INTRODUCTION

Onchocerciasis (river blindness) is an essentially rural parasitosis endemic to the valleys and foothills of mountainous areas along streams where the vectors breed. The etiologic agent is the filaria worm *Onchocerca volvulus* that lives as an adult in subcutaneous nodules within its human host. Ocular lesions usually arise between five and six years after infection.

The worms are white and filamentous. Adult males are relatively small, some 2–4 cm long, while the females attain a length of 40–50 cm. The females are viviparous and discharge microfilariae 200–300 microns long. These microfilariae can live in the skin of their host for up to 30 months, and fertile females have a life-span of up to 15 years.

About a year after infection microfilariae can be found around the adult worms’ subcutaneous nodules. These microfilariae migrate to nearby skin areas where they are sometimes ingested by man-biting flies of the genus *Simulium*. They then seek to penetrate the thoracic musculature of these intermediate hosts, and after six or seven days, without undergoing multiplication, develop into an infective form about 700 microns long that is motile and has a fully developed digestive tract. The infective form then migrates to the fly’s proboscis, from where it can enter another human when the insect bites again. The most suitable time for *Simulium* flies to introduce *O. volvulus* into a human host is on hot days, when the person’s skin is moist with sweat and the pores are open.

The account presented here describes the ecologic characteristics of onchocerciasis foci in the Americas and the *Simulium* vectors implicated up to the present time (see Figure 1). The description deals with each of the affected countries in turn (Guatemala, Mexico, Venezuela, Brazil, Colombia, and Ecuador), considering first those where the disease was discovered earliest.

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2 Coordinator of the Vector Studies Section and PAHO/WHO Adviser, Instituto de Biomedicina, Centro Piloto, Apartado No. 357, Villa de Cura, Aragua 2126, Venezuela.
FIGURE 1. Geographic distribution of onchocerciasis foci, and of confirmed and suspected onchocerciasis vectors, in the American Tropics.
GUATEMALA

Onchocerciasis was discovered in America in 1915 by the Guatemalan scientist Rodolfo Robles, who with great skill described the parasite and clinical picture, reported ocular lesions for the first time, and implicated insects of the genus *Simulium* (the “blackfly” *Simulium metallicum* and the “alazán” *Simulium ochraceum*) as vectors of this new American disease (1). Credit for important early work is also due Victor Manuel Calderón, who in 1920 reported observing the intermediate stages of *O. volvulus* in the thoracic muscles of Guatemalan blackflies (2).

Subsequently, in 1934, a group of Harvard University researchers led by Richard Strong (3) demonstrated that *S. ochraceum*, *S. metallicum*, and *Simulium callidum* were seriously implicated in the transmission of *O. volvulus* to man. In 1935 the Ministry of Public Health of Guatemala began a campaign against onchocerciasis. And between 1943 and 1948 De León (4-7) carried out a series of entomologic research projects designed to establish the taxonomy of the vectors that also produced descriptions of seven new species of the family Simuliidae in Guatemala.

A major study by Dalmat (8) on the taxonomy, biology, and ecology of both the immature stages and the adults of Guatemalan simulids was published in 1955. Dalmat devoted half his work to redescribing 41 species (three belonging to the genus *Cnephia*, two to the genus *Gigantodax*, and 36 to the genus *Simulium*) and providing keys for identifying larvae, pupae, and adults of both sexes. He also described the geographic distribution of the vectors in detail and reported that both *S. metallicum* and *S. callidum* bred in warercourses ranging from small creeks to major rivers, had zoophilic habits, and became agitated when fed on human bait.

Largely because of its strictly anthropophilic habits, Dalmat concluded that the principal vector of onchocerciasis in Guatemala was *S. ochraceum*. This insect, which feeds intermittently on human bait without appearing attracted to other animals, has immature stages that are found in small creeks at altitudes ranging from 900 to 1,500 meters. It was suggested that the insect’s low rate of natural infection with *O. volvulus* could be attributable to deaths resulting when large numbers of microfilariae were ingested. The author indicated that in areas where *S. ochraceum* was rare or absent, *Simulium haematopotum*, *S. veracruzianum*, and *S. exiguum* (= *S. gonzalezii*) could be the principal transmitting agents.

Also, De León (7) found that 1.86% of 631 *S. metallicum* females and 0.89% of 433 *S. ochraceum* females captured in endemic areas of Guatemala were naturally infected by microfilariae that he classified as *O. volvulus*. Similarly, Gibson (9) reported in 1965 that over a period of a year he found 1.04% of 1,734 *S. metallicum*, 0.38% of 1,839 *S. ochraceum*, and 0.62% of 162 *S. callidum* to be naturally infected.

In 1966 De León and Duke (10) reported results obtained with two volunteer carriers of *O. volvulus*, natives of the West African forest and the Sudan savanna, who, together with two Mayan Indians, let themselves be bitten by local Guatemalan vectors. When *S. ochraceum* bit the Mayan Indians it ingested an average of 390 Guatemalan microfilariae but produced only 2.5 metacyclic
forms—indicating that on the average 0.65% of the microfilariae ingested developed into infective forms under experimental conditions, while the rest of the microfilariae were apparently destroyed by the insect. When the same vector ingested an average of 14 West African forest microfilariae per bite, it produced an average of 0.25 metacyclic forms, yielding an average survival rate of 1.8%. Ingestion of microfilariae from the Sudan savanna did not lead to development of the infective form in S. ochraceum, S. metallicum, or S. callidum. The authors also established that simuliids can be used for xenodiagnosis of American onchocerciasis, since insects recently fed on infected subjects yielded a higher concentration of microfilariae than insects from the same regions before feeding.

