Six new species of the Anopheles leucosphyrus group, reinterpretation of An. elegans and vector implications

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Abstract. Among Oriental anopheline mosquitoes (Diptera: Culicidae), several major vectors of forest malaria belong to the group of Anopheles (Cellia) leucosphyrus Dönitz. We have morphologically examined representative material (> 8000 specimens from seven countries) for taxonomic revision of the Leucosphyrus Group. Six new species are here described from adult, pupal and larval stages (with illustrations of immature stages) and formally named as follows: An. latens n. sp. (= An. leucosphyrus species A of Baimai et al., 1988b), An. cracens n. sp., An. scanloni n. sp., An. baimaii n. sp. (formerly An. dirus species B, C, D, respectively), An. mirans n. sp. and An. recens n. sp. Additionally, An. elegans (James) is redescribed and placed in the complex of An. dirus Peyton & Harrison (comprising An. baimaii, An. cracens, An. dirus, An. elegans, An. nemophilius Peyton & Ramalingam, An. scanloni and An. takasagoensis Morishita) of the Leucosphyrus Subgroup, together with An. baisasi Colless and the An. leucosphyrus complex (comprising An. balabacensis Baisas, An. introatus Baisas, An. latens and An. leucosphyrus). Hence, the former Elegans Subgroup is renamed the Hackeri Subgroup (comprising An. hackeri Edwards, An. pujutensis Colless, An. recens and An. sulawesi Wakoed). Distribution data and bionomics of the newly defined species are given, based on new material and published records, with discussion of morphological characters for species distinction and implications for ecology and vector roles of such species. Now these and other members of the Leucosphyrus Group are identifiable, it should be possible to clarify the medical importance and distribution of each species. Those already regarded as vectors of human malaria are: An. baimaii [Bangladesh, China (Yunnan), India (Andamans, Assam, Meghalaya, West Bengal), Myanmar, Thailand]; An. latens [Borneo (where it also transmits Bancroftian filariasis), peninsular Malaysia, Thailand]; probably An. cracens (Sumatra, peninsular Malaysia, Thailand); presumably An. scanloni (Thailand); perhaps An. elegans (the Western Ghat form of An. dirus, restricted to peninsular India); but apparently not An. recens (Sumatra) nor An. mirans [Sri Lanka and south-west India (Karnataka, Kerala, Tamil Nadu)], which is a natural vector of simian malarias. Together with typical An. balabacensis, An. dirus and An. leucosphyrus, therefore, the Leucosphyrus Group includes about seven important vectors of forest malaria, plus at least a dozen species of no known medical importance, with differential specific distributions collectively spanning > 5000 km from India to the Philippines.

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Introduction

Among the anopheline mosquito fauna of the Oriental Region, the most important vectors of forest malaria belong to the Anopheles leucosphyrus Group (Reid, 1949, 1968), classified in Neomyzomyia Series (Christophers, 1924) of subgenus Cellia Theobald of Anopheles Meigen (Harbach, 2004). The geographical distribution of the Leucosphyrus Group ranges from the southern islands of the Philippines through most of mainland South-east Asia to the Chinese islands of Hainan and Taiwan in the east and westward to southern India and Sri Lanka (Peyton, 1990). Adult males and females of all species in the Leucosphyrus Group have a distinctive broad white-scaled band covering the apex of the hindtibia and base of hindtarsomere 1. Taxonomy of the Leucosphyrus Group was first revised by Colless (1956), who recognized six species (including two subspecies) and five geographical forms of doubtful status, two of which were named as subspecies by Colless (1957): An. balabacensis introitus for the Kepong Form and An. balabacensis baisasi for the Luzon Form. Peyton (1990) corroborated Colless' classification and recognized 14 formally named species, six unnamed species and two geographical forms; he also subdivided the Leucosphyrus Group into Elephants, Leucosphyrus and Riparis Subgroups, based on differential length ratios of the adult female proboscis/forefemur and maxillary palpus/proboscs. Because we ascertained that An. elegans belongs to the An. dirus complex of the Leucosphyrus Subgroup, as explained below, we realign the Elephants Group and propose to rename it the Hackeri Subgroup.

As treated in this paper and its sequel (Sallum et al., 2005), the Leucosphyrus Subgroup consists of two widespread and often sympatric complexes of sibling species, generally known as An. dirus s.l.* and An. leucosphyrus s.l., plus An. baisasi Colless in the Philippines and a poorly known form in Con Son island, Vietnam. The Dirus Complex includes An. dirus Peyton & Harrison (An. dirus s.s.* or species A), three previously unnamed species (An. dirus B, C and D), An. elegans (=An. dirus E), An. takasagoensis Morishita and An. nepomphilus Peyton & Ramalingam. The Leucosphyrus Complex includes An. balabacensis Baisas, An. introitus Colless and An. leucosphyrus Dönitz (An. leucosphyrus s.s. = species B of Baimai et al., 1988b) plus one previously unnamed species (An. leucosphyrus A). The Riparis Subgroup remains unchanged with three recognized species: An. cristatus King & Baisas, An. macartthuri Colless and An. riparis King & Baisas. The Hackeri Subgroup has three recognized species (An. hackeri, An. pujatensis and An. sulawesi) plus two previously unnamed species, one known as An. leucosphyrus Sumatra Form and the other previously misidentified as An. elegans (Colless, 1956; Reid, 1968; Peyton, 1990; Harbach, 2004).

Peyton & Harrison (1979) described An. dirus based on morphological features of the adult, pupal and larval stages. Later, Peyton & Harrison (1980) removed An. takasagoensis from synonymy with An. balabacensis based on morphological evidence and hybridization tests between An. dirus and An. takasagoensis. Other studies of the Dirus and Leucosphyrus Complexes showed that they were groups of apparently isomorphic but reproductively distinct species. Discovery of most members of the Dirus Complex was achieved primarily with crossing studies, cyto genetics (chromosome banding patterns), allozyme data, DNA probes and DNA hybridization (Hii, 1984b; Bibowo et al., 1984; Baimai et al., 1987, 1988a; Panyim et al., 1988; Green et al., 1992; Andhio et al., 1995). Cytogenetic studies on members of the Leucosphyrus Group in Thailand and peninsular Malaysia showed differences in the amount and distribution of heterochromatin in the sex chromosomes, suggesting that An. dirus s.l. comprised at least four genetically distinct genetic species: these were designated An. dirus A, B, C and D (Baimai et al., 1981, 1984; Hii, 1982; Bibowo et al., 1984). Kanda et al. (1981, 1983) studied nine geographical populations of the Leucosphyrus Group collected in Thailand and Malaysia: from morphological characters, hybridization tests and cyto genetics they found various degrees of relatedness between the populations, concluding that An. balabacensis and An. dirus were not specifically distinct. More recently, however, molecular methods (DNA-based polymerase chain reaction, PCR) have been developed to differentiate members of the Dirus Complex (Audtho et al., 1995; Xu et al., 1998; Walton et al., 1999; Huong et al., 2001; Manguin et al., 2002), confirming the status of species A, B, C and D. Also, two species in the Leucosphyrus Group, An. leucosphyrus A and B, were recognized from mitotic chromosome karyotypes and cross-breeding experiments (Baimai et al., 1988b).

Hitherto, three members of the Leucosphyrus Group – An. balabacensis, An. dirus s.l. and An. leucosphyrus s.l. – have been considered to be of epidemiological importance because

* Senso stricto (s.s.) means 'in the strict sense', i.e. the exact species. Senso lato (s.l.) means 'in the broad sense', i.e. any or all members of the species complex.

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they are highly competent vectors of human malaria parasites in South-east Asia. Moreover, *An. balabacensis* and *An. leucosphyrus* s.l. transmit *Wuchereria* parasites causing lymphatic filariasis in Borneo (Zuluet al., 1957; White, 1983). However, the involvement of members of the Leucosphyrus Group in the epidemiology of human malaria and filariasis is not fully understood because the species involved in transmission are difficult to distinguish using morphological characters. These species can be identified only by examining morphological characters of associated adult, pupal and larval stages, or by genetic methods (chromosomal characters and molecular diagnostics). To facilitate identification of known species, in preparation for taxonomic revision of the Leucosphyrus Group (Sallum et al., 2005), this paper formally describes and names six new species based on morphological features, and settles the taxonomic position of *An. elegans*.

Materials and methods

We employed standard methods for mounting, storing and microscopic examination of anopheline mosquitoes (http://wrbu.si.edu/wrbu.html), with emphasis on adults associated with pupal and larval skins, after their collection from the field by many collaborators using various sampling methods (Service, 1993). Terminology for morphological characters follows Harbach & Knight (1980; 1981), except we used Belkin (1962) for wing veins and Willkerson & Peyton (1990) for wing spots. The toothed margin index of the pupal paddle was defined by Colless (1955) to express the ratio of the lengths: (a) from the tip of the inner basal tubercle of the paddle to the base of the most distant marginal tooth and (b) from the same point to the base of seta 1-Pa. The basal extention of the PSD spot (see Wing spot abbreviations) on vein R as compared to the HD, PSP and PSD spots on the costa defines the level of extension of the PSD (Peyton & Ramalingam, 1988). Level 1 is defined as the PSD on vein R not extending basally beyond the PSD on the costa, level 2 as the PSD extending basally but not beyond 0.5 of the PSP, level 3 as the PSD extending basally beyond 0.5 of the PSP but not to the level of the HD, level 4 as the PSD extending basally to the level of the HD but not beyond 0.5 of the HD, level 5 as the PSD extending basally beyond 0.5 of the HD but not beyond the HD, and level 6 as the PSD extending basally beyond the HD. The number of pale interruptions on PSD-PD spots is defined as the sum of pale interruptions on PSD and PD spots of vein R.

Abbreviations

Acc. no., collection accession number; AFRIMS, Armed Forces Research Institute of Medical Sciences, Bangkok, Thailand; ASA, allele-specific amplification; BMNH, The Natural History Museum, London, U.K.; F, female; H-banding, heterochromatin bands of the chromosome; ITS2, internal transcribed spacer 2 of the ribosomal DNA; L, larva; Le, larval exuvia; M, male; mtDNA, mitochondrial DNA; NMNH, National Museum of Natural History, Washington D.C., U.S.A.; P, pupa; PCR, polymerase chain reaction; Pe, pupal exuvia; RFLP, restriction fragment length polymorphism; SCAR, sequence characterized amplified regions. Wing spots: AD, apical dark spot; ASP, accessory sector pale spot; HD, humeral dark spot; HP, humeral pale spot; PD, posterior dark spot; PHP, prehumeral pale spot; PP, preapical pale spot; PSD, presector dark spot; PSP, presector pale spot; SCP, subcostal pale spot; SD, sector dark spot; SP, sector pale spot. An asterisk (*) after the life stage means that at least part of it is illustrated. Complete lists of specimens examined and distribution maps for each species will be provided later (Sallum et al., 2005), along with illustrations of relevant parts of adults, fourth-instar larva and pupa, showing taxonomic character states, plus identification keys to the *An. leucosphyrus* group of species.

**Leucosphyrus subgroup**

**Leucosphyrus Complex**

*Anopheles (Cellia) latens* Sallum & Peyton, sp.n.

Etymology: the name *latens* is from Latin, meaning concealed, secret, hidden, latent.

*Anopheles leucosphyrus* of Leicester, 1903: 291 (bionomics).

*Myzomyia leucosphyrus* of Daniels, 1908: 1 (*An. hackeri* and *An. leucosphyrus* mixed, bionomics); Leicester, 1908a: 7 (bionomics); Leicester, 1908b: 18 (F, M, bionomics, probably mixed with *An. hackeri*); Leicester, 1908c: 267 (feeding behaviour, probably mixed with *An. hackeri*).

*Neomyzomyia elegans* of James & Stanton, 1912: 59.

*Anopheles leucosphyrus* of Kanda et al., 1981: 321 (hybridization, taxonomy); Kanda et al., 1983: 193 (phylogeny, chromosomal polymorphism); Takai et al., 1984: 145 (genetics); Takai, 1986: 45 (in part, electrophoresis, Sarawak); Harbach et al., 1987: 241 (bionomics); Chang et al., 1995: 192 (bionomics); Seng, 1999: 454 (bionomics).

*Anopheles leucosphyrus* species A of Baimai et al., 1988b: 44 (cytogenetics, crossbreeding); Peyton, 1990: 197 (taxonomy).

Female. Head: proboscis uniformly dark-scaled, length 1.92–2.25 mm (mean 2.11 mm), ratio of length to forefemur length 1.06–1.16 (mean 1.12), maxillary palpus length 1.62–2.15 mm (mean 1.89 mm), ratio of length to proboscis length 0.81–0.95 (mean 0.89), ratio of length to forefemur length 0.91–1.07 (mean 1.00), ratio of length of palpomeres 3/4 1.62–2.08 (mean 1.77), 3/5 2.17–2.87 (mean 2.44), 4/5 1.22–1.62 (mean 1.37), 4–5/3 0.84–1.08 (mean 0.98), palpomeres 2 and 3 with narrow apical band of silvery white.
scales, apical pale band of pal pomere 4 variable, absent, smaller or larger than those of pal pomeres 2 and 3, scales pale cream-coloured to golden, slightly contrasting with those on pal pomeres 2 and 3, pal pomere 5 dark-scaled at base, with apical band of pale cream-coloured to golden scales, length of apical pale band 0.17-4.00 (mean 1.18) length of basal dark band of pal pomere 5, ratio of length of apical pale band of pal pomere 4 to length of basal dark band of pal pomere 5 0.0-1.67 (mean 0.51). Thorax: pleural setae as follow: 1-4 upper proepisternal, 0-2 prespiracular, 0.63-0.74mm 6-11 usually double or triple, 7-11 with 4-11 branches, 6-11 with 12-20 branches, 7-11 usually with 4 branches (3-6), 8-CT single to triple, 9,12-CT usually triple (2-5). Setae 9-11,111 lightly pigmented, 9-IV-VIII pigmented light brown, slightly darker at base. Abdomen: setae 6-1 usually triple (2-4), 7-11 with 3-9 branches; 1-11 dendritic, with >30 fine branches arising from strong basal stem, 6-11 double or triple, 7-11 with 4-11 branches, 8-11 always absent, 9-II very short, stout, arising cephalad from posterior margin of segment, length 0.01-0.014mm (mean 0.011mm), 10-11-II rarely present; 1-111 with 5-10 branches, 5-111 with 6-11 branches, 6-11 usually double (2,3), 9-III short, stout, length 0.01-0.03mm (mean 0.02mm); 1-IV with 3-7 branches, 5-IV with 4-8 branches, 6-IV single to triple, 9-IV short, length 0.02-0.05mm (mean 0.04mm), ratios of length of 9-IV/9-III 1.25-4.0 (mean 2.36) and 9-IV/9-V 0.19-0.52 (mean 0.36); 1-IV usually single (2-4), 5-V with 3-5 branches, 6-V usually single (1,2), 9-V long, simple, length 0.08-0.12mm (mean 0.10mm); 1-V1 usually triple (2,3), 5-V1 with 3-7 branches, 6-V1 single to triple, 9-V1 long, frequently simple, occasionally with minute denticles, length 0.09-0.13mm (mean 0.11mm); 1-VII double or triple, 5-VII with 4-7 branches, 6-VII usually double (1,2), 9-VII long, frequently simple, sometimes with minute denticles, length 0.09-0.12mm (mean 0.11mm); 9-VIII with 12-20 branches. Paddle: lightly tanned, buttress slightly darker, midrib faint, outer basolateral serrations prominent, filamentous spicules on outer apical margin and most of inner margin prominent; setae 1-Pa strong, darkly pigmented, 2-Pa with 1-3 branches; toothed margin index 0.86-0.94 (mean 0.91), paddle teeth well developed, teeth broad at base tapering to blunt apex and widely spaced from each other.

**Male.** Essentially as in female except for sexual characters. Wing generally paler with reduced scaling, pale spots usually longer than in female. Pal pomere 2 with patch of pale scales at middle of dorsal surface, extending to lateral surface, apex of pal pomere 2 bare; pal pomere 3 dark-scaled, with long dorsal patch of pale scales at middle, extending to lateral surface, apex of pal pomere 3 with broad band of pale scales interrupted by short patch of dark scales at apex of ventrolateral surface; pal pomeres 4 and 5 mostly pale-scaled with narrow basal band of dark scales. Abdomen: sternum VIII covered with pale cream-coloured scales.

**Pupa** (Fig. 1; Table 1). Position and development of setae as figured; range and modal number of branches in Table 1. Measurements and counts from 20 to 22 specimens. Integument without distinctive colour pattern, mostly light brown to yellowish; sterna II-V with narrow dark band near anterior margin. Cephalothorax: setae 1-3-CT about equal in length, 5-CT with 3-8 branches, 6,10,11-CT with 2-4 branches, 7-CT usually with 4 branches (3-6), 8-CT single to triple, 9,12-CT usually triple (2-5). Setae 9-II,111 lightly pigmented, 9-IV-VIII pigmented light brown, slightly darker at base. Abdomen: setae 6-1 usually triple (2-4), 7-11 with 3-9 branches; 1-11 dendritic, with >30 fine branches arising from strong basal stem, 6-11 double or triple, 7-11 with 4-11 branches, 8-11 always absent, 9-II very short, stout, arising cephalad from posterior margin of segment, length 0.01-0.014mm (mean 0.011mm), 10,11-II rarely present; 1-111 with 5-10 branches, 5-111 with 6-11 branches, 6-11 usually double (2,3), 9-III short, stout, length 0.01-0.03mm (mean 0.02mm); 1-IV with 3-7 branches, 5-IV with 4-8 branches, 6-IV single to triple, 9-IV short, length 0.02-0.05mm (mean 0.04mm), ratios of length of 9-IV/9-III 1.25-4.0 (mean 2.36) and 9-IV/9-V 0.19-0.52 (mean 0.36); 1-IV usually single (2-4), 5-V with 3-5 branches, 6-V usually single (1,2), 9-V long, simple, length 0.08-0.12mm (mean 0.10mm); 1-V1 usually triple (2,3), 5-V1 with 3-7 branches, 6-V1 single to triple, 9-V1 long, frequently simple, occasionally with minute denticles, length 0.09-0.13mm (mean 0.11mm); 1-VII double or triple, 5-VII with 4-7 branches, 6-VII usually double (1,2), 9-VII long, frequently simple, sometimes with minute denticles, length 0.09-0.12mm (mean 0.11mm); 9-VIII with 12-20 branches. Paddle: lightly tanned, buttress slightly darker, midrib faint, outer basolateral serrations prominent, filamentous spicules on outer apical margin and most of inner margin prominent; setae 1-Pa strong, darkly pigmented, 2-Pa with 1-3 branches; toothed margin index 0.86-0.94 (mean 0.91), paddle teeth well developed, teeth broad at base tapering to blunt apex and widely spaced from each other.

