A COMPARATIVE ANALYSIS OF THE VENTRAL BRUSH AND ITS ATTACHMENT TO SEGMENT X OF FOURTH-STAGE LARVAE IN TRIBE AEDINI (DIPTERA: CULICIDAE)

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ABSTRACT. A comparative anatomical analysis of the ventral brush and its attachment to segment X of 4th-stage larvae was conducted for the genera and subgenera in tribe Aedini. Four types and 18 subtypes are recognized and examples of each are described and illustrated. A key distinguishing the types and subtypes is included. Some comments concerning the phylogenetic utility of the ventral brush are provided.

KEY WORDS Fourth-stage larva, seta 4-X, ventral brush, grid, boss, Aedini, Culicidae

INTRODUCTION

The large tribe Aedini currently includes 12 genera and 55 subgenera (Reinert 2001). Some subgenera (e.g., Finlaya Theobald and Ochlerotatus Lynch Arribalzaga of genus Ochlerotatus) include numerous diverse groups of species. These groups could be better defined if additional stable characters were employed. One feature, the ventral brush (seta 4-X) and its attachment to segment X of the 4th-stage larvae, seems to provide important information for defining taxa at the species group and higher taxonomic levels. Therefore, to better utilize this character, the structures comprising the ventral brush and its attachment to segment X are described and grouped in recognizable type, subtype, and form categories. A total of 4 types and 18 subtypes are recognized. Each of the proposed subtype categories also includes a description of the saddle (i.e., incomplete or complete ventrally) because in some of the subtypes part of the ventral brush is inserted in the ventral margin of the saddle.

MATERIALS AND METHODS

A comparative anatomical analysis of the ventral brush and its attachment to segment X of 4th-stage larvae of tribe Aedini (Culicidae: Diptera) was conducted. Species from all genera and subgenera (except subgenus *Chaetocruiomyia* Theobald) in the tribe were examined. Larvae of subgenera *Belkinius* Reinert and *Indusius* Edwards are unknown. Representatives (1–10 specimens) of approximately 38% of the currently named species (for which the 4th-stage larvae are known) in Aedini were evaluated. Fourth-stage larvae or larval exuviae mounted on microscope slides were used for the evaluation.

Figures 1-4 illustrate the different types and subtypes of the ventral brush and its attachment to segment X and the saddle (other structures, such as anal papillae, setae 1-3-X, and spicules are not shown). All precratal setae are shown on the illustrations (at least their alveoli) and only 1 seta of each pair of cratal setae is illustrated (or at least their bases when numerous setae occur). Illustrations are not drawn to the same scale.

Definitions of structures and setal types used here to characterize the ventral brush and its attachment to segment X of 4th-stage larvae are primarily those of Harbach and Knight (1980, 1982), but some are modified and others are new.

Structures

Boss = A more or less sclerotized elevated area without a defined grid located at the base of the ventral brush, but setae may possess very short to short, dark extensions at bases of alveoli and these are connected with the elevated area.

Boss seta = One of the ventral brush setae borne on a boss.

Cratal seta = One of the ventral brush setae borne on a grid.

Grid = The network of sclerotized ridges that bear the cratal setae of the ventral brush; with a transverse grid bar at the base of an individual seta; sometimes with lateral grid bars.

Lateral grid bar = One of the more or less strongly developed longitudinal sclerotizations forming the lateral margins of a grid.

Preboss seta = One of the ventral brush setae borne anterior to a boss.

Precratal seta = One of the ventral brush setae borne anterior to a grid.

Saddle = A dorsal sclerite often covering most of the dorsal and lateral surfaces of abdominal segment X; sometimes continuous ventrally.

Seta 4-X = Any seta of the ventral brush, the variable number of paired or unpaired setae arising from the ventral longitudinal midline of abdominal segment X; the most caudal (posterior) seta is designated as seta 4a-X, the next cephalad (anterior) seta as 4b-X, and so on (Belkin 1962, Knight and Laffoon 1971).

