Bull. Org. mond. Santé
Bull. Wld Hlth Org. 1957, 16, 509-522

# BIONOMICS OF THE VECTORS OF ONCHOCERCIASIS IN THE ETHIOPIAN GEOGRAPHICAL REGION

BOTHA DE MEILLON, D.Sc., Ph.D.
*Chief of the Department of Entomology,*
*South African Institute for Medical Research,*
*Johannesburg, Union of South Africa*

SYNOPSIS

Of the two proved *Simulium* vectors of onchocerciasis in Africa, the more widespread and the easier to identify is *S. damnosum.* The identity of *S. neavei* is less easily established, and a summary of the present position regarding the *S. neavei* complex is given. The bionomics of the immature stages and adult females of *S. damnosum* and *S. neavei* are discussed in detail, and consideration is also given to the relation of each species to disease. Distribution maps are included.

Two species of *Simulium*, namely, *S. damnosum* Theobald 1903 and *S. neavei* Roubaud 1915, are known to be vectors of onchocerciasis in Africa. A third, *S. renauxi* Wanson & Lebied 1950, is said to be a vector in the western Belgian Congo but this species is now regarded as a synonym of *neavei* by Freeman & de Meillon.[11] A few other species are known to attack man readily—namely *albivirgulatum* Wanson & Henrard 1944, shown by Wanson & Henrard [42] to be a non-vector, since microfilariae of *volvulus* do not develop beyond the thoracic stage; *merops* de Meillon 1950 bites man readily in Ngamiland but there is no onchocerciasis; similarly, the disease is absent in Madagascar, where *imerinae* Roubaud 1906 and *neireti* Roubaud 1905 bite. The absence of the disease may, of course, be due to the fact that it has not yet been introduced. In Angola *wellmanni* Roubaud 1906 was originally caught biting viciously. Dr Wellmann records that the flies were feared by the natives and on one occasion caused him to move camp; elsewhere in southern Africa and Ruanda Urundi [10] it does not bite. It is not known to transmit onchocerciasis. In the Dongola area of the northern Sudan, *griseicolle* Becker 1903 occurs in vast swarms, and although only a small percentage bite man the number of flies is so enormous that they constitute a definite nuisance,[27] yet onchocerciasis is unknown in this region. *S. gariepensis* de Meillon 1953—a biting species very similar in behaviour, and, for that matter, in morphology, to *griseicolle*—occurs in the southern Orange Free State, where onchocerciasis is unknown.

## S. damnosum

This was the first proved vector of onchocerciasis.[3] The species is widespread in Africa and fortunately easy to recognize in the female sex. There has been very little doubt about its identity in all stages over this vast area.

### *Immature stages*

*Eggs.* A blood meal is necessary for the development of eggs. In the Congo,[42] the gravid female does not go below the water surface but deposits her eggs in clusters of about 250 on damp surfaces such as stones, leaves, twigs, etc., which are partly submerged. Lewis [28] records the number of eggs deposited in captivity by one female as 529 in the Sudan; he did not observe egg-laying in nature. The eggs hatch shortly after deposition and the first-stage larva migrates to deeper water. Hughes [23] believes it possible that where rivers dry up completely the species survives in the form of a resistant egg which can withstand desiccation.

*Larvae.* In the process of migration many first-stage larvae are swept away by the current, and this no doubt serves to disseminate the insects over a large area.

Larvae appear to be indiscriminate feeders. They hang with their heads pointing downstream and with their mouth brushes constantly in motion. In this manner food particles and even inert matter is transferred to the mouth and swallowed, and matter in suspension is thus concentrated in the larval gut. It is easy to see that if such suspended matter contained insecticide the larva would in the course of time accumulate, by its own efforts, a lethal dose. It seems quite likely that this fortunate accident of nature is responsible for the comparative ease with which control may be achieved with relatively minute doses of DDT added to rivers and streams. Wanson & Henrard [42] report six larval moults and maturity in five days in Leopoldville. Outside the tropics larval life is no doubt longer.

*Pupae.* The mature larva spins a discrete cocoon and pupates inside. Pupae are often scattered over stones, leaves, twigs, etc., but sometimes they occur in dense masses over rocky surfaces. Cocoons may be spun inside caddis-fly tunnels. An unusual site for pupae is reported by Lewis,[27] who found them attached to mud in the Nile. The pupal stage at Leopoldville lasts four days.

### *Adult female*

The most comprehensive work on adult females is by Wanson & Lebied,[44] Wanson, Courtois & Lebied [41] in the Belgian Congo and Lewis [27, 28] in the Sudan. Except where otherwise indicated most of what is given below is taken from these authors.

