

The zoogeography of *Aedes* (*Diceromyia*) Theobald (Diptera: Culicidae)¹

by

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Introduced by Botha de Meillon

SUMMARY

The geographical distribution of the subgenus *Diceromyia* is confined chiefly to the savanna and forest fringe areas of the Ethiopian and Oriental Regions. Eight species are limited to the former area and eleven to the latter, with no species occurring in both regions. The hypothesis is presented that the subgenus evolved from an *Aedimorphus* stock in the Indian area and dispersed to the Ethiopian Region when the climate and vegetation of the intervening area were more propitious. As the climate changed in the connecting area, the favourable environmental corridor ceased to exist and the populations of the two areas dispersed and evolved in their respective regions. The present ranges of the species correspond more or less with definite climatic and vegetative zones found in the Oriental and Ethiopian Regions. All recorded collection localities for the subgenus are listed in two appendices and are plotted on distribution maps.

INTRODUCTION

The mosquito subgenus *Aedes* (*Diceromyia*) Theobald is confined to the Ethiopian and Oriental Zoogeographical Regions and as regards number of species is about evenly represented in each area. Eleven species are limited to the Oriental Region and eight are found in the Ethiopian Region, and of these one is endemic to Madagascar. No species occurs in both regions. A review of the subgenus and a discussion of the species in Southeast Asia is given by Reinert (1970), while most species from the Ethiopian Region are covered by Edwards (1941), Hopkins (1952) and Muspratt (1955).

The *Diceromyia* share certain characters with other subgenera of *Aedes*. The palpi of the male are similar to those found in some *Stegomyia*, *Ochlerotatus* and *Finlaya*, while the antennae are typical of *Aedimorphus*. The paraproct and the toothed aedeagus of the terminalia are similar to those of *Aedimorphus* and *Stegomyia*. The adult habitus of the *Diceromyia* has a semblance to members of *Aedimorphus*, *Stegomyia* and *Finlaya*. Other characters and similarities are discussed by Reinert (1970) and Mattingly (1959).

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PLACE OF ORIGIN

The morphological and ecological resemblances of the *Diceromyia* to the Indian *Aedes* (*Aedimorphus*) *nummatus* Edwards, which is apparently plastic in its choice of bamboos or tree holes as breeding sites, suggest that the subgenus may have evolved from an *Aedimorphus* stock in the Oriental Region and that one group, breeding in tree holes, dispersed westward into Africa while the other group, breeding in bamboos, spread into Southeast Asia. The present African species of *Diceromyia* breed almost exclusively in tree holes. The Indian species *Aedes micropterus* (Giles), *periskelatus* (Giles), *reginae* Edwards and *ramachandrai* Reuben breed primarily in tree holes, while the usual breeding habitat of the other Oriental species is in bamboos.

An alternate hypothesis is that the subgenus may have evolved in Africa from group A of *Aedimorphus* (Edwards, 1932:166), since there are marked affinities between the two groups, and then dispersed to the Oriental Region. A third possibility is that the *Diceromyia* arose from some ancestral *Aedimorphus* stock in the intervening area between Africa and Eurasia and that, prior to being eliminated in the area by unfavourable environmental conditions, populations of the subgenus dispersed into the Ethiopian and Oriental Regions.

The place of origin of the *Diceromyia* is purely speculative, but the hypothesis that the subgenus was derived from an Indian *Aedimorphus* stock and spread into Africa seems a likely choice.

ROUTE OF DISPERSAL

A corridor extending from India, by way of the Mediterranean area, to Africa provides a route of dispersal for the *Diceromyia* that seems most plausible. The present distribution, as given by Mattingly (1952), of another tree-hole-breeding species complex, *Aedes* (*Stegomyia*) *unilineatus* (Theobald), *grantii* (Theobald), and *cretinus* Edwards, in India, Crete, Macedonia, Transcaucasia and Africa provides some evidence for this route of dispersal. The range from the Mediterranean area into Southeast Asia—namely, Morocco, Tunisia, Iran, Kazakh S. S. R., Pakistan, and Thailand—of *Aedes* (*Ochlerotatus*) *pulchritarsis* (Rondani) also adds credibility to this pathway of dispersal between the Oriental and Ethiopian Regions.

