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Diversity and Distribution of Orchid Bees (Hymenoptera: Apidae) with a Revised Checklist of Species

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Diversidade e Distribuição de Abelhas Euglossinas (Hymenoptera: Apidae), com uma Lista Revisada de Espécies

RESUMO - O objetivo do presente estudo foi investigar os padrões de distribuição e diversidade das abelhas euglossinas (Euglossina). Análises de agrupamento e de correlação foram aplicados a dados extraídos de 28 levantamentos de euglossinas na Região Neotropical. Os 28 sítios de coleta agruparam-se em três regiões biogeográficas principais que, de forma geral, correspondem à Bacia Amazônica, à Mata Atlântica e à América Central. As três áreas, assim como as sub-regiões de cada uma delas, coincidem, em geral, com os componentes biogeográficos identificados para outras abelhas e organismos com base em análises filogenéticas. A Floresta Amazônica, como um todo, apresentou a fauna mais rica e os mais elevados índices de endemismo. A Mata Atlântica, por outro lado, apresentou a fauna mais pobre e os mais baixos índices de endemismo. No entanto, há que se destacar que um importante bioma neotropical, o cerrado, é praticamente desconhecido no que diz respeito à sua fauna de abelhas euglossinas. Pelo menos 30% das espécies listadas são endêmicas de cada bioma. Uma lista atualizada das espécies de Euglossina é apresentada.

PALAVRAS-CHAVE: Amazônia, Mata Atlântica, Região Neotropical, conservação, taxonomia

ABSTRACT - The aim of this study was to investigate the diversity and distribution patterns of orchid bees (Euglossina). Cluster and correlation analyses were applied to data extracted from 28 orchid-bee surveys throughout the Neotropical Region. The 28 sampling sites were grouped in three main biogeographic areas that roughly correspond to the Amazonian Basin, the Atlantic Forest and Central America. These three regions, as well as subregions within each of them, correspond approximately to biogeographic components identified through phylogeny-based analyses for other bees and organisms. The Amazonian Forest as a whole has the richest fauna and the highest levels of endemism. The Atlantic Forest, on the other hand, showed the poorest fauna and the lowest levels of endemism. However, a major neotropical biome, in which orchid bees are known to occur, has not been sampled yet, the savanna-like cerrado. At least 30% of the species are endemic to each biome. An updated checklist of the species of Euglossina is provided.

KEY WORDS: Amazon, Atlantic Forest, conservation, Neotropics, taxonomy

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Consideration of broad geographic patterns is critical to conceptual development and empirical evaluation of hypotheses in ecology, as well as in conservation and evolutionary biology. Documenting the way in which diversity differs across a given region and understanding the mechanisms that produce such variation are critical steps in the design of regional (and global) conservation strategies and the implementation of regional management plans (Lyons & Willig 2002).

Orchid bees [Hymenoptera: Apidae: Apini: Euglossina (following the proposition of Roig-Alsina in Roig-Alsina & Michener 1993)] frequently are the only pollinators of hundreds of plant species in the Neotropics (revised by Dressler 1982). Since aromatic compounds attractive to orchid bees were discovered in the 1960's (Dodson *et al.* 1969), several inventories have been carried out in an attempt to characterize the local faunas of these bees. Differences in sampling methodology, however, require care to be taken when comparison among local samples is attempted, as noted by Morato (1998) and Nemésio & Morato (2004, 2006). Methodological variations involved include diversity of chemical baits employed; duration of seasonal and daily sampling periods and whether bees are trapped or hand-netted. Moreover, in some cases, bees were identified in the field but not collected.

In spite of these problems, much data have become available in the last 35 years and an attempt to characterize the regional faunas of orchid bees should be made. Nevertheless, since there are no hypotheses for the phylogenetic relationships among the species of most orchid-bee genera, and no such hypothesis will be achieved soon, no historical analysis of orchid bee distribution can be attempted at the moment. The aim of this paper, thus, was to employ the available data on orchid bee distributions in a descriptive analysis, to gain a better understanding of their patterns of geographic distribution.

Material and Methods

Distribution patterns for orchid bees were searched in two ways. First, data obtained from a set of local orchid bee surveys were employed in cluster analyses to delimit biogeographic regions based on faunistic similarity of sites across the Neotropics. After this, all known orchid-bee species were assigned to the regions identified above, according to their known geographic distributions, so that regional species-richness and endemism rates could be compared. In preparing the data matrix and a check list of orchid bee species (Appendix 1), a series of taxonomic decisions had to be made. The problems encountered and the way they were dealt with are explained in Appendix 1.

Data basis of local orchid bee faunas. Data employed in the cluster analyses described below were extracted from many surveys conducted by several researchers across the Neotropical Region (Fig. 1). To reach a reasonable degree of standardization, the data were selected according to the following criteria: (i) we used only results from surveys in which male orchid bees were attracted to aromatic baits (collected using bait traps and insect nets, or attracted but not collected); (ii) the number of specimens (or percentage) of each orchid bee species collected in the area had to be available, since they are necessary for cluster analyses. Thus, simple lists indicating presence/absence were not considered; (iii) cineole (or eucalyptol), one of the most attractive baits, had to be used; (iv) at least two of the following five baits had to be used in addition to cineole: vanillin, benzyl acetate, methyl salicylate, eugenol, and skatole. The use of at least two of these baits together with cineole would make it possible to attract a high percentage of the orchid bee species occurring in a given site (*e. g.* Rebêlo & Garófalo 1997, Morato *et al.* 1992, Bezerra & Martins 2001); (v) for most studies, when more then one site was sampled in the same region, the results of all samples were pooled together and the average frequency of these regional samples was employed in the analyses. Exceptions to these were the two sites at Tambopata Reserve, Peru (Pearson & Dressler 1985), three Costa Rican sites (Janzen *et al.* 1982), and two sites in northeastern state of São Paulo, Brazil (Rebêlo & Garófalo 1997), due to the differences in habitat, elevation or to long distances

Fig. 1. Sampling sites for Euglossina, which data were employed in this study. Data from the multiple sites in Rio Grande do Sul state (RS), Brazil, were merged. Codes of the areas are given in the text and in Table 1.

between sites. On the other hand, in the state of Rio Grande do Sul (Wittmann *et al*. 1988), several sites were sampled in different parts of the state (see Fig. 1), but only the total data were presented. In one case (Oliveira & Campos 1996), in which two sites were sampled for both the understory and canopy, the sites were pooled; however, data from the canopy and understory were considered separate from each other. This was done to check the degree of distinctiveness between understory and canopy faunas, when data from all the Neotropical Region were considered. Data from all other sites employed in our study pertain to understory orchid bee fauna.

The selected studies were: Janzen *et al.* (1982) and Ackerman (1983), for Evergreen Tropical Forests in Central America; Pearson & Dressler (1985), Becker *et al.* (1991), Morato *et al.* (1992), and Oliveira & Campos (1996), for the Amazonian Forest; Wittmann *et al.* (1988) for the Subtropical Atlantic Forest of the state of Rio Grande do Sul, Brazil; Rebêlo & Garófalo (1991, 1997), for the semi-deciduous Atlantic Forest of northeastern region of the state of São Paulo, Brazil; Bonilla-Gómez (1999) for the Atlantic Rain Forest in the Reserva Florestal de Linhares, in the state of Espírito Santo, Brazil; Peruquetti *et al.* (1999) for the seasonal semi-deciduous Atlantic Forest of Viçosa, southeastern Minas Gerais, Brazil; Nemésio & Silveira (2007) for four fragments of semi-deciduous Atlantic Forest in Belo Horizonte, state of Minas Gerais, Brazil; Nemésio (2004) for nine Atlantic Forest fragments around Belo Horizonte and three sites in the Atlantic Forest of the Reserva Particular do Patrimônio Natural da Serra do Caraça, central Minas Gerais, Brazil; Nemésio & Silveira (2006) for a large remnant of semi-deciduous Atlantic Forest, the Parque Estadual do Rio Doce, Eastern Minas Gerais, Brazil; Tonhasca Jr. *et al.* (2002) for the Atlantic Rain Forest of the Desengano region, state of Rio de Janeiro, Brazil; Bezerra & Martins (2001), for the Atlantic Rain Forest of the state of Paraíba, Brazil; Neves & Viana (1997) for a mangrove area in southern state of Bahia, Brazil; Neves & Viana (1999) for a gallery forest immersed in a caatinga matrix in northern Bahia, Brazil; Rebêlo & Cabral (1997) for a western coastal lowland zone in the state of Maranhão, Brazil; Silva & Rebêlo (1999) for Amazonia in the state of Maranhão, Brazil; Silva & Rebêlo (2002) for Cajual Island, Maranhão, Brazil; and Brito & Rêgo (2001) for a secondary forest in Alcântara, Maranhão, Brazil (see Fig. 1 for exact localization of the areas and Table 1 for acronyms used in this paper).