*Behaviour after hatching.* Immediately after hatching, females gather on vegetation near the breeding-places at Leopoldville. From here they fly to obtain a blood meal and then again return to vegetation near the breeding-places. Here they rest until the eggs are mature, a matter of about four days. Control measures, in the form of DDT smoke distributed from the air, were instituted as a result of this knowledge and were immediately successful. Lewis agrees that no blood feeding takes place during egg development and reports that adults may be absent near breeding-places if there is no suitable shelter for them.

*Length of life.* At Leopoldville *damnosum* is considered to be a species of reduced longevity. After a single blood meal eggs are matured in four days and deposited between the fifth and seventh days. If the female feeds again after the first egg-laying the length of life would be about three weeks. In the laboratory, Blacklock [3] found the greatest length of life to be about 10 days. Lewis, on the other hand, believes it possible that flies can live for weeks or months and comments on the fact that flies live longer in the wet than the dry season. This author gives an account of age estimation based on state of development of the ovaries and microfilariae, condition of the halteres and peritrophic membrane, and general external appearance. These features are useful for separating young from old flies but cannot, of course, give an accurate estimate of age beyond a week or so.

*Range of flight.* There is ample evidence that *damnosum* can fly long distances, especially when aided by wind. Gibbins [16] records 40-50 miles (65-80 km) in Uganda and Lewis mentions 6-12 miles (10-20 km) as common and 18 miles (30 km) as rare. The latter author believes that it can probably cover greater distances than those recorded. Hargreaves [20] records 25 miles (40 km). An interesting observation has been made by Lebied,[25] who reports that the thoracic stage of the microfilaria of *Onchocerca volvulus* causes impairment of flight in infected females and that this accounts for the fact that the disease in man is often confined to quite small foci. Lewis, on the other hand, records infected flies up to nearly 12 miles (20 km) from the nearest breeding-place. Crosskey [8] reports fly-per-boy-hour densities of up to 3 as much as 7 miles (11 km) from the breeding-places. He draws attention to the finding that an infection rate of 16.5% is to be found among inhabitants of the Galma valley 10 miles (16 km) or more away from breeding-places.

*Food.* Although pollen grains, bits of tissue, sugars and grit have been recorded from the intestine and diverticulum, blood is a first requirement. Over much of its range its principal host is man, but no accurate information based on precipitin tests is available. Adults have also been taken on goats,[3] birds,[26] birds and game,[20] donkeys,[27] and donkey and dog.[8] In many parts of Africa *damnosum* does not attack man at all. As flies are usually collected where they attack man, it is quite certain that the range of the zoophilous race or strain is greater than reported.

*Biting habits.* The adults prefer the lower extremities of man when feeding. Crosskey [8] finds that the legs are preferred even if the catchers lie down. In Sierra Leone Blacklock [3] found that they bit in the open provided harbourage in the shape of bush was not far away. In the Sudan, on the other hand, Lewis reports biting in open desert, in fact he says "*S. damnosum* will bite almost anywhere out of doors by day . . . " and " the flies bite more in the open than in the bush, and a clearing 200 metres wide seems to act as a feeding ground . . . " Differences in biting habit are to be expected and it is as well to keep this in mind before preventive measures in the shape of clearing, etc., are undertaken. Crosskey [8] finds that long hair protects both man and dog.

The flies do not enter habitations to feed if these are dark. Biting, however, will take place on shaded verandahs, open sheds and other buildings. The exact degree of darkness required to prevent biting has not been determined. Biting can take place throughout the day and is obviously related to climatic conditions. Lewis, for instance, found that in the northern Sudan, during the relatively cold winter, biting did not commence before 10 a.m. (see also Crosskey [8]). There may be an appreciable difference in the numbers which bite each day and it is as well to keep this in mind when making surveys. It is also known that some individuals are more attractive to the fly than others; further, Crosskey [8] finds that Africans are more readily attacked than Europeans.

*Seasonal changes in numbers.* There is some evidence on this, but systematic collecting has not been carried out extensively. In northern Nigeria Crosskey [8] finds flies more prevalent during the marked wet season, whereas in the south, where wet and dry seasons are not readily distinguishable, the flies are abundant all the year round. This is corroborated by evidence from the Gold Coast [23] and the Belgian Congo.[40] In addition, as Lewis found, the number may vary for inexplicable reasons. Local conditions will obviously play an important role. In some areas rain may interfere with breeding and encourage it in others. At the same time high air moisture favours adult longevity and activity and hence dispersion. It is evident that seasonal changes will have to be determined for each locality and that such knowledge is essential before control schemes are embarked on.

