

Notes on the Systematics of Culex (Melanoconion)
Taeniopus Dyar and Knab and Related Species, Gathered
During Arbovirus Investigations in Panama¹

Pedro Galindo
Gorgas Memorial Laboratory
Apartado 1252
Panama, R. de P.

1. Introduction - During the past ten years, the writer has participated in long-term investigations on the ecology of arboviruses, carried out by members of the staff of Gorgas Memorial Laboratory in a tropical rain-forest area near Almirante, Panama. Soon after the beginning of these studies it became evident that Culex mosquitoes of the subgenus Melanoconion were important in the transmission of arboviruses.

The impossible task of separating species of this subgenus on female characters and of studying vector-host relationships of mosquito taxa that could not even be named, called for thorough systematic studies of the local species involved in arbovirus transmission in the Almirante area.

The present contribution is a preliminary summary of some of the findings obtained in these studies, with particular emphasis on the systematic relationships and synonymy of Culex taeniopus D. and K. and related species.

2. Separation into taxa of wild-caught females - Of a total of 32 species of Melanoconion found in the Almirante area, less than a dozen were suspected to be involved in the transmission of arboviruses. Among these, it was possible to recognize females of seven different types, with similar feeding habits. All seven seemed to prefer the blood of rodents, but also attacked mammals and birds, both in the canopy of the forest and on the ground. These different types could not be named at the time and were designated by capital letters. Later, the writer was successful in obtaining laboratory-reared progeny of many individually isolated females of all these types. After a comparative study of the male terminalia and immature stages of these forms, it became possible to identify the seven taxa. During the process of identification it was necessary to carry out a thorough study of the systematics involved, results of which are included in the discussion of each species. At the end of the individual discussion of the species, notes have been added on the phylogenetic relationships between species of this complex, and between the complex and other species of Melanoconion.

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3. Identification of the species - The following taxa were identified by the method described above:

TYPE A - A medium-sized species with females generally dark in color having dark pleura and broad silvery rings at both ends of the hind tarsal joints. Common in the lowland swampy forest and in peridomestic situations around Almirante. This species was identified as what is currently known as Culex taeniopus.

Culex (Melanoconion) taeniopus Dyar and Knab, 1907, was described from a single female collected near Bluefields, Nicaragua. Later, Howard, Dyar and Knab (1915), reported the species as breeding in "rocks along the course of a stream in a forest in Panama". This record is probably referable to C. pseudotaeniopus, then unknown, as C. taeniopus does not breed in this habitat. Dyar (1925) described a male type from Venezuela as the male of C. taeniopus, and this interpretation has been generally accepted in the identification of this species.

A comparison of Almirante material with topotypical males and females of C. taeniopus, collected by Dr. Peter Frank, of the Middle America Research Unit, near Bluefields, Nicaragua, reveals no differences between them. However, definitive proof of the conspecificity of the Almirante and Bluefields populations will have to await the finding of immature stages at the type locality. Until such time, the writer accepts Dyar's interpretation of this species.

TYPE B - A rare species similar to Type A but definitely paler in color. Rarely encountered in the lowland forest. Larvae found breeding among rocks in forest streams with clear water, along the slopes of the mountains to the southwest of Almirante. This taxon was identified as Culex pseudo-taeniopus Galindo and Blanton, 1954. This species can be separated from taeniopus by details of the male terminalia and particularly by the peculiar shape of the pupal trumpets, which are unmistakable. Rozeboom and Komp (1950) were actually referring to this species, then undescribed, when they assigned to C. taeniopus pupal trumpets: ". . . aberrant for a Melanoconion, being widened and flattened at the tips, with a peculiar transverse cleft". Breeding habits of these two species also differ, as the immature stages of C. taeniopus are found in deeply shaded lowland swamps full of dead leaves and debris, particularly in close association with the base of swamp palms.

TYPE C - A fairly large, dark species with dark legs and no basal abdominal bands. Anterior part of mesonotum with a patch of golden scales showing various designs. Larvae found in deeply shaded forested swamps but usually in deeper and more open waters than C. taeniopus. Until males and females were bred out of a single egg batch, females could not be associated with any of the known Melanoconion males taken at Almirante, as the conspicuous patch of golden scales present on the mesonotum of the female is lacking on the corresponding male. When finally associated, they proved to be Culex menytes Dyar, 1918, which was recently synonymized under Culex spissipes (Theobald), 1903, by Takahashi (1968). The writer is in agreement with this synonymy.

