CHAPTER 7

RACES AND VARIETIES OF A. GAMBIAE ANTHROPOPHILY AND ZOOPHILY

Study of A. gambiae var. melas

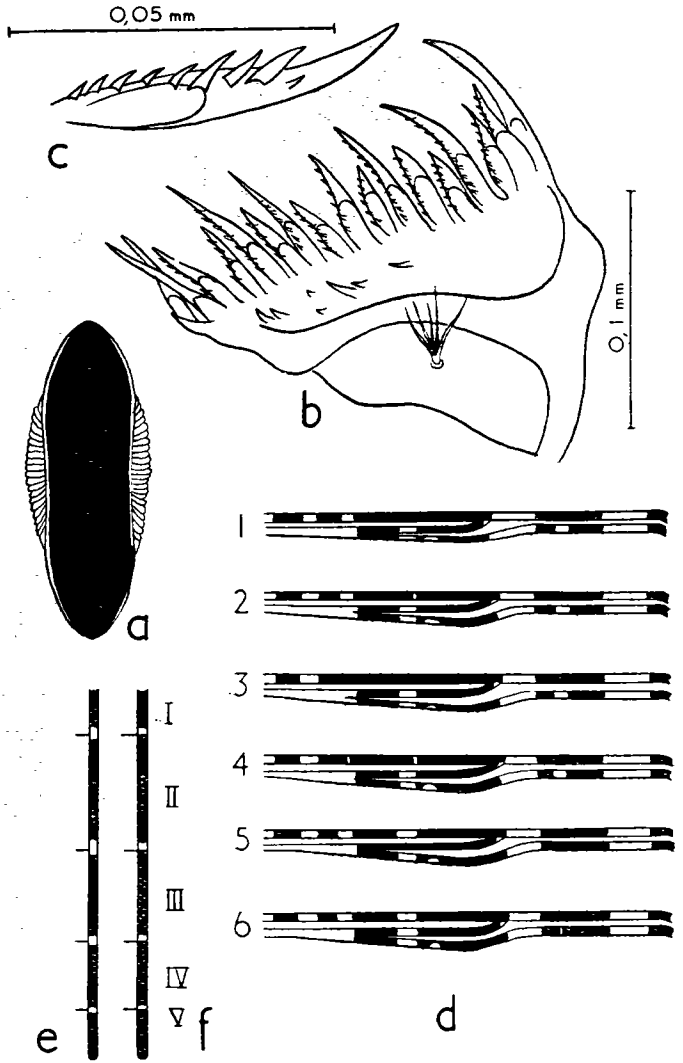
Morphological characters—Differences between gambiae and melas

In the coastal regions of Africa, *A. gambiae* is represented by one variety —*A. gambiae melas*. It is probable that the first specimen described by Theobald,[371] in 1903, as a *gambiae* with a dark integument, with palpi possessing a dark supplementary band, and with reduced ringing on the anterior tarsi and fewer pale spots on the wings, belonged to the variety *melas*. At the same time, Dutton [105] mentioned the discovery of *gambiae* larvae in breeding-places containing sea-water. Although these two observations may not have been connected, most workers agreed with Barber & Olinger [15] and Evans [112] that melanism was associated with development in brackish water, while remarking that the continental *gambiae* was not able to survive in breeding-places which gave rise to *melas*. That this was impossible had already been pointed out by Le Moal,[223] who, having found larvae in marshes with a salinity of 24 g of NaCl per litre, at Dakar, observed that larvae taken from fresh water died when they were transferred to the water of these marshes.

In 1944, Ribbands [289] established that the larvae of *gambiae* and of *melas* showed a clear distinction in the formation of the comb of the VIIIth segment; in *gambiae*, it was composed of groups of uneven teeth of which only the short ones were spiculate, while in *melas*, the teeth were almost equal and all were spiculate with the occasional exception of the two teeth situated at the ends. At the same time, this author [290] showed that, although *gambiae* could not develop in a breeding-place containing more than 11.9 g of NaCl per litre, *melas* completed its cycle in a breeding-place containing 47.6 g, and that there was no correlation between the number of *melas* showing the additional black band on the palpi and the salinity of the water in which the anopheles had been reared (70% of the *melas* could not be distinguished from typical *gambiae*).

Muirhead-Thomson [259] demonstrated an essential difference between the eggs of typical *gambiae* and those of *melas*, the latter being distinguished by the extreme reduction of the distance between the floats and the striated border (fig. 20, **a**). This worker noted that the eggs deposited

FIG. 20. MORPHOLOGICAL CHARACTERS OF A. GAMBIAE VAR. MELAS



a = egg
b = comb of segment VIII, showing supplementary denticles on the body
c = tooth of the comb, isolated
d = variations in wing ornamentation
1 specimen M'Bour 32
2 specimen M'Bour 59
3 specimen Dakar 13
4 specimen Bignona 72
5 specimen Bignona 114
6 specimen Conakry 21
e = anterior tarsus of *A. gambiae*
f = anterior tarsus found in some *A. gambiae melas*

by females with quadrimaculate palpi belonged to typical *melas* and concluded that the *gambiae* females possessing such palpi were, in fact, *A. gambiae melas*. On the basis of these observations he proposed that the variety *melas* be raised to the rank of species, and confirmed his opinion by proving that hybrid males resulting from a *gambiae-melas* cross were sterile.[262] However, cross-breeding carried out in Nigeria showed that males of the F_1 generation were not sterile, matings between F_1 males and F_1 females being fertile, although the eggs deposited did not hatch.[270]

The criterion of quadrimaculate palpi therefore seems to be invalid and to have very little systematic importance. We have already seen (page 41) that, in French West Africa, purely continental *gambiae* may show quite a high percentage of females with four bands on their palpi, and Bruce-Chwatt [52] has pointed this out in Nigeria, noting besides that, in the lagoon area of Lagos, the additional black band was missing in 95% of *melas* identified by the structure of the eggs. Similarly, of all the *melas* that we were able to examine, we verified that, on an average, 25% showed palpi that were typical of *gambiae*.

