

THE DORSAL APOTOME OF PUPAE AND FOURTH-INSTAR LARVAE OF CULICIDAE (DIPTERA), A STRUCTURE OF PHYLOGENETIC SIGNIFICANCE

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ABSTRACT. The development of the pupal dorsal apotome was examined and compared in representatives of the families Culicidae, Chaoboridae, Corethrellidae, and Dixidae. Illustrations of the pupal dorsal apotome for 73 species, in 25 genera, are provided to show the differences and similarities between taxa. The 4th-instar larval dorsal apotome is compared and illustrated for the 3 subfamilies of Culicidae. The phylogenetic significance of the dorsal apotome of the pupae and 4th-instar larvae is discussed.

KEY WORDS Phylogenetics, dorsal apotome, mosquitoes, pupae, larvae

Based on a cladistic analysis of the anatomical characteristics of larvae (22 features), pupae (2 features), and adults (6 features), Wood and Borke (1989) included the 4 families Dixidae, Corethrellidae, Chaoboridae, and Culicidae within the infraorder Culicomorpha, superfamily Culicoidea. Their listing of the families was with the phylogenetically older one (Dixidae) listed first to the

most recent one (Culicidae) listed last. However, Pawlowski et al. (1996), utilizing ribosomal RNA gene sequences, found "... the sister-group relationship between Culicidae, Chaoboridae and Corethrellidae was clearly confirmed, the Dixidae, traditionally considered as closely related to these two families, were not placed close to them on our trees."

Table 1. Taxa evaluated having pupal dorsal apotome with a single sclerite.^{1,2}

Family Chaoboridae	
<i>Chaoborus</i> sp. (S)	
Family Corethrellidae	
<i>Corethrella appendiculata</i> Grabham (I)	<i>Corethrella longitubus</i> Belkin, Heinemann, and Page (I)
<i>Corethrella brakeleyi</i> (Coquillett) (S)	<i>Corethrella wirthi</i> Stone (S)
<i>Corethrella librata</i> Belkin, Heinemann, and Page (I)	
Family Dixidae	
<i>Dixella scitula</i> Belkin, Heinemann, and Page (I)	<i>Paradixa fuscineris</i> (Tonnoir) (I)
<i>Dixina solomonis</i> Belkin (I)	<i>Paradixa harrisi</i> (Tonnoir) (I)
<i>Mesodixa biambulacra</i> Belkin, Heinemann, and Page (I)	<i>Paradixa neozelanaica</i> (Tonnoir) (I)
<i>Nothodixa campbelli</i> (Alexander) (I)	<i>Paradixa tonnoiri</i> Belkin (I)
Family Culicidae	
Subfamily Anophelinae	
<i>An. (Ano.) atropos</i> Dyar and Knab (S)*	<i>An. (Ker.) neivae</i> Howard, Dyar, and Knab (I)*
<i>An. (Ano.) barberi</i> Coquillett (S)*	<i>An. (Ker.) pholidotus</i> Zavortink (I)*
<i>An. (Ano.) bradleyi</i> King (S)*	<i>An. (Nys.) albanus</i> Wiedemann (S)*
<i>An. (Ano.) campestris</i> Reid (I)*	<i>An. (Nys.) aquasalis</i> Curry (I)*
<i>An. (Ano.) crucians</i> s.l. Wiedemann (S)*	<i>An. (Nys.) noroestensis</i> Galvao and Lane (I)*
<i>An. (Ano.) earlei</i> Vargas (S)*	<i>An. (Nys.) oswaldoi</i> (Peryassu) (I)*
<i>An. (Ano.) punctipennis</i> Dyar and Knab (S)*	<i>An. (Nys.) strodei</i> Root (I)*
<i>An. (Ano.) quadrimaculatus</i> s.s. Say (S)*	<i>An. (Ste.) kompi</i> Edwards (S)*
<i>An. (Ano.) walkeri</i> Theobald (S)*	<i>An. (Ste.) nimbus</i> (Theobald) (S)*
<i>An. (Cel.) aconitus</i> Doenitz (I)*	<i>Bi. (Bir.) gracilis</i> Theobald (I)*
<i>An. (Cel.) culicifacies</i> Giles (I)*	<i>Bi. (Bru.) hollandi</i> Taylor (S)*
<i>An. (Cel.) minimus</i> Theobald (I)*	<i>Bi. (Bru.) obscura</i> Tenorio (I)*
<i>An. (Cel.) pampanai</i> Buettiker and Beales (I)*	<i>Bi. (Nbi.) confusa</i> Bonne-Wepster (I)*
<i>An. (Cel.) varuna</i> Iyengar (I)*	<i>Bi. (Nbi.) soesiloi</i> (Strickland and Chowdhury) (I)
<i>An. (Ker.) bambusicolus</i> Komp (I)*	<i>Ch. bathana</i> (Dyar) (S)*
<i>An. (Ker.) bellator</i> Dyar and Knab (I)*	<i>Ch. bonneae</i> Dyar (S)*
<i>An. (Ker.) homunculus</i> Komp (I)*	<i>Ch. fajardoii</i> (Lutz) (S)*

¹ Abbreviations of genera and subgenera of Culicidae follow Reinert (1975, 1982, 1991).

