A Review of the Systematics and a
Proposed Scheme of Internal Classification of the
New World Subgenus Melanoconion of Culex
(Diptera, Culicidae)^{1,2}

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ABSTRACT. This review of the New World subgenus Melanoconion of Culex includes taxonomic history, previous schemes of internal classification, revised subgeneric characters, summaries of bionomics, medical importance and distribution, discussions of included species, diagnostic features for separating Melanoconion from other related subgenera of Culex, its affinities and phylogenetic relationships. The taxonomic characters used are discussed and figured, followed by a detailed outline of the proposed scheme of internal classification, keys to sections, groups and/or subgroups and definitions of sections. A conspectus of taxonomic changes, including 2 transferred taxa, 10 provisionally rejected names and 5 new synonyms, is appended. Based on the study of types and/or available topotypic material, the male genitalia of 6 valid species are figured: phlabistus, saramaccensis, creole, pifanoi, idottus and ernsti.

INTRODUCTION

Among the major groups of New World mosquitoes, the genus *Culex*, subgenus *Melanoconion* is very important as it contains species which are natural or potential vectors of various arboviruses, including Venezuelan Equine Encephalomyelitis (Aitken et al. 1968, 1969; Galindo et al. 1966; Galindo and Srihongse 1967; Galindo and Grayson 1971; Galindo 1978). However, since the pioneer studies by Rozeboom and Komp (1950) and Foote (1954), little progress has been made in the systematics of the whole subgenus. During this period, some 60 additional species were described but only a few local or restricted studies of certain groups were made (Galindo 1969; Duret 1969c; Belkin, Heinemann and Page 1970). When I initiated a revision of the medically important *Melanoconion* species during 1976-1977, I soon found that most of the species in the subgenus were very inadequately known and that nearly every

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Form Approved OMB No. 0704-0188 aspect of the systematics was in a very confused state. Because of this situation, both taxonomic and nomenclatural problems have been frequently encountered in identifying specimens to species or even to subgenus. With the extensive collections of numerous reared specimens from the project "Mosquitoes of Middle America" (Belkin et al. 1965) and the large number of the types at the U. S. National Museum, my study has been expanded to cover the entire subgenus and related subgenera. As a result of this study, additional significant data on the morphology of the adults and immatures have been obtained. Part of this study dealing with the comparative female cibarial armature has been published (Sirivanakarn 1978b).

The present paper is a preliminary review of the fundamental aspects of the systematics of *Melanoconion*. To provide a basis for further study of the species on a geographic or group level, the subgenus is characterized and a scheme of internal classification based on the morphology of adults and immatures is proposed. Also included in this review are my conclusions on the current status of 23 nominal taxa whose types and/or available topotypic material I have examined during the course of this study. The terminology used in the descriptions, taxonomic discussions and keys generally follows Harbach and Knight (1980, 1981) except for the special terms used in describing certain elements of the male genitalia, which follow that of Sirivanakarn (1979) and Sirivanakarn and Heinemann (1980).

I am most grateful to the late Dr. John N. Belkin for stimulating discussions, advice, assistance and encouragement prior to his untimely death in April 1980. In memory of Dr. Belkin, this paper is dedicated to him.

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SYSTEMATICS

TAXONOMIC HISTORY

The status of *Melanoconion* underwent several changes in interpretation and taxonomic treatment from 1906 until 1950 when the subgeneric concept of the group as a whole became more stabilized. For an understanding of certain fundamental aspects of the systematics of this large and difficult subgenus, an account of its historical development is summarized below.

Melanoconion was originally proposed as a distinct genus by Theobald (1903) separated from the genus Culex primarily in the adults by the broad squamous scales of the wings and included 6 nominal species: atratus Theobald 1901, humilis Theobald 1901, rima Theobald 1901 (currently transferred to the Old World Culex, subgenus Eumelanomyia Theobald 1909), indecorabilis Theobald 1903, luteopleurus Theobald 1903 and spissipes Theobald 1903. (1905) studied the male genitalia of atratus and selected this species as the type of Melanoconion. Dyar and Knab (1906) synonymized Melanoconion with the genus Culex and proposed Mochlostyrax as a distinct genus with caudelli Dyar and Knab 1906 as its type. The latter was recognized only in the larva by the presence of a single row of spinelike comb scales. In Howard, Dyar and Knab (1915), both Melanoconion and Mochlostyrax were considered synonyms of Culex without recognition even as groups. Subsequently, Dyar (1918a), in his comparative study of the male genitalia, restored Melanoconion and Mochlostyrax as subgenera of Culex. In the same paper, Dyar also proposed Choeroporpa as a subgenus of Culex with anips Dyar 1916, as type. Included within Choeroporpa were most of the species he earlier placed in Culex or Mochlostyrax. While there was considerable confusion in the subgeneric placement of the species, Dyar (1918b) recognized Helcoporpa as another subgenus with menytes Dyar 1918, as type. This was followed by the restoration of Gnophodeomyia Theobald 1905 (type species: inormata Theobald 1905) as a subgenus with the proposal of Anoedioporpa as a replacement name for subgenus Isostomyia Coquillett 1906 (Dyar 1923).

In the "Mosquitoes of the Americas", Dyar (1928) made significant changes in his treatment of Melanoconion and Mochlostyrax. In this monograph, only Melanoconion and Mochlostyrax were considered as subgenera of Culex. The previously recognized subgenera Choeroporpa and Helcoporpa and the newly recognized Dinoporpa (type-species: trifidus Dyar 1921) were reduced to sections of Mochlostyrax; Tinolestes Coquillett 1906 (type-species: latisquama Coquillett 1906), Gnophodeomyia and Anoedioporpa to sections of Melanoconion, in which he also included americanus (Neveu-Lemaire) 1902 and antillummagnorum Dyar 1928 of the subgenus Micraedes Coquillett 1906.

In the subgeneric classification of New World Culex by Edwards (1932), the interpretation and arrangement of species of Melanoconion and Mochlostyrax were different from that of Dyar (1928). In Edwards' treatment, Melanoconion was considered as a subgenus with Gnophodeomyia, Asebeomyia Aiken 1911 (type species: Cx. epirus Aiken 1909), Tinolestes, Choeroporpa, Helcoporpa and Dinoporpa as its synonyms; the subgenus Mochlostyrax was restricted to the species in the Mochlostyrax section of Dyar (1928); Anoedioporpa was synonymized with the subgenus Isostomyia (currently transferred to Trichoprosopon), and americanus and antillummagnorum were transferred to the subgenus Micraedes. During the same year Komp and Curry (1932) proposed Upsiloporpa as

a new subgenus of *Culex* for their new species *haynei*. Later, Komp (1935) found this species to be the same as *menytes* Dyar 1918 and in consequence *Upsiloporpa* became another synonym of *Melanoconion*.

In the thirties and forties, Edwards' classification was largely followed (Senevet and Abonnenc 1939, Lane 1939, Floch and Abonnenc 1947) except for the transfer of *ocellatus* Theobald 1903 from *Microculex* Theobald 1907 to *Melanoconion* by Lane and Whitman (1943).

The most important contribution to the stability of the subgeneric concept of Melanoconion occurred when Rozeboom and Komp (1950) treated both Melanoconion and Mochlostyrax as a single subgenus with excellent illustrations of the male genitalia of some 90 species. In the "Neotropical Culicidae" by Lane (1953), the subgeneric treatment of Rozeboom and Komp was largely followed except for the resurrection of Tinolestes from Melanoconion as a separated subgenus, to include those species with a short palpus in the Immediately following Rozeboom and Komp's study, Foote (1954) found the larvae of the species of Mochlostyrax distinct from those of Melanoconion, leading him to consider it as a separated subgenus. Eventually Foote's recommendation was adopted in the mosquito catalog of Stone, Knight and Starcke (1959). More recently, however, Belkin (1968) and Belkin, Heinemann and Page (1970) again considered Melanoconion and Mochlostyrax to form a single subgenus. In brief, Belkin (1968) transferred breviculus Senevet & Abonnenc 1939 and cauchensis Floch & Abonnenc 1945, previously assigned to Tinolestes by Lane (1953), to Melanoconion and reinterpreted the subgenus Tinolestes to include only latisquama. These changes and others recommended by Belkin have currently been adopted in the revised mosquito catalog of Knight and Stone (1977) and in the recent revisions of Aedinus, Tinolestes and Anoedioporpa by Berlin and Belkin (1980).

In the present review, *Melanoconion* is considered as a subgenus of *Culex* largely in the sense of Rozeboom and Komp (1950), Belkin (1968) and Belkin, Heinemann and Page (1970). It primarily contains species with a long palpus in the male and includes most nominal species currently listed in the catalog (Knight and Stone 1977) and its supplement (Knight 1978). The only exceptions are 2 transferred taxa, 10 provisionally rejected names and 5 new synonyms as indicated in the discussion of included species.

PREVIOUS SCHEMES OF INTERNAL CLASSIFICATION

Previous attempts at a broad scheme of classification of *Melanoconion* were by Dyar (1928), Edwards (1932) and Rozeboom and Komp (1950). However, due to changes in the subgeneric treatment of *Melanoconion* involving repeated resurrection and synonymy of several generic group taxa, the schemes developed by these authors are extremely confusing and in need of improvement. Since certain characters used and the grouping of species established by these authors have been found to be of some significance in developing the new scheme proposed here, their classifications are briefly discussed below.

In treating the subgenera Mochlostyrax and Melanoconion, Dyar (1928) recognized 8 sections (4 in each subgenus), based largely on the shape of the gonostylus of the male genitalia and to a certain extent on the type of larval comb scales. The 4 sections recognized in the subgenus Mochlostyrax were: Dinoporpa with trifidus, Helcoporpa with menytes (currently = spissipes),

Mochlostyrax with caudelli and 5 other related nominal taxa, and Choeropora with some 69 nominal taxa. The 4 sections recognized in the subgenus Melanoconion were: Tinolestes with latisquama, Gnophodeomyia with aikenii (currently = ocossa and panocossa), Melanoconion with atratus and 8 other nominal taxa, and Anoedioporpa with conservator and 6 other related nominal taxa. All of these sections except Choeroporpa and Melanoconion are natural groups and 2 of these (Tinolestes and Anoedioporpa) have been elevated to subgeneric rank by Belkin (1968) and Berlin and Belkin (1980). The sections Choeroporpa and Melanoconion are, on the other hand, largely composite and artificial, consisting of several unrelated forms not further classified by Dyar.

In Edwards' scheme (Edwards 1932), the subgenus was subdivided into 3 groups on the basis of certain conspicuous characters of the adults. These are: Group A with taeniopus and 3 other nominal taxa, characterized by the narrow scales on the vertex and presence of tarsal markings on at least the hindleg; Group B with chrysonotum, spissipes and 5 other nominal taxa, characterized by the narrow scales on the vertex, the dark tarsi and anterior half of scutum covered with golden scales; and Group C with some 70 included species, characterized by the broad scales on the vertex, the dark tarsi and the entirely dark scales on the scutum.

The classification by Edwards is artificial as pointed out by Rozeboom and Komp (1950). None of the 3 groups Edwards recognized reflect the true relationships that are evident when a classification is based on the male genitalia. The scheme developed by Rozeboom and Komp was largely adopted from that of Dyar. The only significant change from that of Dyar was in combining both Melanoconion and Mochlostyrax into a single subgenus. Within the subgenus, all the sections except Anoedioporpa (Melanoconion, Tinolestes, Gnophodeomyia, Dinoporpa, Helcoporpa, Choeroporpa and Mochlostyrax) and their included species that were originally established by Dyar on the basis of the male genitalia were retained. As indicated in Dyar's scheme, the various species in the Choeroporpa and Melanoconion sections are obviously not closely related, but no further attempt was made by Rozeboom and Komp to recognize any of these as groups or subgroups.

Since Rozeboom and Komp, two species groups have been recognized and defined. One of these was by Galindo (1969) who recognized the *Culex spissipes* group on the basis of the male genitalia and larval characters while the other was by Duret (1969c) who recognized the *ocellatus* group on the basis of distinctive adult features and male genitalia. Both of these groups are redefined in the broad scheme of classification proposed in this study.

SUBGENERIC CHARACTERS

Based on the morphology of the adults and immatures of atratus, the type-species of Melanoconion, and various other species, the subgenus is characterized as follows:

FEMALES. In general as figured for atratus (Fig. 1). Usually small or medium sized, wing length ranging from 2-3 mm. Head. Decumbent scales on vertex varying from narrow, linear or crescent shaped in center to entirely broad, ovate; erect scales numerous, usually entirely dark, sometimes pale whitish or partially pale golden. Palpus and proboscis entirely dark; palpus 0.16-0.20 of proboscis length; antenna as long as proboscis. Thorax. Acro-

stichal setae on scutum absent (except spissipes); scutal integument usually dark brown to nearly black, sometimes pale brown or yellowish brown; antealar and supraalar areas without dark rounded spots (except ocellatus and related species); scales on anterior half of scutum usually entirely dark, infrequently partially pale golden, producing a distinct pattern. Antepronotum with row of setae only, scales absent. Pleural integument usually slightly paler or concolorous with scutum, sometimes pale white or yellow, contrasting with that of scutum; scale patch present on lower posterior surface of mesokatepisternum, present or absent on upper corner and upper median area of mesanepimeron; metameron without microsetae. Legs. All segments usually without conspicuous coloration or entirely dark, sometimes with white knee spots on apices of femora and/or white rings at joints of hindtarsomeres 1-Plume scales on all wing veins usually short, broad ovate or squamous, rarely long, narrow, linear or clavate. Abdomen.usually with distinct basolateral pale spots or sometimes with complete basal pale bands, rarely entirely dark scaled.

FEMALE CIBARIAL ARMATURE. As figured for atratus (Fig. 3). Cibarial dome triangular or ovoid, dark-pigmented and strongly denticulate; cibarial teeth 3-12, all large, columnar, hollow, sometimes more numerous, narrow, entirely pigmented.

MALES. In general as described for females. Head. Palpus long, exceeding proboscis by at least 0.5 of palpomere 5, infrequently slightly shorter than or subequal to proboscis; palpomeres 4,5 moderately to strongly plumose, rarely non-plumose. Flagellar whorls of antenna usually strongly plumose; secondary whorls of short setae distad of normal whorls not developed.

MALE GENITALIA. Variously modified, with the following subgeneric characters. Segment VIII. Caudal margin of tergum shallowly to deeply Segment IX. emarginate. Shape, size and setae of tergal lobe variously developed. Gonocoxite. Usually conical-comma shaped, sometimes broad ovoid, globose, oblong or rectangular. Subapical Lobe. Proximal and distal divisions strongly developed, widely separated, each with basal columnar stem of varied length; columnar stem of proximal division distally divided or undivided, bearing on its apex 2 curved or straight rodlike setae; columnar stem of distal division shorter than or sometimes as long as proximal, bearing on its apex 1 large hooked rod, 2 acute bladelike setae, 3,4 densely packed foliforms and/or 1 or more variously modified leaves. Gonostylus. from simple sickle-shaped to strongly modified. Phallosome. Aedeagus usually without sclerotized upper tergal bridge connecting the 2 lateral plates; lateral plate in lateral aspect with narrowly or broadly sclerotized basal hook, its distal part simple with apex tapering into single point or broadly expanded tergally and sternally, forming simple pointed or bifurcate tipped apical tergal process, median conical, quadrate process and/or sternal hooked Proctiger. Apical crown usually with a comblike row of 5-12 flattened, apically blunt or pointed teeth; paraproct narrow; cercal sclerite largely membranous; basolateral sclerotization broad triangular, oval or digitiform.

