Rev. Biol. Trop., 22(1): 187-200, 1974

Bionomics of black flies (Diptera: Simuliidae) in Costa Rica.
I. Species biting man, with an epidemiological summary for the Western Hemisphere*

by

B.V. Travis,** Mario Vargas V.,***
and J. Clyde Swartzwelder****

(Received for publication March 18, 1974)

ABSTRACT: In the Western Hemisphere there are listed 61 species of black flies which are recorded as biting man in the Neotropical Region and 37 in the Nearctic Region. Five neotropical species, *Simulium quadrivittatum, S. metallicum, S. callidum, S. haematopotum* and *S. paynei,* were collected while biting man in Costa Rica. The greatest biting rates in Costa Rica were at altitudes of 0 to 1500 m.

As part of a program to study the bionomics of biting Diptera in Costa Rica, observations were initiated in July 1968 on the black flies. For the first year of the project, observations and collections of black flies were made at monthly intervals in 53 streams located in the Central Valley. During the second year, observations were continued at bimonthly intervals in 28 of these 53 streams and in 47 additional streams located mostly outside the Central Valley. It was hoped that the biometrical data assembled from these studies would be helpful in a better understanding of the biology and distribution of

* Louisiana State University International Center for Medical Research and Training (LSU-ICMRT), San José, Costa Rica. This investigation was supported in part by the United States Army Medical Research and Development Command, Contract DADA-17-68 C-8023. The findings in this report are not to be construed as an official Department of the Army position unless so designated by official documents.

** Louisiana State University, School of Medicine New Orleans, La. Visiting Professor, on leave from Cornell University, Ithaca, N.Y.

*** Universidad de Costa Rica, Facultad de Microbiología, Departamento de Parasitología, San José, Costa Rica, C.A.

**** Louisiana State University, School of Medicine, New Orleans, La.

species of black flies and that such data would be useful in past and future epidemiological interpretations of disease organisms transmitted by these flies (TRAVIS and VARGAS, 40; VARGAS and TRAVIS, 46).

Because of the general strong reaction to bites and to the transmission of disease organisms by black flies it seemed appropriate to start assembling lists of black fly species recorded in the Western Hemisphere as biting man. Also it seemed appropriate to make some brief comments on the disease organisms transmitted to man by these flies.

In the Western Hemisphere two lists of species are available, VULCANO (47) lists 253 species in the Neotropical Region, and STONE (35) 111 species and one subspecies in the Nearctic Region (north of Mexico).

With the two lists of species as guide lines for valid names, preliminary lists were prepared from the literature of species that were recorded as biting man. Each record has one documentation for the species in each country. In most cases the documentation is not necessarily the original. As the nomenclature at the subgeneric level is still a matter of debate, only the generic names are used.

The species are arranged alphabetically, with the generic names separated by a comma from the trivial name. The names of the describers of the various species are not added in this report as they are included in the two published lists.

SPECIES RECORDED BITING MAN

NEOTROPICAL REGION

The records for the neotropics include those published for the Latin American countries, and also the records for the biting adults from our Costa Rican studies.

In Table 1 are included the 61 species that are recorded in the literature as biting man in the neotropics. In tables 2 and 3 are summarized the average numbers of biting adults taken in Costa Rica at various altitudes during a two-year study. Table 2-A includes the data obtained from collections at 53 streams in the Central Valley during the year 1968-69. The major objectives were to concentrate on the larvae, pupae and reared adults. The biting adults collected were almost exclusively those that were biting the members of the survey team during the time spent collecting the immatures. With few exceptions the total time spent with the observations of each stream site was one hour during the period 9 AM to 1 PM. There were, with few exceptions, four field workers making the observations and collections. Thus, the average number of adults per stream site was based on approximately four man-hours per observation and 12 monthly observations, or a total of 48 man-hours per stream site.

