

**BAIMAIA, A NEW SUBGENUS FOR *ANOPHELES KYONDAWENSIS*
ABRAHAM, A UNIQUE CRABHOLE-BREEDING ANOPHELINE IN
SOUTHEASTERN ASIA**

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Abstract.—*Baimaia*, n. subg., is introduced as a new subgenus of *Anopheles* for the unusual crabhole species, *An. kyondawensis* Abraham, in Southeast Asia. A diagnosis of the subgenus is provided that features unique anatomical characters of the adult, larval, and pupal stages of the type species. The larva of *An. kyondawensis* is redescribed and the previously unknown adult female, adult male, and pupa are described in detail. The affinities of *Baimaia* and *An. kyondawensis* are discussed in terms of their position in the phylogeny of Anophelinae, and their bionomics and distribution are reviewed.

Key Words: Culicidae, Anophelinae, taxonomy, mosquito

Abraham (1947) described *Anopheles* (*Anopheles*) *kyondawensis* from larvae found in shallow ground pools along streams near the village of Kyondaw (Moulmein Township, Mon State) in southern Myanmar. The species was not encountered again until 1966 when a single larva was found in a crabhole at Ban Pha Man located near the Laos border in Nan Province of Thailand (Harrison and Scanlon 1975). Harrison and Scanlon (1975) suggested that the larvae collected by Abraham in Myanmar may have been swept out of freshwater crabholes by high water because they were found in association with larvae he identified as *An. (Cellia) leucosphyrus* Dönitz [probably *An. baimaii* Sallum and Peyton (recently described in Sallum et al. 2005) since it is the dominant species of the Leucosphyrus Group in Myanmar], which “normally occur in small temporary ground

pools that follow flooding or rains.” In 1979, another larva was collected from a stream in Huai Kop, Sai Yok District of Kanchanaburi Province in western Thailand (Harrison et al. 1991). Likewise, it is likely that this larva may have been dislodged from a crabhole because the margin of the stream where it was captured was lined with these habitats at water level. Oo et al. (2004) found one larva of *An. kyondawensis* in a shaded pool along a stream in the vicinity of Innwaing near the type locality during collections made in Myanmar between May 1998 and March 2000. These authors did not indicate whether the pool was associated with crabholes. Material examined during the present study, however, confirms that *An. kyondawensis* does in fact breed in burrows created by freshwater crabs. This material consists of larvae, and adults reared from larvae and pupae col-

lected from crabholes in Ban Tham Sua, Tak Province, located in northwestern Thailand.

Reid and Knight (1961) included *An. kyondawensis* in the Culiciformis Group of subgenus *Anopheles* based on the reduced setae 5,6,7-C, and other setae of the larval head capsule. Harrison and Scanlon (1975) considered this placement tentative until the adult and pupal stages were known. Following the discovery of the previously unknown adult and pupal stages, we initiated studies of this species, and after having considered all of the unique features in the adult, larval, and pupal stages noted below, we concluded that *An. kyondawensis* does not belong in any currently recognized species group of *Anopheles*.

The traditional classification of subfamily Anophelinae included three genera: *Anopheles* Meigen, *Bironella* Theobald, and *Chagasia* Cruz. The phylogenetic relationships of these genera, based on a cladistic analysis of morphological data (Harbach and Kitching 1998), reflect the intuitive hypothesis (Ross 1951) that Anophelinae is a monophyletic clade comprised of *Chagasia* in a sister-group relationship to *Bironella* + *Anopheles*. Molecular phylogenies inferred from nuclear and mitochondrial gene sequences also support this hypothesis of relationships (Besansky and Fahey 1997; Foley et al. 1998; Krzywinski et al. 2001a, b), but more recent studies based on both morphological (Sallum et al. 2000, Harbach and Kitching 2005) and molecular data (Sallum et al. 2002) suggest that *Anopheles* is a paraphyletic assemblage relative to *Bironella*. In the absence of support for the generic status of *Bironella*, Sallum et al. (2000) formally synonymized this taxon with *Anopheles s.s.* This synonymy, however, is not supported (see below) by the later studies of Sallum et al. (2002) and Harbach and Kitching (2005), which indicate that *Bironella* should be regarded as a subgenus of *Anopheles*.