FUPAE. In general as figured for atratus (Fig. 3) with the following subgeneric characters. Pigmentation of integument usually pale, cream-colored, sometimes brown or yellow. Trumpet. Meatus varied in length,

usually cylindrical, sometimes slightly modified; pinna narrow or broad oblique, with distinct meatal slit extending from its ventral margin to 0.3-0.5 of trumpet length, rarely absent. Cephalothorax. Seta 8-C usually 4-6 Seta 10-C branched, sometimes double or triple, rarely single. Metanotum. usually multiple, sometimes 3-5 branched; 11-C single or double. Abdomen. Setae 5-IV-VI at least double or usually more branched; 6-III-VI usually 3-5 branched, sometimes single or double; 9-VIII placed at caudolateral angle of Broad, obovate; outer margin segment VIII or removed cephalad. Paddle. without fringe of hairlike spicules; setae 1,2-P present, usually moderately to well developed.

In general as figured for atratus (Fig. 4) with the following LARVAE. Broader than long, usually with prominent subgeneric characters. Head. lateral ocular bulge; seta 2-C usually absent, sometimes present; 5-C weakly to strongly developed, single or branched; 6-C long, always single. Antenna usually as long as or slightly shorter than head length, sometimes length and thickness reduced; seta 1-A usually large and strongly plumose, rarely reduced. Thorax. Spiculation usually present, lightly to strongly developed, sometimes absent; setae 7,8-P well developed; 7-P usually triple (2-6); 8-P Spiculation weaker than on thorax; setae 6usually double (1-6). Abdomen. I, II usually double, sometimes triple; 7-I usually single, sometimes double. Comb scales usually numerous, forming patch, all subequal or differentiated in size, with normal fringe of fine spicules, sometimes relatively few, enlarged, spinelike, forming patch or arranged in a single row. Segment VIII. Tubular, distally 1,2 usually with basal sclerotized plate. Siphon. tapering, length varied, usually ranging between 0.8-1.2 mm, sometimes shorter or longer; pecten teeth 8-16, in a close-set row, rarely widely spaced, usually with fine barbs of numerous denticles; subventral tufts 3-8 pairs, moderately to strongly developed, length varied from about as long as to 2-6 times longer than siphon width at points of insertion, usually inserted beyond pecten to about 0.75 of siphon length from base, sometimes placed inside pecten to almost at apex of siphon; dorsolateral setae usually 2 pairs, sometimes 3 or 4, scattered between 0.3-0.75 of siphon length; 2-S usually well developed and apically hooked, usually with submedian accessory spine; dorsal and ventral valves of spiracular apparatus well developed; median caudal filament present or absent. Anal Segment. Saddle complete, attached acus absent; caudolateral margin lightly spiculate, sometimes practically bare or with dense row of several long spines; ventral brush (4-X) with 5,6 pairs of setae.

BIONOMICS

far as known, almost all Melanoconion species are breeders. The only exceptions are occilatus and 3 other related species whose breeding sites are exclusively in leaf axils of epiphytic bromeliads. Both pupae and larvae of groundpool forms have are laid singly or in a batch. been collected from a variety of habitats, including pools in forest or jungle swamps under heavy shade, artificial or natural ponds, marshes, lakes, margin of slowly moving rivers and canals, partially shaded or exposed to full sun-The elevation usually ranges from near sea level to $50~\text{m}_{\odot}$ species (taeniopus) has been known to breed in underground water of coral The jungle groundpool limestone rock or in borrow pits at bases of trees. habitats usually contain fallen leaves, branches and roots of trees, whereas those in open areas, such as marshes, ponds, lakes or canals, usually contain Immatures of certain floating pistia, reeds and other aquatic vegetation.

species are very difficult to find. Adults have frequently been collected in numbers while resting during the day on fallen leaves, tree trunks, moist soil and emergent vegetation. Several species have also been taken in numbers from light and animal baited traps. They are nocturnal in activity and several species have been known to feed on blood of a variety of vertebrates (birds, lizards, mice, man).

MEDICAL IMPORTANCE

As far as known the following species are important as natural or potential vectors of Venezuelan Equine Encephalomyelitis and various other strains of arboviruses: taeniopus, ocossa, panocossa, pedroi, vomerifer, portesi, delpontei and crybda (Galindo 1978; Aitken and Galindo 1966; Aitken et al. 1968, 1969; Degallier et al. 1978, 1979; Cupp, Scherer and Ordonez 1979; Sirivanakarn and Jakob 1981b).

DISTRIBUTION

Melanoconion is primarily neotropical in distribution with the greatest number of species occurring in Middle America which, in the sense of Belkin et al. (1965), includes Central America, the West Indies and the northern part of South America north of the Amazon river. The entire reported range covers a considerably broader area, extending from the southern part of the United States southward through all the countries in Central America, South America east of the Andes and islands of the West Indies. Its southern limit extends from the east coast of Sao Paulo, Brazil through Paraguay to the west as far as Buenos Aires Province, Argentina. On the Pacific side west of the Andes, the subgenus extends from Colombia southward as far as Peru.

DISCUSSION OF INCLUDED SPECIES

In the mosquito catalog of Knight and Stone (1977) and its supplement by Knight (1978), about 162 species are listed under *Melanoconion*. Since then, some corrections, including revalidation, synonymy and descriptions of new species have been made by Sirivanakarn (1978a, 1979), Sirivanakarn and Belkin (1980), Sirivanakarn and Degallier (1981), Sirivanakarn and Galindo (1980) and Sirivanakarn and Jakob (1979, 1981a). As a result, the total number of taxonomically valid species was then adjusted to 165. In addition, after further study of types and topotypic material and a critical analysis of the original and subsequent descriptions, I am making the following taxonomic changes, thus reducing the total number of valid species to 149.

(1) Transferred Taxa. I have examined topotypic specimens of breviculus Senevet & Abonnenc 1939 and a male paratype of cauchensis Floch & Abonnenc 1945 and found that both are more closely related to latisquama of the subgenus Tinolestes (Berlin and Belkin 1980) than to any Melanoconion species. This is evident from the following combination of characters: (1) male palpus is about half the length of the proboscis; (2) flagellomeres of male antenna with a distinct secondary whorl of short setae distad of normal whorl; (3) metameron with a group of several microsetae and (4) apical crown of proctiger with over 20 densely packed teeth. Other general adult features, such as the yellow pleural integument, the general facies, the relatively sparse long setae of the flagellar whorls, the type of decumbent scales on the vertex and the type of wing scales all indicate that both taxa belong to Tinolestes

instead of *Melanoconion*. On this basis, I therefore transfer them to that subgenus. For comparative purposes, certain characters of the male genitalia of these 2 species are illustrated in Fig. 10,13,14,17,19 and 20.

- (2) Rejected Names. These include 10 nominal taxa whose identity cannot be determined either from the examination of the existing types or from the original descriptions. Most of these species were previously assigned to species of uncertain position or validity by Rozeboom and Komp (1950:98), because their male genitalia were unknown. It appears most likely that these forms were described under other names, but this cannot be determined with any degree of certainty. To avoid possible confusion in taxonomy and nomenclature of Melanoconion, I chose at this time to provisionally reject these names by assigning them to 2 categories: taxa dubia and nomina dubia as discussed by Smith (1970). I am also recommending that these names should not be used until the specimens from the type-localities are recovered and definitely proved to be conspecific with the types.
- (a) Taxa Dubia. Falling into this category are the following nominal taxa: humilis Theobald 1901, nigricorpus (Theobald 1901), indecorabilis (Theobald 1903), nigrescens (Theobald 1907), fasciolatus (Lutz 1904), lugens Lutz 1905, gravitator Dyar & Knab 1906 and decorator Dyar & Knab 1906. primary types (holotypes, lectotypes) of humilis, nigricorpus, indecorabilis, nigrescens and lugens are still in existent but those of fasciolatus, gravitator and decorator were lost and could not be located at the institutions where they were reported to be deposited (Belkin 1968; Belkin, Schick and Heinemann 1971). The types of nigricorpus and indecorabilis are pinned females only but those of humilis and nigrescens are males with their genitalia missing or presumably lost. The figure of the male genitalia of nigrescens in Rozeboom and Komp (1950, Pl. X, 57) is, in fact, that of clarki Evans 1924 while the figure for this species in Lane (1953:480-481) most probably applies to that of implicatus Senevet & Abonnenc 1939. The syntype male of lugens and the male genitalia were in extremely poor condition and it was not possible to determine its identity. A critical examination of the existing types and analysis of the original descriptions have shown that all of these taxa are typical of Melanoconion, but none can be associated with any known members in the subgenus.
- (b) Nomina Dubia. Included in this category are 2 nominal taxa: chrysothorax (Peryassu) 1908 and epirus Aiken 1909 whose types are non-existent and their identity as determined from the original description has shown that both are probably members of other Culex subgenera instead of Melanoconion. lectotype male of chrysothorax designated by Belkin (see Belkin, Schick and Heinemann 1971:23) at the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil was later found to be lost when Belkin and I visited that institution in January of 1980. From a detailed translation of the entire original description by Peryassu (1908), I finally concluded that chrysothorax is most probably a Microculex because of the following descriptive features: (1) male palpus with 4 white rings at bases of palpomeres 2-5; (2) scutum with 3 longitudinal white stripes alternating with dark stripes; (3) antepronotum covered with white narrow scales and (4) tarsi with basal white rings. In addition, the description and the photograph of the chrysothorax larva and notes on the breeding sites (bromeliads, marshy area) by Peryassu also suggest that the specimens before him were a Microculex, most probably a member of the imitator series of Lane and Whitman (1951). Since it has not been possible to associate chryso-

thorax with any known members of Microculex, I therefore relegate it to a The same conclusion is also made for epirus, originally nomen dubium. described as Culex by Aiken (1909), but later the author placed it in a distinct genus with a combination Asebeomyia epirus (Aiken 1911:193, foot-From Aiken's notes, it is most likely that epirus is Cx. quinquefasciatus Say because of the following statements: "To the genera above described two new ones will probably fall to be added. One is domestic species which came near Gnophodeomyia but has the femora swollen apically and basally as in Melanoconion... The larvae are found in house, in cistern and bath water and the adults have a peculiarly disrespectful affection for tender integument, the lips, nostrils and other exposed mucous membrane receiving their attention. The name Asebeomyia would be proper for this new genus. Into this genus will come my Culex epira (B.G. Medical Annual for 1908, p. Because of the dubious subgeneric status of epirus, I also consider the name Asebeomyia as a nomen dubium with a recommendation that it should be eliminated from the current synonymy with Melanoconion.

- (3) New Synonyms. Based primarily on the study and comparison of the types and/or available topotypic material, the following nominal taxa are considered as new synonyms: (1) kerri Duret 1968 (=phlabistus Dyar 1920); (2) implicatus Senevet & Abonnenc 1939 is transferred from the previous synonymy of nigrescens (Theobald 1907) by Lane (1951, 1953) and Casal (1963) to the synonymy of saramaccensis Bonne-Wepster & Bonne 1919(1920); (3) seneveti Clastrier 1970 (=contei Duret 1968); (4) thomasi Evans 1924 (=bastagarius Dyar & Knab 1906) and (5) venezuelensis Anduze 1948(1949) (=simulator Dyar & Knab 1906).
- (4) Identity of 6 valid species. The identity of the following 6 species is extremely difficult to determine from the original and/or subsequent descriptions and figures of the male genitalia. To alleviate this problem, the male genitalia, primarily from the types of these species are illustrated in Fig. 23, 24 and 25. These species are: phlabistus Dyar 1920, saramaccensis Bonne-Wepster & Bonne 1919(1920), creole Anduze 1948(1949), pifanoi Anduze 1948(1949), idottus Dyar 1920 and ernsti Anduze 1948(1949). These species can be distinguished readily from the rest of Melanoconion by comparing the figures of the male genitalia with those in Rozeboom and Komp (1950) and in the subsequent publications by Komp and Rozeboom (1951), Galindo and Blanton (1954), Galindo and Mendez (1961), Duret (1954-1969), Duret and Barreto (1956), Clastrier (1968-1972) and other recent authors.

DISCUSSION OF DIAGNOSTIC CHARACTERS

The majority of Melanoconion species can generally be separated from most species of related subgenera of Culex (Aedinus, Anoedioporpa, Belkinomyia, Carrollia, Micraedes, Microculex, Tinolestes) in all stages by the keys recently published by Berlin and Belkin (1980:3-6). However, because of several overlaps in the characters of one or more stages of these subgenera, it is important that identification should be based on at least 2 or more characters in each stage. Caution should be taken in relying on the broad decumbent scales on vertex of the adult head in couplet 10(9) of Berlin and Belkin's key, since this character largely applies to the species in the Melanoconion section only, but not to those in the Ocellatus and Spissipes sections (see proposed scheme and keys to sections). The following is a summary of diagnostic characters that will separate most Melanoconion species

from members of related subgenera.

(1). In the adults, the females can be readily separated from Carrollia by the absence of metallic coloration on the legs and terga of the abdomen; from Micraedes and Microculex by the absence of acrostichal setae (except spissipes), the darker scales and integument of the scutum, the absence of narrow scales on antepronotum, the usually broader plume scales on wing veins and tarsal marking if present, embracing both ends of tarsomeres 2-4, whereas in Microculex, this marking is entirely basal; from Belkinomyia by the presence of basolateral whitish spots on abdominal terga II-VII and the absence of microsetae at base of halter; from Aedinus by the coarser and relatively sparse scutal scales and the usually dark or blackish integument of the scutum versus tan or reddish-brown in Aedinus; from Anoedioporpa by the absence of scales on antepronotum, the broader and shorter plume scales of wing veins and the generally darker scutal and pleural integument; and from Tinolestes by the dark versus tan brown antepronotum and the absence of microsetae on metameron.

The males of *Melanoconion* can easily be separated from *Aedinus*, *Anoedioporpa*, *Belkinomyia*, *Micraedes* and *Tinolestes* by the longer palpus which is at least 0.75 to longer than proboscis length, whereas in all of these related subgenera, the palpus is reduced to 0.16 to at most 0.5 of proboscis length; and from *Microculex* and *Carrollia* by the same characters given above for the females.

- (2). In the male genitalia, Melanoconion can be readily separated from Aedinus, Belkinomyia, Micraedes and Microculex by the elongated columnar stems of proximal and distal divisions of the subapical lobe and the variously developed distal part of the lateral plate of the aedeagus; from Anoedioporpa by the presence of scales on basal tergal surface of the gonocoxite and the usually well developed tergal lobe of segment IX; from Carrollia by the presence versus the absence of distal division of the subapical lobe and different modifications of the gonostylus; and from Tinolestes by the reduction in the number of teeth on the proctiger crown, which range from 5-12 versus 20 or more in Tinolestes.
- (3). In the pupa, all Melanoconion species except ocellatus and related forms can be readily separated from related subgenera by the presence of a distinct meatal slit or cleft extending from the pinna of trumpet and by the several branched abdominal setae 1,5-III-VI.
- (4). In the larva, Melanoconion can be separated from Aedinus by the absence of acus attached to the anal saddle and the usually longer and narrower pecten teeth of the siphon; from Anoedioporpa and Tinolestes by the presence versus the absence of a distinct basal sclerotized plate of setae 1,2-VIII and the serrated versus the unserrated pecten teeth of the siphon; from Belkinomyia by the usually well developed seta 1-III-VI of the abdomen and the usually strongly developed subventral tufts of the siphon; from Carrollia by the tubular versus fusiform shape of the siphon, the longer and thicker antennal shaft and the prominent ocular bulge of the head capsule; from Microedes by head seta 6-C single versus triple and non-stellate setae 1,3 of the thorax and abdomen (except ocellatus and related species); and from Microculex by the strong seta 8-P versus the reduction of this seta and the more strongly developed subventral tufts of the siphon.

