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MORPHOLOGY AND EVOLUTION OF THE LARVAL MAXILLA AND ITS IMPORTANCE IN THE CLASSIFICATION OF THE SABETHINI (DIPTERA: CULICIDAE)¹

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ABSTRACT. Several larval maxillary structures of previously unknown or confused homology were investigated in species and genera of the tribe Sabethini. Particularly important discoveries were made with regard to the maxillary brush, its structural homologs, and the development of an associated apical tooth-like process of the maxillary body. The specific determination of homologous structures of the larval maxilla explains the morphological similarities and differences exhibited by groups of seemingly related and unrelated taxa. The findings are of considerable use in understanding phylogenetic relationships and defining supraspecific categories. Structural relationships and homologies, and their significance, are discussed. *Isostomyia* Coquillett is elevated from a subgenus of *Runchomyia* Theobald to generic rank based on larval maxillary structure and correlated distinctions in the adult, larval, and pupal stages.

INTRODUCTION

No other group of mosquitoes displays the complexity and diversity of larval structure that is found in the tribe Sabethini. Unfortunately, this diversity of structure has been used very little in classification, and the majority of the genera and subgenera are presently based on adult morphology. Inattention to larval morphology is responsible for the many unnatural groups of species now known to exist within the tribe, especially for groups defined by Lane and Cerqueira (1942) and Lane (1953) for New World taxa and Mattingly (1980, 1981) and other authors for Old World taxa. Studies by Zavortink (1979), Harbach and Peyton (1990, 1991, 1992), and Harbach (1991) eloquently demonstrate the value of using larval characters in recognizing monophyletic groups within the tribe.

Although larval mouthparts have been described and illustrated in some more recent taxonomic studies, the character states of mouthparts have not been used to define supraspecific categories or to determine phylogenetic relationships. In this paper we describe the basic components of the larval maxilla, recognize and define modifications of homologous structures for the first time, introduce new terminology, and examine phylogenetic implications of maxillary structures in the tribe Sabethini. Convergent developments are noted for some genera and subgenera of sabethine and aedine mosquitoes.

MATERIALS AND METHODS

Fourth-instar larvae preserved in ethanol and larval exuviae mounted on microscope slides were used in this study. Heads were removed from preserved larvae and transferred to a drop of clove oil under a stereoscopic microscope where the maxillae and mandibles, and in some cases the labiohypopharynx, were removed using finely sharpened stainless steel minuten nadeln inserted into applicator sticks. The dissected mouth-

¹ The views of the authors do not purport to reflect the views of the Department of the Army or the Department of Defense.

² Reprint requests: Walter Reed Biosystematics Unit, Museum Support Center, MRC 534, Smithsonian Institution, Washington, DC 20560.



parts were transferred to a thin layer of copal-phenol mixture on a microscope slide, properly positioned, and placed in an oven at 45–50°C for at least 24 h. Cover slips were then added over a drop of euparal, and the slides returned to the oven for an additional 2–3 wk. In most cases the head and body of the larva were mounted on the slide with its mouthparts. The mouthparts of one or more specimens were dissected for each species studied, and the maxillae of at least one species of each genus and most subgenera of the tribe Sabethini were examined.

Maxillae typical of all sabethine genera are illustrated in this report. New morphological terminology and abbreviations are introduced for highly modified or derived structures, otherwise the terminology and abbreviations recommended by Harbach and Knight (1980) are used throughout. Specimens used in this study are deposited in the National Museum of Natural History, Smithsonian Institution, and the University of Sao Paulo, Brazil.

OBSERVATIONS AND DISCUSSION

Because the head of the mosquito larva is basically prognathous, the mouthparts are considered as anterior appendages. The maxillae are typically flattened lobes borne obliquely on the transverse margin of the lateralialia where they lie ventral to the mandibles. For simplicity, the surface of each maxilla adjacent to a mandible is considered to be dorsal, the side bearing the maxillary palpus is lateral, the side near the midline of the head is mesal, and the surface lying adjacent to the lateralialia is ventral (Knight and Harbach 1977).

The basic components of the larval maxilla (labeled in Figs. 1A,B;5C,D) include the maxillary palpus (MPlp), merostipital sclerite (mSS), laciniastipes (LSt), galeastipes (GSt), and the cardo (Cd) (Harbach and Knight 1977, 1980). For the most part, these components are separate and distinct only in certain aedine genera, e.g., *Opifex* Hutton and *Haemagogus* Williston, and we postulate that

this condition represents the culicid ground plan. In most genera, the laciniastipes and galeastipes are indistinguishably fused to form the main body of the maxilla (maxillary body, MxBo), the merostipital sclerite is either fused with or incorporated into the base of the maxillary palpus, and the cardo is an independent structure. Among the genera of Sabethini, this condition is present in *Maorigoeldia* Edwards (Fig. 1A,B), most *Wyeomyia* Theobald, and the nominotypical subgenus of *Topomyia* Leicester (Fig. 1C). In other sabethine genera, the cardo is either joined with the base of the maxillary palpus (*Trichoprosopon* Theobald, *Tripteroides* Giles), united with the maxillary body (*Limatus* Theobald, some *Suaymyia* Thurman of *Topomyia*, and some *Wyeomyia*), or fused with the palpus and body of the maxilla to form a single structure (*Sabethes* Robineau-Desvoidy, *Malaya* Leicester, *Johnbelkinia* Zavorlink). These three character states—(1) fusion of the palpus and cardo, (2) fusion of the cardo and maxillary body and (3) fusion of the palpus, cardo and maxillary body—are derived conditions that evidently occurred independently in several sabethine taxa. Among non-sabethine genera, the cardo and palpus are fused in *Aedeomyia* Theobald and *Hodgesia* Theobald, and all three components are fused with each other in the subgenus *Lutzia* Theobald of *Culex* Linnaeus and the nominotypical subgenus of the genus *Psorophora* Robineau-Desvoidy. The cardo is weakly developed in species of *Phoniomyia* Theobald, *Runchomyia* Theobald, *Isostomyia* Coquillett (new status as genus, see below), *Shannoniana* Lane and Cerqueira, and the subgenus *Suaymyia* of *Topomyia*, and its seta (6-Mx) seems to arise from the membrane at the proximal margin of the maxillary body.

The larval maxilla bears two principal functional structures that play a role in feeding. In most mosquitoes, the apex of the maxillary body (galeastipes) bears a prominent collection of spicules known as the **maxillary brush** (MxB) and the dorsomesal margin (laciniastipes) bears three rows or patches of spicules known as the **laciniarastra**. The maxillary

brush and the most mesal of the laciniarastra (= laciniarastrum 1, hereafter referred to simply as the **laciniarastrum**, LR) are variously modified to feeding in different ways on different kinds of food. In no other group of mosquitoes are the modifications more striking than the homologous structures in certain genera and subgenera of the tribe Sabethini.

The maxilla in Sabethini has taken two different courses of evolution. In one, the modified maxillary brush has become the primary functional feature, and in the other, leading toward the genus *Sabethes*, the laciniarastrum has become the dominant feature. The dominance of one feature over the other is not entirely complete in species of the subgenus *Ctenogoeldia* Edwards of *Runchomyia*.

