THE *ANOPHELES (ANOPHELES) CRUCIANS* SUBGROUP IN THE UNITED STATES (DIPTERA: CULICIDAE)[1]

BY

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ABSTRACT. *Anopheles (Anopheles) bradleyi* King, *An. (Ano.) crucians* Wiedemann and *An. (Ano.) georgianus* King are taxonomically redefined by morphology, ethology and distribution, and established as the *crucians* subgroup of the *An. (Ano.) punctipennis* (Say) species group. This study involved the examination of over 1,800 specimens and the preparation of 15 full-page illustrations. Species descriptions include sections on: type-data, synonymy, descriptions of female, male, pupa, and larva, distribution, taxonomic discussion, bionomics and medical importance. Keys for the *crucians* subgroup are presented for male genitalia, pupae and 4th stage larvae. Additional keys are presented, in an appendix, to separate the *crucians* subgroup from the other southeastern United States anophelines.

The 1st through 4th stage larvae of *bradleyi* and *crucians*, the 4th stage larva of *georgianus* and the pupae of *bradleyi* and *georgianus* are completely illustrated for the first time. Tables with the ranges of setal branching are included for the 4th stage larvae and pupae of each species.

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INTRODUCTION

Since 1950, work on United States anopheline and culicine taxonomy has inadequately kept abreast of advances in basic descriptive taxonomy and taxonomic techniques made in mosquito studies for other regions of the world. Belkin's exacting studies (1950, 1952, 1953, 1954, 1960, 1962) established a chaetotaxy system for the larval and pupal stages based on homologous setal innervations. Belkin (1962) demonstrated that pupal morphological characters

are as taxonomically relevant as adult and larval characters. These concepts and techniques have been extensively used in publications by the Bernice P. Bishop Museum, Mosquito Fauna of the Papuan Subregion, the Mosquitoes of Middle America Project, the Southeast Asia Mosquito Project, and the Medical Entomology Project (Smithsonian Institution) in taxonomic studies of other regions of the world. However, only a few taxonomists have used these modern taxonomic methods on the North American mosquitoes (Barr and Barr 1969; Lacey and Lake 1972; Reinert 1970a,b,c,d,e,f,g, 1971; Zavortink 1969a,b, 1970, 1972).

In other respects, anopheline research is advanced in the United States. The cytogenetic studies by Kitzmiller and associates (1963-1974) and the predator/parasite-host association studies by Chapman (late 1960's to early 1970's) are examples. However, these highly specialized studies are based on species that are poorly defined and incompletely described. For example, of the 16 anopheline species recorded from the continental United States, the majority do not have the larval and/or pupal stage completely described and illustrated.

This study was undertaken to help eliminate for the *An. crucians* subgroup the inadequacies mentioned above. Four objectives were proposed: 1) To test the authenticity of the species involved by use of morphology, ethology and distribution; 2) To update the taxonomy and descriptions of the subgroup members by use of currently accepted taxonomic techniques and nomenclature; 3) To completely illustrate the pupal stage and all the larval stages for the subgroup members; and 4) To review the early literature for the subgroup in light of current taxonomic and behavioral concepts and try to establish species' identities for the early references.

MATERIALS AND METHODS

Materials. Specimens studied were obtained from a number of Federal and State agencies and/or collected and reared by the authors. A majority of the specimens were borrowed from the collections of the United States National Museum (USNM) through the Medical Entomology Project (MEP), Smithsonian Institution. Hence, specimens not otherwise designated, *e.g.* (UCLA), will be deposited in the USNM. Included in the USNM material were many historically significant specimens, including the holotype, allotype and paratypes of *Anopheles bradleyi* and *georgianus*.

A total of 1,828 specimens were examined, including 999 adults, 68 male genitalia preparations, 209 pupal skins and 552 whole larvae and larval skins. Most of the *bradleyi* and *crucians* collected by the authors have associated larval and pupal skins. No *georgianus* specimens were collected during the study. Early stage larvae of *georgianus* were not available for examination. Some *bradleyi* and *crucians* salivary chromosome slides prepared by Dr. R. D. Kreutzer, Youngstown State University, Youngstown, Ohio, were examined.

Methods. Collection procedures, recording of data and mounting techniques for male genitalia, whole larvae, and pupal and larval skins generally followed the procedures described in Belkin (1962).

Special terminology is used here for certain adult and pupal characters. The interpretation of scale colors is extremely important. The terms "dark",

"mixed" and "pale" as applied to scale coloration on the head, palps, proboscis and wings of *bradleyi*, *crucians* and *georgianus* require definition. Scale color is influenced significantly by the orientation and intensity of the light source. The terms "dark" and "pale" have been used by Belkin (1962), Belkin et al. (1970) and others in morphological descriptions of the imago, but the terms usually are not defined. Here, "dark" refers to scales or scaled areas that are black, medium to dark gray, dark brown or opaque. "Pale" scales or scaled areas are white, creamy, light gray, light brown or opalescent. The term "mixed" refers to an area where individual scales are intermixed light gray (brown) and dark gray (brown). These areas are neither dark nor pale. The word "opaque" is loosely interpreted as a dull, non-transparent color. Wing scales often appeared iridescent, hence the word "opalescent". Paddle refractile index means the ratio of the maximum length of the paddle to the length of the lateral paddle margin (either serrated and/or with fringe hairs) that is refractile to light (Reid 1967).

The arrangement of this presentation generally follows a format established by Dr. J. N. Belkin, University of California (Los Angeles), in his mosquito publications. For easier understanding, the Historical Review is presented chronologically. A synopsis for the subfamily Anophelinae, genus *Anopheles*, and subgenus *Anopheles*, precedes the *crucians* subgroup description. Illustrations are placed after the references in order to maintain continuity in the manuscript. Several publications, notably Belkin (1950, 1952, 1953 and 1962), Knight (1971) and Knight and Laffoon (1971), were relied upon for current interpretations of setal arrangement and terminology. The terms instar(s) and stage(s) were used as defined by Anderson *et al.* (1971).

A synonymy is given for each species. The taxonomic references for *bradleyi* and *georgianus* are considered complete. The types, paratypes and other specimens of *bradleyi* and *georgianus* were examined. The illustrations are considered composites in that the single specimen concept was not adhered to completely. The appendix tables for pupal and larval setal branching are based on a minimum of 10 specimens (except 6 *georgianus* pupae). Consequently, some setal ranges reflect observations on several hundred specimens. Descriptions are composites because of the number of specimens examined (1,828). Systematics, bionomics, medical importance, and distribution for each species are based on the literature, and occasionally on our interpretation of the literature. Specimens listed in the distribution sections have been coded, *i.e.*, "P" = pupal skin, "WL" = whole larva, "L" = larval skin, and "G" = a male genitalia slide preparation. Brackets "[]" indicate our opinions. Abbreviations used for literature references conform to the most recent CBE style manual (1972: 152-65) and the 1974 List of Serials, Bioscience Information Service of Biological Abstracts (BIOSIS).

HISTORICAL REVIEW

Systematics. Studies of North American anopheline mosquitoes began in the early 1800's with reports often appearing in journals that covered a wide variety of subjects. Most original descriptions at this time were based entirely on adult characters. Wiedemann, a renowned German taxonomist, described *Anopheles crucians* from specimens collected in Pennsylvania and New Orleans,

Louisiana in 1828. *Anopheles crucians* is the eighth oldest anopheline species name, and is the primary species in the subgroup considered in this study. In the original description, Wiedemann incorrectly described the palpal coloration on his *crucians* specimens. Consequently, Coquillett (1900), Theobald (1901), Felt (1904), Smith (1904), and Blanchard (1905) compounded the error by using similar statements. Howard (in Coquillett 1906) examined Wiedemann's types in the Naturhistorisches Museum, Vienna, Austria in 1905, and confirmed the types to be *crucians* as recognized in the United States, but did not correct the palpal discrepancy. Ludlow (1906) recognized this inaccuracy and suggested it would be easier to correct if the mosquito changed its markings. Theobald (1907) followed Ludlow and corrected this error in Volume IV of his monograph. Later, part of Wiedemann's original description appeared in the monograph by Howard, Dyar and Knab (1917).

Although Smith (1904) and Dyar (1905, 1906) recognized the usefulness and stability of larval characters, and Mitchell (1907) developed larval keys, early twentieth century American culicidologists continued to rely primarily on adult characters for classification. Larval chaetotaxy was not fully utilized until the works of Howard, Dyar and Knab (1912-1917) became the standard references on the North American mosquitoes. This 4 volume treatise contained many descriptions and/or keys to the 4th stage larvae, adults, eggs, and male genitalia of the mosquitoes known to occur in North America. Headlee (1921), Hardenburg (1922), Herms (1923), Beyer (1923), and others constructed anopheline keys based on the monograph, but included personal observations such as Headlee's description of the antenna of *crucians* [=*bradleyi*]. Root (1922a,b) developed an anopheline classification using adult, 4th stage larvae, and male genitalia characters. Root's work represented the most natural classification of the United States anophelines published to that time.

In 1924, Root found that *crucians* larvae collected in Lee County, Georgia, differed from those collected in marshes near the Chesapeake Bay. Those from the marsh were like the *crucians* that Smith, Howard, Dyar and Knab, Headlee, and others had been collecting and describing for several years. However, the *crucians* in Lee County more closely resembled *quadrimaculatus* Say and *punctipennis* (Say). From this, Root concluded that *crucians* actually consisted of a freshwater race and a brackish water race, capable of being differentiated in the 4th larval stage but indistinguishable as adults.

Russell (1925) published an excellent paper describing the 4th stage larvae of the common freshwater anophelines of the southern United States. He delineated and categorized the dorsal larval chaetotaxy useful in anopheline identification. He recognized the distinctiveness of setae 0, 2 on abdominal segments IV - V. Root (1929) published the first key separating *crucians* into 2 races. Bradley (1932a), apparently unaware of Root's 1929 key, described a *crucians* variety collected in Florida which would not key out in Russell's 1925 key. In 1936, Bradley, in a key to the 4th stage anopheline larvae of the southern United States, included 2 races of *crucians*.

Bellamy (1939), collecting in southern Georgia, found anopheline larvae that resembled the brackish water race of *crucians*. The collections were made 50 - 150 miles from the coast, and in fresh water. King, after examining these specimens, and reexamining the other 2 races, confirmed the presence of another variety related to *crucians*. King (1939) established the following taxonomic

status for *crucians* and related varieties: *Anopheles crucians* var. *bradleyi* King for the brackish water variety, *Anopheles crucians* var. *georgianus* King for the one Bellamy discovered, and *Anopheles crucians* var. *crucians* Wiedemann. King (in King *et al.* 1942) raised the varieties to full species.

Miles (1945) tabulated the 4th stage larval chaetotaxy of *bradleyi*, *georgianus* and *punctipennis* presented by previous investigators, and Bickley (1945) and Dodge (1946) added further observations separating the species. Roth (1945) studied the variations and aberrations of setal branching within the genus *Anopheles* and observed structural anomalies of the inner [2-C] and outer [3-C] clypeals on *crucians* larvae. Few variations or anomalies were observed on *bradleyi* or *georgianus* larvae, probably because of the few specimens examined.

Early larval stages received little attention by the anopheline investigators of the early 1900's. Russell (1925) made some observations on early instars of *crucians*, but did not continue these studies. Hulburt (1941) first constructed a key to separate 1st stage *crucians* larvae from the other common anophelines in the southern United States. Breeland (1951) discussed the early stages of the 3 common *Anopheles* in southern Georgia, but did not include *bradleyi* or *georgianus*. In 1963 and 1966, Dodge published keys to the larval stages of North American Culicidae, but did not treat the *crucians* subgroup in detail.

The pupae of North American anophelines were usually dismissed as uninteresting, and of little taxonomic use. King (1939) briefly described the pupae of *bradleyi*, *crucians* and *georgianus*. Knight and Chamberlain (1948) developed a chaetotaxy system for pupae, but did not discuss the *crucians* subgroup. In 1949, Penn and Darsie, independently, published keys illustrating and differentiating the pupae of *bradleyi*, *crucians* and *georgianus*. The pupal chaetotaxy of this subgroup has not received recent consideration.

The egg of *crucians* [=*bradleyi*] was first illustrated by Mitchell in 1907. Howard, Dyar and Knab used Mitchell's figures in Volume II of their monograph, but switched the labels on the figures of the eggs of *crucians* and *punctipennis*. Bellamy and Repass (1950) compared the eggs of *crucians* and *georgianus* and found that regardless of the overlap between them, eggs from each species produced only progeny of that species. Breeland (1953) also described egg variations in *crucians*. Vargas (1941) described *bradleyi* eggs.

Felt (1904) first described the male genitalia of some North American anophelines, and Howard, Dyar and Knab (1912-1917) included illustrations of the male genitalia, but the illustrations were too small to be useful. Root (1923) published drawings of the male genitalia that were taxonomically useful in separating some *Anopheles* species. King (1939) illustrated the claspette of *crucians* and the related varieties. However, Ross and Roberts (1943), Matheson (1944), Roth (1944), Carpenter *et al.* (1946) and Carpenter and LaCasse (1955) presented only general illustrations of the male genitalia of *crucians*.

Cytogenetic studies on the *crucians* subgroup were initiated in 1965 (Kitzmiller *et al.*, in Wright and Pal [Ed.] 1967). Preliminary results indicated the *crucians* subgroup was closely related to the *maculipennis* complex of North America. Kreutzer *et al.* (1970) published chromosomal maps indicating *bradleyi* and *crucians* were closely related, probably differing by 5 or less paracentric inversions. Concurrent hybridization studies showed at least partial reproductive isolation (Kreutzer and Kitzmiller 1971).

Bionomics. It was impossible to separate many of the early publications into either taxonomic or ecological categories. Entomologists in the early 1900's were often unable to develop an ecological study without first constructing descriptions and/or keys for the species involved. However, several excellent ecological studies were conducted during this time. Most of the early investigations were made in Atlantic coastal plain areas. One of the first workers to mention *crucians* was Howard (1896). In a treatise on household insects, he listed *crucians* as one of the species which would enter dwellings in search of a blood meal. Dyar (1902) collected adult *crucians* [=*bradleyi*] at Bellport and Amaganset, Long Island, New York, but was unable to locate the larvae. He did not survey brackish habitats for anopheline larvae. However, Smith (1904) found immature *crucians* [=*bradleyi*] in the brackish waters along the New Jersey coast. Grossbeck (1913) and Brehne (1913), in independent studies, also reported it in salt marsh habitats.

In 1918, Metz studied the ecology and ethology of adult and larval *crucians* in a freshwater swamp near Montgomery, Alabama. The swamp was about 3 km long and had a ditch emptying refuse from a chemical plant into it at its upper end. Collections from the swamp consisted almost entirely of *crucians* larvae, which were not found in the immediate vicinity outside the swamp. In other studies conducted in 1918, Metz (1919b) found the diet of anopheline larvae consisted of a heterogenous mixture of plants and animals. Little preference was observed between living or dead organisms. However, Barber (1927) reported that dead organic matter was not as desirable as live, and that algae, bacteria, and infusoria were staple ingredients in the diet of most larvae. Metz (1919b) also showed that most *Anopheles* larvae preferred water that was free of pollution, but that *crucians* larvae thrived in waters with a high mineral content. Metz concluded that *crucians* exhibited a marked difference in its ovipositional site selection, as well as in physiological adaptability, from *punctipennis* and *quadrimaculatus*. The acidity of water inhabited by *crucians* larvae was determined by Boyd (1929), Frohne (1939), Fletcher (1946), and Vogt (1947) to be between pH 4.0-8.9. Renn (1941) discussed the feeding mechanism of *crucians* and *quadrimaculatus*. He found that larvae utilized 2 methods of feeding and were able to adopt whichever method best suited the situation.

One species of the subgroup, *i.e.*, *bradleyi*, inhabits brackish water. Griffitts (1921, 1928a,b) found *crucians* [=*bradleyi*] larvae abundant in salt marshes along the Atlantic coast and Chapman (1959) reported *bradleyi* larvae from New Jersey salt marshes with a salinity above 50 percent. Knight (1965) determined the chemical composition of the soil underlying brackish water habitats in North Carolina. More recently, LaSalle and Knight (1973, 1974) studied the effects of ditching on salt marsh mosquitoes, including *bradleyi*.

Behavioral observations and studies on members of this subgroup are numerous. Some early records on adult activity are Smith (1904) and Headlee (1921). More recently a number of authors have investigated host selection and the flight activity of *bradleyi* and *crucians* (Bidlingmayer 1967, 1974; Edman 1971; Knight 1954; Nayar and Sauerman 1970a,b, 1974; Schaefer and Steelman 1969).

Host-pathogen relationships involving *crucians* were first recognized by Couch (1945). He recovered and described *Coelomomyces dodgei* Couch and *C. lativittatus* Couch from *crucians* larvae collected in Georgia. In addition,

C. punctatus Couch, *C. bisymmetricus* Couch, and *C. quadrangulatus* Couch were found in *crucians*. A *Coelomomyces* species was also recovered from immature *bradleyi* (Chapman, Woodard *et al.* 1970), and *C. quadrangulatus* was found in a *georgianus* larva from Georgia (Couch & Dodge (1947). Species of 2 protozoan genera, *Nosema* and *Thelohania* (Microsporidea: Nosematidae), have been found in *bradleyi* and *crucians* larvae (Chapman, Clark and Petersen 1970). Mermithid nematodes (Nematoda: Mermithidae) belonging to the genera *Gastromermis* and *Romanomermis* have been recovered from *bradleyi* and *crucians* larvae (Petersen and Chapman, 1970, Petersen and Willis 1971) and may prove to have biological control potential.

Distribution. Table 1 depicts the general distribution of the subgroup (Carpenter and LaCasse 1955, Carpenter 1968, 1970, 1974; King *et al.* 1960). Distribution is further discussed under each species.

Table 1. DISTRIBUTION OF THE *AN. CRUCIANS* SUBGROUP.

	An. crucians	*An. bradleyi*	*An. georgianus*
Alabama	X	X	X
Arkansas	X		
Connecticut	X		
Delaware	X	X	
District of Columbia	X		
Florida	X	X	X
Georgia	X	X	X
Illinois	X		
Indiana	X		
Iowa	X		
Kansas	X		
Kentucky	X		
Louisiana	X	X	X
Maryland	X	X	
Massachusetts	X		
Mississippi	X	X	X
Missouri	X		
New Jersey	X	X	
New Mexico	X		
New York	X	X	
North Carolina	X	X	X
Ohio	X		
Oklahoma	X		
Pennsylvania	X		
Rhode Island	X		
South Carolina	X	X	X
Tennessee	X		
Texas	X	X	
Virginia	X	X	

Table 1 (Continued)

	An. crucians	*An. bradleyi*	*An. georgianus*
Bahamas	X		
Belize	X		
Dominican Republic	X		
Guatemala	X		
Haiti	X		
Honduras	X	X	
Jamaica	X		
Mexico	X	X	
Nicaragua	X	X	
Puerto Rico	X		

Medical importance. The medical significance of *crucians* and the *crucians* subgroup remains unresolved. Beyer *et al.* (1902) considered *crucians* [?species] a capable malaria vector, but Felt (1904) disregarded it as such. King (1916) and Mitzmain (1916a)experimentally proved *crucians* a capable vector of *Plasmodium falciparum* (Welch 1897) and *P. vivax* (Grassi and Feletti 1890). Natural malarial infections in *crucians* were reported in Florida (Metz 1919a) and in Louisiana (Mayne 1919). Dyar (1922) considered *crucians* a serious malaria vector.

Metz (1918) and Mayne (1926b)found that the incidence of malaria in the human population was low where *crucians* was the prevalent anopheline present. Bull and King (1923), Barber *et al.* (1927) and Edman (1971) reported *crucians* preferred large and small vertebrates to humans as sources of blood meals. In the only laboratory study involving *bradleyi*, Boyd *et al.* (1936) demonstrated *falciparum* transmission.

In an endemic malaria zone in South Carolina, Sabrosky et al. (1946) reported a higher incidence of malaria infection in *crucians* than in *quadrimaculatus* Frohne *et al.* (1950) continued this study, but reached no definite conclusions. The relationship of *crucians* and the *crucians* subgroup to avian malaria was investigated inconclusively by Hunninen et al. (1950), Hunninen (1951), Atchley (1952) and Young and Burgess (1961).

Kissling *et al.* (1955) and Chamberlain *et al.* (1958) suggested *crucians* might be a vector of certain arboviruses in the United States. Cache Valley arbovirus (Holden and Hess 1959) and Tensaw arbovirus (TV) (Coleman 1969), members of the Bunyamwera group of arboviruses (Casals and Whitman 1960), have been isolated from the *crucians* subgroup, *i.e.*, *bradleyi* and/or *crucians*. Chamberlain, Sudia and Coleman (1969) reported that in southern Alabama 74.4 percent of the TV isolates were from *crucians*, and Sudia, Coleman and Chamberlain (1969) demonstrated TV transmission by *crucians*. Stamm *et al.* (1962) Sudia *et al.* (1968), and Chamberlain, Sudia, Work *et al.* (1969), conducting arbovirus studies in the southeastern United States, recovered Eastern encephalitis (EEE), Venezuelan encephalitis (VEE) and California encephalitis (LaCrosse) virus strains from *crucians*.

In addition, 2 other California group arboviruses (Keystone and Trivittatus) were isolated from *crucians* in Florida (Taylor *et al.* 1971, Wellings *et al.* 1972). Cache Valley virus was recovered from a mixture of *bradleyi* and *crucians* specimens in the Del-Mar-Va Peninsula (Buescher *et al.* 1970). The significance of these arbovirus isolations is discussed later.

SYSTEMATIC TREATMENT

Subfamily Anophelinae. The subfamily Anophelinae consists of 3 genera and 6 subgenera (Reid 1968). In this paper, only the genus *Anopheles* Meigen 1818, with over 360 species widely distributed in the world, is discussed.

Genus *Anopheles*.* Characterized by the following: ADULT. Scutellum rounded, with continuous row of setae; wing vein M after the crossvein and vein Cu_1 curved or straight, not wavy; male maxillary palpus club-shaped; male with one large claw on foreleg. PUPA. Trumpet short, open, with margin having at least one cleft of varying width and depth; seta 9 simple, spinelike, inserted on posterior corners of abdominal segments II - VII; seta 2-P ventral. LARVA. Seta 4-P nearer to 5,6,7-P than to 1,2,3-P; 1-M not palmate; spiracular lobe rarely with stigmal process on median dorsal valve, without fringe setae on ventrolateral valves.

The genus *Anopheles* is the only representative of the subfamily in the United States. Six subgenera are recognized worldwide: 1) *Anopheles* Meigen 1818 - Cosmopolitan; 2) *Cellia* Theobald 1902 - Eastern Hemisphere; 3) *Kerteszia* Theobald 1905 - Neotropical; 4) *Lophopodomyia* Antunes 1937 - Neotropical; 5) *Nyssorhynchus* Blanchard 1902 - Neotropical; 6) *Stethomyia* Theobald 1902 - Neotropical. *Anopheles* and *Nyssorhynchus* are represented in the United States by 16 species (Table 2). Carpenter and LaCasse (1955) summarized the fauna north of Mexico and Carpenter (1968, 1970, 1974) and Darsie (1973) have updated this work.

Reid and Knight (1961) revised the divisions of the subgenus *Anopheles* established by Edwards (1932). They based their revision in part on the shape of the pupal trumpets. Those species with pupae bearing wide funnel-shaped trumpets were considered the laticorn section; those with simple semitubular type were placed in the angusticorn section.

**Anopheles* Meigen. 1818. System. Beschr. Europe. Zweifl. Insekten. 1:10. There are 23 synonyms for this genus, a complete list is presented in Stone, Knight and Starcke 1959.

Table 2. CLASSIFICATION OF THE ANOPHELINE MOSQUITOES NORTH OF MEXICO.

SUBFAMILY Anophelinae

GENUS *Anopheles*

SUBGENUS *Anopheles*

Anopheles series
(*maculipennis* species group)
atropos Dyar and Knab 1906
earlei Vargas 1943
freeborni Aitken 1939
occidentalis Dyar and Knab 1906
quadrimaculatus Say 1824
walkeri Theobald 1901

(*plumbeus* species group)
barberi Coquillett 1903
judithae Zavortink 1969

(*pseudopunctipennis* species group)
franciscanus McCracken 1904
pseudopunctipennis Theobald 1901

(*punctipennis* species group)
bradleyi King 1939
crucians Wiedemann 1828
georgianus King 1939
perplexens Ludlow 1907
punctipennis (Say) 1823

SUBGENUS *Nyssorhynchus*

albimanus Wiedemann 1820

Briefly, their classification is:

Laticorn section	Angusticorn section
Arribalzagia series	*Anopheles* series
Christya series	*Cycloleppteron* series
Myzorhynchus series	*Lophoscelomyia* series

The *Anopheles* series, the only series represented in the United States, is thought to be the most advanced of the 6 series. This series primarily occurs in the Nearctic, Oriental and Palearctic regions, but is also represented by a few, mostly mountainous species in the Neotropical region, and

Table 3. NORTH AMERICAN SPECIES GROUPS IN THE *ANOPHELES* SERIES (AFTER REID AND KNIGHT 1961).

Character	*maculipennis* sp. group	*plumbeus* sp. group	*pseudopunctipennis* sp. group	*punctipennis* sp. group
Distribution	Holarctic	Holarctic	Nearctic - Neotropical	Nearctic
Pronotal lobes	Without scales	Without scales	With or without scales	With scales
Wings	Dark, with clusters of darker scales	Dark, or with pale fringe spots	Pale spots present	Pale spots present
Legs	Dark or with pale marks, tarsi dark	Some pale marks, tarsi dark	Pale marks, tarsi usually dark	Pale marks tarsi dark
Scutal integument	Center often gray	Center often gray	Center gray, sides dark	Center gray, sides often dark, or mottled gray-black
Male				
parabasal spines	2	2	2	2
leaflets	Present	Absent	Present	Present
Larva				
3-C	Usually many branches	Simple or few branches	Simple	Many branches

one species, *concolor*, in the Ethiopian region. *Anopheles* series characters are: 1) Abdomen and coxae lack scales; 2) Leg scales uniformly colored, tarsi rarely banded; 3) Forefemur slender, not swollen on basal half; 4) Vertex scales narrow or very narrow; 5) Female palpus thin, not shaggy; and 6) Larval seta 11-P usually simple.

The *Anopheles* series is as diverse morphologically as geographically and has been divided into groups (Reid and Knight 1961). This diversity ranges from small, fragile, drab species to large, ornate species, and is conducive to subdivision. There are 8 groups recognized, with 4 occurring in the United States (Table 3). Kitzmiller *et al.* (1967) considered *punctipennis* a member of the *maculipennis* species group, yet they found *punctipennis* quite distinct and with the least affinity to this group. This distinctness supports the decision of Reid and Knight (1961) to consider *punctipennis* in a separate species group from the *maculipennis* species group.

Anopheles bradleyi, *crucians*, and *georgianus* belong in the *punctipennis* species group. These 3 species will be shown later to be morphologically similar, particularly the early larval instars and adult stages. Based on this evidence, *i.e.*, morphological similarity, and the criteria established by King (1939), these 3 species should be considered a species subgroup within the *punctipennis* species group.

ANOPHELES (ANOPHELES) CRUCIANS SUBGROUP

The *crucians* subgroup can be differentiated from other members of the group by the following characters: ADULT. *Head*. Palpus with 3 pale scaled areas (apical and basal portion of segments 3, 4 and 5 entirely pale-scaled). *Thorax*. Scutal integument mottled gray-black. *Wing*. Costa entirely dark-scaled except fringe at tip; anal vein with alternating pale and 3 dark-scaled areas; midsection of vein always dark. *Male genitalia*. Claspette lobes fused, triangular, with 3-5 apical and external setae, all acute; lobes on tergum 9 long, slender, apically rounded. PUPA. Only *crucians* can be readily separated from the other species by 0 on III-V usually having 3 or more branches. See the key for *bradleyi* and *georgianus*. 4TH STAGE LARVA. (*crucians*) - setae 0,2 on III-V nearly equal in size and multibranched; (*bradleyi*) - 1-III, VII, 0.50 - 0.66 smaller than 1 on IV-VI, 5-I much longer than 4-I, 1-P usually simple; (*georgianus*) - 1-III, VII rudimentary, 1 on IV-VI well developed.

Keys to the anopheline species in the southeastern United States appear in the Appendix.

KEYS TO THE *ANOPHELES CRUCIANS* SUBGROUP.

MALE GENITALIA*

1. Claspette usually with 3 setae on each side (Fig. 7). . *bradleyi*
Claspette usually with 4 setae on each side (Fig. 1). . *crucians*
. . . . . (Fig. 13) *georgianus*

PUPAE

1. Seta 0-IV large, usually with 2 - 6 branches; 0-V large, with 3 - 11 branches (Fig. 2) . . . . . *crucians*
Setae 0-IV,V small, simple or bifid, rarely trifid 2

2.(1) Seta 1-IV with 5 - 9 branches (usually 5 - 6); 1-V with 3 - 6 branches; 5-IV with 5 - 10 branches; 5-V with 3 - 8 branches; 5-VI with 3 - 5 branches (Fig. 8) . . *bradleyi*
Seta 1-IV with 9 - 14 branches; 1-V with 6 - 10 branches; 5-IV with 12 - 17 branches; 5-V with 8 - 16 branches; 5-VI with 9 - 13 branches (Fig. 14) . . . . . *georgianus*

LARVAE

1. Setae 0 on IV-V with 4 - 13 branches, nearly equal in size to 2 on IV-V; 8-III with 6 - 12 branches; 13-III with 6 - 12 branches (Fig. 3) . . . . . *crucians*
Setae 0 on IV-V simple, or with 2 - 3 branches, much smaller than 2 on IV-V; 8-III with 2 - 6 branches; 13-III with 4 - 8 branches 2

2.(1) Seta 5-II with 5 - 9 branches (usually 5 - 6); 9-III with 5 - 9 branches (usually 5 - 6); 11-I with 4 - 6 branches; 1-III appearance more like 1-IV than 1-II (Fig. 9) . . . . . *bradleyi*

Seta 5-II with 7 - 14 branches (usually 9 - 11); 9-III with 7 - 11 branches (usually 7 - 9); 11-I with 6 - 10 branches; 1-III appearance more like 1-II than 1-IV (Fig. 15) . . . . . *georgianus*

*Male genitalia characters are reliable only on 70 - 75 percent of specimens and should be confirmed by associated immature skins.

ANOPHELES (ANOPHELES) CRUCIANS WIEDEMANN

Anopheles crucians Wiedemann 1828. TYPE: Adults, Pennsylvania and New Orleans, Louisiana. Lectotype: Female, New Orleans (Orleans Parish), Louisiana, designation by Belkin (1968).

