Review of a Bromeliad-Ovipositing Lineage in *Wyeomyia* and the Resurrection of *Hystatomyia* (Diptera: Culicidae)

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ABSTRACT   Problems associated with the monophyly of *Wyomyia* Theobald are discussed and part of the classification is revised. One problematical component of the cladogram is a lineage of primarily bromeliad-ovipositing mosquitoes that include the type species *Wyeomyia grayii* Theobald. When the characters used in the cladistic analysis are partitioned by life stage the arrangement displayed by the combined data does not appear among the various topologies based on a single life stage. However, further analyses support the unique arrangement from the combined data and the following changes in classification are made to reflect the pattern of relationships implied by that cladogram. *Phoniomyia* Theobald is reduced to a subgenus in *Wyeomyia*. The name *Hystatomyia* Dyar is resurrected for 7 species currently without subgeneric placement. Two species representing 2 well-defined groups within *Hystatomyia* are redescribed and illustrated in larval, pupal, and adult stages. *Wyeomyia esmeraldasi* (Levi-Castillo) is transferred from *W.* (*Phoniomyia*) to *W.* (*Hystatomyia*). *Wyeomyia intonca* Dyar and Knab is removed as a junior synonym of *Wyeomyia circumcincta* Dyar and Knab.

KEY WORDS   Sabethine mosquitoes, cladistics, total evidence, partitioned analyses, classification

SABETHINE MOSQUITOES EXHIBIT a wide range of behaviors atypical for nematoceran flies that have stirred the interest of field biologists for years. Although it is not uncommon to find arthropods inhabiting the fluids of phytotelmata (Fish 1983, Frank 1983), sabethines have invaded these habitats with a tenacity matched by few groups of insects. Pitcher plants, leaf axils, tree holes, bamboo, flower bracts, decaying fruit pods, and ground litter provide suitable sites for oviposition and development throughout the tropics, where the group reaches its greatest diversity.

A cladistic analysis using exemplars representing all genera and most subgenera of Sabethini demonstrates that although the tribe is monophyletic, 3 of the 13 genera are not (Fig. 1; Judd 1996). *Tripteroides* Giles, *Runchomyia* Theobald, and *Wyeomyia* Theobald are paraphyletic as currently recognized. Within *Wyeomyia,* the nominal subgenus is likely to be polyphyletic. These results strongly suggest that reclassification of Sabethini and particularly *Wyeomyia* is required if the classification is to reflect natural groups (sensu Hennig 1966). A recent species group revision by Albuquerque Motta and Lourenço de Oliveira (1995) restricted *Dendromyia* to 5 species, leaving the remaining 38 species (Knight and Stone 1977) without subgeneric placement. Those species affected by the changes of Albuquerque Motta and Lourenço de Ol-

iveira (1995) and included in the analysis, can be identified in Fig. 1 by the absence of a subgeneric name following the abbreviation for *Wyeomyia*. The phylogenetic hypothesis based on explicit cladistic analysis (Fig. 1; Judd 1996) provides a framework from which to establish the new classification. The discussion that follows focuses on a lineage embedded well within *Wyeomyia* (Fig. 1, component A; Judd 1995, 1996). With the exception of 1 unplaced species, these focal taxa appear to be restricted to ovipositing and developing in fluid-filled bromeliads.

Historical and Phylogenetic Considerations. Component A (Fig. 1) is the most disparate combination of *Wyeomyia* taxa on the cladogram and includes species from the subgenera *Dendromyia* Theobald (sensu Knight and Stone 1977), *Dodecamyia* Dyar, *Nunezia* Dyar, and the nominal subgenus, as well as *Phoniomyia* Theobald (sensu Knight and Stone 1977). Dyar (1928: Table 1) classified these species into 6 subgenera in 2 genera. Subsequent revisions by Edwards (1932) and Correa and Ramalho (1956) closely aligned the focal taxa with the currently accepted classification (Knight and Stone 1977, Ward 1992, Albuquerque Motta and Lourenço de Oliveira 1995). The trends in mosquito classification that led to the current classification problems were discussed by Judd (1996) and will not be repeated here. However, to date, a thorough examination of all taxa assigned to *Wyeomyia* has not been published.

Phylogenetic studies that use an exemplar approach can yield misleading results if groups represented are inadequately sampled or if monophyly is a problem

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These results were first presented at the 1993 annual meeting of the American Mosquito Control Association.

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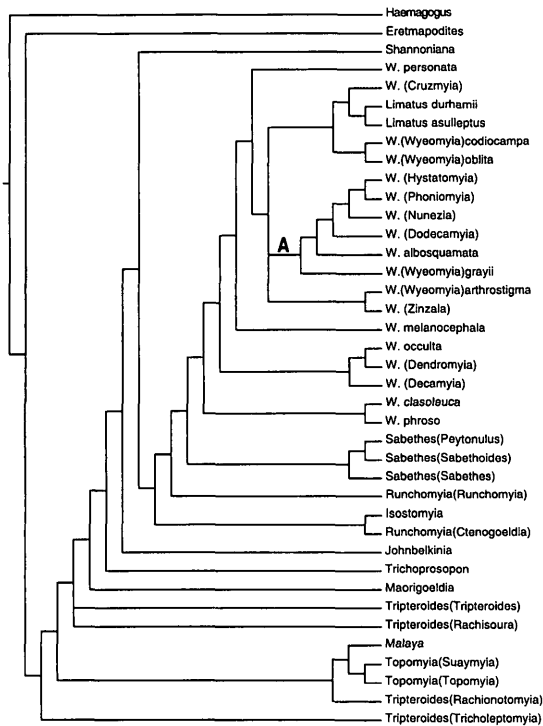
Fig. 1.   Sabethine relationships based on SAW data from Judd (1995 1996). The tree length is 281 steps with a 0.54 CI and an 0.77 RI. (A) Bromeliad-ovipositing lineage.

Table 1.   Comparison of classifications following Dyar (1928) and recent works of Knight and Stone (1977), Ward (1992), and Albuquerque Motta and Lourenço de Oliveira (1995) for focal taxa

Dyar 1928	Classification as of 1995
Dendromyia Theobald	*Wyeomyia* subgenus
Hystatomyia Dyar	Synonym *Wyeomyia*
circumcincta (Dyar & Knab)	Unplaced
intonca (Dyar & Knab)	Synonym circumcincta
coenonus (Howard, Dyar, and Knab)	Unplaced
autocratica (Dyar & Knab)	Unplaced
lamellata (Bonne-Wepster & Bonne)	Unplaced
luteoventralis (Theobald)	Unplaced
Eunicemyia Dyar & Shannon	Synonym *Wyeomyia*
albosquamata (Bonne-Wepster and Bonne)	Unplaced
Wyeomyia	Stable
Dyarina Bonne-Wepster & Bonne	Synonym *Phoniomyia*
tripartita Bonne-Wepster & Bonne	*Phoniomyia*
syn. muhlensi Petrocchi	*Phoniomyia*
syn. fuscipes Edwards	*Phoniomyia*
trinidadensis (Theobald)	*Phoniomyia*
syn. lassalli Bonne-Wepster & Bonne	*Phoniomyia*
pallidoventer (Theobald)	*Phoniomyia*
Nunezia Dyar	Stable
bicornis (Root)[a]	Stable
Dodecamyia Dyar	Stable
aphobema Dyar	Stable
splendida Bonne-Wepster & Bonne	*Phoniomyia*
quasilongirostris Theobald	*Phoniomyia*
incaudata Root	*Phoniomyia*
pilicauda Root	*Phoniomyia*
Wyeomyia Theobald	Stable
synonym *Phoniomyia*	Genus
longirostris Theobald	*Phoniomyia*
pertinans (Williston)	Unplaced
syn. grayii Theobald	Type *Wyeomyia* by subsequent designation

[a] Original designation *W. (Eunicemyia)* based on larvae only.

(Wheeler et al. 1993). Therefore, additional analyses on the focal group (component A, Fig. 1) were performed using a modified procedure described by Schuh and Farris (1981). The purpose of this exercise was 2-fold. First, selected clade analysis (SCA, Judd 1998) is an approximate test of stability of the component. In other words, can the relationships observed for component A in Fig. 1 be reproduced using a reduced taxon set? Second, what relationships do the characters suggest when partitioned by individual life stages? Because mosquito classification is based primarily on adult characters, it is of historical interest to examine the soundness of such decisions. Clade stability serves as a measure for assessing the current state of mosquito classification.

Materials and Methods

A detailed description of the combined phylogenetic analysis, including character codings, taxa selection, and data matrix for the tree in Fig. 1, can be found elsewhere (Judd 1996). A brief description of SCA is included here; a more thorough discussion of the procedure is in Judd (1998). The taxa in component A (Fig. 1) were reanalyzed separately as a reduced taxon set. *Hemagogus* Williston and *Eretmapodites* Theobald remain as outgroups and *W. personata* (Lutz) was included because it had the smallest cladistic distance (sensu Farris 1967) to component A of an ambiguously resolved group on the cladogram (Fig. 1). A total of 9

taxa was included in SCA. Characters were given equal weights and run unordered in PAUP 3.1.1 (Swofford 1993). Because fewer taxa were included, an algorithm that found all possible trees was implemented in these analyses. Successive approximation weighting (SAW) was used to select among equally parsimonious cladograms (Farris 1969, Carpenter 1988). Data sets were partitioned such that 4 tree sets resulted: combined, larval, pupal, and adult.

Terminology used to describe morphological structures of adults and larvae follow McAlpine et al. (1981), and for pupae Harbach and Knight (1980). Illustrations are sometimes based on several individuals because difficulties arose from the poor condition of available material or specimen preparation.