It seems, therefore, that the distinguishing character seen in the morphology of the egg may be the only one that enables *gambiae* females to be differentiated from those of *melas*. However, at Lagos, Bruce-Chwatt [49] found that a small proportion of the females laid eggs which were of an intermediate type and which could be attributed to neither of the two forms. Such eggs exist in about 3% of the batches and show constant differences in size.[270]

As far as the larvae are concerned, the character of the comb on segment VIII appears uniform. The only variations we have been able to find concern the denticulations on the teeth at the ends, which may or may not be spiculate, and the presence of supplementary denticles on the body of the comb (fig. 20, **b**, **c**).

Attempts to find stable morphological characters which would allow of the differentiation of the adults have not been crowned with success. Bruce-Chwatt [48] has shown that the pharyngeal armatures of the typical female and of the variety are identical in every way. The few males that we were able to dissect showed the hypopygium of typical *gambiae*. We have, on the other hand, observed the association of certain morphological characters in females collected from the Lower Ivory Coast and from Guinea, and in specimens (determined by examination of the eggs after dissection) we have received from Senegal and Casamance.

These characters are the following:

(1) *Wings:* Extension of dark areas and corresponding reduction of the pale spots on the costa, the subcostal vein, and the first longitudinal veins (fig. 20, **d**).

(2) *Palpi :* Quadrimaculate.

(3) *Legs :* Ringing of the anterior tarsi reduced to the apical portion of the segments (fig. 20, **e** and **f**).

The association of the characters observed in various localities and regions is evident from the following figures, which indicate the percentage of *gambiae* showing the characters mentioned :

	Wings	*Palpi*	*Legs*
Bignona (Casamance) . . .	91.8	70.0	83.0
Dakar (Senegal)		90.0	17.0
M'Bour (Senegal)		72.5	74.5
Ivory Coast		71.7	28.0
Guinea	14.0	60.0	80.0

It is therefore clear that the most easily identified *melas* came from Casamance and Guinea. Specimens from Senegal and the Ivory Coast did not show noticeable variations in wing ornamentation.

One must, nevertheless, wonder whether *melas* specimens which display characters (1), (2), and (3) at one and the same time do not merely represent a geographical variety, because the extension of the dark areas on the costa has been found in some females whose eggs have been shown, on examination, to belong to the type-species. On the other hand, none of the *gambiae* that we examined in the coastal districts showed the reduced ringing of the anterior tarsi—a character which appears to be vested in *melas*.

Larval breeding-places

The preference of *A. gambiae melas* for brackish waters confines this species to the coastal zones, where the lagoons and swamps are subject to tidal action. Although known in Nigeria,[15, 49] in Sierra Leone,[259, 289, 290, 380] and in Gambia,[57] where its role in transmitting malaria is as important as that of *gambiae*, until recently, *melas* had not been discovered in the French territories on the west coast of Africa. We were able to demonstrate its presence at Dakar, where it had been suspected, at M'Bour (Senegal), and in the coastal districts of the Casamance. Furthermore, we were able to find larval breeding-places at Conakry (Guinea), and along the coastal line of lagoons in the direction of Portuguese Guinea, as well as at Grand Bassam (Ivory Coast). These larval breeding-places, which are highly characteristic in Guinea, are formed by the swamps of a mangrove, *Avicennia nitida*, and of a grass, *Paspalum vaginatum*, situated behind the belt of the mangrove, *Rhizophora racemosa*, and affected by tides.

The larvae occurred in greater numbers in the swamps containing *Paspalum* alone than in those where this grass was associated with *Avicennia*. In the Ivory Coast, the zone in which we found *melas* consisted of a huge *Paspalum* swamp where the influence of the tides was considerably reduced. The role of *melas* in the transmission of malaria seems negligible in this region, because the species is rare, probably on account of the limited extent of suitable breeding-places. On the other hand, at Conakry, and along the coastline of Guinea, there is a different state of affairs: *melas* can be found there in large numbers, and may be considered responsible for a high rate of endemic malaria.

The amount of NaCl in the breeding-places where *melas* was discovered proved to be very variable: 8.4-27 g per litre at Conakry; 0.3-17.2 g per litre along the coastline of Guinea; 24-53.2 g at Dakar; 0.1-4.89 g at Grand Bassam.

Special features in the biology of the adults

We collected or identified a greater number of *melas* females in outside shelters than in dwellings. Thus, at Casamance, for instance, out of a batch of 48 females identified by their eggs, the distribution of collecting places (November 1949) was found to be as follows:

Dwelling-huts	17
Deserted huts	9
Empty canaris	6
Hollow trunk of a fallen tree	6
Crack in a silk-cotton tree	5
Vegetation surrounding a breeding-place	5

At Dubreka (French Guinea), a minute number of females was captured in dwellings (7 in 4 hours in 32 huts) while 13 females were collected in 2 hours from cracks in trees, beneath pirogues upside down on the banks of the Soumba, and from the midst of vegetation near breeding-places.

These captures show that, in *A. gambiae melas*, there is marked exophily which may explain the difficulties encountered in searching for the adults in houses in towns (Conakry, Dubreka, Grand Bassam). This exophily is accompanied by a high maxillary index (about 15: e.g., 15.1, for the Casamance area, and 14.8, for Guinea), with the number of teeth varying from 12 to 19 per single maxilla, and from 12.5 to 18 per pair of maxillae, the distribution being established as follows:

12.5	2.1 %	15.5	15.4 %
13	1.0 %	16.0	17.2 %
13.5	6.4 %	16.5	9.6 %
14	10.7 %	17.0	4.3 %
14.5	9.6 %	17.5	2.1 %
15	20.6 %	18.0	1.0 %

These characters of exophily and of multidenticulation of the maxillae suggest a tendency to zoophily that our observations on the Soumba (7-8 October 1949) seem to confirm.

