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# VARIATION IN MORPHOLOGICAL CHARACTERS OF ADULTS OF THE *AEDES* (*STEGOMYIA*) *SIMPSONI* COMPLEX FROM UGANDA, KENYA, AND SOUTH AFRICA (DIPTERA: CULICIDAE)

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**ABSTRACT.** Examination of adult *Aedes simpsoni* (Theobald) *s.l.* from locations in Uganda and Kenya showed more variation than reported previously. Four patterns of white banding on the midtarsomeres were identified, and they occurred in varying frequencies in samples from different locations. The length of the tarsal bands was distributed continuously within samples from different locations and was variable among progeny of single mothers. This character therefore is not diagnostic of species in the complex. Midtarsomeres 1 and 2 have longer white bands in the majority of males and females of anthropophilic populations in Kenya and Uganda, but there is considerable overlap between the anthropophilic and nonanthropophilic biotypes. A few females in some samples did not bear a tooth on all claws of the fore- or midlegs. Twelve patterns of scutal lines occurred in varying frequencies in samples from different locations. A scutal pattern with long inner lines and short outer lines was most common, with an average occurrence of 51.2% in females and 32.2% in males. An H-pattern of scutal lines was more frequent in males (42.1%) than in females (12.1%), indicating a sex association. Three tergal banding patterns were defined. We conclude that the nominotypical *Ae. simpsoni* in southern Africa is a distinct species different from the more widespread *Ae. lilii* (Theobald) in tropical Africa. *Aedes bromeliae* (Theobald) cannot be distinguished from the latter based on characters presently described as diagnostic.

## INTRODUCTION

Philip (1929) demonstrated that *Aedes* (*Stegomyia*) *simpsoni* (Theobald) transmits yellow fever virus under laboratory conditions. Yellow fever virus was later isolated from two lots of this species from Bwamba County, western Uganda (Mahaffy et al. 1942). Since then, *Ae. simpsoni* has been shown to be an important vector of yellow fever virus in East Africa. The species was largely responsible for the greatest recorded African epidemic of yellow fever, which occurred in Ethiopia from 1960 until 1962 (Haddow 1968). It was suspected of being a vector in the yellow fever epidemic that occurred in Sudan in 1959 (Haddow 1968).

Theobald (1905) originally described *Stegomyia simpsoni* from Transvaal, South Africa. Later, Theobald (1910) described *Stegomyia lilii* Theobald from Bor, Sudan, and in the following year (1911) he described *Stegomyia bromeliae* Theobald from Kampala Swamp, Uganda. These three species were differentiated by the color of the scales on the scutum and tarsomeres and the presence or absence of teeth on the tarsal claws. However, they were extremely similar and difficult to separate. Edwards (1912) synonymized both *Stegomyia lilii* and *S. bromeliae* with *S. simpsoni*. Later, Edwards (1941) recognized two forms: *Aedes* (*Stegomyia*) *simpsoni s.s.* and *Ae. simpsoni* var. *lilii*. He described *Ae. simpsoni* as having a pair of narrow yellow lines running the length of the scutum and all claws of the female simple. He characterized *Ae. simpsoni* var. *lilii* as having the narrow yellow lines more or less abbreviated in front, usually not reaching forward beyond the middle of the scutum, or sometimes absent; the main white patches of the scutum somewhat larger; and the claws of the fore- and midlegs of the female usually, but not always, toothed.

Haddow et al. (1951) observed variation in the light-colored scales on the scutum and abdomen of *Ae. simpsoni.* They observed that abdominal terga II and III often did not bear basal white bands. They noted that the other characters for *Ae. simpsoni* var. *lilii* fell within the normal range of variation of *Ae. simpsoni* described by Edwards (1941).

Gillett and Van Someren (1972) described 12 patterns of yellow and white scales on the scutum of *Ae. simpsoni* from Chaggaland, Tanzania. The biting behavior differed among mosquitoes with different patterns. Some patterns occurred more frequently among specimens caught biting humans in the morning, and other patterns occurred more frequently among specimens caught in the afternoon.

Recently, Huang (1979) considered *Ae. simpsoni* to be a complex comprised of at least three species. *Aedes simpsoni s.s.* is described as having fore- and midtarsal claws simple and fore- and midtarsomere 2 with white scales on the basal 0.83–0.90 of the dorsal surface. It is restricted to South Africa. *Aedes bromeliae* is described as having fore- and midtarsal claws toothed, foretarsomere 2 with white scales in the basal 0.50 of the dorsal surface, midtarsomere 1 with white scales forming a white stripe on the basal 0.75–0.83 of the posterior surface, and midtarsomere 2 with white scales in the basal 0.66-0.75 of the dorsal surface and at least the basal 0.66 of the posterior surface. *Aedes bromeliae* is a common, widespread species in the Afrotropical region and is believed to be the species from which Mahaffy et al. (1942) isolated yellow fever virus. *Aedes lilii* is described as having fore- and midtarsal claws toothed and fore- and midtarsomere 2 with white scales in the basal 0.50 of the dorsal surface. This species also is widely distributed across Africa, but is less prevalent. The difficulties that arose in trying to apply the criteria used by Huang (1979) to differentiate *Ae. bromeliae* and *Ae. lilii* prompted our study of variation of the *Ae. simpsoni* complex.

## MATERIALS AND METHODS

Immature stages or adults of *Ae. simpsoni s.l.* were collected from nine locations in Uganda, three in Kenya, and one in South Africa. At Kinyarwanda (0° 03′ N, 32° 27′ E) and Lunyo Farm (0° 04′ N, 32° 28′ E), both located near Entebbe on the northern shore of Lake Victoria, and at Bwayise (0° 27′ N, 32° 34′ E), northeast of Kampala, a single collection was made every 14 days for a period of one year. Collections also were made at Nkokonjeru (0° 14′ N, 32° 58′ E), about 70 km east of Kampala, and at Maya (0° 11′ N, 32° 25′ E), about 60 km west of Kampala, but not at regular intervals. Several other collections were made at the following places: Bussi Island (0° 02′ N, 32° 24′ E), about 10 km west of Entebbe; Nsadzi Island (0° 06′ N, 32° 37′ E), about 40 km southeast of Entebbe; Mubuku irrigation scheme (0° 16′ N, 30° 08′ E), in western Uganda; Ntandi Village (0° 48′ N, 30° 08′ E), Bwamba County, western Uganda; Taveta (3° 24′ S, 37° 48′ E), Kenya, on the northern edge of Mount Kilimanjaro; Kwale (4° 16′ N, 39° 22′ E) and Rabai (3° 55′ N, 39° 34′ E), along the coastal plain of the Indian Ocean, Kenya; and Oslo Beach, Natal, about 100 km south of Durban, South Africa. Only a few specimens were collected from Rabai, Kwale, Taveta, Mubuku, Bussi Island, and Nsadzi Island. Progeny of only a single female from Oslo Beach were examined. These populations, however, are included in this study to show the extent of variation within and between populations.

