

## The Maxillary Index

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### Abstract

Preventive Medicine was given the possibility of reducing the incidence of malaria by vector incrimination and control at the beginning of the 20<sup>th</sup> century. However, vector incrimination proved to be far from simple and attracted a number of approaches, one based on the maxillary armature of adult female anophelines. This article looks at the theory behind this innovative approach and traces its progress until, after thirty five years, it proved to be a false trail.

**Key words:** maxillary index, *Anopheles*

### Introduction

Incrimination of the genus *Anopheles* in the transmission of human malaria in the closing years of the nineteenth century (Dobson, 1999) transformed the importance of these mosquitoes from merely pestiferous to dangerous vectors of disease, and began the taxonomic, bionomic and physiological studies which continue today.

Early studies in the Holarctic Zoological Region showed that adult forms of the common domestic *Anopheles* (now known as the Maculipennis Group of *Anopheles*), in addition to dark legs, carry more or less distinct clusters of scales on particular areas of a dark wing field (excluding the fringe which may or not carry pale scales). However, it soon became obvious that some of these mosquitoes were more domestic than others and also differed in other behavioural aspects, many pertinent to involvement in malaria transmission. At the start of the twentieth century Sergent & Sergent (1903) remarked on size differences between adult *Anopheles maculipennis* from Algeria and from France. However, it was only in the years between the two twentieth century world wars that the problem of *Anopheles maculipennis* and its involvement in malaria transmission was seriously tackled.

Roubaud (1920) was amongst the first to be involved, when he described how diversion to blood feeding on cattle in France afforded protection to the human population against malaria in parts of Normandy. In Italy, Grassi (1921) also reported the existence of a zoophilic form of *An. maculipennis* and Falleroni (1924, 1926) remarked on differences in egg morphology, an observation with far reaching consequences (Hackett & Missiroli, 1935). In the Netherlands there were reports of enormous populations of *An. maculipennis* in malarious and malaria-free regions alike, of long-winged and short-winged forms and of aquatic development in both fresh and saline waters. In the same country some over-wintered in cold shelters where the females were inactive until the following Spring, but others over-wintered in warm shelters where blood feeding (but without consequent ovarian development) and malaria transmission continued into the winter (de Buck, 1926; de Buck *et al.*, 1930, 1932; Swellengrebel, 1929; Swellengrebel & de Buck, 1933; Swellengrebel *et al.*, 1937; van Thiel, 1927, 1939).

Most workers agreed that morphological identification and classification of the different forms was essential for vector identification. However, one school of thought (Roubaud, 1921) argued that all that was necessary was a method of discriminating between 'races' which habitually fed on human blood and 'races' which habitually fed on cattle. This article outlines the long and contentious history of this approach to vector identification.

### **Roubaud's premise and investigations in the Holarctic during the 1920s**

Each of the paired maxillae of adult mosquitoes consists of a long flattened stylet, the tip of which bears backward pointed teeth. Discussing the disappearance of malaria from Denmark between 1830 and 1900, Wesenburg-Lund (1920-1921) suggested that the number of these maxillary teeth may be related to *Anopheles* host preference, and that a more thorough investigation of the maxillary armature of these mosquitoes might be revealing. Grassi (1921) took an early interest and in a paper describing work on *Anopheles maculipennis* collected near Naples mentioned, in addendum but without further comment, that he found no difference between the maxillary dentition of 107 specimens collected in a house and 107 specimens collected in a pig sty.

However, it was Roubaud (1921, 1922) who made the first investigations of a possible link between anopheline maxillary dentition and vector status and who set the discriminatory criteria. After examining specimens of *An. maculipennis* (then regarded as a single polymorphic species) obtained from different places in metropolitan France, Corsica and Macedonia, he concluded that specimens from malarious and malaria free areas could be distinguished by examination of the paired maxillae of adult female specimens. He put forward the premise that during the long association of *An. maculipennis* with thin skinned humans, evolutionary pressure selected a paucidentate, almost compulsory anthropophilic species. Then, with the much later domestication of cattle, conditions became favourable for selection of female mosquitoes better equipped for piercing thicker hides, resulting in the evolution of paucidentate, human oriented and multidentate, cattle oriented 'races'.