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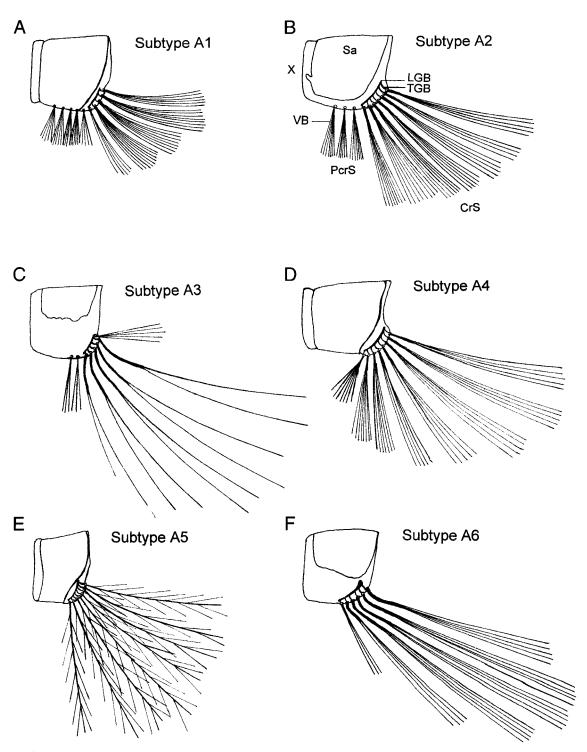


Fig. 1. Segment X of 4th-stage larvae. (A) Subtype A1, Aedes (Edwardsaedes) imprimens; (B) Subtype A2, Aedes (Aedimorphus) vexans; (C) Subtype A3, Ochlerotatus (Ochlerotatus) muelleri; (D) Subtype A4, Ochlerotatus (Ochlerotatus) scapularis; (E) Subtype A5, Aedes (Huaedes) wauensis; and (F) Subtype A6, Ochlerotatus (Finlaya) chrysolineatus. Abbreviations: CrS, cratal seta; LGB, lateral grid bar; PcrS, precratal seta; Sa, saddle; TGB, transverse grid bar; VB, ventral brush; X, segment X.

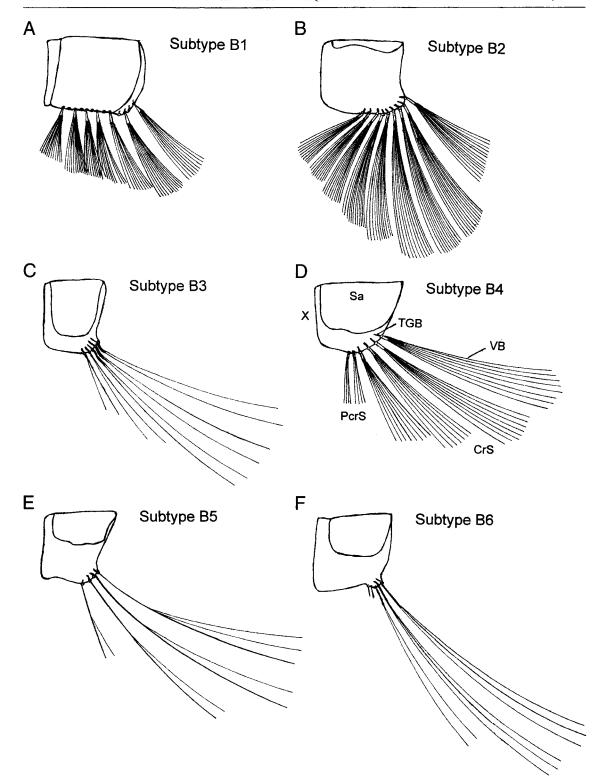


Fig. 2. Segment X of 4th-stage larvae. (A) Subtype B1, Psorophora (Psorophora) columbiae; (B) Subtype B2, Ochlerotatus (Nothoskusea) chathamicus; (C) Subtype B3, Aedes (Stegomyia) aegypti; (D) Subtype B4, Ochlerotatus (Kenknightia) dissimilis; (E) Subtype B5, Ochlerotatus (Macleaya) tremula; and (F) Subtype B6, Ayurakitia griffithi. Abbreviations: CrS, cratal seta; PcrS, precratal seta; Sa, saddle; TGB, transverse grid bar; VB, ventral brush; X, segment X.