Cluster analysis. Similarity between all site-pairs was calculated using the frequency of each species in the selected samples. The percent similarity-index of Renkonen was employed for this calculation. According to Wolda (1981), when small samples are compared, this index is relatively insensitive to sample size and species diversity, as compared to other similarity indexes. Moreover, it has other desirable characteristics – (i) only presence of common species adds up to the similarity between two sites and (ii) the contribution of any given species to the total similarity can be readily accessed, being equal to its minimum observed frequency in the two sites compared.

Based on these similarities, the areas were grouped using UPGMA (Sneath & Sokal 1973). Two sets of data were used: (i) all the orchid bee species, and (ii) only *Euglossa* species. For Rio Grande do Sul, Brazil, only data for all orchid bee species were used, since only seven individuals of *Euglossa* were caught, four of which were not identified to species level (Wittmann *et al.* 1988).

Checklist of orchid bee species. The known geographic distribution of each valid species of Euglossina was established through the available literature and included as Appendix 1. The species are organized there according to their occurrence in the three major regions defined by the analyses described above: Atlantic Forest (including the Subtropical Rain Forest of southern Brazil, the Semideciduous Atlantic Forest in the interior of the states of São Paulo and Minas Gerais, and some other vegetational types within the Atlantic Forest domain, such as the mangrove area in southern Bahia); Amazon Forest (including parts of northern South America – the so-called Venezuelan Corridor, and Peruvian and Ecuadorian areas east to the Andes); and Central America (including the Caribbean islands, northern Colombia, Mexico and southern United States). These are not homogeneous areas and include different areas of endemism within their limits, such as the Panamanian Endemic Zone (Kimsey 1982), which is included in the Central American region (see also Amorim & Pires 1996, Camargo 1996, Camargo & Pedro 2003). In general, however, these divisions represented areas of relatively high similarity (see results) and are generally coincident with biogeographic areas delimited through phylogeny-based analyses of data obtained for other groups of animals (see Discussion). In addition to these three major regions, species common to two adjacent areas (Atlantic Forest and Amazon Basin or Amazon Basin and Central America) were treated separately. Pan-neotropical species, species with disjunct geographic distributions, and species endemic to other biomes were also included in Appendix 1.

Results

Faunistic regions. When the 28 study areas were grouped according to the similarity of their orchid bee faunas (Figs. 2 and 3), the sites within the Atlantic Forest domain were clustered separately from the sites within the Amazonian Forest domain. These groupings were similar both when all Euglossina and when only species of *Euglossa* were considered. When all Euglossina were included in the analysis, part of the Central American fauna grouped with the Amazonian fauna, but part of the fauna from Costa Rica (Parque Nacional Santa Rosa) was quite distinct from the other regions (Fig. 2). However, when only *Euglossa* were included in the analysis, the Central-American local faunas clustered together as one distinct group (Fig. 3). The position of the Alcântara area (in the northeastern Brazilian state of Maranhão – MA4) also changed depending on the data set employed in the analysis. When all Euglossina were considered, Alcântara clustered with the Atlantic Forest areas, albeit with low similarity; when only species of *Euglossa* were considered, it clustered with the Amazonian region,

Table 1. Number of bees and species, sampling method, chemical baits used and frequency of the commonest orchid bee species in 28 areas in the Neotropics.

Areas	Authors	No. bees	No. species	Method[1]	Baits[2]
Rio Grande do Sul - RS	Wittmann *et al.* (1988)	639	5	IN	C, SK, V
Faz. Santa Carlota (SS) – SP1	Rebêlo & Garófalo (1991)	892	8	IN	C, E, V
EEZ – SP2	Rebêlo & Garófalo (1997)	736	10	IN	C, E, V
Faz. Santa Carlota (SI) – SP3	Rebêlo & Garófalo (1997)	906	14	IN	C, E, V
Viçosa – SMG	Peruquetti *et al.* (1999)	893	10	BT	AB, C, E, SM, V
Belo Horizonte 1997 – BH1	Nemésio & Silveira (2007)	1,325	14	IN	AB, C, CM, E, V
Belo Horizonte 1999 – BH2	Nemésio (2004)	2,146	14	IN	AB, C, CM, E, V
Res. Serra do Caraça - RSC	Nemésio (2004)	236	10	IN	AB, C, CM, E, V
Parque Estadual Rio Doce – EMG	Nemésio & Silveira (2006)	1,183	18	IN	AB, BI, BM, BZ, C, CM, CR, DB, E, SK, SM, T, V
Rio de Janeiro – RJ	Tonhasca Jr. *et al.* (2002)	3,653	21	IN	C, CM, E, SK, SM, V
Espírito Santo – ES	Bonilla-Gómez (1999)	16,177	31	OBS	C, E, SM, SK, V
Mangrove Bahia – BA1	Neves & Viana (1997)	1,144	12	BT	C, E, SM, V
Gallery Forest – BA2	Neves & Viana (1999)	527	7	IN+BT	BB, C, CM, E, V
Paraíba – PB	Bezerra & Martins (2001)	1,082	9	BT	AA, AB, C, E, SM, V
Lowland Coast. zone – MA1	Rebêlo & Cabral (1997)	1,153	9	IN	BB, C, E, SM
Buriticupu – MA2	Silva & Rebêlo (1999)	1,740	37	IN	BB, C, E, SM, V
Cajual Island – MA3	Silva & Rebêlo (2002)	339	19	IN	C, E, SM, V
Alcântara – MA4	Brito & Rêgo (2001)	467	19	IN	BB, C, E, SM, V
Amazon 1991 – AM1	Becker *et al.* (1991)	290	16	BT	C, SK, SM
Amazon 1992 – AM2	Morato *et al.* (1992)	1,242	27	IN	AB, C, E, SM
Amazon 1996 understory – AM3	Oliveira & Campos (1996)	1,145	33	BT	AB, BB, C, CM, E, SK, SM, V
Amazon 1996 canopy – AM4	Oliveira & Campos (1996)	1,277	35	BT	AB, BB, C, CM, E, SK, SM, V
Peru – Floodplain – PE1	Pearson & Dressler (1985)	1,178	18[3]	IN	AA, AB, AC, AlB, C, CM, dC, E, EC, pC, pCy, pE, Pi, SK, SM, V
Peru – Terra Firme – PE2	Pearson & Dressler (1985)	1,661	18[3]	IN	AA, AB, AC, AlB, C, CM,CR, DC, E, EC, pCy, pE, Pi, SK, SM, V
Panama – PAN	Ackerman (1983)	21,842	44	OBS	AB, C, BB, BI, BM, BZ, CM, dC, E, G, L, SK, SM, 2pEA, 2pE, V
Costa Rica – CNP – CR1	Janzen *et al.* (1982)	961	27	IN	AB, C, CM, E, SM
Costa Rica – SNRP (300 m) – CR2	Janzen *et al.* (1982)	720	20	IN	AB, C, CM, E, SM
Costa Rica – SNRP (5 m) – CR3	Janzen *et al.* (1982)	480	12	IN	AB, C, CM, E, SM

[1] Method: IN = insect net; BT = baited traps; OBS = identification in the field, without collecting

[2] Baits: AA = anisyl acetate; AB = benzyl acetate, AC, cresyl acetate; AlB = benzyl alcohol; BB = benzyl benzoate; BI = β-ionone; BM = β-myrcene; BZ = methyl benzoate; C = 1,8-cineole or eucalyptol; CM = methyl trans-cinnamate; CR = *p* -cresol; DB = dimethoxibenzene; DC = D-cresol methanol; dC = d-carvone; E = eugenol; EC = Ethoxy cinnamate; G = geraniol; L = linalool; pCy = *p* -cymere; pE = phenyl ETOH; Pi = piperonol; SK = skatole; SM = methyl salicylate; T = *p*-tolyl acetate; 2pE = 2-phenyl ethanol; 2pEA = 2-phenyl ethyl acetate; V = vanillin

[3] Thirty nine species were collected, but only the 18 most common species included numbers of specimens, but these represented at least 98% of the captured bees.