On the edge of a boat moored 30 m (approximately 100 feet) away from a swampy uninhabited island, 900 m (984 yards) from the island of Dofili and from the village of Coperaing, and 1,500 m (approximately 1 mile) from Dubreka, between 10.30 p.m. and 1 a.m. (after a wait of some minutes), we caught by lamplight 43 very aggressive females. Collected before they could bite, they were examined on our return to Dubreka, and in 19 of them blood was already present in the stomach. Microscopical examination showed that nucleated red corpuscles (bird ?) were present in one of the blood samples; the remaining 18 lots of stomach-contents were kept on filter-paper, and were later analysed at Bobo-Dioulasso by the precipitin method. No positive reaction was recorded with the antisera then at our disposal—human, bovine, and porcine—which thus demonstrates that it is possible that, in the uninhabited islets of the littoral, *melas* feeds on an animal yet to be determined.

Anthropophilic and Zoophilic Populations of A. gambiae

A. gambiae in uninhabited regions

More and more observations tend to show that the behaviour of *A. gambiae* is subject to considerable variations which often cannot be attributed to climatic differences. Habitually regarded as a typically endophilic (house-frequenting) and anthropophilic anopheles, *gambiae* nevertheless displays in many districts quite opposite tendencies, which allow one to suspect that biological races exist within the species. It is clear that *A. gambiae* occurs in totally uninhabited regions where the only possibilities of feeding lie in the presence of a wild fauna. Dutton & Todd [106] have found this species in deep forest in the Congo, far from any dwelling. Hopkins [179] points out that very many *gambiae* have been collected in the uninhabited valley of Lambwe in south-west Kenya; he refers to the observation made by Chorley who, in deep bush, near larval breeding-places, found females most of which were engorged and entered the tents at 6.30 or 7 a.m. Roubaud (in Marneffe et al.[243]) mentions having been bitten by *gambiae* in uninhabited regions of the Upper Gambia populated only by big game. More recently, Haddow [152] has shown that the relation between the captures of *gambiae* in uninhabited forest in the Bwamba County (Uganda) and the captures made in plantations was 48 to 1. With his colleagues,[154] he was able to collect in the Semliki forest more than 30,000 specimens of this species, which represented 93%

of all the species captured. Finally, Bagster Wilson (personal communication, 1950) told us that he had proved that, in the northern frontier district of Kenya, a large number of *gambiae* were attacking man in places totally devoid of dwellings.

Thus, we have numerous examples of the presence and activity of *gambiae* in the absence of man, examples which allow one to suppose that the species can subsist on the local fauna, and which suggest that, in these observations, we are dealing with a zoophilic race.

Distinguishing characters of gambiae populations

We have already recorded [172] the observations which led us, after examining *A. gambiae* populations originating from Bamako (Sudan), and from Bobo-Dioulasso and its environs, to describe two races of *gambiae*. We based our opinion on the differences it was possible to establish in a certain number of characters—morphological (size, colour of the integument, maxillary armament) and biological (choice of larval breeding-places and behaviour of the adults).

More extensive research has made us abandon the distinguishing characters of size and coloration, which are subject to geographical modifications and cannot be attributed to any racial difference whatsoever, and have proved too inconstant to be valid.

On the other hand, this research has allowed us to extend the study of the maxillary armament and to add the technique of precipitin reactions to our investigation methods. We shall therefore set out the results of the study of *gambiae* populations as a function of maxillary armament, of trophic preferences, of choice of larval breeding-places, and of behaviour (exophily-endophily).

Maxillary index

Studies of the maxillary index, following the research of Roubaud, led him and his colleagues to make a careful investigation into the vector role of the anopheles in the Far East. Roubaud, Toumanoff & Gaschen [315] demonstrated a close relationship between the maxillary index and the power to infect in *A. hyrcanus sinensis*, *A. vagus*, *A. minimus*, *A. aconitus*, *A. jeyporiensis*, and *A. maculatus*; on the other hand, the maxillary index was utilized to distinguish the two varieties, *sundaica* and *litoralis*, of *A. ludlowi*.[317]

The species showing a mean maxillary index of 11 (paucidentate species) were the only vector-species of malaria in Tonkin, those with a high

maxillary index, from 14.2 to 15.6 (multidentate species), playing only a minor role in the transmission of malarial infection.

According to Roubaud : " Faunae showing undifferentiated zoophily are faunae whose maxillary index is not noticeably high, generally less than 14. These faunae are the most dangerous for man, from the point of view of malaria " [307] (page 556).[e]

In tropical Africa, Sautet & Marneffe, after examining *A. gambiae* from the French Sudan, recorded that " the mean [maxillary] index varies between 15 and 17 teeth, the extreme figures being 14 and 19 " [330] (page 355).[f] No precise information on the conditions in which the anophelines were captured accompanies this assertion, which therefore cannot be interpreted. The only other figure available, relating to captures made in human habitations, was quoted by da Cruz Ferreira,[117] who attributed to the species a mean maxillary index of 13, but pointed out the difficulties encountered in its determination.

The two observations available are, therefore, contradictory, the first expressing, but with reservations, a tendency towards zoophily, the second demonstrating a marked anthropophily.

TABLE XXIV. DISTRIBUTION OF THE MAXILLARY INDEX IN FEMALE GAMBIAE

Maxillary index *	Paucidentate *gambiae* (%)	Multidentate *gambiae* (%)
10.5	1.7	—
11	1.5	—
11.5	4.7	—
12	3.1	1.4
12.5	4.7	2.8
13	22.2	1.8
13.5	27.0	5.6
14	8.0	8.4
14.5	20.6	15.1
15	4.7	13.4
15.5	1.8	21.7
16	—	11.5
16.5	—	14.7
17	—	—
17.5	—	2.2
18	—	—
18.5	—	1.4

* Number of teeth per pair of maxillae

Our own research led us to distinguish two populations of *gambiae* with a distinctive maxillary armament (see table XXIV) :

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e " Les faunes à zoophilisme indifférencié sont des faunes dont l'index maxillaire est peu élevé, généralement inférieur à 14. Ce sont les faunes les plus dangereuses pour l'homme, au point de vue malariologique."

f " ... que l'indice [maxillaire] moyen oscille entre 15 et 17 dents, les chiffres extrêmes étant de 14 et 19."