These experiments, together with others carried out by Duke (11) in Venezuela, demonstrated that African and American onchocerciasis differ in many respects, and that (as indicated previously by Figueroa Marroquin—12) the latter can be regarded as an indigenous disease. The arguments in favor of this theory were confirmed by Duke et al. (13) in 1967, after they succeeded in infecting a chimpanzee from Cameroon with Guatemalan metacyclic forms of O. volvulus. These O. volvulus were taken to Africa in specimens of S. ochraceum that had previously bitten volunteers harboring large parasite loads. When microfilariae appeared in the chimpanzee's skin, the animal was exposed to the bites of S. damnosum, but at the end of seven days the American strain had not developed into the infective stage in the principal African vector.

Bain et al. (14) reported in 1974 that only 1 to 2% of all the microfilariae ingested by S. ochraceum were able to evolve in the insect's musculature, and that 98% of the microfilariae were destroyed immediately after ingestion. Along this same line, Omar and Garms (15) reported the following year that numerous chitinous teeth in the buccopharynx of S. ochraceum destroy large numbers of microfilariae, allowing only some 2.6% through to enter the thoracic musculature. In contrast, the buccopharynx of S. metallicum is toothless, and although the insect tends to ingest relatively few microfilariae, most (some 74.5%) of those ingested succeed in migrating to the insect's thorax.

In 1975 Garms (16) reported natural vector infection rates on five Guatemalan coffee plantations where onchocerciasis was endemic to be 0.3% in S. metallicum, 0.2% in S. callidum, 1.3% in S. gonzalezi, and 1.9% in S. ochraceum. This last species had a lower O. volvulus infection index than did the local human populations affected by onchocerciasis. It was also found that only three S. ochraceum females were parasitized by third stage O. volvulus larvae out of a total of 3,513 insects examined, and that only two out of 3,121 S. metallicum examined were found to contain filariae morphologically distinct from O. volvulus.

Around the same time, Collins et al. (17) determined the level of infection of S. ochraceum exposed to 10 volunteers with very low and average numbers of microfilariae in the skin. This was done both qualitatively (by finding the percentage of insects infected) and quantitatively (by finding the average number of infective larvae in each insect), with the object of ascertaining S. ochraceum's effectiveness as a reservoir of O. volvulus infection.
The volunteers were divided into three groups. The first consisted of three people from whom feeding insects had taken an average of 12.5 microfilariae and had produced an average of 0.02 infective larvae. The second included four people from whom feeding insects had taken averages of 24.2 to 44.7 microfilariae and had produced an average of 0.12 to 0.17 infective larvae. The third group was comprised of three people from whom feeding insects had taken an average of 51.1 to 117.8 microfilariae and had produced an average of 0.51 to 1.69 infective larvae. It appeared that the last group of persons must play the most important role in transmission of onchocerciasis. This finding indicates that the percentage of insects infected is a more significant indicator regarding effective individual transmission than is the average number of filariae found per infected insect.

In the late 1970s, Collins (18) found *O. volvulus* infectivity rates in *S. ochraceum* and *S. callidum* to be 0.31% and 0.41%, respectively. When multiplied by their respective total biting densities, however, the infective biting density of *S. ochraceum* came out to be 79 times that of *S. callidum*. The number of viable larvae that are required for effective transmission was calculated by multiplying the infective biting density by the average number of larvae per infected insect. *S. ochraceum* was found to have the highest infective bite density, and also the effective transmission capacity associated with the human population suffering from onchocerciasis. These findings showed that a high *S. ochraceum* bite density was required to maintain the endemic at its then current levels.

Around the same time, Cupp and Collins (19) studied the gonadotrophic cycle of *S. ochraceum*. They found that a gonadotrophic harmony exists—i.e., that after a single ingestion of blood it is possible to observe complete development of the follicles in all the ovarioles simultaneously. Ovigenesis was found to take 48 to 60 hours. After oviposition the rest of the follicular cells (yellow body) were found to remain visible at the end of the ovariole for about 150 hours.

Under the same laboratory conditions, Collins (20) experimentally infected *S. ochraceum* and *S. metallicum* with *O. volvulus*. Larval development in *S. ochraceum* was found to be synchronic and regular, so that the filariae reached the thoracic muscles and evolved into infective larvae in close to 192 hours after a single ingestion of blood. In contrast, their development in *S. metallicum* was asynchronic and delayed. Between eight and 10 days after feeding, the author observed one infective larva, together with a few residual microfilariae and first-stage larvae that were atrophied and deformed. He concluded that development of *O. volvulus* in *S. ochraceum* is compatible with the intensive transmission associated with human onchocerciasis (21).

Also in the late 1970s, Garms and Ochoa (22) found that an average of 10.2% of the parous *S. ochraceum* females collected in endemic areas were carrying first or second stage *O. volvulus* larvae, and that 1.7% were carrying metacyclic forms. Outside the endemic foci no *O. volvulus* infections of *S. ochraceum* were found. By comparison, the rates of natural *O. volvulus* infection in *S. metallicum* and *S. callidum* were found to be very low, both in endemic areas (2.0% and 2.5%, respectively) and
in areas without known human onchocerciasis (1.1% and 1.0%, respectively). The authors concluded that the vector capacity of *S. metallicum* was extremely low, noting that only four females among the 7,743 insects captured in endemic areas (0.05% of the total number of insects biting) appeared to be infected, and some of the infecting larvae were not *O. volvulus*.