Results and Discussion

Selected clade analysis of the combined data set resulted in 2 equally parsimonious cladograms (Fig. 2 A and B) of 81 steps with a 0.74 CI and a 0.68 RI. Neither of the cladograms using characters of equal weight are congruent with the pruned arrangement from Fig. 1 (component A), although the arrangement
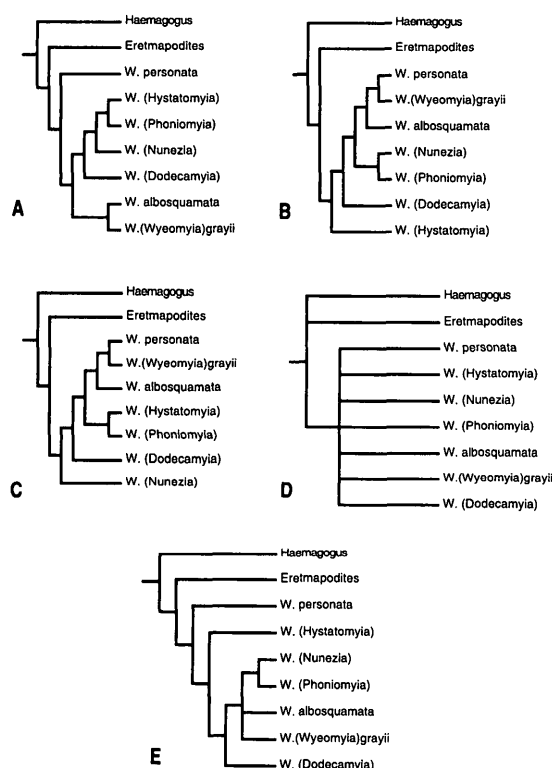
Fig. 2. Results of Selected Clade Analysis (SCA) on component A of Fig. 1. (A and B) Two topologies generated from simultaneous analysis of larval, pupal and adult characters for the selected taxa. (C) Single topology generated by only larval characters. (D) Strict consensus tree of 26 topologies from the pupal characters. (E) Single topology resulting from analysis of adult characters only.

in Fig. 2A differs only at the basal node from the pruned arrangement. Application of SAW to the data retained the arrangement of Fig. 2A, but discarded the tree of Fig. 2B. When only larval characters were analyzed 1 tree resulted (Fig. 2C; 37 steps; CI = 0.78, RI = 0.77). Like the discarded tree in Fig. 2B, the larval character analysis exchanged only the position of *W. (Hystatomyia)* Dyar and *W. (Nunezia)* Dyar. The pupal data analysis yielded 26 trees of 16 steps (CI = 0.88, RI = 0.86). These data were uninformative as evidenced by the strict consensus tree (Fig. 2D). None of the 26 trees is congruent with combined or larval topologies and weighting the data did not reduce or change earlier results. Finally, the adult data produced 1 tree (Fig. 2E), 22 steps in length with a 0.80 CI and a 0.79 RI. SAW did not alter these results.

The resulting 30 trees from the reduced taxon set and the various life stage partitions are all unique arrangements. As previously mentioned, the SAW preferred hypothesis of the combined data set (Fig. 2A) differs only in the arrangement of the basal node from the pruned component (Fig. 1). Simultaneous analysis of all characters (Fig. 1) and SCA (Fig. 2A) topologies are consistent with one another if the basal node is collapsed in each, converging on the same arrange-

ment. This minor rearrangement of *W. grayii* Theobald and *W. albosquamata* Bonne-Wepster and Bonne (Fig. 2A) is an artifact of different character interactions in the reduced taxon set of SCA. Further studies (additional characters and taxa, Judd, in prep.) support the arrangement observed in component A (Fig. 1) and demonstrates the stability of the component to data set perturbation. Results of SCA on component A and the original data analysis using all taxa and characters (Fig. 1) provide strong evidence for simultaneous data analysis. One argument commonly voiced by advocates of total evidence (e.g., Kluge 1989, Barrett et al. 1991) is that simultaneous analysis of data can result in unique arrangements that may remain hidden if character sets are analyzed separately. In the original data set, component A (Fig. 1) was the only component of 10 examined that was not supported by at least 2 of the life stage partitions (Judd 1998).

The observation of character disagreement between insect life stages is not new. Past attempts (Weismann 1882, Dyar and Knab 1906, Alexander 1930, Crampton 1930, Rohlf 1963, Michener 1977, Roback and Moss 1978) have failed to find a congruent classification based on characters from different life stages. De Beer (1954) coined the term "mosaic evolution" to describe taxa that possessed a mixture of apomorphic and pleisomorphic characters, and it was within this context that adaptational paradigms were constructed to account for the incongruence of classifications. Nonetheless, it is likely that many of these failures were caused by methodological error (e.g., evolutionary taxonomy, phenetics; see Farris 1971). Current cladistic approaches, such as total evidence (Kluge 1989), bury the problem of taxonomic incongruence by shifting the theoretical emphasis to character congruence (Judd 1998). However, if only a total evidence approach is used, character information that can delimit the boundaries of difficult groups can be obscured or not observed.

For example, in component A, if only adult characters are examined, our interpretation is significantly different than if larval characters are used as the framework for the hypothesis. Classifications constructed from these data partitions would be useful only for special purposes, such as in identification keys, but should be avoided for formal classifications if they are to be meaningful representations of phylogeny. In this study, combining the data are more robust than any of the life stage arrangements and provides the best choice for constructing the revised classification (Fig. 1). It could be argued that because each life stage suggests a different arrangement of the taxa, collapsing the preexisting subgenera and *Phoniomyia* into the nominal subgenus would be the wisest strategy. However, mosquito taxonomy has long used the nomenclatural category of subgenus to identify inclusive groupings. Abandoning these subgeneric names could cause confusion among systematists and the users of taxonomic products worldwide resulting in greater instability than currently exists. In addition, the Sabethini is arguably the least well known of the
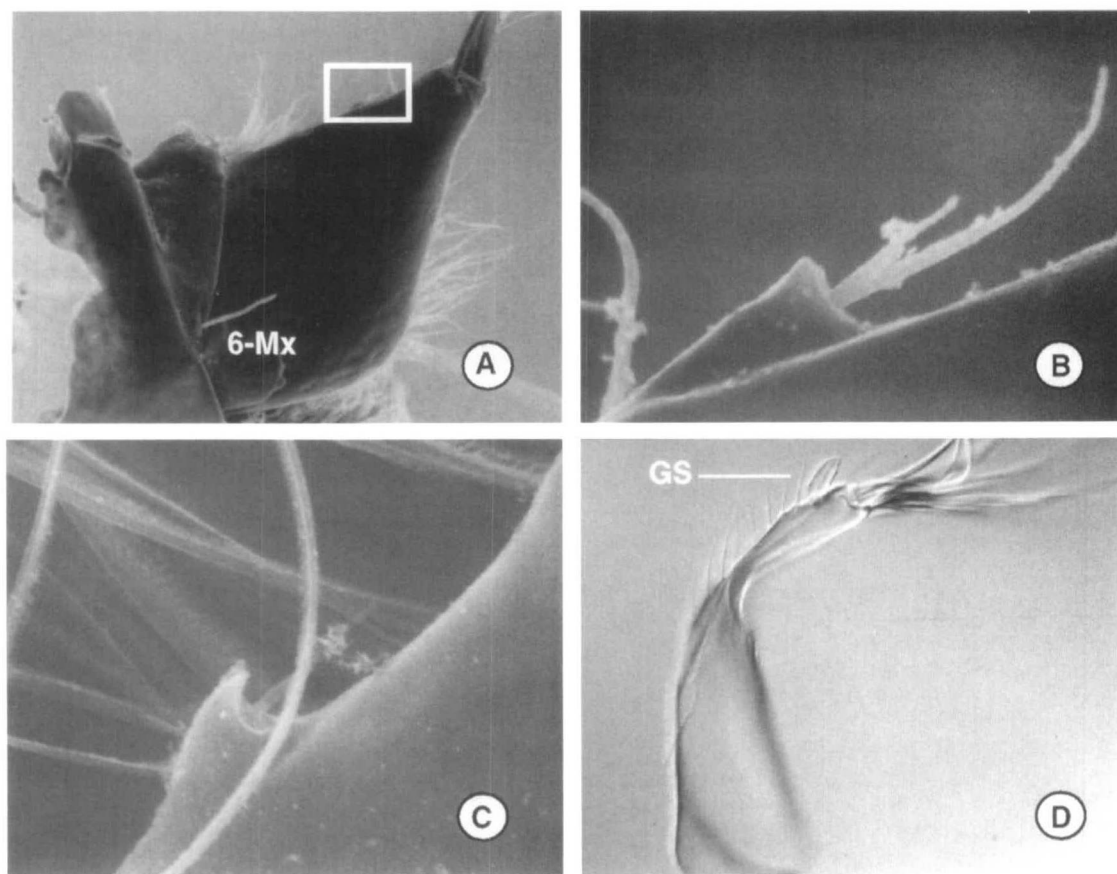
Fig. 3.　Characters of the larval maxilla and male terminalia. (A and B) *Wyeomyia* (*Hystatomyia*) *circumcincta*. (A) Maxilla, ventral aspect, box indicates location of seta 3-Mx. (B) Seta 3- Mx. (C) *Wyeomyia* (*Phoniomyia*) *splendida*, seta 3-Mx. (D) *Wyeomyia* (*Phoniomyia*) *longirostris*, gonocoxite. GS, gonostylus; 6-Mx, seta 6 of palpifer.

mosquito tribes and numerous species await description (Judd 1998). Therefore, until the boundaries for the nominal subgenus are more clearly defined, I have chosen to retain the subgenera *Dodecamyia* (monotypic, but a species complex) and *Nunezia* (2 valid and 1 new species), although clearly little knowledge is imparted from the category in these cases. Given this decision, the question then becomes, what should be done with the 7 unplaced species identified as "spp. group A" in Judd (1995, 1996)? If only the arrangement from Fig. 1 is considered, the subgeneric boundaries become arbitrary. Diagnostic characters, such as subapical placement of the male gonostylus, occur in both groups. The plant host information adds to this dilemma, because larvae from these 2 *Wyeomyia* groups are commonly collected together in areas of overlap (e.g., Trinidad). Therefore, the strongest evidence for recognizing another subgenus is the data provided by the differing life stage arrangements of SCA (Fig. 2). From these data, and considering past classifications (Dyar 1919, 1928), the following changes are recommended to revise the classification for part of *Wyeomyia*.

Resurrection of *Hystatomyia* Dyar. The species group discussed in this section is currently without

subgeneric placement in *Wyeomyia* (Albuquerque Motta and Lourenço de Oliveira 1995), although the group was treated previously as a junior synonym of *W.* (*Dendromyia*) by most authors (e.g., Knight and Stone 1977). These species form a monophyletic group within *Wyeomyia* and the name *Hystatomyia* Dyar (1919) is available for these taxa. Focus was placed on these taxa because they are diagnostically distinct from other species within *Wyeomyia* and their position within the phylogenetic framework (Fig. 1; designated as *Wyeomyia* sp. A group in Judd 1996) strongly suggests they are the sister group to *Phoniomyia* (sensu Knight and Stone 1977). *Phoniomyia* and these species share a unique structural modification of the larval maxilla not observed in other mosquitoes: seta 3-Mx is produced on the outer margin of the maxilla in a cuplike extension of the cuticle (Fig. 3 A–C).