Table 2-B includes data from collections at 47 stream sites outside the Central Valley. Each of these streams was observed bimonthly for one

TABLE 1

Black fly species recorded in the literature as biting man in the Neotropical Region

Species	Country	References
amazonicum, Simulium	Venezuela	BRICEÑO IRAGORRY, VARGAS & DIAZ NAJERA (4)
annulatum, Simulium	Argentina	WYGODZINSKY & COSCARON (48)
anthracinum, Austrosimulium	Argentina	VARGAS (42)
antillarum, Simulium	Antilles, Mexico	VARGAS (42)
	Cuba	DIAZ NAJERA (11)
avidum, Simulium	Mexico	HOFFMANN (20)
callidum, Simulium (=*S. mooseri*)	México, Guatemala	VARGAS (42)
	Colombia	GUTTMAN (18)
	Costa Rica	TRAVIS, VARGAS & SWARTZWELDER*
clarki, Simulium	Panamá	VARGAS (42)
deagostinii, Simulium	Argentina	COSCARON (6)
delpontei, Simulium	Argentina	VARGAS (42)
dinelli, Simulium	Argentina	VARGAS (42)
downsi, Simulium	Mexico	VARGAS & DIAZ NAJERA (43)
	Guatemala	DALMAT (7)
dureti, Simulium	Chile	COSCARON (6)
escomeli, Simulium	Ecuador	LEON & WYGODZINSKY (23)
exiguum, Simulium	Ecuador	LEON & WYGODZINSKY (23)
	Colombia	BARRETO (2)
	Guatemala	DALMAT (7)
flavopubescens, Simulium	Brazil	VARGAS (42)
ganalesense, Simulium	Mexico	VARGAS & DIAZ NAJERA (43)
gonzalesi, Simulium	Mexico	VARGAS & DIAZ NAJERA (44)
gonzalezherrejoni, Simulium	Mexico	DIAZ NAJERA (13)
guianense, Simulium	British Guiana	VARGAS (42)
haematopotum, Simulium	Mexico	VARGAS (42)
	Costa Rica	TRAVIS, VARGAS & SWARTZWELDER*
	Guatemala	DALMAT (7)
	Panamá	FAIRCHILD (14)
ignescens, Simulium	Ecuador	LEON & WYGODZINSKY (23)
inaequale, Simulium	Argentina	VARGAS (42)
incrustatum, Simulium	Brazil	VARGAS (42)
infuscatum, Simulium	Brazil	VARGAS (42)
jacumbae, Simulium	Guatemala, Mexico	COSCARON (6)
jerezensis, Simulium	Mexico	DIAZ NAJERA (13)
jujuyense, Simulium	Argentina, Ecuador	LEON & WYGODZINSKY (23)
lahillei, Simulium	Argentina	BARRETO (2)

TABLE 1 (Cont.)

Black fly species recorded in the literature as biting man in the Neotropical Region

Species	Country	References
lane-portoi, Simulium	Brazil	VARGAS (42)
limbatum, Simulium	Venezuela	VARGAS (42)
lugubre, Simulium (=S. guianense)	Venezuela	VARGAS (42)
lutzianum, Simulium	Venezuela	VARGAS (42)
mediovittatum, Simulium	Mexico	VARGAS & DIAZ NAJERA (45)
meridionale, Simulium	Mexico	VARGAS (42)
metallicum, Simulium	Mexico, Guatemala Costa Rica, Panama Venezuela, Trinidad	VARGAS (42)
	Colombia	GUTTMAN (18)
minusculum, Simulium	Brazil, Paraguay Costa Rica	VARGAS (42)
moorei, Simulium	Chile	VARGAS (42)
ochraceum, Simulium	Mexico, Guatemala Panama, Venezuela	VARGAS (42)
opalinifrons, Simulium	Chile	COSCARON (6)
orbitale, Simulium	Brazil, Paraguay	COSCARON (6)
pachecolunai, Cnephia	Guatemala	DALMAT (7)
panamense, Simulium	Costa Rica	ZELEDON & VIETO (49)
paraguayense, Simulium	Argentina, Brazil, Paraguay, Venezuela	COSCARON (6)
paynei, Simulium	Costa Rica	TRAVIS, VARGAS & SWARTZWELDER*
pertinax, Simulium	Brazil, Argentina Paraguay	VARGAS (42)
pruinosum, Simulium	Brazil	VARGAS (42)
pseudocallidum, Simulium	Mexico	DIAZ NAJERA (12)
pseudohaematopotum, Simulium (=S haematopotum)	Mexico	HOFFMAN (20)
pulverulentum, Simulium	Venezuela	BRICEÑO IRAGORRY (3) VARGAS (42)
quadrivittatum, Simulium	Cuba, Costa Rica Jamaica, Panama Venezuela, Puerto Rico	VARGAS (42)
riveti, Simulium	Ecuador	VARGAS (42)

TABLE 1 (Cont.)

