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M. W. SERVICE

Studies on the biology and taxonomy of *Aedes (Stegomyia) vittatus* (Bigot)
(Diptera: Culicidae) in Northern Nigeria

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**Studies on the biology and taxonomy of *Aedes (Stegomyia) vittatus* (Bigot)
(Diptera: Culicidae) in Northern Nigeria**

By M. W. SERVICE

The Nature Conservancy, Monks Wood Experimental Station, Huntingdon, England

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With 2 Plates and 17 Text-figures

SYNOPSIS

An account is given of the ecology of *Aedes vittatus* in Northern Nigeria. Oviposition sites are described, and the differential hatch and susceptibility of eggs to high and low temperatures investigated. The effect of high and low temperatures on larvae and pupae and their susceptibility to desiccation is discussed. The duration of the larval instars and pupae and the periodicity of pupation are recorded, and predators, host preferences, diel biting cycles, seasonal incidence and attempts to establish colonies are described. A detailed taxonomic study is given of the adult, pupa and all four larval instars. The distribution, taxonomic position and origins of *Ae. vittatus* are discussed.

I. INTRODUCTION

THE only species of mosquito with the habit of breeding in rock-pools that has been so far studied in any detail is *Aedes atropalpus* (Coquillett) (James, 1964; Shaw & Maisey, 1961), but there has been no general investigation of the bionomics of this

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species. The habitats of its larvae differ from those of the larvae of *Ae. vittatus* (Bigot) in that they consist of larger rock-pools situated along streams near rapids or waterfalls. Their associated fauna indicates the presence of nearby running water and is probably not specially adapted to rock-pools. The small size of the rock-pools studied in the present work allows the relationship of the species constituting the macrofauna to be easily observed. It also makes them liable to sudden and rapid desiccation, so that the fauna is of a specialised type that must either vacate the pools at these periods, e.g. adult beetles and Hemiptera, or be capable of entering a state of diapause that can withstand dehydration, e.g. *Aedes* eggs, larvae of *Poly-pedilum vanderplanki* Hinton and adults of *Actinolainus hintoni* Lee. *Ae. vittatus* is particularly well suited to such an environment, as its eggs can tolerate desiccation for many months, and the very rapid rate of metamorphosis of the larvae minimises the likelihood of the immature stages being killed by the pools drying out.

Ae. vittatus is of interest as it is atypical of the subgenus *Stegomyia* Theobald both taxonomically and ecologically. The spiculate antennae and unpaired tufts proximal to the barred area of the ventral brush of the larvae are characters associated more with the subgenus *Aedimorphus* Theobald than with *Stegomyia*. The presence of scales on the clypeus of the adult and the structure of the male terminalia are also more typical of *Aedimorphus* species. The preference of females for ovipositing in rock-pools is in marked contrast to all other members of the subgenus in Africa, which breed primarily in tree-holes and domestic containers. Although its larval habitats limit its local distribution to areas where rock-pools occur, it is exceptional in having a very widespread geographical distribution, being found throughout the greater part of the Ethiopian zoogeographical region, much of the Oriental region and in parts of the Mediterranean subregion of the Palaearctic region. Its presence in the relatively cool climate of the Pyrenees and Kenya Highlands, where it is found up to 6900 feet (Eldoret), and in the very humid and hot areas of tropical Africa and Asia shows that the species must have an exceptional tolerance to a wide temperature range. Finally, *Ae. vittatus* may be of medical importance, as Philip (1929) demonstrated that it could transmit yellow fever virus under laboratory conditions, and Lewis (1943) suspected it as a natural vector in the Sudan.

For these reasons the biology of *Ae. vittatus* was investigated at a rock outcrop in the Kaduna area of the Northern Guinea Savannah of Nigeria from 1960 to 1963, and the taxonomy of all larval instars, pupal stage and adults investigated. The chorionic pattern of the egg is given elsewhere (Hinton & Service, 1970).

II. DESCRIPTION OF THE WORKING AREA

(1) General

All work carried out in the present survey was restricted to the Northern Guinea Savannah, a large area lying in between the Southern Guinea Savannah and the Sudan Savannah. In this area the five months from October to March constitute the severe dry season, during which time humidities drop and extremes of temperatures are experienced. In late November to January it is relatively cool, but in February to March maximum temperatures are recorded. The dryness of this period is accentuated by a strong dust-laden easterly wind, known as the "harmattan", which blows in from across the Sahara and produces localised dust storms. The first rains of the wet season have little visible effect on the land, as the dry porous soils rapidly soak up all surface water.

Most of the field work was carried out at a granite outcrop situated about 20 miles N.N.E. of Kaduna in the uninhabited Anara Forest Reserve, about 120–150 yards from the Kaduna–Jos laterite road. The outcrop was approximately 300 yards in diameter without any overhanging vegetation and fully exposed to the sun. It was characterised by scant vegetation of grass and climbers such as *Acacia ataxacantha*

De Candalle, *Canthium venosum* (Oliv.) Hiern and other types of plants, e.g. *Stegonotaenia araliacea* Hochst and *Ficus* spp. Numerous hollows and small rock holes, which when full of water provided many larval habitats for *Ae. vittatus*, occurred in the outcrop (Plate I). The nearest village to this site, Kangimi, contained about 200 people and was about two miles to the north. The next nearest village was Katabu, situated about three miles south and containing about 500 people. A field station of the Sleeping Sickness Service sited two and half miles from the outcrop provided daily rainfall records. A few observations were also made in Anguwun Rimi village, situated some 22 miles S.S.W. of the rock outcrop near the Kaduna River, and at the Veterinary Investigation Training Centre about five miles S.E. of the rock outcrop.

All times given are local times, which are one hour faster than G.M.T.

(2) *The Rock-pools and Their Associated Fauna and Flora*

The several hundred rock-pools on the outcrop at the working site could conveniently be divided into two distinct categories. One category consisted of small elliptical hollows, very regular in outline, averaging in size $9\frac{3}{4} \times 14$ inches across and 2 inches deep, the smallest being about $8\frac{1}{2} \times 11$ inches and the largest $10\frac{1}{2} \times 17$ inches, with depths of about $\frac{3}{4}$ and 5 inches, respectively (Plate I, pools 1-8). There was about half an inch of mud and detritus at the bottom of the pools, and their capacity when full of water was about four pints. It is believed that they were made in some past epoch by indigenous tribes grinding grain on the rock surface. Similar formations are found in Western Nigeria (Baldry, *personal communication*), in the Jos area (Boorman, 1961) and in the Sudan (Lewis, 1943). The other category consisted of pools irregular in outline (Plate I, pools I-V), measuring approximately 2-5 feet across and about 2-5 inches deep. These have undoubtedly been caused by natural weathering of the rock surface.

The absolute maximum and minimum temperatures recorded in the small pools over several 24-hour periods were 46.5° and 21.0° C., respectively. The pH of the water in the pools, measured with a Lovibond Comparator, varied from 7.2 to 8.4, and there was no appreciable difference between the alkalinity of the small and large pools. The only Angiosperm in the rock-pools was *Dopatrium longidens* Skan, a rooted emergent aquatic member of the Scrophulariaceae growing only in water-filled rock-pools in savannah areas of Africa. Nearly all the larger, and about half of the small, rock-pools contained this plant, the shoots of which first appear in late May or early June. Towards the end of the rains, in about October, although many of the pools still contain water, the plant dies down, its seeds remaining dormant in the mud at the bottom of the pools during the dry season and germinating the following rains. A few eggs of *Ae. vittatus* were found on it.

Only one vertebrate, a frog of the genus *Rana* subgenus *Ptychadena*, was found in the pools; a specific name could not be given because all collected specimens were juveniles that had not fully developed their adult characters. The following insects were found in the pools: *Anisops jaczewski* Hutchinson, *A. adonis* Hutchinson, *Micronecta* spp., *Laccotrephes* spp., *Bradynopyga strachani* (Kirby) and *Pantala flavescens* F., *Helochares rugipennis* J. Balfour-Browne, *Berosus nigriceps* (F.), *Canthydrus bisignatus* Wehn, *Laccophilus adpersus* Boheman, *Uvarus octoguttatus* (Régimbart), *Sternolophus ? solieri* Castelnau, one specimen of an unidentifiable *Enochrus* (*Methydrus*) sp. and unidentified species of *Berosus* and *Helochares* (*Agraphydrus*), *Polypedilum vanderplanki* Hinton, *Anopheles gambiae* Giles, *Culex grahami* var. *farakoensis* Hamon; and larvae of *Stratiomys* and *Odontomyia* in a few pools containing decaying organic matter. No larvae of *Uranotaenia nigripes* Theobald, a species which is known to occur in the general area and which breeds predominantly in rock-pools, were found in any of the pools on this, or neighbouring rock outcrops.

A high level of organic pollution was produced in one of the small pools that was regularly contaminated by the faeces of baboons (*Papio anubis*) in the dry season (and possibly also in the rains); this resulted in a dense growth of slimy green algae, which was absent from other pools, and abnormally high densities of bacteria and various protozoa. Larvae of Stratiomyids, Syrphids and *Ae. vittatus* taken from this pool were heavily infected with Peritrichida and fungi (see p. 125). The only record of larvae of *Culex decens* Theobald/*C. invidiosus* Theobald was from this pool.

III. OBSERVATIONS ON IMMATURE STAGES

(1) Larval Habitats

Larvae of *Ae. vittatus* are found predominantly in pools in rock outcrops or river beds, and even in pools formed in coral (Wiseman, Symes, MacMahon & Teesdale, 1939). They have also been recorded from a variety of habitats including domestic utensils, hoofprints, boats, wells (Hopkins, 1952), bamboo pots (Harris, 1942) and tree-holes (Kerr, 1933; Peters, 1956), and the present author has found larvae on several occasions at the peak of the breeding season in open floodwater concrete drains. In the present work, however, no larvae of *Ae. vittatus* were found in 578 collections from tree-holes in Anguwun Rimi village, and, although cylindrical gourds of *Lagenaria siceraria* (Malina) Standley provide suitable artificial oviposition sites for tree-hole-breeding mosquitoes (Service, 1965a), no larvae of *Ae. vittatus* were found in 1928 collections from such gourds placed in either Anguwun Rimi or in the Anara Forest Reserve about one and half miles north west of the outcrop, or in gourds suspended at a height of about six feet from trees situated at the base of the rock outcrop.

As larvae of *Ae. vittatus* have been recorded from clay pots, 12 unglazed clay pots about one foot high and 10 inches in diameter were placed amongst the scant vegetation of the rock outcrop from July to September, 1961 (*i.e.* during the rainy season). No larvae were found on 1st or 6th July, but thereafter larvae were regularly found each week in about half of the pots examined during each week throughout the period of observation, which ended on 15th September. It seems therefore that adults oviposit in the pots, although there are numerous water-filled rock-pools in the area, and that at least some eggs hatch soon after oviposition.

No *Aedes* eggs were found on the water surface in the pots, but a few occurred in irregular batches inside them near the water line. No *vittatus* eggs were found on the inner sides of 18 pools examined on three separate occasions, but the rough and speckled surfaces of the sides of the rock-pools would make the eggs extremely difficult to locate. On five occasions, 7, 11, 19, 25, and 27 unhatched *Aedes* eggs were found on the stems of *D. longidens* growing in the pools. In two instances the eggs were situated well above the water line and would have hatched only after the plant had died down and the pools been reflooded the following rainy season. Three of the egg batches were soaked in filtered rock-pool water; after two days larvae of *Ae. vittatus* hatched from two batches but none did so from the third.

(2) Hatching

Fully developed young larvae contained within mature *Aedes* eggs usually enter a state of diapause that is only broken when the eggs are soaked and subjected to a suitable hatching stimulus (Bacot, 1916, 1917; Shannon & Putman, 1934) such as agitation, cooling and other shock treatments (Christophers, 1960) and plant auxins (Abdel-Malek, 1948). The most common hatching stimulus is a reduction in the dissolved oxygen content of the water, brought about by either physical, chemical or biological means (Gjullin, Hegarty & Bollen, 1941). It has also been shown that in *Ae. triseriatus* (Say) changes in the duration of daylight stimulate hatching (Baker, 1935).

Not all eggs in a batch laid by an *Aedes* mosquito hatch at the same time when soaked; they may hatch in instalments over a relatively long period, and a certain proportion may require several separate soakings followed by periods of desiccation before hatching occurs. This characteristic is well defined in some tree-hole-breeding *Aedes* species (Service, 1965a). Genetic studies of the variation in the hatching response of eggs of *Ae. aegypti* (L.) (Gillett, 1955a, 1955b), showed that variability in hatching was an inherited property, but that as the depth of diapause varied greatly in eggs from a single batch, a multiple mechanism was involved. Staggered, or differential, hatching is obviously advantageous in species of *Aedes* that breed in small transient collections of water, such as tree-holes (Service, 1965a), which are liable to rapid desiccation.

It seemed that eggs of *Ae. vittatus* would also hatch differentially, otherwise all the eggs in the mud of the rock-pools would hatch after the first showers of the rainy season, which rarely produce sufficient water to last through the time required for the development of the aquatic stages. Mud samples were collected from eight different pools during the dry season in December 1960 and were soaked for three days in plastic bowls containing tap water, all larvae that appeared being counted and removed. The samples were then dried out in the sun for three to five days before being resoaked for another three days. This procedure was repeated until each sample received eight soakings.

Few eggs hatched during the first soaking, and surprisingly most hatched on the second and third soakings, very few larvae being obtained from the sixth soaking and none after this (Table I). It would seem to be more advantageous if more than two or three soakings were required to produce maximum hatching, to ensure that this

TABLE I.—Numbers and percentages (in parentheses) of eggs of *Ae. vittatus* hatched from mud samples

Mud sample numbers	Number of eggs hatched on various soakings							
	First	Second	Third	Fourth	Fifth	Sixth	Seventh	Eighth
1	0	27 (36)	33 (43)	0	16 (21)	0	0	0
2	0	22 (37)	26 (44)	11 (19)	0	0	0	0
3	12 (9)	62 (44)	35 (25)	21 (15)	0	11 (8)	0	0
4	0	48 (53)	16 (18)	21 (23)	5 (6)	0	0	0
5	0	29 (26)	47 (42)	17 (15)	0	19 (17)	0	0
6	7 (9)	27 (33)	28 (34)	0	8 (10)	11 (14)	0	0
7	18 (12)	38 (26)	62 (43)	16 (11)	11 (8)	0	0	0
8	0	41 (41)	38 (38)	22 (22)	0	0	0	0

occurred when the rainy season was firmly established. The greatest hatch of *Aedes* species that bred in tree-holes was produced by the first soaking, but provided that the eggs were deposited high enough in the tree-holes a certain volume of water would be required before they were soaked (Service, 1965a). A similar stratification, however, cannot occur with the eggs of *Ae. vittatus*, as they are contained in the mud at the bottom of the pools. Mud samples 1, 3, 5, and 6 show that, as with the tree-hole-breeding *Aedes* of the area, it is possible to soak some eggs and not get a hatch, although both previous and subsequent soakings initiated hatching.

The effect of prolonged soaking in water on the hatching of *vittatus* eggs was investigated by collecting six mud samples in December and dividing each into two equal parts (samples "a" and "b"). One half of each of the samples (1a-6a) was soaked in tap water continuously for 52 days and all larvae counted and removed daily; the other halves (1b-6b) were soaked for three days, and after removal of the larvae the mud was allowed to dry out. At the end of the 52 days' continuous soakings, the mud samples were allowed to dry out for five days, and then these and the other samples, which had only received a short three-day soaking, were resoaked for three days on four separate occasions (Table II). Most eggs from both series of

TABLE II.—Numbers and percentages (in parentheses) of eggs of *Ae. vittatus* hatched from mud samples

Mud sample numbers	No. eggs hatched daily from samples soaked continuously					No. eggs hatched from samples previously soaked continuously			
	1st day	2nd day	3rd day	4th day	5th-52nd day	1st resoaking	2nd resoaking	3rd resoaking	4th resoaking
1a	17 (57)	11 (37)	2 (7)	0	0	0	0	0	0
2a	18 (38)	21 (44)	6 (13)	3 (6)	0	0	0	0	0
3a	0	0	0	0	0	0	0	0	0
4a	0	8 (42)	3 (16)	8 (42)	0	0	0	0	0
5a	0	0	0	0	0	0	0	0	0
6a	11 (34)	21 (66)	0	0	0	0	0	0	0

	No. eggs hatched daily from samples soaked for only 3 days			No. eggs hatched from samples previously soaked for only 3 days			
	1st day	2nd day	3rd day	1st resoaking	2nd resoaking	3rd resoaking	4th resoaking
1b	0	0	0	37 (52)	27 (38)	7 (10)	0
2b	8 (29)	18 (44)	2 (7)	46 (43)	35 (32)	19 (18)	8 (7)
3b	17 (44)	22 (56)	0	58 (62)	31 (33)	4 (4)	0
4b	11 (34)	18 (56)	3 (9)	28 (33)	47 (55)	7 (8)	3 (4)
5b	0	22 (100)	0	26 (34)	48 (62)	3 (4)	0
6b	14 (66)	7 (33)	0	44 (60)	29 (40)	0	0

samples hatched during the first two days of soaking; few hatched on the third day, and in samples soaked continuously none hatched after four days. Hatching in samples (1b-6b), which were subjected to alternate periods of soaking and desiccation, confirmed that when *vittatus* eggs are given short soakings most hatch on the second and third soakings (*i.e.* first and second resoakings). No eggs hatched from any samples previously given a continuous soaking. Continuous immersion of the samples may have resulted in the establishment of various pathogens in the muddy water which may have killed any remaining unhatched eggs. Because mud samples were collected from the field and the eggs not extracted from them, the original number of eggs in the samples is not known. To discover whether there is any egg mortality due to continuous soaking in the absence of mud, three strips of blotting paper on which eggs of *Ae. vittatus* were deposited were immersed in water continuously for 40 days. Three similar strips of blotting paper with eggs were soaked for three days and then dried. At the end of the period of continuous soaking the samples were allowed to dry out, and then all samples (1a-3a and 1b-3b) were given three separate soakings of three days' duration. Yeast was added to the water to provide a hatching stimulus. Results (Table III) differ from those shown in Table II in that most eggs in samples (1a-3a) hatched on the first day of soaking, and in samples (1b-3b), which were only given short soakings, maximum hatch occurred during the first soaking. Few eggs hatched on the second, and very few on the third, soakings (*i.e.* first and second resoakings). As with the mud samples, no eggs hatched from samples previously given prolonged soakings when they were resoaked. These differences between the pattern of the differential hatch of eggs on blotting paper and in mud samples may be correlated with the difference in intensity of the hatching stimuli. That produced by the yeast medium was probably stronger, and consequently more eggs hatched on both the first soaking and the first day of soaking. Prolonged soaking resulted in the failure of eggs to hatch in both experiments. This is unlikely to happen in the field, since most pools dried out for short periods during the wet season. They rarely contained water continuously for 2-3 weeks, which might be long enough to cause mortality of some eggs.

