BIONOMICS AND SYSTEMATICS OF THE ORIENTAL ANOPHELES SUNDAICUS COMPLEX IN RELATION TO MALARIA TRANSMISSION AND VECTOR CONTROL

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Abstract. The taxonomic history, distribution, bionomics, systematics, and vector control strategies for the Anopheles sundaicus complex are reviewed in relation to malaria epidemiology. The lack of data on the bionomics, insecticide resistance, and vector capacity, as well as the general lack of surveillance and monitoring of potential vector populations, make the development of targeted control measures problematic. It will be necessary to elucidate, characterize and identify all members of the complex to determine their distributions, disease relationships, ecological relationships, and resistance to insecticides. This knowledge is essential for epidemiological studies, the design and implementation of appropriate vector control measures, and the development of strategies for monitoring and assessing the potential risk of malaria outbreaks due to members of the complex.

INTRODUCTION

Malaria control strategies aim to decrease human morbidity and mortality by limiting parasite transmission. The identification of vector species and knowledge of their ecology and behavior is essential for epidemiologic studies and the design and implementation of appropriate vector control strategies. Among morphologically indistinguishable anopheline species, distinct ecoethologic differences have been used to identify putative species associated with malaria transmission. These putative species are now recognized as distinct genetic species.

In southeast Asia, vector studies and malaria control are focused mainly on three major species complexes: Anopheles dirus Peyton & Harrison, An. minimus Theobald, and An. sundaicus Rodenwaldt. The An. dirus and An. minimus complexes are well known because they are widespread throughout southeast Asia, whereas the An. sundaicus complex has been investigated to a much lesser degree because the species occur mainly in coastal areas. The ecology, behavior, and/or vectorial capacity of An. sundaicus s.l. have been described for populations in India, Indonesia, Malaysia, Vietnam, Myanmar, Thailand, and Cambodia. However, comparisons of the main characteristics of populations across the distribution of the taxon are wanting.

The probability that An. sundaicus represents a complex of species was hypothesized on the basis of ecoethologic differences and isolation of populations on the coastal areas and islands of southeast Asia. The recent use of genetic and molecular tools confirmed the genetic isolation of species that comprise the An. sundaicus complex. Considered an efficient malaria vector taxon, An. sundaicus s.l. has been a principal target of mosquito control programs even though links between biologic characteristics and vectorial capacity have not been clearly defined.

The aim of this report is to consolidate available information about the An. sundaicus complex as a foundation for further investigation and a better understanding of the individual species across their ranges of distribution. Unless otherwise noted, An. sundaicus refers to An. sundaicus s.l. in the discussion of this report.

DISTRIBUTION

The distribution of An. sundaicus includes coastal areas (Figure 1) from northeastern India to southern Vietnam (low the 11th parallel), south to the Nicobar, Andaman, and Indonesian islands. The taxon occurs in southern Sulawesi but is absent from the Philippines and has not been reported from southern Borneo (Figure 1). It has been observed in Pakistan and two localities in northwestern India, but these observations require verification.

Environmental changes due to human activities seem to be causing the disappearance of the taxon from coastal areas. Recent field surveys in southwestern peninsular Malaysia and the eastern coastal region of India (Figure 1) suggest that An. sundaicus no longer occurs there. Earthen embankments were built in peninsular Malaysia to prevent intrusion of sea water and profound ecologic and salinity changes occurred in India, which probably altered or eliminated potential larval habitats. In other countries such as Pakistan, field records are not recent and the occurrence of An. sundaicus is uncertain. In addition, local populations of An. sundaicus are known to have a fluctuating, patchy distribution in space and time, changing through the year in response to the availability of adequate breeding sites.

In general, the distribution of An. sundaicus on the coastal areas and islands of southeast Asia is poorly known due to a paucity of available data.