Synonymy. *Anopheles crucians* of Howard 1896 (distribution), 1900a (distribution), 1900b (A*, distribution), 1902 (A*, distribution in part); Theobald 1901 (A*, distribution in part), 1907 (L*, distribution in part), 1910; Giles 1900, 1902 (distribution in part); Coquillett 1900 (A), 1906 (A); Blanchard 1905 (A*, distribution in part); Ludlow 1906 (A); Dyar 1905, 1906, 1922 (distribution in part), 1928 (♂*, L*); Howard, Dyar and Knab 1912-1917 (A*, ♂*, L*, E, distribution in part); Christophers 1913, 1924; Mitzmain 1916a (malaria); King 1916, 1921 (malaria); Metz 1918 (A, L), 1919a (malaria); Mayne 1919, 1926b (malaria); Chandler 1921 (distribution); Root 1922a,b (♂*); Komp 1923 (A*), 1941 (A*, L), 1942 (A*, ♂*, L*); Hegner *et al.* 1923 (A*); Barber *et al.* 1924 (A, L, P); Russell 1925 (L*); Clark 1926 (distribution); Covell 1927 (A, L, distribution in part); Barber *et al.* 1927 (malaria); Griffitts 1928a,b (distribution in part); Boyd 1929, 1930 (bionomics); Boyd and Weathersbee 1929 (bionomics); Boyd and Aris 1929 (malaria); Matheson 1929, 1944 (A*, L*, distribution in part); Perez 1930 (A, L); Edwards 1932 (A, distribution in part); Matheson 1932 (A*, L, distribution in part); Turner 1933 (distribution); Quinby 1938 (distribution); Tulloch 1939 (A, L); Bradley and King in Moulton 1941 (A, L, bionomics); Komp in Moulton 1941 (A, L); Rozeboom in Moulton 1941 (A); King and Bradley in Moulton 1941a (A*, ♂*, L, distribution); King and Bradley in Moulton 1941b (A, L, distribution); Simmons in Moulton 1941 (malaria); Renn 1941; Hurlbut 1941 (L); Huffaker 1942 (A); King *et al.* 1942 (A*, P*, L, sp. status); Bellamy 1942 (L); Kumm 1942 (distribution); Carr and Hill 1942 (A, L, malaria); Frohne 1942 (L); Schmitt 1942, 1943 (L, distribution in part); Roth 1944 (♂*), 1945 (L*); Hill and Hill 1945, 1948 (distribution in part); Bickley 1945 (L); Couch 1945 (L, parasitism); Sabrosky *et al.* 1946 (malaria); Fletcher 1946 (L); Michener 1947 (A, L); Bates 1949a (A); Darsie 1949 (P*); Frohne and Hart 1949 (A); Freeborn in Boyd 1949 (A, L); Penn 1949 (P*); Vargas and Palacios 1950, 1956 (A*, ♂*, L*); Bellamy and Repass 1950 (E*); Frohne *et al.* 1950 (malaria); Breeland 1951 (L*), 1953 (L*, E*); Knight 1954 (A); Ferguson and McNeel 1954 (distribution); Horsfall 1955 (distribution, medical); Carpenter and LaCasse 1955 (A*, ♂*, L*, bionomics, distribution); Bargren and Nibley 1956 (A, bionomics); Love and Smith 1958 (A); Favorite and Davis 1958 (A); Chamberlain *et al.* 1958 (arbovirus); Stone *et al.* 1959 (distribution); Foote and Cook 1959 (A*, L*, medical); Provost 1959 (A, bionomics); Holden and Hess 1959 (arbovirus); Chapman 1959 (L); Stojanovich 1960 (A*, L*); King *et al.* 1960 (A*, ♂, L, bionomics, distribution); Tinker and Stojanovich 1962 (P*); Forattini 1962 (distribution); Clements 1963; Dodge 1963, 1966 (L*); Belkin *et al.* 1966 (distribution); Porter 1967 (distribution); Bidlingmayer 1967, 1974 (A, bionomics); Belkin *et al.* 1966 (bionomics); Carpenter 1968, 1970, 1974 (distribution); Carestia and Horner 1968 (A); Smith and Enns 1968 (distribution); Peterson *et al.* 1968 (L, parasitism); Sudia *et al.* 1968 (arbovirus); Sudia, Coleman and Chamberlain 1969

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*An illustration is presented

(arbovirus); Sudia, Newhouse and Chappell 1969 (arbovirus); Coleman 1969 (arbovirus); Hardin and Poolson 1969 (distribution); Edman and Bidlingmayer 1969 (A, bionomics); Knight and Wonio 1969 (A, ♂, L*, P); Chamberlain, Sudia and Coleman 1969 (arbovirus); Chamberlain, Sudia, Work *et al.* 1969 (arbovirus); Gladney and Turner 1968 (distribution); Belkin *et al.* 1970 (A*, ♂*, L*, P*, distribution); Kreutzer and Kitzmiller 1970, 1971 (L, genetics); Kreutzer *et al.* 1970 (A, L, genetics); Chapman, Clark *et al.* 1970 (L, parasitism); Sublette and Sublette 1970 (distribution); Hayes 1970 (distribution); Gerberg 1970 (A); Petersen and Chapman 1970 (L, parasitism); Chapman, Woodard *et al.* 1970 (L, parasitism); Stryker and Young 1970 (A); Harden *et al.* 1970 (A); Sudia *et al.* 1971 (A, arbovirus); Parsons and Howell 1971 (distribution); Bickley *et al.* 1971 (distribution); Bertram 1971 (distribution); Edman 1971 (A, bionomics); Petersen and Willis 1971 (L, parasitism); Chapman *et al.* 1972 (L, parasitism); Chapman and Glenn 1972 (L, parasitism); Siverly 1972 (A*, L*, distribution); Grothaus and Jackson 1972 (A); Roberts 1972 (A); Schreck *et al.* 1972 (A); Blume *et al.* 1972 (A); Parsons *et al.* 1972 (distribution); Cupp and Stokes 1973 (A); Siverly and Shroyer 1974 (♂*); Tempelis 1975 (A, bionomics); Wolff *et al.* 1975 (distribution); Mullen 1975 (A).

?Anopheles pictus and *ferruginosus* of Coquillett 1900 (A).

?Anopheles punctipennis of Theobald 1905 (A); Prout 1909; Johnson 1919.

Anopheles crucians - freshwater race or form of Root 1924b,c (L), 1929 (L*); Matheson 1932 (A, L); Bradley 1936 (L); Dozier 1936 (A, L); Herms and Gray 1940 (A).

Anopheles crucians - inland or freshwater variety of Bradley 1932a (L); Boyd and Stratman-Thomas 1934 (A, malaria); Boyd *et al.* 1936 (A, malaria); King *et al.* 1939 (A*, P*, L).

Anopheles crucians var. *crucians* of King 1939 (A, ♂* in part, L* in part, P); Vargas 1940b (L).

Anopheles crucians crucians of Ross and Roberts 1943 (A*, ♂*, L*); Schoof and Ashton 1944 (distribution); Quinby 1941 (L); Matheson *in* Moulton 1941 (A, malaria); Russell *et al.* 1943 (A, L); Carpenter *et al.* 1946 (A*, ♂*, L*); Brennan 1951 (distribution); Yamaguti 1952 (A*, ♂*); Bargren 1953 (L).

Anopheles bradleyi-crucians complex of Schaefer and Steelman 1969 (A, bionomics); Buescher *et al.* 1970 (arbovirus).

Description. Females are distinguished from other North American species (except *bradleyi* and *georgianus*) by the last palpal segment being entirely pale scaled, segment 3 pale scaled basally, segment 4 pale scaled apically and basally; costa without pale spots except at tip; and 1A with 3 dark scaled areas (basally, medially, and apically). The pupa has seta

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*An illustration is presented

0 on IV-V with 2 - 11 long branches. The larva has 2-C simple; 3-C with more than 20 branches; and 0 on III-V with 4 - 13 branches and nearly equal in size to 2 on III-V.

FEMALE. (Fig. 1). *Head.* Vertex with pale erect scales expanded and notched at tip; interocular space narrow, with pale short scales and elongate pale frontal setae; antennal pedicel and flagellomere one with a few mixed scales; palpus with erect scales on basal 0.33 and decumbent scales distally, scales dark except narrow pale band on base of segment 3, narrow apical and basal bands on 4, and 5 entirely pale scaled; proboscis dark with decumbent scales, forefemur/proboscis ratio nearly 1:1. *Thorax.* Anterior promontory scales pale, elongate; scutum integument dark brown and pale with acrostichal and median prescutellar lines darker, setae on above 3 lines often appear gold, anterior promontory, acrostichal, dorsocentral, lateral prescutal, fossal, antealar, and supraalar groups of setae long and dark; scutum with long thin pale scales; prescutellar space with fine pale setae except immediately cephalad to scutellum; scutellum with long dark setae and short, thin pale scales; anterior pronotum with dark scales dorsally and with 8 - 10 long, dark setae; other pleural setae are, 5 - 10 (7,8) propleural, 2 - 5 (3,4) spiracular, 3 - 6 prealar, 3 - 4 upper and 3 - 7 lower mesepisternal, 6 - 12 upper and 0 lower mesepimeral setae. *Wing.* Costa black scaled to apical pale spot, subcosta dark; Radius dark scaled except for small area of pale scales near base at R_s; R_s with pale scales medially; R_1 dark except for pale tip; R_{2+3} pale scaled medially; R_2 dark except distal 0.20 pale; R_3 dark with pale scaled area near distal end, distal 0.20 dark scaled; R_{4+5} usually mixed gray, basal and preapical areas dark, tip pale; Media with basal and median parts dark, apical portion often gray or light gray; M_{1+2} and M_{3+4} with apical and basal 0.25 dark, Cubitus dark, *i.e.*, black, medium to dark gray, or dark brown; basal 0.5 and apical 0.25 of Cu_1 dark scaled, median 0.25 pale scaled; Cu_2 medium gray or brown, usually not black; 1-A with basal, median and apical areas dark scaled, and pale areas on either side of median dark area; crossveins r-m, m-cu dark scaled, humeral crossvein without scales; fringe scales dark except for pale area extending from tip of R_1 to R_{4+5}, often interrupted by dark fringe at R_3. *Halter.* Knob dark scaled with sparsely scattered setae. *Legs.* Coxae without scales, upper midcoxa with 2 - 5 setae, the lower usually stouter than the upper; femora, tibiae and tarsomeres long, slender, and unicolorous dorsally and ventrally, with sparsely scattered setae and dark decumbent scales; apex of femur and base of tibia pale. *Abdomen.* Integument unicolorous dorsally and ventrally; numerous dark setae dorsally, medially and ventrally.

MALE. (Fig. 1). *Head.* Like female except palpus dark scaled with 2 apical segments flattened and club-like; antenna strongly plumose. *Genitalia.* Basimere with a few scales laterally and ventrally; 2 parabasal spines on tubercle; internal spine inserted on distal 0.5 of basimere; claspette lobes fused with 3 - 5 (usually 4) flattened setae situated in pairs, dorsal (lateral) pair nearly equal in size and shape, ventral pair with the most distal seta longer and stouter than other; distal end of aedeagus with 6 - 8 acute leaflets; 9th tergum with long, slender lateral lobes.

PUPA. (Fig. 2, Appendix Table 2). Integument usually tan to light brown. *Cephalothorax*. Seta 7 usually long and simple; 10 often simple, stout and long; 11, 0.50 - 0.75 as long as 10, with 4 - 11 branches; 12 nearly as long as 10 with 3 - 8 branches. *Trumpet*. Darkly pigmented, deep meatal cleft, meatus 0.33 as long as trumpet, often with small spiny spur on lateral rim of pinna. *Abdomen*. Seta 5-I with 1 - 5 branches (usually 2 - 4), as long as segment; 6-I with 3 - 11 branches (usually 5 - 8), up to 1.25 longer than segment; 0-II with 1 - 2 branches; 0 on III-IV with 2 - 6 branches; 0-IV rarely unbranched or with 7 branches; 0-V with 3 - 11 branches; 1 on II-VI well developed; 1-II with 5 - 18 branches, stem as stout as 1-III; 1-III with numerous branches (8 - 17); 1-IV with 8 - 21 branches, 0.5 as long as segment V; 1-V usually with 10 - 14 branches, 0.5 - 0.7 as long as segment VI; 1-VI usually with 6 - 12 branches, 0.50 - 0.66 as long as segment VII; 2-IV with 4 - 18 branches; 2-V with 3 - 9 branches; 3 on III-IV with 4 - 12 branches; 3-V with 3 - 7 branches, sum of branches of both 3-V, 8 - 13; 5-IV with 8 - 18 branches, 0.50 - 0.66 as long as segment V; 5-V with 4 - 17 branches, 0.50 - 0.66 as long as segment VI; 5-VI with 5 - 16 branches, 0.50 - 0.66 as long as segment VII; 5-VII with 2 - 11 branches, 0.50 - 0.66 as long as segment VIII; 6-II with 2 - 10 branches, 0.50 - 0.75 as long as segment; 6-III with 4 - 13 branches, 0.25 - 0.33 as long as segment; 6 on IV-V with 3 - 9 branches, 0.25 - 0.50 as long as respective segment; 7-I with 2 - 8 branches, 0.50 - 0.75 as long as 6-I; 7-IV with 1 - 4 branches, 0.20 - 0.25 as long as segment; 7-V with 1 - 6 branches, 0.20 - 0.25 as long as segment; 7-VI simple or bifid, 0.25 - 0.50 as long as segment; 7-VII simple or bifid, 0.50 - 0.75 as long as segment; 9 on III-VIII deeply pigmented; 9-IV, 0.50 - 0.66 longer than 9-III; 9-VII, 3 to 5.5 as long as wide; 10 on III-V with 2 - 6 branches, approximately 0.5 as long as following segment. *Paddle*. Refractile margin 0.55 - 0.80 as long as paddle; margin serrate on refractile portion with very fine hairs beyond to apex and for short distance on inner margin; 1-P simple or bifid, stout and attenuate; 2-P simple or bi- or trifid.

4TH STAGE LARVA. (Fig. 3, Appendix Table 5). *Head*. Darker than thorax and abdomen; antenna base approximately as wide as tip; antenna with numerous spines; 1-A with 4 - 10 branches (usually 4 - 5) inserted on basal 0.25; 2 and 3-A attenuated and serrated on one edge; 4-A with 4 - 6 branches; 2-C long, simple, rarely bifid, bases nearly always separated by less than diameter of an alveolus; 3-C with 20 to more than 40 broom-like branches; 3-C, 0.50 - 0.75 as long as 2-C; 4-C simple or with 1 - 4 distal branches; 5,6,7-C long, plumose, well developed with 12 - 25 branches; 11-C as long as antenna, with 20 to more than 60 branches. *Thorax*. Seta 1-P simple, bi- or trifid, 0.25 - 0.50 as long as 2-P; 2-P with 7 - 14 branches, arising from tubercle; 3-P simple, closer to 2-P than 1-P is to 2-P; 3-P nearly equal in size to 1-P; 4-P stout with 12 - 21 branches, arising from tubercle, closer to 5-P than to 3-P, 1.25 - 1.33 as long as 2-P; 5,6-P with common tubercle, 6-P simple and as long or longer than 7-P; 7,8-P well developed, nearly equal in length; 9,10,11,12 on P, M, and T arise from common tubercle on each segment; 9,10-P, M,T long, simple; 11-P,M,T short, simple; 12-P long, simple; 12-M short and simple; 12-T short with 1 - 4 branches; 13-P with 12 - 20 branches; 14-P with 5 - 11 branches; 1-M stout, well developed; 2,3,5-M usually simple and long;

4-M with 3 - 7 branches, caudal to 3 and 5-M; 6,7-M with 3 - 6 branches, 7-M less than 0.5 as long as 6-M; 14-M with 8 - 18 branches; 3-T with flattened leaflets; 5,7,8-T well developed and nearly equal in size; 6-T with 3 - 6 branches, less than 0.2 as long as 5-T; 13-T with 2 - 6 branches. *Abdomen.* Anterior tergal plates on I-VII approximately 0.25 width of segment; posterior tergal plates on III-VII, that on VII larger than rest; seta 0-II with 2 - 6 branches; 0-III with 4 - 6 branches; 0-IV with 4 - 9 branches; 0-V with 5 - 13 branches; 0-VI with 4 - 7 branches; 0 on VII-VIII with 3 - 5 branches; 0 on III-V nearly equal or equal in size to 2 on III-V; 0-VII approximately 0.66 as large as 0-III; 1-I with 3 - 8 flattened pale leaflets; 1-II with 7 - 21 leaflets; 1 on III-VI nearly equal in size, darkly pigmented, with 8 - 24 leaflets with serrate margins; 2-I with 4 - 9 branches; 2-II with 8 - 14 branches; 2-III with 6 - 14 branches; 2-IV with 5 - 16 branches; 2-V with 5 - 14 branches; 0,2 on III-V conspicuous; 3-VI caudal to I-VI; 4-V with 4 - 11 branches; 5-I with 5 - 9 branches; 5-II with 6 - 11 branches; 5 on III-V with 5 - 8 branches; 5-VI with 5 - 11 branches; 5-VII with 5 - 9 branches; 5-VIII with 4 - 8 branches; 6,7 on I-II well developed and nearly equal in length; 6-III well developed, at least 0.75 as long as 6-II, with 11 - 18 branches; 6 on IV-V with 2 - 3 branches, and approximately 0.75 as long as 6-III; 6 on VI-VII nearly equal in size, less than 0.2 as long as 6-V, and with 2 - 5 branches; 7-III with 2 - 7 branches, approximately 0.33 as long as 7-II; 8-II with 6 - 10 branches; 8-III with 6 - 12 branches; 8 on IV-V with 3 - 9 branches; 8 on VI-VII with 3 - 8 branches; 8 on III-IV nearly equal in size to 2 on III-IV; 9-I with 5 - 10 branches; 9-II with 6 - 11 branches; 9-III with 8 - 13 branches; 9 on IV-V with 9 - 12 branches; 9-VI with 7 - 11 branches; 9-VII with 3 - 7 branches; 9 on I-VI closer to 6 on I-VI than 5 on I-VI is to 6 on I-VI; 10 on I, III-VI simple or bifid, 10-III occasionally with 3 or 4 apical branches; 10 on I, III-V, 0.50 - 0.75 as long as the respective segment; 10-II with 2 - 6 branches; 10-VII with 2 - 8 branches; 11-I with 5 - 9 branches; 11 on II-IV, VII with 1 - 4 branches; 11 on V-VI with 2 - 4 branches; 11 on III-V approximately equal in size and caudal to 12 on III-V; 12-I with 1 - 4 branches, 12-II simple or bifid; 12 on III-V with 2 - 6 branches; 12 on VI-VII simple; 13-I with 2 - 4 branches; 13-II with 4 - 12 branches; 13-III with 6 - 12 branches; 13 on IV-V with 4 - 6 branches; 13-VI with 7 - 13 branches; 13-VII with 3 - 4 branches; spiracular lobe seta 1 with 4 - 7 branches; 2-S with 4 - 7 branches, inserted on pecten plate; 3,4,5-S minute; 6-S simple or bifid, approximately 0.5 as long as 1-S, 7-S minute, inserted at apex of spiracular valve; 8,9-S inserted caudally on spiracular lobe, 2 - 6 branches, approximately equal in length to 6-S; 11,12,13-S minute, medially and distally inserted on spiracular lobe; pecten with 9 - 11 long teeth and 8 - 10 shorter teeth grouped 2 or 3 together; 1-X usually longer than saddle.

Distribution. (Fig. 2). *Anopheles crucians* is primarily eastern North American in distribution and has been collected in all states east of the Mississippi River except Maine, Michigan, New Hampshire, West Virginia, Wisconsin and Vermont. It is most widely distributed in the southeastern and central Atlantic states, and probably occurs only in the south central and southern portions of New York, Pennsylvania, Ohio, Illinois and Indiana. In Kentucky and Tennessee, *crucians* is found primarily along the Mississippi and Ohio River drainages.

West of the Mississippi River *crucians* has been reported in 8 states, *i.e.*, Arkansas, Iowa, Kansas, Louisiana, Missouri, New Mexico, Oklahoma and Texas. It is not common in any of these except Texas and those states including portions of the Mississippi River drainage basin. Barber (1939) reported *crucians* from Artesia, New Mexico. Subsequently, Sublette and Sublette (1970) and Wolff *et al.* (1975) included it in the New Mexico fauna, but did not report recent collections. The Iowa and Kansas collections were made by a Federal government mosquito survey team (Communicable Disease Center 1951).

A total of 426♀, 108♂, 94P, 94WL, 104L and 51G specimens were examined, including the following from the United States:

Alabama: Waxahachee Creek, 30-X-1914, Le Prince 1♂. Paint Creek nr. Lock 12, 12-XI-1914, Le Prince, 1♀. Coosa Run, 21-IV-1915, 1♀. Mobile, 10-VI-1915, R. H. Von Ezdorf, 1♂; 11-VI-1915, Von Ezdorf, 2♀; 14-VI-1915, Von Ezdorf, 1♂; 17-VI-1915, Von Ezdorf, 11♀, 5♂; 22-VI-1915, Von Ezdorf, 9♀. Point Clear, 9-V-1953, W. L. Seal, 2WL. Arkansas: Stuttgart, 9-VIII-1914, J. A. Le Prince, 1♀. Plissville, V-1915, Von Ezdorf, 1♀. Delaware: Summit Bridge, 4-VIII-1966, R. W. Lake and J. Harrison, 1♀, 1♂, 1WL. District of Columbia: "D. C", 27-IV-1893, 1♀. Florida: "Fla.", Dyar, 2G; $1052B_3$, 1L; $1124B_4$, 14-VIII-1933, 1G. Miami, 11-XI-1921, G. F. Moznette, 22♀, 1♂, 1G; 1-X-1943, W. W. Wirth, 1♀; 9-XII-1942, W. W. Wirth, 1♀. Lake Alfred, 12-V-1928, Fla. Agr. Exp. Sta., 1♀. nr. Orlando, 3-XI-1931, G. H. B., 1G. Zellwood, 11-VIII-1932, 1♂, 1G; 28-II-1938, T. E. McNeel, 1♀, 1♂, 2P, 2L. Ocala, 11-IX-1933, CCC Survey, 4♀. Cocoa, 5-X-1937, T. E. McNeel, 1L. Lake Okeechobee, Warners Camp north shore, III-1903, J. H. Egbert, 1♀. Madison, "1956", 16-II-1938, W. V. King, 1♂, 1P, 1L; 27-IX-1945, Hampton, 1♀. Boca Raton, 8-IX-1943, 4♀; 12-XI-1943, 4WL. Camp Blanding, 27-II-1943, L. Roth, 1G; 31-III-1943, 2♂; 20-VI-1944, L. Roth, 2WL; 17-VII-1944, L. Roth, 1WL. Tyndall Air Field, 31-III-1943, L. Roth 1G; 7-IV-1943, L. Roth, 2G; 23-V-1945, 1♀. Dale Mabry Field, 2-IV-1943, L. Roth, 1G. Ft. Barr, 27-III-1943, L. Roth, 1G. Hendricks Air Field, 14-VII-1944, L. Roth, 1WL. Drew Air Field, 16-VIII-1944, L. Roth, 2WL. Perry, 6-V-1944, D. C. Thurman, 1♀. Tallahassee, 17-IX-1944, 1♀. Jacksonville, 25-IX-1944, D. C. Thurman, 1♀; Naval Air Station, 12-VI-1948, Comd. Hirst, 1♀. Starke, 10-X-1944, D. C. Thurman, 2♀. Lake City, 2-I-1945, 2♀. Gainesville, 30-I-1945, Hunt, 3WL. Leesburg, 2-IX-1945, Krueger, 2G. Live Oak, 3-VIII-1945, Braswell, 3♀, 1♂. Sumter Co., 14-VIII-1945, D. C. Thurman, 1♀. Marco, 5-VIII-1946, Love, 1♀. Florida City, 7-XI-1947, J. S. Haeger, 1WL, 1G. Upper Matecumbe, 7-XI-1947, J. S. Haeger, 1WL. Lower Matecumbe Key, 5-XII-1947, J. S. Haeger, 1WL; 11-II-1948, J. S. Haeger, 1WL. Dade Co., 10-II-1948, J. S. Haeger, 4WL. Boca Chica, 5-V-1958, J. H. Hirst, 1G. Big Pine Key, 11-III-1948, Johnson, 1♀. Suwannee River, 28-IV-1948, D. C. Thurman, 1♀. Green Cove Springs, "295", 28-XII-1951, K. L. Knight, 1P, 1L. Georgia: Brunswick, 23-V-1915, R. H. Von Ezdorf, 7♀. Waycross, 30-VIII-1915, Von Ezdorf, 6♀, 2♂; 31-VIII-1915, Von Ezdorf, 32♀, 3♂; 1-IX-1915, Von Ezdorf, 3♀. Quitman, "1957", 16-II-1938, W. V. King and R. E. B., 1♀, 1P, 1L; P. Bennett Farm, 20-VI-1974, T. G. Floore, 5♀, 2♂, 8P, 10L; Elsberry Farm, 21-VI-1974, T. G. Floore, 3♀, 2♂, 6P, 6L. Hinesville, 27-III-1941, G. H. B., 1L. Camp Stewart, 6-IV-1943, L. Roth, 3G; 16-VII-1944, 2WL. Ft. Benning, 29-X-1942, L. Roth, 1G; 26-VII-1944, 2WL. Chatham Air Field, 13-VI-1944,

1WL; 27-VI-1944, L. Roth, 1WL; 3-VII-1944, L. Roth, 4WL; 16-VIII-1944, L. Roth, 1WL. Camp Gordon, 26-VII-1944, L. Roth, 3WL. Hunter Air Field, 8-IV-1943, L. Roth, 1G; 10-VII-1944, 1WL. Moody Air Field, 8-VII-1942, L. Roth, 5G; 9-X-1942, L. Roth, 1G; XII-1942, 5WL; 11-I-1943, 1WL; 26-I-1943, L. Roth, 7WL; 17-III-1943, L. Roth, 1WL; 8-IV-1943, L. Roth, 5G; 26-IV-1943, L. Roth, 1WL; 17-VI-1944, L. Roth, 3WL; 20-VI-1944, L. Roth, 1WL; 10-VII-1944, L. Roth, 1WL; 28-VII-1944, L. Roth, 3WL. Louisiana: Mound, 4-VI-1914, D. L. Van Dine, 1♀; 27-IV-1915, Van Dine, 1♀; 4-V-1915, Van Dine, 1♀; 8-V-1915, Van Dine, 1♀; 17-V-1915, Van Dine, 1♂. Houma, V-1928, R. L. Turner, 1♀. Port Jackson, 3♀, 1♂. Alexandria, 16-IV-1943, W. W. Wirth, 1♀; 1-II-1943, W. W. Wirth, 1G; 8-II-1943, W. W. Wirth, 2WL; 20-IV-1943, W. W. Wirth, 1WL. Monroe, 28-I-1943, W. W. Wirth, 2WL. New Orleans, X-1943, R. H. Goodale, 5WL. Lake Charles, "130", 28-VII-1973, H. C. Chapman, 10P, 11L, 3G. Maryland: Laurel, VII-1903, Dr. Lyons, 1♀. College Park, 28-V-1933, F. C. Bishopp, 1♂; 28-VI-1933, F. C. Bishopp, 1♀; 25-VIII-1933, F. C. Bishopp, 1♀. Anne Arundel Co., Mayo, 3-VIII-1969, R. LaSalle, 3♀. Worcester Co., Hickory Point Rd., 25-X-1972, J. F. Burger, 1♀, 1P, 1L. Mississippi: Lucedela, VI-1915, Von Ezdorf, 11♀, 4♂. Greenville, 3-VIII-1914, J. A. Le Prince, 22♀, 1♂. Harmon, 29-V-1915, D. L. Van Dine, 1♂. Camp Van Dorn, 6-IV-1943, L. Roth, 1G. Flora, 6-IV-1944, 1WL; 19-VII-1944, 2WL. Missouri: Hannibal, 13-VIII-1941, L. D. Beadle, 1♀. Joplin, 13-IX-1942, A. B. Gurney, 1G. New Jersey: Nixon, 23-VIII-1966, P. H. Thompson, 2♀; 26-VIII-1966, P. H. Thompson, 2♀; 31-VIII-1966, P. H. Thompson, 2♀; 2-IX-1966, P. H. Thompson, 3♀; 7-IX-1966, P. H. Thompson, 7♀; 18-IX-1966, P. H. Thompson, 2♀. North Carolina: Hendersonville, 24-III-1913, W. B. W. Howe, 1♀. Roanoke Rapids, 21-24-VI-1914, J. A. Le Prince, 1♀. Ft. Bragg, 8-X-1926, R. L. Turner, 1♂; 23-XII-1942, F. N. Young, 1G; 25-VIII-1973, "135", T. G. Floore, 1♂; 25-VIII-1973, "136", T. G. Floore, 1♀, 1L; 25-VIII-1973, "138", T. G. Floore, 4♀, 1♂, 3P, 3L, 1G. Highlands, IV-V-1936, R. C. Shannon, 41♀, 1♂. "N.C.", An. 75., D. F. Ashton, 1P, 1L. Elizabeth City, 13-VI-1944, D. F. Ashton, 2WL. Maxton, 21-V-1943, A. B. Klots, 1♀; 22-V-1943, A. B. Klots, 1♀, 1♂; 8-IX-1943, A. B. Klots, 1♀. Camp Mackall, 5-VI-1944, L. Roth, 1WL; 10-VI-1944, L. Roth, 1WL; 26-VI-1944, L. Roth, 2WL; 1-IX-1944, L. Roth, 1WL. Goldsboro, 2-V-1969, R. LaSalle, 1♂, 2L; "122", 19-V-1973, T. G. Floore, 5♀, 1♂, 7P, 1WL, 7L, 2G; "123", 19-V-1973, T. G. Floore, 1♀, 1P, 1L; "124", 19-V-1973, T. G. Floore, 1P, 3WL, 1L. Aberdeen, 12-IV-1969, R. LaSalle, 4♂, 6L. Bladen Co., 15-VII-1972, T. G. Floore, 1♀. Benson, 15-VII-1972, T. G. Floore, 31♀, 21♂, 9P, 1WL, 13L, 4G. Wayne Co., Seymour Johnson AFB, 21-VII-1973, T. G. Floore, 2♀, 4P, 4L. Raleigh, N.C.S.U. Schenck Forest Farm, 16-X-1974, B. A. Harrison, 10♀, 4♂, 13P, 3L (BAH). South Carolina: Anderson, 20-V-1912, Jennings, 1♀. Columbia, 12-IX, W. H. Sligh, 1♀. Hartsville, 24-30-VI-1914, J. A. Le Prince, 5♀, 2♂; 26-30-VI-1914, J. A. Le Prince, 3♀. Ft. Jackson, 7-IV-1943, L. Roth, 1G; 21-IV-1944, L. Roth, 2WL. Myrtle Beach, 31-X-1943, 1WL; 27-VI-1944, L. Roth, 1WL; 10-VII-1944, L. Roth, 1WL; 27-VII-1944, 1WL. Charleston A.A.F., 17-VIII-1944, 1WL. Santee-Cooper Reservoir, 1-VIII-1944, C. W. Sabrosky, 1♀; 21-VIII-1944, Sabrosky, 1♀; 22-VIII-1944, Sabrosky, 2♀; 28-VIII-1944, Sabrosky, 1♀; 30-VIII-1944, Sabrosky, 1♂; 11-IX-1944, Sabrosky, 1♂; 14-IX-1944, Sabrosky, 1♀; 18-IX-1944, Sabrosky, 1♂; 20-IX-1944, Sabrosky, 1♂; 25-IX-1944, Sabrosky, 4♀, 2♂; 26-IX-1944, Sabrosky, 1♂; 27-IX-1944, Sabrosky, 1♀; 29-IX-1944, Sabrosky 5♀, 3♂; 31-X-1944, Sabrosky, 1♂; 10-XI-1944, Sabrosky, 4♀, 1♂; 17-XI-1944, Sabrosky, 1♀; 26-III-1945, Sabrosky, 2♂. St. Paul, 11-X-1944, Sabrosky

1♂. Manning, 7-XII-1944, Sabrosky, 1♂. Tennessee: Braden, 11-IX-1933, CCC Survey, 1♂. Obion Co., Walnut Log, IX-1933, L. L. Williams, Jr. 1♀. Texas: Buna, 14-XI-1902, Hopkin U.S., 1♀. Mission, 5-II-1924, R. L. Turner, 1♀; 5-IV-1924, R. L. Turner, 1♀. Brownsville, X-1923, R. L. Turner, 1♀. Virginia: Lake Drummond, 29-X-1906, H. S. Barber, 1♀, 1♂. Ft. Eustis, 20-V-1927, J. M. Hewilt, 6♀. Accomack Co., New Church, 19-VIII-1972, J. F. Burger, 4♀, 6♂, 11P, 11L; Assateague Island, 27-VIII-1972, J. F. Burger, 1P, 1L.