TABLE III.—Numbers and percentages (in parentheses) of eggs of *Ae. vittatus* hatched from blotting paper strips

Blotting paper strip number	No. eggs hatched daily from samples soaked continuously				No. eggs hatched from samples previously soaked continuously			
	1st day	2nd day	3rd day	4th–40th day	1st resoaking	2nd resoaking	3rd resoaking	4th resoaking
1a	26 (65)	11 (28)	3 (8)	0	0	0	0	0
2a	18 (67)	9 (33)	0	0	0	0	0	0
3a	33 (61)	21 (39)	0	0	0	0	0	0
	No. eggs hatched daily from samples soaked for 3 days			No. eggs hatched from samples soaked previously for only 3 days				
	1st day	2nd day	3rd day	1st resoaking	2nd resoaking	3rd resoaking	4th resoaking	
1b	29 (78)	8 (22)	0	18 (64)	8 (29)	2 (7)	0	
2b	27 (84)	4 (13)	1 (3)	6 (100)	0	0	0	
3b	29 (73)	11 (28)	0	17 (68)	4 (16)	4 (16)	0	

(3) *Effects of Temperature*(i) *Field observations on eggs*

Because *Ae. vittatus* survives the dry season as eggs in the dry mud at the bottom of the rock-pools, temperatures attained by this mud during the very hot dry season were of interest. Unfortunately instruments capable of recording both fluctuations and durations of temperature over 24 hours were not available, so it was necessary to use an ordinary mercury-filled glass thermometer. From September 1962, when some of the pools started to dry out, to March 1963, when the rainy season was becoming re-established, the temperatures of the mud in six pools, selected at random twice a month, were recorded by covering the thermometer bulb with dry mud. Since it was the upper limits of the temperature range that were of interest, all readings were taken at 1230–1330 hours local time, when it was considered that the highest temperatures would be experienced. Most of these recorded temperatures were between 39.5° and 41.5° C., the most commonly recorded being the last. The lowest and highest temperatures were 38.0° and 42.5° C., respectively. No large differences between the temperature of the mud in different months of the dry season were apparent, but from January to March (usually the hottest part of the dry season) temperatures were generally 1–2° C. higher than at other times. It is not known how long these high temperatures are maintained, but, since some larvae do hatch from eggs contained in this mud in the following rains, some eggs must be capable of surviving at least short exposures to these high temperatures. Further, acclimatisation (Mellanby, 1954) through exposure to gradually increasing temperatures of the dry season may increase the ability of eggs to withstand higher temperatures in the field than they are shown to do in the laboratory, where they are suddenly exposed to high test temperatures. The question of acclimatisation is also discussed in reference to the larvae (pp. 111, 117).

(ii) *Laboratory observations on eggs*

Eggs were obtained either from blotting paper that had been placed in the pools during the preceding rainy season, or from gravid females that had oviposited in the laboratory. These were stored at about 26° C. and 75–85 per cent. relative humidity and were at least six weeks old when used in the experiments.

Blotting paper strips with eggs were placed for varying intervals of time in an electric incubator, which had reached and maintained the desired test temperature for at least two hours. It was impossible to maintain constant temperatures in the

incubator during 24-hour exposures, and the temperatures given in Table IV are the maximum and minimum recorded during these periods. To prevent any sharp drop in humidity, three evaporating basins of water were kept in the incubator. After exposure eggs were removed and soaked for three days in water containing yeast as a hatching stimulus, after which they were removed, dried and given three more soakings. Percentage mortalities were calculated from the total number of eggs exposed and the number which hatched. In the controls, eggs were removed from storage, kept at ordinary laboratory temperatures and soaked four times in tap water. A hatch of 76–89 per cent. resulted; those that did not hatch were regarded as indicative of control mortality, irrespective of whether they were really dead, and all test mortalities were corrected (Abbott, 1925) for this apparent control mortality. Complete mortality is not experienced with short exposure periods of 10 minutes until a temperature of 50° C. is reached (Table IV); longer exposures progressively lower the temperature giving complete mortality, and all eggs died after 24 hours' exposure to only 41°–42° C.

TABLE IV.—Mortalities of eggs submitted to different temperatures for various time intervals. A dash denotes that no eggs were subjected to this temperature.

Temperature (°C.)	Duration of exposure of eggs									
	10 minutes		1 hour		3 hours		6 hours		24 hours	
	No. ex-posed	Percent-age mortality	No. ex-posed	Percent-age mortality	No. ex-posed	Percent-age mortality	No. ex-posed	Percent-age mortality	No. ex-posed	Percent-age mortality
32·1–33·5	—	—	—	—	—	—	—	—	52	2
34·2–37·4	—	—	—	—	—	—	—	—	48	9
37·5–40·0	—	—	—	—	—	—	—	—	73	67
41·1–42·3	—	—	—	—	—	—	—	—	71	100
39	76	3	96	6	66	6	46	8	—	—
40	84	2	74	16	69	4	66	14	—	—
41	71	10	76	13	54	7	43	19	—	—
42	83	8	81	17	62	15	42	33	—	—
43	64	12	71	21	73	33	48	82	—	—
44	78	11	52	32	74	83	69	100	—	—
45	94	18	78	75	81	100	54	100	—	—
46	78	17	70	100	63	100	—	—	—	—
47	56	30	71	100	—	—	—	—	—	—
48	107	38	—	—	—	—	—	—	—	—
49	82	74	—	—	—	—	—	—	—	—
50	62	100	—	—	—	—	—	—	—	—
51	48	100	—	—	—	—	—	—	—	—

Temperature and mortality have been plotted on arithmetic probability paper so that the LT 50s could be obtained visually (figs. 1, 2). With 24-hour exposures the arithmetic means of the temperature ranges have been used. To try to overcome the difficulties of comparing the LT 50 from the different exposure periods used by various workers, the LT 50s have been plotted against exposure periods and temperatures (fig. 3), so that either the temperature or the exposure period causing 50 per cent. mortality could be determined.

There is no information on how long the high temperatures mentioned above may continue in the field, but from the figures just given it would appear that about 50 per cent. of the eggs would be killed at 39·5°, 41·5° and 42·5° C., if the eggs were exposed to these temperatures for about four, seven and 17 hours respectively (fig. 3). It is however unlikely that any appreciable mortality of eggs occurs in the field owing to high temperatures in rock-pools, which are the principal larval habitats. Nevertheless, it must be remembered that the investigations were not undertaken at the edge of the geographical distribution of the species, where limiting climatic conditions

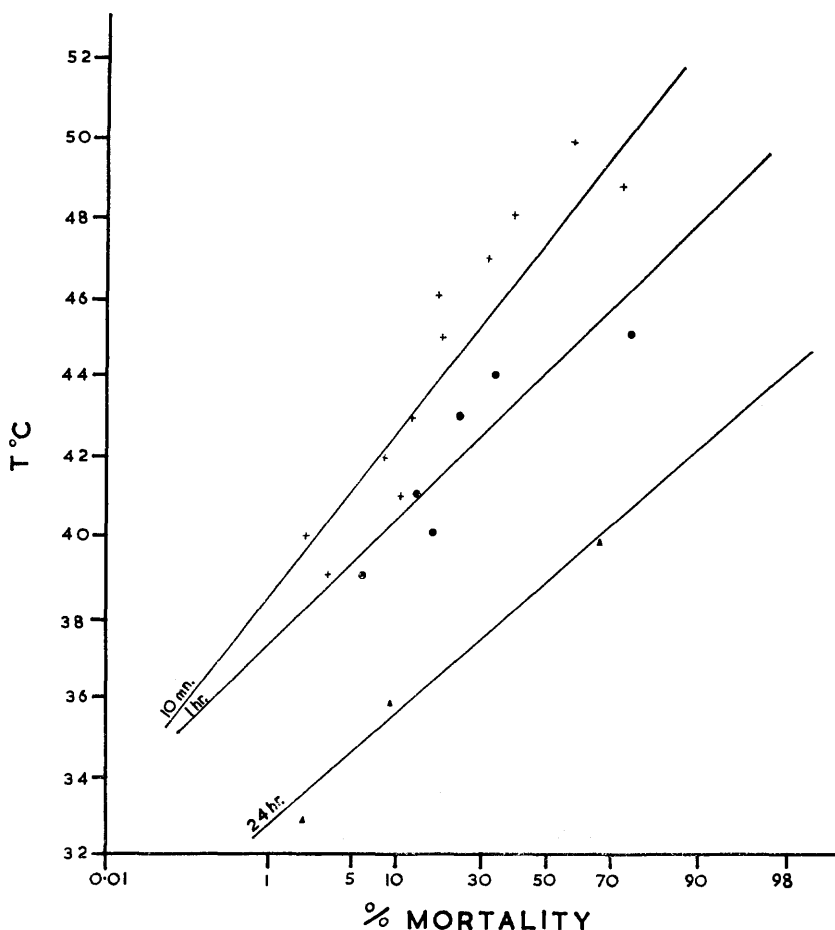


FIG. 1.—Mortality of eggs of *Ae. vittatus* exposed for 10 minutes, one hour and 24 hours to various temperatures.

might be expected to prevail. Acclimatisation (Mellanby, 1954) to increasing high temperatures of the dry season might explain the ability of eggs to withstand high temperatures in the field.

Although in the study area minimum temperatures rarely fell below 15° C. the survival of eggs at lower temperatures is of interest in understanding the limit of the distribution of *Ae. vittatus* in the more temperate areas. Consequently, a few eggs were subjected to low temperatures. There were difficulties in maintaining constant low temperatures, and eggs were exposed to a temperature range. An air-conditioned room provided temperatures of 15.3° and 17.5° C., and by altering the cold setting of a refrigerator a short range of lower temperatures was obtained; exposure periods varied from one to six days. The procedure for the controls, the hatching technique and the assessment of mortalities was as described above (p. 108).

Six days' exposure to temperatures down to 15.3° C. had no detrimental effect on the eggs, but at 11.8°–14.8° C. appreciable mortality occurred with exposures of three days or more, and below this temperature all eggs were killed at exposures of three days or more (Table V). Few hatched at temperatures of about 10° C. (8.2°–11.3° C. range) after even short exposures, and longer exposures gave complete mortality. There are no published results on the effect of low temperatures on eggs of *Ae. vittatus*, but Christophers (1960) concluded that short exposures to low temperatures had little effect on eggs of *Ae. aegypti*, although several days at 10° C. or below

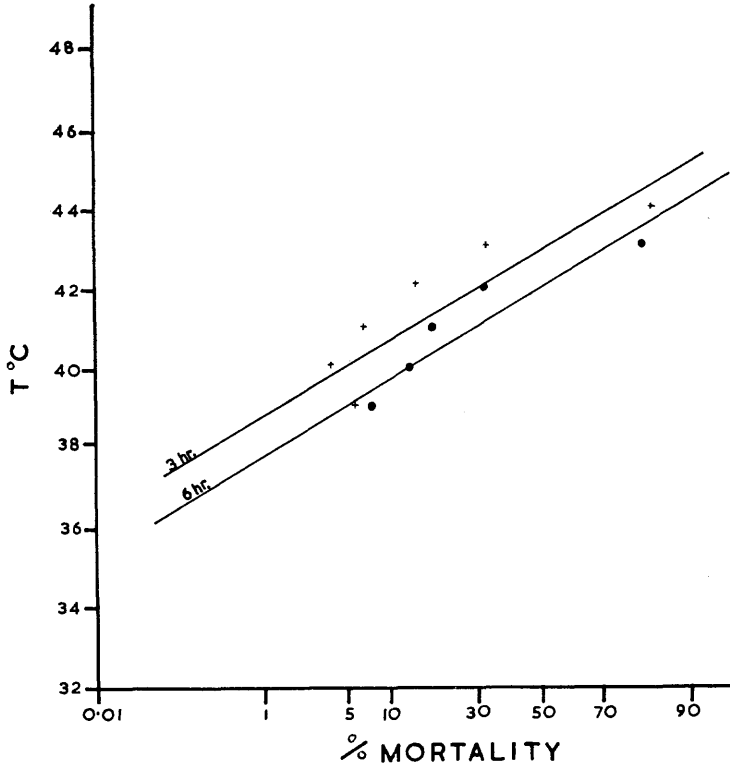


FIG. 2.—Mortality of eggs of *Ae. vittatus* exposed for three and six hours to various temperatures.

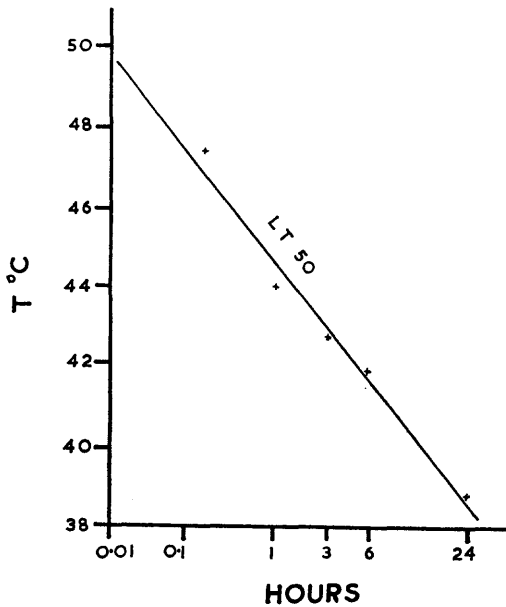


FIG. 3.—Values of LT 50 of eggs of *Ae. vittatus* at different exposure periods and temperatures.

TABLE V.—*Effect of low temperatures on mortalities of eggs*
Percentage mortalities after various exposure periods

Temperature (°C.)	1 day		2 days		3 days		6 days	
	No. exposed	Percentage mortality	No. exposed	Percentage mortality	No. exposed	Percentage mortality	No. exposed	Percentage mortality
15·3–17·5	56	0	61	4	44	8	78	7
11·8–14·8	58	6	48	0	65	53	69	74
8·2–11·3	77	76	76	71	49	100	73	100

caused high mortalities. It seems that the cold tolerance of eggs of *Ae. vittatus* and *Ae. aegypti* is similar and, depending on the duration of the exposure period, temperatures of about 10° C. and below cause high, or total, mortality.

(iii) *Field observations on larvae and pupae*

Nieschulz, Bedford & du Toit (1934) commented on the warm temperature of the water in rock-pools containing larvae of *Ae. vittatus*, and Vanderplank (Hinton, 1951) noted that the temperature in one pool near Kaduna was 35° C. Boorman (1961) found that in nine rock-pools at Vom the temperature varied between 28·6° and 35·8° C. These appear to be the only records of water temperature for this type of habitat.

In 1962 maximum and minimum temperatures were recorded, by means of two mercury-filled maximum and minimum thermometers, twice a month in two pools over a period of 24 hours. Since it was desired to continue these readings through the dry season, when the pools are normally dry, they were artificially filled with water twice a month. In the rains the lowest temperature (21·0° C.) occurred in June, August and October, and the highest (46·5° C.) in June, July and August. In the dry season, the lowest temperature (12·5° C.) was recorded in December and January, and the highest (38·0° C.) in November. The relatively low maximum temperatures recorded in the dry season, which is the hottest part of the year, probably resulted from a cooling effect of a rapid rate of evaporation of water from the pools during this period when humidities are very low.

(iv) *Laboratory observations on larvae and pupae*

Larvae and pupae were acclimatised by keeping them at 25°–28° C. for 12 hours before exposure to the higher test temperatures. They were then isolated on a nylon gauze strainer to drain off surplus water and transferred to water in porcelain evaporating dishes contained in the incubator, which had reached and maintained the test temperature for at least two hours. No food was given to the larvae during the exposure periods, which varied from 10 minutes to 24 hours. As it was impossible to maintain constant temperatures during 24-hour exposures, the temperature range, as indicated by a maximum and minimum thermometer placed in the incubator, is given. After the required exposure period, larvae were transferred to glass beakers containing about 400 ml. of water and placed in small cloth cages. The larvae were given yeast and finely-ground oats as food. After a 24-hour holding period, dead and moribund specimens were counted and mortalities assessed. In the controls larvae and pupae were transferred to evaporating bowls, kept at normal laboratory temperatures and at the end of 24 hours, a period equal to the longest exposure period, placed in beakers containing 400 ml. water and given food. There was no control mortality. Criteria for dead and moribund larvae were those recommended by the World Health Organization (Anon., 1960). The same criteria were applied, where appropriate, to the pupae. During the holding periods, a few adults emerged from the pupae, and a few larvae pupated; such specimens have been omitted from

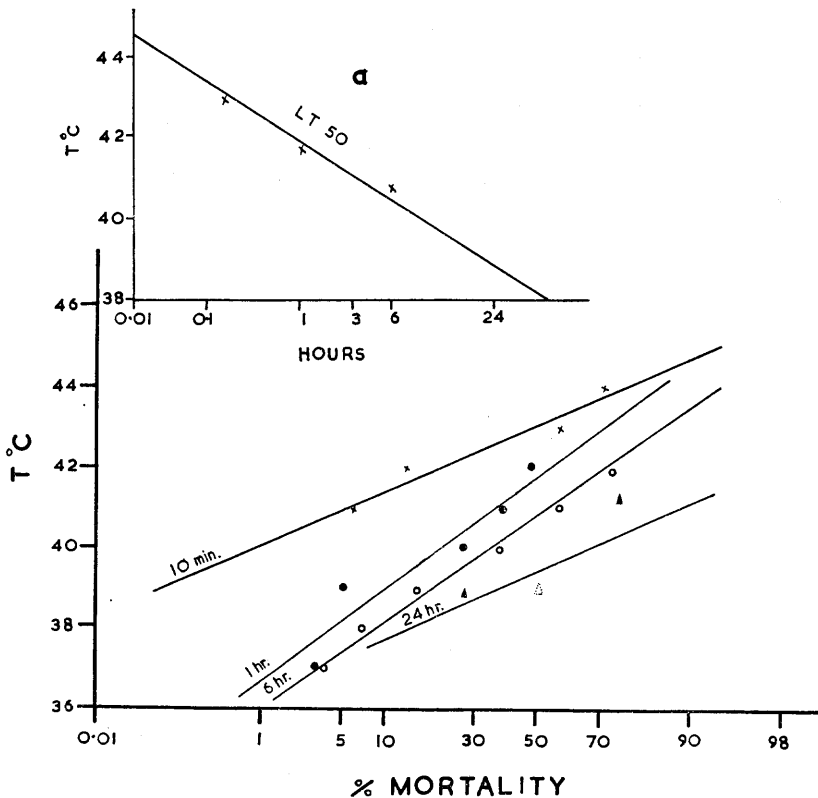


FIG. 4.—Mortality of first instar larvae of *Ae. vittatus* exposed to various temperatures; (a) values of LT 50.

the results. No allowances were made, however, for any first or second instar larvae that changed into succeeding instars during the holding period, or during the 24-hour exposure period, because the rapid rate of larval development would make any such adjustments impractical.

Although several workers have investigated the effect of temperature on larval mortality (Barr, 1952; Christophers, 1960; Davis, 1932; Farid, 1949; Macfie, 1920; Pal, 1943; Wright, 1927; and others), it is difficult to compare their results because the experimental conditions were not standardised. Most workers have referred to the thermal death point (LT 100), but Pal (1943) also calculated the LT 75 and some workers (Farid, 1949; Bar-Zeev, 1957) gave the LT 50. Barr (1952) departed from the usual procedure of keeping the exposure period constant and varying temperature, by exposing all larvae to 42° C. and varying the exposure times.

In the present trials, to facilitate comparisons with published results on other mosquito species, both the LT 50, obtained graphically by plotting the results on arithmetic probability paper, and the LT 100 are given. The exact values of the LT 100 were not determined; they are in between the observed values giving complete mortality and the succeeding low temperatures. The difference between these two temperatures was small, and it was not considered that the extra experimental work involved in getting the precise values was justified.