**Larva** (Fig. 1; Table 2). Position and development of setae as figured; range and modal number of branches in Table 2. Measurements and counts from 10 to 24 specimens. Head: integument light brown to yellowish either with or without pattern of darkened spots, if dark spots present, as follows: 1 dark spot placed posteriorly on dorsal apotome; 2 lateral spots on dorsal apotome posterior to setae 8-C, posteriorly on frontal ec dysial line; 1 dark spot ventral on lateralia enclosing setae 12-C; 2 dark spots on labiogula posterior to hypostomal suture; head length 0.60-0.70mm (mean 0.67mm), width 0.63-0.74mm (mean 0.68mm), antenna length 0.25-0.30mm (mean 0.28mm), ratio of distance between base and seta 1-A to antenna length 0.31-0.42 (mean 0.38), setae 2-C long, usually single (1,2), with minute sparse spicules on distal 0.5, 3-C single, length 0.07-0.09mm (mean 0.08 mm), distance between bases of 2-C and 3-C 0.03-0.04mm (mean 0.04mm), 4-C posterolateral of 2-C, single, length 0.04-0.07mm (mean 0.06mm), never reaching base of 2-C, distance between insertions of 2-C and

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Fig. 1. *Anopheles latens* sp.n. Pupa (male): CT, cephalothorax; GL, genital lobe; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Millimetre scale bars.
Table 1. Number of branches for pupal setae of *Anopheles latens*: range (mode). n.c. = not counted.

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Table 2. Number of branches for setae of fourth-instar larva of *An. latens*: range (mode).

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4-C 0.06–0.10 mm (mean 0.08 mm), ratio of length of 4-C to distance between insertions of 2-C and 4-C 0.51–0.88 (mean 0.74), distance between bases of 3-C and 4-C 0.06–0.09 mm (mean 0.07 mm), 5-C longer than antenna, extending beyond anterior margin of head, with 7–11 branches, 6-C with 8–14 branches, 7-C with 9–16 branches. Thorax: tubercles of all large setae light brown; seta 1-P with 10–17 branches, stem stout, not noticeable expanded, flattened basally, arising from large tubercle, tubercle frequently separated from that of 2,3-P or rarely both tubercles joined at base, each tubercle with small, inconspicuous apical lip arising from posterodorsal side and projecting forward over bases of 1,2-P, 14-P with 5–8 branches; 4-M with 2–4 branches, 6-M usually triple (3,4), 14-M with 5–11 branches; 3-T weakly developed, palmarily broad lanceolate leaflets with minute apicolateral serrations and apical filament; 1-X long, single, inserted on saddle; pecten with 4–6 long teeth alternating with 6–10 short teeth, with 11–15 total teeth.

Material examined. HOLOTYPE: adult male with associated larval and pupal exuviae on microscope slide, acc. no. 08161–10, collected by AFRIMS team, 25 May 1980, deposited in the NMNH. Type locality: THAILAND, Phangnga, Ban Bang Kao (8°35’N 98°32’E). PARATYPES: INDONESIA, Kalimantan, Salaman (3°49’S 115°5’E), 19–24 September 1986, acc. no. IDK 43, 1F, 1M, 2Le, 2Pe. MALAYSIA (EAST), Sabah, Beaufort (5°20’N 115°45’E), 4 April 1970, acc. no. S-368, 1M, 1Le, 1Pe. THAILAND, Chumphon, Pathiu, Ban Chong Rakam, Ban Chong Mut, Mu 3 (10°44’N 99°18’E), 18 September 1978, acc. no. 08007(3), progeny, 1F, 1M, 3Le, 3Pe. Nakhon Si Thammarat, Tung Song, Nam Tok (8°10’N 99°30’E), 1983, acc. no. TS39 (F–2), progeny, 1F, 3M, 5Le, 5Pe, 3; Tung Yai, Ban Tham Phae Dan (8°22’N 99°20’E), 3–8 December 1985, acc. no. TY001, progeny, 2F, 2M, 4Le, 5Pe. Phangnga, Ban Bang Kao (8°35’N 98°32’E), 25 May 1980, acc. no. 08161, 6F, 8M, 11Le, 1Pe; 25 May 1980, acc. no. 08162, 3F, 2M, 5Le, 5Pe. Songkhla: Sadao, Padang Besa, Khao Rup Chang (6°40’N 100°19’E), 12 December 1986, acc. no. PB53, progeny, 4F, 1M, 4Le, 5Pe. Paratypes deposited in the NMNH. Total material of An. latens examined: 263 specimens comprising 73F, 43M, 55Le, 69Pe, 23 L derived from 52 separate collections from natural habitats (28 adults, 24 immatures) and 10 progeny broods.

Distribution. Anopheles latens is known from Indonesia (Kalimantan), east Malaysia (Sabah, Sarawak), west Malaysia (Malay States, Kelantan, Negeri Sembilan, Pahang, Perak, Perlis and Selangor) and Thailand (Chumphon, Nakhon Si Thammarat, Narathiwat, Phangnga, Satun and Songkhla).

Bionomics. The importance of An. latens as vector of human malaria parasites, and bancroftian filariasis parasites is not well established because this species has been largely misidentified as An. leucosphyrus. Probably most of the literature records regarding An. leucosphyrus from Indonesia, east and west Malaysia and Thailand are An. latens. Based on the published records for An. leucosphyrus from the localities mentioned before, An. latens seems to be an important vector of human malaria parasites and also involved in the transmission of bancroftian filariasis in Sarawak (Zulueta & LaChance, 1956; Zulueta, 1956, 1957). In a mountainous area in the tropical rain forest of Sarawak, An. latens was found to be more abundant in farm huts than in village settlements. The malaria transmission was more intense in former than in latter, but in both ecotypes, females were attracted more to humans than to CDC light traps. The inoculation rate of An. latens in farm huts was 0.023 (Seng et al., 1999). Also, An. latens was incriminated as a vector of both human malaria and Bancroftian filarial parasites in villages and in forested areas situated 0.5 km from the villages. Females activity peaked around midnight in forested areas and soon after dusk in village settlements (Chang et al., 1995). These differences in the peak activity may be related to changes in the microenvironmental conditions in both ecotypes, thus the humidity is lower indoors than outdoors during the night and the opposite in the dusk. Human bait collections at a remote village located in a heavily forested area in south Kalimantan, Indonesia, showed that An. latens and An. balabacensis were predominant outside houses in villages, whereas the number was lower in nearby forest. The sporozoite infection rate was 1.0% for An. latens, slightly less than 1.3% for sympatric An. balabacensis (Harbach et al., 1987).

Like other members of the Leucosphyrus Complex, An. latens breeds in forests where larval habitats are mostly in shaded temporary pools and natural containers on the ground. In west Malaysia, immatures were found in a muddy pool in a cart track running through dense jungle and in the longitudinal half of a bamboo stem on the ground (Leicester, 1903), and in jungle streams in Selangor, Jugra (Leicester, 1908a).

Collections in Thailand for this study included immatures of An. latens from ground pools along stream margins, flood pools, seepage pools, sandy pools in stream banks, small shallow running streams and elephant footprints. The water was either fresh or stagnant, turbid or clear, sometimes with some degree of pollution and decaying leaves. The habitats were partially or heavily shaded in primary and secondary rain forests of mountains or valleys at elevations ranging from 76 to 520 m above sea level. Immatures were found in association with those of many other mosquito species: Aedes orbitae Edwards, Aedes vexans (Meigen), Anopheles baimaii sp.n., An. bengalesis Puri, An. intratolus Colless, An. macarthurii Colless, An. maculatus Theobald, An. p. jutens Colless, An. nemophilous Peyton & Ramalingam, Culex spp. including Cx. fraudatrix (Theobald),
**Systematics.** The Leucosphyrus Complex includes four species: *An. balabacensis*, *An. introitalus*, *An. latens* (as *An. leucosphyrus*) and *An. leucosphyrus* s.s. (Peyton, 1990).

Based on hybridization and cytogenetic evidence, Kanda *et al.* (1981) suggested that specimens from populations of Sabah, and Kuching (SWK) and Niabet (SWN) in Sarawak, Malaysia, belonged to a separate species they termed *An. leucosphyrus sensu stricto*. Later, Kanda *et al.* (1983) using chromosomal polymorphisms confirmed that both SWK and SWN populations belonged to their *An. leucosphyrus s.s.* Using seven protein loci, Takai (1986) was able to distinguish five taxa within the *An. leucosphyrus* group and confirmed the hypothesis of Kanda *et al.* (1981, 1983) that specimens of *An. leucosphyrus* from SWK belonged to a distinct species. Finally, Baimai *et al.* (1988b) found cytogenetic evidence that *An. leucosphyrus* s.l. included two allopatric species, one inhabiting Borneo, west Malaysia, and southern Thailand (designated as *An. leucosphyrus* A), the other confined to Sumatra (An. leucosphyrus s.s.). Based on Baimai *et al.*'s findings, we conclude that specimens termed *An. leucosphyrus s.s.* by Kanda *et al.* (1981, 1983) and Takai (1986) were *An. latens*.

*Anopheles latens* is morphologically more similar in all life stages to *An. leucosphyrus* than to any other species of the Leucosphyrus Complex. The adult males and females of *An. latens* are indistinguishable from those of *An. leucosphyrus*; however, they can be separated from *An. introitalus* and *An. balabacensis* by having the PSD spot of vein R extending basally to or beyond the level of the HD spot on the costa, from level 4 to level 6, and the apical pale band of palpmere 5 distinctly cream-coloured or yellowish contrasting with the silvery white bands of palpmere 2 and 3. In *An. introitalus* and *An. balabacensis*, the PSD spot of vein R usually does not extend basally beyond the level of the PSD spot on the costa (level 1) and rarely extends into the distal 0.5 of the HD spot of the costa (level 4), but never reaches or extends beyond level 5; the apical pale band of palpmere 5 is white or whitish, not strongly contrasting with the silvery white bands of palpmere 2 and 3. The pupal stage of *An. latens* cannot be distinguished from those of *An. balabacensis* and *An. introitalus* but some individuals can be distinguished from that of *An. leucosphyrus* by having seta 7-II with 4–11 branches, seta 2-VII with 3–6 branches and 2-V with 2–5 branches, whereas in *An. leucosphyrus* seta 7-II 2–6 branches, 2-VII 2,3 branches and 2-V always triple. Although useful to separate some individuals of these two species, the pupal characters overlap in *An. leucosphyrus* and *An. latens*, thus they should be used with caution for species separation. The fourth-instar larva of *An. leucosphyrus* and *An. latens* can be distinguished from those of *An. balabacensis* and *An. introitalus* by having the tubercles of seta 1-P and 2-P without a posterodorsal tooth, or at most with a weak and inconspicuous lip projecting forward over the base of each seta, and with the tubercles of both setae usually well separated, occasionally joined basally. In *An. balabacensis* and *An. introitalus*, the basal tubercle of setae 1-P and 2-P are joined basally, and each tubercle has a prominent tooth or spine arising from the posterodorsal margin that projects over the base of the seta. The fourth-instar larvae of *An. latens* and *An. leucosphyrus* are indistinguishable. Since these two species are allopatric, their distributions should be considered when making identifications.

**Dirus complex**

*Anopheles* (*Cellia*) *cracens* Sallum & Peyton, sp.n.

**Etymology:** the name *cracens* is Latin for neat, graceful.

*Anopheles balabacensis* Perls/Thair Form of Reid (1968) (taxonomy).


*Anopheles balabacensis* peritensis of Yong *et al.*, 1983: 611 (electromorphs, species differentiation); Ward, 1984: 260 (nomen nudum).


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bionomics); Baimai et al., 1988d: 372 (polytene chromosomes); Baimai et al., 1988a: 333 (crossbreeding, heterochromatin); Baimai et al., 1988c: 151 (bionomics, distribution); Yasothonrrnikul et al., 1988: 703 (RFLP); Damrongphol & Baimai, 1989: 563 (egg morphology); Green et al., 1992: 29 (enzyme electromorphs); Audtho et al., 1995: 107 (DNA hybridization); Poopittayasataporn & Baimai, 1995: 426 (polytene chromosome, phylogeny); Sithiprasana et al., 1996: 483 (methoprene resistance); Walton et al., 1999: 24 (ASA PCR species identification); Huong et al., 2001: 615 (PCR species identification); Manguin et al., 2002: 46 (SCAR multiplex PCR, species identification).

Anopheles leucophurus Petits (IMR) of Kanda et al., 1981: 321 (hybridization, phylogeny).

Female. Head: proboscis length 1.97–2.25 mm (mean 2.11 mm), ratio of length to forefemur 1.09–1.17 (mean 1.13), maxillary palpus length 1.82–2.10 mm (mean 1.96 mm), ratio of length to proboscis length 0.89–0.97 (mean 0.93), ratio of length to forefemur length 1.01–1.12 (mean 1.05), ratio of length of palpomeres 3/4 1.67–1.92 (mean 1.78), 3/5 2.18–2.78 (mean 2.45), 4/5 1.20–1.56 (mean 1.37), 4/5–3/5 0.88–1.05 (mean 0.97), palpomeres 2–4 with narrow apical silvery white bands, pale scales of palpalome 5 white to pale cream-coloured, length of apical palpalome of palpalome 5 1.43–3.67 (mean 2.12) length of basal dark band of palpalome 5, ratio of length of apical palpalome of palpalome 4 to length of basal dark band of palpalome 5 0.50–1.25 (mean 0.88). Thorax: pleural setae as follow: 1–3 upper proepisternal, 1–3 prespiracular, 3–5 prealar, 3–6 upper mesokatepisternal, 2,3 lower mesokatepisternal, 3–5 upper mesepimeral. Wing: length 3.21–3.74 mm (mean 3.45 mm), pale scales on all veins light cream-coloured, spots on costa and subcosta slightly more obviously cream-coloured, not strongly contrasting with other spots; PHP spot of costa always present, prominent or reduced, HP spot always present, small, PSP and SP spots always present, prominent, ASP spot always absent, PP spot 0.75–1.44 (mean 1.14) length of SCP spot, AD spot 1.56–3.00 (mean 2.13) length of PP spot, PSD spot of vein R extending basally from level 1 to level 5 on one or both wings, PDS spot of vein R with 1–3 small pale interruptions, SD spot of vein R with 1–5 pale interruptions, number of pale interruptions on PSD-PD spots of vein R 4–9 on each wing, ratio of length of cell R2 to vein R3+5 1.33–1.95 (mean 1.66), ratio of length of cell R2 to cell M1+2 1.23–1.38 (mean 1.30). Legs: foretarsosomes 2 and 3 with prominent basal and apical pale spots, dark area of foretarsosome 2 with or without 1–3 pale spots on dorsal surface mostly pale-scaled on dorsal surface with small dark median band, mostly dark-scaled on ventral surface, foretarsosome 3 with apical and basal palpalome bands, bands sometimes poorly developed, foretarsosome 4 noticeably pale-scaled at base, apical palpalome band usually prominent, rarely inconspicuous, foretarsome 5 mostly dark-scaled with pale scales at apex, foretarsosomes 1–5 mostly dark-scaled on ventral surface, basal and apical palpalome bands of ventral surface absent or present but less evident than those on dorsal surface; midtarsosome 2 usually without basal pale band, rarely with inconspicuous basal pale band, median dark region usually with 1–3 pale spots, rarely entirely dark-scaled, basal and apical pale bands complete or incomplete, midtarsosome 3 with apical palpalome band more distinct on dorsal surface, midtarsosome 4 and 5 with complete or incomplete apical palpalome bands, sometimes mostly pale-scaled on ventral surface; hindtarsosome 2 with apical palpalome band, basal palpalome band absent or inconspicuous, median dark part entirely dark-scaled or with 1–7 small pale spots, hindtarsosome 3 with apical palpalome band, hindtarsosome 4 with apical and complete or incomplete basal palpalome bands, hindtarsome 5 usually without basal palpalome scales, sometimes with inconspicuous basal palpalome band, apical palpalome band always present. Abdomen: tergum VI usually with 2–5 pale cream-coloured to tan scales on posterolateral margin, tergum VII variable, with few or occasionally several posterolateral scales, scales vary from pale cream-coloured to tan to dark, tergum VIII with a large posteromeral patch of pale cream-coloured to golden scales; sternum VI with small patch of dark scales posteromedially, sternum VII with posteromeral patch of dark scales, rarely with 2.3 lateral pale scales, sternum VIII with small anterolateral patch of whitish scales.

Male. Essentially as in female except for sexual characters. Wing: generally paler with reduced scaling, pale spots usually longer than in female. Palpomere 2 with dorsal patch of pale scales at middle, extending onto lateral surface, apex of palpomere 2 bare; palpomere 3 with long median dorsal patch of pale scales at middle, extending onto lateral surface, apex of palpomere 3 with broad band of pale scales covering dorsal, lateral and ventral surfaces except for narrow ventrolateral line of dark scales; palpomeres 4 and 5 mostly pale-scaled with narrow basal band of dark scales, basal dark band of palpomere 5 with short extension on ventral surface not reaching apex. Abdomen: sternum VIII covered with pale cream-coloured scales.