(%)	CR2	CR3	PAN	CR1	PE1	PE2	AM4	AM1	AM2	AM3	AM4	EMG	MA1	MA3	ES	BA1	BA2	SMG	RJ	PB	MA2	SP1	SP2	RSC	SP3	BH1	BH2	RS
Eg. analis	0	0	0	0	0	0	0.2	0	0	0.3	0	47	0	0	17	0	0	0	5	0	0	0	0	0	0	0	0	0
Eg. chalybeata	0	0	0	0	21	24	9	32	21	21	3	0	1.5	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Eg. cordata	0	0	0	0	0	0	0	0	0	0	2	0.2	63	69	44	45	51	15	23	12	4	17	0	0	0.2	0.5	0	0.5
Eg. imperialis	1.7	0.8	24	34	6	11	0.5	2	0.7	0.5	0	0	0	0	7	2	0	0	0	0	3	0	0	0	0.2	0.2	2	0
Eg. pleosticta	0	0	0	0	0	0	0	0	0	0	0	5	0	0	1	0	0	1	2	0	33	52	72	0	27	0.6	0.5	0
Eg. stilbonota	0	0	0	0	0	0	28	53	32	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eg. viridissima	65	76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
El. cingulata	1	0.6	8	4	2	1	0.1	0	0.7	0.4	24	20	18	3	3	0	0	22	11	6	2	0	0	4	0	0.5	0.2	0
El. nigrita	1	0.6	8	0.1	0	0	0	0	0	0	0.9	10	8	7	10	49	16	55	28	30	4	10	11	26	28	46	51	1

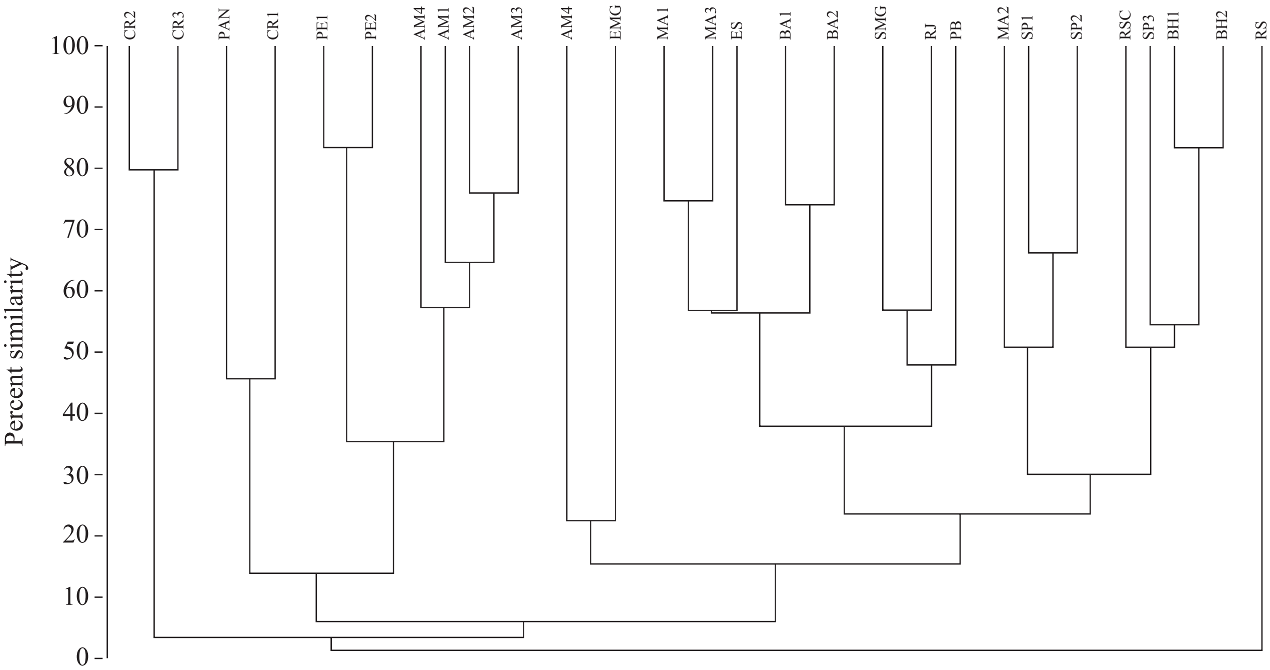

Fig. 2. Clustering of the 28 sampling sites in the Neotropical Region, according to the similarity of their fauna of Euglossina. See Table 1 for codes of the areas. Numbers above site acronyms refer to frequencies of the most important species in defining the groups shown in the dendrograms.

also with low similarity. Lastly, when all Euglossina were considered, the Amazonian Forest clustered first with part of Central America (Panama and the southernmost site of Costa Rica), then with the Atlantic Forest, and finally with the two remaining Costa Rican sites. When only species of *Euglossa* were considered, the Amazonian Forest, including the Peruvian sites, clustered first with the Atlantic Forest and, then, with the Central American region.

The orchid bee fauna of the Brazilian state of Rio Grande do Sul showed almost no similarity with any other area. Thus, in general, there were three distinct groups in South America (Amazonia, Atlantic Forest, and Subtropical Rain Forest, the latter represented by Rio Grande do Sul), and one group for Central America, with two distinct and weakly related subgroups (Panama and southwestern Costa Rica, on one side, and the two northwestern Costa Rican sites, on the other). The association among these major groups was very weak and will be considered below.

Rio Grande do Sul, Brazil. The extremely high frequency of *Eufriesea violacea* (Blanchard) (almost 98% of the bees in the samples) was the main responsible for the dissimilarity between Rio Grande do Sul and the other Atlantic Forest regions. This species was recorded in other sites in the states of São Paulo (SP1, SP2 and SP3), Minas Gerais (EMG, RSC and SMG) and Espírito Santo (ES). Nevertheless, its abundance was always below 5% of the total orchid-bee community in all these areas. The very low frequencies (1% or less) of *Euglossa cordata* (L.) and *Eulaema nigrita* Lepeletier, species widely distributed in the Neotropics and particularly abundant in the Atlantic Forest domain, also contributed for the distinction between Rio Grande do Sul and the Atlantic Forest sites in southeastern and northeastern Brazil.

Atlantic Forest domain. With both sets of data (all Euglossina and only species of *Euglossa*), three subgroups were evident in the Atlantic Forest areas:

- Subgroup 1 (BH1, BH2, RSC, SP1, SP2, SP3, and MA2) constituted mostly by inland, semi-deciduous Atlantic Forest in close proximity with the cerrado (Brazilian savanna). The large frequencies of *El. nigrita*, *Euglossa fimbriata* Rebêlo & Moure, *Euglossa pleosticta* Dressler, and *Euglossa truncata* Rebêlo & Moure are primarily responsible for the clustering of these sites. This subgroup can be further divided in two clusters: (i) BH1

(%)	CR2	CR3	PAN	CR1	PE1	PE2	AM4	AM3	AM2	AM1	MA4	MA1	BA1	MA3	SGM	BA2	PB	ES	RJ	MA2	SP1	SP3	SP2	RSC	BH1	BH2	EMG
Eg. analis	0	0	0	0	0	0	0.2	0.3	0	0	0	0	0	0	0	0	0	20	8	0	0	0	0	0	0	0	69
Eg. chalybeata	0	0	0	0	27	27	10	23	36	34	5	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Eg. cordata	0	0	0	0	0	0	0	0	0	0	3	90	91	82	77	61	54	52	38	5	19	0.3	0	0	1	0	0.2
Eg. fimbriata	0	0	0	0	0	0	0	0	0	0	0.3	0.4	0	0.3	9	37	0	*	1	6	0	39	8	7	27	18	0.6
Eg. imperíalis	2	1	32	47	7	12	0.5	0.6	1	2	0	0	5	0	0	0	0	8	0	4	0	0.3	0	0	1	3	0
Eg. pleosticta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	1	4	42	58	41	88	0	1	1	7
Eg. securigera	0	0	0	0	0	0	0	0	3	0	0	0	0.7	0.7	4	2	0	0.3	12	0.7	0	0.2	0	9	17	7	3
Eg. stilbonota	0	0	0	0	0	0	30	43	48	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eg. viridissima	76	88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