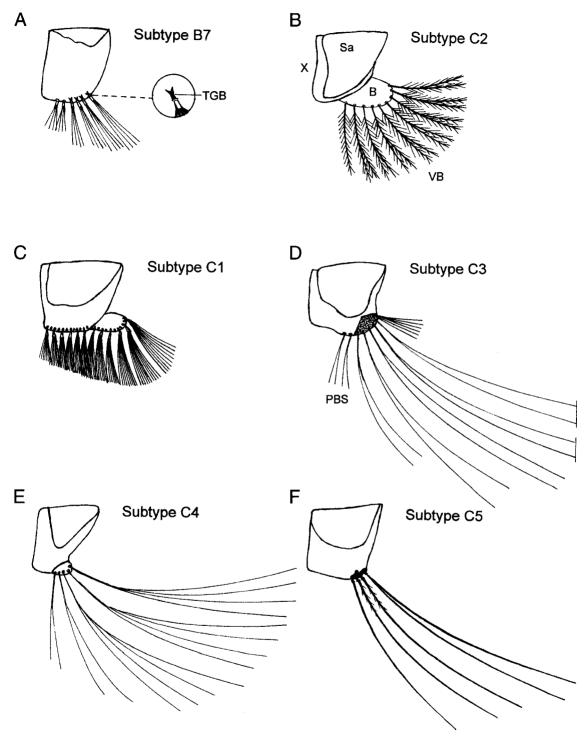


Fig. 3. Segment X of 4th-stage larvae. (A) Subtype B7, Armigeres (Armigeres) subalbatus; (B) Subtype C2, Ochlerotatus (Molpemia) pecuniosus; (C) Subtype C1, Ochlerotatus (Mucidus) laniger; (D) Subtype C3, Ochlerotatus (Kompia) purpureipes; (E) Subtype C4, Ochlerotatus (Finlaya) poicilius; and (F) Subtype C5, Eretmapodites quinquevittatus. Abbreviations: B, boss; PBS, preboss seta; Sa, saddle; TGB, transverse grid bar; VB, ventral brush; X, segment X.

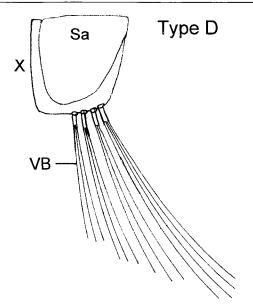


Fig. 4. Segment X of 4th-stage larva. Type D, *Aedes* (*Christophersiomyia*) *thomsoni*. Abbreviations: Sa, saddle; VB, ventral brush; and X, segment X.

Transverse grid bar = One of the transverse sclerotizations supporting the base of an individual cratal seta; sometimes joined laterally by lateral grid bars.

Ventral brush = Setae 4-X; usually a more or less linear series of irregularly paired setae borne posteroventrally on the midline of abdominal segment X; often divided into 2 groups, a posterior group of cratal/boss setae borne on a grid/boss and an anterior group of precratal/preboss setae not borne on the grid/boss.

Setal types

Aciculate = Seta furnished with slender needlelike processes along the stem; the processes are somewhat flexible but often appear to be rigid.

Bifurcated = Seta with 2 branches of equal or nearly equal length arising together, usually below the distal third, commonly at the base.

Branched = Seta with branches radiating from or near the base, originating as divisions of the main stem or arising along the length of the main stem. **Fanlike** = Seta with branches spreading out in a single plane from a short or moderately long stem. **Forked** = Seta with a few branches arising beyond the basal third of the main stem.

Pectinate = Seta with long branches arising at regular intervals from 1 side of the main stem; a few small, sparsely arranged branches may arise from the opposite side.

Plumose = Seta with numerous usually regularly arranged branches arising on either side of the main stem; the branches on either side may be directly opposite one another or alternate.

Simple = Seta without lateral or apical processes. **Single** = Seta unbranched; simple or aciculate.

The different types and subtypes of the ventral brush that I have recognized are described below. Some subtypes may have more than 1 form. An attempt was made to describe all types and subtypes and most forms of the ventral brush of Aedini; however, because all species of the tribe were not available for examination, some additional forms may exist. One or more examples of species possessing each type, subtype, and form are listed. Type and subtype categories are determined 1st by the point of attachment of the setae in the ventral brush (e.g., to a grid, to a boss, or neither), next by the development of the grid (e.g., both transverse and lateral grid bars or only transverse grid bars) or boss (e.g., large, medium, or small), and then by the placement and development of the setae of the ventral brush (e.g., cratal/boss, precratal/preboss, single, multiple branched, plumose, stems short, moderately long or long, and so on).

A key that distinguishes the types and subtypes is provided. Lengths and sizes of structures (e.g., stems of setae, size of boss) used in the key and descriptions can be seen in Figs. 1–4.

TYPES, SUBTYPES, AND FORMS OF VENTRAL BRUSH AND ITS ATTACHMENT TO SEGMENT X

Type A

Ventral brush with all or most setae attached to a grid composed of both transverse and lateral grid bars.