Discrimination between these 'races' was possible by counting the teeth (denticles) on the blades of each of the paired maxillae. Many specimens carry unequal numbers of maxillary teeth (Sergent *et al.*, 1922; Shannon, 1924; Trenszt, 1931), and counts were recorded as a Maxillary Index (M.I.), defined as the total number of teeth on both maxillae divided by two or, in series of counts, means of the individual indices. A maxillary index of less than 14 was taken to indicate almost obligatory anthropophily, and hence potentially dangerous or actual vectors; an index of between 14 and 15 indicates extreme orientation to cattle blood, to the extent that this group can be discounted as vectors of malaria; specimens with an index of more than 15 are also cattle oriented but are more readily diverted to humans if and when their preferred hosts are seasonally or occasionally absent or rare, so that specimens with very high maxillary indices may be vectors in some situations.

The difference in the maxillary indices of the strongly human (M.I.<14) and cattle (M.I.=14-15) oriented 'races' is small, and in practice discrimination between them caused practical difficulties, the first being definition of a tooth or denticle. Roubaud simply stated that he used a No. 7 microscope objective, without mentioning the eyepiece or make of microscope, but French workers following his methods in general used a magnification of 600-650x (Toumanoff, 1934). Other workers using different microscopes and high (oil immersion) magnifications, encountered difficulties of differentiating between real denticles and secondary serrations and it was only if and when procedures were adequately described that counts could be comparable.

Adverse criticism was not long in coming. Langeron (1922) doubted the value of Roubaud's maxillary index theory, stating that the number of specimens examined were insufficient to permit valid conclusions. Martini (1922) stated that larvae developing at lower water

temperatures often produced larger adults which probably, on average, have more maxillary teeth. In a further paper (Martini, 1924) he said he found *An. elutus* (= *sacharovi*) to have fewer maxillary teeth than *An. maculipennis* (= *sensu lato*) and, where both occur in the same locality, individuals developing in warmer water have fewer teeth. He maintained that the number of teeth is not a simple racial characteristic but is environmentally modified. He added that summer generations of both these mosquitoes are smaller on average than the spring generation and it is probable that maxillary dentition is also related to overall size. Furthermore, as malaria is rarer in cooler regions it is probable, in general, that there is inverse parallelism between the number of teeth of all species and malaria incidence.

Measuring wing length, de Buck (1926) discovered longer winged paucidentate and shorter winged multidentate *An. maculipennis* in the Netherlands, and reported that the latter carried malaria. No difference was found in the maxillary index of *An. maculipennis* collected from stables or from houses in the Netherlands, and, unlike Martini (1922), the Dutch investigators found no correlation between water temperature and the maxillary index. Neither was the maxillary index influenced by salinity of the larval sites. Following the discovery of malaria transmission by mosquitoes overwintering in houses, examination of overwintering specimens collected from non-malarious areas and exhibiting gonotrophic dissociation (n=11,612) or gonotrophic concordance (n=8,665) produced maxillary indices of 18.0 and 17.0 respectively (Swellengrebel, 1929, Swellengrebel & de Buck, 1933).

Shannon (1924) examined a small number of Nearctic specimens under (dry) 440x magnification. *Maculipennis* Group females from California (n=19) had counts of between 13 and 19 teeth, and this compared with counts of between 15 and 21 in specimens collected in British Columbia. In two of the Californian specimens one of the maxillae was missing and there were variations of up to 2 teeth between each of the paired maxillae of the other specimens. The maxillary index of all specimens examined was 15.3. However, he considered it to have little value because Chico, where he collected his Californian specimens, was malarious whereas the maxillary index signified zoophily according to Roubaud's observations in France. He questioned Roubaud's assumption that man was the original natural host and that 13 was the original maxillary index of *An. maculipennis* and that additional teeth came with increasing zoophily. He stated that bovids (bison) were numerous in North America long before humans appeared as a rival source of blood, and that cattle were possibly instinctively the preferred host. There was little further interest in the maxillary index in America, though Prado (1929) reported maxillary indices of 14 for *An. braziliensis* and of 10 for *An. cruzii* in a Brazilian malarious area from which cattle were absent.

