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Citation	, 18(1), 57-127
Issue Date	1971-10
Doc URL	http://hdl.handle.net/2115/27518
Type	bulletin (article)
File Information	18(1)_P57-127.pdf

Observations on the Bionomics of Some Neotropical Xylocopine Bees, with Comparative and Biofaunistic Notes (Hymenoptera, Anthophoridae)[1][2]

By

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(*With 59 Text-figures and 7 Tables*)

Contents

Introduction

Among numerous groups of bees the subfamily Xylocopinae or carpenter bees has certain characteristic bionomic features. Recent studies confirm interesting social systems in some genera of this group, *Exoneura*, *Allodapula*, etc. (Michener 1962b, 1964a, 1965, 1968). But the genera with simpler modes of life are none the less worth study for some remarkable bionomic characters such as prolonged adult life, coexistence of mother and offspring, plasticity in nesting habits, etc. Our knowledge of this group is still insufficient, mainly due to their scarcity in temperate regions, where most comprehensive studies have been carried out. In the present paper, we described our observations on the bionomics of some Neotropical species, made mostly in southern Brazil, partly in Paraguay. The results are in most species casual and often incomplete. Nevertheless we believe these notes may stimulate further comparative studies in the Neotropical region, where the bionomic information is still scanty in comparision with the rich xylocopine fauna.

Most nests examined were collected in two localities, Curitiba and Castro,

Table 1.   Main climatic conditions in Curitiba and Castro (from Ostea *et al.* 1954)

locality	Curitiba				Castro			
	mean temperature (°C)			rainfall (mm)	mean temperature (°C)			rainfall (mm)
month	maximum	mean	minimum		maximum	mean	minimum	
January	26.5	20.1	16.0	182.7	26.4	19.7	15.3	197.6
February	26.3	20.1	16.0	148.9	26.4	19.6	15.2	150.2
March	25.4	19.2	15.3	105.0	26.0	19.1	14.7	110.7
April	23.2	17.1	13.0	75.5	23.7	16.7	11.8	78.4
May	20.5	14.3	9.6	88.1	21.2	13.6	8.0	92.1
June	18.9	12.9	8.0	104.2	20.2	12.2	6.4	98.4
July	18.9	12.1	6.8	69.3	19.9	11.3	5.1	65.1
August	20.2	13.5	8.1	84.6	21.5	12.8	6.4	88.6
September	20.7	14.5	9.9	123.8	21.7	14.4	8.8	113.2
October	22.1	15.9	11.6	122.1	23.2	16.1	10.9	124.6
November	24.5	17.7	13.1	119.9	24.7	17.6	12.4	132.2
December	25.7	19.3	14.9	138.3	26.1	19.3	14.4	162.8

including their outskirts, both in the State of Paraná.   The annual weather condi-
tions in these two localities are shown in Table 1.   For comparative notes, the
previous papers on the bionomics of the subfamily were consulted as far as possible,
but no complete bibliographical survey was attempted.   Besides collecting nests,
some adult bees were captured on flowers in the course of two periodical wild bee
samplings made at São José dos Pinhais near Curitiba (cf. Sakagami, Laroca and
Moure 1967) and at Boa Vista, Curitiba.   By incorporating the data from these
surveys, the present paper forms a part of our serial work on the wild bee
biofaunistics and biocoenotics in Eastern Paraná.

1.   The genus *Xylocopa* Latreille

The previous observations on the bionomics of Neotropical large carpenter bees
or *Xylocopa* were reviewed by Malyshev (1931).   Later Hurd (1958) published some
additional observations and Hurd and Moure (1963) made a reference list on nesting
habits and nesting substrates, based upon an extensive bibliographical survey.
However, there is no single Neotropical species the annual life cycle of which was
precisely followed as in some temperate species, for instance, *X. valga* (Malyshev
1931) and *X. virginica* (Rau 1933).   In our observations, too, the annual cycles
were not completely traced.

In the present paper, each nest is separately described and illustrated, with special
emphasis on the contents, both immatures and adults, because extraction of *Xylocopa*
nests, particularly those in timber, often confront various circumstantial difficulties so that
precise description is relatively rare.   Each nest is abbreviated as *Ar-1, Br-3*, etc.; the two
letters represent the species name (*Ar=artifex, Br=brasilianorum*, etc.), and the numerals
are given in each species according to the date of nest discovery irrespective of the years,
starting from July, the southern mid winter.   In each nest the height of the entrance means

that from the ground level.   Lateral burrows[1] are designated in each nest with A,B,C, etc., and the length is measured from the point of ramification.   If necessary, cells in each lateral are indicated as I, II, III, etc., starting from the oldest cell.   The partitions separating cells are also numbered in the same way, for instance, the partition between cells I and II is called partition I.   In many nests in timber, laterals contain one to several barrel shaped enlargements indicating either traces of old cells or rudiments for future cells. The distinction between these two categories is often difficult and the term *cell cast* (CC) is used for both.   Sexes of pupae were not recorded in some species.   Wings ($♀♂$) and mandibles ($♀$) of adult inhabitants were examined to estimate relative ages, using the following degrees: Wings$=$W, mandibles$=$M, W_1, M_1, intact; W_2, M_2, slightly worn; W_3, M_3, moderately worn; W_4, M_4, considerably worn; W_5, M_5, heavily worn.   In some nests ovaries of females were examined and classified as follows: O_1, rudimentary; O_2, slightly swollen; O_3, moderately developed; O_4, with mature or submature eggs.   The relation of these classes to relative age is $O_1{\to}O_2{\to}O_3{\to}O_4{\to}O_3{\to}O_2{\to}O_1$, where symbols O′ was used if the degenerating phase was confirmed.   To capture all adult inhabitants, nests were taken as far as possible under adverse weather or in late afternoon though this was often impossible during trips.

Each nest is interpreted (abbrev. *IP*) with special reference to the two points: 1) History of the nest, especially the relation of the foundress ($G_1=$first generation) and the individuals found in the nests, which (G_n) could be either the foundress or her children (G_2) or grandchildren (G_3), etc.   Further discussions are given in 1.1.3 and 1.2.2.   2) Temporal position of the nest in the annual cycle, either in hibernating phase or in brood rearing phase.   In the latter case an emphasis is placed on whether the adult females in the nest belong to the hibernating generation ($=$females emerged in the last summer and started brood rearing activity after hibernation) or the summer generation (females produced by hibernating generation and producing the next hibernating generation).   Under the subtropical climate, hibernation does not result in complete cessation of flight activity, though brood rearing activity is interrupted.

Some architectural characters common to all species studied are summarized as follows: 1) All nests except one (*Ci-4*) were found in dead and dry substrates. 2) Nest entrances were made against the grain, never from the cut surface of the substrates. 3) With one dubious exception (*Ar-4*), all entrances found on the horizontal or oblique surface were excavated on the underside of the substrate (*Ci-2,3,5; Nr-1, Gr-1, Br-1, Au-1, Fr-4*). 4) Nest entrances were always open, usually more or less circular but often irregular, especially when made on hardwood substrates (*X. hirsutissima* and *X. augusti*, cf. Fig. 20).   5) In all timber nesting species, the nest consisted of a short entry canal made across the grain, and several laterals mostly made along the grain, though occasionally running obliquely (Figs. 16, 17, 26).   In some nests the end of the entry canal was enlarged, forming a chamber into which laterals opened (Figs. 14, 17). 7) Inner walls of laterals and cells were smooth.   A special waterproof lining (*X. valga*, Malyshev 1931) was not sought.   8) Lateral cell walls were straight in *X. ciliata* and *X. artifex*, barrel shaped in all other timber nesting species. 9) Cell length was often quite variable even within the same lateral.   10) Although not precisely examined in all instances, cell

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1) In *X. ciliata* and *X. artifex*, the terms upper and lower sections are used instead of laterals.

partitions were flat and rough with a spiral pattern on the inner side, concave and smooth on the outside. 11) Except in *X. ciliata*, pollen loaves were mostly elongate rectangular with round angles, mostly attaching to the lateral cell wall along most of their ventral surfaces.

Most of these characters, excluding 4), 6), 8) and 11), are noted also in the previous records of other species.

The names of the species studied by other authors and cited in subsequent pages are given here according to the recent usage (Hurd and Moure 1963), with the names used by the original authors if different. In subsequent pages, the years of publication are cited only when necessary.

Xylocopa (Afroxylocopa) nigrita (Fabricius): Smith 1859 after Malyshev 1931 (Sierra Leone).

X. (Alloxylocopa) appendiculata circumvolans Smith: Iwata 1956 (Japan).

X. (Biluna) auripennis Lepeletier: Iwata 1964 (Thailand).

X. (B.) tranquebarorum (Swederus): *X. orichalcea*, Iwata 1938a, *X. pictifrons*, Iwata 1964 (Formosa).

X. (Copoxyla) iris (Christ): Malyshev 1947 after Grandi 1961 and Bonelli 1967 (Russia); Grandi 1961 (Italy); *X. cyanescens*, Bonelli 1967 (Italy).

X. (Cyaneoderes) caerulea (Fabricius): Jacobson 1927 after Malyshev 1931 (Sumatra).

X. (Ctenoxylocopa) fenestrata (Fabricius): Kapil and Dhaliwal 1968a, b, 1969 (Punjab).

X. (Gnathoxylocopa) sicheli Vachal: Brauns 1913 (South Africa).

X. (Koptortosoma) aestuans (Linné): Horne 1872 after Malyshev 1931, Dover 1924 (India); Mellor 1928 after Malyshev 1931 (Egypt).

X. (K.) caffra (Linné): Skaife 1952 after Kapil and Dhaliwal 1968a (S. Africa).

X. (K.) confusa Pérez: Jacobson 1927 after Malyshev 1931 (Sumatra).

X. (K.) pubescens Spinola: Kapil and Dhaliwal 1968a, 1969 (Punjab).

X. (K.) ruficeps Friese: Iwata 1938a (Formosa).

X. (Megaxylocopa) fimbriata Fabricius: Bodkin 1917 (British Guiana), Janzen 1966 (Mexico).

X. (Mesotrichia) flavorufa (De Geer): Brauns 1913 (South Africa).

X. (M.) torrida (Westwood): Loveridge 1923 after Malyshev 1931 (Tanganyika).

X. (Neoxylocopa) brasilianorum sonorina Smith: Hurd 1958 (Pacific Islands).

X. (N.) b. varipuncta Patton: *X. varipuncta*, Nininger 1916 after Malyshev 1931 (the United States).

X. (Nodula) amethystina (Fabricius): Zollinger 1846 after Malyshev 1931 (Java).

X. (Notoxylocopa) tabaniformis orpifex Smith: Cruden 1966 (California); *X. orpifex*, Nininger 1916 after Malyshev 1931 (the United States).

X. (Nyctomelitta) tranquebarica (Fabricius): Jacobson 1927 after Malyshev 1931 (Sumatra).

X. (? Platynopoda) chloroptera Lepeletier: Horne 1872 after Malyshev 1931 (India).

X. (Platynopoda) latipes (Drury): Beeson 1938 after Kapil and Dhaliwal 1968 a (India); Jacobson 1927 after Malyshev 1931 (Sumatra); Sakagami and Yoshikawa 1961 (Laos).

X. (Schoenherria) macrops Lepeletier: Strand 1912 after Malyshev 1931 (Paraguay).

X. (Stenoxylocopa) nogueirai Hurd and Moure: Hurd and Moure 1960 (S. Brazil).

X. (Xylocopa) valga Gerstaecker: Malyshev 1931 (Russia).

X. (X.) violacea (Linné): Réaumur 1748 after Malyshev 1931 (France); Friese 1923 (Europe); Hardouin 1943, 1948 (France).

X. (Xylocopoides) californica arizonensis Cresson: Hurd 1958 (California).

X. (X.) c. californica Cresson: Cruden 1966 (California).

X. (X.) virginica texana Cresson: *X. texana*, Howard 1893 after Malyshev 1931 (Florida).

X. (X.) virginica (Linné): *X. virginica*, Rau 1933 (Missouri); Hurd 1958 (North Carolina, Washington, D.C., Kansas); Balduf 1962 (Illinois); Krombein 1967 (Maryland).

X. (Zonohirsuta) sauteri Friese: Iwata 1938 a (Formosa).

Proxylocopa (Proxylocopa) olivieri Lepeletier: Guthbier 1916 after Malyshev 1931 (S. Russia).

1.1. Observations on *Xylocopa*

1.1.1.   *X. (Nanoxylocopa) ciliata* Burmeister (Figs. 1∼3)

All previous nests records of this dwarf species indicate its dependence on hollow stalks of *Eryngium* spp. (Umbelliferae) (Malyshev 1931, Hurd and Moure 1961, '63). Nine nests, *Ci-1* to *9*, examined by us were all except one (*Ci-9*) collected from floral stalks of *Eryngium eburneum* in secondary grasslands in the State of Parana. *Ci-1, 4, 6∼8* were in erect stalks (80∼180 cm high) and *Ci-2,3,5* in the horizontal sections of stalks broken at heights of 40∼50 cm. *Ci-9* was found in a erect branch of *Escallonia montevidensis* (Saxifragaceae). These stalks and branch were mostly dry but *Ci-3* was still green at the base and *Ci-4* was green in the part occupied by the nest.

Nest entrance are 40∼45 cm high in the case of erect stalks, circular or slightly longer than wide and so beveled that the opening is wider exteriorly, with inner and outer diameters 7∼9×6∼8 mm (mean 7.8×7.0) and 10∼13×9∼10 mm (mean 11.3×9.3) respectively. The margins are sometimes but not always neatly smoothed. Each nest consists of a single burrow, both ends of which are in most cases compactly filled with fragments of pith, apparently taken from the walls of the hollow cavity. In *Ci-1* and *6* the nest entrances are located at the bottom of the burrow. In other nests, the burrow extends in both directions from entrance; in nests in erect stalks the upper section is always longer. Diameter of nest burrow (a) and that of stalks where containing burrow (b) are in *Ci-1* to *9* respectively as follows (in mm): 18/10, 16/9.5, 18/12, 19/12, 13/8, 16/11, 18/10, 20/15, 15/11. Walls of burrows are, except *Ci-4* and *5*, the newly started nests, neatly smooth.

Brood cells, found only in *Ci-1* and *3*, are quite variable in length, 13∼15 mm, exceptionally 20 mm, and as wide as burrow. Cell partitions are 1.5∼2.0 mm thick in *Ci-1* and 3.0∼3.5 mm thick in *Ci-3* at center, reaching 3 and even 5 mm at periphery. Pollen loaves are quite variable in shape; two loaves in *Ci-1* were nearly triangular, with two anterior projections and attaching to cell walls only with these and other two ventral projections (Fig. 1), that is, with the shape similar to the loaves of *X. valga* (Malyshev). Two loaves in *Ci-3* had no such projections, one (cell V) was attached to the cell wall along its entire ventral surface, the other only by its two ends (Fig. 2).

Nests examined:

Ci-1 (Fig. 1): São José dos Pinhais, Nov. 24 '61. Upper section 17 cm, 3 cells, I. medium larva, II. small larva, III. egg. An amorphous pollen mass

attaching to outer surface of Partition III. Lower section 3 cm, empty. Adult: 1♀ (W_2M_2). *IP*: Apparently nest recently constructed by G_1♀ of hibernated generation.

Ci-2: Tarumá, Curitiba, Feb. 16 '62. Nest burrow 7.2 cm long, without cells. Adult: 1♀ ($W_1M_1O_1$). *IP*: Burrow just started by G_1 ♀ either for hibernation or for brood rearing.

Ci-3 (Fig. 2): Locality and date=*Ci-2*. Apical (as to the stalk) section 10 cm, 5 cells, I. post feeding larva, II. large feeding larva already started defecation, III. medium larva. IV small larva. V. pollen loaf without immature. Basal section 8 cm, 1 cell, with pollen loaf alone, and amorphous pollen mass on inner wall of the burrow in front of Partition I. No adult. *IP*: Presence of pollen mass indicates the active foraging until soon before nest examination, and two cells closed without oviposition may suggest the senility of the nest owner (Malyshev 1931, '36), though similar instances were observed also in nests of other species not always made by old females (for instance, *Ar-3, Au-7, Hi-9*).

Ci-4 and *5*: Castro, March 11 '62. *Ci-4*: Upper section 12 cm, lower section only 0.5 cm. *Ci-5*: Length of burrow not exactly measured, about 10 cm. In both nests wall of burrow still not smoothed. Each inhabited by 1♀ (both W_1 M_1). *IP*: Nest burrows just started, probably for hibernation.

Ci-6~8: Castro, April 6 '62. *Ci-6*: Upper section only, 5.6 cm, with cleaned wall. *Ci-7*: Upper section 5.5 cm, with cleaned wall, lower section 4 cm, wall just being elaborated. Each inhabited by 1♀ ($W_1M_1O_1$). *IP*: Certainly burrow each occupied by 1 juvenile ♀ for hibernation. *Ci-8* was an abandoned nest ca. 15 cm long, with no occupant, inhabited by a spider.

Ci-9: (Fig. 3): São José dos Pinhais, April 26 '62. Branch containing nest was broken and the upper part lost. Nest burrow longer than 12 cm. Lower section only 1.5 cm without cell. Upper section with traces of at least 3 cell partitions. Adult: 1♀ ($W_5N_5O_2'$). Ovaries indicating previous activity by the presence of yellow bodies. *IP*: Apparently the old mother still surviving in the nest after dispersal of progeny.

Although less familiar than the nidification in timber, the use of hollow or pithy stems or stalks is fairly widespread in *Xylocopa*. Reviewing the nesting habits of various species, Hurd and Moure (1963) cited such preference at least in some species of *Lestis*, the Australian vicariant of *Xylocopa*, and of the following subgenera of the latter: *Nanoxylocopa, Schoenherria, Copoxyla, Gnathoxylocopa, Xylocopa, Xylomelissa* and *Epixylocopa*. The most well known cases are *X. sicheli* and *X. iris*. *X. sicheli* nests exclusively in green stalks of *Aloe* (Brauns). Its singular mandibles are specially adapted for this purpose. *X. iris* nests in a variety of stems and stalks, and has the trait of cutting down the upper portion of the stalks it uses either from the inside or from the outside. This behavior is explained as an adaptation for protecting the nest from swinging by wind (Malyshev 1947, Grandi, Bonelli). Although intimately linked with *Eryngium* as nest substrate, *X. ciliata* developed no such particular adaptations, either

morphological or ethological. The longer upper section of the burrow is similar to that of *X. iris*, but not *X. sicheli*.

Two nests with immature stages, *Ci-1* and *3*, show that nests are started at quite different seasons. The exact dates of nest foundation are unknown, but can be estimated from previous information on the duration of immature stages, summarized in Table 2. If the duration of immature stages in *X. ciliata* falls within the range shown in the table, which is quite variable among species, and if the relative age of the oldest immature individual in *Ci-1* and *3* is assumed respectively

Table 2. Previous records on the duration of immature stages in *Xylocopa*. E (Egg), L (Larva), fL (Feeding larva), pL (Postfeeding larva), pP (Prepupa), P (Pupa)

Species (Citation)	Duration of each stage (in days)				Total
X. nigrocincta (Strand 1912)					26
X. fenestrata (Kapil & Dhaliwal 1968a)	E 2.8~3	L 10.8~11.8		pP 7 P 12	30.8
X. violacea (Reaumur 1748)	E /	fL 21	pL 5~6	P 7~8	E+33-35
X. tabaniformis orpifex (Nininger 1916)	E 7	fL 22~28		pP+P 15~19	40~45
X. latipes (Beeson 1938)	E 6-7	L 21		P 14~15	42
X. fimbriata (Bodkin 1917)	E /	fL 21	pL 2	P 21	E+43
X. virginica (Krombein 1967)	E 5~8	fL 11	pL 7	P 21	44~47
X. valga (Malyshev 1931)	E 5	fL 14~21	pL 7	P 14~21	45
X. iris (Bonelli 1967)	E 7	fL 15~18	pL 6~12	P 30	58~67
X. caffra (Skaife 1952)	E 19~24	fL /	pL 14~15	P 30+	83~90
X. brasilianorum varipuncta (Nininger 1916)	E 7	fL 30	pL 20	P 40	100

as at the midpoint of feeding larva and postfeeding larva, it is estimated that oviposition was, respectively, 8~30 days and 15~47 days before the discoveries of the nests, or during late October to middle November in *Ci-1* and during early January to early February in *Ci-3*. The first case is clearly a nest made by a hibernated female. On the other hand, the second one is too late to be similarly interpreted. It may be either a nest founded by a summer generation female or the second nest of a hibernated female, as recorded for *X. valga* (Malyshev). The fact that two pollen loaves were sealed without oviposition favors the second assumption, because similar aberrant behavior has been recorded for senile females (Malyshev 1931, '36). Even if this interpretation is true, the other nest taken on the same day, *Ci-2*, contained a young female apparently produced by a hibernated female. Thus it is assumed that the summer generation is partial even if occurs.

Other nests except *Ci-8* were certainly in hibernating state. Some old mothers also enter hibernation *(Ci-9)*, but it is unknown whether they survive until the next spring or not. No nest examined shows the successive use by more than one generation. This is understandable from the fragile nature of the preferred substrate.

Three types of defensive behavior by females were observed: Closing of the entrance by means of the metasomal dorsum *(Ci-1)*, attempting to sting and expulsion of a yellowish fluid from the anus *(Ci-6)*. The first type of defense is known in several species, *X. appendiculata* (Iwata 1956), *X. tranquebarorum* (Iwata 1938 a), *X. auripennis* (Iwata 1964), *X. torrida* (Loveridge) and *X. virginica* (Rau), and the expulsion of fluid in *X. fenestrata* (Kapil and Dhaliwal 1968b).

### 1.1.2. *X. (Stenoxylocopa) artifex* Smith (Figs. 4～6)

The previous information on the nesting habits of this Neotropical bamboo carpenter bee was reviewed by Hurd and Moure (1960) in relation to the bionomics of an allied species, *X. nogueirai*. The following records of nine nests, *Ar-1～9*, all collected in the State of Parana, are supplementary to the previous records. All nests were found within internodal hollow cavities of erect bamboo culms, *Ar-8* and *9* in *Bambusa* sp. and the other ones in *Merostachys* sp. *Ar-4* was found in the horizontal section of a broken culm, but it is plausible that the nest was made when the culm was erect. Internodal sections used for nesting were all dead and dry, though the basal part of the culm containing *Ar-1* was still green.

Nest entrances are located from 28 to 120 cm (mean 68 cm) high, and all but *Ar-9* opened below the middle of their internodal cavity. Nest entrances are usually with neatly made interior margins and so beveled that the opening is slightly larger exteriorly and usually longer than wide. The exterior diameters (longitudinal and transversal, in mm) in some nests are 8.5×7.1, 9×9, 10×8, 7.8×7 and the interior ones 6×5.5, 8×7.5, The nest cavity is cleaned but otherwise not particularly elaborated. The outer diameter of the internodal section used for nests and the corresponding inner diameter of the burrow (in parentheses) are in mm, 20 (8～10), 19 (14), 15 (12～13), 15 (12), 20 (14), ? (10.5～12), 18 (12.5), 18 (12).

Brood cells were found in *Ar-4* and *8*, and traces of removed partitions in *Ar-9*, except for two remains in *Ar-9*, all in the section above the entrance. Cell lengths are 13～14 mm, exceptionally 18 mm. In contrast to *X. nogueirai*, no particular partition between the top of the cavity and the bottom of the first cell was found except in *Ar-8*. Cell partitions are 0.8～1 mm thick at the center and 1.5 mm at periphery in one case, and 1.0 mm at periphery in another case. No complete pollen loaf was observed.

Nests examined:

Ar-1: Boa Vista, Curitiba, Aug. 19 '63. Cavity 12 cm, lower section infested by fungus. Adults: 3 ♀♀ (all $W_1M_1O_1$) and 3 ♂♂ (all W_1). One ♂ very small, head width 4.5 mm whereas 2 others 5.4 and 5.6 mm respectively. *IP*: Apparently
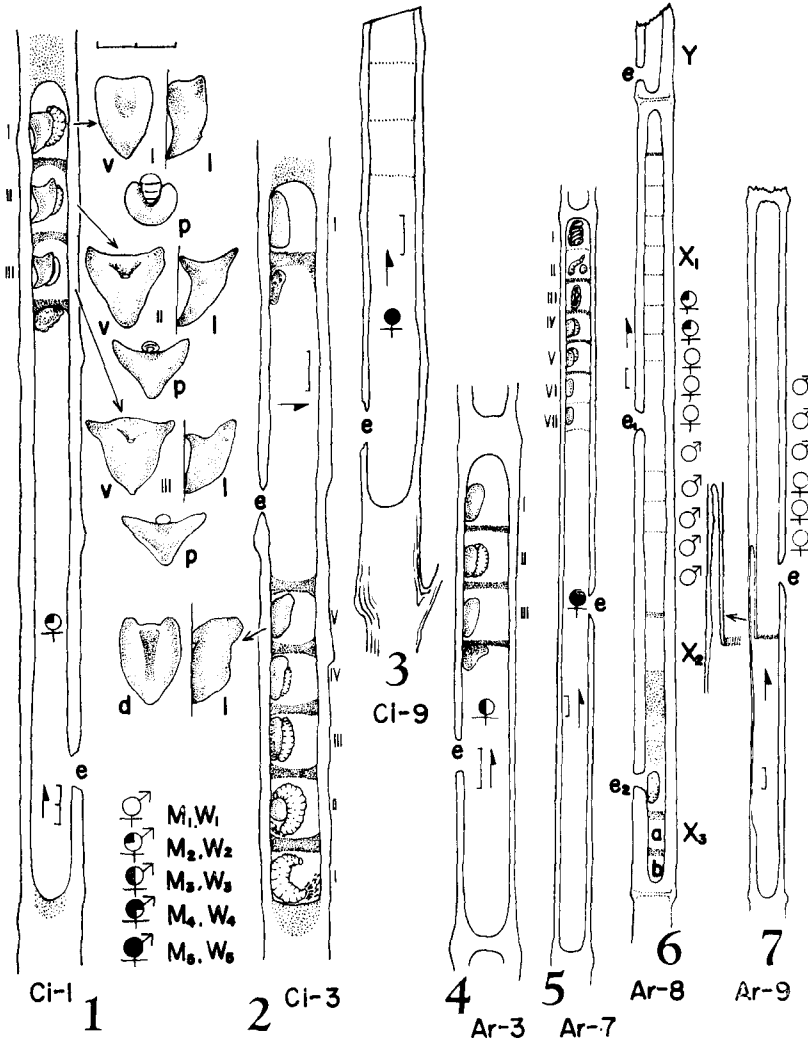
Figs. 1~7. Nests of *Xylocopa ciliata* (1~3) and *X. artifex* (4~7). In these and subsequent figures, nest numbers are shown below figure numbers. Scale lines represent 1 cm, arrows indicate upward direction and "e" nest entrance. Cells are numbered with Roman numerals. Adults are shown with ♀ or ♂, giving relative ages by mandibular ($M_1 \sim M_5$ in ♀♀) or wing wear ($W_1 \sim W_5$ in ♂♂) as shown in Fig. 1, bottom. In Figs. 1 and 2, shape of pollen loaves, ventral (v), dorsal (d), lateral (l) and posterior (p) views. Letters in Fig. 6 are explained in text.

indicating the final stage of communal hibarnation by juvenile association, probably consisting of sibs.

