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**RESTORATION OF *VERRALLINA* TO GENERIC RANK IN  
TRIBE AEDINI (DIPTERA: CULICIDAE) AND DESCRIPTIONS  
OF THE GENUS AND THREE INCLUDED SUBGENERA**

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**Abstract.** *Verrallina* is restored as a genus in tribe Aedini. Rationale for this action is discussed. The genus includes three subgenera (*Harbachius*, new subgenus, *Neomacleaya*, new status and *Verrallina*). Subgenus *Verrallina* is divided into the Butleri Series and Carmenti Series. Ninety-four named species are included in the genus and each is assigned to a subgenus and/or series and, where required by the International Code of Zoological Nomenclature, the spelling of specific names is corrected to agree in gender with *Verrallina*. The genus, three subgenera and two series are defined and described. Detailed descriptions and illustrations are included for the type species of the genus, subgenera and nominotypical species of the two series. Keys to adults, female and male genitalia, pupae and fourth-instar larvae of the three subgenera are provided. An appendix lists the current status of life stages and/or structures described and illustrated for all species assigned to the genus. A conspectus of taxonomic changes is given. Abbreviations for the genus and three subgenera are provided.

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## INTRODUCTION

*Verrallina* Theobald is restored as a genus in tribe Aedini and includes three subgenera (i.e., *Harbachius* Reinert, new subgenus; *Neomacleaya* Theobald, revalidated as a subgenus and with *Aioretomyia* Leicester as a synonym; and *Verrallina*). The discussion section of the genus includes rationale for this action and principal distinguishing features of the genus that separate it from the other genera of Aedini. The following is an overview of the history of the genus.

*Aedes butleri* was described as a new species by Theobald in his "Monograph of the Culicidae" (1901, Vol. 2, page 230). Theobald (1903:295) described *Verrallina* as a new genus and he included in it *butleri* along with two other species. Of these three species, only *butleri* is currently retained in the genus; the other two species are placed in other genera (i.e., *nigra* Theobald in *Ficalbia* Theobald and *smithii* Coquillett in *Wyeomyia* Theobald). In 1905 (page 35), Theobald included this species under "GENUS UNCERTAIN." Blanchard (1905:417) selected *butleri* as the logotype for genus *Verrallina*. Later, Theobald (1907:238) described genus *Neomacleaya* and included in it a single new species, *Neomacleaya indica* Theobald. Leicester (1908:185) described genus *Aioretomyia* and included six species of which three are currently included in *Verrallina*. Edwards (1913:229) synonymized *Verrallina*, along with two other genera (i.e., *Neomacleaya* and *Aioretomyia*), with genus *Aedes* Meigen. Later (1917:221) he transferred the species included in *Verrallina*, *Neomacleaya* and *Aioretomyia*, along with several additional species, to subgenus *Aedes* Meigen of genus *Aedes*. This arrangement was followed by subsequent authors (notably Barraud 1928, 1931, 1934; Edwards 1922a, 1922b, 1928, 1932; Dyar and Shannon 1925; Edwards and Given 1928; Laffoon 1946; King and Hoogstraal 1947; Wijesundara 1951; Knight and Hull 1951, 1953; Stone et al. 1959) until Belkin (1962:412) resurrected *Verrallina* as a subgenus of genus *Aedes* and provisionally included *Neomacleaya* and *Aioretomyia* as synonyms. Belkin stated that the South Pacific species of *Verrallina* had little in common with the type species of subgenus *Aedes* (i.e., *Ae. cinereus* Meigen) but appeared to be quite similar to the type species of *Verrallina* (i.e., *Ae. butleri*). Delfinado (1967:1) removed *Neomacleaya* from synonymy with *Verrallina*, resur-

rected it as a subgenus of *Aedes*, and included in it primarily Oriental species previously included in *Aedes*, *Aioretomyia*, *Neomacleaya* and *Verrallina*; she mentioned that *Neomacleaya* was closely related to both *Verrallina* and *Aedes sensu stricto*. Huang (1968:1) followed Belkin (1962) and placed in *Verrallina* the species occurring in the Papuan Subregion. However, Klein (1973:1) followed Delfinado (1967, 1968) and treated the species from Cambodia in subgenus *Neomacleaya*. A new interpretation of subgenus *Verrallina* was presented by Reinert (1974:3) and included the separation of the subgenus into two sections (i.e., A and B) and divided the first section into three series (i.e., I = *carmenti* Series, II = *butleri* Series and III = *indicus* Series). He included *Neomacleaya* and *Aioretomyia* as synonyms of subgenus *Verrallina* in genus *Aedes*. Descriptions were given for each of these categories and he assigned each of the currently valid species to one of the categories. In 1984, Reinert gave a slightly revised description of subgenus *Verrallina* and treated the species occurring in Sri Lanka. Subsequent authors have followed Reinert's (1974, 1984) treatment (notably Tanaka et al. 1979; Apiwathnasorn 1986; Lee et al. 1987; Ward 1992).

*Verrallina* is herein restored to generic rank in tribe Aedini based on the criteria outlined below. The following definition of genus *Verrallina* is primarily taken from Reinert (1974, 1984), but revised and modified, and includes three subgenera, *Harbachius*, *Neomacleaya* and *Verrallina*. Ninety-four named species are included in the genus and each is assigned to a subgenus and/or series and, where required by the International Code of Zoological Nomenclature, the spelling of specific names is corrected to agree in gender with *Verrallina*. The proposed abbreviation for genus *Verrallina* is *Ve.* and for subgenus *Harbachius* is *Har.* The previously used abbreviations for subgenera *Neomacleaya* (*Nma.*) and *Verrallina* (*Ver.*) (see Reinert 1975, 1991) remain the same.

Species within genus *Verrallina* are easily assigned to subgenera *Harbachius* and *Neomacleaya* and the Carmenti Series of *Verrallina*. Based on the new definitions of the subgenera and series, as defined herein, some of the species previously assigned to Section A, Series II (*butleri* Series) by Reinert (1974:9) have been reassigned to subgenus *Neomacleaya* while the rest remain in the Butleri Series of subgenus *Verrallina*. The species retained in the Butleri Series possess female genitalia with the lower vaginal sclerite and spermathecal eminence more developed than the species in the Carmenti Series. Also, the gonocoxite of the male genitalia of species in the Butleri Series tends to be more developed than those of the Carmenti Series; however, the structural development of the phallosome and proctiger of the two series are the same and differ from those of subgenera *Harbachius* and *Neomacleaya* as discussed below. Fourth-instar larvae of the Butleri Series are similar to those of the Carmenti Series except seta 13-C is branched and seta 2-X tends to possess more branches in *Ve. butleri*, *Ve. iriomotensis* (Tanaka and Mizusawa) and *Ve. lugubris* (Barraud) which is similar to *Neomacleaya*. Also, the fourth-instar larvae of *Ve. dux* (Dyar and Shannon) and *Ve. iriomotensis* have comb scales with a median apical spine. This small assemblage of five species (Butleri Series) occupies a position somewhat between subgenera *Neomacleaya* and *Verrallina* but shares more important features with the latter subgenus and is therefore included in this subgenus but in a separate series. Appendix A lists the current status of life stages and structures described and illustrated for species assigned to genus *Verrallina*. It is noted that for a number of species several life stages/structures remain unknown or not described.