Anopheles crucians occurs in Mexico - Neuvo Leon, San Luis Potosi, Veracruz and Yucatan (Vargas 1940b, 1950, Vargas and Palacios 1950); Central America - Nicaragua, Belize [British Honduras], Guatemala (Clark 1926, Brennan 1951, Kumm 1942, Kumm and Ram 1941); and several Caribbean Islands - Jamaica, Cuba, Dominican Republic and Puerto Rico (Belkin *et al.* 1970, Hill and Hill 1948, Komp 1942, Kumm and Ram 1941, Pritchard and Pratt 1944 and Tulloch (1937a). Honduras is added to the list based on a single specimen seen during this study. Specimens examined from some of these countries were: Bahamas: New Providence, "BAH40", 3-4-VIII-1972, Chew and Rogers, 8♀ (UCLA); "BAH45", 5-VIII-1972, Rogers, 1L (UCLA). Belize: Sierra de Agua, IV-1946, A. J. Walker, 2♀ (UCLA). "BHA138", 1967, Mosq. Mid. Amer. 1♀ (UCLA). "BH366", 1967, Mosq. Mid. Amer., 1♀ (UCLA). Cuba: San Antonio de los Banos, 1-VII-1903, Dr. J. H. Pazos, 4♀. Cayamas, 5-VI-1904, E. A. Schwarz, 1♀; 11-VI-1904, E. A. Schwarz, 1♀; Baker, 1♀. "Cuba", #23, Carr, 3♀; "CUB9", Mosq. Mid. Amer., H. P. Carr, 3♀ (UCLA); "CUB15", VI-1939, H. P. Carr, 2♀ (UCLA); "CUB29", R. B. Hill, 3♂ (UCLA); "CUB34", R. B. Hill, 4♀ (UCLA). Pinar del Rio, 1938, Carr, 1G. Dominican Republic: Jayaco, 12-VI-1960, G.R.R., 7♀, 9♂, 10P, 10L, 3G. San Felipe, "RD0298", 13-IX-1971, T. Rogers, 1♀ (UCLA). Guatemala: Dept. Guate, 4 mi S. Amititlan, 9-XII-1949, J. M. Brennan, 1♀. Honduras: "HON99", Mosq. Mid. Amer., 1♀ (UCLA). Jamaica: St. Elizabeth Parish, II-1928, M. F. Boyd, 10♀; "JA357", Black River, 10-IX-1965, J. Belkin and W. Page, 1♀ (UCLA); "JA358", Black River, 11-IX-1965, J. Belkin and W. Page, 9♀ (UCLA); "JA794", Black River, 13-14-IX-1967, W. Page, 2♀ (UCLA). "Jamaica", Mosq. Mid. Amer., 6♀. St. Catherine Parish, Spanish Town, "JA6", 21-I-1964, H. Tucker, 1♀, 1P, 1L; "JA34", 6-II-1964, H. Tucker, 1♀, 1P, 1L (UCLA); "JA36", 6-II-1964, H. Tucker, 1♀, 1P, 1L (UCLA).

Taxonomic Discussion. Wiedemann's original description initiated confusion that accompanied this species and subsequently, the other members of the subgroup for several years. First, he incorrectly described the pale scaled areas on the palps, implying that they were white at the bases of all the segments, and in addition, he confused *crucians* wing pattern with that of *punctipennis* (see Howard, Dyar and Knab 1917: 1026). Secondly, Wiedemann listed 5 adults collected in Pennsylvania and New Orleans, Louisiana as types. Belkin (1968) resolved this latter problem by designating a specimen from New Orleans as lectotype. The Historical Review addresses the systematics of *crucians* and the subgroup chronologically.

The *crucians* subgroup adults can be separated from the other anopheline adults in the United States by the wing scale color pattern on vein 1A. This vein has 3 nearly equal length dark scaled areas (basal, median, and apical) and 2 pale areas on either side of the median dark area. Differentiating adult *crucians*, *bradleyi* and *georgianus* is difficult. Typically, *crucians*

have vein Cu dark out to the fork; this is also true for *georgianus* adults, but this vein is frequently pale on *bradleyi* (see Taxonomic Discussion for *bradleyi*). Vein R at R_s usually has a distinct, pale spot. No one character or set of characters were found to distinguish adult *crucians* from *georgianus* or *bradleyi* with Cu dark scaled. Adult morphological characters, *i.e.*, palpal coloration, wing color pattern, and thoracic setal arrangement, have so much intergradation that a key to the adults on external structures was not attempted (see Taxonomic Discussion for *bradleyi*). Adult male *crucians* are indistinguishable from male *bradleyi* and *georgianus* (except genitalia, see key).

The pupae in this subgroup are very useful taxonomic tools for species determination, yet were inadequately studied in the past. On *crucians*, setae 0 on IV-V are large, 0-IV usually with 2 - 6 branches and 0-V with 3 - 11 branches, respectively while on the other 2 subgroup members, they are small and simple or bi- or trifid distally. Seta 1-IV has 8 - 21 branches on *crucians* (cf. 5 - 9 *bradleyi*). Seta 2-IV usually has more than 7 branches on *crucians*, but fewer than 7 on *georgianus*. Seta 7-C is usually simple, but was occasionally bifid (FL30-4; Zellwood, FL 1961-8). Seta 8-C is usually simple, but was bifid on 4 specimens (F150-21; F150-22; F120-4 and F1120-5). Specimen 2201-3-L16, Accomack Co., VA had an extra seta 5-VII.

The 4th stage larva is the most reliable stage for separating *crucians* from the other United States anophelines, including the other subgroup members. Following Root's (1924b) discovery of 2 races [=species] of *crucians*, and his complete chaetotaxy descriptions of *quadrimaculatus* and *punctipennis* (1924c), Russell (1925) described the chaetotaxy of *crucians*. This was incomplete however, in that he did not describe the ventral setae. Fourth instars of *crucians* always have seta 0 on III-V equal to or slightly smaller than 2 on III-V and 0 on III-V is always multibranched as is 2 on III-V (cf. *bradleyi* and *georgianus*). Seta 0-IV has 4 - 9 branches, and 2-IV has 5 - 16. Seta 1-III on *crucians* is equal to or slightly subequal to 1-IV, however, some variations in relative size of these setae occur in both *crucians* and *bradleyi* (see *bradleyi*). For this reason, the relative size of 1-III is not a stable character, as indicated by many earlier authorities. However, seta 1 on III-IV is reliable in distinguishing *crucians* from *georgianus*. On *georgianus*, 1-III is approximately 0.2 the size of 1-IV, and morphologically different. Seta 8 on II-V always has 3 or more branches, usually 5 or more; 8-II has 6 - 10, 8-III with 6 - 12 branches compared to 3 - 5 and 2 - 6 on *bradleyi* and 2 - 5 and 3 - 4 on *georgianus*. In addition, seta 3-VIII has 8 - 12 branches, and 13-III has 6 - 12 branches (cf. *bradleyi* and *georgianus*).

The branching of 0 on IV-V and 2 on IV-V on the 3rd stage larvae is also dependable for separating *bradleyi* from *crucians*. In *crucians*, both setae are bi- or trifurcate and nearly equal in size. On *bradleyi*, 0 is minute and simple and 2 on IV-V is usually much larger and simple. No dependable character(s) were found to separate 1st and 2nd stage *crucians* larvae from *bradleyi*. The branching and relative size of some setae may prove of value, but this type of analysis of early stage larvae was not attempted.

Roth (1945) observed structural anomalies of the inner [2-C] and outer [3-C] clypeals on *crucians* larvae. Roth's slides, deposited at the USNM, were studied both to confirm the identifications and to observe the anomalies. In addition to these variations, several other variations or aberrations were noted during this study. These included: NC93 #4 (13-VI-1944) - with 4-C, usually simple or bifid, possessing 3 or 4 branches, and 10-C, usually simple or bifid, having 3 branches; DE 572 (4-VIII-1966) with 6-IV, 4-branched, not 2 - 3 branches as usual; FL, Boca Raton (12-XI-1943) - 4-C with 3 branches; VA, Accomack Co., (2201-3-L6) - 4-C with 3 branches; GA, Camp Stewart (26-VII-1944) - 2-C with 3 branches; GA, Camp Stewart (16-VII-1944) - 6-IV with 4 branches; NC93 #1 (13-VI-1944) - 4-C with 3 branches, and 10-C with 4 branches. In addition, the last specimen possess characters intermediate between *bradleyi* and *crucians*: 0-III very small and bifid; 0 on IV-V approximately 0.5 as large as 2 on IV-V, but with 5 - 6 branches; 1-III slightly smaller than 1-IV and 8 on III-IV branched as in *crucians*. Zellwood, FL (1961-3) - 10-C with 3 branches; NC75, D.F.A. - with 2-C, 3-branched and 6-III with only 6 branches. This specimen had no data and is presented merely to show anomalies. JA34-10, Jamaica had 6-IV with 4 branches. Variation and anomalies often occur on taxonomically important setae and as Roth (1945:267) stated, "not all specimens collected will fit every character described..."

Bionomics. Immature *crucians* develop in permanent or semipermanent freshwater pools, ponds, streams, swamps or along lake margins. The water may be acid or alkaline, although acid water seems to be preferred. Metz (1918) studied *crucians* development in a highly acid Alabama swamp. The water had a high concentration of sulfate, sodium, potassium and ferrous ions as a result of contamination by a chemical plant. The water contained very little plant and animal life, but maintained a large population of *crucians* larvae. Larvae of *quadrimaculatus* and *punctipennis* were found in nearby streams, but not in the swamp. Metz found in laboratory and field experiments that *crucians* larvae matured in the water sustaining the other species, and that the other species developed in the swamp water. He suggested that the physiological differences observed between the larval habitats of *punctipennis*, *quadrimaculatus* and *crucians* might reflect oviposition site selection by the adults. Oviposition discrimination has been shown for many species (Clements 1963), but not in the *crucians* subgroup.

The hydrogen ion concentration (pH) preference of *crucians* larvae has been investigated by Mayne (1926a), Boyd (1929), Frohne (1939), Fletcher (1946) and Vogt (1947). Boyd determined optimal pH values to be 5.24 in North Caroline and 6.99 for Georgia. He never found *crucians* larvae in water more acid than pH 4.6 or more alkaline than pH 8.0. Fletcher (1946), however, increased these extremes to 4.0 and 8.9.

In addition to the pH, the microfauna, amount of vegetation and the numbers and kinds of predators influence larval maturation. Metz (1918, 1919b) suggested the bulk of the larval food supply in the swamp was disintegrated plant tissue. He found the diet consisted of a heterogenous mixture of plants and animals. Little preference was observed between living and dead organisms. However, Barber (1927) reported that dead organic matter was less desirable than live, and that algae, bacteria and infusoria were stable ingredients in the diet of most larvae. Frohne (1939) considered desmids an

important food source and developed a classification of ponds based upon the desmid flora. Renn (1941) studied the mechanism employed by feeding *crucians* and *quadrimaculatus* larvae. He found feeding to be indiscriminate with any surface particle being seized. While feeding, the head is rotated 180° and the mouth positioned just under the water surface. The maxillary palps, maxillae and submentum extend through the surface forming a funnel into the buccal cavity. The paired mouth brushes rotate, creating eddies moving the food toward the mouth. This method of feeding, termed "eddy", occurred when the food - bacteria, protozoa, fungi and algae, was abundant throughout the water. Another method, "interfacial", was also described. In this method, the food approached the mouth in a straight line from all directions at approximately the same rate of flow. "Interfacial" feeding was employed when the food was primarily on the water surface, and occurred when the water surface tension was highest. Second and 3rd stage larvae tended to use this method more than the "eddy" method. Fourth stage larvae used either the "eddy" or "interfacial" method of feeding depending on the availability of food.

In addition to selectivity of favorable oviposition sites by the female and the availability of a food source, larvae require a certain degree of protection from predators. This protection is usually afforded by the aquatic vegetation immediately surrounding the larvae, but the type and number of predators are also important. Root (1924b) and Bradley (1932b) observed, in situations where larvae-eating fish were abundant, that predation was highest among larger larvae when aquatic vegetation and debris were less than moderately dense. Root observed in one pond that larvae were abundant when the pond was full and the larvae were sheltered in the grassy banks, but the number of larvae decreased as the pond dried up, eliminating much of the protective shoreline vegetation. Hixson (1943) in a study of anopheline larvae in 2 ponds near Gainesville, Florida, found the efficiency of predators depended on larval size. In one pond with a fish fauna, the fish preyed on the larger larvae while overlooking smaller larvae. The efficiency of the fish depended on the ability of the larger larvae to remain secluded in the vegetation. In the pond void of fish, water scavenger beetles were numerous. Their predation on larvae was not dependent on size, but on the ability of the larvae to remain motionless in the protected areas. All other predators, excluding fish, were in about equal proportions in both ponds. Hixson concluded predation was very high in most natural habitats.

In addition to predators, pathogens interfere with the maturation of anopheline larvae. These pathogens include protozoa, fungi, bacteria, viruses and nematodes. Microsporidan protozoan species of *Nosema* and *Thelohania* have been reported from *bradleyi* and/or *crucians* (Kellen *et al.* 1966, Chapman, Clark and Petersen 1970). The *Nosema* infection in *crucians* was a laboratory infection, and not in the wild population. While some protozoans (flagellates - *Blastocrithidia, Crithidia, Leptomonas;* eugregarines - *Lankesteria,* neogregarines - *Caulleryella;* internal ciliates - *Tetrahymena*) may not be detrimental, the microsporidan species are pathogenic and offer possibilities as biological control agents because they are lethal to both larvae and adults (Chapman *et al.* 1972). The fungi (Coelomomycetaceae: *Coelomomyces*) occur in 11 genera of mosquito species (Chapman *et al.* 1972). *Coelomomyces dodgei* Couch was described from *crucians* larvae collected in south Georgia (Couch 1945),

and *Coelomomyces lativittatus* Couch was also described from *crucians* by Couch and Dodge (1947). *Coelomomyces punctatus* Couch, *C. bisymmetricus* Couch, *C. sculptosporus* Couch, *C. cribrosis* Couch, *C. keilini* Couch, and *C. quadrangulatus* Couch have also been recovered from *crucians* larvae (Couch and Dodge 1947). Chapman and Glenn (1972) reported *C. dodgei* infected 50 percent of the *crucians* larval population in a 4.5 year study, and *C. punctatus* infected 33 percent of the *crucians* larvae in a 2.5 year study. These study areas were 2 ponds near Lake Charles, Louisiana. Few pathogenic bacteria have been reported in *Anopheles* and none for the *crucians* subgroup (Chapman *et al.* 1972). A cytoplasmic polyhedrosis virus (CPV) was recovered from *crucians* larvae by Chapman, Clark and Petersen (1970). Two genera of mermithids (Nematoda: Mermithidae) parasitize *crucians* larvae. Petersen *et al.* (1968) and Petersen and Chapman (1970) recovered *Romanomermis* and *Gastromermis* species from *crucians* larvae. Petersen and Willis (1971) found that *Reesimermis nielseni* Tsai and Grundmann, parasitized 52 percent of the *crucians* larvae at 5 study sites.

Anopheles larvae usually do not enter into any overwintering stage in their more southern range (Barber *et al.* 1924). Barber *et al.* (1924) reported *crucians* larvae in Alabama, Georgia and Louisiana to be common all winter and demonstrating the same behavior as in the summer, but found that in fully shaded situations during the winter months (January, February) it took 45 days for larvae to mature, 19 more than in April. Balfour (1928) found *crucians* overwintered as larvae in North Carolina. Development of the larvae was retarded, but continued during the winter months. He reported larvae could withstand 10 days of -4° and mature. Boyd (1929) established the optimal water temperature for normal growth to be approximately 20°C. Frohne and Hart (1949) called this behavior hibernation since the larval period was extended, occasionally up to 100 days, yet normal development was resumed with a return of favorable water temperature. In the northern part of its range, *crucians* does diapause, passing the winter as larvae in the substrate.

Anopheles crucians is most numerous along the coastal plain areas of the eastern and southeastern United States. Inland as the elevation increases, it becomes less numerous. It has not been reported from the Smokies or other mountainous regions. *Anopheles crucians* is most numerous in the cypress swamps of southern Georgia and northern Florida (Carpenter and LaCasse 1955). It rarely is found in brackish water. Chapman (1959) reported *crucians* in impounded salt marshes having a mean salinity of 4.3 percent (range 0.3 - 16.7) of mean ocean salinity, but it was one of the least salt-tolerant species investigated in the New Jersey salt marshes. Larvae of *crucians* are often associated with *Anopheles quadrimaculatus* Say, *An. punctipennis* (Say); *Culex restuans* Theobald, *C. erraticus* Dyar and Knab; *Culiseta melanura* (Coquillett) and *Aedes* and *Psorphora* species. In North Carolina *crucians* larvae were collected in a small woodland pool, semi-permanent pools, a seepage area, a woodland stream, a lake and in a plastic swimming pool.

Bidlingmayer (1967, 1974) utilized a combination of sampling methods and data in an investigation of some Florida mosquitoes. He found the most effective trapping methods for male and female *crucians* were the truck trap and the New Jersey trap with a white incandescent light. However, Bargren and

Nibley (1956) found that more *crucians* were attracted to New Jersey traps with blue lights than with white lights. Bidlingmayer (1967) found that *crucians* is primarily crepuscular, and collected more *crucians* in the evening than in the morning (1.5:1). Some *crucians* were collected at night at which time the suction-light method proved more successful. The suction-light trap is a suction trap with a 60W frosted white bulb suspended over the intake funnel. The mean number of female *crucians* captured with this method was 53.9/trap night compared to 40.9 and 6.2 for the NJLT and suction trap respectively. Males were less often captured at any time. Landing rate counts on humans compared with New Jersey trap data indicated *Aedes sollicitans* (Walker) would bite 267 times more often than *crucians*. Harden *et al.* (1970), Blume *et al.* (1972) and Schreck *et al.* (1972) investigated the effectiveness of carbon dioxide (CO_2) associated with other trapping methods. Harden *et al.* (1970) found that with CO_2 supplementing their landing rate study, 78 percent more *crucians* were collected, as well as 8 additional species.

Provost (1959) using New Jersey light traps in studies in several Florida localities found more female *crucians* were captured at new moon than at full moon. This ratio was 7:1. Although moon phases affected New Jersey light trap catches, Bidlingmayer (1967) found *crucians* was more active at night during the full phase, *i.e.*, nocturnal illumination increased flight activity, but reduced the New Jersey light trap efficiency. Crepuscular activity was not affected by moon phases. Truck-trap data indicated flight activity was reduced when the temperature lowered to 18°C. Mayne (1926a) found *crucians* would not bite when the temperature was below 22°C. Humidity and/or rainfall did not influence flight activity (Bidlingmayer 1967). In 1974, he investigated feeding activity and egg stage development relative to flight activity. During the crepuscular period and new moon, 22.5 percent of truck trap captured *crucians* were engorged, and 40.6 percent females carried fully developed (stage V) eggs.

Barber *et al.* (1927) and Bull and King (1923) considered *crucians* [subgroup] zoophilic. Schaefer and Steelman (1969) and Edman (1971) substantiated this. Schaefer and Steelman, working in a saltmarsh situation, found 70 percent of 307 specimens (*bradleyi* - *crucians*) had fed on cattle; Edman reported 99 percent of 506 engorged *crucians* contained mammalian blood with 71 percent of that being rabbit blood. Schaefer and Steelman recorded 0.5 percent had fed on avian blood, Edman reported 3 percent. Neither found specimens with human blood. However, Cupp and Stokes (1973) found 12 of 68 (18 percent) *crucians* collected with a New Jersey light trap and 2 of 25 (8 percent) collected in a dog-baited trap had recently fed on humans in Jefferson Parish, Louisiana.

Barber *et al.* (1925) and Boyd (1930) collected *crucians* adults in stables, on porches or under houses. In the summers of 1927 and 1928 Boyd collected 402 of 427 (94 percent) *crucians* in these situations and only 14 inside houses. Only one male for every 91 females was collected by Barber *et al.* (1925). MacCreary (1941) found *crucians* more numerous at ground level, *i.e.*, 1.2 - 1.5 m above the ground, and less than one percent at an elevation of 30.5 m.

Anopheles crucians can be reared in a properly maintained insectary following the procedures given by Gerberg (1970).

Medical Importance. The medical significance of *crucians* is still undetermined. Early medical entomologists were unable to demonstrate *Plasmodium* transmission by *crucians* (Beyer *et al.* 1902, Felt 1904). King (1916) in laboratory experiments established the 3 common southeastern anophelines as vectors of malarial parasites. He recovered *Plasmodium falciparum* (Welch) oocysts and/or sporozoites from 75 percent of the *crucians* examined, but did not investigate the susceptibility of *crucians* to *Plasmodium vivax* (Grassi and Feletti). Simultaneously, Mitzmain (1916a) reported *crucians* [?species] a suitable laboratory host for *vivax*.

Mayne (1919) reported a naturally infected *crucians* from northern Louisiana, and Metz (1919a) reported 2 naturally infected *crucians* in Polk Co., Florida. Dyar (1922) stated *crucians* was a serious vector of malaria. But, Metz (1918) near Montgomery, Alabama, and Mayne (1926b) studying *crucians* in the Okefenokee Swamp, reported that where it was the only anopheline present or the prevalent one, malaria was low or absent. Later, Barber *et al.* (1927) reported experiments in which 40 percent of 222 dissected laboratory-reared *crucians* were infected with *falciparum* and *vivax*. In summarizing previous studies, they found that less than one percent of 1446 dissected wild *crucians* were infected. Barber *et al.* (1927) considered *quadrimaculatus* the most efficient vector, and agreed with Bull and King (1923) that *crucians* was primarily zoophilic. This was later substantiated by Boyd and Stratman-Thomas (1934), who reported both insectary-reared and wild-caught *crucians* were reluctant to feed on human hosts. These authors also found that when the gametocyte density was low, *crucians* infectivity was minimal, and that laboratory-reared *crucians* were more susceptible to *falciparum* infection than to *vivax*. Other field investigations by Mayne (1926b), Boyd (1930) and Griffitts (1931) have also indicated *crucians* was not an important malaria vector. However, Sabrosky et al. (1946) reported a sporozoite infection of 3.28 percent in *crucians* collected in an endemic malaria area near Santee Swamp, South Carolina. This was a higher infection rate than he found in *quadrimaculatus*. Twenty-six percent of the *crucians* were heavily infected as compared to 18 percent of the *quadrimaculatus*. Precipitin tests of 226 recently engorged wild *crucians* revealed that 47.3 percent had fed on equines, and none on humans or birds. Frohne *et al.* (1950) continued the study in Clarenden, South Carolina, in 1947 and 1948, and found that sporozoite rates continued higher in *crucians* than in *quadrimaculatus* and were within the size range of *P. falciparum* and *vivax*. Attempts to infect canaries with these sporozoites failed, as did attempts to infect *crucians* with known avian malarias. Frohne *et al.* (1950) drew no conclusions from their study, but considered the *crucians* infections the principal reason for the continued malaria prevalence in an area where human parasitemia was almost eliminated.

The susceptibility of *crucians* to avian malaria was investigated further by Hunninen et al. (1950), Hunninen (1951) and Atchley (1952). In 1950, Hunninen et al. reported negative results, but in 1951 Hunninen succeeded in obtaining 6 *P. relictum* (Grassi and Feletti) sporozoite infections. In both studies, *crucians* was the least

susceptible species studied. Atchley (1952) failed to infect birds or humans with sporozoites recovered from *crucians*, and Young and Burgess (1961) reported *cians* was not susceptible to *Plasmodium malariae* (Laveran). The status of *crucians* as an important natural vector of human *Plasmodium* spp. remains unresolved.

Until 1959 no arbovirus transmission had been directly attributed to *Anopheles* (Reeves 1965). That year in East Africa, *An. funestus* Giles and *gambiae* Giles were found to be the primary vectors of O'nyong-nyong fever (Haddow *et al.* 1960, Corbet *et al.* 1961). This previously unknown virus had affected over one million persons (Mattingly 1969). Since 1959 over 20 arboviruses have been reported from as many anopheline species (Chamberlain 1963). Preliminary arbovirus studies in the United States suggested *crucians* was a capable host of Eastern equine encephalitis virus (EEE) (Kissling *et al.* 1955, Chamberlain *et al.* 1958). Subsequent investigations resulted in the isolation of at least 8 arbovirus strains in wild *crucians* (Table 4).

Arbovirus studies conducted in southern Alabama by Stamm *et al.* (1962) in 1957-1958 resulted in the isolation of EEE from *crucians*. *Culiseta melanura* (Coquillett) was the only other species (of 29 studied) with a positive EEE isolation. Subsequent investigation by Sudia *et al.* (1968) in the same area resulted in the isolation of EEE, a LaCrosse strain of the California group arboviruses and Tensaw virus (TV) in *crucians*. *Anopheles crucians* was the most numerous species collected, representing 43 percent of 39,989 live mosquitoes captured. The Tensaw virus was reported by Coleman (1969) as a new member of the Bunyamwera group of arboviruses (Casals and Whitman 1960). The prototype strain was isolated in *crucians* near the Tensaw River in southern Alabama (Coleman 1969). Chamberlain, Sudia and Coleman (1969) reported 74 percent (116/156) of the TV isolations were from *crucians*. Isolations were made in southwest Alabama, southeast Georgia and central and south Florida between 1960-1963. In Tampa Bay area of Florida in 1962 another high TV infection rate was encountered (28 isolations from 5,747 *crucians*, 1:204). Tensaw virus antibody was not found in any bird tested, but Sudia, Coleman and Chamberlain (1969) found high, long-lasting viremia in several mammals, *i.e.*, dogs, cats, rabbits (*Sylvilagus* spp.) and cotton rats (*Sigmodon hispidus* Say and Ord). Subsequent arbovirus investigations by Chamberlain, Sudia, Work *et al.* (1969), Taylor *et al.* (1971) and Wellings *et al.* (1972) in Florida led to the isolation of Venezuelan equine encephalitis (VEE) and the Keystone and Trivittatus strains of the California group of arboviruses from *crucians*.

Cache Valley virus (Holden and Hess 1959), another member of the Bunyamwera group of arboviruses, has also been isolated from the *crucians* subgroup. This virus was isolated from one of 82 pools of mixed *bradleyi* and *crucians* collected on Chincoteague and Assateague Islands on the Del-Mar-Va Peninsula (Buescher *et al.* 1970). The principal member of the subgroup in this study area was *bradleyi*, yet a few specimens of *crucians* may have been involved. The primary mosquito hosts for this virus were *Aedes sollicitans* and *Ae. taeniorhynchus* (Wiedemann). The vertebrate hosts for this virus proved to be large vertebrates (cattle, horses, deer and man) with rare isolations from rodents (3/211 tested).

Table 4. ARBOVIRUS ISOLATIONS FROM THE *ANOPHELES CRUCIANS* SUBGROUP IN THE UNITED STATES, 1953-1970.*

Virus	State	Year	References
EEE**	GA	1953	Chamberlain *et al.* (1954)
EEE	LA	1953	Kissling *et al.* (1955)
EEE	GA	1956	Karstad *et al.* (1957)
EEE	AL	1958	Stamm *et al.* (1962)
EEE	FL	1962	Taylor *et al.* (1968)
		1963-70	Wellings *et al.* (1972)
SLE	FL	1962	Chamberlain *et al.* (1964)
			Dow *et al.* (1964)
Tensaw (Bunyamwera group)	AL	1960	Sudia *et al.* (1968)
			Coleman (1969)
Tensaw	FL	1963-70	Taylor *et al.* (1971)
Tensaw	AL,FL,GA	1959-63	Chamberlain, Sudia and Coleman (1969)
VEE	FL	1963-64	Chamberlain, Sudia, Work *et al.* (1969)
		1968	Sudia, Newhouse and Chappell (1969)
VEE	TX	1971	Sudia and Newhouse (1971)
Keystone (CE)	FL	1963-70	Taylor *et al.* (1971)
Trivittatus (CE)	FL	1963-70	Taylor *et al.* (1971)
LaCrosse (CE)	AL	1963	Sudia *et al.* (1971)
South River (CE)	NJ	1960	Sudia *et al.* (1971)
Cache Valley (Bunyamwera group)	Del-Mar-Va Peninsula	1961	Buescher *et al.* (1970) (*bradleyi-crucians*)

*All isolations from *crucians* only, except in the case of Cache Valley.
**Laboratory induced infection; remaining isolations from wild-caught specimens.

The pathological significance of Cache Valley or Tensaw viruses has not been determined. However, the above data provide substantial proof that *crucians* and probably *bradleyi* are enzootic vectors of these arboviruses in the United States.

ANOPHELES (ANOPHELES) BRADLEYI KING

Anopheles crucians var. *bradleyi* King 1939. TYPE: Holotype and associated larval and pupal skins; Brevard Co., Florida, near St. Johns River, February 5, 1958. T. E. McNeel (USNM).

Synonymy. *Anopheles crucians* of Dyar 1902 (A, L); Howard 1902 (A, distribution in part); Theobald 1901, 1907, 1910 (distribution in part); Smith 1904 (A*, L*); Felt 1904 (A); Blanchard 1905 (distribution in part); Mitchell 1907 (A*, L*, E*); Morse 1910 (A, L); Howard, Dyar and Knab 1912-1917 (A*, ♂*, L*, E*, distribution in part); Brehne 1913 (A, L); Grossbeck 1913 (L); Griffitts 1921, 1928a,b, (A, L); Headlee 1921, 1945 (A*, L*, E*);

Hardenberg 1922 (A*, L*); Beyer 1923 (A*, L); Matheson and Shannon 1923 (L); Komp 1923 (L in part); Bonne and Bonne-Wepster 1925 (L in part); Viosca 1925 (L); Covell 1927 (A, L); Matheson 1929(A*, L*, E*, distribution in part); Bishopp *et al.* 1933 (A); MacCreary and Stearns 1937 (A); Tulloch 1937a,b (A, L); Cory and Crosthwait 1939 (bionomics).

Anopheles crucians - brackish water race or form of Root 1924b,c (L), 1929 (L); Bradley 1936 (L); Dozier 1936 (A, L).

Anopheles crucians - coastal, brackish water variety of Bradley 1932a (L); Boyd *et al.* 1936 (A, malaria); King *et al.* 1939 (A*, P*, L); Stearns 1940 (A, L); Mulhern 1941 (A), 1942 (A), 1943 (A).

Anopheles crucians var. *bradleyi* of King 1939 (A, ♂*, P, L*); Vargas 1940b(L), 1941 (E).

Anopheles crucians bradleyi of Matheson in Moulton 1941 (malaria); Ross and Roberts 1943 (A, L*); Russell *et al.* 1943 (A, L); Carpenter *et al.* 1946 (A*, ♂, L*, distribution in part); Schoof and Ashton 1944 (L, distribution); Vogt 1947 (L); Yamaguti 1952 (A*, ♂*); Bargren 1953 (L); Nayar and Sauerman 1970a,b, 1974 (A, bionomics).

