STUDIES IN RELATION TO MALARIA.

II.

THE STRUCTURE AND BIOLOGY OF ANOPHELES
(*Anopheles maculipennis*).

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(*From the Pathological and Morphological Laboratories of the University of Cambridge.*)

(*Continued from page* 484, *Vol.* I.).

Resting Position of the Imago.—Geographical Distribution of the Species.—Habitat.—Modes of Dissemination and Migratory Flights.—Hibernation of the Imago.—Longevity.—Oviposition, and the Influence of Food thereon.—Parthenogenesis.—Numerical Proportion of Sexes.—Number of Generations during a Season.—Food.—Influence of Heat, Cold, Light, Colour, and Sound.—Sense of Smell and Taste.

ALL recent authors (Ross, Grassi, etc.)[1] are agreed that an essential generic difference exists between *Anopheles* and *Culex* with regard to the position assumed by the imago when at rest. Whereas in *Anopheles* the proboscis and body are almost in a line, so that the insect has not inaptly been compared to a brad-awl (Christy), *Culex* presents a hump-

[1] See Bibliography, p. 75, and p. 484, vol. I., this *Journal;* as also at the end of this paper.

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backed appearance, as figured by Waterhouse (Howard, 1900, p. 34), and, apart from this, the axes of the proboscis and body do not correspond, but form an obtuse angle with each other, the proboscis pointing more towards the surface upon which the insect rests. The structure of *Anopheles* is altogether more slender and graceful, and the legs are considerably longer and more slender than those of *Culex*. In both genera the imago rests either upon four or six legs, the more frequent position being the former, the hind pair being held so that the tarsal joints are elevated and, especially in *Culex*, curved upward. In *Anopheles* the tarsi may be slightly turned upward, but usually they are straightened, the bend being at the femoro-tibial articulation. In a box in which the insects are confined we have frequently opportunities of observing a peculiar rotatory motion of the hind legs, whose function would appear to be largely tactile. When approached by a flying insect the hind legs are used to push away the intruder, and when in search of food the hind leg appears not infrequently to guide the insect. This was especially seen when the insects were fed upon banana or sugar and milk, for in walking about, if the tarsal extremity of the hind leg touched upon a moist surface, the insect immediately turned round and proceeded to feed. Judging from their extended position whilst flying the hind legs doubtless act as balancers. As far as we are aware, Ross was the first to draw attention to the habit of "standing on its head" which characterises *Anopheles*, although we now know that different species behave somewhat differently in this respect, some pointing away at a greater angle from the surface than do others. Sambon and Low (1900) have criticised the statement of Ross and Austen (1899) that the position of the genus *Anopheles* is characteristic, *i.e.* "practically at right angles to the surface," on which it is resting, for they found *A. maculipennis* resting at but a slight angle, *A. superpictus* rested at most at an angle of 45° when the hind feet were raised, whilst *A. pseudopictus* held its body almost at right angles. Gray (Dec., 1900, p. 1820) of St Lucia observed *A. albitarsus* to rest at an angle of 45°, and Christy (1900, p. 1821) has found three out of four species of *Anopheles* in Bombay to assume the position described by Ross. The statement by Sambon and Low, that the "resting position of mosquitoes loses all importance" is therefore misleading. The position is distinctly an aid in recognizing the members of the genus, even if they rest at but slight angles to the surface. In any case Waterhouse was right in the terse statement, "Whatever may be the attitude of *Anopheles*, it is all in one line. *Culex* is angular, humpbacked." In *Culex*, moreover, the abdomen may be parallel to the surface, or its extremity may be directed toward the surface, and owing to its shorter legs its body hugs the surface more closely than that of *Anopheles*.

In the case of *A. maculipennis*, Howard (1900, p. 31) finds that when it rests on a vertical wall its body stands at an angle of 10° to 20°, at times at 30° to 40°, sometimes almost parallel, in the latter case a hind or middle leg being not infrequently broken off. In our observations made on males and females we have noticed the fly resting on vertical surfaces at angles corresponding to those given by Howard. When hanging from a horizontal surface, the angle measured 50° to 70°. When resting on a horizontal surface, the body was nearly parallel, slightly elevated posteriorly (10° or less) or even slightly depressed.

Geographical Distribution of A. maculipennis.

In the paper by Nuttall, Cobbett and Strangeways-Pigg (*Journ. of Hygiene,* vol. I., p. 5) it is recorded that *A. maculipennis* has been found in England, Wales, Scotland, Ireland, Scandinavia, Germany, Austria, Russia, Holland, Denmark, Italy and the adjacent islands, Canada, and the United States. Howard (June, 1901, p. 113) states that this species is found almost everywhere in the United States, for he has seen specimens from the States of New Hampshire, Connecticut, New York, the District of Columbia, Maryland, Virginia, Florida, Texas, Louisiana, Indiana, Illinois, Minnesota, and Oregon, whereas Packard recorded its presence at Brunswick, Maine, in 1861–63. Cropper (p. 49, this *Journal*) has found the species in Palestine.

Habitat.

There is reason to believe that *Anopheles* do not as a rule wander far from their breeding-places, and consequently we shall find the imagines near to those places which we have described as suitable habitats for the larvae (vol. I., p. 70). Some writers have claimed that the distribution of certain species of *Anopheles* coincided with that of human habitations, but this has certainly not been supported by further experience. (See further under Hibernation.)

Modes of Dissemination.

In addition to the data mentioned on p. 8, vol. I. of this *Journal*, with regard to the mode of dissemination of mosquitoes, through winds, trains, ships, and streams we would record the following facts. Howard (1901, p. 20) says he is incredulous regarding the supposed long flights of mosquitoes since he has had occasion in many cases to observe that mosquitoes breed close to localities where their breeding-places had not been suspected. Weeks, of Bayside, Long Island, does not agree with Fernald's observation (cited by us, vol. I.) for he finds many breeding-places in the immediate vicinity of Cold Spring Harbour. Fermi and Lumbao (22 Aug., 1900, p. 180) referring to *Culicidae* in Sassari, state that the females do not travel far because they obtain sufficient food from sucking the blood of man and animals. Howard (1901, p. 17) writes: "In the summer of 1900, Mr W. J. Matheson, living at Lloyd's Neck, Long Island (U.S.A.), a spot formerly infested by mosquitoes to an extraordinary degree, by intelligent exterminative measures succeeded in practically stopping the breeding of mosquitoes upon this narrow neck of land. It resulted that his house was mosquito-free until toward the end of August. Then, after a gentle and continuous wind of two or three days' duration, specimens of another kind of mosquito put in their appearance in large numbers. The explanation was obvious. These mosquitoes had traversed a strip of water forming one of the entrances from Long Island Sound to Oyster Bay, for a distance of a mile or a little more, aided by the gentle and continuous wind."