Dispersal of the *Diceromyia* between the two regions may conceivably have taken a route through the southern portion of Arabia or, as mentioned previously in the third hypothesis on the origin of the subgenus, it may have spread from a point in the intervening area into both Eurasia and Africa. These routes of dispersal seem less likely but provide alternatives to the first-mentioned hypothesis.

The absence of the subgenus from the Seychelles, Agalega, Laccadive and other islands in the Indian Ocean suggests that the *Diceromyia* did not cross this water barrier but dispersed by one of the routes described above.

In any case, dispersal between the two zoogeographical regions probably occurred when the climate in the intervening area was more favourable than the arid conditions that exist today. The climate would have provided the necessary temperature and amounts of rainfall needed for the development of vegetation suitable for mosquito breeding. The supposition that a forest provided continuity between the two regions and then ceased to exist would be in accordance with the proposed dispersal and distribution of the *Diceromyia*.

During the Oligocene a land connection became well established between

Africa and Eurasia (Kurten, 1969; Darlington, 1957). These authors base their ideas, as to the time of the land connection, on mammalian fossil records. Moreau (1952) and George (1962) believe that a forest also extended across this intervening area and provided a route of dispersal for the fauna of the two regions. Moreau's hypothesis is based mainly on his studies of the avifauna and flora of Africa and Asia. These studies would support the premise that the environment was favourable, so that the *Diceromyia* may also have dispersed between the two areas during this epoch. Later, towards the end of the Miocene or early Pliocene, the corridor became dry and lost its forests (Moreau, 1952; George, 1962). As the corridor became more arid it formed an effective barrier between the Oriental and Ethiopian *Diceromyia*. The resulting isolated populations then dispersed and evolved in their respective regions. The vicissitudes in the African biomes succeeding the separation of the *Diceromyia* are presented by Moreau (1963) and help one in perceiving the possible pathways of dispersal and evolution of the subgenus on this continent.

RANGE OF THE SUBGENUS

Edwards (1941:460) states that the present distribution of mosquitoes, as of other groups of animals or plants, is conditioned by present factors of climate, association or isolation, by the permanence of these factors in the past and by evolutionary changes in the organisms themselves. Therefore, the present distribution of the subgenus may throw light on past events, and vice versa. However, any discussion on either aspect of the subject must be largely speculative because of the lack of sufficient fossil records.

The present distribution of each species of *Diceromyia* is shown on the maps (figs. 1-4) and is based on all available published collection records. In the Oriental Region none or only fragmentary collections have been made of the mosquitoes from a number of areas such as the Chittagong Hill Tracts of East Pakistan, Burma, Cambodia, Laos, Vietnam and much of Indonesia. In Africa, Gillies and de Meillon (1968:264) list the following areas in which the fauna is still very incompletely known: Angola, Central African Republic, western Cape Province, the central part of the Congo basin, Mozambique, southern and western Tanzania, Zambia and most of the semi-arid areas. Additional data from the Middle and Near East is also needed. Information from these areas could add much to the understanding of the mosquitoes of the Oriental and Ethiopian Regions.

The collection records shown on the maps are listed in appendix 1 for the Ethiopian Region and in appendix 2 for the Oriental Region. These collection localities are indicated by the following format: countries are in capital letters, districts and provinces, where known, are in italics and place names have the first letter capitalized.