Both anthropophilic and nonanthropophilic populations of *Ae. simpsoni s.l.* were sampled. The Bwamba, Taveta, Rabai, and Kwale populations were described previously as anthropophilic and the Entebbe and Bwayise populations as nonanthropophilic (Gibbins 1942; Gillett 1951, 1955; Van Someren et al. 1955; Gillett and Van Someren 1972; Mukwaya 1971, 1974, 1976; Parker et al. 1972). Collections carried out at Nkokonjeru and Maya gave biting rates with human hosts comparable with those of Bwamba (Lutwama and Mukwaya, unpublished data). McCrae (personal communication) observed in the 1970s that the Mubuku population was anthropophilic. Collections from Mubuku and Bussi Island indicated high biting rates with human hosts, while at Nsadzi Island no mosquitoes were caught biting humans and there were no complaints of day-biting mosquitoes from the inhabitants of the island.

Larvae and pupae were collected from *Colocasia* and banana plants with a pipette. Adults of nonanthropophilic populations were collected with hand sweep-nets. Females of anthropophilic populations were collected with human bait. Eggs were collected at several locations by placing strips of cloth as oviposition substrates in the axils of banana and *Colocasia* plants. Some females collected in the field were placed individually in 7.5 × 2.5 cm glass tubes prepared for egg laying. The eggs from each female were hatched separately and the larvae reared to the adult stage.

Adults that emerged from field-collected or laboratory-reared immatures were held for about 24 hr and then killed with ethyl acetate. The mosquitoes were pinned, labeled, and kept in a frost-free refrigerator to dry and harden for at least three days. Each collection from Kinyarwanda, Lunyo Farm, and Bwayise was examined separately. After they laid two or three batches of eggs, field-collected females were killed and pinned for morphological examination and comparison with their progeny.

The following morphological characters were examined:

**Banding of tarsomeres.** White bands at the base of midtarsomeres 1 and 2 of pinned specimens were examined. Sexual variation in banding was compared for different populations, and seasonal variation was ascertained for the Kinyarwanda, Lunyo Farm, and Bwayise populations.

The lengths of the tarsomeres and their bands were measured along the posterior surface of individual tarsomeres under a binocular microscope with an eyepiece micrometer. The length of the band of white scales was measured from the base of the tarsomere to the end of the farthest white scale. Apart from the specimens from South Africa, the farthest white scales were on the posterior surface. They occurred on the dorsal surface on the specimens from South Africa. The ratio of the length of the band of white scales to the length of each tarsomere was computed from these measurements. Comparisons of the mean tarsal band lengths for each sex were made in the different populations.

**Dentition of tarsal claws.** The presence or absence of teeth on the tarsal claws was determined by removing both fore- and midlegs from 30 males and 100 females from each of the Kinyarwanda, Lunyo Farm, Bwayise, and Nkokonjeru populations, mounting the legs of individual mosquitoes in Canada Balsam, and examining the legs under a low power microscope.

**Scutal line patterns.** Variation in color and arrangement of scutal lines was examined in a total of 1,491 females and 1,136 males.

**Tergal banding patterns.** The presence of white scales on the abdominal terga was determined for 583 females and 546 males from different populations.

## RESULTS

**Banding of midtarsomeres.** Four banding patterns were identified in the *Ae. simpsoni* complex. Figure 1 is a diagrammatic representation of the patterns as observed on midtarsomeres 1 and 2. On individual mosquitoes, there was a similar pattern on the fore- and midtarsomeres. The different patterns are described as follows:

Pattern A: Midtarsomeres 1 and 2 with basal white bands ending sharply without any extension. White bands usually less than 0.6 of the tarsomeres on the posterior surface (range 0.3–0.6, mean = 0.5).

Pattern B: Midtarsomere 1 with basal white band generally short but with an extending narrow stripe (range 0.5–0.8, mean = 0.7). Midtarsomere 2 with basal white band relatively short (range 0.5–0.7, mean = 0.6), without an extension, or with a slight extension on the posterior surface.

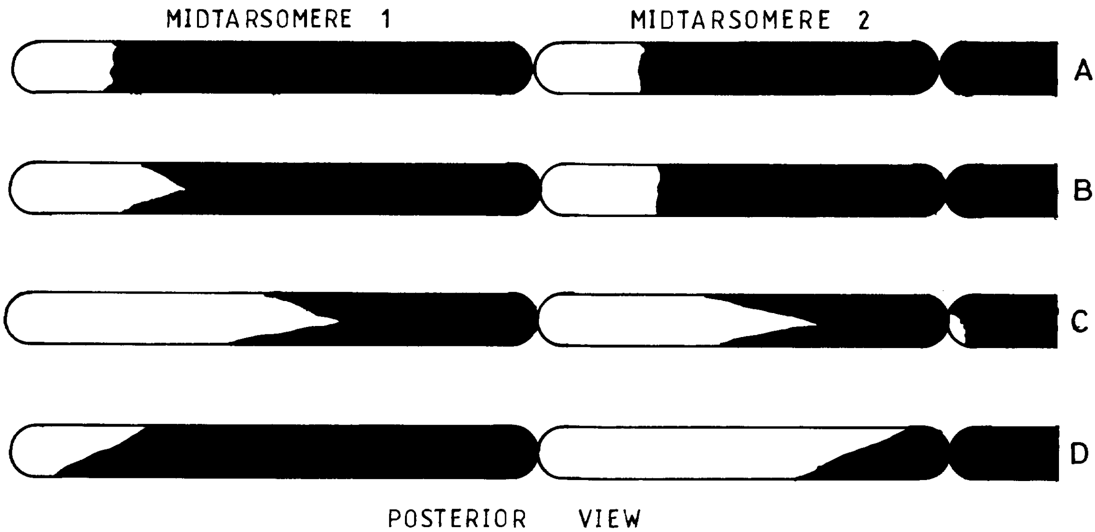


Fig. 1. Tarsal banding patterns on midtarsomeres 1 and 2 of *Aedes simpsoni s.l.*

Pattern C: Midtarsomere 1 with basal white band on the posterior surface relatively long (range 0.7–1.0, mean = 0.8). Midtarsomere 2 also with long white band and stripe on the posterior surface as long as that on midtarsomere 1.

