

# The Geographical Distribution of the Anophelini.

by

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The Anophelini are now generally treated of as a single genus. This genus, however, contains at the lowest computation about 120 species and is spread over the greater part of the globe. When distributional areas are mapped out, it is seen that numbers of species of similar or dissimilar characters are associated and occupy the same faunal areas. Based largely on the work of HOWARD, DYAR and KNAB in America, EDWARDS in regard to African species, STANTON, SWELLENGREBEL and SWELLENGREBEL-DE GRAAF in Malay, TAYLOR in Australia and others I have drawn up a list of substantiated species of the world with the countries from which they have with certainty been recorded.

From such a list the existence of faunal areas is very apparent. At a first approximation there can be distinguished the following:

Tropical South American.	Mediterranean.
Central American.	African.
Argentine.	Indian.
North American.	Oriental.
Palaeartic.	Australasian.

According to HOWARD, DYAR and KNAB (1) there are distinguishable in Tropical America in connection with mosquitos two faunal regions, the one including Brazil, with the countries to the east of the Andes, and the Lesser Antilles, the other including Central America, Mexico, the Greater Antilles and the Pacific coast of South America. There are 12 species of anopheles, as far as known, peculiar to the former and 6 peculiar to the latter region. Peculiar to the two regions taken together there are 24 species known. From the Argentine have been recorded chiefly species common also to the above areas, so that there is no definite evidence, beyond the occurrence of two peculiar species (*A. annulipalpis* Arrib. and *A. pictipennis* Phillippi) pointing to a distinctive fauna in the south of the continent. In extent these three regions together are identical with the Neotropical realm of mammalian distribution,

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To the North American area are restricted 8 species, whilst two more species extend into the previously mentioned realm viz. *A. pseudopunctipennis* Theo., which ranges along the Pacific seaboard from North California through Central America to the western Argentine, and *A. crucians* Wied., which besides being found in the S. E. United States occurs in the Greater Antilles.

In Europe the well known species *A. maculipennis* Meigen, *A. bifurcatus* L. and *A. plumbeus* Stephens, form a characteristic fauna. The area of distribution of these species evidently closely corresponds, at least in the west, to the Palaearctic region of mammalian distribution. Taking the distribution of *A. maculipennis* as a guide, the southern limits of this area have now been followed through northern Africa, Palestine, Mesopotamia and as far as the south Caspian. *A. maculipennis* has also been recorded from Formosa (2). If this be correct the anopheline palaearctic area must have a vast extension through northern Asia, but I have been unable to find in the literature any definite reference to far northern species on the east coast of the Asiatic continent, and the extension of the European species thus far requires careful verification.

Between the Palaearctic area and the African is a peculiar region which has considerable claim to be considered distinct though there is an element of overlapping involved. This corresponds to the Mediterranean sub-region of mammalian zoogeography. It includes, besides the countries bordering the Mediterranean, a considerable tract of the Middle East, extending as far as the North West Frontier of India and Turkestan. In addition to species derived from neighbouring faunas, there are certain species peculiar to this sub-region viz. *A. sergentii* Theo., *A. superpictus* Grassi, *A. turkhudi* Liston, *A. pulcherrimus* Theo., and possibly others not yet clearly differentiated.

To the African continent south of the Sahara and to its immediate neighbourhood, there are peculiar at least 10 species of very wide distribution and 14 other species of more localised occurrence. Egypt possesses a fauna partly of Mediterranean type, but at least

The African area may therefore be considered as including the African continent south of the Sahara, Egypt, south Arabia and Madagascar and the neighbouring islands. It thus corresponds with the exception of the inclusion of the Malagasy region, to the Ethiopian region of mammalian distribution. It is remarkable that one species very characteristic of the region viz. *A. mauritanus* Grandpré has recently been recorded by SWELLENGREBEL and SWELLENGREBEL-DE GRAAF from Java and Sumatra. Otherwise the only species of the African fauna occurring far from the borders of the African continent are *A. maculipalpis* Giles and *A. umbrosus* Theo., both of which have a wide distribution in the Oriental region.