Black fly species recorded in the literature as biting man in the Neotropical Region

Species	Country	References
rubrithorax, Simulium	Brazil, Argentina Venezuela, British Guiana	VARGAS (42)
sanguineum, Simulium	Colombia, British Guiana, Lesser Antilles	SMART (32)
scutellatum, Simulium	Colombia	VARGAS (42)
scutistriatum, Simulium	Brazil	VARGAS (42)
simplicicolor, Simulium	Brazil	VARGAS (42)
tenuipes, Simulium	Chile	VARGAS (42)
trivittatum, Simulium	Mexico	VARGAS (42)
veracruzanum, Simulium	Guatemala	DALMAT (7)
versicolor, Simulium	Venezuela,	VARGAS (42)
vittatum, Simulium	Canada, U. S., Mexico	VARGAS (42)

year (1969-70) by a three-man-team, or approximately 18 man-hours per year.

The data in Table 2 show that outside the Central Valley the greatest biting rates were at altitudes of 500-1000 m, with the maximum rates inside the Central Valley at 500-1500 m. Part of the low biting rates above 1500 m may be a reflection of fewer streams at the higher altitudes.

To obtain some data on the annual variability of black fly production and the biting adults, 28 streams were selected from the 53 in the Central Valley for bimonthly observations for a 12-month period. The data for the first year 1968-69 (Table 3-A) were obtained by selecting bimonthly data from the monthly observations for a 12-month period. These same 28 streams were also observed on a bimonthly basis for the year 1969-70 (Table 3-B). The 1968-69 observations (Table 3-A) of these 28 streams were based on six bimonthly observations of each stream site for approximately 24 man-hours. In 1969-70 (Table 3-B) there were only three observers, thus, there was a total of 18 man-hours of observations of each stream site.

At least under the conditions from which the biting adults were obtained, a very low biting rate on man was actually indicated. Perhaps methods can be devised that will be more conducive to higher biting rates. The numbers of biting adults are surprisingly similar for the two years of observations (Table 3-A and B.).

In all of our Costa Rican records of biting adults the predominant species were *S. quadrivittatum* (534 specimens) and *S. metallicum* (160 specimens). Three other species *S. callidum* (7 specimens), *S. paynei* (1 specimen) and *S. haematopotum* (4 specimens) were taken only rarely. The *S. quadrivittatum* and the *S. metallicum* were both taken mostly at altitudes of

TABLE 2

Black fly adults (Simulium) *collected while biting man during 1968-69 and 1969-70 at different altitudes in Costa Rica*

Altitude (m)	Number collection sites	Total flies	Average number of biting adults per site and species				
			quadrivittatum	*metallicum*	*callidum*	*paynei*	*haematopotum*
A. 53 sites observed in 1968-69 (Central Valley)							
500-1000	17	32	0.6	1.1	0.1	0	0
1001-1500	23	236	7.3	2.8	0.2	0	0
1501-2000	8	11	0.4	1.0	0	0	0
2001-2500	3	1	0	0.3	0	0	0
2501-3000	2	1	0	0	0	0.5	0
B. 47 sites observed in 1969-70 (outside the Central Valley)							
0-500	32	72	2.0	0.1	0	0	0.1
501-1000	13	147	9.9	1.0	0.1	0	0
1001-1500	1	0	0	0	0	0	0
1501-2000	0	0	0	0	0	0	0
2001-2500	0	0	0	0	0	0	0
2501-3000	0	0	0	0	0	0	0

TABLE 3

Black fly adults (Simulium) *collected while biting man during 1968-69 and 1969-70 at different altitudes in Costa Rica*

