EXPERIMENTS ON THE DEVELOPMENT OF MALARIA PARASITES IN THREE AMERICAN SPECIES OF ANOPHELES.

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Plates 98 to 105.

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The early results of experiments to determine the susceptibility of *Anopheles punctipennis* to infection with the parasites of tertian malaria have been recorded in two recent articles by the writer (1915–1916). In these it was shown that this species is an efficient host of *Plasmodium vivax*, and in the second article a foot-note was appended stating that it had also proven to be a host of *Plasmodium falciparum*, the parasite of estivo-autumnal malaria.

In the present paper are given further details of this series of experiments in which the susceptibility of *Anopheles crucians*, as well as of *Anopheles punctipennis*, has been established. The information acquired upon the relative susceptibility of these two species together with *Anopheles quadrimaculatus* is also included.

A study of the literature applying to this subject has revealed the fact that an extremely small amount of experimental work has actually been done with the species of *Anopheles* occurring in the United States. The experiments with *Anopheles punctipennis* were contradictory and inconclusive, and, as stated in the previous articles, the impression had become current that it was not a factor in the transmission of malaria. The proof of its efficiency as a host of malaria parasites does not, of course, establish the degree of its importance in the transmission of malaria. This depends as well upon its food habits in relation to man, its prevalence, and distribution.

In regard to *A. crucians*, nothing has been found in the early literature which establishes with certainty the proof of its susceptibility, although it has been included among the efficient hosts by several authors, notably Howard, Dyar, and Knab (1912), and Knab (1913). They refer to the experiments reported by Beyer, Pothier, Couret, and Lemann (1902), as Dupree (1905) undoubtedly does also in accrediting the proof to Couret and Beyer. The statements are evidently based upon a misinterpretation of the report.

The results of the experiments by Beyer and his associates may be summarized as follows: With *A. crucians*, no infections were obtained with tertian parasites in two specimens or with quartan parasites in three specimens, while none were tested with estivo-autumnal malaria. With *A. quadrimaculatus*, one specimen of three became infected with tertian malaria and two specimens of five with quartan. The five fed on blood containing estivo-autumnal parasites were negative. Their incrimination of *A. crucians* as a host of estivo-autumnal malaria was based on epidemiologic considerations.

Mitchell (1907) made the statement that Dupree had shown her the parasites in the salivary glands of three species (*A. quadrimaculatus*, *A. crucians*, and *A. punctipennis*). Dupree himself, however, made no reference to his having obtained infected specimens of *quadrimaculatus* or *crucians*.

Recently Mitzmain (1916) obtained negative results with 219 *A. punctipennis* dissected from 3 to 38 days after multiple bites on individuals whose blood contained varying numbers of estivo-autumnal crescents. One specimen of three *A. crucians* fed on one of the gamete carriers showed an infection.

The susceptibility of *A. quadrimaculatus* was established by the work of Thayer (1900), who obtained positive results with this species for both estivo-autumnal and tertian malaria—(one infected specimen with the former and two with the latter). Woldert (1901) conducted nine experiments with *A. quadrimaculatus*. The first experiment with tertian malaria failed. Fourteen specimens dissected in the following six experiments with tertian were all negative. In the last two, with estivo-autumnal malaria, two positive specimens were found among the seven dissected. Berkeley (1901) succeeded after repeated experiments in inoculating *A. quadrimaculatus* with the tertian parasite. Hirshberg (1904) obtained eight infected *A. quadrimaculatus* in a series of forty-eight fed on five estivo-autumnal gamete carriers. Beyer, Pothier, Couret, and Lemann reported infections in this species after the ingestion of the parasites of tertian and quartan malaria.

A fourth species of *Anopheles* (*A. pseudopunctipennis*), reported from the Southern United States, was found positive for the parasite of estivo-autumnal malaria in experiments by Darling (1910) in the Panama Canal Zone. Out of thirty-one specimens dissected, four were found to be infected. From the small number infected under the most favorable artificial conditions, and because of the fact that relatively few of this species are taken in dwellings, Darling concludes that *pseudopunctipennis* is only slightly concerned in the transmission of malaria.

The importance of the accurate determination of the exact relation of each species of *Anopheles* to malaria transmission has been emphasized by the results of a number of noteworthy investigations, which have shown that the greatest variation in susceptibility exists among the different species of this genus. Some species are entirely immune, while certain species manifest a difference in susceptibility to the different species of malaria plasmodia. Walker and Barber (1914) have given an excellent discussion of these phases of the subject in the introduction to their paper on "Malaria in the Philippine Islands."

EXPERIMENTAL.