(1) A multidentate population with a mean maxillary index of 15, the number of teeth per maxilla varying from 12 to 19 and, per pair of maxillae, from 12 to 18.5;

(2) A paucidentate population with a mean maxillary index of 13.5, the number of teeth per maxilla varying from 10 to 16 and, per pair of maxillae, from 10.5 to 15.5.

The multidentate *gambiae* came from captures made in the bush, far from any habitation, in bushes, holes in trees, and cracks in the ground, on steep river-banks, on the mosquito-nets that we set up when journeying on our surveys, and finally—and we shall discuss later the explanation of their presence—in dwellings at Bamako and on the outskirts of Bobo-Dioulasso, in October on the one hand, and in September-October, on the other.

The paucidentate *gambiae* were collected in the main built-up areas of the Upper Volta and the Sudan, in human habitations, animal-pens, and various other shelters (ruined huts, wells, vegetation, holes in trees, etc.).

Table XXV gives a résumé of the maxillary characteristics of some of these populations to which we shall refer again when studying trophic preferences (page 134).

Furthermore, from collections made during our surveys or from specimens sent us by the doctors in charge of sectors of the Service général d'Hygiène mobile et de Prophylaxie, we established the maxillary index of *A. gambiae* for a certain number of localities:

	%		%
Abengourou (Ivory Coast)	12.7	Gaoua (Upper Volta) . .	13.8
Bignona (Casamance) . .	13.5	Kolda (Casamance). . . .	12.8
Bouaké (Ivory Coast). . .	13.0	Mamou (Guinea)	12.9
Daloa (Ivory Coast) . . .	12.5	Man (Ivory Coast) . . .	13.2
Danané (Ivory Coast) . .	13.0	N'Zérékoré (Guinea) . . .	13.8
Dédougou (Upper Volta) .	13.4		

A high maxillary index does not necessarily signify true zoophily. Roubaud & Toumanoff [314] have shown that, in *A. maculatus*, *A. kochi*, *A. maculipalpis*, and *A. philippinensis*, "the raising of the maxillary index ... does not imply ... solely and exclusively zoophilic tendencies" (pages 837-838).[g]

That is why it is important to supplement the study of maxillary armament with that of trophic preferences determined by the precipitin method.

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[g] " ... l'élévation de l'indice maxillaire ... ne traduit pas ... purement et exclusivement les aptitudes zoophiles."

TABLE XXV. MAXILLARY ARMAMENT IN VARIOUS GAMBIAE POPULATIONS

Population No.	Date of capture	Place of capture		Mean maxillary index	Number of teeth	
		Locality	Type		minimum	maximum
1	October 1948	Bamako	Dwellings	15.0	13	18
2	September–October 1948	Environs of Bobo-Dioulasso	Dwellings	15.5	12	19
3	December 1948	Grand Bassam	Breeding-place Bs. 13	15.9	14	19
4	August 1949	Subdivision of Houndé	In bush, on mosquito netting	15.2	13	19
5	September 1949	Subdivision of Bobo-Dioulasso	In bush	15.0	13	18
6	September 1949	Subdivision of Bobo-Dioulasso	In bush	14.8	12	17
7	October 1949	Subdivision of Bobo-Dioulasso	In bush, on mosquito netting, and in a small truck	15.3	12	18
8	October 1949	Subdivision of Houndé	In bush	15.1	14	19
9	May 1950	Subdivision of Bobo-Dioulasso	In bush, near the Black Volta	14.7	13	18
10	August 1948–May 1950	Bobo-Dioulasso	Dwellings	13.2	10	16
11	January 1949–June 1950	Sakaby	Dwellings	12.1	10	15
12	March 1949–February 1950	Bobo-Dioulasso	Pigsties	13.5	11	16
13	May and July 1949	Sikasso	Dwellings	12.4	10	15
14	September 1949–June 1950	Bobo-Dioulasso area	Cattle-pens	13.8	10	16
15	February and December 1949	Ouagadougou	Dwellings	12.0	10	15
16	February 1949–June 1950	Upper Volta	Wells	13.0	10	16
17	June 1949–June 1950	Bobo-Dioulasso area	Various shelters	12.8	10	15
18	May 1950	Ségou	Dwellings and pirogues	13.2	11	16
19	May–June 1950	Subdivisions of Banfora and Houndé	Cattle-pens	12.5	10	14

Trophic preferences

It is Davis & Philip [76] to whom we owe the first data on the feeding of *gambiae*. In 1931, these workers found that 81.9% (154 out of 188) of the females collected at Lagos contained human blood, but they mentioned that there were no cattle nearby. The following year, Symes [367] published the results of numerous experiments carried out in several districts in Kenya ; they are summarized below :

District	*Number of tests made*	*Reactions to human antiserum*	
		negative	*positive*
Eldoret	42	11	31
Isiolo	651	69	582
Kakamega	44	5	39
Kisumu	38	20	18
Kitale	65	19	46
Nairobi	104	34	70
South Kavirondo	24	4	20

This worker also established that the species is essentially anthropophilic, as shown by the figures below:

	District	
	Taveta	*Trans-Nzoia*
Number of tests made	191	290
Negative tests	45	49
Positive tests:		
Man	125	192
Ox	10	7
Goat	1	2
Man + bullock	6	11
Man + goat	1	23
Man + bullock + goat	3	6

Furthermore, Kauntze & Symes [194] published the following figures, from Taveta (Kenya), which showed that, according to the reaction of the precipitating sera, more than 70% of the *gambiae* in dwellings where the people and the cattle lived side by side were engorged with human blood, a fact which bears witness to a high anthropophilic index:

Antiserum	*Number of tests made*	*Positive tests*	
		Number	*%*
Human	202	142	70.3
Bovine	202	11	5.4
Caprine	56	7	12.5
Human + bovine	202	4	2.0
Human + caprine	56	1	1.8

These facts were confirmed later, under the same conditions, by Gibbins [137] in Uganda, De Meillon [88] in Mozambique, and Haddow [150] in Kenya. In 1938, Corradetti [68] found an anthropophilic index of 57.4% in the Uollo region of the high Abyssinian plateaux, at an altitude of more than 1,800 m (5,900 feet). At Nairobi, Symes [368] examined 1,500 *gambiae* captured in dwellings, and gave the following figures of reaction to precipitating sera:

Human	78%
Human + bovine	3%
Bovine	1.5%

Finding that, in the French Sudan, 55% of the reactions to human antiserum were positive, Sautet & Marneffe [330] concluded that, in this territory at least, *gambiae* was clearly anthropophilic. Examining 25 *gambiae* in Ruanda Urundi, Jadin & Fain [184] found 11 engorged with human blood, 1 with pig blood, and 1 with ox blood.