Pattern D: Midtarsomere 1 with short basal white band on the posterior surface (range 0.3–0.5, mean = 0.4). Midtarsomere 2 with very long white band and stripe (range 0.8–1.0, mean = 0.9) on the posterior surface. The white bands were longer dorsally than ventrally, extending diagonally across the tarsomere.

Some variation occurred in patterns B and C. In some mosquitoes, the white band was long and wide and the posterior extension wide, whereas in others, the basal white band was short and the posterior extension quite narrow. In other mosquitoes, the basal white band and the posterior extension were not continuous. In yet others, the posterior extension itself had black scales interspersed with the white.

Table 1 shows the frequency of tarsal banding patterns. Pattern C was more common in all East African samples. The specimens from South Africa were pattern D. Lunyo Farm had fewer mosquitoes with pattern C and more with patterns A and B. Samples from Mubuku, Nkokonjeru, Bwamba, Taveta, Kwale, and Bussi Island had relatively high percentages of mosquitoes with pattern C compared with samples from Kinyarwanda, Lunyo Farm, Bwayise, and Nsadzi Island.

More males had longer white bands than did females (Table 2). Females had predominantly patterns A and C, whereas males had predominantly pattern C.

Seasonal variation in the frequency of tarsal banding patterns in samples from Bwayise, Lunyo Farm, and Kinyarwanda is shown in Fig. 2. No clear or significant trend was detected among the patterns for the three sites.

The ratios of the lengths of the tarsal bands relative to the lengths of the tarsomeres were calculated for 810 males and 932 females. Student's *t*-test (confidence interval = 95%) indicated a significant difference in the length of the tarsal bands on fore- and midtarsomeres 1 and 2 between males and females of most samples. In the following samples, males were not significantly different from females: foretarsomere 1—Taveta; foretarsomere 2—Taveta, Oslo Beach, Maya, Bussi, and Nsadzi islands; midtarsomere 1—Taveta, Kwale, and Oslo Beach; and midtarsomere 2—Taveta, Rabai, and Bussi Island. Only the Taveta

**Table 1.** Tarsal banding patterns[1] on midtarsomeres 1 and 2 in populations of *Ae. simpsoni s.l.*

| Population | Grid location | Method[2] of collection | No. of mosquitoes examined | Frequency (%) of pattern A | B | C | D |
|---|---|---|---|---|---|---|---|
| Lunyo Farm | 0° 04′ N, 32° 28′ E | L, E | 300 | 28.0 | 19.3 | 52.7 | 0.0 |
| Kinyarwanda | 0° 03′ N, 32° 27′ E | L, E | 520 | 26.3 | 15.8 | 57.9 | 0.0 |
| Maya | 0° 11′ N, 32° 25′ E | L, E, A | 84 | 22.7 | 13.6 | 63.7 | 0.0 |
| Nsadzi Island | 0° 06′ N, 32° 37′ E | L | 29 | 20.7 | 13.8 | 65.5 | 0.0 |
| Bwayise | 0° 27′ N, 32° 34′ E | L, E | 300 | 19.0 | 13.7 | 67.3 | 0.0 |
| Bussi Island | 0° 02′ N, 32° 24′ E | L, A | 52 | 16.0 | 14.0 | 70.0 | 0.0 |
| Mubuku | 0° 16′ N, 30° 08′ E | L, A | 59 | 15.3 | 8.3 | 76.4 | 0.0 |
| Nkokonjeru | 0° 14′ N, 32° 58′ E | L, E, A | 109 | 14.7 | 10.1 | 75.2 | 0.0 |
| Taveta | 3° 24′ N, 37° 48′ E | A | 39 | 10.3 | 12.8 | 76.9 | 0.0 |
| Bwamba | 0° 48′ N, 30° 08′ E | L, E, A | 135 | 5.2 | 5.2 | 89.6 | 0.0 |
| Rabai | 3° 55′ S, 39° 34′ E | E | 23 | 0.0 | 0.0 | 100.0 | 0.0 |
| Kwale | 4° 16′ S, 39° 22′ E | L | 38 | 0.0 | 2.6 | 97.4 | 0.0 |
| Oslo Beach | 29° 53′ S, 31° 00′ E | E | 16 | 0.0 | 0.0 | 0.0 | 100.0 |

[1] Tarsal banding patterns as in Fig. 1.
[2] L, collected as larvae and pupae; E, collected as eggs on ovitraps; A, collected as adults (human-baited catches).

population did not show significant differences between males (n = 7) and females (n = 32) for the length of the tarsal bands on any of the tarsomeres.

Analysis of variation in the lengths of tarsal bands on fore- and midtarsomeres 1 and 2 indicated significant differences in the means between populations. Some of the populations, however, had small samples sizes: males from Taveta (n = 7), Oslo Beach (n = 8), Nsadzi Island (n = 12), Rabai (n = 15), and Kwale (n = 20); females from Oslo Beach (n = 8), Rabai (n = 8), and Nsadzi Island (n = 17). Table 3 shows the mean lengths of the tarsal bands on fore- and midtarsomeres 1 and 2 of males and females. Males from

**Table 2.** Tarsal banding patterns[1] on midtarsomeres 1 and 2 of male and female mosquitoes in populations of *Ae. simpsoni s.l.*

