

A HANDBOOK OF THE AMAZONIAN SPECIES OF  
*ANOPHELES (NYSSORHYNCHUS)* (DIPTERA: CULICIDAE)<sup>1</sup>

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CONTENTS

INTRODUCTION . . . . .	2
MATERIAL AND METHODS . . . . .	3
SYSTEMATICS . . . . .	4
TAXONOMIC CHARACTERS . . . . .	5
Adult Females . . . . .	5
Male Genitalia . . . . .	6
Fourth Stage Larvae . . . . .	7
BIONOMICS . . . . .	8
MEDICAL IMPORTANCE . . . . .	9
PLATES 1-5 . . . . .	11
ILLUSTRATED KEYS TO THE AMAZONIAN SPECIES OF <i>ANOPHELES</i> ( <i>NYSSORHYNCHUS</i> ) . . . . .	16
DISCUSSIONS, BIONOMICS, MEDICAL IMPORTANCE AND DISTRIBUTION OF SPECIES	
1. <i>Anopheles</i> (Nys.) <i>argyritarsis</i> . . . . .	34
2. <i>Anopheles</i> (Nys.) <i>darlingi</i> . . . . .	35
3. <i>Anopheles</i> (Nys.) <i>allopha</i> . . . . .	37
4. <i>Anopheles</i> (Nys.) <i>braziliensis</i> . . . . .	39
5. <i>Anopheles</i> (Nys.) <i>oswaldoi</i> . . . . .	41
6. <i>Anopheles</i> (Nys.) <i>galvaoi</i> . . . . .	42
7. <i>Anopheles</i> (Nys.) <i>evansi</i> . . . . .	43
8. <i>Anopheles</i> (Nys.) <i>aquasalis</i> . . . . .	45
9. <i>Anopheles</i> (Nys.) <i>ininii</i> . . . . .	47
10. <i>Anopheles</i> (Nys.) <i>rangeli</i> . . . . .	48
11. <i>Anopheles</i> (Nys.) <i>nuneztovari</i> . . . . .	49

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12. <i>Anopheles</i> (Nys.) <i>strodei</i> . . . . .	51
13. <i>Anopheles</i> (Nys.) <i>rondoni</i> . . . . .	53
14. <i>Anopheles</i> (Nys.) <i>benarrochi</i> . . . . .	54
15. <i>Anopheles</i> (Nys.) <i>triannulatus</i> . . . . .	55
ACKNOWLEDGMENTS . . . . .	56
REFERENCES . . . . .	57
PLATES 6-24 . . . . .	63

## PLATES

1. Map of Amazonia . . . . .	11
2. Morphology of adult: general . . . . .	12
3. Morphology of adult: thorax, legs, abdomen . . . . .	13
4. Morphology of male genitalia: <i>oswaldoi</i> . . . . .	14
5. Morphology of larva: <i>oswaldoi</i> . . . . .	15
6. Distribution of <i>argyritarsis</i> , <i>darlingi</i> , <i>lanei</i> , <i>pictipennis</i> and <i>sawyeri</i> . . . . .	63
7. Distribution of <i>albitarsis</i> , <i>allopha</i> and <i>braziliensis</i> . . . . .	64
8. Distribution of <i>albimanus</i> , <i>triannulatus</i> , <i>strodei</i> , <i>rondoni</i> and <i>benarrochi</i> . . . . .	65
9. Distribution of <i>oswaldoi</i> , <i>evansi</i> , <i>aquasalis</i> , <i>ininii</i> and <i>anomalophyllus</i> . . . . .	66
10. Distribution of <i>galvaoi</i> , <i>rangeli</i> , <i>trinkae</i> and <i>nuneztovari</i> . . . . .	67
11. Hypothesized phylogenetic tree of <i>Argyritarsis</i> Section . . . . .	68
12. Hypothesized phylogenetic tree of <i>Albimanus</i> Section . . . . .	69
13. <i>Anopheles</i> (Nyssorhynchus) <i>argyritarsis</i> : larva . . . . .	70
14. <i>Anopheles</i> (Nyssorhynchus) <i>darlingi</i> : larva . . . . .	71
15. <i>Anopheles</i> (Nyssorhynchus) <i>allopha</i> : larva . . . . .	72
16. <i>Anopheles</i> (Nyssorhynchus) <i>braziliensis</i> : larva . . . . .	73
17. <i>Anopheles</i> (Nyssorhynchus) <i>evansi</i> : larva . . . . .	74
18. <i>Anopheles</i> (Nyssorhynchus) <i>aquasalis</i> : larva . . . . .	75
19. <i>Anopheles</i> (Nyssorhynchus) <i>ininii</i> : larva . . . . .	76
20. <i>Anopheles</i> (Nyssorhynchus) <i>rangeli</i> : larva . . . . .	77
21. <i>Anopheles</i> (Nyssorhynchus) <i>nuneztovari</i> : larva . . . . .	78
22. <i>Anopheles</i> (Nyssorhynchus) <i>strodei</i> : larva . . . . .	79
23. <i>Anopheles</i> (Nyssorhynchus) <i>benarrochi</i> : larva . . . . .	80
24. <i>Anopheles</i> (Nyssorhynchus) <i>triannulatus</i> : larva . . . . .	81

## INTRODUCTION

Malaria is currently highly endemic throughout most of Amazonia. The primary anopheline vectors of this disease in Amazonia are members of the subgenus *Nyssorhynchus*, the most important of which is *Anopheles darlingi*. Unfortunately, many of the species in this subgenus are morphologically extremely similar, so that species identification is often very difficult. Primarily for this reason and because of numerous taxonomic changes, previous keys are often unreliable for the differentiation of the species of *Nyssorhynchus* occurring in this region. We have attempted to reconcile some of these difficulties in this handbook by (1) providing keys and illustrations for the adult females, male genitalia and larvae for the species of *Nyssorhynchus* occurring in Amazonia, (2) discussing differentiating taxonomic characters for each currently recognized Amazonian species and (3) providing a brief summary of the bionomics and medical importance of each species.

This handbook and its keys pertain only to those species of *Nyssorhynchus* known to exist in Amazonia: *argyritarsis*, *darlingi*, *allopha*, *braziliensis*, *oswaldoi*, *galvaei*, *evansi*, *aquasalis*, *ininii*, *rangeli*, *nuneztovari*, *strodei*, *rondoni*, *benarrochi* and *triannulatus*. The other species of *Nyssorhynchus* occurring outside of Amazonia occasionally appear in the general discussion of the taxonomic characters, bionomics, medical importance and distribution maps, but have been omitted from the keys. These latter species are presented only to give an overview of the subgenus. Although *trinkae* occurs along the eastern margin of Amazonia (pl. 10), this species presently is not known to occur in the tropical forest of Amazonia and, therefore, is not included.

## MATERIAL AND METHODS

The information and many of the illustrations presented in the handbook have been extracted (often verbatim or *in toto*) and consolidated from two recent revisions, one on the *Albimanus* Section (Faran 1980) and the other on the *Argyritarsis* Section<sup>3</sup>. For a complete list of the pertinent literature, and for a detailed discussion of the material and methods, systematics, and descriptions of the species in the subgenus *Nyssorhynchus*, refer to these two papers.

Amazonia, as represented by the tropical forest, is delimited for the purposes of this handbook as including northern Brazil, the Guianas, the eastern margins of Venezuela, Colombia, Ecuador and Peru, and northern Bolivia (pl. 1; Meggers 1977); it is sometimes referred to in this paper as simply the "Amazon."

The majority of the material for this study was collected (or acquired) by the project Mosquitoes of Middle America (MOMA), University of California, Los Angeles (UCLA) and the Medical Entomology Project (MEP), Smithsonian Institution, Washington, DC.

**TERMINOLOGY.** The terminology and abbreviations are largely those of Harbach and Knight (1980). The form of presentation is essentially that of Belkin (1962). Regarding the chaetotaxy of the immatures, branching for those setae considered to be taxonomically important is usually listed as 2 sets of figures. The first set of numbers after the seta represents the frequency of at least 75% of the observations. The set of numbers following this "75% range" is the entire range of all observations; if the 75% range and the entire range are the same, then only one set of figures is listed. Following Harbach and Knight (1980) a number of new terms are used for the adult thorax, palpus, antenna, tarsi and male genitalia, and the larval spiracular plate. In addition, a few special terms are used for the wing spots of the adult, the ventral and dorsal lobes of the claspette (ventral and dorsal claspettes) of the male genitalia, and abdominal tergal plates of the larva. These terms are listed in the chapter on taxonomic characters and illustrated on plates 2-5.

**KEYS.** Illustrated identification keys are given for the adult females, male genitalia and fourth stage larvae. For each couplet in the key, it is very important to read the *entire* first half of the couplet before proceeding to the second half. In the figures, a number in parentheses associated with an arrow indicates to which couplet the structure pertains; these parenthesized numbers are used when different portions of a single figure are used for more than one couplet.

**DISCUSSIONS.** The beginning of this section for each species pertains to the important differentiating characters for the adult female, male genitalia and larva. When pertinent to this handbook, affinities, evolutionary trends, and intrapopulational and geographical variations are presented.

<sup>3</sup> Linthicum, Kenneth J. 1978. A revision of the *Argyritarsis* Section of the subgenus *Nyssorhynchus* of *Anopheles*. Ph.D. dissertation. University of California, Los Angeles. 409 p.

**BIONOMICS.** Unless otherwise stated, those data on the habitat of the immatures have been extracted from the MOMA field collection records on file at the Smithsonian Institution. Additional information about the natural history of each species has been taken from the literature.

**MEDICAL IMPORTANCE.** A brief summary of the medical importance of each species is included following the bionomics. This section is only a summary, and does not in any way attempt to be an inclusive discussion of the literature. It pertains primarily to malaria and what is known concerning the vector capacity of each species.

**DISTRIBUTION.** The known distribution is given for each species and is also outlined on plates 6-10. On these plates, a solid line broken by a dotted line implies uncertainty regarding the distribution of that particular species within the area bordered by the dotted line (for example: pl. 8, *rondoni*; pl. 10, *galvaoi*).

**FIGURES and PLATES.** The drawings in the key are referred to as figures (fig.) to distinguish them from the other drawings in the handbook that are designated as plates (pl.). In addition to the figures in the key to the larvae, the complete illustration for the fourth stage larva of each species is included following the distribution maps (except for *oswaldoi*, pl. 5).

## SYSTEMATICS

### Plates 11, 12

The subgenus *Nyssorhynchus* has been subdivided into two sections, the Argyritarsis Section and the Albimanus Section (Faran 1980). The 2 sections are closely allied to each other and together form a tight, well-defined taxon. The entire subgenus is restricted to the Neotropics except for *albimanus* which extends into the Nearctic. The Albimanus Section is distinguished from the Argyritarsis Section in the adults primarily by the basal dark band on hindtarsomere 5, and in the male genitalia by the variously developed, fused ventral lobes of the claspette (ventral claspette). Only on the basis of these two characters can these sections be readily differentiated. The Myzorhynchella group has been excluded from consideration because of the paucity of material available for study, and because of its uncertain taxonomic position.

The Argyritarsis Section includes 8 valid species that we have separated into 2 groups, the Albitarsis Group and Argyritarsis Group. The more ancestral Argyritarsis Group has been separated into 4 subgroups: the Argyritarsis Subgroup composed of *argyritarsis* and *sawyeri*, and the monotypic Lanei, Pictipennis and Darlingi Subgroups. We have divided the Albitarsis Group into 2 subgroups, the monotypic Braziliensis Subgroup and the Albitarsis Subgroup composed of 2 species, *albitarsis* and *allopha*. We no longer consider *allopha* to be a junior synonym of *albitarsis* but a separate, distinct species (see discussion section for *allopha*).

Faran (1980) divided the Albimanus Section into 2 groups, the monotypic Albimanus Group and the Oswaldoi Group. The Oswaldoi Group has been separated into 2 subgroups, the monotypic Triannulatus Subgroup, and the Oswaldoi Subgroup composed of 12 species, which is further separated into the Oswaldoi Series and the Strodei Series. Faran (1980) referred to these latter 2 taxa as the Oswaldoi Complex and the Strodei Complex. Within the Oswaldoi Series, 2 separate phyletic lines are discernible on the basis of the structure of the ventral lobe of the claspette of the male genitalia. One line is composed of *oswaldoi*, *galvaoi*, *evansi*, *aquasalis*, *ininii* and possibly the relict *anomalophyllus*, and the other by *rangeli*, *trinkae* and *nuneztovari*. It is important to mention that *evansi* is now considered to be the senior synonym of *noroestensis* (Faran 1981), and no longer a *nomen dubium* (Faran 1980), or the senior synonym of *strodei* (Knight and Stone 1977). The Strodei Series contains *strodei*, *rondoni* and *benarrochi*. *An. strodei* and *rondoni* are very closely related, but their relationship to *benarrochi* is difficult to determine as *benarrochi* is the most



derived species in the section. *An. benarrochi* has been placed in the Strodei Series only because of the derived similarity of its male genitalia with those of *strodei* and *rondoni*.

### TAXONOMIC CHARACTERS

The following is a summary of the pertinent characters used for species identification. The most reliable characters for species identification are in the male genitalia and the larva. The external morphology of the adult female, particularly in the case of the Oswaldoi Subgroup, is very similar interspecifically and usually variable intraspecifically. For this reason, the key to adult females may not always be entirely reliable when used by itself. It is *highly* recommended that one refer to the species discussions when attempting to identify any species in this subgroup, and to correlate those data with the information given on the bionomics and distribution. As has been emphasized by Belkin (1962), it is best to examine more than one specimen. To be certain of an identification, the immatures should be individually reared, and slides prepared of their exuviae and of the genitalia of the corresponding males to permit the correlation of characters in the different life stages. Where morphologically similar species occur sympatrically it is doubly important to use more than one developmental stage. Lastly, it must be emphasized that not all the populations from every locality where each species exists were examined. Thus, the range of variation reported is conservative, and although sufficient in most cases, may be exceeded in some individuals. Also, as indicated by Arnell (1973), the illustrations of the larvae show only the modal condition of the setal branching and cannot represent the variation that occurs within a species.

#### Adult Females

##### Plates 2, 3

The important differentiating characters in the adult female are the (1) maxillary palpo-meres 4,5, (2) presence or absence of scales on mesanepimeron, (3) number of setae on posterior margin of scutellum, (4) banding patterns of legs, (5) relative lengths, and presence or absence of wingspots, (6) dark caudolateral scale tufts of abdomen and (7) presence or absence of scales on first abdominal sternum.

The new terminology (Harbach and Knight 1980) used in the keys, discussions and illustrations for the head, thorax and legs is listed here after the old terminology, and is illustrated in plates 2 and 3.

Old Name	New Name
anterior pronotum	antepnotum
meron	mesomeron
mesepimeron	mesanepimeron
palpal segment	palpomere
postnotum	mesopostnotum
posterior pronotum	postpronotum
propleuron	proepisternum
spiracular area	prespiracular area
sternopleuron	mesokatepisternum
tarsal segment	tarsomere
torus	pedicel

The scale banding patterns in the fore- and midtarsus, as in the hindtarsus, are important diagnostic characters. The dorsal surface of the fore- and midtarsomere 1 is predominantly dark, speckled with light scales and with a light apical band usually less than 0.1 the length of the tarsomere. The

ventral surfaces of the fore- and midtarsomeres 1,2 are light; the ventral surfaces of fore- and midtarsomeres 3-5 are often speckled with dark scales, varying from completely light to dark. Foretarsomere 1 has a white to golden apical band in some species. Foretarsomere 2 has a narrow to wide, light-scaled band in apical 0.15-0.95. Foretarsomere 3 is light scaled in apical 0.1-0.9. Foretarsomeres 4,5 are from dark to predominantly light. Midtarsal markings are generally as in the foretarsus except that the ventral surface usually is darker, and the apical light bands, when present, are white to golden, usually darker than on the foretarsus. The dorsal surfaces of midtarsomeres 2,3 are from completely dark to light in apical 0.4. Midtarsomere 4 is usually dark, occasionally with an apical light band (*ininii*). Midtarsomere 5 is from completely dark to completely light. Hindtarsomere 1 is predominantly dark with a speckling of light scales on the ventral surface, a longitudinal light streak on the anterior surface and sometimes a yellow to white band at the apex. Hindtarsomere 2 is highly variable, with a dark band in basal 0.05-0.90. Hindtarsomeres 3,4 are completely white or with a dark basal band present on either one (*rondoni*, uncommon variants) or both tarsomeres (uncommon variants). Hindtarsomere 5 is from completely white to dark in about basal 0.5.

The wing venation and wing spots are illustrated in plate 2. The special terminology used for the wing spots is modified from Zavortink (1973). Vein C usually has a basal, humeral, subbasal, presectoral, sectoral, subcostal and preapical light-scaled spot; the subbasal, presectoral and subcostal light spots are sometimes absent. Vein  $R_s-R_{2+3}$  is variable, more or less predominantly dark, with 3 or 4 dark spots, 2 or 3 light spots and with or without an extra subcostal light spot. Veins  $R_2$  and  $R_3$  have 2 or 3 light spots. Vein  $R_{4+5}$  has 2 small to moderately large dark spots, one subcostal, the other preapical. Vein M has a subcostal dark spot that in some species reaches the furcation; M may or may not have a sectoral dark spot of variable length. Vein  $M_{1+2}$  has 2 dark spots, and  $M_{3+4}$  has 1 dark spot. The base of vein Cu is light with a small to medium sectoral dark spot usually not reaching furcation. Vein  $Cu_1$  is predominantly light, with usually 3 small, dark spots, 2 toward base in sectoral-subcostal region and 1 preapical. Vein  $Cu_2$  is light except for a small to moderate preapical dark spot. Vein A is predominantly light, with 2 dark spots, 1 subbasal and 1 subcostal. The apical light fringe spot is conspicuous and is small to large; fringe of remainder of wing is largely dark with light areas where veins intersect wing margin except occasionally for  $R_1$ ; usually there is an additional moderately long, light fringe spot present between base of wing and apex of vein A.

## Male Genitalia

### Plate 4

The subgenus *Nyssorhynchus* is characterized by the fusion of the ventral lobes of the claspette to form a single median structure, and by the single parabasal seta. The claspette in *Nyssorhynchus* is divided into a dorsolateral lobe (dorsal lobe of Harbach and Knight 1980) and an apically fused, membranous, mesoventral lobe (ventral lobe of Harbach and Knight 1980). To avoid possible confusion, which could occur because of the various uses of the term "lobe" in reference to the structure of the ventral lobe of the claspette, we shall refer to the ventral and dorsal lobes of the claspette simply as the "ventral claspette" and the "dorsal claspette" respectively. The species in this subgenus have 2 accessory setae and a single internal seta.

The new terminology (Harbach and Knight 1980) used in the keys, discussions and illustrations for the male genitalia is listed here after the old terminology, and is illustrated in plate 4.

Old Name	New Name
accessory spine	accessory seta
basal apodeme	apodeme of gonocoxite
clasper	gonostylus
internal spine	internal seta
parabasal spine	parabasal seta

sidepiece  
tergomedial bristle

gonocoxite  
tergomedial seta

**DORSAL CLASPETTE.** In the Argyritarsis Section the dorsal claspette possesses reliable characters for species delineation. The dorsal seta (leaflet) of the dorsal claspette of *darlingi* and *braziliensis* has a well-developed basomesal projection, while that of all the other species in the section is without a basomesal projection.

**VENTRAL CLASPETTE.** The fused ventral claspette best delimits the taxa within the subgenus and has been used most often to divide the subgenus into different groups, subgroups and series. All the species in the Argyritarsis Section lack spicules on the ventral claspette, whereas all the species in the Albimanus Section, except for *albimanus* and *triannulatus*, possess spicules. "Spicules" is used here to denote the vestiture present on the ventral claspette rather than "setae" previously used in Faran (1980), as these processes lack the aveolus characteristic of true setae. The various components of the ventral claspette used in the key and the discussions, such as the basal lobules, preapical plate, refringent structure, membranous area, median sulcus and mesal cleft, are illustrated in plate 4.

**PHALLOSOME.** We believe that primitively in *Nyssorhynchus* the aedeagus had sclerotized, long, serrated, subapical leaflets. This condition is present in all species in the Argyritarsis Group and in *anomalophyllus* of the Albimanus Section. In all other species sclerotized, serrated leaflets are absent. However, in several species of the Oswaldoi Series remnants of leaflets still occur as unserrated, membranous, basolateral expansions of the apex of the aedeagus. Wherever width of aedeagus is used, it refers to the width of the aedeagus at the base of the apex (subapex where lateral sclerotizations extend ventromedially to form an incomplete tube; referred to as the ventromesal subtriangular projections). Length of apex of aedeagus refers to distance from the subapical, collar-like, ventromesal subtriangular projection to apex of aedeagus.

#### Fourth Stage Larvae

##### Plate 5

Many characters in the larvae of *Nyssorhynchus* correlate with characters in the adult and male genitalia to clearly define the separate taxa. The chaetotaxy is very important for species identification.

**HEAD.** The important setae are 2,3-C, and the length and branching of 4-C. Setae 2,3-C may be (1) of subequal or unequal lengths and (2) single and simple, barbed or plumose with branches short to long and occasionally dendritic. The relationship between the approximation of setae 2-C (inner clypeals) and setae 3-C (outer clypeals) is given by the **clypeal index**, which is the distance between the insertions of seta 2-C and seta 3-C on one side of the head divided by the distance separating insertions of setae 2-C (pl. 5).

**ANTENNA.** Seta 1-A in the ancestral condition is small; it is large and independently derived in *benarrochi* and *ininii*.

**THORAX.** Seta 1-P in the ancestral condition is plumose and multibranched with filiform branches; in the derived state, 1-P is palmate with lanceolate branches. Other important characters are (1) presence or absence of common sclerotized tubercle for setae 1,2-P or 1-3-P, (2) approximation of setae 1-P from opposite sides and (3) seta 3-T filiform or with lanceolate branches.

**ABDOMEN.** Primitively, seta 1-I has filiform branches; this condition is present only in *argyritarsis* and *darlingi*. Seta 1-I in *sawyeri* may represent an intermediate condition with very weakly developed lanceolate leaflets. In all other species seta 1-I has well-developed lanceolate leaflets. Important characters for species identification include (1) size and number of branches of setae 11-I, 13-I-IV, and 0-II, (2) location and size of seta 5-I,II, (3) width of leaflets of palmate seta 1-II-VII and (4) in the Argyritarsis Section, the varied development of the multiple tergal plates on segments I-VIII. In the Argyritarsis Section the median tergal plate is usually moderately large, strongly scler-

otized and located on or near the anterior margin of segments I-VIII. Accessory median and accessory submedian tergal plates are present caudad of the median tergal plate, and are usually subspherical or ovoid, and small (only about 0.05 the area of the median tergal plate). The accessory median tergal plates are (1) oriented longitudinally on the midline 0.1 the length of the segment from the anterior margin, (2) always absent on segment I, (3) single or absent on segment II, (4) single (*argyritarsis*, *darlingi*, *braziliensis*) or sometimes double (*allopha*) on segment III and (5) single and without lobes (*argyritarsis*) or bilobed (*allopha*, *darlingi*, *braziliensis*) or trilobed (*allopha*, *braziliensis*) or with 2,3 round plates (*allopha*) on segments IV-VII. The accessory submedian tergal plates are (1) usually in pairs with one immediately on each side of midline located 0.5 length of segment from anterior margin of segment, (2) present or absent in *argyritarsis*, (3) present on segments I-VII of *allopha*, *braziliensis* and *darlingi* as 1 or 2 pairs.

**SPIRACULAR LOBE.** In Faran (1980) the term lateral arm of the "spiracular apparatus" was used to denote the lateral arm of the "median plate of the spiracular apparatus" of Harbach and Knight (1980). We are following the latter authors' usage of the term "median plate." In the ancestral condition the lateral arm of the median plate of the spiracular apparatus is either nonexistent or short. There has been an independent increase in the size of the lateral arm in *triannulatus* and, to a lesser degree, in *ininii*. The dentition of the pecten is important as a group character in the *Argyritarsis* Section and is a secondary key character in species diagnosis in the *Albimanus* Section.

**ANAL SEGMENT.** In the *Albimanus* Section there appears to be a trend for the insertion of seta 1-X to migrate from a dorsal position within the saddle, to a position on or near the ventral margin of the saddle. In the most derived case (*oswaldoi*) seta 1-X is not inserted on the saddle at all, but ventrad of it. Seta 1-X is moderately long to long in all species except *benarrochi*. The anal gills are short in *aquasalis*, and in all other Amazonian species of *Nyssorhynchus*, they are moderately long to very long.

## BIONOMICS

The immature stages of the subgenus *Nyssorhynchus* are found predominantly in ground water. They occur in a variety of habitats such as ponds, lakes, stream and river margins, seepage and drainage areas, ditches, flooded meadows and pastures, reservoirs, swamps, ground pools, borrow pits, and animal and vehicle tracks. *An. aquasalis* is the only species primarily restricted to the coast; this species preferentially occurs in brackish water such as in mangrove swamps and coastal ground pools. However, *aquasalis* is capable of living in fresh water and often is collected several kilometers from the coast. *An. argyritarsis*, although usually found in ground pools, occasionally is collected in artificial containers such as tin cans and animal watering troughs. *An. triannulatus*, *ininii* and *allopha* commonly are found in lakes, ponds or large ground pools. *An. triannulatus* is the only species clearly shown often to be closely associated with a specific plant; it is usually collected in or between the rosette crowns of *Pistia stratiotes* Linnaeus. *An. allopha* is always found with some vegetation such as green algae, *Eichhornia* spp., *Ceratophyllum* spp. and *Salvinia* spp. *An. darlingi* is often collected in mats of *Ceratophyllum* spp. along the margins of rivers and canals in partial or well-shaded areas. *An. evansi* and *braziliensis* are usually collected in forests or areas of secondary vegetation. *An. oswaldoi*, *ininii* and *triannulatus* adults are usually collected in the interior of forests, although the larvae may be collected from ground pools in interspersed secondary growth areas. *An. rondoni* occurs in ditches, puddles, flooded meadows, etc., in southern Brazil and northern Argentina, and is not reported further north than the southern margin of upper Amazonia.

Regarding altitudinal distribution, *strodei* has been collected at the highest elevations (1600 m) for any species of *Nyssorhynchus*, although it also occurs at lower elevations. *An. rangeli* and, to a lesser extent, *benarrochi* are principally found at intermediate elevations (200-1000 m), such as

in the upper Amazon and the llano plateau region of Colombia, extending south to Mato Grosso and Bolivia. *An. aquasalis* normally occurs on or near the coast usually at elevations less than 400 m. The remainder of the Amazonian species are found at low to intermediate elevations.

Host preference studies for several species indicate that these mosquitoes feed predominantly on large mammals such as dogs, cats, cattle, pigs, goats, donkeys and man; occasionally some feed on fowl. In all known cases, the species feed readily on man when given the opportunity (*ininii* and *galvaoi* have not been studied in this respect). The adults are active either crepuscularly or nocturnally except for those of *triannulatus* and *braziliensis*, which may be somewhat diurnal. Most of the species are exophilic and zoophilic except, in certain instances, for *aquasalis*, *nuneztovari*, *darlingi* and *allopha*.

### MEDICAL IMPORTANCE

*An. darlingi* is a very efficient vector of malaria in northern and northeastern Brazil as well as in numerous other areas in South America. Wherever this species occurs along with malaria, *darlingi* females are almost always found naturally infected. *An. darlingi* is highly endophagous and anthropophilic. In addition to malaria, this species has also been suspected of being a vector of human filariasis. It has transmitted *Wuchereria bancrofti* (Cobbold) in the laboratory and has been collected naturally infected with this parasite.

*An. allopha*, although usually not a primary vector of malaria, may act as a secondary vector (Galvao 1940). This species will readily attack man and at times is very endophilic. It has been experimentally infected with malaria parasites and has been collected naturally infected.

*An. braziliensis*, like *allopha*, is not a primary vector of malaria but is capable of malaria transmission under the proper ecological conditions (Deane, Causey and Deane 1948). Normally this species is exophilic and zoophilic; however, in some regions of Amazonia when domestic animals are absent, *braziliensis* will readily enter houses and bite man. It has been collected naturally infected with *Plasmodium* spp. *An. argyritarsis* is generally considered not to be a primary vector of malaria but may be important when it occurs at high densities. Although it is rarely found inside houses and rarely attacks man, *argyritarsis* has been found naturally infected with malaria parasites.

*An. aquasalis* is a primary vector of malaria in the Lesser Antilles, and in Trinidad and Tobago. Along the coast of Brazil, the Guianas and possibly Venezuela, it is always a potential vector but usually only important when it occurs in large numbers. *An. aquasalis* feeds readily on man and is commonly collected in houses. In the past it has been an important vector of malaria in coastal Brazil.

*An. nuneztovari* is a primary vector of malaria in western Venezuela and northern Colombia, and is a probable vector in Suriname; in some areas where it occurs in Venezuela, spleen indices have been close to 100% (Gabaldon and Guerrero 1959). In Venezuela and Colombia the vector potential of *nuneztovari* has been reported to depend on the density of the nearby vegetation surrounding regions of habitation, which may be correlated with the vector's greater life expectancy and density in the forest (Hamon, Mouchet *et al.* 1970). In the Amazon basin *nuneztovari* has not been reported as being important as a vector of malaria.

*An. triannulatus* does not seem to be an important vector of malaria. This species was implicated as a possible vector during an epidemic at a boys' school near Maracay, Venezuela (Benarroch 1931), and once was found to have a natural oocyst infection (Gabaldon and Cova Garcia 1946b). Several investigators have experimentally infected *triannulatus* with *Plasmodium vivax* (Grassi and Feletti) and *P. falciparum* (Welch); however, it is much more refractory to infection than *albimanus*.

According to Correa (1938), *strodei* transmitted malaria at the Fazenda Santa Alice, Sao Paulo, Brazil; he reported a natural infection rate of 1.2%. Other Brazilian workers have experi-

mentally infected *strodei* with *Plasmodium vivax*, although there have not been any other reports implicating *strodei* as a vector.

Very little is known regarding the vector potential of *rangeli*, *evansi*, *rondoni* and *oswaldoi*. *An. evansi* was found naturally infected once in Ribeira, Sao Paulo, Brazil by Correa and Ramos (1942b). Lucena (1940) reported finding *oswaldoi* var. *metcalfi* naturally infected in Pontesinha, Brazil; however, Lucena may have been studying *aquasalis* rather than *evansi*. *An. oswaldoi* has been experimentally infected with *P. vivax* and *P. falciparum* (Fonseca and Fonseca 1942; Rozeboom 1942). *An. rangeli* has been suspected of transmitting malaria in Ecuador (Forattini 1962), but it has never been shown to be naturally infected. *An. rondoni* was investigated in Jujuy, Argentina, during the malaria season by Davis and Shannon (1928), and it was not found naturally infected nor was it possible to infect it experimentally with *P. falciparum*, *P. vivax* or *P. malariae* (Grassi and Feletti) in 3 different experiments. Nevertheless, Shannon and Del Ponte (1927) stated that Davis was able to infect *rondoni* in other experiments. Nothing is known about the vector potential of *ininii* or *galvaoi*.