Anopheles bradleyi of King and Bradley in Moulton 1941a (A, ♂, L, distribution); King and Bradley in Moulton 1941b (A, L, distribution); Bradley and King in Moulton 1941 (bionomics); King *et al.* 1942 (A, L, to sp. status); King *et al.* 1943 (distribution); Roth 1944 (♂*), 1945 (L*); O'Neal *et al.* 1944 (distribution); Middlekauff and Carpenter 1944 (distribution); Dorer *et al.* 1944 (distribution); Dorsey 1944 (distribution); Matheson 1944, (A, ♂, L, E*); Bradley *et al.* 1944 (distribution); Bickley 1945 (L); Petersen and Smith 1945 (distribution); Miles 1945 (L*); Miles and Rings 1946 (distribution); Dodge 1946, 1963, 1966 (L); Miles and Hill 1948 (distribution); Freeborn 1949 (distribution); Darsie 1949 (P*); Penn 1949 (P*); Vargas and Palacios 1950 (A, L), 1956 (distribution); Barnes *et al.* 1950 (distribution); Sheppard 1951 (distribution); Darsie *et al.* 1951 (L); McNeel and Ferguson 1954 (distribution); Carpenter and LaCasse 1955 (A, ♂, L*); Horsfall 1955 (A, L, distribution, medical); Stone *et al.* 1959 (distribution); Chapman 1959 (L); Johnson 1959 (L); King *et al.* 1960 (A, L, distribution); Forattini 1962 (distribution); Knight 1965 (L); Belkin *et al.* 1966 (bionomics); Lomax 1967 (L); Petersen *et al.* 1968 (L, parasitism); Harden and Poolson 1969 (L, distribution); Gladney and Turner 1968 (distribution in part); Kreutzer *et al.* 1970 (genetics); Petersen and Chapman 1970 (L, parasitism); Belkin *et al.* 1970 (distribution); Chapman, Clark *et al.* 1970 (L, parasitism); Chapman, Woodard *et al.* 1970 (L, parasitism); Bickley *et al.* 1971 (distribution in part); Evans and McCuiston 1971 (distribution); Kreutzer and Kitzmiller 1971 (genetics); LaSalle and Knight 1973, 1974 (bionomics).

Anopheles bradleyi-crucians complex of Schaefer and Steelman 1969, in part (A, bionomics); Buescher *et al.* 1970, in part (arbovirus).

Description. The characters given for female *crucians* also apply for *bradleyi*. On the pupa, seta 0 on III-VI is small, simple, rarely bifid or

*An illustration is presented.

trifid; 2 on III-V usually has less than 5 branches. The larvae have seta 0 on III-VI small, simple or bifid, and 1-III more closely resembles 1-IV than 1-II.

FEMALE. (Fig. 7). *Head.* Vertex scales pale, erect, expanded at tip; interocular space narrow with short erect pale scales, frontal setae pale elongate; antenna pedicel and flagellomere one with scattered mixed scales; palpus with dark erect scales on basal 0.33, decumbent scales toward the apex, segment 5 entirely pale scaled, segment 4 with apical and basal pale bands, and segment 3 with basal pale band; proboscis with dark decumbent scales, forefemur/proboscis ratio nearly 1:1. *Thorax.* Integument mottled brown with darker acrostichal and median prescutellar lines; golden setae along these lines, remaining setae darker; anterior promontory scales pale and elongate; scutum with long thin pale scales; anterior promontory, acrostichal, dorsocentral, lateral prescutal, fossal, antealar and supraalar regions with long dark setae; prescutellar space with pale long setae except just cephalad to scutellum; scutellum with long dark setae and paler short scales; anterior pronotum with dark scales dorsally and 8 - 10 long dark setae; pleural setae are 3 - 8 propleural, 2 - 5 spiracular, 6 - 9 prealar, 3 - 5 upper and 3 lower mesepisternal, 7 - 13 upper and 0 lower mesepimeral *Wing.* Costa black scaled to apical pale spot; Subcosta dark; Radius dark; R_1 dark except for pale tip; R_s dark; R_{2+3} with apical pale area; R_2 with apical tip pale; R_3 with median area pale extending to near tip, tip dark; R_{4+5} basal 0.2 and apical 0.2 dark, median area mixed or pale; basal and median area of Media dark or mixed, apical area pale; M_{1+2} with basal and apical 0.20 dark, median area pale; M_{3+4} base dark, median area pale, apical 0.33 dark; Cubitus with pale or mixed scales sometimes light to median gray or brown; Cu_1 basal 0.25 - 0.33 dark, median area pale, apical 0.25 dark; Cu_2 basal 0.50 - 0.66 pale, apical 0.50 - 0.33 dark; 1-A with basal, median and apical dark areas with a pale area on either side of median dark area; crossveins r-m and m-cu dark scaled, humeral crossvein scaleless; fringe scales dark except for pale spots from R_1 to R_3 and at R_{4+5}, fringe opposite R_3 dark or mixed. *Halter.* Knob with dark scales and scattered setae. *Legs.* Coxae without scales, upper midcoxa with 2 - 4 setae, lower setae stouter than upper; femora, tibiae and tarsomeres long, slender and unicolorous, with dark decumbent scales and scattered dark setae; apex of femur and base of tibia pale. *Abdomen.* Integument unicolorous with numerous dark setae.

MALE. (Fig. 7). *Head.* Palpus entirely dark scaled, last 2 segments flattened and club-like; antenna plumose. *Genitalia.* Basimere usually without scales, with 2 parabasal spines and one internal spine; claspette lobes fused with 3 - 5 (usually 3) flattened setae, usually one distal ventral seta and 2 dorsal (lateral) setae or 3 setae nearly evenly separated from each other; the distal ventral seta stouter than the rest; aedeagus with 6 - 8 attenuated leaflets; 9th tergum with long and slender lateral lobes.

PUPA. (Fig. 8, Appendix Table 3). Light tan to light brown. *Cephalothorax.* Seta 5 with 4 - 7 branches; 7 long simple; 10 long, slender, often bifid at apex; 11 often as long as 10 with 3 - 9 branches; 12, 1.25 - 1.50 longer than 10, with 3 - 5 branches. *Trumpet.* Darkly pigmented; meatal cleft approximately 0.33 as long as trumpet; usually with setal spur on pinna.

Abdomen. Seta 0-II usually simple; 0 on III-VII usually simple or bifid, rarely trifid; 1 on II-III usually with 5 - 7 branches; 1-IV with 5 - 9 branches, 0.50 - 0.75 as long as segment V; 1-V with 3 - 6 branches (usually 3 or 4), 0.66 to equal length of segment VI; 1-VI with 2 - 5 branches, 0.5 to nearly as long as segment VII; 1-VII usually simple or bifid; 2 on IV-VII with 2 - 6 branches (usually 3 or 4); 3 on III-V with 3 - 8, 4 - 7 and 3 - 7 branches respectively; sum of branches of both 3-V, 6 - 13; 4-I with 3 - 10 branches, approximately 0.5 as long as seta 5; 5-IV with 5 - 10 branches, 0.50 - 0.75 as long as segment V; 5-V with 3 - 8 branches, 0.66 to equal length of segment VI; 5 on VI-VII with 3 - 6 branches, 5-VI, 0.50 - 0.75 as long as segment VII, 5-VII, 0.66 - 0.75 as long as segment VIII; 6-I with 2 - 7 branches, as long as or 1.25 longer than 5-I; 6 on II-III with 2 - 6 branches, 6-II, 0.50 - 0.75 as long as segment, 6-III, 0.33 - 0.50 as long as segment; 7-I with 2 - 7 branches, 0.50 - 0.75 as long as seta 6; 7-II with 2 - 5 branches; 7 on III-V with 1 - 6 branches, usually bi- or trifid; 7-VI usually simple or bifid, 0.33 - 0.66 as long as segment; 7-VII usually simple, 0.33 - 0.75 as long as segment; 8-II simple or bifid; 8 on III-V usually simple, bi- or trifid, equal to or slightly smaller than 7 on III-V; 8 on VI-VII usually simple or bifid, 0.25 - 0.50 as long as seta 7 on VI-VII; 9 - I usually simple; 9 on II-VIII darkly pigmented; 9-III approximately 0.5 as long as 9-IV; 9-VII not more than 3.5 - 5.5 times as long as wide; 10 on III-IV usually simple or bifid; 10-V with 1 - 3 branches, 0.33 - 0.50 as long as segment; 10 on VI-VII usually simple or bifid. *Paddle*. Refractile margin 0.65 - 0.80 length of paddle; portion beyond serrated margin with scattered fine hairs to apex, no fine hairs on inner margin; 1-P acute, stout, simple or bifid; 2-P simple or with 2 - 3 distal branches.

4TH STAGE LARVA. (Fig. 9, Appendix Table 6). *Head*. Darker than thorax or abdomen; antenna base slightly wider than tip; antenna deeply pigmented with numerous spines; 1-A with 3 - 6 branches, inserted on basal 0.25 of antenna; 2,3-A acute with one edge serrate; 4-A with 4 - 6 branches; 2-C long, simple with bases separated by less than diameter of an alveolus; 3-C with 16 to more than 30 broom-like branches, usually 20 or more, 0.50 - 0.75 as long as 2-C; 4-C simple; 5,6,7-C long and plumose; 8-C with 3 - 4 branches; 9-C with 2 - 5 branches; 10-C simple, bi- or trifid; 11-C as long as antenna, usually with more than 40 branches. *Thorax*. Seta 1-P usually simple, 0.25 - 0.33 as long as 2-P; 2-P arising from tubercle, with 6 - 12 branches; 3-P simple, inserted closer to 2-P than 1-P is to 2-P, approximately 0.33 as long as 2-P; 4-P stout with more than 12 branches, inserted closer to 5,6,7-P than to 1,2,3-P; 5,6-P arise from common tubercle, 6-P long, simple; 7,8-P well developed with 15 - 31 branches; 9,10,11,12 on P, M, and T on common tubercles, 9,10-P,M,T long and simple; 11-P,M,T short and simple; 12-P long, simple, 12-M short, usually simple, 12-T short and usually bi- or trifid; 13-P with 8 - 15 branches; 14-P with 5 - 10 branches; 1-M stout with 8 - 36 branches; 2,3,5-M usually simple; 4-M with 1 - 3 branches; 6,7-M with 3 - 6 branches; 7-M approximately 0.5 as long as 6-M; 8-M with 10 - 18 branches; 14-M with 8 - 15 branches; 3-T with flattened leaflets; 5,7,8-T well developed and nearly equal in length; 6-T with 3 - 6 branches; 13-T with 2 - 4 branches. *Abdomen*. Anterior and posterior tergal plates as on *crucians*; seta 0 on II-VIII usually simple or bifid, rarely trifid; 1-I with 3 - 8 flattened, slightly pigmented leaflets; 1-II with 5 - 10 partially pigmented leaflets; 1-III with 8 - 16

leaflets, not as well developed and approximately 0.66 as long as 1-IV; 1 on IV-VI well developed, nearly equal in size; 1-VII resembling 1-II more than 1-VI; 2-I with 2 - 4 branches; 2-II with 4 - 8 branches; 2-III with 3 - 6 branches; 2 on IV-V with 1 - 4 branches (usually 1 - 2); 3-VI simple, caudal to 1-VI; 4-V with 3 - 5 branches; 5-I with 4 - 5 branches; 5-II with 5 - 9 branches; 5-III with 4 - 9 branches; 5 on IV-V with 4 - 9 branches; 5 on VI-VII with 6 - 9 branches; 6,7 on I-II well developed and nearly equal in size; 6-III slightly shorter than 6 on I-II, with 11 - 19 branches; 6-IV with 3 - 4 branches, as long as 6-III; 6-V with 2 - 3 branches, 0.75 or as long as 6-IV; 6 on VI-VII less than 0.2 as long as 6-V, with 2 - 5 branches; 7-III with 2 - 6 branches, less than 0.33 as long as 7-II; 7 on IV-VI with 2 - 5 branches, 7 on V-VI approximately 0.25 shorter than seta 7 on preceding segment; 7-VII with 3 - 6 branches; 8-II with 3 - 5 branches; 8-III with 2 - 6 branches; 8 on IV-VI with 2 - 5 branches; 9-I with 5 - 8 branches; 9-II with 5 - 10 branches; 9-III with 5 - 9 branches; 9-IV with 5 - 11 branches; 9 on V-VI with 5 - 12 branches; 9-VII with 3 - 5 branches; 10 on I,III-VI usually simple or bifid; 10-II with 1 - 6 branches; 10-VII with 3 - 5 branches; 11-I with 4 - 6 branches; 11 on II-IV usually simple or bifid; 11-V with 2 - 4 branches; 11 on VI-VII with 1 - 4 branches; 12-IV with 2 - 5 branches; 12-V with 2 - 3 branches; 13-I with 2 - 5 branches; 13-II with 3 - 7 branches; 13-IV with 3 - 8 branches; 13-V with 3 - 4 branches; 13-VI with 3 - 10 branches; 13-VII with 2 - 3 branches; seta 1 on spiracular lobe with 4 - 8 branches; 2-S on pecten plate, with 3 - 5 branches; 3,4,5-S minute; 6-S simple or bifid; 7-S usually simple, inserted at apex of spiracular valve; 8,9-S with 2 - 4 and 3 - 5 branches respectively; 11,12,13-S minute; pecten with 8 - 10 long and 8 - 12 short teeth, short teeth single or paired; 1-X as long or longer than saddle.

Distribution. (Fig. 8). *Anopheles bradleyi* occurs from New York to Texas in the United States, and south into Mexico, Honduras and Nicaragua. A total of 277♀, 85♂, 83P, 83WL, 226L, 15G specimens were examined including those from the following states: Alabama: Mobile, 21-III-1944, L. Roth, 2L; 23-III-1944, L. Roth, 2♀, 3♂. Delaware: Rehoboth, 30-VIII-1923, H. G. Dyar, 1♀. Lewes, 28-VIII-1933, D. MacCreary, 2♀; 4-VI-1935, 2♀. Leamin, 17-IX-1936, 1WL. Port Mahon, 18-VIII-1949, MacCreary, 1WL. Leipsic, 28-IX-1965, R. W. Lake, 1♀, 1♂, 1WL. Florida: Mayport, 1WL; 10-VII-1944, 1WL; 11-VII-1944, 1WL. Daytona Beach, 1WL. "Fla." 1G. Orlando, 13-XI-1931, G. H. Bradley, 3♀, 1♂, 7L; 2-XII-1931, G. H. Bradley, 1♀, 2♂, 3L. Brevard Co., St. John's River, 5-II-1938, T. E. McNeel, 3♀, 3♂ (type-series); 25-II-1938, T. E. McNeel, 8P, 10L, 1G (type-series) [note date difference between adults and associated immature skins of type-series]. Alachua, 3-X-1944, D. C. Thurman, 1♀. Ft. George, 16-VIII-1945, Pritchard, 2♀, 1♂. Pineland, 18-IV-1947, Gill, 1♀. Cocoa, 11-III-1948, Haiston, 1♀. Dade Co., 2-VI-1948, Heidt, 1WL; Fisher Island, 26-IV-1951, Pratt, 4WL. Lee Co., Sanibel Island, 4-XI-1948, Miller, 1WL. Duval Co., McBridge, 2-III-1956, Logan, 2WL. Louisiana: New Orleans, 28-I-1900, H. A. Veazie, 1♀; 27-III-1915, 1♂; 1-I-1932, A. L. Melander, 10♀. Lake Catherine, 8-VI-1901, G. D. Beyer, 1♀, 2♂. Jackson Beach, 13-V-1906, 1♂. Buras, 28-I-1928, T. H. D. Griffitts, 27♀; Buras, 5WL, 5L. Port Jackson, 1♀, 1♂. Lake Charles, 10-X-1973, Chapman, 5P, 7L, 2G. Rapids, 7-IV-1943, W. W. Wirth, 1♀. Maryland: Chesapeake Beach, 4-VII-1903, A. Busck, 5♀; VIII-1906, T. Pergrande, 4♀; 19-20-VI-1933, F. C. Bishopp, 14♀, 3♂, 1G; 28-VII-1933, F. C. Bishopp, 5♀. Crisfield, 15-VIII-1932, 3♀;

16-VIII-1933, F. C. Bishopp, 7♀; 24-VIII-1933, F. C. Bishopp, 1♀. Ocean City, 14-IX-1913, H. G. Dyar, 3♀; 16-VIII-1932, F. C. Bishopp, 2G. Piney Point, VI-1906, T. Pergande, 1♀. Eastern Shore, Fishing Creek, 12-16-IX-1960, J. W. Fitzgerald, 1♀. Mississippi: Biloxi, 6-XII-1902, J. Broskie, 1♀; 24-I-1928, R. L. Turner, 1♀. Miss. State, X-1904, E. S. G. Titus, 1♀. Miss. River, Ocean Station, 1♀, 1♂. Keesler Field, 29-30-VII-1943, Poole and Young, 4L; 7-VI-1944, L. Roth, 1L. Gulfport Field, 22-IV-1944, 1L. New Jersey: Woodbine, VIII-1901, Kotinsky, 1♀. Cape May, IX-1922, J. M. Aldrich, 3♀. Dias Creek, 1938, 5♀. Nixon, 1-IX-1966, P. H. Thompson, 1♀. New York: Bellport, 15-IX-1901, H. G. Dyar, 12♀. North Carolina: Carteret Co., New Port River, "F99", 1-VI-1972, T. G. Floore, 10♀; "F100", 7-VI-1972, T. G. Floore, 11♀, 11♂. Carteret Co., Davis, "F101", 17-VI-1972, T. G. Floore, 19P, 6WL, 81L; "F112 and F113", 5-VII-1972, T. G. Floore, 1P, 17WL, 16L; 12-VII-1972, R. LaSalle, 1P, 8WL, 3L; "104 and 105", 5-VIII-1972, R. LaSalle, 31♀, 27♂, 33P, 8WL, 61L, 8G. Carteret Co., North River, "F115", 6-VII-1972, T. G. Floore, 2P, 19WL, 12L. South Carolina: Beaufort, 25-V-1912, A. H. Jennings, 1♀. Myrtle Beach, 16-V-1944, 2♀; 17-VII-1944, A. H. Halff, 1♀, 1P, 1L. Georgetown, Coastal Airport, 1-15-V-1972, R. Zack, 9♀, 4♂; Coastal Airport, 16-30-V-1972, R. Zack, 6♀, 8♂; Santee Delta, 1-15-V-1972, R. Zack, 27♀, 4♂; Santee Delta, 16-30-V-1972, R. Zack, 9♀, 6♂. Texas: Smith Point, 2-X-1918, H. S. Barber, 1♀; 7-XI-1918, H. S. Barber, 2♀. Brownsville, 19-III-1924, R. L. Turner, 1♂. Seabrook, 22-I-1934, J. S. Smith, 1♀. Galveston, 30-IX-1961, Moore, 1♀. Virginia: Newport News, C. B. Ransome, 1♀. Virginia Beach, 20-IX-1911, H. G. Dyar, 1♀. Langley Field, 6-X-1924, B. B. Warriner, 1♀. Ft. Monroe, 6-VI-1927, 3♀. Accomack Co., Assateague Island, Ragged Pt., 1972, J. F. Burger, 5♀, 2♂, 8P, 8L; 1973, J. F. Burger, 3♀, 2♂, 5P, 5L. Unknown: Dyar and Caudell, 2♀.

In Mexico *bradleyi* has been collected from the states of Campeche, Tabasco, Tamaulipas, Veracruz, Yucatan and Quintana Roo (Vargas and Palacios 1950). Although Tulloch (1937b)reported brackish water *crucians* from Puerto Rico, and Hill and Hill (1948) collected *crucians* in mangrove swamps in slightly brackish water in Jamaica, no recent investigators have collected *bradleyi* on these islands. Belkin *et al.* (1970) suggested that *bradleyi* may occur on Jamaica. The following specimens in the USNM extend the distribution of *bradleyi* to include Honduras and Nicaragua. Honduras: Puerto Castilla, K. B. Maxwell, 6♀; 6-VIII-1943, K. B. Maxwell, 1♀; 5-XII-1943, K. B. Maxwell, 1♀; 17-III-1944, K. B. Maxwell, 4♀. Puerto Castilla, Nav. Med. Sch. Ser. 26, Coll. 1003, 1-III-1944, 5♀; Nav. Med. Sch. Ser. 26, Coll. 455, 8-III-1944, 5WL. Nicaragua: Bluefields, 1♀.

Taxonomic Discussion. The first larval key and partial description of *bradleyi* was made by Smith (1904). He separated *crucians* [=*bradleyi*], *maculipennis* [=*quadrimaculatus*] and *punctipennis* based on the color of the antennae and the size of the gills on segment X. He characterized the gills on "*crucians*" as being half as long as those on the other 2 species, and the antennae as being brown not yellowish. Smith recognized *crucians* [=*bradleyi*] differed from *quadrimaculatus* and *punctipennis*, but did not detect differences between the freshwater and brackish water "*crucians*". Root (1924b) first recognized the larval habitat, physiological and morphological differences between the 2 "races" of *crucians*.

Adult *bradleyi* differ from the other United States anophelines by the general characters given for *crucians*. Most adult *bradleyi* are indistinguishable from *crucians* or *georgianus* (cf. *crucians*). On approximately 50 percent of *bradleyi* specimens, vein Cu is pale scaled out to the fork. Since this character is unreliable in a series, it should not be depended upon to confirm identifications. The male resembles males of *crucians* and *georgianus* except for the genitalia characters given above, *i.e.*, claspette spines, usually with 3 evenly spaced setae or with one stout ventral and 2 dorsal (lateral) setae. Accurate identification can be made only from the pupal and larval stages or adults with associated immature skins.

Anopheles bradleyi pupae are separated from *crucians* primarily by the size and branching of seta 0 on IV-V. On *bradleyi*, 0 on IV-V is usually simple or bifid (cf. *crucians*). Seta 1-IV has 5 - 9 branches on *bradleyi*, usually more than 12 on *crucians* and from 9 - 14 on *georgianus*; I-V on *bradleyi* has 3 - 6 branches, compared to 3 - 17 and 6 - 10 on *crucians* and *georgianus*. Seta 2-IV has 3 - 9 branches on *bradleyi*, but 4 - 18 on *crucians*. On *bradleyi*, 5 on III-V has fewer branches than found on *crucians* or *georgianus*. Seta 5-IV on *bradleyi* has 5 - 10 branches (cf. *crucians* and *georgianus*).

Fourth stage larvae of *bradleyi* are distinguished from *crucians* by comparing the number of branches and the size of seta 0 on III-V to 2 on III-V. On *bradleyi*, 0 on III-V is small and simple or occasionally bi- or trifid; on *crucians*, seta 0 is multibranched and large. Seta 2 on III-V on *bradleyi* has 3 - 6, 1 - 3 and 1 - 4 branches respectively (cf. *crucians*), and is much larger than seta 0 of the same segment. In addition, seta 8 on II-III has 6 or less branches on *bradleyi* (cf. *crucians*). Seta 1-III was used in some earlier studies to separate *bradleyi* from *crucians*, *i.e.*, on *bradleyi* 1-III was considered to be smaller than 1-IV, while on *crucians* 1 on III-IV were considered equal in size. We found this, in most cases, true for *bradleyi*, *i.e.*, seta 1-III is 0.50 - 0.66 as large as 1-IV; however, on some *crucians*, 1-III is noticeably smaller than 1-IV, *i.e.*, approximately 0.66 as large as 1-IV. For this reason, we do not consider this character as reliable as other characters for separating *bradleyi* larvae from *crucians*.

Fourth stage larvae of *bradleyi* and *georgianus* are less easily distinguished, but subtle differences occur. Seta 0 on III-V is small and usually simple on both. The comparison of seta 1-III to 1 on II,IV proved a reliable character. On *bradleyi*, 1-III morphologically resembles 1-IV more than 1-II; on *georgianus*, 1-III resembles 1-II more (see Figs. 9 and 15). In addition, 2-III on *bradleyi* has fewer branches (3 - 6) than *georgianus* (4 - 10). Seta 5-III has 4 - 9 branches on *bradleyi* and 6 - 11 on *georgianus*. Setae 10,11,12-III of *bradleyi* are usually simple, but 2 - 3 branched on *georgianus*. Seta 10-VI is simple or occasionally bi- or trifid on *bradleyi*; on *georgianus* it has 3 - 5 branches. The gills on segment X on *bradleyi* are only about half as long as the gills on *georgianus*. On the head capsule of *bradleyi*, 13-C usually has 4 - 5 branches compared to 5 - 9 on *georgianus*. Thoracic seta 1-P is usually simple on *bradleyi*, but usually has several (2 - 5) apical branches on *georgianus*.

Third instar *bradleyi* appear to have 0 on IV-V small and simple (cf. *crucians*). Second and 1st instar *bradleyi* appear morphologically similar to *crucians*.

Roth (1945) noted 2 aberrations on *bradleyi* larvae; the following variations were observed during this study: Leipsic, DE (28-IX-1965) 10-C with 3 branches, usually 10-C is simple or bifid; Gulfport, MS (22-IV-1944) 3-C is branched at the base; F113 has 1-P with 5 branches; variation from the usual branching on 6-IV occurred on Brevard Co., FL (1958-13), Accomack Co., VA (3281-1-L10), St. Johns River, FL (1958-12, 1958-2, 25-II-1938). Kesler Field, MS (29-30-VII-1943) had 5-I, 3-branched, 2-IV split at base, and one stem of 2-IV had 3 branches at the apex.

A brief description of *Anopheles atropos* Dyar and Knab is included because in certain areas along the Atlantic and the Gulf coasts, both *atropos* and *bradleyi* are commonly collected from the same habitat. *Anopheles atropos* may be separated from *bradleyi* by the following characters: ADULT. The palpal segments of *atropos* are entirely dark scaled or with faint yellow apical bands, the vertex scales and frontal setae are dark and the wings are entirely dark scaled; PUPA. Seta 3-V with 1 - 3 branches, paddle refractile index 0.50 - 0.65; inner margin of paddle with dense fine hairs on apical 0.75; trumpet without spiny lateral spur on pinna; 4TH STAGE LARVA. Seta 2-C usually has minute branches on the distal half, 3-C has 5 - 10 branches, which are not broom-like in appearance, 3-C is approximately 0.5 as long as 2-C; 8,9-C are simple or bifid; 0 on III-IV minute and simple; and 1-III is approximately 0.33 - 0.50 as large as 1-IV (cf. *bradleyi* - description).

The holotype, allotype, and several paratypes of *bradleyi* at the USNM were examined. The pupal skins were poorly mounted, probably in Hoyer's, yellowed badly, and of negligible taxonomic value. The larval skins were in better condition, but dark. Adults were in good condition.

A cytogenetic investigation of *bradleyi* and *crucians* polytene chromosomes was conducted by Kreutzer *et al.* (1970) and Kreutzer and Kitzmiller (1971) conducted hybridization experiments with these 2 species. Their taxonomic data suggests that the *bradleyi* strain they used (Vero Beach, Florida) had larval seta 3-C with 5 - 10 branches. No *bradleyi* larvae seen during this study had less than 16 branches on 3-C; all *bradleyi* larvae from Florida had 20 or more branches on 3-C. These discrepancies suggest that Kreutzer *et al.* (1970) and Kreutzer and Kitzmiller (1971) were misidentifying *atropos* larvae as *bradleyi*. These 2 studies are discussed in more detail in the Discussion and Summary section.

Bionomics. Larvae of *bradleyi* typically occur in brackish water situations along the Atlantic and Gulf coasts, and less often in coastal freshwater habitats. Larvae of *bradleyi* have never been reported far inland, although adults are probably periodically blown inland. Root (1924b) and Bradley (1932a) first recognized the presence of 2 races of *crucians*, *i.e.*, brackish and freshwater. Many earlier reports of *crucians* from brackish or salt water actually referred to *bradleyi*.

Griffitts (1921) studied the relationship of salinity to the breeding of some American anophelines. At Hampton, Virginia, he found *crucians* [*bradleyi*] larvae associated with *Aedes sollicitans* larvae in salt marshes where no other anophelines were found. The primary vegetation in this marsh was *Distichlis spicata* (Linnaeus). Similar results were obtained at Lake Rudee, near Virginia Beach, and York River, West Point, Virginia. Lake Rudee had a salt concentration of 34.6 percent sea water, and produced only *crucians* [=*bradleyi*]. Lake Holly, 200 m away, was freshwater and contained only *quadrimaculatus* larvae. In a nearby barn, 67 *crucians* [?*bradleyi*] adults were captured as compared to 85 *quadrimaculatus*. The York River site, a brackish water pond created by damming the salt marsh, approximated 50 percent sea water. *Anopheles crucians* [=*bradleyi*] larvae were collected in any site containing brackish water, and would develop in either salt water or freshwater. Bradley (1932a) recorded the salinity of the water from which *bradleyi* were recovered in Florida as 3.9 percent. Chapman (1959) reported *bradleyi* larvae in brackish water ranging in salinity from 0.5 to 55.8 percent. In New Jersey the mean salinity for unimpounded marshes from which *bradleyi* larvae were collected was 28 percent. *Anopheles quadrimaculatus* larvae are rarely found where the salinity is greater than 1.5 percent and although *punctipennis* possesses a wider range in its larval habitat than the other species, it is never found in brackish water (Griffitts 1921).

In North Carolina, *bradleyi* was collected in *Juncus* salt marshes on the Newport and North rivers. Frequent tidal flooding made the *Juncus* marshes excellent sites for larval maturation. The Newport River site consisted of ditched and unditched sections. Ditched areas had shorter wet intervals than unditched sections, but were completely flooded 14 - 21 times a month. Ground pools contained water long enough for larval maturation. Predominant vegetation was Black Needlerush - *Juncus roemerianus* Scheel, Saltgrass - *Distichlis spicata* (Linnaeus) and Saltmeadow cordgrass - *Spartina patens* (Aiton). Larvae were collected from natural ground pools and man-made depressions up to a meter wide and 2 - 8 cm deep. Emergent, floating and submerged living and dead vegetation was present in all the sites, and the water was turbid and colored. Salinity ranged from 4 percent to a high of 32 percent. The depressions were usually shaded part of the day. Larvae of *Aedes sollicitans*, *Ae. taeniorhynchus* (Wiedemann) and *Anopheles atropos* were associated with *bradleyi*. Another site, near Davis, also produced numerous *bradleyi*.

Nayar and Sauerman (1970a,b, 1974) have shown that under a constant temperature of 27°C and 12 hours of light, *bradleyi* pupation exhibited a distinct circadian rhythm. Initiation of pupation occurred 138 hours after hatch and the duration of pupation was 105 - 107 hours. In their standard rearing environment consisting of 75 larvae/pan, a basic food ration and 2 times and 4 times basic food rations, in 0.05 or 0.20 dilution sea water, onset of pupation occurred 189 hours after egg hatch.

Dyar (1902), Smith (1904) and Headlee (1921, 1945) studied the behavior of adult *crucians* [=*bradleyi*] in coastal habitats in New York and New Jersey. Smith and Headlee called it "The Daylight *Anopheles*" stating that it initiated flight before dark, *i.e.*, exhibited crepuscular activity. Biting counts conducted in Carteret and Pamlico counties, North Carolina, substantiate this.

In 1972 during one hour of biting count study at Newport River, 40 *bradleyi* were captured between 2030 and 2130 hrs; 48 percent were captured during the first 30 minutes. It was completely dark by the end of the second 30 minutes. Some *bradleyi* were always captured after dark. At North River in 1971, 11 *bradleyi* were captured by the biting count method between 2130 and 2230 hrs (LaSalle and Knight 1973). New Jersey Light Trap data from Newport River and Davis indicate *bradleyi* outnumbered *atropos* (1,667 to 1,049 at Davis over 8 months) (LaSalle and Knight 1973, 1974; personal observation).