| | Males | | | | | Females | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Frequency (%) of pattern | | | | | Frequency (%) of pattern | | | |
| Population | n[2] | A | B | C | D | n[2] | A | B | C | D |
| Lunyo Farm | 140 | 11.4 | 19.3 | 69.3 | 0.0 | 160 | 42.5 | 19.4 | 38.1 | 0.0 |
| Kinyarwanda | 246 | 13.0 | 15.5 | 71.5 | 0.0 | 274 | 31.8 | 13.2 | 45.6 | 0.0 |
| Maya | 62 | 9.7 | 19.3 | 71.0 | 0.0 | 61 | 22.6 | 16.1 | 61.3 | 0.0 |
| Nsadzi Island | 12 | 0.0 | 8.3 | 91.7 | 0.0 | 17 | 35.3 | 17.6 | 47.1 | 0.0 |
| Bwayise | 143 | 4.9 | 14.0 | 81.1 | 0.0 | 157 | 31.8 | 13.4 | 54.8 | 0.0 |
| Bussi Island | 19 | 5.3 | 10.5 | 84.2 | 0.0 | 31 | 22.6 | 16.1 | 61.3 | 0.0 |
| Mubuku | 28 | 0.0 | 0.0 | 100.0 | 0.0 | 32 | 25.8 | 16.1 | 58.1 | 0.0 |
| Nkokonjeru | 56 | 0.0 | 1.8 | 98.2 | 0.0 | 53 | 24.5 | 13.2 | 62.3 | 0.0 |
| Taveta | 7 | 0.0 | 14.3 | 85.7 | 0.0 | 32 | 12.5 | 15.6 | 71.9 | 0.0 |
| Bwamba | 54 | 0.0 | 0.0 | 100.0 | 0.0 | 81 | 8.6 | 8.6 | 82.8 | 0.0 |
| Rabai | 15 | 0.0 | 0.0 | 100.0 | 0.0 | 8 | 0.0 | 0.0 | 100.0 | 0.0 |
| Kwale | 20 | 0.0 | 0.0 | 100.0 | 0.0 | 18 | 0.0 | 5.6 | 94.4 | 0.0 |
| Oslo Beach | 8 | 0.0 | 0.0 | 0.0 | 100.0 | 8 | 0.0 | 0.0 | 0.0 | 100.0 |

[1] Tarsal banding patterns as in Fig. 1.
[2] Number of mosquitoes of each sex examined.

**Table 3.** Mean length of tarsal bands of fore- and midtarsomeres of male and female mosquitoes in populations of *Ae. simpsoni s.l.*

| | Foretarsomere 1 | | Foretarsomere 2 | | Midtarsomere 1 | | Midtarsomere 2 | |
|---|---|---|---|---|---|---|---|---|
| Population | Males | Females | Males | Females | Males | Females | Males | Females |
| Lunyo Farm | 0.49 bc[1] | 0.32 ab | 0.55 ab | 0.49 a | 0.80 bcd | 0.64 bc | 0.73 a | 0.64 a |
| Kinyarwanda | 0.52 bc | 0.32 ab | 0.57 b | 0.50 a | 0.78 bcd | 0.63 ab | 0.76 ab | 0.67 a |
| Maya | 0.36 a | 0.28 ab | 0.52 a | 0.50 a | 0.75 ab | 0.60 ab | 0.74 a | 0.69 ab |
| Nsadzi Island | 0.45 abc | 0.23 a | 0.53 ab | 0.53 abc | 0.81 bcd | 0.63 abc | 0.82 bcd | 0.71 ab |
| Bwayise | 0.45 abc | 0.26 ab | 0.54 ab | 0.49 a | 0.82 cd | 0.66 bc | 0.76 abc | 0.69 ab |
| Bussi Island | 0.43 ab | 0.25 ab | 0.54 ab | 0.50 a | 0.76 abc | 0.60 ab | 0.74 ab | 0.69 ab |
| Mubuku | 0.46 abc | 0.29 ab | 0.60 bc | 0.53 ab | 0.83 cd | 0.66 bc | 0.81 bcd | 0.68 ab |
| Nkokonjeru | 0.46 abc | 0.25 a | 0.55 ab | 0.51 a | 0.84 d | 0.65 bc | 0.80 abc | 0.69 ab |
| Taveta | 0.47 abc | 0.44 cd | 0.54 ab | 0.58 bc | 0.89 de | 0.77 cd | 0.80 abcd | 0.77 bc |
| Bwamba | 0.57 c | 0.40 bc | 0.65 cd | 0.58 bc | 0.84 d | 0.74 c | 0.86 d | 0.81 c |
| Rabai | 0.58 c | 0.43 cd | 0.64 cd | 0.53 ab | 0.91 e | 0.84 d | 0.83 cd | 0.83 c |
| Kwale | 0.83 | 0.58 d | 0.70 d | 0.65 d | 0.91 e | 0.99 d | 0.87 d | 0.86 c |
| Oslo Beach | 0.31 a | 0.25 ab | 0.67 cd | 0.77 d | 0.42 | 0.41 a | 0.84 cd | 0.89 c |

[1] Means within a column followed by a similar letter are not significantly different from each other by Duncan's multiple range test ($P > 0.05$).

Kwale, Rabai, and Bwamba had long bands on all tarsomeres. Males from Maya had short bands on all tarsomeres. The samples of males from other locations had intermediate tarsal band lengths. Males from Oslo Beach had the shortest bands on fore- and midtarsomere 1 and the longest bands on fore- and midtarsomere 2.

Females from Kwale had long bands on all tarsomeres, the longest being foretarsomere 2 and midtarsomere 1. Females from Oslo Beach had the longest bands on fore- and midtarsomere 2. Samples exhibiting the shortest bands of white scales on the tarsomeres varied with the tarsomeres. Females from Nsadzi Island had the shortest bands on foretarsomere 1, those from Bwayise had the shortest on foretarsomere 2, those from Oslo Beach had the shortest on midtarsomere 1, and those from Lunyo Farm had the shortest on midtarsomere 2. Females on nonanthropophilic populations were mostly short-banded, whereas those of anthropophilic populations were mostly long-banded.

**Dentition of tarsal claws.** The presence of a tooth on the claws on the fore- and midlegs is characteristic of females of the *Ae. simpsoni* complex other than *Ae. simpsoni s.s.* However, on some females from Uganda, the tooth was missing on some of the claws. Figure 3 shows combinations of claw and tooth arrangements from different samples. The frequency of these arrangements in four populations is shown in Table 4. We examined 952 claws of males collected at different locations in Kenya and Uganda and observed no difference within and between samples from the different locations. All the claws were similar to arrangement A, but the outer claw on each leg was longer than the inner.

**Scutal line patterns.** The length of the inner as compared with the outer scutal lines was used as the major distinguishing character in the recognition of 12 patterns (Fig. 4). The inner scutal lines were long, extending about two-thirds the length of the thorax, as in patterns 1, 2, and 8; or they were intermediate, extending only about half the length of the thorax, as in patterns 3 and 4; or they were short, about one-third the length of the thorax, as in patterns 5–7 and 9. The outer scutal lines were either intermediate, as in patterns 1–5 and 11, or short, as in patterns 6, 7, and 10. Patterns 1, 3, and 6 had white scales joining the two middle scutal lines, making an "H" pattern. Patterns 8–11 had two scutal lines only, either the inner two (patterns 8 and 9) or the outer two (patterns 10 and 11). Pattern 12 did not have scutal lines.

