MOUTHPARTS OF MALE AEDES (STEGOMYIA) MOSQUITOES

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ABSTRACT. Mouthparts of adult males of 17 strains of 8 species from the subgenus *Stegomyia* of the genus *Aedes*, including 5 strains of *Aedes aegypti* and 6 strains of *Aedes albopictus*, were examined. Lengths of maxillae, mandibles, maxillary palpi, and proboscises were measured under light microscopy and their detailed structures were examined by scanning electron microscopy. Lengths were presented as ratios to proboscis lengths. In contrast to previous reports, mandibles were found in all 5 strains of male *Ae. aegypti* examined. Variations in maxillary and mandibular lengths were significant among strains, even within *Ae. aegypti* and *Ae. albopictus*. High variation of these structures among and within species indicates that the average length of these structures in only 1 species may not be a reliable representative of a subgenus, and those of 1 strain may not be reliable for a species. However, their range in length (maxillae 0.13–0.50, mandibles 0.04–0.17 length of the proboscis, together with their delicate structures and the large coefficient of variation, suggest that they exist only as vestigial structures. A positive correlation was found between lengths of maxillae and those of mandibles, but mandibles are usually shorter than maxillae. The hypopharynx is discernible from the labium wall by its texture and border, and this suggests that it was a free stylet in the past.

KEY WORDS Aedes, Stegomyia, maxilla, mandible, hypopharynx, male mouthparts

INTRODUCTION

Because most female mosquitoes feed on blood, their mouthparts are highly specialized for piercingthe host skin and sucking blood. The piercingsucking tools, known collectively as the fascicle, contain 1 pair of teeth-bearing maxillary stylets, 1 pair of mandibular stylets, a labrum, and a hypopharynx with its salivary canal. All these structures are packed in the gutterlike labium and constitute a proboscis.

The labrum forms a food canal and provides rigidity for the fascicle, whereas the maxillae anchor themselves to the host skin by their teeth. Whether the mandibles play an active role during piercing as in other bloodsucking nematoceran flies (Downes 1970), or simply serve as a closure of the distal opening of the labral food canal (Clements 1992) is not clear. The hypopharynx, which partially makes the ventral closure of the labral food canal, enters the host skin together with other parts and releases saliva from a gutter on its surface (the salivary canal) during feeding.

Male mosquitoes do not take blood. Their food sources are mainly floral and extrafloral nectaries, honeydew (Foster 1995), or even plant tissue (Schlein and Muller 1995). Their mouthparts are not developed for piercing. The maxillae and mandibles are much shorter than the proboscis (Vizzi 1953, Snodgrass 1959, Downes 1970, Clements 1992) and are considered to be functionless (Vizzi 1953, Snodgrass 1959), as in nonbloodsucking nematocerans (Downes 1970). On the other hand, the labrum and the hypopharynx do reach the tip of the proboscis. The hypopharynx, with its salivary canal, fuses with the inner wall of the labium and may form the ventral closure of the labral food canal (Clements 1992). As a result of the elevation of the subgenus Ochlerotatus to generic rank by Reinert (2000), the subgenera Stegomyia and Aedes remain in the genus Aedes, whereas subgenera Ochlerotatus and Finlaya belong to the genus Ochlerotatus. To avoid confusion, references to previous comparative morphological studies of subgenera will be on the basis of the older classification. The implications of the Reinert classification on these studies will be discussed later.

Marshall and Staley (1935) reported variations of maxillae and mandibles among male mosquitoes from the United Kingdom. They found maxillary stylets to be present in 8 subgenera examined, but the lengths of the stylets were found to be highly variable among the subgenera, whereas mandibles were absent in subgenera Aedes and Ochlerotatus of the genus Aedes. Marshall and Staley regarded the lengths of these structures as characteristic to each subgenus. However, because they examined only 1-4 species from the United Kingdom for each subgenus, whether these attributes are common throughout each subgenus is not clear. Vizzi (1953) reported a wide range of individual variation in mouthpart lengths of male Anopheles quadrimaculatus Say, even for specimens taken from 1 laboratory colony.