² I, published illustration of pupal exuviae examined; S, specimen of pupal exuviae examined; *, condition of larval dorsal apotome confirmed on specimen and/or published illustration.

Table 2. Taxa evaluated having pupal dorsal apotome with 2 sclerites.^{1,2}

Family Culicidae	
Subfamily Culicinae	
Tribe Aedeomyiini	
<i>Ad. (Ady.) catasticta</i> Knab (I)*	<i>Ad. (Ady.) squamipennis</i> (Lynch Arribalzaga) (S)*
Tribe Aedini	
<i>Ae. (Abr.) papago</i> Zavortink (S)*	<i>Ae. (Muc.) quasiferinus</i> Mattingly (S)*
<i>Ae. (Adm.) alboscuteclatus</i> (Theobald) (S)*	<i>Ae. (Neo.) lineatopennis</i> (Ludlow) (S)*
<i>Ae. (Adm.) senyavinensis</i> Knight and Hurlbut (S)*	<i>Ae. (Not.) chathamicus</i> Dumbleton (I)*
<i>Ae. (Adm.) vexans</i> (Meigen) (S)*	<i>Ae. (Och.) canadensis</i> (Theobald) (S)*
<i>Ae. (Aed.) cinereus</i> Meigen (S)*	<i>Ae. (Och.) dupreei</i> (Coquillett) (S)*
<i>Ae. (Aed.) esoensis</i> Yamada (S)*	<i>Ae. (Och.) infirmatus</i> Dyar and Knab (S)*
<i>Ae. (Ala.) brevitibia</i> (Edwards) (S)*	<i>Ae. (Och.) mitchellae</i> (Dyar) (S)*
<i>Ae. (Alb.) ngong</i> van Someren (S)*	<i>Ae. (Och.) muelleri</i> Dyar (S)*
<i>Ae. (Ayu.) peytoni</i> Reinert (S)*	<i>Ae. (Och.) taeniorhynchus</i> (Wiedemann) (S)*
<i>Ae. (Azt.) ramirezi</i> Vargas and Downs (I)*	<i>Ae. (Och.) tormentor</i> Dyar and Knab (S)*
<i>Ae. (Blk.) aurotaeniatus</i> Edwards (I)*	<i>Ae. (Och.) vigilax</i> (Skuse) (S)*
<i>Ae. (Bot.) helenae</i> Reinert (S)*	<i>Ae. (Par.) ostentatio</i> (Leicester) (S)*
<i>Ae. (Can.) indonesiae</i> Mattingly (S)*	<i>Ae. (Par.) thailandensis</i> Reinert (S)*
<i>Ae. (Can.) masculinus</i> Mattingly (S)*	<i>Ae. (Pro.) triseriatus</i> (Say) (S)*
<i>Ae. (Cha.) tulliae</i> Taylor (I)*	<i>Ae. (Rhi.) longirostris</i> (Leicester) (S)*
<i>Ae. (Chr.) thomsoni</i> (Theobald) (S)*	<i>Ae. (Scu.) albolineatus</i> (Theobald) (S)*
<i>Ae. (Dic.) franciscoi</i> Mattingly (S)*	<i>Ae. (Sku.) pembaensis</i> Theobald (I)*
<i>Ae. (Dic.) whartoni</i> Mattingly (S)*	<i>Ae. (Stg.) aegypti</i> (Linnaeus) (S)*
<i>Ae. (Edw.) imprimens</i> (Walker) (S)*	<i>Ae. (Stg.) albopictus</i> (Skuse) (S)*
<i>Ae. (Fin.) alboteniatus</i> (Leicester) (S)*	<i>Ae. (Ver.) atrius</i> Barraud (S)*
<i>Ae. (Fin.) chrysolineatus</i> (Theobald) (S)*	<i>Ae. (Ver.) butleri</i> Theobald (S)*
<i>Ae. (Fin.) crossi</i> Lein (S)*	<i>Ae. (Ver.) carmentis</i> Edwards (S)*
<i>Ae. (Fin.) fuscipalpis</i> Belkin (S)*	<i>Ae. (Ver.) yusafi</i> Barraud (S)*
<i>Ae. (Fin.) geniculatus</i> (Olivier) (S)*	<i>Ar. (Arm.) alkatrii</i> Toma, Miyagi, and Syafruddin (I)*
<i>Ae. (Fin.) leonis</i> Colless (S)*	<i>Ar. (Arm.) baisasi</i> Stone and Thurman (S)*
<i>Ae. (Fin.) longipalpis</i> (Grunberg) (S)*	<i>Ar. (Arm.) subalbatus</i> (Coquillett) (S)*