A rise of only 1° C. can result in a large increase in mortality (Table VI). The relationship between temperature and mortality at different exposure periods is shown for the first to fourth instar larvae in figures 4–7, and the LT 50s are plotted

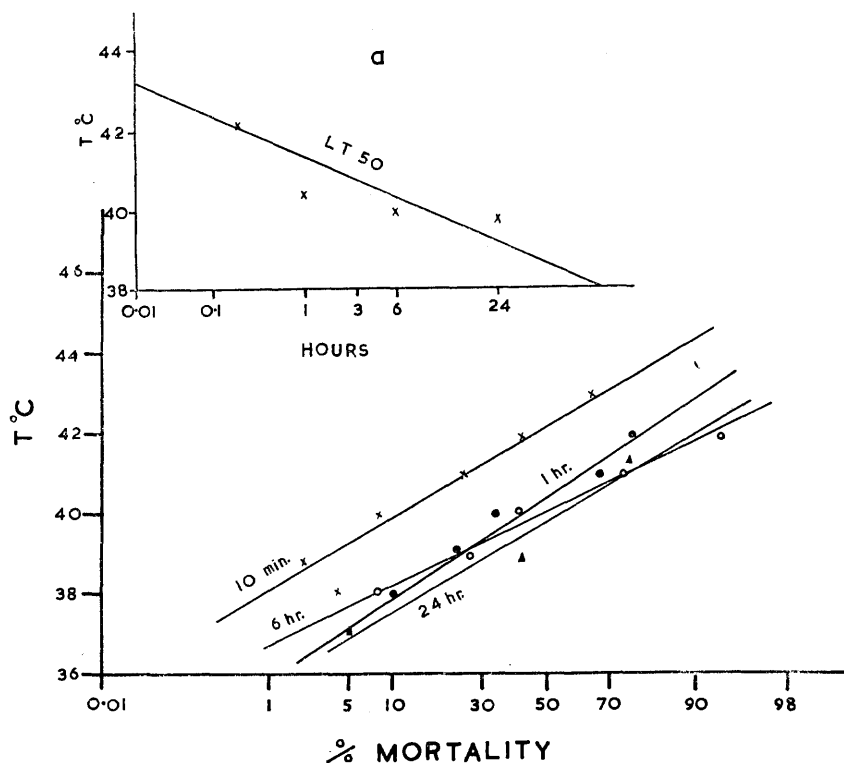


FIG. 5.—Mortality of second instar larvae of *Ae. vittatus* exposed to various temperatures; (a) values of LT 50.

in figures 4a-7a. Values of pupae exposed for 24 hours (fig. 8) have not been plotted, but by obtaining the appropriate LT 50 from figure 4a, and by using the approximate LT 100 (Table VI) a tentative line has been drawn for first instar larvae given an exposure time of 24 hours. Although increased exposure results in lowering the values of the LT 50, these do not differ greatly in larvae given one, six or 24-hour exposures; the greatest difference between these values, and also between the LT 100s, are observed in pupae given one and six hour exposures (Table VII). There are also relatively small differences (0.5°-3.1° C.) between the LT 50 and LT 100 of any larval instar or pupae. Mellanby (1960) has already suggested that little is gained by obtaining the LT 50 in preference to the thermal death point (LT 100), especially as the former entails considerably more experimental work. However, the small differences between the susceptibilities of the different immature stages of *Ae. vittatus* are better illustrated by the LT 50s, because it has been more accurately established, than by the thermal death point.

Some workers (Karamchandani, 1935; Macfie, 1920) have found the pupae of mosquitoes to be more resistant than the larvae to heat; others (Ramsay & Carpenter, 1932; Thomson, 1940) have found the reverse, and Wright (1927) and Barr (1952) found that in some species the pupae, and in others the larvae, were more resistant to high temperatures. Decreasing resistance to heat was observed in the eggs and first to fourth instar larvae of *Anopheles minimus* Theobald (Thomson, 1940), and Barr (1952) found younger instar larvae of three *Anopheles* species were more resistant to high temperatures than were later instars. In the present experiments pupae of *Ae. vittatus* were appreciably more resistant to heat than were larvae. There was relatively little difference between the susceptibilities of second and third instar larvae, but first and fourth instar larvae were the most and least resistant, respectively.

TABLE VI.—*Effect of high temperatures on mortalities of larvae and pupae. A dash denotes that no larvae were exposed to this temperature*

Temperature (°C.)	First instar		Second instar		Third instar		Fourth instar		Pupae	
	No. tested	Percent- age mortality	No. tested	Percent- age mortality	No. tested	Percent- age mortality	No. tested	Percent- age mortality	No. tested	Percent- age mortality
10 minute exposure periods										
36	50	0	50	0	52	0	35	0	—	—
37	50	0	48	0	50	0	40	0	—	—
38	49	0	30	4	49	0	45	0	—	—
39	38	0	31	2	31	0	30	7	25	0
40	52	0	46	8	52	2	51	22	30	0
41	44	6	50	24	51	20	32	47	35	3
42	50	13	50	42	53	40	47	60	30	5
43	56	57	52	65	54	70	50	100	45	10
44	57	70	50	100	50	100	55	100	40	28
45	50	100	50	100	50	100	—	—	35	37
46	52	100	—	—	—	—	—	—	30	100
47	53	100	—	—	—	—	—	—	31	100
1 hour exposure periods										
36	50	0	48	0	50	0	50	0	—	—
37	49	3	47	0	50	0	51	0	—	—
38	50	5	30	10	51	5	52	8	—	—
39	52	5	50	23	58	10	53	28	—	—
40	50	27	30	34	47	37	54	44	28	0
41	50	38	57	68	56	47	50	50	27	5
42	48	47	56	77	52	67	50	81	30	20
43	51	100	50	100	50	90	46	100	30	40
44	52	100	49	96	50	100	50	100	31	53
45	—	—	50	100	51	100	—	—	30	100
46	—	—	—	—	—	—	—	—	30	100
6 hour exposure periods										
36	52	0	48	0	45	0	50	0	—	—
37	51	3	51	0	50	0	55	0	—	—
38	50	7	50	8	50	10	55	15	25	0
39	48	15	52	26	50	37	50	38	24	0
40	56	37	48	41	50	45	49	51	31	3
41	50	57	51	74	50	63	50	71	38	37
42	48	73	50	93	51	81	48	84	35	81
43	52	100	51	100	50	100	36	100	32	100
44	51	100	50	100	49	100	50	100	35	100
24 hour exposure periods										
36·2–38·0	60	0	32	5	50	2	50	8	35	0
38·5–39·4	60	27	38	41	52	37	48	41	35	0
40·5–42·1	62	74	40	76	48	81	49	87	35	67
41·6–43·3	58	100	41	100	50	100	50	100	40	100
44·2–46·2	57	100	40	100	48	100	50	100	40	100

TABLE VII.—*Values of LT 50 and LT 100 (in °C.) for larval instars and pupae*

Exposure periods	First instar		Second instar		Third instar		Fourth instar		Pupa	
	LT 50	LT 100	LT 50	LT 100	LT 50	LT 100	LT 50	LT 100	LT 50	LT 100
10 minutes	43·1	45	42·2	44	42·2	44	41·4	43	45·5	46
1 hour	41·8	43	40·4	43	40·9	44	40·6	43	43·8	45
6 hours	40·8	43	40·0	43	40·1	43	39·9	43	41·4	43
24 hours	39·5	43	39·8	43	39·8	43	39·5	43	?	43

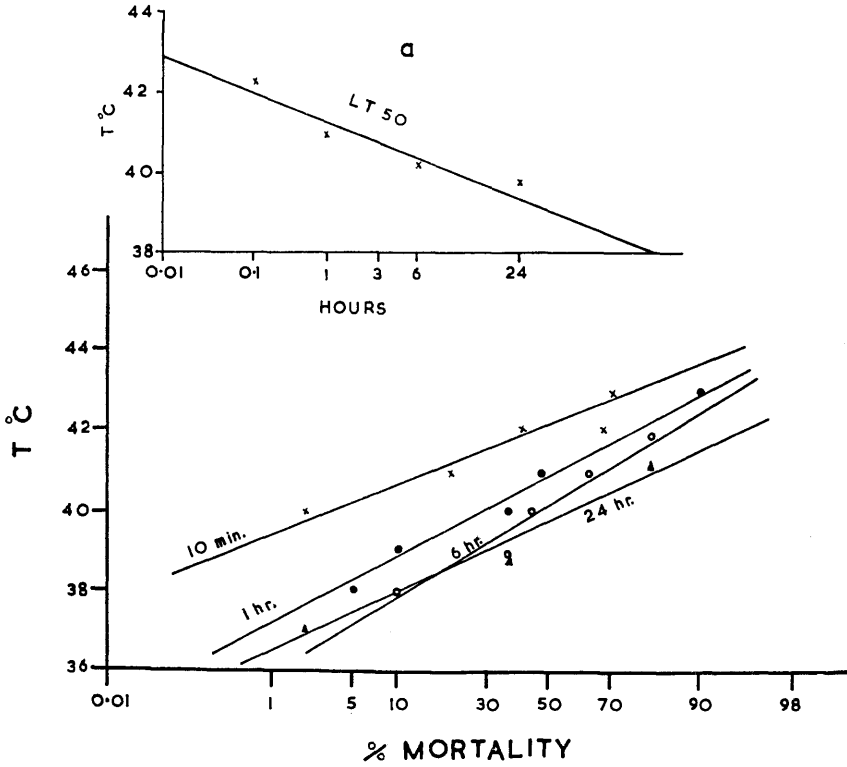


FIG. 6.—Mortality of third instar larvae of *Ae. vittatus* exposed to various temperatures; (a) values of LT 50.

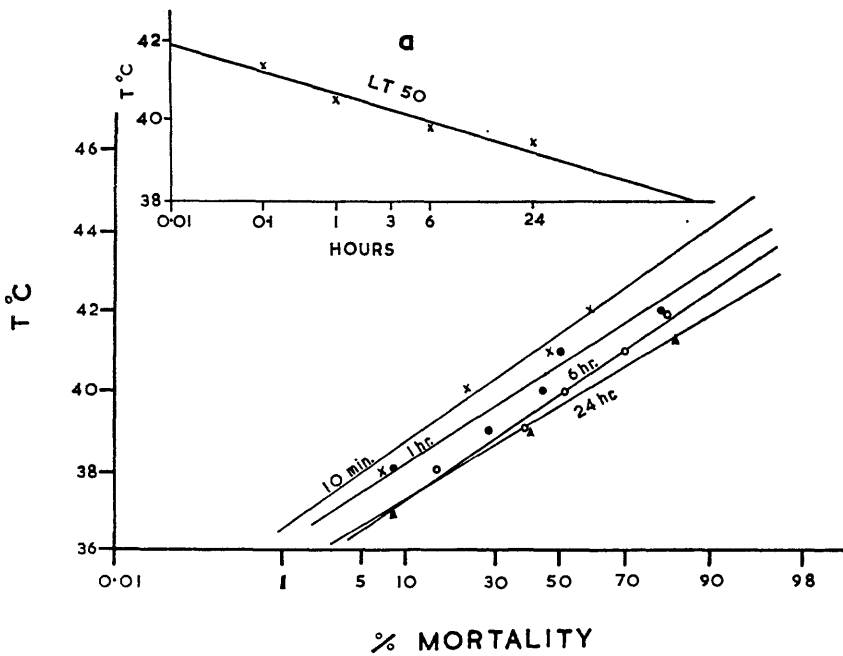


FIG. 7.—Mortality of fourth instar larvae of *Ae. vittatus* exposed to various temperatures; (a) values of LT 50.

Differences between the LT 50s of the pupae and fourth stage larvae, the most and least resistant stages, decreased with prolonged exposure periods, being 4.1°, 3.2° and 1.5° C. for exposure periods of 10 minutes, one and six hours, respectively.

The susceptibilities of larvae of *Ae. vittatus* do not appear to differ appreciably from those of other species. De Meillon (1934) found that a temperature of just over 45° C. for one hour gave complete mortality of larvae of *Anopheles gambiae*, and Bates (1949) gave the thermal death point for *A. pharoensis* Theobald as 40° C. Marcoux, Salimbeni & Simond (1903) found thermal death point of *Ae. aegypti* for one hour's exposure was 39° C., and Christophers (1960) found that three minutes at 46° C., 15 minutes at 45° C. or 30 minutes at 43° C. resulted in complete mortality of larvae of *Ae. aegypti*. The only record for *Ae. vittatus* is that of Boorman (1961). He found that three minutes at 45.5° C. killed two out of 13 (16 per cent.) larvae and three minutes at 48° C. killed 13 out of 14 (93 per cent.) larvae, and that an exposure of one hour at 36.5° C. gave complete mortality amongst the 25 larvae tested. In the experiments just described, complete mortality was only achieved after one hour at 43° C.

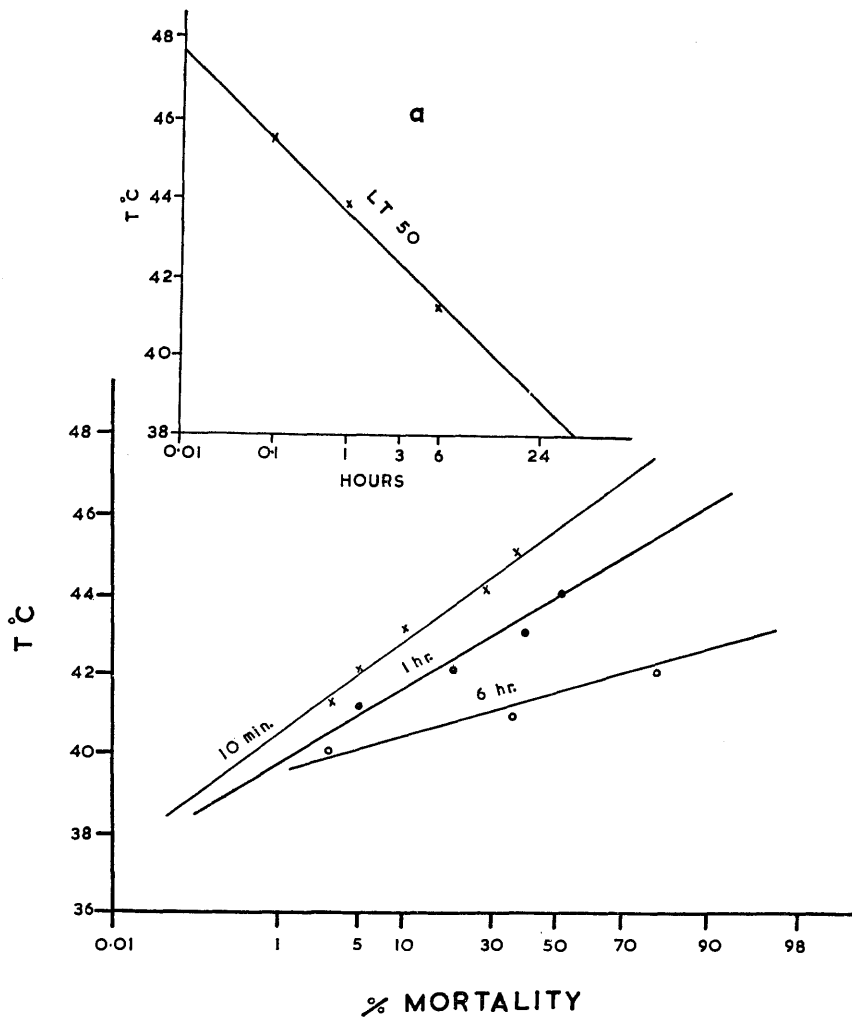


FIG. 8.—Mortality of pupae of *Ae. vittatus* exposed to various temperatures; (a) values of LT 50.

Because acclimatisation might affect the resistance of larvae to high temperatures, an attempt was made to study this phenomenon. As larvae were normally kept at 25°–28° C. prior to testing, four batches of 50 fourth instar larvae were acclimatised to 36.5°–38° C. by placing them in an incubator for 48 hours. Two batches were then given six hours' exposure in another incubator at 43° C. and the other two batches at 45° C. As controls, larvae were kept at 25°–28° C. for 48 hours before they were subjected to the same test temperatures. After a 24-hour holding period, all larvae in the controls and all acclimatised larvae submitted to 45° C. were dead, but only 78 per cent. of those previously acclimatised and then exposed to 43° C. died. This indicates that acclimatisation increased the tolerance of larvae of *Ae. vittatus* to high temperatures.

All pupae of *Ae. vittatus* died after 10 minutes at 46° C. or one hour at 45° C., and 40 per cent. mortality resulted from one hour at 43° C. There is less information on the effect of temperature on mosquito pupae, but Macfie (1920) found that "few pupae of *Ae. aegypti* survived 45° C. and all were killed at 46° C.". Christophers (1960) obtained complete mortality of pupae of *Ae. aegypti* after three minutes at 48° C. and 15 minutes at 45° C., and 64 per cent. mortality resulted from one hour at 43° C. Boorman (1961) recorded that five minutes at 45.5° C. killed 19 out of the 20 (95 per cent.) pupae of *Ae. vittatus* tested, and that three minutes at 48° C. killed all the 14 pupae exposed. There therefore appears to be little difference between the thermal susceptibility of the pupae of *Ae. aegypti* and *Ae. vittatus*.

In the rainy season maximum temperatures of the water in the rock-pools in June–August rose above 43° C., which in the laboratory caused complete mortality in all larval instars after an hour's exposure. Further, as complete mortality occurred in all larval instars after only 10 minutes at 44°–45° C., it would appear that larvae in the rock-pools would be killed after only very short exposures to high temperatures. There was, however, no evidence that this happened in the field. Holstein (1954) found that larvae of *Anopheles gambiae* tolerated higher temperatures in the field than in the laboratory, and Mackerras & Lamerle (1949) found that under field conditions *A. punctulatus* Dönnitz completed its development at 40° C., whereas in the laboratory larvae died at 37° C. Caution is therefore needed in interpreting laboratory data in terms of what happens in the field. The ability of larvae under natural conditions to withstand higher temperatures than they do in the laboratory is therefore probably due both to acclimatisation to higher temperatures before the maximum temperatures are reached, and to the occurrence in the field of a more gradual heat gradient leading to these high temperatures.

The effect of low temperatures on fourth instar larvae and pupae was investigated. As in the experiments with eggs (p. 109), a temperature range was used, and the absolute maximum and minimum temperatures recorded during the exposure periods are

TABLE VIII.—Effect of low temperatures on mortalities of batches of 50 fourth instar larvae and pupae. A dash denotes that no pupae were exposed to this temperature

Temperature (°C.)	Percentage mortalities after various exposure periods						Remarks
	6 hours		24 hours		48 hours		
	Larvae	Pupae	Larvae	Pupae	Larvae	Pupae	
24.4–25.3	0	—	0	—	0	—	No visible effects
20.2–22.5	0	—	6	—	6	—	Movements slightly slower
15.2–17.6	6	—	0	0	3	5	Movements definitely slower
12.5–15.3	10	0	10	5	22	18	Movements very slow
8.3–11.6	3	15	42	45	83	100	} Feeding appears to have ceased in larvae
6.0–7.5	30	44	77	100	100	100	
4.3–5.1	93	100	100	100	100	—	

given in Table VIII. An air-conditioned room provided temperatures from 15.5°–22.5° C., and a refrigerator gave a short series of lower temperatures. After exposure for periods ranging from six to 48 hours, larvae and pupae were transferred direct to tap water at normal room temperatures; controls were maintained as before but kept for 48 hours before being given food. Mortalities were assessed as previously. At temperatures down to 15.2° C. larvae and pupae were little affected, apart from movements being slightly slower, but at 12.5°–15.3° C. a significant reduction in movement and an increase in mortality were observed. At 8.3°–11.6° C. larvae appeared to stop feeding, and both larvae and pupae entered a chill coma, exposures of 24 and 48 hours resulting in high mortalities.