Tables 5 and 6 show the frequency of dif-

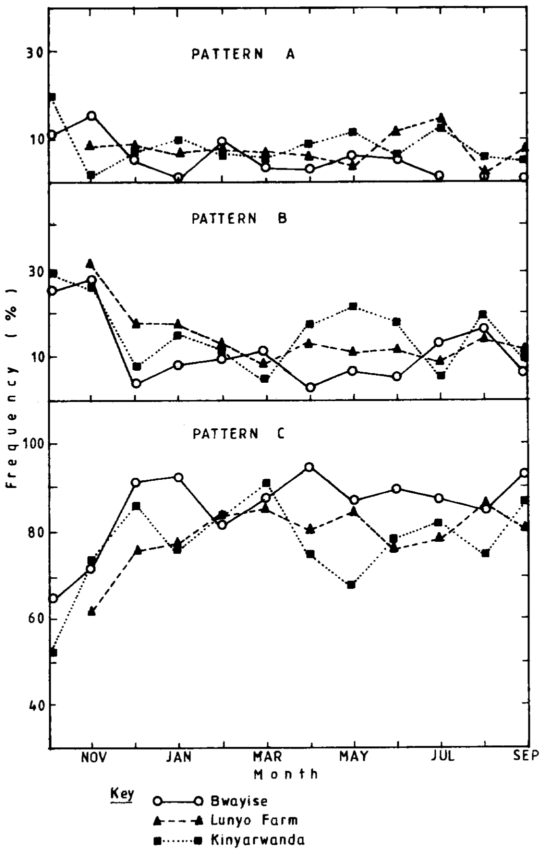


Fig. 2. Variation in frequency (%) of tarsal banding patterns on midtarsomeres 1 and 2 of *Aedes simpsoni s.l.* from Bwayise, Lunyo Farm, and Kinyarwanda over a period of one year.

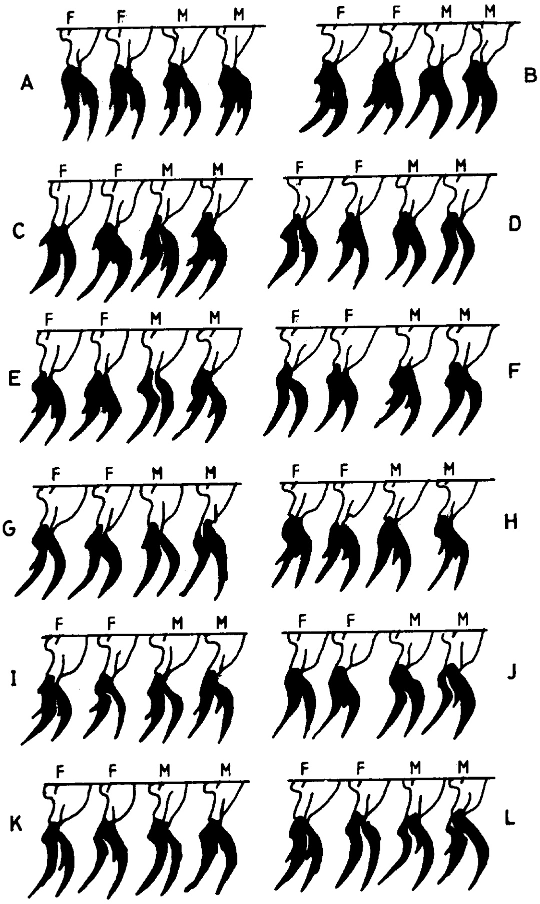


Fig. 3. Dentition of fore (F)- and midclaws (M) of *Aedes simpsoni s.l.*

ferent scutal line patterns on males and females from different locations. Pattern 2 was the most common on both males and females of all populations examined except for males from Kwale, Rabai, and Bwayise. The frequency of pattern 2 was 51.1% on females and 31.1% on males. All patterns occurred on females, but patterns 7, 11, and 12 did not occur on males. Pattern 7 occurred on only a few females from Nkokonjeru and Lunyo Farm. The overall average frequency of pattern 7 was only 0.1%. Pattern 1 was the fourth most common on females but second on males. Pattern 4 occurred in similar proportions on males and females.

The H patterns (Fig. 4, patterns 1, 3, and 6) were more frequent on males than on females, 43.2% and 10.5%, respectively. In nonanthropophilic populations (Bwayise, Lunyo Farm, Kinyarwanda, and Nsadzi Island), 48.4% of males and 21.4% of females had H patterns; in anthropophilic populations (Bwamba, Maya, Mubuku, Bussi Island, Nkokonjeru, Rabai, and Kwale), 42.6% of males and 8.1% of females had H patterns. Females from nonanthropophilic populations, therefore, had a higher frequency of H patterns than did those from anthropophilic populations.

Specimens from Oslo Beach (eight males and eight females, progeny of a single mother) had very long middle scutal lines (longer than shown in Fig. 4, pattern 2). The lines extended from the prescutellar area to the an-

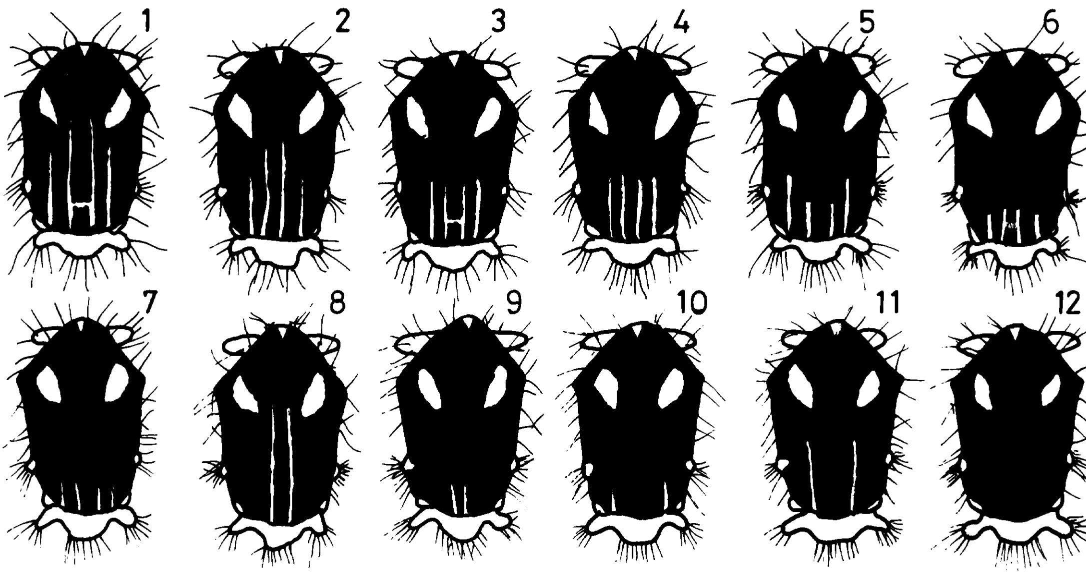


Fig. 4. Scutal line patterns of *Aedes simpsoni s.l.* (grouped according to length of inner as compared with outer scutal lines and presence of white scales joining the middle scutal lines).