*Breeding-places.* Rocky rapids, waterfalls, cascades, cataracts and races with well-aerated broken water appear to be preferred over most of its range. The idea, prevalent in former times, that this represents the sole type of breeding-place, however, is wrong. In the Sudan breeding takes place in placid Nile water flowing at 2 km per hour. At Leopoldville preference was shown for water flowing at 3-4 km per hour and faster-flowing water was not favoured. Breeding is not confined to the larger rivers. At Jinja, Uganda, larvae and pupae are found in very great concentration on rocks in the Owen and Ripon Falls. Below these, and for many miles lower down the Nile, pupae and larvae may be found in the slowly running water. The concentration is never as intense as in the falls, but naturally the population is spread over a much wider area and the number of adults produced must be enormous. Barnley,[1] for instance, estimates that on the vegetation which he could reach in a 100-yard stretch of the Nile near Bujagali Falls in Uganda there were over five million larvae and pupae. It is as well to remember that larvae of all stages are continuously being swept downstream from rapids and falls and it is possible that many specimens, collected in placid waters lower down, originated in this way. For control this is rather important. In parts of Africa where observations have been made breeding proceeds throughout the year though numbers may be restricted during the dry season. Hughes [23] believes that in areas where rivers dry up completely *damnosum* may survive in the form of a resistant egg. This is rather important and requires thorough investigation. Crosskey [8] believes that in northern Nigeria, with a distinct dry season, survival is ensured by minimal breeding on a small scale in residual trickles of water. Few adults are derived from such breeding-places, and they may be overlooked unless a very careful search is made over many boy-hours.

Lewis has commented on the unexpected appearance of adults at the end of the dry season and three weeks before breeding-places became available. These adults were undamaged, and he suggests that they may have been sheltering in crevices, rocky clefts, etc., during the time when breeding-places were non-existent.

Other workers have also commented on the higher adult catches on bait boys after river flooding.[7, 23] Crosskey [7] believes this to be due to a sudden increase in fly population rather than to an increase in biting activity.

It seems to the present writer that resistance to desiccation by stranded pupae has not been sufficiently investigated. In Kenya and in South West Africa, for instance, he found many pupae—not *damnosum*—on dry vegetation well above water level. When such pupae were transferred to the laboratory and placed in an atmosphere of high humidity the flies hatched.

### *Relation to disease*

Because of its liking for man and wide distribution *damnosum* is the more important vector of onchocerciasis in Africa. The original observations of Blacklock [3] in Sierra Leone have been amply confirmed by Wanson and colleagues at Leopoldville and by Lewis in the Sudan.

Since Blacklock's original observation, *damnosum* has been proved to transmit or is suspected of transmitting onchocerciasis in the following territories: Nigeria;[7, 37] Liberia;[2] Bas Lomami, Belgian Congo;[35] Gabon;[12] Sankuru, Belgian Congo;[22] Uele, Belgian Congo;[9, 39] southern Sudan;[4, 24, 28] Uganda;[15] Fernando Po;[33] Nyasaland;[18] Tukuyu, Tanganyika;[21] Leopoldville, Belgian Congo;[42] Cameroons (Kershaw, quoted by Crosskey [7]); and, as reported at the Conference on African Onchocerciasis held in Leopoldville in 1954, Moyen Congo, Chad, and Angola.

The skin changes which are sometimes seen in cases of onchocerciasis are not due to irritation caused by the bites of the fly but to the presence of microfilariae.[29]

The developmental cycle of the microfilariae in the insect host is well known and not worth repeating. It is, however, worth noting some aspects of Lewis's work in the Sudan on this subject. He finds that in spite of the very large numbers of larvae—200 or more—which may be taken in by *damnosum* the average number of infective larvae per fly is only about three. The principal cause of death of larvae is apparently imprisonment by the peritrophic membrane which is secreted by *damnosum* as soon as blood feeding commences. Flies which take up too many larvae are killed. In addition, it has been shown by Wanson that larvae in the infective stage are easily lost when a fly feeds on sugar water and presumably nectar in nature. Lewis also draws attention to the rapid changes in infection rates which may occur even during a single day. It is therefore possible that in fact very few flies can actually infect man, and the relationship between infective flies and the risk of infection is not a simple one as with mosquitos and malaria, for example. This may account in part for the fact that long residence in an onchocerciasis area is required before infection of man results. At Mvolo, for instance, Lewis calculated, from a consideration of the percentage of infective flies, that the risk of infection to man amounted to the inoculation of one worm every three minutes during the biting hours. It would appear difficult to avoid infection under these circumstances and yet many of the inhabitants are free of onchocerciasis and visitors are exposed to very little risk of infection.