AFFINITIES AND PHYLOGENETIC RELATIONSHIPS

As evident in this and previous studies (Sirivanakarn 1978b, Berlin 1969, Valencia 1973, Adames and Galindo 1973, Berlin and Belkin 1980), Melanoconion is related to Aedinus, Anoedioporpa, Belkinomyia, Carrollia, Micraedes, Microculex and Tinolestes. These relationships are evident in the following characters: (1) in the male genitalia, the presence of the so-called "basal hook" of the lateral plate of the aedeagus; (2) in the female cibarial armature, the oval or heart-shaped cibarial dome, which is strongly denticulate, and the development of the cibarial teeth; (3) in the pupa, the position of seta 2-VI which is laterad of seta 1-VI and (4) in the larva, the single seta 6-C, the reduction of seta 3-P and the presence of at least 2 pairs of dorsolateral setae on the siphon. In the Neotropics, this combination of characters is phylogenetically important and provides a clear-cut separation of *Melanoconion* and related subgenera from the rest of *Culex*. Although their relationships have not yet been studied in detail, it is evident that Melanoconion and its related subgenera belong to single major monophyletic line unique to the New World. Within this line, Melanoconion is the largest and most diverse. It comprises several distinct groups, some of which appear to be generalized and primitive, exhibiting characters in one or more stages overlapping with those of related subgenera. Since the majority of Melanoconion species are primarily ground pool breeders whereas, those of the related subgenera are breeders in treehole, bamboo, artificial or natural containers (Anoedioporpa, Carrollia), epiphytic bromeliads (Micraedes, Microculex) and crabholes (Tinolestes, Belkinomyia), it is conceivable that their evolution probably took place primarily through specialization in breeding sites. The mechanism of speciation somewhat resembles that of the Culex subgenera Eumelanomyia and Lophoceraomyia in the Oriental and Indomalayan regions (Sirivanakarn 1972, 1977).

On a broader comparative basis, Melanoconion and related subgenera exhibit certain characters similar to the subgenus Neoculex of Culex and the genera Galindomyia and Deinocerites. Neoculex is worldwide in distribution with only a single species (derivator) occurring in the Neotropics, whereas Galindomyia and Deinocerites are exclusively New World. The similarity with Neoculex is evident in the typical comblike row of the proctiger crown of the male genitalia and in the reduction of seta 3-P of the larvae. The similarity with Galindomyia and Deinocerites is evident particularly in the development of the female cibarial teeth, the type of gonostylus and proctiger crown of the male genitalia. These similarities are obvious particularly in Belkinomyia and Tinolestes as discussed by Adames and Galindo (1973), Belkin and Hogue (1959), and Adames (1971). Further detailed study of the relationships of these Culex subgenera and the genera Galindomyia and Deinocerites should contribute to a better knowledge of their phylogeny as well as to the improvement of the present classification of the genera and subgenera in the tribe Culicini of Belkin (1962).

TAXONOMIC CHARACTERS

Basic to the proposed scheme of internal classification of *Melanoconion* presented here is the determination of phylogenetic importance of the characters of the adults and immatures. The following is a summary of characters that are important in delimiting and recognizing species groups at various levels.

ADULT CHARACTERS.

The significant characters of the head are: (1) vestiture of decumbent scales in the center of the vertex. As shown in Fig. 5 A-F, the decumbent scales vary from narrow, linear or crescent shaped to entirely This character is particularly important in broad, ovate and appressed. determining sections, but is of limited value at the group or subgroup levels and (2) length of male palpus relative to proboscis. In general, the male palpus in Melanoconion exceeds the length of proboscis by at least 0.5 the length of palpomere 5. However, in a few groups, the male palpus is slightly shorter than or subequal to the proboscis. This is significant only in the delimitation of a few primary groups. Other characters of the head, such as the partially pale white decumbent scales, may be significant in defining a few groups and subgroups but are of no value at the section level and for the The same applies to the partially golden majority of groups and subgroups. erect scales of the vertex, which may be of specific diagnostic value, but not significant as a group character.

Thorax. The significant characters of the thorax are: (1) presence or absence of dark round spot on antealar and supraalar areas of the scutum; (2) color of scutal integument, which varies from pale or tan to dark brown or blackish; (3) presence of acrostichal setae, which is significant only in the delimitation of the Spissipes group, whereas this character is absent in all other groups of Melanoconion; and (4) presence or absence of scale patches on the upper corner of mesokatepisternum and median surface of mesanepimeron (Fig. 6 A-F). Other characters of the scutum, such as golden scales on its anterior half and partially pale scales on the prescutellar space and scutellar lobes, may be of specific diagnostic value, but are not significant as group characters.

Legs. In general, the legs are entirely dark or without distinctive coloration except for the presence of knee spots on the apices of the femora and/or banding on hindtarsomeres 1-5, which are diagnostic of only a few species and groups.

Wing. The only important character of the wing is the vestiture of the plume scales on veins R_2 , R_3 and R_{4+5} , which vary from long, narrow, linear or clavate to short and broad ovate as shown in Fig. 7 A-F.

Abdomen. In general, nearly all groups of Melanoconion have distinct basolateral white spots on abdominal terga II-VII. These spots may extend dorsad to form complete basal bands, particularly in the males. However, in one group (Jubifer), these spots and bands are absent or not clearly marked and are therefore significant in the separation of this group.

FEMALE CIBARIAL ARMATURE. As shown in Figs. 8 and 9, the development and number of the cibarial teeth are significant at the group levels, and are sometimes also of specific diagnostic value.

MALE GENITALIA. The various components of the male genitalia are, in practically all cases, of great taxonomic significance. However, in the past only the modifications of the shape of the gonostylus and certain features of the subapical lobe were used (Dyar 1928, Rozeboom and Komp 1950). Based on a

broad comparative study of each element of the male genitalia, the various modifications of the following characters are listed according to the degree of their phylogenetic significance: (1) lateral plate of the aedeagus (Figs. 10, 11, 12); (2) development of the proximal and distal divisions of the subapical lobe (Figs. 14, 15, 16), including also the specialized setae on each division; (3) modifications in the apical half of the gonostylus (Figs. 17, 18); (4) modifications of the tergal lobe of segment IX (Figs. 20, 21, 22) and (5) the general outline or shapes of the gonocoxite (Fig. 13).

PUPA. The characters of phylogenetic importance in the pupa are: (1) position of seta 9-VIII, which is at or near to caudolateral angle of the segment or removed cephalad; (2) branching of seta 11-C; (3) development of seta 5-C; (4) branching of setae 8,9-C; (5) branching of seta 5-IV-VI; (6) branching of seta 3-I-III and (7) branching of seta 6-III-VI. Other features, such as the shape, length of trumpet and presence or absence of a meatal slit extending from pinna of the trumpet are also important at different group levels.

LARVA. The following larval characters, listed in order of importance, are: (1) development of ocular bulge on the head capsule; (2) length and thickness of the antennal shaft; (3) presence or absence of seta 2-C; (4) branching of seta 5-C; (5) position of seta 14-C relative to seta 15-C; (6) branching of setae 7,8-P; (7) branching of seta 4-P; (8) development of seta 1-M, T; (9) branching of seta 7-I; (10) branching of seta 6-I,II; (11) number and type of comb scales; (12) development of subventral tufts of the siphon; (13) number of dorsolateral setae of the siphon; (14) length and shape of the siphon and (15) development of spicules on caudolateral border of the saddle. Most of these characters are significant at the section level but are of less importance at the group or subgroup levels because of considerable overlap possibly due to parallelism or convergence.

PROPOSED SCHEME OF INTERNAL CLASSIFICATION

The first step in this classification is to recognize several primary groups (groups and subgroups). These primary groups are then assembled into major sections on the basis of the type of basal hook of the lateral plate of the male genitalia, the type of decumbent scales in the center of the vertex and other features of the adults, the position of seta 9-VIII of the pupa and certain combinations of larval chaetotaxy as given in the keys. The detailed outline of this scheme and the placement of species into different sections, groups and subgroups are shown below.

Subgenus MELANOCONION

OCELLATUS SECTION: ocellatus Theobald 1903, nigrimacula Lane & Whitman 1943, punctiscapularis Floch & Abonnenc 1946, flochi Duret 1969.

SPISSIPES SECTION:

- (1) Spissipes group: spissipes Theobald 1903
- (2) Taeniopus group:
 - (a) Taeniopus subgroup: taeniopus Dyar & Knab 1907
 - (b) Vomerifer subgroup: vomerifer Komp 1932, portesi Senevet & Abonnenc 1941, sacchettae Sirivanakarn & Jakob 1981
 - (c) Pedroi subgroup: pedroi Sirivanakarn & Belkin 1980,

epanastasis Dyar 1922, crybda Dyar 1924, adamesi Sirivanakarn & Galindo 1980

- (3) Paracrybda group:
 - (a) Paracrybda subgroup: paracrybda Komp 1936, delpontei Duret 1969
 - (b) Pereyrai subgroup: pereyrai Duret 1967
- (4) Ocossa group: ocossa Dyar & Knab 1919, panocossa Dyar 1923
- (5) Jubifer group: simulator Dyar & Knab 1906, jubifer Komp & Brown 1935
- (6) Faurani group: faurani Duret 1968
- (7) Nicaroensis group: nicaroensis Duret 1967
- (8) Lopesi group: *lopesi* Sirivanakarn & Jakob 1979

MELANOCONION SECTION:

- (1) Atratus group: atratus Theobald 1901, dunni Dyar 1918, zeteki Dyar 1918, commevynensis Bonne-Wepster & Bonne 1919(1920), ensiformis Bonne-Wepster & Bonne 1919(1920), caribeanus Galindo & Blanton 1954, trigeminatus Clastrier 1970
- (2) Distinguendus group:
 - (a) Putumayensis subgroup: putumayensis Matheson 1934, phlabistus Dyar 1920, bahiense Duret 1969
 - (b) Distinguendus subgroup: comminutor Dyar 1920, maxinocca Dyar 1920, alcocci Bonne-Wepster & Bonne 1919(1920), distinguendus Dyar 1928, productus Senevet & Abonnenc 1939, nicceriensis Bonne-Wepster and Bonne 1919(1920), patientiae Floch and Fauran 1955
 - (c) Chrysonotum subgroup: chrysonotum Dyar & Knab 1906
 - (d) Galindoi subgroup: galindoi Komp & Rozeboom 1951
 - (e) Rorotaensis subgroup: rorotaensis Floch & Abonnenc 1946
- (3) Trifidus group: trifidus Dyar 1921
- (4) Saramaccensis group: saramaccensis Bonne-Wepster & Bonne 1919(1920)
- (5) Erraticus group:
 - (a) Erraticus subgroup: erraticus (Dyar & Knab 1906), invocator Pazos 1908, aureonotatus Duret & Barreto 1956
 - (b) Clarki subgroup: clarki Evans 1924
 - (c) Psatharus subgroup: psatharus Dyar 1920
- (6) Educator group: theobaldi (Lutz 1904), educator Dyar & Knab 1906, inadmirabilis Dyar 1928, rachoui Duret 1968, keenani Galindo & Mendez 1961, mistura Komp & Rozeboom 1951, cristovaoi Duret 1968
- (7) Intrincatus group:
 - (a) Intrincatus subgroup: intrincatus Brethes 1916, misionensis Duret 1953, johnsoni Galindo & Blanton 1954, mutator Dyar & Knab 1906, sursumptor Dyar 1924, ybarmis Dyar 1920, bequaerti Dyar & Shannon 1925, quadrifoliatus Komp 1936, equinoxialis Floch & Abonnenc 1945, rabanicolus Floch & Abonnenc 1946, pifanoi Anduze 1948(1949), trilobulatus Duret & Barretto 1956, trisetosus Fauran 1961, silvai Duret 1968, milwardi Xavier & Da Silva Mattos 1972
 - (b) Eastor subgroup: eastor Dyar 1920
 - (c) Idottus subgroup: idottus Dyar 1920, fairchildi Galindo & Blanton 1954, ronderosi De Linero 1967, ferreri Duret 1968, sardinerae Fox 1953

- (d) Tecmarsis subgroup: tecmarsis Dyar 1918
- (e) Andricus subgroup: andricus Root 1927
- (f) Penai subgroup: penai Sirivanakarn 1979

(8) Bastagarius group:

- (a) Bastagarius subgroup: bastagarius Dyar & Knab 1906, tourmieri Senevet & Abonnenc 1939, coppenamensis Bonne-Wepster & Bonne 1919(1920), comatus Senevet & Abonnenc 1939, creole Anduze 1948(1949), intonsus Galindo & Blanton 1954
- (b) Iolambdis subgroup: iolambdis Dyar 1918, corentynensis Dyar 1920, limacifer Komp 1936, confundior Komp & Rozeboom 1951, quasihybridus Galindo & Blanton 1954, bifoliatus Duret & Barretto 1956, dureti Casal & Garcia 1968, dolichophyllus Clastrier 1970
- (9) Evansae group: evansae Root 1927, batesi Rozeboom & Komp 1948, johnnyi Duret 1968, changuinolae Galindo & Blanton 1954

(10) Inhibitator group:

- (a) Inhibitator subgroup: inhibitator Dyar & Knab 1906, albinensis Bonne-Wepster & Bonne 1919(1920), phlogistus Dyar 1920, plectoporpe Root 1927, oedipus Root 1927, carcinophillus Dyar & Knab 1906, flabellifer Komp 1936, kummi Komp & Rozeboom 1951, wepsterae Komp & Rozeboom 1951, bejaranoi Duret 1953, orfilai Duret 1953, ernsti Anduze 1948(1949), vidali Floch & Fauran 1954, mesodenticulatus Galindo & Mendez 1961, contei Duret, ernanii Duret 1968, abonnenci Clastrier 1970, pavlovskyi Casal & Garcia 1967, amitis Komp 1936
- (b) Egcymon subgroup: egcymon Dyar 1923, elephas Komp 1936, serratimarge Root 1927, isabelae Duret 1968

(c) Mulrennani subgroup: mulrennani Basham 1968

(11) Conspirator group: conspirator Dyar & Knab 1906, elevator Dyar & Knab 1906, terebor Dyar 1920, dyius Root 1927, jocasta Komp & Rozeboom 1951, lucifugus Komp 1936, madininensis Senevet 1936, aliciae Duret 1953, martinezi Casal & Garcia 1968, olimpioi Xavier, Da Silva & Da Silva Mattos 1970

(12) Pilosus group:

- (a) Pilosus subgroup: pilosus Dyar & Knab 1906, innovator Evans 1924, unicornis Root 1928, rooti Rozeboom 1935
- (b) Caudelli subgroup: caudelli Dyar & Knab 1906, alogistus Dyar 1918, vexilifer Komp 1936, lacertosus Komp & Rozeboom 1951, foliafer Komp & Rozeboom 1951, arboricolus Galindo & Mendez 1961, galvaoi Duret 1968, garcesi Duret 1968, palaciosi Duret 1968
- (13) Peccator group: peccator Dyar & Knab 1909, abominator Dyar & Knab 1909, anips Dyar 1916

KEYS TO SECTIONS, GROUPS AND SUBGROUPS OF MELANOCONION

ADU LTS

1. Scutum with pair of large, round black spots on antealar and supraalar areas; plume scales on veins R_2 , R_3 and R_{4+5} of wing long, narrow, clavate or linear (Fig. 7 A, B) . . . OCELLATUS SECTION

	Scutum without above character; plume scales on veins R_2 , R_3 and R_{4+5} of wing short, broad ovate or squamous (Fig. 7 C-F)
2(1).	Decumbent scales in center of vertex of head largely or partially narrow, linear or crescent shaped; broad decumbent scales restricted to lateral patch at side of eye (Fig. 5 B-D) 3
	Decumbent scales of vertex entirely broad (Fig. 5 E, F) MELANOCONION SECTION (in part)
3(2).	Narrow decumbent scales of vertex numerous, extending from coronal suture to lateral margin; lateral patch of broad scales small, or rather indistinct (Fig. 5 B) SPISSIPES SECTION (in part)
	Narrow decumbent scales of vertex fewer, restricted to small central area along coronal suture; lateral patch of broad scales large, or very distinct (Fig. 5 C, D)
	SPISSIPES SECTION
4(3).	Acrostichal setae present on scutum; female: scales on anterior two-thirds of scutum entirely or partially golden, rarely entirely dark
	Acrostichal setae absent or not developed; female: scales on most parts of scutum entirely dark
5(4).	Erect scales of vertex entirely pale golden or yellow; male: pal- pomeres 4 and 5 non-plumose or with only few weak short setae .
	Erect scales of vertex entirely dark, or sometimes partially pale golden in center; male: palpomeres 4 and 5 plumose or with several strong bristlelike setae 6
6(5).	Abdominal terga II-VII without basolateral pale spots . Jubifer group
	Abdominal terga II-VII with distinct basolateral pale spots 7
7(6).	Size relatively small, wing length 2.3-2.7 mm; female cibarial teeth minute, entirely dark, about 30 in number (Fig. 8 B)
	Size relatively large, wing length usually exceeding 3.0 mm; female cibarial teeth large, columnar, basally hollow or transparent, 10-17 in number (Fig. 8 D-F) (Taeniopus group) 8
8(7).	Scales on prescutellar area and scutellar lobes partially pale whitish; hindtarsus with white bands at joints of tarsomeres 1-5
	Scales on prescutellar area and scutellar lobes entirely dark; hindtarsus with or without white bands at joints of tarsomeres