Subtype A1: Five to 9 pairs of cratal setae, moderately long, and fanlike with short stems bearing multiple (5–12) branches. Anterior pair of cratal setae often with only transverse grid bars, whereas remainder of cratal setae with both transverse and lateral grid bars. Several (normally 4–8, occasionally 2,3) precratal, shorter setae bearing 4–11 branches and inserted ventrally in a row on midline of saddle. Ventral brush with total of 10–25 setae. Saddle complete ventrally. Examples: Aedes (Edwardsaedes) imprimens (Walker) (Fig. 1A), Ochlerotatus (Ochlerotatus) mcdonaldi (Belkin).

Subtype A2: Five to 11 pairs (rarely 4 pairs) of cratal setae, moderately long or long, and fanlike with short or moderately long stems bearing multiple (2–20, usually 3–14) branches. Few to numerous (2–12, usually 2–5) precratal setae, each bifurcate or normally multiple-branched (3–11), fanlike, and attached more or less in line ventrally on midline of segment X. Ventral brush with total of 10–29 setae. Saddle complete or incomplete ventrally but often large and covering dorsal and much of lateral surfaces of segment X.

Form 1. Ventral brush with posterior pair (4a-X) of cratal setae long. Saddle incomplete ventrally. Examples: Aedes (Aedimorphus) vexans (Meigen)

(Fig. 1B), Ochlerotatus (Ochlerotatus) excrucians (Walker), Ochlerotatus (Mucidus) painei (Knight).

Form 2. Ventral brush with posterior pair (4a-X) of cratal setae short with 6–8 branches. Saddle incomplete ventrally. Examples: Ochlerotatus (Finlaya) biocellatus (Taylor), Ochlerotatus (Finlaya) australiensis (Theobald).

Form 3. Ventral brush with posterior pair (4a-X) of setae long. Saddle complete ventrally. Examples: Ochlerotatus (Ochlerotatus) atlanticus (Dyar and Knab), Ochlerotatus (Ochlerotatus) fulvus pallens (Ross).

Subtype A3: Five or 6 pairs of long cratal setae with long stems bearing few (2–7, usually 2,3) branches. Few (2–4, usually 2) short precratal setae, each with few (2–5, usually 2,3) branches. Ventral brush with total of 12–14 setae. Saddle incomplete ventrally.

Form 1. Posterior pair of setae (4a-X) short and with short stems bearing 3-5 branches. Example: Ochlerotatus (Ochlerotatus) muelleri (Dyar) (Fig. 1C).

Form 2. Posterior pair of setae (4a-X) moderately long or long, and with long stems bearing 2-5 branches. Example: *Ochlerotatus* (Finlaya) geniculatus (Olivier).

Subtype A4: Five to 10 pairs of cratal setae, moderately long or long, fanlike, with short or moderately long stems bearing multiple (3–14, usually 5–14) branches, posterior setae long whereas anterior setae shorter. Precratal setae absent (few species with some specimens with 1 seta near grid anteriorly and without grid bar). Ventral brush with total of 10–21 setae. Saddle complete or incomplete ventrally

Form 1. Lateral grid bar thin. Saddle complete ventrally. Examples: Ochlerotatus (Ochlerotatus) scapularis (Rondani) (Fig. 1D), Ochlerotatus (Ochlerotatus) sollicitans (Walker).

Form 2. Lateral grid bar strongly developed and wide, especially posterior portion. Saddle incomplete ventrally. Examples: *Ochlerotatus (Finlaya) hatorii* (Yamada), *Ochlerotatus (Finlaya) macfarlanei* Edwards.

Subtype A5: Seven or 8 pairs of long, strongly plumose, cratal setae; those at midlength of grid longer than those on anterior and posterior areas. Precratal setae absent. Ventral brush with total of 14–16 setae. Saddle complete ventrally. Example: Aedes (Huaedes) wauensis Huang (Fig. 1E).

Subtype A6: Six or 7 pairs of long cratal setae, several of posterior setae with long stems bearing few (2–7, usually 3,4) long branches. Precratal setae absent. Ventral brush with total of 12–14 setae. Saddle incomplete ventrally. Examples: Ochlerotatus (Finlaya) chrysolineatus (Theobald) (Fig. 1F), Ochlerotatus (Finlaya) notoscriptus (Skuse).

Type B

Ventral brush with all or many setae attached to a grid composed of transverse grid bars. Lateral grid bars absent. Subtype B1: Grid weakly developed, with transverse bars very short or short, and attached to 6–12 cratal setae. Cratal setae more or less paired in irregular line posterior to saddle, moderately long, fanlike, with short stems usually bearing 8–12 (range 6–15) branches. Numerous (7–13) precratal setae inserted in line along most of ventral midline of saddle, setae shorter, and fanlike with short stems and bearing multiple (5–14) branches. Ventral brush with total of 16–25 setae. Saddle complete ventrally. Examples: Psorophora (Grabhamia) columbiae (Dyar and Knab) (Fig. 2A), Psorophora (Janthinosoma) ferox (Von Humbolt).