It is a pleasure to name the new subgenus *Harbachius* in honor of Dr. Ralph E. Harbach, The Natural History Museum (NHM), London, United Kingdom, in recognition of his many outstanding contributions to the biosystematics and morphology of the Culicidae.

## MATERIALS AND METHODS

The taxonomic treatment includes a detailed description of genus *Verrallina* followed by keys to adults, female and male genitalia, pupae and fourth-instar larvae of the three subgenera, and by descriptions of subgenera *Harbachius*, *Neomacleaya* and *Verrallina* (including Butleri Series and Carmenti Series). Each subgenus and series description is followed by a listing of all included species. The description and discussion of genus *Verrallina* is detailed in order to provide as much information as possible for comparative purposes. The type species of each subgenus and the nominotypical species of the Butleri Series and Carmenti Series are completely described and pertinent stages and/or structures are illustrated. Tables of the observed branching of setae (range followed by mode in parentheses) are given for the pupae and fourth-instar larvae of the type/nominotypical species of the three subgenera and the two series of subgenus *Verrallina*. Synonymy and taxonomic literature references are provided for the genus and each subgenus. Appendix B provides a conspectus of taxonomic changes. In Appendix A the following abbreviations/symbols are used, ♀ = female, ♂ = male, g = genitalia, P = pupa, L = fourth-instar larva and E = egg. Current country names are as listed in Merriam-Webster's Geographical Dictionary (1997, 3rd Ed., Merriam-Webster, Inc., Springfield, MA).

Measurements of slide-mounted and pinned specimens were made with an ocular micrometer having a linear scale of 100 divisions and calibrated using a stage micrometer. The scale used for the illustrations is in millimeters. Male genitalia are described in the prerotation position. Chaetotaxy and nomenclature used follow Harbach and Knight (1980, 1982), except for terminology proposed by Reinert (1990, 1999b) and Reinert et al. (1997).

## TAXONOMIC TREATMENT

### GENUS *VERRALLINA* THEOBALD

*Verrallina* Theobald, 1903:295 (type species: *Aedes Butleri* Theobald, 1901:230; first of 3 included species, selected by Blanchard 1905:417).

*Aedes* of Theobald 1901:230 (in part); Giles 1902:481; Brunetti 1907:367, 1920:141 (in part); Edwards 1913:229 (in part), 1922a:264 (in part); Senior-White 1923:52 (in part); Mattingly 1956:794; Stojanovich and Scott 1965:11, 1966:47; Stone et al. 1966:50 (in part); Russell 1996:229.

*Verrallina* in part of Blanchard 1905:417; Leicester 1908:196; Theobald 1910b:494; Brunetti 1912:491.

*Aedes* (genus uncertain) of Theobald 1905:35.

*Skusea* of Blanchard 1905:417 (in part); Theobald 1907:542 (in part), 1910a:32 (in part), 1910b:488 (in part); Bancroft 1908:55; Brunetti 1914:55; Taylor 1914a:465.

*Pseudoskusea* of Taylor 1912:27.

*Uranotaenia* of Brunetti 1914:73.

*Lepidotomyia* of Taylor 1914b:191.

*Aedes* (*Aedes*) of Edwards 1917:221 (in part), 1922b:468 (in part), 1932:174 (in part); Dyar and Shannon 1925:79; Edwards and Given 1928:344; Barraud 1928:363, 1934:277; Paine in Paine and Edwards 1929:307; Borel 1930:283; Brug 1932:79, 1934:512; Taylor 1934:21

(in part), 1944:76; Bonne-Wepster and Brug 1937:41; Causey 1937:414; Bohart 1945:65, 1957:65; Laffoon 1946:228; King and Hoogstraal 1947:113; Bonne-Wepster 1948:320, 1954:243; Penn 1949:62; Carter 1950:89; Wijesundara 1951:173; Knight and Hull 1951:214, 1953:471; Iyengar and Menon 1956:789; Stone and Knight 1956:227; Chu 1958:112; Stone et al. 1959:204 (in part); Iyengar 1960:68; Stone 1963:131; Assem and Bonne-Wepster 1964:102; Army Mosquito Project 1965:33; Stojanovich and Scott 1965:11, 1966:47; Stone et al. 1966:50; Knight and Stone 1977:70 (in part).

*Aedes* (?*Skusea*) of Edwards 1921:76.

*Aedes* (*Skusea*) of Brug 1924:437.

*Aedes* (*Verrallina*) of Belkin 1962:412; Stone 1963:131, 1970:152; Army Mosquito Project 1965:29; Stone et al. 1966:50; Steffan 1966:213; Huang 1968:1; Basio 1971:32; Marks 1973:66; Stone and Delfinado 1973:310; Reinert 1974:1, 1976:206, 1984:1, 1999a:78; Hochman and Reinert 1974:8; Matsuo et al. 1974:440; Tenorio 1976:53; Knight and Stone 1977:167; Sasa et al. 1977:159; Taylor and Maffi 1978:212; Knight 1978:34; Miyagi and Toma 1979:14; Tanaka et al. 1979:436; Jayasekera and Chelliah 1981:6; Tsukamoto 1982:305; Tsukamoto and Horio 1985:494; Apiwathnasorn 1986:14; Lee et al. 1987:250; Lu et al. 1988:51; Evenhuis and Gon 1989:203; Townsend 1990:52; Linley et al. 1991:593; Ward 1992:190; Reinert and Harbach 1992:253.

*Aedes* (*Neomacleaya*) of Delfinado 1967:1, 1968:1; Stone 1970:153; Basio 1971:21; Stone and Delfinado 1973:302; Klein 1973:1; Tanaka and Mizusawa 1973:625; Hochman and Reinert 1974:7; Tenorio 1976:54; Knight and Stone 1977:115; Lu and Li 1982:34; Lu and Su 1987:30.

The following description of *Verrallina* is based on the named species included in the three subgenera of the genus.

**FEMALES.** *Head.* Antenna dark brown, 0.76-1.42 length of proboscis, pedicel with few very short fine setae and usually few small broad scales mesally, flagellomere 1 with basal area pale and with several small scales; clypeus bare; maxillary palpus dark-scaled, 4-segmented, short, 0.11-0.21 length of proboscis; proboscis dark-scaled, 0.84-1.55 length of femur I; eyes contiguous or nearly contiguous dorsally (subgenera *Neomacleaya* and *Verrallina*) or separated dorsally (subgenus *Harbachius* and *Ve. mccormicki* (Belkin)); ocular line with broad scales and often with few curved narrow scales, setae dark and well developed; scales on head broad and decumbent or if few curved narrow pale scales present they are restricted to coronal suture (most species of subgenus *Neomacleaya*) and few semierect forked scales near ocular line in *Harbachius*; occiput with several to numerous erect forked scales, decumbent scales broad and/or narrow. *Thorax.* Scutal integument usually dark; scutum covered with curved narrow dark scales, some species also with curved narrow pale scales forming small patches (usually on following areas--anterior promontory, antedorsocentral, lateral scutal fossal, supraalar, and occasionally on margins of prescutellar area); prescutellar area bare (few species with narrow median stripe of scales on anterior portion); dark setae on following areas--few anterior promontory, several to numerous acrostichal (anterior and posterior), few antedorsocentral, several to numerous dorsocentral (anterior and posterior), scutal fossal (anterior, lateral, median, and usually posterior), several to numerous antealar, numerous supraalar, few posterior medial scutal, 1 parascutellar; scutellum with patch of curved narrow scales and several long and short setae on each lobe; mesopostnotum bare (except *Ve. virilis* Leicester and Marks species No. 171 with 1,2 setae); pleural integument usually dark; antepronota widely separated, broad scales usually absent but occasionally present, 7-28 short and long setae; postpronotum with curved narrow scales dorsally (few species with scales apparently absent) in