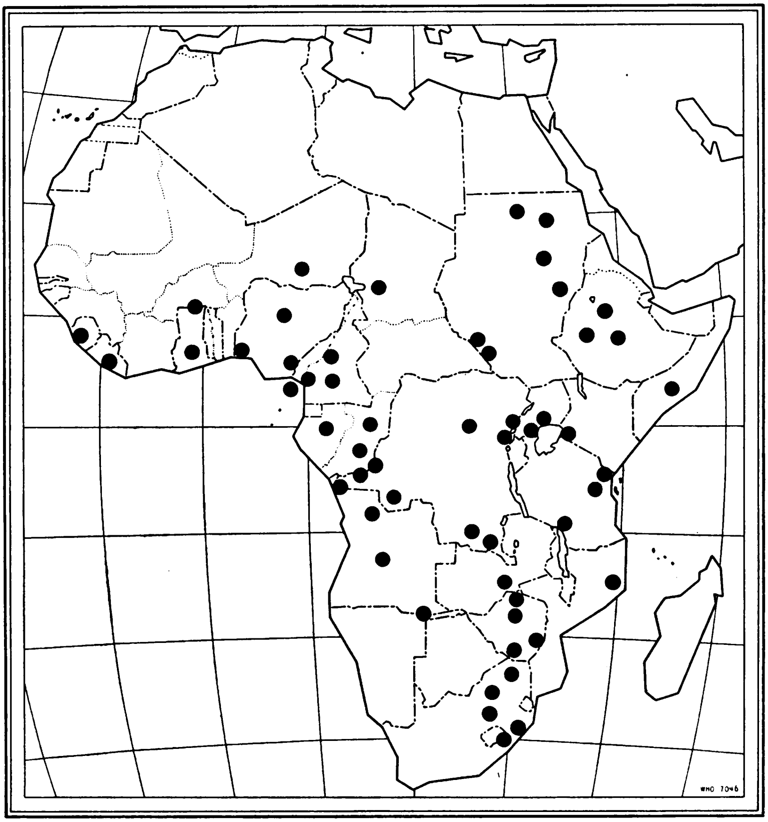
Lewis shows that the main season of transmission is during the rains, for then the adult flies are more numerous and more widely spread.

The fly is actually very much more widely spread than the disease. The distribution of onchocerciasis is, of course, not accurately known but there are many areas in which it is definitely absent and in which *damnosum* is known to occur. An explanation of this anomaly readily comes to mind —namely, that *damnosum* is known not to bite man over quite extensive areas in which it is presumably essentially zoophilic. However, there are areas, for instance, in the Sudan, and probably elsewhere, where the anthropophilic strain is fairly abundant and yet no onchocerciasis is known. Two possible solutions suggest themselves: firstly, that the disease has not been introduced, but that when it is, it will be transmitted; and, secondly, that local conditions for one reason or another do not favour transmission.

*Distribution* (see Fig. 1)

Mr Paul Freeman of the British Museum and I have seen specimens from Sudan, Abyssinia, Sierra Leone, Gold Coast, Cameroons, Liberia, Nigeria, Uganda, Kenya, Belgian Congo, Ruanda Urundi, Tanganyika, Nyasaland, Portuguese East and West Africa, Northern and Southern Rhodesia, Transvaal, Natal, and South West Africa. Additional records

**FIG. 1. DISTRIBUTION OF SIMULIUM DAMNOSUM IN ETHIOPIAN GEOGRAPHICAL REGION**



of specimens not seen by us come from the French Cameroons [19] and Dahomey,[34] and, as reported at the 1954 Conference on African Onchocerciasis, from Moyen Congo, Chad, Upper Volta, Angola, and Somalia.

Generally, the fly is widely distributed over the whole region with the exception of Madagascar, the Mascarenes and the Seychelles.

## S. neavei Complex

While the identity of *damnosum* is easily established and beyond dispute, the same can certainly not be said of *neavei*. The recent discovery of the breeding-places of this and other phoretic species has certainly shed much light on the problem, but the position is not quite clear yet and may be summarized as follows.