There is little information on the lethal effects of low temperatures on the larvae and pupae of *Aedes* species, but Mellanby (1960) found that larvae of *Ae. aegypti* acclimatised to 30° C. entered a chill coma at 10° C., and Bar-Zeev (1957) found that they died at 4° and 8° C.; Christophers (1960) discovered that 24 hours at 4° C. resulted in a chill coma, and that most of the larvae died after 48 hours' exposure. From the few available results it appears that larvae and pupae of *Ae. aegypti* and *Ae. vittatus* respond similarly to cold temperatures, and that larvae are slightly more cold-tolerant than pupae.

(4) Duration of Larval Instars and Pupal Stage

Several workers have found the development time of larvae in their natural habitats to be shorter than that observed in the laboratory, and both Ferreira (1945) and Holstein (1954) considered that the lower temperatures usually encountered in the laboratory were the principal cause. However, the differences between the food available under laboratory and field conditions may be a contributory factor. To investigate the duration of the immature stages under normal field conditions the following observations were made.

During the dry season of 1961 to 1962 pieces of dry mud were collected from rock-pools, which were known to be favoured oviposition sites, and stored in the laboratory. In the following May three pools were selected from which all mud and water was removed, so ensuring that no larvae of *Ae. vittatus* were contained in them. The mud samples were then soaked in these pools in filtered rain water at 1100 hours and removed 12 hours later. The pools were then covered with sandfly netting to prevent oviposition and the escape of the adults that emerged from pupae. They were inspected daily at about 1100 hours, and all larvae were removed, classified in the field according to their instar and then either placed in the same pools or in others that did not contain larvae or eggs. After all larvae had pupated and adults emerged, the same mud samples were re-soaked in the pools several times. The mean daily minimum and maximum water temperatures during the experiments, as recorded in one of the pools, were 21.9° and 41.6° C., respectively. The combined soakings produced 110 larvae. All first instar larvae completed their development within 24 hours, and 66 and 34 per cent. of second instar larvae completed their development in one and two days, respectively. Two, 71 and 27 per cent. of the third instar larvae completed their developments in one, two and three days, and about 29, 45, 18 and 9 per cent. of fourth instar larvae took two, three, four and five days, respectively. In 94 per cent. of the individuals the pupal period lasted two days, and in 4 and 2 per cent. one and three days, respectively. The first pupa appeared on the fifth day after soaking, and the first adult emerged on the seventh day.

Other observations during 1960–63 showed that the first pupae sometimes appeared four days after soaking in June and after five to six days in the cooler months of October, November and December. Boorman (1961) reported the appearance of pupae of *Ae. vittatus* in rock-pools in four days after rain. Philip (1962) found in southern Nigeria that adults of *Ae. vittatus* emerged on the sixth, seventh and eighth

days after soaking scrapings from rock-pools; presumably pupae were formed on the fourth to sixth days, which is in good agreement with results obtained in the present experiments. Lamborne (1930) cites the even shorter period of three days between rain and the appearance of pupae of *Ae. vittatus* in Nyasaland.

(5) Periodicity of Pupation and Sex Ratios

The males of *Ae. aegypti* emerge first because of the shorter duration of the male larval life (Christophers, 1960). To discover whether this was so with *Ae. vittatus*, all pupae appearing each day were collected from 12 pools, on their first day of appearance at the beginning of the rains and on four successive days. Combined results from all the pools showed that females formed 30 per cent. of the 43 pupae collected on the first day and 40, 57, and 70 per cent. of those collected on the following days. Of the few pupae (26) collected on the fifth day only 46 per cent. were females, probably because some of these represented a new generation. The total numbers of pupae collected (1592) gave a sex ratio of female : male of 1 : 1.1. In the laboratory 153 pupae were isolated within an hour of pupation, and their pupal duration was recorded. The mean duration of pupal life for the females was 44.8 hours and that for the males 45.0 hours. This difference is not significant ($P > 0.1$) and, even if it had been, would not have been sufficient to account for the emergence of males one to two days earlier than females. It is concluded therefore that the observed difference in emergence dates is due to a faster growth rate of male larvae.

Several workers have observed periodic pupation in mosquitoes (Goma, 1959; Halcrow, 1956; Shute, 1956). In preliminary investigations 317 newly formed pupae of *Ae. vittatus* were collected from bowls containing third and fourth instar larvae at three-hourly intervals. Times of sunrise and sunset were 0620 and 1845 hours, respectively; the only artificial illumination was from a 40 W. tungsten bulb for periods of 5–15 minutes while the pupae were collected. Results showed that 82 per cent. pupated between 1800 and 0600 hours and that the number pupating between 2400 and 0300 hours formed a peak representing 38 per cent. of the total. On six alternate working nights 225 pupae were collected at hourly intervals from 1800 to 2400 hours and from 2400 to 0600 hours. The maximum number of pupae collected in any one hour was 52 pupae collected between 2400 and 0100 hours, representing 23 per cent. of the total.

(6) Resistance of Larvae and Pupae to Desiccation

Fourth instar larvae (253) and pupae (223) were isolated on filter paper to remove all surface water, after which they were transferred to dry filter paper for varying periods in order to test their resistance to desiccation. The filter papers were then dropped into glass beakers containing 400 ml. of tap water, and mortalities were assessed after a 24-hour recovery period. In the controls, larvae (79) and pupae (46) were isolated on damp filter paper but resoaked again immediately afterwards. No larvae pupated or adults emerged from the pupae during the exposure periods, but both pupation and emergence occurred during the recovery period. Consequently, live pupae resulting from larvae, and adults emerging from pupae, were counted into the totals as representing live larvae and pupae respectively. Desiccation for less than two hours had little or no effect on the larvae (3–6 per cent. mortality) and pupae (0–10 per cent. mortality), but the percentage mortality increased from 29 and 32, respectively, after two and a half hours, to complete mortality after five and seven hours. About half the larvae and pupae died after three hours' exposure. Control mortality was less than 1 per cent.

Boorman (1961) isolated both pupae and larvae of *Ae. vittatus* on dry filter paper and recorded only 4 per cent. mortality amongst pupae after two hours; six hours' desiccation caused complete mortality. With larvae, the maximum duration of

desiccation he employed, one and three-quarter hours, resulted in only 9 per cent. mortality. It appears that his results are in general agreement with those of the present author.

These results show the ability of larvae and pupae to survive on a dry surface, but they do not simulate conditions experienced in the field. In rock-pools larvae and pupae experience more gradual desiccation, and when all surface water has evaporated they are surrounded in, or covered by, damp mud. In further trials 203 larvae and 72 pupae were isolated in beakers containing about 1 inch of wet mud. These were placed upside down at an angle of about 45° for 30 minutes to drain off all free water. They were then returned to an upright position, the larvae and pupae gently pushed away from the sides of the beakers, and the mud allowed to dry out for periods of one to six days in a humidity of about 80–90 per cent. Finally, the mud was flooded with tap water and mortalities assessed as previously. In the controls 43 larvae and 27 pupae were isolated on the mud for about 5–10 minutes and then reflooded. There was little larval mortality (0–19 per cent.) for periods of isolation up to three days. Four and five days' isolation on the mud caused mortalities of 56 and 86 per cent., respectively, and all larvae died after six days' exposure. Only 16 per cent. of the pupae died after two days' isolation on the mud; none were exposed for longer periods, as the emergence rate would have been high. There was no control mortality of the larvae or pupae. It is unlikely, however, that larvae and pupae survive as long as two days in the field on mud, because the rock-pools are fully exposed to the sun and the mud will usually dry out completely in less than this time.

(7) *Predators and Pathogens of Larvae and Pupae*

(i) *Field observations on predators*

Field observations showed that tadpoles of the genus *Rana* subgenus *Ptychadena*, nymphs of waterscorpions and dragonflies attacked larvae of *Ae. vittatus*. From July to September 1961 the incidence of *Ae. vittatus*, tadpoles and nymphs of waterscorpions and dragonflies was therefore recorded in 20 small and 19 large pools selected at random, some of which contained *Dopatrium longidens* (Table IX). It was only discovered at a later period that adults of *Anisops* attacked larvae of *Ae. vittatus*, and no investigations were made on this predator.

In calculating the percentage occurrence of the predators, all pools that were dry at the time of inspection were omitted. An analysis of variance shows that although wide fluctuations exist there is no significant difference between the percentage of small and large pools containing any of these predators ($P > 0.5$). Larvae of *Ae. vittatus* were found in a higher proportion (72.2 per cent.) of small ponds than larger ones (58.7 per cent.) ($0.01 < P < 0.05$). There were wide variations in the number of tadpoles per pool, the mean number being 11.50. The mean numbers of waterscorpion and dragonfly nymphs were 1.75 and 2.85, respectively. Attempts to determine the total of these animals in the larger pools were unsuccessful because of the difficulty experienced in locating all of them.

To assess the potentialities of these predators, three pairs of small pools with moderately thick growths of *D. longidens* were selected and all larvae and predators removed. They were then each stocked with 100 third and fourth instar larvae of *Ae. vittatus* and a known number of predators, which had been kept in glass beakers without food for the previous 24 hours. The number of larvae destroyed in each pool over a period of 48 hours was recorded. All three animals fed upon the larvae (Table X), but tadpoles were the most effective predators. When the weed was cut down to about the level of the mud in some of the pools, which were re-stocked with larvae and predators, predation by the waterscorpion and dragonfly nymphs was not affected, but the mean number of larvae destroyed by the tadpoles was greater ($P < 0.01$).

TABLE X.—Number of mosquito larvae in rock pools destroyed by predators in 48 hours

	No. larvae	Predator	No. larvae destroyed	
			Weed present	Weed absent
Pool 1	100	4 Tadpoles	59	76
Pool 2	100	4 Tadpoles	70	84
Pool 3	100	2 Waterscorpions nymphs	14	12
Pool 4	100	2 Waterscorpions nymphs	14	18
Pool 5	100	4 Dragonfly nymphs	20	22
Pool 6	100	4 Dragonfly nymphs	24	19

(ii) *Laboratory trials with predators*

Third and fourth instar larvae, or pupae, were used, and the predators were starved for 24 hours prior to their introduction to the bowls, except when the frequency with which the tadpoles fed was investigated. Medium blue coloured plastic bowls containing five pints of tap water, having a surface of about 115 sq. inches and with 0.5 inches of mud at the bottom, were used as receptacles in the trials, giving a laboratory habitat approaching the mean volume (4 pints) and surface area (95.5 sq. inches) of the rock-pools. The smaller volume of water in the pools in relation to the surface area was due to their sloping sides. Water temperature during the trials fluctuated between 24.3° and 27.7° C. After 24, 48 and 72 hours the number of larvae destroyed by the predators was assessed by subtracting those remaining alive from the total introduced. This does not necessarily equal those that were eaten, as the tadpoles, for example, sometimes killed more larvae than they ate, but the number killed is more important than the quantity of food devoured in assessing the effect of the predators. The numbers eaten will depend to some extent on the size of the predators, and the following figures refer to the lengths of the predators used in these trials, figures in parentheses being the sizes of the largest specimens seen in the rock pools. Tadpoles, including tail, 1.3–1.4 inches (1.4 inches, and those with all four limbs developed, but without tails, 0.5 inch); waterscorpion nymphs, including respiratory apparatus, 1.4–2.2 inches (2.6 inches); nymphs of *Bradinopyga strachani* 0.6–0.7 inch (0.7 inch). From information supplied by Mr. R. M. Gambles it appears that the ante-penultimate and penultimate (tenth and eleventh) instars of *B. strachani* were used in the trials.

Results are presented in Table XI and analysed in Table XII. The number of larvae eaten within the first 24 hours was considerably greater than that eaten in subsequent 24 hour periods. This is presumably because the predators had to make up for their enforced starvation period, in addition to satisfying their normal hunger requirements during a 24-hour period. The number devoured in the next 24 hours (*i.e.* 48–72 hours) was similar to that in the previous period, indicating that a normal level of feeding was maintained. Because of this initial high intake of food, it is better to compare the number of larvae and pupae eaten by the predators over a longer period, such as 48 hours. Tadpoles were the most efficient predators: the mean number of larvae destroyed in 48 hours was 19.0, compared with 7.3 and 5.5 by the waterscorpion and dragonfly nymphs (Table XII).

Because adults started to emerge from the pupae towards the end of the trials, all pupae offered to the predators that had not been eaten after 36 hours were removed and replaced by a similar number of new pupae (Table XI). Significantly fewer pupae than larvae were eaten by all predators ($P < 0.001$); this was most marked with dragonfly nymphs as the predators (Table XII) and may be accounted for by

TABLE XI.—Number of mosquito larvae and pupae destroyed by various predators. A dash denotes that no trials were conducted for this period

Bowl number	No. predators in larval (L) and pupal (P) bowls		Number of larvae (L) and pupae (P) destroyed															
			24 hours				48 hours				72 hours							
			Larvae (L)		Pupae (P)		Total		Per predator		Total		Per predator		Total		Per predator	
1	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
2	6 tadpoles	6 tadpoles	100	80	78	30	13.0	5.0	—	46	—	7.7	—	59	—	—	—	9.8
3	6 tadpoles	6 tadpoles	100	80	89	28	14.8	4.7	—	45	—	7.5	—	59	—	—	—	9.8
4	6 tadpoles	6 tadpoles	100	80	71	24	11.8	4.0	—	36	—	6.0	—	45	—	—	—	7.5
5	6 tadpoles	6 tadpoles	100	80	80	35	13.3	5.8	—	56	—	9.3	—	67	—	—	—	11.2
6	6 tadpoles	2 waterscorpion nymphs	100	30	69	5	11.5	2.5	—	9	—	4.5	—	12	—	—	—	6.0
7	6 tadpoles	2 waterscorpion nymphs	100	30	77	4	12.8	2.0	—	6	—	3.0	—	10	—	—	—	5.0
8	6 tadpoles	6 dragonfly nymphs	100	30	78	4	13.0	2.0	—	7	—	3.5	—	7	—	—	—	3.5
9	6 tadpoles	6 dragonfly nymphs	200	30	81	3	13.5	1.5	122	6	20.3	3.0	158	6	26.3	3.0	—	3.0
10	6 tadpoles	6 dragonfly nymphs	200	30	102	0	17.0	0	132	1	22.0	0.2	156	1	26.0	0.2	—	0.2
11	6 tadpoles	6 dragonfly nymphs	200	30	94	3	15.7	0.5	98	3	16.3	0.5	116	5	19.3	0.8	—	0.8
12	6 tadpoles	6 dragonfly nymphs	200	30	75	2	12.5	0.3	106	2	17.7	0.3	138	3	23.3	0.5	—	0.5
13	2 waterscorpion nymphs	6 dragonfly nymphs	50	30	12	0	6.0	0	16	0	8.0	0	18	0	9.0	0	—	0
14	2 waterscorpion nymphs	6 dragonfly nymphs	50	—	14	—	7.0	—	17	—	8.5	—	19	—	9.5	—	—	—
15	2 waterscorpion nymphs	6 dragonfly nymphs	50	—	11	—	5.5	—	13	—	6.5	—	18	—	9.0	—	—	—
16	2 waterscorpion nymphs	6 dragonfly nymphs	50	—	13	—	6.5	—	19	—	9.5	—	22	—	11.0	—	—	—
17	2 waterscorpion nymphs	6 dragonfly nymphs	50	—	10	—	5.0	—	14	—	7.0	—	16	—	8.0	—	—	—
18	6 dragonfly nymphs	6 dragonfly nymphs	50	—	5	—	2.5	—	9	—	4.5	—	10	—	5.0	—	—	—
19	6 dragonfly nymphs	6 dragonfly nymphs	50	—	24	—	4.0	—	33	—	5.5	—	41	—	6.8	—	—	—
20	6 dragonfly nymphs	6 dragonfly nymphs	50	—	18	—	3.0	—	33	—	5.5	—	40	—	6.7	—	—	—
21	6 dragonfly nymphs	6 dragonfly nymphs	50	—	26	—	4.3	—	37	—	6.2	—	42	—	7.0	—	—	—
			50	—	15	—	2.5	—	23	—	3.8	—	29	—	4.8	—	—	—

TABLE XII.—Mean numbers and standard deviations (S.D.) of mosquito larvae and pupae destroyed by predators

	Mean no. larvae and S.D.			Mean no. pupae and S.D.		
	24 hours	48 hours	72 hours	24 hours	48 hours	72 hours
Tadpoles	13.6±1.8	19.0±2.2	23.7±2.9	4.9±0.7	7.6±1.2	9.1±1.3
Waterscorpion nymphs	5.4±1.5	7.3±1.6	8.7±1.8	2.0±0.4	3.5±0.7	4.4±1.2
Dragonfly nymphs	3.5±0.2	5.5±1.2	6.3±1.8	0.2±0.2	0.3±0.2	0.4±0.3

differences in the pattern of movement of the larvae and pupae, and the different parts of the environment they occupy. For example, dragonfly nymphs, and to a lesser extent those of waterscorpions and tadpoles, browse over the mud at the bottom of their containers, and therefore come into regular contact with the larvae of *Ae. vittatus*, which are predominantly bottom feeders. Pupae, however, unless disturbed from the water surface, are rarely in this part of the environment and presumably have less contact with the predators.

It was realised that feeding might not be random throughout the day but might be characterised by diel cyclical activity. Detailed investigations of this were not undertaken, but some observations on the feeding pattern of tadpoles were carried out. To avoid any initial high predation none of the tadpoles used in the trials was starved beforehand. They were introduced into the larval bowls during darkness, at 0330 hours local time, so that any increase in feeding occurring during changes in light intensity at sunrise (0624) could be correlated to a natural diel rhythm and not to any disturbance caused by their introduction. Bowls were maintained under conditions of natural illumination except for short periods during the night when at three-hourly intervals the numbers destroyed were assessed. Feeding is mainly confined to the daylight hours, with a maximum in the first part of the morning (Table XIII). Probably the decrease in feeding at night is associated with (i) a general reduction in activity of both predators and prey and (ii) difficulties experienced by the predators in locating their prey under conditions of poor illumination. If this hypothesis is correct, it is reasonable to assume that, with the onset of daylight, normal activity is resumed, and feeding increases to a maximum to satisfy the food deficit resulting from reduced feeding at night, after which a comparatively low level of feeding is maintained.

TABLE XIII.—Number of mosquito larvae destroyed by tadpoles at various time intervals

Bowl number	No. larvae	No. larvae destroyed									
		0300–0600 hours	0600–0900 hours	0900–1200 hours	1200–1500 hours	1500–1800 hours	1800–2100 hours	2100–2400 hours	2400–0300 hours	0300–0600 hours	0600–0900 hours
1	100	3	10	13	7	4	4	0	0	1	9
2	100	5	13	11	3	5	5	4	2	2	10
3	100	3	10	15	7	3	7	3	5	2	11
4	100	4	14	17	11	0	0	0	0	0	14
Total	400	15	47	56	28	12	16	7	7	5	44

No cannibalistic tendencies amongst the predators, or predation between them, were recorded in the field. Laboratory observations showed that waterscorpion nymphs will eat tadpoles, but that the predation is lessened if an abundant supply of mosquito larvae is present.

