OCCURRENCE OF MESOPOSTNOTAL SETAE AND SCALES IN THE FAMILY CULICIDAE[1]

BRUCE A. HARRISON[2] AND WILLIAM E. BICKLEY[3]

ABSTRACT. A survey of specimens and the literature was conducted to determine the presence, distribution and possible phylogenetic significance of mesopostnotal setae and/or scales on adults throughout the family Culicidae. The distribution in the family is tabulated with detailed notes for the species in each taxon having the character, and 4 species with the character are illustrated. The presence and frequency of the character in various taxa of the tribes Aedini, Culicini and Sabethini are discussed highlighting differences in given taxa between the Eastern and Western Hemispheres. Phylogenetic considerations regarding the correlation of the character with the subtropics/tropics, phytotelmic immature habitats, and the origin of the current distribution of the character are discussed.

INTRODUCTION

To many mosquito taxonomists and identifiers in the Holarctic Region the mesopostnotum of mosquitoes is usually bare and not used in taxonomic decisions. On the other hand, workers in the subtropics and tropics must be alert for the presence or absence of scales and/or setae on this structure, as they can be highly significant for separating various mosquito taxa. This structure has been called the metathorax, metanotum or the postnotum by numerous authors over the years. Harbach and Knight (1980) designated this structure "mesopostnotum" (Mpn), following Patton and Evans (1929). We are using the term "mesopostnotum" instead of "postnotum" as used by Owen (1977) and McAlpine (1981) to conform with the terminology used for the postnotum of the metathorax of culicids, i.e., metapostnotum (Owen 1977, Harbach and Knight 1980). Theobald (1901a) found that the presence of setae on the mesopostnotum (as metanotum) was valuable in separating genera, and Theobald (1901b: 95) mentioned that setae (as chetae) on this structure were very important for characterizing the genus *Wyeomyia* and that setae and scales were important for recognizing the genus *Trichoprosopon*. In the same paper, Theobald classified the genera *Sabethes* and *Eretmapodites* in the section having the mesopostnotum (as metanotum) "nude". This may have been an oversight on his part, or the Mpn structures were rubbed off of the specimens he studied. Edwards (1932) also recognized the value of Mpn setae, and in keys or descriptions he referred to 15 genera whose species lacked Mpn setae, or nearly always lacked them. He also recognized 10 genera whose species had or usually had setae on the Mpn.

The mosquito taxon usually associated with the presence of Mpn setae is the tribe Sabethini, but not all sabethine species possess them. Some New World workers have come to rely on Mpn setae or scales as a constant character in sabethines, e.g., Galindo et al. (1951) made the following statement in the descriptions of 2 new *Wyeomyia* species: "Postnotum bare except for the usual tuft of hairs present in all sabethines." Belkin (1962) stated that the Mpn in sabethines is often keeled and with setae or scales, but frequently may be bare and smooth. Similarly, species in the subfamily Culicinae, particularly the tribes Aedini and Culicini are generally considered to lack Mpn setae, however, there are exceptions as noted below.

Actually, an appreciable number of species are known to deviate from what might be considered a norm, i.e., that setae or scales on the Mpn is a sabethine character. Furthermore, the references noting many of these deviates are obscure or not generally known. Consequently, we decided to undertake a survey of the species with and without Mpn setae and/or scales to: (1) assemble and review the literature on this character; (2) determine how widespread this character is in the family Culicidae; and (3) see if the character may be useful in understanding the phylogeny of the Culicidae.

MATERIALS AND METHODS

Much of this survey involved a search through published species descriptions, particularly in those genera where the Mpn character is variable. Although we have not examined every species in taxa such as *Wyeomyia*, *Aedes* or *Culex (Melanoconion)*, we tried to confirm the presence of Mpn setae and/or scales on all of the species in the smaller taxa where the character has been listed as present. In this regard, we were fortunate to have examined many species of different taxa over the last few years, and to have access to the mosquito collection located at the National Museum

[1]The views of the authors do not purport to reflect the position of the Department of the Army or the Department of Defense (para 4-3), AR 360-5.

[2]Department of Entomology, Walter Reed Army Institute of Research, Washington, DC, 20307-5100. Address for reprints: Walter Reed Biosystematics Unit, Museum Support Center, Smithsonian Institution, Washington, DC, 20560.

[3]6516 40th Avenue, University Park, MD, 20782.

of Natural History, Museum Support Center, Smithsonian Institution, Washington, DC. The classification and the names of the taxa follow Knight and Stone (1977), Knight (1978), Ward (1984) and Gaffigan and Ward (1985). The numbers listed in the various tribes, genera and subgenera are close estimates (usually underestimates) and not to be construed as final numbers. We believe there are hundreds of culicid species still to be discovered, particularly among the sabethines and other groups utilizing natural plant receptacles. In Table 1 the numbers appearing in parentheses refer to numbered notes in the results section, and after each taxon one or more authorities are listed. In addition, one or both of us have examined specimens in all of the genera and subgenera listed in this study, and for most of the species mentioned. When we use the term "bare" it means the absence of setae and scales. This strict definition was not used by some earlier authors, e.g., Lane (1953) used nude to mean the absence of setae, even when scales were present.

RESULTS AND NOTES

Table 1 shows the distribution of the Mpn character in the family Culicidae as determined by our survey. Of the 3 subfamilies, Anophelinae, Culicinae and Toxorhynchitinae, only the culicine tribes, Aedini, Culicini and Sabethini include species with Mpn setae and/or scales. Tables 2-3 provide the frequency of this character in the genera included in these 3 tribes. To date, no reports have been found of Mpn setae and/or scales on members of the other 7 tribes of Culicinae, i.e., Aedeomyiini, Culisetini, Ficalbiini, Hodgesiini, Mansoniini, Orthopodomyiini, and Uranotaeniini. Furthermore, we have not seen Mpn setae and/or scales on species in these tribes. Table 4 lists the primary oviposition habitats of the taxa containing species with Mpn setae/scales.

Nine genera are currently recognized in the tribe Aedini, and Mpn setae and/or scales have been found on only certain species of the following 5 genera, *Aedes* (cosmopolitan), *Armigeres* (Oriental), *Eretmapodites* (Afrotropical), *Haemagogus* (Neotropical) and *Heizmannia* (Oriental). All 3 genera in the tribe Culicini, i.e., *Culex* (cosmopolitan), *Deinocerites* (Neotropical and subtropical) and *Galindomyia* (Neotropical), have representatives with this character. Nine of the 12 genera in the Sabethini have species with this character: *Johnbelkinia* (Neotropical), *Limatus* (Neotropical), *Phoniomyia* (Neotropical), *Runchomyia* (Neotropical), *Sabethes* (Neotropical), *Shannoniana* (Neotropical), *Trichoprosopon* (Neotropical), *Tripteroides* (Oriental) and *Wyeomyia* (Nearctic and Neotropical). The expression of this character in the above genera is as follows (numbers coincide with numbers in Table 1).

(1) *Aedes* is the largest genus in the family, with over 940 species. However, only 2 species are known to possess Mpn setae. Reinert (1974: 95) reported that the male holotype of *Ae. (Verrallina) virilis* (Leicester) has one long and one short setae on the Mpn. In addition we found one male and one female of 13 specimens of *virilis* from Sabah, Malaysia, with a single short seta on the Mpn. The second species, Marks sp. No. 171 of Lee et al. (1987: 253), is an undescribed member of the subgenus *Verrallina* from the Australasian Region. We were unable to find other species of *Aedes* with this character.

(2) The genus *Armigeres* has only one species that has Mpn setae and a small group of pale scales, i.e., *flavus* (Leicester), in the subgenus *Leicesteria*. Macdonald (1960) discussed this peculiarity and stated that the Mpn is bare on all the other species in *Leicesteria*. We have examined 20 of the 46 species in the genus, including 13 of the 31 species in the subgenus *Armigeres*, and found this character only on *flavus*. Thurman (1959) and Stone et al. (1959) placed *flavus* in a separate subgenus, *Leicesteriomyia*, using the Mpn character as a major portion of their justification. However, Macdonald (1960) synonymized this subgenus under *Leicesteria* on the basis of his very detailed and comprehensive morphological and ecological studies of this subgenus. *Armigeres flavus* has both setae and scales on the mesopostnotum. During this study we examined 12 specimens of *flavus* and noted a range of 1-6 setae (mode 3) and a range of 0-3 scales (mode 0).