Hystatomyia can be distinguished from other subgenera of *Wyeomyia* by characteristics of the male genitalia and pupal trumpet. The position of the gonostylus is subapical on the inner margin of the gonocoxite in adult males (Figs. 4B, 5 E and F, 13). With the exception of 1 species group in *Phoniomyia* (Fig. 3D), the subapical placement of the gonostylus is not ob-
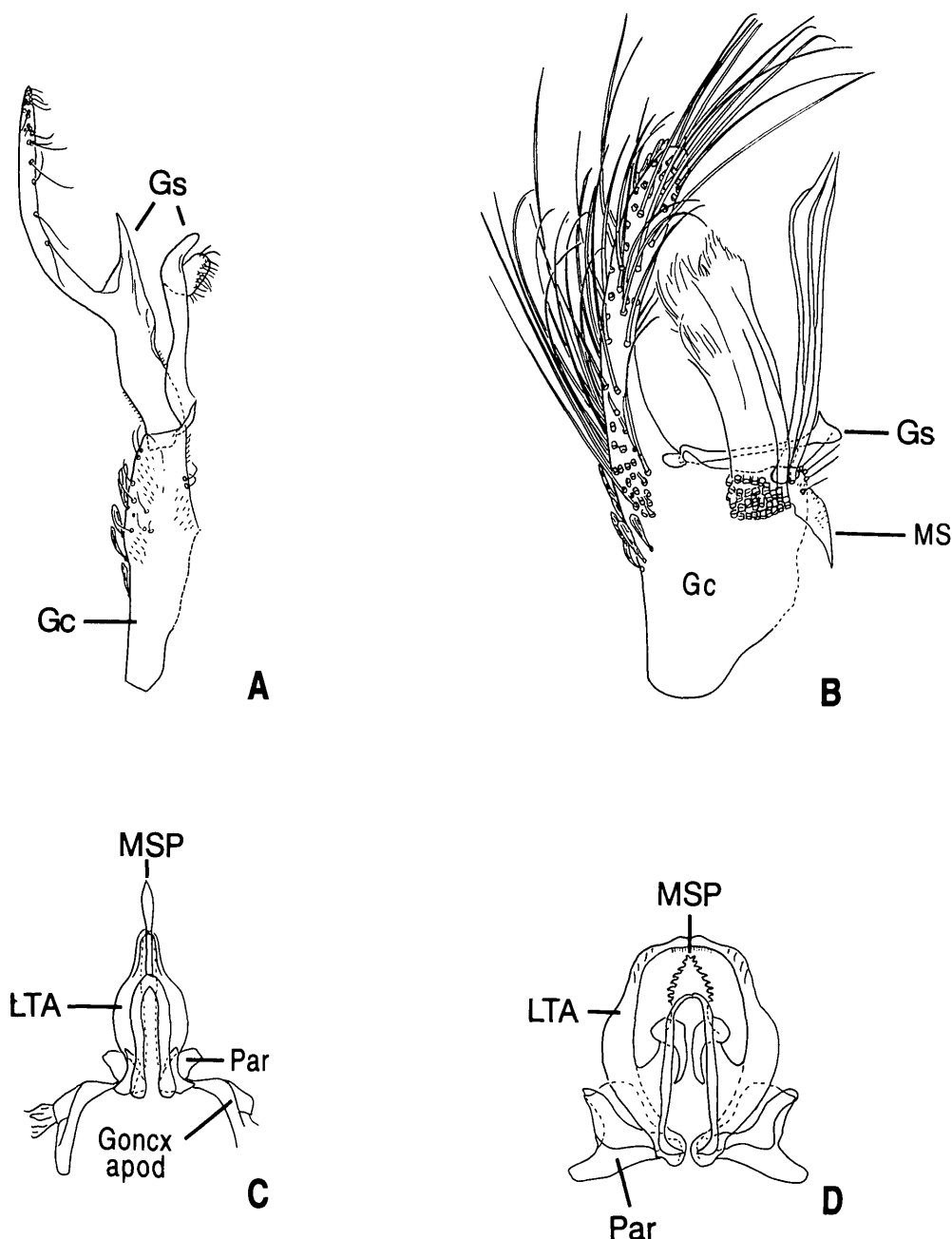
Fig. 4.   Structures of male terminalia in *Wyeomyia*. (A and C) *Wyeomyia* (*Phoniomyia*) *trinidadensis* (B and D) *Wyeomyia* (*Hystatomyia*) *circumcincta*. (A and B) Gonocoxite and gonostylus. (C and D) Aedeagus. Gc, gonocoxite; Goncx apod, gonocoxal apodeme; Gs, gonostylus; LTA, lateral tergal arm; MS, mesal sclerite; MSP, median sternal plate; Par, paramere.

served in other sabethines. In *Phoniomyia*, species with a subapical gonostylus differ from *Hystatomyia* by the following: the well-developed mesal sclerite on the gonocoxite is absent (compare Fig. 4 A and B) and the gonostylus is only slightly removed from the apex and on the outer surface of the gonocoxite. No characters are known that will separate adult females of *Hystatomyia* from other *Wyeomyia* species. The length

of the reticulate portion of the pupal trumpet is exaggerated in species placed in *Hystatomyia*. The elongate trumpets illustrated in Fig. 6 A and B are typical and not observed in any other New World sabethine taxa. As mentioned previously, larvae may be diagnosed by the position of seta 3-Mx on the outer margin of the maxillae. In addition, *Hystatomyia* larvae can be separated from *Phoniomyia* by the presence of a peg-

like sensillum on the apex of the maxillary palpus (Fig. 11 E and F), although the sensillum is minute and difficult to see.

Seven species are included here within the subgenus *Hystatomyia: W. circumcincta* Dyar & Knab (type species), *W. intonca* Dyar & Knab, *W. coenonus* Howard, Dyar & Knab, *W. autocratica* Dyar and Knab, *W. lamellata* (Bonne-Wepster & Bonne), *W. lopezii* Cova Garcia, Sutil Oramas & Pulido, and *W. esmeraldasi* (Levi-Castillo) (new combination, removed from *Phoniomyia*). Ten undescribed species are in the USNM collection (Washington, DC) separated by Belkin during the Mosquitoes of Middle America project.

Two well-defined species groups are within *Hystatomyia.* These 2 groups differ in characteristics of male terminalia. In the group represented here by *W. circumcincta* (Fig. 4B), the gonocoxite lacks a mesal subapical lobe and the gonostylus is elongate with an apex of variable form, but always broader than the median section. The *W. autocratica* (Fig. 13) group possesses a mesal subapical lobe on the gonocoxite and the gonostylus is reduced in length, one half to one-third the size of those in the other species group.

Earlier descriptions of species in *Hystatomyia* are inadequate, especially for the immature stages. Therefore, a species from each of the 2 groups is redescribed in detail below. Detailed descriptions of species that represent the 2 groups will be useful for future revisionary works that attempt to solve some of the current problems in the classification of *Wyeomyia.*

Wyeomyia (*Hystatomyia*) *circumcincta* Dyar & Knab

Wyeomyia circumcincta Dyar & Knab, 1907: 210–211. TYPE: Lectotype male (adult). Locality: Panama, Canal Zone, Tabernilla, 10 July 1907, A. Busck (USNM #10857, Stone and Knight, 1957). References: Belkin et al. 1965, Lane 1953, Lane 1945, Lane and Cerqueira 1942, Dyar 1928, Bonne and Bonne-Wepster 1925, Dyar and Shannon 1924, Dyar 1925, Dyar 1923, Dyar 1919, Howard et al. 1913.

Wyeomyia macrotus Dyar & Knab (1907: 212). TYPE: Lectotype female (adult). Locality: Panama, Boquerón River, 23 May 1907, A. Busck (USNM #10862, selection by Stone and Knight, 1957). Synonymized by Dyar (1928).

Wyeomyia andropus Dyar & Knab (1908: 68). TYPE: Lectotype male (adult). Locality: Panama, Portobelo, Fort San Felipe, 4 January 1909, A. H. Jennings (USNM #11989, selection by Stone and Knight 1957). Synonymized by Dyar (1928).

Female. Wing 2.40 mm. Small-sized mosquito, dorsum densely covered with bronze scales with a blue metallic sheen, wing scales mostly decumbent and concolorous with scutum. Outer surface of legs covered with bronze scales. *Head* (Fig. 5A). Covered with decumbent scales only; mostly concolorous with scutum, except area surrounding dorsal pair of orbital setae and genae immediately behind compound eye covered with patch of white scales of variable size.

Dorsal orbital setae strong, yellow; lateral orbital setae weaker, brown. Interocular space, pedicel, and clypeus without scales. Proboscis 1.6 mm., area between base and apex stout, thickened; apex enlarged. Labium completely covered with bronze scales. Antenna only slightly shorter than proboscis. Palpus (Fig. 5B) two-segmented, segment 1 globose, segment 2 elongate; 2 segments combined slightly longer than clypeus and covered with bronze scales. *Thorax.* Pronotal lobes widely separate. Scutum with anterior patch of white scales of variable size, these extending ventrolaterally. Color of dorsal scales described above, scales becoming broader posteriorly. Scutellum (Fig. 5C) trilobed, appearance enhanced by broad, decumbent scales occurring on the apex of the posterior margin of each lobe along with 4–5 stout brown setae. Mediotergite (Fig. 5C) convex with 6–8 pale, yellowish setae. Pleuron covered with white scales, except for anterior portion of katepisternum, paratergite, meron, and metapleuron, these nude. Pleural chaetotaxy reduced: anterior pronotum, 6–8 setae; prespiracular seta, 1 seta; postspiracular setae absent; proepisternal setae, 3–4 pale setae; prealar setae, 6–8 pale setae; lower katepisternum, 2–3 weak setae; upper katepisternal setae, absent; 4 metepisternal setae (posterior to spiracle, below halter). Legs: forecoxae and trochanter covered with white scales; midcoxae and trochanter nude; hind coxae and trochanter nude. Femora, tibiae, tarsomeres with outer surface covered with bronze scales with metallic blue, green, and violet reflections. Inner surface of foreleg with line of cream-colored scales extending from femur to tarsomere 5. Midleg femur and tibia with inner line of cream-colored scales, tarsomeres 1–5 covered with brown scales. Hind leg femur with inner line of cream-colored scales, tibia inner surface with intermittent white scales and tarsomeres 1–5 covered with brown scales. *Abdomen.* Dorsum covered with bronze scales with metallic blue reflections, sternum covered with white or cream-colored scales. Dorsoventral line straight. Spermathecal capsules: 3, tear-drop shaped.

Male. Like female except as follows. *Head.* Antennal whorls with slightly longer setae. Proboscis with patch of white scales at base and thin line of subapical white scales. *Thorax.* Midleg with inner cream-colored line extending from femur to midpoint of tarsomere 1. Tarsomere 1 with bronze scales extending to midpoint of tarsomere 2. Tarsomere 2 (midpoint) through tarsomere 5 covered with bright white scales. Claws of midleg modified, different in size and shape (Fig. 5D). Hind leg with white line on inner surface of femur and tibia, tarsomere 1–5 covered with bronze scales.