Ar-2: Locality and date=*Ar-1*. Cavity ca. 30 cm. Adult: 1 ♀ (W$_1$M$_1$O$_1$). *IP*: Solitary hibernation.

Ar-3 (Fig. 4): Boa Vista, Curitiba, Nov. 9 '63. Burrow 12.1 cm. Upper section 7.2 cm with 3 cells I. pollen loaf alone, II. small larva with loaf, III. pollen loaf alone. An amorphous pollen mass on outer surface of Partition III. Lower section 4.1 cm, no cells. Adult: 1 ♀ (W$_2$I$_2$O$_4$). *IP*: Apparently nest stated by the hibernated female in ealry spring.

Ar-4: Locality and date=*Ar-3*. Found in the horizontal section of a culm, probably broken after nest foundation, because nest entrace found at the upperside of the culm, a position avoided in hitherto known horizontal nests of *Xylocopa*. Cavity 32 cm, apical and basal section 24.4 and 7.0 cm respectively.

Remains of 1 ♀ and 1 ♂ dead in the cavity and two cocoons of an unidentified parasitic Hymenoptera at bottom of basal section. *IP*: Probably bees are posthibernating juveniles killed by parasites or by disorientation of nest.

Ar-5: Boa Vista, Nov. 25 '63. One ♀ just excavating a nest entrance on the surface of a culm of *Merostachys* was noticed at 14:15 (15°C). The bee escaped at our approach. Ten minutes later, she returned and continued the work for one minute before departure, leaving a shallow depression of 4×4 cm. The place was revisited on Nov. 27 (12:13) and the entrance was already complete. The bee left seven minutes after our arrival and returned after six minutes without bringing pollen, and stayed in the nest until our departure (13:00). *IP*: It is uncertain whether the female belongs to hibernating generation or summer generation.

Ar-6: Boa Vista, Dec. 9 '63. Cavity 24 cm. Upper and lower sections 15.2 and 8 cm, with no cell. Adult: 1♀ (W$_4$M$_4$O$_2$). *IP*: To late to be regarded as the first nest founded by a hibernated female, and too worn for a summer generation female. Possibly a second nest of a hibernated female.

Ar-7 (Fig. 5): Boa Vista, Dec. '63. Nest opened on Jan. 15 '64. several days after collecting. Cavity 36.8 cm, upper (A) and lower (B) sections 19 and 17 cm. A, 7 cells, I. dead dry pupa with pigmented eyes, II. large larva of an unidentified parasitic hymenopteran and half consumed pollen loaf, III. cocoon of a parasitic hymenopteran, IV and V. each with dead larva on pollen loaf, VI and VII. pollen loaf alone. Partitions I, VI, VII already destroyed. Adult:1 dead ♀ (W$_4$M$_4$). *IP*: Some immatures were certainly killed by parasites. It is uncertain whether the removal of partitions and absence of larvae on pollen loaves was caused by parasites, because the nest was opened a considerable time after collecting. It is probable, however, that the nest represents the later stage of brood rearing activity.

Ar-8 (Fig. 6): Abranches, Curitiba, March 23 '63. One nest entrance (e) opening into a damaged internode infested by fungi (Y), and two other entrances (e$_1$, e$_2$) into the internode (X, 38.6 cm long) next below Y. The upper part of X with traces of partitions, indicating 8 cells above (X$_1$, 15.2 cm) and 2 below (X$_2$,

17.4 cm) e_1. The uppermost part of X_1 narrow, separated from the rest by a partition (2 mm thick) about 1 cm from the top. A similar partition seen in X_2, 9.4 cm below e_1. The rest of X_2 partly filled with fine wood particles; the lowest part X_3 with two cells (a, b) filled with dead spiders, certainly served as the nest cavity of a hunting wasp. Adults: 5 ♀♀ (2 $W_2M_2O_2$, 1 $W_1M_1O_2$, 2 $W_1M_1O_1$) and 5 ♂♂ (all W_1). *IP*: Seemingly e_2 indicates the old nest cavity and e_1 a later nest, the progeny from which (G_2) were collected by us in the hibernating state. The correspondence of the number of bees and traces of old cells favors this assumption.

Ar-9 (Fig. 7): Morretes, April 21 '65. Nest cavity 35 cm long, upper and lower sections 9.8 and 15.8 cm respectively. Walls of lower section infested by termites and the section closed 2.6 cm below entrance by a partition of wood particles and soil, apparently made by termites. Adults: 3 ♀♀ (all $W_1M_1O_1$) and 3 ♂♂ (all W_1). *IP*: Apparently communal hibernation of juveniles in the old nest, invaded later by termites.

The nesting habits observed by us coincide with the previous records of this species and *X. nogueirai*. The only difference is the terminal partition made between the end of the nest cavity and the first cell, which seems to be regular in *X. nogueirai* but was not found in *X. artifex* except for *Ar-8* (not mentioned in pervious records of *X. artifex*). It is possible that this partition is made facultatively according to the situation. The closing of a cell after preparation of the pollen loaf, without oviposition (*Ar-3*), is recorded in *X. nogueirai*, too (cf. also *Ci-3*). One nest of *X. artifex* with 15 cells is recorded but in this case the sharing of a common nest cavity by two females is suggested (Hurd and Moure 1960). Our meager data do not give any conclusive evidence on the number of generations per year. Hurd and Moure (1960) observed nests of *X. nogueirai* in various stages in mid February in Cosmópolis, the State of São Paulo, including those with eggs, which favors the presence of a summer generation. All adults in *Ar-1* and all males and one female in *Ar-8* carried 30~100 small mites on the mesosoma and first metasomal tergum.

The utilization of bamboo culms is regarded as a special type of the nidification in hollow stalks discussed in 1. 1. 1. A tedious effort to perforate the hard and resistant surface of a bamboo internode is compensated by the omission of later burrowing and the substrate resistant enough to protect the contents. The preference for bamboo culms as nesting substrates is recorded in various subgenera of *Xylocopa* as follows: *Xylocospila, Schoenherria, Notoxylocopa, Neoxylocopa, Stenoxylocopa, Xylocopa, Biluna and Koptortosoma* (Hurd and Moure 1963). Some of these records may indicate merely a wide tolerance for various substrates and plasticity in site selection. For instance, *X. violacea* usually nests in dead and slightly rotten wood, but can accept bamboo tubes offered artificially (Hardouin 1943, '48). In some other cases the preference seems more definite. According to Kapil and Dhaliwal (1968 a), *X. pubescens* and *X. fenestrata* nearly exclusively nest in bamboo culms used for roofs of huts in Punjab. The highest specialization to this habit is exhibited by two subgenera, *Stenoxylocopa* in the Neotropics and

Biluna in the Oriental region, both provided with similar adaptive modifications of mandibles.

Moreover the nesting habits of these two subgenera are similar in the following points (concerning *Biluna* cf. Iwata 1938a, 1964): 1) The nest entrance is always made on the surface of a hard internode, never utilizing broken or cut ends as do most renting bees and wasps. 2) The nest entrance is slightly longer than wide and so beveled that the opening is larger exteriorly. 3) The nest entrance opens in most cases into the lower half of the internode. 4) Cells are mainly made from the top of the cavity downward. 5) Cell walls are straight, not barrel shaped. 6) Cell partitions are very thin, at periphery 0.9 mm in *X. nogueirai* (thicker in *X. artifex* as given above, perhaps variable according to conditions), 1.8 mm in *X. auripennis* (Iwata 1964) and 0.7 mm in *X. tranque-barorum* (Iwata 1938 a). In the last species, the thickness at the center is only 0.2 mm. 7) Old cavities are reused.

A possible ethological difference between the two subgenera is that material for partitions is take in *Biluna* from a definite place near the entrance, while no such observation has been made in *Stenoxylocopa*. In general, however, greater similarity than difference prevails between two subgenera, offering an instance of convergence in spite of their remote phyletic relation (Hurd and Moure 1960, '63).

1.1.3. *X. (Neoxylocopa) nigrocincta* Smith (Fig. 8)

According to Strand (1912) this species nests in dead branches of *Cerdella* and *Sapium* or in a dead shrub, *Lippia urticoides*, in Paraguay. A single nest was observed by us as follows:

Ni-1 (Fig. 8): Campus of Facultad de Agronomia y Veterinária de San Lorenzo, 30 km south of Asuncion, Paraguay, Jan. 15 '62. Found in a horizontal straight and heavily rotten log 380 cm long and 5 cm wide, held about 2 m high for supporting vines. Nest entrances neatly circular and 12 mm in diameter. After a very short entry canal nest branched in four laterals, A∼D, all opening in an elongate vestibule chamber (Fig. 8). Except for D, traces of barrel shaped cell casts clearly recognized: A. 16 cm, 6 CC; B. 17.2 cm, 8 CC; C. 7 cm, 3 CC; D. 6 cm, no CC. Diameter of burrow 1.3∼1.4 cm, old cell casts 18∼20 mm long, 16∼17 mm in maximum diameter and 14∼15 mm at constriction. A thin layer of pollen deposition observed on the bottom of lateral A. Adults: 1 ♀ (W_2M_2) and 1 ♂ (W_1). *IP*: In all probability two young bees are the progeny of the previous generation which excavated the nest. The pollen deposition could be interpreted either as indicating start of brood rearing activity or, as recorded in *X. virginica* (Rau), as food storage before hibernation. The first interpretation, which admits the reuse of old cells and the occurrence of at least two generations per year, seems to be more plausible, because the time is too early for the beginning of hibernation. The start of brood rearing activity before the dispersal of a communally living male is recorded in *X. tranquebarorum* (Iwata 1938 a) and plausible in *X. brasilianorum* (cf. 1. 1. 5.).

   The reuse of old nest burrows has already been mentioned in 1.1.2. Besides the bamboo bees, reuse is recorded in several other species (1.2.2.) and confirmed or suggested in species observed by us as indicated subsequently. On the other hand, when and how a given nest with more than one lateral, each possessing barrel like cell casts as in *Ni-1*, was founded is a problem not always easy to answer correctly. Because this problem appears frequently when such nests are examined, some possible instances are enumerated below:

 G_1: Founded by the lone female found in the nest examined.

   G_1': Founded by a lone female but becoming *communal* (Michener 1969) by later invasion of other females.

   G_{2a}: After G_1 or G_1' succeeded by a daughter who reused old cell casts.

   G_{2b}: As in G_{2a} but the daughter making her own cells by extending pre-existing laterals.

   G_{2ab}: Combination of G_{2a} and G_{2b}, that is, cells are partly reused and partly newly made.

   G_{2a}', G_{2b}', G_{2ab}': As in G_2 but succeeded by more than one daughter.
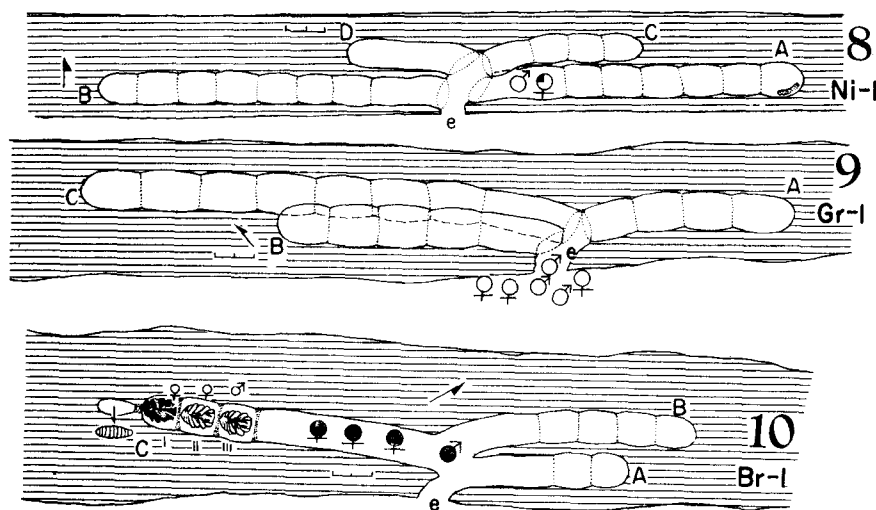
Figs. 8~10. Nests of *Xylocopa nigrocincta* (8), *X. grisescens* (9) and *X. brasilianorum* (10). Scale line represent 2 cm. In these and subsequent figures, laterals are shown by A, B, C,..Further explanation as for Figs. 1~7 and in text.

   In G_1 and G_1' young adult females found in the nest are the daughters of the foundress (or foundresses in G_1'), while in G_2 the granddaughters of the foundress. Theoretically a given nest can be utilized through several generations. In such a case, if G_{nb}, the nest may show a complicate labyrinthine system, whereas, if G_{na}, the burrow system may not differ much from the original system, though such repeated reused of old cell casts is less probable. Among the cases enumerated

Table 3.   Previous records on the number of cells produced by one female in
various species of *Xylocopa* (m=mean, mx=maximum)

Species (Authors)	Number of cells	Species (Authors)	Number of cells
X. amethystina (Zollinger 1846)	6~10, m 8	*X. nogueirai* (Hurd & Moure 1960)	m 5, mx 7
X. artifex (Hurd & Moure 1960)	6, mx 15		
X. fenestrata (Kapil & Dhaliwal 1968a)	m 6.14	*X. ruficeps* (Iwata 1938a)	ca. 8
		X. tranquebarorum (Iwata 1938a)	m 6, mx 8
X. iris (Malyshev 1947)	5~7		
„ (Grandi 1961)	6~11	*X. valga* (Malyshev 1931)	16~19
„ (Bonelli 1967)	7	*X. violacea* (Reaumur 1748)	18
X. nigrita (Smith 1859)	5~6	„ (Hardouin 1948)	12
		X. virginica (Rau 1933)	6~7

above, G_1' is seemingly rare, judging from the developed defensive behavior of many species.   Probably such communal life in the brood rearing season is possible only among individuals that lived together throughout the juvenile stage.   Iwata (1938a) recorded an instance in *X. tranquebarorum* interpreted as such reunion of previous nest mates.   The distinction of other cases is not easy, but the number of cell casts is indicative to some degree.   Thus, if G_1 (or G_{na}), the number of cell casts must remain within the number of cells produced by a single female, that is, hardly exceeding 20, as shown by previous records of various species (Table 3).

Returning to nest *Ni-1*, the number of cell casts, 17, is realized in some species, but higher than the average capacity in the genus, that is, the nest is probably older than G_1.   No further identification is possible but G'_{2b} or G'_{2ab} are plausible judging from the small number of cells produced per female in other *Neoxylocopa* species described subsequently.   Therefore the nest is interpreted as started by a lone female, succeeded by at least two daughters and their offspring, the grandchildren of the foundress, were probably collected by us $(G_n=G_3)$.

1.1.4.   *X. (Neoxylocopa) grisescens* Lepeletier (Fig. 9)

Only one nest of this species, probably the largest form of *Neoxylocopa*, was examined:

Gr-1 (Fig. 9):   Caculé, State of Bahia, July 22 '61.   Found in a fallen tree fixed only by a part of the root system.   The trunk, about 7 cm in diameter and quite rotten, laying nearly horizontally and swung by wind.   Nest entrance neatly circular, 16×17 cm in diameter.   All three laterals, A, B, C, provided with cell casts: A. 11 cm, 4 CC; B. 12 cm, 4 CC; C. 22.4 cm, 7 CC.   Cell casts quite variable in length 30 (3 cases), 28 (5), 25 (6) and 23 mm (1), 20~22 mm in maximum width and 18~19 mm wide at constrictions.   Adults: 3♀♀ (all W_1M_1) and 3♂♂ (all W_1).   *IP*: Juvenile association for hibernating and probably grandchildren (G_3) of the foundress as in *Ni-1*, judging from the number of cell casts.

1.1.5. *X. (Neoxylocopa) brasilianorum* (Linné) (Fig. 10).

X. brasilianorum has a wide distribution and is divided into several subspecies. Correspondingly, there are several nest records taken from various localities, including at Pacific Islands, where *X. b. sonorina* has recently dispersed through human interference (Hurd 1958). Nevertheless, no accurate description of nests taken in Brazil has so far been published. Only one nest was examined by us;

Br-1 (Fig. 10): Along the road between Morretes and Paranaguá, State of Paraná, April 21 '65. Found in an obliquely standing dead three about 8 cm in diameter, with dry and brittle wood. Nest entrance approximately circular, 15 mm in diameter, about 1 m high. Five other shallow holes excavated above and below the entrance, indicating abandoned efforts to make nests. Nest with tree vertical laterals, A and B above and C below entrance, all opening to short, obliquely ascending entry canal. A. 8.9 cm, 4 CC; B. 12.8 cm, 4 CC; C. 13.2 cm, 3 cells. I. quite pigmented ♀ pupa, II. white ♀ pupa, III. white ♂ pupa. Laterals about 18 mm wide at proximal parts. Cell casts $19 \sim 20$ mm long and about 18 mm in maximum diameter. A narrow chamber containing a larva of the meloid genus *Cissites* found at the end of lateral C, as recorded in *X. frontalis* (Hurd 1958). The chamber 22 mm long and 8 mm wide, separated from C-I by sawdust plug for 4 mm. Parasite with head directed toward C-I. Adults: 3 ♀♀ (all W_5M_5), and 1 ♂ (W_5). *IP*: The most plausible interpretation of the status of this nest is as follows: Founded by a lone female (G_1), succeeded by three daughters (G_2), which were captured by us. Each female worked in one lateral, either reusing old cell casts or making one new cell or more (G'_{2ab} in 1.1.3.). Their offspring already emerged and left the nest in A and B, while still remaining in C.

However, there are some problems which cannot be explained with precision: 1) The date of the first oviposition by the adult females is unknown. Applying the previous records on the duration of immature stages (Table 2) in general, the pupa in C-I is assumed to be from an egg laid one to two months ago. But if the duration given by Nininger for *X. brasilianorum varipuncta* is applied, which is 100 days, the longest among various records, it must have been laid at the beginning of January. At any rate, it is likely that the old females in the nest belonged to the summer generation. 2) The presence of one worn male is remarkable, because it suggests his continuous co-existence with sisters during brood rearing activities by the latter, unless he was an alien individual that later drifted in from the outside. Anyhow, his presence shows a quite long life span in males. 3) If our interpretation is correct, the number of cells produced per female is remarkably low. This peculiarity is also suggested in other species of *Xylocopa* and *Ceratina* described subsequently. 4) In spite of the presence of *Cissites* larva, all three pupae in lateral C were intact and no trace in other cells indicated damage by parasites.

1.1.6. *X. (Neoxylocopa) augusti* Lepeletier (Figs. $11 \sim 15$)

Some previous records of nests of this species are cited by Hurd and Moure

(1963) but no precise description has so far been published. Hurd and Moure note its preference for structural timbers, first of all, fence posts, in the State of Paraná. Most of eight nests studied by us, *Au-1~8*, all taken in the same state, were also found in fence posts.

Nest structure in general resembles that in the three species described above. Nest entrance circular or slightly longer than wide (16.5 × 14 mm in *Au-5*, 17 × 12 in *Au-7*, 18×15 in *Au-8*) when made in relatively soft substrates, but rather irregular and elongate when nest substrates are hard and resistant (31×12 mm in *Au-1*, also irregular in *Au-2~4*), probably made in part utilizing pre-existing slits. Short entry canal is excavated across the grain, from which several laterals go either in parallel or in opposite directions, mostly along the grain. In case of parallel excavation, laterals are often made in close proximity, so that the wooden substrate separating them is as thin as 2 mm, as already mentioned by Schrottky (1904). Further short laterals made obliquely or perpendicularly across the grain were formed in several nests. Laterals 16~18 mm wide with smooth walls. Cells are barrel shaped, 20 mm long, 17~18 mm in maximum diameter and 15~16mm wide at constriction. Cell partitions are 2 mm thick at center and 4~5 mm at periphery.

Nests examined:

Au-1 (Fig. 1): Uberaba, Curitiba, July 27 '63. Found in a slender dead and half fallen tree at the bank of Rio Iguaçu. Nest in the horizontal part of the trunk about 9 cm in diameter and entrance about 22 cm high. All seven laterals except A with old cell casts: A. 4 cm, no CC; B. 7 cm, 2 CC; C. 14 cm, 2 CC; D. 5 cm, 4 CC; E. 4 cm, 1 CC; F. 4 cm, 2 CC; G. 6 cm, 2 CC. Distance between ends of C and G 11 cm. A narrow chamber of *Cissites*, probably *C. maculata*, found at the end of D. Adults: 9 ♀♀ (1 $W_2M_2O_2$, all others $W_1M_2O_2$). *IP*: Nest was probabyl started by a lone foundress (G_1, cf. 1.1.3.). Judging from the number of cell casts, more than one daughter (G_2) used the nest and extended laterals by adding new cells. Certainly they also reused some old cell casts (G'_{2ab}), because, unless postulating the later invasion of some females, the number of progeny found in the nest (G_3) is seemingly too large in comparison with the number of cell casts confirmed, assuming the presence of some males already dispersed. One slightly worn female is probably starting the excavation of lateral A.

Ar-2~4: Tarumá, Curitiba, Oct. 15, '61. Three irregular nest entrances on a fence post of imbuia (*Phoebe porosa*, Laureriaceae), respectively at 30 (*Au-2*), 60 (*Au-3*) and 114 cm (*Au-4*) high. No precise observation was made but *Au-2* contained 2 ♀♀ and *Au-4* 2 ♂♂, all juveniles after hibernation. *Au-3* was an old abandoned nest with one upper lateral (8 cm long) and two lower ones (8 and 7 cm). One of the lower laterals contained an old nest of a megachilid bee and at discovery was occupied by an ant colony.

Au-5 (Fig. 12): Boa Vista, Curitiba, Nov. 27, '63. Nest entrance found in a dead branch (8 cm in diameter) of a living citrus tree (*Citrus aurantium*) at 4 m high. Nest with short entry canal and two vertical laterals. Lower lateral,
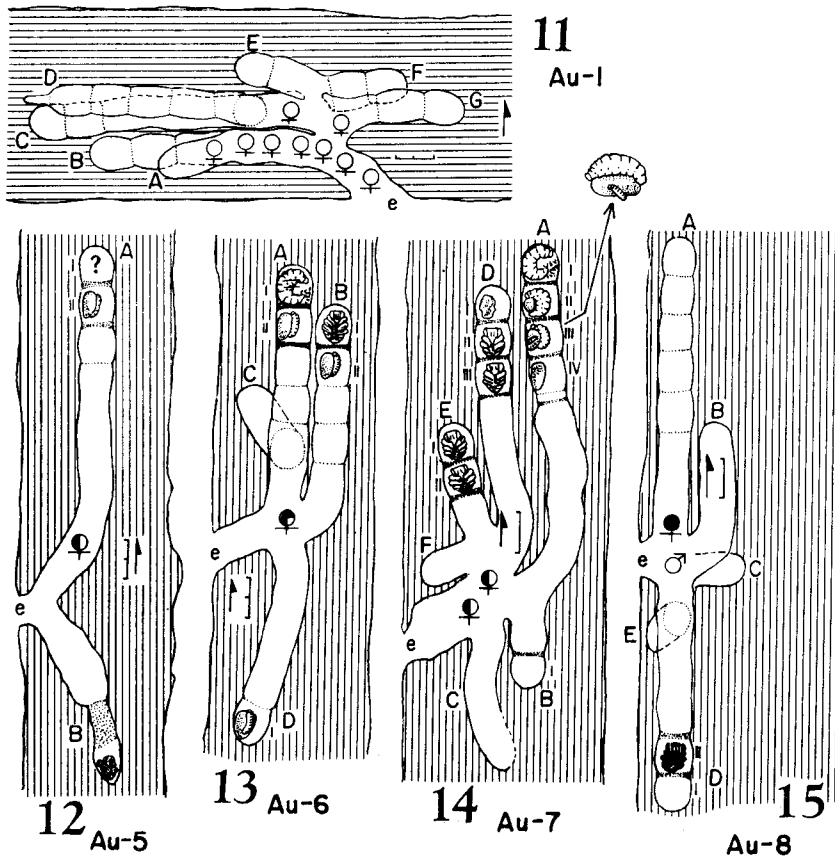
Figs. 11~15. Nests of *Xylocopa augusti*. Scale lines represent 2 cm. Further explanation as for Figs. 1~10 and in text.

B, seemingly once used by a coleopterous larva, with diameter enlarged to 22 mm; a narrow chamber at the lower end was closed with sawdust from the upper part and harbored young isopods. Upper lateral, A, about 18 cm long with two cells, I. content lost, II. small larva, and a cell cast below II. Adult: 1 ♀ ($W_3M_3O_3$). *IP*: Nest could be regarded as an incipient one started by a lone foundress (G_1) belonging to the hibernating generation, with a third cell now under preparation as in G_1 of 1.1.3. But the female is too worn to be regarded as starting the nest recently. An alternative interpretation, the foundation of a second nest using a pre-existing old burrow, is more likely and can explain reasonably the condition of the lower lateral, too.