(3) *Eretmapodites* is a genus confined to the Afrotropical Region. According to Edwards (1941) this is the only taxon in Africa with species having Mpn setae. He noted the presence of a small tuft of bristles in *chrysogaster* Graham, *dracenae* Edwards, *forcipulatus* Edwards, *grahami* Edwards, *inornatus* Newstead, *intermedius* Edwards, *penicillatus* Edwards, *semisimplicipes* Edwards, *silvestris* Ingram and de Meillon, and *subsimplicipes* Edwards. On the basis of Edwards' statement we infer that the following species also possess Mpn setae: *argyrurus* Edwards, *leucopus* Graham, *melanopous* Graham, *oedipodeios* Graham, and *plioleucus* Edwards. Additionally, Edwards (1941) noted that *quinquevittatus* Theobald, and *tonsus* Edwards lack Mpn setae.

Our observations of a small number of specimens from Cameroon, Sierra Leone, and Ivory Coast confirm the presence of Mpn setae on *chrysogaster, dracenae, grahami, leucopus, oedipodeios, semisimplicipes,* and *silvestris*. We have seen specimens of *quinquevittatus* with the Mpn bare.

Since 1941, *parvipluma* Edwards, *productus* Edwards and *wansoni* Edwards have been elevated from subspecies to species. The subspecies, *brevis* Edwards and *conchobius* Edwards are still subspecies and subspecies *stanleyi* Edwards has been synonymized under *oedipodeios*. We have not seen specimens of these taxa and do not know if they have Mpn setae. Regarding *forcipulatus*, Edwards (1941: 234) noted that the Mpn setae were reduced to 1-2 or absent.

An additional 24 species of *Eretmapodites* have been

Table 1. Distribution of mesopostnotal setae/scales in the family Culicidae.

Taxon	Mpn Setae and/or Scales			Basic references
	Present	Present or absent	Absent	
Anophelinae			0	Belkin (1962)
Culicinae		+/0		See below
Aedeomyiini			0	Belkin (1962)
Aedini		+/0		See below
Aedes		+/0 (1)*		Reinert (1974) and Lee et al. (1987)
Armigeres		+/0 (2)		Macdonald (1960)
Eretmapodites		+/0 (3)		Edwards (1941)
Haemagogus		+/0 (4)		Zavortink (1972) and Arnell (1973)
Heizmannia		+/0 (5)		Mattingly (1970) and present study
Opifex			0	Belkin (1962)
Psorophora			0	Carpenter and LaCasse (1955)
Udaya			0	Mattingly (1958)
Zeugnomyia			0	Baisas and Feliciano (1953)
Culicini		+/0		See below
Culex		+/0 (6)		Rozeboom and Komp (1948) and present study
Deinocerites		+/0 (7)		Adames (1971)
Galindomyia		+/0 (8)		Stone and Barreto (1969) and present study
Culisetini			0	Belkin (1962)
Ficalbiini			0	Belkin (1962)
Hodgesiini			0	Belkin (1962)
Mansoniini			0	Belkin (1962)
Orthopodomyiini			0	Belkin (1962)
Sabethini		+/0 (9)		See below
Johnbelkinia	+ (10)			Zavortink (1979a)
Limatus	+ (11)			Edwards (1932)
Malaya			0	Belkin (1962)
Maorigoeldia			0	Belkin (1962)
Phoniomyia	+ (12)			Theobald (1903), Lane (1953) and Correa and Ramalho (1956)
Runchomyia	+ (13)			Zavortink (1979a)
Sabethes	+ (14)			Edwards (1932)
Shannoniana	+ (15)			Zavortink (1979a)
Topomyia			0	Edwards (1932) and Thurman (1959)
Trichoprosopon	+ (16)			Lane (1953) and Zavortink (1979a, 1981)
Tripteroides		+/0 (17)		Mattingly (1981)
Wyeomyia	+ (18)			Lane (1953) and Belkin et al. (1970)
Uranotaeniini			0	Belkin (1962)
Toxorhynchitinae			0	Belkin (1962)

*Refer to numbered notes in text.

Table 2. Frequency of mesopostnotal setae/scales in the tribes Aedini and Culicini with included genera.

Category	Number species with Mpn character	Number species in category	Frequency of Mpn character in category	Zoogeographical regions* where character found
Aedini	55	1,146	0.048	AA, AT, NT, O
Aedes	2	940	0.002	AA, O
Armigeres	1	46	0.022	O
Eretmapodites	18**	44	0.409	AT
Haemagogus	9	32	0.281	NT
Heizmannia	25	30	0.833	O
Opifex	0	1	-	SP
Psorophora	0	47	-	NA/NT
Udaya	0	2	-	O
Zeugnomyia	0	4	-	O
Culcini	12	759	0.016	NT
Culex	4	740	0.005	NT
Deinocerites	7	18	0.389	NT
Galindomyia	1	1	1.0	NT

*Australasian (AA), Afrotropical (AT), Nearctic (NA), Neotropical (NT), Oriental (O), South Pacific (SP).
**Probably an underestimate as 24 species of *Eretmapodites* were unavailable for examination.

Table 3. Frequency of mesopostnotal setae/scales in the tribe Sabethini and included genera.

Category	Number species with Mpn Character	Number species* in category	Frequency of Mpn character in category	Zoogeographical regions** where character found
Sabethini	226*	377*	0.599	NA, NT, AA, O
Johnbelkinia	3	3	1.0	NT
Limatus	8	8	1.0	NT
Malaya	0	12	-	AT, O
Maorigoeldia	0	1	-	SP
Phoniomyia	23	23	1.0	NT
Runchomyia	11	11	1.0	NT
Sabethes	30	30	1.0	NT
Shannoniana	3	3	1.0	NT
Topomyia	0	38	-	O
Trichoprosopon	13	13	1.0	NT
Tripteroides	19***	119	0.160	AA, O
Wyeomyia	116	116	1.0	NA, NT

*Many species of Sabethini are undescribed, and many more remain to be discovered.
**Australasian (AA), Afrotropical (AT), Nearctic (NA), Neotropical (NT), Oriental (O), South Pacific (SP).
***Probably an underestimate as 14 species of subgenus *Rachisoura* were unavailable for examination.

described since 1941. White (1980) listed 44 species in this genus. Most of these more recently described species were differentiated on the basis of male genitalic characters, and other characters such as Mpn setae were rarely mentioned. The Smithsonian Afrotropical mosquito collection is limited in comparison with the British and French collections and we have not been able to examine specimens of the 24 more recently described species. Rickenbach and Eouzan (1970) described *ferrarai* and *germaini*; Ferrara and Eouzan (1974) described *rickenbachi* and *adami*; and Rickenbach

and Lombrici (1975) redescribed *leucopus* and *productus* and described *brenguesi* and *jani*. These 8 species were differentiated by genitalia, and Mpn setae were not mentioned. Rickenbach et al. (1976) listed 32 species of *Eretmapodites* in Cameroon, but they did not mention Mpn setae and/or scales.

(4) Of the 32 species currently recognized in the Neotropical genus, *Haemagogus*, the 8 species (4 unnamed) recognized by Zavortink (1972) in the subgenus *Conopostegus* apparently do not exhibit Mpn scales or setae, and only 9 of the 24 species in the subgenus *Haemagogus* have Mpn setae or scales. Those 9 species belong to the Splendens Section of Arnell (1973: 69), which is characterized, in part, by having 1-2 small posteromesal setae on the mesopostnotum. They are: *aeritinctus* Galindo and Trapido, *argyromeris* Dyar and Ludlow, *boshelli* Osorno-Mesa, *celeste* Dyar and Nunez Tovar, *chalcospilans* Dyar, *iridicolor* Dyar, *lucifer* Howard, Dyar and Knab, *regalis* Dyar and Knab, and *splendens* Williston. Members of both subgenera were examined during this study and no deviations from the above statements were noted.