Altitude (m)	Number collection sites	Total flies	Average number of biting adults per site and species				
			quadrivittatum	*metallicum*	*callidum*	*paynei*	*haematopotum*
A. 1968-69 observations on 28 stream sites selected from the 53 streams in the Central Valley							
500-1000	5	12	1.4	0.8	0.2	0	0
1001-1500	15	181	8.7	3.3	0.1	0	0
1501-2000	6	9	0.5	1.0	0	0	0
2001-2500	0	0	0	0	0	0	0
2501-3000	2	1	0	0	0	0.5	0
B. 1969-70 observations on the 28 selected stream sites in the Central Valley							
500-1000	5	20	2.2	1.8	0	0	0
1001-1500	15	179	10.0	1.8	0.1	0	00
1501-2000	6	8	0	1.3	0	0	0
2001-2500	0	0	0	0	0	0	0
2501-3000	2	0	0	0	0	0	0

0-1500 m with the greatest numbers occurring at altitudes of 1000 to 1500 m. The seven specimens of *S. callidum* were taken principally at altitudes of 500-1000 m. The single specimen of *S. paynei* was collected at 2630 m and the four *S. haematopotum* at 60 m.

Nearctic Region

In Table 4 are listed 37 nearctic species which are recorded as biting or annoying man north of Mexico.

INCRIMINATED VECTORS

Neotropical Region

Onchocerciasis: In the neotropics onchocerciasis was first diagnosed by Robles (30) in the Pacific coast of Guatemala. That same year Brumpt (5) described a new species of *Onchocerca, O. caecutiens,* in Latin America. Maldonado (24) gave a historical account of the disease in the neotropics. At the present time active foci are known to be in Mexico, Guatemala, and Venezuela; autochthonous cases are reported from Colombia and Surinam and possibly also in Brazil. There still remain many unanswered problems on the distribution and transmission of *Onchocerca* to man. For instance, of the many species of black flies that are recorded as biting man, only about half a dozen species are reasonably well documented as transmitters of *O. volvulus,* the only disease organism clearly shown to be transmitted by black flies.

The species that have been incriminated as vectors of *Onchocerca* in the neotropics are: *S. ochraceum, S. metallicum* and *S. callidum* (Dalmat, 7). There is some laboratory evidence that *S. mangabeirai* (Vargas and Diaz Najera, 45), *S. gonzalezi* (=*S. exiguum*), *S. haematopotum,* and *S. veracruzanum* may also be vectors (Gibson and Dalmat, 17).

It is interesting that the same most important vector species occur from Mexico in the north to Costa Rica and from Costa Rica to the northern portions of South America. Although these same species occur in Costa Rica, there is no report of human onchocerciasis in this country. The importance of *S. callidum* must be reevaluated as a result of the separation of *S. pseudocallidum* from the *S. callidum* complex by Diaz-Najera (12).

As might be expected in the literature, the certified transmitters of *Onchocerca* were in the lists of anthropophilic species. However, the fact that a given species of black fly is anthropophilic is no proof that the species will be a transmitter of *Onchocerca.* It might be assumed that some species have mixed host preferences and normally may be zoophilic. However, in the absence or in low populations of animal hosts these species may be forced to be strongly anthropophilic. It also might be assumed that a reasonably high population of intermediate hosts such as black flies will be needed to maintain the required transmissions that assure survival of the parasites for which they are vectors.

TABLE 4

Black fly species recorded in the literature as biting or as pests of man in the Nearctic Region