Male Genitalia (Figs. 4 B and D, 5 E and F): *Segment VIII.* Segment covered with small, fine setae. Sternum with a pair of small setae on anterior portion, larger setae occurring midway and extending along posterior margin. Scales broad, flat on lateral posterior margin. Tergum densely covered with broad, decumbent scales, long setae on lateral and posterior margins. *Segment IX:* Sternum with anterior margin weakly emarginate, triangular, consisting of thin strip of sclerite partially fused to gonocoxal lobes separated by
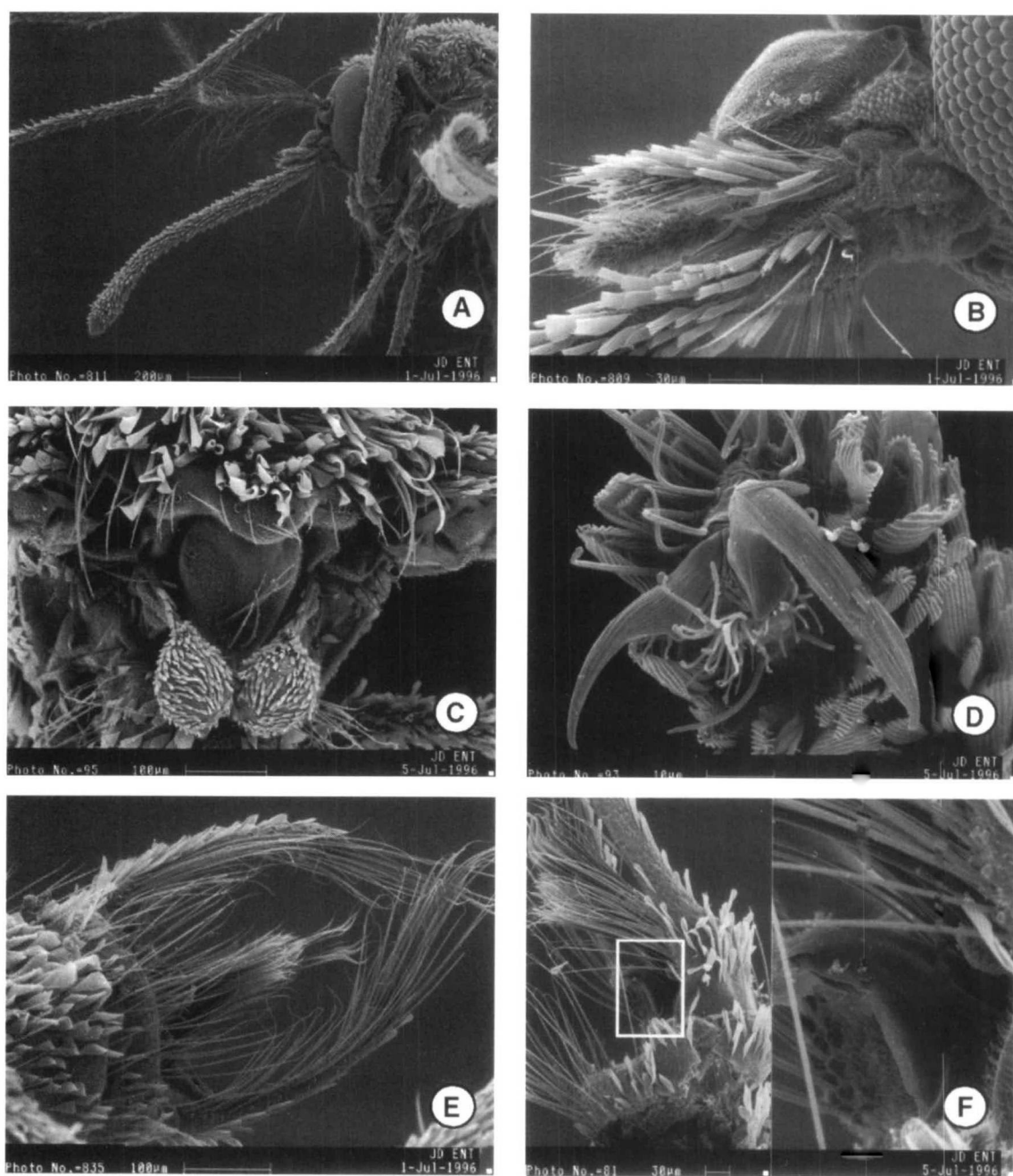
Fig. 5. *Wyeomyia circumcincta.* (A) Structures of the head. (B) Two-segmented maxillary palpus. (C) Thoracic structures including trilobed scutellum, mediotergite, and halteres. (D) Male claw of midleg. (E) Dorsal aspect of male terminalia. (F) Lateral aspect of male terminalia, left, box indicates location of proctiger, right, close-up of proctiger.

weak line of flexion. Tergum dark, broadly emarginate on anterior margin, posterior margin fused to gono- coxites, with 2 or 3 elongate, flat, outwardly curved setae on each lobe. *Gonocoxite* (Figs. 4B and 5E). Arms appearing fused at base with segment IX. Basal portion broad with strongly developed mesal lobes. Mesal lobe membranous with 25–30 subapical elongate, flat setae more or less in circular pattern. Arms narrow and curved inward. Each arm densely covered with scales

and well-developed setae. Inner surface of arm with setae restricted to area extending posteriorly from midpoint to apex. *Gonostylus* (Fig. 4B). Length 0.15 mm. Located on inner margin of gonocoxite at the point where lobe constricts to form arm. Base of gono- stylus wider than median section, apex triangular. *Me- sal Sclerite.* Sclerite surrounding gonostylus, extending from mesal margin of gonocoxal lobe posteriorly to- ward apex of gonocoxite. Apical region not defined,
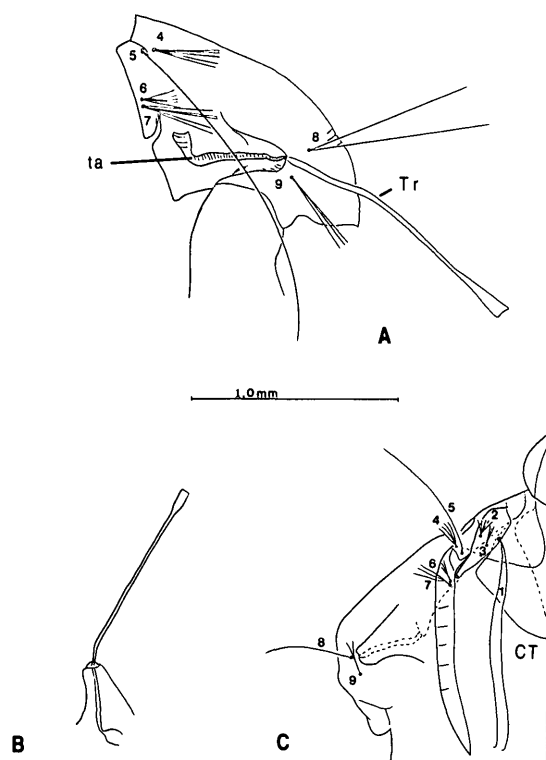
Fig. 6. Cephalothorax of pupal exuviae. (A) *Wyeomyia circumcincta* (B and C) *Wyeomyia autocratica.* (A and C) Cephalothorax. (B) Trumpet. CT, cephalothorax; ta, trachoid section of the trumpet; Tr, reticulate section of the trumpet; 1–9, cephalothoracic setae.

fusing with other sclerotized areas. Mesal region darkened, separating lobes internally and just posterior to aedeagus. Six strong, elongate, flat setae on posterior mesal margin of each lobe; 3 of these setae stout, flat, with apices constricted, curved inward. Other 3 setae shorter, apices not constricted. *Aedeagus* (Fig. 4D). Tergal bridge forming upside-down V fused at base with lateral tergal arm. Lateral tergal arms broad at base, narrowing subapically with dorsal margin emarginate, and apices fused with posterior margin serrate. Median sternal plate spatulate with lateral and apical margins emarginate not extending beyond apex of lateral tergal arms. Paired, conical, darkly sclerotized structures with truncate, concave apices near base of median sternal plate. *Proctiger* (Fig. 5F). Weakly sclerotized at base with 2–3 weakly defined teeth, 1 tooth prominent of variable form. Dorsal surface with 3–5 small setae.

Pupa. (Figs. 6A and 7A). Chaetotaxy as figured. *Cephalothorax* (Fig. 6A). Pigmentation uniform, light golden tan, except at apex of posterior scutal angle, this unpigmented. Seta 1 weakly hooked at apex. Seta 8 branched. Ecdysial sutures weak or absent. *Trumpet.* Brown, length 1.02–1.23 mm. Width significantly narrowed, 0.02 mm. Apex slightly swollen, not >0.05 mm. *Metanotum and Abdomen* (Fig. 7A). Cuticle weakened and hyaline on dorsum of segment I surrounding seta

1. Only ventral setae 10-I, 11-I present. Some specimens with singular circular pit located immediately lateral of ventral midline. Segments II–VIII concolorous with cephalothorax. Minute, uniformly spaced spicules on segments VIII. Intersegmental sclerites darkly pigmented posterior to segments II, III, IV, and V. Only ventral seta 10-II, 11-II present. Seta 5-III-VI single, elongate, extending length of 2.5 abdominal segments. Seta 14-VIII present. *Paddle.* Uniformly oblong, narrowing at apex. Short, 0.7 length of seta 9-VIII. Surface glabrous, lateral margins spiculate. Midrib prominent, width 0.01 mm and extending just short of caudal margin. *Male Genital Lobe.* Longer than paddle, oblong with apex attenuated.