Subtype B2: Grid with dark, moderately long, slender, transverse grid bars. Nine pairs of long, 8–15 (usually 10–13) branched, fanlike, cratal setae with short stems and with few anterior and 1 posterior pair of setae shorter. Precratal setae absent. Ventral brush with total of 18 setae. Saddle incomplete ventrally. Example: Ochlerotatus (Nothoskusea) chathamicus (Dumbleton) (Fig. 2B).

Subtype B3: Grid with dark, elongate, slender, transverse bars. Four or 5 pairs of cratal setae, single, bifurcated or with few (3–5, usually 3,4) branches at base or at apex of short stem, and simple or aciculate. Precratal setae absent. Posterior setae long whereas anterior setae shorter. Ventral brush with total of 8–10 setae. Saddle complete or incomplete ventrally.

Form 1. Saddle complete ventrally. Example: *Aedes (Stegomyia) tongae* Edwards.

Form 2. Saddle incomplete ventrally. Examples: Aedes (Stegomyia) aegypti (Linnaeus) (Fig. 2C), Heizmannia (Mattinglyia) achaetae (Leicester).

Subtype B4: Grid with dark, moderately long, slender, transverse bars. Three to 5 pairs of long cratal setae with short or moderately long stems, each single or bearing 2–12 (usually 2–5) long branches. Few (2, rarely 1) shorter, precratal setae, single or with 2–11 (usually 2–5) branches. Ventral brush with total of 8–10 setae. Saddle incomplete ventrally. Examples: Ochlerotatus (Finlaya) ingrami (Edwards), Ochlerotatus (Kenknightia) dissimilis (Leicester) (Fig. 2D).

Subtype B5: Grid with weakly developed, very short to short, slender, transverse bars. Four pairs of moderately long, single to 3-branched, cratal setae with long stems. Precratal setae absent. Ventral brush with total of 8 setae. Saddle incomplete ventrally. Example: Ochlerotatus (Macleaya) tremula (Theobald) (Fig. 2E).

Subtype B6: Grid with dark, moderately long, slender, transverse bars. Two pairs (rarely with 3 pairs) of very long cratal setae with short stems bearing few (2–4) branches. Precratal setae consisting of 1 or 2 moderately long, single to 3-branched setae next to cratal setae and 1 or 2 very short, slender, single or 2-branched setae anteriorly. Ventral brush normally with 6 or 7 (range 6–8) total setae. Saddle incomplete ventrally. Example: Ayurakitia griffithi Thurman (Fig. 2F).

Subtype B7: Grid with dark, very short or short, relatively thick, transverse grid bars with terminal ends forked. Normally 5 pairs of relatively short or moderately long cratal setae with short stems usually bearing 2–5 (range 2–14) branches, inserted in more or less irregular line. Setae attached to transverse grid bars except for few (2,3) anterior precratal setae. Ventral brush normally with 10 (rarely 11,12) total setae. Saddle small and incomplete ventrally. Examples: Armigeres (Armigeres) subalbatus (Coquillett) (Fig. 3A), Armigeres (Leicesteria) dentatus Barraud.

Type C

Ventral brush with all or most setae attached to a sclerotized boss.

Subtype C1: Boss large, composed of moderately pigmented and sclerotized, elongate, somewhat oval-shaped structure borne posteroventrally and projecting caudally from segment X. Numerous (14–22) moderately long setae inserted in row midventrally on boss. Usually 11–16 (range 6–16) preboss setae, most somewhat shorter, and inserted in a row along ventral midline of segment X. Ventral brush with total of 22–36 setae, each multiplebranched, fanlike, and with short stem. All setae each with short, dark, sclerotized extension at base of alveolus. Saddle incomplete ventrally. Examples: Ochlerotatus (Mucidus) laniger (Weidemman) (Fig. 3C), Ochlerotatus (Mucidus) quasiferinus (Mattingly).

Subtype C2: Boss exceptionally large, composed of heavily pigmented and sclerotized, more or less oval-shaped structure borne posteroventrally from segment X, and with most of structure projecting caudally. Numerous (15–19) setae, single or 2,3-forked, stout, dark, strongly aciculate to plumose, and inserted in slightly irregular row along ventral and posterior midline of boss. With or without 3 or 4 preboss setae. Ventral brush with total of 17–22 setae. Saddle incomplete ventrally but large and covering dorsal and most of lateral surfaces of segment X. Examples: Ochlerotatus (Molpemyia) auridorsum (Edwards), Ochlerotatus (Molpemyia) pecuniosus (Edwards) (Fig. 3B).