Species	Country	References
arcticum, Simulium	U. S.	PETERSON (26)
	Canada	SOMMERMAN, SAILER & ESSELBAUGH (34)
aureum, Simulium	U. S.	STONE & JAMNBACK (37)
	Canada	PETERSON (27)
bicorne, Simulium	U. S. (Pest)	PETERSON (26)
canonicola, Simulium	U. S.	PETERSON (27)
caudatum, Prosimulium	Canada	SHEWELL (31)
corbis, Simulium	Canada	HOCKING & RICHARDS (19)
decorum, Simulium	U. S.	ANDERSON & DEFOLIART (1)
	Canada	DAVIES & PETERSON (8)
defoliarti, Simulium	Canada (Pest)	PETERSON (26)
doveri, Prosimulium	Canada	PETERSON (28)
esselbaughi, Prosimulium	Canada	SOMMERMAN (33)
exigens, Prosimulium	U. S. (Pest)	PETERSON (27)
flaviantennum, Prosimulium	U. S. (Pest)	PETERSON (26)
fontanum, Prosimulium	Canada (Pest)	DAVIES, PETERSON & WOOD (9)
fulvum, Prosimulium	Canada	PETERSON (27)
fuscum, Prosimulium	U. S.	ANDERSON & DEFOLIART (1)
	Canada	DAVIES & SYME (10)
*hirtipes, Prosimulium**	U. S.	STONE & JAMNBACK (37)
	Canada	HOCKING & RICHARDS (19)
hunteri, Simulium	U. S.	DAVIES & PETERSON (8)
	Canada	PETERSON (26)
jenningsi, Simulium	U. S.	STONE & SNODDY (38)
	Canada	DAVIES, PETERSON & WOOD (9)
johannseni, Simulium	U. S.	JOBBINS-POMEROY (21)
latipes, Simulium	U. S.	STONE & JAMNBACK (37)
longistylatum, Simulium	Canada	DAVIES, PETERSON & WOOD (9)
luggeri, Simulium	Canada	FREDEEN (16)
magnum, Prosimulium	U. S.	STONE & SNODDY (38)
meridionale, Simulium	Canada	FREDEEN (16)
mixtum, Prosimulium	U. S.	ANDERSON & DEFOLIART (1)
multidentatum, Prosimulium	Canada	DAVIES & PETERSON (8)
mutata, Cnephia	U. S.	STONE & SNODDY (38)
	Canada	DAVIES & PETERSON (8)
nyssa, Simulium	U. S. (Pest)	STONE & SNODDY (38)
parnassum, Simulium	U. S.	STONE & SNODDY (38)
	Canada	HOCKING & RICHARDS (19)
pecuarum, Cnephia	U. S.	JOHANNSEN (22)
pictipes, Simulium	U. S.	STONE & SNODDY (38)
pugetense, Simulium	U. S.	STONE & JAMNBACK (37)
tescorum, Simulium	U. S.	STONE & BOREHAM (36)
trivittatum, Simulium	U. S.	PETERSON (26)
tuberosum, Simulium	U. S.	STONE & SNODDY (38)
	Canada	DAVIES, PETERSON & WOOD (9)
venustum, Simulium	U. S.	STONE & JAMNBACK (37)
	Canada	PETERSON & WEST (29)
vittatum, Simulium	Canada	TWINN (41)
	U. S.	STONE & SNODDY (38)

* *Prosimulium hirtipes* is now thought to be limited to the Eastern Hemisphere and represented in the Western Hemisphere by at least three sibling species, *P. fontanum, P. fulvum* and *P. mixtum.*

Carate: LEON and WYGODZINSKY (23) pointed out that in the neotropics as early as 1862 Juan León of México believed that the disease called "mal de pinto" or "carate" was transmitted by "jejenes" (black flies). PEÑA CHAVARRIA and SHIPLEY (25) reviewed the disease and presented some epidemiological evidence that black flies may transmit the disease called carate. The primary evidence is that the disease is distinctly more common in the vicinity of streams and particularly in areas of high black fly biting rates. The method of transmission of the causative organism *Treponema carateum*, is still unknown.

Venezuelan equine encephalitis (*VEE*) and *vesicular stomatitis*: Two additional disease organisms have been recently isolated from black flies in Colombia. These are the viruses that cause VEE, (TRAPIDO, 39) and vesicular stomatitis (H. TRAPIDO, personal communication). The role of black flies in transmitting these viruses is yet to be learned.

NEARCTIC REGION

Typhoid and *pellagra*: In the Nearctic Region no disease is known to be transmitted to man by black flies. However, in the literature of the early 1900's these insects were accused of transmitting ethiologic agents causing typhoid and pellagra. Some strong evidence for the transmission of pellagra by black flies in the U.S. was presented by FORBES (15). Of course we now know that this problem is caused by a vitamin deficiency.

Equine encephalitis (*EE*): Black flies (*S. johannseni*) were experimentally infected with EE when fed on infected birds in Wisconsin. Also this virus was isolated from a pool of *S. meridionale* collected from a turkey brooder house (ANDERSON and DEFOLIART, 1).