Barber *et al.* (1924) at Gulfport, Mississippi, observed a large adult population of *crucians* [*?bradleyi*] and subsequently found the larvae producing this adult population 19.2 km off the coast on an island. Numerous adults were found on the island, and were eager to feed. MacCreary and Stearns (1937) reported *crucians* [=*bradleyi*] dispersed at least 5.5 km to an island offshore.

Although the salinity of the water reflects the larval habitat, *i.e.*, freshwater versus salt water, it is not the best indicator of site selection by ovipositing females. Knight (1965) considered the salinity of extracted soil water to be a reliable indicator of oviposition site selection because it approximates the existing conditions at oviposition, particularly for *Aedes sollicitans* and *Ae. taeniorhynchus*. Knight (1965:156-158) determined the total soluble salt concentration, *i.e.*, the specific conductance of the water expressed as millimhos/centimeter (mmhos/cm), for 5 common coastal North Carolina species. The specific conductance was highest for *bradleyi* (range 12.8 - 24.3 mmhos/cm, avg. 18.0). This was significant in that the average was 5.3 mmhos/cm more than the average for *Ae. sollicitans* and 15.5 mmhos/cm more than the average for *Ae. vexans* (Meigen), a common freshwater aedine mosquito. The slight minimal differences (2.6 mmhos/cm: 1.3 mmhos/cm) recorded between *sollicitans* and *vexans* distinctively separated the salt marsh and freshwater breeding aedine mosquitoes and established *bradleyi* as a brackish water inhabitant.

The effect of predators on larval populations of *bradleyi* has not been studied. However, several pathogens have been recovered from *bradleyi* larvae. Kellen *et al.* (1966) and Chapman, Clark and Petersen (1970) reported *Parathelohania* (as *Thelohania*), a protozoan, from *bradleyi* larvae. Petersen *et al.* (1968) and Petersen and Chapman (1970) successfully infected *bradleyi* larvae with the mermithids, *Gastromermis* and *Romanomermis*. In addition, a fungus, *Coelomomyces* sp., has been reported from *bradleyi* larvae (Chapman, Woodard *et al.* 1970).

Anopheles bradleyi larvae can be reared to adults following the methods of Nayar (1967, 1968) and Nayar and Sauerman (1970a).

Medical Importance. In general, it was not possible to determine which species - *bradleyi* or *crucians* - early malaria investigators examined. Ecological and/or larval habitat data usually were not included in these malaria studies. Some studies undoubtedly included *bradleyi*, either in part or as the only source of their "*crucians*" pool. Barber *et al.* (1927) probably included both *bradleyi* and *crucians* adults. Boyd *et al.* (1936) conducted the

only experiments comparing susceptibility of the freshwater [=*crucians*] and coastal [=*bradleyi*] forms of *crucians* to *P. falciparum* malaria. They infected *bradleyi* experimentally, but no natural infections have been reported.

Only one arbovirus study has implicated *bradleyi* as a vector of arboviruses. Buescher *et al.* (1970) isolated Cache Valley virus from the *crucians* subgroup (as *bradleyi-crucians*) on the Del-Mar-Va peninsula. They tested 82 pools (3097 specimens) of *bradleyi-crucians* for this arbovirus and found one positive pool. The proximity of their collection sites to brackish water suggests that most of their specimens were *bradleyi* adults.

ANOPHELES (ANOPHELES) GEORGIANUS KING

Anopheles crucians var. *georgianus* King 1939. TYPE: Holotype and associated larval and pupal skins; Brooks Co., Georgia, near Quitman, February 16, 1938, R. E. Bellamy and W. V. King (USNM).

Synonymy. Anopheline resembling the brackish water race of *crucians* - Bellamy 1939 (L).

Anopheles crucians var. *georgianus* of King 1939 (A, ♂*, P, L*, distribution) and Vargas 1940a(A), 1940b (L).

Anopheles crucians georgianus of Matheson in Moulton 1941 (malaria); Ross and Roberts 1943 (A, L*); Russell *et al.* 1943 (P, L, distribution); Schoof and Ashton 1944 (distribution); Carpenter *et al.* 1946 (A, ♂, L*, distribution); Yamaguti 1952 (A*, ♂*); Bargren 1953 (L).

Anopheles georgianus of Bradley and King in Moulton 1941 (bionomics); King and Bradley in Moulton 1941a (L); King and Bradley in Moulton 1941b (distribution); King *et al.* 1942 (sp. status); Frohne 1942 (distribution); Bellamy 1942 (L); King *et al.* 1943 (distribution); Bradley *et al.* 1944 (distribution); Matheson 1944 (A, ♂, L, distribution); Middlekauff and Carpenter 1944 (distribution); Roth 1944 (♂*); Wirth 1944 (L); Bickley 1945 (L); Carpenter *et al.* 1945 (distribution); Miles 1945 (L); Petersen and Smith 1945 (distribution); Miles and Rings 1946 (distribution); Carpenter and Chamberlain 1946 (distribution); Weathersbee and Arnold 1947 (distribution); Michener 1947 (L); Couch and Dodge 1947 (L, parasitism); Miles and Hill 1948 (distribution); Darsie 1949 (P*); Penn 1949 (P*); Freeborn 1949 (distribution); Bellamy and Repass 1950 (E*); Sheppard 1951 (distribution); Carpenter and LaCasse 1955 (A, ♂, L*, distribution); Horsfall 1955 (distribution); Stone *et al.* 1959 (distribution); King *et al.* 1960 (A, L, distribution); Dodge 1963, 1966 (L); Belkin *et al.* 1966 (bionomics); Carpenter 1968, 1970 (distribution).

Description. Females resemble *bradleyi* and *crucians*. Pupal seta 0 on II-VII simple, rarely with 2 - 3 branches; 5 on III-V well developed usually with more than 8 branches. Larval seta 0 on II-VII simple, rarely bifid;

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*An illustration is presented

1-III more like 1-II than 1-IV; 6-IV with 3 - 6 branches.

FEMALE. (Fig. 13). *Head.* Vertex scales pale, erect, expanded and notched at apex; interocular space narrow with short pale erect scales and elongate pale frontal setae; antennal pedicel with a few mixed scales, flagellomere one with some pale or mixed scales; palpus with dark erect scales on basal 0.33 giving shaggy appearance; distal scales decumbent; segment 5 entirely pale scaled, segment 4 with narrow apical and basal pale bands, segment 3 with narrow basal pale band; proboscis with erect dark scales basally, dark decumbent scales apically; proboscis/forefemur ratio approximately 1:1. *Thorax.* Anterior promontory scales erect, long and pale, scutum integument mottled brown, acrostichal and median prescutellar lines darker with pale setae along lines; remaining setae darker; anterior promontory, acrostichal, dorsocentral, lateral prescutal, fossal, antealar and supralar regions with long dark setae; scutum with long pale scales; prescutellar space with long pale setae; scutellum with long dark setae and shorter pale scales; anterior pronotum dark scaled dorsally, with long dark setae; pleural setae: 6 - 8 propleural, 3 - 5 spiracular, 4 - 6 prealar, 4 - 5 upper and 6 lower mesepisternal, 7 - 11 upper and 0 lower mesepimeral setae. *Wing.* Costa dark scaled to apical pale spot; subcosta dark; Radius dark scaled except for pale scales at R_s; R_1 dark except pale tip; R_s basal 0.5 dark, apical 0.5 pale; R_{2+3} apical 0.5 pale; R_2 tip pale; R_3 basal 0.5 and apical 0.2 dark scaled, median area with pale scales, R_{4+5} with mixed dark and pale scales, tip pale; Media with dark scales on basal portion, rest mixed or pale scaled; M_{1+2} with basal 0.33 and apical 0.25 dark, median pale; M_{3+4} basal 0.2 and apical 0.25 dark, median pale; Cubitus entirely dark; Cu_1 basal 0.33 - 0.50 and apical 0.2 dark, median with mixed or pale scales; Cu_2 basal 0.5 pale and apical 0.5 dark scaled; 1-A with basal, median and apical dark areas, pale areas on either side of dark median area; crossveins r-m and m-cu dark scaled, humeral cross vein scaleless; fringe scales dark at R_3, pale from R_1 to R_3 and from R_3 to R_{4+5}. *Halter.* Knob dark scaled with some dark setae. *Legs.* Coxae without scales, upper midcoxae with 3 - 4 setae; femora, tibiae and tarsomeres long and slender with dark decumbent scales and scattered dark setae, pale spots at apex of femur and base of tibia. *Abdomen.* Integument unicolorous with numerous dark setae.

MALE. (Fig. 13). *Head.* Palpus entirely dark scaled with 2 apical segments flattened and club-like; antennae strongly plumose. *Genitalia.* Basimere without scales; pair of parabasal spines inserted on a tubercle; internal spine on distal 0.5 of basimere; claspette lobes fused, with 4 strongly attenuated setae, usually in pairs; ventral (distal) setae stouter than others and approximately 0.2 - 0.5 longer than dorsal setae, dorsal (lateral) pair nearly equal in size and shape; aedeagus usually with 6 attenuated leaflets at apex; 9th tergum with long, slender lateral lobes.

PUPA. (Fig. 14, Appendix Table 4). Integument tan to light brown. *Cephalothorax.* Seta 5 usually with 8 - 10 branches; 7 long, slender and simple; 12 with 3 - 5 branches, approximately 1.20 - 1.25 longer than 10. *Trumpet.* Darkly pigmented with deep meatal cleft, meatus 0.25 - 0.33 as long as trumpet; usually with spiny spur or pinna. *Abdomen.* Setae 0 on II-VII

simple, occasionally bi- or trifid; 1-II with 5 - 11 branches; 1-III with 7 - 11 branches; 1-IV with 9 - 14 branches, 0.5 - 0.7 as long as segment V; 1-VI with 3 - 6 branches, 0.5 - 0.7 as long as segment VII; 2-IV with 4 - 7 branches; 2-V with 5 - 7 branches; 2 on VI-VII with 5 - 8 and 4 - 6 branches respectively; 3 on II-III with 3 - 8 branches; 3-IV with 5 - 12 branches; 3 on V-VII with 2 - 7 branches; sum of branches on both setae 3-V, 6 - 9; 4-I with 7 - 10 branches, approximately 0.5 as long as 5-I; 5-III with 5 - 13 branches; 5-IV with 12 - 17 branches, 0.50 - 0.66 as long as segment V; 5-V with 8 - 16 branches, 0.66 - 0.75 as long as segment VI; 5-VI with 9 - 13 branches, 0.66 - 0.75 as long as segment VII; 5-VII with 2 - 9 branches, 0.50 - 0.66 as long as segment VIII; 6-II with 3 - 6 branches, 0.66 - 0.75 as long as segment; 6-III with 4 - 9 branches, 0.66 - 0.75 as long as segment; 6-IV with 3 - 5 branches; 6 on V-VI with 1 - 3 branches; 7-I with 6 - 11 branches, 0.50 - 0.75 as long as 6-I; 7-II with 5 - 9 branches; 7-III with 3 - 6 branches; 7-IV with 2 - 5 branches; 7-V with 3 - 5 branches; 7-VI with 1 - 4 branches, 0.66 - 0.75 as long as segment; 7-VII simple, 0.75 - 0.90 as long as segment; 8 on III-VII with less than 5 branches, usually bi- or trifid; 9-III approximately 0.5 as long as 9-IV; 9-VII 3 - 5 times as long as wide. *Paddle*. Refractile margin 0.65 - 0.90 length of paddle; paddle margin beyond serrate portion with fine hairs to apical portion of inner margin; 1-P stout, attenuate, simple or split apically; 2-P with 2 - 4 branches.

4TH STAGE LARVA. (Fig. 15, Appendix Table 7). *Head*. Darker than thorax or abdomen; base of antenna as wide as tip; antenna not deeply pigmented, with many spines; 1-A with 4 - 6 branches, usually 5 - 6, inserted on basal 0.25 of antenna; 2,3-A attenuate, serrate on one edge, 4-A with 4 - 7 branches; 2-C long, simple, bases separated by less than diameter of an alveolus; 3-C with 23 to more than 38 broom-like branches, 0.50 - 0.75 as long as 2-C; 4-C usually bifid; 5,6,7-C long, plumose; 8-C with 3 - 6 branches; 9-C with 3 - 5 branches; 11-C as long as antenna usually with more than 40 branches. *Thorax*. Seta 1-P usually with 2 - 5 apical branches; 2-P stout with 9 - 15 branches, arising from tubercle, 1.50 - 1.66 longer than 1-P; 3-P simple or bifid, approximately equal in size to 1-P, closer to 2-P than 1-P is to 2-P; 4-P stout, arising from tubercle, closer to 5-P than 3-P, with 16 - 24 branches; 5,6-P arise from common tubercle, 6-P long and simple; 7,8-P well developed, approximately equal in length; 9,10,11,12 on all 3 thoracic segments arise on common base; 9,10-P,M,T simple; 11-P,M,T short simple, 12-P long simple; 12-M short with 1 - 3 branches; 12-T long with 3 - 7 branches; 13-P with 15 - 20 branches; 14-P with 5 - 8 branches; 1-M stout, well developed, arising from tubercle; 2-M usually with 2 - 5 apical branches; 3,5-M simple or bifid; 4-M with 2 - 5 branches; 6,7-M with 3 - 8 branches, 7-M usually 0.50 - 0.66 as long as 6-M; 8-M arising from tubercle and well developed; 14-M with 6 - 12 branches; 3-T with flattened leaflets; 5,7,8-T well developed and nearly equal in size; 6-T with 2 - 8 branches, usually 6 - 8; 13-T with 2 - 5 branches. *Abdomen*. Anterior and posterior tergal plates as on *crucians*. Zero on II-VII usually simple; 1 on 1-III with few small flattened pale leaflets; 1 on IV-VI nearly equal in size, with 15 - 26 dark serrated leaflets; 1-VII less than 0.2 as large as I-VI; 2-I with 3 - 5 branches; 2 on II-III with 4 - 9 and 4 - 10 branches respectively; 2 on IV-V with 2 - 5 branches; 2-VI with 3 - 6 branches; 2-VII with 4 - 7 branches; 2-VIII with

5 - 8 branches; 3-VI usually simple, caudal to 1-VI; 4-V with 4 - 6 branches; 5-I with 4 - 7 branches; 5-II with 7 - 14 branches; 5-III with 6 - 11 branches; 5-IV with 5 - 8 branches; 5 on V-VII with 6 - 11 branches; 5-VIII with 3 - 4 branches; 6,7 on I-II well developed and nearly equal in size; 6-III well developed with 14 - 26 branches; 6-IV with 3 - 6 branches, usually 5 - 6; 6-V with 2 - 4 branches; 6 on VI-VII with 2 - 5 branches, less than 0.2 as long as 6-V; 7 on III-VII with 2 - 5 branches, 0.2 or less as long as 7-II; 8-II with 2 - 5 branches; 8 on III-VII with 2 - 6 branches, usually 2 - 4; 9-I with 6 - 11 branches; 9-II with 7 - 12 branches; 9-III with 7 - 11 branches; 9-IV with 9 - 13 branches; 9-V with 9 - 13 branches; 9-VI with 8 - 11 branches; 9-VII with 3 - 5 branches, 9 on I-VII inserted closer to 6 on I-VII than 5 on I-VII is to 6 on I-VII; 10 on I-II usually bi- or trifid; 10 on III-IV with 2 - 3 branches; 10-V simple or with 2 - 3 branches; 10-VI with 3 - 5 branches; 10-VII with 2 - 7 branches; 11-I with 6 - 10 branches, 0.50 - 0.66 as long as segment; 11-II with 2 - 4 branches, 0.66 - 0.75 as long as segment; 11-III with 2 - 3 branches, approximately 0.25 as long as segment; 11 on IV-VI with 1 - 4 branches, approximately 0.25 as long as the segment; 12-I with 3 - 6 branches; 12-II with 1 - 3 branches; 12 on III-V with 2 - 3 branches, approximately 0.25 as long as respective segments; 12 on VI-VII simple or bifid; 13-I with 2 - 4 branches; 13-II with 4 - 9 branches; 13 on III-IV with 4 - 6 and 3 - 6 branches respectively; 13 on I-IV approximately 0.25 as long as the segment; 13-V with 3 - 5 branches, 0.33 - 0.66 as long as the segment; 13-VI with 5 - 7 branches; 13-VII with 2 - 3 branches; spiracular lobe seta 1 with 3 - 4 branches; 2-S with 4 - 7 branches, inserted on pecten plate; 3,4,5-S minute; 6-S simple or bifid; 7-S minute, inserted at apex of spiracular valve; 8,9-S inserted caudally on spiracular lobe, with 3 - 4 branches; 11,12,13-S minute; pecten with 9 - 11 long and 13 - 15 short teeth, the short teeth often in pairs or groups of 3; seta 1-X as long or longer than saddle.

Distribution. (Fig. 14). *Anopheles georgianus* occurs only in the southeastern United States. It has been collected from 7 states (Alabama, Georgia, Florida, Louisiana, Mississippi, North and South Carolina). A total of 6♀, 4♂, 32P, 29WL, 16L, 2G specimens were examined from the following states: Florida: Jacksonville, 24-IX-1942, 1♂. Camp Blanding, 1WL; 26-VII-1944, 4WL; 15-III-1946, S. O. Hill, 1WL. Panama City, 10-IV-1943, 1WL. Tallahassee, 12-II-1945, M. W. Provost, 1♀. Barrancis, 26-II-1946, 1WL. Holmes Co., Ponce de Leon, 8-IV-1948, Thurman and Calloway, 1WL; 28-IV-1948, Thurman and Calloway, 1♀, 2WL. Georgia: "Ga153", R. E. Bellamy, 3WL. Brooks Co., "Br296", 21-X-1937, R. E. Bellamy, 1WL; "Ga75", 11-I-1938, R. E. Bellamy, 1♀, 2P, 2L; Quitman, "Fla1955", 26-XI-1937, R. E. Bellamy, 1WL, 1G; Quitman, "Fla1957", 16-II-1938, W. V. King and R. E. Bellamy, 3♀, 2♂, 29P, 11L, 1G (type-series). Thomas Co., "Ga74", 10-I-1938, R. E. Bellamy, 1♂, 1P, 1L. Sumter Co., "F.C. 3398", 10-V-1950, R. E. Bellamy, 2L. Camp Stewart, 1-XII-1942, Wm. C. Grimn, 1WL. Camp Gordon, 17-IX-1946, 1WL. Louisiana: Camp Polk, "310", 30-I-1942, R. W. Bunn, 1WL; "La68", 22-VII-1942, W. W. Wirth, 1WL. Camp Livingston, 15-IV-1942, 1WL; 8-II-1943, W. W. Wirth, 1WL. North Carolina: Ft. Bragg, 9-VIII-1943, D. F. Ashton, 5WL. Camp MacKall, 22-VIII-1944, L. Roth, 1WL. South Carolina: Ft. Jackson, 20-VII-1944, 4th S.C.M. Lab., 1WL.

Taxonomic Discussion. Bellamy (1939) collected anopheline larvae near Quitman, Georgia, about 120 km from the coast, that morphologically resembled the brackish water race of *crucians* previously described by Bradley (1932a, 1936). After collecting additional specimens of this mosquito, King (1939) described it as *crucians* variety *georgianus*. In King *et al.* (1942), King raised the varietal names to full species rank. Although Carpenter *et al.* (1946), Yamaguti (1952) and others considered *georgianus* a subspecies of *crucians*, we are following Carpenter and LaCasse (1955), Horsfall (1955) and King *et al.* (1960) and considering *georgianus* a distinct species. Besides characters used by the above authors to justify the species status of *georgianus*, we have found additional larval and pupal characters to support the distinctness of this taxon.

Adults are currently indistinguishable from *crucians* and dark-winged specimens of *bradleyi*. A few adult *georgianus* were larger than either *bradleyi* or *crucians*, however, this trend was not constant. The dark fringe spot opposite vein R_3 usually is distinctive, but some reared *crucians* with associated immature skins collected near Quitman, Georgia, also exhibited this dark fringe spot. Vein Cu and Cu_2 coloration on *georgianus* is identical to that of *crucians*. The male genitalia are similar to the other subgroup members, especially *crucians*.

Anopheles georgianus is distinct from *bradleyi* and *crucians* only in the pupal and larval stages. Pupae of *georgianus* can be separated from *bradleyi* and *crucians* by using the branching of 0 on III-VI, 2-IV, and the number of branches of setae 1,5 on IV-V. Seta 0 on III-VI on *crucians* is large and multibranched: 2 - 7 on III; 1 - 7 on IV; 3 - 11 on V; 2 - 5 on VI. On *georgianus* (and *bradleyi*) seta 0 is usually small, simple or bifid. Seta 2-IV has 4 - 7 branches on *georgianus*, while 2-IV usually has more than 7 branches on *crucians*. Setae 1,5-IV on *georgianus* have 9 - 14 and 12 - 17 branches respectively; on *bradleyi* these setae have 5 - 9 and 5 - 10 branches respectively. Setae 1,5-V on *georgianus* have 6 - 10 and 8 - 16 branches; on *bradleyi* they have 3 - 6 and 3 - 8 branches respectively.

Larvae of *georgianus* have 0 on III-V small, simple or bifid. On *crucians* these setae are always multibranched and nearly as large as seta 2 on III-V. Seta 1-III on *georgianus* more closely resembles 1-II than 1-IV. This character separates *georgianus* from *crucians* as well as from most *bradleyi*. Seta 8-III on *georgianus* has 3 - 4 branches; on *crucians* 8-III has 6 - 12 branches. Larvae of *georgianus* are more difficult to separate from *bradleyi*. In addition to the general difference in appearance of seta 1-III, 5-II on *georgianus* has 7 - 14 branches compared to 5 - 9 on *bradleyi*, 6-IV on *georgianus* has 3 - 6 branches (usually on 3 on *bradleyi*) and 11-I has 6 - 10 branches on *georgianus* while only 4 - 6 on *bradleyi*.

Pupal slides were not examined to determine if any variations or aberrations occurred because the pupal skins were poorly mounted, and it was difficult to determine the range in setal branching. An insufficient number of slides were adequately mounted to allow detailed taxonomic evaluation. One variation was observed; the larva on slide F1 1957-7 (16-II-1938) had 2 branches on the right seta 2-C.

The holotype, allotype and paratypes examined were only in fair condition. The pupal mounts, in fact, were poorly mounted with the cephalothorax folded or with the entire exuvia in one piece. Whole larval mounts were dark, particularly those examined from Louisiana and North Carolina. Larval skins, in general, were better prepared than pupal skins or whole larvae, but were deteriorating or drying out. Most of the larval skins were excessively stretched and it was difficult to determine exact setal positions. Adult specimens were in better condition with only a few legs and wing scales missing from the entire series housed at the USNM. Most specimens examined were mounted in the late 1930's and early 1940's. Two larval slides, one containing 3 whole larvae, prepared by Bellamy in 1950 were found in the general laboratory collection of a course the senior author was taking at North Carolina State University.

Bionomics. Immature *georgianus* were found in pastureland seepage areas, hoofprints, and potholes (Bellamy 1939, King 1939). Typical habitats were 10 - 35 cm in diameter and about 5 cm deep (Wirth 1944). He characterized the habitat as clear water situations with filamentous algae and grassy margins. Wirth considered the pitcher plant, *Sarracenia purpurea* Linnaeus, an indicator of the typical habitat. In southern Mississippi, Michener (1947) collected *georgianus* larvae from shaded pools full of decaying leaves. The water was stained brownish-black, and not clear. These habitat descriptions suggest a distinct microhabitat. The last reported collection of *georgianus* was Bellamy and Repass (1950).

The lack of published reports of *georgianus* in the last 25 years leads one to suggest: 1) that *georgianus* has not been reported recently due to insufficient collecting, probably as a direct result of the curtailment of investigation associated with the conclusion of the National Malaria Eradication Program in the early 1950's (Andrews 1951); 2) that urbanization and 20th century technology, including the increased usage of pesticides, have altered or eliminated its microhabitat, and *georgianus* has been unable to adapt or to maintain its populations.

Our attempts to collect *georgianus* at Quitman, Georgia, the type-locality, and in North Carolina were unsuccessful. More investigations throughout the southeastern United States will probably lead to the collection of *georgianus*. No information on adult behavior is available.

With the exception of one report no predator/pathogen studies have involved *georgianus*. Couch and Dodge (1947) reported that of 38 *Coelomomyces quadrangulatus* Couch collections from Georgia in 1945, 13 were from *crucians* and one was from *georgianus*.

Medical Importance. No published malaria or arbovirus investigations have involved *georgianus*.

UNDETERMINED SPECIMENS

The following 69♀ and 24♂ adults were not identified due to overlapping wing scale coloration. In the absence of associated immature skins they have been labeled *bradleyi-crucians* complex. Alabama: Grandview Park, 23-III-1944, 2♂. District of Columbia: Washington, IX-1906, T. Pergande, 1♀. Catholic University, 4-X-1906, T. Pergande, 1♀. Florida: Paradise Key, 23-II-1919, Schwarz and Barber, 3♀; 27-II-1919, A. Wetmore, 1♀. Miami, 1-XI-1921, G. F. Moznette, 1♀. Orlando, 2-XII-1931, 1♀. Jacksonville, 25-IX-1944, D. C. Thurman, 1♀. Duval Co., 12-X-1944, D. C. Thurman, 1♂. Tallahassee, 15-X-1944, 2♀, 1♂. Gainesville, 24-XI-1944, D. C. Thurman, 1♀; 30-I-1945, 2♀. Tyndall Field, 23-V-1945, 1♀. Lake City, 1-X-1945, 1♂. Pineland, 18-IV-1947, Gill, 1♀. Grant, 6-XII-1947, McNaught, 1♀. Ft. Clinch, 11-II-1948, Decker, 1♀. Ormond Beach, 25-IV-1952, C. Sabrosky, 1♀. Spring Grove, 20-IX-1901, A. O. Hiscock, 1♀. Maryland: Piney Point, 2♀; 29-VI-1904, T. Pergande, 2♀, 4♂. VI-1906, T. Pergande, 3♂. Crisfield, 15-VIII-1932, 5♀; 16-VIII-1933, F. C. Bishopp, 6♀. Chesapeake Beach, 19-20-VI-1933, F. C. Bishopp, 3♀, 1♂; 28-VII-1933, F. C. Bishopp, 2♀, 1♂. Salisbury, 8-IX-1932, 1♀. Worton, 17-VIII-1933, F. C. Bishopp, 1♀. Princess Anne, 21-IX-1933, F. C. Bishopp, 1♀. Mississippi: Harmon, "4704.2", 22-V-1915, 1♀. New Jersey: Cape May, VII-1930, J. M. Aldrich, 1♀. South Carolina: McClellonville, 12-X-1906, 1♀. Beaufort, "152", 25-V-1912, Jennings, 1♀. Santee-Cooper Reservoir, 25-IX-1944, C. W. Sabrosky, 3♀; 26-IX-1944, C. W. Sabrosky, 1♂; 27-IX-1944, C. W. Sabrosky, 1♂; 1-XI-1944, C. W. Sabrosky, 1♂; 10-XI-1944, C. W. Sabrosky, 3♂; 27-XI-1944, C. W. Sabrosky, 1♀, 1♂. Texas: Mission, 5-II-1924, R. L. Turner, 1♀. Brownsville, 15-II-1924, R. L. Turner, 1♀; 18-I-1940, 1♀. Virginia: Richmond, Mrs. Slosson, 1♀. Emporia, 22-VIII-1915, T. H. D. Griffitts, 1♂. British Honduras: Belize, 31-X-1939, 8♀. Costa Rica: Buco del Toro, 1♀. Cuba: LaHavane, 1907, 1♂. Centra Jaronu, 17-XI-1927, H. K. Plank, 1♀. Guatemala: Dept. Guate, 4 mi S. Armititlan, 9-XII-1949, J. M. Brennan, 1♂. Mexico: Tampico, Jos. Goldberger, 1♀; 22-I-1926, J. A. LePrince, 1♀. Cobos Camp, Tuxpam R., 17-II-1921, J. A. LePrince, 2♀.

DISCUSSION AND SUMMARY

Several topics require more discussion or need to be summarized. These include: 1) species groups and phylogeny, 2) recent genetic studies on the *crucians* subgroup, 3) the morphology and distribution of the subgroup, and 4) continuing research.

Assigning closely related anopheline species to categories, called groups or complexes, dates back at least to Theobald (1901), who used the term "Sinensis Group" for *An. sinensis* Wiedemann and similar species. More recently, exacting taxonomic, ecological, ethological and cytogenetic studies have exposed a number of closely related groups of species or sibling species as defined by Mayr (1969). However, some of the proposed groups still need clarification. The *punctipennis* species group (Reid and Knight 1961) is one of these. Reid and Knight proposed this group to include *bradleyi*, *crucians*, *georgianus*, *perplexens* and *punctipennis*. Baker and Kitzmiller (1964), using cytogenetic evidence, considered *punctipennis* a member of the *maculipennis* species complex. This was modified somewhat by Kitzmiller *et al.* (1967), who

retained *punctipennis* in the *maculipennis* species complex, but as a distantly related species (or species complex) that needed further clarification. Reid and Knight (1961) characterized the anterior pronotal lobes as being scaleless on species in the *maculipennis* and *punctipennis* species groups. However, all specimens of *punctipennis* and the *crucians* subgroup examined during this study have scales on the anterior pronotal lobes. The presence or absence of scales on the anterior pronotal lobes has been shown highly significant in defining species groups in the *Anopheles*, *Lophoscelomyia* and *Myzorhynchus* Series in the subgenus *Anopheles* (Reid and Knight 1961, Reid 1968). Regardless of the Reid and Knight oversight, their 1961 species group classification will be followed here because further morphological evidence has been found that links *punctipennis* with the *crucians* subgroup and separates it from the *maculipennis* species group. Another reason for supporting the Reid and Knight classification is conflicting evidence regarding the relationship of *punctipennis* to the *maculipennis* species group. Kitzmiller and Baker (1965) presented evidence that the chromosomes of *punctipennis* are much more similar to chromosomes of *earlei*, than to other members of the *maculipennis* species group. Yet attempts crossing *punctipennis* with *aztecus* Hoffman, *freeborni* and *quadrimaculatus* were more successful than attempts crossing *punctipennis* with *earlei* (Kitzmiller *et al.* 1967). Thus, attempted hybridization studies (Kitzmiller and Baker 1965, Kitzmiller *et al.* 1967) have not confirmed a relationship between the described similarities and actual affinity. Apparently no efforts have been made to hybridize *punctipennis* with either *bradleyi* or *crucians*.

The *punctipennis* species group can be divided into 2 subgroups, *i.e.*, the *punctipennis* subgroup including *perplexens* and *punctipennis*, and the *crucians* subgroup including *bradleyi*, *crucians* and *georgianus*. Although the *punctipennis* species group may not be a natural assemblage, the *punctipennis* subgroup and *crucians* subgroup represent monophyletic sibling species assemblages. In the *crucians* subgroup, *crucians* is probably the ancestral species because: 1) its distribution is nearly totally sympatric with the distribution of *bradleyi* and *georgianus*; 2) it is physiologically and ecologically much more adaptable, with populations in its distribution occupying habitats very similar to those of *bradleyi* and *georgianus*; and 3) its immature stages are intermediate to *bradleyi* and *georgianus* in setal branching numbers. The evolution and speciation processes leading from *crucians* to *bradleyi* or *georgianus* are uncertain, and remain undetermined at this time.

