i.e., Nelson tree) of which is depicted in figure 7. Only two of the resultant topologies are strictly supported while the third is ambiguously supported (Nixon and Carpenter, 1996).

The topology resulting from this analysis

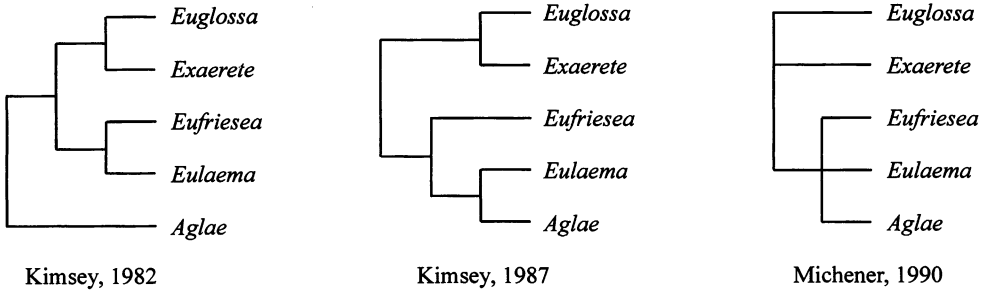


Fig. 6. Previously proposed phylogenies for tribe Euglossini.

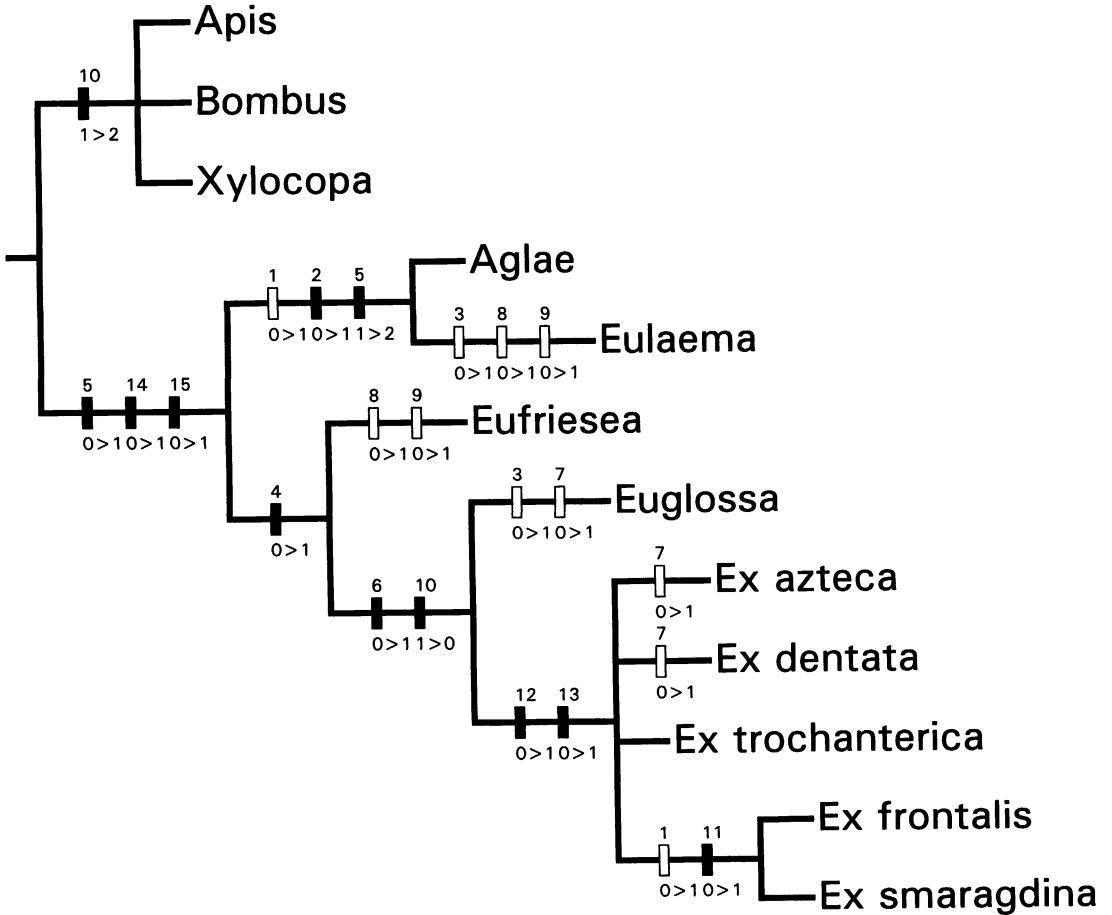


Fig. 7. Phylogeny of Euglossini derived from cladistic analysis of data presented in table 2 (strict consensus of 3 trees, length 22, CI 0.77, RI 0.85). Black bars indicate unreversed changes, white bars indicate homoplastic character transitions. The character number is indicated above the bar and the state change is indicated below.

differs most notably in the position of *Eufriesea*, which is grouped with a *Euglossa* + *Exaerete* clade. Both Kimsey (1982, 1987) and Michener (1990) grouped *Eufriesea* with the genera *Eulaema* and *Aglae*. The grouping presented here is supported by the presence of a strong sternal groove into which the elongate proboscis fits when in repose. This character is absent in the outgroup taxa, *Eulaema*, and *Aglae*. Kimsey (1982, 1987) assumed that the absence of this character was a derived reversal, the presence of such a groove was plesiomorphic for the tribe, and was thereby unavailable to group *Eufriesea* with *Euglossa* and *Exaerete*. Kimsey's alternative grouping of *Eufriesea* with *Eulaema* and *Aglae* was supported by the pointed apical margin of the male hind tibia (although absent in *Aglae*), the presence of the gonocoxal projection (also absent in *Aglae*), and the linear volsella. *Aglae* was considered "so highly modified" (Kimsey, 1987: 68) that the absence of some of these character states were a priori considered reductions and overlooked. *Aglae* is indeed remarkably unique among euglossine genera as Kimsey described, yet her position appears unjustified by outgroup comparison and the presence of a sternal groove is here interpreted as derived while the sole character fixed across the three taxa in Kimsey's arrangement (the linear volsella) is considered plesiomorphic for the tribe. The genus *Euglossa* is believed, once again, to be a fairly derived group of orchid bees and sister to the genus *Exaerete*. Thus, *E. moronei* implies that the genus *Euglossa* is at least 20 Ma, with the origin and more basal diversification of the orchid bees occurring sometime before in the early Eocene or perhaps even the Paleocene.