Pupa (Fig. 2, Table 3). Position and development of setae as figured; range and modal number of branches in Table 3. Measurements and counts from 20 to 75 specimens. In general similar to An. latens except for following characters. Sterna II–VII with narrow dark band near anterior margin. Cephalothorax: 5-CT with 5–7 branches, 8, 10-CT normally double (1–3), 9, 11,12-CT usually triple (9, 2–4, 11, 12, 2–5). Seta 9-II–VII very lightly pigmented, 9-VIII light brown, slightly darker at base. Abdomen: seta 6-II usually double (1–3), 7-II with 3–7 branches; 6-II single to triple, 7-II with 3–7 branches, 8, 10-11-II absent, 9-II length 0.01–0.02 mm (mean 0.01 mm); 1-IIII with 5–17 branches, 5-II usually double, 9-II length 0.01–0.03 mm (mean 0.02 mm); 1-IV with 4–13 branches, 5-IV with 6–14 branches, 6-IV always single, 9-VI long, usually with small spines, length 0.04–0.11 mm (mean 0.08 mm), ratios of length of 9-IV/9-III 2.00–6.86 (mean 4.35) and 9-IV/9-V 0.41–0.96 (mean 0.78); 1-V with 2–6 branches, 5-V with 5–9 branches, 9-V usually with minute denticles, length 0.09–0.12 mm (mean 0.11 mm); 1-VI with 2–4 branches, 5-VI with 4–8 branches, 6-VI single, 9-VI usually with minute denticles, length 0.10–0.13 mm (mean 0.11 mm); 1-VII single
Fig. 2. *Anopheles cracens* sp.n. Pupa (male): CT, cephalothorax; GL, genital lobe; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Circle shows basal details of setae 1-3-P. Millimetre scale bars.
Table 3. Number of branches for pupal setae of *Anopheles cracens*: range (mode). n.c. = not counted.

<table>
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<th>Paddle</th>
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</tr>
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</tr>
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<td>6</td>
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<tr>
<td>8</td>
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<td>-</td>
</tr>
<tr>
<td>9</td>
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<tr>
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Table 4. Number of branches for setae of fourth-instar larva of *An. cracens*: range (mode).

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<td>IV</td>
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</tr>
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<td>16</td>
<td>1</td>
<td>4-7 (7)</td>
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</table>

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to triple, 5-VII with 4-8 branches, 9-VII usually with minute denticles, length 0.09-0.13 mm (mean 0.11 mm); 9-VIII with 12-18 branches. Paddle: seta 2-Pa single or double; toothed margin index 0.80-0.92 (mean 0.87), teeth well developed, strong, widely separated.

Larva (Fig. 2, Table 4). Position and development of setae as figured; range and modal number of branches in Table 4. Measurements and counts from eight to 29 specimens. In general as described for An. latens except for following characters. Head: integument very lightly pigmented, without pattern of dark spots; length 0.59-0.77 mm (mean 0.70 mm), width 0.66-0.82 mm (mean 0.75 mm); antenna length 0.26-0.32 mm (mean 0.29 mm), ratio of distance between base and seta 1-A to antenna length 0.30-0.53 (mean 0.40); seta 3-C length 0.07-0.10 mm (mean 0.08 mm); distance between bases of 2-C and 3-C 0.03-0.05 mm (mean 0.04 mm); 4-C length 0.05-0.10 mm (mean 0.07 mm), either extending to or not reaching base of 2-C, distance between insertions of 2-C and 4-C 0.06-0.10 mm (mean 0.08 mm), ratio of length of 4-C to distance between insertions of 2-C and 4-C 0.73-1.09 (mean 0.92); distance between base of 3-C and 4-C 0.06-0.09 mm (mean 0.07 mm); 5-C longer than antenna, not reaching anterior margin of head, with 7-12 branches, 6-C with 9-16 branches, 7-C with 11-16 branches. Thorax: tubercles of all large setae very lightly pigmented, light tan to pale straw-yellow; seta 1-P with 7-20 branches, tubercle of 1-P joined to tubercle of 2-3-P, each tubercle with a strong apical tooth arising from posterodorsal side and projecting forward over bases of 1.2-P, 14-P with 4-8 branches; 4-M double or triple, 6-M 2-5-branched, 14-M with 4-8 branches; 3-T moderately developed, palmate, with 3-6 leaflets. Abdomen: seta 1-I with 4-10 leaflets, 2-3-I single to triple; seta 1-II more developed than 1-I, palmate, with 5-17 leaflets; 3-IV double or triple, 13-IV with 3,4 branches, ratio of length of 13-IV to 10-IV 0.54-0.79 (mean 0.65); 1-VII with 7-13 leaflets; 1-X long, single, inserted in marginal notch or at edge of saddle; 11-16 pecten teeth, 3-5 long teeth alternating with 7-12 short teeth.

Material examined. HOLOTYPE: adult female with associated larval and pupal exuviae on microscope slide, acc. no. MH0023(1)-4, collected by V. Baimai and R. G. Andre, 28 April 1982, from progeny brood, deposited in the NMNH. Type locality: MALAYSIA (WEST), Terengganu, Kampong Tapah (5°6′N 102°55′E). PARATYPES: MALAYSIA (WEST): Terengganu: Kampong Dura (5°6′N 102°55′E), 28 April 1982, collection (accession) number MH0008 (1), progeny, 3F, 5M, 8Le, 8Pe; same data, 28 April 1982, progeny, acc. no. MH0016 (1), 6F, 4M, 10Le, 10Pe, 1L; Kampong Tapah (5°6′N 102°55′E), 28 April 1982, acc. no. 0023 (1), progeny, 5F, 3M, 8Le, 8Pe, 41. THAILAND: Chumphon: Wang Mai, Ban Jo Po Ro (10°29′N 98°55′E), 20 September 1978, acc. no. 08099, 1F, 2M, 3Le, 3Pe, 1L; Phangnga: Khao Pak Cham (8°17′N 98°23′E), 13 October 1986, acc. no. 1560, 2M, 2Le, 1Pe, Phangnga: Tanod, Ban Le Chang Kha (7°10′N 99°30′E), February 1985, acc. no. PT-23 (1), progeny, 4F, 4Le, 4Pe. Paratypes deposited in the NMNH. Total material of An. cracens examined: 330 specimens comprising 82F, 39M, 93Le, 95Pe, 211, derived from 15 separate collections from natural habitats (12 adult, 3 immature) and 12 progeny broods.

Distribution. Anopheles cracens is known from Indonesia (Sumatra Island), west Malaysia (Perlis, Terengganu) and Thailand (Chumphon, Phangnga, Phattalung).

Bionomics. Anopheles cracens is an anthropophilic species, showing peak biting activity at 1900–2100 hours and a low level of activity throughout the night outdoors in Phatthalung, Thailand (Baimai et al., 1988c). In Sabang Island (Pulau Weh), Aceh, Sumatra, An. cracens was captured biting humans at night (J. E. Hudson). In west Malaysia, adult females were also captured in human-bait collections at night in secondary tropical rain forest and in villages in localities situated either in mountainous or hilly areas. Presumably An. cracens is an important vector of human malaria, but this requires investigation now it can be identified. A study on the susceptibility to the simian malaria parasite Plasmodium cynomolgi B strain in comparison to other South-east Asian Anopheles showed that 77% of An. cracens were infected (Klein et al., 1991). In another study, An. cracens was orally infected with Brugia pahangi microfilariae, but the infectivity rate was lower than that of An. stephensi Liston (Zahedi & White, 1994). Studies on the susceptibility of a colony of An. cracens to DDT, fenitrothion, propoxur and malathion showed a considerable degree of tolerance to the first two chemicals (Hii, 1984a). Anopheles cracens was found to be stenogamous in the laboratory (Sucharit & Choochote, 1983) and this facilitated many experimental studies of An. dirus species B cited above.

In Thailand, immatures were taken from elephant and other animal footprints. The water was fresh, stagnant, temporary, clear or coloured, in full sun or partial shade. The larval habitats were in secondary rain forest situated in both plains and mountainous areas. Immatures of Ae. caecus, Ae. oribatae, An. baimnai sp.n., An. barbirostris Van der Wulp and An. kochi Dönitz were found in association with An. cracens.

Systematics. Anopheles cracens was first distinguished from An. balabacensis and An. dirus by its distinctive mitotic and meiotic karyotypes and the larval salivary gland polytene chromosome banding patterns of individuals from a population designated as An. balabacensis Perlis Form (Baimai et al., 1981). Morphometrics of the male genitalia and the frequency of clasper movement also showed differences between An. cracens (as An. balabacensis Perlis Form) and An. dirus (Bangkok colony) (Sucharit & Choochote, 1983). Further examination of the polytene chromosomes and crossingbreeding of laboratory colonies by Hii (1985) confirmed the status of An. dirus and revealed another species designated as An. dirus species B (= An. cracens). Additional studies of cytogenetics and hybridization (Baimai et al., 1984, 1988a,d; Hii, 1984b, 1985; Wibowo et al., 1984; Baimai & Traipakvasin, 1987; Baimai, 1988a; Baimai, 1995) plus morphological and morphometric characters of the immature
stages, were taken to confirm the specific status of *An. cracens* within the Dirus Complex (Hii, 1986; Damrongphol & Baimai, 1989). Diagnostic enzyme electrophors, DNA probes and DNA markers have been developed to separate members of the Dirus Complex and to confirm their species status, including *An. cracens* (Yasoonthornrikul *et al.*, 1988; Green *et al.*, 1992; Audtho *et al.*, 1995; Walton *et al.*, 1999; Huong *et al.*, 2001; Manguin *et al.*, 2002). Backcrosses of hybrids between *An. dirus* and *An. cracens* showed that autosomes as well as the X chromosome might contribute to sterility (Hii, 1984b, 1985).

Adults of *An. cracens* can be recognized by the following combination of characters: (1) proboscis uniformly dark-scaled, slightly longer than the forefemur, ratio 1.09–1.17 (mean 1.13); (2) PSD spot of vein R with 1–3 small pale interruptions; (3) ASP spot always absent from costa; (4) hindtarsome 4 always with either a complete or incomplete basal pale band; (5) hindtarsome 5 usually dark-scaled at base, rarely with an inconspicuous pale band; (6) apical white band of hindwings with a dark extension into the basal portion; (7) vein 1 A without a noticeably longer pale spot at the level of the PSD spot of the costa; (8) PSD spot of vein R frequently extending basally to level 3 and level 4, less frequently to level 5, and rarely to level 1 and level 2; (9) sternum VI with a small postero-lateral patch of dark scales present in both sexes.

Fourth-instar larvae of *An. cracens* can be recognized by the following combination of characters: (1) pigmentation of sclerotized structures very light, inapparent, light tan to pale straw-yellow, the margins of sclerotized tubercles of the larger setae, the anterior and posterior tergal plates, and the saddle not discernable, the head capsule (except for very dark collar), including antenna, uniformly very pale tan to straw-coloured, larger setae light brown, seta 1-III-VI slightly darker, small scattered nearly colourless spicules on inner ventral aspect of antenna and on posterior-lateral surface of saddle; (2) seta 3-C single; (3) seta 5-C longer than antennae; (4) basal sclerotized tubercle of seta 1-P with prominent tooth or spine arising from postero-dorsal margin; (4) tubercles of setae 1,2-P broadly joined basally; (5) seta 1-P small and weak, not noticeably expanded basally, with 7–20 branches; (6) seta 4-C short, either not reaching base of 2-C or extending slightly beyond it, ratio of length of 4-C to distance between the insertions of 2-C and 4-C 0.73–1.09; (7) seta 3-C short, extending to or only slightly beyond anterior margin of head; (8) seta 1-II palmae, weakly developed, with 5–17 narrow, lanceolate leaflets; (9) seta 2-IV,V with 3–5 branches; (10) seta 1-X inserted in a marginal notch or at the edge of the saddle; and (11) seta 14-P with 4–8 branches. Distinction of *An. cracens* based on pupal characters is more difficult, but the overall pigmentation of the pupa is distinctive in comparison to other members of the Dirus Complex. Especially evident is the lack of pigmentation of seta 9-III-VII, which are very light yellow, only slightly darker than the integument. Additionally for *An. cracens*, the male genital lobe of the pupa is noticeably constricted at mid-length.

**Anopheles (Cellia) scanloni** Sallum and Peyton, sp.n.

**Etymology:** This species is named in honour of the late John E. Scanlon, whose studies on *Anopheles* represent an enormous contribution to knowledge of malaria epidemiology and vector species in Asia.


**Female.** Head: proboscis length 1.64–2.27 mm (mean 1.95 mm), ratio of length to forefemur length 1.07–1.14 (mean 1.10), maxillary palpus length 1.52–2.15 mm (mean 1.82 mm), ratio of length to proboscis length 0.90–0.98 (mean 0.93), ratio of length to forefemur length 1.00–1.10 (mean 1.03), ratio of length of palpomeres 3/4 1.53–2.00 (mean 1.75), 3/5 2.18–2.71 (mean 2.43), 4/5 1.22–1.50 (mean 1.42), 4–5/3 0.91–1.08 (mean 0.99); palpomeres 2–4 with narrow apical white bands, pale scales of palpomere 5 white to pale cream-coloured, length of pale band of palpomere 5 1.00–3.50 (mean 1.87) length of basal dark band of palpomere 5, ratio of length of apical pale band of palpomere 4 to length of basal dark band of palpomere 5 0.28–2.00 (mean 0.79). Thorax: pleural setae as follows: 1,2 upper proepisternal, 0–2 prespiracular, 3–5 prealar, 3–5 upper mesokatepisternal, 2–4 lower mesokatepisternal, 2–4 upper mesepimeral. Wing: length 2.63–3.72 mm (mean 3.08 mm), pale scales on all veins light cream-coloured, spots on costa and subcosta slightly more obviously cream-coloured but not strongly contrasting with other spots, PHF spot of costa absent to prominent, HP spot reduced or small but rarely absent, PSP spot always present, reduced or prominent, SP spot always present, prominent, ASP spot always absent, PP spot 0.13–1.60 (mean 0.84) length of subcostal pale SCP spot, AD spot 1.10–4.75 (mean 2.10) length of PP spot, PSD spot of vein R extending basally from level 1 to level 5 on one or both wings, PSD spot of vein R entirely dark-scaled or with 1–2 pale interruptions, SD spot of vein R with 1–3 pale interruptions, 2–7 pale interruptions on PSD-PD spots of vein R on each wing, ratio of length of cell R2 to R3+6 1.25–1.70 (mean 1.39), ratio of length of cell R2 to cell M1+2 170 M. A. M. Sallum *et al.*
1.14–1.41 (mean 1.27). Legs: forefemur 2 and 3 with complete or incomplete basal and apical palpal bands, middle dark region of forefemur 2 entirely dark-scaled or with 1.3 pale spots, forefemur 4 with basal pale band, apical palpal band reduced or absent, forefemur 5 mostly dark-scaled, apical palpal scales reduced or absent, forefemur 2–5 mostly pale-scaled along ventral surface, pale spots absent or less noticeable than on dorsal surface; midtarsomers 2–4 usually dark-scaled with small apical patch of pale scales on dorsal surface, occasionally apical palpal patches inconspicuous, midtarsomer 5 dark-scaled with faint apical palpal band; hindtarsi 2, 3 mostly dark-scaled with small apical palpal band, hindtarsi 4 with apical and basal palpal bands, hindtarsi 5 with basal and apical palpal bands, basal palpal band sometimes absent or reduced to dorsal palpal patch, apical palpal band always present. Abdomen: tergum VI without scales, tergum VII with few sparse dark scales on posterior margin, tergum VIII with large postero medial patch of yellowish to golden scales; sternum VI without scales, sternum VII with post- comedial patch of dark scales, sternum VIII variable, without out scales or with few lateral palpal scales, with anterolateral patches of pale scales.

**Male.** Essentially as in female except for sexual characters. Wing generally paler with reduced scaling, pale spots usually longer than in female. Palpmere 2 with long patch of dark scales at middle extending laterally, apex of pal pmere 2 bare; palpmere 3 with long dorsal patch of pale scales at middle, extending laterally, apex of palpmere 3 with broad basal band of pale scales covering dorsal, lateral and ventral surfaces except for narrow, ventrolateral spot of dark scales, palpmere 4 and 5 mainly pale-scaled with narrow basal band of dark scales. Abdomen: sternum VIII covered with yellowish to golden scales.

**Pupa** (Fig. 3, Table 5). Position and development of setae as figured; range and modal number of branches in Table 5. Measurements and counts from 20 to 30 specimens. In general as described for An. latens except for the following characters. Sternum II–VII with narrow, dark band near anterior margin. Cephalothorax: 5,11–CT frequently triple (5, 2–5; 11, 1–4), 6–10,12–CT usually double (see Table 5 for ranges). Abdomen: seta 6–1 usually double (1–3), 7–I with 3–5 branches; 1–II with more than 20 fine branches, 6–11 usually double (1,2), 7–I with 2–5 branches, 8,10,11–II absent, 9–II length 0.01–0.02 mm (mean 0.01 mm); 5–III with 6–10 branches, 9–III length 0.02–0.03 mm (mean 0.02 mm); 1–I with 4–7 branches, 6–IV single, 9–IV length 0.03–0.10 mm (mean 0.05 mm), ratio of length of 9–IV/9–III 1.09–4.75 (mean 2.31), ratio of 9–IV/9–V 0.13–0.38 (mean 0.21); 1–V usually double (1–3), 5–V with 3–6 branches, 9–V usually simple, rarely with 1.2 minute denticles, length 0.08–0.13 mm (mean 0.11 mm); 1–VI usually double (1–3), 5–VI with 3–6 branches, 6–VI single or double, 9–VI usually simple, rarely with 1.2 minute denticles, length 0.10–0.13 mm (mean 0.12 mm); 1.6–VII single or double, 5–VII with 3–6 branches, 9–VII usually simple, rarely with 1,2 minute denticles, length 0.11–0.14 mm (mean 0.12 mm); 9–VIII with 9–17 branches. Paddle: filamentous spicules on outer apical margin either absent or sparse, always absent on inner margin; seta 2–Pa single; toothed margin index 0.82–0.90 (mean 0.86), paddle teeth narrow, tapering to acute apex.