BIONOMICS: FIRST EVIDENCE OF A SPECIES COMPLEX

Immature stages. The immature stages of An. sundaicus inhabit sunlit bodies of stagnant water, including ponds with vegetation and floating algae, swamps, mangrove wells, rockpools, and particularly shrimp/fish ponds along the coast or irrigated by inland sea water canals, which are reported as favorable habitats in Vietnam and Indonesia. Sea water aquaculture was known during the 18th century in Jakarta to be favorable for malarial mosquitoes, which were most likely An. sundaicus. Lagoons and creeks blocked river mouths are also favorable sites for An. sundaicus larvae. Since the majority of suitable larval habitats are provided with saline water from the sea, An. sundaicus has been described as mainly a brackish water breeder in coastal areas. However, the taxon has been found in inland sites with either brackish or freshwater. In southern Vietnam, where no permanent freshwater breeding sites have been encountered, sea water canals contribute saline water to larval habitats.
Anopheles sundaicus larvae breed in inland freshwater ponds in India,\textsuperscript{31,50} Car Nicobar island,\textsuperscript{46} peninsular Malaysia,\textsuperscript{51} Sarawak (Malaysian Borneo),\textsuperscript{22} and Indonesia.\textsuperscript{15,24,28} Published data indicate that larvae tolerate salinity ranging from 0\% to 11\% (Figure 2), i.e., from freshwater (<0.05\%) to much greater concentrations than sea water (3.5\%). Over time, salinity in ponds changes as a result of rainfall, inundation by sea water, and evaporation.\textsuperscript{27,30} Soeparno and Lair\textsuperscript{15} and Kikuchi and others\textsuperscript{52} noted that the levels of salinity in coastal habitats are affected by tidal movements. Therefore, any comparison of salinity must be done cautiously, as indicated by the different optimal ranges shown in Figure 2. Phan\textsuperscript{30} noted a positive correlation between salinity and vector density, with peak density at the start of the rainy season. This correlation shows the importance of salinity tolerance in larval development. In addition, Collins and others\textsuperscript{28} noted that An. sundaicus females in southern Sulawesi readily oviposit in freshwater if no brackish water sites are available.

The wide range from freshwater to saline breeding sites was one of the differences that led mosquito workers to hypothesize that An. sundaicus was a species complex.\textsuperscript{22} Either different species accounted for observed ecologic differences or one euryhaline species was tolerant to a wide range of salinity. Compared with salinity, the pH of larval habitats is not so variable, ranging from 7 to 8.5 in India, Vietnam, and Java (Indonesia).\textsuperscript{9,14,31,47} Filamentous floating algae and aquatic plants appear to be crucial for the development of An. sundaicus larvae.\textsuperscript{14,47} Aquatic flora supplies food (micro-algae and bacteria) and protection against predators.\textsuperscript{15,53,54} In Bengal, India, Iy-
enger\textsuperscript{55} found a direct relationship between surface algae together with submerged vegetation and breeding sites. Exceptions include sites on the Coral Beach of India\textsuperscript{59} and rockpools on Pandan Beach in the Lundu District of Sarawak (Malaysian Borneo),\textsuperscript{22} where no vegetation was present. Freshwater plants such as Salvinia sp.\textsuperscript{53} and Eichhornia crassipes (water hyacinth)\textsuperscript{52} are associated with the absence of An. sundaicus larvae, but since immature stages occur in freshwater habitats these plants seem to be more a barrier to oviposition than indicators of unfavorable breeding places.\textsuperscript{52}

**Adult behavior.** Differences in adult behavior are also indicators of species diversity. *Anopheles sundaicus* exhibits both endophagy and exophagy. It is mainly endophilic and anthropophilic, but also exhibits exophilic and zoophilic (Table 1). Indoor application of insecticide for vector control showed the presence of exophagic, endophagic, and zoophilic An. sundaicus in areas of the Nicobar islands and Vietnam where the vector was previously known to be endophagic, endophilic, and anthropophilic.\textsuperscript{11,50} Females exhibit a peak of biting activity from 8:00 pm to 3:00 am depending on locality. Adventitious biting in dark houses during the day has been observed in Vietnam,\textsuperscript{10,14} but humans are generally at higher risk of being bitten indoors while sleeping during the night. *Anopheles sundaicus* is capable of flying long distances, ranging from 1.6 to 9 km,\textsuperscript{13,27,40,56} but blood feeding depends on the location and availability of hosts and insecticide pressure.

Due to its ecologic and behavioral plasticity, *An. sundaicus* has adapted to a range of coastal and inland environmental situations. The main requirement is the presence of sunlit breeding sites with fresh or brackish water, floating algae, and non-invasive vegetation in coastal areas and on islands. Adult females are mainly anthropophilic and endophilic. Comparison of the biology of *An. sundaicus* with that of the more intensely studied *An. gambiae* complex in Africa or the *An. minimus* complex in Asia suggested the existence of a species complex in the absence of other evidence. Investigation based on genetic tools confirmed that *An. sundaicus* is a complex of species.

