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NEW CLASSIFICATION FOR THE COMPOSITE GENUS *AEDES* (DIPTERA: CULICIDAE: AEDINI), ELEVATION OF SUBGENUS *OCHLEROTATUS* TO GENERIC RANK, RECLASSIFICATION OF THE OTHER SUBGENERA, AND NOTES ON CERTAIN SUBGENERA AND SPECIES

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ABSTRACT. The composite genus *Aedes* is divided into 2 genera, *Aedes* and *Ochlerotatus*, on the basis of consistent primary characters of the female and male genitalia. *Ochlerotatus* is separated into 2 sections. Additional supplemental features of the female and male genitalia, 4th-stage larvae, and pupae are provided for the separation of the genera and sections as well as a discussion of exceptions and comparisons. This classification is based on a morphological examination of specimens of over 65% of the currently recognized species and all subgenera previously included in *Aedes* and representative material of all subgenera and genera of tribe Aedini. Published literature was examined and evaluated. All currently recognized subgenera are assigned to the appropriate genus. The proposed new generic classification provides better defined genera and a more natural arrangement of included taxa. Armigerini is formally recognized as a synonym, in part, of Aedini.

KEY WORDS *Aedes, Ochlerotatus,* Aedini, Armigerini, taxonomy

INTRODUCTION

The original description of *Aedes* by Meigen (1818), written in German and also in Latin, was very brief and included a single species, *Aedes cinereus* Meigen. A translation to English, provided by the late George C. Steyskal, Gainesville, FL, of the description follows: antennae extending forward, filiform, 14-segmented, in male long plumose, in female bristly; proboscis extending forward, as long as dorsum of thorax; palpi very short; wings scaly, lying down. Christophers (1960) discussed the history and rationale for not using the diaeresis in the generic name *Aedes*; also, this is covered by Article 27 of the *International Code of Zoological Nomenclature.*

Investigators who have examined *Aedes* have consistently recognized that it was heterogeneous. Typical comments concerning the genus are ". . . its internal classification is in great need of revision" (Belkin 1962), "A polymorphic genus; most characters extremely variable" (Tanaka et al. 1979), and "A very large heterogeneous genus in which subgenera, or species groups within major subgenera, are far more readily characterized than the genus itself" (Lee et al. 1982). Mattingly (1971) in his keys to the life stages of mosquito genera of the world, noted numerous exceptions in genus *Aedes.* Harbach and Kitching (1998) in their phylogeny and classification of Culicidae discussed the problematic nature of the genus. As a result of its heterogeneous nature, *Aedes* has been difficult to define and was often characterized by a combination of characters or the lack of characters as typified by the statement of Hopkins (1952): "This very large genus has larvae which are distinguished more by the absence of peculiar characters than by their presence." This has resulted in a generic level taxon that is poorly defined, generally without definitive features, and undoubtedly heterogeneous. Recent actions (Reinert 1999c, 2000b, 2000c) have partially remedied this by removing several groups from the genus (i.e., *Ayurakitia* Thurman and *Verrallina* Theobald were restored to generic rank, and *Sinoaedes* Gong and Lu was placed in synonymy with subgenus *Mattinglyia* Lien of *Heizmannia* Ludlow).

The 1st comprehensive treatment of *Aedes* was published by Edwards (1932). He included 24 subgenera in the genus, most of which had previously been treated as genera. Edwards' definition of *Aedes* contained many characters that were variable and few that were constant. Subsequent authors have followed his arrangement of the genus and subgenera, but with some modification.

Edwards (1932, 1941) indicated that *Aedes* could be divided into numerous subgenera primarily on the basis of the structure of the male genitalia and the form of the male maxillary palpus. He divided the subgenera into 2 main groups. The 1st group was defined primarily by the male genitalia having claspettes present, arising from the basosternal area of the gonocoxite and normally in the form of a fingerlike process bearing a hooked filament apically, and a phallosome that was undivided, scoop-shaped, and without teeth. The 2nd group possessed male genitalia with structures corresponding to the

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claspettes but in the form of a hairy basal lobe or plaque, never as a fingerlike process with a hooked appendage, and a phallosome that was divided into lateral plates that were variously toothed. Edwards (1941) stated, however, that "Some small and anomalous subgenera do not fit easily into either of these groups . . . ."

Belkin (1962) proposed a division of the genus on characters of the male genitalia (i.e., proctiger with cercal setae present or absent and the aedeagus simple or complex) and the 4th-stage larvae with seta 12-I present or absent. His study was based principally on material from the South Pacific area and included 12 subgenera of *Aedes* and 2 other genera of Aedini. He recognized that the genus must be studied on a worldwide basis before it could be truly evaluated, understood, and possibly reorganized.

Even though *Aedes* has not been evaluated on a worldwide basis since Edwards (1932), considerable work has been done on the included subgenera. Much of this work benefited from the works of Belkin (1951, 1952, 1953, 1962) in which the stability of the chaetotaxy of the 4th-stage larva and pupa was established and its taxonomic importance was demonstrated. In 1962, Belkin set a new standard for providing detailed descriptions and illustrations of the life stages of subgenera included in *Aedes*. Following this format, numerous revisionary studies of subgenera have been published, such as Marks (1962, 1964) (*Chaetocruiomyia* Theobald); Belkin (1968) (*Nothoskusea* Dumbleton); Knight (1968) (*Finlaya* Theobald, in part); Huang (1968) (*Huaedes* Huang), (1972, 1977, 1979, 1990, 1997) (*Stegomyia* Theobald); Berlin (1969) (*Howardina* Theobald); Zavortink (1970) (*Abraedes* Zavortink), (1972) (*Abraedes, Aztecaedes* Zavortink, *Gymnometopa* Coquillett, *Kompia* Aitken, and *Protomacleaya* Theobald); Schick (1970) (*Protomacleaya,* in part); Reinert (1970, 1973b) (*Diceromyia* Theobald), (1973a) (*Aedimorphus* Theobald), (1973c) (*Bothaella* Reinert), (1976a) (*Edwardsaedes* Belkin and *Indusius* Edwards), (1976b) (*Rhinoskusea* Edwards), (1979) (*Isoaedes* Reinert), (1981) (*Paraedes* Edwards), (1982a) (*Belkinius* Reinert), (1985) (*Scutomyia* Theobald), (1986) (*Albuginosus* Reinert), (1990) (*Kenknightia* Reinert), (1993) (*Molpemyia* Theobald), (1999a) (*Rusticoidus* Shevchenko and Prudkina), (1999b) (*Zavortinkius* Reinert), (2000a) (*Fredwardsius* Reinert); Tyson (1970) (*Mucidus* Theobald); Arnell and Nielsen (1972) (*Ochlerotatus* Lynch Arribalzaga, in part); Arnell (1976) (*Ochlerotatus,* in part); Abercrombie (1977) (*Christophersiomyia* Barraud); and Tanaka et al. (1979) (*Aedes* Meigen, in part; *Finlaya,* in part; *Ochlerotatus,* in part; *Stegomyia,* in part). Additional stability in the nomenclature of all life stages of Culicidae has resulted from the publication *Taxonomists' Glossary of Mosquito Anatomy* by Harbach and Knight (1980, 1982) and its precursory parts published in *Mosquito Systematics Newsletter* and *Mosquito Systematics* between 1970 and 1978 by these authors and the late Jean L. Laffoon.