<i>Ae. (Fin.) macfarlanei</i> (Edwards) (S)*	<i>Ar. (Lei.) magnus</i> (Theobald) (S)*
<i>Ae. (Fin.) oreophilus</i> (Edwards) (S)*	<i>Er. inornatus</i> Newstead (S)*
<i>Ae. (Fin.) papuensis</i> (Taylor) (S)*	<i>Er. leucopous</i> Graham (S)*
<i>Ae. (Fin.) poicilius</i> (Theobald) (S)*	<i>Er. penicillatus</i> Edwards (S)*
<i>Ae. (Fin.) reinerti</i> Rattanarithikul and Harrison (S)*	<i>Er. silvestris</i> Ingram and De Meillon (S)*
<i>Ae. (Fin.) togoi</i> (Theobald) (S)*	<i>Hg. (Con.) leucocelaenus</i> Dyar and Knab (I)*
<i>Ae. (Geo.) kabaensis</i> Brug (S)*	<i>Hg. (Hag.) janthinomys</i> Dyar (S)*
<i>Ae. (Gym.) mediovitatus</i> (Coquillett) (S)*	<i>Hg. (Hag.) spagazzinii</i> Brethes (S)*
<i>Ae. (Hal.) australis</i> (Erickson) (I)*	<i>Hz. (Hez.) complex</i> (Theobald) (S)*
<i>Ae. (How.) walkeri</i> (Theobald) (I)*	<i>Hz. (Hez.) reidi</i> Mattingly (S)*
<i>Ae. (Hua.) wauensis</i> Huang (S)*	<i>Hz. (Hez.) persimilis</i> Mattingly (S)*
<i>Ae. (Iso.) cavaticus</i> Reinert (S)*	<i>Op. fuscus</i> Hutton (S)*
<i>Ae. (Ken.) dissimilis</i> (Leicester) (S)*	<i>Ps. (Gra.) columbiae</i> (Dyar and Knab) (S)*
<i>Ae. (Ken.) harbachi</i> Reinert (S)*	<i>Ps. (Jan.) cyanescens</i> (Coquillett) (S)*
<i>Ae. (Kom.) purpureipes</i> Aitken (S)*	<i>Ps. (Jan.) ferox</i> (Von Humboldt) (S)*
<i>Ae. (Lep.) aurimargo</i> Edwards (S)*	<i>Ps. (Pso.) ciliata</i> (Fabricius) (S)*
<i>Ae. (Lev.) geoskusea</i> Amos (I)*	<i>Ps. (Pso.) howardii</i> Coquillett (S)*
<i>Ae. (Lor.) amesii</i> (Ludlow) (S)*	<i>Ud. argyrurus</i> (Edwards) (S)*
<i>Ae. (Mac.) tremulus</i> (Theobald) (S)*	<i>Ze. gracilis</i> Leicester (S)*
<i>Ae. (Mol.) pecuniosus</i> Edwards (S)*	<i>Ze. lawtoni</i> Baisas (S)*
<i>Ae. (Muc.) laniger</i> (Wiedemann) (S)*	
Tribe Culicini	
<i>Cx. (Acl.) belkini</i> Stone and Penn (I)*	<i>Cx. (Lut.) halifaxii</i> Theobald (I)*
<i>Cx. (Ads.) amazonensis</i> (Lutz) (I)*	<i>Cx. (Mca.) bisulcatus</i> (Coquillett) (I)*
<i>Cx. (And.) conservator</i> Dyar and Knab (I)*	<i>Cx. (Mel.) erraticus</i> (Dyar and Knab) (S)*
<i>Cx. (Bel.) eldridgei</i> Adames and Galindo (I)*	<i>Cx. (Mel.) pilosus</i> (Dyar and Knab) (S)*
<i>Cx. (Car.) iridescens</i> (Lutz) (I)*	<i>Cx. (Ncx.) leonardi</i> Belkin (I)*
<i>Cx. (Cui.) nigropunctatus</i> Edwards (S)*	<i>Cx. (Ncx.) territans</i> Walker (S)*
<i>Cx. (Cux.) quinquefasciatus</i> Say (S)*	<i>Cx. (Tha.) dispectus</i> Bram (I)*
<i>Cx. (Cux.) restuans</i> Theobald (S)*	<i>Cx. (Tin.) laisquama</i> (Coquillett) (I)*
<i>Cx. (Cux.) salinarius</i> Coquillett (S)*	<i>De. cancer</i> Theobald (S)*
<i>Cx. (Cux.) tarsalis</i> Coquillett (S)*	<i>De. pseudes</i> Dyar and Knab (S)*
<i>Cx. (Eum.) brevipalpis</i> (Giles) (S)*	<i>Ga. lei</i> Stone and Barreto (I)*
<i>Cx. (Lop.) peytoni</i> Bram and Rattanarithikul (S)*	

Table 2. Continued.