	1-5
9(8).	Upper border of mesokatepisternum with an even curved row of 9-12 strong setae; if white bands present on hindtarsus, then apices of all femora with distinct white knee spots Pedroi subgroup
	Upper border of mesokatepisternum with an irregular row of 7,8 weaker setae; if white bands present on hindtarsus, then apices of all femora without distinct knee spots Vomerifer subgroup
10(3).	Pleural integument generally light yellowish or nearly whitish, contrasting sharply with dark scutal integument; female cibarial teeth minute, 30-40 in number (Fig. 8 B) SPISSIPES SECTION (in part)
	Pleural integument more or less same color as scutum, if lighter, then with a striking pattern of dark and pale stripes running across mesokatepisternum and mesanepimeron; female cibarial teeth large, hollow, columnar, 5-8 in number (Fig. 8 G-L) MELANOCONION SECTION (in part)
	MELANOCONION SECTION
11(10).	Pleural integument with striking pattern of dark and pale stripes; upper corner of mesokatepisternum usually with patch of several pale scales
	Pleural integument without pattern of stripes as above or uniformly brownish; upper corner of mesokatepisternum with or without patch of few pale scales Distinguendus group 12
12(11).	Anterior two-thirds of scutum largely or entirely golden scaled
	All parts of scutum entirely dark scaled
13(12).	Upper corner of mesokatepisternum with distinct patch of scales Distinguendus subgroup
	Upper corner of mesokatepisternum without scales Putumayensis subgroup
14(2).	Size minute, wing length usually about 1.5 mm, not exceeding 2.0 mm; male: palpus slightly shorter or subequal to proboscis length.
	Size large or medium, wing length at least 2.2 mm; male: palpus longer than proboscis by at least 0.5 of palpomere 5 15
15(14).	Plume scales on wing veins R_2 , R_3 , and R_{4+5} of wing relatively narrow, clavate; male: palpomeres 4 and 5 weakly plumose and short
	Plume scales on above wing veins usually broad ovate or squamous;

	male: palpomeres 4 and 5 moderately to strongly plumose and long
16(15).	Upper corner of mesokatepisternum with few to several scales forming a distinct patch (Fig. 6 E)
	Upper corner of mesokatepisternum without scales (Fig. 6 F) 19
17(16).	Median surface of mesanepimeron with broad whitish scale patch (Fig. 6 E) Erraticus group (in part) Erraticus subgroup; Clarki subgroup
	Median surface of mesanepimeron without scale patch 18
18(17).	Female: Cibarial teeth short, broad, hollow, 5-7 in number; cibarial dome small, broad conical (Fig. 9 A); male: palpomers 4 and 5 moderatley to strongly plumose . Erraticus Group (in part)
	Female: Cibarial teeth long, narrow, entirely pigmented, 40-60 in number (Fig. 9 H,I); cibarial dome large, hemispherical; male: palpomeres 4 and 5 weakly plumose Peccator group
19(16).	Decument scales of vertex predominantly pale whitish or grayish; female: cibarial teeth 3 in number (Fig. 9 F, G)
	Decumbent scales of vertex partially pale to entirely dark; female: cibarial teeth 5 or more in number (Fig. 9, B-E) 20
20(19).	Scutal and pleural integument dark brown or black; decumbent scales of vertex entirely dark Intrincatus group (in part) Tecmarsis subgroup; Intrincatus subgroup
	Scutal and pleural integument usually light brown; decumbent scales of vertex usually pale along eye margin, dark toward center
21(20).	Median posterior surface of mesopostnotum with a distinct patch of microsetae
	Median posterior surface of mesopostnotum without microsetae
22(21).	Lower posterior part of mesanepimeron usually with a patch of microscopic scalelike setae (Fig. 6 C) Bastagarius group

	Lower posterior part of mesanepimeron without above character (Fig. 6 F)
	MALE GENITALIA
1.	Basal hook of lateral plate of aedeagus in lateral aspect broadly sclerotized or in form of broad sternally rounded plate (Fig. 10 A-I)
	Basal hook of lateral plate of aedeagus narrowly sclerotized or in form of slender curved arm (Fig. 11, 12) MELANOCONION SECTION
2(1).	Distal part of lateral plate tapered into single caudal process only; basal hook rather short and bluntly pointed (Fig. 10 A) OCELLATUS SECTION
	Distal part of lateral plate with elongate apical tergal process and short hooked or straight apical sternal process (Fig. 10 B-G, I), if not so modified, then basal hook long and broadly rounded on sternal margin (Fig. 10 H)
3(2).	Apical crown of proctiger large, compact, with dense row of 20 or more teeth (Fig. 19 A) breviculus and cauchensis (here transferred to subgenus TINOLESTES)
	Apical crown of proctiger small or moderate in size, with comblike row of 5-15 teeth (Fig. 19 B, D) SPISSIPES SECTION 4
	SPISSIPES SECTION
4(3).	Gonocoxite broad, more or less rectangular (Fig. 13 D); gonostylus with strong dorsal spine in preapical portion (Fig. 17 G); teeth of proctiger crown very thick (Fig. 19 B) Nicaroensis group
	Gonocoxite slender conical or ovoid (Fig. 13 A, F); gonostylus without preapical dorsal spine as above; teeth of proctiger crown slender (Fig. 19 D)
5(4).	Preapical portion of gonostylus strongly angulate or upturned (Fig. 17 B); lobe of IX tergum large, hill-like (Fig. 20 G) Spissipes Group
	Preapical portion of gonostylus normal or not modified as above (Figs. 17 I, K, Fig. 18 A, C); lobe of IX tergum not as above
6(5).	Apical portion of gonostylus with dense tuft of numerous filaments on ventral surface (Fig. 18 A); proximal division of subapical lobe with peculiar rounded pit ventrad of base of columnar stem Lopesi group

	Apical portion of gonostylus without above character; proximal division of subapical lobe without rounded pit
7(6).	Lobe of IX tergum long, digitiform (Fig. 20 H); median apical margin of distal portion of lateral plate convex or rounded Taeniopus group (in part) Taeniopus subgroup
	Lobe of IX tergum short, moundlike or ovoid (Fig. 20 E, F, I, J); median apical margin of distal portion of lateral plate straight or concave
8(7).	Columnar stem of proximal division of subapical lobe with hyaline sheathlike seta and flat hooked seta adjacent to base of rodlike setae a and b (Fig. 14 F)
	Columnar stem of proximal division without above specialized setae
9(8).	Columnar stem of distal division divided into 2 secondary stalks (Fig. 14 F)
	Columnar stem of distal division not divided Taeniopus group (in part) Pedroi subgroup
10(8).	Distal division of subapical lobe with broad leaf (Fig. 14 H); columnar stem of proximal division long and not divided apically . 11
	Distal division of subapical lobe without broad leaf; columnar stem of proximal division short and apically divided with base of rods α and b clearly separated Faurani group
11(10).	Lobe of tergum IX poorly developed, apical margin flat, with row of 5-7 setae (Fig. 20 F); base of distal division of subapical lobe with petiolate leaf
	Lobe of IX tergum well developed or not as above (Fig. 20 I, J); base of distal division of subapical lobe with leaf of different shape than above
12(11).	Goncoxite broad conical; lobe of IX tergum small, oval or mound-shaped (Fig. 20 I, A); subapical crest of gonostylus weakly developed . Taeniopus group (in part) Vomerifer subgroup
	Gonocoxite ovoid or narrow conical; lobe of IX tergum larger, typically oval or broadly prominent (Fig. 20 J); subapical crest of gonostylus strongly developed Jubifer group
	MELANOCONION SECTION
13(1).	Gonocoxite small, narrow, oblong (Fig. 13 C); gonostylus evenly narrowed and simple, subapical crest absent (Fig. 17 D)

	Gonocoxite conical, obovoid or globose (Fig. 13 A, E, F); gonostylus variously modified, subapical crest usually present 14
14(13).	Gonostylus distally divided into 3 long, slender curved arms (Fig. 17 F); lobe of IX tergum elongate, polelike, (Fig. 21 C) Trifidus group
	Gonostylus not modified as above; lobe of IX tergum variously modified, but not as above
15(14).	Gonocoxite greatly enlarged, globose (Fig. 13 E); gonostylus large, with strong subapical crest of spines and wavy hairlike tuft on outer submedian prominence (Fig. 17 H) Peccator group
	Gonocoxite not modified as above; gonostylus variously modified, but not as above
16(15).	Distal part of lateral plate in lateral apsect with an elongate apical tergal process and a hooked apical sternal process (Fig. 11 D-I)
	Distal part of lateral plate with a short apical tergal process, a slender or stout spinelike or quadrate median process and/or apical sternal process (Fig. 12 A-I)
17(16).	Apical tergal process bifurcate at tip (Fig. 11 D, E, G-I) 18
	Apical tergal process tapered into a single point (Fig. 11 F) Saramaccensis group
18(17).	Apical tergal process long and narrow, projecting caudad; apical sternal process basal in position (Fig. 11 D, E) Distinguendus group
	Apical tergal process moderately to very broad; apical sternal process more or less at same level as apical tergal process (Fig. 11 G-I)
19(18).	Upper point of bifurcate apical tergal process blunt or rounded (Fig. 11 D) Putumayensis subgroup
	Upper point of bifurcate apical tergal process abruptly pointed (Fig. 11 E) Distinguendus subgroup; Chrysonotum subgroup; Rorotaensis subgroup; Galindoi subgroup
20(18).	Upper point of bifurcate apical tergal process blunt, with a series of teeth; apical sternal process long, with apex projecting basad (Fig. 11 I) Educator group
	Upper point of bifurcate apical tergal process ending in a point or without teeth; apical sternal process short, with apex projecting caudad (Fig. 11 G, H) Erraticus group (in part) 21

21(20).	Columnar stem of proximal division distally divided into 2 divergent secondary stalks (Fig. 16 G) Erraticus subgroup Columnar stem of proximal division not divided (Fig. 15 D)
22(16).	Apical median process of lateral plate conical, spinelike or with apex produced into a point tergad (Fig. 12 A-C). Intrincatus group (in part)
	Apical median process of lateral plate broad quadrate or rectangular with flat or truncate apical margin or with tergal and sternal angles produced into strong spines (Fig. D-J)
23(22).	Lobe of IX tergum forceplike (Fig. 22 E); gonostylus very thick and evenly broad, subapical crest of spicules not distinct (Fig. 18 H)Penai subgroup
	Lobe of IX tergum and gonostylus not modified as above 24
24(23).	Lobe of IX tergum slender, very long, and tubular (Fig. 22 D) Tecmarsis subgroup
	Lobe of IX tergum not modified as above
25(24).	Columnar stem of proximal division distally divided into 2 secondary stalks (Fig. 16 B, D)
	Columnar stem of proximal division not distally divided (Fig. 16 A, C)
26(25).	Distal division with distinct leaf at base or apex; columnar stem of proximal division with secondary stalks clearly separated from one another (Fig. 16 B)
	Distal division without leaf; columnar stem of proximal division with secondary stalks largely overlapped at bases (Fig. 16 D) Andricus subgroup
27(26).	Basal stem of distal division long, columnar, with all setae situated on extreme apex Eastor subgroup
	Basal stem of distal division short, with setae situated from median to apical portion (Fig. 16 B) Intricatus subgroup
28(25).	Leaf of distal division broad, oval; columnar stem of distal division slender and long (Fig. 16 A) Erraticus group (in part)
	Leaf of distal division narrow, with characteristic hooked apex; columnar stem of proximal division thicker and shorter (Fig. 16 C). Intrincatus group (in part) Idottus subgroup
29(22).	Apical sternal process absent (Fig. 12 E-G) Conspirator group

	Apical sternal process present (Fig. 12 D, E, H, I) 30
30(29).	Apical sternal process of lateral plate basal in position (Fig. 12 H, I), apex of gonostylus swollen or forming prominent head (Figs. 17 L, 18 L) Pilosus group
	Apical sternal process of lateral plate submedian or subapical in position or at same level as apical tergal process (Fig. 12 D, E), apex of gonostylus not forming prominent head 32
31(30).	Lobe of IX tergum small, fingerlike (Fig. 22 F) Pilosus subgroup
	Lobe of IX tergum very large, sac-like (Fig. 22 H)
32(30).	Apical sternal process well developed; apical median process prominent, and usually with row of distinct teeth on apical margin (Fig. 12 E) Inhibitator Group
	Apical sternal process poorly developed; apical median process not well developed, its apical margin smooth, irregular or with few teeth confined to tergal angle (Fig. 12 D)
33(32).	Gonostylus enlarged and strongly modified (Fig. 17 J, 18 J) 34
	Gonostylus not modified as above or normal Inhibitator subgroup
34(33).	Lobe of IX tergum enlarged, sac-like (Fig. 22 G); gonostylus as illustrated in Fig. 17 J Egcymon subgroup
	Lobe of IX tergum not modified as above; gonostylus as illustrated in Fig. 18 J
35(32).	Tergal angle of apical median process with at least 2 distinct denticles Bastagarius group (in part) Iolambdis subgroup
	Tergal angle of apical median process ending in a point 36
36(35).	Columnar stem of proximal division distally divided into 2 divergent stalks; apical median process of lateral plate relatively small, apical margin irregular Evansae group
	Columnar stem of proximal division not clearly divided into 2 stalks as above (Fig. 16 E, F); apical median process of lateral plate larger, apical margin smooth Bastagarius group (in part)
1.	Trumpet very slender and long, at least 1.0 mm; meatus without narrow
	slit or cleft extending from ventral margin of pinna; seta 5-C remarkably strong, its length about as long as trumpet; seta 9-VIII strong, as long as paddle length OCELLATUS SECTION

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	Trumpet short to moderately long, 0.3-0.8 mm; meatus with distinct slit or cleft extending from pinna; setae 5-C and 9-VIII not as strong as above
2(1).	Seta 9-VIII placed at or close to caudolateral angle of segment; seta 11-C usually double SPISSIPES SECTION
	Seta 9-VIII placed distinctly cephalad of caudolateral angle of segment; seta 11-C usually single MELANOCONION SECTION 9
	SPISSIPES SECTION
3(2).	Seta 5-IV double, 1.5 times as long as segment V; pinna of trumpet narrow, its length, including slit about 0.3 total length of trumpet
	Seta 5-IV 3-8 branched, shorter to slightly longer than segment V; pinna, including slit about 0.5 total length of trumpet 4
4(3).	Setae 3-I, II and 9-VII, VIII usually double 5
	Setae 3-I,II and 9-VII, VIII usually single 8
5(4).	Seta 10-C 3-5 branched 6
	Seta 10-C 8-15 branched Taeniopus group (in part) 7
6(5).	Meatus of trumpet thick and moderately or strongly swollen in middle; seta 6-III-VI usually single Spissipes group
	Meatus of trumpet slender and uniformly cylindrical; setae 6-III-VI double or triple Taeniopus group (in part)
7(5).	Seta 4-I strong, subequal to 3-I; 6-III-VI usually triple Vomerifer subgroup
	Seta 4-I minute, much shorter than 3-I; 6-III-VI usually single or double
8(4).	Caudolateral angle of segment VIII strongly produced into sharp point; pinna of trumpet moderately to strongly flared
	Caudolateral angle of segment VIII not produced as above; pinna of trumpet not flared or same diameter as meatus. Paracrybda group
	MELANOCONION SECTION
9(2).	Trumpet thin and long, index 10 or greater
	Trumpet rather thick, short to moderately long, index usually 5-8, sometimes lower