Au-6 (Fig. 13): Taken together with *Au-5* from the same branch. Nest entrance 37.5 cm above that of *Au-5*. Nest with 3 upper laterals (A~C) and one lower

one (D). A. 10 cm; 2 cells and 2 CC, I. postfeeding larva, II. young larva; B. 10 cm, 2 cells and 2 CC, I. white pupa, II. young larva; C. 2 cm, opening into proximal part of A, no cell; D. 10 cm, 1 cell with young larva. Adult: 1 ♀ ($W_4M_4O_2'_{\sim3}$). A and B separated by wall only 2 mm thick. Interestingly cells B-II and D-I not sealed. *IP*: Judging from the number of cells and cell casts, the nest was made by a lone female and succeeded by a daughter (G_2), the female found in the nest, who made probably a few new cells, that is, G_{2b} or G_{2ab} (1.1.3.), using two laterals alternately, as shown by the relative age of immatures in A and B, probably in the order of B-I →A-I→A-II or B-II or D-I. A marked age difference between two immatures both in A and B suggests the ovipositions made with an interval of 10∼20 days (cf. Table 2). Another possiblity is the occurrence of communal nesting of more than one female in the nest, G_2', followed by the death or dispersal of some female or females, leaving only one. It is not impossible that the female found in *Au-5* was an ex-inhabitant of *Au-6*. If such was the case, the number of progeny reared is remarkably low, for the female in the nest already showed degeneration of ovaries.

Au-7 (Fig. 14): Castro, Dec. 31 '62. Found in a fence post of *Eucalyptus* about 10 cm in diameter. Nest entrance 118 cm high, followed by a remarkably enlarged entry canal from which issued six laterals: A. 8.5 cm, 4 cells, I. post-defecation larva, II. large larva on half consumed loaf, III. ditto, accompanied with a small beetle larva, possibly *Cissites*, IV. pollen loaf alone: B. 3.4 cm, 1 empty but sealed cell and 1 CC; C. 3.5 cm, no cell and cell cast; D. 6.5 cm, 3 cells, I. dry pollen mass alone, II and III each with pupa; E. 2.8 cm, 2 cells each with pupa; F. 1.2 cm, no cell. Adults: 2 ♀♀ ($W_3M_3O_{3\sim4}$), in both ovaries degenerated (or rudimentary) but the left ovary with one mature egg. *IP*: two females are the daughters, G_2, of a lone foundress, reusing old cell casts. Probably some new cells were added by them, because, if not, the number of cells produced by the daughters is smaller than that made by the foundress. The females examined may be the mothers of the immatures found ($=G_3$), each working in two laterals, that is, first in E (or D) then in A (or B). However, an alternative interpretation, that the females were elder sisters of the pupae in laterals just developing their ovaries, cannot completely be rejected. Three interesting facts concerning this nest are: 1) a sealed cell without content (B-I), 2) a cell with pollen loaf alone and sealed not at the lower constriction, but a little below (A-IV), and 3) a fairly large intact larva found together with a parasite (A-III).

Au-8 (Fig. 15): Castro, March 11 '62. Found in a fence post of *Eucalyptus* about 10 cm in diameter, with entrance about 1 m high. Nest with five laterals: A. 15.3 cm, 5 CC; B. 7.9 cm, no cell; C. 2.5 cm, no cell; D. 7.9 cm 2 cells, I. empty, II. black ♀ pupa; E. 1.6 cm, issued from D, no cell. Adults: 1♀ (W_5M_5) and 1 ♂ (W_1). *IP*: Apparently nest at the final stage of brood rearing activity. The occurrence of some other juvenile adult inhabitants is not probable because the nest was taken in cold weather. Therefore, it is inferred that juveniles left the nest, leaving the mother, a brother and an unemerged sister. The nest was either founded by the female in the nest (G_1) or she is a daughter of the foundress (G_{2a}

or G_{2ab}). In either case it is possible that the old female belongs to the summer generation, unless the nest is her second one.

The observations given above show the tendency of this species to make labyrinthine nests in structural timbers. Nest reuse is seemingly frequent. The presence of two generations per year is still not conclusive but probable from two cases, *Au-7*, *Au-8*. The most interesting fact is the occurrence of two unsealed cells, each with a larva, probably the first record in *Xylocopa*. The females are quite aggressive at their nests, closing nest entrances with the metasomal dorsum at a disturbance as does *X. ciliata*.

1.1.7. *X. (Neoxylocopa) hirsutissima* Maidl (Figs. 16~25)

Hurd and Moure (1961) recorded from Paraná a fence post containing active nests of *X. augusti*, *X. hirsutissima* and *X. frontalis*, which has been a unique authentic nest record of this species. Fortunately we could examine twelve nests, all taken in Castro (*Hi-3, 4, 5, 6, 7, 8, 11, 12*) and its suburb, Santa Quitéria (*Hi-1, 2, 9, 10*), in the State of Paraná. All nests were made in fence posts of imbuia bordering pastures. The posts were 6 to 11 cm (mostly 8~10 cm) in diameter, of a very hard and resistant nature.

Nest entrances were found at 25 (*Hi-1*), 40 (*Hi-8*), 42.5 (*Hi-9*), 60 (*Hi-2*), 90 (*Hi-11*), 93 (*Hi-7*) and 148.5 and 151.5 cm (*Hi-6*) high, mostly not neatly made, either irregularly circular (18~20 mm in diameter) or elongate (28~45 cm, *Hi-6*), often not well elaborated (Figs. 20, 22), probably because of the resistant nature of the substrate. The burrow system is similar to that of *X. augusti*, consisting of a short entry canal and several, mostly vertical laterals 19~22 mm wide, usually running along the grain. Laterals are often nearly straight and juxtaposed closely nearby as in *X. augusti*, separated from one another by thin walls, occasionally down to 0.5 mm thick. Further, one upper lateral and one lower one are often made in line with one another (cf. Figs. 18, 21, 23, 24, 25). But as in *X. augusti*, nests often possess short oblique or even transverse laterals (Figs. 20, 23, 19). Cells are 17~20 mm long, 16~18 mm in maximum diameter and 14~16 mm wide at the constriction; partitions are 1.5~2 mm thick at center and about 3~3.5 mm at periphery.

Nests examined:

Hi-1 and *2* (Fig. 16): July 16, '62. The post contained five nests; three upper ones were examined. The part occupied by these nest, *Hi-1*, *Hi-2* and *Fr-2* (cf. 1.1.8.) had a labyrinthine appearance due to ·the complicated burrow system. *Hi-1* contained one juvenile hibernating female ($W_1M_1O_1$) and four laterals: A. 9 cm, 4 CC; B. 6 cm, 3 CC; C. 4 cm, 2 CC; D. 5 cm, 1 CC. The distance between the ends of A and *Fr-2*, E only 2 mm, and B and *Fr-2*, G connected to each other by means of a narrow canal 3 mm wide, seemingly made by a *Cissites* larva. *Hi-2* was an old abandoned nest, identified to *X. hirustissima* from the width of the laterals. Nest with two entrances, two laterals contained nests of an unidentified
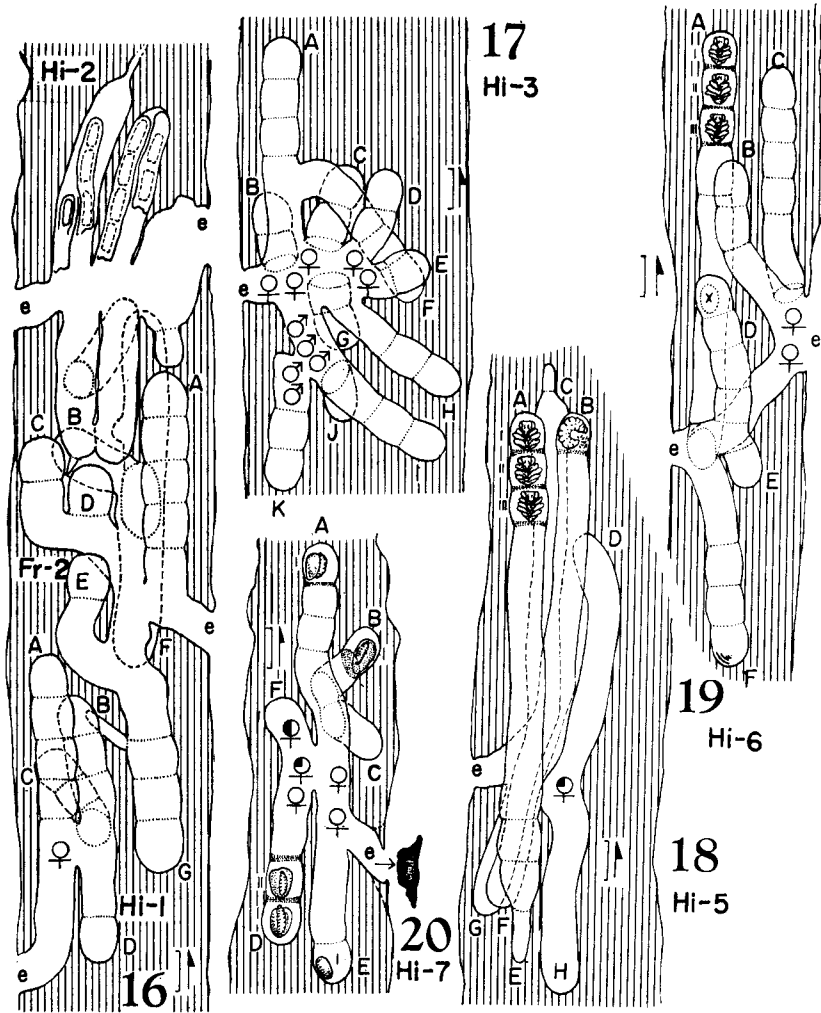
Figs. 16~20. Nests of *Xylocopa hirsutissima* (*Fr–2* in Fig. 16=*X. frontalis*). "X" in Fig. 19 is a spider's sac. Further explanation as for Figs. 1~10 and in text.

trypoxylonid wasp. Some laterals only 2 mm from those of *Fr-2*. *IP*: Both nests are either made by lone foundresses or later extended by daughters (G_1 or G_{2b} or G_{2ab}). *Hi-2* was, however, more likely to be used by more than one generation, judging from burrow system, two entrances and enlarged vestibule chamber.

    Hi-3 (Fig. 17): August 16, '62. Nest with 11 laterals opening into a widened entry canal: A. 10 cm, 3 CC; B. 4 cm, 1 CC; C. 4 cm, 2 CC; D. 5 cm, 1 CC; E. 3 cm, 1 CC; F. opening to A. 8 cm, 2 CC; G 4 cm, 1 CC; H. 8 cm, 2 CC; I. 7 cm,

2 CC; J. opening to I. 8 cm, 2 CC; K. 7 cm, 2 CC. Irregular arrangement of laterals unusual. Some laterals made obliquely across very hard grain. Adults: 5 ♀♀ (4 $W_1M_1O_1$, 1 $W_1M_1O_2$) and 5 ♂♂ (all W). *IP*: Certainly the nest was near the end of communal hibernation by juvenile adults. Probably succeeded by more than one daughters of the foundress, which was the mother of the adults found in the nest (G_3), and extended by the addition of new cells, with or without reuse of old cell casts (G'_{2b}, and G'_{2ab}).

Hi-4: Sept. 31, '61. Not examined in detail. Nest with a few adults which escaped at examination and 4 laterals each with 3, 4, 5 and 1 CC. A burrow of *Cissites*, 20 mm long and 8 mm wide, at the end of one lateral. *IP*: Probably in the final stage of communal hibernation as in *Hi-3*.

Hi-5 (Fig. 18): Nov. 5 '61. Nest with 8 laterals, among which A-E (24.6 cm, with a *Cissites* tube, 14 mm long at the end of E, B-F (25 cm), C-G (26.4 cm), D-H (23 cm) are respectively continuous. 3 pupae in A, 1 postdefecation larva in B and 2 CC in E. Adult: 1 ♀ (W_2M_2). *IP*: Judging from its relatively young age, the single adult female may be one of the elder sisters of the immatures, representing the summer generation, probably emerged from E. The small number of cells and cell casts is strange in comparison with long laterals, making reliable interpretation difficult, unless some accidental interruption of brood rearing activity is assumed.

Hi-6 (Fig. 19): Nov. 5 '61. Found in the same post harboring *Hi-7*, at about 17.5 cm above the entrance of the latter. Provided with 2 entrances connected to each other with a canal, containing 5 laterals: A. 20 cm, 3 cells each with pupa and 1 long CC; B. 8 cm, 2 CC; C. 11 cm, 4 CC; D. 7 cm, 4 CC, at the end with an egg sac of a spider (x); E. 2 cm, 1 CC; F. 10 cm, 3 CC; at the end with wooden dust. Adults: 2 ♀♀ (both W_1M_1). *IP*: Presence of two entrances is difficult to interpret but the fusion of two originally independent nests is not excluded. Another possibility is the succession of the original nest by more than one daughter of the foundress. These daughters made another entrance and added some new cells with or without reuse of old cells (G'_{2b} or G'_{2ab}), producing the females found in the nest (G_3), which belong to the summer generation.

Hi-7 (Fig. 20): Nov. 15 '61. With 5 laterals: A. 9.4 cm, 1 cell with young larva and 2 CC; B. 3.6 cm, 1 cell with young larva; C. 2.4 cm, no cell and cell cast (B and C opening into A); D. 7.4 cm, 2 cells each with young larva; E. 7 cm, 1 cell with still incomplete pollen mass; F. 3 cm, no cell and cell cast. Adults: 5 ♀♀, No. 1 W_1M_1, No. 2 W_1M_2, No. 3 W_2M_2, Nos. 4 and 5 each W_3M_3. *IP*: Females are summer generation daughters (G_2) of the lone foundress now reusing old cell casts, because if all cells are newly made, the number of old cells is less than that of adults emerged from them. But addition of one or two new cells is not excluded (G'_{2b}, G'_{2ab}). How the females shared the laterals is unknown, but the following assumption is likely: No. 5, D or A+B; No. 4, A+B or D; No. 3, E; Nos. 1 and 2, still not starting brood rearing activity.

Hi-8 (Fig. 21): Nov. 27 '61. With 4 laterals, forming two continuous ver-

tical burrows, AC and BD. A. 10 cm, 4 CC; B. 5 cm, 1 cell with young larva and 1 small partitioned space with small but elaborated pollen mass (x in Fig. 21); C. 8 cm, 4 CC and at the end an old *Cissites* tube 8 mm long, 5.4 mm wide; D. 5.4 cm, 2 CC. Adult: 1 ♀ ($W_3M_3O'_3$). *IP*: Probably nest made by a lone foundress and reused by a daughter ($G_n=G_2$). But the contents are enigmatic. In comparison with the age of the inhabitant, the immature is too young and too few in number. Is the female an invader making her second nest? Or, has the female laid an egg after a long pause from the previous oviposition? "Cell" II in B is noteworthy, with the length only 4 mm and not barrel shaped, containing a small but well elaborated pollen mass and sealed normally, being comparable to abnormal behavior found in senile females of *X. valga* by Malyshev.

Hi-9 (Fig. 22): Dec. 15 '61. Nest entrance found at the upper end of a natural crack 11 cm long and 2.5 cm wide on a fence post. With 2 laterals: A. 5 cm, 3 CC, the second cast connected to the outside by a narrow canal filled with wooden dusts, probably made by a *Cissites* larva; B. 4 cm, 1 cell with pollen loaf alone, but normally sealed. Adult: 1 ♀ (W_3M_3), one ovary still rudimentary while the other with a growing oocyte. *IP*: Case not easy to interpret. Assumption I: Nest is a small but old one previously made by a lone female. One daughter (summer generation) succeeded it and prepared a cell before the development of the ovary ($G_n=G_2$). But such premature provisioning is unknown in non social Xylocopinae and the age is a little older. Assumption II. Nest was
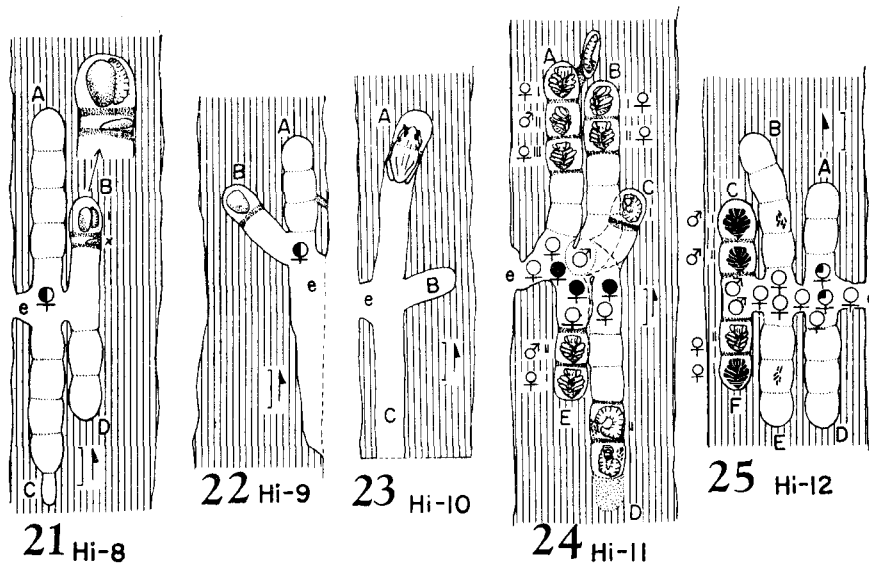
Figs. 21~25. Nests of *Xylocopa hirustassima* (continued). Scale lines represent 2 cm. Streaks in Fig. 25, B and E, are traces of defecation. Further explanation as for Figs. 1~10 and in text.

started by the female captured (summer generation, $G_n=G_1$). Three children already dispersed but the mother made an abnormal cell at her senility. But her age is still not too old and the departure of the progeny is too early. Assumption III: The female is an invader making her second nest as a reproductive anomaly. As in II, the age is still not old but this assumption is more likely than the other two.

Hi-10 (Fig. 23): Dec. 15, '61. An old abandoned nest found in the same post with *Hi-9*, in all probability made by *X. hirsutissima*. With 3 laterals: A. 10 cm, with a small frog; B. 3 cm, C. more than 18 cm. Inner walls fairly smooth. *IP*: Nest abandoned relatively recently, judging from the walls of burrows. The frog probably invaded after abandonment, because *X. hirsutissima* could easily defend the nest against a frog of such small size.

Hi-11 (Fig. 24): March 11 '62. With 5 laterals: A. 10 cm, 3 cells, I. ♀ pupa, II. ♂ pupa, III. ♀ pupa and 2 CC, at the end with a tube of *Cissites*; B. 10 cm, 2 cells, both with ♀ pupa and 2 CC; C. 3 cm, 1 cell with post feeding larva; D. 12 cm, 2 cells each with post feeding larva and 2 CC, at the end with a space filled with wooden dust for 18 mm; E. 7 cm with 2 cells, I. ♀ pupa, II. ♂ pupa. Adults: 7 ♀♀ (3 $W_1M_1O_1$, 1 $W_1M_1O_2$, 1 $W_5M_5O'_3$, 1 $W_5M_5O'_3$, 1 $W_5M_5O'_2$) and 1 ♂ (W_1). *IP*: Apparently nest reused by the offspring ($G_n=G_2$) from a single foundress, with possible addition of some new cells (G'_{2ab}), and at the end of brood rearing activity. How five laterals were shared by three old females is unknown. Of course the earlier deaths of other females are not excluded. Provenance of five juvenile adults is not clear. It is assumed that some of them emerged from cell casts in A and B. But in this case the order of development becomes inverse. Moreover, even if four adults emerged in such way, a fifth must be an invader, because its emergence from D is hardly possible. In general, the assemblage is regarded as a compound family before hibernation, consisting of three sisters with their offspring.

Hi-12 (Fig. 25): April 8 '62. With 6 laterals, forming 3 continuous vertical burrows, AD, BE, CF: A. 5.2 cm, 2 CC; B. 8 cm, 4 CC; with trace of larval defecation; C. 4.4 cm, 2 cells each with black ♂ pupa; D. 6.4 cm, 3 CC; E. 6.4 cm, 3 CC with trace of larval defecation: F. 4.4 cm, 2 cells, I. black ♀ pupa, II. white ♂ pupa, Adults: 9 ♀♀ (4 $W_1M_1O_1$, 2 $W_1M_2O_2$, 1 $W_1M_1O_2$, 2 escaped) and 2 ♂♂ (both W_1). *IP*: Either the work of a lone foundress (G_1), the offspring of which are in part still before emergence but mostly entering communal hibernation ($G_n=G_2$), or the bees captured are the grandchildren of the foundress ($G_n=G_3$). The latter assumption is likely from the small number of cells seemingly produced by a single female in other nests. In either case, the mother or mothers produced G_n probably belong to the summer generation. Two females seemingly participating in the removal of partitions and other minor work, judging from slightly worn mandibles.

From the conditions of examined nests, this species resembles *X. augusti* in: 1) Preference for structural fence posts, 2) Preparation of many laterals and

short, often unused ones, 3) Frequent reuse of laterals and cells by one or more daughters, 4) Occasional communal nests (*Hi-7, 11*). As to the first item, the species is characterized by the preference for hard posts of imbuia, suggesting its adaptation to this man-made environment. The number of cells produced by a single female seems to be very small, in maximum only five (*Hi-5, Hi-11*). Comparison of immatures in *Hi-5, 6, 7*, and *Hi-11*, all obtained in the same locality, favors the recognition of at least two generations per year. As in *X. augusti*, two abnormal cells sealed without eggs were observed.

### 1.1.8. X. (Megaxylocopa) frontalis (Olivier) (Figs. 16, 26~31)

The nests of this giant species, distributing throughout South America, have been recorded several times (Hurd and Moure 1963), but a precise description was given only by Hurd (1958). The eurytopic nature of nest substrates (Hurd and Moure 1963) was confirmed by our observations on seven nests, *Fr-1~7*, too.

As in *X. augusti* and *X. hirsutissima*, nests often form a labyrinthine system with numerous laterals, occasionally separated from one another by walls less than 2 mm thick. The nest entrance is more or less circular, 15~17 mm in diameter when made in soft substrates (*Fr-1, 5, 6*), but becoming irregular in hard substrates (*Fr-3*, 33×15 mm, partly using a natural crack). Reflecting the body size, burrows are wide, 20~22 mm in diameter, with the inner surface smoothed. Cell lengths and widths are quite variable, 19~25 mm (mean 22 mm) and 18~24 mm (m. 21 mm) respectively. Partitions are 2~3 mm (m. 2.6 mm) thick at the center and 4.5~6 mm (m. 5 mm) at periphery.

Nests examined:

Fr-1 (Fig. 26): Livramento do Burmado, State of Bahia, July 13 '61. Discovered by the return of a female at 15:00. Made in dead but still erect trunk of a palm, *Cocos nucifera*, of about 28 cm in diameter. Entrance made at about 6 m high. The very soft wood was occupied by a labyrinthine system of laterals about 50 cm long, only the part near the entrance was examined and shown in Fig. 26. Several larvae and pupae were present but only 1 postdefecation larva shown in the figure was accurately recorded. Adults: Except several adults which escaped, 3 ♀♀ (1 W_5M_5, 2 W_1M_1), 5 ♂♂ (all W_1) and, interestingly, 1 ♀ (W_1M_1) of *X. grisescens*. *IP*: It is worth mentioning that the nest contained immatures, although taken at the middle of the Southern Hemisphere winter. Under the tropical climate of Bahia, hibernation might be obscure, even if it occurs, not might sharply interrupt brood rearing activity. On the other hand, the invasion of an old *X. grisescens* female was seemingly possible only under the decreased brood rearing activity due to low temperature, which might lower the defense and hostility to alien individuals. Judging from the complexity of burrow system, the nest must have been used by two or more generations successively.

Fr-2 (Fig. 16): Santa Quitéria, Castro, State of Paraná, July 16 '62. Found in a fence post of imbuia together with 2 nests of *X. hirsutissima* (cf. *Hi-1* and *2*). With relatively long entry canal and 7 laterals, occupying nearly the whole
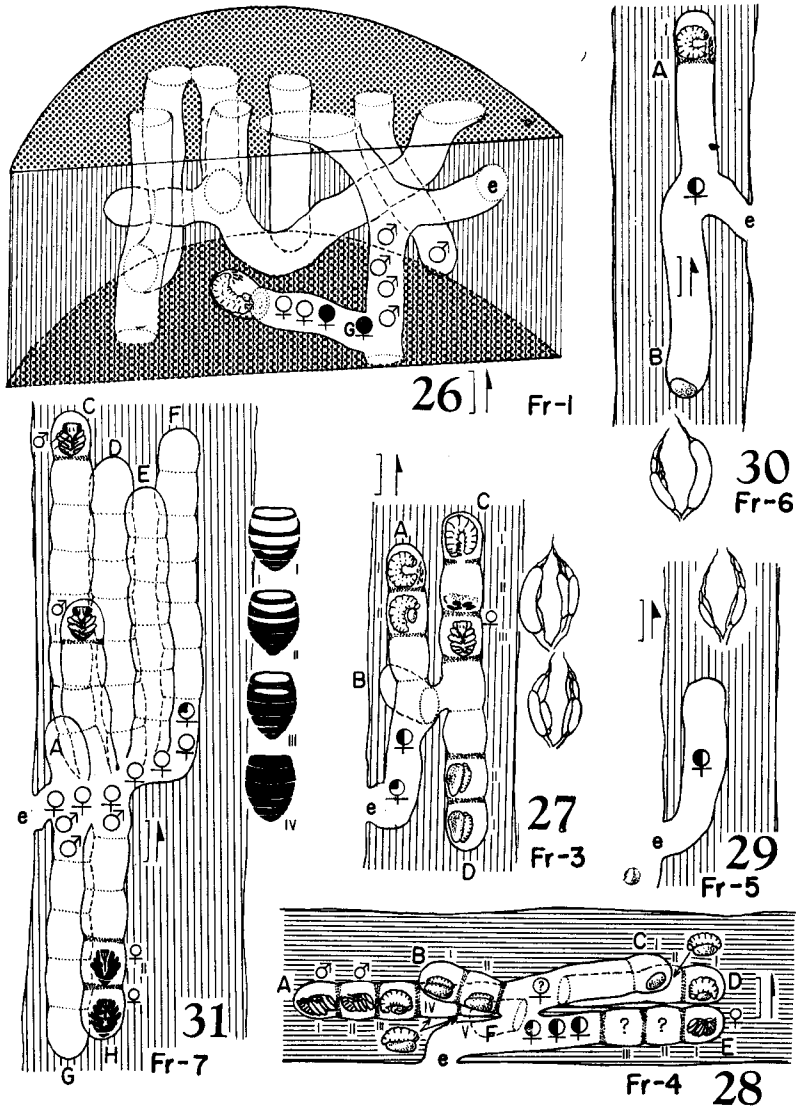
Figs. 26~31. Nests of *Xylocopa frontalis*. Ovaries of adult females are illustrated in Figs. 27, 29 and 30, and gradual pigmentation of female metasoma in Fig. 31. G♀ in Fig. 26 means a *X. grisescens* female. Adults shown with "?" are escaped females whose relative ages are unknown (Fig. 28). Further explanation as for Figs. 1~10 and in text.

interior of the post together with *Hi-1* and *2* for nearly 50 cm: A. 10 cm, 4 CC; B. 4 cm; C. 4 cm; 1 CC; D. 2 cm, 1 CC; E. 5 cm, 1 CC; F. 8 cm; G. 10 cm, 3 CC. A tube by *Cissites*, 27 mm long and 6 mm wide at G, cell cast III. Adults: escaped. *IP*: Apparently adults are in hibernation. The number of cell casts, 10 in total, could be the product of a single female, but as interpreted in other species, the addition of some cells by successors is not improbable.