Most sabethines have a maxillary brush much like that found in the majority of non-sabethine species of the subfamily Culicinae. The typical brush consists of a number of independent, basally articulated, flexible elements which serve to collect food particles from the palatal brushes. In the derived condition, all or most of the elements are partially or completely coalesced into a single articulated structure. We hypothesize that the first step in this transformation is represented by the agglutination of some brush spicules, similar to the condition exhibited by the maxillary brush of *Tripteroides nepenthicola* (Banks) (Fig. 2A,B). Further coalescence of spicules resulted in the formation of a structure referred to here as the **maxillary bundle** (MxBn) (= maxillary stylus of Harbach and Knight 1980). The maxillary bundle consists of partially fused, bound or ensheathed spicules, with clear evidence of individual elements internally or at least apically (Figs. 3;4;5A,B), and is generally flexible. From this derived state, further transformation gave rise to a rigid **maxillary claw** (MxC), which represents the completely fused and unrecognizable elements of the maxillary brush (Figs. 6;7A,B). In some cases, the bundle and claw are accompanied by a number of independent basal spicules (labeled MxB in Figs. 4C,D;7A,B), which is further evidence that

these structures evolved from the typical brush. Concomitant with the transition from brush to claw, the derived structures became distinctly hinged basally and partially opposed obliquely toward the mouth. The functional aspects of these modifications are presently unknown, but they appear to be adaptations for collecting food by sweeping, scraping, or clasping.

The presence of an apical process of the maxillary body is typical of sabethine larvae. The exact homology of this feature is unknown, but it may have originated as a simple elongation of the apex of the maxilla or as a modification of the most distal element of the laciniarastrum. In the majority of sabethines, the structure has the appearance of a small bump or protuberance (Figs. 1;2), but in certain others it is developed into a prominent tooth- or claw-like process (**apical tooth**, AT). With the exception of *Sabethes* and a few *Wyeomyia* (see below), a well differentiated apical tooth appears to have evolved in concert with the maxillary bundle and claw. The maxilla of *Sabethes* bears a typical brush, except that it is much reduced in size and the individual elements are simple spicules (Fig. 8A,B). The dominant feature of the *Sabethes* maxilla is the strongly developed prong- or claw-like apical tooth (Fig. 8A,B), which probably plays a specialized role in the acquisition of food.

In those taxa where a specialized apical tooth is developed in conjunction with a bundle or claw, the body of the maxilla is long and slender and the elements of the laciniarastrum are often weakly developed (except *Shannoniana*). Members of the subgenus *Ctenogoeldia* of *Runchomyia* bear an apical tooth that is almost as large as the associated maxillary bundle (Fig. 3A,B), while species of the nominotypical subgenus of *Runchomyia* possess an apical tooth that is much longer than the associated bundle (Fig. 3C,D). The adaptive significance for the presence of an apical tooth together with a bundle or claw is unknown, but it is obvious that this condition and the one observed in *Sabethes* represent two very different lines of descent.

Table 1. Summary of apical maxillary structures among the genera, certain subgenera and groups of the tribe Sabethini.^a

Taxon	Brush	Bundle	Claw	Prominent Tooth	Distribution ^b
<i>Limatus</i>	Yes	—	—	—	NW
<i>Malaya</i>	Yes	—	—	—	OW
<i>Maorigoeldia</i>	Yes	—	—	—	OW
<i>Phioniomyia</i>	Yes	—	—	—	NW
<i>Tripteroides</i> (except <i>Rachisoura</i>)	Yes	—	—	—	OW
<i>Tripteroides</i> (Mabinii Group)	Yes	—	—	Yes	OW
<i>Trichoprosopon</i>	Yes	—	—	—	NW
<i>Topomyia</i> (<i>Topomyia</i>)	Yes	—	—	—	OW
<i>Wyeomyia</i>	Yes	—	—	Yes/No ^c	NW
<i>Wyeomyia</i> (<i>Prosopolepis</i> Group)	Yes	—	—	Yes	NW
<i>Sabethes</i> ^d	Yes	—	—	Yes	NW
<i>Topomyia</i> (<i>Suaymyia</i>) ^e	—	Yes	—	—	OW
<i>Johnbelkinia</i>	—	Yes	—	Yes	NW
<i>Runchomyia</i> (<i>Ctenogoeldia</i>)	—	Yes	—	Yes	NW
<i>Runchomyia</i> (<i>Runchomyia</i>)	—	Yes	—	Yes	NW
<i>Isostomyia</i>	—	—	Yes	Yes	NW
<i>Shannoniana</i>	—	—	Yes	Yes	NW
<i>Tripteroides</i> (<i>Rachisoura</i>)	—	—	Yes	Yes	OW

^a Not intended to show phylogenetic relationships.

^b NW = New World; OW = Old World.

^c It is apparent that there are several distinct phyletic lines within some currently recognized subgenera of *Wyeomyia*, particularly *Dendromyia*. These groups are too numerous and too poorly known to be listed here separately. The genus needs to be revised.

^d The unique apical tooth in *Aedes* (*Diceromyia*) *kanarensis* bears a resemblance to that in *Sabethes* (*Davismyia*) *petrocchia* (see Harbach and Peyton 1991:Fig. 3), except that it has a differentiated bulbous tip (see Tewari et al. 1990:Fig. 3).

^e Similarly developed in *Heizmannia* (*Mattinglyia*) *discrepens*.

Table 1 summarizes the development of the apical structures of the maxilla in the genera, certain subgenera and groups of the tribe Sabethini. Species of *Limatus* (Fig. 9C,D), *Maorigoeldia* (Fig. 1A,B), *Malaya* (Fig. 1D), *Topomyia* (*Topomyia*) (Fig. 1C), *Phioniomyia* (Fig. 9B), *Tripteroides* (except *Rachisoura* Theobald), and *Trichoprosopon* (Fig. 2C,D) have a typical maxillary brush. Other exceptions, besides *Rachisoura*, occur in the genus *Tripteroides*. The maxillae of *Tripteroides mabinii* Baisas and Ubaldo-Pagayon (Fig. 7C,D) and *Tripteroides riverai* Miyagi, Toma and Tsukamoto, currently regarded as members of the subgenus *Tripteroides*, have a long acuminate apical tooth, suggestive of *Sabethes*, and the maxillary brush is borne basolaterally on the dorsal side opposite the maxillary palpus. Other modifications include partially coalesced maxillary

brush elements in species like *Tripteroides nepenthicola* (Fig. 2A,B) (subgenus *Tricholeptomomyia* Dyar and Shannon) and the presence of a small apical tooth together with a denticulate laciniarastrium in species like *Tripteroides coheni* Belkin (see Belkin 1962:Fig. 388) (subgenus *Polylepidomyia* Theobald).