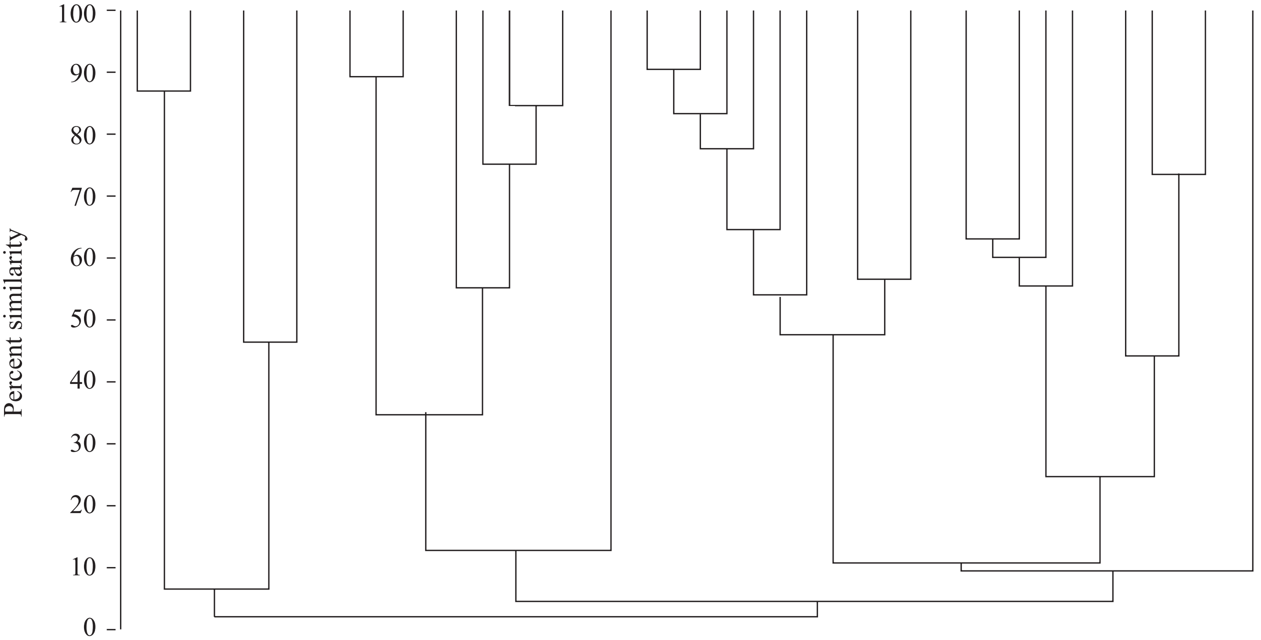

Fig. 3. Clustering of 27 areas in the Neotropical region, according to the similarity of their fauna of *Euglossa.* See Table 1 for codes of the areas. Numbers above site acronyms refer to frequencies of the most important species in defining the groups shown in the dendrograms. * = frequencies below 0.05%.

+ BH2 + RSC, which have a high frequency of *El. nigrita* and *Eg. truncata* in common, and (ii) SP1 + SP2 + SP3 (also inland, in the southernmost portion of this cluster) + MA2 (a disturbed forested area in the Amazonian part of Maranhão), where *Eg. pleosticta* was the most frequent species (33% or more of the specimens). *Eg. pleosticta* was also the dominant species of *Euglossa* in SP3 (41%) and, for this reason, this site moved from the first cluster to the second one when only species of this genus were considered in the analysis (Fig. 3). However, as *Eg. fimbriata* and *El. nigrita* were present at almost the same frequencies as *Eg. pleosticta* in SP3, but in lower frequencies in the rest of the second cluster, this cluster joined the first one when all Euglossina were considered (Fig. 2). In the first cluster (Belo Horizonte region), *Eg. pleosticta* does occur, but in very low frequencies (Nemésio & Silveira 2007).

- Subgroup 2 (BA1, BA2, MA1, MA2, SMG, PB, ES and RJ) is represented mostly by coastal forest. The exception is SMG, which, notwithstanding, is closer to the coast than the other areas in Minas Gerais clustered in Subgroup 1 (BH1, BH2 and RSC). *Eg. cordata* was the dominant *Euglossa* species in all these areas and, in five of them (BA2, ES, PB, MA1, and MA3), it was the dominant orchid-bee species. In some areas (SMG, BA1, RJ, PB, and BA2), *El. nigrita* was very common (it was the dominant species in SMG, BA1, and RJ). This subgroup cannot be clearly divided into clusters, since the internal arrangement of its sites greatly changed when all Euglossina or only *Euglossa* were considered (mainly due to the different frequencies of *El. nigrita*) (Figs. 2 and 3). As *Eg. cordata* was rare in or absent from the seven areas of Subgroup 1, its frequency seems to be the main factor to separate these two Atlantic Forest subgroups.
- Subgroup 3 seems to be the result of the incidental grouping of two areas (EMG and MA4) with low similarity to each other and with the rest of the Atlantic Forest areas. In fact, these areas were grouped only when one considers all Euglossina (Fig. 2), since *Eulaema cingulata* (Fabricius) was responsible for most of the similarity between these two areas. When only species of *Euglossa* were considered, MA4 grouped with the Amazonian areas (Fig. 3). The dominant species in MA4 was *Euglossa piliventris* Guérin-Méneville, which occur only in low frequencies in MA2, MA3, and AM3. EMG represented a singular fauna within the Atlantic

Forest fragments. There, the dominant species was *Euglossa analis* Westwood (47% of all Euglossina), a species that was also relatively abundant in ES (17%) and that occurred in lower frequencies in RJ (5%) and in some Amazonian areas (AM3 and AM4 – less than 1%). EMG showed a moderate similarity to RJ (36%) and ES (33%), which are relatively close in the same domain (see Fig. 1). Moreover, EMG and ES are part of the same hydrographic basin. *Eg. cordata* was present in high frequencies in these two latter areas (44% of all Euglossina in ES and 23% in RJ) and was responsible for clustering them in Subgroup 1. In contrast, in EMG this species represented only 0.2% of the orchid bees.

Amazonian Forest domain. [AM1, AM2, AM3, AM4, PE1 and PE2 (AM4 = canopy; PE1 = floodplain; PE2 = Terra Firme)]. Brazilian (central-eastern Amazonia) and Peruvian (western Amazonia) areas shared several species with *Euglossa chalybeata* Friese, the only present in high frequencies in both regions, as the main responsible for joining them. The Brazilian areas clustered in a separate group because they share a dominant species (28% - 53% of all orchid bees), *Euglossa stilbonota* Dressler, which was not recorded in the Peruvian areas. On the other hand, *Euglossa ignita* Smith and *Eg. chalybeata* are the dominant species in the Peruvian Amazon, with frequencies varying between 21% and 27% of all Euglossina. Both species are present in the Brazilian Amazon, the former in low frequencies, while the latter was the second most common species and accounted for ca. 25% of all Euglossina.

It must be emphasized that all sites sampled in the Brazilian Amazon are in the same area, ca. 90 km north of Manaus. Thus, the high similarity among these sites was expected. On the other hand, it is interesting to note that the canopy fauna (AM4) was the most distinctive among the ones in the Brazilian Amazonian sites, sharing only about 50% similarity with them.

Central America. The four Central American sites were divided into two subgroups, which were weakly related to each other: Panama (PAN) and Corcovado National Park, southwestern Costa Rica (CR1), in one cluster, and the two areas in Parque Nacional Santa Rosa, northwestern Costa Rica (uplands, CR2 and lowlands, CR3), in the other. They were in the same cluster when only species of *Euglossa* were considered (Fig. 3). *Euglossa tridentata* Moure (26%) and *Euglossa imperialis* Cockerell (24%) were the most common species in Panama. This latter species was dominant at CR1 (34%) and occurred in very low numbers in northwestern Costa Rican sites, but these two species were primarily responsible for clustering these areas together, with a very low similarity index (ca. 6% - Fig. 3). When all Euglossina were considered, CR2 and CR3 form an isolate branch that unites to a large group formed by the Atlantic Forest + (Amazonian Forest + PAN and CR1) (Fig. 2). This occurred because *Euglossa viridissima* Friese was by far the most common species at both sites in northwestern Costa Rica (65% in CR2 and 76% in CR3), but was absent from all other sites.