It is difficult to make any inferences of zoogeographical patterns within the Euglossini at the generic level owing to the widespread distribution of the genera. The complete absence of subgeneric or species-level cladograms also prohibits such a discussion. Despite these difficulties the following observations seem apparent. The genus (and the tribe for that matter) must have previously been more widely distributed in the Caribbean than it is today with subsequent extinction occurring. Apparently there were at least two dispersal events for euglossines into the West Indies. The earliest

one, for which no species survived to the present day, occurred sometime during or prior to the Miocene. The apparent lack of affinities between *E. moronei* and any extant subgenus or species group (see Diagnosis above) suggests that a lineage of *Euglossa* had been widely distributed on an ancient Mesoamerican land mass or had at some point invaded the ancient West Indies, perhaps from South America, and been influenced by the tectonic changes in the region. In either case, this species eventually, along with any other orchid bees that may have been with it, perished from the region as the land mass became fragmented and islands became submerged and reconstituted. This is also true for other bee genera that are known as amber inclusions but are today extinct in the Greater Antilles [e.g., *Chilicola* (Colletidae: Michener and Poinar, 1996), *Heterosarus* (Andrenidae: Rozen, 1996), *Neocorynura* (Halictidae: Engel, 1995)]⁴. The most recent orchid bee colonization seems to have been from Central America into Jamaica, after the island surfaced from the Gulf sometime in the middle Miocene about 20 Ma (Steineck, 1974; Buskirk, 1985), which is supported by the seeming affinities of the endemic *E. jamaicensis* with species in southern Mexico and Costa Rica (Dressler, 1978). Trinidad and Tobago are South American in faunal composition and geological origin (a pattern that holds for the euglossine fauna of these islands) and do not represent a dispersal event into the Caribbean.