**GENETIC CONFIRMATION OF A SPECIES COMPLEX**

Genetic tools were used to establish beyond doubt that *An. sundaicus* is a species complex. Cytogenetic and enzymatic studies were first carried out on populations from Thailand and Indonesia (Java and Sumatra) that resulted in the discovery of three forms, informally designated forms A, B, and C.\textsuperscript{54,55} A fourth cytotype named D was identified on Car Nicobar Island.\textsuperscript{57} Form A was collected from coastal areas of Thailand, Sumatra, and Java. Form B was mainly collected in the freshwater sites at South Tapanuli in northern Sumatra in association with form A, where it comprised 92.9% of the females captured in September 1993 and 87.5% in September 1994. Form B was also found with form A in a brackish water area at Purwojero in southcentral Java, where it comprised 9.9% of the collections. Form C was only found in one coastal locality at Asahan in northeastern Sumatra, where it occurred in sympatry with both species A and B (48.4% A, 14.5% B, and 37.1% C). The presence of forms A and B at both freshwater and brackish water sites seemed to dispel the hypothesis that populations with different ecologic requirements might represent different species. In fact, use of the cytochrome b and cytochrome oxidase I mitochondrial markers later showed that mosquitoes reared from an inland freshwater pond near Miri and a brackish water rock pool on the shore of the South China Sea in the Lundu District of Sarawak were the same species.\textsuperscript{58} Based on the formal taxonomic recognition and definition of *An. sundaicus* s.s. as the species encountered in Miri and Lundu,\textsuperscript{29} Dusfour and others\textsuperscript{58} demonstrated that form A in the coastal areas of Vietnam and Thailand is a different genetic species of *An. sundaicus* complex.

The genetics of *An. sundaicus* are poorly explored, but the limited chromosomal, isozyme, and molecular studies confirmed that the taxon is a species complex. However, the molecular studies were based on some different populations than the chromosomal and isozyme studies, and the results cannot be correlated entirely. Further investigation using the

| Country                  | Trophic preference | Resting preference | Biting preference          | Source                |
|--------------------------|-------------------|--------------------|---------------------------|-----------------------|
| Cambodia                 | Exophagy          | Endophily          | Anthropophily             | Chow 1970\textsuperscript{16} |
| Cambodia (Nicobar/Andaman) | Exophagy/ endophagy | Endophily          | Zoophily/ anthropophily   | Webster 2000\textsuperscript{59} |
| India (Andaman/Oriissa) | Endophagy         | Endophily          | Anthropophily             | Covell 1927\textsuperscript{70} |
| India (Nicobar)          | Exophagy          | Exophily           | Zoophily/ anthropophily   | Covell and Singh 1942\textsuperscript{21} |
| Indonesia (western Java) | Endophagy         | Endophily          | Zoophily                  | Kalra 1978\textsuperscript{11} |
| Indonesia (central Java) | Endophagy         | Endophily          | Anthropophily             | Kumari and others 1993\textsuperscript{41} |
| Indonesia (Sulawesi)     | Endophagy         | Endophily          | Zoophily                  | Kumari and Sharma 1994\textsuperscript{72} |
| Malaysia                 | Exophagy          | Exophily           | Zoophily/ anthropophily   | Nandi and others 2000\textsuperscript{73} |
| Malaysia (Sarawak)       | Endophagy         | Endophily          | Zoophily/ anthropophily   | Ikemoto 1982\textsuperscript{74} |
| Thailand                 | Exophagy          | Zoophily           | Anthropophily             | Akiyama 1984\textsuperscript{75} |
| Vietnam                  | Endophily         | Anthropophily      | Zoophily                  | Kinnwardoyo and Yoga 1987\textsuperscript{47} |
| Vietnam                  | Exophily          | Anthropophily      | Zoophily                  | Collins and others 1979\textsuperscript{28} |
| Vietnam                  | Exophily          | Anthropophily      | Zoophily/ anthropophily   | Moorhouse and Wharton 1965\textsuperscript{76} |
| Vietnam                  | Endophily         | Anthropophily      | Zoophily                  | Chow 1970\textsuperscript{16} |
| Vietnam                  | Exophily          | Anthropophily      | Zoophily                  | Gould and others 1966\textsuperscript{59} |
| Vietnam                  | Exophily          | Anthropophily      | Zoophily                  | Giang and others 1980\textsuperscript{77} |
| Vietnam                  | Exophily          | Anthropophily      | Zoophily                  | Phan 1998\textsuperscript{70} |
same markers and the same populations is required to clarify the number of species that comprise the complex.

**ANOPHELES SUNDAICUS: A MALARIA VECTOR**

Differences in the adult behavior and larval habitats of *An. sundaicus* are indicative of an increased risk of contact with humans. *Anopheles sundaicus* is considered as either a major vector or secondary vector of malaria depending on region and country.\(^{15,54}\) It was previously regarded as a secondary vector in Thailand.\(^ {18,59}\) However, because of its occurrence close to tourist sites, it is now considered as a potential major vector.\(^ {17}\) In contrast, it has been regarded as the principal vector in coastal areas of India\(^ {23}\), Vietnam,\(^ {14}\) and Indonesia.\(^ {15,48}\) Kirnowardoya and Yoga\(^ {47}\) observed that malaria transmission at Chilacap on Java fluctuated widely, not only from year to year, but also from locality to locality during the same year. In the meantime, *An. sundaicus* was responsible for local epidemics in Orissa, India from 1930 to 1940,\(^ {31}\) in Calcutta in 1936,\(^ {60}\) in Vietnam from 1965 to 1985,\(^ {30}\) and in Indonesia in 1985.\(^ {47}\) Outbreaks in Indonesia are also linked to Calcutta in 1936,\(^ {60}\) in Vietnam from 1965 to 1985,\(^ {30}\) and in Indonesia in 1985.\(^ {47}\) The role of *An. sundaicus* in malaria transmission has been defined as heterogeneous. As such, it poses a threat for malaria epidemics and endemicity in areas of economic development, notably shrimp farming and tourism. Consequently, it is important to monitor populations to better define the actual or potential role of *An. sundaicus* in malaria transmission. The ecologic and behavioral plasticity of this taxon poses difficulties for the development of appropriate vector control strategies.