In the Public Health Reports published by the U.S. Marine Hospital Service (vol. xvi., 9 Aug., 1901, p. 1792) two communications relative to the dissemination of mosquitoes are published by members of the Service. P. C. Kalloch (surgeon) writes from the Gulf Quarantine Station "that the captain of the ship *America*, arriving in quarantine July 24, stated that mosquitoes came aboard the vessel on the previous night, at a distance of at least 10 miles from land, the nearest point being Chandeleur Island. The opinion prevails in this locality that mosquitoes are blown by south-west winds from the Louisiana marshes to this island, a distance of 10 to 20 miles, and the experience of this summer seems to accord with the opinion. Mosquitoes were very few in number until the middle of July, when, after several days of south-west winds, the number was vastly increased. At that time there was no other local condition to explain the sudden increase."

The second communication is one by H. C. Cumming (passed assistant surgeon), regarding the presence of mosquitoes on board the Spanish bark *Maria Blanquer*, which arrived at the South Atlantic Quarantine Station from Rio Janeiro. The master was positive that

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there were no mosquitoes on board until the twenty-second day out, when some were noticed in the water tank when opened. The water had come from Rio Janeiro. The mosquitoes became so numerous on the journey as to constitute a veritable plague, the people on board having to cover themselves to have rest. The U.S. Quarantine officer reports, "When the forecastle was opened, after fumigation, mosquitoes could be scooped up by the hand."

Further instances of the supposed influence of railways in the dissemination of mosquitoes are given by Howard (1901, pp. 25—28), who quotes letters from various correspondents. One of these claims that there were no mosquitoes in the city of Mexico before the railways were built from Tampico and Vera Cruz, mosquitoes being very numerous in both of these low-lying places. Lounsbury, Government Entomologist at Cape Town, wrote that the railway had been responsible for the dissemination of mosquitoes in many parts of South Africa, and another correspondent "gives details of a precisely similar introduction of mosquitoes into a high lying Missouri town." Howard cites an observation at Winchester, Virginia. This place was at one time a favourite summer resort, mosquitoes being almost unknown until the establishment of a night train service during summer at a time when the water-works of the town were extended without provision for adequate drainage. "As a result, with the arrival of the mosquitoes from Baltimore there was a plentiful supply of standing water all through the city, and conditions were thus perfect for the development of mosquitoes in enormous numbers." It does not seem to us that this last case is convincing, for given a suitable supply of water, the local mosquitoes, however small in numbers, would have sufficed for the stocking of the numerous new breeding-places.

Migratory Flights.

Hitherto no migratory flights have been observed in connection with *Anopheles*. In view of the very positive statements of some authors to the effect that the flight of the *Culicidae* is very limited, it seems desirable to cite the following observations recorded by Howard, in which however neither the genus nor species of *Culicidae* involved is mentioned. The conditions which bring about such migrations are unknown. Howard (June 1901, p. 22) cites a personal letter from J. D. Mitchell, of Victoria, Texas, in which that gentleman states that he has twice had occasion to observe mosquito migrations. On the first occasion (October 1879), "A fairly strong easterly wind had been blowing

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for three days; on the evening of the third day the mosquitoes arrived, flying high about fifty feet, and looking like a cloud or mist coming from Carancahua Bay. At the ranch they set everything on fire that had blood in it, and all work was suspended by unanimous consent... little or nothing was done for nearly five days; by this time the main body had passed, though plenty remained to make everything uncomfortable for about two weeks. This migration was from east to west and the line was about three miles wide...." It would appear as if the mosquitoes had originated from a marsh eighteen square miles in extent, situated at a distance of 35 miles as the crow flies. This flight crossed two expanses of water which were respectively five miles and one mile broad.

The second migration occurred from the same place in the year 1886. This time the flight was narrower but denser. "They clouded the sky, bent down the grass with their weight, and made all drift-wood and ground the same colour. All stock left the shore and went north outside the line of marsh. The wind was light and from the south, and did not affect the mosquitoes in their flight, which was westward; the main flight was low, ten or twelve feet high and always in the same direction." The flight lasted almost three days, stragglers being left behind. Enquiries showed that the flight extended over a distance of 50 or 60 miles. This flight crossed four expanses of water, which measured respectively 1, 2, 3, and 4 miles.

Similar migrations have been observed in connection with other insects, scattered observations being found in entomological literature. The phenomenon may possibly be due to the over-stocking of a given locality by a species. It would seem probable that the sound produced by the flight of numerous insects of one species might exert an influence upon the formation of these swarms, for as we shall see later sound plays a very important part in the life of mosquitoes.

Hibernation of Imago.

We have referred already to the seasonal occurrence of the imago and larvae and to the hibernation of the larvae of *Anopheles*, and have seen that apparently only the larvae of *A. bifurcatus* survived the winter in cold climates. Entomologists agree that *Culicidae* hibernate as imagines. Nuttall wrote (1899, p. 111) that Finsch (1876) made observations on the Siberian Tundras which led him to believe that the imago of *Culex* hibernated beneath the moss. "Sterling (1891) saw

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mosquitoes at Mackinaw, Sault Ste. Marie in March, 1844, when the snow, which lay 2 to 4 feet on the ground, was being melted by the sun. The insects appeared in thousands, and bit his party until sundown. Stewart (1891), of North Carolina, saw mosquitoes appear in swarms in March, when several feet of snow lay on the ground. They "literally blackened the banks of snow in sheltered places. These were evidently the insects of the previous summer which were wintering over. The Indians told us that the mosquitoes lived over the winter, and the old ones are the most annoying to them." Westwood (1872–76) noted the hibernation of gnats in his house at Oxford, the insects being troublesome during winter evenings. Wade (1884) saw *Culex ciliatus* Fabr. hibernate in his cellar; Aaron (1890) and Young (1881) have made similar observations.