10(9).	Seta 6-III-VI usually 5,6 branched Atratus group
	Seta 6-III-VI usually double or triple Distinguendus group (in part)
11(10).	Seta 9-VIII 4 branched; 5-IV 4-6 branched Putumayensis subgroup
	Seta 9-VIII 5,6 branched; 5-IV double or triple Distinguendus subgroup
12(9).	Seta 9-VII double or triple Trifidus group
	Seta 9-VII at least 4 branched
13(12).	Meatus of trumpet thick, uniform in width or swollen in apical 0.5.
	Meatus of trumpet slender to moderately thick, usually uniform in width but not swollen in apical 0.5
14(13).	Meatus of trumpet distinctly swollen in apical 0.5, apical margin more or less rounded
	Meatus of trumpet not swollen in apical 0.5, apical margin truncate.
15(14).	Trumpet 0.45-0.5 mm long; seta 5-IV 5,6 branched Distinguendus group (in part) Rorotaensis subgroup
	Trumpet 0.25-0.35 mm long; seta 5-IV 4 branched . Saramaccensis group
16(14).	Seta 8-C 3,4 branched; 6-III-VI usually double Distinguendus group (in part) Chrysonotum subgroup
	Seta 8-C 5-8 branched; 6-III-VI usually 3,4 branched Erraticus group (in part) Erraticus subgroup
17(13).	Seta 6-III-VI usually 5,6 branched Educator group
	Seta 6-III-VI usually 1-3 branched
18(17).	Seta 6-III-VI usually single Erraticus group (in part) Psatharus subgroup
	Seta 6-III-VI usually double or triple
19(18).	Seta 3-II, III usually double Intrincatus group; Bastagarius group
	Seta 3-II, III usually single
20(19).	Trumpet relatively short, usually 0.35 mm in length; paddle seta 2-P very distinct, 3,4 times as long as 1-P Pilosus group

	Trumpet relatively long, 0.4-0.5 mm in length; paddle seta 2-P rather indistinct or distinct, at most 2 times as long as 1-P
21(20).	Seta 1-C usually triple; 5-V usually triple Conspirator group
	Seta 1-C usuallly 4,5 branched; 5-V 4-6 branched . Inhibitator group; Evansae group
	LARVAE
1.	Thorax and abdomen with several strong stellate setae; caudolateral margin of saddle with long spinelike spicules OCELLATUS SECTION
	Thorax and abdomen without strong, stellate setae as above; caudo-lateral margin of saddle with short, minute spicules 2
2(1).	Seta 8-P 4-6 branched; 7-P usually 4,5 branched SPISSIPES SECTION
	Seta 8-P usually double or single; 7-P usually triple or double 8
	SPISSIPES SECTION
3(2).	Abdominal seta 7-I double; comb scales numerous, all with apical fringe of evenly fine spicules
	Abdominal seta 7-I single; comb scales rather few in number, some strongly differentiated into large acute spines
4(3).	Setae 2,3-A of antenna subapical; seta 1-M single, strong, as long as 5-M; median caudal filament of spiracular apparatus of siphon remarkably long Spissipes group
	Setae 2,3-A of antenna apical; seta 1-M 1-3 branched, small, considerably shorter than 5-M; median caudal filament of spiracular apparatus of siphon not as long as above Taeniopus group
5(4).	Seta 5-C 4,5 branched; seta 6-I,II double Taeniopus subgroup
	Seta 5-C 7-9 branched; seta 6-I, II triple 6
6(5).	Siphon with prominent rows of strong subventral tufts, their length 3-4 times as long as siphon width at point of insertion; pecten teeth without distinct basal denticle Vomerifer subgroup
	Siphon without promenent row of subventral tufts as above, all tufts rather weak, relatively short and widely spaced, 1-2 times as long as siphon width at point of insertion; pecten teeth with strong basal denticle Pedroi subgroup

/(3)•	Seta /-P triple; siphon with 7 pairs of subventral tufts Paracrybda group
	Seta 7-P 4,5 branched; siphon with 4,5 pairs of subventral tufts
8(2).	Seta 2-C present, 14-C distinctly cephalad of 15-C; saddle without distinct spicules on caudolateral border Jubifer group
	Seta 2-C absent, 14-C at same level as or slightly cephalad of 15-C; saddle with distinct spicules on caudolateral border . MELANOCONION SECTION
	MELANOCONION SECTION
9(8).	Siphon rather thick and short, 0.45-0.60 mm in length; subventral tufts 7,8 pairs, all remarkably long, forming brushlike row from inside pecten to near extreme apex of sipon
	Siphon slender, moderately to very long, usually 1.0 mm or at least 0.70 mm in length; subventral tufts 4-6 pairs, weakly or strongly developed, but not as above, forming weak or prominent row usually from beyond pecten to about 0.75 of siphon length from base
10(9).	Siphon with 3,4 pairs of small dorsolateral setae inserted between 0.3 and 0.75 of its length from base Atratus group
	Siphon with 2 pairs of small dorsolateral setae inserted between 0.5 and 0.75 of its length from base
11(10).	Siphon slender and relatively long, 1.5-2.0 mm; subventral tufts weakly to moderately developed, widely spaced, not forming a dense row . Distinguendus group (in part)
	Siphon thicker and shorter than above, usually 0.90-1.2 mm in length; subventral tufts stronger, closely spaced or forming a prominent row
12(11).	Seta 7-I double; subventral tufts of siphon 3,4 times as long as siphon width at point of insertion Putumayensis subgroup
	Seta 7-I single; subventral tufts of siphon shorter or rather inconspicuous, about as long as siphon width at point of insertion. • • • • • • • • • • • • • • • • • • •
13(11).	Seta 8-P single; 7-P usually double; 4 or 5 distal pecten teeth strongly enlarged and closely packed Trifidus group
	Seta 8-P usually double; 7-P usually three or more branched; distal pecten teeth not strongly enlarged or closely packed as above

14(13).	Comb scales 7-27, their apices terminating in a sharp spine 15
	Comb scales 30-50, their apices rounded or truncate and fringed with evenly fine spicules
15(14).	Siphon strongly tapered and curved dorsad in distal portion; hooked seta 2-S of siphon enlarged and prominent . Distinguendus group (in part) Rorotaensis subgroup
	Siphon gradually tapered and straight in distal portion; hooked seta 2-S of siphon weakly to moderately developed 16
16(15).	Ventral brush (seta 4-X) of saddle composed of 5 pairs of setae . 17
	Ventral brush of saddle composed of 6 pairs of setae 18
17(16).	Seta 4-P double; siphon 0.85 mm; subventral tufts 3-4 times as long as siphon width at points of insertion Saramaccensis group
	Seta 4-P single: siphon longer, at least 1.0 mm; subventral tufts shorter, about 2 times as long as siphon width at points of insertion
18(16).	Seta 4-P single; integument of thorax and abdomen covered with very conspicuous spicules
	Seta 4-P double; integument of thorax and abdomen not covered with distinct spicules as above Educator group
19(18).	Seta 5-C single or double; 3-P usually double and long, about 0.5 length of setae 1,2-P . Distinguendus group (in part)
	Seta 5-C 4,5 branched; 3-P 7-10 branched and short, about 0.3 length of setae 1,2-P . Erraticus group (in part) Erraticus subgroup
20(14).	Seta 1-C (preclypeal spine) short, flattened and apically blunt; pecten teeth short, broad, conical, with apices not projecting beyond ventral margin of siphon . Erraticus group (in part)
	Seta 1-C long, spiniform, or sharply pointed apically; pecten teeth long, narrow, spinelike, with apices projecting beyond ventral margin of siphon
21(20).	Seta 4-P usually double; 1-M reduced, rather inconspicuous, its length at most 0.50 of 3-M Intrincatus group (in part) . 22
	Seta 4-P usually single; 1-M well developed and very distinct, its length subequal to or longer than 3-M
22(21).	Setae 2,3-A of antenna apical Idottus subgroup

	Setae 2,3-A subapical
23(22).	Seta 4-P widely separated, its length about 0.3 distance between bases of the pair; spiculation of thorax and abdomen distinct
	Seta 4-P close together, its length about as long as distance between bases of the pair; spiculation of thorax and abdomen indistinct
24(23).	Seta 5-C usually single; 12-C distinct, 4,5 branched; siphon with median dark ring Tecmarsis subgroup
	Seta 5-C usually double; 12-C indistinct, 2-4 branched; siphon without median dark ring Intrincatus subgroup
25(21).	Seta 7-P usually double; 3-P usually double or triple (1-5b) Conspirator group
	Seta 7-P usually triple; 3-P usually 4-6 branched 26
26(25).	Seta 4-C close together near dorsal midline; 12-C double or triple . Bastagarius group (in part)
	Seta 4-C widely separated; 12-C at least 4 branched (4-6b) 28
27(26).	Seta 5-C 3-6 branched Bastagarius subgroup
	Seta 5-C single or double Iolambdis subgroup
28(26).	Seta 2-VIII double; siphon/saddle ratio usually more than 3 Inhibitator group
	Seta 2-VIII single; siphon/saddle ratio usually less than 3
29(9).	Seta 7-C 10-12 branched; 12-C double Intrincatus group (in part) Andricus subgroup
	Seta 7-C 4-7 branched; 12-C 5,6 branched Pilosus group 30
30(29).	Seta 4-C double, minute or rather indistinct Pilosus subgroup
	Seta 4-C multiple, large and very distinct Caudelli subgroup

OCELLATUS SECTION

FEMALE. As described for the subgenus with the following characteristics: Head. Decumbent scales in center of vertex narrow, numerous, occupying an extensive area from coronal suture to near sides of eyes; lateral patch of broad appressed scales small; erect scales usually entirely white, sometimes brown. Thorax. Scutum with a pair of dark eyelike spots on antealar and supraalar areas. Pleuron with a broad vertical scale patch extending from

upper corner to lower posterior border of mesokatepisternum. Legs. Without any distinctive ornamentation. Wing. Plume scales on all veins long, narrow, linear or clavate. Abdomen. Terga II-VII without basolateral pale spots or basal transverse pale bands.

FEMALE CIBARIAL ARMATURE (Fig. 8 A). Cibarial teeth about 40, all very narrow and distally filamentous; hollow area on central axis of teeth absent.

MALE. In general as in female. *Head*. Palpus varying from 0.75 to as long as proboscis; palpomeres 4,5 non-plumose or with only a few short setae. Flagellar whorls of antenna strongly plumose.

MALE GENITALIA. Segment IX (Fig. 20 A). Tergal lobe small, mound-shaped, bearing 6-12 weak setae; interlobar space wide. Gonocoxite (Fig. 13 A). Slender, conical-comma shaped, sometimes broad oval or swollen at middle. Subapical Lobe (Fig. 14 A). Columnar stems of proximal and distal divisions well developed, widely separated and not distally divided. Gonostylus (Fig. 17 A). Shape normal or without special modification, subapical crest of spicules absent or poorly developed. Phallosome (Fig. 10 A). Aedeagus in tergal aspect with a distinct tergal bridge connecting the 2 lateral plates; basal hook of lateral plate broadly sclerotized, relatively short with sternal margin tapered into a blunt point; distal part simple, with a narrow caudal process only. Proctiger (Fig. 19 F). Apical crown small, with 4,5 teeth.

PUPA. Cephalothorax. Seta 5-C remarkably strong and long, subequal to trumpet length. Trumpet. Very long, slender, about 1.0 mm; pinna small, meatal slit absent. Metanotum. Seta 11-C single. Abdomen. Seta 5-IV-VI double or triple, remarkably long, at least 2 times as long as following segment; 6-III-VI long, single; 9-VIII double, remarkably strong, as long as paddle, inserted at or close to caudolateral angle of segment VIII. Paddle. Broad, hemispherical and largely pale; setae 1,2-P minute, inconspicuous.

Ocular bulge not prominent; seta 2-C absent; mental plate LARVA. Head. with 8,9 lateral teeth on each side of median tooth. Antenna relatively short and thin, less than 0.5 head length; seta 1-A short, weakly developed. Thorax. Spiculation absent; setae 7,8-P single; 0-P, 1-M, T and 13-T strong, stellate. Abdomen. Seta 6-I, II triple; 7-I double; 1-I-VI, 3-I-VI and 13-I-VI strong, stellate. Comb scales numerous, 30-40, all narrow, with apical fringe normal or barbed with evenly fine spicules. Setae 1,2-VIII without basal sclerotized plate. Siphon. Slender, distally tapering; moderately to very long, 1.25-2.0 mm; pecten teeth about 8, widely spaced, all without distinct barb of fine denticles; subventral tufts 5 pairs, each double, all strong, 4,5 times as long as siphon width at points of insertion; dorsolateral setae 2 pairs, inserted between 0.5-0.75 of siphon length from base; 2-S strong, simple and hooked. Anal Segment. Caudalolateral margin of saddle strongly spiculate or with numerous, long spinelike spicules; ventral brush (4-X) with 5 pairs of setae.

DISCUSSION. The Ocellatus section of 4 closely related species (ocellatus, nigrimacula, punctiscapularis and flochi) is the most distinctive of the 3 sections of Melanoconion and might even be recognized as a separated subgenus. This section corresponds to the ocellatus group of Duret (1969:113-134), characterized in the adults by the presence of a pair of dark, eyelike

spots on the antealar and supraalar areas of the scutum and by other distinctive features as indicated in the keys. It exhibits a rather bizarre combination of characters with the male genitalia typical of *Melanoconion*, the dark spots of the scutum of the adults like *Cx. stonei* Lane & Whitman 1943 and *shopei* Forattini & Toda 1966 of *Microculex* and the pupa and larva of *Micraedes* (Berlin 1969). Since members of the Ocellatus section and the latter 2 subgenera breed in leaf bases of epiphytic bromeliads, it is possible that their similarity is due to convergence. Further study on the relationships among these distinct lines would significantly contribute to a more natural classification of the groups.

The distribution pattern of the members of the Ocellatus section appears to be localized and widely disjunct over a large biogeographic area. The reported range extends from Colombia eastward through northern South America and southward as far as Sao Paulo, Brazil. Adult biology and medical importance are unknown.

SPISSIPES SECTION

FEMALE. As described for the subgenus with the following characteris-Decumbent scales in center of vertex largely narrow, numerous, Head. usually occupying an extensive area, sometimes restricted to a small triangular patch along coronal suture; lateral patch of broad appressed scales usually small, sometimes large, extending dorsad to posterolateral area; erect scales usually entirely dark, rarely partially pale golden. Thorax. integument dark brown to nearly black; scales usually entirely dark, sometimes partially pale golden on anterior half of scutum or partially whitish on prescutellar space and scutellar lobes. Pleuron usually without scale patch except on lower posterior surface of mesokatepisternum, latter sometimes with a small scale patch on its upper corner. Legs. Usually without distinctive ornamentation, sometimes with distinct white rings at joints of hindtarsomeres 1-5 and/or whitish knee spots on apices of femora. Wing. Plume scales on all veins short, broad ovate or squamous. Abdomen. Terga II-VII usually with distinct basolateral pale spots; basal transverse pale bands usually absent, rarely present.

FEMALE CIBARIAL ARMATURE (Fig. 8 B-F). Cibarial teeth varied, usually large, columnar, 10-17, with hollow area largely restricted to basal portion, sometimes small, toothlike, numerous, 20-40, all entirely pigmented.

MALE. In general as in female. *Head*. Palpus usually exceeding proboscis by at least 0.5 of palpomere 5, rarely shortened or subequal to proboscis; palpomeres 4,5 moderately to strongly plumose. Flagellar whorls of antenna strongly plumose.