### CONTROL STRATEGIES

Eradication of *An. sundaicus* was included in the anti-malarial programs undertaken in many southeast Asian countries in the 1950s. The strategy was based on the application of DDT inside houses.\(^ {7,13,30}\) The unforeseen consequence was the rapid resistance of mosquitoes to DDT (Table 3). However, *An. sundaicus* remained susceptible in a few malaria foci of India.\(^ {9,31}\) Other insecticides were used in areas where DDT resistance occurred, but few records report whether *An. sundaicus* has developed resistance. To circumvent or decrease the extent of resistance and avoid wasteful indoor spraying where *An. sundaicus* is exophilic or exophagic, control efforts focused on environmental alteration of breeding sites, particularly in Indonesia.\(^ {42}\) The elimination of brackish water habitats by drainage was effective in decreasing vector den-

### Table 2

| Country              | Year    | Sporozoite rate (%) | Source                        |
|----------------------|---------|---------------------|-------------------------------|
| Bangladesh           | 1952    | 4.3                 | Nasiruddin 1952\(^ {53}\)     |
| Cambodia             | 1977    | 0.4                 | Klein 1977\(^ {79}\)          |
| India (Calcutta)     | 1936    | 3.6                 | Sen 1938\(^ {60}\)           |
| India                | 1948    | 2.7                 | Nagpal and Kalra 1997\(^ {31}\) |
| Indonesia (Sulawesi) | 1953    | 0.04                | Bonne-Webster and Swellengrebel 1953\(^ {78}\) |
| Indonesia (Sulawesi)| 1973    | 0.07                | Collins and others 1979\(^ {28}\) |
| Indonesia (Java)     | 1952–56 | 0.04–0.3            | Sundaraman and others 1957\(^ {56}\) |
| Indonesia (Flores)   | 1991    | 4.2                 | Marwoto and Arbani 1991\(^ {79}\) |
| Malaysia (Sabah Province) | 1957 | 1.65                | Malaria Report 1957 cited in Chow 1970\(^ {16}\) |
| Thailand             | 1986    | 0                   | Gould and others 1966\(^ {29}\) |
| Vietnam (Go Cong Province) | 1961    | 2.9                 | Phan 1998\(^ {40}\)          |
| Vietnam (Go Cong Province) | 1971    | 4.4                 | Phan 1998\(^ {40}\)          |
| Vietnam (Ho Chi Minh Province) | 1968 | 1.03                | Nguyen Tang Am and others 1993\(^ {14}\) |
| Vietnam (Mekong Delta) | 1968     | 0.18               | Hien 1968\(^ {37}\)         |
| Vietnam (Tra Vinh Province) | 1975 | 2.7                 | Giang and others 1980\(^ {27}\) |
| Vietnam (Bac Lieu Province) | 1998 | 0                   | Coosemans and others 1998\(^ {29}\) |


CONCLUSIONS

Due to its plasticity and capacity to transmit malaria, members of the *An. sundaicus* complex represent a threat to coastal and island populations of humans in southeast Asia. The capacity of *An. sundaicus* to develop in seawater, various concentrations of brackish water, and freshwater is not linked to a particular species, but to an ability of the species to adapt to available sites. However, its presence is restricted along the coast, supporting the hypothesis of larval tolerance to freshwater rather than a wide degree of adaptability. The capacity to develop in a range of habitats from freshwater to seawater is not unusual in anopheline mosquitoes that is known for its plasticity and capacity to transmit malaria, as well as the general lack of surveillance and monitoring of potential vector populations, make the development of targeted control measures problematic. The results of recent molecular and phylogenetic analyses of the *An. sundaicus* complex will foster further study of these mosquitoes. The next step should be the elucidation, characterization, and identification of all members of the complex that includes four identified species: *An. sundaicus* s.s. and species A confirmed by molecular markers and species B and C. Such work is needed to determine the distributions, disease relations, environmental characteristics, and insecticide resistance of the individual species. This knowledge is essential for epidemiologic studies, the design and implementation of appropriate vector control measures, and the development of strategies for monitoring the spatio-temporal fluctuations of *An. sundaicus* needed to assess the potential risk of malaria outbreaks.

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