First assessment of the orchid-bee fauna (Hymenoptera: Apidae) at Parque Estadual do Rio Preto, a cerrado area in southeastern Brazil

André Nemésio & Luiz R. R. Faria Jr.

Laboratório de Sistemática e Ecologia de Abelhas, Departamento de Zoologia, ICB, Universidade Federal de Minas Gerais. Caixa Postal 486 -Belo Horizonte, MG. 30.123-970, Brazil. E-mail: nemesio@ornitologia.com.br or andre.nemesio@bol.com.br

Abstract

Male euglossine bees were sampled with chemical attractants in September 2003 at five sites at Parque Estadual do Rio Preto, Minas Gerais state, Brazil. Two sites were located in typical "cerrado" area, two in gallery forests and one in "campo rupestre" formation. We collected 222 bees of ten species; *Euglossa melanotricha* was the most common at every site, followed by *Euglossa fimbriata*, and cineole was the most attractive bait. Comparisons with Atlantic Forest fragments suggest a relatively high diversity of orchid bees in the cerrado domain.

Keywords: Euglossina, chemical baits, Insecta.

Introduction

Orchid bees (Hymenoptera: Apidae: Apini: Euglossina) are primarily neotropical bees occurring from southern United States (Minckley & Reyes, 1996) to southern Brazil (Wittmann et al., 1988) and northern Argentina (Pearson & Dressler, 1985). This subtribe is composed of approximately 200 species distributed in five genera, and this is the only subtribe among Apini which presents no species with eusocial behaviour (Michener, 1990). Male euglossine collect aromatic compounds at flowers, storing them in their posterior tibia (Dodson et al., 1969) but the biological functions of these compounds are not fully understood. However, it was suggested that these substances promote recognition of males by females at the moment of mating (Eltz et al., 1999).

Euglossina are important pollinators of several plant species in the families Orchidaceae, Gesneriaceae, Araceae, Euphorbiaceae and Solanaceae (Williams, 1982). Orchid bees are regarded as forest insects (Dressler, 1982; Morato et al., 1992; Oliveira & Campos, 1995) and, as a consequence, most samplings of orchid bee faunas are carried out in forested areas (Pearson & Dressler, 1985; Powell & Powell, 1987; Becker et al. 1991; Rebêlo & Garófalo, 1991, 1997; Morato et al. 1992; Oliveira & Campos, 1995; Bezerra & Martins, 2001; Tonhasca Jr. et al., 2002; Nemésio, 2003). Few published studies have been performed in other biomes (Neves & Viana, 1997, 1999) with only one in a cerrado area (Rebêlo & Cabral, 1997). The bee fauna of the "cerrado" domain is poorly known due to few

Received:21-X-2003 Accepted:25-X-2004 Distributed 31-XII-2004 assessments in this biome (see Silveira & Campos, 1995; Carvalho & Bego, 1996; Viana et al., 1997).

The Parque Estadual do Rio Preto (PERP) is located in the municipality of São Gonçalo do Rio Preto, state of Minas Gerais, southeastern Brazil, in the Serra do Espinhaço range. It has an area of ca. 10,000 ha, mostly covered with "cerrado sensu stricto" and "campo rupestre" (high elevation rocky field) vegetation, varying from about 700 to 1,826 m above sea level. The Espinhaço range includes an area of approximately 1,000 km in length and 50-100 km in width (Menezes & Giulietti, 2000). This mountain range separates two important biomes in its central and southern portion: the Atlantic forest on the eastern slope, and the "cerrado" on the western slope (see Melo-Júnior et al., 2001). The Espinhaço range invertebrate fauna is almost unknown, and considered a priority area for scientific investigation. The few areas on which there is some information suggest that the invertebrate fauna of this region has exceptional importance (Silveira, 1998).

The main goal of this paper is to report on a rapid and intensive chemical sample of the orchid-bee fauna at PERP in the dry season.