Most species of *Wyeomyia* also have a typical maxillary brush (Fig. 9A), but some have maxillae with derived apical structures. One species, *Wyeomyia confusa* (Lutz), originally described from a female, was placed in the genus *Prosopolepis* Lutz, which is currently regarded as a synonym of the subgenus *Dendromyia* Theobald. The larva described and illustrated some 37 years later as this species appears to have a long maxillary bundle (see Lane and Cerqueira 1942:Figs. 412 and 413, and Lane 1953:Fig. 983) like some species of *Johnbelkinia*, and it may actually belong to a

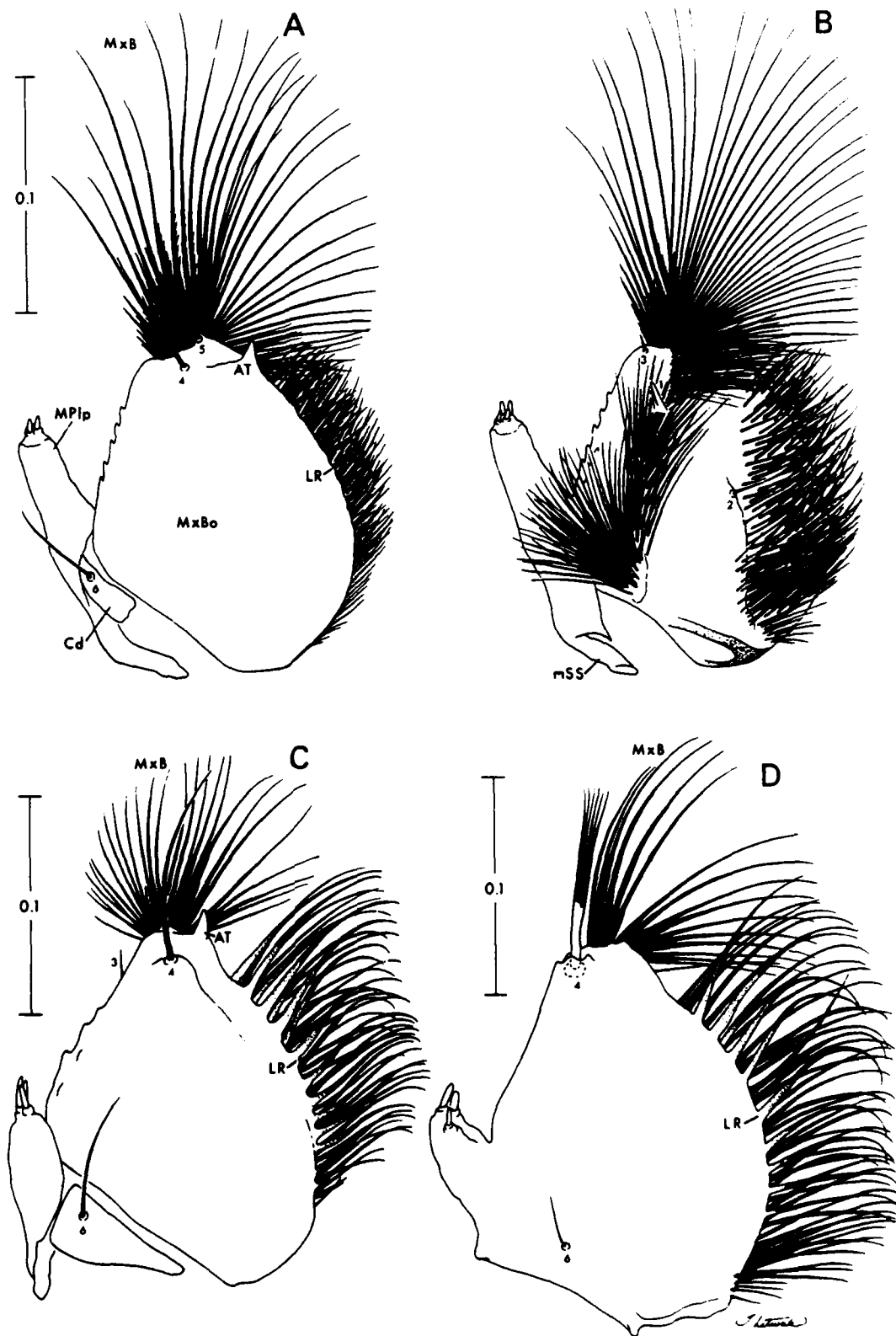


Fig. 1. Maxillae of (A,B) *Maorigoeldia argyropus* (Walker), (C) a species of *Topomyia* (*Topomyia*), and (D) *Malaya genurostris* Leicester. A,C,D. Ventral views; B. dorsal view. Scales in mm.

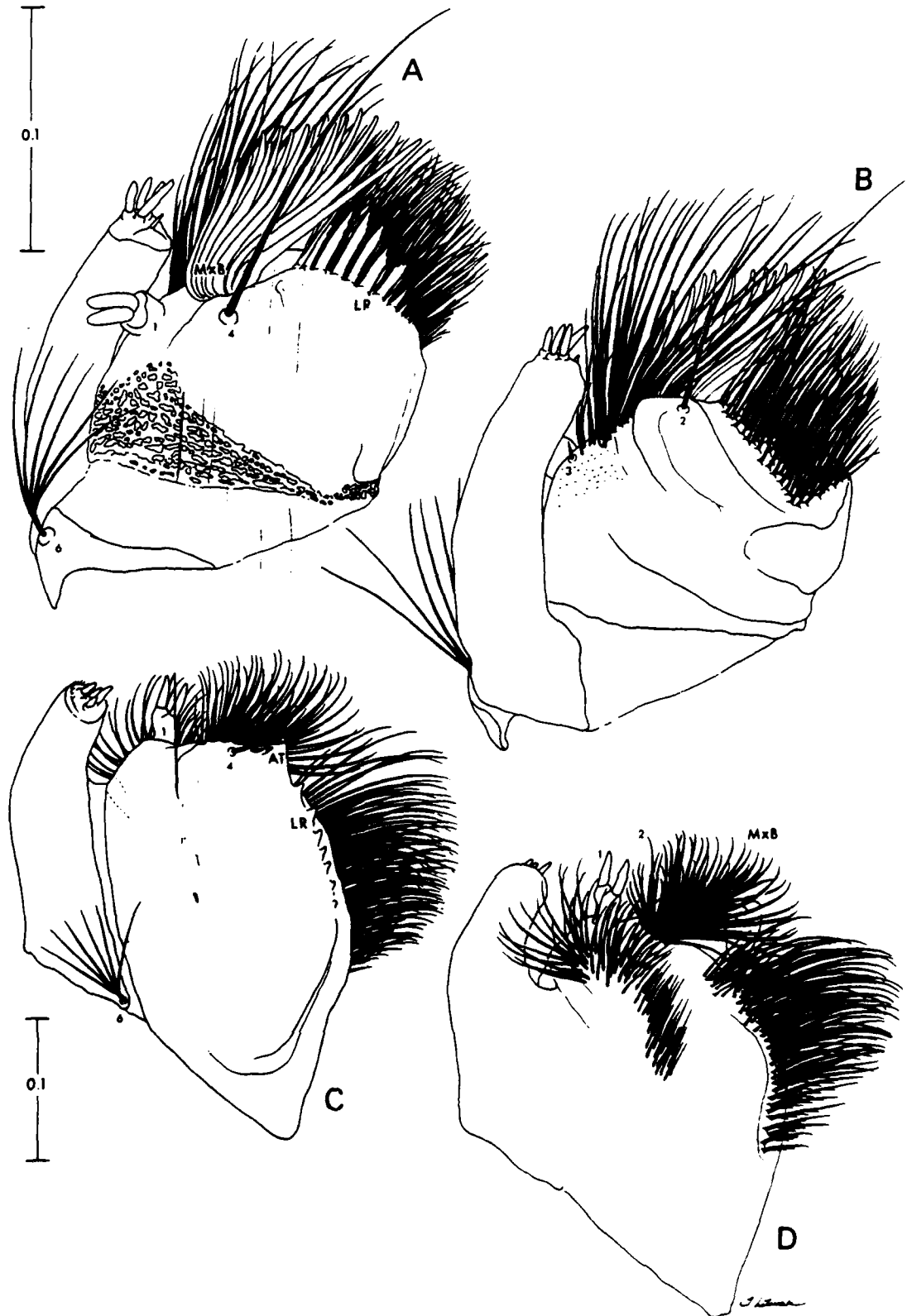


Fig. 2. Maxillae of (A,B) *Tripteroides (Tricholeptomya) nepenthicola* (Banks) and (C,D) *Trichoprosopon digitatum* (Rondani). A,C, Ventral views; B,D, dorsal views. Scales in mm.