Tribe Culisetini	
<i>Cs. (All.) longiareolata</i> (Macquart) (I)*	<i>Cs. (Cus.) incidens</i> (Thomson) (I)*
<i>Cs. (Cli.) melanura</i> (Coquillett) (S)*	<i>Cs. (Cus.) inornata</i> (Williston) (S)*
Tribe Ficalbiini	
<i>Fi. minima</i> (Theobald) (S)*	<i>Mi. (Ing.) milloti</i> Grjebine (I)*
<i>Fi. uniformis</i> (Theobald) (I)*	<i>Mi. (Mim.) chamberlaini</i> Ludlow (S)*
<i>Mi. (Ing.) bernardi</i> (Doucet) (I)*	<i>Mi. (Mim.) gurneyi</i> (Belkin) (I)*
<i>Mi. (Ing.) beytouti</i> (Doucet) (I)*	<i>Mi. (Mim.) hispida</i> (Theobald) (I)*
<i>Mi. (Ing.) grjebinei</i> Brunhes (I)*	<i>Mi. (Mim.) splendens</i> Theobald (I)*
Tribe Hodgesiini	
<i>Ho. malayi</i> Leicester (S)*	<i>Ho. solomonis</i> Belkin (I)*
Tribe Mansoniini	
<i>Cq. (Aus.) tenuipalpis</i> (Edwards) (I)	<i>Ma. (Man.) titillans</i> (Walker) (I)*
<i>Cq. (Coq.) lutea</i> (Belkin) (I)*	<i>Ma. (Man.) uniformis</i> (Theobald) (S)*
<i>Cq. (Rhy.) nigricans</i> (Coquillett) (I)*	<i>Ma. (Mnd.) bonnaeae</i> Edwards (S)*
<i>Ma. (Man.) leberi</i> Boreham (I)*	
Tribe Orthopodomyiini	
<i>Or. anopheloides</i> (Giles) (I)*	<i>Or. siamensis</i> Zavortink (I)*
<i>Or. fascipes</i> (Coquillett) (I)*	<i>Or. signifera</i> (Coquillett) (S)*
<i>Or. phyllozoa</i> (Dyar and Knab) (I)*	<i>Or. wilsoni</i> Macdonald (S)*
Tribe Sabethini	
<i>Jb. longipes</i> (Fabricius) (I)*	<i>Tp. (Rac.) stonei</i> Belkin (I)*
<i>Jb. ulopus</i> (Dyar and Knab) (I)*	<i>Tp. (Rah.) coheni</i> Belkin (I)*
<i>Li. durhamii</i> Theobald (S)*	<i>Tp. (Tri.) roxasi</i> Baisas and Ubaldo-Pagayon (I)*
<i>Mg. argyropus</i> (Walker) (I)*	<i>Tp. (Trp.) purpuratus</i> (Edwards) (I)*
<i>Ml. solomonis</i> (Wharton) (I)*	<i>Tr. compressum</i> Lutz (I)*
<i>Ru. (Iso.) lunatum</i> (Theobald) (I)*	<i>Tr. pallidiventer</i> (Lutz) (I)*
<i>Ru. (Run.) frontosum</i> (Theobald) (I)*	<i>Wy. (Cae.) fernandezyepezi</i> Cova Garcia, Sutil Oramas, and Pulido F (I)*
<i>Ru. (Run.) reversum</i> Lane and Cerqueira (I)*	<i>Wy. (Den.) forcipenis</i> Lourenco de Oliveira and da Dilva (I)
<i>Sa. (Dav.) petrochiae</i> (Shannon and del Ponte) (I)*	<i>Wy. (Exm.) arborea</i> Galindo, Carpenter, and Trapido (I)*
<i>Sa. (Pey.) aurescens</i> (Lutz) (I)*	<i>Wy. (Wyo.) haynei</i> Dodge (S)*
<i>Sa. (Sab.) gymnothorax</i> Harbach and Petersen (I)*	<i>Wy. (Wyo.) mitchellii</i> (Theobald) (S)*
<i>Sa. (Sbn.) xhyphydes</i> Harbach (I)*	<i>Wy. (Wyo.) vanduzeei</i> Dyar and Knab (S)*
<i>To. (Sua.) spathulirostris</i> Edwards (S)*	<i>Wy. (Zin.) fishi</i> Zavortink (I)*
<i>To. (Top.) javaensis</i> Miyagi and Toma (I)*	
<i>To. (Top.) lindsayi</i> Thurman (I)*	
<i>To. (Top.) spathulirostris</i> Edwards (S)*	
Tribe Uranotaeniini	
<i>Ur. (Pfc.) anhydor</i> Dyar (I)*	<i>Ur. (Ura.) lowii</i> Theobald (S)*
<i>Ur. (Pfc.) bimaculata</i> Leicester (I)*	<i>Ur. (Ura.) sapphirinia</i> (Osten Sacken) (S)*
Subfamily Toxorhynchitinae	
<i>Tx. (Lyn.) portoricensis</i> (Roeder) (I)*	
<i>Tx. (Lyn.) rutilus</i> (Coquillett) (S)*	<i>Tx. (Tox.) brevipalpis</i> Theobald (I)*
<i>Tx. (Tox.) amboinensis</i> (Doleschall) (I)*	<i>Tx. (Tox.) splendens</i> (Wiedemann) (I)*

¹ Abbreviations of genera and subgenera of Culicidae follow Reinert (1975, 1982, 1991).