The subgenus Stegomyia of the genus Aedes includes vectors of human filariasis and a number of viral diseases and is a dominant subgenus in the Oriental Region (Huang 1979). However, reports on mouthparts of male Stegomyia are limited to those dealing with Aedes aegypti (L.). Christophers (1960) and Lee (1974) described the structures of mouthparts of both males and females under light microscopy and scanning electron microscopy, respectively. Both of these authors stated that mandibles are absent in males of Ae. aegypti.

Species	Strain	n
Aedes aegypti	Makassar, Indonesia	20
	Liverpool	18
	Jakarta, Indonesia	13
	Timor, Indonesia	15
	Polewali, Indonesia	20
Aedes albopictus	Matsumoto, Japan	18
	Polewali, Indonesia	12
	Tanegashima, Japan	15
	Makassar, Indonesia	11
	Okinawa, Japan	11
	Mambi, Indonesia	10
Aedes paullusi	Seram, Indonesia	20
Aedes scutellaris	Seram, Indonesia	20
Aedes riversi	Kabeshima, Japan	17
Aedes flavopictus	Seburi, Japan	10
Aedes galloisi	Kyongi-do, Korea	18
Aedes pseudoalbolineatus	Mambi, Indonesia	9

 Table 1.
 Aedes (Stegomyia) species and strains examined.

' The Liverpool strain originally was collected in Thailand.

Our preliminary observation suggested the presence of maxillae and mandibles of males in some species of the subgenus *Stegomyia*. Thus, our objectives were to describe the mouthparts of male *Aedes* (*Stegomyia*) species, with confirmation of the morphological status of mandibles of *Ae. aegypti* males; and to examine whether the lengths of maxillae and mandibles are common attributes throughout species belonging to this subgenus.

MATERIALS AND METHODS

Specimens included 17 strains of 8 species from 3 species groups of Stegomyia: Ae. aegypti represented the aegypti group; the scutellaris group included Aedes albopictus (Skuse), Aedes paullusi Stone and Farner, Aedes scutellaris (Walker), Aedes riversi Bohart and Ingram, Aedes flavopictus Yamada, and Aedes galloisi Yamada; and Aedes pseudoalbolineatus Brug represented the albolineatus group. For Ae. aegypti and Ae. albopictus, 5 and 6 strains were examined, respectively (Table 1). Identifications were based on keys of Wepster (1954), Huang (1979), and Tanaka et al. (1979). Numbers of specimens varied from 9 to 20 individuals, depending on availability. Specimens were reared from larvae collected in the field or obtained from laboratory colonies, and kept alive for at least 24 h after emergence. Until examination, specimens were kept in 70% ethanol.

Because the labium, labrum, and hypopharynx in male *Stegomyia* are almost the same length and reach the tip of the proboscis, we measured only the lengths of maxillae, mandibles, maxillary palpi, and the proboscis (the length of the labium from the base of the prementum to the tip of the labella) (Fig. 1). All measurements were converted to millimeters and then presented as ratios of proboscis lengths (Marshall and Staley 1935). This enabled

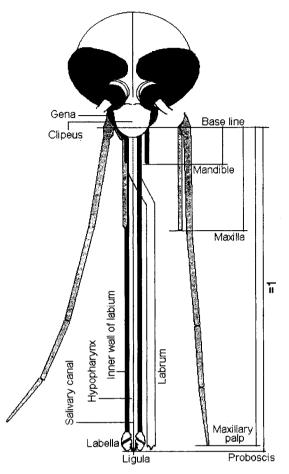


Fig. 1. Head and mouthparts of a male of Aedes (Stegomyia).

us to compare the relative lengths of the structures, because the absolute values are affected by body size. We measured the lengths of maxillary palpi, because they are a well-developed functional organ in males (Clements 1992) and are connected directly to the base of maxillary stylets. The lengths of maxillary palpi can be used to compare the extent of variation between structures with functions and those without function.