Grassi (1900, pp. 84—86) says that he has never found the males of *A. maculipennis* hibernating, but only the females, all of these being fecundated. The development of the eggs was retarded by the cold, and advanced with the onset of warm weather, when the female would again begin to bite. The imago was very frequently encountered in houses, stables, chicken-houses, especially in heated apartments. In central and southern Italy they were found to hibernate in cabins and grottos, although less numerous in these situations. The imagines begin to disappear in February, and vanish to a greater extent in March, when at times none are to be found. These insects have presumably flown out, and died after depositing their eggs. He states (p. 47) that but few *A. bifurcatus* hibernate as imagines. A few *A. superpictus* were found hibernating in grottos.

Mr Theobald informed us last year that the imagines of *A. maculipennis* which have hibernated in England disappear early in May, "no doubt to oviposit and then die." We have found this species hibernating in the cellar of a house in Cambridge, and have caught them occasionally during the winter, as has also Mr Verrall at Newmarket (*v.* tables on p. 16, vol. I. of this *Journal*). Annett and Dutton have since (27 April, 1901) reported the finding of hibernating imagines in similar situations in north and mid-Cheshire during the month of February. Howard (1900, p. 12) states that Dr Thayer of Baltimore observed *A. crucians* and *A. quadrimaculatus* (*A. maculipennis*) hibernating in enormous numbers in barns near New Orleans, clustering on the roofs and on the walls. We find, like other observers, that the female imagines live longer in captivity as winter approaches, and it is presumed that such insects would successfully hibernate under natural conditions.

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Longevity of the Imago.

'rom what has just been stated there appears to be no evidence the male imagines hibernate, and this sex has in all probability ch shorter life than the female. Grassi (1900, p. 58) states that he only keep *Anopheles* alive for a month in the laboratory. Howard), p. 11) could only keep *A. maculipennis* alive for eight days in iement during the summer, but Woldert kept them alive for ys on banana alone. In the autumn they lived for 50—60 days nfinement, these being insects which would probably have hiber- . We succeeded in the summer of 1900 (July—August) in ng females alive on a diet of banana and water for 14 to 56 days, ng found essential to keep the atmosphere moist and the food both of which conditions are apt to be neglected. We have also that the females were able to live longer in captivity as winter ached. We have found that unfed males and females, confined diately after their escape from the pupa-case and maintained at 20° C., survived two to three days. That *Culicidae* may survive r unfed is indicated by the observation of Veazie (Howard, 1901, of New Orleans, who found some to survive unfed for five days, as Mitchell in Texas claims that he has seen them survive unfed days. In the last case the conditions of moisture are not stated, o information is given regarding the species, the temperature, nor insect started to fast on a full stomach.

iere is every reason to believe that the imagines may survive longer in their natural state than they do in confinement. We presently refer to the influence of the character of the food upon vity.

Oviposition.

'ith the exception of Kerschbaumer (1901, p. 54) nobody has ed to have observed the process of oviposition and as far as we no one has witnessed copulation. After numerous attempts made en 8 p.m. and 2 a.m., Kerschbaumer found that both *Anopheles* and , at any rate in captivity, only oviposited in the early morning hours. itnessed the process but once in *Anopheles*, thrice in the case of a s of *Culex*. He does not however describe the process (excepting far as he says the insect rested directly upon the water) and what s of *Culex* has already long been known. He found that unfed

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captive *Anopheles* hardly ever seemed to lay a full complement of eggs. A female laid a batch of 146 eggs, and subsequently laid six more. We have already referred (vol. I., pp. 49—51) to the behaviour of the eggs after being laid. Observations upon captive insects have shown that the nature of the food supplied has a considerable influence upon fertilization and oviposition. Thus Ross, Annett and Austen (1900, p. 21) found that if *Anopheles* males and females were placed together and fed on fruit no fertilization nor oviposition took place even after weeks of confinement. The contrary was the case when the females were fed on blood. Fertilized females laid a second batch of eggs after receiving a meal of blood, but did not do so when kept on a fruit diet. Grassi (1900, p. 85) had seen the female of *A. maculipennis* suck blood some hours after oviposition and the insect survived for some days in the laboratory. He thought that the process of oviposition might be repeated several times. Both Grassi and Ross and his colleagues have concluded that blood is essential for the reproduction of the species which they studied. Austen (30 March, 1901) writes, "The experience of the members of the Sierra Leone Expedition of the Liverpool School of Tropical Medicine showed that eggs are laid only by female *Anopheles* which have had a natural feed of blood, and that naturally fed specimens invariably laid eggs after two to three days." Specimens reared from the egg, and kept for some time with males, then isolated in test-tubes and allowed to suck blood, never laid eggs. The inference drawn is that a meal of blood is a necessary preliminary for fertilization. According to the Report of the Expedition, "The following law is likely to hold good for the *Culicidae* which feed on man, at least for the common species:—Although these gnats can live indefinitely on fruit, the female requires a meal of blood both for fertilization and the development of her ova. In other words, the insects need blood for the propagation of their species." It was found that "previously fed and fertilized insects would lay a second batch of eggs after a second meal of blood without a second fertilization, but never laid a second batch of eggs without a second meal of blood," that is, one fertilization sufficed for several batches of eggs, but one meal of blood for only one batch of eggs.

Annett, Dutton and Elliott (1901, p. 37) fed some *Anopheles* on blood, others on banana, varying the conditions of the experiments. They reached conclusions confirmatory of the preceding, viz. that a purely vegetable diet is insufficient for the propagation of the genus *Anopheles*; that blood is necessary for the development of the ova; that blood must be available regularly at least every two days for the

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› develope; that the power of propagation is acquired in a very time from the appearance of the imago, and is vigorous during ıole life of the insect when the latter is fed on blood; that one ;ation by the male suffices for a considerable period of ova :tion. They found that unfertilized fully-developed ova may be l for as long as four weeks by the female.