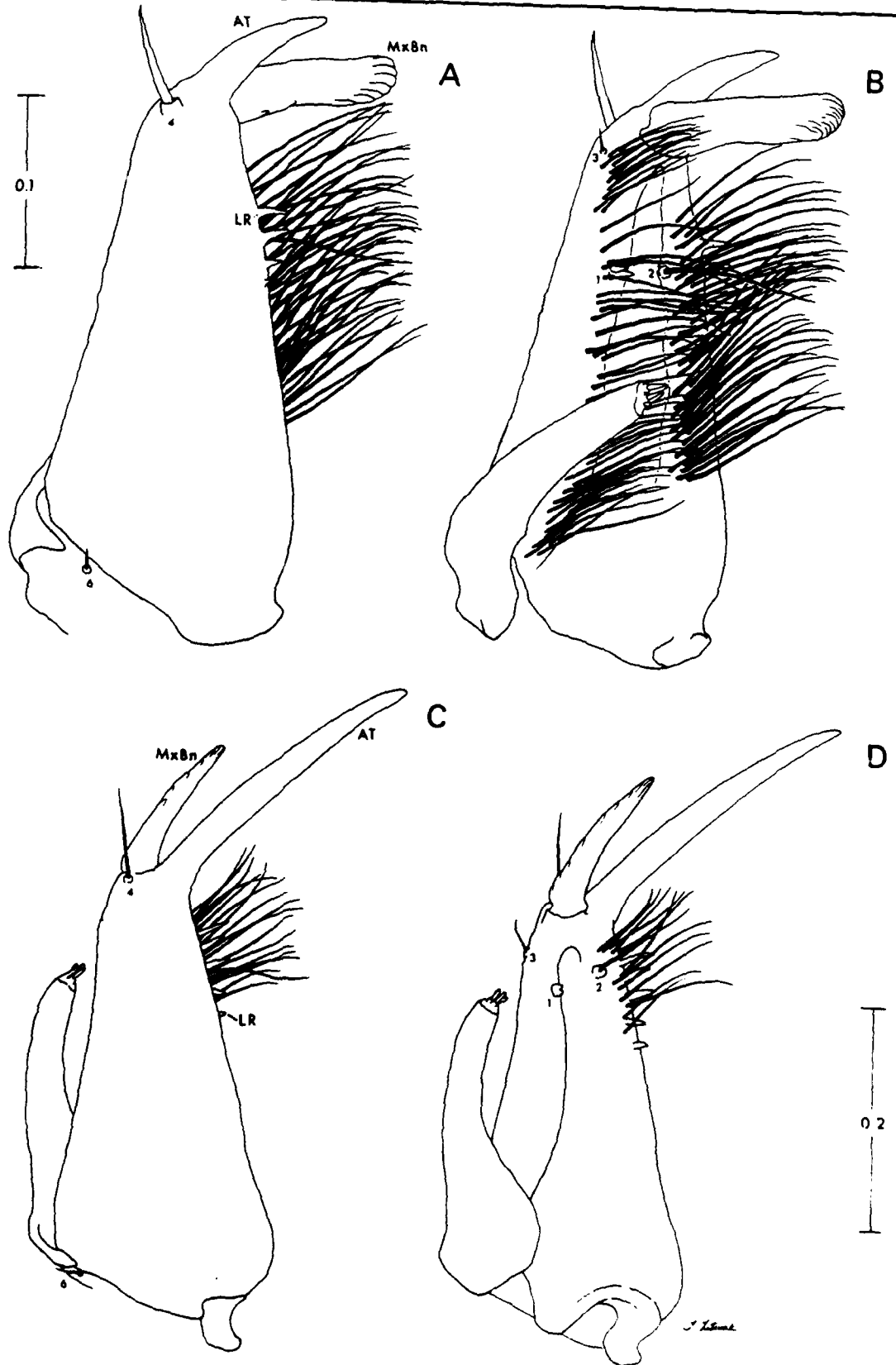


Fig. 3. Maxillae of (A,B) *Runchomyia (Ctenogoeldia) magna* (Theobald) and (C,D) *Runchomyia (Runchomyia) rapax* (Dyar and Knab) (not currently recognized as a valid species). A,C. Ventral views; B,D. dorsal views. Scales in mm.