Material and methods

Study sites

Data were collected in five sites of distinct cerrado (*sensu lato*) physiognomies (see Eiten, 1972; Silva & Bates, 2002) at Parque Estadual do Rio Preto. Site-1: a typical cerrado (savanna) formation, at an elevation of ca. 800 m above sea level (18°07'04"S - 43°20'42"W); Site-2: "campo rupestre", at an elevation of ca. 950 m (18°08'15"S - 43°20'59"W); Site-3:

a gallery forest immersed in a matrix of cerrado, at an elevation of ca. 830 m ($18^{\circ}05'26''S - 43^{\circ}20'30''W$). This gallery forest was a tiny corridor along Córrego da Lapa, a small river; Site-4: a gallery forest along Rio Preto, the largest water course inside PERP, at an elevation of ca. 750 m ($18^{\circ}08'10''S -$ 43+20'15''W). The canopy at this site was much denser and higher (tallest trees around 15 - 20 m) than that at Site-3; Site-5: another cerrado area, distinct from Site-1 due to the presence of more arboreal elements (typical "cerradão"), at an elevation of ca. 820 m ($18^{\circ}07'46''S - 43^{\circ}22'15''W$).

Sampling

Male euglossine bees were collected at a single fixed spot in each site, between 11:00 and 16:00, when they are most abundant at baits in southeastern Brazil (unpublished data). Each site was sampled in a single day between September 13 and 24, 2003. Ten aromatic compounds were tested for their attractiveness to male euglossine bees: benzyl acetate, 1,8cineole, eugenol, methyl trans-cinnamate, methyl salicylate, pcresol acetate, ß-ionone, skatole, dimethoxibenzene, and vanillin. They were used to saturate cotton wads that were hung from branches at about 1.5 m above the soil surface and distant from each other at least 2 m. Bees attracted to these lures were captured with entomological nets, killed with ethyl acetate and pinned. The substance to which each bee was attracted and the local and day it was collected were recorded. All specimens collected are deposited at the Entomological Collection of the Department of Zoology, Universidade Federal de Minas Gerais. Bees were identified with the aid of taxonomic keys and by comparison with specimens previously identified by specialists.

Results

A total of 222 male euglossine bees belonging to eight species were collected at the five sites at PERP (Tab. 1). Besides the eight species recorded, additional random samplings at this area revealed the presence of *Euglossa pleosticta* Dressler and *Euglossa leucotricha* Rebêlo & Moure. A single male of the former species was attracted to cineole and some males of *Eg. leucotricha* were attracted to cineole and methyl trans-cinnamate. Thus, the total number of species known to exist at PERP is ten.

Euglossa melanotricha Moure was the most common species in each site, followed by *Eg. fimbriata* Rebêlo & Moure. *Euglossa imperialis* Cockerell and *Eulaema nigrita* Lepeletier contributed 13 individuals each, and the remaining species contributed one or two individuals each (Tab. 1).

Cineole was the most attractive bait, where eighty-one percent of the 222 male orchid bees were collected. Eleven percent of the specimens were collected on eugenol, 5% on methyl cinnamate and the remaining three percent were collected on vanillin, skatole, p-cresol acetate, and β -ionone. Dimethoxibenzene, methyl salicylate, and benzyl acetate were not attractive during this study, although two *Eg. imperialis* were collected in bait traps containing methyl salicylate during the same period in a cerrado area at PERP.

The highest abundance was seen in Site-1 (savanna), followed by Site-4, Site-3 (both riparian forests), Site-2 (field), and Site-5 (savanna - Tab. 1).

Table 1 -	Number of specifients of each species conected at PERP according to the site and attractive ball. $B = D$ -follow, $C = 1,8$ checked, $E = 1,8$
	eugenol; K = skatole; M = methyl <i>trans</i> -cinnamate; P = p-cresol acetate; V = vanillin.

Number of environment of each environment of the DEDD exampling to the site and etteration both D _ h instance C

Species		Site 1				Site 2	2	Site 3				Site 4				Site 5			Т
	С	E	М	B	С	E	v	С	E	М	Р	С	E	K	М	Р	С	E	
Euglossa fimbriata Rebêlo & Moure		03	06	_	07	04	_	17	02	01	_	16	01	02	_	_	08	01	84
Eg. imperialis Cockerell	04	-	-	_	01	-	-	01	-	-	-	06	_	-	01	-	-	-	13
Eg. melanotricha Moure	21	03	03	_	11	04	_	20	01	01	-	25	01	_	-	-	13	03	106
Eg. securigera Dressler	01	-	-	_	-	-	-	-	-	-	-	01	_	-	-	-	-	-	02
Eg. stellfeldi Moure	01	-	-	01	-	-	-	-	-	-	-	-	_	-	-	-	-	-	02
Eg. townsendi Cockerell	-	_	_	_	_	_	_	01	_	_	_	_	_	_	_	_	_	_	01
Eg. truncata Rebêlo & Moure	-	-	-	_	-	01	-	-	-	-	-	-	_	-	-	-	-	-	01
Eulaema nigrita Lepeletier	03	-	_	_	02	_	01	03	-	_	01	01	_	-	-	01	01	-	13
Total individuals		06	09	01	21	09	01	42	03	02	01	49	02	02	01	01	22	04	222
Grand total individuals		62			31			48				55				26			
Total species		06			05			05				05					03 08		