The Oriental region likewise is characterised by a very considerable number of species having a wide distribution within certain faunal boundaries. Numerous characteristic species of this region occur throughout India from the extreme north west to the extreme south including Ceylon, also throughout the Malay Peninsula and the Malay Archipelago. According to SWELLENGREBEL and SWELLENGREBEL-DE GRAAF (4) the eastern boundary of the region in respect to anopheles distribution includes Celebes, beyond which an Australasian element becomes predominant. The Philippine fauna is composed of well known oriental species as is that of Tonkin, South China and Formosa. The species recorded from Hong Kong as a result of Dr. MACFARLANE'S mosquito survey (5) are all forms commonly met with in India; the same identity is noticeable in the list of species recorded by TSUZUKI, SECRETE and others from Formosa. How far further north this oriental anopheline fauna extends I have not been able to ascertain.

In the Indian area certain species occur which are not encountered further east. Some of these are species of the Mediterranean region, but two at least have a special Indian distribution viz. *A. culicifacies* Giles and *A. stephensii* Liston. On the whole the Indian region may be described as possessing an anopheline fauna of an impoverished Malayan type, but with some element in addition.

New Guinea, the Solomon Islands and Australia evidently form a distinct faunal province. The common anopheline throughout is *A. annulipes* Walker, which is found as far south as Tasmania.

These are the chief anopheline faunas. If others exist they are of the nature of subdivisions of these, or have not yet come sufficiently into prominence to enable one to detect their existence with certainty.

In order to advance further in an understanding of the nature of these faunas, it is necessary to analyse their constitution in

relation to the natural affinities of the various species composing them. This can only be done after a close study of the morphological characters of the anophelini and in particular of the features of the male genitalia, which afford a most instructive clue to the classification of this group.

THEOBALD'S subdivision of the anophelini into genera based on scale characters has not been found altogether satisfactory.

A more satisfactory classification, which I have outlined in a previous communication (6) commences by a subdivision of all anopheles into three groups, precisely separable by the type of the male genital armature. It is then, and then only, possible satisfactorily to subdivide further into groups of species shewing distinct natural affinities and corresponding in the main to various genera and subgenera of authors.

Formerly I have termed these three major divisions Protanopheles, the group of American Cellias, and Deuteroanopheles.

These names are not satisfactory and I propose here to speak of them respectively, for reasons which will be more apparent later, as Protanopheles, Neoanopheles<sup>1)</sup> and Palaeoanopheles. If these divisions were treated as genera they would, by rules of nomenclature, be respectively *Anopheles*, type species *A. maculipennis* Meigen, *Nyssorhynchus*, type species *A. argyritarsis* Rob. Desv. and either *Myzomyia* with type species *A. rossii* Giles or *Pyretophorus* with type species *A. costalis* Theo. For the present, however, I merely wish to use the terms in a descriptive sense and for convenience,

In the Protanopheles (with two spines at the base of the clasper) can readily be distinguished the following subgenera: *Anopheles* (sensu stricto), including *Coelodiaezis* and *Stethomyia* and excluding the next group; *Patagiomyia*, including anopheles-like species with spotted wings and tufted prothoracic lobes; *Myzorhynchus*; *Cyclolepton*; and *Arribalzagia*.

In Neoanopheles (with genitalia of the general type of the above but with a single large spine at the base and other distinctions) are included the sub-genera *Cellia*, *Dendropaedium* and probably *Myzorhynchella* of DYAR (7). This group is of great interest because, though

<sup>1)</sup> I have previously used the name Neoanopheles to designate the multi-spotted species of the *annulipes* group, an example of which *A. leucosphyrus* Dönitz, was made the type species of the genus *Neomyzomyia* by JAMES. I think it is better to employ this term as used above and to refrain from naming the *Neomyzomyia* group otherwise than as a subgenus for the present.

it possesses genitalic characters of the general type of the Protanopheles, its members simulate in wing markings etc. anophelines of the third group to be mentioned, with which it is certain they are not directly connected.