MATERIALS AND METHODS

During the last 30 plus years, I have had the opportunity to examine the morphology of specimens of all the 43 currently recognized subgenera of *Aedes* and the 10 other genera of Aedini (i.e., *Armigeres* Theobald,[2] *Ayurakitia, Eretmapodites* Theobald, *Haemagogus* Williston, *Heizmannia, Opifex* Hutton, *Psorophora* Robineau-Desvoidy, *Udaya* Thurman, *Verrallina,* and *Zeugnomyia* Leicester). I have studied all life stages where available but have devoted special attention to a study of the female genitalia of the subgenera and genera of the tribe. I am convinced that the structures of the female genitalia offer some of the best characters for partitioning generic, subgeneric, and group level taxa. In several pending papers, I will treat these structures in detail. The male genitalia also have been extensively studied and offer outstanding characters for grouping similar taxa of Aedini at all levels. Characters described for the male genitalia are in the prerotation sense. Now that the 4th-stage larvae of more species have been accurately described and illustrated in detail it has become evident that this stage presents a wealth of characters not only for distinguishing species but also for organizing and defining higher level taxa. The pupal and egg stages have not received thorough evaluations, but as more species in various groups, subgenera, and genera are described and illustrated, character trends are emerging. Unfortunately, worldwide, a considerable number of species in Aedini still have not been adequately described and illustrated in all stages.

Illustrations showing examples of the primary and supplemental characters used below to distinguish the 2 genera and the 2 sections of *Ochlerotatus* can be seen in Figs. 1–4. Parts A–C of Fig. 1 are original. Other figures are electronically modified and reconfigured from those in the following publications: Figs. 1E, 2A, 2B, and 4C, 4D from Zavortink (1972); Figs. 2E–2I and 3A–3C, 3E, 3F from Reinert (1973a); Figs. 3H, 3I from Reinert

[2] Li and Lu (1997:280–281) removed *Armigeres* from Aedini and placed it in a new monogeneric tribe, Armigerini. However, I believe *Armigeres* should be retained in Aedini because the new tribe is not equivalent in rank relative to other tribes of Culicidae and the characters given by Li and Lu (page 281) to define Armigerini are similar to members of other genera of Aedini (e.g., male genitalia with the gonostylus having multiple gonostylar claws in a row also is found in numerous species of subgenus *Aedimorphus* of *Aedes*; and the larval siphon without a pecten also is found in several species of *Eretmapodites*). Therefore, Armigerini is hereby formally recognized as a synonym, in part, of Aedini.

(1976a); Figs. 1D, 2C, 2D, and 4A, 4B from Arnell (1976); Fig. 3G from Reinert (1981); Fig. 3J from Reinert (1982a); and Fig. 3D from Reinert (1993). Figures are not drawn to the same scale.

TAXONOMIC ACTIONS

On the basis of my examination of the morphology of over 65% of the currently recognized species (Knight and Stone 1977; Knight 1978; Ward 1984, 1992) and all subgenera previously included in *Aedes,* representative material of all subgenera and genera of Aedini, and the published literature, I hereby propose the division of the composite genus *Aedes* into 2 genera, *Aedes* Meigen and *Ochlerotatus* Lynch Arribalzaga, and the latter genus into 2 sections. This action necessitates the restoration of *Ochlerotatus* to generic rank. The divisions are based on consistent primary features of the female and male genitalia, and supplemental features of the female and male genitalia, 4th-stage larvae, and one pupal character. No apparent consistent differences in adult habitus were noted for the 2 genera.

I do not lightly undertake the division of genus *Aedes* because many of the species transferred to genus *Ochlerotatus* are vectors of disease pathogens, have medical and veterinary importance, and have long been known as *Aedes.* However, I believe the creation of more natural and better defined genera are valid reasons for proposing this change and outweigh the initial inconvenience of the generic change of the affected species. Fortunately, the transfer of numerous species from *Aedes* (masculine) to *Ochlerotatus* (masculine) does not result in changing the gender of the species names (*International Code of Zoological Nomenclature,* Article 31b). The proposed 2-letter abbreviation is *Oc.* for *Ochlerotatus,* and *Ae.* remains the same for *Aedes.* Three-letter abbreviations used for subgenera follow Reinert (1975, 1982b, 1992).

Primary characters defining the genera

Genus Aedes: Female genitalia have the insula tonguelike and without setae (Fig. 1C); male genitalia have the proctiger without setae (Fig. 2E) and the phallosome has the aedeagus consisting of 2 lateral plates that usually bear teeth laterally and/or apically (Figs. 2E, 2F, 2I, 2J).

Genus Ochlerotatus: Female genitalia have the insula liplike and bearing well developed setae laterally (Figs. 1A, 1B); male genitalia have the proctiger bearing cercal setae that are tiny and all the same size (Figs. 2A, 2C), and the phallosome has the aedeagus simple and scooplike, troughlike, or tubelike (Figs. 2A, 2C).

Supplemental features supporting the partition of the genera

Genus Aedes: Female genitalia have the insula usually with a few tiny tuberculi (often each bearing a minute to small spicule) that are situated more or less medially (Fig. 1C); male genitalia have the claspette developed as a basal mesal lobe bearing setae (Figs. 2E, 2G, 2H) or otherwise developed, but not developed as a single, elongate, columnar stem with a terminal bladelike filament, and have the gonostylus variously developed (Figs. 2E and 3E–3J) (e.g., with distal portion expanded, or bifurcated, or trifurcated, or with rows or patches of short stout spicules, or with more than 1 gonostylar claw, or without a gonostylar claw); and 4th-stage larvae have seta 12-I absent (Fig. 3B), the ventral brush (seta 4-X) is borne on a grid (some groups also may have a few precratal setae) (Fig. 3C), and seta 4-M is normally branched (Fig. 3A) (single in some species).

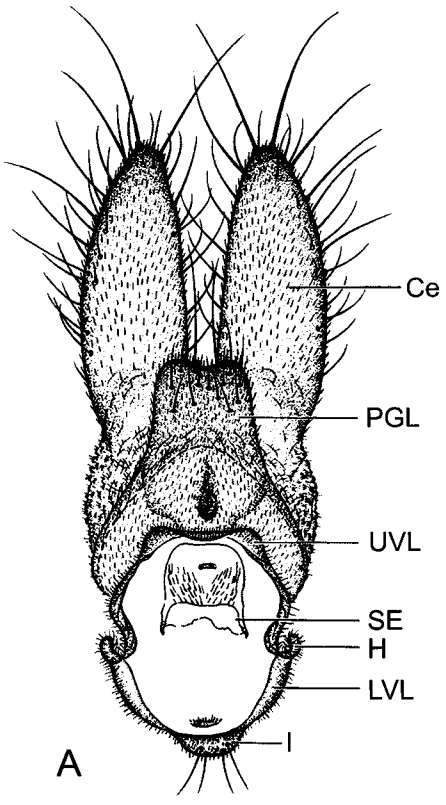
Genus Ochlerotatus: Male genitalia have the claspette developed as a moderately long to long, narrow, columnar stem with a terminal flattened filament (Figs. 2A–2D) (except in subgenera *Geoskusea, Howardina, Kenknightia,* and *Rhinoskusea*), and the gonostylus is moderately long to long, relatively narrow throughout its length but with the distal portion narrower and somewhat curved mesally, and with a single gonostylar claw that is long, narrow, uniformly thick throughout its length, and attached at the apex of the gonostylus (Figs. 2A, 2C).