Fr-3 (Fig. 27): Castro, Paraná, Nov. 22 '61. Found in a fence post of imbuia, about 150 cm long. Nest entrance 113 cm high, irregular and elongate, probably made by using a natural crack. With relatively long entry canal ascending for 5.7 cm and 4 laterals (C and D forming a continuous burrow): A. 7 cm, 2 cells, I. post defecation larva, II. large feeding larva, and 1 CC; B. 4.2 cm; C. 9 cm, 3 cells, I. large beetle larva (not *Cissites*), II. immature probably destroyed by parasite, III. white ♀ pupa; D. 7 cm, 2 cells, I. medium feeding larva, II. small larva, and 1 CC. Adults; 2 ♀♀, No. 1, W_3M_3, left ovary with an egg soon before oviposition, right ovary well developed; No. 2, W_2M_2, with well developed ovaries, though without mature egg (cf. Fig. 27). Partition I of C had a large orifice and Cell II contained fecal remains of *Xylocopa* and some unidentified matter. *IP*: Case interesting but difficult to interpret adequately: 1) From the relative age and ovarian conditions, adults are not the sisters of the immatures described and they are not mother and daughter. 2) Cells found in the nest are either all made by the foundress and reused by the adults found in the nest (A_1), or partly added by the latter (A_2), or all made by them (A_3). Among these possibilities, A_1 is most plausible from the number of cells. If A_2, the number of cells made by the foundress was very few, though this is not completely excluded from the relatively small number of cells made by a single female in other nests (cf. also *X. brasilianorum*, *X. augusti* and *X. hirsutissima*). If A_3, one female, probably No. 2, is a later invader. 3) Laterals were either shared between two females (B_1), or cared exclusively by one female (B_2), or partly used communally by both (B_3). B_2 is most plausible from the continuous gradient of immatures in the order of C→A→D, probably worked by No. 1. If B_1, the reproductive activity of No. 1 continued for a considerable time, because she, the older female, possessed still an egg ready to lay in her ovaries. B_3, the quasisocial association (Michener 1969, cf. 1.2.5.) is least plausible. 4) Two females are either sisters (C_1) or one, probably No. 2, is an invader (C_2). If A_3 is the case, always C_2. Assuming the invasion as a rare event, C_1 is more likely than C_2. Consequently $A_1B_2C_1$ may be the most probable interpretation, followed by $A_2B_2C_1$. In both cases, the participation of only one female, probably No. 1, in brood rearing is assumed. Another female, No. 2, must be younger or her ovaries would mature much later. Applying the record on the duration of immature stage in *X. fimbriata*, a species close to *X. frontalis* (Table 2), the white pupa in C-III is assumed to be from an egg laid about one month ago. This suggests that two females belong to the hibernating generation.

Fr-4 (Fig. 28): Rio Claro, State of São Paulo, Nov. 29 '63. Found in a

Eucalyptus beam 8 cm in diameter, supported horizontally 90 cm high. In the same beam was another incomplete and abandoned entrance hole. With 6 laterals opening into relatively long entry canal, all made along the grain: A. 10.4 cm, 5 cells, I and II. ♂ pupae, III∼V. large feeding larvae; B. 4 cm, 2 cells with young feeding larvae; C. 7 cm with 1 cell under provisioning; D. 10 cm, 2 cells with large feeding larvae; E. 9 cm, 3 cells, I. ♀ pupa, II and III. contents lost; F. 2 cm, no cell and cell cast. Adults: 4 ♀♀ (3 W_3M_3, 1 escaped). *IP*: It is assumed that each female worked at least in one lateral, A, B, D and E, and that one of them which worked in B was relatively young and continued brood rearing activity in C. As in *Fr-3*, brood rearing was probably started about one month ago, so that the females belonged to the hibernation generation. Probably the nest was founded by a lone female and enlarged by her daughters, with addition of some new cells ($G_n = G_2$).

Fr-5 (Fig. 29): San Lorenzo, Paraguay, Jan. 15 '62. Found in a dead branch of a living tree in the Campus of Facultad de Agronomia y Veterinária de San Lorenzo. Entrance about 2 m high. With only one burrow of 7.1 cm long, with no cell and cell cast. Adult: 1 ♀ ($W_1M_3O_2$), with crop full of nectar. *IP*: Apparently at the beginning of nest foundation, probably by a female of the summer generation.

Fr-6 (Fig. 30): Found with *Fr-5* in the same branch about 50 cm above the latter. With 2 laterals above and below the short entry canal: A. 8 cm, 1 cell with post defecation larva; B. 9 cm, with amorphous pastelike pollen mass on the bottom. (In *Fr-5* and *6*, the presence or absence of cell casts was not critically examined). Adult: 1 ♀ (W_2M_3), with one ovary considerably developed and the other with an egg ready to lay. *IP*: The female is starting brood rearing activity at a stage more advanced than in *Fr-5*. Meanwhile, the presence of one postdefecation larva is enigmatic. If it is a sib of the female, the age difference is remarkable and the number of cells produced by their common mother is very small. On the contrary, if the larva is her offspring, brood rearing is characterized by a remarkable interruption. Even if the latter is the case, the female must belong to the summer generation.

Fr-7 (Fig. 31): Santa Quitéria, Castro, Paraná, April 8 '62. Found in a fence post 11 cm in diameter. Entrance about 80 cm high. With 8 laterals opening into vestibule chamber: A. 2.5 cm, a heap of sawdust attaching on the bottom; B. 8.4 cm, 1 cell with black eyed ♂ pupa and 2 CC; C. 1 cell with black eyed ♂ pupa and 6 CC; D. 15 cm, 6 CC; E. 13.4 cm, 5 CC; F. 16.5 cm, 6 CC; G. 12 cm, 4 CC; H. 11 cm, 2 cells each with black ♀ pupa and 2 CC. Adults: 7 ♀♀ (1 $W_2M_2O_2$II, 1 W_1 M_1O_2III, 1 $W_1M_1O_1$IV, 3 $W_1M_1O_1$I, 1 escaped. I∼IV show the degrees of pigmentation on metasomal terga, cf. Fig. 31). *IP*: Apparently a communal juvenile association at the beginning of hibernation. Nest with 35 cells and cell casts indicates habitation by at least two generations, probably more. Sawdust found in A may indicate the activity of a female with M_2, suggesting the occurence of minor nesting activity during the juvenile stage.

The nests described above show the wide preference of this species for nesting substrates. The nest structure resembles that of *X. augusti* and *X. hirustissima*, especially in the excavation of many laterals, running side by side and often leading to the formation of a complicated system (cf. *Fr-1, 2, 7*). Further, the presence of more than one female in the same nest in the brood rearing season is seemingly not rare. They may live communally sharing several laterals among them. But further comparative study is required because some instances are not easy to interpret as simple communal associations (*Fr-4*, and also parly *Fr-5*). This species apparently has two generations per year under subtropical climate. According to Bertoni and Schrottky (1909) some nests of this species are started in late summer in Paraguay, while old nests contain larvae, pupae and young adults emerging in early summer. This observation favors the presence of two generations per year. The integument of female adults seems to be pigmented gradually after emergence (*Fr-7*), though without such remarkable delay as is seen in many stingless bees.

1. 2.   Comparative notes on *Xylocopa*

Based upon the descriptions given above, some aspects of the bionomics of *Xylocopa* are discussed subsequently.

1.2.1.   Nest substrates and nest structure

The species the nests of which were studied by us are divided into two groups according to their preference for nest substrates, those preferring hollow stalks or culms, and those nesting in timber. Probably the former group, represented by *X. ciliata* and *X. artifex*, is derived from the latter by specialization. The fact that they make nest entrances on the side walls of stalks or culms against the grain, never on the cut surface as practiced by most stem- and branch-nesting bees, indicates their secondary origin.

Concerning the second group, to which all other species belong, the preference for structural timbers is conspicuous in *X. augusti*, *X. hirsutissima* and *X. frontalis*. *X. frontalis* seems relatively eurytopic whereas *X. hirsutissima* shows a strong attachment to fence posts, at least in Castro and the vicinity. As commented by Hurd (1958) and Hurd and Moure (1963), such a synanthropic tendency in certain species must affect the distribution and make up of local *Xylocopa* faunas. Under ever increasing human impact, *Xylocopa* had to be thrown, together with all other animals, from their original habitats in the primary vegetation into a series of man-made environments. Many species must decrease their density by the alternation of cultivated lands and secondary vegetation, but some others survived or probably even increased through the adoption of various artificial substrates. Probably the three species mentioned have been adapting to such environments for a century or more and may sustain their life under moderate urbanization.

The nest structure in the species studied essentially coincides with the previous information as summarized at the beginning of Section 1. Here must be

given a few words on the barrel shaped cells found in all species except *X. ciliata* and *X. artifex*. This type of cells appears to be not rare in the genus (cf. Hurd and Moure 1960, p. 817 r), but definite descriptions or illustrations of the cell shape are relatively rare, only as follows (timber nesting species alone):

Not barrel shaped: *X. valga* (Malyshev, rarely barrel shaped), *X. violacea* (cf. Malyshev 1931), *X. virginica* (Rau, Hurd 1958, Balduf.)

Barrel shaped: *X. nigrita* (Smith), *X. ruficeps* (Iwata 1938a), *X. sauteri* (Iwata 1938a), *X. tabaniformis* (Davidson, cf. Malyshev 1931).

The results given in the present study suggest that barrel shaped cells are widespread in the genus. It is recommended to notice this point in further studies, because after the emergence of immatures, the barrel shaped cells can be traced as cell casts which are often useful in the interpretation of relative age and state of nests, as made in the present study.

1.2.2. Nest reuse

Nest reuse is classified into two categories: Reuse of nest burrow and of cells. Here the discussion is given only concerning the former, leaving the latter in 1.2.3. There are several previous records for timber nesting species of the successive use of nest entrances and laterals. Definite cases are known in *X. californica arizonensis* (Hurd 1958), *X. ruficeps* and *X. sauteri* (Iwata 1938a) and *X. virginica* (Rau, Balduf). Iwata (1956) cited the prolonged reuse of the same nest burrows of *X. appendiculata circumvolans*, in the rafters of the Buddist's temple, Hôryu-Ji in Nara, Japan, the world oldest wooden building, and assumed continuous use for about one hundred years.

Among the species studied by us, nest reuse by *X. ciliata* was not confirmed and probably is absent, judging from the fragile nature of substrate. Reuse was also not confirmed in *X. artifex* but was recorded by Hurd and Moure (1960). In all timber nesting species, reuse is suggested in may instances either by the complicated burrow system or by cells and cell casts too numerous to be the product of a single female as well as the number and relative age of the inhabitants. In these nests the adults captured (G_n) were related to the foundresses (G_1) or her children (G_2) or grandchildren (G_3) as follows:

$G_n = G_3$: *Ni-1, Gr-1, Au-1, Hi-3.*
$G_n = G_2$: *Br-1, Au-6, Au-7, Hi-5, Hi-6, Hi-7, ?Hi-8, Hi-11, Fr-3.*
$G_n = G_1$ or G_2: *Au-8, Hi-12, Fr-2, Fr-6, Fr-7.*
$G_n \neq G_1$: *?Hi-2, Fr-1.*

Thus 20 out of 30 nests studied are regarded as reused. Among the other ten nests, four (*Au-2~4, Hi-4*) were not closely studied and four others (*Hi-1, 9, 10, Fr-2*) were difficult to interpret. Only two nests, *Au-5* and *Fr-5*, were headed each by a single foundress. Although reuse is attested in many cases only indirectly, yet the frequent occurrence of this phenomenon is obvious, indicating a widespread tendency for economy of labor in the genus. However, the case $G_n = G_2$ was more frequent than $G_n = G_3$ and no cases of $G_n > G_3$ were

recognized. The relative scarcity of nests with long laterals involving more than five cell casts shows that nests are in most cases not infinitely ramified and extended. Janzen (1966) suggested the possible development of a tendency against nest overcrowding in *X. fimbriata*, as a mechanism to secure nest substrates. In a slightly different sense, his hypothesis might be applicable to our observation, too. Of course such danger of destroying substrates may be reduced when nests are reused mainly by the reuse of cells, with preparation of few new cells and little burrow extension. In such case one can determine G_n exactly only by observing nests continuously through many years as did by Rau for *X. virginica*.

1.2.3. Cell reuse

It is interesting that the reuse of cells, a simple labor-saving device, developed only in a few groups of bees (Michener 1964): some halictine bees (Sakagami and Michener 1962), some euglossine bees (Bennett, cf. Zucchi, Sakagami and Camargo 1968) and honeybees. In contrast to these bees in which laterals are either absent or differentiated from cells, xylocopine bees basically adopt the linear or allodalous cell arrangement (Malyshev 1936) and make cells within laterals themselves. In the species not making barrel shaped cells (cf. 1.2.1.), the reuse of cells has no positive meaning. Some species such as *X. virginica* (Rau), *X. artifex* (Hurd and Moure 1960) and *X. tranquebarorum* (Iwata 1938a) clean old laterals and prepare there new cells. This could be called the reuse of spaces where previous cells were made but is difficult to regard as the reuse of old cells themselves.

On the other hand, "the reuse of cells" has a more specific meaning when a species making barrel like cells reuses the previous cell casts for later brood rearing. However, the crucial evidence for such occurrence is virtually unknown, except for a possible instance in *X. ruficeps* (Iwata 1938a). This is due to the absence of cocoons and conspicuous linings on cell walls in *Xylocopa*. Malyshev (1931) reports the presence of some elaboration on cell walls in *X. valga*, but this does not result in the formation of duplicate cell lining as known in reused cells of some Neotropical halictine bees (Sakagami and Michener 1962).

> If a lateral contains several cells casts (*Y*), or several cells with immatures (*X*) in the terminal part followed by some cell casts (*Y*) in the proximal part, the formation of *Y* can be explained in three ways: 1) *Y* represents cell rudiments newly prepared. 2) *Y* corresponds to old cells and *X* was made by recent excavation. 3) Both *X* and *Y* are old cells and the part *X* is now being reused. The case 1) is possible when only one or two cell casts exist after cells already sealed, but is less likely when several casts are in series as in many nests described in the present paper. On the other hand, it is difficult to identify a given case either with 2) or 3).

In the nests studied by us, reuse is certain in *Au-1* and *Hi-7*, in which the number of adults captured cannot reasonably be explained unless reuse of some cells is admitted. Further, reuse is plausible in some other nests, for instance, *Au-6*, *Hi-3*, *Hi-11*. These items of evidence were applied to other nests, which in many

cases could be explained by either reuse or addition of new cells (G'_{2b} or G'_{2ab}) as noted in the interpretation of each nest. Thus our knowledge on this trait requires further accumulation of information for various species.

1.2.4. Number of cells produced by a single female

Unfortunately our data are inadequate to estimate the number of cells produced by a female, mainly due to the scarcity of nests in which both cessation of oviposition and absence of the beginning of emergence were confirmed. Some instances, which are seemingly at or near the end of cell production, are as follows:

> *Ar-7*: 1 old ♀ and 7 cells, *Ar-8*: 5♀♀ and 5♂♂ (all young) and remains of 10♀♀ cells; *Br-1*: 3 old ♀♀ living together and 9 cells (divided in 3, 4, 2); *Au-7*: 2♀♀ and 10 cells (2 empty, divided in 3, 7); *Au-6*: 1♀ and 5 cells; *Hi-5*: 1♀ and 4 cells; *Hi-11*: 3♀♀ and 14 cells (=4.6 cells per ♀); *Fr-3*: 1 or 2♀♀ and 7 cells; *Fr-4*: 4♀♀ and 13 cells (3.2 cells per ♀).

The number of cells per female, especially in timber nesting species (*Br, Au Hi, Fr*), is rather low in comparison with the number recorded for other species as summarized in Table 3. It is open to further studies whether this low number is characteristic to the species studied or not.

A more precise figure is the number of cells per lateral. As given in Table 4, most laterals contain less than five cells or cell casts, most frequently 3~4 (A similar tendency is known in *X. valga*, Malyshev). This tendency is particularly conspicuous in *X. hirsutissima*. Bees that made linear cell arrangement have a problem to be solved at the emergence of immatures. The oldest individual, emerging in the terminal cell, must get the outlet either by patiently awaiting the emergence of young sibs or by making its way through cells with young, without destroying the latter. Although various devices have arisen among bees to solve this difficulty (cf. 2.2.7.), the preparation of a limited number of cells per burrow or lateral decreases the difficulty to some degree. In the species nesting in narrow

Table 4. Number of cells per lateral in nests of *Xylocopa*.

If the laterals have partitioned cells alone, only such laterals the last cells of which contain immatures older than full grown larvae were chosen. If the laterals have cell casts, the combined number of partitioned cells and cell casts was employed.

Number of cases observed \ Number of cells	1	2	3	4	5	6	7	8	Total
X. artifex							1	1	2
X. nigrocincta			1			1		1	3
X. grisescens				2			1		3
X. brasilianorum		1	1	1					3
X. augusti	1	6	1	4	1				13
X. hirustissima	7	9	8	5					29
X. frontalis	2	6	8	4	3	2	1		26
Total	10	22	19	16	4	3	3	2	79

stems or stalks, this must be done by the preparation of a second nest. In the species prefering ample substrates such as soil or timber, however, this can be achieved by the excavation of more than one lateral. It is still premature to conclude that the number of cells per lateral is smaller in the latter group than in the former. But this aspect is worthy of notice in future studies. As to the arrangement of sexes in each lateral, our data are insufficient to show any particular tendency as given by Malyshev (1931).

1.2.5. Aggregation and association

Some species of *Xylocopa*, for instance, *X. valga* (Malyshev), seem to be relatively "solitary". But previous records often show the formation of "colonies" in certain species. In such case it is not always clearly mentioned whether many nests concentrate within a limited space or several individuals live together in the same nest.

The first instance, corresponding to *aggregation* of Michener (1969), is known in the following species: *X. aestuans* (Mellor), *X. californica californica* (Cruden), *X. confusa* (Jacobson), *X. flavorufa* (Brauns), *X. fimbriata* (Bodkin, a tendency counteracting overcrowding was discussed by Janzen), *X. frontalis* (Bertoni and Schrottky), *X. latipes* (Jacobson, Sakagami and Yoshikawa), *X. nogueirai* (Hurd and Moure 1960), *X. sauteri* (Iwata 1938a), *X. tabaniformis orpifex* (Cruden), *X. tranquebarorum* (Iwata 1938a), *X. virginica* (Rau).

In our observations, the following cases represent the construction of more than one nest in the same substrate: *Au-2~4, Au-5~6, Hi-1~2+Fr-2, Hi-6~7, Fr-5~6*. The nidification of two species in the same substrate is also recorded by Hurd and Moure (1961, *X. hirustissima, X. augusti* and *X. frontalis*) and Cruden (1966, *X. californica californica* and *X. tabaniformis orpifex*).

The second instance, the living together of more than one individual in the same nest is recorded: *X. artifex* (Hurd and Moure 1960), *X. fenestrata* (Kapil and Dhaliwal 1968a), *X. frontalis* (Hurd 1958). *X. nogueirai* (Hurd and Moure 1960), *X. ruficeps* (Iwata 1938a), *X. tranquebarorum* (Iwata 1938a), and *X. virginica* (Rau). In these cases, however, it is often not mentioned either the association consists of juvenile adults before or after hibernation (including the mother or not) as discussed in 1.2.6., or of females in brood rearing period. The latter instance is definitely recorded only in *X. artifex, X. nogueirai, X. tranquebarorum* and *X. virginica*.

In our observations the following instances are regarded as such co-existence of brood rearing females: A) Cases indicating the previous co-existence by the arrangement of laterals and number of cell casts: *Au-1, Hi-3, Hi-6,? Hi-12, Fr-1, Fr-7*, B) Ditto, by the co-existence of post-reproductive females: *Br-1*. C) Actual co-existence of brod rearing females: *Au-7, Hi-7*. B+C) *Hi-11, Fr-3, Fr-4*.

Nextly the nature of this association is considered. As no caste system has so far recorded in *Xylocopa*, the association must be either *communal* (a group of females utilizing a single composite nest, each making and provisioning her own cells) or (a small colony in which two to several females of about the

same age and probably the same generation cooperatively construct and provision cells, more than one bee working on a given cell, Michener 1969). Theoretically the communal association can be subdivided into two types: 1) Each female with her particular section, for instance, lateral, within the nest. 2) Each without such section but with her own cells. The second type could be expected in the species making heterodalous or anodalous nests (Malyshev 1936), though difficult to prove. In the species making linear or allodalous nests, however, the second type is unlikely to occur unless a complete alternation of cell construction and provisioning occurs between the females living together. Consequently the communal use of a lateral in *Xylcopa* may lead obligatorily to the appearance of a quasisocial association. Such communal use is suggested when the number of females with well developed ovaries is higher than the number of laterals containing eggs and very young larvae. No instance in nests studied by us fulfils this condition. *Fr-3* and *Fr-4* are quite interesting but can be regarded as communal as given in the interpretations of these nests. Applying Morgan's law of parsimony in a modified sense, it may be safe to conclude that *Xylocopa* does not exhibit association higher than the communal type. Correspondingly, the inhibition of ovarian development, a criterium for a higher level, the semisocial association of Michener, must not appear among the females living together, though we could examine this only in *Fr-3* which was slightly aberrant as already described.

However, one peculiarity in *Xylocopa* must be mentioned. In contrast to the bees making allodalous nests in soil, nests of *Xylocopa* usually have no long main burrow and laterals are often relatively short. This may increase the chance of encounters among inhabitants. Furthermore, Rau (1933, p. 246) observed in *X. virginica* food regurgitation between nest mates as follows: "Twice I have actually seen a mother, busy with her tunnelling and seldom leaving her burrow, accept food at her entrance from the mouth of a sister who attempted to enter". Considering this remarkable observation, a trait absent in social halicitine bees and only exceptionally reported even in bumblebees (Sakagami and Zucchi 1965), together with the nest structure facilitating frequent contacts, it is inferred that interindividual relations are quite intimate in communal associations of *Xylocopa*. Finally the data in *Br-1* show that males occasionally stay in the nests even after the beginning of brood rearing activities by females. A similar instance is also recorded in *X. tranquebarorum* (Iwata 1938a). Such an event apparently possible only by the unusually long male life span, which is exceptional among the various groups of bees (Malyshev 1931).

1.2.6. Hibernation

All previous records on temperate *Xylocopa* species show that both sexes of young adults emerge in summer and enter hibernation (cf. *X. valga*, Malyshev; *X. virginica*, Rau 1933; *X. appendiculata circumvolans*, Iwata 1944). The importance and peculiarity of this long juvenile stage, lasting from late summer to the next spring, was stressed by Rau. Hibernation by adults is also confirmed in some tropical or subtropical species: *X. aestuans* (Dover, Horne), *X. chloroptera* (Horne),

X. fenestrata and *X. pubescens* (Kapil and Dhaliwal 1968a), *X. nogueirai* (Hurd and Moure 1960), *X. latipes* (Beeson). The record of the absence of hibernation in *X. virginica texana* in Florida (Howard) was rejected by Malyshev (1931). We still have no crucial information on the presence or absence of any inactive period under humid rainforest climates.

Many hibernating nests in our study contained more than one juvenile adult: *Ar-1* (3 ♀♀ 3 ♂♂), *Ar-8* (5 ♀♀ 5 ♂♂), *Gr-1* (3 ♀♀ 3 ♂♂), *Au-1* (9 ♀♀), *Au-2* (2 ♀♀), *Au-4* (2 ♂♂), *Hi-3* (5 ♀♀ 5 ♂♂), *Hi-4* (several adults), *Hi-12* (9 ♀♀ 2 ♂♂), *Fr-1* (more than 2 ♀♀ and 5 ♂♂), *Fr-7* (7 ♀♀ 3 ♂♂). Solitary hibernation was observed in *Ci-4, 5, 6, 7, Ar-2* and *Hi-1*. As seen from these cases, many nests contain both sexes. This seems to be a rule in many species: *X. macrops* (Strand), *X. sicheli* (Brauns), *X. violacea* (Pérez) and *X. virginica* (Balduf). The segregation of sexes in separate nests as recorded in *X. pubescens* and *X. fenestrata* (Kapil and Dhaliwal 1968a) is exceptional.

Some hibernating nests studied by us contained old worn adults, either together with (*Au-8*, March 11; *Hi-11*, March 11; *Fr-1*, July 13) or without juveniles (*Ci-9*, April 26). These records show that the temporal co-existence of mother and her adult offspring is not rare in a subtropical climate, whereas it is absent (*X. virginica*, Rau) or exceptional (*X. violacea*, Pérez; *X. valga*, Malyshev 1931) in some temperate species. Under subtropical and tropical climates, mother-offspring meeting and their temporal co-existence are recorded in *X. nogueirai* (Hurd and Moure 1960 in the State of Minas Gerais, Brazil) and *X. frontalis* (Bertoni and Schrottky). Jacobson (1927, cf. Malyshev 1931) recorded the survival of the old mother until the daughters started their own nests (*X. caerulea*). All our nests were observed at the incipient phase of hibernation, so that it was uncertain whether the old mothers could survive to the next spring or not. A single exception, *Fr-1*, obtained in July in Bahia, was discovered by the flight activity of one female and the nest contained some immatures. It is not unlikely that hibernation becomes indistinct in the tropical climate of Bahia. In Southern Brazil hibernation starts at late March (*Ci-4, 5, Ar-8*) or April (*Ci-6, 7, 9, Ar-1, 2, Hi-3*) and continues to August, sometimes to September (*Hi-4*) or even October (*Au-2, 4*).

However, hibernating adults probably make some flights from nests, especially on warm days (cf. Section 3). The flight activity of *X. brasilianorum* was observed in Mendoza, Argentina, from June to August (Jörgensen 1909, after Malyshev 1931). Rau recorded in *X. virginica* food storage and partial excavation of burrows in the incipient stage of hibernation. The observation in *Fr-6* indicates such partial elaboration within the nest.