The third group, Palaeoanopheles (with four or five quite delicate spines at the base of the clasper) includes the subgenera *Myzomyia*, *Pyretophorus*, *Nyssorhynchus* (in the ordinary use of the term) and *Cellia*. These subgeneric names, however, require a good deal of modification to make them satisfactory. For the purpose of following the distribution of species, it is better to deal for the time with such natural groups of closely related species as can with certainty be recognised. The following can be distinguished: (1) the *culicifacies-funestus* group, practically *Myzomyia* after excluding the *A. rossii* group, (2) the *superpictus* group, including the species *A. turkhudi*, *A. superpictus*, *A. transvaalensis* etc., (3) the *marshalli* group, including the Oriental *A. jeyporiensis*, (4) the *rossii* group, (5) the *costalis* group, (6) *Nyssorhynchus* (as the term is ordinarily employed, but excluding group 8. Strictly speaking this should now be *Neocellia*). (7) *Cellia*, as applied to certain of the old world species and (8) the *annulipes* group.

The species *A. atratipes* Skuse and *A. stigmaticus* Skuse from Australia, *A. watsoni* Leic., *A. natalensis* Hill and Haydon and some others are as yet impossible to class as they have not been sufficiently studied, and in particular the male genitalia have not been described.

With this digression we may return to the faunas, studying these in relation to the distribution of natural groups.

One of the most striking faunal features is due to the peculiar distribution of the genus *Anopheles* s.s. in relation to that of the remaining groups. If the distribution of *Anopheles* s.s. be examined, it will be seen that whilst this genus as previously defined extends over almost the whole world, it is especially in the northern hemisphere that it is dominant and appears in its most typical form. South of the limits of the North American and Palaeartic areas the genus is chiefly represented by species that have been usually classed as *Stethomyia*. In this form the sub-genus extends over the Brazilian area (*A. nimba*), Mediterranean area (*A. algeriensis*), the Oriental area (*A. aitkenii*) and into the Australian region (*A. corethroides*). In its typical form it occurs only as rare species of which only two are known, *A. culiciformis* and *A. brevipalpis*. In the northern zone, represented by the North American and Palaeartic faunas, moreover,

the sub-genus *Anopheles* is unassociated with the many other sub-genera which are found in other parts of the globe.

Until a certain latitude is reached the sub-genus *Anopheles* holds the field. It is then, in North America, associated with *Patagiamyia*. *Patagiamyia* is well represented in the South Western States (*A. crucians*, *A. punctipennis*) and as *A. pseudopunctipennis* on the Pacific Coast. It appears again in the Himalayas, the Assam Hills and Upper Burmah, and as montane forms in scattered localities of high altitude in the Oriental region. This may represent a true montane constituent of the Oriental fauna, or it may be the edge of, and outliers from, an unknown southern palaeartic of Central Asia.

Though the species in the North American and Palaeartic areas respectively are distinct, yet the two faunes are evidently closely related and presumably only recently differentiated. They have no resemblance in their constitution to that of any other area and may suitably be dealt with together as a single major division. To a large degree this division is distinct, not so much by reason of its positive characters, as by the fact that, whether originally present or not, there are now no representatives of many genera everywhere else present.

Turning to the new world we find that the Brazilian and Central American areas together are the only region in which occurs the peculiar protanopheline sub-genus *Arribalzagia*. This sub-genus, whilst perhaps shewing *Myzorhynchus* affinities, is entirely and obviously distinct, both in its very marked general facies and in genitalic characters. To these areas also is entirely restricted the group of *Cellia* like genera (*Cellia*, *Dendropaedium* and *Myzorhynchella* of DYAR) forming my second group of Neotanopheles.