subgenus *Verrallina*, or scales absent in subgenus *Harbachius*, 3-10 posterior setae, some species also with few short fine setae, proepisternum with patch of broad white scales and 4-21 setae on upper area, lower area bare (except *Ve. adusta* (Laffoon), *Ve. andamanensis* (Edwards), *Ve. margarsen* (Dyar and Shannon) and *Ve. sohni* (Reinert) with small patch of short fine setae on median area); paratergite bare (except *Ve. indica* occasionally with few narrow pale scales); subspiracular area, prespiracular area and mesomeron bare; postspiracular area with or without scales, 2-12 setae; mesokatepisternum with upper and lower patches of broad scales, 1-7 upper and 4-19 lower setae, some species also with few short fine setae on anterior, dorsal and ventral areas; prealar area usually without scales, 4-22 setae; mesepimeron (Fig. 14) with patch of broad white scales near center, 5-33 setae dorsally and/or posterodorsally of scale patch, also with few (2,3) (e.g., *Ve. indica*) to numerous fine hairlike setae located posteriorly and/or ventrally to scale patch (setae in some species restricted to lower posterior margin of scale patch (e.g., *Ve. butleri* and *Ve. carmenti*) while others with numerous setae along entire posterior margin of scale patch and extending to near ventral margin of sclerite (e.g., *Ve. unca*)) in subgenera *Neomacleaya* and *Verrallina* (absent in subgenus *Harbachius*); metameron usually bare (short fine setae and small pale scales present in *Ve. gibbosa* (Delfinado) and members of the Andamanensis Group). *Legs*. Coxae I-III with several setae and patch of pale scales, I also usually with brown scales; trochanters I-III with few short setae and small scales; femora I and II with anterior surfaces brown-scaled, II occasionally with pale-scaled stripe ventrally, I with posterior surface brown-scaled with pale-scaled longitudinal stripe dorsally, II with posterior surface with pale-scaled longitudinal stripe ventrally, III with anterior and posterior surfaces pale-scaled except for anterodorsal and posterodorsal longitudinal dark-scaled stripe; tibiae I-III usually brown-scaled, I and II occasionally with longitudinal pale-scaled stripe on posterior surfaces; tarsi I-III dark-scaled; posttarsi I, II with ungues variable, III with ungues simple in subgenera *Neomacleaya* and *Verrallina* and toothed in subgenus *Harbachius*. *Wing*. Dorsal and ventral veins dark-scaled (some species with few pale scales at base of costa and/or on remigium, e.g., *Ve. yusafi* (Barraud)), scales not broad; alula with narrow to moderately broad scales on margin; upper calypter with several setae on margin; 1-3 remigial setae. *Halter*. Pedicel pale; capitellum covered with pale and/or dark scales. *Abdomen*. Tergal scaling variable, all dark-scaled or with pale-scaled patches and bands, usually with basolateral pale-scaled patches, tergum I always with basolateral patch of broad pale scales; sternal scaling variable, from completely pale- to dark-scaled, usually with pale-scaled broad basal bands and apical areas dark-scaled; terga and sterna with numerous short setae, mostly along posterior margins. *Genitalia*. Tergum VIII with numerous broad scales covering apical 0.50-0.84, basal 0.1-0.7 retracted into segment VII, moderately to heavily pigmented, wide, base usually slightly concave, apex gently convex or slightly concave, numerous short and moderately long setae scattered over apical 0.24-0.88, basolateral seta present or absent (some species with small bulla instead of seta), covered with minute spicules, VIII-Te index 0.35-0.80, VIII-Te/IX-Te index 1.05-6.84; sternum VIII with numerous broad scales covering much of apical 0.78-0.96, moderately to heavily pigmented, wide, base concave mesally, apex with shallow to moderately deep median indentation and with small lobe on each side of midline, setae on lobe thin or stout, numerous short and moderately long setae scattered over most of surface, covered with minute spicules, apical intersegmental fold unpigmented, VIII-S index 0.47-0.80; tergum IX moderately to heavily pigmented, wide, short and usually ribbonlike, setae absent (several setae present in *Ve. gibbosa* (Delfinado) and *Ve. yusafi* and rarely one seta on one side in few other species), IX-Te index 0.12-0.83; insula ill-defined, small, unpigmented, with 2-7 small tuberculi (usually each with minute spicule) in subgenera *Neomacleaya* and *Verrallina* or insula absent and replaced by median apical U-shaped portion of lower vaginal sclerite in subgenus *Harbachius*; lower vaginal lip moderately to heavily pigmented,

narrow, with spicules at least on basal portion, with or without small heavily pigmented median projection caudally, lower vaginal sclerite lightly to heavily pigmented, variable in shape and number, with or without spicules; upper vaginal lip moderately to heavily pigmented, variable in shape and development, may have median posterior area developed into vertical shield (subgenus *Neomacleaya*) or horizontal shield (subgenus *Harbachius*), with or without spicules, upper vaginal sclerite moderately to heavily pigmented, variable in shape and development, very large, often nearly covering wall of vagina; spermathecal eminence well defined, heavily pigmented, depth shallow to deep, simple to complex, with or without spicules, heavily pigmented spinelined pouch present (subgenus *Harbachius*) or absent (subgenera *Neomacleaya* and *Verrallina*); postgenital lobe short to moderately long, narrow to moderately broad, apex rounded or with small to very deep median indentation, 5-29 setae on each side of midline, 11-57 total setae, covered with small spicules, dorsal PGL index 0.47-1.78, ventral PGL index 0.43-2.13; proctiger with minute spicules; cercus more or less triangular in outline, short to moderately long, usually broad at base, apex acute, covered with minute to small spicules, dorsal surface with number of short and moderately long setae scattered over most of surface, few long setae at apex, ventral surface with several short to moderately long setae along outer margin and becoming more numerous distally, usually with numerous broad scales on dorsal surface, cercus index 1.76-4.27, cercus/dorsal PGL index 2.42-5.30; 3 spermathecal capsules, 1 large, 1 medium and 1 small in size, heavily pigmented, elliptical or ovoid, usually with narrow or broad short pigmented neck connected with spermathecal duct, few to several small spermathecal capsule pores near orifice; accessory gland duct base unpigmented to moderately pigmented.