There appear to be few published records of tadpoles eating mosquito larvae (e.g. Barber & King, 1927; Boorman, 1961; Laird, 1947; Pruthi, 1928), although there must be many instances in which they form a significant part in their diet.

However, Boorman (1961) found by direct observations, and also by gut analyses, that tadpoles of an unidentified genus of frog preyed upon larvae of *Ae. vittatus* in rock-pools, and although Philip (1962) presented no observations on predation, he reported that mosquito larvae were absent from rock-pools containing numerous tadpoles. Similarly, Lewis (1943) found that there were fewer late instar larvae of *Ae. vittatus* in pools containing dragonfly nymphs. Neither of these two observations was confirmed in the present work. There are several references to waterscorpions feeding on mosquito larvae (*vide* Jenkins, 1964), and some of these refer to the genus *Laccotrephes*.

There are many records of various species of dragonfly nymphs eating mosquito larvae (*vide* Jenkins, 1964), but Corbet (1962) considered dragonfly nymphs were unlikely to be much value in controlling any specific organisms, because they are facultative feeders. It is reasonable to conclude that they will not normally produce any marked reduction in a particular species unless they occupy an environment where there is no, or very little, choice of prey. Such a niche is unfavourable, as there is danger of the prey becoming eradicated, and this could lead to cannibalism amongst the nymphs, resulting in destruction of the local population. It is difficult to assess the importance of these predators in reducing the local population of *Ae. vittatus*, since some predation may occur between the predators and there is no information on the importance of other aquatic insects in their diets; some of these, such as Chironomid larvae, were often very abundant in the pools and possibly formed a major element in the diet of some of the predators.

(iii) *External pathogens of larvae and pupae*

Larvae from one of the rock-pools had heavy infestations of Peritrichida and external fungal hyphae (p. 104), but because of the much greater frequency of multiple infestations it was impossible to collect sufficient specimens which had only one infestation and so study individually their effect. Several records exist of mosquito larvae being infested by *Vorticella* spp. and various fungi (*vide* Jenkins 1964), but this appears to be the first report concerning *Ae. vittatus* infested by *Vorticella*-like Protozoa.

Infested larvae and pupae were characterised by their characteristic greyish fuzzy appearance, their sluggish movements and markedly slower response to external alarm stimuli. Examination of 18 first, 22 second, 38 third and 76 fourth instar larvae and 68 pupae showed that none of the first, and only five (22.7 per cent.) of the second instar were infested but that all later instar larvae and pupae were infested with either one or both of these plants. There were few Peritrichida, and no fungi, on the larval head capsule and its appendages and no infestations on the siphon. The anal papillae were the most heavily infested region of the body. Fungal hyphae extended over both ventral and dorsal surfaces of the thorax and abdomen, and *Vorticella* and fungi were distributed over the cephalothorax and abdomen of the pupae, but none occurred on the paddles.

There was no appreciable difference in the mortality of adults obtained from healthy and from infested larvae and pupae collected from rock-pools and reared in the laboratory. Some infested larvae, however, and a larger number of the infested pupae, but no uninfested larvae or pupae, died during transportation to the laboratory.

Probably relatively little mortality amongst either larvae or pupae of *Ae. vittatus* in the field is due directly to these pathogenic infestations, but as infested individuals appear to possess less vigour, significant mortality may result in an unfavourable environment where they are under stress. Further, as infested larvae are much slower in their reactions to alarm stimuli, a greater proportion possibly fail to escape from any predators in the pools.

IV. OBSERVATIONS ON ADULTS

(1) *Host Preferences*

Although *Ae. vittatus* has a widespread distribution, there is relatively little information on adult feeding habits. It bites man readily in certain areas of Africa (Kerr, 1933; Lewis, 1943; Mouchet & Rageau, 1964; Service, 1963; and others), whereas in other regions it rarely feeds on man (Muspratt, 1956; Teesdale, 1959; van Someren, Teesdale & Furlong, 1955). When Magoon traps (Magoon, 1935) were used about five miles to the south-east of the rock outcrop at the Veterinary Investigation and Training Centre, *Ae. vittatus* were among the many mosquitoes taken in traps baited with sheep and pigs (Service, 1964). No *Ae. vittatus*, however, were taken when the trap was placed on the rock outcrop (Plate II) and baited with goats, sheep, pigs and monkeys (*Erythrocebus patas patas* (Schreber)), although seven males and 84 females were caught when the author entered the trap in the early evening on four occasions.

About 44 hours were spent searching for adults resting in crevices and cracks in the rock and amongst its scant vegetation. A total of 230 females and 47 males of *Ae. vittatus* were caught (Table XIV). Fifty-eight of the unfed females were dissected;

TABLE XIV.—*Numbers and physiological condition of Ae. vittatus and other mosquitoes caught amongst vegetation and rock crevices*

Species	Caught amongst vegetation					Caught from rock crevices				
	Un-fed	Blood fed	Gra-vid	Total		Un-fed	Blood fed	Gra-vid	Total	
				fe-males	Males				fe-males	Males
<i>Aedes vittatus</i> (Bigot)	75	40	77	192	32	17	18	3	38	15
<i>Ae. unilineatus</i> Theobald	0	0	1	1	0	0	0	0	0	0
<i>Ae. sp. indet.</i>	1	0	0	1	0	0	0	0	0	0
<i>Anopheles gambiae</i> Giles	2	1	0	4	1	2	1	0	3	0
<i>A. funestus</i> Giles	0	0	0	1	1	3	0	0	3	0
<i>A. flavicosta</i> Edwards	0	0	1	1	0	0	0	0	0	0
<i>A. pretoriensis</i> (Theobald)	1	0	0	1	0	1	0	0	1	0
<i>A. domicolus</i> (Edwards)	2	0	0	2	0	0	0	0	0	0
<i>Culex poicilipes</i> (Theobald)	3	0	0	3	0	0	0	0	0	0
<i>C. nebulosus</i> Theobald	5	0	1	7	1	0	0	0	0	0
<i>C. grahami</i> var. <i>farakoensis</i> Hamon	0	0	0	2	2	0	0	0	0	0
<i>C. spp. indet.</i>	2	0	0	2	0	0	0	0	0	0

49 of these (84 per cent.) had ovaries in stage II of Christophers (1911), and their uncoiled tracheoles showed them to be nulliparous (Detinova, 1945). Nineteen per cent. of the females dissected were unfertilised and this, together with the presence of 47 males in the catch, showed that many were newly emerged adults. No mosquitoes were caught from nine hours of sweeping vegetation, mostly grass, up to 70 yards from the base of the rock outcrop. Results of precipitin tests on the 58 blood-fed females have already been published (Service, 1965*b*). There were no double feeds. A little over half had fed on porcupine and about a fifth on birds and on man; there were few feeds on goats, sheep or bovids and none on monkeys. Porcupines appear to be the principal host of *Ae. vittatus* in this area, but in regions where they are absent some other host must be used. Smith (1955) suggested that species vary their feeding preferences according to the locality and availability of the various possible hosts.

(2) *Diel Biting Cycles*

It was not possible to carry out continuous 24-hour human bait catches to obtain the diel biting cycle of this species. A series of 12 shorter catches, each of about

3 hours' duration, however, covered all hours of the day. In these, two men sat on the rock outcrop and caught in test tubes all mosquitoes alighting on them; during darkness light was provided by a small hurricane lamp and the intermittent use of torches. Of the 16 men employed in these catches, no two worked longer than four hours at a time, often less, and every effort was made to see that any one couple did not introduce any bias in the catches by working during only one interval of time. Little feeding occurred during 2300–1600 hours local time. *Ae. vittatus* appears to have a relatively short crepuscular biting period, with maximum activity from 1800 to 2100 hours (fig. 9). The fluctuations in the numbers of males were similar to those of the females.

In an earlier series of direct human bait catches carried out from 1800 to 0600 hours, *Ae. vittatus* was the most common anthropophilic *Aedes* mosquito, forming 47.6 per cent. of the *Aedes* catch (Service, 1963).

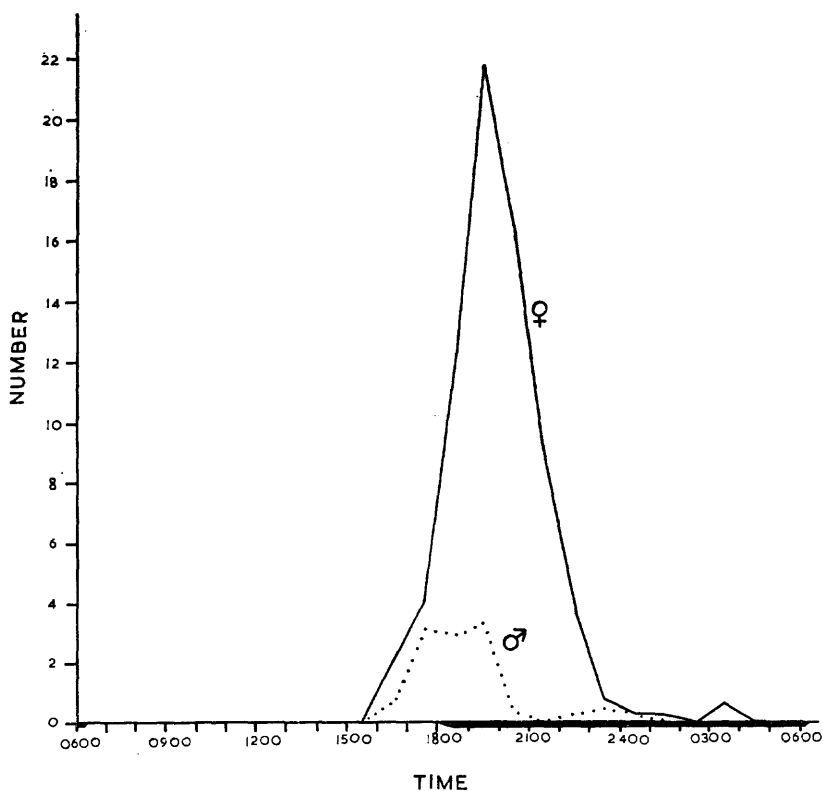


FIG. 9.—Mean numbers of females and males of *Ae. vittatus* landing on one man per hour.

(3) Catches Inside Huts

Apart from *Culex pipiens fatigans* Wiedemann, *Mansonia uniformis* (Theobald) and *M. africana* (Theobald), culicine species are rarely found resting inside huts in West Africa. In the Kaduna area no *Ae. vittatus* was found amongst a total of 48,380 mosquitoes caught in 6425 pyrethrum-spray sheet collections in village huts and town houses and of 5308 mosquitoes collected biting man inside huts. However, van Someren, Teesdale & Furlong (1955) have recorded it biting with equal intensity both in and out of doors, and recently adults were caught in light-traps placed in village huts in the Kaduna area of Nigeria (Service, in press).

(4) *Seasonal Incidence*

Investigations into the seasonal incidence of the adults near Kaduna (Service, 1963) showed that the greatest number of adults occurred in May, and that none was recorded in the dry season from December to March. At the rock outcrop adults are absent from November or December to about March or April. In the higher rainfall areas of southern Nigeria, adults are in evidence during most of the year. Small differences in seasonal occurrence may also exist between localities in the same general area. At sites such as the rock outcrop, its seasonal incidence depends only on rain water filling up the pools. In other areas where *Ae. vittatus* breeds in rock-pools in river beds, its seasonal incidence depends both on direct rainfall and on the water level of the rivers.

(5) *Attempts to Establish a Colony*

Several attempts were made to establish a colony. The first was made in July–September 1961 in an insectary, in which temperature and humidity could not be controlled, but which housed a flourishing colony of *Ae. aegypti*. Large numbers of late instar larvae in enamel bowls were placed in a 2.5 feet cube cage having a wooden floor and framework, with the sides and top covered in plastic mosquito gauze. Illumination in the cage could be altered by putting various amounts of brown paper over the sides and top. This type of cage was successful in both Lagos and Kaduna for establishing colonies of *Ae. aegypti*. Emergent adults were supplied with 10 per cent. cane sugar solution and offered blood meals from anaesthetised guinea-pigs placed either in or on the top of the cage. Small unglazed clay pots, four to five inches high with openings about three and a half inches in diameter containing tap water were introduced into the cages as oviposition sites. Although both sexes fed on the sugar solution, females could not be induced to feed on the guinea-pigs. In July–August the following year chickens, with many of the breast feathers removed and strapped to boards, were placed in the cage. Although both *Ae. aegypti* and *C. p. fatigans* fed on such chickens, adults of *Ae. vittatus* refused to feed on the birds. Neither would they take a blood-meal when the author's arm was introduced into the cage, during the day, evening or at night. Final attempts were made in July–August 1963. The cage was transferred to a room having a temperature of about 27° C. and a relative humidity of 85–90 per cent., but adults still refused to feed either on the author's arm or on guinea-pigs. In 1969, however, three unfertilised females obtained from soaking mud samples were successfully fed on the author, and these, and also unfed females, were easily inseminated by artificial mating techniques using decapitated males. Mating, however, was not a problem in establishing a colony, because dissections showed that 81 and 87 per cent. of the 58 and 38 females removed from the cages in 1962 and 1963, respectively, were fertilised.

Boorman (1961), working in Nigeria, although he was not successful in establishing a colony of *Ae. vittatus*, managed to obtain a few fertile eggs. Colonies have been successfully established with Mediterranean strains of the species (Callot, *personal communication*; Coluzzi, *personal communication*; Freyvogel & McClelland, 1969), and a colony of a strain from Rhodesia has been established in North America (Freyvogel & McClelland, 1969). It is possible that the ease of establishing colonies of this species varies according to the strains used.

V. TAXONOMY AND DISTRIBUTION

(1) *Introduction*

Edwards (1932) divided the subgenus *Stegomyia* into four groups, which he designated A, B, C, and D; a fifth group was added by Knight & Rozeboom (1946) and called group E by Knight & Hurlburt (1949). Bohard (1956) created two more groups, F and G, and Belkin (1962) added group H. There have been several trans-

fers of species amongst the original four groups, and also from these into the newer ones, but *Ae. vittatus* still occupies its unique position, in group D. Adults may be distinguished by the following combination of characters:— a scaly clypeus, pale banded proboscis, all broad scutellar scales, three pairs of white scutal spots, presence of lower mesepimeral bristles, white ring near middle of the tibia, highly modified style in the male genitalia, basal lobe without strongly modified setae, convex form of tergite IX and the absence of a ventral arm in the paraproct. Distinguishing characters of the larvae consist of a usually spiculate antennae, antennal seta usually branched, head seta C (no. 5) single, comb teeth in a single irregular row and not arising from a plaque, single lower caudal seta (no. 3), ventral brush with one or more precratal setae, and its setae more strongly branched than in other species. The pupae are unusual in having the paddle edge with only minute spicules. In many of these characters the species is reminiscent of the subgenus *Aedimorphus*.

Belkin (1960) found that there were cords of tissue, presumably nerves, connecting larval setae to their pupal homologues. This enabled, for the first time, the perfect correlation of larval and pupal hairs. In the present work hairs were identified by the criteria set out by Belkin (1952) on the position of the setae, by the underlying setae of following instars and by their relative position to one another. Nomenclature adopted for the larval work is basically that of the revised form of Belkin (1953) together with the alterations suggested by Belkin & Hogue (1959), but, as suggested by Belkin (Barr & Myers, 1962), the numberings of abdominal hairs 11 and 12 have been interchanged. The pupal chaetotaxy is essentially that of the two above papers by Belkin, except that, as proposed by Barr & Myers (1962), abdominal seta 10 becomes 7, seta 7 changes to seta 9 and, because of the interchanging of hairs 11 and 12 in the larvae, seta 12 becomes seta 10. There has been no change in numbering of setae 3 and 4, which were found by Barr & Myers (1962) to have reversed their positions on some segments of *Culiseta inornata* (Williston) and *Culex pipiens quinquefasciatus* Say (= *C. p. fatigans*), because the nerves connecting fourth instar setae to those of the pupae were not seen and there was therefore no evidence that this reversal took place in *Ae. vittatus*. Whenever possible characters on both sides of the specimens, e.g. right and left sides, have been examined. In the descriptions of the various stages given below, the numbers in parentheses after the setal numbers give the range of branching.

Aedes (Stegomyia) vittatus (Bigot)

Culex vittatus Bigot, 1861, *Ann. Soc. ent. Fr.* (4) 1 : 227.

For full synonymy see Stone, Knight & Starcke (1959) and Mattingly (1965).

Types.—*vittatus* ♀, Corsica, lost; *brumpti*, cotype ♂♂ and ♀♀, Harar, lost; *albopuncta*, ♀, Sierra Leone, in B.M. (N.H.).

Distribution.—North-Chad (Rioux, 1959), Iles d'Hyere (Timon-David, 1928), France, mainland (Callot, 1951); see Mattingly (1965) for comprehensive list of other localities.

(2) Detailed description of the stages of *Ae. vittatus*

First instar larvae

(Based on 30 specimens; fig. 10)

Head.—No distinct ocular bulge, pigmentation uniform dark brown except for slightly lighter ocular areas and a black heavily sclerotised egg breaker. No distinct collar. Antennae lighter pigmented than rest of head capsule, spicules very sparse and pale, shaft hair (*i.e.* hair 1) plumose, lightly pigmented and situated at 0.33 distance from antennal base and composed of 2.4 ± 0.5 branches. All dorsal and ventral hairs of head capsule non-plumose, single and pale in colour. Mentum with 7–8 teeth on each side of central tooth.

Thorax.—Integument smooth, nude throughout and unpigmented, meso- and metathoracic spiracular rudiments not developed. Larger hairs plumose or sub-plumose and weakly pigmented, basal tubercles small and unpigmented, smaller hairs very pale and non-plumose.

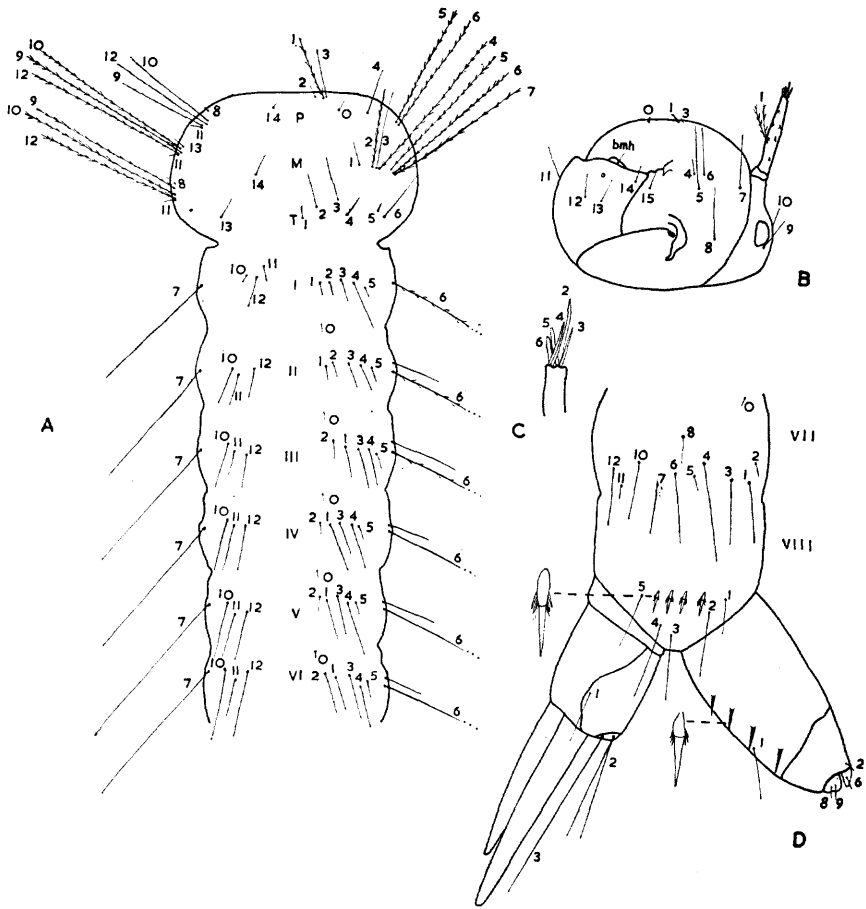


FIG. 10.—Chaetotaxy of first instar larva: (A) thorax and abdomen; (B) head; (C) tip of antenna; (D) terminal abdominal segments.