Larva (Figs. 8 A and C, 9, 11, 12; head capsule drawn from exuviae). Chaetotaxy as figured. *Cranium.* Oval with anterior margin produced, slightly wider than long. Margin straight between setal pair 1-C (Figs. 8A and 11A). Cranial setae 4–14 branched. Occipital foramen with dorsolateral slit extending anteriorly 0.30 mm anteriorly. *Antenna.* 0.26 mm in length. Antennal seta 1 bifid located on dorsal surface of apical 3rd. *Hypostoma:* (Fig. 11B), median tooth prominent with 9–10 teeth decreasing in height toward lateral margin. *Mandible* (Fig. 11 C and D). Anterior tooth extended with 3 smaller teeth below. Dorsal teeth absent. *Maxillae* (Fig. 3 A and B): Seta 3-Mx on outer margin of maxilla in sclerotized pocket or notch. Laciniarastrum with small apical tooth. Palpus (Fig. 11 E and F) with 4 apical sensilla, 1 peg-like, other 3 cone-shaped. Palpus, palpiger, maxillary body separate. Palpiger hyaline, seta 6-Mx single. *Labiohypopharynx* (Fig. 11 G and H). Lateral premental teeth fused, aligned longitudinally; prementoligular teeth extending posteriorly, midway between seta 1 and ventral premental spicules; prementoligular teeth confined to lateral margin between setal pairs 2,3 and 4,5. *Thorax* (Figs. 9, 12A). Surface glabrous. *Abdomen.* Surface glabrous. *Segment VIII* (Figs. 8C, 12 B–D): Comb teeth numerous, extending to ventrolateral area. Individual teeth with lateral and apical margin spiculate. *Siphon* (Figs. 8C, 12 E–F). Length 1.01 mm. Pecten elongate, spinelike, in single row, number appears variable, 3–7 (although many appear to have been removed during mounting). *Anal Segment* (Abdominal segment X, Figs. 8C, 12 B and D). Saddle incomplete, covered with rows of intermittently spaced spicules. Paired, fanlike, 8-branched accessory setae on ventral surface, sclerite absent between setae (Figs. 8C and 12B).

Bionomics. Larvae are found in fluid-filled bromeliads. In Panama, known from species of *Tillandsia.*

Distribution. Known from Belize, Panama, Colombia, Brazil, and Bolivia.

Systematics. One of 2 species groups in *Hystatomyia* is comprised of *W. circumcincta, W. coenonus, W. intonca,* and *W. esmeraldasi.* The holotype of *W. esmeraldasi* is apparently lost, therefore placement within this species group is based on illustrations from the original description (Levi-Castillo 1955). *W. intonca* is here removed from synonymy with *W. circumcincta. W. intonca* differs in larval chaetotaxy and the shape of the male gonostylus.
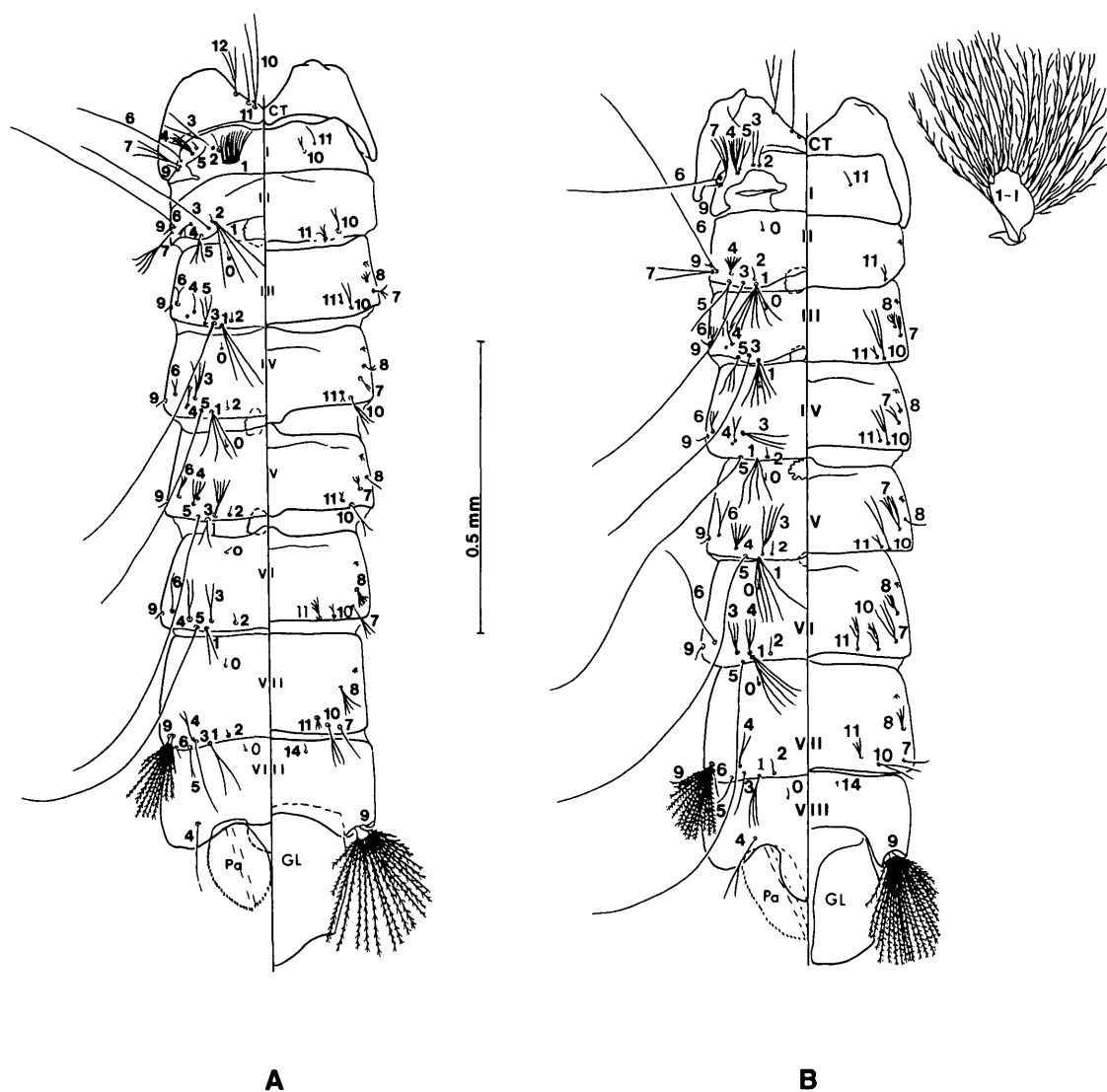
A   **B**

Fig. 7. Pupal chaetotaxy of metathoracic and abdominal segements. (A) *Wyeomyia circumcincta.* (B) *Wyeomyia autocratica*, seta 1-I enlarged. CT, cephalothoracic 3rd segment; GL, genital lobe; Pa, paddle; Arabic numerals, homologous setae; Roman numerals, abdominal segments (dorsal aspect left of the longitudinal line, ventral aspect right of the line).

Material Examined (USNM). PANAMA: 7 pinned females, 5 pinned males, 15 male genitalia slide-mounted, 22 reared larval and pupal exuviae, and 2 whole larvae. PANAMA: Canal Zone, Barro Colorado Island, Bocas del Toro, Almirante, Isla Colon, Punta de Pena, Colon, Portobelo, Darien, Morti, Pucro.

Wyeomyia (Hystatomyia) autocratica
Dyar & Knab

Wyeomyia autocratica Dyar and Knab, 1906: 230; Pl. XVI, fig. 77. TYPE: Holotype larva (mounted on slide, apparently lost). Pupal exuviae and pinned male with the abdomen dissected and slide-mounted from the same locality (see Stone and Knight 1957). Type Locality: Trinidad, locality and date not specified, F. W.

Urich (USNM #9986). References: Belkin et al. 1965, Stone and Knight 1957, Lane 1953, 1945, Lane and Cerqueira 1942, Dyar 1928, Bonne and Bonne-Wepster 1925, Dyar and Shannon 1924, Howard et al. 1915).

Female. No adult specimens available. Two pupal exuviae with associated larval skins examined are female. However, the adults were not found in the Belkin collection deposited at USNM.

Male. Wing 2.56 mm. Small, similar in size to *W. circumcincta*, dorsum densely covered with bronze scales with faint blue-green metallic sheen, wing scales decumbent, bronze-colored with faint magenta reflection on anterior margin. Outer surface of legs covered with bronze scales. *Head.* Covered with wide, decumbent scales only; most scales bronze, except for row of white scales encircling compound eyes and
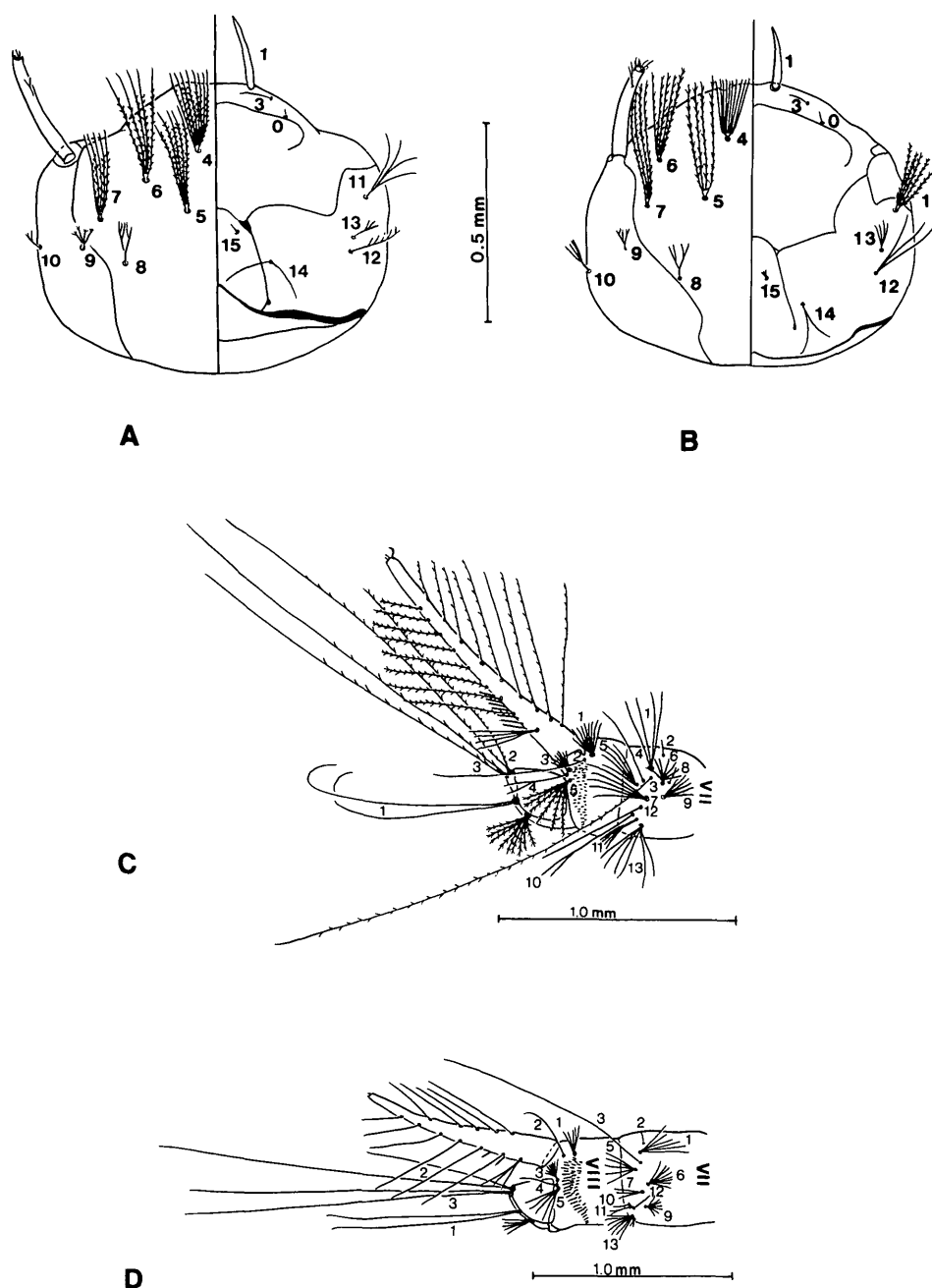
Fig. 8.   Head and terminal segments of larvae. (A and C) *Wyeomyia circumcincta.* (B and D) *Wyeomyia autocratica.* (A and B) Cranium (dorsal aspect left of the longitudinal line, ventral aspect right of the line). (C and D) Abdominal segments VII–X, lateral aspect. Arabic numerals, homologous setae; Roman numerals, abdominal segments.