ıat other conditions may influence oviposition has been shown by ɔft (5 June, 1901), who observed mosquitoes in captivity which ntly did not lay eggs on clean water, whereas they often ovi-ɨ in putrid water. Bancroft does not state to what genus these itoes belonged.

though there can be no doubt as to the necessity of blood for the ;ation of the species under the conditions of the experiments l above, it seems to us quite premature to lay down any law would apply to the life-history of these insects under natural ions. In the above experiments the mosquitoes as a rule appear 'e only had the choice between the banana and blood. The fact ıe insects did not propagate on banana and did on blood does not that blood is a condition *sine quâ non.* Before we can reach such :lusion we must know more about the food which these insects ɘek in nature, and on this point we have very little information. ;he insects, at any rate in limited numbers, frequently have access ɔd is of course clear from the mere fact that they are necessary ɘ distribution of malarial and certain filarial parasites. But this scientific proof of blood being necessary to the propagation of sects. We certainly need exact and further studies upon the l food of the *Culicidae.*

Parthenogenesis.

e only direct reference to parthenogenesis which we have found ; of Howard (1901, p. 4), who states that Kellogg in California ed it in a species of mosquito, the genus of which is not men-. A female insect which escaped from the pupal covering whilst ›tivity almost immediately laid eggs, which hatched out, the almost reaching maturity. "There was no other mosquito in r and certainly no mating." Annett, Dutton and Elliott (1901,), in their Report on the Malaria Expedition to Nigeria, state ome captive *Anopheles* (species not mentioned) were seen to ;s without having been fertilized, but in this case the eggs did .tch out.

Numerical Proportion of Males and Females.

Rees (March 1901, p. 290) states that "When mosquitoes are bred in captivity the males, as a rule, hatch out first, and in greater numbers than the females." We have found no similar statement elsewhere, and the observations we have made do not tend to confirm his observation. The proportion of males to females has always appeared to us to be fairly equal, and we have counted the sexes on several occasions.

Number of Generations during the Season.

Observations made by Italian observers indicate that between three and four generations of *Anopheles* may be developed during a season. Kerschbaumer (1901, p. 85) observed four generations to occur in Austria. The first appeared in April and the beginning of May, the second appeared in the beginning of June and first week of July, the third appeared in the end of July and the first three weeks of August, the fourth between the middle of September and the middle of October. He could find no larvae of *A. maculipennis* after the middle of October. In these cases the number of generations was determined by the finding of young larvae. Basing his calculation upon the assumption that a female may lay 150 eggs, and assuming further that all the descendants lived, he figured that the number of descendants calculated up to the fourth generation would number 31 millions. Our observations tend also to show that about four generations may develope during a season in the neighbourhood of Cambridge.

Food of the Imago.

In view of the enormous numbers of *Culicidae* which occur in certain countries, especially where there are few animals from which they can suck blood, naturalists have hitherto agreed in considering them essentially vegetable feeders. In any case but an infinitesimal number ever have an opportunity of sucking blood, and in the vast majority of cases it would appear that it is but the female which feeds on blood. Dimmock (1881) considered that the male could not suck blood, he wrote, "Upon anatomical grounds I believe that male mosquitoes take liquid food, although I never dissected their stomachs to see what this food was. They have mouth-parts and pharynx developed sufficiently to suck liquids...."

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The statement has been made that a few species of *Culicidae* exist in which the males suck blood. Stiles informed Howard (1901, p. 37) that he was once bitten near Leipzig by what was apparently a male *Culex nemoralis*. We shall certainly gain more knowledge on the subject now that so much attention is being given to this interesting group throughout the world. In the case of *Culex salinus* Ficalbi, it is stated that the male has mouth-parts like the female and that it is capable of sucking blood. It is quite possible in the case of the observation made by Stiles that the insect was an anomaly. Certainly in the case of *Anopheles maculipennis* the female only has mouth-parts adapted for penetrating the skin (see pp. 464—467, vol. I., this *Journal*).

In Nuttall's monograph (1899, p. 113) notes will be found regarding the food of *Culicidae*. Various species have been seen to feed on bananas, melons, and other fruits. Smith, of Rutgers College, New Jersey (Howard, p. 34), has seen mosquitoes (*Culex sollicitans* ?) feeding on wild-cherry blossoms: "So abundant were they that he captured hundreds by sweeping his net over the blossoms." Joly (May 1901, p. 258) says that he has seen mosquitoes rise in clouds from over-ripe mangoes, lying on the ground, as also from bananas and oranges, although they preferred the first. Nuttall states that Murray (1885) saw *Culex* destroy very young trout, the adult insect, as Aaron puts it, "literally sucking out their unsuspecting little brains before they could escape." Combes (1896) made a similar observation on the Island of Anticosti. The mosquitoes attacked the "petits poissons filiformes" and sucked out their heads. When released the little fish turned belly upward and floated on the water, dead. These mosquitoes were also seen to attack an allied species of insect while the latter were issuing from the pupa-case. At this time the fly is still very soft, and it is readily sucked out by the other species which attack it. Howard (1901, p. 34) was informed by Veazie that he had seen *Culicidae* feeding on the soft-skinned pupa of *Cicada*, whilst Hagen in the north-western States saw one feed on the chrysalis of a butterfly. Brakeley informed Howard that he had seen mosquitoes sucking the blood of a black terrapin.

Referring to *Anopheles*, we find that Grassi (1900, p. 84) states that the males never contained food (cap. III.) and that he had never seen male *A. maculipennis* feed. His observations however are not final, for we have repeatedly seen them feed ravenously on bananas, sugared cherries, dried figs, sugar, and milk. Howard (1900, p. 12) states that the males of other *Culicidae* have been also observed to feed, sipping up water, molasses and beer, and Gray of St Lucia (1900) noted that *Culex pipiens* (?) had a predilection for port wine. We see then that it is abundantly established that the male *Culicidae* do feed upon nutrient and even intoxicating fluids.

A number of authors have dwelt upon the importance of *blood* as a normal article of diet for the female *Anopheles*. Speaking of *A. maculipennis* Grassi (1900, pp. 82—83), says that the ordinary food of the female is blood, although Ficalbi has seen them suck up vegetable juices, and even the contents of latrines, and Grassi has seen them feed on unripe maize, water, and sugar and water. He kept them on this diet for a month at 15° to 25° C., but observed that their numbers decreased. He concludes, "In breve si può dire che alle femmina degli Anofeli la dieta vegetale non basta e il sangue è indispensabile." He says that they only appeared to suck the blood of warm-blooded animals, usually that of mammals, exceptionally that of birds, also that they are more attracted to large than to small animals. The same author (1900, p. 1307) mentions elsewhere in a footnote that he has kept *A. maculipennis* alive for a long time (how long, not stated) on a diet of melon. James (1900, p. 535) in India found that he could only keep *A. rossii* and another undetermined species of *Anopheles* alive for 4 or 5 days on a banana diet, whereas if he occasionally fed them with blood they lived for 14 to 18 days. Ross, Annett and Austen (1900, pp. 20—21) saw both the males and females of *A. funestus* and *A. costalis* feed on banana. The female digested a meal of blood in one to three days depending upon the size of the meal. Grassi (1900, p. 84) observed that the female *A. maculipennis* required 10 or more days to dispose of a meal, when the thermometer registered 15° C., but only 40—50 hours in summer-time. Bancroft (5 June, 1901) has found dried dates to be an excellent food for mosquitoes, better than bananas, which he was the first to suggest: "they do not get rotten or even mouldy; and there is no necessity, as with banana, to change for fresh every three or four days; a single date hung in the mosquito cage will serve throughout the experiment however long it may last. Mosquitoes fed on dates live longer, and many species that will not live in confinement more than three days on banana, *e.g.* *Anopheles musivus*, Skuse, *Culex vittiger*, Skuse, thrive on dates and live for upwards of a month." Our observations are in substantial agreement with these.