Richness and endemism along the Neotropical Region. Two hundred and seven species of five genera of Euglossina are currently recognized (see Appendix 1), one species in *Aglae* Lepeletier & Serville, seven in *Exaerete* Hoffmannsegg, 27 in *Eulaema* Lepeletier, 65 in *Eufriesea*, and 107 in *Euglossa.* Two of these species are only known as fossil specimens preserved in Dominican amber (Engel, 1999): *Eufriesea melissiflora* (Poinar) and *Euglossa moronei* Engel. Moreover, two undescribed species of *Eufriesea* (Schwartz Filho & Laroca 1999, D. Yanega, pers. comm.) and two of *Euglossa* (Bembé 2004) have been recognized but have not been published yet. So, the total number of orchid bee species reaches, at least, 210 species.

The Amazon Basin is the area with the highest number of species — 127. In Central America, 76 species of orchid bees were recorded and 62 species were recorded in the Atlantic Forest (Appendix 1). The endemism is also highest in the Amazon Basin — 77 species. In Central America 40 extant endemic species are found, whereas 27 orchid-bee species are endemic to the Atlantic Forest.

Discussion

Distribution and diversity. Dendrograms resulting from cluster analyses do not necessarily bear any phylogenetic or historical information. However, the main biogeographic regions suggested by our analyses are much coincident with biogeographic components identified on basis of phylogenetic analyses of other bee groups, flies (Diptera) and primates (Camargo 1996, Amorim & Pires 1996).

These papers suggested an ancient division of South America in a northwestern, mainly Amazonic, component and a southeastern one, including the southeastern limits of Amazonia, the Atlantic Forest, the cerrado and the caatinga. These papers also suggested divisions of the northwestern component in three sub-components – (i) a basal one composed by the northern pacific coast of South America plus Central America; (ii) a southwestern Amazonic region and (iii) a northeastern Amazonic region. Moreover, area cladograms obtained by Camargo (1996) and Camargo & Pedro (2003), based on the phylogenies of three genera of meliponine bees, suggest the existence of a coastal and an interior region in the Atlantic Forest component, what is coincident with data presented in this paper. Although relation between specific geological events and these biogeographic divisions were not confidently established yet, the coincidence of results obtained from such diverse group of animals suggests these biogeographic regions to be real historic entities. It seems, thus, that the regions indicated by the analyses presented here also coincide with historical biogeographic units.

It is surprising that historic units as close as the interior and coastal regions of the Atlantic Forest still can be distinguished through the analysis of data from a group of powerful flyers such as the orchid bees, which might be expected to easily disperse along the whole domain. This is probably due the ecological differences between the evergreen rainy forests of the coast and the semi-deciduous seasonal forests in the interior. Bees in the interior areas inhabit forests with lower canopies and with understories more exposed to sunlight and wind than those near the coast (Rizzini 1979).

Although many euglossine species do have wide geographic ranges, many of them are very restrictive in respect to the kind of environment they inhabit in nature. Thus, some of them, such as *Eg. analis* and *El. niveofasciata* (Friese), are only found in the very interior of humid, close-canopy forests and are unable to cross narrow bands of deforested land (Powell & Powell 1987). Others, such as *El. nigrita* and *Eg. cordata,* on the other hand, seem to be best adapted to drier, illuminated environments (e.g. Morato *et al.* 1992, Silva & Rebêlo 2002, Tonhasca Jr. *et al.* 2002, Nemésio 2004). It should be noted that many of these latter species are the same found in the cerrado (Nemésio & Faria Jr. 2004), the savannic vegetation that covers central Brazil. This suggests that the cerrado and the Atlantic Forest would have clustered together, if data from the former domain were available for our analyses, as the southeastern biogeographic component of South America devised by Amorim & Pires (1996), Camargo (1996) and Camargo & Pedro (2003).

A few odd positionings of specific sites or regions in the dendrogram deserve some discussion. Thus, the Brazilian state of Rio Grande do Sul appears as a distinctive branch at the base of the dendrograms, isolated from all other sampling sites. However, this region would be expected to cluster with other sites in Atlantic Forest domain. It could be argued that this region was sampled only during the summer months, the only season when adult *Eufriesa* are active (Kimsey 1982). The high abundance of *Ef. violacea* in that region, which made it so dissimilar to all other sites, could, then, represent an overestimation of its actual frequency. Nonetheless, even overestimated, the abundance of *Ef. violacea* in Rio Grande do Sul was surprisingly high since, in other places, species of this genus are always captured in low numbers, never above 5% of the individuals (e.g. Rebêlo & Garófalo 1991, 1997, Peruquetti *et al.* 1999, Nemésio 2004). This led authors to generally consider species of *Eufriesea* as rare (e.g. Kimsey 1982, Nemésio & Silveira 2004, Nemésio 2005a).

Furthermore, samplings in the intervening region between Rio Grande do Sul and other sites in the Atlantic Forest (southern São Paulo and the states of Paraná and Santa Catarina) were not available when our analyses were carried on. Samplings in these areas could have made the transition between Rio Grande do Sul and the other sites in the Atlantic Forest smoother than that shown in Fig. 2. This is supported by results published recently by Sofia & Suzuki (2004) and Sofia *et al.* (2004) for northern Paraná state. In this region, frequencies of *Ef. violacea* ranged from 33% to 50%. On the other hand, the number of species found by these authors was also higher than that observed in Rio Grande do Sul and included larger frequencies of some species, such as *El. nigrita, Eg. pleosticta* and *Eg. fimbriata,* which are particularly common in other sites of the Atlantic Forest. These works by Sofia and colleagues, published when our paper was under review, fit the kind of transition we would expect to find in Paraná and Santa Catarina. Otherwise, the impoverishment of the euglossine fauna toward southern South America, already shown by Rebêlo (2001), just fits the well-recognized general trend of decreasing diversity associated to increasing latitude (e.g. Begon *et al.* 1986).

The fluctuation of the sampling sites in Maranhão among the Amazonian and Atlantic Forest sites also calls attention. Geographically speaking, Maranhão is much closer to the Amazonian domain than to the region currently covered by the Atlantic Forest. Nevertheless, when the biogeographic areas recognized by Amorim & Pires (1996), Camargo (1996) and Camargo & Pedro (2003) are considered, the state is on the boundary between the northwestern and the southeastern South American components.

Historically, it has been suggested that connections between the Amazonian and the Atlantic Forests existed in the near past, until Europeans reached South America (e.g. Coimbra-Filho & Câmara 1996). If this is true, the coastal region of Maranhão was probably part of the transition zone between those biomes, and the current composition of its euglossine fauna is just a testimony of this. Ecologically, the fragmentation and disturbance of the Amazonian forests in Maranhão may have allowed for their recently colonization by species such as *El. nigrita* and *Eg. cordata.* These species, which are the main responsible for clustering areas of Maranhão with those in the Atlantic Forest, seem to be well adapted to open and/or disturbed areas, as indicated above.

Generally speaking, the two main regions devised in the Amazonian region (western, in Peru, and Central, in Brazil) correspond to the two main subdivisions of the northwestern biogeographic component of South America, as suggested by Amorim & Pires (1996), Camargo (1996) and Camargo & Pedro (2003). This region, however, is very badly sampled. In our analyses, it was represented by two sets of sites from two restricted areas. For a better understanding of the relationships among the local Amazonian faunas, more areas must be sampled in different regions of that domain. Additional sampling in areas in southeastern Amazonia (southern state of Pará and northern state of Tocantins), southwestern Amazonia (Brazilian states of Acre and Rondonia and north of Mato Grosso) as well as in northern South America (Colombia, Venezuela) and on the western Andean slopes are important to test the concordance of similarity patterns with historic patterns in euglossine faunas in northern South America.