#### ABBREVIATIONS FOR ADULT PLATES 2 AND 3

A	anterior	Mtn	metanotum
Ap	antepnotum	Mtpn	metapostnotum
L	lower	Mts	metepisternum
Mam	mesanepimeron	PA	postspiracular area
Mem	metameron	Ppn	postpronotum
Mks	mesokatepisternum	Ps	proepisternum
Mpn	mesopostnotum	PsA	prespiracular area
Msm	mesomeron	SA	subspiracular area
Mtm	metepimeron	U	upper

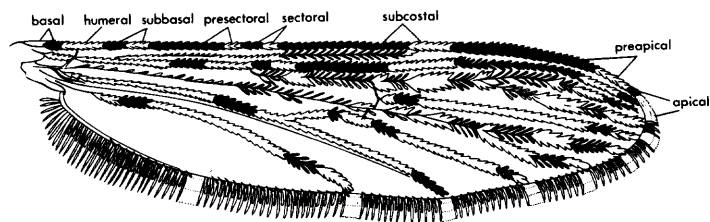
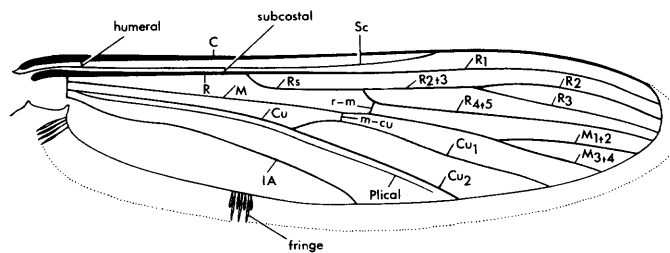
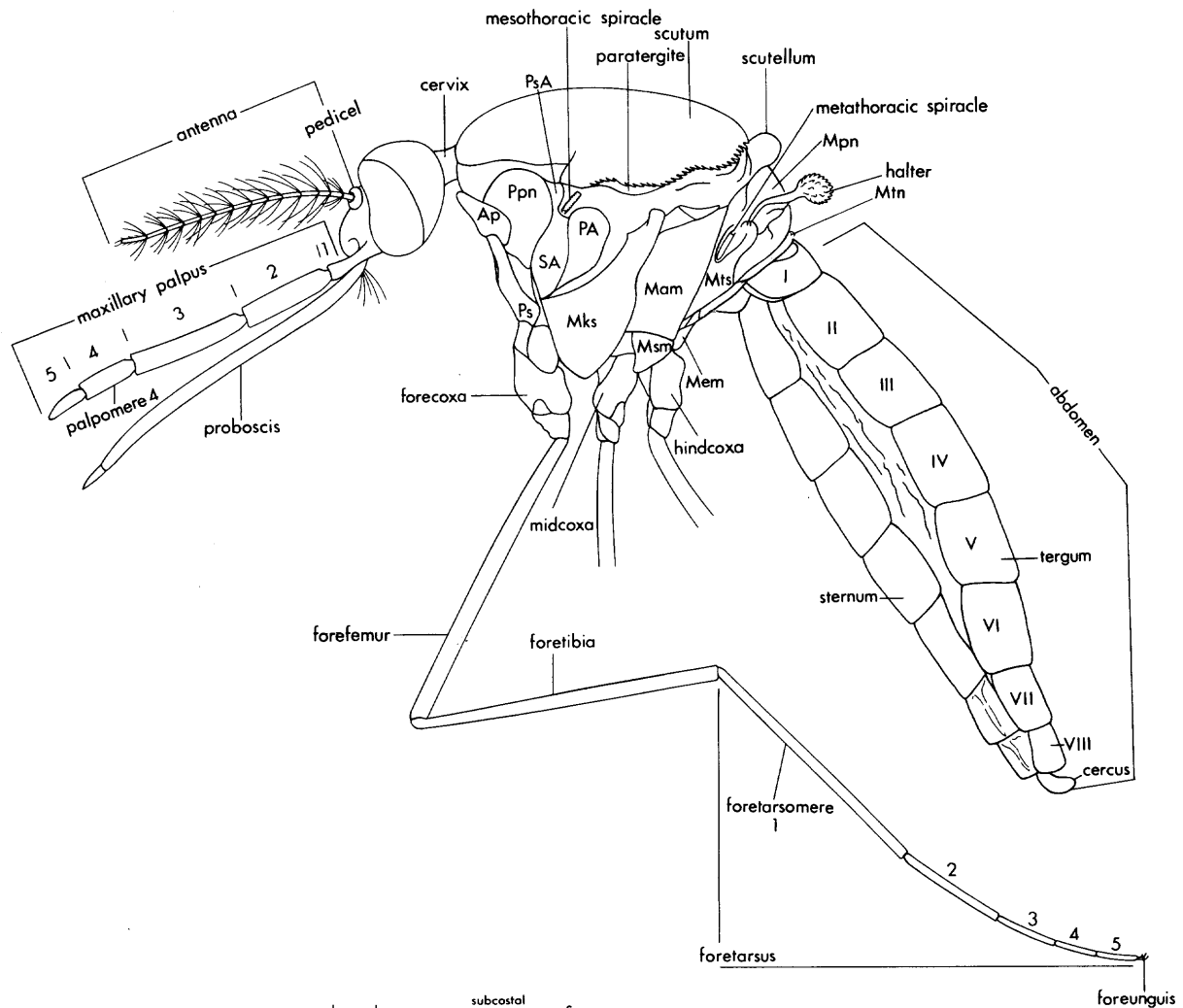
#### ABBREVIATIONS FOR LARVAL PLATE 5

A	antenna	PT	pecten
C	cranium	S	spiracular lobe
M	mesothorax	SAP	spiracular apparatus
Mx	maxilla	T	metathorax
P	prothorax		

# P1.1



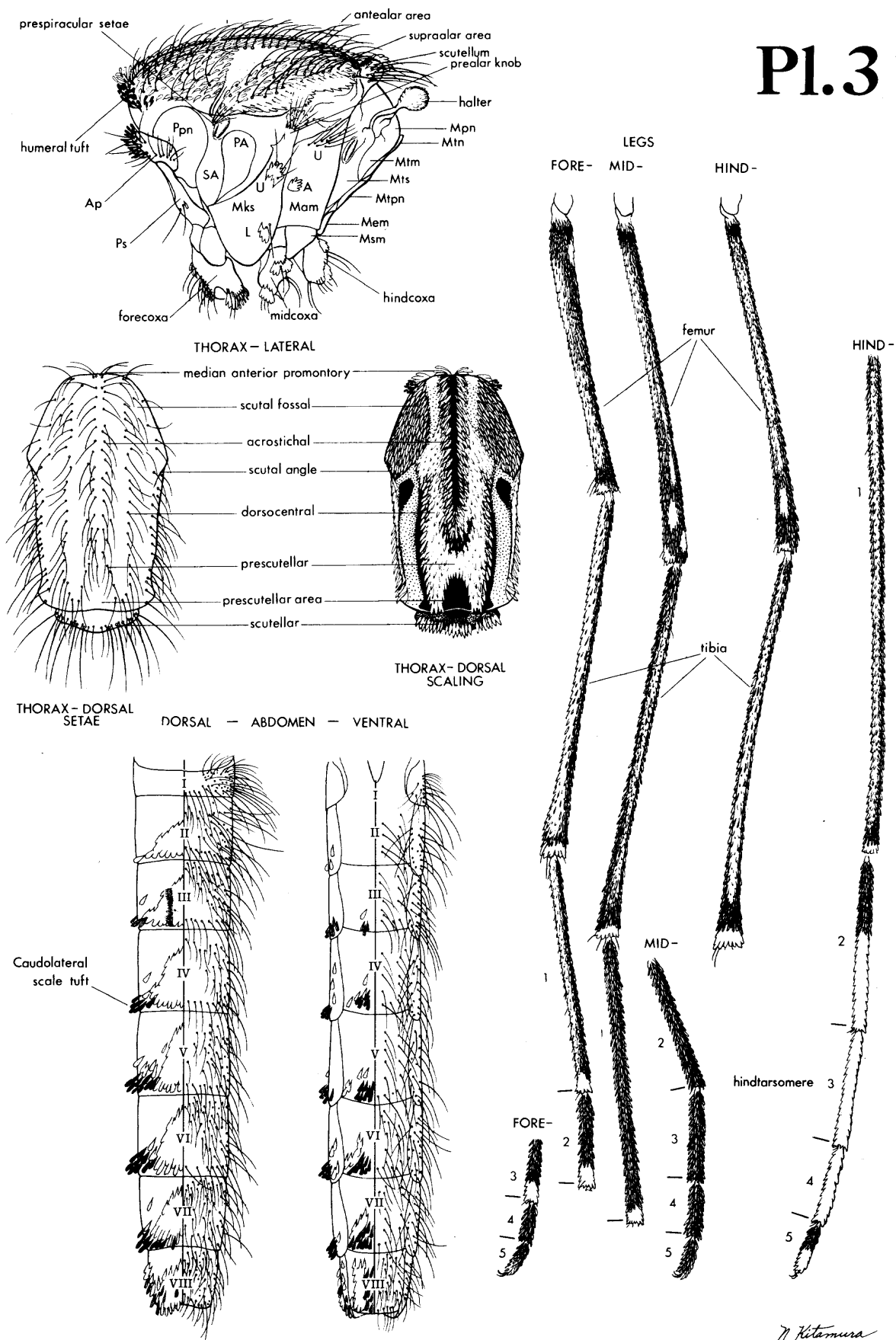
# Pl.2



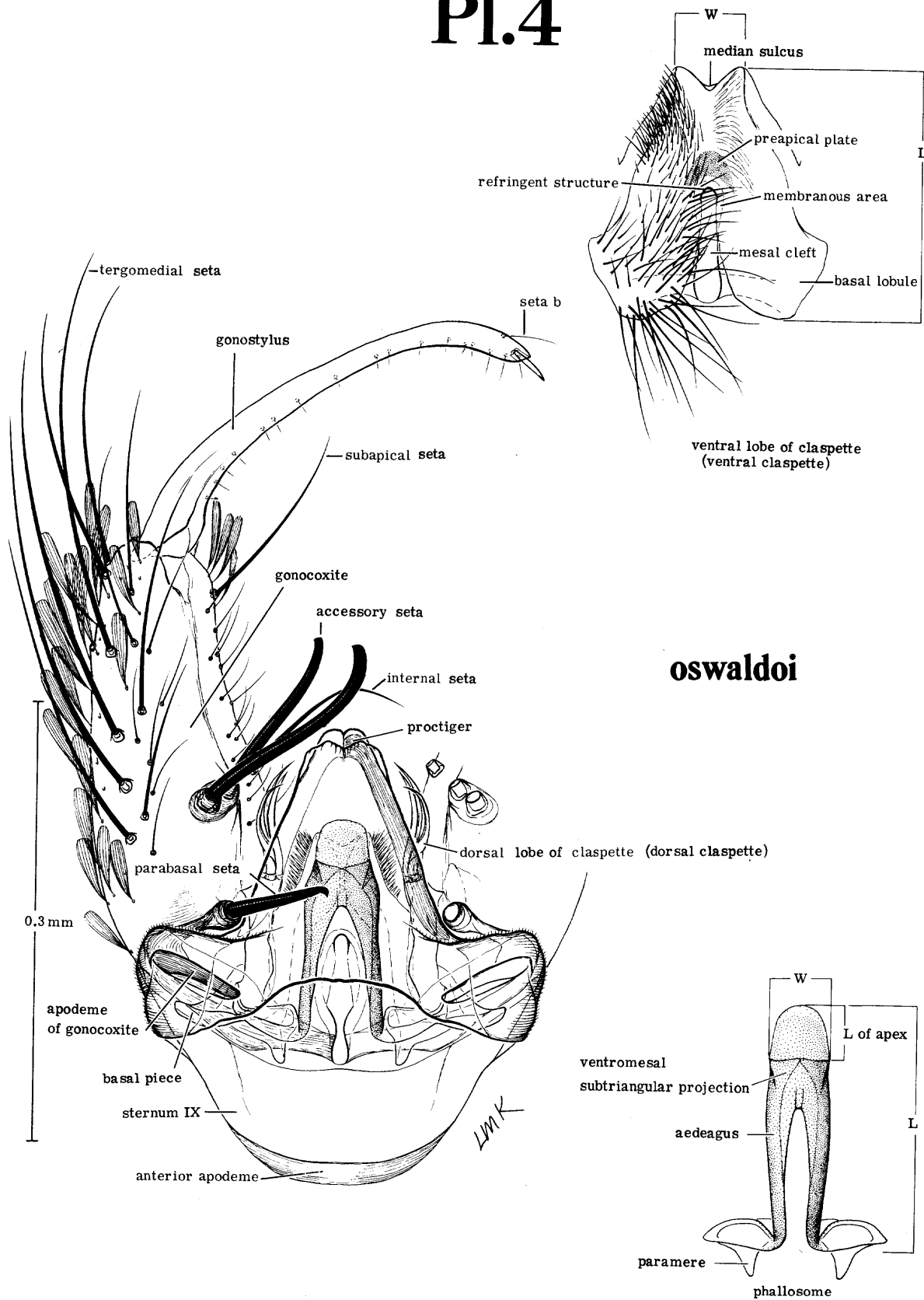
*A. Dery*



## Pl.3

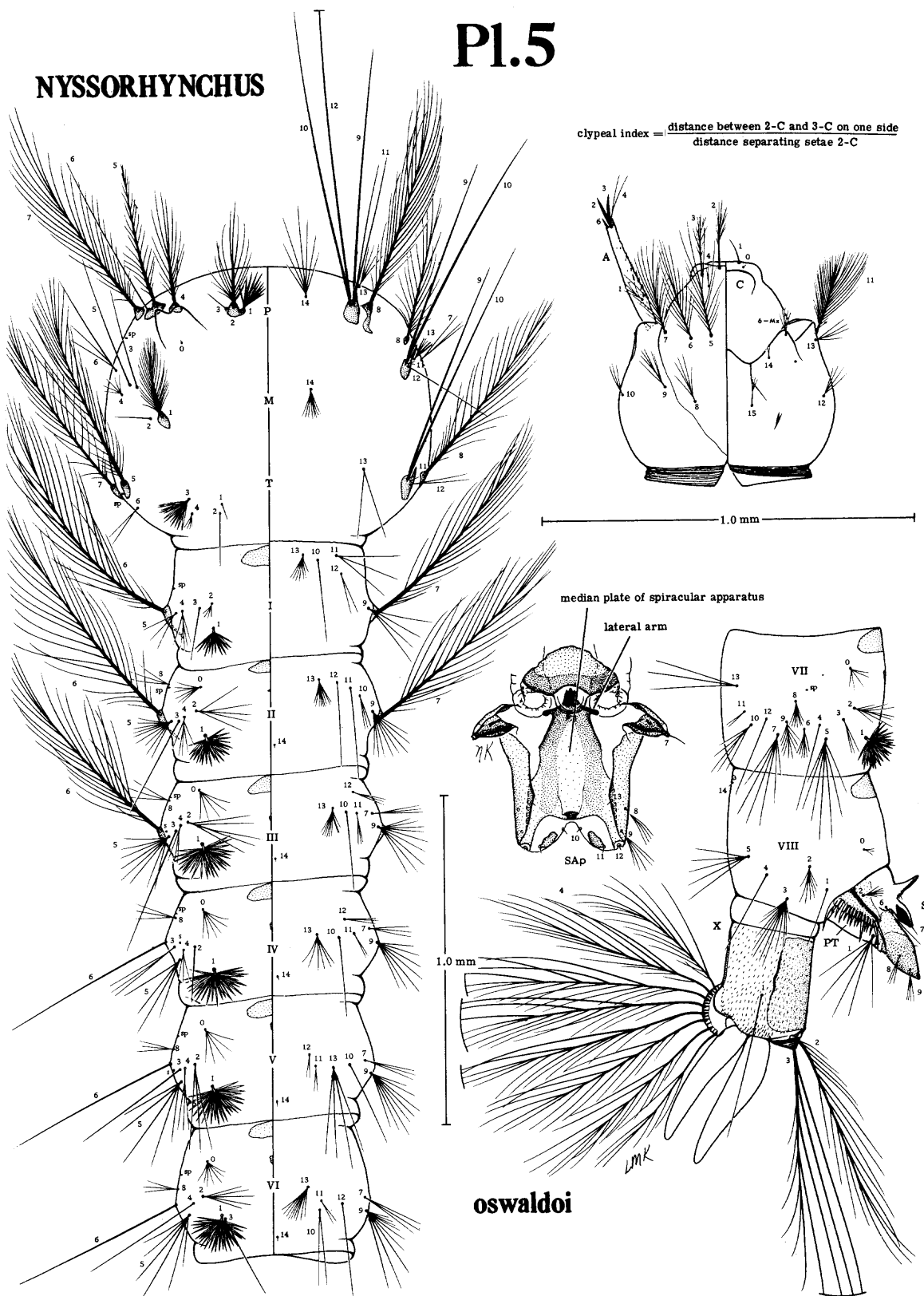


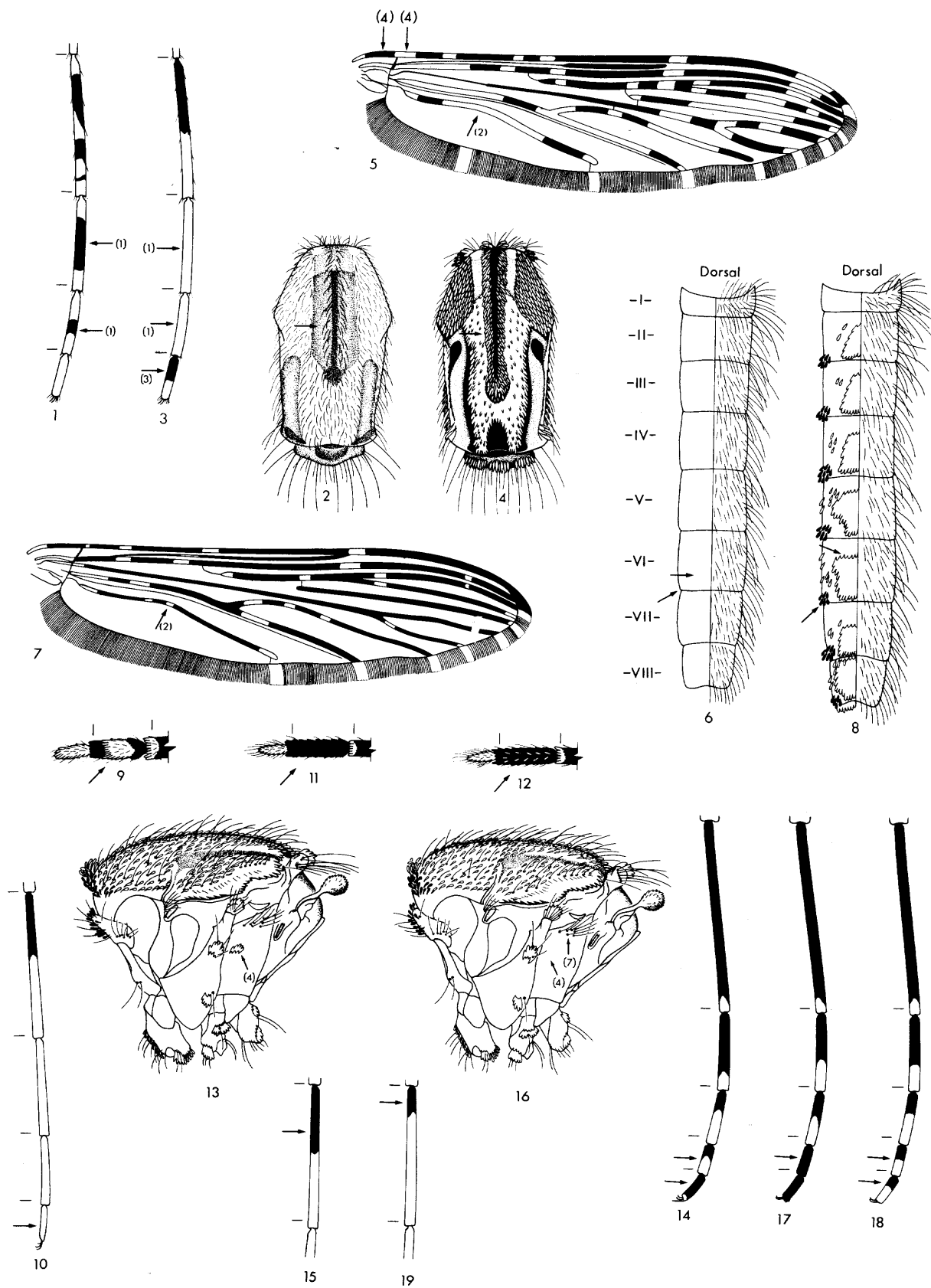
## Pl.4



**NYSSORHYNCHUS****P1.5**

clypeal index =  $\frac{\text{distance between 2-C and 3-C on one side}}{\text{distance separating setae 2-C}}$





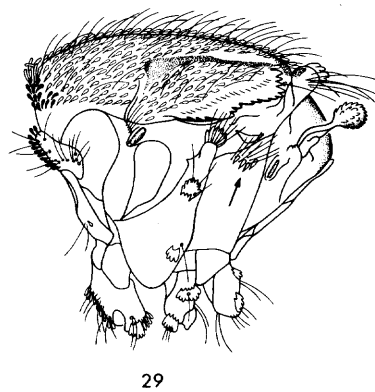
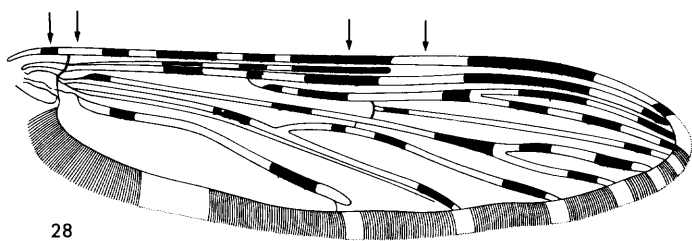
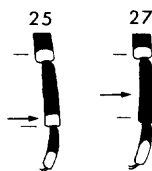
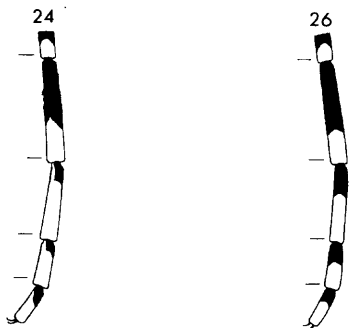
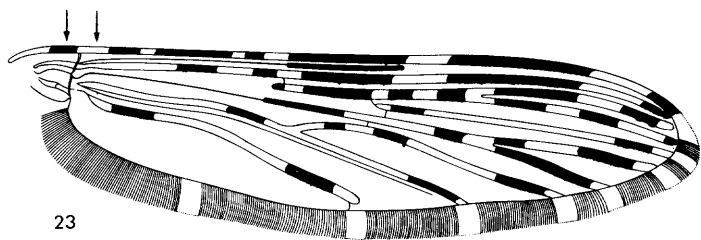
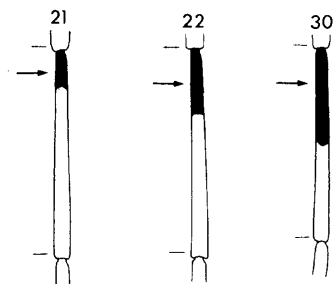
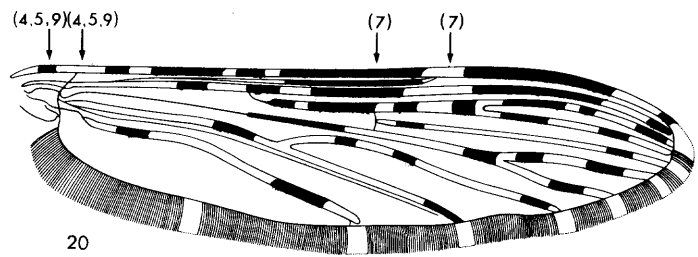
FIGURES 1-19

# ILLUSTRATED KEYS TO THE AMAZONIAN SPECIES OF *ANOPHELES* (*NYSSORHYNCHUS*)

## FEMALES

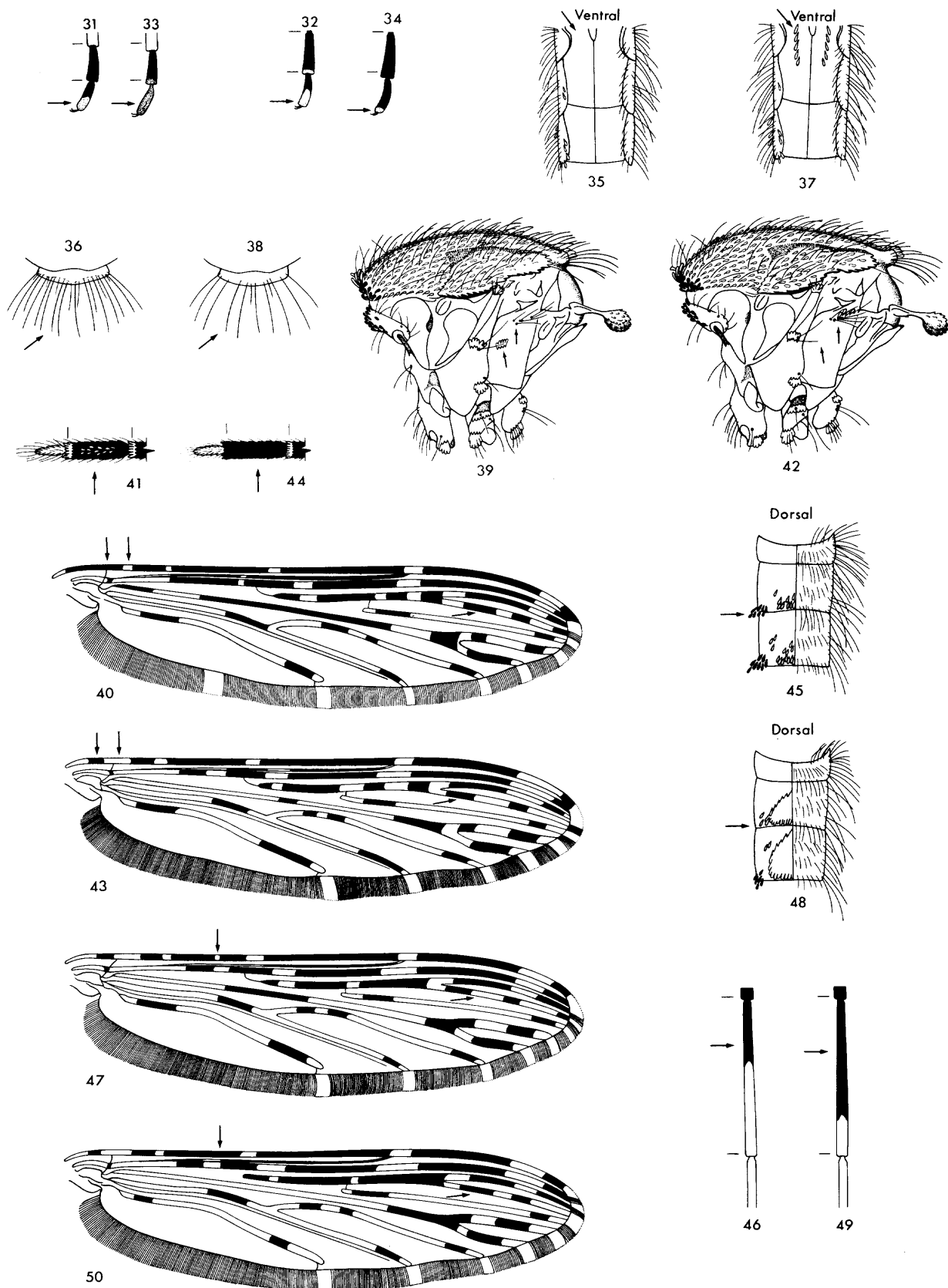
(*6. galvaoi* and *13. rondoni* not included; see species discussions)

1. Hindtarsomeres 3 and 4 not entirely white (fig. 1); acrostichal and dorsocentral areas at most with scattered scales (fig. 2); wings variable . . . . . Subgenera *Anopheles*, *Lophopodomyia*, *Kerteszia* and *Stethomyia*  
Hindtarsomeres 3 and 4 entirely white, except in unusual variants (fig. 3); acrostichal and dorsocentral areas with numerous scales (fig. 4); wings with distinct light and dark spots (fig. 5) (Subgenus *Nyssorhynchus*) . . . . . 2
- 2(1). Abdominal terga II-VII without obvious scales or caudolateral scale tufts (fig. 6); vein 1A more than 0.5 dark (fig. 7) . . . . . Myzorhynchella group  
At least some of abdominal terga II-VII with obvious scales and caudolateral scale tufts (fig. 8); vein 1A 0.5 or more light (fig. 5) (*Albimanus* and *Argyritarsis* Sections) . . . 3
- 3(2). Hindtarsomere 5 with a basal dark band (fig. 3); palpomere 4 with at least some white or cream on mediolateral surface (fig. 9) (*Albimanus* Section) . . . . . 4  
Hindtarsomere 5 entirely white (fig. 10); palpomere 4 dark (fig. 11), or with light and dark scales intermingled on mediolateral surface (fig. 12) (*Argyritarsis* Section) . . . 11
- 4(3). Anterior mesanepimeron (Mam) with a conspicuous patch of light scales (fig. 13); foretarsomere 4 with a light band in apical 0.40-0.65 (fig. 14); foretarsomere 5 predominantly dark (fig. 14); hindtarsomere 2 dark in basal 0.4-0.7 (fig. 15); vein C humeral light spot small, 0.5-1.3 length of basal dark spot (fig. 5); small species . . . . . *15. triannulatus*  
Anterior mesanepimeron (Mam) without a patch of light scales (fig. 16); foretarsomere 4 predominantly dark (fig. 17), or if light in more than apical 0.3 then foretarsomere 5 about 0.5 or more apically light (fig. 18) and/or hindtarsomere 2 less than 0.4 basally dark (fig. 19); vein C humeral light spot large, greater than 1.5 length of basal dark spot (fig. 20) except in *nuneztovari*; moderately large to large species . . . . . 5



FIGURES 20-30

- 5(4). Hindtarsomere 2 with basal dark band usually less than 0.25 length of tarsomere (fig. 21); vein C humeral light spot greater than 1.5 length of basal dark spot (fig. 20) . . . . 6
- Hindtarsomere 2 with basal dark band usually equal to or greater than 0.25 length of tarsomere (fig. 22), *if* less than 0.25 *then* vein C humeral light spot less than 1.5 length of C basal dark spot (fig. 23) . . . . . 7
- 6(5). Foretarsomere 4 all light to rarely more than 0.3 basally dark (fig. 24); midtarsomere 4 with a light band in apical 0.15-0.25 (fig. 25); foretarsomeres 3-5 predominantly cream to white, dark scales often present only on dorsobasal surface of tarsomere (fig. 24); foretarsomere 2 light in apical 0.35-0.55 (fig. 24); foretarsomere 3 light in apical 0.70-0.86 (fig. 24) . . . . . *9. ininii*
- Foretarsomere 4 at least 0.3 basally dark to all dark (fig. 26); midtarsomere 4 all dark (fig. 27); dark basal bands on foretarsomeres 3-5 almost completely encircling each tarsomere, dark scales usually absent from ventral surface (fig. 26); foretarsomere 2 light in apical 0.20-0.45 (fig. 26); foretarsomere 3 light in apical 0.50-0.85 (fig. 26) . . . . . *5. oswaldoi*
- 7(5). Subcostal light spot of vein C usually greater than 0.5 (0.45-1.00) length of subcostal dark spot (fig. 28); upper mesanepimeron (Mam) often with 1-4 light obovate scales (fig. 29); hindtarsomere 2 usually dark in basal 0.25-0.35 (fig. 22); humeral light spot of vein C usually large, 1.8-3.5 (1.0-3.7) length of basal dark spot (fig. 28) . *10. rangeli*
- Subcostal light spot of vein C almost always less than 0.5 length of subcostal dark spot (fig. 20); upper mesanepimeron (Mam) usually without light scales (fig. 16); hindtarsomere 2 and humeral light spot of vein C variable . . . . . 8
- 8(7). Hindtarsomere 2 dark in about basal half, 0.40-0.55 (0.3-0.6) (fig. 30); light wing spots at least on veins C and R light cream to yellowish, not white . . . . . *8. aquasalis*  
*14. benarrochi*
- Hindtarsomere 2 dark in less than basal 0.40 (fig. 22), *or if* greater than 0.40 *then* light wing spots white, not light cream to yellowish . . . . . 9
- 9(8). Vein C humeral light spot less than 2.0 (0.7-1.7) length of basal dark spot (fig. 23) . . . . . *11. nuneztovari*
- Vein C humeral light spot equal to or greater than 2.0 length of basal dark spot (fig. 20) . . . . . 10



FIGURES 31-50



- 10(9). Light scales on wing (at least anterior veins) and coxae (usually) gray to cream to yellow, not white; foretarsomere 5 cream, gray or golden in apical 0.30-0.50 (fig. 31); midtarsomere 5 gray to cream in about apical 0.5 (fig. 32) . . . . . **7. *evansi***

Light scales on wing and coxae usually white or very light cream; foretarsomere 5 usually golden to brown (fig. 33), occasionally differentiated into 0.5 dark, 0.5 light; midtarsomere 5 usually cream in less than apical 0.3 (fig. 34) . . . . . **12. *strodei***

- 11(3). Sternum I completely bare, without white scales (fig. 35); scutellum usually with more than 12 large, dark setae on posterior margin (fig. 36) . . . . . 12

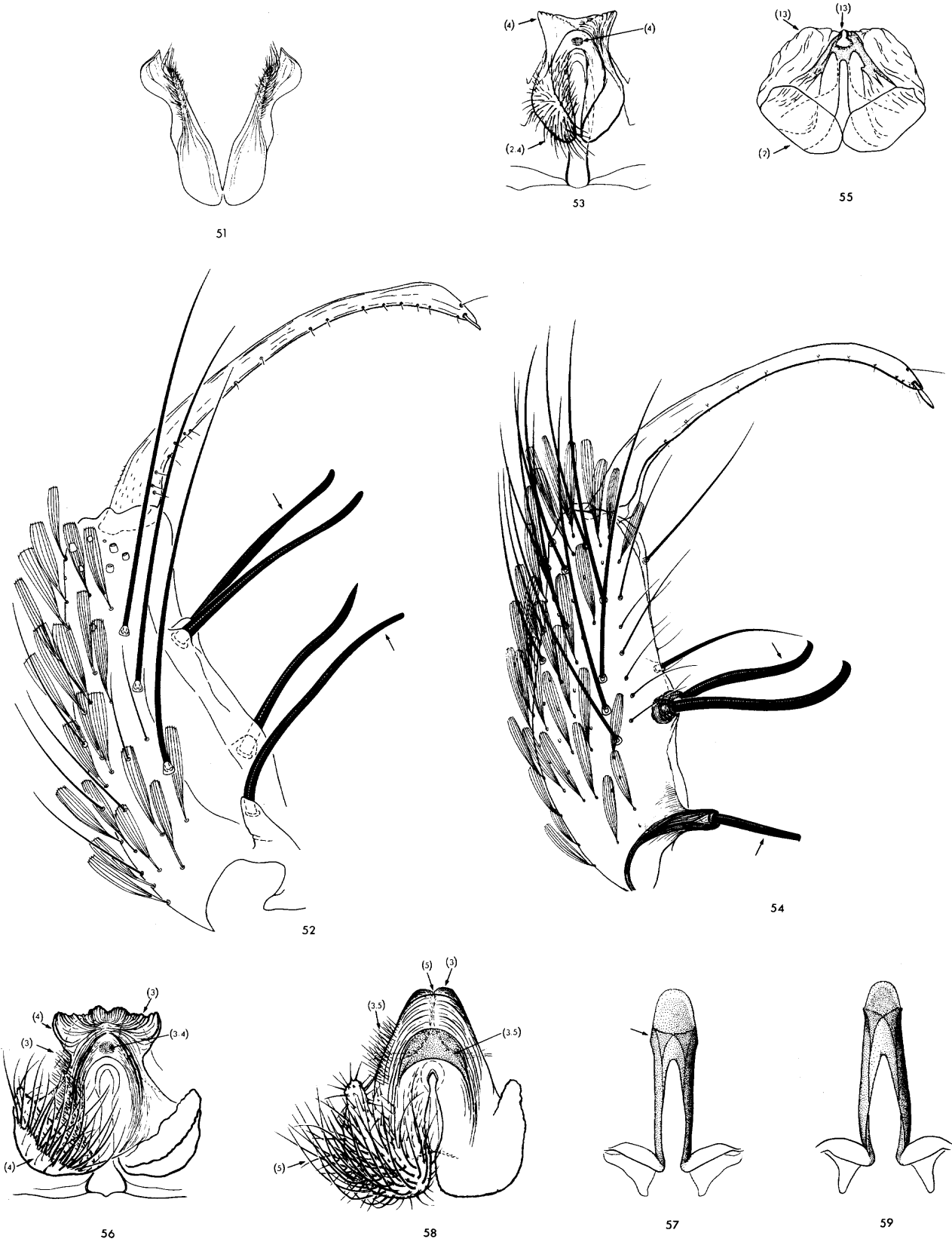
Sternum I with 2 longitudinal rows of white scales (fig. 37); scutellum usually with fewer than 12 large, dark setae on posterior margin (fig. 38) . . . . . 13

- 12(11). Anterior mesanepimeron (Mam) with a distinct patch of light scales (fig. 39); upper mesanepimeron (Mam) without scales (fig. 39); vein C with basal dark spot greatly enlarged, about 4.0 of humeral light spot (fig. 40); vein  $R_3$  with 3 dark spots (fig. 40); palpomere 4 with scattered white scales on mediolateral surface (fig. 41) . **2. *darlingi***

Anterior mesanepimeron (Mam) bare (fig. 42); upper mesanepimeron (Mam) with a line of light scales (fig. 42); vein C with basal dark spot not greatly enlarged, at most equal to humeral light spot (fig. 43); vein  $R_3$  with 2 dark spots (fig. 43); palpomere 4 without scattered light scales on mediolateral surface (fig. 44) . . . . . **1. *argyritarsis***