² I, published illustration of pupal exuviae examined; S, specimen of pupal exuviae examined; *, condition of larval dorsal apotome confirmed on specimen and/or published illustration.

While conducting a morphologic taxonomic study of the Quadrimaculatus Complex of the genus *Anopheles* Meigen (Reinert et al. 1997), I noted and illustrated differences in the development of the pupal dorsal apotome. Crawford (1938) previously illustrated the dorsal apotome (as vertical plate) of 15 Malayan species of *Anopheles* and suggested that the shape of this structure "appeared to vary to some extent specifically." Also, most authors who have illustrated the pupal cephalothorax have included the dorsal apotome, but without any written mention or description of it. Harbach and Knight (1980) provided the following definition of the dorsal apotome of pupae "... the cranial area

bounded laterally by the frontal ecdysial lines and apically by an imaginary line between the most apical parts of the frontal ecdysial lines In mosquito pupae, perhaps homologous with the dorsal apotome of mosquito larvae." In slide-mounted specimens of pupal exuviae (positioned in a flattened aspect [Reinert et al. 1997]) the dorsal apotome projects from the median anterior margin of the cephalothorax in a manner appropriate for comparative study.

After noting differences in the structure of the dorsal apotome in the pupae of the Quadrimaculatus Complex (5 sibling species), this structure was compared to species in other mosquito genera and