**Larva** (Fig. 3, Table 6). Position and development of setae as figured; range and modal number of branches in Table 6. Measurements and counts from 18 to 40 specimens. In general as described for An. latens except for the following characters. Head: integument light brown to yellowish, with or without pattern of darkened spots, in present spots as follow: 1 small spot posteriorly at dorsal apotome and 2 well developed dark spots slightly anterior to it; a more developed, single dark spot posterior to seta 6–C in area between seta 8–C, and 2 small dark spots laterally; 2 lateral dark spots at dorsal apotome, posterior to seta 7–C; 1 dark spot ventrally on lateralia in the area of insertion of seta 12–C; a faint dark spot on lateralia bordering frontal ec dysial line; 1 dark spot on labiogula laterally at level of posterior tentorial pit; head length 0.60–0.73 mm (mean 0.67 mm), width 0.68–0.78 mm (mean 0.74 mm); antenna length 0.29–0.32 mm (mean 0.30 mm), ratio of distance between base and seta 1–A to antenna length 0.26–0.48 (mean 0.34); seta 2–C simple; 3–C length 0.07–0.10 mm (mean 0.09 mm); distance between bases of 2–C and 3–C 0.03–0.04 mm (mean 0.04 mm); 4–C single to triple, length 0.10–0.22 mm (mean 0.13 mm), extending beyond base of 2–C, distance between insertions of 2–C and 4–C 0.06–0.10 mm (mean 0.08 mm), ratio of length of 4–C to distance between insertions of 2–C and 4–C 1.20–3.26 (mean 1.70); distance between bases of 3–C and 4–C 0.05–0.08 mm (mean 0.07 mm); 5–C shorter than antenna, not reaching anterior margin of head, with 8–11 branches, 6–C with 10–14 branches, 7–C with 8–16 branches. Thorax: seta 1–P with 10–13 branches, tubercle of 1–P frequently separate from tubercle of 2,3–P, or rarely joined to tubercles of 2,3–P on one side, each tubercle with well developed apical tooth arising from posterdorsal side and projecting forward over bases of 1,2–P; 4–M with 2,3 branches, 6–M triple, 14–M with 7,8 branches; 3–T moderately developed, palmate, with 3,4 weak, nearly transparent lanceolate leaflets arising from a long narrow stem. Abdomen: seta 2–I usually double (1–3), 3–I single or double, 9–I with 3,4 branches; 1–II more developed than 1–I, with 10–16 leaflets, stem more pigmented than leaflets; 3–IV single or double, 13–IV triple, ratio of length of 13–IV to 10–IV 0.70–0.88 (mean 0.80); 1–III with 9–13 leaflets, leaflets normally without apical collateral serrations, rarely few leaflets with minute apical collateral serrations; pecten teeth 12–17 with 4–6 long teeth alternating with 7–11 short teeth.

**Material examined. HOLOTYPE: adult female with associated larval and pupal exuviae on microscope slide, acc. no. 08126–15, collected by AFRIMS team, 18 November 1979, deposited in the NMNH. Type locality: THAILAND, Kanchanaburi, Sai Yok (Office of Livestock) 14°21'N 98°59'E. PARATYPES: Kanchanaburi, Nam Tok, Khao Na Chang (14°13'N 99°5'E), 6 June 1965, acc. no. 0225 1M, 1F, 1Le, 1Pe; Phao Phu Thong (13°54'N 99°24'E), 21 September 1973, acc. no. 06537, 2F, 1Le, 1Pe; Hual Ma, Khamin (14°38'N 99°00'E), 24 November 1979, acc. no. 06537, 2F, 1Le, 1Pe; Hual Ma, Khamin (14°38'N 99°00'E), 24 November 1979, acc. no.
Fig. 3. *Anopheles scanloni* sp.n. Pupa (female): CT, cephalothorax; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; PP, pecten plate; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Circle shows basal details of setae 1-3-P. Millimetre scale bars.
Table 5. Number of branches for pupal setae of *An. scanloni*: range (mode). n.c. = not counted.

<table>
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<th>Seta no.</th>
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<th>Abdominal segments</th>
<th>Paddle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
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<td>II</td>
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<td>1</td>
</tr>
<tr>
<td>1</td>
<td>2.3 (2)</td>
<td>-</td>
<td>&gt;20</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>3-6 (5)</td>
<td>4-7 (5)</td>
</tr>
<tr>
<td>3</td>
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<tr>
<td>4</td>
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<td>2-6 (4)</td>
<td>3-7 (4)</td>
</tr>
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<td>2-5 (3)</td>
<td>1-3 (2)</td>
<td>2-7 (3)</td>
</tr>
<tr>
<td>6</td>
<td>1.2 (2)</td>
<td>1-3 (2)</td>
<td>1.2 (2)</td>
</tr>
<tr>
<td>7</td>
<td>2-4 (2)</td>
<td>3-5 (3)</td>
<td>2-5 (3)</td>
</tr>
<tr>
<td>8</td>
<td>1-3 (2)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>1-3 (2)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>1-4 (2)</td>
<td>-</td>
<td>1.2 (1)</td>
</tr>
<tr>
<td>11</td>
<td>1-4 (3)</td>
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</tr>
<tr>
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<td>1-3 (2)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>13</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>-</td>
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</table>

Table 6. Number of branches for setae of fourth-instar larva of *An. scanloni*: range (mode). n.c. = not counted.

<table>
<thead>
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<td>M</td>
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</tr>
<tr>
<td>1</td>
<td>1</td>
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<td>1</td>
<td>7-12 (11)</td>
<td>2-3 (3)</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>1-4 (1)</td>
<td>13-18</td>
<td>2-3 (2)</td>
</tr>
<tr>
<td>5</td>
<td>8-11 (9)</td>
<td>n.c.</td>
<td>28-37 (28)</td>
</tr>
<tr>
<td>6</td>
<td>10-14 (11)</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>7</td>
<td>8-16 (10)</td>
<td>14-25 (22)</td>
<td>2-4 (3)</td>
</tr>
<tr>
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<td>17-29 (23)</td>
</tr>
<tr>
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<td>1</td>
</tr>
<tr>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>26-29 (29)</td>
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<td>1</td>
</tr>
<tr>
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<td>1-3 (1)</td>
<td>2-3 (2)</td>
</tr>
<tr>
<td>13</td>
<td>5-8 (6)</td>
<td>4-5 (5)</td>
<td>4-5 (5)</td>
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<tr>
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<td>n.c.</td>
<td>5-8 (6)</td>
<td>7-8 (8)</td>
</tr>
<tr>
<td>15</td>
<td>n.c.</td>
<td>-</td>
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08153, S, 6M, 10Le, 10Pe; Ban Plai Huai, Kaeng Riang (14°24'N 99°5'E), 7 June 1982, acc. no. 09137(1), progeny, 16F, 12M, 28Le, 28Pe; Ban Tab Tao, Mu 2 (14°24'N 99°9'E), 8 June 1982, acc. no. 09139 (14), progeny, 5F, 4M, 8Le, 8Pe; Ban Huai Duan (14°24'N 99°9'E), 10 June 1982, acc. no. 09142(2), progeny, 19F, 24M, 42Le, 42Pe; Tha Kradan, Ban Phu Takai, Mu 3 (14°27'N 99°5'E), 1 July 1981, progeny, acc. no. 09120 (1), 12F, 11M, 26Le, 22Pe. All collected by AFRIMS staff team. Phattalung, Tanod, Ban Lo Chang Kra (7°10'N 99°30'E), February 1985, acc. no. PT15, progeny, 3F, 2Le, 2Pe, 11, collected by V. Baimai. All paratypes deposited in the NMNH. Total material of *An. scanloni* examined: 1358 specimens comprising 221 F, 14 M, 8Le, 8Pe; Ban Huai Duan (14°24'N 99°5'E), 10 June 1982, acc. no. 09137(1), progeny, SF, 8Le, 8Pe; Ban Phu Taka, Mu 3 (14°27'N 99°5'E), I July 1982, ace. no. 09139(1), progeny, SF, 8Le, 8Pe; Tha Kradan, Ban Phu Takai, Mu 3 (14°27'N 99°5'E), I July 1981, progeny, acc. no. 09120 (1), 12F, 11M, 26Le, 22Pe. The water was always fresh, stagnant, coloured or clear, sometimes with a degree of pollution, and in partial shade. Larval habitats were in primary bamboo groves, tropical rain forest, deciduous forest and scrub environments situated in mountains and also in valleys at elevations from 75 to 480 m above sea level. Immatures were found in association with *An. barbirostris*, *An. kochi*, *An. maculatus* Theobald, *An. nigerrimus* Giles, *An. vagus* Dönitz, *Cx. fuscocapillus* Theobald, *Cx. infantulìa* Edwards, *Cx. minor* (Leicester), *Oc. assamensis* (Theobald) and *Oc. gubernatoria* (Giles).

**Systematics.** Based on the distinctive H-banding pattern of metaphase sex chromosomes, Wibowo *et al.* (1984) distinguished *Anopheles scanloni* (as *An. dirus C*) from *An. balabacensis*, *An. dirus* and *An. cracens* (as *An. dirus B*). Several crossing, chromosomal and RFLP studies confirmed the species status of *An. scanloni* (Baimai *et al.*, 1984, 1987, 1988d; May, 1987; Baimai, 1988a, 1988b; Yasothornsrikul *et al.*, 1988; Sawadipanich *et al.*, 1990; Audtho *et al.*, 1995; Poopitayasataporn & Baimai, 1995). Scanning electron micrographs of the eggs of *An. scanloni* and *An. dirus* showed that the pattern of the outer chorionic cells between the frill and the floats may be useful for distinguishing between these species (Damrongphol & Baimai, 1989). The banding pattern of the larval salivary gland polytene chromosomes showed interspecific differences, particularly at the free ends of the X, 2R and 2L arms, between *An. scanloni*, *An. dirus* and *An. cracens* (Baimai *et al.*, 1988d). The species status of *An. scanloni* was also based on isozyme electromorphs (Green *et al.*, 1992), a non-radioactive DNA hybridization method (Audtho *et al.*, 1995), an allele-specific polymerase chain reaction of the ITS2 region of rDNA (Walton *et al.*, 1999), and nucleotide sequence data of the COI mitochondrial gene (Walton *et al.*, 2000). More recently, a PCR test employing species-specific primers was developed to separate four species of the Dirus Complex, including *An. scanloni* (Huong *et al.*, 2001), and a multiplex PCR-based method using species-specific primers (Manguin *et al.*, 2002). Studies on the population genetic structure of *An. scanloni* employing 11 microsatellite loci showed that there is a high degree of differentiation between the northern and the southern populations, suggesting the presence of two incipient species (Walton *et al.*, 2001).

The adult of *An. scanloni* can be recognized by the following combination of characters: (1) proboscis dark-scaled, slightly longer than forefemur, ratio of proboscis length to forefemur length 1.07-1.14 (mean 1.10); (2) PSD spot on vein R normally with 1, 2 pale interruptions; (3) ASP spot absent on costa; (4) hindtarsomere 4 with basal pale band; (5) apical white band on hindtibia with dark linear extension into basal portion of ventral surface (occurs only in specimens from Kanchanaburi) or without dark extension; (6) longest pale spot of vein 1A is at the level of the PSD spot; (7) PSD spot of vein R extending from level 1 to level 5 on one or both wings, most frequently to level 3 or 4; (8) pale spots and bands along dorsolateral surface of foretarsomer 1 and 2 usually small, discrete, occupying less surface than the dark portions along this surface; (9) pale spots on foretarsomere 1 usually not fused, not forming long lines or splashes of pale scales along entire length, often restricted to 2-4 spots; (10) middle dark area of foretarsomere 2 usually without pale spot on dorsal surface, occasionally with 1-3 small pale spots.

The fourth-instar larva of *An. scanloni* can be recognized by the following combination of characters: (1) 3-C single; (2) seta 1-II not fully developed; (3) 5-C shorter than antenna, not reaching anterior margin of head; (4) seta 1-X inserted on the saddle; (5) tubercle of seta 1-P usually separate, occasionally narrowly joined to tubercle of 2,3-P on one side; (6) 2-C single and simple; (7) 4-C long, extending well beyond base of 2-C, ratio of length of 4-C to distance between the insertions of 2-C and 4-C 1.20-3.26; (8) length of seta 4-C varying from 0.10 to 0.22 mm (mean 0.13 mm).

The pupa of *An. scanloni* can be distinguished by the absence of a fringe of filamentous spicules on the inner margin of the paddle. However, *An. elegans* exhibits polymorphism for this character and some individuals may be misidentified as *An. scanloni*. Therefore, since *An. scanloni* and *An. elegans* are allopatric, geographical distribution should also be considered when separating *An. scanloni* from *An. elegans* on the basis of pupal characters alone.

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Anopheles (Cellia) baimaii Sallum & Peyton, sp.n.

**Etymology:** this species is named after Prof. Visut Baimai for his valuable contributions to systematics of the Leucophaeus Group.


**Female.** Head: proboscis length 1.97–2.38 mm (mean 2.09 mm), ratio of length to forefemur length 1.01–1.14 (mean 1.08), maxillary palpus length 1.77–2.18 mm (mean 1.96 mm), ratio of length to proboscis length 0.88–1.00 (mean 0.94), ratio of length to forefemur length 0.96–1.05 (mean 1.00), ratio of length of palpomeres 3/4 1.50–1.67 (mean 1.63), 3/5 2.08–2.78 (mean 2.27), 4/5 1.25–1.67 (mean 1.39), 4–5/3 0.96–1.20 (mean 1.06), palpomeres 2–4 with narrow apical silvery white bands, pale scales of palpomere 5 white to pale cream-coloured, length of pale band of palpomere 5 1.00–2.33 (mean 1.39) length of basal dark band of palpomere 5, ratio of length of apical pale band of palpomere 4 to length of basal dark band of palpomere 5 0.37–1.00 (mean 0.64). Thorax: pleural setae as follow: 1–3 upper proposternal, 0–4 prespiracular, 2–6 prealar, 3–5 upper mesokateminal, 1–3 lower mesokateminal, 3,4 upper mesepimeral. Wing: length 3.09–3.54 mm (mean 3.39 mm), pale scales of all veins light cream-coloured, spots on costa and subcosta more obviously cream-coloured, sometimes bordering on pale golden, pale spots on remaining veins lighter, not strongly contrasting with others; ASP spot always absent, PP spot 0.38–2.00 (mean 1.01) length of SCP spot, AD spot 1.15–4.17 (mean 2.11) length of PP spot, PSD spot of vein R extending basally from level 1 to level 5 on one or both wings, PSD spot of vein R entirely dark or with 1–4 small pale spots, sum of pale spots on PSD-PD spots of vein R 3–10 for each wing; ratio of length of cell R5 to vein R5, 2.17–1.77 (mean 1.48), ratio of length of cell R5 to cell M1, 1.12–1.26 (mean 1.19). Legs: foretarsomere 2 variable, sometimes entirely pale-scaled along dorsal and lateral surfaces, or dark-scaled with basal and apical pale bands, middle dark area variable, usually mostly pale along dorsal and lateral surfaces, dark scales restricted to 1, 2 middle dark bands, less frequently mostly dark-scaled, with or without 1,2 pale spots, foretarsomere 3 dark-scaled with basal and apical pale bands, foretarsomere 4 usually dark-scaled with basal and apical pale patches, occasionally dark part less distinct, pale scales varying from light brown to tan, foretarsomere 5 entirely pale-scaled or with indistinct tan to light brown basal band, pale at apex, foretarsomeres 2–5 tan-scaled along ventral surface, basal and apical pale bands less noticeable or absent on ventral surface; midtarsomeres 2–4 with apical patches of pale scales more evident on dorsal surface, sometimes pale patches poorly evident, midtarsomere 2 variable, entirely dark-scaled or with 1,2 pale spots on dorsal surface, midtarsomere 5 variable from tan to light brown or dark at base and pale at apex; hindtarsomeres 2 and 3 with apical pale bands, hindtarsomere 2 with 1–3 pale spots on middle dark region, occasionally reduced to 1,2 pale scales, hindtarsomeres 4 and 5 with basal and apical pale bands, sometimes reduced to few basal and apical pale scales on hindtarsomere 5. Abdomen: tergum VI sometimes with 2–4 pale cream-coloured scales on postero medial margin, tergum VII with few brownish scales on posterior margin, tergum VIII covered with cream-coloured to yellowish to golden scales, scales sometimes reduced to small postero medi al patch; sternum VI usually without scales or occasionally with 1–4 dark postero medi al scales.

**Male.** Essentially as in female except for sexual characters. Wing generally paler with reduced scaling, pale spots usually longer than in female. Palpomere 2 with dorsal patch of pale scales at middle, apex of palpomere 2 bare; palpomere 3 with long dorsal patch of pale scales at middle extending laterally, apex of palpomere 3 with broad band of pale scales covering dorsal, lateral and ventral surfaces except for narrow ventrolateral line of dark scales at apex; palpomeres 4 and 5 pale-scaled with basal dark bands of dark scales, sometimes reduced to very narrow dark band on palpomere 5, more visible on dorsal and ventral surfaces, scales on lateral surface entirely pale or tan at base, dark band of palpomere 5 with ventral dark extension, not reaching apex of palpomere. Abdomen: sternum VIII covered.
with white to pale cream-coloured scales centrally, scales yellowish laterally.

*Pupa* (Fig. 4, Table 7). Position and development of setae as figured; range and modal number of branches in Table 7. Measurements and counts from 20 to 38 specimens. In general as described for *An. latens* except for the following characters. Sternum II-VII with narrow dark bands near anterior margins, usually darker on segments II-V. Cephalothorax: seta 5-CT with 3–7 branches, 6,7-CT usually double (6, 8, 1–3; 7, 2 or 3), 10-CT with 2–5 branches. Seta 9-IV-VIII light to medium brown, slightly darker at base. Abdomen: seta 6-I usually double (2,3), 7-I with 3–5 branches; 6-II single to 5-branched, 7-II with 2–5 branches, 8,10,11-II absent, 9-II length 0.01–0.02 mm (mean 0.01 mm); 5-III with 6–14 branches, 9-III length 0.01–0.02 mm (mean 0.02 mm); 5-IV with 4–10 branches, 6-IV single or double, 9-IV length 0.02–0.09 mm (mean 0.04 mm), ratios of length of seta 9-IV/9-III 1.15–4.40 (mean 2.15) and seta 9-IV/9-V 0.20–0.84 (mean 0.42); 5-V with 4–7 branches, 6-V always single, 9-V length 0.04–0.12 mm (mean 0.10 mm); 1-IV usually double (1–3), 6-VI single, 9-VI length 0.07–0.13 mm (mean 0.10 mm); 1-VII single or double, 5-VII with 3–7 branches, 9-VII length 0.09–0.14 mm (mean 0.11 mm); 9-VIII with 9–16 branches. Paddle: 2-Pa single or double; toothed margin index 0.76–0.88 (mean 0.84), paddle teeth well developed, teeth tapering to acute apex, teeth widely separated.