Discussion

Differences among sites

The observed differences among sites, both regarding abundance and richness, should be viewed with care, since only one sampling was carried out in each site. Influence of meteorological factors, such as sunlight, wind, and temperature on activity of bees is well known (see Linsley 1958). During this assessment, changes in weather conditions could be observed. For example, in site-2 the day was completely cloudy until 11:00, when sampling was started. After this time, weather conditions changed dramatically and at noon no cloud could be seen. At site-3, on the other hand, weather was quite hot during all the morning and few clouds could be seen. However by 13:30, the sky became completely cloudy and no bees were collected there after 15:00. These situations are contrasting with those of sites 1 and 4, where the weather conditions were more stable during all day, with a hot weather and clear sky. This kind of variation in climatic conditions may affect the abundance of orchid bees (AN, pers. obs.). Differences among sites may also reflect different climatic conditions, since temperature seems to be the most important factor limiting flight activity in Aculeata (Käpylä, 1974; see Burrill & Dietz, 1981).

It should be pointed out, however, that Eg. *imperialis* was abundant at the most developed forest (site-4) than at the other sites. More than 50% of the individuals of this species were collected in this site.

Species richness

The ten euglossine species observed at PERP were more than the number of species observed in a well preserved (but smaller) Atlantic Forest remnant in eastern Minas Gerais state during the end of the dry season (Nemésio, 2003). In other studies performed at the southernmost portion of the Serra do Espinhaço range, where samplings were carried out during a whole year, the total (year round) observed richness varied from 10 (Reserva Particular do Patrimônio Natural da Serra do Caraça, unpublished data) to 17 species (Belo Horizonte city, Nemésio & Silveira, in press). It should be noticed that all these studies were carried out in semideciduous Atlantic Forest remnants and not in cerrado and campo rupestre areas, as in the present study. Given that euglossines have been regarded as typical forest insects, it is interesting to note that the species richness recorded during the present study is similar to those of most forested areas in nearby regions. Moreover, the fact that sampling at PERP was carried out only during the end of the dry season suggest that the number of species is probably higher, since some euglossine bees (particularly members of the genus *Eufriesea* Cockerell) are highly seasonal and are only active during the wet season. This richness is, thus, remarkable, especially considering that in the only other study performed in a cerrado area, Rebêlo & Cabral (1997) recorded nine species during an entire year, with two samplings per month.

Species composition

Three of the ten collected species, El. nigrita, Eg.

townsendi, and Eg. imperialis, are among the most widespread euglossine bees, occurring from Central America to southern Brazil - Eg. imperialis and Eg. townsendi reach São Paulo state and El. nigrita reaches Rio Grande do Sul state in Brazil (Rebêlo & Garófalo, 1991 and Wittmann et al., 1988 respectively). The low incidence of El. nigrita is noteworthy, since this species has been considered as typical of open areas (Morato et al., 1992; Nemésio & Silveira, in press). However, El nigrita shows a dramatic population decline at the end of the dry season (AN, pers. obs.). Thus, whereas the mean annual frequencies of this species in the Belo Horizonte city region is about 50% of the total community of orchid bees, it drops to 10% or less at the end of the dry season (unpublished data). The same phenomenon may be responsible for its low frequencies at PERP.