Section I: Fourth-stage larvae have seta 12-I present (Fig. 4A) (except in 6 species, see discussion section below), the ventral brush (seta 4-X) is attached to a grid (Fig. 4B) (some groups also may have a few precratal setae) or in the 2 small-sized subgenera *Molpemyia* (Fig. 3D) and *Mucidus* it is attached to a very large and posteriorly projecting boss, seta 4-M is branched (Fig. 4A) (rarely single), and seta 3-V (and also normally seta 3-III,IV) is at least 2 times the length (often much longer) of seta 5-V (and also normally seta 5-III,IV) (Fig. 4A) (except variable in subgenus *Protomacleaya,* some *Finlaya,* and a few other species); and pupal setae 1–6-VI normally have 3 or more of the setae branched (Fig. 1D).

Section II: Fourth-stage larvae do not have seta 12-I (Fig. 4C), and the ventral brush (seta 4-X) is attached to a small boss (Fig. 4D), seta 4-M is single (Fig. 4C) (rarely branched), and seta 3-V (and also normally seta 3-III,IV) is shorter than, or normally less than 1.5 times the length of, seta 5-V (and also normally seta 5-III,IV) (Fig. 4C), but very rarely is seta 3-V (and seta 3-III,IV) near 2 times the length of seta 5-V (and seta 5-III,IV); and pupal setae 1–6-VI are single (Fig. 1E) (few species with 1–3 of the setae with 2, 3 branches).

Key based on female genitalia

Insula tonguelike, without setae ..... *Aedes*
Insula liplike, with well-developed setae .....
..... *Ochlerotatus*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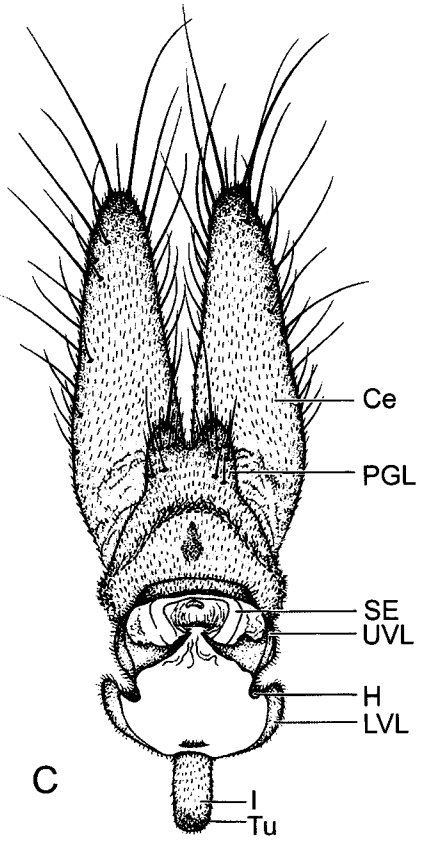
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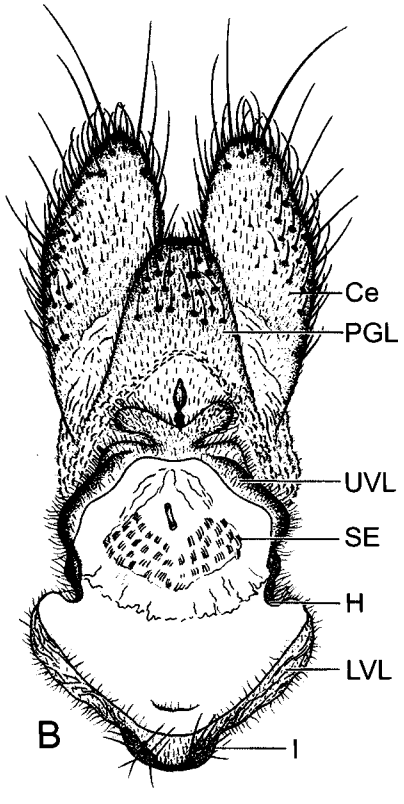
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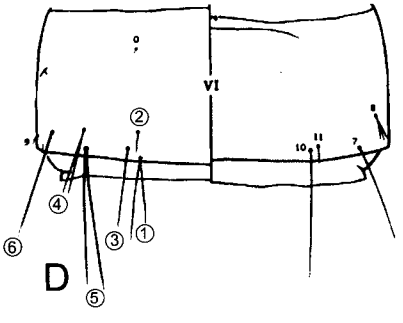
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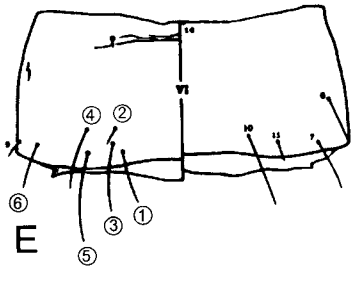
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Key based on male genitalia

Proctiger without cercal setae,[1] aedeagus consisting of 2 lateral plates usually bearing teeth laterally and/or apically ..... *Aedes*

Proctiger with tiny cercal setae; aedeagus simple and scooplike, troughlike, or tubelike .... *Ochlerotatus*

[1] Except for a few species (see discussion section).

Key based on 4th-stage larvae

1. Seta 12-I absent 2
   Seta 12-I present[1] .... *Ochlerotatus,* Section I
2. Setae of ventral brush attached to grid[1] .... *Aedes*
   Setae of ventral brush attached to small boss .. .. *Ochlerotatus,* Section II

[1] Except for 6 species (see discussion section).