terior promontory, almost touching the median spot of broad white scales on the anterior border of the scutum. The H patterns were not distinct on some males. The white scales that join in the middle scutal lines to form the H pattern were not close together, so the cross line was not continuous. H patterns were

**Table 4.** Frequency of tarsal claw groups[1] on females of four populations of *Ae. simpsoni s.l.*

| Tarsal claw group | Frequency (%) | | | |
|---|---|---|---|---|
| | Kinyarwanda (n = 100) | Bwayise (n = 100) | Nkokonjeru (n = 100) | Oslo Beach (n = 8) |
| A | 97.0 | 95.0 | 80.0 | 0.0 |
| B | 0.0 | 0.0 | 1.0 | 0.0 |
| C | 1.0 | 0.0 | 2.0 | 0.0 |
| D | 0.0 | 0.0 | 1.0 | 100.0 |
| E | 0.0 | 1.0 | 1.0 | 0.0 |
| F | 0.0 | 0.0 | 1.0 | 0.0 |
| G | 0.0 | 0.0 | 2.0 | 0.0 |
| H | 0.0 | 0.0 | 2.0 | 0.0 |
| I | 1.0 | 1.0 | 3.0 | 0.0 |
| J | 1.0 | 2.0 | 4.0 | 0.0 |
| K | 0.0 | 1.0 | 2.0 | 0.0 |
| L | 0.0 | 0.0 | 1.0 | 0.0 |

[1] Tarsal claw groups as in Fig. 3.

not observed on any of the females from Oslo Beach.

**Tergal banding patterns.** Three patterns were recognized: variant A (the normal or most common) had a basal white band on abdominal terga II–VIII, variant B had a basal white band on terga III–VIII, and variant C had a basal white band on terga IV–VIII (Fig. 5). Specimens from South Africa were similar to variant A in having a band of white scales on abdominal terga II–VIII, but differed by having wider bands (about 0.6 of the length of the tergum).

Table 7 shows the frequency of different tergal banding patterns from different locations. A small percentage (less than 20%) of males and females in all populations was variant C. Between 15% and 50% of males and females in different populations were variant B. All specimens from Oslo Beach had wide basal white bands on abdominal terga II–VIII.

**Comparisons of isofemale progeny.** The progenies of 61 female *Ae. simpsoni s.l.* from Kinyarwanda, Bwayise, Bwamba, and Nkokonjeru were examined (data for some of these progenies are presented in Tables 8 and 9), and the following observations were made: i) The lengths of the basal white bands on fore- and midtarsomeres 1 and 2 were quite variable in the progeny of one mother (Table 8). Similar differences were observed for the progenies of mothers from other sites. ii) Male mosquitoes generally had longer tarsal bands than did their female siblings. iii) The pattern of banding on midtarsomeres 1 and 2 was variable in the progeny of a single female. The percentages of the various patterns are shown in Table 9. iv) All progenies examined had toothed claws. v) The progenies of only two of 33 mothers from different populations examined for variation in the scutal line patterns had the same scutal line pattern: the progeny from Oslo Beach (eight males and eight females) and those of a mother from Nkokonjeru (13 males and nine females). Progenies of other mothers had at least three patterns of scutal lines. vi) Progenies of 17 mothers from different populations were examined for the presence of white bands on the abdominal terga. The progeny of every mother included variants B and C. More than 78% of all progeny were variant A.

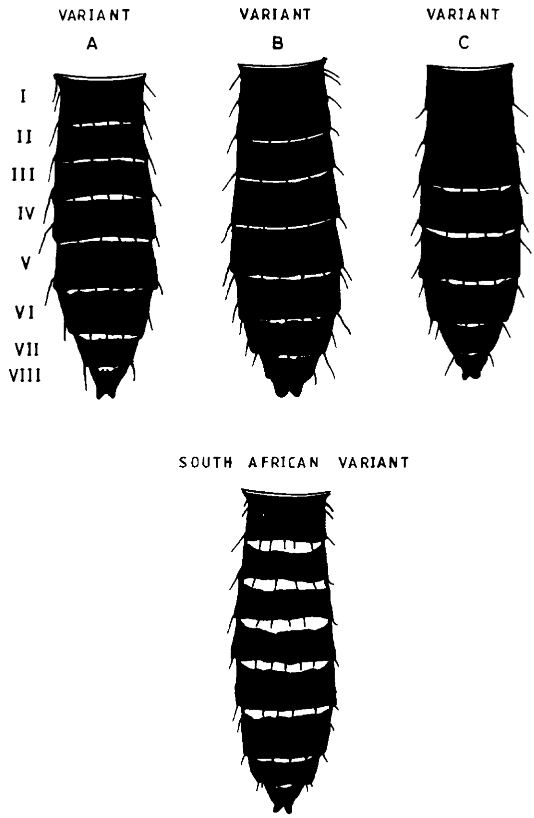


Fig. 5. Tergal banding patterns of *Aedes simpsoni s.l.*

## DISCUSSION

Variation in the length of the white tarsal bands of *Ae. simpsoni,* as described previously, led to the conclusion that *Ae. simpsoni* comprises a species complex (Huang 1979, 1986; Huang and Ward 1982). Morphologic and morphometric observations in the present study have shown that the length of the tarsal bands has a continuous distribution