TYPE D - A small species with dark legs. Pleura light-colored with four discrete dark spots, two on sternopleuron and two on mesepimeron. The commonest species of Melanoconion in biting collections with human bait. Larvae extremely difficult to find in nature. Always encountered in deeply shaded, shallow pools in lowland swamps, choked with dead leaves and other debris, usually within the buttressed roots of trees. This turned out to be the toptotypical population of Culex vomerifer Komp, 1932. The synonymy of this species was revised by Aitken and Galindo (1966) who resurrected C. portesi from the synonymy of vomerifer and placed cayennensis Floch and Abonnenc as a synonym of it.

TYPE E - A medium-sized dark species very similar to C. taeniopus but tarsal rings much narrower. This taxon was identified as the toptotypical population of Culex mychonde Komp, 1928. The describer of this species (Komp, 1935) synonymized it with C. opisthopus Komp, 1926, described from Puerto Castilla, Honduras.

Belkin (1969), in studying the closely related forms cedecei Stone and Hair, 1969, from Florida, annulipes Theobald, 1907, from Jamaica and opisthopus from Honduras, could find no differences in the male terminalia of these three populations. He further found that material from Florida had "very restricted" tarsal rings, which were more conspicuous in the Honduras specimens and extremely variable in the Jamaica population. He only had larvae from Florida and Jamaica in front of him, which he found almost identical, but ". . . conforming to a type unique in Melanoconion in the distal displacement of the 2 subdorsal siphonal tufts". In view of the lack of immature stages from Honduras (opisthopus) and from Panama (mychonde), he decided to resurrect annulipes Theobald from the synonymy of taeniopus D. and K. and to place cedecei as a synonym of it, keeping the specific name opisthopus Komp to refer to the Honduras and Panama populations.

The writer has had the opportunity to compare all stages of toptotypical populations of mychonde and cedecei. While male terminalia of the two forms are very similar, there are slight differences in the outer arm of the subapical lobe. The differences in the hind tarsal markings noted by Belkin (loc. cit.) between cedecei and opisthopus are also quite constant between cedecei and mychonde. Markings in cedecei are evanescent and almost absent, while in mychonde are more conspicuous, although much narrower than in taeniopus, as noted before. However, in view of the variations observed by Belkin in annulipes it would seem dangerous to attempt separating this complex into species by this character alone. The immature stages of cedecei and mychonde appear identical to the writer. The apical displacement of the subdorsal hairs of the siphon cited by Belkin (loc. cit.) in cedecei is also present in the mychonde population. Actually this is not a specific, but rather a group character, as it is shared by other Melanoconion related to the species under consideration. This will be further discussed below. The breeding habits of cedecei and mychonde populations are totally different. While mychonde breeds in deeply shaded forest swamps with dead leaves and vegetable debris, usually associated with C. spissipes, cedecei is said to breed in solution holes in coral limestone.

In view of Belkin's findings and the close morphological similarities in the immature stages and male terminalia of cedecei and mychonde, the writer hereby proposes to keep the specific name annulipes Theobald to refer to all of these closely related allopatric populations and thus places in its synonymy opisthopus Komp and mychonde Komp, as well as cedecei, already placed there by Belkin. The marked differences in breeding habits and the constant differences found in the tarsal markings between forms cedecei and mychonde suggests that this is a polytypic species which breaks up into at least 3 geographical races or subspecies. However, this will have to be substantiated by a thorough study of all stages of Central American and Mexican populations. For the time being, the writer considers opisthopus and cedecei subspecifically distinct from annulipes.

TYPES F and G - Type F is a large species with abdomen, mesonotum and occiput covered mostly with dark scales. Pleura light-colored with three conspicuous dark spots, two on sternopleuron and one on mesepimeron. Type G is also a large, dark species, with dark legs, pleura and mesonotum. The latter bears a light pattern of golden scales. Occiput with erect pure golden scales in the middle, bordered by dark erect ones. Abdomen with broad basal abdominal bands.

While these two types can be readily separated on external characteristics of the adult, it was discovered that they possess male terminalia which appear identical in every respect and which are in turn identical with the terminalia of C. taeniopus. Immature stages of these three sympatric populations in Almirante differ and are ecologically isolated, as they occupy very different habitats. It has been noted that C. taeniopus larvae and pupae are found breeding in shallow pools of deeply shaded swamps, usually closely appressed to the base of the trunk of palms. On the other hand, "Type F" larvae have been found exclusively deep within rodent burrows dug at the edge of forest swamps, whose lower galleries have been flooded by a rising water table. The third form, "Type G", breeds in sunlit, open swamps choked with floating sedges and grasses. Despite the identical nature of the male terminalia of these three forms, there appears little doubt that they represent distinct sympatric species which have become genetically isolated through differences in breeding and, perhaps, in mating habits.