(5) The genus *Heizmannia* is confined to the Oriental Region and contains 30 species in 2 subgenera (Mattingly 1970, Knight and Stone 1977, Tanaka et al. 1979). The subgenus *Mattinglyia* has 5 species that do not have Mpn setae or scales (Reinert 1973). An examination of *achaetae* (Leicester), *catesi* Lien, *discrepans* Edwards, and *thelmae* Mattingly, in this subgenus revealed no Mpn setae. The remaining 25 species, in the subgenus *Heizmannia*, can be recognized by the presence of Mpn setae, and also scales on some species. These species are: *aurea* Brug, *aureochaeta* (Leicester), *chandi* Edwards, *chengi* Lien, *communis* (Leicester), *complex* (Theobald), *covelli* Barraud, *demeilloni* Mattingly, *funerea* (Leicester), *greenii* (Theobald), *himalayensis* Edwards, *indica* (Theobald), *kana* Tanaka, Mizusawa and Saugstad, *kanhsienensis* Tung, *lii* Wu, *macdonaldi* Mattingly, *mattinglyi* Thurman, *persimilis* Mattingly, *propinqua* Mattingly, *proxima* Mattingly, *reidi* Mattingly, *scanloni* Mattingly, *scintillans* Ludlow, *taiwanensis* Lien, and *viridis* Barraud. We examined 17 of the above 25 species and confirmed the presence of Mpn setae, and in the case of *complex* and *taiwanensis*, scales also. Seven of the remaining 8 species of subgenus *Heizmannia* are described as having Mpn setae. We have not seen specimens or the description of *kanhsienensis* Tung.

(6) *Culex* is the second largest genus in Culicidae, containing over 740 species in 20 subgenera. In major revisions this genus is generally described as having the mesopostnotum bare (Lane 1953, Belkin 1962, Tanaka et al. 1979). However, this is an oversight, as at least one species with Mpn setae has been known in the subgenus *Melanoconion* since the report of Rozeboom and Komp (1948). In addition, we have discovered Mpn setae on 3 previously described species in the subgenus *Carrollia*. At least 21 species are now recognized (3 remain unnamed) in the Neotropical subgenus *Carrollia* (Valencia 1973, Knight 1978, Ward 1984). Although possessing the classic characters of the genus *Culex*, members of this subgenus have diverged from the classic *Culex* habitus in also possessing conspicuous metallic ornamentation, as is more commonly seen in the tribes, Aedini and Sabethini. During routine identification of South American specimens we discovered that *bonnei* Dyar, typically possesses a group of 4 lower Mpn setae (Fig. 1A). Examination of an additional

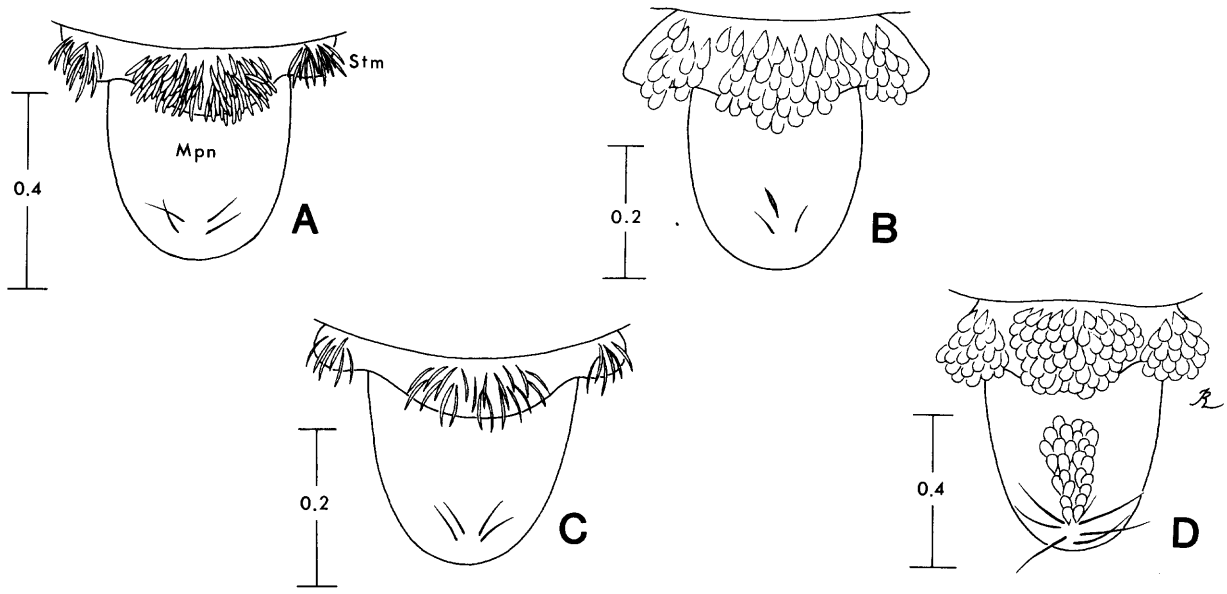

Figure 1. Mesopostnotal setae and/or scales and scutellar scales on: (A) *Culex (Car.) bonnei,* (B) *Galindomyia leei,* (C) *Culex (Mel.) batesi,* and (D) *Trichoprosopon digitatum*.

40 specimens of *bonnei* from Brazil, Colombia and French Guiana revealed that this is not an anomaly, but probably a fixed character for this species. We also examined adults of an additional 14 species of this subgenus, and Mpn setae were generally absent, with the following exceptions. Five of 35 specimens of *metempsytus* Dyar, from Costa Rica and Panama had from 2 to 4 short, curved, dark setae, and 3 of 40 specimens of *urichii* Coquillett, from Colombia and Brazil, had 1 and 4 setae, respectively. Valencia (1973) included *metempsytus* in his Bihaicolus Group, which he considered more primitive, while *bonnei* and *urichii* were included in the Iridescens Group, which he considered more derived. In preserved *Carrollia* specimens, the halteres frequently are shriveled and cover the posterior part of the mesopostnotum; thus, the Mpn setae are difficult to see.

Sirivanakarn (1983) recognized 149 valid species in the Western Hemisphere subgenus *Melanoconion*, and several new species have been described since, thus, over 150 species are now recognized. Rozeboom and Komp (1948) described a new species, *batesi*, with 10 or fewer Mpn setae. This has been overlooked by most *Culex* workers, except Sirivanakarn (1983). Lane (1953: 309) described the mesopostnotum of *Culex* as, "postnotum nude", but on page 491 he quoted the original description of *batesi*, which clearly mentions 10 or less Mpn setae. Sirivanakarn (1983) used the presence of Mpn setae to differentiate his Evansae Group in a key, and listed 4 species in this group, viz., *evansae* Root, *batesi* Rozeboom and Komp, *johnnyi* Duret, and *changuinolae* Galindo and Blanton. We examined 8 specimens of *batesi* from Ecuador, 7 had pale golden Mpn setae (Fig. 1C), while one specimen apparently had the setae rubbed off. Two specimens also exhibited 2 or 3 pale scales. The lectotype and one female paralectotype of *evansae* were examined and the lectotype, although badly damaged and rubbed, appears to have 1 Mpn alveolus. The paralectotype has the Mpn bare. The following additional specimens in the NMNH labelled as Evansae Complex or nr. *evansae* had Mpn setae or alveoli: 3 males, 2 females (Brazil); 1 male (Ecuador); 17 males (French Guiana); 1 male, 3 females (Panama); and 1 female (Peru). Usually from 2 to 6 dark setae were present on these specimens, however, 2 males from French Guiana each possessed one alveolus, much like the lectotype of *evansae*. We did not examine specimens of the other 2 species in Sirivanakarn's Evansae Group.

(7) *Deinocerites*, a Neotropical genus of crab hole inhabiting mosquitoes, currently contains 18 species, of which 7 have been recorded with Mpn setae (Adames 1971). Adames (p. 36) listed *dyari* Belkin and Hogue, *barretoi* Adames, and *nicoyae* Adames and Hogue, the 3 members of the Dyari Group, as usually having a few lower Mpn setae. He also listed *epitedeus* (Knab), *panamensis* Adames, and *colombianus* Adames, 3 of the 5 members of the Epitedeus Group as usually having 2 or more lower Mpn setae. *Deinocerites* (as *Dinomimetes*) *epitedeus* was noted by Snodgrass (1912: 60) to have one or 2 coarse spinelike "bristles" near the posterior margin of the Mpn. In the Pseudes Group, Adames noted that one species, *mcdonaldi* Belkin and Hogue, usually has one middle Mpn seta. The remaining species apparently do not exhibit this character.