LIST OF WORLD SPECIES OF DICEROMYIA

Oriental Region

franciscoi Mattingly, 1959
iyengari Edwards, 1923a
kanarensis Edwards, 1934
micropterus (Giles, 1901)
periskelatus (Giles, 1902)
platylepidus Knight and Hull, 1951
punctipes Edwards, 1921
ramachandrai Reuben, 1967
reginae Edwards, 1922
scanloni Reinert, 1970
whartoni Mattingly, 1965

Ethiopian Region

adersi (Edwards, 1917)
bananea Wolfs, 1958
fascipalpis (Edwards, 1912)
flavicollis Edwards, 1928
furcifer (Edwards, 1913)
grassei Doucet, 1951
taylori Edwards, 1936
zethus De Meillon and Lavoipierre, 1944

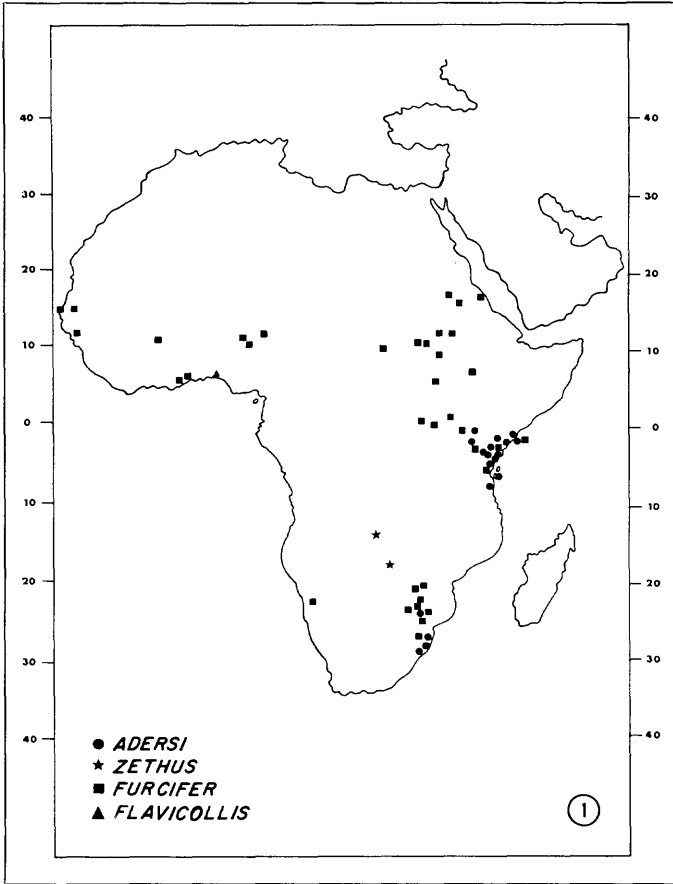


Fig. 1. Distribution of *Aedes (Diceromyia)* in the Ethiopian zoogeographical region.

DISTRIBUTION IN THE ETHIOPIAN REGION

In Africa the distribution of the subgenus follows a pattern very similar to the boundaries of the periodically dry savanna climate **Aw** of Koppen (1931). This is a tropical rainy climate with a periodic dry season during the winter. The plotting of the collection records on the maps (figs. 1 and 2) shows that the range of *Diceromyia* species forms a belt from Senegal east across the continent to Sudan, where there is an extension north and east to Eritrea. The belt forms a southeastward extension from Sudan to Zanzibar and then south to Natal with a noticeable westward bulge encompassing Rhodesia. The distribution of the subgenus also occupies a small strip of similar climate along the southern margin of Ghana and Nigeria. Two other isolated collection locations, one on the west tip of the Republic of Congo and another in Madagascar, also have more or less similar climates. These climatic belts have temperatures and a

rainfall periodism that is conducive to the formation of the savanna and forest fringe vegetation which provides the principal breeding habitats of the *Diceromyia*. Zonal climate is one of the most important barrier systems or limiting factors in animal distribution according to Darlington (1957), and the range of the *Diceromyia* agrees with this supposition. Reference to Mattingly (1952, 1953), who lists the altitude and annual rainfall for many African localities, will give the reader a better understanding of the areas in which the *Diceromyia* occurs.