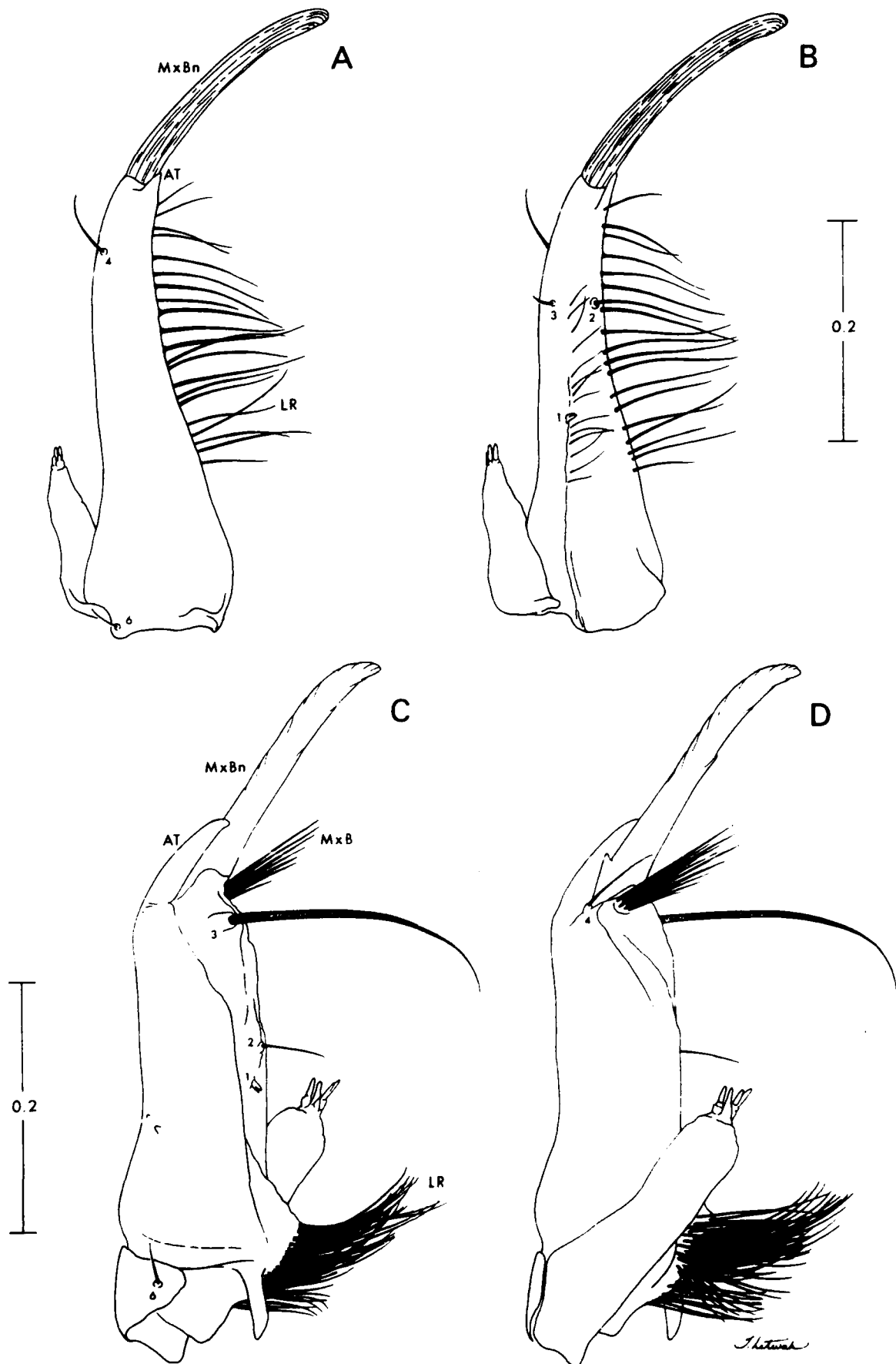


Fig. 4. Maxillae of (A,B) a species of *Topomyia (Suaymyia)* and (C,D) *Topomyia (Suaymyia) imitata* Baisas. A,C. Ventral views; B,D. dorsal views. Scales in mm.

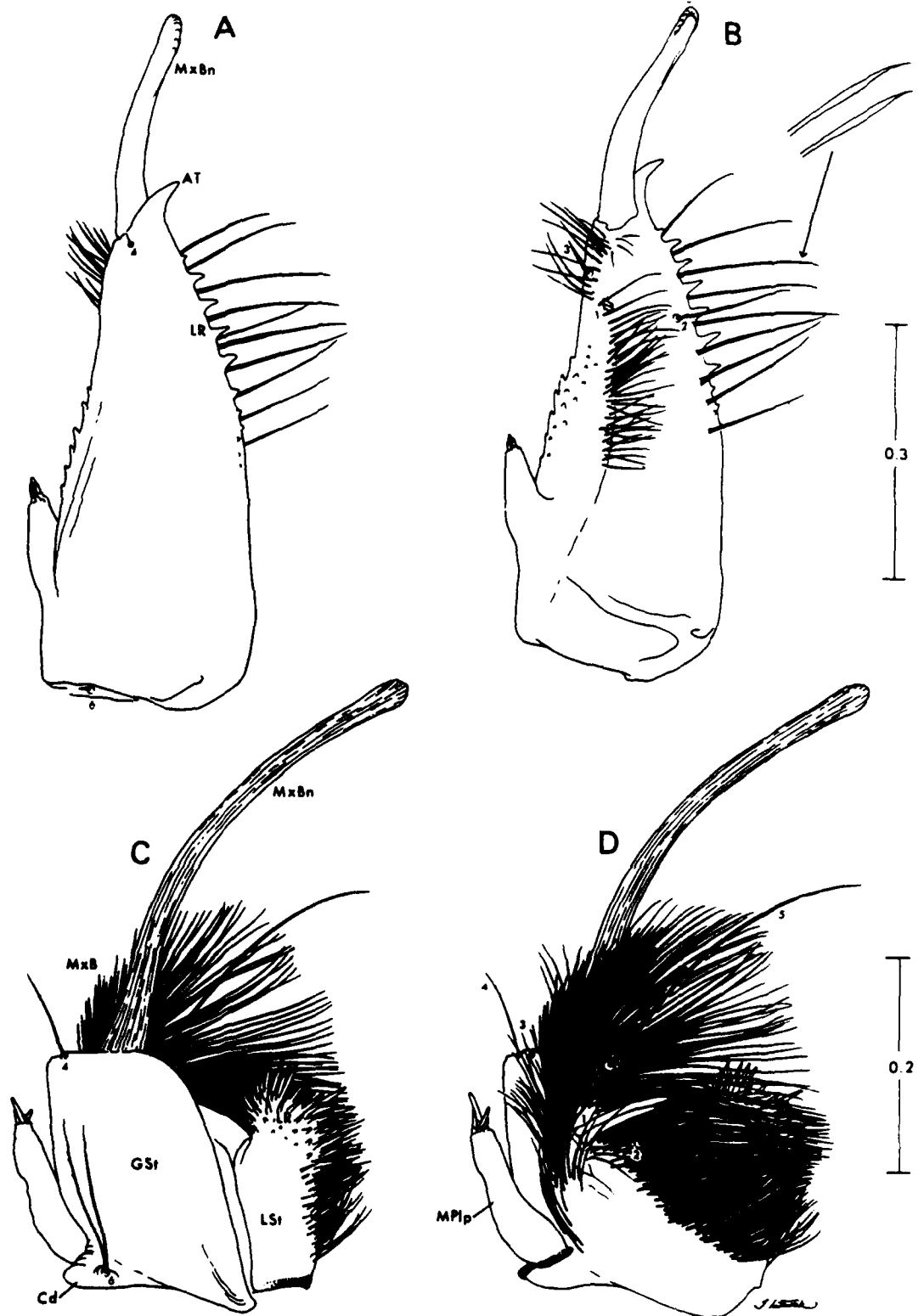


Fig. 5. Maxillae of (A,B) *Johnbelkinia longipes* (Fabricius) and (C,D) *Heizmannia (Mattinglyia) discrepans* (Edwards). A,C, Ventral views; B,D, dorsal views. Scales in mm.