(8) *Galindomyia* is a monotypic genus of crab hole inhabiting species known only from Colombia and Ecuador (Adames and Arzube 1975, Adames and Galindo 1975). The single species, *leei* Stone and Barreto, is described as occasionally having a small posterior tuft of Mpn setae near the midline (Stone and Barreto 1969). Three specimens of *leei* were examined from Esmeraldas Province, Ecuador and Mpn setae (2) were present on only one specimen, while all 3 specimens possessed from 1 to 4 Mpn scales (Fig. 1B).

(9) Publications on the tribe Sabethini pertaining to the Western Hemisphere normally list the presence of Mpn setae and/or scales as a differentiating character for species in that tribe (e.g., Lane 1953, Belkin et al. 1970). Apparently, the presence of Mpn setae/scales is a good character for identifying Western Hemisphere sabethines. However, most Eastern Hemisphere sabethines lack Mpn setae/scales. Approximately 377 valid species are recognized in the tribe and slightly over half (54.9%) are known in the 8 Western Hemisphere genera: *Johnbelkinia* Zavortink, *Limatus* Theobald, *Phoniomyia* Theobald, *Runchomyia* Theobald, *Sabethes* Robineau-Desvoidy, *Shannoniana* Lane and Cerqueira, *Trichoprosopon* Theobald, and *Wyeomyia* Theobald. In the Eastern Hemisphere, the remaining 42.5% of the valid species occur in 4 genera: *Malaya* Leicester, *Maorigoeldia* Edwards, *Topomyia* Leicester and *Tripteroides* Giles. The only Eastern Hemisphere sabethines exhibiting Mpn setae (no scales) are certain species in *Tripteroides*. Accordingly, authors should consider species from both hemispheres when making generalized statements about sabethines. This is particularly true as this is probably the least known and understood tribe in the Culicidae. Most species probably remain undiscovered because of their affinity for phytotelmic (= inhabiting small pools of water within or upon plants) oviposition sites.

(10) *Johnbelkinia* is a Neotropical genus described by Zavortink (1979a) for 6 nominal species previously included in the old composite genus *Trichoprosopon*. Zavortink recognized 3 of these 6 nominal species as valid: *leucopus* (Dyar and Knab), *longipes* (Fabricius) and *ulopus* (Dyar and Knab). These 3 species possess numerous Mpn setae, and *leucopus* often has dark iridescent Mpn scales, while *longipes* and *ulopus* usually lack scales on the Mpn.

(11) The genus *Limatus* contains 8 valid species, all restricted to the neotropics. The species in *Limatus* are all supposed to have Mpn setae and some possess Mpn scales. However, Lane (1953: 1045) possibly caused confusion on this point by describing *Limatus* as having, "Postnotum nude, median portion with hyaline scales which easily

become detached." The 8 valid species are: *andinus* Levi-Castillo, *asulleptus* (Theobald), *durhamii* Theobald, *flavisetosus* De Oliveira Castro, *guayasi* Levi-Castillo, *hoffmani* Root, *martiali* Senevet and Abonnenc, and *pseudomethysticus* (Bonne-Wepster and Bonne). Belkin et al. (1970) described the female of *hoffmani* as having a median patch of 10-20 light golden setae preceded by an equal number of broad golden scales. Clastrier and Claustre (1978) described the female of *martiali* as having a tuft of 5 or 6 golden setae on the posterior part of the Mpn, and as lacking scales on the Mpn.

(12) The Neotropical genus, *Phoniomyia*, contains 23 species, all of which are supposed to possess Mpn setae (Theobald 1903, Correa and Ramalho 1956). Also, many of the species may exhibit scales on the Mpn. Bonne-Wepster and Bonne (1921) described *lassalli* as lacking Mpn scales. Lourenco-de-Oliveira (1983) described a new species, *deanei*, as having some setae on the median portion of the Mpn.

(13) *Runchomyia*, another Neotropical taxon, was restored to generic status by Zavortink (1979a) in his preliminary reclassification of the composite genus *Trichoprosopon* (Zavortink 1979b). In this new classification, Zavortink recognized 15 available species names in *Runchomyia*, of which he considered 11 as valid species. These 11 species were listed by Ward (1984) according to their subgeneric designation. The 11 species are: *cerqueirai* (Stone), *espini* (Martini), *frontosa* Theobald, *humboldti* (Lane and Cerqueira), *lunata* (Theobald), *magna* (Theobald), *paranensis* Brethes, *perturbans* (Williston), *reversum* (Lane and Cerqueira), *theobaldi* (Lane and Cerqueira), and *walcotti* (Lane and Cerqueira). All of these species are presumed to exhibit Mpn setae and some may possess Mpn scales.

(14) The Genus *Sabethes*, another Neotropical taxon, contains approximately 30 valid species. Edwards (1932) stated that species in this genus have Mpn setae. Lane (1953) considered all *Sabethes* to have Mpn setae, but gave very incomplete descriptions and only mentioned 2 species as also possessing Mpn scales, they are: *belisarioi* Neiva and *tarsopus* Dyar and Knab. Lane (1953) specifically mentioned that *amazonicus* Gordon and Evans, has the "postnotum nude", i.e. without scales. *Sabethes forattinii* Cerqueira, was described as having the Mpn without scales, but with a group of setae (Cerqueira 1961).

(15) The genus *Shannoniana* was also elevated to generic status by Zavortink (1979a, 1979b). Zavortink recognized 4 available species names in this Neotropical genus, and he considered 3 as valid species. He indicated that he was aware of an additional 12 new undescribed species, and that "scores more" await discovery. The 3 valid species listed by Ward (1984) are: *fluviatilis* (Theobald), *moralesi* (Dyar and Knab), and *schedocyclia* (Dyar and Knab). These 3 species possess Mpn setae. According to Lane (1953), *fluviatilis* does not exhibit Mpn scales.

(16) In his preliminary reclassification of the genus *Trichoprosopon*, Zavortink (1979a, 1979b, 1981) indicated that 21 species were recognized (several undescribed) that would remain in the Neotropical genus *Trichoprosopon*, and he listed 20 available species names he was placing in this genus. Ward (1984), with Zavortink's approval, listed 15 of the available names as valid, with 13 as species and 2 as varieties, they are: *andinum* Levi-Castillo, *brevipes* (Da Costa Lima), *castroi* Lane and Cerqueira, *compressum* Lutz, *compressum* var. *mogilasium* (Dyar and Knab), *digitatum* (Rondani), *digitatum* var. *townsendi* Stone, *evansae* Antunes, *lampropus* (Howard, Dyar and Knab), *lanei* (Antunes), *obscurum* Lane and Cerqueira, *pallidiventer* (Lutz), *simile* Lane and Cerqueira, *soaresi* Lane and Cerqueira, and *vonplesseni* (Dyar and Knab). It is generally accepted that all of these species and varieties exhibit a tuft of Mpn setae, and some, e.g., *compressum* and *digitatum* (Fig. 1D), also exhibit Mpn scales. Lane (1953) indicated the Mpn of *obscurum* was "nude."

