STUDIES ON THE TAXONOMY, DISTRIBUTION AND ECOLOGY OF PHLEBOTOMINE SANDFLIES OF VENEZUELA

by

MARIA DORA FELICIANGELI DE PIÑERO
Dottore in Scienze Biologiche
(Universitá degli Studi diRoma)
DIC

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Department of Pure and Applied Biology,
Imperial College of Science and Technology
Silwood Park, Ascot,
Berkshire. SL7 5PY

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ABSTRACT

The present study represents the first major review of Venezuelan sandfly taxonomy and ecology.

Species of sandflies known at present are listed and assigned to their currently recognized taxonomic positions.

Five new species have been discovered and are described and another five species are recorded for the first time in Venezuela.

A new synonym has been created after a re-examination of the holotype of Lutzomyia marajoensis (Damasceno & Causey, 1944) which proved to be Lutzomyia walkeri (Newstead, 1914). The name Lutzomyia dubitans (Sherlock, 1962) is resurrected for another fly which was incorrectly recognized as L. marajoensis (Damasceno & Causey, 1944). Morphometric data from L. walkeri and L. dubitans have been used to quantify characters for the separation of the two species.

Morphological anomalies of Venezuelan sandflies are described in 5 species: L. trinidadensis; L. dubitans; L. shannoni; L. lichyi and L. gomezi and an unidentified male fly.

Illustrated Keys for the identification of the species are provided. Proven and incriminated vectors of leishmaniasis are considered.

Searches were made for sandflies in different States of Venezuela. The results are added to previous records and distribution maps plotted and correlated with ecological habitats.

An ecological study of the phlebotomine fauna was carried out at San Esteban, an endemic focus of cutaneous leishmaniasis, for one year. Information about the relative abundance, occurrence, seasonal fluctuations,

anthropophily and zoophily of sandflies and the efficiency of different trapping methods is collated and statistically analyzed.

The vector potential of each species present in the focus is estimated on the basis of parasite infection rates, the correlation between the specific population density and the incidence of leishmaniasis in the area.

The results suggest that the fly suspected as the major vector of cutaneous leishmaniasis in Venezuela, L. panamensis, does not, in fact, play any role in parasite transmission at San Esteban.

A strategy for future research is outlined in the light of the present results.

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1. GENERAL INTRODUCTION

1.1 Phlebotomine Sandflies and American Leishmaniases

The medical importance of Phlebotomine sandflies, haematophagous Diptera belonging to the family Psychodidae, stems especially from their ability to transmit flagellates of the family Trypanosomatidae, genus Leishmania.

A major interest of parasitologists in these protozoa arises from both the abundance of clinical variations of the leishmaniases and from the seriousness of some forms of the disease. Visceral leishmaniasis (kala-azar) when not properly treated, causes a high mortality and muco-cutaneous leishmaniasis produces disfiguring manifestations in the affected people. Zuckerman & Lainson (1977) enumerate a series of reasons that contribute to the importance of this group of diseases as a serious problem of public health. Among others they indicate:

1. the fact that, particularly in Latin America, leishmaniasis is restricted to the poorer sectors of the community;
2. the difficulties of both treatment (lengthy, expensive and generally late) and control (at present, not feasible for the sylvatic zoonoses);
3. the low level of medical interest in a disease that lacks the drama associated with fatal infections such as occur in yellow fever or malaria.

A recent classification of Leishmania of the New World has been given by Lainson & Shaw (1979) who, in addition to Leishmania chagasi Cunha and Chagas, 1937, the causative organism of Neotropical kala-azar, recognize 9 species or subspecies that infect man, causing different

forms of cutaneous disease viz: Leishmania mexicana mexicana Biagi, 1953; Le.* mexicana amazonensis Lainson & Shaw, 1972; Le mexicana pifanoi Medina & Romero, 1959; Le. mexicana aristedesi Lainson & Shaw, 1979; Le. braziliensis braziliensis Vianna, 1911; Le braziliensis guyanensis Floch, 1954; Le. braziliensis panamensis Lainson & Shaw, 1972 and Le. peruviana Velez, 1913. Another recently described species, Le. garnhami Scorza et al., 1979, can be added to the list.

Le. mexicana mexicana causes "chiclero's ulcer", the histopathology of which is pathognomonic of this parasite. The ear, which can become completely mutilated, is the most commonly affected organ. This form of leishmaniasis is most prevalent in Central America.

Le. mexicana amazonensis usually produces single or scanty lesions without special preference in localisation. It is also the causative organism of Brazilian cases of diffuse leishmaniasis. It has been recorded in Brazil and probably exists in some countries including southern Venezuela (Pifano et al., 1973).

Le. mexicana pifanoi produces a florid form of the disease called "leishmaniasis tegumentaria diffusa". This is a leprosy-like form, interpreted by some authors as due to a peculiar immunological state of the patient and not to a different species of the parasite (Convit et al., 1972). It has been described in Venezuela, on the north-east coast of Brazil and in Amazonas State.

Le. mexicana aristedesi has been isolated from wild rodents and one marsupial in Panama. Lainson & Shaw (loc.cit.) consider that "although no human cases have been reported to date, it is quite likely

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*The abbreviations Le. and L. are used to avoid confusion between the genera Leishmania and Lutzomyia respectively.

that they do occasionally occur".

Le. braziliensis braziliensis is the aetiological agent of the classical form, "espundia", which shows the most disfiguring clinical features. It is characterised by sole or scanty lesions often followed by metastases to the nasopharyngeal tissues with serious effects on breathing, speaking and swallowing. This form is found in Brazil, Peru, Ecuador, Bolivia, Colombia, Paraguay and Venezuela.

Le. braziliensis guyanensis causes "pian-bois", a form of leishmaniasis which is manifested by the usual chronic ulcers which are frequently multiple, due to a metastatic spread along the lymphatics or by the blood circulation. At the moment, this form is known only from the Guyanas and N.E. Brazil.

Le. braziliensis panamensis has been found in Panama, and possibly extends south into Colombia. The lesions are usually single, but sometimes may become multiple due to metastatic spread; it rarely, if ever, causes espundia.

Le. peruviana produces the classical "uta", a benign clinical form since it usually spontaneously regresses. It is found only in the Peruvian Andes. Lesions are usually single.

Le. garnhami is a new species of Leishmania showing a peculiar and unique organelle. It produces cutaneous lesions unique in people living at a height of 800 to 1,800m in urban and rural areas of the Venezuelan Andes region (Scorza et al., 1979a).

From the large amount of available evidence, it is not doubted that all the parasites causing the Neotropical leishmaniases are, like the Old World forms, transmitted by phlebotomine sandflies. In the

New World, this is a large subfamily, Phlebotominae, about 350 Neotropical species of which are presently known.

About 25 species are proven or suspected to transmit Neotropical leishmaniasis of one form or another, but the roles of comparatively few have been confirmed beyond doubt (Lainson & Shaw, 1979).

One difficulty in proving which sandflies transmit Leishmania is the lack of laboratory colonies of sandflies. The establishment and maintenance of colonies of these insects in the laboratory is usually laborious and expensive, and many colonies have been abandoned (Johnson & Hertig, 1961; Christensen, 1972b).

Two Neotropical species, Lutzomyia longipalpis (Lutz & Neiva, 1912) and Lutzomyia flaviscutellata (Mangabeira, 1942), have been recently established as closed colonies (Killick-Kendrick et al., 1977a; Ward, 1977b) leading to studies on the ultrastructure and life cycle of Le. mexicana amazonensis in L. longipalpis (Killick-Kendrick et al., 1974; Molyneux et al., 1975) its transmission to hamsters by bite (Killick-Kendrick et al., 1977b) and some aspects of the host-parasite relationship (Killick-Kendrick et al., 1977c) and to provide overwhelming evidence of the role of L. flaviscutellata as a vector of Le. mexicana amazonensis in Brazil (Ward et al., 1977).

Since suitable prophylactic and control methods of the cutaneous forms are not still available, attempts to resolve the outstanding problems of the biology of the vectors, discussed by Killick-Kendrick (1978), must be made in order to have a better understanding of the epidemiology.

Almost all forms of leishmaniasis are zoonoses in which man is an accidental host. Visceral leishmaniasis is generally peridomestic, with the dog as the main reservoir, but the Neotropical cutaneous leishmaniases

(except the Peruvian form) are sylvatic, the known reservoirs of which are rodents, marsupials and edentates.

Bustamante (1948) made the first summary of the epidemiology of leishmaniasis in the New World; later, Deane (1958) and Deane & Deane (1964) analysed the problems of visceral leishmaniasis in South and Central America, while Lainson & Shaw (1973) especially emphasised the cutaneous forms. More recently, Ward (1977a) in a wide analysis of the distribution and incidence of the leishmaniases in the various countries of America, summarized the epidemiological changes that occurred during the last three decades.

1.2 Leishmaniases in Venezuela

In Venezuela all clinical forms except "uta" have been observed, but in spite of a great deal of work further studies are necessary to explain the epidemiological features of the leishmaniases in this country. Even the true incidence of disease is not known, cases of leishmaniasis are often unnotified or untreated. The 101 cases of visceral leishmaniasis (Ward, 1977a) and 13,676 cases of dermal leishmaniasis (Archives of The Department of Dermatology, 1977, in: Aguilar, 1981) which are on record in Venezuela undoubtedly form only a small part of the actual number of cases.

In Venezuela, kala-azar is a rural and sylvatic disease with a sporadic incidence (Pifano, 1954), and is not epidemic, as in India. The geographical distribution of the endemic foci is limited to 14 out of 23 states (Fig. 1) (Romero, 1965).

Dermal leishmaniases occur in 21 of 23 States (Table 1), but cases are generally restricted to humid and wooded locations in the foothills of mountain regions.

In Venezuela the dog is the only proven reservoir of kala-azar (Amaral et al., 1961a; Torrealba et al., 1961, 1964) and very little is known about the reservoirs of the parasites of dermal leishmaniases. Some isolates from wild rodents; Heteromys (Torrealba et al., 1972), Zygodontomys (Kerdel-Vegas & Essenfeld.Yahr, 1966) and Proechimys (Convit, 1968) are thought to belong to the Le. mexicana complex (Lainson & Shaw, 1979). Dogs and donkeys found with leishmanial skin lesions (Pons, 1968; Bonfante et al., 1973, 1981) may represent accidental infections forming no part in a true chain of transmission of L. braziliensis sensu lato, although the possibility that they may contribute to the spread of

cutaneous or mucocutaneous leishmaniasis of man in some places cannot yet be excluded (Aguilar, 1981).

Further studies are necessary to demonstrate the identity of animal and human strains. Isolation and typing of parasites from man are important since they are still treated as "unidentified subspecies of Leishmania braziliensis complex" (Lainson & Shaw, 1979).

Five species of Venezuelan sandflies: Lutzomyia longipalpis (Lutz & Neiva, 1912), Lutzomyia panamensis (Shannon, 1926), Lutzomyia migonei (França, 1920), Lutzomyia flaviscutellata (Mangabeira, 1942) and Lutzomyia townsendi (Ortiz, 1960) have been seen naturally or experimentally infected with promastigotes thought to be Leishmania spp. Their role as vectors is still "suspected" but not fully demonstrated.

In 1943 Pifano reported catching L. longipalpis infected with a kind of "leptomonas" very similar to the parasites of the same form, developed in cultures of protozoa from a human dermal lesion.

Later, one of 14 L. longipalpis caught feeding on a dog infected with Le. chagasi was seen to be infected with promastigotes when dissected 4 days later (Amaral et al., 1961b). This observation, and the fact the geographical distribution of kala-azar and L. longipalpis overlap, and that the same species of sandfly was found naturally infected with promastigotes in other endemic foci of kala-azar in Latin America, led Amaral et al. (1961b) to conclude that L. longipalpis was the "probable" vector of visceral leishmaniasis in Venezuela.

Similarly Pifano et al. (1959) incriminated L. panamensis as the vector of dermal leishmaniasis on the basis of the following observations: (i) Pifano (1941) had caught specimens naturally infected with pro-

mastigotes, (ii) this species is highly anthropophilic, and (iii) one of his colleagues, who served as bait in a Shannon trap in an endemic focus of dermal leishmaniasis, developed a typical leishmanial lesion two months later. L. panamensis was the only species caught feeding on man. L. migonei was found infected with promastigotes thought to be Le. braziliensis (Pifano, in: Forattini, 1959) but no further evidence of its role as a vector was supplied.

L. flaviscutellata has also been found with promastigotes which, when inoculated into a hamster, caused a lesion containing amastigotes indistinguishable from those of Le. amazonensis pifanoi (Pifano et al., 1973).

L. townsendi has been shown to be susceptible to infection by a parasite first described as "Le. braziliensis sensu lato" but later referred to as "L. mexicana (?)" (Mogollón et al., 1977; Carnevali & Scorza, 1976). It is thought to be the vector of Le. garnhami, on the basis of its ecological association with the parasite in the Venezuelan Andes (Scorza et al., 1979a).

The present study was intended:

1. to update the taxonomy of the sandflies in Venezuela, to create a new check-list of the species, and to review their taxonomic position and illustrate the principal characters used in original keys for their identification;
2. to review the known geographical distribution of Venezuelan sandflies, map the distribution of each species and relate available records to biohabitats.

3. to collect the scattered information on biological and ecological aspects of each species in Venezuela and prepare a preliminary bibliography of Venezuelan sandflies.
4. to gather new information on the ecology of sandflies in an endemic focus of cutaneous leishmaniasis in Venezuela; and
5. to establish a type-collection of Venezuelan sandflies for reference purposes.

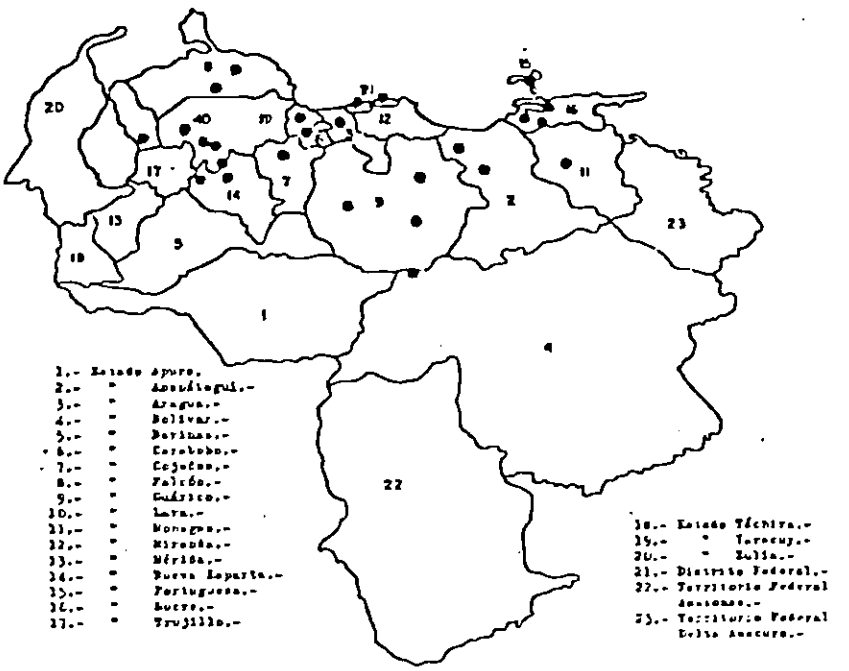


Fig. 1. Endemic foci of visceral leishmaniasis in Venezuela (after Romero , 1965).

	1955-65	1970	1971	1972	1973	1974	1975	1976	1977	Total
Dtto. Federal	9	-	5	4	1	-	-	1	13	33
Anzoátegui	41	23	3	17	22	9	9	20	13	156
Apure	23	-	-	-	2	3	3	2	-	33
Aragua	250	-	15	1	11	27	6	6	10	326
Barinas	1.597	57	57	56	43	36	28	36	10	1.895
Bolívar	217	12	12	8	3	5	2	1	-	260
Carabobo	91	6	48	25	16	38	-	1	32	257
Cojedes	77	-	-	-	-	-	-	-	-	77
Falcón	89	-	1	1	-	-	1	1	-	93
Guárico	61	-	-	1	-	-	-	1	-	63
Lara	240	-	71	23	16	28	76	31	24	511
Mérida	2.151	36	29	41	49	39	60	42	37	2.482
Miranda	123	-	3	22	50	10	9	7	4	228
Monagas	-	-	-	6	8	12	9	11	7	53
Portuguesa	282	67	53	30	31	10	24	27	10	534
Sucre	26	-	4	17	31	20	48	44	125	310
Táchira	2.310	329	103	104	74	54	147	64	64	3.049
Trujillo	1.368	54	117	111	121	103	62	101	25	2.062
Yaracuy	145	21	24	20	16	12	32	16	16	306
Zulia	752	14	28	35	24	16	21	25	9	924
T.F.Amazonas	6	-	-	-	-	-	-	-	18	24
VENEZUELA	5.866	412	571	517	518	402	535	437	415	10.674

Table 1. Number of cases of cutaneous and muco-cutaneous leishmaniases diagnosed by the Dermatology Services in Venezuela (1955 - 1977) (Archives of the Department of Dermatology, Caracas).

2. REVIEW OF THE SYSTEMATICS OF PHLEBOTOMINE SANDFLIES

2.1 Classification at the level of the Family and Sub-families

Sandflies are insects belonging to the order Diptera, sub-order Nematocera, family Psychodidae. They are small (1-5 mm), and have a hairy body and long, delicate legs. The thorax is convex and the wings, which are lanceolate, are also covered with hairs. When at rest, the wings are directed upwards and outwards, making an angle with the body, like small butterflies

From the description of the first sandfly, Bibio papatasi, Scopoli until now the classification of sandflies has been controversial. In the present work only the most recent contributions are summarized since several specialists (Lewis et al., 1977; Martins et al., 1978; Ready et al., 1980) have recently reviewed and discussed the history of the taxonomy of sandflies in depth.

The flies have been divided into taxa for practical convenience, or as a result of their morphology or suspected phylogeny. This has given rise to several different systems of classification. Nevertheless, the arrangement of the family Psychodidae in six sub-families is now unanimously accepted. Six sub-families can be easily separated by the following characters given by Young & Fairchild (1974):

1. Trichomyinae (Cosmopolitan)
   a. Radius of wings with 4 branches
   b. $R_2 + R_3$ fused in a single vein
   c. Wing broad and rounded
   d. Mandibles absent

2. Sycoracinae (Palearctic, Pantropical)
   a. Radius of wings with 4 branches

b. $R_2 + R_3$ fused in a single vein

c. $R_2 + R_3$ and R_4 forked distal to emission of R_5

d. r-m cross-vein prominent

e. Wing broad and rounded

f. Mandibles present

3. Horaiellinae (China, India)

a. Radius of the wings with 4 branches

b. $R_2 + R_3$ fused in a single vein arises from R_5 proximal to R_4

c. r-m cross-vein faintly discernible

d. Wing elongate

e. Mandibles present

4. Psychodinae (Cosmopolitan)

a. Radius of wing with 5 branches

b. Palpi with 4 segments

c. Eyes with eye-bridge

d. Antennal segment nodiform or barrel-shaped

5. Bruchomyinae (Pantropical, Neartic, Australia, New Zealand)

a. Radius with 5 branches

b. Palpi with 5 segments

c. Eyes without eye-bridge

d. Antennal segments pyriform or subcylindrical

e. ♀ mouth parts not adapted for blood-sucking: mandibles absent

f. ♀ with 1 spermatheca

g. Aedeagus of male entire

6. Phlebotominae (Cosmopolitan)

   a. Radius with 5 branches

   b. Palpi with 5 segments

   c. Eyes without eye-bridge

   d. Antennal segments pyriform or subcylindrical

   e. ♀ mouth-parts with well developed mandibles adapted for blood-sucking

   f. ♀ with 2 spermathecae

   g. Aedeagus of male bifid.

2.2 Classification at the level of genera.

Of the six sub-families of Psychodidae, only Phlebotominae are haematophagous, and it is only flies of this sub-family which transmit leishmaniasis.

For more than thirty years there has been controversy over the generic names of phlebotomine sandflies (e.g. Theodor, 1948, 1965; Fairchild, 1955; Barretto, 1955; Forattini, 1971, 1973; Lewis et al., 1977; Ready et al., 1980, 1981; Williams, 1981). At first, this sub-family contained the single genus Phlebotomus Rondani. In 1948 Theodor proposed the division of the Old World and the New World sandflies into four genera: Phlebotomus and Sergentomyia for the Old World species and Lutzomyia and Brumptomyia for American forms.

Two new genera, Warileya Hertig and Hertigia Fairchild, were later described and named by Hertig (1948) and Fairchild (1949). In 1955 Fairchild published one of the most detailed papers on the classification of Neotropical sandflies, in which he advocated the retention of the generic name Phlebotomus for all but the species placed in the genera Warileya and Hertigia. In suggesting this, he hoped to avoid confusion and keep the name Phlebotomus for medically important and bloodsucking psychodid sandflies.

Barretto (1955) accepted the genus Brumptomyia of Theodor (loc.cit.) but rejected Lutzomyia, placing the majority of New World species in the genus Sergentomyia.

Later, Barretto (1961, 1962) and Fairchild (Young & Fairchild, 1974) accepted the four genera proposed by Theodor in 1948. Theodor created the basis for the modern classification of New World sandflies (Theodor, 1965), listing naming 250 American species. Martins & Morales (1972) raised

this number to 292. New radical proposals on the systematics of sandflies were given by Forattini (1971, 1973). He raised four sub-genera to generic status and rejected the use of the informal categories "groups" and "series". The sub-family Phlebotominae was therefore divided in 9 genera: Phlebotomus and Sergentomyia, for the Old World, Lutzomyia, Viannamyia, Pressatia, Pintomyia, Psychodophygus and Warileya for the New World.

However, this classification has not yet been accepted by the majority of specialists. Young & Fairchild (1974) considered that his system was based on too few characters and was therefore unnecessarily artificial. Martins et al. (1978) judged that many of the supraspecific taxa defined by Forattini (1971, 1973) were heterogeneous, his definition of taxa cumbersome and obvious natural relationships between species, were obscured.

Lewis et al. (1977) emphasized that, after 285 years since the description of the first sandfly, there was a need to agree to a stable classification of these insects. They suggested the "compromise of retaining well known names of family, sub-family and genera and the use of sub-genera and species-groups as a method to express new ideas." They recommended that the philosophy of Abonnenc & Leger (1976) should be followed to keep generic names to a minimum and their contents broad. A biogeographical concept and practical convenience were the main reasons supporting the division of the sub-family into the 5 genera (Phlebotomus, Sergentomyia, Lutzomyia, Brumptomyia and Warileya).

The argument of academic convenience was also emphasized by Martins et al. (1978). In addition to 5 genera given by Lewis et al. (1977), Martins et al. (1978) maintained the genus Hertigia, as proposed by

Young & Fairchild (1974), with the hope of keeping a "common language" amongst sandfly taxonomists. However, they thought that Hertigia should be a junior synonym of Warileya. Ready et al. (1980) challenged the "stable classification" proposed by Lewis et al. (loc.cit.) and gave reasons for a "flexible classification" of sandflies. They supported the rank of genus for the subgenus Psychodopygus and having re-examined the different criteria on which previous systems were based, used a comparative analysis of characters to explain their support.

Ready et al. (loc.cit.) described "exclusive" characters for their proposed genera, i.e. Warileya, Brumptomyia, Psychodopygus, Phlebotomus and Sergentomyia, but none for Lutzomyia. The absence of unique characters for the genus Lutzomyia is a weak point in their "comparative" character analysis.

In their historical review of the systematics of sandflies Ready et al. (1977) mentioned Forattini's classification but only treated the genus Psychodophygus which Forattini had subdivided in 2 subgenera: Psychodophygus and Trichophoromyia. They pointed out that, following Fraiha et al. (1971) and Fraiha & Ward (1974), the genus Psychodophygus proposed by them contained only the species of the former subgenus.

The lack of investigation and discussion of the status of any of the other subgenera recognized by Lewis et al. (1977) and Martins et al. (1978), constitutes another weak point in their argument.

They admitted that consequently "their approach might be attacked as lacking unity" but cite Linnaeus' dictum "it is the genus that gives the characters and not characters that make genus" in support of their action. Characters are indispensable tools for the taxonomist, but the way in which these tools are used sometimes creates confusion.

The main morphological characters used to distinguish the genus Brumptomyia from the genus Lutzomyia (i.e. the form of the interocular suture and the arrangement of the horizontal cibarium teeth) undoubtedly constitute a "decided" gap between the two genera, as defined by Mayr (1969). Practical convenience and medical importance were considered and used by Lewis et al. (1977) to support well defined morphological differences. The conclusions they offer are, however, still a "compromise". Although I agree that "classification must not be created solely as a reliable easy to-use filing system "(Ready et al., loc.cit.) the proposition of Lewis et al., appears to me to be logical, at least in the short-term until important gaps are filled. For example, it is striking that there are at least 85 Neotropical species of sandflies for which only one sex is known. The parallelism of having 2 major groups in each hemisphere separated on the basis of one morphological character (the female cibarium) and the use of variation in medical importance "must have looked very attractive" to Lewis et al. (loc.cit.) and were critizised by Ready et al. (loc.cit.). However the latter workers failed to offer a more attractive solution and their classification appears illogical and confused.

At the end of their discussion they defined 3 characters to distinguish Psychodophygus from Brumptomyia. These work perfectly, being the same characters, mentioned above, used to separate Brumptomyia from Lutzomyia. They also give three "distinctive" characters to separate Psychodopygus and Lutzomyia, two of which overlap in practice. These are the "mountainlike" or "volcanic" exochorionic sculpturing of eggs, and the abdominal, mostly recumbent abdominal setae on tergites 2-6, with erect setae restricted to segments 2-4, "characteristic" of Psychodopygus"; these characters, however, are also shown by L. flavis-

cutellata of the subgenus Nyssomyia.

Although Ready et al. (loc.cit.) themselves admit that "the variable nature of the palpal formula has persuaded taxonomists to assign little weight to palpal characters" they use, as an "exclusive" character for Psychodopygus the 5th decidedly short palpal segment. It is indeed true that this character separates Psychodopygus on the one hand from Brumptomyia Phlebotomus and Sergentomyia, all three of which have 5th palpus segments which are constantly long. However, the monotypic subgenus Hertigia of the genus Warileya, and some species in the genus Lutzomyia, have a short 5th palpal segment and this character cannot be considered "exclusive" to Psychodopygus.

The full comparison of Psychodopygus with other sub-genera and species groups is indispensable if it is to be raised to the rank of genus. Moreover this rise in status is difficult to justify at present because the ranking of sub-genera and groups is far from stable (Lewis et al., loc.cit.; Martins et al., loc.cit.). It could be argued that several other subgenera have as much right as Psychodopygus to be raised to generic rank. The imbricated spermathecae of Psychodopygus are no more distinctive than the paired sclerotized structures of Viannamyia spermathecae or the presence of spines on the hind femur in Pintomyia.

To conclude, morphology, biogeography, phylogeny, practical convenience and medical importance are sufficiently strong reasons at the moment to support the classification proposed by Lewis et al. (1977) and followed by Martins et al., that is five genera: Phlebotomus and Sergentomyia for Old World flies and Lutzomyia, Brumptomyia and Warileya for New World flies.

Of these five genera, four (Phlebotomus, Sergentomyia, Brumptomyia and

Lutzomyia) show:

1. Wing relatively narrow, pointed at tip
2. $R_2 + R_3 + R_4$ forked beyond r-m cross-vein
3. Dististyle shorter than basistyle

The genus Warileya has the following characters:

1. Wings broad, rounded at tip
2. $R_2 + R_3 + R_4$ forked before, above, or just slightly beyond r-m cross-vein
3. Dististyle of male longer than basistyle

With some exceptions, species of the two Old World genera lack or just have one group, episternal setae, but in the American species two groups are clearly evident. Brumptomyia is separated from Lutzomyia by the following characters:

Brumptomyia:

1. Interocular suture complete
2. Dististyle with 5 large spines
3. Basistyle with a basal tuft or patch of setae and with 1-6 setae (in a row) on the distal portion
4. Cibarium of the female with 4 longitudinal rows of hind teeth, fore teeth lacking

Lutzomyia:

1. Interocular suture incomplete
2. Dististyle of male genitalia with 1-6 major spines
3. Cibarium of female with 1 row of hind (horizontal) teeth, often with fore (vertical) teeth.

3. TAXONOMY OF VENEZUELAN SANDFLIES

3.1 Introduction

After a re-examination of the early taxonomic literature and a critical appraisal of recent studies, Lewis et al. (1977), in an attempt to resolve the present confusion in the systematics of phlebotomine sandflies, have recently proposed a practical system for a classification of these medically important insects. For reasons given in Section 2.2 above, this system is adopted in the present study of Venezuelan sandflies.

Recently Martins et al. (1978) published an extensive account of American phlebotomine sandflies. Although the classification proposed by these authors is different from that of Lewis et al., at the level of sub-genera and species-groups, their paper is especially useful because it lists all species and their geographical distribution by country and by locality.

Research into the taxonomy and distribution of sandflies in Venezuela has mainly been linked to epidemiological studies in endemic foci of leishmaniasis. During a review of the literature on South American Sandflies my attention was drawn to the fact that many more sandfly species have been recorded in two neighbouring countries than in Venezuela itself. 108 species are known in Colombia (Martins et al., 1978; Young, 1979; Morales & Minter, 1981) and 176 in Brazil (Martins et al., 1978), but only 39 in Venezuela (Martins et al., 1978). Although Brazil is much larger than Venezuela, this relatively low number of species is thought to be explained mainly by a lack of research in Venezuela rather than by the assumption that there is a poor sandfly fauna in that country.

An adequate background knowledge of the taxonomy of sandflies is a prerequisite to the understanding of the epidemiology of the leishmaniases (WHO, 1979). Since it seemed clear that less is known of the sandflies of Venezuela than of many other countries in which the Neotropical leishmaniases are endemic, it was decided to make new collections of sandflies in Venezuela and to re-examine existing collections with a view to updating the taxonomy and geographical distribution of phlebotomine sandflies of that country. The results of this study are presented in this section of the present work.

3.2 Materials and methods

During the past two decades, a series of studies on kala-azar and cutaneous leishmaniases, mostly undertaken by Dr. J.W. Torrealba for research or teaching pusposes, has been carried out at the University of Carabobo, Valencia, Venezuela.

In this work a large collection of sandflies has been amassed from different parts of the country; this has provided part of the material studied in the present work.

New surveys of sandflies have also been made in three States: Carabobo, Cojedes and Apure. The sandflies of Apure had never previously been studied.

Field sampling methods.

For a complete understanding of the total phlebotomine population in an area, several different collecting methods must be used. No single trapping technique will catch all species present in any one area. Even if several species are caught by one method, it is most unlikely that they will be equally sampled.

The methods used in this work were chosen on the basis of availability and proven efficiency.

1. Sampling the adult resting population. Adult flies resting on tree trunks, in tree holes, in the dark crevices between buttresses and in the litter on the forest floor were found with a torch and collected with an oral aspirator. Sometimes flies were disturbed by rapping on the tree trunks or, if this was unsuccessful, with cigarette smoke.

These day-time collections of resting adults are much less time

consuming than night captures. Furthermore, they are of particular value in catching non-phototropic and non-anthropophilic sandflies.

2. Sampling adults by human and animal bait catches. Adults of sandflies, as of other haematophagous insects, are usually caught biting human or animal baits. Crepuscular and nocturnal collections were the most useful because sandfly activity was at a peak at this time.

3. Sampling adults by light traps. Shannon traps (Shannon, 1939) made from muslin and lit by a kerosene lantern, and C D C light traps (Sudia & Chamberlain, 1962) were used at night to catch phototropic species. The species composition of catches with these two traps was very similar.

Laboratory methods.

For routine identification, the sandflies were mounted in Berlese's fluid. The fluid is soluble in water and has two special advantages: (i) it has an excellent refractive index for revealing transparent structures like spermathecae and (ii) the mounting procedure is rapid. Slides were ringed with transparent nail polish after drying in an incubator at about 37°C for one month.

The taxonomic characters used for the differentiation and the classification of Phlebotomine sandflies were the following:

A - Ascoids or geniculated spines: hyaline spines situated on most antennal segments, well differentiated from other spines by their refringence and shape; on ascoids of some sandflies there is a pair of backward projecting prolongations called "posterior spurs".

B - Palps: generally in the description of species palpal formulae

are recorded. This is done by listing the segments in order of length from the shortest to the longest. In the Keys the length of 3rd and 5th palpal segment is also related and compared.

C - Pharynx: this is the suction pump that continues posteriorly from the cibarium. The posterior part is sometimes armed with spines or striae.

D - Cibarium: this is constituted of 3 plaques, 1 ventral and 2 dorso-lateral . The basal part of the ventral plaque presents the cibarial armature formed by hind (or horizontal) and fore (or vertical) teeth.

E - Cibarial arch: this is a chitinous arch situated before the cibarium. It can be complete or incomplete.

F - Spermathecae: these lie in a pair at the level of the VIII abdominal segment. The shape of the spermathecae and the relative lengths of individual and common ducts are used in the Keys.

G - Genitalia of the male: these consist of four paired parts: styles, aedegai, (divided in basistyle and dististyle), parameres and lateral lobes. The presence or absence of setae and/or spines and the shape and length of many of the parts are diagnostic characters for the identification of males of the species.

H - "Alpha" and "Delta" of the wing: "alpha represents the length of the anterior branch of the 2nd longitudinal vein (R_2); "delta" gives the length of the portion of the 1st longitudinal vein (R_1) measured from the tip to the level of the 2nd bifurcation of R_2. (Other measurements not used in the present Keys, are (i) "beta": the distance between the 1st and the 2nd bifurcation of R_2 and (ii) "gamma": the distance between the level of the first bifurcation of R_2 and the level

of the transversal vein r-m.).

I - The ratio of FI (= antennal segment n° 3) length to L (labrum) length is useful in separating some species and has been used in the present work.

In describing the new species, measurements were done following the methods given by Young (1979).

Distribution maps

The geographical distribution of Venezuelan sandflies is presented in the form of distribution maps for each species. These were plotted according to the system developed by the Medical Ecology branch of NAMRU-5 (Ash, 1972; Ash & McConnell, 1975).

This method provides a simple and uniform system for recording the distribution of plants and animals.

All published records and new records from recent sandfly catches and from a re-examination of existing collections (present study) were mapped.

The Venezuelan area was divided into a grid of 15' squares, each representing about 25 Km^2. Each square in which one or more records were available was marked. Maps were made for each species. Occasionally the distribution of several species which did not overlap are plotted on the same map.

Map references for the localities (Appendix 1) were obtained from the Nis Gazetteer (1961) and from Maps of the Direction of National Cartography and Maps elaborated by the Ministry of Healthy (Dirección de Malariologia y Saneamiento Ambiental)by State and County, whenever

available.

Occasionally collection sites were not found in any of these sources and coordinates cannot be given for them. An indication of the position of such sites is based on a proximity to named roads and larger villages; the county in which they occur was given whenever possible.

The ecological map of Venezuela by Ewel & Madriz (1968) divides the country into various "life zones". A life zone is defined as the widest division of the climatic habitat which exerts a dominant influence on the ecosystem (Holdridge, 1964). This ecological map (Fig. 52) was used in an attempt to relate sandfly distribution to the different habitats.

3.3 Results

In 1978 Martins et al. listed 39 species of Venezuelan sandfly. This number was raised to 46 by Feliciangeli (1980) and, in the present work is increased to 58 (Table 2).

The sandfly fauna includes 3 species of Brumptomyia viz: B. devenanzii (Ortiz & Scorza, 1963) (female unknown), B. beaupertuyi (Ortiz, 1954) and B. avellari (Costa Lima, 1932) which was recently found in Venezuela by Ramirez et al. (1976).

Although Brumptomyia galindoi (Fairchild & Hertig, 1947) was reported from Lara State by Pifano & Ortiz (1952), and was included in the Venezuelan fauna by Martins et al. (loc.cit.) it probably does not occur in Venezuela. Scorza et al., (1967) re-examined the specimen from Lara State and concluded that the fly was B. beaupertuyi. B. galindoi is therefore not included in the present work.

The remaining 55 species are of the genus Lutzomyia. In accordance with Martins et al., (loc.cit.), four species previously reported from Venezuela are excluded from this list. Lutzomyia dendrophila (Mangabeira, 1942) and Lutzomyia furcata (Mangabeirea, 1941) are omitted because no collection localities were given (Pifano et al., 1962a). Lutzomyia pifanoi (Ortiz, 1972) and Lutzomyia gibsoni (Pifano & Ortiz, 1972) are considered synonyms of Lutzomyia shannoni (Dyar, 1929) and Lutzomyia fischeri (Pinto, 1926) respectively (Martins et al., 1978).

Two species accidentally omitted by Martins et al. (loc.cit.) are added to the list of Venezuelan sandflies. They are Lutzomyia triacantha (Mangabeira, 1942) reported by Pifano (1962) in Portuguesa State and Lutzomyia verrucarum (Townsend, 1913) reported by Floch & Abonnenc (1950-1953) from Carabobo State and by Pifano (Pifano & Ortiz, 1952)

Table 2. List of the species of phlebotomine sand flies found in Venezuela. Symbols show which sexes are known and described; the symbol in parentheses indicates that the ♂ is known but has yet to be described (modified from Feliciangeli, 1980).

GENUS (SUBGENUS) OR SPECIES GROUP	SPECIES	SEX
Brumptomyia	avellari (Costa Lima, 1932)	♂♀
	beaupertuyi (Ortiz, 1954)	♂♀
	devenanzii (Ortiz & Scorza, 1963)	♂
Lutzomyia		
(Evandromyia)	begonae (Ortiz & Torres, 1975)	♂♀
	sp. of Monay	♂
(Lutzomyia)	gomezi (Nitzulescu, 1930)	♂♀
	ignacioi Young, 1972	♂♀
	lichyi (Floch & Abonnenc, 1950)	♂♀
	longipalpis (Lutz & Neiva, 1912)	♂♀
(Nyssomyia)	anduzei (Rozeboom, 1942)	(♂)♀
	antunesi (Coutinho, 1939)	♂♀
	flaviscutellata (Mangabeira, 1952)	♂♀
	hernandezi (Ortiz, 1965)	♂♀
	olmeca bicolor Fairchild & Theodor, 1971	♂♀
(Pintomyia)	fischeri (Pinto, 1926)	♂♀
(Pressatia)	dysponeta (Fairchild & Hertig, 1952)	♂♀
	triacantha (Mangabeira, 1942)	♂♀
	sp. of Chiricoca	♂
(Psychodopygus)	panamensis (Shannon, 1926)	♂♀
	parimaensis (Ortiz & Alvarez, 1972)	♀
	squamiventris (Lutz & Neiva, 1912)	♂♀
(Trichophoromyia)	ubiquitalis (Mangabeira, 1942)	♂♀
baityi group	baityi (Damasceno, Causey & Arouck, 1945)	♂
cayennensis group	atroclavata (Knab, 1913)	♂♀
	cayennensis cayennensis (Fairchild & Hertig, 1948)	♂♀
	micropyga (Mangabeira, 1942)	♂♀
	venezuelensis (Floch & Abonnenc, 1948)	♂♀
	yencanensis (Ortiz, 1965)	♂♀
	sp. of La Vaquira	♀
longispina group	conviti Ramirez-Perez, Martins & Ramirez, 1976	♂♀
	longispina (Mangabeira, 1942)	♂♀
migonei group	dubitans (Sherlock, 1962)	♂♀
	migonei (Franca, 1920)	♂♀
	walkeri (Newstead, 1914)	♂♀
oswaldoi group	trinidadensis (Newstead, 1922)	♂♀
pilosa group	pilosa (Damasceno & Causey, 1944)	♂♀
	sp. of Bitichas	♀
saulensis group	saulensis (Floch & Abonnenc, 1944)	♂♀
shannoni group	abonnenci (Floch & Chassignet, 1947)	♂♀
	dasymera (Fairchild & Hertig, 1961)	♂♀
	lutziana (Costa Lima, 1932)	♂♀
	punctigeniculata (Floch & Abonnenc, 1944)	♂♀
	shannoni (Dyar, 1929)	♂♀
verrucarum group	columbiana (Ristorcelli & van Ty, 1941)	♂♀
	evansi (Nunez-Tovar, 1924)	♂♀
	nuneztovari (Ortiz, 1954)	♂♀
	ottolinai (Ortiz & Scorza, 1963)	♂♀
	ovallesi (Ortiz, 1952)	♂♀
	townsendi (Ortiz, 1960)	♂♀
	verrucarum (Townsend, 1913)	♂♀
	serrana (Damasceno & Arouck, 1949)	♂♀
	sp. of Loma Abajo	♂♀
vexator group	ceferinoi (Ortiz & Alvarez, 1963)	♂
	scorzai (Ortiz, 1965)	♂♀
	erwindonaldoi (Ortiz, 1978)	♂
Ungrouped	rangeliana (Ortiz, 1953)	♂♀
	torrealbai Martins, Ordonez & Falcao, 1979	♂
Inadequately described species	maracayensis (Nunez-Tovar, 1924)	♂

in Merida State.

While the paper by Martins et al. was in press, 2 species were collected in Venezuela for the first time. These were Lutzomyia columbiana (Ristorcelli & Van Ty, 1941) (Martins, pers. commun.) and Lutzomyia pilosa (Damasceno & Causey, 1944) from Trujillo State, (Ramirez Perez et al., 1979). In addition, four new species have been described from Venezuela during this time. Lutzomyia begonae (Ortiz & Torres Rojas, 1975) and Lutzomyia conviti Ramirez Perez et al., 1977, were both found in Territorio Federal Amazonas. Lutzomyia torrealbai Martins et al., 1977 came from Trujillo State and Lutzomyia erwindonaldoi (Ortiz, 1978) came from the boundary of Trujillo and Zulia States.

In the present study, 10 more Lutzomyia species have been added to the list of Venezuelan sandflies, making a total of 58 species of this sub family. Five new species were discovered in previously unidentified material in two collections (Universidad de Carabobo and Universidad de los Andes) (See 3.3.1). Another five species are recorded here for the first time from Venezuela. (See 3.3.4.).

The species Lutzomyia dubitans (Sherlock, 1962) has been resurrected after synonymizing Lutzomyia marajoensis (Damasceno & Causey, 1944) with Lutzomyia walkeri (Newstead, 1974). (See 3.3.2). Anomalies occurring in several species have been described. (See 3.3.3)

A new check-list is presented (See 3.3.5) with a brief summary of the characteristics of each subgenus and species-group and a list of the species which form them. For each species references are given for the first description and any redescription of the adults, for the description of immature stages and for any Keys in which the species occur.

All available references were cited except for the most studied species when only the most recent papers on biology and ecology are quoted.

Special attention has been paid to the precise localities in Venezuela from which sandflies have been collected.

A brief note about taxonomic and/or biological aspects is also given for species for which there is information. Because of the variability of habits and behaviour of the species according to different habitats, only observations made in Venezuela have been reported; unless otherwise stated, the information is from the papers cited for the geographical distribution. Illustrated taxonomic Keys for the identification of females and males are presented (See 3.3.6).

Both sexes of 44 species have been described and all are included in the Keys of the species. Only the males of Lutzomyia baityi (Damasceno, Causey & Arouck, 1945), Lutzomyia ceferinoi (Ortiz & Alvarez, 1963), L. erwindonaldoi, L. torrealbai, Lutzomyia sp. of Chiricoca, Lutzomyia sp. of Monay and the females of Lutzomyia parimaensis (Ortiz & Alvarez, 1972), Lutzomyia sp. of La Vaquira and Lutzomyia sp. of Bitichas are included in the Keys; the other sex of these species are unknown. The male of Lutzomyia anduzei (Rozeboom, 1942) is known but not yet described, (Young 1979), and is consequently omitted from the Key. Lutzomyia maracayensis (Nuñez-Tovar., 1924) is an "inadequately described species" (Martins et al., 1978) and for this reason, although included in the list, has also been omitted from the Key.

Sandflies were caught in 52 new localities. In addition, flies from another 15 localities, which had been mounted but not identified, were examined and identified. Sandflies from a total of 67 new sites are therefore recorded (See 3.3.4. and 3.3.5.).

3.3.1 New species of the genus Lutzomyia

Descriptions of 5 new species of Lutzomyia, found in the present work are given in this section. In accordance to the International Code of Zoological Nomenclature (ICZN 1964, 1974) no names are here assigned to these new taxa.

Lutzomyia sp. of La Vaquira (Fig. 2)

Female (n = 3). Head: length 0.36 (0.33-0.38) mm, width 0.31-0.33, length/width 1.08-1.16. Eyes separated by 0.13 mm = ca. 10 facet diameters. Antennae: Segment 3 (= Flagellomere I) 0.17 (0.16-0.19) mm long = length of II + III. Ascoids of A4 (= FII) simple and short. Palps (n = 2). Length of segments in mm: 1, 0.035-0.038; 2, 0.113-0.093; 3, 0.150-0.138; 4, 0.138-0.123; 5, 0.330, palpal formula: 1, 2, 4, 3, 5. Labrum: 0.22 (0.20-0.23) mm. long. Index FI/L.0.77. Cibarium with 4 straight triangular hind teeth and 4-5 vertical teeth at each side of the middle line; with an odd medium tooth-like process. Chitinous arch absent, pigmented patch comparatively dark. Pharynx as figured 0.5 mm long. Pleura with 5-12 upper and 3-5 lower episternal setae. Wing: length 1.74 (1.73-1.75) mm, width 0.50 (0.45-0.58) mm. Length of veins in mm. alpha 0.29, beta 0.30, delta 0.11, gamma 0.26 mm; indices alpha/beta = 0.97, alpha/delta = 2.66, alpha/gamma = 1.12. Legs. Length of femora, tibiae, basitarsis and tarsi. (Slide no. 2059-A): foreleg: 0.70, 0.63, 0.37, 0.58 mm, midleg: 0.66, 0.77, 0.41, 0.60 mm, hindleg missing; (Slide no. 2059-C) foreleg and midleg missing, hindleg: 0.72, 0.92, 0.49, 0.65 mm. Spermathecae as shown (Fig. 2), large and sausage-like, individual ducts long, common duct not visible.

Material examined: Holotype ♀, Slide no. 2059-A, (British Museum, N.H.), 2 Paratype ♀♀: Slide no. 2059-B (University of Carabobo, Parasitologia, Maracay, Venezuela) and Slide no. 2059-C (University of Carabobo,

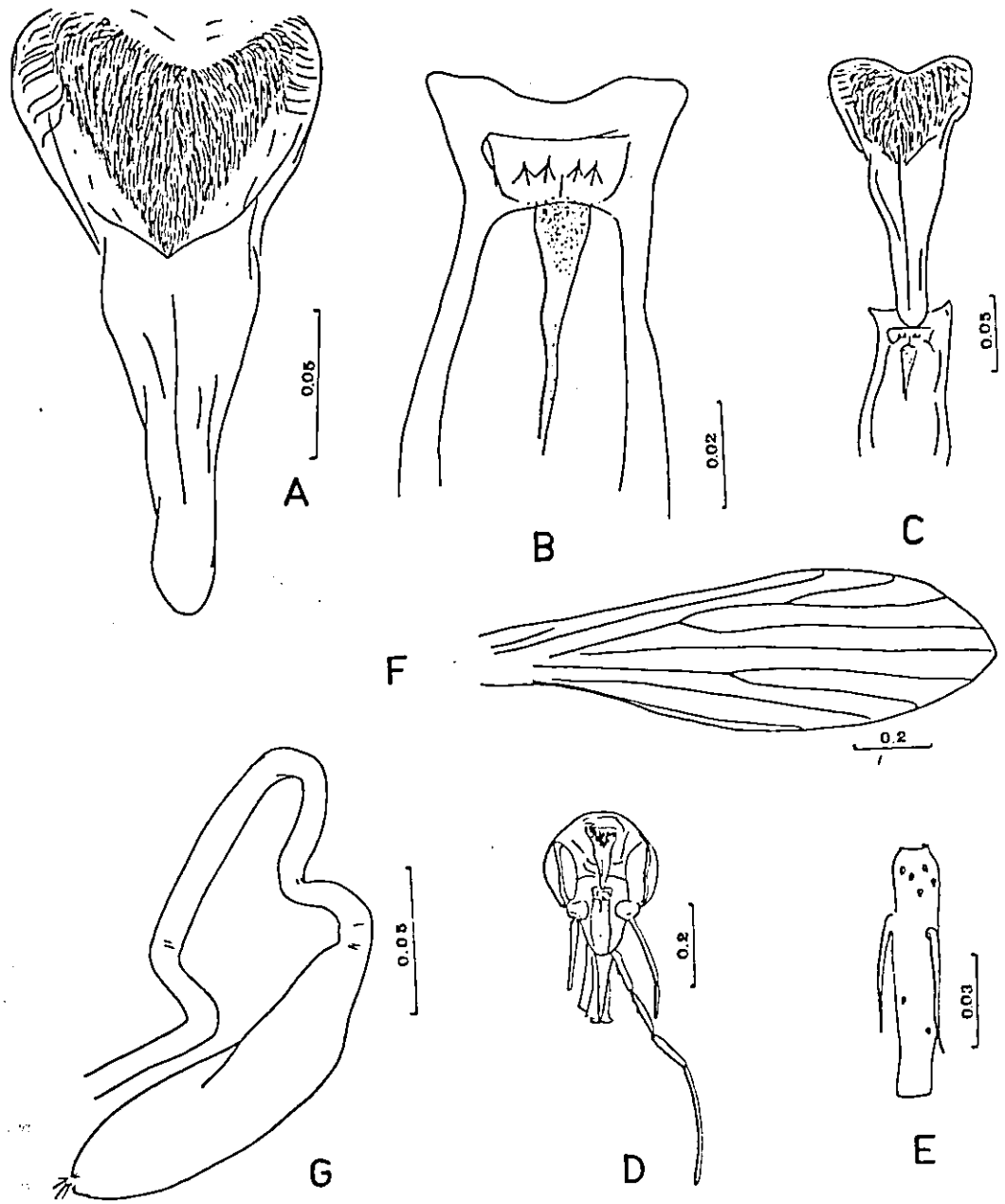


Fig. 2. Lutzomyia (cayennensis group). L. sp. of La Vaquira. Female : A. Pharynx; B. Cibarium; C. Pharynx and cibarium; D. Head; E, Flagellomere II; F. Wing; G. Spermatheca.

Parasitologia, Valencia, Venezuela). Locality type. La Vaquira, Municipio (= county) El Pao, Cojedes State, Venezuela, 20 June, 1977,Coll. Elio Fernandez.

Discussion: This species differs from other Lutzomyia mainly in the peculiar shape and armature of its spinose pharynx. It somewhat resembles the pharynx of the species of the cayennensis group, series atroclavata, L. atroclavata (Knab, 1913) and L. venezuelensis (Floch & Abonnenc 1948); however, it differs from those in the presence of the crowded spines over the transverse ridges. In addition, the spermathecae are undoubtedly distinct. It is also worth mentioning that the odd medial "tooth" in the cibarium somewhat resembles that of L. vexator (Coquillet, 1907) and L. vindicator (Dampf, 1944), but not in other characters.

On the basis of these considerations we tentatively assign this species to the cayennensis group, series atroclavata, pending the discovery of the male. L. sp. of La Vaquira was collected in a tree hole during the day, together with L. longipalpis (3♂♂ and 4♀♀), L. cayennensis (5♂♂ and 3♀♀) and L. rangeliana (1♂ and 5♀♀).

It will be with great pleasure that I shall name this my first described species, in honour of Dr. David J. Lewis whose invaluable orientation in the study of the taxonomy of sandflies has roused my curiosity and enthusiasm for this group of insects.

Lutzomyia sp. of Bitichas (Fig. 3). -

Female (Holotype). Head: length 0.31 mm, width 0.29 mm. length/width index = 1.06. Eyes separated by 0.11 or by distance = ca. 6.5 facet diameters. Antennae: Segment 3 (= Flagellomere I) 0.24 mm long, 1.2 x length of II + III. Ascoids of FII simple, their distal tips reaching

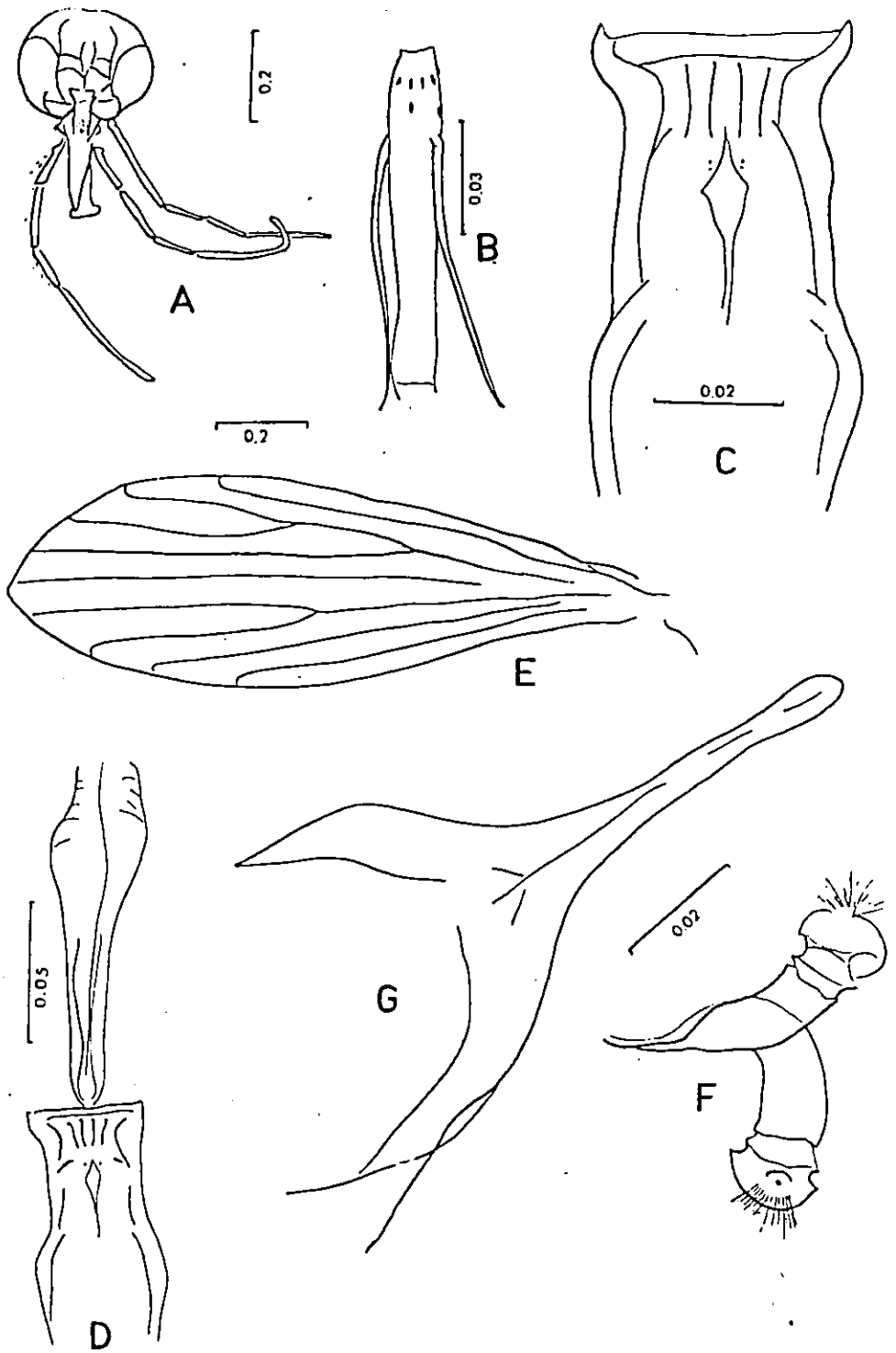


Fig. 3. Lutzomyia (pilosa group).L.sp. of Bitichas.
Female : A, Head; B, Flagellomere II;
C. Cibarium; D. Pharynx and Cibarium; E. Wing;
F. Spermathecae; H. Furca.

to or beyond end on all flagellomeres except the last. Palps: length of palpal segments in mm. : 1, 0.023; 2, 0.103; 3, 0.138; 4, 0.100; 5, 0.320. Palpal formula: 1, 4, 2, 3, 5. Labrum 0.16 mm long. Index F I/L 1.47. Cibarium with 4 long, horizontal teeth as figured, chitinous arch absent, pigment patch well defined, Pharynx unarmed, 0.10 mm long. Pleura with 5 upper and 4 lower episternal setae. Wing length 1.62 mm. long. Length of wing vein: Alpha 0.36 mm, beta 0.29 mm, delta 0.16 mm, gamma 0.19 mm; indices alpha/beta = 1.24; alpha/delta = 2.25; Alpha/gamma = 1.89. Legs: Length of femora, tibiae, basitarsis and tarsis 2+3+4+5. Foreleg: 0.67, 0.68, 0.38, 0.60 mm: midleg: 0.66, 0.81, 0.46, 0.60 mm; hindleg 0.69, 0.95, 0.50, 0.64. Spermathecae as illustrated (Fig. 3), exceedingly small, narrowing abruptly to individual ducts only the beginnings of which are visible. Common duct not discernible.

Material examined: Holotype ♀ Slide no. 710. Locality Type. Bitichas, Municipio San José, Trujillo State, Venezuela, elev. 1500 m, 7 Nov. 1972, Pedro Manzanilla, deposited at the British Museum (N.H.).

Discussion: The cibarial armature of the female places the species in the pilosa group Theodor, 1965. The females of the three species which comprise this group, L. pilosa, (Damasceno & Causey, 1944), L. mangabeirana Martins, Falcão & Silva, 1963 and L. chassigneti (Floch & Abonnenc, 1944), are almost indistinguishable. Their spermathecae are tubular and smooth, continuing indefinitely into individual ducts. This new species differs from them notably in the shape of the spermathecae, which show a slight but definite distal constriction and an abrupt continuation into very delicate individual ducts.

The specimen examined was the only one captured by a simple aspirator from a hollow tree between 15.10 h and 15.40 h. Feeding habits, associate

species and any other biological or ecological data are unknown but it is likely that, like the other members of this group, this species is not abundant, since it was found in an area comprising 280 localities, explored during 5 years work (1971-1976) which yielded 42,000 specimens belonging to 17 species (Mogollón et al, 1977).

I will dedicate this species to Dr. José Witremundo Torrealba, a great Venezuelan parasitologist and an inestimable friend whose premature death has moved me deeply.

Lutzomyia sp. of Loma Abajo. (Fig. 4, 5 and 6).

Male (n = 2) Head: length 0.31, width 0.27, length/width index = 1.15. Eyes separated by 0.12 mm or distance ca. 7.2 facet diameters. Antennae: Segment 3 (= Flagellomere I) 0.27 mm, nearly 1.14 x length II + III. Ascoids of FII simple and short, not reaching the end of the segment. Palps: length of palpal segments: 1, 0.023; 2, 0.132; 3, 0.129; 4, 0.104; 5, 0.177; palpal formula: 1, 4, 3, 2, 5. Labrum length, 0.22 mm; F I/L 1.23. Cibarium with small numerous vestigial teeth, chitinous arch atypical, pigment patch narrow. Pharynx: length 0.14 mm. Pleura with 4 upper and 3 lower episternal setae. Wings partially folded, length 1.52 mm, width not measurable. Length of vein sections: alpha 0.37 mm, beta 0.17 mm, delta 0.09 mm, gamma not measurable: indices alpha/beta = 2.18, alpha/delta = 4.11. Legs. Femora, tibia and basitarsi: Foreleg: 0.77, 0.89, 0.54. Midleg: 0.74, 1.05, 0.6; Hindleg lacking. Genitalia: Style (0.12 mm long) with 4 spines and a small subterminal bristle. The basal spines are situated at the same level and implanted on well marked relatively long tubercles. Coxite (0.23 mm long) bearing two groups of hairs, being (i) the basal tuft built by numerous and fine, closely inserted setae and (ii) the distal group sparse but well defined. Paramere rounded at the end and variable according to angle of view,

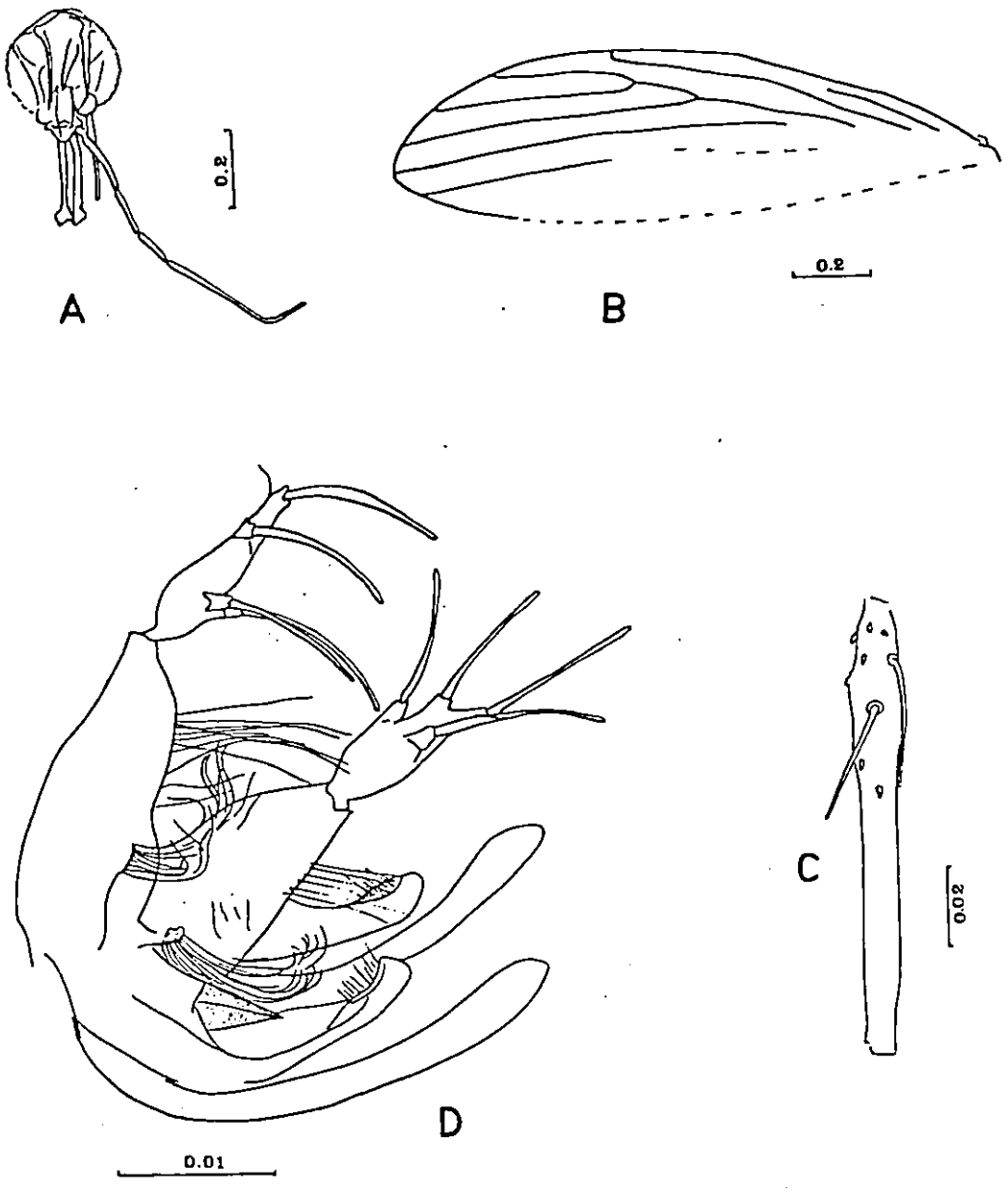


Fig. 4. Lutzomyia (verrucarum group) L.sp. of Loma Abajo. Male : A, Head; B, Wing; G. Flagellomere II; D. Genitalia.

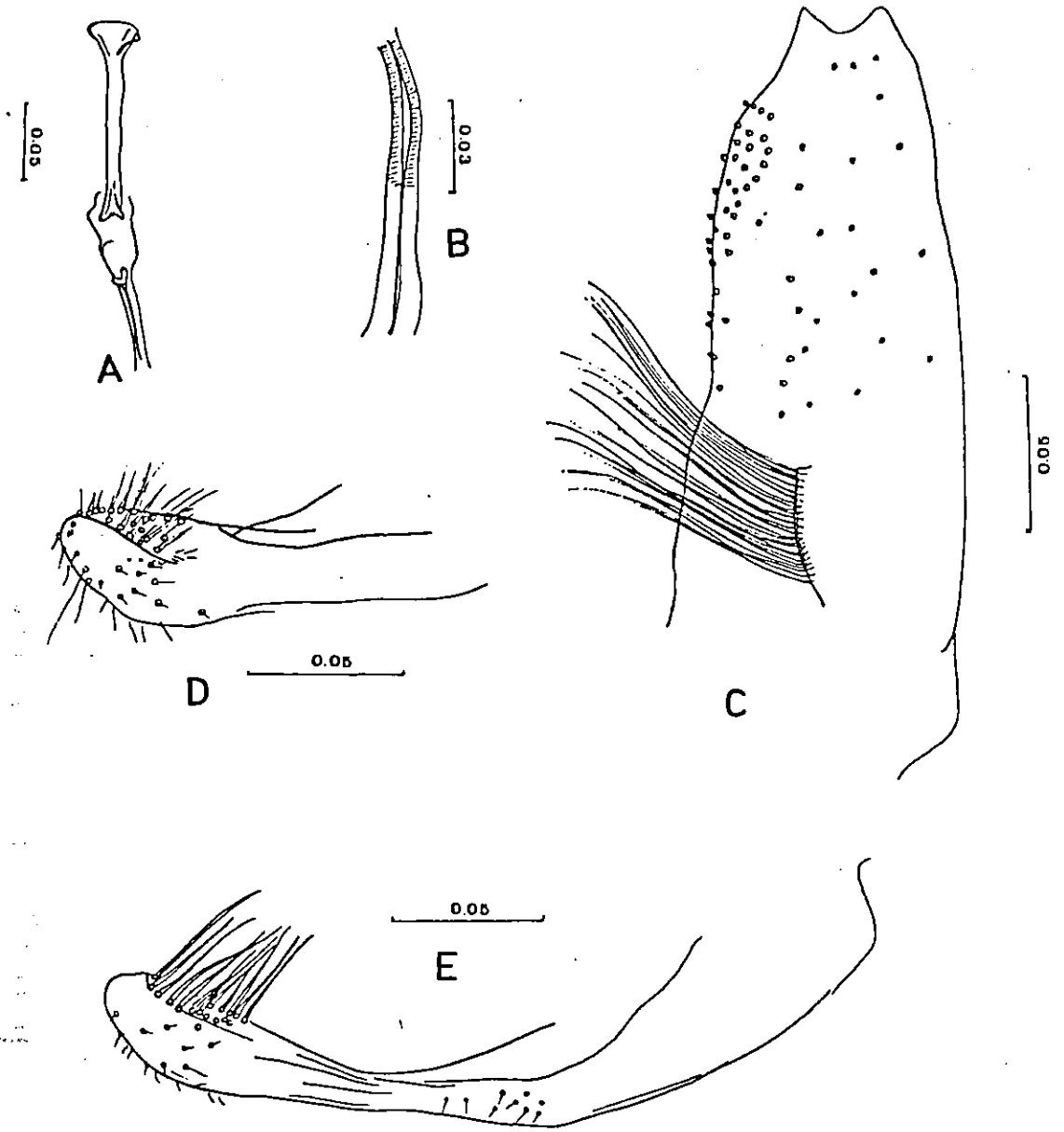


Fig. 5. Lutzomyia (verrucarum group). L.sp. of Loma Abajo. Male : A. Genital pump; B. Distal end of genital filaments; C. Coxite : basal tuft and sockets of distal tuft; D. Dorsoventral view of a paramere; E. Lateral view of a paramere.

as depicted (Fig. 5), upholding dorsal setae at the tip. Lateral lobe (0.58 mm) longer than coxite. Aedeagus subtriangular (0.06 mm). Genital pump (0.132 mm long), each filament 0.56 mm long or approximately 4.23 x length of pump, filament tips simple, very slightly enlarged apically.

Female (n = 4). Head: length 0.402 (0.38-0.41) mm, width 0.396 (0.382-0.408) mm, length/width index 1.01. Eyes separated by 0.17 = ca 8-9 facets diameters. Antennae: Segment 3 (= Flagellomere I) 0.31 mm long, 1.14 x length of II + III. Ascoids of F II simple and short. Palps. Length of segments in mm : 1, 0.038; 2, 0.122; 3, 0.164, 4, 0.110; 5, 0.279; palpal formula: 1, 4, 2, 3, 5. Labrum length 0.23 mm. Ratio FI/L = 1.35. Cibarium with numerous fine teeth of different sizes which continue laterally, appearing twisted in different positions according to the mounting; numerous vertical teeth concentrated in the middle also present; pigmented patch absent. The cibarial armature widening anteriorly showing a chitinous structure crossing its ventral wall, different from the typical arch. Pleura with 13-18 upper and 1-4 lower episternal setae. Wing: length 2.33 (2.30-2.38) mm. width 0.74 (0.73-0.76) mm. Length of vein sections: alpha 0.61 (0.60-0.63) mm, beta 0.25 (0.21-0.30) mm, delta 0.21 (0.20-0.22) mm, gamma 0.24 (0.22-0.26) mm; indices alpha/beta = 2.44, alpha/delta = 2.90, alpha/gamma = 2.54. Legs. Femora, tibiae and basitarsis (n = 1). Foreleg: 0.91, 1.05, 0.43; midleg: 0.87, 1.29, 0.73 mm, hindleg: 0.96, 1.55, 0.76 mm. Spermathecae sac-like and wrinkled, individual ducts stocky, common duct not discernible.

Material examined. ♂ holotype, slide no. 1038, Loma Abajo, Municipio Cegarra, State Trujillo, Venezuela, 1 June 1970, Mr. Pedro Manzanilla. ♀ allotype, slide no. 1733, La Vega de Tosto, State Trujillo,

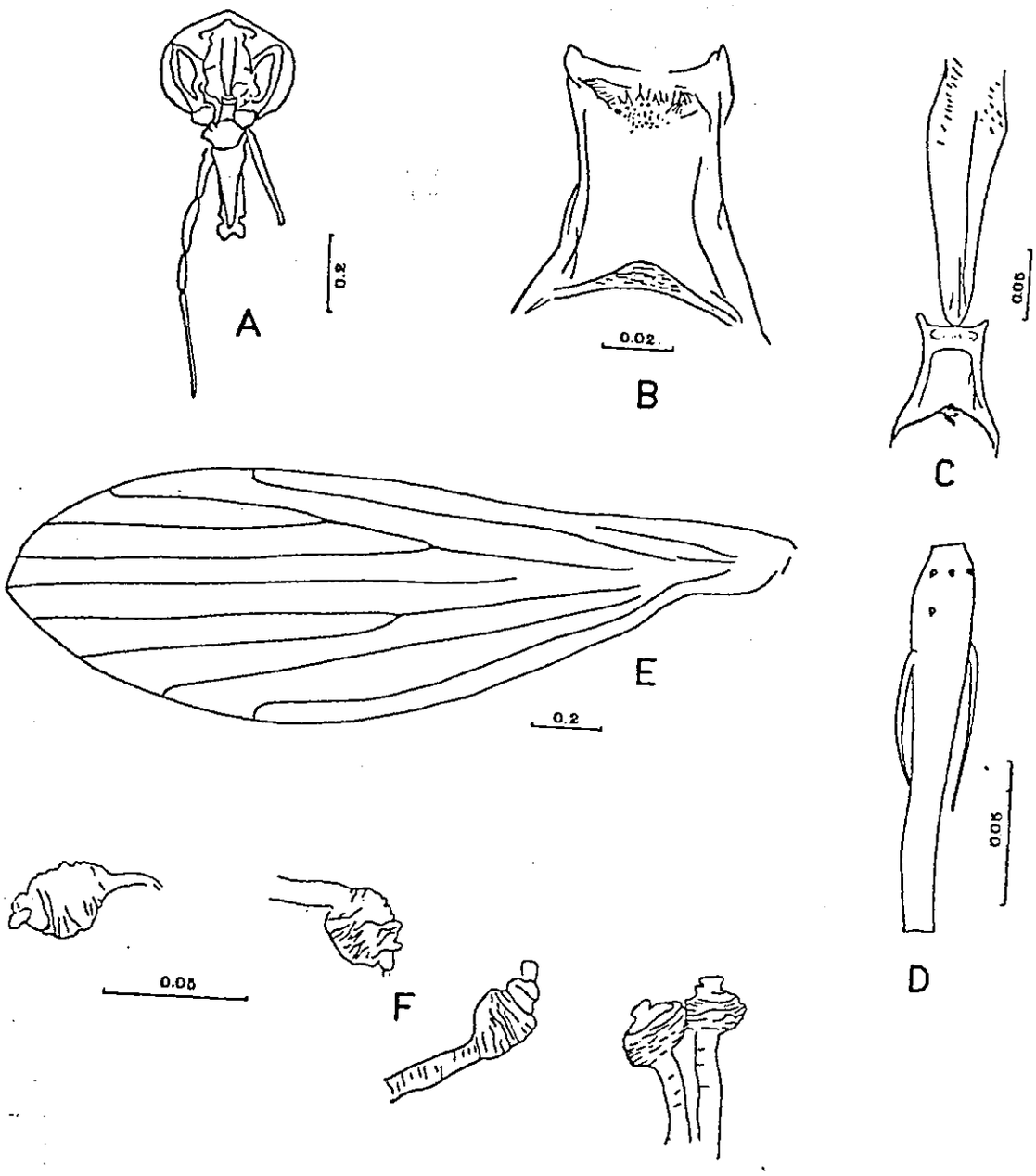


Fig. 6. Lutzomyia (verrucarum group) L.sp. of Loma Abajo. Female : A. Head; B. Cibarium; C. Pharynx and Cibarium. D. Flagellomere II; E. Wing; F. Spermathecae.

Venezuela, 4 April 1978 (both deposited at the British Museum, N.H.); Paratypes: 1 ♂ (no. 428, Vitisay, Mpio. Monsenor Jauregui, State Trujillo, 28/6/1972); 2 ♀♀, no. 1734-A, 1734-B, Vitisay, 4/4/1978; 1 ♀, no. 1740, Hato San Pablo, State Trujillo, 7/4/1978; all at University of Carabobo, Parasitologia, Maracay, Venezuela. Allotype and paratypes also collected by Mr. P. Manzanilla.

Discussion. When the two males on which the description is based were first examined, they were labelled as L. columbiana. The difference is, however, obvious when the characters of these two species are compared: L. columbiana shows only one definite group of hairs on the coxite, a paramere strongly clubbed and the basal spines of the style not implanted on tubercles. This new species shows two groups of hairs in the coxite, the paramere narrows centrally and gently widens to form an oval tip and the basal spines of the style are inserted on well-marked tubercles. The remaining species of the verrucarum group (series verrucarum), which bear a subapical group of long hairs on the coxite, are Lutzomyia moralesi Young, 1979; Lutzomyia verrucarum (Townsend, 1913) and Lutzomyia andina Osorno, Osorno & Morales, 1972. L. sp. of Loma Abajo is easily distinguishable from L. moralesi because the latter lacks the subterminal bristle, the setae of the basal tuft are thicker and the paramere shows a distal lobe on the ventral margin. L. verrucarum has a very peculiar paramere completely different from this species and the proximal spines of the style are not inserted on long and evident tubercles. L. andina, the most closely related species, shows a more clubbed paramere and a shorter basal spine enlarged and truncated at the end. The described female is considered to be the same species: the spermathecae are typical of the verrucarum group and the cibarium of the male shows numerous vestigial teeth which indicate the corres-

pondence with the cibarial armature of the female. In addition, two females were later found in the same place as the male paratype.

Prof. A. Vianna Martins has examined other males from the same collection no. 428 (Vitisay, 28/6/1972) and agrees that the flies belong to a new taxon (pers. commun.). The initial misidentification of this new species as L. columbiana at first suggested that this species should be removed from the list of Venezuelan sandflies. However, Prof. Martins (pers. commun.) states that Dr. Arredondo has recently reported the finding of L. columbiana in Venezuela, in the Yacambú National Park. It is therefore considered best to retain L. columbiana in the list until Arredondo's material can be examined.

Lutzomyia n. sp. of Chiricoca (Fig. 7).

Male (Holotype). Head: length 0.36 mm, width 0.34 mm. Length/width index = 1.06. Eyes separated by 0.13 mm. or by distance = ca 7.4 facet diameters. Antennae: Flagellomere I (= segment 3) 0.25 mm. long = length of II + III. Ascoids simple and long reaching the end of the respective segments. Palps: length of palpal segments in mm.: 1, 0.045; 2, 0.109; 3, 0.123; 4, 0.097; 5, 0.212. Palpal formula: 1, 4, 2, 3, 5. Labrum length, 0.20 mm; FI/L = 1.0. Pharynx length, 0.15 mm. Cibarial arch incomplete. Pleura with 14 upper episternal setae, lower setae lacking. Wing: length 1.97 mm, width 0.55 mm. Length of vein sections: alpha 0.47 mm, beta 0.28, gamma 0.19, delta 0.08; indices alpha/beta = 1.69; alpha/gamma = 2.45, alpha/delta = 6.18, beta/gamma = 1.45. Legs. Femora, tibia, basitarsi and tarsi 2 + 3 + 4 + 5. Foreleg: 0.76, 0.96, 0.52, 0.69. Midleg: 0.72, 0.99, 0.53, 0.62. Hingleg: 0.85, 1.17, 0.57, 0.65. Genitalia: Style (0.20 mm. long) with three major spines and two small setae: one subterminal and the other in the middle of the two other spines. Coxite bearing three tufts: one apical and one median formed

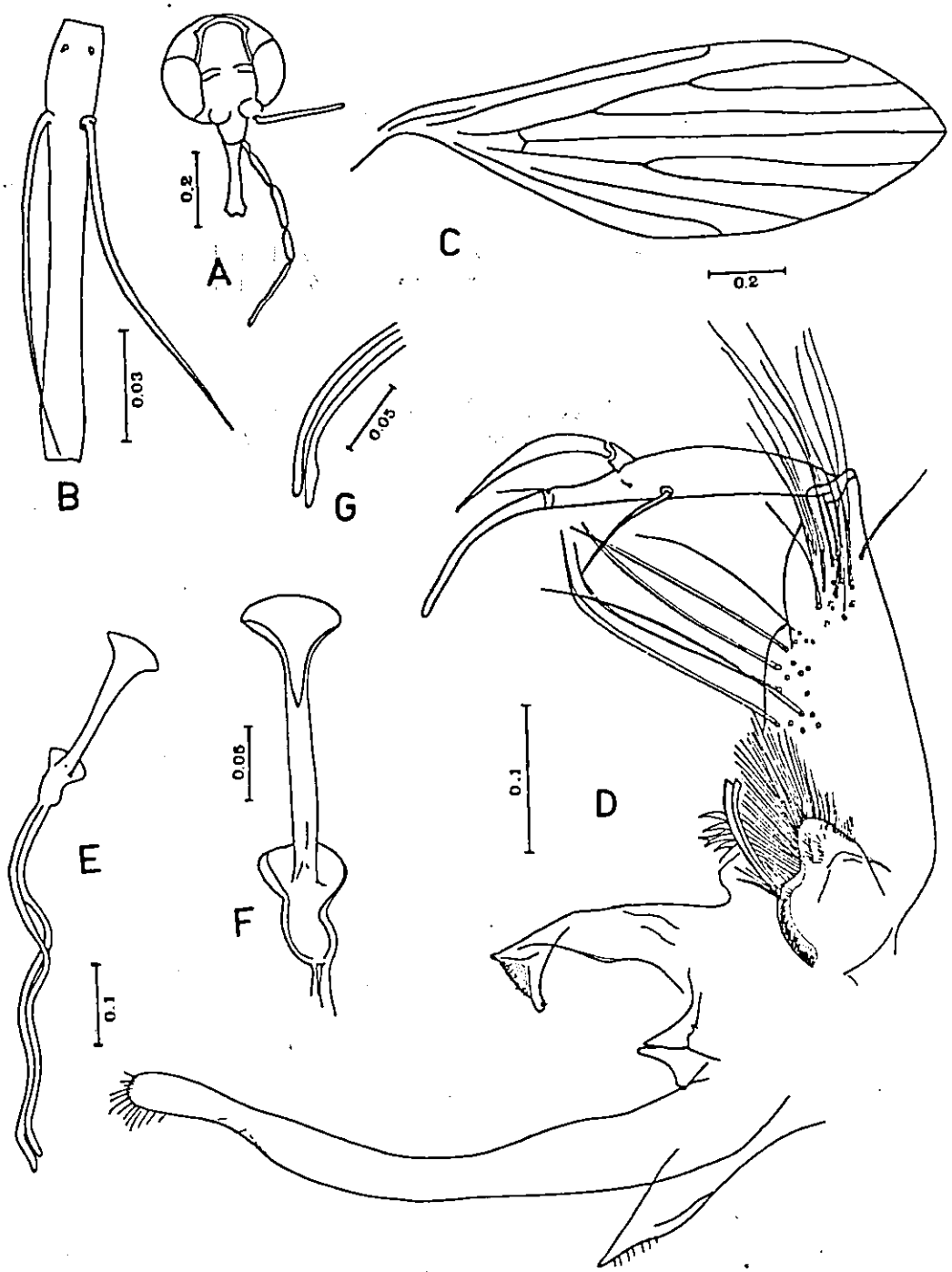


Fig. 7. Lutzomyia (Pressatia) L.sp. of Chiricoca.
Male : A. Head; B. Flagellomere II; C. Wing;
D. Genitalia; E. Pump and genital filaments;
F. Genital pump. G. Distal end of genital filaments.

of long hairs and the basal tuft, which consists of two parts. The basal tuft arises from a well-chitinized ridge, the inferior part formed by two lamellar setae with square ends, which cross 7-8 transparent and pointed setae (Fig. 41). The latter spines merge with the numerous thin and straight spines of the superior part, which lies on a rounded and wide protuberance. Paramere narrowed in the middle, widens at the end in two processes, the dorsal small, the ventral larger which enclose a rounded area covered by fine hairs. Aedeagus short (0.037 mm) and conical. Genital pump 0.19 mm. long and genital filaments 0.51 mm, 2.6 x length of pump, striated in the distal third, excepting the tips, which gently enlarge taking the shape of a human foot. Lateral lobe much longer than basistyle (0.46 mm).

Material examined. ♂ holotype, slide no. 3699. (British Museum, N.H.). Type locality: Chiricoca, M. pio San Camilo, Apure State, Venezuela 8. 7. 1981. Collector: Mr. Juan Pulido. This species was collected amongst roots of a tree with L. antunesi, L. gomezi and L. shannoni.

Discussion. The male of L. sp. of Chiricoca undoubtedly belongs to the subgenus Pressatia: it shows a dististyle with three spines and two small setae, a basistyle with a tuft consisting of two parts, a paramere with two characteristic processes, dorsal and ventral, and the lateral lobes curved and tapering.

The holotype has been compared with types of all the species of the same subgenus, except of L. calcarata Martins & Da Silva, 1964. The new species is completely different from L. dysponeta (Fairchild & Hertig, 1952), which shows only one simple tuft on the coxite, and from L. triacantha (Mangabeira, 1942) and L. equatorialis (Mangabeira, 1942); the superior tuft of both of which are small, with few short setae.

L. camposi (Rodriguez, 1952), L. choti (Floch & Abonnenc, 1941) and L. trispinosa (Mangabeira, 1942) have a very distinct, rather stocky paramere, while that of the male of Chiricoca is comparatively slender like the paramere of L. calcarata. This paramere of the latter species seems to be inverted in relation to that of the new species, and the superior process of the paramere is larger in L. calcarata than in L. sp. of Chiricoca. The apparent shape of the paramere, is however, largely due to the position of the specimen. The shape of the tuft of the coxite of L. calcarata, as depicted and described by Martins & Da Silva, seems to be completely different from the paramere of the new species. The Authors point out that it is formed of two tufts. The lower is implanted on a small tubercle and comprises 3-4 foliaceous setae, curved and pointed at the apex. The upper tuft is close to the anterior tuft and is formed by straight and fine setae implanted on a well-developed tubercle. There is no mention of the chitinized ridge from which the tuft arises, which is so evident in L. sp. of Chiricoca. The two parts of the tuft in this species merge indefinitely into each other, and the two modified lamellar setae with square ends are very distinctive.

Two other differences are notable: beta of the wing is larger than gamma in L. sp. of Chiricoca while they are about the same size in L. calcarata, and the 5th palpal segment is shorter in the new species than in all the other species of the subgenus.

Lutzomyia sp. of Monay (Fig. 8).

Male (Holotype). Head: length 0.32 mm. width not measurable because of the lateral position. Antennae: Flagellomere I (= segment III) 0.24 mm, nearly = length of II + III. Ascoids simple, no posterior spurs, their tips not reaching the end of their respective segments. Palps: length

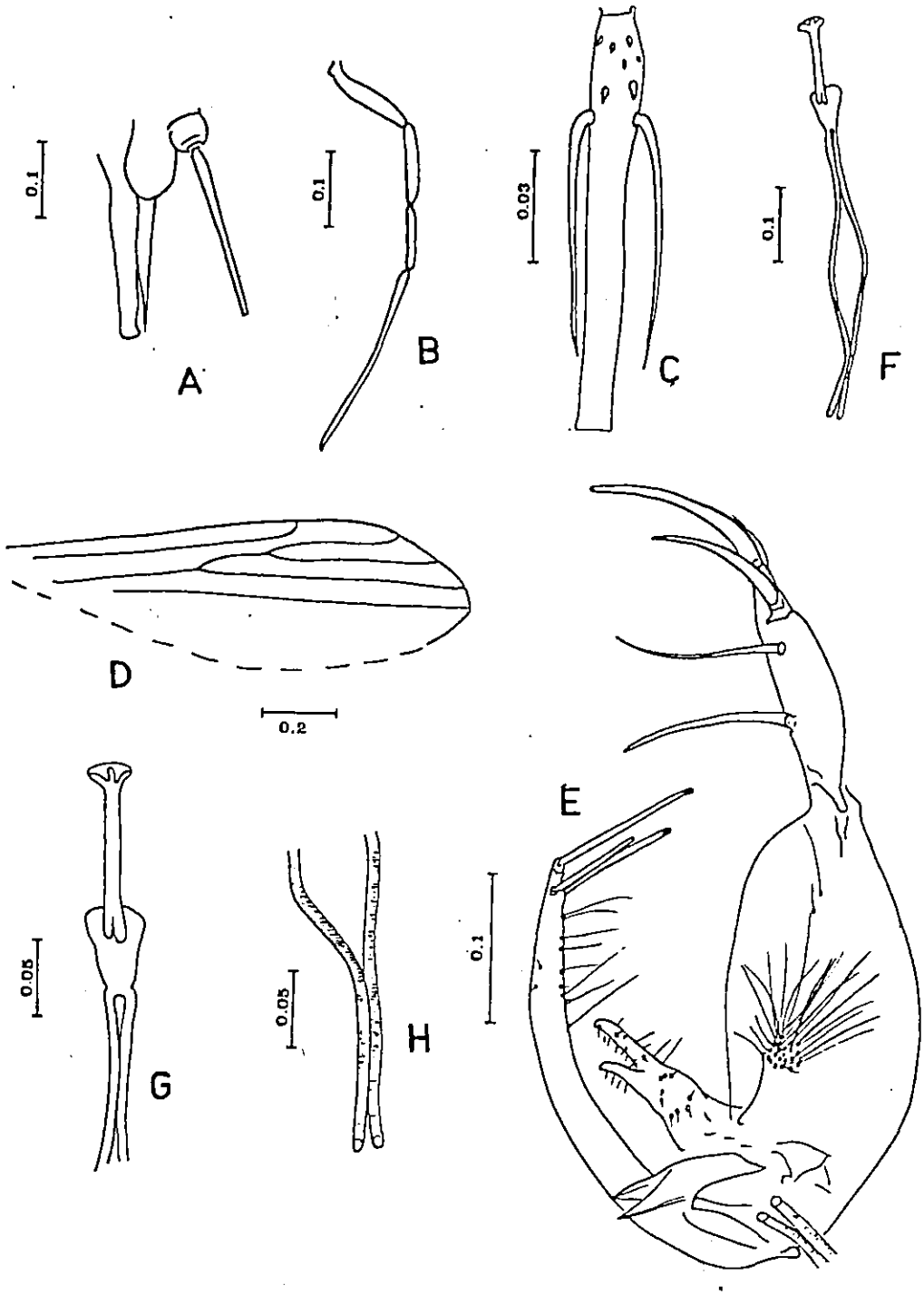


Fig. 8. Lutzomyia (Evandromyia) L.sp. of Monay.
Male : A. Flagellomere I and labrum; B. Palp;
C. Flagellomere II; D. Wing; E. Genitalia;
F. Pump and genital filaments; C. Genital pump;
H. Distal end of genital filaments.

of palpal segments in mm: 1, 0.045; 2, 0.092; 3, 0.118; 4, 0.092; 5, 0.262; palpal formula: 1, (2, 4), 3, 5. Labrum length, 0.18 mm; FI/L = 1.3. Pleura with 11 upper and 1 lower episternal setae. Wings partially folded, length 1.49 mm, width not measurable. Length of vein sections: alpha 0.27 mm, beta 0.196 mm, gamma 0.194 mm; delta 0.083; indices alpha/beta = 1.38, alpha/gamma = 1.39; alpha/delta = 3.27. Legs. Femora, tibia, basitarsi and tarsi 2 + 3 + 4 + 5 (mm). Foreleg: 0.66, 0.68, 0.40, 0.5. Midleg: 0.62, 0.78, 0.45, 0.53. Hindleg: 0.69, 0.96, 0.53, 0.59. Genitalia. Style (0.17 mm long) with 4 strong spines situated at different levels and 1 subterminal seta. Coxite with a tuft of about 24 setae emerging from lightly sclerotized sockets. Paramere bifurcate, with arms of different lengths. The undivided portion and the lower arm more heavily sclerotized. Few short hairs are scattered on both proximal portion and arms. Aedeagus elongate and triangular (0.12 mm. long), and genital filaments 0.39 mm, 3.14 x length of pump. The distal two-thirds of the genital filaments are clearly striated, apart from the tips which are smooth and cylindrical. Lateral lobe (0.32 mm. long) pointed at tip and bearing three distal modified setae, striated at the end.

Material examined. ♂ Holotype, slide no. 394. (British Museum, N.H.) Locality Type: Rio Monosnoy, near Monay, Trujillo State, Venezuela, February 1978, (Coll.) Prof. J.V. Scorza.

Associated species: Lu. atroclavata, Lu. micropyga, L. evansi, L. longipalpis, L. pilosa and L. walkeri. These flies were collected together in a tree hole, in which a bitch was living with a litter of puppies.

Discussion. The features of the male of Monay, viz. dististyle with four major spines and one subterminal seta, paramere bifurcate, lateral lobe curved upward, pointed at tip and with three long spatulate setae

at the end, are characteristic of the genus Lutzomyia, subgenus Evandromyia, series infraspinosa. Young & Arias (1977) have recently discussed the position of the species grouped in this subgenus and keyed the males. They placed seven species in the series infraspinosa. In two of these, L. bourrouli (Barreto & Coutinho, 1941) and L. pinottii (Damasceno & Arouck, 1956), the paramere is undivided but in the others it is bifurcate. In this last group, L. cerquerai (Causey & Damasceno, 1945) differs from the new species in not showing a definite tuft of setae on the coxite, and L. brachiphalla (Magabeira, 1941) has a basal tuft of 4-5 setae and only two spatulate setae on the lateral lobe. The remaining species are L. begonae (Ortiz & Torres, 1975), L. infraspinosa (Mangabeira, 1941) and L. inpai Young & Arias, 1977. L. begonae was described by Ortiz & Torres as having a trifurcate paramere, but Young & Arias (loc.cit.), after seeing Brazilian specimens, considered the most inferior arm of the paramere as an acute process on the ventral margin of the lower arm and included this species in the series infraspinosa. According to Young & Arias, the process permits differentiation of L. begonae from L. infraspinosa.

The paramere of the male of Monay is clearly bifurcate and therefore different from L. begonae. It also differs from L. infraspinosa, since the undivided portion of the paramere in the new species is about the same size as the divided distal part, i.e. of the longer arm of the paramere, while in L. infraspinosa this arm is longer than twice the undivided portion.

The most closely related species to Lutzomyia of Monay seems to be L. inpai, notwithstanding that they can be easily separated by two main differences. The undivided portion of the paramere of L. inpai is covered by numerous fine hairs, while this area in L. sp. of Monay presents

only a few scattered short and strong hairs. The genital filaments of L. inpai are very thick and swollen towards the distal ends, which are pointed; the genital filaments of the new species are cylindrical with truncate tips.

This species is described from one specimen which Prof. J.V. Scorza collected and kindly placed at my disposal. Following Prof. Scorza's suggestion, this species will be named after Mr. J. Mogollón (Ministerio de Sanidad y Asistencia Social, Dirección de Malariologia y Saneamiento Ambiental, Servicio de Endemias Rurales, Trujillo State), an invaluable field worker, who has collected thousands of sandflies in Trujillo State.

3.3.2 Synonymy of Lutzomyia marajoensis (Damasceno & Causey, 1944) with Lutzomyia walkeri (Newstead, 1914) and resurrection of Lutzomyia dubitans (Sherlock, 1962).

The recent discovery of L. walkeri (Newstead, 1914) in Venezuela (Apure State, present work) led me to re-examine the taxonomy of this sandfly.

L. walkeri was the first described species of the Group migonei of Theodor (1965). This group was divided by Young & Fairchild (1974) into three series: migonei, costalimai and walkeri. The walkeri series contains ten species, two of which, L. marajoensis (Damasceno & Causey, 1944) and L. gasti (Sherlock, 1962), are closely related to L. walkeri.

In a recent revision of the Psychodid Flies of Colombia, Young (1979) pointed out that L. walkeri and L. marajoensis are easily distinguishable, but treated L. gasti as a junior synonym of L. walkeri. In a remounted male of the type series of L. walkeri, he observed the presence of the complex aedeagus, with a posterior cylindrical projection which is emphasized by Sherlock in his description of L. gasti. This character has also been described by Llanos (1973) for Peruvian specimens of L. walkeri.

A study of the original description of L. gasti and a comparison with the lectotype and paralectotypes of L. walkeri at the British Museum (N.H.), supports the synonymy suggested by Young (1979). However, it was noticed that the peculiar structure of the aedeagus is not always evident, apparently depending on the mounting medium and the position of the specimen. Hence, Lewis (1967b) made no mention of this character in the redescription of the species and Young (loc. cit.) had to remount specimens in order to see it.

I could clearly observe this structure in only 36% of my specimens. The flies in which it was not visible had to be distinguished from L. marajoensis, which has also been recorded in Venezuela (Pifano et al., 1962, Ramirez Perez et al., 1978). Several specimens identified as L. marajoensis are in the collection of the University of Carabobo and were available for comparison.

A study of these flies, the results of which will be given in detail below, led to the conclusion that there are certainly two species. One of them is L. walkeri (Newstead, 1914), but the other species is different from L. walkeri and from the original description and pictures of L. marajoensis given by Damasceno & Causey (1944).

The L. marajoensis holotype, loaned by the National Museum, Washington, D.C., proved to be identical to the lectotype and paralectotypes of L. walkeri at the British Museum (N.H.). By chance, both specimens mounted on the holotype slide clearly show the posterior projection of the aedeagus. Therefore L. marajoensis (Damasceno & Causey, 1944) becomes a synonym of L. walkeri (Newstead, 1914), as Forattini suggested (1973).

Although the majority of Authors have recognized two distinct species, it is evident that the name L. marajoensis was incorrectly applied to a distinct taxon.

Fairchild & Hertig (1961) discussed the differences between specimens of L. marajoensis from Venezuela, Colombia, Trinidad and Panama and the holotype. In considering the variability among individuals of the same area, they advanced the possibility that L. marajoensis might represent only geographical variants of L. walkeri. However, they refrained from synonymyzing them and retained two separate

species. Their drawings of L. marajoensis are different from those of Damasceno & Causey, in that the two basal spines of the dististyle are situated at about the middle of the segment and at the same level.

The same features are seen in the redescription of L. marajoensis from Venezuela by Pifano et al. (1962a)who said: "basistyle with two spines implanted at different levels, the basal ones anterior to the middle of the segment..."

Sherlock (1962), in examining specimens from Colombia from the same collection seen by Fairchild & Hertig (1961), decided to create a new species which he named Lutzomyia dubitans. His description fits Fairchild & Hertig's (1961) drawings of L. marajoensis. In comparing L. dubitans with the description and the pictures of Damasceno & Causey, Sherlock noted the following difference: "the distribution of the spines of the dististyle, which in the new species are not 3 distal, but two distal and two in the middle of the segment". Later, several authorities on sandflies (Vianna Martins, 1978; Young, 1979) considered L. dubitans to be a synonym of L. marajoensis (Damasceno & Causey, 1944).

This now appears to be incorrect; L. marajoensis, with the exception of the specimens described by Damasceno & Causey (1944), seems actually to be L. dubitans. I think, therefore, that the name L. dubitans (Sherlock 1962) should be resurrected. This is the earliest name available for this taxon, which is distinct from L. walkeri (Newstead, 1914). In support of this proposal, I have tried to determine and quantify characters which distinguish L. walkeri from L. dubitans. The results of these observations are given below.

The aim of the comparison was to show whether or not the arrangement of the spines, the ratio FI/L and width of individual ducts/common duct

are species-specific, in spite of geographical variability.

Material and Methods

The characters studied and statistically analyzed were:

(i) the relative position of the basal spines of the dististyle (males);

(ii) the width of the individual sperm ducts relative to the width of the common duct, (females);

(iii) the ratio of Flagellomere I (= antennal segment 3)/length labrum-epipharynx length = FI/L (both sexes).

Males - Two groups of males L. walkeri (Fig. 9), groups 1 and 2 and one group of males L. dubitans (Fig. 9), group 3, were compared.

Group 1 was 14 ♂♂ from Apure State, collected in tree holes during April 1981. Group 2 was 13 ♂♂ collected from different localities of Venezuela at different dates, kept at the University of Carabobo, misidentified as "L. marajoensis". Group 3 was 6 ♂♂ from different places in Venezuela, kept at the U.C., plus 3 ♂♂ deposited at the British Museum (N.H.), both also misidentified as "L. marajoensis".

For each specimen the following measurements were taken (Fig. 9)

B - 4 = the distance between the basal and the apical limit of the style, thus, the total length of the segment;

B - 1 = the distance between the basal limit of the style and the middle of the socket of the basal or more proximal spine (spine 1);

B - 2 = the distance between the basal limit of the style and the middle of the socket of the spine 2;

1 - 2 = the distance between the middle of the socket of the spine 1 and the middle of the socket of the spine 2;

2 - 4 = the distance between the middle of the socket of the spine 2 and the spine 4.

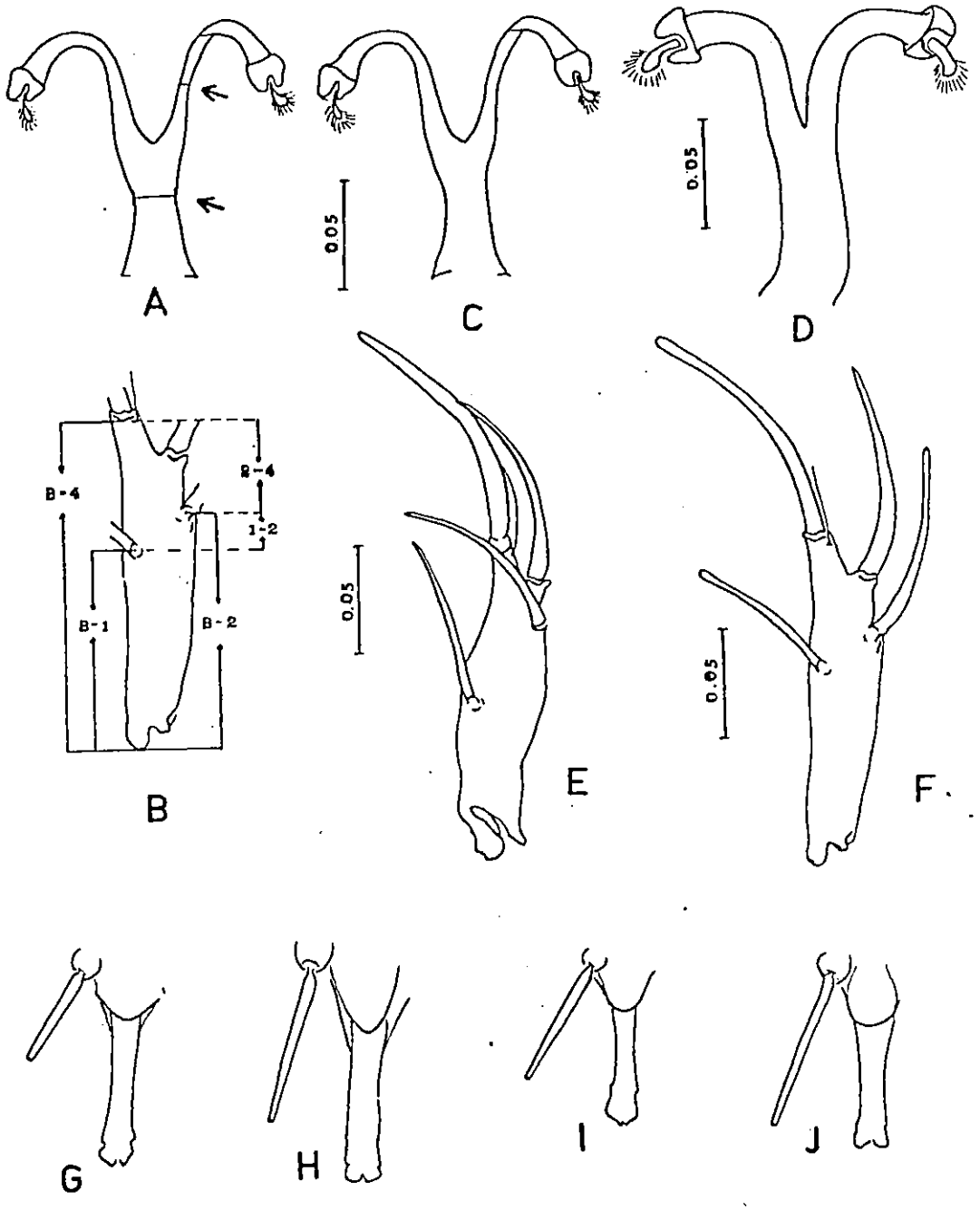


Fig. 9. Lutzomyia (migonei group)
A. and B. measurement points used for spermathecae ducts and styles; C. Spermathecae of L. walkeri; D. Spermathecae of L. dubitans; E. Style of L. walkeri; F. Style of L. dubitans; G. to J. Labra and Flagellomeres I: G. L. walkeri ♂; H. L. walkeri ♀; I. L. dubitans ♂; J. L. dubitans ♀.

Females - Two groups of females, 6 of L. dubitans from different areas of Venezuela and 10 of L. walkeri (Apure State) were compared.

The measurements taken were; (i) the width of the narrowest point of the individual ducts and (ii) the width of the narrowest point of the common duct (Fig. 9).

For both sexes the length of the FI was related to the length of the labrum-epipharynx taken from the apex of the clypeus to the tip of the proboscis. For these measurements, 6 specimens from the L. walkeri group were chosen at random to get the same sample size as for L. dubitans.

All the means were compared using Student's t test. Other qualitative characters, the shape of paramere, the aspect of the tuft of basistyle, etc. have been re-examined and are discussed below.

Results

Males

1. Styles: In Tables 3 to 5 and Figs. 10 to 13 the results of style measurements are given. They establish the position of the spines on the dististyle, in relation to the length of the segment. In Tables 6 and 7 the results of the statistical analysis are shown. There was no difference in the total length of the dististyle of the two species. Both groups of L. walkeri show the following characters:

(i) spine 1 is always in the middle of the segment (B-1/B-4 = 0.51);

(ii) spine 2 is always on the distal anterior quarter of the segment (B-1/B-4 = 0.77 to 0.79). No statistical differences were found between the two samples.

(iii) The separation of spines 1 and 2 and of 2 and 4 in relation to the total length of the style (B4) are more variable: (1-2/B-4 =

Table 3. Style measurements for L. walkeri from Apure

Specimen No.	Position of spines on the style (μm)				
	B-4	B-1	B-2	1-2	2-4
2967-1-1	150	80	118.75	38.75	31.25
2967-1-2	147.5	77.5	117.75	40	30
2967-1-3	147.5	70	112.5	42.5	35
2967-4-4	143.75	71.25	113.75	42.5	30
2967-5-5	156.25	83.75	121.25	40	32.5
2967-5-60	151.25	73.75	125	51.25	26.25
2967-5-61	146-25	75	117.5	42.5	28.75
2967-5-7	143.75	73.75	118.75	45	25
2964-9-9	152.5	77.5	121.25	43.75	31
2995-10	156.25	80	122.5	42.5	33.75
2955-26	146.25	73.75	116.25	42.5	30
2967-6-1	140	71.25	108.75	36.25	32.5
2967-6-2	140	70	105	35	35
2967-6-3	145	77.5	120	42.5	25

Table 4 Style measurements for L. walkeri (overall).

Specimen No.	Position of spines on the style (µm)				
	B-4	B-1	B-2	1-2	2-4
111	152.5	75	116.25	41.25	36.25
1417	150	77.5	111.25	35	37.5
1654	147.5	73.5	108.75	33.5	40.5
541	151.25	81.25	117.5	36.25	33.75
1656	150	80	111.25	36.25	33.75
1655	145	72.5	112.5	40	32.5
543-1	153.75	78.75	120	41.25	33.75
543-2	151.25	75	116.25	41.25	35
1655-1	158.75	80	125	45	33.75
1654-1	157.5	77.5	120	42.5	37.5
1870	148.75	75	111.25	36.25	37.5
1990	132.5	67.5	107.5	40	25
25	157.5	83.75	120	36.25	37.5

Table 5 Style measurements for L. dubitans (overall)

Specimen No.	Position of spines on style (µm)				
	B-4	B-1	B-2	1-2	2-4
57-1	148.75	88.75	108.6	20.0	40
57-2	145	77.5	101.25	23.75	43.75
90-3	161.25	87.5	112.5	25	48.75
107	155	88.75	107.5	18.75	47.5
1979	153.75	90	110	21.25	42.5
128	140	75	97.5	22.5	42.5
BM-1961	145	87.6	107.5	16.25	41.25
BM-1622	152.5	86.25	113.75	25	40
BM-4736	142.5	80	96.25	16.25	45

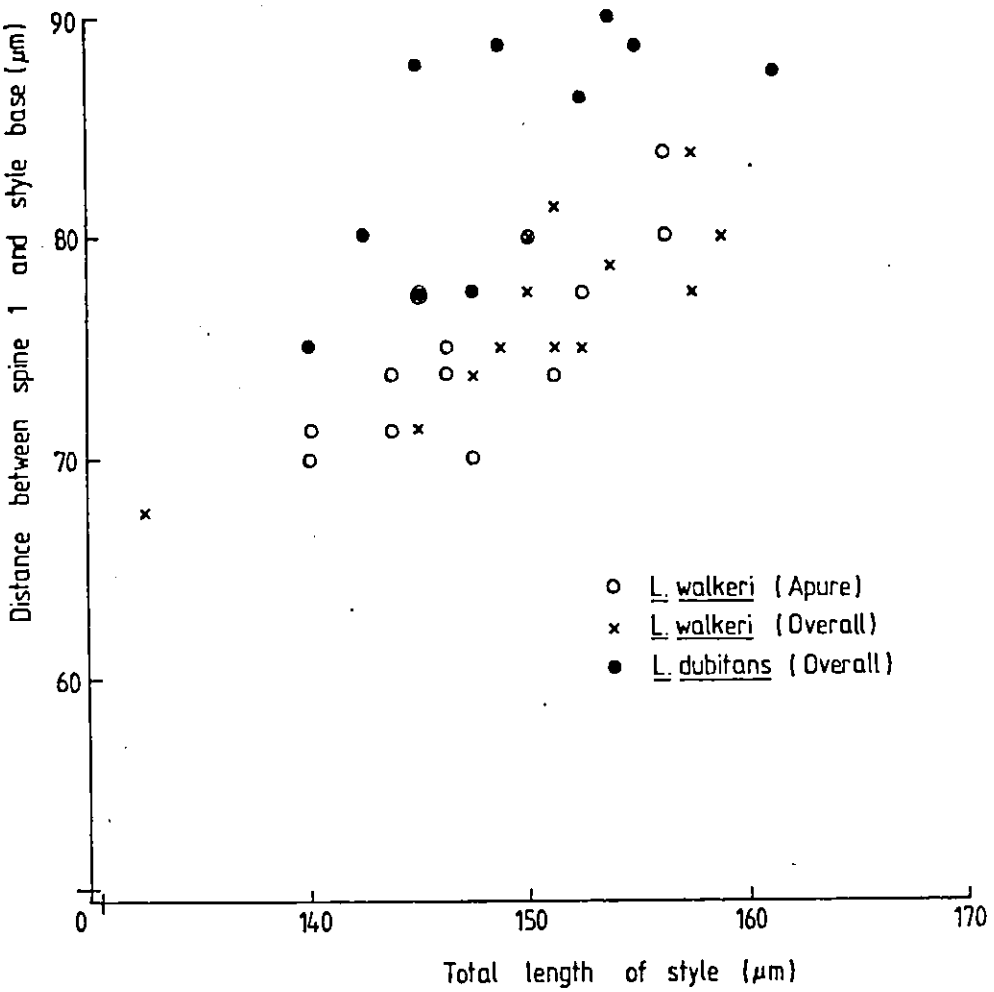


Fig. 10. Distance between spine 1 and style base plotted against the total length of style.

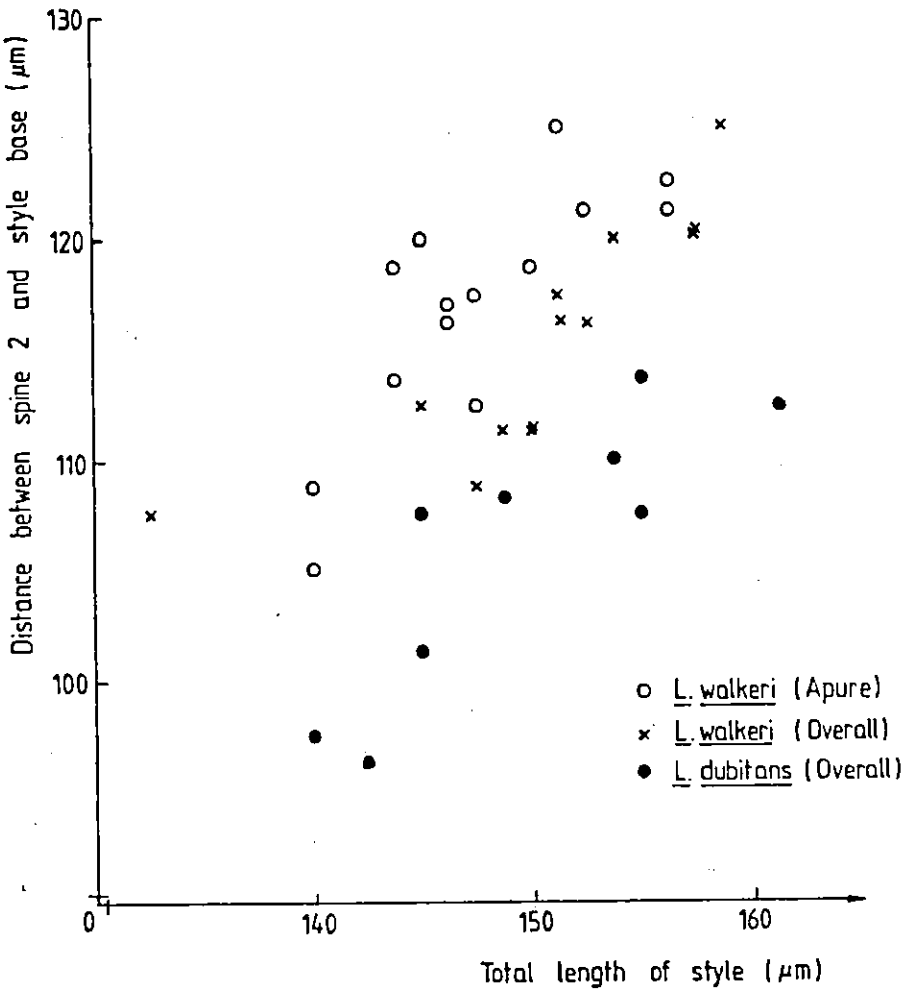


Fig. 11. Distance between spine 2 and style base plotted against the total length of style.

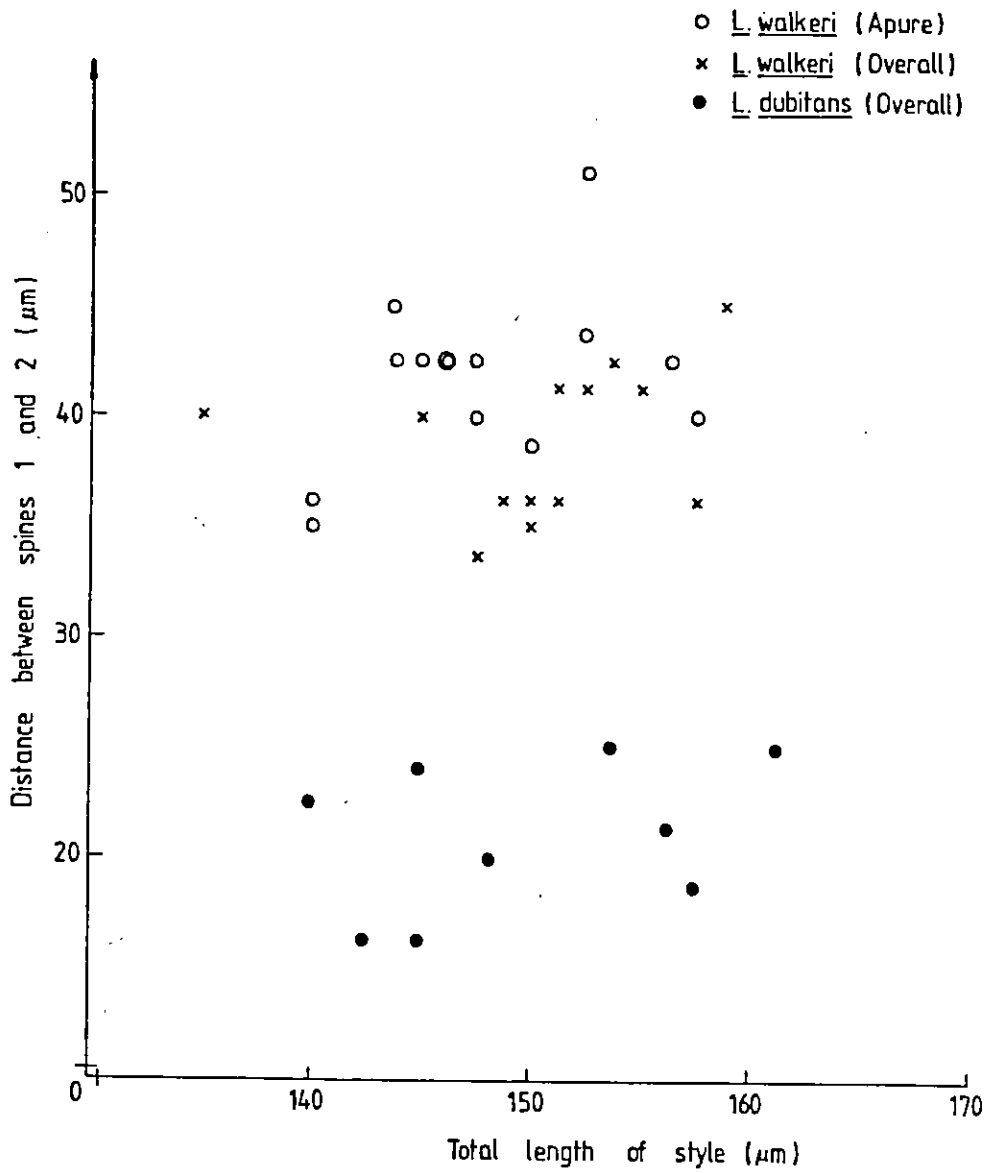


Fig. 12. Distance between spines 1 and 2 plotted against the total length of style.

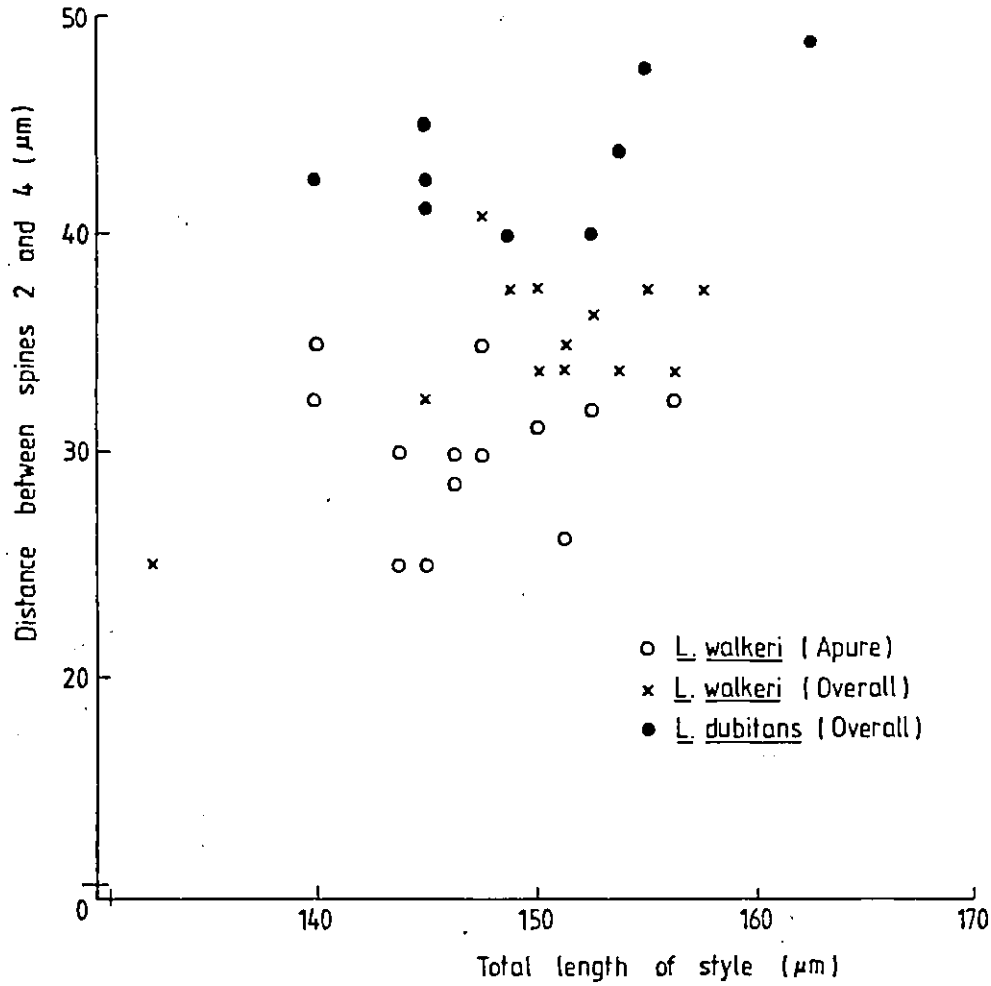


Fig. 13. Distance between spines 2 and 4 plotted against the total length of style.

