Biological Observations on a Neotropical Parasocial Bee, *Eulaema nigrita*, with a Review on the Biology of Euglossinae (Hymenoptera, Apidae). A Comparative Study[1) 2)]

By

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(*With 21 Text-figures, 2 Plates and 9 Tables*)

The female of the handsome golden and black Euglossa Surinamensis visits the cajú trees, and gathers with its hind legs a small quantity of the gum which exudes from their trunks. To this it adds the other material from the neighbouring bushes, and when laden flies off to its nest. H.W. Bates *Naturalist on the River Amazons*.

Contents

Introduction

The aim of the present paper is twofold, first to give the full account of observations made on nest architecture and behavior of an euglossine bee, *Eulae-*

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2) Dedicated to Prof. Theodosius Dobzhansky at his 70th birthday (Jan. 25 1970).

ma (*Apeulaema*) *nigrita* Lepeletier (*cf.* Zucchi 1966, Zucchi MS), together with some notes on nests and flower visits of *Euplusia auriceps* (Friese) and *Euglossa* (*Euglossa*) *cordata* Linné, secondly to summarize the previous information published on the biology of the Subfamily Euglossinae.

The euglossine bees form, together with bumblebees (Bombinae), stingless bees (Meliponinae) and honeybees (Apinae), the Family Apidae[1]), which represents by its behavioral differentiation one of the summits in invertebrate evolution. Comparing the biological information so far obtained, however, we at once notice a conspicuous unbalance among these four groups. Although there are still much to be clarified as to the complicated life of honeybees, they are certainly biologically one of the best known insects (Ribbands 1953, v. Frisch 1965, etc.). Our knowledge on bumblebees is still far less satisfactory than on honeybees, but the outline of their mode of life is already well recognized as compiled by Free and Butler (1959). Concerning stinglees bees, the previous information was summarized by Schwarz (1948), followed by Moure, Nogueira-Neto and Kerr (1958). Thereafter some interesting facts on behavior have successively been recorded (Esch 1967, Lindauer and Kerr 1958, Kerr 1950, Nogueira-Neto 1954, Sakagami *et al.* 1963, Sakagami and Zucchi, 1966, 1968). But the biology of this Pantropic group is a rich but still insufficiently explored treasure, in spite of their highly evolved social organization, attaining a level comparable to honeybees. Finally the biology of euglossine bees is least known. Virtually no single species has biologically precisely been studied. Nevertheless they form an important link for the full understanding of apid evolution. Fortunately we could discover a nest of *Eulaema nigrita*, transfer it into an observation case and study their intranidal behavior, which has so far been concealed from any specialists of bee biology. The obtained results are still fragmentary in many aspects but involve some interesting novelties in comparison with the behavior of the other three groups.

In preparing the descriptions of these results, we felt the necessity of compiling the previous information on the biology of Euglossinae. Obviously we need a number of studies for the future, specially planned and executed for this group. But such work is, or has been, not always easy to realize, because of their tropically limited range, their scarcity and secretive mode of life. Consequently the majority of previous information is incidental and fragmentary. Attempts to summarize such records were tentatively made by Schrottky (1907) and Friese (1930, 1941). Maa (1953) gave a synoptic table of both morphological and biological features of four groups of Apidae. But none of them tried to gather all available records nor to analyse them sufficiently. Fortunately, several papers on the biology of Euglossinae, much more precise than those in earlier times, have recently been published, encouraging for the advance of our knowledge on these bees. In such circumstance, it

1) The classification system differs among specialists. Michener (1944) : The Subfamily Apinae with four tribes, Euglossini, Bombini, Meliponini and Apini; Moure, Nogueira-Neto and Kerr (1958) : The Family Apidae with four subfamilies, Euglossinae, Bombinae, Meliponinae and Apinae; and Michener (1965a) : The Family Apidae with three subfamilies, Euglossinae, Bombinae and Apinae (with Meliponini and Apini). Here we follow the system by Moure *et al.*, simply for the convenience in discussions.

may be appropriate to give a compilation of previous records, to facilitate further studies of this fascinating, but so far ignored group.

Probably because of its rather singular external appearance, the Subfamily Euglossinae has occasionally been placed outside of Apidae (for instance, Handlirsch 1925), but it shares several good characters with other apid groups, though some of them such as the possession of developed corbiculae are secondarily modified in parasitic genera. Within Apidae Euglossinae is (Pl. IV–B) distinguished by a number of conspicuous features, including brilliantly metallic integument (Plate IV), extraordinary prolongation of glossa, peculiarily concave male sternum VIII, highly differentiated male legs, etc. All four groups of Apidae are quite distant one another, but Euglossinae may stand relatively closer to Bombinae than the other two highly social groups. Maa (1953) considers Euglossinae as the most primitive among four groups, without giving sufficient explanation. But it is still premature to give any definite conclusion from the morphological point of view, because beside some apparently primitive features, this group possesses some highly specialized ones. Sociologically it is certainly most primitive in the sense that many species are seemingly solitary or possessing only weakly developed social system (*cf.* Section 4). For the time being, however, it may be wise to avoid a careless amalgamation of biological and morphological interpretations.

Since a monograph by Friese (1899) a good number of species had been described but no attempt to establish the taxonomic framework had been made until Moure (1950) gave a key to the genera. Thereafter he described a number of additional species (1963～1967a) and gave a check list of so far known species (1967b). According to his system, the present status of the subfamily is summarized as follows:

Genera and main characters	Subgenera and main characters	Number of species in Moure (1967 b)
Euglossa Latreille 1802 Nonparasitic, small to medium sized, brilliantly metallic with poor pubescence	*Euglossa* s. str. (Pl. IV-A, 1,2,4) Small, male mandibles bidentate, glossa long	39
	Euglossella Moure 1967 (Pl. IV-A, 3,5). Small, male mandibles tridentate, glossa long	15
	Glossura Cockerell 1917 (Pl. IV-A, 6～9, B). Medium, glossa very long	12
Euplusia Moure 1943 (Pl.IV-A, 12～23) (=*Plusia* Hoffmannsegg 1817) Nonparasitic, medium to large, moderately metallic and haired		45+
Eufriesea Cockerell 1908 (Pl. IV-A, 11) Ditto, with large plate like mesoscutellum		1

Eulaema Lepeletier 1841 (=*Eulema* auct.) Large to very large, less metallic and more hairy	*Eulaema* s.str. (Pl.IV-A, 27, 30~32) Metasoma extensively metallic, male face without white marks	14
	Apeulaema Moure 1950 (Pl.IV-A, 26,28,29) Metasoma less metallic, male face with white marks	6
Aglae Lepeletier et Serville 1825 (Pl.IV-A, 25) Parasitic, brilliantly metallic, body flat, mesoscutellum plate like		1
Exaerete Hoffmannsegg 1817 (Pl.IV-A, 24) (=*Chrysantheda* Perty 1833). Parasitic, brilliantly metallic, mesoscutellum tuberculate		5
		In total 137

Certain biological differences among these genera will subsequently be mentioned. Concerning the nonparasitic genera, three items are specially noteworthy: 1) Absence of typical subterranean nidification by self-excavation. 2) Abundant use of resin for nidification and 3) Appearance of an incipient social complexity in some species. Furthermore, males of many species have a special preference for the flowers of certain, often quite definite orchid species, accompanied with a peculiar behavior sequence.

In geographical distribution, the subfamily is typically Neotropical. Moure (1967b) gives a map indicating the distribution of each genus. The northernmost limit is given by the two following records: *Euplusia simillima* Moure et Michener from Maguarichic and Barranca del Cobre, both in the western side of the Cordillera of Chihuahua, Mexico, and *Eulaema polychroma* Mocsáry from Brownsville, Texas. In the Caribbean Islands, they do not go further beyond Jamaica and Trinidad. Southward,in the Pacific coast they stop at the north of the Peruvian desert, while in the Atlantic side reach Southern Brazil, Paraguay and Northern Argentina. The southern limit is given by *Euplusia chalybaea* (Friese) from Córdoba. Generally speaking the distribution pattern closely resembles that of the Neotropical stingless bees. Vertically it is plausible that they rarely nidificate at high altitudes, though, being excellent fliers, many specimens have bee recorded from the altitudes of more than 1,000 m. The highest record of the nidification is that of *Euplusia nigrescens* (Friese) (*cf. 1.3.3.*), found at 1,600 m in the Colombian East Andes (Vogel 1963).

Materials and Methods

In subsequent pages, each particular topic of biology is treated in separate section. In each section, our own observations are first given, followed by the review of previous information and discussions on the samt topic. But in sections where we have no sufficient original data, these will be incorporated in the general

review. Before entering into results and discussions, some remarks on our procedures are explained herewith.

1. Sources of previous information: We attempted to consult and read all literature so far published on the euglossine biology. It is always possible some brief notes scattering among not easily accessible periodicals escape from the survey. But we believe all important papers and most of short notes were compiled in our review. The sources of information we gathered together are given in Table 1 and in references, shown with asterisks. The table contains the following items in each species, on which some biologial notes have so far been published:

1) Recent scientific name mostly based upon Moure (1967 b).

2) Names used by each author who observe some aspects of biology, provided the names are different from Moure except for the omission of subgeneric designation.

3) Author and date of publication (*cf.* References).

4) In parentheses, localities where the cited species was observed. In case of Ducke, all information was, unless specially mentioned, obtained in Belém do Pará and the vicinity, including Marajo and Macapá. Similarly most localities cited in Dodson and Frymire 1961 b and Dodson, 1966~1967 are in Costa Rica, Peru and Ecuador.

5) Aspects of biology observed, given with the following gothic abbreviations: **B.** Miscellaneous notes on behavior; **D.** Immature stages and development; **H.** Host of parastic species; **HP.** Habitat preference and phenology; **FV.** Flower visits; **M.** Foraging of nesting materials; **N.** Nest sites and nest architecture; **OR.** Male visits to orchids, Araceae, etc.; **SO.** Social organization; **P.** Parasites and other associated animals; **TV.** Visits to decayed wood, etc. including observations on male tibial organ.

Some difficulties concerning tabulation are mentioned. Formerly one of us (S.F.S.) mentioned an inevitable incertitude of scientific names cited in this kind of tables (Sakagami and Michener 1962). In the present case, too, some names are probably invalid. Erroneous identifications and resulting changes of names are inevitable in taxonomically still not well revised groups. The results are serious in taxonomic studies, but often more in biological ones. Let us explain this by an example. One observer, say **G**, took some biological notes on a particular species, which was identified either by himself or by a contemporary specialist to species *A*. Later, however, it was confirmed that the name *A* had been preoccupied by *B*. Correspondingly the species observed by G may automatically be called *B*. But later it was discovered that *B* was a composite species, involving B_1, B_2, etc., being so similar that previous authors could not separate them. In such instance, it is often impossible to know the correct name of the specimens observed by **G**. Contrary to the specimens used for taxonomic studies, the specimens, with which biological observations were made, rarely remain in museums. Or, the observers might send the specimens to the specialsit for identification, often without annexing the labels noting the occurrence of biological data. Thus the value of such specimens are lost within the accumulation of further specimens, often partly accerelated by the lack of interest upon the biological data by museum experts.

There is another source of misidentification. Many observers send the specimens at least once to the specialists. Thereafter, however, they may continue the observations upon "this" species. By this way, often observations of closely allied species, or even those quite remote but superficially similar ones, are mixed. Nevertheless, certain remarkable biological differences often exist just in such species-pair as exemplified by the separation of two sibling species in *Ammophila* (Adriaanse 1947), *Trigona* (Michener 1959) and *Parischnogaster* (Yoshikawa, Ohgushi and Sakagami 1969), which are distinguished more

easily by biological features. This is particularly important for Euglossinae, which contain some groups consisting of closely similar species such as *Euglossa cordata* complex and *Eg. ignita* complex, species superficially closely similar such as *Eulaema meriana* and *El. seabrai*, and some remarkable cases of parallelism in color pattern found between *Eulaema* and *Euplusia* (*Cf.* Plate IV-A, 20~23 versus 26~29). Virtually Ducke (1901~'02) recorded two very different types of nests of *Euglossa* "*cordata*", one is aerial hanging from twigs or leaves, another is made within small cavities. As shown later, it is certain that his "*cordata*" is composite, consisting of at least two different species (*cf. 1.2.* and *1.3.1.*).

In order to minimize such defect, we applied in Table 1 the following marks:

No asterisk: Specimens used by these authors were examined by recent experts, or not but the identity is probably correct because the species is quite distinct, without superficially similar species, or, there are other reasons which make the validity of the identification plausible.

Single asterisk: The identity is probably correct, but without sound basis.

Double asterisks: The identity is dubious by the presence of allied species, confusion in synonymy, etc.

Obviously this procedure is incomplete, but it may decrease the misinterpretation. On this occasion, we would like to emphasize the importance of preserving biologically observed specimens in appropriate places, with adequate labels noting the presence of such records, even if they would be, as is often the case, in poor conditions.

In subsequent citations, the generic names are abbreviated as follows: *Euglossa* = *Eg.*, *Euplusia*=*Ep.*, *Eufriesea*=*Ef.*, *Eulaema*=*El.*, *Exaerete*=*Ex.*, *and Aglae*=*Ag.*

Table 1. List of the species biologically observed

Euglossa s. str.

Eg. alleni Moure MS. Dodson & Dressler after Dodson 1967, **OR.**

Eg. analis Westwood 1840 (Plate, IV-A-2). Bodkin 1918* (Demerara, Brit. Guiana), **N, SO**; Vogel 1966 (Manaus), **TV,** (Uaupés, Amazonas), **OR.**

Eg. (*Euglossa*) *bicolor*, Ducke 1902a*, **FV, OR**; 1902 b*, **HP, OR.**

Eg. bicolor, Myers 1935* (Upper Ireng River, Brit. Guiana), **OR**; Vogel 1963 (Sierra Macarena, Colombia), **OR, FV,** 1966, (Manaus) **TV.**

Eg. azureoviridis Friese 1930. Dodson 1965a after 1967, **OR**; Dressler 1967 (Costa Rica), **OR, TV.**

Eg. championi Cheeseman 1929. Dressler after Dodson 1967, **OR.**

Eg. cordata (Linné 1785) (Plate, IV-A-1). Lucas 1878** (Cayenne), **N, SO**; Friese 1899** (Obidos, Pará), **N, SO**; Schulz 1902** (Belém), **N, SO, TV, FV**; v. Ihering 1904** Schrottky 1907**, (Araguary, Goias), **N**; Ducke 1903**, **N, SO** (Photo only); 1906 b**, **FV** (Ducke records two types of nests, apparently of different species. *Cf. 1.3.1.* and *1.2.*); Bodkin 1918* (Brit. Guiana), **N, FV, B**; Friese 1930** (San José, Costa Rica), **N**; Michener 1954 (Panamá), **FV, OR**; Allen, 1952, '55, after Dodson 1967, **OR**; Vogel 1963 (Sierra Macarena, Colombia), **OR**; Cruz-Landim 1963 & '67, **Wax glands**; Cruz-Landim *et al.* 1965, **TV**; Bennett 1966 (Trinidad), **N, P**; Dodson 1969, **FV, OR**; Vogel 1966 (Amazonic basin), **FV, B,** (Piracicaba. SP), **OR, TV**; Dodson 1962, Dressler, Dressler & Dodson, after Dodson 1967, **OR**; Dressler (1967), **OR**; Ferreira MS (Rio Claro, SP), **N, SO**; Nogueira-Neto unpub.* (São Paulo), **N, SO**; Zucchi *cf. 1.1.5* & *6.2.3.* (Ribeirão Prêto, SP).

Euglossa (*Euglossa*) *cordata*, Ducke 1901**, **FV, OR, TV, HP, N, SO**; 1902 a**, **OR, N**; 1902 b** **HP, FV, OR, N.**

Eg. cyanosoma Moure MS. Sakagami & Laroca *cf. 6.3.* (Antonina, Paraná), **B.**

Eg. dodsoni Moure 1965. Moure 1965, **OR**; Dodson 1966 (Costa Rica), **N, SO, FV, P**; Dressler after Dodson 1967, **OR.**

Eg. dressleri Moure MS. Dressler after Dodson 1967, **OR.**

Eg. gorgonensis Cheeseman 1929. Dodson 1966, **FV, OR**; Dressler after Dodson 1967, **OR.**

Eg. hansoni Moure 1965. Dodson 1966, **FV, OR**; Dressler after Dodson 1967, **OR.**

Eg. hemichlora Cockerell 1917. Dodson 1966 (La Elsa and Rio Branco, Ecuador), **FV, N, B, SO**; Dodson 1965 a after 1967, **OR.**

Eg. viridissima, Dodson & Frymire 1961 b, **FV, N, B, SO**; Dodson 1962 b, **OR.**

Eg. melanotricha Moure 1967. Sakagami, Laroca & Moure 1967 a (Campo Alegre, Goias), **N, SO, D.**

Eg. nigropilosa Moure 1965. Moure 1965, **OR**; Dodson 1966, **FV, OR,** Dodson 1965 a after 1967, **OR.**

Eg. orichalcea Moure MS. Dressler after Dodson 1967, **OR.**

Eg. purpurea Friese 1899. Dressler after Dodson 1967, **OR**; Dressler 1967 (Costa Rica), **TV.**

Eg. townsendi Cockerell 1904. Dressler after Dodson 1967, **OR**; Dressler 1967, **OR.**

Eg. variabilis Friese 1899. Friese 1930** (San José, Costa Rica), **N** (Friese describes aerial nests of "*variabilis*", but after Moure 1967 b, *Eg. variabilis* is unknown from Central America); Bennett 1966 (Trinidad), **N,P.**

Eg. cf. *variabilis*, Dodson 1965a, Dressler, after Dodson 1967, **OR.**

Euglossa (Euglossella)

Eg. augaspis Moure 1966. Dodson 1966, **OR**; Dodson 1965 a after 1967, **OR.**

Eg. cyanura Cockerell 1917. Dressler after Dodson 1967, **OR**; Dressler 1967, **OR.**

Eg. decorata Smith 1874. (Plate, IV-A–5) .Dodson 1966, **FV, OR**; Dodson 1962 a after 1967, **OR.**

Eg. (*Euglossa*) *decorata*, Ducke 1802, b, **HP.**

Eg. mandibularis Friese 1899 (Plate, IV-A–3).

Eg. aenescens Friese 1925 (MG, Brazil), **FV.**

Eg. mixta Friese 1899. Dodson 1966, **OR**; Dressler after Dodson 1967, **OR.**

Eg. polita Ducke 1902.

Eg. (*Euglossa*) *polita*, Ducke 1902, a, b, **FV, HP.**

Eg. singularis Mocsáry 1899.

Eg. meliponoides, Ducke 1902, a, **FV.**

Eg. viridis (Perty 1833).

Eg. azurea, Ducke 1902, a, b,* **FV, TV, HP.**

Eg. viridissima Friese 1899. Friese 1922** (San José, Costa Rica), **N, HP**; 1925** (San José, Costa Rica), **N, P**; 1930** (San José, **N, FV** 1941**, **N**; Ostlund, Pollard after Dodson 1967, **OR.**

Eg. cf. *viridissima*, Dressler after Dodson 1967, **OR.**

Euglossa (Glossura)

Eg. asarophora Moure et Sakagami. MS. (Pl. IV-A–8). Dressler after Dodson 1967, **OR.**

Eg. chalybeata Friese 1926. Vogel 1966 (Rio Mamoré, Acre), **B.**

Eg. consimilis Moure et Sakagami MS. Vogel 1966 (Rio Humea), **FV.**

Eg. ignita Smith 1874. (Plate, IV-A–6). Ducke 1901**, **HP, FV, OR, TV**; 1902 b*, **HP, FV, OR**; Dodson 1966 (Iquitos, Peru, etc.), **FV, N, SO, OR**: Roberts & Dodson 1967 (Iquitos), **N, SO, D, B, P**; Dressler, Dodson 1962 a, '65 a, after 1967, **OR.**

Eg. (*Euglossa*) *piliventris*, Ducke 1901*, **HP, FV, OR, TV.**

Eg. igniventris Friese 1925. Friese 1925 (San José, Costa Rica), **FV**; Dressler after Dodson

1967, **OR**; Dressler 1967, **OR.**

Eg. intersecta Latreille 1838. (Plate, IV-A–9). Zucchi *et al.* MS (Belém), **N, SO, D.**

Eg (*Euglossa*) *brullei*, Ducke 1901, **OR, TV, HP.**

Eg. (*Glossura*) *brullei*, Dodson (Iquitos), **N, FV, P, SO.**

Eg. imperialis Cockerell 1922. Dodson 1966, **FV**; Roberts & Dodson 1967 (Limón, Costa Rica), **N, SO, D, P**; Dressler after Dodson 1967, **OR.**

Eg. piliventris Guérin. (Pl. IV-A–7, B). Bodkin 1918 (Brit. Guiana), **FV**; Janiver 1955 (Yungas, Bolivia), **FV, N, B, D, SO**; Dressler after Dodson 1967, **OR.**

Eg. (*Euglossa*) *piliventris*, Ducke 1902, a, **HP, FV, TV**; 1902 b, **OR, TV.**

Euglossa (? subgenus)

Eg. vogeli Moure MS. Vogel 1966 (Colombia), **FV.**

Euplusia

Ep. auriceps (Friese 1899). Zucchi *cf. 1.1.4, 2.4, 6.2.3.* (Ribeirão Prêto, SP), **N, D, OR, P.**

Ep. chrysopyga (Mocsáry 1898). Dodson 1966, **OR, FV.**

Ep. combinata (Mocsáry 1897). Dressler after Dodson 1967, **OR.**

Ep. concava (Friese 1899). Dressler after Dodson 1967, **OR.**

Ep. duckei (Friese 1923).

Euglossa (*Eulema*) *duckei*, Ducke 1902, a, **FV.**

Ep. elegans (Lepeletier 1841).

Euglossa (*Eulema*) *elegans*, Ducke 1901*; **FV, B**; 1902 b, **HP, FV.**

Ep. fallax (Smith 1854).

Euglossa (*Eulema*) *fallax*, Ducke 1901*, **FV.**

Ep. laeniventris (Ducke, 1902).

Euglossa (*Eulema*) *laenvientris*, Ducke 1902 a, **HP, FV**; 1902 b, **FV.**

Euglossa laeniventris, Ducke 1906 b, **FV.**

Ep. macroglossa Moure 1965. Moure 1965, **OR**; Dodson 1965 a after 1967, **OR.**

Ep. nigrescens (Friese 1923) (Plate, IV-A–18 & 19).

Euglossa (*Eumorpha*) *longipennis*, Friese 1925 (San José, Costa Rica), **FV**; Vogel 1963 (Huila, 1,600 m, Colombia), **N.**

Euplusia longipennis, Sakagami & Sturm 1965 (Florencia-Neiva, 1,300~1,500 m, Colombia), **N, D, P, SO** (It is open to the question whether Costa Rican and Colombian specimens belong to the same species).

Ep. ornata (Moscáry 1896). (Plate, IV-A–21). Dodson 1966, **FV, OR**; 1965 a after 1967, **OR.**

Euglossa (*Eulema*) *ornata*, Ducke 1901, **FV.**

Euglossa (*Eulema*) *limbata*, Ducke 1902 b*, **HP, FV.**

Ep. purpurata (Mocsáry 1896). (Plate, IV-A–12). Dodson 1966, **OR**; Vogel 1966 (Manaus), **TV**; Dodson after Dressler 1967 (Iquitos), **TV.**

Euglossa purpurata, Ducke 1906 a* (Tabatinga, Amazonas), **MC.**

Ep. schmidtiana (Friese 1925). Dodson 1966, **FV, OR**; 1965 a after 1967, **OR**; Dressler 1967 (Cerro Campo, Panamá), **B, TV.**

Ep. superba (Hoffmannsegg 1817). Dodson 1966, **FV, OR**; Dodson 1967, **OR.**

Ep. ? superba, Arlé after Dressler 1967 (Belém-Brasilia Highway), **TV.**

Ep. surinamensis (Linné). Dodson 1966 (Ecuador). **FV, HP, MC, N, D**; 1967, **OR.**

Centris surinamensis, Möbius 1865* (Altona), **N.**

Euglossa surinamensis, Bates 1863* (Santarem, Pará), **N, MC**; Bodkin 1918* (Brit. Guiana), **FV, N.**

Euglossa (*Eulema*) *smaragdina*, Ducke 1901*, **HP, FV, MC, B.**

Euglossa (*Eulema*) *smaragdina* forma genuina, Ducke 1902 a*, **N, HP.**; 1902 b*, **N, HP.**

Euglossa smaragdina, Ducke 1903,* N (Photo alone); 1906 a, **P.**
Eulaema brusei, Cockerell 1916 (Brit. Guiana), **N.**
Euplusia smaragdina, Sakagami 1965 a (Manaus), **N, D**; Dodson & Frymire 1961 b(Ecuador), **FV, N, B, SO, MC, OR.**
Ep. violacea (Blanchard 1840). (Plate, IV-A–14 & 15). Sakagami & Michener 1965 (São Carlos, SP), **N, SO**; Vogel 1966 (Iguaçu, Paraná), **FV.**
Euglossa violacea, Schrottky 1901, 1902 (São Paulo), **FV, N, MC**; v. Ihering 1904 (Itu, São Paulo), **N**; Hoehne 1932 (São Paulo), **OR.**
Eumorpha violacea, Schrottky 1907 (Paraguay), **HP.**
Centris (*Euplusia*) *violacea*, Michener 1953 (Brazil), **D.**
Ep. violascens (Mocsáry 1898). Sakagami 1965 a (Paraguay), **N, MC, SO**; Cruz-Landim *et al.* 1965 (Brazil), **TV.**
Ep. sp. 1. *Eulema dimidiata*, Lucas (Girard) 1878 (Cayenne), **N.** (Probably an *Euplusia*, judging from the use of bark pieces for nest, possibly *Ep. ornata*).
Ep. sp. 2. *Euglossa* (*Eulema*) *smaragdina* var. *concava*, Ducke 1902 b, **FV, HP** (Probably not *concava*, which is a Central American species after Moure 1967 b).
Ep. sp. 3. *Euglossa* (*Eulema*) *smaragdina* var. *flaviventris*, Ducke 1902 b, **HP** (After Moure 1967 b, *flaviventris* is synonymous to *surinamensis* (=*smaragdina*), but Ducke distinguishes *flaviventris* and *smaragdina* genuina).
Ep. sp. 4. *Euplusia nigrita*, Vogel 1966 (Piracicaba, SP), **OR.** *Euglossa* (*Eumorpha*) *magretti* var. *nigrita* is synonymous to *Ep. nigrescens*. But it is dubious that Vogel's species is identical with the Andean *nigrescens*.

Eufriesea

Ef. pulchra (Smith 1854), (Plate IV-A-11).
Euglossa (*Eumorpha*) *pulchra*, Ducke 1901, **FV, B**; 1902, **FV.**

Eulaema s. str.

El. basicincta Moure MS. (Plate IV-A-32).
El. basalis (Nomen nudum), Bennett after Dodson 1967, **OR**; Bennett MS (Trinidad), **OR.**
El. bennetti Moure 1967. (Plate IV-A-31). Bennett after Dodson 1967, **OR**; Bennett MS (Trinidad), **OR.**
El. bomboides (Friese 1923). Dodson & Frymire 1961 b, **FV, OR**; Dodson 1966, **FV, OR.**
El. leucopyga Friese 1898. Dodson 1966, **FV, OR**; Dodson 1967, **OR.**
El. luteola Moure 1967. Dodson after Dressler 1967, **B.**
El. meriana (Olivier 1789). (Plate IV-A-27). Dodson 1966, **FV,OR,N**; Vogel 1966 (Amazonas), **FV, TC, MC, OR, B**; Dodson 1965 a after 1967, **OR**; Wille unpub. (Costa Rica) **N.**
Euglossa dimidiata, Bodkin 1918 (Brit. Guiana), **FV, B.**
Euglossa (*Eulema*) *dimidiata*, Ducke 1901*, **HP, FV, OR**; 1902 a*, **OR**, 1902 b*, **HP, FV, OR**; Friese 1941 (Guayaquil, Ecuador), **N, SO, P.**
Euglossa (*Eulaema*) *dimidiata*, Ducke 1906 b,*, **FV, OR**: Michener 1954 (Juan Mina, Panamá), **FV.**
Eulaema dimidiata, Dodson & Frymire 1961 b (Ecuador), **OR, FV, N.**
El. nigrifacies Friese 1898. Dressler after Dodson 1967, **OR**; Dressler 1967 (Cerro Campo, Panamá), **OR, B.**
El. polyzona (Mocsáry 1897). Dodson 1966. **FV, OR**; Vogel 1966 (Belém), **MC**; Dodson 1967, **OR.**
Euglossa (*Eulema*) *polyzona*, Ducke 1901, 1902 b, **FV, B, TV**; 1902 a, **B.**
El. seabrai Moure 1960. Dodson 1966, **FV**; Dodson 1965 a after 1967, **OR.**
El. speciosa (Mocsáry 1897). Dodson & Frymire 1961 b, **OR**; Dodson 1966, **FV, OR**;

Dressler after Dodson 1967, **OR**.

El. ? *speciosa*, Dressler 1967, **B**.

El. terminata (Smith 1874). (Plate IV-A-30). Bennett 1965 (Trinidad), **N, B, P, SO, D, MC**; Bennett MS (Trinidad), **OR**.

Eulaema (Apeulaema)

El. boliviensis Friese 1898. Dodson 1966, **FV, OR**; Dodson 1967, **OR**.

El cingulata (Fabricius 1804). (Plate IV-A-26). Dodson & Frymire 1961 b (Ecuador), **OR, FV, MC,** (Balzapamba 775 m, Ec.), **N, D, SO, B, MC**; Vogel 1963 (Rio Gnatiquia, Colombia), **OR**; Sakagami & Michener 1965 (Juan Mina, Panamá), **N, SO**; Dodson 1966 (Ecuador, **OR, FV, MC**, (Balzapamba), **N, D, SO, B, MC, P**; Vogel 1966 (Manaus, Amapá), **FV**, (Belém), **B**; (Crüger 1865, Allen 1952, Dodson 1962 a, Dodson 1965 a, all after Dodson 1967, **OR**.

Euglossa (*Eulema*) *fasciata*, Ducke 1901, 1902 b, **FV, OR**; Friese 1930 (Guayaquil, Ecuador), **N, SO**, (Costa Rica), **FV**.

Euglossa fasciata, Ducke 1906 b, **FV, OR**; Myers 1935 (Wanaina, Brit. Guiana), **FV**.

El. mocsaryi (Friese 1899). Dodson 1966, **FV**.

Euglossa (*Eulema*) *mocsaryi*, Ducke 1901*, **FV, OR, HP**; 1902 a, **MC**; 1906 b; **HP, FV,**

El nigrita (Lepeletier 1841). (Plate IV-A-28). Moure 1946 (Rio de Janeiro), **N, P,**; Cruz-Landim *et al.* 1965 (Rio Claro, SP), **TV**; Sakagami 1965 b (Rio Claro, SP), **TV**; Dodson 1966, **FV, OR**; Vogel 1966 (Itatiaia, State of Rio de Janeiro), **TV, OR**; Zucchi *et al. cf.* sections *1–7* (Ribeirão Prêto, SP), **N,SO, D, B FV, P, MC.**

Euglossa (*Eulema*) *nigrita*, Ducke 1901, **HP**, 1902 a, **N, OR, B**; 1902 b, **FV, OR, B.**

Euglossa nigrita, Schrottky 1901 (São Paulo), **FV, TV, B**; Ducke 1903, **N, D, P**; Bodkin 1918 (Georgetown, Brit. Guiana), **N**; Myers (Yupunari, Brit. Guiana), **N, D, P.**

Centris nigrita, Schrottky 1907 (Paraguay), **FV.**

El. polychroma (Mocsáry 1899). (Plate IV-A-29). Dodson 1966, **FV, OR**; Dressler after Dodson 1967, **OR**; Dressler 1967 (Mexico), **OR**, (Cerro Campo, Panamá; Caracas), **B.**

Euglossa fallax, Ducke 1902 a*, **MC.**

Euglossa surinamensis, Friese 1930* (Costa Rica), **FV.**

Euglossa sp. Porsch 1955* (Costa Rica), **OR.**

Eulaema tropica, Dodson & Frymire 1961 b, **OR, FV, MC**; Wille 1963 (Costa Rica), **FV**; Lopez 1963 (Mexico), **TV.**

Euglossa fallax, Ducke 1902*, **MC.**

Aglae

Ag. caerulea Lepeletier et Serville 1825. (Plate IV-A-25). Ducke 1902 a, **B**; 1902 b, **B, FV**; Myers 1935, (Yupunari, Brit. Guiana), H; Dodson 1966, **FV**; Vogel 1966 (Sierra Macarena, Colombia), **FV.**

Exaerete

Ex. dentata (Linné 1758). Ducke 1906 a, **H**; Vogel 1966 (Iguiaçu, Paraná), **FV**; *Chrysantheda dentata*, Ducke 1901, **FV, B.**

Ex. frontalis (Guérin 1845). Friese 1941 (Guayaquil, EC.), **H**; Dressler 1967, **OR.** *Chrysantheda frontalis*, Ducke 1901, **FV, B**; 1902 a, **FV.**

Ex. smaragdina (Guérin 1845). (Plate IV-A-24). Ducke 1903, **H**; 1906, **FV**; Moure 1946

(Rio de Janeiro), **H**; Dodson & Frymire 1960 b, **FV**; Dodson 1966, **FV**; Vogel 1966 (Florencia, Colombia), **FV**, (Belém), **B**; Dressler after Dodson 1967, **OR**; Dressler 1967, **OR**; Zucchi (Ribeirão Prêto), **H, D**; (*cf. 2. 4. & 6*).

2. *Original observations*: *El. nigrita* is, together with *El. cingulata*, one of the commonest and most ubiquitous *Eulaema* species. Unlike the other members of the genus, this species is widely distributed in relatively arid areas south of Amazonic basin, monopolizing the southernmost part of the generic range. According to Moure (1967b), the norhternmost limit is Costa Rica and the southern limits are southern Brasil and northern Argentina. The species is common in the Interior of the State of São Paulo.

A nest was discovered by Mr. W. P. Avelar on January 9, 1966 with in the Campus of the Faculty of Medicine of Ribeirão Prêto. After making some observations upon foraging activities, the nest entrance was closed with a piece of plastic cloth on the evening of February 9. The nest was excavated on the next day, ten minutes after the application of carbon dioxyde. The excavated cell cluster was, together with the unique female alive, first transferred into a provisonal case, then, after the death of the female, in February 11, into the observation case.

Considering the timidity of the adults shown at field observations, the observation case was made to reproduce the orginal nest site (Fig. 2) as far as possible. (Fig. 1) A large rectangular hole was excavated undert he floor of the apiary house. Within the hole a section

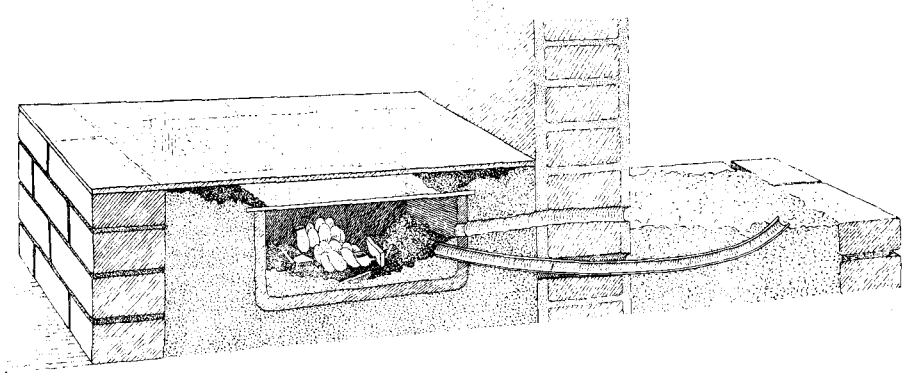

Fig. 1. Observation case containing cell cluster of *El. nigrita*, covered with double glass-lids.

of $72 \times 59 \times 20$ ccm was enclosed with bricks. An earthen trough of $35 \times 15 \times 15$ ccm was put within the section and the space between trough and brick walls was filled with soil. The interior of the trough was filled with soil and pieces of broken tiles up to the half of its depth and the cell cluster was placed there (*cf.* Pl. V). Finally the tops of both trough and brick enclosure were covered with glass plates. The trough was communicated with the outside by means of a plastic tube, through the wall of the apiary.

On February 16 the spread of molds on the surface of the cell cluster was noticed. According to the advice by Prof. W.E. Kerr, the diluted (1 gr./1 l water) solution of Mangate, a commercial fungicide, was applied by a fine brush on cell surface. Further the invasion of various animals, ants, spiders, roaches and crickets were frequent until the emergence of adults. They were removed once per week. On March 20, the emergence of the first adult was noticed, and the observation of intranidal behavior was started. The sequence of observations is summarized in the following chronicle:

Jan. 9: Discovery of nest; Jan. 10~Fev. 9: Observations at nest site, at noon, usually 20~30 min., with full day observations on Jan. 18 and 19; Feb. 10: Excavation of nest; Feb. 11: Transference into observation case; Feb. 16: Application of fungicide; Feb. 26: Ditto; March 20: First emergence of adult. Start of observations of adult behavior; April 22. Last emergence of adult; May 2. Nest taken from the observation case.