The experiments reported below were conducted in New Orleans during the months of November and December, 1915, and January, 1916. The adult mosquitoes of the two species, *Anopheles quadrimaculatus* and *Anopheles punctipennis* were bred from larval material supplied by Mr. D. L. Van Dine, of the Bureau of Entomology, from Mound, La. Since no bred material of *Anopheles crucians* was available, specimens collected in the open were used. A flight of this species into the city occurred at this time and upon examination it was found that only a very small proportion of them had had blood meals. The specimens used for infecting purposes were selected from the ones in which no distention of the abdomen with blood or developed ova could be detected.

The experimental mosquitoes were given but one meal of infected blood. They were fed individually, not in lots as is usually done, so that the fact of their having fed was thus made certain in each case. Before the blood meal and afterwards, the diet consisted of raisins and water. Between the times of the blood meal and dissection, each specimen was kept in a separate container.

In Table I is given a part of the data obtained from the examinations of females of *Anopheles punctipennis* after they had fed on estivo-autumnal gamete carriers. The examinations were made at intervals ranging from 7 to 46 days. In all, twenty-two specimens were fed on two patients. Two specimens were not examined. On one of the patients four feedings were made on different days. Case 514 showed a medium number of gametes in the blood, but since no other species besides *punctipennis* were fed on this case, a satisfactory explanation of the negative results cannot be made.

TABLE I.

Results of Experiments with Anopheles punctipennis and Estivo-Autumnal Parasites.

Specimen No.	Date of feeding.	Date of dissection.	Interval.	Result of examination.		Case No.
				Midgut.	Salivary glands.	
	1915	*1915*	*days*			
602.1	Nov. 13	Dec. 30	47	–	+	511
602.2	" 13	" 15	32	–	–	511
617.1	" 13	Nov. 25	12	–	Not examined.	511
617.2	" 13	—				511
617.3	" 13	Dec. 6	23	–	–	511
618.1	" 13	" 29	46	–	–	511
618.2	" 13	" 27	44	–	–	511
618.3	" 13	" 27	44	–	–	511
612.6	" 22	" 21	29	–	–	511.5
626.1	" 22	" 21	29	+	+	511.5
617.4	" 23	" 14	21	+	+	511.6
618.5	" 23	Nov. 30	7	–	–	511.6
620.1	" 23	Dec. 15	22	+	–	511.6
		1916				
601.1	Dec. 23	Jan. 17	25	–	–	514
601.2	" 23	" 14	22	–	–	514
601.3	" 23	–				514
601.4	" 23	" 17	25	–	–	514
604.1	" 23	" 15	23	–	–	514
606.1	" 23	" 15	23	–	–	514
607.1	" 23	" 14	22	–	–	514
607.2	" 23	" 14	22	–	–	514
610.1	" 23	" 17	25	–	–	514

Total No. dissected.. 20
" " infected.. 4
Per cent " 20
" " " of those fed on Case 511 only.................. 33

In Specimen 602.1, the salivary glands contained only a very few sporozoites. In No. 626.1, one oocyst and one empty capsule were found upon the stomach, and the salivary glands contained large numbers of sporozoites in all the lobes of both sets. In No. 617.4 (Figs. 7, 8, and 14), one oocyst and one empty capsule were present on the stomach. The oocyst showed well developed sporoblasts. The salivary glands of this specimen were heavily infected with sporozoites. In No. 620.1, eight oocysts were counted on the stomach, five of which were placed toward the anterior end of the enlargement of the midgut. Two of the oocysts were in the last stage of development before the release of the sporozoites, and four were large but without visible sporoblasts. The measurement of the latter gave: 47 by 48, 31 by 37, 35 by 40, and 48 by 55 microns. The other two were very small—not over 20 microns in diameter.

In Table II are shown the results of the examination of females of *Anopheles punctipennis* after feeding on tertian gamete carriers. Further details of this series have been given in a previous article (King, 1916).

TABLE II.

Results of Experiments with Anopheles punctipennis and Tertian Parasites.

Specimen No.	Date of feeding.	Date of dissection.	Interval.	Result of examination.		Case No.
				Midgut.	Salivary glands.	
	1915	*1915*	*days*			
612.1*	Nov. 6	Nov. 24	18	+	−	509
612.2	" 6	" 15	9	+	Not examined.	509
612.3	" 6	Dec. 1	25	−	−	509
614.1†	" 6	Nov. 26	20	+	+	509
614.2	" 6	" 13	7	+	Not examined.	509
614.3	" 6	" 13	7	+	" "	509
612.5‡	" 12	Dec. 2	20	+	+	510

Total No. dissected.. 7
" " infected.. 6
Per cent " 85

* Figs. 2, 3, and 4. † Figs. 9 and 11. ‡ Fig. 10.