Table 6. Style measurements ($\bar{X}$ and σ) of L. walkeri and L. dubitans

Species and origin	B - 4		B - 1		B - 2		1 - 2		2 - 4	
	$\bar{X}$	σ	$\bar{X}$	σ	$\bar{X}$	σ	$\bar{X}$	σ	$\bar{X}$	σ
L. walkeri (Apure)	147.59	5.18	75.35	4.17	117.07	5.47	41.78	3.91	30.42	3.3
L. walkeri (Overall)	150.48	6.76	76.73	4.26	115.19	5.22	38.82	3.43	34.94	3.75
L. walkeri (Pooled)	148.98	6.05	76.00	4.19	116.16	5.34	40.36	3.92	32.6	4.15
L. dubitans	149.30	6.84	84.59	5.56	106.09	6.32	20.97	3.41	43.47	3.11

Table 7. "t" test comparison of style measurements of L. walkeri and L. dubitans

Species and origin	B - 4	B - 1	B - 2	1 - 2	2 - 4
L. walkeri[1] Apure Versus L. walkeri overall	1.25	0.83	0.91	2.08*	3.32**
L. walkeri[2] Pool Versus L. dubitans	0.13	4.91**	4.69**	13.23**	7.18**

1. DF = 25, 2. DF = 34

* $0.05<P<0.01$

** $0.01<P<0.001$

0.26 to 0.28 and 2-4/B-4 = 0.21-0.23). The sample of individuals from one area (Apure State) was more uniform and typical of L. walkeri: the two basal spines were far apart and the distance between the three apical spines was short.

The position of the spines in L. dubitans showed the following patterns:

(i) spine 1 is found towards the apex of the style (B1/B4 = 0.59),

(ii) spine 2 is always on the median anterior quarter of the segment (B-2/B-4 = 0.71);

(iii) spines 1 and 2 are closer than those in L. walkeri (1-2/B-4 = 0.14);

(iv) spines 2 and 4 are wider apart (2-4/B-4 = 0.29).

When all measurements of L. walkeri were pooled and compared with those of L. dubitans, the differences were highly significant. All the graphs (Figs. 10 - 13) show two groupings, one of which is formed by the pooled L. walkeri measurements and the other by the measurements of L. dubitans.

2. FI/L - Measurements and comparison of Flagellomere 1 and labrum lengths confirm previous observations on the three groups of sandflies (Tables 8, 9). No statistical difference was found between the two samples of L. walkeri, while highly significant differences were noticed in the length of the Flagellomere I and the corresponding ratio FI/L between L. walkeri and L. dubitans. In L. walkeri FI length is about the same as L length ($\bar{X}$ = 0.99 ± 0.06); in L. dubitans FI is about one and a half times as long ($\bar{X}$ = 1.45 ± 0.13).

Females

1. Sperm ducts: The comparison between (i) minimum width of individual sperm ducts; (ii) minimum width of common sperm duct and; (iii) the

Table 8. Comparison of Flagellomere I (FI) and Labrum (L) length in males of *L. walkeri* and *L. dubitans*.

Specimen No.	Length of Flagellomere I (FI) and Labrum (L) in µm.					
	L. walkeri (Apure State)		*L. walkeri* (Overall)		*L. dubitans* (Overall)	
	FI	L	FI	L	FI	L
1	198.24	207.68	212.4	224.2	306.8	188.8
2	217.12	224.20	174.64	177	295.0	217.12
3	212.4	214.76	219.48	200.6	273.76	184.08
4	212.4	195.88	226.56	221.84	318.6	188.8
5	174.64	202.96	212.4	214.76	271.4	205.32
6	198.24	200.6	221.84	212.4	278.48	207.68
$\bar{X}$	202.28	207.68	211.22	208.41	290.67	198.63
σ	15.66	10.34	18.74	17.51	19.31	13.21

Table 9. "t" test comparison of FI, L and the FI/L ratio in males of *L. walkeri* and *L. dubitans*.

Species and origin	FI	L	FI/L
*L. walkeri** Apure V.	0.91	0.09	1.10
L. walkeri overall			
*L. walkeri*** pool V.	9.42**	1.39	10.35**
L. dubitans			

DF = 10
DF = 16
** P<0.001

ratio individual ducts/common duct are given in Tables 10 and 11. They show highly significant differences between L. walkeri and L. dubitans. The width of individual ducts in L. walkeri is less than $^{1}/3$ (= 0.28) of the common duct; the width of individual ducts in L. dubitans is about ½ (= 0.48) of the common duct.

Measurements and comparison of Flagellomere I and labrum lengths in females also show considerable differences between L. walkeri and L. dubitans (Tables 12, 13), the ratio FI/L is smaller in L. walkeri (= 0.73) than in L. dubitans (= 0.96).

A synopsis of the main reliable characters useful for the identification of these two species is shown in Table 14.

Discussion

In previous papers on L. walkeri (Newstead, 1914) and L. dubitans (Sherlock, 1962), discussed in the introduction to this section, the difficulty in separating these two closely related species is clearly shown. The problem apparently arose when differences in the characters used were considered as evidence of geographical variation.

When qualitative observation is insufficient or difficult, quantification of some of these characters is helpful in distinguishing the two species. In the male, the presence of the posterior process of the aedeagus remains to support the special status of L. walkeri as considered by Young (1979). In flies lacking this structure, it is advisable to check the position of the basal spines in relation to the base of the dististyle. These measurements have proven to be constant and reliable. The variability noticed by Fairchild & Hertig (1961) mainly concerned the relative distance between spines. However, the statistical comparison of the distances spine 1 and style base, spine 2

Table 10. Sperm duct measurements for *L. walkeri* and *L. dubitans*

Specimen No.	*L. walkeri*		*L. dubitans*	
	Narrowest point common duct (µm)	Narrowest point individual ducts (µm)	Narrowest point common duct (µm)	Narrowest point individual duct (µm)
1	20	5 5	25	12.5 -
2	17.5	5 5	27.5	12.5 12.5
3	17.5	5 5	30	15 12.5
4	20	5.25 -	25	12.5 12.5
5	15	4.5 5	25	12.5 -
6	17.5	5 5	27.5	12.5 12.5
7	17.5	5 4.5		
8	18.8	5 5		
9	17.5	5 5		
10	17.5	5 5		

Table 11. "t" test comparison of sperm duct measurements for *L. walkeri* and *L. dubitans*.

Species	Narrowest point common duct (µm)			Narrowest point individual ducts			Ratio $ID/_{CD}$		
	$\bar{X}$	σ	t	$\bar{X}$	σ	t	$\bar{X}$	σ	t
L. walkeri	17.88	1.45		4.96	0.17		0.28	0.02	
			10.09*			41.75**			18.13*
L. dubitans	26.7	2.04		12.75	1.45		0.48	0.02	

* $P<0.001$, DF = 14

** $P<0.001$, DF = 27

Table 12. Comparison of Flagellomere I (FI), Labrum (L) length and ratio FI/L in females of L. walkeri and L. dubitans

Specimen No.	Length of Flagellomere I (FI) and Labrum (L) in µm					
	L. walkeri			L. dubitans		
	FI	L	FI/L	FI	L	FI/L
1	207.68	287.92	0.7213	271.4	292.64	0.9274
2	177.00	271.40	0.6522	261.96	271.4	0.9652
3	198.24	252.52	0.7850	280.84	290.28	0.9675
4	177.00	224.2	0.7902	261.96	273.76	0.9569
5	181.72	261.96	0.6922	247.80	252.52	0.9813
$\bar{X}$	188.32	259.6	0.7282	264.79	276.12	0.9597
σ	13.9	23.71	0.06	12.3	16.26	0.02

Table 13. "t" test comparison of FI, L and FI/L ratio in females of L. walkeri and L. dubitans

Species	FI	L	FI/L
L. walkeri			
	9.21*	1.28	8.24*
L. dubitans			

* $P<0.001$, DF = 8

Table 14. Differences between L. walkeri (Newstead, 1914) and L. dubitans (Sherlock, 1962).

L. walkeri	L. dubitans
Males	
♂♂	
1 - Aedeagus complex with a dorsal cylindrical or fan-shaped projection	2 - Aedeagus simple without projection
2 - Basal spine on dististyle on middle or the basal half of the segment; 2nd spine on the distal anterior quarter of the style.	2 - Basal spine on dististyle always on the distal half of the segment and close to the 2nd spine on the medial anterior quarter of the segment.
3 - F I (= Antennal segment no. 3) about the same length of L (labrum)	3 - F I about 1½ times the length of L
4 - Tuft of the basistyle inconspicuous, always formed by less than 20 setae	4 - Tuft of the basistyle very conspicuous, always formed by more than 20 setae
♀♀	
1 - Wide and stumpy spermathecae, individual ducts and common duct	1 - Elongate and delicate sperm athecae, individual ducts and common duct.
2 - Individual sperm ducts about 1/3 as wide as common duct.	2 - Individual sperm ducts about ½ as wide as common duct
3 - F I about ¾ times the length of L.	3 - F I about the same length as L.

and style base and spine 1 and 2, revealed striking differences between L. walkeri and L. dubitans. Spine 1 and 2 are more separate in L. walkeri than in L. dubitans. Therefore in the former species the basal spine appears close to the style base, while the other three spines lie grouped at the end of the style. In L. dubitans spines 1 and 2 are close together and 3 and 4 lie next to each other at the distal end (Fig. 9.). The ratio Flagellomere I: labrum is proposed as another new character. It is easily visible and significantly different in the two species, for both sexes.

The aspect of the basal tuft of the coxite is another useful feature. The greater number of setae in L. dubitans noticed by Sherlock (1962) and by Fairchild (see Lewis, 1967; referred to "L. marajoensis") is difficult to measure. However, after observing several specimens it does appear to be a conspicuous difference. The shape of the paramere was shown by Young (1979) to be another possibly distinguishing character. It appears to be slightly bent ventrally in L. dubitans while it is straight in L. walkeri. This character may be helpful with some specimens, but it may be affected by mounting.

The shape of the spermathecae and sperm ducts is an important, reliable and easy character to separate the female of L. walkeri and L. dubitans. When they are not completely visible, quantitative characters such as the ratios individual sperm ducts/common duct and FI/L are useful.

In conclusion, it is necessary to use as many characters as possible in order correctly to identify these two species. Correct identification is important because the distribution of these two species overlaps, as is already demonstrated in Colombia and Trinidad (Young, 1979) and is now reported for Venezuela (See 3.3.7).

3.3.3. Anomalies of Venezuelan Sandflies

In 1971 Abonnenc et al. reviewed the morphological abnormalities of sandflies. They pointed out that the more common anomalies were of the genitalia of the males, particularly the presence of supernumerary spines on one side of the style.

They listed 34 sandfly specimens with supernumerary spines, nineteen of which belonged to 10 species of the Old World (Sergentomyia minuta (Rondani, 1843); Phlebotomus papatasi (Scopoli, 1786); P. major Annandale, 1910; P. perniciosus Newstead, 1911; S. africanus (Newstead, 1912); P. mascittii Grassi, 1908; P. orientalis Parrot, 1936; S. clydei (Sinton, 1928); P. ariasi Tonnoir, 1921; and S. ingrami (Newstead, 1914) and the remaining fifteen to 10 species of the New World (Lutzomyia fischeri (Pinto, 1926); L. mangabeirana (Barreto & Coutinho, 1941); L. ayrozai (Barreto & Coutinho 1910); L. travassoi (Mangabeira, 1942); L. aragaoi (Costa Lima, 1932); L. baduelensis (Floch & Abonnenc, 1941); L. rorotaensis (Floch & Abonnenc, 1944); L. pacae (Floch & Abonnenc, 1943); L. whitmani (Lutz & Neiva, 1912); L. longipalpis (Lutz & Neiva, 1912)).

A reduction in the number of style spines, by atrophy or fusion, seemed to be much rarer, since the authors reported only 4 individuals of four species with this abnormality viz: one P. major which had two spines fused, giving 4 spines in the abnormal style and 5 in the normal one; one S. minuta which had only three instead of four spines in both styles; one L. pacae with a unilateral reduction to three spines, not four, and one S. simillimus (Newstead, 1914) with only one apical spine on one style and the normal number of 4 on the other.

Of particular interest are the anomalies in the cibarium of the females. A reduction of the number of the cibarial teeth was observed

by Parrot & Habibi (1946) in S. minuta parroti (Adler & Theodor, 1927) and in S. clydei by Qutubuddin (1961), and the absence of the pigment patch in S. ingrami was noticed by Kirk & Lewis (1951).

A peculiar anomaly not referred by Abonnenc et al (1971) was observed in Venezuelan sandflies. Ortiz (1963) found one male, classified by him as belonging to the "group cayennensis-micropygus", which showed one mid-leg with deformation and fusion of the 5th tarsal segment and one hind leg also deformed, reduced in size, and lacking the s. One striking fact in Abonnenc's paper is the omission of the already known cases of gynandromorphism in P. ariasi (Rioux et al., 1965) and in L. longipalpis (Sherlock, 1958), which may be considered as a teratological malformation.

Only a few other records of abnormalities have been reported in the Old World since Abbonenc's review. Dancensco & Chadli (1979) again observed one supernumerary spine on one style of P. papatasi, while Kaul & Wattal (1979) described the reduction of the number of spines of the dististyle in P. papatasi and S. babu babu. Four more cases of gynandromorphism have been described, one of S. minuta (Rioux et al. 1974), two of P. orientalis (Ashford, 1974), and another of S. minuta (Addadi & Dedet, 1977).

In the New World, Almeida (1970) noticed anomalies in L. umbratilis Ward & Fraiha, 1977, misidentified by him as L. anduzei (Rozeboom, 1942) (Ward & Fraiha, 1977). One male of this species had three spines and another five spines instead of the normal four on the dististyle. Almeida (loc.cit.) also reported a similar anomaly in L. rorotaensis (Floch & Abonnenc, 1944) with six spines instead of the normal five on one style. Later (1971), Chaniotis described two examples of gynandromorphism in two females of L. trinidadensis (Newstead, 1922) and Llanos et al. (1975)

found a female of L. serrana (Damasceno & Arouck, 1949), the spermathecae of which differred considerably from the typical, being completely smooth, possibly as a consequence of the distention produced by an enormous number of spermatozoa. Williams & Carvalho (1979) published a drawing of a female of L. dispar which lacked the hind teeth and showed the fore teeth clustered around the middle line while Young (1979), in over 103 females of L. pia (Fairchild & Hertig, 1961), noticed 3 specimens with 5 teeth instead of the normal four.

In this note the anomalies observed in morphological studies of sandflies of Venezuela are described:

1. One teratological unidentified male (Figs 14, 15) (El Pilón de Valle Hondo, Cojedes State, 1.12.1981);
2. Four males of L. trinidadensis (Newstead, 1922) with one supernumerary spine on the dististyle (Figs 16 to 19) (San Esteban, Carabobo State, 25.7.1979; 16.2.1981 and 6.7.1981. Solano, Cojedes State, 13.10.1981);
3. One male of L. dubitans (Sherlock, 1962) with reduction of the number of spines (Fig. 20) (Las Rosas, Cojedes State, 22.5.1979);
4. Two females of L. trinidadensis with five teeth instead of the normal four in the cibarium (Fig. 21) (San Esteban, Carabobo State, 1.3.1979 and 9.7.1979);
5. One female of L. shannoni (Dyar, 1929) also with five teeth instead of four (Fig. 22) (El Pilón de Valle Hondo, 7.10.1981);
6. Three females of L. lichyi (Floch & Abonnenc, 1950) with the same anomaly (Figs 23 to 25) (El Pilón de Valle Hondo, 21.11.1981, 3.12.1981; Solano, 13.6.1981);
7. One female of L. gomezi (Nitzulescu, 1931) with five teeth and another L. gomezi with only three teeth in the cibarium (Figs 26,27)

(Sarare Abajo, Apure State, 24.7.1981; Chiricoca, Apure State, 20.7.1981).

The abnormal male, shown in Figs. 14, 15 has only one coxite with a small tuft borne on an elongate and hyaline tubercle. The single style has eight spines of different sizes. The single stout paramere shows a definite depression at the end. The lateral lobes and cerci are paired as usual. There is no trace of any pump or genital filaments. The F III (= antennal segment 5) of one antenna and the F IV (= antennal segment 6) of the other are abnormally swollen. There was no trace of teeth in the cibarium nor of other features typical of females which could support the idea of an intersex. It was impossible to ascribe this fly to a known species by the characters shown.

The identification of the anomalous males of L. trinidadensis was based on the size and the position of the five spines of the dististyle, the medial scattered hairs on the coxite and the sharpened parameres. All of them showed one extra spine on one style. As shown in the pictures, (Fig. 16 to 19), the additional spine usually lies at about the same level as the basal spines. In one specimen (Fig . 17) the sub-apical spine appeared thicker than usual.

The first anomalous specimen of L. trinidadensis caught in San Esteban was in a sample of 892 males collected during one years work in the locality; this represents 0.11% of abnormality.

The male from Las Rosas, (Fig. 20) was identified as L. dubitans by (i) the presence of a conspicuous basal tuft in the coxite, (ii) the position of the basal spines of the style at about the middle of the segment and (iii) the spoon-shaped tips of the genital filaments. However, one of the styles had 3, not the normal 4, spines and there

was no evidence of an extra socket.

L. dubitans is a comparatively rare species and was represented only by 2 males and 1 female out of a total of 2110 sandflies trapped in weekly collections during 1978-1979. One of these two males was abnormal but, because of the extremely small sample, the abnormality cannot be expressed as a percentage.

Among 481 females of L. trinidadensis collected in San Esteban during the same period as the males, two anomalous specimens were found (0.42%). They had a typical pharynx and spermathecae but the cibarium showed only one supernumarary tooth (Fig. 21).

No further data than those listed can be added in relation to L. shannoni and L. lichyi. The 2 abnormal females, L. gomezi, were in a sample of 47 females (4.25%).

Such sporadic abnormalities should be considered separately from the more common intraspecific variability as seen in L. bahiensis (Mangabeira & Sherlock, 1961) in which 20% of about a thousand specimens showed wide variations in the number of the spines on the style (Sherlock, 1963). This phenomenon seems also to be very common in L. alphabetica (Fonseca, 1936) and L. torrealbai Martins et al., 1979, and is therefore best considered as a characteristic of an aberrant species (Martins et al., 1979) rather than "common anomalies" (Forattini, 1973).

The type and frequency of abnormalities in the morphology of sandflies are important for correct specific identifications. However, the origin and significance of the abnormalities remain unknown. The possibility of a relationship with some form of parasitism has been suggested by Welch (1963) and by Lewis & Buttiker (in press).

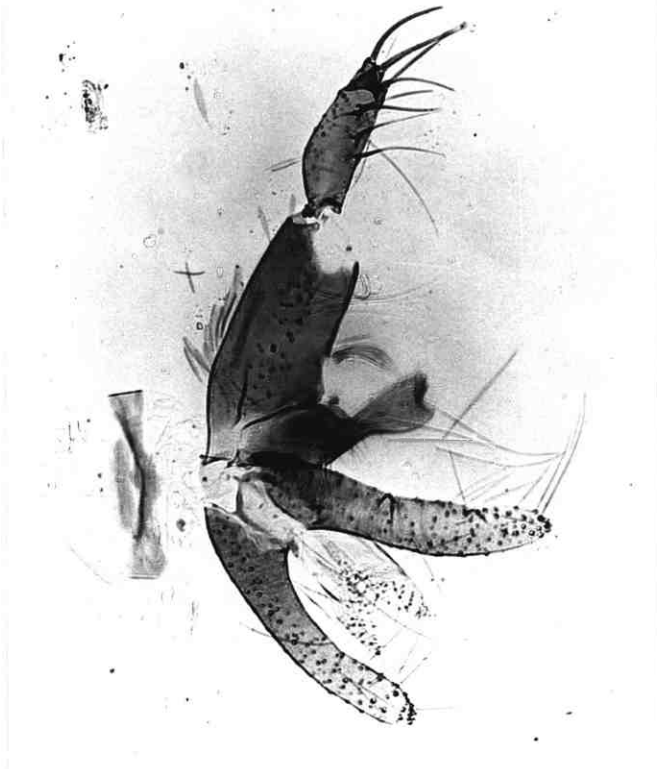


Fig. 14. Anomalous Lutzomyia sp. : Male genitalia showing only one coxite, one style with 8 spines and one paramere.

Fig. 15. Anomalous Lutzomyia sp : head showing the FIII and FIV of the antennas abnormally swollen.

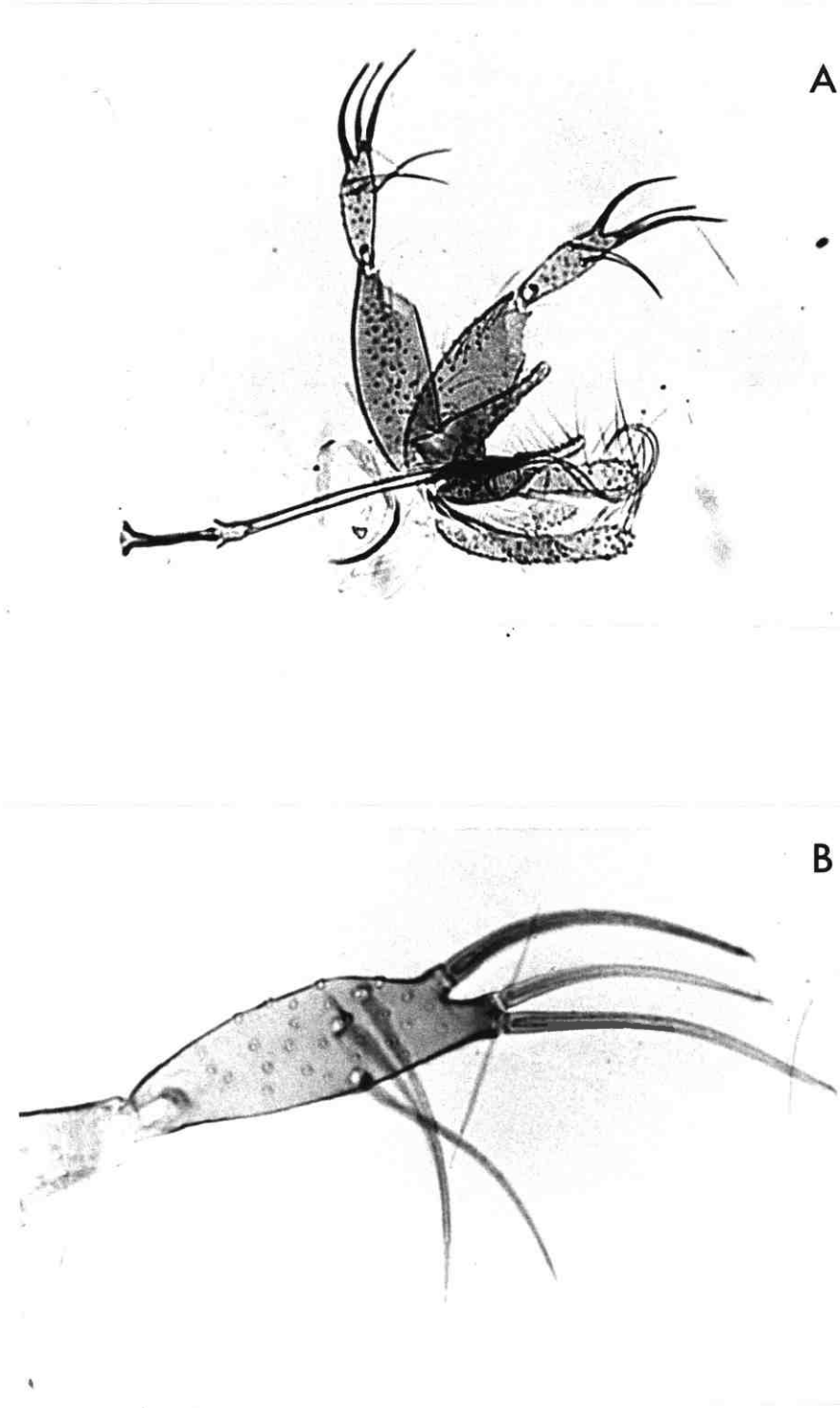


Fig. 16. Anomalous L. trinidadensis (specimen 1): Male showing one style with 5 spines. A. General view of genitalia. B. Detail of the abnormal style.

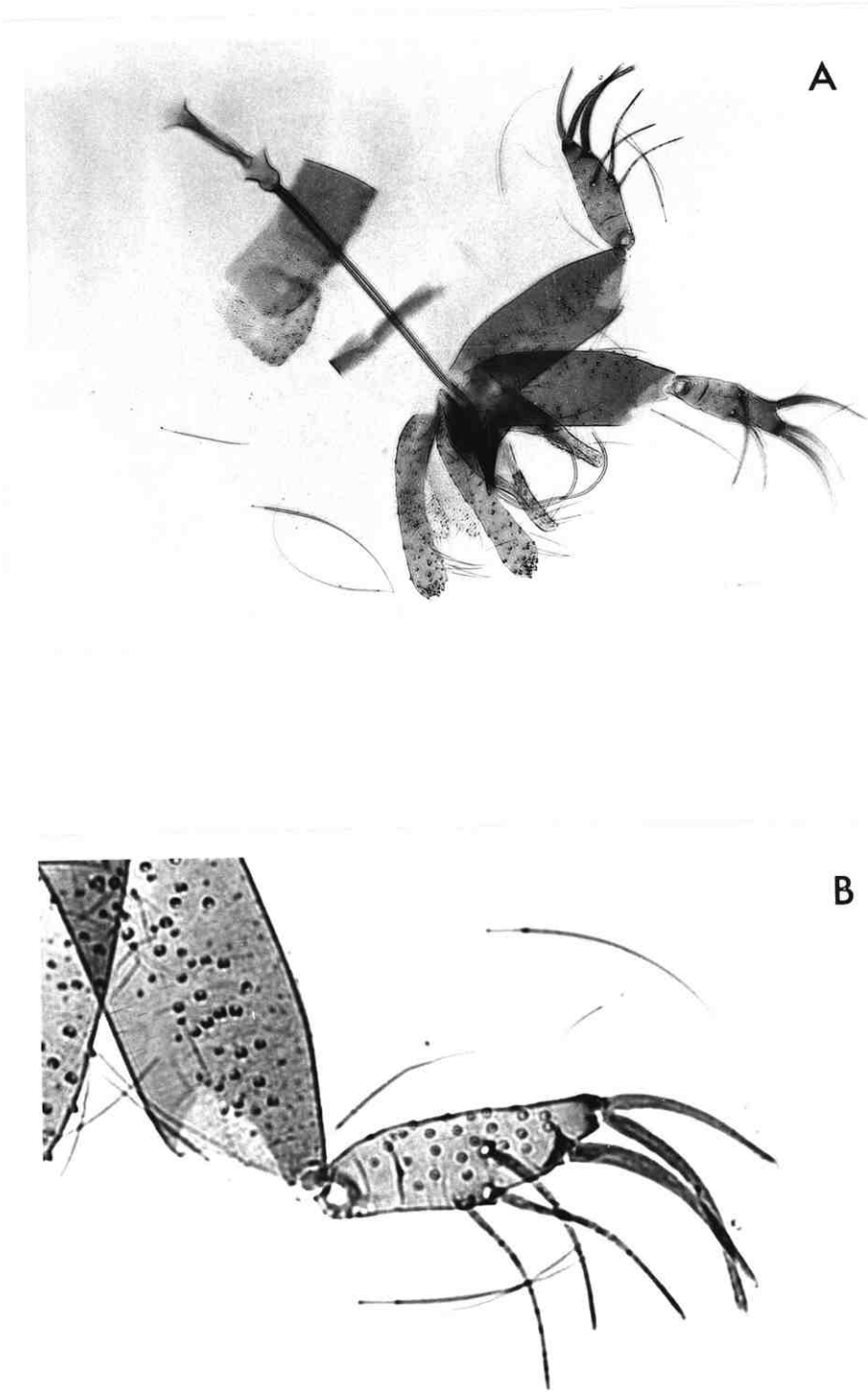


Fig. 17. Anomalous L. trinidadensis (specimen 2): Male showing one style with 5 spines. A. General view of genitalia. B. Detail of the abnormal style.

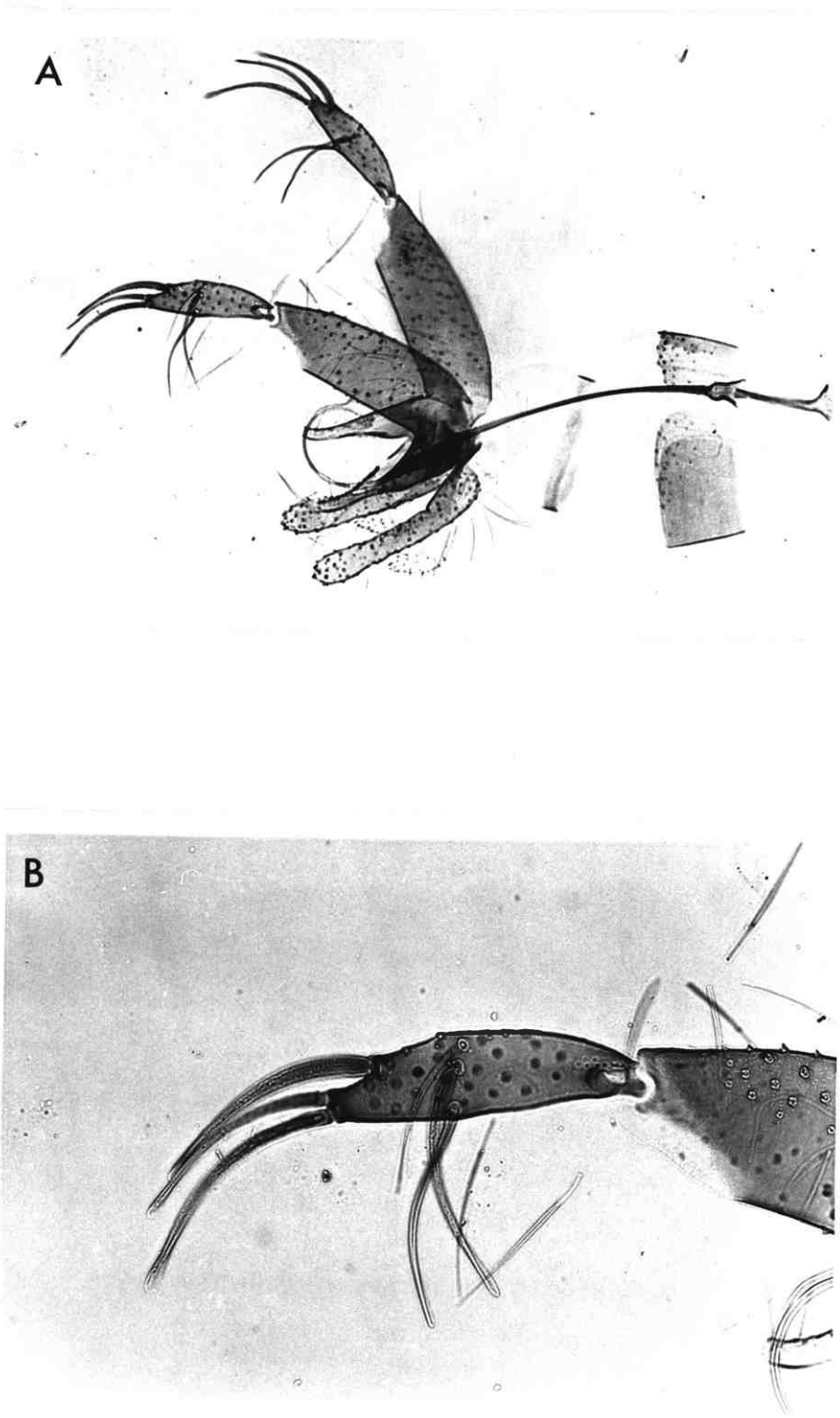


Fig. 18. Anomalous L. trinidadensis (specimen 3): Male showing one style with 5 spines. A. General view of genitalia. B. Detail of the abnormal style.

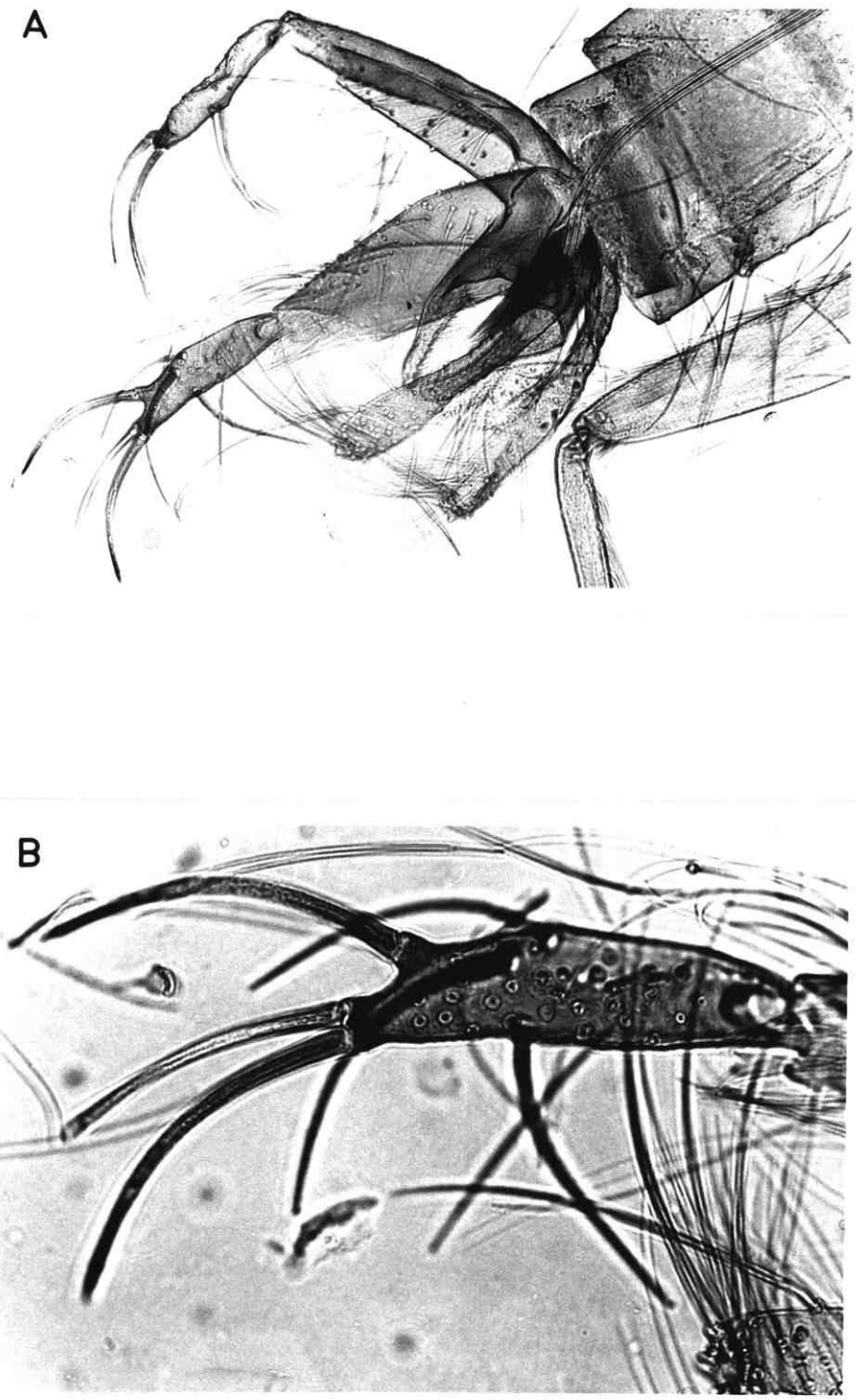


Fig. 19. Anomalous L. trinidadensis (specimen 4): Male showing one style with 5 spines.
A. General view of genitalia.
B. Detail of the abnormal style.

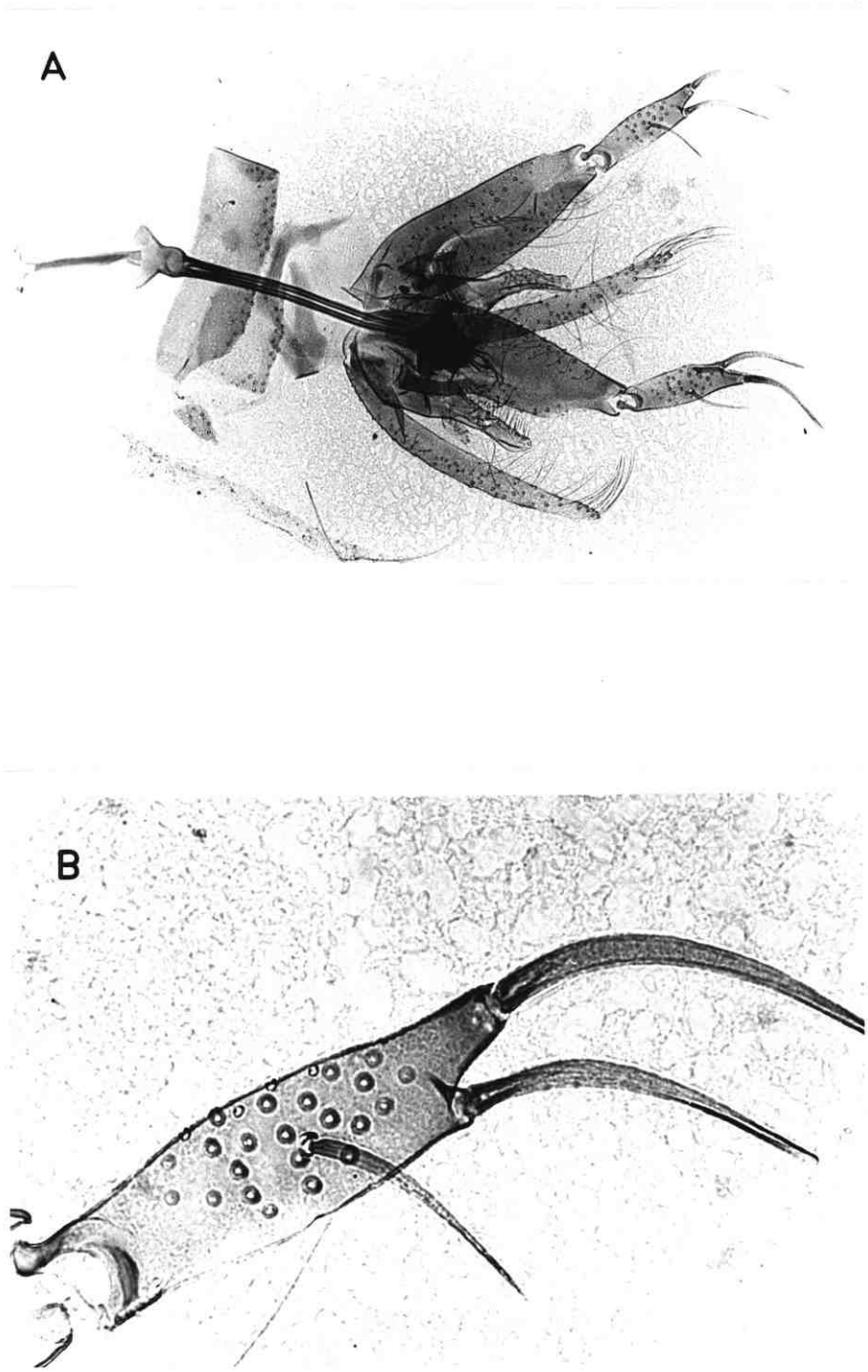


Fig. 20. Anomalous L. dubitans: male showing one style with 3 spines. A. General view of genitalia. B. Detail of the abnormal style.

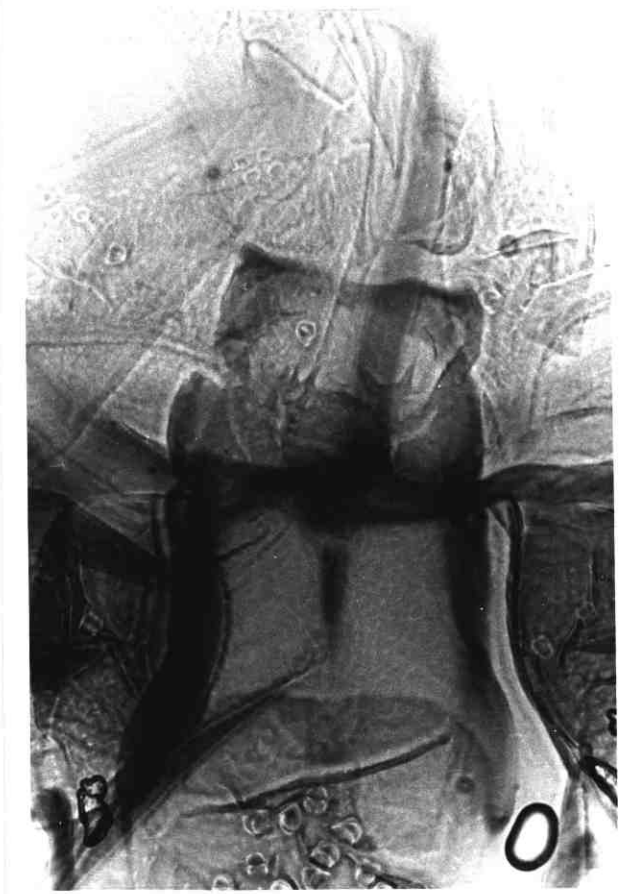


Fig. 21. Anomalous L. trinidadensis: female cibarium showing five teeth instead of the normal four

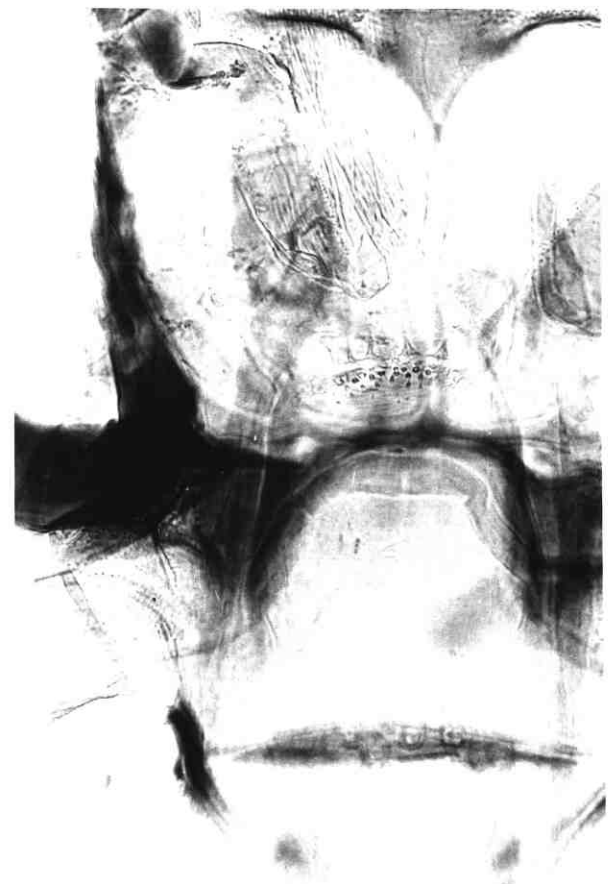


Fig. 22. Anomalous L. shannoni: female cibarium showing five teeth instead of the normal four

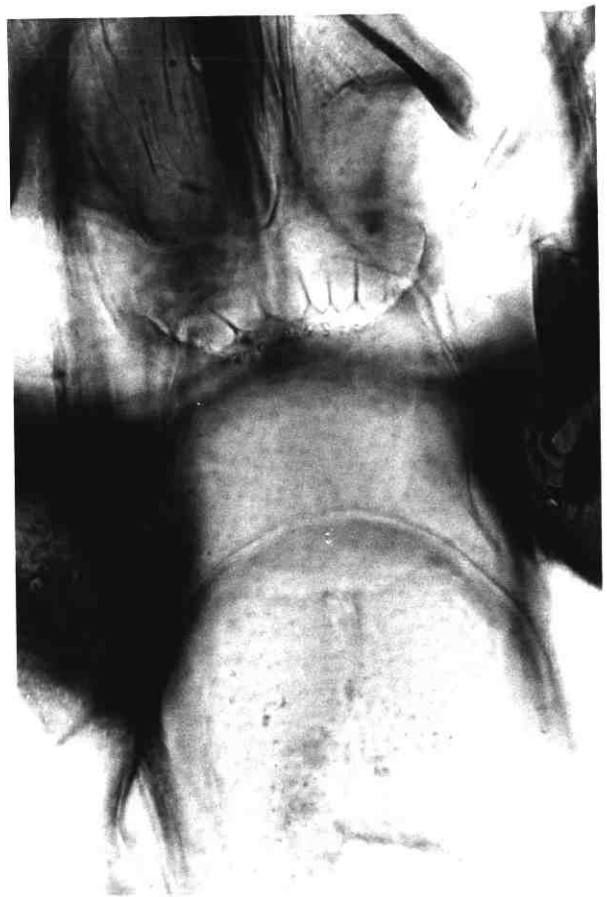


Fig. 23. Anomalous L. lichyi (specimen 1): female cibarium showing five teeth instead of the normal four.

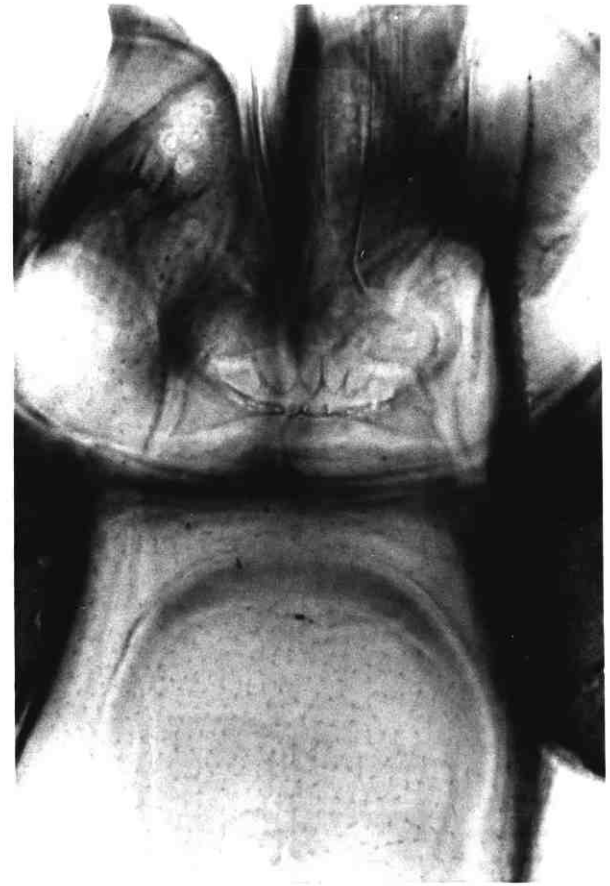


Fig. 24. Anomalous L. lichyi (specimen 2): female cibarium showing five teeth instead of the normal four.

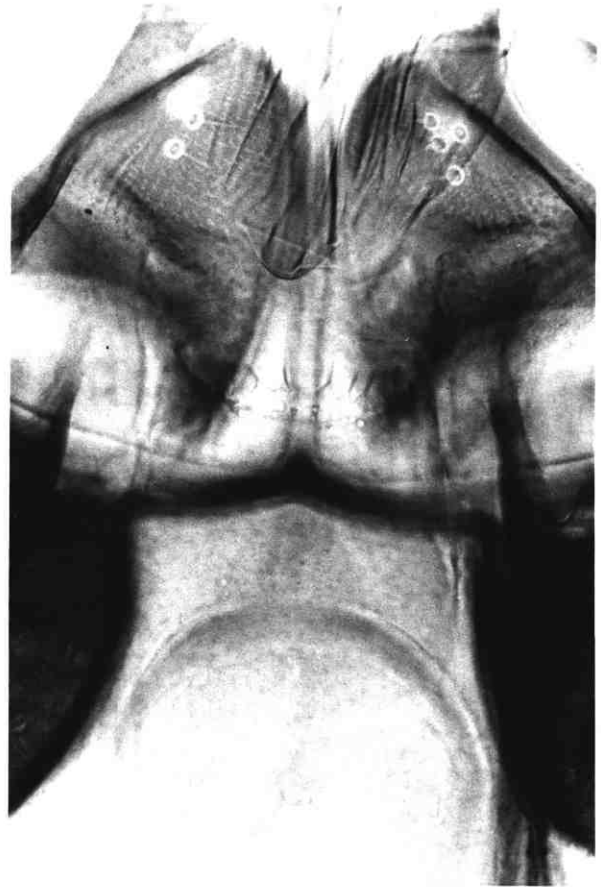


Fig. 25. Anomalous L. lichyi (specimen 3): female cibarium showing five teeth instead of the normal four.

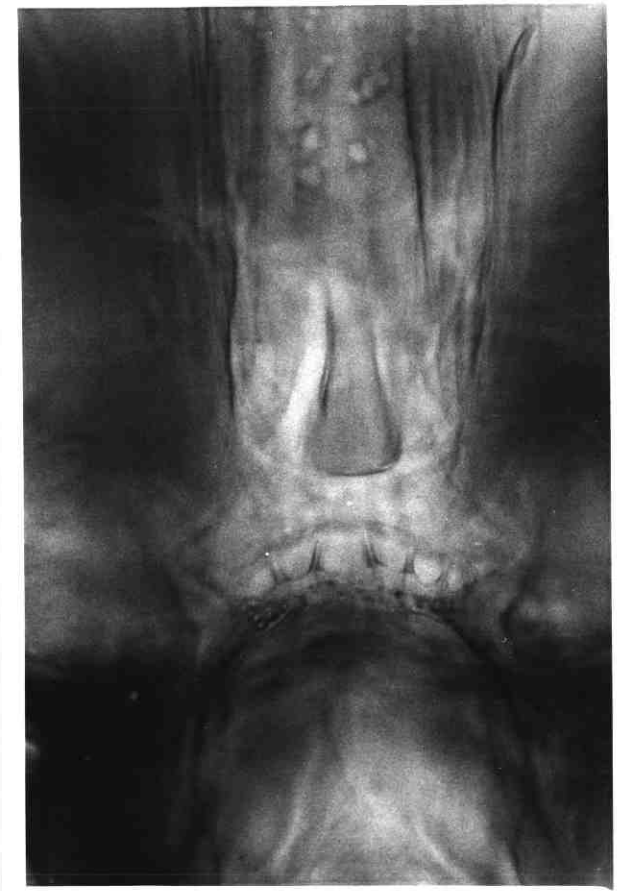


Fig. 26. Anomalous L. gomezi: female cibarium showing 5 teeth instead of the normal four.

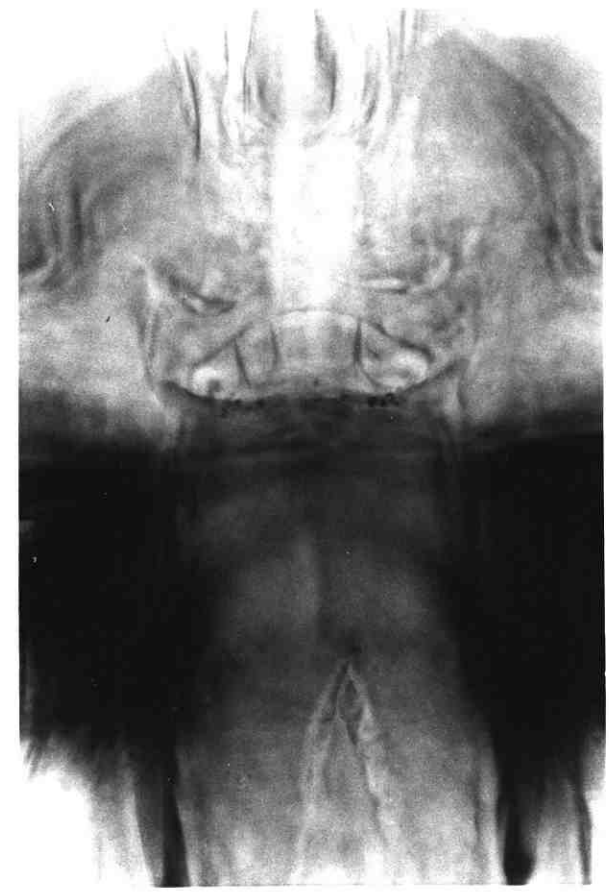


Fig. 27. Anomalous L. gomezi : female cibarium showing 3 teeth instead of the normal four.

3.3.4 New Records of Species and of the Distribution of Sandflies in Venezuela

Five species are here recorded for the first time in Venezuela.

1. Lutzomyia serrana (Damasceno & Arouck, 1949).

Material examined: 1 ♂, locality : Loma Bastidas, Municipio (= county) San Lazaro, Trujillo State, 2 March 1977. Collector Mr. Pedro Manzanilla. Habitat: This species was collected at day-time under dead leaves.

2. Lutzomyia saulensis (Floch & Abonnenc, 1944).

Material examined: 4 ♂♂ 1 ♀, Pio Paez, M. pio Codazzi, Apure State, 23 April 1981; 8 ♂♂ 2 ♀♀, El Novillo, Mpio Codazzi, Apure State, 24 April 1981; 2 ♀♀, Guaramacaco, Mpio Codazzi, Apure State, 29 April 1981. Mr. Juan Pulido. Habitat: All specimens were collected in tree holes.

3. Lutzomyia walkeri (Newstead, 1914).

Material examined: Apure State: 4 ♂♂ 9 ♀♀, Guaramacaco, Mpio Codazzi, 27 April 1981; 14 ♂♂ 9 ♀♀ same locality, 29 April 1981; 1 ♂, El Novillo, M. pio Codazzi, 24 April 1981; 1 ♀ P.to Paez, M pio Codazzi 24 April 1981; 1 ♀ Mata da Silva; Mucurita. Habitat: tree bark, termitaria. Trujillo State : 1 ♀ Cumbre de la Sierra, 17 Dec. 1972; 3 ♂♂, 1 ♀ El Volcán, Mpio Monsenor Jauregui, 6 Sept. 1972; 1 ♂, Sabana Grande, M. pio Candelaria, 4 June 1975; 6 ♂♂, same data but 22 May 1975; 1 ♂ , El Mamón, Mpio Candelaria, 13 Aug 1974; 2 ♂♂, Las Cocuizas, M.pio La Concepción, 25 Nov. 1975. Mr. Pedro Manzanilla; 1 ♀, Rio Monosnoy Feb. 1978, Prof. Scorza.
Cojedes State: 1 ♂, Boca de Cero, Mpio El Pao, 5 Nov, 1980. Mr. Temistocles Gonzalez. Habitat : between stones, roots, tree holes.

4. Lutzomyia abonnenci (Floch & Chassignet, 1947).

Material examined: 1 ♂ July 1981, El Pilón de Valle Hondo, Cojedes State. Collectors: Mr. Elio Fernandez and Mr. Pedro Aular.

5. Lutzomyia olmeca bicolor Fairchild & Theodor, 1971.

Material examined: 4 ♀♀, Apr. 1979; 1 ♂, May 1979; 3 ♂♂, 2 ♀♀ June 1979; 1 ♂ 1 ♀ Aug 1979; 2 ♀♀ Oct 1979; 3 ♂♂ Nov. 1979; 5 ♂♂ 3 ♀♀ Dec. 1979; 2 ♂♂, 4 ♀♀, Jan 1980; 1 ♀ Feb. 1980, San Esteban, Mpio P.to Cabello, Carabobo State. Collectors: Mr. Pedro Aular and Mr. Elio Fernandez. Habitat: This species was collected biting man and in light traps.

New geographical records by State, localities and counties.

Cojedes State. Collectors : T. Gonzalez, O. Vargas

Material examined:

1 - Charcote, Romulo Gallegos:

L. trinidadensis: 2 ♂♂, 1 Oct. 1980; 2 ♂♂ 16 Oct. 1980; 2 ♂♂, 22 Oct. 1980; 4 ♂♂, 29 Oct. 1981; 1 ♂ 1 ♀, 19 Feb. 1981; 4 ♂, 18 May 1981.

L. punctigeniculata: 1 ♂, 1 Oct. 1980; 3 ♂♂, 16 Oct. 1980; 5 ♂, 22 Oct. 1980; 5 ♂ 29 Oct. 1980, 5 ♂ 1 ♀ 9 Dec. 1980;

L. micropyga: 1 ♂, 1 ♀, 10 Oct. 1980; 3 ♂♂, 1 ♀ L. micropyga 3 ♂♂, 22 Oct. 1980; 2 ♂♂, 1 ♀, 9 Dec 1980; 1 ♂, 18 May, 1981.

L. shannoni: 2 ♂♂, 16 Oct. 1980; 2 ♂♂, 22 Oct. 1980; 1 ♀, 29 Oct. 1980; 1 ♂, 12 Dec. 1981.

L. cayennensis: 1 ♀, 29 Oct. 1980;

L. longipalpis: 2 ♀♀, 29 Oct. 1980; 1 ♂, 18 May 1981.

L. rangeliana: 1 ♂, 18 May, 1981.

L. atroclavata: 1 ♂, 18 May, 1981.

2 - Tierra Caliente, Manrique

L. trinidadensis: 14 ♂♂, 23 Oct. 1980; 5 ♂♂, 2 ♀♀, 4 Nov. 1980; 5 ♂♂, 8 Jan. 1981; 7 ♂♂, 4 ♀♀, 17 Feb. 1981; 7 ♂♂, 3 ♀♀, 18 Feb. 1981; 26 ♂♂, 23 ♀♀, 19 Feb. 1981; 14 ♂♂, 6 ♀♀, 25 Feb. 1981; 5 ♂, 10 March, 1981; 10 ♂♂, 1 ♀, 13 May 1981.

L. atroclavata: 1 ♂, 4 Nov. 1980; 1 ♂, 8 Jan, 1981; 7 ♂♂, 2 ♀♀, 17 Feb. 1981; 4 ♂, 2 ♀♀, 18 Feb. 1981; 7 ♂♂, 23 ♀♀, 19 Feb. 1981; 5 ♂♂, 25 Feb. 1981; 3 ♂♂, 10 March 1981; 3 ♂, 13 May 1981.

L. lichyi: 1 ♂, 23 Oct. 1980; 4 ♂♂, 2 ♀♀, 17 Feb. 1981.

L. panamensis: 1 ♂, 19 Feb. 1981; 1 ♂, 13 May 1981.

L. punctigeniculata: 1 ♂, 1 ♀, 18 Feb. 1981.

L. rangeliana: 2 ♂, 2 ♀, 13 May 1981.

3 - Potrero Largo, Manrique

L. trinidadensis: 9 ♂♂, 2 ♀♀, 10 March 1981; 1 ♂, 13 May 1981

L. atroclavata: 3 ♂♂, 1 ♀ 10 March 1981;

L. lichyi: 1 ♂, 1 ♀, 13 May, 1981.

4 - Hacienda Vieja, Manrique

L. trinidadensis: 41 ♂♂, 7 ♀♀, 24 Feb, 1981.

L. lichyi: 1 ♂, 3 ♀♀, 24 Feb, 1981.

L. gomezi: 1 ♂, 1 ♀, 24 Feb, 1981.

L. atroclavata: 7 ♂ 24 Feb, 1981.

L. micropyga: 1 ♂, 2 ♀♀, 24 Feb, 1981.

L. rangeliana: 2 ♂, 24 Feb, 1981.

5 - La Morita, El Pao San Juan Bautista

L. trinidadensis: 2 ♂♂, 1 ♀, 2 Oct. 1980

L. micropyga: 5 ♂♂, 2 Oct, 1980

L. longipalpis: 5 ♀♀, 2 Oct, 1980

L. punctigeniculata: 2 ♂♂, 2 Oct, 1980.

L. evansi: 1 ♀, 2 Oct, 1980.

6 - Zambrano, El Pao

L. longipalpis: 39 ♂♂, 4 ♀♀, 23 Oct, 1980; 16 ♂♂, 5 ♀♀, 30 Oct. 1980;

L. gomezi: 21 ♂♂, 23 Octo. 1980; 54 ♂♂, 1 ♀, 30 Oct. 1980;

L. evansi: 9 ♂♂, 1 ♀, 23 Oct. 1980; 6 ♂♂, 1 ♀, 30 Oct. 1980.

L. trinidadensis: 4 ♂♂, 3 ♀♀, 23 Oct. 1980.

L. micropyga: 1 ♀, 23 Oct. 1980.

L. dubitans: 1 ♂, 30 Oct. 1980.

7 - Las Rosas, San Carlos

L. trinidadensis: 2 ♂♂, 1 ♀, 23 Oct. 1980.

L. punctigeniculata: 2 ♂♂, 23 Oct. 1980.

8 - Solano, San Carlos

L. trinidadensis: 9 ♂♂, 1 ♀, 23 Oct. 1980

9 - Boca de Cero, El Pao

L. trinidadensis: 8 ♂♂, 2 ♀♀, 5 Nov. 1980.

L. longipalpis: 2 ♂♂, 5 Nov. 1980.

L. cayennensis: 1 ♂, 1 ♀, 5 Nov. 1980.

L. micropyga: 1 ♀, 5 Nov. 1980.

L. walkeri: 1 ♂, 5 Nov. 1980.

10- La Ceiba, San Carlos

L. trinidadensis: 8 ♂♂, 3 ♀♀, 30 Oct. 1980.

L. punctigeniculata: 5 ♂♂, 30 Oct. 1980

L. shannoni 1 ♂, 30 Oct. 1980.

L. rangeliana 1 ♂, 30 Oct. 1980.

11- Mapurite, San Carlos

L. punctigeniculata: 2 ♂♂, 30 Oct. 1980.

L. evansi: 1 ♂, 30 Oct. 1980.

L. shannoni: 2 ♂♂, 30 Oct. 1980.

L. antunesi: 3 ♂♂, 30 Oct. 1980.

12- Las Galeras, El Pao

L. trinidadensis: 1 ♀, 6 Nov. 1980.

13- San Carlos (INAGRO)

L. rangeliana: 3 ♂♂, 30 Jan. 1981;

L. trinidadensis: 1 ♂, 13 Feb. 1981.

Apure State. Collector: Mr. Juan Pulido

Material examined:

1 - Guaratico, Mantecal.

L. antunesi: 29 ♂♂, 15 ♀♀, 26 Sept. 1978; 5 ♂♂, 3 ♀♀, 28 Sept. 1978; 31 ♂♂, 18 ♀♀, 26 Oct. 1978.

L. shannoni: 1 ♂, 26 Sept. 1978; 4 ♂♂, 2 ♀♀, 28 Sept. 1978; 1 ♀, 26 Oct. 1978.

L. gomezi: 1 ♀, 26 Sept. 1978.

2 - Guaramaco, Codazzi

L. trinidadensis: 14 ♂♂, 14 ♀♀, 27 April 1981; 22 ♂♂, 14 ♀♀, 29 April 1981.

L. antunesi: 17 ♂♂, 14 ♀♀, 27 April 1981; 10 ♂♂, 21 ♀♀, 29 April 1981.

L. walkeri: 4 ♂♂, 7 ♀♀, 27 April 1981; 14 ♂♂, 10 ♀♀, 29 April 1981.

L. saulensis: 2 ♀♀, 29 April 1981.

L. cayennensis: 1 ♀, 27 April 1981, 1 ♀, 29 April 1981.

L. shannoni: 1 ♀, 27 April 1981.

3 - El Novillo, Codazzi

L. saulensis: 8 ♂♂, 2 ♀♀, 24 April 1981.

L. trinidadensis: 9 ♂♂, 4 ♀♀, 24 April 1981.

L. walkeri: 1 ♀ 24 April 1981.

4 - La Blanquita, Mpio. San Camilo

L. gomezi: 8 ♂♂, 1 ♀, 25 July 1981

L. antunesi: 1 ♂, 25 July 1981.

5 - Payara, Mpio. San Juan de Payara (CDC)

L. antunesi: 1 ♀, 26 Nov. 1981.

6 - Montaña La Puerta, Mpio. El Amparo

L. antunesi: 2 ♂♂, 1 ♀, 20 Aug. 1981.

L. panamensis: 1 ♀, 20 Aug. 1981.

L. dubitans: 1 ♂, 20 Aug. 1981.

7 - Los Rancheros. Mpio. San Vicente.

L. shannoni: 4 ♂♂, 2 ♀♀, 27 Oct. 1981.

L. punctigeniculata: 3 ♀♀, 27 Oct. 1981.

8 - Santa Elena, Mpio Elorza

L. punctigeniculata: 9 ♂♂, 1 ♀, 12 Dec. 1981.

L. antunesi: 14 ♂♂, 11 ♀♀, 12 Dec. 1981.

L. shannoni: 3 ♂♂, 1 ♀, 12 Dec. 1981.

9 - Santa Lucia, Achaguas.

L. panamensis: 4 ♀♀, 22 June 1981; 7 ♂♂, 12 ♀♀, 24 June 1981.

L. migonei: 1 ♂, 1 ♀, 22 June 1981; 1 ♂, 2 ♀, 24 June 1981.

L. antunesi: 10 ♂♂, 2 ♀♀, 24 June 1981.

L. shannoni: 1 ♀, 24 June 1981.

L. dubitans: 1 ♀, 24 June 1981.

L. rangeliana: 1 ♂ , 24 June 1981.

10- El Carrao, Apurito

L. gomezi: 2 ♂♂, 1 ♀, 20 June 1981.

L. punctigeniculata: 2 ♀♀, 20 June 1981.

L. rangeliana: 1 ♂, 20 June 1981.

L. migonei: 1 ♂, 20 June 1981.

11- Puerto Paez, Codazzi

L. saulensis: 4 ♂♂, 1 ♀, 23 April 1981.

L. trinidadensis: 1 ♂, 6 ♀♀, 24 April 1981.

L. walkeri: 1 ♂, 1 ♀, 24 April 1981.

L. antunesi: 1 ♂, 5 ♀♀, 23 April 1981.

12- Los Morichales, Mpio San Vicente

L. antunesi: 2 ♂♂, 1 ♀, 23 Oct. 1981.

L. micropyga: 1 ♂, 1 ♀, 23 Oct. 1981.

L. punctigeniculata: 1 ♀, 23 Oct. 1981.

L. shannoni: 9 ♂♂, 5 ♀♀, 23 Oct. 1981.

13- Caño Regreso, Mpio Urdaneta

L. gomezi: 24 ♂♂, 9 ♀♀, 23 July 1981.

L. shannoni: 12 ♂♂, 1 ♀, 23 July 1981.

L. trinidadensis: 1 ♂, 23 July 1981.

14- Sarare Abajo, Mpio Urdaneta

L. antunesi: 2 ♂♂, 2 ♀♀, 24 July 1981.

L. gomezi: 91 ♂♂, 14 ♀♀, 24 July 1981.

L. ovallesi: 1 ♂, 1 ♀, 24 July 1981.

L. shannoni: 2 ♂♂, 1 ♀, 24 July 1981.

L. micropyga: 1 ♂, 24 July 1981.

15- Guayabital. Mpio Guasdualito.

L. antunesi: 4 ♂♂, Aug. 1981.

L. gomezi: 5 ♂♂, 5 ♀♀, Aug. 1981.

16- San Carlos del Meta, Codazzi

L. antunesi: 5 ♂♂, 1 ♀, 25 April 1981.

L. trinidadensis: 1 ♂, 25 April 1981.

17- Cajutal, Peñalver

L. trinidadensis: 4 ♂♂, 1 ♀, 23 Feb. 1981.

18- Hato La Tigrera, Peñalver

L. shannoni: 8 ♂♂, 3 ♀♀, 24 Feb. 1981.

L. cayennensis: 7 ♀♀, 24 Feb. 1981.

L. punctigeniculata: 1 ♀ 24 Feb. 1981.

19- Chiricoca, San Camilo

L. gomezi: 27 ♂♂, 12 ♀♀, 21 July 1981; 19 ♂♂, 5 ♀♀, 20 July, 1981.

L. antunesi: 2 ♀♀, 21 July 1981; 2 ♂♂, 20 July 1981.

L. shannoni: 1 ♀, 21 July 1981; 1 ♀, 20 July 1981.

L.sp. (Pressatia) 1 ♀, 21 July 1981; 1 ♂, 20 July 1981.

L. micropyga: 1 ♂, 21 July 1981.

20- Mata de Silva, Mucurita.

L. shannoni: 12 ♂♂, 1 ♀, 24 Oct. 1981.

L. rangeliana: 17 ♂♂, 7 ♀♀, 24 Oct 1981.

L. walkeri: 1 ♀ , 24 Oct 1981.

L. gomezi: 2 ♂♂, 24 Oct. 1981.

Carabobo State, Collectors: Elio Fernandex, Pedro Aular

1 - Los Cocos, Democracia

L. trinidadensis: 34 ♂♂, 12 ♀♀, 9 June 1977.

L. ovallesi: 2 ♂♂, 4 ♀♀, 9 June 1977.

L. venezuelensis: 7 ♂♂, 3 ♀♀, 9 June 1977.

L. micropyga: 1 ♂, 9 June 1977.

2 - Guache, Guigue

L. trinidadensis: 37 ♂♂, 22 ♀♀, 17 June 1977.

L. atroclavata: 9 ♂♂, 5 ♀♀, 17 June 1977.

L. evansi: 1 ♀, 17 June 1977.

3 - Yuma, Guigue

L. trinidadensis: 35 ♂♂, 5 ♀, 17 June 1977.

L. ovallesi: 50 ♂♂, 8 ♀♀, 17 June 1977.

L. rangeliana: 5 ♂♂, 17 June 1977.

L. atroclavata: 1 ♂, 17 June 1977.

4 - El Pueblito, Guigue

L. trinidadensis: 17 ♂♂, 57 ♀♀, 22 June 1977.

L. rangeliana: 4 ♂♂, 2 ♀♀, 22 June 1977.

L. ovallesi: 4 ♂♂, 22 June 1977.

5 - S.ta Inès, Belén

L. trinidadensis: 15 ♂♂, 64 ♀♀, 22 June 1977.

L. ovallesi: 1 ♀ 22 June 1977.

6 - Las Colonias, Guigue

L. trinidadensis: 25 ♂♂, 18 ♀♀, 30 June 1977.

L. atroclavata: 59 ♂♂, 45 ♀♀, 30 June 1977.

L. cayennensis: 3 ♂♂, 6 ♀♀, 30 June 1977.

L. lichyi: 20 ♂♂, 4 ♀♀, 30 June 1977.

L. ovallesi: 56 ♂, 5 ♀♀, 30 June 1977.

L. migonei: 1 ♂, 30 June 1977.

7 - Belén

L. gomezi: 1 ♂, 30 June 1977.

L. lichyi: 4 ♂♂, 1 ♀ , 30 June 1977.

L. ovallesi: 72 ♂♂, 17 ♀♀, 30 June 1977.

8 - El Corozo

L. lichyi: 5 ♂♂, 30 June 1977

L. ovallesi: 51 ♂♂, 5 ♀♀, 30 June 1977.

9 - El Caneto, Belén

L. trinidadensis: 36 ♂♂, 3 ♀♀, 30 June 1977.

L. ovallesi: 19 ♂♂ 30 June 1977.

L. lichyi: 5 ♂♂, 1 ♀, 30 June 1977.

L. gomezi: 1 ♂, 30 June 1977.

L. rangeliana: 2 ♂♂, 30 June 1977.

L. venezuelensis: 1 ♂, 30 June 1977.

10- Agua Linda, Tocuyito

L. trinidadensis: 60 ♂♂, 19 ♀♀, 6 July 1977.

L. atroclavata: 2 ♂♂, 1 ♀, 6 July 1977.

L. ovallesi: 1 ♂, 6 July 1977.

L. rangeliana: 1 ♂ , 6 July 1977.

11- El Naipe, Tocuyito

L. trinidadensis: 50 ♂♂, 18 ♀♀, 6 July 1977.

L. atroclavata: 3 ♂♂, 1 ♀, 6 July 1977

12- Carabobo, Tocuyito

L. trinidadensis: 29 ♂♂, 26 ♀♀, 6 July 1977

L. atroclavata: 11 ♂♂, 6 July 1977

L. rangeliana: 5 ♂♂, 6 July 1977

L. micropyga: 1 ♀, 6 July 1977

13- Las Animas

L. atroclavata: 10 ♂♂, 9 June 1977

L. trinidadensis: 5 ♂♂, 10 ♀♀, 9 June 1977

L. cayennensis: 7 ♀♀, 9 June 1977

L. rangeliana: 1 ♂, 9 June 1977

14- El Cambur

L. cayennensis: 39 ♂♂, 30 ♀♀, 9 June 1977

L. atroclavata: 29 ♂♂, 5 ♀♀, 9 June 1977

L. trinidadensis: 4 ♂♂, 1 ♀, 9 June 1977

15- Pueblo Nuevo

L. trinidadensis: 8 ♂♂, 1 ♀, 20 June 1977

L. ovallesi: 2 ♀♀, 20 June 1977

L. cayennensis: 2 ♂♂, 1 ♀, 20 June 1977

16- La Arenosa

L. trinidadensis: 55 ♂♂, 26 ♀♀, 18 July 1977

17- San José

L. trinidadensis: 69 ♂♂, 31 ♀♀, 18 July 1977

L. punctigeniculata: 1 ♂, 18 July 1977

L. lichyi: 1 ♀, 18 July 1977

L. gomezi: 3 ♂♂, 18 July 1977

18- El Tigre

L. trinidadensis: 55 ♂♂, 26 ♀♀, 18 July 1977

3.3.5. Check-list of Venezuelan Sandflies

Species of the genus Brumptomyia Franca & Parrot, 1921.

1. Brumptomyia avellari (Costa Lima)

Phlebotomus avellari Costa Lima, 1932: 47 (♂, Brazil)

Ortiz, 1963: 320 (♀ Keyed). Ortiz & Scorza, 1963: 354 (♂ Keyed)

Flebotomus avellari: Mangabeira, 1942b: 225 (♂, ♀ immatures).

Brumptomyia avellari:Carneiro & Sherlock, 1964: 315 (pupa, Keyed).

Forattini, 1973: 122 (gen review). Martins et al.1978: 10 (refs., distr.). Young, 1979 : 34 (♂ Keyed, refs., distr.).

Territorio Federal Amazonas: Atabapo (Ocamo)

(Ramirez Perez et al. 1976. Rev. Brasil. Biol. 36 (3):599)

This species, found near the boundary with Brazil, was collected in an armadillo burrow. Young (loc.cit.) also refers to trapping this fly in light traps.

2. Brumptomyia beaupertuyi (Ortiz)

Phlebotomus beaupertuyi Ortiz, 1954: 235 (♂, Venezuela) Pifano et al. 1962a.: 383, 387 (♂, ♀ Keyed), 411-412 (♀ descr., ♂ redescr.). Ortiz, 1963a : 322 (♀, redescr.). Ortiz & Scorza, 1963: 350 (♂ , Keyed). Scorza et al. 1967 : 193 (♂, Keyed). Ortiz, 1968a : 533 (ecology).

Phlebotomus galindoi (not galindoi of Fairchild & Hertig, 1947)

Pifano & Ortiz, 1952: 137 ; Scorza et al. 1967: 179 (as synonym of beaupertuyi).

Brumptomyia beaupertuyi: Fraiha et al. 1970: 468 (♂, Keyed)

Forattini, 1973: 522 (gen. review). Martins et al. 1978: 11 (Refs. distr.), Ramirez Perez et al., 1978: 52 (♂, ♀ Keyed). Young,

1979: 36 (♂ Keyed, refs., distr.)

Aragua: Rancho Grande (Scorza & Ortiz, 1960. Ztschr. Tropenmed. Parasitol. 11: 433 Ramirez Perez, et al, 1978. Bol. Dir. Malariol. y San. Amb., 18 (1): 43).

Carabobo: El Cambur (Present work).

Lara: Duaca: (Ortiz, I. 1954, Acta Biol. Venez. 1 (14): 235).

Miranda: Agua Blanca. Guatopo (Pifano et al. 1962a. Arch. Venez. Med. Trop. Parasit. Med. 4(2) : 369), Valles del Tuy (Pifano et al. 1962c. Arch. Venez. Med. Trop. Parasit. Med. 4(2) : 149).

This species was collected in light traps (Shannon trap), and in resting places of animals. Ortiz (1968a)associated B. beaupertuyi with armadillos and bats.

3. Brumptomyia devenanzii (Ortiz & Scorza)

Phlebotomus (Brumptomyia) devenanzii Ortiz & Scorza 1963: 351 (♂ , Venezuela); 354 (♂, Keyed). Scorza et al, 1967: 190 (listed). Ortiz, 1968a: 533 (ecology).

Brumptomyia devenanzii Ramirez Perez et al. 1978: 52 (♂ Keyed). Martins et al. 1978: 14 (dist. refs.).

Aragua: Rancho Grande (Ortiz & Scorza, 1963. Acta Biol. Venez. 3(23): 341; Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb., 18(1) : 43).

The male described was collected with a Khan tube at 1175 m above sea-level from uncovered roots of big trees. The female of this narrowly distributed species is still unknown.

Species of the genus Lutzomyia Franca, 1924 found in Venezuela

Sub-genus Evandromyia Mangabeira, 1941:216.

Antennal ascoids simple. 5th palpal segment much longer than 3rd.

Male: Basistyle usually with a basal tuft of hair arising from a chitinized ridge. Dististyle with 4 well developed spines at different levels and a subterminal seta. Parameres simple or bifurcated (series infraspinosa) or trifurcated (series monstruosa), partly chitinized. Lateral lobes long, equal to or greater than the length of the basistyle, with 2-3 spatulate hairs (series infraspinosa) or unarmed (series monstruosa).

Female: Cibarium with 4 horizontal teeth and few small vertical teeth; pigment patch defined and cibarial arch complete. Body of the spermathecae elongate or sac-like.

Series infraspinosa.

4. Lutzomyia begonae (Ortiz & Torres Rojas)

Phlebotomus begonae (Ortiz & Torres Rojas, 1975: 101 (♂ , Venezuela)

Lutzomyia begonae Young & Arias, 1977: 63 (♀ (descr.), ♂ (redescr.) 67-68 (Keyed). Arias & de Freitas, 1977: 516 (bionomics).

Terr. Federal Amazonas: El Gavilán (Ortiz & Torres Rojas, 1975. Revista del Inst. Nac. de Higiene. 8 (1-2): 101).

The original description of L. begonae by Ortiz states that the paramere of this species is trifurcated, and the pictures show in detail 3 arms, the ventral one quite pronounced. Young & Arias (loc.cit.) in the redescription of the male, based on Brazilian specimens, considered the "paramere bifurcated, the lower arm with a ventral acute process" which is actually difficult to observe in the picture. They considered the differences as the result of geographical variation and regarded the Brazilian specimens as being conspecific with L. begonae.

In 1977, 69 females caught by Arias & Freitas in Brazil (loc.cit.) were named L. begonae but L. begonae males, though caught on an earlier occasion, were absent from the catch that year. The only male collected

was L. infraspinosa. Females of L. begonae and L. infraspinosa are indistinguishable (Young & Arias, loc.cit.), and the females caught by Arias & Freitas may therefore have been L. infraspinosa. Comparison of flies from the L. begonae type locality (Venezuela) with the Brazilian flies may help to clear this confusion. Large samples from both areas would show the limit of any geographical variation and finally allow flies from both areas to be considered conspecific or heterospecific.

5. Lutzomyia sp. of Rio Monosnoy (♂, Venezuela, present work).

Trujillo: Rio Monosnoy near Monay

The female of this new species is unknown. The only male was found with L. atroclavata, L. longipalpis, L. evansi, L. micropyga and L. pilosa in a tree hole. Taxonomic characteristics are discussed in the description.

Sub-genus Lutzomyia Franca, 1924: 10

Antennal ascoids simple. 5th palpal segment long, greater than segments 3+4.

Male: Basistyle with a basal tuft or 4 or more long and well developed hairs. Dististyle with 4 spines (series cruciata) or 4 spines and a subterminal seta (series longipalpis). Parameres unarmed (series cruciata) or with 2-5 long spines often in the shape of "antelope horns" (series longipalpis). Lateral lobes approximately of the same length or longer than the basistyle.

Female: Cibarium with 1-10 horizontal teeth, regularly distributed vertical teeth; pigment patch discrete and cibarial arch complete. Spermathecae with no imbricated segments (series longipalpis) or pear-shaped with a rounded apical segment (series cruciata); individual ducts long.

Series longipalpis

6. Lutzomyia longipalpis (Lutz & Neiva)

Phlebotomus longipalpis Lutz & Neiva, 1912 : 89 (♂, ♀ Brasil), Ortiz, 1942: 166 (Venezuela). Pifano & Ortiz, 1952: 141, 147 (♂, ♀ Keyed). Deane, 1958: 431 (incriminated vector of Le. donovani). Sherlock & Sherlock. 1959: 229 (rearing). Guitton & Sherlock, 1969: 383 (immature stages). Pifano et al., 1962b: 17 (ecology). Ortiz, 1968b: 57 (Keyed).

Phlebotomus otamae Nuñez Tovar, 1924. 44p. (♂)

Phlebotomus almazani Galliard, 1934b : 193 (♀).

Lutzomyia longipalpis: Osorno et al., 1969: 379 (♂, ♀ redescr. Colombia). Killick-Kendrick et al. (1974): 187 (Leishmania life cycle) Forattini, 1973: 213 (gen. review). Ward & Ready, 1975: 50 (eggs, morphology) Lewis, 1975: 500 (mouthparts). Killick-Kendrick et al., 1977a: 429 (rearing). Killick-Kendrick et al., 1977b : 105 (exper. infection with L. mexicana amazonensis)Killick-Kendrick et al., 1977_c 191 (Leishmania life-cycle). Martins et al., 1978: 22 (refs., distr.). Ready, 1979: 413 (eggs production) Young, 1979: 51 (♂, ♀ Keyed), 56 (refs. distr.).

Aragua: Valles de Aragua. (Pifano F. et al 1962b. Arch. Venez. Med. Trop. Parasit. Med., 4(2): 17).

Quebrada Apamate, La Sureña , Rio Cura, El Ingenio, Augustia, Barbacoas, Palambra, Q.da Dos Hermanas, Paso del medio, Paso de los Indios, Guanabano, Guanasnal, Lagunita, Q.da Honda, Piedras Pintadas, El Onoto, Los Bagres, Mata de Café, Corocito, El Ocumo, Macuaya, Agua de Maiz, Paya, (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18(1): 43).

Carabobo: Isla de Otama (Nuñez Tovar, 1924. Mosq. y Flebotomos de

Venezuela: 44):

Cojedes: El Tinaco. (Briceño Iragorry & De la Plaza, 1934. "Medical" Rev. Clin. Luis Razetti, 8 : 112). La Váquira, Charcote, Zambrano, Boca de Cerro (Present work).

Falcon: Mene de Mauroa (Ortiz, I. 1942. Bol. Lab. Clin. Luis Razetti, Año 3, 2 (9) : 162).

Guarico: Altagracia de Orituco: Parapara, San Francisco de Tiznado, San José de Tiznado, Santa Maria de Ipire, Zaraza, Baragua, Ribas (Amaral et al. 1961. Gac. Med. 70 (7-9) : 389).

Nueva Esparta: Isla Margarita: Guayacán, (Pifano & Morrell, 1973. Arch. Venez. Med. Trop. Parasit. Med. 5(2) : 129).

Portuguesa: Guanare (Pifano et al. 1962. Arch. Venez. Med. Trop. Parasit. Med. 4(2) : 1).

Sucre: Barbacoas, Cangrejal, El Tacal, Mariquitar, Petare, (Henriquez et al. 1970 Rev. ta Venez. San. Asist. Soc. 35 : 761).

Trujillo: (Mogollón et al. 1977. Bol. Dir. Malariol. y San. Amb., 17 (3): 206). Rio Monosnoy (Present work).

Yaracuy: Valles del Yaracuy (Iriarte, D.R. 1952. Bol. Lab. Clin. Luis Razetti, Año XII (35-36), 16 : 487), San Felipe (Pifano, F. 1943. Bol. Ent. Venez., 2 (2): 99).

Pifano, in Yaracuy State, found L. longipalpis infected with promastigotes (1941). Amaral et al. (1961b)confirmed the presence of these flagellates in the anterior gut of specimens caught in Guarico State, and pointed out the presumed epidemiological importance of this species in the trasmission of visceral leishmaniasis in Venezuela. In Pifano's et al. (1962b) observations on the ecology of L. longipalpis, he noted that it has a neutral phototropism and, in consequence, is only sporadically caught in Shannon traps. It is abundant in the neighbourhood of the "ranchos", the rural dwellings, and in places where hens, dogs,

pigs and goats sleep. Resting places are usually dark and free from draughts and this species is frequently collected between roots, in holes of trees or from hiding places of animals. Scorza et al. (1968d) noted that Lu. longipalpis fed preferentially on domestic animals but, in their absence, was anthropophilic. The altitudinal distribution of this species is from 300 m to 1880 m above sea-level (Mogollón et al., 1977).

7. Lutzomyia lichyi (Floch & Abonnenc)

Phlebotomus lichyi Floch & Abonnenc, 1950: 1 (♀ , Venezuela)

Floch & Kramer: 387 (♂).

Phlebotomus foliatus: Mirsa & Ortiz, 1952: 249 (♂). Fairchild & Hertig, 1958: 203 (as synonym of vexillarius)

Phlebotomus vexillarius: Fairchild & Hertig, 1952. 514 (♂, ♀)

Pifano et al. 1962a: 385 (Keyed).

McConnell & Correa, 1964: 527 (infected fungi). Floch & Kramer, 1965 (as synonym of lichyi). Hanson, 1968: 90 (immature stages).

Scorza et al. 1968a: 35 (bionomics).

Lutzomyia vexillaria: Martins et al, 1963: 335 (Brazil)

Lutzomyia lichyi: Arjona et al., 1971: 93 (biting records)

Forattini, 1973: 259 (gen. review). Lewis, 1975a:500 (mouthparts)

Martins et al., 1978: 22 (refs., distr.). Young, 1979: 51 (♂, ♀ Keyed), 54 (refs., distr.).

Aragua: Rancho Grande (Ortiz & Scorza 1963. Acta Biol. Venez., 3 (23): 341; El Negrito, Loro Arriba, La. Barquera, Guiripa San José, Golfo Triste, Las Adjuntas, Las Caobas, Tierra Negra, Agua Fria, Bejucal, Taguarigua, Guambra, Los Algarrobos, Monte Oscuro, Los Mamires Guanasnal, El Altar, Los Vargas, La Trinidad, El Ocumo, El Cortejo, Malpica, Quebrada Guayabo, Corral Viejo, Cataure, Semen, El Omoto,

Tunas, Caicara, Los Bagres, Quebrada Caney, El Toro, El Chino Agua de Maiz, Tucupido, (Ramirez Perez et al. 1978, Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Carabobo: Rio Borburata (Floch & Abonnenc, 1950. Publ. n 208), El Corozo, Belén, San José, Las Colonias (Present work).

Cojedes: Las Rosas (Aguilar, 1981. Thesis U.C., 132 pp).

Tierra Caliente: Hacienda Vieja (Present work).

Distrito Federal: Caracas (Mirsa & Ortiz, 1952. Rev. San. Asist. Soc. 17 (3-4): 249)

Merida: El Salado (Calderón, L. 1973. Acta Cient. Venez. 24: 87)

Miranda: Guatopo (Pifano et al., 1962a) Archs. Venez. Med. Trop. Parasit. Med., 4: 369), Los Chorros (Mirsa & Ortiz, 1952. Rev. San. Asist. Soc. 17 (3-4): 249)

Nueva Esparta: Isla de Margarita: Las Piedras (Pifano & Romero, 1964. Gac. Med. Caracas, 72 (7-12): 425)

Sucre: Cumanacoa (Pifano & Romero, 1964. Gac. Med. Caracas 72 (7-12): 473).

Trujillo: (Mogollón et al., 1977. Bol. Dir. Malariol. y San. Amb. 17 (3): 206).

This sandfly has frequently been taken off human bait but is considered by Scorza et al. (1968d) to be sylvatic, never domestic, and only sporadically anthropophilic and it has long flight and indifferent phototropism. Pifano (1960) reported that the majority of L. lichyi were caught in nests and tree-holes.

Like L. gomezi, L. lichyi has a wide altitudinal distribution, from 200 to 1800 m above sea-level (Mogollón et al., 1977).

Series Cruciata

8. Lutzomyia gomezi (Nitzulescu)

Phlebotomus gomezi Nitzulescu 1931: 247 (♀, Venezuela). Fairchild & Hertig, 1948a: 252 (Taxonomy). Fairchild & Hertig, 1953: 382 (♂, ♀ descr.). Hanson, 1968: 60 (larva, pupa).

Flebotomus gomezi: Barretto, 1946a:3-7, 21 (♂, ♀ , Brazil)

Phlebotomus japignyi: Floch & Abonnenc, 1944b:2 (♂ , ♀ , French Guyana). Fairchild & Hertig, 1948a: 252 (as synonym of gomezi)

Flebotomus suis: Rozeboom, 1940: 8 (♂, ♀ , Panama). Barretto, 1946: 1 (as synonym of gomezi). Fairchild & Hertig, 1948a: 252 (as synonym of gomezi)

Phlebotomus trinidadensis Theodor, 1932: 22 (♀)

Lutzomyia gomezi: Tesh et al., 1971: 153 (Natural host preferences). Tesh et al. 1972: 90 (Natural host preferences). Chaniotis et al. 1971a: 339 (pop. dynamics). Chaniotis et al. 1971b: 815 (man-biting) Forattini, 1973: 240 (gen. review. distr.). Lewis 1975a: 500 (mouthparts morphology). Rutledge & Ellenwood, 1975a:71 (ecology: the species complement). Rutledge & Ellenwood, 1975b:78 (ecology: hydrologic and physiographic relations). Rutledge & Ellenwood, 1975c:83 (ecology: phytologic and edaphic relations). Rutledge et al., 1975d:179 (ecology: light traps). Ward & Ready, 1975: 128 (eggs). Rutledge et al., 1976: 1149 (ecology: a transect study). Miles et al., 1976: 531 (mating behaviour). Zimmerman et al., 1977. (egg). Martins, 1978: 122 (refs, dist.). Young 1979: 51-52 (♂, ♀ Keyed), 56-59 (refs, dist.). Christensen & Herrer, 1980b:188 (infeccion with L. mexicana). Christensen & Herrer, 1980a. 522 (host attraction). Porter & DeFoliart, 1981:81 (ecol).

Apure: Guaratico, El Carrao, Mata de Silva, Chiricoca, Caño Regreso, Sarare Abajo, La Blanquita, Guayabital, (Present work).

Aragua: Maracay, San Mateo, (Iriarte D. 1952 Bol. Lab. Clin. Luis Razetti Año XII, 16 (35-36): 487; Polanco, Monte Oscuro, Golfo

Triste, El Negrito, Las Marias, Las Adjuntas, San José, Guambra Taguarigua, Las Caobas, Guiripa, Tierra Negra, Loro Arriba, Las Quebraditas, El Onoto, Guanasnal, La Lagunita, Quebrada Honda, Quebrada Guayabo, Cataure, Semen, Los Bagres, El Toro, Tucupido, Quebrada Jabillar, Gabante, Periquito, La Trilla, Aponte, Puerto Colombia, El Paraparo, (Ramirez Perez et al 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Barinas: (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti, Año XII, 16 (35-36): 487).

Carabobo: Belén, San José, San Esteban (Present work).

Cojedes: Las Rosas (Aguilar, 1981. Thesis. U.C. 132pp). Hacienda Vieja, Zambrano, (Present work).

Distrito Federal: Caracas (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti, Año XII, 16 (35-36): 487)

Falcon: Churuguara, Mene de Mauroa, (Ortiz, I. 1944. Bol. Lab. Clin. Luis Razetti, Año 5, 4 (14): 247.

Guarico: Altagracia de Orituco (Mirsa, A. 1954. Rev. San Asist. Soc. 19: 189).

Miranda: Guatopo, Los Chorros, Ocumare del Tuy (Ortiz, I. 1950. Arch. Venez Pat. Trop. Parasit. Méd., 2 (1): 83).

Monagas: Caripito (Martins et al 1978. American Sandflies. Acad. Brasil. Ciencias, Rio de Janeiro, R.J. 195 pp).

Nueva Esparta: Isla de Margarita: Las Piedras: (Pifano & Morrell 1964. Gaceta Méd. Caracas, 72 (7-12): 425).

Portuguesa: Guanare (Pifano et al 1962. Arch. Venez. Med. Trop. Parasit Med. 4 (2): 1).

Sucre: Cumanacoa (Pifano & Romero. 1964. Gaceta Méd. Caracas 72 (7-12): 473)

Tachira: La Colorada, San Cristobal (Nitzulezcu, V. 1931. Ann. Parasit.

Hum. Comp. 9 (3): 247).

Trujillo: (Mogollón et al 1977. Bol. Dir. Malariol. y. San. Amb. 17 (3): 206).

Yaracuy: San Felipe (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti Año XII 16 (35-36): 487)

Zulia: Bachaquero, Cabimas, (Ortiz & Peña Garcia. 1948. Apuntes Cient. 1 (2): 6), Rio Negro, Zipayare (Marmol León P. 1968 Kasmera, 3 (1): 61).

This species, with a wide geographical and altitudinal distribution in Venezuela, has been caught in holes of trees and also biting man, attracted by a Coleman lamp; it is considered to be anthropophilic. L. gomezi, a vector of cutaneous leishmaniasis in Panama, is suspected by Pifano (1960) to play a similar role in Venezuela.

9. Lutzomyia ignacioi Young

Lutzomyia ignacioi Young, 1972: 312 (♂, ♀)

Merida: (Young, D. 1972. J. Med. Ent. 9 (4): 312).

Except for the taxonomy this species is completely unknown.

Sub-genus Nyssomyia Barretto, 1962: 91.

Antennal ascoids simple. 5th palpal segment shorter, equal or a little longer than the 3rd segment.

Male: Basistyle without basal tuft. Dististyle with 4 spines, one of which is terminal and without subterminal seta. Parameres and lateral lobe simple.

Female: Cibarium with 6-12 horizontal teeth and 2-8 rows of vertical teeth; pigment patch defined and cibarial arch complete. Spermathecae segmented with 5-20 well defined annulations and head voluminous. Common duct long, short, or absent.

10. Lutzomyia anduzei (Rozeboom)

Phlebotomus anduzei Rozeboom, 1942: 91 (♀, Venezuela).

Lutzomyia anduzei: Ward, 1976: 228 (larva, descr., Keyed). Ward & Fraiha 1977: 315 (♀, redescr.). Arias & de Freitas, 1977: 512 (biting records).

Bolivar: Gran Sabana (Rozeboom, 1942. Bol. Entomol. Venez. 1: 91)

The description of L. umbratilis Ward & Fraiha, 1977, a closely related species to L. anduzei, and the re-examination of the early literature, led these Authors to the conclusion that all previous references to L. anduzei were actually congruous with L. umbratilis. Therefore at the present, the geographical distribution of L. anduzei is assumed to be limited only to Venezuela and Brazil (Amazonas) where it was caught biting man and horse.

The male of this species is still undescribed. The precise locality where the female described by Rozeboom was collected was not reported.

11. Lutzomyia antunesi (Coutinho)

Phlebotomus antunesi Coutinho, 1939: 181 (♂, Amazonas, Brazil). Barretto 1950: 108 (Keyed): Floch & Abonnenc, 1952: 36 (♂, Keyed), 99 (♀, descr.). Pifano et al. 1962a : 385 (♂, Keyed) Llanos 1964a : 372 (♂, descr., Peru). Wijers & Linger, 1966 (biting man, Surinam).

Phlebotomus intermedius var. acutus Floch & Abonnenc 1942: 3

Phlebotomus balourouensis Floch & Abonnenc, 1944a: 1

Phlebotomus machicoensis Floch & Abonnenc, 1944a: 8

Lutzomyia antunesi Aitken et al., 1968: 264 (biting man, Trinidad). Lewis et al., 1970: 215 (parous rates). Shaw et al., 1972: 720 (biting man, Brazil). Llanos, 1973: 33 (♂, redescr., Peru). Ward & Ready, 1975: 128 (egg). Lewis 1975a:500 (mouth parts).

Ward, 1976: 227 (larva, descr., Keyed). Zimmerman et al., 1977; 575 (egg cf. to ylephiletor). Martins et al., 1978: 97 (refs, distr.), Young, 1979: 150 (♂, ♀ Keyed) 151 (full refs, distr.).

Apure: Guaratico, Guaramaco, Santa Lucia, P.to Paez, San Carlos, del Meta, Chiricoca, La Blanquita, Sarare Abajo, Los Morichales, Santa Elena, Payara, Montaña La Puerta, Los Mangones, Guayabital, (Present work).

Cojedes: Las Rosas, (Aguilar, 1981, Thesis U.C., 132pp), Mapurite (Present work).

Portuguesa: Guanare (Pifano et al. 1962. Arch. Venez. Med. Trop. Parasit. Méd. 4 (2): 1)

Territorio Federal Amazonas: Atabapo (Ramirez Perez et al 1976. Rev. Brasil, Biol. 36 (3): 599).

Trujillo: El Rincón, La Placita, (present work).

This species, which has been collected in Venezuela in armadillo burrows and tree holes, has been reported biting man in Brazil and Trinidad. Young therefore suggests that "it should not be ruled out as a potential vector".

12. Lutzomyia flaviscutellata (Mangabeira)

Phlebotomus apicalis: Floch & Abonnenc, 1943: 25 (♂, ♀ , French Guyana). Barreto, 1946b:534 (as synonym of flaviscutellata).

Lutzomyia flaviscutellata: Fairchild & Theodor 1971: 153 (♂, ♀ , redescr., refs, distr). Shaw & Lainson 1972: 709 (ecology, Brazil). Shaw et al., 1972: 718 (feeding habits) Forattini, 1973: 428 (♂, ♀ , biology; distr.). Pifano et al., 1973: 145 (biting man, nat. infection with promastigotes, Venezuela). Ward et al., 1973: (collecting data). Ward & Ready, 1975: 128 (egg, descr.). Lewis,

1975a: 501 (mouth parts). Lewis, 1975b: 363 (taxonomy, distr.). Tikasingh, 1975: 228 (pop. dynamics, infection with Leishmania, Trinidad). Ward, 1976: 227 (immatures., descr. larvae Keyed). Llanos et al., 1976: 480 (Peru). Arias & de Freitas, 1977: 517 (biting records). Ward, 1977b:469 (rearing); Ward et al., 1977: 265 (bite transmission of Leishmania mexicana amazonensis to hamsters). Martins et al, 1978: 98 (refs, distr.). Young, 1979: 150 (♂, ♀ Keyed), 153 (refs., distr.).

Aragua: La Trilla, Aponte, (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Territorio Federal Amazonas: Nyiayobateri (Sierra Parima) (Pifano et al., 1973: Arch Venez. Med. Trop. Parasit. Med. 5 (2): 145)

L . flaviscutellata was caught in Southern Venezuela biting man (Pifano et al., 1973). Maceration of the gut of females in saline solution showed the presence of promastigotes which, when inoculated intradermally in hamsters, produced a lesion containing amastigotes indistinguishable from those of Le. mexicana pifanoi. The possible identity of this parasite with Le. mexicana amazonensis has been advanced by Lainson & Shaw (1973). The role of Lu. flaviscutellata as a vector of the latter parasite to man has been demonstrated by Ward et al., 1977).

The present known distribution of this sandfly in Northern Venezuela (Ramirez Perez et al., loc.cit.) has been put in doubt by the discovery of L . olmeca bicolor in the same area (c.f. L . olmeca bicolor, page 112).

13. Lutzomyia hernandezi (Ortiz)

Phlebotomus hernandezi: Ortiz, 1965b:412 (♂, Venezuela)

Psychodopygus hernandezi: Forattini, 1973: (♂, review)

Lutzomyia hernandezi: Martins et al, 1978: 99 (refs, distr.).
Ramirez Perez et al. 1979: 259 (♀ descr., ♂ redescr.).

Trujillo: Panamerican Highway near Caja Seca (Ortiz, 1965. Arch. Venez. Med. Trop. Parasit. Méd. 5 (1): 411). Agua Clara (Present work).

Tachira: Caño Amarillo (Ramirez Perez et al.,1979. Rev. Brasil. Biol. 39: 259).

L. hernandezi was collected amongst aerial roots in a tree hole. The known geographical distribution of this species is at present restricted to Venezuela.

14. Lutzomyia olmeca bicolor: Fairchild & Theodor.

Lutzomyia olmeca bicolor: Fairchild & Theodor, 1971: 157 (♂, ♀ Canal Zone, Colombia). Christensen & Fairchild, 1971: 302 (Panama) Chaniotis et al., 1971a : 344 (pop. dynamics, Panama). Chaniotis et al.1971b: 415 (man-biting activity). Christensen et al., 1972: 55 (collecting data, Panama). Chaniotis et al., 1972: 95 (resting sites). Chaniotis 1974 : 501 (Keyed) Lewis, 1975b: 363 (taxonomy). Rutledge & Ellenwood 1975a:73 (ecology: breeding sites). Herrer & Christensen, 1976: 62 (collecting data). Ward, 1976: 238 (larva Keyed, cf. to flaviscutellata). Martins et al., 1978: 101 (refs, distr.). Young, 1979: 150 (♂, ♀ Keyed), 155 (refs., distr.). Christensen & Herrer, 1980a: 522 (host attraction).

Phlebotomus apicalis: (not apicalis of Floch & Abonnenc, 1943). Johnson & Hertig, 1961: 765 (rearing). Thatcher, 1968a:295 (Panama); Hanson, 1968: 46 (larva, pupa, descr.).

Lutzomyia flaviscutellata: (not flaviscutellata of Mangabeira, 1942a): Tesh et al., 1971: 153 (blood meals).

Psychodopygus olmecus: Forattini 1973: 89 (gen. review)

Carabobo: San Esteban (Present work)

Cojedes: Las Rosas (originally recorded as L. flaviscutellata)

(Aguilar, 1981: Thesis U.C. 132pp).

This species was found in Venezuela from material which had been misidentified as L. flaviscutellata. There has been no opportunity in the present work to examine specimens from other localities. In view of the close relationship of these two species, the identity of L. flaviscutellata from previous work perhaps needs to be confirmed.

One female of L. olmeca bicolor from Las Rosas (10 Oct. 1978), collected under litter in a peridomestic area was infested by a mite, which was examined and identified by Mr. D. Macfarlane (British Museum, NH) as Suidasia medanensis of the family Acaridae.

Sub-genus Pintomyia Lima, 1932: 44

Antennal ascoids with short posterior spurs. 5th palpal segment longer than 3 + 4. Hind femure with a longitudinal row of 3-8 short spines.

Male: Basistyle with a basal tuft composed of hair-like setae. Dististyle with 4 spines, one of which is terminal and with a subterminal seta. Parameres and lateral lobes simple, unarmed.

Female: Cibarium with 4 horizontal teeth and 2 or 3 rows of vertical teeth. Cibarial arch complete. Spermathecae without defined head, show thin walled cylindrical capsules and short sclerotized ducts. Intracellular ducts open in the distal part of the body.

15. Lutzomyia fischeri (Pinto)

Phlebotomus fischeri Pinto 1926: 373 (♂, Brazil). Theodor, 1932: 22 (♀). Coutinho & Barretto, 1941: 423 (bionomics). Barretto,

1941b:385 (larva, pupa, egg). Llanos, 1973: 33 (♀, redescr., Peru). Forattini, 1973: 500 (gen. review).Martins et al, 1978: 27 (refs.distr.).

Phlebotomus gibsoni: Pifano & Ortiz, 1972: 29

Territorio Feder. Amazonas: Niyayobateri (Sierra Parima) (Pifano & Ortiz, 1972. Rev. Inst. Nac. de Higiene. 5 (1): 29.

This species, collected in Venezuela (at 800 m from a tree hole), in Peru and Brazil was found to be highly anthropophilic and was collected inside houses.

Sub-genus Pressatia Mangabeira, 1942: 131

Antennal ascoids simple or with very short posterior spurs. 5th palpal segment longer than 3 + 4, sometimes than 2 + 3 + 4.

Male: Basistyle with a basal tuft which consists of two or three parts: one of two dorsal lobes with fine hairs and a ventral tubercle bearing leaf-like setae. Many species also show a group of hairs near the distal end of basistyle. Parameres with a dorsal and/or ventral process. Lateral lobes long, tapering and upwardly curved.

Female: Cibarium with 4 horizontal teeth and 2 groups of small lateral teeth. Cibarial arch complete. Spermathecae with a small "head" and the body like a cylindrical capsule with delicate thin walls. Individual ducts, short and chitinized, open in a wide, membranous common duct.

16. Lutzomyia dysponeta (Fairchild & Hertig)

Phlebotomus dysponetus: Fairchild & Hertig, 1952: 505 (♂, ♀ Panama). Hanson, 1961: 320 (breeding sites). Marmol León, 1968:29(♂, redescr.). Hanson, 1968: 42 (larva, Keyed), 56 (breeding sites).

Phlebotomus triacanthus: Rodriguez, 1950: 6 (not triacanthus of Mangabeira 1942).

Lutzomyia dysponeta: Thatcher, 1968b:1142 (breeding sites). Chaniotis

et al., 1971a: 344 (pop. dynamics, Panama); Christensen & Fairchild, 1971: 302 (Panama). Chaniotis et al., 1972 (resting sites). Christensen, 1972a: 88 (listed). Christensen et al., 1972: 57 (collecting data); Christensen & Herrer, 1973: 579 (collecting data). Lewis, 1975a: 502 (mouth parts). Rutledge et al., 1975a: 71 (ecology: species complement). Rutledge et al., 1975c: 83 (ecology: phytologic and edaphic relations). Rutledge et al., 1975d: 179 (ecology: light trap). Martins et al., 1978: 55 (refs., distr.). Young, 1979: 96 (♂, Keyed) 98 (refs., distr.). Christensen & Herrer, 1980a:522 (host attraction).

Pressatia dysponeta: Forattini, 1971: 106 (listed). Forattini, 1973: 515 (gen. review).

Zulia: Zipayare (Marmol León, P. 1968. Kasmera, 3 (1): 61)

In a review of this species, Young (loc.cit.) summarizes available knowledge of this species. Young points out that immature stages of this species have not been described but Hanson (1968) states that the larva is indistinguishable from that of L. camposi.

17. Lutzomyia triacanthus (Mangabeira)

Flebotomus triacanthus: Mangabeira, 1942a: 119 (♂, Brazil). Mangabeira, 1942c: 242 (♀, immatures). Floch & Abonnenc, 1952: 14 (Keyed). Pifano et al., 1962a: 1 ♂, Keyed).

Pressatia triacantha: Forattini, 1973: 520 (gen. review).

Lutzomyia triacantha: Lewis, 1975a: 502 (mouth parts). Martins et al., 1978: 56 (refs, distr.). Young, 1979: 96 (♂, Keyed), 100 (refs., distr.).

Portuguesa: N-E of Guanare (Pifano et al., 1962. Archs Venez. Med. Trop. Parasit. Méd. 4 (2): 419.

The precise place of collection of this species in Venezuela is not

well defined because it was caught with many other species from tree holes and/or resting places of animals.

18. Lutzomyia sp. of Chiricoca (♂, Venezuela, present work).

Apure: Chiricoca (present work)

Sub-genus Psychodopygus Mangabeira, 1941: 231

Antennal ascoids simple. 5th palpal segment shorter than 3rd and 4th.

Male: Basistyle without tuft. Dististyle with 1 large terminal spine and 3 small spines near it. Parameres simple or very complex with 3 large and 1 small seta (series squamiventris), or with thick tuft of setae and 2-4 large setae (series panamensis), or simple (series arthuri).

Female: Cibarium with 4-8 horizontal teeth and several rows of vertical teeth. Cibarial arch present. Spermathecae imbricated , that is with segments telescoped into each other.

Series squamiventris

19. Lutzomyia squamiventris (Lutz & Neiva)

Phlebotomus squamiventris:Lutz & Neiva, 1912: 89 (♀, ♂ Brazil)

Phlebotomus squamiventris: Lutz & Neiva, 1912: 94 (♀, ♂)

Flebotomus (Psychodopygus) complexus Mangabeira, 1941: 36 (♂)

Psychodopygus complexus: Forattini, 1971: 105. Forattini, 1973: 407 (♂, gen. review). Ward & Ready, 1975: 50 : 128 (egg).

Lutzomyia squamiventris: Martins, Maciel & Silva, 1968: 10 (♀). Martins, 1978: 37 (refs., distr.).

Aragua: Maracay (Nuñez-Tovar, M. 1924. Mosq. y Flebotomos de Venezuela. 44pp).

Bolivar: Gran Sabana (Pifano & Ortiz 1952. Rev. San. Asist. Soc. 17 (1-2): 137).

Series panamensis

20. Lutzomyia panamensis (Shannon)

Phlebotomus panamensis: Shannon, 1926: 192 (♂, ♀ Panama). Fairchild & Hertig, 1951 : 399 (♂, ♀ descr.). Pifano et al. 1959: 229 (vector of dermal leishmaniases in Venezuela). Johnson & Hertig, 1961: 764 (rearing). Pifano et al., 1962a : 369 (♂, ♀ redescr. Keyed). Ortiz, 1972b: 22 . (Keyed). Hanson, 1968: 65 (larva, pupa, Keyed).

Phlebotomus squamiventris: Costa Lima, 1932: 25

Phlebotomus davisi: Pifano, 1943: 100. Ortiz, 1947: 521.

Psychodopygus panamensis: Forattini, 1973: 89 (gen review); Ward, 1976: 239 (larva, Keyed).

Lutzomyia panamensis: Barretto,1966: 142 (Keyed) Christensen et al., 1969: 1090 (infection with Leishmania braziliensis). Chaniotis et al., 1971a: 339 (population dynamics). Tesh et al., 1972: 90 (blood meals). Chaniotis & Correa, 1974; 115 (biting habits). Chaniotis 1974: 501 (Keyed). Lewis, 1975a: 502 (mouth parts). Rutledge & Ellenwood, 1975: 72 (breeding sites). Rutledge et al., 1975d: 179 (ecology). Martins et al., 1978: 43 (refs., distr.). Young, 1979: 168-169 (♂, ♀ Keyed), 190 (refs., distr.). Christensen & Herrer, 1980a: 522 (host attraction). Porter & DeFoliart, 1981: 81 (ecology).

Apure: Santa Lucia, Montaña La Puerta (Present work).

Aragua: Choroni (Albornoz et al. 1968. Dermat. Venez. 7 (3-4): 659) Ocumare de la Costa (Pifano & Ortiz, 1952. Rev. San. Asist. Soc. 17 (1-2): 137), San Mateo (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti, Año XII, 16: 487; Loro Arriba, Las Marias, Periquito, La Trilla, Aponte, Puerto Colombia, El Paraparo, (Ramirez Perez et al, 1978. Bol. Dir. Malariol. 18 (1): 43).

Barinas: (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti Año XII, 16: 487).

Bolivar: Gran Sabana (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti. Año XII, 16: 487).

Carabobo: Alpargaton, (Pifano & Ortiz, 1952. Rev. San. Asist. Soc.

17 (1-2): 137), San Esteban (Present work).

Cojedes: Las Rosas (Aguilar, 1981. Thesis U.C., 132pp), Tierra Caliente (Present work).

Falcón: Mene de Mauroa (Ortiz, I. 1942. Bol. Lab. Clin. Luis Razetti. Año III, 2(9): 162).

Guarico: Altagracia de Orituco (Mirsa, A. 1954. Rev. San. Asist. Soc., 19: 189)

Lara: Barquisimeto (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti. Año XII, 16: 487)

Miranda: Guatopo (Pifano et al. 1962a Arch. Venez. Med. Trop. Parasit. Méd., 4: 369), Ocumare del Tuy (Ortiz, I. 1950. Arch. Venez. Med. Trop. Parasit. Med., 2: 83).

Nueva Esparta: Isla de Margarita:Guayacán (Pifano & Morrell, 1973 Arch. Venez. Med. Trop. Parasit. Méd. 5(2): 129).

Portuguesa: Guanare (Pifano et al 1962. Arch. Venez. Med. Trop. Parasit. Méd., 4(2): 1)

Sucre: Cumanacoa (Martins et al., 1978. American Sandflies: 44).

Trujillo: (Mogollón et al 1977. Bol. Dir. Malariol. y San. Amb. 17 (3): 206).

Yaracuy: San Felipe (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti, Año XII, 16: 487), Valle de Aroa (Pifano, F. 1962. Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 25).

Zulia: Zipayare (Marmol León, P. 1968. Kasmera 3 (1): 61)

In an endemic area of tegumentary leishmaniasis (Yaracuy State), Pifano (1941) found L. panamensis infected with flagellates similar to culture forms of "Le. braziliensis." Later Pifano et al. (1959) observed the natural transmission of this parasite by means of L. panamensis to a member of a team who was carrying out studies in another endemic area

(Guatopo). The patient had typical leishmanial lesions on the limbs, with abundant parasites. On another occasion, promastigotes were found in the anterior gut of female L . panamensis at the same time as an outbreak of leishmaniasis was registered in the population.

Scorza et al., (1968d) reported that L . panamensis is optionally anthropophilic and has long flight; it enters dwellings attracted by light (positive phototropism). Pifano collected this species biting man, attracted by a Coleman lamp and caught one male in a hole of a crab. All Authors agree that it is a wild, peri-sylvatic and peri-domestic sandfly. From the point of view of altitudinal distribution, Mogollón et al. (1977) noticed that L . panamensis is found only in areas of low altitude and high temperature.

Ungrouped

21 Lutzomyia parimaensis (Ortiz & Alvarez)

Phlebotomus parimaensis Ortiz & Alvarez, 1972: 139 (♀). Martins et al. 1978: 169 (inadequately described species).

Territorio Federal Amazonas: Nyayobateri (Sierra Parima) (Ortiz & Alvarez, 1972. Rev. Inst. Nac. de Higiene. 5 (2-3): 139)

This peri-sylvatic species was collected in a tree-hole. It is positively phototropic and is anthropophilic, attacking man in the hours of the evening.

Sub-genus Trichophoromyia Barretto, 1962: 91.

Antennal ascoids simple. 5th palpal segment subequal to 3rd, always shorter than 3 + 4.

Male: Basistyle with one or two groups of spine-like or hair-like setae. Dististyle with 4 spines, one of which is terminal and without sub-terminal seta. Parameres simple or complex. Lateral lobes simple.

Female: Cibarium with 8-14 horizontal teeth and vertical teeth; pigment patch and cibarial arch complete. Spermathecae segmented with a well developed "head", individual ducts long, common duct long, short or absent.

22. Lutzomyia ubiquitalis (Mangabeira)

Flebotomus ubiquitalis: Mangabeira, 1942a:158 (♂, Brazil).

Phlebotomus basispinosus: Barretto & Coutinho, 1943: 185 (♂)

Phlebotomus cauchensis: Floch & Abonnenc 1943: 22 (♂); 1944: 5, 17 (♀).

Psychodopygus (Trichophoromyia) ubiquitalis Forattini, 1973: 481: (♂, ♀).

Lutzomyia ubiquitalis: Martins et al. 1978: 87 (refs., distr.).

Territorio Federal Amazonas: Atabapo (Ocamo) (Ramirez Perez et al., 1976. Rev. Brasil. Biol. 36 (3): 599).

This species was collected in an armadillo burrow.

Baityi Group Theodor, 1965: 194.

Antennal ascoids simple. 5th palpal segment longer than 3rd and than 4th.

Male: Basistyle with a basal tubercle bearing long setae or short spines, and with a group of 4-8 strong straight setae on the distal part. Dististyle with 4 short, stubby spines, two of which are terminal. Parameres simple, broad. Lateral lobes simple.

Female: Cibarium with 4 horizontal teeth and numerous small vertical teeth. Spermathecae exceedingly small, sausage-shaped with a short individual duct and no discernable common duct.

23. Lutzomyia baityi (Damasceno, Causey & Arouck)

Flebotomus baityi, Damasceno, Causey & Arouck, 1945: 22 (♂).

Phlebotomus baityi: Pifano et al., 1962a:386 (♂, Keyed). Marmol

León, 1968: 31 (♂, redescr.).

Lutzomyia baityi: Forattini, 1973: 274 (gen. review). Martins et al., 1978: 158 (refs., distr.). Young, 1979: 102 (refs, distr.).

Zulia: Zipayare (Marmol León, P. 1968. Kasmera, 3(1): 61).

The specimen found in Venezuela was collected in a tree hole. Ortiz (1968a)associated this species with armadillos and bats.

Cayennensis group Theodor 1965: 186.

Antennal ascoids simple. 5th palpal segment longer than 2 + 3.

Male: Basistyle without basal tuft (series cayennensis and chiapanensis) or with tuft (series atroclavata). Dististyle with 4 spines (series cayennensis and atroclavata) or 5 spines (series chiapanensis), two of which are terminal; subterminal seta absent. Parameres and lateral lobes simple.

Female: Cibarium with 4 to over 30 longitudinal teeth in a comb-like arrangement, many, few or no vertical teeth. Pharynx spinose at posterior end. Spermathecae pear-shaped, segmented at the base, with a globose apical segment.