Black fly adults vary in their choice of vertebrate hosts; for instance, some species feed mostly on birds. These ornithophilic species may be of considerable importance in maintaining a virus such as EE by passing the virus from bird to bird. Some species seem to select mammals such as horses and cattle, and some are at least reasonably anthropophilic.

RESUMEN

De las especies de simúlidos señaladas en el Hemisferio Occidental como picadoras del hombre, 61 corresponden a la Región Neotrópica y 37 a la Región Neártica.

Durante los dos años dedicados a este estudio, cinco especies neotropicales picaron al hombre en alguna oportunidad. De acuerdo con un orden decreciente de antropofilia tales especies fueron: *Simulium quadrivittatum* (534 especímenes), *S. metallicum* (160 especímenes), *S. callidum* (7 especímenes), *S. haematopotum* (4 especímenes) y *S. paynei* (1 espécimen). Dado el interés epidemiológico se señala las principales especies de simúlidos incriminadas como vectores, especialmente de oncocercosis, en el Hemisferio Occidental.

En Costa Rica la mayor frecuencia de picadas por parte de los simúlidos al hombre se encuentra entre los 0 y los 1500 m sobre el nivel del mar.

ACKNOWLEDGEMENTS

The authors wish to express their thanks to a number of people for their help with the necessary local arrangements. Special thanks are extended to the Staff of the Louisiana State University International Center for Medical Research and Training (LSU-ICMRT) and also to the laboratory and field assistants, Roberto Echeverri (ICMRT) and Guillermo Zúñiga (Universidad de Costa Rica). Thanks are also extended to Dr. A. Díaz Nájera of México for kindly loaning specimens, for reviewing this paper, and for supplying additional references.

The authors would appreciate being advised by the readers of species not included in Tables 1 and 4 that were missed in the literature review. These records can be sent to B.V. Travis, Department of Entomology, Cornell University, Ithaca, N.Y. 14850.

LITERATURE CITED

1. ANDERSON, J. R., & G. R. DEFOLIART
1961. Feeding behavior and host preferences of some black flies (Diptera: Simuliidae) in Wisconsin. *Ann. Entomol. Soc. Amer.*, 54: 716-729.

2. BARRETO, P.
1969. The Species of black flies found in Colombia (Diptera: Simuliidae). *J. N.Y. Entomol. Soc.*, 77: 31-35.

3. BRICEÑO IRAGORRY, L.
1943. Nota sobre Simúlidos del Valle de Caracas. *Bol. Lab. Clin. "Luis Razetti", Caracas*, 3: 182-186.

4. BRICEÑO IRAGORRY, L., L. VARGAS, & A. DIAZ NAJERA
1953. Algunos caracteres morfológicos de *Simulium amazonicum* Goeldi, 1905 (Insecta, Diptera). *Rev. Inst. Salubr. Enferm. Trop. (Méx.)*, 13: 243-245.

5. BRUMPT, EMILE
1919. Una nouvelle filaire pathogène parasite de l'homme (*Onchocerca caecutiens*, n. sp.). *Bull. Soc. Path. Exot.*, 12: 464-473.

6. COSCARON, S.
1969. Nuevos datos relacionados con la importancia sanitaria de los simúlidos. (Insecta: Diptera). *Rev. Soc. Entomol. Ar.*, 31: 73-76.

7. DALMAT, H. T.
1955. The black flies (Diptera, Simuliidae) of Guatemala and their role as vectors of onchocerciasis. *Smithsonian Misc. Collect.*, 125: 1-425.

8. DAVIES, D. M., & B. V. PETERSON
1956. Observations on the mating, feeding, ovarian development and oviposition of adult black flies (Simuliidae: Diptera). *Can. J. Zool.*, 34: 615-655.

9. DAVIES, D. M., B. V. PETERSON, & D. M. WOOD
1962. The black flies (Diptera: Simuliidae) of Ontario. I. Adult identification and distribution with descriptions of six new species. *Proc. Entomol. Soc. Ont.*, 92: 70-154.