On the other hand, there was continued interest in Europe. After eight years work, Roubaud (1928) considered that stable environmental conditions during all stages of the mosquito life cycle was one of the most important factors affecting its freedom of host choice. He reasoned that, following the imposition of hydrological regulations, increasingly stable environments were expanding in France, leading to the gradual evolution of the zoophilic 'race' of *An. maculipennis*.

### **Investigations in the western Palaearctic during the 1930s**

During the 1930s egg morphology became increasingly accepted as the most reliable method of discriminating between the various forms of *An. maculipennis*, but attempts to differentiate between vector and non-vector populations by examination of maxillary dentition continued.

Ekblom & Ströman (1931) reported that in Sweden only 2.3% of *An. maculipennis* maxillae carried as few as 14 teeth; all other specimens examined possessed 15-27 teeth, and the overall maxillary index of 17.8 was higher than anywhere else in Europe. They considered this was not due to shortage of hosts other than man, but rather to latitude. Eight old museum specimens collected at the beginning of the nineteenth century proved to have between 16 and

19 maxillary teeth (M.I.=17.1), showing there had been no change in the last 100 years, during which locally transmitted malaria had disappeared.

Trensz (1931) examined specimens with a high (oil immersion) magnification, giving differences in the number of denticles carried (from side to side) by each maxilla, and included a statistical treatment of his results. He concluded that the maxillary index should be based, not on individual insects, but rather on individual maxillae, and concluded that Roubaud's theory was based on too few specimens to be valid. This brought a prompt (pre-publication) and a forthright reply from Roubaud (1930), who considered Trensz's statistical analysis unnecessary, stating that examination of samples of 10,000 specimens is more inaccurate, because fatigue would produce greater inaccuracy than would statistical error in dealing with smaller samples of less than 100 individuals, a view shared by Senior White (1937). Roubaud (1932a, b) reported that paucidentate, anthropophilic and multidentate, zoophilic *An. maculipennis* retain their preferences over three generations.

In further investigations in Algeria, Sergent & Trensz (1933) reported that the *An. labranchiae* egg form, with a M.I. of 14-15 is, according to the premise of Roubaud, definitely zoophilic. Nevertheless, it is the only form of *An. maculipennis* present in malarious regions, and had definitely not become less dangerous in the localities studied, where conditions have long favoured the development of zoophily. Moreover, where malaria disappeared from the Departemente of Correze (Limoussin) in France during the 19th century, the resident *An. atroparvus* egg form has a M.I. of 16 -17, and in non-malarious Alsace, the resident *An. messeae* egg form has a M.I. of 15.6. Roubaud (1935) reported that in Morocco, the newly described *An. sicaulti* egg form, since synonymised with *An. labranchiae* (de Zulueta *et al.*, 1983), had a maxillary index of 13.7 and fed on humans by preference.

Roubaud & Gaschen (1933) considered that egg morphology was insufficiently distinctive to differentiate between all *An. maculipennis* 'races' and Weyer (1933a, b) expressed the opinion that though variations in size may be influenced by climate and larval habitats, the maxillary index is the only constant difference between the *An. atroparvus* and *An. messeae* egg forms, though this difference is no more than a denticle.

Working in Corsica with the *An. labranchiae* and *An. elutus* (= *sacharovi*) egg forms, Gaillard & Sautet (1935) reported a M.I. in both forms of 12 to 14 during the summer malaria season, and 13 to 16 in winter and stated that these may correlate with suitable larval conditions at the beginning of summer which then deteriorate until the first rainfall in September, so that only robust females with a high M.I. survive to hibernate.