Throughout 1977 Onofre Ochoa (23) investigated the natural infection of vectors in the pilot study area of San Vicente Pacaya, at an altitude of 750 m. The highest rate of *S. ochraceum* infectivity observed was 1.6% (in the month of September). The annual average rate of parous females found among the collected *S. ochraceum* specimens was 42.9. A total of 46 metacyclic larvae morphologically indistinguishable from *O. volvulus* were obtained from 16 specimens of *S. ochraceum*. In contrast, the rate of *O. volvulus* infection found in *S. metallicum* and *S. callidum* was very low; furthermore, these infections were not considered to be of human origin in view of the insects' marked zoophilic tendency and the impossibility of making a correct identification. The authors concluded that *S. ochraceum* was the sole effective vector of *O. volvulus*, and that the status of *S. metallicum* as an *O. volvulus* transmitter was still uncertain.

To ascertain seasonal variations of *S. ochraceum* populations, Takaoka (24) did research from August 1978 to January 1980 at the headwaters of two major rivers that flow through the endemic areas of Escuintla Department. His findings showed that at the end of the dry season *S. ochraceum* larvae were confined to permanent streams at intermediate altitudes. During the rainy season, however, the immature stages spread to numerous temporary rain-fed creeks. At the headwaters of the two rivers the adult population was at its peak from October to December.

As they reported in 1981, Monroy et al. (25) were able to determine that temperature plays a key role in experimental development of *O. volvulus* in *S. ochraceum* and *S. metallicum*. Under laboratory conditions, temperature was found to directly affect the survival of both insects, there being lower survival at higher temperatures and higher survival at lower temperatures. Temperature was also found to affect the time required for development of *O. volvulus* larvae. Thus, the higher the temperature, the shorter the time required for the nematode to complete its development in the insect. In addition, the authors found that a temperature between 18°C and 30°C was required to permit complete development of infective larvae in both species of simulid. For *S. ochraceum* the optimum transmission temperature was found to lie between 22°C and 24°C, because that temperature permitted the highest survival rate.

However, other laboratory experiments carried out by Takaoka (26) and Takaoka et al. (27) have shown that daily exposure to lower temperatures (14-18°C) during the night assists *O. volvulus* larval development in *S. ochraceum* and also enhances the longevity of *S. ochraceum* adults. These findings help to explain why transmission of onchocerciasis has continued without interruption in a region of temperate climate in Guatemala where there are appreciable differences between daytime and nighttime temperatures.

During the late 1970s and early 1980s, Tada et al. (28) and Tada
(29) carried out another study of an epidemiologic nature in San Vicente Pacaya. Using a single skin biopsy, they examined 2,153 persons, of whom 664 (30.8%) proved positive for *O. volvulus*. They also found that altitude played an important role in the parasitosis, with transmission occurring mainly at altitudes between 600 and 1,300 m. Out of 1,217 persons examined by simultaneous biopsy and nodule palpation, 587 proved positive by one or both methods; 101 nodules were detected, mostly in children or persons who had lived in areas of low endemicity. It was concluded that both diagnostic methods needed to be used in order to accurately determine the prevalence of the disease in Guatemala.

Regarding areas affected by onchocerciasis in Guatemala, only seven of the country's 22 departments are involved. No new transmission foci have been reported recently, and the known foci appear to have grown smaller. In 1981 García Manzo (30) reported that the endemic area included three biomes (using Holdridge's classification). These were (1) the wet tropical biome, (2) the wet premontane biome, and (3) the very wet premontane biome. The very wet premontane biome was located near the Pacific, and the others were found in Huehuetenango Department.

According to this same report (30), Robles' disease (ocular onchocerciasis) is distributed in two main areas—that occupied by the Sierra Madre mountain range along the south coast on the Pacific (at an altitude of 600–1,200 m) and that of the Cuchumatanes area of Huehuetenango Department (a continuation of the Soconusco focus in Mexico). According to Aguilar et al. (31), around 1981 the area involved covered approximately 5,130 square kilometers containing 343,000 inhabitants, of whom some 30,000 were infected.

**MEXICO**

In 1923 Fülleborn (32) reported seeing onchocerciasis nodules on the head of a five-year-old Mexican child who attended his clinic in Hamburg, Germany. In 1925 (33) Bustamante reported that the disease probably existed in the Monte Cristo Valley of Chiapas State. In 1926 the presence of this disease was demonstrated unequivocally in both Chiapas and Oaxaca.

Regarding other research in Mexico, in 1931 Torroella (34) first observed microfilariae in the anterior chamber of the eye of an onchocerciasis patient. Using wild females, Hoffmann (35, 36) accomplished the first experimental infections of *S. metallicum*, *S. callidum*, and *S. ochraceum* with *O. volvulus*. Dampf (37, 38) made important studies of the biology and distribution of the simuliid transmitters in endemic areas. In 1949 Vargas and Ruiz Reyes (39) reported natural infection of *S. exiguum* (= *S. gonzalezi*) with intermediate stages of *O. volvulus*. Later, Vargas (40) added the names of two other possible vectors—*Simulium haematopota* (which is very troublesome in the states of Michoacán and Guerrero) and *S. veracruzianum* (in the state of Veracruz). In addition, Vargas and Díaz Nájera (41) carried out a study of Mexican simuliid morphology and systematics in the 1950s, and Vargas (42) wrote an important monograph entitled "Simüliids del Nuevo Mundo" (Simuliids of the New World) that was published in 1945.
Regarding entomologic factors that relate to interruption of onchocerciasis transmission in Mexico and Guatemala, in 1960 Vargas (43) noted that the risk of contracting onchocerciasis for the first time depends primarily on the number of bites that a susceptible individual receives and on the extent to which the local population of female simuliiids are parasitized by infective larvae. This means that a high density of biting females combined with few human reservoirs would produce a very low rate of simuliiid-transmitted infection.