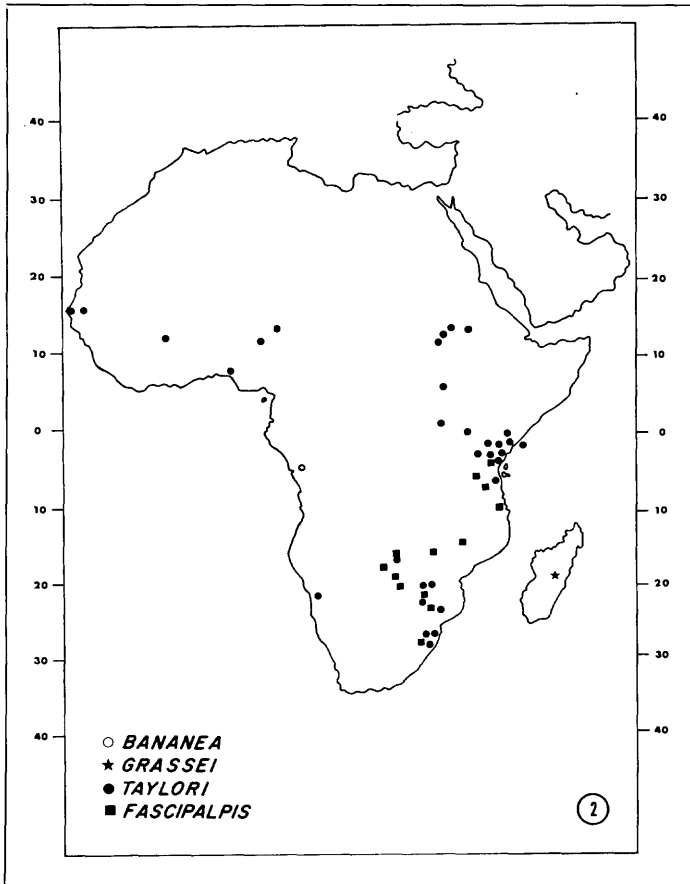


Fig. 2. Distribution of *Aedes* (*Diceromyia*) in the Ethiopian zoogeographical region.

Species of this subgenus, as well as other *Aedes*, are well adapted to the above-mentioned climate and habitat as demonstrated by their eggs which are capable of withstanding desiccation for extended periods of time (Muspratt, 1955:174). The finding of *Aedes furcifer* and/or *taylori* at Okimbahe, a semi-desert area in South West

Africa with an annual rainfall between $2\frac{1}{2}$ and 5 inches, exemplifies the ability of these species to withstand dry seasons and semi-arid areas by means of the erratic hatching and drought resistance of the eggs. Muspratt (1956), for example, kept dried eggs of *Aedes furcifer* for more than 14 months and still obtained hatching when they were flooded. Another factor important in the distribution of the *Diceromyia* is the flight range of the adults. Mattingly (1962:31), while discussing biological factors involved in the distribution of mosquitoes, points out that flight range is an important factor in dispersal and that savanna species probably cover much larger distances than forest species, mainly because of the restricted habitat of the latter. A continuous forest serves as a barrier to non-forest species and may help to explain the distribution of the *Diceromyia* in the climatic belts surrounding the tropical forests in Africa. This is particularly true of *Aedes furcifer*, *taylori* and *fascipalpis*, which have wide ranges. Three of the eight Ethiopian species, namely, *Aedes bananea*, *flavicollis* and *grassei*, however, are known only from their type localities, while an additional species, *zethus*, has been collected from only two locations. These latter four species have isolated ranges in various parts of the region, indicating that they may be relict or relatively new species.

DISTRIBUTION IN THE ORIENTAL REGION

The range of the subgenus in the Oriental Region is confined mainly to the warm temperate rainy climates with dry winters (Koppen's **Cw** type) and tropical rainy climates with dry winters (**Aw** type). The distribution of the Oriental species (figs. 3 and 4) follows a belt more or less along these climatic zones. The range extends from north-west and central India south along both coasts and then throughout most of Thailand and south through the Malay Archipelago to Sumba in the Lesser Sunda Islands.