Series cayennensis

24. Lutzomyia cayennensis (Floch & Abonnenc)

Phlebotomus cayennensis: Floch & Abonnenc, 1941a:14 (♂, French Guyana); 1948a : 1 (♀) Fairchild & Hertig 1948a: 460 (♂, ♀ redescr.). Floch & Abonnenc, 1952: 37, 46 (♂, ♀ Keyed), 138-142 (♂, ♀ redescr.). Pifano & Ortiz, 1952: 143, 148 (♂, ♀ Keyed). Rosabal, 1954: 10 (♂, redescr.). Johnson & Hertig, 1961: 773 (rearing). Pifano et al., 1962a:385, 388 (♂, ♀ Keyed), 400-401 (♂, ♀ redescr.). Ortiz, 1965a:205 (♀, Keyed). Hanson, 1968: 53-55 (larva, pupa, descr.).

Lutzomyia cayennensis: Lewis, 1967a:76 (class, ♀ Keyed). Christensen

et al., 1972: 57 (collecting data). Forattini, 1973: 122 (gen review). Lewis, 1975a: 502 (mouth parts). Martins et al., 1978: 60 (refs., distr.). Young, 1979: 213 (♂, ♀ Keyed, refs., distr.).

Apure: Guaramaco, Mata de Silva, Hato la Tigrera (Present work)

Aragua: Choroní (Albornoz et al., 1968. Dermat. Venez. 7(3-4): 659; Quebrada Apamate, Los Conucos, La Sureña, El Ingenio, Augustia, El Guayabito, Polanco, Los Mamires, Diana, Paso de los Indios, Quebrada, Honda, El Cedral, Tucutunemo, Corocito, Quebrada Guayabo, Macuaya, La Pavona, Agua de Maiz, Tucupido , Rio Arriba, Hacienda Punta Larga, Paya, Rancho Grande, (Ramirez Perez et al. 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Carabobo: Pueblo Nuero, Las Animas, El Cambur; Las Colonias, San Esteban, (Present work).

Cojedes: San Rosas (Aguilar, 1981. Thesis U.C. 132pp).

Charcote: Boca de Cerro, La Váquira (Present work).

Distrito Federal: Caraballeda (Pifano & Ortiz, 1952. Rev. San Asist. Soc. 17 (1-2): 137).

Falcón: Hombre Pintado, Mene de Mauroa (Pifano & Ortiz 1952. Rev. San. Asist. Soc. 17 (1-2): 137.

Guarico: Altagracia de Orituco (Mirsa, D. 1954. Rev. San. Asist. Soc. 19: 189).

Miranda: Guatopo (Pifano et al., 1962a. Arch. Venez. Med. Trop. Parasit. Méd. 4 (2): 369), Los Chorros (Mirsa, M. 1954. Rev. San. Asist. Soc. 19 (1-2): 139).

Portuguesa: Guanare (Pifano et al. 1962. Arch. Venez. Méd. Trop. Parasit. Méd. (2): 1)

Sucre: Cumanacoa (Pifano & Romero. 1964. Gaceta Méd. Caracas 72 (7-12): 473).

Yaracuy: San Felipe (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti. Año XII, 16 (3-4): 487.

Zulia: Bachaquero, Rio Negro (Floch & Abonnenc, 1948a,Publ. No. 166), Zipayare (Marmol León, P. 1968. Kasmera, 3(1): 61).

L. cayennensis is a species with a wide geographical distribution and high prevalence (Ortiz, 1968a). It has been collected from holes of trees and resting places of animals.

25. Lutzomyia micropyga (Mangabeira)

Flebotomus micropygus: Mangabeira, 1942a:132 (♂, ♀, Brazil).

Phlebotomus micropygus: Pifano et al., 1962a:385 (♂ Keyed), 402-403 (♂, ♀ , descr.). Ortiz & Scorza, 1963: 342 (collecting data, Venezuela). Ortiz, 1965a:209 (♀ Keyed). Scorza et al., 1967: 190 (dist., ♂ , ♀ Keyed). Lucena, 1967: 274 (♂ redescr.).

Lutzomyia micropyga: Thatcher, 1968b:1142 (breeding sites, Panama) Tesh et al., 1971: 153 (blood meal). Chaniotis et al., 1971a: 344 (pop. dynamics). Chaniotis et al., 1972: 95 (resting places). Forattini, 1973: 310 (gen. review). Llanos, 1973: 34 (♂, ♀ redescr.). Llanos et al., 1976: 480 (♀ , redescr.). Martins et al., 1978: 63 (refs., distr.). Young, 1979: 213 (♂, ♀ Keyed), 215 (refs, distr.).

Apure: Chiricoca, Los Morichales, Sarare Abajo, (Present work).

Aragua: Rancho Grande (Scorza & Ortiz, 1960. Ztschr. Tropenmed. Parasitol., 11: 433; Rio Cura, Monte Oscuro, La Barquera, Taguarigua, Las Adjuntas, El Negrito, Polanco, Boca de Onoto, El Altar, Zuata, Paso del Medio, La Majada, Tucutunemo, Rio Arriba, Casupito, Quebrada Jabillar, La Concepción, El Tigre, Quebrada Apa, La Trilla, Bahia de Cata, El Paraparo, (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18(1): 43).

Carabobo: Los Cocos, Carabobo, (Present work).

Cojedes: Las Rosas (Aguilar, 1981. Thesis U.C., 132pp); Charcote, Hacienda Vieja, La Morita, Zambrano, Boca de Cerro, (Present work).

Miranda: Guatopo (Pifano et al. 1962a) Arch. Venez. Med. Trop. Parasit. Méd. 4 (2): 369).

Zulia: Zipayare (Marmol León P. 1968. Kasmera, 3(1): 61.

L. micropyga has been associated with rodents and small reptiles and it is usually found in tree holes.

26. Lutzomyia yencanensis (Ortiz).

Phlebotomus yencanensis (Ortiz, 1965a:205 (♂,♀).

Aragua: Rancho Grande (Ortiz, I. 1965a:Acta Biol. Venez. 4 (7): 205).

L. yencanensis generally lives in tree holes (Ficus macrosyce, Chimarrhis microcarpa) it has[a] very short flight and is saurophilic.

Series atroclavata

27. Lutzomyia atroclavata (Knab)

Phlebotomus atroclavatus Knab, 1913: 135 (♂, ♀, Trinidad). Dampf, 1947a:296 (♂, redescr.). Fairchild & Hertig, 1948b:455 (♂, ♀ redescr.). Fairchild & Trapido, 1950: 405, 409 (♂, ♀ Keyed). Floch & Abonnenc, 1952: 34, 47 (♂, ♀ Keyed), 107 (♂, ♀ redescr.). Scorza & Ortiz, 1960: 434 (biology). Pifano et al., 1962a:387, 389 (♂, ♀ Keyed), 398 (♂, ♀ redescr.). Fauran et al., 1966: 904 (♂, redescr.).

Phlebotomus tejerae Larrousse, 1922: 71, 73 (♂, ♀ Venezuela) Dyar, 1929: 120 (as synonym of L. atroclavatus).

Phlebotomus guadeloupensis: Floch & Abonnenc, 1945: Dampf, 1947a: 302 (as synonym of atroclavatus). Courmes et al., 1966: 217 (as possible vector of kala-azar in Guadeloupe).

Lutzomyia atroclavata: Theodor, 1965: 195 (♀). Forattini, 1973:

281 (gen. review). Martins et al., 1978: 129 (refs. distr.). Young, 1979: 212, 213 (♂,♀ Keyed), 218 refs., distr.).

Aragua: Choroní (Albornoz et al. 1968. Dermat. Venez. 7 (3-4): 659, Rancho Grande (Scorza & Ortiz. 1961. Bol. Venez. Lab. Clin. 5-6: 23; La Sureña, Los Conucos, Quebrada Apamate, Los Dos Montes, El Guayabito, Angustia, Rio Cura, El Ingenio, El Loro Arriba, Guiripa, Golfo Triste, San Pedro, Vallecito, Los Algarrobos, Taguarigua, El Bejucal, Tierra Negra, Las Quebraditas, Diana, Bocade Onoto, Palambra, Paso del Medio, Quebrada Dos Hermanas, El Guanabano, Guanasnal, El Nicual, El Valle, Zuata, Los Vargas, Paso de los Indios, Quebrada Honda, Piedras Pintadas, El Onoto, Las Tunas, Los Bagres, El Chino, Quebrada Caney, Corral Viejo, El Cedral, Quebrada Guayabo, Tucutunemo, Mata de Cafe, El Ancon, Malpica, Corocito, El Saman, Macuaya, Chaguaramos, Caicara, La Majada, El Ocumo, Agua de Maiz, La Pavona, Rio Arriba, Sabana Grande, Hacienda Punta Larga, Pedregal, Paya, Polvorin, Las Vegas, Rio Tuy, Quebrada Seca, Paso de Tapiche, La Luisa, El Ingenio, Santa Rosa, Tiara, Boca de Cagua, San Francisco, Pao Zarate, Curiepe, Quebrada Jabillar, Cañadote, Santo Domingo, Los Blancos, Pozo Azul, La Gavilana, La Concepción, Quebrada Apa, El Tigre, El Guayabo, Quebrada Calanche, La Ceiba, Pie del Cerro, Ingenio Bolivar, La Curia, Casupito, Corocito, Puerto Colombia, El Paraparo, (Ramirez Perez et al. 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Carabobo: Las Animas; El Cambur, San Esteban, Guache, Yuma, Las Colonias, Agua Linda, El Naipe, Carabobo (Present work).

Cojedes: Charcote, Tierra Caliente, Potrero Largo, Hacienda Vieja, (Present work).

Falcón: Mene de Mauroa, (Ortiz, I. 1944. Bol. Lab. Clin. Luis

Razetti, Año V, 14: 247).

Lara: (Scorza et al., 1967: Acta Biol. Venez. 5: 179)

Miranda: Guatopo, (Pifano et al. 1962a. Arch. Venez. Med. Trop Parasit. Méd. 4: 369) Valles del Tuy (Pifano et al. 1962c. Arch. Venez. Med. Trop. Parasit. Méd. 4: 149).

Nueva Esparta: Isla Margarita: Las Piedras (Pifano & Romero, 1964. Gac. Méd. Caracas: 72: 425).

Portuguesa: Guanare (Martins et al. 1978. In press).

Sucre: Cumanacoa (Pifano & Romero, 1964. Gac. Méd. Caracas 72: 473).

Trujillo: Panamerican Highway near Caja Seca (Ortiz, I. 1965. Arch. Venez. Med. Trop. Parasit. Med. 5(1): 411); Rio Monosnoy (Present work).

Zulia: Altagracia; Bachaquero, Mene Grande, Rio Negro, (Pifano & Ortiz,1952. Rev. San Asist. Soc. 17 (1-2): 137), Zipayare (Marmol Leon, P. 1968. Kasmera 3(1): 61).

Yaracuy: San Felipe (Pifano, F. 1943. Bol. ent. Venez. 2(2): 99).

Although Ortiz (1968a) associated L. atroclavata with rodents and small reptiles, this species has been collected by Pifano et al. (1962c) biting man,to whom it was attracted by light. This sandfly has a wide geographical distribution and high prevalence.

28. Lutzomyia venezuelensis (Floch & Abonnenc)

Phlebotomus venezuelensis Floch & Abonnenc, 1948b : 1 (♂, Venezuela).

Scorza & Ortiz, 1960: 434 (ecology). Pifano et al., 1962a: 387, 389 (♂, ♀ Keyed), 403-404 (♂, ♀ , redescr.).

Phlebotomus zulianensis Floch & Abonnenc, 1948b: 5 (♀). Pifano & Ortiz, 1952 (♀, Keyed). Scorza & Ortiz, 1960: 434 (as probable synonym of venezuelensis). Pifano et al., 1962a: 403 (as synonym of venezuelensis).

Lutzomyia venezuelensis: Lewis, 1975a: 502 (mouth parts). Martins et al., 1978: 132 (refs., distr.). Young, 1979: 213 (♂, ♀ Keyed), 220 (refs., distr.).

Aragua: Rancho Grande (Ortiz & Scorza. 1963. Acta Biol. Venez. 3 (23): 341; Tucupido, (Ramirez Perez et al., 1978. Bol Dir. Malariol. y San. Amb. 18(1): 43).

Carabobo: Los Cocos, El Canuto (Present work)

Guarico: Altagracia de Orituco (Floch & Abonnenc, 1948. Publ. No. 178).

Lara: Duaca (Pifano & Ortiz, 1952. Rev. San Asist. Soc. 17 (1-12): 137.

Miranda: Guatopo (Pifano et al. 1962a. Arch Venez. Med. Trop. Parasit. Méd. 4 (2): 369).

Portuguesa: Biscucuy Road (Ortiz & Alvarez, 1963).

Zulia: Bachaquero, Rio Negro, Selva de Tamanaco (Floch & Abonnenc, 1948. Publ. No. 178).

L. venezuelensis has been collected among stones and holes of trees. It has a wide geographical distribution in Venezuela and bites

rodents and small reptiles (Ortiz, 1968a).

29. Lutzomyia sp. of La Váquira (♀, Venezuela, present work)

Cojedes: La Váquira.

This species has been found in Venezuela from tree-holes associated with L. longipalpis, L. cayennensis and L. rangeliana

Longispina Group Theodor 1965: 189

Antennal ascoids simple. 5th palpal segment longer, over 1.5 times the length of the 3rd.

Male: Basistyle without basal tuft, but sometimes with a row of long ventral hairs. Dististyle long with 4 large spines and a small sub-terminal seta. Basal spine isolated and terminal spine standing on a long process. Parameres divided into 2 or 3 parts. Lateral lobes simple.

Female: Cibarium with 4 horizontal teeth. Cibarial arch incomplete. Spermathecae pear-shaped with a terminal knob.

30. Lutzomyia longispina (Mangabeira)

Flebotomus longispinus (Mangabeira 1942a:186 (♂, Brazil).

Mangabeira 1942d:251 (♀, larva, egg, descr.).

Phlebotomus longispinus: Floch & Abonnenc, 1952: 33, 48 (♂, ♀ Keyed).

Pifano et al., 1962a:385, 389 (♂, ♀ Keyed). Hanson, 1968: 88 (larva, cf. to triramulus).

Lutzomyia longispina: Forattini, 1973: 172 (gen. review). Lewis 1975a: 502 (mouth parts). Martins et al., 1978: 114 (refs., distr.). Young, 1979: 121 (♂, ♀ Keyed, refs., distr.).

Bolivar: Gran Sabana (Pifano & Ortiz, 1952. Rev. San. Asist. Soc. 17 (1-2): 137).

31. Lutzomyia conviti Ramirez Perez, Martins & Ramirez

Lutzomyia conviti Ramirez Perez, Martins & Ramirez, 1976: 599 (♂, ♀, Venezuela).

Territorio Federal Amazonas: Atabapo (Ramirez Perez et al. 1976. Rev. Brasil. Biol. 36 (3): 599)

This species was collected in an armadillo burrow.

Migonei Group Theodor 1965: 182.

Antennal ascoids simple. 5th palpal segment longer, over 1.5 times the length of the 3rd.

Male: Basistyle with basal tuft of setae. Dististyle with 4 spines and a small subterminal seta. Parameres simple or with modified setae. Lateral lobes simple.

Female: Cibarium with 4 horizontal teeth. Cibarial arch incomplete. Spermathecae are either narrow tubes or smaller or longer round or elliptical capsules.

Series migonei

32. Lutzomyia migonei (França)

Phlebotomus migonei França, 1920: 230 (♂, Paraguay). Theodor, 1932: 19 (♂, ♀) Barretto, 1941b:380 (egg, larva, pupa). Pifano et al., 1962a:387, 388 (♂, ♀ Keyed).

Phlebotomus rangeli Nuñez-Tovar, 1924: 45 (♂, ♀).

Phlebotomus araozi Patterson & Shannon, 1926: 33 (♂,♀).

Lutzomyia migonei: Forattini, 1973: 274 (gen. review). Lewis, 1975a: 500 (mouth parts). Martins et al., 1978: 138 (refs., distr.). Young, 1979: 62 (♂, ♀ Keyed), 63 (refs., distr.).

Aragua: Choroní, Maracay, Ocumare de la Costa (Carbonell, O. 1938. Parasitologia en Venezuela y Trabajos del Doctor M. Nuñez-Tovar); Rio Cura, El Ingenio, Los Dos Montes, San Pedro, El Loro Arriba, Guiripa, Las Caobas, La Barquera, Monte Oscuro, Polanco,

Tucutunemo, El Samán, Caicara, Macuaya, El Ocumo, Quebrada Apa, El Guayabo, El Tigre, Pie del Cerro, San Miguel, Gabante, Pozo Azul (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Apure: Santa Lucia, El Carrao, (Present work).

Carabobo: Las Colonias (Present work).

Distrito Federal: Caracas (Iriarte, D. 1943, Bol. Lab. Clin. Luis Razetti, Año IV, 3: 189)

Merida: El Salado (Calderón, 1973. Acta Cientif. Venez. 24: 87).

Miranda: Los Chorros (Mirsa, M. 1954. Rev. San.Asist. Soc. 19 (1-2): 139)

Portuguesa: Guanare (Pifano et al., 1962 Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 1).

Sucre: Cumanacoa, (Pifano & Romero, 1964. Gac. Méd. Caracas 72: 473).

Trujillo: (Mogollón et al. 1977. Bol. Dir. Malariol. y San. Amb. 17 (3): 206).

L. migonei is anthropophilic (Ortiz, 1968a),but seems also to be attracted to domestic animals since Pifano collected it biting a bait horse. It is a widely distributed species in areas of low altitude and high temperature (Mogollón et al., 1977). L. migonei has been found naturally infected by promastigotes thought to be those of Le. braziliensis braziliensis in Venezuela (Pifano 1943; Pifano et al., 1954; Forattini 1959) and in Brazil (Forattini, 1973). In this second country it is considered as a suspected vector (Forattini, 1973).

Series walkeri

33. Lutzomyia dubitans (Sherlock)

Phlebotomus dubitans, Sherlock, 1962: 324 (♂, Colombia). Forattini, 1973: 292 (as synonyms of L. walkeri). Martins et al., 1978:

134 (as synonym of L. marajoensis).

Phlebotomus marajoensis (not marajoensis of Damasceno & Causey, 1944). Fairchild & Hertig, 1961: 237 (♂,♀ descr.). Pifano et al., 1962a: 386 (♂, ♀ Keyed, redescr.). Sherlock. 1962: 327 (cf. to dubitans). NEW SYNONYM.

Lutzomyia marajoensis, Barretto, 1962: 98 (listed). Martins et al., 1962: 381 (Brazil). Martins et al., 1963: 334 (Brazil). Lewis, 1967b:132 (cf. to walkeri) Forattini, 1971: 101 (listed). Osorno et al., 1972: 23 (Colombia). Christensen, 1972a:88 (listed). Forattini, 1973: 292 (as synonym of L. walkeri) Christensen & Herrer, 1973: 579 (Panama). Lewis, 1975a: 500 (mouth parts). Ramirez Perez et al., 1978: 43. Martins et al., 1978: 134 (refs., distr.). Young et al., 1979: 62 (♂, ♀ Keyed), 63 (refs., distr.) NEW SYNONYM.

Apure: Santa Lucia, Montaña La Puerta (Present work).

Aragua: Quebrada Apamate, San Pedro, Agua Fria, La Barquera, El Loro Arriba, Golfo Triste, Boca de Onoto, Quebrada Honda, El Guanabano, Piedras Pintadas, El Chino, Quelrada Guayabo, Macuaya, Caicara, La Majade, El Rincón, El Ocumo, Agua de Maiz, Hacienda Punta Larga. (= L. marajoensis) (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Carabobo: San Esteban, Los Guayos, La Glorieta, La Velén (Present work).

Cojedes: Zambrano (Present work). Las Rosas (= L. marajoensis) (Aguilar, 1981. Thesis U.C. 132pp).

Falcon: Hombre Pintado (Pifano & Ortiz. 1952. Rev. San. Asist. Soc. 17 (1-2): 137).

Miranda: Guatopo (Pifano et al., 1962a. Arch. Venez. Méd. Trop. Parasit. Med. 4(2): 369).

Portuguesa: Guanare (Pifano et al., 1962. Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 1).

Sucre: Cumanacoa (Pifano & Romero, 1964. Gac. Méd. Caracas 72 (7-12): 473).

Zulia: Zipayare (Marmol León, P. 1968. Kasmera 3(1): 61)

L. dubitans has been caught in resting places of animals. It is believed to be associated with armadillos and bats (Ortiz, 1968a).

34. Lutzomyia walkeri (Newstead)

Phlebotomus walkeri Newstead, 1914: 188 (♂, ♀ , Bolivia-Brasil) Fairchild & Hertig, 1961: 250 (cf. to marajoensis).

Phlebotomus gasti Sherlock, 1962: 326 (♂, Colombia).

Lutzomyia gasti: Theodor, 1965: 182 (listed). Lewis, 1967: 131 (listed) Forattini, 1971: 103 (listed) Christensen, 1972a: 88 (Panama). Osorno et al., 1972a:23 (Colombia). Forattini, 1973: 348 (gen. review).

Lutzomyia walkeri: Lewis, 1967b:132 (♂, ♀ redescr.). Llanos, 1973: 31 (♂, ♀ redescr.). Forattini, 1973: 274 (gen. review). Lewis, 1975a: 500 (mouth parts) Martins et al., 1978: 135 (refs., distr.). Young, 1979: 62, 63 (♂, ♀ Keyed), 67 (refs., distr.).

Apure: Guaramaco, Pto Paez, El Novillo (Present work)

Cojedes: Boca de Cerro (Present work).

Trujillo: Cumbre de la Sierra, Sabana Grande, El Volcán, El Mamón, Las Cocuizas, Rio Monosnoy (Present work).

Oswaldoi Group Theodor, 1965: 187.

Antennal ascoids simple. 5th palpal segment.

Male: Basistyle without tuft. Dististyle with 5 large spines. Parameres and lateral lobes simple.

Female: Cibarium with 4 horizontal teeth and 1-2 rows of vertical

teeth. Pharynx unarmed or with posterior spines. Spermathecae segmented with an enlarged segment or long, smooth and sausage-shaped.

35. Lutzomyia trinidadensis (Newstead)

Phlebotomus trinidadensis Newstead, 1922: 47 (♂, ♀, Trinidad). Fairchild & Hertig, 1948: 253 (♂, ♀, redescr.). Hanson, 1961: 320 (larva) Johnson & Hertig, 1961: 765 (rearing). Pifano, 1962a: 384, 388 (♂, ♀ Keyed) 407 (♂, ♀ redescr.). McConnell & Correa, 1964: 523 (naturally infected with trypanosomes, gregarines and fungi). Thatcher & Hertig, 1966: 46 (host preferences). Hanson, 1968: 84 (larva, pupa, descr.)

Phlebotomus (Neophlebotomus) cruciatus Dyar, 1929: 119.

Phlebotomus yucatanensis Galliard, 1934a:1 (♂, ♀, Mexico). Fairchild & Hertig, 1948a:255 (as synonym of trinidadensis). Mirsa, 1953: 63 (rearing).

Phlebotomus yucatanensis var. baduelensis Floch & Abonnenc, 1941a: 4 (♂, French Guyana). Fairchild & Hertig 1948a:255 (as synonym of trinidadensis).

Phlebotomus longipalpis: Ristorcelli & Van Ty, 1941: 252 (♀, Colombia) not longipalpis of Lutz & Neiva, 1912.

Phlebotomus villelai Mangabeira 1942a:196 (♂, Brazil). Barretto, 1946b:527 (as synonym of baduelensis). Fairchild & Hertig, 1948a: 255 (as synonym of trinidadensis). Dampf, 1947b: 423.

Phlebotomus baduelensis Floch & Abonnenc 1944c:1 (♂, ♀, French Guyana). Fairchild & Hertig, 1948a:255 (as synonym of trinidadensis. Floch & Abonnenc, 1952: 41, 44 (♂,♀ Keyed), 163-167 (♂, ♀ redescr.).

Lutzomyia trinidadensis: Tesh et al., 1971: 153 (blood meals). Chaniotis et al., 1971a: 344 (pop. dynamics, Panama). Chaniotis

1971: 459 (♀ gyandromorphism). Chaniotis et al., 1972: 95 (resting sites). Christensen, 1972b: 683 (rearing) Christensen et al., 1972: 57 (collecting data, infected with nonleishmanial flagellates, Panama). Forattini, 1973: 90 (gen. review). Lewis, 1975a: 502 (mouth parts). Rutledge & Ellenwood, 1975a: 71 (ecology, species complement), 1975c: 87 (breeding sites). Williams, 1976: 615 (infected with flagellates and worms). Martins et al., 1978: 73 (refs, distr.). Young 1979: 223 (♂, ♀ Keyed), 227 (refs., distr.). Scorza et al., 1979: 35 (ethology).

Apure: Guaramacaco, El Novillo, Pto Paez, Caño Regreso, San Carlos del Meta, Cajutal (Present work).

Aragua: (Albornoz et al., 1968. Dermat. Sanit. 7 (3-4): 659), Rancho Grande, (Scorza & Ortiz, 1961. Bol. Venez. Lab. Clin. 5-6: 23; Los Dos Montes, Quebrada Apamate, Los Conucos, La Sureña, Rio Cura, La Ceiba, El Ingenio, Angustia, El Guayabito, Barbacoas, Golfo Triste, Polanco, Las Marias, La Barquera, Vallecito, El Negrito, San Pedro, Monte Oscuro, Las Adjuntas, Tierra Negra, Los Algarrobos, Loro Arriba, Taguarigua, Bejucal, Las Caobas, Las Quebraditas, Boca de Onoto, Diana, Los Mamires, El Valle, Palambra, Quebrada Honda, Quebrada Dos Hermanas, Paso del Medio, Paso de los Indios, Los Vargas, Zuata, El Nicual, Guanasnal, Macuaya, Corocito, El Ocumo, Malpica, Quebrada Guayabo, El Rincon, La Majada, Caicara, Tucutunemo, El Onoto, Las Tunas, Chaguaramos, El Samán, El Ancón, La Lagunita, Los Bagres, El Cortijo, El Cedral, Corral Viejo, Quebrada Caney,

El Chino, Cataure, Semen, Piedras Pintadas, Agua de Maiz, La Pavona, Sabana Grande, Rio Arriba, Tucupido, Las Vegas, Paya, Polvorín, Pedregal, Hacienda Punta Larga, Casupito, Corocito, Rio Tuy, El Ingenio, La Luisa, Paso de Trapiche, Quebrada Seca, Quebrada Jabillar, Santa Rosa, Tiara, Boca de Cagua, San Francisco, Pao de Zarate, Santo Domingo, Cañadote, Curiepe, San Miguel, Los Blancos, Pozo Azul, La Gavilana, La Concepción, Quebrada Apa, El Molino, El Tigre, El Guayabo, Quebrada Calanche, Pie del Cerro, Ingenio Bolivar, La Curia, Aponte, La Trilla, Periquito, Bahia de Cata, Puerto Colombia, El Paraparo, (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San Amb. 18 (1): 43).

Carabobo: La Arenosa, San José, El Tigre, Pueblo Nuevo, Las Animas, El Cambur, El Naipe, Carabobo, San Esteban, Agua Linda, El Canuto, Los Cocos, Guache, Yuma, El Pueblito, S.ta Ines, Las Colonias (Present work).

Cojedes: Charcote, Tierra Caliente, Potrero Largo, Hacienda Vieja, La Morita, Las Rosas, Solano, Zambrano, Boca de Cerro, La Ceiba, Las Galeras, San Carlos (Present work)

Falcón: Mene de Mauroa (Iriarte, D. 1952. Bol. Lab. Clin. Luis Razetti Año XII 16: 487)

Lara: Duaca (Pifano & Ortiz. 1952. Rev. San. Asist. Soc. 17 (1-2): 139).

Miranda: Guatopo (Pifano et al. 1962a. Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 369).

Neuva Esparta: Isla Margarita: Las Piedras (Pifano & Romero, 1964. Gac. Méd. Caracas 72 (7-12): 425)

Portuguesa: Guanare (Pifano et al. 1962. Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 1).

Sucre: Cumanacoa (Pifano & Romero. 1964. Gac. Méd. Caracas 72 (7-12): 473).

Trujillo: Panamerican Highway near Caja Seca (Ortiz, I. 1965).

Yaracuy: San Felipe (Pifano & Ortiz. 1952. Rev. San. Asist. Soc.: 137).

Zulia: Bachaquero, Rio Negro, Selva de Tamanaco: (Floch & Abonnenc, 1948. Publ. No. 178), Zipayare (Marmol León, P. 1968, Kasmera 3(1): 61).

This species, usually collected from holes in trees, has been associated with rodents and small reptiles by Ortiz (1968a). 76% of 25 samples examined by Tesh et al., (1971) by precipitin tests reacted with reptile-amphibian antiserum. However, in a recent study on the behaviour of this species, Scorza et al. (1979b)point out that this species feeds on mule (62%), horse (11%), man (11%), pig (11%) and cow (4%).

Pilosa Group, Theodor 1965: 194

Antennal ascoids simple. 5th palpal segment longer than one half the length of the 3rd and twice of the 4th.

Male: Basistyle without basal tuft, although a median or distal patch may be present. Dististyle with 3 spines, the median being small but lacking a small subterminal seta. Parameres and lateral lobes simple.

Female: Cibarium with 4-5 long uniquely shaped horizontal teeth. Spermathecae as small rounded capsules with slender knobs, show long individual ducts; common duct absent.

36. Lutzomyia pilosa (Damasceno & Causey)

Phlebotomus pilosus Damasceno & Causey, 1944: 339 (♂, Brazil). Barretto, 1950: 102 (♂ Keyed. Floch & Abonnenc, 1952: 30 (♂ Keyed). Pifano et al., 1962a:385 (♂ Keyed).

Lutzomyia pilosa: Forattini, 1973: 209 (gen. review). Martins et al., 1978: 152 (refs., distr.). Ramirez Perez et al., 1979: 39 (♀. descr.). Young, 1979: 231 (♀, descr., refs., distr.).

Miranda: Valles del Tuy (Pifano et al., 1962c. Arch. Venez. Méd. Trop. Parasit. Méd. 4 (2): 149).

Tachira: Caño Amarillo (Ramirez Perez et al., 1979. Rev. Brasil. Biol. 39: 259).

Trujillo: Rio Monosnoy (Present work). Ortiz (1968) associates this species with bats and armadillos.

37. Lutzomyia sp. of Bitichas (♀, Venezuela, present work).

Trujillo: Bitichas (Present work).

Saulensis Group Lewis et al., 1977:

Antennal ascoids simple. 5th palpal segment long, more than 3 + 4.

Male: Basistyle with a basal tuft of few straight setae, paramere conspicuous. Dististyle with 4 spines and a sub-terminal bristle.

Female: Cibarium with 4 horizontal teeth, cibarial arch complete, pigmented patch well developed. Spermathecae typical with bubble-like expansions.

38. Lutzomyia saulensis (Floch & Abonnenc)

Phlebotomus saulensis, Floch & Abonnenc, 1944: 11 (♂, French Guyana). Floch & Abonnenc, 1952: 35, 112, (♂, Keyed, redescr.). Pifano et al., 1962a:386, 389 (♂, ♀ Keyed, Venezuela)

Phlebotomus pinealis Floch & Abonnenc, 1944: 11 (♀ , French Guyana). Fairchild & Hertig, 1958: 204 (as synonym of saulensis). Hanson, 1968: 69 (1st instar larva).

Lutzomyia saulensis: Chaniotis et al. 1971a:344 (pop. dynamics) Chaniotis et al., 1972: 95 (resting sites). Shaw & Lainson,

1972: 710 (infected with nonleishmanial flagellates). Llanos, 1973: 34 (♂, ♀ , redescr.). Lewis 1975a: 504: (Mouth parts). Martins et al., 1978: 34 (refs., distr.). Young 1979: 69 (refs., distr.).

Apure: El Novillo, Pto Paez, Guaramaco, (Present work).

Shannoni Group Theodor 1965: 189

Antennal ascoids with posterior spurs. 5th palpal segment longer than 3rd and 4th.

Male: Basistyle without basal tuft. Dististyle with 4 large spines and no subterminal seta. Parameres and lateral lobes simple.

Female: Cibarium with 4-6 horizontal teeth. Spermathecae as smooth, elongate capsules with long individual ducts.

39. Lutzomyia abonnenci (Floch & Chassignet)

Phlebotomus abonnenci Floch & Chassignet, 1947 : 1 (♂, French Guyana). Fairchild & Hertig, 1950: 526 (as a variant of shannoni). Floch & Abonnenc, 1952: 38 (Keyed), 151-52 (♂, redescr.). Sherlock & Carneiro, 1964: 206 (reproductive system).

Lutzomyia abonnenci: Christensen, 1972a: 88, 89 (as a valid species) Miles et al., 1976: 532 (mating aggregation). Martins et al., 1978: 106 (refs., distr.). Young, 1979: 108 (♂, ♀ Keyed), 109 (refs. distr.).

Cojedes: El Pilón de Valle Hondo, (Present work).

Martins et al. (1978) reported two known areas of distribution for L. abonnenci viz: a Northern one (Panama and Colombia) and a Southern one (Brazil and Peru).

The discovery of this species in Venezuela fills the gap between the two areas.

40. Lutzomyia dasymera (Fairchild & Hertig)

Phlebotomus dasymerus Fairchild & Hertig, 1961: 237 (♂, ♀, Panama). Marmol León, 1968: 31 (♂, redescr.). Hanson, 1968: 55 (1st instar larva).

Lutzomyia dasymera: Chaniotis et al., 1971a:344 (pop. dynam. Panama). Christensen et al., 1972: 57 (collecting data). Forattini, 1973: 293 (gen. review). Martins et al., 1978: 154 (refs, distr.). Young, 1979: 108-109 (♂, ♀ Keyed), 111 (refs. distr.).

Zulia: Zipayare (Marmol León, P. 1968. Kasmera 3 (1): 61).

The four males of L. dasymera found in Venezuela were taken from a tree-hole.

41. Lutzomyia lutziana (Costa Lima)

Phlebotomus lutzianus Costa Lima, 1932: 49 (♂, Brasil).

Phlebotomus sp. de Cayenne, Floch & Abonnenc, 1945a:3 (♂, ♀)

Lutzomyia lutziana: Forattini, 1973: 310 (gen. review). Martins et al., 1978: 145 (refs., destr.).

Territorio Federal Amazonas: Atabapo, (Ramirez Perez et al., 1976 Rev. Brasil. Biol. 36 (3): 599). L. lutziana was caught from from an armadillo burrow.

42. Lutzomyia punctigeniculata (Floch & Abonnenc)

Phlebotomus punctigeniculatus Floch & Abonnenc, 1944a:5 (♂, ♀ French Guyana). Fairchild & Hertig, 1950: 425 (taxonomy). Pifano & Ortiz, 1952: 144-146 (♂, ♀ Keyed), 153 (♂, ♀ redescr.). Pifano et al., 1962a:385, 388 (♂, ♀ Keyed) 397 (♂, ♀ redescr.).

Phlebotomus christophersoni Damasceno & Causey, 1944: 347 (♂, Brazil) Fairchild & Hertig, 1950: 526 (as a synonym of punctigeniculata).

Lutzomyia punctigeniculata: Tesh et al., 1971: 153 (blood meal).

Chaniotis et al., 1971a:344 (pop. dynamics, Panama). Llanos 1973: 33 (♂, redescr.). Forattini, 1973: 293 (gen. review). Lewis 1975a: 502 (mouth parts) Arias & de Freitas, 1977: 507 (biting records). Martins et al., 1978: 108 (refs., distr.). Young, 1979: 108 (♂, ♀ Keyed), 115 (refs., distr .).

Apure: Los Rancheros, Santa Elena, El Carrao, Los Morichales, Hato La Tigrera (Present work).

Aragua: Choroní (Albornoz et al., 1968. Dermat. Venez. 7 (3-4): 659; El Guayabito, El Ingenio, Angustia, Boca de Onoto, El Chino, El Onoto, El Samán, Macuaya, Tucupido, Agua de Maiz, La Pavona, Hacienda Punta Larga, Aponte (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18(1): 43).

Carabobo: San José, San Esteban, (Present work).

Cojedes: Charcote, Tierra Caliente, La Morita, Las Rosas, La Ceiba, Mapurite, (Present work).

Lara: Duaca (Pifano & Ortiz, 1952. Rev. San Asist. Soc. 17 (1-2): 137).

Miranda: Guatopo (Pifano et al. 1962a. Arch. Venez. Med. Trop. Parasit. Méd. 4 (2): 369).

Portuguesa: Guanare (Pifano et al., 1962. Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 1).

Zulia: Rio Negro (Floch & Abonnenc, 1948. Publ. No. 178), Zipayare (Marmol León, P. 1968. Kasmera 3(1): 61).

According to Ortiz (1968a) L. punctigeniculata in Venezuela is anthropophilic. Pifano (1962c) collected it using a horse as bait and from tree-holes and resting places of animals. In the Amazon Basin of Brasil, it was shown also to be anthropophilic but it refused to bite a horse. (Arias & de Freitas, loc.cit.).

43. Lutzomyia shannoni (Dyar)

Phlebotomus (Neophlebotomus) shannoni Dyar, 1929: 121 (♂, Panama). Fairchild & Hertig 1950: 523 (collecting data). Johnson & Hertig 1961: 765 (rearing). Hanson, 1968: 78 (larva, pupa.).

Phlebotomus bigeniculatus Floch & Abonnenc, 1941b: 3-7.

Flebotomus shannoni Barretto, 1946a:7 (♂,♀)

Flebotomus limai Fonseca, 1935: 61 (♀)

Phlebotomus limai Barretto & Coutinho, 1940: 127.

Phlebotomus pifanoi. Ortiz, 1972a: 21.

Lutzomyia shannoni: Chaniotis et al., 1971a:339 (pop. dynamics, Panama). Tesh et al., 1971: 150 (blood meal). Tesh et al., 1972: 88 (blood meal). Chaniotis et al., 1972: 91 (resting sites). Ward et al., 1973: 174 (man biting). Zeledón & Alfaro, 1973: 416 (infected with promastigotes). Forattini, 1973: 178 (gen. review). Chaniotis et al., 1974: 369 (mark-release-recapture). Lewis, 1975a: 500 (mouth parts). Miles et al., 1976: 532 (mating aggregation). Martins et al. 1978: 109 (refs., distr.). Young, 1979: 109 (♂, ♀ Keyed), 117 (refs., distr .).

Apure: Guaratico, Guaramaco, Los Rancheros, Santa Elena, Santa Lucia, Los Morichales, Caño Regreso, Sarare Abajo, Hato La Tigrera, Chiricoca, Mata de Silva (Present work).

Aragua: Rancho Grande (Scorza & Ortiz. 1961. Bol. Venez. Lab. Clin. 5-6: 23; Los Dos Montes, Los Conucos, La Sureña, Angustia, Rio Cura, El Ingenio, El Guayabito, San Pedro, Las Caobas, Las Adjuntas, El Negrito, Polanco, La Lagunita, El Samán, Macuaya, Tucutunemo, El Cortijo, El Ocumo, Agua de Maiz, Rio Arriba, Sabana Grande, El Ingenio Bolivar, Corocito, Hacienda Punta Larga (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Cojedes: Charcote, La Ceiba, Mapurite (Present work).

Distrito Federal: Caracas (Martins et al., 1978 loc.cit.).

Falcón: Mene de Mauroa (Pifano & Ortiz, 1952. Rev. San. Asist. Soc. 17(1-2): 137).

Miranda: Guatopo (Pifano et al. 1962a. Arch. Venez. Med. Trop. Parasit. Méd. 4 (2): 369).

Portuguesa: Guanare (Pifano et al., 1962. Arch. Venez. Med. Trop. Parasit. Méd. 4 (2): 1).

Sucre: Cumanacoa (Pifano & Ortiz, 1952. Rev. San. Asist. Soc. 17 (1-2): 137).

Territorio Federal Amazonas: Nyiayobateri (Sierra Parima) (Pifano & Ortiz 1972. Revista Inst. Nac. de Hygiene. 5(1): 29).

Trujillo: (Mogollón et al., 1977. Bol. Dir. Malariol. y San. Amb. 17 (3): 206).

Yaracuy: San Felipe (Pifano & Ortiz. 1952. Rev. San. Asist. Soc. 17 (1-2): 137).

This anthropophilic species has been collected in tree holes, biting man and with Shannon traps. Phototropism and a high prevalence are characteristics of this sandfly, which is widely distributed and related to foci of cutaneous leishmaniasis (Ortiz, 1968a). It is usually found from 15 to 600 m above sea-level, appearing only sporadically up to 1800 m (Mogollón et al., 1977). In view of its biological characteristics, Scorza (personal communication) suggests that the epidemiological importance of L. shannoni deserves further investigation.

Verrucarum Group Theodor 1965: 183

Antennal ascoids simple. 5th palpal segment longer, over 1.5 times the length of the 3rd, and as long as or longer than segments 2 + 3.

Male: Basistyle with basal tuft. Dististyle with 4 large spines

and a small subterminal seta, (series verrucarum), or with 3 large spines and a small subterminal seta (series serrana). Median two spines inserted close together on the same horizontal level. Parameres and lateral lobes simple.

Female: Cibarium with 4 horizontal teeth and 1-2 rows of vertical teeth. Cibarial arch complete or nearly so. Spermathecae wrinkled, sac-like.

Series verrucarum

44. Lutzomyia columbiana (Ristorcelli & Van Ty)

Phlebotomus colombianus Ristorcelli & Van Ty, 1941: 13 (♀, Colombia). Rozeboom, 1947: 705 (♂). Sherlock, 1962: (♂,♀)

Phlebotomus monticolus var. incarum: Ristorcelli & Van Ty, 1941: 266 (♀, Colombia). Rozeboom, 1947: 705 (as synonym of columbiana)

Lutzomyia columbiana: Forattini, 1973: 206 (gen. review). Martins et al., 1978: 126 (refs., distrib.). Young, 1979: 72 (♂, Keyed), 77 (refs, distr.).

Lara: Parque Nacional de Yacambú (Martins, V.A. pers. commun.).

This species has been included in the list of sandflies of Venezuela because it has been recently discovered there (Martins, pers. commun.).

45. Lutzomyia evansi (Nuñez-Tovar)

Phlebotomus evansi Nuñez-Tovar, 1924: 44 (♂, Venezuela). Ristorcelli & Van Ty, 1941: 255 (♂,♀). Mirsa, 1953: 63 (rearing). Pifano et al., 1962a:386, 390 (♂,♀ Keyed), 412 (♂, ♀ redescr.).

Phlebotomus squamiventris: Dyar & Nuñez-Tovar, 1926: 155. Dyar, 1929: 121, 124 (♂, Keyed, ♀).

Lutzomyia evansi: Llanos, 1973: 34 (♂, ♀ redescr.). Forattini, 1973: 122 (gen. review). Martins et al., 1978: 126 (refs., distr.). Young, 1979: 72 (♂ Keyed), 78 (refs. distr.).

Aragua: San Mateo (Iriarte, D. 1943. Bol. Lab. Clin. Luis Razetti Año 4, 3: 1 89; La Sureña, El Guayabito, La Ceiba, La Barquera, Las Adjuntas, Las Marias, Monte Oscuro, Vallecito, Onoto, Boca de Onoto, Paso de los Indios, Paso del Medio, La Palambra, Quebrada Honda, Quebrada Dos Hermanas, Guanasnal, El Ocumo, El Cortijo , Macuaya, Malpica, Quebrada Guayabo, Corral Viejo, Corocito, Cataure, Semen, Las Tunas, El Samán, El Ancón, Mata de Café, Los Bagres, El Cedral, Quebrada de Caney, El Chino, El Onoto, El Toro, Piedras Pintadas, La Pavona, Agua de Maiz, Quebrada Seca, Santo Domingo, Quebrada Calanche, La Curia, Polvorín, Paya, La Trilla, Aponte, (Ramirez Perez et al., 1978. Bol. Dir. Malariol y San. Amb. 18 (1): 43).

Carabobo: Mariara: (Nuñez-Tovar, 1924. Mosquitos yFlebotomos de Venezuela: 44), Guache, San Esteban (Present work).

Cojedes: Las Rosas (Aguilar, 1981 Thesis, U.C. 132pp); La Morita, Zambrano, Mapurite (Present work).

Distrito Federal: Macuto (Iriarte, D. 1943. Bol. Lab. Clin. Luis Razetti Año IV, 3: 189).

Falcón: Mene de Mauroa (Ortiz, I. 1944. Bol. Lab. Clin. Luis Razetti Año V 4: 247).

Guarico: Altagracia de Orituco (Floch & Abonnenc, Publ. No. 178).

Miranda: Guatopo (Pifano et al., 1962a. Arch. Venez. Med. Trop. Parasit. Méd. 4: 369), Ocumare del Tuy (Ortiz, I. 1950. Arch. Venez. Pat. Trop. Parasit. Méd. 2 (1): 83).

Nueva Esparta: Isla de Margarita: Las Piedras (Pifano & Romero. 1964. Gac. Méd. Caracas. 72 (7-12): 425).

Portuguesa: Guanare (Pifano & Romero. 1962. Arch. Venez. Med. Trop. Parasit. Med. 4(2): 1)

Trujillo: (Mogollón et al., 1977. Bol. Dir. Malariol. y San.

Amb. 17 (3): 206); El Rincón, Rio Monosnoy (Present work).

Zulia: Bachaquero, Rio Negro, Selva de Tamanaco (Floch & Abonnenc, 1948. Publ. No. 178), Zipayare (Marmol Leon, P. 1968. Kasmera 3 (1): 61).

L. evansi has been collected on several occasions from human bait and is therefore assumed to be anthropophilic. Pifano & Romero (1964) suspected this species was a vector of visceral leishmaniasis in Sucre State, but several years later Henriquez et al. (1970) found L. longipalpis (the only proven Neotropical vector of this form of the disease) in that area. However, because of its prevalence, wide geographical and altitudinal distribution, and the fact that it is related to foci of dermal leishmaniasis, this species is particularly interesting.

46. Lutzomyia nuneztovari: (Ortiz)

Phlebotomus nuñez-tovari: Ortiz, 1954: 232 (♂, Venezuela). Scorza & Ortiz, 1960: 434 (ecology). Pifano et al., 1962a:387 (♂ Keyed). Scorza et al., 1967: 194, 195 (♂, ♀ Keyed), 196 (collecting data).

Lutzomyia nuneztovari: Forattini, 1973: 265 (as synonym of L. ovallesi). Martins et al., 1978: 127 (refs., distrib.). Young, 1979: 72 (♂, Keyed), 83 (♀ descr., refs., distr.).

Aragua: Rancho Grande (Scorza & Ortiz 1960. Ztschr. Tropenmed. Parasit. 11: 433)

Lara: Duaca (Ortiz, I. 1954. Acta Biol. Venez. 1 (14): 231).

L. nuneztovari: has been collected from tree-holes. Young (loc.cit.) recently described the female and discussed the synonymy proposed by Forattini with which Martins et al. (loc.cit.) disagreed.

47. Lutzomyia ovallesi (Ortiz)

Phlebotomus ovallesi: Ortiz, 1952: 155 (♂, Venezuela). Ortiz, 1954:

239 (♂ redescr.); Lewis & Garnham, 1959: 87 (♀, descr. Belize). Scorza & Ortiz, 1960: 434 (ecology). Hanson, 1961: 317 (breeding sites). Johnson & Hertig, 1961: 765 (rearing). Pifano et al., 1962a:387, 389 (♂, ♀ Keyed), 404 (♂, ♀ redescr.). Strangways-Dixon & Lainson, 1962: 297 (infected with flagellates, Belize). McConnell & Correa, 1964: 527 (infected with fungus). Hanson, 1968: 64 (larva, pupa, descr.).

Lutzomyia ovallesi: Tesh et al., 1971: 153 (blood meals). Chaniotis et al., 1972: 95 (collecting data). Christensen et al., 1972: 57 (light trap). Forattini, 1973: 122 (gen. review). Lewis, 1975a: 500 (mouth parts). Rutledge et al., 1975d:181 (ecology). Martins et al., 1978: 128 (refs., distr.). Young, 1979: 72 (♂, Keyed), 84 (refs., distr.).

Apure: Sarare Abajo (Present work).

Aragua: Rancho Grande (Scorza & Ortiz 1961. Bol. Venez. Lab. Clin. 1 (14): 239; Loro Arriba, Guiripa, Las Caobas, La Barquera, Guambra, Las Adjuntas, Polanco, Golfo Triste, Monte Oscuro, Las Marias, El Ocumo, El Cortijo, Malpica, Quebrada Guayabo, Corral Viejo, Caicara, El Onoto, Las Tunas, El Ancón, Los Bagres, Quebrada Caney, El Chino, El Toro, Tucupido, Cañadote, Gabante, Polvorín, (Ramirez Perez et al., 1978; Bol. Dir. Malariol.y San Amb. 18 (1): 43).

Carabobo: El Corozo, Belén; Las Colonias, Los Cocos, Yuma, El Pueblito, S.ta Ines, Agua Linda, Pueblo Nuero, San Esteban (Present work).

Cojedes: (Scorza et al. 1967., Acta Biol. Venez. 5: 180), Las Rosas (Aguilar, 1981. Thesis U.C. 132pp).

Distrito Federal (Scorza et al. 1967., Acta Biol. Venez. 5: 180).

Lara: Duaca (Ortiz, I. 1954. Acta Biol. Venez. 1 (14): 239).

Miranda: Guatopo (Pifano et al., 1962a. Arch. Venez. Med. Trop. Parasit. Med. 4: 369).

Portuguesa: Guanare (Pifano et al., 1962. Arch. Venez. Med. Trop. Parasit. Med. 4(2): 1).

Sucre: Cumanacoa (Pifano & Romero, 1964. Gac. Med. Caracas 72 (7-12): 473).

Trujillo: (Mogollón et al., 1977. Bol. Dir. Malariol. y San. Amb. 17 (3): 206).

Yaracuy: San Felipe (Ortiz, I. 1952. Rev. San. Asist. Soc. 17: 153).

L. ovallesi, usually caught in tree-holes, has been shown to be strongly anthropophilic in Venezuela (present work). It is distributed from 200 to 1800 m above sea-level, has a high prevalence and is related to foci of cutaneous leishmaniasis.

48. Lutzomyia townsendi (Ortiz)

Phlebotomus townsendi Ortiz, 1959: 23 (♂, Venezuela). Ortiz & Scorza, 1963: 347 (♂, ♀ descr.). Scorza et al., 1968a: 28 (bionomics); 1968b: 41 (biting preferences); 1968c: 52 (gonadotrophic circle); 1968d: 87 (anthropophily). Mogollón et al., 1977: (altitudinal distr.). Martins et al., 1978: 129 (refs., distr.).

Aragua: Rancho Grande (Ortiz, I. 1959. Bol. Venez. Lab. Clin. 3: 37; Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Merida: El Salado: (Calderón, 1973). Acta Cientif. Venez. 24: 87); Merida (Carnevali & Scorza. 1976. Bol. Dir. Malariol. y San. Amb. 16(4): 333).

Trujillo: (Mogollón et al., 1977. Bol. Dir. Malariol. y San.

Amb. 17 (3): 206).

Biological and ecological characteristics of L. townsendi, defined by Ortiz (1959) as an "interesting representative of the Venezuelan phlebotomine fauna", have been studied by Scorza et al., (1968 a, b, c).

This species moves in short flight. It is easily collected in holes of trees (Chimarrhis microcarpa, Gyranthera caribensis, Endlecheria tschudyana), with human or animal baits, and is caught in large numbers in Shannon traps. In spite of its positive phototropism, it has never yet been caught in houses. Observations on its feeding preferences in nature and in captivity have shown that it is optionally anthropophilic but also bites wild animals including Didelphis marsupialis, Proechymis sp. and Heteromys anomalus. It is believed to be the only species that feeds on man and domestic animals in localities as high as almost 2000 m above sea-level: all habitats of this species are at high altitude from 800 to 1900 m (Mogollón et al., 1977), and its abundance and activity depend directly on the height. Observations on the gonotrophic features of L. townsendi have shown that it is possible to differentiate nulliparous from parous females by inspection of the ovarioles, oviducts and the Malpighian tubules (Scorza et al., 1968c). Carnevali & Scorza (1977) experimentally infected this species with a Venezuelan strain of "Le. braziliensis sensu lato" and discussed its possible role in the transmission of suburban and rural leishmaniasis peculiar to high regions.

49. Lutzomyia verrucarum (Townsend)

Phlebotomus verrucarum: Townsend, 1913: 107 (♂, ♀, Peru), 1914:57 Shannon, 1929: 78; Hertig, 1942; Herrer, 1949-51: 119 (biology) Pifano & Ortiz 1952: 142-148 (♂,♀ Keyed).

Lutzomyia verrucarum: Forattini, 1973: 100 (gen.review); Martins

et al. 1978: 129 (refs.; distr.).

Carabobo: Rio Borburata (Floch & Abonnenc, 1950-53. Bol. ent. Venez. 9 (1-4): 3).

Merida: (Pifano & Ortiz, 1952. Rev. San Asist. Soc. 17 (1-2): 137-151).

50. Lutzomyia sp. of Loma Abajo (♂, ♀ Venezuela, present work).

Trujillo: Loma Abajo, Vitisay, La Vega de Tosto, Hato San Pablo (Present work).

Series serrana

51. Lutzomyia ottolinai (Ortiz & Scorza)

Phlebotomus (Pifanomyia) ottolinai Ortiz & Scorza, 1963: 345 (♂, ♀ Venezuela). Scorza & Ortiz, 1967: 194, 195 (♂, ♀ Keyed).

Lutzomyia ottolinai: Forattini, 1973: 265 (♂, discussion). Martins et al., 1978: 116 (refs., distr.).

Aragua: Rancho Grande (Ortiz & Scorza, 1963. Acta Biol. Venez. 3 (23): 341; Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18(1): 43).

The habitat of L. ottolinai appears to be restricted to tree-holes.

52. Lutzomyia serrana (Damasceno & Arouck)

Phlebotomus serranus: Damasceno & Arouck, 1949: 843 (♂, Brazil). Fairchild & Hertig, 1961: 237(♂, ♀ descr.). Hanson, 1961: 320 (breeding sites). Johnson & Hertig, 1961: 765 (rearing). Hanson, 1968: 76 (larva, pupa).

Phlebotomus guayasi: Rodriguez, 1956: 76 (♂, ♀ Ecuador). Fairchild & Hertig, 1961: 237 (as synonym of serranus).

Lutzomyia serrana: Tesh et al., 1971: 152 (blood meals). Chaniotis et al., 1971a: 345 (pop. dynamics, Panama). Tesh et al., 1972: 89 (blood meals). Forattini, 1973: 123 (gen. review). Llanos et al., 1975: 668 (anomaly). Martins et al., 1978: 117 (refs.,

distr.). Young, 1979: 71 (♂, Keyed), 73 (refs. distr.).

Trujillo: Loma Bastidas (Present work).

The only male found in Venezuela was collected under litter on the forest floor.

Vexator Group Theodor 1965: 183

Antennal ascoids simple. 5th palpal segment longer than 3rd, but shorter than 2 + 3 + 4.

Male: Basistyle with an inner tuft. Dististyle with 5 spines. Parameres and lateral lobes simple.

Female: Cibarium with 4 horizontal teeth. Cibarial arch not well defined. Spermathecae segmented (series peruensis) or like small capsules (series vexator).

53. Lutzomyia ceferinoi (Ortiz & Alvarez)

Phlebotomus ceferinoi Ortiz & Alvarez, 1963: 285 (♂, Venezuela). Martins et al., 1978: 78 (refs., distr.).

Portuguesa: Biscucuy (Ortiz & Alvarez, 1963. Salud públ.Caracas 5 (23): 285).

The species, of unknown habits, was collected under stones.

54. Lutzomyia scorzai (Ortiz)

Phlebotonus scorzai: Ortiz, 1965: 28 (♂, ♀ Venezuela). Scorza et al., 1967: 191 (♂, ♀ Keyed).

Lutzomyia scorzai: Forattini, 1973: 213 (gen. review). Martins et al., 1978: 81 (refs., distr.). Young, 1979: 196 (♂, ♀ Keyed), 204, 205 (refs.; ♂, ♀ redescr.; distr.).

Aragua: Rancho Grande (Ortiz, 1965. Acta Biol. Venez. 5 (2): 25; Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

L. scorzai has been collected from tree-holes and in a Shannon trap.

Females showed a marked anthropophilism.

55. Lutzomyia erwindonaldoi: (Ortiz, 1978).

Phlebotomus erwindonaldoi(Ortiz, 1978: 205 (♂).

Trujillo: Caja Seca (Ortiz, I. 1978. Bol. Dir. Malariol. y San. Amb. 18(3): 205).

This recently-described species was collected in tree-holes, with the closely related species L. ceferinoi, and with L. atroclavata and L. lichyi. The main distinguishing characters given by Ortiz (1978) were the filamentous genital ducts, at present unique in males with 5 spines on the dististyle.

Ungrouped

56. Lutzomyia rangeliana (Ortiz)

Phlebotomus rangelianus, Ortiz, 1952: 153 (♂, Venezuela). Pifano et al., 1962a:384, 389 (♂,♀ Keyed), 406-407 (♂, ♀ descr.).

Lutzomyia rangeliana: Forattini, 1973: 293 (gen. review). Martins et al., 1978: 166 (refs., distr.). Young, 1979: 235 (refs., distr.).

Apure: Santa Lucia, El Carrao, Mata de Silva (Present work).

Aragua: Quebrada Apamate, Las Conucos, Barbacoas, El Ingenio, El Guayabito, Vallecito, Zuata, Paso del Medio, Quebrada Dos Hermanas, Palambra, El Onoto, Los Bagres, El Chino, Quebrada El Caney, Quebrada Guayabo, Tucutunemo, La Lagunita, El Ancón, El Samán, Macuaya, Chaguaramos, Las Tunas, Pedregalito, La Majada, Caicara, El Cortijo, La Pavona, Hacienda Punta Larga. (Ramirez Perez et al., 1978. Bol. Dir. Malariol. y San. Amb. 18 (1): 43).

Carabobo: Las Animas, Yuma, El Pueblito, El Caruto, Agua Linda,

Carabobo, San Esteban (Present work).

Cojedes: Las Rosas (Aguilar, 1981. Thesis, U.C. 132pp).

Charcote, Tierra Caliente, Hacienda Vieja, La Ceiba, San Carlos (Present work).

Lara: Duaca (Ortiz, I. 1952. Rev. San. Asist. Soc. 17: 153).

Miranda: Guatopo (Pifano et al., 1962a. Arch. Venez. Med. Trop. Parasit. Méd. 4(2): 369).

Nueva Esparta: Isla de Margarita: Las Piedras. (Pifano & Romero 1964. Gac. Med. Caracas. 72 (7-12): 425).

Portuguesa: Guanare (Pifano et al., 1962. Arch. Venez. Med. Trop. Parasit. Med. 4(2): 1).

Sucre: Cumanacoa (Pifano & Romero. 1964. Gac. Med. Caracas 72 (7-12): 473).

L. rangeliana has been caught from holes in trees, and is associated with armadillos and bats (Ortiz, 1968).

57. Lutzomyia torrealbai Martins, Ordoñez de Fernandez & Falcão.

Lutzomyia torrealbai Martins, Ordoñez de Fernandez & Falcão, 1979: 431 (♂, Venezuela).

Trujillo: La Vega de Tosto El Volcan, Vitisay, Escorá, Altamira, (Martins, O. de Fernandez & Falcão 1979. Rev. Bras. Biol.: 431).

Martins et al (1979) considered this species, which frequently shows a variable number of spines on the dististyle, as an aberrant species and refrained from assigning it to any group, pending the discovery of the female.

Inadequately described species

58. Phlebotomus maracayensis Nuñez-Tovar

Phlebotomus maracayensis Nuñez-Tovar, 1924: 43 (♂, Venezuela)

Martins et al., 1978: 169 (refs., distr.).

Aragua: Tucupido (Nuñez-Tovar, 1924. Mosquitos y Flebotomos de Venezuela: 43).

Yaracuy: Valles del Rio Yaracuy (Pifano, F. 1943. Bol. ent. Venez. 2: 99)

3.3.6. Illustrated Keys for the identification of Venezuelan sandflies

This Key is a revised and updated version of that published in 1980 (Feliciangeli, 1980). 12 new species have been included.

Key to the species of the Genus Brumptomyia in Venezuela

1. Females.....2

Males.....3

2(1). Palpal formula: 1.2.4.3.5. Fore teeth absent (Fig..28B).....avellari

-Palpal formula: 1.4.2.3.5. One row of 5-6 fore teeth present... (Fig..28D).....beaupertuyi

3(1). Dististyle with 2 apical spines, 2 basal spines implanted on a tubercle at the middle and another one approximately in an intermediate position between the two pairs (Fig. 28F)....beaupertuyi

-Dististyle with 2 apical spines and the other 3 situated approximately at the middle, 2 of them being implanted on a tubercle.....4

4(3). Basistyle with a row of 6 strong spines on the inner distal part. Paramere dorso-ventrally flattened (Fig..28A)....avellari

-Basistyle with a row of 5 strong spines on the inner distal part. Paramere finger-shaped(Fig..28G).....devenanzii

Key to the species of the Genus Lutzomyia in Venezuela

Females

1. Hind femur with a longitudinal row of 3-8 short spines. Cibarium with 4 cylindrical hind teeth. Spermathecae cylindroid with a flat head..(Fig..33A,B).....fischeri

-Hind femur without spines.....2

2(1). Antennal ascoids with long posterior spurs. Spermathecae elongate and smooth.....3

-Antennal ascoids without such posterior spurs.....4

3(2). Spermathecae sausage-shaped. Cibarium with 4 hind teeth (Fig. 45 G,H).....shannoni abonnenci

-Spermathecae striated at base. Cibarium with 6 pairs of hind teeth (Fig. 45 C,D).....dasymera

4(2). 5th palpal segment shorter than, or subequal to, 3rd segment..5

-5th palpal segment longer than 3rd segment.....13

5(4). Spermathecae imbricated.....6

-Spermathecae not imbricated but annulated.....8

6(5). Individual ducts of spermathecae longer than the body and partly striated, partly smooth.(Fig..35A).....squamiventris

-Individual ducts of spermathecae shorter than the body and completely striated.....7

7(6). Cibarium with 4 triangular hind teeth. Terminal segment of body of spermathecae asymmetrical (Fig..35D).....panamensis

-Cibarium with 4 fine hind teeth. Terminal segment of body of spermathecae symmetrical (Fig..35H).....parimaensis

8(5). Cibarium with 4-5 pairs of hind teeth. Individual sperm ducts striated for 1/5 of their length and then smooth. Spermathecae with 6-7 distinct rings...(Fig..32.A,B).....anduzei

-Cibarium with 3-6 pairs of hind teeth. Individual ducts smooth.....9

9(8). Spermathecae with tongue-shaped head.....10

-Spermathecae not as above.....11

10(9). Cibarium with 6-7 hind teeth. Genital fork stem slender (Fig..32.J,K).....flaviscutellata

-Cibarium with 8-10 hind teeth. Genital fork stem broad (Fig..32.L,M).....*olmeca bicolor*

11(9). Cibarium with 8 hind teeth, spermathecae irregularly segmented with a small head (Fig..32.G,H).....*hernandezi*

-Cibarium with 10-12 hind teeth, spermathecae regularly segmented.....12

12(11). Spermathecae with 5-6 distinct rings and a small head (Fig. 32D).....*antunesi*

-Spermathecae with more than 10 distinct rings and a large head (Fig. 36B).....*ubiquitalis*

13(4). Pharynx spinose at posterior end.....14

-Pharynx without posterior spines.....20

14(13). Pharynx widens abruptly at the posterior end.....15

-Pharynx widens gradually at the posterior end.....17

15(14). Pharynx heavily spinose, but without transverse ridges (Fig. 2A).....sp. of *La Vaquira*

-Pharynx with few spines and numerous transverse ridges or striae.....16

16(15). Cibarium with 4 small triangular hind teeth. Spermathecae smooth throughout with a defined base (Fig..39.A,C)....*atroclavata*

-Cibarium with 4 large triangular hind teeth. Spermathecae with basal folds and undefined base (Fig..39,.F,G)...*venezuelensis*

17(14). Cibarium with 5-15 pairs of hind straight teeth in a comb-like arrangement (Fig. 38B).....18

-Cibarium with 2-4 pairs of hind teeth, not as above.....19

18(17). "Delta" of wing very long, more than ½ of "alpha", hind spines of pharynx longitudinally arranged.....*cayennensis*

-"Delta" of wing very short, never reaching ½ of "alpha", hind spines of posterior pharynx ordered in characteristic

transverse rows.....yencanensis

19(17).Cibarium with 2 pairs of hind teeth inclined and converging towards the middle line. Spermathecae smooth and sausage-shaped (Fig..42.B,C).....trinidadensis

-Cibarium with 3-4 pairs of hind teeth slightly oblique. Spermathecae pear-shaped and irregularly segmented at base (Fig..38.E,F).....micropyga

20(13).Cibarium with numerous fine hind teeth, spermathecae wrinkled, sac-like (Fig..6F).....sp. of Loma Abajo

-Cibarium with 4-8 stout hind teeth.....21

21(20).Cibarium with 6-8 hind teeth.....22

-Cibarium with 4 hind teeth.....23

22(21).Spermathecae cylindroid and annulated, the annuli being of uniform length and width (Fig. 30C).....longipalpis

-Spermathecae sausage-shaped (Fig..46B).....punctigeniculata

23(21).Cibarial arch absent.....24

-Cibarial arch present.....25

24(23).Spermathecae tubular and smooth, continuing indefinitely into broad individual ducts (Fig..43B).....pilosa

-Spermathecae with a definite distal constriction and continuing abruptly into delicate individual ducts (Fig. 3F).....sp. of Bitichas

25(23).Cibarial arch ill-defined at the middle or incomplete.....26

-Cibarial arch well-defined or complete.....29

26(25).Spermathecae globular.....27

-Spermathecae annulated.....28

27(26).Spermathecae pear-shaped, annulated at the bases (Fig..31C).....gomezi

-Spermathecae nearly sperical, finely striated at the

bases (Fig..40D).....conviti

28(26).Spermathecae cylindrical continuing indefinitely into long individual ducts (Fig..49.C,D).....scorzai

-Spermathecae conical, truncated at base, continuing abruptly into short individual ducts (Fig..48K).....serrana

29(25).Spermathecae with a small head and the body like a cylindrical capsule. Individual ducts short and chitinized....30

Spermathecae otherwise.....31

30(29).Spermathecae with the head flat and large.(Fig..34A)..dysponeta

-Spermathecae with the head globular and reduced (Fig..34E).....triacantha

31(29).Spermathecae wrinkled.....32

-Spermathecae otherwise.....41

32(31).Individual ducts of spermathecae absent, body of spermathecae saclike (Fig..50B).....rangeliana

-Individual ducts of spermathecae present.....33

33(32).Body of spermathecae continuing indefinitely into individual ducts.....34

-Body of spermathecae continuing abruptly into individual ducts.....36

34(33).Individual ducts very long; spermathecae finely striated, pear-shaped (Fig..47F).....evansi

-Individual ducts short.....35

35(34).Spermathecae conical, annulated (Fig..48H).....ottolinae

-Spermathecae tubular, wrinkled with incomplete annulations (Fig.29B).....begonae

36(33).Spermathecae with a clear constriction separating the first 6 folds of body from the rest; thin individual ducts (Fig..47B).....ovallesi

-Spermathecae without constriction.....37

37(36).Head of spermathecae deeply implanted.....38

-Head of spermathecae superficially implanted.....39

38(37).Head of spermathecae well developed, spermathecae spherical (Fig..40B).....longispina

-Head of spermathecae small, spermathecae cylindroid (Fig..47I).....nuneztovari

39(37).End segment of body of spermathecae large, globular and well-defined. Individual ducts thin (Fig..48B)..townsendi

-End segment of body of spermathecae small and ill-defined. Individual ducts thick.....40

40(39).Common duct of spermathecae tubular..(Fig..48E)....verrucarum

-Common duct of spermathecae wide and globular.(Fig..47E).columbiana

41(31).Individual ducts shorter than common duct. Spermathecae distally conical with basal part vesciculate (Fig..44C).....saulensis

-Individual ducts subequal or longer than common duct.....42

42(41).Individual ducts subequal to common duct.....43

-Individual ducts longer than common duct.....45

43(42).Spermathecae large, almost spherical (Fig..46D)....lutziana

-Spermathecae capsule-shaped.....44

44(43).Individual sperm ducts about ½ as wide as common duct. FI about the same length as L. (Fig..41.F,G)..dubitans

-Individual sperm ducts about 1/3 as wide as common duct. FI about ¾ the length of L. (Fig..41,J,K).....walkeri

45(42).Cibarium with 1 or 2 small lateral teeth at each side. Spermathecae pear-shaped with terminal globular segment and annulated at the base (Fig..30.E,F).....lichyi

-Cibarium without lateral teeth.....46

46(45). Spermathecae smooth and tubular..(Fig..41B).....migonei

-Spermathecae annulated with a large terminal knob (Fig..31F).....ignacioi

Key to the species of the Genus Lutzomyia in Venezuela

Males

1. Hind femur with a longitudinal row of 3-8 short spines. Basistyle with a tuft of few hair-like setae. Dististyle with 4 spines, and a subterminal seta. Paramere simple, unarmed...(Fig..33C).....fischeri

-Hind femur without spines.....2

2(1). Antennal ascoids with long posterior spurs.....3

-Antennal ascoids without such long posterior spurs.....5

3(2). Paramere complex, wide at base, which bears a rounded appendix with long setae, and narrow at end where it curves strongly upward and inward...(Fig..45A).....dasymera

-Paramere simple.....4

4(3). Paramere tapers gradually and is covered with hairs on distal ½....(Fig..45E).....shannoni

-Paramere narrows at the middle and has only few hairs at tip...(Fig..45I).....abonnenci

5(2). 5th palpal segment shorter than, or subequal to, 3rd segment...5

-5th palpal segment longer than 3rd segment.....12

6(5). Basistyle with a patch of setae.....7

-Basistyle without patch of setae.....9

7(5). Patch of setae situated on distal part of basistyle. Paramere simple. Lateral lobe longer than basistyle (Fig..32F).....hernandezi

-Patch of setae situated at middle of basistyle.....8

8(7). Basistyle quite dilated. All spines of disistyle at different levels. Lateral lobe a little shorter than basistyle...(Fig..36C).....ubiquitalis

-Basistyle slightly dilated. The 2 basal spines of dististyle at about the same level. Lateral lobe as long as basistyle..(Fig..32E).....antunesi

9(6). Dististyle with 4 large spines.....10

-Dististyle with 1 large terminal spine and 3 small spines or setae.....11

10(9). Genital pump much longer than style..(Fig..32I)..flaviscutellata

-Genital pump shorter or equal to length of style...(Fig..32N).....olmeca bicolor

11(9). Basistyle very dilated with a median constriction. Dististyle with 1 terminal spine and 3 small adjacent setae. Paramere peduncular and rectangular at end with 2 superior process, one of them racket-like..(Fig..35C)..squamiventris

-Basistyle not dilated with 2 or 3 long setae in the distal part. Dististyle with 4 short spines. Paramere with 3 wide dilations, 2 of them bearing a thick tuft of foliaceous setae, the last elongated, with 2 fine and long setae at end...(Fir..35F).....panamensis

12(5). Dististyle with 3 spines.....13

-Dististyle with more than 3 spines.....19

13(12). Dististyle with 3 spines and 1 seta.....14

-Dististyle with 3 spines and 2 setae.....16

14(12). Basistyle with an extended loosely arranged patch of setae that occupies the distal $\frac{1}{2}$..(Fig..43A).....pilosa

-Basistyle with a basal tuft of setae.....15

15(14).Tuft on basistyle formed by 5 curved and widely spaced setae. Paramere quadrangular. "Alpha" of wing longer than "beta" (Fig..48L).....*serrana*

-Tuft on basistyle formed by a few straight and closely spaced setae. Paramere spatula-shaped. "Alpha" of wing less than twice the length of "beta"..(Fig..48I)..*ottolinai*

16(13).Dististyle with 1 small sub-terminal seta and the other long, situated in the basal ½. Paramere characteristic, clog like...(Fig..50A).....*rangeliana*

-Dististyle with 2 small setae close to spines.....17

17(15).Basistyle with 1 simple basal tuft with 4 foliaceous setae...(Fig..34B).....*dysponeta*

-Basistyle with 1 basal tuft with two distinct parts.....18

18(17).Basistyle with 1 basal tuft with 8-10 setae bent over at the tips and a reduced superior lobe with few fine, short setae..(Fig..34C,D).....*triacantha*

-Basistyle with 1 basal tuft of 8-10 foliaceous setae, 2 of them modified with square ends and a conspicuous superior lobe with numerous fine long setae..(Fig..7D).

.....sp. of *Chiricoca*

19(12).Dististyle with 4 spines.....20

-Dististyle with 5-6 spines.....46

20(19).Dististyle with a subterminal seta.....21

-Dististyle without subterminal seta.....36

21(20).Paramere forked.....22

-Paramere not forked.....25

22(20).Lateral lobe with 3 strong upper spines at tip. Basistyle with a basal tuft of 14-18 setae implanted on small tubercles.....23

-Lateral lobe without 3 strong upper spines at tip. Basistyle with an inner fringe of long and strong setae.....24

23(22).Paramere trifurcate. Genital filaments swollen and pointed at the tips..(Fig..29C).....L. begonae

-Paramere bifurcate. Genital filaments cylindrical and truncated at the tips..(Fig.8E,H).....sp. of Monay

24(22).Both arms of paramere rounded, horizontally directed dorsally covered with many curved setae..(Fig..40C)...longispina

-Each arm of paramere curved and pointing toward the other with straight setae on the lower and upper edges (Fig..40F)..conviti

25(21).Paramere armed.....26

-Paramere unarmed.....27

26(25).Paramere with 2 long spines in the shape of "antelope horns". Basistyle with a basal tuft of long setae (Fig..30A).....longipalpis

-Paramere with a long cylindrical process bearing 2 modified leaf-like spines. Basistyle with a basal fan-shaped tuft of setae implanted on a tubercle..(Fig..30D).....lichyi

27(25).Basistyle with 1 tuft of setae.....28

-Basistyle with 2 tufts of setae.....35

28(27).Basal tuft of basistyle very conspicuous.....29

-Basal tuft of basistyle quite small.....32

29(28).Tip of genital filaments spoon-shaped with a central tubercle.....30

-Tip of genital filament simple.....31

30(29).Aedeagus complex with a dorsal projection. Basal spine of the dististyle at the middle, 2nd spine on the distal anterior quarter of the segment. FI about the same length as L...(Fig..41.H,I).....walkeri

-Aedeagus simple without a dorsal projection. Basal spine of the dististyle always far from the middle and close on the medial anterior quarter of the segment. FI about 1½ times the length of L...(Fig..41.D,E).....dubitans

31(29).Dististyle with 2 spines on distal part and the other 2 in basal part, almost at the same level (Fig..47D)...columbiana

-Dististyle with 3 very close spines on distal ½ and a 4th near the base ..(Fig..48A).....townsendi

32(28).Paramere markedly bent on lower edge of distal part. Tuft on basistyle of 5-7 short setae..(Fig..41C).....migonei

-Paramere straight and horizontally directed.....33

33(32).Paramere stout and quadrangular. Tuft on basistyle of 5 long and straight setae..(Fig..44A).....saulensis

-Paramere quite slender.....34

34(33).Paramere finger-shaped with an external hyaline lobe (Fig..47C).....ovallesi

-Paramere spatula-shaped without such hyaline lobe (Fig..47G).....evansi

35(27).Basal spines of the style inserted on distinct, rather long, tubercles. Paramere rounded at the end (Fig..4D, 5D,E).....sp. of Loma Abajo

-Basal spines of the style not inserted on tubercles. Paramere with a ventral prominence..(Fig..48D).....verrucarum

36(20).Basistyle with patch or tuft of setae.....37

-Basistyle without tuft or patch of setae.....42

37(36).At least 1 pair of spines of dististyle at the same level....38

-Spines of dististyle all at different levels.....40

38(37).Each apical spine of dististyle at the same level, basal spines at different levels. Basistyle with a tuft of

4-5 fine setae implanted on a tubercle. Paramere simple, rectangular with scattered hairs and 1 seta..(Fig..37)...baityi

-Each apical spine at a different level, the basal spines each at the same level.....39

39(38).Basistyle with a basal patch of 5-8 closely spaced setae...(Fig..47H).....nuneztovari

-Basistyle with a patch of 10-12 loosely arranged setae...(Fig..31D).....ignacioi

40(37).Basistyle with a median patch of fine setae (Fig..39H).....venezuelensis

-Basistyle with a basal tuft of setae.....41

41(40).Basistyle with a basal tuft of long setae implanted on a sub-circular, raspberry-like tubercle..(Fig..31A)...gomezi

-Basistyle with a basal tuft of 4 foliaceous long setae...(Fig..39D).....atroclavata

42(36).Paramere conical, distally pointed and covered with numerous long setae, tuft like. Lateral lobe nearly as long as basistyle..(Fig..46A).....punctigeniculata

-Paramere finger-shaped, with short scattered hairs.....43

43(42).Cibarium with vestiges of a comb-like row of hind teeth.....44

-Cibarium without a comb-like row of hind vestigial teeth.....45

44(43)."Delta" of wing very long, more than ½ of "alpha"..cayennensis

-"Delta" of wing very short, never reaching ½ of "alpha"..yencanensis

45(43).Lateral lobe much longer than basistyle..(Fig.46E)..lutziana

-Lateral lobe subequal to basistyle..(Fig..38G).....micropyga

46(19).Basistyle with a loose median patch of setae. Paramere simple, finger like at end. Lateral lobe shorter than basistyle...(Fig..42D).....trinidadensis

-Basistyle with a compact basal tuft.....47

47(46).Basistyle with a tuft of 2-3 adjacent setae..(Fig..49A)..scorzai

-Basistyle with 10 or more long and strong setae.....48

48(47).Dististyle with 5 or 6 spines all at different levels...(Fig..50C).....torrealbai

-Dististyle with 5 spines, 2 distal, 2 basal at about the same level and 1 close to the distal ones.....49

49(48).Hairs of tuft of basistyle implanted on chitinised slightly scattered sockets. Genital filaments normal (Fig..49.F,G).....ceferinoi

-Hairs of tuft of basistyle implanted on lightly pigmented adjacent sockets. Genital filaments extremely fine and delicate...(Fig..49H).....erwindonaldoi

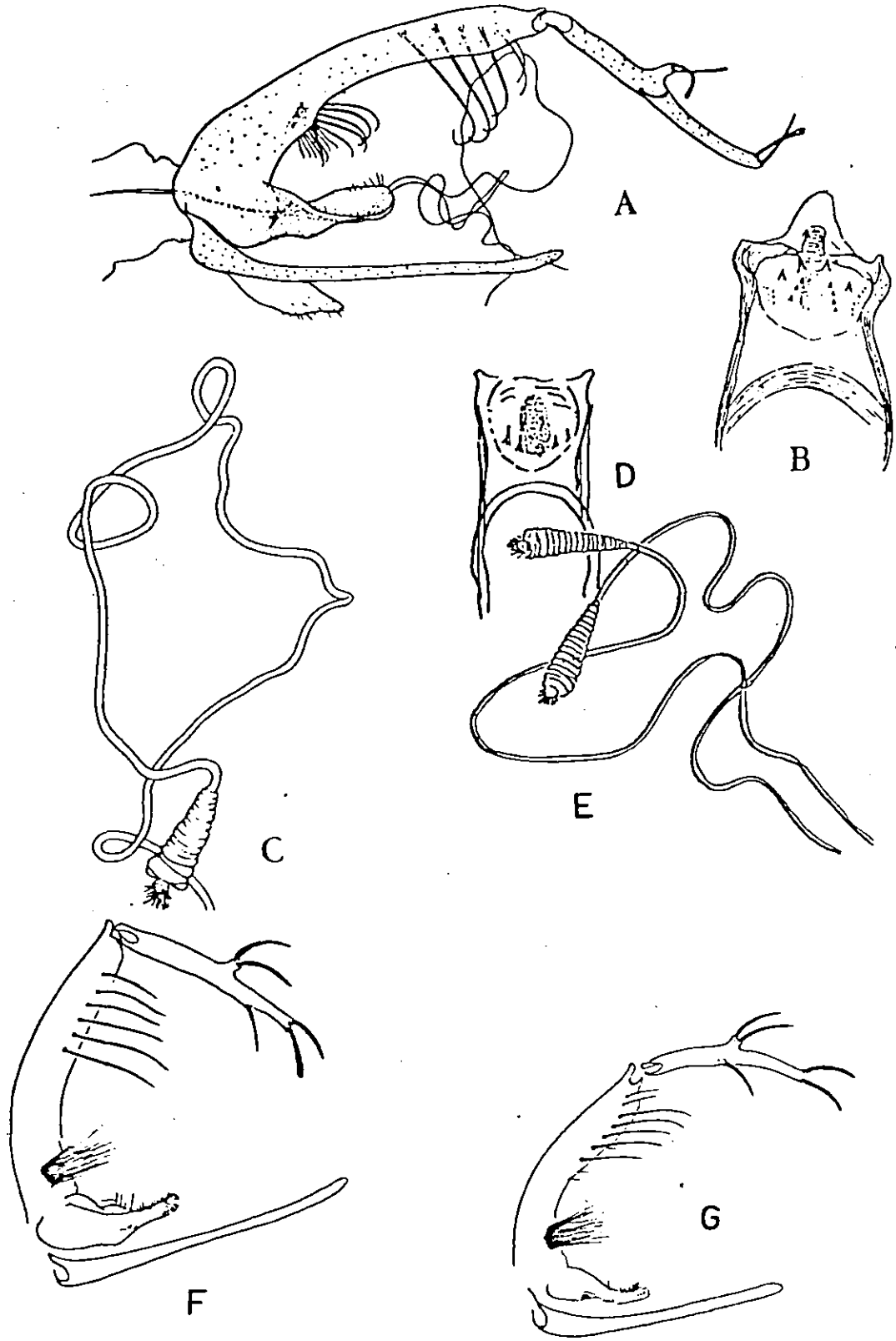


Fig. 28. Brumptomyia avellari : A. ♂ genitalia; B. ♀ cibarium; C. spermathecae (after Mangabeira 1942). B. beaupertuyi : D. ♀ cibarium; E. spermathecae (after Ortiz, 1963); F. ♂ genitalia (after Forattini, 1973). B. devenanzii : G. ♂ genitalia (after Ortiz 19).

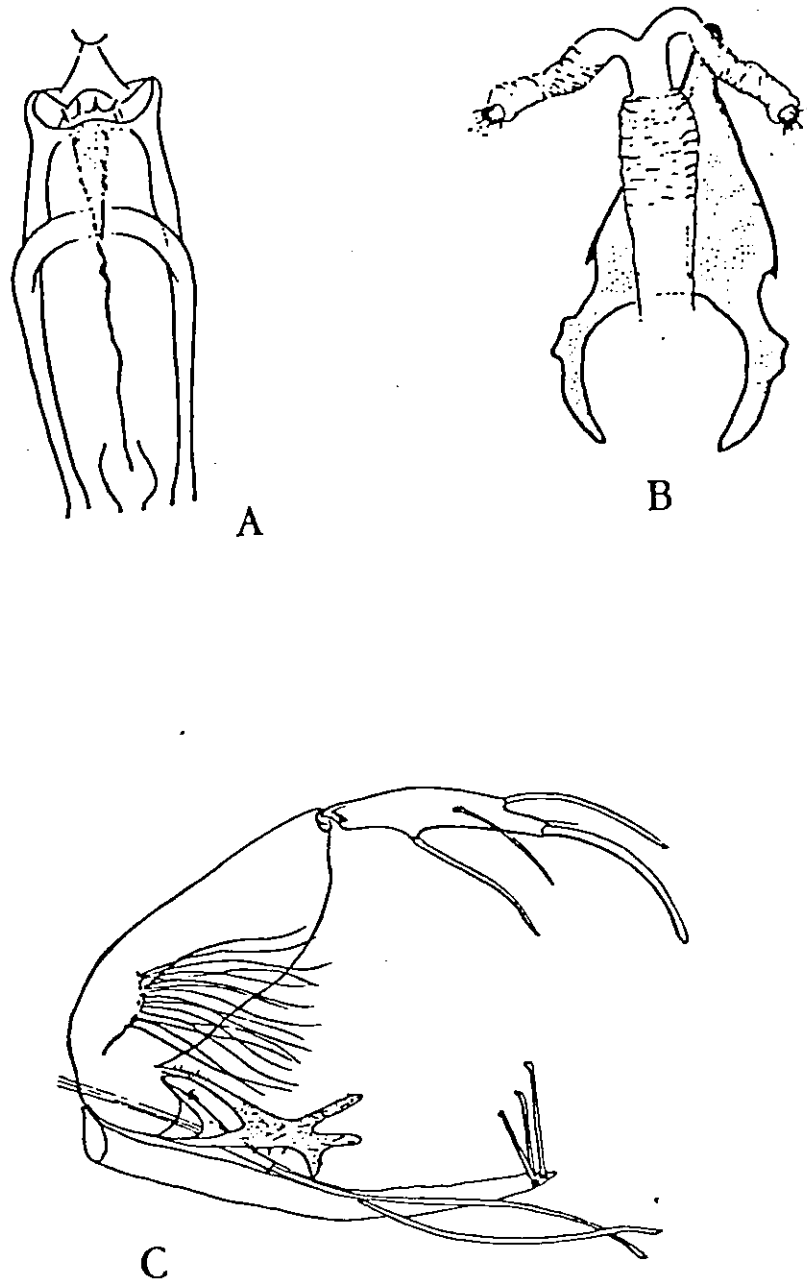


Fig. 29. Lutzomyia (Evandromyia) begonae : A. ♀ cibarium
B. spermathecae (after Young & Arias 1977);
C. ♂ genitalia (after Ortiz & Torres 1975).

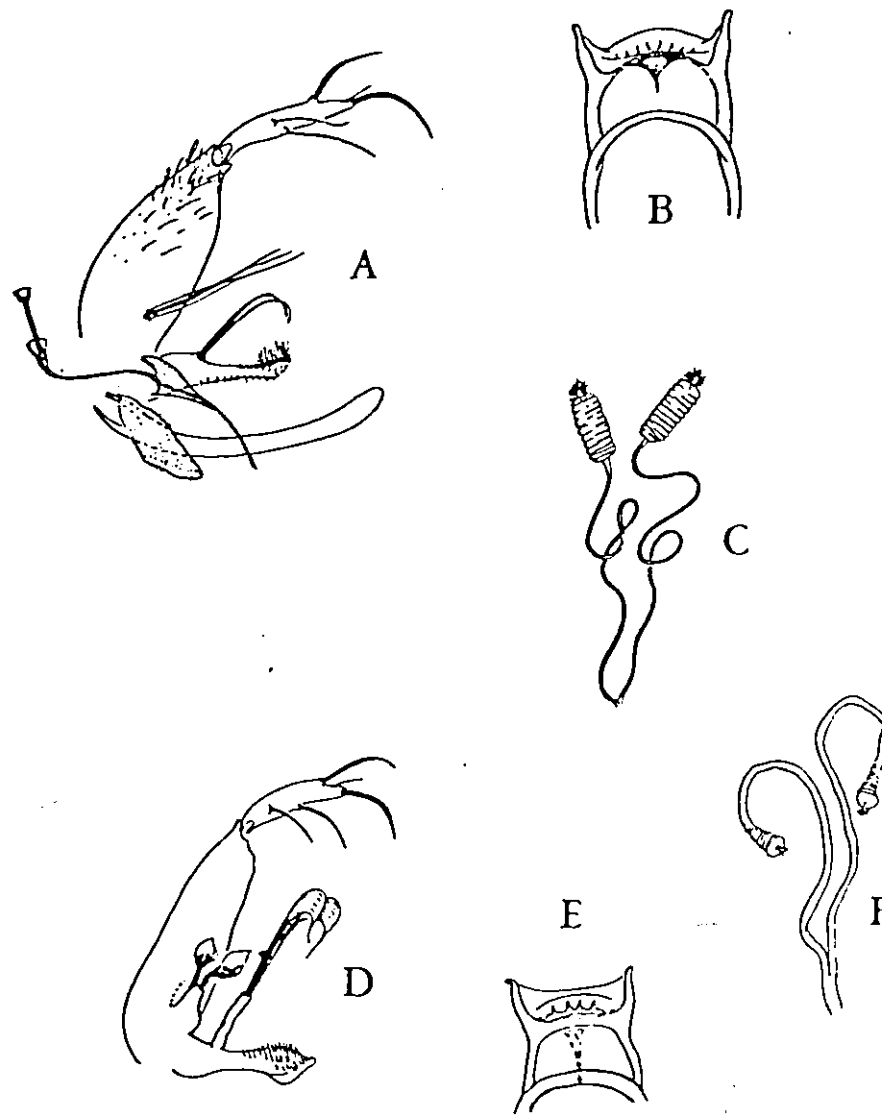


Fig. 30. Lutzomyia (Lutzomyia) longipalpis : A.♂ genitalia; B. ♀ cibarium; C. spermathecae. L.(L.) lichyi: D. ♂ genitalia; E. ♀ cibarium; F. Spermathecae (after Forattini 1973).

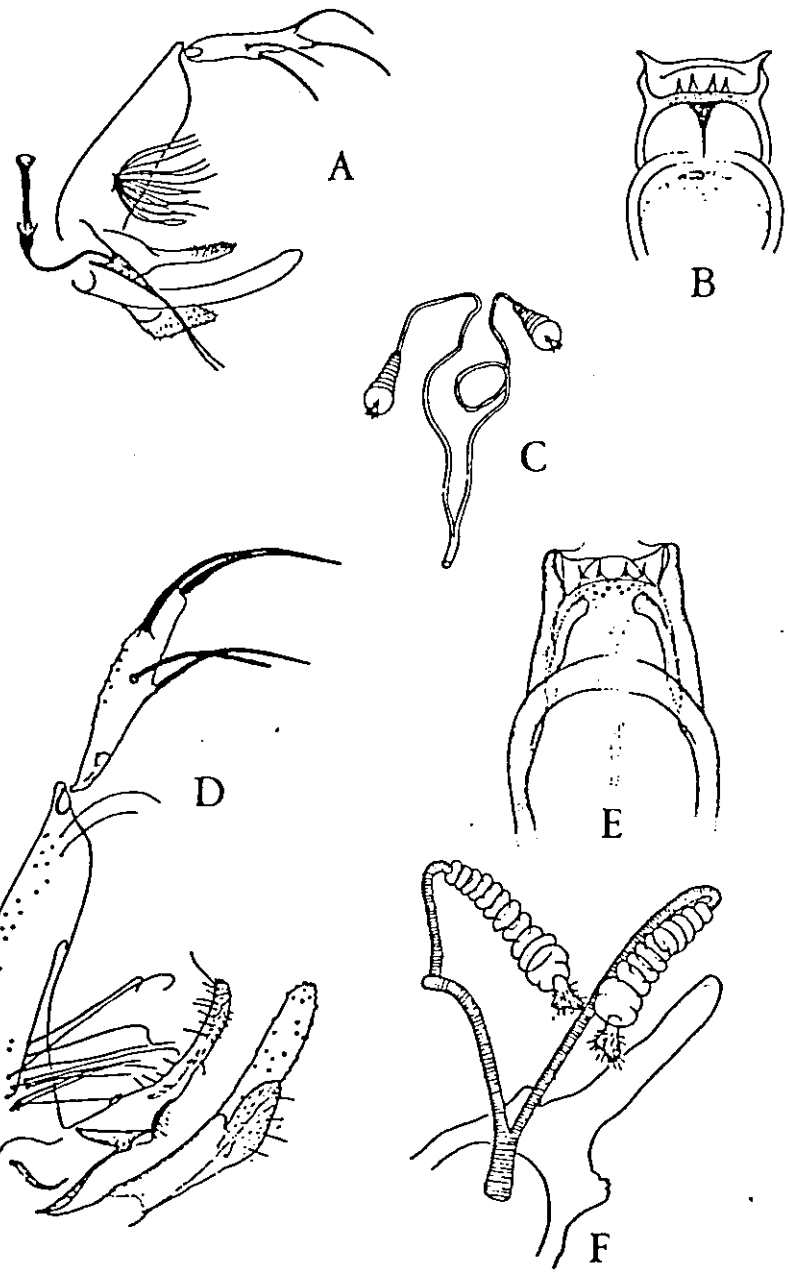


Fig. 31. Lutzomyia (Lutzomyia) gomezi: A.♂ genitalia; B. ♀ cibarium; C. spermathecae (after Forattini 1973). L.(L.) ignacioi: D. ♂ genitalia; E. ♀ cibarium; F. spermathecae (after Young, 1972).

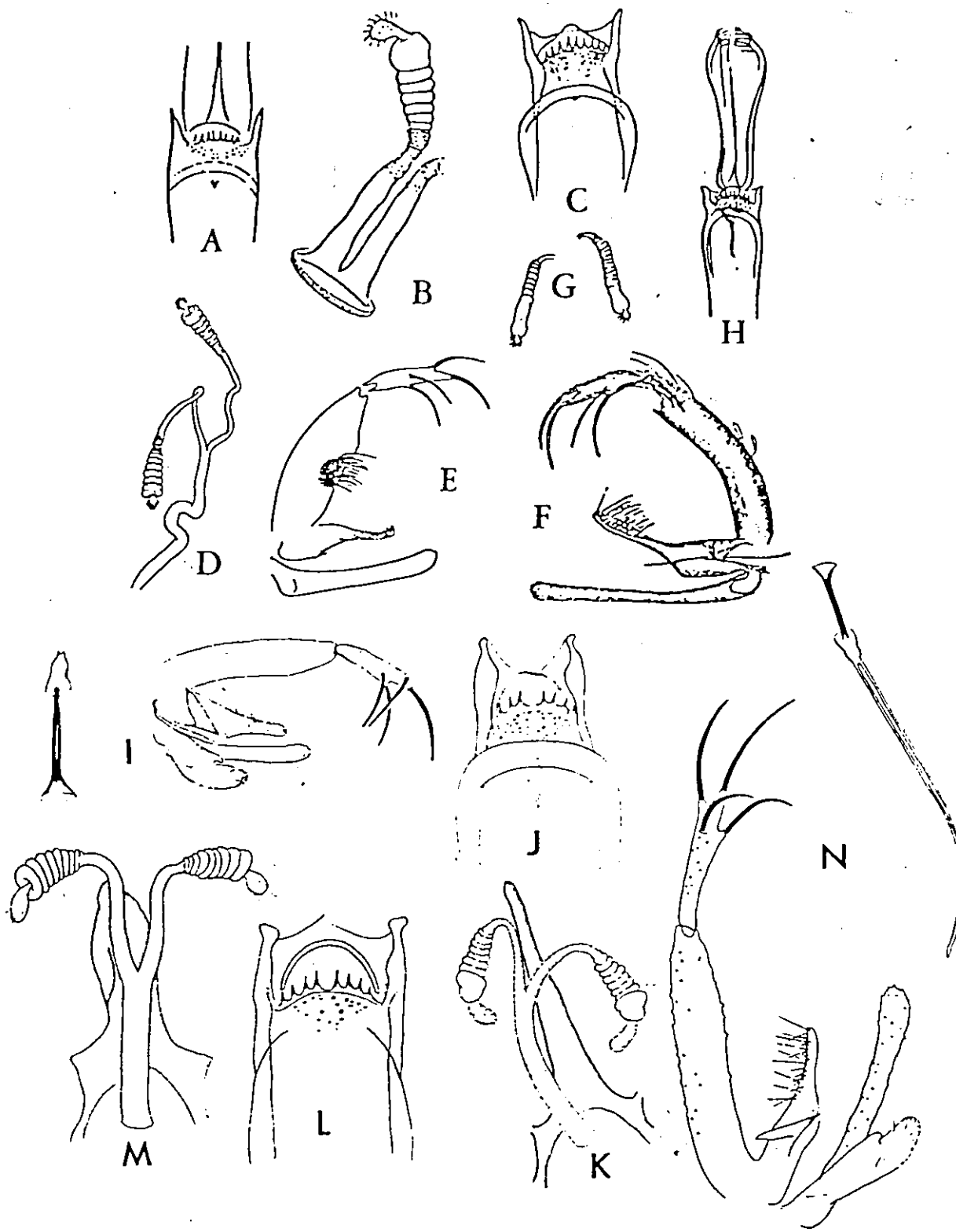


Fig. 32. Lutzomyia (Nyssomyia) anduzei: A. ♀ cibarium; B. spermathecae (after Rozeboom, 1942); L. (N.) antunesi : C. ♀ cibarium; D. spermathecae; E. ♂ genitalia (after Forattini, 1973). L. (N.) hernandezi : F. ♂ genitalia (after Ortiz, 1965); G. spermathecae; H. ♀ cibarium (after Ramirez Perez et al., 1979). L. (N.) flaviscutellata: I. ♂ genital pump and genitalia; J. ♀ cibarium; K. spermathecae. L. (N.) olmeca bicolor : L. ♀ cibarium; M. spermathecae; N. ♂ genital pump and genitalia (after Young 1979).

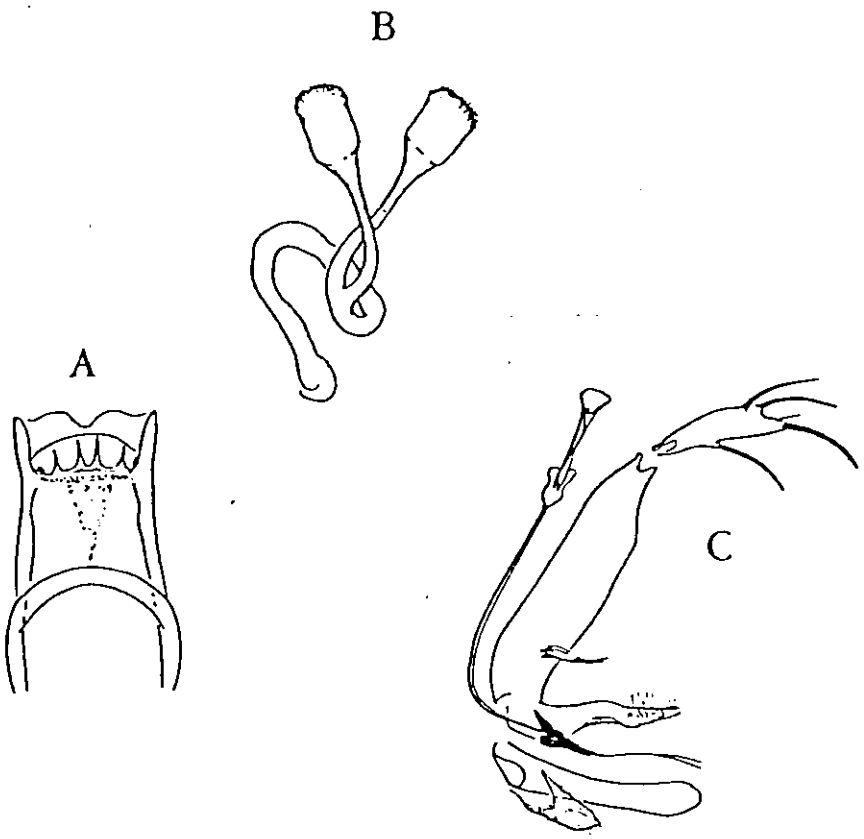


Fig. 33. Lutzomyia (Pintomyia) fischeri : A. ♀ cibarium; B. spermathecae; C. ♂ genitalia (after Forattini 1973).

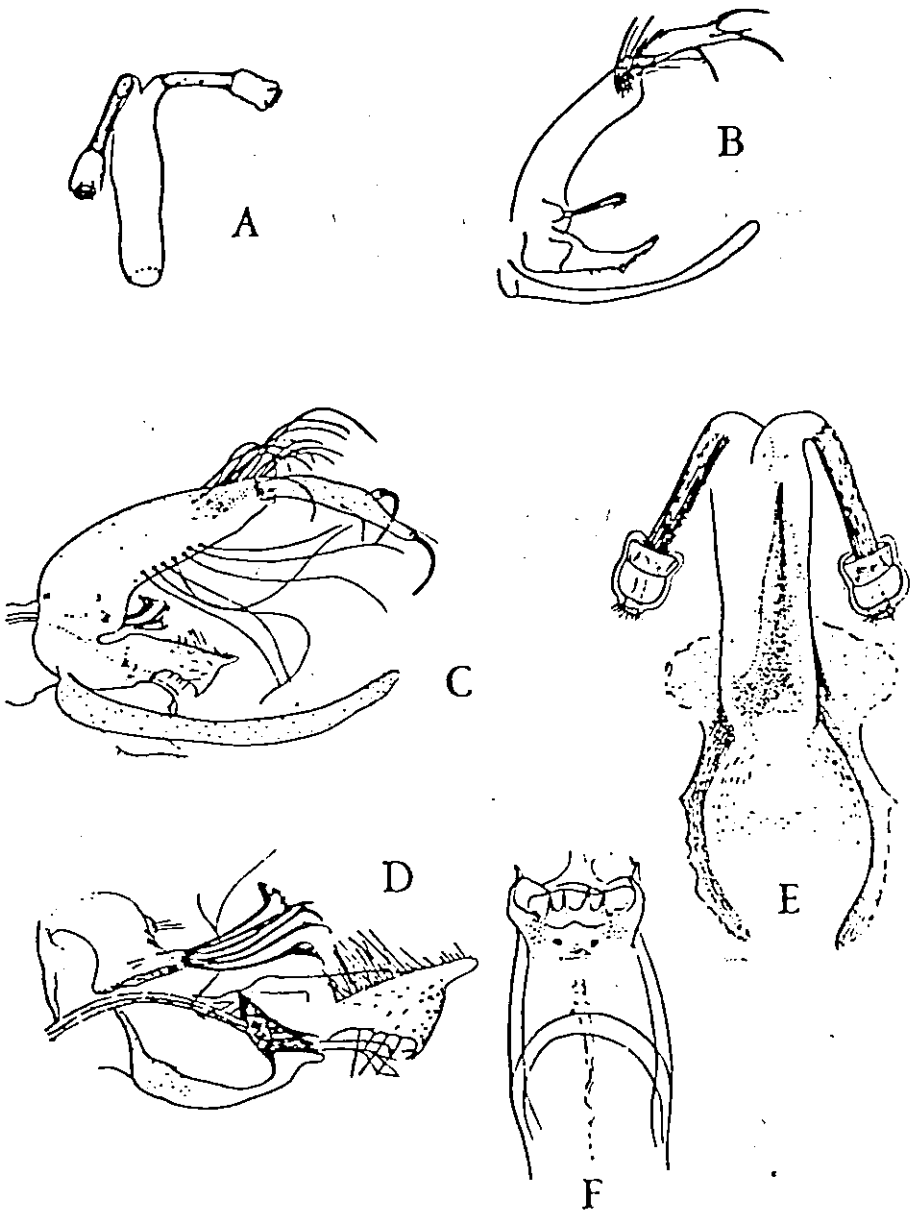


Fig. 34. Lutzomyia (Pressatia) dysponeta : A. spermathecae, B. ♂ genitalia (after Forattini 1973). L (P.) triacantha : C. ♂ genitalia; D. detail of ♂ genitalia; E. spermathecae; F. ♀ cibarium (after Mangabeira 1942).

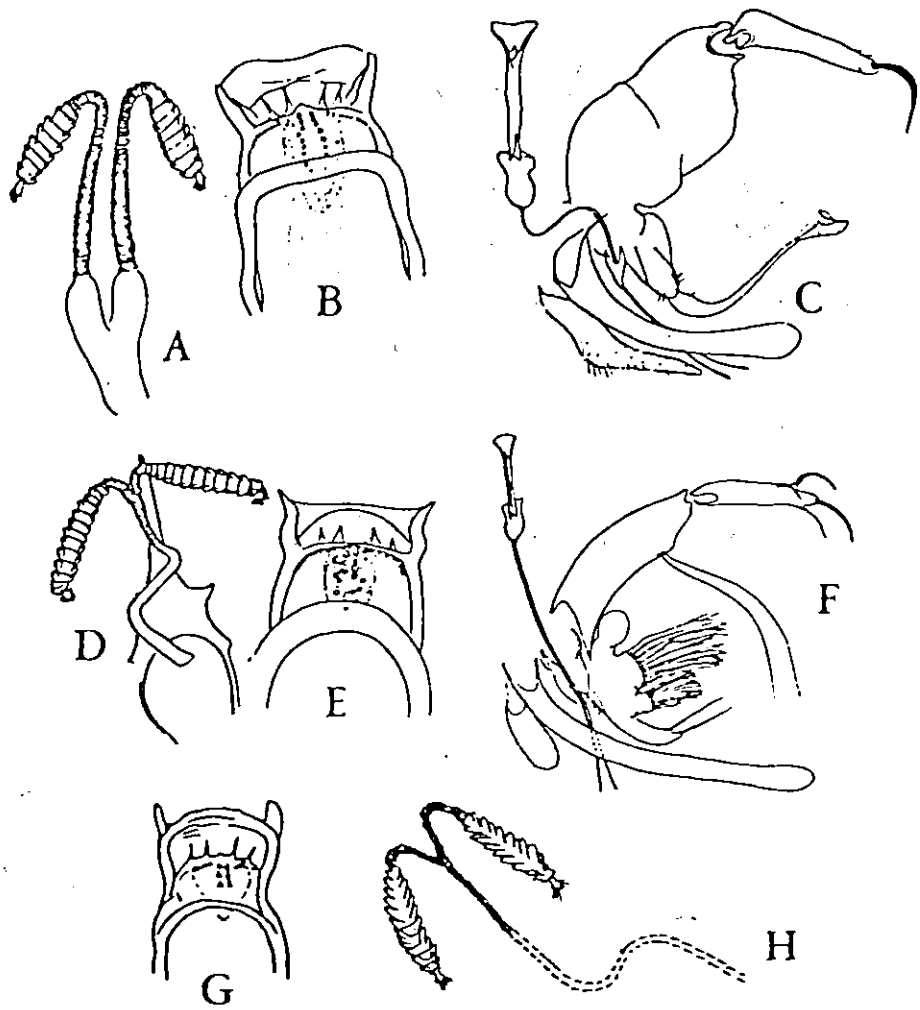


Fig. 35. Lutzomyia (Psychodopygus) squamiventris: A. spermathecae; B. ♀ cibarium; C. ♂ genitalia. L.(P.) panamensis : D. spermathecae; E. ♀ cibarium; F. ♂ genitalia (after Forattini 1973). L. (P.) parimaensis: G. ♀ cibarium; H. spermathecae (after Ortiz, 1972).

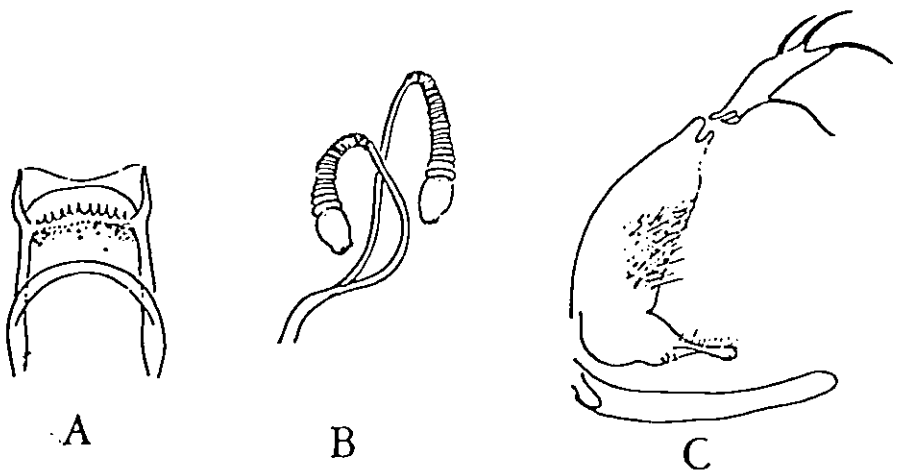


Fig. 36. Lutzomyia (Trichophoromyia) ubiquitalis: A. ♀ cibarium; B. spermathecae; C. ♂ genitalia (after Forattini 1973).

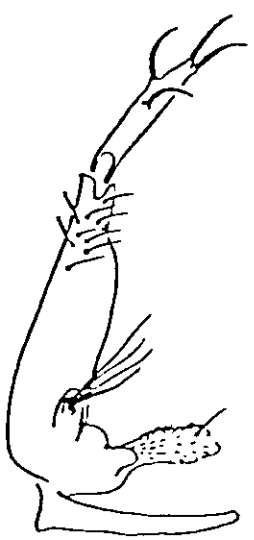


Fig. 37. Lutzomyia (baityi group). L. baityi : ♂ genitalia (after Forattini 1973).

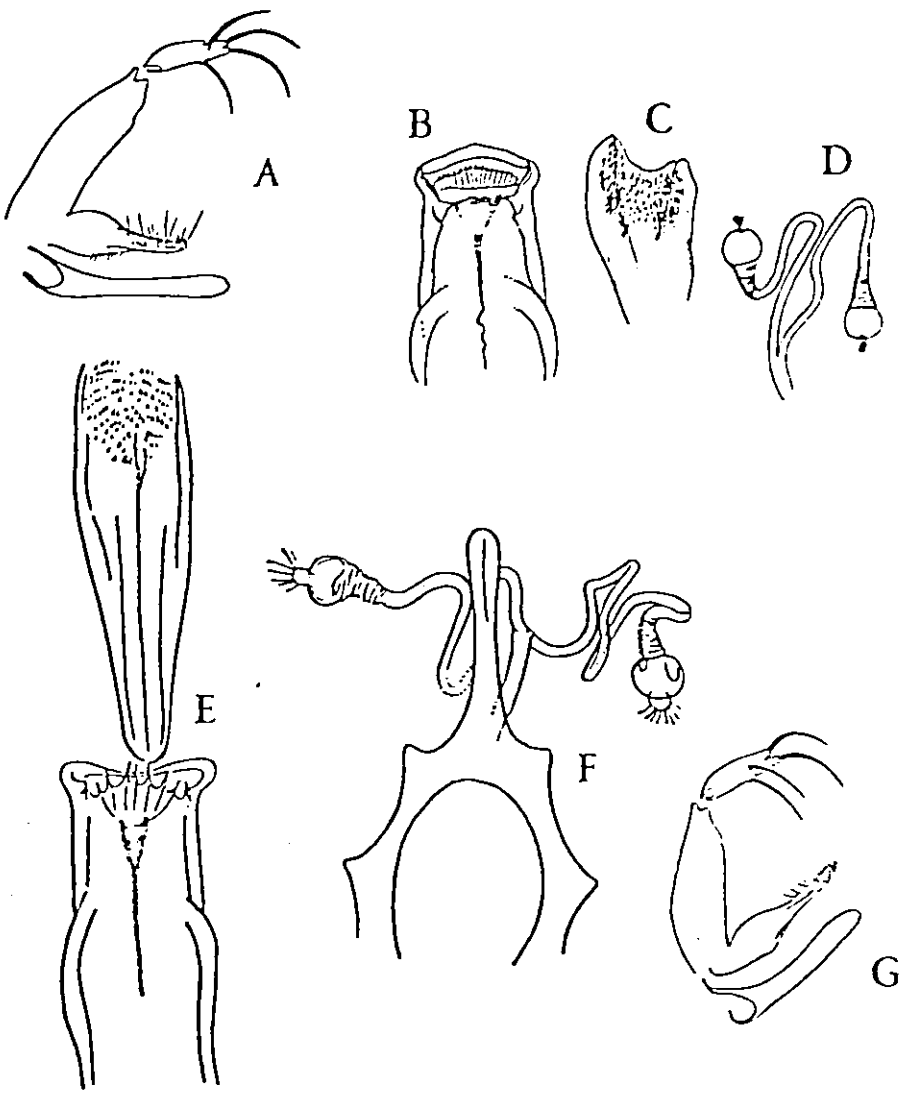


Fig. 38. Lutzomyia (cayennensis group). L. cayennensis cayennensis : A. ♂ genitalia; B. ♀ cibarium; C. pharynx; D. spermathecae. L. micropyga: E. ♀ cibarium, F. spermathecae (after Llanos et al., 1976); G. ♂genitalia (after Forattini, 1973).

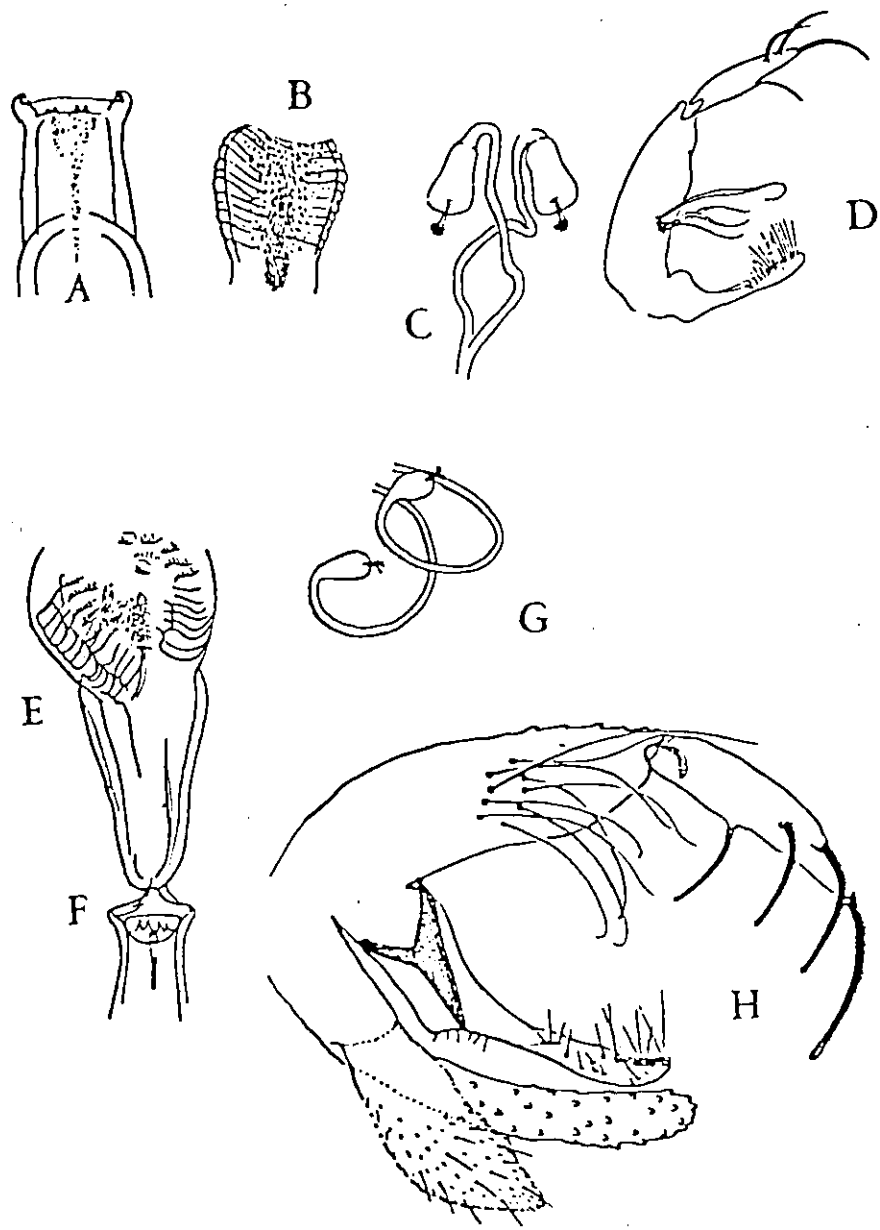


Fig. 39. Lutzomyia (cayennensis group). L. atroclavata: A. ♀ cibarium (after Young & Fairchild 1974); B. pharynx; C. spermathecae; D. ♂ genitalia (after Forattini 1973). L. venezuelensis: E. pharynx; F. ♀ cibarium; G. spermathecae (after Floch & Abonnenc 1948); H. ♂ genitalia (after Young & Fairchild 1974).

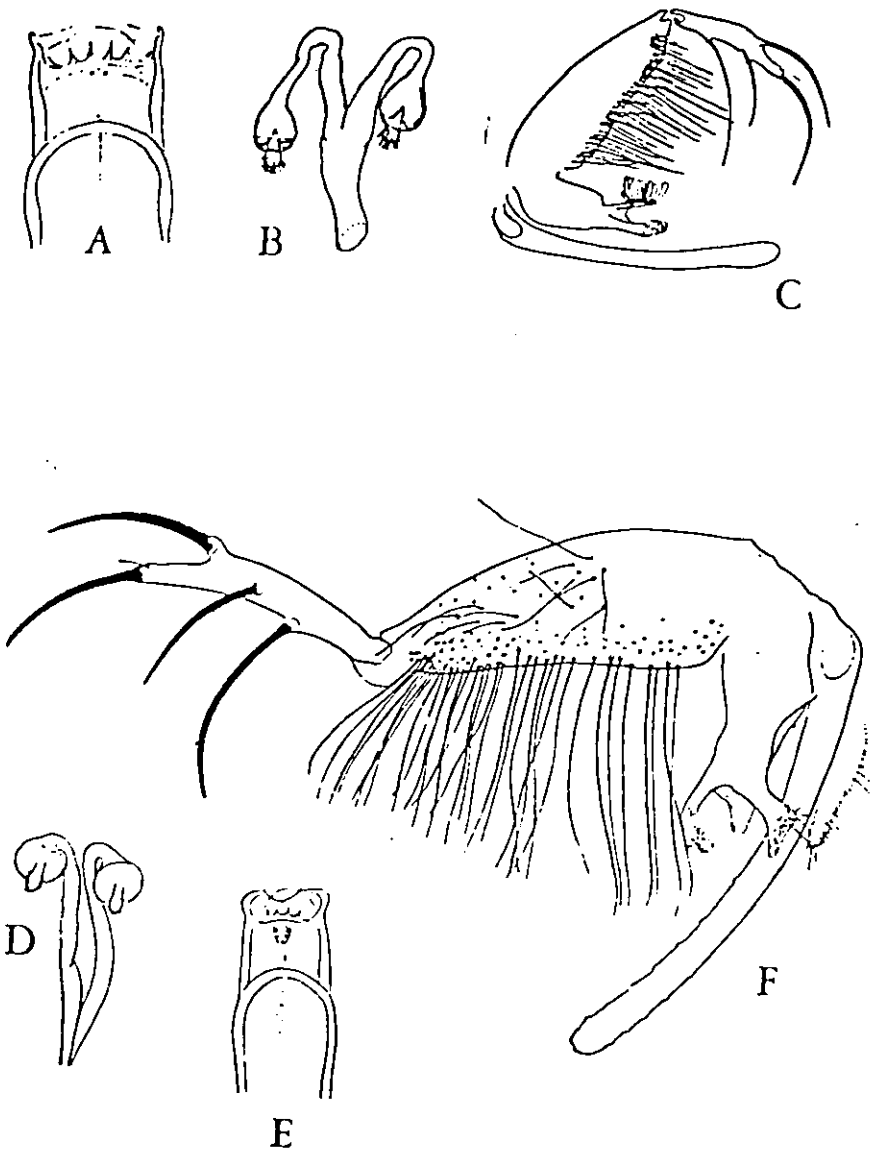


Fig. 40. Lutzomyia (longispina group). L. longispina: A. ♀ cibarium; B. spermathecae; C. ♂ genitalia (after Forattini 1973); L. conviti : D. spermathecae; E. ♀ cibarium; F. ♂ genitalia (after Ramirez-Perez et al., 1976).