Taking account of independent lines of evidence, especially sequence data for the

slowly evolving single-copy nuclear *white* gene, Krzywinski and Besansky (2003) hypothesized that *Bironella* diverged from the main lineage of *Anopheles* following the earlier separation of *Chagasia*. Although this hypothesis is not supported by the morphological and molecular phylogenetic studies of Sallum et al. (2000 and 2002, respectively), it is not inconsistent with the results of the more recent cladistic analysis of Harbach and Kitching (2005), one aim of which was to investigate the phylogenetic position of *An. kyondawensis*. This latter analysis placed *An. kyondawensis* as sister to *Bironella* + all other *Anopheles*, with *Chagasia* as sister to these three taxa. Although this arrangement of taxa, expressed parenthetically as *Chagasia* + (*An. kyondawensis* + (*Bironella* + other *Anopheles*)), raises questions concerning the biogeography of anophelines, support for this set of relationships (assessed using Bremer and relative Bremer support) is strong and indicates that both *An. kyondawensis* and *Bironella* are independent lineages relative to the rest of Anophelinae (see Harbach and Kitching (2005) for a full assessment of relationships and character support). These results agree with the suggestion by Sallum et al. (2002) that "*Bironella* may be plausibly regarded as a subgenus of *Anopheles*", and imply in accordance with application of the principle of equivalent rank (Hennig 1966) that *An. kyondawensis* should also be afforded subgeneric rank. Hence, a new subgenus is proposed herein for this species.

MATERIALS AND METHODS

This study is based on a small number of larvae, and adults reared from larvae and/or pupae collected from crabholes (as indicated above), and the holotype larva of *An. kyondawensis* deposited in The Natural History Museum (NHM), London (see Material examined following the species description). Because the medium in which the holotype was mounted on a microscope slide had turned black with age, the speci-

men was removed following the procedures of Brown and De Boise (2005) and remounted in Euparal on the same slide. The head and dissected mouthparts of the larva were mounted under a separate coverslip. Following stereoscopic examination, the head of the only available female was removed, cleared in 5% NaOH for 2 h at 50°C, and mounted, with the mouthparts separated from the head capsule, in euparal on a microscope slide for more detailed study. The genitalia of 2 available males were also dissected and likewise cleared and mounted on individual microscope slides. Pinned adults were examined under simulated natural light; dissections, larvae, and larval and pupal exuviae were studied with differential interference contrast optics. Measurements and counts were made from all available specimens. Numbers in parentheses represent modes, when apparent, of the reported ranges. The anatomical terminology and abbreviations used in the descriptions and illustrations, respectively, follow Harbach and Knight (1980, 1982). The symbols ♀, ♂, Le, Pe, and L used in the literature summary and material examined sections for *An. kyondawensis* represent female, male, larval exuviae, pupal exuviae, and fourth-instar larva, respectively. An asterisk (*) after one of these symbols in the literature summary section indicates at least part of the life stage was illustrated in the publication cited.

TAXONOMIC TREATMENT

Anopheles subgenus *Baimaia*, Harbach, Rattanarithikul, and Harrison, new subgenus

Type species.—*Anopheles kyondawensis* Abraham, 1947.

Diagnosis.—*Baimaia* appears to be related to subgenus *Anopheles* Meigen, especially the Aitkenii, Alongensis, and Culiciformis Groups, but differs principally in features of the male genitalia, which are unique within genus *Anopheles*. The gonocoxite does not have differentiated parabas-

al and inner setae, and the gonostylus is flattened and mitten-shaped distally and lacks a gonostylar claw. Males also have uniquely developed maxillary palpi, which are straight and very nearly cylindrical with palpomeres 4 and 5 barely swollen and only slightly flattened. Adults lack thoracic scaling, and females have a dense covering of long sensilla between the antennal whorls that depart a fuzzy appearance to the antennae. The immature stages are found in crab-holes, or in pools after having been washed out of these habitats. Pupae have a trumpet that appears undifferentiated and intermediate between angusticorn and laticorn, spiracular scars of abdominal segments II–VII and seta 9–II–VIII borne ventrally, seta 1–III plumose, and a long fringe of spicules on the inner and outer margins of the paddle. Larvae have strongly inwardly curved antennae, setae 5,6,7-C reduced, long, single, compressed or flattened, somewhat lanceolate setae on the thorax and abdomen, and setae 6–IV–VI as long as setae 6–I–III. *Baimaia* is monobasic: see in the Systematics section following the description of *An. kyondawensis* for discussion.

Etymology.—*Baimaia* is a patronymic honoring Prof. Visut Baimai of Mahidol University, Bangkok, for his many important contributions to our knowledge of the cytogenetics and systematics of *Anopheles* mosquitoes in southeastern Asia. We have chosen to Latinize Visut's surname by adding the feminine suffix “-a” rather than the masculine “-us” because *Baimaia* is more euphonious and easier to pronounce (*Bī-mī-ā*). The three-letter abbreviation *Bmi.* is recommended for this subgenus.