- 13(11). Caudolateral scale tufts well developed on abdominal segment II (fig. 45); hindtarsomere 2 with basal 0.3-0.4 dark (fig. 46); vein C with or without a small presectoral light spot (fig. 47); vein  $R_3$  with 3 dark spots (fig. 47); abdominal terga II-IV with relatively few light scales (fig. 45) . . . . . **4. *braziliensis***

Caudolateral scale tufts absent on abdominal segment II (fig. 48); hindtarsomere 2 with basal 0.45-0.90 dark (fig. 49); vein C never with presectoral light spot (fig. 50); vein  $R_3$  with 1 or 2 dark spots (fig. 50); abdominal terga II-IV with numerous light scales (fig. 48) . . . . . **3. *allopha***

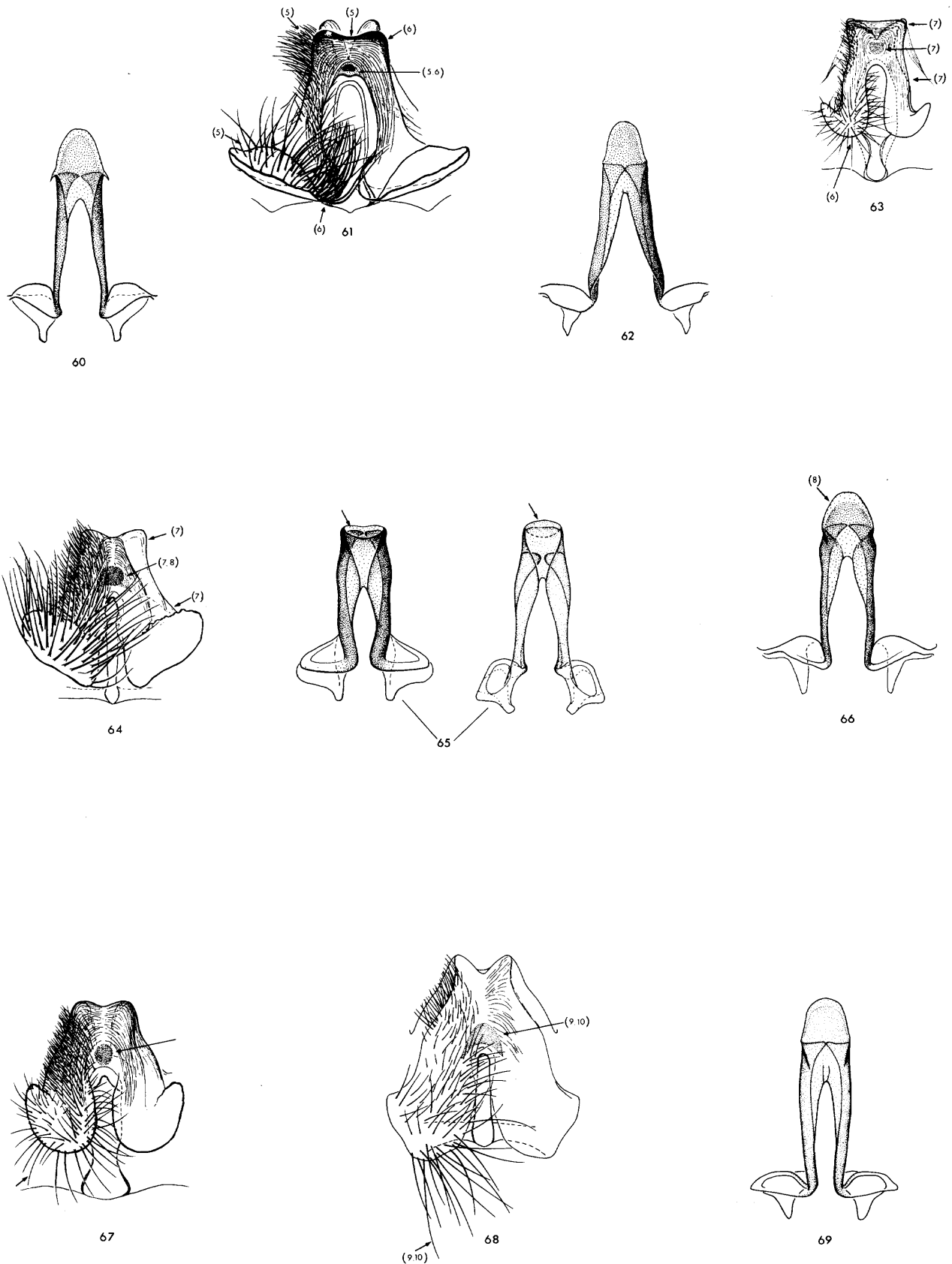


FIGURES 51-59

## MALE GENITALIA

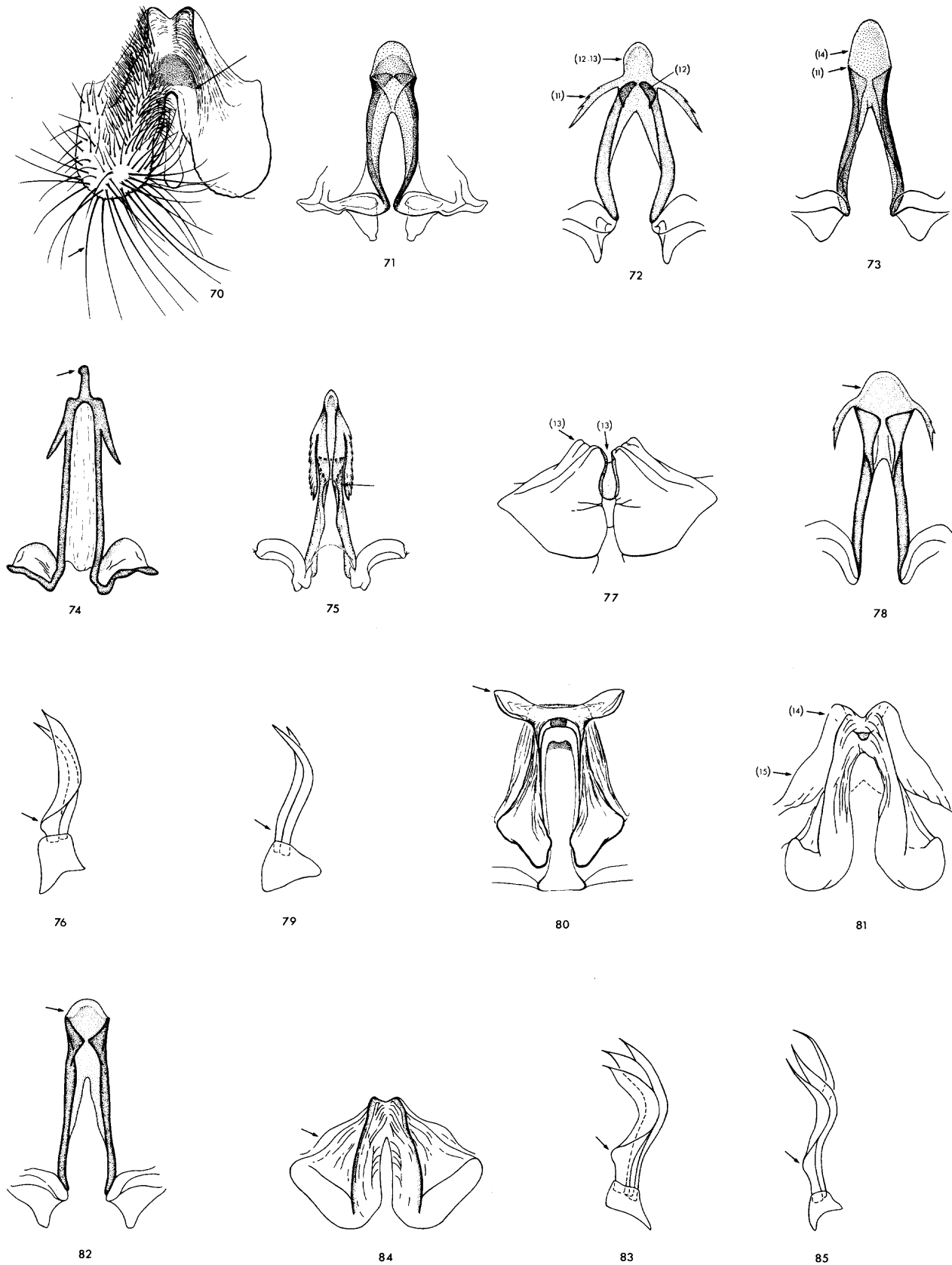
(13. *rondoni* not included; see species discussion)

1. Ventral claspette not apically fused into single structure (fig. 51); gonocoxite with more than one parbasal seta, *or if* one *then* longer than 0.3 length of gonocoxite (fig. 52) *or* not arising from prominent tubercle; gonocoxite with or without accessory seta(e) (fig. 52) . . . . . Subgenera *Anopheles*, *Lophopodomyia*, *Kerteszia* and *Stethomyia*
- Ventral claspette apically fused into a single structure (fig. 53); gonocoxite with one parbasal seta of less than 0.3 length of gonocoxite arising from a prominent tubercle and with 2 accessory setae (fig. 54) (Subgenus *Nyssorhynchus*) . . . . . 2
- 2(1). Ventral claspette with spicules (fig. 53) . . . . . 3
- Ventral claspette without spicules (fig. 55) . . . . . 11
- 3(2). Ventral claspette with apex rugose or deeply striated, and moderately to strongly expanded laterally into rounded or pointed lobe, spicules on lateral margins not extending toward apex as far as level of apical margin of preapical plate (fig. 56); apex of aedeagus without leaflets (fig. 57) . . . . . 4
- Ventral claspette with apex neither rugose nor deeply striated nor laterally expanded, spicules extending to apex or at least as far as level of apical margin of preapical plate (fig. 58); apex of aedeagus with or without leaflets . . . . . 5
- 4(3). Ventral claspette small, about 0.33 length of gonocoxite, apex moderately expanded laterally, apicolateral margins sharply angled and moderately pointed (fig. 53); basal lobule of ventral claspette small, narrow, curving mesad, with spicules along basal margin short, about equal to or slightly longer than width of aedeagus (figs. 53, 59); preapical plate of ventral claspette heavily sclerotized (fig. 53) . . . . . 14. *benarrochi*
- Ventral claspette large, about 0.5 length of gonocoxite, apex strongly expanded laterally, apicolateral margin produced into large, rounded lobe with basal and lateral margins convex and apical margin weakly concave (fig. 56); basal lobule of ventral claspette large, with spicules along basal margin long, about 2.0-3.5 width of aedeagus (figs. 56, 57); preapical plate of ventral claspette weakly to moderately sclerotized (fig. 56) . . . . . 12. *strodei*



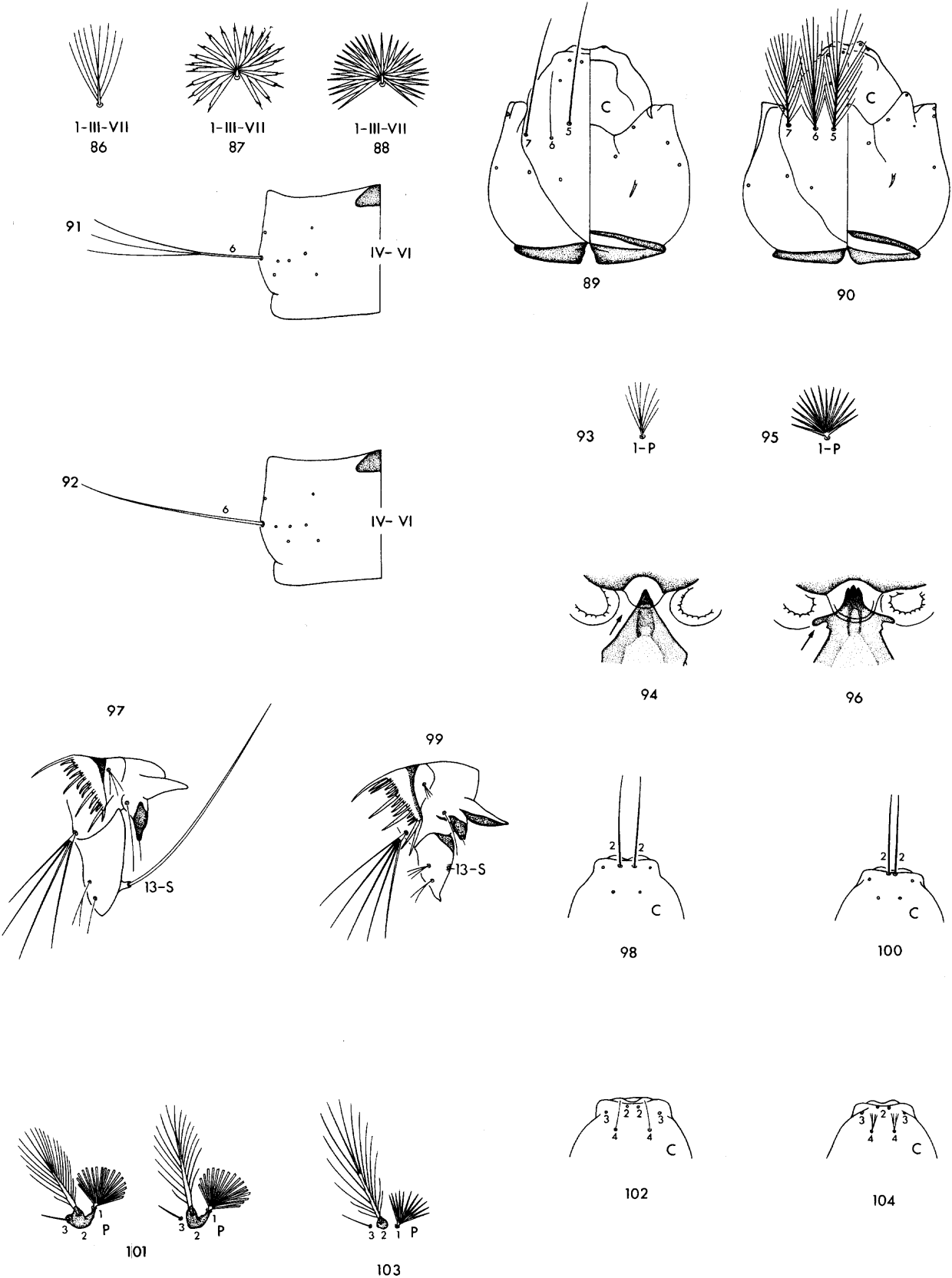
FIGURES 60-69

- 5(3). Ventral claspette strongly conoid, with a very small median sulcus at apex, spicules on lateral margins (exclusive of basal lobule) short and extending toward apex only as far as level of apical margin of preapical plate, spicules along basal margin of basal lobule long about 2.0-3.0 width of aedeagus, preapical plate very large, crescent shaped and heavily sclerotized (figs. 58, 60) . . . . . *9. ininii*
- Ventral claspette not strongly conoid, either truncate or with a moderately small to large median sulcus at apex, spicules on lateral margins extending to or nearly to apex, spicules along basal margin of basal lobule short to long, preapical plate small to large (fig. 61) . . . . . 6
- 6(5). Ventral claspette with a concentration of long spicules about 1.5 width of aedeagus on basomesal margin of basal lobule directed caudally into mesal cleft, wide at apex (width 0.4-0.5 length of claspette) with abruptly angled, rounded lateral margins, preapical plate small, oval and heavily sclerotized (figs. 61, 62) . . . . . *10. rangeli*
- Ventral claspette without spicules concentrated on basomesal margin of basal lobule, shape and preapical plate varied (fig. 63) . . . . . 7
- 7(6). Ventral claspette with apex moderately broad to broad, width at apex about 0.5-0.6 length of claspette, lateral margins of claspette not tapering appreciably medially toward apex, preapical plate moderately small and semicircular to oval (fig. 63) . . . . . *11. nuneztovari*
- Ventral claspette with apex moderately narrow to narrow, width at apex about 0.3 length of claspette, lateral margins of claspette tapering toward apex, preapical plate variously developed (fig. 64) . . . . . 8
- 8(7). Aedeagus truncate or weakly rounded at apex (fig. 65); preapical plate of ventral claspette moderately large, semicircular to oval, heavily sclerotized (fig. 64) . . . . . *7. evansi*
- Aedeagus well rounded at apex (fig. 66); preapical plate of ventral claspette variously developed . . . . . 9
- 9(8). Ventral claspette with spicules along basal margin of basal lobule moderately short about equal to or slightly longer than width of aedeagus, preapical plate moderately small, circular to oval and weakly to occasionally strongly sclerotized (figs. 66, 67) . . . . . *8. aquasalis*
- Ventral claspette with spicules along basal margin of basal lobule long about 2.0 or more width of aedeagus, preapical plate large and moderately to strongly sclerotized (figs. 68, 69) . . . . . 10



FIGURES 70-85

- 10(9). Ventral claspette with spicules along basal margin of basal lobule about 2.0 width of aedeagus, preapical plate large, usually crescent shaped and moderately to strongly sclerotized (figs. 68, 69) . . . . . *5. oswaldoi*
- Ventral claspette with spicules along basal margin of basal lobule very long about 3.0 width of aedeagus, preapical plate strongly sclerotized, large and circular to semicircular with small basolateral projections (figs. 70, 71) . . . . . *6. galvaoi*
- 11(2). Aedeagus with a pair of strong, sclerotized subapical leaflets (fig. 72) . . . . . 12
- Aedeagus without subapical leaflets (fig. 73) . . . . . 14
- 12(11). Aedeagus hook-like at apex (fig. 74), *or if* not hooked *then* ventromesal subtriangular projection of aedeagus located about 0.5 from base of aedeagus (fig. 75) . . . . . Myzorhynchella group
- Aedeagus not hook-like at apex, ventromesal subtriangular projection subapical immediately basad of subapical leaflets (fig. 72) . . . . . 13
- 13(12). Ventral claspette with apex broad and truncate, median sulcus small, often indistinct (fig. 55); apex of aedeagus egg shaped, longer than wide (fig. 72); dorsal leaflet of dorsal claspette with distinct basomesal projection (fig. 76) . . . . . *2. darlingi*
- Ventral claspette with apex narrow, median sulcus well developed (fig. 77); apex of aedeagus broadly rounded, width 1.5 of length (fig. 78); dorsal leaflet of dorsal claspette without a basomesal projection (fig. 79) . . . . . *1. argyritarsis*
- 14(11). Apex of ventral claspette expanded laterally into large, auriculate lobe (fig. 80); apex of aedeagus about 1.5 as long as wide (fig. 73) . . . . . *15. triannulatus*
- Apex of ventral claspette not expanded laterally into large, auriculate lobe (fig. 81); apex of aedeagus as wide as or wider than long (fig. 82) . . . . . 15
- 15(14). Ventral claspette with lateral margins slightly expanded laterally from apex to about 0.5 from base (fig. 81); dorsal leaflet of dorsal claspette with a distinct basomesal projection (fig. 83) . . . . . *4. braziliensis*
- Ventral claspette with lateral margins strongly expanded laterally from apex to about 0.5 from base (fig. 84); dorsal leaflet of dorsal claspette without a prominent basomesal projection (fig. 85) . . . . . *3. allopha*



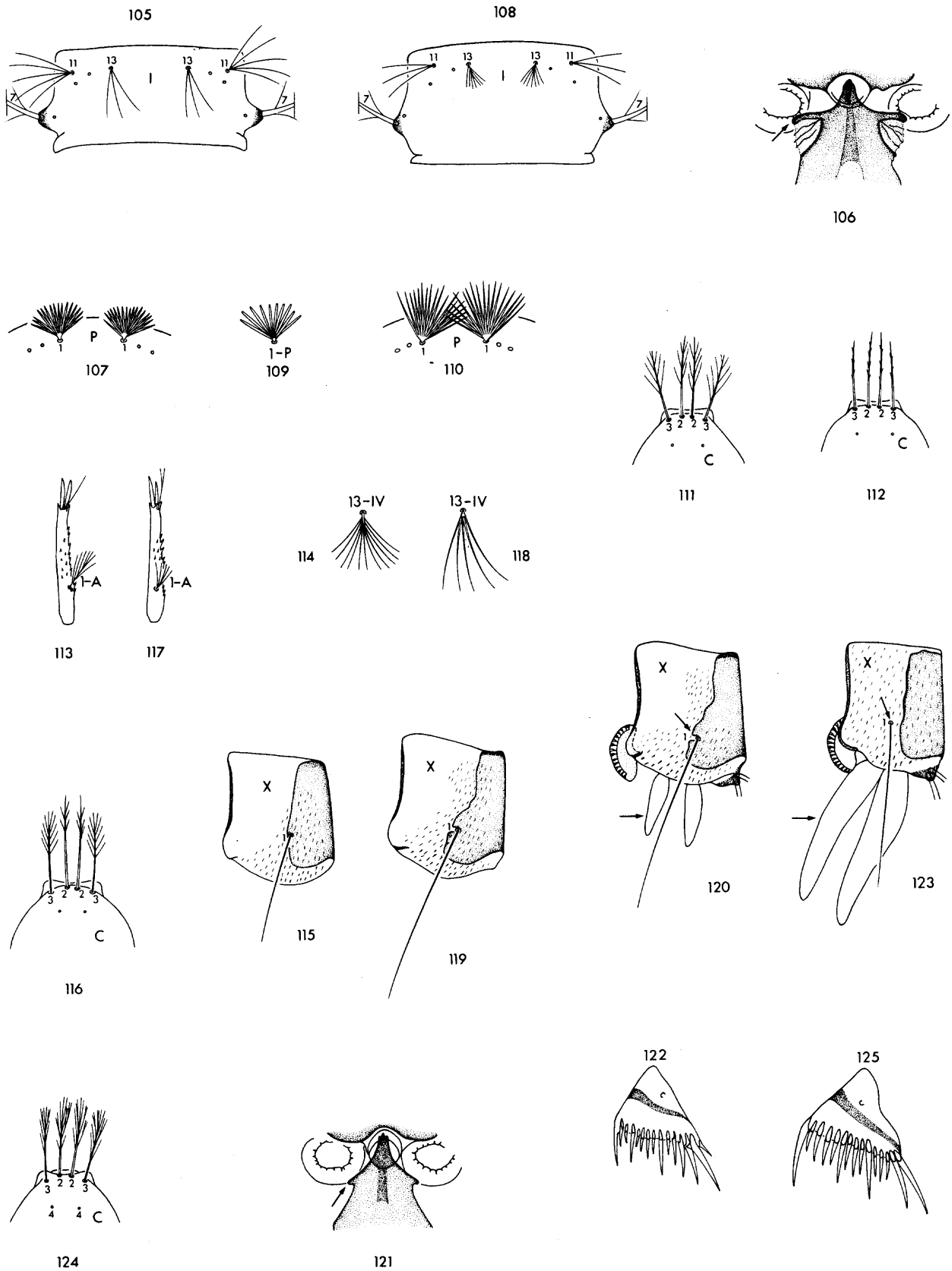
FIGURES 86-104



## LARVAE

(6. *galvaoi* and 13. *rondoni* not included)

1. Setae 1-III-VII with filiform branches (fig. 86) or lanceolate leaflets with notched margins (fig. 87) . . . . . Subgenera *Anopheles*, *Lophopodomyia*, *Stethomyia*  
 Setae 1-III-VII with smooth-margined lanceolate leaflets (fig. 88) (Subgenera *Kerteszia*, *Nyssorhynchus*) . . . . . 2
- 2(1). Setae 5-7-C single or forked (fig. 89) . . . . . Subgenus *Kerteszia*  
 Setae 5-7-C plumose (fig. 90) (Subgenus *Nyssorhynchus*) . . . . . 3
- 3(2). Setae 6-IV-VI branched (fig. 91) . . . . . Myzorhynchella group  
 Setae 6-IV-VI single (fig. 92) (*Albimanus* and *Argyritarsis* Sections) . . . . . 4
- 4(3). Seta 1-P plumose or branched with filiform branches, never palmate (fig. 93); lateral arms of median plate of spiracular apparatus not projecting free laterally (fig. 94) . . 5  
 Seta 1-P always palmate with lanceolate branches (fig. 95); lateral arms of median plate of spiracular apparatus projecting free laterally, short to long (fig. 96) . . . . . 6
- 5(4). Seta 13-S very strongly developed, long, about 2.2-2.5 length of saddle (fig. 97); setae 2-C widely spaced, clypeal index about 1.5 (fig. 98) . . . . . 2. *darlingi*  
 Seta 13-S not strongly developed, never long (fig. 99); setae 2-C closely approximated, clypeal index greater than 4.0 (fig. 100) . . . . . 1. *argyritarsis*
- 6(4). Setae 2-C closely approximated, clypeal index 2.5 or greater (fig. 100) . . . . . 7  
 Setae 2-C widely separated, clypeal index less than 2.5 (fig. 98) . . . . . 8
- 7(6). Seta 1-P often with blunt-tipped leaflets (fig. 101); 4-C usually single, long, extending to near or beyond insertion of 2-C (fig. 102); 1-3-P or 1,2-P sharing common tubercle (fig. 101). . . . . 4. *braziliensis*  
 Seta 1-P with acuminate leaflets (fig. 103); 4-C 1-4 branched, small to moderately small, usually not extending to near or beyond insertion of 2-C (fig. 104); 1-3-P not sharing common tubercle (fig. 103), rarely 1,2-P share common tubercle . . . . 12. *strodei*



FIGURES 105-125

- 8(6). Seta 11-I large, usually 5-7 branched (3-7) (fig. 105); 13-I large, usually 3 branched (2-4) (fig. 105); lateral arm of median plate of spiracular apparatus long, directed laterally (fig. 106); 1-P with 15-20 (13-20) very narrow to narrow lanceolate leaflets, leaflets not overlapping with leaflets of 1-P of opposite side (fig. 107) . . . **15. triannulatus**

Seta 11-I moderately large, 2-4 branched (fig. 108); 13-I small to moderately large, usually more than 3 branched (fig. 108); lateral arm of median plate of spiracular apparatus very short to moderately long (except long in *ininii*) (fig. 96); 1-P with usually 9-16 (8-18) narrow to broad lanceolate leaflets (fig. 109), *if* more than 16 branched *then* leaflets overlapping with leaflets of 1-P of opposite side (fig. 110) . . . . . 9

- 9(8). Seta 3-C (and usually 2-C) plumose in about apical half, with distinct, moderately long to long branches (fig. 111) . . . . . 10

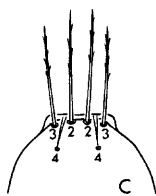
Setae 2,3-C single, and simple or barbed (fig. 112) . . . . . 12

- 10(9). Seta 1-A long, at least 2.0 width of antenna at point of insertion (fig. 113); 13-IV small, usually 10-13 branched (6-13) (fig. 114); 1-X moderately short, as long as or slightly longer than saddle (fig. 115); 3-C with moderately long branches, 2-C single and barbed (fig. 116) . . . . . **14. benarrochi**

Seta 1-A short to moderately short, always less than 2.0 width of antenna at point of insertion (fig. 117); 13-IV moderately large, usually 5-7 branched (3-8) (fig. 118); 1-X longer than saddle (fig. 119); 2,3-C with branches subequal in length or branches of 3-C slightly longer than those of 2-C (fig. 111) . . . . . 11

- 11(10). Seta 1-X inserted on saddle, on or near ventral margin (fig. 120); anal gills usually short, about 0.5 length of anal segment (fig. 120); 2,3-C with simple branches, rarely dendritic (fig. 111); lateral arm of median plate of spiracular apparatus very short (fig. 121); pecten with shorter median teeth mixed medium and short (fig. 122) . . **8. aquasalis**

Seta 1-X not inserted on saddle (fig. 123); anal gills long, as long as or longer than anal segment (fig. 123); 2,3-C with usually dendritic branches (fig. 124); lateral arm of median plate of spiracular apparatus moderately long (fig. 96); pecten with shorter median teeth mostly subequal (fig. 125) . . . . . **5. oswaldoi**



126



127



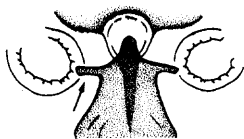
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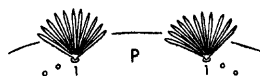
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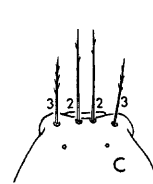
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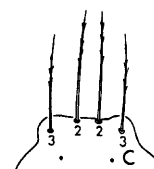
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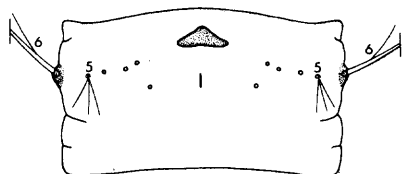
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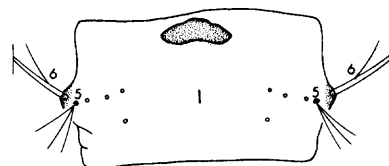
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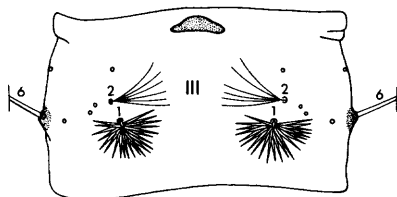
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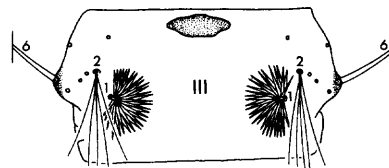
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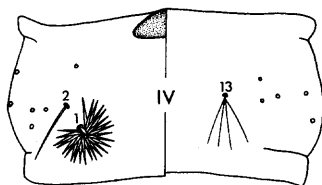
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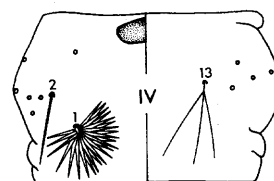
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FIGURES 126-140

- 12(9). Seta 4-C single or 2-4 forked, moderately long to long, usually extending to near or beyond insertion of 2-C (fig. 126), *if* moderately long (0.30-0.60 length of 3-C) *then* 13-V 4-6 branched (4-7) (fig. 127) . . . . . **11. nuneztovari**
- Seta 4-C variously branched, short to moderately long, usually not extending to base of 2-C (fig. 104), *if* moderately long (0.30-0.45 length of 3-C) *then* 13-V almost always 3 branched (3-5) at least on one side (fig. 128) . . . . . 13
- 13(12). Seta 1-A long, about 2.0 width of antenna at point of insertion (fig. 129); lateral arm of median plate of spiracular apparatus long, directed laterally (fig. 130) . . . **9. ininii**
- Seta 1-A short, as long as or slightly longer than width of antenna at point of insertion (fig. 131); lateral arm of median plate of spiracular apparatus short to moderately short, directed caudolaterally (fig. 121) . . . . . 14
- 14(13). Seta 1-P with 14-19 (14-22) leaflets overlapping with leaflets of 1-P of opposite side (fig. 110); 3-C 0.65-0.75 length of 2-C (fig. 132) . . . . . **3. allopha**
- Seta 1-P with 8-14 leaflets not overlapping with leaflets of 1-P of opposite side (fig. 133); 3-C 0.8-1.0 length of 2-C (fig. 134) . . . . . 15
- 15(14). Seta 5-I short, inserted 0.75-1.00 its length from lateral margin of abdomen (fig. 135); 2-III relatively short, 1.5-2.0 length of leaflets of 1-III (fig. 136); 2,13-IV moderately short, slightly longer than leaflets of 1-IV (fig. 137) . . . . . **10. rangeli**
- Seta 5-I moderately short, inserted less than 0.75 its length from lateral margin of abdomen (fig. 138); 2-III longer than 2.0 length of leaflets of 1-III (fig. 139); 2,13-IV moderately long, about 1.5 length of leaflets of 1-IV (fig. 140) . . . . . **7. evansi**

*1. Anopheles (Nyssorhynchus) argyritarsis* Robineau-Desvoidy 1827

Plates 6, 11, 13

**DISCUSSION.** *An. argyritarsis* can be distinguished in the female by (1) terga II-IV entirely covered by cream scales, (2) basal dark spot of vein C 0.4-1.0 length of humeral light spot, (3) hind-tarsomere 2 dark in basal 0.4 or less, (4) foretarsomere 1 dark in basal 0.92-0.94, (5) frontal tuft of head with 8 or 9 pairs of long setae, (6) interorbital space moderately wide, about 0.6-0.8 width of pedicel of antenna, (7) anterior mesanepimeron (Mam) never with scales, (8) upper mesanepimeron (Mam) always with a line of light scales, (9) vein  $R_3$  with 2 dark spots and (10) palpomere 4 without scattered light scales on mediolateral surface; in the male genitalia by (1) ventral claspette with narrow apex and rounded apical lobes, median sulcus at apex well developed, mesal cleft only about 0.15 length of claspette, and refringent structure weakly developed, (2) apex of aedeagus broadly rounded, width 1.5 length, (3) dorsal leaflet of dorsal claspette without a basomesal projection, (4) sternum IX without distinct anterior apodeme, (5) parabasal seta with short basal tubercle, spine 2.8 length of its tubercle and (6) apodeme of gonocoxite about 0.3 length of gonocoxite; and in the larva by (1) seta 1-P plumose with filiform branches, (2) setae 3-T and 1-I not palmate, usually with filiform branches, (3) seta 8-C usually double or triple, (4) accessory submedian tergal plates of abdomen usually not completely absent, (5) collar moderately narrow, about 0.35 mm, (6) seta 3-C about 0.65 length of 2-C, (7) seta 4-C extending just to base of 2-C, (8) seta 13-S not strongly developed, never long, (9) setae 2-C closely approximated, clypeal index greater than 4.0 and (10) lateral arm of median plate of spiracular apparatus not projecting free laterally.

**BIONOMICS.** The immature stages of *argyritarsis* have been collected in the following habitats: stagnant ponds, swamps and marshes, drainage ditches, rain pools, wet meadows, forest streams, ground pools, animal tracks, springs, artificial containers such as tin cans and animal water troughs, rock holes, and river and stream margins. These sites were usually in full sun or partial shade, rarely in deeply shaded areas. They contained some type of grassy vegetation and, to a lesser extent, green algae. The water was clear or turbid, but not obviously polluted or brackish. The sites were most often in areas of secondary growth such as plantations, cultivated fields, pastures and sunny forest clearings. Reports by other workers, in general, are in agreement with collection records of MOMA.