Abdomen.—Integument smooth and nude throughout, unpigmented except for specialised structures on segments VIII–X, spiracular rudiments on segments I–VII not developed. Comb consists usually of 4–5 weakly sclerotised scales situated in an irregular single row; siphon sclerotised on about distal 0.26–0.41 of its length, pale brown-grey; siphonal hair single and non-plumose, situated at about 0.7 distance from base. Pecten consists usually of 4–5 pointed sclerotised spines, of which 1 is distal to tuft. Ratio of siphonal length to its width at base 1.6 ± 0.2 , gills subequal and about twice length of saddle segment. Saddle dark brown and incomplete, no ventral brush. All abdominal hairs single, only the larger ones on a few segments plumose or sub-plumose. Hairs 0 and 14 could not be found and appear to be absent, hair 8 was not present on the metathorax and abdominal segment 1. No dorsal sensilla on segments III–V.

Second instar larvae

(Based on 26 specimens; fig. 11)

Head.—No distinct ocular bulge, pigmentation darker brown than on first instar larva, ocular areas and antennae paler. No collar but a very thin dark occipital ring present. Sculpturing less distinct than on preceding instar. Antennal hair darker than antenna, situated at about 0.37 distance from base and composed of 1–3 branches; spicules very small dark apically and sparse. All dorsal and ventral hairs lighter than head capsule. Seta 0–3(1), 4(1–2), 5(1), 6(1–2), 7(1–3), 8(1–2), 9(1), 10–11(1–2), 12(1), 13(1–2), 14–15(1), *bmh* (1). Mentum with 10–11 teeth on each side of a central tooth.

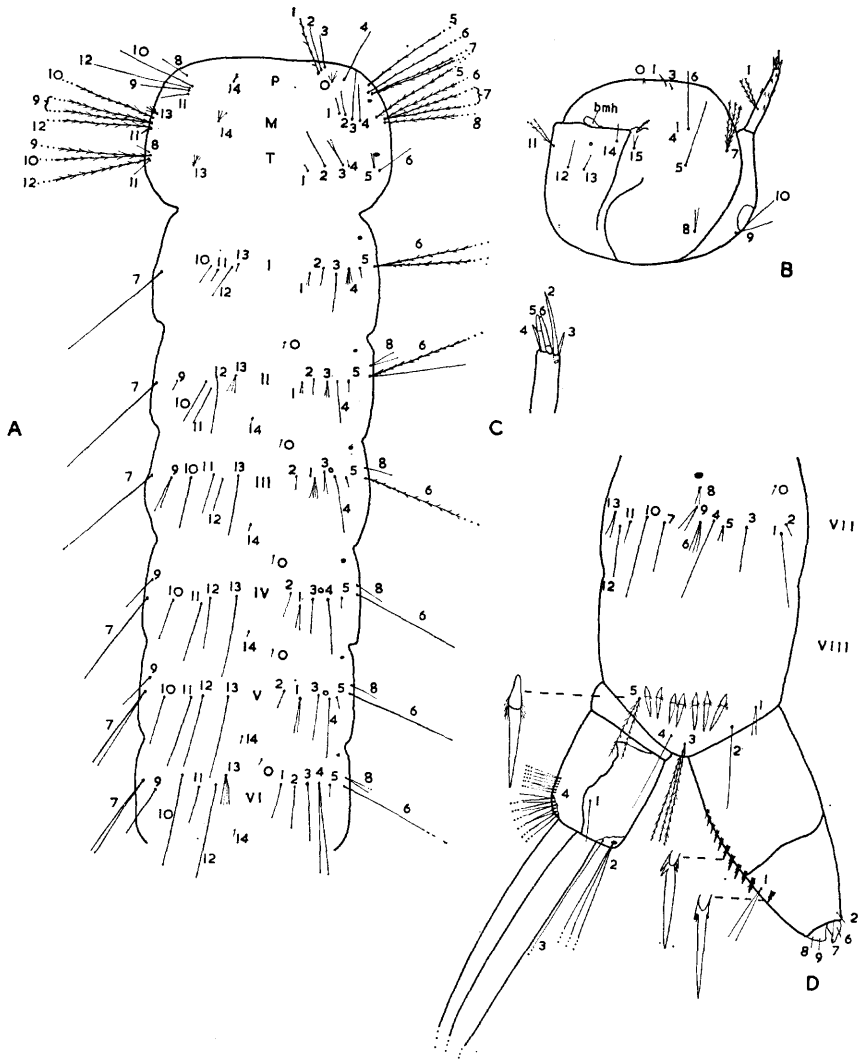


FIG. 11.—Chaetotaxy of second instar larva of *Ae. vittatus*: (A) thorax and abdomen; (B) head; (C) tip of antenna; (D) terminal abdominal segments.

Thorax.—Integument smooth and nude throughout, unpigmented, meso- and metathoracic spiracles present as small distinct black sclerotised spots. All hairs darker than integument, prothoracic tubercles relatively small and pale but meso- and metathoracic ones well developed and dark brown. Hair 7 appears for the first time on prothorax but is absent from the metathorax. Prothorax: seta 0(2-4), 1-6(1), 7(1-2), 8-12(1), 14(1-4). Mesothorax: seta 1-6(1), 7(1-2), 8(1), 9(1-3), 10-12(1), 13(2-4), 14(3-5). Metathorax: seta 1-2(1), 2(2-3), 4(1), 5(1-2), 6(1), 8-12(1), 13(3-5).

Abdomen.—Integument smooth and nude throughout, unpigmented except for specialised structures on segments VIII-X. Spiracular rudiments developed as very small black spots on segments I-VII, dorsal sensillum present on segments III-V between hairs 3 and 4. Hairs 8 and 9 absent from segment 1, but hairs 9 and 13 appear for first time on segments II-VII. Comb consists of 8-9 weakly sclerotised pointed scales arranged in a single irregular row. Siphon sclerotised on about distal 0.33-0.54 of its length; siphonal hair inserted at about 0.67 from base, with 2-3 branches. Ratio of siphonal length to basal width 1.9 ± 0.2 . Pecten consists usually of 8-10 pointed sclerotised spines, of which 1-2 are distal to siphonal hair. Gills subequal, about 4 times length of saddle segment. Saddle dark brown and incomplete. Ventral brush with 6 paired and 6 unpaired (pre-cratel) tufts, of which the former are mainly single although occasionally 2-branched, and the latter mainly single but may also be 2-branched. Seg. I: seta 1(1-2), 2-3(1), 4(4-5), 5(1), 6(2), 7(1-2), 10-13(1). Seg. II: seta 0(4), 1(1-2), 2(1), 3(3-4), 4-5(1), 6(2), 7(1), 8(1-2), 9-12(1), 13(3-4), 14(1). Seg. III:

seta 0(1), 1(2-4), 2(1), 3(1-2), 4-8(1), 9(1-2), 10-14(1). Seg. IV: seta 0(1), 1(2-3), 2(1), 3(1-2), 4-6(1), 7(2-3), 8-11(1), 12(1-2), 13-14(1). Seg. V: seta 0(1), 1(2-3), 2(1), 3(1-2), 4-6(1), 7(2-3), 8(1-2), 9-11(1), 12(1-2), 13-14(1). Seg. VI: seta 0(1), 1(2-3), 2-3(1), 4(3-4), 5-6(1), 7(3-4), 8(3-4), 9-10(1), 11(1-2), 12(1), 13(3-4), 14(1). Seg. VII: seta 0-2(1), 3(1-2), 4(1), 5(2-4), 6(3-4), 7(1), 8(2-3), 9(1-2), 10-12(1), 13(3-4). Seg. VIII: seta 1(1-2), 2(1), 3(4-5), 4(1-2), 5(1-2). Seg. X: seta 1(1), 2(2-3), 3(1), 4a-f(6), 4g-l(6).

Third instar larvae

(Based on 30 specimens; fig. 12)

Head.—No distinct ocular bulge, pigmentation dark brown, ocular areas paler, but antennae with about same degree of pigmentation as head capsule. No collar, but a very thin dark occipital ring present. Sculpturing indistinct. Antennal hair about same colour as antennae, situated at about 0.36 from base and composed of 2-3 branches; spicules very small, sparse and with dark apices. Smaller hairs of head paler than head capsule, but larger ones darker. Seta 0-3(1), 4(2-3), 5-6(1), 7(3-4), 8(3-4), 9-10(1), 11(2-3), 12(1), 13(2-3), 14(1), 15(1-2), *bmh*(1). Mentum with 11-12 teeth on either side of a central one.

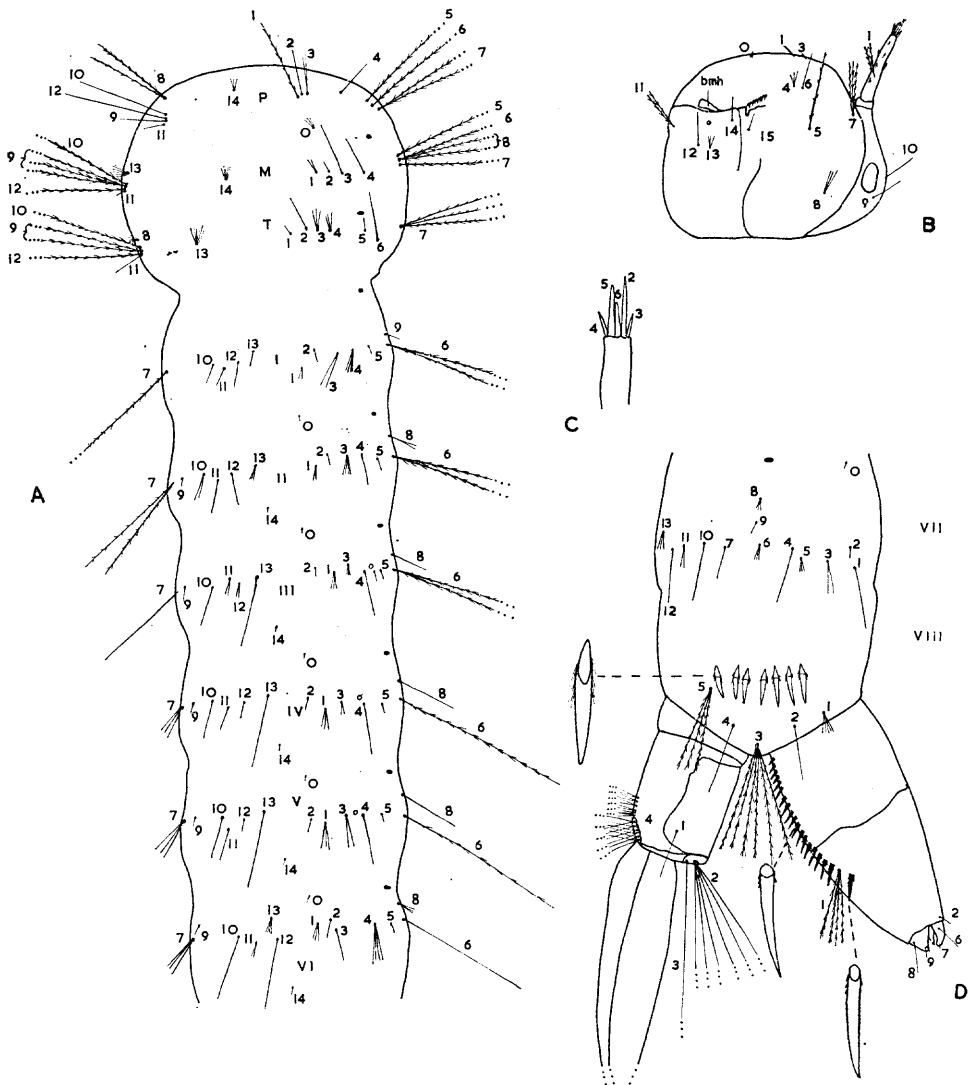


FIG. 12.—Chaetotaxy of third instar larva of *Ae. vittatus*: (A) thorax and abdomen; (B) head; (C) tip of antenna; (D) terminal abdominal segments.

Thorax.—Integument smooth and nude throughout, unpigmented, meso- and metathoracic spiracular rudiments present as distinct black sclerotised spots. All hairs darker than integument, prothoracic tubercles relatively small and pale, but meso- and metathoracic tubercles well developed and dark brown. Hair 7 appears for first time on metathorax. Prothorax: seta 0(5-6), 1-2(1), 3(1-2), 4-6(1), 7(2), 8(1-2), 9-12(1), 14(2-4). Mesothorax: seta 1(1-2), 2-4(1), 5(1-2), 6(1), 7(1-2), 8(2-3), 9(2-4), 10-12(1), 13(5-7), 14(4-6). Metathorax: seta 1-2(1), 3(2-3), 4(3-4), 5-6(1), 7(3-4), 8(4-5), 9(1-2), 10-12(1), 13(6-7).

Abdomen.—Integument smooth and nude throughout, unpigmented except for specialised structures on segments VIII-X. Spiracular rudiments present on segments I-VII, dorsal sensillum occurs on segments III-V. Hair 9 appears for first time on segment I. Comb consists of 8-9 weakly sclerotised pointed scales arranged in an irregular row. Siphon brown and sclerotised on distal 0.58-0.70 of its length; siphonal tuft inserted at about 0.62 from base, with 4-5 branches. Ratio of siphonal length to basal width 1.62 ± 0.1 . Pecten consists of 18-20 long brown spines, of which the more distal are often curved, and 1-2 are distal to siphonal tuft. Gills subequal and about 5 times length of saddle segment. Saddle brown and incomplete. Ventral brush with 6 paired tufts, of which the proximal ones have 3-4 branches and the distal ones mainly 2 but occasionally 3 branches, and 6 unpaired tufts, latter with 3 or 4 branches proximally and 2 branches distally. Seg. I: seta 1(1-2), 2(1), 3(1-2), 4(5-7), 5(1), 6(2), 7(1-2), 9(1-2), 10-13(1). Seg. II: seta 0(1), 1(1-2), 2(1), 3(4-5), 4-5(1), 6-7(2), 8(1-2), 9(1), 10(1-2), 11-12(1), 13(2-3), 14(1). Seg. III: seta 0(1), 1(2-3), 2(1), 3(2-3), 4-5(1), 6(1-2), 7-8(1), 9(2-3), 10(1), 11-12(2-3), 13-14(1). Seg. IV: seta 0(1), 1(3-4), 2(1), 3(3-4), 4-6(1), 7(2-4), 8-10(1), 11-12(1-2), 13-14(1). Seg. V: seta 0(1), 1(2-3), 2(1-2), 3(2-3), 4-6(1), 7(2-3), 8-11(1), 12(1-2), 13-14(1). Seg. VI: seta 0(1), 1(3-4), 2-3(1), 4(3-4), 5(1), 6(1-2), 7-8(3-4), 9(1), 10(1-2), 11(2-3), 12(1), 13(4-5), 14(1). Seg. VII: seta 0-2(1), 3(2-3), 4(1), 5-6(3-4), 7(1), 8-9(1-2), 10(1), 11(1-2), 12(1), 13(3-4), 14(1). Seg. VIII: seta 1(3-4), 2(1-2), 3(5-7), 4(1), 5(3-4). Seg. X: seta 1(1), 2(4-6), 3(1), 4a-f(6), 4g-l(6).

Fourth instar larvae

(Based on 30 specimens; fig. 13)

Head.—Ocular bulge not very pronounced, pigmentation dark almost black, but ocular areas and antennae paler. Collar absent, but a distinct thin black occipital ring present. Sculpturing moderately well developed but indistinct because of intensity of pigmentation. Antennal hair slightly paler than antenna, situated at about 0.39 distance from base, and composed usually of 2-3 hairs, spicules very small and fewer than on third instar larvae, occasionally absent, their apices dark. Smaller hairs paler than on head capsule, larger ones darker. Seta 0-3(1), 4(2-3), 5-6(1), 7(5-7), 8-9(1), 10(1-2), 11(3-4), 12(1), 13(3-4), 14(1), 15(3-4), *bmh* (1). Mentum with 12-14 teeth on each side of a central tooth.

Thorax.—Integument smooth and nude throughout, unpigmented, meso- and metathoracic spiracular rudiments present as distinct black sclerotised spots. All hairs darker than integument, prothoracic tubercles relatively small, but others well developed and dark brown. Prothorax: seta 0(5-7), 1-2(1), 3(1-2), 4-6(1), 7-8(2-3), 9-12(1), 14(5-7). Mesothorax: seta 1(2-4), 2(2-3), 3-6(1), 7-8(1-2), 9(3-4), 10-11(1), 12(1-2), 13(8-10), 14(5-7). Metathorax: seta 1(1-3), 2(1-2), 3(5-7), 4(2-4), 5-6(1), 7(5-6), 8(6-7), 9(1-2), 10-12(1), 13(6-8).

Abdomen.—Integument smooth and nude throughout, unpigmented except for specialised structures on segments VIII-X. Spiracular rudiments present on segments I-VII, dorsal sensillum on segments III-IV. Comb consists of 6-9 sclerotised pointed brown spines arranged in a slightly irregular row. Siphon brown and sclerotised along its entire length, except for a very small pale area at extreme base; siphonal tuft composed of 4-6 hairs inserted at about 0.69 distance from base. Ratio of siphonal length to basal width 1.62 ± 0.1 . Pecten consists of 19-22 long dark brown, almost black, pointed spines, of which the distal ones are curved, and 1 is distal to the siphonal tuft.¹ Gills subequal and about 5 times length of saddle segment. Saddle dark brown and incomplete. Ventral brush with 6 unpaired and 6 paired tufts, latter with 2-3 branches distally and 4-5 branches proximally, and unpaired tufts with about 8-9 branches. Seg. I: seta 1(2-4), 2(1), 3(1-2), 4(7-9), 5(2-3), 6(2-4), 7(2-3), 9(1-2), 10-13(1). Seg. II: seta 0(1), 1(1-2), 2(1), 3(7-9), 4(1), 5(1-2), 6(2), 7-8(2-3), 9-12(1), 13(8-10). Seg. III: seta 0(1), 1(5-7), 2(1), 3(2-3), 4-5(1), 6(2), 7(3-5), 8(1-2), 9-10(1), 11(2-4), 12(2-3), 13-14(1). Seg. IV: seta 0(1), 1(3-5), 2(1), 3(1-3), 4-5(1), 6(2), 7(3-5), 8(1), 9(1-2), 10(1), 11-12(1-2), 13-14(1). Seg. V: seta 0(1), 1(2-4), 2(1), 3(2-3), 4-6(1), 7(4-6), 8-10(1), 11(1-3), 12(1-2), 13-14(1). Seg. VI: seta 0(1), 1(2-3), 2-3(1), 4(2-4), 5(1-2), 6(1), 7(3-5), 8(2-4), 9-10(1), 11-12(1-2), 13(6-8), 14(1). Seg. VII: seta 1-2(1-2), 3(2-4), 4(1), 5(1-2), 6(5-7), 7(1), 8(4-6), 9(1-2), 10(1), 11(1-2), 12(1), 13(6-8). Seg. VIII: seta 1(4-6), 2(1-3), 3(8-11), 4(1), 5(2-4). Seg. X: seta 1(1-2), 2(7-9), 3(1), 4a-f(6), 4g-l(6).