MALE GENITALIA. Segment IX (Fig. 20 D-J). Tergal lobe variously developed. Gonocoxite. Usually conical-comma shaped, sometimes swollen at middle, ovoid or slightly modified. Subapical Lobe (Fig. 14 E-H). Columnar stems of proximal and distal divisions well developed, that of proximal not distally divided. Gonostylus (Fig. 17 B, G, I, K, 18 A, C). Usually normal or unmodified, sometimes angulate or swollen distad of median curvature; subapical crest poorly or strongly developed. Phallosome (Fig. 10 D-I). Aedeagus without upper tergal bridge; basal hook of lateral plate broadly sclerotized and with rounded sternal margin, distal part usually produced tergad and

sternad, with an elongate beaklike apical tergal process and a short, hooked sternal process or spine, sometime simple or represented by a single caudal process only. *Proctiger*. Apical crown small, with a comblike row of 7-12 teeth.

PUPA. Cephalothorax. Seta 5-C reduced or not strongly developed. Trumpet. Usually long, uniformly cylindrical or sometimes swollen in middle, length varying from 0.65-0.7 mm, sometimes shorter, funnel-shaped; pinna broad with meatal slit extending to 0.3-0.5 of total length of meatus. Metanotum. Seta 11-C usually double, rarely single. Abdomen. Seta 5-IV-VI two or more branched, shorter to slightly longer than following segment; 6-III-VI moderately developed, usually single or double, sometimes 3,4 branched; 9-VIII 1-4 branched, short, inserted at caudolateral angle of segment. Paddle. Broad, hemispherical, entirely pale or partially pigmented; setae 1,2-P distinct.

LARVA. Head. Ocular bulge prominent; seta 2-C present or absent; mental plate with 5-7 lateral teeth on each side of median tooth. Antenna long, stout, subequal to head length; seta 1-A long, strongly plumose. Spiculation present or absent; setae 7,8-P usually 4-6 branched, sometimes 7-P triple or double and 8-P single; 0-P, 1-M,T and 13-T normal, not stellate. Seta 6-I, II usually triple, sometimes double; 7-I usually double, sometimes single; 1,3 and 13-I-VI normal not stellate. Comb scales usually numerous, 30-40 or more, with even fringe of fine spicules or sometimes posterior scales strongly differentiated into large, elongate spines. Siphon. Usually slender, relatively long, sometimes thicker and short, 0.8-1.7 mm; pecten teeth 5-10, with fine barb of delicate denticles; subventral tufts weakly to strongly developed, usually 5 pairs, sometimes 3, 6 or 7, their length varying from 1 to 4 times as long as siphon width at points of insertion; dorsolateral setae usually 2 pairs, sometimes 3, inserted between 0.5-0.75 of siphon; 2-S strong or moderately developed, usually with submedian accessory spine, sometimes simple. *Anal Segment*. Caudolateral margin of saddle usually lightly spiculated, sometimes practically bare; ventral brush (4-X) with 6 pairs of setae.

The Spissipes section recognized here includes most of the DISCUSSION. species previously assigned by Galindo (1969) to his Culex spissipes group on the basis of the male genitalia and larval characters. In this study, the group is broadly interpreted and treated as a section to also include other species which exhibit the following shared characters: (1) in the male genitalia, the broadly sclerotized basal hook of the lateral plate; (2) in the general adult features, the largely narrow decumbent scales in the center of the vertex; (3) in the pupa, the insertion of seta 9-VIII at caudolateral angle of segment VIII; and (4) in the larva, the usually 4-6 branched setae 7,8-P and double seta 7-I and/or the presence of seta 2-C. Of all stages, the shape of the basal hook of the male genitalia and the pupal character noted above are the most characteristic and, I believe, are also of great importance in indicating the relationships among the species placed in this section. outlined in the proposed scheme, the 19 species of the Spissipes section apparently fall into 8 natural groups: Spissipes, Taeniopus, Paracrybda, Ocossa, Jubifer, Faurani, Nicaroensis and Lopesi. These groups can be readily separated by the characteristic male genitalia and certain features of the adults, pupa and larva, as indicated in the keys. The immatures of the Faurani, Nicaroensis and Lopesi groups are not yet known, thus these groups are provisionally assigned to this section primarily on the basis of the male

genitalia and adult characters.

Of the 3 sections of *Melanoconion*, the Spissipes section is apparently the most generalized and primitive, exhibiting the type of lateral plate of the male genitalia similar to that of the subgenera *Anoedioporpa* and *Tinolestes*. Certain groups of this section, particularly the Spissipes and Taeniopus groups also exhibit female cibarial teeth similar to those of *Tinolestes*, *Belkinomyia* and *Galindomyia* (Sirivanakarn 1978). This evidence suggests that these groups probably share a common ancestor with *Anoedioporpa*, *Tinolestes*, *Belkinomyia* and *Galindomyia*.

The Spissipes section is the most important of all sections of Melano-conion in the natural transmission of arboviruses. As indicated in the section of medical importance, at least 8 species (taeniopus, ocossa, panocossa, pedroi, vomerifer, portesi, delpontei and crybda) are currently known to be natural or potential vectors of Venezuelan Equine Encephalomyelitis and various other strains of arboviruses.

The distribution of the Spissipes section covers the entire reported range of the subgenus. Its center of distribution appears to be in Central America where the majority of the species occur, particularly in jungle swamps or open marshy areas along the Atlantic coast.

MELANOCONION SECTION

FEMALE. In general as described for the subgenus with the following characteristics. Head. Decumbent scales in center of vertex usually entirely broad and appressed, sometimes narrow, forming a relatively small triangular patch along coronal suture; lateral patch of broad appressed scales large or very conspicuous; erect scales entirely dark. Thorax.Scutal integument usually dark brown, sometimes pale reddish, yellowish or with orange tinge; all scales usually entirely dark or same color as underlying integument. Pleuron usually without scale patch on upper corner of mesokatepisternum and upper median surface of mesanepimeron, sometimes scale patches present. Legs. Usually without any distinctive ornamentation. Wing. Plume scales on all veins usually short, broad ovate or squamous. Abdomen. Terga II-VII with distinct basolateral pale spots or sometimes with complete basal transverse pale bands.

FEMALE CIBARIAL ARMATURE (Fig. 8 G-L, Fig. 9 A-I). Cibarial teeth usually large, hollow columnar, 3-8 in number, sometimes more numerous, narrow, with or without hollow area at bases or on axis.

MALE. In general as in female. *Head*. Palpus usually exceeding proboscis by at least 0.5 of palpomere 5, rarely as long as or subequal to proboscis; palpomeres 4,5 weakly to strongly plumose, rarely non-plumose. Flagellar whorls of antenna strongly plumose.

MALE GENITALIA. Segment IX (Figs. 21, 22). Tergal lobe variously modified. Gonocoxite (Fig. 13 C, E, F). Small to large, conical, oblong or globose. Subapical Lobe (Figs. 15, 16). Columnar stems of proximal and distal divisions usually well developed, that of proximal usually divided into 2 divergent stalks, sometimes undivided; specialized setae and leaves on each division variously developed. Gonostylus (Figs. 17 D, F, H, J, L-N; 18 B, D-

L). Variously modified from simple, sickle shape to being strongly swollen, forming a prominent head beyond median curvature, distal portion undivided (except trifidus). Phallosome (Figs. 11, 12). Aedeagus without upper tergal bridge (except penai); basal hook of lateral plate narrowly sclerotized, or in form of a slender curved rod, its distal part simple or variously modified with bifurcate tipped apical tergal process, apical sternal spinelike process and/or median, pointed or truncate process. Proctiger. Apical crown comblike, with 7-12 teeth, rarely more numerous.

PUPA. Cephalothorax. Seta 5-C not strongly developed. Trumpet. Moderately long, 0.35-0.60 mm, more or less uniformly cylindrical; pinna broad with meatal slit extending to about 0.3 of total length of meatus. Metanotum. Seta 11-C single. Abdomen. Seta 5-IV-VI with 3 or more branches, usually shorter than following segment; 6-III-VI usually at least three or more branched, sometimes double; 9-VIII 3-7 branched, always removed cephalad of caudolateral angle of segment. Paddle. Broad, hemispherical and usually entirely pale or transparent; setae 1,2-P moderately to well developed and distinct.

Head. Ocular bulge always prominent; seta 2-C absent; mental LARVA. plate with 5.6 lateral teeth on each side of median tooth. Antenna long, stout, subequal to head length; seta 1-A strongly plumose. Thorax. lation moderately to strongly developed; seta 7-P usually triple or sometimes double; seta 8-P usually double or sometimes single; 0-P, 1-M,T and 13-T weakly to strongly developed but not stellate. Abdomen. Seta 6-I, II usually double, sometimes triple; 7-I usually single, rarely double; 1,3,13- I-VI normally developed, not stellate. Comb scales usually numerous, 20-50 with normal fringe of fine spicules or with distinct apical median spine, sometimes 7-12, all large, spinelike, in a single row. Siphon. Length varying from 0.65-2.2 mm, usually about 1.0 mm; pecten teeth 7-16 or more, all usually narrow and increased in length toward proximal portion of siphon; subventral tufts usually well developed, 4-8 pairs, forming a prominent row usually from beyond pecten to about 0.75 of siphon length, sometimes extending to near apex, their length varying from 1-6 times as long as siphon width at points of insertion; dorsolateral setae usually 2 pairs, sometimes 3 or 4; seta 2-S Anal Segment. moderately to strongly developed. Caudolateral margin of saddle lightly to moderately spiculated; ventral brush (4-X) with 5,6 pairs of setae.

DISCUSSION. The Melanoconion section recognized here is the largest and most complex of all 3 sections of Melanoconion. Included within this section are some 125 species most of which were previously segregated into sections Dinoporpa, Choeroporpa, Mochlostyrax, Melanoconion and Gnophodeomyia by Dyar (1928) and Rozeboom and Komp (1950). In this study, all of these sections are combined into the single Melanoconion section on the basis of the following shared characters: (1) in the male genitalia, the narrowly sclerotized basal hook of the lateral plate; (2) in the general adult features, the usually broad appressed decumbent scales of the vertex (except Atratus and Distinguendus groups); (3) in the pupa, the position of seta 9-VIII which is removed cephalad of caudolateral angle of the segment and the usually single seta 11-C of metanotum; and (4) in the larva, the usually double seta 6-I,II, single seta 7-I, triple or double seta 7-P and double seta 8-P.

The members of the Melanoconion section are strongly differentiated from

one another by the modification of the various components of the male genitalia, but less so or not at all in the external features of the adults, female cibarial armature and the immature stages. Most of the species in this section are known only from males and the taxonomic status of several nominal forms remains uncertain. Based primarily on the male genitalia and to a certain extent also on other stages of several known species, 13 groups are These are: Atratus, Distinguendus, Trifidus, Saramaccensis, Erraticus, Educator, Intrincatus, Bastagarius, Evansae, Inhibitator, Conspirator, Pilosus and Peccator. As outlined in the proposed scheme, six of these groups (Distinguendus, Erraticus, Intrincatus, Bastagarius, Inhibitator and Pilosus) are further subdivided into subgroups. The relationships between or among these groups are very difficult to interpret because of the extreme diversity or overlap in one or more stages. However, from the detailed comparative study of each component of the male genitalia and the analysis of the distribution of similar genitalic characters among the various groups, indications of the probable relationships are evident. Possibly of great importance are the trends in the modification of the distal part of the lateral plate of the aedeagus. Based on this character, there appear to be 3 distinct lines, with the Atratus, Distinguendus and Intrincatus groups that represent the ancient stocks from which the other groups were probably The three lines are composed of the following groups: (1) Atratus derived. and Trifidus (2) Distinguendus, Saramaccensis, Erraticus, Educator and perhaps also Peccator; and (3) Intrincatus, Bastagarius, Evansae, Inhibitator. Conspirator and Pilosus. The relationship between the Atratus and Trifidus groups is evident in the type of lateral plate as shown in Fig. 11 A and B; that of the Distinguendus and 4 other groups is evident as shown in Fig. 11, D-I; and that of Intrincatus and 5 other groups is evident as shown in Fig. 12 The modification of the lateral plate in the Intrincatus line largely involves the development of the apical median process which is absent in the Atratus and Distinguendus lines. This process is probably developed from the upper point of the bifurcate tipped apical tergal process of the Distinguendus and Erraticus types. Other modification of the lateral plate in the Intrincatus line also involves the reduction or expansion of the apical median process, and loss or shifting in position of the apical sternal hooked process as shown in the Bastagarius, Inhibitator, Conspirator and Pilosus groups.

The Melanoconion section is the most widespread and has been reported from all areas within the range of the subgenus. As in the Spissipes section, its center of distribution appears to be in Central America and adjacent areas in northern South America where all of the groups and most of the subgroups are represented. As far as known, all species in this section are typical groundpool forms. Adults of various species are relatively common and have been captured in practically all types of collections. The adult biology and medical importance are largely unknown. Currently, only 3 species, iolambdis, elevator and dunni, have been reported to harbor certain strains of arboviruses (Galindo 1978).