Anopheles (*Baimaia*) *kyondawensis*

Abraham, 1947

(Fig. 1)

Anopheles (*Anopheles*) *kyondawensis* Abraham, 1947 (L*); Delphin and Rao 1957 (L key); Reid and Knight 1961 (classification); Reid 1968 (L key); Kyi 1971 (distribution); Rattanarithikul and Harrison 1973 (L* key); Harrison and Scanlon

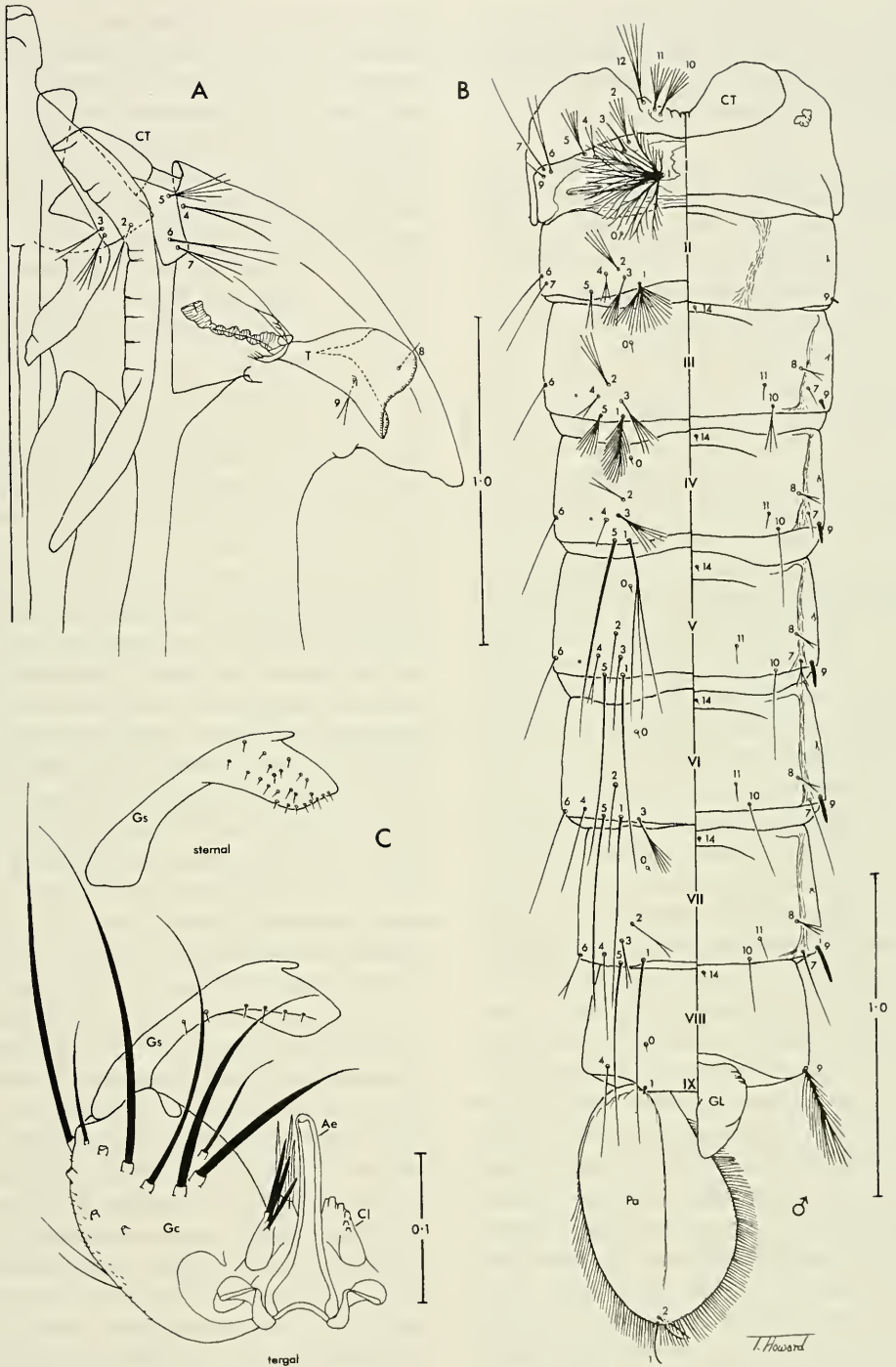


Fig. 1. Pupa and male genitalia of *Anopheles (Baimaia) kyondawensis*. A, B, Pupa: (A) left side of cephalothorax, dorsal to right; (B) dorsal (left) and ventral (right) aspects of metathorax and abdomen. C, Male genitalia, aspects as indicated. Ae = aedeagus; Cl = claspette; CT = cephalothorax; Gc = gonocoxite; GL = genital lobe; Gs = gonostylus; Pa = paddle; T = trumpet; I-VIII = abdominal segments I-VIII; 0-14 = setal numbers for specified areas, e.g., seta I-III. Scales in mm.

1975 (L*, distribution, taxonomy); Harrison et al. 1991 (collection record); Harbach 1994, 2004 (classification); Oo et al. 2004 (collection record).