TABLE XXVI. RESULTS OF PRECIPITATION REACTIONS CARRIED OUT ON VARIOUS GAMBIAE POPULATIONS

	Paucidentate *gambiae*		Multidentate *gambiae*	
	Captures in dwelling-huts	Captures in animal-pens and natural shelters	Captures in the bush	Captures in dwelling-huts
Number of tests made . .	1,328	314	597	325
Negative tests	115	21	177	17
Percentage	*8.7*	*6.7*	*29.6*	*5.2*
Positive tests with various antisera:				
Man	1,165	261	103	113
Percentage	*87.7*	*83.1*	*17.3*	*34.8*
Ox	40	11	66	103
Percentage	*3.0*	*3.5*	*11.1*	*31.7*
Man + ox	8	—	12	92
Percentage	*0.6*	—	*2.0*	*28.3*
Pig	—	17		
Percentage	—	*5.4*		
Man + pig	—	4		
Percentage	—	*1.3*		
Antelope			239	—
Percentage			*40.0*	—
Man + antelope			—	—
Percentage			—	—

The use of precipitin reactions, applied either, immediately after capture, to the fresh stomach-contents, or, later, to the dried blood preserved on filter-paper, enabled us to record the results which are summarized in table XXVI, in which the *gambiae* populations are classified into four groups:

(1) paucidentate *gambiae* captured in dwelling-huts;

(2) paucidentate *gambiae* captured in animal-pens and in various shelters;

(3) multidentate *gambiae* captured in the bush;

(4) multidentate *gambiae* captured in dwelling-huts.

These data allow us to take into account the enormous percentage of positive reactions to human antiserum given by paucidentate *gambiae* in dwelling-huts as well as in natural shelters. The presence of *gambiae* in cattle-pens and pigsties does not necessarily signify that one is dealing with zoophilic mosquitos, since 83.1% of the specimens captured in these animal shelters were engorged with human blood.

In another connexion, an interesting fact to note is the percentage of positive reactions to human or bovine blood among the *gambiae* captured

in the bush. This is explained by the incessant movement of herds and their herdsmen who, coming from the middle valley of the Niger, cross the Sudanese zone of the open savannas to reach the Lower Ivory Coast and central Guinea. Bernet [28] has pointed out the flights of *gambiae* accompanying the migrant herds in desert areas, and has drawn attention to the malaria prevalence among the Peuhls shepherds.

The proof that it is possible for *gambiae* to feed on wild animals (e.g., antelopes) and on migrant herds confirms the hypothesis put forward by Roubaud (in Marneffe et al.[243]) when he said: "We should ask ourselves if, in its exophilic state, *gambiae* does not also attack animals as *vagus* does in Indo-China, and if colonies of the mosquito are not maintained by wild fauna away from human communities".[h]

If we reconsider the populations enumerated earlier (see table XXV), we shall find, on reading tables XXVII and XXVIII, that the results given by precipitin tests on the anophelines which comprise these populations show only practically negligible differences and may be considered as remarkably uniform.

The presence of multidentate gambiae at Bamako (population 1) and in the environs of Bobo-Dioulasso (population 2) can be explained by the proximity of extensive natural organic breeding-places (whose role in the development of populations with a high maxillary index will be noted), the dwellings then serving as shelters for anopheles, of which nearly 32% contain only bovine blood, but which can, on occasion, bite man. On the other hand, we ought not to forget that these populations have been found in localities which are resting places for migrant herds.

TABLE XXVII. FOOD PREFERENCES AS A FUNCTION OF MAXILLARY ARMAMENT IN MULTIDENTATE GAMBIAE (ZOOPHILY)

Population No.	Mean maxillary index	Percentage of females giving positive precipitation tests with antisera					negative tests
		man	ox	man + ox	antelope	man + antelope	
1	15.0	32.0	28.0	23.0	—	—	17.0
2	15.5	39.3	33.6	18.7	—	—	8.4
4	15.2	—	18.4	—	31.7	—	49.9
5	15.0	12.0	13.9	2.7	48.0	—	23.4
6	14.8	20.0	9.4	6.1	27.4	—	37.1
7	15.3	8.8	12.1	0.9	44.1	—	34.1
8	15.1	10.4	24.0	1.9	29.8	—	33.9
9	14.7	16.8	10.1	1.1	43.0	—	39.0

[h] "Il y aurait lieu de se demander si le *gambiae* n'attaque pas aussi les animaux en condition d'exophilie, comme le fait le *vagus* en Indochine, et si même les peuplements du moustique ne sont pas entretenus par la faune sauvage, en dehors des collectivités humaines."

TABLE XXVIII. FOOD PREFERENCES AS A FUNCTION OF MAXILLARY ARMAMENT IN PAUCIDENTATE GAMBIAE (ANTHROPOPHILY)

Population No.	Mean maxillary index	Percentage of females giving					
		positive precipitation tests with antisera					negative tests
		man	ox	man + ox	pig	man + pig	
10	13.2	91.2	1.4	0.1	—	—	7.3
11	12.1	86.5	4.0	2.5	—	—	7.0
12	13.5	70.8	—	—	17.9	5.2	6.1
13	12.4	75.8	2.8	1.4	—	—	20.0
14	13.8	84.6	12.0	—	—	—	3.4
15	12.0	83.4	1.7	0.8	—	—	14.1
16	13.0	80.6	2.7	—	4.0	—	12.7
17	12.8	72.0	4.8	—	5.2	0.8	17.2
18	13.2	80.8	—	—	—	—	19.2
19	12.5	70.2	19.4	—	—	1.4	9.0

It may therefore be supposed that the high percentage of positive reactions to bovine antiserum is due to the presence of animals, but that, in addition, the anopheline populations have been able to follow the herds in their migration and, in the localities where the latter are stationary, to orient themselves towards anthropophily.