¹ Very occasionally no such spine.

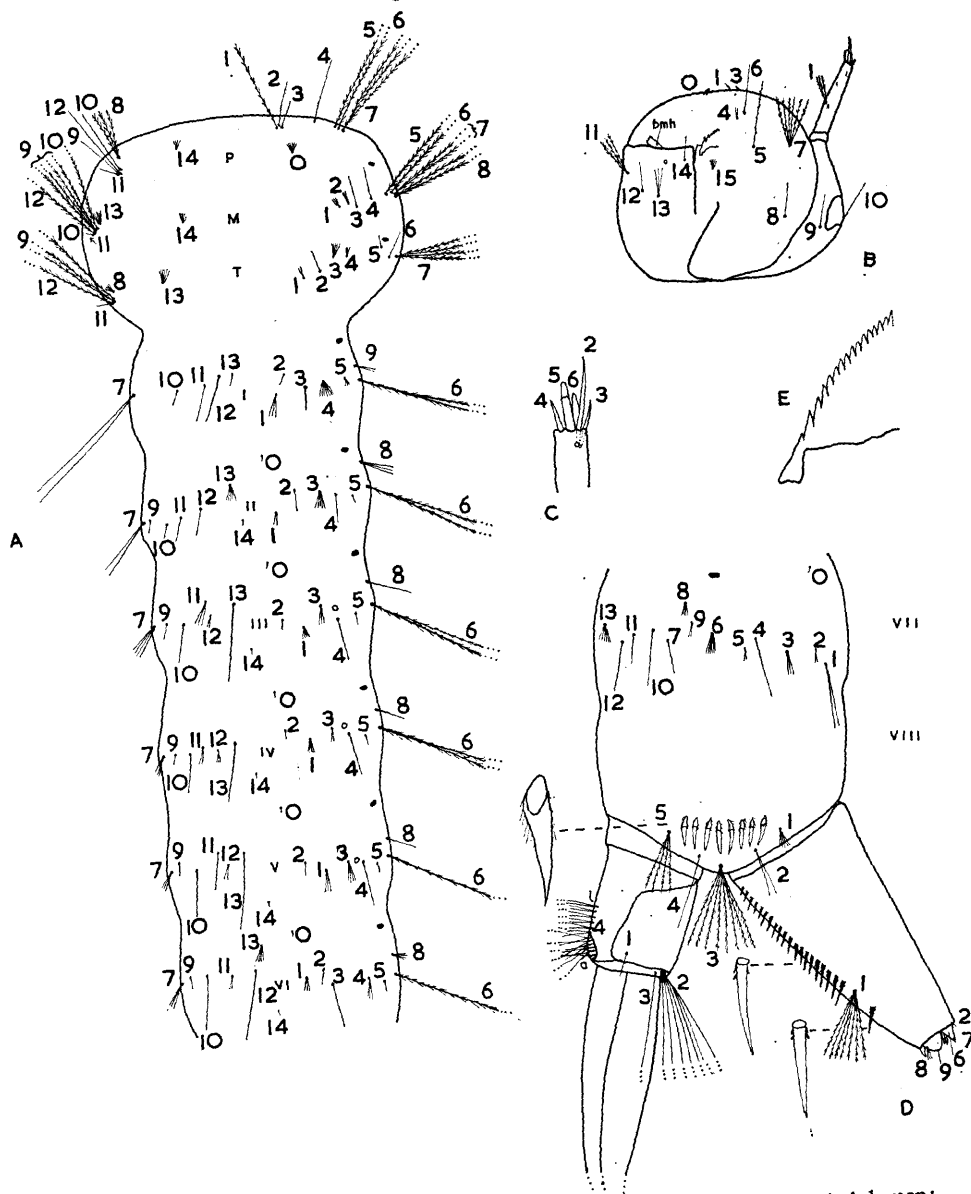


FIG. 13.—Chaetotaxy of fourth instar larva of *Ae. vittatus*: (A) thorax and abdomen; (B) head; (C) tip of antenna; (D) terminal abdominal segments; (E) one side of mentum.

Pupae

(Based on 28 specimens; fig. 14)

Cephalothorax.—Pigmentation light brown, darker areas occur surrounding trumpets and on metanotum. Tracheoid part of trumpets very light brown, pinna darker. Tracheation extends entire length of meatus, pinnae sharply conical and with a deep opening about 0.5 as long as pinna, slit absent. Trumpets about 2.8 times as long as median width, ratio of length to tracheoid: meatus 1.9 ± 0.1 . Seta 1(1-2), 2(1-3), 3(1-2), 4(1-3), 5(2-5), 6(1-2), 7(1-3), 8(2-3), 9(1), 10-11(1-2), 12(1-3).

Abdomen.—Pigmentation pale but darker areas occur on anterior median parts of first few segments, particularly on segment 11; in general pigmentation becomes progressively paler on posterior segments. Hairs 8 and 14 appear to be absent from segment 11. Paddles very pale, outer margin

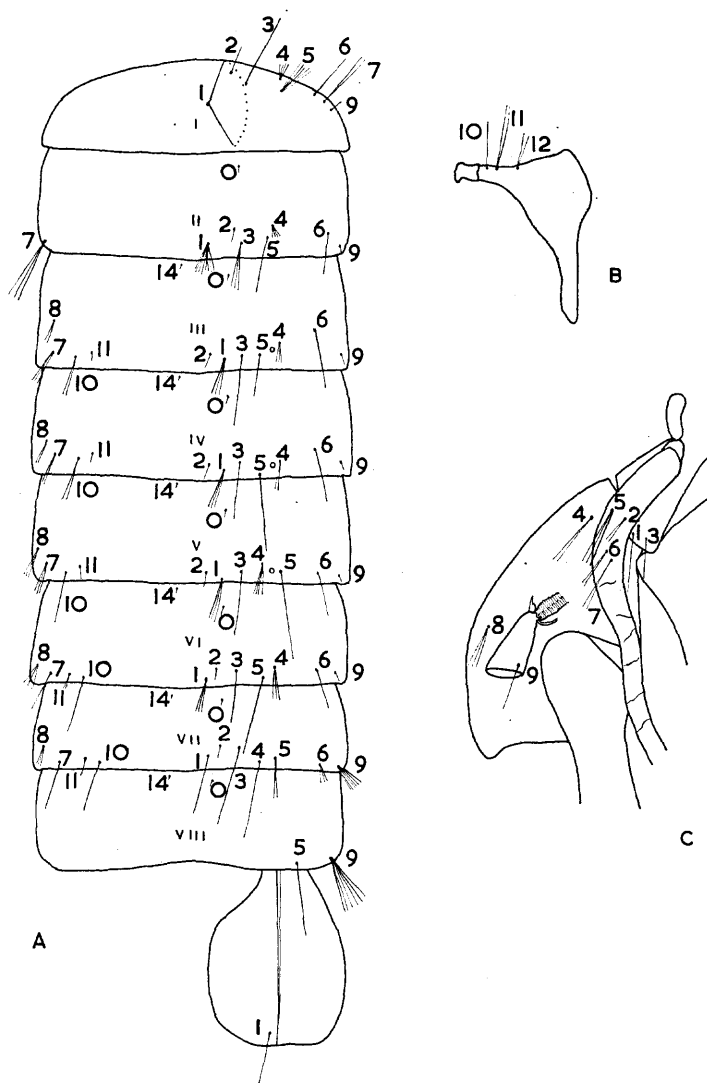


FIG. 14.—Chaetotaxy of pupa of *Ae. vittatus*: (A) abdomen; (B) metanotum; (C) one half of cephalothorax.

weakly sclerotised and very finely spiculate for about 0.54–0.73 of its length, inner margin very faint and without spicules. Mid-rib weakly sclerotised and very finely spiculate. Ratio of paddle length to greatest breadth 1.02 ± 0.04 . Male genital lobes darker, extending to 0.77 length of paddles and very finely spiculate over much of both ventral and dorsal surfaces (based on 12 specimens). Female lobes dark as in male and extending to about 0.41 length of paddles, very finely spiculate dorsally in the centre (based on 16 specimens). Hair 3 of abdominal segment III usually single, but in one specimen was split into 4 branches (no specimens were seen in which it had 3 branches). Seg. I: seta 1(12–21, dendroid), 2(1–3), 3(1–2), 4(4–6), 5(5–7), 6(1–3), 7(2–3), 9(1–2). Seg. II: seta 0(1), 1(7–11), 2(1–2), 3(2–3), 4(4–7), 5(1–2), 6–7(1–3), 9(1–2). Seg. III: seta 0(1), 1(3–5), 2(1), 3(1–4), 4(3–5), 5–6(1), 7(1–3), 8(3–5), 9(1), 10(1–2), 11 and 14(1). Seg. IV: seta 0(1), 1(2–4), 2(1), 3(1–2), 4(2–3), 5(1–2), 6(1), 7–8(2–4), 9(1), 10(1–2), 11(1–3), 14(1). Seg. V: seta 0(1), 1(1–3), 2(1), 3(1–2), 4(3–5), 5(1–2), 6(1), 7(3–6), 8(2–4), 9(1), 10–11(1–2), 14(1). Seg. VI: seta 0(1), 1(2–3), 2(1–2), 3(1), 4(1–3), 5(1), 6(1–2), 7(1), 8(2–4), 9(1), 10–11(1–2), 14(1). Seg. VII: seta 0(1), 1(1–3), 2(1), 3–5(1–2), 6(3–5), 7(1–2), 8(3–5), 9(4–7), 10(1), 11(1–2), 14(1). Seg. VIII: seta 0(1), 5(1), 9(7–10). Seg. X: seta 1(1).

Adults

(Based on 30 specimens, unless otherwise stated; figs. 15-16)

Female

Head.—Eyes black, narrowly separated behind, narrow margin of white scales adjacent to eyes on vertex and continuous in front with frontal tuft, which is composed of long narrow white scales. Vertex with decumbent curved brown-black scales, erect scales black. Two dorsolateral patches of white decumbent scales behind eyes. Clypeus with lateral patches of white scales. Palps 0.4 mm. long, about 0.21 length of proboscis, black scaled below, upper surface with band of white scales about one-third from base and apex broadly pale. Antennae 1.7 mm. long, about 0.85 length of proboscis, torus with many white scales on inner and outer surfaces, first flagellar segment with scattered white scales. Proboscis about 1.9 mm. long, may be totally black scaled or have in the middle a band of varying width or whitish scales, better developed ventrally than on dorsal surface. (An examination of 177 adults showed that in only 9.6 per cent. was the pale band present; there were large monthly variations in the proportion having the pale band, but no difference in the incidence of those with it in the wet and dry seasons.)

Thorax.—Integument of scutum varies from dark brown to black in different specimens. Ground colour of scales usually dark brown, occasionally black, and a few adults have light brown scales; distribution of areas of white scales as illustrated in figure 15, a few scattered, isolated, narrow white scales also occurring on dorsum. Acrostichal, dorsocentral and prescutellar bristles all well developed. Scutellum covered on all three lobes with broad white scales, but a few black ones may be present on apex of middle lobe. Broad white scales are present on anterior pronotum (*apn*), propleuron (*pl*), posterior pronotum (*ppn*), subspiracular area (*ss*), postspiracular area (*ps*), upper (*ust*) and lower (*lst*) sternopleurae and upper mesepimeron (*ume*); lower mesepimeron (*lme*) devoid of scales; paratergites (*ptg*) usually appear nude, but in a few specimens narrow white scales are evident. Number and percentage occurrence (in parentheses) of pleural bristles: *apn*—13 (90), 12 (6), 11 (4); *pl*—7 (63), 6 (26), 5 (11); *ppn*—7 (100); *ps*—6 (72), 5 (28); *ust*—17 (80), 16 (9), 15 (11); *lst*—7 (62), 6 (10), 5 (28); *ume*—11 (72), 10 (18), 9 (10); *lme*—4 (100). Wing about 2.6–3.7 mm. long, scales of veins dark brown-black, but at extreme base of costa a few broad white scales present. A few scattered white scales often but not always present on costa and vein 1, and may extend to as far as one-third from wing root. Halteres with stems devoid of scales and knob white-scaled. *Fore leg*: coxa and trochanter with scattered white scales, femur mainly dark but white scales at extreme base, and anterior face with scattered white scales, a distinct narrow band of white scales one-fifth from apex, apex narrowly pale, posterior face as for anterior surface but with a few more scattered white scales; tibia dark-scaled except for a few white prebasal scales and a narrow band at

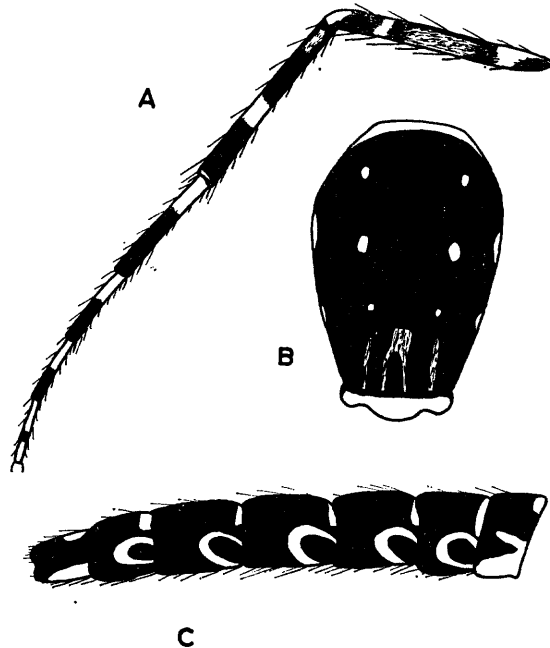


FIG. 15.—Adult female of *Ae. vittatus*: (A) hind leg; (B) scutum; (C) lateral aspect of abdomen.

about one-third from base continuing round to posterior face, which is otherwise dark; tarsal segments 1-3 with white apical bands about 1.5 times as long as broad, segments 4 and 5 all dark. *Mid-leg*: coxa and trochanter with scattered white scales, femur with base narrowly white, scattered white scales on anterior surface and a narrow band of white scales one-fifth from apex, which is narrowly pale, posterior face much as for anterior face; tibia dark except for a few scattered prebasal white scales and a narrow white band of scales one-third from base continuing on posterior face, which is otherwise all dark; tarsal segments as for fore leg. *Hind leg* (fig. 15): coxa and trochanter with numerous white scales as in mid-leg, femur extensively white-scaled from base to just prior to a narrow band of white scales situated one-fifth from apex, which is narrowly white, posterior surface mainly white-scaled on basal half, distal part mainly dark-scaled; tibia with 2-4 white prebasal scales, broad band of white scales about half way from apex, which has a white spot anteriorly, posteriorly surface as in mid-leg; tarsal segment 1, with basal one-third white, segment 2 with basal one-third to one-half white, segment 3 with basal half white, segment 4 with basal three-fourths white, and segment 5 all white. Fore and mid-tarsi with claws strongly developed.

Abdomen.—All dark scales black, not brown, cerci dark. Tergite 1 black, but narrow white central band extending to near apical margin, tergites II-VI with narrow white basal bands of scales, tergite VII with a central area of broad white scales extending to about one-third of segment. Lateral aspects of tergites I and VII with white markings, other segments with distinctive loops of white scales (fig. 15). Sternites I-VI with lateral and central areas of white scattered scales, sternite VII with 2 median longitudinal white lines of scales extending from base to near apex.

Male

General appearance as for female. Palps about 2.5 mm. long and 1.1 length of proboscis when stretched out straight, last 4 segments (II-VI) with conspicuous white broad basal bands of scales about as wide as long. Proboscis about 2.3 mm. long, and in 146 specimens examined completely black. Antennae about 1.8 mm. long, 0.76 length of proboscis. Genitalia as in figure 16. Style a very characteristic shape, being greatly expanded apically in horizontal plane, covered with narrow scales dorsally and some minute setulae ventrally. A small number of minute sensillae near base of terminal appendage, which is strongly curved and devoid of setae. Basal lobe along inner edge with small spines which are curved along the basal corner, scattered setae near inner edge, very fine setae present on outer area. Paraprocts without any ventral arm, tergite IX concave. The phallosome with about 14 coarse well developed teeth.

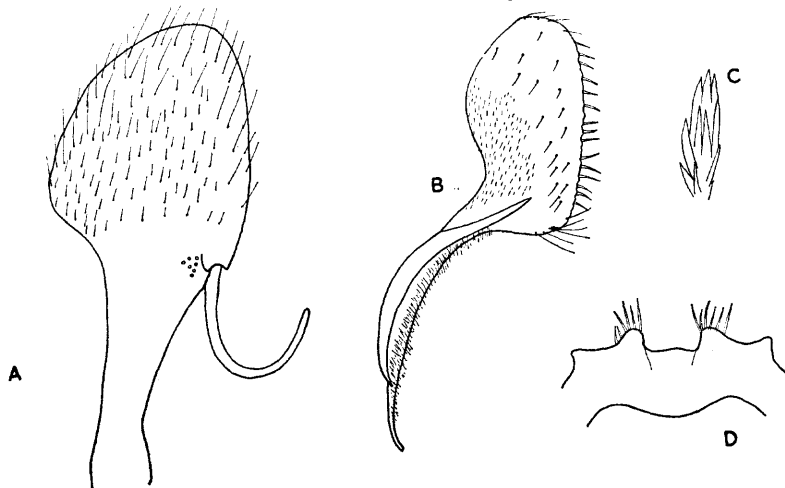


FIG. 16.—Male terminalia of adult *Ae. vittatus*: (A) style; (B) basal lobe of paraproct; (C) phallosome; (D) ninth tergite.

Taxonomic note

Despite careful examination no trace of hair 14, which is admittedly minute, could be found in the first instar larvae. The transitory abdominal hairs, 9 and 13, which are absent from first instar larvae, but which appear in either second or third instars, were both first found in the second instar. The dorsal sensilla on abdominal segments III-V first appeared in the second instar larvae. As found by Mattingly & Knight (1956) and also by Muspratt (1956), the antennae of the fourth instar larvae

are not always spiculate as was supposed by Hopkins (1952), who used the presence of spicules as a diagnostic character in his larval keys; even when they are present, they may be very difficult to locate. Mattingly (1965) mentions that there are "often 1-2 pecten teeth distal to the subventral tufts" of fourth instar larvae; in the specimens examined by the author, except when there was no such spine, there was always one spine after the tuft. It is of interest to note that Hopkins (1952) described the larvae of *Ae. vittatus* twice (Mattingly, 1965), the description on page 178 being mistakenly given as that of *Ae. minutus* Theobald.

Mattingly (1965) used a different nomenclature (Belkin, 1962) from that used here for his figure of the pupa of *Ae. vittatus*, but, with the exception of seta 7 the numbers of the setae mentioned in this paragraph are the same in both systems. In general the abdominal chaetotaxy of the pupa agrees with that given by Mattingly (1965), but the positions of setae 4 and 5 on segment 1 are reversed, on the same segment one of the more lateral hairs is labelled as 8 whereas in the present work it is identified as seta 9, and hairs 1 and 2 on segment VII also have their positions reversed. Mattingly identifies the paddle hair as seta 7 (which on the present nomenclature would be seta 9), whereas in the present account it is identified as seta 1. Finally he does not illustrate setae 0 and 14.