Results and Discussions

1. Nests

Up to the present, most nests of Euglossinae have been discovered by chance. Only Bennett (1965) discovered a nest of *El. terminata* by tracing mud foraging females. He also succeeded to induce the nidification of *Eg. cordata* and *Eg. variabilis* into artificial wooden boxes. We shall first describe the structure of nests of *El. nigrita*, *Ep. auriceps* and *Eg. cordata* observed by us. Thereafter the previous records on the euglossine nest architecture will be reviewed and discussed.

1.1. Original observations

1.1.1. Nest site and nest arrangement in Eulaema nigrita: The nest studied by us was discovered at a slightly sloped ground, with a sparse growth of grasses not completely shading the entrance. The area was encircled by walls and trees, not receiving direct sun beams except for 11:00~14:00. The entrance (Fig. 2, top) was circular, about 1.5 cm in diameter, bordered by a flat rim of soil but with no specialized turret. At the dicovery, a triangular resinous piece of unknown significance was found near the margin, which was not replenished after its removal.

The entrance was followed by a burrow down to 25 cm below the soil surface, where the latter opened to a large pre-existing, apparently artificially formed cavity. The entrance burrow was 1.8~2.0 cm wide, descending vertically and slightly winding, the inner walls were not particularly lined. The cavity was found in one of these tubes at the depth of about 70~80 cm below the soil surface, supported by several resinous pillars (Fig. 2). A dark stinking mass of 2 ccm, apparently the material used for cell construction was placed near the cluster. Otherwise no particular lining was confirmed in the surrounding of the cell cluster. Several broken and partly decomposed cadavers of bees were scattered within the cavity, which indicated the absence of removal of deads and the lasting use of the cavity by more than one generation (*cf. 3.3.1* and *4.1*). The nest arrangement clearly shows the use of the pre-existing cavity by bees. The fact that the diameter of the entrance burrow did not markedly vary throughout its course

Fig. 2. Cross section of nest of *El. nigrita* at nest site. Top, entrance seen from above.

implies the later refinement, but, judging from the nest arrangement in previous records, it is unlikely that bees made the burrow entirely by self-excavation.

1.1.2. Cell cluster of El. nigrita: The cell cluster (Fig. 3) was about 12 cm long and 5 cm wide, consisting of 43, reddish brown cells, tightly fused one another, forming a rigid mass, producing a strong camphor odor, probably of resin taken from *Proteum* (Burseraceae). The cell arrangement is relatively regular though not

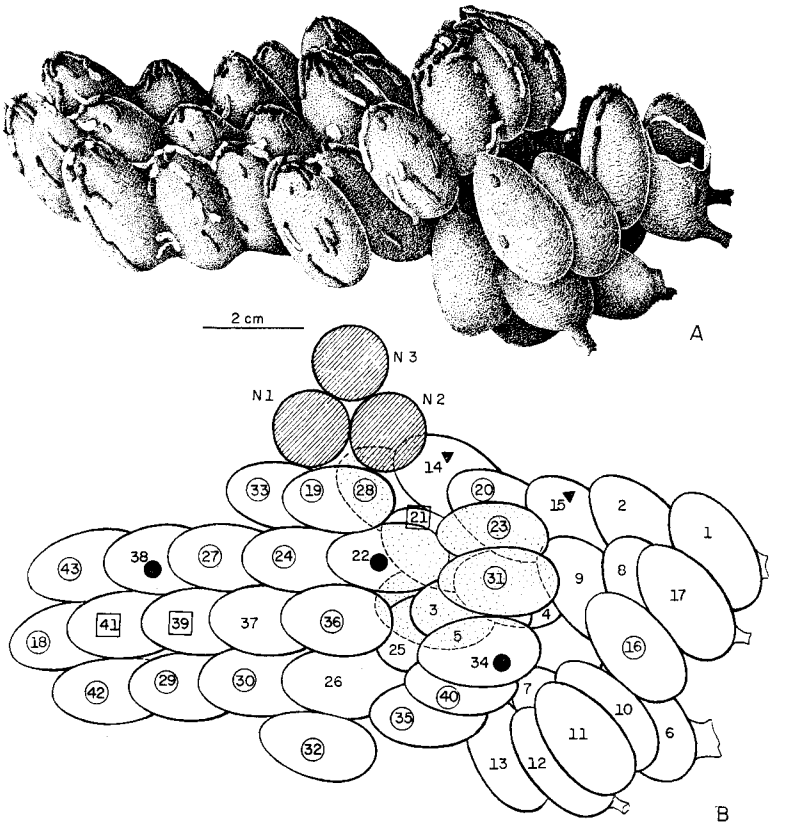

Fig. 3. Cell cluster of *El. nigrita*. A. Seen laterally. Right-lower part is the older part, some cells with cicatrices, the emergence holes closed later. B. Ditto, slightly obliquely seen. Contents: Circled, major females; Black circles, minor females; Squares, males, Triangles, Occupied by *Euborella ambigua* (*cf.* Section 8). Other cells are old or the contents not examined. N 1–3 are those made after the introduction into the observation case.

properly be called comblike. The cluster was divided into two parts. One involves cells Nos. 1 ~ 13, all old and empty. The other part, involving all other cells, constructed later above the former part. The orientation of cells is different

between these two parts, indicating a later dislocation. Within each part, the long axes of the cells, more or less vertical, were approximately in pararell with each other, but the tops and bottoms of the cells were not strictly in the same plane, and the contour of each cell was well recognized from the outside.

The cell cluster is fixed by means of a number of pillars at one side and at the bottom, which are made from the material same to that used for cells. Length and diameter of pillars are variable as shown by the following examples:

Lateral pillars		Bottom pillars		
Length	Diameter	Length	Diameter	(in mm)
2.5	4.0×2.0	6.0	6.0×2.0	
5.0	15.0×8.0	3.0	3.0×4.0	
5.0	3.0×6.0	2.0	3.0×2.0	

Probably the pillars are successively added to and strengthened in the course of the growth of the cell cluster, as a device to prevent serious dislocation of cell cluster.

1.1.3. Structure of brood cells in El. nigrita: Cells are ovoid (measurements in Table 3) (Fig. 4), elliptical in cross section. The cell walls are thick at sides and bottom, thinner at the top, the outermost layer of the wall is occasionally partly in common. But the cell wall is usually made without utilizing that of the previous cells, along which the new one is made, though the cells are later tightly fused for each other.

The cell surface is slightly rugose but well elaborated, provided with several irregular but predominantly longitudinal keels (Figs 3A, 4A) of 1～2 mm wide and 12 mm in the maximum length. Four kinds of materials, from which these keels are made, are distinguished: 1) Reddish brown and brittle, 2) Gray to nearly black, viscous and plastic, with strong camphor odor. 3) Milky white and plastic, probably of resinous origin. 4) White and brittle, probably taken from excrement of fowls, because visits of *El. nigrita* to a poultry farm were occasionally observed. These materials are never used in mixture. Further each single keel is rarely made entirely from a single kind of material. Most keels show a mosaic of these four materials, which suggests more or less synchronous preparation of several keels. The significance of these keels is unknown. They are absent or vistigeal on old cells, probably indicating later removal.

The cell wall is divided into two layers (Fig. 3, Nos. 1 and 2 in C). The outer layer is dark reddish brown, 0.7～0.8 mm thick, mainly made from animal excrement mixed with pale resin and a small quantity of dark resin, at first rather plastic but later becoming very hard. The inner layer is only one fourth thick of the outer one, thickest at the bottom, entirely made from predominantly black resin of strong camphor odor, and water impermeable. In cells containing pupae, the inner surface of the wall is smooth and shining, except for the top (*cf.* Fig. 4 A,B), tightly covered by the adhering cocoon, the texture of which will be described in *2.3.*

Some cells possessed at their upper lateral wall each one cicatrix (Fig. 3,A), prepared from the same material used for the other part of the cells but slightly depressed and the texture is rougher. This part is easily detached by a gentle push, leaving a neatly circular hole. As described in *3.2.2.*, these cicatrices are emergence holes closed by adult females. Cells with such cicatrices are always empty. No evidence of the reuse of cells was obtained. The process of cell construction is later given in *3.2.3.*

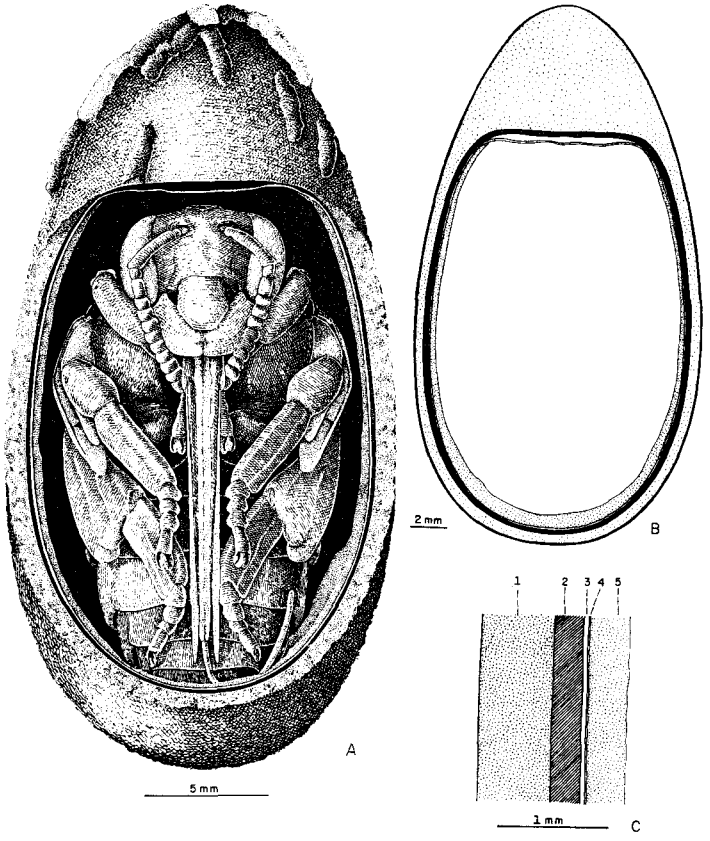

Fig. 4. Cell structure in *El. nigrita*. A. Cross section with pupa (cell top with resinous keels). B. Ditto, shown schematically. C. Cross section of cell wall, showing five layers (the outermost layer at left). Nos. 1–2, cell wall, 3–4, cocoon, 5. larval feces.

1.1.4. Observation on a nest of Euplusia auriceps: A nest of this species was discovered on May 10 1968 in Tanquinho, a small town between Rio Claro and Piracicaba, State of São Paulo by Dr. W.D. Hamilton (Imperial Coll. Sci. Techn., London) who kindly offered us the material on May 20, together with the information

on nesting site: "The nest was found within the wall made from clay and tiles of a small abandoned hut. The entrance hole was made in clay, about 1 m high above the ground, resembling the nest hole of certain spiders, followed by a short vertical burrow of 1.5 cm wide, which bent perpendicularly at the depth of ca. 6 cm from the entrance, continuing further for ca. 7 cm (Fig. 5, left)". Four cells, the last one still in construction, were found in the latter section, arranged in a series (*allodalous arrangement* in Malyshev 1936), forming a solid tube of 6.8 cm long and 1.4 cm wide near the end, 2.7 cm wide near the bending of the burrow (Fig. 5, right A). The long axis of each cell was, however, quite deviated one another. Especially the last cell was made semi-perpendicularly to the long axis of the tube. The nest owner was found in the entrance section, with quite worn wings and mandibles.

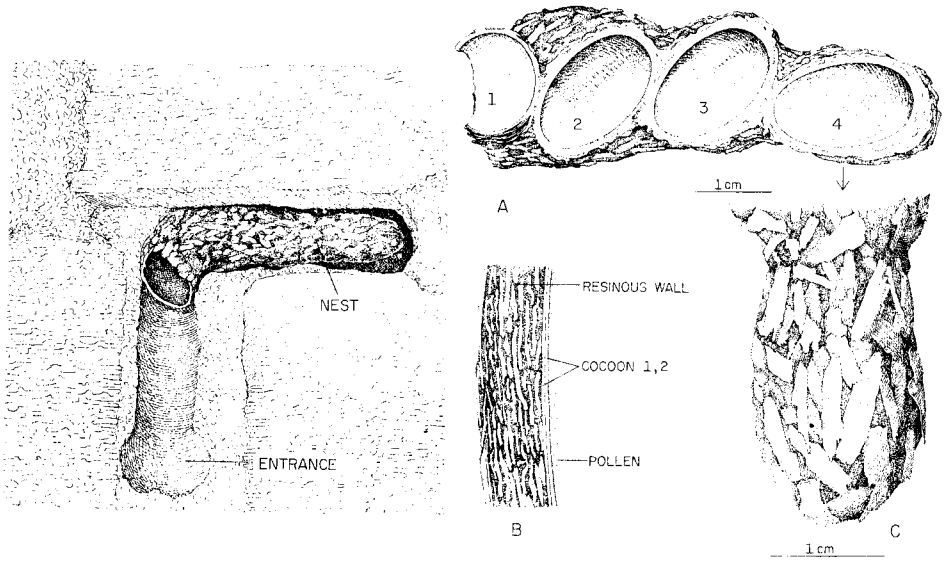

Fig. 5. Nest of *Euplusia auriceps*. Left. Nest arrangement. Right. A. Cross section of cell series. B. Cross section of cell wall. C. Outer surface of cell.

The cell wall was made of small pieces of leaves and barks, firmly fused one another with resin (Fig. 5 right C), with a slight admixture of mud, apparently added to occasionally from the inner wall of the burrow. The maximum thickness of the wall was 4~5 mm. The inner wall was smooth and polished, though the vegetable pieces were visible here and there. Internally cells were elongate oval, 17 mm long and 11 mm wide. External dimension, difficult to determine precisely because all cells formed a solid tube, was about 25 mm long in the first cell.

1.1.5. Observation on a nest of Euglossa cordata made in an abandoned wasp's nest: *Eg. cordata* is one of the commonest and most ubiquitous euglossine species, the nests of which have repeatedly been recorded, though some of older records are suspicious as to the identity of the species (*cf.* table 1, and *1.3.1.*). The nest described here was dicovered in December, 1967 by Prof. W.E. Kerr within an abandoned nest of a wasp, *Polybia occidentalis scutellaris* (White), found at Fazenda Monte Alegre, Ribeirão Prêto. The wasp is one of the commonest polybine species in the locality. The nest is variable both in shape (spherical, elongate, companiform, etc.) and nest sites, sometimes persisting nearly 30 years (Maule-Rodrigues 1968). The nest of the wasp and of *Eg. cordata* were already quite damaged when discovered. The entrance was located on the outer envelope of the wasp's nest (Fig. 6), neatly circular, of 5 cm in diameter, facing an interspace

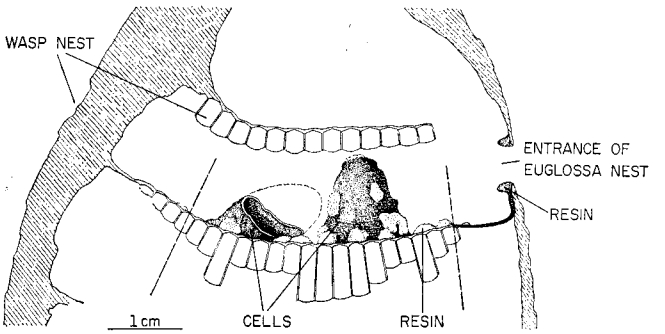

Fig. 6. Nest of *Euglossa cordata* made within an abandoned nest of a wasp, *Polybia occidentalis*.

between two combs made by wasps. Externally there was no more particular construct, but internally provided with a complete rim made from dark resin. This resinous lining was extended downward and further inward, forming a bridgelike vestibule for the area where an accumulation of pale resin and cells were found. The exact number of cells was undetermined, but at last three dead, pigmented pupae, two females and one male, were found, one within an intact cell, another in a damaged cell and the third exposed. The intact cell was externally 12 mm long and 13 mm wide at the base, with an abnormal conical shape. The outer wall was very irregular, made from dark resin, on which some pieces of pale resin were deposited. The inner dimension was 11 mm high and 6 mm wide, and the wall was 0.6 mm thick at the upper part. Beside the resinous lining mentioned above, resinous particles were deposited here and there on the upper surface of the wasp's comb, where the cells were found, but the complete coating was absent.

1.2. Nest site preference in Euglossinae: The number of species, the nests of which have so far been recorded, is still a fraction of the total number of

euglossine species. Nevertheless the previous information enables to give a perspective of the nesting habits. We first deal with the nest site preference. The previous records are summarized in Table 2.

Before dealing with these data, one remark on a discrepancy found in earler records must be preceded. Ducke writes that *Eg. cordata* makes two very different types of nests, one is aerial with an outer envelope and the other made within more or less closed cavities. On the other hand, Friese regards aerial nests as produced by *Eg. variabilis*, and concealed ones by *Eg. cordata*. These earlier records are inevitably cited in Tables 1 and 2 under the names adopted in the original papers. It is uncertain what species was actually observed in each of them, because of the presence of several small, brilliantly metallic species allied to *Eg. cordata*. The fact so far established is the presence of two distinct biological groups, which may or may not correlate to the morphological grouping, as to the nest site preference in small Euglossas allied to *Eg. cordata*. Among the previous records, only the following cases are authentic as to the species name: Aerial nests. *Eg. dodsoni* (Dodson 1966); Concealed nests: *Eg. cordata* (Bennett 1966, Ferreira MS), *Eg. variabilis* (Bennett 1966), *Eg. hemichlora* (Dodson 1966), *Eg. melanotricha* (Sakagami, Laroca and Moure 1967 a). It is likely that both groups involve a number of species. Further observations with authentic identifications are specially required for these species. Although found within a hollow tree, the nest of "*Eg. cordata*" recorded by Schulz (1902) appears to belong to the aerial type, judging from the presence of the spherical envelope.

Table 2. Nest site preference in Euglossinae

1. *Nests completely or nearly completely exposed*
   - 1.1. Nests attaching on twigs or stems: *Eg. variabilis*, Friese (Mocsáry) 1898, Friese '30, '41; *Eg. cordata*, Ducke '02 b (partim); *Eg. dodsoni*, Dodson '66; *Eg.* sp. Girard (*cf.* Lucas).
   - 1.2. Nests attaching under leaves: *Eg. cordata*, Ducke '20 a, b(under palm leaves), Bodkin (under leaf); *Eg. variabilis*, Friese '41 (under palm leaves).
   - 1.3. Nests on soil surface: *Ep. nigrescens*, Vogel '62, Sakagami & Sturm (on vertical bank covered with plants).
2. *Nests semi-exposed within incomplete cavities or at allied situations*
   - 2.1. Nests at crevices of walls: *Ep. surinamensis*, Bates (or of trees), Dodson & Frymire '61 b; Dodson '66(cane walls of rail road stations), Cockerell '16 (chinks between floor and posts of a hut); *Ep. violacea*, Sakagami & Michener '65; *Eg. hemichlora*, Dodson '66 (between boards in a building).
   - 2.2. Nests at spaces under eaves or ceilings: *Ep. surinamensis*, Möbius, Ducke '01, '02 a, b, Bodkin (top of roof beam), Sakagami '65 a (under palm leaves used for eave), Dodson & Frymire '61 b, Dodson '66 ("Hundreds of nests attached to the ceilings over sidewalks throughout the downtown of Babahoyo, Ecuador").
   - 2.3. Nests at miscellaneous spaces: *Eg. cordata*, Friese '30, '40 (between folds of hanging clothes), Nogueira-Neto unpub. (under tile covering an artificial nest of *Melipona scutellaris*); *Eg. viridissima*, Friese '41 (under bark).
3. *Nests in nearly completely closed cavities*
   - 3.1. Nests within hollow trees: *Eg. cordata*, Schulz (freely hanging within hollow), Ducke '01 a, '02 (in decayed hollow tree), Friese '30, '41; *Eg. viridissima*, Friese '22, '25, '30 (in wooden stumps or bamboo stems though written as under bark in 1941); *Ep. surinamensis*, Bodkin; *Ep. violascens*, Sakagami '65 a; *El. cingulata*,

Sakagami & Michener (60 cm above ground), Dodson '66; *El. meriana*, Friese '41, Dodson '66 (6 fts above ground); *El. nigrita*, Myers (ca. 4 fts above ground).

3.2. Nests within subterranean cavities: *Eg. analis*, Bodkin; *El. cingulata*, Dodson & Frymire '61 b, Dodson '66 (in embarkment of loosely piled stones covered with soil); *El. meriana*, Dodson '66; Wille unpub; *El. nigrita*, Zucchi *et al. cf. 1.1.1.*; *Eg. cordata*, Lucas (possibly subterranean as the cell cluster contained fine rootlets).

3.3. Nests within subterranean animal nests: *El. nigrita*, Ducke '03 (in an abandoned termite nest), Sakagami unpub. (One female in the collection of Departamento de Zoologia, Secretaria da Agricultura, São Paulo, labelled "Fazenda Cachoeirinha, Jatai, Goias, Outubro, Ninho em capinzeiro abandonado", that is, from an abandoned termite nest), Moure '46 (in an abandoned nest of leaf-cutting ants); *Eg. imperialis*, Roberts & Dodson (in an abandoned nest of a land crab or small mammal); *Eg. melanotricha*, Sakagami, Laroca & Moure (in a hollow within a still occupied termite nest).

3.4. Nests within abandoned overground animal nests: *Ep.* sp. 1, Girard (Lucas) (in galleries of cerambycid beetles, etc.); *Ep. auriceps* Zucchi *et al. cf. 1.4.1.* (possibly using the nest of another animal); *El. terminata*, (in an ant nest in a limb 50 fts above ground); *Eg. cordata*, Ducke '01 (in a nest of *Ep. surinamensis*); v. Ihering, Schrottky '07 (in a nest of a polybine wasp), Ducke '01 (in termite eaten beams), Bodkin (in a nest of *Sceliphron fistulare*), Ferreira MS (in old nest holes of *Xylocopa*), Zucchi et al. *cf. 1.1.5.* (in an abandoned nest of *Polybia*); *Eg. hemichlora*, Dodson '66 (in a termite eaten beam); *Eg. intersecta*, Dodson '66 (in still occupied termite nests in a dead tree, one nest ca. 7 fts, another ca. 3 fts above ground), Zuchi, Oliveira & Camargo MS (in a still occupied nest of *Nasutitermes* sp. in a dead tree, 35 cm above ground).

3.5. Nests within man-made cavities, etc. *Eg. cordata* and *Eg. viridissima*, Friese '22, '25, '30 (in bamboo stems); *Eg. viridissima*, Friese (in chest); *Eg. cordata*, Ducke '01, '02 b, '03 (in keyholes), Bodkin (in various curious places, inside of disused heel of cotton, interior of empty cartridge case, eye-pieces of polariscope, keyholes, small cavities in timber); *Eg. cordata* and *Eg. variabilis*, Bennett '66 (induced to nest in small boxes); *Ep. surinamensis*, Bodkin (artificial holes in timber); *El. nigrita*, '03 (in aboriginal urn in museum exhibition), Bodkin (in hollow beam of the dining hall of the large hotel); *Eg. piliventris*, Janvier (in hollow in walls of chimnys); *Eg. ignita* Dodson '66, Roberts & Dodson (in fern fibers wrapped around bases of orchids hung from ceiling); *Eg.* sp. Girard (Lucas) (in dried nutshell).

It is not easy to express the relative preference quantitatively based upon the records in Table 2. Many earlier records do not cite the number of nests observed, and some authors apparently cite same observations in repetition. Ignoring these defects, the relative preference among three genera for various nest sites is given by the following arbitrary weights:

	Exposed		Semi-exposed	Concealed	
	Aerial	Overground		Overground	Subterranean
Euglossa	+		+	##	+
Eupluisa		±	##	+	
Eulaema				#	#

Although the sharp distinction between semi-exposed and concealed, or subterranean and overground situations is difficult, each genus possesses certain characteristic tendency. *Euplusia* prefers relatively exposed situations. But it is plausible that some nests of this genus found from semi-exposed places were originally made at more or less concealed corners of such sites. Concerning nests of *Ep. surinamensis* Dodson writes: "In most cases, nests seemed to have been started under cover or in a cavity but as they grew in size they extended into the open".

Well closed cavities are prefered by *Eulaema*. Many *Euglossa* species prefer similar but, corresponding to the lesser body size, narrower spaces. But this genus developed another, quite different type of nest site preference as shown by aerial nests made by *Eg. dodsoni* and some other species.

The use of abandoned animal nests, in particular, those made by ants and termites, is relatively frequent, apparently caused by the availability of such cavities in tropical regions. Silvestri (1903) recorded a similar preference by some other solitary bees. The solitary or only primitively social mode of life in Euglossinae must prevent further specialization to these favorable habitats, as seen in some stingless bees making their nests exclusively within still occupied ant or termite nests (Schwarz 1948, Kempf-Mercado 1961, Kerr *et al.* 1967). It is noteworthy that nests of *Eg. melanotricha* and *Eg. intersecta* were found within still partly occupied termite nests.

Another remarkable fact is the scarcity of nests discovered from real subterranean cavities. Most records classified into subterranean nests under 3.2. and 3.3. in Table 2 virtually do not deal with those made in typical subterranean cavities formed under the horizontal ground. The nest of *El. nigrita* described in the present paper is rather exceptional. On this aspect, Euglossinae shows an arboricolous tendency more definitely than principally terricolous Bombinae, even though not so strongly as in Apinae and Meliponinae. Probably the frequent use of overground cavities developed in connection with the avoidance of excessive moisture on one hand, and the availability of such sites under humid tropical climate on the other hand.

At any rate many species are relatively eurytopic as shown by the wide preference range in certain repeatedly recorded species, for instance, *El. nigrita*, *Ep. surinamensis* and *Eg. "cordata"*. In connection with this, definite synanthropic tendencies in some species must be mentioned. One of the most remarkable cases is given by Janvier (1955), who discovered the nests of *Eg. piliventris* in the chimneys used by the natives of Bolivian Yungas and made the following note:

"Ils frequent les appentis dans lesquels pour attendre les cheminées, planer devant un rideau de fumée, le franchir ou s'élancer d'un vol en flèche a travers la flamme pour se glisser furtivement dans des orifices dissimules dans la couche de suie. Les murailles composées des blocs de pierre enfouis dans une páte argilleuse, fendillée par la chaleur, se pretent au travaux de perforation des abeilles".

In *Eulaema* such synanthropism is seemingly not common. But Bodkin records

the nidification of *El. nigrita* in a hollow beam of the large dining hall of one of the largest hotels in Georgetown, Brit. Guiana. "The bee passed to and fro apparently quite regardless of the proximity of human beings." This response makes a strong contrast to the timidity observed in the nest of the same species observed by us (*cf. 3.1.4.*), indicating an interesting habituation process. These instances of synanthropism suggest the survival of some euglossine species as so-called *Kulturfolger* under mild urbanization in tropical America, as comparable to some stingless bees (*Trigona jaty* in South America and *T. iridipennis* complex in Tropical Asia and Oceania).

Occasionally it is noted that nest cavities are enlarged by their own efforts. Concerning the nests of *Eg. ignita* made in the chunk of tree fern fibers, Dodson (1966, *cf.* also Roberts and Dodson 1967) writes that the cavity is enlarged by the bees by biting of the fibers. Bennett also suggests the enlargement of the original cavity in *El. terminata*, and Zucchi *et al.* (MS) similarly in *Eg. intersecta*. However, all previous records inform the use of pre-existing cavities or preparation of *anodalous nests* (Malyshev 1936) in Euglossinae. Thus, it shares the loss of self-exacavation with three other groups of Apidae, sharply contrasting to the closest relative, Anthophoridae, most so far biologically observed nonparasitic species of which make their nests by self-excavation into substrata, either soil or wood (Linsley, MacSwain and Smith 1956, Michener and Lange 1958 b).

1.3. Nest structure in Euglossinae: The information now available on the nest structure of nonparasitic Euglossinae tells the following characters common to all members: 1) Use of pre-existing cavities (independent or *anodalous* nests in Malyshev 1936). 2) Absence of elaborated nest entrance. 3) Use of resin for cell building, mixed or not with other materials, being soft and pliable when fresh, becoming extremely hard later, (*ectostoechal* in Malyshev). 4) Cells mostly made by building, not by excavation (independant or *automorphous* cells in Malyshev), though the formation of cells by excavating the accumulated materials is known in *Eg. intersecta* (Zucchi et al. MS).[1] 5) Cells radial symmetric and oval, made more or less in contact. 6) Differentiation of cell wall into outer and inner layers with different texture, but with no special lining by self-produced substance. 7) Larval food extremely moist, paste like.

Other architectural characters are variable among genera so that each genus is separately reviewed and discussed. The number of cells in each nest, ranging from several to hundreds, is discussed in Section 4, in relation to the social organization. The sizes of cells in previous records are summarized in Table 3.

The data in Table 3 show a marked variability often even in the same species. This is certainly caused by the difference in the performance of cell construction under various conditions. Inner dimensions may be less variable.

1) Similar plasticity is known in some halictine bees, making cells either by building or excavation (Stockhammer 1966), although the principal technique in this group is, in contrast to Euglossinae, excavation.

Table 3. Sizes of brood cells (in mm)

Species	Author	Length	Width	Thickness of wall	Remarks
Eg. cordata	Bodkin 1918	ca. 10	5		
"	Schrottky 1907	10	7		
"	Ferreira MS	15	7		
"	Zucchi *et al.* (*1.1.5.*)	(11)	(6)	0.6	Inner dimension
Eg. dodsoni	Dodson 1966	11	6–6.5	0.3–1.0	
Eg. hemichlora	"	12	7–8	.05–0.8	
Eg. melanotricha	Sakagami *et al.* 1967a	11–14	6.5–9	0.8–1.7	
Eg. viridissima	Friese 1922	11–12	5–6		
Eg. ignita	Dodson 1966	16	9	0.4–0.8	
Eg. imperialis	Roberts & Dodson 1967	(15)	(8)	0.75	Inner dim.
Eg. intersecta	Dodson 1966	25	15		
"	Zucchi *et al.*	18	11	1–4	
El. cingulata	Sakagami & Michener '65	24–25 (22–23)	15–16 (12.5–14)	1–1.5	Inner dim.
"	Dodson 1966	20	15–17	2.5	
El. meriana	Friese 1941	30–35	20–23		From the figure
	Dodson 1966	35	20–22	3–3.5	
El. nigrita	Myers 1935	30	17		
"	Zucchi *et al.*	27–29 (m=28) (19–22)	13–15 (m=14) (12–13)	m=1.0	Inner dim.
El. terminata	Bennett 1965	28–30	20–24	2.5–8	Thickness of inner resinous layer 0.4–0.9 mm
Ep. surinamensis	Möbius 1856	20	12		
"	Ducke 1902 b	16	11		
"	Bodkin	15	10		
"	Dodson 1966	19–21	15–20		
Ep. auriceps	Zucchi *et al.* (*1.1.4.*)	25 (17)	14 (11)	4–5	Inner dim.
Ep. nigrescens	Sakagami & Sturm 1965	25–40	18–28	5–6 often 10	
Ep. violacea	Sakagami & Michener '65	22	13	2–2.5	
Ep. violascens	Sakagami 1965 a	22	13	2–2.5	

1.3.1. Nest structure in Euglossa: All so far biologically known species of *Euglossa* are characterized by the abuse of exogenous materials other than resin. Occasional admixture of other materials is possible. Zucchi *et al.* found the inclusion of damaged wooden particles in the outermost layer of cells of *Eg. intersecta* the nest of which was found within a termite nest. However, there is no observation on the abundant use or collecting by females of such materials. The admixture of self-producing wax is so far not confirmed but possible, because

Cruz-Landim (1963, 1967) recently discovered the presence of wax gland on the penultimate metasomal tergum of *Eg. cordata*.

The oldest record of the nest of *Euglossa* is that by Lucas (1878): "Made from black, hard and waterproof resinous substance, with rough surface, 65 mm wide, 45 mm in long and 15~20 mm thick, containing about 25 round, rather irregular cells separated by thick partitions". In all probability this description deals with a nest made within a cavity. Except for this record all so far recorded nests are classified into two distinct types, *aerial* and *concealed*.

Aerial nests are recorded several times, but, except for *Eg. dodsoni* (Dodson 1966), the descriptions are incomplete and the species observed are not accurately identified (*cf. 1.2.*). Therefore we shall first cite the description by Dodson, then compare the previous records with it. Dodson writes:

"The whole nest is made of resin and is about the size of a walnut, 27~31 mm high, 21~29 mm wide and 15~18 mm thick. It is round in outline and flattened on the front and rear faces. The entrance is a hole on the front side opposite the point of attachment of the nest to the plant. The nest is firmly attached to the plant and is built part-way around it. It is light brown to nearly amber in color when first constructed and is soft and pliable. It generally turns ashen-white with age and becomes very hard. The diameter of the opening is 4~5 mm. The outside shell varies 0.75~1.5 mm thick and inflexed and thickened around the opening where it may be 3 mm thick. Cells are constructed of resin like the outside shell. The cap of the cell is usually thin, showing small individual masses of resin, unlike solid resin of other parts of cells and the outside wall. The axes of cells tend to be vertical but vary to horizontal. Cells are first constructed in the lower part of the nest and these are vertical. The upper part is then largely filled with cells oriented in various ways".

The previous records accord to the citation in the following points: Round, similar to walnut in shape and size, with pale colored outer shell (Girard after Lucas 1878, Mocsáry after Friese 1899, Friese 1930, both from illustrations); Entrance at the side opposite the point of attachment (Mocsáry after Friese). Occasionally the entrance seems to be lengthened to form a short tube (Mocsáry after Friese). Schulz (1902) records a quite large aerial nest, hanging within a hollow tree, 7~8 cm in diameter and the wall 1.5 mm thick, provided with a slightly curved entrance tube of 2 cm long and 8 mm thick. Friese (1930) (1930) illustrates a nest of 18~24 mm in diameter and 25~27 mm in height, being comparable to those of *Eg. dodsoni*. He writes, in contrast to the case in *Eg. dodsoni*, that cells in aerial nests are more horizontal while those in concealed nests are more or less vertical.

Concealed nests are made within more or less closed pre-existing cavities. The entrance is usually not provided with particular constructs. Dodson (1966, *Eg. ignita*) and Janvier (1955, *Eg. piliventris*) definitely writes the absence of such constructs, though Janvier mentions the lining of the entrance. This does not mean that the entrance is left with no elaboration. In a nest of *Eg. intersecta* observed by Zucchi *et al.*, the original entrance found at a side of the root of a big

fallen tree was about 15 mm in diameter, but constricted with resin to 9 mm, in a neatly circular form, projecting about 2 mm from the root surface. This observation coincides with our own given in *1.1.5.* According to Bennett (1966), *Eg. cordata* opens a small circular hole in the resin just large enough for passage. The hole is never closed when the bee leaves the nest but is always sealed in the evening, or often during the day when working inside. The closing of the entrance at night is also recorded in *Eg. ignita* (Roberts and Dodson 1967).

Most recent records refer to the coating, at least partly, of the inner walls of the nest cavity, and, if present, of the entrance canal (Zucchi *et al.* in *Eg. intersecta*): *Eg. ignita*, *Eg. hemichlora*, *Eg. intersecta* (Dodson 1966), *Eg. imperialis* (Roberts and Dodson 1967), *Eg. intersecta* (Zucchi *et al.*), *Eg. piliventris* (Janvier 1955), *Eg. cordata* (Zucchi *et al. cf. 1.1.5.*), *Eg. cordata* (Nogueira-Neto pers. comm.). Ducke (1902 b) writes the absence of particular coating but his figure (1903) shows the occurrence of resinous coating at least partly. Dodson reports that in *Eg. ignita* inner walls of nest cavities are partly lined with resinous material less than 1 mm thick and the inner surface is smooth. When nests are partly opened the orifices are immediately sealed, even if the glass or plastic plates are applied to. Friese (1930) presents the figure of a nest of *Eg. cordata*, which shows such coating. He also writes as to *Eg. viridissima* that the upper and lower ends of the nest cavity are closed by resinous walls. The same elaboration was recently observed in a nest of *Eg. cordata* found in an old burrow of *Xylocopa* (Ferreira MS). *Eg. cordata* and *Eg. variabilis* observed by Bennett (1966), using glass lid wooden boxes, sealed all cracks and joints on the insides of the boxes with resin. *Eg ignita* reared by Dodson (1966) in a small cage smeared resin on the crevices of nest boxes. Up to the present, the absence of any inner wall coating is definitely recorded only in a nest of *Eg. melanotricha* made within a hollow termite nest, probably due to the large size of the cavity (Sakagami, Laroca and Moure 1967 a).

The size of the nest cavity is variable according to nest sites: *Eg. piliventris*, 8～10 cm long, 6～8 cm wide and high (Janvier 1955), *Eg. hemichlora*, 12 cm l, 1～3 cm w (Dodson 1966); *Eg. cordata* 7～8 cm l, 3～5 cm w and 1.5～2 cm h (Nogueira-Neto personal comm.); *Eg. intersecta*, 9.5 cm l and 6.5 cm w (Zucchi *et al.* MS); *Eg. viridissima* 10 cm l within hollow stem of 22 cm l and 3 cm w (Friese 1925); *Eg. cordata* and *Eg. variabilis*, induced to nest in boxes of 10×6×4.5 ccm in inside dimension (Bennett 1966); *Eg. imperialis*, 13 cm l 13 cm w 11 cm h (Roberts and Dodson 1967); *Eg. cordata*, 24.5 cm l and 1.5 cm w (Ferreira MS). The cavities would be smaller and more irregular in shape when made at unusual places as given in Table 2 (3.5). The largest cavity so far recorded is that used by *Eg. melanotricha* (25 cm in diameter and 12 cm high, Sakagami, Laroca and Moure 1967 a).