Rees (March, 1901, p. 292) observed that the *Anopheles* with which he worked bit more readily at times when the hand which was offered them had been previously immersed in warm water. We have had no

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difficulty in persuading *A. maculipennis* to bite in confinement. We have fed them on human blood and by placing a rabbit within the tent in which the insects were confined. They did not feed upon a toad (*Bufo vulgaris*) nor upon a large earthworm although the flies were hungry. A male was seen to feed upon the body juices of a crushed spider. Rose-buds covered with *Aphides* offered a great attraction, doubtless because of the sugary substances present, which were moistened with dew. Both sexes feed ravenously on sugar and milk or sugar and water, the females becoming very fully distended. (See further above under "Oviposition.")

Kept in a suitable vessel of which the atmosphere is sufficiently moist, or in which water or fresh banana is kept and renewed, the female remains alive for a considerable time. Females were kept alive in captivity during the summer (July and August) for two to eight weeks. During this time their abdomens were frequently seen to be distended with banana juice. A number of flies were repeatedly fed with blood. When the temperature ranged between 20° and 26° C. they willingly sucked blood every two or three days. After a full meal the abdomen is greatly swollen and tense. At first the blood gives the abdomen a bright red colour, which changes to a lake as digestion proceeds. (See vol. I., Plate X.). After a full meal or even whilst sucking, a drop of intestinal contents is frequently expelled from the anus.

Effect of Heat and Cold upon Anopheles maculipennis.

We have referred elsewhere to the effect of cold in retarding the development of the larvae (vol. I., p. 69, this *Journal*) and we have seen that they became more active during warm weather, feeding more continuously and growing more quickly. During cold weather it has commonly been observed that the imagines of all the *Culicidae* become torpid, and cease to be troublesome. Insects caught in cold cellars during the winter become active when warmed, and it has been frequently noted that they will then readily suck blood. In other words the *Culicidae* behave very much like other insects with regard to their activity under varying conditions of temperature. The larval forms as we have shown (pp. 451—453) of *A. bifurcatus*, at any rate, may resist degrees of cold considerably beneath zero Centigrade. As far as we know no recorded observations have as yet been made in this respect upon imagines.

Behaviour of the Imago to Light.

The preference of some species of *Anopheles* for dark and shady places has been repeatedly noted by observers in various parts of the world. During the day-time the imagines congregate in caverns, grottos, beneath the shade of trees and bushes, within the precincts of dwellings and barns, beneath bridges, etc. It is true that they have been observed to be present during the daytime, but frequently they are absent except on clouded days. They fly about chiefly towards sunset and until sunrise. We are able to confirm the earlier statements of Grassi in this respect, and similarly Sambon (26 Jan. 1901) writing of *A. maculipennis* which he studied in the Roman Campagna in July and August writes that the imagines appeared "very punctually a few minutes after sunset and disappear again a few minutes before sunrise." We have repeatedly had occasion to watch the insects (*A. maculipennis* and *A. bifurcatus*) we had in captivity observing this rule. When boxes were placed near the window the insects retreated into the shadiest parts and remained quietly resting throughout the day. About the time of sunset a loud buzzing came from the boxes, and the insects promptly fed upon any substances that were present and which they generally neglected throughout the day. At night when confined in a room, tent, or gauze net, they invariably crowded to the side which was illuminated by a lamp, apparently seeking an exit in this way. If confined within a lamp-chimney they fly towards the end which is held towards the light, evidently with the same object. It has been claimed as a matter of common experience in mosquito-ridden countries, that a room can be rid of the insects to a certain extent by keeping it dark and placing a light in an adjoining apartment, the door being left ajar.

However Ross, Annett and Austen (1900, p. 38) state that lights in a room tend to prevent gnats from biting "not by attracting them, as many suppose; but more probably by alarming them."

Colour.

The behaviour of the insects towards various colours has not as yet received sufficient attention. Whilst engaged with experiments upon the influence of shade and colour we came upon a few data cited in the recent literature.

Austen (March 1901, p. 341) writes, "If the walls of the room be white-washed, with a dark dado, it is interesting to note that the

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insects will always be found upon the dark strips, and never on the white portions of the wall." Buchanan (April 1901) in India notes that "The men who collect the living *Anopheles* say that the *Anopheles* hide in a black coat, but avoid a white coat, so they hang up one or two black coats in the Hospital Ward" when they desire to catch the imago. Neither Austen nor Buchanan say anything about the influence of colour. The first as far as we know to refer directly to the influence of colour is Joly (May 1901, p. 259) who made observations on mosquitoes in Madagascar. He states, without saying what genus, that mosquitoes there were more attracted to black than to red soil, or to white sand. Persons wearing black shoes and socks were more bitten than when these articles of apparel were white. Brown clothes protected less than those of white or blue. He states that the natives of Madagascar know the attraction black offers to mosquitoes and for this reason hang up a black cloth on the rafters of the room for the insects to collect upon. Joly observed that a yellow haired dog was very much less bitten than a black one. For the same reason the natives are more bitten than the whites, although they suffer less from the after effects.

It seemed to us to be a matter of considerable practical utility to determine what influence, if any, colour exerted upon a known malaria-bearing species of mosquito. And we deem our results sufficiently striking to make it worth the while for those who are engaged in similar studies abroad to take the matter up systematically. Our experiments certainly indicate that *Anopheles maculipennis* is attracted by some colours and repelled by others, a matter which would have its *practical application in the choice of the colour of clothing and the interior of rooms* in malarious districts. We are moreover inclined to believe that suitably constructed coloured boxes, or *colour-traps*, might be of practical utility in and about houses infested with mosquitoes. By periodically closing the boxes and sweeping out the contained insects into a receptacle, or, possibly by rendering the interior of the boxes sticky a considerable number of mosquitoes might be destroyed.