Most hibernating adults are discovered in old nests. But there are several records of extranidal hibernation as follows: *X. macrops* (Nests of other larger *Xylocopa* species, Strand), *X. valga* (subterranean cavities, Malyshev), *X. violacea* (Nests of *Anthophora*, Friese 1901), *Proxylocopa olivieri* (Nests of *Anthophora* and other bees, Gutbier 1916) (All from Malyshev 1931). In the present study all hibernating adults in timber nesting species and *X. artifex* were

found in old nests. On the other hand, the hibernating adults of *X. ciliata* (*Ci-4, 5*) were found in nests probably newly prepared by them. This is understood from the fragile nature of nest substrates preferred by this species.

The dispersal of some adults from old nests is recognized by the presence of solitary hibernation and marked imbalance in sex ratio in some nests containing many juveniles (for instance, *Au-1, Hi-12* mentioned above). The opposite instance, the invasion of some adults, is recorded in *X. appendiculata circumvolans* (Iwata 1956) and in *Hi-11*. The occasional invasion of other species is also suggested by the co-existence of *X. frontalis* and *X. grisescens* in *Fr-1*. Horne (1872 after Malyshev 1931) records an instance of communal hibernation of *X. aestuans* and *X. chloroptera*.

1.2.7. Number of generations per year

This problem was commented in 1.1.1. and referred to under each of the species observed by us. The previous records on temperate species show nearly unanimously a single generation per year. Friese (1923) assumed two generations in *X. violacea* in the Mediterranean area, but Malyshev (1931) considered all previous records including tropical species as showng monovoltinism, regarding the multivoltine trends suggested in *X. sicheli* (Brauns) and *X. virginica texana* (Howard) as dubious.

However, later observations on the occurrence of certainly newly made nests in February (*X. nogueirai*) and March (*X. artifex*, both by Hurd and Moure 1960) favor the presence of at least two generations under subtropical climate. Another extreme is the recent work by Kapil and Dhaliwal (1968a) with *X. fenestrata* and *X. pubescens*. These authors assert the occurrence of four generations in Punjab, India: 1. March ~ early May, 2. and 3. June ~ mid September, 4. Mid September ~ October. Further they refer to *X. latipes* as multivoltine from the observation by Beeson. Kapil and Dhaliwal (1969) confirmed the beginning of food provisioning by a laboratory-reared female nine days after emergence. Although food storage by hibernating juvenile females was observed by Rau (*X. virginica*), the above mentioned observation shows that some females can start nests without the intervention of a long juvenile stage. However, the report of four generations per year seems to need more precise evidence. Especially, they assume the second and third generations without definite evidence, seemingly by inference from the duration of immature stages, 739 hrs. or ca. 30 days. But a simple use of this duration to estimate the number of generations must be made cautiously. Already Rau (1933) mentioned that *Xylcopa* is exceptional among Hymenotpera by their "lazy" biorhythm, spending 4 ~ 9 hours for a single foraging trip and doing little work after returning. Iwata (1944, 1968) mentioned the low maturation speed of ovarian eggs and stressed the corresponding "slow life-speed" of adults. Certainly the assumptions, however suggestive for xylocopine biology, must be tested by concrete evidence. But they are worthy of consideration in estimating the number of generations.

The clear solution of the problem must be made by the periodical observations

of numerous nests in the same locality. But this is not always easy to do, especially for timber nesting species. Occasionally examined nests may be regarded tentatively as the product of the summer generation, provided they fulfil the following conditions: 1) The oldest cells contain eggs or young larvae in mid to late summer. 2) Mother or mothers are still not too worn, and 3) Nest contents show no particular abnormalities suggesting senility of the mother. The first criterium depends on local climate, time of nest foundation by the hibernating generation and duration of immature stages (cf. Table 2). No instance completely fulfilling these criteria was obtained by us. But *Br-1*, *Au-8*, *Hi-11*, *Fr-5*, *Fr-6* were interpreted as the products by the summer generation. It is possible that *Ci-2*, *Ci-3*, *Ar-6* and *Ni-1* were also made by the summer generation. Finally, the comparison of *Hi-5~7* favors the presence of a summer generation. Consequently it seems that some Neotropical *Xylocopa* species have at least two generations per year in a subtropical climate, although the summer generation could be produced only partially. Nothing is known on the sequence of generations under a humid equatorial climate.

1.2.8. Miscellaneous notes

Some nests studied by us showed abnormalities. Pollen loaves sealed without receiving eggs were found in *Ci-3* (2 cases), *Ar-3*, (2) *Au-7* (1), *Au-8* (1, sealed without loaf), *Hi-8* (1) and *Hi-9* (1), in total eight cells. Some of these cases may represent the senility of adult females as suggested by Malyshev (1931, '36). But cases in *Ar-3*, I and *Au-8*, D-I cannot be regarded as such because later cells were normally provided with immatures. These cases could be interpreted, though with no concrete evidence, as showing a discrepancy between maturation of eggs and the maternal behavior cycle. Another more interesting abnormality is two unsealed cells with immatures, found in *Au-6*. Malyshev (1936) writes that *Ceratina callosa* and probably also *X. valga* occasionally do not seal the last cell which is guarded by the mother. Unfortunately we have no evidence either to support or to reject this assertion.

Concerning the animals associated with nests of *Xylocopa*, our observations are incomplete because no animal was accurately identified. As parasites, however, the burrows of *Cissites* were found in many nests, *Br-1*, *Au-1*, *Hi-4, 5, 8*, and *Fr-2*, all made at the ends of the laterals as recorded by Hurd (1958, *X. frontalis* and *X. nigrocincta*), indicating the frequent attack by this meloid beetle. It was also observed that old nests of *Xylocopa* attracted bees, wasps, termites, spiders, ants, isopods and even a frog, offering them suitable nesting sites or shelters.

2. The genus *Ceratina* Latreille

In spite of the richness of the *Ceratina* fauna in the Neotropical Region, both in species and individuals, few studies have so far been published on the species inhabiting this vast area. Schrottky (1914) made some notes on two species, *C. aspera* and *C. gomphrenae* in Paraguay. Friese (1925) mentioned the nidification

of *C. ingara* and two species of *Calloceratina* in bamboo culms in Costa Rica. Recently Michener and Eickwort (1966) gave some bionomic notes on two species in Costa Rica. Probably these are all the contributions so far made on the bionomics of Neotropical species. Our fragmentary observations on five species, all made in the State of Paraná, Brazil, are supplementary to these previous records.

The description of each nest is made basically following the system adopted for *Xylocopa* (cf. pp. 60∼61). Nests in all cases consist of a simple burrow, so that the term "lateral" is not used. Occasional empty spaces between two sealed cells, being a characteristic of the genus, are designated with I′, II′, III′ . . . ., starting from the bottom as in normal cells, and the partitions before these spaces are also shown with same numerals.

As in *Xylocopa* the names of the species studied by other authors and cited in subsequent pages are given here. The classification of *Ceratina* is still incomplete, so that subgeneric names are mentioned only for some species. *Ceratinula* Moure, an independent genus according to Prof. Pe. J.S. Moure, who identified all species studied by us, is regarded here as a subgenus, simply for convenicence' sake. On the other hand, *Pithitis* Klug is considered as an independent genus (Hirashima 1966).

Ceratina (Ceratina) cucurbitina Rossi: Grandi 1961 (Italy); Friese 1923 (Europe).

C. (C.) iwatai Yasumatsu: Iwata 1964 (Japan); Tano 1964 (Japan).

C. (C.) megastigmata Yasumatsu et Hirashima: Shiokawa 1969 (Japan).

C. (Ceratinidia) flavipes Smith: Tano 1964 (or *C. japonica* ?, Japan); Shiokawa 1966, 1969 (Japan).

C. (C.) "hieroglyphica" Smith: Iwata 1938b (Formosa).

C. (C.) japonica Cockerell: Iwata 1932, '44 (or *flavipes* ?, Japan); Shiokawa, 1966, 1969 (Japan).

C. (C.) lieftincki v. d. Vecht: Sakagami and Yoshikawa 1961 (Thailand).

C. (Ceratinula) sp.: Michener and Eickwort 1966 (Costa Rica, cited subsequently as *Cl.* sp.).

C. (Neoceratina) australensis Perkins: Michener 1962 a (Australia).

C. (Zaodontomerus) calcarata Robertson: Rau 1928 (Missouri).

C. (Z.) dupla Say: Comstock 1895, Graenicher 1909, both after Iwata 1932 (the United States).

C. (Z.) ignara Cresson: Michener and Eickwort 1966 (Costa Rica).

C. aspera Schrottky: Schrottky 1914 (Paraguay).

C. callosa Fabricius: Malyshev 1913, 1936 (S. Russia); Rabaud 1923 (France); Friese 1923 (Europe).

C. chalcites Latreille: Ponomareva 1958 (C. Asia); Grandi 1961 (Italy).

C. cyanea Kirby: Malyshev 1936 (S. Russia); Friese 1923 (Europe).

C. dallatorreana Friese: Daly 1967 (California, introduced).

C. dentiventris Gerstaecker: Friese 1923 (Europe); Grandi 1961 (Italy).

C. ferghanica F. Morawitz: Ponomareva 1958 (Central Asia).

C. gomphrenae Schrottky: Schrottky 1914 (Paraguay).

C. gravidula Gerstaecker: Friese 1923 (Europe).

C. nigroaenea Gerstaecker: Friese 1923 (Europe).

C. unicolor Friese: Iwata 1938b (Formosa).

Pithitis smaragdula (Fabricius): *Ceratina smaragdula*, Sakagami and Yoshikawa 1961 (Thailand); *Ceratina binghami*, Iwata 1938b (Formosa); *C. binghami*, Kumar, Kapil and Atwal 1968, Kapil and Kumar 1969 (Punjab).

2.1. Observations on *Ceratina*

2.1.1. *C. (Ceratinula) muelleri* Friese (Fig. 32)

A single nest was discovered on October 27 1962 in Curitiba.

Mu-1 (Fig. 32): Found in a oblique (ca. 45°), dead and dry pithy twig of a shrub. Entrance at cut end of twig, 60 cm high, with no particular constriction. Nest burrow 16 cm long and 2 mm wide, with 2 cells, I. small larva, II. egg, and (III) a half built pollen loaf still not partitioned. Adult: 1♀ (W_1M_1).

Cells 7.5 mm long, partitions 1 mm long, outer surface smooth and slightly concave, inner surface nearly flat, pollen loaves conspicuously elongate, attaching to the cell wall with its entire ventral surface. *IP*: Apparently nest recently started.

2.1.2. *C. (Ceratinula) oxalidis* Schrottky (Fig. 33)

Three nests, *Ox-1 ~ 3*, of this dwarf species were examined, all discovered at a secondary grassland in São José dos Pinhais near Curitiba in dry, erect (*Ox-2,3*) or inclined (*Ox-1*, ca 45°) stalks of *Eupatorium litorale* (Compositae), with diameters 3 (*Ox-1*), 2.8 (*Ox-2*) and 3 mm (*Ox-3*) respectively. Nest entrances are made at the broken or cut ends of the stalks 50 ~ 70 cm high, circular and not particularly constricted. Nest burrows are 14.5, 9.6 and 21 cm long respectively and 1.8 (*Ox-1*) and 2 mm (*Ox-2 ~ 3*) wide, walls without visible lining.

Nest examined:

Ox-1: May 14 '62. No cell, partition or immature. Adults: 3 ♀♀ (all W_1M_1) and 3 ♂♂ (all W_1). *IP*: Apparently nest at the incipient stage of hibernation.

Ox-2 (Fig. 33): June 12 '62. Contents from the top as follows (cf. Fig. 33): A, B. 2 adult ♀♀ ($W_1M_1O_1$ with a mass of nematodes in metasoma, and $W_1M_1O_2$); C. black ♀ pupa facing to entrance; D. mature post-feeding larva still in defecation; E. partition, 4.8 cm from entrance, characters not studied; F. cocoon containing dead and decapitated ichneumonid pupa; G. compact ball made from mixture of pollen and pithy fragments; H. mass of pithy fragments; I. trace of an old partition; J. final partition; K. old cocoon of a hunting wasp. *IP*: Both adult females seem to be juveniles, being the elder sister of pupa and larva found in the burrow. No partition observed between these immatures. Their position and order suggest later transport by adults. The part below partition E is difficult to interpret but assumed as follows: First the stalk was used by a hunting wasp for nidification (K). Later, probably after the emergence of its progeny, the burrow was adopted by *C. oxalidis* for nidification and the nest was infested by the ichneumonid parasite. However, the nest was destroyed including the parasite, and a new nest was established by the female, which was the mother of the individuals found in the nest.

Ox-3: May 14 '62. Walls of the upper half (13 cm) of burrow quite aged while those of the lower half not well cleaned. Adults: 2 ♀♀ (both $W_1M_1O_2$). *IP*: Judging from the walls the burrow was deepened for hibernation. Ovaries of

two females were relatively swollen. It is open to the question whether the hibernation with this condition is general or not.

C. oxalidis is common in and near Curitiba and the results shown in Table 5 were obtained by two periodical samplings made in São José dos Pinhais and Boa Vista (cf. Section 3). Nest contents given above show that some bees enter hibernation in May, probably already in April, but some nests still contain immatures. Probably such immatures are not produced by the females soon after hibernation. Thus, it is plausible that the species partially has two generations per year under the local climate, with the peaks at September and December (cf. Table 5). The alternative possibility, the preparation of a second nest by some females is not rejected. But this may not be universal, because it means prolonged nesting activity lasting approximately from September to March for some females.

Table 5. Capture records of *Ceratina oxalidis* in two samples taken periodically in São José dos Pinhais (SJP) and Boa Vista (BV). ♀ p=females carrying pollen

Month	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	Total
SJP													
♀			17	3	4	8	2					6	40
♀ p			16	3	3	8	2					5	37
♂	1	5	14	2		9	5		2			1	39
BV													
♀	4		1	1	4		2			2			14
♂	1	6	1	1			1						10

2.1.3. *C. (Crewella) rupestris* Holmberg (Figs. 34~36)

Four nests, *Ru-1~4*, were collected in Castro, all from erect stalks of *Vernonia westiniana* (Compositae), growing in a "Campo Sujo", each with diameter 8~9 mm at base, about 6~7 mm at nest entrance. All stalks were dry but that with *Ru-1* was still green at the base. Nest entrances are made circularly at the broken or cut ends of the stalks at 30~50 cm high. Nest burrows are not particularly lined, 5~7 mm wide, constricted to 4~4.5 mm at entrances. In *Ru-2*, the part immediately below the entrance was widened to 6 mm, compared to the rest which was about 5 mm wide, though not so conspicuously widened as in *Ceratinidia* (cf. 2.2.2.). Cells are 11.5~12 mm long in *Ru-1* and 9~10 mm in *Ru-2*, walls parallel, not barrel shaped, with no visible lining. Partitions are smooth and concave exteriorly, flat and rough interiorly, about 3 mm thick at periphery, 2 mm at center. Pollen loaves were not closely studied but appeared more oval than in other species. The abdominal tips of the larvae in *Ru-1*, I, II and *Ru-2*, II, III were fixed to cell walls by means of adhessive exuviae. At the time of collection, the adult showed not attempt to escape as frequently practiced by *C. asuncionis*.
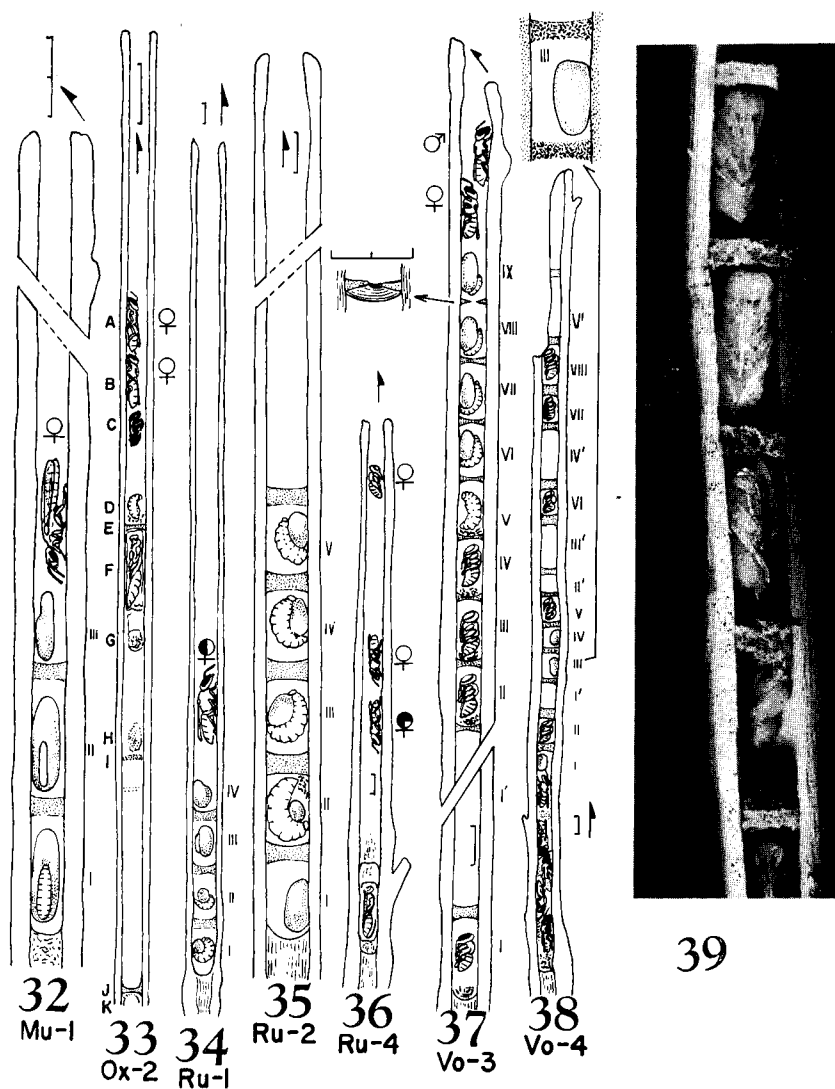
Figs. 32~39. Nests of *Ceratina muelleri* (32), *C. oxalidis* (33), *C. rupestris* (34~36) and *C. vollitans* (37~39). In *Ceratina* nests adults are illustrated. Scale lines represent 0.5 mm. Marked size difference among pupae is shown in Fig. 39 (Scale=5 mm). Further explanation as for Figs. 1~10 and in text.

Nests examined:

Ru-1 (Fig. 34): January 3 '64. Burrow 21 cm long, 3 cells: I. large feeding larva, II. medium feeding larva, III. small feeding larva. An incomplete pollen

mass above partition III. Adult: 1♀ ($W_3M_3O_4$). *IP*: Nest at the peak of brood rearing activity.

Ru-2 (Fig. 35): January 3 '64. Length of burrow not precisely measured. With 5 cells: I. pollen loaf alone, II. large feeding larva, III ~ V. medium feeding larvae. Adult: 1♀ (W_3M_3). *IP*: Probably a nest the foundress of which finished her brood rearing activity.

Ru-3: February 8 '63. Burrow 11 cm long, with 1 ♂ pupa and 1 ♀ pupa, both pigmented. Partitions already removed. Adults : 4 ♀♀ (all W_1M_1) and 2 ♂♂ (all W_1). *IP*: Certainly nest after the emergence of adults leaving two pupae. It is uncertain whether the females would start new nests or enter hibernation.

Ru-4 (Fig. 36): February 8 '63. Burrow 13 cm. At the bottom an elongate cocoon containing an ichneumonid pupa. Above the cocoon a mass of pithy fragments, probably produced by the removal of partitions. One white ♀ pupa 1.2 cm below entrance, not separated by partitions. Adults: 2 ♀♀ ($W_4M_4O_1'$, $W_1M_1 O_1$). *IP*: Nest is comparable to *Ru-3*, but the foundress is still surviving, resulting in the meeting of the mother and her adult daughter. The position of a single pupa suggests its transport by one of the adults. The number of progeny is very small. It is possible that some other adults already dispersed elsewhere, though the ichneumonid must have devoured one or more immatures.

2.1.4. *C. (Rhysoceratina) vollitans* Schrottky (Figs. 37 ~ 39)

Four nests of this species, *Vo-1~4*, are each peculiar in certain respects and are separately described below.

Vo-1: Boa Vista, Curitiba, Nov. 27 '63. No data taken at collecting and no adult found. The nest contained 8 cells, all separated by empty spaces, which were slightly shorter than the cells. The nest was brought to laboratory and cut longitudinally. Both pieces were fastened together and the contents were periodically examined by removing one piece for a short time. On Nov. 28, contents were as follows: I. post defecation larva, II. post feeding larva, III. large feeding larva, IV. pollen loaf alone, V. large feeding larva, VI and VII. medium feeding larvae, VIII small feeding larva. The duration of the feeding larval stage was about 19 days (from VIII), of the post feeding stage 6~8 days (from III ~ VIII) and total duration of immature stages excluding the egg approximately 55 days (from VI and VIII). Thus the pupal stage is estimated as 28~30 days. Adults emerged on January 10 '64 from I and II, and on Jan. 13 from III. On the same day, all three adults moved to IV and devoured there the remaining pollen loaf. On January 22, two adults emerged from V and VI and also went to IV for pollen. On January 27 all immatures except VIII had become adults. All partitions were removed and fragments were loosely packed in the bottom of the burrow. *IP*: Certainly the nest was made by a post hibernating female. Regular alternation of brood cells and empty spaces is noteworthy.

Vo-2: Castro, Jan. 4 '64. Found in an oblique dead branch of a composite shrub. Nest entrance at the cut end 40~50 cm high, constricted to 2.5 mm. Burrow 23.2 cm long, the bottom section filled with loose fragments of pith for 4.2

cm, 2∼3 adults, probably juveniles were found but not closely examined. *IP*:
Difficult to correctly interpret for the lack of sufficient data. Probably inhabitants
were newly emerged adults, which had removed partitions and packed fragments
at the bottom of the burrow.

   Vo-3 (Fig. 37): Castro, Jan. 4 '64. Found in a dead and inclined (ca. 45°)
branch of a living *Baccharis* sp. (Compositae). Nest entrance on the partly
broken end of the branch at ca. 50 cm high. Nest burrow 17 cm long, 3 mm wide,
widened to 3.5∼4 mm near entrance, which was constricted to 3 mm. Walls of
burrow and cells without visible lining, and cell walls parallel, not barrel shaped.
Nine cells and 1 empty space as follows: I. black eyed pupa, I'. empty 6 cm, II∼
IV. white pupae, V. postdefecation larva, VI-IX. large, medium, small and
very small larva respectively. Cells 7 mm long in I∼III, 6.5 mm in others.
Partitions biconcave, 2 mm thick at periphery and 1 mm at center in I, while
thinner in others, respectively 1 and 0.1∼0.3 mm thick. Partition VIII perforated
centrally (cf. Fig. 37). The last cell, IX, without closure. Four pupae directed
upwards. Pollen loaves attaching to cell walls with most of their ventral surfaces.
Egg probably laid on pollen loaf and not in contact with the cell wall, judging from
the position of larva in cell IX. Adults 1 ♀ (W_1M_1) and 1 ♂ (W_1). *IP*: The
duration from pupation to black eyed pupa is approximately 7∼8 days (from *Vo-2*,
cell I), so that cell I received an egg about 32∼34 days ago, that is, about in early
December. This time is too late for nest foundation by a post hibernating female
and the number of cells is too many for a second nest by such female. Probably
this represents an early nest made by a summer generation female. The nest is
enigmatic in some aspects. The presence of a long empty space and two juvenile
adults could be explained as the bees emerged from the space mentioned and took
the way to the entrance, passing over their young sibs, repairing the partitions.
This is not always impossible because such penetration through younger cells without
damaging younger sibs as pupae or old larvae and repair of removed partitions were
observed in *C. flavipes* (Tano 1964, cf. 2.2.7.). However, it is likely that they might
damage small larvae on pollen. The repair of partitions by mothers is confirmed by
Tano, but juveniles do not repair partitions perfectly as seen in this nest.
Moreover, the empty space involved no fecae and fragments of pith. Consequently
the invasion of two juveniles from the outside is held as an alternative interpreta-
tion, even though this is not very likely. The stalk was provided with a relatively
thin core of pith. Probably this relates to the thinness of the partitions.

   Vo-4 (Fig. 38): Taboão, Curitiba, Jan. 7. '63. Found in a dead twig of a
shrub. Nest entrance 50 cm high. The apical part, including the entrance,
broken at collecting. Nest burrow 20 cm long and 3 mm wide, without mother.
Bottom section free of partitions for 5.5 cm, containing 5 juvenile adults (sex
unrecorded) and loose heaps of pithy fragments. A pollen loaf without an
immature was near the top of the bottom section. Apparently the partitions below
it was removed by juveniles. Counting this loaf as cell I, there were 8 cells (I∼
VIII) and 5 empty spaces (I'∼IV') arranged as in Fig. 38: I. pollen loaf alone,

II. pupa, III and IV. each with pollen loaf alone, V ∼ VIII. each with pupa. Cell walls parallel, without visible lining. Cells 6 mm, but cell VIII 10 mm long. Empty spaces 6 (I′), 4(II′), 11 (III′), 13 (IV′) and 15 mm (V′) long. Partitions 2 ∼ 3 mm thick at periphery. Pollen loaves as in *Vo-3* . All pupae directed upwards. *IP*: Inserting the total duration of immature stages (cf. *Vo-1*) to the data described, the nest is estimated as founded in mid November. It is difficult to determine whether it was made by a post hibernating female or by an earliest summer generation female. It is possible that the nest is a second nest made by a hibernated female, judging from the presence of loaves without eggs.

The comparison of these meager data favors the presence of more than one generation under the local climate. Furthermore the frequent appearance of empty spaces seems to be characteristic of the species. Fig. 29 shows a part of a nest of this species. Unfortunately no detailed note on this nest was made. But the orientation of pupae, partitions, and accumulation of feces are seen in the figure. A marked difference in body size, characteristic of many *Ceratina* species, is recognized among pupae.