In contrast to aerial nests, resin used in concealed nests, both for cells and coating, is reported nearly unanimously as dark colored (Ducke 1902 a,b, Schrottly 1907, Friese 1925, '30, '41, Janvier 1955, Dodson 1966, both for *Eg. hemichlora* Zucchi *et al.*). Particularly Ducke and Friese stress the difference between aerial and concealed nests on this character.

Most previous records suggest the parallel construction of upward directing cells in close contact as the pattern basic to the cell arrangement in *Euglossa*. This pattern, when typically expressed, produces an incomplete pre-comb arrangement as seen in *Eg. cordata* (Friese 1930, Bennett 1966), *Eg. imperialis* (Roberts and Dodson 1967), *Eg. ignita* (Dodson 1966) and *Eg. melanotricha* (Sakagami, Laroca and Moure 1967 a). But the tendency to follow the pattern is seemingly not firmly established so that easily modified according to the situation, particularly by the spatial limitation, resulting in a more or less irregular cluster of cells (*Eg. cordata*, Ducke 1903, Friese 1941; *Eg. hemichlora*, Dodson 1966; *Eg. intersecta*, Zucchi *et al.* MS). Even without such external limitation, some cells are isolately made or tops and bottoms of neighbouring cells are often not in the same planes, and the longitudinal axes often not paralleled. In *Eg. hemichlora*, cell axes tend to be horizontal. Janvier (1955) writes and illustrates that cells in *Eg. piliventris* take any directions, made on any places, ceiling, sides and bottom of the nest cavity, built approximately perpendicular to the cavity walls. When a nest contains many cells, new cells are formed above older ones, so that two or more irregular tiers are resulted in *Eg. imperialis*, Roberts and Dodson (1967), *Eg. ignita*, Dodson (1966), *Eg. melanotricha*, Sakagami, Moure and Laroca (1967 a). A more definite tendency to comb formation is recorded by Friese (1922, '25, '30, '41). According to him, *Eg. viridissima* arranges the cells in the same plane. But his illustration (1922) to show this horizontal comb arrangement is not always clear.

Cells are elliptical or elongate oval in all species. The outer surface is rough while inner surface is smooth (*Eg. dodsoni*, *Eg. hemichlora*, *Eg. ignita*, Dodson 1966; *Eg. imperialis*, Roberts and Dodson 1967; *Eg. viridissima* Friese 1922; *Eg. intersecta*, Zucchi *et al.* MS; *Eg. melanotricha* Sakagami, Larcoa and Moure 1967 a). The cell wall is often partly common between two neighbouring cells in contact (*Eg. melanotricha*, *Eg. ignita*). The top of the cell is reported as thinner in *Eg. hemichlora*, or made less compact, with mammiferous projection in *Eg. melanotricha*.

1.3.2. Nest structure in Eulaema: As reviewed in *1.2.*, all so far discovered nests of *Eulaema* have been recorded from more or less closed cavities, the sizes of which are fairly large, for instance 5 inches in diameter and height in *El. nigrita* (Myers 1935), 1 feet in diameter in *El. cingulata* (Dodson 1966). No particular elaboration of the entrance and the canal leading to the cavity (1 m long in a nest of *El. cingulata*, Dodson 1966) is mentioned and Bennett notes the absence of any such structure in *El. terminata*. On the other hand, Ducke (1903) records short entrance tubes in two nests of *El. nigrita*. Myers found in a nest of the same species a constriction of the original entrance by means of clay, leaving the neatly circular entrance hole. These records suggest, together with our observation in *1.1.1.* some minor elaboraton by bees at least in *El. nigrita*.

How the nest mass or cell cluster is fixed within the nest cavity is variable among previous records. Dodson (1966) reports two nests of *El. cingulata* and

one of *El. meriana*, all suspended from the ceilings of the cavities or attached to tree rootlets included in the cavities. Myers and Ducke (one nest) record each the nest mass of *El. nigrita*, both lying on the bottoms of the cavity. Moure (1946) writes that his nest of the same species had no connection to the cavity walls by means of pillars. On the other hand, Sakagami and Michener (1965) found a nest of *El. cingulata* attached to the wall of the cavity by means of one short but thick pillar. The presence of such pillars as described in *1.1.2.* seems to be facultative in the genus.

In contrast to *Euglossa*, all previous records do not refer to the resinous coating of the walls of the cavities. Dodson positively touches upon the absence of such coating in *El. cingulata* and the nest of *El. nigrita* studied by us also possessed no coating on the cavity walls. Probably this trait represents, together with the nest materials given below, one of the most distinct ethological characters, which separates *Eulaema* from *Euglossa*.

The nest materials are resin, mud and animal excrement. Previous records are cited as follows: Ducke 1903, *El. nigrita* : In one nest cells are made from "einer vegetablischen Bestandteilen gebildeten aus Regenpfützen zusammengetragenen schwarzgrauen Erde", both in- and outsides covered with resin taken from Burceraceae, grayish when fresh, becaming whitish with age. In another nest cells are mostly made from horse dung, only internally coated with resin. Myers 1935, *El. nigrita* : Clay and resin, but probably using excrement, too, because he mentions an irregular mist heap of dark, fecal smelling material beside the cell cluster. Michener and Sakagami 1965, *El. cingulata*: Mainly from resin, mixed with a dark colored substance, probably animal excrement. Dodson 1966, *El. cingulata*: Mixture of mud, human feces and resin from *Proteum* sp.; *El. meriana*: Mainly made from mud, mixed with resin. Bennett 1965, *El. terminata*: Mainly from mud, including fine rootlets, apparently admixed at foraging, internally coated with resin. These records indicate the use of resin with an abundant mixture of mud or animal excrement. The relative choice of these two materials seems to be variable even within the same species (*cf. El. nigrita*). In each nest, however, one of them seems to prevail, probably caused by the attachment of the foragers to particular sources.

There have been recorded two types of cell arrangement, *combed* in *El. meriana* (Friese 1941) and *clustered* in all other species so far observed. The latter type is probably comparable to the nest arrangement of most *Euglossa* making concealed nests. The parallel construction of vertical, upward directing cells in close contact approximately in the same plane appears to be the pattern basic to this genus, too. This tendency is easily disturbed in large nests and the arrangement becomes more or less irregular as in our nest described in *1.1.2.* (Fig. 3). Cells may attach obliquely near the tops or bottoms of the older ones, often not taking vertical orientation, so that the whole arrangement becomes quite irregular (*cf.* Figure by Ducke 1903, Friese 1930). Bennett (1965) traced the development of a nest of *El. terminata* precisely based upon the dates of newly emerged adults.

The cluster developed approximately upward and laterad but with a considerable irregularity.

In contrast to such rather irregular cell arrangement in many species, Friese illustrates a beautifully arranged nest of *El. meriana*. Each cell lies in the same plane and the whole forms a horizontal comb. The contours of the top and bottom of each cell are still traced from the outside but not so distinctly as in other species. Another nest of this species recorded by Dodson (1966) contained only two cells. A third nest found by Dr. A. While in Guacimo, Costa Rica, was very large. Through his kindness, one of us (S.F.S.) had an opportunity to see it and confirmed the comb arrangement identical with that shown by Friese.

Cells are more or less similar in all species, and essentially to those in *Euglossa*, except for the larger size (Table 3) and the admixture of mud or animal excrement in the outer cell wall, resulting in the distinct separation of outer and inner layers (*1.1.3.*). Cell walls are often common when two cells are made side by side (Bennett, Dodson, both in *El. cingulata* and *El. meriana*). The top is thinner, containing more resin in *El. cingulata* (Dodson 1966), no particular difference except for thickness in *El. nigrita* (*1.1.3.*), *El. meriana* (Dodson 19 66) and *El. terminata* (Bennett 1965). The different texture of the top part depends on the process of operculation after oviposition as described in *3.3.3.* It is worth mentioning that external keels observed in *El. nigrita* (*1.1.3.*) have not been recorded in any other observations.

1.3.3. Nest structure in Euplusia: All so far discovered nests of *Euplusia* are common, and distinguished from those of *Euglossa* and *Eulaema*, in the use of bark or allied vegetable materials mixed with resin. On the other aspects, too, the nest structure is more or less similar among species and approximately identical with that of *Ep. auriceps* described in *1.1.4.* A remarkable exception is *Ep. nigrescens*, the nest of which is referred to later. The following old comment by Girard (*cf.* Lucas 1878) on an "*Eulaema*" nest apparently deals with a nest of *Euplusia*: "Les cellules sont grossièrement construits avec une matière gomo-résineuse, solidifiées et reliées par des copeaux de vois très minces, comme feuillets." On the other hand, the description and illustration by Möbius (1856), the oldest biological account known on Euglossinae, is very precise: "The nest was found under the eave, made by oval-round cells, which *ziemlich in einer Richtung aneinanderhangen*. The outer cell wall is made with pieces of bark, each about 5∼10 mm long and tightly attached one another by gummi and wax. The inner wall is made by dark brown wax, about 0.5 mm thick, and the inner surface is smooth and polished. The basal end of the cell is rounded, while the apical end truncate" (*El. surinamensis*). The wax cited in the description may mean resin. Otherwise this description may be applied to all other species, as far as the cell structure is concerned, especially as to the cell wall made by pieces of bark tightly attached by dark resin, the inner surface smooth, and the outer side covered with rather larger and much loosely attached pieces of bark (Ducke 1902 b, Dodson and Frymire 1961b, Sakagami 1965a, Dodson 1966, all *Ep. surinamensis*; Sakagami and Michener 1965, *Ep. violacea*). In two instances, bark is replaced by other materials (Cockerell

1916, wood shavings; Bodkin 1918, flakes of plaster, both in *Ep. surinamensis*).

The successive construction of cells in a tubular form, or, *allodalous arrangement* (Malyshev 1936) is also given in all records except for *Ep. violascens*, the nest examined of which had still only one cell (Sakagami 1965 a). The number of cells in each series is up to 4 (Dodson and Frymire 1961 b, Dodson 1966), 2～3, rarely more (Ducke 1902 b), 1～4 (Sakagami 1965 a) in *El. surinamensis*, 1～3 in *Ep. violacea* and 4 in *Ep. auriceps* (Zucchi *et al. cf. 1.1.4.*). These tubes are made either linearly or in curve. Often several tubes are made side by side (Ducke, Dodson and Frymire, Dodson, Sakagami) and occasionally arranged so irregularly that a complicated cell cluster is formed (Möbius, Bodkin 1918). But even if such is the case, the basic allodalous arrangement is retained in each unit-series (Sakagami and Michener).

Usually lateral walls of successive cells are continuous, without outer demarcation between cells. But some species, for instance, *El. surinamensis* (Sakagami 1965 a) seems to be plastic on this aspect, often showing demarcation or even complete separation between cells. The rounded basal end and truncate apical end of the cell noted by Möbius are recognized in *El. surinamensis* (Sakagami 1965 a) and *El. violacea* (Schrottky 1902, '07, Sakagami and Michener 1965). Sakagami (1965 a) also records that the whole tubular series can be covered with a large assemblage of loosely attached pieces of bark (*cf.* also Ducke 1903). Such outer envelope may be discovered in other nests made in not completely closed places.

As given above, cells are externally truncate at the apical end, but internally always elliptical or oval as in *Euglossa* and *Eulaema* (even in *Ep.. nigrescens* as referred to below), with walls consisting of two layers, the outer one in average thicker than in *Euglossa* and *Eulaema* (*cf.* Table 3) made from bark and resin, while the inner one, very thin, from resin alone, provided with smooth surface but no special lining. The orientation of cell is vertical in a nest of *Ep. violascens*, oblique and downward directing in *Ep. surinamensis* (Sakagami 1965 a) and not precisely give in other records.

Ep. nigrescens is remarkable by the aberrant nest structure, being quite different from other species as follows: 1) Made on the exposed ground surface. 2) Mostly made from sulphur yellow, not dark, resin. 3) Use of bark (occasionally replaced by moss) extremely reduced, mostly attached on the outer surface of the cell, not incorporated in cell wall which is very thick. 4) Outer surface of cell provided with a peculiar papillate architecture. 5) Inside of cell provided with a differentiated structure, consisting of A. Fragile and easily detached cell lid, made from pieces of bark loosely attached one another with a bit of resin. B. Cup-like antechamber with smooth wall. C. Resinous partition including porous interspace filled with pieces of bark. D. Proper cell interior. 6) In most cells antechamber and cell interior connected by means of a canaliculus penetrating resinous partition. 7) Cells built either isolately or grouped to 12. When grouped, cells arranged either in parallel or obliquely but never showing the genuine

allodalous arrrangement (*cf.* Fig. 7, Ep-4).

Except for the use of bark and resin, the nest structure of this species does not share any characters with the other members of the genus. The presence of a differentiated vestibule is unique among all euglossine species, probably among all bees. It is worth to mention that *Ep. nigrescens* morphologically does not differ much from the other congeneric species, for instance, *Ep. violacea*. This would reflect a rapid change of the nest architecture as an adaptation to the high Andean environment.

1.4. Evolution of euglossine nest structure: The review presented above clarified within the limit of our present knowledge both common features and group diversity found in euglossine nest structure. There is no feature common to all genera while absent in any other bee groups. All common features enumerated at the top of *1.3.* are replicated in some other bees. Therefore we shall trace the evolution of nest structure from the standpoint of group diversity.

This problem called attentions of Friese. In three successive papers (1922, 1930, 1941), he published his idea upon the evolution of euglossine nest structure in parallel with morphological differentiation. The following schema is cited from the last work, which is also one of the last papers of his prolific, though occasionally confusing contributions to melittology during half a century: (Roman and Arabic designations were added to by us. Some changes in scientific names are given as follows: *dimidiata→meriana*, *fasciata→cingulata*, *smaragdina→surinamensis*, *aenescens→mandibularis*, *brullei→intersecta*, *mariae→mariana*).

		Morphological	Biological
I.	*Eulaema*	Bumbelbee like with hair bands: *dimidiata, fasciata, polyzona*	0. Linear nest, from resin and pieces of bark: *smaragdina* 1. Irregular cluster, from resin and mud: *fasciata, nigrita* 2. Combed, from resin and mud: *dimidiata*
II.	*Eumorpha*	Medium sized, metallic, no hair bands: *violacea, aenescens, brullei, mariae*	1. Linear nest, from resin and pieces of bark: *violacea*
III.	*Euglossa*	Smallest, metallic, nearly naked: *cordata, viridissima, ignita*	Nest purely made from resin 1. Within cavity, clustered: *cordata* 2. Under bark, combed: *viridissima,* 3. Aerial, with pale outer shell: *variabilis*

In this schema, *Eumorpha* is an invalidated name. *Em. violacea* and *Em. mariae* go, with his *Eulaema smaragdina*, to *Euplusia*, and *Em. aenescens* and *Em. brullei* to *Euglossa*. Thus his group I–0 disappears, included within his II–1. After these changes, the designations given in the schema correspond to those in Fig. 7, which shows all so far known

euglossine nest patterns schematically. (It is uncertain what species is meant by his *variabilis*, though it apparently deals with the species making aerial nests as in *Eg. dodsoni*).

The gradual development through three steps is an interesting idea and not always inconceivable, if the relation is not regarded as strictly linear, such as *Eulaema→Euplusia→Euglossa*. But the problem is not simple even if only nesting habits are dealt with, because at least three features are involved here: nest site, nesting materials and cell arrangement, each of which must separately be considered and the higher steps in one feature do not necessarily link with those in another feature.

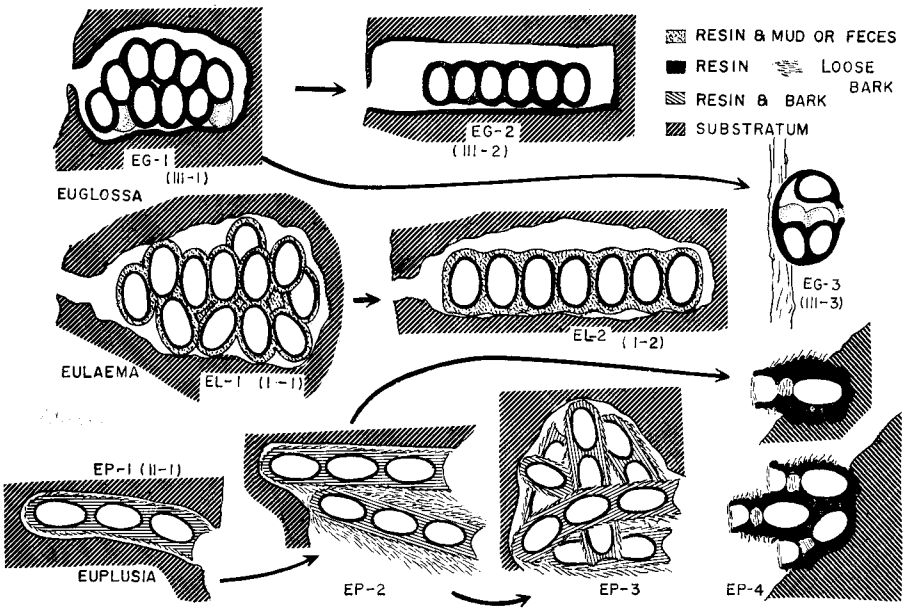

Fig. 7. Various patterns of nest arrangement in Euglossinae. Abbreviations: Eg, El, Ep, respectively three genera mentioned. I–1, I–2, etc, are types proposed by Friese (1941). Eg–2 was drawn based upon records by Friese (1922～'41) but the exact pattern is uncertain.

Obviously the preference for overground nest sites is a secondary acquisition in bees, or in most Aculeata. The shift from the primary soil dwelling habit to the epigaeic nidification evolved in diverse bee groups independently: Colletidae (*Hylaeus*), Halictidae (*Augochlora, Megalopta*) Megachilidae (most groups), Xylocopinae (complete shift except for *Proxylocopa*, Guthbier 1916) and Anthophorinae (*Clisodon*). Here the Family Apidae is outstanding by the virtual loss of self-

excavation into substrata. The use of subterranean cavities is still frequent in bumblebees, occasional in euglossine bees, and probably of the secondary acquisition in certain stingless bees (*Geotrigona*, *Schwarziana*, etc.). The next step is the change of the preference from more or less closed cavities to exposed situations. In solitary bees the latter case is relatively rare, only known in some megachilid bees (*Chalicodoma*, *Dianthidium*, etc., *cf.* Linsley 1958). In Apidae bumblebees did not develop this trait (Dias 1960). But at least two groups of stingless bees *Trigona* s. str. partly, *Dactylurina*) make aerial nests. Finally honeybees are regarded primarily making such aerial nests. The preference for concealed cavities by *Apis mellifera* and *cerana* is presumably of the secondary acquisition. Therefore, in Euglossinae, too, the preference for more or less closed cavities is regarded the primitive trait, represented by all known *Eulaema*, most *Euglossa* and some *Euplusia*. From this condition the tolerance for semi-closed nest sites as in many *Euplusia*, and finally the nidification at exposed places as in *Eg. dodsoni* and *Ep. nigrescens* were derived. In conclusion three groups do not form a linear series but show independent development as to nest site preference.

It is not easy to decide the relative antiquity of the preference for various nesting materials, resin, mud, animal excrement and bark in this case. The animal excrement was probably adopted later, as a substitute for mud, when a large amount of this material has become available, probably intensified under increased human activities. It could be inferred that mud and bark were used piror to resin, which was more difficult to manipulate. Virtually in some megachilid bees using resin together with other materials, often resin is used to line the inside of the cell made from other materials (Malyshev 1936). But the alternative hypothesis, the use of resin later incorporated with other materials, is also conceivable. This is especially likely as to bark. Unlike megachilid bees, which transport both resin and other materials in mouth, all so far studied apid bees use the mouth part only to carry away deads and other debris from nests, never to carry any materials in nests. Consequently the pieces of bark cannot be brought back without using the viscosity of resin already deposited on corbiculae (*cf. 3.2.1.*). On the other hand, it is open to the question whether the same idea can be applied to *Eulaema*, in which resin and mud (or animal feces) are carried back independently. There is the observation which favors the earlier adoption of resin than mud. In our nest of *E. nigrita*, resin was collected mostly by the females which were just possessing the cell under construction or provisioning (*cf. 3.4.1.*). Even if mud was adopted prior to resin by the ancestral Euglossinae, it is probable that the mixed use of resin developed rapidly, thanks to its excellent quality to protect the content of the cell against molds, one of the worst enemies under humid tropical climate. At least it is certain that the use of resin is fairly fixed, while that of other materials relatively plastic, which is also recognized by the reduced use of bark in *Ep. nigrescens*.

The discovery of the rudimentary wax gland in *Euglossa* (*1.3.1.*) suggests a tendency to the use of self-produced wax as in three other apid groups. It is

interesting that the use of resin is still maintained in most stingless bees. Even honeybees, the combs of which are nearly entirely made from wax, collect resin. This trait, called propolization in apiculture, varies among species, or races, strong in *A. florea* and some races of *A. mellifera* (for instance, Caucasian, *A.m. remipes*) and virtually absent in *A. cerana* and Middle-East races of *A. mellifera* (Sakagami 1960).

Thirdly the cell arrangement in euglossine nests is discussed. So far known types of cell arrangement given in Fig. 7 are classified into three types. Clustered (Eg–1, El–1, Ep–4, Eg–3), combed (Eg–2, El–2) and allodalous (Ep–1, Ep–2, Ep–3). Concerning the first two types, combed nests certainly developed from clustered ones. Combed nest is the most advanced type concerning the spatial economy and evolved independently in Halictinae (Sakagami and Michener 1962), Nomiinae (Guthbier 1916, Batra 1966), stingless bees (Schwarz 1948, Kerr and Laidlaw 1956), social wasps (*cf.* Richards and Richards 1961), reaching the summit in honeybees.[1] Moreover, independent evolution of combed nests is suggested even within a restricted group, for instance, in Halictinae (*Evylaeus, Augochloropsis, Augochlorella, Halictus* s. str., etc. *cf.* Sakagami and Michener 1962). Combed nests in *Eulaema* and *Euglossa* could be one instance of such parallel evolution. Recently Michener (1961) asserted the possibility of the reversed instance in stingless bees, the secondary derivation of clustered nests from combed ones due to spatial limitation. In Euglossinae there is no evidence to support this opinion. But such plasticity is not excluded in another sense. Many previous records indicate both *Euglossa* and *Eulaema* have a tendency to make cells vertically and to build them one by one in close contact. This tendency may result, in the absence of spatial limitation, in an incomplete horizontal comb, as seen in *El. nigrita* (Fig. 3), *Eg. cordata* (Bennett 1966), *Eg. melanotricha* (Sakagami, Laroca and Moure 1967 a).[2] Probably this tendency is prevailing in both genera, but it is not so firmly fixed that easily modified by spatial limitation or further development of nests, resulting in an irregularly clustered arrangement (*cf. 1.3.2.*). Thus these species are seemingly going and returning at the middle of the way to comb formation, instead of returning to clustered nests after the acquisition of comb system as suggested by Michener in stingless bees.

The third type, allodalous arrangement, is exclusive in *Euplusia* and universal to the genus except for *Ep. nigrescens*, retained even when the arrangement is complicated by the fusion of several unit-series (*Ep. violacea, cf. 1.3.3.* and Fig.

1) According to the system by Malyshev (1936), only nests of social wasps and honeybees, in which cells are synchronously, not successively constructed one by one, are called "comb", while combs formed by successive cell construction are classified as *pseudocombs*. Here the term *comb* is used in the wider sense, including both types.

2) It is possible that combed nests of *Eg. viridissima* reported by Friese (1922, '30, '41) virtually belong to this type. Although cited as combed type (Fig. 7, Fig. 2) from his statement, it is uncertain whether the nests of this species are typically combed as those of *El. meriana*.

7, Ep–3). The allodalous arrangement represents in itself a regularity, reflecting its evolution from a more irregular, or exactly, randomly made type. In burrowing bees, for instance, its derivation from branched type nests is likely (Sakagami and Michener 1962). In Euglossinae, however, it is not easy to assume the type ancestral to allodalous nests. One possible explanation for the development of this type is suggested from the old note by Girard (*cf.* Lucas 1878), recording the nests of probably *Euplusia* in the burrows of beetles. Another similar instance is the nest of *Ep. auriceps* described in *1.1.4.* If this genus once acquired the preference for such nest sites, the walls of which cannot be excavated and the diameters do not permit to make more than one cell in parallel, the allodalous arrangement may be the inevitable consequence. The maintenancle of this arrangement after the extension of nest site preference for relatively open spaces may explain the present situation in the genus. It is uncertain whether this preference for limited spaces developed directly from the burrwoing habit of some groups ancestral to Euglossinae or after the adoption of the use of any small cavities as in *Eulaema* and *Euglossa*. If the latter is the case, the type ancestral to allodalous nests would be the irregular arrangement of cells, built either separately or occasionally in contact. Such prototype produced clustered nests in *Eulaema* and *Euglossa* on one hand, and allodalous nests on the other hand. Probably this is the limit of our inference within the present knowledge.

Finally two additional instances are briefly commented on. The nest of *Ep. nigrescens* is clustered. It is difficult to assume that this remarkable nest with highly specialized cell structure is the type ancestral to the allodalous type in other species of *Euplusia*. This case indicates that even so firmly established trait can secondarily modify under particular condition. Another point worth mentioning is the coating of inner walls of nest cavities found in *Euglossa* (*1.3.1.*), but not in *Eulaema* and *Euplusia*. Free aerial nests with outer envelope, made by *dodsoni* and some other species of *Euglossa*, could evolve easily from the presence of such trait.

Summarizing, we obtained the following evolutional trends:

Nest sites :

Abandonment of self-excavation	→	Closed subterranean cavities *Euglossa* ± *Euplusia* + *Eulaema* ++	→	Closed overground cavities *Euglossa* ++ *Euplusia* + *Eulaema* ++	→ Semiclosed overground cavities *Euglossa* + *Euplusia* ++	→ Aerial *Euglossa* ± Exposed *Ep. nigrescens*

Nesting materials: (H. 2 is more likely than 1)

Hypothesis 1

(Mud) → Mud + Resin → *Eulaema*
Resin → *Euglossa*
Resin + Bark → *Euplusia*

Hypothesis 2

(Resin)—→ Resin — *Euglossa*
|→Resin + Mud — *Eulaema*
|→Resin + Bark — *Euplusia*

Cell arrangement:

Burrowers→ Builders→ Closely contact in parallel → Combed *Eulaema* +, *Euglossa* ±
(Irregular arrangement) → Closely contact in parallel → *Eulaema* ++, *Euglossa* ++
With outer envelope *Euglossa* ±
Closely contact in series→ *Euplusia* ++
|→In parallel *Ep. nigrescens*

At the present we cannot combine these three trends to have one reasonable evolutional course as did by Friese (1941). Within each group, some secondary differentiations appeared: Formation of combed nests, aerial nidification and peculiar cell structure. While the origins of these secondary courses are not always difficult to assume, we cannot have a clear picture upon the interrelation among three genera. This fact indicates the quite old ramification among them, the common ancestral type of which was already lost in the very past. At least ethologically the distances among three genera are assumed to be not smaller than those among any "genera" in three other groups of Apidae, however Euglossinae socially remains at an incipient stage.

2. Immature stages

In this section, diagnostic characters of larva and pupa of *El. nigrita* are first given and compared with those of other euglossine species. Thereafter, some additional items of information concerning immature stages are gathered together.

2.1. Larval and pupal morphology of El. nigrita:

Predefecation larva (Fig. 8, described according to the system by Michener 1953): About 28.5 mm long and 6.3 mm wide at middle. *Head capsule* (Fig. 9, A, B): Distinctly wider than long (2.3 mm: 1.6 mm), only slightly constricted from thorax, rather weakly sclerotized without conspicuous marginal thickenings and setae. Posterior tentorial pit inconspicuous. Seen frontally median cleavage line distinct; laterofrontal covexity without tubercle but with slightly sclerotized, rather elongate patch immediately above and mesad of antenna. Antenna slightly longer than height of broad basal convexity, apically without papillae (in the sense of Roberts and Dodson 1967, not Michener 1953). Epistomal suture merely represented by gently arched transverse depression between distinctly sclerotized anterior tentorial pits. Labioclypeal suture clear but hidden by raised apex of clypeus. Labrum bilobed, apically with minute setae, laterally distinctly sclerotized especially at base. *Mouth parts* (Fig. 9 E, F): Mandible short and robust, conspicuously sclerotized, especially at upper margin, not strongly tapering apically; Apex rather obliquely truncate; inner surface without cusp but with borad and deep apical concavity margined by ridge; upper margin with one large tooth midway; lower margin roundly but distinctly bending, with distinct subapical tooth. Maxilla apically not bent inward,

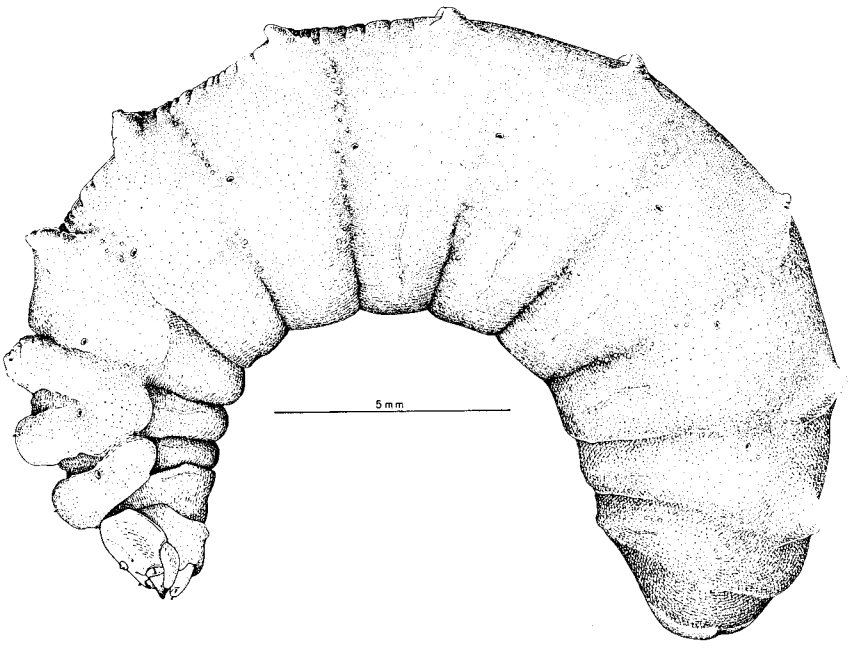

Fig. 8. Predefecation larva of *El. nigrita*

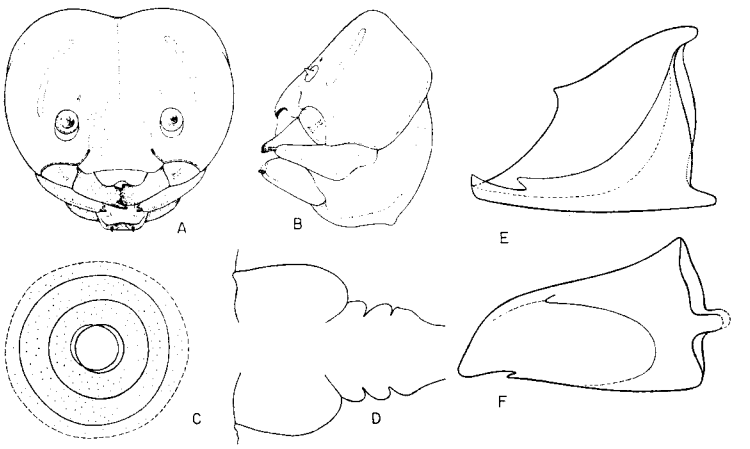

Fig. 9. Head (frontal and lateral views A, B), tracheal opening, (C, cross section D) and mandible (ventral and inner views. E,F) of larva of *El. nigrita*.

gradually tapering apically; Outer surface with minutest setae; Apex roundly pointed; galea about half as long as palpus, without apical setae; palpus longer than doubled basal width but shorter than tripled width. Labial lobe not fused with maxilla, parallel sided, apex linear with rounded lateral angles; with scattered minutest setae; pre- and postmentum clearly marked by depression; salivary opening transverse, nearly as wide as interpalpal distance, marked by weakly sclerotized lips; palpus nearly twice as long as wide. *Postcephalic segments* : Intersegmental lines weak, interrupted on side. Lines between cephalic and caudal annulets weak except on thoracic segments. Dorsolateral tubercles on thoracic segments conspicuous, highest dorsolaterally but homogenously elevating beyond level of spiracle, dorsomedially longitudinally depressed, dorsolaterally without marked conical elevation, only feebly raised, not particularly sclerotized, each with fine short spine. Dorsolateral tubercles on abdomen less conspicuous, distinct on anterior segments, gradually weakening postward, all represented by conical elevation without sclerotization or spines. Body without setae but inconspicuous spicules on dorsal surface. Spiracle (Fig. 9 C, D) with shallow atrium, outer rim inconspicuous, inner wall without spine, ridge or annulation. Primary tracheal opening narrowed by collar approximately as wide as atrial opening. Peritreme complete and flat.

Pupa (*cf.* Michener 1954 b): No tubercle or spinous projection on scape, vertex, frons, pronotum, mesoscutum, mesoscutellum, metanotum, tegula, wing and tibia. Coxa with apical spine, those on mid and hind coxae conspicuous. Fore and mid trochanters with dull apical process, pointed but not forming spine. Fore and mid femurs basoventrally roundly projecting. Body without long seta. Metasomal tergum II and following ones each with subapical row of spicules.

2.2. Some comparative remarks on larval morphology: Michener (1953) described the larva of *Ep. violacea*. Recently Roberts and Dodson (1967) described the larva of *Eg.* (*Glossura*) *imperialis* and gave a comparison of the larvae of *Glossura*, *Euglossa* and *Euplusia*. Comparing these descriptions with that of *El. nigrita*, the following synopsis was tentatively prepared:

Characters	*Euglossa*	*Glossura*	*Euplusia*	*Eulaema*
Dorsolateral tubercles of thoracic segments	Short transverse ridge	Concial	Short transverse ridge	Prominent transverse elevation
Setae on head capsule and dorsal surface of postcephalic segments	Very sparse	Very sparse	Very sparse	Absent
Tubercle on cephalic laterofrontalc onvexity	Probably Present	Present	Present	Absent
Galea of maxilla	Small	Large	Large	Large
Papillae of antenna	2, quite large	6–10, small	4–5, large	Absent

Beside these differences, the following characters in *El. nigrita* are worth mentioning for precise comparison in future. 1) Intersegmental lines and lines separating caudal and cephalic annulets weak (=*Glossura*), 2) Dorsolateral tubercles of abdominal segments relatively well developed though not sclerotized.

3) Laterofrontal convexity of cephalic capsule with a pair of elongate, weakly sclerotized patches (≠*Euplusia*, =*Glossura*, after the figures). 4) Epistomal suture weak (≠*Euplusia*, *Glossura*). 5) Apical margin of mandible distinctly concave (≠*Euplusia*, ≒*Glossura*). 6) Lower margin of mandible with distinct subapical tooth (≠*Euplusia*, *Glossura*). 7) Maxillary galea without long seta (≠*Euplusia*, *Glossura*). 8) Pre- and postmentum separated (≠*Euplusia*, =*Glossura*). 9) Labium and maxilla not fused (=*Glossura*, ≠*Euplusia* after the figures by Michener, and Roberts and Dodson).

Most remarkable deviations of the larva of *El. nigrita* from the other species so far recorded are probably, 1) Absence of body setae, 2) Absence of cephalic tubercle, 3) Presence of prominent subapical tooth on lower margin of mandible, and 4) Absence of antennal papillae. On the other hand, all so far known euglossine larvae are distinguished from those of other species of the Family Apidae by the following characters: 1) Relatively long antenna. 2) Broad mandible not tapering apically. 3) Presence of distinct maxillary galea. 4) Primary tracheal opening narrowed by collar. The presence of body setae except in *El. nigrita* agrees to bumblebees, but no euglossine larvae possess differentiated spines in tracheal atrium characteristic to bumblebees.

Michener (1953) pointed out a paradoxical phenomenon, the possession of many primitive characters by the larvae of bee groups, the adults of which are of rather specialized types, and explained this by the reverse evolution. Euglossinae, including *El. nigrita*, is certainly one of such groups, retaining more primitive characters (8 out of 11 characters enumerated by Michener) than in any other groups of Apidae, but Roberts and Dodson prefer to explain the fact by a delayed development.

2.3. Some additional notes on immature stages:

Egg size: All so far known eggs of Euglossinae seem to be of the same shape, cylindrical, distinctly curved and the head pole slightly larger than the caudal one. The size is recorded: *El. nigrita*, 6 mm long and 0.9 mm wide; *Ep. surinamensis*, 6 mm long and 1 mm wide (Ducke 1902 b, Sakagami 1965 a); *Eg. imperialis*, 5 mm long and 1 mm wide (Roberts and Dodson 1967); *Eg. piliventris*, 2.5 mm (sic !) long. Except for *Eg. piliventris*, the record of which is probably erroneous, all belonging to the medium sized egg in Iwata and Sakagami (1966). The egg index (egg length/mesosomal width of adult female) in three species is respectively 0.77, 0.80 and 0.88, all distinctly higher than in bumblebees, honeybees and stingless bees except *Melipona*.