Table III shows the results obtained with specimens of *Anopheles crucians* fed upon an estivo-autumnal gamete carrier. A total of thirty-five females were fed during a period of 5 days, but this species lived poorly in captivity, and sixteen which died soon after the blood meal were unsuitable for examination. The fact that they were "wild" mosquitoes and not bred, as were the other two species, may account for this high mortality. Seven other specimens which were used in another experiment could not be included in the tabulation.

TABLE III.

Results of Experiments with Anopheles crucians and Estivo-Autumnal Parasites.

Specimen No.	Date of feeding.	Date of dissection.	Interval.	Result of examination.		Case No.
				Midgut.	Salivary glands.	
	1915	*1915*	*days*			
703.1	Nov. 23	Dec. 7	14	–	–	511.6
703.2	" 23	" 16	23	–	–	511.6
703.4	" 23	" 3	10	–	Not examined.	511.6
703.6	" 23	" 13	20	+	–	511.6
703.8	" 23	" 16	23	–	+	511.6
703.9	" 23	" 20	27	–	+	511.6
703.12	" 23	" 9	16	+	Not examined.	511.6
705.8	" 24	" 24	30	–	+	511.7
709.1	" 27	" 27	30	+	+ (?)	511.9
710.2	" 27	" 21	24	+	–	511.9
710.3	" 27	" 26	29	+	+ (?)	511.9
710.4	" 27	" 27	30	+	–	511.9

Total No. dissected.. 12
" " infected.. 9
Per cent " 75

Specimen 703.6 (Figs. 1, 5, and 6), had a very large number of oocysts on the stomach; the number was estimated at 75 after 39 had been counted. These ranged in size from 24 to 50 microns in diameter, the majority probably between 40 and 50. No. 703.8 had a medium infection of the center lobes of the salivary glands (compare Fig. 12). A heavy infection of all the lobes of the glands existed in No. 703.9. Five oocysts were present on the stomach of No. 703.12. Two of these measured 34 by 37 microns. In No. 705.8 a small number of sporozoites were found in the salivary glands. In No. 709.1, one large oocyst, 50 by 60 microns, was present on the stomach. The condition of the salivary glands was such that the presence of sporozoites could not be definitely ascertained. One oocyst measuring 45 microns in diameter was found on the stomach of No. 710.2. In No. 710.3, one oocyst was present on the stomach and the glands seemed to contain sporozoites, but their condition made the diagnosis uncertain. In No. 710.4, one oocyst was seen on the stomach.

Table IV shows the infections occurring in specimens of *Anopheles quadrimaculatus* with tertian parasites, and Table V with estivo-autumnal parasites.

TABLE IV.

Results of Experiments with Anopheles quadrimaculatus and Tertian Parasites.

Specimen No.	Date of feeding.	Date of dissection.	Interval.	Result of examination.		Case No.
				Midgut.	Salivary glands.	
	1915	*1915*	*days*			
349.2	Nov. 2	Nov. 11	9	−	Not examined.	507
351.3	" 2	" 6	4	−	" "	507
352.7	" 2	" 10	8	−	" "	507
352.8	" 2	" 9	7	+	" "	507
352.9	" 2	" 12	10	+	" "	507
365.1*	" 6	Dec. 7	31	+	+	509
365.2	" 6	−				509
372.1	" 6	−				
373.1	" 6	Nov. 16	10	+	−	509
373.2	" 6	" 19	13	+	Not examined.	509
373.3	" 6	−				
347.6	" 12	Dec. 9	27	−	+	510
365.5†	" 12	" 9	27	−	+	510
365.6	" 12	" 13	31	−	−	510
371.1	" 12	−				
373.4	" 12	−				
373.5‡	" 12	Nov. 30	18	−	+	510
374.1	" 12	−				

Total No. dissected.. 12
" " infected.. 8
Per cent " 66

* Figs. 16 and 17. † Fig. 13. ‡ Fig. 15.

TABLE V.

Results of Experiments with Anopheles quadrimaculatus and Estivo-Autumnal Parasites.