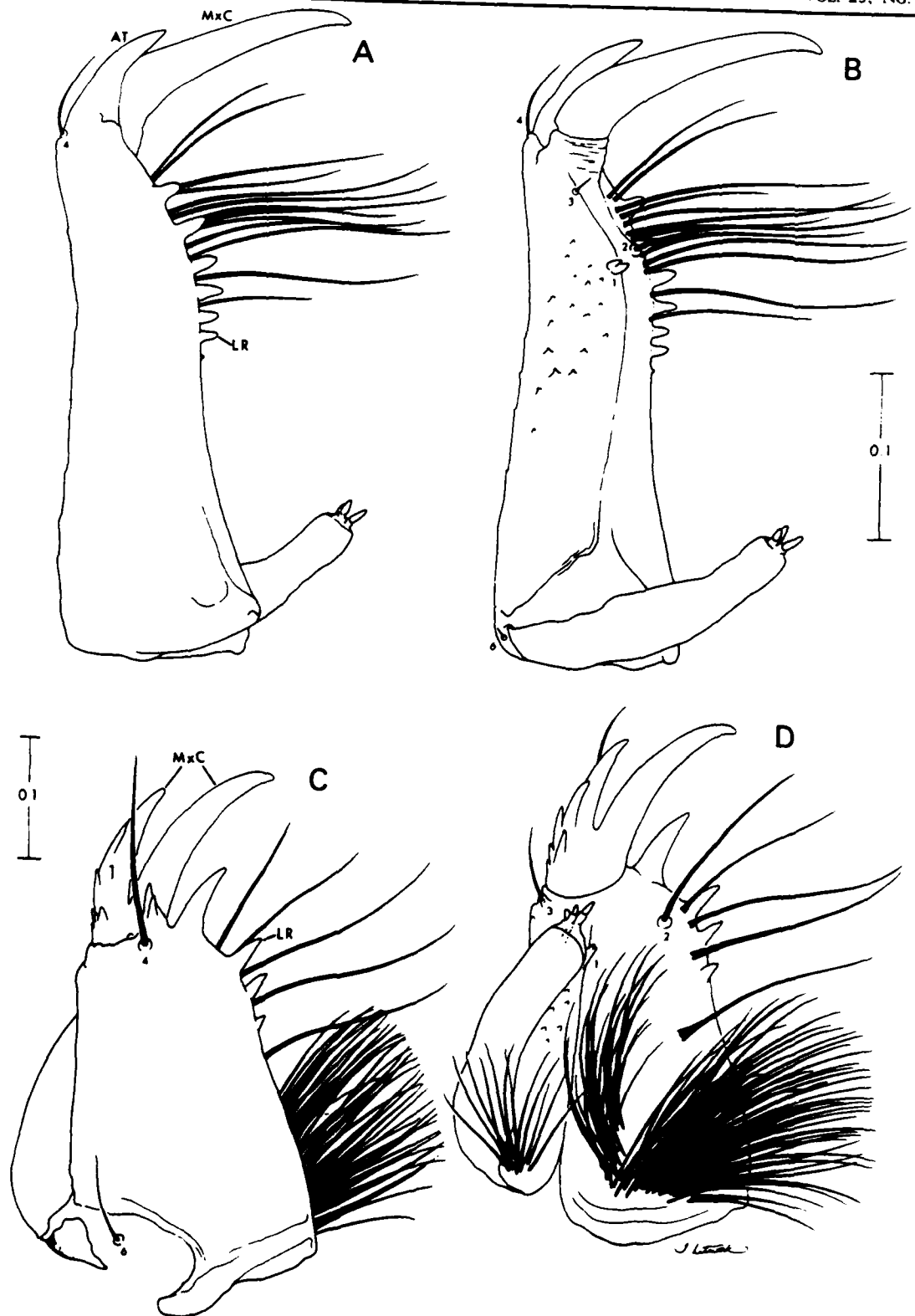


Fig. 6. Maxillae of (A,B) *Isostomyia perturbans* (Williston) and (C,D) *Shannoniana moralesi* (Dyar and Knab). A,C. Ventral views; B,D. dorsal views. Scales in mm.

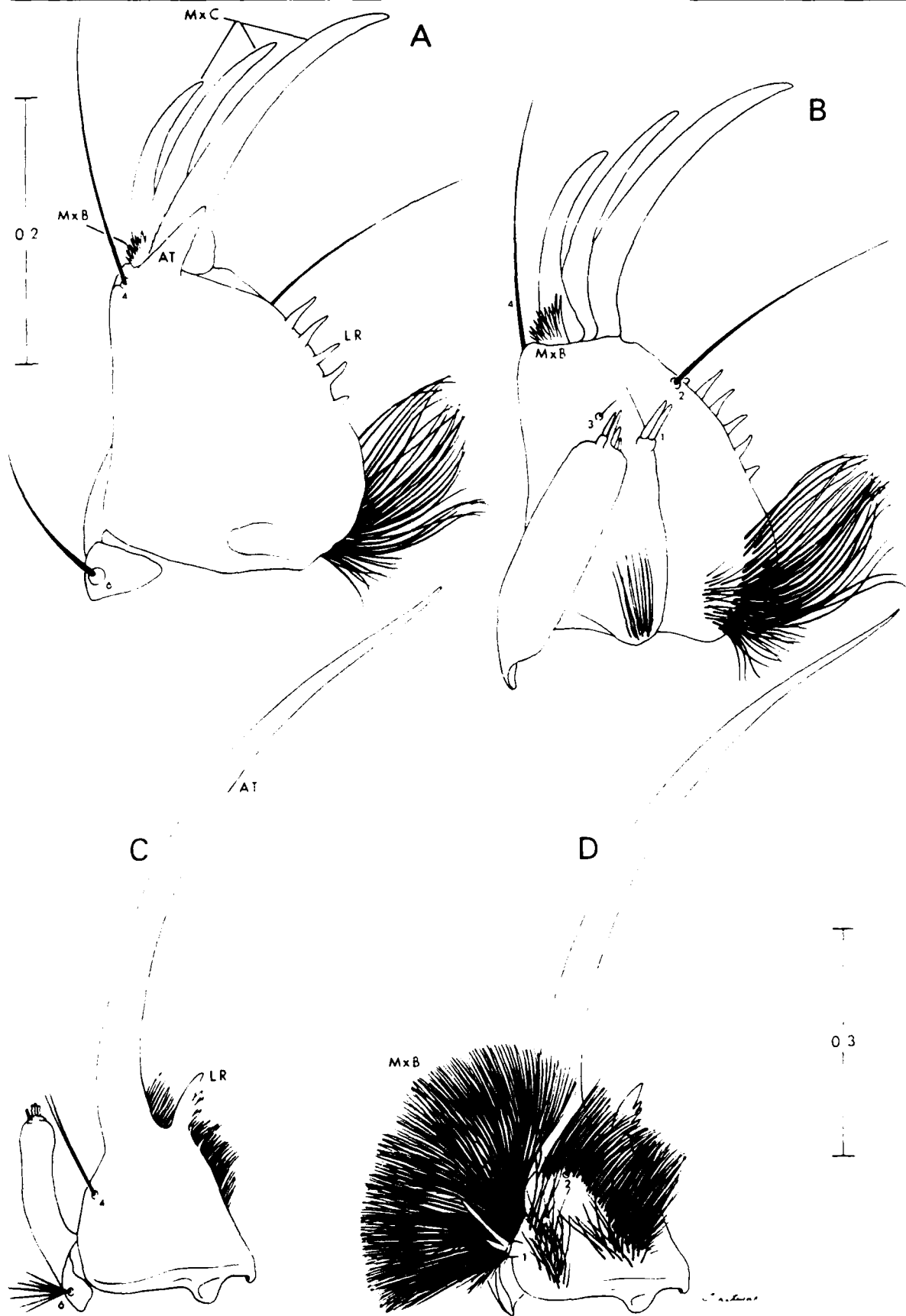


Fig. 7. Maxillae of (A,B) *Tripteroides (Rachisoura) stonei* Belkin and (C,D) *Tripteroides (Tripteroides) mahinii* Baisas and Ubaldo-Pagayon. A,C, Ventral views; B,D, dorsal views. MxB omitted from maxilla shown in C. Scales in mm.