### *S. neavei*

The typical species occurs in Uganda and Kenya. In the western Belgian Congo occur specimens which differ very slightly from typical *neavei* and have been described under the name *renauxi* Wanson & Lebied.[45] At the moment, *renauxi* is considered to be a synonym of *neavei*.

Over its whole range, *neavei* is predominantly anthropophilic and an important vector of onchocerciasis. The immature stages are found attached to the carapace of the crabs *Potamonautes niloticus* M. Edwards in Kenya and, according to Wanson & Holemans,[43] of *P. lueboensis* and *P. lirrangensis* in the western Congo.

### *S. woodi*

This is known from Nyasaland, Northern Rhodesia, Tanganyika, Kenya and Ethiopia. It is very similar to *neavei* but separable in Kenya from both this species and *nyasalandicum* by colour and male terminalia. Specimens intermediate between it and *neavei* occur in Northern Rhodesia and others resembling *nyasalandicum* in colour in Ethiopia. In Kenya it is not anthropophilic but in both Northern Rhodesia and Tanganyika specimens have been captured on human bait. The Ethiopian specimens come from an onchocerciasis region but it is not known if they were the vectors. In Kenya the immature stages are found only in the exhalant passages of the crab *Potamonautes niloticus* and the pupae differ slightly from those of *neavei* and *nyasalandicum*.

### *S. nyasalandicum*

This is known from Nyasaland, Kenya, Uganda and (?) Tanganyika. It is very near to *neavei* but separable in Kenya, at least, by colour and male terminalia. In Kenya it bites man very rarely. The Tanganyika specimens reported by Hawking [21] as *neavei* were caught on human bait and it may be an anthropophilic species there, but the identity of the specimens is not beyond question. In Kenya the early stages are found in association with crabs as in *neavei*, and the pupae of these two are not separable as far as is known. Its role in the transmission of onchocerciasis is not known but in Kenya it is not considered to be of any importance.

It is obvious from the above that much remains to be done on the *neavei* complex.

So far as we know the most important member of the complex is undoubtedly *neavei* and summarized below are the salient features of its bionomics.

## S. neavei

The most comprehensive work on *neavei* deals with observations in Kenya;[5, 13, 30, 31] in addition there is some information from the Belgian Congo.[14, 22, 38, 40, 43]

### *Immature stages*

*Eggs.* In the laboratory gravid females can be induced to oviposit on damp filter paper. Under these circumstances the eggs in a batch number about 100 and turn a rich golden colour soon after deposition. In the Kavirondo I obtained over 100 batches of eggs laid by females on filter paper and not a single larva hatched, even when the papers were transferred to swift- or slow-running waters. This experience is in sharp contrast to that of Wanson at Leopoldville, who found that *damnosum* eggs hatched almost immediately after deposition. Dr Wanson kindly informs me that in the western Congo the eggs of *neavei* are not found on crabs but on vegetation, etc., near the cascades in which *Potamonautes* lives. Presumably the larvae migrate after hatching and seek out the crab host. Each egg cluster contains 150-250 eggs and the clusters do not show the golden colour reported for laboratory specimens.

*Larvae.* Larvae have only been found living in apparent phoretic association with crabs (*Potamonautes niloticus* in Kenya, and *P. lueboensis* and *P. lirrangensis* in the western Congo). They are found attached round the eye stalks, mouth parts, bases of the legs and dorsum of the carapace. The larvae probably share the food torn up by the crab, as suggested by Marlier[32] for two other species which live in phoresis with mayfly nymphs.

*Pupae.* The mature larva spins its cocoon and pupates on the crab host and especially around the sides of the carapace. McMahon[31] records a single pupa on a mayfly nymph, and I have hatched a single adult from a large bunch of vegetation cut in a fast-running river in Kenya. These are chance findings, however, and the main site of pupal attachment is the crab.

*Biology of the larval and pupal host.* Little information is available and the following is from McMahon.[31] At least three species of crab were found in the breeding-grounds but only *P. niloticus* appeared to be used. This crab is almost entirely restricted to cascades and rocky falls exposed to the sun in rivers and large tributaries. Very rarely is it found in the shade, never in swamps or in smaller streams. *P. niloticus* apparently has a wider distribution than *neavei*, which is restricted to altitudes between 4000 and 6000 feet (1200-1800 m) in Kenya.