Female.—*Head*: Vertex with sparse long, dark, narrow, truncate erect scales medially (centrally), abruptly graded into equally long attenuate setae laterally and anteriorly, latter indistinguishable from ocular setae that are removed from eye margin, decumbent scales absent; frontal tuft comprised of few slender piliform scales and 4 long forward projecting setae, scales and setae slightly paler (more golden) than those of vertex. Clypeus without scales. Antenna length about 1.5 mm; pedicel bare, yellowish; flagellum with dense covering of relatively long anteriorly curved setalike sensilla between antennal whorls, flagellomere 1 with a few inconspicuous narrow scales on dorsomesal surface among most proximal setae and sensilla, other flagellomeres without scales. Proboscis long and slender, entirely dark-scaled, labella paler than prementum, with 6 long and few shorter basal setae that fan out from ventral and lateral surfaces, length about 2.35 mm, $1.15\times$ length of forefemur, slightly longer than maxillary palpus (about $1.1\times$). Maxillary palpus long and slender (palpomere 5 very slightly swollen), length about 2.15 mm, entirely dark-scaled, palpomeres 1 and 2 with semierect scales, palpomere 1 with 1 long and several shorter setae, palpomere 2 with few short inconspicuous setae on proximal half, palpomeres 4 and 5 with rather widely spaced, short, inconspicuous, forward-projecting setae on ventrolateral margin. Cibarial armature absent. *Thorax*: Without scales; integument light brown. Scutum with prominent dark brown setae on all areas (anterior promontory, acrostichal, dorsocentral, lateral prescutal, fossal, antealar, supraalar, and prescutellar areas); parascutellar seta equally prominent. Scutellum evenly rounded with many long and few short dark brown setae. Mesopostnotum bare. Antepnotum with row of dark

brown setae along anterior margin. Postpronotum with 1–3 inconspicuous setae on extreme posterodorsal margin (could be confused for prespiracular setae). Pleura with dark setae as follows: 1 upper proepisternal, 1 prealar, 1 upper mesokatepisternal, 2 lower mesokatepisternal, 3 or 4 upper mesepimeral, no lower mesepimeral. *Wing*: Length 3.25 mm; entirely dark-scaled; humeral crossvein and alula without scales; cell M_2 about 0.55 length of cell R_2 ; cell M_2 about 0.6 length of vein M_{2+3} . Dorsal surface with elongate semierect scales on R_3 , R_{2+3} , R_2 , proximal 0.5 of R_3 , M_{2+3} , and distally on 1A, remaining veins with decumbent spatulate scales; ventral surface with similar scales on middle of R_1 , R_{4+5} and distally on CuA and 1A. *Halter*: Pedicel mainly pale, scabellum and capitellum dark, capitellum dark-scaled. *Legs*: Slender; coxae without scales, prominent dark brown setae on anterior surface of forecoxa, outer surface of midcoxa and posterior surface of hindcoxa; trochanters with dark scales and short dark setae on ventral surfaces; femora, tibiae, and tarsi entirely dark-scaled; forefemur length about 2.05 mm, 0.87 length of proboscis. *Abdomen*: Integument dark brown dorsally, lighter ventrally; without scales; with long brown setae.

Male.—Like female except antennal whorls with more numerous and much longer setae, long setalike sensilla only present on 2 terminal flagellomeres, which are disproportionately long compared to the other flagellomeres, apical flagellomere about 0.75 length of penultimate flagellomere, which is $4\times$ longer than more proximal flagellomeres. Maxillary palpus slightly shorter than proboscis; palpomeres 4 and 5 nearly cylindrical, very slightly expanded. Same numbers of pleural setae as in female except 2–4 upper mesepimeral setae present. *Genitalia* (Fig. 1C): Tergum IX without setae; sternum IX small, not fused to tergum. Gonocoxite relatively short and stout, without scales, setae on dorsolateral, lateral, and ventrolateral areas strongly developed, more distal ones longer than gonocoxite

Table 1. Range of numbers of branches for pupal setae of *Anopheles (Baimaia) kyondawensis*.

Seta No.	Cephalothorax CT	Abdominal Segments								Paddle P
		I	II	III	IV	V	VI	VII	IX	
0	—	—	1	1	1	1	1	1	—	—
1	2,3(2)	~300	14-21	26-36(28)	1-4(4)	1	1	1	1	1
2	2,3(2)	5-9	3-5(5)	3,4(4)	1,2(2)	1,2(2)	1,2(2)	2	—	2
3	2	1,2(1)	3-9(7)	5-11	8-11	1-5(1)	5,6	1-3(3)	—	—
4	2,3(2)	2,3(3)	1-3(3)	2,3(2)	1-3(2)	2,3(3)	1	1	—	—
5	2-6(2)	3-6(5)	2,3(2)	7-11(8)	1,2(1)	1	1	1	—	—
6	2	2-4	1-3(2)	1	1	1	1	1,2(2)	—	—
7	2,3(3)	1	1-3(1)	1-4	1-3(2)	1,3(3)	1	1-3(1)	—	—
8	1,2(1)	—	m	2,3(2)	1-3(2)	1,2(2)	2,3	3,4(3)	—	—
9	1-4(2)	1	1	1	1	1	1	1	—	—
10	4-6(4)	—	—	2-4	1	1	1	1-3(2)	—	—
11	5-7(6)	—	—	1	1	1	1	1	—	—
12	4-6(5)	—	—	—	—	—	—	—	—	—
14	—	—	—	1	1	1	1	1	—	—