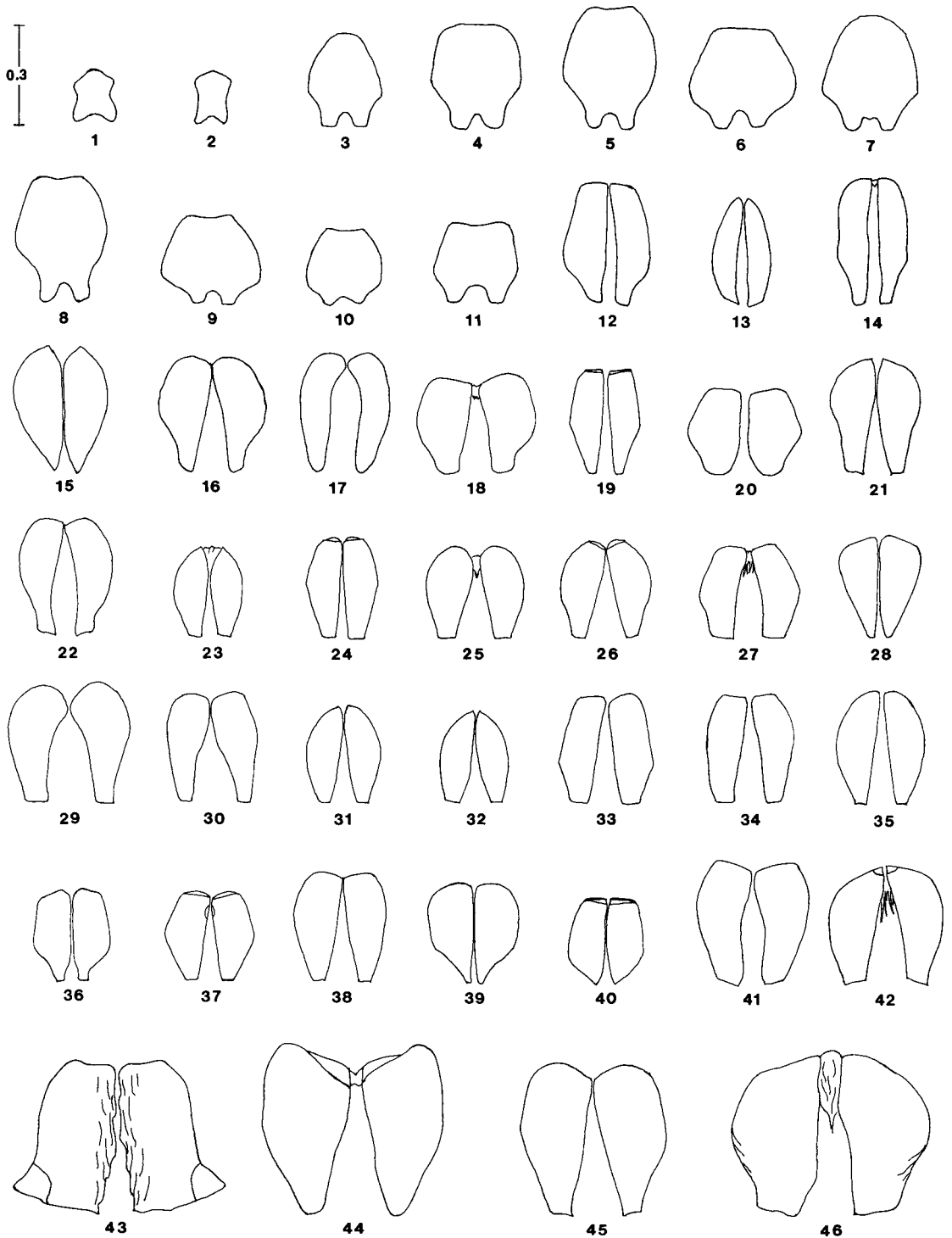


Fig. 1. Dorsal apotome (DAP) of pupae; drawn from pupal exuviae; all DAPs drawn to same scale, 0.3 mm. 1, *Corethrella brakeleyi*, ♂, Florida, USA; 2, *Corethrella wirthi*, ♂, Florida, USA; 3, *Bironella hollandi*, ♂, Solomon Islands; 4, *Anopheles quadrimaculatus* s.s., ♂, Minnesota, USA; 5, *An. atropos*, ♂, Florida, USA; 6, *An. earlei*, ♂, Wisconsin, USA; 7, *An. barberi*, ♂, Florida, USA; 8, *An. bradleyi*, ♂, Louisiana, USA; 9, *An. punctipennis*, ♂, Wisconsin, USA; 10, *An. crucians* s.l., ♂, Louisiana, USA; 11, *An. albimanus*, ♀, Florida, USA; 12, *Orthopodomyia signifera*, ♂, Florida, USA; 13, *Limatus durhamii*, ♀, Costa Rica; 14, *Wyeomyia vanduzeei*, ♂, Florida, USA; 15, *Aedes aurimargo*, ♂, Papua New Guinea; 16, *Ae. wauensis*, ♀, Papua New Guinea; 17, *Ae. tremulus*, ♂, Australia;

major differences were observed that seem to be of phylogenetic significance. In specimens and/or published illustrations (e.g., Knight and Chamberlain 1948, Belkin 1962, Belkin et al. 1970, Zavortink 1972; publications of the Mosquitoes of Middle America Project, Southeast Asian Mosquito Project, Medical Entomology Project, Walter Reed Biosystematics Unit, and others) the dorsal apotome appears as a single more or less oblong sclerite in species of the subfamily Anophelinae (genera *Anopheles*, *Bironella* Theobald, and *Chagasia* Cruz) and as a structure consisting of 2 longitudinal sclerites connected by a membrane mesally in the subfamilies Culicinae (i.e., tribes Uranotaeniini, Culicini, Aedeomyiini, Hodgesiini, Culisetini, Ficalbiini, Mansoniini, Orthopodomyiini, Aedini, and Sabethini) and Toxorhynchitinae (Knight and Stone 1977). Tables 1 and 2 list the broad range of taxa evaluated during this study (4 families, 3 subfamilies, 10 tribes, 42 genera, 102 subgenera, and 233 species).

The pupal dorsal apotome in species of Dixidae, Corethrellidae, and Chaoboridae is represented as a single sclerite, suggesting that this is the plesiomorphic state and the divided condition is the apomorphic state. Therefore, the development of the pupal dorsal apotome supports the contention of most authors that the Anophelinae is the most primitive subfamily of the Culicidae. From the examination of specimens and/or published illustrations it seems that the shape and development of the dorsal apotome of pupae also may be of value at other taxonomic levels (e.g., separation of genera, subgenera, species groups, and some species). The dorsal apotomes of various pupae of families (2), subfamilies (3), genera (25), subgenera (46), and species (73) are illustrated (Figs. 1 and 2) to show the differences or similarities observed between taxa.