**Table 5.** Frequency of scutal line patterns[1] of males of different populations of *Ae. simpsoni s.l.*

| | | Scutal line patterns | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population | n[2] | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Lunyo Farm | 254 | 34.2 | 46.5 | 2.7 | 7.5 | 5.5 | 2.0 | 0.0 | 0.8 | 0.8 | 0.0 | 0.0 | 0.0 |
| Kinyarwanda | 310 | 42.3 | 43.2 | 3.2 | 5.2 | 4.2 | 1.3 | 0.0 | 0.3 | 0.0 | 0.3 | 0.0 | 0.0 |
| Maya | 81 | 11.1 | 40.7 | 4.9 | 13.6 | 18.6 | 11.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bwayise | 284 | 34.9 | 34.5 | 9.7 | 4.3 | 5.8 | 0.0 | 0.7 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bussi Island | 9 | 11.1 | 11.1 | 0.0 | 33.4 | 22.2 | 22.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Mubuku | 21 | 15.0 | 30.0 | 20.0 | 35.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Nkokonjeru | 110 | 37.1 | 41.4 | 5.2 | 7.4 | 4.7 | 3.0 | 0.0 | 0.6 | 0.5 | 0.1 | 0.0 | 0.0 |
| Bwamba | 47 | 21.3 | 34.0 | 8.5 | 19.2 | 8.5 | 8.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Rabai | 10 | 40.0 | 20.0 | 20.0 | 10.0 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Kwale | 10 | 40.0 | 20.0 | 20.0 | 20.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Average | | 27.4 | 31.1 | 9.7 | 16.1 | 9.3 | 6.1 | 0.0 | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 |

[1] Scutal line patterns as in Fig. 4.
[2] Number of mosquitoes examined.

**Table 6.** Frequency of scutal line patterns[1] of females of different populations of *Ae. simpsoni s.l.*

| | | Scutal line patterns | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population | n[2] | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Lunyo Farm | 279 | 16.5 | 58.4 | 1.4 | 6.1 | 8.6 | 1.8 | 0.4 | 3.6 | 1.4 | 0.7 | 0.0 | 1.1 |
| Kinyarwanda | 425 | 15.5 | 54.6 | 3.3 | 12.9 | 7.3 | 0.2 | 0.0 | 2.8 | 0.2 | 0.2 | 0.2 | 0.2 |
| Maya | 82 | 4.9 | 37.8 | 0.0 | 25.6 | 31.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bwayise | 270 | 20.7 | 38.3 | 3.0 | 18.2 | 12.7 | 2.2 | 0.2 | 1.9 | 0.0 | 0.0 | 0.0 | 1.1 |
| Bussi Island | 15 | 6.7 | 53.3 | 0.0 | 15.3 | 20.0 | 6.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Mubuku | 21 | 4.5 | 63.6 | 0.0 | 9.1 | 18.2 | 4.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Nkokonjeru | 310 | 4.5 | 32.6 | 1.9 | 20.3 | 34.5 | 5.2 | 0.3 | 0.3 | 0.3 | 0.0 | 0.0 | 0.3 |
| Bwamba | 68 | 5.9 | 57.4 | 0.0 | 20.6 | 11.8 | 4.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Rabai | 11 | 0.0 | 54.5 | 0.0 | 18.2 | 9.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 9.1 | 0.0 |
| Kwale | 10 | 0.0 | 70.0 | 0.0 | 20.0 | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Average | | 7.9 | 51.0 | 0.1 | 16.6 | 17.1 | 2.5 | 0.1 | 0.9 | 0.2 | 0.1 | 0.9 | 0.3 |

[1] Scutal line patterns as in Fig. 4.
[2] Number of mosquitoes examined.

within and among populations. Based on single family progeny results, the length of the white tarsal band appears to be a polygenic character. The average length of the bands and the type of banding pattern on midtarsomeres 1 and 2 were variable for samples from different locations. Lengths of tarsal bands also varied from mosquito to mosquito, so that a single mother produced offspring identifiable as *Ae. lilii* and *Ae. bromeliae* following Huang's (1979) and Huang and Ward's (1982) designations.

As these variations are of a continuous nature, tarsal bands cannot be used to identify different species within the complex. Only the tarsal banding pattern of the South African population (pattern D) was distinctive, a characteristic of *Ae. simpsoni s.s.* It should be noted, however, that only a single progeny was examined. A larger sample may show a greater range of variation. The banding pattern observed on the mosquitoes from South Africa is similar to that described by Huang (1979) and Huang and Ward (1982) for *Ae. simpsoni.* Differences in the lengths of the white bands and their frequencies in the different populations may be interpreted as due to genetic or environmental factors.

Fluctuations in the percentages of mosquitoes with different tarsal banding patterns

**Table 7.** Frequency of abdominal banding patterns[1] of different populations of *Ae. simpsoni s.l.*

| | Frequency of pattern | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| Population | A | B | C | A | B | C |
| Lunyo Farm | 56.5 | 39.4 | 4.1 | 65.1 | 32.8 | 2.1 |
| Kinyarwanda | 43.0 | 37.9 | 19.1 | 53.1 | 34.1 | 12.8 |
| Maya | 65.0 | 33.8 | 1.2 | 55.0 | 42.6 | 2.4 |
| Nsadzi Island | 49.5 | 48.3 | 2.1 | 62.4 | 34.1 | 3.5 |
| Bwayise | 54.3 | 43.7 | 1.9 | 63.6 | 34.0 | 2.4 |
| Bussi Island | 66.8 | 33.2 | 0.0 | 74.8 | 23.8 | 1.4 |
| Mubuku | 71.4 | 18.4 | 10.2 | 56.7 | 30.1 | 13.2 |
| Nkokonjeru | 61.2 | 38.8 | 0.0 | 58.7 | 41.3 | 0.0 |
| Bwamba | 54.3 | 26.6 | 19.1 | 60.9 | 26.6 | 12.5 |
| Rabai | 55.4 | 31.9 | 12.7 | 53.4 | 28.8 | 18.2 |
| Kwale | 51.1 | 29.6 | 19.3 | 47.3 | 38.5 | 14.2 |

[1] Abdominal banding patterns as in Fig. 5.

**Table 8.** Length of tarsal bands relative to lengths of fore- and midtarsomeres 1 and 2 in the progeny of a single female *Ae. simpsoni s.l.* from Bwayise.

| Mosquito number | | Sex | Length of band: Foretarsomere 1 | Foretarsomere 2 | Midtarsomere 1 | Midtarsomere 2 | Tarsal banding pattern[1] |
|---|---|---|---|---|---|---|---|
| NKK | 1 | F | 0.26 | 0.50 | 0.56 | 0.68 | C |
| | 2 | F | 0.22 | 0.50 | 0.71 | 0.59 | B |
| | 3 | F | 0.76 | 0.44 | 0.79 | 0.64 | C |
| | 4 | F | 0.24 | 0.83 | 0.75 | 0.63 | C |
| | 5 | F | 0.25 | 0.43 | 0.71 | 0.59 | B |
| | 6 | F | 0.19 | 0.26 | 0.81 | 0.59 | B |
| | 7 | F | 0.26 | 0.62 | 0.56 | 0.56 | A |
| | 8 | F | 0.28 | 0.55 | 0.58 | 0.61 | A |
| | 9 | M | 0.31 | 0.53 | 0.88 | 0.91 | C |
| | 10 | M | 0.20 | 0.59 | 0.86 | 0.65 | B |
| | 11 | M | 0.57 | 0.50 | 0.78 | 0.71 | C |
| | 12 | M | 0.28 | 0.59 | 0.81 | 0.67 | C |
| | 13 | M | 0.74 | 0.44 | 0.83 | 0.64 | B |
| | 14 | M | 0.29 | 0.47 | 0.75 | 0.60 | B |
| | 15 | M | 0.87 | 0.77 | 0.81 | 0.61 | B |
| | 16 | M | 0.43 | 0.59 | 0.76 | 0.71 | C |

[1] Tarsal banding patterns as in Fig. 1.