The sharp differences between the northwestern Costa Rican sites and the southwestern area + Panama should not be ignored and wait for an explanation. The species list of Colombian orchid bees (Bonilla-Gómez & Nates-Parra 1992) suggests that, if data on local faunas were available for this country, they might have acted as a link between southern Central America and the Amazon Forest, eventually placing Amazonia closer to Central America than to the Atlantic Forest, as suggested by the phylogeny-based analyses of Amorim & Pires (1996), Camargo (1996) and Camargo & Pedro (2003). A closer relationship between orchid bee faunas of Central America and the northern Pacific coast of South America and Central America, as suggested by the area cladograms of Amorim & Pires (1996), Camargo (1996) and Camargo & Pedro (2003), can also be antecipated from the results of Dick *et al.* (2004), which indicated the Andes as an effective barrier for the gene flow between populations on its eastern and western slopes. Whether or not this will show to be true depends on the proportion of speciation events that have occurred after the uplift of the Andes. According to Camargo (1996) and Dick *et al.* (2004), most of them occurred recently, in response to climatic and environmental changes.

It should be kept in mind that part of the heterogeneity found among sites inside each of the geographic regions recognized here may be due to human activity. Fragmentation and disturbance of natural vegetation may have lead to the reduction (some times extinction) of local populations of some species and to the increasing (sometimes invasion) of the populations of other species in specific sites. Thus, for a reliable picture of orchid bee biogeography to be constructed, it is urgent that areas suffering high deforastation rates, such as the southern portion of the state of Pará or the state of Rondônia (both in Brazil), are sampled.

Endemism and richness variation among regions. Peruquetti *et al.* (1999, p.107) suggested that the species richness of Euglossina in the Atlantic Forest domain was higher than that of the Central Amazon. The analysis of the data in the Appendix suggests otherwise. One problem is that they compared a list of every species ever collected in the whole Atlantic Forest domain to the species collected in a few specific sites, all in the same region of the Amazon Basin, during one-year samplings. Moreover, they included, among the 57 species they assigned to the Atlantic Forest domain, two unidentified species of *Eufriesea* and four of *Euglossa,* which are not known to be different from each other or from other species already present on their list. Also, *Euglossa chalybeata iopoecila* Dressler, *Eulaema bombiformis niveofasciata* (Friese), and *Eulaema meriana flavescens* (Friese) are there listed as subspecies.

When lists of all species ever collected in Central America and in the Amazon Basin are compared to the complete list of species from the Atlantic Forest, the latter presents the poorest orchid bee fauna among the three geographic areas compared, even when species that are not strictly endemic to this biome are included. Examples of the latter are *Euglossa melanotricha* Moure, *Eg. truncata*, *Eg. securigera* Dressler, and *Eg. fimbriata* which are present in the cerrado (Brazilian savanna – Nemésio & Faria Jr. 2004). Nevertheless, as discussed before, the Atlantic Forest and the cerrado seem to be part of a single major southeastern biogeographic component of South America (Amorim & Pires 1996, Camargo 1996, Camargo & Pedro 2003). This suggests a close historic relationship and not simple dispersion and/or interchange of faunistic elements between these two seasonal semi-deciduous domains.

The degree of endemism in the Atlantic Forest is also the lowest of all three regions. It is difficult to determine whether the low orchid bee endemism in the Atlantic Forest is an actual characteristic of the biome or whether it is the result of five centuries of fragmentation. After all, orchid bees are not easily caught without the aid of the attractive compounds which were discovered only in the 1960's (Dodson *et al.* 1969) and all the scarce records of orchid bees (mostly of female specimens) prior to that date were fortuitous. Since it is impossible to know how much of the original fauna of the Atlantic Forest was sampled, it may be useful to look at what is known from other taxa, such as birds.

The comparison with birds seems reasonable, since orchid bees are known for their remarkable flight capability and because them, as birds but contrary to other bees, are most diverse and abundant in tropical forests (Michener 1990). For birds, good estimates were made before most of the fragmentation of this biome occurred. Although many species are currently threatened by extinction (Birdlife International 2000), only two bird species [*Cyanopsitta spixii* (Wagler) and *Mitu mitu* (L.)] did become extinct (and only recently) in the wild (see Nemésio 2001). All other species remain and most of them are still found in the same areas where earlier naturalists found them (Sick 1997, Tobias *et al.* 2006), in spite of deforestation. Thus, we may suppose that extinction was probably not high among orchid bees. If this is true, then, contrary to what seems to be true for other taxa, the Atlantic Forest is not a hotspot (Mittermeier 1999) for orchid bees. Most of the species listed as endemic to this domain are tolerant to open areas or to high elevations.

Eulaema seabrai Moure, which has been treated as a species typical of dense forest (Dressler 1979, Oliveira 2000) was recently collected in an urban area close to Belo Horizonte (Nemésio & Silveira 2004). Among the most common orchid bees listed as endemic in Appendix 1, only *El. flavescens* (Friese) seems to be exclusively associated to the typical coastal Atlantic Rain Forest. It should be emphasized, however, that the Atlantic Forest is not a homogeneous domain concerning orchid bee fauna. Some species, as the recently described *Euglossa anodorhynchi* Nemésio, are restricted to southern Brazil (Nemésio 2006) and other ones, such as *Eg. mandibularis* Friese and *Ef. violacea* are distributed from southern to southeastern Brazil. Other species, such as *El. flavescens*, *El. niveofasciata*, *Eg. cyanochlora* Moure, are restricted to areas ranging from Paraíba, in northeastern Brazil, to Espírito Santo and Rio de Janeiro in the east.

On the other hand, the euglossine fauna of Amazonia seems to be composed of a high number of species intolerant to open and/or disturbed habitats (Morato 1994), some of which fail to cross only a few dozen meters of open space between forest fragments (Powell & Powell 1987). A remarkable difference between the Amazonian and the Atlantic Forest faunas (and, to a lesser extent, the Central American fauna) is the low frequencies of species of *Eulaema* in the former, although the Amazon Forest and northern South America present the highest number of species in this genus (Oliveira 2000). In the Atlantic Forest, *El. nigrita* and, to a lower degree, *El. cingulata* are among the most common species (in all the 13 areas of Atlantic Forest, *El. nigrita* is one of the most common species and in three areas *El. cingulata* is also common). In contrast, no species of *Eulaema* figures among the most common species in the Amazonian areas and only in southern Costa Rica, among the Central American sites, does the frequency of *El. meriana* (Olivier) reach 14% of all orchid bees. As the Atlantic Forest, the Amazon Basin is far from homogeneous concerning the orchid bee fauna. Although several species are widespread, some are restricted to limited regions of the domain. For example, *Eg. stilbonota* and *Eg. piliventris* have only been collected in eastern Amazonia, whereas *Eg. rugilabris* Moure, *Eg. lugubris* Roubik, and *Eg. occidentalis* Roubik are restricted to western Amazonia (see Roubik 2004).

The differences between the species composition of the Amazonian areas and of the Central American ones are also outstanding. The Amazonian forest shares more species with the Atlantic Forest than with Central America (Appendix 1). Two explanations are possible: (i) the data reflect the original community composition of the Amazonian and Central

American biotas, each with a high level of endemism, or (ii), the observed similarities are due to poor sampling of vast Amazonian areas, especially in its northern portion. This second hypothesis is supported by the fact that most Central American "endemic" species reach northern Colombia (Bonilla-Gómez & Nates-Parra 1991) and might also be present in the subsampled Amazonian areas of Venezuela, Colombia, and northern Brazil. Most species of Amazonian birds, a well sampled taxon in the area, are also present in Central America (Ridgely & Tudor 1989, 1994), and a similar pattern may be obtained for orchid bees after these areas are better sampled. It is then necessary to consider that sampling orchid bees to answer the questions posed above is an urgent task, since the fast destruction of native vegetation throughout their ranges may create artificial gaps in the geographic distribution of the involved species.

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Appendix 1

In preparing the check list below, several taxonomic problems were found. Following, are the explanations of these problems and the way they were dealt with.