10. DAVIES, D. M., & P. D. SYME
1958. Three new Ontario black flies of the Genus *Prosimulium* (Diptera: Simuliidae). II. Ecological observations and experiments. *Can. Entomol.*, 90: 744-759.

11. DIAZ NAJERA, A.
1961. Nota acerca de *Simulium* (*Psilopelmia*) *antillarum* Jennings, 1915, nueva especie para México (Diptera: Simuliidae). *Rev. Inst. Salubr. Enferm. Trop.* (*Méx.*), 21: 79-92.

12. DIAZ NAJERA, A.
1965. Acerca de un nuevo simúlido mexicano (Diptera: Simuliidae). *Rev. Inst. Salubr. Enferm. Trop.* (*Méx.*), 25: 25-45.

13. DIAZ NAJERA, A.
1969. Simúlidos de Aguas Calientes y Zacatecas. Descripción de seis especies del subgénero *Psilopelmia* y datos de dimorfismo. *Rev. Invest. Salud Pública*, (*Méx.*), 29: 21-63.

14. FAIRCHILD, G. B.
1940. Notes on the Simuliidae of Panamá. (Dipt., Nematocera). *Ann. Entomol. Soc. Amer.*, 33: 701-719.

15. FORBES, S. A.
1912. On black flies and buffalo gnats (*Simulium*) as possible carriers of pellagra in Illinois. *27th. Rept. Sta. Entomol. Ill. Bull.*, 159: 21-52.

16. FREDEEN, F. J. H.
1958. Black flies (Diptera: Simuliidae) of the agricultural areas of Manitoba, Saskatchewan, and Alberta. *Proc. Tenth Int. Congr. Entomol.*, 3: 819-823.

17. GIBSON, C., & H. DALMAT
1952. Three new potential intermediate hosts of human onchocerciasis in Guatemala. *Amer. J. Trop. Med. Hyg.*, 1: 848-851.

18. GUTTMAN, D.
1972. The biting activity of black flies: (Diptera: Simuliidae) in three types of habitats in western Colombia. *J. Med. Entomol.*, 9: 269-276.

19. HOCKING, B., & W. R. RICHARDS
1952. Biology and control of Labrador black flies (Diptera: Simuliidae). *Bull. Entomol. Res.*, 43: 237-257.

20. HOFFMANN, C. C.
1930. Los simúlidos de la región onchocercosa de Chiapas (con descripción de nuevas especies). *An. Inst. Biol.* (*Méx.*), 293-306.

21. JOBBINS-POMEROY, A. W.
1916. Notes on five North American buffalo gnats of the genus *Simulium U.S.D.A. Bull.*, 329: 1-48.

22. JOHANNSEN, O. A.
1934. Aquatic Diptera. 1. Nematocera, exclusive of Chironomidae and Ceratopogonidae. *Cornell Univ. Agr. Exp. Sta. Memoir*, 164: 1-71.

23. LEON, L. A., & P. WYGODZINSKY
1953. Los simúlidos del Ecuador (Diptera). *Bol. Inf. Cient. Nac.*, 6: 269-288.

24. MALDONADO, J. F.
1965. *Helmintiasis del Hombre en América.* Editorial Científico-Médica, Barcelona. 529 pp.

25. PEÑA CHAVARRIA, A., & P. G. SHIPLEY
1925. Contribución al estudio de los carates de América Tropical. *Rev. Med. Latino-Amer.*, 10: 3-76.

26. PETERSON, B. V.
1959. Observations on mating, feeding and oviposition of some Utah species of black flies (Diptera: Simuliidae). *Can. Entomol.*, 91: 147-155.

27. PETERSON, B. V.
1959. Notes on the biology of some species of Utah blackflies (Diptera: Simuliidae). *Mosq. News*, 19: 86-90.

28. PETERSON, B. V.
1970. The *Prosimulium* of Canada and Alaska (Diptera: Simuliidae). *Mem. Entomol. Soc. Can.*, 69: 1-216.

29. PETERSON, D. G., & A. S. WEST
1960. Control of adult black flies (Diptera: Simuliidae) in the forests of Eastern Canada by aircraft spraying. *Can. Entomol.*, 92: 714-719.