*Adult female*

*Behaviour after hatching.* Little is known. It appears, however, that the adults are much more sensitive to climatic conditions than are those of *damnosum*. Their presence in large numbers in certain types of wooded country suggests that after hatching they gather in selected sites, which may be some distance from the breeding-places. Hissette [22] in the Congo and Buckley [5, 6] in Kenya found that certain requirements are necessary for adult harbourage—namely, presence of fast-running rivers, well-wooded banks, hilly or mountainous terrain. If these conditions obtain near breeding-grounds then adults are found close at hand; otherwise, the adults migrate, possibly for considerable distances, to preferred sites. McMahon [30] also believes that bush, not dense thicket, bordering rivers favours adult harbourage. Buckley [6] in Kenya showed that bush clearing could entirely eliminate *neavei* adults.

Dr Wanson informs me that in the western Belgian Congo adults are to be found in dense forest galleries in which the humidity reaches 96%, whereas 500 metres away where the air is drier (50% humidity) one is rarely attacked.

*Length of life.* No information is available. In the laboratory the adult females may be kept alive for a matter of 10 days. In captivity they die almost immediately after egg-deposition. It is quite certain that in nature they live very much longer than this, as adults with torn wings, badly rubbed thoraces and abdomens and other signs of advanced age can be taken in nets in long grass near streams.

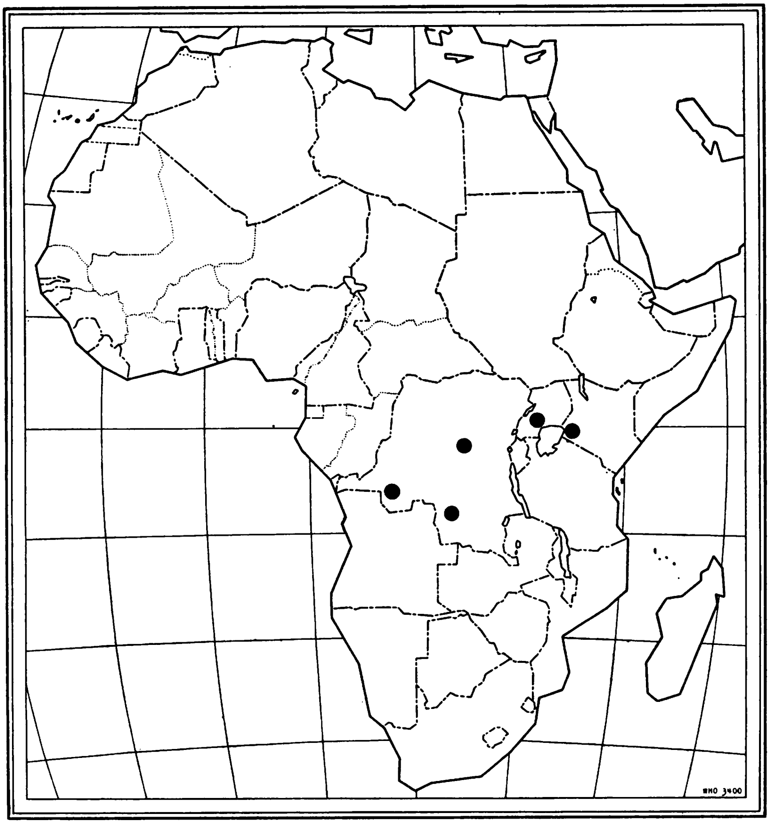
*Range of flight.* Once adults have congregated in the forested habitat which suits them they do not leave it except for short feeding sorties of perhaps 50 yards (45 m) into open country. McMahon [30] comments on the restricted flight range of *neavei.* He records it biting as far as 700 yards (640 m) from a river but the greatest density occurred within 300 yards (275 m).

How far adults will fly from breeding-places in search of suitable harbourage is not known.

*Food.* As far as is known the adults are almost entirely anthropophilic. I have taken one on a donkey in Kenya, but at the same time they were being caught at the rate of about 100 per hour on human bait.

*Biting habits.* As with *damnosum*, the adults prefer the lower extremities, but when the human bait is sitting down they will attack the upper parts of the body with equal avidity. Adults will bite in bright open sunshine provided suitable harbourage is close at hand. Adults are not known to enter habitations.

FIG. 2. DISTRIBUTION OF SIMULIUM NEAVEI IN ETHIOPIAN GEOGRAPHICAL REGION



*Relation to disease*

*Neavei* is reported to be a vector of onchocerciasis in Sankuru, Belgian Congo;[22, 38] Kwango, Belgian Congo;[14, 45] Nyanza Province, Kenya.[5, 30] The evidence incriminating *neavei* is based on the dissection of wild-caught flies and on epidemiological evidence, but there is little doubt that it is well founded.