Subgenera included in each genus

Genus Aedes: *Aedes, Aedimorphus, Alanstonea* Mattingly, *Albuginosus, Belkinius, Bothaella, Cancraedes* Edwards, *Christophersiomyia, Diceromyia, Edwardsaedes, Fredwardsius, Huaedes, Indusius, Isoaedes, Leptosomatomyia* Theobald, *Lorrainea* Belkin, *Neomelaniconion* Newstead, *Paraedes, Pseudarmigeres* Stone and Knight, *Scutomyia, Skusea* Theobald, and *Stegomyia.*

Genus Ochlerotatus, *Section I: Chaetocruiomyia, Finlaya, Geoskusea* Edwards, *Halaedes* Belkin, *Kenknightia, Levua* Stone and Bohart, *Macleaya* Theobald, *Molpemyia, Mucidus, Nothoskusea, Ochlerotatus, Protomacleaya, Pseudoskusea* Theobald, *Rhinoskusea, Rusticoidus,* and *Zavortinkius.*

Genus Ochlerotatus, *Section II: Abraedes, Aztecaedes, Gymnometopa, Howardina,* and *Kompia.*

DISCUSSION

During this study, only morphological characters that consistently separated genera *Aedes* and *Ochlerotatus* were selected as primary characters. Characters listed as supplemental features are very useful in partitioning the genera and sections but have some exceptions. The primary characters combined with the supplemental features reliably distinguish the 2 genera and 2 sections of *Ochlerotatus.* Numerous other characters, in all life stages, also were examined and evaluated but were found to be too inconsistent to be of value at the generic level; however, many appeared to have utility in distinguishing other taxa (e.g., subgenera and species groups). Other consistent distinguishing features for separating these genera may be discovered when a detailed examination is made of structures not fully evaluated during this study, such as mouthparts of 4th-stage larvae, chaetotaxy and structure of 1st-stage larvae and pupae, and the structure of eggs. Few molecular studies dealing with species in Aedini have been published (e.g., Wesson et al. 1992, Kumar et al. 1998). Unfortunately, these studies treated only a few species and genera; however, they generally appear to provide additional support for the above proposed separation of genera. Future molecular studies should evaluate and compare much larger numbers of species, subgenera, and genera of Aedini and should link their results with morphological features.

Exceptions to the characters for the genera and sections given above, of which I am aware, are discussed below. Also, other comments pertaining to the classification of genera and subgenera of Aedini are provided.

In male genitalia of genus *Aedes,* the phallosome has the aedeagus divided into 2 lateral plates that normally bear several stout lateral and/or apical teeth and the plates are usually not, or are only weakly, fused apically. Species of subgenus *Christophersiomyia* appear to have 2 lateral plates of the aedeagus that have the distal portions strongly curved mesally and fused at the apex and are without teeth (except *Ae. gombokensis* Mattingly, which has 2, 3 short stout teeth laterally). Species of subgenus *Bothaella* have the distal portion of the lateral plates of the aedeagus curved mesally and fused at the apex, and each plate bears 3–8 short or long teeth (teeth are weakly developed in *Ae. helenae* Reinert). Species in subgenus *Lorranea* appear to have the aedeagus divided into 2 lateral plates in which the apices are lightly fused and slightly extended posteriorly. The aedeagus of some subgenera (e.g., *Alanstonea, Diceromyia,* and *Isoaedes*) have numerous long, stout, curved teeth laterally and apically, but the apices of the lateral plates appear to be strongly fused. The aedeagus is unknown and the claspette is only partly known for the monotypic subgenus *Indusius* (see Reinert 1976a).

The gonostylus of the male genitalia in genus *Aedes* normally is variously developed (e.g., distal portion is expanded, or is bifurcate, or is trifurcate, or has rows or patches of short stout spicules, or has 2 or more gonostylar claws, or has the gonostylar claw absent), but rarely is it developed as in

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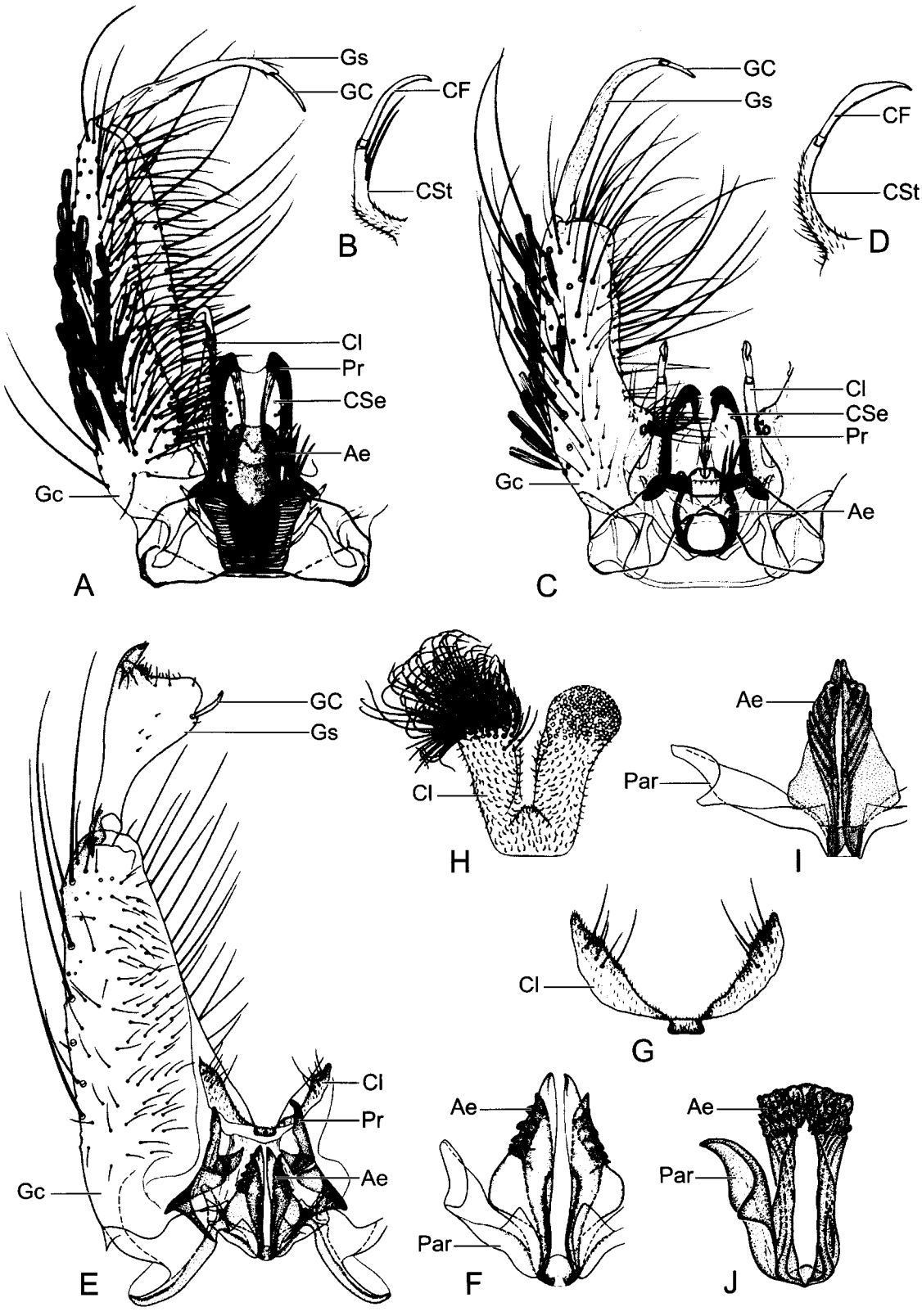
Fig. 1. (A–C) Female genitalia showing structures; (D, E) pupal segment VI showing setae. (A, D) *Ochlerotatus* (*Ochlerotatus*) *scapularis* (Rondani); (B, E) *Ochlerotatus* (*Aztecaedes*) *ramirezi* (Vargas and Downs); (C) *Aedes* (*Aedimorphus*) *domesticus* (Theobald). Abbreviations used: Ce, cercus; H, hinge; I, insula; LVL, lower vaginal lip; PGL, postgenital lobe; SE, spermathecal eminence; Tu, tuberculus; UVL, upper vaginal lip; VI, abdominal segment VI. Larger numbers in circles on D and E signify distinctive setae.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genus *Ochlerotatus*. However, a few species have the gonostylus moderately long to long, relatively narrow throughout its length, and with a single terminal gonostylar claw (e.g., *Ae.* (*Aedimorphus*) *natronius* Edwards, *Ae.* (*Diceromyia*) *kanarensis* Edwards, *Ae.* (*Diceromyia*) *micropterus* (Giles), *Ae.* (*Diceromyia*) *reginae* Edwards, *Ae.* (*Isoaedes*) *cavaticus* Reinert, *Ae.* (*Neomelaniconion*) *bergerardi* Pajot and Geoffroy, *Ae.* (*Neomelaniconion*) *monotrichus* Edwards, and species of subgenera *Christophersiomyia* and *Huaedes*) except that the gonostylar claw is usually differently developed. In subgenus *Stegomyia* the gonostylus superficially resembles those of genus *Ochlerotatus*, but the distal portion is somewhat expanded and the gonostylar claw is attached subapically (except the gonostylar claw appears to be attached apically in *Ae. novalbopictus* Barraud [see Huang 1972]). Subgenera *Aedes, Indusius, Neomelaniconion,* and *Skusea* have the gonostylus attached subapically to the gonocoxite and the gonocoxite has the sternal area developed into an apical projection. The gonostylar claw is absent in *Ae.* (*Stegomyia*) *desmotes* (Giles) and subgenera *Aedes, Belkinius, Edwardsaedes, Indusius,* and *Paraedes*. The latter 2 subgenera have short spicules forming filelike ridges on the distal portion of the gonostylus. The gonostylus of *Ae.* (*Fredwardsius*) *vittatus* (Bigot) has the distal portion greatly expanded and bears numerous, relatively long spicules in rows on one side, but this species also bears a narrow, strongly curved, gonostylar claw. The gonostylus is bifurcate in all or some species of subgenera *Aedes, Aedimorphus, Diceromyia, Edwardsaedes, Paraedes,* and *Skusea*. Two or more gonostylar claws are present in many species of subgenus *Aedimorphus*. Species of subgenus *Pseudarmigeres* usually have, in addition to the gonostylar claw, several stout spicules on the mesal margin that resemble gonostylar claws. Species of subgenus *Skusea* possess a comblike row of closely set, stout, blunt-tipped spicules.