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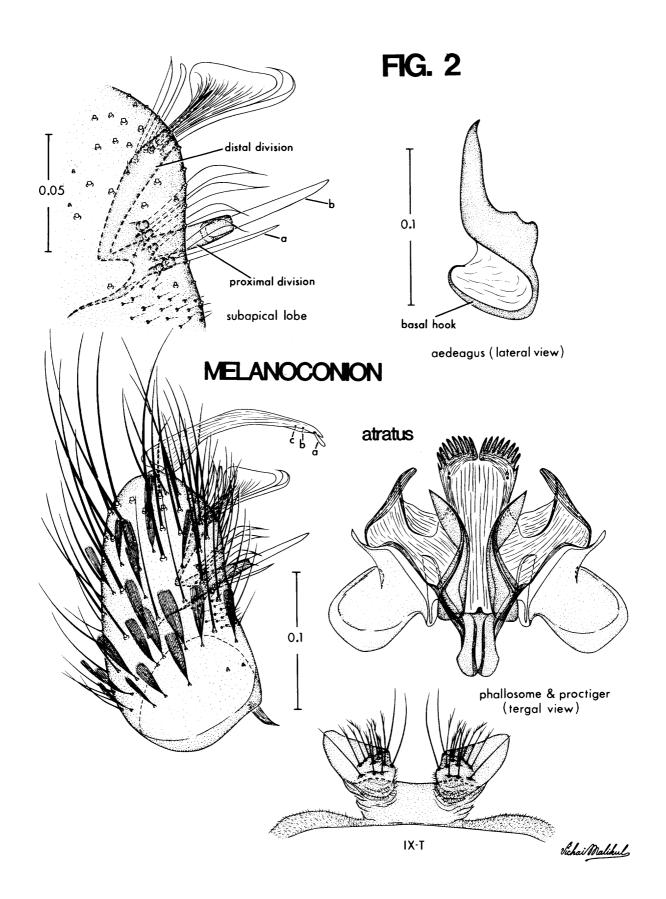
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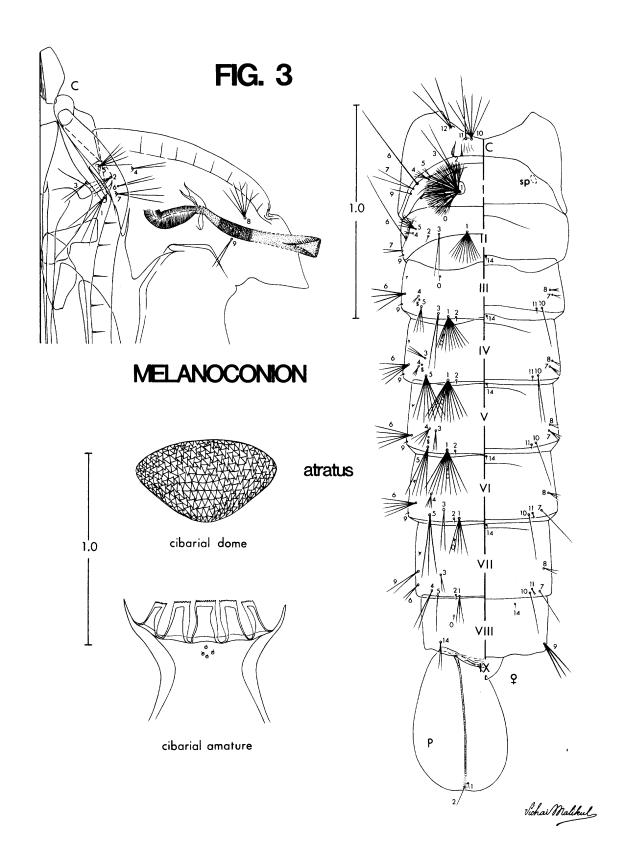
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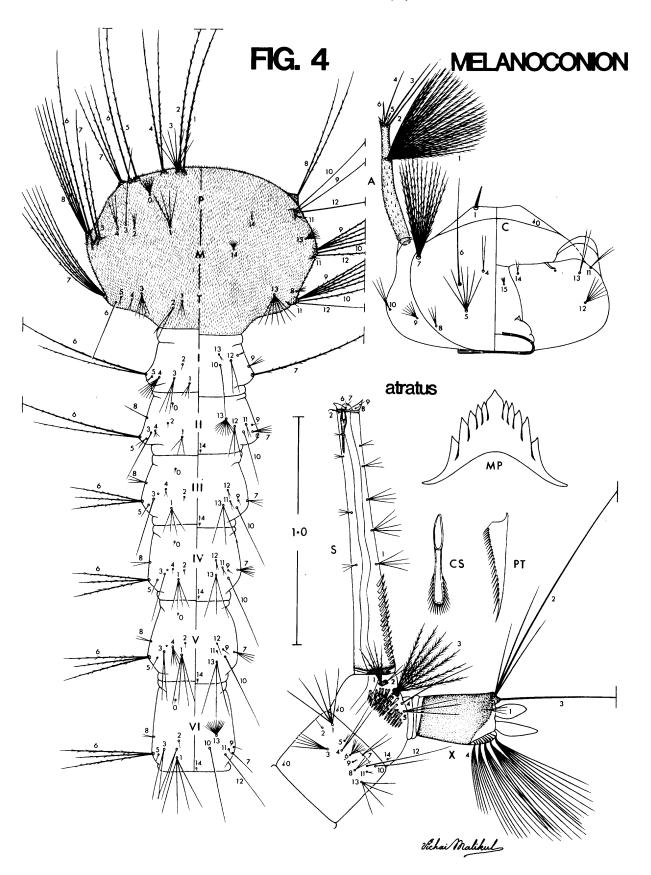
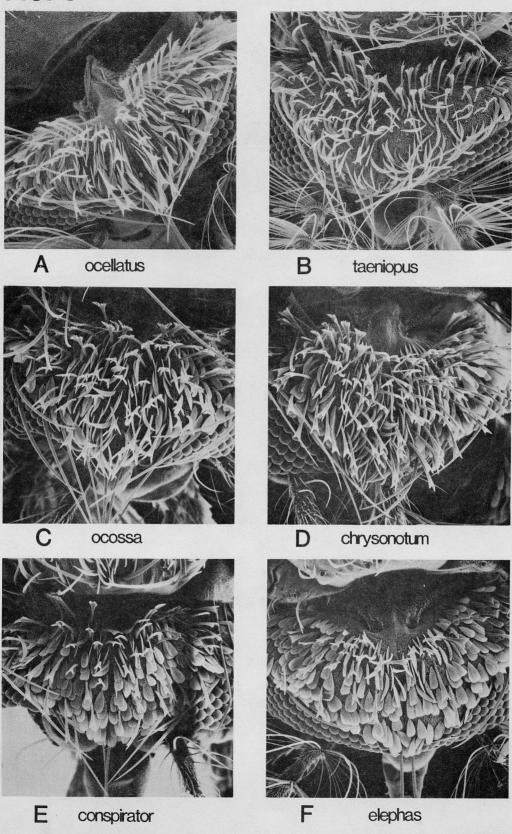


FIG. 5 Types of Decumbent Scales on Vertex of the Head



E

erraticus

FIG. 6 Thorax: Pleural Scale Patches spissipes A ocellatus B vomerifer dunni

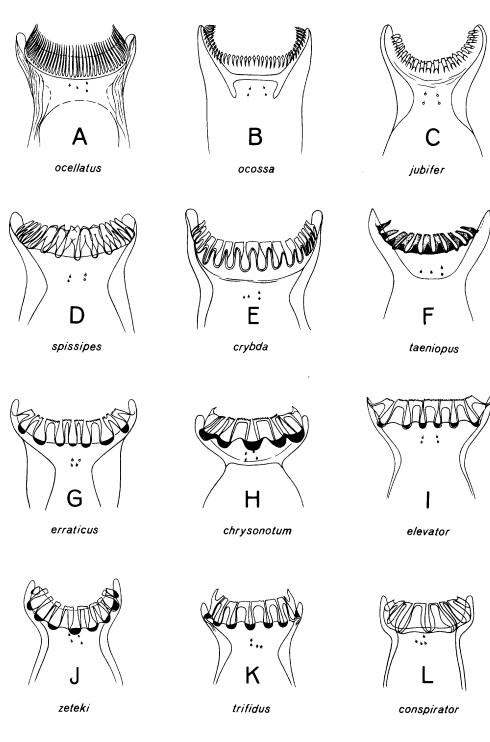
F

conspirator

FIG. 7 Types of Plume Scales of the Wing wernsn clavat X 275 A ocellatus X 675 B clavate bread X 270 chrysonotum D X 675 ovale E X 270 spissipes F X 675

FIG. 8

Female Cibarial Armature



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Richai Malikul

FIG. 9

Female Cibarial Armature

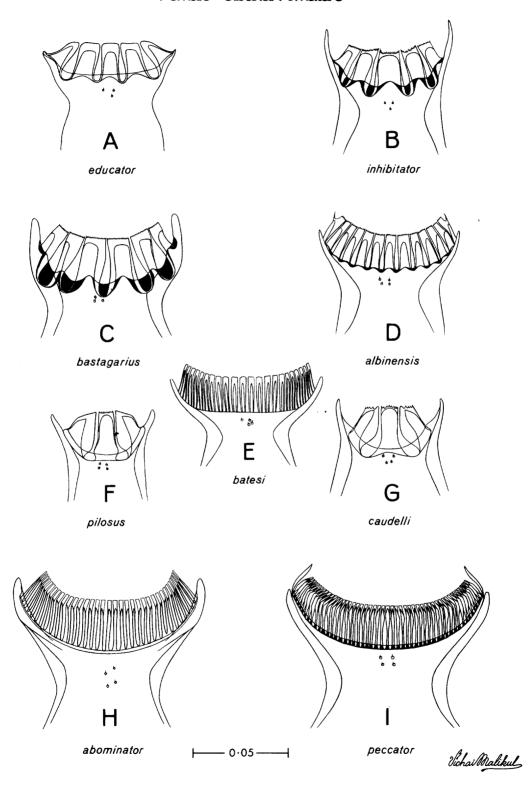
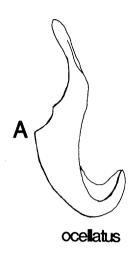
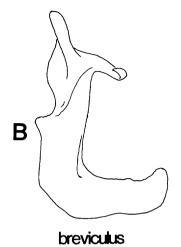
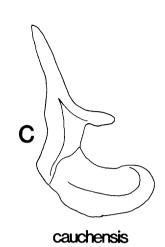


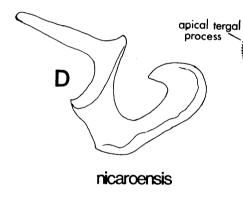
FIG. 10

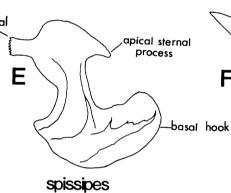


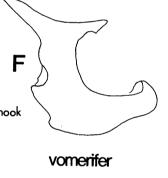


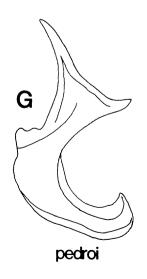


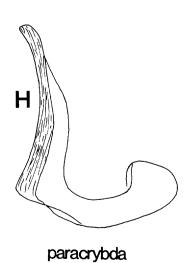












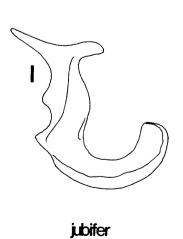


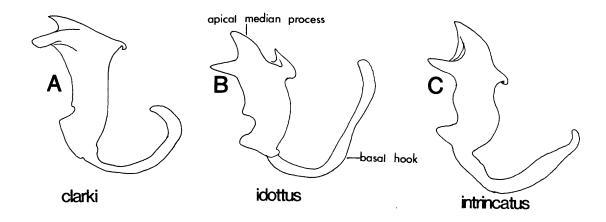
FIG. 11 Male Genitalia: Lateral Plate of aedeagus В anips trifidus atratus apical tergal process D apical sternal process basal hook putumayensis chrysonotum saramaccensis