occiput, additional white scales between dorsal orbital setae and vertex, boundaries of white scales on vertex not well defined. Dorsal orbital setae strong, golden-yellow, lateral orbital setae weaker, brown. Interocular space, pedicel, clypeus without scales. Surface of clypeus weakly punctate. Proboscis 1.68 mm., area between base and apex narrow, elongate, apex enlarged. Labium with patch of white scales on ventral surface at base of proboscis, all other scales bronze. Antenna 0.75 length of proboscis. Palpus apparently 2-segmented; slightly longer than clypeus and covered with bronze scales. *Thorax.* Pronotal lobes widely separate. Scutum with ill-defined anterior patch of white scales of variable size, this extending ventrolaterally. Color of dorsal scales described above, scales becoming broader posteriorly. Scutellum apparently tri-
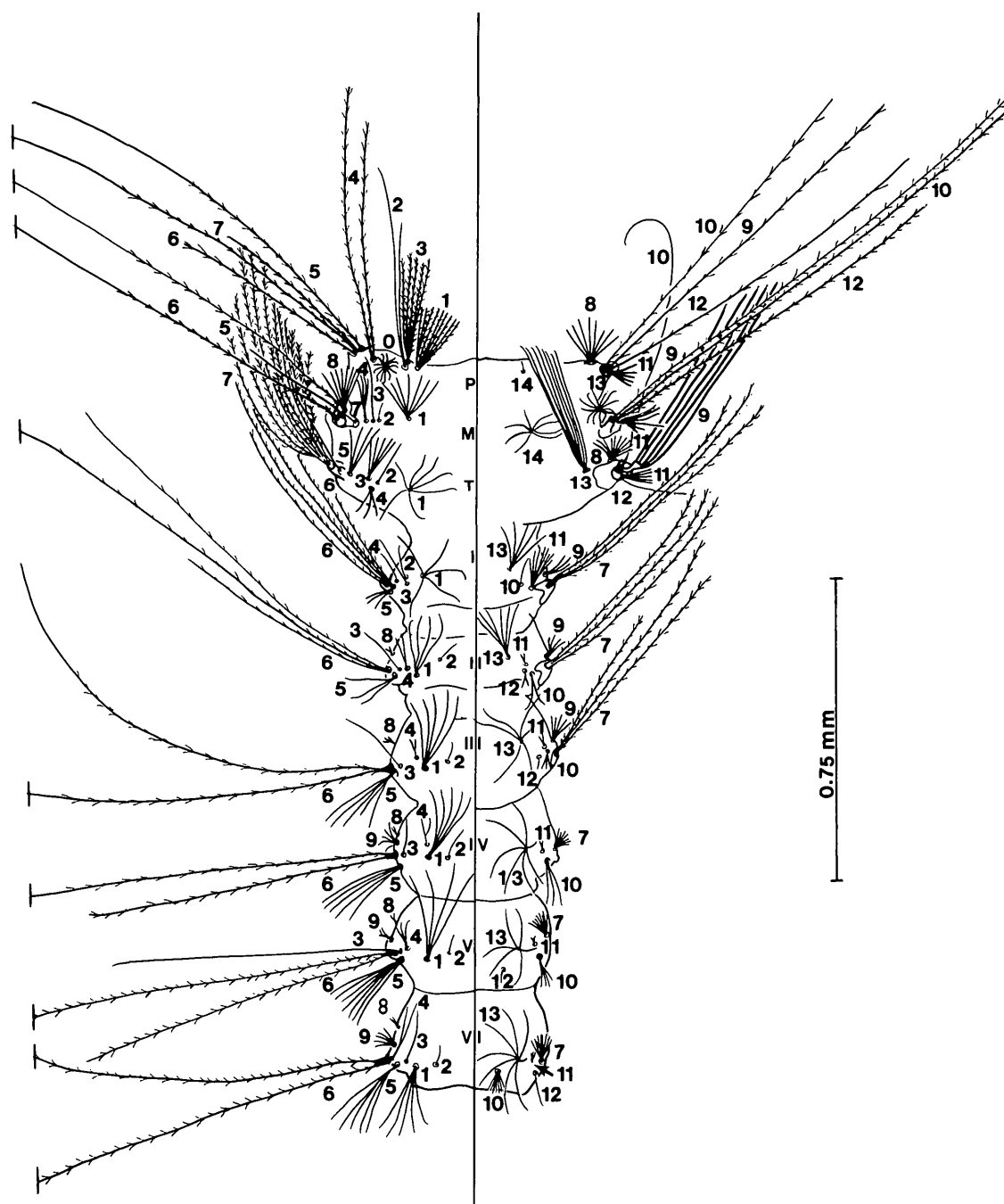
Fig. 9. Larval chaetotaxy of *W. circumcincta* for thoracic and abdominal segments I–VI. P, prothoracic segment; M, mesothoracic segment; T, metathoracic segment; Arabic numerials, homologous setae; Roman numerals, abdominal segments (dorsal aspect left of the longitudinal line, ventral aspect right of the line). Seta 0 on all abdominal segments omitted for clarity.

lobed, appearance enhanced by broad, decumbent scales occurring on apex of posterior margin of each lobe along with 4–5 stout golden-brown setae. Mediotergite convex with 6–8 pale, yellowish setae. Pleuron covered with white scales, except for anterior portions of katepisternum, meron, metapleuron these nude. Paratergite not visible. Pleuron chaetotaxy reduced: anterior pronotum, 6–8 setae; prespiracular