Cocoon: The cocoon of *El. nigrita* is consisting of two layers (Nos. 3 and 4 in Fig. 3 C). The outer layer is chestnut colored, rough and resistant. The inner layer, easily separable from the outer one, is finer and paler, here and there inlaid with viscous and brilliant granules. The deposition of whitish yellow pulverized larval feces (No. 5 in Fig. 3C) was noticed also between two layers, thicker at the bottom of the cell, indicating the defecation during cocoon spinning. The cocoon

tightly adheres to the cell wall except for the top where a narrow interspace exists between cocoon and cell wall (Fig. 3 A, B). The cocoon of *Ep. auriceps* is also consisting of two layers as in *El. nigrita*, but the larval feces was found within the inner layer.

The cocoon of Euglossinae, first recorded by Möbius (1856) seems to be more or less of the similar texture among species, mostly brownish, silky and tightly adhering to the inner wall of the cell (*Ep. violacea*, *Ep. cingulata*, Sakagami and Michener 1965 a; *El. terminata*, Bennett 1965; *Eg. dodsoni*, *Eg. hemichlora*, *El. cingulata*, Dodson 1966), though reported a little less tightly adhering in *Ep. surinamensis* (Dodson 1966) and more easily detached in *Ep. nigrescens* (Sakagami and Sturm). Bennett (1965) records a narrow interspace between cocoon and cell wall at the top of the cell as in *El. nigrita*. Friese (1922) notes absence of cocoon in *Eg. viridissima*. Probably the cocoon was overlooked because so tightly adhered to the wall.

According to Michener (1964 a) cocoon spinning and lining of cell wall by adult female with self-secreting material have a negative correlation. Larvae of sphecoid wasps spin the cocoon but adults do not line the cell. The primitive bees such as Colletidae and Halictidae line the cell wall but do not spin the cocoon. Michener is of the opinion that spinning and lining materials are produced from the same gland, which mature in later larval stages in sphecoid wasps but in adults in the primitive bees. This plausible shift of the function was again reverted in some specialized bees such as megachilid and apid bees, which made cocoon but did not line the cell wall.

Opinions differs as to the defecation at pupation among the authors. In *El. nigrita* and *Eg. intersecta* (Zucchi *et al.* MS) feces are found between outer and inner layers of the cocoon, while feces are reported as voided inside the cocoon, usually at the end of the cell in *El. terminata* (Bennett 1965), *El. cingulata*, *Ep. surinamensis*, *Eg. dodsoni*, *Eg. ignita* (Dodson 1966), *Ep. surinamensis* (Sakagami 1965 a), *Ep. violacea* (Sakagami and Michener 1965), *Eg. imperialis* (Roberts and Dodson 1967) and *Ep. auriceps* (Zucchi *et al.*). Roberts and Dodson stress this trait as peculiar to Euglossinae, unlike the other cocoon spinning groups such as bumblebees and megachilid bees, which defecate before spinning. One might assume the presence of feces between two layers of the cocoon indicated the reuse of the same cell successively. But the different texture of two layers excludes this possibility. Faegri (after Løken 1961 b) photographed the presence of feces between two layers of the cocoon in *Bombus lucorum* (Linné). Further critical observations are required on this problem.

2.4. Duration of immature stages: In our nest of *El. nigrita*, the duration of immature stages was not directly confirmed. But an indirect estimation was made from the following inference: 1) Dates of the emergence of adults from the cell cluster brought in the observation case are divided into two separate periods, The majority of adults, 24 individuals (18 ♀♀, 3 ♂♂ and 3 those not sexed), emerged more or less continuously during March 20 to April 6, but two females and one male, with a pause, during April 19～22, from cells Nos. 41～43. 2) As seen in Fig. 3B, these cells occupy, together with cell No. 18, one end of the cell cluster. No. 18 contained a white female pupa when opened on March 1. Judging from the

proximity of No. 18 and Nos. 41～43, the latter cells are assumed as prepared approximately at the same time, giving an estimation of the pupal stage of about 50 days. 3) These cells are assumed to be provisioned and oviposited on January 18～19, for no foraging trip was observed since these days. Therefore, the duration from oviposition to pupation is estimated as about 39 days, and the total duration of immature stages as about 2 months.

The duration of immature stages was partly observed in *Ep. auriceps*. On May 23 1968, a small window of about 3×3 mm. sq. was perforated in the wall of the first cell (made at the end of the burrow, *cf. 1.1.4.* and Fig. 5). Through this window, which was opened only at observations,the conditon of the occupant was intermittently observed. During May 23～November 11, 173 days, the occupant remained as postdefecation larva. Since that day, the occupants of two other cells were observed simultaneously as follows:

Date		Cell 2	Cell 3	Cell 4
Nov.	11	Pale colored pupa	Dark eyed pupa	White pupa
	19	Dark pupa, first movement	Pale colored pupa	〃
	21	Greenish	〃	〃
	22	Green	〃	〃
	25	〃, buzzing	〃	〃
	27	Emergence	Pale colored pupa	White pupa
	28		Dark pupa	Dark eyed pupa
Dec.	2		First movement	Pale colored pupa
	13		Emergence	Dark pupa
	23			〃
Jan.	3			Emergence
		Ex. smaragdina ♀	*Ep. auriceps* ♂	*Ep. auriceps* ♂

The prolonged diapause in postdefecation stage is regarded normal, because the occupants in cells 2 and 3 were more or less of the similar stages. Moreover the length of total immature stage, 211+x days approximately corresponds to that given by Ducke as to *Ep. surinamensis* (*cf.* below). Beside the discovery of the parasitism by *Ex. smaragdina* it is interesting that the occupant of cell 4, made earlier than cell 3, was in younger stages, which facilitated the successive departure emerged adults.

The records on the duration of preimaginal life in Euglossinae are still meager. But as cited below together with some comparable data, it is remarkably longer than in other groups of Apidae. The prolonged duration in *Euplusia* is of particular interest, because they spent "winter" as preimaginal stages, not as adults as in all other apid bees, under tropical (*Ep. auriceps*) or even equatorial climate (*Ep. surinamensis*).

Duration of Immature stages (in days)

Species	Egg	Larva	Prepupa	Pupa	Total	Author
Ep. surinamensis	6	—	—	—	Ca. 250 (Feb.-Dec.)	Ducke 1902 b
Eg. cordata	—	14	—	—		Ducke 1901
Eg. ignita	3	25	..... 35		63	Roberts and Dodson 1967
El. cingulata	—	—	—	—	ca. 120	Dodson 1966
El. nigrita	..... ca. 40			50	ca. 90	Zucchi *et al.*
El. terminata	—	—	—	—	>63	Bennett 1965
Bombus atratus Worker	6	7	5–6	8–12	ca. 28	Sakagami, Zucchi and Akahira 1967
Bombus lapidarius Worker	4	..... 7		12	22–23	Sladen 1912
Bombus agrorum Worker 1947	4–6	..... 10–19		10–18	32.0	Brian 1961
1948	4–7	..... 7–15		10–20	34.1	〃
Melipona quadrifasciata						Kerr 1950
Worker	4.5–6.5	7–8	5–5.5	15.5–18	34–37	
Queen	〃	〃	4.5–5	11.5–15	30–34	
Trigona postica Worker	2	13	..... 31–33		46–48	Sakagami and Akahira unpub.
Apis mellifera Worker	3	6(5)	3	9	21(20)	*Auct.*
Queen	3	9	2	5	16	〃

3. Female Behavior

Up to the present no detailed direct observation on the behavior of Euglossinae, particularly that within the nest, has been published. Dodson (1966) reported some observations on the behavior of *Eg. ignita*. Bennett observed that behavior of *Eg. cordata* and *Eg. variabilis* by means of special nest boxes, but his results have still only partly be published (1966). In this section all our observations on female behavior of *El. nigrita* are described each topic separately, each followed by discussions and reference to previous information if any. The results involve some social behavior, but the discussions on this topic will be given in the next section.

In our nest of *E. nigrita*, most females left the nest a few days after their emergence. Only three females, emerged on March 24 from Cell 22, on April 1 from Cell 34 and April 5 from Cell 38, (*cf.* Fig. 3B) remained for a long period in the nest. The following observations were mainly made with these females, which were relatively smaller than those abandoned the nest. Henceforth these two types are called respectively major and minor females, the significance of which upon the social organization will be discussed in the next section.

The individual marking, indispensable for precise behavior observations, was not undertaken, in fear of their timidity, exhibited when one female was marked on January before transfering the nest into the laboratory (*3.3.1.*). This defect was partly compensated by certain recognition marks in wings, legs, etc. in some individuals, which made continuous observations possible. One minor female, called *A*, was specially favorable for continuous day to day observations of behavior by the lack of terminal segments of the left antenna by the emergence.

3.1. Intranidal maintenance bahavior and interindividual behavior: At first some intranidal behavior patterns are described, which mainly relate to self-maintenance.

3.1.1. Emergence: The emergence hole is invariably perforated at the upper lateral wall of the cell. The hole is made with mandibles but the application of some buccal secretion for softening the wall is likely, because during the process a small paste like pellet accumulates between mandibles, which is intermittently removed by transverse movements of the head. The exact duration spent for emergence is unknown. One female spent 63 min. to enlange the inicial hole of 2×2 mm sq. up to the size allowing the passage. Another female spent 45 min. for a comparable performance and a third female required 130 min. The perforation of emergence hole is mostly done without help by other adults. But two times we noticed a rudiment of such help. One case is cited: One adult female approached to a cell, from which a young female was just emerging. The former inspected the hole with antennae, then, though during a brief time, only about 30 sec., scraped the margin of the hole with mandibles. The help at emergence is well established in honeybees and stingless bees, and, though more haphazard, in bumblebees (Sakagami and Zucchi 1964). The rudimentary appearance of this trait in *El. nigrita* might be regarded as a case comparable to the "generic" behavior proposed by Haas (1965).

According to Bennett (1965), the emergence hole is made at the top of the cell in *El. terminata*, but at the upper lateral wall when another cell is built above the first one. The emergence through a hole made at the top is also recorded in *Eg. ignita* (Dodson 1966). On the other hand, Myers (1935) observed the emergence from holes made at lateral walls in *El. nigrita*, though the parasite, *Ag. caerulea*, emerged from the top. The emergence hole made laterally seems to be rather a rule, as far as judging from the illustrations of cells after emergence shown by Ducke (1903, *Eg. cordata*, *El. nigrita*), Friese (1930, *El. cingulata*), Friese (1941, *El. meriana*), Sakagami and Michener (1965, *Ep. violacea* and *El. cingulata*), Sakagami (1965 a, *Ep. surinamensis*). A definite exception to this rule is *Ep. nigrescens*, which emerges from the top, apparently conditioned by its peculiar cell structure. The trait to emerge through the lateral hole may become an obstacle to the evolution of comb system. In *El. meriana*, Friese (1941) and *Eg. viridissima* (Friese 1922), both making incomplete combs, the emergence holes seem to be made not so laterally as in other species. Apparently the emergence from the cell top must be a necessary prerequisite for the development of much typical comb system as in honeybees and stingless bees.

Another situation exceptional to the rule is the allodalous nests of *Euplusia* made within the pre-existing narrow burrows (*cf.* Table 2, 3.4. and *1.1.4.*), where the emergence through

lateral holes is difficult just as in case of many other bee groups making alloladous nests. Virtually the males of *Ep. auriceps* observed by us (*cf. 2.3.*) left the cells through the holes made at their tops.

Lucas (1878) supposed that newly emerged adults of *Eg. cordata* might leave cells through the holes made by solving the walls with some exudate. The same assumption was held by Friese (1925) as to *Eg. viridissima*. Although the use of some secretion is suggested in our observation given above, the main effort is certainly achieved through mandibular action. The perforation of hardened resinous wall must be a tedious task for many species. In *Eg. ignita*, the emergence required one to two hours after the bees began to chew through the cell wall (Dodson 1966). In *Ep. nigrescens* with special cell structure, one male emerged after continuous gnawing lasting 3 hrs (Sakagami and Sturm 1965).

Newly emerged audlts possess fully pigmented hair coat, being capable to walk and fly exactly same as in older adults. This lack of *callow stage* contrasts sharply to other three apid groups, the newly emerged adults of which are morpho-physiologically still imperfect. The full functioning of various activities is accomplished a few days after emergence and flight activities much later in honeybees (Sakagami and Maruyama 1956, Sekiguchi and Sakagami 1966) and also in stingless bees. Such callow stage is well known in most higher ants, while relatively inconspicuous in bumblebees (Sakagami and Zucchi 1965), indicating its correlation to the relative height of social evolution.

3.1.2. Self-cleaning: Soon after emergence adults make self-cleaning as in other apid bees. Unlike these groups, however, the duration is very short in *El. nigrita*. Thereafter self-cleaning appears under diverse situations, but less frequently than in other three apid groups. It appears constantly after the return from a foraging trip, carrying either pollen or nesting materials, and lasts 15～40 sec. The sequence is usually as follows : The metasoma is slightly raised and the venter is cleaned by alternative use of hind legs. Thereafter the metasomal dorsum is cleaned in a similar manner. Wings are also cleaned with hind legs. Cleaning of antennae, mandibles and the lower half of the head is followed by using fore legs, but these acts appear less frequently. Otherwise, the behavioral sequence is more or less similar to that in other apid groups. But the synchronous use of mid legs for cleaning the mesosomal dorsum, seen in bumblebees (Sakagami and Zucchi 1965) was not observed. An unusual cleaning posture is reported by Dodson (1966) in *Eg. ignita*, which hang from the ceiling of the cage with mandibles and cleaned themselves using all six legs.

3.1.3. Resting and patrolling: Unlike other apid bees having higher social systems, the time spent for resting is brief in *El. nigrita*. After finishing one task, most individuals make a brief self-cleaning and start patrolling or enter into a new task, usually without resting. Prolonged resting appears only under the following two situations: 1) At night. When cell construction is started by one female at late afternoon, she continues the performance to night (*3.2.3.*). Except for this task, there is usually no activities at night. 2) After intense participation in

outdoor activities. One instances is cited: One female engaged herself in the foraging of cattle feces throughout the forenoon, then she kept the immobility on a cell during 31 min. before starting the next activity.

At resting the head is slightly lowered, mandibles are closed, antennal scapes, wings and legs are tightly in contact to the body (Fig. 10 A). All external movements cease except for rhythmic contraction of metasoma. Resting is made always on a cell, never on the nest floor. When one female possesses a cell just constructed, or in the course of provisioning, she always rests sitting on the orifice or side wall of the cell. With this position, she defends the cell against other individuals approaching nearby (*3.1.4.*).

After resting or finishing one task, female bees frequently wander to and fro within the nest. During this patrolling they often stops the walk for 2～6 sec., keeping the body high on mid and hind legs, raising fore legs and opening and closing mandibles. This posture expresses a weak alertness (Fig. 10 B). It happens frequently when the observation case was opened for cleaning, or observations continued too long. The prolonged wandering is also made by a female attempting to select the site for cell construction, holding the construction material between mandibles.

Observing the behavior of a small colony of *Bombus artatus* Franklin, introduced into an artificial case, Sakagami and Zucchi (1965) were impressed by the sluggish disposition of many individuals. Usually at least one fourth of the inhabitants were in rest without any performance. The presence of numerous "unemployed" individuals is a rule in colonies of ants and honeybees. Sekiguchi and Sakagami (1966) regarded this as one of the important factors for the division of labor among honebyee workers. The continuous activity of *El. nigrita* is sharply contrasting to such laziness, which would develop parallel to the advanced social organization. It would be fruitful to compare the diurnal rhythm of resting-patrolling-task performance among bees at different social steps.

3.1.4. Interindividual relations and defensive behavior: As mentioned at the top of this section, some females abandoned the nest a few days after emergence and three minor females remained for a considerable time. Consequently some observations were made on interindividual relations. They behaved much more independently one another than in bumblebees (Brian 1952, Sakagami and Zucchi 1965). At encounter of two females, they give way for each other. Except for this simple mutual avoidance, no direct communicative acts and regurgitation are noticed. The aggressive disposition is evoked rarely, under the following two situations: 1) When one female approaches to another which is just discharging her loads of construction material at the storing place, or working there with material, the latter stops the task and enters in the alert posture (Fig. 10 B). By further approach of the former bee, the latter inclines the body to the side opposite to the approaching bee, and raises the mid leg. The opponent usually retreats by this alert posture and the former bee returns to her work interrupted.

2) As noted in *3.1.3.*, each brood cells is guarded by the owner, which rests in the night on or near it. When another female approaches the cell, the owner opens her mandibles and occasionally bites the legs or wings of the opponent which retreats without further resistance. Wing buzzing before attack was observed only once and the use of sting for attack never.

Against men the individuals observed by us were extremely timid. Before the transference of the nest into the observation case, foraging activities were observed at the nest site. On January 18 10:21, one female was marked with yellow paint (Fig. 15 A, M and t'). Her subsequent behavior was abnormal during the day, remaining in the nest for a long time or leaving the nest for a long time and returning without load. She recovered her regular activity only on the next day (Fig. 15 B). Such delayed influence of marking is rare in honeybees, stingless bees, bumblebees and halictine bees observed by us. But the timidity could sometimes be inhibited by a habituation, as shown by the indifference of *El. nigrita* nesting in a dining room (Bodkin 1918, *cf. 1.2.*).

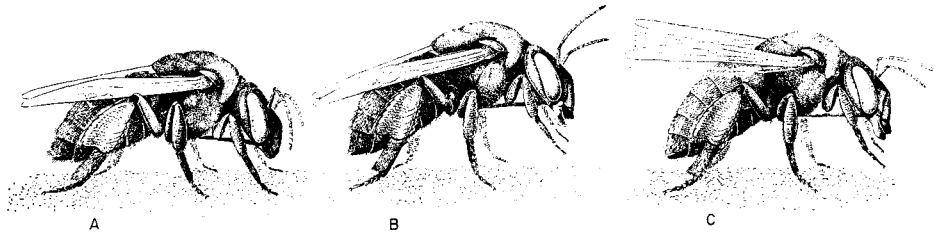

Fig. 10. Three postures taken by females of *El. nigrita* in the nest. A. Resting. B. Weakly alert. C. Mild defense.

When females are disturbed by means of finger, stick, etc., they produce loud and lasting buzzing and open and close the mandibles (=first defensive posture, Fig. 10 C). Holding them with pincette, they cling to the substratum with mandibles but no attack is made. The defensive posture described above, inclination of body and raising of mid leg (=second defensive posture), quite resembles the mild defensive posture observed in bumblebees (Sakagami and Zucchi 1965), suggesting a common phyletic origin. *El. nigrita* does not exhibit, however, the behavior comparable to the strong defensive posture in bumblebees, sitting upside down and assuming a posture with legs, mandibles and sting against the enemy, similar to the posture shown by cornered felid species. Probably this posture developed in bumblebees in connection with the advanced social organization. The absence of any noticeable interindividual relations in *El. nigrita* is impressive. This indicates a possibility of the appearance of a primitive social organization based upon only two prerequisites: Homing to a common place and mere mutual tolerance without advanced interindividual cohesion.

3.2. Building activities: Building activities are divided into two dinstinct

groups: A. Foraging of material and B. Building of brood cells, pillars, etc. In most solitary bees, these two activities usually alternate regularly as ABABAB.. In *El. nigrita* such a chain performance is broken and, as in most social bees, one activity is made rather independently from the other, each with its own rhythm.

3.2.1. Foraging of construction materials: Foraging of construction materials and of larval food are often performed by one and the same individual on the same day (*cf.* Marked bee in Fig. 15 B, which brought in first feces two times, followed by food five times, then again resinous material one time). The nesting materials foraged by our bees were animal feces and resin. The material most abundantly foraged was cattle feces, nextly human feces. Judging from the color and consistency of the loads, the bees seem to frequent the same sources successively. This constancy, comparable to the flower constancy in many bee groups, appears to occur in other species, too. Bennett (1965) located a nest of *El. terminata* by tracing the bees collecting mud from the same place. The other material, resin, was brought in, in total, about one third of the total input of feces. Both feces and resin are carried back deposited on corbiculae. Resinous loads are smaller, about one half of fecal loads and better prepared, being compact and kidney shaped, with strong camphor odor, presumably taken from *Proteum*.

Beside feces and resin, fibers of the seeds of epiphytic Bromeliaceae were occasionally brought in together with two main materials and deposited at the storing place, which was used in common among all foraging females. Later the fibers were used for construction mixed with feces or resin. Probably the fibers were incidentally attached to the resinous material deposited on corbiculae when females visited flowers of Bromeliaceae for nectar intake, just as the admixture of fine rootlets in mud used for construction by *El. terminata* (Bennett). Collecting of mud, repeatedly reported in *Eulaema*, including *El. nigrita* (*cf. 1.3.2.*), was not observed in our nest, although the mud on the floor of the observation case was occasionally mixed with feces and resin at the storing place and used for building.

After returning to the nest, foraging females go straight to the storing place and discharge the loads on corbiculae by alternate scratching by mid legs. Thereafter, they make rapid self-cleaning and usually immediately start the next foraging trip. Resin is left without further manipulation so that a pair of kidney shaped loads are identified for a long time. Fecal loads are pressed to the previous heap by foragers before their departure for the next trip. Mandibles and fore legs are used $8 \sim 10$ times for pressing. Each pressing is accompanied with rapid buzzing, lasting about five sec. This buzzing is produced only by foragers, not by other females working at the storing place. Resin and feces do not form separate deposits, intermingling at the storing place. Further remarks on foraging trips are given in *3.3.1.*

Previous records on foraging of nesting materials are cited. A. *Resin*: *Ep. surinamensis* from Cajû trees (Bates 1863), *Eg. ignita* from Burseraceae, *Ep. surinamensis* from *Spondias dulcis* (Anacardiaceae) (Dodson and Frymire 1961 b), *Spondias purpurea* (Dodson 1966).

B. *Animal faces*: *El. nigrita* (S.F.S. found a female in the collection of Departamento de Zoologia, Secretaria da Agricultura de São Paulo, labelled "from animal excrement"), *El. cingulata* (human feces, Dodson 1966). C. *Mud*: *El. terminata* (Bennett 1965), *El. polychroma* (Ducke 1902 a), *El. meriana* and *El. polyzona* (Vogel 1966). D. *Bark*: *Ep. purpurata* (from Melastomaceae, Ducke 1902 a), *Ep. violacea* (Schrottky 1901, '02, from conifers). While in *Eulaema* mud and animal faces are carried back by trips made independently from resin foraging, *Euplusia* developed an interesting behavior. As cited in the prologue of the present paper, Bates (1863) observed *Ep. surinamensis*, first collecting resin, then adding bark to this sticky matter on corbiculae. The same trait is also observed in *Ep. purpurata* by Ducke (1906) and one of us (S.F.S.) examined some *Euplusia* females in the collection of Prof. Pe. J.S. Moure, CMF, carrying abundant pieces of bark attached to resinous loads on their corbiculae.

3.2.2. Closure of emergence holes and discussion about the reuse of cells: As mentioned in *1.1.3.*, some cells in our nest of *El. nigrita* had each a circular cicatrix (Fig. 3 A), which was the emergence hole closed later. The closure of emergence hole is plastic both in the time at which each female does it and the manner of the performance. It is either made soon after emergence or by older bees. The work is executed either continuously or intermittently, but it is rare that holes remain open for a long time. The material used is the mixture of feces and resin, taken from the storing place on the nest floor. The performance proceeds through the alternation of two phases, collecting of material and working (filling the material and smoothing it) at the hole with mandibles and fore legs. In one instance, in which the task was continuously done by one and the same female, the hole was closed 19 min. after the start of the performance and further six minutes were spent until the final removal of the female. Both reuse of old cells by refurbishing and application of the material from old cells for other building activities were not observed.

The closure of old cells is also reported by Myers (1935) in *El. nigrita*. He found six cells provided with cicatrices similar to those in our nest. He concluded the reuse of cells but his inference is not always definitive. Bennett (1965) assumed such reuse in *El. terminata* without definite evidence. Roberts and Dodson showed a photograph suggesting the probable reuse in *Eg. imperialis*. The definite evidence was obtained by Bennett, who wrote to one of us (S.F.S.) as follows: "I have definitely established that cells are used more than once,—in one instance where a female was parasitized by a conopid emerging female remained in the same box and provisioned the cell from which she emerged". This observation is important because the reuse of old cells, a seemingly simple device and is performed in all social wasps, has arisen in bees only in *Apis* and certain halictine bees (Michener 1964 a, Sakagami and Michener 1962, Michenr and Lange 1958 a, Sakagami and Moure 1967).

In *Euglossa*, which make their cells from resin alone, females often tear apart the material from old cells and use it anew for construction. In *Eg. ignita* (Dodson 1966) and *Eg. melanotricha* (Sakagami, Laroca and Moure 1967 a), old cells were torn down nearly to the bottoms and new cells were constructed above them.

3.2.3. Cell construction: Only three cells were constructed since the transference of the cell cluster into the observation case (Fig. 3 A, N 1–3), but

the behavior sequence is more or less similar in all cases, characterized by its consistency, that is, the majority of the work is performed by a single female since the start to the end nearly continuously and with no help. Other females participate in only at the final phase of the work, by adding resin to the inner wall, smoothing the inner wall and manipulating the cell collar, but always in the absence of the proper owner, which, returning to the cell, violently drives away

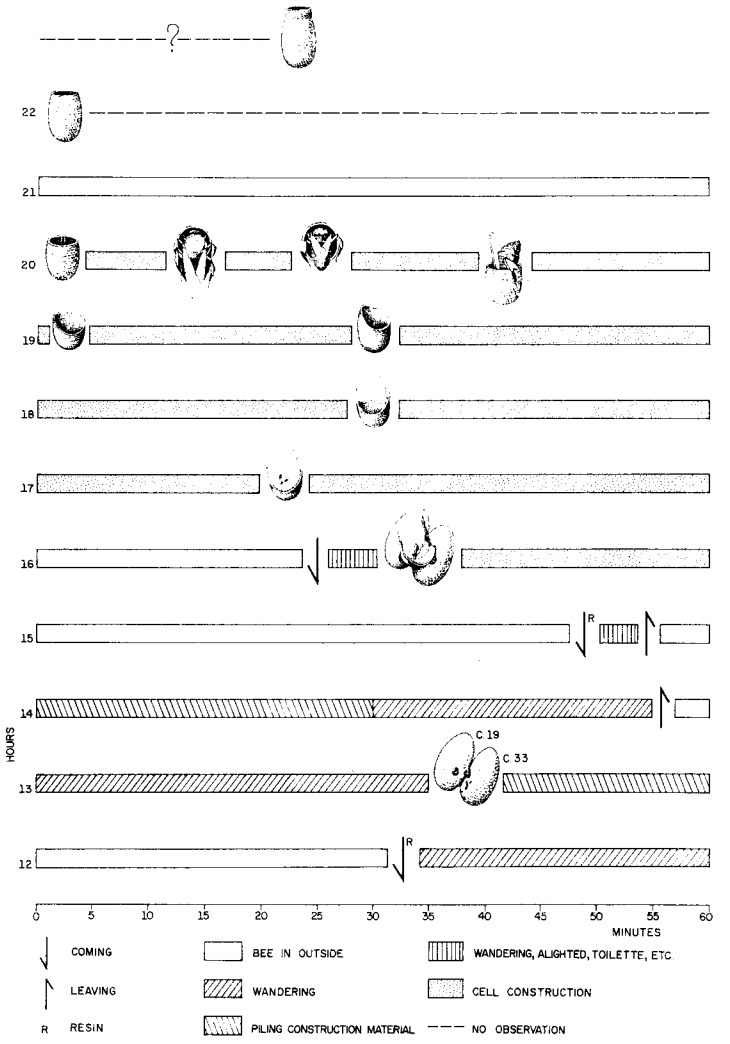

Fig. 11. Chronological sequence of cell construction in *El. nigrita*, observed in a minor female, *A*, on March 29, 1966, intervened by departures and returns, bringing in resin or not (In this and subsequent figures, "construction material" given in legend means feces).

other females.

Fig. 11 illustrates the chronological sequence of the construction of Cell N 1 by the female *A*, on March 29, her sixth day after emergence (*cf.* Fig. 20). In observing this female since 12:00, small deposits of construction material were noticed on the side walls of two cells. Thereafter, her behavior was still inconsistent, making wandering within the nest, self-cleaning and departure and return bringing in resin. After 16:30, however, the work was executed consistently through the alternation of the following phases: A. Working with material heaped at the place where the cell is under construction. B. Wandering. C. Collection of material at the storing place. D. Bringing back material to the cell. A precise sequence of which is partly reproduced in Fig. 12. Since the cell reached more than the half of its final height, the work was mainly made by inserting the fore body into the interior of the cell, three postures of which were shown in Fig. 11. In any case, the material was brought in with mandibles, pressed to the wall with mandibles and fore legs, and distended with mandibles. The construction lasts for a long time, in the case mentioned in Fig. 11, 10 hrs and 5 min. since the first deposition of the material to the end. Fig. 13 reproduces the time required

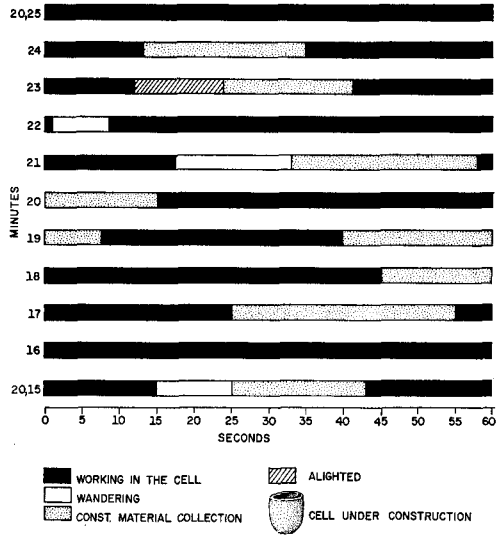

Fig. 12. Chronological sequence of cell construction. Precise record during 10 min., (20 : 15–20:25), showing the alternation of collection of material and construction.

for the completion of one cell, by combining the observations with N1 (A∼H) and N 2 (H∼). The cell ready to receive the larval food is tubular, 2.5 cm long, wider at the lower part (1.6 cm), slightly constricted above (1.1 cm) and provided with the characteristic collar, which is made from nearly pure resin, thick and viscous, with the upper margin serrated and the inner wall smoothed.

Against the process described above, performed continuously by a single female, the final lining of the inner cell wall and preparation of the collar represent a separate phase. Other females also participate in these activities. Moreover the performance is made rather intermittently, during more than one day (Fig. 13), even after the beginning of provisioning.

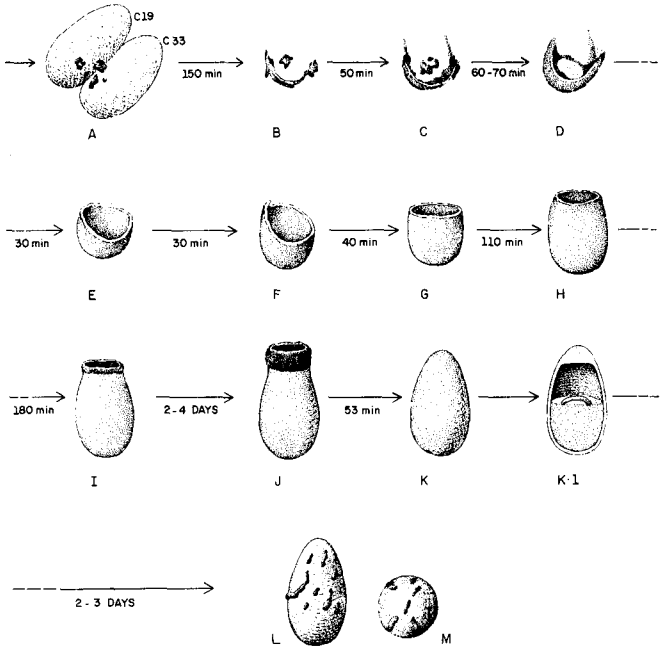

Fig. 13. Time spent for each phase of cell construction in *El. nigrita*.

Up to the present no detailed observation has been published upon the cell construction in Euglossinae. Bennett (1966) observed the behavior of *Eg. cordata* and *Eg. variabilis* directly. But his observations are still not published except for the following note: "Usually each cell is provisioned and sealed before another is started". Probably this is true to *El. nigrita*, if the behavior sequence of each particular female is concerned. As far as our observations go, the manner of cell construction in *El. nigrita* differs from that in other solitary bees making ectostoechal cells in the absence of the strict alternation of foraging of material (*F*) and cell construction (*C*). Material brought in the nest is provisionally deposited at the common storing place and at construction transported (*T*) to the place where the cell is built. Consequently, instead of an alternation of *FCFCFC*... as in many solitary bees, there are two independent series of performance, *FFFFF*... and *TCTCTC* ..., which are either divided among different females or can appear at different times in the same female. However, this seapration is seemingly not always the

rule general to Euglossinae. The alternation of foraging and construction, accompanied with direct application of foraged material would be expected in solitary species and probably in the solitary phase of facultatively social species (*cf.* the next section).

In general the behavior sequence of cell construction closely resembles that of queens and laying workers of bumblebees, especially in the following points: 1) The cell construction is performed since the start to the completion by the continuous work of a single female. 2) The process goes through the alternation of material collection and construction. 3) The participation of other individuals is limited, and only appears in the absence of the proper cell owner (Sahagami and Zucchi 1965). Therefore the cell construction process is sharply contrasting to that in stingless bees and honeybees, in which each cell is made through successive and independent activities of a number of workers (Sakagami, Montenegro and Kerr 1965). On the other hand, the behavior pattern in cell construction resembles that in stingless bees, especially in the insertion of the fore body into the half made cell, the formation of collar and the manner of operculation as described in *3.3.3.*

It was mentioned that the final phase of cell construction, lining of inner wall and preparation of the collar forms a separate part. These activities are made intermittently even during the provisioning. This synchronous performance of provisioning and cell construction seems to occur in a more exaggerated manner in some species of *Euglossa*. Janvier (1955) writes that *Eg. piliventris* starts the provisioning when about three fourth of the cell is completed. Dodson (1966) notes that *Eg. ignita* provisions the cell as it is being constructed. One might homologize this trait to the final phase of cell construction in *El. nigrita*, because *Euglossa* uses only resin for building. But Sakagami (1965 a) found a cell of *Ep. violascens* still half built but already filled with larval food. Consequently, the cell construction in Euglossinae seems to be quite variable among groups, the separation of material foraging and construction on one hand, and synchronous execution of construction and provisioning on the other hand. These two extremes deviate markedly from the stereotypy found in most ectostoechal solitary bees.

3.2.3. Other building activities: The operculation of the cell which received an egg is described in *3.3.3.* As described in *1.1.3.* operculated cells of *Eg. nigrita* were provided with longitudinal keels. In cells newly made within the observation case, these keels were added to successively during 2～3 days after operculation (Fig. 13). This task is not performed as a continuous work by a single female, but by several females of different ages. Even females soon after emergence participate in it, after a brief post-emergence self-cleaning. The work is made with the highest consistency and intensity in afternoon, after the cessation of flight activities, continuing to 19～22:00, that is, when only cell construction is the activity seen in the nest. The female takes a small piece of material from the storing place, then wanders within the nest, holding the material in mandibles and puts it on the wall of the cell. The presence of this deposit seems to release the further addition of material, resulting in the formation of a longitudinal keel.

The reinforcement of pillars is also made by any females. The work is not

consistent as in cell construction. One female may interrupt the work midway and another may succeed the position, just as in the cell construction in stingless bees (Sakagami, Montenegro and Kerr 1965) and building activities other than cell construction in bumblebees (Sakagami and Zucchi 1965).

Dodson (1966) put nests of *Eg. ignita* in a cage and observed the behavior of emerged bees. Females dismantled old cells and worked resin into crevices of the film boxes into which the nests had been placed. This is virtually the unique direct observation so far made on building activities of Euglossinae.

3.3. Provisioning, oviposition and cell operculation: The final part of the female behavior in *El. nigrita* deals with the core of brood rearing activities. The amount of observations is insufficent but enough to show the qualitative aspect of this important behavior.

3.3.1. Flight activities: At first some comments on flight activities in general, including foraging of both larval food and construction materials, are given, mainly based upon full day observations made on January 18 and 19 at the nest site before the transference of the cell cluster into the observation case (Fig. 15). During this period at least three females participated in foraging, but only one female was found when the nest was excavated on February 10.

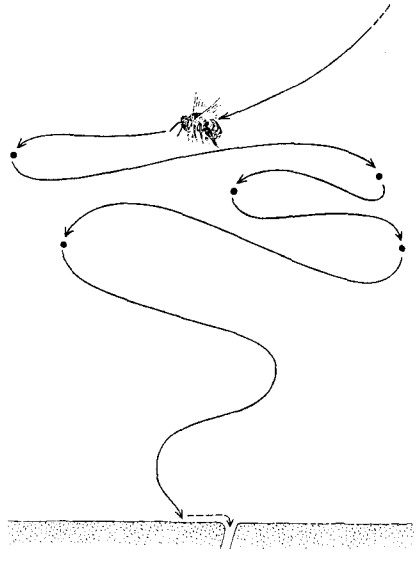

Fig. 14. Orientation flight of a female of *El. nigrita* returned from a trip.

The behavior of returning bees is more or less similar in all cases. They stop at the height of 30~40 cm and make circular flights of about 50 cm in the maximum diameter, during 3~10 sec., then swiftly descend, land at the point about 5~10 cm apart from the entrance and walk to the entrance (Fig. 14). The

departure from the nest is simpler. After a loud buzzing, females appear at the entrance and immediately ascends to the height of ca. 50 cm, where they make a brief orientation flight for 1～3 sec., directing the head to the entrance, then disappear. When disturbed, the female faces toward the source of the disturbance at each turning point of circular flights. At each "facing toward", the bee lowers for a moment, then again begins to ascend.