The most comprehensive work is that of Buckley and McMahon in the Nyanza Province of Kenya. Here the disease is mainly restricted to an area lying between 5000 and 6000 ft (1500-1800 m), which again coincides with the greatest concentration of *neavei*. Buckley found the incidence of onchocerciasis to vary a great deal within the compass of as little as 10 miles (16 km). He examined such obvious possible contributing factors as the customs and habits of the people, topography, fly density and terrain without their yielding a reasonable explanation. He thinks that the infectivity rates in flies in these different areas may account for the patchy distribution of the disease, but no evidence is produced. McMahon, on the other hand, investigated onchocerciasis in a smaller area and found that *neavei* was present in greatest density in areas of highest human infection. He found an over-all infection rate of 10% in flies but did not discriminate between proboscis, thorax or intestinal infections. The percentage of infective flies was probably much lower.

In the western Belgian Congo Geukens found an infection rate of 100% in the local population. This is higher than reported from any other area. Dr Wanson informs me that in this region he dissected 300 flies and found 50% with larvae, 10% of which were infective. He notes that this is much higher than reported for *damnosum* at Leopoldville.

As far as is known, *neavei* is anthropophilic and associated with onchocerciasis throughout its range. In some localities it is associated with *damnosum* but the relative importance of each species under these circumstances has not been assessed. It appears, however, that in those places where the two occur together *neavei* is of greater importance.

*Distribution* (see Fig. 2)

Specimens considered to be this species have been seen by Paul Freeman and myself from Western Ankole and Kigura, Uganda; Nyanza, Kenya; and Kasai, Belgian Congo. Other records are from Sankuru, Belgian Congo,[22] and Bas Lomami, Belgian Congo.[36] There is also a record from Natal, Union of South Africa,[17] which is almost certainly wrong. Hawking's [21] record from Njombe, Tanganyika, is now considered to refer to *nyasalandicum*.

## RÉSUMÉ

Deux espèces de *Simulium* (*S. damnosum* et *S. neavei*) sont connues comme vectrices de l'onchocercose dans la région éthiopienne.

La première espèce, dont l'auteur décrit en détail la biologie, est largement répandue dans toute cette région, à l'exception de Madagascar, des Mascareignes et des Seychelles. Elle est aisément identifiable, et les divers stades de son développement sont bien définis.

D'après les observations faites au Soudan, le nombre moyen de microfilaires infectantes est de trois par moucheron — bien que le chiffre de 200 ait été avancé. Les moucherons meurent parfois d'avoir ingurgité trop de larves. Les larves aussi peuvent être détruites dans le corps des moucherons, emprisonnées par la membrane sécrétée par l'insecte au moment où il va se gorger de sang. D'une façon générale, le pouvoir infectant d'un insecte peut varier beaucoup au cours de la même journée. Il est possible que le

nombre de *Simulium* réellement infectants soit peu élevé. Le rapport entre l'insecte infectant et le risque d'infection n'est pas simple, comme il l'est dans le paludisme par exemple. C'est probablement l'une des explications du fait que la maladie n'est généralement contractée qu'après un long séjour dans une région infectée et qu'une partie de la population reste indemne.

*S. damnosum* est plus répandu que la maladie. Dans certaines zones, l'espèce est zoophile et ne pique pas l'homme. Dans d'autres, où la souche anthropophile est fréquente, il est possible que la maladie n'ait jamais été introduite (et que, si elle l'était, la transmission se produirait) ou bien que les conditions ne soient pas favorables à la transmission.

Si la détermination de l'espèce *damnosum* est admise sans conteste, celle du complexe *neavei* (*S. neavei, S. woodi, S. nyasalandicum*) est loin de l'être. L'espèce *neavei* typique se rencontre dans l'Ouganda et le Kenya. Dans toute son aire de distribution, *neavei* est anthropophile; sa présence est liée à celle de l'onchocercose. Les larves vivent en association avec les crabes *Potamonautes* sur lesquels elles sont fixées.