Genus *Eulaema*. We follow Oliveira (2000) and treat all *El. meriana* (Olivier) recorded for the Atlantic Forest as *El. flavescens* (Friese). All *El. bombiformis* recorded for the Atlantic Forest were treated as *El. niveofasciata,* following Moure (2003) and Nemésio (2005b). Dressler (1979) mentioned the distribution of *El. polyzona* (Mocsáry) to include "Guianas and Amazon basin to Espirito Santo" (Dressler 1979:151) but no specimen from Espírito Santo is mentioned in the literature. According to Oliveira (2000), *El. polyzona* is endemic to Amazonia and, for this reason, it was also excluded from the Atlantic Forest species list. Moure (2003) described some new *Eulaema* species, but some of them are considered junior synonyms by Oliveira (pers. comm.), whose opinion we follow here: *El. pallescens* Moure is a synonym of *El. meriana* and *El. stenozona* Moure is a synonym of *El. terminata* (Smith). Also according to Oliveira, *El. mimetica* Moure is a synonym of *El. tenuifasciata* (Friese) and *El. quadrifasciata* (Friese) is also a synonym of *El. meriana*.

Genus *Euglossa*. *Eg. amazonica* Dressler, *Eg. avicula* Dressler, and *Eg. modestior* Dressler were listed as occurring in Parque Estadual do Rio Doce (EMG site), eastern Minas Gerais (*Eg. avicula* also in SMG site) by Peruquetti *et al.* (1999). One of us (AN) has checked the specimens mentioned by them and found that the species designated as *Eg. amazonica* in their paper is, in fact, *Eg. pleosticta*. There were also some specimens of *Eg. truncata* from Viçosa (SMG), which were misidentified as *Eg. amazonica* (Peruquetti *et al.* 1999:108), and specimens of at least three different species (e.g. *Eg. securigera* Dressler,) as *Eg. modestior*. *Eg. avicula* was recently considered a junior synonym of *Eg. townsendi* Cockerell (see Ramírez *et al.* 2002), but Bembé (2004) states that it is, in fact, a synonym of *Eg. heterosticta* Moure and we follow Bembé's opinion here. Bembé also considers the following synonymies: *Eg. gaianii* Dressler as a junior synonym of *Eg. hemichlora* Cockerell; *Eg. ultima* Moure as a junior synonym of *Eg. deceptrix* Moure, *Eg. charapensis* Cockerell as a junior synonym of *Eg. aureiventris* Friese; *Eg. cyanaspis* Moure as a junior synonym of *Eg. cordata* (Linnaeus) (we do not follow this latter synonymy here), and *Eg. violaceifrons* Rebêlo & Moure as a junior synonym of *Eg. despecta*. *Eg. azureoviridis* Friese has been considered a *nomen nudum* (Bembé 2004). On the other hand, Bembé (2004) treats *Eg. erythrochlora* as a subspecies of *Eg. hemichlora* and we chose not to follow his opinion in this regard. We do not recognize any subspecies in any orchid bee genus and, thus, we maintain the specific status to *Eg. erythrochlora*. The bees listed as *Euglossa cybelia* Moure and *Euglossa* cf. *nigropilosa* Moure for Rio de Janeiro in Tonhasca Jr. *et al.* (2002) were examined and both are the same species which was recorded in the states of Pernambuco and Alagoas (Darrault *et al.* 2006) and coast of São Paulo (AN, pers. obs.) as *Eg. ioprosopa* Dressler. *Eg. sapphirina* Moure has disjunct distribution. This species was collected in some Atlantic Forest areas and in Central America. However, we could not find any record for this species in the areas in between. *Eg. allosticta* Moure and *Eg. bursigera* Moure, until recently considered endemic to Central America and northern Colombia, were recorded for Brazilian Amazon (Nemésio, 2005c and Martines *et al.*, unpublished data, respectively).

Genus *Eufriesea*. Two species of *Eufriesea* considered by Kimsey & Dressler (1986) as synonyms were revalidated by Moure (1999): *Ef. smaragdina* (Perty), and *Ef. auriceps* (Friese). We follow Roubik & Hanson (2004) and list *Ef. smaragdina* as valid and endemic to the Atlantic Forest domain but we consider here *Ef. auriceps* as a senior synonym of *Ef. danielis* (Schrottky) (**syn. nov.**). Nevertheless, the status of *Ef. auriceps* and *Ef. violascens* (Mocsáry) remain to be checked, since Kimsey (1982) considered both species as synonyms. The species *Ef. aridicola* Moure, Neves & Viana, *Ef. faceta*, and *Ef. nordestina*, both of Moure authorship are here considered as valid but deserves further studies. *Ef. simillima* (Moure & Michener) considered by Kimsey & Dressler as synonym of *Ef. caerulescens* (Lepeletie) is considered a valid species by D. Yanega (pers. comm.) and is accepted as such here. On the other hand, we follow Moure (1999) and Roubik & Hanson in treating *Ef. xantha* (Kimsey) as a junior synonym of *Ef. vidua* (Moure). Finally, *Ef. nigrohirta* was treated by Moure (1967) and Kimsey (1982) as endemic to Amazonia, since its holotype is labeled as collected in Pará. Nonetheless, it has only been collected in the altitude fields of eastern Brazil (Silveira *et al.* 2002, Nemésio 2005a) and for this reason, it is included in the list of species endemic to the Atlantic Forest domain. It is important to call attention to the species *Ef. yepezi* (Moure). Its name was only published in the erratum published by the journal where the original article was published, in the subsequent number. Maybe for this reason, this species has not been listed by Ramírez *et al.* (2002) and Roubik & Hanson (2004) in their checklists.

Checklist and geographic distribution of the known species of Euglossina.

Endemic to Central America (including southern North America and northern South America) – 41 species
Eufriesea anisochlora (Kimsey, 1977)
Ef. caerulescens (Lepeletier, 1841)
Ef. corusca (Kimsey, 1977)
Ef. dressleri (Kimsey, 1977)
Ef. lucifera Kimsey, 1977
Ef. mexicana (Mocsáry, 1897)
Ef. pallida (Kimsey, 1977)
Ef. rufocauda (Kimsey, 1977)
Ef. rugosa (Friese, 1899)
Ef. schmidtiana (Friese, 1899)
Ef. simillima (Moure & Michener, 1965, in Moure, 1965)
Ef. venusta (Moure, 1965)
Euglossa alleni Moure, 1968
Eg. asarophora Moure, 1969
Eg. championi Cheesman, 1929
Eg. crininota Dressler, 1982
Eg. cyanaspis Moure, 1968
Eg. cyanura Cockerell, 1917
Eg. dissimula Dressler, 1978
Eg. dodsoni Moure, 1965
Eg. dressleri Moure, 1968
Eg. erytrhrochlora Moure, 1968
Eg. flammea Moure, 1969
Eg. hansoni Moure, 1965
Eg. heterosticta Moure, 1968
Eg. hyacinthina Dressler, 1982
Eg. igniventris Friese, 1925
Eg. jamaicensis Moure, 1968 – Endemic to Jamaica
Eg. maculilabris Moure, 1968
Eg. micans Dressler, 1978
Eg. nigrosignata Moure, 1969
Eg. obtusa Dressler, 1978
Eg. oleolucens Dressler, 1978
Eg. purpurea Friese, 1899
Eg. tridentata Moure, 1970
Eg. turbinifex Dressler, 1978
Eg. villosa Moure, 1968
Eg. villosiventris Moure, 1968
Eg. viridissima Friese, 1899
Eulaema polychroma (Mocsáry, 1899)
Exaerete azteca Moure, 1966
Common to Central America + Amazon Basin – 19 species
Eufriesea chrysopyga (Mocsáry, 1898)
Eufriesea concava (Friese, 1899)
Ef. duckei (Friese, 1923)
Ef. elegans (Lepeletier, 1841)[1] – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Ef. macroglossa (Moure, 1965) – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Ef. ornata (Mocsáry, 1896)
Ef. pulchra (Smith, 1854)
Euglossa allosticta Moure, 1969
Eg. bursigera Moure, 1970
Eg. cybelia Moure, 1968
Eg. deceptrix Moure, 1968
Eg. gorgonensis Cheesman, 1929
Eg. variabilis Friese, 1899
Eulaema bombiformis (Friese, 1899)
El. luteola Moure, 1967
El. meriana (Olivier, 1789)
El. nigrifacies (Friese, 1898)
El. speciosa (Mocsáry, 1897)
Exaerete trochantherica (Friese, 1900)
Endemic to the Amazon Basin – 86 species
Aglae caerulea (Lepeletier & Serville, 1825)
Eufriesea auripes (Gribodo, 1882)
Ef. bare González & Gaiani, 1989
Ef. boharti (Kimsey, 1977)
Ef. chaconi González & Gaiani, 1989
Ef. chalybaea (Friese, 1923)
Ef. combinata (Mocsáry, 1897)
Ef. convexa (Friese, 1899)
Eufriesea. distinguenda (Gribodo, 1882)
Ef. eburneocincta (Kimsey, 1977) – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Ef. excellens (Friese, 1925)
Ef. fallax (Smith, 1854)
Ef. flaviventris (Friese, 1899)
Ef. formosa (Mocsáry, 1908)
Ef. fragrocara (Kimsey, 1977)

Continue

Continuation.