Subtype C3: Boss medium, composed of pair of heavily pigmented and sclerotized, more or less triangular or oval structures. Setae attached along ventral midline of boss. With or without 1 or 2 shorter, preboss setae. Ventral brush with 5–8 pairs of setae, each single, bifurcated or with few (3–6, usually 3,4) branches, and normally long on middle area, shorter on anterior area, and some species with short, posterior pair. Saddle incomplete ventrally.

Form 1. Ventral brush with 5 or 6 pairs of setae with short to moderately long stems bearing 2-6 branches, setae long except anterior pair shorter. Examples: *Haemagogus* (*Haemagogus*) splendens

Williston, Ochlerotatus (Gymnometopa) mediovittatus (Coquillett).

Form 2. Ventral brush with 5–8 pairs of setae, single or 2-branched with long stems, setae long except anterior pair shorter and posterior pair (4a-X) short and single or with 4–15 branches. Examples: Ochlerotatus (Aztecaedes) ramirezi (Vargas and Downs), Ochlerotatus (Kompia) purpureipes (Aitken) (Fig. 3D).

Subtype C4: Boss medium, composed of pair of lightly (often) to moderately (occasionally) pigmented and sclerotized, more or less triangular structures on posteroventral area of segment X. Normally 5 pairs of setae attached to ventral margin of boss, each with heavily pigmented alveolus and long, slender stem bearing few to several (3–7, usually 4,5) long branches, often slightly pectinate at point of branching. Ventral brush with total of 10 setae, posterior setae long whereas anterior setae shorter. Boss may be very lightly pigmented and shape difficult to distinguish in some larval exuviae. Saddle incomplete ventrally. Examples: Ochlerotatus (Finlaya) neogeorgianus (Belkin), Ochlerotatus (Finlaya) poicilius (Theobald) (Fig. 3E).

Subtype C5: Boss small, composed of pair of small, heavily pigmented and sclerotized, relatively narrow, more or less elongate structures on each side of ventroposterior area of segment X. Structures bearing 4–6 pairs of stout, dark, single to 3-branched setae ventrally, most with very short, dark, sclerotized extension at base of alveolus. With or without 2 shorter preboss setae bearing 2 or 3 branches. Ventral brush with total of 8–12 setae, normally long except anterior pair sometimes shorter. Saddle incomplete ventrally. Examples: Eretmapodites quinquevittatus Theobald (Fig. 3F), Aedes (Alanstonea) brevitibia (Edwards).

Type D

Ventral brush with setae arranged in irregular row with grid and boss absent. Six to 8 moderately long setae normally bearing 2-4 (range 2-7) branches on short, stout stems, inserted in an irregular row on midventral area ventroposterior to large saddle. Saddle incomplete ventrally. Examples: Aedes (Christophersiomyia) ibis Barraud, Aedes (Christophersiomyia) thomsoni (Theobald) (Fig. 4).

KEY TO TYPES AND SUBTYPES

1	Ventral brush with all or many setae at-
	tached to a grid or a boss 2
_	Ventral brush with setae not attached to a
	grid or a boss Type D
2(1)	Ventral brush with all or many setae at-
	tached to a grid
-	Ventral brush with all or most setae at-
	tached to a boss (Type C) 15
3(2)	Grid with both transverse and lateral grid
	bars (Type A)