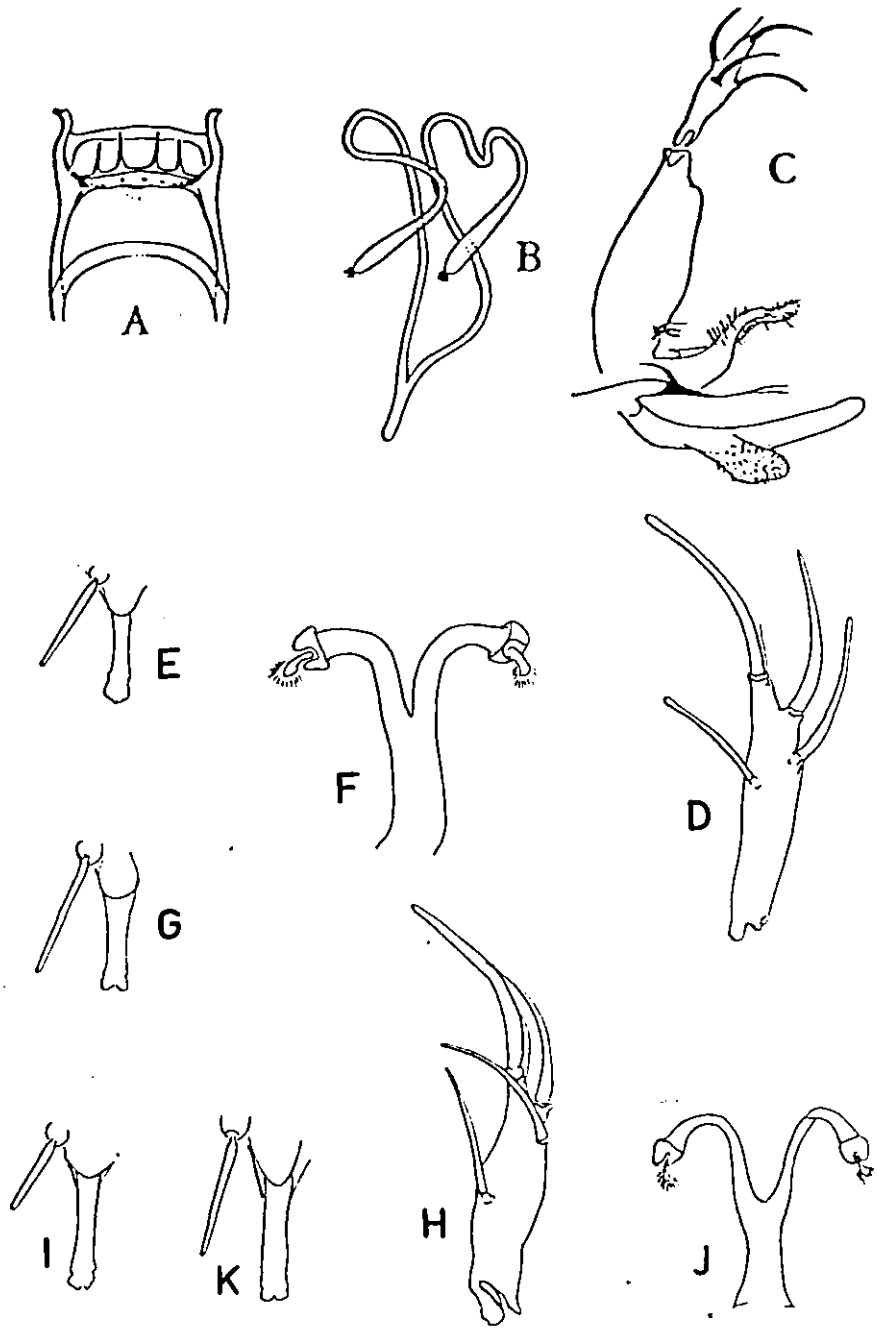


Fig. 41. Lutzomyia (migonei group). L. migonei: A. ♀ cibarium; B. spermathecae; C. ♂ genitalia (after Forattini 1973). L. dubitans : D. ♂ style; E. ♂ Flagellomere I (FI) and Labrum (L); F. spermathecae; G. ♀ FI and L. L. walkeri : H. ♂ genitalia; I. ♂ FI and L; J. spermathecae; K. ♀ FI and L. (present work).

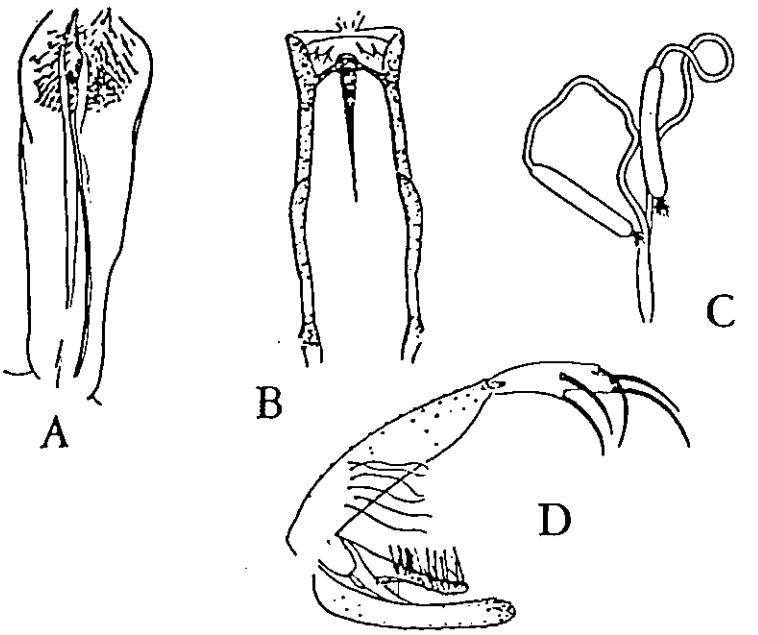


Fig. 42. Lutzomyia (oswaldoi group). L. trinidadensis: A. pharynx; B. ♀ cibarium; C. spermathecae; D. ♂ genitalia (after Forattini 1973).

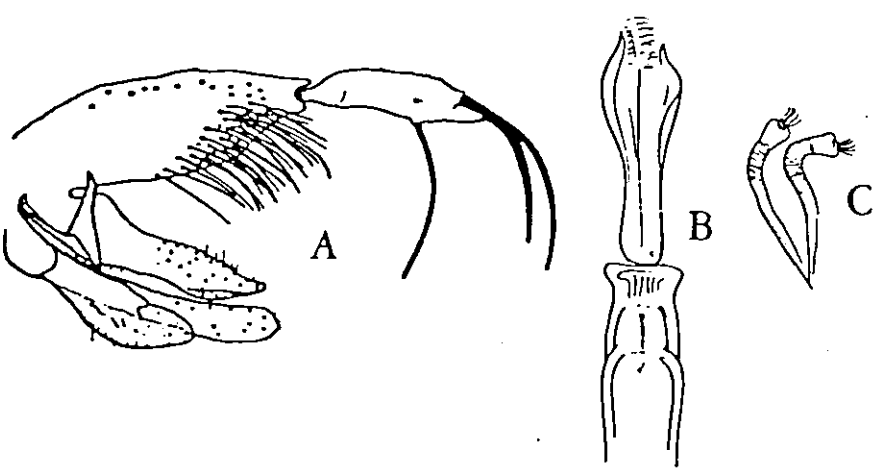


Fig. 43. Lutzomyia (pilosa group). L. pilosa: A. ♂ genitalia (after Young & Fairchild, 1974); B. ♀ pharynx and cibarium; C. spermathecae (after Ramirez Perez et al. 1979).

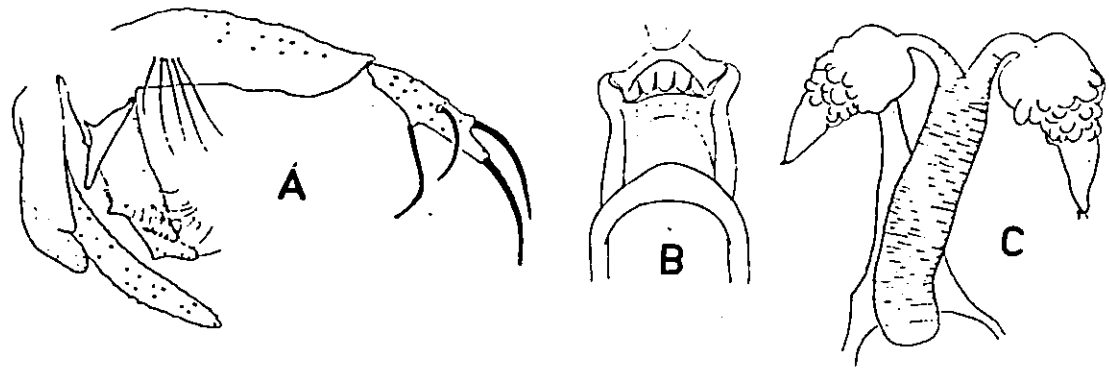


Fig. 44. Lutzomyia (saulensis group). L. saulensis: A. ♂ genitalia; B. ♀ cibarium; C. spermathecae (after Young, 1979).

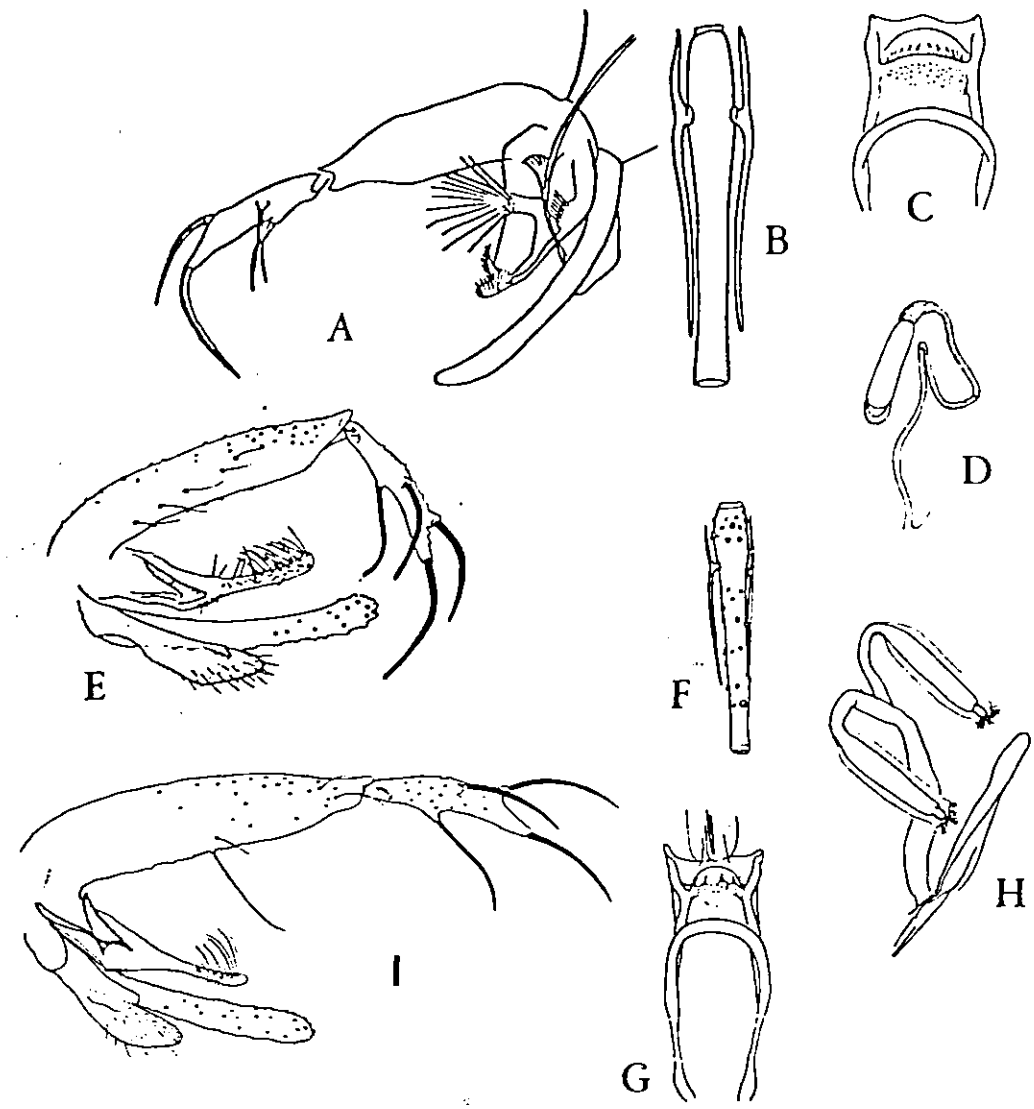


Fig. 45. Lutzomyia (shannoni group). L. dasymera: A. ♂ genitalia; B. antennal ascoids (after Marmol Leon 1968); C. ♀ cibarium; D. spermathecae (after Forattini 1973). L. shannoni E. ♂ genitalia; F. antennal ascoids; G. ♀ cibarium; H. spermathecae (after Fairchild & Hertig 1950); L. abonnenci: I. ♂ genitalia (after Young 1979).

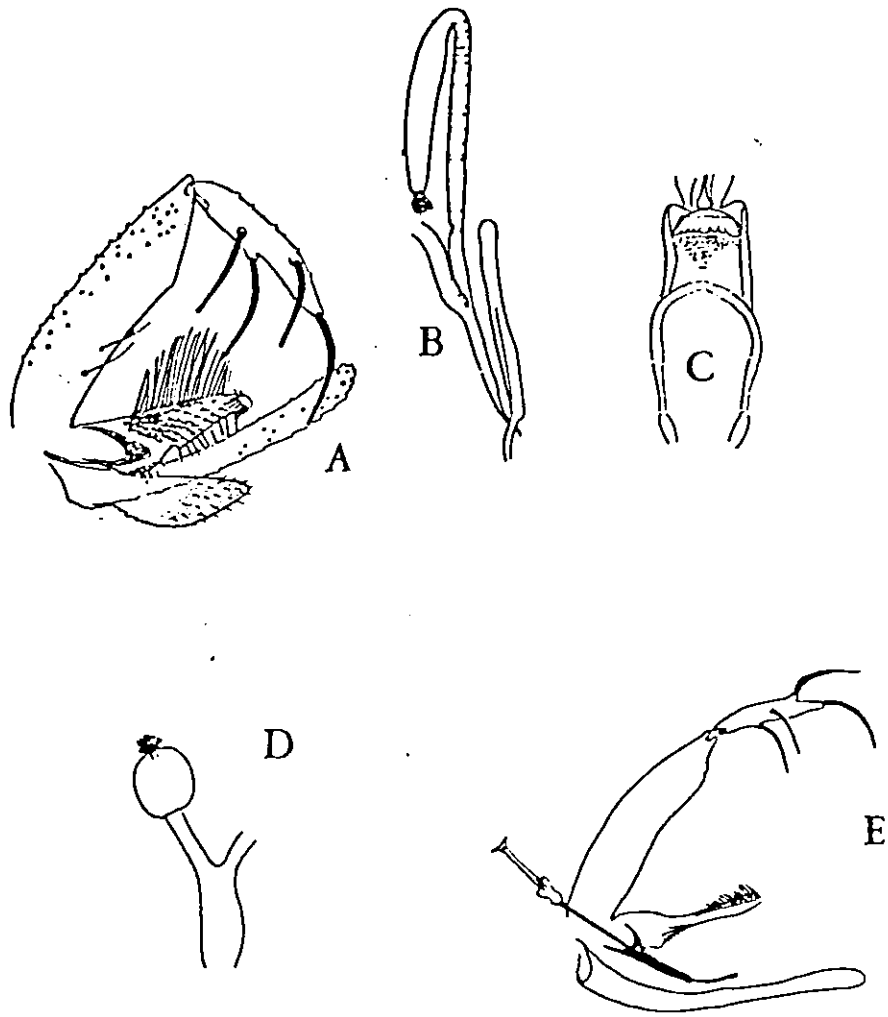


Fig. 46. Lutzomyia (shannoni group). L. punctigeniculata; A. ♂ genitalia; B. spermathecae; C. ♀ cibarium, (after Fairchild & Hertig 1950).
L. lutziana : D. spermathecae; E. ♂ genitalia (after Forattini 1973).

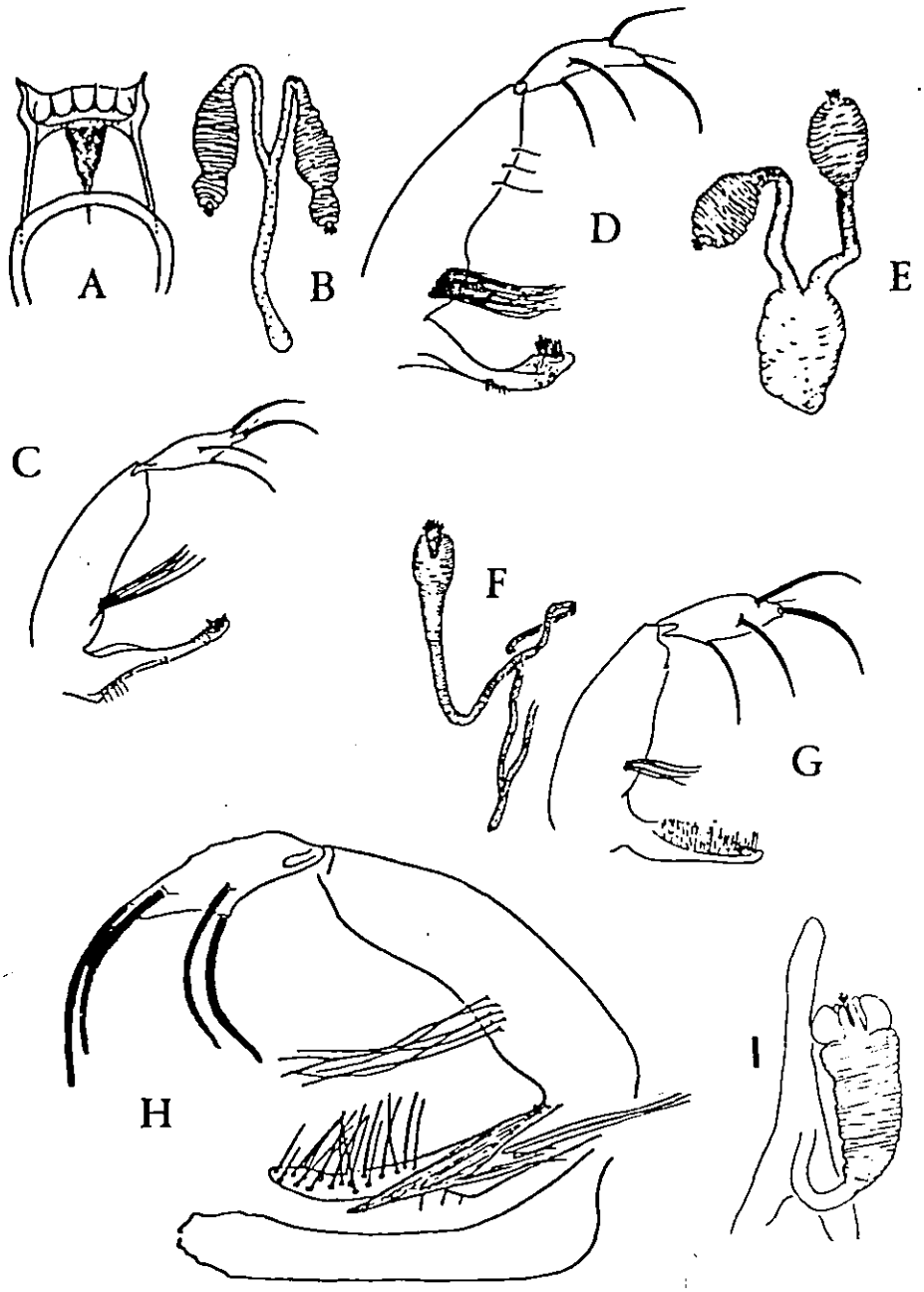


Fig. 47. Lutzomyia (verrucarum group). L. ovallesi: A. ♀ cibarium; B. spermathecae; C. ♂ genitalia. L. columbiana: D. ♂ genitalia; E. spermathecae. L. evansi: F. spermathecae; G. ♂ genitalia (after Forattini 1973). L. nuneztovari: H. ♂ genitalia (after Ortiz 1954); I. spermathecae (after Young 1979).

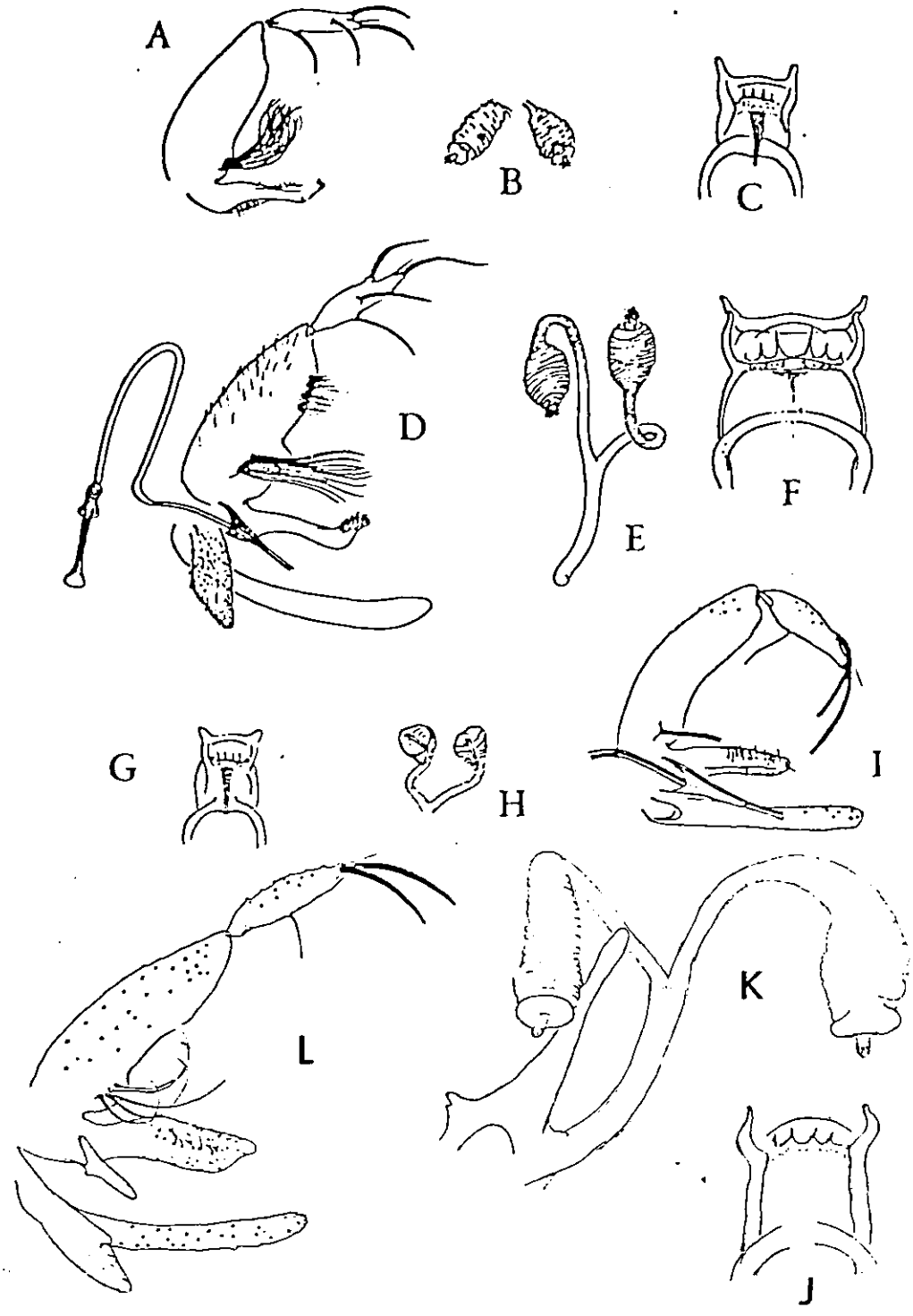


Fig. 48. Lutzomyia (verrucarum group). L. townsendi: A. ♂ genitalia (after Forattini 1973). B. spermathecae; C. ♀ cibarium (after Ortiz & Scorza 1963). L. verrucarum: D. ♂ genitalia; E. spermathecae; F. ♀ cibarium (after Forattini 1973). L. ottolinai : G. ♀ cibarium, H. spermathecae; I. ♂ genitalia (after Ortiz & Scorza 1963). L. serrana. J. ♀ cibarium; K. spermathecae; L. ♂ genitalia (after Young 1979).

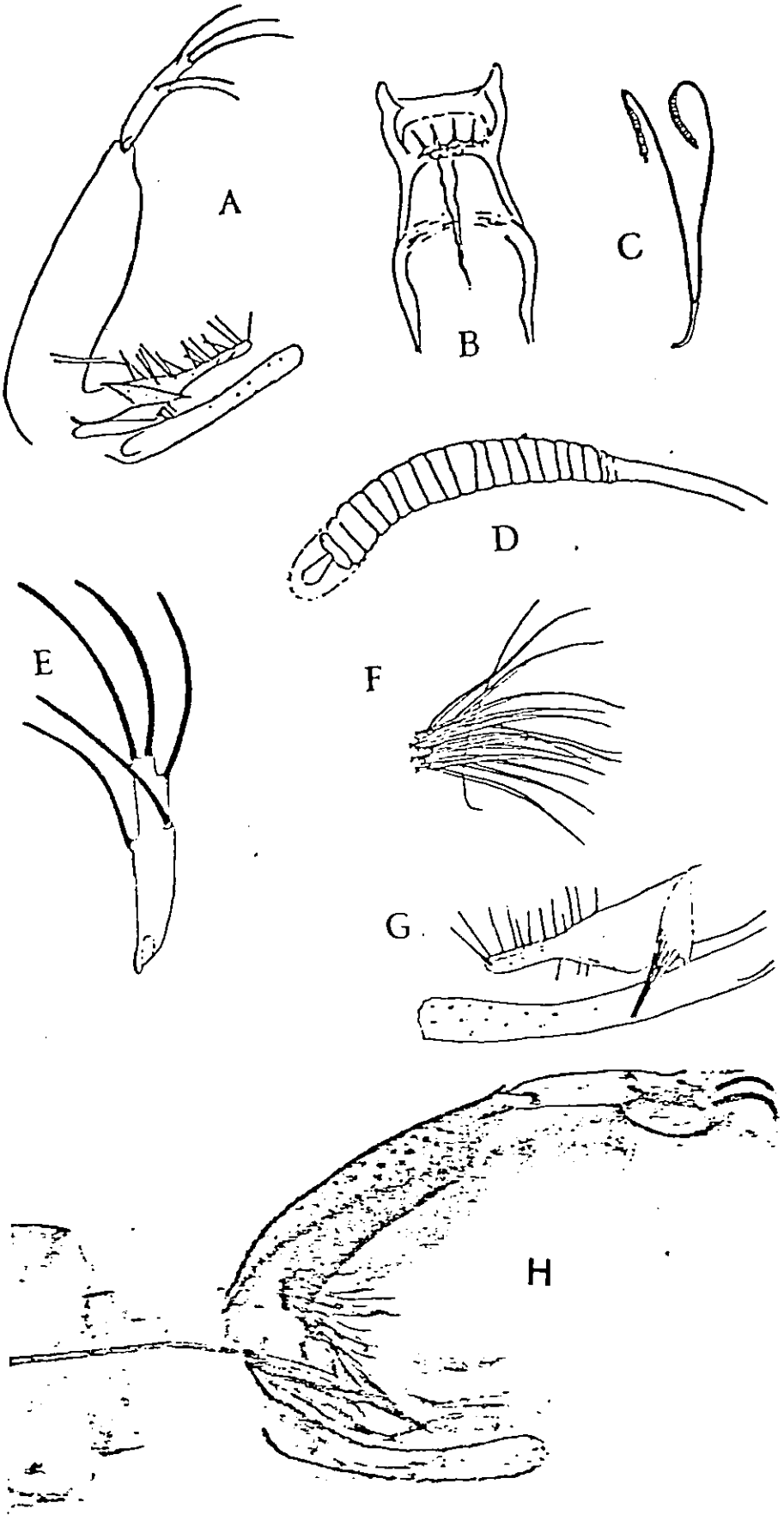


Fig. 49. Lutzomyia (vexator group). L. scorzai : A. ♂ genitalia; B. ♀ cibarium; C. D. spermathecae (after Ortiz 1965). L. ceferinoi: E. dististyle; F. tuft of basistyle; G. paramere and lateral lobe (after Ortiz & Alvarez 1963). L. erwindonaldoi : H. ♂ genitalia (after Ortiz 1978).

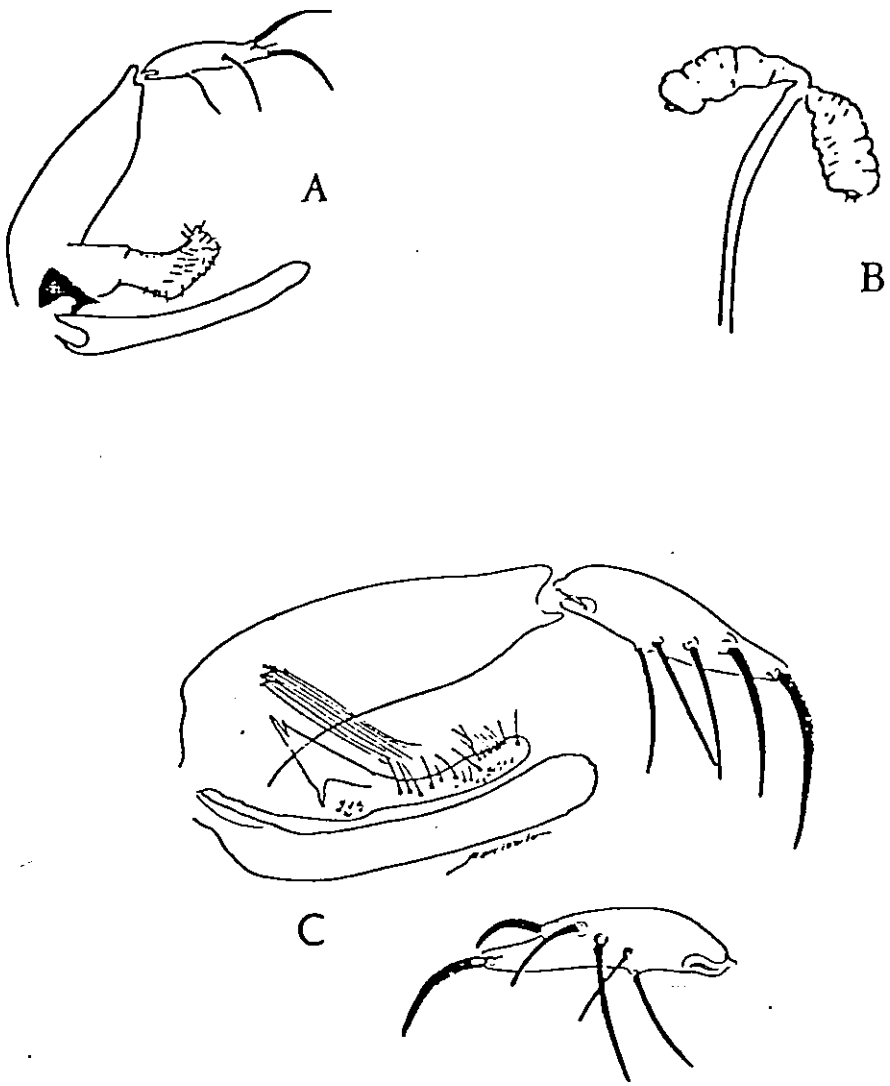


Fig. 50. Ungrouped. L. rangeliana : A. ♂ genitalia (after Forattini 1973); B. spermathecae (after Pifano et al. 1962). L. torrealbai: C. ♂ genitalia (after Vianna Martins et al 1977).

3.3.7 Geographical distribution of Venezuelan sandflies

Venezuela is a South-American country of about 912.000 km^2, between latitude $0^o45'$ and $12^o15'$ North and longitude $59^o45'$ and $73^o30'$ West. Fig. 51 shows the administrative division of the country into 23 States and the principal features of the physiogeography of Venezuela. This includes three mountain groups reaching up to 5,000 m. above mean sea level viz: the Andes in the East, the "Cordillera de la Costa" fringing the Caribbean coast in the North and the "Escudo Guayanes" in the South. The central area is occupied by the "Llanos".

Twenty two "life zones" have been described in Venezuela (Fig. 52, Ewel & Madriz, 1968). Because the climate and vegetation are very varied in the mountainous areas, these places contain many different life zones. The extensive flat areas show more uniformity.

In Fig 53 the collection area is shown; this gives an idea on the differences in intensity with which different parts of Venezuela have been surveyed for phlebotomine sandflies. Geographical coordinates for the sites are given in Appendix 1.

There are no records for two Western States: Anzoategui and Territorio Federal Delta Amacuro, only one report for Monagas, Bolivar and Barinas, two reports for Portuguesa, Merida, Lara, Falcón and Nueva Esparta States, three reports for Tachira, Distrito Federal, Territorio Federal Amazonas and Yaracuy and five references for Zulia, Miranda and Sucre.

Many more sandfly collections have been made in the remaining 6 States: Apure, Aragua, Carabobo; Cojedes, Guarico and Trujillo. Those form a small area, about 1/5 of the total.

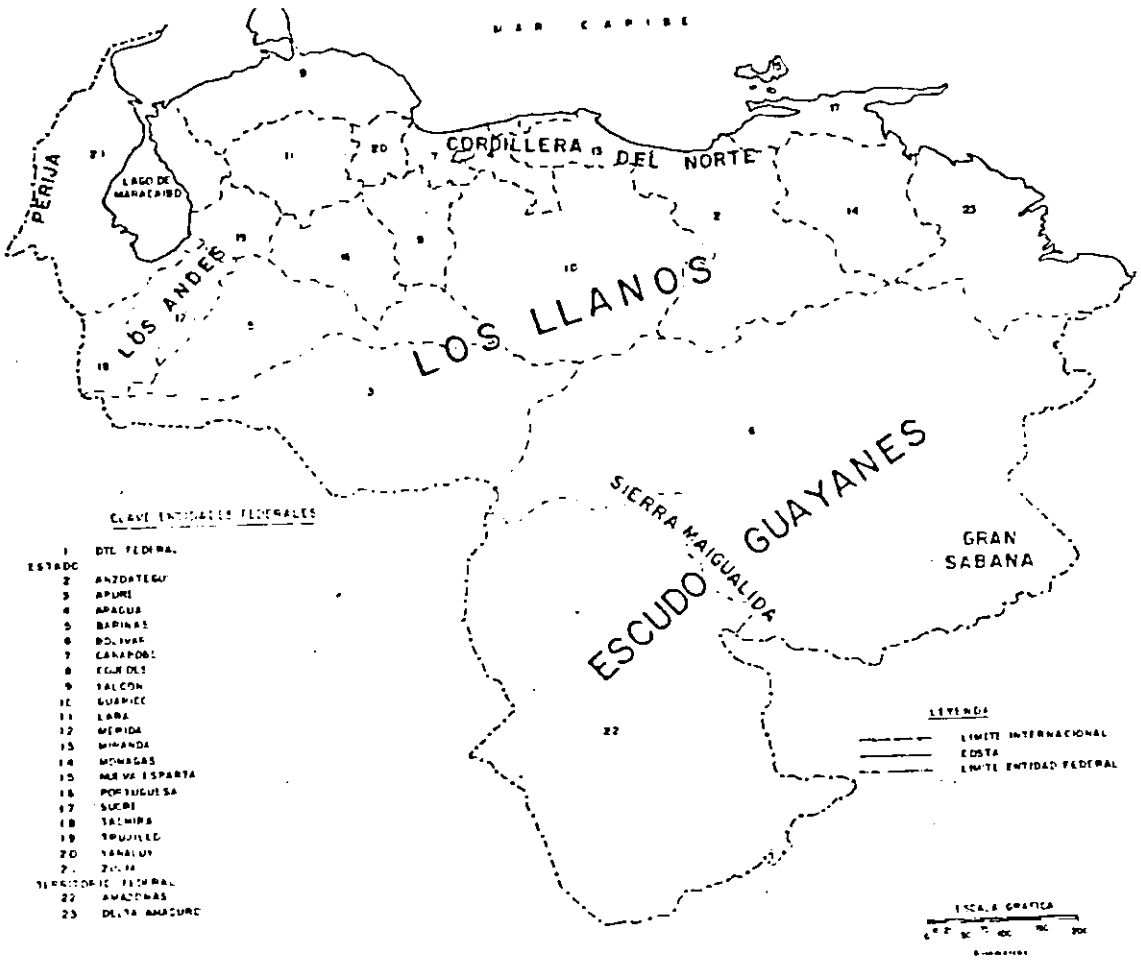
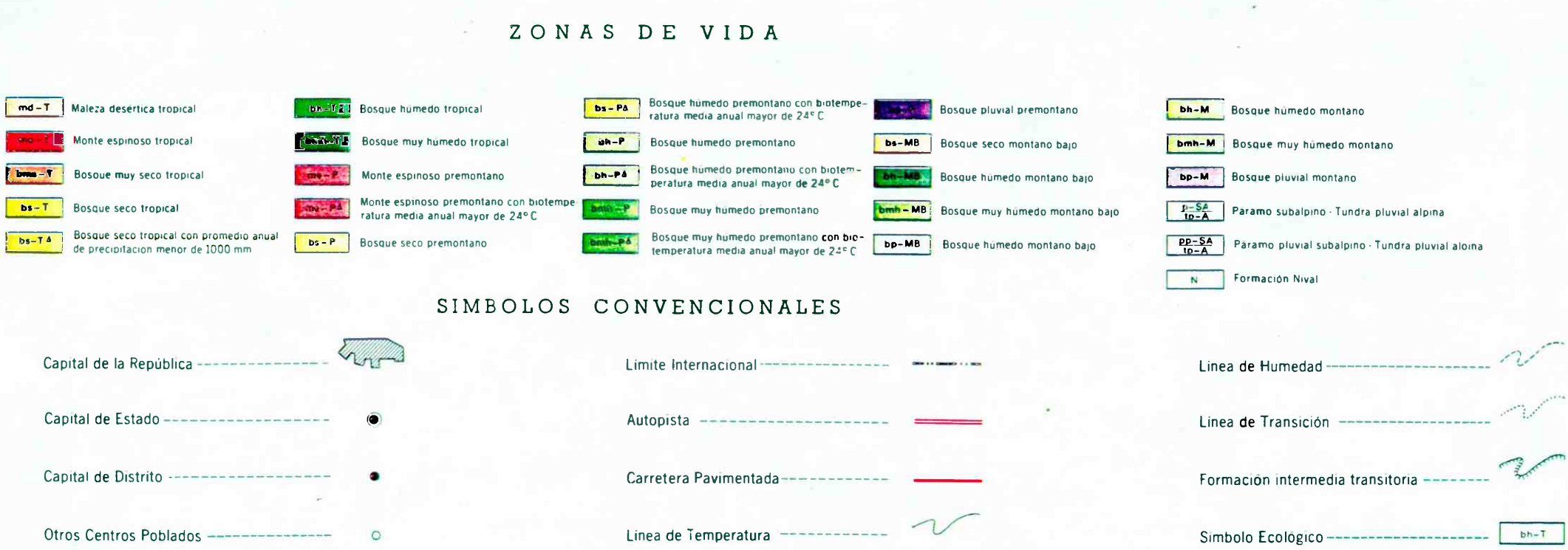


Fig. 51. Administrative divisions and main geographical features of Venezuela (after Ewel & Madriz 1968).

Fig. 52. Life zones of Venezuela (after Ewel & Madriz 1968); Key to the Map.



FUENTE : MINISTERIO DE AGRICULTURA Y CRIA - FONDO NACIONAL DE INVESTIGACIONES AGROPECUARIAS 1976.
COLABORACIÓN : INSTITUTO INTERAMERICANO DE CIENCIAS AGRICOLAS DE LA ORGANIZACIÓN DE ESTADOS AMERICANOS - ZONA ANDINA 1965. - MARNR - DIRECCIÓN DE CARTOGRAFÍA NACIONAL.


MAR CARIBE
OCEANO ATLANTICO
REPUBLICA DE VENEZUELA
MAPA ECOLOGICO
ZONA EN RECLAMACION

Table 15. Distribution of Venezuelan sandflies according to the life zones.

	LIFE ZONES								
	Tropical wet forest (bmh-T)	Tropical moist forest (bh-T)	Tropical dry forest (bs-T)	Tropical very dry forest (bms-T)	Tropical thorn woodland (me-T)	Lower Montane wet forest (bmh-P)	Lower Montane moist forest (bh-P)	Lower Montane dry forest (bs-P)	Lower Montane dry forest (bs-P)
L. longipalpis			x	x	x		x	x	x
L. panamensis		x	x	x	x	x	x		
L. lichyi		x	x		x	x	x		x
L. gomezi		x	x	x	x	x	x		x
L. cayennensis		x	x	x		x	x	x	x
L. micropyga		x	x			x	x		x
L. venezuelensis		x	x	x			x	x	
L. atroclavata		x	x	x	x	x	x	x	x
L. migonei		x	x	x		x	x	x	x
L. dubitans		x	x			x	x		x
L. walkeri	x		x				x		
L. trinidadensis		x	x	x	x	x	x	x	x
L. punctigeniculata			x	x		x	x		x
L. shannoni		x	x	x		x	x	x	x
L. evansi		x	x	x	x	x	x		x
L. ovallesi		x	x			x	x		x
L. rangeliana		x	x		x		x	x	x
L. townsendi	x	x							
L. begonae		x							
L. ignacioi	x								
L. anduzei							x		
L. antunesi		x	x						
L. flaviscutellata						x	x		
L. olmeca bicolor		x	x						
L. hernandezi		x					x		
L. fischeri							x		
L. dysponeta			x						
L. triacantha			x						
L. squamiventris							x		x
L. parimaensis						x			
L. ubiquitalis			x						
L. baityi			x						
L. yencanensis		x							
L. longispina							x		
L. conviti		x							

Table 15 (Continued)

	LIFE ZONES								
	Tropical wet forest (bmh-T)	Tropical moist forest (bh-T)	Tropical dry forest (bs-T)	Tropical very dry forest (bms-T)	Tropical thorn woodland (me-T)	Lower Montane wet forest (bmh-P)	Lower Montane moist forest (bh-P)	Lower Montane dry forest (bs-P)	Lower Montane dry forest (bs-P)
L. pilosa		x	x						
L. saulensis			x						
L. abonnenci			x						
L. dasymera			x						
L. lutziana		x							
L. columbiana	x								
L. nuneztovari		x						x	
L. verrucarum	x		?						
L. ottolinai		x							
L. serrana									
L. ceferinoi		x							
L. scorzai		x							
L. erwindonaldoi		x							
L. torrealbai	x						x		
L. maracayensis							x		
L. .sp. of Chiricoca		x							
L. .sp. of La Vaquira			x						
L. .sp. of Monay			x						
L. sp. of Bitichas							x		
L. sp. of Loma Abajo							x		
B. avellari		x							
B. beaupertuyi		x	x			x		x	
B. devenanzii		x							

* For symbols in brackets see legend of Fig. 52.

Trujillo State has been very well explored. 42,000 sandflies were collected in 280 localities in an intensive study carried out by the Dirección de Malariologia y Saneamiento Ambiental and the University of Carabobo. The altitudinal distribution of the anthro pophilic species from 0 to 1900 m was analyzed (Mogollón et al., 1977) but unfortunately a full record of sandflies caught and the areas explored were not given. Precise locations could be found only for unidentified specimens from that collection, which have since been re-examined and named (present study). Species recorded by Mogollón et al., (loc.cit.) without details of their collection sites, are denoted on the maps by a square in the centre of Trujillo State.

In Figs. 54 to 79 the known distribution of the 53 species of sandflies found in Venezuela is shown.

Map coordinates were used to locate the precise area where the sandflies were collected and these were correlated with the various life zones. Sandflies have been caught in only 9 of 22 life zones (Table 15) (though this figure can only be an approximation - like the life zone maps themselves).

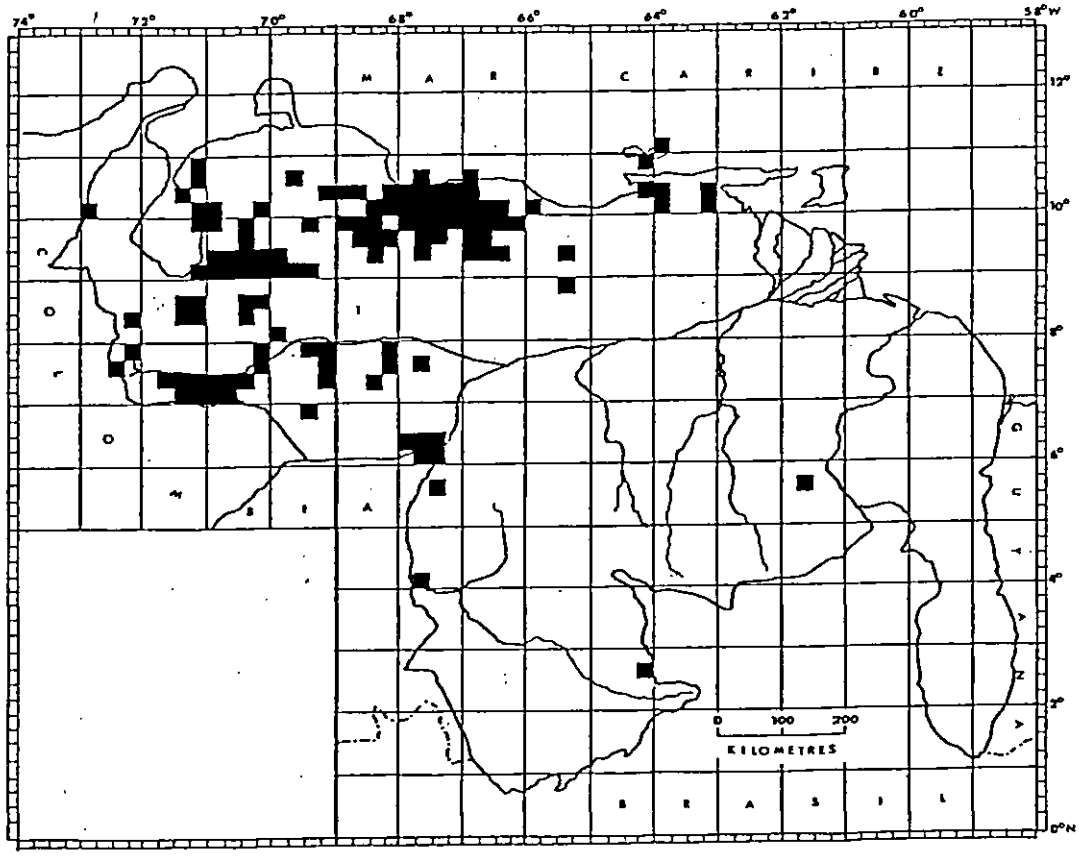


Fig. 53. Areas in Venezuela surveyed for sandflies.

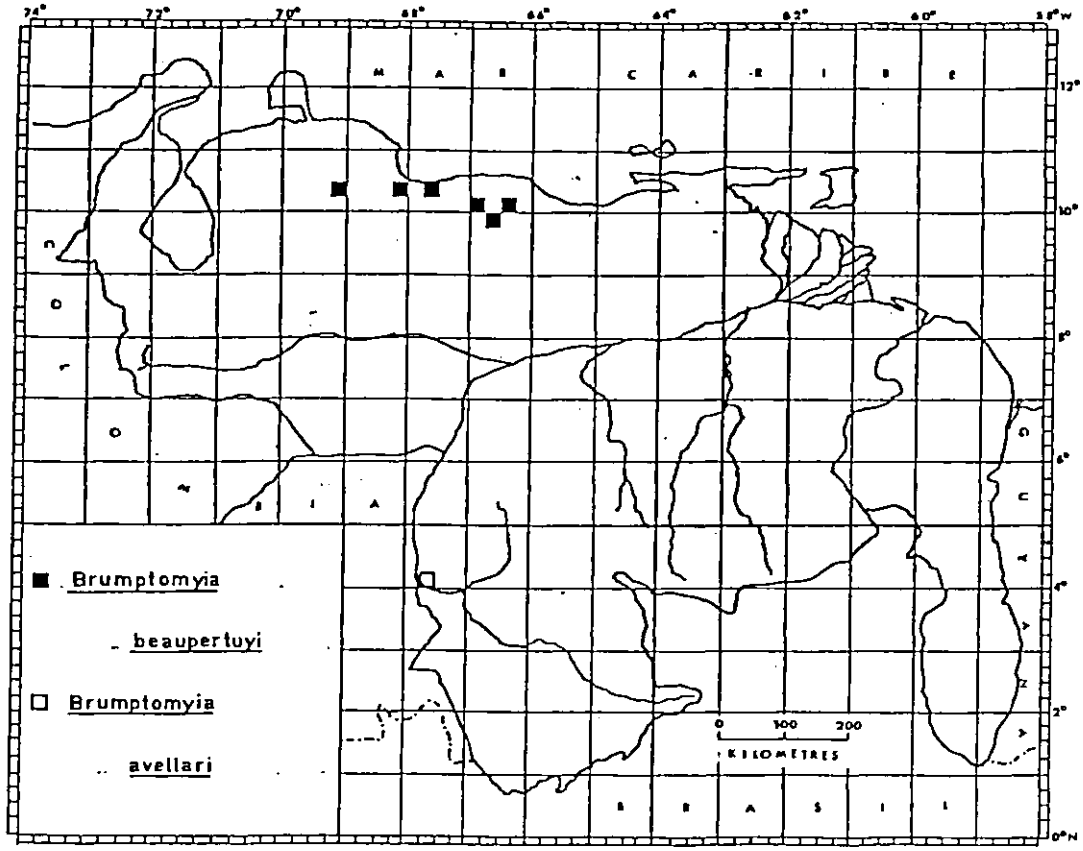

Brumptomyia
beaupertuyi
Brumptomyia
avellari
0 100 200
KILOMETRES

Fig. 54

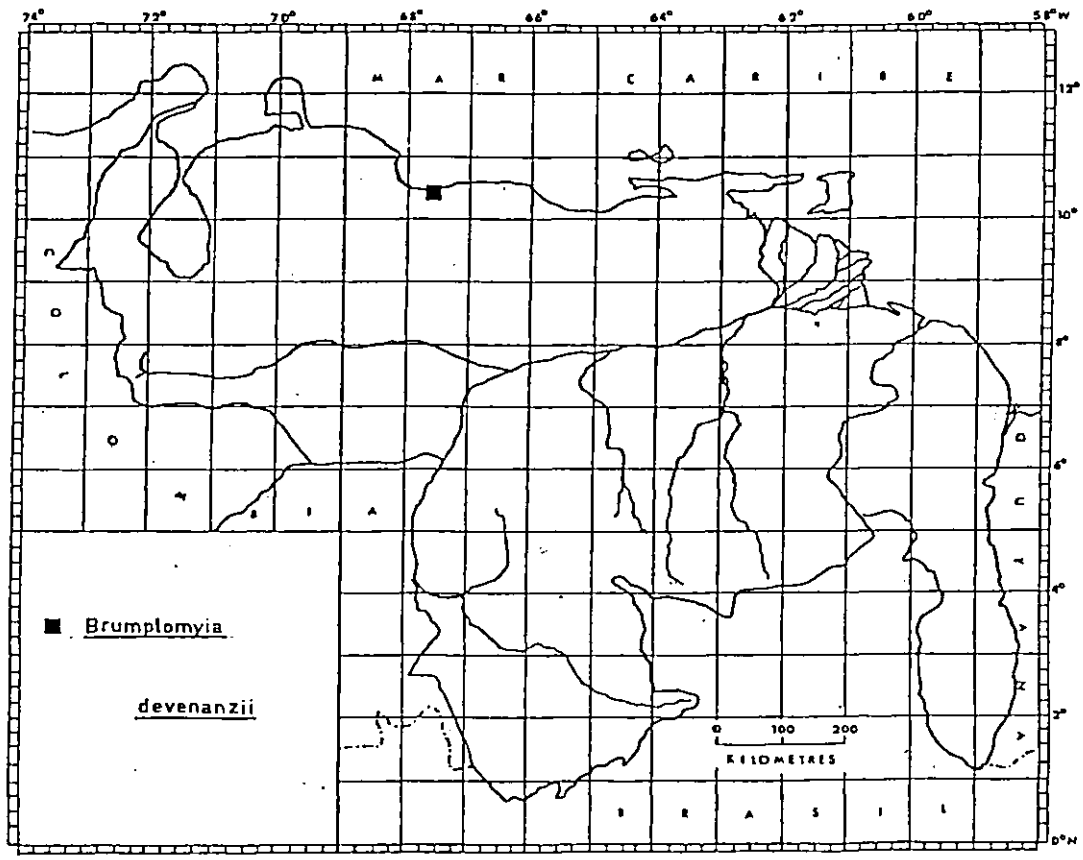

Brumptomyia
devenanzii
0 100 200
KILOMETRES

Fig. 55

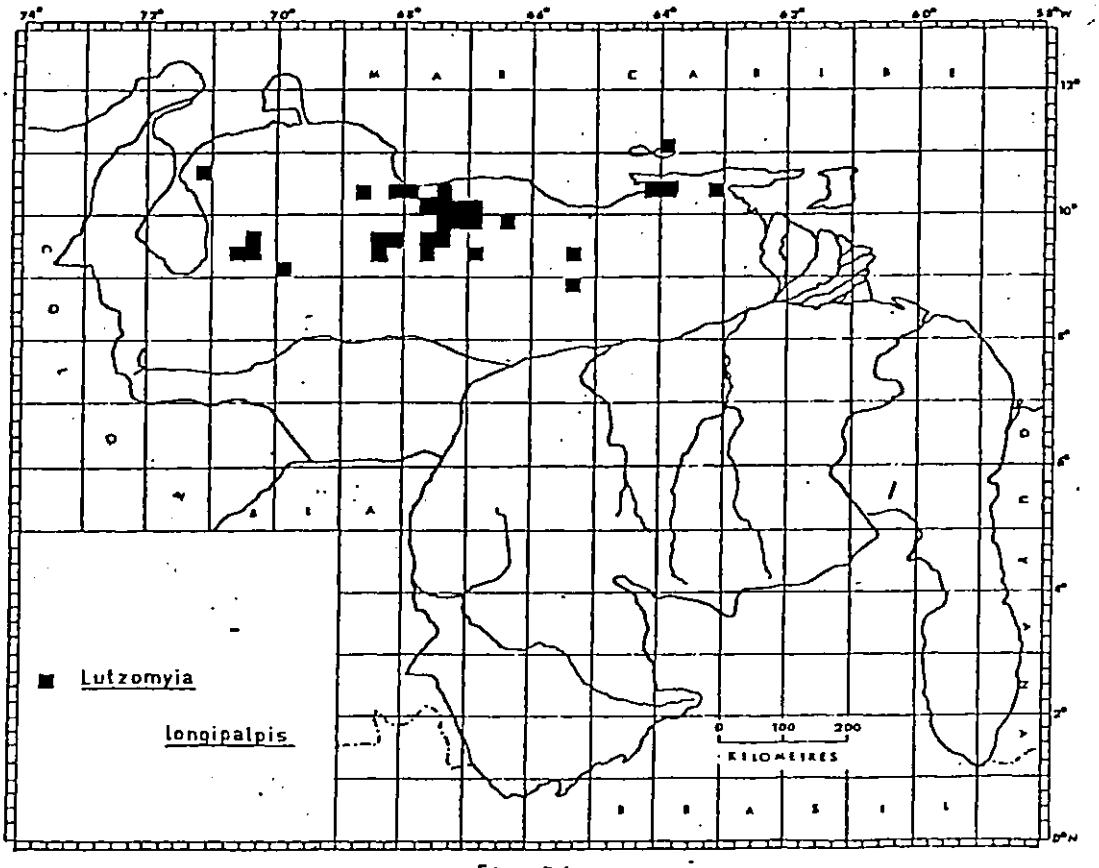

Lutzomyia
longipalpis
0 100 200
KILOMETRES

Fig. 56

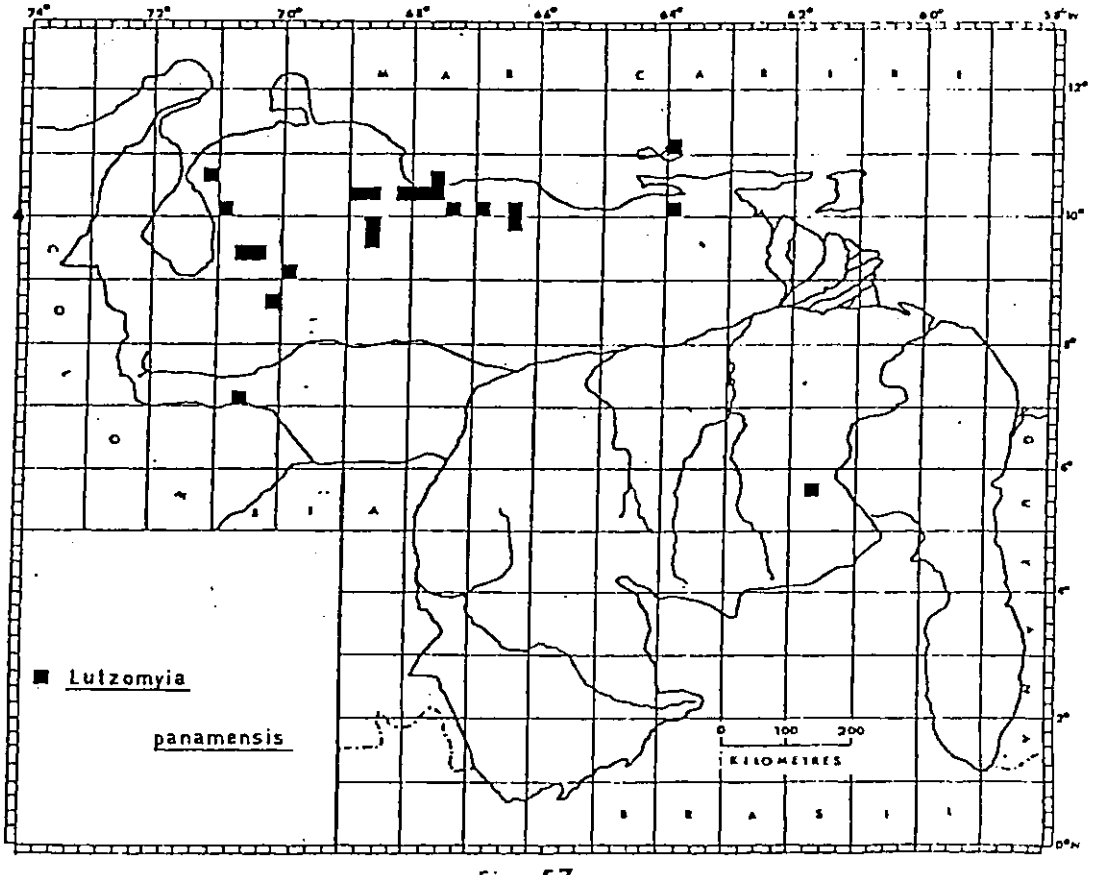

Lutzomyia
panamensis
0 100 200
KILOMETRES

Fig. 57

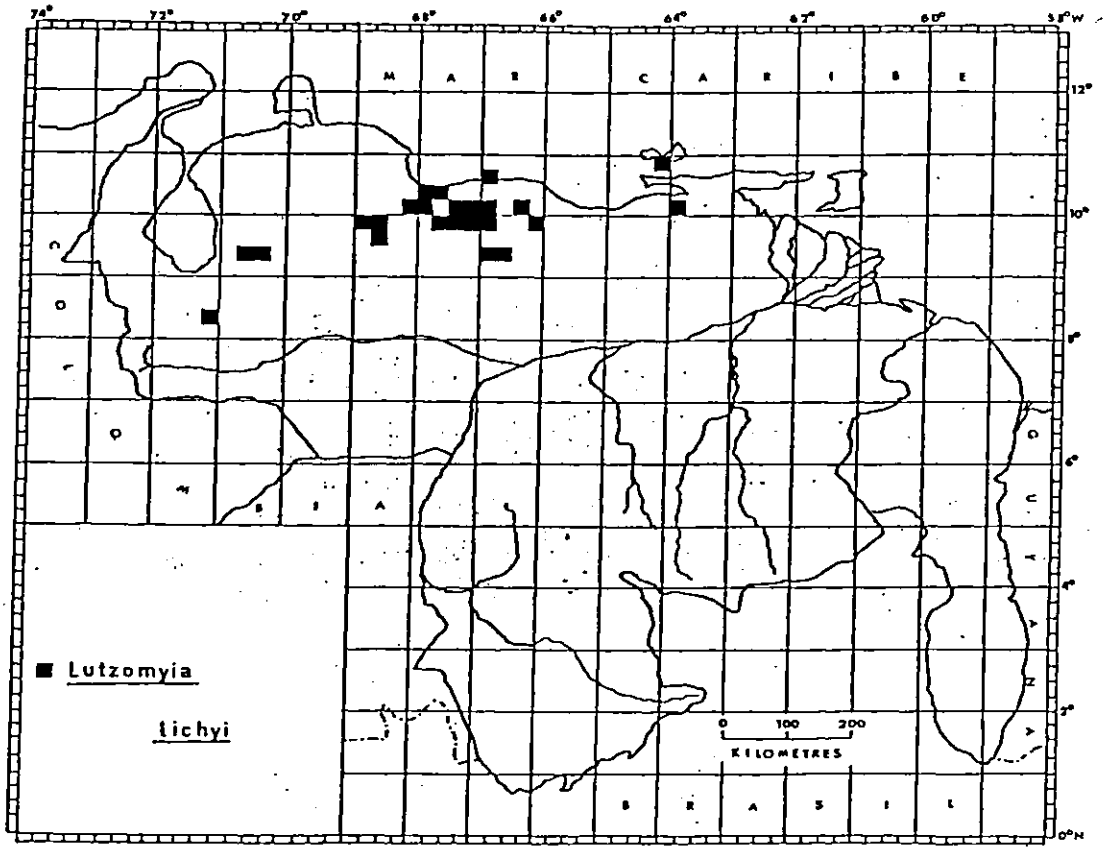

Lutzomyia
lichyi
0 100 200
KILOMETRES

Fig. 58

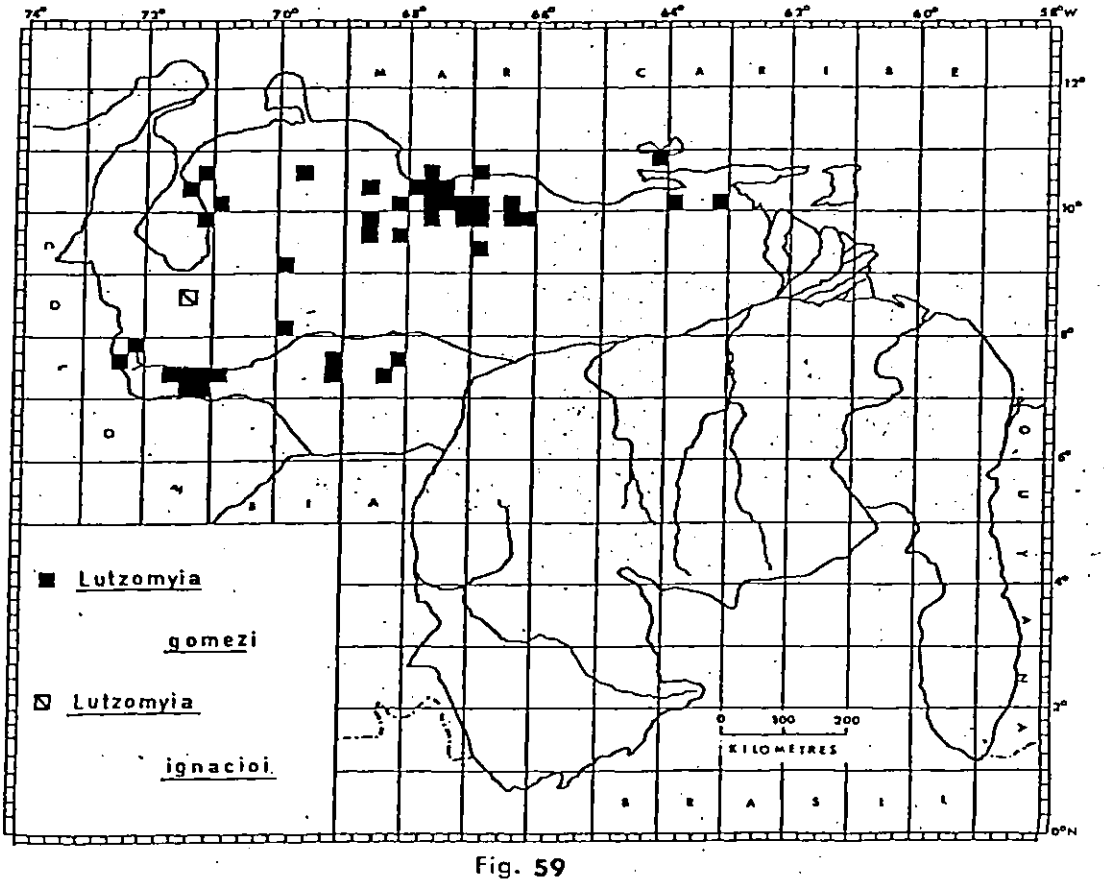
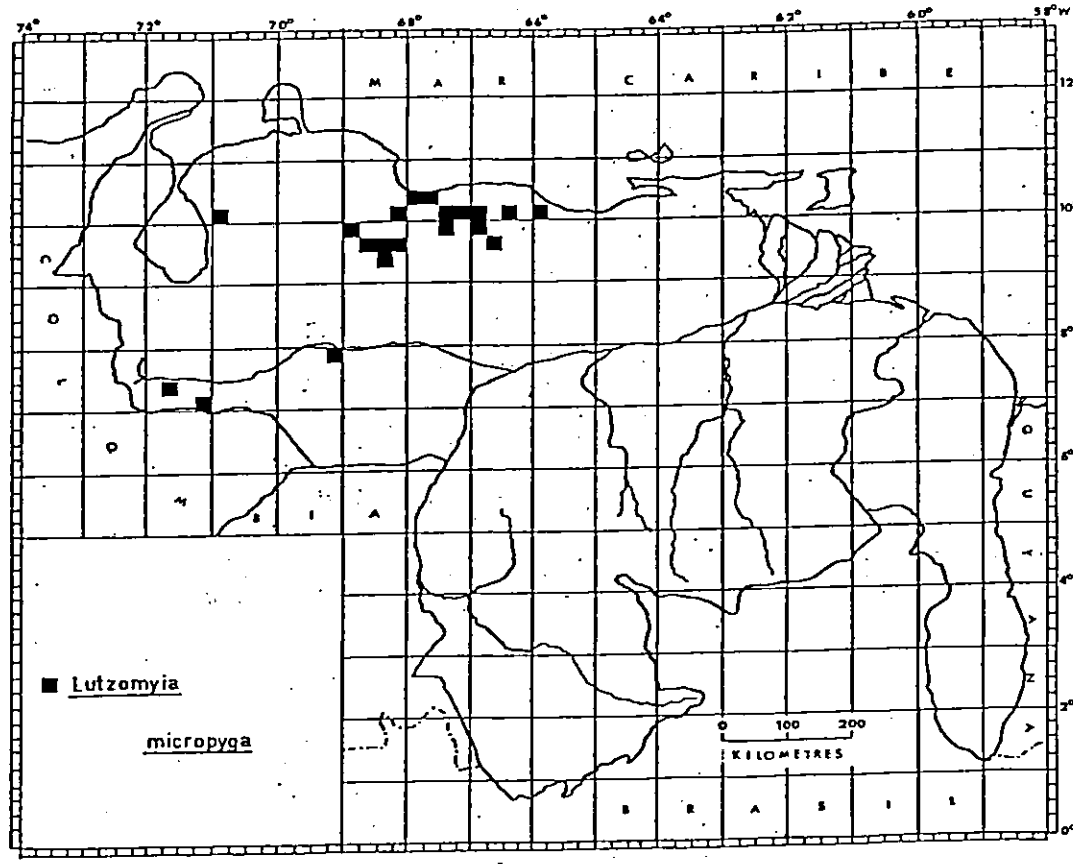

Lutzomyia
gomezi
Lutzomyia
ignacioi
0 100 200
KILOMETRES

Fig. 59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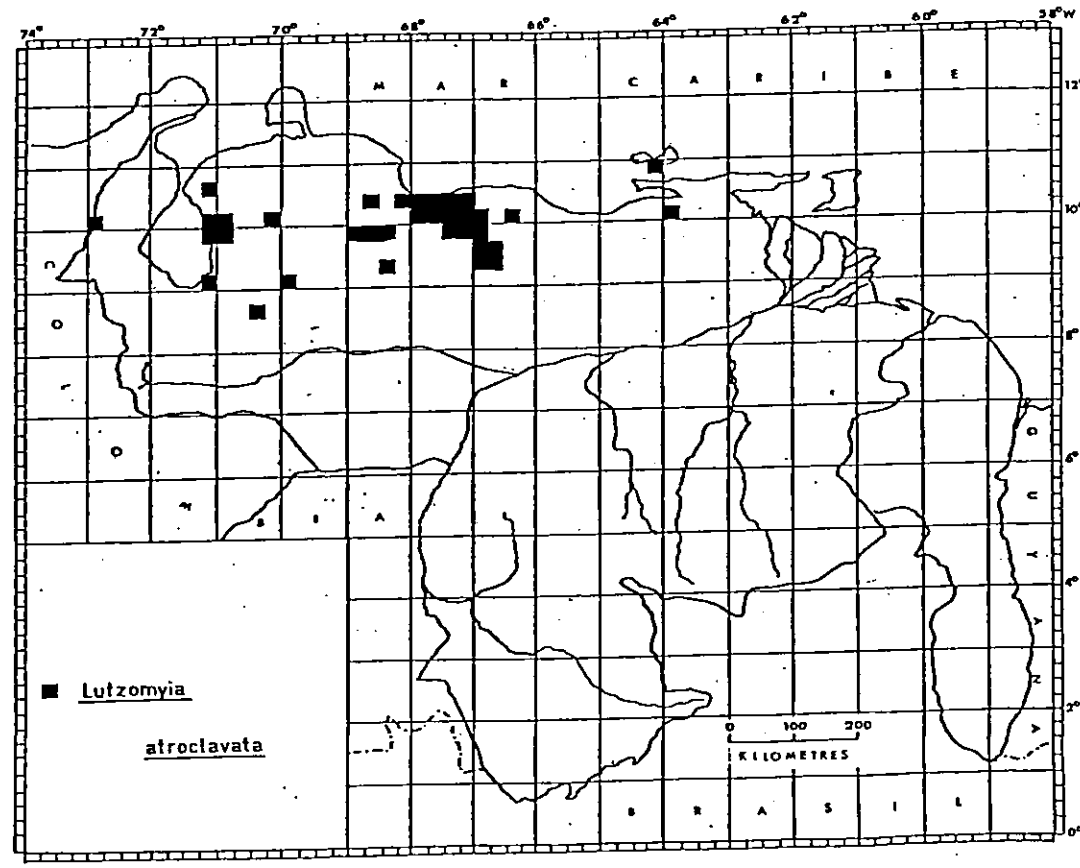
B R A S I L
Lutzomyia
micropyga
0 100 200
KILOMETRES

Fig. 60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B R A S I L
Lutzomyia
atroclavata
0 100 200
KILOMETRES

Fig. 61

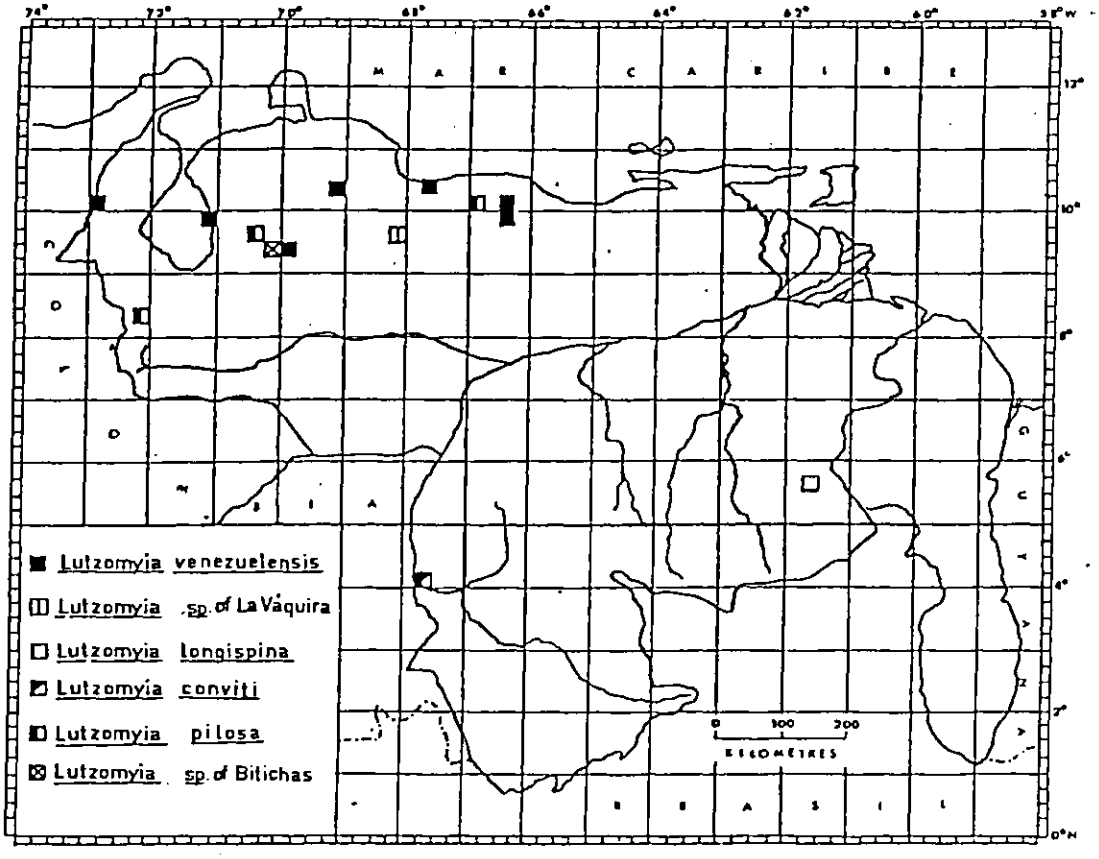

Lutzomyia venezuelensis
Lutzomyia sp. of La Vaquira
Lutzomyia longispina
Lutzomyia conviti
Lutzomyia pilosa
Lutzomyia sp. of Bitichas
KILOMETRES

Fig. 62

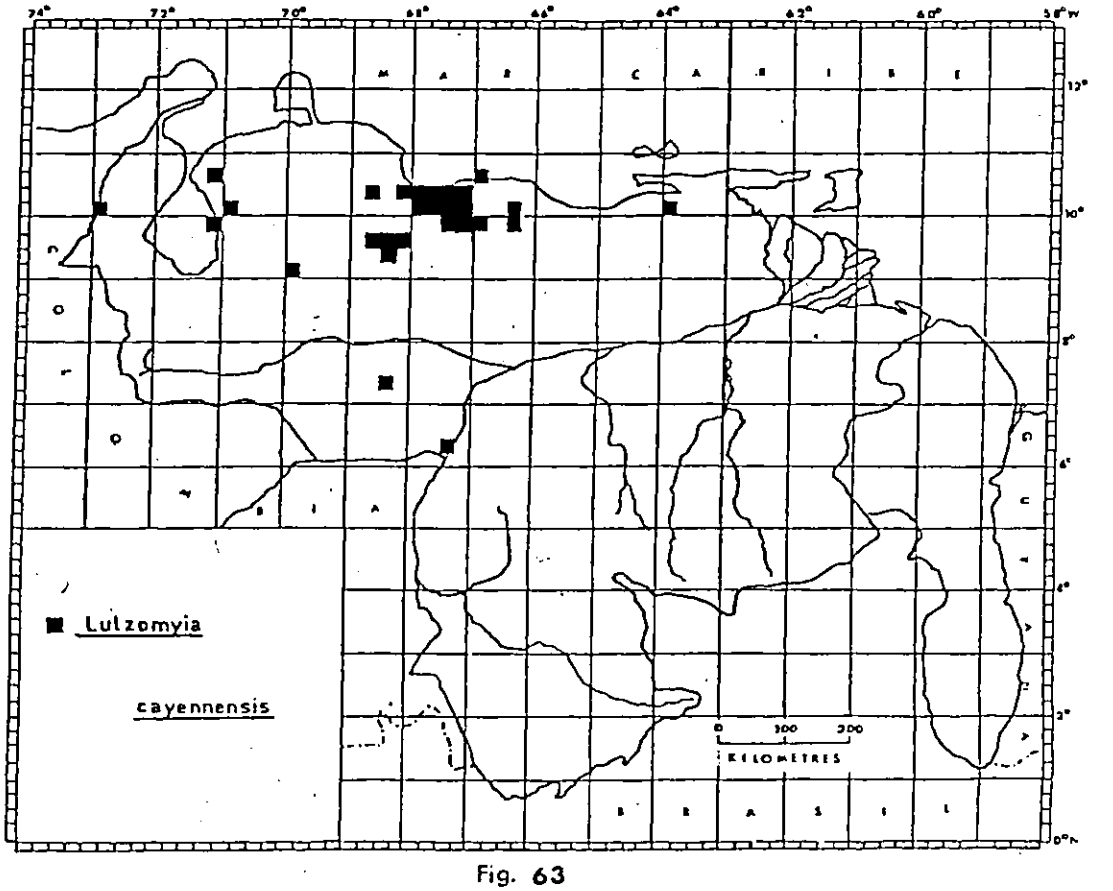

Lutzomyia
cayennensis
KILOMETRES

Fig. 63

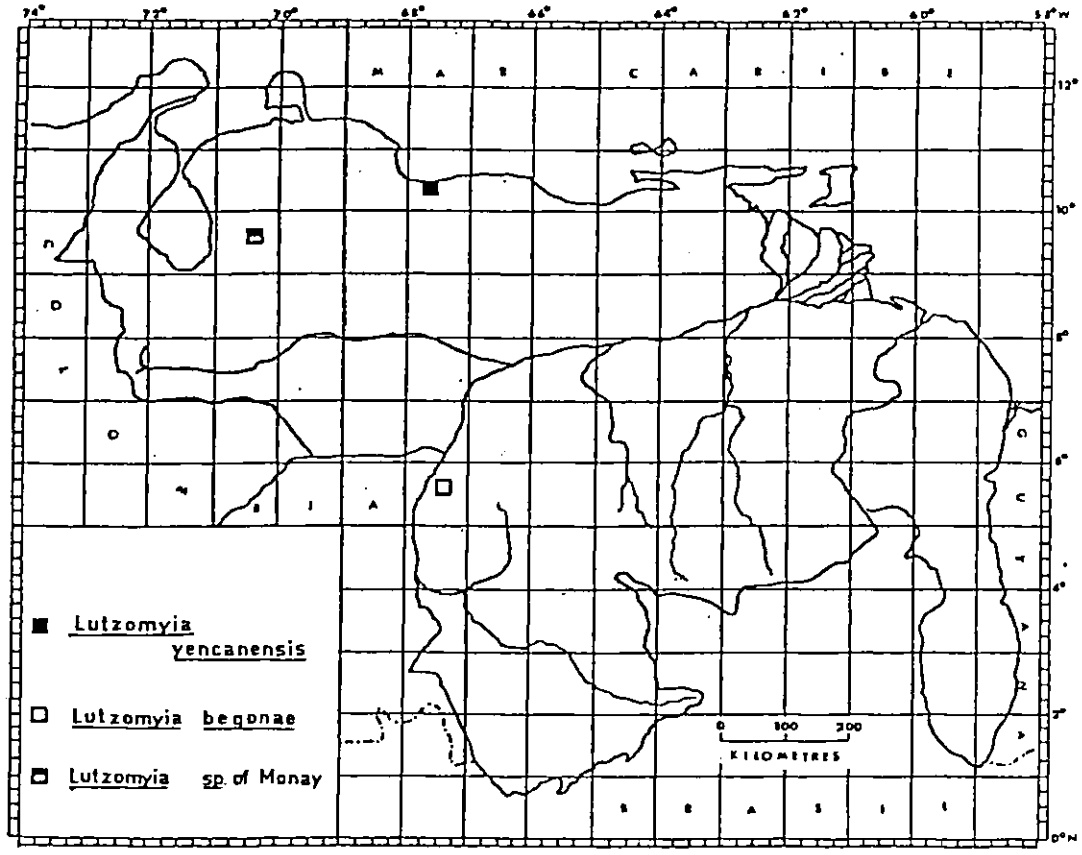

Lutzomyia yencanensis
Lutzomyia begonae
Lutzomyia sp. of Monay
0 100 200
KILOMETRES

Fig. 64

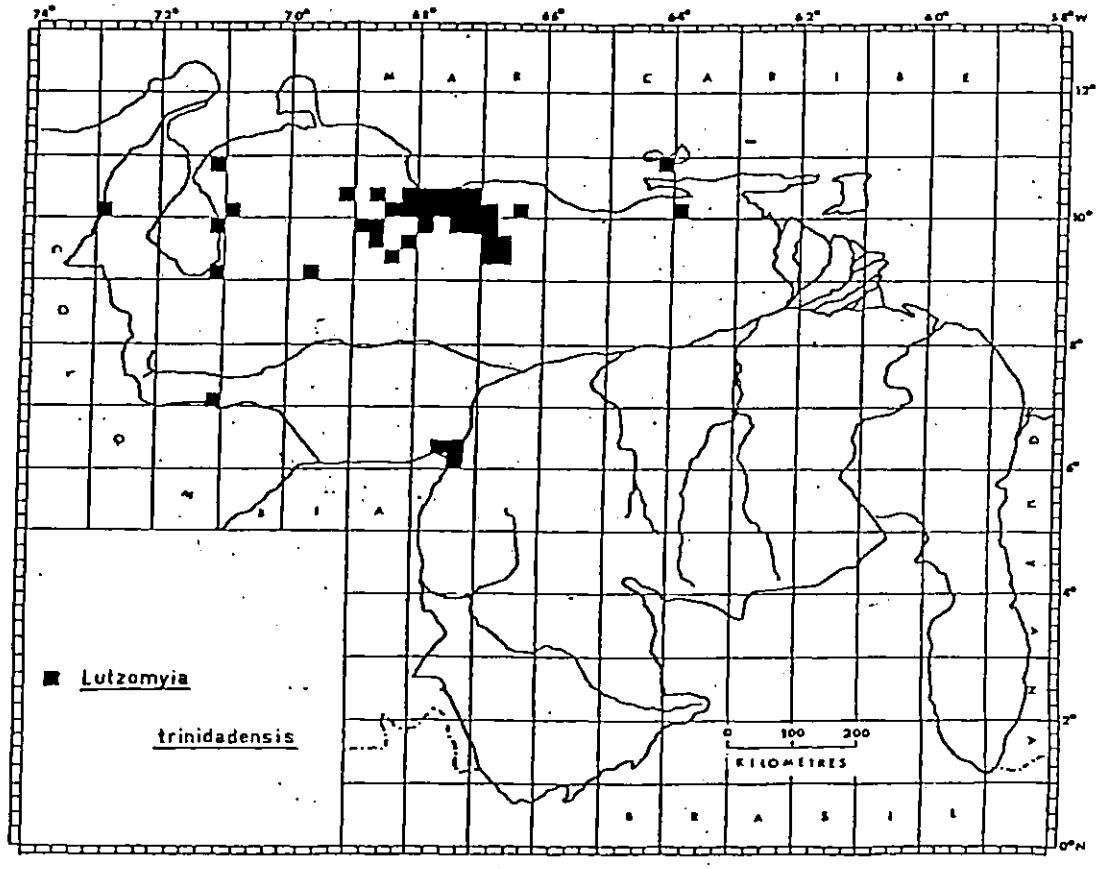

Lutzomyia trinidadensis
0 100 200
KILOMETRES

Fig. 65

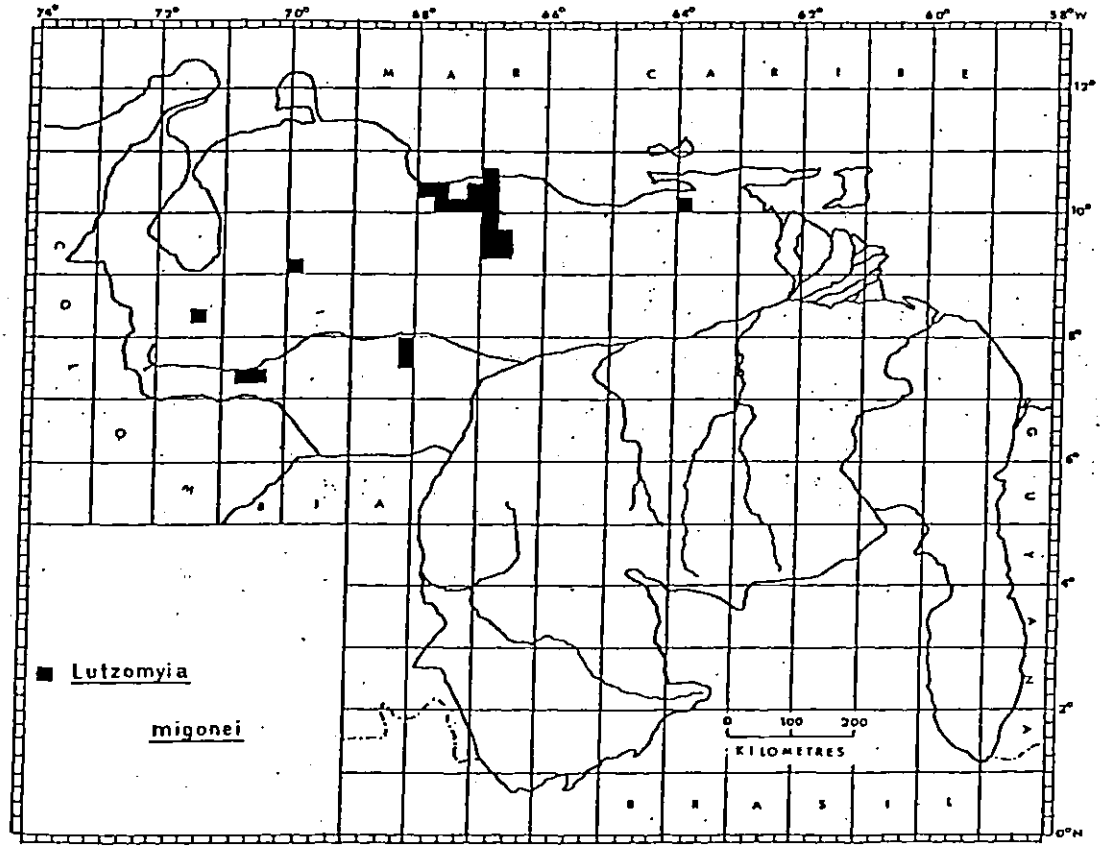

Lutzomyia
migonei
0 100 200
KILOMETRES
MARCARIBE
BRASIL

Fig. 66

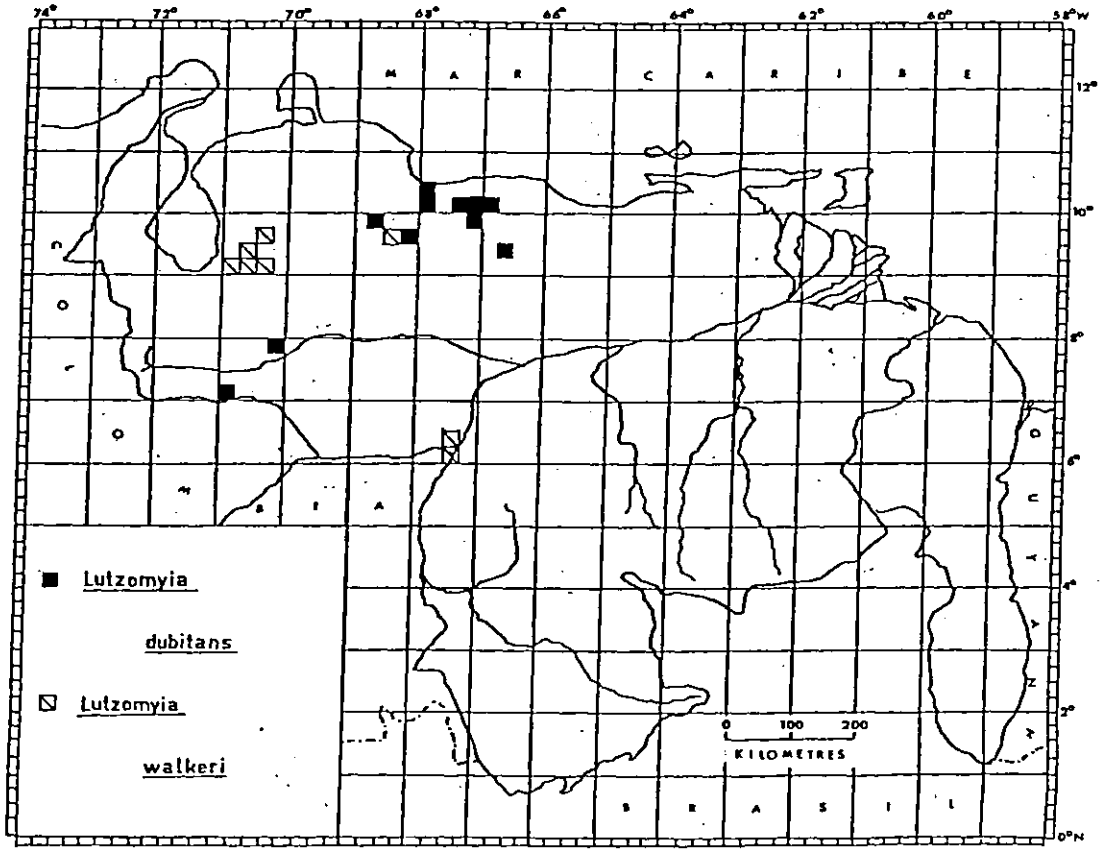
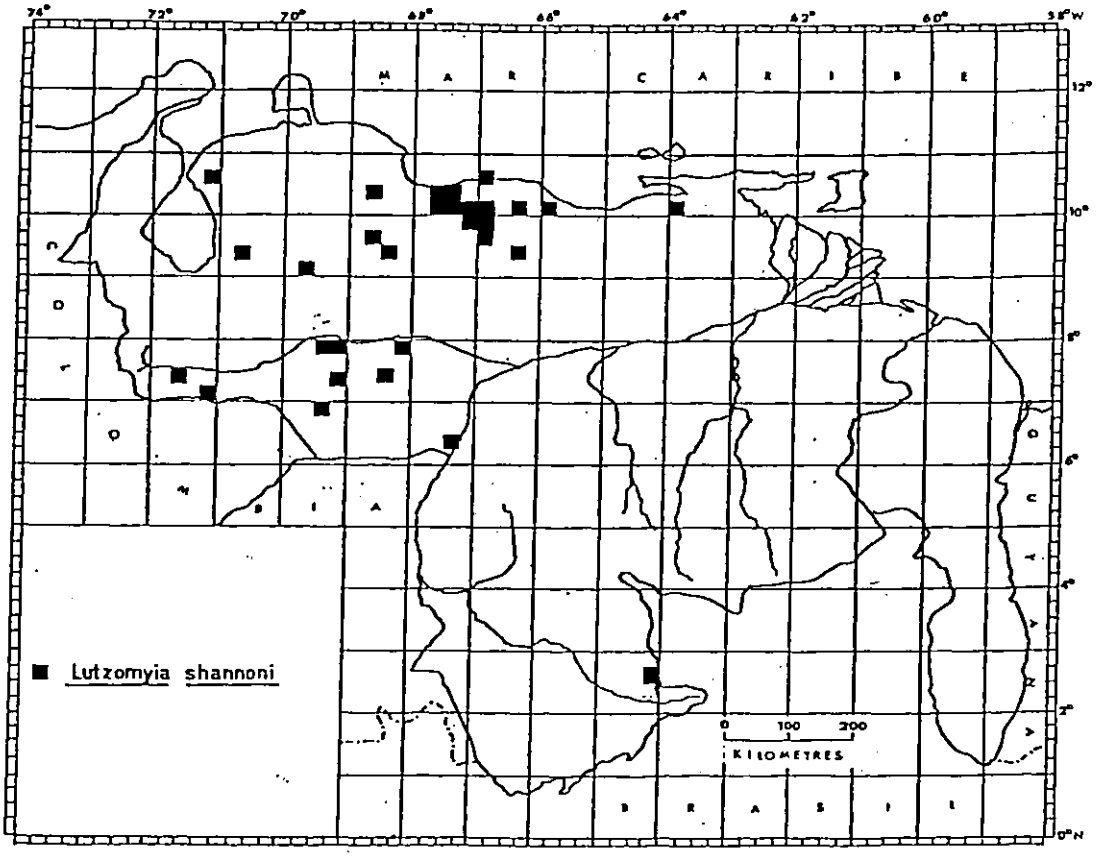

Lutzomyia
dubitans
Lutzomyia
walkeri
0 100 200
KILOMETRES
MARCARIBE
BRASIL

Fig. 67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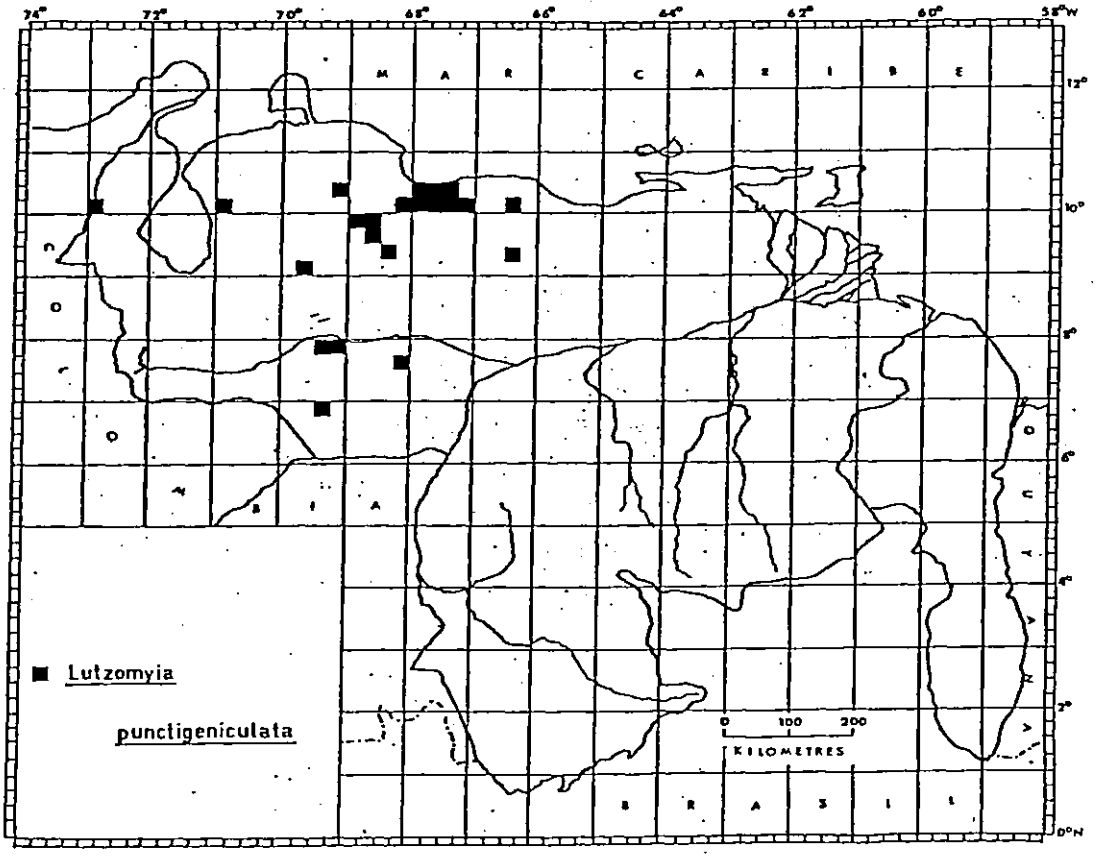
G U I A N A
B R A S I L
Lutzomyia shannoni
0 100 200
KILOMETRES

Fig. 68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G U I A N A
B R A S I L
Lutzomyia
punctigeniculata
0 100 200
KILOMETRES

Fig. 69

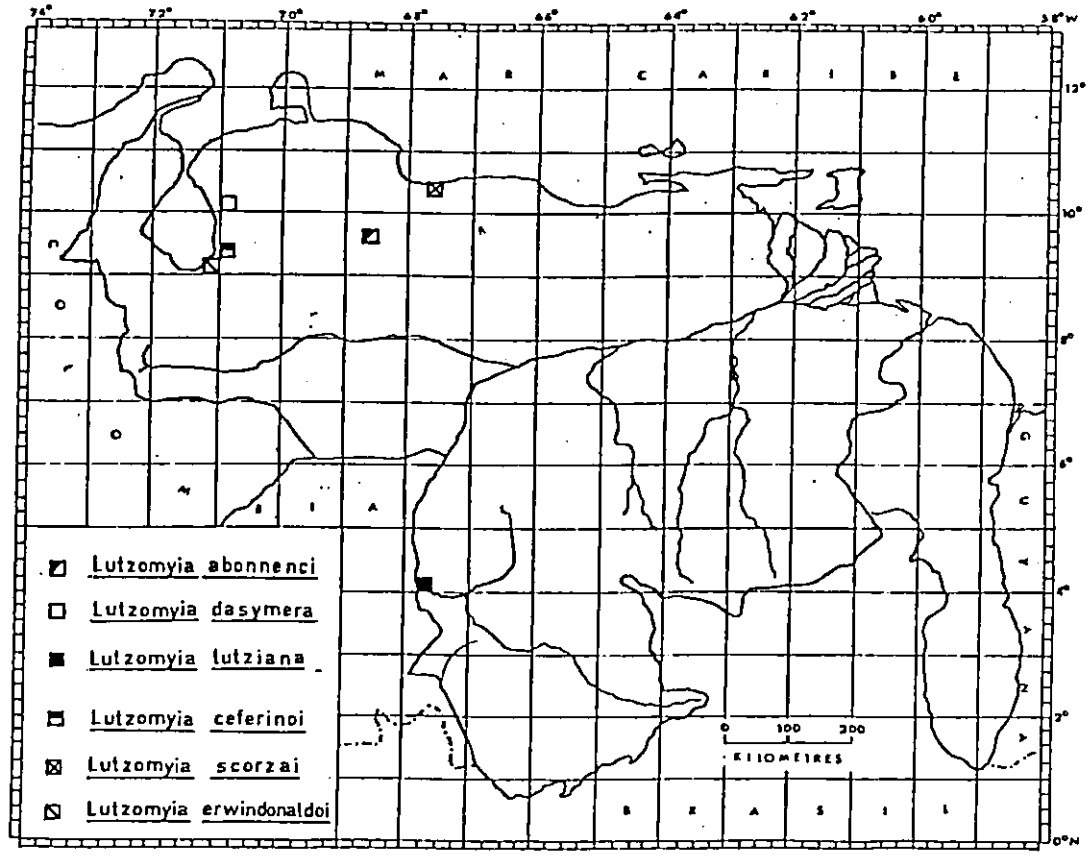

Lutzomyia abonnenci
Lutzomyia dasymera
Lutzomyia lutziana
Lutzomyia ceferinoi
Lutzomyia scorzai
Lutzomyia erwindonaldoi
0 100 200
KILOMETRES

Fig. 70

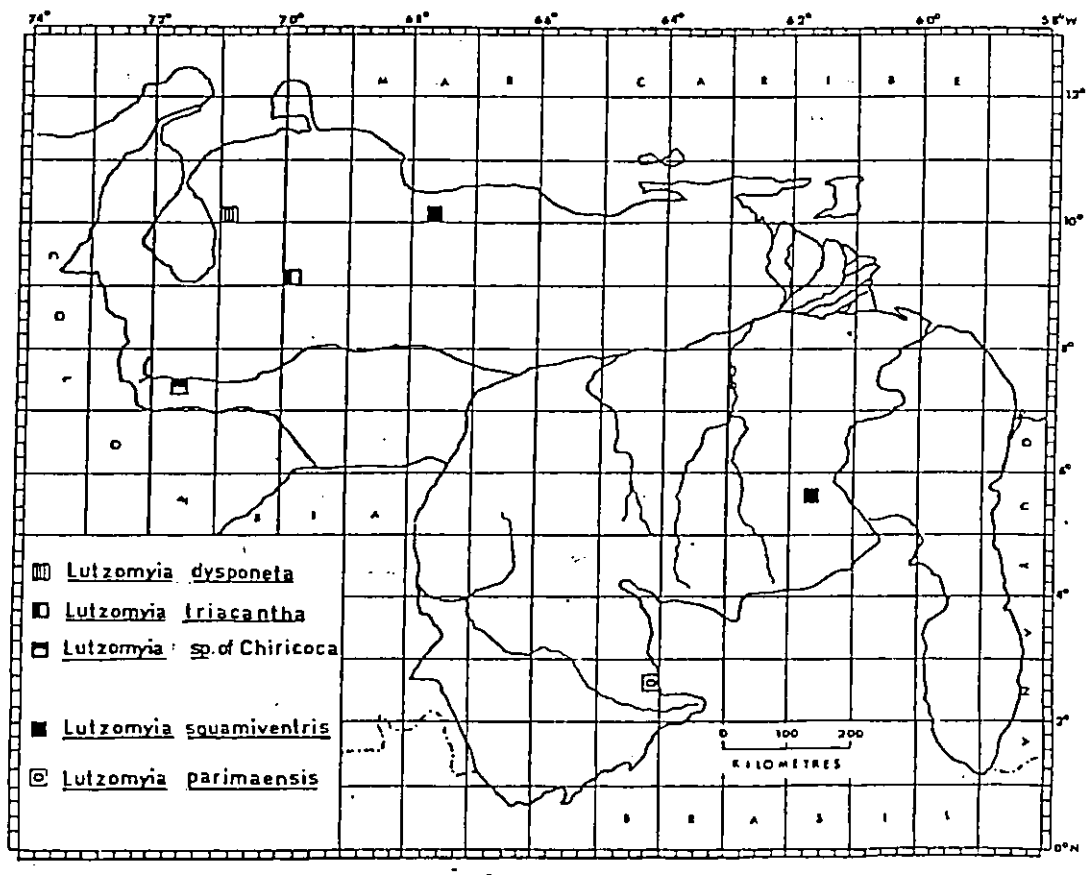

Lutzomyia dysponeta
Lutzomyia triacantha
Lutzomyia sp. of Chiricoca
Lutzomyia squamiventris
Lutzomyia parimaensis
0 100 200
KILOMETRES

Fig. 71

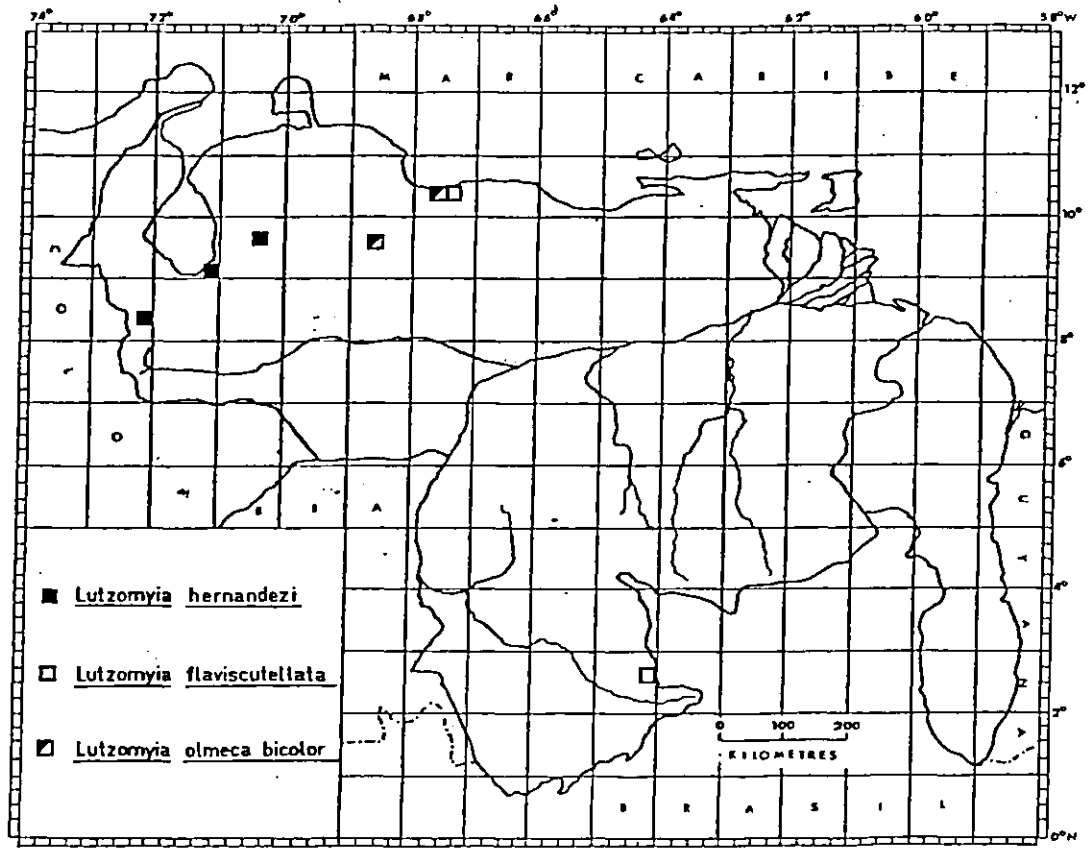

Lutzomyia hernandezi
Lutzomyia flaviscutellata
Lutzomyia olmeca bicolor
0 100 200
KILOMETRES

Fig. 72

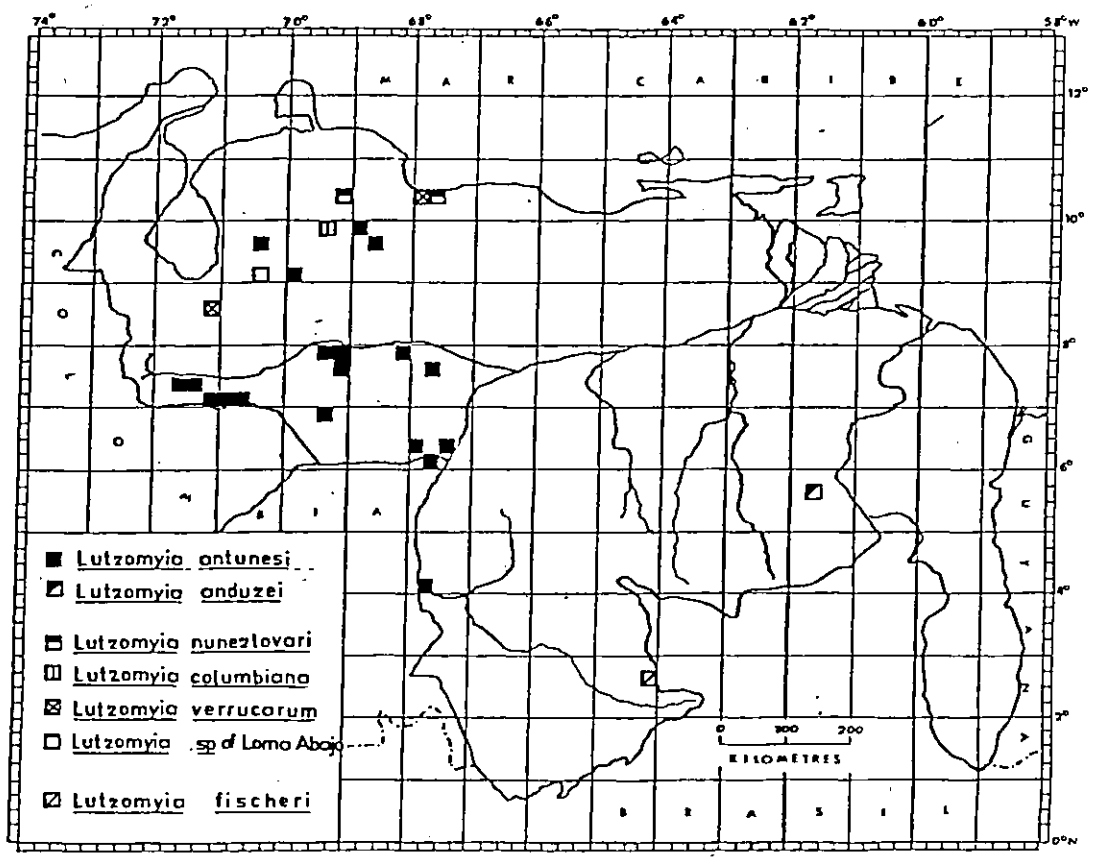
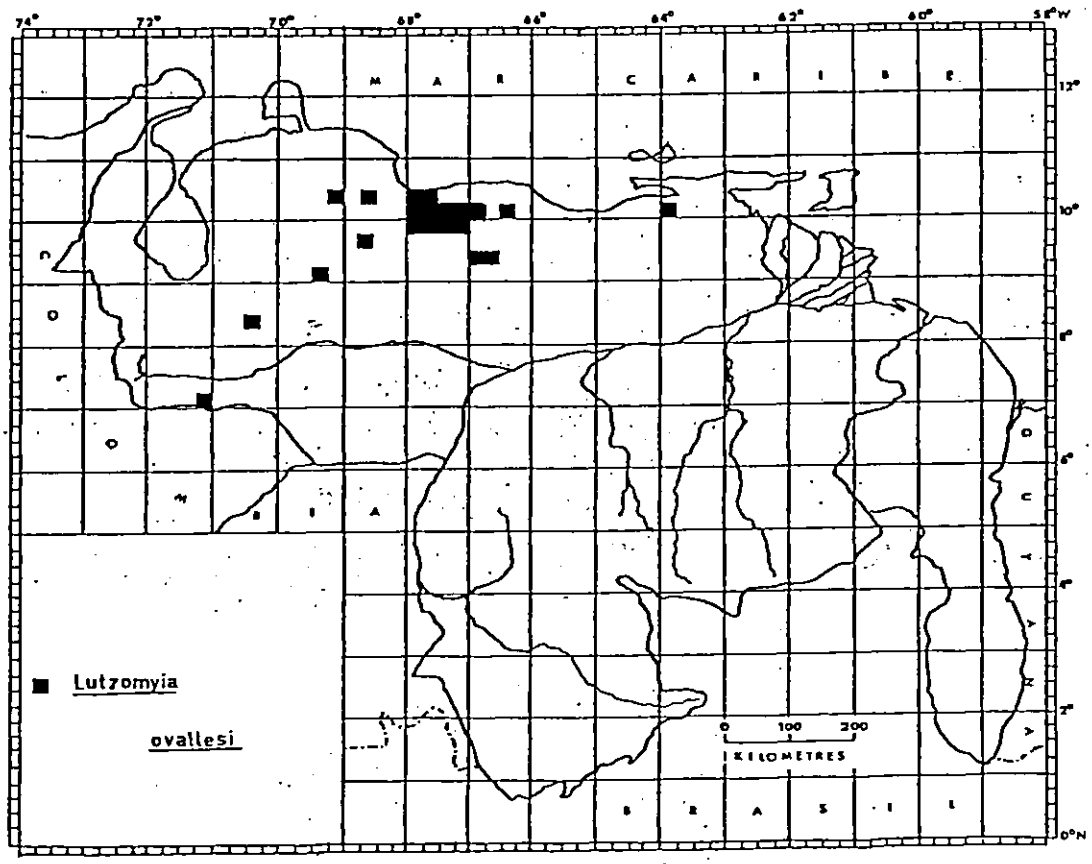

Lutzomyia antunesi
Lutzomyia onduzei
Lutzomyia nunestovari
Lutzomyia columbiana
Lutzomyia verrucarum
Lutzomyia sp of Lomo Abajo
Lutzomyia fischeri
0 100 200
KILOMETRES

Fig. 73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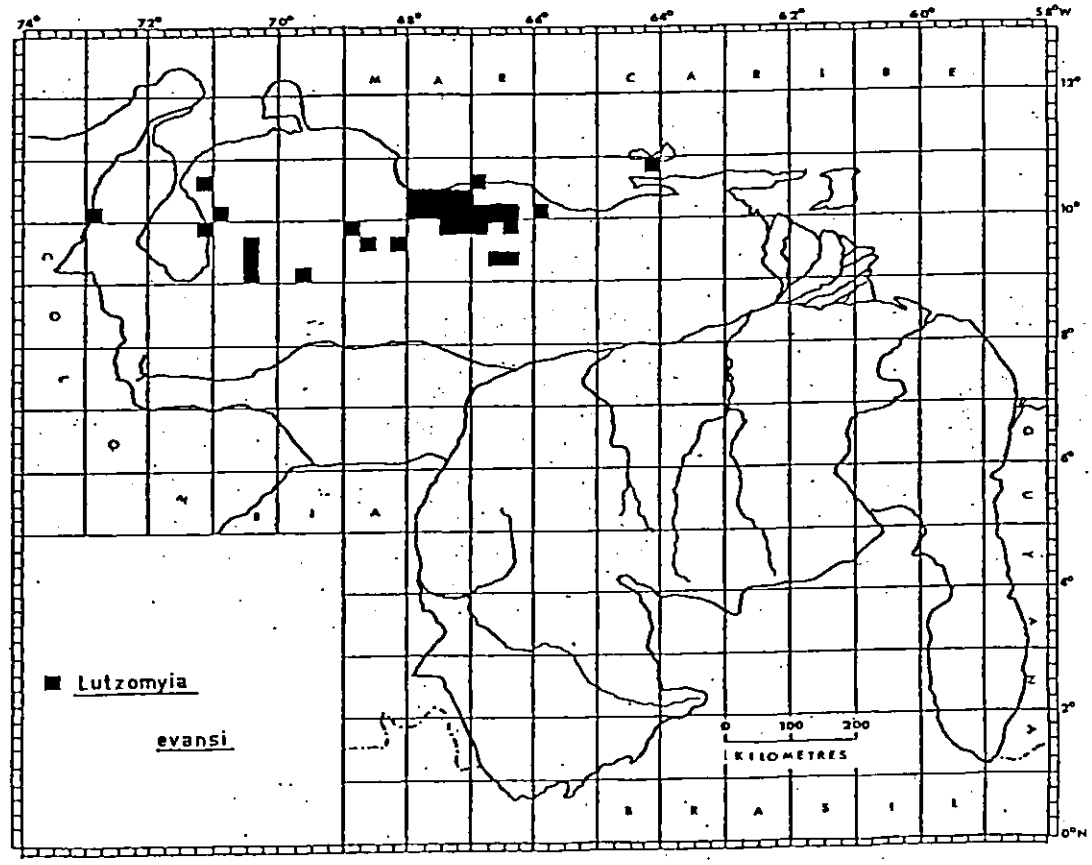
V E N E Z U E L A
B R A S I L
Lutzomyia
ovallesi
0 100 200
KILOMETRES

Fig. 74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C O L O M B I A
V E N E Z U E L A
B R A S I L
Lutzomyia
evansi
0 100 200
KILOMETRES

Fig. 75

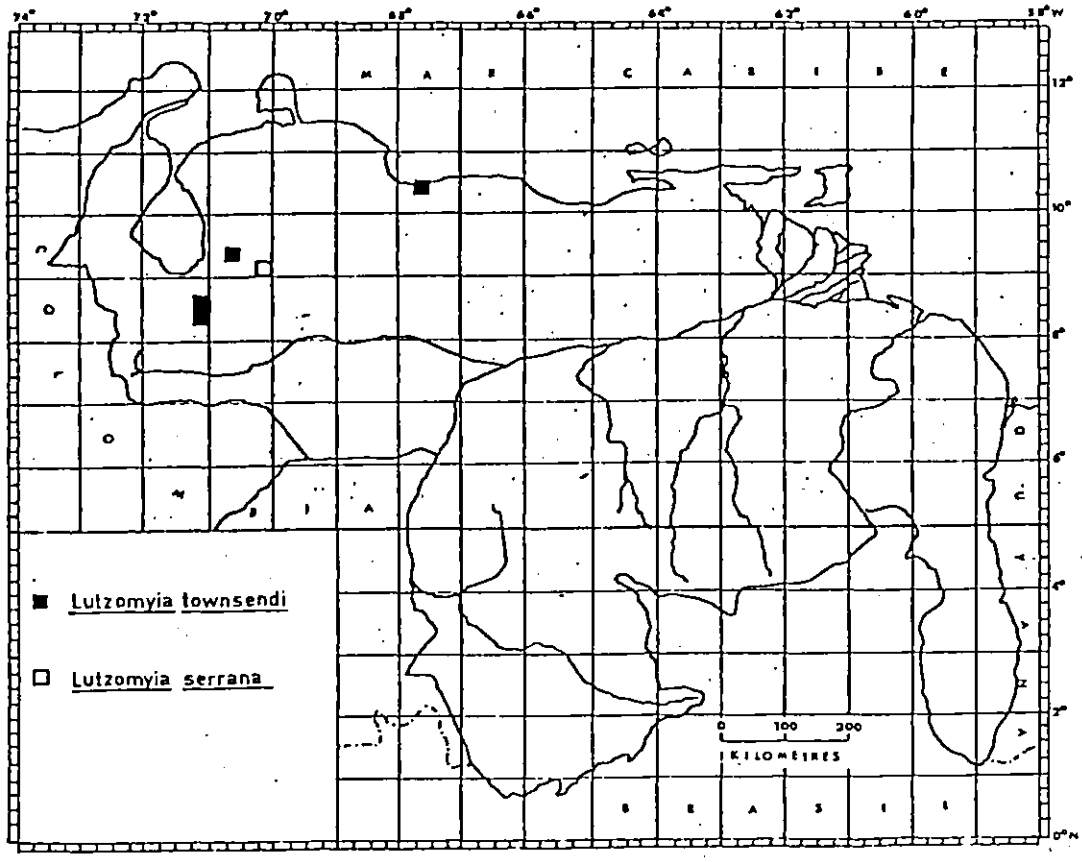

Lutzomyia townsendi
Lutzomyia serrana
0 100 200
KILOMETRES

Fig. 76

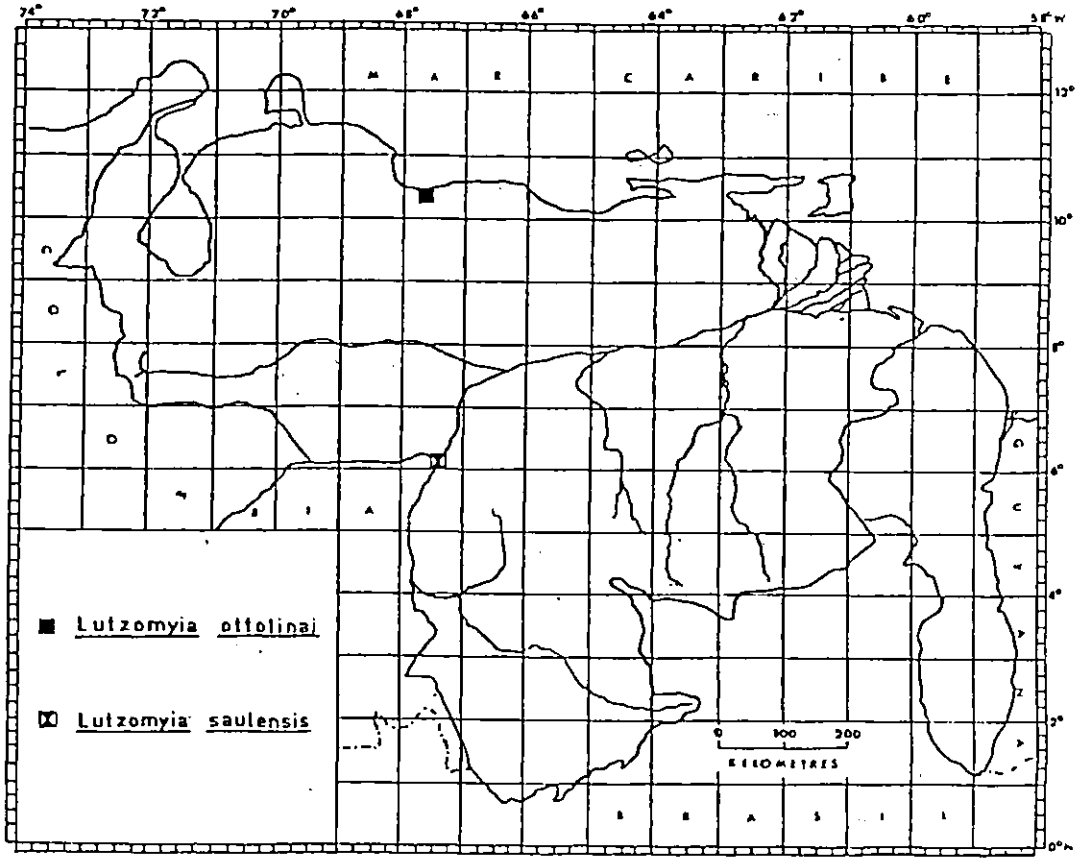
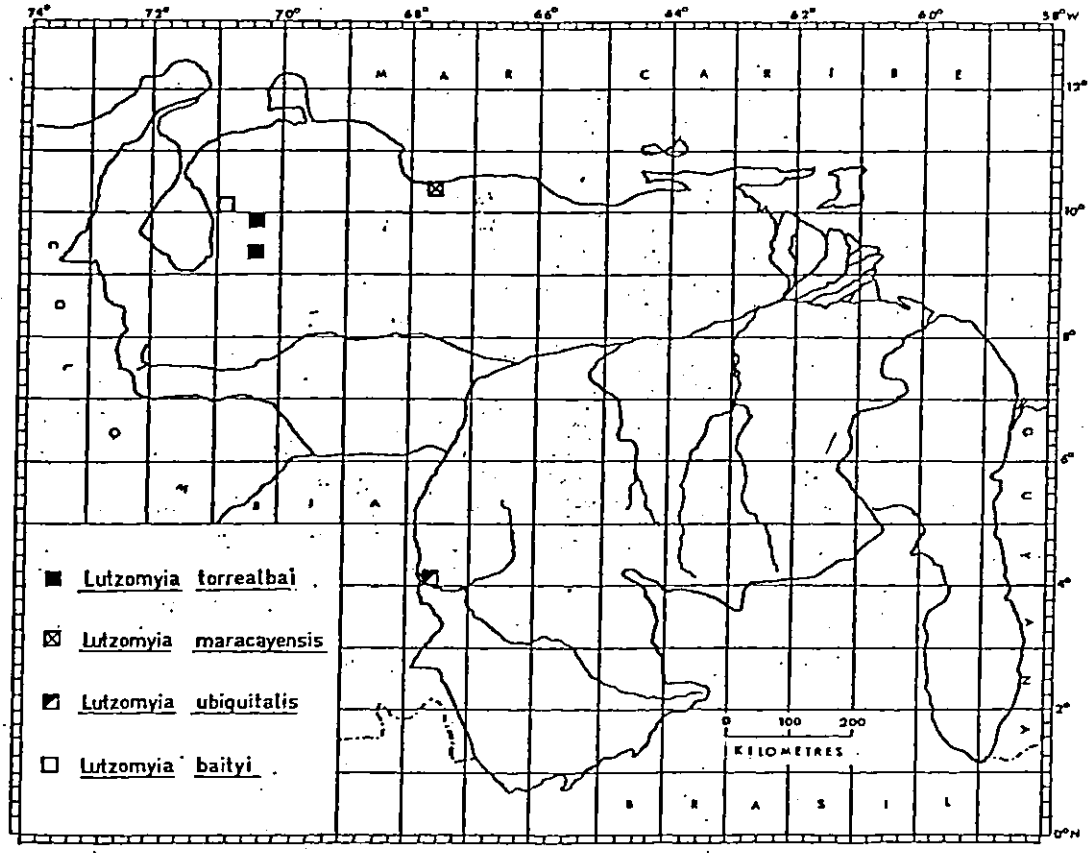

Lutzomyia ottolinai
Lutzomyia saulensis
0 100 200
KILOMETRES

Fig. 77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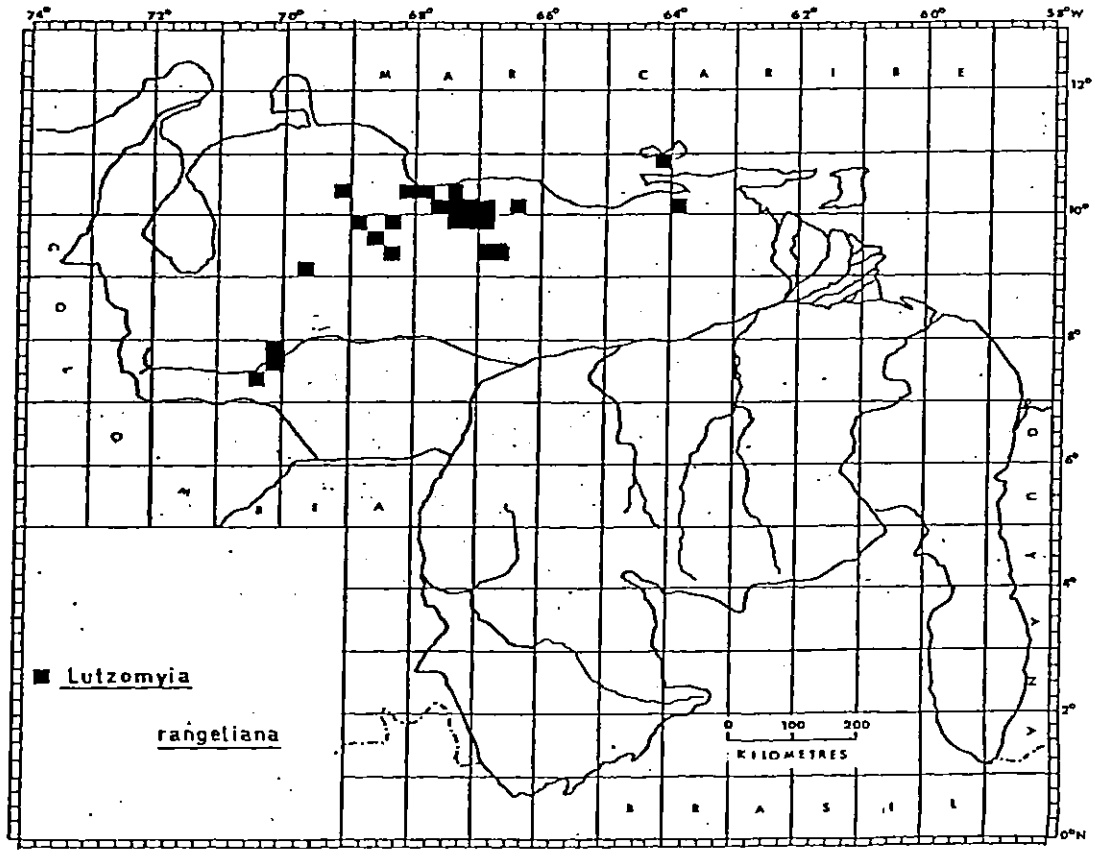
BRASIL
Lutzomyia torrealbai
Lutzomyia maracayensis
Lutzomyia ubiquitalis
Lutzomyia baityi
0 100 200
KILOMETRES

Fig. 78


74°
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2°
0°N
BRASIL
Lutzomyia rangeliana
0 100 200
KILOMETRES

Fig. 79

3.4 Discussion

When Kirk & Lewis (1951) gave a survey of the sandflies of the Ethiopian region, they stated that they could give only "approximate numbers of species in view of the constant changes in the knowledge of the species".