The gonostylus of the male genitalia of *Oc. brygooi* (Brunhes) (subgenus *Zavortinkius*) has the middle portion broadly expanded. In subgenus *Levua,* the gonostylus bears a pair of short, stout, curved, and pointed gonostylar claws subapically. The gonostylar claw of *Oc.* (*Geoskusea*) *kabaenensis* (Brug) and *Oc.* (*Geoskusea*) *baisasi* (Knight and Hull) is relatively short and has a somewhat flared apex; the apex in the latter species also has a few small notches. In *Oc.* (*Finlaya*) *elsiae* (Barraud), *Oc.* (*Finlaya*) *shortti* (Barraud), and *Oc.* (*Pseudoskusea*) *postspiraculosus* (Dobrotworsky), the gonostylus bears 2 or more stouter setae subapically that are somewhat like the terminal gonostylar claw but thinner. The gonostylar claw is sinuous in *Oc.* (*Rusticoidus*) *rusticus* (Rossi).

In *Aedes,* 2 species, *Ae.* (*Diceromyia*) *kanarensis* and *Ae.* (*Stegomyia*) *calceatus* Edwards, have a few very long, stout setae on the proctiger of the male genitalia, but because of their unusual development, I consider these to be a departure from the normal. Also, a few species of Edwards' (1932) Group C of subgenus *Aedimorphus* (e.g., *Ae. argenteopunctatus* (Theobald), *Ae. minutus* (Theobald), and *Ae. punctothoracis* (Theobald)) have a few tiny cercal setae on the proctiger; their presence appears to be a reversal.

Within Aedini, the claspettes and the basal mesal lobes are homologous structures that can be identified as such by their connection basomesally to the spiculate, more or less narrow, somewhat troughlike, aedeagal guide (see Reinert [1999b] as adapted from Wood [1991]; =interbasal lobe, in part, of Freeborn [1924]; =median lobe of Schick [1970]; =interbasal fold of Tanaka et al. [1979]) that is situated ventral to the phallosome. Freeborn (1924) should be examined for a comparative examination of this structure within Culicidae. This structure has apparently been nearly lost in species of subgenus *Geoskusea* because it appears to be reduced to the spiculate aedeagal guide and a short thin strip extending laterally onto the basosternal portion of the mesal surface of the gonocoxite and bears 1 or a few short, thin, inconspicuous setae. Species of subgenus *Howardina* (see Berlin 1969) have the claspette developed as a spiculate, somewhat elongate lobe, with the basal portion usually somewhat expanded, and with a single, apical, stout, setalike filament (2 apical setae in *Oc. aureolineatus* (Berlin) and *Oc. ioliota* (Dyar and Knab), but 1 seta is shorter and slightly thinner). Also, according to Berlin (1969), the claspette is completely absent in the male genitalia of the 2 species in the Whitmorei Group of subgenus *Howardina*; however, this should be reevaluated to see if this structure has been reduced to only an aedeagal guide. The development of the short claspette bearing a stout setalike filament in subgenus *Howardina* is somewhat similar to that of species in subgenus *Kenknightia* of *Ochlerotatus* (see Reinert 1990). Species of subgenus *Levua* and *Oc.* (*Ochlerotatus*) *antipodeus* Edwards have a stout setalike