In attempting to name types "F" and "G" the writer became faced with the fact that the only name available for a "dark legged" Melanoconion with "taeniopus-like" terminalia was Culex crybda Dyar, 1924, described from Colombia. Provisionally, the writer assigned the name crybda to the commonest of the two forms which was "Type F", also taking into consideration the fact that this type occurs in Trinidad, where Aitken (personal communication) was also referring to it as "Culex crybda", while, to the writer's knowledge "Type G" had not been found outside Panama. Thus literature from Panama (Galindo et al., 1966) and from Trinidad (Aitken et al., 1969) which refers to C. crybda, is referring to "Type F", with dark tarsi, abdominal tergites without broad basal bands, dark mesonotum and occiput and light-colored pleura with two dark spots on the sternopleuron and a single spot in the mesepimeron.

In the hope of finding an available name for "Type G" the writer began a critical examination of other species synonymized under C. taeniopus, namely, C. annulipes (Theobald), and C. epanastasis Dyar, 1922. C. annulipes has ringed hind tarsi, so it could not be "Type G" which has dark tarsi. Besides, Belkin (loc. cit.) has shown that annulipes has male terminalia quite distinct from C. taeniopus, as discussed under "Type E".

Culex epanastasis, the second name synonymized under C. taeniopus, was described from the Canal Zone and became the subject of interest to the writer. In checking the original description of this species it was determined that, despite the fact that Dyar stated: "The single male type is much damaged", he went on to say: "Abdomen entirely black. Legs black, the femora narrowly pale beneath, tips of femora distinctly white".

From this description it is obvious that Komp (1935) was in error when he synonymized epanastasis under taeniopus D. and K. basing his conclusion on male terminalia characters, as the latter has broad white rings on the hind tarsal joints. It also became apparent that our "Type G" could not be this species as it has broad basal abdominal bands, while epanastasis, was described as with the abdomen "entirely black".

The questions raised by the writer were then two:

- 1) is "Type F" really identical to C. crybda? and
- 2) are epanastasis and crybda one and the same species?

C. crybda Dyar, 1924, was described from Colombia and in 1928 the describer sank the name in the synonymy of taeniopus. Rozeboom and Komp (loc. cit.) resurrected crybda from synonymy basing their conclusion mainly on differences in characters of the pupal trumpets. Actually what they were calling the pupa of taeniopus was that of a third species which was later described as pseudotaeniopus Galindo and Blanton. The pupa of crybda and taeniopus are of the same general type, although there are minor but constant differences between them.

In order to clarify the issue, the writer sent specimens of "Type F" which were being called "crybda", to Dr. Alan Stone, at the U. S. National Museum and asked him to compare them with the type, paying particular attention to the pleural spots. This he kindly did and came to the following conclusion: ". . . I think that you have correctly identified crybda, and your [Type G] is different". In further examining other specimens labeled "C. crybda" in the U. S. National Museum, Dr. Stone found that: "All other specimens . . . appear to agree with crybda except for one. This latter . . . bears the data: Trinidad Rio, Pan. 19-III-12. This, a male, has broad abdominal bands and agrees well with your [Type G]". Dr. Stone kindly loaned this specimen to the writer. A comparison with Almirante material of "Type G" reveals the identical nature of the specimens, thus extending the known range of "Type G" into central Panama.

The writer further asked Dr. Stone to re-examine the type of epanastasis in the light of the newer knowledge mentioned above. After a lengthy discussion of the characters of the type, which is in extremely poor condition, Dr. Stone states: ". . . I think you are reasonable safe in sinking crybda under epanastasis and not your new species [Type G]".

Based on the evidence presented above the writer is hereby resurrecting the name Culex epanastasis Dyar, 1922, from the synonymy of taeniopus Dyar and Knab, 1907, and considers Culex crybda Dyar, 1924, a synonym of epanastasis. The species referred to here as "Type G" appears to be new and will be described shortly in another publication.

Taxonomic relationships between the taxa - Early in the course of this work, it became evident to the writer that all of the taxa discussed above had very close phylogenetic relationships. Their feeding habits, a very generalized type of larva and close affinities between the male terminalia of several species led to this conclusion. The writer proposes to name this complex of species "the Culex spissipes-group" and include in it the following described species of Culex of the subgenus Melanoconion:

- 1 - Culex (Melanoconion) spissipes (Theobald), 1903
Melanoconion spissipes Theobald, 1903
Culex (Helcoporpa) menytes Dyar, 1918 (synonymized by Takahashi, 1968).
Culex (Upsilonporpa) haneyi Komp and Curry, 1932 (synonymized under menytes by Komp, 1935).
- 2 - Culex (Melanoconion) taeniopus Dyar and Knab, 1907
Culex taeniopus Dyar and Knab, 1907
Culex annulipes, Dyar, 1928 (nec Theobald, 1907).
Culex crybda, Dyar, 1928 (nec Dyar, 1924).
Culex epanastasis, Komp, 1935 (nec Dyar, 1922).
- 3 - Culex (Melanoconion) annulipes (Theobald), 1907
Melanoconion annulipes Theobald, 1907
Culex (Mochlostyrax) taeniopus, Dyar, 1928 (in part)
Culex (Melanoconion) annulipes, Belkin, 1969 (resurrected from synonymy).
 ssp. Culex (Melanoconion) annulipes opisthopus Komp, 1926 (here created).
Culex (Choeroporpa) opisthopus Komp, 1926
Culex (Mochlostyrax) mychonde Komp, 1928 (synonymized under episthopus by Komp, 1935).
 ssp. Culex (Melanoconion) annulipes cedecei Stone and Hair, 1968 (here created)
Culex (Melanoconion) cedecei Stone and Hair, 1968 (synonymized under annulipes by Belkin, 1969).
- 4 - Culex (Melanoconion) epanastasis Dyar, 1922 (here resurrected from synonymy of taeniopus).
Culex (Choeroporpa) epanastasis Dyar, 1922
Culex (Mochlostyrax) taeniopus, Komp, 1935 (in part)
Culex (Choeroporpa) crybda Dyar, 1924 (here synonymized).
- 5 - Culex (Melanoconion) vomerifer Komp, 1932
Culex vomerifer Komp, 1932
Culex portesi, Lane, 1951 (nec Senevet and Abonnenc, 1941).
Culex cayennensis, Lane, 1951 (nec Floch and Abonnenc, 1945).
- 6 - Culex (Melanoconion) paracrybda Komp, 1936
- 7 - Culex (Melanoconion) portesi Senevet and Abonnenc, 1941
Culex portesi Senevet and Abonnenc, 1941
Culex (Melanoconion) vomerifer, Lane, 1951 (in part).
Culex (Melanoconion) cayennensis Floch and Abonnenc, 1945 (synonymized by Aitken and Galindo, 1966).

- 8 - Culex (Melanoconion) pseudotaeniopus Galindo and Blanton, 1954
Culex taeniopus, Howard, Dyar and Knab, 1915 (in part, breeding place)
Culex taeniopus, Komp and Rozeboom, 1950 (in part, pupal morphology).
- 9 - Culex (Melanoconion) pereyrai Duret, 1967
- 10 - (?) Culex (Melanoconion) faurani Duret, 1968

The species C. faurani has been included in the group because the describer suggests that it is: "Near to the C. crybda - taeniopus group, or to vomerifer". However, examination of the illustration of the male terminalia leads the writer to suspect that it belongs with C. educator and related species, rather than in this group.

Definition of the group is based on larval characters of species 1, 2, 3, 4, 5, 7, and 8. Species 6 and 9 whose larvae are undescribed have been included because of close similarity of their male terminalia with other species of the group. Definition is as follows: Larva usually dark in color; siphon long; subdorsal hairs of siphon displaced apically (only partially in C. spissipes); lateral hair No. 7 of abdominal segment I with 2 branches; antennae homogeneously dark from base to apex.

The displacement of the subdorsal hairs of the siphon is unique in Melanoconion. The presence of 2 branches in hair 7 of abdominal segment I is also unique in the subgenus, as all other species known to the writer have this hair single. The homogeneous dark color of the antennae is shared by few species of the subgenus, as the large majority of Melanoconion larvae have bicolored antennae.

The only seemingly aberrant species of the group is spissipes, which does not appear as closely related to the other species as they are to each other. Displacement of the subdorsal hairs of the siphon is not as pronounced in spissipes as in the other species and it presents a very peculiar type of male terminalia. However, many other characters of the larva and pupa show the affinities that exist between spissipes and other species of the complex.

The center of distribution of the group appears to be the Amazon river basin, where the greatest number of species are to be found. From here it spreads north and south throughout the lowland forests of the neotropical faunal zone, with one form, C. annulipes cedecei, extending its range to the border area between the neotropical and nearctic zones. Near the center of distribution, many of the species occur together, but this sympatric association becomes progressively less pronounced as one moves away from the center. The mechanism by which such closely related populations have become genetically isolated and speciation has taken place, is one of the interesting problems that this group of mosquitoes presents to the modern systematists of the Culicidae.

In order to save space the writer has not included in the references below works cited under each of the taxa involved in such well-known treatises as: Dyar's "Mosquitoes of the Americas" and Stone, Knight and Starcke's "A synoptic catalog of the mosquitoes of the World".

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