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Distribution of African Malaria Mosquitoes Belonging to the *Anopheles gambiae* Complex

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The distribution of malaria vector mosquitoes, especially those belonging to species complexes that contain non-vector species, is important for strategic planning of malaria control programmes. Geographical information systems have allowed researchers to visualize distribution data on maps together with environmental parameters, such as rainfall and temperature. Here, Maureen Coetzee, Marlies Craig and David le Sueur review our current knowledge on the distribution of the members of the Anopheles gambiae complex.

The *Anopheles gambiae* Giles complex comprises six named species¹, one unnamed species² and several 'incipient' species^{3,4}. It includes two of the most effective vectors of malaria parasites in Africa. In dealing with the distribution of this important group of insects, it is appropriate to consider the history of the complex, the methods of identification and their implications for research and control operations.

History

Before 1962, *An. gambiae* was considered to be a single, biologically variable species. However, in the early literature⁵, there were many reports of variation in the larval habitats and adult female resting behaviour and feeding preferences. This caused some concern when

residual insecticide spraying of houses was adopted as the routine method for malaria control. First, the irritating properties of DDT caused avoidance behaviour in adults, reducing the effectiveness of the control programmes in West Africa. Second, large numbers of *An. gambiae* larvae could still be collected in areas where malaria transmission had effectively been controlled, although outdoor-resting adults were shown to have fed on cattle. This was interpreted at the time as being selection for behavioural resistance within a single species. The reasons for these apparent changes in behaviour were unknown and it was feared that the outdoor populations could return to their previous human-biting, indoor-resting ways⁶.

The first real evidence for the specific distinctiveness of the saltwater-breeding members of the group was presented in the mid-1940s, although this was largely ignored at the time. Hybrid male sterility between two freshwater-breeding populations was reported in the 1950s and early 1960s, but was not considered to be evidence of interspecific differences between the two⁶. However, by 1964, five species were recognized, with Paterson⁷ presenting evidence that the three freshwater-breeding species did not mate in Nature. Evidence for a new sixth species from Uganda was presented by Davidson and Hunt⁸. The six species were formally assigned the following scientific names: species A: *An. gambiae*; species B: *An. arabiensis*; species C: *An. quadriannulatus*; species D: *An. bwambae*; East African salt-water breeder: *An. merus*; and West African salt-water breeder: *An. melas*. The latest addition to the complex, reported in 1998, is known as *An. quadriannulatus* species B from Ethiopia, and is yet to be named². Debate still surrounds the issue of the specific status of the West African incipient species of *An. gambiae*, although it is becoming increasingly evident that they are, in fact, distinct biological species⁴.

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Species identification methods and relevance to control programmes

Species complexes containing morphologically cryptic species that vary in their behaviour and vectorial capacity present a very real problem to malaria control programme managers. In large areas of Africa, *An. gambiae* and *An. arabiensis* occur in sympatry. Because both are good vectors of malaria parasites, it might seem unnecessary to carry out expensive identification procedures when the control methods to be applied are probably going to be the same. However, assessing the impact of control measures can only be effective if the abundance and proportion of the various species are determined both before and after implementation of the control programme. It is when control measures fail that the reasons can be found in correct identification; for example, the Garki project⁹, and insecticide resistance in *An. arabiensis* in Zimbabwe¹⁰. Furthermore, the marked exophily of *An. arabiensis* poses a very real

Box 1. Countries and Islands Represented in the *Anopheles gambiae* Database

Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Cape Verde Islands, Central African Republic, Chad, Comoros Islands, Congo, Côte d'Ivoire, Democratic Republic of Congo, Equatorial Guinea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea Bissau, Kenya, Liberia, Madagascar, Mali, Mauritania, Mauritius, Mozambique, Namibia, Niger, Nigeria, Réunion, São Tomé, Saudi Arabia, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Uganda, Yemen, Zambia, Zimbabwe.