and gonostylus, setae on inner and parabasal areas not developed or distinct from other prominent setae on dorsomesal surface; gonostylus short, curved, laterally flattened, and expanded in distal half, expanded portion with thumblike projection at approximately middle of lateral margin and relatively sparse covering of minute setae on ventral surface, dorsal surface with sparse row of similar setae that extends onto proximal portion; gonostylar claw absent. Aedeagus long and slender, leaflets absent; claspette a single undivided lobe, bearing a close-set apical row of 6 (apparent) similar, straight setae.

Pupa (Fig. 1A, B).—Character and positions of setae as illustrated; numbers of branches in Table 1. *Cephalothorax*: Evenly and lightly to moderately pigmented. Seta 4-CT significantly longer than 5-CT, approaching length of 6-CT. *Trumpet*: Undifferentiated and intermediate between angusticorn and laticorn; without tracheoid area; pinna without fold opposite cleft (1 of 3 available specimens with an unnatural fold due to mounting), rim thin and uniform. *Abdomen*: Evenly and moderately pigmented; length 2.9-3.0 mm. Spiracular scars of segments II-VII borne ventrally near middle of lateral margins. Seta 9-II-VIII inserted ventral to caudolateral corner

of segments, 9-II-III short, peglike, 9-IV-VII progressively longer and more sharply pointed on succeeding posterior segments, 9-VII ventral and inserted close to 7-VII (but when mounted, see Fig. 1B, appears to be near posterolateral corner), 9-VIII long, with well-developed branches (14-23); 1-III plumose, with 26-36 branches, 1,5-IV-VII equally strongly developed, 1.4-1.6× length of tergum, all single except 1-IV with 1-4(4) branches arising well beyond base; 3-III anterior to 1-III; 7-IV-VII, and sometimes 7-III, inserted on fold line, 7-V-VII at posterior margin of sternum. *Genital lobe*: Length 0.30 mm in male; 0.18 mm in female. *Paddle*: Lightly pigmented; asymmetrical, outer part broadest in basal half, inner part broadest in distal half; length about 0.75 mm, width about 0.50 mm, index about 1.5; refractile border about 0.25 paddle length; long dense spicules on both inner and outer margins, about 0.5 length of seta 1-Pa. Seta 1-Pa relatively long, single, curved; 2-Pa double, about 0.8 length of 1-Pa.

Larva, fourth-instar.—As illustrated by Rattanarithikul and Harrison (1973) and Harrison and Scanlon (1975) except where noted below; ranges of setal branching in Table 2. *Head*: Slightly wider than long, length 0.67 mm, width 0.70-0.82 mm;

Table 2. Range of numbers of branches for fourth-instar larval setae of *Anopheles (Baimata) kyondawensis*.