30. ROBLES, R.
1919. *Enfermedad de Robles.* Academia de Ciencias Médicas, Físicas y Naturales, Guatemala (ed.), 1963. p. 58-82.

31. SHEWELL, G. E.
1959. New Canadian black flies (Diptera: Simuliidae) *Can. Entomol.*, 91: 686-697.

32. SMART, J.
1940. Simuliidae (Dipt.) from British Guiana and the Lesser Antilles. *Trans. Roy. Entomol. Soc. London*, 90: 1-10.

33. SOMMERMAN, K. M.
1964. *Prosimulium esselbaughi* n. sp., the Alaska *P. hirtipes* 2. (Diptera: Simuliidae). *Proc. Entomol. Soc. Wash.*, 66: 141-145.

34. SOMMERMAN, K. M., R. I. SAILER, & C. O. ESSELBAUGH
1955. Biology of Alaskan black flies (Simuliidae, Diptera). *Ecol. Monogr.*, 25: 345-385.

35. STONE, A.
1965. Family Simuliidae, p. 181-189. *In A catalog of the Diptera of America north of Mexico.* U.S.D.A. Handbook 276.

36. STONE, A., & M. M. BOREHAM
1965. A new species of *Simulium* from the southwestern United States (Diptera: Simuliidae). *J. Med. Entomol.*, 2: 164-170.

37. STONE, A., & H. A. JAMNBACK
1955. *The black flies of New York State (Diptera: Simuliidae).* N.Y. State Mus. Bull., N° 349. 144 pp.

38. STONE, A., & E. L. SNODDY
1969. The black flies of Alabama (Diptera: Simuliidae). *Auburn Univ. Agr. Expt. Bull.,* 380: 1-93.

39. TRAPIDO, H.
1971. *Venezuelan encephalitis. Proc. of the workshop symposium on Venezuelan encephalitis.* PAHO Scientific publication Nº 243. Washington, D.C. pp. 163-164.

40. TRAVIS, B. V., & M. VARGAS V.
1972. Bionomics of black flies in Costa Rica. II. An ecological consideration. *Proc. 57th Ann. Meeting N. J. Mosq. Exterm. Assoc.*: 111-112.

41. TWINN, C. R.
1936. The black flies of eastern Canada (Simuliidae, Diptera). *Can. J. Res. Sec. D.,* 14: 97-150.

42. VARGAS, L.
1945. *Simúlidos del Nuevo Mundo.* Monografía Nº 1 del Inst. Salubr. Enf. Trop. (Méx.). 241 p.

43. VARGAS, L., & A. DIAZ NAJERA
1951. Nota sobre los simúlidos de México y su distribución geográfica (Diptera: Simuliidae). *Rev. Inst. Salubr. Enf. Trop.* (*Méx.*), 12: 89-100.

44. VARGAS, L., & A. DIAZ NAJERA
1953. *Simulium* (*Notolepria*) *gonzalesi* n. sp. (Insecta, Diptera). *Rev. Inst. Salubr. Enf. Trop.* (*Méx.*), 13: 235-239.

45. VARGAS, L., & A. DIAZ NAJERA
1957. Simúlidos Mexicanos. *Rev. Inst. Salubr. Enf. Trop.* (*Méx.*), 17: 143-399.

46. VARGAS V., M., & B. V. TRAVIS
1973. Bionomía de los simúlidos (Diptera: Simuliidae) en Costa Rica. IV. Localización y descripción de los lugares de recolección. *Rev. Biol. Trop.,* 21: 143-175.

47. VULCANO, M. A.
1967. Family Simuliidae, p. 1-44. *In A catalogue of the Diptera of the Americas south of the United States.* 16. Dept. Zool., Secret. Agric. São Paulo, Brazil.

48. WYGODZINSKY, P., & S. COSCARON
1967. A review of *Simulium* (*Pternaspatha*) Enderlein (Simuliidae, Diptera). *Bull. Amer. Mus. Nat. Hist.,* 136: 49-116.

49. ZELEDON, R., & P. L. VIETO
1957. Contribución al estudio de los Simúlidos de Costa Rica (Diptera: Nematocera). I. Sobre el *Simulium panamense* Fairchild, 1940. *Rev. Biol. Trop.,* 5: 19-33.