This concept is applicable to this attempt to update the check-list of phlebotomine sandflies from Venezuela, which, at the moment, contains 58 species.

The position of a few of these species is presently doubtful but whenever species are thought probably to exist in the country, they have been included.

A peculiar case is represented by L. maracayensis. The description of this species was in the first period of the study of sandflies, when identification mainly was based on external morphology. Therefore this "inadequately described species" will probably remain in that position for ever, because of the lack of specific valid characters and lack of type material. It is also possible that it has been described under another name, but there is no evidence of this possibility sufficiently strong to maintain this species in the list.

The distribution of L. verrucarum in sites of high altitude, according to Martins et al. (1978), is restricted to Peru. There are, however, two records from Venezuela. One, of females only, from Carabobo State (near the Caribbean Coast; Floch & Abonnenc, 1950-53) must be considered doubtful because of the low altitude of the collection site and because of the difficulty of identifying females of this group in the absence of associated males. The second report, of flies of unspecified sex, is of L. verrucarum caught by Anduze in the Andean region (Merida)

(Pifano & Ortiz 1952). Confirmation of this record should be sought by finding males (Young, 1979), but the high altitude of the collection site suggests that this species probably exists in Venezuela and that it should be kept in the check-list for the moment.

The presence of L. columbiana, a recently-found species, also needs further confirmation, with precise data on the specimens collected.

In the present work, descriptions of three new sandflies have been made on only one specimen. This is by no means ideal, but the concept of Perfiliev (1968) that "when new sandflies are found which resemble a certain species, it is better to describe a new species. It is easier to make the new name a synonym after further study, than to divide a collective form", has been followed. However, these descriptions, like previous descriptions based on only one specimen, will doubtless need revision. More specimens have to be found and descriptions supported by statistical data are important to determine the variability of a character and to avoid or eliminate synonymies. An example of its utility has been given in the comparative study of L. walkeri and L. dubitans (Section 3.3.2).

Both sexes are known only for 44 of the 58 Venezuelan species of Phlebotomine sandflies. Of the remaining 12 species the corresponding sex has to be found and described. Biological data are necessary to supplement and support taxonomic opinions, for instance to determine the correspondence of sexes.

The species concept of Mayr (1942, 1963), in which the species is an objective unit distinguished by reproductive isolation, shows the species as primarily a biological rather than a morphological entity. This attribute is of great importance in the recognition of sibling

species (none of which has yet been found in sandflies), and of morphologically similar species. An example is given by the recently described Lutzomyia llanosmartinsi Fraiha & Ward, 1980 from Peru, which had been confused with Lutzomyia amazonensis (Root, 1934). The solution of this taxonomic problem was only possible by rearing L. amazonensis from Brazil, which provided males found to be very different from the male of L. amazonensis as described by Llanos et al. (1975) (Fraiha & Ward, 1980).

It has been suggested that biochemical methods, such as electrophoretic studies on genetic polymorphism, will probably be useful in the systematics of sandflies and in the analysis of population structure and the differentiation of closely-related taxa (Ward et al., 1981a, b). The analysis of cuticular components has been successful in the differentiation of anopheline and blackfly species-complexes (Carlson & Service, 1979; Carlson & Walsh, 1981). Such techniques must be regarded as helpful future tools for taxonomic studies of phlebotomines.

The number of species known from Venezuela is low in comparison with the number of species of neighbouring countries. With the exception of the Andes, the boundaries between Venezuela and neighbouring countries are artificial and do not represent ecological barriers likely to affect the range of distribution of sandflies. In Venezuela there is a variety of habitats, some of which are common to either Colombia or Brazil. It is certain that the distribution of at least some of the species at present unknown in Venezuela, but recorded in the neighbouring countries, will be found to extend into that country. The recent discovery of L. saulensis, L. abonnenci, L. serrana, L. olmeca bicolor, and L. walkeri in Venezuela are evidence of this. When searches for sandflies are intensified, other gaps in the distribution of sandflies will be filled. The relatively

poor number of collections in Venezuela is one of the explanations for the comparatively low number of species of presently-known Venezuelan sandflies.

The chorology of the sandfly fauna within the country is for the same reason at this moment rather difficult to be carried out.

In an attempt to correlate the species distribution with the ecological habitats, at least 17 species were found apparently able to flourish in the majority of the life zones in which sandflies have been collected. However, it is known that the life zone concept of Holdridge (1964) can only give a general idea of a classification of the world's vegetation. The question whether life zones are real in nature or whether they are simply a convenient but arbitrary classification still remains open (MacArthur, 1972).

On the other hand, tropical species of animals and plants are known often to have a patchy geographic distribution for reasons that have no obvious relation to the climate or habitat (MacArthur, 1972). Therefore the presence of the same species in two very different life zones, like tropical moist forest and tropical thorn woodland, might be interpretated as the result of the presence of similar microenvironments in the two zones.

Some doubts have arisen in relation to the distribution of two species. Over 50 years ago, L. squamiventris was recorded for the first time in Maracay (Aragua State) by Nuñez-Tovar (1924). Although sandflies of this state are the best studied, L. squamiventris has not been found again in a recent intensive collection by Ramirez Perez et al., 1978.

These workers referred to the presence of L. flaviscutellata in a zone which is very close to the distribution area of L. olmeca bicolor.

When this record is considered in the light of what is known of the American distribution of these two species, it is clear that it requires confirmation. The distribution of L. olmeca bicolor ranges from Central America (Panama) to Colombia, Ecuador and Venezuela. L. flaviscutellata is presently known only in South America, with Trinidad the most northern place of distribution. If its presence in the centre of Venezuela is confirmed, L. flaviscutellata and L. olmeca bicolor are sympatric in this area.

The temptation to correlate the distribution of the two suspected vector species, L. longipalpis and L. panamensis, with the geographical distribution of kala-azar and cutaneous leishmaniases respectively, is particularly attractive. In spite of the limitations of collections already discussed, there appears to be a reasonable concordance between the known distribution of L. longipalpis (Fig. 56) and foci of kala-azar in Venezuela (Fig. 1). The distribution of L. panamensis (Fig. 57) is different from that of L. longipalpis. It seems to follow the mountainous group of the Andes in the East and the "Cordillera de la Costa" in the North. Presumably, it is not a coincidence that the distribution of cutaneous leishmaniasis is thought to be confined to the foothills of mountain regions (Pifano, 1960).

No speculations on the distribution of other Venezuelan sandflies and leishmaniasis can be made without more information. Distribution maps of these lesser known species are considered simply as guides for further studies, and as starting points in attempts to delineate their true ranges of distribution in relation to ecological habitats.

4. ECOLOGY OF VENEZUELAN SANDFLIES : ADULT POPULATION DYNAMICS OF SANDFLIES AT SAN ESTEBAN, CARABOBO STATE, MARCH 1979 - MARCH 1980

4.1 Introduction

In order to understand the natural history of sandfly-transmitted diseases, it is necessary to study (i) the vector's seasonal distribution, (ii) the diversity of species and their relative abundance and (iii) the degree of anthropophily and zoophily of each species. Systematic field work furthermore offers the advantages of additional information on insect ethology and the efficacy, reliability and applicability of the methods used.

In the Americas, this kind of study has been carried out in Brazil (Shaw & Lainson, 1972), Panama (Chaniotis et al, 1971a, b) and Trinidad (Tikasingh, 1975). Results for the same species in different places have often been compared, but this cannot be done for Venezuelan species without more information.

The studies cited above were mainly carried out in sylvatic habitats. In the present work, in an endemic focus of cutaneous leishmaniasis in Venezuela, the adult population dynamics of 13 species of sandflies were studied in 3 different habitats: viz: houses, a peridomestic area and a sylvatic site.

4.2 Study area.

Geographical situation.

San Esteban is a small village in the District of Puerto Cabello, Carabobo State, 10° 26' North, 68° 01' West and at an altitude of 85 m above sea level (Fig. 80).

The hilly sinuous valley in which the village is spread out is crossed by a stream bearing the same name, which divides it into two parts. The northern side is connected by the main asphalted road to Puerto Cabello (17 km away), one of the most important ports of the Caribbean Sea. The southern side is limited by the foothills of the mountain range called "Serrania de la Costa".

Phytogeographic and Zoogeographic aspects.

The area of San Esteban was originally moist tropical forest but it has been disturbed for four centuries by the settlement of man.

Three plant associations can be distinguished: (i) agricultural, (ii) secondary forest and (iii) primary forest.

The "conuco", the small individual cultivated field of the Venezuelan farmer, is mostly of beans (Phaseolus vulgaris, Vigna sinensis), maize (Zea mays), and various tubers (Solanum tuberosus, Manibot esculenta, Beta vulgaris, Daucus carota etc.). Cultivation of bananas (Musa sapientum, M. paradisiaca), avocado (Persea americana), cocoa (Theobroma cacao), coffee (Coffea arabica) and citrus fruits (Citrus spp.) is done within the well-advanced secondary forest, a result of wood-felling and fire.

Remnants of the original primary forest persist along the river

edge and at high altitudes. Ficus spp. (Moraceae), with their enormous tubular roots, Ceiba pentandra (Bombacaceae), Anacardium excelsum (Anacardiaceae), Caroupita guayanensis (Lecythidaceae), Terminalia spp. (Combretaceae), form the upper canopy level, 30-40 m above the ground.

The branches of these tall trees bear numerous epiphytes of the families Bromeliaceae, Orchidaceae and Araceae.

A second level is formed by trees up to 20 m high including palms of the genera Scheelea, Bactriz, Socratea, Iriartea and many lianas. Luehea (Tiliaceae), Grislea (Lythraceae), Heliconia, form a shrub layer. The ground flora is scanty because little light penetrates the well-developed canopy and the deposits of leaf litter are shallow.

The vertebrate fauna include a large variety of reptiles, birds and mammals. The latter, as potential reservoir hosts of leishmaniasis, are of particular interest.

The most common mammals include monkeys (Alouatta ursina, Cebus apella apella, C. a. bruneus), ant-eaters (Tamandua tetradactyla), squirrels (Sciurus granatensis), armadillos (Dasypus novemcinctus), rabbits (Sylvilagus braziliensis), sloths (Bradypus infuscatus), rats (Heteromys, Orizomys, Proechimys, Zigodontomys etc) and bats (eg Phascellodomus hastatus).

Human population and leishmaniasis.

At present, 354 houses with about 1500 inhabitants form the village. There is one primary school and a dispensary which is visited once a week by a medical doctor.

The activities of the villagers are related to their sex and age: women are traditionally engaged in housework and helping the old men farm. The young men usually prefer the heavy, but well-paid work at

the port.

New cases of leishmaniasis, reported regularly over ten years, show that San Esteban is an endemic focus of the cutaneous disease. The monthly distribution of the assumed first appearance of the primary lesion, in a total of 115 cases, as judged by the physician, reported during 1967-1976 (Giordanelli et al., 1975-1976), is presented with an attempt to correlate these appearances with the monthly fluctuations of sandflies (Fig. 81).

Climate

From March 1979 to March 1980 records of the temperature (T) and relative humidity (RH) were made with 3 thermohygrographs placed at the 3 collecting stations: a house in the village, the peridomestic area (about 20 m from the same house) and the sylvatic area (200 m from one of the last houses in the village).

A rain-gauge , available from August 1979 to August 1980, was sited at the sylvatic station.

Four daily readings were taken from the continuous records at 02 h, 08 h, 14 h, and 20 h and the means for T and RH were calculated.

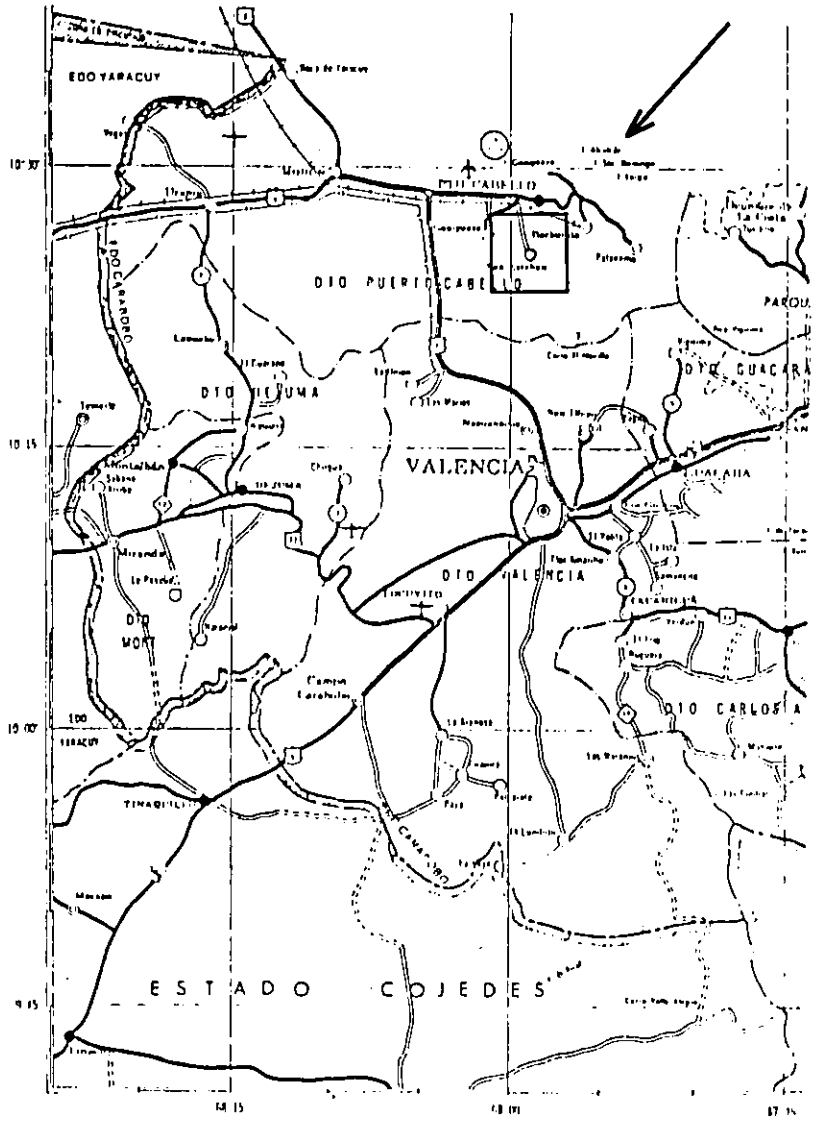


Fig. 80. Location of San Esteban, Carabobo State, Venezuela.

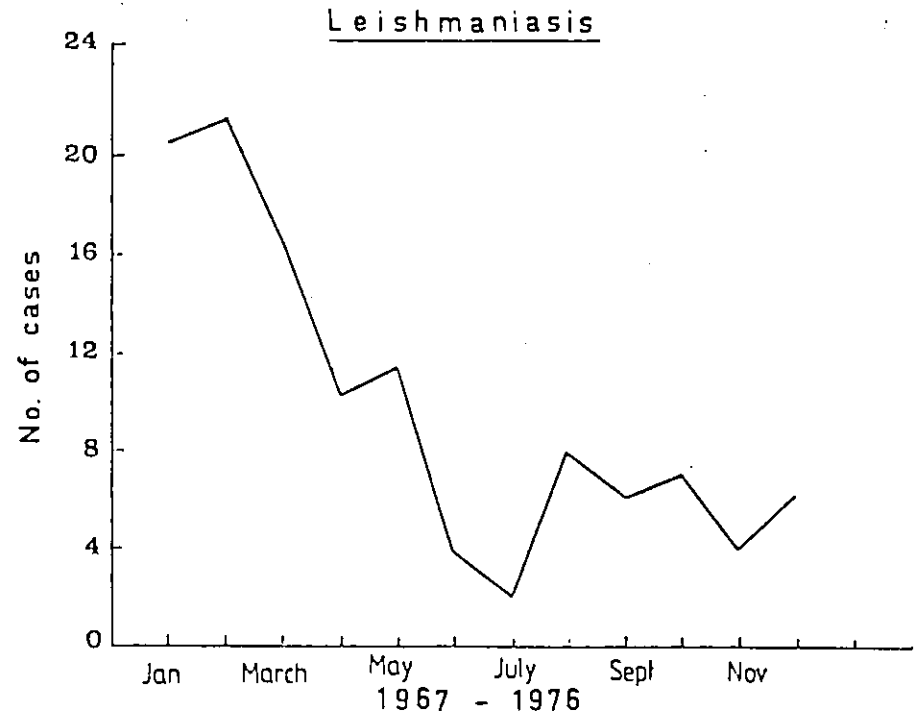


Fig. 81. Incidence of cutaneous leishmaniasis (1° lesions) at San Esteban (Venezuela) (1967 - 1976).

4.3 Materials and methods

The main purpose of the work was to provide a qualitative and quantitative analysis of the sandfly population and to record the relative seasonal densities of each species, by comparing successive samples taken in a standard way. This type of sampling does not require randomization in regard to the area, as recommended for estimating total populations (Morris, 1960).

Collecting stations were selected to include areas close to and distant from human activity. 3 distinct biotopes in the study area were chosen: (i) one house in the centre of the village; (ii) the peridomestic area (20 m from the same house) and (iii) the field (200 m from one of the last houses of the village).

Flies were caught from resting sites or coming to feed on man. Each of the two standard sampling methods was used twice a month, once in the morning (0800 - 1100h) and once at night (1900-2200). Catches were made on the same day of each week and each method was used on alternate weeks. The observations were continued for one year (March 1979-March 1980). The flies caught were recorded, with the catching method and time of day caught, for each month. It was not possible to trap sandflies for exactly three hours in each session, so the numbers caught were corrected for trap time, as explained below (Appendix 3).

Searches in domestic resting sites included the exploration of internal and external walls and household goods. Insects, located with the help of a lamp, were captured using an oral aspirator.

Trees were searched in an attempt to detect the natural resting sites of sandflies. Aerial roots, trunks and especially shaded crevices between buttresses were explored; sandflies were often caught after

being disturbed by cigarette smoke.

Direct bait catches were made so that anthropophilic sandfly species could be recognized and the relative probability of a man being bitten in the 3 different habitats estimated. The collections were carried out by two people: one served as bait and the other as collector. The bait sat with his shirt off and his trousers rolled up to the knee. Sandflies were caught as they attempted to feed.

Twice a month, during night catches, three additional catching methods were used. 1 Shannon trap with a kerosene lantern and no bait and 1 battery-operated CDC miniature light-trap were placed at the field station at about 2 m above ground level. The normal round collapsible frame of the CDC trap was replaced by a gauze-covered cage (20 cm^3) to make carriage easier. The cage was kept in a damp box.

In the peridomestic area flies were caught coming to animal bait, either pig or cow, depending on availability.

The efficacy of light traps had already been assessed (Chaniotis 1971a; Rutledge, 1975d). Their use showed which species of sandflies were positively phototropic. Such flies are more likely to be attracted to houses at night than species which are not attracted to light.

The collections from pig and cow gave an indication of the zoophily of each species and of the degree with which the presence of domestic animals may perhaps interrupt the flight of sandflies towards houses.

Occasional collections among stones at the edges of the stream, litter on the forest floor, animal burrows and animal baited traps were

attempted. This was difficult and, when it was found that the results were inconsistent, these collections were stopped.

After collection, the insects were transferred from aspirators to disposable plastic pots. The bottom of these pots was perforated and lined with plaster of Paris. The tops were covered with gauze. Pots containing flies were carried to the laboratory in polystyrene boxes with a wet cloth inside to maintain the humidity. The catches were sorted at the laboratory, and sandflies were mounted in Berlese's medium, sexed and identified to species.

Search for leishmanial infection.

Five thousand and twenty one females comprising 54 L. atroclavata, 121 L. cayennensis, 22 L. olmeca bicolor, 318 L. gomezi, 397 L. ovallesi, 2582 L. panamensis, 2 L. punctigeniculata, 12 L. shannoni and 1513 L. trinidadensis collected by the various techniques from March 1979 to July 1981, were dissected in saline and examined for leishmanial promastigotes.

Preparations which showed flagellate infections were stained by Giemsa's stain for identification of the form of the parasite.

2263 L. panamensis, 414 L. ovallesi and 41 L. gomezi were washed in detergent solution, triturated in saline solution and inoculated subcutaneously into golden hamsters. Pools ranged from 17 to 594 sandflies per inoculation. The 22 hamsters inoculated were observed for 6-8 months.

Statistical Methods

The counts of sandflies have been analysed using GENSTAT, a statistical

package developed at Rothampstead Experimental Station (Alvey *et al.* 1977) and the analysis is described fully in the Appendices. Detailed significance levels are not included in the main body of the text since only those differences significant at the 0.05 level, or more significant, are included.

4.4 Results

Definition of terms.

For the study of the phlebotomine fauna at San Esteban several terms are here used, in the sense explained below.

The "species composition" of a fly population describes the species within it, the population limits being a particular area or habitat.

"Abundance" expresses the number of each species collected.

"Relative abundance" is the ratio of the total number of each species to the total number of sandflies collected.

The term "occurrence" will be used in this paper in two senses: qualitative and quantitative.

In the qualitative sense, occurrence is defined as the presence of one species in a definite place or habitat whereas, in quantitative terms, it is calculated as the number of collections in which the species occurs.

The term "absolute occurrence" is a measure of collecting success, being the ratio of the number of collections in which the species was found, to the total number of collections carried out during the study period.

The term "relative occurrence" describes the efficiency of each capture method for each fly species. It is expressed as the number of collections by a given method in which the species occurred, divided by the total number of collections made using that method.

4.4.1 Metereological observations

In Table 16 and Fig. 82 are shown the recordings for temperature which decreased from the house ($\bar{x}$ = 26.8 $\pm$ 1.04) through the peridomestic area ($\bar{x}$ = 24.5 $\pm$ 0.73) to the field ($\bar{x}$ = 23.01 $\pm$ 0.90).

The mean Relative Humidity (Table 17, Fig. 82) was similar in all 3 stations (House: $\bar{x}$ = 75.26 $\pm$ 2.65; peridomestic station: $\bar{x}$ = 77.08 $\pm$ 4.15; field station: $\bar{x}$ = 76.6 $\pm$ 3.86).

Although differences in average RH were negligible, values for minimum RH were significantly different for the three habitats. During the dry season (January-April) the values for minimum RH in the house and in the peridomestic site quickly reached 60% and stayed at about this level until July. In the sylvatic site, the minimum humidity was less than 60% until September, when it slowly increased till December. The minimum RH decreased dramatically in the dry season in this habitat.

The rainfall ranged from a monthly minimum of 0.5 mm to a maximum of 144.4 mm, the total annual precipitation was 773.20 mm (Table 18). The resultant climatogram (Fig. 83), built following Walter & Lieth's method (1960, 1967), reveals a 4 month dry season (January to April) and an 8 month wet season (May to December). The wet season had two peaks of rainfall, one around June - July and the other at the end of the year. The driest month was March and the wettest December.

Table 16. Mean Temperatures (°C) recorded at three collecting stations in San Esteban during 1979-1980.

		1979										1980		
		M	A	M	J	J	A	S	O	N	D	J	F	M
House	Monthly mean (σ)	25.7 (1.93)	27.7 (0.91)	27.4 (0.65)	27.6 (0.76)	27.9 (0.88)	27.6 (0.88)	27.8 (0.68)	27.2 (0.91)	27.6 (1.23)	26.1 (1.31)	25.5 (0.84)	25.0 (1.79)	25.8 (1.14)
	Mean of maxima (σ)	28.9 (1.35)	29.6 (1.64)	30.1 (1.14)	30.2 (0.72)	31.2 (0.71)	30.7 (1.16)	31.3 (0.98)	30.4 (1.15)	30.3 (1.44)	29.4 (1.19)	28.3 (1.24)	29.0 (0.96)	29.8 (1.32)
	Mean of minima (σ)	24.7 (1.14)	25.6 (0.92)	25.0 (0.60)	25.2 (0.37)	25.5 (0.65)	25.0 (1.08)	25.1 (0.92)	25.0 (0.64)	25.0 (0.79)	24.0 (1.35)	23.2 (0.94)	22.0 (0.85)	22.6 (1.58)
Peridomestic habitat	Monthly mean (σ)	24.9 (1.15)	25.6 (0.88)	25.5 (1.05)	25.3 (0.84)	23.7 (0.87)	23.8 (0.80)	24.5 (0.87)	24.7 (1.31)	25.0 (0.92)	24.0 (0.94)	24.2 (0.80)	23.2 (1.59)	24.6 (1.55)
	Mean of maxima (σ)	29.6 (1.41)	29.9 (1.25)	30.5 (2.20)	30.4 (1.10)	28.9 (1.80)	28.6 (1.16)	30.2 (1.44)	29.9 (1.47)	30.2 (1.24)	28.7 (1.52)	29.2 (1.09)	29.1 (1.23)	29.7 (0.91)
	Mean of minima (σ)	22.1 (1.31)	23.5 (0.50)	23.2 (0.68)	22.5 (0.38)	20.4 (0.56)	20.3 (0.71)	20.9 (0.83)	21.8 (1.47)	22.1 (0.99)	21.5 (1.13)	20.6 (0.93)	18.7 (1.59)	19.6 (2.11)
Field habitat	Monthly mean (σ)	22.8 (0.88)	25.5 (3.10)	23.5 (0.92)	23.0 (1.55)	23.2 (0.86)	22.6 (1.11)	23.3 (1.09)	23.0 (0.99)	22.0 (1.28)	22.9 (2.29)	22.3 (0.83)	21.8 (2.28)	23.3 (1.38)
	Mean of maxima (σ)	26.0 (1.04)	26.5 (2.19)	28.3 (1.68)	27.0 (1.70)	28.0 (1.17)	26.9 (1.31)	28.4 (1.48)	27.3 (1.15)	25.3 (1.97)	25.2 (1.10)	26.9 (0.48)	25.9 (1.58)	28.1 (0.98)
	Mean of minima (σ)	19.7 (1.50)	20.8 (1.41)	20.3 (0.58)	20.8 (0.47)	19.6 (0.46)	19.8 (0.55)	20.1 (0.59)	20.7 (0.67)	19.7 (1.31)	20.4 (1.01)	19.9 (0.62)	17.7 (0.95)	18.3 (1.55)

Table 17. Relative humidity (%) recorded at three collecting stations in San Esteban (1979-1980).

		1979										1980		
		M	A	M	J	J	A	S	O	N	D	E	F	M
House	Monthly mean (σ)	72.2 (5.29)	76.6 (3.08)	75.8 (4.96)	76.0 (5.41)	74.9 (4.22)	76.4 (4.08)	76.3 (2.63)	78.1 (2.35)	76.6 (3.39)	79.1 (4.11)	75.0 (3.08)	72.0 (5.02)	69.4 (3.89)
	Mean of maxima (σ)	81.3 (4.88)	84.9 (3.47)	84.2 (3.61)	86.9 (1.66)	85.6 (1.53)	86.2 (2.52)	86.7 (2.69)	87.6 (2.69)	87.3 (3.48)	87.9 (3.95)	84.3 (1.81)	84.3 (3.24)	80.5 (2.70)
	Mean of minima (σ)	61.5 (7.39)	65.2 (4.69)	62.0 (6.61)	65.6 (8.31)	58.3 (5.99)	63.2 (2.52)	58.5 (7.5)	63.2 (5.89)	64.6 (5.58)	63.7 (5.78)	63.7 (5.53)	54.3 (7.51)	51.4 (6.65)
Peridomestic habitat	Monthly mean (σ)	77.1 (4.78)	79.3 (3.29)	81.7 (4.12)	79.5 (6.45)	77.9 (4.91)	80.3 (4.43)	76.7 (4.11)	81.6 (3.31)	78.1 (3.5)	77.2 (4.44)	75.2 (5.28)	68.7 (6.10)	68.8 (4.19)
	Mean of maxima (σ)	81.6 (1.15)	90.6 (1.45)	91.4 (1.16)	90.2 (0.42)	89.2 (8.04)	89.0 (0.37)	89.2 (0.60)	87.4 (3.18)	90.0 (3.47)	89.3 (3.86)	84.9 (2.67)	83.2 (3.01)	85.7 (1.81)
	Mean of minima (σ)	55.6 (7.94)	61.1 (7.32)	59.3 (6.02)	60.1 (6.00)	52.5 (8.04)	55.5 (8.35)	50.7 (8.03)	55.2 (8.11)	55.0 (5.38)	56.8 (8.90)	50.8 (5.42)	43.8 (6.08)	41.4 (6.11)
Field habitat	Monthly mean (σ)	69.6 (3.72)	74.1 (4.85)	74.4 (5.20)	75.1 (3.83)	77.6 (4.65)	80.4 (4.63)	79.6 (4.10)	81.5 (3.88)	81.6 (2.10)	78.2 (5.82)	77.6 (3.15)	75.0 (4.85)	70.7 (3.79)
	Mean of maxima (σ)	80.2 (2.84)	80.9 (1.35)	80.2 (2.05)	78.8 (0.83)	86.1 (1.04)	84.9 (1.05)	84.6 (0.63)	84.8 (0.73)	83.6 (1.84)	84.7 (0.50)	85.3 (0.70)	84.4 (1.18)	84.7 (1.58)
	Mean of minima (σ)	51.1 (8.88)	53.9 (7.69)	55.7 (9.28)	60.6 (12.2)	53.6 (7.68)	60.8 (9.15)	56.6 (9.87)	63.0 (7.06)	65.5 (5.98)	70.0 (3.94)	63.3 (5.19)	53.1 (7.35)	45.2 (6.49)

Table 18. Rainfall (mm.) recorded at San Esteban (Venezuela)from August 1979 to July 1980.

	1979					1980						
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July
Total	49.7	104.8	122.3	91.4	144.4	5.4	11.2	0.5	4.6	41.4	102.4	95.1
Max 24 hs	19.8	20.6	25.3	21.0	30.2	4.2	6.3	0.4	2.8	14.1	28.5	21.5
Min 24 hs	1.0	0.2	0.8	0.7	0.3	0.3	0.7	0.1	0.2	0.1	0.5	0.5
Daily mean (σ)	1.71 (4.72)	3.74 (5.31)	4.08 (6.32)	3.05 (5.3)	5.55 (9.28)	0.27 (0.94)	0.43 (1.28)	0.01 (0.07)	0.22 (0.64)	1.38 (3.49)	3.41 (2.85)	3.17 (1.8)

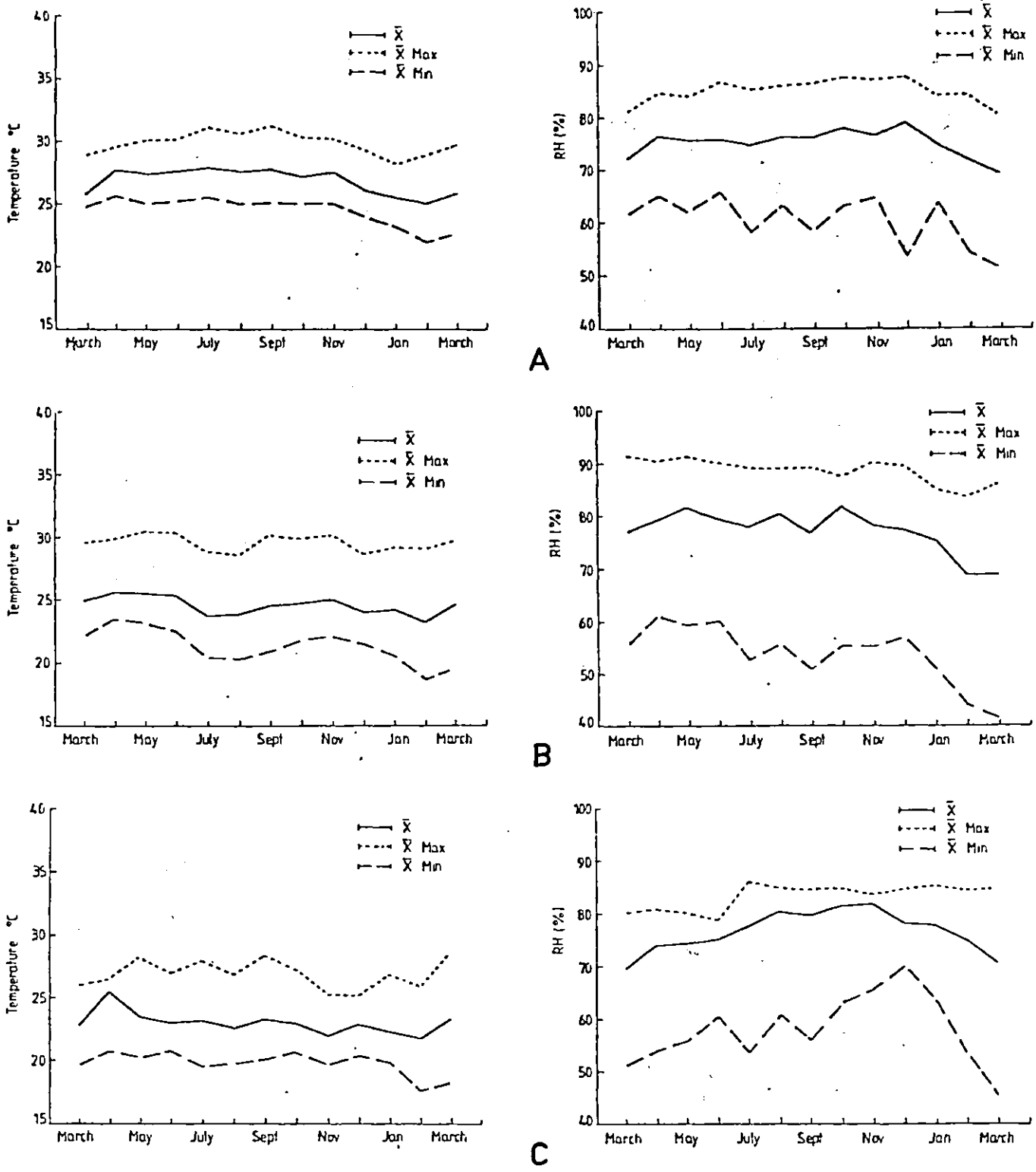


Fig. 82. Metereological data (Temperature and Relative Humidity), recorded during 13 month study period at the collecting stations in San Esteban, Venezuela.
A: House; B: Peridomestic Area; C: Sylvatic area.

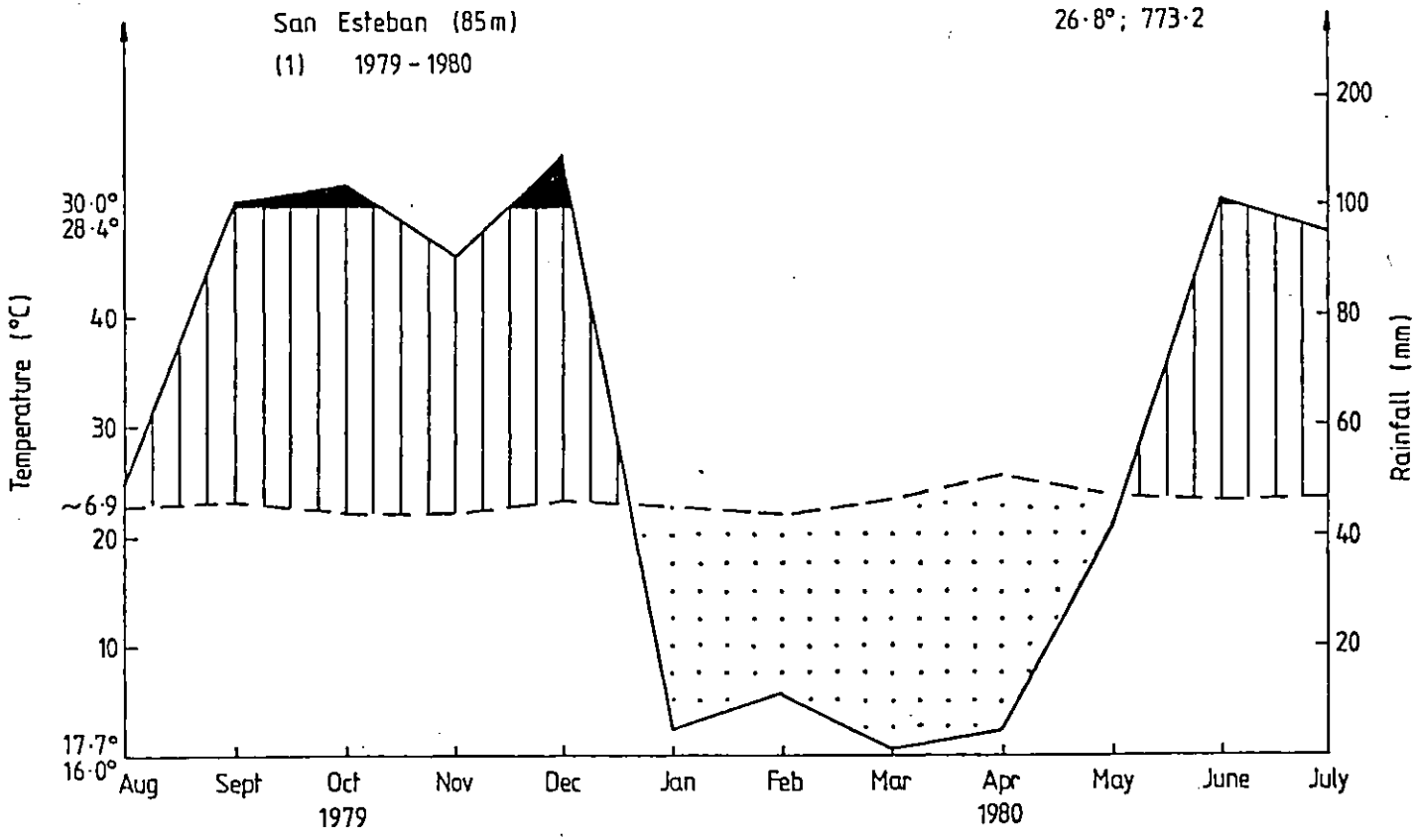


Fig. 83. Climatogram at San Esteban (Venezuela) (1979 - 1980).

4.4.2 Sandfly population structure: species composition in relation to habitat, catching method and time of catching.

During 13 months of the study period, a total of 10,723 sandflies (9,061 ♀♀ and 1,662 ♂♂), representing 13 species were collected.

Table 19 shows the species composition, giving the number of sandflies by species and sex, the sex ratio and the abundance of each species.

Table 20 shows the 'occurrence' of sandflies using a different scoring method.

The trapping methods were limited, and some species were undoubtedly under-represented because of their ecology and behaviour. Abundance, occurrence and the terms "relative" and "absolute" must therefore be applied with caution when comparing the results for different species.

Tables 19 and 20 allow separate comparison of species with respect to (i) abundance and occurrence, (ii), occurrence in relation to the habitat, and (iii) occurrence in relation to catching methods. In Appendix 2 are shown the monthly number of insects/man/hour by habitat and method, during morning and evening hours. In Tables 21 and 22, this information is summarized giving the average numbers of insects taken during the period study by man and by hour, divided by the total number of collections by day and by night.

4.4.2a. Abundance and occurrence

The most abundant species in the study area was L. panamensis, which represented 68.7% of the total catch (Table 19), followed by L. trinidadensis (12.8%), L. ovallesi (9.78%) and L. gomezi (6.02%).

These same species, in a different order, also scored most highly

Table 18. Monthly totals for each sandfly species caught at San Esteban, Venezuela, from March, 1979 to March 1980.

Species	Month	1979										1980			Total ♀♀ or ♂♂	Total ♀♀ + ♂♂	Sex ratio ♀♀ : ♂♂	Abundance
		March	April	May	June	July	August	Sept.	October	November	December	Jan.	February	March				
L. atroclavata	♀♀	4	2	4	6	1	2	4	2	1		1	4		31	119	1 : 2.84	1.11%
	♂♂	24	4	8	1	5	2	8	9	11	2	11	8		88			
L. cayennensis	♀♀	4		1	4	4	1	2	4	1	8	3	4	3	37	88	1 : 38	0.82%
	♂♂	3			8	1	3	5	7	4	16	2	2	2	51			
L. dubitans	♀♀										1				1	1	1 : 0	0.03%
	♂♂														0			
L. evansi	♀♀												1		1	1	1 : 0	0.03%
	♂♂														0			
L. gomezi	♀♀	3	18	13	20	15	19	19	46	56	19	38	106	8	382	646	1 : 0.69	6.02%
	♂♂	11		2	7	4	57	83	70	3	8	19	20		264			
L. olmeca bicolor	♀♀		4		3		1		2	3	3	4	1		21	32	1 : 0.52	0.50%
	♂♂			1	2		1				6	2			11			
L. ovallesi	♀♀	10	150	3	10	7	5	11	7	53	24	410	263		876	1,049	1 : 0.07	9.78%
	♂♂	1	5	2	1	1		2	2	2		8	47		73			
L. panamensis	♀♀		52	270	1,748	458	282	348	587	1,668	585	1,037	166	11	7,113	7,364	1 : 0.04	68.67%
	♂♂		7	8	89	23	9	10	38		38	22	31		251			
L. punctigeniculata	♀♀							1					1		2	6	1 : 0.5	0.06%
	♂♂				1						1		2		4			
L. rangeliana	♀♀														0	1	0 : 1	0.009%
	♂♂						1								1			
L. shannoni	♀♀				1		1	1	3	3	6		1		15	42	1 : 1.8	0.39%
	♂♂			1			2	8	13	1	1	1			27			
L. trinidadensis	♀♀	80	31	47	44	54	21	33	29	31	53	38	29	23	481	1,373	1 : 1.85	12.80%
	♂♂	74	41	148	45	72	43	48	53	65	114	115	54	22	892			
Brumptomyia sp.	♀♀				1										1	1	1 : 0	0.009%
	♂♂														0			
Monthly Total	♀♀	71	287	338	1,837	539	333	318	880	1,828	887	1,530	578	46	9,061	10,723	1 : 0.18	
	♂♂	113	67	163	162	306	318	142	171	85	176	181	164	24	1,662			

Table 20. Relative and absolute occurrence by habitat and trapping methods of sandfly species at San Esteban, Venezuela (March 1979 - March 1980).

Habitat / Method / Species	House		Peridomestic Area				Silvatic Area				No. occasions collected	Absolute frequency (%)
				Biting								
	Walls (25)*	Biting man (26)	Tree (25)	Man (26)	Pig (8)	Cow (4)	Tree (25)	Biting man (26)	Shannon trap (23)	CDC trap (13)		
L. atroclavata	12	-	76	7.69	-	-	28	-	8.70	7.69	34	16.9
L. cayennensis	16	3.85	68	3.85	-	-	24	-	4.35	15.38	32	15.9
L. dubitans	-	-	-	-	-	-	-	-	-	7.69	1	0.05
L. evansi	-	-	-	-	-	-	-	-	4.35	-	1	0.05
L. gomezi	28	15.38	8	50	87.5	75.0	16	42.3	91.3	84.61	83	41.3
L. olmeca bicolor	-	7.69	-	-	-	-	-	3.85	47.83	23.01	17	8.46
L. ovallesi	-	7.69	8	26.92	50	-	44	34.62	78.3	69.23	62	30.8
L. panamensis	48	26.92	28	50	100	100	28	57.69	91.3	100	107	53.2
L. punctigeniculata	-	-	8	-	-	-	12	-	-	-	5	2.49
L. rangeliana	-	-	-	-	-	-	4	-	-	-	1	0.05
L. shannoni	-	-	40	3.85	37.5	50	8	7.69	8.69	-	22	10.9
L. trinidadensis	28	3.85	88	11.5	12.5	-	92	-	4.35	23.07	61	30.3
Brumptomyia sp.	-	-	-	-	-	-	-	-	4.35	-	1	0.05

*Numbers in brackets indicate the total number of collections.

in the measure of the occurrence. L. panamensis was detected in 53% of the collections and L. gomezi, although not represented by many individuals, was found in 41.3% of the samples. The absolute occurrence of L. ovallesi and L. trinidadensis was about 30%. L. cayennensis, L. atroclavata and L. shannoni, with low absolute occurrence (10-17%), were most the common species in collections in trees. L. olmeca bicolor, although never found resting, was often caught in light-traps (Table 20).

Values of the absolute occurrence are dependent on the efficiency of the combined collection methods. Consequently, though a species may be constantly present in an area, the value for its absolute occurrence can be low if it is detected only by a limited number of methods.

The relative occurrence by method therefore appeared to be the more sensitive measure to separate common species from rare species. Those species which reached a relative occurrence of about 50% or more at any time in any habitat using any method, were considered as common species, i.e. L. panamensis, L. ovallesi, L. gomezi, L. trinidadensis, L. atroclavata, L. cayennensis, L. shannoni and L. olmeca bicolor. The other species, L. punctigeniculata, L. rangeliana, L. evansi, L. dubitans, and Brumptomyia sp., were considered rare species. Samples of rare species were too small to justify a statistical analysis and this was done only with "common" species.

4.4.2b. Composition in relation to the habitat

The presumed sylvatic origin of Neotropical sandflies was once more supported by the observation that specimens of all the species detected were collected at the field site (Table 21 and 22). Eight of thirteen species (61.5%) were encountered in the peridomestic habitat and seven of thirteen (53.8%) in the house. The average number of insects of these

Table 21. Sandflies/man/hour ($\bar{x}$) caught in day time, by habitat and collecting method (San Esteban, Venezuela, March 1979 - March 1980).

Species ♀♀ ♂♂	House		Periodmestic habitat		Field site	
	WALLS	BITING MAN	TREES	BITING MAN	TREES	BITING MAN
L. atroclavata	0.06 0.03		0.33 1.86	0.05	0.24 0.32	
L. cayennensis	0.19		0.56 0.72		0.08 0.13	
L. dubitans						
L. evansi						
L. gomezi			0.03		0.06 0.03	
L. olmeca bicolor						
L. ovallesi			0.03		0.11 0.06	0.05
L. panamensis	0.06		0.64 0.36	0.06		0.13
L. punctigeniculata			0.03		0.36	
L. rangeliana					0.03	
L. shannoni			0.08 0.10		0.03	
L. trinidadensis	0.12 0.19		3.77 8.89	0.03	8.49 16.06	
Brumptomyia sp.						
All species ♀♀ ♂♂	0.42 0.22		5.39 11.95	0.06 0.08	9.09 17.00	0.18

Table 22. Sandflies/man/hour ($\bar{x}$) caught at night by habitat and collecting method (San Esteban, Venezuela, March 1979 - March 1980).

Species ♀♀ ♂♂	HOUSE		PERIDOMESTIC HABITAT				FIELD SITE			
	WALL	MAN	TREES	MAN	PIG	COW	TREES	MAN	SHANNON	CDe
L. atroclavata			0.12 0.57				0.03		0.04	0.03
L. cayennensis	0.08	0.08	0.32 0.36	0.06			0.09 0.06		0.007	0.06 0.04
L. dubitans										0.04
L. evansi									0.015	
L. gomezi	0.28 0.65	0.38 0.15	0.04	3.24 4.98	15.25 34.5	3 38.5	0.18 0.03	2.68 0.27	1.98 1.69	1.85 0.10
L. olmeca bicolor		0.07						0.03	0.24 0.32	0.09
L. ovallesi		0.31	0.09 0.25	0.71 0.04	1 0.75		0.67 0.06	16.93	6.63 0.89	1.58 0.10
L. panamensis	3.57 0.30	4.17	0.42 0.03	17.38 0.06	58.0 1.75	143.5 5.0	5.17 0.22	20.58 0.21	72.42 2.68	56.67 2.21
L. punctigeniculata							0.04			
L. rangeliana										
L. shannoni			0.25 0.12	0.19	0.25 1.00	4.50		0.07	0.09 0.01	
L. trinidadensis	0.06 0.03	0.08	1.48 7.53	0.11	0.50		3.46 1.54		0.05	0.09
Brumptomyia sp									0.007	
All species	3.9 1.06	5.00 0.15	2.71 8.9	21.39 5.37	74.5 38.5	146.5 48.0	9.59 1.94	40.27 0.51	80.24 5.81	60.42 2.46

species caught with the same methods in the neighbourhood of the house was higher than at the field site (Tables 21 and 22).

4.4.2c. Composition in relation to capture methods.

The occurrence and abundance of sandflies in relation to capture methods is directly related to specific habits.

Collections from human bait detected 3 anthropophilic species: L. panamensis, L. ovallesi and L. gomezi. They were encountered attacking man in all habitats, but were found rarely on trees and, when present, were always in low numbers.

Collections in trees were especially successful for non-anthropophilic species: L. trinidadensis, L. atroclavata and L. cayennensis, frequently associated inhabitants of tree holes. L. shannoni was found with a relatively low frequency and low density on trees and then only in the peridomestic habitat.

In analysing the results of collections on domestic animals it is necessary to note that the first four months of observation (March - June 1979) were missing and that collections from pig and cow were limited to only four months (July - October 1979). However, as March - June was the period of lowest density for all species, it is possible to compare results obtained biting man with those biting pig. All anthropophilic species were attracted by this host and the frequency of attack of two of them was higher for pig than for man. While the number of L. ovallesi caught on pig was similar to that caught on man, many more L. gomezi and L. panamensis were caught on the pig than on human bait.

Light traps proved to be the most efficient method of capture, since 86.6% of all species were trapped by Shannon and CDC traps combined.

The Shannon trap gave better results than CDC traps in terms of numbers and density of species trapped, except for L. trinidadensis and L. cayennensis. Both these species are known not to be phototropic. Catches were made more frequently using CDC than Shannon Traps, CDC sampling a larger air volume by suction, than do Shannon Traps, (Table 20).

The numbers of L. panamensis attracted by light was overwhelming in relation to all other species. Although L. ovallesi and L. gomezi were regularly trapped by light-traps, they were always in low numbers. L. olmeca bicolor, a species thought not to be abundant, was caught several times in light-traps.

4.4.2d. Composition in relation to the time of capture

Anthropophilic sandflies usually, but not always, feed at night or during the few hours of twilight before sunset and after sunrise. This crepuscular and nocturnal biting activity was seen in the present study, human bait being more frequently attacked at night than in daylight. In contrast, more sandflies were aspirated from trees during daylight than at night (Tables 21 and 22).

Males predominated in tree catches from the peridomestic area by day and night, and from the field site during the day. Curiously, more females than males were caught from the field area at night.

A summary of all aspects of the studies considered above is presented in Tables 23 and 24 and Figs. 84 to 86. The relative abundance of the common species is expressed as the number of sandflies caught per man, per hour with all methods used, by day and night, throughout the study period. The most closely associated species fell into the two groups: (i) the anthropophilic species L. panamensis, L. ovallesi and L. gomezi

and (ii) the non-anthropophilic species, L. trinidadensis, L. atroclavata and L. cayennensis. L. shannoni and L. olmeca bicolor are treated separately because they show no strong preferences. Though found biting man, their attacks were rare compared with their abundance.

Table 23. Relative abundance of the anthropophilic species at San Esteban, Venezuela (March 1979-March 1980).

	♀♀	♂♂	Tot	%
L. panamensis	7,113	251	7,364	81.3
L. ovallesi	976	73	1,048	11.57
L. gomezi	382	264	646	7.13
	8,471	588	9,058	100

Table 24. Relative abundance of non-anthropophilic species at San Esteban, Venezuela (March 1979-March 1980).

	♀♀	♂♂	Tot	%
L. trinidadensis	481	892	1,373	86.9
L. atroclavata	31	88	119	7.53
L. cayennensis	37	51	88	5.57
	549	1,031	1,580	100

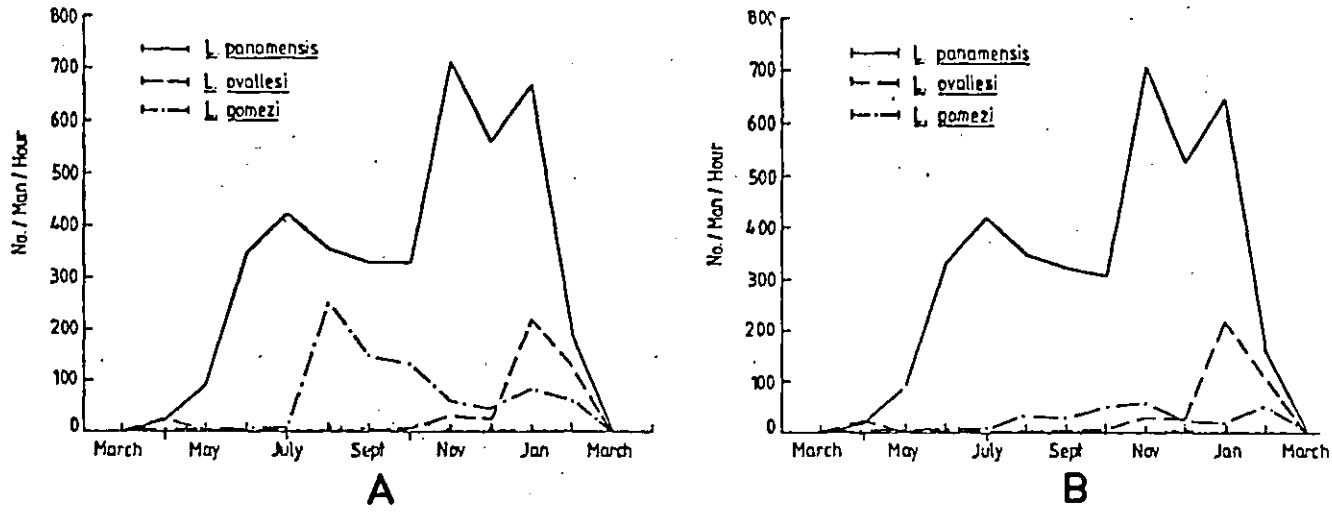


Fig. 84. Relative abundance of total population (A) and Females (B) of dominant anthropophilic species at San Esteban during 13 months (March 1979 - March 1980).

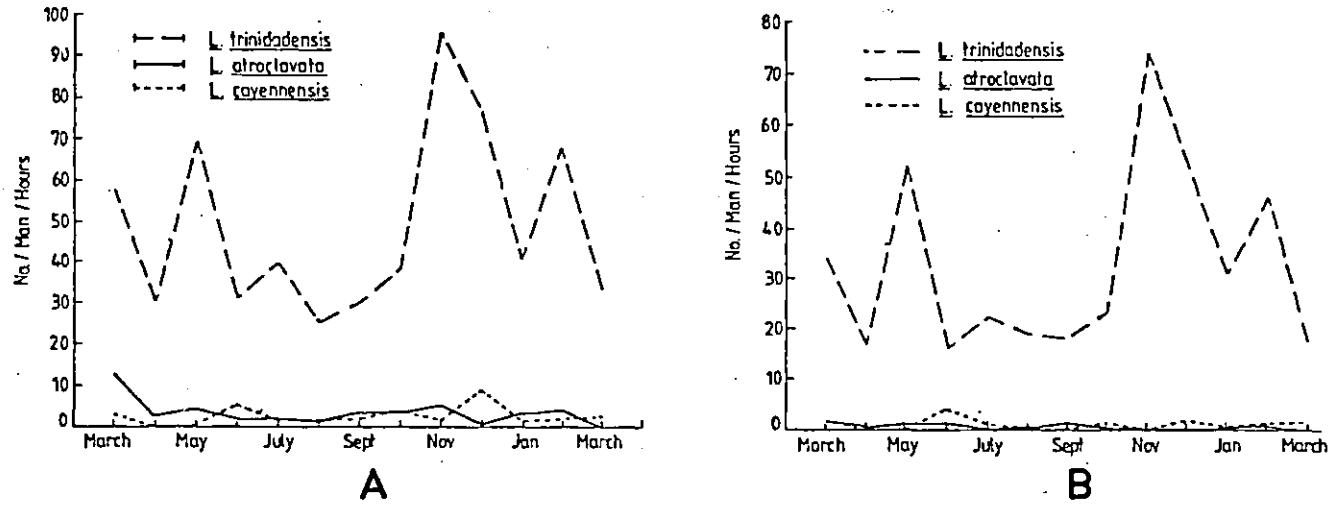


Fig. 85. Relative abundance of total population (A) and Females (B) of dominant non-anthropophilic species at San Esteban during 13 months (March 1979 - March 1980).

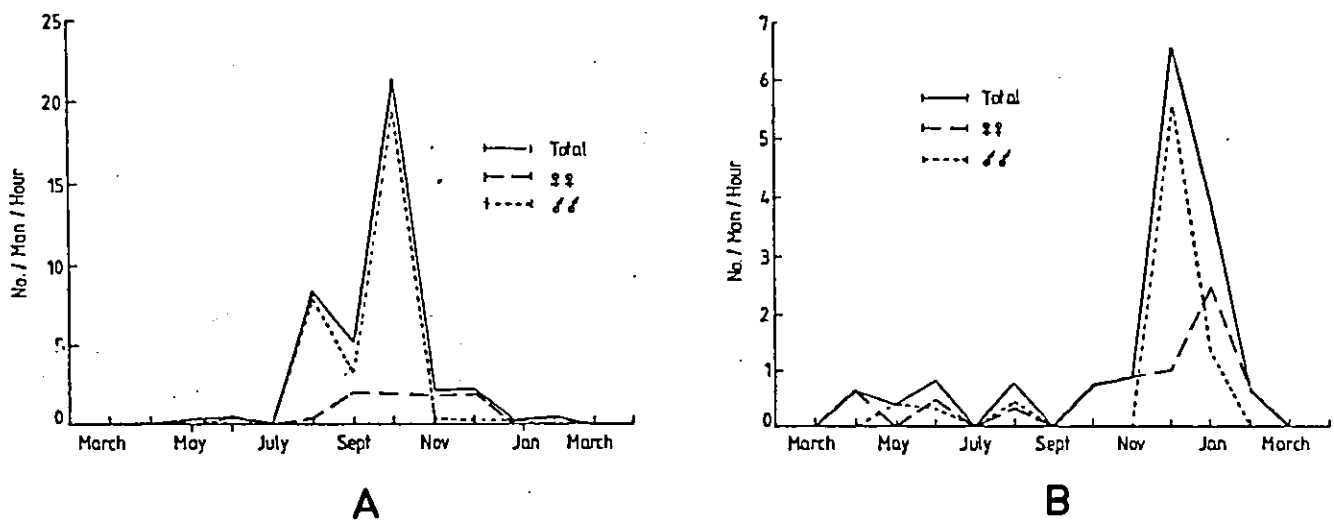


Fig. 86. Relative abundance of L. shannoni (A) and L. olmeca bicolor (B) at San Esteban, Carabobo State, Venezuela (March 1979 - March 1980).

4.4.3 Seasonal fluctuations

As stated above, catching methods were not used uniformly during the period of study; collections with the CDC trap were started in June 1979 and those on pig and cow began in July and were stopped in November 1979. On two occasions (in March and September 1979), one of the two Shannon traps failed. A constant sampling time of 3 hours had been initially planned but several problems prevented this regime being maintained. For instance, the exploration of the houses had to be delayed sometimes because of locked doors. Though late starts could be compensated for by late finishes, the catch was different because of the hourly fluctuations in the activity of sandflies. Collection times using human bait were affected by the density of sandflies: at times so many flies were feeding that the men found it impossible to remain still and some flies were disturbed. Several times sudden rain forced the removal of a Shannon trap and the interruption of the catch.

In order to make the results of seasonal fluctuations comparable, only the results from methods used every month have been taken into account. The numbers of sandflies collected were divided both by the time employed and number of collectors, and were expressed as number of sandflies/man/hour. For the Shannon trap, the time of exposure of the trap, the time of collection and the number of collectors were taken in consideration.

For each species, graphs of seasonal trends and the most abundant collections deserving special comment are presented.

The outstanding feature of the population dynamics of L. panamensis (Fig. 87 A) was a clear correlation with rainfall. The population began

to increase immediately after the first rains in April and reached a first peak in June when total rainfall for the year exceeded 100 mm. This peak was followed by a decrease in the population size in the following two months, coinciding with a drop in rainfall. An increase in rainfall in September was accompanied by a second increase in the size of the L. panamensis population. Later, the population appeared out of phase with the rainfall by one month.

Fig. 87B, C, D show the results of collections biting man at night in the three habitats. Although flies were more frequently found resting on walls than feeding on bait, the highest densities were observed biting man, reaching a maximum of 18 man/hour in September. This high level of biting activity in September coincided with an increase in abundance of sandflies in the peridomestic habitat, where the peak was represented by more than 100 sandflies/man/hour. In the field site, the greatest density was comparatively lower (80 man/hour) and was seen in November (Fig. 87D). The Shannon trap caught a larger number of sandflies than the CDC trap (Fig. 87 E,F), with November and January being the months with the highest densities.

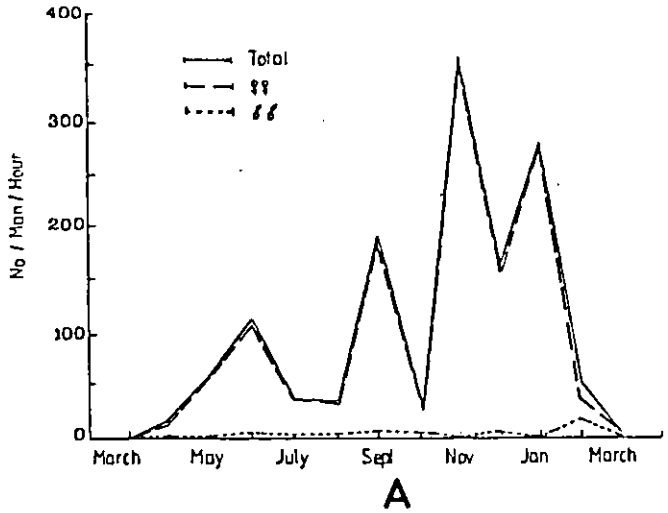
Fig. 87G shows the number of L. panamensis/man/hour collected on pig. The high attraction of this species to domestic animals is evident. Peaks of high densities were recorded in November and February when the number of specimens biting man in the peridomestic area was comparatively lower.

The sex ratio in all captures throughout the year showed an overwhelming preponderance of females.

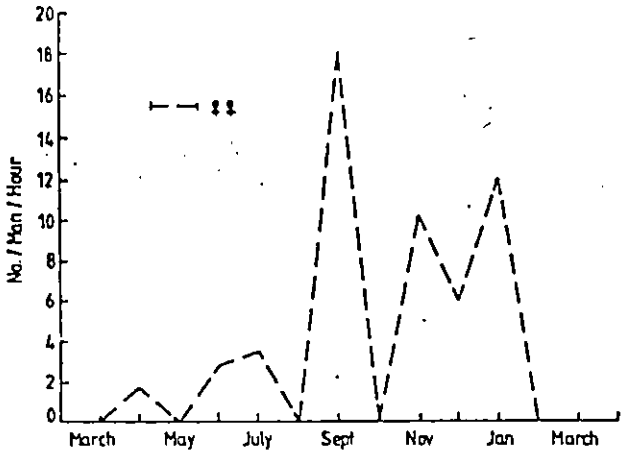
L. gomezi showed a different pattern from that of L. panamensis. The size of the population was extremely low during the dry season (March

Fig. 87. L. panamensis : Seasonal fluctuations of the total population (A)*. Monthly collections at night : biting man in the house (B), biting man in peridomestic habitat (C), biting man in sylvatic habitat (D), with Shannon trap (E), with CDC trap (F), biting pig (G). (San Esteban, Venezuela, March 1979 - March 1980).

*Only methods which were used in each month of the year have been combined in this figure (see text).



A



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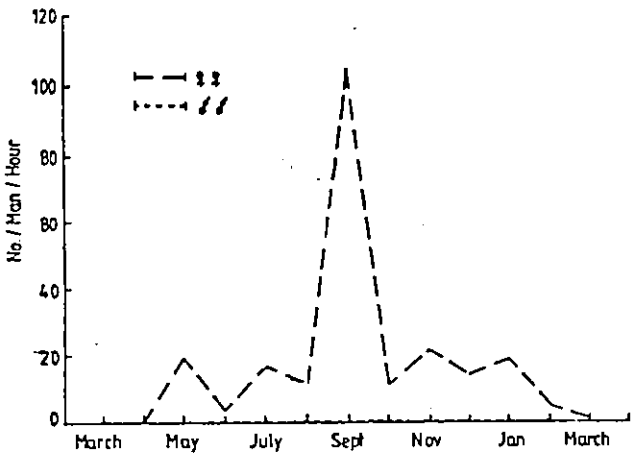

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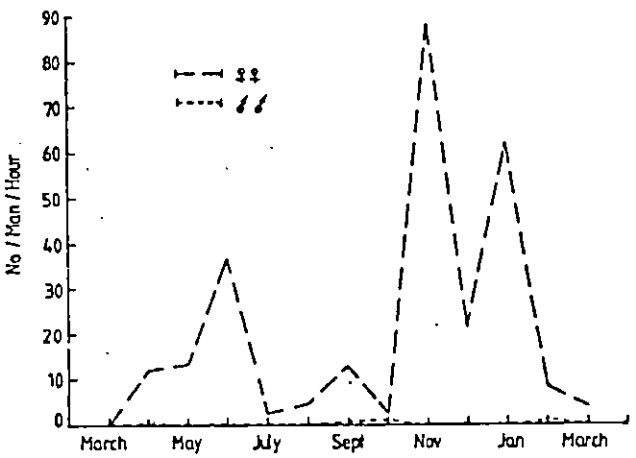

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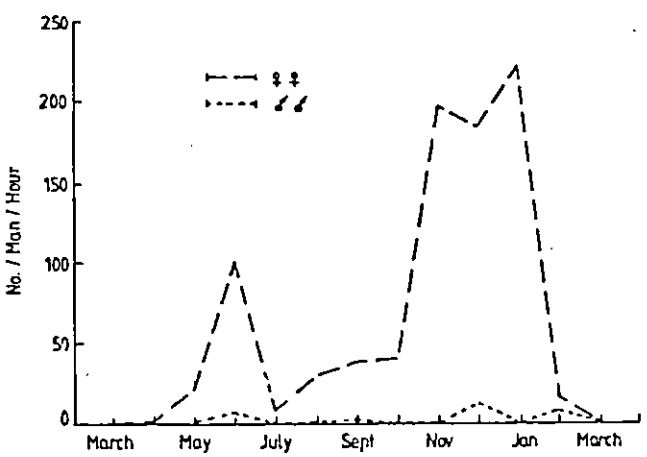

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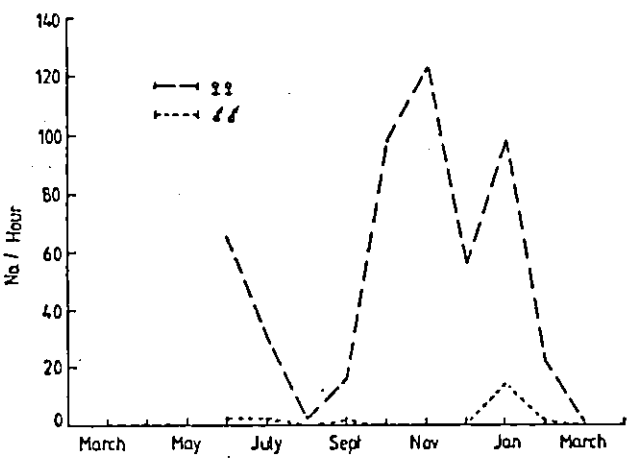
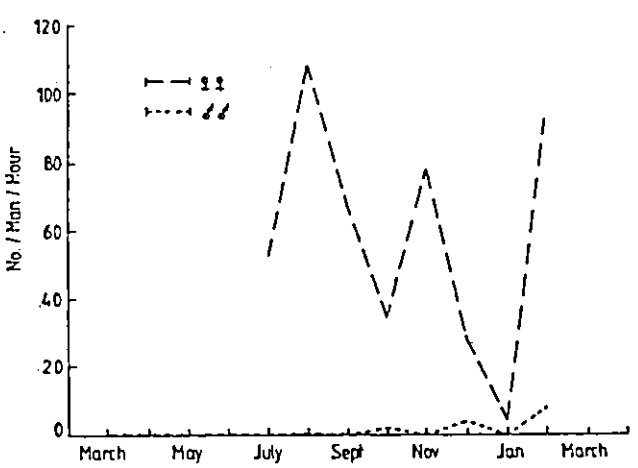


F



G

Fig. 87

to July) and increased abruptly in August, particularly on human bait in the peridomestic habitat. In the next three months (September - November), the population fell and there was then a slight increase towards January of the next year (Fig. 88).

The number of L. gomezi attracted by light traps was much lower than L. panamensis.

The sex ratio in this species varied with the catching habitat. Males prevailed over females in catches from human and pig bait in the peridomestic area while in the field habitat, males were more common from human bait and light traps (See section 4.4.2c).

The seasonal changes in the L. ovallesi population are shown in Fig. 89A. Though detected every month, there was a sudden "explosion" at the beginning of the year. Only catches in the field habitat are shown since, although this fly occasionally entered houses and was found in the peridomestic habitat, it occurred in these places at very low densities. In contrast, the number of sandflies which attacked man in the field was very high, exceeding the highest densities of L. panamensis (Fig. 87). This catching constituted the major part of the total fly population.

Very few specimens of L. ovallesi were caught in light-traps (Fig. 89B,C). The fly was never caught on cow and was caught on pig on only half the occasions it was offered as bait. The number of females caught was much greater than that of males.

L. trinidadensis population dynamics showed two peaks in fly density in May and November, immediately before and after the first two peaks of rainfall, respectively (Fig. 90A). Trees were the main

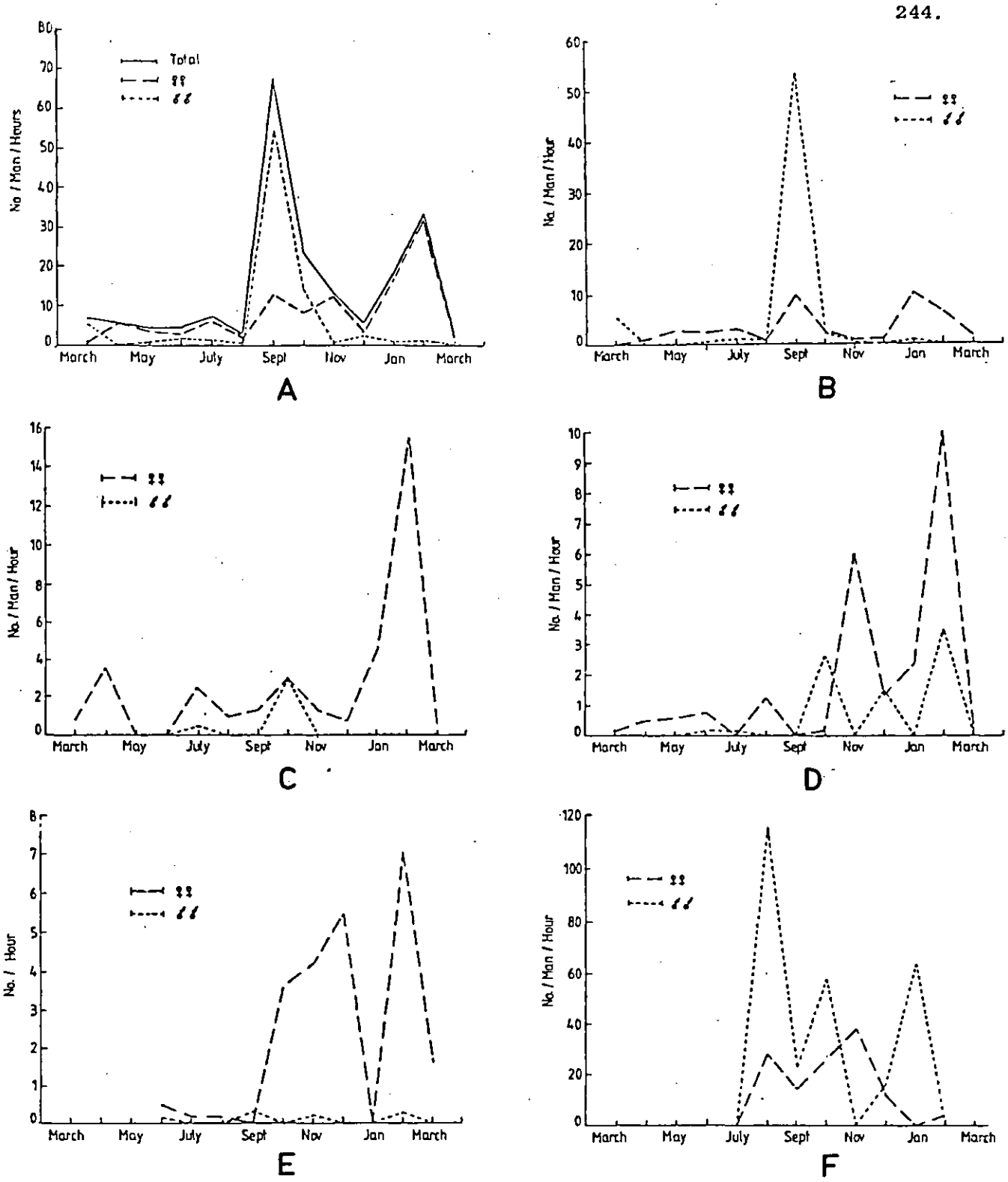


Fig. 88. L. gomezi: seasonal fluctuations of the total population (A)*. Monthly collections at night : biting man in peridomestic habitat (B), biting man in sylvatic habitat (C), with Shannon trap (D), with CDC trap (E), biting pig (F). (March 1979 - March 1980).

*Only methods which were used in each month of the year have been combined in this figure (see text).

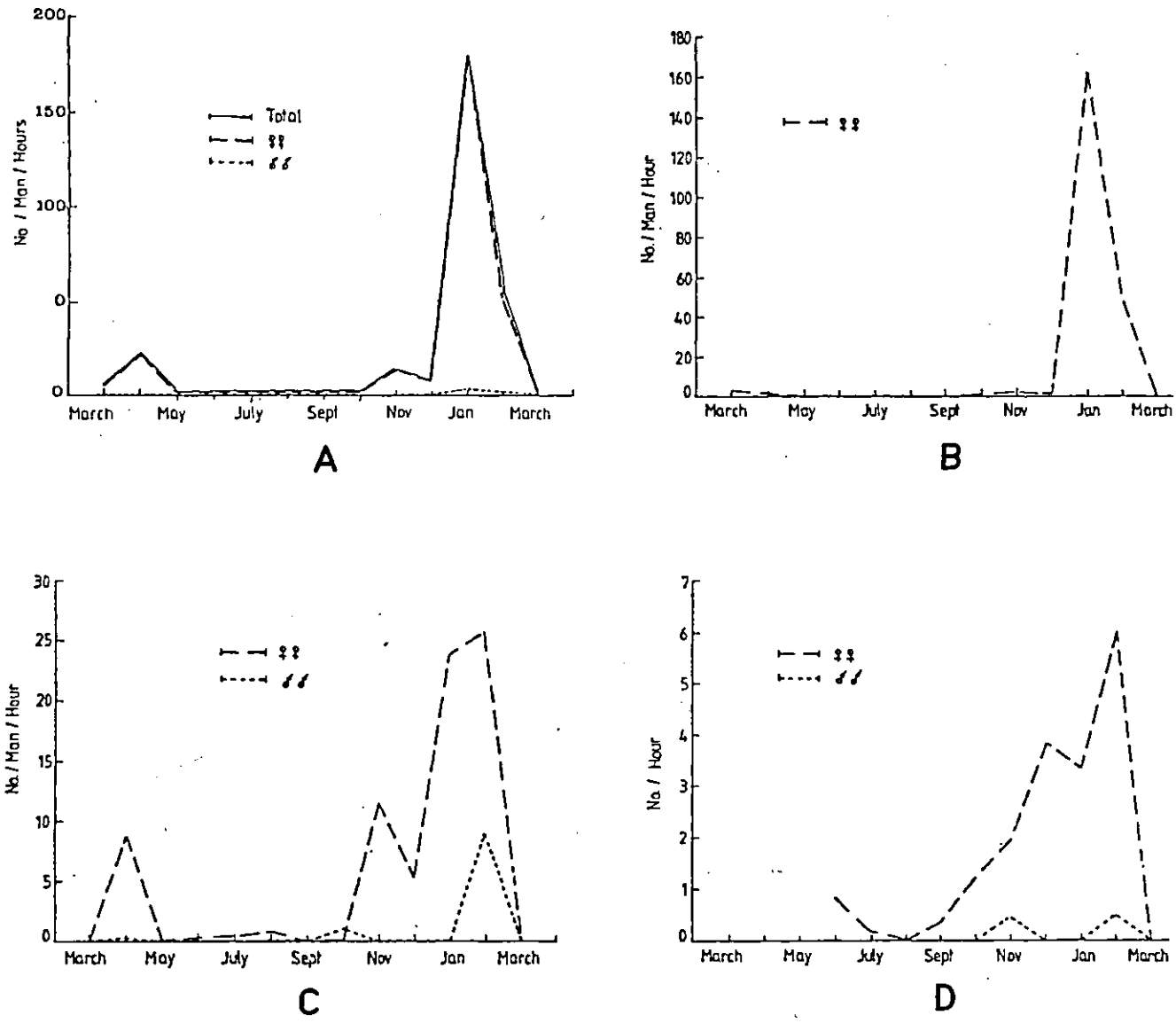


Fig. 89. L. ovallesi: Seasonal fluctuations of the total population (A)*. Monthly collections at night : biting man in sylvatic habitat (B); with Shannon trap (C), with CDC trap (D), (March 1979 - March 1980).

*Only methods which were used in each month of the year have been combined in this figure (see text).

source of the collected population. Samples from the peridomestic habitat during the day and at night were similar in size and in sex composition with a predominance of males (Fig. 90B,C). In contrast, in the field the number of sandflies caught at night was relatively small and the proportion of females relatively high compared with day catches (Fig. 90 D,E).

The majority of L. atroclavata (Fig. 91) and L. cayennensis (Fig 92) were caught in the morning. Though in low densities, they were present throughout the year and in all habitats. The highest density of L. atroclavata was reached in March 1979 and of L. cayennensis in December. L. atroclavata males were more common than females throughout the year. L. cayennensis males also predominated towards the end of the year, but early in the year females were more common.

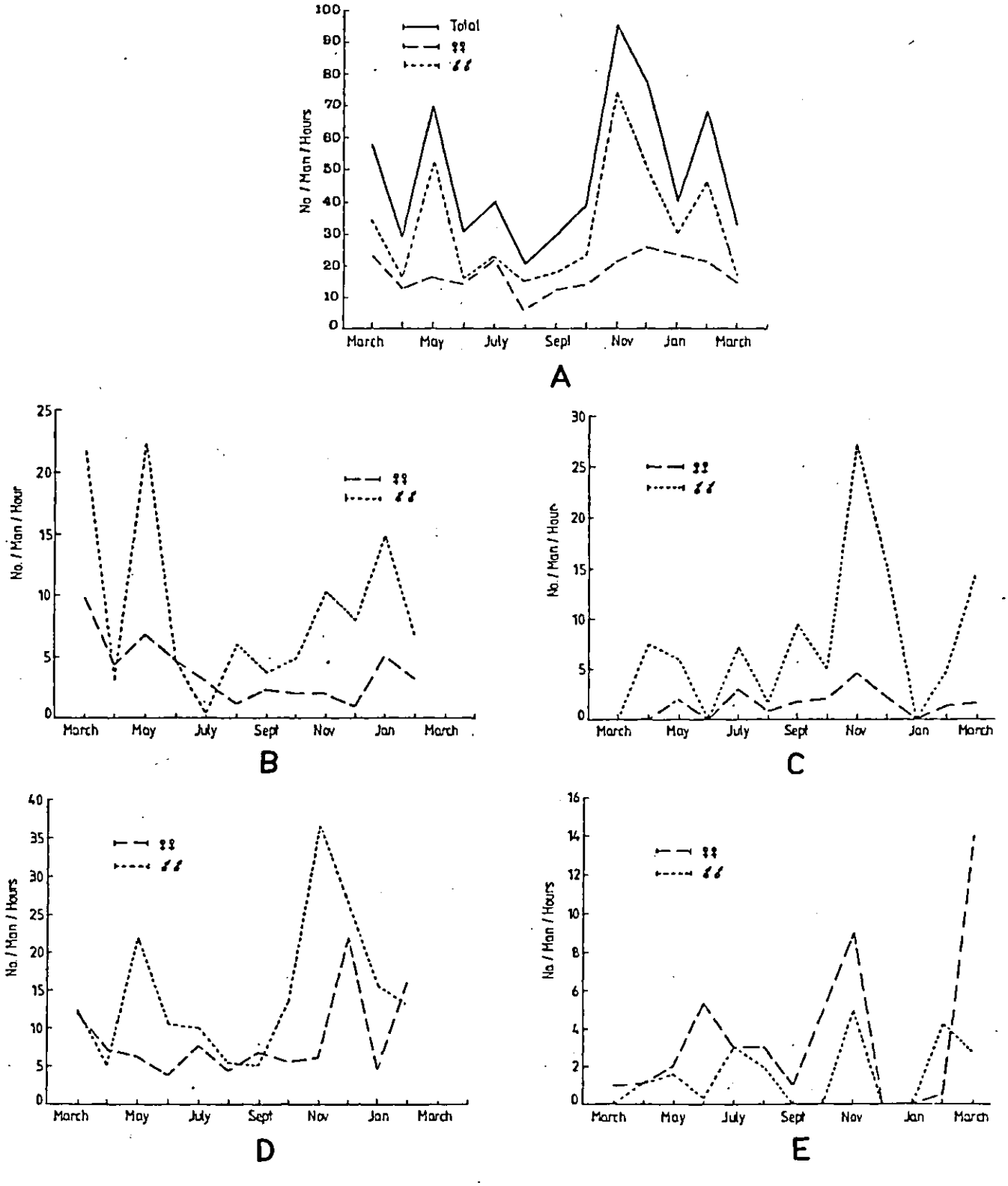


Fig. 90. L. trinidadensis: Seasonal fluctuations of the total population (A)*. Monthly collections in peridomestic habitat : during the day (B), at night (C). Monthly collections in sylvatic habitat : during the day (D), at night (E). (San Esteban, Venezuela, March 1979 - 1980).

*Only methods which were used in each month of the year have been combined in this figure (see text)

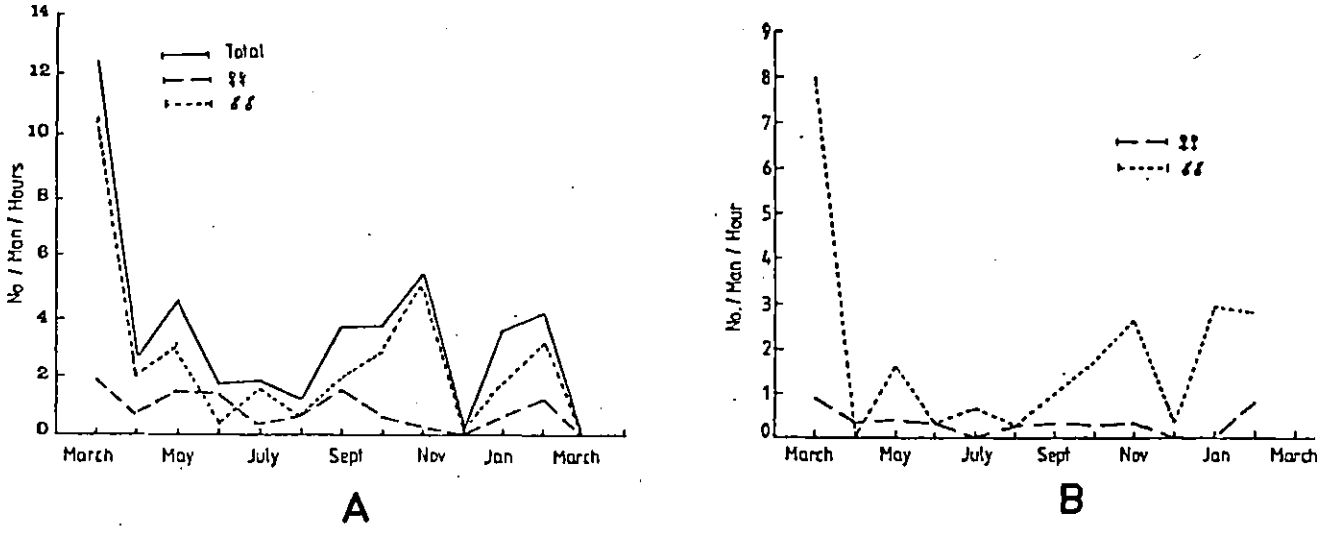


Fig. 91. L. atroclavata : Seasonal fluctuations of the total population (A)*. Monthly collections in trees at day-time (B).

*Only methods which were used in each month of the year have been combined in this figure (see text).

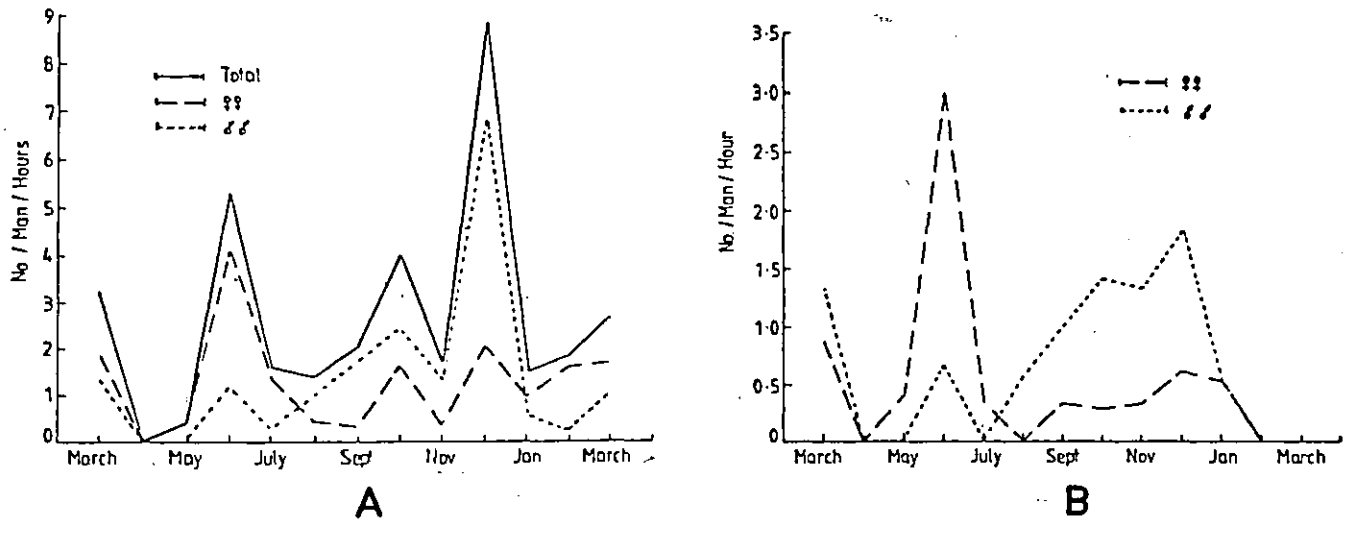


Fig. 92. L. cayennensis: Seasonal fluctuations of the total population (A)*. Monthly collections in trees at day-time (B).

*Only methods which were used in each month of the year have been combined in this figure (see text).

4.4.4 Search for leishmanial infection

No leishmanial infection was found. 2 of 2582 L. panamensis (0.08%), 51 of 1513 L. trinidadensis (3.37%), 4 of 121 L. cayennensis (3.3%) and 2 of 54 L. atroclavata (3.7%) showed either epimastigote or trypomastigote forms.

None of the hamsters inoculated with triturated specimens developed leishmaniasis.

4.5 Discussion

4.5.1. Sandfly population structure: species composition, occurrence and abundance.

The species composition of a sandfly population can be considered as the result of geographical and metereological conditions and the resultant soil-type and vegetation. Similarities in species composition can therefore be expected in places which show similar conditions, provided the same collecting methods are used.

During March 1979 - March 1980, 13 species of sandflies formed the phlebotomine fauna at San Esteban, an endemic focus of cutaneous leishmaniasis in Venezuela.

The majority of these species were also caught by Pifano et al., (1962c)in localities at similar latitude and altitude, with ecological features comparable to those of San Esteban, a partially cleared area of lowland forest. These were around Araguita, Miranda State, at 100 m above sea level. Both Araguita and San Esteban are in the foothills of the "Serrania de la Costa". Pifano et al. collected 17 species which included all species found at San Esteban, except L. olmeca bicolor. Albornoz et al. (1968) found 5 species: L. panamensis, L. trinidadensis, L. atroclavata, L. cayennensis and L. punctigeniculata in Choroni, another focus of cutaneous leishmaniasis at about 50 m above sea level.

Often specific sandfly assemblages can be found in areas with similar conditions, even if they are far apart in terms of distance. L. trinidadensis, L. shannoni, L. ovallesi, L. panamensis and L. cayennensis were among 22 species collected during 6 years in Belize (Williams, 1970). The same 5 species were found at Limbo Station, Panama (Chaniotis, et al. 1971a) with L. gomezi and L. punctigeniculata. The L. gomezi -

L. panamensis association was later recognized as a real entity since it was demonstrated that these species have a strong tendency to occur together (Rutledge et al., 1975d). Similarly, six of the species present in San Esteban were collected at Sasardi, Panama (Christensen et al., 1972) i.e. L. panamensis, L. gomezi, L. ovallesi, L. trinidadensis, L. cayennensis and L. dubitans (cited as L. marajoensis). All except L. dubitans had high relative occurrence and were classified as "common species" at San Esteban (see Section 4.4).

Sandflies have been collected in Providencia, Colombia (Porter & De Foliart, 1981), an area which is very different from San Esteban, lying along the border between "tropical wet forest" and "tropical wet premontane forest" at an altitude of 400 to 800 m. Not surprisingly, only 4 species which occur at San Esteban were found (L. panamensis, L. gomezi, L. shannoni and L. olmeca bicolor). Only two of the species found at San Esteban (L. gomezi and L. shannoni) were also seen in the Serra dos Carajas in Brazil, an area of high altitude (Ward et al., 1973). A wide geographical distribution and perhaps also the relative abundance of a species may be considered as indicators of its success. Sometimes the two characters show some correlation in that wherever the fly occurs it is very abundant and nowhere is it found in low numbers. L. trinidadensis is an example of such a fly. It was the most abundant species found resting on trees at San Esteban and in Belize (Williams, 1970), Panama (Chaniotis et al., 1971a; Christensen et al., 1972) and Colombia (Young, 1979). Young (loc.cit.) pointed out its "interesting distribution" indicating that, in Colombia, L. trinidadensis is very common and abundant in Northern Choco, but appears to be absent in forest along the Pacific coast in Valle Department.

In Trujillo, Venezuela, Mogollón et al., (1977) observed both

the occurrence and abundance of L. townsendi were positively correlated with the altitude.

L. panamensis, the dominant man-biting species in San Esteban (81.3%), also showed a marked predominance at Teresita, at an altitude of 35 m in Colombia (86%) but formed only 12% of the man-biting species at Limbo Station (50 - 180 m) in Panama (Chaniotis et al., 1971a) and only 3% at Providencia in Colombia (400 - 800 m) (Porter & De Foliart, 1981).

It seems therefore that the occurrence and abundance of L. panamensis are together inversely correlated with altitude, the higher the collection site the rarer the fly.

L. gomezi is a very widely-distributed species. Its range includes El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Equador, French Guyana, Peru and Brazil (Martins et al., 1978). This species occurred in San Esteban in all habitats but at relatively low abundance. In Trujillo State L. gomezi was found in only 7% of the localities below 300 m and about 25% of localities at 1000 m above sea level (Mogollón et al., loc.cit.). The latter authors concluded that this species seems to be more successful between 200 m and 1,800 m. This positive correlation between occurrence, abundance and altitude might explain the low density of L. gomezi at San Esteban, a place of low elevation.

4.5.2 Specific features in relation to the habitat

Significant statistical differences were found between the size of the sandfly population in the 3 habitats explored. (Tables A3.9 - A3.16).

Seven species of sandflies were found at San Esteban in houses: 3 (L. panamensis, L. gomezi and L. ovallesi) were classified as anthropophilic because they were regularly collected biting man. The other three (L. trinidadensis, L. atroclavata and L. cayennensis) were non-anthropophilic species which were mainly found resting on walls and in shelters. Occasionally both sexes were caught alighting on man. L. olmeca bicolor was collected biting man in the house as well as in the sylvatic site. However, this species is only considered weakly anthropophilic.

Flies may enter houses either in search of food or as a result of positive phototaxis. It is unlikely that the 3 non-anthropophilic species were attracted by light, since they were not frequently caught by the two light traps. The poor attraction of L. trinidadensis to light has been noticed also by Chaniotis et al. (1971a); and Christensen et al. (1972).

L. atroclavata never alighted on man and only 1 male of L. cayennensis and 1 female of L. trinidadensis were caught on man during a year of collections. It is concluded that these three species are not anthropophilic. This was in agreement with the observations in the peridomestic and in field habitats. Williams (1970) reported similarly low numbers of L. trinidadensis on man in Belize and Tesh et al. (1971) found that 76% of blood meals of L. trinidadensis reacted with reptile-amphibian antisera, confirming the general belief that L. trinidadensis is a saurophilic species (Ortiz, 1968a;Forattini, 1973; Young, 1979). It is likely that L. trinidadensis, L. atroclavata and L. cayennensis

enter houses in search of geckos and other small lizards which abound in the cracked walls of the rural houses. However Scorza et al. (1979b) recently pointed out that L. trinidadensis can have a wider range of hosts. In Trujillo State they caught 62% of their specimens biting mule, 11%, man; 11% horse; 11% pig; and 4% cow.

The finding of L. panamensis in houses is presumably the result of both positive phototaxis and anthropophily. This is indicated by high numbers of flies caught both in light-traps and biting man in peridomestic and field habitats.

L. gomezi and L. ovallesi probably only enter human dwellings in search of a bloodmeal, since they show little if any phototaxis. The numbers of these species attracted to light-traps in sylvatic places was low in comparison with the populations attracted to man.

In contrast, though of low overall abundance, many more specimens of L. olmeca bicolor were caught in light-traps than biting man and they probably enter the houses as a result of phototaxis alone. They show no marked anthropophily and possibly bite man only when in accidental contact. The behaviour of L. olmeca bicolor at Sasardi (Panama) was similar to that observed at San Esteban. "It was taken regularly in small to moderate numbers, mostly in Malaise and light-traps but also 19 times biting man" (Fairchild & Theodor, 1971). Later it was indicated as the dominant species collected in forest from litter and in rodent-baited castor oil traps (Christensen et al., 1972). In Colombia, Providencia area, L. olmeca bicolor was rarely found biting man (Porter & De Foliart, 1981).

Tree searches in the peridomestic area showed that L. atroclavata, L. cayennensis and L. shannoni tend to concentrate in this habitat.

L. shannoni, which was very abundant in trees in Belize (Williams, 1970), in Panama (Chaniotis et al., 1971a; Christensen, 1972) and in Colombia (Porter & De Foliart, 1981), was very poorly represented in San Esteban.

The paucity of anthropophilic species (L. panamensis, L. ovallesi and L. gomezi) found in trees in the present study has also been observed in Belize (Williams, 1970), Panama (Chaniotis et al., 1971a) and in Brazil (Ward et al., 1973). The resting sites of these species still remain an enigma. Though Rutledge et al. (1976) suggested that L. panamensis rested in tree trunks, in tree hollows, green plants and forest litter, the number caught in such sites seems too small to indicate a general trend. Their presence in the peridomestic area was mainly detected by human and animal baits.

L. gomezi was caught in larger numbers in the peridomestic habitat than in houses and in the field site, indicating a definite preference for sites cleared of vegetation. This result agrees with the observation of Fairchild & Hertig (1948a) who defined this species as "probably semidomestic" having found it biting man "both outdoors and in houses, even in quiet urban areas" in Panama. Johnson et al. (1963) and Thatcher & Hertig (1966) found this species to be very common in an area of secondary growth.

Another relevant feature of this species in the peridomestic habitat is the predominance of males in all the catches, especially on the hosts. 17 females were caught probing or feeding and 32 males were caught "dancing" on man by Miles & Foster (1977) in Panama. At San Esteban the males were caught landing on the host and their presence in such large numbers must be another example of mating aggregation as indicated by Miles & Foster (loc.cit.). This phenomenon was also observed in

L. shannoni attracted to pig, man and cow. A similar observation for this species was also reported by Miles & Foster (loc.cit.), and Williams (1970). This last author also recorded L. shannoni as the third most abundant man-biting species after L. cruciata and L. panamensis. Because of the low relative occurrence of female L. shannoni biting man, this species was not considered to be truly anthropophilic at San Esteban Only a few man-biting L. shannoni were caught in Panama (Chaniotis et al., 1971a; b), in Brazil (Ward et al., 1973), at Curiche, Colombia (Young, 1979) and at Providencia, Columbia (Porter & De Foliart, 1981).

The predominant species in the sylvatic area were the non-anthropophilic L. trinidadensis and the anthropophilic L. panamensis and L. ovallesi.

L. panamensis, a successful species ranging from southern Mexico, through Belize, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Peru and Brazil (Martins et al., 1978) has been demonstrated as highly anthropophilic in mature, disturbed and secondary forest (Porter & De Foliart, 1981).

At San Esteban it attacked man in similar numbers in the forest and in the peridomestic habitats. The same pattern was seen at Providencia, Colombia, where it predominated in cleared sites, (Porter & De Foliart, 1981). Though Porter & De Foliart (loc.cit.) considered that the fly's behaviour varies with the area, Rutledge et al., (1976) found this species to be virtually absent from catches made within a clearing.

In contrast, L. ovallesi is without doubt a sylvatic species which probably strays into houses and the peridomestic habitat in search of a blood-meal. The distribution of this species is limited to Central America and Northern South America (Martins et al., 1978). Its behaviour seems to be variable. In Panama, Chaniotis et al. (1971a, b) never caught

L. ovallesi biting man, although densities in trees were appreciable. In contrast, it was caught on man in Colombia and British Honduras, (Osorno Mesa et al., 1972; Williams, 1970). In Venezuela it was also considered to be decidely anthropophilic with a wide distribution between altitudes of 100 m to 1800 m in Trujillo State (Mogollón et al., 1977). In a cloud forest of North-central Venezuela it was, however, very rare (Scorza, 1972).

4.5.3. Specific features in relation to capture methods.

A comparison was made between all the collection methods during the months in which domestic animals were used as bait. This showed that certain methods were more efficient at catching flies and that these varied with the species of fly. The differences were statistically significant (see Tables A3.9-A3.16). The efficiency of each method was dependent on the behaviour and activity of the sandflies. The results from the comparison have already been partly discussed in relation to the 3 collection habitats (Section 4.5.2).

As previously observed (Chaniotis et al., 1971a), light traps proved to be a useful and reliable collecting method for surveying the phlebotomine fauna, since they attracted most of the species present.

Results from animal-baits were of particular interest. The attraction of L. panamensis to man, pig, and cow seems to be of similar intensity. Though there were differences, e.g. more flies biting cow than pig and more biting pig than man, these may be the result of differences in surface area of hosts, rather than differences in "attractiveness".

The behaviour of L. ovallesi was different from L. gomezi. Both attacked pig more than man, but L. ovallesi did not bite cow at all, whereas L. gomezi attacked the cow about as often as the man.

These "anthropophilic" sandflies are probably often diverted from entering houses and attacking man by the attraction of domestic animals in the neighbourhood. Zooprophylaxis might therefore be one method of reducing man-fly contact in endemic foci of leishmaniases in which sandflies show a similar behaviour.

4.5.4. Specific features in relation to the time of capture

The comparison of different methods in relation to the hour of capture showed highly significant differences for all the common species at San Esteban except L. shannoni (Tables A3.9-A3.16).

Most of the non-anthropophilic species found in their resting sites were collected during morning hours, and there was very little diurnal man-biting activity of anthropophilic sandflies. Nevertheless, a few L. panamensis were seen to be active in daylight in all the habitats and L. ovallesi was occasionally found attacking man in the field site during the morning. Porter & De Foliart (1981) observed a low level of diurnal activity of anthropophilic species at Providencia, Colombia. They thought this was because there was no avid man-biting species with a distinct preference for the forest floor where they are easily disturbed by man. However, at San Esteban such an avid feeder does exist in the form of L. panamensis, the breeding sites of which are thought to be decaying leaves and forest litter (Hanson, 1961; Johnson & Hertig, 1961; Rutledge & Ellenwood, 1975a, b, c). Human bait is possibly less likely to be attacked when motionless on a chair than when walking. Movement may stimulate flies resting on nearby ground vegetation to attack and feed, as Williams (1970) observed with L. olmeca olmeca. However, Ward et al. (1978) found no evidence of increasing man-biting activity of L. flaviscutellata when vegetation was disturbed at dawn.

Another explanation is simply that an upright man may be more attractive than a seated one. However, Shaw et al. (1972) found that seated bait caught more L. flaviscutellata than upright bait.

It is likely that diurnal attacks are atypical and accidental for the majority of sandflies and the typical behaviour is to feed between dusk and dawn. However, Fraiha et al. (1971) reported a high biting activity of L. wellcomei throughout the day and night.

4.5.5. Seasonal fluctuations

Long-term studies on the population dynamics of a vector species are of inestimable value in planning a control strategy and to determine the most effective time to mount an attack (Killick-Kendrick, 1978).

Seasonal fluctuations in population densities which result from the changing metereological patterns in different geographical regions have been widely studied.

In the Neotropics, mean daily temperatures may differ by only two or three degrees throughout the year and therefore have little effect on sandfly populations. In this part of the world, rainfall and the consequent levels of humidity appear to be the most important determinants of the seasonal densities of many species of sandflies.

The pattern of seasonal variation of a fly population has been seen to differ with the area studied. Such variations may be the result of local metereological fluctuations and differences in the biotic and abiotic characteristics of each region. Occasionally very severe or very mild weather may also cause unusual troughs or peaks in a sandfly population. In spite of all these variables, a general pattern predominates in the Neotropics i.e. an increase in population density during the wet season followed by a decrease in the dry season (Barretto, 1943; Fairchild & Hertig, 1951; Pifano et al., 1960; Johnson et al., 1963; Scorza et al., 1968; Chaniotis et al., 1971a). This pattern exists for all but a few species which show increases in the dry season. The behaviour of each species varies so little over successive years or areas that the terms "wet-season species" or "dry-season species" have often been used to describe a fly (Chaniotis, 1971a; Rutledge et al., 1976).

The correlation between fluctuations in total sandfly population at San Esteban with the mptereological conditions have not been analysed in the present study. This is because of the bias created by fluctuations in L. panamensis which formed most of the collections. All species have therefore been treated separately and results will be discussed in the same manner.

Anthropophilic species

L. panamensis. This species, considered primarily as a wet season species in Mexico, Panama and Colombia (Biagi & Biagi, 1953; Johnson et al., 1963; Chaniotis et al., 1971a; Rutledge et al., 1976; Christensen & Herrer, 1980a;Porter & De Foliart, 1981) showed the same tendency at San Esteban (Venezuela).

The population density was lowest from February to May. This coincided with the dry weather, when the normal habitats used for sandfly breeding would be unsuitable for that purpose. Sandfly eggs, larvae and pupae are known to be highly susceptible to extreme conditions of dryness. The wetting of the forest floor improves breeding conditions substantially and an increase in the population size is evident after the first rain. However, once the rainfall exceeded 100 mm the adult population size decreased. A similar pattern has been observed and discussed in other places and with other species. In Panama, Chaniotis (1971a) indicated that "rain was beneficial to the sandflies when it occurred in moderate amounts and was evenly distributed, but became detrimental when it inundated the ground". In Brazil Ward et al., (1973) observed that a monthly rainfall of more than 200 mm was harmful to L. flaviscutellata. Excessive dampness and immersion in water kills the immature stages of sandflies (Chaniotis et al., 1971a). When Rutledge et al. (1975a) studied the production of phlebotomine sandflies

on the open forest floor in Panama, they obtained the smallest collections of L. panamensis during the rainy season. Frequent erosion of breeding sites is known to occur (Rutledge & Mosser, 1972; Rutledge & Ellenwood, 1975b).

The man-biting activity of L. panamensis in the sylvatic habitat was low in the dry season, when four flies were caught in light-traps, and high when fly densities were high, in the wet weason. This behaviour is unlike that observed in Canal Zone, Panama (Chaniotis et al., 1971b), where the man-biting activity of L. panamensis was highest in the dry season, when light trap collections were relatively small. Chaniotis et al. (1971b) concluded that this species "is a good potential vector mainly because of its strong seasonal peak in the dry season when man enters the forest for recreation and camping". However, Porter & De Foliart (1981) considered the observation by Chaniotis et al. (1971b) to be an "apparent exception" to the usually observed behaviour of L. panamensis.

The man-biting activity of L. panamensis reached a maximum in the domestic and peridomestic habitats two months earlier than in the sylvatic habitat. By the time biting activity had peaked in the sylvatic site, late in the wet season, the activity in the two other places was falling.

This result suggests that there are two separate populations, experiencing different biotic and abiotic conditions. There is probably a stable peridomestic population and all L. panamensis approaching houses at dusk do not therefore come from sylvatic resting places (Pifano et al., 1960). Doubt is therefore cast on the value of "clearing, development of the land and thinning of trees" which Rutledge et al., (1976) suggested as a method of control for this species. Low relative humidity appears

strongly to influence the fly population. Humidity differs between the sylvatic and peridomestic habitats, the peridomestic habitat becoming quite humid (60% minimum) some months earlier than the other. Breeding sites may be more easily damaged by heavy rains in the peridomestic area. Cultivation and building lead to more numerous rain pools around houses than in sylvatic habitats, where the natural processes of absorption, percolation and seepage are not disturbed.

L. gomezi. This species was considered as a "dry-season species" at Gamboa, Canal Zone, Panama (Chaniotis, 1971a), at Sasardi, Panama (Christensen et al., 1972) and on the Pacific coast of Panama (Christensen & Herrer, 1980a) but behaved as a typical wet-season species elsewhere in the Panama Canal Zone (Rutledge et al., 1976). The population dynamics of adult populations of L. gomezi at San Esteban seemed to reflect two different situations in the peridomestic and in the field habitats, as seen in L. panamensis.

For 6 months from the late dry season to the early wet season (March to August), the population was very low. A population explosion, mostly of male flies, occurred in the peridomestic habitat in the second half of the wet season. The population then began to fall with further rainfall, but a second peak was later observed at the beginning of the dry season. In contrast, in the sylvatic habitat, the maximum population density was reached in February, so in that area L. gomezi behaved as a typical dry-season species.

Local factors, such as T and RH already discussed for L. panamensis, might in part explain this variability, which may not be "an aberration" as defined by Rutledge et al. (1976). These same authors pointed out that breeding populations of L. gomezi are more strongly affected by local and seasonal factors of the environment than those of L. panamensis.

L. ovallesi seasonal fluctuations at San Esteban show that this species is a true "dry-season species", as was observed also in Panama (Christensen & Herrer, 1980a). The sudden population explosion of this species, after a long period of virtual absence, and its equally sudden disappearance a short time later, constitutes a peculiar feature. The temporal distribution of adult populations of L. ovallesi and L. panamensis in this area seem to be remarkable: L. ovallesi arrives just when the L. panamensis population is declining and replaces it very successfully as a man-biter.

The virtual absence of L. ovallesi during the long period of heavy rains is probably a result of either asthenobiosis or diapause of an immature stage which allows this species to survive in the adverse conditions.

The phenomenon of asthenobiosis has been suggested by Scorza et al. (1968) to explain sharp rises in the size of sandfly populations immediately after the first rains. This involves the arrested development of an immature stage which is "reactivated" as soon as moisture levels rise. The dormancy induced and terminated immediately by changes in temperature or moisture has also been used to explain quiescence of sandfly larvae in laboratory conditions (e.g. Killick-Kendrick, 1978).

A true diapause involves a prolonged and predetermined period of arrested development of an insect which is not immediately reversible and which is the result of intrinsic rather than extrinsic factors (Ready & Croset, 1980).