As this implies, a given simuliiid species' role in transmitting the disease (leaving aside factors relating to the filaria worm, man, and the environment) depends on (a) the vector species' degree of susceptibility to the parasite, (b) the number of biting females existing at a given moment, (c) their propensity to take blood from people instead of other vertebrates, (d) the number of gonadotrophic cycles involved, and (e) the insects' longevity in nature. In general, a person may receive the first and subsequent infective doses of *O. volvulus* at intervals depending on the timing of the initial and final stages of the seasonal transmission cycle. However, this only occurs at certain altitudes (between 500 and 1,600 meters). Transmission does not occur at sea level. It has been noted that the areas endemic for onchocerciasis are located around human settlements and near watercourses. The vectors neither rest within houses nor preferentially bite people within houses. Vargas (44) also found that the distance from a breeding ground over which onchocerciasis could be transmitted often corresponded to the maximum flying distance of the adult simuliiid. This does not imply that a single insect would commonly be a transmitter, but rather that the range of a dense population of adult simuliiids capable of transmitting onchocerciasis would determine the size of the area involved.

No current statistics are available on the prevalence of human infection with *O. volvulus* in Mexico. However, Salazar-Mallén (45, 46) reported in 1975 and 1977 that prevalences close to 70% existed in some endemic areas and that some purported reduction of morbidity had been due to diagnostic error attributable to systematic nodule removal—a practice that considerably reduced the number of people with tumors without directly affecting parasitism by microfilariae in the skin.

Overall, it is roughly estimated that some 40,000 people are infected in Mexico, and that the affected regions cover an area of some 8,900 square kilometers. In 1962 García Sánchez and Chávez (47) stated that the focus with the largest number of infections was in southern Chiapas, and that the next largest was in Oaxaca. Coast erysipelas of the kind described in Guatemala has not been reported in Chiapas; however, notable skin discoloration has been seen, sometimes producing a greenish tinge, and this appears to be the source of the so-called "mal morado" (purple sickness) applied to such alterations in Mexico (Vargas—48). According to Beltrán-Hernández (49), as of 1983 onchocerciasis was not a public health problem in Mexico. He indicated that a quarter of the cases were asymptomatic, that severe ocular lesions progressing toward blindness were unknown, and that the number of people blinded by the disease was very small.
According to Salazar-Mallén (46), in the mid-1970s there were three onchocerciasis foci in Mexico. The largest was in Soconusco, in the southern part of the state of Chiapas, located between latitudes 15°4' and 15°57' N and longitudes 90°5' and 93°7' W with an area of some 6,800 square kilometers. A second focus was also located in the state of Chiapas further north, this being the "chamula" focus situated between latitudes 16°52' and 17°7' N and longitudes 92°29' and 92°40' W and covering an area of some 700 square kilometers. A third focus was in the state of Oaxaca, at a place called Alto Papaloapan to the west of the "chamula" focus, between latitudes 17°25' and 17°48' N and longitudes 96°12' and 96°40' W and covering some 1,400 square kilometers.

**VENEZUELA**

The first known onchocerciasis focus in Venezuela was discovered in the eastern part of the country in the late 1940s (50). Its discoverers (Potenza, Febres Cordero, and Anduze) captured *S. metallicum* and *S. exiguum* in the endemic zone but did not prove natural infection. In 1951 Guzmán (51) reported finding a case in the state of Miranda that marked discovery of another endemic area in central Venezuela. Arends et al. (52) reported finding the disease in the state of Aragua in 1954, and in 1957 García Ocampo et al. (53) reported seeing a case with ocular lesions originating in the state of Carabobo.

As reported in 1961, the ability of *S. metallicum* to act as a principal vector for onchocerciasis was demonstrated by Peñalver (54), who studied histologic sections of insects fixed in formalin and stained with hematoxylin-eosin. Of 1,226 *S. metallicum* examined, 104 (8.5%) were found to be infected; however, the highest positive indices of infection were found among females captured at endemic foci in the states of Aragua and Miranda (this index of 12.5% included *S. metallicum* containing any of the three larval stages of *O. volvulus*). In addition, *S. exiguum* was implicated as a second transmitter in the coastal mountain range, even though this insect's small size appeared to permit development of only a small number of nematodes.

During the 1960s, in response to an invitation from the Government of Venezuela, Lewis (55), an entomologist with the British Museum of Natural History, studied the biology of vectors in endemic areas of San Antonio de Maturín in eastern Venezuela. He found that *S. metallicum* preferred to bite the lower extremities of human subjects, while *S. exiguum* alit indifferently on the upper and lower parts of the human body. He also found that the immature stages of *S. metallicum* inhabited small streams 25 to 50 cm in width, while the larvae and pupae of *S. exiguum* were collected in rivers whose beds measured five meters or more across.

In 1965 Rivas et al. (56) published a study on the geographic distribution of onchocerciasis in nine states where the overall prevalence of infection was found to be 39.94 per thousand inhabitants examined, and where the infection had been diagnosed in nearly 17,000 people. The clinical part of the study detected nodules in 23% of the onchocerciasis patients studied. The commonest ocular lesion found, ac-
counting for 47.59% of the total, was keratitis. In addition, microfilariae were found in the anterior chamber of the eye in 11.17% of the infected subjects. The methods used to diagnose infection with *O. volvulus* were the Mazzotti test and skin biopsy. Regarding transmission, the principal vector was found to be *S. metallicum*; the observed infection rate in collected *S. metallicum* specimens was 2.8 infected insects per thousand examined.

As reported in 1970, Duke (11) brought two Africans carrying *Onchocerca volvulus* (one native to the West African jungle and the other to the Sudanese savanna) to Venezuela. When *S. metallicum* and *S. exiguum* were allowed to feed on these African volunteers, they ingested the African microfilariae without difficulty, but the worms did not develop into the infective stage. In contrast, when the two vectors were allowed to feed on two Venezuelan carriers, ingested microfilariae were able to reach the infective stage. However, *S. exiguum* was found to be a vector of low susceptibility since most of the parasites did not reach the third larval stage, their development halting at the “sausage” stage. By comparison, *S. metallicum* turned out to be four to 10 times more efficient as a principal vector than *S. exiguum*. In this regard, it is noteworthy that when *S. metallicum* females ingested an average of 10 microfilariae, the latter were well tolerated, but when they ingested more than 20, many of the insects died in the first 24 hours after their blood meal.