* Larva* (Fig. 4, Table 8). Position and development of setae as figured; range and modal number of branches in Table 8. Measurements and counts from 15 to 40 specimens. In general similar to *An. latens* except for the following characters. Head: integument light brown to yellowish, usually without pattern of dark spots but if present as follows: 2 small dark spots posteriorly on dorsal apotome; one dark spot slightly anterior them; one dark spot centrally on dorsal apotome posterior to seta 5-C; 2 lateral spots on dorsal apotome between insertions of setae 7-C and 8-C along dorsal ecdysial line; 2 dark spots on lateralia, 1 placed in area of 12-P insertion and 1 slightly posterior; and 2 dark spots on labiogula at level of hypostomal suture; head length 0.62–0.75 mm (mean 0.67 mm), width 0.66–0.81 mm (mean 0.76 mm); antenna length 0.28–0.34 mm (mean 0.31 mm), ratio of distance between base and seta 1-A to antenna length 0.25–0.40 (mean 0.32); seta 2-C usually simple, rarely with 1, 2 minute spicules on apical 0.5, 3-C length 0.06–0.10 mm (mean 0.08 mm), distance between bases of 2-C and 3-C 0.03–0.04 mm (mean 0.04 mm), 4-C posterolaterad of 2-C, single or double, length 0.07–0.12 mm (mean 0.09 mm), extending to or beyond base of 2-C, distance between insertions of 2-C and 4-C 0.08–0.13 mm (mean 0.10 mm), ratio of length of 4-C to distance between insertions of 2-C and 4-C 0.67–1.0 (mean 0.94), distance between bases of 3-C and 4-C 0.08–0.13 mm (mean 0.09 mm), 5-C longer than antenna, not reaching anterior margin of head, with 8–12 branches, 6-C with 10–16 branches, 7-C with 9–14 branches. Thorax: tubercles of all large setae yellowish to light brown; seta 1-P with 13–22 branches, tubercle of 1-P joined to tubercle of 2,3-C, each tubercle with prominent, apical tooth arising from posterior dorsal side and projecting forward over bases of each seta, 14-P with 4–7 branches; 4-M with 2,3 branches, 14-M with 4–8 branches; 3-T moderately developed, somewhat palmate, with 3–8 leaflets arising from long slender stem. Abdomen: seta 1-I small, somewhat palmate, with 4–8 leaflets, 2-I single to triple; 1-II similar to 1-I with 4–13 leaflets; 3-IV double or triple, 13-IV with 3,4 branches, ratio of length of seta 13-IV to 10-IV 0.46–0.88 (mean 0.71); 1-VII with 10–16 lanceolate leaflets, leaflets frequently smooth, sometimes with minute apicolateral serrations, apical filament poorly defined; 1-X long, single, inserted in marginal notch or on edge of saddle; 11–16 pecten teeth, with 3–5 long teeth alternating with 8–11 short teeth.

**Material examined.** HOLOTYPE: adult female with associated larval and pupal exuviae on microscope slide, acc. no. TH1690(11)-15, collected by V. Baimai, 7 August 1989, progeny, deposited in the NMNH. Type locality: THAILAND, Mae Sot, Ban Kariang, Tham Rua (16°40'N 98°44'E), 27 June 1975, acc. no. [072], 11F, 12M, 19Le, 17Pe; all collected in 1975, progeny, deposited in the NMNH. Total material of *An. baimaii* examined: 5620 specimens comprising 1355F, 988M, 1404Le, 1657Pe, 3061, derived from 295 separate collections from natural habitats (74 adult, 225 immature) and 84 progeny broods.

**Distribution.** *Anopheles baimaii* is known from Bangladesh (Chittagong), India (Andaman Islands, Assam, Meghalaya,
Fig. 4. Anopheles baimaii sp.n. Pupa (female): CT, cephalothorax; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; PP, pecten plate; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Circle shows basal details of setae 1–3–P. Millimetre scale bars.
### Table 7. Number of branches for pupal setae of *An. baimai*: range (mode). n.c. = not counted.

<table>
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<tr>
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<th>Abdominal segments</th>
<th>Paddle P</th>
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<td>5-8</td>
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<td>2-5</td>
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<td>8</td>
<td>1-3</td>
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</tr>
<tr>
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<td>2-3</td>
<td>1</td>
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<tr>
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<tr>
<td>11</td>
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<tr>
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### Table 8. Number of branches for setae of fourth-instar larva of *An. baimai*: range (mode). n.c. = not counted.

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<th>Seta no.</th>
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<th>M</th>
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</table>
Bionomics. Females of An. baimaii were collected from cowsheds and hospitals in Assam, Cachar District, India (Ramsay, 1930) and at a settlement of brick-makers in a series of constructions made of bamboo, called 'bashas', at Chunati near Chringa, Bangladesh (Macan, 1950). Anopheles baimaii seems to be an important vector of human malaria parasites in some areas in Thailand, Burma, Bangladesh and northeastern India (Rahman et al., 1977; Rosenberg & Maheswary, 1982; Rosenberg, 1982; Dutta et al., 1989a, 1989b, 1991; Green et al., 1991; Prakash et al., 1997b, 2001; Xu et al., 1998; Chareonviriyaphap et al., 2000). For example, An. baimaii was the vector responsible for holoendemic malaria in a forest community of Bangladesh, with up to 3.8% sporozoite rate, although transmission occurred only during the 7-month monsoon. Females were both exophagic and endophagic with biting activity pattern irregular, related neither with rainfall nor other climatic parameters. Generally the biting activity peaked from 22.00 to 02.00 hours. Also, mostly adult females live long enough to reach infectivity to P. falciparum (Rosenberg & Maheswary, 1982). Numbers biting indoors were greatly diminished in DDT-sprayed houses, and they fed earlier than in unsprayed houses. In Assam, India, in an isolated village of the rainforest-fringe, during the monsoon season, the vectorial capacity of An. baimaii for P. vivax was higher than for P. falciparum, decreasing after the monsoon to zero in the cold dry season (Prakash et al., 2001). Malaria prevalence and vector density were higher in locals closer to the forest in Naga Hills with An. minimus as well as An. baimaii as vectors (Prakash et al., 2000b). In upper Assam, biting activity of An. baimaii began at 19.00 hours, ended at 05.00 hours and was most intense between 21.00 and 03.00 hours (Prakash et al., 2005). During the post-monsoon season, peak biting activity was from 03.00 to 05.00 hours, whereas in the pre-monsoon and monsoon season it was from 21.00 hours to midnight. The anthropophilic index was 92.3% (Prakash et al., 1997a). In northeastern areas of India, An. baimaii is highly anthropophilic, biting throughout the night with several activity peaks from 20.00 to 03.00 hours (Dutta et al., 1996). Light trap collections in human dwellings in villages at the fringe of forest in Dibrugarh District, Assam, showed that An. baimaii was one of the most common mosquito species frequenting houses but it was the only anopheline species collected in an isolated village (Prakash et al., 1997b, 1998b). Species density was related to seasonality, peaking in July, but it was very low in the dry, cool months. Positive correlation was observed between mosquito density and rainfall that occurred 2 weeks prior to collections (Prakash et al., 1997b). In Nagaland, India, An. baimaii was found in low densities, but was more abundant during the monsoon season (Misra et al., 1993). Anopheles baimaii was the most common of 12 Anopheles species collected in Changland District, Arunachal Pradesh in July and August, and some individuals were found positive for sporozoites in Tirap and Arunachal Pradesh Districts, Assam, where sporozoites were found in the salivary glands of one specimen (Dutta et al., 1989a, 1992). During a longitudinal study of malaria transmission carried out in three villages in Boko PHC, Assam, at the same time that indoor DDT spraying was being used for malaria control, An. baimaii was found in low numbers, and few specimens were positive for sporozoites (Nandi et al., 1993). The sporozoite rate was 1.6% and the parous rate was 64.7% in an isolated village at the forest fringe in Assam, where malaria transmission increased with the increase in density of An. baimaii (Prakash et al., 1997b). In north-eastern localities in West Bengal, An. baimaii was observed to be an anthropophilic species (Nandi et al., 2000). Also, in Jalpaiguri districts of west Bengal, An. baimaii was more common during rainy months and found in close association with human environments (Nandi et al., 1996).

In Thailand, adults of An. baimaii were collected biting humans in primary and secondary evergreen forest, primary and secondary deciduous forest, primary and secondary rain forest, secondary rain forest mixed with fruit plantations, orchards and rubber plantations, banana and pineapple plantations, villages, villages with fruit plantations, inside houses, and also in the canopy of rain forests 16.5 m above ground level.

The larval habitats of An. baimaii are similar to those of An. dirus. Although An. baimaii can share the same habitats with An. dirus, the former is more common in temporary breeding places than the latter (Rattanarithikul et al., 1995). Immatures of An. baimaii have been found in domestic elephant and animal footprints, wheels and cart tracks along paths and roads, animal wallows, seepage pools, flood pools, pools in drying and dried streambeds and stream margins, ground pools, flood pools, large flood pools, seepage pools, limestone pools, sandy pools in banks of streams, shallow streams, ditches, flooded ditches, charcoal pits, small and large rock pools, swamps and rice paddies. The water was always fresh, stagnant, clear, turbid or sometimes with some degree of pollution. The pools were generally less than 2 m wide and 30 cm deep, under partial or heavy shade, or sometimes in sunlit areas. The larval habitats were inside primary bamboo groove forest, primary and secondary rain forest, primary and secondary deciduous forest, primary and secondary evergreen forest, secondary scrub in villages, secondary forest mixed with fruit plantations, evergreen rain forest, rubber tree plantations, village with fruit plantations, and orchards and villages located in valleys, hilly and mountainous areas.

In India, immatures of An. baimaii were collected in a well, 100 m above sea level. In Upper Brahmaputra Valley, Assam, immatures were found exclusively in forested areas (Khan et al., 1998), whereas in a forest-fringe village in Assam, immatures were taken from small, shallow, rain-filled, temporary, shady and partly shaded puddles and ground pools during rainy months. In dry months, immatures were taken from permanent streams in the forest adjoining a village (Prakash et al., 1997c). In Changland District, Arunachal Pradesh, An. baimaii is also a forest species found in small stagnant ground pools, completely or partially shaded by plants in open jungle (Dutta et al., 1989b).
In Bangladesh, during the annual 6-month monsoon season, immatures of *An. baimaii* was found in puddles on footpaths, and in turbulence pits at the heads of drainage gullies that held water for at least 5 days. In the dry season, the breeding places were in streams about 3 km distant from the malaria focus. Immatures seem to be well adapted to small temporary pools. Eggs were laid above the water line and remained viable for about 2 weeks. Interestingly, larvae of *An. baimaii* were observed to leave a draining pool and crawl as far as 53 cm, sometimes to another pool. Also, larvae remained alive up to 94 h at the bottom of drained pools (Rosenberg, 1982).

During field collections carried out for the present study, immatures were collected from turbulence pit ground pools, turbulence pits, a narrow sand gully head, large pools, large turbulent pools in the middle of a stream bed, small ground pools, ground pools in a foot path, ground pools under a large steel bridge, stream pools, stream bed pools, head waters of streams, stream margins, cave pools, pools along roads, culvert pools, riverside pools, ditches on roads, ditches in streams, puddles in villages, sluggish streams, a stream bed below factory tank seepage, tank runoff and a pothole. The water was always fresh, stagnant, clear, turbid, sometimes dark or brownish, usually in heavy or partial shade or in full sun. The larval habitats were situated in tropical rain forest, in mountainous, hilly areas or in valleys.

In Yunnan Province, southern China, larvae of *An. baimaii* were found in habitats situated near villages; however, no adults were captured in CDC light traps with UV or incandescent bulbs during 57 night collections (Moore *et al.*, 2001). Baimai *et al.* (1984) showed that *An. baimaii* is highly polymorphic for chromosome inversions and that the distribution of the polymorphisms may be associated with the geography and epidemiology of malaria transmission.

**Systematics.** Using evidence from the heterochromatin of the metaphase sex chromosomes, Baimai *et al.* (1984) found support for a fourth species within the Dirus Complex, which was designated as *An. dirus* D. The species status of *An. baimaii* was confirmed by: crossing experiments and chromosomal differences (Baimai *et al.*, 1987, 1988e); a DNA probe based on 7000 recombinant clones derived from wild females (Panyim *et al.*, 1988); a non-radioactive DNA probe method (Audhio *et al.*, 1995); nucleotide sequence of the ITS2 of rDNA (Xu & Qu, 1997; Xu *et al.*, 1998); allele-specific amplification in the nucleotide sequence of ITS2 (Walton *et al.*, 1999); a PCR based method (Huong *et al.*, 2000); and a SCAR marker and multiplex PCR-based method (Manguin *et al.*, 2002). Additionally, Green *et al.*, 1991 found support for the hypothesis that the four chromosomal/electrophoretic forms of the Dirus Complex represented four distinct biological species, and Damrongphol & Baimai (1989) pointed out diagnostic morphological characters of the egg, useful for distinguishing *An. baimaii* from the other members of the complex. The phylogenetic relationships among five species of the complex, including *An. baimaii*, were investigated employing data on the fixed inversion of 3Rb and inversion polymorphism of the X chromosome (Poopittayasataporn & Baimai, 1995). Using 11 microsatellite loci, Walton *et al.* (2001) showed that *An. dirus*, *An. baimaii* and *An. scanloni* are very distinctive; however, no differentiation was observed either within or between *An. dirus* and *An. baimaii* based on COI gene sequences. The genetic diversity was higher in *An. baimaii* than in *An. dirus*, suggesting that expansion occurred first in *An. baimaii* and then in *An. dirus* (Walton *et al.*, 2000).

Adults of *An. baimaii* can be recognized by the following combination of characters: (1) proboscis dark-scaled, slightly longer than forefemur, ratio of proboscis length to forefemur length 1.01–1.14 (mean = 1.08); (2) PSD spot of vein R rarely entirely dark-scaled, frequently with 1 or 2 pale interruptions on one or both wings; (3) ASP spot absent on costa and usually on subcosta; (4) hindtarsomere 4 with pale scales dorsally at base; (5) hindtarsomere 3 with a minute basal pale band; (6) apical pale band on hindtibia entirely white, without a dark extension into the basal portion; (7) vein 1A occasionally with a long pale spot at level of the PSD spot at least on one wing, when present this spot is always the longest pale spot of vein 1A; (8) combination of pale spots and bands along the dorsolateral surface of foretarsomeres 1 and 2 dominate the dark portions along this line, often two or more of these pale spots on tarsomere 1 are fused, forming long lines or splashes of pale scales; (9) foretarsomere 2 often has the pale band and spots fused, is completely pale dorsally, or the pale spots and bands are longer, reducing the dark areas in the middle to narrow bands; (10) the PSD spot on vein R usually extends basally from level 1 to level 5, most often to level 1, level 3 and level 4.

The fourth-instar larva of *An. baimaii* can be distinguished from other members of the Dirus Complex except *An. cracens* by the following combination of characters: (1) 5-C noticeably longer than antenna; (2) basal sclerotized tubercle of seta 1-P with a prominent tooth or spine arising from the posterodorsal margin; (3) seta 4-C short, usually not reaching or extending beyond the base of 2-C, less frequently extending 0.3 beyond base of 2-C, the ratio of 4-C length to the distance between the insertions of 2-C and 4-C 0.67–1.31 (mean = 0.94); (4) seta 3-C extends to or slightly beyond anterior margin of head; (5) seta 1-X inserted in a marginal notch or at the edge of the saddle; and (6) seta 14-P with 4–8 branches.

Except for *An. scanloni* and the male pupa of *An. cracens*, the pupal stage of *An. baimaii* is indistinguishable from those of the other members of the Dirus Complex. As mentioned above, the pupal paddle of *An. scanloni* does not have a fringe of spicules on its inner margin, whereas it is always present in *An. baimaii*. Additionally, in the pupa of *An. cracens*, the male genital lobe is noticeably constricted at midlength, but not constricted in *An. baimaii*.

*Anopheles* (Cellia) elegans (James)

**Myzomyia** (?) *elegans* James, 1903. In Theobald, 1903: 51 (F* wing, scales) (new species of James, possibly a variety of
An. leucosphyrus. Type specimens: Holotype pinned female, BMNH, London. Type locality: India, Karnataka, Kârvâr.

Anopheles balabacensis of Reid, 1970: 56 (in part, systematics).


Anopheles elegans of Townsend, 1990: 36 (type information).

Anopheles leucosphyrus of Christophers, 1933: 177 (type information).

Anopheles leucosphyrus balabacensis of Colless, 1956: 76 (taxonomic notes, type information).

Anopheles leucosphyrus var. elegans of Cogill, 1903: 330 (larval bionomics, in part); James & Liston, 1940: 82 (wing, page 83); Reid, 1949: 46 (taxonomic notes, in part, type information).

Neomyzomyia elegans of Theobald, 1910: 29 (transferred to genus Neomyzomyia; in part, F, Fig. 11); James & Liston, 1911: 106 (F wing).