The fixation of orchid specialization across the tribe Euglossini suggests that it is a primitive characteristic of the tribe and was already present in the common ancestor of all orchid bees (Schultz et al., 1996). Therefore, given the presumed phylogenetic position of this species within the genus *Euglossa*, it too was presumably a regular visitor of orchids. If this is indeed the case, then this is the oldest record of the specialized association between orchids and their bee visitors. Moreover, the

⁴ Poinar (1998a: 34) enigmatically considers these genera, except *Heterosarus*, to be entirely extinct when each is actually alive and well in the modern mainland bee faunas. In an accompanying note (Poinar, 1998b) he incorrectly asserts that euglossines do not occur in the West Indies while *E. jamaicensis* is endemic to at least one of these islands (other species also occur in Trinidad: see Introduction). He also incorrectly assigns the panurgine genus *Heterosarus* (under the lapsus *Heterosaurus*) to the Halictidae (1998a: 34)!

presence of *E. moronei* and *Eufriesea melisiflora* indirectly indicates that the Orchidaceae was a component of the Oligocene-Miocene flora of Hispaniola. A presumed orchid seed exists in a private collection of Dominican amber (D. A. Grimaldi, personal commun.), which would be the only fossil orchid and would support this notion. In lieu of a definitive fossil orchid, the addition of Orchidaceae to this paleoflora remains an assumption. Similar inferences have indirectly added significant floral components to these ancient forests. For example, the presence of palm bugs (Heteroptera: Thaumastocoridae) and fig wasps (Hymenoptera: Agaonidae) indicates the presence of palm and fig trees, respectively (Grimaldi, 1996).

Resolution of the relationships among euglossines would potentially provide greater insights into orchid bee biogeography as well as a foundation upon which to examine in greater detail the bee-orchid association and coevolution. As it presently stands we know that males of all of the nonparasitic genera pollinate the orchid tribes Cymbidieae, Epidendreae, and Maxillarieae while *Exaerete* males visit Maxillarieae (the orchid associates of *Aglae* remain to be discovered). As was also observed by Oliveira (1998), the distribution of these tribes mapped on euglossine phylogeny (no matter what topology is preferred) provides little information for understanding bee-orchid coevolution. Future work should focus on cladistic studies of species-level relationships, particularly in the genus *Euglossa*, coupled with studies on the relationships among orchids (the foundations of which can be found in Dressler, 1993). Such lower-rank analyses will also create the framework for finer discussions of euglossine biogeography, possible morphological specialization, and patterns in species-specific chemical blends. For the time being, however, we can only marvel at the complexity of orchids and their bee visitors and, like Darwin (1862), speculate on the even greater story of their union that awaits our discovery.