## REFERENCES


1. Barnley, G. R. (1952) *Uganda J.*, **16**, 113
2. Bequaert, J. C. (1929) *The insect carrier of* Onchocerca volvulus *in Liberia.* In: *Transactions of the Fourth International Congress of Entomology, Ithaca, N.Y., 1928*, Tring, vol. 2, p. 605
3. Blacklock, D. B. (1926) *Ann. trop. Med. Parasit.*, **20**, 1
4. Bryant, J. (1935) *Trans. roy. Soc. trop. Med. Hyg.*, **28**, 523
5. Buckley, J. J. C. (1949) *J. Helminth.*, **23**, 1
6. Buckley, J. J. C. (1951) *J. Helminth.*, **25**, 213
7. Crosskey, R. W. (1954) *Ann. trop. Med. Parasit.*, **48**, 152
8. Crosskey, R. W. (1955) *Ann. trop. Med. Parasit.*, **49**, 142
9. D'Hooghe, M. (1934) *Ann. Soc. belge Méd. trop.*, **14**, 153
10. Fain, A. (1950) *Rev. Zool. Bot. afr.*, **43**, 228
11. Freeman, P. & de Meillon, B. (1953) *Simuliidae of the Ethiopian region*, London
12. Gaillard, H. (1932) *Bull. Soc. Path. exot.*, **25**, 167
13. Garnham, P. C. C. & McMahon, J. P. (1947) *Bull. ent. Res.*, **37**, 619
14. Geukens (1950) *Ann. Soc. belge Méd. trop.*, **30**, 1483
15. Gibbins, E. G. (1935) *Uganda J.*, **2**, 272
16. Gibbins, E. G. (1936) *Trans. roy. ent. Soc. Lond.*, **85**, 217
17. Gibbins, E. G. (1938) *Ann. trop. Med. Parasit.*, **32**, 21
18. Gopsill, W. L. (1939) *Trans. roy. Soc. trop. Med. Hyg.*, **32**, 551
19. Grenier, P. & Rageau, J. (1949) *Bull. Soc. Path. exot.*, **42**, 513
20. Hargreaves, H. (1925) *Annual report of the Government Entomologist.* In: *Annual report of the Department of Agriculture, Uganda*, Entebbe, pp. 21-28
21. Hawking, F. (1940) *Ann. trop. Med. Parasit.*, **34**, 211
22. Hissette, J. (1932) *Ann. Soc. belge Méd. trop.*, **12**, 433
23. Hughes, M. H. (1952) *W. Afr. med. J.*, **1**, 3
24. Kirk, R. (1947) *Ann. trop. Med. Parasit.*, **41**, 357
25. Lebied, B. (1950) *Une nouvelle théorie endémiologique*, Léopoldville
26. Le Roux, P. (1930) In: *Pan-African Agricultural and Veterinary Conference . . . 1929. Papers of the veterinary section*, Pretoria, p. 110
27. Lewis, D. J. (1948) *Trans. roy. ent. Soc. Lond.*, **99**, 475
28. Lewis, D. J. (1953) *Bull. ent. Res.*, **43**, 597
29. Loewenthal, L. J. A. (1943) *Ann. trop. Med. Parasit.*, **37**, 147
30. McMahon, J. P. (1940) *Trans. roy. Soc. trop. Med. Hyg.*, **34**, 65
31. McMahon, J. P. (1951) *Bull. ent. Res.*, **42**, 419

32. Marlier, G. (1950) *Rev. Zool. Bot. afr.*, **43**, 135
33. Najera, A. L. (1935) *La* Onchocerca volvulus *en Fernando Poo.* In: *Primer Congreso nacional de Sanidad, 1934. Actas,* Madrid, vol. 4, pp. 241-293. (Abstracted in *Rev. appl. Ent. B,* 1936, **24**, 213)
34. Roubaud, E. & Grenier, P. (1943) *Bull. Soc. Path. exot.*, **36**, 281
35. Schwetz, J. (1930) *Ann. Soc. belge Méd. trop.*, **10**, 1
36. Schwetz, J. (1932) *Ann. Soc. belge Méd. trop.*, **12**, 549
37. Sharp, N. A. D. (1927) *Ann. trop. Med. Parasit.*, **21**, 415
38. Strong, R. P. (1937) *Trans. roy. Soc. trop. Med. Hyg.*, **30**, 487
39. Van den Berghe, L. (1941) *Ann. Soc. belge Méd. trop.*, **21**, 63
40. Wanson, M. (1950) *Ann. Soc. belge Méd. trop.*, **30**, 667
41. Wanson, M. Courtois, L. & Lebied, B. (1949) *Ann. Soc. belge Méd. trop.*, **29**, 373
42. Wanson, M. & Henrard, C. (1945) *Rec. Sci. méd. Congo belge,* No. 4, 113
43. Wanson, M. & Holemans, K. (1951) *Ann. Parasit. hum. comp.*, **26**, 93
44. Wanson, M. & Lebied, B. (1948) *Rev. Zool. Bot. afr.*, **41**, 66
45. Wanson, M. & Lebied, B. (1950) *Rev. Zool. Bot. afr.*, **43**, 309