Visit the website of the Department of Medical Entomology, South African Institute for Medical Research/University of the Witwatersrand for more information or access to the database and bibliography: <http://www.wits.ac.za/fac/med/entomology/medento.htm>

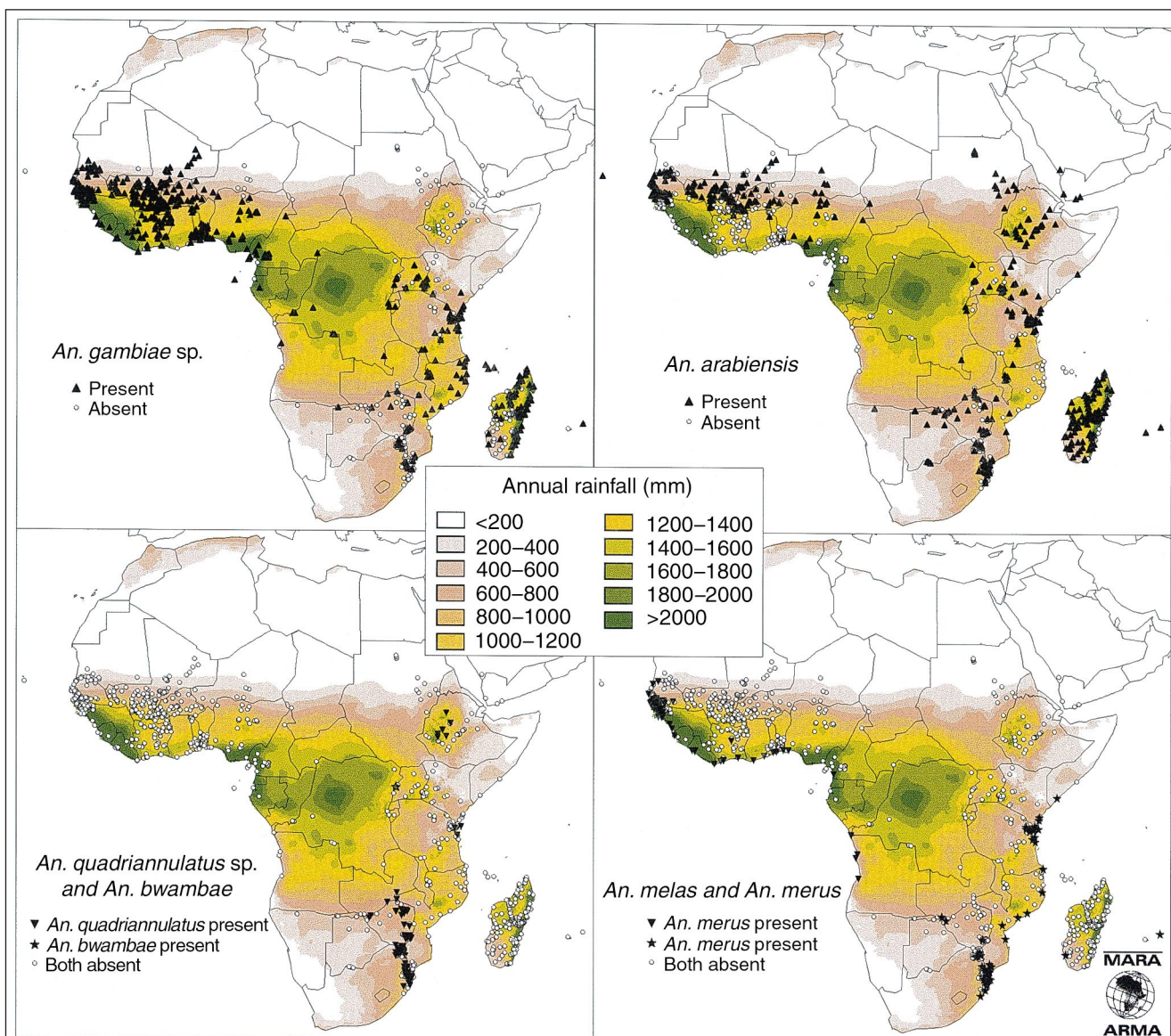


Fig. 1. Collection sites where the six named species of the *Anopheles gambiae* complex have been found (closed symbols), against mean annual rainfall. Open circles indicate collection sites where the species were not recorded, although this does not mean that they are absent from these sites (see text). (*An. gambiae*, n = 542; *An. arabiensis*, n = 475; *An. quadriannulatus*, n = 93; *An. bwambae*, n = 1; *An. melas*, n = 65; *An. merus*, n = 55). 'sp.' after *An. gambiae* and *An. quadriannulatus* indicates that these taxa include more than one species.