(17) The genus *Tripteroides* Giles, is an Oriental/Australasian/ South Pacific taxon that is still relatively poorly known. In Knight and Stone (1977), 113 species were listed in 3 subgenera. However, Mattingly (1980, 1981) began a reclassification of this genus and recognized 5 subgenera. At present, there are approximately 119 valid species recognized. As noted below, most of these species lack Mpn setae and/or scales. The subgenus *Polylepidomyia* Theobald, which is confined to the Australasian Region, contains 18 species that have the Mpn bare. The subgenus *Rachionotomyia* Theobald, contains 13 Indian, Southeast Asian and Oriental-Palaearctic species, of which only one, *edwardsi* (Barraud) in India and Southeast Asia, has a tuft of Mpn setae (Barraud 1934). The third subgenus, *Rachisoura* Theobald, contains 27 species that are confined to the Australasian and South Pacific regions. Knight and Stone (1977) transferred *mabinii* Baisas and Ubaldo-Pagayon to the subgenus *Tripteroides*. Three species of *Rachisoura* definitely lack Mpn setae or scales, i.e., *exnebulis* Bonne-Wepster, *fuscipleura* Lee, and *latisquama* (Edwards). Five species, i.e., *confusus* Lee, *felicitatis* Bonne-Wepster, *filipes* (Walker), *leei* Peters, and *longipalpatus* Lee, definitely have Mpn setae, but apparently no scales. Belkin (1962) described *mathesoni* Belkin, *stonei* Belkin and *torokinae* Belkin, as having 2-4 minute setae (frequently absent) and no scales. One species, *flabelliger* Bonne-Wepster, has Mpn setae and white scales (Van den Assam 1959). Sloof (1961) described *tityae* as having only 5-8 white Mpn scales. Authors of the remaining 14 species failed to mention Mpn setae and/or scales, viz., *adentata* Van den Assam, *bisquamatus* Lee, *brevirhynchus* Brug, *cuttsi* Van den Assam, *fuliginosus* Lee, *kingi* Lee, *pallidus* Lee, *papua* Brug, *pilosus* Lee, *plumiger* Bonne-Wepster, *simplex* Brug, *sylvestris* (Theobald), *szechwanensis* Hsu, and *vanleeuweni* (Edwards).

The fourth subgenus, *Tricholeptomyia* Dyar and Shannon, contains 9 species that are restricted to the Philip-

pines in the Southeast Asian subregion. Eight of the 9 species exhibit a small tuft of Mpn setae, they are: *apoensis* Baisas and Ubaldo-Pagayan, *belkini* Baisas and Ubaldo-Pagayan, *christophersi* Baisas and Ubaldo-Pagayan, *delpilari* Baisas and Ubaldo-Pagayan, *microcala* (Dyar), *nepenthicola* (Banks), *roxasi* Baisas and Ubaldo-Pagayan, and *werneri* Baisas and Ubaldo-Pagayan. The single species having the Mpn bare is *barraudi* Baisas and Ubaldo-Pagayan.

The fifth and largest subgenus, *Tripteroides* Giles, contains about 51 species which are distributed through northeastern India eastward to Japan and south through Malaysia and Indonesia, New Guinea and northern Australia to the Solomons and Santa Cruz Island, Fiji (Mattingly 1981). Mattingly (1981: 79) described the members of this subgenus as having the Mpn bare.

(18) There are at least 116 valid species of *Wyeomyia*. As members of the tribe Sabethini, all of these species are supposed to possess a tuft of Mpn setae (Lane 1953). However, Belkin et al. (1970) reported that 2 species, *albosquamata* Bonne-Wepster and Bonne, and *surinamensis* Bruijning, have scales, but no setae. Zavortink (1985) described *zinzala* as having long strongly developed Mpn setae and "sometimes a few dark scales." This genus, like most of the other sabethine genera is very poorly known, and because of the association of most species with bromeliads in the Neotropical forests, there must be numerous undescribed species. E. L. Peyton (pers. comm., 1990) suggests that there are at least 160 species in the genus, based on the specimens deposited in the Smithsonian Institution. We have not encountered specimens of *Wyeomyia* that have the Mpn entirely bare.

DISCUSSION

References to mesopostnotal setae and/or scales were scattered throughout the mosquito literature, and then only in the adult descriptions or group discussions. One obvious result of this survey is finding the high frequency in which the mesopostnotum has been overlooked or ignored, even to the present, and not included in descriptions. Recent descriptions of new mosquito species have become increasingly lengthy and complex, causing suggestions that shorter diagnostic descriptions would suffice. A survey such as this one highlights the value and need for thorough descriptions. Diagnostic descriptions may meet the requirements of the International Code of Zoological Nomenclature (ICZN) to validate species in pure alpha level taxonomic works, however, the taxonomy of the Culicidae has long since reached a level requiring highly detailed descriptions for beta and gamma level considerations.

The distribution of Mpn setae/scales in the family Culicidae is restricted to only 3 of the 10 tribes in the subfamily Culicinae, namely, Aedini, Culicini and Sabethini. Only about 5% of the currently known Aedini species possess the character, and of those, 83.6% occur in the Eastern Hemisphere (Table 2). In the Western Hemisphere the only members of the Aedini possessing the character are 9 species of *Haemagogus*, all belonging to the subgenus *Haemagogus*. In the Eastern Hemisphere most of the species of *Eretmapodites* (Afrotropical) probably possess the character, however, we were unable to confirm this because of limited material in the Smithsonian collection and because of inadequate descriptions for many of the species. The remaining species of Aedini with this character occur in the Oriental and/or Australasian regions. Genus *Heizmannia*, often mentioned as the Eastern Hemisphere equivalent of *Haemagogus*, has Mpn setae/scales on the 25 species in the subgenus *Heizmannia*, but lacks this character on the 5 species in the subgenus *Mattinglyia*. One species of *Heizmannia* in Korea, *lii* Wu, is the northernmost (35°N) species that possesses this character in the Eastern Hemisphere. The Oriental genus *Armigeres* only has one species with Mpn setae/scales. This genus apparently is most closely related to the Afrotropical *Aedes* subgenus, *Pseudarmigeres*, whose species do not possess this character (Edwards 1941). *Aedes* is cosmopolitan and is the largest culicid genus with 41 subgenera that utilize a wide variety of immature habitats. The presence of Mpn setae on only 2 species of *Aedes* in the subgenus *Verrallina* from the Oriental and Australasian regions was a surprise.

In the tribe Culicini there are only 3 genera and all 3 possess species with Mpn setae/scales (Table 2). However, only about 0.5% of the species in *Culex* are known to possess this character and they occur in the subgenera *Carrollia* and *Melanoconion*. *Culex* is also cosmopolitan and is the second largest culicid genus, with 20 subgenera. The presence of Mpn setae/scales only in the monotypic Neotropical genus *Galindomyia*, and in certain Neotropical species of *Culex* and *Deinocerites* was also unexpected.

In the Eastern Hemisphere the presence of Mpn setae/scales in the tribe Sabethini is unusual (Table 3). Of the 4 sabethine genera in the Eastern Hemisphere, only the genus *Tripteroides* has species with this character, and then only in 3 of 5 subgenera, i.e., *Rachionotomyia, Rachisoura* and *Tricholeptomyia* (Mattingly 1981). The 3 Eastern Hemisphere sabethine genera without species exhibiting the character are *Malaya, Maorigoeldia* and *Topomyia*. The genus *Malaya* is Oriental, Afrotropical and Australasian in distribution, and in the Afrotropical region it is the only representative of the Sabethini. The genus *Maorigoeldia* is an isolated monotypic genus found only in New Zealand (South Pacific). Belkin (1962) hypothesized that *Maorigoeldia* probably arose through a primitive *Tripteroides* ancestor. This ancestor must have lacked the Mpn character as do a majority of *Tripteroides* to this day, including members of subgenus *Polylepidomyia* in Australia and Tasmania. The third genus, *Topomyia*, is Oriental

and in many ways resembles species found in the Neotropical genera related to *Trichoprosopon*. Although *Topomyia* species do not possess Mpn setae/scales, they have a similar unique character not found in any other genus in the Eastern Hemisphere except *Toxorhynchites*, i.e., setae and scales on the metepisternum that are usually ventral and caudal to the metathoracic spiracle (Marks 1971). There are 38 recognized species of *Topomyia*, with 28 definitely having this character (usually as setae), 4 described as lacking this character, and the status on the remaining 6 is unknown.

In the Western Hemisphere all of the described species of Sabethini apparently exhibit Mpn setae/scales, and both setae and scales are present on many species. On certain species, e.g., *Trichoprosopon digitatum*, the scales are translucent and difficult to see (Fig. 1D). On others, the pale to black color of the Mpn setae serves as a useful taxonomic character (e.g., *Sabethes*). The location of the setae and/or scales on the mesopostnotum may also be of taxonomic value. The northernmost species possessing the Mpn setae/scales in the Western Hemisphere is *Wyeomyia smithii* (Coquillett) which extends to approximately 55°N latitude in Canada.