*An. argyritarsis* occurs predominantly at low to intermediate elevations. According to Root (1926) *argyritarsis* in Brazil is mainly a highland and interior species, although it is also present in the foothills of the coastal plain. Galvao (1940) has reported that the larvae are incapable of surviving large variations in pH and temperature. The adults are exophilic and crepuscular, being most active in the evening and in the early morning hours. Galvao, Lane and Correa (1937) stated that in April only a single specimen of *argyritarsis* was captured in a house in Novo Oriente, Sao Paulo, Brazil. In Palmeiras, Bahia, Brazil, *argyritarsis* is very rarely found in houses and appears to be indifferent to humans (Pinto 1939).

**MEDICAL IMPORTANCE.** In general *argyritarsis* is not considered to be an important vector of malaria in either Central and South America, or in the Lesser Antilles. Several attempts to experimentally infect *argyritarsis* have been unsuccessful (Darling 1910; Benarroch 1931). Similarly, a number of workers have examined the salivary glands and midguts of field-caught *argyritarsis* and have not found *Plasmodium* infections (Stephens 1921; Davis 1927; Benarroch 1931; Godoy and Pinto 1923; Earle 1936). However, according to Pinto (1939), Paterson in 1911, and Neiva and Barbara in 1917 demonstrated the transmission of *P. vivax* by *argyritarsis* in Argentina. In the state of Rio de Janeiro, Brazil, Boyd (1926) found mature oocysts and sporozoites in 8% of the females of *argyritarsis* from Porto das Caixas and Itamby, and Davis (in Boyd 1926) found oocysts in 3.6% of those from Sant'Anna. Unfortunately, until 1926 when Root described *darlingi*, and for several years thereafter, *darlingi* was continuously mistaken for *argyritarsis*. *An. darlingi* has since been

shown to be a very efficient vector. It is most likely, particularly in Rio de Janeiro, that the reports of *argyritarsis* being naturally infected as well as endophilic actually pertain to *darlingi*.

**DISTRIBUTION** (pl. 6). *An. argyritarsis* is the most widespread species in the Argyritarsis Section. It is usually found at elevations up to 100 m, often in interior plains, but also along the margins of coastal foothills. *An. argyritarsis* occurs as far north as the state of Guerrero, in the Sierra Madre del Sur of Mexico, and throughout most of Central America. *An. argyritarsis* is the only species in the Argyritarsis Section to extend into the Lesser Antilles, being found throughout the Windward Islands and in the Leewards north to Montserrat. In South America, *argyritarsis* occurs in Colombia, Venezuela, the Guianas, Brazil, Bolivia, Paraguay, Uruguay and the northern provinces of Argentina. West of the Andes *argyritarsis* extends as far south as the Department of Narino in Colombia.

## 2. *Anopheles (Nyssorhynchus) darlingi* Root 1926

Plates 6, 11, 14

**DISCUSSION.** *An. darlingi* can be distinguished from all other species in the Argyritarsis Section in the female by (1) anterior mesanepimeron (Mam) always with a distinct patch of light scales, (2) upper mesanepimeron (Mam) never with a line of scales, (3) interorbital space narrow, less than 0.3 width of pedicel of antenna, (4) palpomere 4 with scattered white scales on mediolateral surface, (5) scales of scutum predominantly yellowish, (6) vein C with basal dark spot greatly enlarged, about 4.0 length of humeral light spot and (7) vein R<sub>3</sub> with 3 dark spots; in the male genitalia by (1) ventral claspette with apex broad and truncate, median sulcus small, often indistinct, (2) dorsal leaflet of dorsal claspette with a well-developed basomesal projection, (3) tergum VIII covered with light golden scales, (4) sternum IX not emarginated on anterior border, (5) aedeagus at least 0.5 length of gonocoxite and (6) apex of aedeagus egg shaped, longer than wide, with large sclerotized leaflets and distinct, heavily sclerotized, collarlike, subapical, ventromesal subtriangular projections; and in the larva by (1) seta 13-S very strongly developed, about 2.2-2.5 length of saddle, (2) setae 2-C widely spaced, clypeal index about 1.5, (3) seta 4-C double, (4) seta 1-P with filiiform branches arising at apex of a short shaft, (5) seta 3-T palmate, with broad lanceolate leaflets, (6) seta 1-I palmate with lanceolate leaflets arising at apex of a median shaft, (7) seta 1-A arising about 0.35-0.45 from base of antenna, (8) median tergal plate of abdominal segment VIII very large, about 0.60-0.65 width of segment, (9) accessory median tergal plates of abdominal segments III-VII with distinct lobes and (10) pecten without distinct serrations on teeth.

*An. darlingi* is easily recognized in nearly all cases by several unique characters. In the adult, the presence of a white scale patch on the anterior mesanepimeron and the greatly enlarged basal dark spot of vein C immediately identify *darlingi*. No other species in the Argyritarsis Section exhibits either of these characters; *triannulatus* in the Albimanus Section is the only other species of *Nyssorhynchus* with a white scale patch on the anterior mesanepimeron. The male genitalia of *darlingi* is distinguished in the dorsal claspette by the presence of a well-developed basomesal projection on the dorsal leaflet, in the ventral claspette by its truncated apex, and in the aedeagus by the presence of large sclerotized leaflets and by its distinct, heavily sclerotized, subapical, ventromesal subtriangular projections forming a subapical collar. The dorsal leaflet of the dorsal claspette of all other species in the Argyritarsis Group is without a basomesal projection, and the apex of the ventral claspette of these species is never truncate. The aedeagus of the species in the Albimanus Group never has subapical leaflets. The presence of distinct, heavily sclerotized, collarlike, subapical, ventromesal subtriangular projections in *darlingi* is unique in the Argyritarsis Section. The larva of *darlingi* is characterized by the extremely long seta 13-S arising from a large, conspicuous tubercle.

**BIONOMICS.** The immatures of *darlingi* have been collected in streams and ponds with mud bottoms, ground pools, and swamps. Most of the immatures were in partially shaded areas.

All the sites contained grassy or floating vegetation and sometimes green algae. The water was clear, never turbid or polluted. The sites were usually in areas of secondary growth such as plantations or cultivated fields.

Root (1926) collected *darlingi* at the type-locality in patches of *Ceratophyllum* sp. along the margins and in inlets of a small river and canal that had "rather rapid currents." In other places he found the larvae "in mats of surface vegetation in lagoons with almost no current, in small pools full of vegetation and, on one occasion, in a large, bare, muddy road-pool." Pinto (1939) states that Davis collected larvae in debris along the margin of a pool in the state of Parana, Brazil. Shannon (1931) collected *darlingi* in large swamps and marshes, always in areas open to sunlight in the state of Bahia, Brazil. Barretto (1938) found larvae in calm water along the margins of still bays of large rivers. The larvae have been found associated with *Cupressus glauca* that was growing along the margins of reservoirs. Barretto observed that the immatures were usually in areas shaded by trees. He did find some larvae in small collections of water such as springs, wells, mud puddles, animal footprints and roadside ditches, exposed to the sun during most of the day. Shannon (1933) found only a few larvae of *darlingi* in the Amazon and concluded that this species occurs in large bodies of still water (*igapos*) along tributaries of the Amazon River. Galvao, Lane and Correa (1937) encountered very few larvae of *darlingi* (as *darlingi paulistensis*) in Novo Oriente, Sao Paulo, Brazil, despite the large number of adults found in houses. Stage and Giglioli (1947) stated that in Guyana *darlingi* occurs on the coast in large bodies of fresh water such as irrigation canals, rice fields, flooded cane fields and pastures; while in the interior, it is found in seepage swamps, forest streams and rainwater pools.

*An. darlingi* is usually found in regions characterized by elevated relative humidity and high annual rainfall, as it seems to be vulnerable to dry seasons. It is not present in much of northeastern Brazil where the dry season is long and drought often occurs (Deane, L.M., Causey and Deane 1946). Root (1926) observed in the state of Rio de Janeiro that the species did not become abundant until rather late in the rainy season, and that the increase coincided with the onset of cooler weather.

During May in the state of Rio de Janeiro, Root (1926) observed that in Porto das Caixas, *darlingi* was as abundant inside houses as *albitarsis*, and in houses in Sant'Anna, it was more common than either *albitarsis* or "*tarsimaculatus*." He concluded that *darlingi* was definitely an endophilic species. A number of workers have verified that when a bait animal is used as a form of mosquito control outside houses, more specimens of *darlingi* are still found inside the houses than on the bait animal. When compared to "*tarsimaculatus*," *pseudopunctipennis*, *strodei*, *triannulatus* and *punctimacula*, *darlingi* is by far the most common anopheline inside houses (Davis 1931; Davis and Kumm 1932; Shannon 1933). Galvao, Lane and Correa (1937) recorded the percentages of anophelines found in houses in Novo Oriente, Sao Paulo, and found that in March 1936, 100% of the anophelines inside houses were *darlingi*, in February 1937, 91%, in April 1937, 82%, and in May 1937, 80%.

Deane and Damasceno (1948) stated that the postfeeding resting sites in houses are the vertical surfaces; 99% of the adults they studied in Brazil clung to walls in houses, and most were within 2 m of the floor. The adults of *darlingi* have been observed to disperse as far as 200-1500 m (Davis and Kumm 1932; Deane 1947). Recent behavioral studies concerning *darlingi* by Roberts, Alecrim, Tavaris and McNeill (1981) at Floresta, Amazonas, Brazil, a field site along the Ituxi River, indicate that *darlingi* feeds readily indoors and outdoors. Preliminary results indicate a bimodal peak in the biting activity of *darlingi*, the largest peak occurring about 30 minutes after sunset and another smaller peak just before sunrise; a few females have been observed to feed throughout the day and night both inside and outside the house. The majority of engorged and unengorged females were consistently found resting on the ceiling inside their study house, although a large minority were collected resting on the walls. In 2 nights of human biting collections at a site 10 m from the house, *darlingi* was the only mosquito collected; whereas at a site 20 m from the house 7 other culicid species were caught, 5 of which were other anophelines. Essentially only *darlingi* was biting man



in and immediately around the house. Charlwood and Wilkes (1979) also observed a pronounced peak in biting activity of *darlingi* at dawn and dusk (by nulliparous females).

Essentially all reports in the literature indicate that *darlingi* prefers humans to domestic animals. This evidently is correct, although almost all the adults caught by the MOMA project have been lured to and collected off of domestic animal bait, mainly burros, indicating that *darlingi* is also attracted to large mammals other than man.

**MEDICAL IMPORTANCE.** According to L.M. Deane, Causey and Deane (1946), *darlingi* is "the most efficient indigenous malaria vector in north and northeast Brazil." Horsfall (1955) has stated that most observers agree that *darlingi* is "the most satisfactory component in the insect portion of the reservoir for human plasmodia in Neotropica." *An. darlingi* is a very serious vector throughout its range because of its domestic habits and its great susceptibility to plasmodial infection. Almost all examinations of *darlingi* in nature have yielded either oocysts in the gut or sporozoites in the salivary glands (Benarroch 1931; Davis 1931; Davis and Kumm 1932; Shannon 1933; Correa and Ramos 1942b; Correa 1943; Floch and Abonnenc 1943; Kenney 1946; Floch 1954). Charlwood and Wilkes (1979) applied the Polovodova aging technique (see Gillies 1958) to females of *darlingi* collected in Aripuana, Mato Grosso, Brazil, and reported that 1.5% of the females had oviposited at least 4 times and were old enough to be potential vectors of malaria.

Foote and Cook (1959) stated, "Malaria would become a relatively unimportant disease in South America with the disappearance of *darlingi*." This species probably also contributes to the endemic malaria in the extreme southern part of Mexico as well as the northern part of Central America. It is a vector of malaria in the southeastern jungle, savannah plateau and on the coast in Venezuela. East of the Andes, in Ecuador and probably in Peru, and in the plains of northern Bolivia, *darlingi* is the principal vector of malaria. In Brazil and the Guianas this species is widespread in the lowlands, particularly along waterways, and again is the primary vector of malaria.

*An. darlingi* has been suspected by several workers to be a vector of human filariasis. Davis (1931) collected 200 specimens of *darlingi* in houses in Belem, Para, Brazil, and found that 14 contained filarial larvae. Giglioli (1948) reported that *Wuchereria bancrofti* readily invades the tissues of *darlingi* in Brazil and Guyana. The mosquitoes were given an infective blood meal, and in 13 days 74% showed infection, and 9% had mature worms in their proboscises. In Brazil, Causey, Deane *et al.* (1945) also found *darlingi* infected with filarial worms in nature.

**DISTRIBUTION** (pl. 6). *An. darlingi* is widely distributed. It is usually found at lower elevations along large rivers in the interior, but it may exist in coastal areas and occasionally at higher elevations. *An. darlingi* has been reported to occur as far north as the state of Chiapas, Mexico, near the Gulf of Mexico, at an elevation of 60 m or less (Vargas and Martinez Palacios 1950, 1955). It occurs throughout Belize, Honduras and Guatemala; however, it has not been reported elsewhere in Central America. In South America *darlingi* has been reported east of the Andes in Colombia, Venezuela, Bolivia, Peru, Ecuador, Brazil, the Guianas and Argentina. West of the Andes it extends as far south as the Department of Choco in Colombia. The discontinuity in the distribution of *darlingi* is not understood. Perhaps the species was introduced into northern Central America and has not dispersed throughout the rest of Central America. Or possibly, although unlikely, *darlingi* is present throughout the remainder of Central America but has never been collected.

### 3. *Anopheles (Nyssorhynchus) allopha* (Peryassu 1921)

Plates 7, 11, 15

**DISCUSSION.** *An. allopha* is distinguished from other species in the Albitarsis Group in the female by (1) hindtarsomere 2 with basal 0.45-0.90 dark, (2) vein C with presectoral light spot always absent, (3) interorbital space moderately wide, about 0.6-0.7 width of pedicel of antenna, (4) frontal tuft of head usually composed of 3 to 5 setae, (5) clypeus moderately broad, about 2.0

width of pedicel of antenna, (6) caudolateral scale tufts absent on abdominal segment II, dark brown to black on segments III-VIII, (7) vein  $R_3$  with 1 or 2 dark spots and (8) abdominal terga II-IV with numerous light scales; in the **male genitalia** by (1) sternum IX always less than 0.10 length of gonocoxite, (2) ventral claspette with lateral margins strongly expanded laterally from apex to about 0.5 from base then tapering toward base, (3) median sulcus of apex of ventral claspette distinct, moderately shallow, (4) refringent structure and transparent membranous area of ventral claspette absent, (5) gonocoxite with 4,5 tergomedial setae, (6) dorsal leaflet of dorsal claspette without a basomesal projection and (7) tergum VIII vested with creamy and silvery scales; and in the **larva** by (1) clypeal index usually about 1.3, (2) seta 3-C about 0.65-0.75 length of seta 2-C, (3) accessory median tergal plates on abdominal segments IV-VII single and bilobed or trilobed or with 2,3 round plates, (4) seta 12-C with 5 branches, (5) seta 1-P with 14-19 (14-22) leaflets overlapping with leaflets of opposite 1-P, (6) seta 6-T usually triple, (7) 1-I with 17-19 branches, (8) seta 3-IV triple, (9) seta 4-III 3,4 branched, (10) seta 5-IV,V usually 5-7 branched and (11) seta 7-IV 4,5 branched.

The populations of *allopha* we examined do not exhibit great geographical variation. The only consistent variation appears in the adult, although reared larval and pupal material from the entire geographical range of *allopha* has not been available for study. The adults from southern Brazil show a slight increase in the length of the basal dark band on hindtarsomere 2 and the number of dark scales on vein C of the wing.

We recognize 2 species of what has been called *albitarsis*. One species, *allopha*, occurs throughout most of Brazil, regions of Paraguay, Bolivia, Colombia, the Guianas, Trinidad, Venezuela, Panama, Costa Rica and Guatemala. The other, *albitarsis*, occurs in Argentina, Uruguay, regions of Paraguay and southern Brazil. *An. allopha* is distinguished from *albitarsis* in the **female** by the combination of (1) small to moderate size, (2) hindtarsomere 2 usually with basal 0.4-0.6 dark, (3) vein C never with all of the light spots absent, although they may be reduced to just a few scales, (4) interorbital space moderately wide, usually about 0.6-0.7 width of diameter of pedicel and (5) caudolateral scale tufts usually dark brown on proximal abdominal segments and black on distal segments; in the **male genitalia** by the combination of characters listed above for *allopha* and dorsal claspette with base of pedicel truncate, not rounded; in the **pupa** (not otherwise treated in this handbook) by the combination of (1) small to moderate size, (2) length of paddle about 1.7 of width, (3) seta 2-P always single, (4) length of male genital lobes about 2.6 of width, (5) seta 9-C either single or double, (6) minor distal branches of 1-I (float hair) with several nonuniform melanic patches, (7) seta 2-II with 4-6 branches, (8) seta 5-II weakly developed, double and (9) seta 9-V usually about 2.0 length of seta 9-IV; and in the **larva** by the combination of characters listed above for *allopha*.

**BIONOMICS.** The immatures of *allopha* have been collected from the following habitats: large ground pools, small stream pools, swampy shores of lakes, stagnant ground pools, turbid marshy depressions, small road puddles and small ponds. Most of the immatures were found exposed to full sunlight, rarely were they in partial shade and never in deep shade. Most of the sites contained abundant grassy and herbaceous vegetation. The water was usually clear, and the majority of the sites had a muddy bottom. Most sites occurred in areas of secondary growth such as in open savannahs or along roads.

Root (1926) collected larvae of *allopha* (as *albitarsis*) associated with aquatic vegetation such as green algae, *Eichhornia* spp., *Ceratophyllum* spp., *Salvinia* spp. and *Azolla* spp., and usually not in bare, muddy pools. He stated that *allopha* showed a preference for large bodies of water such as large ponds, marshes, bays and overflows of rivers. To a lesser extent the larvae were collected in small pools and puddles. According to Kumm, Komp and Ruiz (1940), and Arnett (1950) larvae have been found among algal filaments and emergent vegetation in ponds in direct sunlight. Deane, Causey and Deane (1948) reported that the immature sites are principally marshes, grassy spots along the margins of rivers and lagoons rich in organic matter. Forattini (1962) stated that Cova

Garcia found the larvae in brackish water in Venezuela.

The adults can be either exophilic or endophilic. In the state of Bahia, Brazil, Davis and Kumm (1932) reported that *allopsha* (as *albitarsis*) represented 62% of all anophelines caught feeding on a horse used as bait. In Panama, Curry (1934) and Rozeboom (1937, 1938, 1942) stated that *allopsha* (as *albitarsis*) ignores man and does not enter houses; this apparently is also true in Venezuela, Guyana and Trinidad (Rozeboom 1942). On the other hand, in some regions of Brazil *allopsha* is endophilic and readily enters houses. According to L.M. Deane, Causey and Deane (1946), in many parts of eastern Rio Grande do Norte, Paraiba, Pernambuco, Alagoas and in the Amazon basin, *allopsha* (as *albitarsis domesticus*) can be captured in large numbers inside houses both during the day and night. The reasons for the difference in adult female activity patterns in different geographic areas is not understood. According to Horsfall (1955), females feed on whatever animal is available. Downs, Gillette and Shannon (1943) found that *allopsha* will feed freely on man.

**MEDICAL IMPORTANCE.** *An. allopsha* is not a primary vector of malaria throughout most of its range. There is no doubt that *allopsha* will readily attack man under the proper conditions, although only along the coast of Brazil does *allopsha* enter houses and become a potential malaria vector. The percentage of females of *allopsha* that can be experimentally infected with *Plasmodium* is well below that of the females of *darlingi*. According to Galvao (1940), Boyd observed in the Baixada Fluminense, Rio de Janeiro, that 6.2% of the naturally occurring *allopsha* had oocysts, and 2.8% had sporozoites.

In Panama, where *allopsha* is not a malaria vector, Rozeboom (1938) found 4 specimens of *allopsha* (as *albitarsis*) that were infected with *P. falciparum*, but the oocysts failed to mature. Rozeboom suggested the possibility that *allopsha* was introduced into Panama, and that this population is resistant to infection by the Panamanian strain of *P. falciparum*. Probably the principal reason it is not a malaria vector in Panama is its reluctance to attack man (Rozeboom 1938). L.M. Deane, Causey and Deane (1946) observed in Ceara, Brazil, that *allopsha* (as *albitarsis*) constituted 97.6% of the anophelines captured outdoors and only 4.3% of those in houses. They found that during a malaria epidemic in Ceara (1938-1939), in which 24% of the human population was infected, none of the 314 specimens of *allopsha* examined were positive for *Plasmodium*. On Marajo Island, Para, Brazil, in the malarious village of Cachoeira they dissected 224 specimens of *allopsha* and found all negative for oocysts and sporozoites. Further inland, in a non-malarious village they examined 1493 females of *allopsha* and found only 2 infected with oocysts and none with sporozoites.

**DISTRIBUTION** (pl. 7). *An. allopsha* is a tropical species normally found at low elevations, but it has been reported to occur as high as 400 m in the Serra do Cabral in the state of Minas Gerais, Brazil. It probably occurs as far north as Guatemala, and Forattini (1962) reports it from Honduras. It also occurs in Costa Rica and Panama. In South America it is not known how far south *allopsha* extends east of the Andes. All specimens examined from the state of Sao Paulo, Brazil, and from Paraguay were *allopsha*, not *albitarsis*. *An. albitarsis* has been reported from Bolivia, but whether this is actually *allopsha* or *albitarsis* we have not determined. Elsewhere in South America, *allopsha* occurs in the northern coastal areas of Brazil, the Guianas, Colombia, Venezuela and Trinidad. West of the Andes *allopsha* extends as far south as the Department of Valle Del Cauca, Colombia.

#### 4. *Anopheles (Nyssorhynchus) braziliensis* (Chagas 1907)

Plates 7, 11, 16

**DISCUSSION.** *An. braziliensis* can be distinguished from other species in the *Albitarsis* Group in the female by (1) caudolateral scale tufts of abdomen well developed on segments II-VIII, (2) abdominal terga II-IV with relatively few scales, usually with a medial dark scale patch surround-

ed by golden scales, (3) vein C sometimes with a small presectoral light spot, usually represented by only a few white scales, (4) vein  $R_3$  with 3 dark spots and (5) hindtarsomere 2 with basal 0.3-0.4 dark; in the male genitalia by (1) ventral claspette with lateral margins tapering toward narrow apex, apex with moderately shallow median sulcus, (2) preapical plate of ventral claspette weakly developed, (3) dorsal claspette always with distinct basomesal projection on dorsal leaflet, (4) parabasal seta of gonocoxite about 2.5 length of basal tubercle, (5) tergum VIII vested with golden scales, (6) sternum VIII with patch of golden scales on anterior margin and 2,3 rows of long setae along apical margin and (7) sternum IX with anteromesal border not emarginated, posterior border slightly emarginated; and in the larva by (1) setae 2-C moderately closely approximated, clypeal index about 2.7, (2) seta 4-C long, usually single and extending to near or beyond insertion of 2-C, (3) pecten teeth alternating one long and 2,3 short, (4) seta 1-P often with blunt-tipped leaflets not overlapping leaflets of adjacent 1-P, (5) setae 1-3-P or 1,2-P sharing a common tubercle, (6) seta 13-P 5-9 branched, (7) abdominal median tergal plates about 0.20-0.25 width of segment, (8) accessory median tergal plates of abdominal segments II-VII always single and often lobed and (9) integument of head with heavily pigmented band extending anteriorly from collar along arms of frontoclypeal suture to seta 8-C, continuing anteriorly to seta 3-C.

The adults, male genitalia and larvae of *braziliensis* can easily be distinguished from those of other species in the Albitarsis Group. As in all species examined, the larval chaetotaxy is somewhat variable. Not all individuals possess blunt-tipped leaflets on seta 1-P, although the bases of setae 1-P are always widely spaced so that the leaflets from the setae on opposite sides do not overlap. Seta 4-C of the head usually is long and single, but in some populations from Brazil this seta is frequently apically branched. The teeth of the pecten are remarkably uniform and are reliable for species identification throughout this species' range.

**BIONOMICS.** The immatures of *braziliensis* have been found in clear ponds and clear stagnant swamps with mud bottoms, ponds in cultivated fields and a flooded borrow pit along a stream with stagnant water. Most of the immatures were in full sun or in partial shade, never in entirely shaded areas. All the aquatic habitats contained some type of vegetation; they usually had grassy margins with emergent and floating vegetation, and algae. The water was usually clear, but occasionally turbid. Most sites were in areas of secondary growth such as pastures or forest clearings. Other workers have collected *braziliensis* in similar habitats. Root (1926) found it at Lassance, Minas Gerais, Brazil, in large and small ground pools, ponds, marshes and seepage areas, all with considerable vegetation. Galvao (1940) collected the larvae in the city of Sao Paulo, Brazil, in well-lit shallow pools that had a large number of erect emergent plants and abundant algae. In Lassance, Shannon and Davis (1930) found *braziliensis* in spring water at the head of a spring-fed swamp. Deane, Causey and Deane (1948) stated that in northeastern Brazil the larvae of *braziliensis* (as *pessoai*) are principally collected in clear, slow-moving water containing grasses and algae, and usually exposed to the sun.

*An. braziliensis* is exophagous in some regions, rarely entering houses and preferring to feed on animals; elsewhere it is frequently seen inside houses. In northeastern Brazil, Deane, Causey and Deane (1948) reported that only 15 of 527 (2.9%) adults of *braziliensis* (as *pessoai*) captured were from inside houses. In Ceara and Paraiba, Brazil, they found that 0.4% of the anophelines collected inside houses were *braziliensis*, whereas it represented over 20% of the anophelines found outside. The same authors in Amazonia often collected *braziliensis* inside houses where it constituted 50% to 100% of the anophelines examined. It has been suggested that the two different behavior patterns for *braziliensis* in the various regions might be a result of the different lifestyles of the people who live in these areas. The people in northeastern Brazil always have a number of domestic animals near their houses while the people in Amazonia do not. *An. braziliensis* feeds outside on these domestic animals in northeastern Brazil, whereas in Amazonia selection pressure has resulted in *braziliensis* being endophagous (Deane, Causey and Deane 1948).

Where *braziliensis* is common it is active both during the day and night. Deane, Causey and

Deane (1948) investigated the activity pattern of *braziliensis* (as *pessoai*) and concluded that the time of maximum activity is in the evening. Nevertheless, they often observed it feeding in the middle of the day when sunlight is most intense.

**MEDICAL IMPORTANCE.** It is not believed that *braziliensis* is a primary vector of human malaria, but it is possible that this species could act as a secondary vector. As has been mentioned, *braziliensis* may, under the proper conditions (in the absence of domestic animals), enter houses in great numbers and may become involved in malaria transmission. Deane, Causey and Deane (1948) found that one of 122 females of *braziliensis* (as *pessoai*) dissected from Tamucuri, Para, Brazil, had sporozoites. In this particular area conditions were optimal for it to transmit malaria. The prevalence of endemic malaria was very high, and it was probably maintained by *darlingi*. The inhabitants showed a high gametocyte rate, domestic animals were very rare, and *braziliensis* was observed "breeding" very close to houses where subsequently it was encountered biting. Apparently when conditions are such that *braziliensis* may enter houses, it can occasionally transmit malaria. If however, those conditions are not met, *braziliensis* would probably play a very small role in the transmission of malaria.

**DISTRIBUTION** (pl. 7). *An. braziliensis* apparently is rarely found along the coastal plain of South America, but it is distributed throughout the interior in northern South America east of the Andes. To the south, it extends at least as far as the state of Sao Paulo, Brazil, and into parts of Bolivia. It occurs throughout Colombia, Venezuela, the Guianas and Trinidad. It is not found on any of the islands in the Antilles, nor does it occur anywhere in Central America.

#### 5. *Anopheles (Nyssorhynchus) oswaldoi* (Peryassu 1922)

Plates 4, 5, 9, 12

**DISCUSSION.** *An. oswaldoi* can be distinguished from other Amazonian species of the Albimanus Section in the female by the combination of (1) foretarsomeres 2 and 3 cream to white in apical 0.20-0.45 and 0.50-0.85 respectively, (2) foretarsomere 4 all dark to more than 0.3 dark basally, (3) dark basal bands on foretarsomeres 3-5 almost completely encircling each tarsomere, dark scales usually absent from ventral surface, (4) midtarsomere 4 all dark, (5) hindtarsomere 2 less than 0.25 dark basally and (6) vein C with a small, basal dark spot, humeral light spot 1.6-3.0 (1.1-3.8) length of basal dark spot; in the male genitalia by the combination of (1) basal lobule of ventral claspette very large, expanded laterally, with long spicules along basal margin about 2.0 width of aedeagus, (2) lateral and ventral surfaces of ventral claspette (exclusive of basal lobules) with spicules equal to or slightly less than width of aedeagus, (3) preapical plate of ventral claspette large, usually crescent shaped, moderately to heavily sclerotized and (4) aedeagus usually without leaflets; and in the larva by the combination of (1) setae 2,3-C plumose with usually dendritic branches, setae 2-C widely spaced, clypeal index about 1.65, (2) seta 4-C moderately short, (3) setae 8,9-C moderately large, length about 1.5 distance separating setae 5-C, (4) lateral arm of median plate of spiracular apparatus moderately long, (5) median teeth of pecten mostly subequal, (6) seta 1-X not inserted on saddle and (7) anal gills long, as long as or longer than anal segment.

*An. oswaldoi* is most closely related to *evansi*, *galvaoi* and *aquasalis*. The male genitalia of these species are very similar in general appearance. The shape of the preapical plate and the length of the spicules on the ventral claspette of *galvaoi* and *evansi*, and the truncate aedeagus of *evansi* are the only characters which differentiate the male genitalia of these species from *oswaldoi*. There is also considerable overlap in the adult females of *oswaldoi* and *evansi*, which sometimes makes species identification difficult. The larvae of *aquasalis* and *evansi* are similar to those of *oswaldoi*, differing mainly in the characters given above. Although *oswaldoi* may occur sympatrically, in the broad sense, with *aquasalis* and *evansi*, it is ecologically isolated from these species, occurring in fresh, usually well-shaded water in the interior of forests.

**BIONOMICS.** The immature stages of *oswaldoi* are found in the interior, usually in or on the margins of tropical forests, frequently along roads, in cultivated fields or grasslands adjacent to forested areas. They occur in permanent or temporary ground pools, margins of ponds or lakes, swamps, and stream-side pools; the sites most often are found in deeply to partially shaded areas, less often in full sun. The immature stages are commonly collected in the grassy margins of pools with muddy bottoms. Algae and abundant flotsam are present. The water is always fresh and may be turbid or clear.

The adults of *oswaldoi* are largely restricted to the forest. They are exophilic and zoophilic. Of the 6470 adults of *oswaldoi* Deane, Causey and Deane (1948) captured in Para, Brazil, 83 or 1.3% were from inside houses. Although primarily zoophilic, *oswaldoi* feeds freely on man inside the forest such as in the Mojinga Swamp in Panama or in the forest of French Guiana (Curry 1932; Rozeboom 1941; Floch and Abonnenc 1947). Deane, Causey and Deane (1948) reported that the peak in biting activity of *oswaldoi* was between 1800 and 1900 h.

**MEDICAL IMPORTANCE.** *An. oswaldoi* has been experimentally infected with *Plasmodium vivax* and *P. falciparum* by Fonseca and Fonseca (1942) in the state of Sao Paulo, Brazil, and by Rozeboom (1942) in Trinidad; however, it has never been found naturally infected or otherwise implicated in transmitting malaria. Deane, Causey and Deane (1948) dissected 540 females from the northeast of Brazil and found none infected with *Plasmodium*. At present, *oswaldoi* does not seem to be a vector of malaria.

**DISTRIBUTION** (pl. 9). *An. oswaldoi* is distributed throughout South America east of the Andes as far south as the northern provinces (Formosa, Misiones, Salta, Tucuman) of Argentina. It occurs throughout most of Colombia, Venezuela, the Guianas, Brazil, Paraguay and Bolivia; *oswaldoi* also occurs in Ecuador and Peru east of the Andes. Northward, this species extends into Panama and Costa Rica. It is also found in Trinidad, but not in Tobago or any other islands of the Antilles. It is not certain how far south *oswaldoi* occurs west of the Andes.

#### 6. *Anopheles (Nyssorhynchus) galvaoi* Causey, Deane & Deane 1943

Plates 10, 12

**DISCUSSION.** *An. galvaoi* can be distinguished from other Amazonian species of the *Albimanus* Section in the male genitalia by the combination of (1) ventral claspette with basal lobule very large, covered with very long, uniformly distributed spicules about 3.0 width of aedeagus, (2) ventral and lateral surfaces of ventral claspette (exclusive of basal lobules) with short spicules about 0.5 width of aedeagus, (3) preapical plate of ventral claspette heavily sclerotized, circular to semicircular with small basolateral projection and (4) apex of aedeagus rounded, about as wide as long (possibly shorter than that of *oswaldoi*), without leaflets. The female of *galvaoi* is apparently very similar to those of *aquasalis* and *benarrochi*. Since there were only 4 damaged specimens available, we were unable to differentiate the female of *galvaoi* from those of the latter 2 species. Consequently, we have not included *galvaoi* in the key to females. Forattini (1962) states that Correa and Ramalho can distinguish *galvaoi* from *aquasalis* on the basis of the relative lengths of the dark basal spot and humeral light spot of vein C. Forattini reports that in *aquasalis* the basal dark spot is about 0.5 the length of the B<sub>2</sub> (humeral) spot; whereas in *galvaoi*, the basal dark spot is clearly less than 0.5 the length of the humeral light spot. For *aquasalis* this is not always true. Because *aquasalis* and *galvaoi* are not sympatric, there should be no problem in recognizing *aquasalis*.

The male genitalia of *galvaoi* is very similar to those of *oswaldoi* and *evansi*, *galvaoi* differing only by (1) longer spicules on basal lobule of ventral claspette and shorter spicules on ventral and lateral surfaces of the fused portion of ventral claspette when compared to *oswaldoi*, (2) circular or semicircular shape of preapical plate when compared to *oswaldoi* and (3) rounded apex of the aedeagus in contrast to *evansi*.

The larva of *galvaei* was unavailable for this handbook; however, the larva has been described by M.P. Deane, Causey and Deane (1946). From their description and key it seems that *galvaei* most closely resembles *nuneztovari* (as *goeldii*), *evansi* (as *noroestensis*) and *rangeli*. With regard to the larva, these investigators stated, "... it [*galvaei*] can usually be separated from *A. goeldii* in which the posterior clypeal hairs [setae 4-C] are longer and simple or divided far from the base. In *A. goeldii*, *A. noroestensis* and *A. rangeli* the anterior clypeal hairs [setae 2,3-C] have even less numerous and shorter branches, and the leaflets of the abdominal palmate tufts of segments 5 to 7 [seta 1-V-VII] are pointed at the tips." In their key, *galvaei* is distinguished from *evansi* and *rangeli* by palmate setae 1-V-VII possessing apically truncate leaflets.