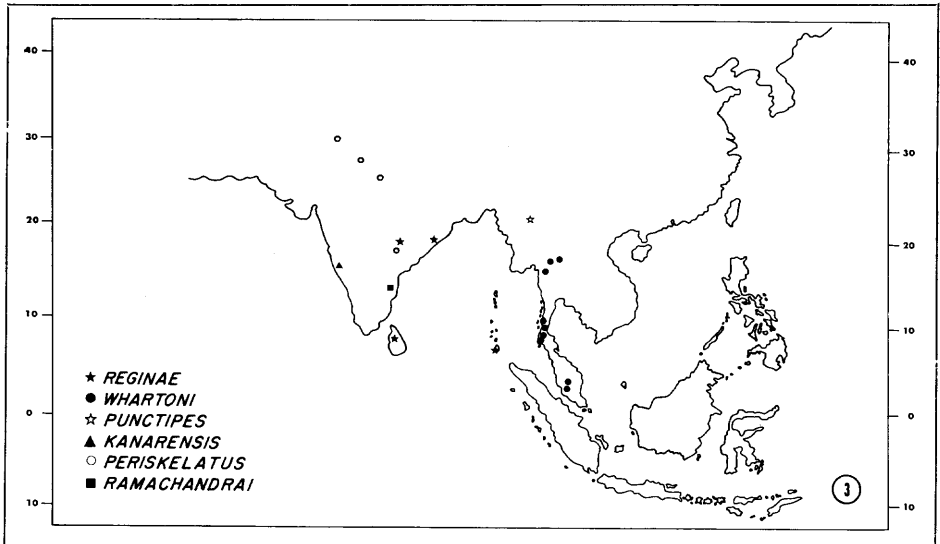


Fig. 3. Distribution of *Aedes* (*Diceromyia*) in the Oriental zoogeographical region.

Aedes micropterus and *periskelatus* have wide ranges associated with the dry tropical and shrub and thorn forests of the Indian area, while *Aedes reginae* has a distribution from Kharghpur, India, south to Ceylon and east to the Nicobar Islands. Although *Aedes iyengari* has the widest distribution in the Oriental Region, its range is fragmented into several locations. A collection at Karwar, India, is disjunct from records occurring in a belt from Calcutta through Assam, Burma and into northern Thailand, and a wide gap separates the Thailand records and the records in Indonesia. The collection of *Aedes iyengari* from Sumba extends the range of the subgenus nearly to Weber's Line, which is the southeastern limit of the subgenus. *Aedes whartoni* has a distribution from north Thailand to the center of the Malaya Peninsula, while the aberrant *Aedes platylepidus* is known from five specimens collected on three islands in the Philippines. The remaining Oriental species are known only from their type localities or have very limited distributions.

Brug and Bonne-Wepster (1947:195) reason that species of mosquitoes which breed in bamboo may be transported throughout the Malay Archipelago in bamboo water containers carried on board primitive crafts. Since bamboo is still used to store drinking water by primitive communities within the area, species of *Diceromyia* may have been spread in the region by this method. A portion of the Malay Archipelago has not been collected in detail and when more information is obtained it may show that the subgenus has a wider range in this region, since favourable climatic conditions and breeding habitats are available.

The subgenus has similar habitat and climatic requirements in both the Oriental and the Ethiopian Regions, where it breeds primarily in tree holes and bamboos found in savanna or along forest fringes. The distribution of the *Diceromyia* in