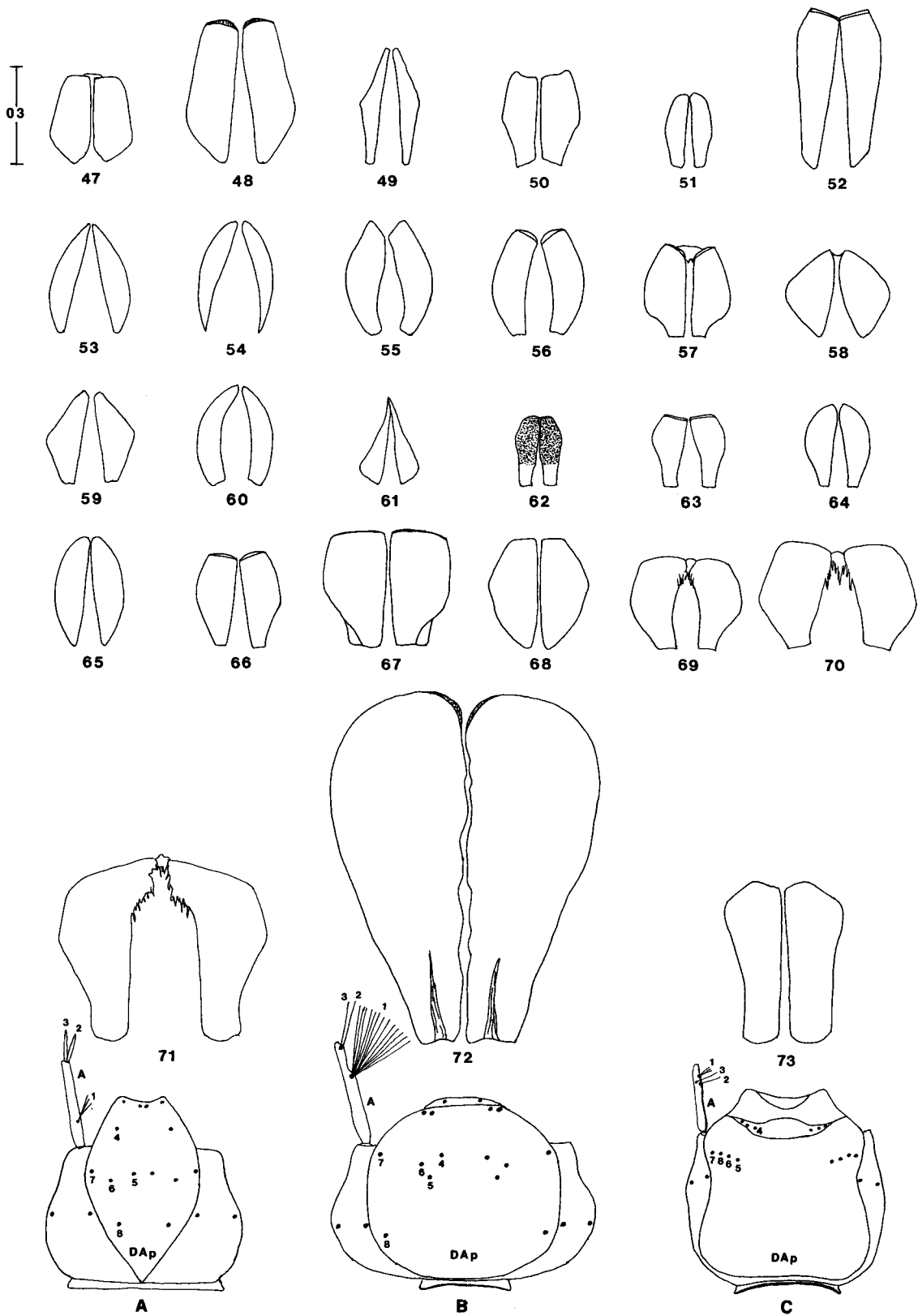
The posterior portion of the dorsal apotome is narrow in 4th-instar larvae of species of Anophelinae (Fig. 2A) and broad in the Culicinae (Fig. 2B) and Toxorhynchitinae (Fig. 2C) (some *Uranotaenia* Lynch Arribalzaga?). As pointed out by others, the Anophelinae also is distinguished as follows: in the 4th-instar larvae the siphon (see discussion in Belkin 1951, 1962; Harbach 1978) consists only of a pair of sclerotized pecten plates, one on each side dorsolaterally, that are connected posteriorly

by a very narrow U-shaped band and located immediately ventral to the spiracular apparatus, Nuttall and Shipley's organ is present dorsally on the prothorax, a tergal plate is situated anteromesally on each of abdominal segments I–VIII, and palmate setae are present (except 10 of 12 species of the Umbrosus Group of *Anopheles*); and the eggs have floats (except absent in a few species, for example, *An. bariensis* James, *An. dthali* Patton, *An. multicolor* Cambouliu, *An. pessoai* Golva and Lane = *An. braziliensis* (Chagas), *An. sawyeri* Causey, Deane, Deane and Sampaio, *An. superpictus* Grassi, and *An. turkhudi* Liston; see Christophers 1933, Causey et al. 1944). In comparison the 4th-instar larvae of Culicinae and Toxorhynchitinae have the siphon developed as an elongate sclerotized tube with the spiracular apparatus situated apically, Nuttall and Shipley's organ is absent, tergal plates are absent on segments I–V (tergal plate present on one or more of segments VI–VIII in *Orthopodomyia*), and palmate setae are absent; and the eggs are without floats. Larvae of the subfamily Toxorhynchitinae (Fig. 2C) have seta 8-C displaced far cephalad on the dorsal apotome, situated between setae 6-C and 7-C, and more or less in a line with setae 5–7-C, and antennal setae 2,3-A are inserted basad of seta 1-A, which distinctively separate them from larvae of the other 2 subfamilies of the Culicidae. In larvae of Anophelinae (Fig. 2A) and Culicinae (Fig. 2B) seta 8-C is inserted noticeably caudad to seta 7-C on the dorsal apotome and is not located in line with setae 5–7-C, and antennal setae 2,3-A are inserted distal to seta 1-A. Terminology used follows Harbach and Knight (1980).