Results of work in Italy (de Moro, 1933; Ottolengi & Rosa, 1935) were inconclusive and the maxillary index varied little between different egg forms in samples of various size:

<i>An. atroparvus</i> egg form from Po Plain	M.I. 14.00-15.00 (range)
<i>An. maculipennis</i> sensu stricto egg form from Po Plain	M.I. 13.50-14.00 (range)
<i>An. elutus</i> (= <i>sacharovi</i> ) egg form from Pontino	M.I. 14.00 (mean)
<i>An. elutus</i> (= <i>sacharovi</i> ) egg form Pontino	M.I. 14.80 (mean)
<i>An. labranchiae</i> egg form from Pontino	M.I. 12.97 (mean)
<i>An. maculipennis</i> sensu stricto egg form from Pontino	M.I. 14.10 (mean)
<i>An. messeae</i> egg form from Pontino	M.I. 14.00 (mean)

In the Iberian Peninsula, Torres Cañameres (1934), working with the *An. atroparvus* egg form in Jaen, Spain, reported differences between paired maxillae of up to 4 denticles. He arrived at a M.I. of 14.9-15.0 (overall range 12-19) in contrast to a previously recorded figure of 15.7. The separate indices for unfed and gorged females were 14.7 and 15.1 respectively. He suggested the difference between these and Roubaud's findings was possibly brought about

by a decrease in mosquito abundance affecting competition for preferred hosts. However, although the maxillary index was well within Roubaud's safety limits, the region was still intensely malarious. Also in Spain, de Buen (1935) examined 920 specimens and reported a M.I. of 15.9. He concluded that if biological races of *An. maculipennis* exist, they cannot be distinguished either by the maxillary index or by wing length. He went on to say that the maxillary index does not vary with the size of the mosquito; mosquitoes are smaller in size at higher temperatures. In laboratory studies in Portugal, Rivera & Hill (1935) reported that the M.I. changed from 16.5 in the P generation to 14.3 in the F7 generation.

### Investigations with Tropical Asian species

Investigations of a link between maxillary dentition and malaria transmission was not confined to the Maculipennis Group but during the 1930s were taken up in the investigation of many *Anopheles* populations elsewhere, notably in south-eastern Asia. Comparisons were made of the maxillary index and malaria infection rate in *An. hyrcanus* var *siniensis* (= *An. sinensis*) and six species of the subgenus *Cellia* which is well represented in the Cochinchina region of south-western Vietnam and Cambodia (Table 1).

This was followed by a wide ranging investigation over two years of the maxillary index of many (mostly *Cellia*) species prevalent in Cochinchina (Table 2). The Maxillary Index in general was reported to rise slightly from Tonkin in a northerly direction to Annam and Laos, and it was suggested that its determination is more valuable than the discovery of infected mosquitoes, an opinion which perhaps explains why maxillary indices and mosquito infection rates were not more often measured simultaneously.

Toumanoff (1935b) went on to say that 5,000 precipitin tests of *Anopheles* blood meals in Indochina showed *An. kochi*, *An. philippinensis* and *An. tessellatus* to be zoophilic, and that in *An. hyrcanus* var. *sinensis* (= *sinensis*), *An. aconitus*, *An. barbirostris*, *An. jeyporiensis*, *An. minimus*, *An. splendidus*, *An. subpictus*, *An. sundaicus*, and *An. vagus* the percentage of human bloodmeals was higher in individuals with the lower maxillary indices. On the other hand, the zoophilic species in the above list had mostly fed on animals even though some had a high percentage of individual counts of 13. However, he considered that precipitin tests from the Mekong delta reacting to bovine blood may indicate feeding on water buffalo rather than cattle.

After examination of 500 specimens of *An. hyrcanus* var. *sinensis* (= *An. sinensis*) collected from a variety of shelters in the vicinity of Shanghai, Ma & Chang (1935) reported a maxillary index of 16.23 (range 13-23). Of these specimens, 285 had equal numbers of teeth on both maxillae, but in the other specimens differences between sides varied from 1-5. Of those collected in human habitations (n=42), 30.9% had a M.I. of less than 14 and 69.1% a M.I. of more than 14. For those collected from other shelters (privies, animal sheds and an outdoor trap) (n= 458), 2.2% had a M.I. of less than 14, and 97.8% a M.I. of more than 14. Treillard (1935) remarked that zoophilic species with a high maxillary index (such as *An. vagus*) may be domestic. However, anthropophilic species with a low maxillary index, and hence the power to transmit malaria, seem to be both domestic and long-lived.