During the whole of the dry and rainy seasons of 1973, Ramírez Pérez et al. (57) studied the age groups of wild female *S. metallicum* specimens captured systematically in the Henry Pittier National Park (a primary wet tropical forest) and in an onchocerciasis focus at Guiripa (secondary forest) in the state of Aragua. The results showed that nulliparous females (which are epidemiologically harmless) were very common throughout the year at the National Park, and that a high percentage of multiparous (potentially dangerous) females appeared in the endemic rural Guiripa area in the dry season. This suggested that the dry season was the time of peak transmission, although the indices of infection and natural infectivity were not estimated at that time.

Ramírez Pérez (58) also succeeded in experimentally infecting *S. metallicum* with *O. volvulus* and in developing infective forms over a period of six days and 16 hours at a temperature that ranged between 25°C and 30°C (the relative humidity was kept at 68–75%). Under the same laboratory conditions, digestion of blood and development of the ovaries (a gonadotrophic cycle) took 48 hours. What these results indicate is that if ovule development takes two days and the microfilariae need between six and seven days to become infective, then the insect must make two or three ovipositions in order to become a potential transmitter in nature.

To determine the endemicity of onchocerciasis in Venezuela and evaluate seasonal variations, Ramírez Pérez et al. (59) carried out a systematic study of the natural infection index in *S. metallicum* collected at eight localities in the country’s central region (in the states of Aragua, Carabobo, and Guárico) throughout the dry and rainy seasons of 1974. They were able to show that the rate of *S. metallicum* infection rises in the dry season and falls in the rainy season. The average number of filariae found per infected insect (including all the stages of
$O.\ volvulus$) ranged from a high of 6.2 in February to a low of 1.2 in November. The highest incidence was recorded in March in a locality (Santa Rosa in Cara-
bobo State) where 13% of the collected insects were infected.

The author also performed a
detailed study (60) of the microscopic morphology of the $S.\ metallicum$ larva, pupa, and adult. The resulting monograph presents a thoroughgoing description of the insect's digestive, circulatory, tracheal, nervous, muscular, and reproductive systems and ancillary organs, giving particular attention to the digestive tract and the thoracic muscles (which are directly involved in the passage and development of the parasite in the vector). It also shows how the morphology of the female changes at different physiologic ages and distinguishes between the innocuous nulliparous and potentially dangerous multiparous forms. Also, by analyzing the epidemiologic determinants of $O.\ volvulus$ transmission to man, the author concluded that it would be necessary to apply larvicides to the permanent creeks during the dry season in order to reduce the rainy season adult population.

In 1975, Rassi et al. (61) discovered a new onchocerciasis focus in the Federal Territory of Amazonas. More specifically, the disease was found to be prevalent among the Yanomama Indians who inhabit an area of 200,000 square kilometers on both sides of the Brazil-
Venezuela frontier (62). Skin biopsies and Mazzotti tests carried out in this region yielded positivity rates ranging from 35.7% (at the Mavaca Mission) to 88.9% (at the Coyowâteri Mission). In the

Parima Mountains (including the upland savannas of Parima A and Parima B at 1,050 m and 950 m, respectively), and in the wet forest of the Little Orinoco (at 250 m), $S.\ pintoi$ had previously been implicated as the principal vector. This finding was based on its high biting density, natural index of infection with the three larval forms of $O.\ volvulus$ (an index reaching 8%), and natural infection index with infective $O.\ volvulus$ larvae (2% in the Little Orinoco area). Also, study of a low area (at about 100 m) including Platanal, Boca de Ocamo, and Tamatama, found metacyclic forms of $O.\ volvulus$ in 0.25% of the cephalic capsules of Simulium amazonicum (sensu Rassi) females captured at Platanal.

A later study of simulids in the Federal Territory of Amazonas, described by Ramírez Perea et al. in 1982 (63), identified 27 species collected as pupae or with human bait. Later works have confirmed that the principal vector of onchocerciasis among the Yanomama groups is $S.\ pintoi$, this having been demonstrated both in nature (64) and experimentally (65). Simulium yarzabali (66), now synonymous with $S.\ incrustatum$ Lutz 1910 (67), sustains some development of $O.\ volvulus$ microfilariae up to the infective stage and could act as a secondary transmitter in the Parima Mountains; but it has not been found infected in the wild (64). In the depart-
ments of Río Negro and Casiquiare the transmitter appears to be another black-
fly, Simulium cuasisanguineum (63); this is probably the species that Rassi et al. (61, 81) identified at first as $S.\ amazonicum$. In 1982 Godoy (68) reported an additional focus among the Amerindians who inhabit the Upper Caura, in the Cedeño District of Bolívar State. He assumed that this focus was a continuation of the Amazonas focus, in which case the vectors involved in transmission are probably the same.
As of 1983, there appeared to be three onchocerciasis foci in Venezuela (67). The first was within the Coastal Mountain Range of the country's north-central zone—a mountainous area including portions of the states of Aragua, Carabobo, Cojedes, Guárico, Miranda, and Yaracuy. The second focus is located to the northeast, in the eastern part of the Coastal Mountain Range, and includes portions of the states of Anzoátegui, Monagas, and Sucre. The third focus is located in the Upper Caura, in the Cedeno District of Bolívar State, in the Parima Mountains, and from the upper Ventuari to the Upper Orinoco to the east of the Federal Territory of Amazonas.