REFERENCES

- Ackerman, J. D.
1983. Specificity and mutual dependency of the orchid-euglossine bees interaction. *Biol. J. Linn. Soc.* 20: 301–314.
- Buskirk, R. E.
1985. Zoogeographic patterns and tectonic history of Jamaica and the northern Caribbean. *J. Biogeogr.* 12: 445–461.
- Chavarría, G., and J. M. Carpenter
1994. Total evidence and the evolution of highly social bees. *Cladistics* 10: 229–258.
- Cockerell, T.D.A.
1904. Descriptions and records of bees. *Ann. Mag. Nat. Hist.*, ser. 7, 14: 21–30.
1908. Notes on the bee-genus *Exaerete*. *Psyche* 15: 41–42.
1927. *Zoology of Colorado*. Boulder: Univ. Colorado Press.
- Darwin, C. R.
1862. On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. London: John Murray.
- Dodson, C. H.
1966. Ethology of some bees of the tribe Euglossini (Hymenoptera: Apidae). *J. Kansas Entomol. Soc.* 39: 607–629.
1967. Relationships between pollinators and orchid flowers. *Atas Simp. Biota Amaz.* 5: 1–72.
1970. The role of chemical attractants in orchid pollination. In K. L. Chambers (ed.), *Biochemical evolution*: 83–107. Corvallis: Oregon State Univ. Press.
1975. Coevolution of orchids and euglossine bees. In L. Gilbert and P. H. Raven (eds.), *Coevolution of animals and plants*: 91–99. Austin: Univ. Texas Press.
- Dodson, C. H., and G. P. Frymire
1961. Natural pollination of orchids. *Missouri Bot. Gard. Bull.* 69: 133–152.
- Dodson, C. H., R. L. Dressler, H. G. Hills, R. M. Adams, and N. H. Williams
1969. Biologically active compounds in orchid fragrances. *Science* 164: 1243–1249.
- Dressler, R. L.
1978. An infrageneric classification of *Euglossa*, with notes on some features of special taxonomic importance (Hymenoptera; Apidae). *Rev. Biol. Trop.* 26: 187–198.
1982a. New species of *Euglossa*. III. The *burigera* species group (Hymenoptera: Apidae). *Ibid.* 30: 131–140.
1982b. Biology of the orchid bees (Euglossini). *Annu. Rev. Ecol. Syst.* 13: 373–394.
1993. Phylogeny and classification of the orchid family. Portland: Dioscorides Press.
- Engel, M. S.
1995. *Neocorynura electra*, a new fossil bee