Female. Head: proboscis length 2.03–2.30 mm (mean 2.20 mm), ratio of length to forefemur length 1.03–1.11 (mean 1.08), maxillary palpus length 1.93–2.20 mm (mean 2.06 mm), ratio of length to proboscis length 0.90–0.99 (mean 0.94), ratio of length of forefemur 0.96–1.02 (mean 1.01), ratio of length of palpspores 3/4 1.53–1.69 (mean 1.59), 3/5 2.06–2.55 (mean 2.28), 4/5 1.31–1.60 (mean 1.44), 4–5/3 1.00–1.16 (mean 1.07), palpspores 2–4 with conspicuous apical bands of silvery white scales, pale scales of palpspore 5 white to pale cream-coloured, length of band of palpspore 5 0.91–1.83 (mean 1.21) length of basal dark band of palpspore 5, ratio of length of apical pale band of palpspore 4 to length of basal dark band of palpspore 5 0.27–0.78 (mean 0.56). Thorax: pleural setae as follow: 2–4 upper proesapisterial, 0–4 prespircipalar, 3–6 prealar, 3–4 upper mesokatepisternal, 2–4 lower mesokatepisternal, 3–4 upper mesepimeral. Wing: length 2.78–3.67 mm (mean 3.33 mm), pale scales on all veins light cream-coloured, spots on costa, subcosta and R1 more obviously cream-coloured, those on vein R and posterior veins lighter, not strongly contrasting with others; PHP, HP and PSP spots of costa prominent or reduced but usually present, SP seta always present and prominent, ASP seta always absent, PP spot 0.63–1.36 (mean 1.00) length of SCP spot, AD spot 2.00–3.20 (mean 2.43) length of PP spot; PSD spot of vein R extending basally from level 2 to level 5 on one or both wings, PSD spot of vein R with 1–4 pale interruptions, sum of pale interruptions on PSD-PD spots of vein R 4–9 for each wing, ratio of length of cell R2 to vein R2+3 1.53–1.98 (mean 1.85), ratio of length of cell R3 to cell R1+2 1.18–1.28 (mean 1.22). Legs: foretarsomeres 2, 3 and 4 with broad basil and apical bands of white scales on dorsal, lateral and anterior surfaces, tan to light brown-scaled along ventral surface, apical and basal pale bands indistinct or absent on ventral surface, foretarsomere 2 sometimes mostly pale-scaled on dorsal, lateral and anterior surfaces, with 2 narrow dark middle bands, foretarsomere 5 mostly dark-scaled with pale scales at apex, occasionally entirely pale-scaled, dark scales on foretarsomeres 4, 5 sometimes tan to light brown; midtarsomeres 2–4 with apical pale band on dorsal, lateral and anterior surfaces, venetal surface entirely dark-scaled, midtarsomere 5 dark-scaled; hindtarsomeres 2, 3 with short apical pale band, hindtarsomere 2 with 1–3 pale patches on middle dark region, hindtarsomere 4 with basal and apical pale bands, hindtarsomere 5 dark with pale scales at apex. Abdomen: tergum VI without scales, tergum VII with few cream-coloured to brownish scales posteriorly, tergum VIII with cream-coloured to golden scales covering apical 0.5–0.8; sternum VI usually without scales, sometimes with 1–3 dark posteromediaal scales, sternum VII with posteromediaal patch of dark scales, sternum VIII with small basolateral patch of pale scales.

Male. Essentially as in female except for sexual characters. Wing generally paler, with reduced scaling, pale spots usually longer than in female. Palpspore 2 with dorsal patch of pale scales at middle extending laterally, apex bare; palpspore 3 with long dorsal patch of pale scales at middle, extending laterally, apex with broad band of pale scales covering dorsal, lateral and venral surfaces, and dark scales at apex of ventrolateral surface, palpspore 4 and 5 mostly pale-scaled with narrow basal band of dark scales, both with longitudinal line of dark scales on ventral surface not reaching apex of palpspore 5. Abdomen: sterna VI and VII with posteromediaal patches of dark scales, sternum VIII covered with pale cream-coloured to yellowish scales.

Pupa (Fig. 5, Table 9). Position and development of setae as figured; range and modal number of branches in Table 9. Measurements and counts from 18 to 20 specimens. In general similar to An. latens except for the following characters. Spermatheca: sexes 5–CT with 3–6 branches, 6–CT single or double, 7,8,12–CT usually double (7, 2–4; 8, 1–3; 9, 8–CT single or double. Seta 9–II–VIII light to medium brown, slightly darker at base. Abdomen: seta 6–II usually double (1,2), 7–I with 2–4 branches; 6–II single or double, 7–II with 3–5 branches, 8,10,11–II absent, 9–II length 0.01–0.0144 mm (mean 0.01 mm); 1–III with 4–6 branches, 9–III length 0.02–0.0244 mm (mean 0.02 mm); 1–IV with 2–6 branches, 5–IV with 4–6 branches, 6–IV single, 9–IV length 0.02–0.05 mm (mean 0.03 mm), ratios of length of seta 9–IV/9–III 1.33–2.44 (mean 1.82) and 9–IV/9–V 0.23–0.46 (mean 0.33); 1–V usually double (1–3), 5–V with 4–7 branches, 6–V single, 9–V length 0.07–0.13 mm (mean 0.11 mm), with or without minute denticles; 1–VI usually single (1–3), 6–VI single or double, 9–VI length 0.10–0.13 mm (mean 0.11 mm), with or without minute denticles; 1–VII single or double, 5–VII with 3–8 branches, 9–VII length 0.11–0.14 mm (mean 0.12 mm), with or without minute denticles; 9–VIII with 10–20 branches. Paddle: filamentous spicule on outer apical margin and inner margin usually prominent and present, rarely absent on inner margin or from both outer and inner margins; seta 2–Pa single or double; toothed margin index 0.78–0.90 (mean 0.85), paddle teeth well developed, tapering to acute apex, teeth widely spaced.
Larva (Fig. 5, Table 10). Position and development of branches as figured; range and modal number of branches in Table 10. Measurements and counts from 20 to 32 specimens unless otherwise indicated. In general similar to An. latens except for the following characters. Head: integument without pattern of dark spots; length 0.68–0.72 mm (mean 0.70 mm) (n 9), width 0.70–0.77 mm (mean 0.74 mm) (n 9), antenna length 0.28–0.32 mm (mean 0.30 mm), ratio of distance between base of seta 1-A to antenna length 0.31–0.44 (mean 0.38); seta 2-C single, simple; 3-C length 0.07–0.10 mm (mean 0.09 mm); distance between bases of 2-C and 3-C 0.03–0.04 mm (mean 0.04 mm), 4-C single, length 0.07–0.10 mm (mean 0.08 mm), extending nearly or beyond base of 2-C, distance between insertions of 2-C and 4-C 0.08–0.11 mm (mean 0.09 mm), ratio of length of 4-C to distance between insertions of 2-C and 4-C 0.80–1.09 (mean 0.93) (n 19); distance between bases of 3-C and 4-C 0.07–0.10 mm (mean 0.08); 5-C as long or slightly longer than antenna, not reaching anterior margin of head, with 5–10 branches, 6-C with 7–13 branches, 7-C with 7–11 branches. Thorax: tubercles of all large setae light brown to yellowish; seta 1-P with 11–17 branches, tubercle of seta 1-P partially joined to tubercle of 2,3-P by an anterior basal bridge, each tubercle with strongly pointed apical tooth arising from posterior dorsolateral side and projecting forward over bases of 1,2-P, 14-P with 4–7 branches; 4-M single to triple, 6-M triple, 14-M with 5–9 branches; 3-T moderately developed, pale, with 3–6 leaflets arising from long slender stem. Abdomen: seta 1-I moderately developed, with 3–6 leaflets, 2-I single to triple, 3-I with 3,4 branches; 1-II moderately developed with 6–10 leaflets; 2-I with 3,4 branches, 3-IV double or triple, 13-IV triple to 4-branched, ratio of length to length of 10-IV 0.53–0.87 (mean 0.67); 2-V with 4,5 branches; 1-VII with 9–13 leaflets, leaflets without apical seta serrations; pecten with 12–15 teeth, 4–7 long teeth alternating with 7–10 short teeth.

Material examined. HOLOTYPE: adult pinned female with the head detached and glued on the same round label with the adult. There are four labels with the specimen: a handwritten label ('Kârwar, Bombay'); a round, handwritten label ('Anopheles elegans, Holotyp., P.F. Mattingly, I.i.1955'). Total material of An. elegans examined: 1155 specimens comprising 176F, 203M, 362Le, 369Pe, 45L, derived from three separate collections from natural habitats (2 adult, 1 immature) and a series from colony.

Distribution. Anopheles elegans is apparently restricted to peninsular India, where it occurs in hill forests of Karnataka and Tamil Nadu, and was known as the Western Ghats form of An. dirus (Bhat, 1988).

Biometrics. Immatures of An. elegans were found in a jungle spring in association with An. culicifomis Cogill and An. fluvialis James in April (Cogill, 1903), and in elephant footprints in association with An. mirans. They were also found in streams, muddy pools, spring pools and tree holes in the Nilgiris District, India (Tewari et al., 1987). Larval habitats were inside the forest and also in betel nut gardens (Bhat, 1988). Adults were collected in human-bait collections, resting on vegetation and in cattle sheds in the Kyasanur area of Shimoga District, Karnataka (Tewari et al., 1987).

Systematics and nomenclature. James (in Theobald, 1903) described An. elegans from an adult female that Cogill had collected in India the year before (Kârwar, Karnataka). James placed the species in the genus Myzomyia and designated the single female he sent to Theobald as 'the type' of An. elegans and reported (p. 54) that it was deposited in the British Museum (Nat. Hist.), presented by the describer.' James also wrote that neither the male nor the immature stages were known. In October of the same year, Cogill (1903) placed Myzomyia elegans in the genus Anopheles and mentioned that two larvae of *A. leucophyrus, Donitz, var. elegans, Theobald' were collected in India. The larvae were collected in a jungle stream in April and no additional larvae were found again until the rains ended. Cogill also described the larva, pupa and adult male, and redescribed the female. It is significant that the wing illustration in Cogill's paper differs from that in Theobald (1903), which is An. elegans. Cogill's illustration probably belongs to one of the specimens collected in September–October James & Liston (1904) considered An. elegans to be a variety of An. leucophyrus, included it in their Group II with An. punctulatus, and confirmed that the only specimens available were collected by Cogill in Kârwar, India. Two wing illustrations appear in James & Liston (1904). The wing illustrated in Plate XI(1) is similar to what Cogill (1903) published and is thus distinct from the wing in Theobald (1903). However, the wing depicted on p. 83 of James & Liston (1904) is identical to that shown on p. 53 in Theobald (1903). In 1910, Theobald described a new genus, Neomyzomyia, and transferred An. elegans to it. He also redescribed An. elegans (because he considered James's description to be inadequate) giving photographs of wings (as Figs 11 and 12) that differ from that of Theobald (1903), especially in having three pale interruptions on the PD spot of vein R1, and in having the PDS spot of vein R with at least one pale interruption (the other pale interruption is not clear in the picture). Moreover, the wings in Figs 11 and 12 are not the same: the latter belongs to a specimen of what appears to be An. baimaii (as described herein) collected by R. White on the Andaman Islands. James & Liston (1911) agreed with Theobald (1910) in considering An. elegans to be a species of Neomyzomyia and reprinted James's original description and wing drawing with some additions from Theobald (1910). Christophers (1933) treated An. elegans as a junior synonym of An. leucophyrus and confirmed that the type was in the BMNH. Reid (1949), however, found no specimen labelled as type among Cogill's specimens deposited in the BMNH but confirmed that one female had the same collection data reported by James in Theobald (1903). The other seven specimens in the BMNH were collected by Cogill in September–October 1902. In the NMNH, there
Fig. 5. *Anopheles elegans*. Pupa (female): CT, cephalothorax; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; PP, pecten plate; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Circle shows basal details of setae 1-3-P. Millimetre scale bars.
Table 9. Number of branches for pupal setae of *Anopheles elegans* range (mode). n.c. = not counted.

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<th>Abdominal segments</th>
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<td>1</td>
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Table 10. Number of branches for setae of fourth-instar larva of *A. elegans* range (mode).

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<th>M</th>
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<td>2-3 (3)</td>
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are also four of Cogill's specimens collected in September–October 1902. Reid (1949) concluded that the description of James & Liston (1904) was based on the specimens collected by Cogill in September–October 1902 and suggested further that James in Theobald (1903) was wrong in designating the specimen collected in April 1902 as the type of *An. elegans*. In a discussion on the validity of the name *An. elegans*, Colless (1956) considered the single female (collected by Cogill, v.02) James sent to Theobald to be *An. l. balabacensis*, and the other specimens to be *An. elegans*. He concluded this because Theobald did not label the single female as the type and because James & Liston's (1904, 1911) descriptions were probably based on specimens collected in September–October. Colless also considered Theobald's designation of the single female collected in April as the 'Type' was an error and the remaining four females and two males (collected by Cogill, x.02) should be considered cytops, from which a lectotype should be designated.

A holotype is defined as 'the single specimen upon which a new nominal species-group taxon is based in the original publication' (Article 73.1: ICZN, 1999). Article 73.1.1 also says 'If an author when establishing a new nominal species-group taxon states in the original publication that one specimen, and only one, is the holotype, or “the type”, or uses some equivalent expression, that specimen is the holotype fixed by original designation'. Article 73.1.3 states, 'The holotype of a new nominal species-group taxon can only be fixed in the original publication and by the original author.' From these three articles, it is clear that the specimen designated as 'the type' by James in Theobald (1903) is the holotype of *An. elegans*. In addition, James clearly wrote that 'the specimen is imperfect' and was collected in April. Since James only sent a single female and only this female was noted in the original description, that specimen is the holotype. Colless (1956) examined Cogill's specimens of *An. elegans* (i.e. original specimens), as well as the correspondence between James and Theobald, and concluded that James sent Theobald a written description, figure of one wing and one female with the suggestion that this specimen might be kept as a type until better specimens could be sent. Examination of the specimen designated as 'the type' by James revealed that it is imperfect, with the head detached from the body and glued to the same label with the pinned adult female. Mattingly recognized the specimen as the holotype of *An. elegans* and added a type label and an additional label on which he wrote 'Anopheles elegans James, Holotype, P.F. Mattingly, 1.ii.1955. We examined the 12 specimens collected by Cogill in 1902, both in April and September–October 1902 (BMNH and NMMH) and discovered that they belong to two distinct species of the Leucosphyrus Group. Because the holotype of *An. elegans* is the specimen designated as the type by James in Theobald (1903), the other specimens collected in September and October belong to an undescribed species that has been largely misidentified as *An. elegans* since Cogill (1903). Furthermore, the holotype shows that *An. elegans* belongs to the Dirus Complex of the Leucosphyrus Subgroup, whereas the undescribed species belongs to the Elegans Subgroup of Colless (1957) and Peyton (1990). Also, *Anopheles dirus* species E (Sawadipanich et al., 1990) is, in fact, *An. elegans*. Because *An. elegans* belongs to the Dirus Complex, the group designated the Elegans Subgroup by Colless and Peyton is now renamed as the Hackeri Group.

Cytogenetic and crossing data confirm that *An. elegans* (as *An. dirus* species E) is a distinct species in the Dirus Complex and is more closely related genetically to *An. baimaii* than to any other member of the complex. Both species, for example, share the same Xa inversion. It seems that *An. elegans* and *An. baimaii* evolved from a common ancestor through allopatric speciation (Sawadipanich et al., 1990).

Adults of *An. elegans* are distinguished, except from *An. scanloni* and *An. baimaii*, by the following combination of characters: (1) proboscis dark-scaled, slightly longer than forefemur, ratio of length to forefemur length 1.03–1.11; (2) PSD spot of vein R rarely extending to level 1, 2 or 3 on at least one wing, frequently extending to level 4 and 5 on one or both wings; (3) PSD spot of vein R usually with 2–4 pale interruptions on at least one wing, rarely with one pale interruption on one wing; (4) ASP spot absent on costa and usually absent on subcosta; (5) hindtarsomere 4 with basal and apical pale bands; (6) hindtarsomere 5 dark-scaled at base; (7) apical pale band on hindtibia entirely white, without dark extension; (8) vein IA with a long pale spot at level of the PSD spot of vein R on at least one wing, this pale spot sometimes reduced but always the longest pale spot of IA; (9) sternum VI usually without scales, occasionally with 1–3 postero medial dark scales.

The fourth-instar larva of *An. elegans* can be recognized by the following combination of characters: (1) seta 5-C as long or slightly longer than the antenna, not reaching the anterior margin of the head; (2) seta 1-X inserted on the saddle; (3) seta 2-C without aciculae; (4) tubercle of seta 1-P narrowly joined to the tubercle of 2,3-P by an anterior basal bridge; (5) tubercle of setae 1,2-P with strong, pointed apical tooth arising from posterodorsal side and projecting forward over base of 1,2-P; (6) seta 4-C not reaching the base or extending slightly beyond the base of 2,3-C, ratio of length 4-C to distance between 2,3-C and 4-C 0.80–1.09. Recognition of *An. elegans* based on pupal characters is not reliable. A few individuals examined did not have a fringe of filamentous spicules on the inner margin of the paddle, and thus they could have been misidentified as *An. scanloni*. Because *An. elegans* and *An. scanloni* are allopatric, their geographical distributions can facilitate their identification.

**Hackeri subgroup (formerly Elegans subgroup)**

*Anopheles* (*Cellia*) *recens* Sallum & Peyton, sp.n.

**Etymology:** the name *recens* is Latin for fresh, young, recent.

*Anopheles* Sumatra species of Peyton, 1990: 197.