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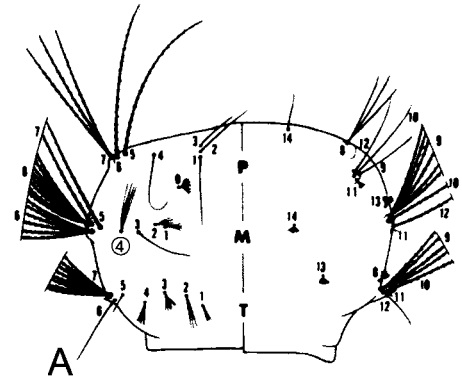
Fig. 2. Male genitalia showing structures. (A, C, E) Genitalia minus right gonocoxite and gonostylus, (E) minus tergum IX; (B, D, G, H) claspette (G and H enlarged); (F, I, J) aedeagus and left paramere (enlarged). (A, B) *Ochlerotatus* (*Aztecaedes*) *ramirezi*; (C, D) *Ochlerotatus* (*Ochlerotatus*) *scapularis*; (E–G) *Aedes* (*Aedimorphus*) *mediolineatus* (Theobald); (H, I) *Aedes* (*Aedimorphus*) *stenoetrus* (Theobald); (J) *Aedes* (*Isoaedes*) *cavaticus*. Abbreviations used: Ae, aedeagus; CF, claspette filament; Cl, claspette; CSe, cercal seta; CSt, claspette stem; Gc, gonocoxite; GC, gonostylar claw; Gs, gonostylus; Par, paramere; Pr, proctiger.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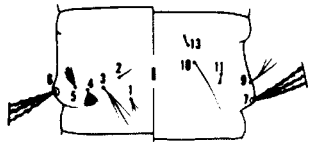
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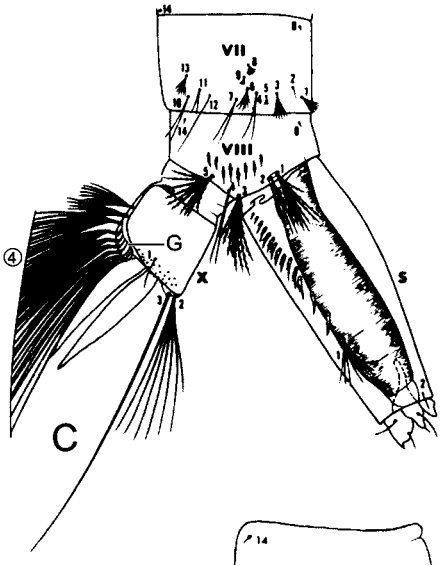
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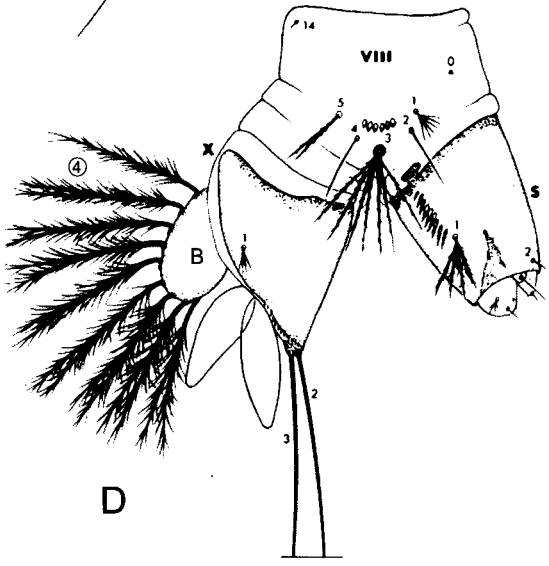
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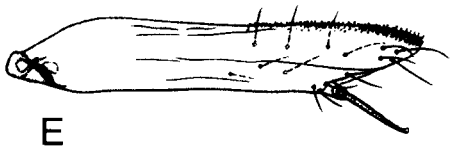
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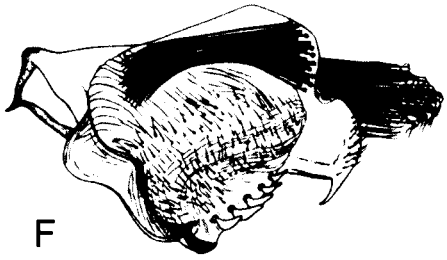
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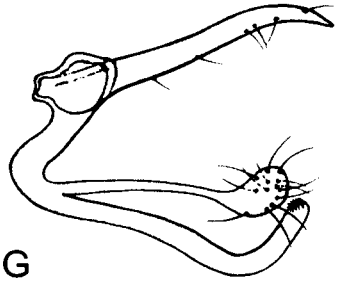
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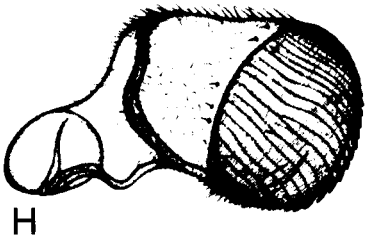
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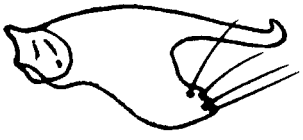
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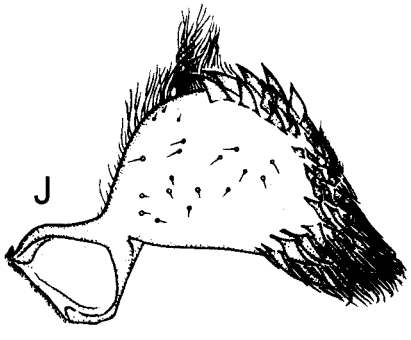
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filament attached apically to a moderately long, columnar, claspette stem.

In *Ochlerotatus,* male genitalia of subgenus *Rhinoskusea* are unusual in that the claspette does not have a filament and is bifurcate in 2 species, and the gonostylus is expanded distally or near midlength and bears a subapical, longitudinally striated, short, gonostylar claw. The claspette of *Oc.* (*Nothoskusea*) *chathamicus* (Dumbleton) has the filament absent and is developed as a bluntly rounded, lobelike process that is densely covered with short, thin setae. In subgenus *Halaedes,* the claspette appears to be developed as an oblong plaque bearing a number of curved lanceolate setae, is connected with its mate by a spiculate aedeagal guide, and the dorsal lateral portion is fused with the basomesal portion of the tergal surface of the gonocoxite. In subgenus *Pseudoskusea,* the claspette is much reduced (similar to subgenus *Geoskusea*), is restricted to a spiculate aedeagal guide and a short thin strip that extends laterally onto the basosternal portion of the mesal surface of the gonocoxite, and bears 2 or a few short, thin, inconspicuous setae. The claspette of subgenus *Rusticoidus* and some species of subgenus *Ochlerotatus* has the stem moderately to greatly swollen subapically or at about midlength (e.g., *Oc. aenigmaticus* (Cerqueira and Costa) and *Oc. atlanticus* (Dyar and Knab)), other species possess a short, thumblike process on the stem subapically or at about midlength (e.g., *Oc. aurifer* (Coquillett), *Oc. clelandi* (Taylor), *Oc. diantaeus* (Howard, Dyar, and Knab), *Oc. imperfectus* (Dobrotworsky), *Oc. intrudens* (Dyar), *Oc. nigrithorax* (Marquart), *Oc. pullatus* (Coquillett), *Oc. sagax* (Skuse), *Oc. sapiens* (Marks), *Oc. thibaulti* (Dyar and Knab), and *Oc. vittiger* (Skuse), whereas other species appear to have an additional basolateral, caudally directed, long process bearing setae in addition to the columnar stem and filament (e.g., *Oc. aenigmaticus, Oc. atlanticus, Oc. pertinax* (Grabham), *Oc. serratus* (Theobald), and *Oc. tormentor* (Dyar and Knab)). The claspette filament is relatively short and transversely annulated in species of subgenus *Rusticoidus.* Detailed comparative studies on the development of the claspette and its relationship with the basomesal structures (lobes, setal groups, specialized setae, etc.) of the gonocoxite are needed. For example, I have observed a narrow sclerotized attachment between these structures in a number of species, and in others it is difficult to determine if the structure is a basomesal lobe of the tergal surface of the gonocoxite or a dorsolateral lobe of the claspette. Additionally, considerable work is needed on the internal classification of species included in subgenus *Ochlerotatus* because, as currently known worldwide, it is very heterogenous and poorly defined.