**Table 9.** Tarsal banding patterns[1] on midtarsomeres 1 and 2 in the progeny of single females of *Ae. simpsoni s.l.* from different populations.

| Progeny number[2] | No. of mosquitoes[3] | Frequency (%) of tarsal banding patterns: A | B | C |
|---|---|---|---|---|
| 19 KND | 15(7) | 26.7 | 0.0 | 73.3 |
| 9 KND | 16(7) | 31.3 | 12.5 | 56.2 |
| 5 KND | 16(6) | 25.0 | 25.0 | 50.0 |
| 6 BY | 10(7) | 20.0 | 10.0 | 70.0 |
| 34 BY | 37(23) | 37.8 | 21.6 | 40.5 |
| 108 BY | 12(4) | 8.3 | 41.7 | 50.0 |
| 1 BWB | 14(9) | 0.0 | 14.3 | 85.7 |
| 4 BWB | 1(7) | 0.0 | 0.0 | 100.0 |
| 28 BWB | 12(4) | 8.3 | 0.0 | 91.7 |
| 56 NKK | 32(17) | 12.5 | 46.9 | 40.6 |
| 58 NKK | 16(6) | 0.0 | 6.2 | 93.8 |
| 59 NKK | 13(11) | 7.7 | 0.0 | 92.3 |

[1] Tarsal banding patterns as in Fig. 1.
[2] KND, Kinyarwanda; BY, Bwayise; BWB, Bwamba; NKK, Nkokonjeru.
[3] Number of females in parentheses.

did not appear to be seasonal. A relationship was seen between sex and the amount of white scaling on the tarsomeres. More males than females had larger bands on midtarsomeres 1 and 2.

If the length of the tarsal bands is associated with biting behavior and considered diagnostic of different species, then *Ae. bromeliae* and *Ae. lilii* must occur sympatrically because mosquitoes with short and long tarsal bands occur together in each of the populations. However, frequencies of the different lengths of tarsal bands give no indication of separation into two or three distinct peaks suggestive of different species. Thus it appears that all the mosquitoes at a single site belong to the same species despite variation in many characters. The distribution map of Huang (1986) showing a number of sympatric occurrences of *Ae. bromeliae* and *Ae. lilii* supports the concept of polymorphic variation in one species.

The absence of teeth on the fore- and midclaws of females is used as a diagnostic character separating *Ae. simpsoni s.s.* from the other species of the complex (Edwards 1941, Gillett and Van Someren 1972, Huang 1979, Huang and Ward 1982). All samples of *Ae. simpsoni s.l.* from East Africa possessed these teeth. However, a few mosquitoes in some of the samples were missing teeth on at least one of the claws. Only a single specimen from the Nkokonjeru population was found without teeth on both the fore- and midclaws. In none of these mosquitoes was there an indication that the teeth had been broken off. The small number of specimens without teeth on one or more tarsal claws does not lead us to question this as a diagnostic character. All 3,866 female claws of a Chaggaland population of *Ae. simpsoni s.l.* examined by Gillett and Van Someren (1972), were toothed. One specimen had two teeth on one claw. It is also worth noting that Edwards (1941) observed that the claws of the fore- and midlegs of *Ae. simpsoni s.l.* females from areas other than southern Africa are usually but not always toothed. Therefore, the occurrence of a single mosquito without teeth on the claws of the fore- and midlegs is not surprising.

Huang (1979) and Huang and Ward (1982) indicated an association between the length of the scutal lines of females and species of the *Ae. simpsoni* complex. Long scutal lines were associated with females of *Ae. simpsoni s.s.,* medium length scutal lines (similar to patterns 1 and 2) were associated with *Ae. bromeliae,* and short scutal lines (similar to patterns 3 and 5) were associated with *Ae. lilii.*

The use of scutal line lengths to discriminate species of the *Ae. simpsoni* complex in East Africa is not supported by our observations. The results of our study show that if *Ae. lilii* and *Ae. bromeliae* are distinct species, then they occur sympatrically at all sites studied because individuals with long and short scutal lines were found at each site. Although the lengths of the scutal lines were not measured, the lengths varied continuously in all populations. Thus, there is no clear boundary between short and long scutal lines. The fact that there are differences in the frequencies of the different scutal patterns in different populations may be due to random fixation of particular, not necessarily adaptive, genes in these populations.

A sex association was observed in the frequency of the H patterns of scutal lines. More males than females bore H patterns in all populations. It was also observed that the H pattern occurred more frequently on females of nonanthropophilic populations than on females of anthropophilic populations. This indicates an association between the scutal line patterns and biting behavior. Earlier, Gillett and Van Someren (1972) observed only a small percentage of females from Chaggaland, an anthropophilic population, with the H pattern of scutal lines.

The scutal line pattern of *Ae. simpsoni* from South Africa was distinct. It has been described by Theobald (1905), Edwards (1941), Huang (1979), and Huang and Ward (1982) to be diagnostic of *Ae. simpsoni s.s.*

Clearly, there is more variation in the morphology and color of *Ae. simpsoni s.l.* than previously reported. There are statistically significant differences between certain populations for some of the characters but few absolute differences. Morphological evidence indicates a species level of difference between the South African *Ae. simpsoni s.s.* population and other populations of the complex. However, no constant morphological differences are evident between the other populations sampled, although intrapopulation variation is high. *Aedes lilii* and *Ae. bromeliae* are not separable on the basis of the morphological criteria proposed by Huang (1979). What is apparent from the tarsomere banding studies is that females with short bands predominate in nonanthropophilic populations, whereas those with long bands predominate in anthropophilic populations.

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