seta not visible; postspiracular setae absent; 4–5 pale proepisternal setae; 7–8 pale prealar setae; 4–5 weak lower katepisternum; setae absent on upper katepisternum; 4 metepisternal setae. Legs: forecoxae with anterior region covered with white scales, entire outer surface of mid- and hind coxae covered with white scales. Foretrochanter apparently nude, mid- and hind trochanters with white scales on the inner surface.
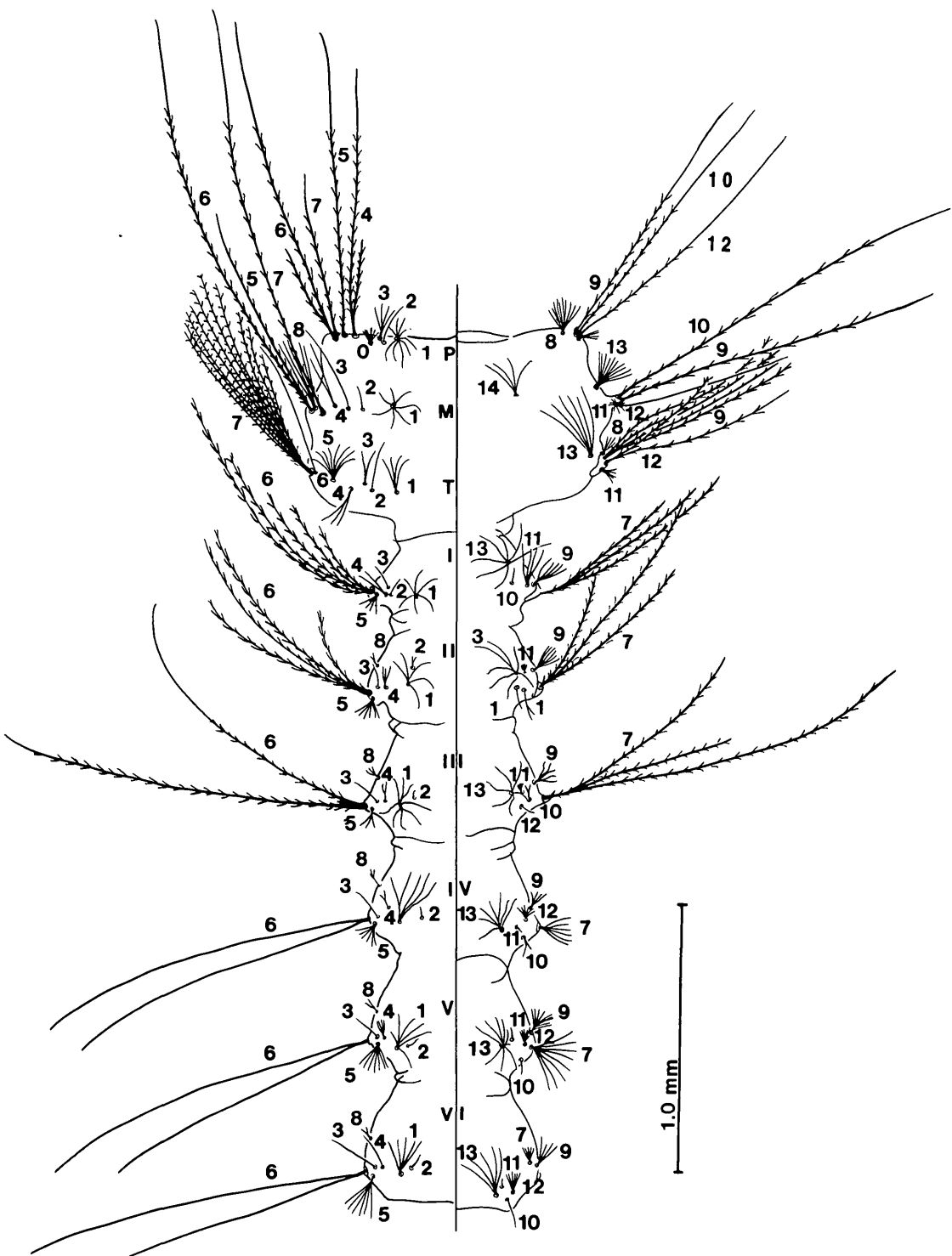
Fig. 10.   Larval chaetotaxy of *W. autocratica* for thoracic and abdominal segments I–VI. Abbreviations follow those in Fig. 9. Seta 0 on all abdominal segments omitted for clarity.
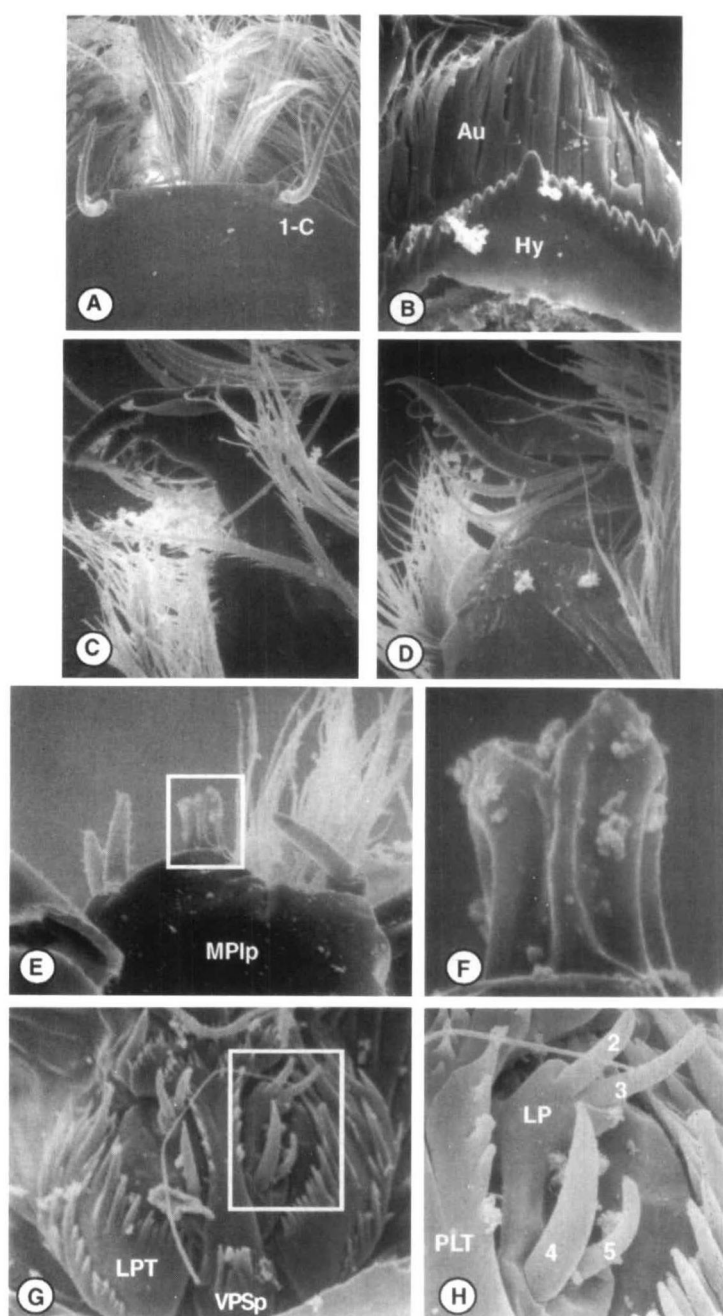
Fig. 11. Structures of larval cranium, *W. circumcincta*. (A) Anterior margin of the cranium. (B) Hypostomal region. (C) Ventral aspect, mandibular teeth. (D) Dorsal aspect, mandibular teeth. (E) Apex of maxillary palpus, box indicates location of peg-like sensilla. (F) Peg-like sensilla. (G) Labiohypopharynx, box indicates location of labial palpus. (H) Labial palp. Au, aulaeum, Hy, hypostoma, LP, labial palpus; LPT, lateral premental teeth; MPlp, maxillary palpus; PLT, prementoligular teeth; VPSp, ventral premental spicules; 1-C, seta 1 cranium; 2–5, setae of labial palpus.

Outer surface of all legs covered with bronze scales, except where mentioned. Femur of foreleg with scales of inner surface primarily cream-colored. Foretibia and tarsomere covered with bronze scales. Foreleg tarsomeres 2–5 with inner surface covered with white scales. Femur, tibia, tarsomere 1 of midleg with inner surface covered with cream-colored scales. Midleg tarsomere 2 with bronze scales only. Midleg tarsomere 3–5 with cream-colored scales on lateral margins. Hind leg with femur, tibia, and tarsomere 1 covered entirely with bronze scales. Hind leg damaged, tarsomeres 2–5 missing. Claws of midleg modified; not equal in size or shape. *Abdomen.* Dorsum covered with bronze scales with faint magenta reflections, sternum covered with
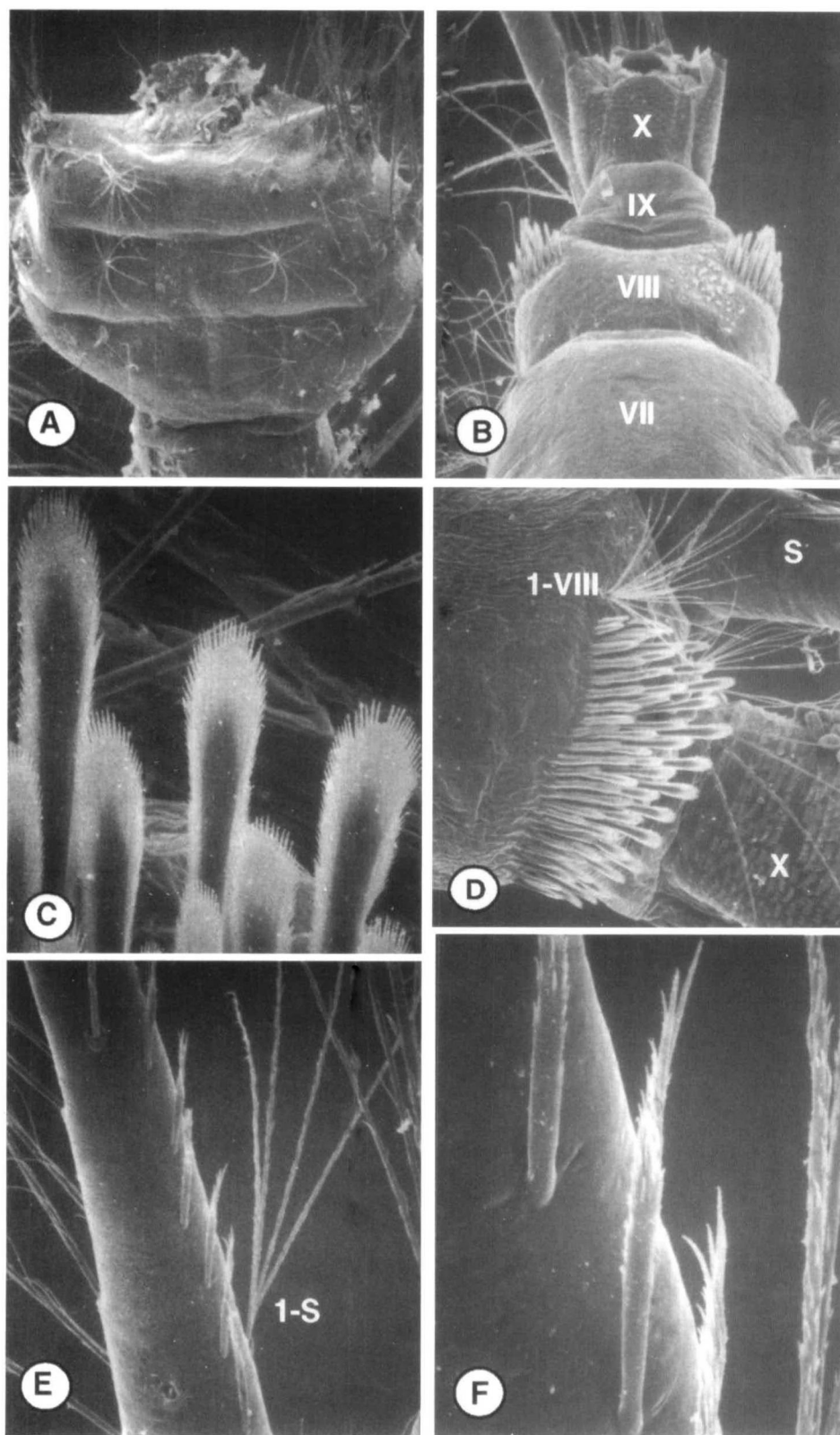
Fig. 12. Larval thoracic and abdominal structures, *W. circumcincta*. (A) Thorax, dorsal aspect. (B) Terminal segments of the abdomen, ventral aspect (C) Comb scales. (D) Abdominal segment VIII, lateral aspect. (E) Single row of pecten. (F) Individual pecten. S, siphon; Arabic numerals, homologous setae; Roman numerals, abdominal segments.
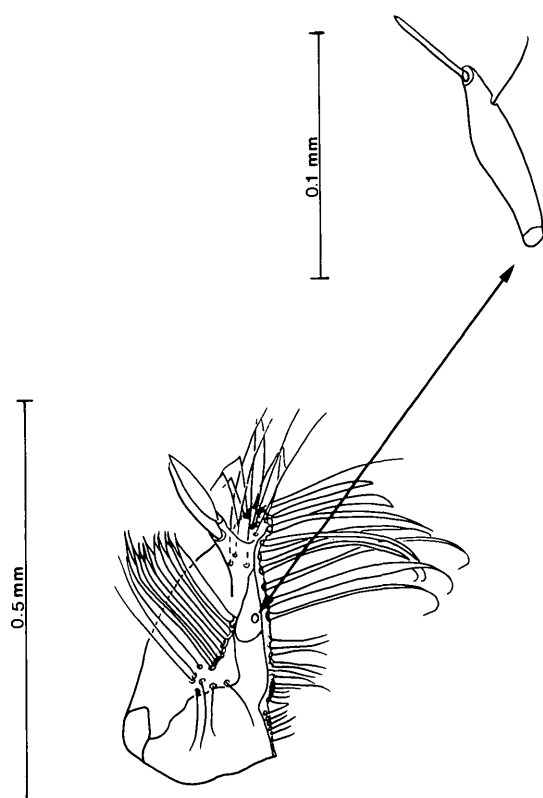
Fig. 13. Gonocoxite and gonostylus of *W. autocratica*. Gonostylus enlarged above the gonocoxite, with arrowhead marking the point of articulation on the inner margin of the gonocoxite.

white or cream-colored scales. Scales of dorsoventral line straight.