Specimen No.	Date of feeding.	Date of dissection.	Interval.	Result of examination.		Case No.
				Midgut.	Salivary glands.	
	1915	*1915*	*days*			
349.1	Nov. 2	Nov. 13	11	–	Not examined.	506
354.1	" 2	" 10	8	–	" "	506
358.1	" 2	" 15	13	–	" "	506
358.2	" 2	" 15	13	–	" "	506
359.1	" 2	–				506
359.2	" 2	" 8	6	–	" "	506
359.3	" 2	" 8	6	–	" "	506
347.7	" 13	Dec. 6	23	–	–	511
350.1	" 13	" 1	18	–	–	511
350.2	" 13	–				
350.3	" 13	" 29	46	–	–	511
350.4	" 13	" 18	35	–	+	511
365.7	" 13	" 28	45	+	–	511
371.2	" 13	Nov. 20	7	–	Not examined.	511
380.1	" 22	–			–	511.5
386.1	" 23	Dec. 14	21	–	–	511.6
390.1	" 23	" 14	21	+	–	511.6
381.1	" 24	" 21	27	–	–	511.7
803.1	" 24	" 15	21	–	–	511.7
381.2	" 26	–				511.8
394.1	" 27	" 22	25	–	–	511.9
396.1	" 29	" 13	14	–	–	511.10
396.2	" 29	" 22	23	–	–	511.10

Total No. dissected.. 19
" " infected.. 3
Per cent " 15
" " " of those fed on Case 511...................... 23

Since no infections resulted from Case 506, the percentage from Case 511 only is shown.

The total number of mosquitoes of the three species examined is too small to permit of very satisfactory comparisons, but the indications of relative susceptibility as shown in Tables VI and VII are of interest. In these only those specimens which were fed on the same gamete carriers have been included. Since the females of

Anopheles crucians were not bred, while those of the other two species were, the results are perhaps not strictly comparable.

TABLE VI.

Comparative Results with Plasmodium vivax.

	A. punctipennis.	*A. quadrimaculatus.*
Total No. dissected	7	7
" " infected	6	6
Per cent "	85	85

TABLE VII.

Comparative Results with Plasmodium falciparum.

	A. punctipennis.	*A. quadrimaculatus.*	*A. crucians.*
Total No. dissected	12	13	12
" " infected	4	3	9
Per cent "	33	23	75

In Table VIII are shown the proportion of gametes to leukocytes in the blood upon which the mosquitoes fed. Case 511 was employed for feeding purposes on several different days extending over a period of 2 weeks. As may be seen from the earlier counts, the numbers of gametes were extremely high.

TABLE VIII.

Comparative Counts of Leukocytes and Gametes Made from Stained Blood Smears Taken at the Time of the Feeding of the Mosquitoes.

Case No.	Species of *Plasmodium.*	No. of leukocytes counted.	Gametes.	Gametes per 100 leukocytes.
509	*P. vivax.*	131	19	14
511	" *falciparum.*	57	300	526
511.5	" "	100	143	143
511.6	" "	200	187	93
511.7	" "	125	171	136
511.8	" "	350	106	30
511.9	" "	350	128	36
511.10	" "	300	56	18
514	" "	281	20	7

The mosquitoes used in the experiments were kept in a darkened, screened box in the laboratory. Temperature and humidity records for the entire period were kept by means of Friez recording instruments placed beside the box. The temperature of this room was usually higher and fluctuated less than the outdoor temperature, and during part of the time the room was artificially heated during the day. The temperature in the laboratory rarely fell below 60°F. On Dec. 28, however, the minimum was 51°, and on the 29th, 49°.

TABLE IX.

Weekly Mean Temperature and Per Cent Humidity (Relative) from November 1, 1915, to January 16, 1916.

Week.	Mean temperature.	Average relative humidity.
	°F.	per cent
Nov. 1–7	76.7	60.3
" 8–14	79.7	65.5
" 15–21	71.6	48.7
" 22–28	73.5	57.6
" 29–Dec. 5	68.5	48.8
Dec. 6–12	72	64.0
" 13–19	68.7	62.0
" 20–26	65.4	54.2
" 27–Jan. 2	64.7	72.2
Jan. 3–9	75	64.4
" 10–16	69.1	51.6

An explanation of the long developmental period of the parasites, as exhibited in these experiments, is undoubtedly found in the temperature conditions prevailing during the time. The length of the sexual cycle is usually given as from 9 to 12 days, but the exact relation of temperature to the period of development has not been carefully ascertained.

SUMMARY.

Since a knowledge of the susceptibility of any species of *Anopheles* to infection with malaria parasites is of great importance in determining its part in the transmission of malaria, the experiments reported here were undertaken, and included the three most prevalent species of this genus occurring in the United States. As a result of these experiments *Anopheles punctipennis* is shown to be an efficient

host of the organisms of tertian and estivo-autumnal malaria, *Anopheles crucians* of estivo-autumnal malaria, at least, and information has been obtained upon the relative susceptibility of these two species and *Anopheles quadrimaculatus.* The latter species has been known to be an efficient host since Thayer's experiments in 1900, and has been considered to be the principal species concerned in the transmission of malaria in the United States.