Genetic studies of the North America anophelines began in the 1950's (Davidson and Mason 1963). Salivary gland chromosome studies of *bradleyi* and *crucians* were initiated in 1965, and preliminary results indicated the 2 species exhibited very few chromosomal differences (Kitzmiller *et al.* 1967). Kreutzer *et al.* (1970) found a difference between *bradleyi* and *crucians* of no more than 5 paracentric inversions, *i.e.*, one on the X chromosome, one on 2R, 2 on 3R, and one on 3L, and also a few minor single band differences. Concurrently, Kreutzer and Kitzmiller (1971) studied the hybridization of *bradleyi* and *crucians* and found at least partial reproductive isolation between these species. The F_1 males were sterile and the hybrid females, when backcrossed with normal males, produced fewer progeny than normal females.

In addition, they found some natural *crucians* populations with X-chromosome aberrations that resembled the standard *bradleyi* configuration and/or some of the hybrid configurations. These aberrations occurred at a very low level in the sampled populations and were significant in demonstrating that the *bradleyi* chromosome banding pattern also occurred in the *crucians* populations.

Unfortunately, the cytogenetic work of Kreutzer *et al.* (1970) and the hybridization study of Kreutzer and Kitzmiller (1971) on *bradleyi* and *crucians* must be seriously questioned for basic taxonomic reasons, *i.e.*, the correct identification of the "*bradleyi*" used in their experiments. No whole larvae, associated immature skins or adults were retained from those studies to confirm their identifications (Kreutzer 1975, *in litt.*). Kreutzer and Kitzmiller (1971) stated that *bradleyi*, *crucians* and *georgianus* "are morphologically very similar, and may be separated with certainty only as fourth instar larvae". These authors tabulated the morphological characters they used to differentiate *bradleyi* from *crucians*, using one adult and 4 larval differences. Kreutzer (1975 *in litt.*) considered the outer clypeal (seta 3-C) character as the best for separating these 2 species. This character was listed (Kreutzer and Kitzmiller 1971) as *crucians* "outer clypeal hairs with 25 to 30 branches" while *bradleyi* "outer clypeal hairs with five to 10 branches". Previous major publications and keys to this subgroup and to United States anophelines list *bradleyi* as having 3-C thickly and dichotomously branched (King 1939, King *et al.* 1960), densely dichotomously branched (Carpenter *et al.* 1946, Carpenter and LaCasse 1955) or 25 or more branches (Stojanovich 1960). The low number of 3-C branches listed for *bradleyi* by Kreutzer and Kitzmiller is identical to the number of branches described for *atropos*, another salt marsh anopheline that can be very common in Florida (King *et al.* 1960, Kreutzer *et al.* 1969). In fact, *atropos* is separated from all the other southeast United States anophelines (except *albimanus* Wiedemann and *barberi* Coquillett) by having only 5 - 10 branches on 3-C (Carpenter *et al.* 1946, Carpenter and LaCasse 1955, King *et al.* 1960, Stojanovich 1960). Further evidence for this species mixup comes from another larval character listed by Kreutzer and Kitzmiller (1971), where they list seta 0 on *bradleyi* as "absent or very much smaller than hair two". Seta 0 on *bradleyi* is always much smaller than seta 2, but it is never absent. However, seta 0 on *atropos* is considerably smaller and difficult to detect, so much so that Carpenter *et al.* (1946) and Carpenter and LaCasse (1955) listed this seta as "obsolete" on *atropos*. The other 2 larval characters Kreutzer and Kitzmiller listed for *bradleyi* are identical on *atropos*, *i.e.*, seta 2 on abdominal segments IV-V is usually single or double and palmate seta 1 on segment 3 is smaller than I-IV. On *atropos* seta 2-C is usually sparsely feathered at the tip (cf. *bradleyi* simple), but 2-C on *atropos* is occasionally simple (Carpenter and LaCasse 1955, King *et al.* 1960). Kitzmiller (1975 *in litt.*) stated that the one adult character, *i.e.*, pale scales on vein Cu stem, was unreliable for separating *bradleyi* from *crucians* in Florida. However, this was the only character in their table that could not be applied to *atropos*.

Larval setal counts made during the present study were based on reared skins with associated pupal skins and adults. These counts show that *bradleyi* normally has 20 or more branches on seta 3-C, but occasionally may have slightly less than 20 [this study (16); Carpenter and LaCasse 1955, Fig. 27c (19)]. The lowest number of 3-C branches recorded for Florida *bradleyi* specimens was 20.

Although most *bradleyi* and *crucians* adults still cannot be separated, the larvae and pupae are easily differentiated. Consequently, adults can be definitely assigned to species by reared associated immature skins. In future cytogenetic studies on sibling species in which the adults cannot be separated and the immatures must be used for identification (*e.g.*, *crucians* subgroup), it would be advantageous to make preparations of polytene chromosomes from adult female ovariole nurse cells. At least 2 different techniques have been described for this type preparation (Coluzzi 1968, Green 1970). Sacrificing the adults in that type study would leave the identifiable immature stages available for confirmation. In the reverse situations, *i.e.*, where adults are identifiable, but immatures are not, then preparations of polytene chromosomes from 4th stage larvae (French *et al.* 1962) can be made from larvae from known mothers and the mothers can be preserved for confirmation.

Publications on morphology and distribution of the *crucians* subgroup, as indicated in the Historical Review and species discussions, before 1939 were often inaccurate. One species, *i.e.*, *crucians*, was recognized, but it clearly occupied at least 2 distinct niches (see *bradleyi* and *crucians* Bionomics). This led to confusion in species descriptions, *e.g.*, Smith (1904: 154) obviously described *bradleyi*, not *crucians*, larvae. Root (1924b) though often not credited, first recognized the presence of 2 races of *crucians* and in 1929 presented a key to separate these races. Bradley (1932b,1936) is usually credited with both of these accomplishments. King (1939) actually first described *bradleyi* as a variety of *crucians*.

The larval keys by Howard, Dyar and Knab (1917), Beyer (1923), Herms (1923), and Komp (1923) utilized the relative size of abdominal seta 1 on III-VII. This character proved unreliable and impractical and Russell (1925) used a combination of dorsal setal characters to develop a practical key to the 3 common anopheline species in the southeastern United States. He observed that setae 0,2 on IV,V were multibranched and nearly equal in size on *crucians*. This easily separated *crucians* from *quadrimaculatus* and *punctipennis*. Russell acknowledged the usefulness of the ventral setae, but failed to utilize them. Root (1924c) had used ventral chaetotaxy in his study of *quadrimaculatus* and *punctipennis*.

In addition to accurate larval descriptions, ecological data, particularly habitat, is a necessary component in species identification within this subgroup. Generally salinity provides an excellent basis for separating *bradleyi* and *crucians*. *Anopheles crucians* has not been reported from water with a high salinity. *Anopheles crucians* has recently been found on the Del-Mar-Va Peninsula in water with chlorinity concentrations up to 0.13 - 0.17 g/l, while *bradleyi* was found in concentrations ranging from 0.1 - 7.9 g/l. Concentrations of 0.13 - 0.17 g/l are probably ecologically "fresh water", since sea water is usually about 19.0 g/l. Thus, the reports by Dyar (1902), Smith (1904), Mitchell (1907), Howard, Dyar and Knab (1912-1917), Griffitts (1921, 1928a,b), and others probably represented more *bradleyi* collections than *crucians*. Based on their descriptions and the ecological data in the reports, we have placed these citations under the correct species, therefore some citations previously listed as *crucians* appear under *bradleyi*, and in some cases, in both synonymies if both species were discussed.

The pupae of the North American mosquito fauna have been largely neglected. The pupal stage is now recognized by most mosquito taxonomists as a valuable aid to mosquito identification and affinities. In some Oriental anopheline groups the pupal stage offers the most reliable taxonomic characters for identifying the included species. King (1939) offered very brief descriptions of *bradleyi* and *georgianus* pupae. The pupal descriptions by Darsie (1949) and Penn (1949) were much more valuable, yet still not complete. Since 1949, Belkin (1952, 1953, 1954) and Knight (1971) have presented corrected interpretations of pupal setal homologies and terminology. However, very few North American pupae have been described using the Belkin system.

Mitchell's (1907) illustration of an egg of *crucians* from a brackish water habitat near New Orleans, is considered herein to be *bradleyi*. Bellamy and Repass (1950) have the first description of *crucians* eggs. Some seasonal variation probably occurs in the eggs of the *crucians* subgroup as Hurlbut (1938) has described in *walkeri* eggs. This is based on the reports by Bellamy and Repass (1950) on the intergradation of characters between the eggs of *crucians* and *georgianus* and Breeland's (1953) discussion of variation in the eggs of some *crucians* collected in southern Georgia. Much work remains to be done on the eggs of North American anophelines, including the *crucians* subgroup.

The mosquitoes of the United States need to be re-examined and where necessary, redescribed utilizing current concepts. The last monographic study of the United States Culicidae was Carpenter and LaCasse (1955), and although Carpenter (1968, 1970, 1974) has updated this work, it is not a complete systematic treatment. The present study has attempted to bring our knowledge of the *crucians* subgroup up to a level equal to that now existing for some mosquito species groups in other regions of the world.

A bio-ecological study in the Delaware, Maryland and Virginia area will set a precedent by utilizing computer systems for the analysis of data (Eldridge, unpublished material). Computer analysis of data and computerized population modeling is a relatively new component to the science of entomology (Moss and Hendrickson 1973).

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LIST OF FIGURE ABBREVIATIONS.

Male Genitalia

AE = Aedeagus
B = Basimere
CL = Claspette
D = Distimere
IX-T = Tergum IX

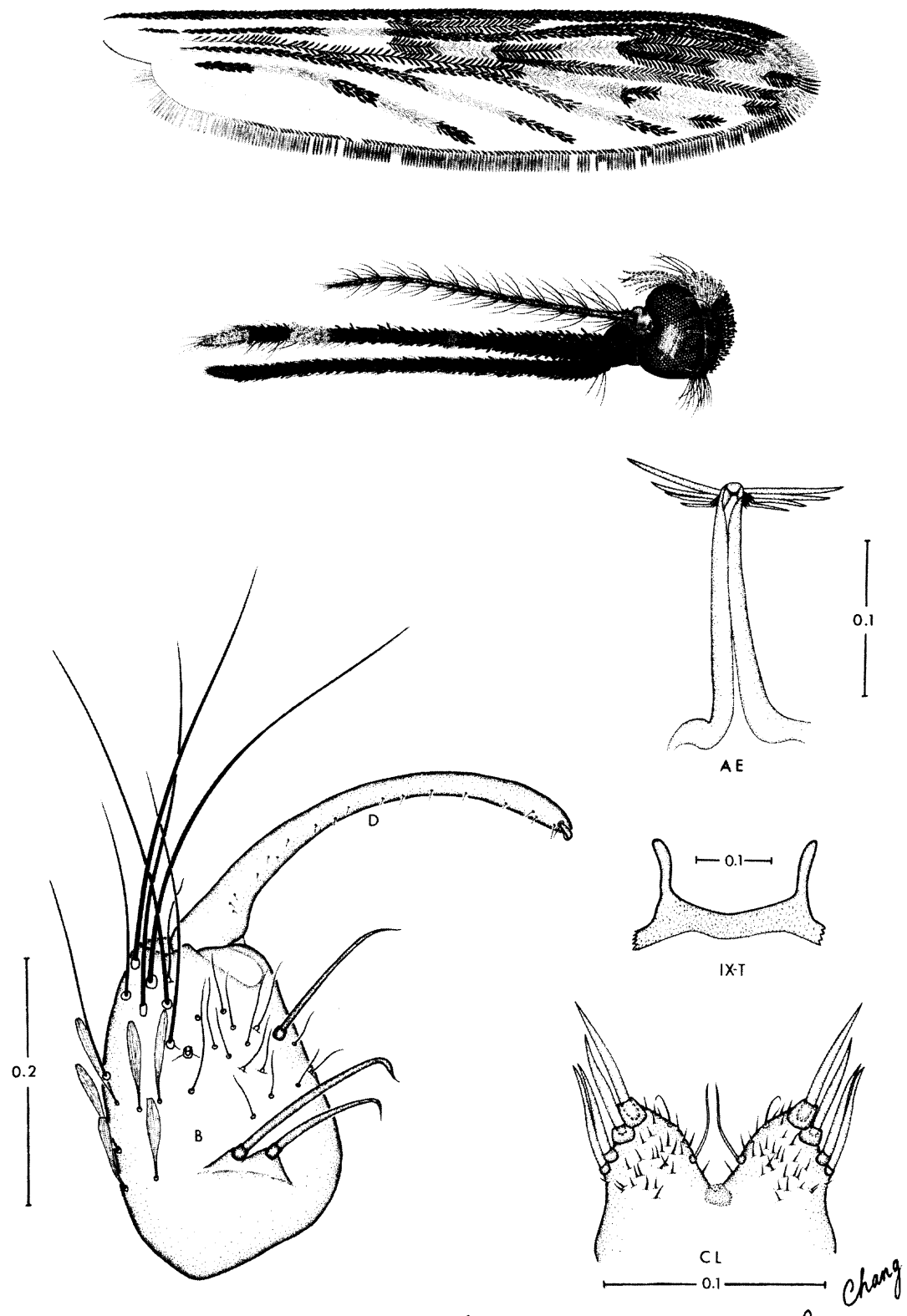
Pupa

C = Cephalothorax
P = Paddle
I-VIII = Abdominal segments I-VIII

Larva

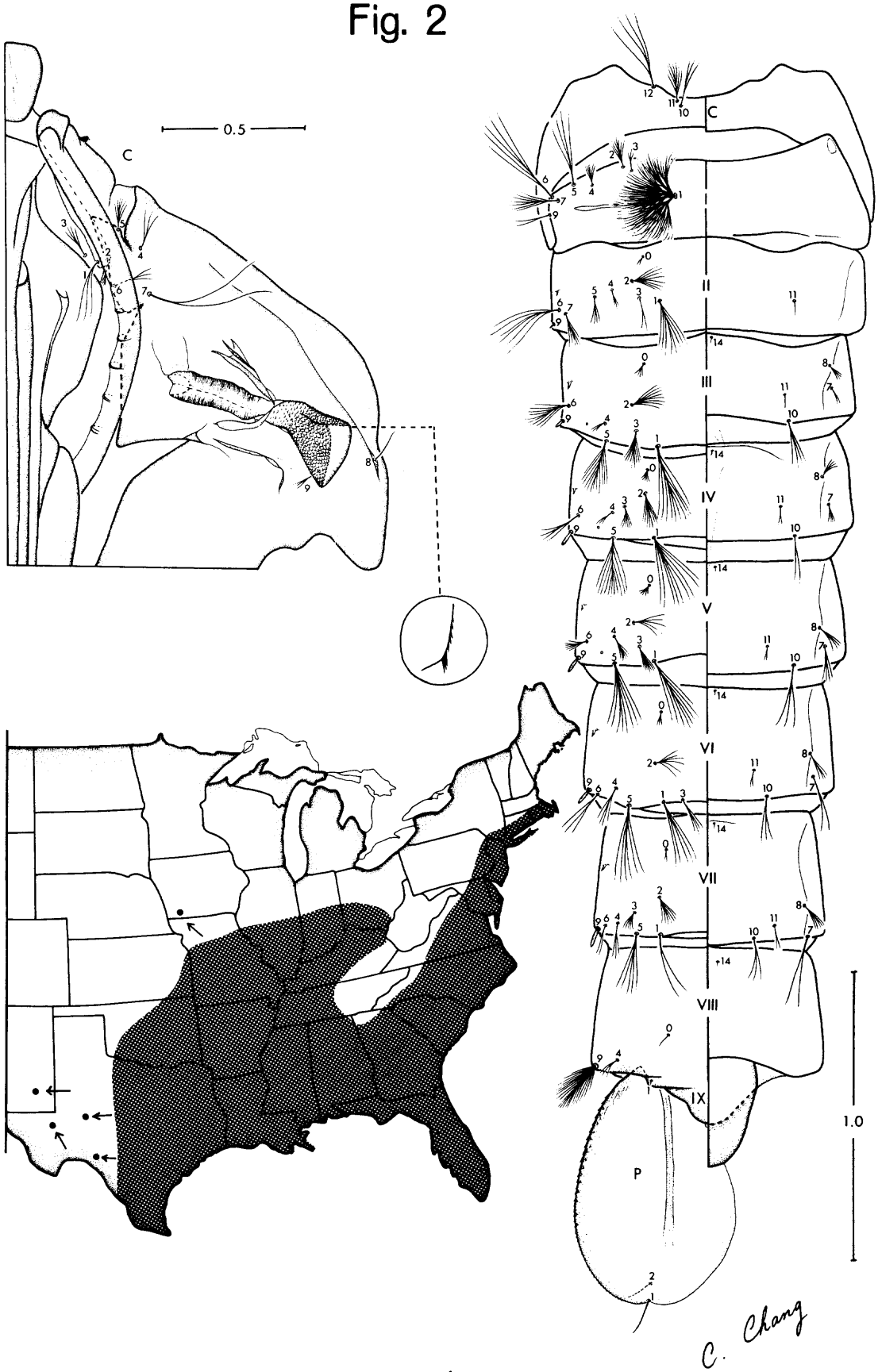
A = Antenna
C = Head
CS = Comb scale
I-VIII,X = Abdominal segments I-VIII,X
M = Mesothorax
P = Prothorax
PPL = Pecten plate
T = Metathorax