**MALES.** Usually similar to females in general habitus. *Head.* Antenna plumose, 0.76-1.27 length of proboscis; maxillary palpus very short, 0.09-0.18 length of proboscis; proboscis 0.93-1.56 length of femur I. *Thorax.* Most setal groups usually with fewer setae. *Legs.* Posttarsi I,II variable, III with unguis simple in subgenera *Neomacleaya* and *Verrallina* (except *Ve. prioekaensis* (Brug) with one unguis with one small tooth) and unguis toothed in subgenus *Harbachius*. *Abdomen.* Terga with lateral setae rather short; tergum VIII wide with number of long caudally directed setae. *Genitalia.* Tergum IX moderately to heavily pigmented, mesal area narrow, setae absent; gonocoxite short, broad, heavily pigmented, mesal surface membranous with minute spicules, dorsal, lateral and ventral surfaces with short to long setae, with one or more dorsoapical and/or ventroapical lobes or fleshy projections or with spiniforms (except absent in *Ve. leilae* (King and Hoogstraal) and *Ve. simplicis* (King and Hoogstraal)), few to numerous scales on lateral and ventral areas; gonostylus attached to gonocoxite subapically in many species, short to moderately long, moderately to heavily pigmented, variable in shape but usually with basal portion somewhat expanded and with few setae, apical portion narrow and curved, gonostylar claw absent; basal mesal lobe variable in development, consisting of plate situated on membranous basomesal area of gonocoxite and strongly fused along sternal margin to tergomesal margin of sclerotized ventral surface of gonocoxite, plate connecting with its mate by narrow band (aedeagal guide) covered with spicules and located ventrad of apical portion of prosopallus, with several to numerous short to moderately long thin setae, some (groups of species) also with lobes, projections or spiniforms; proctiger with paraproct variously developed, many species with paraproct modified into short to long, heavily pigmented projections, other species with paraproct developed into broad contiguous heavily pigmented plates, subbasal area produced into small lobe extending ventrad and articulates at point on dorsal surface of basal piece near base of opisthophallus, base of proctiger fused with tergum X, cercal setae absent; tergum X moderately to heavily pigmented, fused with tergum IX; phallosome complex, composed of opisthophallus, phallus, prosopallus, paramere and basal piece, each developed as follows, opisthophallus--consisting of lightly to heavily pigmented tergal

transverse bridge between basal pieces, located dorsad of phallus and prosophallus and ventrad of proctiger, phallus--consisting of pair of heavily pigmented, narrowly separated, caudally produced aedeagal sclerites fused together by narrow bridge, base extends laterally and is fused to basal portion of prosophallus, apex of phallus forming tergal penis filament extending cephalad, prosophallus--consisting of pair of moderately to heavily pigmented projections or plates (prosophallic sclerites) with bases moderately to widely separated, base attached to paramere, located laterad and slightly ventrad of phallus, paramere--heavily pigmented, short and small in subgenus *Verrallina*, moderately long in subgenus *Neomacleaya* and very long and moderately broad in subgenus *Harbachius*, basal piece--moderately to heavily pigmented, short to long, outer surface broadly attached to basotergal apodeme of gonocoxite; sternum IX heavily pigmented throughout, large, broad, several to numerous short to moderately long setae in patch near median caudal area (except *Ve. yerburyi* (Edwards) with only 2,3 setae), most species of subgenus *Harbachius* and several species of subgenus *Neomacleaya* also with one to few broad scales.

**PUPAE.** Chaetotaxy and other features are summarized as follow. *Cephalothorax.* Setae 1-3-CT approximately equal in length and equally developed; 1-CT single to 5-branched; 2-CT single to 4-branched; 3,6-CT single to 3-branched (6-CT almost always single); 4-CT single to 9-branched; 5-CT with 2-12 branches; 7-CT with 2-9 branches, moderately long to long; 8-CT with 2-11 branches; 9-CT single to 6-branched, close to mesothoracic wing base; seta 10-CT with 2-13 branches; 11-CT single, approximately equal to or slightly longer than 10,12-CT; 12-CT with 2-8 branches. *Trumpet.* Moderately to heavily pigmented; hairlike spicules on inner surface of meatus; index 2.82-5.80. *Abdomen.* Setae 0-II,VII,VIII single; 0-III,IV,VI single or 2-branched; 0-V single to 3-branched; 1-I dendritic, well developed, with 10-38 branches on basal 0.3; 1-II with 3-37 branches; 1-III with 2-14 branches; 1-IV,V single to 10-branched; 1-VI single to 8-branched; 1-VII single to 6-branched; 2-I single or 2-branched, bases of 2,3-I widely separated; 2-II-VII stout in many species; 2-II-V,VII single; 2-VI single or 2-branched; 3-I with 2-8 branches (very rarely single); 3-II usually single (apparently occasionally 2-branched in *Ve. lineata* (Taylor) and *Ve. nigrotarsis* (Ludlow)); 3-III single; 3-IV with 2-10 branches; 3-V single to 7-branched; 3-VI single to 6-branched; 3-VII with 2-9 branches; 4-I with 3-12 branches; 4-II with 2-11 branches; 4-III single to 8-branched; 4-IV single to 5-branched; 4-V with 2-11 branches; 4-VI single to 12-branched; 4-VII single to 7-branched; 4-VIII single to 5-branched; 5-I-III with 2-9 branches; 5-IV,VII single to 6-branched; 5-V,VI single to 4-branched; 6-I,II single to 3-branched; 6-III,V single to 5-branched; 6-IV,VI single to 5-branched; 6-VII single to 9-branched, short, weakly developed; 7-I,IV single to 6-branched; 7-II single to 7-branched; 7-III single to 8-branched; 7-V single to 11-branched; 7-VI single to 4-branched; 7-VII single to 3-branched; 8-III,VII single to 6-branched; 8-IV,VI single to 5-branched; 8-V single to 7-branched; 9-I single to 3-branched; 9-II-VI single; 9-VII single to 4-branched, short, weakly developed; 9-VIII single to 6-branched, short to moderately long, normally thin; 10-I single; 10-III single to 10-branched; 10-IV single to 7-branched; 10-V,VII single to 4-branched; 10-VI single to 3-branched; 11-I single or 2-branched, usually present; 11-III,IV single or 2-branched; 11-V,VI single to 3-branched; 11-VII single to 4-branched; 14-III-VI single; 14-VII,VIII single or 2-branched. *Paddle.* Ovoid; with minute serrations on basal portion of outer margin; with minute spicules on apical portions of outer and inner margins; without hairlike spicules; midrib lightly to moderately pigmented and nearly reaching or reaching apex; seta 1-Pa usually single, occasionally 2-branched; index 1.14-1.70.

**FOURTH-INSTAR LARVAE.** Chaetotaxy and other features are summarized as follow. *Head.* Lightly to heavily pigmented; patch of small spicules over area of compound eye in some species (*Ve. cyrtolabis* (Edwards), *Ve. indica*, *Ve. leicesteri* (Edwards), *Ve. torosa* (Delfinado), *Ve. unca* (Theobald) and *Ve. yerburyi*); setae 0,1,3,18-C single, 1-C well developed, long, thickened;