With *Anopheles punctipennis*, developmental forms of the exogenous or sporogenic cycle of *Plasmodium vivax* were demonstrated in six (85 per cent) of the seven mosquitoes dissected, and the development of *Plasmodium falciparum,* in four (20 per cent) of twenty specimens. These four infections, however, occurred in a series of thirteen specimens fed on one person, so that the percentage was actually 33.

With *Anopheles crucians,* oocysts or sporozoites or both oocysts and sporozoites of *Plasmodium falciparum* were found in nine (75 per cent) of the twelve specimens dissected. No tests were made with this species and *Plasmodium vivax.*

Anopheles quadrimaculatus was employed as a control species in the experiments and became infected in the following ratio: eight (66 per cent) of twelve specimens with *Plasmodium vivax*, and three (15 per cent) of nineteen specimens with *Plasmodium falciparum.*

In determining the relative susceptibility of the three species only those individuals which had fed upon the same gamete carriers are considered. The number of mosquitoes from which the percentages are computed is too small to make the results entirely conclusive, but the indications are that *Anopheles punctipennis* and *Anopheles quadrimaculatus* are equally susceptible to infection with *Plasmodium vivax,* 85 per cent of each species under the same conditions being positive. With *Plasmodium falciparum*, *Anopheles crucians* showed the highest percentage of infection (75 per cent), *Anopheles punctipennis* second (33 per cent), and *Anopheles quadrimaculatus* third (23 per cent).

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EXPLANATION OF PLATES.[1]

PLATE 98.

FIG. 1. Oocysts of *Plasmodium falciparum* in *Anopheles crucians* (No. 703.6).
FIG. 2. Oocysts of *Plasmodium vivax* in *Anopheles punctipennis* (No. 612.1).

PLATE 99.

FIG. 3. Two oocysts of *Plasmodium vivax* in *Anopheles punctipennis* (No. 612.1).

FIG. 4. Five oocysts of *Plasmodium vivax* in *Anopheles punctipennis* (No. 612.1).

PLATE 100.

FIG. 5. Eight oocysts of *Plasmodium falciparum* in *Anopheles crucians* (No. 703.6).

FIG. 6. Ten oocysts of *Plasmodium falciparum* in *Anopheles crucians* (No. 703.6).

PLATE 101.

FIG. 7. An oocyst of *Plasmodium falciparum* in *Anopheles punctipennis* (No. 617.4), showing formation of sporoblasts.

FIG. 8. Same as Fig. 7, more highly magnified.

PLATE 102.

FIG. 9. An oocyst of *Plasmodium vivax* in *Anopheles punctipennis* (No. 614.1). This body contained active sporozoites and was at the point of rupturing.

FIG. 10. The empty capsule of an oocyst of *Plasmodium vivax* in *Anopheles punctipennis* (No. 612.5), after the escape of the sporozoites.

FIG. 11. Two empty capsules of oocysts of *Plasmodium vivax* in *Anopheles punctipennis* (No. 614.1).

PLATE 103.

FIG. 12. A normal salivary gland of *Anopheles crucians*, showing the relation of the three lobes.

FIG. 13. A mass of sporozoites of *Plasmodium vivax* in *Anopheles quadrimaculatus* (No. 365.5). These were expelled from the salivary glands by the pressure of the cover glass.

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[1] The author is greatly indebted to Dr. F. M. Johns for aid in the preparation of the microphotographs of infected mosquitoes, and to Dr. W. S. Thayer of Baltimore for confirmation of his interpretation of several of the preparations.

PLATE 104.

FIG. 14. Sporozoites of *Plasmodium falciparum* in glands of *Anopheles punctipennis* (No. 617.4). (Although a very poor illustration it has been included since it is the only microphotograph obtained of sporozoites in this species of mosquito.)

FIG. 15. Sporozoites of *Plasmodium vivax* in *Anopheles quadrimaculatus* (No. 373.5).

PLATE 105.

FIG. 16. Sporozoites of *Plasmodium vivax* in *Anopheles quadrimaculatus* (No. 365.1). This illustrates the typical clumping in one of the gland cells.

FIG. 17. Same as Fig. 16, more highly magnified.