Roubaud & Toumanoff (1935) went on to explain that though a high M.I. indicates zoophily and a low M.I. indicates anthropophily, there are also zoophilic species with a low M.I. This may be because the process of selection only operates under the stress of competition, when many mosquitoes try to feed on a relatively low number of animals in an enclosed space (endophagy). Such is *An. maculipennis* (sensu lato) and, to a certain degree, *An. hyrcanus* (sensu lato). These factors do not operate on species such as *An. bifurcatus* (= *An. claviger*) which feeds on animals outdoor (exophagy). With exophagic species feeding on wild or domestic animals living outside, there is not the same degree of competition. In Indochina the paucidentate zoophilic species are essentially those which attack animals in the open or in

open shelters. *Anopheles minimus* is endophilic and anthropophilic, and like other species which attack man indoors, has remained paucidentate, humans being more numerous and accessible than animals. However, *An. kochi*, *An. maculatus*, *An. philippinensis* and *An. splendidus*, all of which have low maxillary indices (12.5) have been shown by precipitin testing to be zoophilic and are exceptions to the general rule; but they are not exophagic. *Anopheles vagus* is an 'amphophile', attacking animals indoors and out of doors rather than man, but always rests in domestic shelters. Its variable M.I. suggests that, like *An. ludlowi* (amended by Knight & Stone (1977) to *An. ludlowae*), it has races.

In the hinterland of Shanghai, China, Toumanoff & Hu (1936), performed precipitin tests on the bloodmeals taken by 1604 specimens of *An. hyrcanus* var. *sinsensis* (= *An. sinensis*) collected from various sources. Chang (1936) determined the maxillary index of 500 of these specimens (Table 3) and concluded that this species tends to rest in the shelter in which it takes a blood meal. However, there was very little difference in the maxillary index of specimens using any of the shelters.

In an experiment in the same area, Ma & Chang (1935) collected *An. sinensis* from a cow shed and starved them for 8 days before releasing them into a large chamber, where they were enclosed overnight along with various locally available mammalian hosts. Of the engorged specimens obtained from this experiment, 500 were submitted to precipitin tests to ascertain the source of their blood meals. The maxillary teeth of these same specimens were also examined to see if there may be any correlation with the precipitin tests results (Table 4). The maxillary index of insects feeding on each of these hosts was high and almost identical.

Working in Indonesia (then the Netherlands East Indies), van Thiel (1935) used a high power (oil immersion) objective, which gave a higher count (uniformly for all species) than that used by Roubaud. However, he worked out a reduced count for comparison, with these results:

	% engorged human blood	Maxillary Index
<i>Anopheles hyrcanus</i> var. <i>nigerrimus</i> (= <i>An. nigerrimus</i> )	83	13.0
<i>aconitus</i>	12	11.5
<i>annularis</i>	9	11.5
<i>kochi</i>	4	11.5
<i>maculatus</i>	9	11.5
<i>subpictus</i>	12	13.0
<i>tessellatus</i>	0	11.5
<i>vagus</i>	1	13.0

He went on to say that the few *An. punctulatus* which were also examined had a M.I. of 19.0, the highest of all species examined, and yet it is a dangerous vector, whilst *An. tessellatus* (M.I.=11.5) is the least anthropophilic. *Anopheles vagus*, with a M.I. of 13.0, is one of the least anthropophilic species in Indonesia. He also stated that of two additional species, *An. barbirostris* is near the paucidentate group and *An. sundaicus* near the multidentate group, though the latter is the more anthropophilic of the two. He concluded that the maxillary index is an unreliable guide for this region.

In a long paper Senior-White (1937), after discussing the work carried out to date, summarised his findings with north-eastern Indian anophelines as:

M.I. 12: *An. fluviatilis*, *minimus*, *varuna*, *aconitus*, *pseudojamesi*, *pallidus*, *splendidus*.

M.I. 13: *An. tessellates*.

He concluded that:

1. Evidence is accumulating that Roubaud's original hypothesis is sound, but there are no multidentate anophelines in north-eastern India with which to test it.