There is relatively little variation in the adults, apart from the intensity of the black scaling on the thorax and abdomen and in the degree of pale scaling on the proboscis. Mattingly (1965) states that this pale scaling is variable, but does not refer to any specimens in which it is completely absent; an examination of adults from N. Nigeria, however, showed that it was absent in most instances. A few white scales were observed on the paratergites of a few specimens, but most had this pleuron bare; it is of course possible that they were rubbed off.

(3) *Relation to Other Species of Aedes*

Ae. aegypti and *Ae. vittatus* are the only species of *Stegomyia* that have scales on the adult clypeus, and Mattingly (1957) considered that *Ae. vittatus* was the most primitive surviving member of the subgenus. In considering the origins of *Ae. aegypti*, closely related forms such as *Ae. vinsoni* Mattingly and *Ae. mascarensis* MacGregor provide valuable clues. There are, however, no closely related species to *Ae. vittatus*, and no hybrids, either natural or experimental. The curious style of the male genitalia is most nearly matched by that of the Ethiopian species, *Ae. (Stegomyia) pogonurus* Edwards, although *Ae. (Stegomyia) desmotes* (Giles) from the Indo-Malayan region shows some slight resemblances. The numerous branches of the unpaired tufts of the ventral brush of the larvae, the spiculate antennae and the stout development of seta 5 (C) of the head capsule are characters atypical of the *Stegomyia*, but are similar to those of some *Aedimorphus* species. The characters separating the other eight groups within the *Stegomyia* are not so marked as those that distinguish group D, and in many respects *Ae. vittatus* occupies an intermediate position between these two subgenera. However, without a critical comparison of the phylogeny of the other subgenera and species, little useful purpose would at present be served by creating a new monotypic subgenus for this species.

(4) *Observations on the Past and Present Distribution of Ae. vittatus*

Ae. vittatus could have evolved either in Africa south of the Sahara and invaded the southern zone of the Palaearctic region, or have originated in the southern area of the latter region and with the advent of adverse climatic conditions (e.g. a glacial epoch during the Pleistocene) have been pushed southwards into Africa, at the same time managing to maintain itself in a few scattered localities in the southern Palaearctic. This second hypothesis seems the less likely, as *Ae. vittatus* is not very common in any region of the Palaearctic and is only known from a few localities, although there

appear to be large areas with climatic conditions favourable to its existence. Furthermore, there are very few species of *Stegomyia* in the Palaearctic, the most successful subgenus being *Ochlerotatus* Lynch Arribálzaga, whereas in the Ethiopian region the *Stegomyia* are better represented than elsewhere. Its presence in North African countries such as Algeria, Morocco and Tunisia, and in the Palaearctic, is probably due to its extension from the wetter areas of central Africa during an earlier wet period. With the advent in Africa of a dry period, *Ae. vittatus* was probably eradicated from most of North Africa, but remained as a relic of a bygone age in its present localities.

The principal larval habitats of *Ae. aegypti* are containers, usually man-made (Christophers, 1960), and its widespread distribution is most likely due to its synanthropic habits. However, even this "cosmopolitan" species has not extensively invaded certain areas, such as the Oriental geographical region. In India it is mainly coastal, and it has only comparatively recently begun to spread into inland areas in Malaya (MacDonald, 1956; Reid, 1954). In contrast, *Ae. vittatus* has specialised larval habitats (rock-pools) but after *Ae. aegypti* is the most widely distributed species of the subgenus, extending from a latitude of 30° 51' S. (Margate, Natal) to one of about 43° 50' N. (Hérelt, France), and in addition occurs in inland areas in the Oriental region. It might have been supposed that its specialised larval habitats, which tend to be localised, would have hindered its distribution. Mattingly (1954) considered that its distribution was at least partly geological in Africa, but in Nigeria and most other coastal West African countries there are no apparent geological barriers. It extends from the coastal Mangrove swamps, where early-recent Tertiary deposits such as sands, sandy clays and saline Mangrove silts predominate, to the semi-arid Sudan areas of the extreme north, where loose sands, clays and shales of the Cretaceous-recent Tertiary periods occur. Admittedly, it may be more common in areas where the geology favours the formation of rock-pools, such as those where pre-Cambrian Basement Complex rocks are present.

The limits of the extension of *Ae. vittatus* into the northern hemisphere are probably now climatic, with temperature as the most important limiting factor. Laboratory experiments have shown that the larvae are adversely affected by temperatures of about 12°–15° C., lower temperatures causing high mortality, and that eggs die after prolonged exposures to temperatures below about 10° C. Figure 17 shows its distribution in relation to the January and July 10° C. isotherm for the northern and southern hemisphere, respectively. An examination of meteorological data (Meteorological Office, 1958) shows that considerably lower temperatures (0.5°–2.8° C.) than 10° C. occur during the winter months in the northern part of its range. Evidently *Ae. vittatus* occurs, but is not necessarily common, in areas where the minimum temperatures fall below 10° C. in winter. Eggs of *Ae. vittatus* hatch mainly on the second and third soakings; therefore, where there is heavy precipitation in the winter hatching would be initiated, even if temperatures were unfavourably low. The resultant larvae might be killed by the low temperatures, or the rate of development retarded, making the immature stages very susceptible to periods of desiccation. Even if the species can survive the cold winters at the edge of its distribution, summer temperatures must be sufficiently high to enable the completion of at least one gonotrophic cycle. The occurrence of irregular adverse climatic conditions, such as excessively low temperatures or drought, may be important in the distribution of some species. Such less easily defined phenomena are much more difficult to analyse and correlate in a form that can be compared to the distribution of a species, although in many instances they would probably be more germane than mean climatic values in limiting distribution.

With the limited and crude meteorological data available, it is difficult to correlate with any degree of accuracy the distribution of *Ae. vittatus* with temperature. There is also insufficient knowledge of its biology in temperate areas to justify attempts at

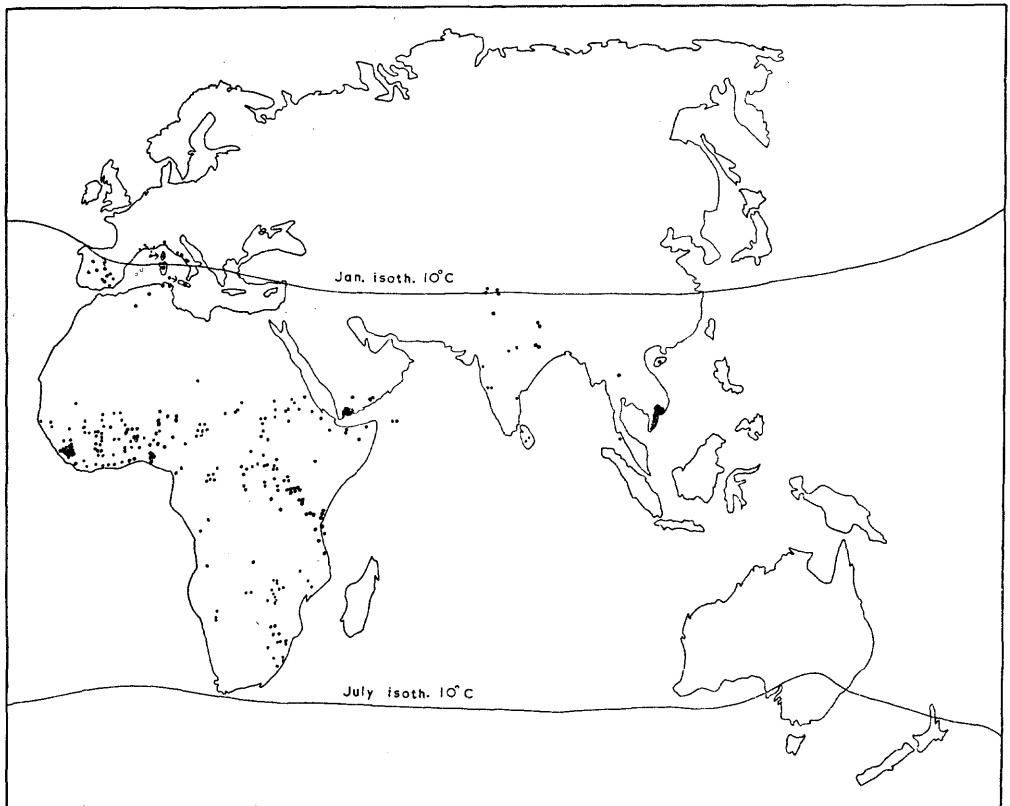


FIG. 17.—Distribution of *Ae. vittatus*; based on Mattingly (1952, 1965) and on unpublished records.

a detailed correlation. Possibly, populations at the edge of its range, such as in the Palaearctic, are more tolerant to cold temperatures than those investigated in Nigeria. Clinal variations are known to exist in mosquitoes, and some of these are probably associated with temperature (Mattingly, 1962). Alternatively the phenomenon of acclimatisation may play a part.

It seems logical to surmise that, as *Ae. vittatus* principally breeds in rock-pools which very often occur in isolated groups, there is in many instances probably little gene flow within the species, and that in some areas the populations consist of distinct demes. Such isolation favours the selection of populations exhibiting genetical, morphological or behavioural differences, but comparative ecological and taxonomic studies are needed for these small differences to become apparent. There have been no such studies on *Ae. vittatus* from different parts of its distribution range, but some divergencies in its behaviour are apparent in the readiness of adults to bite man in some areas of Africa and not others. Also, Freyvogel, Hunter & Smith (1968) and Freyvogel & McClelland (1969) have recently shown differences between the isozymes of esterase and alkaline phosphates of Italian and Rhodesian populations.

VI. SUMMARY

1. The ecology of *Aedes (Stegomyia) vittatus* (Bigot) was studied mainly during 1960–63 in the Kaduna area of the Northern Guinea Savannah of Nigeria.
2. Eggs collected from the field and given various soakings in the laboratory, hatched mainly after the second and third soakings; none hatched after the sixth.
3. Temperatures recorded in the rock-pools showed maxima ranging from 38°

to 42.5° C. in the mud during the dry season and 46.5° C. in the water during the rains. Laboratory experiments showed that the LT 50 after one hour's exposure was 44.1° C. for eggs, 40.6° C. for fourth instar larvae and 43.8° C. for pupae. Eggs, fourth instar larvae and pupae were killed after two days' exposure to 8°–11° C. and below, but little mortality resulted from exposure down to 15° C.

4. The minimum time in the field from egg hatching to adult emergence was six days. Most larvae pupated at night, maximum pupation occurring between 2400 and 0100 hours local time. The shorter time taken by male larvae to complete their development resulted in an initial predominance of male pupae and the emergence of males about a day earlier than females. In the laboratory larvae and pupae survived 2–3 days on damp mud.

5. Field and laboratory studies showed that the most effective predators of the larvae and pupae were tadpoles belonging to a frog of the genus *Rana*.

6. No adults were caught when a Magoon trap was baited with goats, sheep, monkeys and a pig; porcupine was the most important host in the area. *Ae. vittatus* has a relatively short crepuscular biting period, with maximum activity between 1800 and 2100 hours local time.

7. Attempts to establish a colony of the species in the laboratory were unsuccessful.

8. The chaetotaxy of all four larval instars and of the pupae is described, and a detailed description given of the adults.

9. In considering the origins and distribution of the species, it is concluded that it probably evolved in the Ethiopian zoogeographical region, and at a later date spread into the Oriental and southern parts of the Palaearctic regions.

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Rock outcrop at Anara Forest Reserve showing water-filled rock pools; 1-8 small pools, I-V large pools.
M. W. Service



Magoon trap in position at the rock outcrop.

M. W. Service

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GENERAL

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Papers of up to 7000 words (10 printed pages, including figures) may be submitted for *Proceedings Series A* (General Entomology) or *Series B* (Taxonomy) at any time. Longer papers offered for publication in the *Transactions*, must reach the Registrar by 1st October or 1st April, the closing dates for papers for the first and second halves of the volume. A reasonable number of line drawings can be accepted and, for the *Transactions*, a limited amount of half-tone work, but the author will normally be required to pay for half-tone work included in the *Proceedings*. Colour work is accepted only by special arrangement.

Papers by authors who are not Fellows of the Society must be communicated by a Fellow.

Papers are not necessarily published in the order in which they are received; those that require little editing are likely to appear earlier than those that involve much.

Manuscripts are considered on the understanding that their contents be not published elsewhere in substantially the same form; if a preliminary announcement relating to the contents of the paper has been published, this must be stated.

Papers must be concisely written; the Royal Society's *General Notes on the preparation of scientific papers* and the *Style Manual for Biological Journals* (published by the American Institute of Biological Sciences) contain much useful guidance.

Manuscripts must be typed, with double spacing, on one side of paper of uniform size, with a left-hand margin of about $1\frac{1}{2}$ inches. Pages should be numbered at the top. The author should retain one copy of the manuscript in its final form.

Titles must be concise and followed by a short descriptive synopsis, indicative of the aspects of the subject dealt with but not summarising the results or conclusions.

Papers must conclude with a short, factual summary, giving the results obtained and the conclusions reached, except when this is clearly superfluous, as in short papers confined to a few taxonomic descriptions. Nothing should be included in the summary that has not appeared in the text.

Papers intended for the *Transactions* must include a table of contents.

More than three categories of headings should be avoided.

Footnotes should be kept to a minimum and preferably avoided.

On at least the first occasion on which a species is cited in the text, the name of its author must be given in full (except for Linnaeus (L.) and Fabricius (F.)).

Tables

Tables, unless very short, must be typed on separate sheets, their approximate position being indicated in the manuscript.

The components of tables must be appropriately headed, and units of measurement given.

Elaborate tables, such as those printed sideways on the page or including vertical rules, should be avoided.

The same data must not be given both in tables and graphs.

References

All references cited in the text (and only these) must be included in a list of references at the end of the paper; but may be given in the text alone when only one or two, as follows: Smith (1936, *Proc. R. ent. Soc. Lond. (B)* 6 : 304); otherwise, citation in the text must be as follows: Smith (1936); Smith (1936 : 156, fig. 3); (Smith, 1936); (Smith, 1936 : 156, fig. 3). Two works published by the same author in one year must be cited as Smith (1936a) and Smith (1936b). Citations in the list of references must be as follows:

IMMS, A. D., 1957, *A general textbook of entomology*. 9th ed. (revised). x + 886 pp. 606 figs. London.

FENNAH, R. G., 1965, New Species of Fulgoroidea (Homoptera) from the West Indies. *Trans. R. ent. Soc. Lond.* 117 : 95-126.

Titles of periodicals must be abbreviated as laid down in the *World List of Scientific Periodicals*, 4th Edition (1964-65).

Titles of works in languages other than Latin, Romance or Teutonic must be given in English translation, the language of the original being indicated. Transliterations, if needed, must be given in accordance with a recognised scheme such as that laid down in British Standard 2979 : 1959.

If a reference has not been consulted in the original or in photocopy, this must be stated and reference made to the version consulted.

Illustrations

The original drawings for all figures must be supplied and must be drawn to a scale that will permit their reduction (preferably by $\frac{1}{2}$ or $\frac{1}{3}$) to an area not exceeding 8×5 inches inclusive of legend. Authors resident overseas are asked to submit photographs of their drawings in the first instance.

Line drawings must be numbered serially (in arabic numerals) throughout the paper. Authors should either group the figures or give an indication of the grouping. Lettering and numbering must be inserted by the author in black ink, and large enough to be legible when reduced. Labelling should be in words, where this is possible without giving an over-crowded appearance.

Plates are numbered serially throughout the paper. Authors should either mount and number the photographs or give an indication of the required grouping.

Graphs designed to be reproduced as line drawings must be presented on plain or on blue-ruled paper. The use of other colours involves additional cost.

The numbering and lettering of plates and figures must accord with the references in the text.

The scale of a figure, where required, must be indicated by a scale line on the drawing itself.

Legends to illustrations must be typed on a separate sheet, and not attached to the figures or incorporated in the text. The approximate position for each illustration must be indicated, preferably in the galley proof.

The author's name and a brief title of the paper must be written on the back of each illustration.

Proofs

Authors should not insert new matter, or correct faults in style or arrangement, at proof stage. Errors of fact may be corrected in galley proof, but authors may be required to pay for any great amount of alteration. When page proofs are submitted, authors should insert cross references but only errors of typography may be corrected.

Reprints

Authors are entitled to receive 25 copies of their papers free of charge, and they or their departments may buy additional copies if ordered before publication.

The Society's publications are copyright.

TAXONOMY

Papers must conform with the International Code of Zoological Nomenclature and with the published Opinions of the International Commission on Zoological Nomenclature.

A new taxon must be referred to its position in a recognised system of classification, *e.g.* by giving differences from the most closely related taxa.

The description of a new genus must be accompanied by the definite fixation of a type species, for which the term "genotype" must not be used.

The names of taxa proposed for the first time must be followed by the abbreviation *gen. n.*, etc., as appropriate. Replacement names for junior homonyms must be followed by the abbreviation *nom. n.* (The expression *nomen nudum* should not be abbreviated.)

The name of a taxon newly elevated or lowered in rank should be followed by *stat. n.*

When a species is transferred to a genus to which it has not been assigned before, the abbreviation *comb. n.* should follow the first citation of the new combination.

When the synonymy of two or more names is established for the first time, or when doubtful synonymy is fully established, the abbreviation *syn. n.* must be added to the junior synonym.

The author must make clear his intentions regarding the treatment of doubtful species, *e.g.* if there is insufficient evidence to prove the identity of two species, this should be clearly stated.

Types that have been examined by the author should be indicated, preferably in the synonymy.

An author's name, when cited, must follow the name of the taxon without any intervening punctuation. If a species or subspecies is transferred from its original genus, the author's name must then be placed in parentheses.

The name of a subsequent user of a scientific name must be separated from that of the original author by a semicolon.

If misidentifications are cited in synonymies they should be clearly distinguished, preferably by a clear statement of misidentification and not by use of the term "nec".

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original descriptions are to be designated paratypes. The complete data of the holotype and paratypes, and the collection(s) and institution(s) in which they are deposited, must be recorded in the original description. In the presentation of data, larger geographical divisions should precede the smaller (with latitude and longitude of lesser known names) and be followed by the host (if any), date of capture, captor's name (in parentheses) and depository, *e.g.*:

Holotype ♂, BRAZIL: Amazonas, Manaus, on cactus, 6.vii.1938 (*A. Smith*), British Museum (Nat. Hist.).

Paratypes: 2 ♂, same data as holotype, in British Museum (Nat. Hist.); 1 ♂, 2 ♀, BRAZIL: Amazonas, Recife, 1° 28' S., 48° 24' W., 15.vi.1939 (*S. Gonzalez*), author's collection.

When the individuals of a species are not sexed, they must be recorded as 1 ex., 2 ex., etc.

The symbols ♂, ♀ etc. should not be used in cursive text.

Keys should preferably be constructed in couplet form, rather than with the contrasting alternatives separated.

Where detailed treatment of the taxon is given at some distance from the page in which it occurs in the key, the page reference should be inserted in the key after the appropriate name. When the key is a long one, and the sequent couplets are widely separated, the page reference to the second alternative should be inserted after its number.