- species from Dominican amber (Hymenoptera: Halictidae). *J. New York Entomol. Soc.* 103: 317–323.
1997. A new fossil bee from the Oligo-Miocene Dominican amber (Hymenoptera: Halictidae). *Apidologie* 28: 97–102.
- 1998a. A new species of the Baltic amber bee genus *Electrapis* (Hymenoptera: Apidae). *J. Hym. Res.* 7: 94–101.
- 1998b. Phylogeny, classification, and evolutionary ethology of the bee tribe Augochlorini (Hymenoptera: Halictidae). Ph.D. diss., Cornell Univ., Ithaca, NY.
- Farris, J. S.
1988. Hennig86, Version 1.5. Program and documentation. Port Jefferson Station, NY.
- Garófalo, C. A.
1985. Social structure of *Euglossa cordata* nests (Hymenoptera: Apidae: Euglossini). *Entomol. Gen.* 11: 77–83.
1991. Comportamento de nidificação e estrutura de ninhos de *Euglossa cordata* (Hymenoptera: Apidae: Euglossini). *Rev. Bras. Biol.* 52: 187–198.
- Garófalo, C. A., E. Camillo, S. C. Augusto, B.M.V. de Jesus, and J. C. Serrano
1998. Nest structure and communal nesting in *Euglossa (Glossura) annectans* Dressler (Hymenoptera, Apidae, Euglossini). *Rev. Bras. Zool.* 15: 589–596.
- Grimaldi, D. A.
1995. The age of Dominican amber. In K. B. Anderson and J. C. Crelling (eds.), *Amber, resinites, and fossil resins*: 203–217. Washington DC: Am. Chem. Soc. Symp.
1996. *Amber: window to the past*. New York: Am. Mus. Nat. Hist.
- Hoffmannsegg, J. C. von
1817. Entomologische Bemerkungen bei Gelegenheit der Abhandlungen über amerikanische Insekten. *Zool. Mag., Wiedemann* 1: 49–110.
- Iturralde-Vinent, M. A., and R.D.E. MacPhee
1996. Age and paleogeographical origin of Dominican amber. *Science* 273: 1850–1852.
- Kimsey, L. S.
1979. An illustrated key to the genus *Exaerete* with descriptions of male genitalia and biology (Hymenoptera: Euglossini, Apidae). *J. Kansas Entomol. Soc.* 52: 735–746.
1980. The behaviour of male orchid bees (Apidae, Hymenoptera, Insecta) and the question of leks. *Anim. Behav.* 28: 996–1004.
1982. Systematics of bees of the genus *Eufriesea* (Hymenoptera, Apidae). Univ. California Publ. Entomol. 95: 1–125.
1984. The behavioural and structural aspects of grooming and related activities in euglossine bees (Hymenoptera: Apidae). *J. Zool. (London)* 204: 541–550.
1987. Generic relationships within the Euglossini (Hymenoptera: Apidae). *Syst. Entomol.* 12: 63–72.
- Kimsey, L. S., and R. L. Dressler
1986. Synonymic species list of Euglossini. *Pan-Pac. Entomol.* 62: 229–236.
- Latreille, P. A.
1802. *Histoire naturelle des fourmis, et recueil de mémoires et observations sur les abeilles, les araignées, les faucheurs, et autres insectes* Paris: Crapelet.
- Lepeletier de Saint Fargeau, A. L. M.
1841. *Histoire naturelle des insectes, Hyménoptères*. Paris: Roret.
- Lepeletier de Saint Fargeau, A. L. M., and J. G. A. Serville
1825. *Entomologie, ou histoire naturelle des crustacés, des arachnides et des insectes*. In P. A. Latreille (ed.), *Encyclopédie méthodique, histoire naturelle, Insectes* 10: 1–344. Paris: Diderot.
- Linnaeus, C.
1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, vol. 1, ed. 10, reformata. Holmiae [Stockholm]: Salviae.
- Michener, C. D.
1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bull. Am. Mus. Nat. Hist.* 82: 151–326.
1962. An interesting method of pollen collecting by bees from flowers with tubular anthers. *Rev. Biol. Trop.* 10: 167–175.
1974. *The social behavior of the bees: a comparative study*. Cambridge MA: Harvard Univ. Press.
1990. Classification of the Apidae (Hymenoptera). *Univ. Kansas Sci. Bull.* 54: 75–164.
- Michener, C. D., and A. Fraser
1978. A comparative anatomical study of mandibular structure in bees. *Univ. Kansas Sci. Bull.* 51: 463–482.
- Michener, C. D., and G. O. Poinar, Jr.
1996. The known bee fauna of the Dominican amber. *J. Kansas Entomol. Soc.*, suppl. 69: 353–361.
- Moure, J. S.
1964. A key to the parasitic euglossine bees and a new species of *Exaerete* from