The two dominant species, Eg. melanotricha and Eg. fimbriata are abundant in the semideciduous Atlantic Forest of the Belo Horizonte region. Eg. fimbriata was the most common Euglossa species at Parque das Mangabeiras, the largest forest fragment in Belo Horizonte (Nemésio & Silveira, in press). Its presence in high numbers in a typical cerrado area as PERP reinforces the impression that the present orchid bee fauna of the fragmented Atlantic Forest in the interior of Minas Gerais and São Paulo states do not include species apparently dependent of densely forested areas. Eg. melanotricha has only been found in elevations higher than 500 m. It was never collected in areas of typical rainy Atlantic Forest, such as those sampled in Paraíba (Bezerra & Martins, 2001), Espírito Santo (Bonilla-Gómez, 1999), or Rio de Janeiro (Tonhasca Jr. et al., 2002) states. Even in non-coastal areas of low elevations, such as Parque Estadual do Rio Doce (ca. 300m above sea level unpublished data), Eg. melanotricha is absent. Eg. truncata is the dominant species at another large forest fragment (Reserva Particular do Patrimônio Natural da Serra do Caraça, a 11,000 ha area situated at the southern portion of the Serra do Espinhaço range, ca. 60 Km far from Belo Horizonte city) (unpublished data) and also occurs in high numbers at the Belo Horizonte region (Nemésio & Silveira, in press). The rarity of this species (a single male) at PERP is, thus, surprising, even considering the dry season, as is the case of Eg. securigera. Eg. stellfeldi [senior synonym of Euglossa annectans Dressler, 1982 (syn. n.), AN, pers. obs.] is a common species from southern Brazil to Belo Horizonte city region. In Belo Horizonte it is most abundant from November to January, the wettest months in the year. The two males collected at PERP represent the northernmost record for this species. In southern Brazil this species has been collected at sea level (e.g. Florianópolis island) (Kamke et al., 2004). However, in Minas Gerais state it had only been recorded in elevations above 700 m. Eg. leucotricha is a poorly sampled species. It is only known to occur in the states of São Paulo (Rebêlo & Garófalo, 1991), Espírito Santo (Bonilla-Gomez, 1999) and Minas Gerais (Nemésio & Silveira, in press). The males collected at PERP are the northernmost record for this species. Other species are expected to occur at PERP but were not collected, possibly due to the fact that sampling was carried out during the dry season. Species of Eufriesea Cockerell, for example, are seasonal and, at least in southern and southeastern Brazil, are active only during a few months in the wet season (Silveira et al., 2002). Thus, Eufriesea nigrohirta (Friese), a typical species from the

"campos rupestres" of southeastern Brazil, is found at the Serra do Espinhaço range from its southern limits in the Belo Horizonte city region (19° 56' 55"S; 43° 54' 12" W) to the Morro do Pai Inácio (12° 27' 41"S - 41° 28' 34"W), Bahia state, in the north. The PERP, thus, is in the centre of the distribution range of this species in the Serra do Espinhaço and its presence, there is expected during the wet season. Supporting this idea, *Ef. nigrohirta* has been already collected near the village of "Capivari", in the municipality of Serro, MG (ca. 18° 26' 05"S - 43° 25' 11"W; altitude: 1200 m), distant approximately 35 Km (in straight line) from PERP.

Since the highest site sampled at the Rio Preto park was at ca. 950 m and *Ef. nigrohirta* is said to be associated to altitudes above approximately 1300 m (Silveira & Cure, 1993), factors related to altitude may also explain why this bee was not collected during this rapid assessment.

Final comments

Both the richness and the species composition at PERP suggest that the cerrado domain has been underestimated concerning the orchid bee fauna, as it occurs with the bee fauna as a rule (see Silveira & Campos, 1995). Supporting this, Martins (1990) collected eleven orchid bee species at a "cerrado" area in southern Bahia state, without the use of aromatic compounds, which is remarkable. More studies in this domain, which occupies a large area in central Brazil, are necessary in order to understand the patterns of distribution of several euglossine species. Some species regarded as typical of forested areas, such as *Eg. fimbriata*, were collected in large numbers at PERP. These findings suggest that this biome may be important for orchid bees.

Acknowledgements

We thank Dr. Fernando A. Silveira (Universidade Federal de Minas Gerais) for reading and commenting on previous versions of this manuscript; Dr. Benjamin Bembé (Zoologische Staatssammlung München) checked the identification of *Euglossa leucotricha* specimens; Dr. André Hirsch (Pontifícia Universidade Católica de Minas Gerais) calculated the distance between the locality "Capivari" and PERP and helped with coordinates; Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre (UFMG) supported this work; Instituto Estadual de Florestas de Minas Gerais allowed us to sample the area through license # 075/2003.