Diapause, which was well studied in larvae of some Palaearctic sandflies (Ready & Croset, 1980), has also been observed in eggs of the neotropical sandfly L. lainsoni (Fraiha & Ward, 1974) by Ward & Killick-

Kendrick (1974), and in fourth-instar larvae of L. whitmani (Antunes & Coutinho, 1930) by Barretto (1941a). However, no observations of diapause or quiescence have been reported for L. ovallesi. Further studies in laboratory conditions will help to explain the ecological patterns of this anthropophilic species.

Non-anthropophilic species

L. trinidadensis. The 3 peaks in the size of the adult population of L. trinidadensis at San Esteban suggest a direct correlation with the rainfall. Some of the concepts expressed above seem also to be applicable to this species. For instance in this species the first peak appeared at the first rains and may have been derived from asthenobiotic larvae. Excessive rainfall in the late wet period also seems to affect population density. No clear differences were observed between the peridomestic and the sylvatic habitats.

This species has been considered as a wet-season species at Gamboa, Canal Zone (Chaniotis, 1971a) and a dry-season species at Sasardi (Christensen et al., 1972).

L. cayennensis and L. atroclavata.

Unfortunately, only low numbers of L. cayennensis and L. atroclavata were caught. Erratic fluctuations in population size were observed and the sexes peaked at different times. However, because of the small sample size, no clear relationships between the population density and metereological factors can be defined.

L. olmeca bicolor and L. shannoni.

These two species were also caught in very low numbers. It seemed that the size of the population of L. olmeca bicolor was highest during the late wet season and that of L. shannoni highest in the early wet

season. Christensen & Herrer, (1980a) observed a similar pattern for L. olmeca bicolor in Panama.

4.5.6. Sandflies and leishmaniases.

One prerequisite for a sandfly to be a vector of leishmaniases is for it to be susceptible to the parasites.

With the possible exception of urban anthroponotic cutaneous leishmaniasis of the Old World, dermal leishmaniases are zoonoses in which man is an accidental host. A degree of anthropophily and a concommitant attraction towards the reservoirs are an essential condition for a vector.

Pifano (1941) found L. panamensis in Venezuela naturally infected with promastigotes similar to culture forms of Le. braziliensis sensu lato. Its role as a vector of cutaneous leishmaniasis in this country was later suggested by Pifano et al. (1959), based on the evidence that one of the collectors developed leishmanial lesions after exposure to L. panamensis bites.

Natural infection of this species by promastigotes has also been found in British Honduras, but the fact that none of the flagellates induced leishmanial lesions in hamsters, and failed to grow in culture medium or in volunteers, gave strong suspicions that the parasite was not a human Leishmania parasite (Williams, 1970). However, Christensen et al. (1969) gave some parasitological evidence of its role as a vector in Panama when they obtained an experimental infection in hamsters inoculated with a sub-culture of L. braziliensis sensu lato isolated from L. panamensis.

The high anthropophily of this species has been discussed above. Blood meal analyses of 6 L. panamensis (Tesh et al., 1971, 1972) indicated rodents as possible sources of blood for L. panamensis. However, the frequency of this fly in rodent- and marsupial-baited traps was

only 0.6% of the entire catch at Sasardi (Christensen et al., 1972).

In recent studies on host attraction profiles in Panama, (Christensen & Herrer, 1980a), L. panamensis showed a major preference for rodents, though the flies represented only 14.5% of the flies caught on all bait animals. The flies did not show any detectable preference for the two-toed sloth, Choloepus hoffmanni, the principal reservoir host of Le. braziliensis in Panama.

Promastigote forms of Le. braziliensis sensu lato have been seen in natural infections of L. gomezi (Johnson et al., 1963; Schneider & Hertig, 1966) and a Panamanian strain of Le. mexicana was seen to develop in the same fly (Christensen & Herrer, 1980b). This species constitutes one of the suspected vectors of dermal leishmaniasis in Panama (Christensen & Herrer, 1973).

The anthropophily of L. gomezi has been assessed in the present study. However, this species does not seem to be substantially attracted by wild animals. The L. gomezi tested by Tesh et al (1972) for bloodmeal identification, of which "77.8%" reacted with rodent antisera were too few in number (9 specimens) to be considered as representative of the feeding pattern of this species. L. gomezi represented only 0.5% of the sandflies caught with wild animal-baited traps (Christensen & Herrer, 1980a). L. gomezi, a peridomestic fly, probably feeds mostly on man and domestic animals.

L. ovallesi was found infected with both promastigotes and epimastigotes by Williams (1970) in British Honduras. No confirmation was obtained to suggest that any parasites of this fly were leishmaniae of man.

Rodents are likely sources of blood for L. ovallesi (Tesh et al., 1971) but, again, the sample was too small to give a measure of the zoophily of this species.

The population density of a potential vector is an epidemiological factor directly correlated with the risk of parasite transmission.

Transmission of leishmaniasis to man at San Esteban takes place during the dry season. A weak correlation was found between abundance of L. panamensis and the incidence of leishmaniasis.

No natural infection of promastigotes was observed in 2582 specimens dissected. In consequence, in spite of previous opinions and the close contact between L. panamensis and man in all the habitats, doubt is cast on the role of this species as a vector in this area. The same argument can be made for L. gomezi which, furthermore, is not so abundant as L. panamensis.

The appearance of L. ovallesi was accompanied by a prompt outbreak of leishmaniasis. Only 397 L. ovallesi were dissected, which is too small a sample to exclude the possibility of L. ovallesi being infected in this area.

The possibility that flies which do not appear to be highly anthropophilic may in fact be major vectors of leishmaniasis should be considered in foci of the disease. Williams (1970) strongly suggested that although L. olmeca olmeca in British Honduras is not greatly attracted to man it is, nevertheless, responsible for leishmaniasis in rodents and for transmitting the disease to man. Williams explained this apparent contradiction with the hypothesis that the flies normally feeding on rodents and resting on the ground flora were disturbed by men walking

through the vegetation and were stimulated to feed on them.

Rutledge et al.(1976), studying the correlation between sandfly fauna and leishmaniasis in different places in Panama, observed sharply contrasting patterns of distribution between the anthropophilic species and the disease.

They concluded that transmission of leishmaniases to humans in Panama may occur in places or seasons where zoophilic sandfly species are predominant.

L. olmeca bicolor, a common rodent-biting species (Christensen & Herrer, 1980a; Tesh et al., 1972), has also been found to be susceptible to infection by Leishmania parasites. It is regarded as a vector of enzootic leishmaniasis in a zone where human leishmaniasis has not yet been observed even though L. panamensis, which is usually considered a major vector of human leishmaniasis, is abundant and strongly anthropophilic (Christensen et al., 1972).

Reexamination of L. ovallesi and L. olmeca bicolor from San Esteban is necessary if their possible role as vectors of leishmaniasis is to be verified. Rather than repeating the year-round observations, collections could be limited to December, January and February when the two fly populations reach their greatest size. Collections would be made from the ground flora, where L. olmeca bicolor is known to rest. Large numbers of flies would have to be dissected before their capability as vectors of leishmaniasis, both, rodent and human, could be evaluated.

Each microfocus of leishmaniasis has its own peculiar characteristics which are closely related to the rate of transmission and other factors which form the links of the epidemiological chain. The aims of most

epidemiological surveys are to determine this transmission rate, the vectors involved and the appropriate strategy for control. This information only becomes available after the ecology of parasites, sandflies, reservoir and other susceptible hosts has been studied.

5. GENERAL DISCUSSION.

The main aim of this study has been to review and augment the present knowledge of the entomology of the leishmaniases of Venezuela.

The inventory and the analysis of the sandfly fauna and geographical distribution have revealed important gaps yet to be filled. Sandflies of much of the country have never been surveyed and the picture of the present known distribution is clearly incomplete.

This panoramic view gives rise to precise ideas for future work based on comprehensive new collections from all parts of the country.

For 10 species only one sex is known. Intensive searches in the locality of origin and laboratory rearing of these sandflies should help to solve these taxonomic problems.

Confirmation should be sought of some of the early reports and of reports of the finding of single specimens. In pursuing these narrow but precise objectives new questions will certainly arise. If intensive and wide ranging collections are made, it is probable that new species, some of which may be vectors of leishmaniasis, will be found.

As far as possible taxonomic, biological and ecological studies should be made simultaneously. Such work will undoubtedly illuminate the epidemiologies of the various forms of the leishmaniases in Venezuela and, hopefully, might give rise to new ideas of control.

Twenty years ago, L. panamensis and L. longipalpis were first incriminated as vectors of two forms of leishmaniasis in Venezuela. New work to investigate the possible vectorial roles of other species is urgently needed. There has been speculation about the ability of several

species to transmit leishmaniasis, but the criteria of a proven vector (Killick-Kendrick and Ward, 1981) require firm evidence, which is, at the moment, lacking.

In Venezuela all clinical forms of cutaneous leishmaniasis except "uta" have been seen, but almost nothing is known of the epidemiological features of any form. For example, the only vector of Le. braziliensis sensu lato at present recognized in Venezuela is L. panamensis; clearly it cannot be accepted that this species is the only one responsible for the transmission of all forms of the cutaneous disease.

Working groups on parasitological (Scorza et al., 1979a), biochemical (Hernandez et al., 1980; Infante et al., 1980), immunological (Perez et al., 1979a, b) and clinical - epidemiological (Valera et al., 1978) aspects of the disease are developing in the country. An effort is necessary to synchronize programmes and objectives, the final goal of which is the control of the disease.

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APPENDICES

Appendix 1

Geographical coordinates for sandfly collection sites.

	N	W
APURE		
Arichuna	7°42'	67°08'
Caño Regreso	7°05'	71°15'
Chiricoca	7°17'	71°32'
El Carrao	7°40'	68°08'
Guaramaco	6°16'	67°25'
Guaratico	7°30'	69°13'
Guayabital	7°14'	70°48'
La Blanquita	7°28'	71°27'
Los Mangones	7°54'	69°19'
Los Morichales	7°50'	69°10'
Los Rancheros	7°58'	69°30'
Mata da Silva	7°17'	68°19'
Montaña La Puerta	7°13'	70°42'
Payara	7°37'	68°38'
Puerto Paez	6°13'	67°28'
San Carlos del Meta	6°19'	67°49'
Santa Clara	7°01'	69°53'
Santa Elena	6°56'	69°25'
Santa Lucia	7°57'	68°09'
Sarare Abajo	7°14'	71°12'
ARAGUA		
Agua Fria	10°15'	67°10'
Aponte	10°25'	67°45'
Barbacoas	9°28'	66°59'
Boca de Cagua	10°14'	67°04'
Caicara	9°24'	66°35'
Cañadote	9°55'	67°01'
Casupito	10°09'	67°26'
Cata	10°29'	67°44'
Cataure	9°57'	66°51'
Corocito	9°51'	67°08'
Curiepe	10°14'	67°10'
Chaguaramos	10°01'	67°32'
Choroní	10°29'	67°37'
Diana	9°56'	66°52'
El Ancón	10°03'	67°28'
El Bejucal	10°01'	66°58'
El Cedral	10°22'	67°12'
El Cortijo	10°05'	67°25'
El Chino	10°02'	67°18'
El Guanabano	9°58'	67°09'
El Guayabito	9°11'	64°50'
El Guayabo	9°28'	66°56'

	N	W
El Loro Arriba	10°02'	66°57'
El Negrito	9°59'	66°58'
El Nicual	10°04'	67°16'
El Ocumo	10°05'	67°21'
El Onoto	10°00'	66°49'
El Paraparo	10°26'	67°35'
El Saman	9°49'	66°53'
El Tigre	9°40'	66°34'
El Toro	9°27'	66°54'
El Valle	10°25'	67°16'
Golfo Triste	10°00'	66°56'
Guambra	10°03'	67°02'
Guanasnal	9°59'	67°08'
Guiripa	10°03'	67°01'
Ingenio Bolivar	10°13'	67°25'
La Barquera	10°04'	67°02'
La Ceiba	10°02'	67°01'
La Concepción	10°11'	67°31'
La Curia	10°13'	67°22'
La Garilana	10°16'	67°21'
La Lagunita	10°04'	67°27'
La Luisa	10°28'	67°23'
La Majada	10°04'	67°23'
La Pavona	10°03'	67°34'
La Trilla	10°24'	67°25'
Las Adjuntas	10°02'	65°57'
Las Tunas	9°55'	67°03'
Las Vegas	10°01'	67°00'
Los Algarrobos	10°02'	67°12'
Los Bagres	10°05'	67°25'
Los Conucos	10°29'	67°24'
Los Dos Montes	9°43'	66°48'
Los Mamires	9°57'	67°07'
Los Vargas	10°04'	67°05'
Macuaya	10°02'	67°27'
Malpica	9°59'	67°30'
Maracay	10°15'	67°36'
Monte Oscuro	10°01'	66°54'
Ocumare de le Costa	10°28'	67°46'
Palambra	9°56'	67°16'
Pao Zarate	9°57'	67°11'
Paso del Medio	9°55'	67°16'
Paso de los Indios	10°05'	67°08'
Paya	10°15'	67°28'
Pedregal	9°25'	66°52'
Periquito	10°21'	67°38'
Pié del Cerro	10°19'	67°19'
Piedras Pintadas	10°25'	67°52'
Polanco	10°05'	67°03'
Polvorín	10°18'	67°28'
Puerto Colombia	10°30'	67°36'
Quebrada Apa	10°13'	67°21'
Quebrada Calanche	10°25'	67°18'
Quebrada Honda	9°56'	67°14'

	N	W
Quebrada Seca	10°18'	67°01'
Rancho Grande	10°22'	67°41'
Rio Arriba	10°06'	67°18'
Rio Cura	9°51'	66°51'
Rio Tuy	10°19'	67°12'
Sabana Grande	10°03'	67°41'
San Francisco	10°08'	67°15'
San José	9°53'	67°06'
San Mateo	10°13'	67°25'
San Pedro	10°03'	66°56'
Santa Rosa	10°08'	67°14'
Santo Domingo	10°16'	67°12'
Tiara	10°08'	67°09'
Tierra Negra	10°04'	67°01'
Tucupido	10°17'	67°30'
Tucutunemo	10°00'	67°27'
Vallecito	9°54'	67°03'
Zuata	10°10'	67°08'
BOLIVAR		
Gran Sabana	5°35'	61°45'
BARINAS		
Barinas	8°40'	70°12'
CARABOBO		
Borburata	10°2 '	67°58'
Belén	9°59'	67°41'
Carabobo	10°00'	68°09'
El Cambur	10°10'	68°10'
El Naipe	10°02'	68°12'
El Tigre	10°09'	68°25'
Glorieta	10°08'	67°55'
Isla de Otama	10°10'	67°41'
La Arenosa	10°06'	68°06'
Las Animas	10°25'	68°07'
Las Colonias	10°02'	67°46'
Los Chorritos	10°06'	67°14'
Los Guayos	10°02'	67°57'
Mariara	10°17'	67°43'
Pueblo Nuero	10°05'	67°47'
San Esteban	10°26'	68°01'
Santa Inés	9°56'	67°51'
Yuma	10°06'	67°42'

	N	W
COJEDES		
Boca de Cerro	9°39'	68°15'
Charcote	9°26'	68°29'
El Pilón de Valle Hondo	9°44'	68°34'
El Tinaco	9°42'	68°24'
Hacienda Vieja	9°55'	68°50'
La Ceiba	9°35'	68°44'
La Morita	9°46'	68°46'
La Váquira	9°30'	68°10'
Las Galeras	9°28'	68°19'
Las Rosas	9°42'	68°44'
Mapurite	9°40'	68°39'
Potrero Largo	9°46'	68°30'
San Carlos	9°40'	68°36'
Tierra Caliente	9°50'	68°33'
Zambrano	9°37'	68°09'
DISTRITO FEDERAL		
Caracas	10°30'	66°55'
Caraballeda	10°37'	66°50'
Macuto	10°37'	66°53'
FALCON		
Churuguara	10°41'	69°44'
Mene de Mauroa	10°43'	71°01'
GUARICO		
Altagracia de Orituco	9°52'	66°23'
Parapara	9°44'	67°18'
Ribas	9°15'	65°45'
San Francisco de Tiznado	9°36'	67°35'
San José de Tiznado	9°23'	67°33'
Santa Maria de Ipire	8°49'	65°19'
Zaraza	9°21'	65°19'
LARA		
Barquisimeto	10°04'	69°19'
Duaca	10°18'	69°10'
MERIDA		
El Salado	8°26'	71°02'
Merida	8°36'	71°08'

	N	W
MIRANDA		
Agua Blanca	9°54'	66°38'
Guotopo	10°00'	66°25'
Los Chorros	10°30'	66°50'
Ocumare del Tuy	10°00'	66°46'
Valles del Tuy	10°10'	66°50'
MONAGAS		
Caripito	10°08'	63°06'
NUEVA ESPARTA		
Isla Margarita:		
- Guayacán	11°09'	63°56'
- Las Piedras	10°50'	64°10'
PORTUGUESA		
Biscucuy	9°22'	69°59'
Guanare	9°03'	69°45'
SUCRE		
Barbacoas	10°25'	64°14'
Caugrejal	10°30'	63°13'
Cumanacoa	10°15'	63°55'
Mariguitar	10°27'	63°54'
Petare	10°18'	63°15'
TACHIRA		
Cano Amarillo	8°20'	72°10'
La Colorada	7°33'	72°20'
San Cristobal	7°46'	72°14'
TRUJILLO	9°25'	70°30'
Agua Clara	9°42'	70°18'
Altamira	9°42'	70°19'
Caja Seca	9°09'	71°05'
El Mamón	9°16'	70°42'
El Rincón	9°31'	70°21'
El Volcán	9°18'	70°22'
La Placita	9°31'	70°19'
Las Cocuizas	9°29'	70°43'
Rio Monosnoy (near Monay)	9°33'	70°28'
Sabana Grande	9°24'	70°48'

	N	W
TERRITORIO FEDERAL AMAZONAS		
Atabapo	4°03'	67°42'
El Gavilán	5°30'	67°12'
Nyiayobateri	2°30'	64°00'
YARACUY		
San Felipe	10°20'	68°44'
Valle de Aroa	10°26'	68°54'
Valles del Rio Yaracuy	10°35'	68°14'
ZULIA		
Altagracia	10°05'	71°12'
Bachaquero	9°56'	71°08'
Mene Grande	9°49'	70°56'
Rio Negro	10°05'	72°48'
Zipayare	10°13'	70°53'

APPENDIX 2

This appendix shows the raw data of the catches of sandflies at San Esteban (Venezuela)expressed as Number of sandflies caught/man/hour, March 1979 - March 1980). Asterisks indicate collections which were missed. No Tables are presented for L. dubitans, L. evansi, L. rangeliana and Brumptomyia sp. because only 1 specimen of each was caught (see Table 19).

Table A2.1

DURATION OF EACH TRAPPING SESSION (HOURS)
****

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	2.000	3.000	3.000	3.000	3.000	2.500	3.000	3.500	3.000	3.250	3.750	2.250	*
HOUSE	WALL	NIGHT	1.500	2.500	3.000	2.500	2.830	3.000	2.250	2.500	2.500	2.500	2.000	2.750	2.000
HOUSE	HUMAN	DAY	3.000	3.250	3.000	3.000	3.000	2.500	3.000	3.500	2.500	2.500	2.330	2.500	2.000
HOUSE	HUMAN	NIGHT	2.000	1.750	1.000	2.160	2.000	2.580	1.000	2.750	2.160	1.000	2.000	2.500	2.500
PERI-DOMESTIC	TREE	DAY	2.250	3.000	2.500	3.000	3.000	3.500	3.330	3.500	3.000	3.250	3.750	2.500	*
PERI-DOMESTIC	TREE	NIGHT	1.750	2.000	3.000	2.250	3.660	3.500	2.250	2.500	1.330	2.250	2.330	1.500	1.250
PERI-DOMESTIC	HUMAN	DAY	1.500	3.250	3.000	3.000	3.000	2.500	3.000	3.500	2.500	2.500	2.500	2.750	2.000
PERI-DOMESTIC	HUMAN	NIGHT	1.830	2.000	2.500	2.500	2.000	2.580	.410	2.750	2.500	1.000	2.250	2.500	2.000
SYLVATIC	TREE	DAY	2.000	3.000	3.000	2.750	3.000	2.830	3.000	2.000	1.500	2.000	3.750	.500	*
SYLVATIC	TREE	NIGHT	3.000	2.500	2.500	3.000	3.000	1.000	1.000	1.000	1.000	1.250	2.500	3.500	2.000
SYLVATIC	HUMAN	DAY	3.000	1.500	1.000	3.000	3.000	3.580	2.500	1.500	2.000	2.000	2.500	2.750	1.500
SYLVATIC	HUMAN	NIGHT	2.500	2.000	2.500	2.250	2.000	2.000	1.500	2.000	1.500	1.500	2.000	2.000	1.500
SYLVATIC	CDC	NIGHT	*	*	*	3.000	6.000	3.000	3.000	2.500	2.500	1.830	1.500	2.000	2.500
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	.250	.250	.500	.500	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	.250	.250	.500	.500	.500	.250	.250	.250	*
SYLVATIC	SHANNON	NIGHT	7.500	8.750	7.500	6.000	6.250	2.250	.960	1.500	2.500	3.000	1.500	1.500	1.250
SYLVATIC	SHANNON	NIGHT	*	6.250	2.000	6.000	6.250	2.970	*	3.125	1.680	.438	1.500	2.810	*

CATCH OF L ATROCLAVATA
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Table A2.2

FEMALES
=======

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	.330	0	0	.330	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	.880	.330	.400	.330	0	.280	.330	.280	.330	0	0	.800	*
PERI-DOMESTIC	TREE	NIGHT	0	0	.330	0	0	0	.880	.400	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	1.000	0	0	.720	0	.350	.330	0	0	0	.530	0	*
SYLVATIC	TREE	NIGHT	0	0	.160	0	0	0	0	0	0	0	0	.200	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC.	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	.170	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	*	0	.500	.330	0	0	*	0	0	0	0	0	*

MALES
=====

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	.330	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	8.000	0	1.600	.330	.660	.280	1.000	1.710	2.660	.300	2.930	2.800	*
PERI-DOMESTIC	TREE	NIGHT	0	2.000	1.000	0	.540	0	0	1.200	2.250	.400	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	.330	0	0	0	0	0	0	.360	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	2.500	0	0	0	0	.350	1.000	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

CATCH OF L CAYENNENSIS
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Table A2.3

FEMALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	1.000	0	0	.330	1.000	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	.880	0	.400	3.000	.330	0	.330	.280	.330	.610	.530	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	.400	0	.800	0	.400	.400	1.330	.800
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	.800	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	1.000	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	.500	0	0	0	0	.660
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	.250	.200
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

MALES
=====

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	1.000
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	1.000	0	0	0
PERI-DOMESTIC	TREE	DAY	1.330	0	0	.660	0	.570	1.000	1.420	1.330	1.840	.530	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	.270	.400	0	0	0	4.000	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	.360	0	0	.660	.500	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	.500	0	0	0	.280	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	.250	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	.160	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

CATCH OF L. GOMEZI
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Table A2.4

FEMALES
=======

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	.80	.35	0	.44	.80	0	.40	0	0	.80
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	.57	0	0	0	0	2.00	0	1.38	1.00	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	.33	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	1.00	2.80	2.40	3.00	.77	9.75	2.54	.80	1.00	10.20	6.40	1.50
SYLVATIC	TREE	DAY	0	0	.66	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	.40	0	0	0	0	2.00	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	.80	3.50	0	0	2.50	1.00	1.33	3.00	1.33	.76	4.50	15.50	.66
SYLVATIC	CDC	NIGHT	*	*	*	.50	.17	.17	0	3.60	4.20	5.46	0	7.00	1.60
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	12.00	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	28.00	14.00	26.00	38.00	12.00	0	4.00	*
SYLVATIC	SHANNON	NIGHT	.13	.80	.13	.16	0	.44	0	0	9.60	.33	2.66	10.00	0
SYLVATIC	SHANNON	NIGHT	*	.16	1.00	1.33	0	2.02	*	.32	2.37	2.28	2.00	9.95	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	1.20	0	0	.88	6.00	0	0	0	.40	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	2.00	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	.57	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	5.46	0	0	.40	1.00	.77	53.60	2.18	.40	0	.88	0	0
SYLVATIC	TREE	DAY	0	0	.33	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	.40	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	.50	0	0	3.00	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	.17	0	0	.33	0	.22	0	0	.30	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	104.00	42.00	8.00	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	116.00	22.00	58.00	0	16.00	64.00	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	.16	.16	0	0	4.00	0	.66	0	1.33	0
SYLVATIC	SHANNON	NIGHT	*	0	0	.16	.16	0	*	1.28	0	2.28	0	5.68	*

CATCH OF L OLMECA BICOLOR
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Table A2.5

FEMALES
=======

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	.460	0	.500	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	.400	.420	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	.330	0	0	0	0	0	1.000	1.330	.660	0
SYLVATIC	SHANNON	NIGHT	*	.640	0	.160	0	.330	*	.320	0	0	.660	0	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	.400	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	.330	0	.440	0	0	0	1.000	.660	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	4.570	.660	0	*

CATCH OF L OVALLESI
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Table A2.6

FEMALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	1.00	0	0	3.00	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	1.20	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	3.50	0	.40	.50	.38	0	0	0	0	.88	3.60	0
SYLVATIC	TREE	DAY	0	0	0	0	0	0	.66	0	2.00	0	0	0	*
SYLVATIC	TREE	NIGHT	0	1.09	.80	0	0	0	0	1.00	1.00	2.40	2.40	0	0
SYLVATIC	HUMAN	DAY	.33	0	0	.33	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	3.20	1.50	0	0	0	0	0	1.00	2.00	1.33	161.50	49.50	0
SYLVATIC	CDC	NIGHT	*	*	*	.83	.17	0	.33	1.20	1.93	3.82	3.33	6.00	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	2.00	2.00	0	4.00	0	0	*
SYLVATIC	SHANNON	NIGHT	.13	15.65	.13	.33	0	0	0	0	9.20	1.33	10.66	.66	0
SYLVATIC	SHANNON	NIGHT	*	1.76	0	.33	.80	1.68	*	0	13.60	9.14	36.66	50.48	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	.40	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	3.20	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	.54	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	.33	0	.33	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	.33	0	0	0	0	0	0	.40	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	.44	0	0	.50	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	6.00	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	.57	0	0	0	0	0	2.00	0	0	0	3.33	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	14.57	*

CATCH OF L PANAMENSIS
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Table A2.7

FEMALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	.33	.33	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	4.00	10.80	4.94	2.80	2.22	2.40	1.00	10.80	4.30	3.20	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	1.71	0	2.77	3.50	0	18.00	0	10.18	6.00	12.00	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	6.66	1.00	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	1.33	0	0	1.33	0	0	0	2.80	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	.33	0	0	0	0	0	0	.40	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	19.20	3.60	16.50	11.24	104.87	10.90	21.20	14.00	18.60	4.80	1.00
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	1.63	8.00	0	8.33	0	9.00	9.00	0	24.80	6.40	0	0
SYLVATIC	HUMAN	DAY	0	.40	0	.33	0	0	0	0	1.00	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	12.00	13.20	36.44	2.50	4.50	12.66	2.50	88.00	21.30	62.00	8.50	4.00
SYLVATIC	CDC	NIGHT	*	*	*	65.67	31.33	2.33	17.00	98.80	123.00	56.28	98.66	22.50	1.20
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	284.00	160.00	60.00	70.00	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	52.00	108.00	68.00	34.00	78.00	28.00	4.00	92.00	*
SYLVATIC	SHANNON	NIGHT	0	.91	13.06	47.33	2.40	14.66	37.50	4.66	237.60	80.00	174.66	20.66	0
SYLVATIC	SHANNON	NIGHT	*	2.08	28.50	153.50	13.44	43.77	*	73.92	154.07	285.70	266.60	10.66	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	.33	0	.35	0	.44	.40	0	2.00	0	.40	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	DAY	0	.66	0	.66	0	0	3.03	0	0	0	0	0	0
PERI-DOMESTIC	TREE	NIGHT	0	0	0	.44	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	.72	0	0	0	0	*
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	2.00	0	.80	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	.76	1.00	0	0	0	1.00	0
SYLVATIC	CDC	NIGHT	*	*	*	2.67	2.67	.33	1.66	0	0	0	14.60	1.50	*
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	4.00	0	16.00	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	2.00	0	4.00	0	8.00	*
SYLVATIC	SHANNON	NIGHT	0	.23	0	3.17	.16	3.11	2.08	0	0	4.00	0	14.66	0
SYLVATIC	SHANNON	NIGHT	*	.48	2.00	10.16	.80	0	*	0	0	20.57	0	.35	*

CATCH OF L PUNCTIGERICHLATA
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Table A2.8

FEMALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	.440	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	0	.300	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	.360	0	0	0	0	0	0	0	4.000	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	.570	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

CATCH OF L SHANNONI
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Table A2.9

FEMALES
=======

			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	0	0	.330	.610	0	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	.400	0	0	1.500	1.330	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	.440	0	0	0	0	0	0	0	.500	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	2.000	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	2.000	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	0	0	0	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	0	0	0	0	0	0	.330	.280	0	.300	.260	0	*
PERI-DOMESTIC	TREE	NIGHT	0	0	0	0	0	0	.440	.800	.330	0	0	0	0
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	2.430	0	0	0	0	0	0
SYLVATIC	TREE	DAY	0	0	.330	0	0	0	0	0	0	0	0	0	*
SYLVATIC	TREE	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	4.000	0	14.000	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	4.000	0	4.000	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	.320	0	0	0	0	*

CATCH OF L TRINIDADENSIS
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Table A2.10

FEMALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	.500	.330	0	.330	.330	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	.400	.350	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	1.000	0	0	0
PERI-DOMESTIC	TREE	DAY	9.770	4.300	6.800	4.660	3.000	1.140	2.330	2.000	2.000	.920	5.060	3.200	*
PERI-DOMESTIC	TREE	NIGHT	0	0	2.000	0	3.000	.800	1.760	2.000	4.500	2.220	0	1.330	1.600
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	TREE	DAY	12.000	7.330	6.330	3.630	7.600	4.240	6.660	5.500	6.000	22.000	4.530	16.000	*
SYLVATIC	TREE	NIGHT	1.000	1.090	2.000	5.330	3.000	3.000	1.000	5.000	9.000	0	0	.500	14.000
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	.170	0	0	0	.400	.220	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	0	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	.330	0	0	*	0	0	0	0	.710	*

MALES
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			MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
HOUSE	WALL	DAY	0	0	.330	0	2.000	0	0	0	0	0	0	0	*
HOUSE	WALL	NIGHT	0	0	0	.400	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
HOUSE	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	TREE	DAY	21.770	3.000	22.400	4.660	.330	6.000	3.660	4.850	10.330	7.930	14.930	6.800	*
PERI-DOMESTIC	TREE	NIGHT	0	7.500	6.000	0	7.100	1.600	9.330	4.800	27.060	15.550	0	4.610	14.400
PERI-DOMESTIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	.360	0
PERI-DOMESTIC	HUMAN	NIGHT	0	0	.400	0	0	0	0	0	0	1.000	0	0	0
SYLVATIC	TREE	DAY	12.500	5.000	22.000	10.540	10.000	5.300	5.000	13.500	36.660	26.500	15.700	30.000	*
SYLVATIC	TREE	NIGHT	0	1.090	1.600	.330	3.000	2.000	0	0	5.000	0	0	4.280	2.660
SYLVATIC	HUMAN	DAY	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	HUMAN	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	CDC	NIGHT	*	*	*	0	0	0	0	0	0	0	0	0	0
PERI-DOMESTIC	COW	NIGHT	*	*	*	*	0	0	0	0	*	*	*	*	*
PERI-DOMESTIC	PIG	NIGHT	*	*	*	*	0	4.000	0	0	0	0	0	0	*
SYLVATIC	SHANNON	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0	0
SYLVATIC	SHANNON	NIGHT	*	0	0	0	0	0	*	0	0	0	0	0	*

Appendix 3: The Statistical Analysis of Sandfly Catches

by M.D.F. Piñero and A.R. Ludlow

Table A2.1 shows the duration of trapping sessions with each method throughout the 13 months. Asterisks indicate sessions which were omitted, for example, a pig was available for only eight months of the year, while a cow was available for only four. In addition, there were no daytime collections from the two light-traps or from the cow and pig. During the 13th month the daytime collections from humans in the house were also omitted. In view of these omissions, the statistical analysis for each species was divided into three sections.

SECTION A. was restricted to the first six types of collection, i.e. from walls, trees and from humans in each of the three habitats. All collections from the 13th month were excluded. This allowed a comparison between the three habitats, and it identified those sandflies which bit or congregated near humans. It could also have provided a measure of seasonal variation, but that would have excluded insects which responded only to light-traps. The seasonal variation was therefore studied separately.

SECTION B was restricted to those methods which were used without omission over the first 12 months, and catches from the 13th month were excluded. In other words, the analysis was based on the six methods included in Section A, together with the collections from the Shannon light-trap. Both day and night catches were included. This gave the maximum complete information available on seasonal variation. It was used both to chart the month-by-month variation and also to measure the correlations between monthly catches and meteorological data, and leishmaniasis.

SECTION C was restricted to the four months in which a cow was available.

and to night-time catches. This allowed all of the methods to be compared without omitted collections.

The most frequently caught sandfly was L. panamensis and the analysis of catches of this species is described fully before giving comparable results for other species.

L. panamensis - females

SECTION A

Only female sandflies bite, so the catches of males and females have been analysed separately. In addition to sex, the catches of L. panamensis can be classified according to four other factors:

HOUR (day or night)

HABITAT (house, peridomestic area or sylvatic area)

METHOD (methods used by both day and night, i.e. collections from human bait and searching trees or walls).

MONTH

By restricting the analysis in section A to the first 12 months and the first six collection types, it is possible to form a four-way table, classified according to these four factors, in which there are no empty cells. Such a four-way table lends itself to an analysis of variance, but the data are counts of sandflies and these would be expected to have a Poisson rather than a normal distribution. In the past, such counts have been transformed into logs and an analysis of variance performed on the transformed counts. However, the significance levels of such an analysis would not have been affected by the number of sandflies caught; the significance levels would have depended only on the number of replicates of each collection. This overlooks, completely, the fact that each sandfly caught is, in a sense, a separate

experiment and each one increases the confidence placed on any differences which emerge. Thus, if a man were bitten by two sandflies in the house, and by one outside, the difference would be regarded as trivial, but if he were bitten by 2000 in the house and 1000 outside one would say with confidence that the probability of being bitten inside was higher than outside.

To test that difference, using the actual counts of sandflies caught, one might sensibly use a χ^2 test. That can also be done with two, or even three factors. In recent years, however, there has been a major development in analysing such data and Nelder and Wedderburn (1972) have developed methods which amount, more or less, to performing multi-way χ^2 tests with any number of factors. Two powerful computer programs have since been developed using these methods: GLIM (generalised Linear Modelling) and GENSTAT, both produced by the statistics department at Rothampstead Experimental Station. The present analysis has been done using GENSTAT, whose manual is by some 16 authors (Alvey et al. 1977) including Nelder and Wedderburn.

The basic approach of Linear Modelling with GENSTAT is that one calculates expected frequencies of sandflies, and from this calculates the value of χ^2. This is called the DEVIANCE and is analogous to the variance of normal statistics. By the same analogy the χ^2 corresponds to the sum of squares of normal statistics. In a standard analysis of variance one fits more and more factors, and measures the reduction in the sum of squares. This gives a measure of the amount of variation which each factor explains. In an analysis of DEVIANCE one fits factors in turn, and measures the reduction in χ^2, or the amount of DEVIANCE which each factor explains.

Fitting new factors involves recalculating the expected frequencies

with more and more information. Thus, suppose that the following catches of sandflies had been found

	HOUSE	PERIDOMESTIC	SYLVATIC	Total
DAY	20	5	10	35
NIGHT	407	182	404	993
Total	427	187	414	1028

First one would fit the NULL model which used no information except the total number of sandflies caught and the number of cells. The expected frequencies on the null model would all be 1028/6 = 171.33 and the value of χ^2 calculated by the usual formula would be 1088. To fit the factor HOUR one would calculate the expected frequencies in the top row as 35/3 = 11.67 and in the bottom row they would be 993/3 = 331. This gives a considerably smaller χ^2, 110.62, and the difference is due to the factor HOUR. In otherwords the factor HOUR reduces the χ^2 by 1088 - 110.62 = 977.38. Looking that value up in the tables shows that, with one degree of freedom a χ^2 of only 6.64 would be significant at the 1 percent level.

To add the factor HABITAT, one would recalculate the expected frequencies in the way one normally does a χ^2 test, in otherwords the expected frequency in the first cell would be (427x35)/1028 = 14.54. With GENSTAT or GLIM one can add or subtract factors very easily although the values given by GENSTAT are slightly different from those above, because it calculates χ^2 in a slightly different way. Thus, the χ^2 for the null model was 1088 (above) and 1241 with GENSTAT. This was reduced to 110.62 (above) and to 121.6 with GENSTAT when HOUR was fitted. When both HOUR and HABITAT are fitted the GENSTAT value is reduced further to 3.6 while the standard χ^2 would be 3.37.

To test the significance of the factor HOUR one subtracts the DEVIANCE without HOUR fitted from the DEVIANCE with HOUR fitted and this value is looked up in the χ^2 tables with the appropriate number of degrees of freedom. But one can perform this subtraction in two ways, as the following table shows.

ANALYSIS OF DEVIANCE

	DEVIANCE	DF
Null model	1241	5
Null + Hour	121.6	4
Null + Habitat	1123	3
Null + Habitat + Hour	3.602	2

Effect of HOUR alone: 1241.0 - 121.6 =1119.4 (5-4=1 df)

Effect of HOUR (with HABITAT already in): 1123.0 - 3.6 = 1119.4 (3-2=1 df)

Effect of HABITAT alone: 1241.0 - 1123.0 = 118.0 (5-3=2 df)

Effect of HABITAT with HOUR already in): 121.6 - 3.6 = 118.0 (4-2=1 df)

In the example above, the two methods give exactly the same answer, but that will not always be the case. If the two factors are correlated, then fitting each alone will give an inflated estimate of their effects. One should therefore use the second method each time. In otherwords one fits both, or all of the factors and then drops one at a time and measures the change in χ^2.

The degrees of freedom are simply a measure of the information used in calculating the expected values when fitting each factor. Thus, in fitting the NULL model above we used the grand total of counts and so used one degree of freedom. Six cells minus one degree of freedom gives five. When fitting HOUR we used the two marginal totals 35 and

993, but we might have used the grand total and one marginal total, since the other can be calculated from those two. Thus, we used one extra degree of freedom, making two in all, one of which is associated with the factor HOUR. Similarly, we would use the grand total and two marginal totals when calculating the expected values for fitting HABITAT, so 2 degrees of freedom are associated with the factor HABITAT. When fitting both HABITAT and HOUR one uses 1 df for the NULL model, 1 for HOUR and 2 for HABITAT making 4 in all and leaving 2 df associated with the residual deviance.

The essence of Linear Modelling, as developed by Nelder and Wedderburn (1972), is, then, to fit factors in turn. In doing so, one spends degrees of freedom and reduces the χ^2 by a given amount. The factor has a significant effect if the change in χ^2 is cost-effective, in otherwords, if you get a big enough change in DEVIANCE for a given number of degrees of freedom. That is essentially what happens in the analysis of variance. One spends degrees of freedom to reduce the sum of squares, and if the change in sum of squares is cost-effective, then the factor is significant. With balanced experimental designs and a normal distribution, one can estimate the variance due to each factor all at once. With unbalanced designs and with Poisson or binomial distributions it is a bit more complicated, but the underlying logic is the same, and using this approach is more sensitive than a straight forward analysis of variance on the logs of the counts.

The example above is hypothetical because the real data include a complication. The time spent trapping sandflies was not the same for each collection (see Table A2.1). When sandflies were biting in large numbers the human volunteers were not prepared to stay for the standard three hours. When calculating the values of χ^2 however, one

must not divide the number of sandflies caught by the time spent collecting, because that would lose the information about the actual numbers. Instead, one should use the time spent trapping to calculate the expected frequencies, and then compare the expected with the actual frequencies. Suppose, for example, that the trapping sessions had been twice as long in the house than in the other locations. When fitting HOUR one would have calculated the expected frequencies of the top row as (2 x 35)/4, 35/4 and 35/4 or 17.5, 8.75 and 8.75, instead of 35/3 in each case. The bottom row would have been calculated in the same way as (2 x 993/4), 993/4 and 993/4.

Both GENSTAT and GLIM allow one to do this by using an OFFSET variate. Because GENSTAT and GLIM use logs to calculate the expected frequencies one can multiply by time, in effect, by adding the log of time. This is done by calculating a variate LTIMES = LOG(TIMES) and then declaring LTIMES as the OFFSET variate (see Alvey et al. 1972).

After these lengthy preliminaries, we may now discuss the detailed analysis of L. panamensis catches. As mentioned above, there are four factors, HOUR, HABITAT, METHOD AND MONTH. These were first fitted, together, then each was dropped in turn to measure the χ^2 associated with each factor (see the program HOUR in Appendix 4). In addition to the main effects of each factor, the 2-way interaction between every pair of factors was also fitted so that the statistical significance of each interaction could be assessed (the biological significance is discussed below). The interaction between two factors is what one tests with the usual two-way χ^2 test. Thus, in the example above, the χ^2 after fitting both HABITAT and HOUR was 3.6, and the expected frequency for this was calculated in the standard way. Normally, one would look up the value 3.6 in the tables (with 2 df) and if it were

significant (in this hypothetical example it is not), one would conclude that there was a significant effect of HOUR on HABITAT. In other words, at some times of day sandflies were to be found in one place, at others in another. Or one might conclude that sandflies could be caught more easily by day in one place and by night in another. That is the sort of association which the two-way interaction terms measure, but with more than two factors, as we have here, it is necessary to use a sophisticated program like GENSTAT to calculate them. The analysis of deviance for L. panamensis is shown in Table A3.1.

The biological significance of this analysis can best be understood by examining a series of two-way tables (A3.2-A3.7). These show the rate of catching in sandflies per hour, and were calculated by dividing the sandflies caught by the time spent in each collection. The rate was then averaged over the two factors which do not appear in the table. Table A3.2 shows the mean catching rate classified according to HOUR and HABITAT. The mean number caught per hour was 0.15 during the day collections and 9.19 at night. This difference is highly significant as shown by the χ^2 of 1653 in the first row of Table A3.1. The effect of HABITAT was less striking, ranging from 6.93 in the sylvatic area to 2.11 per hour in the house. The χ^2 of 222.9 is still highly significant, but the effect is clearly much smaller than that of HOUR. The mean deviance shown in Table A3.1 is a measure of the change in χ^2 per degree of freedom, and so allows different factors to be compared fairly directly. On this measure the effect of HOUR is at least ten times more important than that of HABITAT. There is a significant interaction between HOUR and HABITAT (row 5 of Table A3.1). This probably arises because the peak catching rate during the day time is in the peridomestic area, which is not where the highest rates are observed at night. Thus,

the day and night-time catches do not tell the same story about the distribution of sandflies and the result is best interpreted as a warning to treat them separately (as has been done in the main text).

Table A3.3 shows the mean catch rate classified according to HOUR and METHOD. More sandflies were found biting humans than by searching walls and trees, and this large difference is statistically significant (row 3 of Table A3.1. The interaction between the two factors is significant (row 6 Table A3.1) which means that the means of the two factors are not telling the whole story. Examining the table, it is at once clear that, during the day, sandflies were found more often on trees and walls than biting humans. Thus, L. panamensis definitely bites humans and does so principally at night.

Table A3.4 shows the catches classified according to HOUR and MONTH. The analysis of monthly catches is the main aim of SECTION B, but here we are able to see whether the DAY/NIGHT differences are at all affected by time of year. The interaction in this case is significant (row 7, Table A3.1), so we must conclude that seasonal factors affect the day/night behaviour of L. panamensis. Inspection of the table shows that June was the best month for daytime catches, while September was best at night. With the large numbers of this species which were caught, it is possible to detect very slight differences which are significant statistically but not biologically. This interaction may be no more than a difference in daytime wind conditions in June. In any event, it shows that catching efficiency was probably not consistent throughout the year. However, the mean deviance is only 7.0, which is the lowest, so this is the least important interaction.

Table A3.5 shows the relationship between trapping METHOD and

HABITAT. The interaction between these two factors is significant (row 8 of Table A3.1) and inspection of the table shows that the two methods give different pictures of the distribution of sandflies within habitats. On the basis of the human-bait catches one should expect a reasonable number of sandflies to be found by searching trees in the peridomestic area, but this was not the case. It is not, perhaps, surprising that searching walls and trees should give inconsistent results, since the surfaces available in the three habitats are so different, so for this species at least the numbers biting man may be the best indicator of distribution within habitats. Even human-bait catches, however, will undoubtedly be affected by local wind conditions and distance from the host to the sandflies' resting place. It will also be affected by movement or quiescence of the host.

Table A3.6 shows the interaction between HABITAT and MONTH, which was again highly significant (row 9 of Table A3.1). It appears that the peak in the house and peridomestic area was in September, whereas it was in November in the sylvatic area, with rather few in September. This suggests that breeding conditions can change independently in the two areas and also that the range of movement of sandflies may not be very great.

Table A3.7 shows the interaction between METHOD and MONTH. The interaction is significant (row 10,Table A3.1) and inspecting the table shows that high numbers in one column are by no means correlated with high numbers in the other. This may reflect the local weather conditions during the time that each sample was made (in otherwords,the trapping efficiency of the two methods) and it is a warning of that type of problem. In view of this, it is right to follow the monthly variations with each method separately,as has been done in the main

body of the text.

To summarise, Table A3.1 shows that all four factors had a significant effect on catching rate, as did all of the two-way interactions. The high levels of statistical significance are due principally to the large numbers caught and with such numbers it is possible that weak effects with little biological importance are statistically very significant. Nevertheless, the statistically significant results are always a sign of some biological or methodological feature which should be examined more closely. In some species the interactions are not significant which means that the main effects alone tell all of the story. When an interaction is found to be significant it means that one should look closely at the two-way table and perhaps split the data up further before coming to any firm conclusion. In the main body of the text this course has been followed, by showing Tables of day and night catches separately, thus allowing a finer view of the way methods and habitats differ. Similarly the graphs of monthly changes are based on trapping methods in each location separately. Significance levels are not given in the main body of the text because only those found to be significant have been included in the more detailed graphical analysis.

The analysis above provides a thumb-nail sketch of L. panamensis. It is a species which definitely bites man, although almost exclusively at night. It hides by day although a few are found and a very few will still bite humans. It is most common in the sylvatic area and least in the house, although local conditions may influence the efficiency of both methods at different times of day and through the year. It appears to peak at different times in the two main areas hence it probably has a limited flight range and its numbers are subject to local

conditions. This sketch is extended by the analysis in Sections B and C, which examine the seasonal variation and the relative efficiency or different methods in more detail.

SECTION B

The monthly variation in numbers of L. panamensis females were analysed using data from both day and night catches with the methods in Section A, together with the collections from Shannon light traps. At first the factors METHOD and MONTH were fitted and the significance of the monthly changes assessed. Then the various meterological measures were used in turn to predict the sandfly catches (having removed the factor MONTH). This allowed one to see which of the meterological variates was the best predictor of sandfly numbers. Since they are to a great extent correlated (e.g. humidity is closely related to rainfall) there seems little point in presenting the full results of this analysis, and only the most important is identified. Finally, the correlation between sandfly numbers and leishmaniasis was examined for each species.

For L. panamensis females, monthly variation was highly significant (χ^2 = 3618 with 11 df.) and the most significant factor was the mean minimum value of relative humidity recorded each day. With a χ^2 of 1969 (1 df.) this measure explained 54% of the total monthly variation. There was a significant correlation with leishmaniasis, but it was very weak indeed (only 2% of the variation in sandflies was correlated with leishmaniasis).

SECTION C

In this phase of the analysis the day-time catches were excluded.

and only those months for which all methods were used were included (July, August, September and October). The main effect of MONTH was first fitted and then the effect of METHOD which caused a change of 1461 in the χ^2 (9 df.). This is highly significant, and the mean catch rates are shown in Table A3.8 where it is clear that much of the highest catching rate was with a cow as bait, but also that L. panamensis females respond to light traps and to pigs.

SUMMARY TABLES

After performing this analysis on each species and sex, the results have been summarised in the following tables.

This section has been prepared jointly with A.R. Ludlow who developed the statistical analysis and wrote the GENSTAT programs which are available from the Department of Pure and Applied Biology, Imperial College, London, U.K.

Table A3.1 Analysis of deviance for L. panamensis.

TERM	DEVIANCE	DF	MEAN DEVIANCE	PROBABILITY
HOUR	1652.8	1	1652.8	< 0.01
HABITAT	222.7	2	111.4	"
METHOD	408.6	1	408.6	"
MONTH	717.2	11	65.2	"
HOUR HABITAT	32.8	2	16.4	"
HOUR METHOD	46.1	1	46.1	"
HOUR MONTH	77.1	11	7.0	"
HABITAT METHOD	134.0	2	67.0	"
HABITAT MONTH	197.7	22	8.0	"
METHOD MONTH	133.3	11	12.1	"

Sandflies caught per hour (L. panamensis females).

A3.2

HABITAT / HOUR	HOUSE	PERIDOME	SYLVATIC	MEAN
DAY	0.03	0.35	0.07	0.15
NIGHT	4.19	9.60	13.78	9.19
MEAN	2.11	4.97	6.93	4.67

A3.3

METHOD / HOUR	HUMAN	TREEWALL	MEAN
DAY	0.07	0.23	0.15
NIGHT	15.07	3.31	9.19
MEAN	7.57	1.77	4.67

A3.4

HOUR / MONTH	DAY	NIGHT	MEAN
MARCH 1979	0.00	0.00	0.00
APRIL	0.07	2.56	1.31
MAY	0.11	7.40	3.76
JUNE	1.22	9.16	5.19
JULY	0.17	5.96	3.06
AUGUST	0.00	3.09	1.54
SEPTEMBER	0.00	24.68	12.34
OCTOBER	0.00	4.13	2.07
NOVEMBER	0.17	20.06	10.12
DECEMBER	0.07	12.82	6.44
JANUARY	0.00	17.68	8.84
FEBRUARY	0.00	2.75	1.38
MEAN	0.15	9.19	4.67

A3.5

METHOD / LOCATION	HUMAN	TREEWALL	MEAN
HOUSE	2.26	1.96	2.11
PERIDOME	9.40	0.55	4.97
SYLVATIC	11.06	2.80	6.93
MEAN	7.57	1.77	4.67

A3.6

LOCATION / MONTH	HOUSE	PERIDOME	SYLVATIC	MEAN
MARCH 1979	0.00	0.00	0.00	0.00
APRIL	0.43	0.00	3.51	1.31
MAY	1.08	4.88	5.30	3.76
JUNE	3.47	2.90	9.19	5.19
JULY	2.11	4.38	2.71	3.06
AUGUST	0.70	2.81	1.13	1.54
SEPTEMBER	5.06	26.55	5.42	12.34
OCTOBER	0.60	2.72	2.88	2.07
NOVEMBER	2.80	5.30	22.25	10.12
DECEMBER	4.20	3.60	11.52	6.44
JANUARY	4.07	5.35	17.10	8.84
FEBRUARY	0.80	1.20	2.13	1.38
MEAN	2.11	4.97	6.93	4.67

A3.7

METHOD / MONTH	HUMAN	TREEWALL	MEAN
MARCH 1979	0.00	0.00	0.00
APRIL	2.35	0.27	1.31
MAY	5.46	2.06	3.76
JUNE	7.19	3.19	5.19
JULY	3.75	2.38	3.06
AUGUST	2.62	0.47	1.54
SEPTEMBER	22.59	2.09	12.34
OCTOBER	2.23	1.90	2.07
NOVEMBER	20.06	0.17	10.12
DECEMBER	6.95	5.93	6.44
JANUARY	15.43	2.25	8.84
FEBRUARY	2.22	0.53	1.38
MEAN	7.57	1.77	4.67

A3.8

METHOD	MEAN
HUMHOUSE	5.38
HUMPERI	35.88
HUMFIELD	5.54
WALLHOUS	3.09
TREEPERI	0.33
TREEFIEL	6.58
SHANNON	14.81
CDC	37.37
COW	143.50
PIG	65.50
MEAN	31.80

Table A3.9 Analysis of deviance for L. atroclavata.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	7.99	7.99	0.01	26.36	26.36	0.01
	HABITAT	2	11.11	5.55	0.01	120.64	60.32	0.001
	METHOD	1	34.99	34.99	0.01	96.80	96.80	0.001
	MONTH	11	10.61	0.96	-	60.19	5.47	0.01
	HOUR HABITAT	2	2.46	1.23	-	5.54	2.77	-
	HOUR METHOD	1	0.00	0.00	-	0.86	0.86	-
	HOUR MONTH	11	11.52	1.05	-	40.53	3.68	0.01
	HABITAT METHOD	2	0.00	0.00	-	0.53	0.27	-
	HABITAT MONTH	22	21.86	0.99	-	26.09	1.19	-
	METHOD MONTH	11	0.00	0.00	-	7.54	0.69	-
B	MONTH	11	10.12	0.92	-			
	MAX. RAINFALL	1	1.44	1.44	-			
	LEISHMANIASIS	1	1.23	1.23	-			
C	METHOD	9	11.13	1.24	-	20.18	2.24	0.05

Table A3.10 Analysis of deviance for L. cayennensis.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	5.19	5.19	0.05	1.95	1.95	-
	HABITAT	2	27.65	13.83	0.01	48.93	24.46	0.01
	METHOD	1	34.04	34.04	0.01	45.79	45.79	0.01
	MONTH	11	30.99	2.82	0.01	47.55	4.32	0.01
	HOUR HABITAT	2	4.14	2.07	-	2.26	1.13	-
	HOUR METHOD	1	5.75	5.75	0.05	2.47	2.47	-
	HOUR MONTH	11	20.65	1.88	0.05	23.86	2.17	0.05
	HABITAT METHOD	2	1.17	0.58	-	9.61	4.81	0.01
	HABITAT MONTH	22	28.05	1.28	-	17.93	0.81	-
	METHOD MONTH	11	4.48	0.41	-	2.47	0.22	-
B	MONTH	11	31.10	2.83	0.01			
	MAX. RAINFALL	1	6.40	6.40	0.05			
	LEISHMANIASIS	1	1.50	1.50	-			
C	METHOD	9	13.02	1.45	-	9.25	1.03	

Table A3.11 Analysis of deviance for L. gomezi.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	233.96	233.96	0.001	141.60	141.60	0.001
	HABITAT	2	55.62	27.81	0.01	31.29	15.64	0.001
	METHOD	1	151.73	151.73	0.001	24.69	24.69	0.001
	MONTH	11	102.96	9.36	0.001	137.35	12.49	0.001
	HOUR HABITAT	2	1.12	0.56	-	4.91	2.46	-
	HOUR METHOD	1	16.41	16.41	0.01	2.87	2.87	-
	HOUR MONTH	11	14.09	1.28	-	11.50	1.05	-
	HABITAT METHOD	2	22.60	11.30	0.01	69.76	34.88	0.001
	HABITAT MONTH	22	65.65	2.98	0.01	77.16	3.51	0.01
	METHOD MONTH	11	29.46	2.68	0.01	51.54	4.69	0.01
B	MONTH	11	183.00	16.64	0.001			
	MEAN MINIMUM TEMPERATURE	1	85.00	85.00	0.001			
	LEISHMANIASIS	1	62.00	62.00	0.001			
C	METHOD	9	165.36	18.37	0.001	611.40	67.93	0.001

Table A3.12 Analysis of deviance for L. olmeca bicolor.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	3.07	3.07	-	0.66	0.66	-
	HABITAT	2	4.36	2.18	-	1.74	0.87	-
	METHOD	1	2.91	2.91	-	1.38	1.38	-
	MONTH	11	6.81	0.62	-	4.49	0.41	-
	HOUR HABITAT	2	0.01	0.00	-	0.01	0.00	-
	HOUR METHOD	1	0.01	0.01	-	0.01	0.01	-
	HOUR MONTH	11	0.01	0.00	-	0.01	0.00	-
	HABITAT METHOD	2	0.01	0.00	-	0.01	0.00	-
	HABITAT MONTH	22	0.00	0.00	-	0.01	0.00	-
	METHOD MONTH	11	0.01	0.00	-	0.01	0.00	-
B	MONTH	11	27.10	2.46	0.01			
	MEAN MINIMUM RELATIVE HUMIDITY	1	11.80	11.80	0.01			
	LEISHMANIASIS	1	1.10	1.10	-			
C	METHOD	9	4.00	0.44	0.05	4.41	0.49	0.05

Table A3.13 Analysis of deviance for L. ovallesi.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	718.27	718.27	0.001	6.07	6.07	0.05
	HABITAT	2	881.05	440.52	0.001	11.82	5.91	0.01
	METHOD	1	612.33	612.33	0.001	9.31	9.31	0.01
	MONTH	11	1413.54	128.50	0.001	31.18	2.83	0.01
	HOUR HABITAT	2	0.75	0.37	-	2.34	1.17	-
	HOUR METHOD	1	24.14	24.14	0.001	0.49	0.49	-
	HOUR MONTH	11	49.30	4.48	0.01	16.25	1.48	-
	HABITAT METHOD	2	3.91	1.95	-	0.71	0.35	-
	HABITAT MONTH	22	91.99	4.18	0.01	7.73	0.35	-
	METHOD MONTH	11	81.09	7.37	0.01	6.85	0.62	-
B	MONTH	11	1629.00	148.09	0.001			
	TOTAL RAINFALL	1	728.00	728.00	0.001			
	LEISHMANIASIS	1	862.00	862.00	0.001			
C	METHOD	9	17.98	1.99	0.05	15.07	1.68	-

Table A3.14 Analysis of deviance for L. panamensis.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	1652.8	1652.8	0.001	5.19	5.19	0.05
	HABITAT	2	222.9	111.4	0.001	2.43	1.21	-
	METHOD	1	408.6	408.6	0.001	9.47	9.47	0.01
	MONTH	11	717.2	65.2	0.001	53.03	4.82	0.01
	HOUR HABITAT	2	32.8	16.4	0.01	30.26	15.13	0.001
	HOUR METHOD	1	46.1	46.1	0.001	9.72	9.72	0.01
	HOUR MONTH	11	77.1	7.0	0.01	29.09	2.64	0.01
	HABITAT METHOD	2	134.0	67.0	0.001	10.23	5.11	0.01
	HABITAT MONTH	22	197.7	9.0	0.001	38.99	1.77	0.05
	METHOD MONTH	11	133.3	12.1	0.001	11.70	1.06	-
B	MONTH	11	3618.00	328.91	0.001			
	MEAN MINIMUM RELATIVE HUMIDITY	1	1969.00	1969.00	0.001			
	LEISHMANIASIS	1	101.00	101.00	0.001			
C	METHOD	9	1460.92	162.32	0.001	70.53	7.84	0.001

Table A3.15 Analysis of deviance for L. shannoni.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	4.75	4.75	0.05	0.05	0.05	-
	HABITAT	2	14.09	7.05	0.01	12.22	6.11	0.01
	METHOD	1	4.27	4.27	0.05	4.85	4.85	0.05
	MONTH	11	27.78	2.53	0.01	17.83	1.62	-
	HOUR HABITAT	2	1.22	0.61	-	1.07	0.53	-
	HOUR METHOD	1	1.36	1.36	-	2.01	2.01	-
	HOUR MONTH	11	1.85	0.17	-	5.34	0.49	-
	HABITAT METHOD	2	9.79	4.89	0.01	0.29	0.15	-
	HABITAT MONTH	22	8.21	0.37	-	5.69	0.26	-
	METHOD MONTH	11	9.84	0.89	-	3.01	0.27	-
B	MONTH	11	34.67	3.15	0.01			
	MEAN RAINFALL	1	49.34	49.34	0.001			
	LEISHMANIASIS	1	60.48	60.48	0.001			
C	METHOD	9	16.40	1.82	-	61.32	6.81	0.001

Table A3.16 Analysis of deviance for L. trinidadensis.

			FEMALES			MALES		
SECTION	TERM	DF	DEVIANCE	MEAN DEVIANCE	PROB.	DEVIANCE	MEAN DEVIANCE	PROB.
A	HOUR	1	107.30	107.30	0.001	184.61	184.61	0.001
	HABITAT	2	374.30	187.10	0.001	756.97	378.49	0.001
	METHOD	1	580.44	580.40	0.001	1183.47	1183.47	0.001
	MONTH	11	39.03	3.55	0.01	225.78	20.53	0.05
	HOUR HABITAT	2	4.29	2.15	-	132.81	66.40	0.001
	HOUR METHOD	1	3.08	3.08	-	2.50	2.50	-
	HOUR MONTH	11	78.77	7.16	0.01	196.82	17.89	0.01
	HABITAT METHOD	2	8.49	4.25	0.05	4.08	2.04	-
	HABITAT MONTH	22	50.84	2.31	0.01	74.93	3.41	0.01
	METHOD MONTH	11	4.42	0.40	-	6.67	0.61	-
B	MONTH	11	36.00	3.27	0.01			
	MEAN MINIMUM RELATIVE HUMIDITY	1	12.00	12.00	0.01			
	LEISHMANIASIS	1	4.00	4.00	0.05			
C	METHOD	9	113.29	11.33	0.001	239.99	26.67	0.001

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RESISTENCIA AL AYUNO EN TRIATOMINOS (HEMIPTERA, REDUVIIDAE) VENEZOLANOS

I — Rhodnius prolixus Stal

M. Dora FELICIANGELI (1), Jorge RABINOVICH (2) y E. FERNANDEZ (1)

RESUMEN

Se estudia la capacidad de resistencia al ayuno en ninfas y adultos de **Rhodnius prolixus** y el efecto del mismo sobre la fecundidad y fertilidad de la hembra y la actividad sexual del macho. Con este propósito se compararon grupos de machos y hembras apareados, ambos mantenidos en ayuno, con grupos de machos y hembras apareados y alimentados semanalmente; machos en ayuno apareados con hembras alimentadas semanalmente y viceversa, hembras mantenidas en ayuno apareadas con machos alimentados semanalmente. Se observó que los estadios ninfales I y II, y los adultos son los menos resistentes al ayuno, siendo la longevidad aproximadamente 1 mes y medio, 3 meses y 1 mes, respectivamente, mientras los estadios intermedios pueden alcanzar hasta un máximo de 7 meses (ninfas III y IV) y 5 meses (ninfas V) aproximadamente. Estos resultados sugieren que este parámetro tiene importancia en relación a la distribución etaria de la población en condiciones naturales, donde se observa una pirámide con base estrecha (ninfas I y II), que se ensancha notablemente a nivel de los estadios III y IV, disminuyendo relativamente a nivel estadio V, y aumentando en la etapa adulta donde evidentemente hay una acumulación de individuos. El efecto del ayuno sobre la producción de huevos es muy marcado, siendo la alimentación indispensable para garantizar la oogénesis. También se observó que la misma está aparentemente afectada por cambios climáticos. También la eclosión de los huevos es reducida en proporción significativa por el ayuno debido probablemente a una disminución en la actividad de las glándulas accesorias del macho, las cuales están encargadas de la secreción de una sustancia peculiar indispensable para la fecundación. Sin embargo, el hecho de que los % más altos de eclosión se registren en huevos puestos por hembras en ayuno apareadas con machos alimentados, permite inferir que es posible tenga importancia el número de espermatozoides en relación al número de huevos presente. La actividad sexual del macho se vé muy reducida cuando es mantenido en ayuno en comparación con la del macho alimentado. Finalmente se destaca que el potencial reproductivo de la población es muy diferente en los varios grupos estudiados, siendo mayor en el caso de hembras alimentadas apareadas con machos mantenidos en ayuno, debido a que la probabilidad de supervivencia de las mismas es mayor (ya que la cópula parece afectar la longevidad tanto de hembras como de machos), y además los espermatozoides se mantienen viables en la espermateca de la hembra hasta 45 semanas después de la cópula. Se discute la importancia de estos resultados en términos poblacionales, ya que garantizaría de manera eficaz la continuidad de las poblaciones en caso que los machos sean afectados por algún factor adverso.

(1) Cátedra de Parasitología, Facultad de Ciencias de la Salud, Universidad de Carabobo, Valencia, Venezuela
(2) Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 1827, Caracas 101, Venezuela

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INTRODUCCION

Varios Autores han documentado la capacidad de ayuno de los triatominos. URIBE[14] observó en una ninfa III estadio de **Rhodnius prolixus** una longevidad de 5 meses bajo esas condiciones y BUXTON[2] refiere, para los adultos, una longevidad promedio de 41 días en machos y de 35 dias en hembras.

PELLEGRINO[8] en ninfas III y IV de **Triatoma infestans** obtuvo una supervivencia, en condiciones de ayuno, de 5 meses en el 48% de los ejemplares estudiados.

TOBAR[13] observa en la misma especie que la resistencia al ayuno está bastante condicionada por el clima, siendo menor a temperaturas muy bajas (5°-15°C) o muy altas (37°C); por otro lado, en **Mepraia spinolai** obtiene una resistencia mayor en larvas (ninfas I a IV) con respecto a ninfas V y de estas con respecto a adultos.

DIAS[4] estudia el ayuno en **T. infestans, R. neglectus y Panstrongylus megistus** confirmando los resultados anteriores de una menor resistencia de las ninfas I y de los adultos, con resultados un poco diferentes para los estadios intermedios con respecto a los obtenidos por PERLOWAGORA[9] en **T. infestans** y COSTA & col.[3] en **R. neglectus**, explicables en términos de las diferentes condiciones de experimentación.

RYCKMAN[12] observa en **T. protracta** que el estadio IV es el más resistente al ayuno, con un máximo de 309 días de inanición, y que totalizando los períodos máximos de supervivencia para cada estadio, teóricamente esa especie de triatomino puede permanecer por un período máximo de 3 años en los estadios ninfales, en caso de no haber un efecto por ayuno en estadios anteriores.

El estudio comparativo del ayuno en especies simpátridas, bajo las mismas condiciones ambientales, puede contribuír con información de valor epidemiológico, ya que el ayuno está directamente asociado al mantenimiento de las infestación en viviendas u otros hábitats temporalmente abandonados.

En este primer trabajo se estudia la capacidad de ayuno en ninfas y adultos de **Rhodnius prolixus**, el principal vector de la enfermedad de Chagas en Venezuela, para compararlo posteriormente con otros triatominos venezolanos, y su efecto sobre ciertas características biológicas como la actividad sexual en el macho, y la fecundidad y fertilidad en las hembras.

MATERIALES Y METODOS

Los insectos, procedentes de una cría mantenida en la Cátedra de Parasitología de Universidad de Carabobo desde el año 1968, fueron mantenidos en condiciones ambientales de laboratorio. Referimos por lo tanto, los datos climáticos registrados en el mismo año en que se llevó a cabo el experimento (1976) en la estación meteorológica experimental de la FAV (Fuerza Aérea Venezolana) más cercana a Valencia. La temperatura media anual fué 24.2°C (máximo = 33.9; mínimo = 12.9), y la humedad relativa promedio 73% (máximo = 100%; mínimo = 22%).

Se utilizaron especímenes recién mudados procedentes de lotes alimentados el mismo dia, con una variación en la fecha de ecdisis de 1 a 3 días.

En frascos de vidrio de 3,9ml de capacidad se aislaron aproximadamente 50 ejemplares de cada estadio ninfal (Tabla I) los cuales fueron mantenidos en ayuno hasta la muerte del último individuo. Contemporáneamente se aislaron en sendos frascos otros lotes de 50 ejemplares de la misma edad morfo-fisiológica los cuales eran alimentados semanalmente y se mantenían como testigo hasta que mudaran al estadio siguiente.

Los lotes de adultos se obtuvieron separando machos y hembras en el V estadio ninfal según el criterio de ESPÍNOLA[4], y apareándolos ocho dias después de la muda al azar, de acuerdo al siguiente esquema: 50 machos con 50 hembras, ambos sexos mantenidos permanentemente en ayuno; 50 machos con 54 hembras, ambos sexos alimentados semanalmente; 50 machos mantenidos en ayuno con 47 hembras que semanalmente eran retiradas del frasco común, alimentadas y regresadas; 50 hembras mantenidas en ayuno con 50 machos semanalmente retirados del frasco común, alimentados y regresados.

También semanalmente se efectuaban censos en todos los frascos anotándose la mortalidad. La alimentación era llevada a cabo utilizando aves de corral.

Con el propósito de evaluar el efecto del ayuno sobre la actividad sexual de los machos, y la fecundidad y fertilidad de las hembras, ya sea apareadas con machos en ayuno o viceversa, cada semana se recolectaban todos los espermatóforos y los huevos de los frascos de adultos. Los espermatóforos eran contados y los huevos almacenados hasta la eclosión para calcular el porcentaje de fertilidad.

Para simplificar el cálculo del número de cópulas por macho por semana (Fig. 3) y del número de huevos puestos por hembra por semana (Fig. 1), se decidió suponer que la mortalidad registrada había ocurrido durante el primer dia de la semana, lo cual permitió calcular los promedios en base a los individuos vivos presentes en el momento del censo. Por ejemplo, si en el censo correspondiente a una cierta semana se encontraron 100 huevos, 48 hembras vivas y 2 hembras muertas, el número promedio de huevos puestos por hembras durante esa semana seria 100/48, considerando que las dos hembras habían muerto el primer día y, por lo tanto, no habían hecho ningún aporte al número total de huevos puestos.

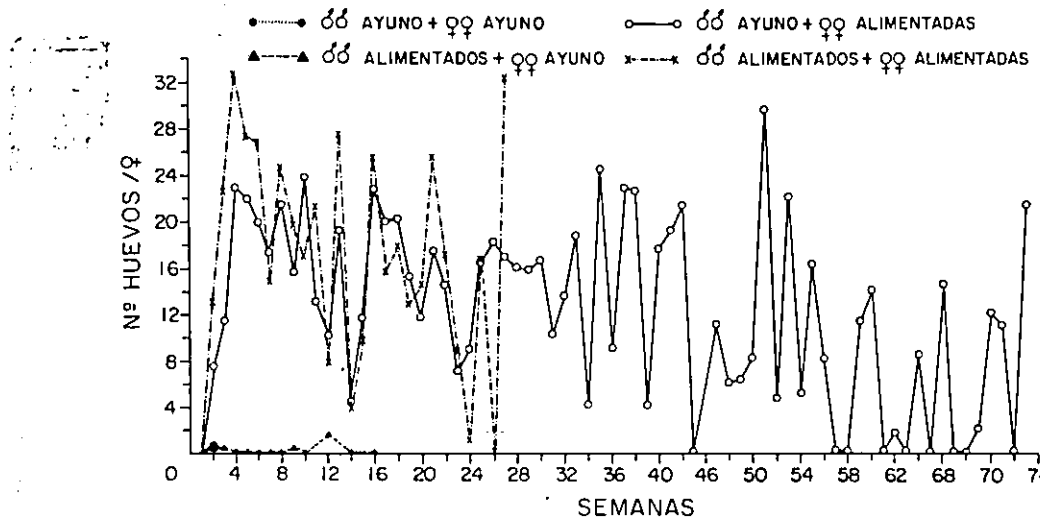

Fig. 1 — Número de huevos puestos por hembras de Rhodnius prolixus bajo diferentes condiciones de alimentación y apareamiento

Un índice de potencial reproductivo de la hembra puede calcularse mediante la sumatoria de los productos de 1x (probabilidad de las hembras de llegar vivas a la edad x) por el número de huevos puestos por hembra a esa edad y por el % de eclosión de los mismos ($\Sigma l_x.N.^{o}h/♀ E_x$). Cada término de la sumatoria permite comparar el esfuerzo reproductor de las hembras para esa edad.

RESULTADOS

La Tabla I muestra la resistencia al ayuno en ninfas de **R. prolixus**. Se observa que las ninfas del estadio I pueden ayunar aproximadamente 1 mes y medio y las del estadio II, más del doble. Los estadios III y IV son los más resistentes al ayuno (aproximadamente 5 meses). Este lapso disminuye considerablemente en las ninfas V, siendo la diferencia estadisticamente significativa con respecto al estadio anterior. Las variaciones altas de la desviación standard pueden ser interpretadas como debidas a la diferencia de contenido alimenticio (reserva), traida del estadio anterior. Totalizando los períodos máximos de resistencia al ayuno en todos los estadios ninfales, se obtiene que esta especie podría sobrevivir un lapso de 698.7 días, o sea, dos años, antes de llegar a adulto.

En los lotes testigo, que eran alimentados semanalmente antes de la muda, se registró una mortalidad muy baja: O% para ninfas I y III, y solamente 2% en los estadios II y IV y 11.7% en el estadio V, pudiéndose considerar estos valores dentro del rango aceptado como resultado de factores como la manipulación de los insectos, la mortalidad debida a la muda, variaciones individuales, etc.

En relación a los adultos se observa que, cuando tanto los machos como las hembras son mantenidos en ayuno apareados sobreviven sólo aproximadamente un mes (Tabla II), y para ambos sexos este resultado es comparable al que se obtiene cuando son apareados con el sexo opuesto alimentado semanalmente. En cambio, cuando se comparó la longevidad de los machos alimentados apareados con hembras alimentadas (Tabla II, columnas C y D) con la de los machos alimentados apareados con hembras en ayuno (Tabla II, columnas G y H), las cuales murieron precozmente, la diferencia resultó ser estadisticamente significativa. También la longevidad fué significativamente mayor en hembras alimentadas que se mantuvieron con machos en ayuno que en hembras alimentadas mantenidas con machos alimentados (Tabla II).

T A B L A I

Resistencia al ayuno (días) de los diferentes estadios ninfales de R. prolixus.

	Estadio				
	I	II	III	IV	V
n	53	50	52	47	51
$\bar{x}$	44.64	91.00	164.90	161.60	114.75
s	10.83	15.56	25.99	43.47	25.97
Rango (mínimo-máximo)	14-56	56-119	105-210	14-210	28-175
t	17.43+	17.51+	0.45++	6.44++	

\+ significativo para $P < 0.01$
++ no significativo

T A B L A II

Longevidad (días) de los adultos de Rhodnius prolixus bajo diferentes condiciones de alimentación y apareamiento

	A ♂♂ 50 + ♀♀ 50 Ayuno	B 50 ♀♀ Ayuno	C ♂♂ 50 + ♀♀ 54 Aliment.	D Aliment.	E ♂♂ 50 + ♀♀ 50 Ayuno	F Aliment.	G ♂♂ 50 + ♀♀ 50 Aliment.	H 50 ♀♀ Ayuno
$\bar{x}$	37,52	40,60	198,24	96,06	34,02	271,21	260,68	45,22
$\bar{s}$	12,06	12,33	118,98	58,16	13,57	116,53	117,68	18,34
$s_{\bar{x}}$	1,71	1,74	16,83	7,91	1,92	17,00	16,64	2,59
Rango (mínimo-máximo)	7-56	7-70	7-420	7-196	7-49	35-504	7-413	7-91

[1]A-E = 1,36: no significativo
[1]B-H = 1,48: no significativo
[1]C-G = 2,64: significativo para $P < 0.01$
[1]D-F = 9,35: significativo para $P < 0.01$

La Tabla III presenta una síntesis de los datos totales relativos a fecundidad y fertilidad de las hembras en distintas condiciones de apareamiento y alimentación.

El número de huevos/♀/semana y el período de oviposición presentan valores muy bajos en los casos en que la hembra es mantenida en ayuno (Fig. 1); los valores más elevados son alcanzados en la curva correspondiente al testigo (machos alimentados con hembras alimentadas), mientras que la curva correspondiente a hembras alimentadas apareadas con machos en ayuno (que ya a la semana número 8 habian perecido), se mantiene con niveles ligeramente inferiores al de la curva anterior; sin embargo la producción de huevos continúa hasta la muerte de la última hembra.

En las dos curvas de hembras alimentadas la oviposición es aparentemente cíclica.

El % de eclosión de los huevos (Fig. 2) disminuye bruscamente en la curva correspondiente a huevos puestos por hembras en ayuno, apareadas con machos en ayuno. En cambio cuando ambos sexos fueron alimentados, los valores obtenidos estuvieron en la gran mayoría comprendidos entre 80% y 100%. En el caso de hembras alimentadas y apareadas con machos en ayuno, los valores de eclosión solo se mantienen entre 80% y 100% durante las pri-

meras ocho semanas, cuando todavía los machos estaban presentes, pero después de la muerte de estos últimos, el porcentaje de eclosión es irregular, pero en general va bajando progresivamente, posiblemente en relación a la disminución del número de espermatozoides en las espermatecas de las hembras; es interesante notar que, hasta la semana número 53, ó sea 45 semanas después de las últimas cópulas, todavía algunos huevos llegaron a eclosionar.

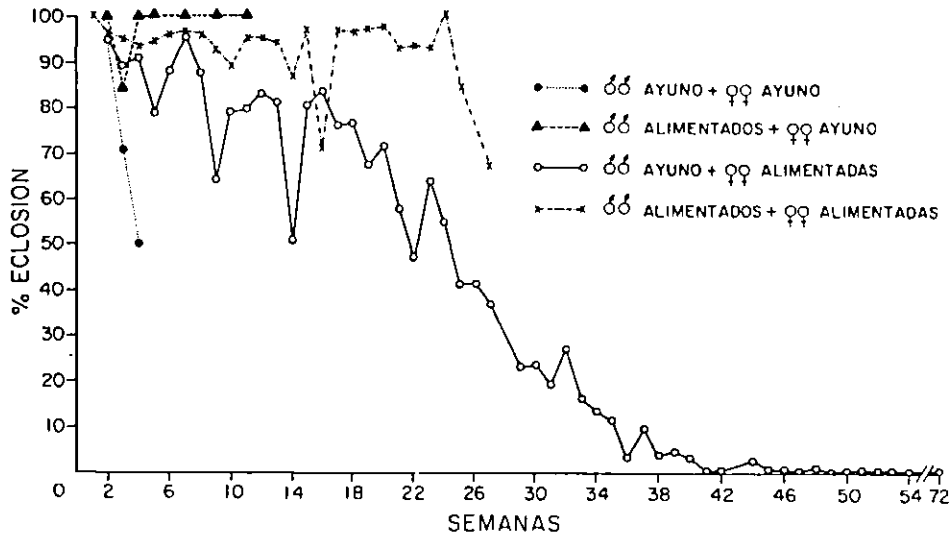

Fig. 2 — Porcentaje de eclosión de los huevos de **Rhodnius prolixus** depositados por hembras sometidas a diferentes condiciones de alimentación y apareamiento

La actividad sexual del macho en función del apareamiento y del ayuno (Fig. 3) muestra ser mayor en el caso de los machos alimentados y apareados con hembras alimentadas, con los valores más altos en las primeras ocho semanas (máximo de 4,4 cópulas/individuos). En el caso de los machos alimentados y apareados con hembras en ayuno, la actividad sexual es menor, disminuyendo a niveles todavía inferiores cuando el macho es mantenido en ayuno.

La relación entre la supervivencia de cada sexo y el potencial reproductivo (expresado por $l_x m_x E_x$, donde x representa la edad en semanas) está resumida en la Fig. 4. La gráfica 4a muestra que la supervivencia de ambos sexos son casi idénticas en condiciones de ayuno, pero muy inferior en los machos, cuando ambos sexos han sido alimentados (Fig. 4b). Comparando las Figs. 4b y 4c se observa claramente la progresiva y rápida caída en la supervivencia de las hembras alimentadas al haber copulado con machos alimentados, mientras que esa caída es sumamente lenta cuando las hembras alimentadas se encontraban con machos en ayuno (Fig. 4c). Es interesante observar que la mayor supervivencia de las hembras con machos en condiciones de ayuno se obtiene aún antes de una reducción notable en el número de machos sobrevivientes; es decir, se confirma la evidencia dada en la Fig. 3, que en condiciones de ayuno la habilidad copulatoria del macho se reduce ya desde la primera semana. En la Fig. 4d se observa que la curva de supervivencia de los machos es más alta que la respectiva curva de la Fig. 4b, confirmándose que la cópula también en los machos, tiene el efecto de reducir la sobrevivencia.

El potencial reproductivo en función de la edad muestra un patrón que sigue fielmente el efecto de la curva de supervivencia de las hembras, aunque también refleja las oscilaciones en la postura de huevos.

DISCUSION

Los resultados de resistencia al ayuno en **R. prolixus** concuerdan en línea general, con los obtenidos por otros Autores (URIBE [14]; BUXTON [2]) y, al igual que en otras especies (PERLOWAGORA [6]; TOBAR [1,3], se observa una mayor

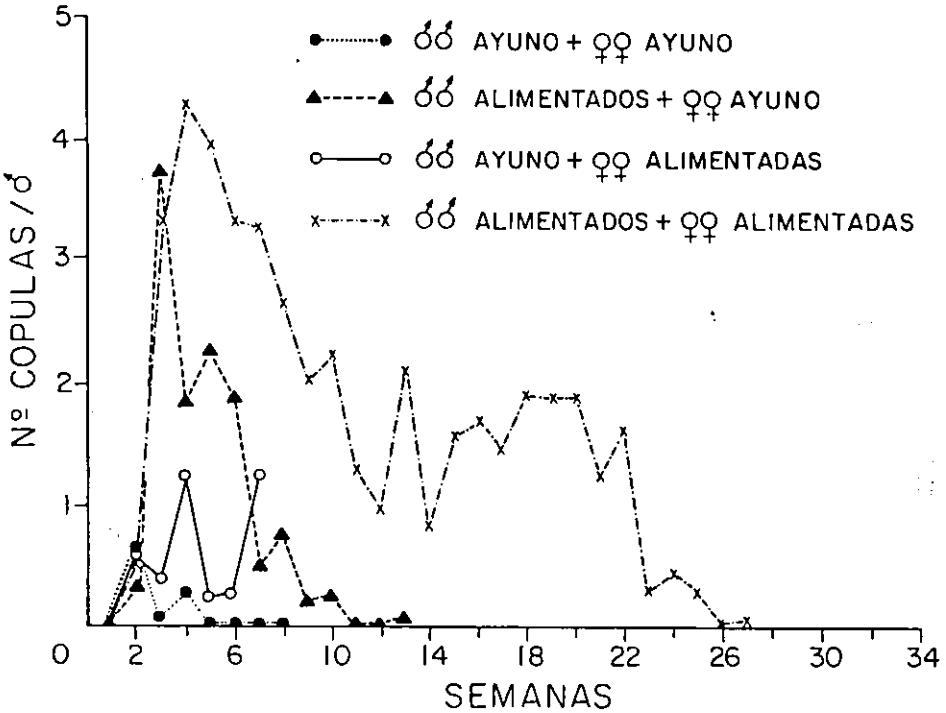

Fig. 3 — Tasa de cópula de Rhodnius prolixus (N.º de cópulas/macho) bajo diferentes condiciones de alimentación y apareamiento

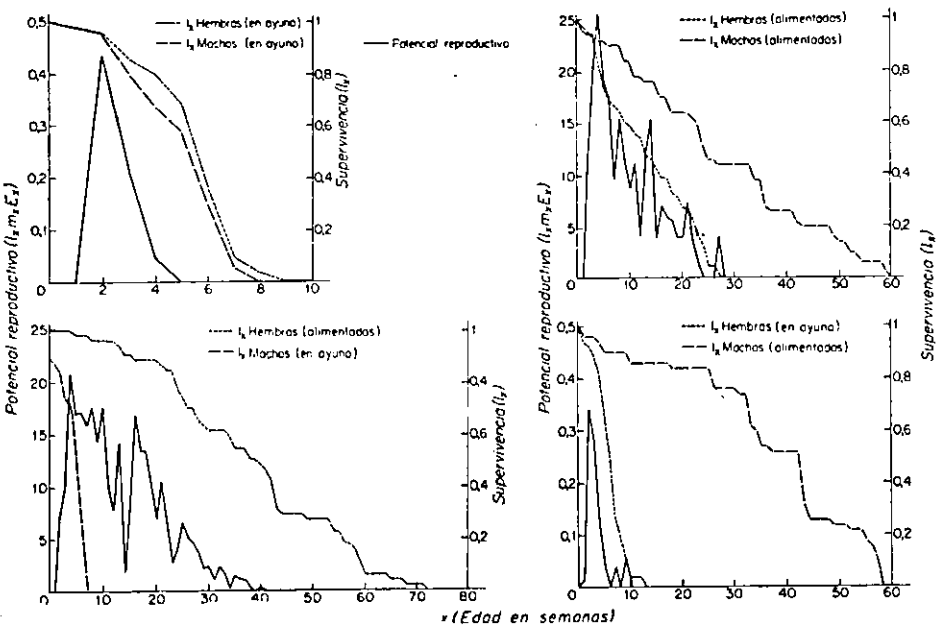

Fig. 4 — Curvas de supervivencia de machos y hembras de Rhodnius prolixus bajo diferentes condiciones de alimentación y supervivencia, y curvas del potencial reproductivo ($l_x m_x E_x$) donde, l_x = probabilidad de llegar vivo a la edad x, m_x = curva de fecundidad (N.º de huevos depositados por hembra de edad x, y Ex = porcentaje de eclosión de los huevos depositados por una hembra de edad x

sobrevida en los estadios intermedios (III y IV) que disminuye un poco en las ninfas V y apreciablemente en los adultos.

Estas observaciones permiten formular una hipótesis relativa a la distribución etaria de las poblaciones naturales. En esas condiciones generalmente se observa una pirámide etaria con una base muy estrecha (ninfas I y II) que se ensancha con los estadios III y IV, disminuye relativamente en el estadio V, para finalmente ensancharse con los adultos. Este patrón, observado tanto en poblaciones domésticas (ROSSELL [11]), como en poblaciones silvestres (FELICIANGELI & TORREALBA [6]), difiere notablemente del patrón obtenido mediante estudios de Tablas de Vida conducidos en el laboratorio.

Si bien por un lado puede adjudicarse la escasez de individuos de I y II estadio a dificultades de su recolección, también es posible que su baja resistencia al ayuno puede producir ese resultado ya que si esos estadios logran alimentarse, inmediatamente mudarán a estadios superiores y, de no lograrlo, mueren rápidamente.

Por otra parte los estadios III y IV, que resisten un largo período de ayuno, son los que se presentan en mayor abundancia relativa. Con las ninfas V ocurrirá lo mismo que en las I y II: las que logran alimentarse mudan y pasan al estadio adulto, y las que no lo logran mueren en mayor proporción que las anteriores en igual tiempo, produciéndose por lo tanto una disminución relativa de la población de dicho estadio.

La resistencia de los adultos al ayuno es muy reducida; sin embargo ellos tienen la ventaja de poder desplazarse con mayor facilidad que las ninfas en búsqueda de alimento y es posible, por lo tanto, que puedan compensar en parte esa desventaja, produciéndose así el ligero incremento de su abundancia relativa que se refleja en la pirámide etaria.

Se concluye que la resistencia al ayuno parece ser de importancia bajo condiciones naturales, no solamente porque es responsable directa del mantenimiento de la infestación en un hábitat determinado, sino también porque influiría sobre la estructura de edades de la población, cuya composición debe ser tomada en cuenta en la aplicación de cualquier medida de control (RABINOVICH [10]).

En los lotes de adultos alimentados la diferente longevidad de los grupos apareados con el otro sexo en ayuno con respecto á la situación en que ambos están alimentados, permite deducir que cópula y oviposición juegan un papel importante en la supervivencia.

Con respecto a la cópula ésta parece afectar más a las hembras que a los machos, ya que cuando ambos sexos eran alimentados semanalmente los machos alcanzaron una longevidad promedio 5 veces mayor, y las hembras solamente 2,4 veces mayor a la del lote en ayuno.

Al analizar los resultados de la oviposición se desprende, como es conocido (ARENDS [1]), que la alimentación es indispensable para la producción de huevos, y además que está aparentemente ligada a un ritmo semanal que podría coincidir con el tiempo necesario para que se cumpla la oogénesis (también en frascos de cria, generalmente se observa que los insectos no oviponen durante la semana siguiente a la alimentación). Dado que posiblemente no todas las hembras comen simultáneamente se explica que haya fluctuaciones de diferente amplitud. Además, el hecho de que las curvas (hembras alimentadas+machos alimentados) y de (hembras alimentadas+machos en ayuno) son bastantes paralelas a lo largo del tiempo, hace pensar que es posible que los cambios de temperatura influyan también sobre la oviposición. En efecto, en la semana 14 la disminución en la producción de huevos fué bastante violenta y correspondió al mes de Enero 1976 cuando fué registrada la temperatura mínima absoluta más baja (12.9°C) de todo el período.

Los valores finales de las curvas corresponden a la situación en que quedaba un solo individuo y por eso se hacen más amplias y más evidentes las fluctuaciones; esto coincide con PERLOWAGORA [9], quién observó que en T. infestans aparentemente no hay una disminución importante de la producción de huevos con el envejecimiento de la hembra sino un mantenimiento de la alternancia de períodos fértiles con periodos estériles.

Comparando las cantidades totales de huevos producidos (Tabla III) se observa que hembras alimentadas apareadas con machos en ayuno producen el doble de huevos que las hembras alimentadas apareadas con machos alimentados. Sin embargo, si calculamos el número de huevos puestos por día por hembra, obtendremos para las primeras 1,74 huevos/ ♀ /

TABLA III

Fecundidad y fertilidad en hembras de Rhodnius prolixus bajo diferentes condiciones de apareamiento y alimentación

	♀♀ Alimentadas + ♂♂ Alimentados	♀♀ Ayuno + ♂♂ Ayuno	♀♀ Ayuno + ♂♂ Alimentados	♀♀ Alimentadas + ♂♂ Ayuno
No. total de huevos puestos	12.357	46	50	25.534
% eclosión	93,63	80,43	94,00	55,35
Máxima edad reproductiva (días)	189	35	112	497
Potencial reproductivo	212,3	0,70	0,94	298,63

día (25.534/54/271,2) y para las segundas 2,57 huevos/♀/día (12.347/50/96.1). Esto por un lado hace pensar que la cópula sea un estímulo para la oviposición y por otro lado explica que lo afirmado anteriormente, que además de la cópula, también la presión de oviposición afecta la longevidad de las hembras.

KHALIFA [7] opina que el éxito de la fecundación por parte del macho es debida no a la cantidad de espermatozoides (de los cuales considera que siempre hay una cantidad en exceso), sino a la cantidad de una sustancia peculiar, probablemente secretada por las glándulas accesorias, que desaparece si los machos son mantenidos en ayuno por 60 días.

Estas observaciones explicán porqué el % de huevos eclosionados baja notablemente en los huevos puestos por hembras en ayuno apareadas con machos también en ayuno. Sin embargo, analizando los % de eclosión que se obtienen cuando los huevos son puestos por hembras alimentadas y apareadas con machos mantenidos en ayuno se observa que las primeras ocho semanas (período de longevidad máxima de los machos), los porcentajes de eclosión se mantienen dentro de los valores límites esperados (80 a 100%) o sea, que aparentemente, no sólo intervienen las condiciones del macho, sino que posiblemente la hembra, cuando está alimentada, produce huevos potencialmente más fértiles o más fácilmente fertilizables. Esta conclusión concuerda con los resultados observados en huevos puestos por hembras no alimentadas apareadas con machos en ayunas donde la mayoría de los huevos puestos eclosionan. A pesar de que el número de huevos puestos era muy pequeño, no debe descartarse la posible importancia del número de espermatozoides para garantizar que casi todos los huevos sean fertilizados. A pesar que KHALIFA[7] admite que el número de espermatozoides está siempre en exceso, no sabemos si al aumentar el número de espermatozoides por huevos aumenta la probabilidad de que éste sea fecundado.

Aún cuando adultos de ambos sexos están alimentados, rara vez todos los huevos de una cosecha llegan a eclosionar; esto posiblemente sea el resultado de variaciones individuales: machos no capaces de copular, hembras más fértiles que otras, etc.

Es importante destacar que el mayor potencial reproductivo de las hembras correspondió al de las hembras alimentadas apareadas con machos en ayuno; esto resulta no sólo por la viabilidad y actividad de los espermatozoides almacenados en las espermatecas sino también de la mayor probabilidad de supervivencia (1_x) de las hembras de este grupo en todos los intervalos de clases de edades. Este fenómeno podria interpretarse como un mecanismo de adaptación poblacional que garantizaria que, si en algún momento llegan a desaparecer o disminuír considerablemente los machos, quede asegurado el mantenimiento de la población.

SUMMARY

Resistance to fast in Venezuelan Triatominae (Hemiptera, Reduviidae). I — Rhodnius prolixus Stal

Resistance to starvation by nymphs and adults of **Rhodnius prolixus** was studied, and its effects on the female's fertility and fecundity, as well as on the male's sexual activity was analyzed. Four groups resulting from the combination of starved and fed individuals were used in the case of adults; the fed individuals were offered a meal on a weekly basis. Maximum longevity of nymphs was observed in instars III and IV (7 months) and instar V (5 months); shorter longevities were observed for instars I (1 month), and II (3 months) and

adults (1 month). This finding might explain the age piramid frequently found in both sylvatic and domestic populations, with a typically enlarged middle section. Egg production is clearly correlated with feeding, but a relationship with some climatic changes was also observed. Egg hatching is significantly reduced by starvation, and this was traced to the accesory glands of the males under starvations as well as to the relationship between the number of spermatozoa and eggs. In general, sexual activity of the male is strongly reduced when kept under starvation. The reproductive potential of the population is very different in the various groups of the experimental design, being highest in the case of fed females with starved males, mainly because the spermatozoa maintained viability up to 45 weeks after copulation took place. The importance of these findings in terms of population control is discussed.

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Domiciliary biting frequency and blood ingestion of the Chagas's disease vector *Rhodnius prolixus* Ståhl (Hemiptera: Reduviidae), in Venezuela*

J. E. Rabinovich**

Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B. C. Canada V6T 1W5

J. A. Leal

Division de Malariología y Endemias Rurales, Ministerio de Sanidad y Asistencia Social, Avenida, Bermudez, Maracay, Venezuela

AND

D. Feliciangeli de Piñero

Cátedra de Parasitología, Facultad de Ciencias de la Salud, Universidad de Carabobo, Valencia, Venezuela

Summary

Demolition of a rural house in the State of Cojedes, Venezuela, provided a collection of 7,934 *Rhodnius prolixus* of which a random sample of 1,415 was weighed within 48 hours. The field weights, coupled with laboratory information of weight loss (in %) with time, average blood ingestion and meal size sufficient to promote moulting, were used to estimate biting rate under domiciliary conditions.

The results show that in this particularly highly infested house, the *R. prolixus* population bites, on the average, at a rate of 58 times/person/day, draining blood at a rate of about 100 cm^3/person/month; this meant a total of 1·2 litres/month from the 11 people inhabiting the house. It was found that the more advanced *R. prolixus* is in its development, the more aggressive it is in securing its meal: 15, 25, 30, 59 and 77% of fed insects of instar 1 through 5, respectively, were able to achieve moulting with only one meal.

Applying the estimated biting rate to *R. prolixus* collections of other 13 demolished houses, with more typical insect population densities, an average biting rate of 9 bites/person/day was obtained; this value was, however, extremely variable, ranging from 0·2 bites/person/day (once every five days) to 33 bites/person/day.

Introduction

Achieving eradication of *Rhodnius prolixus* populations in rural areas in Venezuela is made so difficult by the permanent recolonization of houses by insects from palm trees (Gamboa, 1970; Gomez-Nuñez, 1963), that control measures will have to be geared to obtaining effectiveness by keeping the population size of the vector below "dangerous" levels. Determination of these thresholds of population size that would indicate the necessity of initiating treatment of houses for vector control will require knowledge of several factors that depend upon local conditions (such as location of house, climate, time of year), type of parasite (strain of *Trypanosoma cruzi*), number and health of both people and animals in the house, and proportion of infected vectors in the house. Using a computer simulation model Rabinovich & Rossell (1976) have shown that some of these factors play a role of varying importance in the transmission of *T. cruzi*. Because of ignorance, however, about its actual field value, in all instances an educated guess had to be used for the biting rates of the different instars of *Rhodnius prolixus*.

The purpose of this article is to obtain an estimate of the biting rate of a domiciliary *R. prolixus* population by combining laboratory information and field measurements. This approach assumes that the physiology and the behaviour of the vector in the field and in the laboratory are similar in some respects; because these assumptions have to be verified independently, we consider our estimates of the biting rates to be preliminary approximations. In our discussion we suggest ways in which more precise methods might be developed.

Materials and Methods

As part of a research project to evaluate possibilities of using two species of microhymenopterous parasitoids for biological control of *Rhodnius prolixus*, 14 houses were dismantled and all *R. prolixus* were captured. A random sample of bugs from one of these houses (CBM-17) was then weighed in the laboratory, using a Sartorius electrobalance, accurate to 0·01 mg. These houses were located in Hacienda Vieja, a small village in the State of Cojedes, south-western Venezuela.

Demolition of house CBM-17 was begun at 8 a.m. on March 17, 1977; the inhabitants of CBM-17 (and the other houses also dismantled)

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** On sabbatical leave from: Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 1827, Caracas 101, Venezuela.

made use of their house and maintained their normal activities including sleeping in it the night before. This was considered essential to avoid any possible emigration of insects. Before demolition, all the household articles and personal belongings were taken out of the house and immediately checked for the presence of any insects; all bugs collected were kept in labelled jars.

Demolition was performed in approximately nine hours, using a team of 16 people: the authors, technicians, students, some personnel of the Ministry of Health and local villagers. House CBM-17 was built exclusively of thatched material (both roof and walls were made of palm leaves). The demolition was started by carefully dismantling the walls. For this purpose a white canvas was laid on the ground by the external side of the walls and the imbricated palm leaves were removed one by one; they were first shaken strongly above the canvas, and all falling insects collected; then the palm leaf was beaten with a stick to cause additional insects (if any) to drop on to the canvas; finally, each palm leaf was individually checked, section by section, to verify that no insects remained (this rarely happened).

A similar procedure was applied to the thatched roof. After all the palm leaf material of the roof had been removed, the house structure was also removed and carefully checked for bugs. This is usually a difficult task when the frame is made of bamboo material because the insects frequently hide in the hollow stalks, but in CBM-17 the process was simplified because the frame was made of lumber and small logs. When collection was finished, the rubbish was burned.

All insects were carefully collected with a pair of tweezers made of soft clock springs to avoid pressing or damaging them. The insects were stored in colour-coded jars identifying their origin according to the six following strata: bedroom walls or other (non-bedroom) walls, household articles, upper roof (the crest), lower roof (including the eaves) and the middle roof (the intermediate part).

Part of the field team remained on the site to finish the new house that had already been initiated to replace the one demolished. Another group drove the same evening to Caracas (approximately five hours). The jars were stored at room temperature (approximately 22°C) until the next morning, when a random sample from each stratum was taken for weighing. A relatively constant loss of weight with time is well known in *R. prolixus*, and therefore the operation of weighing the random sample was performed in a period of 48 hours, with a total of 38 hours of weighing activity, performed by four people working in shifts by pairs. A total of 1,415 insects of all instars, plus male and female adults, were weighed (17·8% of the actual population of the house).

To obtain an estimate of the feeding rates the results from house CBM-17 were used in combination with laboratory information; the latter, when obtained from the literature, has been cited accordingly but frequently, unpublished laboratory information of the first author (in preparation, to be published separately) was also used. The estimation procedure is based on a four step method, described in detail in the results section and summarized in Table VII using third instar as an example.

Results

Analysis of distribution of weights

Table I shows, by developmental stage and stratum, the number of *R. prolixus* found in house CBM-17. The total of 7,934 bugs sets a record of domiciliary density for *R. prolixus* and probably for any species vector of Chagas's disease: the highest domiciliary triatomine infestation previously recorded is 6,034 for *Triatoma infestans* in Brazil (DIAS & ZELEDÓN, 1955). It can be seen that although there are slight differences in age structure of *R. prolixus* for different strata, about 50% of the population was found in the bedroom walls.

Table II gives the mean weight of fed insects, by developmental stage and stratum. To obtain Table II the population of weighed insects was analysed in terms of its frequency distribution, which showed a clear bimodal shape. As suggested by BLISS (1967) the two subpopulations (in this case obviously corresponding to fed and unfed insects) were separated visually and then checked for normality by means of the Kolgomorov-Smirnov statistic; in all cases the distribution of fed insects proved to be normally distributed.

Table III shows the results of some statistical analyses performed on the weight distribution and mean weights. In addition to satisfying normality, the variances of the means of the weights (with the exception of third and fifth instars) passed Bartlett's test of homogeneity. With the exception of the

Table I—Number of insects collected after demolition of house CBM-17

	Stage							
Stratum	1	2	3	4	5	Adult	Total	%
Bedroom walls	469	651	1064	1115	519	127	3945	49·7
Roof—low	161	277	553	763	240	75	2069	26·1
Roof—middle	49	63	148	190	128	62	640	8·1
Roof—high	65	90	235	337	214	148	1089	13·7
Other walls	8	25	27	40	17	2	119	1·5
Household articles	3	6	14	27	18	4	72	0·9
Total	755	1112	2041	2472	1136	418	7934	100·0

Table II—Mean weight (mg), standard deviation, and sample size of fed insects in House CBM-17

Stratum	Stage 1	2	3	4	5	Females	Males
Bedroom walls	1·52	6·40	16·35	54·10	128·69	127·95	97·21
	0·41	1·15	4·19	8·80	46·81	22·82	16·64
	16	16	6	50	78	39	53
Roof—low	1·99	6·05	19·66	55·71	135·08	137·75	90·39
	0·56	1·23	5·72	11·35	44·45	29·69	12·96
	13	27	58	90	43	16	10
Roof—middle	1·53	6·27	17·95	53·26	136·44	121·60	86·62
	0·56	1·06	3·83	11·36	26·45	26·56	20·09
	7	16	45	71	42	19	30
Roof—high	—	6·05	19·03	56·98	138·46	119·95	73·59
	—	1·31	2·55	10·71	33·61	24·46	18·92
	—	16	17	18	25	22	35
Other walls	—	—	17·09	53·59	121·30	—	—
	—	—	3·44	8·80	47·66	—	—
	—	—	11	12	6	—	—
Household articles	—	—	—	58·56	142·33	—	—
	—	—	—	13·30	48·28	—	—
	—	—	—	12	9	—	—

Table III—Statistical analysis of the weights of insects from house CBM-17

1. Bartlett test of homogeneity of variances

Stage	Chi-square	DF	Strata†
1	1·4943	2	R-h, R-m, Br
2	0·7835	3	R-h, R-m, R-l, Br
3	16·4898*	4	R-h, R-m, R-l, Br, Ow
4	6·2398	5	all
5	17·4181*	5	all
Females	1·7030	3	R-h, R-m, R-l, Br
Males	3·0517	3	R-h, R-m, R-l, Br

* The hypothesis H_0 = equality of variances is rejected at the 5% level
† R-h = roof-high; R-m = roof-middle; R-l = roof-low; Br = bedroom walls; Ow = other walls

2. Student-Newman-Keul's test comparing mean weights between strata for each stage

Stage	Least square range	Tabulated 5% value	Differences between means
1	0·470	0·487	not significant
2	0·355	1·090	not significant
3	3·310	5·470	not significant
4	5·300	5·308	not significant
5	21·10	63·09	not significant
Females	17·80	21·69	not significant
Males (R-h, Br)	23·62	10·15	significant
Males (R-h, R-1)	16·80	15·21	significant
Males (R-m, R-h)	13·03	8·82	significant

males, the mean weights of fed insects showed no statistically significant differences between strata, therefore in the remainder of this article the weights from all strata were pooled.

With all strata pooled, the analysis of weight frequency distribution was repeated, and again the results for all instars and adults were shown to be normally distributed by the Kolmogorov-Smirnov

Table IV—Statistical analysis of the weights (milligrams) of *Rhodnius prolixus* collected in the field (House CBM-17) and weighed within 48 hours of collection, with all strata pooled

	Developmental Stage													
	1		2		3		4		5		Females		Males	
Statistic	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
Sample size	42	39	52	79	126	141	134	253	121	204	—	96	—	128
Minimum	0·19	0·64	0·30	3·31	0·25	8·39	6·70	23·90	13·10	53·45	—	87·99	—	66·02
Maximum	0·60	3·19	2·20	9·07	8·00	42·23	23·35	92·95	53·20	257·3	—	191·03	—	141·03
Mean	0·42	1·72	1·31	6·17	4·32	18·55	14·28	54·83	40·25	133·8	—	126·05	—	88·09
Median	0·44	1·70	1·32	6·13	4·29	18·58	13·64	55·17	41·00	137·4	—	128·96	—	87·19
Standard dev.	0·09	0·52	0·41	1·68	1·35	·4·71	3·03	10·83	8·21	41·9	—	25·70	—	16·64
Coef. Variation	21·33	30·46	31·51	18·94	31·29	25·39	21·24	19·75	20·42	31·3	—	17·84	—	17·11
Skewness	−0·37	0·34	−0·29	0·16	0·13	1·05	0·50	0·30	−0·85	−0·13	—	0·559	—	0·721
Kurtosis	−0·21	0·62	0·31	−0·25	0·82	4·15	0·18	1·09	1·27	−0·31	—	0·671	—	0·774
K-S Dmax*	0·07	0·09	0·07	0·07	0·07	0·09	0·10	0·06	0·06	0·07	—	0·115	—	0·109

* Kolmogorov-Smirnov statistic testing for a normal distribution

test; Table IV shows the latter's Dmax statistic, as well as the value of the skew and the kurtosis of the frequency distribution of weights. As an example, Fig. 1 shows the frequency distribution of field weights for third instars, with all strata pooled, in weight classes of 1 mg. Actually, after a first visual separation of the two subpopulations, a final "cutting point" was determined subtracting two standard deviations from the mean of the fed insects (for the third instar example: cutting point = 18·6 − [2 × 4·5] = 9·2). The adults were an exception; no bimodality was apparent, and all efforts to separate the original frequency distribution in fed and unfed insects failed.

After a similar procedure was applied to all developmental stages, the number of fed and unfed insects was estimated. Table V gives the percentage of fed insects by instar and by stratum.

Prediction of proportion of unfed population

It was expected that a certain proportion of immature individuals would be found unfed, particularly because there is a well known refractory period after moulting when insects do not feed. BUXTON (1930) gives times from moult to feeding and from feeding to next moult for all instars at 24 and 30°C. We converted these times to percentages of the total developmental time for each instar and averaged the figures for 24° and 30°C to obtain a value more representative of the average CBM-17 temperature of 27°C. These percentages were applied (Table VI) to total developmental times per instar as given by PIPPIN (1970), which were based on larger samples and obtained at daily fluctuating temperatures of 14 to 30°C; in this way new average times from moult to feeding and from feeding to new moult were estimated.

Under the assumption that during a short period of 15 to 30 days the proportion of individuals in each instar is relatively constant, Table VI shows the results of the calculation of the expected number of unfed individuals in the sample weighed. The assumption of a stable instar distribution allows us to compute the number of insects entering each developmental stage per day simply by dividing the number of weighed insects in each instar by the duration of that instar. The last two columns of Table VI show that although there are some discrepancies between predicted and observed values, the differences are relatively small (average of 19·9% error in absolute values); thus, our separation of the fed and unfed subpopulations can be considered acceptable.

Feeding rates and blood ingestion

The reliability of the estimates of biting frequency and amount of blood ingested, based exclusively on the distribution of weights of field-collected insects, is very limited. The reason is that an individual found in the field with a given weight could have arrived at such a value by two courses: (a) from a relatively old meal that was obtained to completion, or (b) from a relatively recent meal that was, due to many possible causes, interrupted before completion. However, because there is currently no method that can provide better estimates under domiciliary situations, the distribution of weights was used in

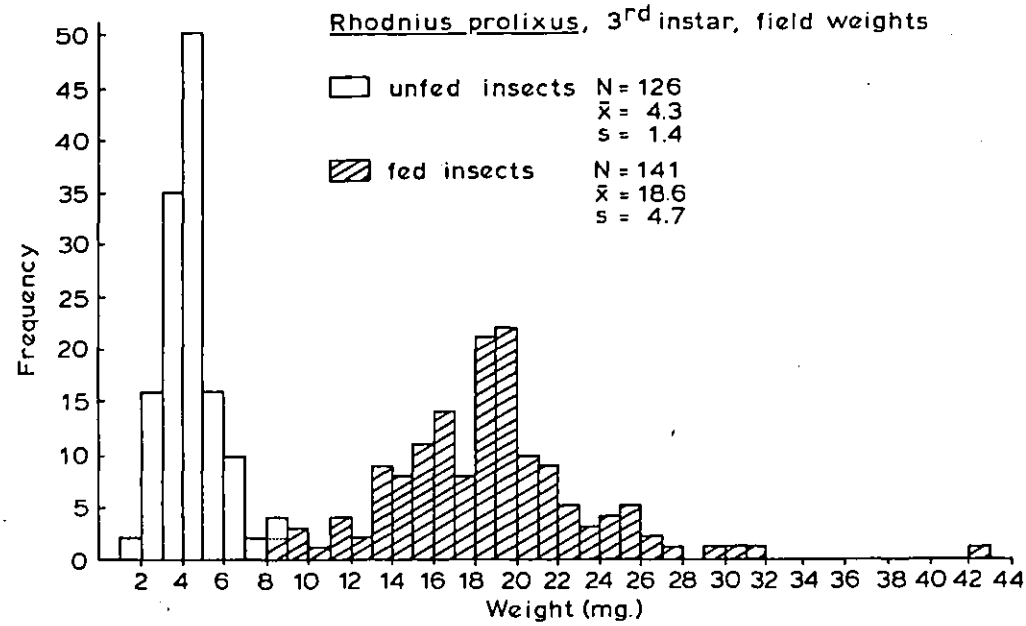

Fig. 1. Histogram of the frequency distribution of the weights of field collected 3rd instar *Rhodnius prolixus*. For the procedure for separating the fed and the unfed populations see text. $\bar{x}$ = mean, s = standard deviation. N = sample size.

Table V—Percentage of fed insects found in each stratum of House CBM-17

	Stage						
Stratum	1	2	3	4	5	Males	
Bedroom walls	53·3	53·3	20·0	100·0	78·0	100·0	100·0
Roof—low	48·2	58·7	63·0	63·8	61·4	100·0	100·0
Roof—middle	33·3	69·6	59·2	58·2	53·9	100·0	100·0
Roof—high	—	66·7	44·7	54·6	54·4	100·0	100·0
Other walls	—	—	47·8	50·0	31·6	—	—
Household articles	—	—	—	70·6	100·0	—	—

conjunction with the following *ad hoc* assumptions about similarities between domiciliary and laboratory insects:

1. the mean and variance of the blood meal is the same;
2. the average loss of weight with time is the same;
3. the average minimum amount of blood necessary to moult is the same;
4. the average developmental time is the same.

Of these assumptions the second is the most easily accepted, for the loss of weight (except for the initial diuresis) is essentially due to digestive activity; this activity is fundamentally determined by temperature, and the laboratory data obtained by the first author and used below corresponds to 27°C, which is very similar to the average temperature of the village of house CBM-17. Assumptions three and four depend basically, although not exclusively, on the validity of assumption one, the last-named being the most unwarranted of all. In the Appendix the effects of changing the laboratory value of the variance of the meal size were evaluated using a Montecarlo simulation.

Laboratory data obtained from daily weighing of individual insects of each stage after their blood meal were fitted to a hyperbolic function of the form $y = x/(a - bx)$ (x = time in days; y = weight loss in %), using a non-linear search computer algorithm. Fig. 2 gives, using the fifth instar as an example, the results of fitting the hyperbola to the laboratory data, expressed as percentage weight losses. The numerical values of the two coefficients of the hyperbolic law are given in Table VIII for all instars.

Table VI—Validation of the fitting by normal distribution procedure for separating fed and unfed insects, by predicting the expected number of unfed individuals among those weighed in House CBM-17

(1) Developmental Stage	(2)* Time from moult to feed as % of total time in the stage (at 24°C)	(3)* Same as (2) (at 30°C)	(4) Average between (2) and (3)	(5)** Total time in stage (days)	(6) (5 × 4) Time from moult to feed (days)	(7) Number of insects weighed	(8) (7/5) No. of insects entering stage per day	(9) (8 × 6) Number expected to be found unfed	(10) Number found unfed in CBM-17	(11) [(10-9)/10]100 Difference between expected and observed (%)
1	48·2	37·5	42·9	16·7	7·2	81	4·9	35	42	+16·7
2	28·0	42·9	35·5	20·7	7·2	131	6·5	47	52	+ 9·6
3	36·1	29·6	32·9	19·7	6·5	267	13·6	88	126	+30·2
4	46·4	31·0	38·7	21·8	8·4	387	17·8	149	134	−11·2
5	18·5	31·8	25·2	27·0	6·8	325	12·0	82	121	+32·2

* Calculated from BUXTON (1930); ** from PIPPIN (1970)

Fig. 2. Weight loss (percentage) as a function of time (days) after feeding for the 5th instar of *Rhodnius prolixus*. Each data point represents the mean of six insects. The line is the best fit to the hyperbolic law of weight loss.

Assigning an initial weight after feeding equal to the average weight obtained in the laboratory (assumption one), the application of the hyperbolic law of weight loss produces the new weights as a function of time. However, for all immature stages, many weight values of the CBM-17 insects would only be attained after 50, 60 and even 70 days (depending on the instar) after the meal if a complete meal had been ingested. But by these times all instars would have moulted to the following stage. Therefore, within the fed group, there must be a set of individuals that had taken a meal smaller than that necessary to moult.

Using PIPPIN's (1970) average developmental times as given in Table VI, and accepting assumption four, the application of the hyperbolic law of weight loss was truncated in order to account for moulting to the following instar (in the case of the third instar, for example, at day 20; see step one, Table VII). On the other hand, for all those individuals that would not achieve moulting, the hyperbolic law of weight loss was applied on an initial weight that was evaluated as the maximum possible not initiating the moulting process (Table IX). In this way the left tail of the weight distribution of the fed bugs was accounted for, and was attributed to individuals that would have to take an additional meal (at least) in order to moult.

Step two combines the results of step one with the field distribution of weights; from the operational point of view it consists of assigning the range of the time since feeding from the first column of step one, Table VII to each weight class; this is done separately for insects that will succeed in moulting without additional meals and for those that will not.

Step three reorganizes the information put together in step two, presenting the frequency of insects (moulting, non-moulting and both combined) that have ingested their meals a given

Table VII—Details of the 4 steps procedure to estimate the biting frequency and the amount of blood ingested, using instar 3 of *Rhodnius prolixus* as an example

STEP 1. Application of the hyperbolic law of weight loss; $y = x/(a - bx)$; $a = -\cdot405$, $b = \cdot442$. Initial weight for fully engorged insects = 46 mg; initial weight of insects with blood meal less than necessary to moult = 19 mg.

Days after feeding	Moulting insects weight (mg)	Non-moulting insects weight (mg)
1	33·7	13·9
2	32·3	13·4
3	31·3	12·9
4	30·4	12·5
5	29·5	12·2
6	28·7	11·9
7	28·0	11·6
8	27·3	11·3
9	26·6	11·0
10	25·9	10·7
11	25·3	10·4
12	24·7	10·2
13	24·0	9·9
14	23·5	9·7
15	22·9	9·5
16	22·4	9·2
17	21·8	9·0
18	21·3	8·8
19	20·8	8·6
20	20·3	8·4
21-43	—	5·0-8·4

STEP 2. Integration of weights obtained by Step 1, and the weights from CBM-17

Distribution of field weights in 5 mg classes		Range of age (in days) of blood meal ingested by insects that will	
Weight	Frequency	achieve moulting	not achieve moulting
5-10	5	—	13-43
10-15	24	—	1-12
15-20	70	—	0
20-25	30	11-20	—
25-30	9	5-11	—
30-35	2	1-4	—
35-40	1	0	—

STEP 3. Organization of the information obtained in Step 2, tabulating the results for insects achieving and not achieving moulting, as a function of the age of the blood meal ingested, using the pivote point of the age range.

Days from meal to demolition	Frequency of insects that		
	moult	don't moult	total
0	1	70	71
2·5	2	—	2
6·5	—	24	24
8·0	9	—	9
15·5	30	—	30
28·0	—	5	5
Mean	12·19	2·99	5·73
S.D.	4·00	6·43	7·17
N	42	99	141

STEP 4. Computation of biting frequency and amount of blood ingested in CBM-17

(a) On the average 3rd instars bite every 5·73 days; so, $(1/5\cdot7) \times 100 = 17\cdot54\%$ of the 3rd instar population bite per day

(b) Of the 17·54%, 29·79% (= 42/141) tak a blood meal "ad libitum" (41·6 mg), and 70·21% (=99/141) take a partial meal size (14·3 mg) that does not allow them to complete development to the following instar

(c) Total 3rd instar population of CBM−17 = 2041; percent fed = 52·8%; N° fed = 1078. Number feeding daily = 189 (= 1078 × 0·1754); blood ingested by full insects = $189 \times 0\cdot2979 \times 41\cdot6 = 2329\cdot6$ mg; not moulting insects = $189 \times 0\cdot7021 \times 14\cdot3 = 1901\cdot9$ mg.
Total blood ingested = 2329·6 + 1901·9 = 4231·5 mg.