2. The oriental fauna contains several species which are not natural malaria carriers but which are paucidentate. Therefore the maxillary index cannot replace dissection to find vectors.
3. The maxillary indices of wild and laboratory mosquitoes cannot be compared.
4. An annual cyclical change in the maxillary index of *An. subpictus* appears to be related to rainfall.
5. The maxillary index can remain constant over wide stretches of country, but there appear to be geographical limits beyond which this is not the case.

After further reflection Senior-White (1954) suggested a formal classification of *Anopheles* trophic preferences, but did not discuss the maxillary index.

### **Tropical African species**

Wanson (1935) reported that *An. gambiae* in the present day Democratic Republic of the Congo (ex Belgian Congo) has two different wing lengths, both with the same maxillary index of 12.24, but did not pursue the matter further.

The 1939-1945 war brought a halt to work on the Maxillary Index, but it recommenced in Africa soon afterwards in attempts to explain observed morphological and behavioural variations in fresh water *An. gambiae*, which was beginning to be suspected of comprising more than one cryptic form of uncertain taxonomic status. Campbell (1951) in The Gambia, Maillot (1955) near Brazzaville and Holstein (1949, 1952) elsewhere in French West Africa reported the existence of multidentate, zoophilic, and paucidentate. anthropophilic 'races', the former choosing larger more or less long lasting larval sites containing large amounts of organic matter and the other choosing smaller, more temporary peri-domestic larval sites, poor in organic content. Goma (1960, 1961), working in Uganda confirmed that paucidentate and multidentate adults emerged from smaller temporary or more permanent larval habitats respectively, but stated that all parts of extensive swamps are not suitable for *An. gambiae*.

Gillies & Shute (1954), by inducing individual wild female *An. gambiae* to oviposit in the laboratory and rearing half of each oviposition in either crowded poorly nourished, or uncrowded, well nourished conditions, demonstrated that maxillary dentition is determined during aquatic development. Individuals developing in better conditions tend to develop more robust maxillae. At the same time Gillies (1954), working with natural populations of *An. gambiae* in Tanzania, showed that in villages in the malarious coastal plain, where widespread tsetse infestation precluded the presence of cattle, and where breeding places were restricted to small, temporary, seasonal rain pools, wild *An. gambiae* females were invariably paucidentate, and required two blood meals for maturation of the first egg batch. By contrast, in an inland swampy malarious area where cattle were numerous, and where larval conditions were more permanent and favourable, *An. gambiae* females were multidentate and a single blood meal invariably led to oviposition.

It was left to Fox & Fox (1955) to have the last word on maxillary indices and 'races' of fresh water *An. gambiae*. They pointed out that since the postulated paucidentate and multidentate 'races' were sympatric, and that their genetic isolation had not been demonstrated, fresh water *An. gambiae* should still be regarded as a single polymorphic species. An unanswerable argument? Yes, that is until Davidson (1962, 1964) and Paterson (1963) with Paterson *et al.* (1963) independently demonstrated genetic isolation between sympatric fresh water populations, and *Anopheles gambiae* sensu lato joined *Anopheles maculipennis* s. l. as a complex of sibling species.

## Conclusions

It was some thirty-five years after the proposition that examination of the maxillary armature of anopheline mosquitoes would allow separation of malaria vector from non-vector forms, that it was proved to be false. It may seem to current workers that Roubaud's concept was so obviously flawed that it should not have been pursued for more than a third of a century. However, he was one of the foremost scientists of his day with an outstanding international reputation and a most enviable track record. In addition to his many other interests, he published over a hundred papers on mosquitoes or mosquito-borne pathogens alone. He attempted to produce laboratory crosses between the different egg types and found at least one naturally occurring mixture of *An. atroparvus* and the type form of *An. maculipennis* which he considered to be a hybrid population.

Roubaud's research covered a much wider range of interest than is usual or even possible today, and included the biology of dipteran pests and vectors of disease, as well as agricultural damage caused by insects and arachnids. His introduction to and spare time study of *Belonogaster* social wasps (Hunt, 2007) are proof of a fertile and productive mind.