Fig. 1



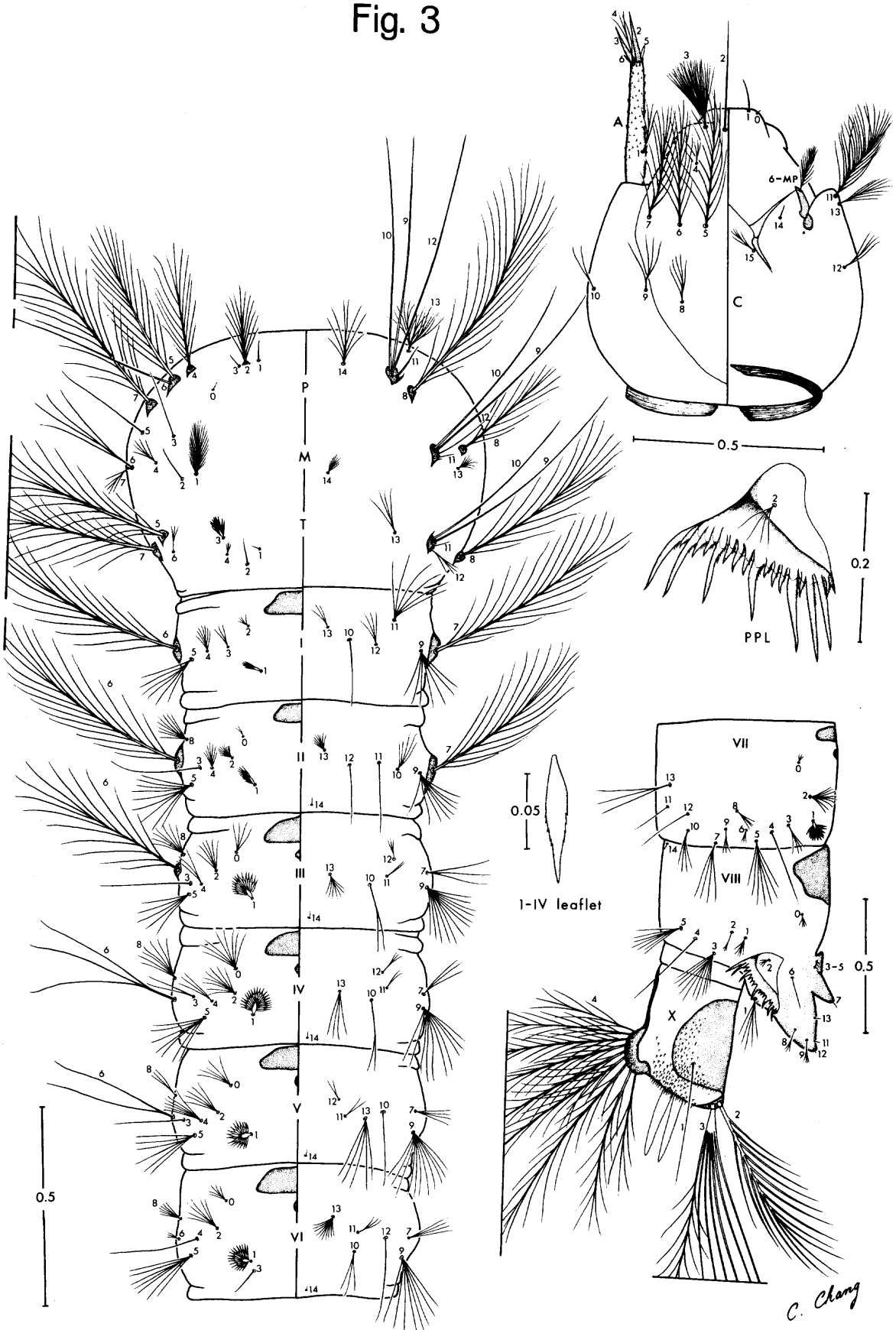
crucians

Fig. 2



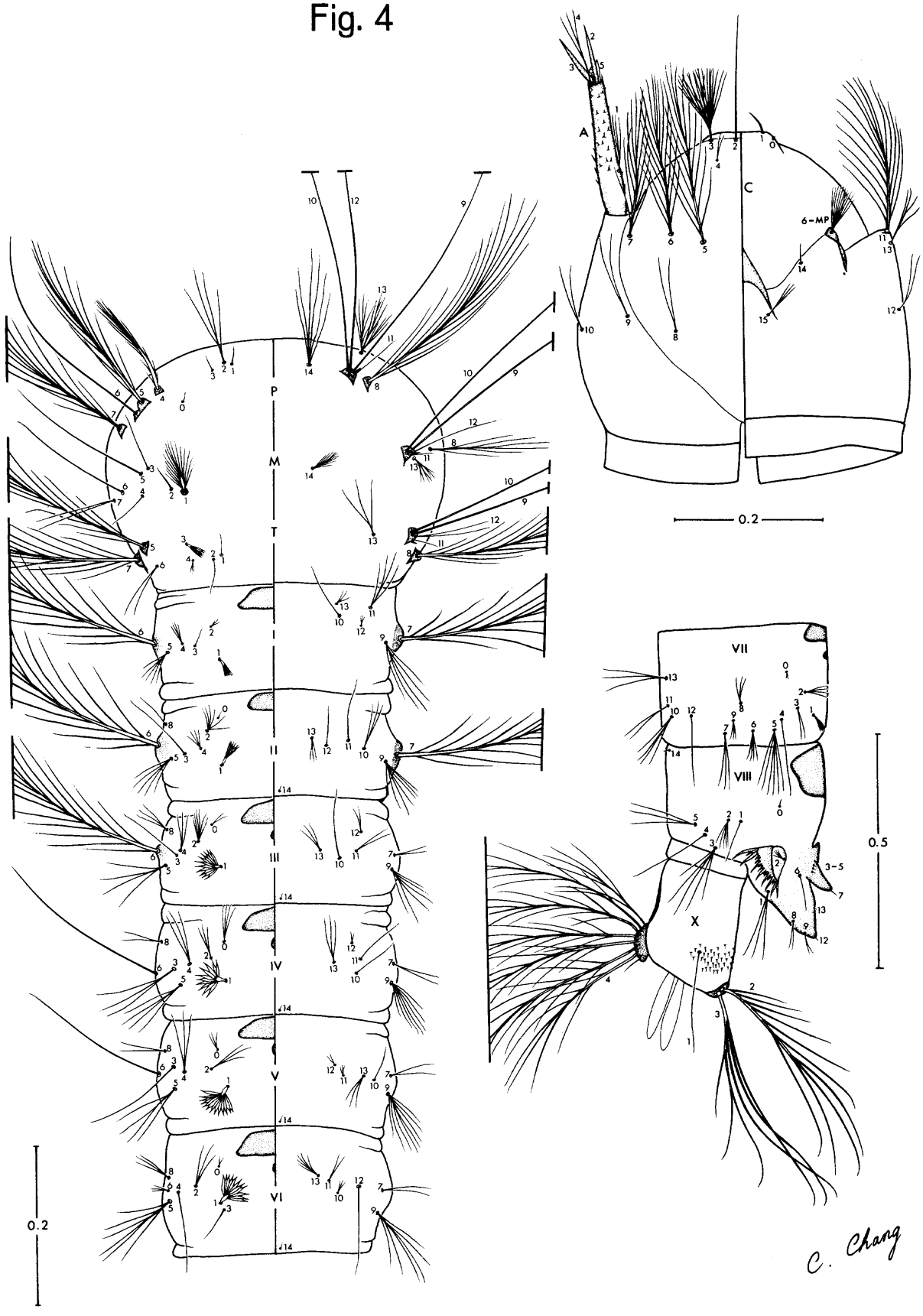
crucians

Fig. 3



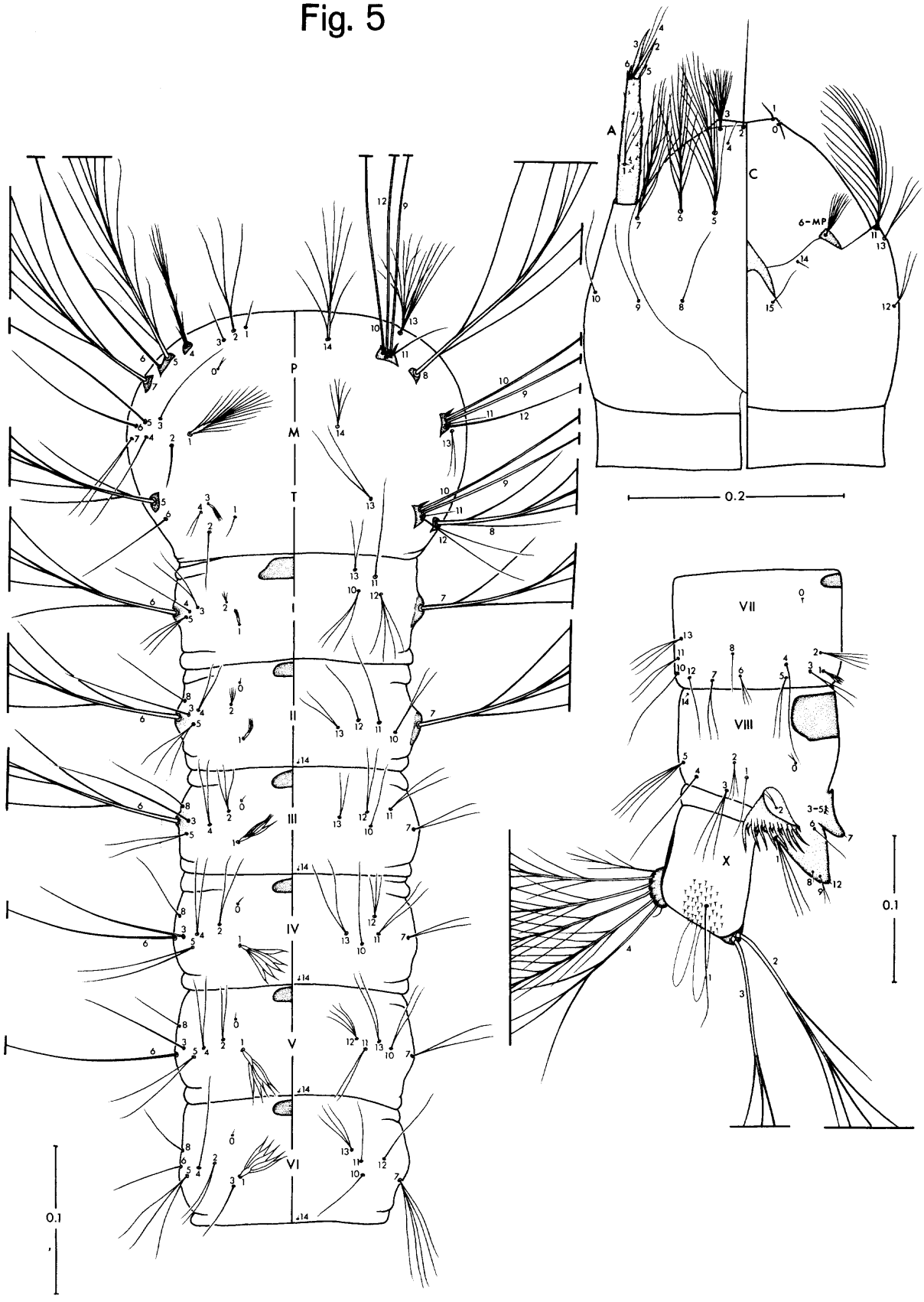
crucians 4th instar

Fig. 4



crucians 3rd instar

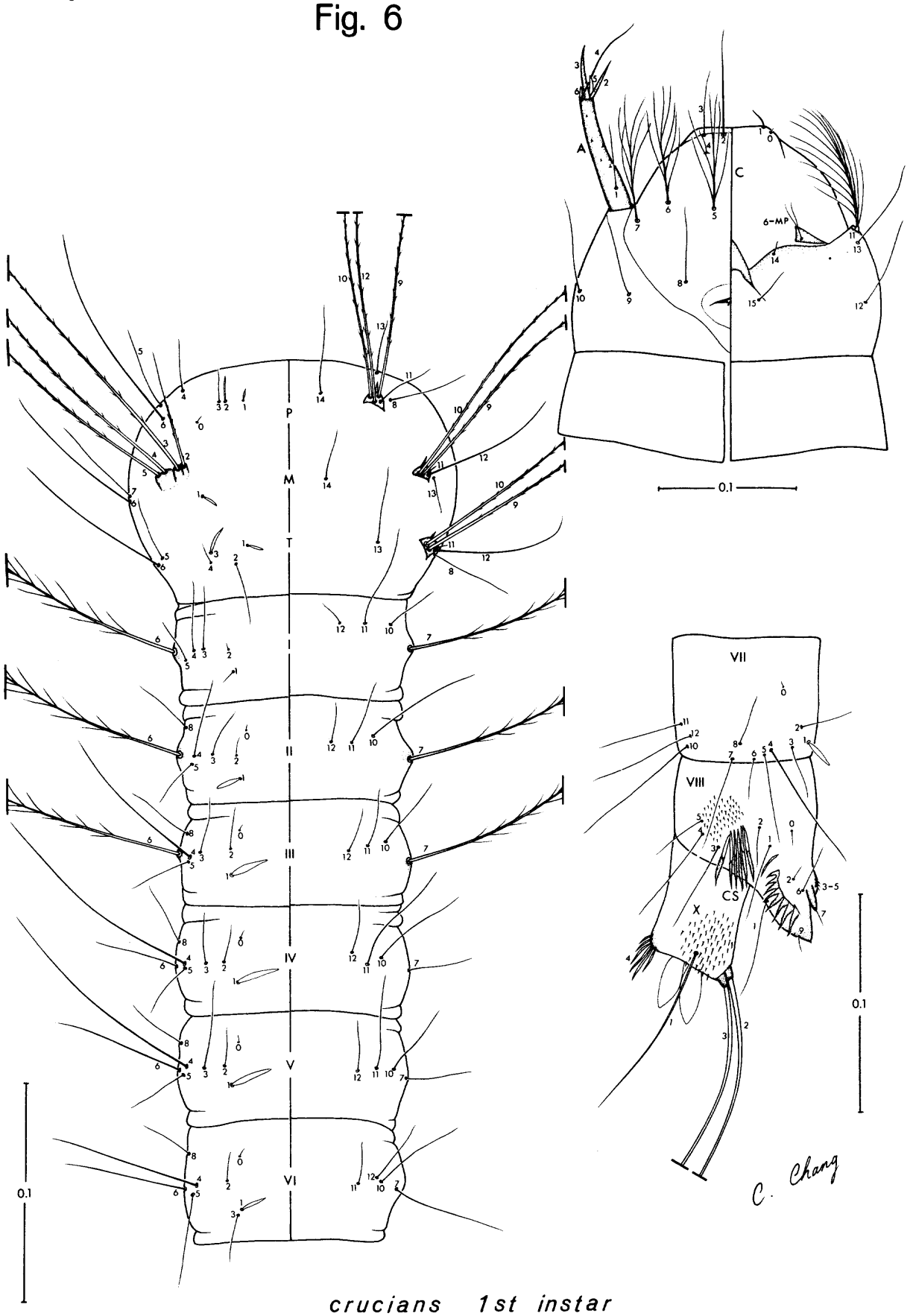
Fig. 5



crucians 2 nd instar

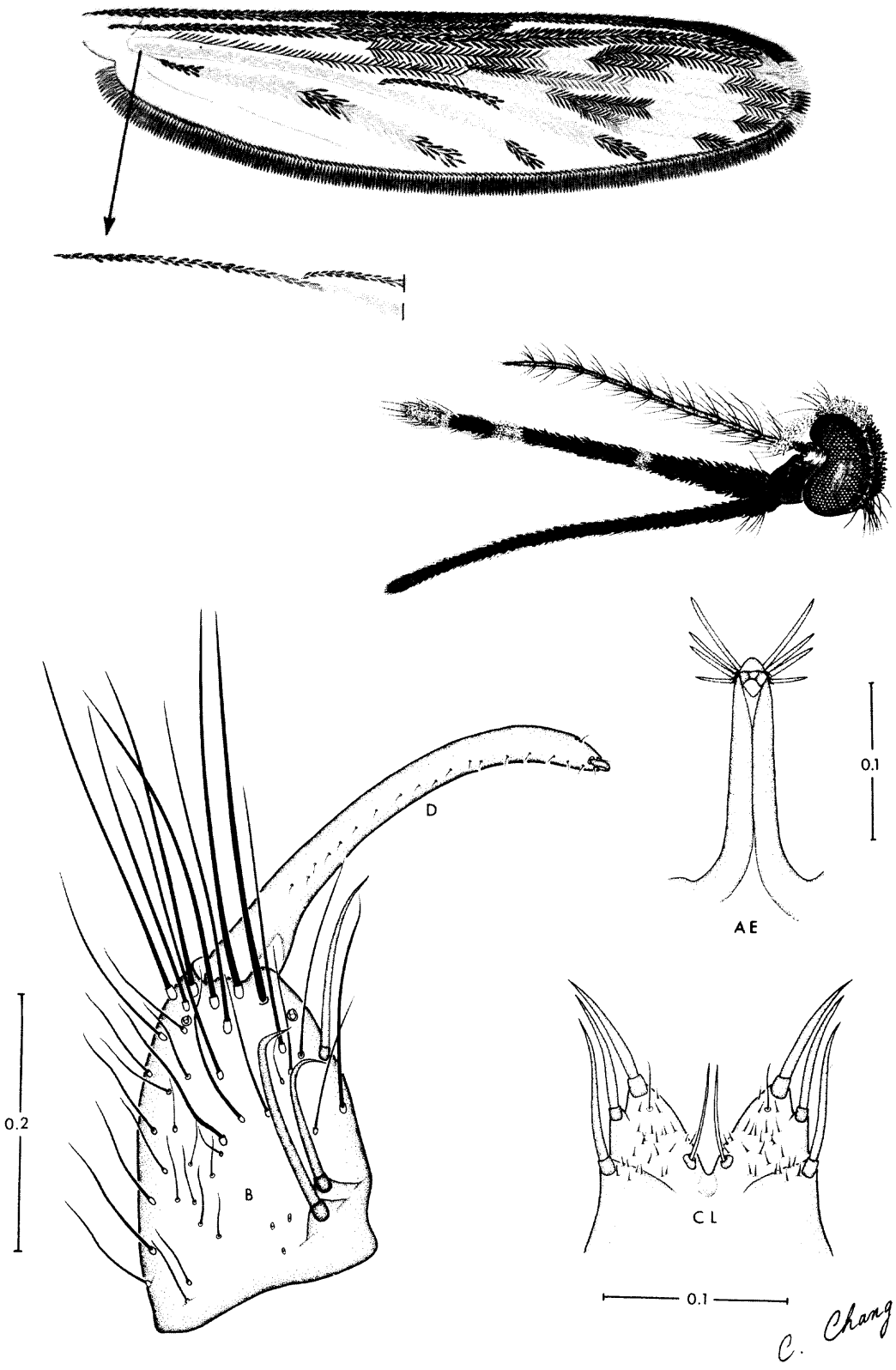
C. Chang

Fig. 6



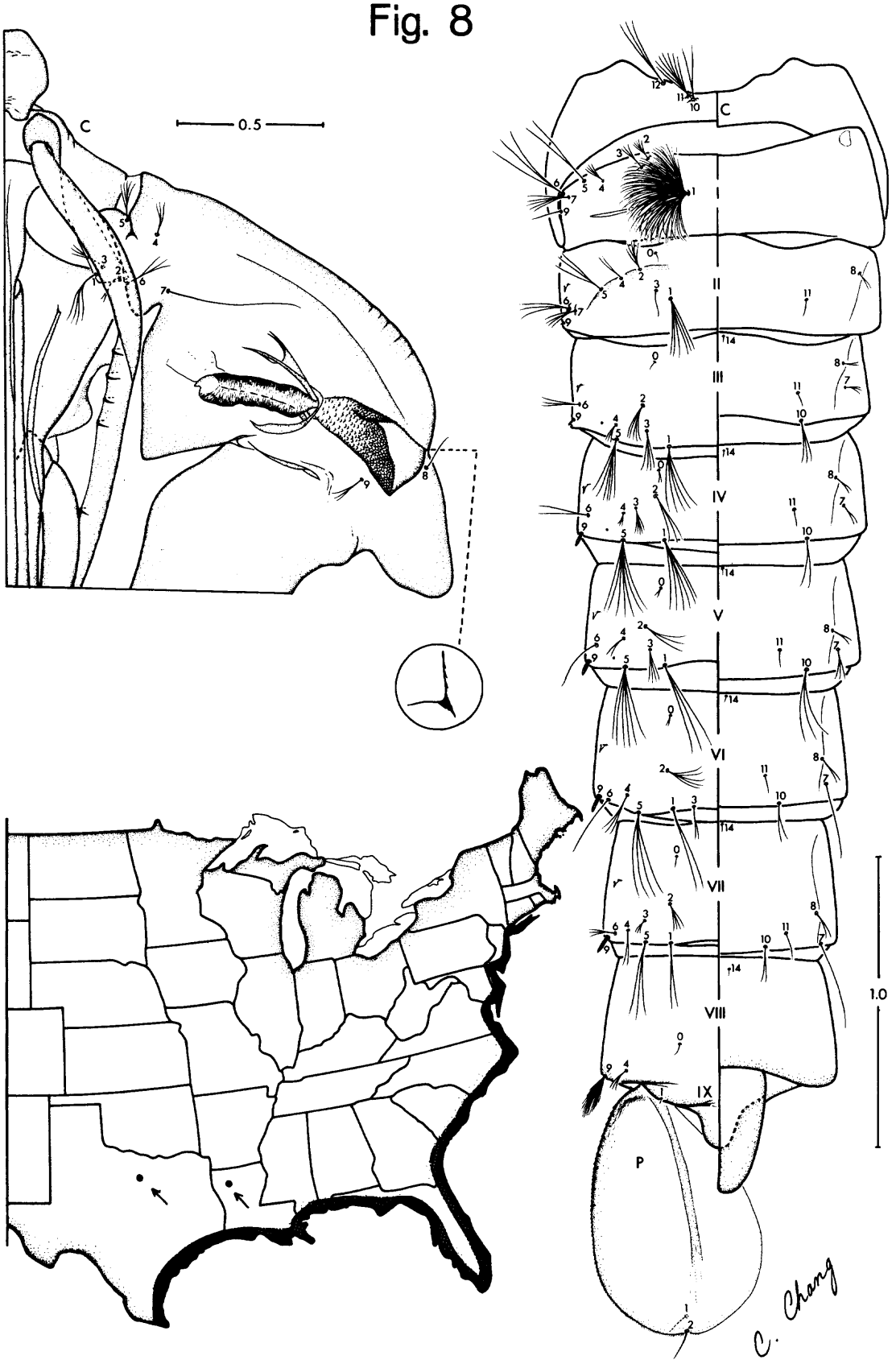
crucians 1st instar

Fig. 7



bradleyi

Fig. 8



bradleyi

Fig. 9

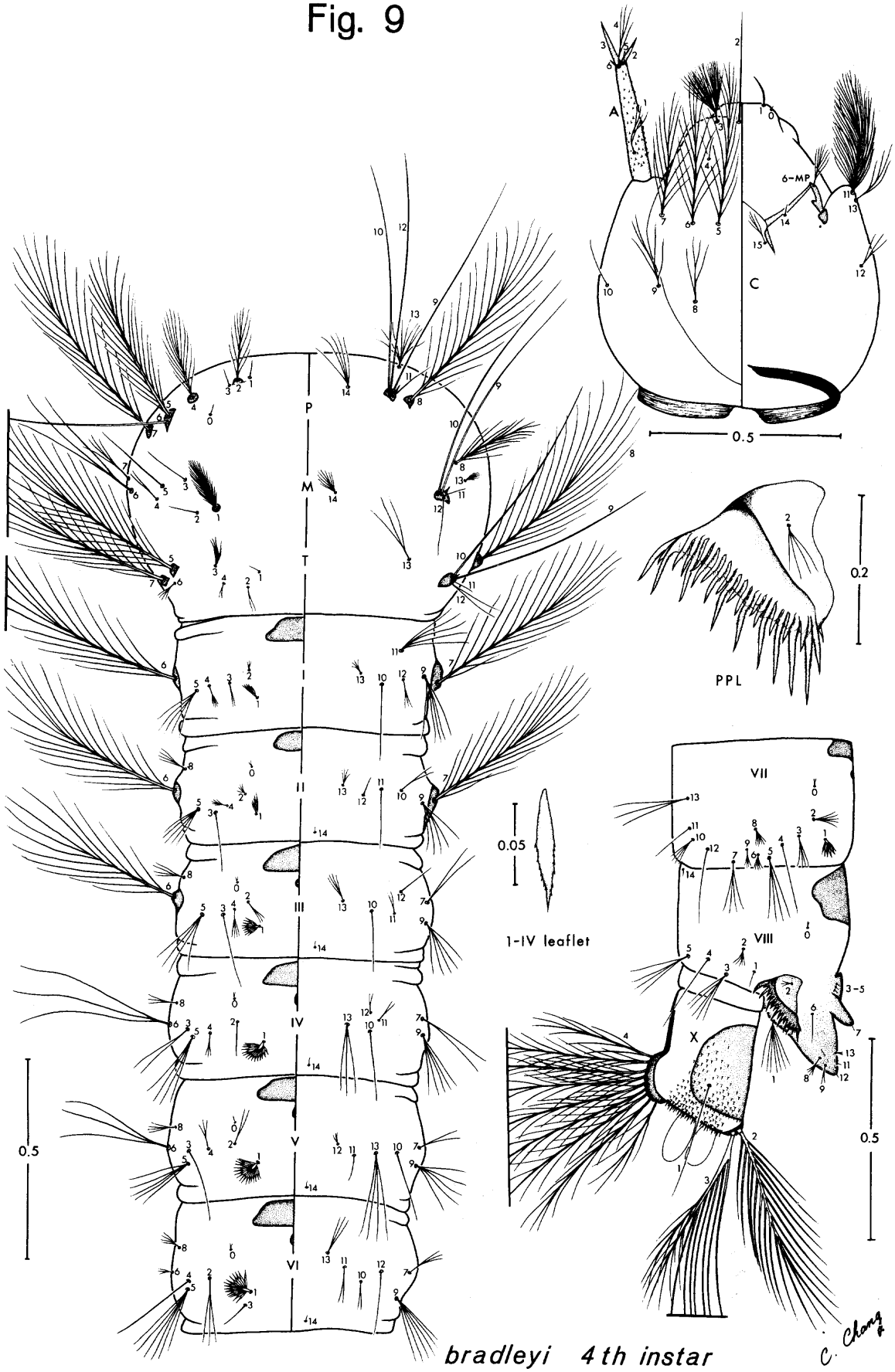
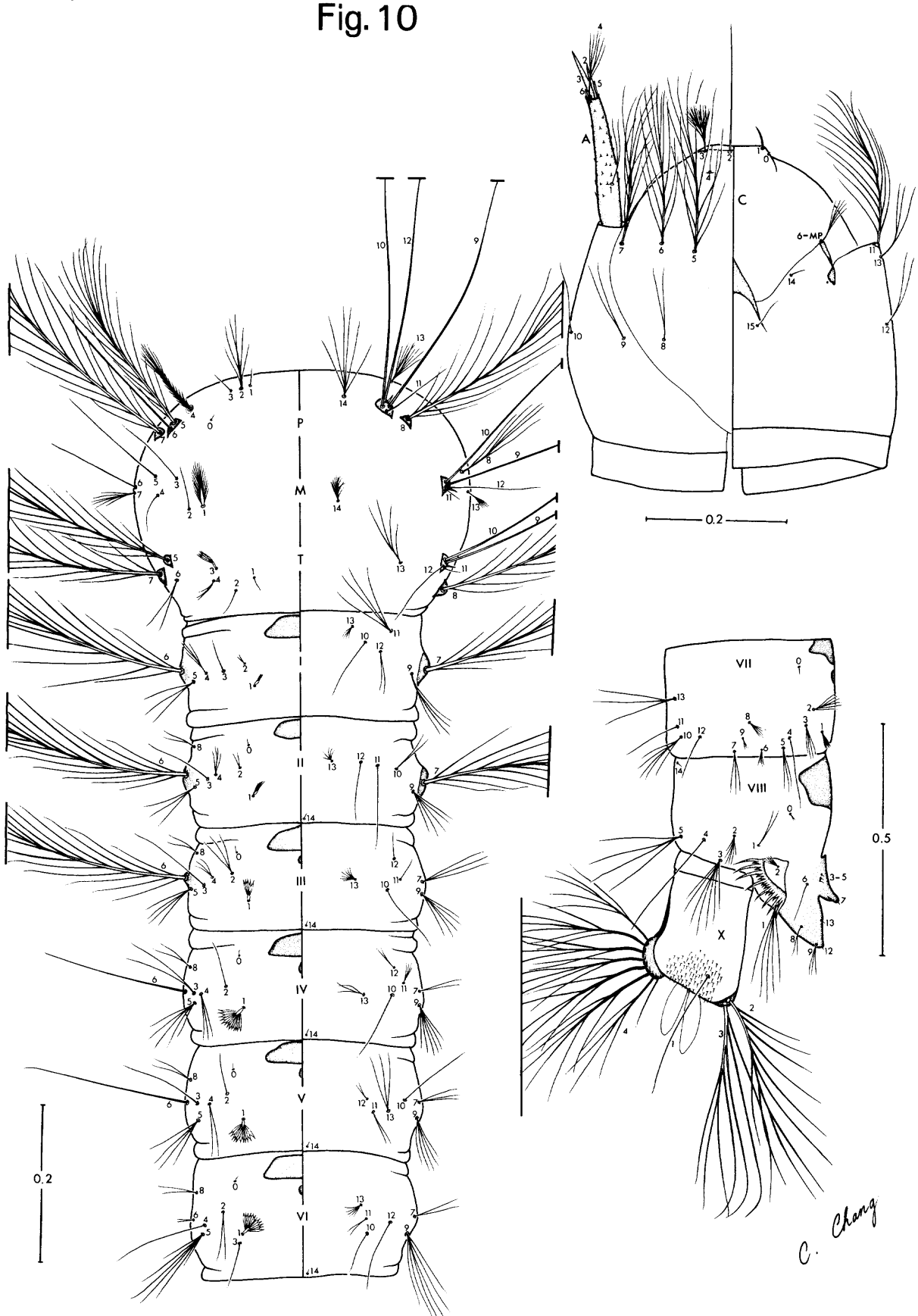
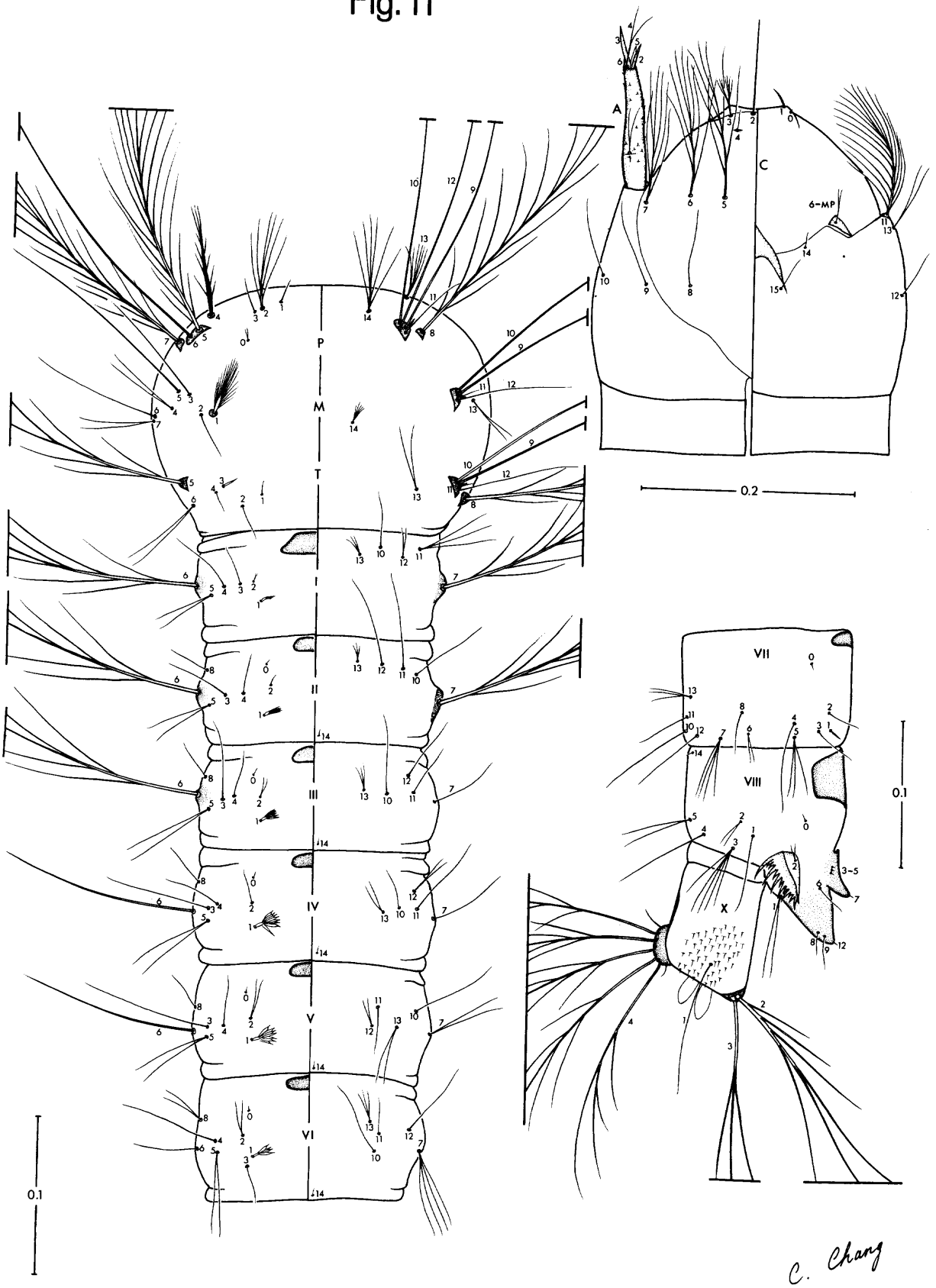

A
C
6-MP
0.5
PPL
0.2
0.05
1-IV leaflet
P
M
T
I
II
III
IV
V
VI
VII
VIII
X
3-5
0.5
bradleyi 4th instar
C. Chang

Fig. 10



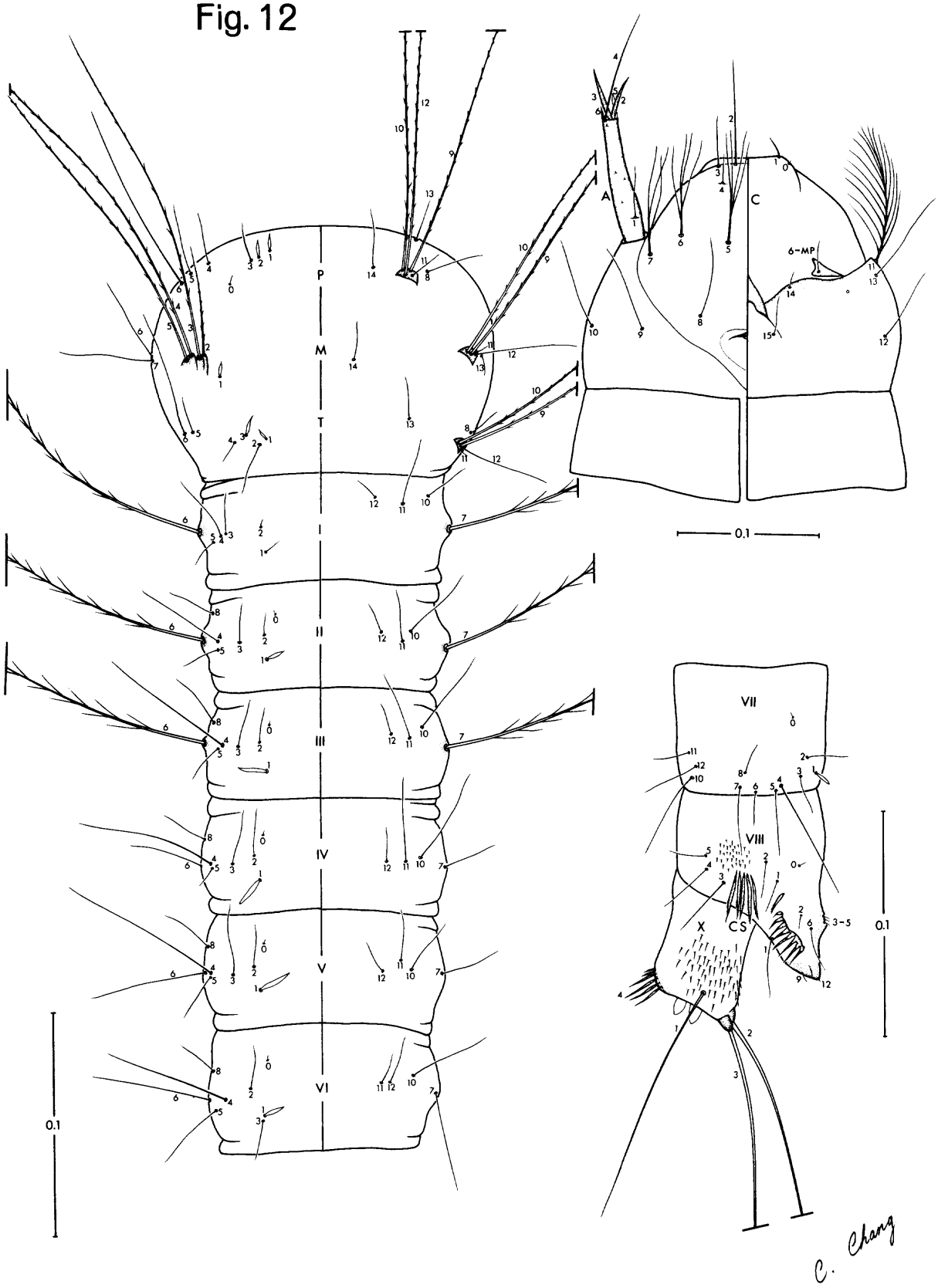
bradleyi 3rd instar

Fig. 11



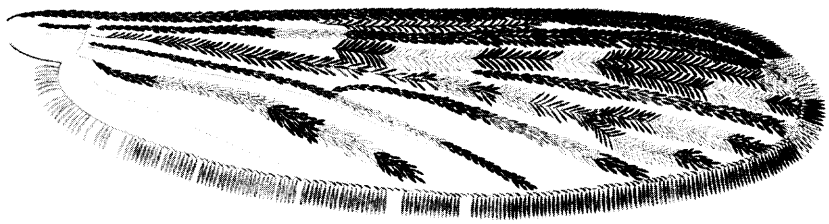
bradleyi 2nd instar

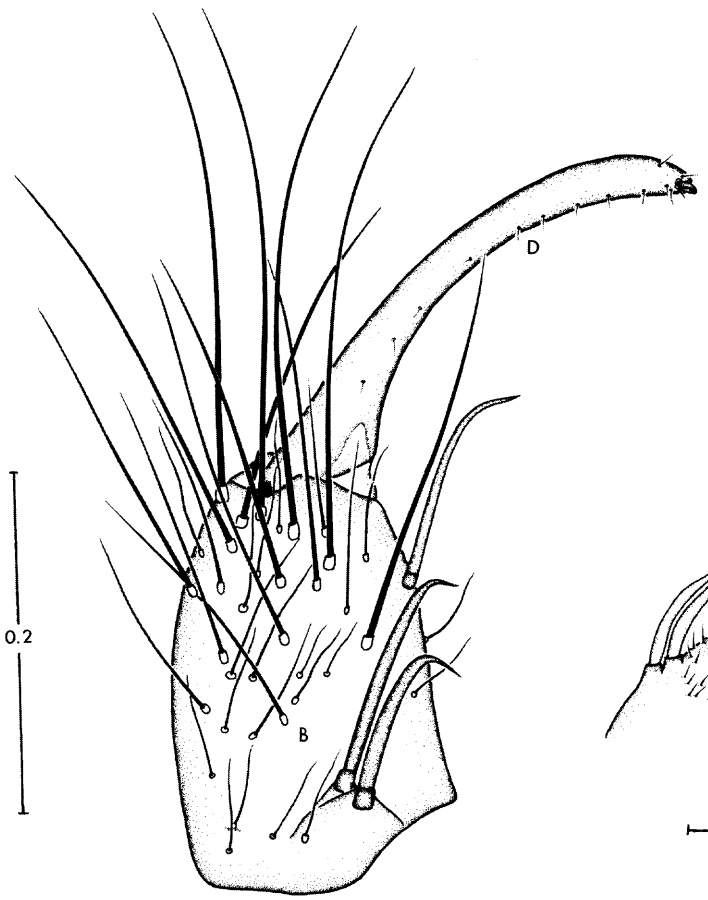
Fig. 12

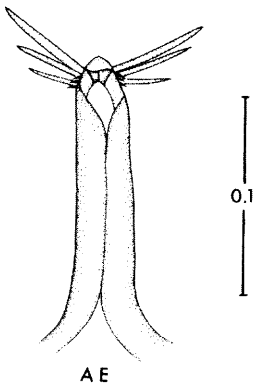


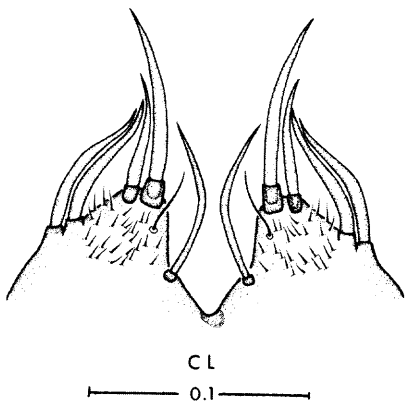
bradleyi 1st instar

Fig. 13



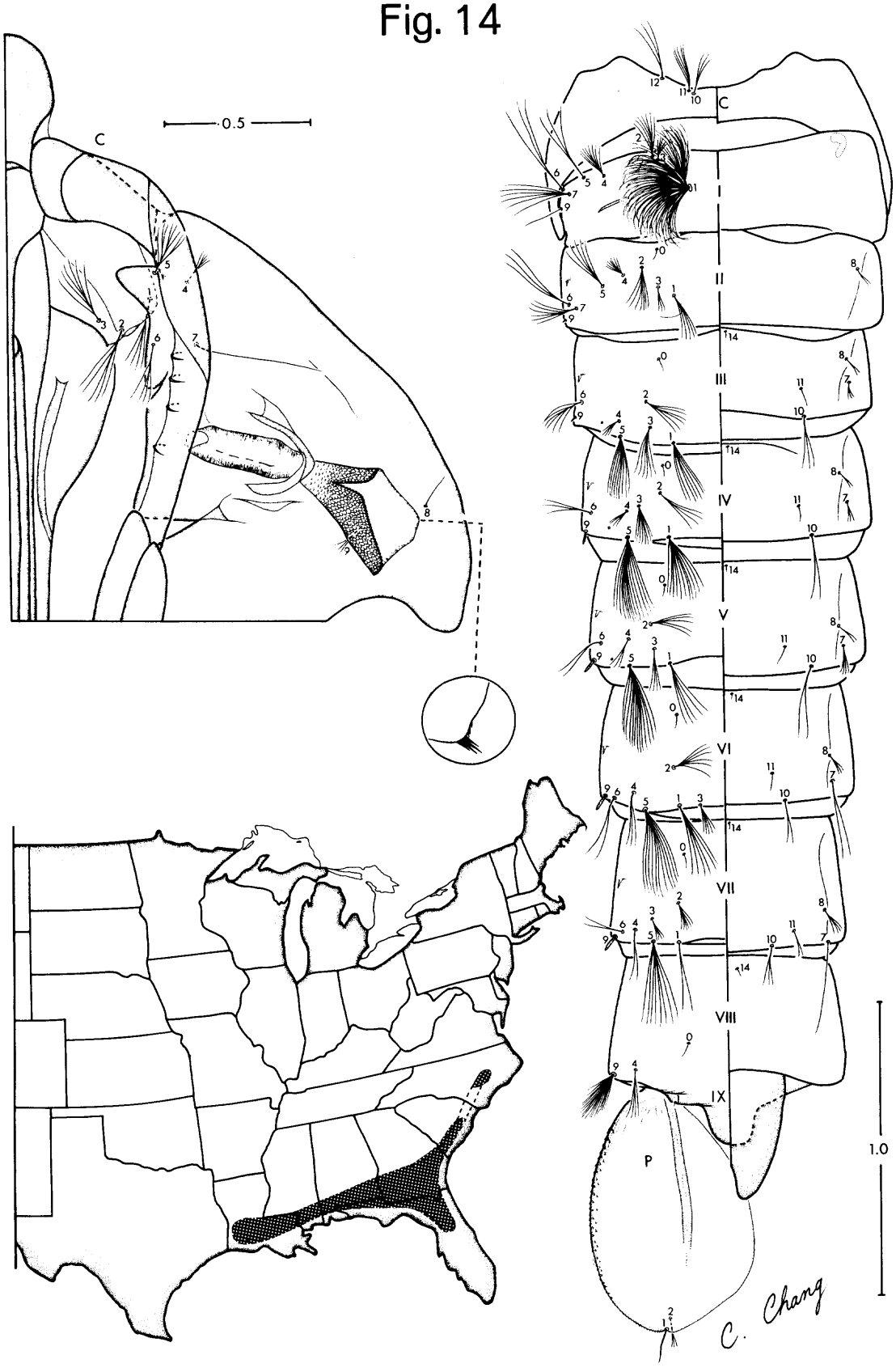






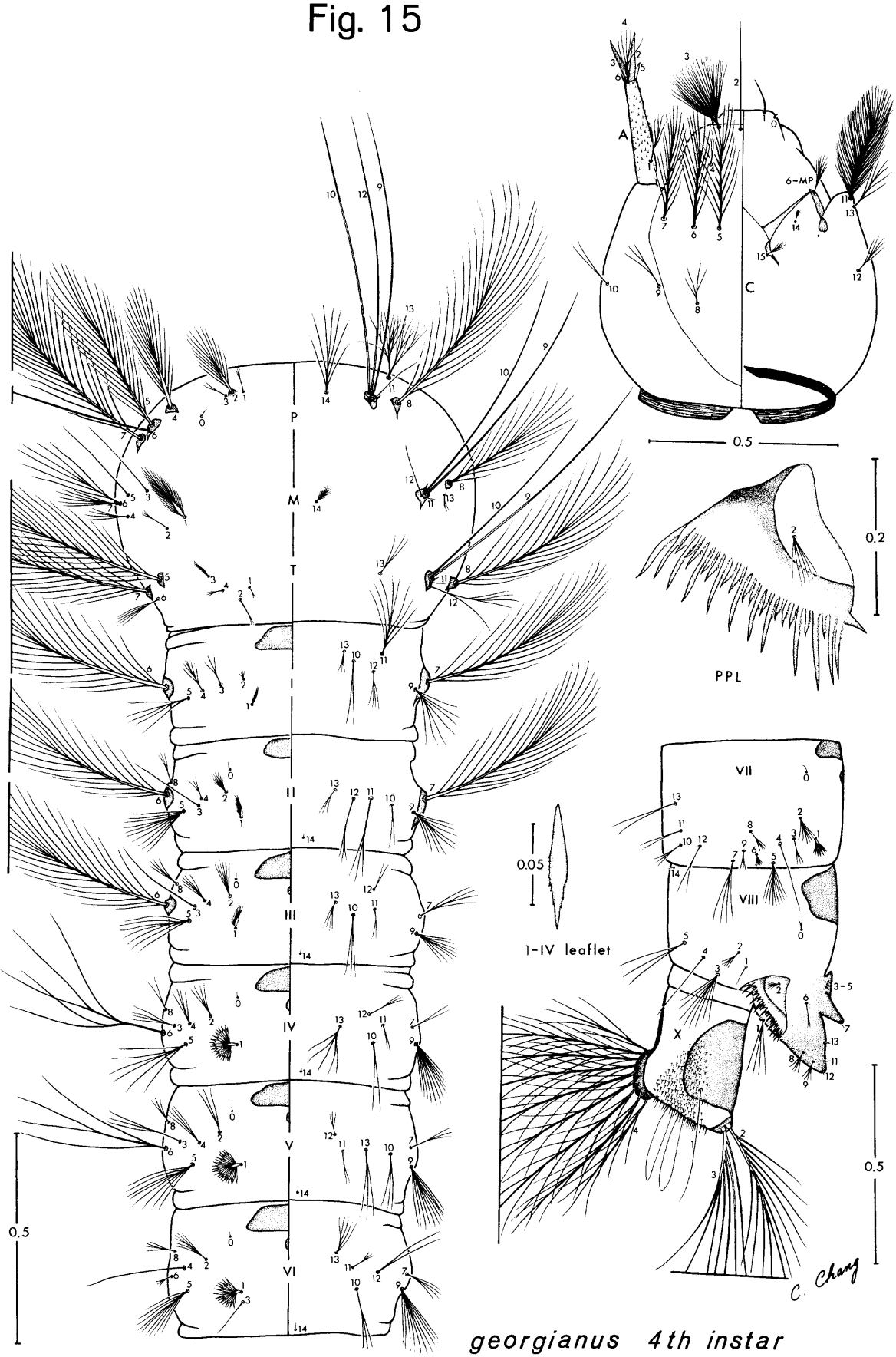
georgianus *C. Chang*

Fig. 14



georgianus

Fig. 15



georgianus 4th instar

Appendix Table 1. KEYS TO THE ANOPHELINE MOSQUITOES OF THE SOUTHEASTERN UNITED STATES.