Of anophelines not in the above sub-genera there are in the Neotropical region (a) *A. nimba* Theo. a *Stethomyia*, (b) the very peculiar *A. vestitipennis* DYAR and KNAB and (c) *A. grabhamii* Theo., the at present unique species forming the sub-genus *Cycloleppterion*. I have had the opportunity of examining this latter species and with DYAR consider it distinct sub-generically from other American species. Further it appears to have the very closest affinities to the old world sub-genus *Myzorhynchus*, in which it might well be included, forming in this case the only representative in the new world of *Myzorhynchus*. The area of distribution of *A. grabhamii* is confined to the Greater Antilles.

The Brazilian and the Central American areas, though in many cases distinct as regards species, are identical as regards the types

of sub-genera concerned. Their faunas are entirely distinct from that of any other region and they obviously form a major subdivision which not only resembles the Neotropical realm of mammals in point of extent, but also in the character of isolation. The features of this region are (a) a high degree of specialisation of protanopheline type, (b) the presence, unlike any other area, of the Neopanopheles branch and (c) the entire absence so far as is known of any representative of the Palaeopanopheles branch. However much the general appearance of a species from this region may resemble forms in the old world, examination of the genitalia shews that this resemblance is entirely superficial. Hence the placing of new world species under such genera as *Myzomyia* and *Cellia* is entirely wrong.

With the above it is probably best for the time to include the Argentine area.

The African, Mediterranean, Indian, Oriental and Australian areas similarly form but one major subdivision comparable with those we have so far dealt with. To this area is restricted the group of Palaeopanopheles, the species of which outnumber those in any other group. The Palaeopanopheles have a distribution which is roughly coincident with that of the ancient Gondwana continent after the separation of South America. As a convenient name I may term it the Palaeotropical area. Like South America this possesses a generally diffused Protanopheline element largely overshadowed, however, by the great development of forms of Palaeopanopheline type.

The species proper to the African and Oriental regions respectively, though usually distinct in the two areas, are related in general affinities so that it is not easy to separate out groups or sub-genera which are peculiar to one or the other. Mapping out the distributional area of the culicifacies-funestus group, this is seen to occur widely throughout both regions, but the number of species is greater in Africa than in the eastern parts of the Oriental region, where for the most part the group is represented by the species *A. minimus* only. The *superpictus* group is represented by a number of species in the African and Mediterranean areas, but does not occur to the east of India. The *marshalli* group is represented by several species in Africa, but by *A. jeyporiensis* Theo. only in the east. The distribution of this latter species is peculiar, since though it occurs in China, it is not recorded from the Malayan Archipelago.

It is possible to view these three groups as in some degree representing progressive differentiation of markings and scale characters

towards a *Pyrethophorus* facies, so that if we recognise such a sub-genus it would represent a line of evolution of an African order.

*Cellia* is represented by several species in the African area but is not a constituent of the Oriental fauna.

*Nyssorhynchus*, or more correctly *Neocellia* shews a reverse phenomenon, for, whilst only four species are African, one of which is Oriental also, there are a great many species of wide distribution in the Oriental region.

The fact that the species peculiar to the Mediterranean area are largely of the *Pyrethophorus* type and include a *Cellia* (*A. pulcherrimus* Theo.) related to the widely disseminated and common African species *A. pharoensis* makes it legitimate to look upon this area as affiliated to the African and even as forming a modified portion of it.

The species *A. annulipes* Wlk. which seems especially to characterise the Australasian region is very probably of Palaeoanopheline type and if so would not argue any special isolation of the Australasian area as occurs in the case of mammals. So far as I can ascertain, however, no one has yet described the genitalia of this species. Whether the very peculiar forms *A. atratipes* and *A. stigmaticus* represent some early Australian element cannot be decided until these forms have been more completely studied and in particular the male genitalia examined.