As seen in Fig. 15, flight activities are not particularly affected by air temperature and insolation. It is interesting, however, that all three females returned without bringing loads before rain (Fig. 15 A, 17–18:00). One female marked on January 18 (Fig. 15, M and ⌊′) did not return to the nest in the evening of January 19, and the numbers of departures and returns on two days do not correspond for each other. Certainly females occasionally spent the night out of the nest, as known in bumblebees (*cf.* Sakagami and Zucchi 1965), being a trait very rare in stingless bees and honeybees. But Dodson (1966) confirmed the presence of

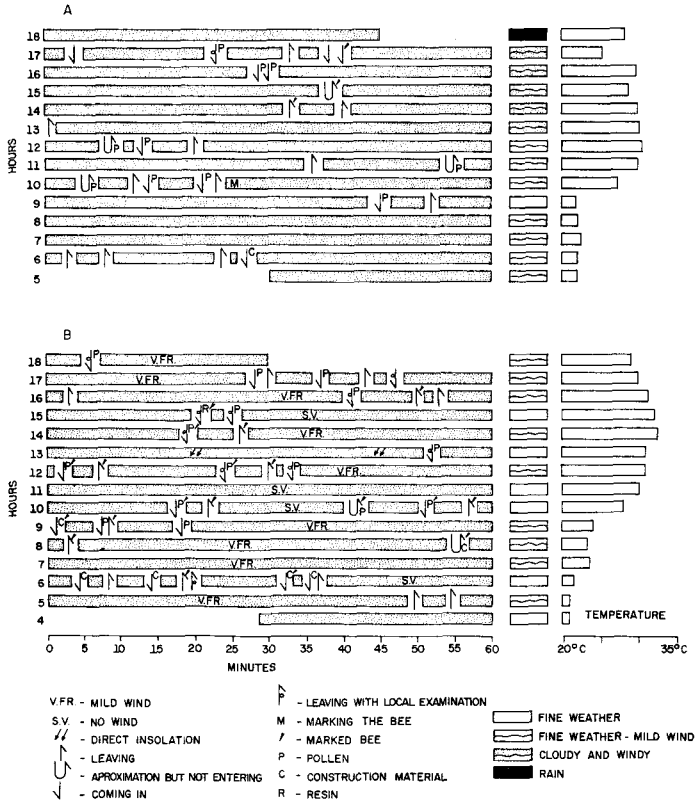

Fig. 15. Full day observations on flight activities of *El. nigrita* at nest site on January 18 (A) and 19 (B).

occupants in each nest of *Eg. ignita* by regular night check.

From the records of the marked female, the mean duration of a single trip was calculated as 52.5 min. Eack foraging trip for larval food lasted 17～109 min (*m.* 56.3 min.) and for construction materal 17.5～58 min. (*m.* 44.5 min.). Within 810 min. of the total observation time, the marked female made five returns with larval food and three with construction material, spending about 64.2% (=520.5 min.) out of the nest. Throughout the observation no guard bee was found at the entrance and no bee left the nest to throw away the refuse matters.

Some previous records concerning flight activities of Euglossinae are summarized. All euglossine bees are excellent fliers, especially by their fascinating ability to hover. Some large species of *Eulaema*, notably *El. meriana*, the largest species (cf. Plate IV-A-27) flies slower, with louder buzzing. They are also presumably strong fliers. Dodson (1962 b) notes that some species could be captured in the Ecuadorian Andes on sunny warm days at more than 10,000 ft above the sea level. Probably they do not nest at such height, only ascending from deep canyons governed by tropical climate.

Few precise records exist on diurnal activities. In general flight activities seem to be intense in morning than in afternoon but not so conspicuously as in many other bees. Schrottky (1901) notes flight activities mainly during 9-15:00 but, though less intensively, seen to 18:00. According to Ducke (1901) flight activities are intense in Belém and the vicinity during 6:00-13:00 but females are seen still at later hours. He also notes that flower visits are observed only to the noon, while foraging of nesting materials to afternoon. Dodson (1966) also found females of *Ep. surinamensis* on *Thevetia* at any hours and flight activities of *El. cingulata* from dawn to dusk. Orchid visits of males of some species (*6.2.2.*) are observed often at early morning, and there seems to occur certain specific difference, *El. cingulata* and *El. meriana* mostly during 6-9:00, never after 10:00 while *Eg. cordata* to the noon (Ducke 1901). The influence of weather conditions upon flight activities is little studied. Ducke (1901) observed visits of *El. cingulata* and *El. meriana* to *Catasetum macrocarpum* under "herrschendem Landregen". Dodson (1966) notes that flight activities of females of *El. cingulata* are not inhibited by light rain. Vogel (1966) recently recorded some fragmentary but interesting notes on extranidal behavior of certain species : *Eg. cordata*, licking of human sweat; *Exaerete smaragdina* (♀), Sleeping in holding the leaf margin in mandibles as practiced in many other Aculeata; *Eg. chalybeata*, Ripening of nectar by rhythmic movements of tongue as in honeybee workers, accompanied with fanning.

The absence of the removal of refuse matters is suggested in other species by the presence of carcasses within the nest. Ducke (1903) detected in a nest of *El. nigrita* two carcasses incorporated in the nest wall and noted that this was frequently seen in large nests of *Eg. cordata*. The presence of carcasses is mentioned in various species: *Eg. ignita* (Dodson 1966), *Eg. viridissima* (Friese 1922), *Eg. cordata* (Ferreira MS), *Eg. imperialis* (Roberts and Dodson 1967), *Eg. melanotricha* (Sakagami, Laroca and Moure 1967 a), *El. nigrita* (Myers 1935, Zucchi *et al. cf. 1.1.1.*), *El. terminata* (Bennett 1965). This fact is interesting in comparison with the cleaning behavior of other apid groups. Bumblebees occasinally throw away the deads from the nest. Honeybees and stingless bees make this but with group differences. While most stingless bees drop the refuse matters after carrying away from the nest entrance, *Hypotrigona* and *Lestrimelitta* throw at the nest entrance. The European honeybee, *Apis mellifera* has a developed cleaning trait but the Asiatic sister, *A. cerana*, has not, resulting in the accumulation of debris on the hive floor (Sakagami 1960).

3.3.2. Provisioning (*cf.* Pl. V): In our nest of *El. nigrita*, foraging of larval food

appeared only when one or more cells ready to be provisioned were present. The behavior sequence of food discharge into the cell is illustrated in Fig. 16. The loads are well prepared, kidney-shaped as resin loads, consisting of pollen with abundant mixture of nectar. The female returned from the trip (Fig. 15 A) wanders the nest floor and goes to the cell. After a brief inspection (B), she turns and inserts the body from the metasomal tip deeply into the cell, showing only the head (C). This posture continues for 60～80 sec., intervened by rotation (D). After leaving the cell, already without loads, she again inserts the body into the cell from the head (E～F), apparently to press the food mass, followed by the final withdrawal, self-cleaning (G) and often the immediate departure for the next trip. The food loads on corbiculae are soft and paste like, not hard and dry as in other bees, both social and solitary. Furthermore, no contraction of the metasoma is observed at pressing of food. The nectar is presumably mixed with pollen already during the trip, not at provisioning as in other solitary bees.

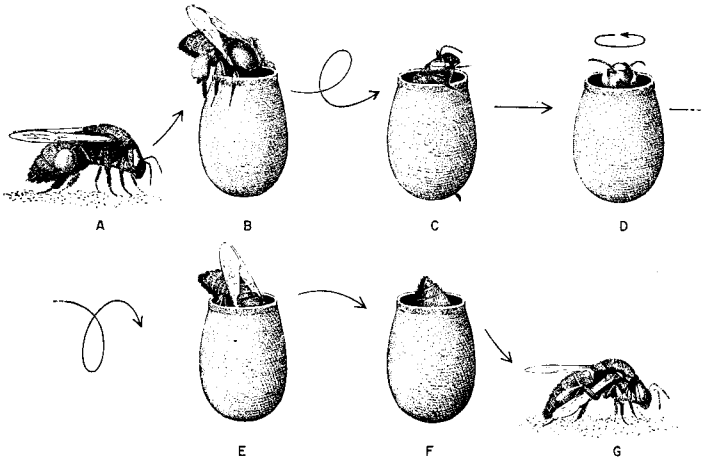

Fig. 16. Behavior sequence of food discharge to a cell by a female returning from a foraging trip.

Fig. 17 presents the process of provisioning in two cells, Nos. N 1 and N 2. In all three cells, provisioning was made by minor females and lasted several days. Provisioning is intervened, as already mentioned, by one or more returns with resin loads and lining of inner cell wall or improvement of cell collar (Fig. 17, Cell 1). The improvement of inner cell wall is also made briefly before departure but rather intensely in the evening. Cell N 1 was provisioned exclusively by a single female, *A*, the cell owner, but in Cells N 2 and N 3 other minor females participated in provisioning. By night, the cell owner sometimes does not ruturn (Fig. 17, Cell 1, April 2). But if present, she sits on or near the cell and guards it against other females (*cf*, *3.1.4.*). The quantity of larval food in two cells is as follows:

Cell	Height of larval food	Number of trips	Weight of larval food	Calculated larval food per trip
N 1	1.4 cm	8	1.05 gr	0.132 gr
N 2	〃	〃	1.34	0.17

The amount per single trip is about 5～10 times heavier than the pollen load (8～22 mg Maurizio 1953) and 2～3 times than the nectar load (average 40 mg, max. 70 mg, Fukuda, Sekiguchi and Moriya 1969) carried back by a single trip by a honeybee worker. Probably the real amount is larger because a part of larval food was taken from the cell and consumed by other females in the absence of the provisioner.

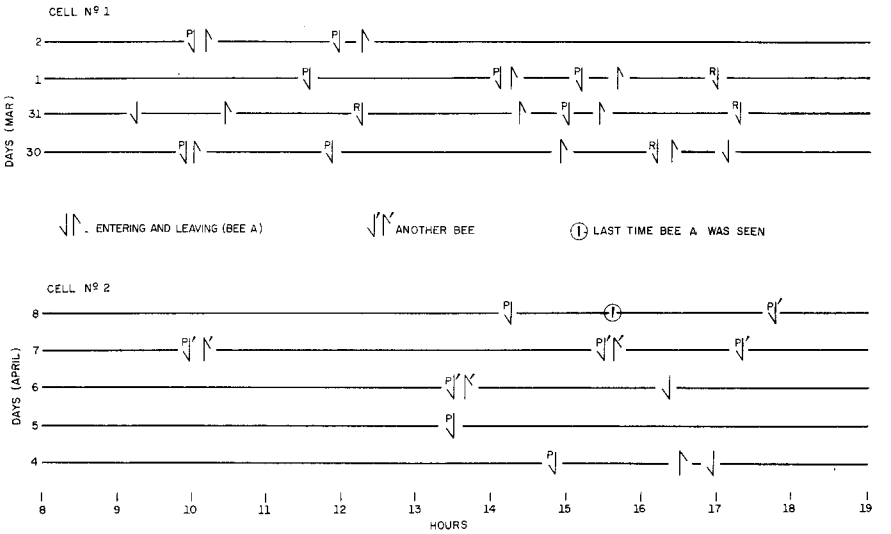

Fig. 17. Chronological sequence of provisioning in Cells N–1 and N–2.

No direct observation on the provisioning in Euglossinae has so far been published, except for a brief note by Janvier (1955), who wrote that about 20 trips were made to provision one cell in *Eg. piliventris*. Viscous, paste like nature of larval food, with a scanty mixture of pollen, is common to all closely observed species: *Eg. cordata* (Ducke 1901, Schulz 1902), *Eg. piliventris* (Janvier 1955), *Eg. dodsoni*, *Eg. hemichlora*, *Eg. ignita*, *El. cingulata* (Dodson 1966), *Eg. imperialis* (Roberts and Dodson 1967), *Eg. melanotricha* Sakagami, Laroca and Moure 1967 a), *Ep. surinamensis* (Ducke 1902 b), Bodkin 1918, Sakagami 1965 a), *Ep. violascens* (Sakagami 1965 a), *El. nigrita* (Ducke 1903, Myers 1935).

3.3.3. Oviposition and operculation: Oviposition and operculation were observed only once, with Cell N 3 on April 12. Fig. 18 reproduces the behavior sequence chronologically. The pre-oviposition behavior began with the improvement of cell collar. At this phase, the collar was thick and short, which were

gradually lengthened through further manipulation (Fig. 18. A→I). The female showed a marked excitement, repeatedly inserting the metasoma or head (B, E) in the cell or worked at the collar (C,D) aften rotating the body around the cell axis. At the insertion of the head, rhythmic openings of genital orifice was noticed several times, two of which synchronized with strong metasomal contractions, by which a transparent fluid was ejected (Fig. 21, F). Judging from the large size of the egg (*cf. 2.3.*), this fluid seems to act as a lubricant for oviposition. Soon before oviposition, the height of the collar attained to 0.4 cm, and the diameter of the cell orifice, ca 1.1 cm at provisioning, was constricted to 0.8 cm (Fig. 21, I). The oviposition (J), confirmed only by the metasomal contraction, lasted 29 sec.

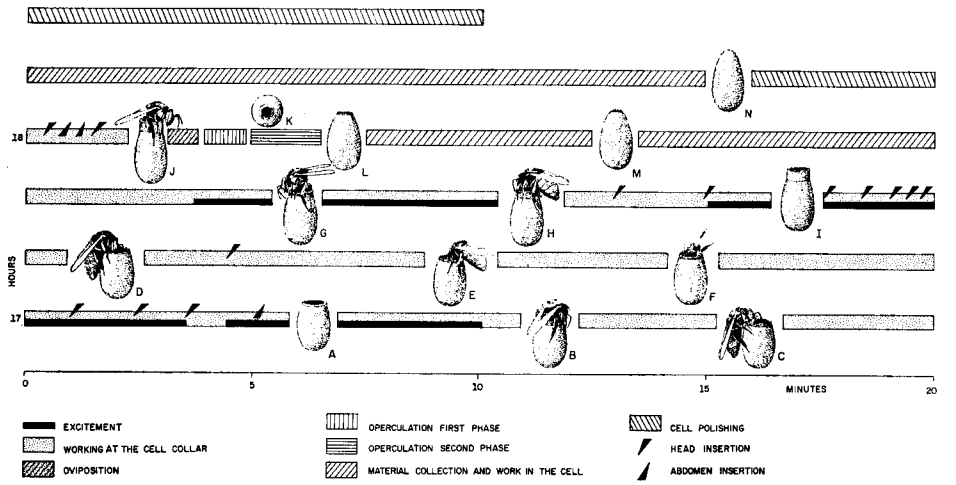

Fig. 18. Chronological sequence of poviposition and operculation in *El. nigrita.*

The operculaton began soon sfter the oviposition, divided into three phases: 1) Rotation phase (50 sec.). Inserting the metasoma into the cell and rotating the body on cell, the female closes the orifice by bending the collar inwardly with mandibles and fore legs. 2) Side work phase (125 sec.). The metasoma is withdrawn and the orifice, narrowed to 3 mm (Fig. 18 K), is closed by pressing the collar with mandibles. 3) Improvement phase (42 min.) The female so far stayed on the cell top begins to collect the material. The bright brown operculum made from pure resin becomes gradually inconspicuous, coated by the material consisting of feces and resin, and is polished externally.

As far as the behavior sequence is concerned, both cell construction and oviposition processes in *El. nigrita* quite resemble those in bumblebee queens (*cf. 3.2.3.* and Sakagami and Zucchi 1965), both performed as a continuous activity by a singl female. The difference is that in *El. nigrita* the two processes are separated by provisioning which continues for several days while in bumblebees

they form a single continuous sequence. On the other hand, the behavior patterns of oviposition and operculation differ from those in bumblebees, rather resembling stingless bees, especially in the succession of rotation and sidework phases and the performance with metasomal insertion. It is open to the question whether this behavioral resemblance bears any phyletic significance or means a mere parallel evolution. The long duration of oviposition porbably correlates to the large egg size. In stingless bees, too, the genus *Melipona* is characterized by the large eggs and long duration of oviposition (Iwata and Sakagami 1966, Sakagami, Montenegro and Kerr 1965).

3.4. Behavioral differences between major and minor females: As mentioned at the top of this section, the females emerged in the observation case were divided into two size groups: most were relatively large while three distinctly smaller. The behavior patterns did not differ but the behavior inventory showed a remarkable difference between these major and minor females. Leaving the discussion of its functional significance in the next section, here is given the result of our observations.

3.4.1. Size and behavior differences: The size difference was easily recognized but the precise measurement (of distance between outer extremities of tegulae) was made only with two females in each group. The female discovered at nest excavation, with heavily worn wings and mandibles, was also measured.

Individual	Mesosomal width (in mm)	
	Minor females	Major females
1	7.66 (the old female)	8.33
2	7.83	8.59
3	7.74	

The essential behavioral difference between two groups is that major females left the nest a few days after emergence while minor ones remained for a long time, The difference in the performance of various tasks between two groups are summarized as follows:

Behavior or task	Minor females	Major females
Foraging of larval food	⫴	−
Cell construction	+	−
Oviposition	+	−
Foraging of resin	⫲	±
Closure of emergence hole	⫲	+
Help at emergence	+	+
Deposition of construction material on cell, transporting it from the storing place	+	⫲
Cell cleaning	+	⫲
Foraging of feces	+	⫴

The frequency of performance was given arbitrarily. As the number of major females was superior to that of minor ones, their contributions might be overesti-

mated. Nevertheless we can notice an important difference. Cell construction, provisioning and oviposition, that is, the essential parts of brood rearing activities, are exclusively made by minor females. Major females did not forage much resin, and inner duties performed by them are mostly of secondary importance, not belonging to the type made continuously and consistently as cell construction. Therefore, the essential part of the maintenance of the nest was executed by minor females. The main role of major females must be played after their dispersal from the nest.

In bumblebees, too, small workers tend to remain in nests and start their flight activities later,or did not make them ultimately (Sakagami and Zucchi 1965). This tendency, smaller workers tending more or less to inner duties, whereas larger ones more to outer duties, seems to be common in many social insects (Pardi 1950). It is noteworthy that a parallel case was found in *El. nigrita*, still with no castes.

3.4.2. Life history of major females: Some major females leave the nest soon after emergence. Others stay a few days in the nest. The behavior does not markedly differ among individuals, so that observations on one particular individual, stayed relatively long in the nest, is cited:

April 6. 9:30. Start of emergence. 10:40. Emergence. 12:00. Self-cleaning.13:00. Wandering on nest floor. 14:00. Resting on cell. 14:30~16:00. Various intranidal activities of minor importance. 16:10. Departure.

April 7. Closer observations are given in Fig. 19. During 9~11:00 she participated energetically in foraging of feces (eight times) and resin (once), with the duration of trips 28.5 sec.~5 min. (*m.* 31 sec.). Thereafter she rested at the side of a cell during 18

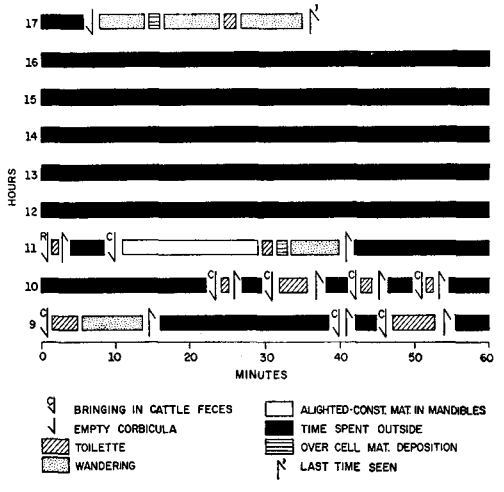

Fig. 19. Chronological sequence of the behavior of a major female on April 7, the day after emergence.

min., keeping a fecal piece in mandibles (given in Fig. 19 "Alighted-Constr. Mat. in Mandibles"). After awaking from this akinetic state, she put the material on a cell and made a small construct of unknown significance. She departed from the nest at 11:42 and after a long absence returned at 17:05. Then she wandered to and fro in the nest, with intervention of self-cleaning and transport of a fecal piece from the storing place to a cell. At 17:36 she again flew away and never returned thereafter.

These observations suggest a weaker cohesion to the nest of major females than minor ones. The first flight was made already at 4.5 hrs after emergence, far earlier than in minor females, and did not return until the next day. The activities seen in Fig. 19 are sporadic, accompanied with rather ambiguous transport of construction material, which is assumed to be the incipient appearance of still not matured construction behavior. The similar trend was, even though not systematically observed, noticed in other major females, too.

By the return of the female mentioned above at 17: 05, her final metasomal segment was half open, and she touched upon there several times with hind legs. This probably indicates the mating, distinctly earlier than in other apid groups (*Bombus atratus*, 3∼5 days after emergence, *Melipona quadrifasciata* 4∼8 days, *Apis mellifera* 5∼6 days, Zucchi unpub.). The mating behavior and related problems are discussed in *6.3.*

3.4.3. Life history of minor females: As already mentioned, many if not all important tasks were mainly performed by three minor females. Their life history, represented by the individual *A*, is cited herewith. This female was not found until 23:00, March 23, so that seemingly emerged on March 24, early morning. Her behavior until the first flight was recorded as follows:

March 24. 8:00. Walking on cells; 8:30. Ditto; 9:10. Closing of the own emergence hole; 9:35. Ditto, but stopped the work and began to close another emergence hole; 9:45. Ditto; 10:40. Ditto; Closed completely; 11:00. Restarting the closure of the own emergence hole; 11:45. Wandering in the nest; 11:47. Again closing the own hole; 11:35. Ditto; 12:28. Closed completely; 13:00∼17:45. Resting, wandering, self-cleaning, etc., always within the nest; 18:00. Resting on the cell cluster; 20:00. Ditto.

March 25 (Fig. 20). 8:00. Absent; 9:25. Return with resin.

March 26∼28 (Fig. 20). During these days, she closed two other emergence holes, repaired pillars (*cf. 3.2.4.*), removed the remain of fungus coat on cells, (*cf.* Pl. V) and made several departures from the nest, bringing in resin or not.

March 29. After performing various intranidal tasks, she started cell construction (*cf. 3.2.3*, Fig. 11).

March 30∼April 2. Provisioning of the cell (Fig. 17, Cell N–1).

April 3. Construction of Cell N 2 and provisioning.

April 4∼8. Provisioning of Cell N 2 (Fig. 17, No. 2). But her provisioning activity became slower, the time spent out of the nest became longer, and provisioning was principally made by another minor female. After April 8, 15:32, the female *A* was no more seen in the nest. If she died then, her adult life is 16 days, which is shorter than the longevity known in other species, unless her death was incidental, or she made a second nest.

Only Dodson (1966) records the longevity of female euglossine bees. As to *Eg. ignita* he writes:" 1) A female ceases to work constructing new cells after about 45 days and

maintains then nest until her death. 2) No precise data on longevity was obtained however most seemed to die after about 60 days under natural conditions. 3) Captive females (kept in small screen cages, 2 ft × 1ft × 1 ft) generally lived for 30 to 60 days.

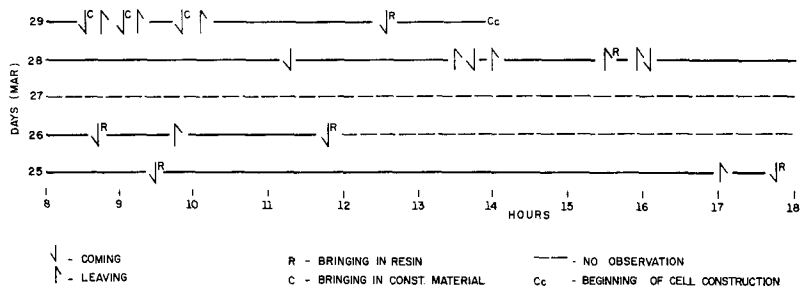

Fig. 20. Behavior sequence of a minor female, *A*, since the day after emergence to the start of cell construction.

4. Social organization

The observations presented in the preceding section, especially those in *3.4.* tell that *El. nigrita* is not a simple solitary species, possessing a sociality however incipient in nature. Few previous records on euglossine biology involve direct observations of behavior. But some casual observations indicate such incipient sociality by the presence of, 1) many cells in a nest, hardly interpreted as the product of a single female, or 2) more than one female in a nest. These records are compiled and discussed in this section, with reference to our own observations given above.

4.1. Solitary life: Here the solitary life is defined as the preparation of one nest or more by a lone adult female, or the mother. The subsequent life history may be variable as follows: 1) The mother dies before or soon after emergence of her daughters. All daughters leave the nest and each of them repeats the life cycle passed through by the mother. Or, one of the daughters succeeds the mother's nest. She and other dispersed sisters behave as the mother did. 2) The mother survives after emergence of her daughters, forming a matrifilial association. Or, the mother dies but more than one daughter remain in the nest, forming a sororal association. In the first case the solitary life is inherent to the specific life pattern, whereas in the latter, it represents the initial phase of the ontogeny leading to a more complicated mode of life. Except for honeybees, stingless bees and some tropical vespid wasps, all so-called social insects pass this solitary phase, at last facultatively, at the start of their life pattern (replaced by a pair instead of a single female in termites).

In the absence of direct observations of nesting behavior, the solitary life is expected when, 1) only one female occurs in the nest and 2) the number of cells in the nest is small. The reduction of the number of progeny in parallel with the

Table 4. Records of presumably solitary nests in Euglossinae

Case	Species and author	Conditions and remarks
1.	*Eg. cordata* (Ducke '03)	Illustration of a nest with 5～6 cells
2.	〃 (Bennett '66)	One nest with 9 cells by 1 ♀, another 13 by 1 ♀. In both, succession of the mother's nest is directly observed
3.	〃 (*cf. 1.1.5.*)	At least 3 cells
4.	〃 (Ferreira MS)	Three old nests, each with 13, 18, 28 cells
5.	*Eg.* "*cordata*" (Friese 1899)	Aerial nest, probably not made by *cordata* (*1.4.1.*), 5 adults emerged (=5 cells)
6.	〃 (Schulz '02)	Aerial nest as in above, 3 cells with 1 ♀
7.	*Eg. dodsoni* (Dodson '66)	8～10 cells per nest, each nest with 1 ♀, distinctly solitary species
8.	*Eg. hemichlora* ('')	With 1 ♀
9.	*Eg. piliventris* (Janvier '55)	8 cells, probably made by 1 ♀, judging from description
10.	*Eg. intersecta* (Dodson '66)	Incipient nest with 1 ♀, still no cell
11.	*Eg. ignita* (Roberts & Dodson '67)	Four nests, 17 cells with 1 ♀, 18 with 1 ♀ ?, 22 with with 1 ♀, 25 cells with 1 ♀. Details in text and in *4.3.*
12.	*Ep. violascens* (Sakagami '65a)	1 cell with 1 ♀
13.	*Ep. nigrescens* (Sakagami & Sturm '65)	1～12 cells per nest
14.	*Ep. auriceps* (*cf. 1.1.4.*)	4 cells with 1 ♀
15.	*El. meriana* (Dodson '66)	2 cells with 1 ♀
16.	*El. cingulata* ('')	4 cells with 1 ♀
17.	〃 (Sakagami & Michener '65)	7 cells with 1 ♀

increased maternal care is a rule in animals. According to Dodson (1966), a single female of *Eg. ignita* makes 9～15 cells in her life time. The nests containing equal to, or less than these figures could tentatively be regarded as cared by a lone female. The previous records fulfilling such condition are summarized in Table 4. Unless particularly mentioned, each record deals with a single nest.

Not all of these records may indicate the obligatory solitary life. The succession of old nests by the progeny is likely to occur. In the second nest in Case 2 (Bennett 1966), the nest owners are traced to the third generation. In such instance, the female found in the nest could not necessarily be regarded as the mother who made the cells found in the nest. Instead it is plausible that she is a newly emerged daughter. If such would be the case, there is no reason to deny the appearance of the nest with pleural females, by subsequent emergence of younger sisters and their stay in the nest. Virtually Dodson (1966) records the stay of a second newly emerged female in an initially solitary nest of *Eg. ignita*. Only the examinations of cell contents and ovarian and spermathecal conditions of adults can bring a definite conclusion. All four nests of *Eg. ignita* observed by Dodson (*cf.* Roberts and Dodson 1967) contained no egg and three of them some pupae or

old cells. It is conceivable that these nests do not represent the solitary nidification but the work made by the preceding generation, probably made solitarily. Unfortunately such exact observations are scarce in other instances. However, most of them could be assumed as the product by a solitary foundress, because the remain of old cells are not particularly mentioned.

Thus the presence of the solitary life in Euglossinae is evident. But this does not mean all cited species possess the obligatory solitary life pattern. Contrarily, the more complicated life is recorded in *Eg. hemichlora* (?), *Eg. intersecta*, *Eg. ignita*, *El. meriana* and *El. cingulata* as referred to in *4.3.* In these species the life pattern can be started solitarily but circumstantially can develop further steps.

Among other species, most *Euplusia* seem to be solitary. But this genus has a tendency to form aggregations as given in *4.2.* In *Euglossa*, *Eg. dodsoni* is recorded as solitary. Probably the other species of *Euglossa* making aerial nests are also solitary (Cases 5 and 6 in Table 4). In these species their trait to make the outside envelope (*1.3.1.*), certainly a secondary acquisition (*1.4.*), may inhibit further development of the social pattern by spatial limitation. Similar antagonism between architectural and social evolutions is also suggested in the Indomalayan stenogasterine wasps. For instance, *Eustenogaster* is usually solitary, probably in part for their elaborate nest envelope, whereas many species of *Parischnogaster*, making nests without envelope, are nonsolitary (Yoshikawa, Ohgushi and Sakagami 1969). The comb formation developed by halictine species of carinate *Evylaeus* seems to disappear in certain species with developed social system (Sakagami and Hayashida 1968). There is no definite evidence upon the presence of obligatory solitary species among other species of *Euglossa* and *Eulaema* making their nests in concealed cavities. Some species, which have a strong preference for narrow spaces, could principally be solitary, but further accumulation of observations, even if fragmentary, is needed to enrich our knowledge on this aspect.

4.2. Aggregations in Euplusia: The term *aggregation* is used in bees when many nests are made independently but in contiguity, irrespective of each nest is either lonely cared or not. This tendency is widespread in burrowing bees. In bees which do not excavate in substrata for nidification, however, aggregations are common in those making their nests at exposed or semi-exposed sites, not in more or less closed cavities, obviously in part conditioned by the availability of favorable sites. In Euglossinae, too, aggregations are reported only in *Euplusia*, which often make nests at relatively exposed sites. (*cf. 1.2.*).

Möbius (1856) illustrates about eight tubular cell series of *Ep. surinamensis*, closely intermingling one another. Dodson and Frymire (1961 b) note that females of the same species work independently but nesting alongside, forming a colony consisting of up to 20 females. Although the synchronous work of several females is not directly observed, the large nest masses are known in some other species. Sakagami and Michener (1965) records a complicated nest mass of *Ep. violacea*, with

some 60 cells. Sakagami and Sturm (1965) illustrates a large nest mass of *Ep. nigrescens*, which contains 21 cells made upon another mass of old cells, thus, in total consisting of at least 40 cells. In these cases the number of cells involved is too large to be regarded as the product of a single female. But cell contents are not examined, so that it is uncertain whether the masses were made by several females synchronously or successively, though the first situation is not always unlikely.

As already mentioned an aggregation does not necessarily postulate the interference among individual nest owners. Such indifference is easily maintained in burrowing bees, in which each nest is distinctly independent, separated by substratum, and possessing its own entrance. In some groups, called communal by Michener (1969), several females share the entrance canal. Even in this case, the independence of each female is usually maintained, each making and provisioning her own cells made in her "particular" canal. The circumstance is different in bees forming exposed or semi-exposed nests. Here each female may work in closer contact with others, because they are not separated by substratum. The distinction between aggregation and communal mode of life disappears in these bees. Nautrally the activity of each bee may fundamentally be independent, as stressed in the classical example of *Chalicodoma* by Fabre (1882). However, it is not excluded that here is a possible start of an advanced social cohesion. In the nest mass of *Ep. violacea*, the cell series probably made by different females intermingled one another, without showing definite spatial separation. Under such circumstance, the partial superposition of the work of each female is not always excluded. Deleurance (1949) observes an aggregation of three females of a megachilid bee, *Osmia emarginata* Lepeletier, participating in the construction of one and the same cell, showing the facultative appearance of *quasisocial* state (Michener 1969, *cf. 4.5.1.*) in this ordinarily solitary species.

On the other hand, we already mentioned that females of *El. nigrita* defend their own cells against other females (*cf. 3.1.4.*), which implied the remnant of the behavior expressed by bees forming aggregations against the invasion of neighbours. But it was also confirmed that their living together involved something more than a mere co-existence of several individuals without cooperation. There would be no reason to deny the appearance of a similar cooperation, however rudimentary and facultative, in some species of *Euplusia* making a *superaggregation*, a composite nest mass, the difference of which from nest masses of some *Euglossa* and *Eulaema* depends ultimately only on the nature of nest sites, either made in exposed situations or in more or less closed cavities.

4.3. Presence of more than one female in the same nest in Euglossa and Eulaema:

Here we deal with one of the most interesting aspects of euglossine biology, the presence of more than one female in the same nest or the evidence which suggests it — a large number of cells in the nest. The previous informantion is given in Table 5 (Abbreviations: O. Old cells; O'. Very old cells; Em. Cells from

Table 5. Records of nests presumably cared by more than one females in Euglossinae (Explanations in text)

Case Species	Author	Numbers of cells and (females)	Remarks
1. *Eg. cordata*	Lucas 1878	25 (12 adults)	Not mentioned whether adults emerged from the cells or they made them. Probably the first assumption more likely
2. *Eg. analis*	Bodkin '18	....	A large subterranean nest with many cells
3. *Eg. viridissima*	Friese '22	ca. 21	From illustration. Presumably a nest made solitarily
4. *Eg.* ref. *cordata*	Nogueira-Neto unpublished	(6∼10)	These females working in the same nest (*cf.* Table 2, 2.3.)
5. *Eg. hemichlora*	Dodson '66	21 (2)	Originally two independent nests fused at collecting ? 14 O+7 Em.
*6. *Eg.melanotricha* (Three cases)	Sakagami, Laroca & Moure '67a	64 (2)	Divided in two clusters, but certainly each not cared by one female. 25 O', 9 O, 8 P, 11 Pr, 6 L, 1 E, 1 N, 3 M
*7. *Eg. ignita* (Three cases)	Roberts and Dodson '67	a 52 (5) b 39±(2) c 34±(5)	41 O, 4 L∼P, 4 L+E 3 N 13 ± O, 25 Em, 1 N 12 ± O, 19+ P, 3 N
*8. *Eg. imperialis*	〃	275 (8)	186 O, 24 P, 27 Pr, 24 L, 8 E, 6N
*9. *Eg. intersecta*	Dodson '66	ca. 73(4)	Divided in two parts, most cells L or P, some O or O'
*10. 〃	Zucchi *et al.* MS	10 (3)	5 P, 4 L, 1 N
11. *El. nigrita* (Three cases)	Ducke '03	a>100(2) b>200 c>21	
*12. 〃	Myers '35	11(3)	1 N, 2 Em, others U or M
13. 〃	Moure '46	>100	
*14. 〃	Zucchi *et al.*	43 (3)	13 O, 25 Em, 5 U or M
15. *El. meriana*	Friese '41	>50	From illustration
16. 〃	Wille unpublished	ca. 85	Most cells produced males
17. *El. cingulata*	Friese '30	42	
*18. 〃	Dodson '66	ca. 386 (25)	Divided in 6 stages. I, 11 O'', II. ca. 25 O', III. ca. 75 O or M, IV. ca. 125, O or M, V. ca 125 Em (all ♀♀),VI. 20 ; Em (12 ♂♂ 3 M), 5 N
*19. *El. terminata*	Bennett '65	53 (4)	8 O, 3 M, 10 U, 29 Em (all ♂♂), 3 N

which adults emerged; P. Cells with pupae or preimagines; Pr. Cells with prepupae; L. Cells with larvae; E. Cells with eggs. N. Cells still before operculation; M. Cells produced parasites or those damaged, broken, etc.; U. Cells from which adults not emerged. Cases with asterisks are discussed in *4.4.*

However, neither the presence of more than one female nor of many cells does not necessarily means the lasting stay of more than one female in the same nest. As shown in *4.1.* the reuse of the same nest site by more than one generation is seemingly not rare in Euglossinae, indicated by the frequent presence of carcasses in nests (*cf. 3.3.1.*). In such case even if the nest is cared by a lone female at a time, the number of cells may be large. Moreover, several females found in the same nest might merely be newly emerged ones before dispersal. Therefore the real co-existence of mature adult females in the same nest is confirmed only by examinations of cell contents and adult ovaries. As seen in Table 5, cell contents are known only in several cases (6~10, 12, 14, 18, 19) and the ovarian condition is recorded only in *Eg. ignita* (Dodson 1966), *Eg. imperialis* (Roberts and Dodson 1967) and *Eg. intersecta* (Zucchi *et al.* MS). Nevertheless, some of these relatively precise records distinctly show that nests are cared synchronously by more than one female as explained in *4.4.*. Moreover the other less precise cases suggest, as a whole, that the occurrence of more than one female is recorded too frequently to be regarded as mere chance discoveries, in comparison with the scarcity of similar records in other solitary bees.