4-C short, with 2-12 weakly developed branches, mesad and slightly cephalad of 6-C; 5,9-C single to 9-branched; 5-C caudad and slightly mesad of 6-C and laterad and caudad of 4-C; 5,6-C bases widely separated, with 1 branch longer than others in many species of subgenus *Neomacleaya* and Carmenti Series of subgenus *Verrallina*; 5-7-C well developed, stout, long, aciculate; 6-C single to 7-branched; 7-C with 2-17 branches, laterad and slightly cephalad of 6-C or 7-C laterad and at same level as 6-C in few species; 8,13-C single to 6-branched; 10,11-C with 2-8 branches, 11-C very short to short; 12-C single to 10-branched; 14-C single (rarely with 2-4 branches), short; 15-C single to 11-branched; ventromedian cervical sclerite moderately to heavily pigmented, moderately large. *Mouthparts*. Dorsomentum heavily pigmented, with 17-45 teeth; lateral palatal brush with mesal filaments pectinate apically; seta 6-Mx single or 2-branched. *Antenna*. Short to moderately long; usually moderately pigmented; spicules scattered over most of shaft, usually more numerous on basal area and longer on outer area near middle; seta 1-A moderately stout, single to 9-branched (usually 2-6), short to moderately long, attached near middle of antennal length, branches more or less flattened; 2-A long, with subapical constriction; 3-A short, 0.20-0.36 length of 2-A; 4-A moderately long, 0.37-0.74 length of 2-A; 5-A with basal area flattened, pigmented, with dorsal spine, apical portion unpigmented; 6-A peglike, short, 0.22-0.39 length of 2-A; 2-6-A all apical. *Thorax*. Seta 0-P with 4-26 branches; 1,7-P single to 3-branched; 2,3-P single to 5-branched; 4-P single to 9-branched; 5-P single (5,6-P with 2 branches in *Ve. nigrotarsis*); 6,10-P single or 2-branched; 8-P long, thickened, usually single (occasionally 2-branched, very rarely 3-branched); 9-P single to 7-branched; 11-P with 2-8 branches; 12-P single to 6-branched; 13-P absent; 14-P single to 4-branched; 1-M with 2-8 branches; 2-M single to 7-branched; 3-M single to 4-branched; 4-M with 3-13 branches; 5,7,12-M single or 2-branched; 6-M with 3-9 branches; 8-M with 4-11 branches; 9-M with 5-12 branches; 10-M single; 11-M single to 3-branched; 13-M with 7-40 branches; 14-M with 3-20 branches; 1-T single to 8-branched; 2-T with 2-10 branches (rarely single); 3-T with 3-21 branches; 4-T single to 11-branched; 5,12-T single to 3-branched; 6-T single to 6-branched; 7-T with 4-12 branched; 8-T with 7-27 branches; 9-T with 2-5 branches; 10-T single or 2-branched; 11-T single to 5-branched; 12-T single to 3-branched; 13-T with 4-23 branches. *Abdomen*. Seta 0-II-V,VII,VIII single; 1-I single to 5-branched; 1-II single to 9-branched; 1-III,VII with 2-13 branches, 1-VII short; 1-IV with 3-15 branches; 1-V with 3-13 branches; 1-VI with 2-11 branches; 1-VIII with 2-10 branches; 2-I-VII single; 2-VIII single to 5-branched, 2-VIII longer than 1-VIII; 3-I with 4-13 branches; 3-II with 3-16 branches; 3-III with 2-13 branches; 3-IV,VII with 2-12 branches, 3-VII short; 3-V with 2-8 branches; 3-VI with 2-10 branches; 3-VIII with 4-12 branches; 4-I with 7-27 branches; 4-II with 4-18 branches; 4-III with 2-8 branches; 4-IV with 2-5 branches; 4-V with 4-15 branches; 4-VI with 2-11 branches; 4-VII single to 7-branched (rarely single); 4-VIII single to 4-branched; 5-I single to 9-branched; 5-II with 2-8 branches; 5-III single to 6-branched; 5-IV single to 4-branched; 5-V single to 5-branched; 5-VI single to 7-branched; 5-VII with 2-10 branches; 5-VIII with 5-15 branches; 6-I single to 4-branched; 6-II single to 6-branched; 6-III single; 6-IV-VI single or 2-branched; 6-VII with 4-18 branches; 7-I single to 3-branched, long; 7-II with 2-12 branches, short; 7-III with 3-15 branches; 7-IV with 2-17 branches; 7-V with 4-17 branches; 7-VI with 2-13 branches; 7-VII single to 10-branched; 8-II single to 4-branched; 8-III-IV single or 2-branched, short; 8-V single to 3-branched, short; 8-VI with 2-9 branches; 8-VII with 2-15 branches; 9-I with 2-7 branches; 9-II single to 4-branched; 9-III,V,VI single or 2-branched; 9-IV single; 9-VII single to 5-branched; 10-I with 2-8 branches; 10-II,III,V,VII single to 6-branched; 10-IV single to 8-branched; 10-VI single to 5-branched; 11-I,VI single to 7-branched; 11-II single to 6-branched; 11-III-V,VII single to 5-branched; 12-I absent; 12-II,VI single to 6-branched; 12-III with 2-6 branches; 12-IV with 2-5 branches; 12-V single to 4-branched; 12-VII single to 10-branched; 13-I single to 3-branched; 13-II with 4-24 branches; 13-

II,IV with 2-12 branches; 13-V with 2-14 branches; 13-VI with 9-62 branches; 13-VII with 4-18 branches; 14-II,IV single; 14-III,V,VIII single or 2-branched; 14-VI,VII single to 3-branched; VIII with comb consisting of 7-25 scales arranged in single, more or less curved, irregular row (*Ve. cuccioi* (Belkin) with two rows, one row very short), scales with stouter median apical spine and short denticles on basolateral areas or with uniformly developed short denticles on lateral and apical areas; 1-X single to 3-branched, moderately long, attached near middle of saddle posteriorly; 2-X single to 11-branched (usually multiple-branched, very seldom 2-branched), moderately long (long and single in *Ve. cuccioi*); 3-X single, very long; ventral brush (4-X) with 8-18 setae on grid and 1-4 precratal shorter setae (usually with 10 setae on grid and 2,3 precratal ones), all multiple-branched; saddle moderately to heavily pigmented, without spines on posterior margin, incompletely rings segment X, acus absent; 4 anal papillae, usually moderately long (short in *Ve. butleri* and very long in *Ve. cuccioi*, *Ve. hamistylus* (Laffoon) and *Ve. robertsi* (Laffoon)). *Siphon*. Lightly to heavily pigmented; moderately long; index 1.44-5.00; acus well developed; pecten on basal 0.49-0.65 (on basal 0.67-0.83 in *Ve. cuccioi*, *Ve. hamistylus*, *Ve. robertsi*, *Ve. similis* (Theobald) and *Ve. trispinata* (King and Hoogstraal)), consisting of 6-17 spines (*Ve. johnsoni* (Laffoon) with 14-20 spines but when 17 or more present basal 2,3 spines much reduced in size), distal 1-5 spines longer and wider spaced than remainder, each spine long, slender and with 1-3 small stout denticles basoventrally, distal 1-4 spines occasionally without denticles; seta 1-S with 2-10 branches, short, base attached on basal 0.62-0.83 of siphon distad of last pecten spine (attached within pecten in *Ve. cuccioi*, *Ve. similis*, and *Ve. trispinata*); 2,6,7,9-S single (6-S short, occasionally 2-branched); 8-S single to 8-branched (usually multiple-branched), short.