Our experiments were made in a large gauze tent which had been erected within a disused photographic establishment, the one end of the tent ending against large windows into which the sunlight poured on bright days. Large stone basins were placed on the floor for the *Anopheles* to breed in, the stock being renewed from time to time.

It was noticed at the beginning that when one entered the tent in dark grey clothes, that the imagoes frequently flew up and settled on the dark cloth, but that they never did this when the person entering

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the tent was clothed in white flannels. To test the influence of colour, a number of pasteboard boxes were taken which measured 20 by 16 cm. and had a depth of 10 cm. The boxes were lined with cloth, having a slightly roughened surface, to which the insects could comfortably cling. All of the fabrics had a dull—not shiny—surface, and each box was lined with a cloth of different colour. The boxes were placed in rows upon the floor and upon each other in tiers, the order being changed each day after the observations had been made. The interior of the boxes was moderately illuminated by light reflected from the surface of the white tent. On 17 days during a month beginning with the middle of June, we counted the number of flies which had accumulated in the boxes. Counts were actually made on 17 sunny and cloudy days, and with the following result:

Colour of Box	Number of *A. maculipennis* counted in each box during 17 days.
Navy blue	108
Dark red	90
Brown (Reddish)	81
Scarlet	59
Black	49
Slate grey	31
Dark green (olive)	24
Violet	18
Leaf green	17
Blue	14
Pearl grey	9
Pale green	4
Light blue (forget-me-not)	3
Ochre	2
White	2
Orange	1
Yellow	0
	512

We see from the above table that dark blue was most attractive, the other colours being less and less attractive in the order of numbers given. A marked fall in the number of insects resting in the boxes begins with the "pearl grey" box. Pale green, light blue, ochre, orange, and yellow, especially the last two colours seemed to repel the insects. The karki-coloured uniform at present in vogue should offer advantages besides invisibility to human foes! These observations on colour were described by one of us in a short note which appeared in the *British Medical Journal* (14 Sept. 1901).

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Mr J. Cropper of Mount Ballan, Chepstow, who read the above note wrote to us (17 Sept., 1901): "Seeing your article on Colour Selection by *Anopheles* reminds me that I found the dark navy-blue lining of my tent this summer (in Palestine) extremely attractive to mosquitoes, almost entirely *Anopheles*—and when the sun got hot I always noticed an increase in their numbers, presumably as they came from the herbage and trees near by. No one ever slept in the tent, and I never found *Anopheles* bite in the daytime[1].'

Moreover Dr H. E. Durham has since informed us that whilst he was studying yellow fever at Parà, Brazil, he was much less bitten about the feet than was his late companion Dr Myers. Dr Durham wore ochre coloured socks, Dr Myers black ones[2].

Hearing.

It would appear to be generally accepted that the organs of hearing are situated in the antennae of the *Culicidae*.

In 1855 Johnston, of Baltimore, U.S., wrote: "That these parts themselves are, in some instances, concerned in collecting and transmitting sonorous vibrations, we hold as established by the observations we have made particularly upon *Culex mosquito*; while we believe, as Newport (*Trans. Entomol. Soc.* II.) has asserted in general terms, that they also serve as tactile organs." Referring to the bulbous enlargement at the base of the antennae, and noting their larger size in the male insect, he says, "The space between the inner and outer walls of the capsule, which we term confidently the auditory capsule, is filled with a fluid of moderate consistency, opalescent, and containing minute spherical corpuscles, and which probably bears the same relation to the nerve as does the lymph in the *scalae* of the *cochlea* of higher animals. The *nerve itself*, of the antenna, proceeds from the first or cerebral ganglion, advances towards the pedicle of the capsule in company with the large *trachea* which sends its ramifications throughout the entire apparatus, and, penetrating the pedicle, its filaments divide into two portions. The central threads continue forwards into the antenna and are lost there; the peripheral ones on the contrary radiate outwards in every direction, enter the capsular space, and are lodged for more than

[1] See also p. 54, this *Journal*.

[2] *Note whilst going to press*: According to a newspaper report which we have seen, our experiments have promptly led to a practical application in the United States Army in the abandonment of the regulation shirt of navy blue in favour of white shirts for service in malarial districts where mosquitoes abound.

half their length in *sulci* wrought in the inner wall or cup of the capsule."..."The intra-capsular fluid is impressed by the shock, the expanded nerve appreciates the effect of the sound, and the animal may judge of the *intensity*, or *distance*, of the source of sound, by the *quantity* of the impression: of the *pitch*, or *quality*, by the consonance of particular whorls of stiff hairs, according to their lengths; and of the *direction* in which the modulations travel, by the manner in which they strike upon the *antennae*, or may be made to meet either *antenna*, in consequence of an opposite movement of that part."

"That the male should be endowed with superior acuteness of the sense of hearing appears from the fact, that he must seek the female for sexual union either in the dim twilight, or in the dark night, when nothing save her sharp humming noise can serve him as a guide." He also notes that the male mosquito is more difficult to catch. The coloured plate which accompanies the interesting contribution gives a very fair representation of the head of a male *Culex* and of the structures under consideration.

An important paper in this connection is that of Mayer (1874) who was familiar with the publication of Johnston. He cemented a male *Culex* with shellac to a glass slide and placed it beneath a $\frac{1}{5}$ objective. He then "sounded successively near the stage of the microscope a series of tuning-forks with the openings of their resonant boxes turned towards the fibrils," and saw that a Ut_4 fork, of 512 vibrations per sec. set certain fibrils in vigorous vibration, whilst others remained comparatively at rest. He measured the amplitudes of the vibrations of the fibrils under the influence of the sound emitted by various tuning-forks. We shall only cite four out of nine such measurements: the Ut_2 fork caused a vibration of ·0042, the Ut_4 fork of ·0504, the Mi_4 fork of ·0126, the Ut_5 fork of ·0168 mm. When the forks were vibrated with lower intensity a corresponding lessening in the amplitude of the vibration was noticeable. Different hairs were seen to vibrate to different notes. He also observed that when the sound came from a direction corresponding to the line continued through the long axis of the antennary hairs that vibration ceased. This led him to suppose that the antennae could register the *direction* whence the sound comes. When he observed the antennae under the microscope he found that vibration ceased, when the hairs pointed towards the source of sound, and on drawing a line in the direction in which the hair pointed, he found that "it always cut within 5° of the position of the source of sound."