We can already conclude from the analysis of *gambiae* populations—on the basis of maxillary armament and food preferences—that these populations can be separated into two types, one characterized by elective anthropophily accompanied by weak dentition, the other by clearly marked zoophily and strong dentition.

Other characters enable us to differentiate even better between the two types of populations..

Choice of larval breeding-places

We have seen (table XXV) a population of *gambiae* (population 3) which showed the very high maxillary index of 15.9. These specimens were reared from larvae and pupae collected at Grand Bassam in an old pirogue abandoned in a swamp and containing stagnant water covered with a thick layer of vegetation. Subsequently, we sought to discover whether any relationship existed between paucidentate and multidentate populations on the one hand, and the nature of the breeding-places on the other. We proceeded to establish the maxillary index of females obtained from specimens in the first instar reared in the water of the breeding-places where they had been collected, this water being analysed. We were able to observe a certain correlation between the dentition of *gambiae* and the amount of dissolved organic matter of vegetable origin in the water of

TABLE XXIX. RELATION BETWEEN THE MAXILLARY INDEX AND THE ORGANIC-MATTER CONTENT OF THE BREEDING-PLACE

Breeding-place	Organic-matter content of breeding-place in milligrams of oxygen per litre	Mean maxillary index
Bfn. II	2.41	15.8
Drs. I	2.37	15.9
Kou. IV	2.28	15.3
Fak. II	2.09	14.7
K. XII	2.00	15.4
K. XIV	1.92	13.2
Bb. XIV	1.83	15.2
Sso. III	1.74	15.2
Bb. V	1.61	15.0
Bfn. XI	1.56	14.8
Sak. XVII	1.51	15.2
Drs. IX	1.48	15.0
Fak. VI	1.39	14.8
Nas. III	1.25	15.5
Bfn. IV	1.20	15.2
Bb. XXV	1.18	13.5
Sso. XII	1.10	12.5
Dd. I	1.04	12.8
Kop. II	0.98	13.8
Drs. III	0.87	13.0
Bb. XIII	0.74	13.5
Dd. II	0.68	13.0
Bb. XXIV	0.63	14.9
Kop. VI	0.45	13.5
Sak. XXXI	0.31	13.2
Kou. II	0.20	13.7
Kop. III	0.12	12.0
Nas. VIII	0.02	13.0

the breeding-places (see table XXIX). The breeding-places with an organic-matter content (in milligrams of oxygen per litre) between 1.20 and 2.41 gave rise to populations with a mean maxillary index of 15.0, while those with a content of between 0.02 and 1.18 furnished us with *gambiae* with a mean maxillary index of 13.2. The extreme indices of 12.0 and 15.9 were obtained from water titrating at 0.12 and 2.37 mg, respectively. Table XXX shows the distribution of individual maxillary indices in certain populations from both types of breeding-place.

We can therefore say that paucidentate populations, with an anthropophilic orientation, will develop preferably in water with a low content of organic matter of vegetable origin, while it is more likely that multidentate populations, inclined to zoophily, will be found in water heavily charged with organic matter. This corresponds, in general, to the distribution of breeding-places in nature; the large natural breeding-places rich in organic material (marshes and swamps) generally occur far from built-up areas, while breeding-places which are poor in organic matter are extremely abundant, particularly during the rainy season, in towns and their immediate vicinity, as a result of the rainfall and of man's activity.

However, the presence of paucidentate *gambiae* in water with much organic matter (population K. XIV) and vice versa (population Bb. XXIV) should be noted. It is probable that, in nature, *gambiae* populations do not always have a choice of breeding-place, and that zoophilic populations may therefore be found living in inorganic breeding-places, and vice versa. On the whole, however, a clear correlation between dentition and the organic-matter content of the water of the breeding-places has been obvious in our breeding experiments.

Exophily and endophily

Sautet,[328] studying the present trend of the fight against adult anophelines, emphasized one of the most important problems which faces the malariologist: the study of exophily in the species, that is, their ability

TABLE XXX. DISTRIBUTION OF THE MAXILLARY INDEX IN CERTAIN POPULATIONS FROM BOTH TYPES OF BREEDING-PLACE

Breeding-place	Organic-matter content of the breeding-place in milligrams of oxygen per litre	Mean maxillary index	Individual maxillary index	Distribution of individuals (%)
Kop. III	0.12	12.0	10.5	15.4
			11	11.5
			11.5	23.1
			12	11.5
			12.5	7.7
			13	15.4
			13.5	7.7
			14	7.7
Bb. XXIV	0.63	14.9	12.5	5.4
			13	0
			13.5	16.2
			14	5.4
			14.5	16.2
			15	10.8
			15.5	21.6
			16	16.2
			16.5	2.7
			17	5.4
K. XIV	1.92	13.2	11.5	8.0
			12	4.0
			12.5	20.0
			13	20.0
			13.5	24.0
			14	8.0
			14.5	4.0
			15	12.0
Drs. I	2.37	15.9	14	6.7
			14.5	3.3
			15	13.3
			15.5	13.3
			16	30.0
			16.5	23.3
			17	6.7
			17.5	3.3

to spend a part of their lives in shelters situated outside human habitations. He has recorded that, very often, anophelines which are dangerous malaria vectors show a very marked tendency to shelter in holes in trees, hollows in the ground, etc. This worker pointed out that this was true of *A. maculipennis* and *A. sacharovi*,[326] and, with his co-workers, of *A. sergenti* and *A. superpictus* in Lebanon,[329] and of *A. gambiae* in the French Sudan [329] and in Mauritania.[331]

The demonstration of exophily in an anopheles makes it necessary to consider methods of imago control which will be as appropriate for houses as for shelters. Swellengrebel & Stack [364] have shown the difficulties which thus await the malariologist who has to deal with an anopheles which, like *A. punctulatus* in New Guinea, transmits malaria outside dwellings. Hinman & Cutkomp,[167] treating only dwellings and habitual shelters of *A. quadrimaculatus*, recorded a failure, and established that the species was present, after DDT sprayings, in stables and in control traps. In Georgia, on the other hand, Fletcher & Krause [119] succeeded in making this species disappear at the same time as *A. crucians* and *A. punctipennis*, by treating only those places which were likely to be used as shelters.