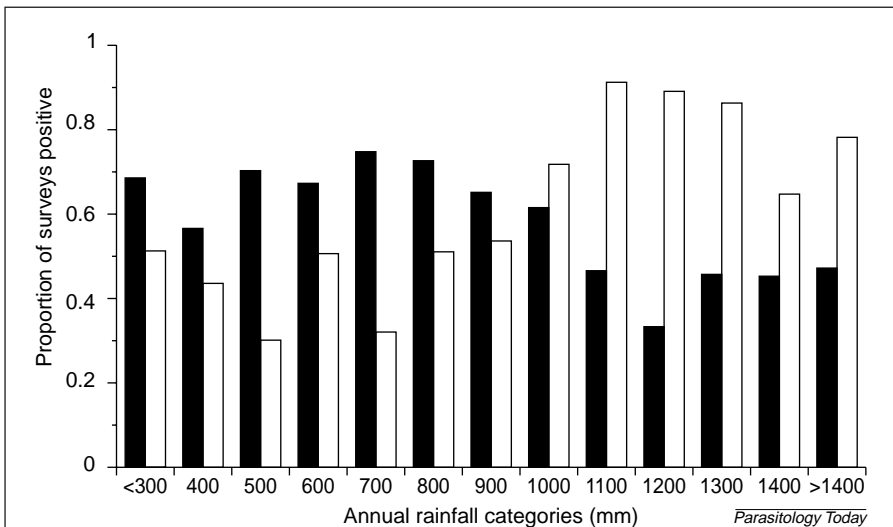


Fig. 2. The proportion of total collection sites ($n = 815$) in which *Anopheles gambiae* (open bar) and *An. arabiensis* (closed bar) were found, plotted against total annual rainfall. The two end categories represent pooled data because there were too few sites in each for further subdivision to be meaningful. Sites for which no rainfall data were available have been excluded.

distribution maps. Distributional records are based solely on identified samples, and come from scientific publications, reports of the Ross Institute of the London School of Hygiene and Tropical Medicine and unpublished records from recognized research institutions that carry out species identifications. The computer programs used were dBASE III Plus and Quattro Pro for the databases and MapInfo for the production of the maps. The database used to compile the maps includes the following categories: country, place name, map coordinates, species, method of collection, date of collection, method of identification, number of specimens identified and the references from which the data were obtained.

Members of the *An. gambiae* complex have been reported from

problem for control measures focused on indoor resting and biting behaviour.

Likewise, in southern Africa the cattle-feeding, normally outdoor-resting, non-malaria vector species *An. quadriannulatus* can sometimes be found resting in houses¹¹. This means that, in areas where *An. quadriannulatus* occurs, monitoring of '*An. gambiae*' populations must be accompanied by accurate species identification so that scarce resources are not wasted on controlling a species that does not transmit malaria parasites. The fact that Ethiopian *An. quadriannulatus* sp. B has been regarded as the same species as its southern African namesake has led researchers into assuming that the behaviour and vector capacity are also the same. This might not be so, and further studies on correctly identified *An. quadriannulatus* sp. B in Ethiopia are needed.

Research studies on host-seeking behaviour, distribution, feeding preferences and response to insecticide impregnated bednets cannot be evaluated without identification of the species under study.

Since the recognition of the complex in 1962, precise identifications of each species have been carried out using various methods. These include chromosomal banding arrangements¹², isoenzyme electrophoresis¹³, crossmating techniques¹⁴, salinity tolerance tests¹⁵ and, most recently, DNA studies using PCR¹⁶.

It is obvious from the above that a working knowledge of where malaria vector species occur is essential for the malaria control programme manager. As a result, distributional and biological data have for many years been collected by entomologists and malariologists throughout Africa. The aim of the present work was to pull together all these records into a single database, produce distributional maps of the members of the *An. gambiae* complex, and provide individual countries with a source of reference material for work carried out in their area.

Data collection and distribution

The collection of distributional data was initiated by the late George Davidson of the London School of Hygiene and Tropical Medicine, UK, who spent much of his retirement collecting and collating data for the

most countries of Africa and its adjacent islands, including Madagascar, as well as Saudi Arabia and Yemen (Box 1). The database has 2537 records, at 1231 localities, from 215 sources, dating from 1944 to the present. It is being updated continuously, as new distributional records appear in the literature. Figure 1 shows the total distribution of each species for the whole of Africa overlaid on mean annual rainfall for the continent. These computerized maps are based on updates of the data produced by Davidson and Lane (unpublished) and presented in Ref. 1.