4.4. Interpretation of some records on the co-existence of females: At first we shall recapitulate our observations on *El. nigrita*. Then, some precise records by other authors are interpreted comparatively. Our observations confirmed: 1) At least three females engaged themselves in foraging activities, though only one was captured when the nest was opened later. 2) Nest was consisting of 13 old cells and 30 later made cells. 3) Most newly emerged females were large and left the nest within a few days, some ones immediately after emergence, others, after participating in some inner tasks and foraging of feces. 4) Three females were smaller, they remained in the nest, participating in all tasks including cell construction, provisioning and oviposition. 5) Each cell is principally built and provisioned by a single female. She defends the cell against other females and oviposited in it. On the other hand, other females occasionally participate in cell construction. Only one cell is built at a time, which is provisioned mainly by the owner, but circumstancially also by other females.

Probably this nest was founded by a lone female, the number of old cells corresponds to the average productivity by such solitary foundation (*cf. 4.1.*). Some females born from these initial cells might leave the nest while others, at least three, stayed and produced 30 later made cells. Therefore, our observations on behavior (*cf.* Section 3) were made at the initial part of the third phase of colony development. Keeping these facts and interpretations in mind, some previous records are briefly discussed.

Case 6. Eg. melantoricha: The presence of many old cells indicates the succession by one or more, likely two generations of the nest site. One dead female and two living ones were found. One of the latter escaped and the other had quite worn wings and mandi-

bles. There were two separate cell clusters, one (A) with 25 O', I E and 1 N, the other (B) with 9 O', 28 L~P, indicating the order of development A→B→A. The distribution of ages of immatures is continuous, hardly regarded to involve two generations while too large (29+1) to be regarded as a product of a single female. The most plausible interpretation is therefore synchronous activities by at least two females. The ratio of numbers of old cells to later made cells and adult females suggests dispersal of some females.

Case 7. Eg. ignita: The large number of old cells in relation to that of cells containing immatures is common to all three nests, implying the succession by one (nest b and c) or more (nest a) generations and dispersal of some females. In nest a ovaries and other features of five females were examined as follows:

Individual	B	C	D	E	F
Ovarian development	+	+	±	∓	∓
Inseminated or not	−	+	−	−	+
Wing wear	−	−	−	+	−
Mandibular wear	−	−	−	+	−

All females, including slightly aged E, seem to belong to the same generation, emerged relatively recently. Ovarian and spermathecal conditions are rather irrgular, but at least E and F are certainly egg layers. These facts suggest, together with the presence of three unfinished cells, synchronous brood rearing activities by three to four females, as already commented by the original authors. In nest b, both females are probably recently emerged, and one female is just making a new cell. Nest c is probably in the stage comparable to a. Furthermore, Dodson (1966) adds to the following noteworthy comments from regular inspections of nests: "1) When only two bees occur, they seem to construct separate groups of cells. 2) In the nests with five bees each, at least one (two in one nest) bee seemed larger, slightly different in color (face golden red rather green-gold) and attacked me in defense of the nest. The other bees were smaller and though they buzzed loudly when disturbed, never seemed aggressive. 3) When females emerge some leave and construct new nests elsewhere, others stay and work with the older bee".

Case 8. Eg. imperialis: The nest cavity was apparently succeeded by probably more than one generation. The number of old cells, 186, is very large. If the nest was succeeded by lone females in each generation, at least the cavity was used by nine generations (average number of cells produced by a single female is about 20 in the maximum, *cf. 4.1.*). It is more likely that the co-existence of several females occurred previously. All eight females discovered were inseminated with fully developed ovaries. As assumed by the original authors, probably all females, at least six of them, worked each with her own cells.

Case 9. Eg. intersecta: The presence of some old cells implies the succession of the nest cavity. But the fact that most cells contained pupae and larvae indicates the relatively young age of the nest and the co-existence of several females in the generation which produced four females found at excavation, which certainly emerged recently, because no unfinished or egg containing cells are recorded.

Case 10. Eg. intersecta: No old cell is recorded so that probably the outcome of the work of a lone foundress. All three females were inseminated. One female was quite worn with fully developed ovaries. The other two were fresh with moderately developed ovaries. The cells from which these females, at least the latter two, emerged were not confirmed. Probably the cells were torn and the material was applied for other purposes. Two younger females would be either daughters or younger sisters of the aged one. It is interesting that they were large (mesosomal width 7.4 and 7.5 mm respectively) than the older female (m.w.=6.8 mm), the fact comparable to our observation in *El. nigrita* (*cf. 3.4.*

1.). As they are both inseminated, it is certain that they returned to the nest from their initial flights.

Case 12. El. nigrita: The presence of three females and only eleven, not too old cells, indicates the work by a lone nest foundress. At least one of her daughter made a new cell. It is uncertain whether the other two are just before dispersal or not.

Case 18. El. cingulata: Age distribution of cell groups beautifully shows the gradual expansion of the nest from the solitary nest foundation (Stage I, 11 cells), succeeded by six generations. The number of cells does not differ between stages IV and V, probably reflecting the dispersal of a relatively large number of females in V. Among 25 females only one was captured from the nest, all others as they approached or left the nest, probably suggesting that a considerable part of them already started the work in the nest. Five unfinished cells reflect the synchronous but probably independent brood rearing activities by several females.

Case 19. El. terminata: As interpreted by the original author, eight old cells may indicate the solitary foundation. At least four daughters remained in the nest and produced the majority of the other cells. Three unfinished cells may show the case similar to that mentioned above.

4.5. Social organization in Euglossinae: Based upon the information given above, though still hardly regarded sufficient, the social organization of Euglossinae is outlined, first of all, to give an impetus for further studies.

4. 5. 1. Social pattern: From the previous records, the following features are likely to be general to euglossine social pattern: 1) Each nest is founded by a lone female. There are many records to support this, whereas no single record gives the positive evidence for pleometrotic foundation. 2) Matrifilial association is seemingly rare, though the possibility is still not definitely rejected. 3) The nest site used by the foundress is often succeeded by daughters. Certain records suggest the succession through generations. The succession by a lone daughter would be possible but there is still no definite evidence for the continuous nest succession in obligatorily solitary species. In *Euplusia* making nests at exposed places, the sedentary disposition often seems to develop a nest aggregation. 4) In *Euglossa*, especially *Glossura*, and *Eulaema*, nests involving more than one female are regarded as the outcome of differential responses among daughters, some ones leave the nest and make their own, each solitarily, while some others remain in old nests. The presence of both solitary and gregarious nests in certain species (*El. cingulata*, *El. meriana*, *Eg. intersecta*, *Eg. ignita*, compare Tables 4 and 5), is explained by this way. 5) The expanding rate of the nest is thus determined by the ratio of dispersing to remaining females, which seems usually higher than 1.0. This may explain the frequent occurrence of large nests with a relatively small number of females. The life cycle is therefore schematicized as in Fig. 21. 6) Among females remaining in the same nests, seemingly there is no caste difference and each cares her proper progeny independently (communal type in Michener 1969). But some observations, especially those obtained in *El. nigrita* (cf. Section 3, especially *3.4.*) show some deviations from this *equivalent and independent coexistence*, in size-correlated behavior differences and partial share of cell construc-

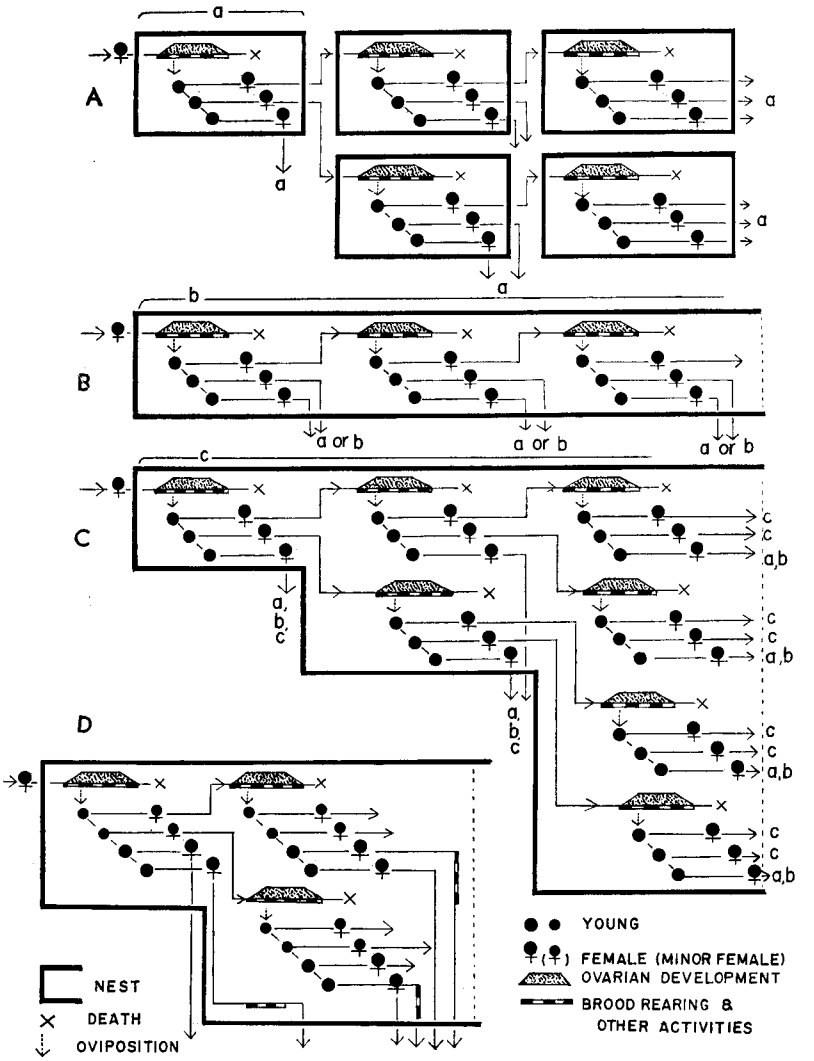

Fig. 21. Schematic representation of social patterns in Euglossinae. For simplicity males and mating are excluded. In A~C, it is postulated that each female produce three daughters. A. Solitary life without succession of nest. B. Solitary life with succession of nest. C. Parasocial life with stay of more than one female in nest and gradual development of nest by repetition of such coexistence of females. (It is postulated in the figure that two out of three daughters stay in nest. Actually more daughters may leave nest than stay in it). D. Parasocial life observed in *El. nigrita*, with production of minor females. (It is postulated that each female produce two minor and two major females. Actually major females leaving nest occupy a larger part of the progeny).

tion and provisioning, corresponding to *quasisocial type* in Michener. He distinguished *semisocial type* from quasisocial one by the presence of division of labor, with both egg layers and workerlike females. Apparently *El. nigrita* does not show such, but behavior differences between minor and major females (*cf. 3.4.*) could be regarded another type of division of labor. Moreover, it is interesting that in our nest only one cell was made at a time, the feature prevailing in semisocial bees.

Summarizing, some *Euglossa* and *Euplusia* species are obligatory solitary, though the latter often make aggregations. Some species in *Eulaema* and *Glossura* certainly reach the communal type in their life cycle ontogeny, with implication of certain quasisocial features.

4.5.2. Further remakrs on certain "social" features: Beside life cycle pattern, some observations, particularly those in *El. nigrita* indicate the presence of some traits, which deviate from those in genuine solitary bees (A), but still far simpler than in more advanced social groups (B). These features are itemized below, aspects A and B separately.

1) Mutual tolerance:

A. The frequent occurrence of nests with several females indicates the presence of mutual tolerance. Virtually each female in our *El. nigrita* nest was indifferent one another, mutually giving way at encounter (*3.1.4.*).

B. However, females expelled others when the latter approached their own cells, suggesting a vestige of mutual antagonism found in solitary bees.

Observing intranidal behavior of various halictine bees, Batra (1968) confirmed the higher interindividual intolerance in principally solitary species than in social species belonging to *Dialictus*. For instance, the aggression was severe in *Augochlora pura* (Say) and *Neocorynura fumipennis* (Friese). *Halictus rubicundus* (Christ) behaved intermediately, the dominant female of which attacked the other one when the latter approached her cell. This situation is comparable to our observations in *El. nigrita*, though no definite rank order was confirmed in the latter. Queens of bumblebees are usually indifferent to workers approaching their cells, but behave aggressively to laying workers (*cf.* Sakagami and Zucchi 1965), which implies the appearance of interindividual intolerance in defense of brood cells, the trait usually absent in groups with advanced caste differentiation.

2) Behavior sequence in building activities:

A. In most solitary bees making ectostoechal cells, cell building and provisioning activities form a stereotyped unit sequence. Building activities consist of repetition of collecting of material (M) and construction (C), followed by foraging of larval food and provisioning (P) and oviposition (O), formulated n (MC)·nP·O. A deviation from such stereotypy, regarded as a prerequisite for advanced social system (Weyrauch 1939, Michener 1969), is noticed in *El. nigrita*. M and C become two independent performance series. Collected materials are once deposited at a storing place (*3.2.1.*). The female constructing a cell repeats transport of

materials from the storing place to the place where the cell is made (T), that is, the behavior sequence consists of two independent series, *n*M and *n*(TC) instead of *n*(MC). Because the storing place is shared by all nest mates, their performance series are not independent but crisscross one another. Further other building activities, closure of emergence holes, preparation of pillars, longitudinal keels on cells and cell collars, as well as the final lining of cell inner walls are made discontinuously by several females (*3.2.2.*~*3.2.3.*). One female often ceases the work halfway, entrusting it to another, which often behaves as her predecessor, resembling the performance pattern in highly social bees.

B. However, the essential part of cell construction is made, as in bumblebees, through the continuous and consistent work by a single female (*3.2.3.*), contrasting to the performance pattern in honeybees and stingless bees. It is interesting that Batra (1964) found an intermediate condition in a social halictine bee, *Lasioglossum zephyrum* (Smith), that is, the completion of a cell by alternate performance by two females.

3) *Provisioning*:

A. The parallel performance of cell construction and provisioning in some species (*3.2.3.*), and participation of more than one female in provisioning a cell, as well as intake of larval food from the cell by some females (*3.3.2.*) in *El. nigrita* show deviations from the way taken in solitary bees.

B. However, clear manifestation of ownership in females concerning their own cells in *El. nigrita* and frequent records of the presence of more than one cell in nests involving more than one female in other species suggest that most species still remain at quasisocial step, not attaining semisocial one.

4) *Absence of advanced integration mechanisms*:

A. Partial cooperation concerning cell construction and provisioning implies that results of the work made by any females can release the preformance of the same act by others, giving a base for indirect communication, which is likely important even in highly social bees (Sekiguchi and Sakagami 1966).

B. However, the social integration is indubitably still very weak, as shown by the absence of elaborated direct communication, effective defensive mechanisms, advanced control of physical conditions and removal of colony metabolic waste (*cf. 3.3.1.*).

5) *Possible polyethism*:

The correlation of body size and behavior found in *El. nigrita* (*3.4.*) is interesting. In this case ovaries of major females were not examined, but the circumstance indubitably indicates their later development. Therefore this cannot be regarded as the caste in the usual sense. Nevertheless, the fact suggests the presence of a division of labor. Most major females remained only a few days in the nest. Nevertheless their contributions would as a whole not be neglegible because they were numerically superior. Examining the collections of Euglossinae in Departamento de Zoologia, Universidade do Paraná and Departamento de Zoologia, Secretaria da Agricultura de Estado de São Paulo, Prof. Pe. J.S. Moure,

CMF and one of us (S.F.S.) noticed some dwarf females, especially in *El. nigrita* and *El. cingulata*. Probably such females correspond to the minor females observed in the present study. Their scarcity also coincides with our result. A similar size difference was found in *Eg. intersecta* (*4.4.*, Case 10), whereas another functional correlation of size difference is suggested in *Eg. ignita* (*4.4.*, Case 7). However, it is still open to the question, even in *El. nigrita*, how such size difference is definitely established and to what degree it correlated to polyethism.

4.5.3. Significance of Euglossinae on social evolution of Hymenoptera: Finally some considerations are given as to the evolutional significance of the presence of communal or quasisocial nests in Euglossinae. The appearance of highly complicated social differentiations in Hymenoptera directly from unorganized assemblages of solitary individuals is hardly conceivable. We must therefore admit the occurrentce of some intermediate steps. Two instances would be postulated: 1) Facultative appearance of an assemblage, consisting of females of equivalent social status bearing complete functions both for self- and group-maintenance, probably caused by the acquisition of mutual tolerance. This may result in brood rearing activities by these females in the same nest (A_1). Later workerlikes may appear from this "equivalent co-existence", probably when such state is still facultative. 2) Facultative apparance of an assemblage of one female with reproductive ability (X) and one or more females without such ability (Y), which are allowed to stay with the former, probably *because of* their reproductive inability (A_2). Later, this state may become obligatory and the X-Y relation may change to the caste system.

Beside such distinction, there is another classification, namely, the association may be either matrifilial (B_1) or intersib (=sororal in Hymenoptera, B_2). Thus we obtain four combinations, A_1B_1, A_1B_2, A_2B_1, A_2B_2. (Assemblages each consisting of unrelated females are possible but not considered here).

Here we notice a remarkable fact: The presence of these intermediate steps has so far been recorded very little, in comparison with numerous cases of obligatory eusocial cases with firmly established caste system (Michener 1969), not to speak of a plenty of solitary cases (Sakagami and Hayashida 1968). This implies the instability of such intermediate steps. Or, such steps, once appeared, must rapidly change to more differentated steps through the selection of replica genes which are reponsible for "altruistic" tendency (Hamilton 1964), or inversely, the return to the solitary condition by the dominance of "selfish" tendency (Michener 1969).

Secondly, the courses through which elaborated social systems evolved from these intermediate steps must be considered. Since 1958 Michener (*cf.* 1969) developed an idea of different social evolutions among Hymenoptera. Wasps, ants and allodapine bees practice the progressive provisioning, so that their differentiated societies seem to develop based upon matrifilial association (=subsocial way). In other social bees of Halictidae and Apidae, the progressive provisioning appears

secondarily at the summit of social evolution, in *Bombus* and *Apis*, never even in stingless bees, in spite of their social differentiation being comparable to, or, in part exceeding that of honeybees. Consequently here the intersib or parasocial associations (including communal, quasisocial and semisocial types) are likely to give an impetus for the development of differentiated societies.

Although all highly developed social Hymenoptera or eusocial groups are matrifilial (B_1), this association is relatively rare in intermediate steps. The case which is most contiguous to eusocial matrifilial groups, A_2B_1, is known only facultatively in allodapine bees (Michener 1965 b), and A_1B_1 in *Belonogaster* wasps in Africa, according to the classic work by Roubaud (1916). On the other hand, intersib or parasocial association, A_1B_2 and A_2B_2, are known in various groups of halictid bees and, as shown in the present paper, in Euglossinae, favoring the hypothesis by Michener. Interestingly enough, the recent study of stenogasterine wasps, the Indomalayan counterpart of *Belonogaster*, confirmed the associations which could better be regarded intersib, A_1B_2, than matrifilial, A_1B_1, because no particular age difference was found among nest mates with developed ovaries and inseminated spermatheca (Yoshikawa, Ohgushi and Sakagami 1969). Therefore parasocial association is likely to occur even in wasps, which are regarded genuinely *subsocial* by Michener.

Recently Hamilton (1964) developed an important idea to explain the evolution of social behavior, the "altruistic" nature of which had been difficult to understand by the ordinary selection theory, which mainly postulated the survival of bearers exhibiting "selfish" trait. He assumes that the altruism is enhanced by the selection not of individuals but of gene replicas, responsible for such traits, carried by their relatives, and that the survival of gene replicas correlates to the degree of relationship between individuals, because the closer is the relationship, the higher the chance of the possession of such genes. This theory adequately explains the frequent appearance of gynarchic social tendency in various Hymenoptera, where, due to its male-haploid sex determination, the degree of relationship between sisters is 3/4, not 1/2 as in most other animals. This theory favors, however, the matrifilial origin instead of intersib one in hymenopteran social systems, because the genetic relation of sister eggs is twice that of niece eggs.

Nevertheless the frequent occurrence of parasocial groups, often showing even an incipient caste differentiation (=semisociality), is undeniable. Some traits found in our nest of *El. nigrita*, removal of molds from cell surface, common use of nesting materials, food intake from cells under provisioning and partial sharing of provisioning, are certainly beneficial for the whole group, probably without too harmful effect upon the individuals which perform these activities, because deaths of some females do not result in the complete wastage of their efforts. Against such advantages, the disadvantage of reduced reproductive efficiency in colonies than in solitary nests, widely known in socialinsects (Michener 1964 b), might counteract. Thus, in many halictine bees and probably euglossine bees, the existence of parasocial groups would always be unstable, circumstancially

returning to the solitary state (*cf.* Michener 1969). In some halictine bees, the opposed chance would occur which increased sociality with incipient caste differentiation, but, in Euglossinae so far no such tendency is confirmed.

Why then all eusocial halictine and apid bees are matrifilial inspite of most intermediate cases are intersib or parasocial, is a problem for the time being difficult to answer. Probably parasocial groups appeared more easily than matrifilial, because the latter necesitated the long life span of females making the co-existence of mother and daughters possible. It is not impossible that mutual tolerance and incipient caste differentiation acquired in parasocial association would often give a background for the establishement of matrifilial association by the prolongation of mother's life span, which, once developed, rapidly replaced parasociality because of their higher chance of selection.

Finally a few words are added to the relation between Euglossinae and other apid groups. Our observations clarified some behavioral resemblance between euglossine and bumblebee females. It is not excluded that both groups evolved from a common ancestral group, which already had a tendency to develop parasocial association frequently. But the final answer will be given only after closer compartive studies of these groups, both in morphology and ethology. Similarly we are still not in the position to give any definite statements on the phyletic relationship of social behavior in Euglossinae and two eusocial apid groups, honeybees and stingless bees.

5. Flower visits

Although the flower visiting habits represent one of the most fascinating problems in melittology, here we confine to present a compilation of previous records, simply because we have virtually made no own observation on this aspect.

5.2. Flowers visited by Euglossinae: Table 6 summarizes previous flower visit records for Euglossinae by various authors. The table excludes the highly specialized relation between certain Orchidaceae (and certain Araceae and Gesneriaceae) and male Euglossinae visiting these plants not for food intake. This relation will be referred to in the next section. Some orchids are visited for food intake as other plants. The records of these normal visits were not completely compiled but only those reported by Dodson (1966) were cited, because we could not refer to various papers concerning orchid visits by Euglossinae.

Table 6. Flower visit records of Euglossinae, excluding special relation with Orchidaceae, Araceae and Gesneriaceae.

Citations are numerically abbreviated as follows: Bodkin 1918 (1), Dodson 1966 (2), Dodson & Frymire 1961 b (3), Ducke 1901 (4), '02 a (5), '02 b (6), '06 b (7), Friese 1925 (8), '30 (9), Janvier 1955 (10), Myers 1935 (11), Michener 1954 (12), '62 (13), Sakagami unpub. (14), Schrottky 1901, '02, '07 (15, 16, 17). Vogel 1963, '66 (18, 19), Wille 1963 (20). Plant names are those given in the original papers. P and N mean visits for pollen and nectar intakes.

	I. DICOTYLEDONEAE	
Ranunculaceae	*Delphinium adjacis*	*El. nigrita* ♀ (17)

Malpighiaceae	? *Banisteria* sp.	*Eg.* (*Glossura*) sp. (19)
	Byrsonima sp.	*El. meriana* ♀P (19)
Geranacieae	*Pelargonium* sp.	*El. nigrita* ♀ (15)
Polygalaceae	*Polygala spectabilis*	*Eg. ignita* ♀♂, *El. cingulata* ♀♂, *El. mocsaryi* ♀♂, *Ex. smaragdina*, *Ex. frontalis* (4); *Eg. cingulata* ♀, *El. mocsaryi* ♀♂ (6)
	P. sp.	*El. meriana* ♂ (6)
Balsaminaceae	*Impatiens balsamina*	*Eg. hemichlora* ♀N (2)
Malvaceae	*Hybiscus rosa-sinensis*	*Ep. surinaemsnsis* ♂ N, *El. nigrita* ♂N (2)
	H. schizopetalus	*Ep. surinamensis* ♂N (2)
	H. sp.	*Ep.* sp. ♂ (3)
Bixaceae	*Bixa orellana*	*Ep. ornata* ♀, *Ep. surinamensis* ♀♂, *El. cingulata* ♀ (4); *Ep. ornata* ♀, *Ep. surinamensis* ♀ (6); *El. cingulata* (3); *El. cingulata* ♀P, *Ep. surinamensis* ♀P, *Eg. hemichlora* ♀P, *El. polychroma* ♀P (2)
Flacourtiaceae	*Oncoba pauciflora*	*Eg. intersecta* ♀, *Eg. ignita* ♀, *El. cingulata* ♀, *El. mocsaryi* ♀, *El. meriana* (4); *Eg. piliventris* ♀♂, *Eg. intersecta* (5); *El. meriana* ♀(6)
Passifloraceae	*Passiflora edulis*	*El. nigrita* ♀(14)
Loganiaceae	*Buddleia* sp.	*Eg. viridissima* (9)
Apocynaceae	*Allamanda neriifolia*	*Eg. cordata*, *Ep. surinamensis*, *Ex. dentata* (4)
	A. sp.	*El. cingulata* ♀♂N, *El. polychroma* ♀♂N (2)
	Amblyanthera sp.	*Ex. frontalis*, *Ex. smaragdina* (4)
	Lacemellea lactescens	*El. meriana* ♀N (19)
	Prestonia mollis	*Eg. viridissima*, *El. bomboides*, *El. cingulata*, *El. meriana*, *El. polychroma* (3); *El. cingulata* ♀♂ N, *El. meriana* ♀♂N, *El. bomboides* ♀♂ N, *El. polychroma* ♀♂N (2)
	P. sp.	*El. meriana* (3); *El. meriana* ♀♂N, *Ep. surinamensis* ♀ N, *Ex. smaragdina* ♀♂N (2)
	P. sp. Nr. 250	*Ex. dentata* (19)
	Tabernaemontana rigida	*Ex.* sp. ♀N (Manaus, 19)
	Thevetia peruviana	*Eg. viridissima* ♂, *Ep.* sp. ♀, *Ep. surinamensis*, ♀, *El. meriana*, *El. cingulata*, *El. bomboides*, *El. polychroma* (3); *El. cingulata* ♀♂N, *Ep. surinamensis* ♀♂N, *Eg. hemichlora* ♀♂N, *El.*

		bomboides ♀♂N, *El. polychroma* ♀♂N, *Ep. superba* ♀N, *Eg. cordata* ♀♂N (2)
Convolvulaceae	*Ipomea* sp.	*Ep. surinamensis* ♀♂, *El. polychroma* ♀♂ (4); *Eg. analis* ♀, *Ep. laeniventris* (5,6) *Eg.* "*cordata*" ♀♂, *Ep. surinamensis* (6) *El.* ♀♂, *Ep. surinamensis* (6)
Solanaceae	*Petunia* sp.	*El. nigrita* ♀ (15)
	Solanum atropurpureum	*Ep. violacea*, *El. nigrita* ♀ (15, 16, 17); *Ep. violascens* (16); *Ep. violacea* ♀P (19)
	S. oocarpum	*El. nigrita* (15, 16)
	S. cf. *quitoensis*	*Eg. ignita* ♀P (2)
	S. toxicarum	*Eg. cordata* ♀, *Eg. ignita* ♀, *Ep. ornata* ♀, *Ep. elegans* ♀, *El. polyzona* ♀, *El. mocsaryi* ♀ (6); *Eg.* (*Glossura*) sp. ♀P (Belém, 19)
	S. sp.	*Eg. mandibularis* (8), *El. cingulata*, ♀, *El. mocsaryi* ♀, *El. polyzona* ♀(6)
	Gen. sp.	*Eg. cordata*, *Eg. piliventris*, *El. surinamensis* (1)
Verbenaceae	*Cornuta grandifloria*	*Eg. cordata* (12)
	Valanerioides jamaicensis	*Eg. dodsoni* ♀N (2)
	Vitex polygama	*Eg. viridis* ♂ (5, 6)
Labiatae	Gen. sp.	*Eg. piliventris* (10)
Bignoniaceae	*Bignonia* sp.	*Eg. viridissima*, *El. cingulata*, *El. meriana* (3)
	Clytostoma sp.	*El. meriana* ♀N (2)
	Tabebuia ipe	*El. nigrita* ♀(14)
	Tecoma sp.	*El. cingulata* ♀♂N, *El. polychroma* ♀♂N (2)
	Gen. sp.	*Eg.* spp. (3)
Gesneriaceae	*Codonanthe* sp.	*El. meriana* ♀N, *El. cingulata* ♀N (19)
	Episcia sp.	*El. polyzona* ♂ (2)
Rosaceae	*Conepia grandiflora*	*El. nigrita* ♀P (15)
Leguminosae	*Cassia alata*	*Ep. elegans* ♀, *Ef. pulchra* ♀, *Ep. surinamensis* ♀♂, *El. cingulata* ♀ (4); *Ep. duckei* (5); *Ep. elegans* ♀, *Ep. surinamensis*, *Ep.* sp. 2 (6); *El. cingulata* ♀P (2)
	C. biflora	*El. polychroma* ♀P (20)
	C. hoffmannseggi	*Ep. elegans* ♀(4)
	C. reticulata	*El. cingulata* (2)
	C. spp.	*El. cingulata* ♀, *Ep. elegans* ♀ (4, 5); *Ep. schmidtiana* (8), *El.* or *Ep.* sp. ♀P (13); *El.* sp. ♀P (19),

		El. speciosa ♀P (2)
	Centrosema brasiliarum	*Ep. surinamensis* ♀♂, *El. cingulata* ♀♂ (4); *Eg.* "*cordata*" ♀♂, *Ep. surinamensis* ♀♂ (6)
	C. plumieri	*Ep. surinamensis* ♂♀ (6)
	C. spp.	*Ep. ornata* ♀, *El. nigrita* (6); *Eg. cordata* ♀N, *Eg.* (*Glossura*) sp. ♀N, *El. cingulata* ♀ NP (19)
	Dalonix sp.	*Ep. surinamensis* ♂N(2)
	Dioclea lasiocarpa	*Eg. polita* ♀ ♂ (5)
	Inga sp.	*El. cingulata* (3)
	Swartzia longestipitata	*El.* sp. ♀p (Amapá, 19)
	Gen. spp.	*Ep. ornata* ♀(4), *Eg. cordata* ♀♂, *Ep. elegans* ♀(6); *Eg. viridissima*, *El. cingulata El. meriana* (3)
Begoniaceae	*Begonia* sp.	*El. nigrita* ♀(15)
Melastomaceae	*Loreija spruceana*	*El. meriana* ♀ P(19)
	Micronia sp.	*El. cingulata* ♀ P(2)
Lecythidaceae	*Eschweilera* sp.	*Eg.* (*Glossura*) sp. ♀P (Belém, 19)
Rubiaceae	*Cephaelis barcellana*	*El. meriana* ♂N(2)
	C. colorata	*Ag. caerulea* ♂N(19), *Ex.smaragdina* as on *Psychoteria* (5)
	Leonurus sp.	*Eg. igniventris* (8)
	Palicourea rigida	*El. nigrita* ♀(11)
	Sabicea aspera	*Eg.* "*cordata*" ♀♂, *Ep. laeniventris* ♀♂, *Ex. smaragdina* ♀♂, *Ag. caerulea* ♀♂ (6)
	S. tomentosa	*Ep. chrysopyga* ♀N, *Eg. hansoni* ♀N (2)
Caprifoliaceae	Gen sp.	*El. nigrita* ♀(15)
	II. MONOCOTYLEDONEAE	
Bromeliaceae	*Aechmea maria-reginae*	*El. meriana* ♂N(2)
	A. sp.	*El. polychroma* ♂N(2)
	Ananas comosus	*El. meriana* ♀♂N, *El. mocsaryi* ♀N, *El. seabrai* ♀N, *Ep. ornata* ♀N(2)
	A. sativus var. *bracteata*	*El. nigrita* ♀(15,16)
Lilliaceae	*Hemerocallis* cult var.	*El. meriana* N♀♂ (2)
Amaryllidaceae	*Eucharis bankeriana*	*Eg. analis* ♀♂(18); *Eg. vogeli* ♂N?(19)
Musaceae	*Heliconia bihai*	*El. cingulata* ♀P, *Eg.* spp. (Brit. Guiana, 11)
Zingaberaceae	*Costus discolor*	*Ex. frontalis* (6)
	C. freidrichcini	*Eg. intersecta* ♀♂N(2)
	C. cf. *grandiflora*	*El. meriana* ♀♂N, *Eg. intersecta* ♀♂N, *El. boliviensis* ♀N, *Eg. nigropilosa* ♀♂N, *Ex. smaragdina* ♀♂N, *Eg. decorata* ♀N (2)
	C. spicatus	*El. meriana* ♀♂(2)

	C. villosissima	*El. leucopyga* ♂N, *El. nigrita* ♂N, *El. meriana* ♀♂B, *El. polychroma* ♀♂N, *El. speciosa* ♀♂N, *Eg. imperialis* ♀♂N, *Eg. gorgonensis* ♀♂N, *Eg. hansoni* ♀♂N, *Eg. ignita* ♂N, *Ep. surinamensis* ♀♂ N, *Ep. schmidtiana* ♂N, *Ex. smaragdina* ♀♂N(2)
	Dimerocostus uniflorus	*Eg. analis* ♀♂ (18); *Eg. consimilis* ♂N, *Ex. smaragdina* ♀N? (19)
	Hedychium coronarium	*Ep. surinamensis* ♀♂N(2)
	Renealmia lativaginata	*Eg. ignita* ♀♂N, *Eg. cordata* ♀♂N, *Eg. intersecta* ♀♂N(2)
Cannaceae	*Canna edulis*	*Eg.* "*cordata*", *Eg. viridissima*, *El. cingulata*, *El. polychroma* (9)
	C. generalis	*El. cingulata* ♀♂N(2)
Maranthaceae	*Calathea insignis*	*El. cingulata* ♀♂N, *Eg. dodsoni* ♂N, *Eg. ignita* N♀♂, *El.polychroma*♀♂N, *El. speciosa* ♀N, *Eg. gorgonensis* ♀♂N, *Eg. hansoni* ♀♂N, *Ex. smaragdina* ♀♂N, *Ag. caerulea* ♀N(2); *Ag. caerulea* ♀N(19)
	C. cf. *ornata*	*El. cingulata* ♀♂N, *El. polychroma* ♀♂N(2)
	C. comosa	*El. cingulata* ♀N, *Eg. superba* ♀N(2)
	C. spp.	*El. cingulata* ♂N, *Eg. dodsoni* ♀N, *Eg. ignita* ♀♂N, *Ag. caerulea* ♀N(2)
	Monotagma laxum	*Eg. ignita* ♀♂N, *Eg. intersecta* ♀♂N, *El. polychroma* ♀♂N (2), *Eg. vogeli* ♂N
	M. tomentosum	*Eg.* (*Eg.*) sp. (2 spp.) N(19)
	M. sp.	*Eg. singularis* (5), *Eg. analis* (3)
	Maranta sp.	*Ep. surinamensis* ♀♂, *El. cingulata* ♀♂, *El. polychroma* ♀♂, *Ex. smaragdina* ♀♂(3)
	Ischnosiphon obliquus & *ovatus*	*Eg. ignita* ♀♂, *Ep. piliventris* ♀♂, *Eg. intersecta* ♀♂, *El. cingulata* ♀♂, *El. mocsaryi* ♀♂ (5)
	I. obliquus	*El. meriana* N(19)
	I. ellipticus	*El.* sp. N(Sierra Macarena, Colombia 19)
	I. sp.	*Eg. ignita* ♀♂, *El. cingulata* ♀♂, *El. mocsaryi* ♀♂(6), *Eg. analis* (18)
	Gen sp.	*Eg. intersecta* ♀♂, *El. cingulata* ♀♂(4); *Eg. piliventris*, *El. cingulata* ♀, *El. mocsaryi* ♀♂(6), *Eg.*

		ignita ♀♂, *El. cingulata* ♀♂, *El. meriana* ♀♂(7).
(Orchidaceae-after Dodson '66)	*Aspacia psitticina*	*El. cingulata* ♀♂N, *El. polychroma* ♀♂N
	Maxillaria grandiflora	*El. cingulata* ♀P′ (=pseudopollen)
	Mx. sanderiana	*El. cingulata* ♀P′
	Cattleya mendelii	*El. cingulata* ♂N?
	C. warszewiczii	*El. polychroma* ♂N?
	C. maxima	*El. polychroma* ♂N?
	Sobralia violacea	*El. cingulata* ♀♂N?, *Ep. surinamensis*, ♀♂N, *El. polychroma* ♂N?, *El. speciosa* ♂N?
	S. cf. *leucoxantha*	*El. speciosa* ♂N?
	S. rosea	*El. polyzona* ♂N?, *Ep. ornata* ♂N?
	S. cf. *weberbaueriana*	*El. polychroma* ♂N?

It is out of our capacity to make a closer analysis of the flower preference of Euglossinae from the data presented in Table 6, first by our limited botanical knowledge, secondly by the incompleteness of the previous information. The latter defect is understood when the tropically limited range of Euglossinae is reminded. Therefore we shall confine ourselves to give a few preliminary remarks.

First of all the table reflects the geographical distribution clearly. At a glance on it any Northern temperate mellittologists may be impressed by the floristic make up different from the flower record lists of the bees familiar to them, characterized by the predominance of tropical or subtropical families, especially, Apocynaceae, Solanaceae, Rubiaceae, Zingaberaceae, Bignoniaceae and Maranthaceae. The large cosmopolitan families are represented by Leguminosae alone.