Table VIII—Value of the coefficients a and b of the fit of the loss of weight laboratory data to the hyperbolic law $y = x/[a - bx]$; y = % weight loss; x = days

Developmental Stage	a	b
1	− 0·1677	0·3090
2	− 0·4706	0·5098
3	− 0·4046	0·4421
4	− 0·5246	0·5550
5	− 0·4995	0·5286
Females	− 0·2342	0·2775
Males	− 0·3568	0·4196

Table IX—Laboratory blood meal information used to calculate tables similar to Table VII for all instars and adults

Developmental Stage	After feeding average weight (mg) of those insects that fed *ad libitum* and achieved moulting	After feeding average weight (mg) of those insects with incomplete meals and not able to moult	Average full blood meal (mg)	Average meal failing to moult (mg)
1	4·0	2·14	3·56	1·70
2	16·6	5·96	15·3	4·65
3	45·9	18·60	41·6	14·3
4	126·0	47·8	111·7	33·5
5	262·2	172·6	221·9	132·3
Females	305·5	—	187·2	—
Males	167·6	—	100·2	—

Table X—Proportion of insects that achieve moulting with only one meal, estimates of biting frequency, and total amount of blood ingested by each developmental stage, for House CBM-17

Developmental stage	Proportion that moults with only one meal	Biting Frequency (bites/insect/day)	Biting Frequency (bites/day)	Amount of blood ingested (mg/day)
1	0·15	0·089	32·3	63·7
2	0·25	0·193	129·2	949·2
3	0·30	0·175	189·1	4,231·5
4	0·59	0·103	166·7	13,337·9
5	0·77	0·119	85·1	17,144·1
Females	—	0·096	19·0	3,463·2
Males	—	0·053	12·0	2,001·6
Totals			633·4	41,491·2

House CBM-17 had 11 people; thus the average per person is: biting = 57·6 bites/person/day; blood drained = 102 cm^3/person/month

Table XI—Estimate of the total actual amount of blood found in the guts of a *Rhodnius prolixus* population in House CBM-17

Stage	Average weight of unfed bug (mg)	Average weight of fed bug (mg)	Blood weight (mg)	Number of insects in the house	% N° of insects found fed	Total blood (mg)
1	0·43	1·72	1·29	755	48·2	469·4
2	1·31	6·17	4·86	1112	60·3	3,258·8
3	4·32	18·55	14·23	2041	52·8	15,334·9
4	14·28	54·83	40·55	2472	65·4	65,556·7
5	40·25	133·84	93·59	1136	62·8	66,767·9
Females	89·6	126·05	36·45	192*	100·0	6,998·4
Males	77·4	88·10	10·70	226	100·0	2,418·2
					Total =	169,804·3**

* In the total collection adults were not differentiated by sex; however the sex ratio of 46% females was applied to the total number of adults found (418), which was the proportion of females obtained from the collection when a random sample of adults was taken for weighing purposes.

** 160,804·3 mg = 152·5 cm^3

Assuming an average urine loss of 40%, the total amount of blood ingested by those bugs was

$$152{\cdot}5 + (152{\cdot}5 \times 0{\cdot}4) = 213{\cdot}5\ cm^3 \text{ of blood}$$

Table XII—Estimation of feeding rate and amount of blood drained by a *Rhodnius prolixus* population in 13 houses in Venezuela. The table was constructed assuming the percentage of population that bites per day and the average blood meal size as given in Table X

CBM House No.	No. of domestic animals	No. of people	Type of roof	Type of walls	Total bug population	Number of bites per person per day	cm^3 of blood drained/ person per month
2	14	8	P*	P	1629	15·1	33·7
3	0	10	P	M*	893	6·8	8·9
4	19	2	P	P	430	13·2	11·4
5	49	8	P	M	183	1·4	1·9
6	30	2	P	M	928	33·0	102·4
7	93	8	P	M	1868	16·9	39·7
9	42	11	P	M	310	2·2	5·4
10	35	9	P	M	604	5·1	14·6
12	21	5	P	M	407	6·3	13·2
13	35	8	P	P	1210	11·5	29·4
14	33	6	P	M	19	0·2	0·7
15	8	7	P	P	171	1·7	2·5
16	16	9	P	P	433	3·4	11·7

Statistics for all houses (2-16) :		Including House No. CBM-17
Number of bites/person/day:		
Mean =	8·98	12·5
S.D. =	9·10	15·7
Coeff. Var. =	101·3%	125·6%
cm^3 of blood drained per person/month:		
Mean =	21·19	26·9
S.D. =	27·38	34·0
Coeff. Var. =	129·2%	126·4%

* P = palm leaves; M = mud walls

number of days before the demolition (the range of time since feeding is here converted to the pivotal value). This step allows us the calculation of the mean number of days from meal to demolition, which in itself represents the average biting frequency.

We analysed separately the biting frequency of the insects that will achieve moulting and of those that will need additional meals to do so. In general we observed for all instars that the average number of days between bites is very similar to the times between feeding and the subsequent moult; for example, the third instar bites on the average every 12·2 days, and the time from feeding to moulting is 13·2 days (difference between columns 5 and 6, Table VI). On the other hand, insects that will need additional meals to moult feed on the average every three days; however, the standard deviation is very high, a reflection of the many zeros, that is to say, of insects that had taken a small meal the night before the demolition was carried out. From this analysis we were able to estimate the proportion of insects of each instar that will need additional meals to achieve moulting, as a function of developmental stage; the results (Table X) indicate that the more advanced *R. prolixus* is in its development, the more aggressive it is in securing its meal.

Step four computes the total amount of blood ingested per day using the estimates of average meal size that promotes or fails to promote moulting (Table IX), and the results of step three in terms of proportion of fed insects that will achieve moulting and those that need additional meals to moult. The arithmetic is straightforward, and the example given in Table VII for the third instar is self-explanatory.

Table X summarizes the estimates of biting frequency and blood ingested by the *R. prolixus* population of house CBM-17. The total amount of blood ingested was estimated to be 1·2 litres per month. In analysing these results one must remember that this was a heavily infested house (the extreme record to date). An indirect way of verifying the order of magnitude of this estimate of blood ingestion can be obtained by calculating the actual amount of blood found in all the insects collected (Table XI): 152 cm^3. As indicated at the bottom of Table XI, if we accept an average loss of urine excretion of 40% in the first 24 hours, those 152 cm^3 of blood represent over 200 cm^3 of blood ingested by the population collected in CBM-17. Thus, it is reasonable to accept 1·2 litres as an estimate of the amount of blood drained per month in that particular house.

Table XIII—Results from a series of 10 runs of a computer simulation programme using the Montecarlo technique, to check the effects of violating the assumption that variability in the blood meal size is the same in the laboratory and in the field. The exercise was applied to data of the 3rd instar

Change in standard deviation (%)	Insects that will moult with one meal		Insects that need more than one meal to moult		No. of days since last meal as a weighed average between the two groups of insects	Percentage (out of 141) that will moult with one meal
	standard deviation of meal size	Mean No. of days since last meal	standard deviation of meal size	Mean No. of days since last meal		
− 75	1·90	14·35	0·89	0·91	5·63	35·1
− 50	3·79	14·04	1·78	1·11	5·98	37·6
− 25	5·69	13·46	2·66	1·41	6·13	39·1
Laboratory	7·58	12·35	3·55	1·61	5·72	38·3
+ 25	9·48	11·77	4·44	2·14	5·88	38·8
+ 50	11·37	10·70	5·33	2·47	5·81	40·4
+ 75	13·25	9·42	6·21	2·99	6·21	43·8
Table VII	7·58	12·91	3·55	2·99	5·73	30·0

Application of CBM-17 estimates to other houses

As part of the field design of the biological control experiment carried out in the State of Cojedes, 13 other houses were demolished to obtain a complete census of their *R. prolixus* populations. Although the detailed results will be published elsewhere, it was of interest to extrapolate the biting rates estimated here to other houses with different *R. prolixus* densities. The results are shown in Table XII, with some construction characteristics, plus the total number of people, domestic animals and bugs. The calculation of the total amount of blood consumed followed a procedure identical to step four, as exemplified in Table VII.

The 13 houses of Table XII can be considered as representative of the region, particularly in terms of number of inhabitants and in size of the bug population. Thus, the average values at the bottom of Table XII can be considered as typical regional figures. On the average every person in a standard rural house will be bitten nine times per day; it should be pointed out that this average value has a coefficient of variation of over 100%, with biting rates that range from 0·2 per day (once every five days) to 33 bites per day.

Discussion

Although the actual variability in the blood meal size taken by *R. prolixus* under domiciliary conditions is not known, there are grounds to assume it should not be much larger than in the laboratory, despite intuitive belief to the contrary. Actually, GILLETT (1967) has shown that laboratory populations of mosquitoes are more variable and slower feeders than wild populations. In our case the variability in the weight of fed bugs within a field sample depends on the variability in the amount of blood ingested but it also depends on the variability within the sample in the length of time since feeding took place. If we assume that bugs are entering each instar, and others progressing to the next instar, at a fairly constant rate over a period of a few weeks (i.e., that the number of individuals within an age class is changing only very slowly), then we can also assume that individuals of different ages since feeding will be fairly evenly represented within the sample. This will tend to contribute significantly to the total variation in weight within the sample, and thus the amount of variability contributed by differences in amount of blood ingested must be significantly less than the figures shown in Table IV. That is, among the bugs that obtain enough blood to proceed in their development to the next stage there does not appear to be a large amount of variability in the size of the meal taken.

The biting rate of a *R. prolixus* population is an essential component in the determination of the probability of transmission of *T. cruzi*, the causal agent of Chagas's disease. The results of the analysis of weight distribution presented here can contribute to evaluations of the risk of transmission of *T. cruzi* in two ways. One way is direct: by the estimates of the feeding rate itself. The ability of *R. prolixus* to defaecate within a few minutes after feeding is well known (DIAS, 1956; PIPPIN, 1970; ZELEDÓN *et al.*, 1977), and thus the proportion of

the population biting every day contributes directly to the estimation of transmission risks.

On the other hand, the results obtained here on the increasing aggressiveness of successive instars in securing meals allows us to estimate a risk value for each developmental stage as a transmitter of *T. cruzi*. This aggressiveness value, coupled with the knowledge of behaviour and pattern of defaecation by instar provided by ZELEDÓN *et al.* (1977), and some information on the life-cycle of the parasite in the insect vector, should be sufficient to formulate a potential transmission index for each developmental stage of *R. prolixus*; this question has not been examined here but is an open door for future research.

There is no doubt that all the conclusions reported here rest fundamentally on the method of estimating field weights and the *ad hoc* explicit and implicit assumptions made. We will not repeat here the argument that we have acknowledged as the weakness of this method; rather, we prefer to suggest a different approach for obtaining similar information to test independently the conclusions presented here. *R. prolixus* is one of the better known insects from the physiological point of view, and the blood digestion processes have been no exception to this. Since the original paper by WIGGLESWORTH (1943) on the fate of the haemoglobin in *R. prolixus*, the literature on this subject has been prolific. [For a recent review of the digestive processes of haematophagous insects GOODING (1972) can be consulted.] As once suggested by GOODING (pers. comm.), if after the blood is ingested by a bug we look at two components: one relatively constant in time (not affected by digestion), and the other altered as a function of the time since the meal was obtained, then their *relative* proportions will be good indicators of the time elapsed since feeding. This is, of course, not a simple task; not only do the components have to be identified, and they have to comply with quite restrictive requirements of sensitivity and constancy, but the complexity of the situation resulting from several "mini-meals", as suggested by our own results, implies that there would probably be a very severe screening of the many candidate components in order to obtain the desired result.

Other factors that affect biting frequency should be investigated under field conditions. FRIEND & SMITH (1977) have made a recent review of the factors affecting feeding by bloodsucking insects in general, with a section dedicated to reduviids. From their review a clear conclusion emerges: most of the factors known to influence feeding by *R. prolixus* have been studied separately; to accept a minimum extrapolation for field conditions the effect of interacting factors should be analysed. For example, degree of abdominal stretch and length of time since previous feeding have both been well documented independently (ANWYL, 1972, and MADDRELL, 1963, for the former; and FRIEND & SMITH, 1975, for the latter). However, as FRIEND *et al.* (1965) have only partially shown, the interaction between both factors seems to be essential.

FRIEND & SMITH (1977) have reported that when free moisture comes in contact with any of the tarsi during feeding, the feeding pattern of *R. prolixus* is immediately broken off; this type of effect, complemented by the observations by WOOD (1953) of the destruction of metacyclic forms of *T. cruzi* by human perspiration, prove that much more has to be done to arrive at a reliable infectivity index of *T. cruzi* transmission by *R. prolixus*.

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Appendix

In order to evaluate the severity of the assumption that the variability of the blood meal size between house and laboratory insects was the same, a computer programme was designed to perform a Montecarlo simulation. This procedure is based upon drawing a random number with a given probability distribution, with which all calculations were made; it is repeated a certain number of times and statistics are computed. In our case the design of the simulation programme reproduced the calculations of Table VII, except that instead of using the actual laboratory mean value, a random value for the blood ingested was drawn from a normal distribution laboratory mean value. The number of draws was 141, to compare the outcome with the third instar's results of Table VII.

For both minimum meal size that promotes moulting and "ad libitum" meal, the laboratory standard deviations were increased and reduced by 25, 50 and 75%. Ten different random series of 141 draws proved to produce a coefficient of variation of approximately 10% for the proportion of insects that need more than one meal to moult, so that more random series of draws were not justified.

Table XIII shows that as the standard deviation of the blood meal size increases, the method described in Table VII produces a smaller estimate of the number of days since the last meal for insects that achieve moulting with one meal, but a larger estimate for those that need additional meals to achieve moulting. However, the total average number of days since the last meal remains relatively constant, showing the compensation of the change in opposite direction of the two groups of insects. In most cases the values differ only in about 10% from the ones calculated in Table VII, which assumes a constant average meal size.

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EXPERIMENTAL PARASITISM OF TRIATOMINAE EGGS (HEMIPTERA: REDUVIIDAE) BY THE MICROHYMENOPTERA *OOENCYRTUS TRINIDADENSIS VENATORIUS* (CHALCIDOIDEA: ENCYRTIDAE) AND *TELENOMUS COSTALIMAI* (PROCTOTRUPOIDEA: SCELIONIDAE)

By M. Dora Feliciangeli[1]

Abstract: *Ooencyrtus trinidadensis venatorius* and *Telenomus costalimai* are natural endophagous parasitoids of *Rhodnius prolixus* eggs in Venezuela. The experimental parasitism by these microhymenoptera was studied in 8 other species of triatomines. *O. t. venatorius* parasitized all species offered, while *Te. costalimai* parasitized only *Rhodnius* spp. Moreover, if the natural host *R. prolixus)* was not available, both parasites were capable of using some alternate host for their reproduction. In *O. t. venatorius,* a positive correlation was observed between the weight of the host egg and average number of emerged progeny; *Te. costalimai* was found to be a solitary parasitoid regardless of host egg weight. It was concluded that *R. prolixus* is the best host species for mass rearing the 2 parasites in the laboratory.

Four species of parasitoid microhymenoptera which feed on eggs of triatomine vectors of Chagas' disease are presently known in the Western Hemisphere.

Telenomus fariai was first found in Brazil in a laboratory colony of *Triatoma megista (=Panstrongylus megistus)* (Costa Lima 1927). Later, it was repeatedly collected in nature in various Latin American countries; in Argentina as an egg parasite of *Triatoma infestans* (Mazza & Jörg 1938), in Bolivia on eggs of *Triatoma sordida* (Mazza 1942), in southern Brazil also on eggs of *Tr. infestans* (Pinto 1942), in Mexico and San Salvador on eggs of *Triatoma phyllosoma pallidipennis* (Peláez 1944, Zeledón 1957), in Perú on eggs of *Panstrongylus herreri* (Lumbreras et al. 1955), and in Costa Rica on eggs of *Triatoma dimidiata* (Zeledón et al. 1970).

In 1950 Pellegrino studied the capacity of this wasp to parasitize other species of triatomines and experimentally obtained its development on eggs of *Triatoma maculata, Triatoma vitticeps* and *Triatoma rubrovaria.* Working out the biology of this microhymenopteron in the laboratory, Zeledón (1957) added *Panstrongylus chinai* to the list of hosts subject to parasitism by *Te. fariai.*

Like Costa Lima (1928) and Pellegrino (1950), Zeledón (1957) found that the average number of wasps emerging per parasitized egg increased with increase in size and volume of the host egg.

Telenomus costalimai was described from Venezuela where it had been found in jars in which *Rhodnius prolixus* was being reared (Ortiz & Alvarez 1959); later it was encountered in eggs of the same host in nature (Feliciangeli 1973, De Santis et al. 1975-1976).

Ooencyrtus trinidadensis, described from Trinidad (Crawford 1913), has been found in Venezuela as a natural parasitoid of eggs of *R. prolixus* (Feliciangeli 1973); the Venezuelan population was designated as *O. trinidadensis venatorius* by De Santis et al. (1975-1976).

More recently in Venezuela, another *Telenomus* sp. as yet unidentified has been observed in nature as an egg parasite of *Psammolestes arthuri.* It has been experimentally induced to parasitize eggs of *R. prolixus,* on which it is now being maintained in our laboratory (Feliciangeli et al. 1978).

Authors of all the papers mentioned above suggested the possibility of using these microhymenoptera in the biological control of the vectors of Chagas' disease, and many studies have been recently carried out with *Te. fariai* (Rabinovich 1970a, b, c, 1971a, b, c, Bosque 1972, Escalante

[1]Cátedra de Parasitología, Escuela de Medicina, Facultad de Ciencias de la Salud, Universidad de Carabobo, Valencia, Venezuela.

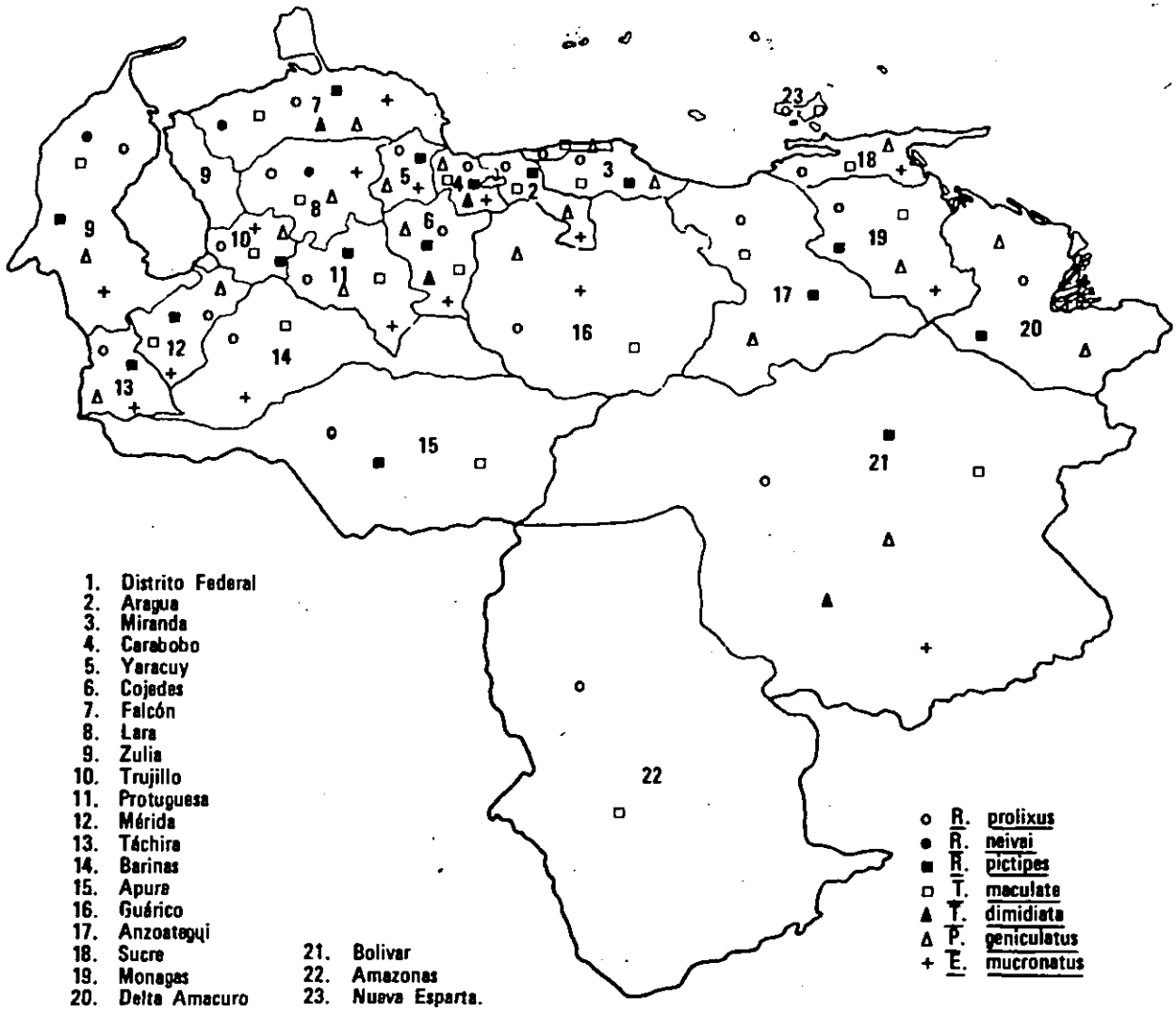

FIG. 1. Geographical occurrence by state of 7 triatomine species in Venezuela (adapted from Otero et al. 1975).

1975). The life cycles and various aspects of host-parasite relationships of *Te. costalimai* and *O. t. venatorius* have been studied (Feliciangeli 1976, Feliciangeli & Rabinovich 1977) to investigate the possibility of using these parasites in the control of *R. prolixus*. This triatomine, which is widely distributed in Venezuela in both domestic and wild habitats (FIG. 1), is the principal vector of Chagas' disease in Venezuela.

The aims of the present work were the following: (1) to investigate the capacity of *Te. costalimai* and *O. t venatorius* to parasitize other species of triatomines, i.e., their potential for exploiting alternate hosts; (2) to investigate whether the number of progeny of these microhymenoptera is dependent on the amount of food available; and (3) to select, from among the species parasitized, those more suitable for mass rearing of these wasps in the laboratory.

MATERIALS AND METHODS

Laboratory colonies of *O. t. venatorius* and *Te. costalimai* were started with specimens collected in Higuerotal, Aragua State, Venezuela, in 1972. These parasites were maintained in a climatic chamber at 28° ± 2°C and 40-50% RH. *R. prolixus* eggs were added approximately every 15 days; no additional food or water was required for their growth.

In addition to *R. prolixus*, the natural host, the following triatomine species were used: *Rhodnius neivai, Rhodnius pictipes, Tr. maculata, Tr. dimidiata, Tr. phyllosoma pallidipennis, Panstrongylus geniculatus* and *Eratyrus mucronatus*, all indigenous to Venezuela except *Tr. phyllosoma*

TABLE 1. Experimental parasitism of Triatominae eggs by 2 microhymenoptera: *Ooencyrtus t. venatorius* and *Telenomus costalimai.**

Triatominae species	Avg. no. of eggs parasitized per ♀		% parasitized eggs without progeny	
	O. t. venatorius	*Te. costalimai*	*O. t. venatorius*	*Te. costalimai*
R. prolixus	4.3 ± 1.6 (50)	15.2 ± 3.7 (29)**	5.5	5.4
R. pictipes	5.1 ± 1.7 (49)	10.8 ± 4.8 (45)	18.2	39.3
R. neivai	3.7 ± 1.9 (38)	6.2 ± 5.1 (24)	14.9	48.3
Tr. maculata	1.6 ± 2 (30)	0 (30)	12.5	—
Tr. dimidiata	0.7 ± 1 (30)	0 (35)	5.3	—
Tr. phyllosoma pallidipennis	0.4 ± 0.7 (20)	0 (27)	0	—
E. mucronatus	0.2 ± 0.5 (16)	— —	33.3	—
P. geniculatus	0.2 ± 0.6 (25)	0 (27)	25	—

*One vial with 1 *O. t. venatorius* and 10 triatomine eggs or 1 *Te. costalimai* and 20 eggs, in each test.
**No. of tests in parentheses.

pallidipennis, which was obtained from Mexico. Colonies of the triatomines have been maintained in the Department of Parasitology, University of Carabobo, for several years followng the standard rearing methods used by Gómez-Núñez (1964) for *R. prolixus*.

Previously it had been observed that *Te. costalimai* has a greater parasitic capacity than *O. t. venatorius* (Feliciangeli 1976). Therefore, each female of the former species was placed with 20 host eggs, and each female of the latter was placed with 10 host eggs in separate vials (1.5 × 5 cm) for 24 h. Eggs provided the wasps ranged in age from 1 day postoviposition to 1 day prehatch. After 24 h, the adult wasps were killed and the host eggs were kept in the climatic chamber until emergence of the parasitic progeny.

The following observations were made. (1) number of parasitized eggs; (2) number of emerged wasps and their sex ratio; (3) number of eggs which did not produce progeny in spite of showing clear signs of parastitism (black in color).

The above tests were repeated several times for the various species of triatomines (see TABLE 1).

To investigate the possible relationship between the emergent parasites and weight of the host egg, 15 eggs of all ages were weighed individually for each triatomine species, and the average weights recorded. To compare the average number of parasite progeny emerged from each host species with the average weight of the corresponding host egg, the correlation coefficient and the regression line equation were calculated.

RESULTS

TABLE 1 shows that *O. t venatorius* was able to parasitize eggs of all the species of triatomines tested, while *Te. costalimai* parasitized only eggs of *Rhodnius* spp.

Parasitism by *O. t. venatorius* was higher in the species of the genus *Rhodnius* than in those of the genus *Triatoma*, being minimal in *Eratyrus* and *Panstrongylus*. Within the genus *Rhodnius*, *R. pictipes* eggs were parasitized in greater numbers than those of *R. prolixus* and *R. neivai*, the differences being significant at 95% and 99% confidence limits, respectively, using the *t*-test (TABLE 2). However, *R. pictipes* is apparently less suitable for the embryonic development of the parasite, as the percentage of the parasitized eggs that failed to produce progeny was higher for this species than for the other 2 (TABLE 1).

In the case of *Te. costalimai*, the number of parasitized eggs per female wasp was higher for *R. prolixus* than for *R. pictipes* and lowest for *R. neivai* (TABLE 1) (all differences significant at $P<0.01$). The mortality rate of parasitized eggs in *R. neivai* and in *R. pictipes* was very high when compared with that

TABLE 2. Statistical significance between average numbers of parasitized eggs from various triatomine species by *Ooencyrtus t. venatorius* and *Telenomus costalimai*.

Triatomine species	*O. t. venatorius*		*Te. costalimai*	
	t	*P*	*t*	*P*
R. prolixus, R. pictipes	2.14	<0.05	7.46	<0.01
R. prolixus, R. neivai	1.65	>0.05	2.24	<0.01
R. pictipes, R. neivai	3.45	<0.01	3.69	<0.01
Tr. maculata, Tr. dimidiata	2.33	<0.05	—	—
Tr. maculata, Tr. phyllosoma pallidipennis	2.61	<0.05	—	—
Tr. dimidiata, Tr. phyllosoma pallidipennis	1.07	<0.05	—	—

of *R. prolixus* (TABLE 1).

The number of progeny of *O. t. venatorius* was proportional to the weight of the host egg (FIG. 2). In the case of *Te. costalimai,* only 1 individual emerged from each egg.

The progeny per female wasp and the number of daughters per mother seem to show a species-specific relationship between host and parasitoid. Among wasps emerged, 75–85% were females for all the species of triatomine eggs, except for *E. mucronatus* eggs, which produced a few wasps with a 1:1 sex ratio.

Te. costalimai is parthenogenetic and its progeny was composed of females only, whose numbers were directly proportional to the numbers of parasitized eggs and inversely proportional to the numbers of eggs not hatching (TABLE 1, 3).

DISCUSSION

In temperate climates, developmental synchrony between parasite and host is very important for effective biological control. In tropical climates, populations generally reproduce continuously and generations overlap. One important factor under these conditions is related to spatial proximity between parasite and host rather than to timing of development. The lack of a very narrow specificity is an added advantage, since it may permit survival of the parasite on nearby populations of alternate hosts. Strain differences in host preferences have been noticed among insect parasitoids (Messenger & van den Bosch 1971). The tachinid parasite *Paratheresia claripalpis,* for instance, commonly attacks both *Diatrea saccharalis* and *Zeadiatrea lineolata* (Lepidoptera: Pyralidoidea) in Venezuela, while the

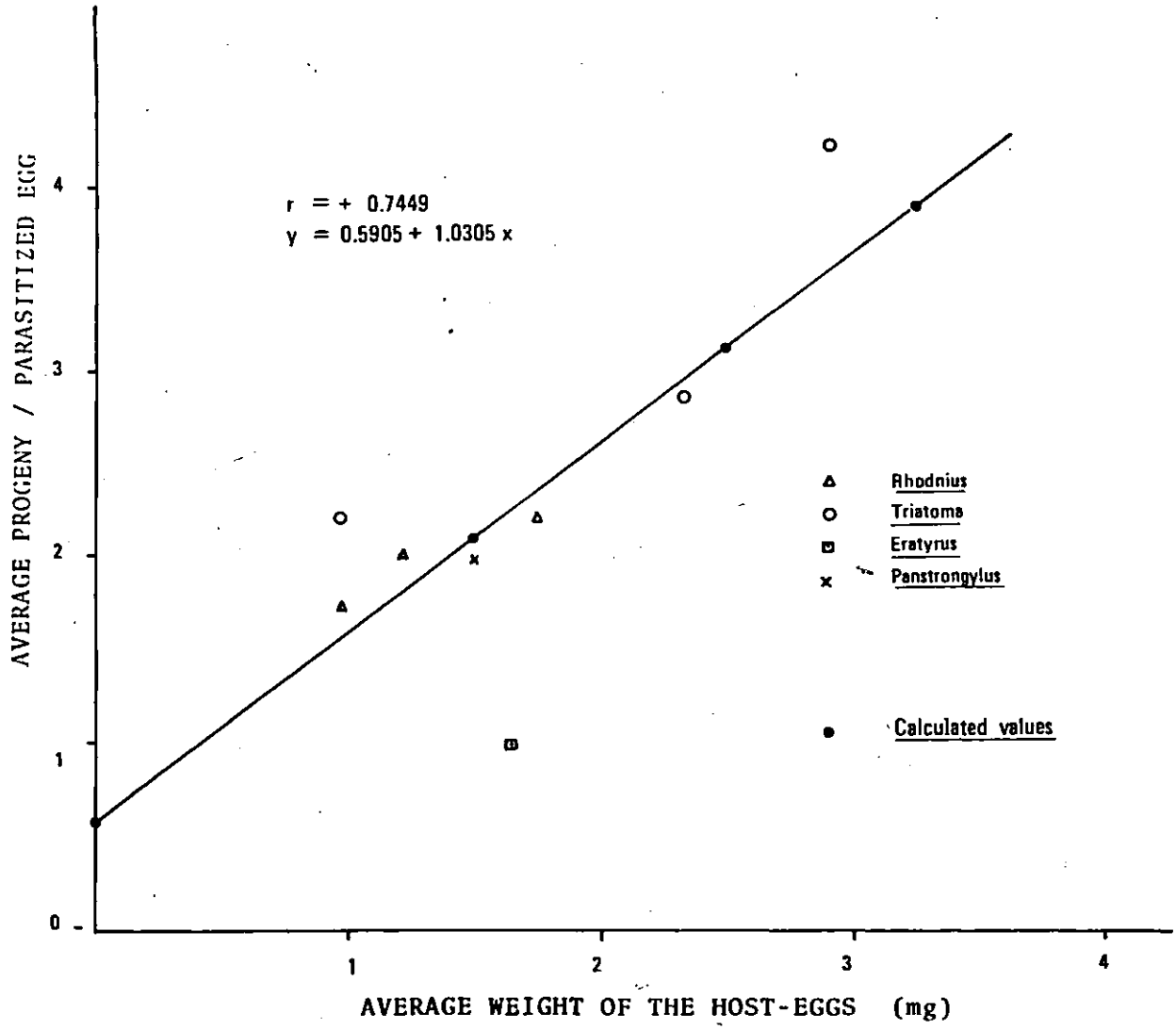

FIG. 2. *Ooencyrtus t. venatorius:* correlation between average weight of parasitized eggs and the average progeny per parasitized egg.

TABLE 3. Some reproductive characteristics of *Ooencyrtus t. venatorius* and *Telenomus costalimai* in various species of triatomines.

Triatomine species	Avg. weight of host egg (mg)	Avg. wasps emerged/ fertile parasitized egg		Progeny/♀	No. of ♀♀/♀	
		O. t. venatorius	*Te. costalimai*	*O. t. venatorius*	*O. t. venatorius*	*Te. costalimai*
R. prolixus	1.8	2.2	1.0	9.2	7.1	14.4
R. neivai	1.2	2.1	1.0	6.5	5.1	6.6
R. pictipes	1.0	1.8	1.0	7.3	5.7	3.1
Tr. maculata	0.9	2.2	0	3.4	2.8	—
Tr. dimidiata	2.3	2.9	0	2.4	2.8	—
Tr. phyllosoma pallidipennis	2.9	4.3	0	1.7	1.5	—
E. mucronatus	1.7	1.0	0	0.1	0.1	—
P. geniculatus	1.5	2.0	0	0.2	0.2	—

latter species is only sporadically parasitized by the fly in Trinidad. Messenger & van den Bosch (1971) suggested that preferences for specific host(s) could be the product of racial differences at the level of parasites or hosts.

Our experiments showed that *O. t venatorius* is capable of parasitizing triatomine eggs of all species in the 4 genera studied; *Te. costalimai* developed only in species of the genus *Rhodnius*. Therefore, *O. t. venatorius* may make use of a much larger range of alternate hosts in Venezuela, where, for instance, the distribution of *Tr. maculata* practically overlaps that of *R. prolixus* (FIG. 1). On the other hand, *Te. costalimai* could parasitize other species such as *R. neivai* and *R. pictipes*, both also present in the country, the latter with a distribution that covers 16 of the 23 states (Otero et al. 1975).

The presence of such alternate hosts, particularly *R. pictipes*, which can be parasitized by both microhymenoptera, could be of special advantage during the initial pressure of biological control when the population of *R. prolixus* might be reduced drastically. *Tr. maculata* lives near human habitations, generally in the nests of hens and pigeons and occasionally enters houses. Moreover, it is distributed over a large area and has a high intrinsic rate of natural increase; consequently *Tr. maculata* is the 2nd most important vector of Chagas' disease in Venezuela (Gamboa 1974, Feliciangeli 1974). *Tr. maculata* could, thus, be an excellent alternate host for *O. t. venatorius*, which, in this situation, would serve as a better agent of biological control than *Te. costalimai*.

Another consideration was the possibility of selecting 1 triatomine species which could be used for mass rearing of the microhymenoptera in the laboratory. Although a positive correlation was found between the weight of the parasitized host egg and the number of progeny of *O. t. venatorius*, it is not possible to exploit this phenomenon in rearing, because the only species which has some advantage is *Tr. phyllosoma pallidipennis*, as it is easily reared in the laboratory and each parasitized egg produces on the average 4 specimens of *O. t. venatorius*. However, since the proportion of eggs parasitized is too low, this species is inadequate to ensure a mass production of the microhymenopteron within a short time. On the other hand, *R. pictipes* eggs are parasitized more often than those of *R. prolixus*, but the latter produces a better wasp yield due to a much lower mortality among the immature stages.

For the above reasons, *R. prolixus* is recommended for establishing mass production of both *O. t. venatorius* and *Te. costalimai*.

With respect to the relationship between hosts and parasitoids, the high wasp mortality recorded in some of the host eggs was probably due to lower adaptation of the parasites to the alternate hosts. Likewise, the variations in correlation between weight of the host egg and the numbers of the progeny produced indicate that physiological specificity may be more important than a quantitative relationship with available food and space.

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A MICROHYMENOPTERAN PARASITE OF EGGS OF *PSAMMOLESTES ARTHURI* (HEMIPTERA: REDUVIIDAE) AND OBSERVATIONS OF EXPERIMENTAL PARASITISM OF EGGS OF *RHODNIUS PROLIXUS* (HEMIPTERA: REDUVIIDAE)

Psammolestes arthuri (Pinto, 1926) is a Triatominae that has only been found in the nests of *Phacellodomus rufifrons inornatus* (Furnariidae). This association with birds explains why it is of little importance in the sylvatic cycle of *Trypanosoma cruzi*, the etiological agent of Chagas' disease (Guerrero, Garcia Martin & Quesada, 1965, Kasmera **2:** 47–97; Carcavallo, Ortega, Ortega & Tonn, 1976, WHO/VBC/17.519). Its geographical distribution is limited to Venezuela (Lent & Jurberg, 1965, Rev. Bras. Biol. **25:** 349–76).

This report is about a microhymenopteran which was found parasitizing eggs of *P. arthuri*. Its potential importance as a parasite of eggs of *Rhodnius prolixus*, the principal vector of Chagas' disease in Venezuela, is demonstrated. This is the 3rd microhymenopteran known in Venezuela to parasitize *R. prolixus* eggs. The other species, *Telenomus costalimai* and *Coencyrtus trinadensis venatorius*, are natural parasites of *R. prolixus* (Feliciangeli, 1973, Rev. Inst. Med. Trop. São Paulo **15:** 235–38).

We collected various nymphal instars and eggs of *P. arthuri* from a nest of *P. rufifrons* from La Encantada, Municipality of Guigue, State of Carabobo. Some of the eggs produced a number of microhymenopterans which belong to the genus *Telenomus* (Scelionidae). Morphologically, these wasps were different from other species collected in Venezuela. They were sexually dimorphic,

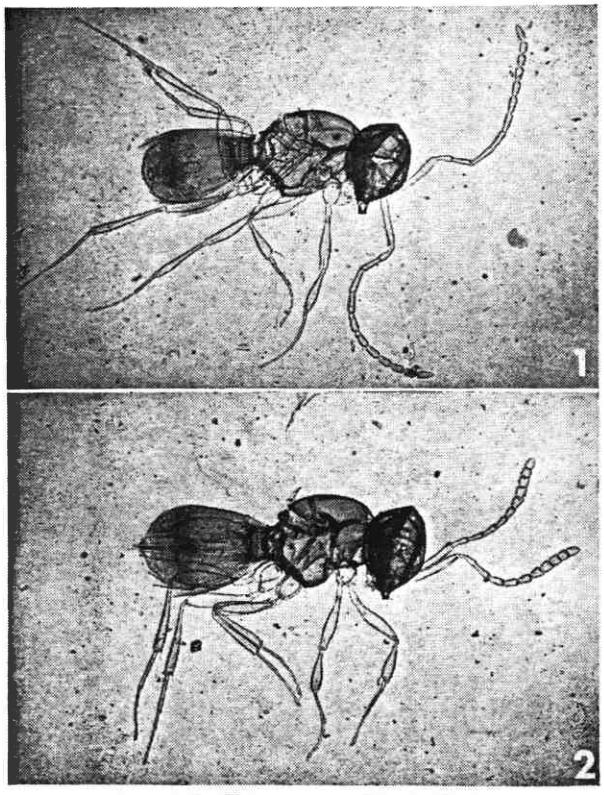

FIG. 1–2. *Telenomus* sp. (1) ♂, (2) ♀.

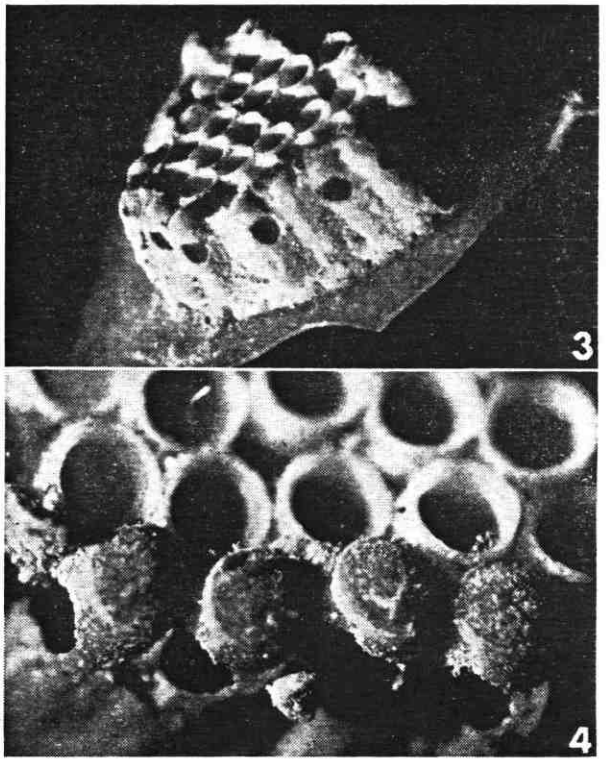

FIG. 3–4. Photograph of eggs of *P. arthuri* parasitized by *Telenomus* sp.

the male having longer antennae than the female with more segments (13 segments in the male, 12 in the female: see FIG. 1, 2).

We sent specimens to Dr L. de Santis of the National University of Plata in Argentina. He confirmed the genus identification and indicated that the species was probably new to the Neotropics. Further study will be done by him (pers. commun.).

The method of parasitism by this wasp is similar to that of other microhymenopterans. The adult female oviposits inside the Triatominae eggs. The resulting larva feeds within the egg, pupates and becomes an adult. The adult wasp cuts an opening with its mandibulae and emerges. The opening is generally in a lateral position and was never observed to be at the operculum.

In nature the eggs of *P. arthuri* are deposited in groups of 3 to 15 and adhere perpendicularly to leaves, sticks, and other materials which make up the nest. Of the eggs we observed, those which were parasitized were located in the most external position in the cluster, while eggs in the center were not parasitized (FIG. 3, 4). This phenomenon might be due to the abundance of the cementing material which the female bug produces after oviposition, which is thicker in the center of the egg batch. Only a single wasp was produced per parasitized egg.

In the laboratory we attempted to rear the microhymenopteran on eggs of *R. prolixus*. The wasp parasitized the eggs and the progeny emerged without difficulty.

We separated 2 groups of wasps. One group contained only virgin females, while the other group contained females and males. Subsequently, each female was placed singly into a vial containing 20 eggs, 0 to 40 hr old, of *R. prolixus*. The 1st group produced only haploid males and the 2nd group produced haploid males and diploid females. Thus, this species appears to be facultatively arrhenotokous.

The eggs of *R. prolixus* were exposed to the wasp for only 24 hr. It was thus possible to pinpoint the date they were parasitized. We determined the incubation period of the microhymenopteran to be 21.7 days $\pm$ 1 day (n=65). The average life span for the adults of both sexes was 5 days, with a maximum of 9 days for males and 7 days for females. The above information was obtained at a temperature of 28° $\pm$ 1 °C and RH of between 50% and 60%.

Rhodnius prolixus and *P. arthuri* occasionally share the same habitat, and both species have a similar geographical distribution. However, the microhymenopteran reported on here has not been found in nature parasitizing the eggs of *R. prolixus*. The ability of this *Telenomus* species to parasitize *R. prolixus* eggs in the laboratory makes it a possible candidate for biological control against *R. prolixus*.—**Maria D. Feliciangeli** and **Elio Fernandez,** Facultad de Parasitologia, Universidad de Carabobo, Valencia, Venezuela, and **R. J. Tonn,** World Health Organization, Chagas' Disease Vector Research Unit, Maracay, Venezuela.

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Comportamiento del microhimenóptero *Telenomus costalimai*

DORA FELICIANGELI de PIÑERO

Telenomus costalimai es un microhimenóptero parasitoide endófago de huevos de *Rhodnius prolixus*. Fue encontrado por primera vez en 1959, por Ortiz & Alvarez (8) en frascos de cría de *R. prolixus* en laboratorio, y reecontrado por Feliciangeli (1), 14 años después, en condiciones naturales en el municipio Higuerotal, estado Aragua.

En estudios anteriores se ha hecho énfasis en la posibilidad de emplear este parasitoide como un agente de control biológico para el principal vector de la enfermedad de Chagas en el país (Feliciangeli, [2]) y se han estudiado algunos aspectos de la biología, como el ciclo de vida, el efecto de la densidad y de la edad del huésped (Feliciangeli, [3]) y la capacidad de parasitismo (Feliciangeli, [4]).

El presente trabajo estudia un aspecto interesante de la relación parásito-huésped en función de condiciones paculiares en las cuales el microhimenóptero puede encontrar el huevo del triatomino.

Dra. Feliciangeli de Piñero, Profesor Agregado de la Cátedra de Parasitología de la Facultad de Ciencias de la Salud. Universidad de Carabobo, Valencia, Venezuela.

MATERIALES Y METODOS

Se utilizaron *R. prolixus* procedentes de una cría mantenida en el insectario de la Cátedra de Parasitología de la Universidad de Carabobo en condiciones ambientales y a un ritmo quincenal de alimentación sobre gallinas. Las hembras de *R. prolixus* generalmente adhieren sus huevos al substrato mediante una substancia cementante. En los frascos de cría, son colocados papeles doblados verticalmente para permitir la oviposición, aumentar la superficie disponible y facilitar a los insectos la llegada a la fuente alimenticia (Gómez Nuñez, [7]). De esta manera, la mayoría de los huevos puestos son obtenidos sobre los papeles; sin embargo, normalmente una pequeña cantidad se encuentra libre en el fondo de los frascos.

La cría de avispas *(T. costalimai)* es rutinariamente mantenida en estufa a 28 ± °C y 50-60% HR, mediante el suministro constante (aproximadamente cada 18-20 días, que corresponde al tiempo de desarrollo huevo-adulto para el microhimenóptero) de los huevos de *R. prolixus* adheridos a los papeles de

los frascos de cría, los cuales son recortados y puestos verticalmente en frascos de 250 ml aproximadamente, en proporción de 1.000 huevos por 100 avispas. Esta proporción garantiza la obtención de parasitismo en 100% de los huevos huéspedes.

En una oportunidad en la cual no se tenían a disposición huevos de *R. prolixus* adheridos y fue necesario utilizar los huevos sueltos en el fondo del frasco de cría, llamó la atención que el parasitismo efectuado por *T. costalimai* fue mucho menor del esperado. A raíz de esta observación se planificó un experimento con el objeto de comparar l capacidad de parasitismo de *T. costalimai* en las dos situaciones.

Hembras de *T. costalimai* de 24-48 horas de edad fueron puestas individualmente en tubos de vidrio (1.5 x 5.0 cm) y abastecidas con 20 huevos (24-48 horas) de *R. prolixus*, diariamente, hasta la muerte. Esos huevos eran expuestos a la avispa durante 24 horas, al cabo de las cuales eran sustituidos por huevos nuevos, retirados y pasados a otros tubos de vidrio rotulados con la fecha correspondiente, para almacenarlos hasta el momento de la emergencia de la progenie.

En un primer grupo (A) de 26 avispas, los huevos fueron ofrecido adheridos a los papeles, y en otro grupo (B) de 30 avispas, fueron ofrecidos libres.

RESULTADOS

Los Cuadros Nº 1 y Nº 2 muestran los resultados del parasitismo efectuado por *T. costalimai* en huevos de *R. prolixus*.

Se observa que el comportamiento de la avispa es bastante uniforme en el grupo A (Cuadro Nº 1) y que se altera completamente frente a la situación, no habitual, de encontrar huevos de *R. prolixus* que no están adheridos al substrato. Solamente 4 avispas del grupo B siguieron el modelo de parasitismo que se observa regularmente en todas las avispas del primer grupo y que se caracteriza por una acción muy eficaz durante el primer día de adulto (10 huevos parasitados), la cual disminuye bruscamente al segundo día. Por otro lado, 2 avispas del grupo B no lograron parasitar ningún huevo durante su vida y una de ellas parasitó uno solamente.

CUADRO Nº 1

***Telenomus costalimai*, Grupo (A): Parasitismo en huevos de *Rhodnius prolixus* adheridos a papel.**
(Número de huevos parasitados por día por avispa)

Día	Avispa Nº																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	14	15	15	14	12	16	15	14	15	15	13	13	17	10	13	15	14	14	14	10	12	14	13	13	12	17.
2	5	3	3	6	3	5	4	3	3	3	5	4	3	6	3	4	4	4	5	6	3	5	3	4	4	6
3	3	3	3	1	2	5	2	2	4	2	1	3	4	5	4	2	4	6	4	1	6	4	6	1	6	4
4	1	6	3	5	4	2	7	7	3	5	4	4	3	5	5	3	5	5	6	4	6	5	3	3	4	3
5	7	4	6	4	7	6	5	4	6	4	5	8	7	4	5	5	6	3	4	2	3	4	2	0	0	6
6	3	3	0	0	0	4	2	2	5	5	0	3	0	2	1	1	5	4	0	5	4	5	–	0	–	0
7	0	3	–	0	–	1	0	2	5	0	0	2	–	1	–	1	1	–	–	0	0	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

CUADRO Nº 2

Telenomus costalimai. Grupo (B); Parasitismo en huevos de *Rhodnius prolixus* libres.
(Número de huevos parasitados por día por avispa).

Día	Avispa Nº																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	5	0	6	4	0	7	1	5	1	1	4	12	1	8	2	6	4	6	13	16	5	4	5	1	5	6	10	0	1	4
2	0	0	4	8	0	3	7	1	0	7	1	8	2	10	10	8	5	0	3	3	4	1	3	0	0	3	7	1	2	0
3	1	0	0	0	0	1	5	1	1	4	1	4	3	3	1	4	1	4	4	5	0	0	0	0	0	0	2	0	6	2
4	1	0	1	1	0	1	7	2	0	8	0	6	0	3	1	7	0	0	3	1	0	0	0	0	0	0	6	2	4	–
5	0	0	0	–	–	0	0	0	0	0	–	5	0	1	0	0	–	–	–	0	–	–	–	0	0	–	0	0	–	–
6	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–
7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

El número total de huevos parasitados por el grupo A fue 839, de los cuales 356 fueron parasitados durante el primer día, mientras el número total de huevos parasitados por el grupo B alcanzó solamente 358. Los promedios de huevos parasitados por avispa dieron respectivamente 32.73 ± 4.64 y 11.93 ± 8.97. Aplicando la prueba "t" de Student, pudimos comprobar que la diferencia observada era estadísticamente altamente significativa ($t = 10.64$; g.l. = 54; $P<0.01$).

En los mismos cuadros puede observarse también la longevidad de las avispas cuyos promedios resultaron ser respectivamente de 7.00 (± 0.65) días para las hembras a las cuales se ofrecieron huevos adheridos y de 5.13 días (± 0.67) para las expuestas a huevos libres ($t = 10.57$; $P<0.01$).

CONCLUSIONES

El experimento llevado a cabo permitió resaltar un aspecto de la relación huésped-parásito que se establece entre el huevo de *R. prolixus* (huésped) y el microhimenóptero *T. costalimai* (su parásito natural). Se evidencia la dificultad con que el parasitismo se realiza en el caso en que el huevo-huésped no se encuentre adherido al substrato, condición ésta menos frecuente en la naturaleza. En efecto, en las casas infestadas por *R. prolixus* generalmente los huevos son encontrados adheridos a los papeles que a menudo cubren las paredes del rancho, bien en cuadros, recortes de periódico, etc., o en cajas de cartón, sacos de papel que frecuentemente cubren el jergón, etc., y en el hábitat silvestre generalmente se observan adheridos a las pencas de las palmeras (Gamboa, [6]). Es evidente que el parasitoide está bien adaptado a esta condición en la cual le es muy fácil parasitar; en efecto, el parasitismo se realiza con éxito generalmente de manera muy rápida, el parasitoide emplea solamente pocos minutos en la exploración del huevo y casi inmediatamente inyecta el ovipositor en el mismo. En cambio, cuando el huevo es libre resbala con mucha facilidad y pudimos observar que en estas condiciones la avispa hace esfuerzos, a veces infructuosos, para sujetarlo y parasitarlo, además, que este "stress" al cual la avispa está sometida, repercute desfavorablemente sobre la longevidad de la misma.

Este aspecto de la relación parásito-huésped podría ayudar a explicar observaciones hechas en otro

experimento (Feliciangeli, [5]) en el cual se ofrecieron a *T. costalimai* huevos de 7 especies de triatominos: 3 del género *Rhodnius*, 3 del género *Triatoma* y 1 del género *Eratyrus*. Todas las especies del género *Rhodnius* cementan sus huevos al substrato durante la oviposición, mientras los de *Triatoma* y *Eratyrus* ponen sus huevos libres y de forma más redonda que los de *Rhodnius*. *T. costalimai* solamente parasitó huevos de las tres especies de *Rhodnius*, pero en ningún momento aceptó o logró parasitar los otros.

Esta aparente especificidad a nivel de género podría estar ligada a una característica de naturaleza fisiológica (por ejemplo la diferente constitución bioquímica del huevo), sin embargo, no se puede excluir la posible intervención de cierta especificidad (etológica) puesto que la habilidad de la avispa podría estar condicionada por los diferentes hábitos de oviposición de los triatominos, los cuales indirectamente repercutirían sobre el éxito del parasitismo.

RESUMEN

Se estudia un aspecto de la relación parásito-huésped entre *Telenomus costalimai* y huevos de *Rhodnius prolixus*, en función de la situación en la cual el parasitoide puede encontrar los huevos huéspedes.

A 26 hembras de *T. costalimai* fueron ofrecidos diariamente 20 huevos nuevos de *R. prolixus* adheridos a papel, situación que se observa generalmente en la naturaleza.

A 30 hembras de *T. costalimai* se ofreció la misma cantidad de huevos, pero libres, situación que ocasionalmente ocurre en condiciones naturales.

Los promedios de huevos parasitados por avispa fueron respectivamente $\bar{x} = 32.73 \pm 4.64$ y 11.93 ± 8.97, los cuales comparados con la prueba "t", mostraron una diferencia altamente significativa. Por otra parte, se observó también que la longevidad de la avispa fue notablemente menor en el caso en que se encontró en presencia de huevos libres.

Estos resultados permiten en parte explicar la dificultad para este microhimenóptero de parasitar especies de triatominos que ponen sus huevos libres, no adheridos al substrato, observación hecha en otro experimento.

SUMMARY

Aspects of the relationship between *Telenomus costalimai* and *Rhodnius prolixus* eggs, its natural host, were studied.

Batches of 20 eggs adherent to paper were offered daily to 26 females of *T. costalimai* kept in individual glass vials. For comparison, batches of 20 eggs that had been laid free were offered to 30 *T. costalimai* also kept in individual vials. The wasps were left with the eggs until they died.

The average number of parasitized eggs in the first group was 32.73 ± 4.64 and in the second, 11.93 ± 8.97; the difference is highly significant. The longevity of the wasp was notably reduced when they were submitted to the stress of depositing their eggs on non-adherent eggs.

This observation may partially explain the difficulty with which this microhymenopteran parasitizes eggs that are usually laid free, as has been observed in other experiments.

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EFECTO DE LA DENSIDAD EN *OOENCYRTUS TRINIDADENSIS* (CHALCIDOIDEA, ENCYRTIDAE), UN PARÁSITO ENDÓFAGO DE LOS HUEVOS DE *RHODNIUS PROLIXUS*, VECTOR DE LA ENFERMEDAD DE CHAGAS EN VENEZUELA

Dora FELICIANGELI y Jorge E. RABINOVICH

RESUMEN

Se evaluó el efecto de la densidad en **Ooencyrtus trinidadensis**, parásito endófago de los huevos de **Rhodnius prolixus**. Se diseñó un experimento de laboratorio, con un número variable de réplicas en el cual se ofreció a diversas densidades de parásitos hembra de 0-48 hs de edad varias densidades e huéspedes. Todas las pruebas fueron realizadas a temperatura y humedad relativa constantes (28± 1°C; 50-60% HR). Se evaluó el efecto de la densidad a través del porcentaje de parasitismo y de la productividad (progenie una geración después), tanto por hembras como por huésped. El porcentaje de parasitismo aumenta rápidamente con el incremento en la densidad de parásitos, aumento que es más acelerado cuanto menor el número de huéspedes disponibles. Se observa que existe un máximo en el número de huéspedes parasitados/hembra que se obtiene a diferentes densidades de huéspedes para diferentes densidades de parásitos. Esto indica una fuerte interacción entre las densidades de parásitos y huéspedes, que también se refleja en la curva de reproducción. La disminución en la progenie por huésped, y el incremento en el número de huéspedes superparasitados indican que el proceso de competencia larval, aunque eficiente, tiene un límite que está en aproximadamente 1 huésped por parásito. Se procesaron los resultados del efecto de la densidad de los parásitos mediante un análisis de varianza de una vía, obteniéndose un efecto estadísticamente significativo para casi todas las densidades de huéspedes utilizadas en todas las variables evaluadas. El efecto de densidad aquí detectado permite recomendar las proporciones de parásitos y huéspedes óptimos para programas de cría masiva con fines de control biológico.

INTRODUCCION

El control biológico descansa sobre la premisa que las densidades de las especies nocivas, tanto en plantas como en animales, están sujetas a control, y probablemente a regulación, fundamentalmente por sus enemigos naturales (parásitos, depredadores y patógenos) (HUFFAKER, MESSENGER & DEBACH [16]). El depredador o parásito que regula en forma más confiable y eficiente la población de su presa o huésped es aquel que tiene con estas últimas una relación densodependiente recíproca (HUFFAKER & MESSENGER [15]). Esto significa que, si el huésped es regulado por su enemigo, a su vez el enemigo está limitado por el número de huéspedes. Más aún, podríamos llegar a aseverar que, si deseamos un agente de control biológico que tenga una capacidad reguladora **eficiente y confiable**, dicho agente deberá necesariamente estar limitado por sus fuentes alimenticias en un grado considerable.

Es, por consiguiente, fundamental en la evaluación de un parásito como agente de control biológico el adecuado conocimiento de las relaciones parásito-huésped bajo diversas condiciones de densidad, tanto del propio parásito como de sus huéspedes. Dentro

Cátedra de Parasitología, Facultad de Ciencias de la Salud. Universidad de Carabobo. Valencia — Venezuela
Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 1827. Caracas 101. Venezuela

FELICIANGELI, D. & RABINOVICH, J. E. — Efecto de la densidad en **Ooencyrtus trinidadensis** (Chalcidoidea, Encyrtidae), un parásito endófago de los huevos de **Rhodnius prolixus**, vector de la enfermedad de Chagas en Venezuela. **Rev. Inst. Med. trop. São Paulo** 19:21-34, 1977.

de este tipo de interacciones es de importancia conocer las llamadas respuestas numérica y funcional de los parásitos a los cambios en la densidad de sus huéspedes. También es de importancia conocer cómo se alteran estas respuestas funcionales y numéricas ante condiciones de diferentes densidades de los propios parásito. Por estas razones fué considerado de interés llevar a cabo una serie de experimentos en los cuales se combinaran diversos niveles de densidad, tanto de los parásitos como de los huéspedes.

Estos fueron los critérios que guiaron el diseño experimental para la evaluación del parasitoide **Ooencyrtus trinidadensis** como un agente potencial de control biológico de los vectores de la enfermedad de Chagas, específicamente del **Rhodnius prolixus**, principal vector de esta enfermedad en Venezuela. Es conocido el hecho que los parasitoides han logrado un control biológico efectivo aproximadamente 4 veces más frecuentemente que los depredadores (DEBACH [2]).

Existen ya numerosos estudios sobre los efectos de la densidad, tanto de los parásitos como de sus huéspedes, en microhimenópteros con perspectivas de transformarse en agentes de control biológico de sus huéspedes (MESSENGER [22]; REINERT & KING [25]; WYLIE [38]; FUJITA & UTIDA [5]; LEGNER [20]; PRICE [24]; VAN DEN BOSH [35]; WALKER [36]; TOSTOWARYK [31]; KUNO [18]; UTIDA [32,34]; ISHIDA [17]; BURNETT [1]; NAKASUJI & col.[23]). También se puede encontrar en la literatura estudios que indican un desarrollo bastante avanzado en la teoría general del problema del efecto de la densidad en microhimenópteros parasitoides (SOUTHWOOD [28]; TAKAHASHI [27,28]; FUJII [4]; UTIDA [31]; KUNO [19]; HASSELL & MAY [11,12]; HASSELL & ROGERS [13], HASSELL & VALEY [14]; HASSELL & HUFFAKER [10]; HASSELL [7,8]; ROGERS & HASSELL [26]; ROYAMA [27]; MAY & col.[21]; WATT [37]).

Desde luego no se pretende extrapolar de una manera directa los resultados de este tipo de experimentos a la eficiencia y confiabilidad de esta especie de parasitoide como un agente de control biológico de su huésped en condiciones de campo. Al no permitir los experimentos de laboratorio aquí presentados la incorporación de la heterogenidad ambiental, ni la relación espacial entre el parasitoide y su huésped, ni las tasas relativas de dispersión de ambos, es evidente que la extrapolación de las interpretaciones logradas en laboratorio a las condiciones de campo son sumamente limitadas. Sin embargo, no sólo logramos comprender mejor las respuestas numéricas y funcionales de la interacción entre el parasitoide y su huésped, sino que además se obtiene una información esencial para diseñar la cría masiva del parasitoide con fines liberación. Este aspecto es de particular importancia en este caso debido a que **O. trinidadensis** es un parasitoide natural de los huevos de **R. prolixus** en Venezuela, implicando que ambas especies han tenido tiempo de coevolucionar para llegar a un estado de equilibrio; dicho estado de equilibrio interferiría con los requisitos de control, y por ello solamente pensamos en la utilización del parasitoide como un mecanismo o agente de control biológico mediante la técnica de la liberación de cantidades masivas del parasitoide.

MATERIALES Y MÉTODOS

Las poblaciones de **Ooencyrtus trinidadensis** var. **venatorius** (DE SANTIS & col. [3]) utilizadas en estos experimentos, tienen su origen en individuos recolectados en el Municipio Higuerotal, Estado Aragua, Venezuela. Esta población fué mantenida en el laboratorio a una temperatura de 28°± 1°C y humedad realtiva entre 50-60%, mediante el suministro constante y exclusivo de huevos de **R. prolixus**, sin necesidad de alimento ni agua.

El huésped, **Rhodnius prolixus**, proviene de una cría mantenida según el método estandardizado de GÓMEZ NUÑEZ [6] en base a la alimentación con aves de corral a un ritmo quincenal para asegurar una adecuada producción de huevos.

Se estudió el efecto de cinco densidades de parásitos (1, 3, 5, 10 y 15) sobre grupos de 5 y 10 huevos de **R. prolixus**, y el efecto de siete densidades de parásitos (1, 3, 5, 15, 20 y 30) sobre grupos de 15, 20, 25 y 30 huevos de **R. prolixus**. Para todas las pruebas siempre se utilizaron **O. trinidadensis** y huevos de **R. prolixus** de 0-48 hs de edad.

Los huevos ofrecidos, recortados individualmente sobre la cartulina en que son de-

positados, fueron pegados con pega incolora e inodora a un papel cuadriculado con el cual se forraba el fondo de cajas de vidrio de Petri de 9 cm de diámetro. El papel cuadriculado permitía una distribución uniforme de los huevos de **Rhodnius prolixus** y las cajas de Petri, por su transparencia, facilitaban la verificación posterior del número de avispas introducidas. La operación de introducir las avispas en las cajas de Petri se realizaba por medio de un microcapturador de vidrio, después de la cual las cajas eran selladas con adhesivo y debidamente rotuladas, dejándose en una estufa a las temperaturas y humedades relativas arriba indicadas durante un lapso de 24 hs.

Al término de este tiempo se retiraban las avispas de la caja de Petri y se recortaban todos los contenidos en la caja para colocarlos en pequeños tubos de vidrio (1,5 x 5 cm), los cuales, tapados con algodón eran guardados de nuevo en estufa durante el tiempo necesario para el desarrollo embrionario de **O. trinidadensis** (14-15 dias) y hasta que la progenie emergida muriera para, de esta manera, facilitar su contaje (19-20 días).

El contaje se efectuaba con la ayuda de una lupa de 10 a 40 aumentos para observar en cada lote de huevos lo siguiente: a) los huevos parasitados vivos de los cuales nacieron avispas; b) los huevos parasitados muertos que mostraban claros signos de parasitismo (ennegrecimiento intenso) pero que no llegaron a producir progenie; c) los huevos no parasitados (de los cuales nacieron **R. prolixus**), y d) los huevos estériles (de los cuales no nacieron ni avispas ni triatominos).

Para cada huevo parasitado vivo se anotó la cantidad de avispas emergidas, tanto machos como hembras, pudiéndose realizar el reconocimiento del sexo en forma rápida y segura por la presencia en la "frente" de un punto que en macho es de color verde brillante, mientras que en la hembra es azul brillante.

Para las distintas combinaciones de números de huevos ofrecidos a diferentes densidades de avispas, se repitieron los experimentos en un número variable de réplicas, desde un mínimo de 4 hasta un máximo de 10.

RESULTADOS

El efecto de la densidad de parásitos sobre el porcentaje de huéspedes parasitados se encuentra en la Fig. 1. Puede observarse que para todas las densidades utilizadas se alcanza entre el 90 y 100% de parasitismo, sólo que este efecto se obtiene más lentamente a medida que existe una mayor disponibilidad de

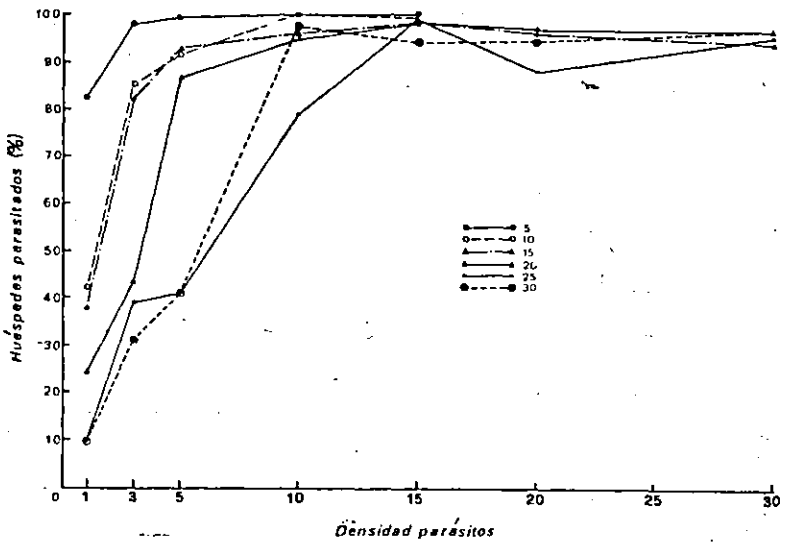

Fig. 1 — Porcentaje de huéspedes parasitados en función de las densidades de los parásitos. Las diferentes curvas corresponden a distintas densidades de huéspedes según se identifica en la figura.

huéspedes. Esto se evidencia por el grado de curvatura del porcentaje de huevos parasitados con la densidad de avispas, que va disminuyendo aceleradamente a medida que aumenta la disponibilidad de huéspedes, que podría interpretarse como una indicación de la existencia de un efecto de interferencia entre las avispas adultas por su acción de parasitismo.

Una de las formas en que podemos poner a prueba la existencia de dicha interferencia consiste en evaluar el efecto de la densidad de los parásitos sobre el número de huéspedes parasitados por hembra, cuyos resultados se presentan en la Fig. 2. El número de huevos parasitados por cada hembra va disminuyendo a medida que la densidad de parásitos va aumentando; para las densidades altas de parásitos se puede observar el efecto de las diferentes densidades de huéspedes disponibles, observándose un mayor número de huevos parasitados por hembra a medida que existe mayor número de huéspedes disponibles. Sin embargo, para densidades bajas de avispas es curioso observar que no hay una tendencia clara del efecto del número de huéspedes disponibles sobre el número de huevos parasitados por hembra; más aún, debido a la forma en que se entrecruzan las curvas, hay aparentemente un óptimo a densidades intermedias de huéspedes disponibles. En efecto, como puede observarse de la Fig. 2, para la densidad de una avispa sola, 15 y 20 huéspedes disponibles producen un mayor número de huevos parasitados por hembra que con 5 y 10 huéspedes disponibles, y aún mucho mayor que con 25 y 30 huéspedes disponibles. Dado que, habiendo una sola avispa hay que descartar cualquier efecto posible de densidad o interferencia entre adultos, podríamos inclinarnos a pensar que existe una reducción de la eficiencia de parasitismo de cada hembra debido a que se va encontrando con huevos parasitados por ella misma en momentos anteriores; a medida que aumenta la disponibilidad de huéspedes disminuye la posibilidad de encontrar más huéspedes parasitados por ella misma, pero a medida que el número de huéspedes disponible aumenta aún más, es decir, a 25 y 30 huéspedes, el número de huéspedes parasitados por hembra vuelve a disminuir, posiblemente debido a un aumento en la demora del tiempo de búsqueda de huevos para parasitar por razones que no alcanzamos a explicarnos.

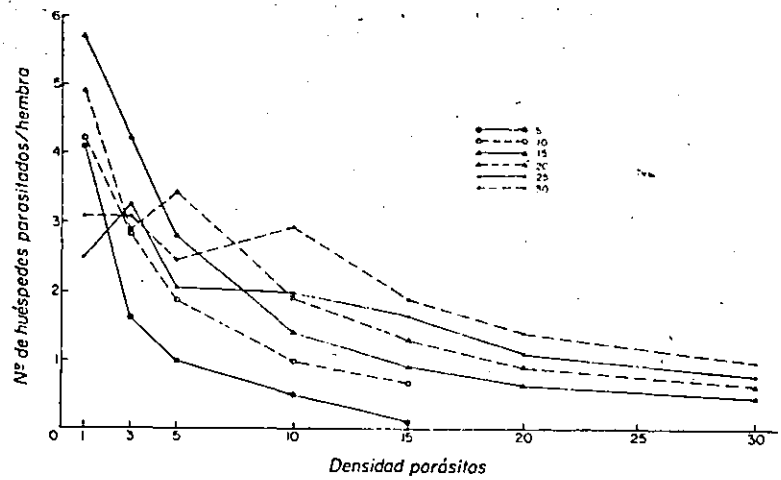

Fig. 2 — Número de huéspedes parasitados por hembra en función de la densidad de parásitos. Interpretación de las curvas igual que en la Fig. 1.

Este efecto se observa más claramente cuando analizamos el número de huevos parasitados por cada hembra en función del número de huéspedes ofrecidos para cada una de las densidades de parásitos utilizadas, como se observa en la Fig. 3. La existencia de una densidad óptima de huéspedes disponibles entre 15 y 20 huéspedes se observa nitidamente

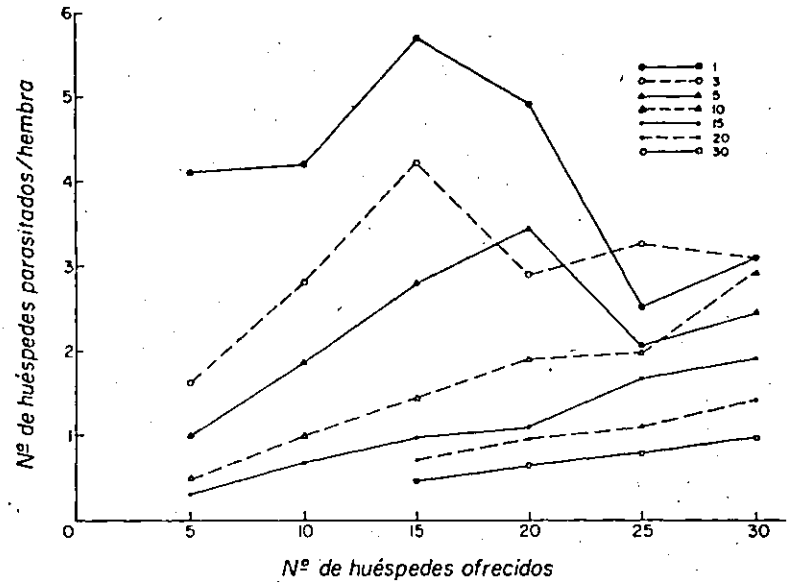

Fig. 3 — Número de huéspedes parasitados por hembra en función del número de huéspedes ofrecidos. Las diferentes curvas corresponden a las distintas densidades de parásitos utilizados, según se identifica en la parte superior derecha de la figura.

para las densidades de avispas de 1, 3, y 5; para densidades de parásitos de 10 y 15 avispas se observa que desaparece dicho efecto dado que el número de huéspedes parasitados por hembra se incrementa de una manera monotónica a medida que aumenta el número de huéspedes ofrecidos. Otra manera de visualizar este efecto es graficando el número de huéspedes parasitados por hembra en función del número de huéspedes ofrecidos por hembra, independientemente de la densidad de parásitos (Fig. 4). Nótese que 3 huéspedes/parásito puede resultar tanto de 3 huéspedes y 1 parásito, como de 15 huéspedes y 5 parásitos, como de 30 huéspedes y 10 parásitos. La Fig. 4 confirma que la eficiencia de parasitismo por hembra aumenta hasta llegar al máximo de 15 huéspedes por parásito.

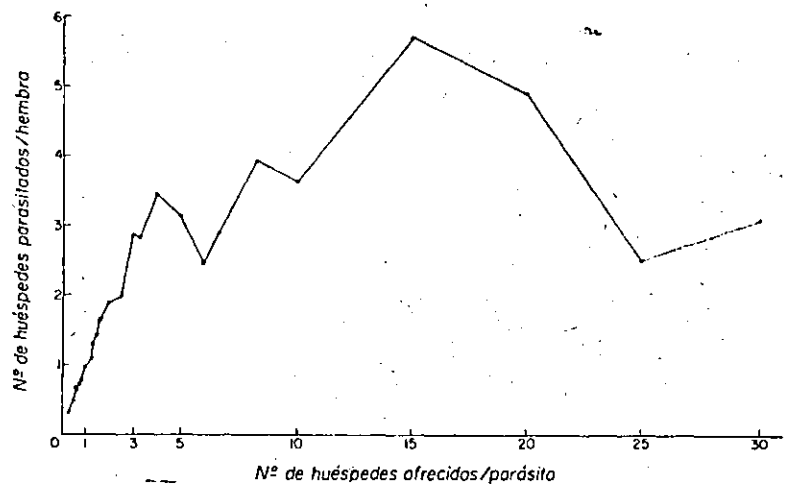

Fig. 4 — Número de huéspedes parasitados por hembra en función de la disponibilidad de huéspedes por parásito. Para una explicación del cálculo de la disponibilidad ver texto.

Cuando pasamos a analizar el efecto de la densidad de avispas sobre la progenie total nacida viva de cada avispa, observamos un resultado como el de la Fig. 5, en el cual se nota una disminución progresiva de la progenie total por avispa a medida que aumenta la densidad de los parásitos. La única excepción a este efecto es cuando existen 30 huéspedes disponibles en que se observa un ligero aumento en el número de las avispas hijas producidas por cada parásito hasta una densidad de 10 parásitos, después de lo cual

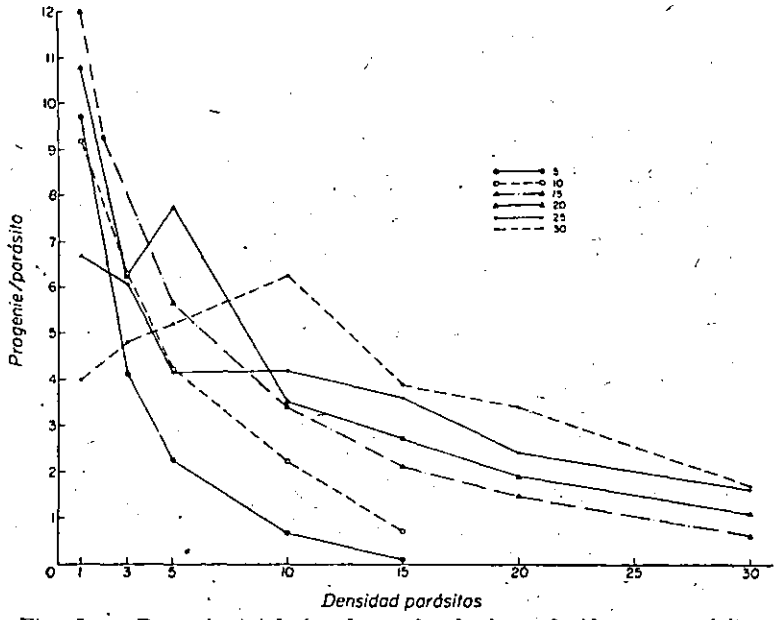

Fig. 5 — Progenie total (macho y hembra) producida por parásito (hembra) en función de la densidad de los parásitos. Las diferentes curvas se interpretan como en la Fig. 1.

se observa una disminución integrándose a la tendencia general para las demás disponibilidades de huéspedes. Este patrón de respuesta es similar al observado para el número de huéspedes parasitados por hembra (Fig. 2), indicando en cierta manera que la productividad de progenie por cada huevo debe ser aproximadamente constante; además también podemos observar que a densidades de 1, 3, y 5 parásitos se obtiene un máximo u óptimo en la producción de progenie para 15 y 20 huéspedes disponibles. Este efecto nuevamente se puede observar con mayor claridad al graficar la progenie viva por avispa en función del número de huéspedes ofrecidos para todas las densidades experimentales de parásitos (Fig. 6).

En la Fig. 7 se observa el efecto de la densidad de parásitos sobre la progenie hembra por cada parásito utilizado. El patrón de respuesta es completamente análogo al de la progenie total por hembra para cada una de las densidades, y el efecto de las diferentes disponibilidades de huéspedes es también similar a esta última. Esto tendería a indicar que, cualesquiera sea la disponibilidad de huéspedes, la proporción de sexos en la progenie debe verse muy poco alterada por las diferentes densidades de parásitos. Esto se observa en la Fig. 8 donde existe un cambio en el porcentaje de hembras dentro de la progenie total sumamente leve, pero con tendencia negativa, a medida que aumenta la densidad de avispas para cualquiera de las disponibilidades de huevos utilizadas.

Otro tipo importante de resultado obtenido de estos experimentos está reflejado en la Fig. 9, donde se ha representado el núme-

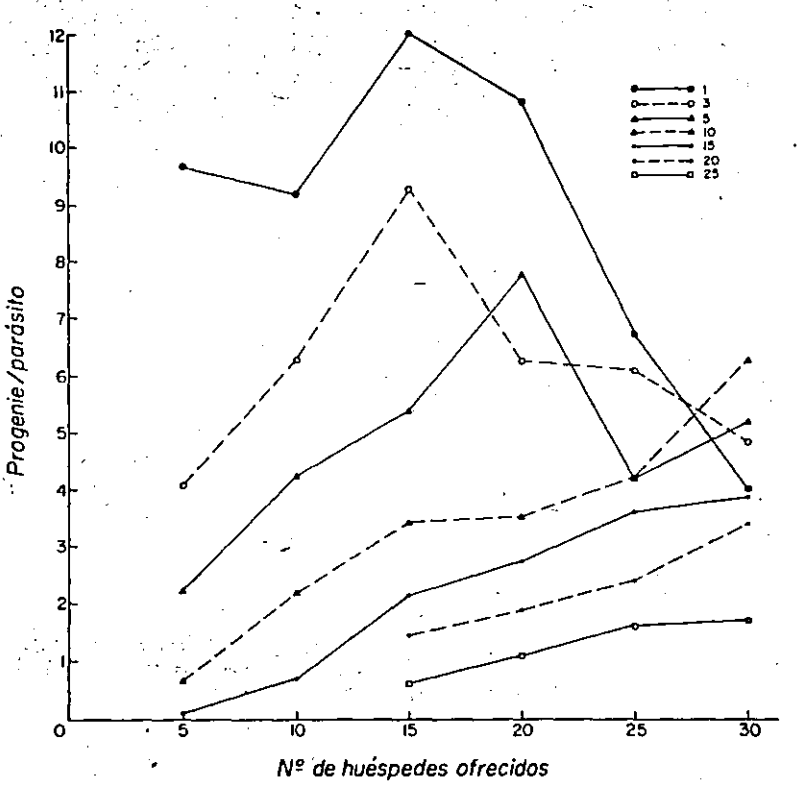

Fig. 6 — Progenie total (macho y hembra) por parásito (hembra) en función del número de huéspedes ofrecidos. Las diferentes curvas se interpretan como en la Fig. 3.

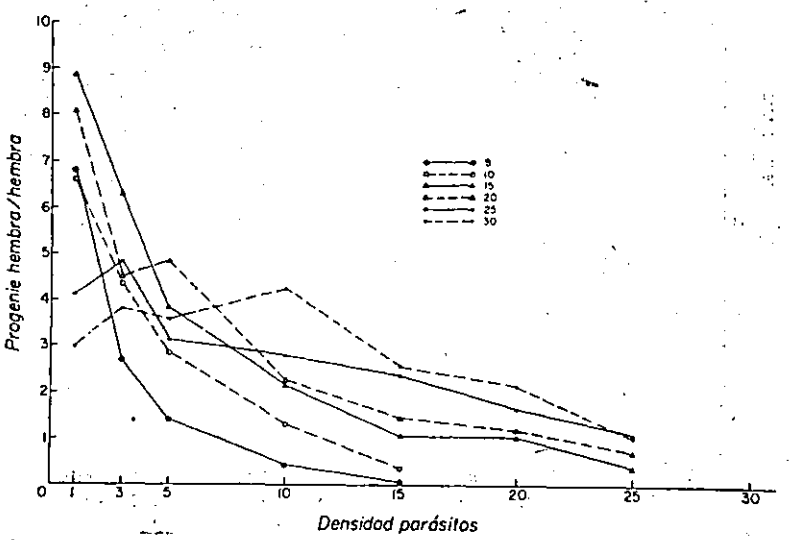

Fig. 7 — Progenie hembra producida por cada hembra de la población en función de la densidad de los parásitos. Las diferentes curvas se interpretan como en la Fig. 1.

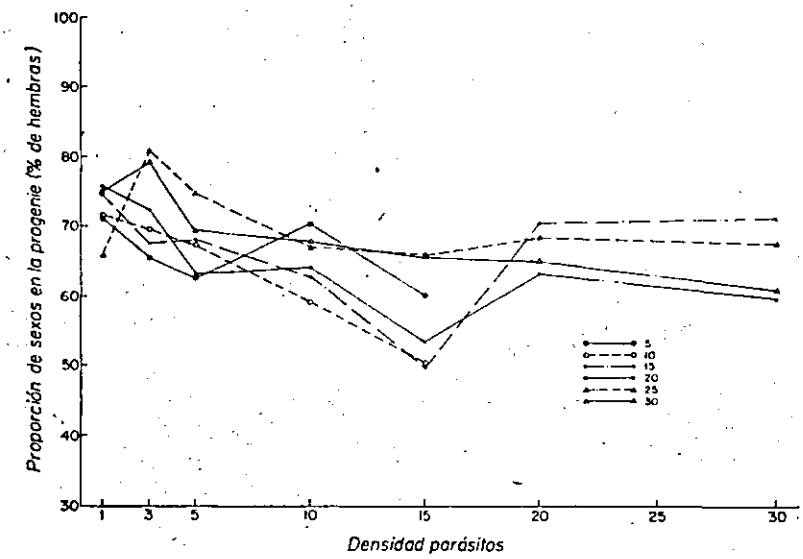

Fig. 8 — Proporción de sexos de la progenie, expresada como porcentaje de hembras, en función de la densidad de parásitos. La interpretación de las curvas es como en la Fig. 1.

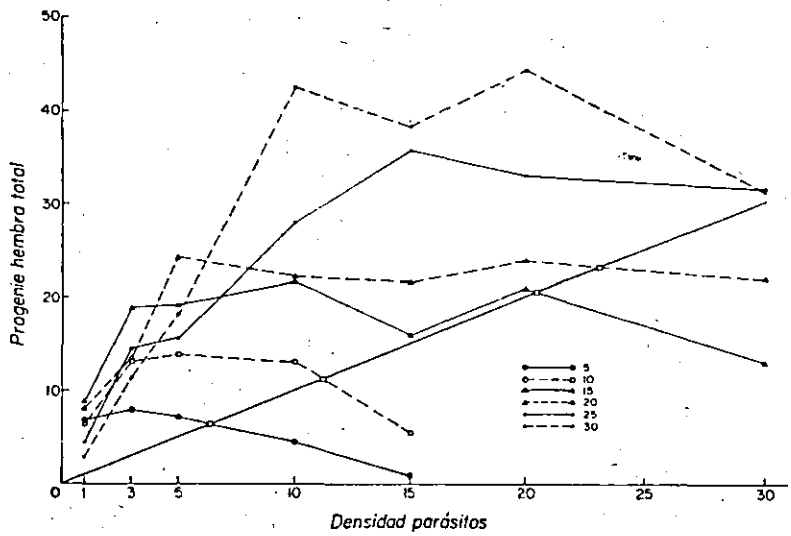

Fig. 9 — Curva de reproducción. Progenie hembra total producida después de un lapso de una generación en función de la densidad de parásitos. Los pequeños cuadrados representan el punto de corte entre cada curva de reproducción a diferentes disponibilidades de huéspedes con la recta de equilibrio, que representa a una población que se autorreemplaza. Las diferentes curvas se interpretan como en la Fig. 1.

ro de hembras una generación después en función del número de hembras madres. Este tipo de curva, muy utilizada en biología pesquera, y conocida como Curva de Reproducción, ha sido también aplicada en ocasiones al caso de los parasitoides entomófagos. En la Fig. 9 están las curvas de reproducción para las seis disponibilidades de huéspedes utilizadas experimentalmente. Como podrá observarse, a medida que la disponibilidad de huéspedes aumenta las curvas se hacen más ascendentes y tienen su punto de inflexión a valores más altos y a densidades de parásitos más altas. Como consecuencia también aumenta progresivamente el valor del punto de intersección con la recta de equilibrio. Esta recta, trazada a 45° en el caso en que ambos ejes estén dibujados a la misma escala, representa aquella condición de equilibrio expresada por una tasa de reemplazo igual a la unidad, es decir, cuando una población de parásitos es reemplazada por una población numéricamente igual una generación después. El punto de corte, por lo tanto, entre las curvas de reproducción y esta recta de equilibrio tiene importancia porque representa el tamaño poblacional a un nivel de equilibrio.

Otros aspectos de interés que se puso de relieve entre los resultados de este trabajo experimental está representado por el aspecto competitivo durante el desarrollo en condiciones de recursos limitados, como lo son los huevos del huéspede para estos insectos parasitoides. En la Fig. 10 se puede observar el efecto de la densidad de las avispas sobre el parasitismo efectivo, expresado como el porcentaje de huevos parasitados que no dió progenie en relación al número total de hue-

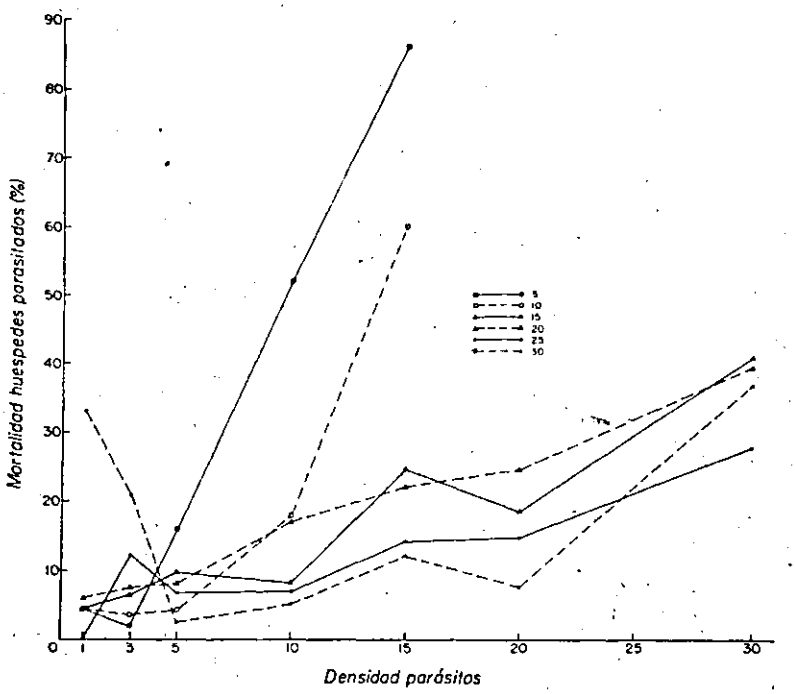

Fig. 10 — Mortalidad de los huéspedes parasitados en función de la densidad de los parásitos. Las diferentes curvas se interpretan como en la Fig. 1.

vos del huésped que fueron parasitados. A medida que aumenta la densidad de avispas este porcentaje de huevos parasitados que no produjo progenie aumenta notablemente, en especial, cuando existe una disponibilidad baja de huéspedes; ésto es un indicador muy claro que existe un proceso competitivo a nivel larval debido a que se deposita un número de huevos de avispa superior a la capacidad de desarrollo que ofrece el recurso que

hay dentro de un huevo del huésped. Este fenómeno competitivo se ve confirmado cuando presentamos los resultados de estos experimentos evaluándolos a través de la variable progenie viva producida por todos los huevos parasitados en función de la densidad de avispas, tal como aparece en la Fig. 11. A diferencia de los resultados de la figura anterior con el aumento en la densidad de los parásitos casi no se observa cambio alguno en la cantidad de descendencia viva que se produce por cada huésped parasitado; en efecto, con la excepción de la disponibilidad de 5 y 10 huéspedes para altas densidades, el número e avispas nacidas por huevo parasitado es de aproximadamente 2.

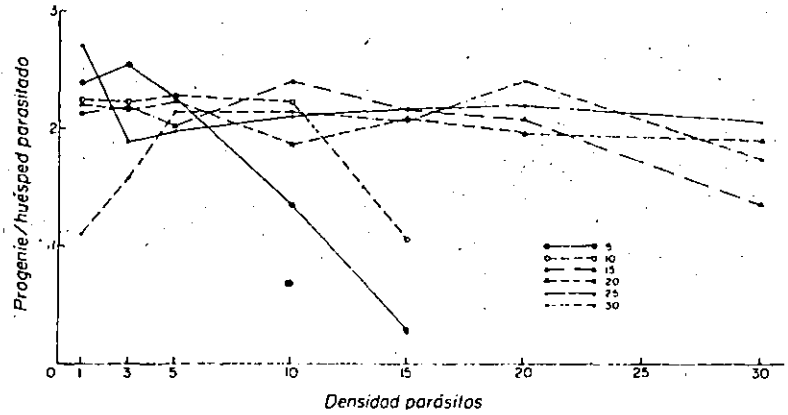

Fig. 11 — Progenie total (machos y hembras) por huésped parasitado en función de la densidad de los parásitos. La interpretación de las curvas es como en la Fig. 1.

Como era de interés conocer si los resultados de estos experimentos, evaluados a través de las diversas variables representadas en las Figs. 1-11, podían interpretarse como efectos estadísticamente significativos, se procedió a llevar a cabo un análisis de varianza de una vía. En la Tabla I encontramos los resultados de este análisis que nos indica que, con sólo três excepciones, todos los efectos de densidad obtenidos son estadísticamente significativos.

TABLA I

Valores del índice F. Resultado del análisis de varianza de una vía que indica la significatividad del efecto de la densidad de los parásitos sobre ocho variables para diferente número de huéspedes disponibles. NS = no significativo, * = significativo al nivel de 5%, ** = significativo al nivel del 1%. Las primeras três variables, por ser porcentajes, fueron transformadas utilizando la transformación de la raíz cuadrada.

Variable	Número de huéspedes ofrecidos					
	5	10	15	20	25	30
Huéspedes parasitados (%)	6,5 **	69,6 **	98,8 **	60,4 **	43,2 **	81,0 **
Huéspedes parasitados muertos (%)	47,0 **	28,6 **	5,9 **	7,6 **	4,3 **	8,4 **
Hembras en la progenie (%)	—	10,7 **	6,9 **	7,3 **	2,49 **	—
Progenie total/huésped vivo	—	2,69 *	1,35 NS	6,4 **	2,23 NS	—
Progenie total/huéspedes totales	36,9 **	10,7 **	4,9 **	0,97 NS	4,82 **	7,51 **
Nº de huéspedes parasitados/hembra	117,4 **	38,3 **	267,9 **	460,3 **	175,5 **	569,8 **
Progenie total/hembra	107,8 **	29,9 **	80,5 **	99,3 **	138,7 **	465,8 **
Progenie hembra/hembra	129,4 **	26,8 **	80,3 **	74,8 **	110,7 **	281,0 **

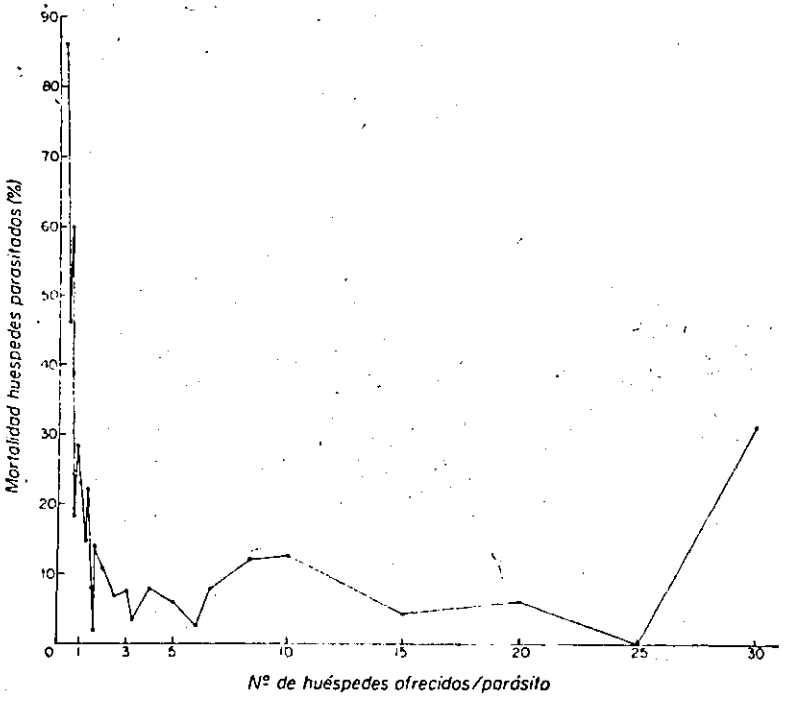

Fig. 12 — Mortalidad porcentual de los huéspedes parasitados en función de la disponibilidad de huéspedes, expresada como número de huevos del huésped por parásito. Para una explicación del cálculo de la disponibilidad ver en el texto la referencia a la Fig. 4.

DISCUSION Y CONCLUSIONES

La evaluación de la existencia de un efecto de densidad en el parasitoide **O. trinidadensis**, a través de su eficiencia de parasitismo y de la progenie producida, indican que dicho efecto existe y que tiene un alto grado de interacción con la densidad de los huéspedes. El efecto de la densidad sobre la eficiencia del proceso de parasitismo demuestra que hay un fenómeno de interferencia, de tipo competitivo, entre los individuos (hembras en este caso) adultos de la población.

Por otra parte, los resultados obtenidos en términos de progenie por hembra, al coincidir en forma notable con los de porcentaje de parasitismo, y la llamativa constancia en la producción de parásitos por huevo huésped, nos indican que también debe existir un proceso competitivo de alta eficiencia durante el desarrollo larval. Sin embargo, esta eficiencia tiene límites bien claros, como se deduce de los resultados presentados en la Fig. 10 ya que es notable el vertiginoso aumento de huevos parasitados que no alcanzan a producir progenie debido a los efectos del superparasitismo.

Dada la compleja interacción densidad parasitoide-densidad huésped que existe entre estas dos especies, una manera de evaluar los límites de la efectividad del proceso de competencia larval se puede obtener al graficar la mortalidad de huéspedes parasitados en función del número de huéspedes ofrecidos por parásito (Fig. 12), de manera similar a la Fig. 4. De esta manera se puede determinar que, mortalidades mayores del 10-15%, sólo se producen cuando la proporción huéspedes/parásito es menor que 1; puesto de otra manera, apenas aumenta el número de parásitos que debe compartir **cada huésped**, se produce un incremento vertiginoso en la mortalidad de los huevos parasitados. La excepción que se observa a 30 huéspedes por pa-

rásito representa posiblemente un efecto espúreo de la variabilidad del experimento a dicha combinación (1 parásito, 30 huéspedes), lo cual es sugerido por haber tenido el coeficiente de variación más alto en toda la serie de densidades (75,1%).

Sin embargo, si la relación parásito-huésped se conserva dentro del limite de **por lo menos** 1 huésped por cada parásito, entonces observamos que el efecto de la densidad no tiene mayor importancia sobre la progenie producida por huevo parasitado.

Por otra parte los resultados de la curva de reproducción (Fig. 9) indican que, según la disponibilidad de huéspedes, existen diferentes densidades de parásitos que pueden considerarse óptimas. Así, por ejemplo, con 30 huevos disponibles, 10 parásitos hembra producirán 40 hembras una generación después, es decir, 0.133 hembras/madre/huésped, mientras que con 15 huevos disponibles, 3 parásitos hembra producirán unas 20 hembras una generación después, es decir, aproximadamente, 0.46 hembras/madre/huésped, o sea, casi cuatro veces más que en la combinación 10 parásitos — 30 huéspedes.

Este tipo de resultados es de gran utilidad en el diseño experimental para la cría masiva del parásito con fines de liberación. En el caso de interesarnos una alta producción sostenida y a largo plazo se sugeriría una combinación de, por ejemplo, 3 parásitos — 15 huéspedes; de necesitarse una alta producción en un lapso breve se recomendaría sacrificar la eficiencia por la productividad y utilizar, por ejemplo, una combinación de 10 parásitos — 30 huéspedes.

SUMMARY

Effects of parasite density on Ooencyrtus trinidadensis (Chalcidoidea, Encyrtidae), an endophagous parasite of Rhodnius prolixus eggs, vector of Chagas Disease in Venezuela

The effect of population density of **Ooencyrtus trinidadensis**, an endophagous parasite of the eggs of **Rhodnius prolixus**, was evaluated experimentally. A variable number of replicates were used of several female parasite densities and host eggs, both 0-48 hs old. All experiments were performed at constant temperature (28± 1°C) and relative humidity (50-60%).

The density effect was evaluated by percent parasitism and progeny production, both per female and per host egg. Percent parasitism increases rapidly with parasite density, being more accelerated the smaller the number of host eggs available. There is a maximum in the number of hosts parasitized per female that shifts towards larger numbers of host eggs available with increasing parasite density, reflecting a strong interaction between parasite and host densities. This interaction is also seen with the reproduction curve.

The results proved statistically significant with a one way analysis of variance. The overall density effects, that reflect both adult parasite interference and larval competition, suggest optimum proportions of parasites and hosts for massive rearing of **O. trinidadensis** for biological control releases.

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Observaciones sobre *Rhodnius prolixus* (Hemiptera, Reduviidae) en su biotopo silvestre *Copernicia tectorum*

DORA FELICIANGELI de PIÑERO
JOSE WITREMUNDO TORREALBA

La comprobación de la existencia de *Rhodnius prolixus* extradoméstico en el estado Guárico, Venezuela en 1961, por Gamboa (5), llevó a modificar considerablemente criterios anteriores sobre la epidemiología y el control de la enfermedad de Chagas en el país.

El transporte pasivo del vector entre las hojas de las palmeras utilizadas en la construcción de la vivienda campesina señalado en 1970 por Gamboa (6), y la dispersión activa del mismo de la palma a la casa referida en 1969 por Gómez-Núñez (7), son mecanismos que favorecen la recolonización de la vivienda por *R. prolixus* y la reintroducción de *Trypanosoma cruzi* procedente del medio silvestre después de la desinfestación de la casa por medio de insecticidas de acción residual.

Dra. Feliciangeli de Piñero, Profesor Agregado de la Cátedra de Parasitología de la Facultad de Ciencias de la Salud. Universidad de Carabobo, Valencia, Venezuela.

Dr. Torrealba, Profesor Asociado de la Cátedra de Parasitología de la Facultad de Ciencias de la Salud. Universidad de Carabobo, Valencia, Venezuela.

A través de exploraciones concentradas especialmente en zonas donde la utilización de la palmera en la construcción de la vivienda es más frecuente, Gamboa (6) llevó a cabo un estudio detallado de la población silvestre de *R. prolixus* delimitando los ecótopos naturales representados por siete especies de palmeras (Familia Aracaceae) y por nidos de aves en su gran mayoría, y analizando además los aspectos de la interrelación de palmeras *R. prolixus*, la importancia de la presencia de nidos de aves y los factores que determinan su infestación.

Posteriormente, en 1973, Pifano (9), definió la relación ecológica entre *R. prolixus* y sus fuentes alimenticias *Didelphis marsupialis* y *Calluromys philander* en la "palma yagua" concluyendo que dicha relación es estable y que permite la existencia de focos naturales de *T. cruzi* fácilmente transferible al rancho.

Más recientemente, en 1976, Tonn y col. (12) estudiaron la población triatomina en el medio silvestre implementando varias técnicas, entre las cuales la

CUADRO Nº 1

Frecuencia de *Rhodnius prolixus* en palmeras *Copernicia tectorum* del caserío El Cumbito, y algunos datos climatológicos de la cercana localidad de Carrizales, estado Guárico, verificados mensualmente, de abril 1975 a febrero 1976

	1975									1976	
	Abr.	May.	Jun.	Jul.	Ago.	Sep.	Oct.	Nov.	Dic.	Ene.	Feb.
Total de palmeras disecadas	15	10	10	10	10	10	10	10	5	10	5
Total de palmeras con *R. prolixus*	9	7	8	7	10	9	9	6	5	6	3
Porcentajes de palmeras positivas	60	70	80	70	100	90	90	60	100	60	60
Total de *R. prolixus* capturados	94	45	67	28	44	44	59	12	30	10	10
Promedio de *R. prolixus* por palmera	6,3	4,5	6,7	2,8	4,4	4,4	5,9	1,2	6	1	2
Número máximo de *R. prolixus* por palmera	28	17	35	14	15	7	19	5	19	3	8
Precipitación total (mm)	—	67	194	49	159	71	136	70	27	1	—
Temperatura media (°C)	30,0	29,5	28,1	26,9	26,7	26,9	26,4	27,6	26,4	27,1	28,1
Temperatura máxima absoluta	37,3	36,6	36,7	34,3	34,6	34,2	33,7	34,5	34,2	35,1	36,0
Temperatura mínima absoluta	19,7	21,8	20,7	18,7	20,5	19,9	18,8	17,5	13,2	14,7	15,7
HR media (%)	64	64	69	68	79	74	78	68	62	52	54

disección de las palmeras fue la que permitió la recolección más cuantiosa de ejemplares. Entre 394 palmeras disecadas, 86,8% fueron positivas, recolectándose 9 especies de triatominos, principalmente *R. prolixus.*

Todos estos estudios sin duda han puntualizado la información cualitativa acerca del alcance de *R. prolixus* en la transmisión de la enfermedad de Chagas; en el presente trabajo se trata de hacer una evaluación cuantitativa de la distribución de la población de este triatomino en la "palma llanera" *(Copernicia tectorum)* a lo largo de aproximadamente un año de observación.

METODOLOGIA

El trabajo fue realizado en el Caserío "El Cumbito", municipio Ortiz, estado Guárico, que se encuentra situado en el Bosque Seco Tropical. Esta zona, compuesta en su mayor parte por "los llanos", se caracteriza por un promedio anual de temperatura entre 22 y 29 °C, con una fuerte sequía de cuatro a seis meses de duración, seguida por una estación con sobrante de agua, (Ewel & Madriz, 2).

Quincenalmente, durante un período de once meses, (abril de 1975 a febrero de 1976) fueron derribadas en el lugar cinco palmeras, y mediante la disección total se recuperó la población triatomina en frascos individuales por palmera, debidamente rotulados. En el laboratorio los insectos fueron clasificados por especie, estadio y sexo; y posteriormente se examinaron las heces de cada individuo en fresco. Para poder efectuar el diagnóstico preciso de los hemoflagelados en fresco, las láminas positivas fueron coloreadas con Giemsa.

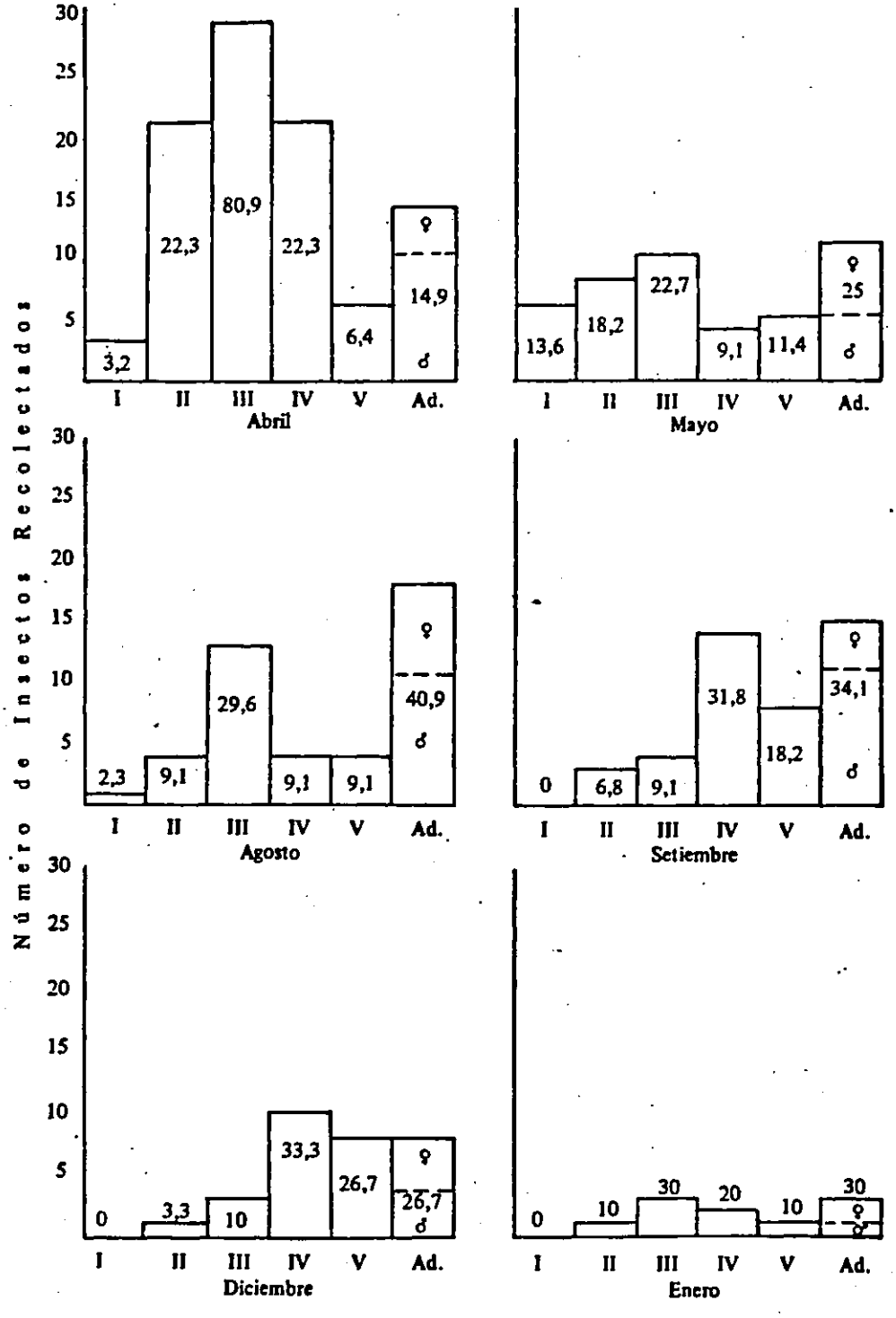
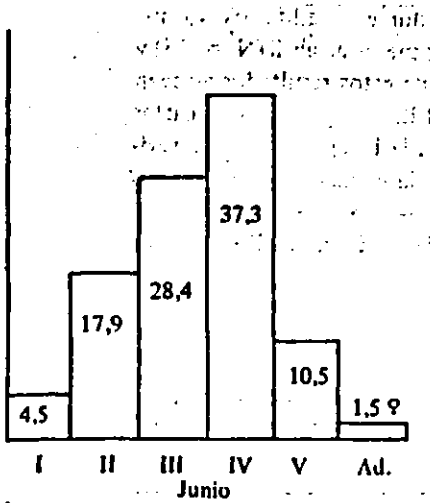
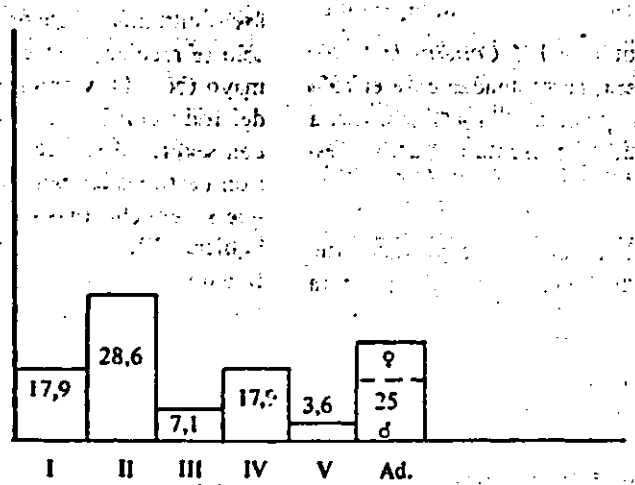
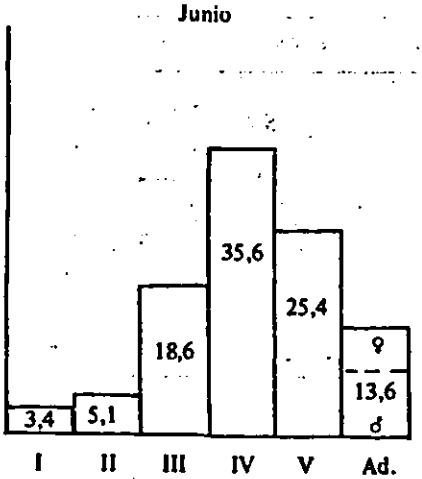
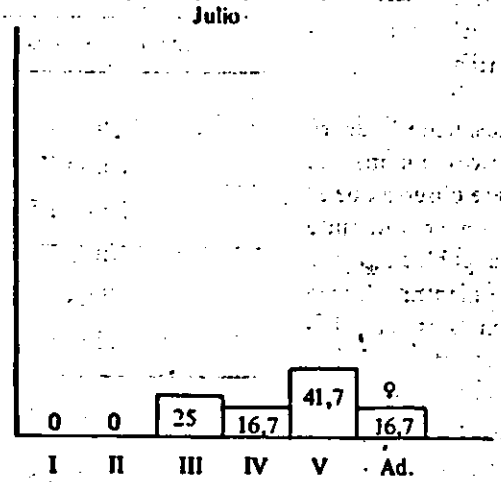


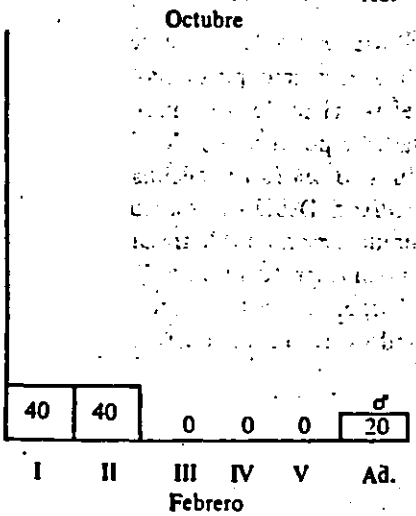
Fig. 1. Porcentaje relativo de cada estadio dentro de











población recolectada en *Copernicia tectorum*.

RESULTADOS

Se disecaron un total de 105 *Copernicia tectorum* de las cuales 83 o sea, aproximadamente el 79% resultaron positivas a *R. prolixus;* 11,4% positivas a *Triatoma maculata* y 3,8% presentaron ambas especies.

El número total de *R. prolixus* capturados fue 443 o sea un promedio de 5,3 ejemplares por palmera positiva.

En el Cuadro Nº 1, se presentan los resultados obtenidos y se refieren los datos climatológicos correspondientes a la Estación Experimental de las Fuerzas Aéreas Venezolanas, más cercana al sitio de trabajo, o sea de la localidad de Carrizales, durante el año 1975-1976, cuando se realizó el trabajo.

En la Fig. 1, se presenta gráficamente la distribución de la población de *R. prolixus* por mes de recolección y por estadio. En ambos se observa que es posible detectar la presencia de *R. prolixus* durante todos los meses del año, siendo la población muy escasa durante los meses de sequía, mientras alcanza los valores más altos de densidad en la estación lluviosa. Así, el número promedio de individuos recolectados por palmera positiva varió de un mínimo de 1,0 para el mes de enero, el mes de mayor sequía, hasta un máximo de 6,7 individuos, correspondió al mes de junio, que fue el mes de más alta precipitación pluvial. Aunque los valores de humedad relativa y temperatura media mensuales no presentan variaciones muy notables, no obstante puede observarse que la menor densidad poblacional coincide con los valores más bajos de HR y de las temperaturas mínimas absolutas registradas en los meses de enero y febrero.

La Fig. 1, permite analizar el porcentaje relativo de cada estadio dentro de la población recolectada mensualmente y se puede observar que la población del II al IV estadio ninfal en abril llega aproximadamente a ser hasta tres veces mayor con respecto a la población de la misma edad en los otros meses del año.

En el Cuadro Nº 2, se expresa la composición etaria de la población total y también se destaca que el porcentaje mayor de la población está generalmente formado por ninfas de III y IV estadio, siendo muy bajo, en proporción, el número de individuos de I estadio. Se hace notar que en el cuadro se omiten los resultados relativos al número de huevos, ya que sólo se recolectaron en los meses de abril (N = 28) y mayo (N = 1), y se cree que estos resultados no sean del todo confiables por el hecho que, para descartar con seguridad su presencia, la búsqueda, o sea la revisión de todas las partes de la palmera, hubiera tenido que ser mucho más cuidadosa, lo cual por otra parte, hubiera dificultado grandemente la realización del trabajo.

CUADRO Nº 2

***R. prolixus:* Composición etaria de la población total (N = 443) recolectada en *Copernicia tectorum* de abril de 1975 a febrero de 1976**

Estadio de desarrollo	Porcentaje
Ninfa I	5,4
Ninfa II	14,7
Ninfa III	21,9
Ninfa IV	24,4
Ninfa V	13,5
Adultos (*)	20,1

(*) Los porcentajes relativos a ♀ y ♂ fueron respectivamente 59,6 y 40,4

T. maculata fue encontrado esporádicamente compartiendo con *R. prolixus* el mismo nicho ecológico. El Cuadro Nº 3, refiere el número de individuos recolectados por estadio y por mes, siendo el número total de 40 individuos, o sea casi la décima parte con respecto a *R. prolixus.* Debido al escaso número de ejemplares capturados, es imposible tratar de establecer alguna relación con respecto a las condiciones bioclimáticas; sin embargo, es oportuno notar que en el mes de abril fue cuando se recolectó el mayor número de individuos.

Infección Natural

El examen de heces, llevado a cabo en 440 *R. prolixus,* permitió establecer que la infección era muy baja para *T. cruzi* (0,23%) y mayor a *T. rangeli* (13,4%). Ninguno de los 40 *T. maculata* apareció infectado.

CUADRO Nº 3

T. maculata: **Ejemplares recolectados en *Copernicia tectorum* de El Cumbito, estado Guárico, de abril de 1975 a febrero de 1976**

Meses	Estadios						
	I	II	III	IV	V	Adulto	
Abril	–	4	7	3	6	2	3
Mayo	–	–	–	1	1	–	–
Junio	–	–	–	1	1	–	–
Julio	2	1	1	–	–	–	–
Agosto	–	–	3	2	–	–	–
Septiembre	–	–	–	–	–	–	–
Octubre	–	–	–	–	1	–	–
Noviembre	–	–	–	1	–	–	–
Diciembre	–	–	–	–	–	–	–
Enero	–	–	–	–	–	–	–
Febrero	–	–	–	–	–	–	–
Totales	2	5	11	8	9	2	3

DISCUSION

El ecótopo silvestre más importante de *R. prolixus* está constituido por distintas especies de palmeras. El estudio de la dinámica poblacional de este vector en la especie *Copernicia tectorum* llevado a cabo a través de la disección sistemática permitió establecer que este nicho ecológico se mantiene constantemente habitado durante todos los meses del año. También se observó que hay una relación bastante estrecha entre la abundancia de la población triatomina y la abundancia de precipitación pluvial que es el factor bioclimático que más relevantes modificaciones sufre durante el año. Sin embargo, en línea general, la población de *R. prolixus* se mantiene escasa en esta especie de palmera, coincidiendo estas observaciones con las de Gamboa (6) y de Tonn y col. (11). Este último señala un promedio de individuos por palmera positiva, todavía inferior al de nosotros (=3,8) pero es posible que la disección de palmeras en esa oportunidad fue realizada solamente durante el período de sequía. La baja densidad de *R. prolixus* puede tener su explicación en las mismas características de esta especie de palmera, la cual presenta un tronco delgado e inerme y la copa poco frondosa, por lo tanto, no es visitada con frecuencia, ni proporciona abrigo permanente a mamíferos de gran tamaño. En efecto, la fauna observada estaba principalmente constituida por lagartijos (género *Phylodactylus*), ratones principalmente del género *Proechymis*, y pequeñas aves. Por cierto que la presencia de nidos en la palmera es un factor determinante de la presencia de *R. prolixus*, inclusive es posible que independientemente de las condiciones macro y/o microclimáticas, la persistencia de una fuente alimenticia constante es la mayor responsable del mantenimiento de una población en una palmera. Esto explicaría cómo muy frecuentemente durante las disecciones se observa que, mientras en una palmera podemos encontrar un número relativamente abundante de individuos, palmeras cercanas resultan negativas.

De cualquier manera, a pesar de la baja densidad, el conjunto de un gran número de palmeras en el llano sin duda constituye un biótopo importante para el mantenimiento del vector.

Los datos relativos a distribución etaria de los estadios dentro de la población, tienen correspondencia con los obtenidos en 1976 por Rossell (10), en *R. prolixus* doméstico. Esto hace pensar que en uno y otro caso pueda intervenir una característica biológica inherente al vector. Experimentos relacionados con la resistencia al ayuno de los diferentes estadios ninfales en condiciones de laboratorio, realizados por Feliciangeli y col. (3), han demostrado que el III y IV estadio son los más resistentes, pudiendo sobrevivir hasta 7 meses sin alimento, las ninfas de V estadio pueden alcanzar hasta 5 meses de ayuno, mientras que el I y II estadio sobreviven de 2 a 3 meses solamente.

Si examinamos la pirámide etaria de los *R. prolixus* capturados en relación a esa característica biológica, podríamos inferir que las ninfas de I y II estadio son más escasas, debido a que no solamente escapan más fácilmente a la captura, sino que también resisten muy poco al ayuno, por lo tanto permanecen muy corto tiempo en ese estadio ninfal: si logran alimentarse, pasan rápidamente al estadio sucesivo, y si no encuentran una fuente alimenticia, en poco tiempo mueren. En cambio, a nivel del III y IV estadio hay un acúmulo de individuos, debido a que tienen la capacidad de poder permanecer por mucho tiempo, e inclusive en proporción mayor que las ninfas de V estadio, las cuales van acumulándose sucesivamente en el estadio adulto.