**Female.** Head: proboscis uniformly dark-scaled or with long ventral patch of pale scales on apical 0.2 of ventral
surface, length 2.28-2.68 mm (mean 2.50 mm), ratio of length to forefemur length 1.16-1.30 (mean 1.21); maxillary palpus length 1.80-2.33 mm (mean 2.10 mm), ratio of length to proboscis length 0.79-0.86 (mean 0.83), ratio of length to forefemur length 0.97-1.05 (mean 1.01), ratio of length of palpmers 3/4 1.67-2.54 (mean 1.94), 3/5 2.50-3.62 (mean 3.05), 4/5 1.22-2.12 (mean 1.60), 4-5 0.70-1.00 (mean 0.85), palpomers 2-4 with narrow apical pale cream-coloured bands, pale scales on palpomere 5 almost yellowish, apical pale band of palpomere 5 0.00-1.00 (mean 0.5) length of basal dark band of palpomere 5, ratio of length of apical pale band of palpomere 4 to length of basal dark band of palpomere 5 0.00-0.67 (mean 0.21). Thorax: pleural setae as follows: 2-5 upper proepisternal, 0-2 prespiracular, 5-9 prealar, 6-7 upper mesokatepisternal, 3-6 lower mesokatepisternal, 3-8 upper mesepimeral. Wing: length 3.64-4.55 mm (mean 4.05 mm), pale scales on all veins light cream-coloured, spots on subcosta and SPC, PP and AP spots of costa more obviously cream-coloured nearly yellowish; HP spot present, prominent, PSP spot rarely absent, SP spot usually present, prominent, ASP spot absent on costa, PP spot 0.79-3.80 (mean 1.31) length of SPC spot, AD spot 1.05-3.63 (mean 2.58) length of PP spot, PSD spot of vein R extending basally from level 2 to level 4 on both wings, PSD spot of vein R with 1-4 pale spots on one or both wings, SD spot of vein R usually with 1, 2 pale interruptions, rarely with 3 pale interruptions on both wings, sum of pale interruptions on PSD-PP spots of vein R 3-8 for each wing; ratio of length of cell R3 to vein R2 1.36-1.79 (mean 1.58), ratio of length of cell R3 to cell M1 1.27-1.48 (mean 1.36). Legs: foretarsomers 2.3 with short basal and apical bands of pale scales, foretarsomer 2 with 2-4 pale spots on middle of dorsal surface, foretarsomer 4 with indistinct basal and apical pale bands, usually without basal pale band, foretarsomer 5 with pale scales at apex or entirely dark-scaled, foretarsomer 2-4 entirely dark-scaled on ventral surface; midtarsomers 2-4 with small, apical patches of pale scales on dorsal surface, midtarsomers 2.3 with 1-3 pale spots on middle dark area, dark-scaled ventrally, midtarsomer 5 entirely dark-scaled; hindtarsomers 2-4 with short apical pale bands, hindtarsomer 2 with 2-4 pale spots on median dark area, hindtarsomer 5 dark-scaled. Abdomen: tergum VI without scales, tergum VII with 2-4 dark scales on posterior margin, tergum VIII with patch of dark scales medially, few golden scales postero-laterally; sternum VI usually without scales, rarely with 2.3 postero-medial scales, sternum VII without scales or with postero-medial patch of dark scales, sternum VIII without scales, rarely with 2.3 antero-lateral pale scales.

Male. Essentially as in female except for sexual characters. Wing generally paler with reduced scaling, pale spots usually longer than in female. Proboscis dark-scaled without ventral patch of pale scales; palpomere 2 with dorsal patch of pale scales at middle, apex of palpomere 2 bare, palpomere 3 with long dorsal patch of pale scales at middle extending laterally, sometimes reaching ventral surface, apex of palpomere 3 variable, with broad band of pale scales covering dorsal and lateral surfaces, with dorsal patch of pale scales, or entirely dark-scaled, palpomere 4 variable, pale-scaled with basal band of dark scales, less frequently with patch of dark scales on ventral and dorsal surfaces, palpomere 5 variable, pale-scaled with basal dark, or with basal dark band with extension along ventral surface not reaching apex of segment, or mostly dark-scaled with lateral patch of pale scales. Abdomen: sternum VIII covered with pale cream-coloured to whitish scales.

Pupa (Fig. 6, Table II). Position and development of setae as figured; range and modal number of branches in Table II. Measurements and counts from 7 to 10 specimens. In general similar to An. latens except for the following characters. Sternal II-VI with narrow dark band near anterior margin. Cephalothorax: seta 5-CT with 3-5 branches, 6-CT single or double, 7-12-CT usually double (see Table II for ranges). Seta 9-IV-VIII light to medium brown, slightly darker at base. Abdomen: seta 6-I usually single (1,2), 7-1 with 2-3 branches; 1-11 dendritic, with 8-18 narrow branches, 6-I single or double, 7-11 double or triple, 8,10,11-II absent, 9-II length 0.01-0.02 mm (mean 0.02 mm); 1-III with 3-5 branches, 5-III with 5-8 branches, 6-III usually single (1,2), 9-III length 0.02-0.03 mm (mean 0.02 mm); 1-IV with 2-4 branches, 5-IV with 4-5 branches, 6-IV single, 9-IV long, always simple, length 0.05-0.08 mm (mean 0.06 mm), ratios of length of 9-IV/9-III 1.92-3.26 (mean 2.27) and 9-IV/9-V 0.33-0.76 (mean 0.44); 1-IV usually double (1,2), 5-V with 4-6 branches, 6-V single, 9-V long, always simple, length 0.11-0.14 mm (mean 0.13 mm); 1-IV single or double, 5-VI with 3-5 branches, 6-VI single, 9-VI always simple, length 0.12-0.15 mm (mean 0.13 mm); 1-VII single, 5-VII with 4-6 branches, 6-VII single, 9-VII always simple, length 0.12-1.15 mm (mean 0.14 mm); 9-VIII with 6-13 branches. Paddle: seta 2-Pa single; toothed margin index 0.84-0.93 (mean 0.89), paddle teeth well developed, tapering to apex, ending in acute apex, widely spaced.

Larva (Fig. 6, Table II). Position and development of setae as figured; range and modal number of branches in Table II. Measurements and counts from 8 to 16 specimens unless otherwise indicated. In general similar to An. latens except for the following characters. Head: integument light brown to yellowish with dark spots on dorsal apatome and labiogula as follow: one dark spot centrally on dorsal apatome, posterior to setae 7-C; a more prominent, single dark spot posterior to area between seta 8-C and 2 small dark spots laterally; 2 lateral dark spots at dorsal apatome, posterior to seta 7-C; 1 dark spot at ventral lateralia near insertion of seta 12-C; 2 dark spots placed laterally at the level of posterior tentorial pit, and a single dark spot posterior to hypostomal ccdysial line; head length 0.75-0.81 mm (mean 0.79 mm) (n 5), width 0.73-0.83 mm (mean 0.76 mm) (n 5); antenna length 0.33-0.40 mm (mean 0.37 mm), ratio of distance between base and seta 1-A to antenna length 0.32-0.43 (mean 0.38); seta 2-C usually rarely with few, sparse, minute spicules; 3-C length 0.11-0.15 mm (mean 0.13 mm) distance between bases of 2-C and 3-C 0.04-0.06 mm.

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Fig. 6. *Anopheles recens* sp.n. Pupa (female): CT, cephalothorax; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; PP, pecten plate; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Circle shows basal details of setae 1-3-P. Millimetre scale bars.
### Table 11. Number of branches for pupal setae of *Anopheles recens*: range (mode).

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### Table 12. Number of branches for setae of fourth-instar larva of *An. recens*: range (mode).

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<td>16-30 (17)</td>
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</table>
New species of the Anopheles leucosphyrus group

(4·C length 0.12-0.17 mm (mean 0·15 mm), extending beyond base of 2·C, distance between insertions of 2·C and 4·C 0·08-0·11 mm (mean 0·09 mm), ratio of length of 4·C to distance between insertions of 2·C and 4·C 1·44-2·0 (mean 1·68), distance between bases of 3·C and 4·C 0·05-0·08 mm (mean 0·07 mm), 5·C shorter than antenna, not reaching anterior margin of head, with 9-12 branches, 6·C with 10-13 branches, 7·C with 11-15 branches. Thorax: tubercles of all large setae light to medium brown; seta 1·P with 14-20 branches, tubercle of seta 1·P usually joined basally to tubercle of 2·P, rarely separate, both tubercles with strong, pointed or somewhat rounded postero dorsal tooth projecting forward over base of 1·2·P, 1·4·P with 5-9 branches; 4·M single or double, 6·M usually 4-branched (3,4), 14·M with 4-7 branches; 3·T somewhat pal mate, with 3-6 leaflets. Abdomen: seta 1-I not palmate, with 3,4 slender branches, 2-I always single, 9-1 with 3,4 branches; 1-11 moderately developed, more pigmented than 1-I, somewhat palmate, with 5-8 leaflets; 2·IV always triple, 3,13 IV single or double, ratio of length of 13-IV to 10-IV 0·91-1·24 (mean 1·11) (n 7); 1·VII with 8-12 leaflets, leaflets with minute apicolate serrations and slender apical filament; 1·X single or double, inserted on saddle; pecten teeth 14-17 teeth, 5-8 long teeth alternately extending with 6-11 short teeth.

Material examined. HOLOTYPE: adult female with associated larval and pupal exuviae on microscope slide, acc. no. IN704-10, collected by U. Malaya team, 5 April 1978, deposited in the NMNH. Type locality: INDONESIA, Sumatra Island, Gunung Dempo (4°2'S, 103°9'E). PARATYPES: same data as holotype, 8·F, 11·M, 6·Le, 6·Pe, 7·Le; acc. no. IN705, 5 April 1978, 2·F, 1M. Other material of An. recens examined: 44 specimens comprising 11·F, 12·M, 7·Le, 7·Pe, 7·Le derived from 2 separate collections from natural habitats (2 immatures).

Distribution. Anopheles recens is known only from Sumatra Island, Indonesia.

Bionomics. Nothing is known about the medical importance of An. recens or the involvement of this species in the transmission of parasites to humans and other animals. Immatures of An. recens were taken from temporary ground pools in cloud forests. The water was fresh, stagnant or slow moving, clear with or without emergent vegetation, and in partial shade or full sun. The larval habitats were located at elevations of 1550 m above sea level.

Systematics. Anopheles recens (as An. leucosphyrus Sumatra species) was included in the Hackeri Group (as Elegans Group) because the proboscis is noticeably longer than the forefemur and the palpus is shorter than the proboscis (Peyton, 1990). Adults can be distinguished by the following characters: (1) proboscis longer than forefemur, ratio of proboscis length to forefemur length 1·16-1·30 (mean = 1·20); (2) proboscis of female entirely dark-scaled or with ventral patch of pale scales on apical 0·2; (3) apical pale band of hindtibia entirely white-scaled or with a patch of dark scales on anterior surface; (4) palpomere 5 entirely dark-scaled or with apical pale band, ratio of length of apical pale band to length of basal dark band 0·00-1·00 (mean = 0·50); (5) PSD spot of vein R extending from level 1 to level 4; (6) PSD spot of vein R with 1-4 pale interruptions; (7) sum of pale interruptions on PSD-PD spots of vein R 3-8 for each wing; (8) SCP, PP and AP spots of costa cream-coloured, almost yellowish, strongly contrasting with other pale spots; (9) tergum VIII with a patch of dark scales medially and a few golden scales posterolaterally; (10) hindtarsomeres without pale scales at base; (11) ASP spot absent from costa; and (12) pale spots on costa small.

The fourth-instar larva of An. recens can be recognized by the following combination of characters: (1) seta 5·C conspicuously longer than antenna; (2) basal selerotized tubercles of setae 1·2·P with prominent tooth or spine projecting from postero dorsal margin forward over the base of each seta; (3) seta 3·C long, extending beyond anterior margin of head; (4) seta 4·C always extending noticeably beyond base of 2·C; (5) seta 1·I with 5-8 very narrow leaflets, leaflets translucent or very lightly pigmented, stem not inflated; (6) seta 13-IV single or double, about length of 10-IV, ratio of length of 13-IV to 10-IV 0·91-1·24 (mean = 1·11); (7) seta 13-IV double; (8) seta 2·VII with 4-6 branches; (9) seta 9·VII with 3,4 branches.

Anopheles (Cellia) mirans Sallum & Peyton, sp.n.

Etymology. The name mirans is derived from Latin 'mirari' meaning to wonder at, look at.


Anopheles balabacensis of Reid, 1970: 56 (in part, west coast of India, systematics).

Anopheles elegans of Colless, 1956: 75 (F*, M, P*, E, taxonomic notes, identification key, distribution); Choudhury et al., 1963b: 243 (vector competence); Choudhury et al., 1963a: 237 (vector competence); Reid, 1968: 303 (F*, taxonomy, bionomics notes, identification key); Nelson et al., 1971: 46 (vector competence); Mendis et al., 1984: 318 (L*, P*, bionomics); Peyton, 1990: 197 (taxonomy).

Neomyzomyia elegans of James & Liston, 1911: 105 (F*, L*, Plate XV).


Female. Head: proboscis uniformly dark-scaled, length 2·17-2·86 mm (mean 2·59 mm), ratio of length to forefemur length 1·19-1·31 (mean 1·25), maxillary palpus length 1·85-2·45 mm (mean 2·22 mm), ratio of length to proboscis length 0·84-0·93 (mean 0·87), ratio of length to forefemur

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length 1.02–1.15 (mean 1.10), ratio of length of palpmores 3/4 1.35–1.77 (mean 1.55), 3/5 1.93–2.54 (mean 2.21), 4/5 1.27–1.73 (mean 1.43), 4–5/3 1.04–1.18 (mean 1.10), palpmores 2–4 with narrow apical silvery white bands, bands similar in size and colour, pale scales of palpmore 5 white, similar to scales on palpmores 2–4, length of apical pale band of palpmore 5 0.83–2.67 (mean 1.40) length of basal dark band of palpmore 5, ratio of length of apical pale band of palpmore 4 to length of basal dark band of palpmore 5 0.33–1.00 (mean 0.6). Thorax: pleural setae as follow: 2–5 upper proepisternal, 0–1 prespiracular, 4–8 prealar, 3,4 upper mesokatepisternal, 2,3 lower mesokatepisternal, 2–6 upper mesepimeral. Wing: length 2.88–4.23 mm (mean 3.64 mm ± 0.34), pale scales of PHP, HP, PSP, SP and SCP spots white on costa, SCP spot pale cream-coloured to yellowish on subcosta, pale scales on remaining veins pale cream-coloured to yellowish, none strongly contrasting with others, PHP spot of costa usually prominent, sometimes reduced, HP, PSP and SP spots always present, prominent, ASP spot absent, PP spot 0.46–1.89 mm (mean 1.00) length of SCP spot, AD spot 1.94–8.00 mm (mean 3.27) length of PP spot, PSD spot of vein R extending basally from level 1 to level 4, often to level 1 and level 2 on one or both wings, PSD spot of vein R without pale interruptions, SD spot of vein R with 1 pale interruption, sum of pale interruptions on PSD-PD spots of vein R always 2 on both wings, ratio of length of cell R3 to vein R2,3,1 1.29–1.80 (mean 1.52), ratio of length of cell R2 to cell M1,2 1.13–1.29 (mean 1.22). Legs: femora, tibiae and tarsomeres dark-scaled and speckled with pale spots; foretarsomere 2 with conspicuous basal and apical pale bands, middle dark area with 1–3 pale spots or entirely dark, foretarsomere 3 with basal and apical pale bands, foretarsomere 4 with basal and apical pale bands, occasionally apical pale band absent, foretarsomeres 5 dark at base, apex pale-scaled, basal and apical pale bands on foretarsomeres 2–5 evident on ventral surface; midtarsomeres 2–4 with apical pale spot on dorsal surface, pale spots not noticeable on ventral surface, midtarsomere 5 pale-scaled at apex; hindtarsomere 2,3 with minute basal pale spot or dark-scaled at base, always with apical pale band, hindtarsomere 4 with basal and apical pale bands, hindtarsomere 5 with basal pale band, rarely entirely dark at base, apex always pale-scaled. Abdomen: tergum VI usually without scales, rarely with few dark scales posteriorly, tergum VII usually without scales, occasionally with few apicolateral scales, tergum VIII covered with golden scales postero-medially, dark scales basally; sternum VI with postero-medial patch of dark scales, sternum VII with postero-medial patch of dark scales, sternum VIII with few, occasionally numerous lateral pale cream-coloured scales.

**Male.** Essentially as in female except for sexual characters. Palpmore 2 with dorsal patch of pale scales at middle, apex of palpmore 2 bare, palpmore 3 with long dorsal patch of pale scales at middle, extending to lateral surface, apex of palpmore 3 with a broad band of pale scales, covering dorsal, lateral and ventral surfaces except for a small ventrolateral patch of dark scales at apex, palpmore 4 mainly pale-scaled with basal dark band extending along ventral surface, palpmore 5 pale-scaled with basal dark band extending along ventral surface and reaching apex. Abdomen: sternum VIII covered with pale cream-coloured to golden scales.

**Pupa** (Fig. 7, Table 13). Position and development of setae as figured; range and modal number of branches in Table 13. Measurements and counts from 20 to 40 specimens. Sterna II–VI with narrow, dark band near anterior margin. Cephalothorax: seta 4-CT usually double (2–4), 5-CT with 3–7 branches, 6-CT single to triple, 7-CT usually triple (2–4), 8-CT single or double, 10-CT single to triple, 11-CT single to 5-branched. Seta 9-III medium to dark brown from base to apex, 9-VIII light brown, darker at base. Abdomen: seta 6-IV single or double, 7-1 with 2–5 branches; 6-IV single or double, 7-II with 2–5 branches, 9-II length 0.01–0.02 mm (mean 0.01 mm), 10-II single to triple, 11-II absent or present; 1-III with 3–8 branches, 5-III with 5–9 branches, 9-III length 0.01–0.02 mm (mean 0.02 mm); 1-IV with 2–6 branches, 5-IV with 4–7 branches, 6-IV single or double, 9-IV short, either with or without minute denticles, length 0.03–0.06 mm (mean 0.04 mm), ratios of length of 9-IV/9-III 1.41–3.23 (mean 2.32) and 9-IV/9-V 0.29–0.52 (mean 0.41); 1-V usually double (1–3), 5-V with 3–7 branches, 6-V single, 9-V long, either with or without minute denticles, length 0.08–0.12 mm (mean 0.11 mm); 1-VI single or double, 5-VI with 4–7 branches, 6-VI single, 9-VI length 0.07–0.14 mm (mean 0.11 mm); 1-VII single or double, 6-VII usually single, 9-VII length 0.08–0.12 mm (mean 0.11 mm); 9-VIII with 8–13 branches. Paddle: seta 2-Pa with 1,2 branches; toothed margin index 0.78–0.94 (mean 0.85), paddle teeth tapering to a pointed, sharply acute apex.