Seta No.	Head C	Thorax				Abdominal Segments												
		P	M	T	I	II	III	IV	V	VI	VII	VII	VII	X				
0	1	2,3(2)	—	—	1	1	1	1	1	1	1	1	1	1	1	1	1	—
1	1	6-9(6)	31-37(33)	1,2(1)	1,2(1)	8-10(9)	14-20(19)	16-21(16)	17-21(18)	14-24(21)	14-20(16)	1	1	1	1	1	1	1
2	1	7-11(10)	2-4(2)	1	1	4-6(5)	2,3(3)	1	1	1	1	1	1	1	1	1	1	1
3	1	1	1	7-12(9)	1	1	1	2,3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)
4	1	18-27(19)	2-4(2)	1-3(2)	3,4(3)	2-5	2-4(2)	2,3(2)	1-3(2)	3-6(4)	3-6(4)	3-6(4)	3-6(4)	3-6(4)	3-6(4)	3-6(4)	3-6(4)	3-6(4)
5	2-6(4)	30-46(44)	1	34-46(41)	2,3(2)	2,3(2)	3	3,4(3)	3-6(4)	5-9(6)	5-9(6)	5-9(6)	5-9(6)	5-9(6)	5-9(6)	5-9(6)	5-9(6)	5-9(6)
6	4,5(4)	1	3-5(3)	1	27-38(27)	30-37(35)	8-11(8)	1	1	1	1	1	1	1	1	1	1	1
7	3-6(4)	27-40(35)	1,2(1)	28-40(28)	22-30(24)	26-36	3,4(4)	2-4(4)	2-4(3)	1	1	1	1	1	1	1	1	1
8	1	28-37(33)	22-31(26)	24-37	—	1,2(1)	1,2(1)	2-6(6)	4-6(5)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)
9	1	1	1	1	3-5	3-8	4-7(5)	1	1	1	1	1	1	1	1	1	1	1
10	1-3(1)	1	1	1	1,2(1)	1,2(2)	1	2-4(4)	2-4(3)	1	1	1	1	1	1	1	1	1
11	34-58	1	1	1	2,3(3)	1	1,2(2)	1,2(1)	1,2(2)	2,3(2)	2,3(2)	2,3(2)	2,3(2)	2,3(2)	2,3(2)	2,3(2)	2,3(2)	2,3(2)
12	2,3(3)	1	1	1	1,2(1)	1	1,2(2)	2-6(6)	4-6(5)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)	4-7(4)
13	4-8(5)	4-6(5)	3-5(4)	1	3,4(4)	4-7(6)	5,6(6)	1-3(2)	1,2(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)	1-3(2)
14	4-6(4)	4,5(4)	3-6(4)	—	—	—	1	5-7(5)	1,2(1)	5-7(5)	5-7(5)	5-7(5)	5-7(5)	5-7(5)	5-7(5)	5-7(5)	5-7(5)	5-7(5)
15	1-3(2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

1-S, 4-6(5)
2-S, 2-5(4)
6-S, 2-3(3)
7-S, 1,2(2)
8-S, 2-4(3)
9-S, 1-3(2)

more or less evenly pigmented, collar and most posterior part of frontal ecdysial line darkly tanned. Seta 1-C long, attenuate; 2-C single, simple, very long, length 0.3–0.4 mm, arising very close to its mate, their alveolar sockets more or less confluent; 3-C short and rather stout, length 0.20–0.25 that of 2-C; 4-C single, slender, simple, about length of 3-C, inserted far forward of 5,6-C, more widely separated from its mate than setae 3-C; 5,6,7-C very short, branched from base; 8,9-C short, single, simple; 11-C well developed, about as long as antenna, plumose. *Antenna*: Cylindrical, markedly curved inward, with relatively few spicules on proximal half of mesal surface; length 0.25–0.28 mm. Seta 1-A very short, length about diameter of antenna at point of insertion on proximal 0.17 of antenna, with 2–5(3) branches from middle of stem; 4-A with 4–10 branches, slightly longer than 2,3-A. *Thorax*: Integument hyaline, smooth. Seta 1-P without setal support plate, with branches arising from short stem; 2-P about 5× length of 1-P, borne on small setal support plate; 3-P single, simple and slightly flattened; 9,10,12-P,M and 9,10-T long, single, simple, common support plates of these setae with very short spine; 12-T short, normally single and slightly flattened (characterized as “bifid distally” by Harrison and Scanlon 1975); 13-T long, single, simple and slightly flattened. *Abdomen*: Integument hyaline, smooth; tergal plates small, less than 0.25 width of segments, segments IV–VII, and sometime III, each with small median accessory tergal plate. Setae 0-II–VIII and 14-III–VIII (14-III–VII incorrectly shown on posterior margins of segments II–VI in illustration of Harrison and Scanlon 1975) minute, single; 1-I minute, usually single, occasionally double, 1-II with slender unpigmented lanceolate leaflets, 1-III–VII fully palmate, leaflets broad, flat and pigmented, with distinct shoulders and apical filaments; 2-IV–VI, 3-I–VI and 4-VI,VII long, single and flattened, 3-IV long, flattened and bifid or trifid distally; seta 5 very

small on segment I and progressively larger on segments II to VII, 5-I usually double, 5-II,III triple and 5-IV–VII increasing in turn on average from 3 or 4 branches to 6 or 7 branches; 6-III as long as 6-I,II, normally with 8 or 9 short widely spaced branches mainly on proximal half (not “flattened” as indicated by Harrison and Scanlon 1975), 6-IV–VI as long as 6-III, simple, 6-VII very small with 2 or 3 branches; 10-I and 13-VII occasionally double, otherwise these setae and 10-V,VI, 11-II, 12-II,VI,VII and 13-V single, simple and flattened; 13-I–IV,VI small, branched from short basal stem. Pecten plate with 14–16 subequal spines, each with strong denticles arising from basal half on dorsal side. Saddle moderately pigmented, length 0.27–0.28 mm; seta 1-X single, simple and slightly flattened, about 1.3× saddle length, inserted close to margin of saddle (incorrectly illustrated on edge of saddle by Harrison and Scanlon 1975).