Summarising the above results we can best indicate the nature of the world's anopheline fauna by the following subdivision:

Holarctic region. The whole of America north of Mexico, Europe and an unknown portion of Asia.

Corresponds closely with the Holarctic region of mammalian distribution, but characterised chiefly by an absence of all sub-genera but *Anopheles* s. s. and *Patagiamyia*.

Neotropical region. America from Mexico south.

Corresponds with the Neogaeic realm of LYDEKKER for mammals, both in area and in evidence of isolation.

Palaeotropical region. Tropical and subtropical Old World.

Including as sub-divisions:

Ethiopian with the Mediterranean area.

Oriental with the Australasian area.

The isolation of the South American area in the case of the anopheline, as in the mammalian fauna, argues that anopheles existed prior to the separation of the South American continent, which might bring the probable origin of the sub-family into Mesozoic times. The

origin of an anopheline fauna in the Gondwana continent would be an interesting fact to substantiate, but could at present scarcely be treated even as an hypothesis. Less hypothetical is the fairly close association which there appears to be between the changes in the mammalian fauna which are known to have occurred in the Pliocene and Miocene and the distribution of the anophelini. If this be admitted we must look upon the African and Mediterranean faunas as Pliocene. That species of African type should extend even very considerably to the east is in agreement with this view, it being known that a mammalian fauna of African type and in the Pliocene not only existed over most of India, but even extended into central Asia. Similarly the present Oriental anopheline fauna may be regarded as "Malayan" in the palaeontological sense, i.e. belonging to a Miocene fauna originally of great extent which flourished in Europe and to which the name "Malayan" was given since a living fauna of this type is still found in Malay. If the Oriental anopheline fauna of the present day is truly derived from this source, then we must look upon it as having once extended much further to the west and as having undergone extensive recession to its present area. The character of the fauna of the Indian region can only be adequately explained in some such way.

The land connection which existed along the southern shore of the ancient Central Mediterranean Ocean across the position of the present Atlantic, linking up the Antilles with Europe, may conceivably have been the reason for the presence of a species of *Myzorhynchus* in the West Indies, but this again would be more an interesting fact to substantiate than an actual hypothesis. Nevertheless in this connection the following remarks of GREGORY, quoted by LYDEKKER are of interest. Dr. GREGORY says: "As I have previously pointed out, the intimate affinity between those (fossil corals) of the West Indies and the Mediterranean can only be explained by the assumption of the existence of a shallow water connection across the central Atlantic in—at latest—Miocene times. That the fauna did not follow along the shores of the North Atlantic Basin, is shewn by its absence from the northern Miocenes of Europe and North America. The evidence now adduced from the fossil corals of Barbados lends support to this view, as shewing that the West Indian fauna is only a fragment of that of the Mediterranean Miocene, and has received nothing from the Pacific."

It will be remembered that there is some reason for supposing the present Oriental anopheline fauna to be an eastern relic of a great Miocene fauna that held sway in Europe. It would be curious if in the

world at the present day there exists both an eastern and a western relic of this great fauna preserved in the distribution of the Anophelini.

*Discussion.*

Dr. DE VOGEL:

I should like to ask Major CHRISTOPHERS if it is known why the borders the mosquito species live are so strictly limited. Dr. SWELLENGREBEL found special Australian species in Celebes and the Molucco's while they were not found in islands belonging to the Asian part of our Archipelago. I think that eggs and larvae could be so easily brought over in native boats in their water reservoirs.

Dr. CHRISTOPHERS:

In regard to Dr. DE VOGEL'S questions it would appear that in spite of apparent facilities for the spread of anophelines, species do not readily extend beyond their natural areas of distribution, or at least they take long periods of time to do so. The reasons that have determined the areas species at present occupy would seem quite possibly, as I have shewn, to be of a geological nature. What we see at the present time as distributional areas would in this case be merely a phase in the rise, spread and decline of anopheline faunas representing those of miocene, pliocene and other ages.

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