FEMALES

1.	Wings with distinct areas of pale scales	2
	Wings entirely dark scaled, but may have spots due to dense scale patches	6
2.(1)	Costa with 4 or more pale areas; hind tarsomeres 3 and 4 entirely pale	*albimanus*
	Costa with no more than 2 pale areas; hind tarsomeres entirely dark	3
3.(2)	Costa with only apical pale spot; anal vein with 3 sharply defined dark spots	*crucians* subgroup
	Costa with subcostal and apical pale spots; anal vein with 1 or 2 dark spots	4
4.(3)	Palpal segments 2-4 with apical pale bands; R_{4+5} and Cu with long pale areas; anal vein with 1 dark spot	*pseudopunctipennis*
	Palpal segments entirely dark; R_{4+5} and Cu entirely dark; anal vein with 2 dark spots	5
5.(4)	Subcostal pale spot on costa large, 0.5 as long to longer than length of preapical dark mark on costa	*.punctipennis**
	Subcostal pale spot on costa reduced (rarely absent), usually 0.33 or less length of preapical dark mark on costa	*.perplexens**
6.(1)	Scutal setae long, approximately 0.5 or more width of scutum; wings without dark scale patches; small species	*barberi*
	Scutal setae less than 0.5 width of scutum; wings often with dark scale patches; large species	7
7.(6)	Vertex scales dark; femora and tibiae without, or with reduced apical pale spots; wings often without dense scale patches	*.atropos*
	Vertex scales pale; femora and tibiae with distinct pale spots; wings with four dense scale patches	8
8.(7)	Palpal segments with apical pale bands; halter knob pale scaled	*.walkeri*
	Palpal segments entirely dark scaled; halter knob dark scaled	*.quadrimaculatus*

*Due to slight overlap in the costal character, adults in the 0.33 - 0.50 category should be confirmed by associated larval skins.

Appendix Table 1 (Continued)

MALE GENITALIA

1. Basimere with 2 large parabasal setae and one slender internal seta . . . . . (Subgenus *Anopheles*) . . 2
Basimere with only one parabasal seta, one internal seta and a pair of accessory setae . . . . . (Subgenus *Nyssorhynchus*) . . . . . *albimanus*

2.(1) Aedeagus without leaflets; 9th tergum without lateral lobes . . . . . *barberi*
Aedeagus with leaflets; 9th tergum with lateral lobes 3

3.(2) Aedeagus leaflets slender and serrated; claspette with setae on dorsal lobe approximately 0.5 length of setae on ventral lobe . . . . . *pseudopunctipennis*
Aedeagus leaflets stout and smooth, or with small basal denticles; claspette with setae on dorsal lobe approximately equal to or slightly shorter than setae on ventral lobe 4

4.(3) Claspette triangular with indistinct dorsal and ventral lobes; lateral claspette setae large and acuminate . . . . . (*crucians* subgroup) . . 8
Claspette not triangular, with dorsal and ventral lobes usually distinct; lateral claspette setae with rounded tips (except *perplexens* and *punctipennis*) 5

5.(4) Aedeagus leaflets with one or more basal denticles; distimere without minute basal setae; 9th tergum lobes usually expanded apically and constricted medianly 6
Aedeagus leaflets without basal denticles; distimere with numerous minute setae on base; 9th tergum lobes usually tapering to narrow points 7

6.(5) Lateral (dorsal) claspette seta(e) capitate or bluntly rounded at apex; apex of ventral lobe of claspette with 1 to 3 (usually 2) large acuminate setae; small setae on ventral lobe of claspette at least 0.33 length of apical setae. . . . . .*quadrimaculatus*
Lateral (dorsal) claspette seta(e) with apex acuminate; apex of ventral lobe of claspette with 1 stout acuminate seta; ventral lobe of claspette with 1 very small seta, less than 0.33 length of apical seta . . . . . .*perplexens**
. . . . . *punctipennis**

*Species identification for these 2 species should be confirmed by wing characters and associated larval skins.

Appendix Table 1. (Continued)

7.(5)	Preapical pair of aedeagus leaflets not over 0.5 length of apical pair of leaflets; distimere with numerous minute setae on basal 0.33 - 0.50	*atropos*
	Preapical pair of aedeagus leaflets over 0.5 length of apical pair; distimere with numerous minute setae only on basal 0.16	*walkeri*
8.(4)	Claspette usually with 3 setae on each side	*bradleyi**
	Claspette usually with 4 setae on each side	*crucians**
	. . . . .	*georgianus**
PUPAE		
1.	Seta 9-VIII spine-like, without branches	2
	Seta 9-VIII with many side branches	4
2.(1)	Trumpet with shallow meatal notch, meatus 0.66 or more as long as trumpet; 1 on IV-VII short, single, less than 0.5 as long as segment; 5-IV short, single	*barberi*
	Trumpet with deep meatal cleft, meatus 0.5 or less length of trumpet; 1 on IV-VII stout, single, as long as or longer than segment; 5-IV with 2 - 7 branches . .	3
3.(2)	Setae 0 on III-V with 2 - 4 branches; 5 on V-VII stout, single	*albimanus*
	Setae 0 on III-V single; 5 on V-VII usually with several lateral branches	*pseudopunctipennis*
4.(1)	Lateral paddle margin with stout, blunt denticles	*walkeri*
	Lateral paddle margin without denticles, may have small fine serrations	5
5.(4)	Sum of branches on both setae 3-V, 6 - 13; (rarely 6); trumpet usually with spiny lateral spur on pinna . . . . . (*crucians* subgroup). .	8
	Sum of branches on both setae 3-V, 3 - 6; trumpet without lateral spur on pinna.	6
6.(5)	Seta 9-VII, 6 or more times as long as wide	*punctipennis*
	. . . . .	*.perplexens*
	Seta 9-VII, 3.5 - 5.5** times as long as wide	7

*Male genitalia characters are reliable on 70-75 percent of specimens and should be confirmed by associate immature skins.

**Infrequent specimens of *atropos* and *quadrimaculatus* may have longer spines. This character is operable on a 95-98 percent level.

Appendix Table 1. (Continued)

7.(6)	Paddle with fine fringe hairs around apex and on apical 0.75 of mesal margin . . . . . *.atropos*
	Paddle without fine fringe hairs on mesal margin, may have few at or near apex . . . . . *.quadrimaculatus*
8.(5)	Setae 0 on IV-V large, with 2 - 11 branches, nearly as large as 2 on IV-V . . . . . *crucians*
	Setae 0 on IV-V small, single or with 2 - 3 branches, much smaller than 2 on IV-V 9
9.(8)	Seta 1-IV with 5 - 9 (usually 5 - 6) branches; 1-V with 3 - 6 branches; 5-IV with 5 - 10 branches; 5-V with 3 - 8 branches . . . . . *bradleyi*
	Seta 1-IV with 9 - 14 branches; 1-V with 6 - 10 branches; 5-IV with 12 - 17 branches; 5-V with 8 - 16 branches . . . . . *georgianus*
LARVAE	
1.	Setae 5,6,7-C small, single; 6 on I-VI plumose . . . . . *barberi*
	Setae 5,6,7-C large, plumose; 6 on I-III plumose, 6 on IV-VI single or with several branches 2
2.(1)	Setae 1,2,3-P arising on common sclerotized base; 1 on I-II well developed, leaflets smooth . . . . . *.albimanus*
	Setae 1,2,3-P arising separately; 1 on I-II with leaflets absent or rudimentary. 3
3.(2)	Seta 3-C simple; 9-M,T short, stout, less than 0.5 as long as 10-M,T . . . . . *pseudopunctipennis*
	Seta 3-C with 5 or more branches; 9,10 on M,T nearly equal length 4
4.(3)	Seta 3-C with 5 - 10 branches . . . . . *atropos*
	Seta 3-C with 15 (usually 20) or more branches 5
5.(4)	Seta 2-C with minute apical branches; 1-P with 3 - 5 stout branches from base. . . . . *walkeri*
	Seta 2-C simple, rarely with apical branches; 1-P short, single or with weak apical branches. 6
6.(5)	Setae 0 on IV-V well developed, with 4 - 13 branches, approximately equal in size to 2 on IV-V. . . *crucians*
	Setae 0 on IV-V minute, simple or with 2 - 3 branches, much smaller than 2 on IV-V 7

Appendix Table 1. (Continued)

7.(6)	Setae 1 on IV-VI nearly equal in size; setae 1-III,VII distinctly smaller* 8
	Setae 1 on III-VII nearly equal in size 9
8.(7)	Seta 1-III appearance more like 1-IV than 1-II; 5-II with 5 - 9 branches; 9-III with 5 - 9 branches; 11-I with 4 - 6 branches . . . . . *bradleyi*
	Seta 1-III appearance more like 1-II than 1-IV; 5-II with 7 - 14 branches; 9-III with 7 - 11 branches; 11-I with 6 - 10 branches . . . . . *georgianus*
9.(8)	Seta 8-C with 8 - 10 branches; alveoli of seta 2-C separated by at least width of one alveolus . . *quadrimaculatus*
	Seta 8-C with 4 - 7 branches; alveoli of seta 2-C usually separated by less than width of one alveolus. 10
10.(9)	All 4 setae 2 on IV-V usually single, infrequently 1 or 2 of 4 setae with 2 or 3 basal branches. . . . *perplexens*
	All 4 setae on IV-V usually with 2 or more basal branches . . . . . *punctipennis*

*Occasionally *bradleyi* have 1-III nearly equal to 1-IV, but 1-VII is always distinctly smaller than 1-VI.

Appendix Table 2. RECORD OF THE SETAL BRANCHING OF THE PUPAE OF *ANOPHELES CRUCIANS*.

Seta	Range	Seta	Range	Seta	Range
Cephalothorax		Abdomen I		Abdomen II (Cont)	
1	3 - 6	1	35+	4	2 - 6
2	3 - 5	2	4 - 10	5	2 - 10
3	4 - 6	3	1 - 3	6	2 - 10
4	3 - 6	4	5 - 13	7	2 - 8
5	4 - 9	5	1 - 5	9	1
6	3 - 6	6	3 - 11	11	1
7	1 - 2	7	2 - 8		
8	1 - 2	9	1 - 3	Abdomen III	
9	1 - 4			0	2 - 7
		Abdomen II		1	8 - 17
Metanotum		0	1 - 2	2	5 - 10
		1	5 - 18	3	4 - 12
10	1 - 4	2	2 - 10	4	2 - 5
11	4 - 11	3	1 - 4	5	6 - 19
12	3 - 8				

Appendix Table 2. (Continued)

Seta	Range	Seta	Range	Seta	Range
Abdomen III (Cont)		Abdomen V (Cont)		Abdomen VII	
6	4 - 13	2	3 - 9	0	1 - 4
7	1 - 5	3	3 - 7	1	1 - 6
8	2 - 5	4	3 - 9	2	3 - 8
9	1 - 3	5	4 - 17	3	3 - 8
10	2 - 5	6	3 - 6	4	2 - 5
11	1 - 3	7	1 - 6	5	2 - 11
14	1	8	2 - 7	6	1 - 4
Abdomen IV		9	1	7	1 - 2
		10	2 - 6	8	2 - 5
0	1 - 7	11	1 - 3	9	1
1	8 - 21	14	1	10	1 - 4
2	4 - 18	Abdomen VI		11	1 - 2
3	4 - 11			14	1
4	1 - 6	0	2 - 5	Abdomen VIII	
5	8 - 18	1	2 - 12		
6	3 - 9	2	3 - 8	0	1 - 3
7	1 - 4	3	2 - 8	1	1
8	2 - 7	4	2 - 4	4	2 - 5
9	1	5	5 - 16	9	7 - 20
10	2 - 6	6	1 - 4	14	1
11	1 - 3	7	1 - 2	Paddle	
14	1	8	2 - 4		
Abdomen V		9	1	1	1 - 2
		10	1 - 3	2	1 - 3
0	3 - 11	11	1 - 2		
1	3 - 17	14	1		

Appendix Table 3. RECORD OF THE SETAL BRANCHING OF THE PUPAE OF *ANOPHELES BRADLEYI*.

Seta	Range	Seta	Range	Seta	Range
Cephalothorax		Metanotum		Abdomen I (Cont)	
1	2 - 6	10	1 - 4	5	2 - 3
2	2 - 3	11	3 - 9	6	2 - 7
3	2 - 4	12	3 - 5	7	2 - 7
4	3 - 6	Abdomen I		9	1 - 2
5	4 - 7			Abdomen II	
6	2 - 5	1	35+		
7	1	2	2 - 9	0	1 - 2
8	1 - 2	3	2 - 5	1	5 - 12
9	2 - 5	4	3 - 10	2	5 - 13

Appendix Table 3. (Continued)

Seta	Range	Seta	Range	Seta	Range
Abdomen II (Cont)		Abdomen IV (Cont)		Abdomen VI (Cont)	
3	1 - 5	6	1 - 5	7	1 - 3
4	2 - 7	7	1 - 5	8	1 - 4
5	2 - 5	8	1 - 4	9	1
6	2 - 6	9	1	10	1 - 3
7	2 - 5	10	1 - 3	11	1
8	1 - 2	11	1 - 2	14	1
9	1	14	1	Abdomen VII	
11	1	Abdomen V		0	1 - 2
Abdomen III		0	1 - 3	1	1 - 3
0	1 - 2	1	3 - 6	2	3 - 7
1	5 - 11	2	2 - 5	3	2 - 6
2	3 - 7	3	3 - 7	4	1 - 3
3	3 - 8	4	2 - 7	5	3 - 5
4	2 - 5	5	3 - 8	6	1 - 3
5	4 - 8	6	1 - 3	7	1 - 2
6	2 - 6	7	2 - 4	8	1 - 6
7	1 - 6	8	1 - 3	9	1
8	1 - 5	9	1	10	1 - 3
9	1	10	1 - 3	11	1
10	1 - 4	11	1 - 2	14	1
11	1 - 2	14	1	Abdomen VIII	
14	1	Abdomen VI		0	1
Abdomen IV		0	1 - 3	1	1
0	1 - 3	1	2 - 5	4	1 - 6
1	5 - 9	2	4 - 6	9	7 - 17
2	3 - 9	3	3 - 7	14	1
3	4 - 7	4	1 - 3	Paddle	
4	3 - 6	5	3 - 6	1	1 - 2
5	5 - 10	6	1 - 2	2	1 - 3

Appendix Table 4. RECORD OF THE SETAL BRANCHING OF THE PUPAE OF *ANOPHELES GEORGIANUS*.

Seta	Range	Seta	Range	Seta	Range
Cephalothorax		Cephalothorax (Cont)		Metanotum	
1	4 - 7	5	5 - 10	10	1 - 3
2	3 - 5	6	3 - 6	11	4 - 8
3	5 - 8	7	1	12	3 - 5
4	3 - 7	8	1		
		9	3 - 5		

Appendix Table 4. (Continued)

Seta	Range	Seta	Range	Seta	Range
Abdomen I		Abdomen IV		Abdomen VI (Cont)	
1	40+	0	1 - 3	4	2 - 3
2	5 - 8	1	9 - 14	5	9 - 13
3	2 - 4	2	4 - 7	6	1 - 3
4	7 - 10	3	5 - 12	7	1 - 4
5	3 - 6	4	4 - 7	8	3 - 5
6	3 - 6	5	12 - 17	9	1
7	6 - 11	6	3 - 5	10	2 - 4
9	1 - 2	7	2 - 5	11	1 - 2
Abdomen II		8	1 - 5	14	1
		9	1	Abdomen VII	
0	1	10	2 - 6		
1	5 - 11	11	1 - 2	0	1
2	6 - 12	14	1	1	2 - 4
3	3 - 8	Abdomen V		2	4 - 6
4	5 - 7			3	4 - 7
5	4 - 6	0	1 - 2	4	1 - 4
6	3 - 6	1	6 - 10	5	2 - 9
7	5 - 9	2	5 - 7	6	2 - 4
9	1	3	3 - 7	7	1
Abdomen III		4	3 - 7	8	4 - 5
		5	8 - 16	9	1
0	1	6	1 - 3	10	3 - 5
1	7 - 11	7	3 - 5	11	1 - 3
2	6 - 10	8	2 - 5	14	1
3	5 - 8	9	1	Abdomen VIII	
4	3 - 5	10	2 - 3		
5	5 - 13	11	1 - 2	0	1
6	4 - 9	14	1	1	1
7	3 - 6	Abdomen VI		4	3 - 5
8	2 - 4			9	8 - 18
9	1	0	1 - 2	14	1
10	2 - 5	1	3 - 6	Paddle	
11	1 - 2	2	5 - 8		
14	1	3	2 - 5	1	1 - 2
				2	2 - 4

Appendix Table 5. RECORD OF THE SETAL BRANCHING ON THE LARVAE OF *ANOPHELES CRUCIANS*.

Seta	Range	Seta	Range	Seta	Range
Antenna		Head		Head (Cont)	
1	4 - 10	1	1	3	20 - 40+
4	4 - 6	2	1	4	1 - 4

Appendix Table 5. (Continued)

Seta	Range
Head (Cont.)	
5	12 - 24
6	12 - 25
7	13 - 25
8	2 - 6
9	3 - 6
10	1 - 4
11	20 - 62
12	2 - 6
13	5 - 14
14	1 - 2
15	2 - 6
6MP	16 - 35
Prothorax	
0	1
1	1 - 3
2	7 - 14
3	1
4	12 - 21
5	18 - 29
6	1
7	20 - 34
8	20 - 30
9	1
10	1
11	1
12	1
13	12 - 20
14	5 - 11
Mesothorax	
1	17 - 33
2	1 - 4
3	1 - 2
4	3 - 7
5	1 - 2
6	3 - 6
7	3 - 6
8	9 - 15
9	1
10	1
11	1
12	1
13	7 - 16
14	8 - 18
Metathorax	
1	1 - 3
2	1 - 3
3	6 - 10
4	2 - 4
5	15 - 26
6	3 - 6
7	16 - 28
8	15 - 26
9	1
10	1
11	1
12	1 - 4
13	2 - 6
Abdomen I	
1	3 - 8
2	4 - 9
3	1 - 4
4	6 - 9
5	5 - 9
6	14 - 28
7	13 - 30
9	5 - 10
10	1 - 2
11	5 - 9
12	1 - 4
13	2 - 4
Abdomen II	
0	2 - 6
1	7 - 21
2	8 - 14
3	1
4	6 - 9
5	6 - 11
6	17 - 25
7	16 - 28
8	6 - 10
9	6 - 11
10	2 - 6
11	1 - 2
12	1 - 2
13	4 - 12
14	1
Abdomen III	
0	4 - 6
1	8 - 16
2	6 - 14
3	1
4	3 - 7
5	5 - 8
6	11 - 18
7	2 - 7
8	6 - 12
9	8 - 13
10	1 - 4
11	1 - 3
12	2 - 5
13	6 - 12
14	1
Abdomen IV	
0	4 - 9
1	14 - 21
2	5 - 16
3	2 - 7
4	3 - 8
5	5 - 8
6	2 - 4
7	2 - 7
8	3 - 9
9	9 - 12
10	1 - 2
11	1 - 4
12	3 - 6
13	4 - 5
14	1
Abdomen V	
0	5 - 13
1	14 - 20
2	5 - 14
3	1 - 2
4	4 - 11
5	5 - 8
6	2
7	2 - 5
8	3 - 9
9	9 - 12
10	1 - 2

Appendix Table 5. (Continued)

Seta	Range	Seta	Range	Seta	Range
Abdomen V (Cont.)		Abdomen VI (Cont.)		Abdomen VIII	
11	2 - 4	13	7 - 13	0	4 - 5
12	3 - 6	14	1 - 2	1	1 - 5
13	4 - 6			2	3 - 9
14	1	Abdomen VII		3	8 - 12
		0	3 - 5	4	1 - 2
Abdomen VI		1	9 - 14	5	4 - 8
0	4 - 7	2	5 - 10	14	1
1	14 - 24	3	2 - 4		
2	6 - 12	4	1 - 2	Spiracular apparatus	
3	1 - 2	5	5 - 9	1	4 - 7
4	1 - 2	6	2 - 5	2	4 - 7
5	5 - 11	7	2 - 8	3	1
6	2	8	3 - 8	4	1
7	2 - 5	9	3 - 7	5	1
8	4 - 7	10	2 - 8	6	1 - 2
9	7 - 11	11	1 - 2	7	1
10	1 - 3	12	1	8	2 - 5
11	2 - 4	13	4 - 5	9	3 - 6
12	1 - 2	14	1		

Appendix Table 6. RECORD OF THE SETAL BRANCHING ON THE LARVAE OF *ANOPHELES BRADLEYI*.

Seta	Range	Seta	Range	Seta	Range
Antenna		Head (Cont.)		Prothorax (Cont.)	
1	3 - 6	15	3 - 4	14	5 - 10
4	4 - 6	6MP	17 - 32		
				Mesothorax	
Head		Prothorax		1	18 - 36
1	1	0	1	2	1 - 3
2	1	1	1 - 5	3	1
3	16 - 30+	2	6 - 12	4	1 - 3
4	1	3	1	5	1
5	13 - 25	4	12 - 20	6	3 - 4
6	14 - 25	5	13 - 27	7	3 - 6
7	13 - 26	6	1	8	10 - 18
8	3 - 4	7	15 - 25	9	1
9	2 - 5	8	18 - 31	10	1
10	1 - 3	9	1	11	1
11	17 - 53	10	1	12	1 - 3
12	2 - 3	11	1	13	8 - 14
13	4 - 5	12	1	14	8 - 15
14	1 - 4	13	8 - 15		

Appendix Table 6. (Continued)

Seta	Range
Metathorax	
1	1 - 2
2	1 - 2
3	2 - 6
4	2 - 4
5	19 - 26
6	3 - 6
7	16 - 24
8	17 - 25
9	1
10	1
11	1
12	2 - 4
13	2 - 4
Abdomen I	
1	3 - 8
2	2 - 4
3	1 - 2
4	4 - 11
5	3 - 5
6	14 - 23
7	15 - 22
9	5 - 8
10	1
11	4 - 6
12	4 - 6
13	2 - 5
Abdomen II	
0	1
1	5 - 10
2	4 - 8
3	1
4	3 - 7
5	5 - 9
6	19 - 28
7	18 - 27
8	3 - 5
9	5 - 10
10	1 - 6
11	1
12	1
13	3 - 7
14	1
Abdomen III	
0	1
1	8 - 16
2	3 - 6
3	1
4	3 - 6
5	4 - 9
6	11 - 19
7	2 - 6
8	2 - 6
9	5 - 9
10	1 - 2
11	1 - 4
12	1 - 3
13	4 - 8
14	1
Abdomen IV	
0	1 - 3
1	13 - 25
2	1 - 3
3	2 - 5
4	3 - 6
5	4 - 7
6	3 - 4
7	2 - 5
8	2 - 4
9	5 - 11
10	1 - 2
11	1 - 3
12	2 - 5
13	3 - 8
14	1 - 2
Abdomen V	
0	1 - 2
1	13 - 20
2	1 - 4
3	1 - 3
4	3 - 5
5	5 - 9
6	2 - 3
7	2 - 4
8	2 - 5
9	5 - 12
10	1 - 2
11	2 - 4
Abdomen V (Cont.)	
12	2 - 3
13	3 - 4
14	1
Abdomen VI	
0	1
1	11 - 20
2	3 - 7
3	1
4	1
5	6 - 9
6	2 - 5
7	3 - 4
8	3 - 5
9	6 - 10
10	1 - 3
11	1 - 4
12	1 - 2
13	3 - 10
14	1
Abdomen VII	
0	1 - 2
1	5 - 12
2	3 - 6
3	2 - 4
4	1
5	4 - 8
6	3 - 5
7	3 - 6
8	3 - 6
9	3 - 5
10	3 - 5
11	1 - 4
12	1 - 2
13	2 - 3
14	1
Abdomen VIII	
0	1 - 3
1	1 - 2
2	4 - 8
3	4 - 8
4	1
5	3 - 7
14	1

Table 6. (Continued)

Seta	Range	Seta	Range	Seta	Range
Spiracular apparatus		Spiracular apparatus		Spiracular apparatus	
1	4 - 8	4	1	7	1 - 3
2	3 - 5	5	1	8	2 - 4
3	1	6	1 - 2	9	3 - 5

Appendix Table 7. RECORD OF THE SETAL BRANCHING ON THE LARVAE OF *ANOPHELES GEORGIANUS*.

Seta	Range	Seta	Range	Seta	Range
Antenna		Prothorax (Cont.)		Metathorax (Cont.)	
1	4 - 6	11	1	12	3 - 7
4	4 - 7	12	1	13	2 - 5
Head		13	15 - 20	Abdomen I	
		14	5 - 8		
1	1	Mesothorax		1	3 - 7
2	1			2	3 - 5
3	23 - 38+	1	19 - 36	3	3 - 5
4	2	2	1 - 5	4	4 - 9
5	10 - 20	3	1 - 2	5	4 - 7
6	13 - 21	4	2 - 5	6	15 - 24
7	14 - 20	5	1 - 2	7	13 - 21
8	3 - 6	6	3 - 6	9	6 - 11
9	3 - 5	7	3 - 8	10	1 - 2
10	2 - 3	8	11 - 18	11	6 - 10
11	22 - 60	9	1	12	3 - 6
12	2 - 5	10	1	13	2 - 4
13	5 - 9	11	1		
14	3 - 8	12	1 - 3	Abdomen II	
15	4 - 7	13	5 - 10		
6MP	7 - 36	14	6 - 12	0	1
				1	6 - 13
Prothorax		Metathorax		2	4 - 9
				3	1
0	1	1	2 - 4	4	3 - 7
1	1 - 5	2	2 - 3	5	7 - 14
2	9 - 15	3	4 - 9	6	18 - 26
3	1 - 2	4	2 - 4	7	17 - 27
4	16 - 24	5	21 - 33	8	2 - 5
5	22 - 31	6	2 - 8	9	7 - 12
6	1	7	19 - 29	10	2 - 3
7	21 - 31	8	17 - 28	11	2 - 4
8	14 - 27	9	1	12	1 - 3
9	1	10	1	13	4 - 9
10	1	11	1	14	1

Appendix Table 7. (Continued)

Seta	Range
Abdomen III	
0	1
1	10 - 18
2	4 - 10
3	1
4	2 - 5
5	6 - 11
6	14 - 26
7	2 - 5
8	3 - 4
9	7 - 11
10	2 - 3
11	2 - 3
12	2 - 3
13	4 - 6
14	1
Abdomen IV	
0	1 - 2
1	16 - 26
2	2 - 5
3	3 - 5
4	3 - 5
5	5 - 8
6	3 - 6
7	2 - 3
8	2 - 4
9	9 - 13
10	2 - 3
11	1 - 4
12	2 - 3
13	3 - 6
14	1
Abdomen V	
0	1 - 2
1	16 - 25
2	2 - 5
3	1 - 3
4	4 - 6
5	6 - 11
6	2 - 4
7	2 - 4
8	2 - 4
9	9 - 13
10	1 - 3
11	1 - 3
12	2 - 3
13	3 - 5
14	1
Abdomen VI	
0	1
1	15 - 20
2	3 - 6
3	1 - 2
4	1
5	6 - 10
6	2 - 5
7	3 - 4
8	3 - 6
9	8 - 11
10	3 - 5
11	1 - 4
12	1 - 2
13	5 - 7
14	1
Abdomen VII	
0	1
1	5 - 8
2	4 - 7
3	2 - 7
4	1 - 4
5	6 - 9
6	2 - 5
7	3 - 4
8	3 - 5
9	3 - 5
10	2 - 7
11	1 - 2
12	2
13	2 - 3
14	1
Abdomen VIII	
0	1 - 2
1	1 - 3
2	5 - 8
3	5 - 8
4	1 - 2
5	3 - 4
14	1
Spiracular apparatus	
1	3 - 4
2	4 - 7
3	1
4	1
5	1
6	1 - 2
7	1
8	3 - 4
9	3 - 4

INDEX

Valid names are in roman type, synonyms and non-valid combinations are italicized. Italicized pages designate the primary treatment of the taxon. Numbers in parentheses under a given species designate pagation for the figures of that species.