A glance at the maps produced here will reveal the areas where the most work has been done. Those parts of the maps that are blank do not necessarily indicate that there are no mosquitoes of the *An. gambiae* complex present, but only that no species identifications have been published from those areas. The reader is cautioned that some distributional points might be inaccurate because of incorrect identifications¹⁷ or incorrect locality data in the original publications. Indeed, original map coordinates placed some records in the wrong country, or in the ocean. In addition, at least one record of *An. gambiae* in southern Africa is known to be the result of laboratory contamination¹⁷.

The database has several other limitations. Over the past 35 years many entomologists and malariologists have studied various aspects of the *An. gambiae* complex throughout Africa. Obviously, each study was carried out independently, using different collection and identification techniques, and without reference to other similar studies. Therefore, the database cannot be used to extract behavioural data, for example, on a wide geographical scale. Some studies included large samples of mosquitoes from well-defined areas, enabling conclusions to be drawn on the relative abundance of the species present. Other data points, however, are the result of a single specimen being identified, and no conclusions can be reached on the presence or absence of other members of the group at these localities. As a result, we have limited our use of the database here to reflect only point data and to produce overall distributional maps for the individual species (Fig. 1).

Recently, a model has been designed to predict the species ranges and relative abundance of *An. gambiae* and *An. arabiensis* using rainfall and temperature data¹⁸. The model is based on a relatively small selection of mosquito distribution data, which might account for the difference between the predicted ranges and those produced by Davidson and Lane (unpublished) and here. It should be possible, however, with careful extraction of certain records from the current database, to improve such models for their predictive value.

Clearly, the distribution of *An. arabiensis* (Fig. 1) is concentrated in the lower rainfall zones, which represent the drier savannah areas. This is in keeping with the known habitat preferences of this species^{1,3}, which are further illustrated in Fig. 2: in collection sites where annual rainfall was <1000 mm, *An. arabiensis* was recorded more often than *An. gambiae*, whereas the reverse was true where rainfall was >1000 mm. Anomalies showing *An. arabiensis* occurring in desert areas (Fig. 1) can be explained by their association with river systems (eg. the Niger in Mali, and the Nile in Sudan). The occurrence of *An. gambiae* in the arid regions of Mali along the River Niger has been shown to be associated with the 'Mopti' chromosomal form¹⁹. Where *An. arabiensis* occurs in equatorial rainforest regions, it is usually associated with a history of extensive land clearance (eg. in Benin City, Nigeria)³, although this is not always the case. The occurrence of *An. quadriannulatus* in Ethiopia at localities with mean annual rainfall figures of >1000 mm (Fig. 1) is in sharp contrast with the southern African data points, where annual rainfall is ~700 mm. This anomaly is explained by the discovery in Ethiopia of a previously undescribed member of the *An. gambiae* complex, with the same polytene chromosome arrangements as *An. quadriannulatus*². It is unknown whether the southern African *An. quadriannulatus* also occurs in Ethiopia.

The incipient species or chromosomal forms of *An. gambiae* and *An. arabiensis* in West Africa have not been differentiated in the database because of the debate still surrounding their specific status^{3,4,6}. Once this problem is resolved, the database will be changed to reflect the distribution of the various species currently within the nominal taxa.

Conclusion

If all the species of the *An. gambiae* complex exhibited identical behavioural characteristics and had the same ability to transmit malaria parasites to humans, then distributional data of the nominal species and those hidden within the taxa (eg. West African incipient species of *An. gambiae*) would not be important. However, as mentioned above, this is not the case, and the species range from excellent vectors of malaria to those not involved in transmission at all. Distribution records thus provide valuable data on where the species occur, and can be used by control programme managers in the planning of strategies to combat malaria in their areas.

It is obvious from the maps presented here that large areas of the continent have no reliable data on the presence or absence of malaria vectors. There is an urgent need for baseline surveys to be carried out in these countries, both on the distribution of the vectors and on the incidence and prevalence of malaria in the human populations.

Those involved in malaria control programmes are encouraged to visit the website (Box 1) containing the database and bibliography. Information from specific countries or regions will gladly be made available on request. The database will continue to be updated periodically as new publications come to hand.

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