Finalmente, los resultados de la baja infección a *T. cruzi*, también reflejan la escasa oportunidad que tienen los individuos de alimentarse de reservorios naturales de parásito. Esta conclusión no contrasta con el hecho de que haya infección mayor por *T. rangeli*, aunque el número de reservorios conocidos para este protozoario sea menor con respecto al primero. En efecto, estos resultados podrían ser consecuencia del canibalismo practicado por ninfas pequeñas hambrientas sobre ninfas mayores recién ingurgitadas. Este fenómeno ya observado por varios autores, entre ellos, en 1914 por Brumpt (1) y Ryckman (11), 1951, fue comprobado recientemente en nuestro laboratorio donde pudimos observar que esta alternativa alimenticia es bastante frecuente y que se presenta bajo dos modalidades: la ninfa caníbal puede ingurgitar sangre o puede ingerir hemolinfa de la recién alimentada. La proporción de estas últimas es normalmente más elevada con respecto a la primera y así ya fue demostrado en 1965 por Marinkelle (8) y uno de nosotros, Feliciangeli (4), cuando se encontró que es posible la transmisión directa de *T. cruzi* de individuo a individuo cuando ingurgitan sangre. Es de esperarse que este mecanismo entre en juego en proporción más elevada en la transmisión de *T. rangeli*.

RESUMEN

Se llevó a cabo un estudio longitudinal de la población de *Rhodnius prolixus* en la palma llanera *Copernicia tectorum* durante el año 1975-1976.

Se observa que la población triatomina ocupa este ecótopo durante todo el año siendo más abundante durante la estación lluviosa y más escasa en el período de sequía.

Se plantea la hipótesis que la resistencia al ayuno sea una componente importante en la distribución etaria de la población, debido a que la cantidad mayor de individuos está agrupada en los estadios III y IV los cuales, en laboratorio son los que mejor soportan la falta de alimento.

Se analizan los resultados de infección a *Trypanosoma cruzi* (0,2%) y a *T. rangeli* (13,4%) en función de la posibilidad de parte de este vector de adquirir la infección de los reservorios naturales y se plantea la posibilidad que el canibalismo puede jugar algún papel en la transmisión, especialmente en relación con *T. rangeli*.

SUMMARY

A longitudinal study of the population of *Rhodnius prolixus* in the palm-tree *Copernicia tectorum* was carried out from april 1975 through february 1976.

It was seen that the triatomine population occupies this ecotope during the whole year, being more abundant in the rainy season and lowest in the drier period.

Resistance to fast seems to be an important factor in the age composition of the population, since the greatest proportion of individuals collected were 3rd and 4 the instar nymphs, which, in the laboratory, are the stages in which survival without feeding is longest.

The difference found in the rates of natural infection of the bugs by *Trypanosoma cruzi* (0,2%) and *T. rangeli* (13.4%) is analysed in relation to the local reservoirs of the parasites and it is suggested that cannibalism might play an important role in the transmission, specially that of *T. rangeli*.

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Queremos expresar nuestro agradecimiento al profesor Leonidas Deane, Profesor Contratado de la Cátedra de Parasitología de la Universidad de Carabobo, por sus valiosas sugerencias en el análisis de los resultados; a la señorita Rosa Bigott, Auxiliar de Laboratorio I de la Cátedra de Parasitología de la Universidad de Carabobo, por su eficiente colaboración técnica y a los señores Rafael Garboza, Auxiliar de Laboratorio II de la Cátedra de Parasitología de la Universidad de Carabobo y Pedro Aular, Visitador Rural del Servicio de Endemias Rurales, de la Zona II de Malariología y Saneamiento Ambiental, por su ayuda en el trabajo de campo.

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Parasitismo de huevos de *Rhodnius prolixus* por los microhimenópteros *Telenomus costa-limai* y *Ooencyrtus trinidadensis* var. *venatorius*

M. DORA FELICIANGELI DE PIÑERO

El término parasitoide, recomendado por Doutt (1959), se aplica a especies que se caracterizan por matar a sus huéspedes, por lo tanto su acción se asemeja más a la de los depredadores, que a la de los verdaderos parásitos.

Este es el caso de los microhimenópteros que oviponen dentro del huevo de triatominos, y las larvas completan su desarrollo alimentándose del contenido de éste.

Actualmente se conocen en el Hemisferio Occidental, cuatro especies de microhimenópteros parasitoides endófagos de huevos de triatominos vectores de la enfermedad de Chagas.

Telenomus fariai, encontrado en 1927 por primera vez por Costa Lima (1) en Brasil en frascos de cría de *Triatoma megista (= Panstrongylus megistus)*; sucesivamente fue recolectado en condiciones naturales en varios países de América Latina por Mazza y Jorg (10); Mazza (11); Pinto (13); Peláez (12), Lumbreras *et al.* (8), Zeledón (15).

Telenomus costa-limai fue encontrado en 1959 por primera vez en Venezuela en frascos de cría de *Rhodnius prolixus* por Ortiz y Alvarez (9) y sucesivamente reencontrado parasitando huevos del mismo huésped en su habitat natural por Feliciangeli (7) y clasificado por De Santis *et al.* (3).

Ooencyrtus trinidadensis, originario de Trinidad, Grawford (2), ha sido encontrado en Venezuela como parasitóide de huevos de *R. prolixus* por Feliciangeli (7) y clasificado como una nueva subespecie: *O. trinidadensis* var. *venatorius* De Santis *et al.* (3).

Más recientemente, también en Venezuela ha sido encontrado otro *Telenomus* sp. parasitando naturalmente huevos de *Psammolestes arthuri* y que, en condiciones experimentales aceptó parasitar huevos de *R. prolixus* con el cual se mantiene actualmente en laboratorio, Feliciangeli y Marino (6), Feliciangeli y Tonn (7).

Dra. Piñero, Biólogo, Profesor Agregado, Cátedra de Parasitología, Escuela de Medicina, Facultad de Ciencias de la Salud, Universidad de Carabobo, Valencia, Venezuela.

En el presente trabajo se estudian:

1. El parasitismo de *T. costa-limai* y *O. trinidadensis* var. *venatorius*.
2. Algunas características reproductivas de estos microhimenópteros en su huésped natural.

MATERIALES Y METODOS

Las colonias de *O. trinidadensis* y *T. costa-limai* fueron iniciadas con especímenes provenientes de Higuerotal, municipio San Francisco de Asís, estado Aragua (año 1972) y mantenidas en laboratorio mediante el suministro constante y exclusivo de huevos de *R. prolixus*, a 28 ± 2 °C y HR = 50 – 60%.

La cría de *R. prolixus*, originaria de Los Naranjos, municipio Negro Primero, estado Carabobo, se encuentra mantenida en el Insectario de la Cátedra de Parasitología desde el año 1967 en base a alimentación con aves de corral a ritmo quincenal, lo que proporciona una producción constante y adecuada de huevos.

Las avispas adultas utilizadas en los experimentos, eran obtenidas de huevos parasitados procedentes de la cría, los cuales habían sido aislados individualmente en frascos de vidrio de fondo plano (1.5 cm de diámetro x 5.0 cm de altura) para seleccionar los que producían hembras solamente, con la finalidad de tener la seguridad de que no estarían fecundadas. Inmediatamente después de la emergencia estas fueron repartidas en dos grupos: algunas fueron apareadas, mientras que las del otro grupo se mantuvieron aisladas. A todas se ofrecieron huevos de *R. prolixus* diariamente (hasta la fecha de su muerte) para que efectuasen la oviposición y poder por lo tanto verificar la capacidad de parasitismo y la progenie producida por hembra.

Siempre se utilizaron huevos-huéspedes de edad conocida (0-48 horas) y adheridos a los papeles que *R. prolixus* utiliza para la ovipostura en los frascos de cría. A *O. trinidadensis* se ofrecieron lotes de 10 huevos y a *T. costa-limai* lotes de 20 huevos debido a que en experimentos preliminares se había observado un mayor parasitismo en esta última especie.

Cada 24 horas los huevos eran retirados y reemplazados por huevos nuevos y los anteriores eran conservados en estufa, debidamente rotulados, hasta la emergencia de la progenie.

Para *O. trinidadensis* se estudió un grupo de 15 hembras fecundadas, y un grupo de 24 hembras no fecundadas, mientras que para *T. costa-limai* se estudió solamente un grupo de 26 hembras no fecundadas, debido à que no se encontraron machos en la cría.

RESULTADOS

1. PARASITISMO

O. trinidadensis. El Cuadro Nº 1 presenta los resultados relativos a hembras fecundadas. El número promedio de huevos parasitados por hembra fue de 28.5 (s = 14.6) y el porcentaje de huevos parasitados que no dio progenie fue 2.6, siendo la longevidad media igual a 12.4 días.

En la Figura 1, se presentan los valores promedio (± s) del número de huevos parasitados diariamente a partir del primer día de vida adulta.

CUADRO Nº 1

Ooencyrtus trinidadensis* var. *venatorius* fecundadas: Parasitismo y progenie producida en huevos de *Rhodnius prolixus

Número de avispa	Número de huevos ofrecidos	Número de huevos parasitados	Progenie producida ♀♀	♂♂	Número de huevos parasitados sin progenie
1	150	44	16	61	0
2	100	28	6	47	0
3	140	35	10	60	0
4	80	22	5	31	2
5	100	26	6	35	1
6	150	45	14	54	1
7	150	41	9	50	3
8	40	4	1	4	0
9	160	42	9	59	2
10	130	30	8	39	0
11	60	10	2	13	0
12	100	25	4	37	1
13	100	27	6	37	0
14	200	47	13	74	1
15	50	1	1	1	0

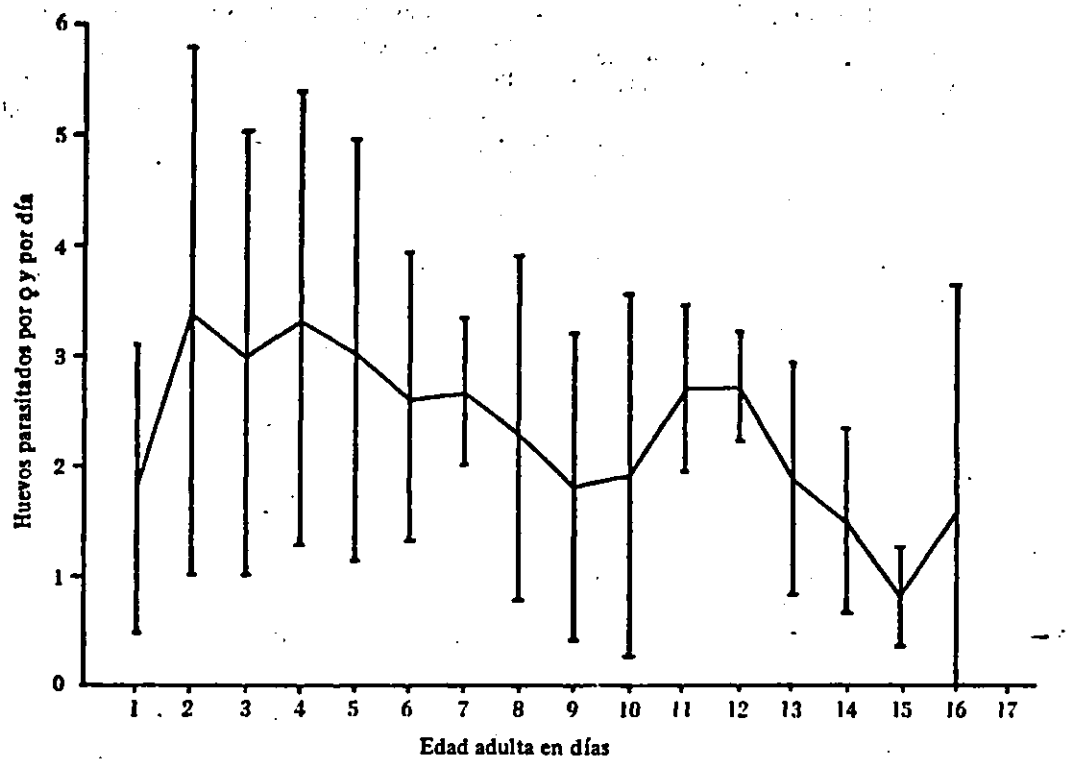

Fig. 1. ***O. trinidadensis*** **fecundadas: Parasitismo de huevos de** ***R. prolixus*** **(x ± s).**

El Cuadro Nº 2, proporciona la misma información relativa a *O. trinidadensis* no fecundadas. En éstas la longevidad promedio fue de 15 días, el promedio de huevos parasitados por hembra fue de 29.6 ± 14.0 y el porcentaje de huevos parasitados sin progenie fue 1.2.

Aplicando la prueba "t" de Student no se encontró diferencia significativa en cuanto a parasitismo en las dos muestras (t = 0.18; g. l. = 37). Los valores de huevos parasitados/día/avispa, se presentan en la Figura 2.

En su aspecto general las dos curvas, relativas a hembras vírgenes (Fig. 1 y 2) se asemejan ya que se observa que en ambos casos el parasitismo es escaso durante el primer día de vida adulta cuando las avispas principalmente parecen dedicadas a alimentarse: se observó en varias oportunidades que pinchan con el ovipositor el huevo-huésped para después ingerir pequeñas gotas del contenido del mismo.

Los valores máximos de parasitismo son alcanzados al 2° y 4° día por las avispas fecundadas (Fig. 1) con un promedio de 3.4 huevos/hembra. Al 9° y 10° día el parasitismo es notablemente más bajo, aumenta de nuevo al 12 y 13 día y finalmente se nota una tendencia a bajar progresivamente con el envejecimiento de la hembra. En las hembras no fecundadas el parasitismo más alto es realizado al 10° día de vida adulta con 3.5 huevos/hembra.

En cuanto a *T. costa-limai* (Cuadro Nº 3) el promedio de huevos parasitados durante toda la vida fue $\bar{x}$ = 32.7 (= 4.6), mayor que *O. trinidadensis* a pesar de tener una longevidad mucho menor que esta última, (long. media = 6.6 días) sin embargo la diferencia entre las medias no fue estadísticamente significativa ni en relación al parasitismo realizado por las hembras fecundadas (t = 1.38; g. l. = 39), ni en relación al parasitismo realizado por hembras partenogenéticas (t = 1.17; g. l. = 48).

La Figura 3 permite observar en esta especie un comportamiento completamente diferente a *O. trinidadensis:* el primer día de vida adulta es la edad de mayor parasitismo con un promedio de 13.8 huevos parasitados por hembra. Este valor cae bruscamente a

CUADRO Nº 2

Ooencyrtus trinidadensis var. *venatorius* partenogenéticas: Parasitismo y progenie producida en huevos de *Rhodnius prolixus*

Número de avispa	Número de huevos ofrecidos	Número de huevos parasitados	Progenie producida ♂♂	Número de huevos parasitados sin progenie
1	160	43	87	0
2	120	30	62	1
3	110	33	61	0
4	150	43	78	1
5	40	7	15	0
6	60	9	17	0
7	70	14	23	0
8	90	12	25	0
9	190	36	59	0
10	110	17	30	0
11	200	47	88	0
12	210	46	83	1
13	130	31	61	1
14	250	48	85	1
15	200	32	62	1
16	160	35	64	1
17	140	35	73	0
18	100	7	13	0
19	140	33	69	0
20	50	10	21	0
21	180	33	64	0
22	200	40	85	0
23	220	51	99	0
24	50	18	38	1

un valor 10 veces menor al tercer día, aumenta ligeramente al 4° y 5° día y de nuevo disminuye hasta 2 huevos/hembra al 7° día, mientras las que alcanzan la longevidad máxima (8 días) ya no están en capacidad de parasitar.

En ningún momento se observó que *T. costa-limai* se alimentaba del huevo de *R. prolixus*, lo cual explicaría la menor longevidad con respecto a *O. trinidadensis*.

2. REPRODUCCION

Ambas especies, *O. trinidadensis* y *T. costa-limai* son maduras sexualmente tan pronto como emergen del huevo-huésped.

En el Cuadro Nº 1 se observa que la progenie de hembras fecundadas estuvo formada por machos y hembras en proporción aproximada de un macho por cinco hembras. El número de hijos promedio producido por hembra fue de 47.5 y el número de hembras/hembra de 40.1.

El Cuadro Nº 2, evidencia que cuando las hembras no están fecundadas pueden oviponer dentro del huevo de *R. prolixus*, pero la progenie producida está en este caso constituida únicamente por machos. El número de hijos producidos/hembra fue igual a 56.8.

T. costa-limai. El Cuadro Nº 3 muestra que las hembras de *T. costa-limai* se reproducen partenogené-

CUADRO Nº 3

Telenomus costa-limai partenogenéticas: Parasitismo y progenie producida en huevos de *Rhodnius prolixus*

Número de avispa	Número de huevos ofrecidos	Número de huevos parasitados	Progenie producida ♀♀	Número de huevos parasitados sin progenie
1	140	32	32	0
2	160	37	37	0
3	120	30	29	1
4	140	30	30	0
5	120	28	27	1
6	140	39	37	2
7	140	35	32	3
8	140	34	34	0
9	160	41	39	2
10	140	34	33	1
11	140	28	27	1
12	140	37	36	1
13	120	34	33	1
14	140	33	33	0
15	140	31	31	0
16	140	31	29	2
17	140	39	37	2
18	120	36	36	0
19	120	33	32	1
20	140	28	27	1
21	140	34	31	3
22	120	37	37	0
23	100	27	27	0
24	120	21	21	0
25	120	26	25	1
26	120	36	34	2

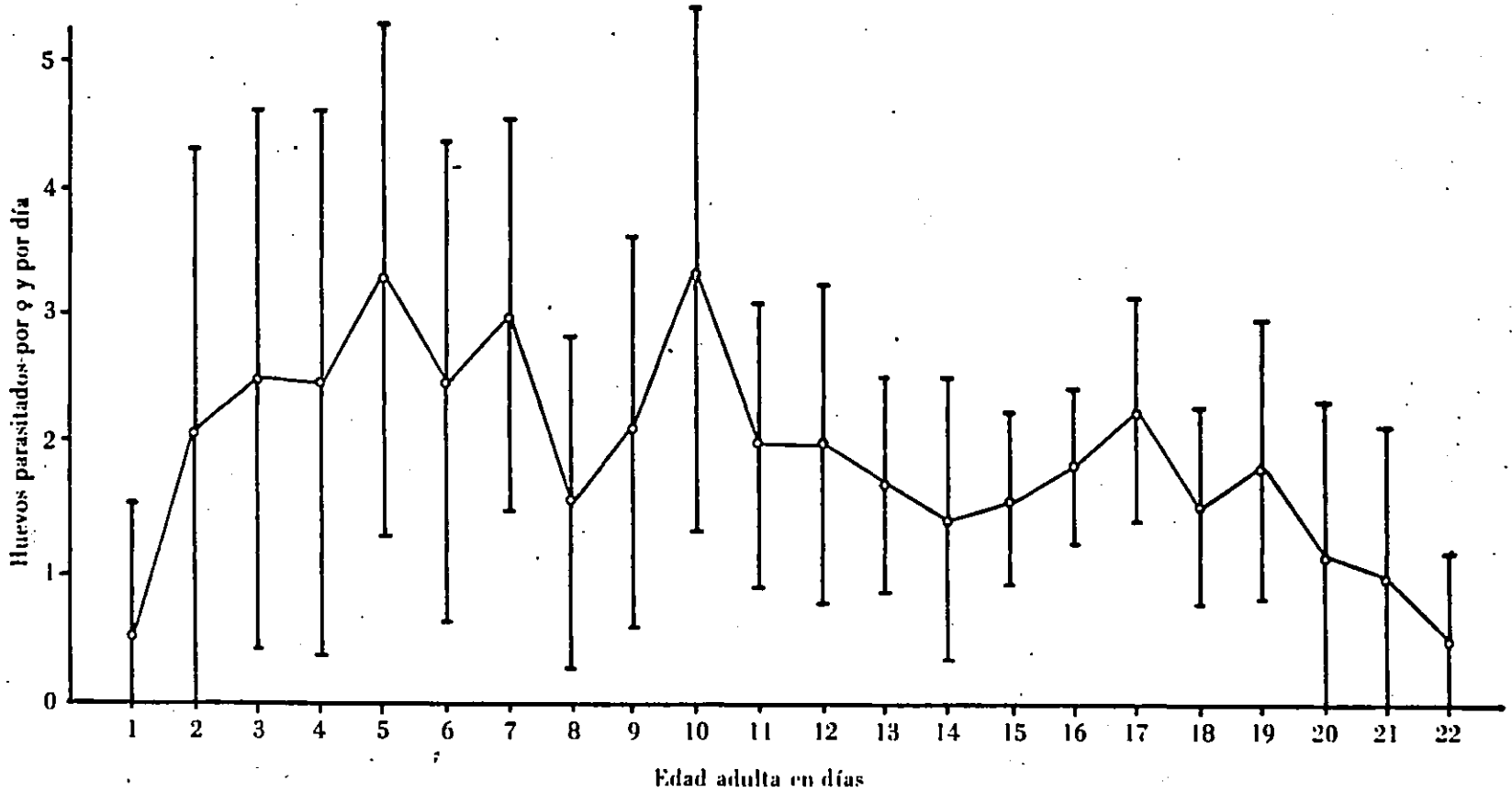

Fig. 2. *O. trinidadensis* partenogenéticas: Parasitismo de huevos de *R. prolixus* (x ± s).

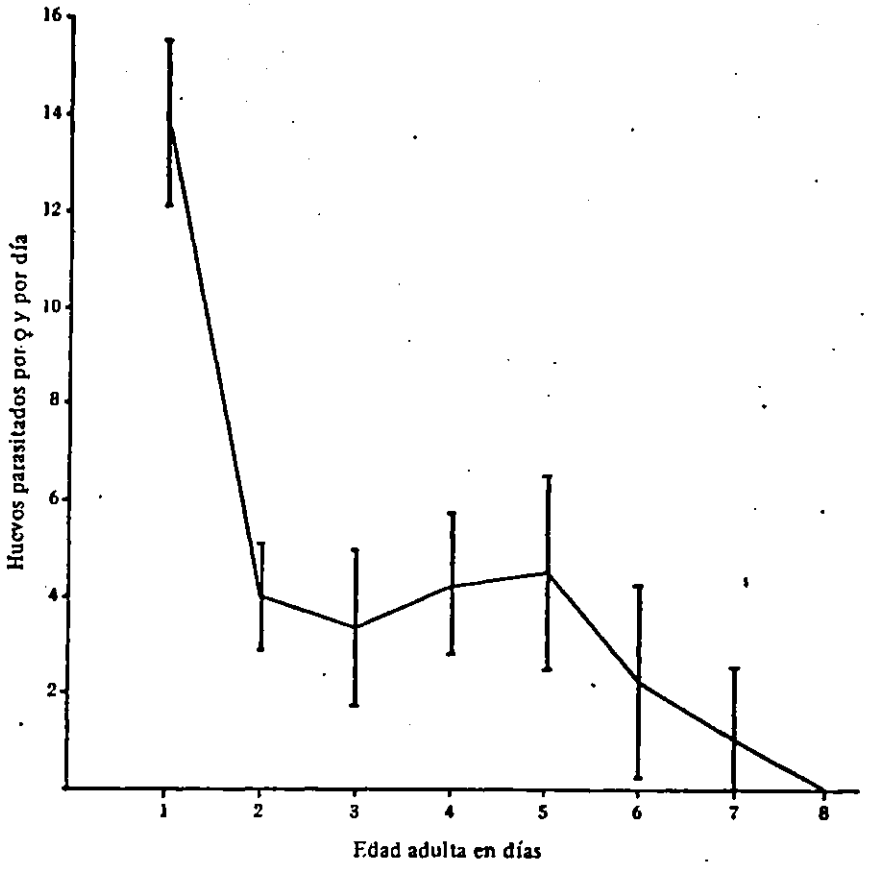

Fig. 3. *T. costa-limai:* Parasitismo de huevos de *R. prolixus* (x ± s).

ticamente pero en este caso la progenie está formada solo por hembras. El número de hembras por hembra fue igual a 31.8.

También se observó diferencia en las dos especies en relación al número de hijos producidos por huevo parasitado. Se notó que en las condiciones experimentales descritas (hembras aisladas en frascos individuales) el número de individuos que puede emerger de un huevo de *O. trinidadensis* parasitado es de uno á tres; mientras que en *T. costa-limai* un huevo parasitado siempre produce un solo individuo.

DISCUSION

El papel de los parásitos y los depredadores en la dinámica de las poblaciones naturales ha sido uno de los problemas más controvertidos en la ecología de las poblaciones. Se han utilizado con éxito enemigos naturales para el control de insectos dañinos, pero las propiedades de esas poblaciones no han sido suficientemente conocidas con anterioridad a su uso como para poder predecir el grado de éxito, ni tampoco se han hecho estudios posteriores a la introducción de las mismas que pudieran dilucidar cuáles factores entraron realmente en juego. (Varley y Gradwell, 1971).

El presente trabajo es el primero de una serie de experimentos cuyos objetivos fue recolectar una información biológica básica, en condiciones de laboratorio, sobre dos microhimenópteros, *O. trinidadensis* y *T. costa-limai*, parásitos naturales de *R. prolixus*, con el propósito de investigar y comparar sus bondades como agentes de control biológico del principal vector de la enfermedad de Chagas en Venezuela y así estimar las posibilidades de su aprovechamiento y el posible grado de éxito que puedan proporcionar en una Campaña de control biológico.

Las observaciones sobre el parasitismo han per-

mitido constatar que las dos especies presentan un comportamiento completamente diferente, aunque el resultado final sea muy parecido.

En efecto, no hay diferencias significativas entre las dos especies en cuanto a cantidad de huevos parasitados lo cual hace pensar en que están capacitadas para competir exitosamente para el aprovechamiento del húesped del cual depende su sobrevivencia; sin embargo, hay diferencias en cuanto a tiempo empleado para efectuar dicho parasitismo. *T. costa-limai,* durante el primer día de vida adulta parasita aproximadamente la mitad de todos los huevos parasitados durante la vida, mientras que *O. trinidadensis* es mucho más lento y necesita mucho más tiempo para lograr el mismo impacto sobre la población del hospedador.

Por lo tanto, si se pensara en la utilización de estos microhimenópteros como agentes de control biológico, dependiendo del enfoque específico de la estrategia a seguir, deberían ponderarse dichas diferencias: *T. costa-limai* parece ofrecer la ventaja de una acción más rápida, por lo tanto sucesivos lanzamientos de este microhimenóptero a muy corto plazo podrían reducir drásticamente la población del hospedador asegurando posiblemente un resultado más efectivo en un tiempo más corto.

Las observaciones sobre la reproducción han llevado a la conclusión que *O. trinidadensis* es una especie arrenotoca o sea que hay producción de machos haploides y hembras diploides, ya que la progenie de hembras fecundadas fue de machos y hembras, mientras que la progenie de hembras vírgenes estaba formada sólo por machos.

En *T. costa-limai* en cambio, se observa un sistema de reproducción teleotoca en que sólo existe producción de hembras partenogenéticas y no es necesaria la presencia de machos.

Es de hacer notar que sólo en tres oportunidades, durante un período de 3 años de mantenimiento de la cría, se ha observado la aparición de un macho, reconocible morfológicamente por la mayor longitud de las antenas (presentan 11 segmentos, uno más que las hembras) y por las genitalia. Este fenómeno podría sugerir que ocasionalmente hay también producción de machos haploides (deuterotoquia).

Las observaciones sobre el número de hijos nacidos por huevo parasitado permiten concluir que *O. trinidadensis* es un parasitoide interno gregario, o sea, que de un solo huésped puede normalmente desarrollarse más de un individuo, mientras que *T. costa limai* es un parasitoide interno solitario ya que siempre emerge un solo individuo por huevo parasitado.

Esto hace pensar en la posibilidad que en *O. trinidadensis,* en determinadas condiciones, pueda evidenciarse el superparasitismo, situación que se establece cuando en el huésped se encuentran más parásitos de los que los tejidos puedan mantener. Los efectos del superparasitismo en los parasitoides gregarios son difícilmente predecibles y pueden afectar notablemente la progenie producida hasta el punto que ningún individuo logra nacer.

La habilidad de la hembra en estimar la capacidad del huésped y la cantidad de progenie ya presente, son entonces factores muy importantes para poder garantizar la sobrevivencia de la especie.

En cambio en el caso de los parasitoides solitarios *(T. costa-limai),* aunque pueda haber superparasitismo, generalmente un solo individuo logra siempre sobrevivir y garantizar por lo tanto la continuidad de la especie.

Es necesario confirmar esta hipótesis con experimentos diseñados a fin de estudiar los efectos de las variaciones de densidad entre huéspedes y parásitos para establecer sí realmente puede haber superparasitismo, cuáles son sus efectos y ponderar la importancia de los mismos para la utilización de una u otra especie.

RESUMEN

El objetivo del presente trabajo fue estudiar el parasitismo de huevos de *Rhodnius prolixus* por dos microhimenópteros autóctonos de Venezuela. Lotes de huevos de *R. prolixus* fueron ofrecidos diariamente, a hembras de *Ooencyrtus trinidadensis* var. *venatorius* y *Telenomus costa-limai* en laboratorio y aisladas individualmente en frascos de vidrio de fondo plano de 1.5 x 5.0 cm. Hembras fecundadas de *O. trinidadensis* parasitaron durante toda la vida un promedio de 28.5 huevos, y hembras no fecundadas parasitaron alrededor de 29.6 huevos.

T. costa-limai no fecundadas, en las mismas condiciones experimentales, parasitaron un promedio de 32.7 huevos de *R. prolixus*, no habiendo por lo tanto diferencia estadísticamente significativa entre las dos especies en relación a la cantidad de huevos parasitados. Sin embargo, el comportamiento de las dos avispas fue muy diferente ya que *T. costa-limai* realizó dicho parasitismo en un tiempo mucho más corto: la longevidad media de esta especie fue de 6.6 días en promedio, mientras la de *O. trinidadensis* fue de 12.4 y 15 días. Esta diferencia parece ser debida al hecho que *O. trinidadensis* se alimenta del huevo-huésped, mientras que *T. costa-limai* solamente utiliza las reservas alimenticias acumuladas durante las fases pre-adultas. Las observaciones sobre la reproducción de estos parasitoides llevó a la conclusión de que *O. trinidadensis* es una especie arrenotoca ya que, cuando es fecundada, la hembra produce machos haploides y hembras diploides, mientras que si no es fecundada, produce machos haploides y hembras diploides.

T. costa-limai presenta en cambio partenogenesis teleotoca ya que normalmente no hay machos y las hembras partenogenéticas sólo producen hembras diploides. También se observó que *O. trinidadensis* es un parasitoide interno gregario ya que de un solo huésped normalmente puede desarrollarse más de un individuo, *T. costa-limai* en cambio, es un parasitoide interno solitario ya que de cada huevo parasitado siempre emerge un solo individuo. Se hacen consideraciones sobre la importancia que estas diferencias biológicas entre las dos especies podrían tener en relación a la utilización de una u otra especie como agente de control biológico para *R. prolixus*.

SUMMARY

This work is a study of parasitism of *Rhodnius prolixus* eggs by two microhymenoptera indigenous to Venezuela. Eggs of *R. prolixus* were daily offered to *Ooencyrtus trinidadensis* var. *venatorius* and *Telenomus costa-limai* reared in the laboratory and individually kept in glass vials (1.5 x 5.0 cm). The averages of parasitized *R. prolixus* eggs through the wasps adult life were 28.5 per fecundated female and 29.6 per virgin female of *O. trinidadensis* and 32.7 per female of *T. costa-limai*.

However, the daily efficiency of *T. costa-limai* was greater, since its adult life span averaged 6.6 days while *O. trinidadensis* female survived 12.4 to 15 days. This difference in survival could be related to the fact that *O. trinidadensis* females feed on the host-egg, while those of *T. costa-limai* do not ingest food during adult life. Observations about the reproduction of these microhyminoptera permitted to conclude that *O. trinidadensis* is an arrhenotokous species, since the female produce haploid males and diploid female when fecundated, and only haploid males if not fecundated. *T. costa-limai* instead presents a thelytokous parthenogenesis because generally there are no males and the females only produce diploid females. It was also observed that *O. trinidadensis* is an internal gregarious parasitoid because several specimens can develop from a single host-egg, while *T. costa-limai* is an internal solitary parasitoid, only one specimen emerging from each parasitized egg. The importance of these biological differences between the two species is discussed in relation to the use of the se microhymenoptera as agents of biological control of *R. prolixus*.

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HIMENOPTEROS PARASITOIDES DE "RHODNIUS PROLIXUS" (HEM.) EN VENEZUELA

por L. DE SANTIS, JULIA A. VIDAL SARMIENTO, J. E. RABINOVICH y DORA FELICIANGELLI DE PIÑERO

SUMMARY: In this paper, Drs. L. De Santis and Julia A. Vidal Sarmiento describes *Ooencyrtus trinidadensis venatorius* new subspecies *(Encyrtidae)* and the allotype male of *Telenomus costalimai* Ortiz et Alvarez, 1959 *(Scelionidae)* and Drs. J. Rabinovich and Dora Feliciangelli de Piñero adds bionomics observations on boths, reared from eggs of *Rhodnius prolixus* Stal, at Higuerotal (Aragua - Venezuela).

Los materiales correspondientes a la especie y subespecie de himenópteros parasitoides que estudiamos en esta nota siguiendo el método que hemos adoptado en nuestros trabajos sobre el grupo, quedan incorporados a las colecciones del Museo de La Plata. Una preparación de *Telenomus costalimai* y una pareja paratipo de *Ooencyrtus trinidadensis venatorius* han sido depositadas en el Departamento de Artropodología del Instituto Nacional de Microbiología, con sede en Buenos Aires; otra será enviada al British Museum (Natural History) de Londres.

La parte taxionómica ha sido elaborada por los doctores De Santis y Vidal Sarmiento, a quienes tendrá que ser acreditada la nueva subespecie que damos a conocer en tanto que los doctores Rabinovich y Feliciangelli de Piñero, son los responsables de la parte bionómica.

SCELIONIDAE

Telenomus costalimai Ortiz et Alvarez

(Figs. 1-2, 6, 8 y 10-12)

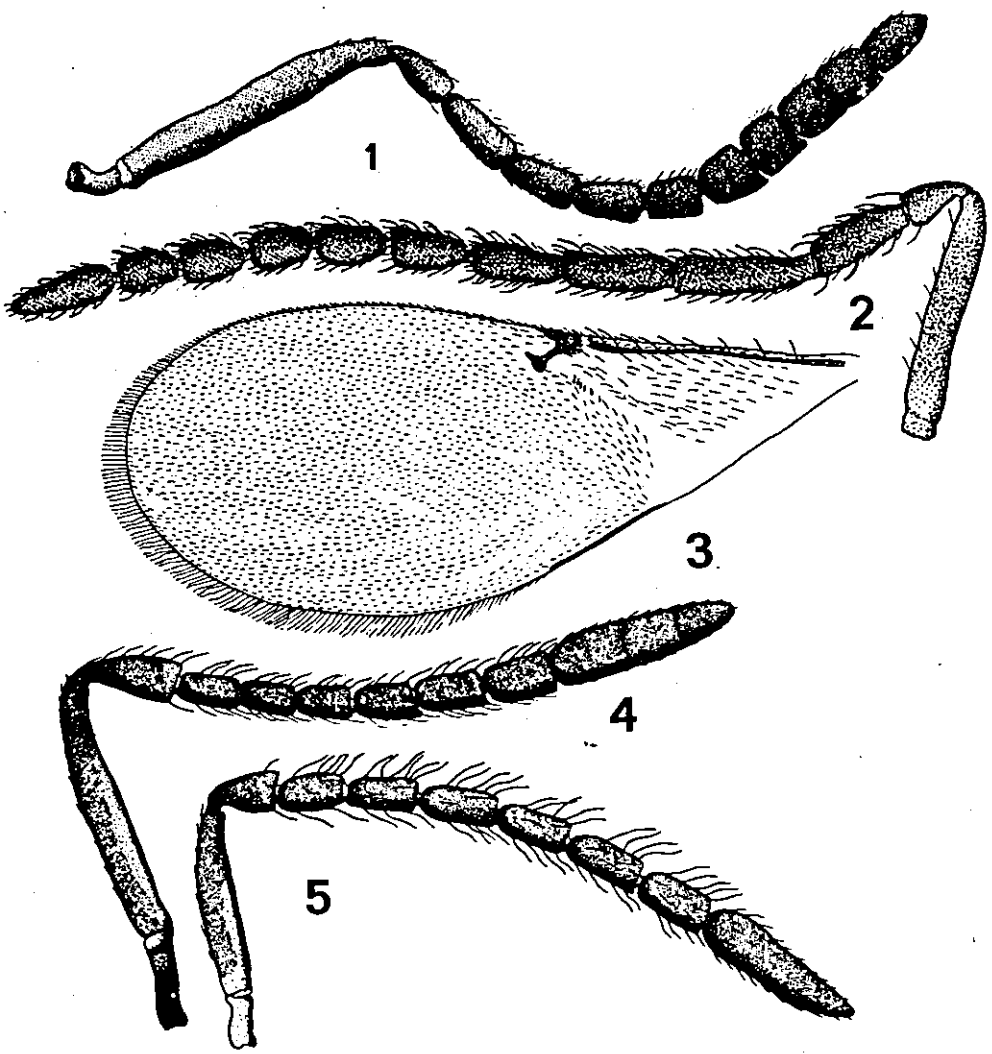
Telenomus costalimai Ortiz et Alvarez, 1959, *Rev. San. Asist. Soc. Caracas*, 24(3-4): 373.

HEMBRA: Puede ser reconocida por la descripción original. Agregamos un dibujo de las antenas (Fig. 1); dimensiones de cada artejo (en mm):

(1) Facultad de Ciencias Naturales y Museo, La Plata, República Argentina.
(2) Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, apartado 1827, Caracas 101, Venezuela.
(3) Cátedra de Parasitología, Facultad de Ciencias de la Salud, Universidad de Carabobo, Valencia, Venezuela.

	Longitud	Anchura		Longitud	Anchura
R.	0,052	0,026	VI.	0,057	0,047
I	0,305	0,047	VII	0,057	0,057
II	0,088	0,036	VIII	0,052	0,057
III	0,093	0,036	IX	0,052	0,057
IV	0,078	0,041	X	0,052	0,052
V	0,057	0,041	XI	0,058	0,047

MACHO: Parecido a la hembra. Antenas conformadas tal como se ve en la figura 2; dimensiones de cada artejo:



Figs. 1 y 2. *Telenomus costalimai* Ortiz et Alvarez. 1, antena de la hembra; 2, antena del macho.

Figs. 3 a 5. *Ooencyrtus trinidadensis venatorius* sp.n. 3, ala anterior de la hembra; 4, antena de la misma; 5, antena del macho.

	Longitud	Anchura		Longitud	Anchura
I	0,259	0,039	VII	0,083	0,039
II	0,072	0,036	VIII	0,072	0,039
III	0,103	0,041	IX	0,070	0,039
IV	0,134	0,036	X	0,065	0,039
V	0,114	0,039	XI	0,060	0,036
VI	0,098	0,041	XII	0,103	0,031

Longitud del cuerpo 1,3.

DISTRIBUCION GEOGRAFICA. Estados Aragua y Yaracuy (Venezuela).

BIONOMIA. Se trata de una especie solitaria, en que las hembras son muy activas, y de comportamiento agresivo, siendo comunes las luchas entre hembras, las cuales con frecuencia pueden llegar a ser mortales. Los machos no demuestran ningún comportamiento de cortejo sexual, son de carácter agresivo, y luego de perseguir a las hembras realizan una cópula que dura pocos segundos. La oviposición dura aproximadamente unos 5 minutos, y se realiza después de un activo comportamiento de inspección por

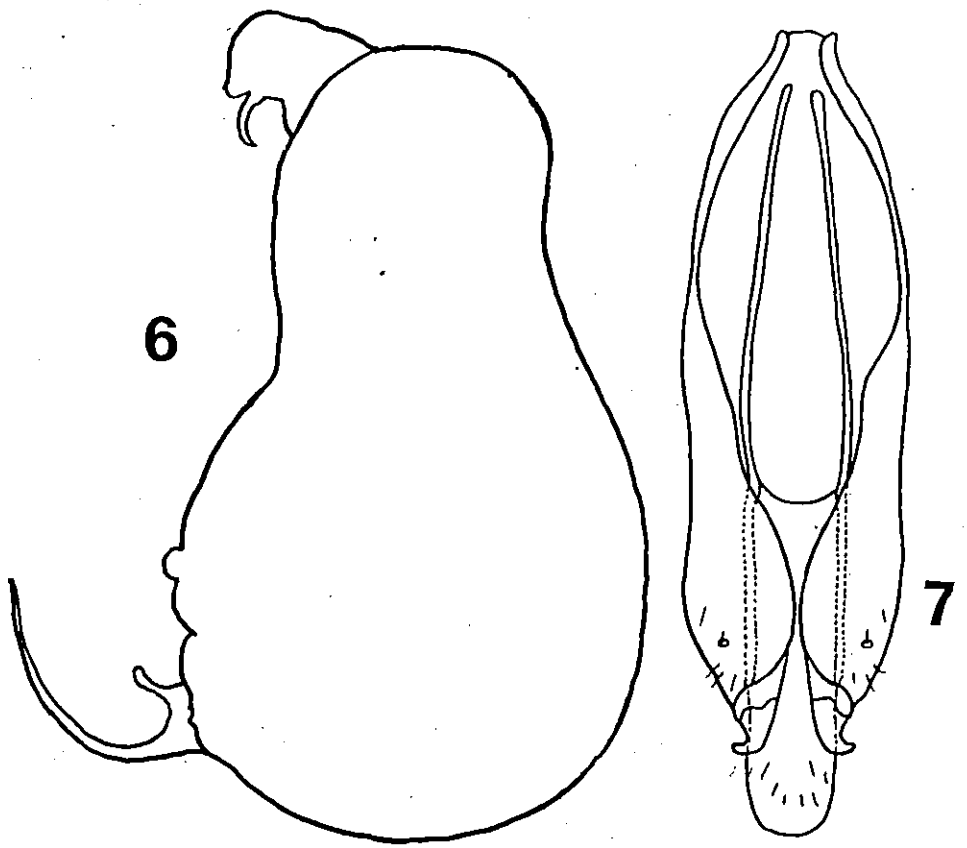
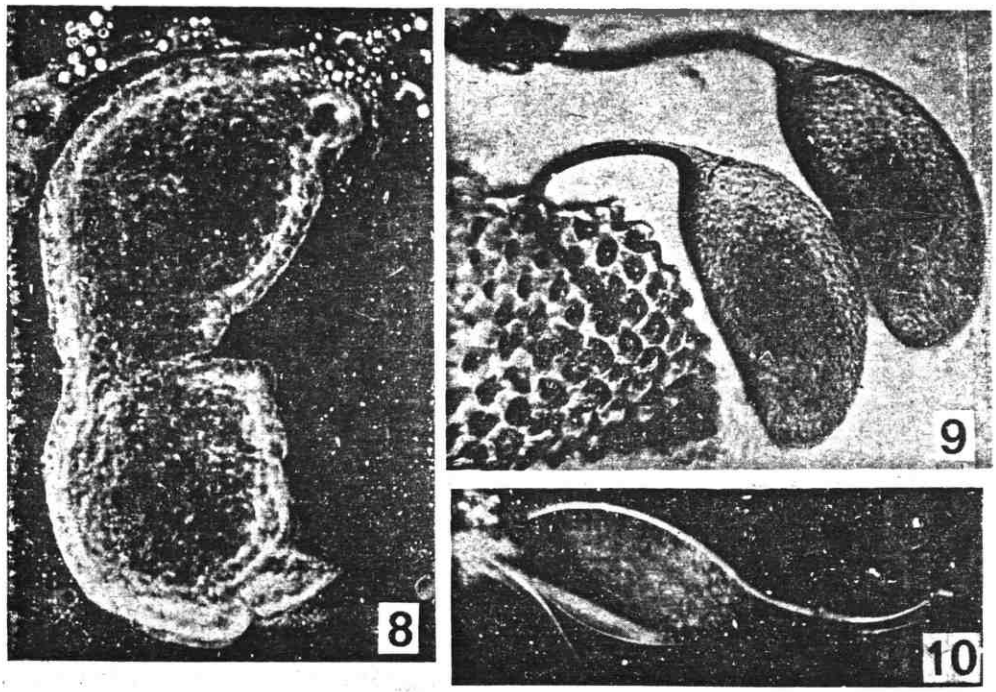


Fig. 6. Contorno de la larva teleaforme de *Telenomus costalimai* 24 horas después de la eclosión (De una microfotografía tomada por el doctor Dan Derling).

Fig. 7. Organo copulador de *Ooencyrtus trinidadensis venatorius* sp.n.



Figs. 8 y 10. *Telenomus costalimai* Ortiz et Alvarez. 8, embrión de 14 horas rodeado por el corion; 10, huevo

Fig. 9. *Ooencyrtus trinidadensis venatorius* sp.n. 9, huevo a las 24 horas de depositado (Detalle de las placas seroscópicas adheridas al corion del huevo del huésped).

(Fotos tomadas pro el doctor Dan Derling).

"tamborilleo" con las antenas. Luego de la oviposición la hembra abandona el hospedador (nunca oviponen en el mismo huevo más de una vez) después de un proceso de marcaje con el ovipositor similar al reportado para *Telenomus fariai*. La inserción del ovipositor puede llevarse a cabo en cualquier parte del corion, con la excepción del opérculo. En general se deposita sólo un huevo por hospedador, el cual es de tipo pedunculado (Fig. 10).

La duración del ciclo de vida desde el huevo hasta la emergencia del adulto es de aproximadamente 20 días, distribuídos entre las diferentes etapas de desarrollo de la siguiente manera: 17 horas como huevo, 55 horas como larva de primer estadio (Fig. 6), 24 horas como larva de 2do. estadio, 72 horas como larva de 3er. estadio, y 312 horas (unos 13 días) como pupa.

La emergencia de machos a partir de los huevos parasitados es sumamente rara. De cada huevo parasitado suele nacer una única hembra, la cual ya está sexualmente madura y en capacidad de comenzar a buscar nuevos hospedadores. Las hembras tienen una longevidad reducida (promedio = 5,1 días) siendo sumamente raro que una hembra llegue a vivir 6 días.

En total una hembra puede llegar a parasitar unos 20 hospedadores durante su lapso de vida, pero el gran esfuerzo de parasitismo se lleva a cabo durante las primeras 24 horas, en que pueden parasitar aproximadamente 15 huevos de *R. prolixus*.

MATERIAL ESTUDIADO: 1 ♂ alotipo y numerosas hembras del Municipio Higuerotal, Estado Aragua, Septiembre 1972, Dora Feliciangelli (Colector).

ENCYRTIDAE

Ooencyrtus trinidadensis venatorius ssp. n.

(Figs. 3 a 5, 7 y 9)

HEMBRA. Negro con reflejos verdosos y pupúreos, mas intensos en la cara y mitad basal del gáster. Región ventral del escapo hasta la línea del tercio apical, amarillento; el resto de las antenas negruzco. Patas amarillentas, más o menos ennegrecidas en las coxas, fémures y tarsos y en un anillo sub-basal en todas las tibias. Alas hialinas con nervaduras parduzcas.

Cabeza reticulada, con punteado poco marcado y esparcido en el frontovértice; mesoescudo también reticulado con punteado setífero; escudete reticulado excepto en el ápice y lateralmente donde es liso y brillante, lo mismo que el gáster.

Ojos ralamente pestañosos, con setas muy cortas; mesoescudo y escudete con setas oscuras, mas largas y esparcidas en este último.

Cabeza tan ancha como el tórax; vista de frente casi circular, tan ancha como larga; escrobas excavadas, reunidas arriba; frontovértice mas bien estrecho igual, casi, a la tercera parte de la anchura de la cabeza; ocelos en triángulo isósceles, los posteriores muy cerca de las órbitas internas correspondientes; mandíbulas con dos dientes y una ancha truncadura oblicua interna; palpos maxilares de 4 artejos, labiales de 3; antenas insertas a igual distancia de la boca y de la línea inferior de los ojos, conformadas tal como se ve en la figura 4; dimensiones de cada artejo:

	Longitud	Anchura		Longitud	Anchura
R	0,067	0,018	VI	0,047	0,026
I	0,207	0,031	VII	0,052	0,028
II	0,078	0,028	VIII	0,052	0,031
III	0,049	0,023	IX	0,062	0,036
IV	0,041	0,023	X	0,044	0,036
V	0,041	0,023	XI	0,044	0,031

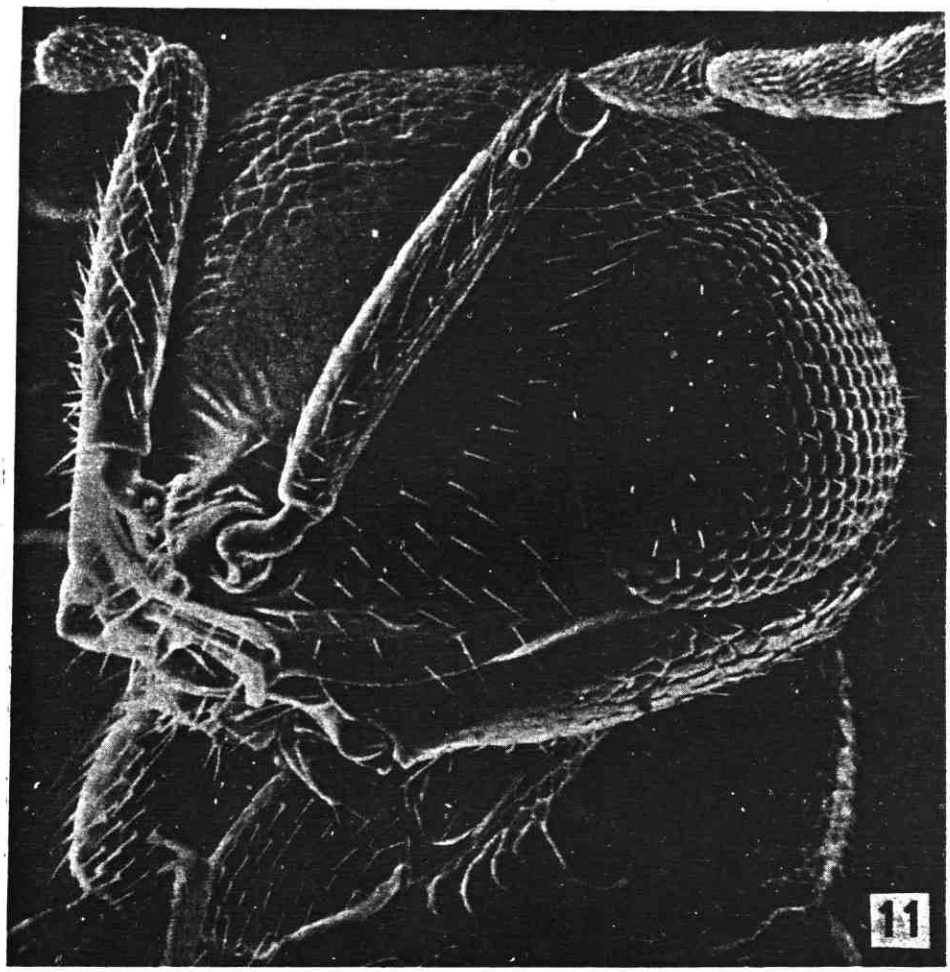
Pronoto bien visible en posición dorsal; mesoescudo ancho, entero; axilas separadas; escudete poco convexo; propodeo corto. Longitud de la alas anteriores (figura 3) 1,054; anchura máxima 0,457; longitud de las pestañas marginales mas largas 0,036; longitudes de las nervaduras submarginal, marginal, postmarginal y estigmática, en la relación siguiente: 30:3:0,5:4. Longitud de las alas posteriores 0,737; anchura máxima 0,190; longitud de las pestañas marginales mas largas 0,051. Espolón de las tibias intermedias mas corto que el basitarso correspondiente (9:11).

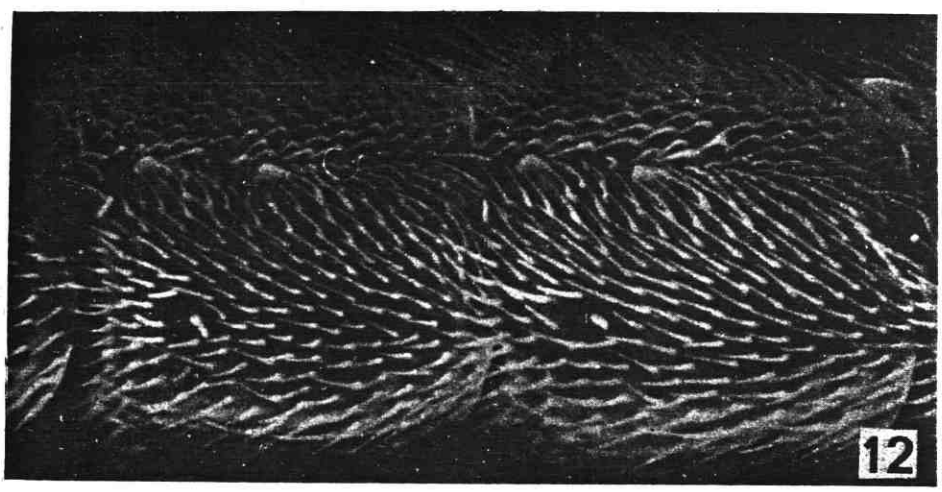
Gáster más corto que el tórax, de contorno subtriangular; oviscapto largo, nace cerca de la base y es apenas saliente.

Longitud del cuerpo 0,95.

MACHO: Se diferencia de la hembra por la coloración y conformación de las antenas.

Cabeza con reflejos verdosos y antenas de color pardo-amarillento conformadas tal como se ve en la figura 5; dimensiones de cada artejo:





Figs. 11 y 12. *Telenomus costalimai* Ortiz et Alvarez. 11, Detalle de la cabeza, parte proximal de las antenas y protórax; 12, detalle de dos artejos del flagelo mostrando los órganos sensoriales, de posible intervención en la detectión de la marca de parasitismo.

	Longitud	Anchura		Longitud	Anchura
R	0,039	0,018	V	0,057	0,023
I	0,145	0,028	VI	0,057	0,023
II	0,047	0,028	VII	0,057	0,026
III	0,049	0,026	VIII	0,056	0,028
IV	0.052	0,023	IX	0,129	0,028

Organo copulador representado en la figura 7.

Longitud del cuerpo 0,69.

DISTRIBUCION GEOGRAFICA: Estado Aragua (Venezuela).

BIONOMIA: Se trata de una especie gregaria, en que las hembras son muy activas en presencia de los machos pero sumamente pasivas cuando se encuentran solas (pueden pasar varias horas inmóviles). No hay una evidente capacidad de vuelo, sino que mas bien los individuos suelen brincar con saltos rápidos o a lo sumo realizar vuelos muy cortos. Existe un cortejo sexual de aproximadamente medio minuto por parte del macho, el cual suele encontrar poca receptividad por parte de las hembras, viéndose obligado a una persecución que suele durar pocos minutos. La cópula en si dura pocos segundos. La hembra, una vez ubicado el huevo de su hospedador, realiza una inspección con sus antenas pero no tiene ningún comportamiento de marcaje. La oviposición va precedida de varias inserciones con el ovipositor que una vez retraído hacen salir un exudado del hospedador que la hembra utiliza para su alimentación. La oviposición en sí dura aproximadamente 30 minutos.

La actividad de oviposición puede resultar en la deposición de hasta 4 huevos en cada hospedador, aunque 3 es la cantidad de huevos mas frecuente. Con una sola inserción del ovipositor se pueden depositar 1 ó 2 huevos, pero es frecuente que una misma hembra parasite mas de una vez, de manera secuencial, el mismo hospedador. La inserción puede realizarse en cualquier parte del corion, incluso a través del ópérculo. El huevo depositado es de tipo encirtiforme y tiene una placa aeroscópica bien desarrollada (Fig. 9).

La duración del ciclo de vida, desde el huevo hasta la emergencia del adulto, es de aproximadamente 14 días, los cuales se distribuyen entre las diferentes etapas de desarrollo de la siguiente manera: 42 horas como huevo, 27 horas en el 1er. estadio larval, 24 horas en el 2do. estadio larval, 72 horas en el 3er. estadio larval y 168 horas (7 días) como pupa. Todos los estadios larvales son libres, pero solo el primero muestra mandíbulas bien desarrolladas.

Las avispas hembras recién emergidas ya están en capacidad de parasitar sus hospedadores. Durante las primeras 24 horas parasitan un promedio de 5,3 huevos, pero esta capacidad suele ir disminuyendo progresivamente con la edad. Las hembras pueden llegar a vivir unas 3 semanas pero la media de su capacidad de vida es de unas 2 semanas (longevidad media = 13,97 días). Un grupo de 35 hembras mantenidas en el laboratorio en un lapso de 24 días parasitó un total de 1.125 huevos de *R. prolixus*.

En las colecciones del Museo de La Plata existen ejemplares de la forma típica *O. trinidadensis trinidadensis* Crawford, 1913, que fueron criados de huevos del lepidóptero *Opsiphanes cassina fabricii* Boisd., en Cumaná, por la doctora Silva Durán, en Noviembre de 1960. Las especies de *Ooencyrtus* de bionomía conocida, se desarrollan ya sea como parásitos primarios o secundarios en los huevos de los hemípteros, coleópteros y lepidópteros.

OBSERVACIONES: Los ejemplares de esta nueva subespecie se diferencian de los

de la forma típica por su coloración mas oscura; además, los machos presentan los artejos del flagelo más estrechos y con setas más largas.

MATERIAL ESTUDIADO: 1 ♀ holotipo, 1 ♂ alotipo y 248 ♀♀ y 87 ♂♂ paratipos, Municipio Higuerotal, Estado Aragua, Septiembre 1972. Dora Feliciangelli (Colector).

Aclaramos, finalmente, que antes de que las dos avispitas que estudiamos en este trabajo fueran identificadas, la doctora Feliciangelli de Piñero publicó algunas observaciones sobre las mismas en la *Revista do Instituto de Medicina Tropical de Sao Paulo*, volumen 15, número 4, páginas 235-238, con 4 figuras, Julho-Agosto, 1973.

Rev. Inst. Med. trop. São Paulo
15(4):235-238, julho-agosto, 1973

CDU 576.985.161.13

HALLAZGO DE HUEVOS DE *RHODNIUS PROLIXUS* PARASITADOS NATURALMENTE POR MICROHIMENÓPTEROS

(NOTA PREVIA)

M. Dora FELICIANGELI (1)

RESUMEN

En esta nota se informa sobre el hallazgo en el campo, de parasitismo natural de huevos de *Rhodnius prolixus* por dos microhimenópteros endófagos. Se notifica como se observó el fenómeno y se hacen consideraciones sobre el posible empleo de estos insectos como una arma promisoria para el control biológico del vector más importante de la Enfermedad de Chagas en Venezuela.

En 1959 ORTIZ [5] encontró en frascos de cría de *Rhodnius prolixus* huevos parasitados por un microhimenóptero de la Flia. Scelionidae y lo clasificó como *Telenomus costa-limai* describiendo la hembra, ya que no consiguió ejemplares machos.

Durante los últimos años RABINOVICH [8, 9], al mismo tiempo que realizaba estudios sobre dinámica poblacional de *Telenomus fariai*, endófago de los géneros *Triatoma* y *Panstrongylus* [1, 6, 7] emprendió busquedas sistemáticas de *T. costa-limai*, en varias regiones del país durante las distintas épocas del año, pero siempre con resultados infructuosos [10].

Recientemente empezamos un estudio sobre dinámica poblacional de *R. prolixus* en su hábitat natural, con el fin de llevar a cabo una prueba para el control de esta especie mediante la autoesterilización de los insectos del medio rural [2]. Para medir el grado de infestación de las casas en experimento, empleabamos el método de la caja GOMEZ-NUÑEZ [4] actualmente usado en varios países de Latinoamerica en la detección de la infestación intradomiciliaria por reduvideos [3].

Durante la revisión de las cajas provenientes de un típico "rancho" construído hace aproximadamente 2 años y nunca rociado con insecticidas, se observó que una de ellas contenía 8 huevos de *R. prolixus* adheridos. Estos presentaban el opérculo cerrado y una perforación circular hacia uno de los polos (Fig. 1). En la parte posterior el resto del contenido del huevo aparecía ennegrecido y después de la disección, a la observación microscopica, se presentó como una única masa semilunar de color rojizo. En la misma caja habían 8 microhimenópteros evidentemente emergídos de los huevos de *R. prolixus*.

Con el propósito de recolectar mayor cantidad de material para establecer una cría de laboratorio, semanalmente se dejaron huevos de *R. prolixus* en cajitas colgadas del techo de la casa y a los 7 días se recogían y se aislaban los que aparecían parasitados.

Cuando empezaron a nacer los primeros individuos en laboratorio, nos dimos cuenta de que se trataba de 2 especies y quizás géneros distintos, ambos endófagos de huevos de *R. prolixus*.

La recolección del material objeto de este trabajo fué efectuada cuando el Autor trabajaba en la Sección de Estudios Biológicos, División de Endemias Rurales, M.S.A.S., Maracay

(1) Instructor, Cátedra de Parasitología. Facultad de Medicina, Universidad de Carabobo, Venezuela

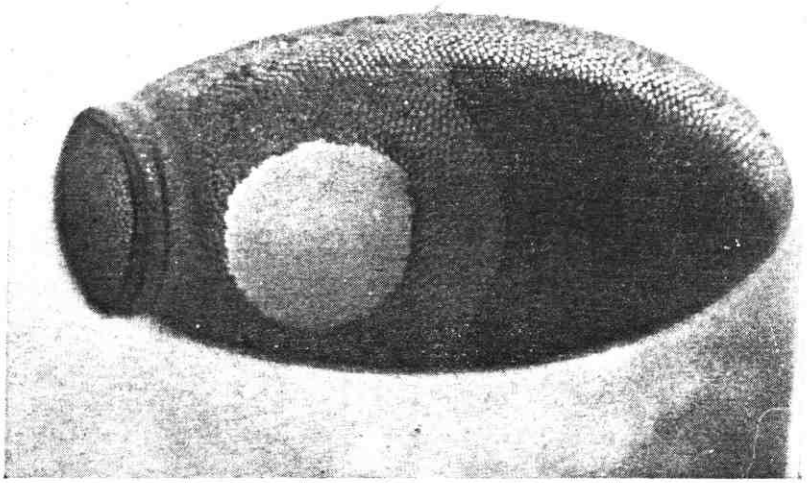


Fig. 1 — Huevo de *R. prolixus* parasitado por un microhimenóptero. (Aumento aproximado: 70 veces al original)

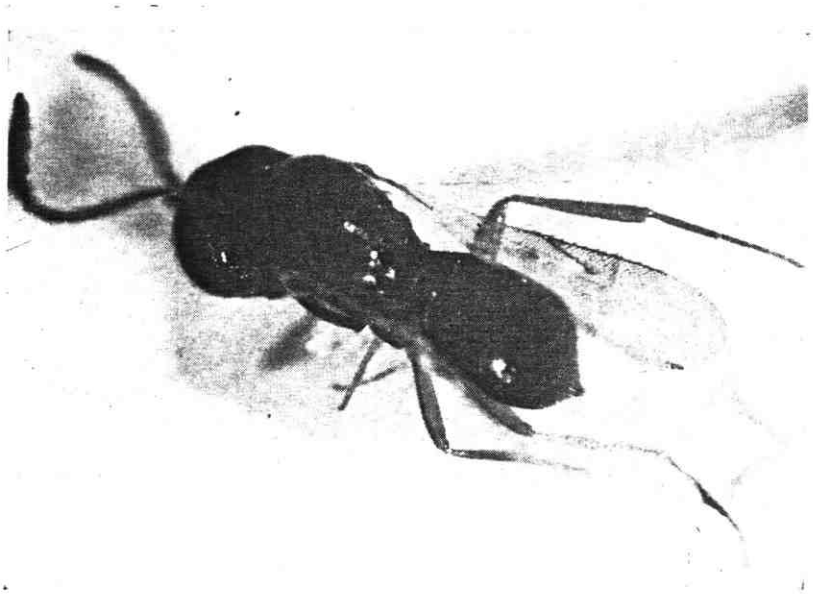


Fig. 2 — Microhimenóptero emergido del huevo de la Fig. 1. (Aumento aproximado: 50 veces al original)

El microhimenóptero que se encontró primero (Fig. 2) es más estilizado, y presenta el abdómen claramente peduncolado, de color negro, liso y brillante.

El segundo (Fig. 3) es más pequeño pero más grueso, presenta el abdómen negro con reflejos de color verdoso y bandas amarillentas claras transversales, por debajo de las cuales, de cada lado, está implantado un grupo de 3 pelos bien desarrollados.

La perforación hecha por este último, para emergir del huevo de *R. prolixus*, es de po-

sición y bordes más irregulares (Fig. 4) y el resto del contenido del mismo se presenta elaborado en pequeñas masas de color rojizo.

Debido a esta diferencia se podría pensar que posiblemente el mecanismo de utilización del huésped sea diferente por parte de los dos parasitoides.

Otro hecho interesante se refiere al número de individuos emergídos del huevos parasitado. Para la avispa de la Fig. 2 fué siempre de 1 por huevo de *R. prolixus* y para la segunda, fué de 1 hasta 6.

Este fenómeno podría depender de la mayor capacidad de la primera en diferen-

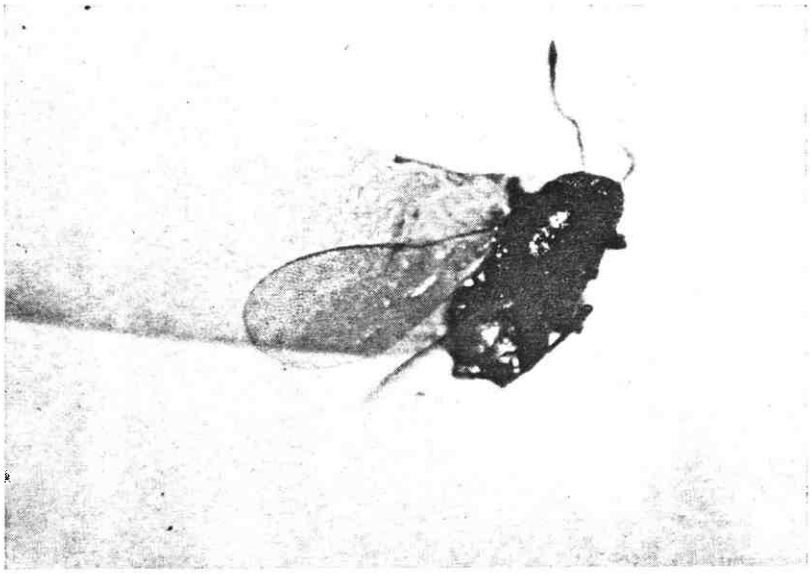


Fig. 3 — Otro microhimenóptero emergido del huevo de *R. prolixus* de la Fig. 4. (Aumento aproximado: 50 veces al original)

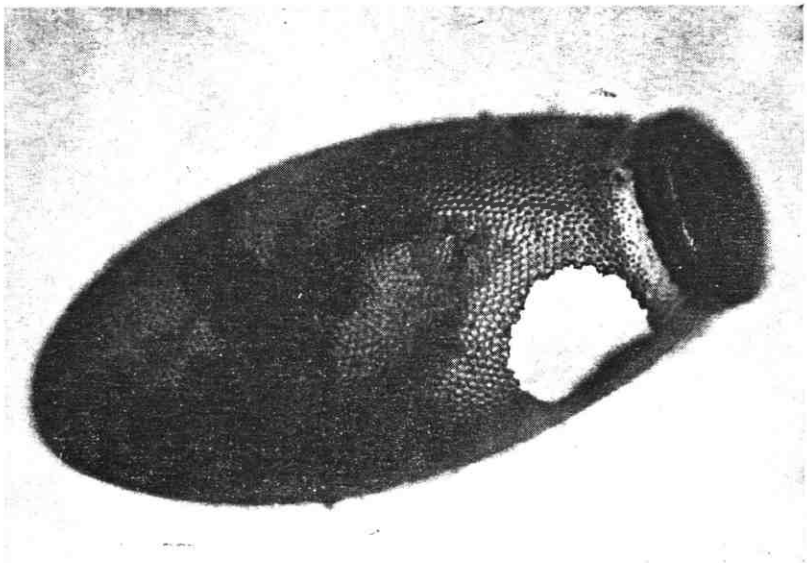


Fig. 4 — Huevo de *R. prolixus* parasitado por el microhimenóptero de la Fig. 3. (Aumento aproximado: 70 veces al original)

ciar huéspedes ya parasitados, ó bien del hecho de que la segunda hembra, al igual que *T. fariai*, pueda oviponer un número variado de huevos en el mismo huésped, ó sea, que se trate de un parasitoide solitario en el primer caso y de un parasitoide de tipo gregario en el segundo.

Además de los hechos antes mencionados, observaciones preliminares comparativas sobre el comportamiento de las dos avispas han revelados también ciertas diferencias. La de la Figura 2 es más rápida, se despleza activamente y efectúa la oviposición en pocos minutos, la de la Figura 3 es más lenta, permanece mucho tiempo inmóvil y lleva aproximadamente media hora para la oviposturа.

Actualmente se está procediendo a la clasificación precisa de los dos microhimenópteros y se están comenzando estudios sobre la biología, ecología y dinámica poblacional de estos insectos debido a la posible importancia que podrían tener para el control biológico de *R. prolixus* del cual constituyen enemigos naturales.

SUMMARY

Rhodnius prolixus *eggs naturally parasitized by endophagous microhymenopterus*

This is a note regarding the finding in the field, of *Rhodnius prolixus* eggs naturally parasitized by two endophagous microhymenopterus. Comments are made on the possibilities of using these insects as a means for biological control of the most important vector of Chagas' Disease in Venezuela.

AGRADECIMIENTOS

Al personal de la Sección de Estudios Biológicos y de la Zona I de la División de Endemias Rurales del M.S.A.S. por las valiosas facilidades prestadas en la recolección del material de campo y a los Dres. J. W. Torrealba y Junia Chaves de Torrealba de la Cátedra de Parasitología de la Universidad de Carabobo, por sus sugerencias en la redacción de esta nota.

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J. Med. Ent. Vol. 9, no. 2: 139–143 28 April 1972

CHEMOSTERILIZATION OF ADULT *RHODNIUS PROLIXUS* BY METEPA[1]

By **M. Dora Feliciangeli**[2]

Abstract: Laboratory-reared adult *Rhodnius prolixus* were tested to observe the effects of metepa on the reproductive capacity of the species. Results indicate that an individual dose of 0.20 mg applied to the thorax produces a suitable fertility reduction but also some undesirable effects. Spermatozoa, female gonads, and movement and longevity of the insect seemed to be most affected by the chemosterilant. Recovery of fertility and induced excessive irritability could reduce the practicality of using this sterilizing agent in the sterile-adult control method. Results suggest investigation of another approach based on the direct application of chemosterilants within infested houses.

Effects of ionizing radiation on *Rhodnius prolixus*, an important Neotropical vector of Chagas' disease, have been studied to evaluate the feasibility of using sterile males for control of the species (Gómez-Núñez et al. 1962, Baldwin & Shaver 1963, Gómez-Núñez et al. 1964). Results indicated that both gamma-and X-irradiation produced total sterility only with doses that also inhibited the insect's mating capability. This paper reports the results obtained in the first of a series of tests designed to investigate the use of chemosterilants for similar purposes. Effects of metepa [Tris 1-(2-methyl) aziridinyl phosphine oxide] on oviposition, fertility, longevity and mating capability are given.

MATERIALS AND METHODS

The *Rhodnius prolixus* were provided by Venezuela's Division of Rural Endemic Diseases, Bureau of Malariology and Environmental Health. They were reared and maintained following a standard procedure (Gómez-Núñez 1964) that produced adults closely comparable in morphological development and physiological age. Test specimens were kept in 1700-ml glass jars. The bugs were fed every 14 days on hen chickens. Sexes were separated during the fifth nymphal stage to avoid unscheduled matings. During the 78 days of the experiment, environmental temperature fluctuated between 28 and 29°C and relative humidity between 52 and 57%.

[1]This investigation was supported in part by Public Health Research Grant AI–05794 from the National Institute of Allergy and Infectious Diseases.

[2]Sección Estudios Biológicos, División Endemias Rurales, Dirección de Malariologia y Saneamiento Ambiental, Maracay, Venezuela.

Metepa doses of 0.05, 0.10, 0.20 and 0.40 mg per specimen were applied. To obtain these doses, 2.5, 5.0, 10.0 and 20.0% solutions were prepared using an 82% commercial metepa concentrate with acetone as the diluent. Each specimen was partially anesthetized with CO_2 and treated with 2 µl of the appropriate solution. Metepa was applied to the thorax by means of a microapplicator.

To determine effects of metepa on fertility and oviposition, 3 groups of 25 pairs were used for each of the 4 metepa concentrations. Treatment was given only to males in one group, to females in another, and to both sexes in the third group. Three control groups, also of 25 pairs each, were used; in one group males, in the other females were treated individually with 2 µl acetone alone; the third group remained untreated. Specimens were treated or introduced as controls 1 week after the final molt, were mated 1 week after treatment and their longevity was subsequently noted every 14 days.

To determine the duration of the effects of metepa on males, new groups of untreated virgin females were paired with the treated males every 14 days and percentage hatching was noted in eggs of each group of females; eggs/female was based on number of eggs per surviving females.

It had been noted in experiments using radiation that insect feeding influenced results; therefore, 1 group of *Rhodnius prolixus*, consisting of 25 pairs for each metepa concentration, was treated before feeding and a similar group after feeding. Feeding was done about 1 week after molting to adult.

Relative insect activity was determined by the use of a photocell counting device. This essentially consisted of a Petri dish, 9 cm in diameter, placed so that its edge rested over a photoelectric cell connected to a counter which advanced 1 unit each time that a bug walked over the cell. This position was chosen because it was observed that the bugs tended to move about the circumference of the dish, in preference to its center. Five bugs at a time were placed in the dish and left there for a period of 10 hr (0800–1800 hrs) during the day and 14 hrs during the night (1800–0800 hrs). Groups were alternated so that a rest period could be given between tests. The number of counts per hr per bug was taken as a measure of the insect activity.

Mating competitiveness of treated males, when challenged by the presence of normal males, was evaluated by observing the percentage of eggs hatching during a period of 3 weeks from 7 jars each containing 200 specimens, of which 100 were normal females and 100 were males in ratios of normal males: treated males as follows: (100:0), (90:10), (70:30), (50:50), (30:70), (10:90) and (0:100). A comparison was then made of observed and expected values. As in previous tests with ionizing radiation, expected values were determined graphically by drawing a straight line connecting the observed hatching percentage from jars containing only normal males to that from jars containing only treated males, using as the abscissa a scale proportional to the normal:treated male ratios (Gómez-Núñez et al. 1964).

To obtain data about mating frequency groups consisting of 5 marked males treated with 0.10 mg of metepa, 5 normal males and 10 normal females, were directly observed and the number of matings per hr recorded. This was done daily for 15 days at the start and at the end of the experiment. Three replicates were made of each test.

All control groups were similarly handled and maintained as the test groups. Significance of the differences was checked by chi-square and t-distribution tests and based on a 5% level.

RESULTS

Mean oviposition values in groups treated with acetone and those not treated were 5.2 and 4.8 egg/female/week respectively; hatching remained within 85–95% in all groups. These differences are normally found between untreated groups of similar size.

Effects of metepa on fertility are given in TABLE 1. The values given correspond to the means of values from 5 observations throughout a period of 78 days. As net reproduction depends on both the quantity of eggs available and percentage of them

TABLE 1. Metepa-induced sterility in *R. prolixus*.

Metepa dose in mg	Treated ♂♂—Untreated ♀♀		Untreated ♂♂—Treated ♀♀		Treated ♂♂ and ♀♀	
	% sterility	Student's "t"*	% sterility	Student's "t"*	% sterility	Student's "t"*
0.00	8.61 ± 2.12	—	7.92 ± 0.65	—	7.94 ± 0.65	—
0.05	43.13 ± 32.84	−2.10	49.04 ± 7.76	−10.56	75.44 ± 17.23	−7.85
0.10	76.34 ± 24.70	−5.46	74.52 ± 4.20	−31.25	94.98 ± 4.70	−36.66
0.20	99.36 ± 0.88	−79.05	91.90 ± 2.66	−61.31	99.40 ± 0.88	−166.99
0.40	100.00 ± 0	−86.23	99.10 ± 1.26	−128.24	99.96 ± 0.05	280.59

*t is given in relation to untreated specimens.

TABLE 2. Changes due to time on the effects of metepa.

Treated sex	Dose in mg	% hatching and (eggs/female) per weeks after treatment		
		0–2 wks	5–7 wks	9–11 wks
♂	0.00	92.5 (17.3)	88.4 (18.6)	92.6 (10.5)
	0.05	11.7 (11.4)	75.8 (18.9)	84.7 (18.7)
	0.10	1.2 (15.8)	36.6 (18.1)	64.4 (16.6)
	0.20	0.0 (16.0)	2.0 (6.3)	4.3 (5.3)
	0.40	0.0 (8.3)	0.0 (5.4)	0.0 (3.1)
♀	0.00	92.5 (17.3)	90.9 (54.9)	92.0 (69.9)
	0.05	78.5 (10.1)	86.1 (33.1)	86.3 (27.1)
	0.10	43.3 (6.4)	80.5 (16.4)	86.6 (21.6)
	0.20	17.8 (4.5)	73.7 (6.7)	76.2 (5.8)
	0.40	19.6 (2.3)	33.3 (0.3)	88.9 (0.4)

hatching, sterility was obtained by the formula given for the Egyptian cotton leafworm (Toppozada et al. 1966) where:

$$\text{Sterility} = 100 - \left(\frac{\text{eggs per treated } ♀ \times \% \text{ hatching}}{\text{eggs per normal } ♀ \times \% \text{ hatching}} \times 100\right)$$

The specific effects of metepa on oviposition, hatching, and the persistence of those effects are given in TABLE 2.

All doses used caused sterility in both sexes and the effect increased according to dosage. Differences in mean % sterility between treated and untreated groups were significant at a level of 1‰ by the t-Student test in all groups except that of males treated with 0.05 mg ($_8t_{0.05} = 2.26$).

Egg hatch in females paired with treated males increased after 5 weeks when dosage was 0.10 mg or less. Oviposition in normal females paired to these males, below normal in the 0.20-and 0.40-mg groups, remained below normal for 11 weeks.

Although egg hatch of treated females was not markedly reduced, oviposition was significantly reduced by doses greater than 0.05 mg ($X^2$0.10 mg = 6.86, $P<0.01$) and the combined effect of hatching and oviposition reduction produced a significant reduction of the fertility in females treated with more than 0.05 mg.

Hatch began to recover in treated females after 2 weeks and approached normality by the end of 11 weeks. On the other hand, oviposition, although increasing in the control groups, decreased with time in the group of females treated with 0.40 mg, and remained below normal in the rest of the treated groups.

TABLE 3. Effect of feeding on metepa-induced sterility.

Metepa dose in mg	Unfed		Fed		
	% hatching	No. of eggs	% hatching	No. of eggs	X/σ
0.00	100.0	2735	100.0	3331	—
0.05	74.8	3029	56.2	4725	16.7
0.10	27.9	1915	16.6	3554	9.9
0.20	0.0	137	2.3	1963	1.8
0.40	0.0	40	0.0	878	—

When both sexes were treated with metepa, the hatch was similar to that obtained when only males were treated, and oviposition was similar to that obtained when only females were treated.

TABLE 3 shows the effect of treatment before or after feeding. Hatching is significantly ($P<0.0^{11}$ 520) reduced, in relation to the values obtained from unfed specimens, when treatment with 0.05 and 0.10 mg of metepa follows feeding.

Average hourly mating frequency for the 15 days immediately after treatment with 0.10 mg was 2.4 for the group of 5 treated males and 1.2 for group of 5 normal ones; but at the end of the 78 days this ratio was reversed and normal males were mating 4.1 times and treated ones 2.4 times.

Insect movement, as measured by the photocell device, progressively increased in direct proportion to dosage. The daily average was 7.7 counts/specimen/hr (SD 4.9) for untreated specimens and 28.8 counts/specimen/hr (SD 12.2) for those treated with 0.40 mg of metepa. Night-time counts were 69.2 (SD 30.9) and 129.4 (SD 48.7) respectively.

Effect of metepa on adult longevity of *R. prolixus* is given in FIG. 1. Male longevity was significantly reduced ($X^2 = 10.1$, $P<0.01$) with a dose of 0.40 mg. Female longevity was significantly reduced with 0.20 ($X^2 = 4.5$, $P<0.05$) and 0.40 mg doses ($X^2 = 6.5$, $P<0.02$).

Treated male competitiveness (FIG. 2) did not approach the values expected when insects were treated with 0.10-and 0.20-mg doses.

DISCUSSION

Results from the tests indicate that metepa, when applied to adult specimens at individual doses of 0.10 mg or more, significantly reduces the fertility of *R. prolixus*. Effects differed according to dose and sex.

Male fertility was reduced in direct relation to dosage increase but after a period of time, depending on dose, fertility was recovered. This suggests that metepa affected mainly the spermatozoa and not the spermatogonia (Fahmy & Fahmy 1964) and, as in other insects (La Chance et al. 1970), consecutive matings accelerated this recovery by the faster replacement of damaged spermatozoa with normal ones.

Treated females showed a somewhat different response to metepa; hatching was reduced to only about 20% by the higher dose used, 0.40 mg, but again subsequently recovered in all females by the end of the test. On the other hand, as in other insects (Chamberlain 1962, Toppozada et al. 1966, Borkovec 1966, Turner et al. 1969, Hafez et al.

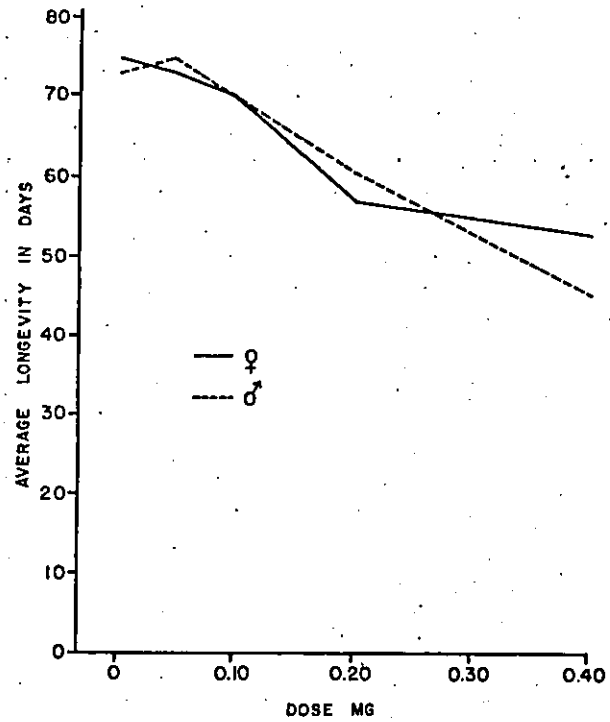

FIG. 1. Effect of metepa on longevity of adult *Rhodnius prolixus*.

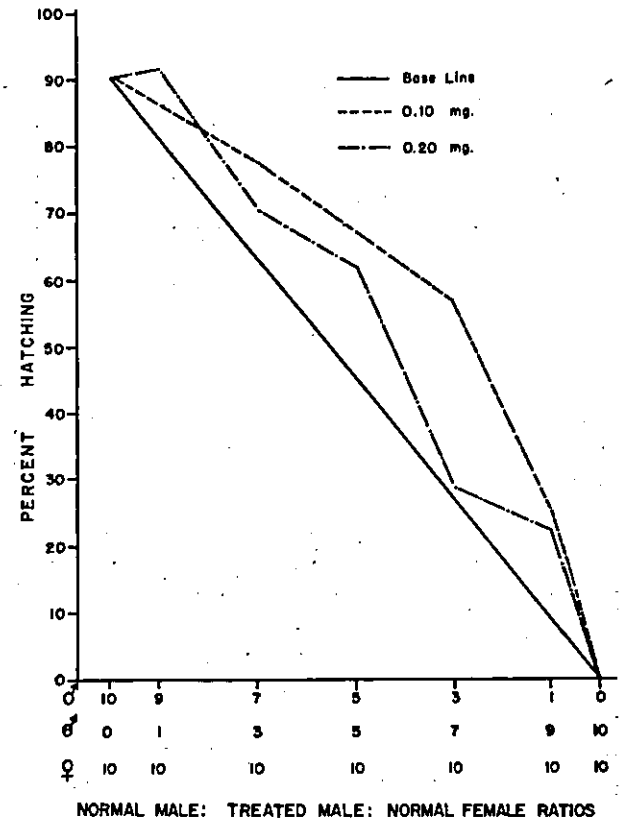

FIG. 2. Comparative competitiveness of metepa-treated ♂ *Rhodnius prolixus*.

1970), the female's egg production capability was significantly reduced in all treated females and continued to decrease throughout the 11 weeks of the test. This suggests 2 possible actions by metepa in female *R. prolixus:* a main one on the gonads (Jalil & Morrison 1969) and a secondary action affecting the eggs, the spermatozoa from the normal males mated to them, or both.

A more complex process apparently was involved with respect to the effect on oviposition of untreated females mated to treated males. The low oviposition observed in untreated females mated to males treated with 0.40 mg could be explained by an inhibition in mating frequency due to irritability in those males, but since this same oviposition reduction was noted in females mated to sexually active males treated with 0.20 mg the results suggest that the sterilant could have been carried into females during copulation as noted in house flies (Chang et al. 1966).

The high hatching obtained in the experiment of mating competitiveness between treated and untreated males contrasts with the high mating frequency observed in the treated males immediately after the treatment. This fact could be explained as the direct result of the harmful action of the chemosterilant on the sperm of the treated males.

Differences noted in hatching when comparing results from specimens fed before treatment with those from specimens fed after treatment contrast with results obtained by the use of ionizing radiations, which suggests that damage by metepa was less generalized than that caused by ionizing radiations (Gómez-Núñez, 1970).

The oviposition increase noted in the fed group can not be considered caused by metepa since feeding in *R. prolixus* stimulates oviposition.

A comparison of results from metepa tests with those from ionizing radiation does not show any definite advantage of one method over the other in regard to the production of sterile males. Nevertheless metepa apparently causes less overall damage to *R. prolixus* and might be worthwhile testing in the field as a sterilant to control house infestation by that and other vectors of Chagas' disease (Feliciangeli & Gómez-Núñez 1969, Gómez-Núñez 1970). Recovery of hatch in time and the interference of induced irritability with mating would be of minor importance in field trials since mean longevity of adult *R. prolixus* under natural conditions is less than 3 weeks (Gómez-Núñez 1969).

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STERILIZZAZIONE DI *RHODNIUS PROLIXUS* ADULTI PER CONTATTO TARSALE CON SUPERFICI PLASTICHE TRATTATE CON METEPA ED EFFETTO RESIDUO DELLE MEDESIME

M. DORA FELICIANGELI (1)

Vengono presentati i risultati di alcuni esperimenti di laboratorio sulla sterilizzazione di *Rhodnius prolixus* adulti esposti per 10', 20' e 30' a superfici di polivinilcloruro trattate con 0.25, 0.50 e 1.0 mg di metepa per cm^2.

E' stato studiato inoltre l'effetto residuo delle medesime superfici 2 mesi ed 8 mesi dopo la loro preparazione.

I dati ottenuti suggeriscono che teoricamente il metodo può essere adeguato per il controllo dei vettori del Mal di Chagas e che sarebbe opportuno effettuare un esperimento pilota di campo in una zona altamente infestata.

INTRODUZIONE

In una revisione dei metodi di lotta genetica per il controllo di insetti vettori, Knipling et al. (1) per quanto riguarda il controllo dei triatomidi, mentre escludono la possibilità dell'immissione di maschi sterili in natura, suggeriscono la tecnica di campo della autochemosterilizzazione, ribadendo allo stesso tempo l'importanza delle ricerche sugli attrattivi.

In precedenti ricerche è stato studiato il comportamento di *R. prolixus* adulti trattati topicamente con metepa (2), e la possibilità di sterilizzare questi insetti per contatto tarsale con superfici plastiche trattate con soluzione di metepa in acetone. Si osservò però che il metodo usato presentava alcuni svantaggi, giacché il solvente scioglieva la plastica e il chemosterilante non si spargeva uniformemente sulle superfici. Le dosi usate provocavano inoltre una mortalità significativa tra gli insetti trattati (3).

(1) *Dirección de Malariología y Saneamiento Ambiental, División de Endemias Rurales, Sección de Estudios Biológicos, Maracay, Venezuela.*

La presente nota illustra i risultati ottenuti da un esperimento simile, usando un solvente che non intacca la plastica, ma con dosi di chemosterilante notevolmente inferiori. Oltre all'efficacia è stato anche studiato l'effetto residuo di dette superfici fino a otto mesi dopo la preparazione. Vengono infine analizzati i fattori inerenti alla applicazione pratica del metodo.

MATERIALI E METODI

Gli esperimenti sono stati effettuati utilizzando scatole di polivinilcloruro (PVC) del diametro di 8,9 cm × 2,1 cm di altezza (superficie utile cm^2 185 circa). Tali scatole sono state trattate con 5 ml di soluzione ciascuna; per ottenere una distribuzione il più possibile uniforme del metepa le scatole venivano agitate delicatamente per qualche minuto, quindi il solvente veniva fatto evaporare tenendo ogni scatola aperta un paio di giorni. Il contenuto in metepa è risultato quindi rispettivamente di circa 0.25, 0.5 e 1.0 mg/cm^2

Per gli esperimenti vennero utilizzati *R. prolixus* allevati in laboratorio in condizioni ottimali di temperatura e U.R. (27°-29°C e 60-70%), separati per sessi al V stadio ninfale. Gli insetti furono esposti alle superfici trattate 7-10 giorni dopo l'evoluzione allo stadio adulto. Per ognuna delle 3 concentrazioni si esposero 4 gruppi di 5 insetti per 10', 20' e 30'. Qualche giorno dopo il trattamento gli insetti furono alimentati su galline ed accoppiati incrociando gruppi di maschi e di femmine entrambi trattati e gruppi di individui con il sesso opposto non trattato. Per ognuna delle tre combinazioni su utilizzarono 3 gruppi di controllo in cui gli individui del sesso corrispondente a quello trattato con metepa erano stati esposti per 30' a superfici trattate col solo solvente.

Dopo l'esposizione al metepa gli insetti trattati sono stati alimentati ogni due settimane, in pari tempo procedendosi alla raccolta delle uova e al cambio delle femmine vergini normali, per poter seguire nel tempo la sterilità dei maschi trattati. La mortalità fu annotata ogni settimana.

Per studiare l'effetto residuo delle superfici trattate l'esperimento è stato ripetuto a due mesi e ad otto mesi dalla preparazione delle superfici con le stesse modalità.

RISULTATI

Come si vede in Tabella 1 i maschi sono più sensibili delle femmine. Naturalmente, quando entrambi i sessi sono trattati, l'effetto si somma. Il risultato è migliore dopo 2 mesi dal trattamento (Nov. 1970); tuttavia, ancora a 8 mesi di distanza si ha una certa azione residua che, con 1 mg/cm^2, e quando entrambi i sessi sono trattati, dà il 96.3% di ova sterili.

La correlazione fra dose ed effetto è abbastanza evidente, specialmente dopo 8 mesi dal trattamento delle capsule (10.1%, 28.6%, 63.1% di sterilità quando le femmine sono trattate con 0.25, 0.50, 1.00; 16.9%, 46.9% e 96.3% quando entrambi i sessi sono trattati con le stesse dosi). In

qualche caso c'è un'apparente discrepanza fra dose ed effetto, come quando nei maschi trattati si ha 99.9% di schiusura con 0.50 mg e 90% con 1 mg; o come quando nelle femmine trattate si ottiene 84.2% con 0.5 e 82.6% con 1 mg); ma queste differenze, non molto significative, possono essere attribuite a variabilità individuale (dato il basso numero di individui esposti) o a variazioni sull'assorbimento del chemosterilante da insetto a insetto. Infatti, basta che qualche individuo nel breve arco di

TABELLA 1

Percentuali di ova sterili prodotte da R. prolixus *esposti per* 10', *in tre epoche successive, alle medesime superfici trattate con* 3 *diverse concentrazioni di metepa* (*tra parentesi il numero di ova osservate*)

	metepa mg/cm²	periodo dell'esposizione		
		Settembre 1970	Novembre 1970	Maggio 1971
♂♂ trattati × ♀♀ normali	0.00	6.7 (878)	17.1 (960)	8.1 (1291)
	0.25	59.7 (876)	100 (1087)	15.7 (1570)
	0.50	99.9 (748)	99.1 (1011)	47.8 (1614)
	1.00	90.1 (671)	90.6 (948)	37.0 (1393)
♂♂ normali × ♀♀ trattate	0.00	8.7 (1412)	7.3 (1094)	7.2 (1423)
	0.25	36.6 (802)	41.2 (615)	10.1 (1062)
	0.50	84.2 (164)	86.6 (187)	28.6 (1156)
	1.00	82.6 (92)	83.6 (122)	63.1 (295)
♂♂ trattati × ♀♀ trattate	0.00	11.9 (1391)	10.0 (1427)	7.8 (1702)
	0.25	72.6 (875)	100 (556)	16.9 (1352)
	0.50	100 (143)	100 (127)	46.9 (1633)
	1.00	100 (56)	100 (125)	96.3 (297)

tempo di 10', si sia fermato in un punto della superficie trattata contenente una quantità di chemosterilante più bassa o sia rimasto in una posizione tale da non aderire perfettamente alla superficie (ad es., per contatto con le sole zampe), perché l'assorbimento di sostanze sia notevolmente diminuito. D'altronde, dai dati osservati, sembra evidente che con le dosi di 0.5 mg si raggiunge già il massimo effetto possibile, per cui la differenza fra l'effetto delle dosi di 0.5 e 1 mg non è significativa.

L'effetto del tempo di esposizione sulla sterilità indotta viene illustrato nella Tabella 2 dove appaiono le percentuali di uova sterili (Sett. 1970) di insetti esposti per 10' 20' e 30' alle superfici trattate e i valori di x/σ corrispondenti alle differenze riscontrate, statisticamente significative ($p<0.01$). Solo con 0.25 mg/cm², sia nei maschi che nelle femmine, raddoppiando il tempo di esposizione da 10' a 20' si rilevò un aumento nella proporzione di uova sterili. E' da notare però che quando si espo-

TABELLA 2

Effetto del tempo di esposizione alle superfici trattate sulla sterilità indotta con metepa in R. prolixus: percentuali di ova sterili osservate

Metepa mg/cm²	♂♂ normali × ♀♀ trattate				♂♂ trattati × ♀♀ normali			
	tempo di esposizione				tempo di esposizione			
	10'	20'	30'	x/σ	10'	20'	30'	x/σ
0.25	59.9	97.8	81.1	10'-20'=25.8 10'-30'=11.9 20'-30'=15.4	35.1	68.2	65.3	10'-20'=12.0 10'-30'=12.1
0.50	99.9	100.0	100.0		84.8	86.2	87.5	
1.00	90.0	100.0	92.2	10'-20'=12.8 20'-30'=11.3	82.6	88.9	88 2	

sero i maschi per 30' a 0.25 e 1.0 mg si ottenne una diminuzione rispetto alla esposizione con 20'; lo stesso comportamento si può riscontrare anche nelle femmine, ma esso non raggiunge valore significativo. Tutti i dati finora presentati sono stati tabulati sul totale di uova raccolte durante la durata degli esperimenti ossia fino ai 44 giorni dopo l'esposizione.

Nella Tabella 3 si mostra il recupero degli insetti durante detto lasso di tempo e la fecondità delle femmine, corrispondenti al primo esperimento (Sett. 1970). Quando si esposero i maschi al metepa nella concentrazione di 0.25 mg/cm² il recupero non fu graduale e completo: con 0.50 mg non fu significativo e con 1.0 mg arrivò al 44.5%. Quando si esposero le femmine si osservò recupero solo con 0.25 mg/cm².

Rispetto alla fecondità delle femmine normali accoppiate con i maschi trattati, si osservano variazioni rispetto al controllo, però non proporzionali al trattamento; in cambio la ovoposizione delle femmine espo-

TABELLA 3

Recupero di R. prolixus *dopo trattamento con metepa: percentuali di schiusura delle uova e, tra parentesi, numero di uova per femmina.*

sesso trattato	metepa mg/cm²	giorni dopo il trattamento		
		16	30	44
♂♂	0.00	93.4 (44.0)	91.6 (35.8)	98.4 (12.4)
	0.25	6.2 (40.5)	36.5 (17.6)	92.2 (29.2)
	0.50	0.0 (36.6)	0.0 (24.5)	0.7 (13.7)
	1.00	0.0 (39.9)	1.6 (12.6)	44.5 (14.6)
♀♀	0.00	95.8 (35.6)	89.9 (51.9)	89.6 (53.7)
	0.25	47.0 (27.0)	63.3 (41.4)	80.6 (32.5)
	0.50	16.8 (15.5)	0.0 (0.9)	0.0 (0.1)
	1.00	18.4 (17.4)	0.0 (1.0)	— (0.0)

ste diminuisce proporzionalmente con tutte le dosi e tende a zero con il tempo.

Nella Fig. 1 si può osservare la mortalità percentuale degli insetti trattati: in tutti gli esperimenti la tossicità fu maggiore per le femmine che per i maschi e nelle prime aumentò proporzionalmente con la dose, mentre nei secondi, osservando i risultati di settembre 1970, quando il fenomeno è più evidente, si nota che la mortalità, nulla con la esposizione a 25 mg/cm², restò stazionaria con 0.50 e 1.0 mg/cm². Nell'ultimo esperimento non si registrò mortalità nei maschi.

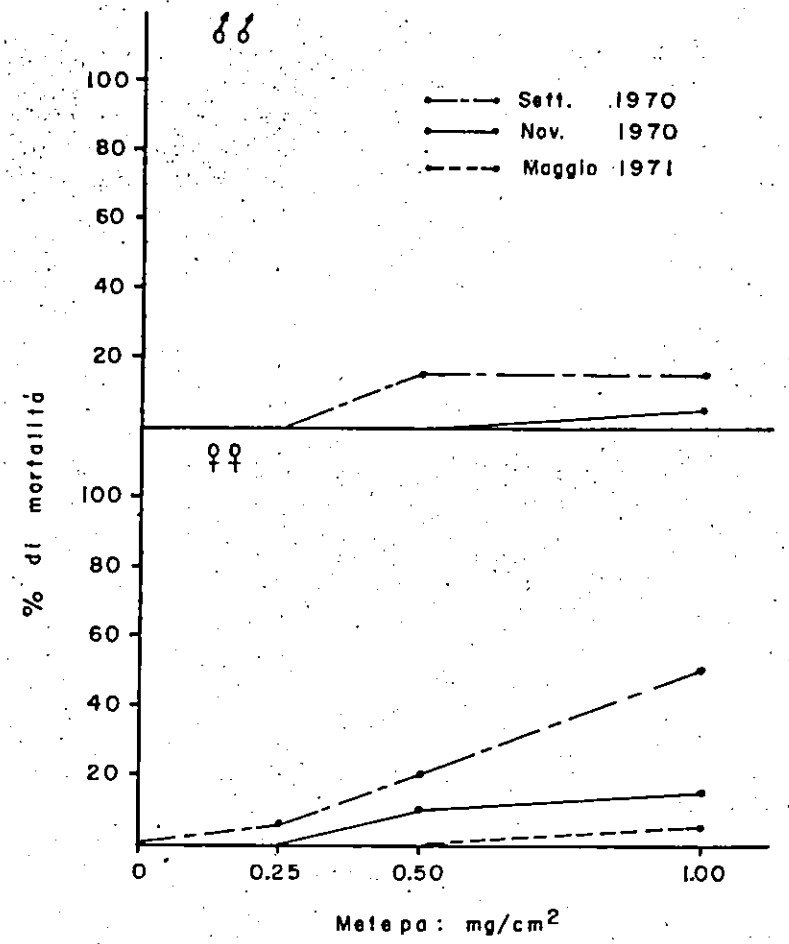

Fig. 1 — Mortalità registrata in *R. prolixus* esposti durante 10', in tre epoche successive, alle medesime superfici plastiche trattate con diverse concentrazioni di metepa.

DISCUSSIONE

In linea generale i risultati ottenuti indicano che le superfici plastiche trattate con metepa nelle tre dosi sperimentate, riducono notevolmente la fertilità di *R. prolixus* adulti quando questi stanno in contatto con le medesime per 10'.

Comparando i risultati ottenuti con 0.50 mg/cm², e con 1.0 mg/cm², sembrerebbe che con una maggior dose, sia nei maschi che nelle femmine, si ottenga un effetto controproducente in quanto a sterilità. Lo stesso fenomeno si osserva con un maggior tempo di esposizione, e ciò potrebbe far pensare a un meccanismo di difesa instaurato dall'insetto

quando viene sottoposto a una dose troppo forte o a un tempo di esposizione troppo prolungato. Tuttavia, non avendo per ora elementi più precisi di giudizio, ci limitiamo a esporre i fatti.

Studiando l'effetto residuo delle superfici si osserva che sono stati ottenuti migliori risultati due mesi dopo la loro preparazione, e ciò farebbe pensare a un maggiore assorbimento della sostanza dopo l'evaporazione del solvente.

I risultati ottenuti otto mesi dopo suggeriscono che l'effetto residuo è tale da poter pensare alla applicazione del metodo per il controllo della popolazione selvatica e che pertanto varrebbe la pena di effettuare una prova di campo pilota in una zona altamente infestata.

Esperimenti di laboratorio attualmente in corso dimostrano che il metepa non esercita nessuna azione « repellente » sugli insetti che arrivano in contatto con le superfici trattate e su queste riposano volentieri.

Per la scelta della dose da utilizzare, resterebbe da studiare comparativamente la motilità degli insetti che entrano in contatto con 0.50 mg di metepa/cm² e con 1.0 mg/cm².

Infine, considerando gli eventuali rischi tossicologici dovuti ad agenti alkilanti nella casa, è prematuro pensare all'applicazione pratica di questo metodo su larga scala, dovendosi sottoporre una simile risoluzione al giudizio di Organismi Internazionali di Sanità Pubblica, che ultimamente hanno manifestato dubbi sulla applicabilità del controllo genetico per i vettori del Mal di Chagas (5). In ogni caso i risultati di tale studio sarebbero comunque di interesse, in quanto si getterebbero le basi del metodo per il possibile uso di futuri chemosterilanti meno nocivi o altre sostanze chimiche con diverso meccanismo di azione e maggiormente specifiche come potrebbero essere, ad esempio, gli ormoni giovanili.

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STERILIZATION OF ADULT *RHODNIUS PROLIXUS* BY TARSAL CONTACT ON PLASTIC SURFACES TREATED WITH METEPA AND ITS RESIDUAL EFFECT

The possible use of auto-chemosterilization technique for the control of *Rhodnius prolixus* the main vector of Chagas' disease in Venezuela has been investigated.

Adult *R. prolixus* of both sexes allowed to crawl on plastic (polyvinylchloride) surfaces treated with 0.25, 0.50 and 1.0 mg of metepa per cm² for 10, 20 and 30 minutes. In order to test the residual effect of the treated surfaces, the experiments were repeated with distinct lots of insects in three successive stages: two days, two months and height months after the treatment.

Table 1 represents the effect of the exposure of the insects during 10' on the treated surfaces. In the first two experiments (Sept. 1970 and Nov. 1970) the following results were obtained: when males were exposed to surfaces treated with 0.50 and 1.0 mg/cm², the percentage of sterile eggs of normal females paired with them was 90.0% or above; when females were exposed, the percentage was above 80.0%; and when both sexes were exposed 100% of sterile eggs was obtained with each dosage. In the last experiment (May 1971), eight months after treatment of the surfaces, the above percentages were notably reduced in the males, and to a lesser extent in the females. But, when both sexes were exposed it reached 96%.

In Table 2 are shown the effects of exposure time on the induced sterility: only by exposing both sexes to a dosage of 25 mg and doubling the exposure time, from 10' to 20' there was a significant statistical increase in the percentage of sterile eggs.

In Fig. 1 are shown the mortality values of treated insects: mortality in females was always higher than in males.

In Table 3 are indicated the data on insect recovery during 44 days after treatment and the effect of metepa on oviposition. It may be noted that with the two higher dosages the sterility induced in the females seems to be irreversible.

In general the results obtained suggest that it would be worthwhile to carry out a pilot field experiment in a zone highly infested with *R. prolixus*, to acquire information on the feasibility of control.

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RICERCHE PRELIMINARI SULLA STERILIZZAZIONE DI *RHODNIUS PROLIXUS* PER CONTATTO TARSALE SOPRA SUPERFICI TRATTATE CON METEPA (OSSIDO DI TRIS-(2-METIL-AZIRIDINIL) FOSFATO)

M. D. FELICIANGELI (1)

Vengono esposti i risultati ottenuti dalle prime esperienze condotte in laboratorio con lo scopo di trovare una superficie atta come supporto al Metepa per la sterilizzazione di *Rhodnius prolixus* adulti per contatto tarsale. Con carta da filtro e carta da ufficio immerse in varie soluzioni di Metepa in acetone non si ottenne sterilità; con scatole di cloruro di polivinile (PVC) con 4 mg e 8 mg di Metepa/cm², si ottenne nei maschi sterilità totale; le dosi usate furono però troppo elevate ed influirono negativamente sulla longevità degli insetti.

INTRODUZIONE

Il Mal di Chagas è una tripanosomiasi umana che interessa soprattutto l'ambiente rurale di vaste regioni del continente americano.

Secondo i più recenti dati epidemiologici stimati dal Ministero di Sanità, il 4% della popolazione presenterebbe, attraverso esame elettrocardiografico, evidente lesione miocardica presumibilmente imputabile a tale malattia.

In Venezuela il vettore di maggiore importanza dal punto di vista epidemiologico è *Rhodnius prolixus*, emittero ematofago con una distribuzione geografica che abbraccia l'82% del territorio comprendendo zone da 0 a 1000 metri di altitudine. Ecologicamente l'insetto occupa due sistemi ben definiti: uno silvestre, dove l'habitat è rappresentato da alcuni tipi di palme e da nidi di uccelli, e l'altro domestico, rappresentato dal « rancho », la casa tipica del contadino venezuelano con il pavimento di terra, le pareti di fango impastato con

(1) *Dirección de Malariologia y Saneamiento Ambiental, División de Endemias Rurales, Sección de Estudios Biológicos, Maracay, Venezuela.*
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paglia sostenute da un intreccio di canne e il tetto di foglie secche di palma e paglia.

I metodi di lotta attuali sono rivolti soprattutto al controllo del vettore per mezzo di insetticidi e al miglioramento della dimora. Allo stesso tempo si sono intensificati gli studi chemioterapici alla ricerca di metodi profilattici specifici; sono stati studiati gli effetti dei raggi X e gamma (1, 2, 3) e sono state intraprese ricerche sull'efficacia di alcuni chemosterilanti. Il Metepa, applicato topicamente al torace dell'insetto, ha dato buoni risultati: una dose di 0.10 mg/insetto produce infatti la sterilità nel 90% dei maschi senza causare mortalità significativa (4, 5, 6).

Il presente lavoro informa sui primi esperimenti condotti in laboratorio nel tentativo di sterilizzare gli insetti per contatto tarsale sopra superfici trattate con Metepa.

MATERIALI E METODI

Gli insetti usati per gli esperimenti erano *R. prolixus* provenienti da una colonia mantenuta in laboratorio in condizioni standard: 27°-29° C e 60-70% di U.R. Maschi e femmine furono separati al V stadio ninfale e 7-10 giorni dopo la evoluzione allo stadio adulto esposti separatamente alle superfici trattate. Alla età di 14 giorni furono alimentati su galline e quindi accoppiati secondo lo schema seguente: maschi trattati con femmine trattate; maschi trattati con femmine normali; e maschi normali con femmine trattate. Si continuò regolarmente l'alimentazione e le uova furono raccolte ogni due settimane. I maschi trattati vennero accoppiati periodicamente con nuove femmine vergini normali per seguirne la sterilità nel tempo.

Le superfici trattate con Metepa erano: carta da filtro e carta da ufficio, in fogli di cm 10×15, e scatole di plastica.

Per l'impregnazione delle carte si usarono soluzioni di Metepa in acetone al 20%, 40% e 60%, giacché precedenti prove avevano dimostrato che con questa ultima concentrazione si otteneva il massimo di assorbimento di sostanza da parte di ambo i tipi di carta. Trattandosi di prove preliminari e non avendo a disposizione apparecchi meccanici per irrorare i fogli con quantità esattamente conosciute del chemosterilante, questi furono impregnati immergendoli in una vaschetta contenente la soluzione. Si cercò di evitare il più possibile la evaporazione del solvente chiudendo il recipiente subito dopo ogni immersione, con un coperchio a bordi smerigliati.

Per quanto riguarda le carte, dalla quantità di soluzione consumata per ogni concentrazione, divisa per il numero di fogli e per l'area di questi (150 cm^2), risultò che approssimativamente si avevano: per la soluzione al 20%, 1,6 mg di Metepa/cm^2, per la soluzione al 40%, 3,2 mg/cm^2 e per la soluzione al 60%, 4,8 mg/cm^2.

Gruppi di 5 insetti furono lasciati per 30' sulle carte trattate coperti da una capsula di Petri di 9 cm di diametro; gli insetti avevano quindi a disposizione 63,6 cm^2 di superficie trattata.

Le scatoline di plastica erano di PVC (cloruro di polivinile della Montecatini), di forma cilindrica, con 8,9 cm di diametro e 2,1 cm di altezza. Si prepararono soluzioni di Metepa in acetone al 12% e al 24% delle quali, con una

buretta, si versarono 2 ml per scatola, corrispondenti a 4 mg e 8 mg di Metepa/cm².

Per poter confrontare nel modo migliore i risultati delle prove con i fogli di carta e le scatoline, si utilizzò di queste ultime solo il fondo, offrendo così ad uno stesso numero di insetti presso a poco la stessa area trattata (cm² 63,2): onde ottenere che gli insetti camminassero sempre sul fondo si usarono come coperchi capsule di Petri, in quanto gli insetti stessi schivano il vetro sul quale di muovono con difficoltà.

Nelle scatole si provarono tre tempi di esposizione: 10', 20' e 30', utilizzando scatole diverse per ogni esperimento. Il controllo era rappresentato da gruppi di 5 insetti esposti per 30' su fogli di carta da filtro, carta da ufficio e scatole di plastica trattate con il solvente.

RISULTATI

I risultati del trattamento dei maschi a mezzo carte sono esposti nella Fig. 1. In Tabella 1 sono invece riportati i dati relativi al trattamento dei due sessi usando le scatole di plastica.

Analizzando i risultati ottenuti con le carte si può rilevare che gli insetti maschi subirono scarsamente l'effetto sterilizzante del Metepa: solo con la concentrazione al 60% si ebbe infatti, con la carta da ufficio, una diminuzione della fertilità, di appena il 28% circa, rispetto al controllo. Con la carta da filtro i valori di fertilità furono

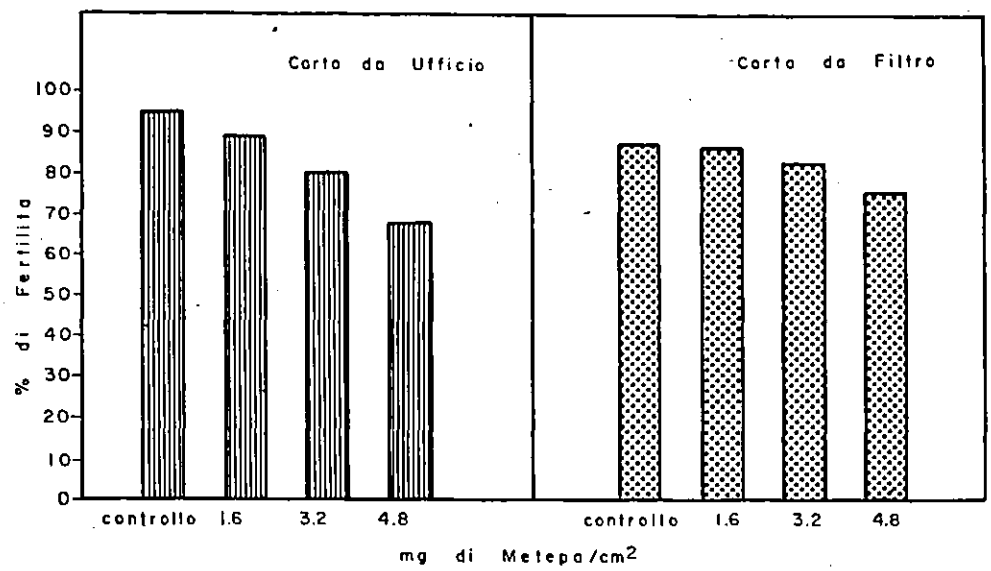

Fig. 1. - *R. prolixus*: % di schiusura di uova di ♀♀ vergini normali accoppiate con ♂♂ posti per 30' in contatto con carta da ufficio e carta da filtro impregnate con varie soluzioni di Metepa in Acetone.

ancora maggiori, ovviamente per il maggior potere di assorbimento di questo tipo di carta.

L'esposizione di femmine a carte trattate non ebbe alcun effetto sterilizzante; accoppiate successivamente con maschi non esposti, le femmine stesse mostrarono valori di fertilità perfettamente normali.

Per nessuna delle tre concentrazioni del chemosterilante si rilevò mortalità tra gli insetti esposti alle carte trattate.

Con le scatole di plastica i risultati furono migliori. La Tabella 1 mostra le percentuali di schiusura di uova ottenute fino a 5 settimane dopo l'esposizione degli insetti alle superfici trattate. L'esperimento non fu proseguito oltre perché dagli studi ecologici effettuati è stato calcolato che la vita media di un *R. prolixus* adulto in condizioni naturali è pari a un mese circa (7).

Quando si esposero maschi e femmine o i soli maschi, con ambedue le dosi sperimentate e per tutti i tempi di esposizione, la fertilità fu sempre uguale a zero. Quando si esposero le femmine i valori di fertilità furono abbastanza alti poiché le femmine sono più resistenti dei maschi. Anche nelle femmine trattate è stata tuttavia osservata una notevole diminuzione della fecondità: il numero di uova deposte/femmina fu infatti molto più basso di quello del controllo.

TABELLA 1

% di fertilità in R. prolixus *adulti esposti a superfici di plastica trattate con Metepa. I dati riportati sono la media dei valori di fertilità ottenuti durante un periodo di 5 settimane dopo la esposizione.* (Tra parentesi: numero di uova deposte/femmina).

	♂♂ trattati + ♀♀ trattate			♂♂ normali + ♀♀ trattate			♂♂ trattati + ♀♀ normali		
	10'	20'	30'	10'	20'	30'	10'	20'	30'
4 mg/cm²	0 (5.8)	0 (16.1)	—	0 (14.1)	0 (23.0)	0 (7.5)	58.3 (2.7)	55.9 (20.2)	59.6 (14.6)
8 mg/cm²	0 (7.8)	0 (10.4)	0 (16.9)	0 (8.7)	0 (30.5)	0 (31.8)	—	27.9 (2.7)	—
Controllo			90.7 (48.3)			87.7 (35.8)			94.0 (50.2)

La mortalità, di cui si prese nota ogni settimana, fu alquanto variabile rispetto alle dosi ed ai tempi di esposizione. Questo risultato trova probabilmente la sua spiegazione nel fatto che la plastica viene intaccata dal solvente e quindi il Metepa si mescola più o meno intimamente ad essa invece di formare, dopo evaporazione dell'acetone, una pellicola sulla superficie.

La mortalità apparve comunque più elevata nelle femmine che non nei maschi; ciò è presumibilmente da imputare al fatto che le femmine, più grosse e pesanti, e striscianti leggermente il voluminoso addome nella deambulazione, entrano maggiormente in contatto con la superficie trattata ed assorbono quindi una maggior quantità di chemosterilante.

DISCUSSIONI E CONCLUSIONI

I diversi risultati ottenuti con l'uso di carte e di scatole di plastica è con ogni probabilità da riferire al potere assorbente delle carte nei confronti del chemosterilante, come anche dimostrato dalle differenze osservate tra i due tipi di carta stessi: con la carta da filtro la sterilità è infatti stata minore che con la carta da ufficio. Se ne conclude che l'uso di carte come supporto per il chemosterilante è praticamente da escludere. Quanto alle superfici di PVC sembra invece che esse possano essere utilizzabili per la sterilizzazione di insetti per contatto tarsale.

L'applicazione pratica delle scatoline contenenti il chemosterilante baserebbe sulla autosterilizzazione degli insetti del campo. Infatti, appendendo le scatoline sulle pareti del « rancho » lungo il percorso notturno dei triatomi dal tetto ai letti e alle amache dove scendono alla ricerca del cibo, si potrebbe con il tempo controllare la popolazione della casa. Questo argomento sarà oggetto di studio in un futuro lavoro. Sono attualmente in corso esperimenti con solventi che non intacchino la plastica e con dosi inferiori a quelle usate nel presente lavoro.

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PRELIMINARY TESTS OF ADULT *RHODNIUS PROLIXUS* STERILIZATION BY TARSAL CONTACT WITH METEPA TREATED SURFACES

The aim of this work was a study of Metepa for the control of some indoor vectors of Chagas'disease. Adult *Rhodnius prolixus* were placed during 30 minutes on bond and filter papers previously dipped in 20%, 40% and 60% Metepa-acetone solutions. Surface concentrations of Metepa resulted respectively 1.6, 3.2 and 4.8 mg/cm². Fertility was inhibited, by 28%, only in those males placed in contact with the 60% solution in bond paper. Males tested on the other concentrations and filter paper showed no fertility changes. Since the marked absorption capacity of the papers used, specially filter, left an insufficient Metepa surface residue, other tests were made using plastic, polyvinylchloride, sheets.

Metepa was applied to these sheets at 4 and 8 mg for cm^2 and adults, both sexes, were placed in contact with them for 10, 20 and 30 minutes periods. Results indicated that males were made totally sterile even by the lowest concentration and shortest contact period used. Female fertility was not significantly affected but oviposition was markedly reduced. Since longevity of treated specimens was also reduced and the acetone used as solvent affected the plastic sheets other tests are in progress using lower Metepa concentrations and a different solvent. These preliminary results suggests that autosterilization by chemical means could be of use for the control of certain indoor vectors of Chagas' disease.

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