References

- Becker, P.; Moure, J. S. & Peralta, F. J. A. 1991. More about euglossine bees in Amazonian Forest fragments. Biotropica, 23: 586-591.
- Bezerra, C. P. & Martins, C. F. 2001. Diversidade de Euglossinae (Hymenoptera, Apidae) em dois fragmentos de Mata Atlântica localizados na região urbana de João Pessoa, Paraíba, Brasil. Revista Brasileira de Zoologia, 18: 823-835.

- Bonilla-Gomez, M. A. 1999. Caracterização da Estrutura Espaço-temporal da Comunidade de Abelhas Euglossinas (Hymenoptera, Apidae) na Hiléia Bahiana. Ph.D. Thesis. Campinas, Universidade Estadual de Campinas. xii + 153 pp.
- Burrill, R. M. & Dietz, A. 1981. The response of honey bees to variations in solar radiation and temperature. Apidologie 12: 319-328.
- Carvalho, A. M. C. & Bego, L. R. 1996. Studies on Apoidea fauna of cerrado vegetation at the Panga Ecological Reserve, Uberlândia, MG, Brazil. Revista Brasileira de Entomologia 40: 147-156.
- Dodson, C. H.; Dressler, R. L.; Hills, H. G.; Adams, R. M. & Williams, N. H. 1969. Biologically active compounds in orchid fragrances. Science, 164: 1243-1249.
- Dressler, R. L. 1982. Biology of the orchid bees (Euglossini). Annual Review of Ecology and Systematics, 13: 373-394.
- Eiten, G. 1972. The Cerrado vegetation of Brazil. Botanical Review, 38: 201-341.
- Eltz, T.; Whitten, W. M.; Roubik, D. W. & Linsenmair, K. E. 1999. Fragrance collection, storage and accumulation by individual male orchid bees. Journal of Chemical Ecology, 25: 157-176.
- Kamke, R.; Zillikens, A.; Steiner, J. 2004. Impacto do cleptoparasita *Hoplostelis belineolata* sobre seu hospedeiro *Euglossa stellfeldi*. In: Anais do XXV Congresso Brasileiro de Zoologia, Brasília, CBZ/UnB, p. 156.
- Käpylä, M. 1974. Diurnal flight activity in a mixed population of Aculeata (Hym.). Annales Entomologici Fennici 40: 61-69.
- Linsley, E. G. 1958. The ecology of solitary bees. Hilgardia 27: 543-599.
- Martins, C. F. 1990. Estrutura da comunidade de abelhas (Hymenoptera, Apoidea) na caatinga (Casa Nova, BA) e na Chapada Diamantina (Lençóis, BA). Dr. Thesis. São Paulo, Universidade de São Paulo. 159 pp.
- Melo-Júnior, T. A.; Vasconcelos, M. F.; Fernandes, G. W.; Marini, M. A. 2001. Bird species distribution and conservation in Serra do Cipó, Minas Gerais, Brazil. Bird Conservation International 11: 189-204.
- Menezes, N. L. & Giulietti, A. M. 2000. Campos Rupestres. In: Mendonça, M. P. & Lins, L. V. (orgs.) Lista vermelha das espécies ameaçadas de extinção da flora de Minas Gerais. Belo Horizonte: Fundação Biodiversitas, Fundação Zoo-Botânica, pp. 65-74.
- Michener, C. D. 1990. Classification of the Apidae (Hymenoptera). University of Kansas Science Bulletin, 54: 75-164.
- Minckley, R. L. & Reyes, S. G. 1996. Capture of the Orchid Bee, *Eulaema polychroma* (Friese) (Apidae: Euglossini) in Arizona, with notes on northern distributions of other Mesoamerican bees. Journal of the Kansas Entomological Society, 69: 102-104.
- Morato, E. F.; Campos, L. A. O. & Moure, J. S. 1992. Abelhas Euglossini (Hymenoptera, Apidae) coletadas na Amazônia Central. Revista Brasileira de Entomologia, 36: 767-771.