Secondly the table shows the predominance of tubular flowers. Exceptions are *Bixa* and Solanaceae, which have relatively open flowers. But they are, together with some legumes, mainly visited by females for pollen, taken with legs, not by their long tongues.

To have another estimate for the preference, especially in relaton to the size of plant families, the entomophilous plant families represented by more than 30 genera within Brazil were chosen from the catalogue by Angely (1960). The families visited by Euglossinae (left) and those not visited (right) are arranged in the following descending order (Number of genera in Brazil parenthesized):

Visited by Euglossinae		Not visited by Euglossinae	
Leguminosae (220)	Labiatae (46)	Compositae (226)	Annonaceae (34)
Orchidaceae (185)	Solanaceae (42)	Euphorbiaceae (104)	Cactaceae (34)
Rubiaceae (127)	Malvaceae (39)	Acanthaceae (79)	Cucurbitaceae (32)
Melastomaceae (83)	Malpighiaceae (36)	Asclepidaceae (79)	Myrtaceae (30)
Bignoniaceae (77)	Bromeliaceae (35)	Scrophulariaceae (59)	
Apocynaceae (64)	Rosaceae (32)		
	Gesneriaceae (31)		

From the left column the above mentioned tendency is more or less confirmed. Exceptions are probably Bromeliaceae and Rosaceae, but the visit to the latter is known only in one instance. On the other hand, we can recognize most families placed in the right column are characterized by small or flat flowers, though with many exceptions.

The preference for relatively tubular flowers is common to many higher or long-tongued bees. Such tendency is different from the so-called oligolecty, the preference for particular pollen sources. Recently it has gradually been clarified that many bees took nectar from a variety of flowers, but pollen from relatively restricted sources. The pollen visiting habits are obviously important from the standpoints of both bee biology and pollination problem. But this does not invalidate the importance of oligotropy as to nectar intake. Concerning the reciprocal adaptation of insects and flowers, nectar-seeking habit seems to play the role more important than pollen-seeking habit, and the evolution of tubular flowers must intimately relate to that of long-tongued insects. Among bees this tendency is best known in bumblebees. They are by no mean strictly oligotropic. The local lists of their flower visits usually cover a wide range of flower species (Probably *Bombus consobrinus* is exceptional. Both sexes of this species specially attach to *Aconitium septentrionale*, Løken 1961a). Nevertheless the predominant visiting trend of bumblebees decidedly shows the preference for long tubular flowers of relatively large size, or those forming a relatively large inflorescence, in particular when compared with honeybees, certainly limited by body size and tongue length (Pittioni 1942). Their large body and long tongue do not permit to take nectar from small isolated and flat flowers. Probably these two factors are responsible for the flower preference in Euglossinae. The size factor may be less important in *Euglossa*, many small species of which are as large as a honeybee workers (Plate IV-A. 1,2,4,5, versus 10), than in *Eulaema* and other genera. But the most important factor must be their extraordinarily long tongue. Among other bees, the longest tongues are possessed by the bumblebees of the subgenus *Megabombus*, exceding 15 mm in queens. But this length is attained even by small species of *Euglossa*. In larger species, the length reaches 30 mm in *El. meriana* or even exceeds this in *Glossura* (Pl.IV-B). Vogel (1963, 1966) notes that the flowers visited by Euglossinae for nectar intake are mainly psychophily. He assumes their partial replacement of the role played by butterflies, which have relatively unimportant significance for tropical rainforest flowers. It is certainly conceivable that Euglossinae partly shares the ecological niche occupied by butterflies for their long tongues. But the following opinion by Robertson (1926 after Percival 1965) must also be reminded. He assumes that butterflies evolved later than bees and have taken possession of the long tongue bee flowers without having been evolved in the fashioning of them. At any rate one difference must be remembered: the tongues of Euglossinae are not coiled as in butterflies. This probably explains a remarkably feature in Table 6, the absence of visiting records to Compositae. This largest plant family indubitably occupies one of the most important food sources for many bee groups,

both short- and long-tongued, including bumblebees. It is also represented by many genera and species in tropical America (*cf.* synoptic presentation of familes given above). Ducke (1901) informs many visiting records to Compositae by various bees in Amazonic Basin and the predominat role of this plant family for bees is, though in Southern Brazil, quantitatively confirmed (Sakagami, Laroca and Moure 1967 b). Virtually we often see a butterfly alighting on composite flower head and extending her coiled proboscis, but we can hardly imagine any euglossine bee using thier long tongue to take nectar from a typical flat composite head. Further observatons might reveal some visits of Euglossinae to composites, but they may never constitute the principally preferred group.

5.2. Flower preference at specific level: Within the general preference trend described above, no strict oligotropy is likely to occur at specific level. The table indicates many flower species visited by *Eulaema*, *Euplusia* and *Euglossa*. Further observations might reveal some differences between *Euglossa* with small and naked bodies and large and hairly *Eulaema*, but at the present there is no evidence to support this assumption. Certain relatively well observed species, for instance, *El. cingulata*, *El. meriana*, *Ep. surinamensis*, *Eg. cordata* and *Eg. ignita* are recorded from a variety of flower species, belonging to different families, probably reflecting their polytropy. The lesser number of records in other species may simply indicate the lack of observation. But there is some instances which suggest a tendency to oligotropy. Ducke (1902, a, b) collected both sexes of *Eg. polita* only from *Dioclea lasiocarpa*, nevertheless this plant was visited by no other species. Furthermore, he notes that *Ex. frontalis* is collected mostly on *Ambylanthera* sp. rarely on *Polygala spectabilis* and *Costus discolor*, and *Ex. dentata* is special fond of *Allemanda neriifolia*. Even if not oligotropic some species may prefer particular flowers. According to Schrottky (1901), females of *Eg. nigrita* visit *Solanum atropurpureum*, *S. oocarpum*, *Petunia*, *Pelargonium* and a Caprifoliaceae species, and males *Ananas sativa* var. *bracteata*, but both always sproadically. On the other hand, he found always a plenty of females on *Conepia grandiflora*, collecting pollen (All observed in State of São Paulo).

5.3. Flower visiting behavior: Few detailed observations exist on the flower visiting behavior of Euglossinae, except for those on the visits to orchids by males (*cf. 6.2.*). Most species approach the flower with characteristic hovering, which is particularly skillful in *Euglossa*. Probably most species extend their long tongues before alighting on flowers (Ducke 1906, Dodson 1966, Vogel 1966, Sakagami various obs.). The same behavior is known in long tongued bumblebees. Studying flower visiting habits of four British bumblebees species, *B.* (*Bombus*) *lucorum* (Linné), *B.* (*Pyrobombus*) *pratorum* (Linné), *B.* (*Thoracobombus*) *agrorum* Fabricius and *B.* (*Megabombus*) *hortorum* (Linné), Brian (1957) found the lowering of tongue before landing only but always in *B. hortorum*, the tongue of which is the longest among bumblebees and probably all bees except for Euglossinae. She also comments on a possible correlation of the development of unusually long tongue in *B. hortorum* to

its rather conservative and stereotyped behavior compared with "psychologically open species" as *B. lucorum*. This could be considered in studying the flower visiting habits of Euglossinae.

Concerning flower visits for pollen, Michener (1962) and Wille (1964) record an interesting behavior by various groups of bees to extract pollen grains from tubular anthers of *Cassia* and *Solanum*. They produce a long buzzing and shout out pollen grains by means of vibration. The lists enumerating bees practicing this technique include *Eulaema* and *Euplusia* spp. (Michener on *Cassia*, recorded in Morelos, Mexico) and *El. polychroma* (Wille, on *Cassia biflora*). Recently Vogel (1966) confirmed the same habit in certain euglossine species.

6. Male behavior

The male behavior of Aculeate Hymenoptera is generally far simpler than in females, usually consisting of food intake and copulation with some associated responses. This is basically true to Euglossinae, but here the behavior inventory is enriched by the occurrence of highly specialized responses observed in their visits to certain orchids and some other plants.

6.1. Miscellaneous notes on male life: At first some miscellaneous records on male life are gathered together. In our nest of *El. nigrita*, more females emerged than males (*cf.* Fig. 3 B). The sex ratio of immatures does not particularly deviate from 1.0 in a nest of *Eg. melanotricha* (Sakagami, Laroca, and Moure 1967 a), a nest of *Eg. imperialis* and some of *Eg. ignita*, while the predominance of one sex over the other is noted in some nests of the last species (Roberts and Dodson 1966). These records may merely show marked individual variations. But there are some other records of much exaggerated deviations (*cf. 4.3.* Table 5): *El. meriana*, Case 16, most cells produced males; *El. terminata*, Case 19, all cells produced males; *El. cingulata*, Case 18, stage V all female (125 ♀♀) and VI all males 12 ♂♂). In the first two cases, it is conceivable that nests were cared by uninseminated females. In the last case, however, a periodic change of the production of two sexes is not excluded. At least the absence of records noting the proterandry, so characteristic in aculeate Hymenoptera, is remarkable and requires further studies.

All males of *El. nigrita* observed by us left the nest at least within the day of emergence. Only one instance was precisely observed: March 22, an emergence hole of 2×2 mm was noticed on Cell 21 at 12:15. The male emerged at 13:30, already with completely black hair coat. He made self-cleaning, walked on the nest floor, left the nest 17 min. after emergence and never returned. This immediate dispersal after emergence is perhaps the rule general to males of Euglossinae, inferred from the absence of adult males in all so far examined nests, and confirmed by Dodson (1966) in *Eg. ignita* and *El. cingulata*. Males of *Eg. ignita* emerged from nests and placed by him in screen cages completely ignored the nests after emergence, whereas females occasionally visited nests and worked there

(Dodoson, *cf. 3.2.4.*). We can recognize here, too, the difference among four groups of Apidae. Males of bumblebees usually stay 2～4 days after emergence (Free and Butler 1959), and those of stingless bees and honeybees for much longer time.

Little is known on the life of males except for flower visits. Dodson (1966) observed a single male of *Ep. surinamensis* was sleeping from ca. 18:15～5:40, eight nights in succession in a tubular cavity 3 cm deep in a termite nest found near Iquitos. Vogel (1966) observed a sleeping male of *El. meriana*, grasping the leaf margin with mandibles (in Manaus). The same posture, widespread in Aculeate Hymenoptera, is also observed in *Eg. ignita*, reared by Dodson (1966) in captivity, hanging with mandibles from the ceiling of the cage.

The adult life span of euglossine males seems to be quite long. Dodson and Frymire (1961 b) marked males of *Ep. surinamensis* in January and observed one of them in May. Under captive condition, males of *Eg. ignita* lived shorter than females, only 13～14 days (Dodson 1966). These males appeared healthy and behaved normally until an hour or so before their deaths. When supplied with orchid flowers (*Peristeria pendula*), males scratched at flowers and lived longer, at least 31 days. Dodson also cites the observation by another investigator, in which male *Euplusia* reared in captivity without orchids did not live longer than 13 days. Males of *El. terminata* reared by Bennett (1965) within gallon jars since emergence also did not live longer than 14 days, in average 8.5 days (n=12) and much shorter when two or more males were placed in the same jar, in average only 5.4 days (n=17). This was caused by frequent combats for possession of the food. The male in possession of the honey-saturated cotton grasped with mandibles the extended tongue of an approaching opponent.

6.2. Visits of males to certain specialized orchid flowers: The reciprocal relations between insects and entomophilous flowers produced a number of incredibly elaborated coadaptations, such as Yucca–Yucca moths, Fig–Fig flies, etc. The relation between male Euglossinae and certain orchid flowers is one of such, relatively unknown but never less complicated. This peculiar relation was first noticed by Crüger (1865). He observed in Trinidad the pollination of some orchids exclusively by male Euglossinae (*El. cingulata* visiting *Catasetum macrocarpum* according to Dodson 1967) and assumed that bees were attracted to the edible inner surface of the flowers. This comment, correct in observation but erroneous in interpretation, was cited by Darwin (1872) in his monograph of orchid pollination. Thereafter records on the intimate relation between male Euglossinae and certain orchids have been published by Ducke, etc. But the edible tissue hypothesis had continued to Allen (1950～'54) and Porsch (1955). The first clue to the intricate relationship was given by Dodson and Frymire (1961 a, b). Thereafter, several valuable contributions have been published in a rapid succession (Dodson 1962 a, b, 1965, a, b, 1966, 1967, Dressler 1967, Vogel 1953, 1966, *cf.* also Moure 1969). Based upon these studies, the peculair behavior of male Euglossinae visiting certain orchids are reviewed and discussed subsequently.

6.2.1. Stimuli releasing male visits to orchids: Although a number of orchid groups as cited in Table 6 are visited by both sexes of Euglossinae for nectar, there are certain groups belonging to Catasetinae, Gongorinae, etc. (Vogel 1966, Dodson 1967, *cf.* also *6.2.5.*), which are solely visited by male Euglossinae. These males are attracted by neither color nor shape, but strong fragrance of the flowers. According to Porsch (1955), the commonest flower color in Catasetinae is green, with or without purple, purple-brown, yellow or white patches, nextly purple, then yellow and finally white. The predominance of green indicates the subordinate role of flower color as attracting stimuli. The minor importance of flower shape is inferred by successful allogamy in Catasetinae by Euglossinae, inspite of a pronounced sexual dimorphism in flowers.

On the other hand, the role of flower odor as guiding stimuli is certainly of the utmost importance. Most *euglossine orchids* are provided with strong odor, aromatic as in *Catasetum* and allied genera, musky as in some *Gongora*, etc. The effect of odor is demonstrated by the behavior of males of *El. polychroma* observed by Porsch, which gave away their ordinary timid disposition and invaded his room, attracted by the odor of *Catasetum* placed on the table. The visits were made only 6:00～7:00 and the fragrance was strongest just during these morning hours. This accords to the observations by Ducke on the swarms of males of *El. cingulata*, *El. meriana*, *Eg. ignita* and *Eg. cordata* on orchids in early morning. Dressler (1967) cites the observation by Janzen in Mexico on male *El. polychroma*, which flew about a quarter of a mile over an open grassy area to reach flowers of *Catasetum integerrimum*. All other reports support the effect of odor. The unique exception is given by Hoehne, who observed swarming of males of *Ep. violacea* to *Cat. cernum*, about at 9:00, and, as this flower was odorless, assumed the action of magnetic or electric rays. Obviously it is premature to conclude the absence of the effect of odor based upon human sensitivity alone.

These odors are emitted from a special tissue found on the inner wall of the labellum, the morphology of which was studied by Porsch (1955) and Vogel (1963). Following the classic edible tissue hypothesis, Porsch considered that this tissue was eaten by male Euglossinae, whereas Vogel regarded it as a kind of osmophore, the source of specific odor. The real function of this tissue was first clarified by Dodson and Frymire (1961 a, b), who also brought to light the functional significance of the singular structure in Euglossinae. In all genera of Euglossinae, including parasitic *Exaerete* and *Aglae*, male fore tarsi are provided with special tufts composed of long specialized hairs. The function of this hair tuft is explained in the next subsection.

6.2.2. Behavior of male Euglossinae on orchid flowers. A review: The observations by Dodson and Frymire (1961 b) are cited as follows: Male Euglossinae are attracted by strong fragrance of Catasetinae and Gongoriane "which provide no food but do exudate intoxicating liquids when scratched. The bees apparently absorb these through chemoreceptive pads located on" the fore tarsi.

"Each scartching continues about 45 secs, then the bees hover in the air a few inches away from the flower, and then repeat the process". "Their immediate reaction to the liquid can only be called intoxication. They loose motor control to a considerable degree, become clumsy and sluggish and lose their wariness. They apparently enjoy the sensation for they return continuously over long periods of time before tiring and flying away". "In *Gongora maculata*, *Eg. viridissima* persisted several hours attaching to particular flowers, repeating the reaction mentioned above". "This habit has made it possible for the orchids to develop intricate pollinating mechanism. The groggy, intoxicating bees can be manipulated by the flowers in a manner which would scare away a "sober" bee, or in other cases, the "sober" bee would be too nimble to effect pollination".

Thereafter, the same behavior pattern was confirmed by Dodson, Dressler and Vogel and important additional information was obtained. First of all, such specialized behavior appears not only at visits to certain orchids, but also to some unrelated plant groups. Already Ducke (1902 a, b) recorded visits of *Eg. cordata*, and *Eg. analis* to *Anthurium regale* (Araceae) and *Anthurium* sp.A and those of *Eg. ignita*, *El. meriana* and *El. cingulata* to *A.* sp.B. Thereafter, visits of male Euglossinae and performance of "scratching" or "brushing" behavior have been found in the following plants:

Araceae, *Spathiphyllum cannaefolium* (*Eg. analis*, *Eg. cordata*, *Eg. viridis*, Vogel 1963; *Eg. analis* Vogel 1966). *Spath.* sp. (*Eg. analis* Myers 1935), *Anthurium andraeanum* (*El. basicincta*, *El. bennetti*, *El. terminata*, Bennett MS). Gesneriaceae, *Gloxinia perennis* (*El. nigrita*, Itatiaia, S. Brazil, Vogel 1966, *El. meriana*, Panamá, Dressler after Vogel 1966), *Drymonia turrialvae* (*Eg.* spp. Dressler). Further, Dodson (1965a, after Dressler 1967) observed the brushing behavior on flowers of an undientified mimosioid legume and a Myrtaceae. Dressler reports some borderline cases. Some species of *Drymonia* are visited by both sexes but brushed by males. He also observed visits of both sexes of some *Euglossa* species to *Bignonia magnifica* but also the brushing behavior by males of *Eg. cordata* and *Ef. pulchra* in the same plant. Studying the floral structure of *Gloxinia perennis*, Vogel (1966) found its convergence to the flowers of euglossine orchids, characterized by emission of a strong aromatic odor, unusual among principally odorless Geseneriaceae, possession of osmophore and reduction of nectary. He also found the intoxication of males which visited this plant continuously. These instances show the parallel evolution of *parfume flowers* (Vogel 1966) with similar pollinating mechanism among unrelated plant groups.

The observations by Vogel coincides with those by Dodson and Frymire, but he assumes that odorous liquids are secreted upon the inner wall of the labellum, so that males merely gathered them by brushing, not by scratching the osmophore. Furthermore, from the absence of any sensillae functioning as chemoreceptors among tarsal tufts, Vogel (1963, '66), supposes the direct influence of intoxicants through antennae or tracheal system. In this case, tarsal tufts may serve merely for absorption and transport of liquids. Then, however, where the odorous liquids

are transported? In connection with this problem, another singular structure characteristic to male Euglossinae must briefly be commented on.

In all genera of Euglossinae, again including two parasitic genera, males have enormously swollen hind tibiae, each with a longitudinal groove along the upper margin, the shape of which is characteristic to each genera. The groove is provided with peculiar hair rows, which are often soaked with oily fluid. Vogel (1963) showed the internal structure of hind legs, using dry specimens of *Eg. viridis*. The interior is mostly occupied by a spongy chitinous sac, which is, through a canal or canals, opens to the groove mentioned above. The inner surface of the sac is covered with numerous branched bristles. He could not determine the function of this sac: either it is a gland to secrete some substance or a reservoir receiving some substance from the outside. But, in observing males of *Eg. analis*, *Eg. cordata* and *Eg. viridis* visiting the flowers of *Sapthiphyllum cannaefolium* and brushing the spadix, he noticed some males rubbing their fore legs on hind legs during hovering, undertaken before the next alighting on the spadix. From this fact Vogel's opinion inclined, though still tentatively, to the reservoir theory.

Subsequent studies favor his assumption. Morphological studies clarified the chitinous sac, or tibial organ, was regarded as the reservoir of exogenous substance (Cruz Landim *et al.* 1965, *El. nigrita*, *Eg. cordata*, *Ep. violascens*; Sakagami 1965 b, *El. nigrita*; Vogel 1966, *Eg. cordata*). Vogel (1966) showed the presence of odor substances in hind tibiae of several species (*Eg. chalybeata*, *El. meriana*, *Ep. purpurata*, *Eg. analis*) and the transference of the substance from fore tarsi to hind tibiae, first in *Eg. analis* visiting *Spath. cannaefolium* as in the previous paper, then in *Eg. cordata* visiting *Catasetum barbatum* and *Ep.* sp. 4 (*cf.* Table 1) visiting *Cat. fimbriatum*. The transference of odor substance from fore tarsi to hind tibiae is made during hovering, but not directly, with intervention of mid legs. Fore legs are simultaneously extended backward and tarsal tufts are drawn through the bristles on the lower surface of mid-basitarsi. Minute droplets of odorous liquid caught by peculiarly curved bristles of mid basitarsi are then transferred to hind tibial organs, again by simultaneous actions. Consequently, Euglossinae is singular among Aculeata, exhibiting the foraging behavior in males. Before dealing with the possible significance of this behavior, our own observations on the same habit are described.

6.2.3. Observations on orchid visits by Ep. auriceps and Eg. cordata: On January 23, 1967, one of us (R.Z.) received eight males of *Ep. auricpes* taken from a female plant of *Catasetum saccatum* var. *typum* in Riberirão Prêto. The orchid with six flowers was transplanted near the laboratory and 25 min. later, the first male visited the plant. The number of males found on or near flowers in subsequent observations are tabulated as follows (E=*Eg. cordata*):

January 23		15:40	1 (A)	8:30	1
14:30	0	16:00	0, rainy	cloudy	
14:45	3	January 24		10:00	0
15:00	2 (Marked as V and A)	8:00	0	10:15	1

11:20	2 (A)	14:00	5	16:30	2 (A), E 1
11:40	3 (A)	14:15	2 (A)	17:00	0
12:15	4 (V), E 1	15:00	3	17:30	0
13:00	4	15:30	0	18:00	0
13:40	4 (A, V), E 1	16:00	1		

Thereafter the visits by V were daily observed until January 27 when the mark was eradicated, and A visited the flowers everyday until February 21, showing a strong adhesion to the particular odor source. The number of male *Ep. auriceps* captured on January 28, 29 and 30 were respectively 36, 14 and 18, whereas only three males of *Eg. cordata* were captured during these three days. These figures are interesting because *Eg. cordata* is not rare in Ribeirão Prêto but *Ep. auriceps* has so far never been collected during three years.

The behavior of *Ep. auriceps* on flowers was similar to that observed by the previous authors, consisting of the alternation of alighting on flowers, brushing in flowers and hovering, the intervals of which were measured in three occasions as follows (all in January 24):

Period of observation	Number of alighting on flowers	Mean interval (sec.) of stay in flowers	hovering
11:21~11:30	10	10.2±3.45	8.0 ±3.96
11:40~11:53	8	13.6±2.87	6.25±2.3
13:40~13:50	18	10.3±2.16	5.9 ±1.86

The bees were very gentle near the flowers, allowing observations from the short distance. At hovering the transference of odor substance from fore tarsi through mid legs to hind tibiae was observed, but the intoxication was not confirmed. The dissection of hind tibiae revealed the odor same to the fragrance of the flowers. The behavior of *Eg. cordata* also consisted of the alternation of alighting, brushing and hovering, but differed from *Ep. auricpes* in, 1) More alert and active at hovering, making closer approach difficult; 2) Repetition of opening and closing of mandibles in flowers without touching to the labellum, 3) Continuous touching on the labellum with antennae; 4) Antennae erected upward at hovering, not half-geniculated postward as in *Ep. auriceps*. The intervals of stay in flower and hovering were measured only four times, with the means 12.25 ±3.40 sec. and 6.75±2.2 sec. respectively.

6.2.4. Visits to decayed wood, etc. by male Euglossinae and significance of odor collection: Beside certain orchid flowers, male Euglossinae often visit decayed wood, tree saps, etc, the places usually ignored by male Aculeata. These records are cited here, because this habit seems to relate the odor storage in hind tibiae. The previous records are compiled in Table 7. These records, rather casual in most cases, reveal as a whole the preference of male Euglossinae for decayed wood, resin, etc. and the observation of brushing behavior at such places by recent authors indicate that odoriferous substances are collected and stored from the sources other than orchid flowers, including resin produced from exotic plants

and such oddy substances as Aldrin, or, more likely, its break-down products. Studying about 8,000 chemicals for luring experiments of the Mexican fruit fly, *Anastrepha ludens* Loew, Lopez (1963), discovered that two compounds, α-ionone and β-ionone, are attractive to *El. polychroma*. These compounds smell as cedar wood odor at higher concentrations, and as violet in diluted solutions. While the control lures attracted no individual, the test lures did 220 males and two females. Dressler (1967) describes his curious experience. Sitting on the porch of Museu Goeldi in Belém, he was pinning some euglossine specimens to an insect box. An *Eg. cordata* male visited the pinned bees, and started brushing on the hind tibia of one male specimen of the same species.

The fact that males of some species visit both orchids or other parfume flowers and extrafloral odor sources led Vogel (1966) to the opinion that each euglossine species had several sources from which odors were collected. For instance *El.*

Table 7. Records of visits to decayed wood, etc. by male Euglossinae

Species	Author	Visited source	Remarks
Eg. piliventris	Ducke '02 b	Tree sap	Visits by both sexes recorded
Eg. intersecta	Ducke '01	Tree sap	
Eg. viridis	"	Sap of *Mangifera indica*	
Eg. "*cordata*"	Schulz '02	Tree sap	Swarming in early morning
Eg. ignita	Ducke '01	Decomposed plant tissue	
Eg. analis	Vogel '66	Decayed wood on earth surface	Wood producing decayed odor
Eg. sp. and *Eg. azureoviridis*	Dressler '67	Rotten log	Brushing observed
Eg. sp.	"	"	"
Eg. purpurea	Dodson & Dressler after Dressler '67	"	"
El. nigrita	Hempel after Schrottky '01	Sap of a conifer	Observed in Campinas, SP
"	Vogel '66	Resin of an introduced cupressoid, *Chamecyparis nutkaensis*	Producing decayed odor
"	Sakagami unpub.	Resin of an introduced conifer	Forming swarming, observed in Rio Claro, SP
El. polyzona	Ducke '02 b		
Ep. superba ?	Arlé after Dressler '67	Rotten log	Brushing observed
Ep. schmidtiana	Dodsen & Dressler after Dressler '67	"	"
Ep. purpurata	Dodson after Dressler' 67	Wooden wall of an old house sprayed with Aldrin	Hundreds of males brushing

nigrita stores both decayed-musky and menthol odors. From these observations, he assumes that the odor collecting by Euglossinae is released by a vareity of organic odor sources and this trait was later utilized by certain orchid groups, resulting in the foraging by males, an unusual trait in Aculeata.[1)]

Based upon this assumption, he altered his previous hypothesis upon the significance of visits to orchds by male Euglossinae. In 1953, he supposed this behavior as gamokinetic, that is, males were attracted by the odors similar to those emitted by females, and brushing behavior was regarded as preliminary to copulation, though the pseudocopula to flowers, famous in certain bees and wasps visiting flowers of *Ophrys* (Kullenberg 1961, allied instances are enumerated by Dodson 1967), is not performed. In 1966, he published another opinion of "borrowed or allochthonous pheromone". Collecting odors from flowers or other sources, males deposit them in tibial organs. The odors are, probably after a modification within sac, later emitted (*cf.* Cruz-Landim *et al.* 1965 and Vogel 1966) to atrract females through the scenting behavior described in *6.3.* Thus the odor substances function like as the sexual pheromones produced autochthonously by males of other bees (*cf.* Kullenberg 1956, Butler 1967).

This hypothesis is interesting and reasonable but more items of evidence must be accumulated in order to explain the curious relation between male Euglossinae and orchids. He itemized himself several questions to be solved in future. Further, the observations by Dodson (1965), cited in. *6.1.* on the shorter life span of captive males deprived of orchid flowers, seem to suggest another aspect of the problem worthwhile to study.

A few words are given as to another hypothesis presented by Vogel (1963) on the similarity between orchid flowers and brood cells of Euglossinae. Based upon this fact he assumes the mimetism by orchids to brood cells to attract male bees. This idea, already criticized by himself (1966), was also rejected by Dressler (1967), noting such flowers as *Gongora* and *Spathiphyllum* scarcely similar to cells. Our knowledge on the nest structure of Euglossinae also does not favor this mimetism. First, the brood cells of *Ep. nigrescens*, mainly based upon which Vogel made his hypothesis, is a remarkable deviation in euglossine cell architecture (*cf. 3.3.3.*). The cells of all other Euglossinae show no resemblance to orchid flowers. Secondly the majority of nests are made within more or less concealed cavities (*3.2.*) where the visual cue may not play the role. Finally males, once leaving nests, usually do not visit them (*6.1.*).

6.2.5. Specific preference of Euglossinae in orchid visits: From the recent accumulation of various observations, it was now firmly established that certain orchid groups posssess an intimate relation to male Euglossinae concerning their pollination. All these orchids produce no nectar but strong fragrance, which is actively collected by male Euglossinae. According to Vogel (1966), such particular

1) In connection with this, he cites the absence of odor foraging on parfume flowers by *Exaerete* and *Aglae*, nevertheless these parasitic genera have tarsal tufts and tibial organs. But Dressler (1967) records the rudimentary brushing behavior in *Ex. smaragdina* and *Ex. frontalis* on some orchids and *Spathiphyllum cannaefolium*.

relation is seen in all genera of Catasetinae (*Catasetum, Mormodes, Cychnoches*) and Gongoriane (=Stanhopeinae, *Gongora, Stanhopea, Coryanthes*, etc.), some genera of Lycastinae, Onicidiinae, Zygopetalinae, Huntleyinae and Crytopodiinae. It is indubitable that male Euglossinae played an important role for the evolution of these groups.

But how intimately Euglossinae relates to the orchid evolution at generic or specific levels? Dodson (1962 b) stresses the importance of euglossine pollinators in orchid evolution, and explained this by the probable speciation in *Stanhopea*, which he called "leap forg speciation". According to him, the basic stock of this genus had relatively small flowers, mostly pollinated by *Euglossa*. From this ancestral type, evolved species suck as *S. intermedia*, the flowers of which were open widely, facilitating the pollination by *Eulaema*. In further speciation some species from this *Eulaema*-pollinated group again turned back to the *Euglossa*-pollinated type, with corresponding change in floral structure. It is not difficult to imagine such isolation due to the size difference of pollinators, when the tiny, honeybee-sized *Eg. cordata* is compared with the huge *El. meriana* (Plate IV–A, 1 versus 27).

On the other hand, Vogel pointed out the absence of strict species-specific relation in Euglossinae-orchid evolution and the total number of euglossine species (=95 in his paper, actually about 140 in the present status) much inferior than the number of *euglossine orchids*. Recognizing the role played by Euglossinae as the background for orchid evolution, he assumed that the rich diversification in shape, color and fragrance in these orchids was not directly selected by euglossine pollinators.

Although we are not sufficiently qualified to discuss this botanical problem, the assertion by Vogel seemingly does not mutually exclusive to the theory stressing the importance of Euglossinae in orchid evolution at lower taxa. Certainly these bees would act as selecting agents neither exclusively nor at every step of flower diversification. But they must play an importance role here and there in the evolution of diverse orchid groups. To obtain a more precise picture upon this problem, we need the accumulation of further data concerning the mutual relation between bees and flowers preferred by them. Based upon the previous contributions, here are given some comments which might be suggestive for future studies.

Dodson (1967) compiled a comprehensive list of so far known pollinators of various orchid species, including all 'euglossine orchids". At a superficial glance in the list, it may be recognized that some euglossine species are pollinated each by more than one species, euglossine and some euglossine species pollinated orchids. But a closer analysis gives several interesint facts as shown in Table 8, which was prepared from Dodosn's list through the following procedures:

1) Only orchid genera solely pollinated by Euglossinae were selected. 2) In each orchid genus, the number of cases observed (one orchid species pollinated by one euglossine species was counted as one) were enumerated. 3) The data on seven principal genera

of elugossine orchids were given separately, while those on the other genera in combination 4) Euglossinae were divided at generic level (regarding *Glossura* as a separate unit). 5) Some euglossine species with numerous records were given separately. 6) Species given by Dodson as *Eg.* sp. were counted each as independent species. *Eg.* cf. *viridissima* and *Eg. viridissima* were regarded each independent species like as in other similar cases. 7) Cases mentioned as "nonpollinating visitors" were excluded.

The facts derived from Table 8 are summarized as follows: 1) Concerning certain orchid genera, *Euglossa* and *Eulaema* behave oppositely. *Gongora*, *Mormodes* and *Peristeria* and principally visited by *Euglossa* while *Catasetum* and *Stanhopea* more by *Eulaema*. 2) Orchid visits by *Euplusia* are relatively scarce in number, nevertheless this genus has more species than *Eulaema* (*cf.* Introduction). Moreover, they relatively ignore the orchid genera actively visited by *Euglossa* and *Eulaema*. In this connection the preference of *Ep. concava* is noteworthy, recorded three cases from *Acineta*, one from *Kegelielia* and one from *Peristeria*. 3) There are certain common euglossine species which are not

Table 8. Euglossinae-orchids relation at generic level (prepared from Dodson 1967. Explanations in text)

Orchids / Euglossinae	Number of cases observed								
	Cata-setum	*Cory-anthes*	*Cychno-ches*	*Gon-gora*	*Mor-modes*	*Stan-hopea*	*Peri-steria*	Other22 genera	Total
Euglossa (+*Euglossella*)									
cordata	4	1		4	2		1	1	13
RLD 2	1		1	1	2			2	7
viridissima					3	2		2	7
dodsoni				2			1	2	5
hemichlora		1		1	1			3	6
mixta		1			4		1		6
Other spp.	3	2	3	13	4	1	6	*14*	46
Total	*8*	*5*	*4*	*21*	*16*	*3*	*9*	*24*	*90*
Glossura									
ignita	1	1	1	2	2	2	1		10
Other spp.	2				2	1	2	1	8
Total	*3*	*1*	*1*	*2*	*4*	*3*	*3*	*1*	*18*
Euplusia									
concava							1	4	5
Other spp.	2	1	1	1		2		7	*14*
Total	*2*	*1*	*1*	*1*		*2*	*1*	*11*	*19*
Eulaema									
cingulata	10	1	4			1		5	21
polychroma	4					1		2	7
meriana	2	1				3		5	11
Other spp.	6	1	1		1	6		5	20
Total	*22*	*3*	*5*		*1*	*11*		*17*	*59*

frequently recorded on orchid flowers. Obviously frequent records of some species such as *El. cingulata*, *El. polychroma*, *El. meriana* and *Eg. cordata* are caused by their predominance throughout tropical America. But the list of Dodson cites few records on such common species as *El. nigrita* (only four cases, two from *Catasetum*, one from *Cychnoches* and one from *Mormodes* (!), the unique record of *Eulaema* from this *Euglossa*-pollinated genus), and *Ep. surinamensis* (only two cases, from *Notylia* and *Pterostemma*), as well as some relatively abundant species as *El. mocsaryi* (no record), *Ef. pulchra* (no record), *Eg. piliventris* (only one record ? from *Catasetum* after Dodson 1967) and *Eg. intersecta* (only one record by Ducke 1901, '02b). This fact indicates either these species have no intimate relation with orchids or they have the preference for some other orchids still not confirmed. 4) Even in genera visited both by *Eulaema* and *Euglossa*, the segregation is noticed at specific level. For instance, in *Catasetum*, *C. barbatum*, *bicolor*, *hookeri* and *luridum* are solely visited by *Eg. cordata* and *C. discolor*, *ebruneum*, *integerrimum*, *macrocarpum*, *macroglossum*, etc. by *Eulaema*. Such segregation is also found in *Stanhopea*.

The relative preference at specific level cannot precisely be analysed by the procedure taken above, which favors the species with wide preference range, while ignores the species with narrow range. Further studies must consider the following two points: 1) To express the relative preference quantitatively. 2) To mention the species not visiting but common in the locality studied. Some related cases are cited from previous records, in the hope of further observations along this line.

Ducke (1901, 1902 a, b) mentions that orchid visits are absent in *Eg. piliventris*, *El. mocsayri*, *Ep. surinamensis*, *Eg. intersecta* (in one case pollinia observed on mesosoma) and rare in *El. nigrita*, nevertheless these species are common in Belém and the vcinity. Another, more important type of observations may be to distinguish principal and accessory pollinators (Dressler 1967). Ducke (1901, '02 a, b) records occasional visitis of *Eg. ignita*, *El. meriana* and *El. cingulata* to *Stanhopea ebrunea*, but mentions they are not effective pollinators. Similar instances are noted by Dodson (1967) and Dressler (1967). In our observations given in *6.2.3.*, *Eg. cordata* could be regarded as accessory pollinator. But the most definite instance is observed by Bennett (MS), not as to orchids but with an aroid, *Anthurium andraenum*, in Trinidad. Visits of male Euglossinae were so frequent that a serious damage of this ornamental was evoked. To prevent the damage, visited males were collected individually. The number of collected males during May 4～June 10, 1963 is cited from his unpublished data: *El. bennetti* 1,745, *El. basicinta* 590, and *El. terminata* 132. The order was same in 1961, too. It must be mentioned that *El. terminata*, the least frequent one, is a well known species, while two others were first discovered as new species by this survey. Moreover, the commonest species, *El. cingulata*, was caught around *Anthurium* but only occasionally.