It is clear, then, how indispensable it is to know the degree of exophily in a species before undertaking an antimalarial campaign with the help of imagocides.

Most of the workers who have studied the biology of *gambiae* in the various regions of its distribution range agree in describing this species as a domestic mosquito, most often found in dwellings. Nevertheless, a continually increasing number of observations indicates that this is not an established fact. Many years ago, Le Moal [223] found the anopheles abundant, during the day, under the awnings of boats and barges on the Senegalese coast, and Blin [37] pointed out the presence of *gambiae* in crab holes on the Dahomey coast. In the Belgian Congo, Newstead, Dutton & Todd [268] recorded that *gambiae* was present in crevices and cracks. From their studies of *gambiae* in Mauritius, Balfour [10] and MacGregor [236] concluded that this species was not a domestic mosquito at all, in view of its rare occurrence in dwellings during the day. This rarity has also been noted in the Transvaal,[90] in Ethiopia,[44] and in Sierra Leone.[32]

Side by side with these observations emphasizing the small number of *gambiae* found during the day in dwellings, others, more interesting, show us the discovery of adults in a great variety of shelters.

Leeson,[210] in Southern Rhodesia, captured 900 *gambiae* along the grassy banks of watercourses, in holes in trees, and in natural cavities in the ground, against 620 in dwelling-huts. In 1931 [211] he mentioned other collections: 309 specimens in crevices in the steep banks of streams and in the walls of small hollows formed in the ground by the erosive

action of the water, against 358 in dwellings. Monier,[257] in Madagascar, showed, as a result of observations made at Ivato and at Tananarive from 1935 to 1937, that only slightly more than half the *gambiae* collected (51.4-58.5%) were found in inhabited houses, the principal other shelter being cattle-pens (24.4-40.9% of the catches). Blacklock & Wilson [32] found the adults of the species at Freetown (Sierra Leone) in hedges, bushes, and hollows in trees, and Symes,[368] at Nairobi (Kenya), found them in bushes and tall herbaceous vegetation. Martin [245] pointed out that, at Addis Ababa, the adults were to be found throughout the year in farmyards and stables, while in spring and autumn it was very rare to find more than a few specimens in dwellings.

In French West Africa, Sautet[327] found adults between the wooden logs partly covering the mouths of wells; and at Bamako (Sudan), Sautet & Marneffe [329, 330] found them in the buttresses of silk-cotton trees.

Their study of the shelters led Sautet & Marneffe to state definitely that the frequented ones were those which gave protection against light, excessive humidity or drought, and wind. Da Cruz Ferreira [117] concluded from his study in Portuguese Guinea that shelters for *gambiae* had to combine the following conditions:

(1) presence of a host (man or animal);

(2) favourable microclimate (little light, moderate temperature and humidity, shelter from the wind);

(3) proximity of breeding-places.

Nevertheless, from our observations it seems that the presence of the host and the proximity of breeding-places are not essential factors in the choice of a shelter during the rainy season, and that they play no part during the dry season. The microclimate would be the determining factor, and this is confirmed by the observations of Soper & Wilson,[355] in Brazil, who explained the absence of *gambiae* from outdoor resting-places by the fact that the invaded region had a sparse vegetation, and was subject to violent insolation, regular winds, and great heat—all elements excluding the existence of protected shelters.

The presence of *gambiae* during the day in outside shelters is not accompanied by a reduction in feeding activity. Bagster Wilson [401] in Tanganyika, Haddow,[152] and Haddow et al.,[154] in Uganda, Sautet & Marneffe [329, 330] in the Sudan, and Vincke (personal communication, 1950) in the Belgian Congo, have all pointed out that this species readily bites man under these conditions. We, ourselves, have been able to verify this fact in the Upper Volta, and, at the present time, in the middle valley of the Niger, both in the Sahelian zone and in the rice-fields of the Office du Niger.

The observations that we were able to make during our stay in French West Africa led us to think that the degree of exophily in anthropophilic populations is much higher than is commonly believed. The captures we made in the dry season gave us a percentage of 53.2 *gambiae* females in dwellings against 46.8 in shelters (see page 103). However, these figures can be criticized, since the factors governing the choice of shelters by aestivating females may be different from those influencing the choice of resting-places by females in the pullulation season.

We utilized, as a criterion of exophily, the presence of males in the shelters, which, as Swellengrebel [360] states, bears witness to the "shelter-ing value" [e] of a place, that is, its fitness for use as a shelter. The presence of males does not necessarily signify that larval breeding-places are nearby, as Lamborn thought; [202] Sautet & Marneffe [329, 330] observed the predominance of males in shelters in the Sudan.

If we total the catches made during the rainy seasons of 1948 and 1949 in the towns and villages, excluding catching stations, of the Upper Volta, the Ivory Coast, and the Sudan, we obtain the following figures:

Gambiae collected in dwellings	3,564 (56.3%)
Gambiae collected outside	2,769 (43.7%)

The distribution of the sexes is as follows:

	Males		*Females*	
	number	%	*number*	%
Caught in dwellings	762	21.4	2,802	78.6
Caught outside	1,547	55.9	1,222	44.1

Much the most frequented shelters were deserted, and often half-destroyed, dwelling-huts, then came wells, cattle-pens and various animal shelters, cracks in trees, and low vegetation surrounding dwellings (table XXXI). In all these shelters, the number of males exceeded that of the females, but in a varying manner.

The precipitin reactions mentioned earlier were carried out on a certain number of the catches that we have just mentioned, and we were able to demonstrate the marked anthropophily of these *gambiae* as well as the paucidentate type of their maxillary armament.