Ef. kimimari González & Gaiani, 1989
Ef. laniventris (Ducke, 1902)
Ef. limbata (Mocsáry, 1897) – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Ef. lucida (Kimsey, 1977)
Ef. magrettii (Friese, 1899)
Ef. mariana (Mocsáry, 1896)
Ef. nigrescens (Friese, 1925) – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Ef. opulenta (Mocsáry, 1908)
Ef. pretiosa (Friese, 1903)
Ef. purpurata (Mocsáry, 1896)
Ef. superba (Hoffmannsegg, 1817)
Ef. theresiae (Mocsáry, 1908)
Ef. velutina (Moure, 1999)
Ef. venezolana (Schrottky, 1902)
Ef. vidua (Moure, 1976)
Ef. violascens (Mocsáry, 1898)
Ef. yepezi (Moure, 1999)
Euglossa amazonica Dressler, 1982
Eg. aureiventris Friese, 1899
Eg. auriventris Friese, 1925
Eg. bidentata Dressler, 1982 – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Eg. bigibba Dressler, 1982
Eg. chalybeata Friese, 1925
Eg. chlorina Dressler, 1982
Eg. cyanea Friese, 1899
Eg. decorata Smith, 1874
Eg. fuscifrons Dressler, 1982
Eg. gibbosa Dressler, 1982
Eg. granti Cheesman, 1929
Eg. hugonis Moure, 1989
Eg. inflata Roubik, 2004
Eg. intersecta Latreille, 1938 – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Eg. laevicincta Dressler, 1982b – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Eg. lazulina Friese, 1923
Eg. lugubris Roubik, 2004
Eg. macrorhyncha Dressler, 1982
Eg. magnipes Dressler, 1982
Eg. modestior Dressler, 1982 – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Eg. mourei Dressler, 1982
Eg. nigropilosa Moure, 1965
Eg. occidentalis Roubik, 2004
Eg. orellana Roubik, 2004
Eg. paisa Ramírez, 2005
Eg. parvula Dressler, 1982
Eg. perfulgens Moure, 1967
Eg. perviridis Dressler, 1985
Eg. piliventris Guérin-Méneville, 1845 – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Eg. platymera Dressler, 1982
Eg. polita Ducke, 1902
Eg. prasina Dressler, 1982
Eg. retroviridis Dressler, 1982
Eg. rugilabris Moure, 1967
Eg. singularis Mocsáry, 1899
Eg. stilbonota Dressler, 1982

Continue

Continuation.

Eg. tiputini Roubik, 2004
Eg. trinotata Dressler, 1982
Eg. viridifrons Dressler, 1982 – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
Eg. viridis (Perty, 1833)
Eulaema basicincta Moure, 2003 – Endemic to Trinidad & Tobago
El. bennetti Moure, 1967 – Endemic to Trinidad & Tobago
El. boliviensis (Friese, 1898)
El. mocsaryi (Friese, 1899) – Reaches Maranhão (Brazil), but not the Atlantic Forest domain.
El. napensis Oliveira, 2006a
El. peruviana (Friese, 1903)
El. parapolyzona Oliveira, 2006
El. polyzona (Mocsáry, 1897)
El. pseudocingulata Oliveira, 2006
El. tenuifasciata (Friese, 1925)
El. terminata (Smith, 1874) – Endemic to Trinidad & Tobago
Exaerete guaykuru Anjos-Silva & Rebêlo, 2006
Ex. lepeletieri Oliveira & Nemésio, 2003
Common to the Amazon Basin + Atlantic Forest – 8 species
Euglossa analis Westwood, 1840
Eg. augaspis Dressler, 1982
Eg. cordata (L., 1758)
Eg. iopyrrha Dressler, 1982
Eg. ioprosopa Dressler, 1982
Eg. liopoda Dressler, 1982
Eg. pleosticta Dressler, 1982
Eg. securigera Dressler, 1982
Endemic to the Atlantic Forest – 26 species
Eufriesea aeneiventris (Mocsáry, 1896)
Ef. aridicola Moure, Neves & Viana, 2001 – restricted to Caatinga in Bahia
Ef. auriceps (Friese, 1899)
Ef. brasilianorum (Friese, 1899)
Ef. dentilabris (Mocsáry, 1897)
Ef. faceta (Moure, 1999)
Ef. nigrohirta (Friese, 1899)
Ef. nordestina (Moure, 1999)
Ef. smaragdina (Perty, 1833)
Ef. tucumana Schrottky, 1902 – restricted to Argentina
Ef. violacea (Blanchard, 1840)
Euglossa annectans Dressler, 1982
Eg. anodorhynchi Nemésio, 2006 – restricted to southern Brazil
Eg. carinilabris Dressler, 1982
Eg. cyanochlora Moure, 1995 – restricted to northeastern Brazil
Euglossa fimbriata Rebêlo & Moure, 1995
Eg. leucotricha Rebêlo & Moure, 1995
Eg. mandibularis Friese, 1899
Eg. melanotricha Moure, 1968 (In: Sakagami et al., 1968)
Eg. perpulchra Moure & Schlindwein, 2002 – restricted to northeastern Brazil
Eg. pictipennis Moure, 1943
Eg. stellfeldi Moure, 1947
Eg. truncata Rebêlo & Moure, 1995
Eulaema flavescens (Friese, 1899)
Eulaema niveofasciata (Friese, 1899)
El. seabrai Moure, 1960
Pan-neotropical distribution – 15 species
Ef. mussitans (Fabricius, 1787)
Ef. surinamensis (L., 1758)

Continue

Continuation.

Euglossa cognata Moure, 1970
Eg. crassipunctata Moure, 1968
Eg. despecta Moure, 1968
Eg. hemichlora Cockerell, 1917
Eg. ignita Smith, 1874
Eg. imperialis Cockerell, 1922 – including the "cerrado" (pers. obs.)
Eg. mixta Friese, 1899
Eg. townsendi Cockerell, 1904
El. cingulata (Fabricius, 1804)
El. nigrita (Lepeletier, 1841) – including the "cerrado" (pers. obs.)
Exaerete dentata (L., 1758)
Ex. frontalis (Guérin-Méneville, 1845)
Ex. smaragdina (Guérin-Méneville, 1845)
Disjunct distribution – 1 species
Eg. sapphirina Moure, 1968 – Atlantic Forest, Colombia, and Central America
Endemic to other biomes – 9 species

Continue

Continuation.

Euglossa natesi Parra-H, Ospina-Torres & Ramírez, 2006 – Colombia and Ecuador, west of Andes
Eg. paisa Ramírez, 2005 – Colombia, west of Andes
Eg. rufipes Rasmussen & Skov – Colombia and Peru, west of Andes
Eg. samperi Ramírez, 2006 – Ecuador, west of Andes
Eulaema bomboides (Friese, 1923) – Ecuador, west of Andes
El. chocoana Ospina-Torres & Sandino-Franco, 1997 – Colombia, west of Andes
El. helvola Moure, 2003 – "Cerrado" (Brazilian Savanna) – Central Brazil and Bolivia
El. leucopyga (Friese, 1898) – Central America to Choco region, Colombia, west of Andes
El. sororia Dressler & Ospina-Torres, 1997 – Colombia, west of Andes
Fossil species – 2 species
Eufriesea melissiflora (Poinar, 1998) – Dominican Amber
Euglossa moronei Engel, 1999 – Dominican Amber