6.3. Territorial behavior and copulation: Ducke (1901–'06) described some specific differences in male activities other than orchid visits: *El. meriana* does not fly after 10:00 and rests on tree trunks, only occasionally making brief flights. *El. polyzona* frequently visits fountains and rotten wood. *El. mocsaryi* and *Ep.*

elegans fly over bushes and *Ep. ornata* over low canopies. *Ag. caerulea* makes restless flights in humid forests and *El. nigrita* visits rotten wood or flies rapidly over lower bushes, not interrupting even under hot midday insolation. Schrottky (1901) found males of *El. nigrita* around trees of *Conepia* which are visited by females for pollen. Bodkin (1918) observed males of *El. meriana*, repeating flying and landing along tree trunks. Some if not all of these records appear to correspond to the territorial behavior recently reported by Vogel (1966) and Dressler (1967). The aggressive disposition in males was shown in *El. terminata* in captivity (*cf. 6.1.*). Mutual chasing at orchid visits were recorded already by Crüger (1865). Porsch (1955) did not observe such behavior in *El polychroma* but Dodson and Frymire (1961 b) observed it in *El. polychroma* and *El. cingulata* and Vogel (1966) in *Eg. cordata* and *Ep.* sp. 4. The term *territorial* is not always appropriate to designate the cases cited below, because the area occupied by each male was not always invaded by other males, but the appearance of combats is likely at such invasions.

Case 1. Eg. chalybeata (Vogel 1966): Two or three males flew around the base of a small palm tree, chasing mutually.

Case 2. El. cingulata (Vogel 1966). The fanning behavior of males was observed three times. In all cases, the male repeated fanning each on the particular tree trunk at the heights of 3~5 m from the ground, and flying around the trunk. At fanning, the head is lowered and the metasoma and hind legs are raised, just as in scenting honeybee workers.

Case 3. El. meriana (Vogel 1966): Similar alternation of fanning and flying around was observed about ten times. The fanning posture was similar to that in *El. cingulata*, but mid legs were extended along the body, not placed on the tree trunk (1.8~3 m high). After each flying, the bees do not always alight on the same spot, changing the place within the extent of about 50×50 cm sq. Flying courses are elliptical or 8-shaped and fairly constant. When another male appeared the fanning male took the air and chased the invader.

Case 4. Eg. hemichlora (Dodson 1966): Two male bees flew back and fourth in front of the stem of a plant a few feet away from the nest (cited in Table 5), "possibly involved in preliminaries to copulation behavior".

Case 5. El. polychroma (Dressler 1967): Each male chooses a smooth barked sapling of 4~8 cm in diameter (at heights 1.5~2 m above the ground) as the focal point and repeats landing and flying around. At landing the head is directed upward and the metasoma is raised. After continuing buzzing with this posture, the male takes the air, circles 2~3 m from the tree and returns and alights on the tree. Once three males were observed circling around a tree without serious combats. Similar behavior was also observed in a small unidentified *Euglossa*.

Case 6. El. nigrifacies (Dressler 1967): Similarly saplings are chosen but males do not land on them. Instead each male makes a zig-zag flight starting at the spot 60~80 cm away from the sapling. After approaching the sapling, he makes normal circling, then repeats zig-zag flights. But Dodson (aftre Dressler 1967) observed in the same species the behavior described in Case 5. Similar alternation of normal and zig-zag flights was observed in *El. luteola* by Dressler who also observed both types as in Cases 5 and 6 in *El. speciosa* ? (not captured).

Case 7. Ep. schmidtiana (Dressler 1967): Each male hovers about 30~40 cm above top of *Heliocarpus* sapling (3 m tall), darting across the sapling and circling widely to repeat

the performance. Chasing of other bees invading the area was observed.

Case 8. Eg. cyanosoma (Sakagami and Laroca, unpub.): In Antonina, Coastal Paraná, the behavior similar to Case 5 was observed. The sapling served as the focal point was visited about 1.5 hrs later and the male still continued the same behavior. Another male also behaved similarly.

Actual copulation was observed two times, both by Dodson (1966, *cf.* Roberts and Dodson 1967). The return of a major female of *El. nigrita* to the nest, propably after copulation, was mentioned in *3.4.2.*

Case 9. El. cingulata: Males make repetition of flying around, buzzing loudly and landing on definite tree limbs or trunks about 5~10 ft above the ground. A single male continued this activity for more than two hours, and returned to the same place on succeeding days. The copulation was observed in such situation. "At 15:00 on a clear sunny day, a female approached and passed near the male several times, then flew to a nearby leaf, clasping it with mandibles. The male followed her, flying back and fourth and hovering over her several times before landing on her dorsum. She then raised her hind legs back over her body and clasped him between meso- and metasoma. Copulation lasted about 5 min."

Case 10. Eg. ignita: Two bees, male and female, hovered around the base of a small tree, about four inches in diameter in virgin forest, buzzing back and fourth and landed regularly. Making several contacts in the air, the female landed and pressed her body and wings tightly the tree. The male hovered over and finally mounted and copulated for about 6 min."

Since the observations by Frank (1941) on the flight path formation in bumblebees, the mating behavior of wild bees has gradually been clarified in various groups. Haas (1960) distinguished several types as follows: 1) *Simple swarming course type*: Many males concerntrate in a narrow swarm area and make within it mating flights, the course of which is not well fixed. They also have no fixed feeding area. This type is practiced by *Andrena chrysosceles* Kirby, and other short lived species and gradually shifts to the next type through intermediate types. 2) *Feeding locality course type*: Males have definite feeding places which are visited during swarm flights. Or the courses leading to feeding places and those pursued in mating flights are largely congruent, exhibited by *Eucera, Melitta* and in the most differentiated manner in *Anthophora,* with precisely directed courses continuously cruised, thus approaching the next type. 3) *Type with swarming courses correlated to feeding localities.* This type, only known in *Bombus* and their parasites, *Psithyrus,* is characterized by the separation of flight path and feeding area, the latter frequently visited during regular cruising of the former. Various species differ one another in the relative height of paths, for instance, *B. lapidarius* flies at tree top level, *B. silvarum, B. pratorum,* etc. over the shrubs and *B. hortorum* above the ground (Haas 1949 a). A flight path has a number of marking spots, where cruising males alight and mark them with odorous secretion of mandibular glands. Males of *Psithyrus* (Haas 1949 b) behave similarly but the paths are connected not by marking spots, but by several particular areas. Arriving these areas, males do not land but make zig-zag flights within each area

before proceeding straight to the next area. 4) *Territorial type*: In the types mentioned above, flight paths of several to many males can overlap, resulting in a network of interwoven paths, which intensifies the scent emitted from paths or marking spots and facilitates the attraction of females (queens in bumblebees). On the other hand, certain megachilid bees (*Osmia*, *Megachile*, *Anthidium*) do not form such communal network of flight paths. Instead, each male possesses a definite area, cruises and feeds within it and defends the area from other males (Haas 1960). A similar territorial behavior is observed in *Bombus mendax* and *B. confusus* (Haas 1949 a), though it is not clearly mentioned whether they feed within their territory or not. The behavior of certain Nearcitic species, *B. auricomus*, *B. morrisoni*, and *B. separatus*, noted by Frison (1930) seems to be of the same type. These species, both Palaearctic and Nearctic ones, are all characterized by well developed eyes, belonging to Section *Boopobombus* Frison, possibly a polyphyletic group.

Now let us examine the observations on male Euglossinae in comparison with the behavior of other bee groups. The characteristic common to all cases cited above as to Euglossinae is the possession of a definite area by one male. The chasing of other males by the occupant is observed in Cases 3, 7 and possibly 1, but not in others, especially in 5. Therefore, Euglossinae seems to belong the type similar to Type 4 in Haas but the defense of the area is not always definite. Another difference from Type 4 would be the segregation of feeding area and "territroy", which indicates, according to Haas (1960), evolutionally a higher step. Mutual chasing of males observed in some areas would be regarded the partial overlap of flight paths among neighbours, but closer observations are required before making precise characterization.

Another characteristic is the occurrence of a focal point within the area occupied. In the course of cruising, the occupant lands on the point (Cases 2, 3, 5, 8, 9) or at least approaches to it with (Case 6) or without (7) zig-zag flights. Because the same species likely land or not on the point (*cf.* Case 6), the behavior could be plastic according to the situation. The significance of this "territorial" behavior is evident from the occurrence of copulation during such behavior. Based upon the scenting behavior found in Cases 2 and 3, Vogel asserted the emission of allochthonous or borrowed pheromone to attract females. But the odorous marking could be achieved without such fanning, when the same area was repeatedly cruised, as inferred from the instance of *Psithyrus* mentioned above.

Finally, the copulating behavior of Euglossinae and bumblebees is briefly compared. Based upon the previous records, bumblebees differ from Euglossinae in the following points: 1) Except for the copulation within the nest (Katayama 1964), male bumblebees catch females in the air, clinging to the metasoma of the latter, although the actual copula is accomplished on the ground or other substrata (Hullkonen 1924 after Postner 1952, Postner 1953, Katayama 1964). 2) Copulation is preceded by the violent touching with antennae by males and usually by the avoidance response by females. 3) From the initial act of the insertion of male genitalia to its completion several minutes are required, and the real copulation

continues for a long period (Hullhonen 2.5 hrs, Postner 3 hrs, Katayama more than 48 min.). A slight discrepancy occurs between Katyama (with *B. ardens*) and Postner (mainly with *B. lapidarius* and *Psithyrus rupestris*). According to Postner, males seem to clasp the metasoma of females during copula, whereas Katayama notes that males tightly attach all legs along body sides and connect with females only by means of genitalia, keeping the body semi-erect above females. Postner (1953) observed the weakening of males after copulation and subsequent deaths a few days after, but only once the death during the copula, which was the rule in honeybees. These descriptions suggest the copulation behavior slightly more differentiated in bumblebees than in Euglossinae. But both are certainly less differentiated in comparison with the highly specialized aerial copulation in honeybees and stingless bees.

7. Associated animals

Linsley and MacSwain (1957, *cf.* also Linsley 1958) classified various animals associated with nests of solitary bees in the following four principal groups: A. Those which in the first larval instar prey upon the egg and in subsequent instars feed upon the stored pollen and nectar; B. Those which parasitize or prey upon the developing or full-grown larva; C. Those which depredate the stored pollen and nectar and destroy, modify, or starve the larva to death, and D. Those which feed upon the contents of old cells and burrow refuse and only through accident have an adverse effect upon the host species. Following this system, the previous information on the animals associated with Euglossinae, obviously still not enough, was compiled in Table 9.

Two parasitic genera of Euglossinae, *Exaerete* and *Aglae*, recently revised by Moure (1964), are the typical examples of parasites which prefer their close relatives as hosts, as well known in anthophorid and megachilid bees. All morphological features clearly show the common origin of parasitic and nonparasitic Euglossinae. But it is still not well studied how the former group derived from the ancestral nonparasitic Euglossinae. Grütte (1935) assumes the resemblance of *Exaerete* to *Euglossa* and that of *Aglae* to *Eulaema* (=*Eulaema*+*Euplusia* in the present paper), and mentions that *Aglae* retains partly characters more primitive than recent *Eulaema*. At any rate, there is no record of parasitism by these genera upon *Euglossa*,, and probably this does not occur, because all known species of *Aglae* and *Exaerete* are distinctly larger than most *Euglossa*, except for certain species of *Glossura*, especially *Eg. intersecta*. Both *Exaerete* and *Aglae* parasitize on *Eulaema*. *Ex. frontalis* and *Ex. smaragdina* parasitize on *Eulaema*, and the latter species and *Ex. dentata* on *Euplusia*. Recently Moure (1964) recognized two groups in *Exaerete*, one including *Ex. frontalis* and *Ex. smaragdina* and showing correlations to *Eulaema*, and the other with *Ex. dentata* and *Ex. azteca* resembling *Euglossa*. The percentage of cells infested in a nest is known in three cases. *Ag. caerulea* (2/11, Myers), *Ex. smaragdina* (about 50%, Moure '46, and 1/3, cf. *2.4.*). Myers observed one beautiful metallic bee, certainly *Aglae*,

Table 9. Animals associated with euglossine nests

Biol. Group	Parasite	Host	Author
A	*Exaerete frontalis* (Euglossinae)	*El. meriana*	Friese '41
A	*Ex. smaragdina* (〃)	*El. nigrita*	Ducke '03, Moure '46
A	*Ex. dentata* (〃)	*El. surinamensis*	Ducke '06 a
A	〃	*El. auricpes*	cf. *2.4.*
A	*Aglae caerulea* (〃)	*El. nigrita*	Myers '35
A	*Stelis* (*Odontostelis*) *bilineolata* (Spinola) (Megachilidae, Hymenoptera)	*Eg. viridissima*	Friese '25
A	〃	*Eg. cordata* and *Eg. variabilis*	Dodson '66
B	*Meloetyphlus attacephalus* Borgmeier (Meloidae, Coleoptera)	*El. terminata*	Bennett '65
B	*M. fuscata* Waterhouse (〃)	*El. cingulata*	Dodson '66
B	*Pelectomoides succincta* Germ. (Rhippiphoridae, Coleoptera)	*El. nigrita*	Ducke' 03 (as a meloid), '06 a
B	*Theronia tacabaya* Cresson (Ichneumonidae, Hymenoptera)	*Eg. dodsoni*	Dodson '66
B	*Monodontomerus argentinus* Brèthes (Torymidae, Hymenoptera)	*Ep. nigrescens*	Sakagami & Sturm '65
B	*Polistomorpha surinamensis* Westwood (Leucospidae, Hymenoptera)	*Eg. ignita*	Roberts & Dodson '67
B	A mutillid wasp (Mutillidae, Hymenoptera)	*Eg. dodsoni* and *Eg. intersecta*	Dodson '66
C or D	A sarcophagid fly (Sarcophagidae, Diptera)	*El. nigrita*	Myers' 35
D?	An acarid mite (Acari)	*Eg. imperialis*	Roberts & Dodson '67
D?	*Uropodina* sp. (Acari)	〃	〃
D	*Solenopsis* sp. (Formicidae, Hymenoptera)	〃	〃
D	*Euborella ambigua* Borelli (Labiduridae, Dermaptera)	*El. nigrita*	Zucchi *et al.*

buzzing loudly in front of the nest of *El. nigrita*, from which he later obtained *Aglae*. Out of this observation, nothing is known on the mode of life of these parasitic genera.

The parasitism by *Stelis bilineolata* on *Euglossa* is also noteworthy. Friese, describing this as *S. abnormis*, reported its attack on *Euglossa*. Cockerell (1931) erected the possibly polyphyletic subgenus *Odontostelis* for this species and *S. cornuta* Bingham known from Burma, by the possession of unusually armed mandibles. Most species of *Stelis* attack nests of megachilid bees, so that the preference for such remote genus as *Euglossa* is unusual and probably of the recent origin. In this connection, the following note by Schwarz (1933) is suggestive: "It would seem probable that *bivittatum* (=*bilineolata*), which is in many of its characters much like *Dianthidium* (*Anthodioctes*) *calcaratum* Friese and may even be derived from it, is an inquiline in the nests of *calcaratum*, as well as those of *Euglossa* mentioned by Friese. It is to be noted, in this connection, that as to place, collector and

date, some of the specimens of *calcaratum* and of *bivittatum* in accord". If such would be the case, the extension of the host range to *Euglossa* is probably caused by the same nesting material employed by phyletically remote host groups, for *Dianthidium* also uses resin as *Euglossa*.

Recently Bennett observed the behavior of *S. bilineolata*, invading artificial glass-lid nest boxes of *Eg. cordata*, and obtained some interesting results (Larvae of *S. bilineolata* was described by Rozen 1966): 1) *Stelis* invades the nest, nudges with mandibles and attempts to sting *Euglossa*, which is forced to abandon the nest. 2) Thereafter *Stelis* closes the entrance from the inside, and stays there for several days, with occasional departures and returns, the latter followed by reclosing. 3) Cells containing eggs or small larvae are opened, the immatures are removed, destroyed and, in case of larva, stung and covered with resin. Then cells receive each one egg and are resealed. 4) Cells containing mature larvae or pupae are not opened but these immatures are killed probably by stinging or squeezing the cell wall from the outside, which indicates the ability of discriminating the contents from the outside. Therefore, this species is singular not only in morphology but also in behavior, especially by the performance of various activities which are usually not made by parasitic bees.

Meloetyphlus fuscatus was found crawling around the nest of *E. cingulata*. Several adult bees carried considerable numbers of their larvae clinging to hairs. A mutillid wasp emerged from a cell in the nest of *Eg. intersecta* began to attack another cell a few hours after emergence. The cell cap was opened with mandibles, and after several unsuccessful attempts to oviposit, each followed by enlargement of the hole, it left the cell and moved to another to repeat the procedure. Dodson suspects the actual oviposition, so soon after emergence and before mating. One adult female of *Polistomorpha surinamensis* attempting to enter a nest of *Eg. ignita* was observed. Nevertheless she was driven out two times, a wasp emerged from the nest about a month later, and all stages of the wasp, egg to adult, were found in the nest. Interestingly a bee larva carried two eggs of the parasite. *Monodontomerus argentinus* is apparently gregarious, one host cell produced about 35 individuals.

Myers found in a nest of *El. nigrita* a number of maggots in a fecal heap (*cf. 3.3.2.*) beside the cell mass, from which a curious yellow-grey sarcophagid fly emerged. *Euborella ambigua*,[1] found from our nest of *El. nigrita* behaved certainly as an unspecialized scavenger (*cf.* Fig. 3, cells marked with triangles).

A few words are to be added concerning the attacks by molds and fungi. Their influence must not be underestimated in humid tropical America. The use of resin for nests could be in part an adaptation to defends molds. Ducke (1902 b) comments on the difficulty to rear the larvae of *Ep. surinamensis*, because they are attacked by molds soon after opening the cell walls.

There is no record of parasites and predators attacking adults, except for the infestation of *Eg. cordata* by a conopid fly (Bennett 1966). Concerning the mimetism, *Dasyllis haemorrhoa* (Asilidae) resembles *El. meriana* (Bischoff, 1927) and *Meloetyphlus fuscatus* (*cf.* Table 9) *El. cingulata*. Several astonishing examples of parallelism in color pattern between *Euplusia* and *Eulaema* (cf. Pl. IV- A, 20–23 versus 26–29) are pointed out.

1) Identified by S.F.S., using the key by Burr (1910).

8. Habitat preference and phenology

In this final section some miscellaneous observations, mainly by Ducke, are cited, which are, however fragmentary, regarded as the basis for the *ecology* of Euglossinae, on which we have virtually still no precise information.

As a whole, the bees seem to prefer rather arid grassland climate (Linsely 1958, Friese 1923), in part reflected by the rich bee faunas in Central Asia, California, Northern Argentina, etc. However, there are a number of groups which exhibit the opposite tendency. Among them, the Family Apidae could first be mentioned by their general attachment to humid forest climate. This character is most clearly expressed by Euglossinae. Although many species are found in relatively arid regions, the heart of their distribution is definitely the vast Amazonic rain forests and their outskirts extending from Central America to Mato Grosso. Under such general inclination to humid and shaded forest, however, there are certain differences in habitat preference among species. Such differences are recognized only after many years' experience, so that it is not strange that only Ducke (1901～'02 a, b) made notes on the habitat preference of Euglossinae. He recognizes two groups in Belém and the vicinity. A. Those prefering relatively dry, open areas: *Eg. cordata*, *El. nigrita*, *Ep. surinamensis*. B. Those prefering relatively humid, shaded areas: *Eg. ignita*, *Eg. piliventris*, *Eg. intersecta* *El. meriana*, *El. mocsaryi*, *El. polyzona*, *Ep. elegans*, *Ep.* sp. 3, *Ag. caerulea*.

Further he notes *Eg. analis* prefers more humid and shaded areas than *Eg. cordata*. *Ep. ornata* seems also intermediate in preference. Males fly in half shaded area in virgin forests and females in cuttings of capoeiras. It is reasonable that three species in group A have a wide geographical range outside of Amazonic Basin, *Eg. cordata* (though Ducke's *cordata* might be a composite species) and *El. nigrita* far southward, and *Ep. surinamensis*, according to Dodson, common in semi-arid regions of coastal Ecuador. Moreover, these species seem to be more tolerable to man-made environments than others (*cf. 1.2.*).

The following notes on the phenology were also prepared from Ducke (1901–'06): In very humid areas surrounding Belém, the bees are seen practically in every month. Regarding the Lower Amazons in general, however, there is a mild alternation of dry and rainy seasons, and the relative abundance of bees follows this shift. The most abundant season is from June to August, they decrease at the peak of dry season in October, then increase by the beginning of rainy season in early December but again decrease after January by heavy rains. The phenology of Euglossinae corresponds to this general trend. In Belém, they are seen practically every month. But in more arid campos in Macapa, they disappear in dry season, leaving only *Eg. cordata* and *Eg. viridis*. As to particular species, Ducke gives the following notes: *Ep. surinamensis*: In Belém, seen every month but breeding activity only during January to April. In Macapa, disappearing in summer dry season; *Ep. ornata*: July～October in Belém. *Eg. polita*: Late April to June, both sexes; *Ex. dentata*: August～October in Belém; *Ex. frontalis*: Male

December ~ April and females August ~ September.

There are some contradictions in his comments. But it is indicated that some species show definite seasonal cycle even under humid equatorial climate. As to other species, Dodson and Frymire (1961 b) record males of *Ep. surinamensis* being common during January to May in Ecuador. Bennett (MS) records the frequent visits of *El. basicincta* to *Anthurium andraeanum* in Trinidad during May ~ August, while concentrations of *El. bennetti* and *El. terminata* in May. Schrottky (1907) writes that *Ep. violacea* is seen in Paraguay during December to March, having only one generation per year, as in *Ep. auriceps* (*cf. 4.3.*) and *Ep. surinamensis* (Ducke 1902 b). The presence of the latter species throughout the year in Belém may be explained by the long life span (*cf. 6.1.*). On the other hand, the following note by Bennett (1966) indicates that *Eg. cordata* has more than one generation per year in Trinidad: "Nest started in August, activity was suspended three times by parasites: the original female, a succeeding daughter, and finally a prasitized granddaughter. The progeny of the last female emerged between December 9 and January 3". The record by Friese (1922) on *Eg. viridissima* also seems to show a similar life cycle in Costa Rica.

Summary

1. The present paper consists of two parts which are not always separately given in text. One is the descriptions of nest structure and intranidal behavior of a Neotropical parasocial euglossine bee, *Eulaema* (*Apeulaema*) *nigrita* Lepeletier, with notes on nests and orchid visits of two euglossine species, *Euplusia auriceps* (Friese) and *Euglossa* (*Euglossa*) *cordata* (Linné). Another part deals with a review of the biology of Euglossinae based upon so far published records.

2. As to nest structure, all euglossine bees are common in the absence of self-excavating nests, the use of resin for nesting material and the elliptical and radial symmetric brood cells without inner wall coated by self-produced substance. Beside these common characters, three principal nonparasitic genera differ in nest structure one another as follows: *Euglossa*: Nests are made by resin alone, with possible admixture of self-produced wax. There are two distinct nest types. One is aerial with resinous envelope. Another type is made in more or less closed cavities, the walls of which are at least partly coated with resin. Cells are mostly clustered but a tendency to comb formation is recorded in one species. *Eulaema*: Nests are made in closed cavities, the wall of which receive no special coating. Nesting material is resin, used with abundant mixture of mud or animal feces. Cells are clustered, but one species shows the comb arrangement. *Euplusia*: Nests are often made at relatively exposed sites, using resin mixed with pieces of bark. Cells are arranged in series (allodalous). One species, *Ep. nigrescens*, deviates markedly from the other species by its peculiar cell structure. As far as the nest structure is concerned, these three genera cannot be arranged along the linear evolutional course as assumed by Friese. For the time being, it is difficult

to assume the ancestral nest structure common to these genera.

3. Larva and pupa of *El. nigrita* were described and some comments were given as to immature stages of Euglossinae, characterized by the longer duration than in other three apid groups, especially in *Euplusia*.

4. Intranidal behavior of Euglossinae was first observed with *El. nigrita*, using a glass-lid observation case. Most females (major females) leave the nest immediately to a few days after emergence, performing or not some intranidal tasks including foraging of feces. A fraction of females (minor females), distinctly smaller than others, however, stay in the nest and participate in cell construction, provisioning, oviposition and other intranidal tasks.

5. Cell construction in *El. nigrita* differs from that in other solitary bees, in the separation of two performance series, foraging of materials and construction itself. Foraged materials, either resin, which is mostly foraged by minor females, or feces, foraged also by major bees, are deposited at the storing place, which is used commonly by all females. Each cell is constructed since the start to the penultimate phase continuously by a single female. Cell construction lasts about 10 hours and proceeds through the alternation of collecting of material from the storing place, transporting of it to the place where the cell is made and construction. During and after construction, the owner female defends the cell against other females approaching nearby. The final part of cell construction, refinement of cell inner wall and cell collar, forms a separate phase, lasting much longer time and made intermittently even after the beginning of provisioning, often with the participation of other minor females, usually in the absence of the owner.

6. Provisioning to each cell is mainly performed by the cell owner during several days, though other minor females participate in it. Oviposition is preceded by prolonged refinement of inner cell wall and cell collar, and immediately followed by the operculation, which is made, except for the final refinement, solely by the cell owner.

7. Other intranidal activities were described and discussed. Within the nest, females of *El. nigrita* are virtually independent one another, avoiding mutually at encounter, without combats except for some situations.

8. The bibliographical survey clarifies most nests of Euglossinae are founded by lone females. Nest cavities are often succeeded by later generations. Some species of *Euglossa* and *Euplusia* are certainly solitary, though nest aggregations frequently develop in the latter genus. In some species of *Euglossa* and *Eulaema*, previous records note the presence of more than one female in the same nest, or the fact suggesting such coexistence, revealed by the large number of cells. These nests are likely to be made by the stay of more than one female in the nest, presumably each working mostly independently. Observations in *El. nigrita* confirm the occurrence of such communal state, with implication of some quasisocial trends. The presence of major and minor females in *El. nigrita* and their functional differentiation suggests a type of division of labor in this species, still with no genuine caste differentiation. Some related problems on social organization were reviewed and

discussed.

9. Previous observations on male behavior were reviewed and discussed, with special emphasis upon the singular behavior, visits to certain specialized orchid flowers, collecting of odor substance from them and storing them in tibial organs. Previous records on flower visitis, animals associated with Euglossinae, as well as some fragmentary notes on habitat preference and phenology on Euglossinae were also reviewed and discussed.

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———— MS. Considerações bionômico-evolutivas sôbre a sociologia de algumas espécies de abelhas. Tese para doutramento.

* ————, Oliveira, B.L. de e J.M.F. Camargo MS. Notas bionômicas sôbre *Euglossa* (*Glossura*) *intersecta* Latr. e descrição de sua larvas e pupa (Euglossini, Apidae).

Addenda

After the completion of the manuscript, the following two publications have come to hand:

*Rudow (Prof.) 1913. Die Wohnungen und Lebenstätigkeiten der honigsammelnden Bienen, Anthophilidae. Ent. Zs. Frankfurt a.M. **26**: 165–166, etc. (With desciption of an aerial nest of "*Euglossa cordata*" (certainly a different species) similar to the nest of *Eg. dodsoni*. *Cf. 1.3.1.*).

*Müller, A. (ed.) 1921. Fritz Müller—Werke, Briefe und Leben. **2.** Briefe und noch nicht veröffentlichte Abhandlungen aus dem Nachlass 1854~1897. Jena, Gustav Fischer. (With fragmentary notes on *Exaerete* and *Euglossa*, including flower visits, especially to *Buddleya* and *Costus*, preference of *Euglossa* males for *Catasteum* and a note on a concealed nest of a blue *Euglossa*, with cells and coating of cavity made from black wax like material — probably the oldest record of the euglossine nest structure).

Explanation of Plate IV

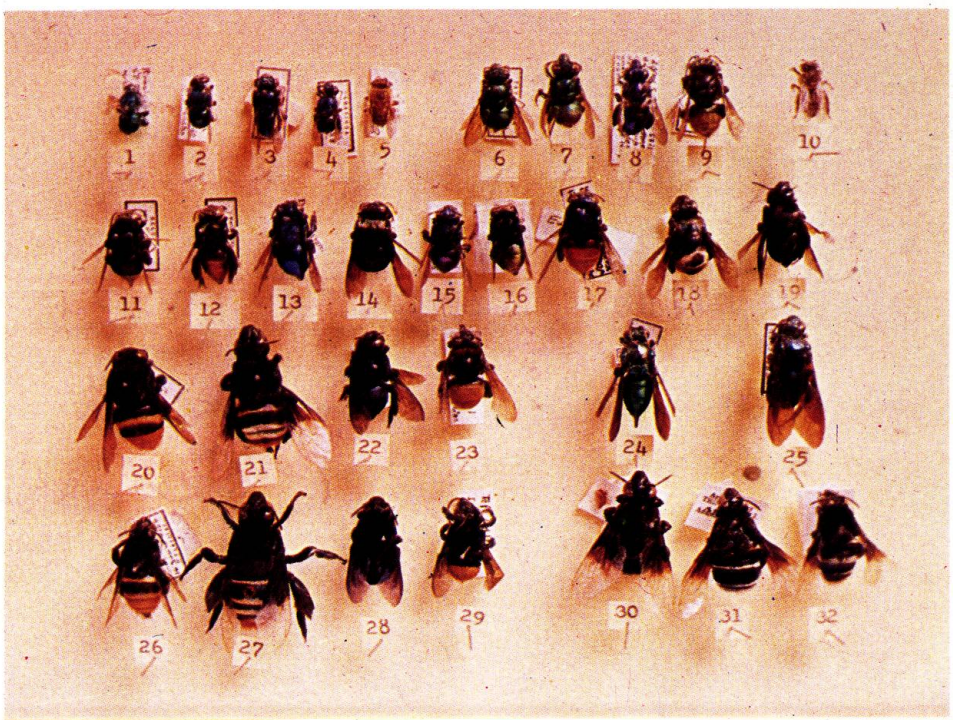
A (Top). Some representative species of Euglossinae (mostly from the collection of Prof. Pe. J.S. Moure, CMF)
1,2,4. *Euglossa* (s.str.) spp. (1. *Eg. cordata* ♂, 2. *Eg. analis* ♂), 3 and 5. *Euglossa* (*Euglossella*) *mandibularis* ♂ and *Eg.* (*Egl.*) *decorata* ♀, 6~9. *Euglossa* (*Glossura*) spp. (6. *Eg. ignita* ♀, 7. *Eg. piliventris* ♂, 8. *Eg. asarophora* ♂, 9. *Eg. intersecta* ♀), 10. Worker of European honeybee for size comparison, 11. *Eufriesea pulchra* ♀, 12~23. *Euplusia* spp. (12. *Ep. purpurata* ♀, 14 and 15. *Ep. violacea* ♂ and ♀, 17. *Ep. mariana* ♀, 18 and 19. *Ep. nigrescens* ♂ and ♀, 21. *Ep. ornata*), 24 *Exaerete smaragdina* ♀, 25. *Aglae caerulea* ♂, 26~31. *Eulaema* spp. (26, *El. cingulata* ♂, 27. *El. meriana* ♂, 28. *El. nigrita* ♀, 29. *El. polychroma* ♀, 30. *El. terminata* ♂, 31. *El. bennetti* ♂, 32. *El. basicincta* ♂.

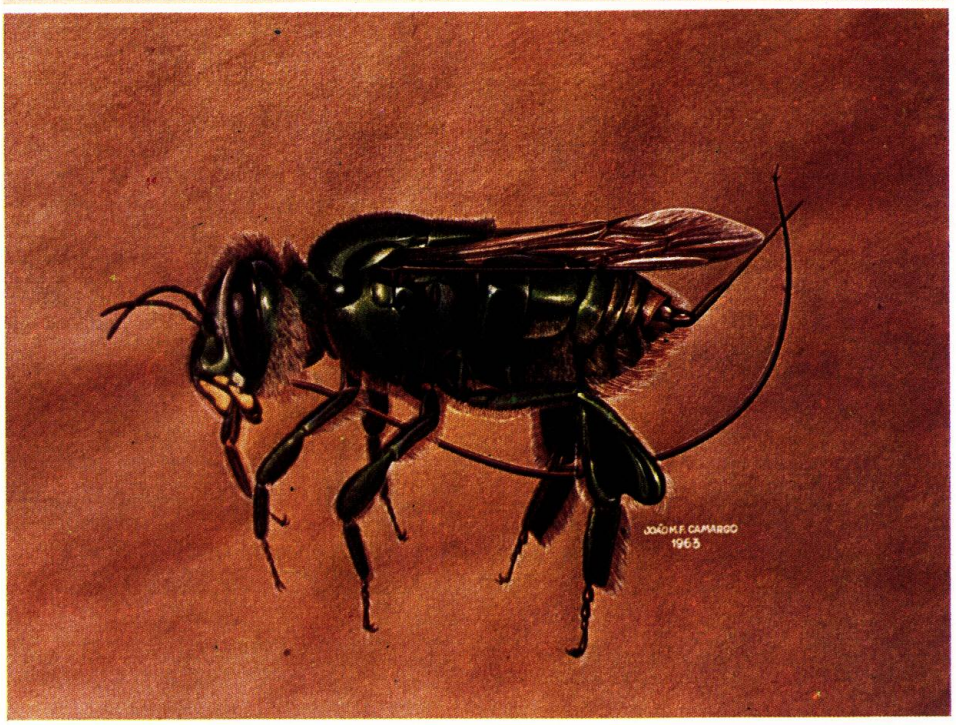
B (Bottom). *Eg.* (*Glossura*) *piliventris* ♀, showing extremely long glossa and corbiculate hind tibia.

Explanation of Plate V

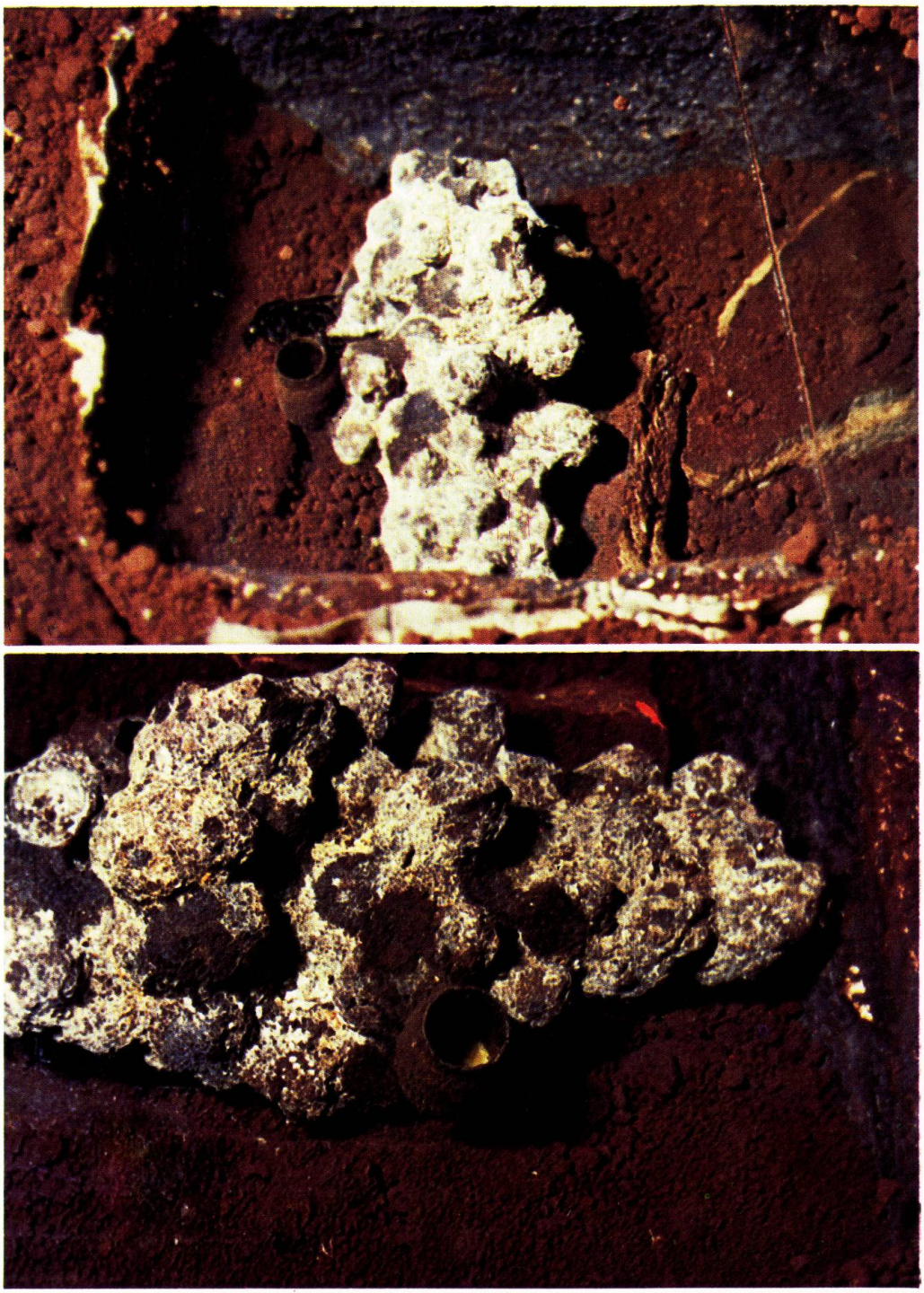
A (Top). Nest cluster of *Eulaema nigrita*, with one minor female provisioning a newly made cell. Nest cluster is still covered with molds, which were later removed by bees.

B (Bottom). Ditto, enlarged, showing deposition of pollen in the cell.





R. Zucchi et al.: Biological Observations on Eulaema nigrita



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