**EGGS.** Seven species of genus *Verrallina* (all in subgenus *Verrallina*) have the egg stage known. Huang (1968:21, 30, 33, 48) illustrated and gave measurements for four species (i.e., *Ve. carmentis* (Edwards), *Ve. funerea* (Theobald), *Ve. lineata* and *Ve. parasimilis* (King and Hoogstraal)). Moriya et al. (1973:52) published a description and scanning electron microphotograph of the egg of *Ve. nobukonis* (Yamada) but did not give the egg measurements, Reinert (1974b:41) described and illustrated the egg of *Ve. dux* and Matsuo et al. (1974:440) gave a description and scanning electron photomicrograph of the egg of *Ve. butleri*. Egg measurement (in microns) of known eggs are: *Ve. butleri* (630-720 x 150-180), *Ve. carmentis* (845 x 140), *Ve. dux* (637-730 x 154-179), *Ve. funerea* (806 x 268), *Ve. lineata* (756 x 206) and *Ve. parasimilis* (1040 x 200). Linley et al. (1991:593) provided a detailed description of the egg for *Ve. funerea* that included numerous electron photomicrographs of the entire egg and various parts and structures. This article should be examined for the most detailed description of the egg for any species within the genus *Verrallina*. Their measurements of the egg of *Ve. funerea* differed from those previously published (i.e., 707.1-848.5 x 151.5-186.9) and they pointed out that the outer chorionic cells of the ventral and dorsal surfaces differed markedly in structure, but that the egg's most distinctive features were its pronounced narrowness relative to length and the unusually large micropylar disk. Linley et al. (1991:607) also indicated that the large tubercles appeared to be more numerous in *Ve. butleri* and probably smaller in relation to the small tubercles, which were less confined to the periphery of the cell field than in *Ve. funerea*.

**DISCUSSION.** As was the practice in the early to mid-1900s, investigators included in subgenus *Aedes* (genus *Aedes*) many species that are currently placed in genus *Verrallina*. They based this placement primarily on features of the adult habitus, short male maxillary palpi and some larval characters. When the importance of male genitalic characters became evident for use in the partition of taxa, several assemblages of species in tribe Aedini were reorganized into different subgeneric and generic arrangements as is evident by the recognition of *Neomacleaya* and *Verrallina*, as used during the 1960s. Reinert (1974) provided a new interpretation for the included

species based on the adults, female and male genitalia, pupae and fourth-instar larvae and included these species in one subgenus (i.e., *Verrallina*) of genus *Aedes* but arranged them into Section A (with three series) and Section B. Now, after having examined all currently recognized subgenera and currently valid genera of tribe Aedini, I am convinced that the new classification proposed here is valid.

Genus *Verrallina* is strikingly different from all other genera and subgenera of tribe Aedini in the remarkably complex development of both the male and female genitalia. These structures are also different from the other genera of family Culicidae, however, the male genitalia show some similarity in the development of the phallosome to those of the monotypic, container-breeding, sabethine genus *Maorigoeldia* Edwards which occurs in New Zealand. Belkin (1962:494, 1968:108) indicated that genus *Maorigoeldia* may be the most primitive sabethine known and this was corroborated in a recent cladistic analysis of generic relationships (Harbach and Kitching 1998). Male genitalia of genus *Verrallina* appear to share similar structures of the phallosome complex with members of family Dixidae (see detailed discussion of the male genitalia of Dixidae by Belkin (1968:8-11)). The above similarities of the male genitalia of genus *Verrallina* with those of Dixidae suggest that this may be the primitive condition in Aedini. Within Aedini, I consider the basal mesal lobe and the claspette of the male genitalia to be homologous structures, but specially developed (see Reinert 1999b).

The very distinctive male genitalia of *Verrallina*, especially the complex development of the phallosome and proctiger, are easily differentiated from the other genera of Aedini and family Culicidae. In *Verrallina*, the absence of a gonostylar claw is shared by the following subgenera of *Aedes*: *Aedes*, *Belkinus* Reinert, *Edwardsaedes* Belkin, *Indusius* Edwards and *Paraedes* Edwards.

Barraud (1928) was the first to recognize the importance of the female genitalia for separating species, but apparently did not realize the importance of these uniquely developed structures at higher taxonomic levels. Development of the female genitalia of *Verrallina* differ in many important aspects from the other genera of Aedini and other genera of Culicidae.

Within Aedini, the presence of fine hairlike setae on the mesepimeron (Fig. 14) located posteriorly and/or ventrally to the scale patch distinguishes the species of subgenera *Neomacleaya* and *Verrallina*; these setae have apparently been lost in the 13 species of subgenus *Harbachius*. These fine hairlike setae are different in structure from lower mesepimeral setae which are stouter, longer and occupy a different position. Fine hairlike setae on the mesepimeron is also found in species of subgenus *Geoskusea* Edwards of genus *Aedes*.

The very short maxillary palpi of males in genus *Verrallina* are strikingly different from the majority of species in genus *Aedes*, but are similar to those of the following small subgenera of genus *Aedes*: *Aedes*, *Belkinus*, *Bothaella* Reinert, *Cancraedes* Edwards, *Christophersiomyia* Barraud, *Huaedes* Huang, *Leptosomatomyia* Theobald, *Nothoskusea* Dumbleton, *Paraedes*, *Rhinoskusea* Edwards, and most species of *Geoskusea* Edwards. Short maxillary palpi of males are also found elsewhere in Aedini in genus *Heizmannia* Ludlow, genus *Zeugomyia* Leicester, and a few species of genus *Haemagogus* Williston. Both males and females of *Verrallina* can be separated from these subgenera of *Aedes* and the other genera of Aedini by the combination of characters listed below.

Pupae of *Verrallina* can be distinguished from those of most of the genera of Aedini by the combination of characters given. However, this life stage has not been investigated thoroughly in all genera and subgenera and when this information becomes available additional and more distinct features may be recognized.

Fourth-instar larvae of genus *Verrallina* have the distal 1-5 pecten spines more widely spaced than those proximally on the siphon, which is similar to many groups that primarily inhabit

fresh water ground pools (e.g., *Aedes* subgenera, *Aedes*, *Aedimorphus* Theobald, *Edwardsaedes*, *Isoaedes* Reinert, *Neomelanicion* Newstead, *Rusticoides* Shevchenko and Prudkin, many *Ochlerotatus* Lynch Arribalzaga and some *Mucidus* Theobald, and some species of genus *Psorophora* Robineau-Desvoidy). Seta 8-P is long, thickened and usually single (occasionally 2-branched, very rarely 3-branched) in *Verrallina*, which differentiates fourth-instar larvae from most genera and subgenera of Aedini; however, 8-P is long and thickened in *Aedes* subgenera *Aedes* (usually 2-branched, rarely single), *Christophersiomyia* Barraud and *Neomelanicion* (with 2,3 branches), *Paraedes* (single) and many *Aedimorphus* and *Ochlerotatus* (usually with 2,3 branches, range single to 4-branched). In fourth-instar larvae of *Verrallina*, the placement and development of setae are fairly uniform within species groups, series and subgenera, but most species possess distinguishing features in this stage. Larvae of the genus are somewhat similar overall to those of subgenera *Aedes* and *Aedimorphus* of genus *Aedes* but can be separated from these subgenera by the positions and development of seta 4-7-C and the combination of other features listed below.