If, on the other hand, we examine the multidentate *gambiae* which were collected in dwellings and proved to be strongly zoophilic, we shall see that their populations comprised a very high number of males—71.2% at Bamako and 63.8% near Bobo-Dioulasso. At the same time,

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[e] Valeur abritante

TABLE XXXI. CAPTURES OF GAMBIAE MADE OUTSIDE DWELLINGS

Type of shelter	*Gambiae* captured		Distribution by sex	
	number	percentage	males (%)	females (%)
Deserted huts	1,822	65.8	52.5	47.5
Wells	594	21.5	62.0	38.0
Cattle-pens	181	6.5	57.5	42.5
Animal shelters	74	2.7	73.0	27.0
Trees	67	2.4	64.2	35.8
Low vegetation	31	1.1	67.7	32.3
Total	2,769	100	55.9	44.1

the average anopheline density per hut, for *gambiae*, showed a considerable increase. While it was represented, for paucidentate populations, by an average figure of 5.6 during pullulation, in the two cases cited above it reached 113.0 and 65.5, respectively. Dwelling-huts therefore play an important role as shelters for these *gambiae* populations, which thus reveal themselves as highly endophilic, in contrast to the anthropophilic populations, which show a high degree of exophily.

Attempts at crossing paucidentate and multidentate gambiae

The study of these different populations of *gambiae* spurred us on to find out whether crossing the two forms would enable us to find arguments in favour of a specific difference.

On several occasions in 1949 and 1950, we crossed the offspring of *gambiae* reared from the first-instar larvae collected in the field, and from which the resulting females were established as belonging to one or other of the two forms. Crossings of paucidentate females with multidentate males, as well as crossings of paucidentate males with multidentate females, were fertile in every case. The females of the F_1 generation showed a dentition of the maternal type, which confirms the work of Roubaud,[307] who demonstrated the hereditary transmission of the maxillary index.

However, crossings between F_1 hybrids, i.e., F_1 paucidentate male and F_1 multidentate female, or F_1 multidentate male and F_1 paucidentate female, gave very disappointing F_2 hybrids, the females of which showed highly variable maxillary indices, belonging either to the multidentate or to the paucidentate type, or, even, to intermediate types.

Nothing in our crossing experiments gave us grounds to suspect a phenomenon of physiological amyxia between the two forms. The percentage

of eggs that hatched and the speed of hatching, the duration of development, and the number of generations obtained were shown to be comparable in every way with those obtained from paucidentate and multidentate populations in control rearings. The number of ovipositions by the hybrids and by the pure populations was similar, and the number of eggs deposited by the females was seen to be remarkably constant and without significant variation, in contrast to what Roubaud & Gaschen [312] noted for *A. maculipennis*.

Systematic position of the populations—Zoophilic possibilities of gambiae

The present position adopted by the systematists makes the results of our research difficult to interpret. The taxonomic position of the species and subspecies of Culicidae is based principally on the differences of the morphological characters in one or another stage in the life of the mosquito. Now, recent experiments concerning *A. gambiae melas*, and the research of Muirhead-Thompson,[264, 265] at Dar-es-Salaam, on a form of *gambiae*, different from *melas*, living in brackish water, incline authors to revise their views on systematics and to ascribe a larger role to biological characters. In view of the uncertain position of these different forms of *gambiae*, we do not propose to name the zoophilic and anthropophilic populations that we have described.

We shall consider it as established that *gambiae* can exist in two forms in the Sahelian and Sudanese savanna zones; one form, paucidentate, displays an elective anthropophily, and the other, multidentate, shows zoophilic tendencies. Corradetti (personal communication, 1952), in East Africa, also had the impression of two biologically distinct forms.

We refer specifically to the Sahelian and Sudanese savanna zones because our investigations were carried out in these regions; recent research suggests that our conclusions may apply to the whole of the Ethiopian region frequented by *gambiae*.

Cambournac [57] has pointed out that, in Mauritius, *gambiae* has been found in deep forest several kilometres from all habitation, and that the anopheline leads a purely woodland life, feeding on stags, which are very abundant in several parts of the island; Tomking & Gebert [375] noted there the anopheles' marked preference for animal shelters. Dowling,[100] for his part, relates that, after an extensive campaign of DDT house-spraying in Mauritius (a campaign which has led to the almost complete disappearance of *A. funestus*), *gambiae* was found in large numbers in cattle shelters (306, against 98 in untreated huts). Although no precipitin tests were made, this worker (personal communication, 1950) thinks that the species must survive on the island thanks to its zoophily. Similarly, in Réunion,

gambiae became exophilic and sylvatic after a DDT house-spraying campaign (Hamon & Dufour [155]). Bruce-Chwatt (personal communication, 1950), studying the results of anti-anopheline control by Gammexane spraying in houses at Ilaro (southern Nigeria), considers that *gambiae* is less endophilic and anthropophilic than is usually thought, and that it shows a certain amount of zoophily. Vincke (personal communication, 1950), who had already pointed out the high percentages of *gambiae* found in stables during the day,[393] kindly told us that experiments he had undertaken in Katanga led him to conclude that, in certain districts, *A. gambiae* shows a very marked degree of zoophily, and that he envisaged the transition of *gambiae* to complete exophily following DDT campaigns, this transition nevertheless being liable to upset the balance of the malaria cycle. In French West Africa, where few observations have been made, Bernet [390] thinks that *gambiae* is a " wild " mosquito, capable of existing on animal hosts, but adapting itself to humans.

The extremely important study of Campbell [59] (which appeared after our research was published in the French edition of this monograph) has confirmed the existence, in British Gambia, of two races of *gambiae*. Indeed, this author has demonstrated the co-existence of two forms—paucidentate (mean maxillary index, 13.1) and multidentate (mean maxillary index, 15.3). The two forms originate from different types of breeding-places, the presence or absence of chlorophyll (photosynthesis) providing the distinguishing characteristic between them (which corresponds to our description of " organic " and "inorganic" breeding-places). In addition, differences in the behaviour of the two forms of *gambiae* in respect of resting-habits have confirmed the distinction made by Campbell.

There is no doubt that further research in other African territories would add considerably to our knowledge of the distribution range of these morphologically and biologically different populations.