**BIONOMICS.** Very little is known about the natural history of *galvaei*. Deane, Causey and Deane (1948) collected the larvae in puddles containing grass and algae exposed to the sun. Forattini (1962) reports that the larvae are found in similar habitats to those of *rondoni*, in puddles and marshes. The females are said to be crepuscular, and they have been collected on animal bait but not inside houses (Deane, Causey and Deane 1948).

**MEDICAL IMPORTANCE.** *An. galvaei* is of no known medical importance.

**DISTRIBUTION** (pl. 10). *An. galvaei* was described from the territory of Acre, Brazil. This species has been reported also to occur in Brazil in the following territories or states: Amazonas, Rondonia, Mato Grosso, Para, Sao Paulo, Rio de Janeiro (?) (Carvalho and Rachou 1951); Goias (?) (Mattos and Xavier 1965); and Bahia (?) and Parana (?) (Rachou and Ricciardi 1951). In Amazonia, Deane, Causey and Deane (1948) collected *galvaei* at Rio Branco, Rio Zinho and Brasileia (Acre), and at Guajara Mirim (Rondonia). Garcia and Ronderos (1962) record *galvaei* from Paraguay.

### 7. *Anopheles (Nyssorhynchus) evansi* (Brethes 1926)

Plates 9, 12, 17

**DISCUSSION.** *An. evansi* can be distinguished from other Amazonian species of the Albi-manus Section in the female by the combination of (1) palpomere 4 often with a dark ventral stripe, (2) hindtarsomere 2 with a dark band in basal 0.25-0.35 (0.2-0.4), (3) foretarsomere 3 with a light band in apical 0.55-0.80, (4) foretarsomere 5 cream, gray or golden in apical 0.3-0.5, (5) midtarsomere 5 usually cream in less than apical 0.3, (6) light wing spots (at least on anterior veins) and coxae (usually) gray to cream to yellow, humeral light spot of vein C usually greater than 2.0 length of basal dark spot, (7) subcostal light spot of vein C moderately large, about 0.30-0.45 length of subcostal dark spot, (8) sectoral and preapical dark spots of vein M moderately large to large and (9) apical light fringe spot moderately large to large and conspicuous; in the male genitalia by the (1) aedeagus truncate or very weakly rounded at apex, subequal to length of ventral claspette, (2) basal lobule of ventral claspette large, expanded laterally, with spicules along basal margin long about 1.5-1.8 width of aedeagus, (3) apex of ventral claspette narrow, width 0.20-0.36 length of claspette and (4) preapical plate of ventral claspette moderately large, semicircular to oval and heavily sclerotized; and in the larva by the combination of (1) setae 2,3-C barbed in about apical half, setae 2-C widely spaced, clypeal index about 1.7 (1.0-2.0), (2) seta 4-C 3,4 branched (2-5), moderately short to moderately long, 0.30-0.45 length of 3-C, (3) seta 14-P 8,9 branched (7-10), with long branches, (4) seta 13-IV 3,4 branched, moderately long, about 1.5 length of leaflets of 1-IV, (5) seta 2-T long, extending beyond caudal margin of thorax, (6) seta 2-III 4-6 branched, large, more than 2.0 length of leaflets of 1-III, (7) seta 2-IV moderately long, about 1.5 length of leaflets of 1-IV, and 2-V very long, 3.0-4.0 length of leaflets of 1-V, (8) seta 5-I moderately short, inserted less than 0.75 its length from lateral margin, (9) seta 13-V very large, about 3.0-4.0 length of leaflets of 1-V, almost always 3 branched (3-5) at least on one side of larva and (10) lateral arm of median plate of spiracular apparatus short to moderately short, directed caudolaterally. *An. evansi* is difficult to diagnose in all stages except for the male genitalia. The larva is almost identical with that of *rangeli* except for the

position of setae 4-C and 5-I,II, and the relative lengths of several of the abdominal setae. The adult is like those of *strodei* and *anomalophyllus* except for the coloration of the scales of the thorax, coxae and wing, and the banding pattern of the foretarsus. Locality data are very useful in distinguishing *evansi* from other Amazonian species of *Nyssorhynchus*, since *evansi* is not believed to occur throughout most of the Amazon. It is known only along the southern and southeastern margins of Amazonia.

*An. evansi* is most closely allied to *oswaldoi* and *galvaoi*, and, to a somewhat lesser extent, to *aquasalis*. The male genitalia differ from those of *galvaoi* and *oswaldoi* primarily in the shape of the apex of the aedeagus, and from that of *oswaldoi* in the shape of the preapical plate (see discussion section for *oswaldoi*). The basal band of hindtarsomere 2 of the adult is the main character separating *evansi* from *aquasalis*, *galvaoi* and *oswaldoi*. Occasionally, females of *evansi* at the variational extremes (with either very small or very large dark bands on hindtarsomere 2) cannot be distinguished from the adults of the latter species. Ecologically, *evansi* occupies a different habitat than either *aquasalis* or *oswaldoi*; it is found in fresh water in secondary growth areas, usually not in forested areas or coastal brackish water habitats.

**BIONOMICS.** The immatures of *evansi* have been collected in both permanent and temporary water habitats in drainage ditches, small ground pools, potholes and along stream margins. The immatures are usually found in fresh water, either exposed to the sun or in partial shade. The water is frequently turbid and brownish. One collection from the state of Rio de Janeiro, Brazil, was from a flooded grassy yard highly contaminated with pig and chicken feces. The immatures have been collected in regions of secondary growth such as in cultivated areas; but they have not been collected in the forest, although they may occur along the margins of forested areas. Additional larval habitats reported in the literature are muddy puddles, rock holes and wells (Deane, Causey and Deane 1948), and marshes and swamps (Galvao 1940).

Most reports indicate that *evansi* is not very anthropophilic or endophilic. Of the 1342 females collected in northeastern Brazil by Deane, Causey and Deane (1948), only 53 or 3.9% were collected in houses. Deane, Causey and Deane (1948) stated that *evansi* (as *noroestensis*) was most abundant during the rainy season (June 1941) in Ceara, Brazil. In 2 days in June, they collected 447 females on animal bait, representing 96.9% of the anophelines captured. During the dry season in December over a 2 day period, they collected only 12 adults, which were 35.3% of the anophelines caught. In host preference studies made between 1730 and 1930 h in June, these investigators collected 38 females on a horse and only one on a man. Biting peaked around sundown, and there was another small peak of activity at dawn, although some individuals could be captured throughout the night.

**MEDICAL IMPORTANCE.** *An. evansi* does not seem to be important as a vector of malaria. Correa and Ramos (1942a, 1942b) dissected 24 females of "*metcalfi*" (presently a synonym of *evansi*) that were collected inside houses in Ribeira, Sao Paulo, Brazil, and found 2 (8.3%) with an oocyst infection of *Plasmodium*. We are not certain that the specimens these authors reported as *metcalfi* were actually *evansi*; however, a photograph of the head capsule of the larva of "*metcalfi*" in Correa and Ramos (1942b) corresponds to that of *evansi*, as does the habitat in which these mosquitoes were collected. Deane, Causey and Deane (1948), after studying *evansi* in many different localities in the northeast of Brazil, stated that all indications are that this species is not important in the transmission of malaria. Forattini (1962) reports that it is possibly a secondary vector. *An. evansi* (as *noroestensis*) from Guaratingueta and Guarujá, Sao Paulo, Brazil, has been experimentally infected with *Plasmodium vivax* by Fonseca and Unti (1943).

**DISTRIBUTION** (pl. 9). *An. evansi* is distributed throughout central and southeastern South America. Its northernmost limits are the southern margins of Amazonia and the northeastern states of Brazil (Maranhao, Ceara). In the west, *evansi* extends to the eastern slope of the Andes. *An. evansi* is reported to occur as far south as the provinces of Chaco, Corrientes, Formosa, Misiones, Salta, Santa Fe and Tucuman in Argentina (Garcia and Ronderos 1962).



8. *Anopheles (Nyssorhynchus) aquasalis* Curry 1932

Plates 9, 12, 18

**DISCUSSION.** *An. aquasalis* can be distinguished from the other Amazonian species in the Albimanus Section in the **female** (except for occasionally *benarrochi*) by the combination of (1) palpomere 4 usually without a distinct ventral stripe of dark scales, (2) light scales on coxae light cream to grayish, not white, (3) foretarsomere 3 highly variable, light in apical 0.4-0.7, (4) hindtarsomere 2 brown in basal 0.40-0.55 (0.3-0.6), (5) vein C with humeral light spot large, 1.5-3.5 length of basal dark spot, and with basal dark spot usually about 0.5 its length from humeral crossvein, (6) subcostal light spot on vein C usually less than 0.5 of subcostal dark spot, (7) apical light fringe spot small to moderate, (8) dark spots on posterior veins distinct and (9) light wing spots at least on veins C and R light cream to yellowish, not white; in the **male genitalia** by the combination of (1) apex of ventral claspette moderately narrow, width at apex about 0.3 length of claspette, (2) basal lobule of ventral claspette broad with uniformly distributed spicules, spicules along basal margin equal to or slightly longer than width of aedeagus and usually not reflexed, (3) lateral and ventral surfaces of ventral claspette (exclusive of basal lobules) with short spicules 0.5 or less width of aedeagus and (4) preapical plate of ventral claspette moderately small, oval to circular and weakly to occasionally strongly sclerotized; and in the **larva** by the combination of (1) setae 2,3-C plumose with 7-12 simple, rarely dendritic branches, setae 2-C widely spaced, clypeal index about 1.67, (2) seta 4-C 1-3 branched, short to moderately short, (3) seta 8-C slightly longer than distance separating insertion of setae 5-C, (4) pecten with median teeth mixed medium and short, (5) lateral arm of median plate of spiracular apparatus very short, (6) saddle with ventral margin irregular, seta 1-X inserted on ventral margin at base of indentation or on saddle near ventral margin and (7) anal gills usually short, about 0.5 length of anal segment, rarely longer. The adults of *aquasalis* are easily distinguished in most cases from all other species in the Oswaldoi Subgroup except for *benarrochi*. Even so, *aquasalis* can usually be distinguished from *benarrochi* by the characters given in the above discussion and by its geographical distribution. Because of the paucity of adult females of *benarrochi* available for study, an attempt has not been made to separate *aquasalis* from the former in the key to the adult females. We believe that separation of these 2 species in the key would lead to misidentification.

The closest allies of *aquasalis* are *oswaldoi*, *galvaoi* and *evansi*. As previously mentioned, the male genitalia of these 4 species are very similar, differing primarily in the shape and sclerotization of the preapical plate, the length of spicules on the ventral claspette, and, in the case of *evansi*, the shape of the aedeagus. *An. aquasalis* does not share as many characters with *galvaoi*, *oswaldoi* and *evansi* as these latter share with each other, but the larvae of all 4 are similar.

**BIONOMICS.** *An. aquasalis* is primarily a brackish water mosquito, even though it has been collected from a wide variety of habitats in both fresh and brackish water. It is more or less restricted to the coast and areas that are influenced by tides, although on certain occasions it has been collected considerable distances inland. Deane, Causey and Deane (1948) collected *aquasalis* 60 km from the coast in the state of Pernambuco, Brazil, in a brackish water lake, Lagoa Salgada. In the Amazon basin, the same authors collected *aquasalis* 140 km from the coast on the right and left banks of the Rio Para. Recently, adults that resemble *aquasalis* have been collected at numerous localities in the Maraba area, Para, Brazil (Roberts, Hoch and Peterson 1981). Since these latter collections were made about 500 km from the coast in fresh water, and the immatures have not been studied, we are reluctant to state that these adults are definitely *aquasalis*. Interestingly, in this region these adults are endophilic with an outdoor to indoor ratio of 3.9 (D.R. Roberts, personal communication). Lucena (1946) collected *aquasalis* 252 km from the coast at Jupi in northeastern Brazil, at an altitude of 750 m, in an area in which the soil had a high salt concentration. In all these instances, except possibly in the Maraba area, salt seemed to be essential for the presence

of *aquasalis* inland from the coast.

The immatures have been collected in mangrove swamps, brackish marshes, flooded meadows, rice fields, sugarcane plantations, ditches, fresh water ponds, pools along stream margins, temporary and semipermanent ground pools, large artificial containers, and crab holes. Although there seems to be a preference for brackish water, many of the specimens examined came from fresh water but usually no farther than 5-8 km from the coast at elevations of 200-300 m; its occurrence in fresh water is particularly common in the Lesser Antilles. Most of the collections were from aquatic habitats in full sun or partial shade, but some were in deep shade, such as in mangrove swamps and in crab holes. The larvae seem to be able to tolerate moderate amounts of pollution. Frequently *aquasalis* is associated with mats of algae.

The adults of *aquasalis* are crepuscular, usually active from dusk to a few hours after sundown. The adult females feed readily on man and on domestic animals, such as cattle, horses, donkeys, dogs, sheep and pigs. They rest inside houses on the walls, normally less than one meter above the floor (Deane and Damasceno 1948). Throughout vast stretches of northeastern Brazil and in some areas of the Guianas and Lesser Antilles, it is the only anopheline that occurs in large numbers inside houses; however, it is reported that less than 10% stay in the house for 24 hours at a time (Deane, Causey and Deane 1948). Feeding preference studies indicate that *aquasalis* is more zoophilic than anthropophilic, except possibly in the Lesser Antilles. Nevertheless, when domestic animals are removed from an area, which has happened in many places because of mechanization, man usually becomes the primary host; under these conditions *aquasalis* becomes a major health threat (Downs, Gillette and Shannon 1943; Giglioli 1959, 1963; Hamon, Mouchet *et al.* 1970). The adults of *aquasalis* are considered to be strong fliers capable of migrating considerable distances.

**MEDICAL IMPORTANCE.** *An. aquasalis* has been a major vector of malaria along the coast of Brazil south to the state of Parana, and in the Lesser Antilles. It is believed not to be a vector in Panama. In Venezuela and the Guianas, *aquasalis* has played a role in residual malaria transmission (Floch 1956; Gabaldon and Guerrero 1959; Giglioli 1959; Hamon, Mouchet *et al.* 1970). *An. aquasalis* has been extremely important as a malaria vector in Trinidad and Tobago, and in northeastern Brazil. It has been incriminated as the major vector of malaria in Grenada (Earle 1936; Root and Andrews 1938), St. Lucia (Earle 1936) and Guadeloupe (Fauran 1962). It has been found naturally infected with *Plasmodium* in Brazil (Fonseca and Fonseca 1942; Coutinho 1943; Correa and Ramos 1944; Deane, L.M. Causey and Deane 1946), Trinidad and Tobago (Downs, Gillette and Shannon 1943), Grenada and St. Lucia (Earle 1936). In all other areas where it is important as a potential vector, it is considered to be an effective vector only when it occurs in large numbers. Thus, its vector effectiveness is dependent on adult density (Deane, L.M., Causey and Deane 1946; Forattini 1962; Senior-White 1951), and to some extent, on the presence of alternate hosts that serve to decrease the number of females feeding on man.

**DISTRIBUTION** (pl. 9). *An. aquasalis* is primarily restricted to the coast, coastal lowlands and coastal waterways influenced by tides, except in the islands of the Lesser Antilles and possibly in Para, Brazil. It occurs from the state of Parana, Brazil, north along the coast, west through the Guianas, Venezuela and Colombia, and into Central America predominantly along the Atlantic side of Panama and Costa Rica to Nicaragua. On the Pacific side of South America, *aquasalis* is reported to occur as far south as the province of El Oro, Ecuador, on the shores of the Gulf of Guayaquil. *An. aquasalis* is present in Trinidad, Tobago and the Lesser Antilles as far north as the Leeward Islands of Antigua and St. Kitts, but it does not occur in the Greater Antilles, Virgin Islands or the Bahama Islands.

9. *Anopheles (Nyssorhynchus) ininii* Senevet & Abonnenc 1938

Plates 9, 12, 19

**DISCUSSION.** *An. ininii* can be distinguished from other Amazonian species of the Albimanus Section in the female by the combination of (1) palpomere 4 with a dark basal band extending distad on the ventral surface to form a distinct, dark, ventral stripe usually not reaching apical dark ring, (2) foretarsomeres 3-5 predominantly cream to white with dark scales often present only on dorsobasal surface of tarsomere, tarsomeres 2 and 3 light in apical 0.45 (0.35-0.55) and 0.75 (0.70-0.86) respectively, tarsomere 4 often all light cream to golden brown or with a small, dark, basal area rarely longer than 0.3 length of tarsomere, tarsomere 5 from about 0.5 basally dark to all cream, (3) midtarsomere 4 with a cream band in apical 0.15-0.25, and tarsomere 5 from completely cream to 0.5 basally dark, (4) hindtarsomere 2 with a dark band in basal 0.17-0.26, (5) wing spots white to very light cream, (6) humeral light spot on vein C about 2.0-3.3 (1.5-3.3) of basal dark spot and (7) subcostal light spot on vein C 0.35-0.70 of subcostal dark spot; in the male genitalia by the combination of (1) ventral claspette strongly conoid, with a very small median sulcus at apex, narrow and rounded at apex, width at apex about 0.3 length of claspette, (2) basal lobule of ventral claspette very large, expanded laterad and usually bent ventrally at base so that spicules on basal margin project caudally, (3) spicules along basal margin of basal lobule very strong and long, 2.0-3.0 width of aedeagus, spicules distributed uniformly over surface of lobule, (4) spicules on lateral and ventral surfaces of ventral claspette (exclusive of basal lobules) short, about 0.5 width of aedeagus, extending toward apex only as far as level of apical margin of preapical plate, (5) preapical plate heavily sclerotized, very large, crescent shaped and (6) apex of aedeagus with or without very small, membranous leaflets; and in the larva by the combination of (1) setae 2,3-C single and barbed in about apical half, setae 2-C widely spaced, clypeal index about 1.25, seta 3-C about 0.8-0.9 length of 2-C, (2) seta 4-C short, not extending to base of 2-C, (3) setae 8,9-C 6-8 branched (5-10), strongly developed, 9-C weakly plumose with moderately long shaft, subequal to 2.0 distance separating insertion of setae 5-C and 6-C, (4) seta 1-A dendritic, 7-9 branches (6-10), long, about 2.0 width of antenna at point of insertion, (5) seta 14-P 7-10 branched (7-13) from moderately long shaft, (6) seta 13-IV 3,4 branched, larger than 13-I-III, (7) lateral arm of median plate of spiracular apparatus long, directed laterally, appearing truncate on lateral margin, (8) seta 1-X inserted on saddle near ventral margin, never on ventral margin at base of indentation and (9) anal gills very long, usually 2.0 or more length of saddle.

The females of *oswaldoi* and *ininii* are very much alike in all characters except for palpomere 4 and the banding patterns of the foretarsus. It is impossible to differentiate these 2 species on the basis of the wing or hindtarsomere 2. Ecologically, *ininii* occurs sympatrically with *oswaldoi*, the immatures being found in many of the same habitats, although *ininii* usually occurs in more open areas than *oswaldoi*.

**BIONOMICS.** Very little is known about the bionomics of *ininii*, particularly for the adults. Almost all the information relating to the larval habitats discussed below came from data recorded on collection forms by J.F. Reinert while in Para, Brazil, in 1974. The immatures of *ininii* are found along grassy margins of ponds, lakes, reservoirs, temporary or permanent ground pools, and animal or wheel tracks, in full sun or occasionally in partial shade. The water is fresh, clear, and with algae and emergent vegetation, although the vegetation is usually scanty in the larval habitat. The general environment in Para was characterized as secondary scrub. The type material of *ininii* was collected in an artificial reservoir in St. Elie, French Guiana (Senevet and Abonnenc 1938). Floch and Abonnenc (1947, 1951) reported that *ininii* occurs in dense vegetation with *An. (Nys.) braziliensis*, *darlingi*, *nuneztovari*, *oswaldoi* and *triannulatus*. Floch and Abonnenc (1951) stated that in 9 years only 6 specimens were collected.

**MEDICAL IMPORTANCE.** Nothing is known about the adult behavior or the medical importance of *ininii*.

**DISTRIBUTION** (pl. 9). *An. ininii* has been collected only in French Guiana and in the state of Para, Brazil.

**10. *Anopheles (Nyssorhynchus) rangeli* Gabaldon, Cova Garcia & Lopez 1940**  
Plates 10, 12, 20

**DISCUSSION.** *An. rangeli* can be distinguished from the other Amazonian species of the Albimanus Section in the **female** by the combination of (1) upper mesanepimeron (Mam) often with 1-4 light obovate scales, (2) foretarsomere 2 with a light band in apical 0.30-0.45 and tarsomere 3 with a light band in apical 0.7 (0.60-0.85), (3) hindtarsomere 2 with a brown band in basal 0.28 (0.24-0.35), (4) wing with several large light spots, humeral light spot of vein C about 1.8-3.5 (1.0-3.7) length of basal dark spot, (5) subcostal light spot of vein C usually greater than 0.5 (0.45-1.00) length of subcostal dark spot, (6) preapical light spot of vein C 0.40-0.65 length of preapical dark spot, (7) presectoral and sectoral dark spots of vein R usually small, (8) vein M predominantly light with sectoral dark spot often indistinct and (9) apical light fringe spot large, conspicuous and usually undivided; in the **male genitalia** by (1) ventral claspette large, apex truncate and wide, width at apex 0.4-0.5 length of claspette, apex with abruptly angled, rounded lateral margins, (2) basal lobule of ventral claspette very large, usually curved ventrally, with long spicules along basal margin about 1.5 width of aedeagus, (3) long spicules along basomesal margin of basal lobule concentrated and directed caudally into mesal cleft, (4) preapical plate of ventral claspette small, oval, heavily sclerotized, convex apically, flat or slightly concave basally, occasionally with small basomesal projection and (5) apex of aedeagus with or without very small, membranous or weakly sclerotized leaflets, apex slightly longer than wide; and in the **larva** by the combination of (1) setae 2,3-C single, and simple or barbed, setae 2-C widely spaced, clypeal index about 1.67, (2) seta 4-C short, not extending to base of 2-C, (3) setae 8,9-C 4-6 (2-6) and 5-7 branched respectively, dendritic, moderately large, (4) palmate seta 1-P with 9-13 (8-14) long, broad leaflets, (5) seta 2-III 3-5 branched (3-6), relatively short, 1.5-2.0 length of leaflets of 1-III, (6) seta 2-IV single, moderately short, slightly longer than leaflets of 1-IV, (7) seta 5-I,II short, inserted 0.75-1.00 its length from lateral margin of abdomen, (8) seta 13-IV 3 branched (3-5), moderately short, slightly longer than leaflets of 1-IV, (9) lateral arm of median plate of spiracular apparatus short and (10) seta 1-X inserted on saddle near ventral margin of saddle or on ventral margin at base of indentation, rarely inserted just ventrad of ventral margin.

*An. rangeli* forms the sister group of *nuneztovari* and *trinkae*. It differs from these 2 species in the female usually by (1) the absence of a ventral dark line on palpomere 4, (2) presence of a few light scales on upper mesanepimeron and (3) presence of a small basal dark spot and a large subcostal light spot on vein C. The male genitalia of these 3 species are very similar, *rangeli* differing only in the (1) presence of a concentration of long spicules along the basomesal margin of the basal lobule, (2) development of the preapical plate and (3) to a lesser extent, structure of the apex of the ventral claspette. The larva of *evansi* is very much like that of *rangeli* and can be distinguished only by the characters given in the key. Locality data are extremely useful in distinguishing the larva of *rangeli* from *evansi*, since the distributions of the 2 species do not overlap, except possibly in Bolivia and southwestern Brazil.

There seems to be no significant variation among the populations we have studied. Intrapopulation variation seems as great as or greater than interpopulational variation. As in all the species in the Albimanus Section, there is considerable variation in the adult female in the relative lengths of the wing spots and in the tarsal banding.

**BIONOMICS.** The immatures of *rangeli* occur in fresh water in marshy depressions, temporary ground pools, animal and wheel tracks, ditches, stream margins, and lakes. They are usually found in full sun or partial shade, and usually not in the forest proper but in open glades, meadows, and scrub or grassland areas. There is frequently abundant vegetation in the aquatic habitat. *An. rangeli* occurs in lowlands and at higher elevations; the highest recorded collection we have was made at 950 m above sea level.

The adults are predominantly exophilic. Rey and Renjifo (1950) collected 2414 anophelines inside houses from September to November near Cucuta, Colombia, of which only 0.62% were *rangeli*. Of the 3722 adults of *rangeli* collected by Deane, Causey and Deane (1948), only 25 or 0.7% were from inside houses. In another study by the latter investigators, 131 hours of collecting in houses resulted in only 5 specimens of *rangeli*; however, in less than 41 hours collecting outside, 1391 individuals were captured. The majority of the specimens were collected on horses or bulls, although many were biting man. In Boca de Acre, Brazil, in a collection made at sundown simultaneously from a cow and a man, 5 females of *rangeli* were collected from the cow and 8 from the man. Elliott (1972) reported that in Peru the peak hours of biting by *rangeli* were 1800-2000 h and 0400-0600 h.

**MEDICAL IMPORTANCE.** Very little is known about the vector capacity of *rangeli*. It does not seem to be a vector of malaria, although Forattini (1962) stated that it has been suspected of transmitting malaria in Ecuador. Deane, Causey and Deane (1948) dissected 363 females from Rio Branco, Acre, Brazil, and found none infected with *Plasmodium*. Rey and Renjifo (1950) did not find *rangeli* naturally infected in the Cucuta area of Colombia during a malaria epidemic in which *Plasmodium falciparum* (18%), *P. vivax* (55%) and *P. malariae* (27%) were present in the human population.

**DISTRIBUTION** (pl. 10). *An. rangeli* occurs in the upper Amazon and Orinoco basins, Colombia, Venezuela, Ecuador (Morona Santiago, Napo, Pastaza), and south through eastern Peru and into northern Bolivia (Beni, Santa Cruz).

### 11. *Anopheles (Nyssorhynchus) nuneztovari* Gabaldon 1940

Plates 10, 12, 21

**DISCUSSION.** *An. nuneztovari* can be distinguished from other Amazonian species of the Albimanus Section in the female by the combination of (1) integument dark brown to very dark brown with considerable contrast between light and dark regions, and light wing spots usually cream at least on anterior veins, (2) usually ventral surface of palpomere 4 with row of dark scales, (3) foretarsomere 2 with a light band in apical 0.2-0.4 (0.15-0.44) and tarsomere 3 with a light band in apical 0.55 (0.40-0.75), (4) foretarsomere 4 with a small, apical cream band, (5) hindtarsomere 2 with a dark band in basal 0.25-0.32 (0.20-0.32), (6) large dark wing spots distinct, humeral light spot of vein C 0.7-1.3 (0.7-1.7) of basal dark spot, (7) subbasal dark spot of vein C usually longer than subbasal light spot, (8) subcostal light spot of vein C 0.20-0.55 of subcostal dark spot, usually less than 0.5 and (9) subcostal and apical dark spots of vein  $R_{4+5}$  and dark spots of  $M_{1+2}$  and  $M_{3+4}$  all very dark and conspicuous; in the male genitalia by the combination of (1) ventral claspette moderately short, 0.25-0.40 length of sidepiece, width at apex about 0.50-0.60 (0.50-0.64) length of claspette, and apex appearing either truncate or with median sulcus, apicolateral margins abruptly angled, lateral margins of claspette not tapering appreciably medially toward apex, (2) basal lobule of ventral claspette moderately expanded laterally, spicules along basal margin moderately long, slightly longer than to 1.5 width of aedeagus but never 2.0 width, spicules distributed evenly over basal surface and radiating in different directions, not concentrated along basomesal margin as in *rangeli*, (3) ventral and lateral surfaces of ventral claspette (exclusive of basal lobules) with short spicules about 0.5 width of aedeagus, (4) preapical plate of ventral claspette moderately small, semi-

circular to oval, and weakly to moderately heavily sclerotized and (5) length of aedeagus 1.33-1.60 (1.31-1.89) length of ventral claspette, apex of aedeagus usually wider than long, moderately rounded and with or without very small, membranous leaflets; and in the larva by the combination of (1) setae 2,3-C single and barbed, setae 2-C widely spaced, clypeal index 1.0-1.3, seta 3-C 0.75-0.90 length of 2-C, (2) seta 4-C single or 2-4 forked, moderately long, 0.30-0.60 length of 3-C, usually extending to near or beyond base of 2-C, (3) palmate seta 1-P with 9-12 (9-15) pigmented, moderately broad leaflets, (4) seta 0-II-VII 5-8 branched (4-10), large, very conspicuous, 0-II subequal to or longer than leaflets of 1-II, (5) seta 13-IV 4-6 branched (3-6), moderate, equal to or slightly longer than leaflets of 1-IV, 13-V 4-6 branched (4-7) and (6) seta 1-X inserted on saddle near ventral margin, on ventral margin at base of indentation, or just ventrad of ventral margin.

Unfortunately, the adult females of *nuneztovari*, *trinkae* and *rangeli* can sometimes be confused due to intraspecific variability and the paucity of reliable differentiating characters. *An. trinkae* is currently not known to exist in the tropical forest of Amazonia so it is necessary only to distinguish *nuneztovari* from *rangeli* in this region.

**BIONOMICS.** The immatures of *nuneztovari* are found in open marshy areas, ponds and lakes (often in the grassy margins), small to large, permanent or temporary ground pools, animal and wheel tracks, and along stream margins; they are found in fresh water exposed to the full sun or in partial shade. Aquatic vegetation may be abundant, and algae are often present. *An. nuneztovari* is collected in the interior or in clearings within the forest, and in areas of secondary growth (scrub), such as around villages.

Elliott (1968, 1972) studied the relationship between the biting activity of *nuneztovari* indoors and outdoors with regard to human activity at 5 localities in Colombia: El Pescado, Rio Fuego, Puerto Reyes, Turbo and Las Aranas. During months of highest adult density, biting reached a peak shortly before midnight, indoor biting being equal to or slightly greater than outdoor. In months of low density biting peaked an hour or so earlier than during the high density season, biting being slightly greater outdoors than indoors. Biting activity was unimodal, not showing early evening or morning peaks. Elliott found that *nuneztovari* usually rests one meter high or less on the walls inside houses, although occasionally (15%) above this height. Because it feeds inside while most people sleep, it is effectively endophilic.

In 1950 Rey and Renjifo reported that in Norte de Santander, Colombia, *nuneztovari* was abundant inside houses between 2200-2400 h. Gabaldon (1972) stated that before spraying the inside walls of houses with DDT in Venezuela, *nuneztovari* was very endophilic, remaining in the houses and resting on the walls and ceiling after taking a blood meal. Spraying of insecticides, however, selected for "intense exophilism." *An. nuneztovari* is still anthropophilic, but immediately upon taking a blood meal, the females leave the house, thereby avoiding a lethal dose of insecticide. Gabaldon stated that, even though strongly exophilic, "*A. nuneztovari* in Venezuela, for example, maintains a human blood preference of around 80%, and a man-biting rate of more than 100 during a night indoors." Gabaldon believes that this intense exophilism has been largely responsible for refractory malaria in Venezuela.

Panday (1977) reported a unimodal distribution of biting activity of *nuneztovari* in Suriname occurring from 1800-1900 h, the peak beginning at the termination of twilight (1830 h, sunset was fixed at 1800 h). Daily collections on human bait at 1800-1900 h (July-December 1976) from 15 m inside the forest resulted in the capture of 13,824 females of *nuneztovari*.

In Para, Brazil, the females seem to be primarily exophagous, unlike *nuneztovari* in Colombia and Venezuela. Deane, Causey and Deane (1948) reported that of the 21,967 females of *nuneztovari* collected, only 411 or 1.9% were captured inside houses. In 29 hours collecting inside houses in Maraba, Para, one specimen of *nuneztovari* was found; however, in 31 hours outside on animal bait, 978 females were captured. Feeding preference studies, comparing a horse and a man as bait, indicate that *nuneztovari* feeds freely on man outdoors. Recent studies, conducted from March 1975 to April 1976 by the U.S. Army Medical Research Unit-Belem (USAMRU) in Palestina (100

km SW of Maraba, Para), also indicate that *nuneztovari* is exophilic and most active at sunset (D.R. Roberts, personal communication). In this region, *nuneztovari* was the dominant anopheline captured in landing and resting collections.

**MEDICAL IMPORTANCE.** *An. nuneztovari* is a major vector of malaria in western Venezuela and northern Colombia. Gabaldon and Guerrero (1959) stated that in some areas where *nuneztovari* was transmitting malaria in Venezuela, spleen indices were close to 100%. They also found that in areas not close to the jungle, malaria disappeared when the local inhabitants took chloroquine; however, in regions near forest, chloroquine failed to stop transmission. Hamon, Mouchet *et al.* (1970) also indicated that the importance of *nuneztovari* depends on the amount and density of vegetation around houses. Vector density is reduced in areas where vegetation has been cleared around houses.

In Suriname, Panday (1977) reported that *nuneztovari* may have been the principal vector of *Plasmodium falciparum* in recent epidemics. He stated that *An. (Nys.) darlingi*, thought to be the primary vector of malignant malaria, has not been captured in the epidemic regions. In these same areas *nuneztovari* has been collected in great numbers.

*An. nuneztovari* has not been reported to be an important vector of malaria in Amazonia other than possibly in Suriname. Recently in the Maraba area of Para, Brazil, D.R. Roberts (personal communication) found both *P. falciparum* and *P. vivax* in the local human population in the absence of a recognized primary vector. Roberts said that in August 1975, 4 teenage members of a colonist family in Gleba 36 (a colonization site) became ill with malaria (3 with *P. falciparum* and one with *P. vivax*; all denied recent travel from their homestead). Although *nuneztovari* occurs in high densities in this region, the entomological and/or epidemiological data are insufficient to implicate this species as a vector. Several other anophelines have been collected in this general locality, such as *ininii*, *oswaldoi*, *strodei*, *triannulatus*, *?aquasalis*, *allopha*, *braziliensis*, *An. (Ano.) mattogrossensis* and *An. (Ano.)* sp. None of these species has been considered a primary vector with the exception of *?aquasalis* which occurs in relatively low numbers. For these reasons, *nuneztovari*, a known or suspected vector in other countries of northern South America, should be carefully investigated as a potential vector in Para, Brazil.

**DISTRIBUTION** (pl. 10). *An. nuneztovari* occurs throughout most of Amazonia; it is also found in northern Colombia and Venezuela, and eastern Panama. It is not known how far south it occurs in Colombia and Venezuela, nor how far west in Amazonia. Cerqueira's report (1943) of *goeldii* from Bolivia may refer to *trinkae* or *nuneztovari*.