2.1.5. *C. (Crewella) asuncionis* Strand (Figs. 40 ∼ 55)

This specis seems one of the commonest wild bees in the Planalto of Eastern Paraná (cf. Section 3). In total 25 nests were collected in Castro, Curitiba and São José dos Pinhais. Among them *As 1∼6* and *23∼25*, all involving adults alone, are conveniently called *hibernating nests* and others *brood rearing nests*. All nests were found in dead and dry stalks or twigs, even if the bases were occasionally still green (*As-7, 9, 10*). Nest substrates are: *Baccharis* sp. (Compositae, *As-4*), *Eupatorium* sp. (Compositae, *As-2, 3, 8, 18*), *Vernonia westiniana* (Compositae, *As-5, 6, 13∼17, 19, 20*), *Escallonia montevidensis* (Saxifragaceae, *As-24, 25*), an unidentified composite (*As-7*), unidentified stalks (*As-9, 11. 21*). These twigs and stalks were mostly erect (*As-1, 2, 7∼10, 13∼15, 17, 19, 20∼24*), partly suberect (*As-4, 5, 6*, ca. 60°) or the state unrecorded. Nest entrances are 15.5 ∼ 65 cm (mean 41 cm) high. The diameters (mm) of stems and burrows of brood rearing nests seem to correlate to some degree as follows:

Burrows	Twigs ≥ 9	≥ 8	≥ 7	≥ 6 mm
≥ 6 mm		1		
≥ 5	2	3	1	
≥ 4	1		2	3

Burrows in brood rearing nests are usually straight, rarely slightly winding when ample pith exists, and the walls are smooth without visible linings. Nest entrances are mostly constricted to 3.5∼4 mm but not in *As-1, 3, 5, 21, 22, 23* (Figs. 42, 44, 53, 54). In *As-15* (Fig. 50) and *18*, the part below the constricted entrance was somewhat widened as a *turning chamber* as seen in *C. flavipes* and *C. japonica* (Tano 1964, Shiokawa 1966), Cells, found only in *As-8* and *10* (Figs. 47, 48) are 10 (*As-8*, I), 8.5 (*As-8*, V, VIII, *As-10*, I), 8 (*As-8*, II, III, IV) and 7.5 mm (*As-8*,

VI, VII) long, with the walls parallel, without visible lining. Partitions are 1.2~
1.5 mm thick at the periphery and 1 mm or less at center, the outer surface concave
and smooth, the inner surface nearly flat and rough. Pollen loaves are 5 mm long,
rectangular, most of the ventral surface attached to the cell walls. An egg found
in *As-8* was laid on the loaf, not in contact with cell wall.

   Nests examined:

   A. Hibernating nests

   As-1 (Fig. 40): Taboão, Curitiba, July 10 '63. Burrow 3 cm long and 3.5
mm wide. Entrance constricted to 2 mm and terminally flared. Bottom opening
into a narrow canal which continues for nearly 30 cm, with a few enlarged cavities.
Fragments of pith loosely packed in the bottom section. Adult: 1 ♂ (W_1). *IP*:
Adoption of an abandoned ant nest for hibernation, with slight elaboration.

   As-2 (Fig. 41): Locality and date=*As-1*. Burrow 2.5 cm long and 4 mm
wide, entrance section constricted to 2.5 mm. Bottom opening into a narrow canal
of more than 23 cm as in *As-1*. Adult 1 ♀ ($W_5M_5O_3'$). *IP*: As in *As-1* adoption
of an abandoned ant nest by a post reproductive mother. It is noteworthy that
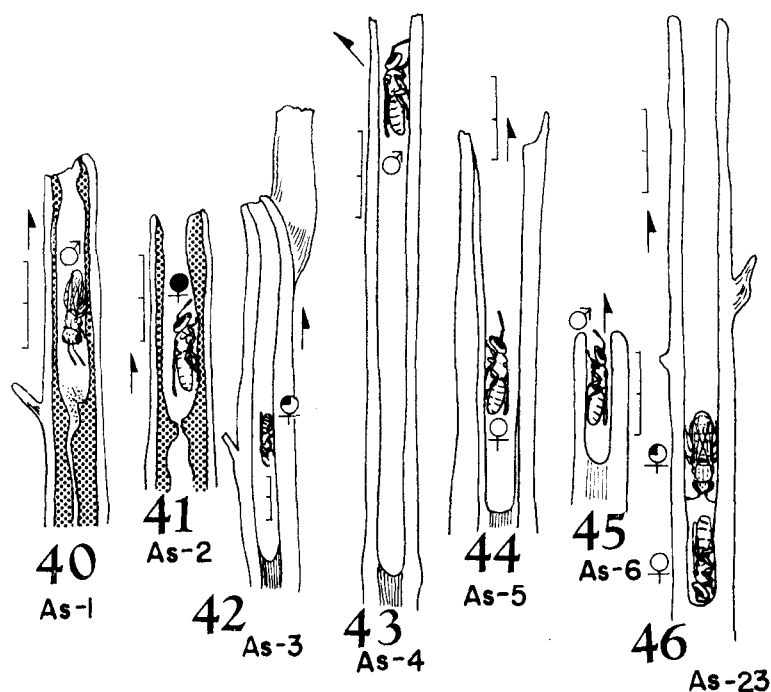
Figs. 40~46. Hibernating nests of *Ceratina asuncionis*. Scale lines represent 1 cm.
Further explanation as for Figs. 1~10 and in text.

ovaries were still considerably swollen, though with yellow bodies showing degeneration.

As–3 (Fig. 42): Locality and date=*As–1*. Burrow 8.5 cm long and 4 mm wide, gradually tapering to entrance (3.5 mm) without conspicuous constriction. Walls old but the bottom section fresh for 1.2 cm, suggesting later extension by the bee. Adult: 1 ♀ ($W_1M_1O_2$). *IP*: Adoption of a preexisting cavity by a juvenile female.

As–4 (Fig. 43): São José dos Pinhais, July 20 '62. Burrow 6.5 cm long and 3 mm wide, widened to 4 mm near entrance. Adult: 1 ♂ (W_1). *IP*: Adoption of a preexisting cavity by a juvenile male.

As–5 (Fig. 44): Castro, July 26 '64. Burrow 4.6 cm long and 3.5 mm wide, gradually widening to entrance (5 mm wide). Walls smooth at bottom for 1.5 cm, rather aged at other parts. Adult: 1 ♀ ($W_1M_1O_1$). *IP*: As in *As*–3.

As–6 (Fig. 45): Locality and date=*As–5*. Burrow only 1.5 cm long and 3 mm wide. Bottom section with walls recently made. Adult: 1 ♂ (W_1). *IP*: As in *As–5*.

As–23 (Fig. 46): Taboão, Curitiba, May 13 '62. Burrow 7 cm long and 4 mm wide with no constriction at entrance. Walls near entrance smeared with pollen. Adults: 2 ♀♀ (W_1M_1, W_2M_2). *IP*: Nest in the initial stage of hibernation by juvenile females. Pollen foraging is suggested.

As–24: Castro, May 14 '62. Burrow 14 cm long and 4 mm wide with no constriction at entrance. Adult: 1 ♀ (W_5M_5). *IP*: As in *As–23*, but by a post reproductive mother.

As–25: Locality and date=*As–24*. Burrow 12 cm long and 3.5 mm wide. Pithy layer well removed. Adult: 1 ♂ (W_5). *IP*: As in *As–24* but with an old male. Probably utilization of preexisting cavity.
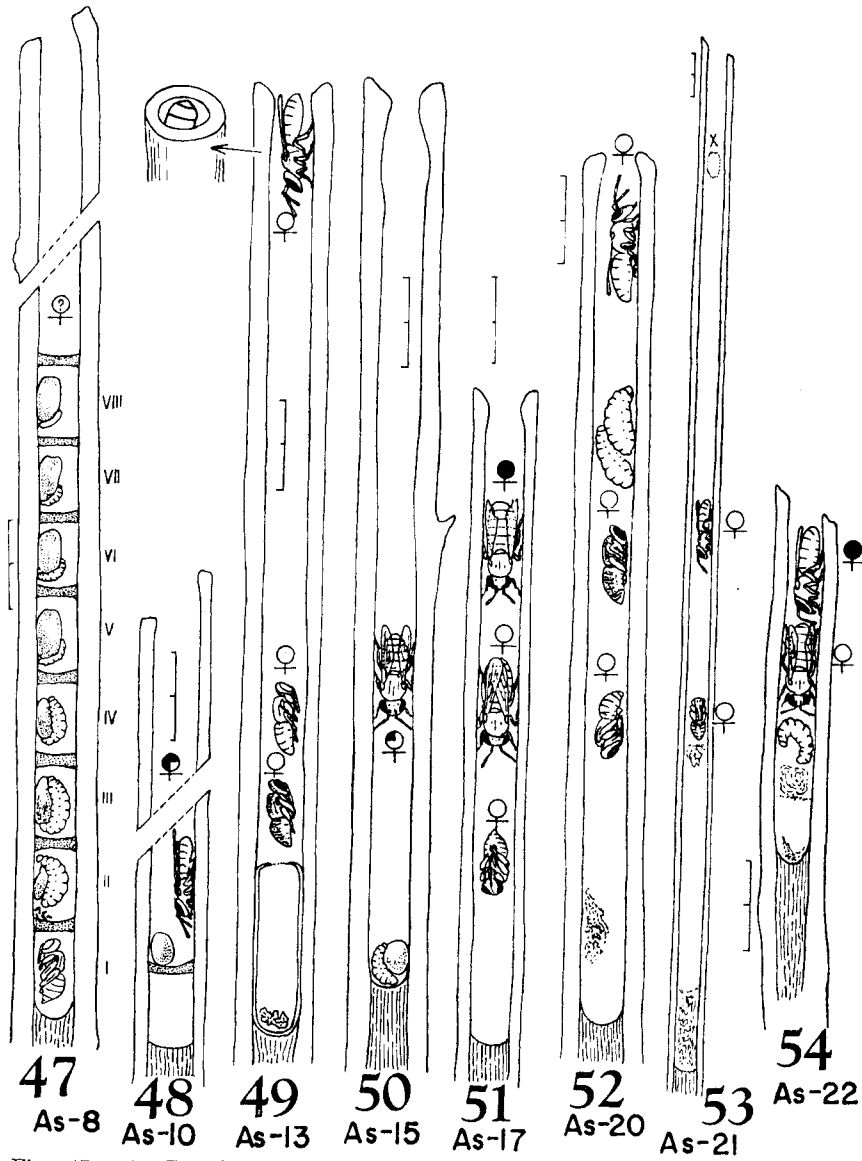
B. Brood rearing nests

As–7: Ahú de Baixo, Curitiba, Sept. 11 '63. Burrow 6.8 cm, with walls apparently smoothed recently. Adult: 1 ♀ (W and M unexamined). *IP*: Probably a nest recently started by a post hibernating female.

As–8 (Fig. 47): Locality and date=*As–7*. Burrow 17.5 cm with 8 cells: I. white pupa, II~III. large feeding larvae starting defecation, IV. medium larva, V~VII. small larvae, VIII. egg. Adult: 1 ♀ (escaped). *IP*: Probably a nest passing the peak of brood rearing activity, showing typical arrangement of immatures.

As–9: Boa Vista, Curitiba, Nov. 9 '63. Burrow 6.7 cm, with recently made walls. Adult: 1 ♀ ($W_5M_5O_3'$), ovaries with yellow bodies showing previous activity. *IP*: Possibly the preparation of a second nest by a female, because the length of the burrow is too short to be a reused nest.

As–10 (Fig. 48): Boa Vista, Nov. 26 '63. Burrow 5.5 cm. One empty cell (I) and an incomplete pollen mass above I, still with oval shape. Adult: 1♀ ($W_4 M_4O_3'O_4'$), one ovary still with a mature oocyte. *IP*: Probably the preparation of a second nest by an old female, behaving abnormally in senility.

Figs. 47 ~ 54.   Brood rearing nests of *Ceratina asuncionis*.   Scale lines represent 1 cm. All nests directed upward.   "X" in Fig. 53 means a spider's egg sac.   Further explanation as for Figs. 1 ~ 10 and in text.

As–11: Boa Vista, Dec. 9 '63. Length of burrow not measured, with 1 white pupa not isolated by a partition. Adult : 1 ♀ (escaped). *IP*: Probably final stage nest made by a post hibernating female. The small number of progeny may indicate either dispersal of other emerged adults or a second nest made by the aged female. A third explanation, the slow progress of brood rearing (Iwata 1938 b) is referred to 2.2.6.

As–12: Locality and date$=$*As–11*. Length of burrow not measured. With 1 dead pigmented pupa. Trace of a removed partition 1 cm from the bottom. Adult: 1 ♀ (W_1M_1). *IP*: As in *As–11*.

As–13 (Fig. 49): Castro, Dec. 26 '64. Burrow 10.9 cm without partitions. Contents from the bottom: An empty cocoon including an exuvium of an ichneumonid (2 cm long), 1 ♀ pigmented pupa, 1 ♀ white pupa, both directed upwards. Adult: 1 ♀ ($W_2M_2O_2$). When discovered, the female was at the entrance, showing her metasomal tip and rhythmically buzzing, probably repairing the entrance section (Fig. 49). After gentle touching with a pencil, she withdrew inside but in 5 sec. again showed the metasomal tip with buzzing. *IP*: Probably a final stage nest of a post hibernating female. At least five eggs were laid (the ichneumonid had attacked at least two immatures). It is uncertain whether the juvenile female was working to reuse the burrow or not.

As–14: Locality and date$=$*As–13*. Burrow 5.2 cm with walls smoothed. No immatures. Adult: 1 ♀ ($W_2M_2O_3$). *IP*: Newly started nest of a summer generation female.

As–15 (Fig. 50): Locality and date$=$*As–13*. Burrow 10 cm. A medium sized feeding larva at bottom on a half consumed pollen loaf not isolated by partition! Adult: 1 ♀ ($W_2M_2O_4'$), ovaries with yellow bodies. *IP*: In all probability nest started by a summer generating female.

As–16: Locality and date$=$*As–13*. Burrow 6.8 cm without partitions. At bottom a cocoon (18 mm long) of ichneumonid with emergence hole, and a loose mass of pithy fragments for 3 mm. Adult: 1 ♀ ($W_5M_5O_2'$). *IP*: Post reproductive nest infested by an ichneumonid. Some juveniles already dispersed, leaving the mother belonging to the hibernating generation.

As–17 (Fig. 51): Castro, Dec. 31 '62. Burrow 7.5 cm, without partitions. One black eyed ♀ pupa about 15 mm above bottom, directed downward. Adults: 2 ♀♀ ($W_1M_1O_1$, $W_5M_5O_3'$). *IP*: Probably final stage brood rearing nest by a hibernating generation female. One juvenile female with her mother.

As–18: Castro, Jan. 4 '64. Burrow 7.2 cm without partition. One pigmented ♂ pupa near bottom. Adult: 1 ♀ ($W_2M_2O_4$). *IP*: As in *As–17*, It is interesting that ovaries of the aged mother showed peak development, with no trace of degeneration.

As–19: São José dos Pinhais, Jan. 21 '63. Burrow 15.2 cm, with walls still rough, not elaborated. Adult: 1 ♀ ($W_2M_2O_4$). *IP*: Adoption of a preexisting cavity. Ovarian condition of the female might indicate failure of establishment of nest.

As–20 (Fig. 52): Taboão, Curitiba, March 6 '63. Burrow 10.3 cm, without partitions. A loose mass of pithy fragments near bottom, probably indicating removed partitions. One black-eyed ♀ pupa 3 cm from bottom, directed downward, 1 pigmented ♀ pupa about 1 cm above the former, directed upward, and 2 fully grown post feeding larvae in contact with each other above the second pupa. Adult: 1 ♀ ($W_2M_2O_2$). *IP*: Later stage brood rearing nest founded by a summer generation female, which probably already died. Arrangement of immatures definitely indicated later transport.

As–21 (Fig. 53): Curitiba, March 12 '63. Burrow 24 cm, without partitions. From bottom, loose mass of pithy fragments (2 cm), empty space (5 cm), loose mass of fragments (0.8 cm) and above it 1 white ♀ pupa. An egg sac of spider near entrance (x). Adult: 1 ♀ ($W_5M_5O_2'$). *IP*: Certainly a later stage brood rearing nest founded by a summer generation female still surviving. Length of burrow indicates the long use. Probably other progeny already emerged and dispersed.

As–22 (Fig. 54): Taboão, Curitiba, March 13 '62. Burrow broken at collecting. From bottom, empty space (2 cm), loose mass of pithy fragments (8 mm) and 1 full grown post feeding larva not partitioned. Adults: 2 ♀♀ ($W_1M_1O_1$, $W_2M_2O_2$). *IP*: Certainly final stage brood rearing nest founded by a summer generation female.

C. asuncionis is one of the predominant wild bee species in and near Curitiba. From two periodical bee surveys executed in São José dos Pinhais and Boa Vista (cf. Section 3), the data on this species were extracted and presented in Fig. 55. The relative ages of males and females are indicated by wing and mandibular wear. The presence or not of pollen loads on legs is given for the females from São José dos Pinhais. The records of the immatures in nests described above are incorporated in the figure. From the figure, the following items of facts and inferences are derived:

1) Number of specimens collected is highest in late autumn and early winter, followed by late winter and early spring, that is, in pre- and posthibernating periods. — The same tendency is also seen in temperate species from the unpublished data on *C. flavipes* and *C. japonica* taken in Sapporo, Northern Japan. 2) Males are collected less frequently than females. — Probably this results from behavioral difference between sexes at flowers. 3) Not only juveniles but also senile adults of both sexes enter hibernation and some survive to the next spring. 4) Pollen foraging occurs even in winter in favorable weather, not only by juveniles but also by senile females. — In *C. flavipes* and *C. japonica*, too, many old females carrying pollen loads are collected in autumn. This trait, unusual in solitary bees, suggests temporal storage by hibernating bees. 5) In spite of the small number of adults collected during the brood rearing season, the wear of mandibles and wings indicates the presence of at least two generations per year, especially when these data are compared with those on immatures and the duration of immature stages given in 2.1.4. (ca. 55 days). But it is likely that these
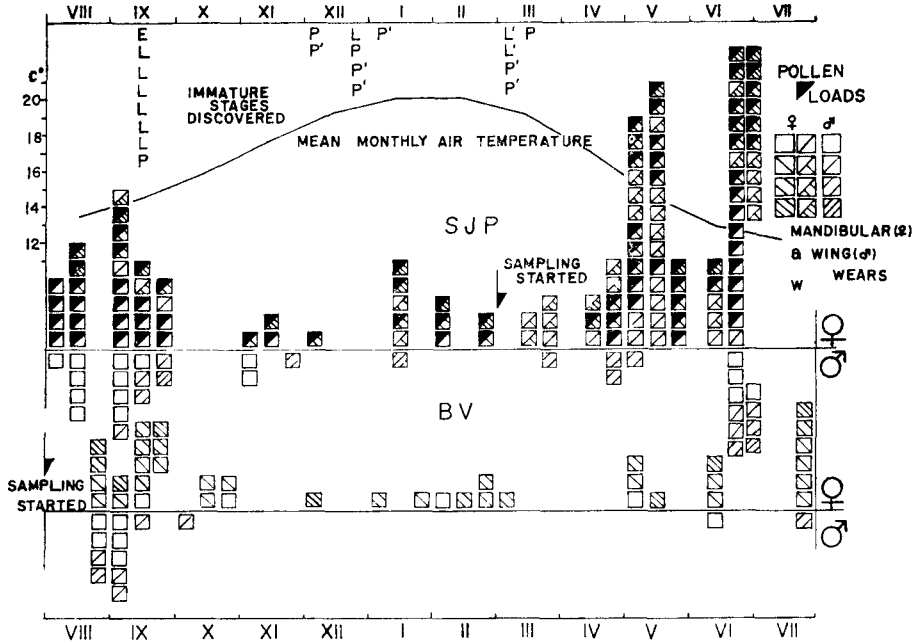
Fig. 55. Phenology of *Ceratina asuncionis* in São José dos Pinhais (SJP, above) and Boa Vista, Curitiba (BV, below), each based upon one year's periodical sampling, started in early March (SJP) and early August (BV) as shown by arrows. Each adult individual is shown by a square, with indication of relative age estimated by mandibular (♀) and wing (♂) wear, each on a scale of 1 ~ 4. In SJP, females with pollen loads are shown with black triangles. Immatures obtained by examination of nests are shown at the top with the following symbols: E (egg), L (feeding larva), L' (post feeding larva), P (white pupa), P' (pigmented pupa).

generations overlap considerably and the summer generation appears only partially.

The small number of immatures per nest with a single exception, *As–8*, probable removal of partitions between post feeding immatures, occasional absence of partitions between feeding larvae, and possible transport of immatures within nests are also worth mentioning. These aspects will be discussed comparatively in the next subsection.

2.2. Comparative notes on *Ceratina*

Our observations on *Ceratina* are fragmentary and incomplete. This incompleteness becomes clearer when we compare our data with the information so far published. But the previous contributions are also frequently incomplete. A brief attempt to compare these data was made by Michener and Eickwort (1966).

But we need to establish a line along which further studies can be undertaken. For this purpose, some aspects of the bionomics of this genus are enumerated and discussed below, irrespective of whether these are touched on in our observations. This treatise was not prepared by the complete bibliographical survey, but we believe most important articles were consulted by us.

2.2.1. Nest substrates

All previous records show the preference for twigs and stalks, mostly provided with a pithy core: *C. aspera*, Schrottky; *C. australensis*, Michener 1962a; *C. calcarata*, Rau; *C. callosa*, Malyshev 1913, Grandi; *C. chalcites*, Ponomareva, Grandi; *C. cucurbitina*, Grandi; *C. dallatorreana*, Daly; *C. ferghanica*, Ponomareva; *C. flavipes*, Tano, Shiokawa 1966; *C. ignara*, Michener and Eickwort; *C. iwatai*, Tano; *C. japonica*, Iwata 1932, Shiokawa 1966; *C. lieftincki*, Sakagami and Yoshikawa; *C. megastigmata*, Shiokawa 1969; *Cl.* sp., Michener and Eickwort; *P. smaragdula*, Kapil and Kumar, Iwata 1938, Sakagami and Yoshikawa, and all species observed by us. The exposure of the pithy surface seems to be prerequisite for nesting (Daly, Ponomareva, Rau), because, in contrast to *Xylocopa*, *Ceratina* has no ability to perforate the resistant outer surface. Rau (1928) assumes that *Ceratina* does not utilize preexisting hollows, because they need pithy fragments to prepare cell partitions. But reuse of preexisting hollows is frequently recorded as follows: *C. dallatorreana*, Daly, nests of other insects; *C. dentipes*, Grandi, culms of wheat; *C. unicolor*, Iwata 1938b, culms of bamboo twigs; *P. smaragdula*, Kapil and Kumar, straws used for roofs. The successive use of one nest cavity is recorded in *C. australensis* (Michener 1962a) and suggested in *C. unicolor* (Iwata 1938 b).

Most nests are recorded as made in erect or suberect substrates with the entrances at the upper ends: *C. australensis*, Michener 1962a; *C. callosa*, Malyshev 1913, Grandi; *C. chalcites*, Grandi; *C. ferghanica*, Ponomareva; *C. flavipes*, Shiokawa 1966; *C. ignara*, Michener and Eickwort; *C. japonica*, Iwata 1932, Shiokawa 1966, and all species observed by us. This may simply mean that such orientation is prevailing in substrates preferred by *Ceratina*. The indifference to the orientation of substrates is suggested in *C. cucurbitina* (Grandi), *C. flavipes* and *C. japonica* (Shiokawa 1966). Nests of *P. smaragdula* observed by Kapil and Kumar (1969) were mostly discovered in straws for roofing, probably oriented with the cut ends directed obliquely downwards. Malyshev (1913) induced *C. callosa* to nest in nearly inverted stalks. The most unusual condition was recorded by Schrottky on *C. gomphrenae*, the nests of which are, according to him, mostly found in dead twigs lying on the ground. It is likely that these were hibernacula rather than brood rearing nests. His comment on the possession of entrances at both ends of twigs strengthens this suspicion.

2.2.2. Entrance structure

Nests in all species so far studied are basically simple burrows, straight or more or less sinuous. The latter condition seems to be found in substrates with

sufficient diameter of pithy cores (*C. chalcites*, Ponomareva; *C. cucurbitina*, Grandi). In such case the diameter often varies in the same burrow. Walls of burrow are smoothed but no particular lining is recorded.

The nest entrance is either constricted or not. A constriction is recorded as follows: *C. callosa*, Malyshev 1913; *C. dallatorreana*, Daly; *C. flavipes*, Tano, Shiokawa 1966; *C. ignara*, Michener and Eickwort; *C. japonica*, Iwata 1932, Shiokawa 1966: *C. lieftincki*, Sakagami and Yoshikawa; *C. unicolor*, Iwata 1938 b; *P. smaragdula*, Kapil and Kumar, *C. asuncionis* and *C. rupestris* in our observations.

In other species the absence of references to this character may indicates its absence or merely that it was overlooked. According to Shiokawa (1969) the constriction in *C. megastigmata* is less conspicuous than in *C. flavipes* and *C. japonica*. The constriction may be prepared facultatively (cf. *C. asuncionis*) depending on the width of the nest burrows. Constriction also occur in most halictine nests. Sakagami and Michener (1962) regarded them as an interesting parallelism in defensive mechanism.

Occasionally the part immediately below the entrance is widened, forming a turning chamber as observed in *C. vollitans* (*Vo-3*) and *C. asuncionis* (*As-15*). In *C. flavipes* and *C. japonica* most nests, excluding some hibernacula, are provided with this structure (Tano, Shiokawa 1966).

In most species the entrances of completed nests are not specially closed. The long life span of mother bees, which survive often to the emergence of their progeny, eliminates the necessity for such a device. But occasional closures of loosely packed pithy fragments are recorded in *C. australensis* (Michener 1962a), *C. callosa* (Malyshev 1913), *C. cucurbitina* (Grandi) and *C. ignara* (Michener and Eickwort). In the last species, the closure could be an extra partition as discussed in 2.2.4.

It is noteworthy that these characters often appear facultatively within a species. The same can be said for the empty spaces referred to 2.2.4. It is possible to stress this as evidence for the plasticity in behavior, as did Rau (1928, '33). But it may be wise to wait further accumulation of observations.