Specimens in 70% ethanol were transferred to 2% KOH solution and heated at 50°C for 2 h. They were then dehydrated by passage through 70%, 90%, and 99% ethanol in this order, and stained with acid fuchsin. Specimens were kept in the staining solution at least for 2 h. Just before examination, the specimens were put on tissue paper for a few seconds to absorb the stain, and then put on a microscope slide. One or 2 drops of Methyl Cellosolve (Nakarai Chemicals, Ltd., Kyoto, Japan) were placed on the specimen, which was then examined under both dissecting and compound microscopes.

First, the head was separated from the body by

using a pair of fine insect pins. The lengths of the proboscis and maxillary palpus were measured under the disecting microscope (magnification $25\times$).

To observe the maxillae and mandibles, maxillary palpi were abducted laterally. The maxillae and mandibles usually were found between the labium and maxillary palpi. The base of the maxilla connects with the maxillary palpus, whereas the base of the mandible connects with the gena by the mandibulogenal link (Jobling 1987). Sometimes it was necessary to pry the labrum up from the labial gutter to find the maxillae and mandibles. If the mandibles still could not be seen, the clypeus, together with the gena and the labrum, was detached from the labium. The starting point for measurement was the point where the maxillary palpi connect with the labium, or the distal point of the gena (Harbach and Knight 1980) (Fig. 1). The maxillae and mandibles originated from the lower and upper sides of this point, respectively. They then were measured under light microscopy with 10×20 or 40×20 magnifications.

Scanning electron microscopy was used to see fine structures and confirm the observation made under light microscopy. Specimens were 1st checked under the light microscope. After the maxillae and mandibles were found, they were transferred to a small poly L-lysine hydrobromide–coated glass slide. The specimens were gradually dehydrated through 70–99% ethanol before they were placed in 99% *t*-butyl alcohol, and then kept in a freezer until they were freeze-dried (with a EIKO ID-2 drier; EIKO, Tokyo, Japan) before gold coating (with a EIKO IB-3 ion coater). The specimens then were examined in a JEOL JSM-5200 LV scanning electron microscope (JEOL, Tokyo, Japan).

Lengths of maxillae, mandibles, and maxillary palpi as ratios to the proboscis were analyzed by the statistical software SSPS version 7.5 (SPSS Inc., Chicago, IL). Because the data distribution was not normal, the Kruskal-Wallis test for multiple independent samples and Spearman's rank correlation were applied. To show the variation, we used box plots (Sokal and Rohlf 1995). Confidence intervals of the median were calculated following McGill et al. (1978). For expression, the McGill's "notch" was changed to "a gray bar," following Benjamini (1988). If the confidence interval bars of 2 medians do not overlap, the medians are significantly different at about a 95% confidence level. To make visual comparisons easier, strains were arranged by order of medians.

RESULTS

General descriptions

The mouthpart structures of species examined were fundamentally the same; hence, only photographs of *Ae. aegypti* are shown here (Figs. 2–4).

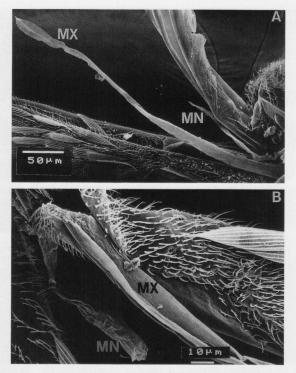


Fig. 2. Maxillae (MX) and mandibles (MN) of *Aedes aegypti* (Makassar). (A) Entire maxilla and the mandible. (B) Irregular shape of the mandible due to its delicate structure. Note that the maxillary base is broader than the mandibular base.

The labrum, as in females, nearly reaches the proboscis tip, the point just before the labellar tip. However, its tip is forked and apparently weaker than the sharp pointed tip of females.

The hypopharynx (Fig. 4) unites with the inner wall of the labium and reaches the proboscis tip at about the same level with the labrum. Although not a free stylet, a distinct border clearly separates the hypopharynx from the labium (Fig. 4). The hypopharynx has a smoother surface than the inner wall of the labium with its longitudinal wrinkles. The salivary canal lays as a gutter on the hypopharynx surface. The hypopharynx tip is fused with the ligula where the salivary canal ends.