The following principal features, in combination, distinguish genus *Verrallina* and can be used in separating this genus from the other genera of Aedini: **in the adults by** (1) scutum and scutellum have only curved narrow scales, (2) paratergite is bare (except *Ve. indica* occasionally has narrow scales), (3) acrostichal area has several to numerous setae (both anterior and posterior) (species of *Harbachius* usually have only a few setae on posterior area), (4) dorsocentral area (both anterior and posterior) has setae, (5) tarsi I-III are dark-scaled, (6) postpronotum has only curved narrow scales dorsally or scales absent, (7) head has decumbent scales of vertex all broad (or if few curved narrow scales are present they are restricted to margins of the coronal suture), (8) wings are dark-scaled (rarely with few pale scales at base of costa and/or remigium) and scales are not broad, (9) alula has narrow to moderately broad scales on margin, (10) antennal pedicel has several very short fine setae and usually a few small broad scales mesally (scales not overlapping or forming a dense patch), (11) mesopostnotum is bare (except 2 species have 1,2 setae), (12) prespiracular area is bare, (13) postspiracular setae are present and (14) male maxillary palpus is very short (0.09-0.18 length of proboscis); **in the female genitalia by** (1) lower vaginal sclerite is present, (2) insula is ill-defined, small, and has few tiny tuberculi in subgenera *Neomacleaya* and *Verrallina* or insula is absent in subgenus *Harbachius* and replaced by an U-shaped median apical sclerotized portion of lower vaginal sclerite, (3) spermathecal eminence is well defined and heavily pigmented, (4) three heavily pigmented spermathecal capsules are present and each is different in size and usually has a short neck, (5) tergum IX is short, wide, and without setae (except two species), (6) upper vaginal sclerite is very large and moderately to heavily pigmented, (7) cercus is more or less triangular in outline and usually has numerous broad scales and (8) tergum VIII and sternum VIII each has numerous broad scales covering most of surface; **in the male genitalia by** (1) phallosome is complex and developed into opisthophallus, phallus, prosophallus, paramere and basal piece, (2) tergum IX is without setae, (3) gonostylus is without a gonostylar claw, (4) proctiger is without cercal setae and paraprocts are usually highly modified into short or long free projections or broad contiguous plates, (5) phallus has a tergal penis filament apically, (6) gonocoxite has one or more well developed lobes or fleshy projections or spiniforms on dorsoapical and/or ventroapical areas (except in two species) and (7) sternum IX is large, heavily pigmented throughout, and has several to numerous setae (usually six or more setae; except one species with only two or three setae); **in the pupae by** (1) setae 1-3-CT are approximately equally developed, (2) setae 6,9-VII are both relatively short and weakly developed, (3) seta 9-VII is single (rarely 2-branched; *Ve. cyrtolabis* usually is single or 2-branched but one specimen was single on one side and 5-branched on the other), (4) seta 9-VIII is single to 6-branched, short to moderately long, and normally thin, (5) seta 1-Pa is single or occasionally 2-branched, (6) bases of setae 2,3-I are widely separated, (7) paddle

is without a fringe of hairlike spicules, (8) setae 1,3-IV are branched (usually multiple-branched, rarely single), (9) seta 3-II,III is moderately long to long and single (3-II apparently occasionally 2-branched in two species) and (10) seta 3-I is branched (very rarely single) and short to moderately long; **in the fourth-instar larvae** by (1) arrangement and development of setae 4-7-C (i.e., seta 4-C is short, multiple-branched and mesad and slightly cephalad of seta 6-C; seta 5-C is caudad and slightly mesad of seta 6-C and laterad and caudad of seta 4-C, bases of setae 5,6-C are widely separated; seta 7-C is laterad and slightly cephalad of seta 6-C or seta 7-C is laterad and at same level as seta 6-C in a few species; setae 5-7-C are stout, branched and approximately equal in length or 7-C is only slightly shorter than 5,6-C (*Ve. unca* has seta 6-C single)), (2) seta 11-C is very short to short and multiple-branched, (3) antennal shaft has numerous spicules, seta 2-A has a subapical constriction, and 2-6-A are all situated apically, (4) seta 7-II is short and branched and seta 7-I is long and single to 3-branched, (5) seta 8-P is long, thickened and usually single (occasionally 2-branched, very rarely 3-branched), (6) setae 1,3-VII are both short and multiple-branched, seta 4-VII is branched (rarely single), (7) seta 8-III-V is single and short, (8) setae 4-M and 2-T are branched, (9) seta 2-X is moderately long and multiple-branched (single in one species) and seta 3-X is very long and single, (10) seta 2-VIII is longer than seta 1-VIII (? except some published illustrations of *Neomacleaya*), (11) seta 6-S is single (occasionally 2-branched), short and seta 8-S is short and usually multiple-branched, (12) saddle incompletely rings segment X, is without spines on posterior margin and acus is absent, (13) pecten has 6-20 (usually 12-16) spines, distal 1-5 spines are wider spaced than remainder, (14) siphon has an acus, (15) setae 5,6-P are single (*Ve. nigrotarsis* is 2-branched) and (16) ventral brush (seta 4-X) usually has 10 setae on grid and two or three precratal shorter setae, all are multiple-branched; and **in the eggs** by (1) width having a pronounced narrowness relative to length, (2) micropylar disk large and (3) outer chorionic cells have ventral and dorsal surfaces differing in structure (it should be noted that the egg is known in only seven species of the genus, only *Ve. funerea* is completely described in detail, and that generic features may become better defined when eggs of more species are fully described and illustrated).

**DISTRIBUTION.** Genus *Verrallina* occupies a geographical range primarily in the Oriental Region from India and Sri Lanka throughout Southeast Asia with an extension north to Japan (Kyushu) and east into the Caroline Islands, New Guinea and southern Pacific islands and south into northeastern Australia. Ranges for subgenera *Harbachius*, *Neomacleaya* and the two series of *Verrallina* are outlined on the map in Figure 1.

## KEYS TO SUBGENERA

### ADULTS

Mesepimeron without fine hairlike setae posteriorly or ventrally to scale patch; tarsus III of both females and males with ungues toothed; eyes separated dorsally .....  
 .....*Harbachius*

Mesepimeron with few to numerous fine hairlike setae posteriorly and/or ventrally to scale patch; tarsus III of both females and males with ungues simple; eyes contiguous dorsally .....*Neomacleaya, Verrallina*

### FEMALE GENITALIA

1. Spermathecal eminence with cephalad produced pouch; insula absent but replaced with U-shaped median apical projection of lower vaginal sclerite, without tuberculi; upper vaginal lip with median area produced into horizontal shield extending over or around spermathecal eminence .....*Harbachius*  
 Spermathecal eminence without pouch; insula ill-defined, small, with few tiny to small tuberculi; upper vaginal lip otherwise .....2
2. Upper vaginal lip with median posterior area developed into large vertical shield caudad of spermathecal eminence; spermathecal eminence deep, complex and with numerous well developed spicules .....*Neomacleaya*  
 Upper vaginal lip without vertical shield; spermathecal eminence shallow, relatively simple, without spicules (except with spicules in Butleri Series) .....*Verrallina*

### MALE GENITALIA

1. Prosophallus very long, greater than 2 times length of phallus; paramere very long, greater than 1.5 times length of phallus .....*Harbachius*  
 Prosophallus and phallus approximately equal in length; paramere noticeably shorter than or moderately long and approximately equal to length of phallus .....2
2. Phallus consisting of pair of moderately long to very long aedeagal sclerites joined mesally at bases by sternal bridge and with narrow, moderately long projection basolaterally extending at approximately right angle; prosophallus consisting of pair of moderately long to long, heavily pigmented, narrow sclerites; paramere moderately long, approximately equal to length of phallus .....*Neomacleaya*  
 Phallus consisting of pair of moderately long aedeagal sclerites joined mesally near midlength by sternal bridge, apices of sclerites contiguous and legs angled outward presenting an A-shaped appearance; prosophallus consisting of pair of moderately long, lightly pigmented sclerites developed into series of overlapping, flattened, leaf-like plates apically<sup>1</sup>; paramere short, noticeably shorter than length of phallus .....*Verrallina*