Geographically, mesopostnotal setae/scales have been found on species in 7 of the major faunal regions; Nearctic, Neotropical, Afrotropical, Palearctic, Oriental, Australasian and South Pacific. This character generally is restricted to genus groups and species confined to the subtropics and tropics between 30°N and 30°S latitudes, except for *Heizmannia lii* in the Oriental Palearctic, *Wyeomyia smithii* in the Nearctic and *Phoniomyia muehlensi* (Petrocchi), *Runchomyia (Run.) paranensis* (Brethes), and *Wyeomyia (Men.) leucostigma* Lutz, which extend south to approximately 35°S latitude in Argentina (Mitchell and Darsie 1985). No attempt was made to define the elevation limitations for the Mpn character.

The most obvious result of this study is the clear association of Mpn setae/scales with the subtropics and tropics where most plants evolved, particularly epiphytic plants. Furthermore, most species having the Mpn character are also phytotelmic in their immature stages (Table 4). The Neotropical sabethines, all of which apparently possess Mpn setae/scales, are definitely correlated to the success and wide distribution of phytotelmata such as bromeliads, aroids, bamboo, etc. In the Eastern Hemisphere there are no bromeliads or an equivalent of these plants except for one species, *Pitcarnia feliciana* (A. Chevalier) Harms and Mildbraed, in West Africa (Richards 1973, Thorne 1973). The nearly complete absence of this plant group must be considered a major factor in the reduced success of the sabethines in the Eastern Hemisphere, particularly in the Afrotropical Region. The restriction of the Mpn character between the 30°N and 30°S latitudes (5 exceptions) would indicate the character evolved in subtropical/tropical

Table 4. Primary oviposition habitats of taxa with Mpn setae/scales.

Taxa	Primary oviposition habitats
Aedini	
Aedes (Verrallina)	Shaded ground pools
Armigeres (Leicesteria)	Phytotelmata
Eretmapodites	Phytotelmata
Haemagogus (Haemagogus)	Phytotelmata
Heizmannia (Heizmannia)	Phytotelmata
Culicini	
Culex (Carrollia)	Phytotelmata
Culex (Melanoconion)	Freshwater marshes, swamps and pools
Deinocerites	Crab holes in brackish water
Galindomyia	Crab holes in brackish water
Sabethini	
Johnbelkinia	Phytotelmata
Limatus	Phytotelmata
Phoniomyia	Phytotelmata
Runchomyia	Phytotelmata
Sabethes	Phytotelmata
Shannoniana	Phytotelmata
Trichoprosopon	Phytotelmata
Tripteroides	Phytotelmata
Wyeomyia	Phytotelmata

ancestors. Accordingly, the exceptions are best explained as: (1) *Wy. smithii*, as an extension from the subtropics into the temperate-boreal zones of the Nearctic through its symbiotic relationship with *Sarracenia purpurea* L., pitcher plants (Ross 1964); and (2) *Hz. lii*, a species trapped on the Korean Peninsula from an earlier warm period when the peninsula enjoyed subtropical or tropical weather. Apparently *Hz. lii* is uncommon in Korea, and found primarily in tree holes (Tanaka et al. 1979). *Heizmannia lii* also occurs in the People's Republic of China, but south of 30°N latitude in Zhejiang Province (Tanaka et al. 1979). The remaining 3 Southern Hemisphere (Neotropical) species probably extend south of 30°S latitude because of their association with a particular phytotelmic habitat.

A possible function of the Mpn setae could be tactile (sensory) monitoring of the dorsal movement of the abdomen by contact with the tergum of the first abdominal segment during mating and oviposition. Certain sabethine species with this character, e.g., *Sabethes chloropterus* (Von Humboldt), have highly specialized adaptations for projecting ova into tiny holes in bamboo (Galindo 1957). However, there are other Western Hemisphere sabethines with Mpn setae that do not have such adaptations (e.g., *Tr. digitatum*, see Lounibos 1983, Lounibos and Machado-Allison 1983). In Aedini, the only species in *Armigeres* with Mpn setae is *Ar. (Lei.) flavus* which also has an unusual oviposition behavior pattern in which ova are deposited on the hindlegs and dipped in the water to hatch (Macdonald 1960). To assist in this specialized behavior, the hindfemur of *Ar. flavus* is much shorter than in the other species of the genus. However, the closely related *Ar. (Lei.) annulitarsis* (Leicester), which does not have Mpn setae/scales, has a similar type of oviposition behavior (Macdonald 1960, Bailey et al. 1975). In view of the above disparities and the presence of Mpn setae/scales on *Deinocerites* and *Galindomyia*, whose species oviposit in crab holes, and on certain species of *Culex (Melanoconion)* and *Aedes (Verrallina)* which typically oviposit in marshes and swamps, the function (if any) of the Mpn setae remains unclear.

PHYLOGENETIC CONSIDERATIONS

A search of the literature for nematocerous Diptera other than Culicidae that possess Mpn setae/scales revealed that certain species in the following families possess this character: Blephariceridae (Hogue 1981), Mycetophilidae (Vockeroth 1981), Sciaridae (Steffan 1981), Anisopididae (Peterson 1981a), Synneuridae (Peterson and Cook 1981), Simuliidae (Freeman and de Meillon 1954, Peterson 1981b), and Chironomidae (Oliver 1981). Using the evolutionary ranking of these families (McAlpine et al. 1981), only the most primitive family, Blephariceridae, has the character throughout the family. Like the Culicidae, the remaining families listed above have only a small portion of their taxa with this character. This is particularly true of genera and species in the Simuliidae and Chironomidae where the character is rare. There is no evidence of Mpn setae/scales in the more primitive families of superfamily Culicoidea, namely, Chaoboridae, Corethrellidae and Dixidae, or in select Culicinae isolated on the New Zealand block (Belkin 1968). However, only a few species of chaoborids, corethrellids, dixids and primitive culicids are still extant. Thus, the absence of this character in these taxa may be a reflection of the decline of these taxa. This may also be true for certain Culicinae tribes that are currently considered more ancestral (Culisetini, Ficalbiini, etc. - see Belkin 1962: 117). We feel Mpn setae and/or scales are an ancestral character in nematocerous Diptera that has been retained in only 3 families of the infraorder Culicomorpha: Culicidae, Chironomidae and Simuliidae. Their occurrence on members of only 3 tribes of Culicinae in family Culicidae is a reflection of their loss in current, more derived taxa.

The current distribution of this character in Culicidae probably arose through certain protoaedines, protoculicines and protosabethines located in warm tropical areas of Gondwana, the southern part of Pangea. With the split up of Gondwana, taxa possessing this character were present on the Indian-Southeast Asian, Antarctica-Australian, African and South American blocks, where the present species evolved and spread to their current distributions. The various culicid components on the above blocks met with varying degrees of success: (1) South America, with the evolving bromeliads, remained isolated for a long period with the sabethines (and the Mpn character) becoming a dominant faunal element; (2) Africa, with practically no bromeliads and severe climatic changes (Raven and Axelrod 1975), lost most of the original sabethines and the Mpn character survived only in the unique aedine genus, *Eretmapodites*; (3) Antarctica, extinction; (4) India-Southeast Asia, separated from Gondwana early, possibly at the same time (Ridd 1971). On the Indian block the aedine genus *Heizmannia* was the most successful line with the Mpn character. The accompanying Southeast Asian block also carried the successful *Heizmannia* as well as the ancestral *Topomyia* line. Otherwise, only *Armigeres flavus* and *Tripteroides edwardsi* in both of these areas, plus those *Tripteroides* in the Philippines have the Mpn character; and (5) Australia, of the successful sabethines, most species lacked the Mpn character, however, with the collision with the Southeast Asian block, the sabethines were rejuvenated by an abundance of bamboo and aroid phytotelmata. We feel the presence of Mpn setae on *Ar. flavus* and the 2 *Aedes (Verrallina)* species represent the presence of a relict character lost by most of the other species in those genera. *Aedes (Verrallina)* is recognized as having an ancestral type of male genitalia, i.e., possessing an opisthophallus (Reinert 1974). We also interpret the presence of Mpn setae/scales in the Neotropical Culicini as relict,

with most of the modern species having lost the character. The species in many of the other tribes, genera and subgenera of Culicinae possibly never possessed the Mpn character because they evolved in the cooler temperate and boreal regions or on Laurasia, the northern part of Pangea. For those without the Mpn character that evolved in the tropics or on Gondwana, their non-association with phytotelmata probably has had some role in the absence of the Mpn/scale character.