ACKNOWLEDGMENTS

Special acknowledgment and appreciation is expressed to: Ralph E. Harbach (The Natural History Museum, London, United Kingdom) for examining the pupal dorsal apotome in several species and for reviewing the manuscript; and to Bruce A. Harrison (North Carolina Department of Environment and Natural Resources, Winston-Salem, NC) and E. L. Peyton (Walter Reed Biosystematics Unit, Smithsonian Institution, Washington, DC) for reviewing the manuscript.

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- 18, *Ae. canadensis*, ♂, Florida, USA; 19, *Ae. thomsoni*, ♀, Thailand; 20, *Ae. papago*, ♂, Arizona, USA; 21, *Ae. cavaticus*, ♀, Thailand; 22, *Ae. franciscot*, ♀, Malaysia; 23, *Ae. lineatopennis*, ♀, India; 24, *Ae. senyavinensis*, ♀, Caroline Islands; 25, *Ae. vexans*, ♀, Florida, USA; 26, *Ae. albolineatus*, ♀, Philippine Islands; 27, *Ae. aegypti*, ♂, Florida, USA; 28, *Ae. peytoni*, ♂, Thailand; 29, *Ae. imprimens*, ♀, Thailand; 30, *Ae. helenae*, ♀, Thailand; 31, *Ae. masculinus*, ♀, Singapore; 32, *Heizmannia* complex, ♀, Malaysia; 33, *Haemagogus spegazzinii*, ♂, Brazil; 34, *Udaya argyrurus*, ♀, Malaysia; 35, *Zeugomyia gracilis*, ♂, Malaysia; 36, *Ae. leonis*, ♂, Malaysia; 37, *Ae. albotaeniatus*, ♀, Thailand; 38, *Ae. chrysolineatus*, ♀, Malaysia; 39, *Ae. crossi*, ♂, Taiwan; 40, *Ae. poicilius*, ♀, Philippine Islands; 41, *Ae. reinerti*, ♀, Thailand; 42, *Ae. triseriatus*, ♀, Florida, USA; 43, *Ae. brevitibia*, ♂, Brunei; 44, *Ae. pecuniosus*, ♂, Australia; 45, *Ae. geniculatus*, ♀, United Kingdom; and 46, *Ae. laniger*, ♀, Philippine Islands.



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Fig. 2. Dorsal apotome (Dap) of pupae; drawn from pupal exuviae; all DAPs drawn to same scale, 0.3 mm. 47, *Culiseta melanura*, ♂, Florida, USA; 48, *Cs. inornata*, ♀, Florida, USA; 49, *Aedeomyia squamipennis*, ♀, Panama; 50, *Mimomyia chamberlaini*, ♀, Malaysia; 51, *Ficalbia minima*, ♂, Malaysia; 52, *Topomyia spathulirostris*, ♀, Malaysia; 53, *Culex brevipalpis*, ♀, Malaysia; 54, *Cx. nigropunctatus*, ♀, Malaysia; 55, *Cx. quinquefasciatus*, ♀, Florida, USA; 56, *Cx. salinarius*, ♂, Florida, USA; 57, *Cx. restuans*, ♂, Florida, USA; 58, *Cx. erraticus*, ♂, Florida, USA; 59, *Cx. territans*, ♀, Florida, USA; 60, *Deinocerites cancer*, ♂, Florida, USA; 61, *Hodgesia malayi*, ♀, Thailand; 62, *Uranotaenia lowii*, ♀, Florida, USA; 63, *Ur. sapphirina*, ♂, Florida, USA; 64, *Ae. butleri*, ♂, Malaysia; 65, *Ae. esoensis*, ♂, Japan; 66, *Ae. dissimilis*, ♀, Malaysia; 67, *Armigeres magnus*, ♂, Thailand; 68, *Eretmapodites silvestris*, ♂, South Africa; 69, *Psorophora columbiae*, ♂, Florida, USA; 70, *Ps. cyanescens*, ♂, Florida, USA; 71, *Ps. ciliata*, ♂, Florida, USA; 72, *Toxorhynchites rutilus*, ♂, Florida, USA; 73, *Opifex fuscus*, ♂, New Zealand. Cranium of Culicidae showing dorsal apotome (DAP) and antenna (A); drawn from larvae; not drawn to scale. A, *Anopheles crucians* s.l.; B, *Culex quinquefasciatus*; C, *Toxorhynchites rutilus*.