Rather than criticising his persistence, it may be better to spare a thought for the parlous state of knowledge of all facets of vector systematics and biology during the first half of the 20th century. Apart from the work of a few pioneer investigators, including Roubaud, the preponderance of current knowledge was gathered after the Second World War, when the discovery of DDT led to the realisation that it may be possible to eradicate some vector borne diseases, and so to vastly increased funding for the research necessary for successful conclusions. Before the end of the century the revolution in information technology facilitated communication and cooperation enormously. Even greater advances in knowledge are now underway with the growth of microbiology, which has already revealed that many of the taxa encountered during the investigations in southern Asia are, like *An. maculipennis* s. l. and *An. gambiae* s.l., assemblages of more or less cryptic species (Harbach, 1994, 2007).

Rather than criticise explorers of false trails, we might give a thought to our own efforts and wonder how they will be viewed by workers of the latter half of the 21st century; and to remember that truism, "the only people who never make mistakes are those who never do anything."

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**Table 1**

Comparison of Maxillary Index and malaria infection (oocyst and/or sporozoite) rates in some *Anopheles* species from Indo-china (after Roubaud, Toumanoff & Gaschen, 1933).

<i>Anopheles</i>	Number Examined	Maxillary Index	Malaria Infection Rate
<i>sinensis</i>	1095	14.2	0.15
<i>minimus</i> *	731	11.6	2.47
<i>aconitus</i> *	266	11.3	1.06
<i>jeyporiensis</i>	183	11.8	2.25
<i>maculatus</i>	53	11.5	3.20
<i>philippinensis</i>	60	11.4	0.00
<i>vagus</i>	1090	15.6	0.00

\* presently regarded as sibling species (Harbach, 1994)

**Table 2**

Maxillary Index of *Anopheles* mosquitoes from Cochinchina.

<i>Anopheles</i>	Cochinchina				West Cochinchina	South Cochinchina	Tonkin
	Morin 1935	Gaschen 1934	Roubaud & Treillard 1934	Toumanoff 1935a	Toumanoff 1935a	Toumanoff 1935a	Toumanoff 1935a
<i>sinensis</i>	15.00	14-16*			15.30	15.10	
<i>aconitus</i> <sup>1</sup>	11.00	11-12*			11.30	11.30	
<i>minimus</i> <sup>1</sup>	11.00	11-12*			11.50	11.30	
<i>culicifacies</i> <sup>2</sup>		11-12*			11.70	12.90	
<i>jeyporensis</i>	11.00						
<i>maculatus</i>					11.70		
<i>splendidus</i>				11.80			11.60
<i>annularis</i>				11.30			11.40
<i>philippinensis</i>				11.40			11.40
<i>kochi</i>							11.70
<i>tessellatus</i>				12.40			12.10
<i>litoralis</i>			12.50				
<i>sundaicus</i>			11.50	13.70			
<i>subpictus</i> <sup>2</sup>				14.30			13.40
<i>vagus</i>	14.00	14-16*			14.10	14.40	

1. presently classified as members of the *An. minimus* species complex (Harbach, 1994)

2. presently regarded as a complex of sibling species (Harbach, 1994)

\*range of individual indices

**Table 3**

Results of precipitin testing of blood meals taken by *An. hyrcanus* var. *sinensis* collected from different sources in the Shanghai region of China, shown with maxillary index of each group (after Toumanoff & Hu, 1936; Ma & Chang, 1935; Chang, 1936).

Source	Positive precipitin tests of bloodmeal					Maxillae examined	
	number	human	cow	pig	Mixed*	number	index
dwelling	172	165	1	1	m/b 5	42	14.78
man bait	193	193	0	0	0	89	16.70
privy	75	75	59	2	m/b 13	26	16.70
cow shed	721	0	715	0	m/b 6	132	16.72
pig shed	443	10	210	223	0	76	15.89

\*m=human b=bovid

**Table 4**

Results of positive precipitin tests made on blood meals taken by 500 *An. hyrcanus* var. *sinensis* collected from a cow shed and held for eight days before being offered a choice of several hosts in a closed chamber, shown together with maxillary index of each host choice group (after Chang, 1937).

Hosts Offered	Positive Precipitin Reactions	Maxillary Index
human	21	17.88
chicken	9	17.77
cow	238	17.79
cat	17	17.67
pig	69	17.66
dog	18	17.47
goat	125	17.10