Systematics.—The number and positions of specialized setae on the gonocoxites of the male genitalia have served as the primary basis for the subgeneric classification of *Anopheles* since the pioneering work of Christophers (1915). Disregarding a few apparent departures from the usual condition in subgenus *Anopheles*, the arrangement and characteristics of these setae are constant within the subgenera. In comparison with the development and positions of these setae in the six traditionally recognized subgenera of *Anopheles* (see Reid 1968: fig. 26), it is obvious that *An. kyondawensis* (Fig. 1C) does not fit within any of these groups. Furthermore, the notion that the specialized gonocoxal setae of *Anopheles* evolved from ordinary setae of the gonocoxite is supported by the relatively unspecialized condition of apparently homologous setae in this species. This, as well as the thin, very nearly cylindrical maxillary palpi of males, with the two apical palpomeres only slightly more swollen than those of *Chagasia*, reinforces the hypothesis that the ancestral stock of *Anopheles*

gave rise to *An. kyondawensis* and a lineage from which all other *Anopheles* evolved.

Disregarding the unique features of the male genitalia, *An. kyondawensis* exhibits a number of characters in common with species of the Alongensis and Culiciformis groups of subgenus *Anopheles*. The adults are small, unadorned insects and the larvae have cranial setae 5, 6, and 7 strongly reduced. The Alongensis Group includes two species (*An. alongensis* Venhuis and *An. cucphuongensis* Vu, Nguyen, Tran, and Nguyen) and the Culiciformis Group includes three species (*An. culiciformis* Cogill, *An. sintoni* Puri, and *An. sintonoides* Ho) (Harbach 2004) in the Oriental Region. Larval habitats utilized by members of the Alongensis Group (known only from Vietnam) include rock holes in a limestone cave and small holes in limestone outcrops in forested hills (*An. alongensis* and *An. cucphuongensis*, respectively). These habitats share a generic likeness to the shaded, cryptic crabholes occupied by larvae of *An. kyondawensis*. Larvae of the Culiciformis Group are found primarily in treeholes and other plant containers. Adult females of *An. kyondawensis* are easily distinguished from those of the Alongensis and Culiciformis Groups by the dense covering of long sensilla between the antennal whorls and the presence of minute setae on the postero-dorsal margin of the postpronotum. The inwardly curved antennae of *An. kyondawensis* are found otherwise only in *An. cucphuongensis* (specimens were unavailable to determine whether this character also occurs in the closely related *An. alongensis*). The flattened single thoracic and abdominal setae on the larva of *An. kyondawensis* are unique, and the pupa is distinguished by the plumose condition of seta I-III and the ventral placement of seta 9-II-VIII. Also, the pupal trumpet of *An. kyondawensis* is undifferentiated and intermediate between the angusticorn- and laticorn-shaped trumpets that Reid and Knight (1961) recognized and used to divide subgenus *Anopheles* into two taxonomic sections, the Angusticorn and

Laticorn Sections. The trumpet of *An. kyondawensis* has a fairly long meatus, a shallow meatal cleft, a pinna that is widely flared, and an uncertain axis. In fact, it is very similar to other primitive species with generalized trumpets, e.g., *An. sintonoides* (see Harrison and Scanlon 1975) and *An. sintoni* (see Tewari and Hiriyan 1992) of the Culiciformis Group.

Harbach and Kitching (2005) recently included *An. kyondawensis* in a phylogenetic study of Anophelinae based on morphological characters. Their findings revealed that *An. kyondawensis* is the earliest taxon derived from an ancestor that gave rise to all other *Anopheles*. A search of the matrix containing 167 characters that occur in species of *Anopheles* that were used in that study revealed 19 characters (numbers 2, 4, 10, 15, 23, 24, 64, 65, 68, 76, 79, 92, 93, 96, 97, 101, 107, 141, and 156) that occur in species of *Anopheles* that retain apparent ancestral (plesiomorphic) characters. Only two of these 19 characters occur in more derived species of subgenus *Cellia* (number 24 in *An. funestus* Giles and 96 in *An. cinereus* Theobald and *An. superpictus* Grassi), as well as species in subgenus *Anopheles*. Of the other 17 characters, two (92, 93) are unique to *An. kyondawensis*, and the remaining 15, plus the two that occur in the three species of *Cellia*, were otherwise found only in *Chagasia* and *Anopheles* (species in subgenera *Anopheles*, *Bironella*, *Kerteszia*, *Lophopodomyia*, and *Stethomyia*). The shared plesiomorphic characters that occur in *An. kyondawensis* and other species are listed in Table 3.