ACKNOWLEDGMENTS

We thank the following personnel of the Department of Entomology, Walter Reed Army Institute of Research (WRAIR): Ralph Harbach, E.L. Peyton and Ronald Ward for critically reviewing the manuscript; Rosetta Trice and James Pecor for typing and final preparation of the manuscript; and Taina Litwak for preparing the illustrations.

LITERATURE CITED

Adames, A.J. 1971. Mosquito studies (Diptera, Culicidae) XXIV. A revision of the crabhole mosquitoes of the genus *Deinocerites*. Contrib. Am. Entomol. Inst. (Ann Arbor) 7(2):1-154.

Adames, A.J. and M.E. Arzube R. 1975. Geographical extension of *Galindomyia leei* Stone and Barreto to Ecuador (Diptera: Culicidae). Mosq. Syst. 7:113-114.

Adames, A.J. and P. Galindo. 1975. Description of the immature stages of *Galindomyia leei* Stone and Barreto, 1969. Mosq. Syst. 7:132-136.

Arnell, J.H. 1973. Mosquito studies (Diptera, Culicidae) XXXII. A revision of the genus *Haemagogus*. Contrib. Am. Entomol. Inst. (Ann Arbor) 10(2):1-174.

Bailey, C.L., S. Vongpradist and K. Mongkolpanya. 1975. Observations of an unusual oviposition habit in *Armigeres (Leicesteria) annulitarsis* (Leicester). Mosq. News 35:564-565.

Baisas, F.E. and P. Feliciano. 1953. Notes on Philippine mosquitoes, XIII. Four new species of *Zeugnomyia* and *Topomyia*. Fieldiana Zool. 33:161-179.

Barraud, P.J. 1934. The fauna of British India, including Ceylon and Burma. Diptera. Vol. V. Family Culicidae. Tribes Megarhinini and Culicini. Taylor and Francis, London, 463 pp.

Belkin, J.N. 1962. The mosquitoes of the South Pacific (Diptera: Culicidae). Univ. Calif. Press, Berkeley and Los Angeles. 2 vols. 608 and 412 pp.

Belkin, J.N. 1968. Mosquito studies (Diptera, Culicidae) VII. The Culicidae of New Zealand. Contrib. Am. Entomol. Inst. (Ann Arbor) 3(1):1-182.

Belkin, J.N., S.J. Heinemann and W.A. Page. 1970. Mosquito studies (Diptera, Culicidae). XXI. The Culicidae of Jamaica. Contrib. Am. Entomol. Inst. (Ann Arbor) 6(1):1-458.

Bonne-Wepster, J. and C. Bonne. 1921. Notes on South American mosquitoes in the British Museum (Diptera, Culicidae). Insec. Inscit. Menst. 9:1-26.

Carpenter, S.J. and W.J. LaCasse. 1955. Mosquitoes of North America (North of Mexico). Univ. Calif. Press, Berkeley and Los Angeles. 360 pp. + 127 pl.

Cerqueira, N.L. 1961. Cinco novos sabetinos da Amazonia (Diptera, Culicidae). Rev. Bras. Entomol. 10:37-52.

Clastrier, J. and J. Claustre. 1978. *Limatus martiali* Senevet et Abonnenc, 1939 et *Wyeomyia nigricephala* n. sp. (Diptera, Culicidae) de la Guyane Francaise. Ann. Parasitol. Hum. Comp. 53:539-546.

Correa, R.R. and G.R. Ramalho. 1956. Revisao de *Phoniomyia* Theobald, 1903 (Diptera, Culicidae, Sabethini). Folia Clin. Biol. 25:1-176.

Edwards, F.W. 1932. Genera Insectorum Diptera, Fam. Culicidae. Fasc. 194. Desmet-Verteneuil, Brussels. 258 pp.

Edwards, F.W. 1941. Mosquitoes of the Ethiopian Region III. Culicine adults and pupae. Brit. Mus. (Nat. Hist.), London. 499 pp.

Ferrara, L. and J.P. Eouzan 1974. Description de deux nouveau *Eretmapodites*, du groupe *oedipodius* Graham, 1909 (Diptera: Culicidae) decouverts au Cameroun *Aedes (Diceromyia) mefauensis* n. sp. Cah. O.R.S.T.O.M. Entomol. Med. Parasitol. 12:3-5.

Freeman, P. and B. de Meillon. 1954. Simuliidae of the Ethiopian Region. Brit. Mus. (Nat. Hist.) Publ. 194:1-224.

Gaffigan, T.V. and R.A. Ward. 1985. Index to the second supplement to "A Catalog of the Mosquitoes of the World", with corrections and additions (Diptera: Culicidae). Mosq. Syst. 17:52-63.

Galindo, P. 1957. A note on the oviposition behavior of *Sabethes (Sabethoides) chloropterus* (Von Humboldt). Proc. Entomol. Soc. Wash. 59:287-288.

Galindo, P., S.J. Carpenter and H. Trapido. 1951. Description of two new species of *Wyeomyia* and the male of *Sabethes tarsopus* Dyar and Knab. Proc. Entomol. Soc. Wash. 53:86-96.

Harbach, R.E. and K.L. Knight. 1980. Taxonomists' glossary of mosquito anatomy. Plexus Publishing, Inc. Marlton, N.J. xi + 415 pp.

Hogue, C.L. 1981. Chapter 8. Blephariceridae, pp. 191-197. *In*: J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

Knight, K.L. 1978. Supplement to a catalog of the mosquitoes of the world (Diptera: Culicidae). Thomas Say Found. Entomol. Soc. Am. 6(Suppl.):1-107.

Knight, K.L. and A. Stone. 1977. A catalog of the mosquitoes of the world (Diptera: Culicidae). Second Edition. Thomas Say Found. Entomol. Soc. Am. 6:1-611.

Lane, J. 1953. Neotropical Culicidae. Univ. Sao Paulo, Sao Paulo, Brazil, 2 vols., 1112 pp.

Lee, D.J., M.M. Hicks, M. Griffiths, M.L. Debenham, J.H. Bryan, R.C. Russell, M. Geary and E.N. Marks. 1987. The Culicidae of the Australasian Region, Vol. 4. Commonw. Dept. Hlth. and Sch. Pub. Hlth. Trop. Med., Univ. of Sidney, Monogr. Ser., Entomol. Monogr. 2. Austr. Gov. Publ. Serv., Canberra. 324 pp.

Lounibos, L.P. 1983. Behavioral convergences among fruit-husk mosquitoes. Fla. Entomol. 66:32-41.

Lounibos, L.P. and C.E. Machado-Allison. 1983. Oviposition and egg brooding by the mosquito *Trichoprosopon digitatum* in cacao husks. Ecol. Entomol. 8:475-478.

Lourenco-de-Oliveira, R. 1983. Sobre uma nova especie de *Phoniomyia* (Diptera: Culicidae) do Rio de Janeiro, Brasil. Mem. Inst. Os. Cruz 78:501-505.

Macdonald, W.W. 1960. Malaysian parasites XXXVIII. On the systematics and ecology of *Armigeres* subgenus *Leicesteria* (Diptera, Culicidae). Stud. Inst. Med. Res. Malaya 29:110-153.

Marks, E.N. 1971. A metapleural generic character in *Topomyia* Leicester. Mosq. Syst. News Letter 3:4-6.

Mattingly, P.F. 1958. The culicine mosquitoes of the Indomalayan area. Part III. Genus *Aedes* Meigen, subgenera, *Paraedes* Edwards, *Rhinoskusea* Edwards and *Cancraedes* Edwards. Brit. Mus. (Nat. Hist.), London. 61 pp.

Mattingly, P.F. 1970. Contribution to the mosquito fauna of Southeast Asia. VI. The genus *Heizmannia* Ludlow in Southeast Asia. Contrib. Am. Entomol. Inst. (Ann Arbor) 5(7):1-104.

Mattingly, P.F. 1980. An interim reclassification of the genus *Tripteroides* with particular reference to the Australasian subgenera. Mosq. Syst. 12:164-171.