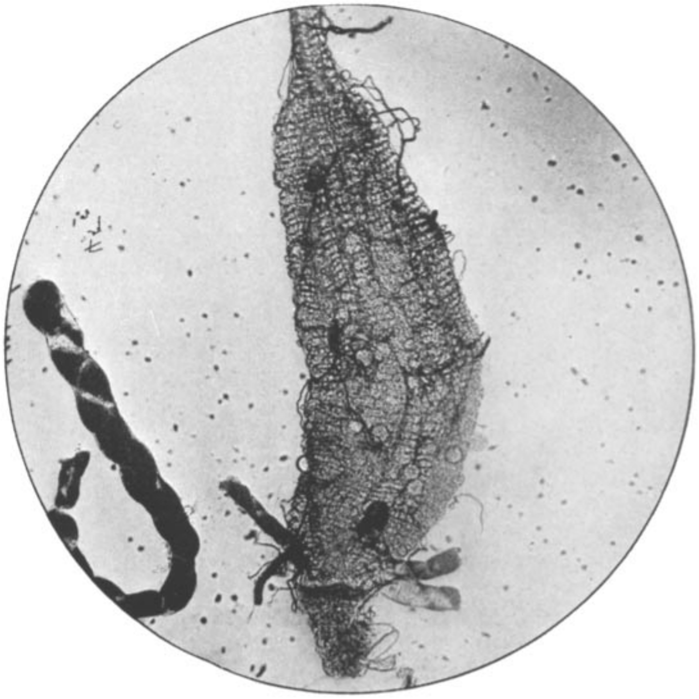

FIG. 1.

FIG. 2.

(King: Development of Malaria Parasites.)

FIG. 3.

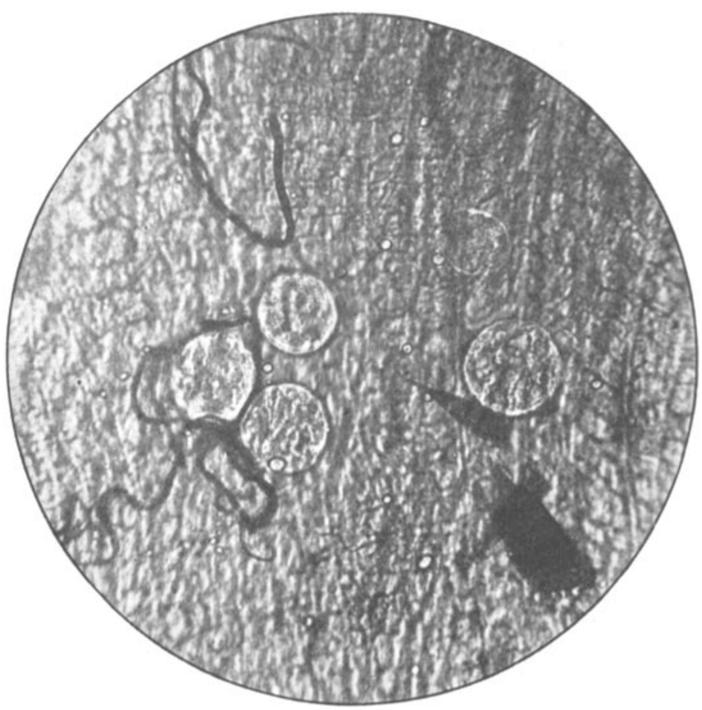

FIG. 4.

(King: Development of Malaria Parasites.)

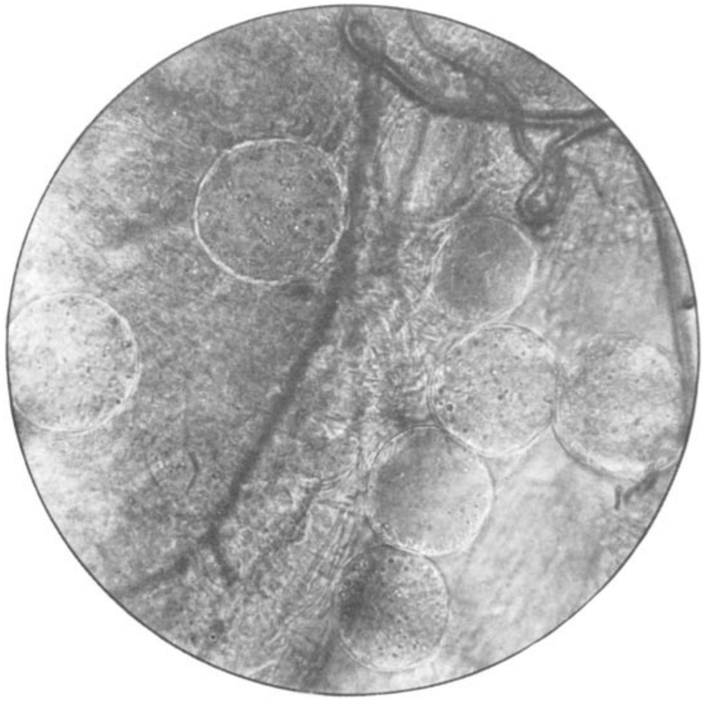

FIG. 5.