Bionomics.—Most of what is known about the bionomics of *An. kyondawensis* is noted in the introduction. The immature stages apparently inhabit crabholes associated with streams or streamlets and are occasionally washed out of these habitats. Larvae have been found only in crabholes and small pools along the sides of streams shaded by forest in hilly and mountainous areas. Species found in association with *An. kyondawensis* in crabholes include *Culex*

Table 3. Shared plesiomorphic characters of *Anopheles* (*Bimaia*) *kyondawensis* that occur in various species in other subgenera of *Anopheles* (*Anopheles*, *Bironella*, *Lophopodomys*, and *Stethomyia*), and *Chagasia* (character numbers taken from Harbach and Kitching 2005). These characters, which are exhibited by taxa that occur in nearly every zoogeographical region, corroborate the more basal position that *An. kyondawensis* occupies in the phylogeny of *Anopheles*, and justify *Bimaia* as a new subgenus.

Species	Zoogeographic Region	No. Shared Characters	Character Nos.
<i>An. (Ano.) aitkenii</i> James	Oriental	3	2,4,15
<i>An. (Ano.) algeriensis</i> Theobald	Palaeartic	2	2,15
<i>An. (Ano.) asiaticus</i> Leicester	Oriental	1	79
<i>An. (Ano.) atropos</i> Dyar and Knab	Nearctic	1	15
<i>An. (Ano.) corethroides</i> Theobald	Australasian	4	2,4,107,141
<i>An. (Ano.) cucphuongensis</i> Vu, Nguyen, Tran and Nquyen	Oriental	1	15
<i>An. (Ano.) implexus</i> Theobald	Afrotropical	1	2
<i>An. (Ano.) interruptus</i> Puri	Oriental	1	79
<i>An. (Ano.) judithae</i> Zavortink	Nearctic	3	15,76,101
<i>An. (Ano.) simtonoides</i> Ho	Oriental	3	4,15,76
<i>An. (Bir.) confusa</i> Bonne-Wepster	Australasian	8	2,4,10,15,24,76,97,101
<i>An. (Bir.) gracilis</i> Theobald	Australasian	6	10,15,24,68,97,101
<i>An. (Bir.) hollandi</i> Taylor	Australasian	7	15,24,64,65,68,97,101
<i>An. (Ker.) bambusicolus</i> Komp	Neotropical	1	76
<i>An. (Ker.) cruzii</i> Dyar and Knab	Neotropical	1	76
<i>An. (Lph.) oiketorakras</i> Osornom-Mesa	Neotropical	1	97
<i>An. (Ste.) nimbus</i> (Theobald)	Neotropical	5	2,24,65,96,107
<i>An. (Ste.) kompi</i> Edwards	Neotropical	5	2,24,65,96,107
<i>Ch. fajardi</i> (Lutz)	Neotropical	7	2,10,23,64,65,141,156

(*Lophoceraomyia*) *bengalensis* Barraud, *Cx. (Lop.) minor* (Leicester), *Cx. (Lop.) spiculatus* Bram and Rattanarithikul, *Uranotaenia (Pseudoficalbia) abdita* Peyton, *Ur. (Pfc.) koli* Peyton and Klein, *Ur. (Pfc.) stricklandi* Barraud, *Ur. (Uranotaenia) macfarlanei* Edwards, and unidentified species of *Verrallina* (Harrison and Scanlon 1975; collection records for the specimens listed below). Larvae collected with *An. kyondawensis* in stream pools include *An. (Anopheles) bengalensis* Puri, *An. (Ano.) insulaeflorum* (Swellengrebel and Swellengrebel de Graaf), and members of the *An. (Cellia) dirus* complex (Abraham 1947, Oo et al. 2004). Adults of this species have never been collected in the wild, and nothing is known about their biology or behavior.

Distribution.—*Anopheles kyondawensis* has been found only in places on either side of the Thai-Myanmar border located rough-

ly between 14 and 17° north (Kanchanaburi and Tak Provinces, Thailand; Mon State, Myanmar), and at one other place (approximately 18°50'N 100°50'E) nearly 400 km northeast of these localities near the Thai-Laos border in Nan Province, Thailand. As noted by Harrison and Scanlon (1975), this suggests that *An. kyondawensis* is more widely distributed in forested hilly and mountainous areas of mainland Southeast Asia.

Material examined.—Eleven specimens: 2 ♂, 1 ♀, 1 Le, 3 Pe, and 4 L, including the holotype. Holotype L, MYANMAR: *Mon State*, Kyondaw [currently Kyondo] (16°36'N 98°04'E), small shallow pool along side of stream, 2 Dec 1943 (NHM). Other specimens, 1 ♂Pe (1-518-18), THAILAND: *Tak Province*, Ban Tham Sua (16°41'N 98°41'E), crabhole in shallow stream in forest, 8 Jun 90 (*Rampa*): 1 ♀Pe (1-520-105), 1 ♂LePe (1-520-13), 2L (1-

520), Ban Tham Sua (16°41'N 98°42'E), crabhole in streamlet in forest, 8 Jun 90 (Chamnonng).

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