Very short maxillary palpi of males are found in *Aedes* in subgenera *Aedes, Belkinius, Bothaella, Cancraedes, Christophersiomyia, Huaedes, Leptosomatomyia, Paraedes,* and most species of *Geoskusea,* but they are also found in *Ochlerotatus* in subgenera *Nothoskusea* and *Rhinoskusea.* Elsewhere in Aedini, short maxillary palpi of males are found in genera *Heizmannia, Verrallina, Zeugnomyia,* and a few species of *Haemagogus.*

Subgenus *Gymnometopa* shares several features with genus *Haemagogus.* Zavortink (1972) alluded to a remote relationship among subgenera *Abraedes, Aztecaedes, Gymnometopa, Howardina,* and *Kompia.* This relationship is supported here as demonstrated by the characterization of Section II of *Ochlerotatus.*

Fourth-stage larvae of subgenera *Abraedes, Aztecaedes, Kompia,* and *Oc. muelleri* (Dyar) share the unusual feature of the posterior pair of seta in the ventral brush (seta 4-X) being short, which appears to be unique for Aedini.

The absence of seta 12-I in the 4th-stage larvae is unusual for genus *Ochlerotatus.* However, 12-I is absent in 4th-stage larvae in subgenus *Howardina,* the monotypic subgenera *Abraedes, Aztecaedes, Gymnometopa,* and *Kompia* (all in Section II), 6 species of subgenus *Ochlerotatus* (i.e., *Oc. impiger daisetsuzanus* (Tanaka, Mizusawa, and Saugstad) [see Tanaka et al. 1979], *Oc. laguna* (Arnell and Nielsen), *Oc. monticola* (Belkin and McDonald), *Oc. muelleri,* and *Oc. varipalpus* (Coquillett)), and *Oc.* (*Chaetocruiomyia*) *tulliae* (Taylor) (see Marks 1962).

Setae of the ventral brush (seta 4-X) are attached to a grid in Section I of *Ochlerotatus,* which is different from Section II but similar to *Aedes.* The ventral brush is attached to a weakly developed grid in 4th-stage larvae of subgenera *Christophersiomyia* and *Macleaya* and some species of subgenera *Finlaya* and *Stegomyia,* whereas in 6 other species, *Ae.* (*Alanstonea*) *brevitibia* (Edwards), *Ae.* (*Leptosomatomyia*) *aurimargo* Edwards, *Ae.* (*Stegomyia*) *aobae* Belkin, *Ae.* (*Stegomyia*) *futunae* Belkin, *Ae.* (*Stegomyia*) *robinsoni* Belkin, and *Ae.* (*Stegomyia*) *tulagiensis* Edwards, the ventral brush is attached to a small boss. In the 4th-stage larva of *Oc.* (*Abraedes*) *papago* (Zavortink), the boss at

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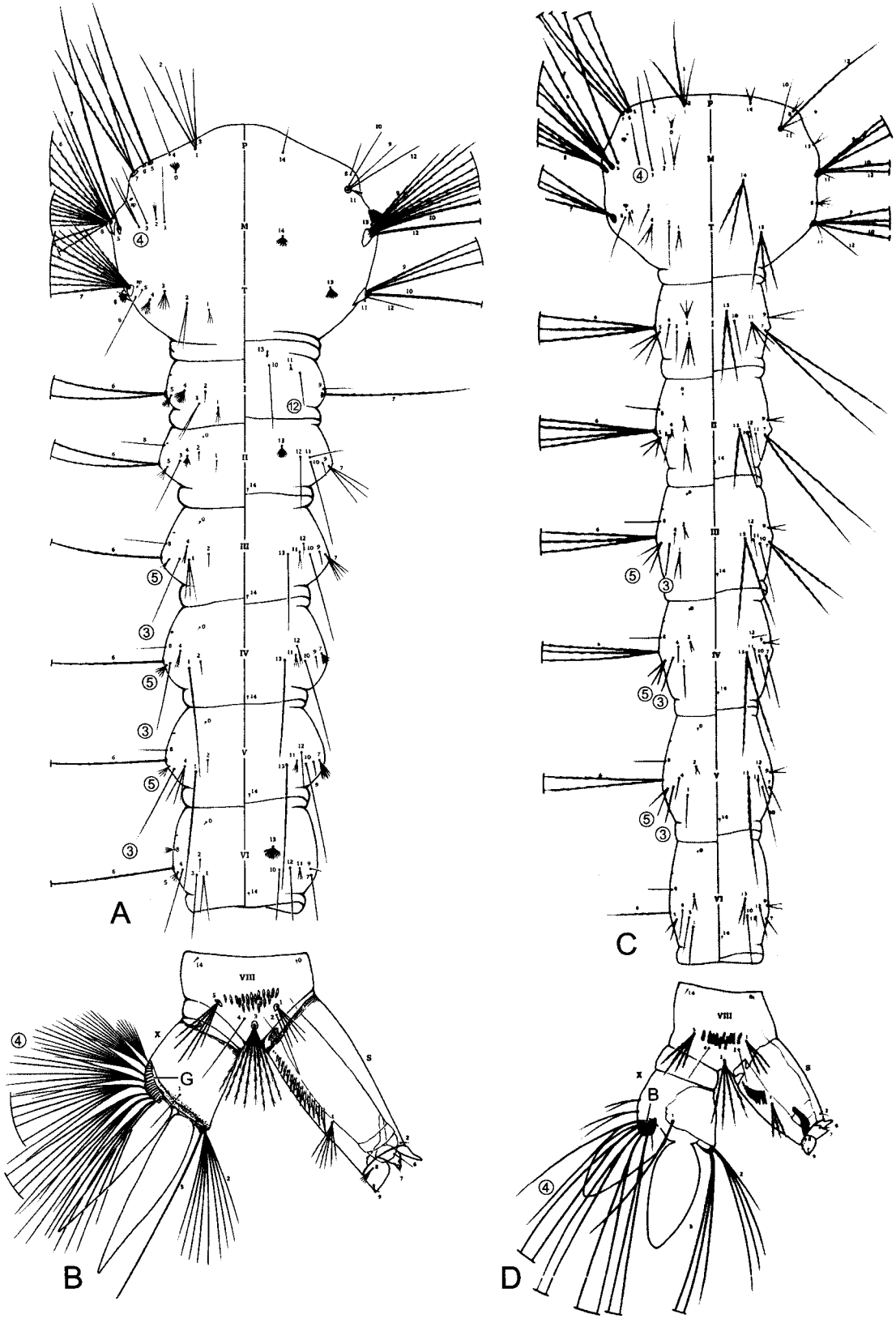
Fig. 3. Fourth-stage larva showing structures. (A) Thorax; (B) abdominal segment I; (C, D) abdominal segments VIII, X and appendages, and segment VII in C; (E–J) gonostylus of male genitalia. (A–C, E) *Aedes* (*Aedimorphus*) *vexans*; (D) *Ochlerotatus* (*Molpemyia*) *pecuniosus* (Edwards); (E) *Aedes* (*Aedimorphus*) *vexans*; (F) *Aedes* (*Aedimorphus*) *pampangensis* (Ludlow); (G) *Aedes* (*Paraedes*) *bonneae* Mattingly; (H) *Aedes* (*Indusius*) *pulverulentus*; (I) *Aedes* (*Edwardsaedes*) *imprimens* (Walker); (J) *Aedes* (*Belkinius*) *aurotaeniatus.* Abbreviations used: B, boss; G, grid; I, VII, VIII, and X, abdominal segments I, VII, VIII, and X with appendages; M, mesothorax; P, prothorax; S, siphon; T, metathorax. Larger numbers in circles signify distinctive setae.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the base of the ventral brush of segment X is weakly developed. The ventral brush is attached to a small but heavily pigmented boss in genera *Eretmapodites* and *Haemagogus.*