Mattingly, P.F. 1981. Medical entomology studies - XIV. The subgenera *Rachionotomyia*, *Tricholeptomyia* and *Tripteroides* (Mabinii Group) of genus *Tripteroides* in the Oriental Region (Diptera: Culicidae). Contrib. Am. Entomol. Inst. (Ann Arbor) 17(5):1-147.

McAlpine, J.F. 1981. Chapter 2. Morphology and terminology - adults, pp. 9-63. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

McAlpine, J.F., B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood. 1981. Chapter 1. Introduction, pp. 1-7. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

Mitchell, C.J. and R.F. Darsie, Jr. 1985. Mosquitoes of Argentina Part II. Geographic distribution and bibliography (Diptera: Culicidae). Mosq. Syst. 17:279-360.

Oliver, D.R. 1981. Chapter 29. Chironomidae, pp. 423-458. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

Owen, W.B. 1977. Morphology of the thoracic skeleton and muscles of the mosquito, *Culiseta inornata* (Williston), (Diptera: Culicidae). J. Morphol. 153:427-460.

Patton, W.S. and A.M. Evans 1929. Insects, ticks, mites and venomous animals of medical and veterinary importance. Part 1. Medical. H.R. Grubb. Ltd., Croydon, Great Britain. 786 pp.

Peterson, B.V. 1981a. Chapter 19. Anisopodidae, pp. 305-312. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

Peterson, B.V. 1981b. Chapter 27. Simuliidae, pp. 355-391. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

Peterson, B.V. and E.F. Cook. 1981. Chapter 21. Synneuridae, pp. 321-324. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.

Raven, P.H. and D.I. Axelrod. 1975. History of the flora and fauna of Latin America. Am. Sci. 63:420-429.

Reinert, J.F. 1973. Notes on the genus *Heizmannia* and the inclusion in subgenus *Mattinglyia* of two species previously placed in *Aedes* subgenus uncertain (Diptera: Culicidae). Mosq. Syst. 5:14-23.

Reinert, J.F. 1974. Medical entomology studies - I. A new intepretation of the subgenus *Verrallina* of the genus *Aedes* (Diptera: Culicidae). Contrib. Am. Entomol. Inst. (Ann. Arbor) 11(1):1-249.

Richards, P.W. 1973. Africa, the "Odd Man Out.", pp. 21-26. *In:* B.J. Meggers, E.S. Ayensu and W.D. Duckworth (ed.). Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Inst. Press, Washington. 350 pp.

Rickenbach, A. and J.P. Eouzan. 1970. Description de quatre *Eretmapodites* nouveaux du groupe *plioleucus* Edwards 1941, captures au Cameroun (Diptera: Culicidae). Cah. O.R.S.T.O.M. Entomol. Med. Parasitol. 8:131-135.

Rickenbach, A., J.P. Eouzan, L. Ferrara and H. Bailly-Choumara. 1976. Donnees nouvelles sur la presence, la frequence et la repartition des *Toxorhynchites* et *Culicinae* (*Diptera, Culicidae*) au Cameroun. 2. Genres *Eretmapodites* et *Culex*. Cah. O.R.S.T.O.M. Entomol. Med. Parasitol. 14:93-100.

Rickenbach, A. and G. Lombrici. 1975. Les *Eretmapodites* du groupe *leucopus* Graham, 1909. Position systematique des deux sous-especes actuellement connues et description de deux especes nouvelles (Diptera: Cu-

licidae). Bull. Soc. Entomol. France 80:39-42.
Ridd, M.F. 1971. South-east Asia as a part of Gondwanaland. Nature 234:531-533.
Ross, H.H. 1964. The colonization of temperate North America by mosquitoes and man. Mosq. News 24:103-118.
Rozeboom, L.E. and W.H.W. Komp. 1948. Three new species of *Culex* (Diptera: Culicidae) from Colombia. J. Parasitol. 34:396-406.
Sirivanakarn, S. 1983. A review of the systematics and a proposed scheme of internal classification of the New World subgenus *Melanoconion* of *Culex* (Diptera, Culicidae). Mosq. Syst. 14:265-333.
Sloof, R. 1961. *Tripteroides (Rachisoura) tityae* (Diptera: Culicidae), a new species from Netherlands, New Guinea. Entomol. Ber. Amst. 21:22-23.
Snodgrass, R.E. 1912. The thorax, pp. 55-60. *In:* L.O. Howard, H.G. Dyar and F. Knab. The Mosquitoes of North and Central America and the West Indies. Carnegie Inst. Wash. Publ. 159.
Steffan, W.A. 1981. Chapter 15. Sciaridae, pp. 247-255. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.
Stone, A. and P. Barreto. 1969. A new genus and species of mosquito from Colombia, *Galindomyia leei* (Diptera, Culicidae, Culicini). J. Med. Entomol. 6:143-146.
Stone, A., K.L. Knight and H. Starcke. 1959. A synoptic catalog of the mosquitoes of the world (Diptera, Culicidae). Thomas Say Found. Entomol. Soc. Am. 6:1-358.
Tanaka, K., K. Mizusawa and E.S. Saugstad. 1979. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). Contrib. Am. Entomol. Inst. (Ann Arbor) 16:1-987.
Theobald, F.V. 1901a. The classification of mosquitoes. J. Trop. Med. 4:229-235.
Theobald, F.V. 1901b. A monograph of the Culicidae or mosquitoes. Vol. 1. Brit. Mus. (Nat. Hist.), London. 424 pp.
Theobald, F.V. 1903. A monograph of the Culicidae or mosquitoes. Vol. 3. Brit. Mus. (Nat. Hist.), London. 359 pp.
Thorne, R.F. 1973. Floristic relationships between tropical Africa and tropical America, pp. 27-47. *In:* B.J. Meggers, E.A. Ayensu and W.D. Duckworth (ed.). Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Institution Press, Washington. 350 pp.
Thurman, E.B. 1959. A contribution to a revision of the Culicidae of northern Thailand. Univ. Md. Agric. Exp. Sta. Bull. A-100:1-177.
Valencia, J.D. 1973. Mosquito studies (Diptera, Culicidae) XXXI. A revision of the subgenus *Carrollia* of *Culex*. Contrib. Am. Entomol. Inst. (Ann Arbor) 9(4):1-134.
Van den Assam, J. 1959. Notes on New Guinean species of *Tripteroides,* Subgenus *Rachisoura* (Diptera, Culicidae) with descriptions of two new species. Tijdsch. Entomol. 102:35-55.
Vockeroth, J.R. 1981. Chapter 14. Mycetophilidae, pp. 223-246. *In:* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (ed.). Manual of Nearctic Diptera. Vol. 1. Agric. Canada Monogr., Ottawa. 674 pp.
Ward, R.A. 1984. Second supplement to "A Catalog of the Mosquitoes of the World" (Diptera: Culicidae). Mosq. Syst. 16:227-270.
White, G.B. 1980. Family Culicidae, pp. 114-148. *In:* R.W. Crosskey, (ed.). Catalogue of the Diptera of the Afrotropical region. Brit. Mus. (Nat. Mus.), London. 1437 pp.
Zavortink, T.J. 1972. Mosquito studies (Diptera, Culicidae) XXVIII. The New World species formerly placed in *Aedes (Finlaya).* Contrib. Am. Entomol. Inst. (Ann Arbor) 8(2):1-206.
Zavortink, T.J. 1979a. Mosquito studies (Diptera, Culicidae) XXXV. The new sabethine genus *Johnbelkinia* and a preliminary reclassification of the composite genus *Trichoprosopon*. Contrib. Am. Entomol. Inst. (Ann Arbor) 17(1):1-61.
Zavortink, T.J. 1979b. A reclassification of the sabethine genus *Trichoprosopon*. Mosq. Syst. 11:255-257.
Zavortink, T.J. 1981. Species complexes in the genus *Trichoprosopon*. Mosq. Syst. 13:82-85.
Zavortink, T.J. 1985. *Zinzala,* a new subgenus of *Wyeomyia* with two new species from pitcher-plants in Venezuela (Diptera, Culicidae, Sabethini). Wasmann J. Biol. 43:46-59.