The maxillae of males, unlike in females, do not have a distinct shape. They are much shorter than the proboscis but usually longer than the mandibles (Figs. 2A, 2B). Under light microscopy, the maxillae are seen as delicate tapelike structures with a pointed, blunt, or sometimes irregular tip. Differing from those of females (Figs. 3B, 3D), the maxillae of males have no teeth (Fig. 3C), no clear transverse striations, but rather unclear thin lines, are present alongside the trunk (Fig. 3A). The widths of the maxillae are narrower than those of females if compared at the base.

Mandibles were present in all species examined,

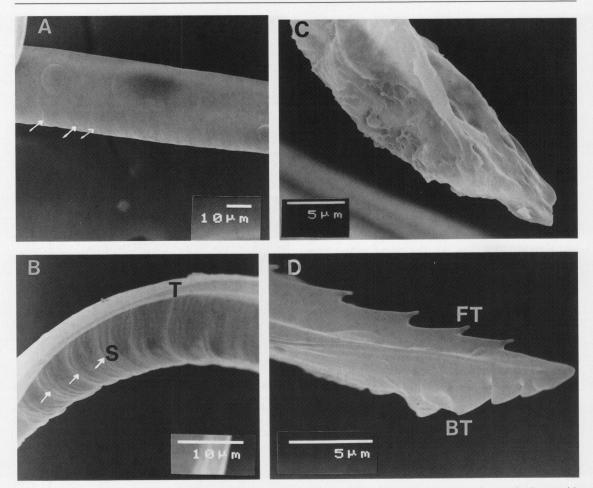


Fig. 3. Differences between maxillae of male and female *Aedes aegypti*. (A) Maxilla of male near its base, with unclear thin lines (arrows). (B) Maxilla of female, at one third of the distance from the tip, with clear transverse striations (arrows). T, trunk; S, transverse striations. (C) Tip of maxilla of male. (D) Tip of maxilla of female, with backward teeth (BT), and smaller forward teeth (FT).

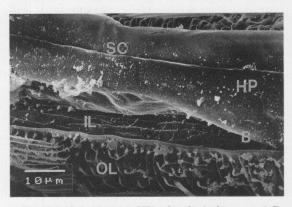


Fig. 4. Hypopharynx (HP) of male *Aedes aegypti*. B, border of hypopharynx; IL, inner wall of labium; OL, Outer wall of labium; SC, salivary canal.

including 5 strains of *Ae. aegypti* (Figs. 2A, 2B). Mandibles, as maxillae, are tapelike structures, but appear to be less sclerotized, narrower, thinner, and more delicate. Their tips are more irregular than those of maxillae (Fig. 2B). As found for maxillae, the widths of the mandibles of males are narrower than those of females.

Lengths

The lengths of proboscises for strains examined varied from 1.90 ± 0.14 mm (mean \pm SD) for Ae. albopictus to 2.45 ± 0.07 mm for Ae. pseudoalbolineatus, depending on different body sizes among strains.

Maxillary palpi range from 0.52 to 1.19 of the proboscis lengths. They are about the same as or a little longer than the lengths of proboscises in *Ae. aegypti, Ae. albopictus, and Ae. paullusi, or a little shorter than the proboscises in <i>Ae. scutellaris, Ae.*

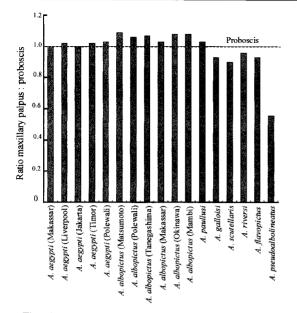


Fig. 5. Average lengths of maxillary palpi of male Stegomyia. Proboscis length = 1.

riversi, Ae. flavopictus, and Ae. galloisi. However, in Ae. pseudoalbolineatus, lengths of maxillary palpi are about one half of the proboscis length (Fig. 5). Statistical tests showed significant differences among all the strains examined (Kruskal-Wallis test, H = 203.7, df = 16, P < 0.001). Significant differences were found even within the same species (Ae. aegypti, H = 11.6, df = 4, P < 0.021; Ae. albopictus, H = 23.3, df = 5, P < 0.001).