The endemic Venezuelan foci are located at altitudes between 400 and 1,000 meters, and from an ecologic standpoint (69) involve three biomes: (1) wet tropical, (2) dry premontane, and (3) wet premontane, the latter typically being composed of coffee-growing areas. The principal vectors involved in transmission are *S. metallicum* in the Coastal Range and *S. pintoi* in the Parima Mountains within the Federal Territory of Amazonas. The secondary vectors are *S. exiguum* to the north and *S. cuasiananguineum* and *S. incrustatum* to the south.

The transmitting insects are more widely distributed at different latitudes and altitudes than is the disease. For example, *S. metallicum* and *S. exiguum* are common in the three mountainous states of Táchira, Mérida, and Trujillo and in Zulia State's Serranía de Perijá; but no onchocerciasis has been reported in any of these areas (70).

The affected areas of the Coastal Range are quite densely populated. According to data obtained from the Institute of Biomedicine, these areas had a total population of about 1.9 million inhabitants in 1974. Beginning in June 1974, a total of 1,628,370 persons in these areas were tested for onchocerciasis, and 40,091 proved positive by the Mazzotti test, yielding an apparent infection rate of 24.6 per thousand inhabitants. In comparing the situation in Venezuela with that in Guatemala and Mexico, Peñalver noted in 1963 (71) that the cutaneous lesions so frequently seen in Mexico and Guatemala were rare in Venezuela, appearing in only 7.5% of the positive cases.

The degree of susceptibility of *Simulium metallicum* to infection with *Onchocerca volvulus* has also been studied in Venezuela (72). The results of that study indicate that despite asynchronous and retarded development, many larvae can develop to the infective stage in *S. metallicum*; and the possibility of infective larvae eventually being inoculated into man is high. It is suggested that the susceptibility of *S. metallicum* in Venezuela to the indigenous strain of *O. volvulus* is relatively high, compared with that of the same species in Guatemala or Colombia.

In addition, the ingestion and development of *O. volvulus* in *Simulium pintoi* from the Parima Mountain region of the Federal Territory of Amazonas in Venezuela have been studied experimentally (73). At a temperature ranging from 16°C to 24°C, the development of *O. volvulus* larvae in *S. pintoi* was synchronous and orderly; no abnormal or deformed larvae were observed. (This synchronous development contrasts markedly with the asynchronous development of *O. volvulus* larvae in *S. metallicum*—73.) Third-stage larvae were first seen in
the heads of flies dying eight or nine days after microfilariae were ingested; 98 of 100 larvae recovered on days 10 through 16 were in the third stage. In conclusion, it is suggested that S. pintoi is an efficient vector of *O. volvulus* due to its high susceptibility, in spite of the high mortality caused by excessive intake of microfilariae.

Finally, a comparative study of onchocerciasis in South and Central America has been made (74) in order to distinguish the features of the disease and its transmission patterns in Guatemala from those in Venezuela. Among other things, it was found that *S. ochraceum*, the Guatemalan vector, apparently differs from Venezuelan *S. metallicum* and *S. pintoi* in the mortality experienced after ingesting large numbers of microfilariae and in the preference exhibited for biting certain portions of the upright human body.

**BRAZIL**

In 1967 Bearzoti et al. (73) reported diagnosing the first known case of onchocerciasis in Brazil, in a child three years of age. In 1972 Moraes and Dias (76) reported another two cases in missionaries living near the Toototöbi River in the north central part of the state of Amazonas. Then, in mid-1974, Moraes and collaborators located new cases in the Surucucú Mountains, where the Yanomama Indians live in the west of the Federal Territory of Roraima (77-79). And in 1976 Rassi et al. (62) reported finding another focus in a new ethnic group, the Maquiritaíres, who live in Auaris in the extreme northwestern part of the Roraima Territory.

The Auaris Mission (latitude 4°8′ N, longitude 64°25′ W), where the latter focus is located, is situated at an altitude of 670 m in a wet premontane biome. A total of 89% of the blackflies previously captured with human bait by Rassi et al. (80) were *S. pintoi*. New observations, reported by Moraes et al. (78) in 1977, indicated that only 8.6% of the Mayongongue Indians (at the only known Maquiritaíre Indian village in Brazil) were infected, as compared to 31.5% of the Sanumá Indians belonging to the Yanomama group that were living at the same locality along the Auaris River under the influence of the Mayongongues.

The Surucucú Mission (latitude 2°50′ N, longitude 63°45′ W, altitude 830 m) is likewise located in a wet premontane biome. Rassi et al. (80) found that the prevalence of onchocerciasis infection was roughly 30% (based on positive biopsies), and that the predominant anthropophilic species, accounting for 95% of the collected vectors, was *Simulium incrustatum*.

The Toototöbi Mission (latitude 1°10′ N, longitude 63°45′ W, altitude 180 m, in a wet tropical biome) was found to have the highest prevalence of infection of the three sites studied, Rassi et al. (80) reporting a positive biopsy rate of 67.4% in persons over 15 years of age. In addition, the Mazzotti test produced a clearly positive response in all the subjects examined. In more recent work, Moraes et al. (79) found 91.7% of the subjects biopsied at the shoulders and buttocks to be infected.

The blackflies captured at the Toototöbi Mission by Rassi et al. (80, 81) were all identified as *S. amazonicum* (*sensu* Rassi), and seven sausage forms of
O. volvulus were found in 972 dissected insects. However, as Rassi himself explained, he was dealing with a complex of several species that were hard to identify, especially since at that time the larvae, pupae, and males of the insects involved were not known. In 1976 Shelley et al. (82) questioned Rassi's identification and provisionally termed the insect Simulium specimen A. Then, in a subsequent publication, Shelley et al. (83) stated with certain reservations that the principal vector of O. volvulus in the Toototobí area was Simulium sanguineum. However, Tidwell et al. (84, 85) redescribed S. sanguineum (sensu strictu) from Colombian topotypes in 1981, after which Shelley et al. (86) provisionally identified the vector in question as Simulium minusculum Lutz, 1910.