_	Grid with only transverse grid bars (Type
	B) 9
4(3)	Precratal setae absent 5
_	Precratal setae present (2 or more) 7
5(4)	Setae of ventral brush strongly plumose;
	anterior pair of setae approximately same
	length as remainder of setae Subtype A5
_	Setae of ventral brush with simple branch-
	es; anterior pair of setae noticeably shorter
	than remainder of setae
6(5)	Setae with short to moderately long stems
- (-)	Subtype A4
_	Setae with long stems Subtype A6
7(4)	Precratal setae inserted ventrally on mid-
,(1)	line of saddle; saddle complete ventrally
	Subtype A1
	Precratal setae not inserted on saddle; sad-
_	•
0(7)	dle incomplete ventrally 8
8(7)	Cratal setae moderately long to long, with
	short to moderately long stems, usually
	multiple branched Subtype A2
_	Cratal setae long, with long stems, usually
	with few branches, some species with pos-
	terior pair (4a-X) of setae short Subtype A3
9(3)	Precratal setae numerous (7-13) and in-
	serted along ventral margin of saddle
	Subtype B1
_	Precratal setae absent or only 1-3, not at-
	tached to saddle 10
10(9)	One to 3 precratal setae
_	Precratal setae absent
11(10)	Grid with very short or short, relatively
11(10)	thick, transverse grid bars with terminal
	ends forked; cratal setae relatively short to
	moderately long Subtype B7
	Grid with moderately long, slender, trans-
_	
	verse grid bars with terminal ends single;
	all or most of cratal setae long or very
10/11)	long
12(11)	Two (rarely 3) pairs of very long cratal
	setae; anterior 1 or 2 precratal setae very
	short; ventral brush with 6 or 7 (rarely 8)
	total setae Subtype B6
_	Three to 5 pairs of moderately long cratal
	setae; precratal setae short to moderately
	long; ventral brush with 8-10 total setae
	Subtype B4
13(10)	Ventral brush setae with long stems; trans-
	verse grid bars very short to short and
	weakly developed Subtype B5
	Ventral brush setae with short stems;
-	transverse grid bars moderately long to
_	transverse grid bars moderately long to long and well developed
14(13)	transverse grid bars moderately long to long and well developed
14(13)	transverse grid bars moderately long to long and well developed
14(13)	transverse grid bars moderately long to long and well developed
- 14(13) -	transverse grid bars moderately long to long and well developed
14(13) -	transverse grid bars moderately long to long and well developed
14(13) -	transverse grid bars moderately long to long and well developed
14(13) - 15(2)	transverse grid bars moderately long to long and well developed
_	transverse grid bars moderately long to long and well developed

	projecting caudally from segment X; ven-
	tral brush composed of 17–36 setae 16
_	Boss medium or small, more or less tri-
	angular or relatively narrow and elongate,
	situated on ventroposterior area of seg-
	ment X; ventral brush composed of 8-16
	setae
16(15)	Boss large; ventral brush setae each mul-
	tiple branched, fanlike, and with short
	stem Subtype C1
_	Boss exceptionally large; ventral brush se-
	tae single or 2,3-forked, stout, strongly
	aciculate to plumose Subtype C2
17(15)	Boss small, composed of pair of relatively
	narrow, more or less elongate structures
	Subtype C5
_	Boss medium, composed of pair of more
	or less triangular or oval structures 18
18(17)	Boss heavily pigmented and sclerotized;
	setae each with alveolus normal, most or
	all attached to boss, and nonpectinate
	Subtype C3
_	Boss often lightly but may be moderately
	pigmented and sclerotized; setae each
	with heavily pigmented alveolus, all at-
	tached to boss, and often slightly pectinate
	Subtype C4
	- 1

DISCUSSION

Aedine 4th-stage larvae inhabiting water in ground pools (e.g., roadside barrow ditches, flooded pastures, forest pools, and so on) normally have the ventral brush and grid well developed, that is, the ventral brush is composed of several to numerous multiple branched, fanlike, cratal setae on a grid with both distinct transverse and lateral grid bars. These larvae also frequently possess several multiple-branched, shorter, precratal setae. Fourth-stage larvae that inhabit water in plant containers (e.g., tree holes, leaf axils, cut bamboo internodes, and so on) and rock holes and artificial containers containing organic debris normally have the ventral brush poorly developed and the grid poorly developed or absent, that is, the ventral brush is usually composed of a few to several setae that are single. bifurcated, or with few branches attached only to transverse grid bars (often these are poorly developed) or to the posteroventral margin of segment X (i.e., *Christophersiomyia*), whereas other groups have the setae attached to grids that also have weakly or partially developed lateral grid bars.

Belkin (1962: 47) classified mosquitoes into 2 principal categories based on sites of the immatures: species inhabitating ground-water habitats, and species inhabiting water in plant-container habitats. He considered ground-water habitats as undoubtedly the primitive breeding sites of Culicidae and plant-container habitats as derived. Aedine species with well-developed ventral brushes (e.g., Sub-

type A1) normally inhabit ground-water habitats, and the strong development of the brush seems to be the more ancestral condition. On the other hand, species with weakly developed ventral brushes (e.g., Subtype B6) inhabit water in plant containers, and the brush seems to be the more derived condition.