Larval seta 3-V is only slightly longer than seta 5-V and seta 5-III,IV is slightly longer than seta 3-III,IV in *Oc.* (*Macleaya*) *tremulus* (Theobald).

Members of the Sexlineatus Section and 2 species (Ioliota Group) of the Walkeri Section of subgenus *Howardina* have seta 13-P developed in the 4th-stage larvae. This seta is also present in subgenus *Bothaella* and the 4 species of subgenus *Stegomyia, Ae. hoguei* Belkin, *Ae. robinsoni, Ae. tulagiensis,* and *Ae. upolensis* Marks.

Fourth-stage larvae of subgenera *Aedes* and *Rusticoidus,* and a few species of subgenus *Ochlerotatus* (i.e., *Oc. crinifer* (Theobald) [see Arnell 1976], *Oc. hexodontus* (Dyar), *Oc. hexodontus hokkaidensis* (Tanaka, Mizusawa, and Saugstad), and *Oc. punctor* (Kirby) [see Tanaka et al. 1979]) are unusual for Aedini in the development of accessory setae on the siphon.

The 4th-stage larva of *Ae.* (*Alanstonea*) *brevitibia* has seta 0-X present, which is unusual for Aedini.

Seta 13-CT is present on the pupal metanotum of a few species of *Aedes,* that is, *Ae.* (*Belkinius*) *aurotaeniatus* Edwards, a few African species of subgenus *Aedimorphus,* and the following species of subgenus *Stegomyia*: *Ae. futunae, Ae. rotumae* Belkin, and *Ae. upolensis* (see Reinert 1980). Setae 13,14-CT are present in *Ae. krombeini* Huang (see Tewari and Hiriyan 1990).

Normally, 3 or more of setae 1–6-VI are branched in pupae of genus *Ochlerotatus* Section I, but most of these setae are single in Section II and in some species of subgenera *Finlaya, Macleaya,* and *Molpemyia,* the Varipalpus Group, and *Oc. muelleri.*

The pupal paddle has a fringe of hairlike spicules in subgenera *Belkinius, Lorrainea,* most *Stegomyia* (except, e.g., *Ae. aegypti* (Linnaeus) and the Dendrophilus Group), a few *Diceromyia* (e.g., *Ae. franciscoi* Mattingly, *Ae. iyengari* Edwards, *Ae. periskelatus* (Giles), and *Ae. tiptoni* Grjebine) of *Aedes,* and subgenus *Abraedes* of *Ochlerotatus.* A similar hairlike fringe of spicules is found in the pupal paddle of genera *Armigeres, Eretmapodites, Heizmannia, Udaya,* and *Zeugnomyia.*

In addition to the previously mentioned characters that distinguish *Aedes* and *Ochlerotatus,* some characters, in various combinations, are useful in separating them from other genera of Aedini, such as, adults have postspiracular setae (except the monotypic subgenus *Kompia* in which their absence I consider to be a reversal), prespiracular setae are absent, upper calypter of the wing has setae on the margin, mesopostnotum is without scales or setae (except in *Oc.* (*Rusticoidus*) *lepidonotus* (Edwards) [see Reinert 1999a] and 4 species of subgenus *Zavortinkius* [see Reinert 1999b]), dorsal margin of the mesomeron is above the base of the hindcoxa (except in *Ae. desmotes*), and the ungues of the male foretarsus are unequal in size (except ungues are equal in size in *Ae.* (*Indusius*) *pulverulentus* Edwards); female genitalia are without lower vaginal sclerites; pupae have seta 1-I well developed and with a number of branches, and the paddle has only 1 seta (i.e., seta 1-Pa); and 4th-stage larvae have a well developed pecten on a normally moderately long siphon and setae 9,10-T are well developed.

Aedes has a distribution in the Old World except for *Ae.* (*Aedes*) *cinereus, Ae.* (*Aedimorphus*) *vexans* (Meigen), *Ae.* (*Stegomyia*) *aegypti,* and *Ae.* (*Stegomyia*) *albopictus* (Skuse) that are found in the New World. The 2 species of subgenus *Stegomyia* are believed to have been introduced to this region. In North America, *Ae. cinereus* exhibits noticeable morphological variability (Wood et al. 1979, Bickley 1980) and is reported from much of the United States and Canada (see Darsie and Ward 1981). The primary range occupied by genus *Aedes* is the Afrotropical and Oriental regions, but a few species occur in the Palaearctic and Nearctic regions (see above). Section I of *Ochlerotatus* is essentially cosmopolitan in distribution. Section II of *Ochlerotatus* occurs in the New World and has a distribution that is primarily Neotropical and centered in the American Mediterranean Region (sensu Belkin 1962) and as reported by Berlin (1969) and Zavortink (1972). However, Section II extends north to the southern part of the United States (*Oc.* (*Abraedes*) *papago* and *Oc.* (*Kompia*) *purpureipes* (Aitken) in southern Arizona; and *Oc.* (*Howardina*) *bahamensis* (Berlin) that was probably introduced into southern Florida [Pafume et al. 1988]) and south to northern Argentina along the Andes.

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Fig. 4. Fourth-stage larva showing structures. (A, C) Thorax and abdominal segments I–VI; (B, D) abdominal segments VIII and X with appendages. (A, B) *Ochlerotatus* (*Ochlerotatus*) *scapularis*; (C, D) *Ochlerotatus* (*Aztecaedes*) *ramirezi.* Abbreviations used: B, boss; G, grid; I–VI, VIII, and X, abdominal segments I–VI, VIII, and X; M, mesothorax; P, prothorax; T, metathorax; S, siphon. Larger numbers in circles signify distinctive setae.

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