- Nemésio, A. 2003. Preliminarly sampling of Euglossina (Hymenoptera: Apidae: Apini) of Reserva Particular do Patrimônio Natural "Feliciano Miguel Abdala", Caratinga, Minas Gerais, southeastern Brazil. Lundiana, 4: 121-124.
- Nemésio, A. & Silveira, F. A. in press. Euglossine bee fauna (Hymenoptera: Apidae: Apini) of Atlantic Forest fragments inside an urban area in southeastern Brazil. **Studies on Neotropical Fauna and Environment**.
- Neves, E. L. & Viana, B. F. 1997. Inventário da fauna de Euglossinae (Hymenoptera: Apidae) do baixo sul da Bahia, Brasil. **Revista Brasileira de Zoologia**, **14**: 831-837.
- Neves, E. L. & Viana, B. F. 1999. Comunidade de machos de Euglossinae (Hymenoptera: Apidae) das matas ciliares da margem esquerda do Médio Rio São Francisco, Bahia. Anais da Sociedade Entomológica do Brasil, 28: 201-210.
- Oliveira, M. L. & Campos, L. A. O. 1995. Abundância, riqueza e diversidade de abelhas Euglossinae (Hymenoptera, Apidae) em florestas contínuas de terra firme na Amazônica Central, Brasil. Revista Brasileira de Zoologia, 12: 547-556.
- Pearson, D. L. & Dressler, R. L. 1985. Two-year study of male orchid bee (Hymenoptera: Apidae: Euglossini) attraction to chemical baits in lowland south-eastern Perú. Journal of Tropical Ecology, 1: 37-54.
- Powell, A. H. & Powell, G. V. N. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. Biotropica, 19: 176-179.
- Rebêlo, J. M. M. & Cabral, A. J. M. 1997. Abelhas Euglossinae de Barreirinhas, zona do litoral da baixada oriental maranhense. Acta Amazonica, 27: 145-152.
- Rebêlo, J. M. M. & Garófalo, C. A. 1991. Diversidade e sazonalidade de machos de Euglossini (Hymenoptera, Apidae) e preferências por iscas-odores em um fragmento de floresta no sudeste do Brasil. **Revista Brasileira de Biologia, 51**: 787-799.
- Rebêlo, J. M. M. & Garófalo, C. A. 1997. Comunidades de machos de Euglossinae (Hymenoptera, Apidae) em matas semidecíduas do nordeste do estado de São Paulo. Anais da

Sociedade Entomológica do Brasil, 26: 787-799.

- Silva, J. M. C. & Bates, J. M. 2002. Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. BioScience, 52: 225-233.
- Silveira, F. A. 1998. Fauna de Invertebrados. In: Costa, C. M. R.; Herrmann, G.; Martins, C. S.; Lins, L. V. & Lamas, I. R. (Ed.). Biodiversidade em Minas Gerais – Um atlas para sua conservação. Belo Horizonte, Fundação Biodiversitas. pp. 49-51.
- Silveira, F. A. & Campos, M. J. O. 1995. A melissofauna de Corumbataí (SP) e Paraopeba (MG) e uma análise da biogeografia das abelhas do cerrado brasileiro (Hymenoptera, Apoidea). Revista Brasileira de Entomologia 39: 371-401.
- Silveira, F. A. & Cure, J. R. 1993. High-altitude bee fauna of Southeastern Brazil: implications for biogeographic patterns (Hymenoptera: Apidae). Studies on Neotropical Fauna and Environment 28: 47-55.
- Silveira, F. A.; Melo, G. A. R. & Almeida, E. A. B. 2002. Abelhas Brasileiras: Sistemática e Identificação. Belo Horizonte, Edição do autor. 253 pp.
- Tonhasca Jr., A.; Blackmer, J. L. & Albuquerque, G. S. 2002. Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic Forest. **Biotropica**, **34**: 416-422.
- Viana, B. F.; Kleinert, A. M. P.; Imperatriz-Fonseca, V. L. 1997. Abundance and flower visits of bees in a cerrado of Bahia, tropical Brazil. Studies on Neotropical Fauna and Environment 32: 212-219.
- Williams, N. H. 1982. The biology of orchids and Euglossine bees. In: Arditti, J. (Ed.) Orchid Biology: reviews and perspectives. Ithaca, Cornell University Press, pp. 120-171.
- Wittmann, D.; Hoffmann, M. & Scholz, E. 1988. Southern distributional limits of euglossine bees in Brazil linked to habitats of the Atlantic- and Subtropical Rain Forest (Hymenoptera: Apidae: Euglossini). Entomologia Generalis, 14: 53-60.