- Mexico (Hymenoptera Apoidea). *Rev. Biol. Trop.* 12: 15–18.
1968. Espécies novas de *Euglossa* da América Central (Hymenoptera, Apidae). *Bol. Univ. Fed. Paraná, Zool.* 3: 13–64.
1989. *Glossuopoda*, novo subgênero de *Euglossa*, e duas espécies novas da Amazônia, do mesmo subgênero (Apidae Hymenoptera). *Mem. Inst. Oswaldo Cruz, Rio de Janeiro, supl.* 4, 84: 387–389.
- Moure, J. S., and S. F. Sakagami
1962. As mamangabas sociais do Brasil (*Bombus* Latr.) (Hym. Apoidea). *Stud. Entomol.* 5: 65–194.
- Nixon, K. C.
1993. CLADOS, Version 1.4.88. Program and Documentation. L. H. Bailey Hortorium, Cornell Univ., Ithaca, NY.
1995. DADA, Version 0.96.1. Program and Documentation. L. H. Bailey Hortorium, Cornell Univ., Ithaca, NY.
- Nixon, K. C., and J. M. Carpenter
1996. On consensus, collapsibility, and clade concordance. *Cladistics* 12: 305–321.
- Oliveira, M. L. de
1998. Interações entre Euglossini e Orchidaceae: uma mini-revisão sob uma perspectiva cladística e biogeográfica. *Encontro sobre Abelhas, Ribeirão Preto* 3: 144–150.
- Plant, J. D., and H. F. Paulus
1987. Comparative morphology of the postmentum of bees (Hymenoptera: Apoidea) with special remarks on the evolution of the lorum. *Z. Zool. Syst. Evolutions-Forsch.* 25: 81–103.
- Poinar, G., Jr.
1998a. *Paleoeuglossa melissiflora* gen. n., sp. n. (Euglossinae: Apidae), fossil orchid bees in Dominican amber. *J. Kansas Entomol. Soc.* 71: 29–34. [Publication date: 9 February 1999]
1998b. Orchid bees. *Mag. Am. Orchid Soc.* 67: 578.
- Roberts, R. B., and C. H. Dodson
1967. Nesting biology of two communal bees, *Euglossa imperialis* and *Euglossa ignita* (Hymenoptera: Apidae), including description of larvae. *Ann. Entomol. Soc. Am.* 60: 1007–1014.
- Roig-Alsina, A., and C. D. Michener
1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). *Univ. Kansas Sci. Bull.* 55: 123–173.
- Rozen, J. G., Jr.
1996. A new species of the bee *Heterosarus* from Dominican amber (Hymenoptera: Andrenidae; Panurginae). *J. Kansas Entomol. Soc. suppl.* 69: 346–352.
- Sakagami, S. F.
1972. Bumble bees collected by the California Academy Lingnan Dawn-Redwood Expedition to Central West China, 1948 (Hymenoptera: Apidae). *Pan-Pac. Entomol.* 48: 153–174.
1975. Some bumblebees from Korea with remarks on the Japanese fauna (Hymenoptera, Apidae). *Ann. Hist.-Nat. Mus. Natl. Hung.* 67: 293–316.
- Sakagami, S. F., S. Laroca, and J. S. Moure
1967. Two Brazilian apid nests worth recording in reference to comparative bee sociology, with description of *Euglossa melanotricha* Moure sp. n. (Hymenoptera, Apidae). *Annot. Zool. Jpn.* 40: 45–54.
- Schultz, T. R., R. B. Cocroft, and G. A. Churchill
1996. The reconstruction of ancestral character states. *Evolution* 50: 504–511.
- 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. *Univ. Kansas Nat. Hist. Mus. Spec. Publ.* 24: 110–123.
- Smith, F.
1874. A revision of the genera *Epicharis*, *Centris*, *Eulema* [sic], and *Euglossa*, belonging to the family Apidae, section Scapulipedes. *Ann. Mag. Nat. Hist.*, ser. 4, 13: 318–322, 357–373, 440–446.
- Steineick, P. L.
1974. Foraminiferal paleoecology of the Montpellier and lower coastal groups (Eocene-Miocene), Jamaica, West Indies. *Paleogeogr. Paleoclimatol. Paleocol.* 16: 217–242.
- Vogel, S.
1966. Parfümsammelnde Bienen als Bestäuber von Orchidaceen und *Gloxinia*. *Österr. Bot. Z.* 113: 302–361.
- Wille, A., and L. C. Chandler
1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera; Meliponini). *Rev. Biol. Trop.* 12: 187–195.
- Zucchi, R., S. F. Sakagami, and J. M. F. Camargo
1969. Biological observations on a neotropical parasocial bee, *Eulaema nigrita*, with a review on the biology of Euglossinae. *J. Fac. Sci. Hokkaido Univ., Zool.*, ser. 6, 17: 271–380.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site <http://nimidi.amnh.org>. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org