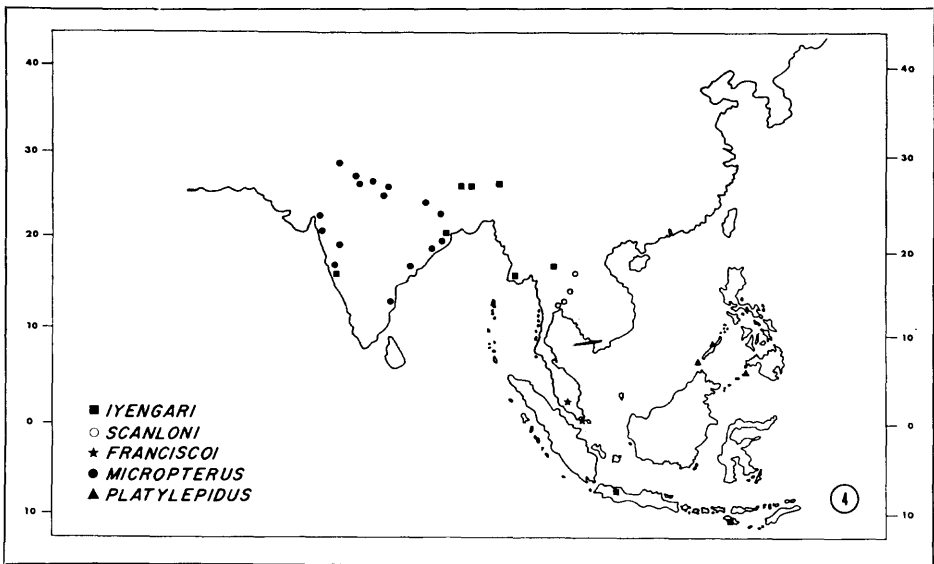


Fig. 4. Distribution of *Aedes* (*Diceromyia*) in the Oriental zoogeographical region.

similar climatic zones in both regions supports Gressitt's theory (1952) that insects do not quickly change their climatic tolerances. He gives as evidence the occurrence together, in ancient deposits of fossils, of groups of organisms that have similar macroclimatic tolerances today, while other evidence suggests some parallels between evolution and dispersal of insects and host-plants with which they are intimately associated.

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APPENDIX 1

Collection Localities of *Aedes* (*Diceromyia*) in the Ethiopian Zoogeographical Region