2.2.3. Cells and cell partitions

Most so far recorded brood cells of *Ceratina* are simple spaces separated by two partitions. Only Ponomareva (1958) mentions that cells of *C. chalcites* are usually parallel sided but occasionally slightly barrel shaped. No such shape was noticed in recent studies on other species (*C. australensis*, Michener 1962 a; *C. flavipes* and *C. japonica*, Shiokawa 1966; *C. ignara* and *Cl.* sp., Michener and Eickwort; *C. megastigmata*, Shiokawa). However, Daly recorded cells of *C. dallatorreana* as feebly barrel shaped, being undetectable to the unaided eye. It is possible that such cryptic barrel shaped cells appear in other species, too. In most species, cell walls have no particular lining, but Daly confirmed in *C. dallatorreana* that walls are water-proof, and assumed the presence of an invisible lining of waxy secretion from sternal glands.

Cell partitions are made of pithy fragments. The structure in various species is summarized in Table 6. The outer surface is usually concave and often smooth, while the inner surface is weakly concave to nearly flat and often rough. But it is dubious whether these records, including our own, were always taken with precision. In *C. flavipes* and *C. japonica*, the curvature of the outer surface is quite variable according to the situation (Shiokawa, person. comm.). Further critical observations are required to determine the relative constancy of these characters among species.

The thickness of the partitions seems to vary even within the same species (*Vo-3* and *4*, Figs. 37 and 38), probably in part depending on the availability of ample material as mentioned for *C. dallatorreana* (Daly). On the other hand, Rau

Table 6. Previous records on the structure of cell partitions in *Ceratina*. Curvature (concave +, weakly concave ±, flat →), texture (smooth +, rough −)

Species (author)	Outer surface		Inner surface		Remarks
	Curvature	Texture	Curvature	Texture	
C. asuncionis (2. 1. 5.)	+	+	± ~ −	−	
C. australensis (Michener 1962 a)	+	+	−	−	
C. chalcites (Ponomareva 1958)	+		+ or −		Solidified with saliva
C. chalcites (Grandi 1961)	+		−		Well pressed
C. cucurbitina (Grandi 1961)	±		±		
C. dallatorreana (Daly 1966)	+	+	±	−	
C. dentiventris (Grandi 1961)	+		+		
C. flavipes (Shiokawa 1966)	+	−	+	−	
C. ignara (Michener and Eickwort 1966)	−		+		
C. japonica (Iwata 1932)	+	+		−	
C. japonica (Shiokawa 1966)	+	−	+	−	
C. megastigmata (Shiokawa 1969)	±	+	±	+	More compact than in *C. flavipes* and *C. japonica*
C. muelleri (2. 1. 1.)	+	+	± ~ −		
C. rupestris (2. 1. 3.)	+	+	−	−	
C. unicolor (Iwata 1938 b)	+	+		−	
C. vollitans (2. 1. 4.)	+		+		
Cl. sp.	+		±		Very thin
P. smaragdula (Kapil and Kumar 1969)	+			−	Iodine colored by saliva

(1928) found in *C. calcarata* that partitions are thicker approximately every three to four cells and thought that three to four cells are made each day. But the deposition of four eggs per day requires verification in view of their large size, one of the largest among insects (Iwata and Sakagami 1966).

Occasionally the partitions are omitted. This will be referred to 2.2.7.

2.2.4. Empty spaces

One of the remarkable characters found in *Ceratina* nests is the occasional presence of empty spaces, inserted between two genuine cells containing immatures. Such structure is not recorded in *C. cucurbitina* (Grandi), *C. dallatorreana* (Daly), *C. dentiventris* (Grandi), *C. ignara* (Michener and Eickwort), *C. lieftincki* (Sakagami and Yoshikawa), *C. megastigmata* (Shiokawa 1969), *C. muelleri* (2.1.1.) and *C. rupestris* (2.1.3.), though the number of appropriate nests examined is not enough in many of these species. On the other hand, such spaces are occasionally recorded in *C. asuncionis* (2.1.5., *As-10*), *C. australensis* (Michener 1962a), *C. callosa* (Malyshev 1913, Rabaud), *C. chalcites* (Grandi), *C. flavipes* and *C. japonica* (Shiokawa 1966), *C. vollitans* (2.1.4.), *Cl.* sp. and *P. smaragdula* (Sakagami and Yoshikawa, Kapil and Kumar).

These empty spaces are often irregular in length in comparison with normal cells. In *P. smaragdula* they are in average longer (12.6 mm) than normal cells (6.7 mm) and range from vestigeal to two times longer than cells (Sakagami and Yoshikawa). In *C. australensis* they are 3 ~ 8 mm long compared to normal cells 4 ~ 7 mm long (Michener 1962a). Several explanations have been offerred for intercellular spaces. Malyshev (1913) thought them as adaptive and stressed their significance as receptacle for fragments of pith produced by the emergence of young bees, as well as for the protection of young immatures passed by their elder sibs just emerged. But Michener and Eickwort (1966) mentioned for *C. ignara* the survivial of immatures passed by sibs in spite of the absence of empty spaces. Tano (1964) directly observed for *C. flavipes* emergence without destructing younger sibs. At any rate the assumption of Malyshev is insufficient to explain facultative appearance of spaces. As to *C. australensis*, Michener (1962 a) explained the empty spaces as showing the interrupted brood rearing activity by prolonged dry weather and resulting flower dearth. But Kapil and Kumar reported them continuously from February to Octover, irrespective of seasonal weather shifts. Rabaud (1923) suggested three possibilities, an improved character, a primitive character, and a character with no apparent significance. Our opinion inclines, for the time being, to the last possibility. Anyhow, the repeated appearance of this character in various unrelated species, belonging to *Pithitis, Ceratinula, Ceratinidia, Neoceratina, Rhysoceratina*, etc., is remarkable, nevertheless it does not become constant in any species.

2.2.5. Pollen loaves and positions of eggs

All so far observed species make more or less elongate pollen loaves with rounded angles. Specific differences appear to exist in the manner of fixing loaves

to cell walls. The loaves are recorded or illustrated as attaching to cell walls by most of their ventral surfaces in *C. asuncionis* (2.1.5.), *C. dallatorreana* (Daly) *C. flavipes* (Shiokawa 1966), *C. japonica* (Shiokawa 1966), *C. lieftincki* (Sakagami and Yoshikawa, though the observation is uncertain), *C. megastigmata* (Shiokawa 1969), *C. muelleri* (2.1.1.) and *C. vollitans* (2.1.4.). In *C. ferghanica*, however, the upper part of the ventral surface is free from the wall (Ponomareva). In *C. callosa* loaves are attaching to walls with their lower part alone and Malyshev (1913) explains it as an adaptation against dessication. An opposite type is reported by Michener (1962a) in *C. australensis*, the loaves of which are attaching to walls with their upper part alone. No precise notes are given as to other species.

The shape of loaves may also differ among species, being relatively rectangular in some species (*C. megastigmata*, Shiokawa 1969) or elongate (*C. muelleri*, 2.1.1.) but closer observations are still needed. The most remarkable feature so far recorded is the ornate margins in *C. australensis* (Michener 1962 a).

Another character of probable specific value is the position of eggs. All observations show that eggs are laid on the posterior half of the dorsal surface of loaves. But there are two distinct locations for the posterior tips of the eggs: A. Tips on loaves. *C. asuncionis* (2.1.5.), *C. chalcites* (Grandi, from the figure), *C. flavipes* and *C. japonica* (Shiokawa 1966), *C. liefincki* (Sakagami and Yoshikawa), *C. muelleri* (2.1.1.), *C. rupestris* (2.1.3.), *C. vollitans* (2.1.4.) and probably *C. ignara* (Michener and Eickwort). B. Tips on cell walls. *C. australensis* (Michener 1962 a), *C. callosa* (Malyshev 1913), *C. cyanea* (Malyshev 1936), *C. dallatorreana* (Daly), *C. megastigmata* (Shiokawa), *P. smaragdula* (Kapil and Kumar).

As in *Xylocopa* (1.2.8), pollen loaves sealed without receiving eggs were found in *C. rupestris* (*Ru-1*) and *C. vollitans* (*Vo-1, 4*). The same event is also recorded in *C. chalcites* (Grandi) and *C. flavipes* (Tano) and could be explained as in *Xylocopa*, either by senility or by a discrepancy between maturation of eggs and the maternal behavior cycle.

2.2.6.   Number of cells per nest and nests with few immatures

The previous data on the number of cells per nest in *Ceratina* are summarized as follows: *C. australensis* (4~12, mean 7.1, Michener 1962a), *C. callosa* (7, Grandi), *C. chalcites* (4~12, Grandi; maximum 10, Ponomareva), *C. cucurbitina* (4~13, Grandi), *C. dallatorreana* (6~8, max. 14, Daly), *C. dentiventris* (5~7, Grandi), *C. ferghanica* (3~8, Ponomareva), *C. flavipes* (min. 4, max. 15, Tano), *C. ignara* (max. 12, Michener and Eickwort), *C. iwatai* (8, Iwata 1964; 8~10, Tano), *P. smaragdula* (1~11, with empty spaces 1~7, Kapil and Kumar), *Cl.* sp. (1~3, Michener and Eickwort). In our observations 9 cells in *Vo-3*, 13 cells in *Vo-4* (3 cells with pollen loaves alone and 5 emerged adults included) and 8 cells in *As-8* are comparable with most of previous records mentioned above.

On the other hand, it is noteworthy that some nests in *C. asuncionis* involved only a few immatures. Obviously such would usually be either incipient nests or old nests from which some progeny already dispersed away. But these interpretations are hardly be applied to some nests such as *As-15* (only one large feeding

larva) and *As-22* (a short burrow with only one postfeeding larva and a juvenile female). Michener and Eickwort (1966) pointed out the small number of cells in *Cl.* sp. and assumed the preparation of more than one nest by each female. Another interpretation was held by Iwata (1938 b, 1964). In *C. unicolor* he found some nests with only a few immatures such as one adult female with one pupa (three cases), one adult female with one egg (two cases). These nests were relatively short, 5∼7 cm long. Pollen loaves and even eggs were found in nest only 2 cm long. On the other hand, two nests with more than one immature were longer. His interpretation is as follows: The female makes at first a short burrow and prepares a pollen loaf and oviposits upon it. Then she postpones the next oviposition until the maturation of the first young. The partition is removed after pupation and the burrow is gradually deepened. If such were the case, however, the time spent to rear a clutch of immatures would be very long. Moreover, a nest recorded by him containing four pupae is difficult to explain by his interpretation involving delayed oviposition. If an egg were laid after the previous immature finished feeding, one would not be likely to find four pupae on the same day, judging from the durations of immature stages given in 2.2.7. Moreover, the gradual deepening of the burrow postulates repeated preparation and removal of partitions. Certainly we cannot reject such a possibility. But the preparation of more than one nest suggested by Michener and Eickwort may be a more simple hypothesis to explain such nests. Malyshev (1913) reported the occasional founding of a second nest, which usually contained only one or two, rarely three to four cells in *C. callosa*. It is not impossible, however, that some species make more than one nest rather regularly. The interpretation given by Iwata would become more plausible if many nests were found, containing at least two immatures with a marked age difference, for instance, one egg and one pupa.

2.2.7. Immature stages, absence of partitions and emergence

As in *Xylocopa*, the larvae of *Ceratina* begin to defecate before finishing the pollen loaves: *C. australensis*, Michener 1962 a; *C. callosa* Malyshev 1914; *C. ignara*, Michener and Eickwort. The duration of immature stages is recorded as follows: *C. australensis*, more than 25 days, Michener 1962 a; *C. callosa*, 1.5∼2 months, Malyshev 1913; *C. dallatorreana*, 33 days, Daly; *C. ferghanica*, one month, Ponomareva; *C. vollitans*, ca. 55 days excl. egg (2.1.4.) *Cl.* sp., 22 days, Michener and Eickwort; *P. smaragdula*, egg 4.34 days, larva and prepupa + pupa 11.31 and 10.96 days respectively at 25°C, 9.96 and 9.73 days at 27.5°C and 8.73 and 8.36 days at 30°C (Kumar, Kapil and Atwal). As to the time required for the completion of a nest, Daly (1966) estimated about 15 days and the survival of the mother for further 18 days.

Frequent omission of partitions is remarkable in *Ceratina* in comparison with other bees. Absence of partitions results from at least two causes, failure to construct them and later removal. The former is recorded in *C. callosa* by Malyshev (1936). He notes that the last cell is often not sealed by a partition and the immature is guarded by the mother. The same case is recorded in *C. asuncionis*

(*As-10, 15, 22*, Figs. 48, 50, 54), *C. australensis* (Michener 1962a), *C. vollitans* (*Vo-3*, Fig. 38) and *P. smaragdula* (Kapil and Kumar). But partitions are often absent between older cells. When partitions are absent in nests before emergence of old immatures, they were originally absent or later removed by the mother. Such instance is recorded in *C. cucurbitina* (Grandi), *C. flavipes* and *C. japonica* (Shiokawa 1966), *C. hieroglyphica* and *C. unicolor* (Iwata 1938b). If several partitions are absent, this might be interpreted as removal by the mother. On the other hand, a single omission at the intermediate part of the nest, as illustrated by Shiokawa (19 66, Fig. 9, *C. flavipes*), suggests the lack of construction. The latter case is interesting because it reminds us of a nest made by an unidentified species of allodapine bee (now placed in the genus *Halterapis*, Michener *in litt.*) described by Brauns (1926), containing several pollen loaves, each with an immature but not separated by partitions.

The later removal of partitions in nests containing old larvae and pupae is seemingly relatively common in some species, notably in *C. asuncionis* (2.1.5.), *C. flavipes* and *C. japonica* (Shiokawa 1966), *C. hieroglyphica* and *C. unicolor* (Iwata 1938b). Many authors record or suggest the departure of emerging juvenile adults by passing over their young sibs, without damaging the latter (*C. calcarata*, Rau 1928; *C. callosa*, Malyshev 1913; *C. cucurbitina*, Grandi; *C. ignara*, Michener and Eickwort), although waiting for the growth of younger sibs is recorded in *P. smaragdula* (Kumar, Kapil and Atwal). Destruction of partitions and locomotion across younger sibs by juvenile adults and mother bees were directly observed in *C. calcarata* (Rau) and *C. flavipes* (Tano). In the latter species, the fragments of pith were pressed by the metasomal tip. Mothers laboriously rebuild partitions by using mandibles and legs, with rotation of metasoma, but juvenile females do not rebuild so skilfully. After emergence, the juveniles often consume parts of pollen loaves still remaining. This is also suggested in *C. dallatorreana* (Daly). Thus, in some *Ceratina* species, the contact of mother and her immatures in later stages is quite common. This shows an interesting contrast to some halictine bees, the cells of which are open during the larval stage but closed later (Knerer and Plateaux-Quénu 1966).

In most species, larvae and pupae are basically directed toward the nest entrance (*C. callosa*, Malyshev 1913; *C. chalcites* and *C. dentiventris*, Grandi; *C. ignara*, Michener and Eickwort; *C. vollitans*, *Vo-3, 4*), but reversed orientation is recorded in *C. asuncionis* (*As-20*), *C. cucurbitina* (Grandi), *C. flavipes* (Tano, Shiokawa 1966), *C. japonica* (Shiokawa 1966). This orientation may evoke a difficulty at emergence when the burrow is too narrow. But Tano (1964) observed in *C. flavipes* that these individuals proceed once to the bottom of the burrow, turn there, and go to the nest entrance. It is possible that reversed orientation was brought in some cases by the movement of immatures, but it is certain that some cases was resulted by the transport of immatures by mothers within the nest burrow. This possibility is suggested by some abnormal arrangement of immatures within nests, such as the presence of older immatures nearer to the entrance than younger ones

(*C. asuncionis*, *As-20*, Fig. 52; *C. hieroglyphica*, Iwata 1938b; *C. oxalidis*, *Ox-2*, Fig. 33), or absence of immature in a cell with larval feces (*C. japonica*, Shiokawa 1966, in a nest still before the emergence of progeny). The transport of immatures for short distances was directly observed for *C. flavipes* (Tano 1964). Consequently we can see in *Ceratina* some ethological resemblances to their cousins, the allodapine bees, which have a developed social system. The tendency to omit or remove partitions and to move the immatures, even though still rudimentary, is noteworthy in this connection (cf. Michener 1962b, 1964, 1965, 1968, Sakagami 1960). Recently the behavior of mother bees in the later half of brood rearing period has closely been studied by Maeta (unpub.) with discoveries of many interesting novelties.

2.2.8. Hibernation

As in *Xylocopa*, all temperate *Ceratina* species pass through the winter as juvenile adults of both sexes. Many species seem to hibernate in old nests. Long burrows containing many adults indicate such use of previous nests (*C. calcarata*, Rau; *C. cucurbitina*, *C. cyanea*, *C. nigroaenea*, *C. callosa*, *C. dentiventris*, *C. chalcites*, *C. gravidula*, Friese 1923; *C. japonica*, Iwata 1932, Shiokawa 1966; *C. flavipes*, Shiokawa 1966). Occasionally up to 30 bees are found in the same hibernaculum (Friese 1923), suggesting invasion of some bees from the outside (Iwata 1944). Yamauchi (*in litt.*) recently found three cases of the communal hibernation of *C. flavipes* and *C. japonica* in Gifu Prefecture, Japan. New excavation of hibernacula is also recorded in *C. flavipes* and *C. japonica*. *C. dalltorreana* seems to hibernate solitarily and the hibernacula are often modified to brood rearing nests in the next season (Daly).

Although we have still no precise life history studies on the species in humid tropics, many subtropical and tropical species have an inactive period as in temperate species: *C. asuncionis*, 2.1.5; *C. australensis*, Michener 1962 a, early October to mid February; *C. oxalidis*, 2.1.2.; In *C. asuncionis* both adoption of old nests (*As-23, 24*) and use of preexisting cavities (*As-1~6, 25*) as hibernacula are recorded. However, the cessation of extranidal activity is less clear than in temperate species. Even in temperate species, occasional departures from nests are recorded in *C. cyanea* (Friese, October 24 in Innsbruck, Austria). Under warmer climates, flight activities are not rare even in winter (*C. asuncionis*, 2.1.5; *C. oxalidis*, 2.1.2.; cf. also Section 3; *P. smaragdula*, Kapil and Kumar). Probably many subtropical and tropical species cease brood rearing but not extranidal activity in winter. In *C. australensis*, both young and old bees enter hibernation as in *C. asuncionis* (2.1.5.), but at low altitudes in Queensland, the larvae are found in all months except January and brood rearing activity seemingly continues nearly uninterrupted throughout the year (Michener 1962a). Consequently it is possible that hibernation or inactivity in winter disappear in humid tropical climates, as suggested for *C. ignara* and *Cl.* sp. in Costa Rica (Michener and Eickwort).

2.2.9. Number of generations per year

Friese (1923) writes that (temperate) *Ceratina* species have one generation per

year. The following temperate species are accurately recorded as monovoltine: *C. callosa*, Malyshev 1913; *C. ferghanica*, Ponomareva; *C. japonica*, *C. flavipes* and *C. megastigmata* (Sakagami, Shiokawa, unpub.). *C. dupla* is regarded as bivoltine by Comstock (1895) but as monovoltine by Graenicher (1909) (both after Iwata 1932). There are two temperate species recorded as bivoltine; *C. calcarata* (Rau 1928, the second generation emerging on July 10~12, in St. Louis, Missouri) and *C. dallatorreana* (Daly). In the latter species, two generations widely overlap and cannot be separated in July and August. It is probable that some hibernating females have nesting activity both before and after hibernation.

As to subtropical and tropical species, it is likely that *C. australensis*, *C. ignara* and *Cl.* sp. have more than one generation per year, though this is not definitely stated. The species observed by us, especially *C. asuncionis*, *C. oxalidis* and *C. vollitans* are also regarded as bivoltine. The extreme instance is reported by Kapil and Kumar (1969) who found nests of *P. smaragdula* with food provisions continuously from February to October, and inserting the data on the duration of immature stages (cf. 2.2.7.), estimated the number of generations per year as six to seven. As already commented in *Xylocopa* (1.2.7.), this approach must carefully be undertaken in Xylcopinae, especially when they report themselves a long adult life span reaching 74 days. Anyhow, our present knowledge is still insufficient to compare the annual cycle of various species.

2.2.10. Miscellaneous notes

All previous records show solitary nidification in *Ceratina*. A unique exception is recorded in *C. australensis* by Michener (1962), who found a nest with one cell just provisioned and two females, both with developed ovaries. On the other hand, the co-existence of mother and her adult progeny in post breeding season is recorded in *C. aspera* (Schrottky), *C. asuncionis* (*As-17*, 2.1.5.), *C. australensis* (Michener 1962 a), *C. callosa* (Malyshev 1936), *C. flavipes* and *C. japonica* (Shiokawa, Maeta unpub.), and *C. rupestris* (*Ru-4*, 2.1.3.).

Concerning natural enemies of *Ceratina*, Daly, Stage and Brown (1967) gave an excellent review. In the present study, nests infested by large ichneumonids were found in *C. asuncionis* (*As-13*, *As-16*), *C. oxalidis* (*Ox-2*), *C. rupestris* (*Ru-4*). In no case was the parasite species identified, but they certainly belong to *Grotea* or allied genera, characterized by size much larger than hosts. Their mode of life is regarded by Cushman (1926, cf. Clausen 1940) as unique type among four ichneumonid modes of life.

3. Biofaunistic notes

As indicated in 2.1.2. and 2.1.5, we made two periodical surveys of wild bees in and near Curitiba, one in São José dos Pinhais (March, 1962 to February, 1963, cf. Sakagami, Laroca and Moure 1967), another in Boa Vista, Curitiba (August, 1963 to September, 1964), both three times per month and three (BV) and four hours (SJP) per time. From these results the data on xylocopine bees were extracted and

analysed as described below, with reference to relative abundance, phenology and flower visits.

3.1. Species collected and relative abundance

The species collected are as follows (Two localities are abbreviated as SJP and BV respectively; III-1, III-2, III-3, etc, mean early, mid and late March, etc.).

1. *Xylocopa (Stenoxylocopa) artifex* Smith: SJP (3♀♀), III-1 (1♀), VI-3 (1♀), IX-1 (1♀); BV (2♀♀ 1♂), X-2 (1♀ 1♂), XII-3 (1♀).

2. *X. (Nanoxylocopa) ciliata* Burmeister: SJP (3♀♀ 2♂♂), VI-3 (2♀♀), IX-2 (1♂), I-2 (1♂), I-3 (1♀).

3. *X. (Neoxylocopa) augusti* Lepeletier: SJP (3♀♀ 1♂), XI-1 (1♀ 1♂), XI-2 (1♀), I-3 (1♀); BV (1♀), XI-1 (1♀).

4. *X.* sp. 1: BV (1♀), IX-2 (1♀).

5. *Ceratina (Crewella) asuncionis* Strand: cf. Fig. 55.

6. *C. (Rhysoceratina) vollitans* Schrottky: BV (3♀♀ 8♂♂), IX-2 (1♂), X-1 (1♀), X-3 (1♀ 1♂), VIII-3 (1♀ 6♂♂).

7. *C. (R.) stilbonita* Moure: BV (3♀♀ 2♂♂), X-3 (1♀), XI-3 (2♀♀ 2♂♂).

8. *C. (Ceratinula) oxalidis* Friese: cf. Table 5.

9. *C. (C.)* sp. 2: SJP (3♀♀ 1♂), VI-3 (1♀ 1♂), IX-2 (1♀), XII-2 (1♀); BV (1♀), VII-3 (1♀).

10. *C.* sp. 1: BV (1♀ 1♂), IX-2 (1♂), VI-2 (1♀).

11. *C.* sp. 2: SJP (1♀), IX-1 (1♀).

12. *C.* sp. 3: SJP (19♀♀ 3♂♂), VI-3 (10♀♀ 1♂), VIII-1 (3♀♀), VIII-2 (3♀♀), IX-1 (2♀♀), IX-2 (1♀ 2♂♂); BV (6♀♀ 1♂), IX-2 (1♀), X-2 (1♀ 1♂), X-2 (2♀♀), VII-3 (2♀♀).

The percentage ratio of xylocopine bees to total bees sampled and the relative abundance of various species between SJP and BV are given in Fig. 56 by applying the occurrence probability method of Kato (cf. Sakagami and Matsumura 1967). In the figure the percentage ratio of each species or groups is given by horizontal bar, the ends of which show the confidence limits ($p=0.05$). In total 8 species with 276 individuals (SJP) and 11 species with 108 individuals (BV) were collected, which constituted about 4.8 (SJP) and 6.0% (BV) of the total bee individuals collected (SJP 3,968; BV 1,920). As shown in Fig. 56 bottom, the differences in percentage ratios between two areas are statistically insignfiicant both in species and individual number. Therefore the mean percentage ratios (5.8%, species; 6.5%, individuals) can be used as an estimate for the relative abundance of xylocopine bees in grassland bee assemblages in Eastern Paraná highlands.

Between two genera, the predominance of *Ceratina* is obvious, occupying a about 96% of total xylocopine individuals taken in both areas. The scarcity of *Xylocopa* is explained by its attachment to woodlands except for *X. ciliata*. Being strong fliers, they could certainly reach the grassland biotopes. But the flowers preferred by them may be relatively scarce there and many flowers attracting other bees could not efficiently be visited by them with large and heavy bodies. We observed numerous *Xylocopa* bees visiting arboreal flowers in and near Curitiba during the periods of two surveys, including *X. frontalis*, which was easily identified from a
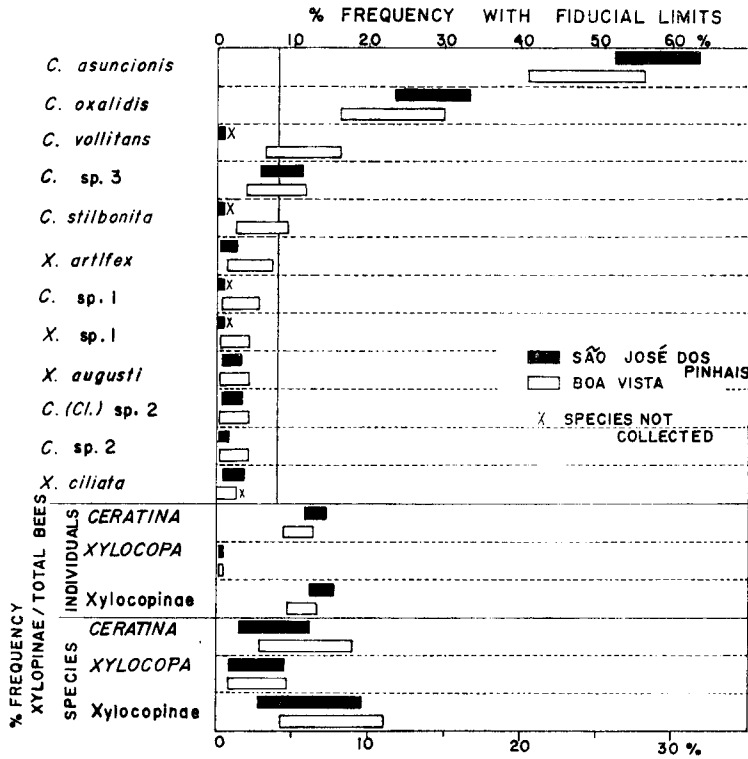
Fig. 56. Relative abundance of xylocopine species in São José dos Phinhais and Boa Vista, shown by occurrence probability method. Vertical solid line means the reciprocal of species number.

distance by its huge body.