"The antennae of the male mosquito have a range of motion in a

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horizontal direction, so that the angle included between them can vary considerably inside and outside of 40°, and I conceive that this is the manner in which these insects during night direct their flight toward the female. The song of the female vibrates the fibrillae of one of the antennae more forcibly than those of the other. The insect spreads the angle between his antennae, and thus, as I have observed, brings the fibrillae, situated within the angle formed by the antennae, in a direction approximately parallel to the axis of the body. The mosquito now turns his body in the direction of that antenna whose fibrils are most affected, and thus gives greater intensity to the vibrations of the fibrils of the other antenna. When he has thus brought the vibrations of the antennae to equality of intensity, he has placed his body in the direction of the radiation of the sound, and he directs his flight accordingly; and from my experiments it would appear that he can thus guide himself to within 5° of the direction of the female."

An attempt which we have made to study the effects of electro-magnetically excited tuning-forks upon male *A. maculipennis* gave unsatisfactory results, this being possibly due to their having been confined for some days in small boxes together with females. We hope however to pursue the subject next season.

Sound produced in Flight.

According to Howard (1901, p. 14) the sound during flight is "apparently produced, as with flies and other dipterous insects, not by the rapid vibration of the wings, but by the vibrations of a chitinous process in the large tracheae just behind the thoracic spiracles. These vibrations are produced by the air during respiration." He furthermore states that the sound produced in its flight is higher in *Culex* than it is in *Anopheles*, adding that "the villain in the play has usually a bass voice."

Our experiments do not support Howard's assertion, with regard to the wing not producing a note, for we have found by cutting off more and more of the wing, that the sound decreased in volume, the note rising progressively. When the wing was cut off quite closely, a very high-pitched note of slight intensity remained, this as we supposed being produced by an internal apparatus such as Howard indicates. It may however be due to respiratory movements which are exaggerated through the efforts at flight, the sound is not produced by the insect in repose. We found that the males gave a higher-pitched note than the females, and that the note was higher in both sexes when they had fed; the greater the meal, the higher the note. Of four unfed females three gave notes within a quarter of a tone of 264 (*i.e.* of 240 to 270 vibrations), the fourth female gave an abnormally low note of about 175 vibrations. Four other females were arranged in the order of the distension of the abdomen by food, the last being largely distended, these gave notes corresponding roughly to 264—281—297—317 vibrations or according to the musical scale, the notes:

Three unfed males gave exactly the same note, viz. corresponding to 880 vibrations  immediately after feeding one gave the note A♯, another which had fed well B♮. The unfed males were more closely concordant than the unfed females, the latter varying over about a semitone. Mr J. W. Capstick, M.A., Fellow of Trinity College, Cambridge, to whom we are greatly indebted for making these ear determinations for us by means of tuning-forks, was not certain that the note given by the males was not one of 440 vibrations. Overtones were obviously strong and it sounded at times as if there were a faint note of 440 vibrations overshadowed by a strong one of 880.

The obvious explanation of the higher note given off by the males is that their wings are markedly narrower and shorter than those of the females. Although a female *Culex pipiens* gave a higher pitched note than a female *A. maculipennis*, we are not at all sure that it was not simply due to the smaller size of the former insect. The male of this species of *Culex* certainly gave a higher pitched note than the female.

But few recent writers refer to the sense of hearing in *Culicidae*. Grassi (1900) states that persons are more liable to be bitten by *Anopheles* when engaged in conversation than when silent. Joly (20 May, 1901) in Madagascar observed that mosquitoes were decidedly affected by music. He states that if he played a stringed instrument all the previously quiescent mosquitoes in the room began to fly about, and if the window were open they flew in from the outside. The same observation was made in the open, in the evenings, whether music was played in the dark or near a lamp. The mosquitoes (genus not mentioned) gathered about the player in great numbers.

Howard (1901, p. 15) was informed by Mr A. De P. Weaver, an

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electrical engineer of Jackson, Miss., that "while engaged in some experiments in harmonic telegraphy, in which a musical note of a certain pitch was produced by electrical means, he was amazed to find that when the note was raised to a certain number of vibrations per second, all mosquitoes, not only in the room where the apparatus was, but also from other parts and from the outside, would congregate near the apparatus and would be precipitated from the air with astonishing force, striking their bodies against the apparatus. He states that he therefore covered a large surface with sticky fly-paper and after sounding the note for a few seconds captured all the mosquitoes in the vicinity. He then devised an apparatus to electrocute them. A section of wire window-screen with the paint removed was mounted on a board and small pins were driven between the meshes, the heads coming flush with the surface of the screen. All the pins were connected together electrically, the whole forming one electrode of the secondary coil of an induction coil, while the wire screen formed the other electrode. An alternating current of high potential was then passed and when the note was sounded the insects precipitated themselves against the screen and were immediately electrocuted. Mr Weaver, unfortunately, does not state whether the males were captured in this way."

In a brief note in the *British Medical Journal* (12 Oct. 1901, p. 1101) Ross states that he has been informed by Mr Brennan, of Jamaica, that he has seen mosquitoes there "respond to such sounds as a continuous whoop or hum," and he goes on to say "I have tried the experience lately, and find swarms gather round my head when I make a continuous whoop."