## 12. *Anopheles (Nyssorhynchus) strodei* Root 1926

Plates 8, 12, 22

**DISCUSSION.** *An. strodei* can be distinguished from the other Amazonian species of the Albimanus Section in the female (except for occasionally *evansi*) by the combination of (1) palpo-mere 4 often with a narrow brown stripe on ventral surface, (2) light scales on coxae usually white or very light cream, (3) foretarsomeres 2 and 3 cream to white in apical 0.25 (0.18-0.35) and 0.5 (0.25-0.80) respectively, (4) foretarsomere 5 usually entirely golden to brown or with a few light apical scales, rarely with apical 0.5 lighter than basal 0.5, (5) midtarsomere 5 usually with a small cream band in less than apical 0.3, (6) hindtarsomere 2 brown in basal 0.35-0.45 (0.3-0.5), (7) light wing spots usually white, occasionally very light cream on vein C, (8) basal dark spot of vein C small, humeral light spot 2.0-4.0 (1.2-4.1) of basal dark spot, (9) subcostal light spot of vein C 0.25-0.50 of subcostal dark spot and (10) abdomen with dark caudolateral tuft scales large and cuneate; in the male genitalia by (1) ventral claspette large, about 0.5 length of gonocoxite, (2) apex of ven-

tral claspette very wide, width at apex 0.5-0.6 length of claspette, without spicules, more or less truncate, rugose or deeply striated, strongly expanded laterally into large rounded lobe that is convex on basal and lateral margins and weakly concave on apical margin, (3) spicules along basal margin of basal lobule of ventral claspette long, 2.0-3.5 width of aedeagus, (4) spicules on lateral margins of ventral claspette extending toward apex only to base of apicolateral lobes, (5) preapical plate of ventral claspette moderate, oval to circular, weakly to moderately sclerotized, moderately well defined and (6) apex of aedeagus without leaflets, slightly longer than wide; and in the larva by the combination of (1) setae 2,3-C single and barbed, setae 2-C closely approximated, clypeal index about 3.0-4.0, (2) seta 4-C 1-4 branched, small to moderately small, usually not extending to near or beyond insertion of 2-C, (3) collar moderately thin dorsomedially, heavily pigmented, (4) setae 1,2-P rarely sharing common tubercle, palmate seta 1-P with 13-17 narrow, acuminate leaflets, 2-P 16-23 branched (16-24), (5) seta 1-M 31-35 branched, ovate in outline, apical branches much shorter than lateral, (6) seta 13-V very large, extending beyond caudal margin of segment and (7) seta 1-X inserted on saddle near ventral margin, or rarely on ventral margin at base of indentation. Foretarsomere 5 in the adults is usually of uniform color, which is unique in the Oswaldoi Subgroup; however, occasionally it is 0.5 apically light, 0.5 basally dark.

The closest ally to *strodei* is *rondoni*. The male genitalia of *strodei* and *rondoni* are almost identical, except that in *rondoni* the setae on the ventral claspette do not extend toward the apex as far as the base of the apicolateral lobes.

**BIONOMICS.** The immatures of *strodei* occur predominantly in ground pools; in addition, the immatures have been collected from animal tracks, ponds, lakes, swamps, stream margins, pot-holes, marshy depressions, ditches, seepage areas and rock holes. *An. strodei* is found only in fresh water, usually in full sun or partial shade but occasionally in deep shade. It occurs over a wide range of elevations, from near the coast to altitudes of 1600 m (Unti 1941). It is commonly found in mountainous areas, plains and plateaus in the interior. The immatures usually are associated with abundant vegetation such as grasses and algae.

The adult females of *strodei* are exophilic, feeding predominantly on mammals other than humans. They only rarely enter houses to feed. In Brazil, Deane, Causey and Deane (1948) collected 1895 adults of *strodei* of which only one was from inside a house. Kumm, Komp and Ruiz (1940) in Costa Rica and Rozeboom (1938) in Panama occasionally found *strodei* inside houses, but usually *strodei* showed a preference for animals and fed outside. The only exception is a paper in which Correa (1938) reported a very high density of *strodei* inside houses at the Fazenda Santa Alice, Sao Paulo, Brazil; 165 females of *strodei* were collected inside houses, which represented 95.3% of all the anophelines captured. In host preference studies using a human and a horse as bait in Alagadico, Brazil, 1942, Deane, Causey and Deane (1948) collected 17 females of *strodei* on the human and 23 on the horse during the crepuscular hours.

**MEDICAL IMPORTANCE.** *An. strodei* does not seem to be an important vector of malaria. It has been incriminated only once as transmitting malaria, and that was by Correa (1938) at the Fazenda Santa Alice, Sao Paulo, Brazil. In that study Correa dissected 163 females collected inside houses and found 2 of them (1.2%) naturally infected with oocysts. Galvao and Lane (1937), Galvao (1938), and Fonseca and Unti (1943) have easily and successfully experimentally infected *strodei* with *Plasmodium vivax*.

**DISTRIBUTION** (pl. 8). *An. strodei* is widely distributed throughout Central America and much of South America east of the Andes. Its northernmost limit is reported to be the state of Veracruz, Mexico, on the Gulf of Mexico; on the Pacific side it is reported from as far north as the border of Costa Rica and Nicaragua. In South America, it is found in northern and eastern Colombia, Venezuela, the Guianas, Brazil, Bolivia, Paraguay and northern Argentina. *An. strodei* occurs along the eastern slope of the Andes in Colombia, Bolivia and northern Argentina; it is presumably also found in eastern Ecuador and Peru, although there are no records. It is not known if it occurs on the Pacific slope of the Andes, although it is reported to occur in the Magdalena River drainage sys-



tem in northern Colombia. The southernmost limit east of the Andes is in the province of Buenos Aires, Argentina. *An. strodei* does not occur on any of the Caribbean islands including Trinidad and Tobago.

### 13. *Anopheles (Nyssorhynchus) rondoni* (Neiva & Pinto 1922)

Plates 8, 12

**DISCUSSION.** We have not included *rondoni* in the keys because it is reportedly very rare in Amazonia, and because no material was available from this region for study (see below and distribution section). The specimens of *rondoni* we examined from Argentina, Bolivia and Paraguay can be distinguished from other Amazonian species in the Albimanus Section in the **female** by (1) pre-scutellar space large, subtriangular, very dark brown to black, (2) foretarsomere 3 light in apical 0.3-0.5, (3) hindtarsomere 2 with a large dark band in basal 0.65-0.85, (4) hindtarsomere 3 with a dark band in basal 0.20-0.35, (5) vein C predominantly dark, subbasal, presectoral and sectoral dark spots fused into a very long, dark spot, occasionally with a few, interspersed, light scales, apical dark spot relatively large, (6) vein  $R_2$  with large preapical dark spot and (7) the preapical dark spot of vein M extending uninterrupted onto  $M_{1+2}$ ; and in the **male genitalia** by the combination of (1) ventral claspette similar to *strodei*, except that spicules usually on basal lobule only, not extending toward apex to base of apicolateral lobe, (2) apex of ventral claspette strongly expanded laterally into large rounded apicolateral lobe which appears slightly heavier than in *strodei* and (3) preapical plate moderate, circular to oval, very weakly sclerotized and ill defined.

*An. rondoni* is the sister species of *strodei*. The male genitalia of these 2 species are almost identical with the exception of the characters mentioned above. Although we did not have the opportunity to study the larva of *rondoni*, several authors (Davis 1933; Galvao 1940; Correa and Ramos 1943) report that the larva is similar to that of *strodei*, differing only in that *rondoni* has (1) fewer branches on seta 1-P (11-14), (2) fewer branches on palmate seta 1-I-VII (20-24) and (3) fewer teeth on pecten.

**BIONOMICS.** Most of this discussion is from the work of Davis and Shannon (1928) on the bionomics of *rondoni* in and around the city of Ledesma, in the villages of Canitas and Calilegua, Jujuy, Argentina, from March 1926 until May 1927. Davis and Shannon first discovered the immatures of *rondoni* along the margin of a reservoir in Ledesma. They soon found that a shallow ditch adjacent to a reedy swamp behind the reservoir was a highly favored aquatic habitat of *rondoni*. Out of that ditch 100 larvae were collected from which 75 adults emerged: 72 were *rondoni*, 2 were *An. (Ano.) pseudopunctipennis* and one was *An. (Nys.) tarsimaculatus*. Later Davis and Shannon encountered the immatures of *rondoni* in clear water, such as in ditches, drying pools along the edges of swamps, a puddle in a road and in heavy growths of grass in a flooded meadow; the aquatic habitats sometimes had considerable detritus, but not algae. The type-specimens were collected on the right margin of the Paraguay River, and later material was collected on the left margin of the S. Lourenco River.

The adults are usually active early in the evening. On one occasion 120 females were collected on a horse, between 1730 and 1800 h, flight commencing while it was still daylight (Davis and Shannon 1928). The females are commonly found inside houses (Shannon and Del Ponte 1927; Davis and Shannon 1928; Pinto 1939). Of 1266 anophelines collected in houses in the area of Ledesma, 118 or 9.3% were *rondoni*. Davis and Shannon concluded that *rondoni* is not as domestic as *pseudopunctipennis*, "but still is found in houses in appreciable numbers."

**MEDICAL IMPORTANCE.** *An. rondoni* has never been incriminated as a vector of malaria. During the malaria season in Jujuy, Davis and Shannon (1928) dissected 88 individuals and all were negative. In 3 different experiments, Davis and Shannon unsuccessfully attempted to infect *rondoni* with *Plasmodium falciparum*, *P. vivax* and *P. malariae*. Shannon and Del Ponte (1927) reported that

Davis was able to infect *rondoni* experimentally; however, we have not found any other reference to that work.

**DISTRIBUTION** (pl. 8). *An. rondoni* occurs primarily in southern and southeastern South America. In Amazonia it has been reported from southern Amazonas, Rondonia and Acre near the Brazil-Bolivian border (Deane, Causey and Deane 1948; Cerqueira 1961). In other states of Brazil, *rondoni* has been reported from Goias, Mato Grosso, Parana, Sao Paulo, Santa Catarina and Rio Grande do Sul. In Bolivia it is known in the departments of Santa Cruz, Beni and Tarija (Cerqueira 1943; Gabaldon and Cova Garcia 1952). The southern distributional limit is in northern Argentina where it has been reported in the provinces of Chaco, Corrientes, Formosa, Misiones, Salta, Santa Fe and Tucuman (Garcia and Ronderos 1962).

#### 14. *Anopheles (Nyssorhynchus) benarrochi* Gabaldon, Cova Garcia & Lopez 1941

Plates 8, 12, 23

**DISCUSSION.** The adult female of *benarrochi* is very similar to that of *aquasalis* and, to a lesser extent, to that of *strodei*. In order to correctly identify these 3 species, the characters given below must be correlated and compared with those given in the discussion sections of the latter 2 species. It must be emphasized that the number of specimens of *benarrochi* available for study was not large. For this reason great care must be taken in identifying the adult female. *An. benarrochi* can be distinguished from the other Amazonian species of the Albimanus Section in the female (except for occasionally *aquasalis*) by the combination of (1) palpomere 4 usually with a row of brown scales on ventral surface, (2) light scales on coxae usually white, (3) foretarsomere 3 with a white band in apical 0.5-0.8, (4) hindtarsomere 2 brown in basal 0.40-0.55 (0.36-0.55), (5) light wing spots cream on anterior veins and white on posterior veins, (6) vein C with humeral light spot about 2.5 or more of basal dark spot, (7) vein R with presectoral and sectoral dark spots moderately small, (8) vein M mostly white, sectoral dark spot present or absent, (9) apical light fringe spot large, unbroken or broken by a few dark scales and (10) dark spots on veins R<sub>3</sub>, M<sub>1+2</sub> and M<sub>3+4</sub>, and Cu subcostal dark spot and A subbasal dark spot often indistinct; in the male genitalia by the combination of (1) ventral claspette small, about 0.33 length of gonocoxite, apex wide, width at apex about 0.5 length of claspette, (2) apex of ventral claspette rugose, moderately expanded laterally with apicolateral margin sharply angled and moderately pointed, appearing truncate or with a median sulcus, (3) spicules on ventral claspette extending toward apex to or nearly to base of apicolateral lobe, (4) preapical plate of ventral claspette small, circular, heavily sclerotized and (5) basal lobules of ventral claspette narrow, curving mesad, with spicules along basal margin about equal to or slightly longer than width of aedeagus; and in the larva by the combination of (1) seta 2-C single and barbed, 3-C plumose with moderately long branches in about apical 0.5, setae 2-C widely spaced, clypeal index about 1.4, (2) seta 4-C small, (3) collar moderately narrow dorsomedially, heavily pigmented, (4) seta 1-A of antenna 5-9 branched, long, at least 2.0 width of antenna at point of insertion, (5) setae 1,2-P not sharing a common sclerotized tubercle, (6) seta 13-IV 10-13 branched (6-13), small, (7) lateral arm of median plate of spiracular apparatus moderately long and thick and (8) seta 1-X moderately short, as long as or slightly longer than saddle, inserted on saddle, on or very near ventral margin.

The closest allies of *benarrochi* are *rondoni* and *strodei*, with which it shares in the male genitalia the nonspiculose, laterally expanded apicolateral lobes and the rugose apical margin of the ventral claspette.

**BIONOMICS.** Very little is known about the natural history of *benarrochi*. The immatures have been collected in stagnant ground pools, abandoned wells and small streams, either exposed to the full sun or partial shade, and in water containing a large amount of organic material (Deane, Causey and Deane 1948; Cerqueira 1961). *An. benarrochi* is not found in the lower Amazon basin,

and no place is it encountered in great abundance (Deane, Causey and Deane 1948).

The females rarely enter houses, and they feed primarily on animals. Of 545 adults of *benarrochi* collected by Deane, Causey and Deane (1948), only 46 or 8.4% were from inside houses. Elliott (1972) reports that the peak hours of biting for the females in Peru are between 1800-2000 h and 0400-0600 h, which correlates with the observation of Deane, Causey and Deane (1948) that *benarrochi* is crepuscular.

**MEDICAL IMPORTANCE.** *An. benarrochi* has never been implicated as a vector of malaria. Deane, Causey and Deane (1948) dissected 31 blood-fed females and found none infected with *Plasmodium*.

**DISTRIBUTION** (pl. 8). *An. benarrochi* is limited primarily to the Orinoco basin and the eastern versant of the Andes, including the llanos plateau region of Colombia, parts of the upper Amazon in Brazil (Rondonia, Acre, Amazonas) and Loreto, Peru.

### 15. *Anopheles (Nyssorhynchus) triannulatus* (Neiva & Pinto 1922)

Plates 8, 12, 24

**DISCUSSION.** The monotypic *Triannulatus* Subgroup can be distinguished from other Amazonian species of the *Albimanus* Section in the female by (1) anterior mesanepimeron (Mam) with a conspicuous patch of silver to white, cuneate scales, (2) palpomere 4 with mediolateral surface having a reduced number of light scales, (3) foretarsomere 4 with a light band in apical 0.55 (0.40-0.65), (4) foretarsomere 5 predominantly dark, occasionally with a few apical golden scales, (5) hindtarsomere 2 dark in basal 0.5 (0.4-0.7), (6) vein C with large dark spots, light spots occasionally obsolete, humeral light spot small, 0.5-1.3 length of basal dark spot, apical dark spot moderately large and conspicuous and (7) vein M with sectoral dark spot usually very large, often 0.7 length of vein; in the male genitalia by (1) ventral claspette without spicules, apicolateral margins produced into 2 large, striated, auriculate, laterally projecting lobes, (2) preapical plate of ventral claspette small, oval, heavily sclerotized and (3) aedeagus long, subequal to length of ventral claspette, with apex about 1.5 as long as wide; and in the larva by the combination of (1) setae 2-C single, and simple or barbed, widely spaced, clypeal index about 1.3, (2) collar narrow dorsomedially, heavily pigmented, (3) palmate seta 1-P with 15-20 (13-20) very narrow to narrow, lanceolate leaflets, leaflets not overlapping with leaflets of 1-P of opposite side, 2-P 16-23 branched, arising from a small pigmented tubercle, (4) seta 14-P 11-14 branched (9-15) from an elongated, flattened shaft, (5) seta 11-I 5-7 branched (3-7), large, and 13-I 2-4 branched, large, (6) seta 13-III,IV 4-6 branched (3-7), large, (7) tergal plate of segment VII large, about 2.0 size of tergal plate VI and (8) lateral arm of median plate of spiracular apparatus long, laterally directed.

**BIONOMICS.** The immatures of *triannulatus* are most commonly collected in permanent ponds, lakes, canals, slow streams or river margins, ditches, and swamps, either exposed to the full sun or partial shade. Occasionally *triannulatus* is collected in semipermanent and temporary rock holes, small ground pools, and animal tracks. The immatures are found in clear, fresh water, never brackish, and are usually associated with *Pistia stratiotes*. Other commonly associated aquatic plants are species of *Eichhornia*, *Azolla*, *Utricularia*, *Jussiaea*, *Elodea* and *Salvinia*.

The adult females are primarily exophilic and zoophilic. They are rarely found inside houses. In French Guiana, Floch and Abonnenc (1944) collected 2102 anophelines in houses, of which 6 were *triannulatus*. Deane, Causey and Deane (1948) reported that of 15,583 specimens of *triannulatus* collected, only 714 or 4.6% were taken in houses. They stated that *triannulatus* feeds outside, although it will readily feed on man. Rozeboom (1938) in Panama found that only 0.5% of the anophelines in houses were *triannulatus*, and the females preferred to feed on pigs rather than humans. In contrast, Gabaldon (1949) reported collecting a large number of *triannulatus* inside a house in the Rio Apure region of Venezuela. Hill (1934) collected *triannulatus* in the area around

Maracay, Venezuela, in stables, houses, dairy farms, and a farm and an orphanage where malaria epidemics were a yearly occurrence. He performed precipitin tests on 262 blood-engorged females and found 14 had fed on man, 173 on horses and 38 on cattle; 37 did not react to the test. He concluded that *triannulatus* "definitely prefers animal blood."

**MEDICAL IMPORTANCE.** Throughout most of its range, *triannulatus* does not seem to be important as a vector of malaria. Only once *triannulatus* was found with a natural oocyst infection and that was in Cojedes, Venezuela (Gabaldon and Cova Garcia 1946a). Benarroch (1931) incriminated *triannulatus* as a possible vector of malaria at a boys' school near Maracay, Venezuela, as it was the most common species present during a malaria epidemic. Hill (1934) stated that when present in a high density, "it is probable that this species can act as a malaria transmitter."

Several investigators (Bonne and Bonne-Wepster 1925; Rozeboom 1935; Floch and Abonenc 1944; Fonseca and Unti 1943) have experimentally infected *triannulatus* with *Plasmodium vivax* and *P. falciparum*. In comparing the susceptibility of *triannulatus* to infection with *P. vivax* and *P. falciparum* with that of *albimanus*, Rozeboom (1935) found a larger percentage of specimens of *triannulatus* refractory to infection. Because of the feeding behavior and low susceptibility to plasmodial infection, *triannulatus* is probably not a serious health threat, except possibly when present in very large numbers.

**DISTRIBUTION** (pl. 8). *An. triannulatus* is widely distributed throughout South America east of the Andes as far south as the Argentine provinces of Chaco, Corrientes, Formosa, Jujuy, Salta, Santa Fe, Tucuman and Misiones. East of the Andes, it occurs throughout Brazil, Paraguay, most of Bolivia, the Guianas, Colombia, Venezuela, Ecuador and Peru. On the Pacific side of the Andes, *triannulatus* extends as far south as Tumbes, Peru. It is found in Central America as far north as central Nicaragua.

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## REFERENCES

- Arnell, J. Hal  
1973. Mosquito Studies (Diptera, Culicidae). XXXII. A revision of the genus *Haemagogus*. Contrib. Am. Entomol. Inst. (Ann Arbor) 10(2):1-174.
- Arnett, Ross H., Jr.  
1950. Notes on the distribution, habits, and habitats of some Panama culicines (Diptera: Culicidae). J. N.Y. Entomol. Soc. 58:99-115.
- Barretto, Mauro P.  
1938. Observacoes sobre a ecologia do *A. darlingi* Root 1926, var. *paulistensis* Galvao, Lane & Correia 1937. Rev. Biol. Hyg. 9:116-132.
- Belkin, John N.  
1962. The mosquitoes of the South Pacific (Diptera, Culicidae). Berkeley, Univ. Calif. Press. 2 vol. 608 p., 412 plates.
- Benarroch, Elias I.  
1931. Studies on malaria in Venezuela. Am. J. Hyg. 14:690-693.
- Bonne, Cornelis and J. Bonne-Wepster  
1925. Mosquitoes of Surinam. R. Colon. Inst. Amst., Afd. Trop. Hyg. 13. 558 p.
- Boyd, Mark F.  
1926. Studies of the epidemiology of malaria in the coastal lowlands of Brazil, made before and after the execution of control measures. Am. J. Hyg., Monogr. Ser. 5. 261 p.
- Carvalho, Francisco Fiere de and R. G. Rachou  
1951. Consideracoes sobre a malaria no Estado do Rio de Janeiro com especial referencia ao Vale do Rio Pirai. Rev. Bras. Malariol. Doencas Trop. 3:473-485.
- Causey, Ottis R., M.P. Deane, O. da Costa and L.M. Deane  
1945. Studies on the incidence and transmission of filaria, *Wuchereria bancrofti*, in Belem. Am. J. Hyg. 41:143-149.
- Cerqueira, Nelson L.  
1943. Lista dos mosquitos da Bolivia (Diptera, Culicidae). Mem. Inst. Oswaldo Cruz Rio de J. 39:15-36.  
1961. Distribuicao geografica dos mosquitos da amazonia (Diptera, Culicidae, Culicinae). Rev. Bras. Entomol. 10:111-168.
- Charlwood, J.D. and T.J. Wilkes  
1979. Studies on the age-composition of samples of *Anopheles darlingi* Root (Diptera: Culicidae) in Brazil. Bull. Entomol. Res. 69:337-342.
- Correa, Renato R.  
1938. O *Anopheles (N) strodei* Root, 1926 como provavel vetor de malaria. Rev. Biol. Hyg. 9:104-109.  
1943. Os vetores de malaria no Estado de Sao Paulo. Arq. Hig. Saude Publica (Sao Paulo) 8(19):121-132.
- Correa, Renato R. and A.S. Ramos  
1942a. Os anofelinos da regio meridional do Estado de Sao Paulo. Arq. Hig. Saude Publica (Sao Paulo) 7(15):37-57.

- 1942b. Do encontro do *A. (N.) darlingi* Root, 1926, e do *A. oswaldoi* var. *metcalfi* Galvao e Lane, 1937, naturalmente infetados com os parasitas malaricos, na regio sul do Estado de Sao Paulo. Arq. Hig. Saude Publica (Sao Paulo) 7(15):379-387.
1943. Nota sistematica sobre *Anopheles (N.) rondoni* (Neiva e Pinto, 1922). Descricao do ovo (Diptera, Culicidae). Arq. Hig. Saude Publica (Sao Paulo) 8(19):135-137.
1944. Os anofelinos da Ilha de Santo Amaro. Arq. Hig. Saude Publica (Sao Paulo) 9(22): 9-16.
- Coutinho, Jose de Oliveira  
1943. Contribuicao para o estudo do *Anopheles (N.) tarsimaculatus* no Distrito Federal, Brasil. Arq. Hig. (Rio de J.) 13:65-77.
- Curry, Delferes P.  
1932. Some observations on the *Nyssorhynchus* group of the *Anopheles* (Culicidae) of Panama. Am. J. Hyg. 15:566-572.  
1934. Breeding of anopheline mosquitoes among aquatic vegetation of Gatun Lake, accompanied by periodic long flights of *A. albimanus* Wied. South. Med. J. 27:644-651.
- Darling, Samuel T.  
1910. Factors in the transmission and prevention of malaria in the Panama Canal Zone. Ann. Trop. Med. Parasitol. 4:179-224.
- Davis, Nelson C.  
1927. *Anopheles pseudopunctipennis* as a malaria transmitter in northern Argentine Republic. Am. J. Trop. Med. 7:167-176.  
1931. A note on the malaria-carrying anophelines in Belem, Para and in Natal, Rio Grande do Norte, Brazil. Riv. Malariol. 10:43-51.  
1933. Notes on some South American mosquitoes. Ann. Entomol. Soc. Am. 26:277-295.
- Davis, Nelson C. and H.W. Kumm  
1932. Further incrimination of *Anopheles darlingi* Root as a transmitter of malaria. Am. J. Trop. Med. 12:93-95.
- Davis, Nelson C. and R.C. Shannon  
1928. The habits of *Anopheles rondoni* in the Argentine Republic. Am. J. Hyg. 8:448-456.
- Deane, Leonidas M.  
1947. Observacoes sobre a malaria na Amazonica brasileira. Rev. Braz. Serv. Espec. Saude Publica 1:1-60.
- Deane, Leonidas M., O.R. Causey and M.P. Deane  
1946. An illustrated key by adult female characteristics for identification of thirty-five species of Anophelini from Northeast and Amazon regions of Brazil, with notes on the malaria vectors (Diptera, Culicidae). Am. J. Hyg., Monogr. Ser. 18:1-18.  
1948. Notas sobre a distribuicao e a biologia dos anofelinos das regioes Nordeste e Amazonica do Brasil. Rev. Braz. Serv. Espec. Saude Publica 1:827-965.
- Deane, Leonidas M. and R.G. Damasceno  
1948. Altura de pouso das femeas de *Anopheles darlingi* e de *Anopheles aquasalis* nas paredes internas das casas. Rev. Braz. Serv. Espec. Saude Publica 2:501-508.
- Deane, M.P., O.R. Causey and L.M. Deane  
1946. An illustrated key by larval characteristics for the identification of thirty-two species of Anophelini from the Northeast and Amazon regions of Brazil, with descriptions of two larvae. Am. J. Hyg., Monogr. Ser. 18:35-50.
- Downs, Wilbur G., H.P.S. Gillette and R.C. Shannon  
1943. A malaria survey of Trinidad and Tobago, British West Indies. J. Natl. Malariol. Soc., Suppl. 2(1). 44 p.

- Earle, Walter C.  
1936. The relative importance of *Anopheles tarsimaculatus*, *Anopheles argyritarsis*, and *Anopheles pseudopunctipennis* as vectors of malaria in the Windward group of the West Indies. *Am. J. Trop. Med.* 16:459-469.
- Elliott, R.  
1968. Studies on man-vector contact in some malarious areas in Colombia. *Bull. W H O* 38: 239-253.  
1972. The influence of vector behavior on malaria transmission. *Am. J. Trop. Med. Hyg.* 21:755-763.
- Faran, Michael E.  
1980. Mosquito Studies (Diptera, Culicidae). XXXIV. A revision of the Albimanus Section of the subgenus *Nyssorhynchus* of *Anopheles*. *Contrib. Am. Entomol. Inst. (Ann Arbor)* 15(7):1-215.  
1981. Synonymy of *Anopheles (Nyssorhynchus) noroestensis* with *An. (Nys.) evansi*, with a description of the male genitalia of the lectotype of *An. (Nys.) evansi* (Diptera: Culicidae). *Mosq. Syst.* 13:86-91.
- Fauran, Pierre  
1962. II.—Compte rendu d'une etude entomologique effectuee en Guadeloupe. *Arch. Inst. Pasteur Guadeloupe* 1961:70-89.
- Floch, Herve  
1954. Exophilie des *Anopheles* et transmission residuelle du paludisme. *Arch. Inst. Pasteur Guyane Fr., Publ.* 346. 7 p.  
1956. La lutte antipaludique en Guyane Francaise. Notre huitieme campagne de pulverisations d'insecticides a effet remanent dans les habitations. *Arch. Inst. Pasteur Guyane Fr., Publ.* 404. 80 p.
- Floch, Herve and E. Abonnenc  
1943. Sur le role de *A. darlingi* Root 1926 dans la transmission du paludisme en Guyane Francaise. *Inst. Pasteur Guyane Territ. Inini, Publ.* 71. 10 p.  
1944. *A. triannulatus* Neiva et Pinto en Guyane Francaise. Morphologie des oeufs et infection experimentale par *P. falciparum* et *P. vivax*. *Inst. Pasteur Guyane Territ. Inini, Publ.* 77. 7 p.  
1947. Distribution des *Anopheles* en Guyane Francaise. *Inst. Pasteur Guyane Territ. Inini, Publ.* 144. 9 p.  
1951. *Anopheles* de la Guyane Francaise. *Arch. Inst. Pasteur Guyane Territ. Inini, Publ.* 236. 91 p.
- Fonseca, J.A.B. da and F. da Fonseca  
1942. Transmissao da malaria humana por anofelinos da serie tarsimaculatus. *Mem. Inst. Butantan (Sao Paulo)* 16:93-124.
- Fonseca, J.A.B. da and O. Unti  
1943. Infeccao experimental de anofelinos de regioes indenes a malaria. *Folia Clin. Biol.* 15:43-52.
- Foote, Richard H. and D.R. Cook  
1959. Mosquitoes of medical importance. *U.S. Dep. Agric., Agric. Handb.* 152. 158 p.
- Forattini, Oswaldo P.  
1962. *Entomologia Medica*. Vol. 1. Sao Paulo, Fac. Hig. Saude Publica. 662 p.
- Gabaldon, Arnoldo  
1949. Malaria incidence in the West Indies and South America. *In* Boyd, Mark F., ed. *Malariology*. Phila., W.B. Saunders Co. 1:764-787.  
1972. Difficulties confronting malaria eradication. *Am. J. Trop. Med. Hyg.* 21:634-639.

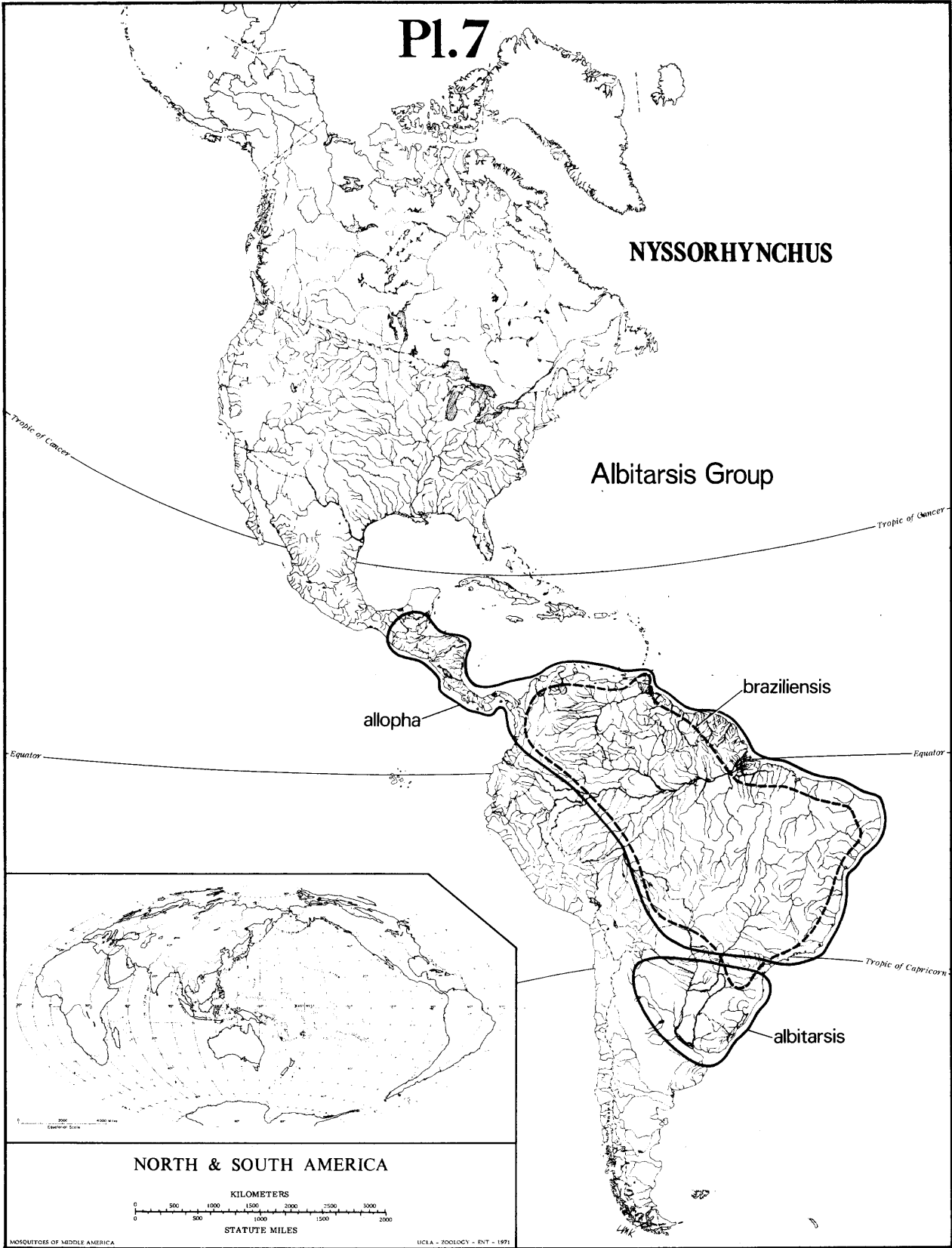
- Gabaldon, Arnaldo and P. Cova Garcia  
 1946a. Zoogeografia de los anofelinos en Venezuela: I. Los dos vectores principales. Tijer-  
 etazos Sobre Malar. 10:19-32.  
 1946b. Zoogeografia de los anofelinos en Venezuela: II. Los vectores secundarios y los no  
 vectores. Tijeretazos Sobre Malar. 10:78-127.  
 1952. Zoogeografia de los anofelinos en Venezuela. IV. Su posicion en la region Neotro-  
 pica y observaciones sobre las especies de esta region. Rev. Sanid. Assist. Soc. 17:171-  
 209.
- Gabaldon, Arnaldo and L. Guerrero  
 1959. An attempt to eradicate malaria by weekly administration of pyrimethamine in areas  
 of out-of-doors transmission in Venezuela. Am. J. Trop. Med. Hyg. 8:433-439.
- Galvao, A.L. Ayroza  
 1938. Sobre a infeccao experimental do *Anopheles strodei* pelo *Plasmodium vivax*. Rev.  
 Biol. Hyg. 9:133-134.  
 1940. Contribuicao ao conhecimento dos anofelinos do grupo *Nyssorhynchus* de Sao Paulo  
 e regioes vizinhas (Diptera, Culicidae). Arq. Zool. Estado Sao Paulo 1:399-484.
- Galvao, A.L. Ayroza and J. Lane  
 1937. Notas sobre os *Nyssorhynchus* de S. Paulo. IV. Sobre a infeccao experimental do  
*Anopheles albitarsis* e *A. strodei* da cidade de Sao Paulo, pelo *Plasmodium vivax*. Folia  
 Clin. Biol. 3:65-69.
- Galvao, A.L. Ayroza, J. Lane and R.R. Correa  
 1937. Notas sobre os *Nyssorhynchus* de S. Paulo. V. Sobre os *Nyssorhynchus* de Novo  
 Oriente. Rev. Biol. Hyg. 8:37-45.
- Garcia, Miguel and R.A. Ronderos  
 1962. Mosquitos de la Republica Argentina. I. Tribu Anophelini (Diptera-Culicidae- Culi-  
 cinae). An. B. Aires Com. Invest. Cient., B. Aires (Prov.) 3:103-212.
- Giglioli, George  
 1948. The transmission of *Wuchereria bancrofti* by *Anopheles darlingi* in the American trop-  
 ics. Am. J. Trop. Med. 28:71-85.  
 1959. Fifteen years experience in malaria eradication in British Guiana. Maintenance poli-  
 cies and residual problems. Riv. Parassitol. 20:279-288.  
 1963. Ecological change as a factor in renewed malaria transmission in an eradicated area.  
 A localized outbreak of *A. aquasalis*-transmitted malaria on the Demerara River estu-  
 ary, British Guiana, in the fifteenth year of *A. darlingi* and malaria eradication. Bull.  
 W H O 29:131-145.
- Gillies, M.T.  
 1958. A modified technique for the age-grading of populations of *Anopheles gambiae*.  
 Ann. Trop. Med. Parasitol. 52:261-273.
- Godoy, Alcides and C. Pinto  
 1923. Estudos sobre malaria. Braz.-Med. 37:29-33.
- Hamon, Jacques J., J. Mouchet, J. Brengues and G. Chauvet  
 1970. Problems facing anopheline vector control. Vector ecology and behavior, during, and  
 after application of control measures. Misc. Publ. Entomol. Soc. Am. 7:28-41.
- Harbach, Ralph E. and K.L. Knight  
 1980. Taxonomists' glossary of mosquito anatomy. Plexus Publ., Inc., Marlton, NJ. 415 p.
- Hill, Rolla B.  
 1934. Feeding habits of some Venezuelan *Anopheles*. Am. J. Trop. Med. 14:425-429.
- Horsfall, William R.  
 1955. Mosquitoes. Their bionomics and relation to disease. Ronald Press, NY. 723 p.