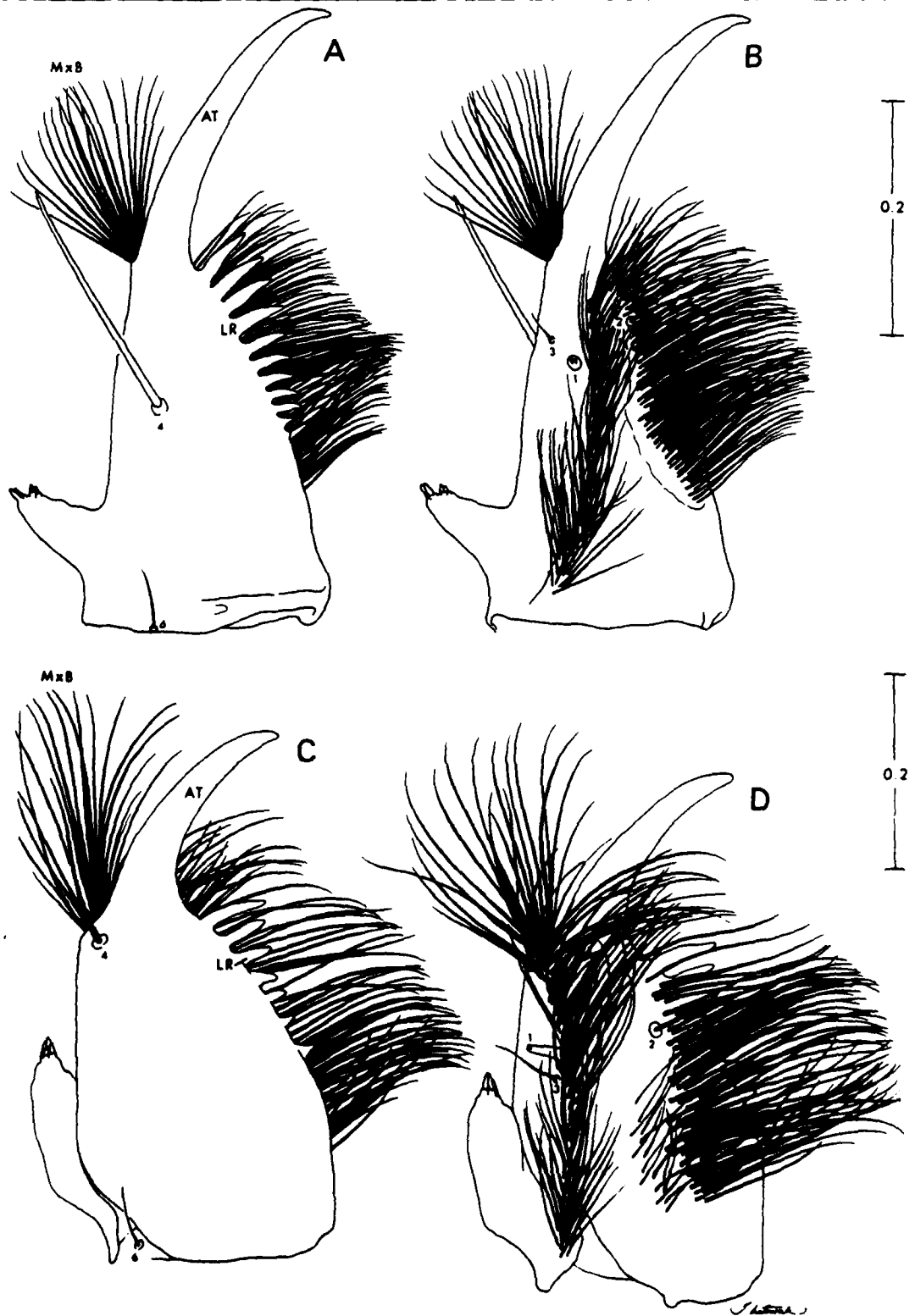


Fig. 8. Maxillae of (A,B) *Sabethes (Sabethoides) chloropterus* (von Humboldt) and (C,D) *Wyeomyia (Dendromyia) ypsipola* Dyar. A,C. Ventral views; B,D. dorsal views. Scales in mm.