To resolve these difficulties, the UNDP/World Bank/WHO Special Program for Research and Training in Tropical Diseases and the Pan American Health Organization assembled a group of specialists active in this field for workshop meetings on the taxonomy of simuliiids of medical importance. These meetings were held at the Oswaldo Cruz Institute in Rio de Janeiro, Brazil, and at the Pilot Center, Vector Studies Section, Institute of Biomedicine in Villa de Cura, Aragua, Venezuela; and their results were reported in World Health Organization documents TDR/FIL/79.1 and TDR/FIL/SIM/82.3 (87, 88). The species under discussion was finally described in 1983 by Ramírez Pérez et al. (63) and was designated S. cuasisanguineum. Typical specimens of this insect, which could be found at Tamatama in the Federal Territory of Amazonas, were subsequently compared with the females captured by Rassi in the vicinity of the Toototobí River.

Colombia

The first case of onchocerciasis discovered in Colombia was reported in 1965 by Assis-Masri and Little (89) among a group of patients suffering from ophthalmologic complications. The focus of the infection was subsequently reported by Little and D'Alessandro (90) as being on the banks of the San Juan de Micay River, which has its headwaters in the Western Mountain Range and flows into the Pacific. The endemic area lies between the settlements of López and San Antonio (latitude 3°N and longitude 77°23' W) at 90 m above sea level in Cauca Department. The area can be regarded as one of transition between a wet tropical biome and a very wet tropical biome, the annual precipitation averaging about 5,000–6,000 mm. Most of the economically active population is engaged in agriculture or mining.

Little and D'Alessandro (90) examined 292 persons from the Micay River area (167 males and 125 females) in the late 1960s. Of these people, 268 were classed as blacks, 16 as whites, and eight as mestizos. Onchocerca infections were detected in 44 persons (22 males and 22 females), representing 15% of the population studied. All but one of the residents found to be infected were blacks. The ages of the infected subjects ranged from seven to 60 years, but the infection rate was found to be highest among people over 30. Only five subjects were found to have microfilariae in their eyes, and none had palpable nodules. Non-palpable nodules were detected in 20 people, six of these being found on the
Thorax, three on the hips, and one on the head. The average number of microfilariae observed was 17.4 per mg of skin, within a range of two to 64 microfilariae per mg. The authors concluded that the infections existing in this Colombian focus appeared to be light.

Trapido et al. (91), by researching historical documents from the year 1717 that were in the Central Archives of Cauca at Popayán, determined that the surnames of 136 black slaves living in the mining area of the Micay River agreed with names of inhabitants in parts of West Africa where onchocerciasis foci exist at the present time. This suggests that the onchocerciasis recently detected in Colombia and Ecuador was brought over from Africa with the slave trade. Preliminary entomologic research on the Colombian focus by Barreto in the 1960s (92) implicated *Simulium exiguum* as the principal and sole transmitter, a finding later confirmed in a 1980 report by Tidwell et al. (93).

Although development of *O. volvulus* to the infective stage has been observed in *S. exiguum* from Colombia, this species does not appear to be a particularly efficient intermediate host under experimental conditions. Results of an entomologic investigation carried out by Tidwell et al. (93) indicated that abnormal development of the parasite was common and that approximately 34% of the larvae observed had not proceeded beyond the first stage five days after ingestion. However, third-stage larvae were recovered late on the fifth day (140 hours after ingestion), and on days six through 10, 27% of the flies were found to harbor third-stage larvae in their heads. The average number of infective larvae per fly was 0.81, and these represented 51% of the third-stage larvae recovered. The highest number of third-stage larvae (nine) was found in the head of a fly dissected on day six.

Duke (11) has suggested that the contribution of *S. exiguum* to the natural transmission of *O. volvulus* in Venezuela is minimal, and that *S. metallicum* is four to 10 times more efficient as an experimental vector. In Colombia, however, data indicate that *S. metallicum* from the Cali area is even less efficient than *S. exiguum* in supporting the development of *O. volvulus* in experimental studies. Tidwell et al. (93) have reported that of 206 *O. volvulus* larvae in *S. metallicum* examined on days seven through 13 after ingestion, 25% were abnormal, 69% had not developed beyond the first stage, and only 10% had reached the third stage. Engorged flies were kept within a temperature range of 22–27°C.

**Ecuador**

Carvajal Huerta et al. (94) and Arzube (95) reported the existence of a focus of onchocerciasis in the Ecuadorian province of Esmeraldas (latitude 0°42' N, longitude 78°54' W) in 1980 and 1981. The endemic zone is located between the settlements of Sapallo Grande and San Miguel de Cayapas at about 30 m above sea level in the western foothills of the Andes Mountains. The climate is hot and humid with an average temperature of 27°C and a relative humidity generally ranging from 70% to 95%. Annual precipitation generally ranges between 2,500 and 4,200 mm, which makes the area a wet tropical biome. The population is classed as 79.4%
black, 14.9% Indian, and 5.7% white. The main sources of employment are farming, hunting, fishing, and mining.

Arzube (96) reported performing biopsy examinations on 87 persons in 1982. *O. volvulus* microfilariae were found in 72 (83%) of the study subjects. Of these, 62 (86%) were blacks and 10 (14%) were Indians belonging to the Capaya group; 42 (58%) were males and 30 (42%) were females. Skin biopsies were taken from 39 infected subjects and weighed. It was found that in 29 (74%) of these subjects the density of microfilariae was higher at the iliac crest than at the scapula. The following clinical manifestations were found in the positive cases: nodules in 45 subjects (63%); dermatitis, pigment changes, and/or skin atrophy in 31 (43%); lymphoadenopathy and/or lymphoedema of the external genital organs in 19 (26%); corneal opacities in 32 (44%); and dermatitis and/or pruritis in 49 (68%).