Maxillae are much shorter than proboscises, with a range of 0.13–0.5 of the proboscis lengths. The Kruskal–Wallis test showed significant differences among all the strains examined (H = 140.6, df = 16, P < 0.001), within *Ae. aegypti* (H = 36.1, df = 4, P < 0.001), and within *Ae. albopictus* (H = 24.6, df = 5, P < 0.001).

Figure 6 shows that a maxilla of Ae. pseudoalbolineatus is the shortest and it is significantly different from those of all the other species. Within the scutellaris group (except Ae. albopictus), the maxillae of Ae. paullusi are significantly longer than those of the other species. Intraspecific variation within Ae. albopictus and Ae. aegypti is considerable, and some strains of Ae. albopictus, as well as some strains of Ae. aegypti, are significantly different from the other species, but some are not. Among strains within the same species, at least the Matsumoto strain of Ae. albopictus apparently is different from the Mambi strain, and the Jakarta and Polewali strains of Ae. aegypti are different from the Timor strain.

The mandibles are shorter than maxillae, with a range of 0.04-0.17 of the proboscis lengths, except for 2 individuals mentioned below. Mandibles, as maxillae, vary among all the strains examined (*H*

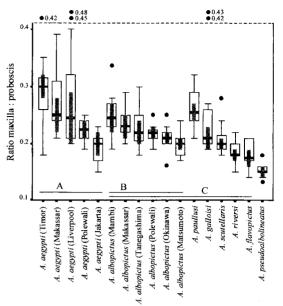


Fig. 6. Variation of maxillary lengths of male *Stego-myia*. The box indicates the interquartile range with the median as a transversal line; upper and lower whiskers are maximum and minimum values within 1.5 of the interquartile range. Outliers (more than 1.5 times of interquartile ranges) are plotted separately and marked with dense circles. Vertical gray bars across the medians are 95% confidence intervals. Horizontal lines at the bottom of the graph are (A) strains of *Aedes aegypti*, (B) strains of *Ae. albopictus*, and (C) *scutellaris* group. The *aegypti* group and *albolineatus*, respectively.

= 148.5, df = 16, P < 0.001), and also within Ae. aegypti (H = 23.7, df = 4, P < 0.001) and Ae. albopictus (H = 13.7, df = 5, P < 0.05).

Figure 7 shows that within the *scutellaris* group (except *Ae. albopictus*), lengths of mandibles of *Ae. paullusi* and *Ae. galloisi* are different from that of *Ae. scutellaris*, as well as from those of *Ae. riversi* and *Ae. flavopictus*. The latter 2 species are different also from *Ae. pseudoalbolineatus* (the *albolineatus* group). Within *Ae. aegypti*, the Makassar strain is clearly different from other strains, whereas strains of *Ae. albopictus* do not vary appreciably (confidence interval bars almost overlap).

Maxillae and mandibles show wide variation in their lengths even within each strain. Examples are the maxillae of *Ae. aegypti* from Timor and the mandibles of *Ae. albopictus* from Makassar. Note that in the Makassar strain of *Ae. albopictus*, 2 unusual mandible lengths occur: 0.41 and 0.45 of the proboscis lengths, which exceed the length of maxillae (0.25 of the proboscis lengths in both cases) in their pairs. These are unique because in all other specimens, maxillae are longer than mandibles. We eliminated the possibility of confusing maxillae as mandibles and vice versa by careful examination of their bases.

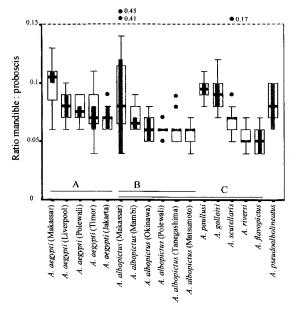


Fig. 7. Variation of mandibular lengths of male *Stego-myia*. For explanation of symbols, see Figure 6.

A significant positive correlation was found between maxillary and mandibular lengths (Spearman's rank correlation r = 0.675, P < 0.01), as shown in Figure 8. Table 2 shows much higher coefficients of variations (CVs) of mandibles (8.9– 106.8) and maxillae (8.1–29.9) as compared to those of maxillary palpi (2.1–5.5).