- Aedes adersi*—KENYA, Gede (van Someren et al., 1955; Bailey, 1947); Penda Kula (Haddow, 1961); Taveta, Mahou (Lumsden, 1955); Kwale, Kaloleni, Vanga, Msambweni, Mombasa, Takaungu, Ganda, Malindi, Mambui (van Someren et al., 1955); Isiolo, Kilifi (Edwards, 1941); Kwa Shekh (Teeddale, 1959); *Pate Island*, Faza (van Someren & Furlong, 1964). SOUTH AFRICA, *Zululand*, St. Lucia; *Natal*, Isipingo Beach (Muspratt, 1955); *Transvaal*, Tzancen (De Meillon et al., 1945). TANZANIA (Tanganyika), Dar-es-Salaam, Tanga, Lindi (Edwards, 1923b; Haworth, 1924; Harris, 1942); (Zanzibar), Mnazi Moja (Edwards, 1917; Aders, 1916).
- Aedes bananaea*—DEMOCRATIC REPUBLIC OF THE CONGO (Belgian Congo), *Bas-Congo*, Banana (Wolfs, 1958).
- Aedes fascipalpis*—BOTSWANA (Bechuanaland), Kasane (De Meillon, 1947); Nata, Francistown (Muspratt, 1955). MALAWI (Nyasaland), Fort Johnson (Edwards, 1941). RHODESIA (Southern Rhodesia), Shamva (Edwards, 1941). SOUTH AFRICA, *Tongaland*, N'dumu (Muspratt, 1959); *Transvaal*, Rolle Siding (Edwards, 1941); Kaapmuiden, Malelane (Muspratt, 1956); Messina (Muspratt, 1955). TANZANIA (Tanganyika), *South Usangu*, Little Ruaha River (Edwards, 1912; Neave, 1912); Tanga (Muspratt, 1959; Harris, 1942); Iringa (Edwards, 1941); Lindi (Haworth, 1924). ZAMBIA (Northern Rhodesia), Livingstone (De Meillon & Lavoipierre, 1944; Muspratt, 1945; Robinson, 1948).
- Aedes flavicollis*—NIGERIA, Lagos (Edwards, 1928); Itowolo (Mattingly, 1949).
- Aedes fuscifer*—ETHIOPIA, *Eritrea* (Stone et al., 1959); Manera (Neri et al., 1968). GAMBIA (Stone et al., 1959). GHANA (Gold Coast), Weshiang (Edwards, 1913); Accra (Macfie & Ingram, 1923; Edwards, 1941). KENYA, Gede (van Someren et al., 1955); Taveta (Lumsden, 1955); Penda Kula (Haddow, 1961). NIGERIA, *Kano*, Kano (Kumm, 1931; Philip, 1931); *Gadua* (Taylor, 1934); *Zaria*, Kaduna (Hanney, 1960; Service, 1964); Kangimi, Anguwun Rimi (Service, 1963). PORTUGUESE GUINEA, Bolama (Edwards, 1941). RHODESIA (Southern Rhodesia), Chipinda Pools on Lundi River, Lone Star Ranch near Lundi (McIntosh et al., 1964; Paterson & McIntosh, 1964). SENEGAL, Dakar, Thies (Hamon et al., 1955). SOUTH AFRICA, *Zululand*, Simbu, Tete (Muspratt, 1956); *Transvaal*, Tzaneen (Ingram & De Meillon, 1929); Rolle Siding (Edwards, 1941; De Meillon et al., 1945); Malelane (Muspratt, 1955); Kaapmuiden (Muspratt, 1956); Potgietersrus (Muspratt, 1956). SUDAN, Nasser, Sobat River (Theobald, 1911); *Kordofan*, Heiban, Nuba Mt. Area, Andona (Lewis, 1942, 1943); Blue Nile (Theobald, 1906); Alleira, Um Dona, Delami, Jebel Deri, Zalutaya; *Darfur*, Zallingei (Edwards, 1941). TANZANIA (Tanganyika), Muhesa (Harris, 1942). UGANDA, Soroti (Edwards, 1941); *Bwamba*, Mongiro (Lumsden, 1952; Haddow et al., 1951); *Karamoja*, Loyoro (Haddow, 1961); Kampala and Entebbe Townships (Hancock, 1930).
- Aedes grassei*—MALAGASY REPUBLIC (Madagascar), Perinet (Doucet, 1951).
- Aedes taylori*—KENYA, Gede (Bailey, 1947); Kwale, Takaungu (van Someren et al., 1955); Taveta, Homer, Njoro, Mahou (Lumsden, 1955); Penda Kula (Haddow, 1961). NIGERIA, *Gadua* (Edwards, 1936); Itowolo (Mattingly, 1949); *Zaria*, Kaduna (Hanney, 1960). RHODESIA (Southern Rhodesia), Chipinda Pools on Lundi River, Lone Star Ranch near Lundi (McIntosh et al., 1964; Paterson & McIntosh, 1964). SENEGAL, Dakar, Thies (Hamon et al., 1955). SOUTH AFRICA, *Zululand*, Dukuduku Forest (Muspratt, 1955). SUDAN, *Kordofan*, Heiban, Nuba Mt. Area (Lewis, 1942, 1943); Fung Reach on Blue Nile, Kostu (Lewis, 1947); Juba, Wad El Magdub (Lewis, 1945). TANZANIA (Tanganyika), Tanga, Moshi, Arusha, Dar-es-Salaam (Harris, 1942). UGANDA, *Karamoja*, Loyoro (Haddow, 1961). ZAMBIA, (Northern Rhodesia), Livingstone (De Meillon et al., 1945; Muspratt, 1945; Robinson, 1948).
- Aedes zethus*—ZAMBIA (Northern Rhodesia), Livingstone (De Meillon, 1943; Muspratt, 1945); Balovale (Robinson, 1948).
- Records of either *Aedes fuscifer* or *taylori*—KENYA, Ganda, Mambui (van Someren et al., 1958); *Pate Island*, Faza (Heisch et al., 1959). SOUTH AFRICA, *Natal*, Isipingo Beach;