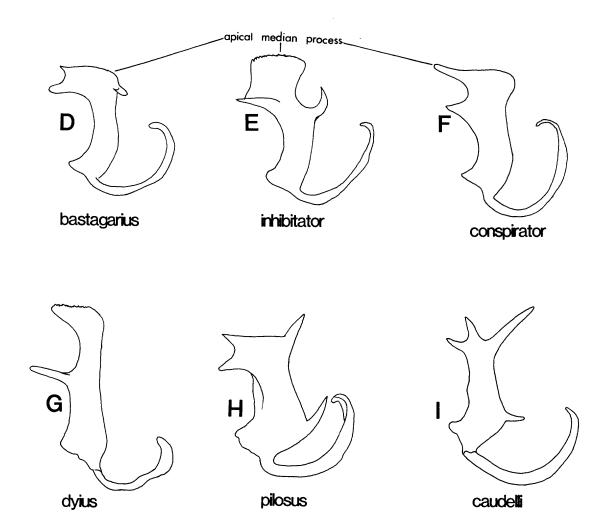
psatharus

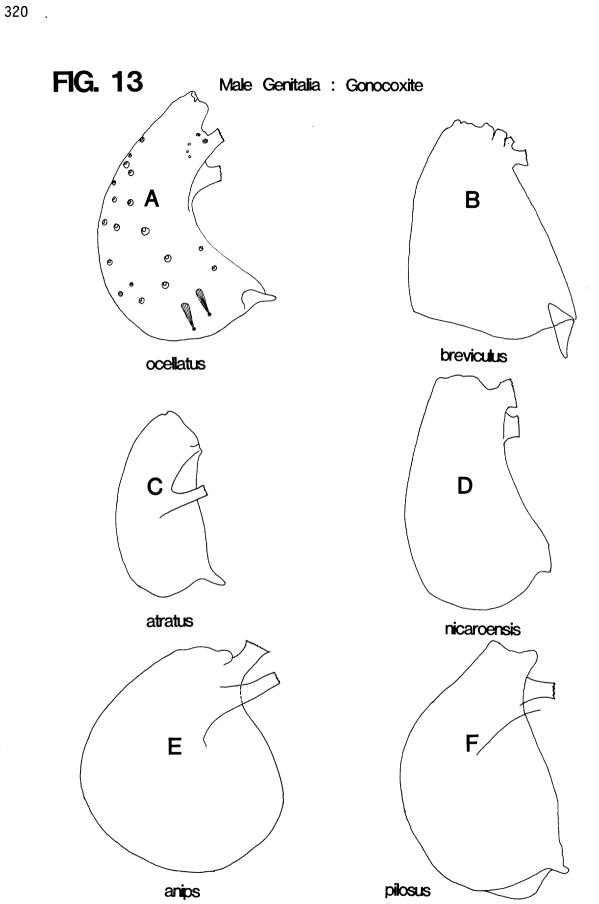
educator

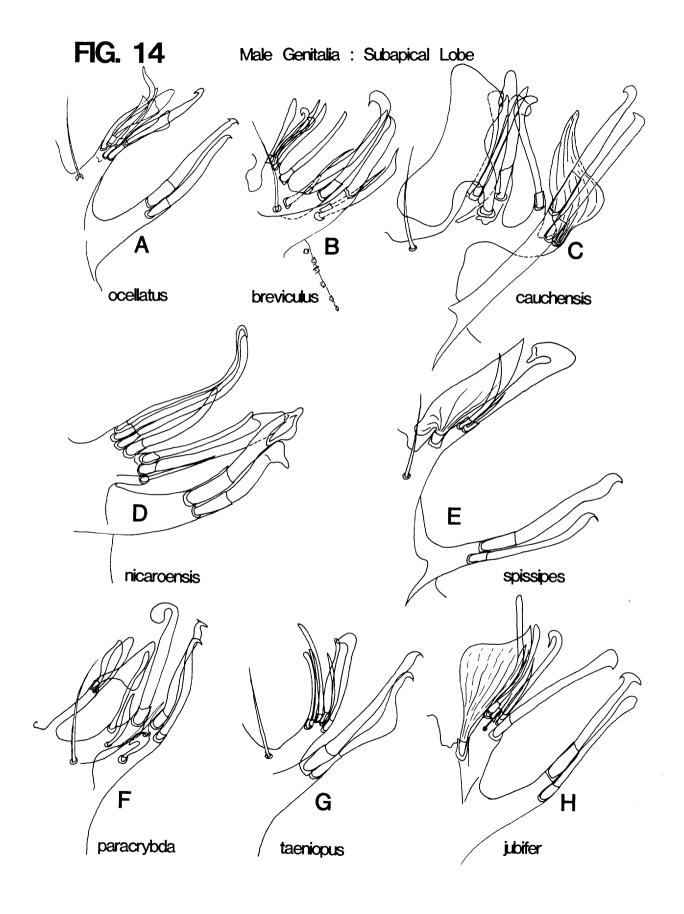
erraticus

FIG. 12 Male Genitalia: Lateral Plate of aedeagus









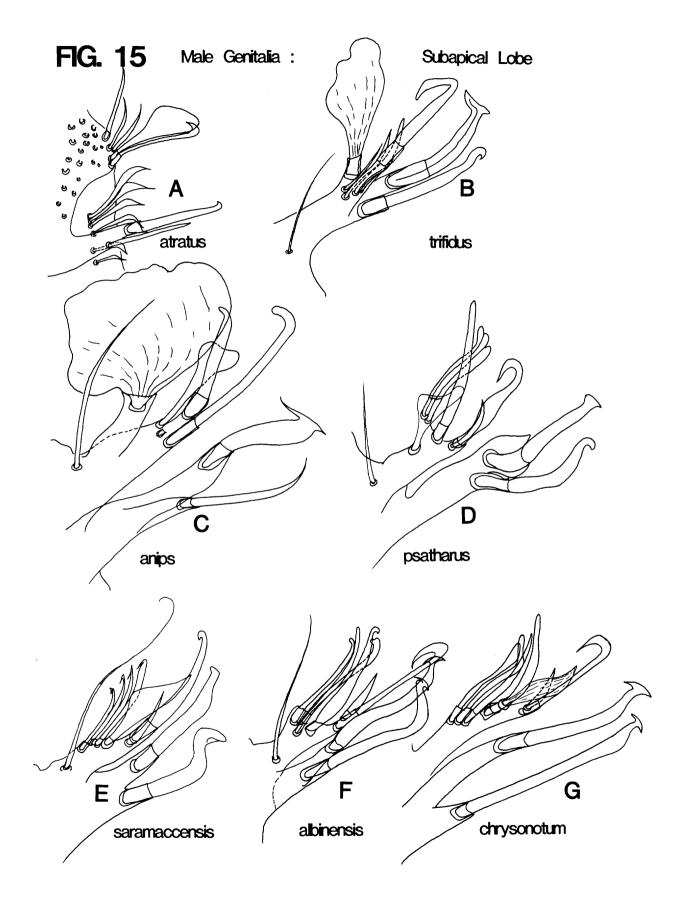
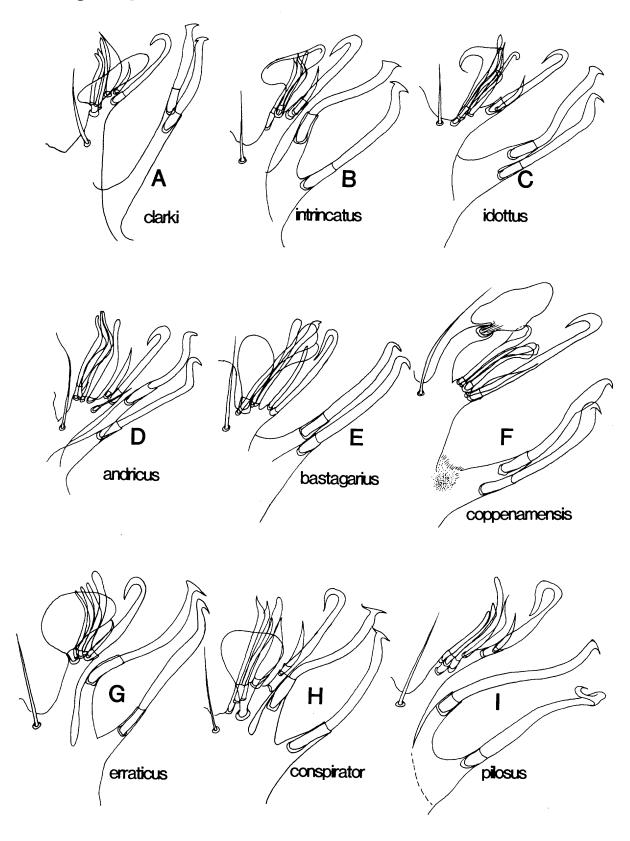
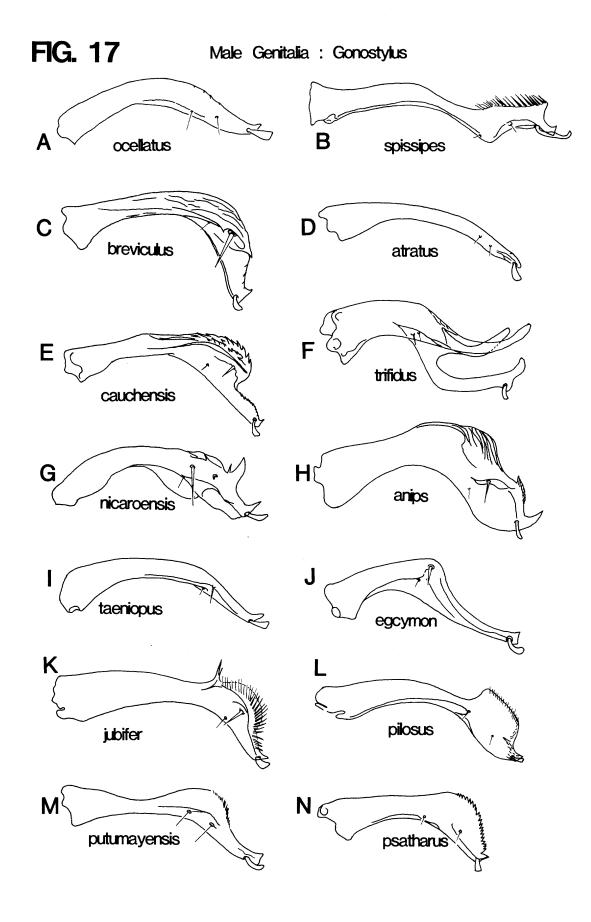


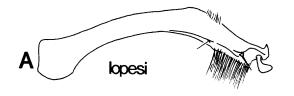
FIG. 16

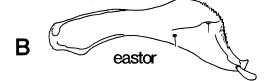
Male Genitalia : Subapical Lobe







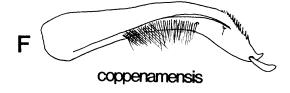




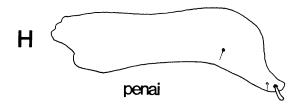


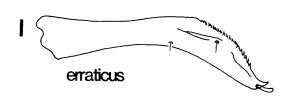


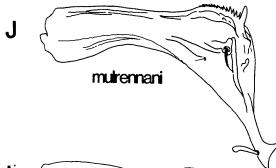


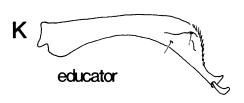












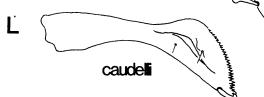


FIG. 19 Male Genitalia: Proctiger Crown breviculus nicaroensis jubifer trifidus

chrysonotum

ocellatus

FIG. 20 Male Genitalia: Lobe of IX Tergui...

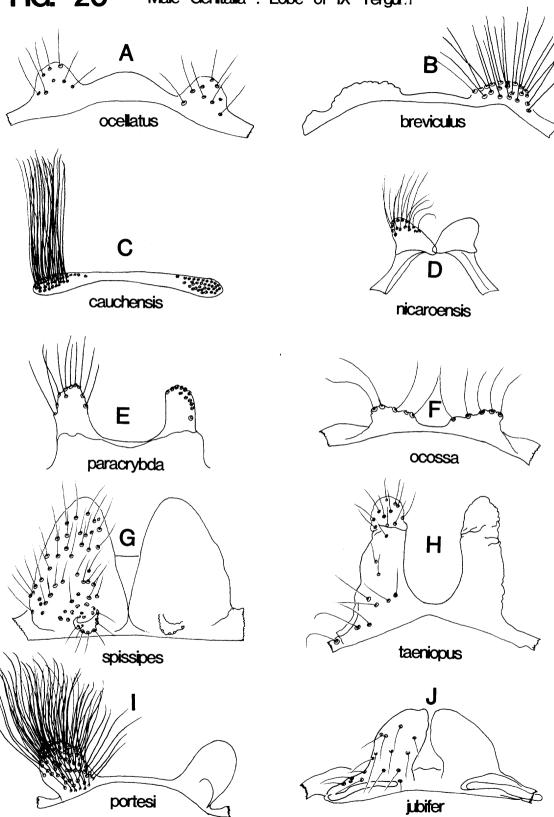
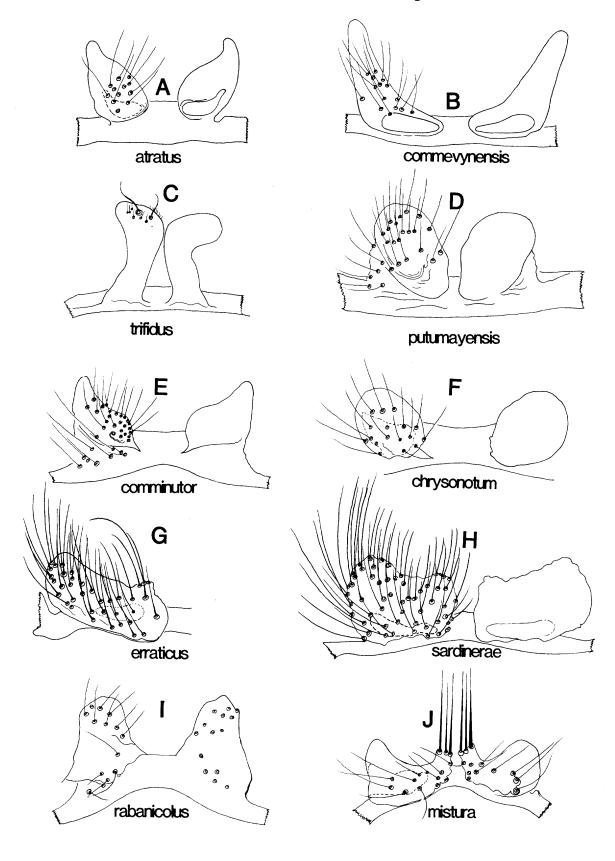


FIG. 21 Male Genitalia: Lobe of IX Tergum



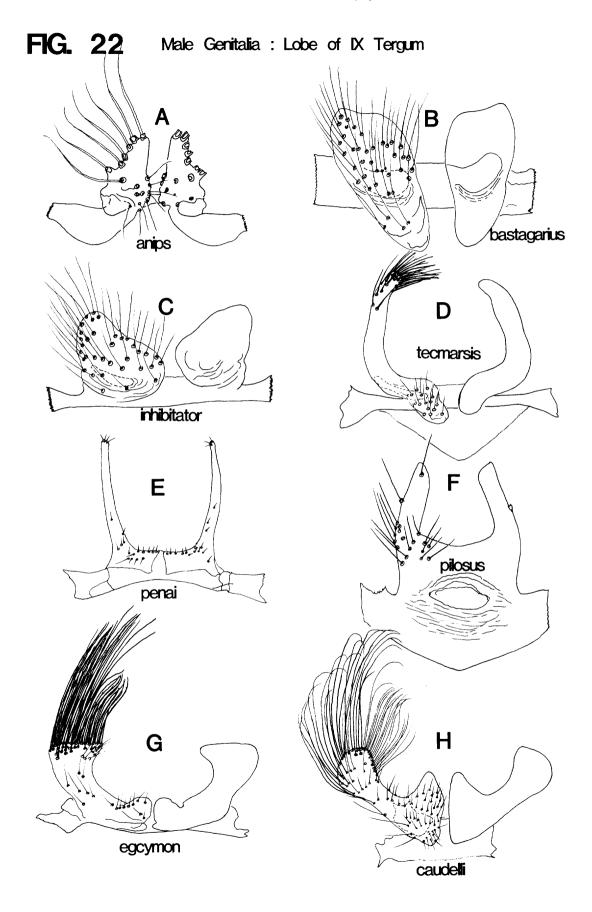
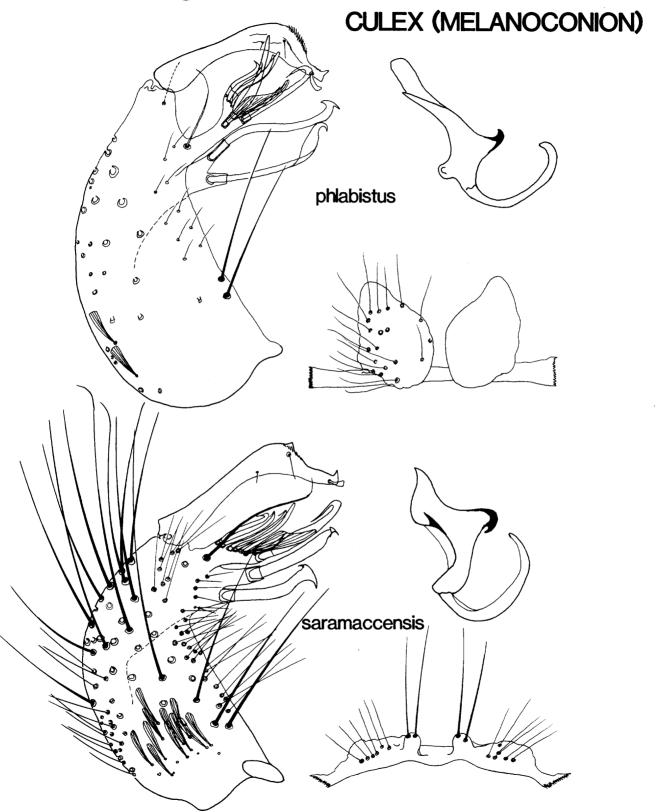
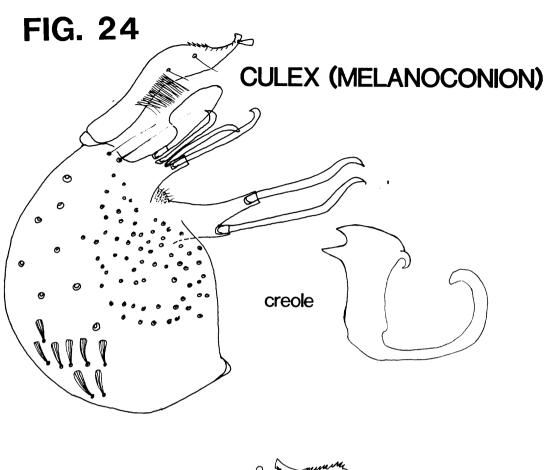
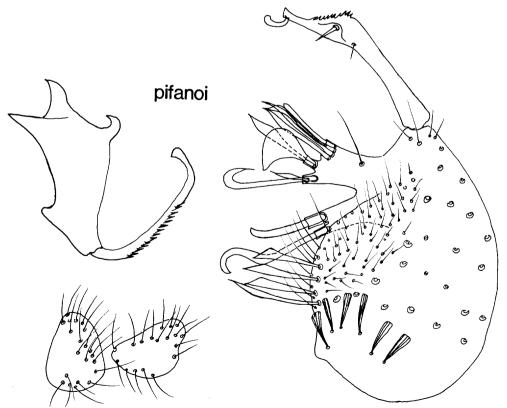
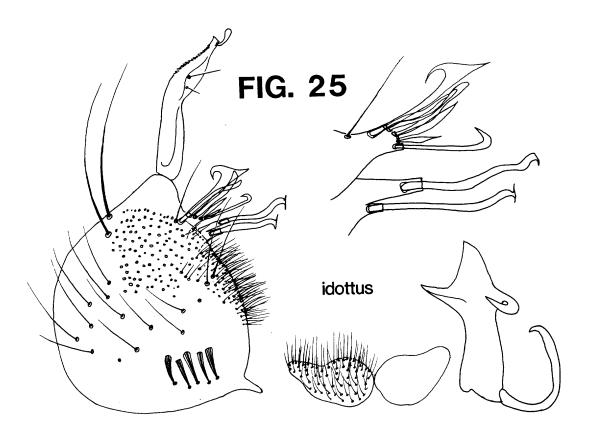


FIG. 23

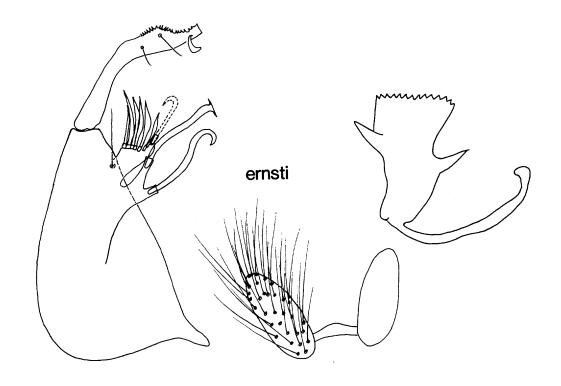








CULEX (MELANOCONION)



APPENDIX

CONSPECTUS OF TAXONOMIC CHANGES

Transferred Taxa

breviculus Senevet & Abonnenc 1939, from subgenus Melanoconion Theobald 1903 to subgenus Tinolestes Coquillett 1906 cauchensis Floch & Abonnenc 1945, from subgenus Melanoconion Theobald 1903 to subgenus Tinolestes Coquillett 1906

Rejected Names

Taxa Dubia: decorator Dyar & Knab 1906; fasciolatus (Lutz 1904); gravitator Dyar & Knab 1906; humilis Theobald 1901; indecorabilis (Theobald 1903); lugens Lutz 1905; nigrescens (Theobald 1907) and nigricorpus (Theobald 1901).

Nomina Dubia: chrysothorax (Peryassu 1908); epirus Aiken 1909 and Asebeomyia Aiken 1911.

New Synonymy

kerri Duret 1968, to synonymy with phlabistus Dyar 1920 seneveti Clastrier 1970, to synonymy with contei Duret 1968 thomasi Evans 1924, to synonymy with bastagarius Dyar & Knab 1906 venezuelensis Anduze 1948(1949), to synonymy with simulator Dyar & Knab 1906

Transferred Synonymy

implicatus Senevet & Abonnenc 1939, from synonymy with nigrescens (Theobald 1907) to synonymy with saramaccensis Bonne-Wepster & Bonne 1919(1920).