DISCUSSION

Huang (1979) reported that the maxillary palpi of males of the subgenus *Stegomvia* are more than 0.50 length of the proboscis, whereas Tanaka et al. (1979) reported that they are 0.80-1.10 lengths of the proboscis for Japanese and Korean species in the *aegypti* and *scutellaris* groups. We found that maxillary palpi vary from 0.52 to 1.19 of proboscis lengths for 8 species belonging to 3 species groups. As stated by Huang (1978a), maxillary palpi of the males of Ae. pseudoalbolineatus are shorter than the proboscis. We found that they ranged from 0.52 to 0.60 proboscis lengths. Maxillary palpi of Aedes laffooni Knight and Rozeboom, Aedes impatibilis (Walker), and Aedes hoogstraali Knight and Rozeboom, all of which belong to the albolineatus group (Huang 1978a, 1978b), are also distinctly shorter than the proboscis. This probably is a characteristic of males of the albolineatus group. Maxillary palpi of other species examined are as long as the proboscis.

All the species and strains, including 5 Ae. aegypti strains, were found to have mandibles. This contrasts with previous reports on Ae. aegypti by Christophers (1960) and Lee (1974), who stated that mandibles do not exist in males of this species.

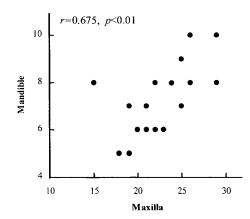


Fig. 8. Correlation between lengths of maxillae and mandibles of male *Stegomyia*. Proboscis length = 100.

Aedes aegypti is known as a highly variable species (Mattingly 1957, Christophers 1960, Huang 1979). The absence of mandibles previously reported for Ae. aegypti possibly is due to intraspecific variation. We examined 5 strains of Ae. aegypti, including those from different parts of Indonesia (Makassar, Jakarta, Timor, and Polewali). All of them had mandibles. Further, mandibles were found in 7 other species of Stegomvia examined. The presence of mandibles is more likely is characteristic of Stegomyia males. Christophers (1960) and Lee (1974) probably failed to find mandibles because they are short and thin and may easily be overlooked. Even when present in live individuals, mandibles may appear to be missing in dead specimens because they are hidden, broken, or have been removed with the gena.

Lengths of maxillae and mandibles are highly variable within the subgenus Stegomyia. Variation

 Table 2.
 Coefficients of variation for mouthparts of male Stegomyia.

Species (strain)	Mandible	Maxilla	Palp
Aedes aegypti (Makassar)	19.7	29.0	5.1
Ae. aegypti (Liverpool)	17.6	22.9	2.1
Ae. aegypti (Jakarta)	13.3	13.7	2.6
Ae. aegypti (Timor)	23.7	21.3	2.8
Ae. aegypti (Polewali)	13.6	8.1	2.1
Aedes albopictus (Matsumoto)	15.9	9.4	3.1
Ae. albopictus (Polewali)	8.9	8.9	3.7
Ae. albopictus (Tanegashima)	19.9	15.1	2.8
Ae. albopictus (Makassar)	106.8	11.7	1.8
Ae. albopictus (Okinawa)	17.9	11.0	2.0
Ae. albopictus (Mambi)	16.4	16.4	5.5
Aedes paullusi	9.2	11.5	2.1
Aedes scutellaris	36.6	11.6	2.7
Aedes riversi	16.2	9.4	2.9
Aedes flavopictus	22.1	13.0	3.9
Aedes galloisi	14.9	29.9	3.4
Aedes pseudoalbolineatus	16.3	9.4	5.2
Average	22.9	14.8	3.2

exists even among strains within the same species (*Ae. aegypti* and *Ae. albopictus*). If multiple strains are examined for other species, similar intraspecific variation, as in *Ae. aegypti* and *Ae. albopictus*, might also be found. Despite this variation, the lengths of maxillae and mandibles of the subgenus *Stegomyia* have distinct ranges (maxillae: 0.13–0.50, mandibles: 0.04–0.17, excluding 2 unusual values). These ranges may be regarded as subgeneric attributes, although species of the *edwardsi* and *w-albus* groups in the Oriental Region (Huang 1979) and species groups of Africa (Huang 1990) have not been examined.