The Ecuadorian onchocerciasis foci are regarded by Guderian et al. (97–100) as divisible into two groups: the main or Santiago focus encompassing localities on the Cayapas, Onzole, and Santiago rivers and their tributaries, and several peripheral foci on different river systems, such as those of the Canande, Cojimíes, Sucio, and Viche rivers. The disease has been found in over 2,000 of the 11,000 people sampled in rural areas, indicating that it afflicts nearly 1% of the 285,000 inhabitants of Esmeraldas Province.

Of 274 simuliiids captured with human bait in the endemic zone by Arzube (96), 206 were found to be *Simulium quadrivittatum*, 59 were *S. exiguum*, and nine were *S. antillarum*. Data presented on experimental infection of these three species in the Santiago focus clearly showed that *S. exiguum* and *S. quadrivittatum* were capable of permitting full development of *O. volvulus* to the infective stage in a short enough time to suggest they could naturally transmit the parasite. *S. exiguum* appeared to be a good host because parasite development in it was synchronous and rapid, and because even high rates of infection had little or no effect on *S. exiguum* mortality after the larvae reached the fly's thoracic musculature (101).

Natural infection rates of *S. exiguum* and *S. quadrivittatum* with filariae were found to be very similar. Of 557 *S. exiguum* dissected, 2.5% of the flies contained filarial larvae and 1.1% contained infective *O. volvulus* larvae. And of 178 *S. quadrivittatum* dissected, 2.2% contained filarial larvae and 1.1% contained infective larvae (101). Also, current data indicate that onchocerciasis transmission in Ecuador is high during the end of the wet season at localities along the middle reaches of the Capayas River.

The paucity of data on *S. antillarum* precludes any conclusions about its susceptibility to filarial infection; but even if it were shown experimentally to be a potential vector of *O. volvulus*, this blackfly would be unlikely to contribute significantly to the epidemiology of the disease in the Santiago focus because of its low anthropophily and human biting rates compared to the two aforementioned species (101).

**SUMMARY**

In all, 12 fly species of the genus *Simulium* have been implicated as confirmed or suspected vectors of onchocerciasis in those six countries (Brazil,
Colombia, Ecuador, Guatemala, Mexico, and Venezuela) with known foci in the Americas.

In Guatemala, the first focus discovered (and also the first focus discovered in the Americas) was described by Rodolfo Robles in 1915. At present, ocular onchocerciasis appears distributed in two main areas, one in mountains near the southern Pacific Coast and the other in the far west along the Mexican border, this latter being an extension of the Soconusco focus of southern Mexico. The principal vector of the disease in Guatemala is *Simulium ochraceum*. Other species implicated as secondary vectors include *S. metallicum* and *S. calidum*.

Among other things, research conducted in Guatemala and Venezuela has shown that African and American onchocerciasis differ in many respects, and that the latter can be regarded as an indigenous disease. Additional research in Guatemala has provided information about the vectors' taxonomy, biology, and ecology; has helped to define the levels of natural *O. volvulus* infection in various vectors; and has elucidated the key role played by temperature in the development of *O. volvulus* inside the vector.

In Mexico there are three known foci. One, the largest, is the Soconusco focus on the Guatemalan border. A second, the so-called “chamula” focus, is slightly further north in Chiapas State. And the third, considerably to the west of the “chamula” focus, is around a place called Alto Papaloapan in Oaxaca State. It has been estimated that some 40,000 people are infected in Mexico, and that the endemic areas cover about 8,900 square kilometers. Vectors implicated or suspected of *O. volvulus* transmission in Mexico include *Simulium ochraceum*, *S. metallicum*, *S. calidum*, *S. exiguum* (= *S. gonzalezi*), *S. haematoptotum*, and *S. veracruza*.

In Venezuela, where over 40,000 people were infected in the mid-1970s, there are three known focal areas. One is among the coastal mountains in the north-central part of the country; a second is to the east in the states of Anzoátegui, Monagas, and Sucre; and the third is far to the south in Bolívar State and the Federal Territory of Amazonas along the Brazil-Venezuela frontier. The principal vectors of onchocerciasis in Venezuela are *S. metallicum* (in the two northern foci) and *S. pintoi* (in the south). Secondary vectors include *S. exiguum* in the north and *S. cuasisanguineum* and *S. incructatum* in the south.

In Brazil, where the disease was first reported in 1967, the focal area is located in the state of Amazonas and the Federal Territory of Roraima near the Venezuelan Frontier. This area, like its counterpart focal areas across the border in southern Venezuela, covers a large area sparsely populated by jungle Indians. Prevalences of infection at specific study sites appear to range from roughly 30% to over 90% of the human population. Initial difficulty in classifying one of the responsible vectors was resolved when this insect was designated *Simulium cuasisanguineum* in 1983. The vectors of onchocerciasis in Brazil include *S. cuasisanguineum*, *S. pintoi*, and *S. incructatum*.

In Colombia, where the first known case of onchocerciasis was reported in 1965, the one established focus is located in the far western part of the country in a mountainous area near the
Pacific Coast. *S. exiguum* has been implicated as the sole transmitter.

In Ecuador, where the existence of an endemic zone was reported in 1980, the focal area is located in the north, close to the Pacific Coast and the Colombian Border. Confirmed or suspected vectors include *S. exiguum*, *S. quadrivittatum*, and *S. antillarum*.

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