**Larva** (Fig. 7, Table 14). Position and development of branches as figured; range and modal number of branches in Table 14. Measurements and counts from 22 to 44 specimens unless otherwise indicated. Head: integument light brown to yellowish with dark spots on dorsal apotome and labiogula as follow: 1 small dark spot at posterior end of dorsal apotome and 2 always slightly anterior; one dark spot posterior to area between seta 8-C and 2 small dark spots laterally; 2 lateral dark spots at dorsal apotome posterior to seta 7-C; 1 dark spot on lateralia in area of insertion of seta 12-C; 2 dark spots laterally at level of posterior tentorial pit; one dark spot placed posteriorly on hypostomal edysial line; head length 0.65–0.74 mm (mean 0.72 mm), width 0.70–0.80 mm (mean 0.76 mm), antenna length 0.29–0.33 mm (mean 0.31 mm), ratio of distance between base of seta 1-A to antenna length 0.32–0.50 (mean 0.39); seta 2-C single, occasionally with minute sparse spicules on apical 0.5; 3-C length 0.07–0.10 mm (mean 0.08 mm), distance between bases of 2-C and 3-C 0.03–0.06 mm (mean 0.04 mm), 4-C single to triple, length 0.10–0.16 mm (mean 0.12 mm), extending beyond base of 2-C, distance between basal insertions of 2-C and 4-C 0.07–0.12 mm (mean 0.09 mm), ratio of length of 4-C to distance between insertions of 2-C and 4-C 1.05–2.12 (mean 1.45), distance between bases of 3-C and 4-C

Fig. 7. *Anopheles mirans* sp.n. Pupa (male): CT, cephalothorax; Pa, paddle; I-IX, abdominal segments of pupa (dorsal on left, ventral on right), numbers on the left side denote seta 9 of designated segments. Larva: C, head; P, prothorax; M, mesothorax; T, metathorax; abdominal segments I-VI left side dorsal, right side ventral; VII-X lateral (left side) view. Circle shows basal details of setae 1-3-P. Millimetre scale bars.
Table 13. Number of branches for pupal setae of *Anopheles mirans*: range (mode). n.c. = not counted.

<table>
<thead>
<tr>
<th>Seta no.</th>
<th>Cephalothorax CT</th>
<th>Abdominal segments</th>
<th>Paddle IX P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>I</td>
<td>II</td>
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<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>n.c.</td>
<td>11-25</td>
</tr>
<tr>
<td>2</td>
<td>2,3 (2)</td>
<td>3-10 (7)</td>
<td>5-7 (6)</td>
</tr>
<tr>
<td>3</td>
<td>2,3 (2)</td>
<td>1-3 (2)</td>
<td>2-5 (3)</td>
</tr>
<tr>
<td>4</td>
<td>2-4 (2)</td>
<td>2-8 (4)</td>
<td>2-5 (3)</td>
</tr>
<tr>
<td>5</td>
<td>2-7 (2)</td>
<td>2-5 (3)</td>
<td>2-5 (2)</td>
</tr>
<tr>
<td>6</td>
<td>1-3 (2)</td>
<td>1,2 (1)</td>
<td>1,2 (1)</td>
</tr>
<tr>
<td>7</td>
<td>2-4 (3)</td>
<td>2-5 (3)</td>
<td>2-5 (2)</td>
</tr>
<tr>
<td>8</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>2-4 (2)</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>1-3 (2)</td>
<td>-</td>
<td>1-3 (2)</td>
</tr>
<tr>
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<td>0-2 (0)</td>
</tr>
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</tr>
<tr>
<td>13</td>
<td>0-2 (0)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>-</td>
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</tr>
</tbody>
</table>

Table 14. Number of branches for setae of fourth-instar larva of *An. mirans*: range (mode).

<table>
<thead>
<tr>
<th>Seta no.</th>
<th>Head no.</th>
<th>Thorax</th>
<th>Abdominal segments</th>
</tr>
</thead>
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<tr>
<td></td>
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</tr>
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<td>1</td>
<td>15-20 (15)</td>
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<tr>
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<td>1</td>
<td>1</td>
<td>10-14 (12)</td>
</tr>
<tr>
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<td>1-2 (1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>1-3 (2)</td>
<td>1</td>
<td>13-18 (13)</td>
</tr>
<tr>
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<td>7-14 (10)</td>
<td>21-51 (33)</td>
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</tr>
<tr>
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<td>10-17 (13)</td>
<td>1</td>
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<td>22-30</td>
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<td>19-28 (28)</td>
<td>19-35 (24)</td>
</tr>
<tr>
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<td>1-6 (2)</td>
<td>1</td>
<td>1-2 (1)</td>
</tr>
<tr>
<td>10</td>
<td>1-2 (1)</td>
<td>1</td>
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</tr>
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<td>1-3 (1)</td>
</tr>
<tr>
<td>13</td>
<td>3-6 (3)</td>
<td>3-6 (5)</td>
<td>4-9 (7)</td>
</tr>
<tr>
<td>14</td>
<td>3-5 (5)</td>
<td>5-12 (8)</td>
<td>6-12 (9)</td>
</tr>
<tr>
<td>15</td>
<td>5-8 (6)</td>
<td>-</td>
<td>-</td>
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</table>
0.05–0.11 mm (mean 0.08 mm), 5-C longer than antenna, extending beyond anterior margin of head, with 7–14 branches, 6-C with 10–17 branches, 7-C with 12–18 branches. Thorax: tubercles of all large setae light to medium brown; seta 1-P with 15–20 branches, tubercle of seta 1-P usually joined basally to tubercle of 2,3-P, rarely separate, both tubercles with strong, pointed or somewhat rounded apical tooth projecting forward over base of 1,2-P, 14-P with 7–12 branches; 4-M single to triple, 6-M usually 4-branched (4,5), 14-M with 6–12 branches; 3-T moderately developed, not palmate, with 5–11 narrow branches arising from distinct level on stem. Abdomen: seta 2-I single to 4-branched, 3-I single to triple, 9-I with 3–7 branches; 1-II poorly developed, more pigmented than 1-I, with 10–17 leaflets arising from distinct level of a moderately pigmented stem, 13-IV with 3,4 branches, ratio of length of 13-IV to 10-IV 0.80–1.14 (mean 0.93); 1-VII with 10–16 moderately broad lanceolate leaflets with minute apicodistal serrations and slender apical filament; 1-X single or double; pecten teeth 13–15, with 5,6 long teeth alternating with 7–10 short teeth.

Material examined. HOLOTYPE: adult female with associated larval and pupal exuviae on microscope slide, acc. no. 316–1, collected by Yiu-Min Huang and Peyton, 18 July 1975, deposited in the NMNH. Type locality: SRI LANKA, Western, Kalutara, Morapitiya, Sinharaja Forest Reserve (6°33'N 80°19'E). PARATYPES: INDIA, Karnañaka (Mysore), Kârâwâr, north Kanara (14°53'N 74°35'E), 3 September 1902, acc. no. 330, 1F; 1 October 1902, acc. no. 332, 1m; acc. no. 333, 1F; acc. no. 335, 1m; acc. no. 336, 1m; acc. no. 357, 10 October 1902, acc. no. 361, 12 October 1902, 1F; acc. no. 373, 29 October 1902, 1F; acc. no. 381, 12 January 1903, 1m. Madras (Tamil Nadu), Nilgiris, Buliar 11°25'N 76°30'E, 13 December 1977, acc. no. 655, 19F, 12M, 13Le, 29Pe; acc. no. 664, 23 December 1977, 4F, 4M, 4Le, 6Pe; acc. no. 676, 12 January 1978, 1F, 3M, 4Le, 4Pe. SRI LANKA, Central, Kandy, Udawatelle Forest Reserve (7°15'N 80°37'E), June 1975, acc. no. 43, 1M, 1Le, 1Pe, all collected by Peyton and Huang; Kandy, Wakarawatta, Roseneath (7°17'N 80°38'E), 25 March 1971, 1L, collected by BA Harrison et al. Sabaragamuwa, Ratnapura, Vaddagala, Sinharaja Forest Reserve (6°24'N 80°27'E), acc. no. 286, 17 July 1975, 1M, 1Le, 1Pe; acc. no. 295, 17 July 1995, 9F, 15M, 19Le, 23Pe. Southern, Galle, Kanneliya Forest Reserve (6°14'N 80°20'E), 9 July 1975, acc. no. 199, 1F, 1Le, 1Pe. Western, Colombo, Labugama Reservoir (6°50'N 80°10'E), acc. no. 422, 7 August 1975, 2F, 4M, 4Le, 4Pe; Kalutara, Morapitiya, Sinharaja Forest Reserve (6°33'N 80°19'E), 18 July 1975, acc. no. 316, 4F, 5M, 4Le, 4Pe, all collected by Huang and Peyton. Paratypes are deposited in the NMNH. Total material of An. mirans examined: 1049 specimens comprising 235F, 183M, 210Le, 359Pe, 63L derived from 94 separate collections from natural habitats (14 adult, 80 immature).

Distribution. Anopheles mirans is known from south-western India (States of Kerala, Karnataka, Tamil Nadu) and Sri Lanka (Central, Sabaragamuwa, Southern, North-western and Western Provinces).

Bionomics. In Tamil Nadu, India, immatures of An. mirans were found in shallow, large and small ground pools, shallow or deep or small rock pools, flood pools and swamps. The water was clear or turbid, in partial or heavy shade, sometimes with decaying leaves. The larval habitats were situated in mountainous areas.

In Sri Lanka, An. mirans immatures were collected in cultivated areas, in ditches along road sides, animal footprints, concrete wells, small rock pools, wheel ruts, ground pools, flood pools, pools along side roads, small or large rock pools, swamps, rock pools along stream edges, and in a semipermanent gem pit. The water was always fresh, stagnant, coloured or turbid or clear, in partial or heavy shade and usually with leaves and sticks. The habitats were in secondary rain forest with mixed scrub vegetation, situated in mountainous terrain, at elevations from 200 to 900 m above sea level. Immatures of An. mirans were found in association with Cx. baliyi Barraud, Cx. fragilis Ludlow, Cx. lasiopalpis Sirivankarn, Cx. minulurus, Cx. minitissima (Theobald), Cx. pallidithorax Theobald, Cx. quadripalpis (Edwards), Cx. uniformis (Theobald), Cx. wardi Sirivankarn, Ur. bicolor and An. maculatus.

Adults of An. mirans were collected at Kandy, Central Province of Sri Lanka, in a small forest (104 ha) bordering the city in central hills of the country at elevation of 518 m above sea level. The vegetation consisted of tall trees with dense undergrowth. Larval habitats were muddy water in car tracks, tyre marks and similar depressions on an infrequently used gravel road. The water was clean except for a few fallen leaves, and it was heavily shaded. Additionally, immatures were found in association with several other Culicinae species but were the only anopheline larva encountered throughout the rainy season. However, when the drought was approaching, immatures of An. mirans declined in numbers (Mendis et al., 1984).

Wild-caught females of An. mirans, from a small locality in foothills of the eastern Nilgiris, were found infected with sporozoites and oocysts of P. cynomolgi Mayer and P. inui Harbesterdeker & von Prowazek (Choudhury et al., 1963b). Additionally, this species was implicated as a natural vector of simian malaria parasites in Sri Lanka where adults were found naturally infected with sporozoites of P. inui shortii Bray and P. fragile Dissainake, Nelson & Garnham (Nelson et al., 1971). In another study, under laboratory conditions, females of An. mirans became infected with simian malaria (P. cynomolgi and P. inui) when fed on Macaca radiata (Saint-Hilaire), but further transmission by these An. mirans was not attempted (Choudhury et al., 1963a).

Systematics. Anopheles mirans has been mostly misidentified as An. elegans since Cogill (1903). Anopheles mirans belong to the Hackeri Subgroup based on the proboscis being noticeably longer than the forefemur. Possible due to its restricted distribution and relative non-availability, this species has received less attention.
than other members of the Leucosphyrus Group. Adult females can be recognized by the following combination of characters: (1) proboscis longer than forefemur (ratio between proboscis length and forefemur length 1.19–1.31); (2) proboscis longer than maxillary palpus, ratio between palpus length and proboscis length 0.84–0.93; (3) proboscis entirely dark-scaled; (4) PS-D spot of vein R without pale interruptions; (5) number of pale interruptions on PS-D-PD spots of vein R always 2; (5) ratio of length of apical pale band of palpmore 5 to length of basal dark band of palpmore 5 0.83–2.67; and (6) apical pale band of hindtibia with continuous dark longitudinal stripe extending into basal portion.

Fourth-instar larvae of *An. mirans* can be recognized by the following combination of characters: (1) seta 5-C conspicuously longer than antenna; (2) basal tubercle of seta 1­-3-C long, extending noticeably beyond base of 2-C; (4) seta 1-11 poorly developed with very narrow leaflets; (5) ratio of length of apical pale band of palpmore 5 to length of basal dark band of palpmore 5 0.83–2.67; and (6) apical pale band of hindtibia with continuous dark longitudinal stripe extending into basal portion.

**Discussion**

With their beautiful adult scale-patterns of fine white spots and dark background facies, all species of the Leucosphyrus Group are readily recognizable from their distinctive broad white tibio-tarsal band on the hind-legs. As they transmit the bulk of forest malaria in oriental countries, these mosquitoes are much feared for the extremely high vectorial capacity of some but not all species, notably the aptly named *An. dirus* – meaning danger. Due to the variability of their elaborate ornamentation, however, separating the many species of this group will always be morphologically challenging. As with other groups of anopheline mosquitoes, therefore, taxonomic progress at the species level has depended increasingly on genetic criteria and specific morphological characters on the immature stages. Combinations of such evidence have allowed us to define the six new species morphologically described and formally named here. They fit the expected criteria (see Fig. 1 in Peyton, 1990) for belonging to the Hackeri Subgroup or the Leucosphyrus Subgroup, based on length ratios of the proboscis/forefemur and the maxillary palpus/proboscis. Thus, we are preparing a taxonomic revision of the complete group (Sallum et al., 2005) including 20 species. This should improve the prospects for understanding their bioecology and specific vector roles, and facilitate better targeting of control operations. Studies on distribution, seasonality, biting activity, feeding habits, longevity, infectivity, vector competence and vectorial capacity depend on the correct identification of such species in each locality. Fortunately it is now possible to distinguish between these species by genetic and molecular procedures, augmented by the morphological characters we have determined.

In the light of these six new species, we have to re-examine the differential distributions and specific biometrics of typical *An. balabacensis*, *An. dirus*, *An. leucosphyrus* and other members of the Leucosphyrus Group, particularly to understand their roles as vectors of malaria (*Plasmodium* spp.) and filaria (*Wuchereria spp.*) parasites among primates in and near forests. For example, *An. latens* (which has been largely misidentified as *An. leucosphyrus* s.s.) is anthropophilic and apparently serves as an important vector of human malaria in villages and forested areas of Sarawak, East Malaysia (Colless, 1956; Zulueta, 1956; Chang et al., 1995), and of South Kalimantan, Indonesia (White, 1983; Harbach et al., 1987). *Anopheles latens* is also responsible for most transmission of *Wuchereria bancrofti* to humans in Sarawak (Zulueta & LaChance, 1956; Zulueta, 1957), whereas *Wuchereria kalimantanii* of leaf monkeys appears to be transmitted by *An. balabacensis* in Kalimantan (Atmosodjono et al., 1993). Even so, *An. balabacensis* is a major vector of malaria in eastern Borneo and adjacent islands.

*Anopheles baimaii* is evidently another important vector of *P. vivax* and *falciparum* in forest, forest fringes and foothill areas throughout its wide range (from India to China), and its vectorial capacity seems to be comparable to that of *An. dirus* in Thailand. Records show that it is vector in Bangladesh (Rahman et al., 1977; Rosenberg & Maheswary, 1982), Burma (Khin-Maung-Kyi & Winn, 1976; Tun-Lin et al., 1995) and north-east India (Dutta et al., 1991; Prakash et al., 2001, 2005). Assessment of the vector role of *An. baimaii* in Thailand is more complex since it occurs in sympathy with other species of the complex (*Baimai* et al., 1991), combining their contributions to the dynamics of malaria transmission. However, *An. baimaii* seems to have a more western distribution, being the predominant member of the Leucosphyrus Group and an efficient vector of human *Plasmodium* in western Thailand (*Baimai* et al., 1988e). Despite being mainly a forest mosquito, *An. baimaii* withstands anthropic environmental changes. In Myanmar, peridomestic populations of *An. baimaii* breed in wells (Tun-Lin et al., 1987; Oo et al., 2003) and have different esterase isozyme profiles from those of forested populations (Tun-Lin et al., 1988).

*Anopheles cracens* is another strongly anthropophilic species (*Baimai* et al., 1988e) that may also contribute to the transmission of both malaria and filaria parasites. Additionally, *An. cracens* is competent to transmit *Plasmodium cynomolgi* (Klein et al., 1991) and *Brugia pahangi* (Zahedi & White, 1994). The other man-biting species such as *An. elegans* in India and *An. scondoni* in Thailand should be checked in relation to the epidemiology of both malaria and filariosis, since they have not been identifiable hitherto, so their vectorial importance may have been underestimated. The non-anthropophilic *Anopheles mirans* may be a natural vector of *P. inui* shortii and *P. fragile* in Sri Lanka (Nelson et al., 1971) as well as *P. cynomolgi* and *P. inui* in foothills of south India (Choudhury et al.,...
1963b), as a laboratory vector, *An. mirans* was readily infected with *P. cynomolgi* and *P. inui* from *Macaca radiata* (Choudhury et al., 1963a).

Under natural forest conditions, most if not all members of the Leucocercus Group apparently feed primarily on monkeys in the tree-tops, transmitting various plasmodia among them. Two species of simian malaria have been detected in *An. dirus* s.l. (Cheong et al., 1965), five species in *An. hackeri* and three species in *An. intralatus*, *An. balabacensis*, *An. pujutenis* and *An. leucosphyrus* s.l. have also been implicated (Warren & Wharton, 1963; Coatney et al., 1971). Presumably all the oriental primate malarias are transmitted to some extent by mosquitoes of the Leucocercus Group. For example, the *Macaca* parasites *Plasmodium knowlesi* and possibly *P. coatneyi* and *P. inui* have been detected in *An. balabacensis* from Palawan Island of The Philippines (Tsukamoto et al., 1978), although *P. cynomolgi* can be harmful to *An. dirus* s.l. under laboratory conditions (Klein et al., 1982). Circumstantial evidence in Sabah led to proof of *An. balabacensis* vector competence for *P. pitheci* and *P. silvaticum* from orang-utans (Peters et al., 1970). Hence, the need to clarify the veterinary as well as medical importance of all species in the Leucocercus Group.

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