Compared with other subgenera of the genus Aedes examined by Marshall and Staley (1935), the subgenus Stegomyia has, on average, longer maxillae with a greater range of length (0.13–0.50) than those of the subgenera Aedes (0.06–0.09), Finlaya (0.20–0.28), and Ochlerotatus (0.20–0.28). Mandibles of males of the subgenus Stegomyia (0.04– 0.17) are more variable than those of the subgenus Finlaya (0.09–0.14), whereas mandibles were not found by these authors for subgenera Aedes and Ochlerotatus.

According to the recent new classification of the genus *Aedes*, subgenera *Stegomyia* and *Aedes* remain in the genus *Aedes*, whereas subgenera *Ochlerotatus* and *Finlaya* belong to the genus *Ochlerotatus* (Reinert 2000). Following this new system, maxillae and mandibles of males appear to be attributes that do not distinguish these genera, as is also the case of maxillary palpi of males (Reinert 2000).

Marshall and Staley (1935) reported that maxillae of species of genera *Orthopodomyia* (0.28– 0.37) and *Culex* (0.09–0.19), as well as their mandibles (*Orthopodomyia*: 0.05–0.07, *Culex*: 0.05– 0.07), are also short. On the other hand, the maxillae of species of the genera *Culiseta* (0.58– 0.94) and *Anopheles* (0.44–0.68), as well as their mandibles (*Culiseta*: 0.07–0.28, *Anopheles*: 0.38– 0.46) were distinctly longer. Other subgenera of *Aedes* and other genera in the Oriental Region are being examined to determine the taxonomic and phylogenetic significance of the mouthparts in males.

As stated by Vizzi (1953) for males of *An. quadrimaculatus,* and by Snodgrass (1959) for females of *Toxorhynchites,* delicate, short, and irregularly shaped maxillae and mandibles suggest the lack of function, at least for piercing. Much higher CV values of maxillae (14.8) and mandibles (22.9) than those of maxillary palpi (3.2) strengthen this view. Structures with function naturally are less variable than those without function, because they need to hold a fixed shape or size to carry out their function. For example, CV values calculated from the data of wing, hind femur, and scutum lengths of female *Ae. albopictus* in the laboratory (Mori 1979, Tables 5–7, 12–14) remain usually less than 5.0, although the absolute lengths vary greatly depending on nutrition and density conditions. Even for wild specimens exposed to diverse nutrition, density, and temperature conditions during larval development, CV values for body size were usually less than 20.0 for mosquitoes breeding in ground pools (Fish 1985). Thus, high variability of maxillae and mandibles of male mosquitoes supports an explanation that they exist just as functionless, vestigial structures (Downes 1970).

The positive correlation that occurs between maxillary and mandibular lengths indicates the simultaneous reduction of both organs in males. The fact that mandibles are usually shorter than maxillae might suggest that mandibles lost their function earlier than did the maxillae.

Snodgrass (1959) stated that the hypopharynx in male mosquitoes is completely fused with the labium and forms the labiohypopharynx. Christophers (1960) recognized the hypopharynx only as a ridge on the labium. On the other hand, Vizzi (1953) found the hypopharynx of *An. quadrimaculatus* to be a sclerotic plate on the labial gutter. We found the hypopharynx of males of *Stegomyia*, although it is not a free stylet, to be a structure clearly discernible from the inner wall of the labium, thus retaining evidence of its free origin. This structure is also found in the genera *Anopheles, Culex*, and *Tripteroides* (unpublished data), and is probably common to other mosquitoes as well.

Because the hypopharynx in female mosquitoes, together with other stylets, enters the host skin during bloodfeeding, the free hypopharynx clearly is correlated with their ability to suck blood. Silva and Grunewald (2000) reported that the hypopharynx of male *Lutzomyia migonei* Franca (Psychodidae) is a free stylet. Probably the earlier form of the hypopharynx of male nematoceran flies was a free stylet. Fusion of the hypopharynx of the male mosquito with the labium may have taken place after the ancestor of the mosquito separated from the sandfly's ancestor.

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