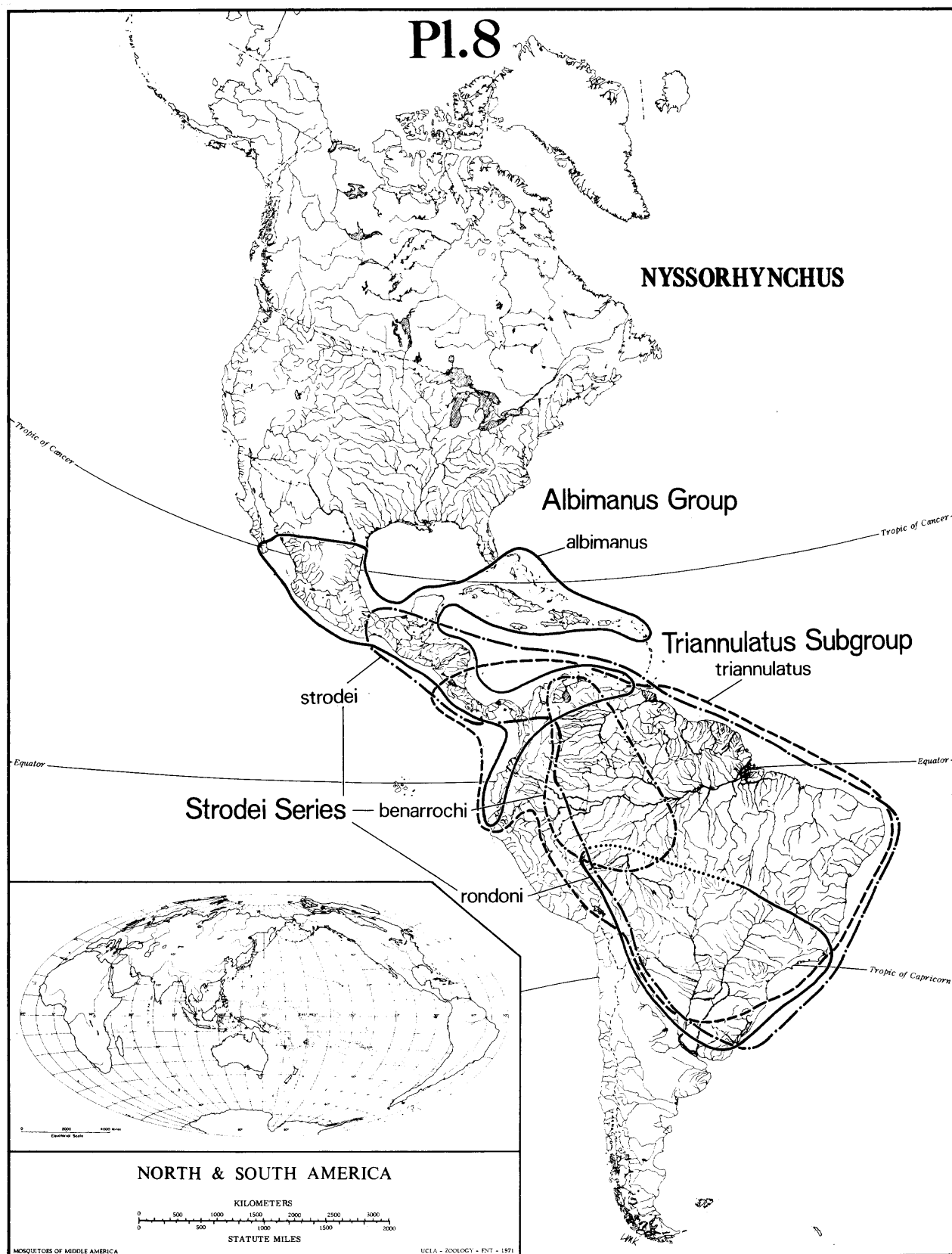


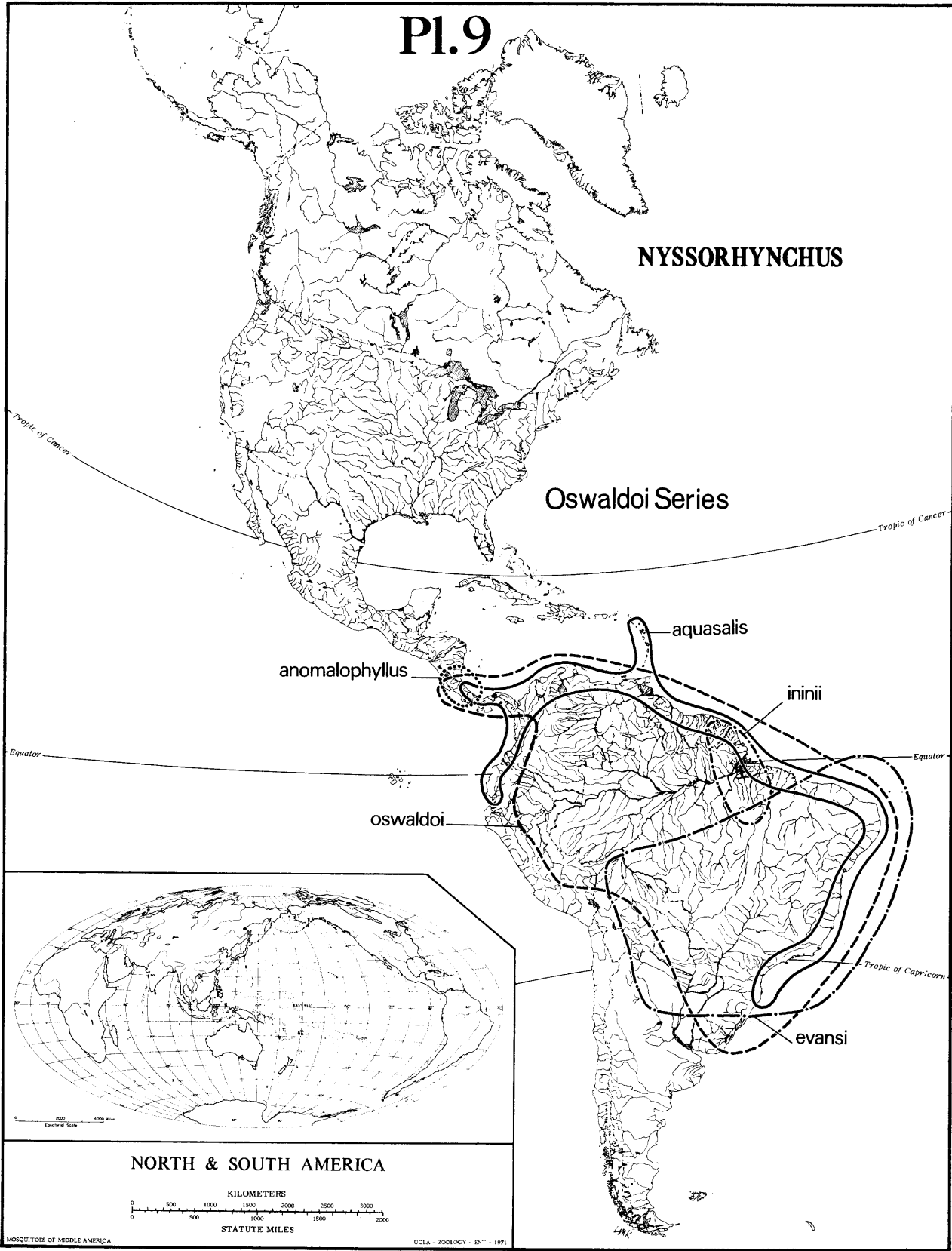
- Kenney, Michael  
1946. Inadequate house screening as a factor in malaria transmission. *J. Natl. Malariol. Soc.* 5:223-227.
- Knight, Kenneth L. and A. Stone  
1977. A catalog of the mosquitoes of the world (Diptera: Culicidae). Ed. 2. Entomol. Soc. Am. (Thomas Say Found., vol. 6), College Park, MD. 611 p.
- Kumm, Henry W., W.H.W. Komp and H. Ruiz  
1940. The mosquitoes of Costa Rica. *Am. J. Trop. Med.* 20:385-442.
- Lucena, Durval T. de  
1940. Os *Nyssorhynchus* de Pernambuco. II. *Anopheles (Nyssorhynchus) oswaldoi* var. *metcalfi* Galvao and Lane, 1937 muito provavel vetor da malaria em Pontesinha. *Folia Med.*, Rio de J. 1940:176-177.  
1946. Esboco ecologico do *Anopheles (N.) tarsimaculatus* Goeldi, 1905 no nordeste brasileiro. *An. Soc. Biol. Pernambuco* 6(1):3-40.
- Mattos, Synezio S. and S.H. Xavier  
1965. Distribuicao geografica dos culicineos do Brasil (Diptera, Culicidae). I—Estado do Goias. *Rev. Bras. Malariol. Doencas Trop.* 17:269-291.
- Meggers, Betty J.  
1977. Vegetational fluctuation and prehistoric cultural adaptation in Amazonia: some tentative correlations. *World Archaeol.* 8:287-303.
- Panday, Roy S.  
1977. *Anopheles nuneztovari* and malaria transmission in Surinam. *Mosq. News* 37:728-737.
- Pinto, Cesar  
1939. Disseminacao da malaria pela aviacao; biologia do *Anopheles gambiae* e outros anofelineos do Brasil. *Mem. Inst. Oswaldo Cruz Rio de J.* 34:293-430.
- Rachou, Rene G. and I. Ricciardi  
1951. Contribuicao ao conhecimento da distribuicao geografica dos anofelinos no Brasil: Estado do Parana (distribuicao por municipios e localidades). *Rev. Bras. Malariol. Doencas Trop.* 3:423-447.
- Rey, Hernando and S. Renjifo  
1950. *Anopheles (N) nunez-tovari* infectado en la naturaleza con *Plasmodium* sp. *Rev. Acad. Colomb. Cienc. Exactas Fis. Nat.* 7:534-538.
- Roberts, Donald R., W.D. Alecrim, A.M. Tavaris and K.M. McNeill  
1981. Observations on the vector ecology of *Anopheles darlingi* Root in Amazonia, Brazil. (In preparation.)
- Roberts, Donald R., A.L. Hoch and N.E. Peterson  
1981. A multidisciplinary program of infectious disease surveillance along the transamazon highway in Brazil. IV. Entomological surveillance. *Bull. Pan. Am. Health Organ.* (In press.)
- Root, Francis M.  
1926. Studies on Brazilian mosquitoes. I. The anophelines of the *Nyssorhynchus* group. *Am. J. Hyg.* 6:684-717.
- Root, Francis M. and J. Andrews  
1938. Malaria and anopheline survey of Grenada, B.W.I. *Am. J. Hyg.* 27:549-579.
- Rozeboom, Lloyd E.  
1935. Infection of *Anopheles bachmanni*, Petrocchi, with *Plasmodium vivax*, Grassi and Feletti, and observations on the bionomics of the mosquito. *Am. J. Trop. Med.* 15:521-528.

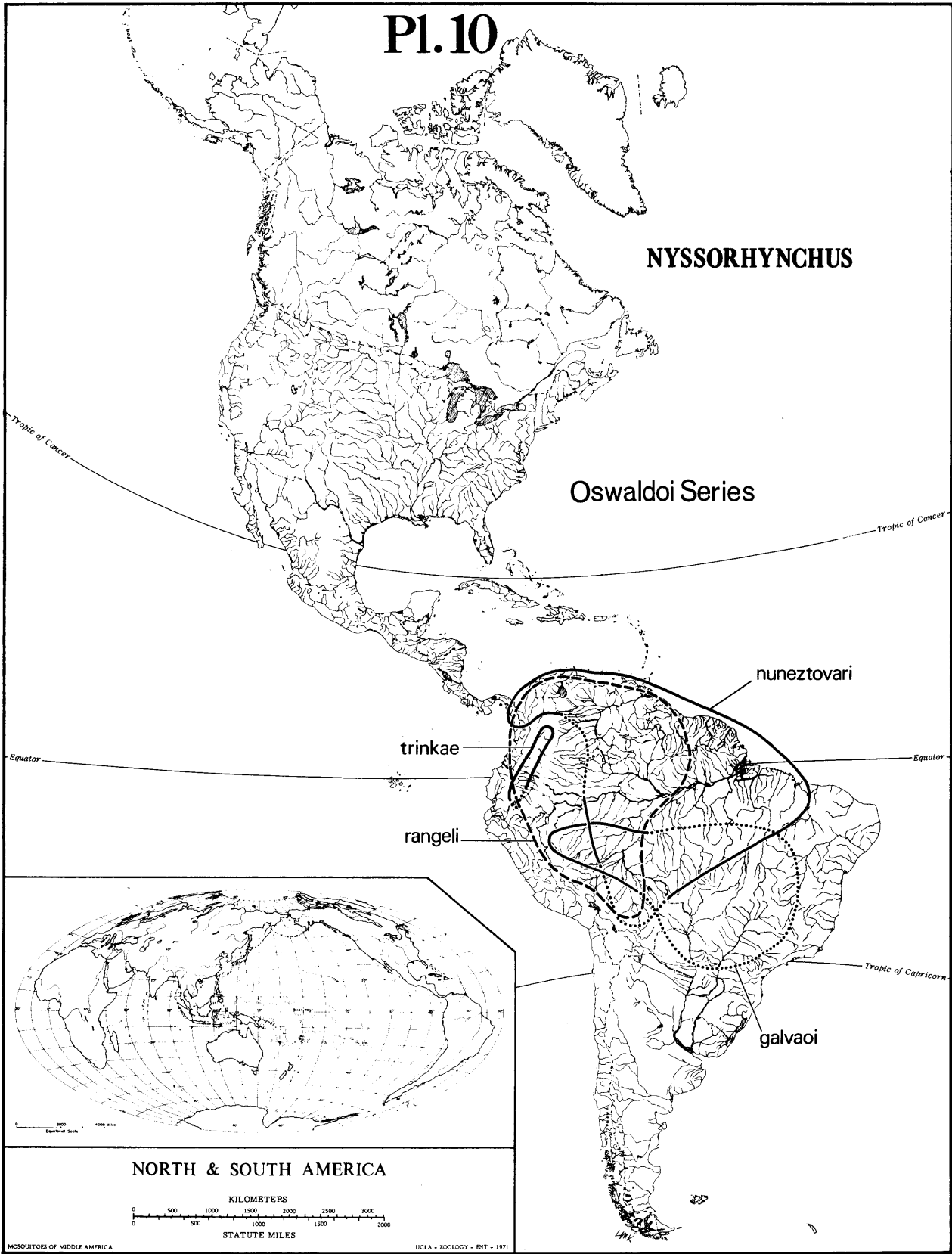
1937. On *Anopheles albitarsis* Lynch Arribalzaga in Panama. South Med. J. 30:590-591.
1938. The role of some common anopheline mosquitoes of Panama in the transmission of malaria. Am. J. Trop. Med. 18:289-302.
1941. Distribution and ecology of the *Anopheles* mosquitoes of the Caribbean region. Am. Assoc. Adv. Sci. Symp. Hum. Malar., p. 98-107. (Publ. 15).
1942. Subspecific variations among neotropical *Anopheles* mosquitoes, and their importance in the transmission of malaria. Am. J. Trop. Med. 22:235-255.
- Senevet, Georges and E. Abonnenc  
1938. Quelques anophelines de la Guyane Francaise. Arch. Inst. Pasteur Alger. 16:486-512.
- Senior-White, Ronald A.  
1951. Studies on the bionomics of *Anopheles aquasalis* Curry, 1932 (contd.). Part II. Indian J. Malariol. 5:465-512.
- Shannon, Raymond C.  
1931. The environment and behavior of some Brazilian mosquitoes. Proc. Entomol. Soc. Wash. 33:1-27.  
1933. Anophelines of the Amazon Valley. Proc. Entomol. Soc. Wash. 35:117-143.
- Shannon, Raymond C. and N.C. Davis  
1930. Observations on the Anophelini (Culicidae) of Bahia, Brazil. Ann. Entomol. Soc. Am. 23:467-505.
- Shannon, Raymond C. and E. Del Ponte  
1927. Informe de una investigacion preliminar sobre los anofeles del Rio Alto Parana, en la Argentina. Rev. Inst. Bacteriol. Malbran, B. Aires 4:706-723.
- Stage, H.H. and G. Giglioli  
1947. Observations on mosquito control in the Caribbean area. Part II. British Guiana. Mosq. News 7:73-76.
- Stephens, John W.W.  
1921. Malaria on a Venezuelan oilfield. Ann. Trop. Med. Parasitol. 15:435-444.
- Unti, Ovidio  
1941. Anofelinos do Vale do Rio Paraiba. *Anopheles (Nyssorhynchus) strodei* Root, 1926 com a descricao de tres variedades novas. Trab. Sao Paulo Serv. Profil. Malar. 33:3-18.
- Vargas, Luis and A. Martinez Palacios  
1950. Estudio taxonomico de los mosquitos anofelinos de Mexico. Mex., D.F., Secr. Salubr. Asist. 143 p.  
1955. Distribucion de los anofelinos de Mexico. Rev. Inst. Salubr. Enferm. Trop. 15:81-123.
- Zavortink, Thomas J.  
1973. Mosquito Studies (Diptera, Culicidae). XXIX. A review of the subgenus *Kerteszia* of *Anopheles*. Contrib. Am. Entomol. Inst. (Ann Arbor) 9(3):1-54.

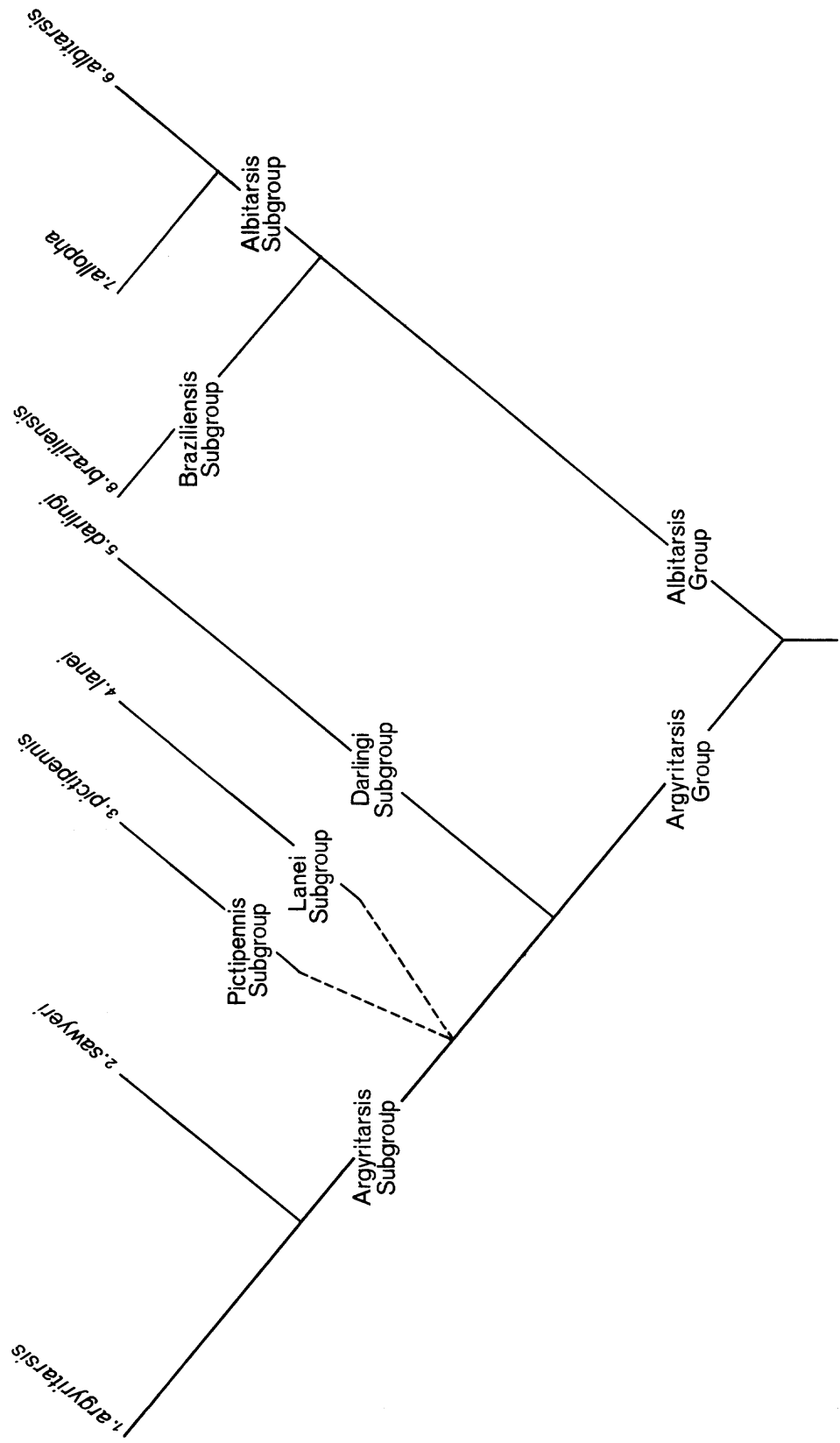






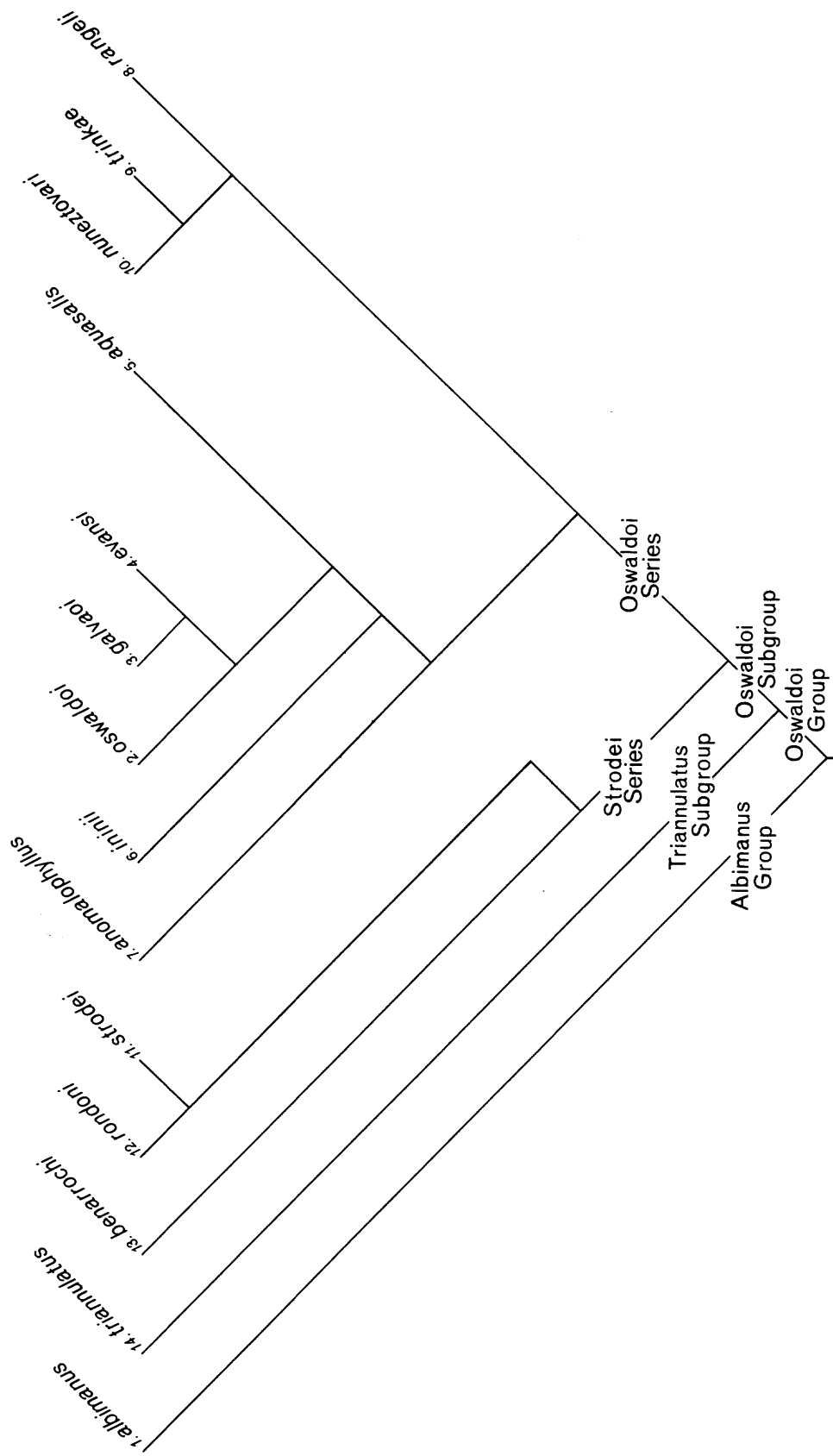






**Pl.11** Argyratarsis Section  
Hypothesized phylogenetic tree  
of the Argyratarsis Section

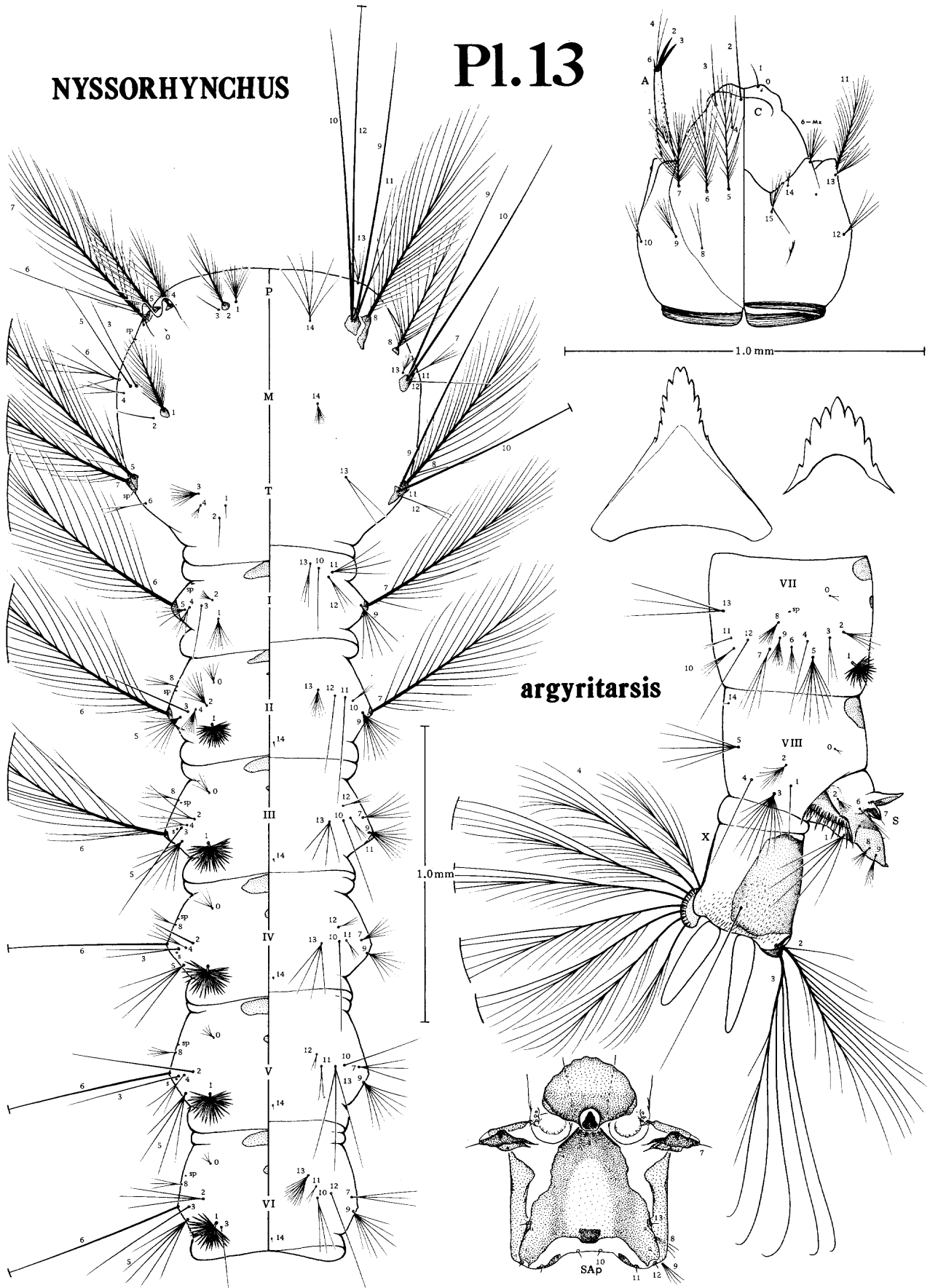


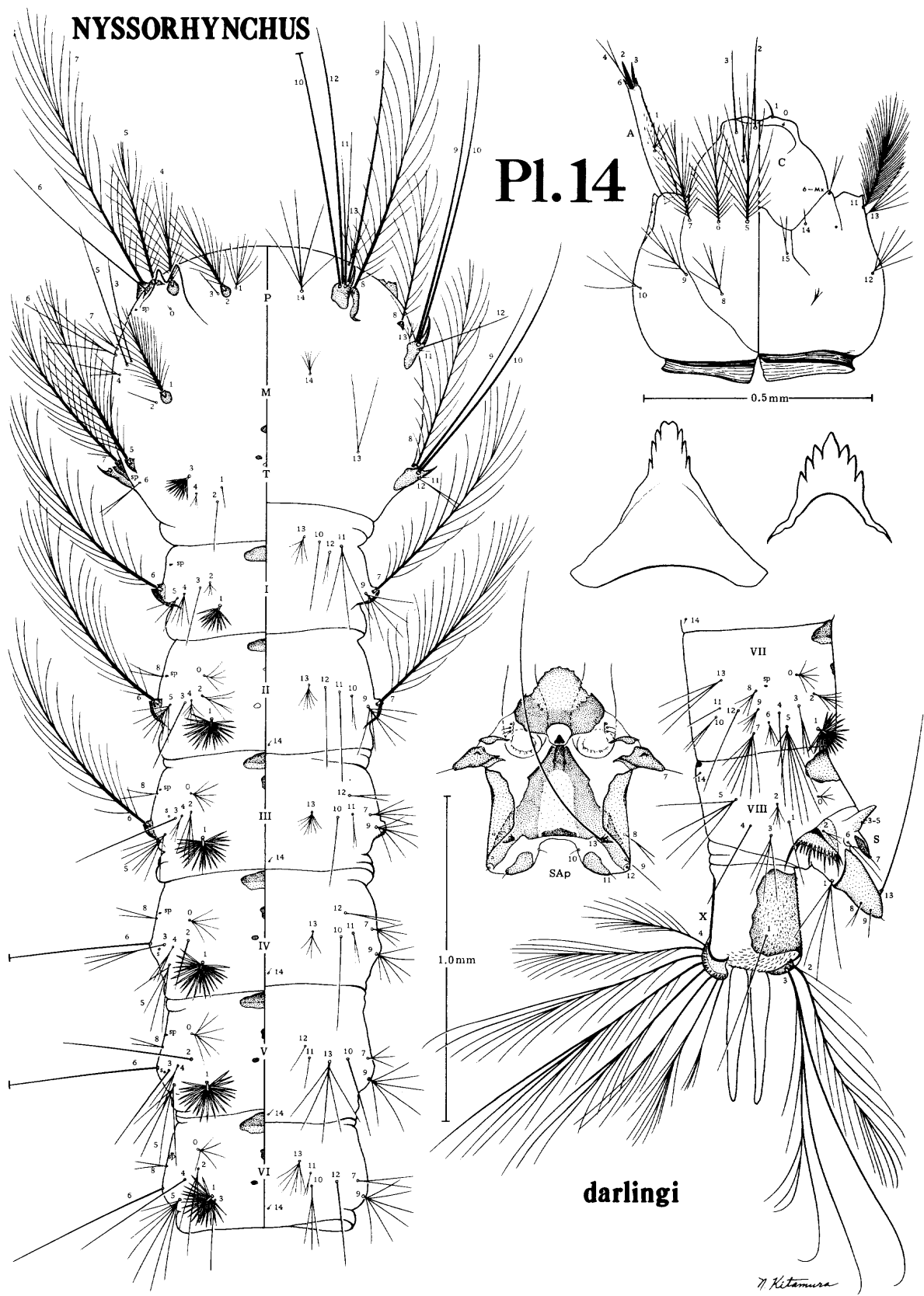


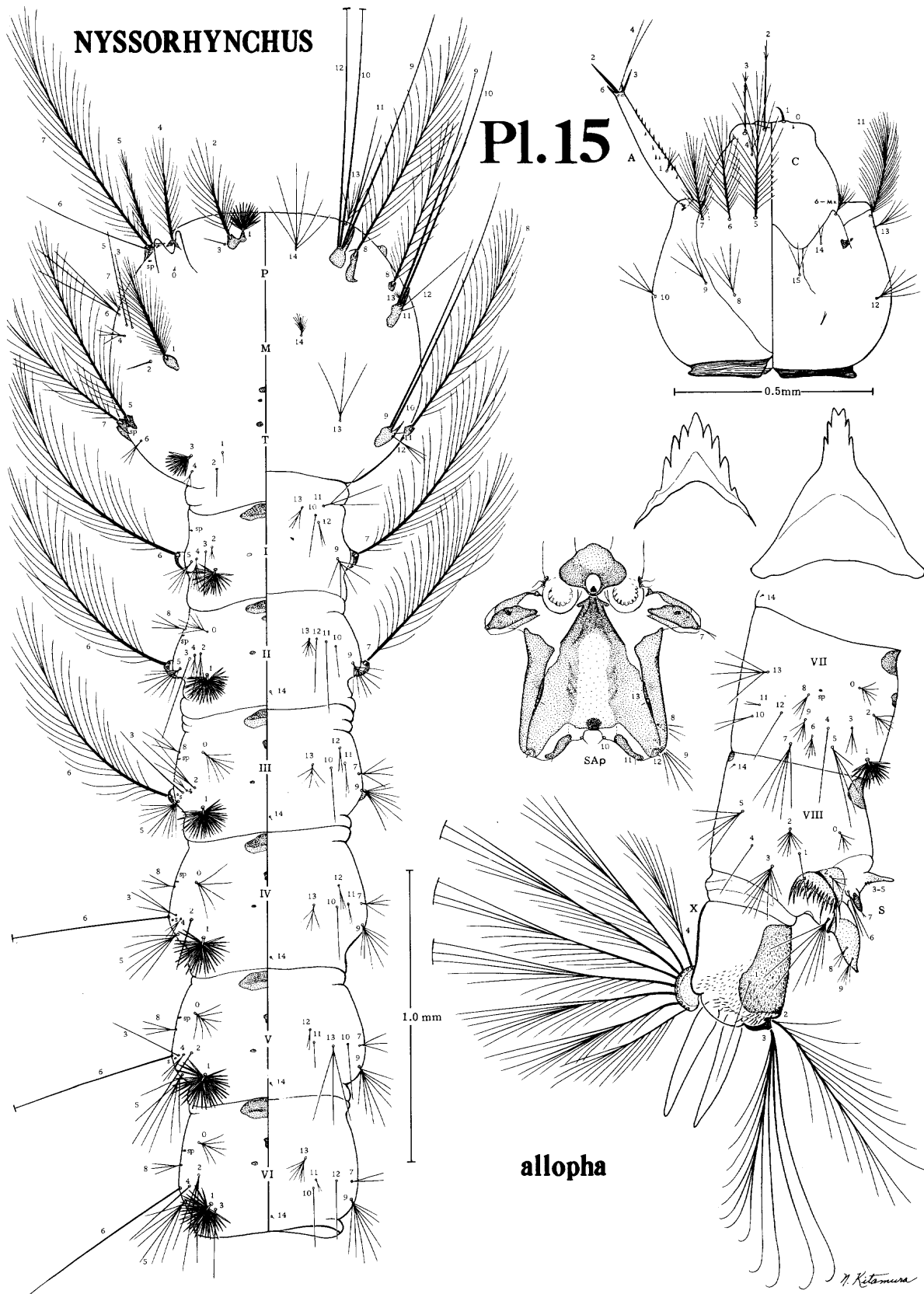
**P1.12** Hypothesized phylogenetic tree of the Albimanus Section.