Based on the type of ventral brush, its attachment to segment X, and the development of the saddle, the plesiomorphic form seems to be a ventral brush consisting of numerous, multiple-branched setae with short, stout stems attached to a well-developed grid (both transverse and lateral grid bars) and with numerous precratal, multiple-branched setae with short stems, inserted on the ventral midline of a saddle that completely encircles segment X. Conversely, the apomorphic condition is a ventral brush with a few, single, simple setae on a poorly developed grid with only transverse grid bars, without precratal setae, and with a small saddle incomplete ventrally. However, the condition of the ventral brush in Type D, in which both the grid and boss are absent, could represent the most derived state because a similar condition occurs in most sabethines (see discussion in Harbach and Kitching 1998: 335) except the ventral brush in this group is restricted to a single pair of setae.

Within a similar larval habitat (e.g., freshwater ground pools), species of more than 1 phyletic line of Aedini may be found and seem to have some structures (e.g., multiple precratal/preboss setae with branches arising from a short stem and inserted in a row) that are similar in development (e.g., Ae. (Edw.) imprimens, Subtype A1; Ps. (Gra.) columbiae, Subtype B1; and Oc. (Muc.) laniger, Subtype C1), but have others that differ (e.g., cratal/ boss setae attached to a grid with both lateral and transverse bars [Subtype A1]; grid with only transverse bars [Subtype B1]; and to a boss [Subtype C1]). Within a subtype (e.g., Subtype A2, Form 1; Ae. (Adm.) vexans, Oc. (Och.) excrucians, and Oc. (Muc.) painei) of a type category (e.g., Type A) convergence of characters seems to have taken place because species in different phyletic lines have similarly developed structures. However, related species apparently can be grouped together based on the named types and subtypes proposed here for those species groups, subgenera, and genera that have been thoroughly studied taxonomically. Conversely, some other large polyphyletic groups (e.g., subgenera Finlaya and Ochlerotatus) seem to require additional taxonomic revision.

Additional general comments concerning the ventral brush and its development and attachment to segment X follow.

Species that have a well-developed lateral grid bar in the 4th-stage larva may have this structure absent or weakly developed in the 3rd-stage larva.

In Types A and B, the cratal setae are usually paired but some specimens may have an odd number of cratal setae. Also, some species may have the cratal setae in a slightly irregular line (e.g., species of genus *Psorophora* Robineau-Desvoidy). The setae on the boss of Type C are more or less paired except for species in Subtypes C1 and C2, in which they are in a row.

The structure comprising the boss seems to have developed from an enlargement of the lateral grid bars. Evidence for this is found in species in which the lateral grid bars are thickened and wider (Subtype A4, Form 2); however, the transverse grid bars are long and well developed. Also, species of Subtype C5 have a small boss composed of a pair of small, heavily pigmented and sclerotized, relatively narrow, more or less elongate structures on the posteroventral area of segment X, and most of the setae bear a very short, dark, sclerotized extension at the base of the alveolus.

The boss in Type C may serve as a strengthening framework for the ventral brush and assist the larva in moving through the water. For example, the very large boss of *Oc. (Mol.) pecuniosus* larvae may provide an advantage in moving through foul and particle-laden water in tree holes.

A small, moderately pigmented, oval structure located dorsally and about midlength of the cratal area was noted in many specimens of *Psorophora* (*Psorophora*) howardii Coquillett. This structure is attached to the apices of a few of the short transverse grid bars and may represent rudimentary lateral grid bars or a boss; however, it is developed differently than in the other species possessing lateral grid bars or a boss.

Within Aedini, the ventral brush of species without either a grid or boss (Type D) was noted in only the plant-container breeding subgenus *Christophersiomyia* of genus *Aedes* (4 species examined). Previously, because of the availability at that time of only 2 damaged larval exuviae of 1 species of *Christophersiomyia*, Reinert (2000) reported that the ventral brush was attached to a weakly developed grid in this subgenus.

A few exceptions to the normal condition of the ventral brush were noted in some taxonomic categories (e.g., subgenera, genera) as follow. Hopkins (1952) reported 4 or 5 pairs of setae in *Eretmapodites pauliani* Grjebine. All species of *Eretmapodites* that I have examined have 4 pairs of setae but I have not seen larvae of *Er. pauliani*. Species of genus *Armigeres* normally have the ventral brush with 10 setae but *Armigeres magnus* (Theobald) has 12. In Subtype B3 the lateral grid bars are absent, but occasionally a specimen was found in which the posterior 2 pairs of setae were connected with short, thin, sclerotized bars.

While reviewing the literature, I found that not all illustrations of the ventral brush, and especially the development of the grid or boss of segment X, were drawn correctly. Specimens need to be carefully examined to insure that published illustrations are accurate.

Based on the present study, the ventral brush

should provide support, when used in combination with other characters, in defining taxa, especially categories within large polyphyletic subgenera and genera.

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