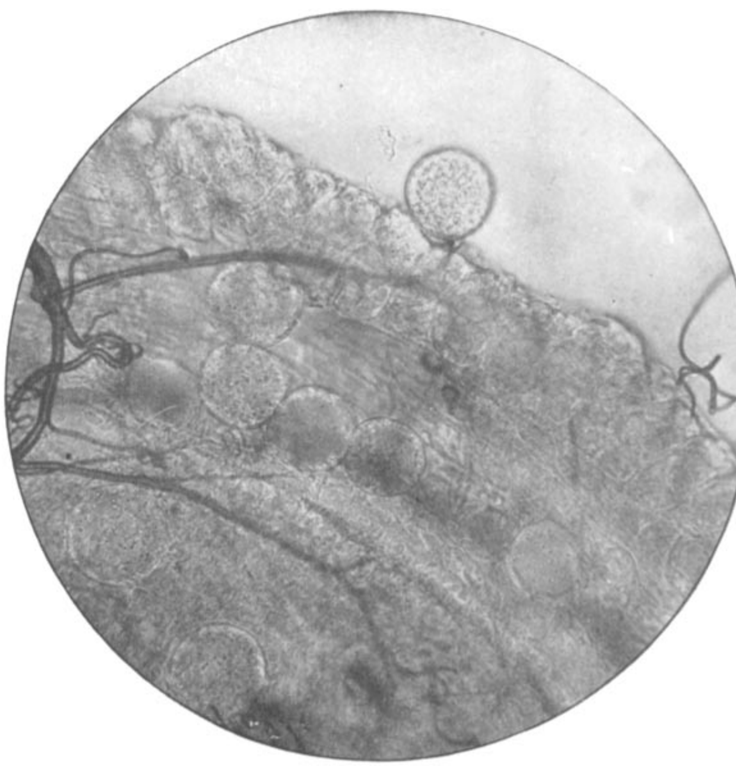

FIG. 6.

(King: Development of Malaria Parasites.)

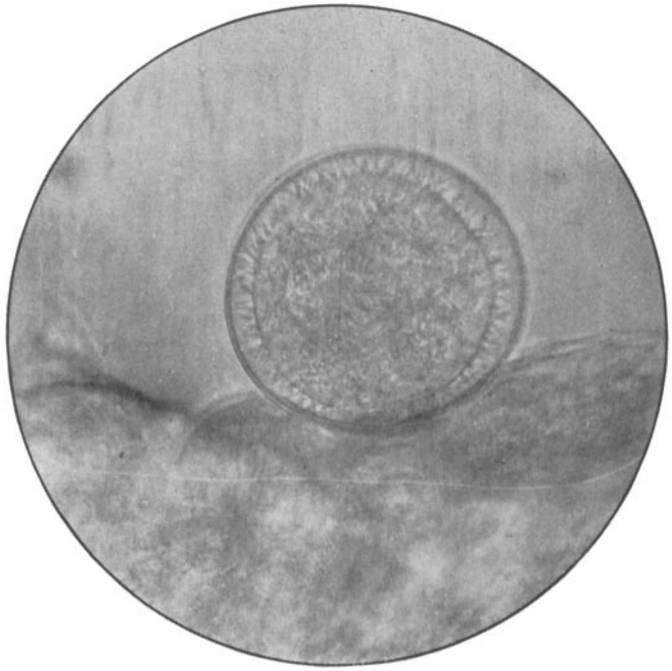

FIG. 7.

FIG. 8.

(King: Development of Malaria Parasites.)

FIG. 9.

FIG. 10.

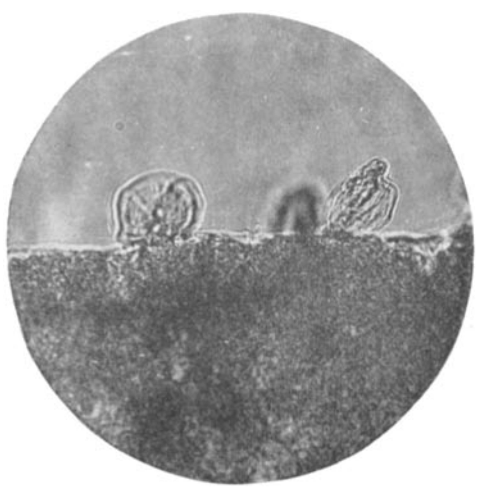

FIG. 11.

(King: Development of Malaria Parasites.)

Fig. 12.