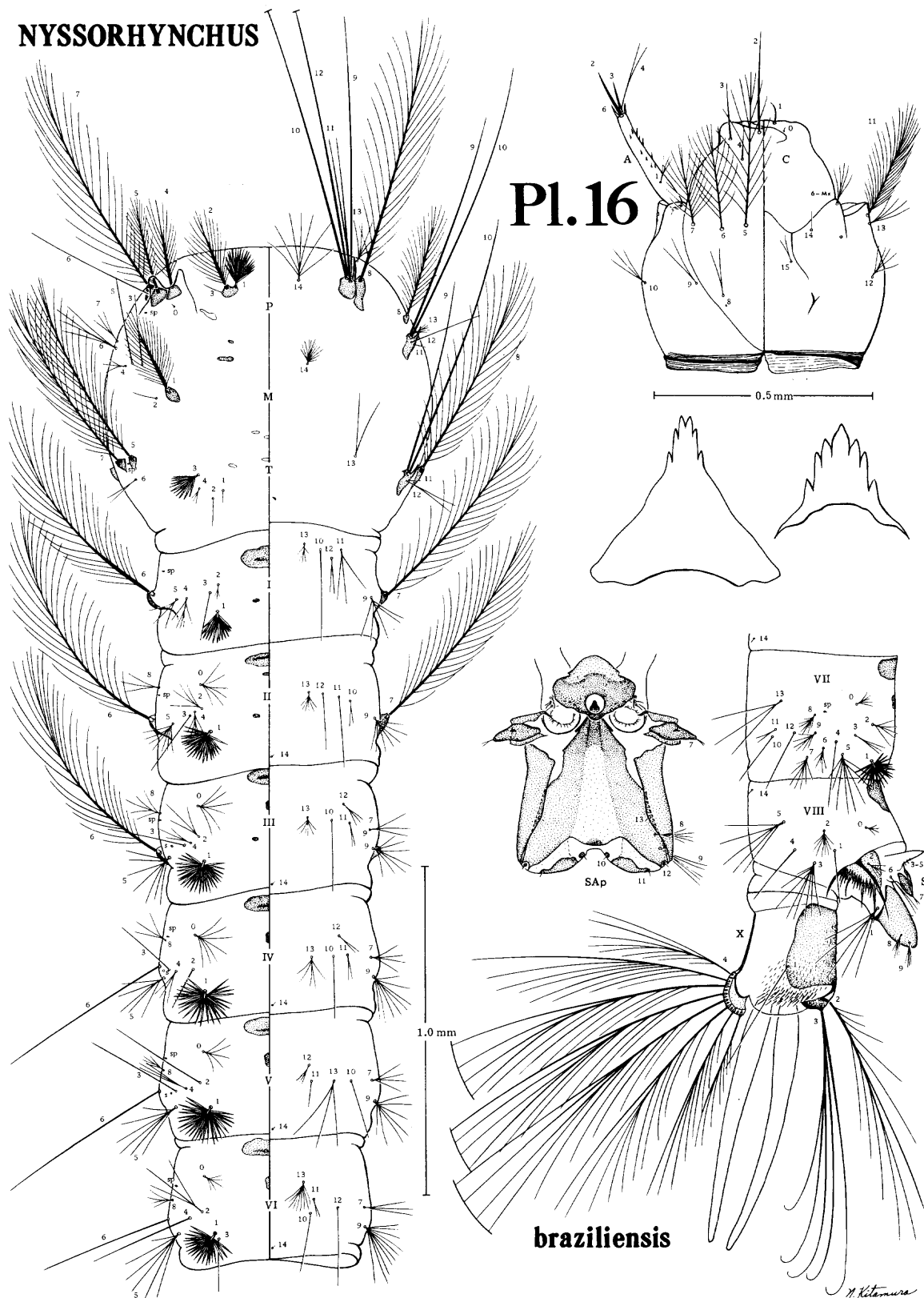
# NYSSORHYNCHUS

# Pl.13



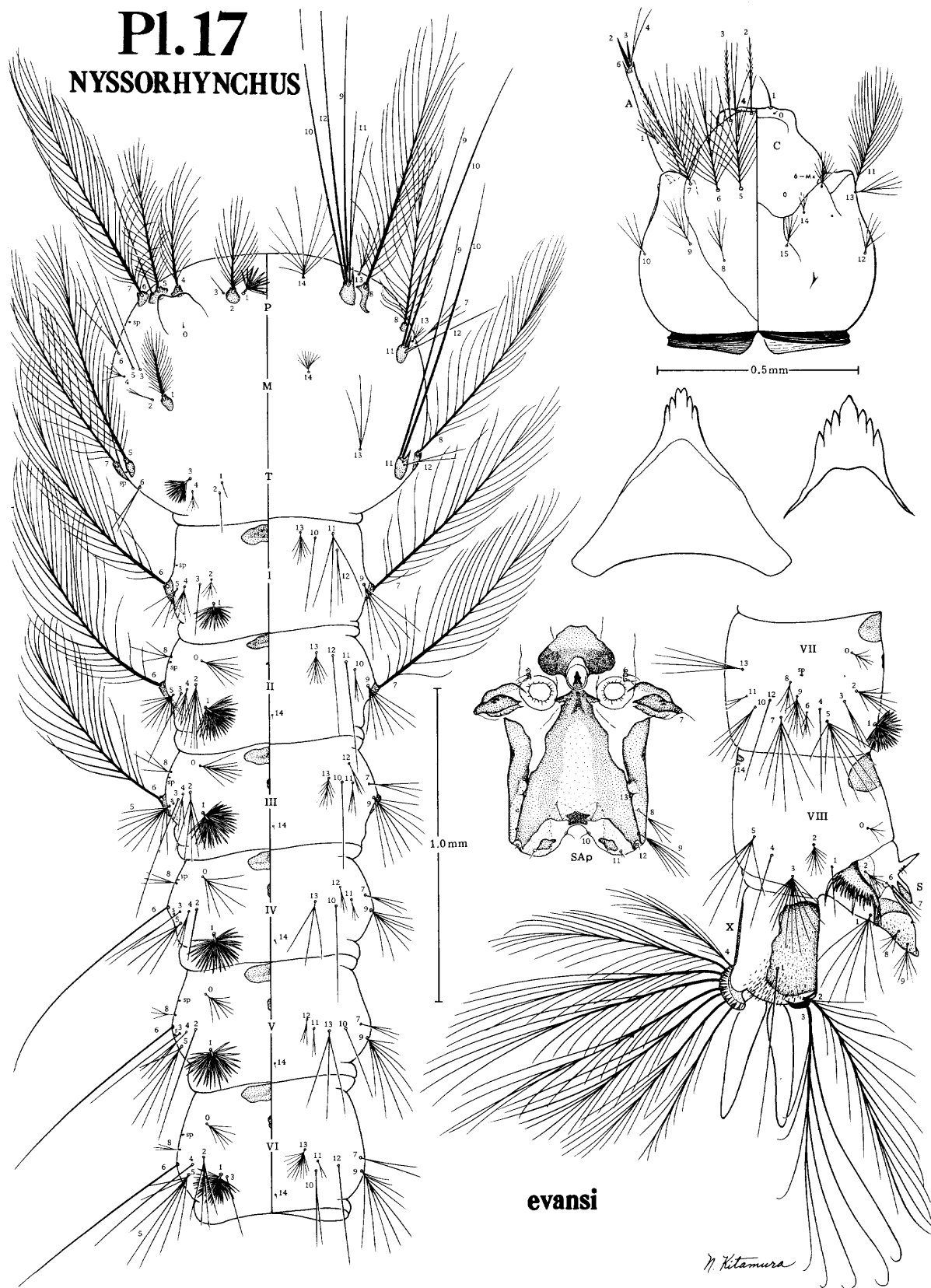


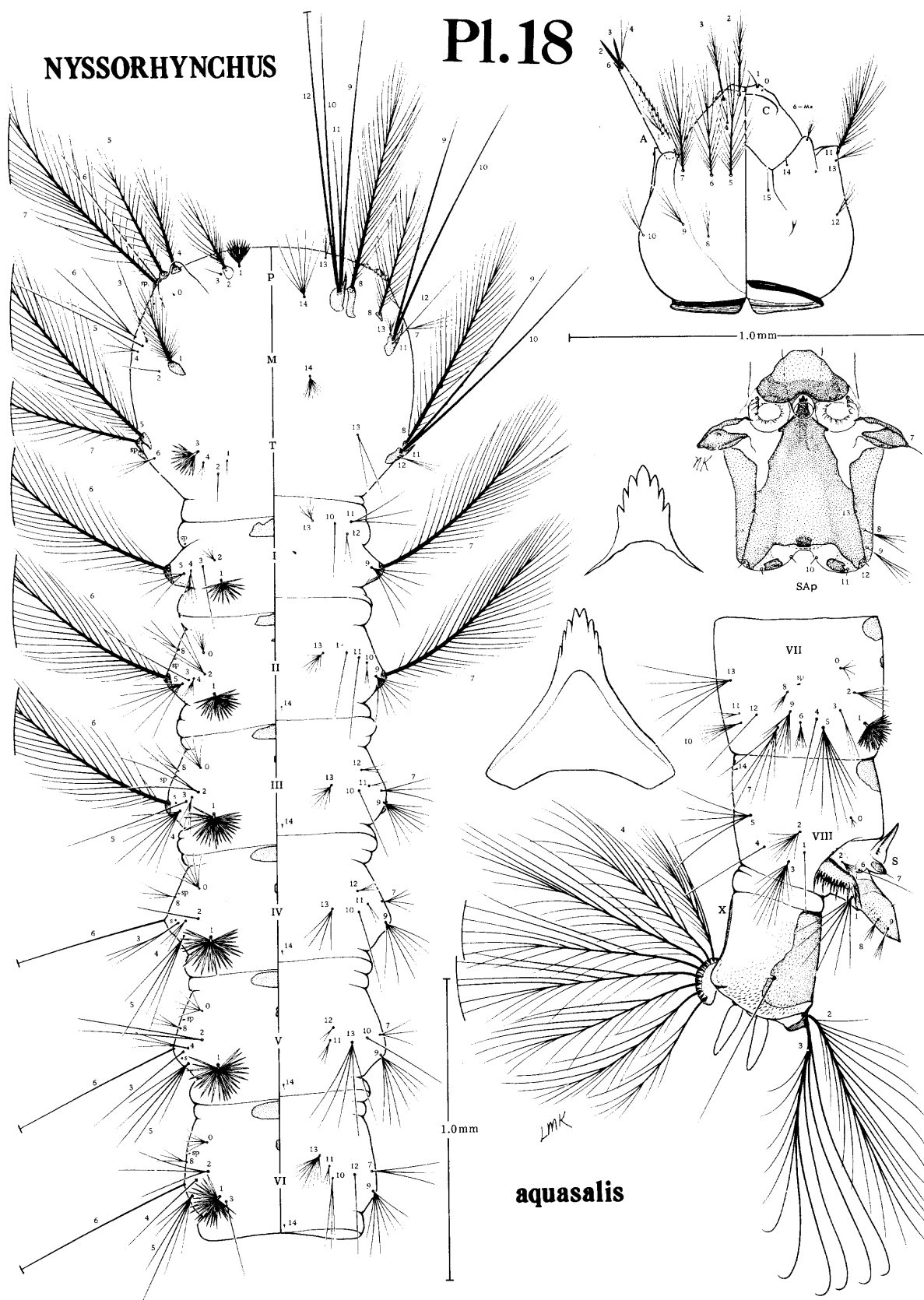


**NYSSORHYNCHUS**

# Pl.17

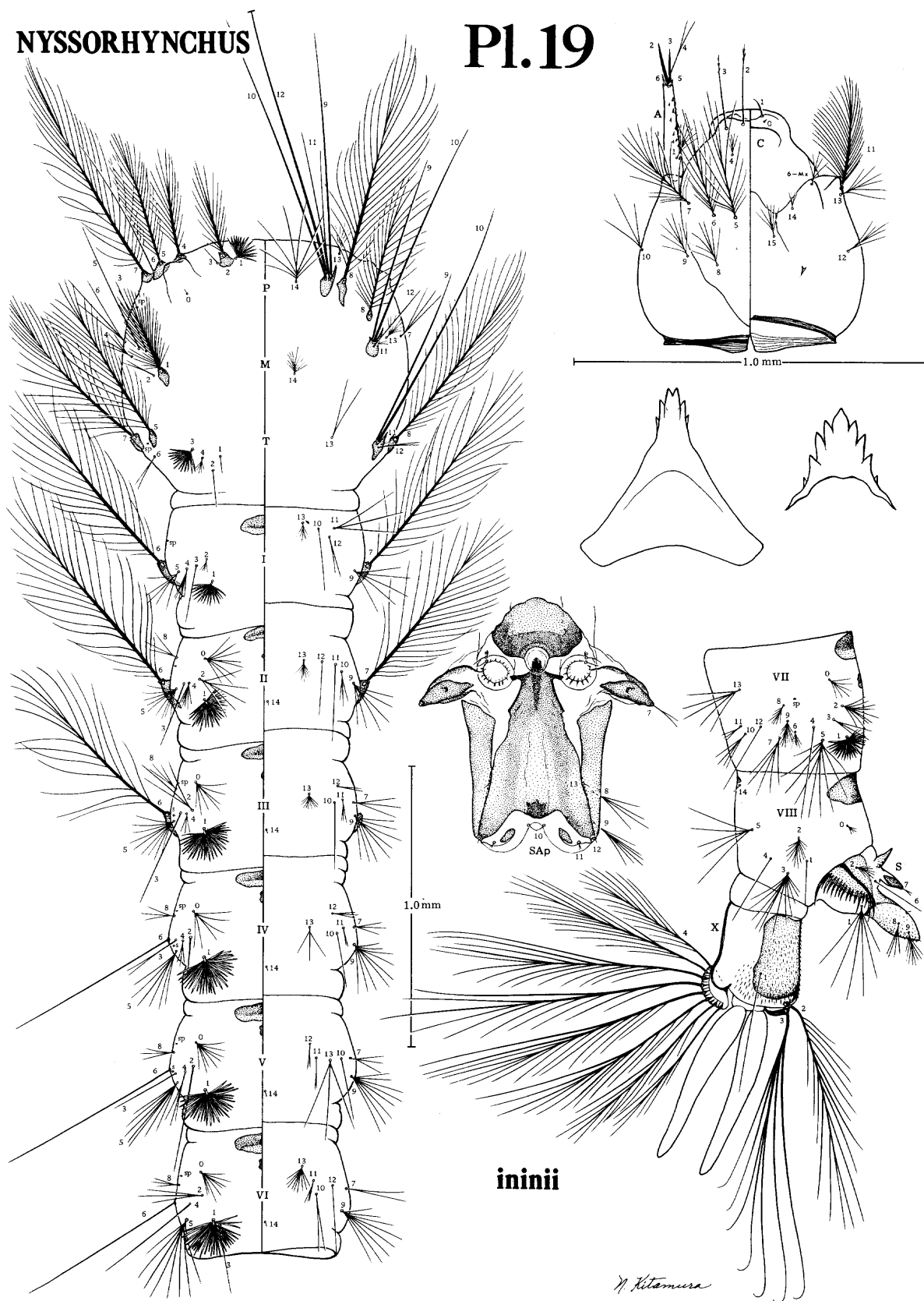
## NYSSORHYNCHUS



**NYSSORHYNCHUS****Pl. 18**

# NYSSORHYNCHUS

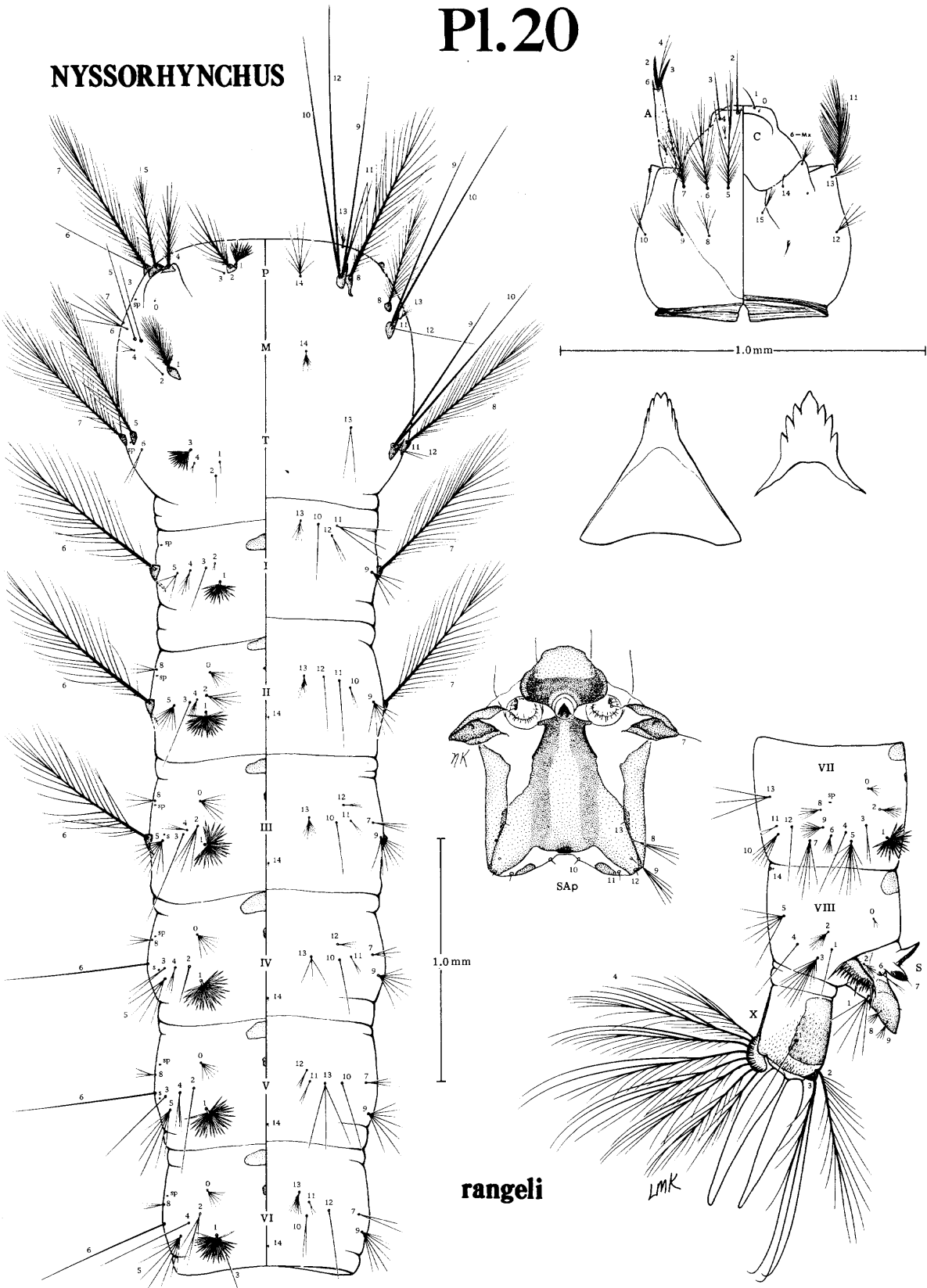
# Pl. 19





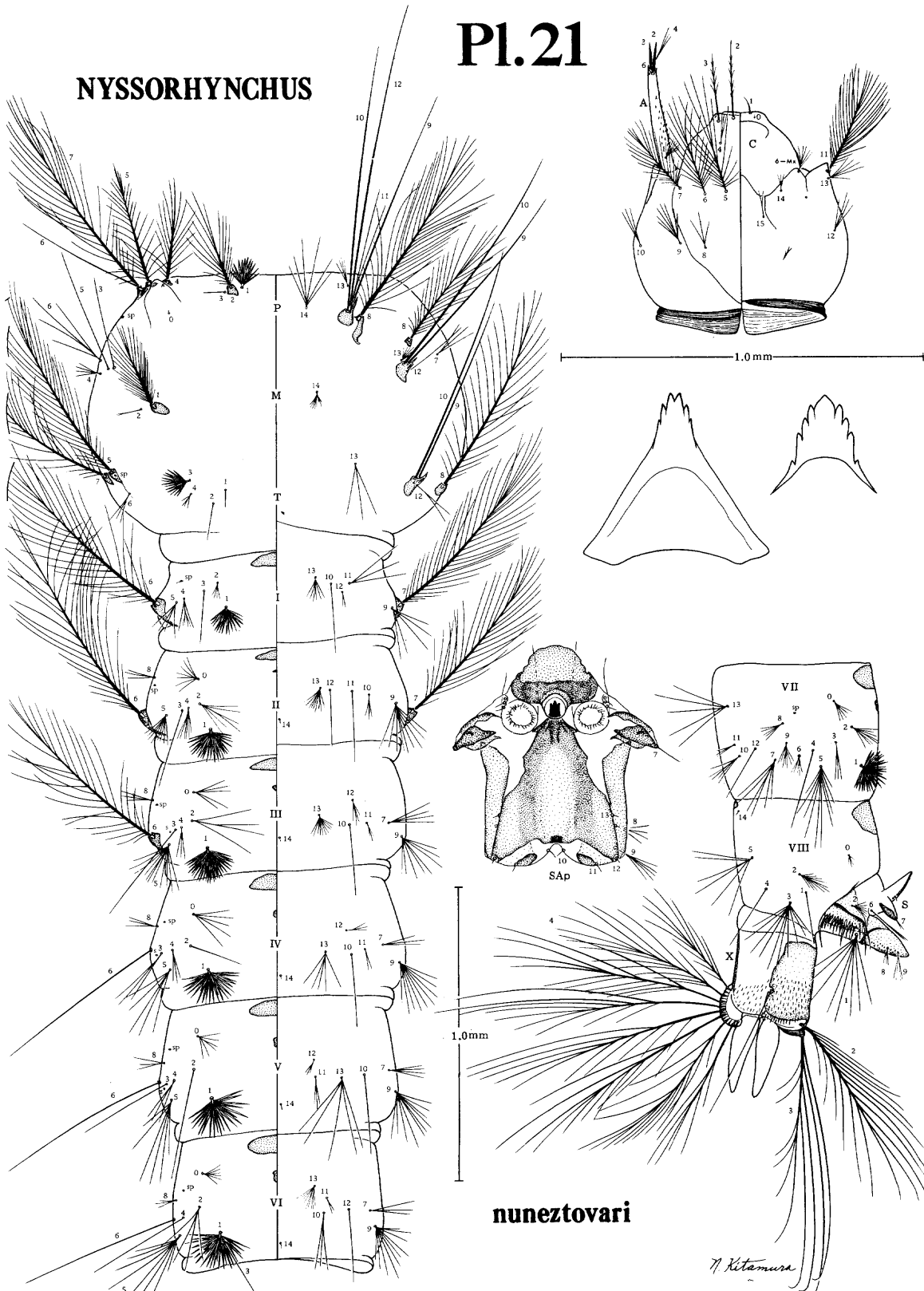
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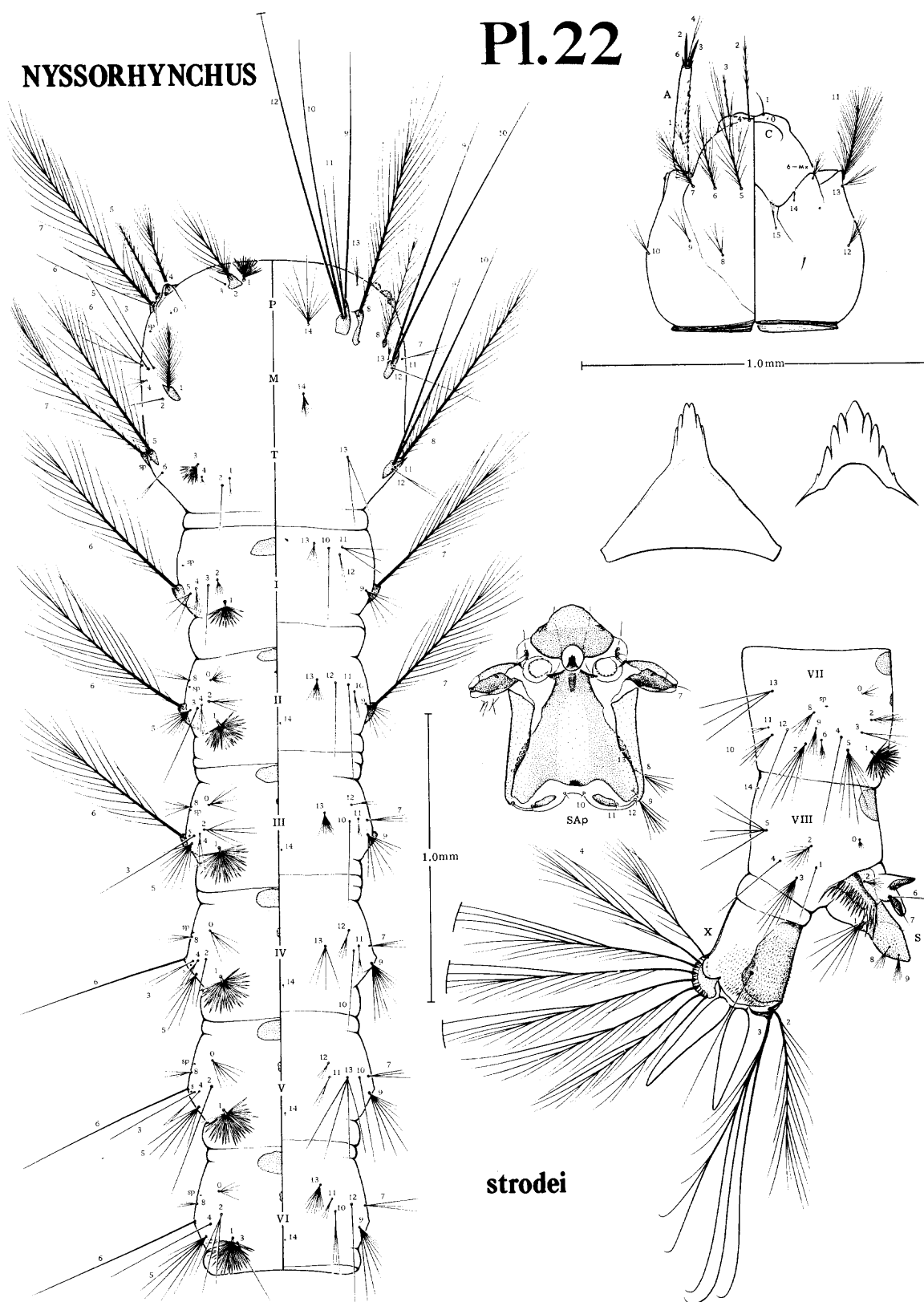
P1.20



## Pl. 21

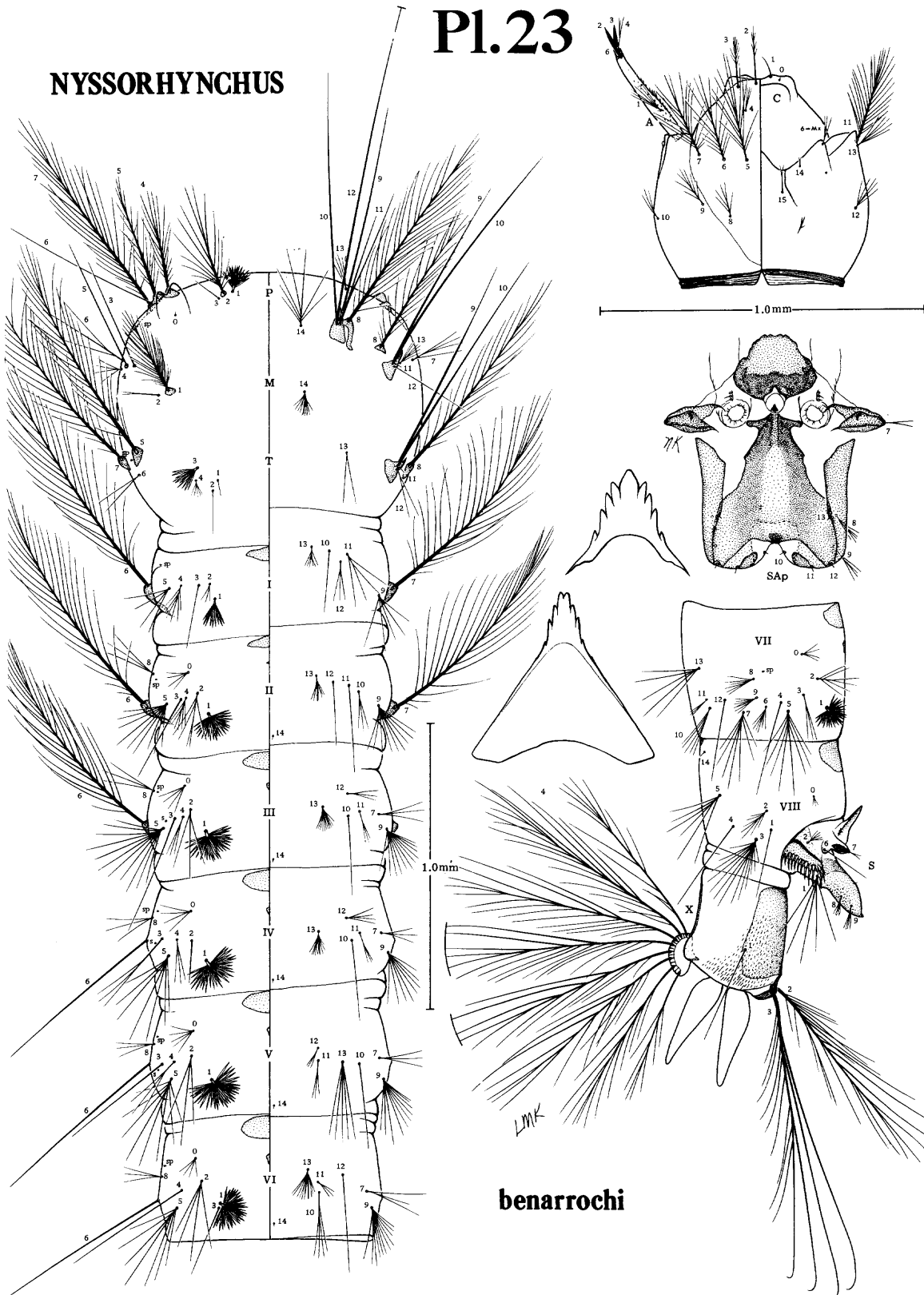
## NYSSORHYNCHUS

**nuneztovari**

**NYSSORHYNCHUS****Pl.22**

# NYSSORHYNCHUS

# Pl.23



**benarrochi**