Concerning relative abundance of each species, too, two localities are similar. A significant difference is noticed only for *C. vollitans* and *C. stilbonita*, collected only in BV. In both areas, *C. asuncionis* and *C. oxalidis* are dominant species, significantly exceeding the reciprocal of species number. Their percentage ratios to total xylocopine individuals are 58 (SJP) and 48% (BV) for *C. asuncionis* and 28 (SJP) and 22 (BV) for *C. oxalidis*, and their ranks in relative abundance among total bee species collected are the 5th (SJP) and 11th (BV) for *C. asuncionis* and 11th (SJP) and 18th (BV) for *C. oxalidis*. Certainly these two species could be regarded as dominant wild bee species in grassland biotopes of Eastern Paraná highlands.

3.2. Phenology

Seasonal trends of xylocopine bees sampled by two surveys are given in Fig. 57, together with climatic conditions. The basic seasonal pattern obviously

resembles that of *C. asuncionis*, the most dominant species, given in Fig. 55. Because of their long life span and hibernation in the adult stages, xylocopine bees can be seen in any month in this climate, without a seasonal succession of different species as in some andrenid and anthophorine bees (Sakagami, Laroca and Moure 1967). Although the number of individuals collected is not large, they were collected more abundantly from late autumn to early spring, both in absolute
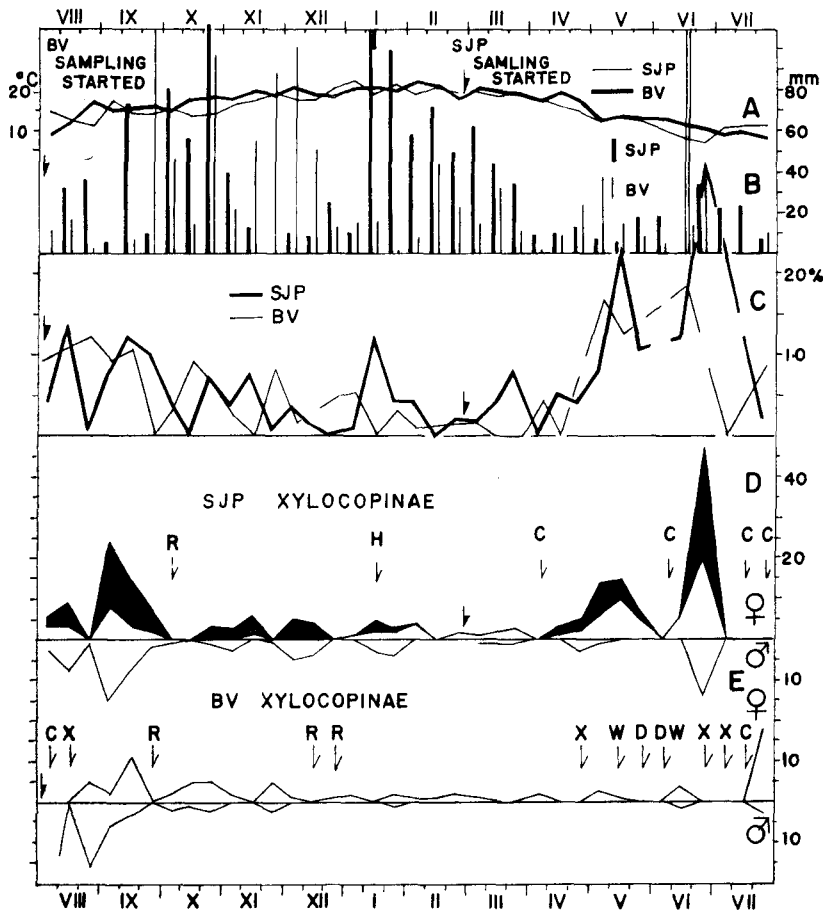

Fig. 57. Phenology of Xylocopinae in São José dos Pinhais (SJP) and Boa Vista (BV). A. Mean 10 days air temperature (SJP, started in early March, 1962; BV, started in early August, 1963, as shown by arrows); B. Rainfall for each 10 days period; C. Percentage of xylocopines to total wild bees captured; D. Individual number of xylocopine bees captured in SJP, female (above, pollen carrying females shown by black part) and males (below); E. Ditto, in BV. In D and E, probable influence of adverse weather is shown by arrows (C, cold; R, rain; H. hot; D. completely cloudy; W. windy; X, not surveyed).

numbers and percentage of total bees taken.   Many individuals were collected in winter on calm, warm days.   The relative abundance in fall to winter apparently in part depends on the scarcity of other bee groups except for Apidae and Halictidae.   At the same time, the emergence of many hibernating adults in fall may be another cause.   However, it was already suggested that some of the species of *Xylocopa* and *Ceratina* have at least two generations per year.   Why we cannot confirm a second peak in summer, corresponding to the emergence of adults reared by the hibernating generation, is uncertain.   Another interesting fact is the presence of numerous females with pollen loads on the legs in fall and winter, recorded only in the survey in SJP (cf. also Table 7 and Fig. 55).   As already commented for *C. asuncionis*, such females certainly are not rearing brood.   This trait is unusual among nonsocial bees, suggesting storage of food or feeding in the nest by these hibernating bees.   Allodapine bees also carry pollen even when they are not feeding larvae (Michener 1968).

3.3.   Flower visits

Most species obtained in the two surveys were collected on flowers.   The flower visits are recorded as follows (p, n in SJP mean the females with and without pollen loads):

   1.   *X. artifex*, SJP: *Senecio* sp. 1 (2n♀♀), *Eupatorium serratum* (1n♀); BV: *Lantana* sp. 1′ (1♀),   *Solanum* sp. 1′ (1♀).
   2.   *X. ciliata*. SJP: *Salvia lachonstachys* (1n♀), *Senecio* sp. 1 (1n♀), *Moritzia dusenii* (2♂♂).
   3.   *X. augusti*. SJP: *Salvia lachnostachys* (2♀♀ 1♂); BV: *Myrcia larvotteana* (1♀).
   4.   *X.* sp. 1. BV: *Senecio oleosus* (1♀).
   5.   *C. (Ceratinula)* sp. 2. SJP: *Escallonia montevidensis* (1p♀), *Senecio* sp. 1 (1p♀, 1♂), *Croton* sp. 1 (1p♀): BV: *Senecio oleosus* (1♀).
   6.   *C.* sp. 2. SJP: *Croton* sp. 1 (1n♀); BV: *Senecio oleosus* (1♀ 1♂).
   7.   *C.* sp. 1. BV: *Senecio oleosus* (1♂).
   8.   *C.* sp. 3. SJP: *Senecio* sp. 1 (16n♀♀ 1♂), *Croton* sp. 1 (2n♀♀ 2 ♂♂), *Prunus* sp. 1 (1n♀ 1p♀ 1♂), *Baccharis articulata* (1♂); BV: *Senecio oleosus* (5♀♀ 1♂), *S. mattfeldianus* (1♀).
   9.   *C. stilbonita*. BV: *Senecio brasiliensis* (2♀♀ 1♂), *Cuphea mesostemon* (1♀), *Senecio* sp. 1′ (1♂).
   10.   *C. vollitans*. BV: *Senecio oleosus* (1♀ 6♂♂), *S. mattfeldianus* (1♀), *S. brasiliensis* (1♀ 1♂), *Schinus englerii* (1♂).
   11.   *C. oxalidis*. SJP: *Eryngium eburneum* (2♂♂), *Escallonia montevidensis* (1p♀ 5♂♂), *Senecio* sp. 1 (7p♀♀ 3♂♂), *Baccharis erioclada* (3♂♂), *Croton* sp. 1 (2n♀♀ 16♀pp 12♂♂), *Baccharis cylindrica* (1p♀ 1♂), *B. spicata* (4n♀♀), *Verbena* sp. 1 (1♀), *Eryngium* sp. 1 (1♂), *Eupatorium* sp. 7 (1p♀ 1♂), *Xyris* sp. 1 (1p♀ 2♂♂), *Baccharis axillaris* (1♂);   BV: *Senecio oleosus* (4♀♀ 2♂♂), *Baccharis malleflora* (1♀ 5♂♂), *Senecio brasiliensis* (4♀♀ 1♂), *Cuphea mesostemon* (1♀),   *Baccharis* sp. 3′ (1♀ 1♂), *Eryngium eburneum* (2♀♀), *Schinus englerii* (1♂).
   12.   *C. asuncionis*. SJP: *Eupatorium serratum* (1n♀), *Vernonia cognata* (3n♀♀), *Eupatorium litorale* (2n♀♀ 1♂), *E.* sp. 2 (3p♀♀), *Vernonia westiniana* (1p♀ 1♂), *Escallonia montevidensis* (1n♀), *Cunila gallioides* (3n♀♀ 1p♀), *Senecio* sp. 1 (29n♀♀ 60p♀♀ 25♂♂), *Croton* sp. 1 (1n♀ 2p♀♀ 2♂♂), *Baccharis cylindrica* (1n♀), *Moritzia dusenii* (2p♀♀ 2♂♂), *Baccharis heliochrysoides* (2p♀♀), *Verbena* sp. 1 (1♂), *Salvia lachnostachys* (1n♀ 3p♀♀ 1♂), *Eupatorium*

sp. 4 (1p♀), *Senecio brasiliensis* (2♂♂), *Eupatorium* sp. 7 (4p♀♀ 4♂♂), *Calea hispida* (1♀);
BV: *Senecio oleosus* (23♀♀ 13♂♂), *Lantana* sp. 1 (1♀), *Vernonia nitidula* (1♀), *Senecio* sp. 1′
(2♀♀), *Vernonia westiniana* (2♀♀), *Baccharis* sp. 2′ (3♀♀), *Eupatorium* sp. 1′ (1♀), Compositae gen. sp. (4♀♀).

In general it is inadequate to consider the flower visiting habits in Xylocopinae
by combining huge *Xylocopa* and dwarf *Ceratina* together. But in our surveys
Xylocopa constitutes a neglegible fraction. The preference for large arboreal flowers
and inflorescences characteristic for *Xylocopa* is not well suggested in the flower
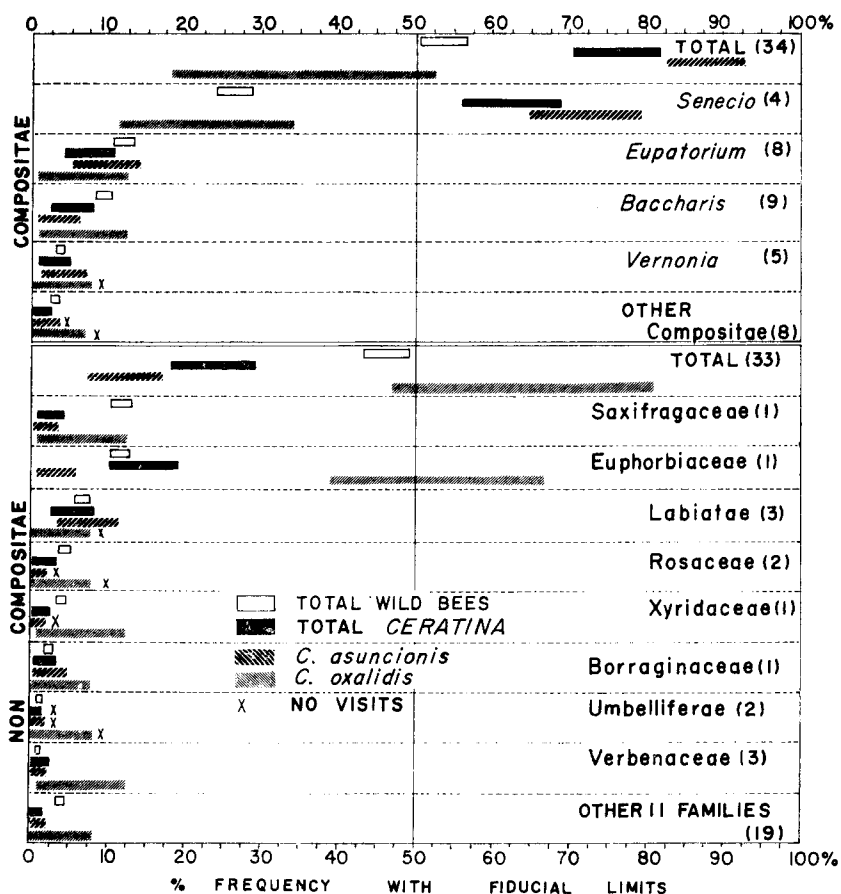records mentioned above. Apparently this means that these records were taken

Fig. 58. Comparison of relative flower visits by females of all wild bees, *Ceratina*
total, *C. asuncionis* and *C. oxalidis* shown by occurrence probability method. Relative
visits are given at generic (composite plants) or family level (non-composites). X means
the absence of visits. Number of plant species visited given parenthetically.

at the periphery of their ordinary life zone. Therefore further consideration of flower visits is given only for *Ceratina*.

Figs. 58 and 59 compare the relative frequencies of visits to flowers by all wild bees (2,944 ♀♀ and 978 ♂♂)[1], all *Ceratina* (180♀♀ 76♂♂) and two dominant species, *C. asuncionis* (122♀♀ 39♂♂) and *C. oxalidis* (34♀♀ 31♂♂), based upon the results of the survey in SJP, females (Fig. 58) and males (Fig. 59) being shown separately. Because of their characteristic life cycle, the adult *Ceratina* are active in any season. Therefore, the comparison is not baised by the discrepancy of phenology between flight periods of bees and blooming periods of flowers, a factor which must be considered in some bee groups such as Anthophorinae, Andrenidae, and Megachilidae.

To facilitate comparison, the occurrence probability method was applied as in Fig. 56. In the figures, percentages of visits to different plant groups are shown by horizontal bars, giving upper and lower fiducial limits ($p=0.05$). Thus the overlap of two bars means the absence of significant difference in relative frequency of visits. As already mentioned in the previous paper, more than the half of the wild bees (both sexes) were collected on composite flowers, a family which outnumbered in species number all the other plant families (34:33). The same tendency is seen in *Ceratina* and for females percentage visits to composites were significantly higher than for all wild bees combined. But this does not necessarily mean a significant preference by *Ceratina* for Compositae. As seen in the figures, a considerable portion of composite visits, both for all wild bees and for *Ceratina* involves visits to *Senecio*. This results from the abundant flowers of *Senecio* sp. 1 blooming from April to October, predominantly May to August, and the only one flower species visited by bees in June and July. During these months of late fall to early spring, only Apidae, Xylocopinae and Halictidae are active as adults, and the number of *Ceratina* collected on flowers is greatest in these months (Fig. 57). Consequently the superficial partiality to Compositae is mainly determined by the coincidence of two phenologies, *Ceratina* and *Senecio* sp. 1.

The lack of specific preference is also shown to other compsite genera, the percentage visits to which show no significant difference between total wild bees and *Ceratina*, except for *Baccharis* (females) and minor genera (males). The same tendency is observed in other plant families, too. In this case, most plant families are represented by a single species (Saxifragaceae-*Escallonia montevidensis*, Euphorbiaceae – *Croton* sp. 1, Xyridaceae - *Xyris* sp. 1, Borraginaceae - *Moritzia dusenii*) or dominanted by one or two species (Labiatae-*Salvia lachnostachys*, *Cunila gallioides*; Rosaceae-*Prunus* sp. 1; Umbelliferae-*Eryngium eburneum* and *E.* sp. 1). A significant difference between *Ceratina* and total wild bees is found in Saxifragaceae, Rosaceae, Xyridaceae and minor families in females, and Euphorbiaceae, Labiatae and Rosaceae in males. But in most cases the number

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1) The figures are corrected and calibrated as to *Trigona spinipes* so that not equal to those given in Sakagami, Laroca and Moure (1967).
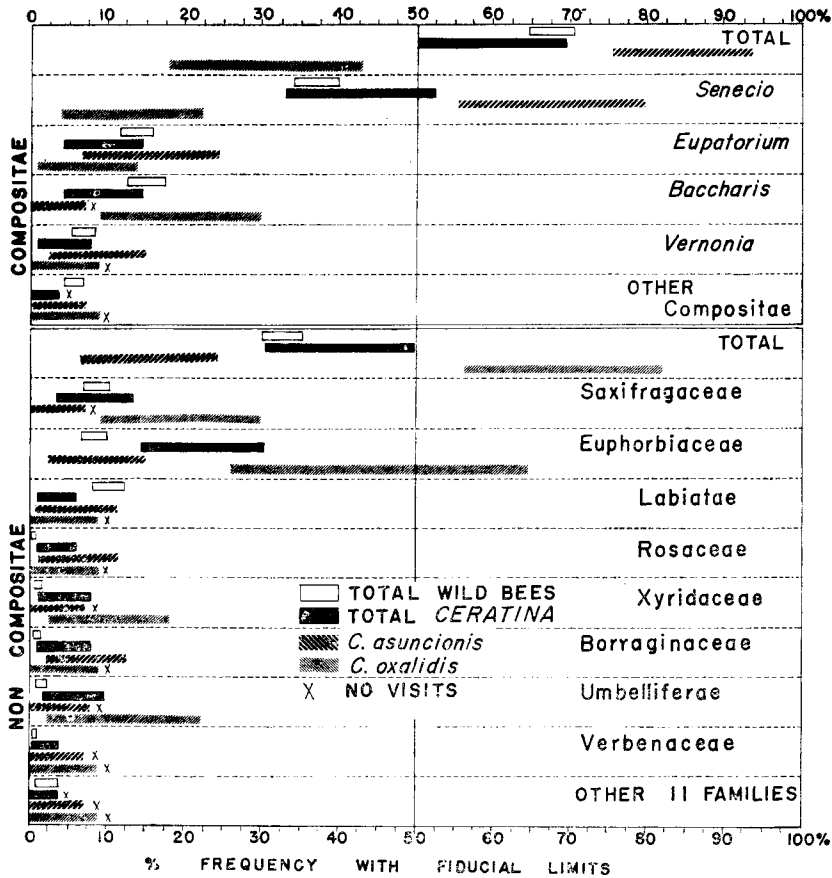
Fig. 59. Comparison of relative flower visits by males of all wild bees, *Ceratina* total, *C. asuncionis* and *C. oxalidis*. Further explanation as for Fig. 58.

of *Ceratina* bees collected is not large enough and the positive cases (=*Ceratina*> total other wild bees) are found only in Euphorbiaceae and Rosaceae (both in males). These facts indicate that the genus behaved as a whole as polytrophic with no marked partiality to any particular flower groups.

The results in Boa Vista are similar, or visits to Compositae are even more prevalent. Among 1,444 females and 404 males of all wild bees collected, 75.4 and 76.1% were respectively captured on Compositae. Further, 47.8 and 44.7% on *Senecio*, predominantly on *S. oleosus* from late autumn to early spring. As to *Ceratina*, among 64 females and 36 males, 92.1 and 94.4% were captured on composites and 71.8 and 77.7% on *Senecio*, mainly on *S. oleosus* as mentioned above. Further details are not given, because visits to other plants were so few.

Table 7. Records of flower visits (individual numbers captured) of *Ceratina asuncionis* and *C. oxalidis* (Figures in parentheses are females with pollen loads)

Flower species	São José dos Pinhais				Flower species	Boa Vista			
	asuncionis		oxalidis			asuncionis		oxalidis	
	♀	♂	♀	♂		♀	♂	♀	♂
Compositae					Compsitae				
Senecio sp. 1	89(69)	25	7(7)	3	*Senecio oleosus*	23	13	4	2
S. brasiliensis		2			*S. brasiliensis*			4	1
Baccharis erioclada				3	*S.* sp. 1'	2			
B. cylindrica	1		1	1	*Baccharis* sp. 3'			1	1
B. spicata			4		*B. malleflora*			1	5
B. heliochrysoides	2(2)				*B.* sp. 2	3			
B. axillaris				1	*Eupatorium* sp. 1'	1			
Eupatorium sp. 2	3(3)				*Vernonia nitidula*	1			
E. serratum	1				*V. westiniana*	2			
E. litorale	2	1			Compositae Gen. sp.	4			
E. sp. 4	1				Non Compositae				
E. sp. 7	4(4)	4	2(2)	1	*Lantana* sp. 1'	1			
Vernonia cognata	3				*Cuphea mesostemon*			1	
V. westiniana	1(1)	1			*Eryngium eburneum*			2	
Calea hispida	1				*Schinus englerii*				1
Non Compositae									
Eryngium eburneum				2					
E. sp. 1				1					
Escallonia monte- *vidensis*	1		1(1)	5					
Cunila gallioides	4(1)								
Salvia lachnostachys	4(3)	1							
Croton sp. 1	3(2)	2	18(16)	13					
Moritzia dusenii	2(2)	2							
Verbena sp. 1		1	1						
Xyris sp. 1			1(1)	2					

Figs. 58 and 59 show a possible difference in flower preference between *C. asuncionis* and *C. oxalidis*. The difference is distinct in the relative avoidance of Compositae in general by both sexes of *C. oxalidis* and by the relative preference by *C. oxalidis* for *Baccharis* (males), Saxifragaceae (males) and especially Euphorbiaceae (both sexes). This difference is suggested, though not statistically significant, by the records of visits to each flower species given in Table 7. In SJP out of 24 flower species tabulated, only six were visited by both while 12 were visited by *C. asuncionis* alone and six by *C. oxalidis* alone. In BV, too, only one out of 14 flower species was visited by both, seven by *C. asuncionis* alone and six by *C. oxalidis* alone. These results indicate different flower preference between two *Ceratina* species dominant in grasslands of Eastern Paraná, probably in part depending on body size, distinctly smaller in *C. oxalidis*.

Summary

1. Nesting habits of thirteen Neotropical species of xylocopine bees, eight *Xylocopa* and five *Ceratina* species, are described, together with some comparative notes on bionomics and the biofaunistic notes obtained in Eastern Paraná.

2. Two species of *Xylocopa*, *X. (Nanoxylocopa) ciliata* Burmeister and *X. (Stenoxylocopa) artifex* Smith, prefer hollow plant cavities for nesting sites, *X. ciliata* floral stalks of *Eryngium* and *X. artifex* bamboo culms. Convergence in nesting habits between two subgenera prefering bamboos, the Neotropical *Stenoxylocopa* and the Oriental *Biluna*, is noted.

3. Nesting habits of all other timber nesting *Xylocopa* species observed, *X. (Neoxyolcopa) nigrocincta* Smith, *X. (N.) grisescens* Lepeletier, *X. (N.) brasilianorum* (Linné), *X. (N.) augusti* Lepeletier, *X. (N.) hirsutissima* Maidl, and *X. (Megaxylocopa) frontalis* (Olivier), coincide in general with previous observations on other species. In all these species many nests have more than one lateral burrow and cells in each lateral are barrel shaped. Special preference for structural timber is suggested for *X. augusti* and *X. hirsutissima*, while *X. frontalis* seems to utilize a variety of nesting substrates.

4. In *X. artifex* and all timber nesting species observed, many nests are seemingly used by more than one generation, and old cells are often reused. The communal use of one nest cavity for brood rearing by more than one female is found in *X. hirsutissima*, *X. augusti*, *X. brasilianorum* and *X. frontalis*. In all these cases, however, the communal use of the some lateral (quasisocial association) is not confirmed.

5. All closely observed species hibernate as juvenile adults of both sexes, often gregariously in the same nests. Some old females also enter hibernation, but it is unknown whether they survive to the next spring or not. In subtropical climates the hibernation inhibits brood rearing activity but some flight activity continues.

6. Most species observed, *X. brasilianorum*, *X. augusti*, *X. hirsutissima*, *X. frontalis* and probably *X. ciliata* and *X. artifex*, seem to have at least two generations per year. Further, encounter and temporal co-existence of mother and her adult progeny seem more common than in temperate species.

7. The pollen loaves sealed without oviposition are frequently found. In one nest of *X. augusti* unsealed cells with immatures were observed. Attack by the parasitic meloid beetle, *Cissites*, is indicated in many nests.

8. Most observed nests of five *Ceratina* species, *C. (Ceratinula) muelleri* Friese, *C. (C.) oxalidis* Schrottky, *C. (Rhysoceratina) vollitans* Schrottky, *C. (Crewella) rupestris* Holmberg and *C. (C.) asuncionis* Strand, are found in dry erect stalks or branches with pithy cores.

9. Nest structures of these species essentially do not differ from that in other species so far recorded. Empty spaces between cells are found in *C. vollitans* and *C. asuncionis* and cells with provisioning but no immatures were found in *C. vollitans* and *C. rupestris*.

10. In *C. asuncionis* most nests in breeding season contain only a few

immatures which are mostly not separated by cell partitions. The transport of immatures by adults is suggested in some nests of this species, *C. oxalidis* and *C. rupestris*.

11. As in *Xylocopa*, *C. asuncionis* and *C. oxalidis* and probably also other species cease brood rearing activity but not flight activity in winter. Winter is passed as juvenile adults of both sexes, but hibernation of old females and probably males to the next spring is seen in *C. asuncionis*. At least *C. asuncionis* and *C. oxalidis* have more than one generation per year.

12. In two wild bee censuses made by periodical sampling in secondary grasslands of Eastern Paraná, the percentage ratio of *Xylocopa* to total wild bees is neglegible, certainly in part due to their weak attachment to grassland habitats. The percentage ratio of *Ceratina* is ca. 5.8% in species number and 6~7% in individual number, relatively low in the favorable season but higher than 10% from late fall to early spring. In both areas, *C. asuncionis* and *C. oxalidis* are most abundant, suggesting their numerical predominance in Eastern Paraná.

13. Most individuals collected in these surveys were captured on composite flowers, especially on *Senecio*. This does not mean a special preference for composites but rather a synchronization between blooming period and high flight activity. A difference in flower preference is observed between two dominant species, *C. asuncionis* and *C. oxalidis*.

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