Golle, Pongola River (Muspratt, 1955); *Transvaal*, Letaba (Ingram & De Meillon, 1929); Waterpoort (Muspratt, 1955). SOUTH WEST AFRICA, Okimbahe (Muspratt, 1955). SUDAN, Mafaza Area, Abu Kidada (Lewis, 1947). UPPER VOLTA, Bobo-Dioulasso, Koumbia (Hamon et al., 1964).

APPENDIX 2

Collection Localities of *Aedes* (*Diceromyia*) in the Oriental Zoogeographical Region

- Aedes franciscoi*—WEST MALAYSIA (Malaya), *Selangor*, Kampong, Sirch, Rantau Panjang (Mattingly, 1959). SINGAPORE, P. Blakang Mati (Mattingly, 1959).
- Aedes iyengari*—BURMA, Rangoon (Barraud, 1934), INDIA, *N. Bengal*, Sukna; *S. Bengal*, Matiabruz, Garden Reach (Barraud, 1934); Calcutta (Senior White, 1934); *Assam* Dibrugarh (Reinert, 1970); *Jalpaiguri*, Meenglas (Edwards, 1923a); Karwar (Barraud, 1928); Kidderpore (Mattingly, 1959). INDONESIA, *Java*, Meester Cornelis (Brug, 1932); Sumba (Bonne-Wepster, 1954); Djakarta (Wijono, 1962; Mattingly, 1959); Bandoeng, Batavia, Purmerend Island (Mattingly, 1959). THAILAND, *Chiangmai*, Doi Pui Mt. (Scanlon & Esah, 1965); Doi Sutep (Reinert, 1970); Northern Thailand (Thurman, 1959).
- Aedes kanarensis*—INDIA, *North Kanara*, Yellapur (Edwards, in Barraud, 1934).
- Aedes micropterus*—INDIA, Allahabad, Lucknow (Giles, 1901); Delhi, Baroda, Pusa, Trombay, Bombay, Poona, Belgaum, Madras (Barraud, 1928); *Bihar*, *Madras*, *Punjab*, *Orissa* (Barraud, 1934). WEST PAKISTAN, Lahore (Barraud, 1928).
- Aedes periskelatus*—INDIA, Shajehanpur (Giles, 1902); Jhansi (Edwards, 1914); Hyderabad City (Qutubuddin, 1945). WEST PAKISTAN, Sadhana (Khokhar & Tariq, 1966).
- Aedes platylepidus*—PHILLIPPINES, *Palawan*, Puerto Princesa; *Balabac*, Cape Melville (Knight & Hull, 1951); *Basilan*, Isabella (Reinert, 1970).
- Aedes punctipes*—BURMA, Maymyo (Edwards, 1921).
- Aedes ramachandrai*—INDIA, *Chittoor*, Musalimadagu and Palmaner Reserve Forests; *Andhra Pradesh* (Reuben, 1967).
- Aedes reginae*—CEYLON, Colombo (Edwards, 1922; Barraud, 1928). INDIA, Kharghpur, Bengal-Nagpur Rly. (Barraud, 1934); Nicobar Islands (Reinert, 1970); un-published record: *N. Arcot*, Venkatapuram (IX. 1962).*
- Aedes scanloni*—THAILAND, *Nakhon Ratchasima*; *Krung Thep*; *Pathum Thani*, Park Kret; *Nontaburi*, Pak Kret; *Udon Thani*, Udornthani (Reinert, 1970).
- Aedes whartoni*—WEST MALAYSIA (Malaya), *Selangor*, Ulu Gombak (Mattingly, 1965); The Gap (Reinert, 1970). THAILAND, *Lampang*; *Nan*; *Phangnga Ranong*; *Tak* (Reinert, 1970).

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