Our attention has moreover been drawn to a letter by Sir Hiram S. Maxim in *The Times* of October 29, 1901. We herewith quote the essential parts of the letter:

"In 1878 I made and erected an apparatus for lighting the grounds of the Grand Union Hotel at Saratoga Springs, New York, by electricity. The lamps employed were rather large and each was provided with its own dynamo machine. One of the lamps worked something like a telephone and gave out a note the pitch of which corresponded exactly with the strips on the commutator passing under the brushes of the dynamo machine. Some of the other lamps would occasionally give off a musical note, but only for a few minutes at a time. With this one, however, the note was practically constant, and no adjustment of the carbons had the least effect upon it. One evening whilst examining this lamp I found that everything in the immediate vicinity was covered with small insects. They did not appear to be attempting to get into the globe, but rather into the box that was giving off the musical note. Upon a close examination of these insects I found that they were all the same kind—viz., mosquitoes, and, what is more, all male mosquitoes. Although there were certainly 200 times as many female mosquitoes on the grounds as males, I was unable to find a single female mosquito that was attracted in the least by the sound. When the lamps were started in the beginning of the evening every male mosquito would at once turn in the direction of the lamp, and as it were face the music, and then fly off in the direction from which the sound proceeded. It then occurred to me that the two little feathers on the head of the male mosquito acted as ears, that they vibrated in unison with the music of the lamp, and as the pitch of the note was almost identical with the buzzing of the female mosquito the male took the music to be the buzzing of the female. I am neither a naturalist nor an entomologist, still I was much interested in this peculiar and interesting phenomenon. I wrote down a full account of it at the time and sent it to a scientific paper, but it appeared to be too stupid to find a place in that particular publication. However, it now appears that others have stumbled across the same thing. A very interesting experiment may be easily made in the following manner:—Obtain a tuning-fork which gives a musical note as much like the hum of the female mosquito as possible. If you strike this fork within 20 ft. of a male mosquito he will at once turn about, face the music, and erect the two little feathers on his head, something after the manner of a cockatoo."

We have collected here a number of perfectly independent observations made with respect to sound upon various species of *Culicidae* in different parts of the world. It is quite evident that the matter requires careful study, for it is not impossible that the knowledge gained might be ultimately put to practical use.

Smell and Taste.

That insects are often particularly sensitive to odours is a matter of wide experience, and this holds also for such as suck blood. As stated by Nuttall (1899, p. 86) the common flea (*Pulex irritans*) is repelled by the smell of the horse, and this insect as also the bed-bug are attracted or repelled by the body-odour of certain individuals. That mosquitoes are more attracted to certain individuals than to others has been frequently noted, and we know that a variety of odorous substances afford protection against the attacks of these insects. So far practical experience has taught us a good deal about repellent odours, but little about those which *attract*, and it would seem to us distinctly useful if such could be discovered, for combined with sticky substances they might be very useful in ridding rooms of these pests. Of the repellent odours we might mention a few, such as the oils of penny-royal, eucalyptus, peppermint, tar; whilst lemon-juice, kerosene, tincture of pyrethrum, sulphur etc. have also been used to afford protection. Joly

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p. 259) has recently observed in Madagascar that mosquitoes ; not stated) were markedly attracted to dried fish.

e have no knowledge as to the situation of the organs of smell. ıot impossible that odours may be appreciated within the tracheal 1.

e know nothing regarding the sense of taste, but that it exists ;arcely be doubted; it is striking how fond the insects are of solutions.

POSTSCRIPT.

ᴇ to p. 452, (vol. ɪ., this *Journal*) Mr Theobald informs us that the *Anopheles* found at Wye in December (reported upon by Annett and Dutton) were those *ifurcatus*. In his opinion this species always lives through the winter in the form; he has never observed hibernating imagines. We have already cited observations with regard to this species on the page referred to above.

rection to be made on p. 479 (vol. ɪ., this *Journal*). Cross out the sentence s 22—23, reading "The absence of scales......generic importance," and read "Mr Theobald informs us that the abdomen is usually nude of scales, but ay be present in the form of narrow spindle-shaped ones, in some species of *les*. He finds that the abdomen may be densely scaled for example in *roensis* Theo., *A. kochi* Dönitz, etc."

(To be continued.)

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*SERGENT, E. (25 Oct. 1901), Existence des Anopheles en grand nombre dans une région d'où le paludisme a disparu. *Annales de l'Institut Pasteur*, T. XV. pp. 811—816. One map. (Made similar investigations to ours upon the geographical distribution of *Anopheles*. He found *A. maculipennis* and *A. bifurcatus* present in large numbers in districts (Loiret, Seine-et-Marne, Seine-et-Oise) whence malaria has disappeared. He comes to essentially the same conclusions as we did regarding the cause of the disappearance of ague, but in view of the *Anopheles* being numerous he does not think that the disappearance is due to a reduction in the number of insects. See under Celli.)

*Smith, T. (15 Jan., 1901), Note on the occurrence of *Anopheles punctipennis* and *A. quadrimaculatus* in the Boston suburbs. *Journ. of the Boston Soc. of the Med. Sciences*, vol. v., pp. 321—324.

*Stephens, J. W. W., Christophers, S. R. and James, S. P. (Oct. 1901), Note on the occurrence of *Anopheles funestus* and *Anopheles costalis* in India. *Indian Med. Gazette*, vol. xxxvi. p. 361.

(Communication of but a few lines, stating that they have found these two species in India where they had not been hitherto described. They prevailed in the planting districts of the Duars. The "interest of the discovery lies in the fact that they are the two species of *Anopheles* which carry malarial infection in Tropical Africa." They are common in India where blackwater fever is most frequent.)

*Voges (1901), Ueber Mosquitointoxikation. Buenos-Aires, Oficina bacteriologica. Review in *Centralbl. f. innere Med.* 1901, No. 44, p. 1085. (States that Naftalan is a sovereign remedy for effects of mosquito-bite when applied immediately. It allays pain, causes redness to disappear, and prevents swelling. Compares its action to specific bacterial(!) antitoxins.)

*Wasielewski, von (1901), Ueber die Verbreitung und künstliche Uebertragung der Vogelmalaria. *Archiv f. Hygiene*, vol. xli. Heft 1, pp. 68—84. (Experiments upon the transmission of proteosomal infection by artificial inoculation to various birds. Reviews the literature; gives numerous interesting facts; he found, contrary to Koch and Ruge, that infected canaries did not acquire immunity after recovery, but suffered from chronic malaria lasting up to 11 months, very few parasites being present in the blood, their presence being only demonstrated by inoculating the blood into fresh animals.)

*Woldert, A. (2 March, 1901), Cultivation of the Estivo-Autumnal Malarial Parasite in the Mosquito, *Anopheles quadrimaculata*. *Journ. of the American Med. Assoc.* vol. xxxvi. pp. 559—563. 5 Figures. *Also* under the title "Original Specimens of Estivo-Autumnal Malarial Parasites in the Middle Intestine of the Mosquito (*Anopheles quadrimaculata*). *Proc. of the Patholog. Soc. of Philadelphia*, n.s., vol. iv., No. 6, April, 1901.