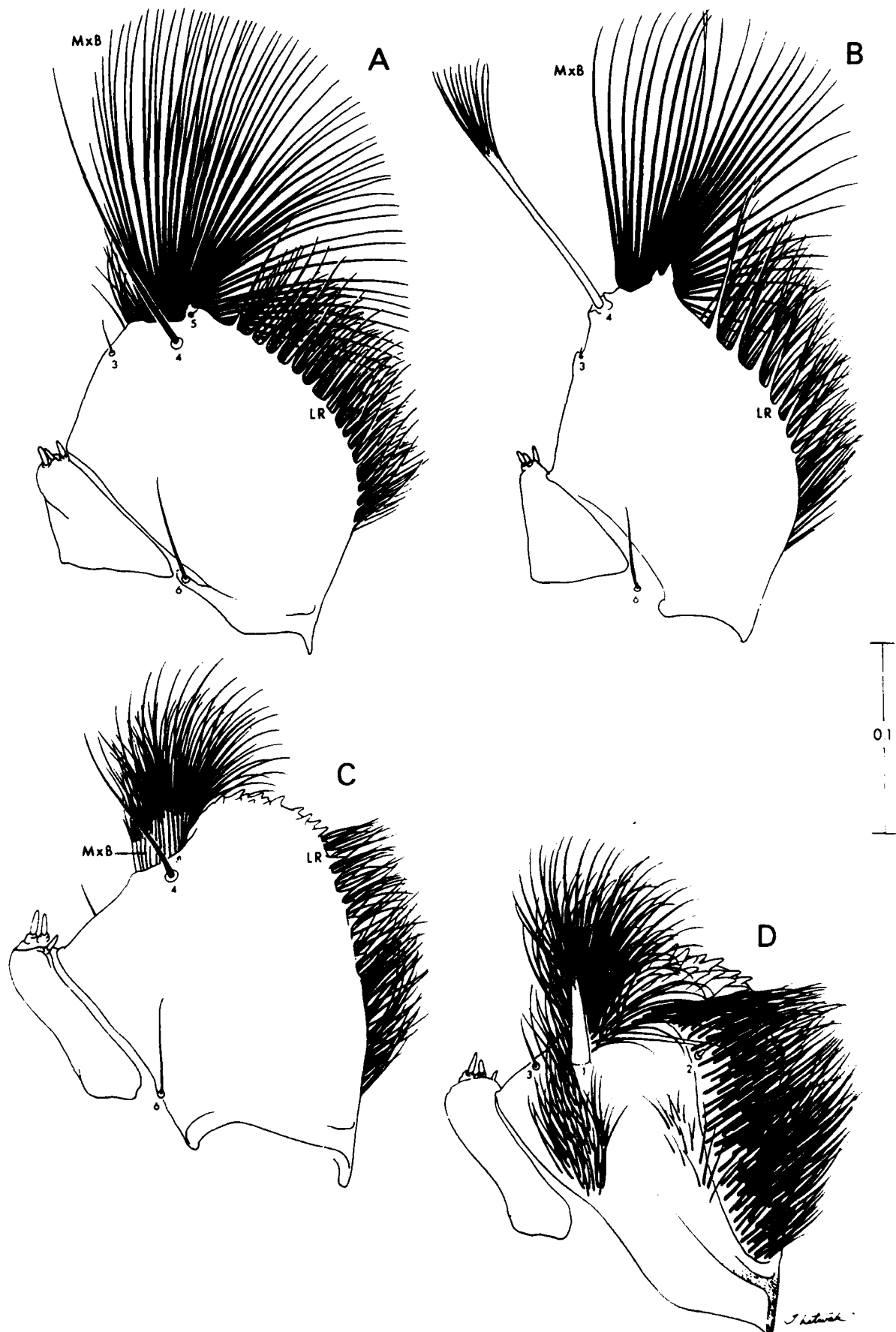


Fig. 9. Maxillae of (A) *Wyeomyia (Wyeomyia) grayii* Theobald, (B) *Phoniomyia edwardsi* Lane and Cerqueira, and (C, D) *Limatus durhamii* Theobald. A-C, Ventral views; D, dorsal view. Scale in mm.

group other than *Wyeomyia*. The specimens that Lane and Cerqueira described and illustrated apparently no longer exist (O.P. Forattini and R.L. de Oliveira, personal communications). Other species subsequently placed in *Prosopolepis* (*Wy. jocosa* Dyar and Knab), or provisionally considered by Heinemann and Belkin (1977, 1978a, 1978b) to be members of this group (*Wy. complosa* (Dyar), *Wy. testei* Senevet and Abonnenc, *Wy. trifurcata* Clastrier, *Wy. ypsipola* Dyar), have a prominent apical tooth and a rather reduced maxillary brush (Fig. 8C,D) much like species of *Sabethes* (Fig. 8A,B). The larvae of these species appear to differ significantly from that illustrated for *Wy. confusa*, suggesting that they may not be related to this species. Species of *Sabethes*, however, are unique among the Sabethini in having the palpus, cardo, and maxillary body combined into a strong, compound structure, from which projects the prominent claw-like apical tooth (Fig. 8A,B). Larvae of the genera *Johnbelkinia* and *Malaya* also have the palpus and cardo fused with the maxillary body, but the apical structures are constructed in a completely different way. Species of *Johnbelkinia* possess a maxillary bundle and an apical tooth (Fig. 5A,B), while species of *Malaya* possess a typical maxillary brush and have a small bump or denticle in place of the apical tooth (Fig. 1D). In general, those species (groups) that possess a prominent apical tooth also have the laciniarstrum developed into a mesal line of stout denticles or small teeth (*Sabethes*, *Prosopolepis*, *Runchomyia*, *Isostomyia*, *Shannoniana*, *Rachisoura*). Likewise, those species (groups) that bear a small bump or protuberance have the laciniarstrum composed of slender, flexible spicules (*Maorigoeldia*, *Phoniomyia*, most *Topomyia*, most *Wyeomyia*, most *Tripteroides*). Exceptions to this are exemplified by species of *Limatus*, *Trichoprosopon*, and certain species of *Tripteroides*, which have the laciniarstrum composed of denticles (Figs. 2C, D; 9C, D), yet the apical process is not much larger than it is in species (groups) that have the laciniarstrum composed of spicules. *Topomyia* (*Suay-*

myia) *imitata* Baisas (Fig. 4C,D) and closely allied species, e.g., *To. decorabilis* Leicester, bear a prominent apical tooth but the laciniarstrum is represented by slender spicules rather than denticles.

The maxillary bundle is present in species of *Johnbelkinia*, *Runchomyia*, and *Topomyia* (*Suaymyia*). A maxillary claw is present in species of *Shannoniana*, *Isostomyia*, and *Tripteroides* (*Rachisoura*). *Suaymyia* differs from the others that have a bundle in being an Old World group, indicating that the maxillary bundle may have arisen independently in this taxon. Since the structure of the maxilla seems to be an especially important source of evidence for monophyly, the subgenera *Suaymyia* and *Topomyia* may be more distantly related than current congeneric status indicates.

Zavortink (1979) provisionally recognized three subgenera within the genus *Runchomyia*, the nominotypical subgenus, *Ctenogoeldia* and *Isostomyia*, but stated that his treatment was "possibly too conservative, and the subgenera perhaps deserve generic rank." *Isostomyia* is elevated to generic status here because it is apparent from maxillary structure that it does not belong in the genus *Runchomyia*. Species of *Isostomyia* bear a maxillary claw (Fig. 6A,B) while those of the subgenera *Runchomyia* and *Ctenogoeldia* possess a maxillary bundle (Fig. 3). The phylogenetic importance of this difference is corroborated by the distinctive differences in all life stages indicated in the keys prepared by Zavortink (1979). The adults of these two groups exhibit a particularly striking difference in scutal scaling. These scales are moderately broad to broad and flat in *Isostomyia* and narrow and curved in the two subgenera of *Runchomyia*.

Although *Tripteroides* (Old World) appears to be very close to *Trichoprosopon* (New World) (Lee 1946) (compare Fig. 2A,B with 2C,D), and separation of these genera is "particularly difficult" (Mattingly 1981), this does not seem to be true of the subgenus *Rachisoura* based on maxillary structure. The multi-pronged maxillary claw found in spe-

cies of this group (Fig. 7A,B) appears to represent a completely different line of descent from any New World taxon, except possibly *Shannoniana*.

Many species of mosquitoes in unrelated groups are known to share analogous morphological traits. That evolutionary modification of the maxilla has involved independent change in structure and function is obvious in the case of *Heizmannia (Mattinglyia) discrepans* (Edwards) (Fig. 5C,D) and *Aedes (Diceromyia) kanarensis* Edwards (see Tewari et al. 1987:Fig. 2 and Tewari et al. 1990:Fig. 3, respectively). The former bears a well developed maxillary bundle and the latter a uniquely developed apical tooth. The principal reason for mentioning these species is to make two points: (1) species or groups with similar modifications of the maxillary brush may not be descended from a common ancestor, and (2) groups containing species with differently modified maxillae and maxillary substructures probably are not monophyletic since absolute differences in maxillary development appear to be supraspecific in nature based on our studies of the Sabethini. Whether similarities in maxillary structure and function are the result of convergent or divergent evolution may never be known, but within natural groups, all of the members appear to have a maxilla built upon a common plan, with variation among the various members resulting in the adaptation of each to its own mode of life. The higher the category, the greater the degree of variation, but the common plan is always discernible.

This has been a preliminary study of maxillary structure in taxa of the tribe Sabethini. An attempt was made to examine the maxillae of type species of all nominal genera and subgenera within the tribe, but nearly half of these were unavailable for study. Once these species and others are examined and studied, it is likely that the specific determination of developmental states of the larval maxilla will explain the morphological similarities and differences exhibited by groups of related and unrelated taxa. This information is also likely to be of considerable use in understanding

phylogenetic relationships and defining supraspecific categories. The result will be a more stable classification, which is necessary for developing reliable keys and accurately identifying specimens.

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