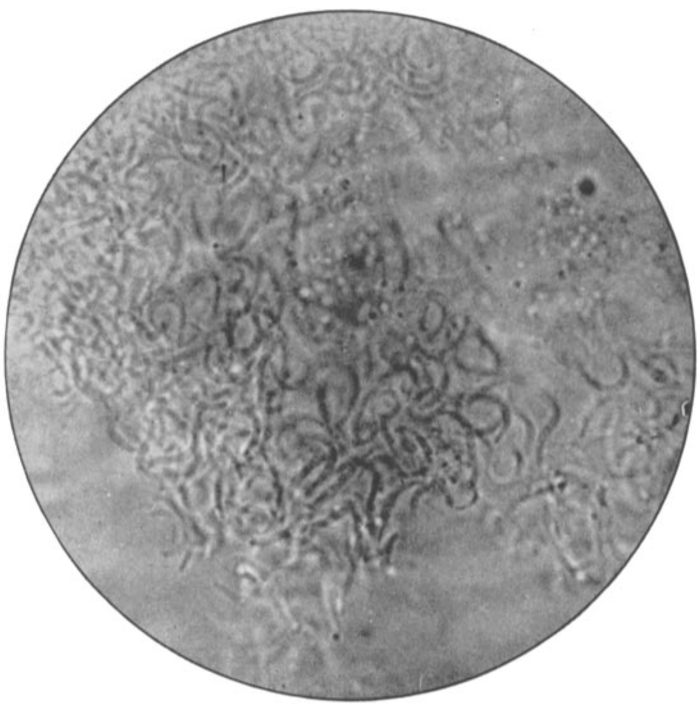

Fig. 13.

(King: Development of Malaria Parasites.)

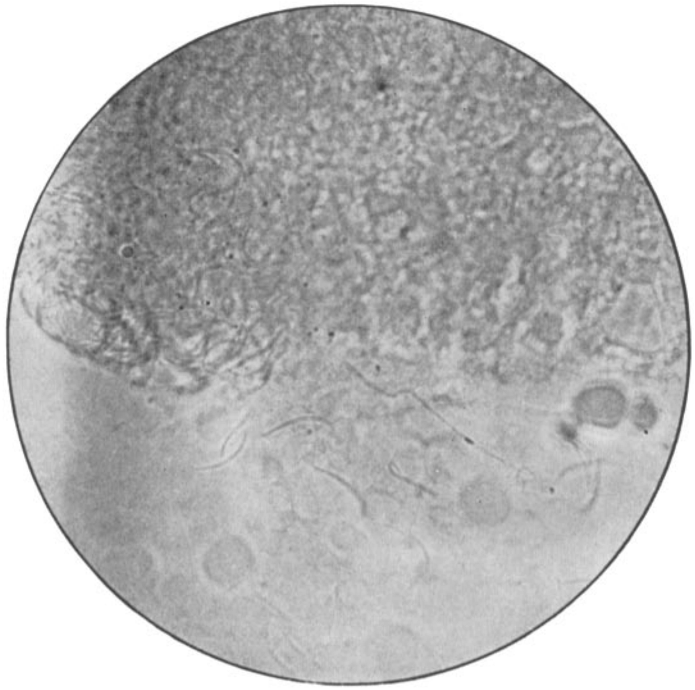

FIG. 14.

FIG. 15.

(King: Development of Malaria Parasites.)

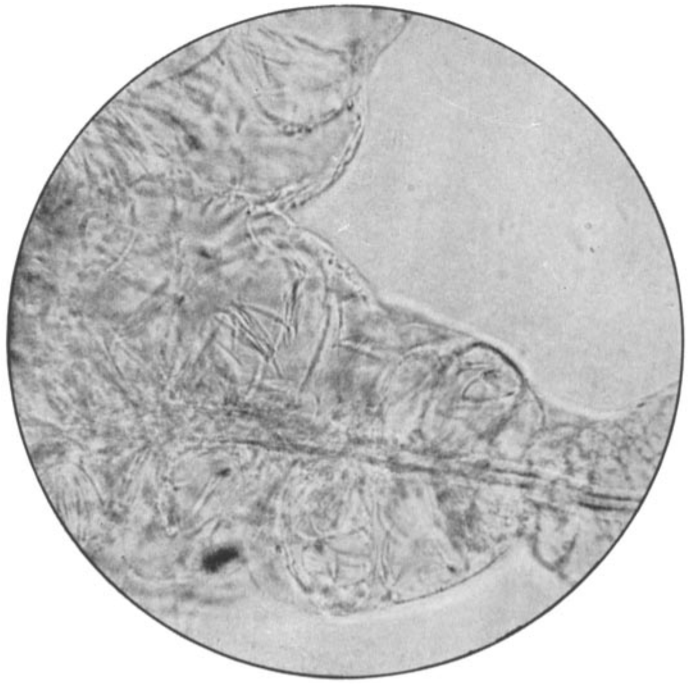

FIG. 16.

FIG. 17.

(King: Development of Malaria Parasites.)