Male Genitalia (Fig. 13). *Segment VIII.* Surface of sternum and tergum covered with fine setae. Sternum with anterior margin with pair of small setae, larger setae beginning midway on segment and extending along posterior margin. Tergum with posterior marginal setae only. *Segment IX.* Sternum with anterior margin weakly emarginate, forming upside-down V, narrowing laterally, fused with tergum. Tergite with anterior margin deeply emarginate forming 2 broad lateral lobes with 3 or 4 stout, dorsoventrally flat setae at apex. *Gonocoxite.* Anterior margins free with mesal margins broadly fused and forming small lobe at base of each arm. Arm of gonocoxite with longitudinal row of 8–12 flat, stout, featherlike setae. Subapical mesal lobe produced on inner margin distal to featherlike setae, apex of lobe containing pair of broad, dorsoventrally flat, short setae. Arm of gonocoxite with posterior margin narrowed and lobelike with 4–6 dorsoventrally flat, featherlike setae. *Gonostylus.* Subapical, produced midway along inner margin of gonocoxal arm. Appearance fingerlike, width more or less uniform throughout. Gonostylus with stout, spinelike seta at apex, a 2nd normal type seta subapically on outer margin. *Mesal sclerite.* Joined on midline of gono-

coxal lobe, consisting of narrow strip of sclerite, this extending up arm of gonoxite, apparently enveloping base of gonostylus. *Aedeagus.* Apex of lateral tergal arms fused, extending anteriorly, fusing basally with tergal bridge. Median sternal plate spatulate, lateral and apical margins emarginate not extending beyond apex of lateral tergal arms. Paired, conical, darkly sclerotized structures with truncate, concave apices near base of median sternal plate. *Proctiger.* Weakly sclerotized at base with 1–2 teeth produced at apex. Upper surface of membrane with 5–6 small setae.

Pupa (Figs. 6 B and C, 7B). Chaetotaxy as figured. *Cephalothorax.* Pigmentation uniform, light golden tan, except at apex of posterior scutal angle, this unpigmented. Seta 1 weakly hooked at apex. Seta 8 unbranched. Ecdysial sutures absent. *Trumpet:* Brown, length 0.84–1.14 mm. Width significantly narrowed, frequently <0.02 mm. Apex slightly swollen, not >0.05 mm. *Metanotum and Abdomen.* Cuticle weakened, hyaline on dorsum of segment I surrounding seta 1. Seta 11 on ventral surface, all other setae apparently absent. Some specimens with singular circular pit located immediately lateral of ventral midline. Segments II–VIII concolorous with cephalothorax. Minute, uniformly spaced spicules on segments II–VIII. Intersegmental sclerites darkly pigmented posterior to segment II, III, IV, and V. Seta 11-II present, all other setae apparently absent. Seta 5-IV–VI single and elongate, extending length of 2.5 abdominal segments. Seta 14-VIII present. *Paddle.* Uniformly oblong, narrowing at apex. Short, 0.7 length of seta 9-VIII. Surface glabrous, lateral margins spiculate. Midrib prominent, width 0.02 mm and extending just short of caudal margin. *Male Genital Lobe.* Longer than paddle, oblong with apex attenuated.

Larva (Figs. 8 B and D, 10). Chaetotaxy as figured. *Cranium.* Oval with anterior margin produced, slightly wider than long. Margin straight between setal pair 1-C. Cranial setae 4–14 branched. Occipital foramen with dorsolateral slit extending anteriorly 0.20 mm anteriorly. *Antenna.* 0.26 mm long. Antennal seta 1 located on inner dorsal margin of apical 3rd. *Hypostoma.* Median tooth prominent, with 10 teeth decreasing in height toward the lateral margin. *Mandible.* Anterior tooth extended, with 3 smaller teeth below. Dorsal teeth absent. *Maxillae.* Seta 3-Mx on outer margin of maxilla, in sclerotized pocket or notch. Laciniarastrum with small apical tooth. Palpus, palpiger, maxillary body separate. Palpus bearing 4 sensilla at apex, 3 coneshaped, 1 peglike. Palpiger hyaline, seta 6-Mx single or bifid. *Thorax:* Surface glabrous. *Abdomen.* Surface glabrous. *Segment VIII. Siphon.* Length 0.93–0.99 mm. Pecten elongate, spinelike, in single row, number appears variable, 2–13 (although many appear to have been removed during mounting). *Anal Segment.* Saddle incomplete covered with rows of intermittently spaced spicules. Paired, fanlike, 8-branched accessory setae located on ventral surface, sclerite absent between setae.

Bionomics. Larvae have been collected in fluid-filled bromeliads. Collection records report *Aechmea*

nudicalulis (L.), *A. bromelicola*, and *Gravisia aquilega* (Salisb.) as plant hosts.

Distribution. Known only from Trinidad.

Systematics. This species is related mostly closely to *W. lamellata* and *W. lopezii.* These 3 form a 2nd species group in *Hystatomyia.*

Material Examined (USNM, FSPUSP). TRINIDAD: 2 pinned males, 2 male genitalia slide-mounted, 18 reared larval and pupal exuviae, 7 whole larvae. TRINIDAD: Saint Andrew, Saint George, Tamana.

Reduction of *Phoniomyia* Theobald. Cladistic analyses (Judd 1995, 1996) unambiguously place *Phoniomyia* within the genus *Wyeomyia.* Further, when characters from larval, pupal, and adult life stages are analyzed simultaneously, *Phoniomyia* is always placed as the sister group of *Hystatomyia.* Extreme elongation of the proboscis in adults of *Phoniomyia* is often used to diagnose species. However, use of this character has caused species belonging to other subgenera to be included in *Phoniomyia* (Judd 1996). Ease of recognition, by virtue of autapomorphies, has long influenced the nomenclatural rank of taxa in systematics. Although the acceptance of paraphyletic groups is pleasing to some, it is misleading and is not sound scientific practice. I agree that species in *Phoniomyia* can be diagnosed more easily than other sabethine groups, however, these species are only modified members of *Wyeomyia.* Therefore, and in keeping with the classification of Dyar (1928), *Phoniomyia* is reduced to a subgenus of *Wyeomyia.* The subgenus *Phoniomyia* contains the following 22 species: *Wyeomyia* (*Phoniomyia*) *longirostris* Theobald-type species, *W. antunesi* Lane & Guimaraes, *W. bonnei* (Lane & Cerqueira), *W. davisi* (Lane & Cerqueira), *W. deanei* (Lourenço de Oliveira), *W. diabolica* (Lane & Forattini), *W. edwardsi* (Lane & Cerqueira), *W. flabellata* (Lane & Cerqueira), *W. fuscipes* Edwards, *W. galvaoi* (Correa & Ramalho), *W. incaudata* Root, *W. lassalli* (Bonne-Wepster & Bonne), *W. lopesi* (Correa & Ramalho), *W. muehlensi* Petrocchi, *W. pallidoventer* (Theobald), *W. palmata* (Lane & Cerqueira), *W. pilicauda* Root, *W. quasilongirostris* Theobald, *W. splendida* Bonne-Wepster & Bonne, *W. theobaldi* (Lane & Cerqueira), *W. trinidadensis* Theobald, and *W. tripartita* (Bonne-Wepster & Bonne).

Remaining Taxa. The only remaining species from component A (Fig. 1) left without subgeneric placement is *W. albosquamata.* Formerly placed in the subgenus *Dendromyia* (sensu Knight and Stone 1977), it was clearly misplaced. The following 3 characters of the larval maxilla place *W. albosquatmata* in this clade: palpifer separate from body of maxilla and palpus, presence of a small apical tooth, and a spineform laciniarastrum. To resurrect *Eunicemyia* Dyar & Shannon (1924) for this species alone would continue the proliferation of monotypic subgenera in this and other lineages and serves no useful purpose. Further, I hesitate to include this species in the nominal subgenus until the boundaries are defined more clearly.

The type species for *Wyeomyia* is *W. grayii* and it appears as the basal taxon in Fig. 1, component A. The nominal subgenus is not demonstrably monophyletic,

but which species should be included is unclear. This subgenus is badly in need of revision. Species belonging to this group occur among 3 sister clades in Fig. 1. Additional analyses adding more taxa and characters have clarified relationships and 2 of the more obvious problems, *W.* (*Wyeomyia*) *codiocampa* + *W.* (*Wyeomyia*) *oblita* and *Limatus*, will be addressed in the near future (Judd, in prep).

Conclusions

The Sabethini require reclassification. The 31 species assigned to *Dendromyia* by Edwards (1932) and left without subgeneric placement by the revision of Albuquerque Motta and Lourenço-de-Oliveira (1995) have available names (see Judd 1996, table 1). Although it might be tempting to resurrect Dyar's available names, the characters of these species have not been thoroughly studied. In addition, it is clear from my results (Judd 1995, 1996) that use of "traditional characters" or single character systems will not lead to a classification that is natural. Belkin (in Heinemann and Belkin 1977) used some of Dyar's available names in his publications on the *Mosquitoes of Middle America*; however, he clearly stated in bold text that "It should be particularly noted that the subgeneric division of *Wyeomyia* used here is completely different from the currently accepted system and was instituted purely to facilitate preliminary identifications, and, as stated above, in no way constitutes a change in taxonomy." There is no harm in leaving these taxa unplaced and it will encourage robust revisionary work on sabethines.

How one organizes taxa into groups and names them is open to considerable debate (Miyamoto 1985, Bryant 1994, Carpenter et al. 1995, Liden and Oxelman 1996, Lee 1996, Carroll 1997). Simultaneous analysis provides the best hypothesis for the data in my study (Judd 1996, 1998), and it is upon this framework that much of the reorganization is focused. However, some of these nodes are susceptible to perturbation as tested by SCA (Judd 1998) and addition of new data (Judd, in prep.). Partitioning characters is an option for exploring the effects of specific characters independent of a "total evidence" analysis. Mapping characters on to the partitioned and combined trees demonstrates that some characters are better for resolving specific areas of the tree than others and that certain characters are more homoplastic (e.g., larval mouthparts).

Evolution should not be an a priori consideration in cladistic analyses (Brady 1985). However, once the framework is provided through empirical analysis of data, carefully constructed questions can be used to test the pattern. This article focuses on a lineage of mosquitoes restricted to developing and ovipositing in plant-held fluids. Homoplasy is an indicator that investigator error or some phenomenon other than common ancestry affects the character. Partitions that restrict character sets to a particular life stage can provide additional insight into these areas.

Acknowledgments

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