**PUPAE**

1. Trumpet with basal 0.4 somewhat expanded; lateralia with area of well developed cuticular ocular facets of compound eye .....*Harbachius*  
 Trumpet with basal 0.4 usually not expanded, with more or less uniform width throughout or with apical area expanded; lateralia without or with area of poorly to moderately developed cuticular ocular facets of compound eye .....2
2. Seta 2-IV-VI (in most species) thin, with bases more caudad than bases of setae 4-IV-VI; seta 9-VIII usually single or 2-branched .....*Neomacleaya*  
 Seta 2-IV-VI (in most species) somewhat stouter, with bases more cephalad than bases of setae 4-IV-VI; seta 9-VIII usually with 3-6 branches (except single or 2-branched in Butleri Series) .....*Verrallina*

**FOURTH-INSTAR LARVAE**

1. Seta 1-A single or 2-branched<sup>2</sup>; seta 7-C usually with 2-4 (range 2-7) branches<sup>2</sup> .....  
 .....*Harbachius*  
 Seta 1-A with 3-9 branches<sup>3</sup>; seta 7-C with 5-17 branches .....2
2. Seta 7-I with 2,3 branches; seta 2-X with 5 or more branches; comb scales with stout median apical spine and small denticles on basolateral area .....*Neomacleaya*  
 Seta 7-I single; seta 2-X with 2,3 branches (rarely single or with 4-8 branches); comb scales rounded apically and with uniformly developed short denticles on lateral and apical margins (except two species of Butleri Series with a median apical spine) .....  
 .....*Verrallina*

<sup>1</sup>*Verrallina lugubris* with single leaf-like plate per prosophallic sclerite.

<sup>2</sup>*Verrallina cononensis* (Reinert) with one aberrant larva and with seta 1-A single on one side and 3-branched on other and seta 7-C with 7 branches on one side.

<sup>3</sup>*Verrallina indica* rarely with seta 1-S with 2 branches.

SUBGENUS *HARBACHIUS* REINERT, NEW SUBGENUS

Type species: *Aedes yusafi* Barraud, 1931

*Verrallina* in part of Leicester 1908:198; Brunetti 1912:491.

*Skusea* in part of Theobald 1910a:33, 1910b:491.

*Aedes* in part of Edwards 1913:230, 1922b:264; Brunetti 1920:144; Senior-White 1923:55; Yamada 1932:228.

*Aedes* (*Aedes*) of Edwards 1917:222 (in part), 1922b:468 (in part), 1932:176 (in part); Barraud 1928:364 (in part), 1931:612 (in part), 1934:281 (in part); Laffoon 1946:230 (in part); LaCasse and Yamaguti 1950:100; Sasa et al. 1950:635; Knight and Hull 1951:215 (in part), 1953:471 (in part); Stone and Knight 1956:227; Bohart 1956:32; Hara 1957:63 (in part); Stone et al. 1959:204 (in part); Moriya et al. 1973:54; Knight and Stone 1977:70 (in part); Knight 1978:15 (in part).

*Aedes* (? *Aedimorphus*) of Hsiao and Bohart 1946:23.

*Aedes* (*Neomacleaya*) of Delfinado 1967:4 (in part), 1968:2 (in part); Stone 1970:153 (in part); Basio 1971:22 (in part); Klein 1973:5 (in part); Stone and Delfinado 1973:302 (in part); Reinert 1973:252; Hochman and Reinert 1974:7 (in part); Harrison et al. 1974:153 (in part); Tenorio 1976:54 (in part); Knight and Stone 1977:115 (in part); Kaur 1992:374 (in part).

*Aedes* (*Verrallina*) of Reinert 1974:11 (in part), 1976:206 (in part), 1977:366, 1984:12 (in part), 1999a:78 (in part); Tenorio 1976:54 (in part); Sasa et al. 1977:159 (in part); Knight 1978:34 (in part); Miyagi and Toma 1979:16 (in part); Tanaka et al. 1979:439 (in part); Jayasekera and Chellian 1981:7 (in part); Apiwathnasorn 1986:15 (in part); Townsend 1990:35 (in part); Darsie et al. 1992:26; Ward 1992:191 (in part); Stojanovich and Scott 1995:70.

The following are primary features of the subgenus.

**ADULTS.** *Head.* Eyes separated dorsally. *Thorax.* Mesepimeron without fine hairlike setae posteriorly or ventrally to scale patch. *Legs.* Posttarsus III of both female and male with unguis toothed.

**FEMALE GENITALIA.** *Lower vaginal sclerite.* Forming pair of heavily pigmented, ribbonlike plates along floor of vagina and attached to lower vaginal lip throughout entire length, fused at apex and developed into median, U-shaped projection, sclerite without spicules. *Postgenital lobe.* Relatively narrow, apex with shallow median indentation or broadly rounded. *Insula.* Absent but apparently replaced with median apical U-shaped projection of lower vaginal sclerite, without tuberculi. *Spermathecal eminence.* Relatively simple, shallow, without spicules, with heavily pigmented spinelined pouch cephalad. *Upper vaginal lip.* With median posterior area produced into large horizontal shield extending over or around spermathecal eminence. *Tergum VIII.* Moderately long, moderately wide, index about 0.58-0.80, scaled area reduced and more distal. *Sternum VIII.* With numerous stouter setae on pair of median apical lobes, scaled areas smaller.

**MALE GENITALIA.** *Gonocoxite.* Basotergal apodeme moderately broad. *Proso-phallus.* Consisting of pair of very long, narrow, heavily pigmented sclerites approximated apically, greater than two times length of phallus. *Phallus.* Consisting of pair of short to moderately long aedeagal sclerites joined mesally at bases by sternal bridge, with narrow, short to moderately long projections basolaterally extending at approximately right angles. *Opisthophallus.* Usually long,

occasionally moderately long, with caudal margin sharply rounded or pointed mesally. *Paramere*. Very long, greater than 1.5 times length of phallus. *Basal piece*. Very long.

**PUPAE.** *Cephalothorax*. Lateralial with area of well developed cuticular ocular facets of compound eye. *Trumpet*. Usually with basal 0.4 somewhat expanded. *Abdomen*. Seta 2-IV-VI thin, with bases more cephalad than bases of seta 4-IV-VI; seta 9-VIII usually with 2,3 branches.

**FOURTH-INSTAR LARVAE.** *Head*. Seta 7-C usually with 2-4 (range 2-7) branches (single on one side of one aberrant specimen of *Ve. consonensis*); seta 8-C branched; seta 13-C with 2-5 branches (rarely single). *Antenna*. Seta 1-A single or 2-branched (one aberrant specimen 7-branched on one side of *Ve. consonensis*). *Abdomen*. Seta 7-I single; seta 2-X with 3-6 branches; comb scales with stout median apical spine and short denticles basolaterally.

***Verrallina (Harbachius) yusafi* (Barraud)**

(Figs. 2, 6, 10, 14, 20)

*Verrallina yusafi* is the type species of subgenus *Harbachius* and is completely described below.

**FEMALE.** *Head*. Antenna dark brown, 1.11-1.21 length of proboscis, pedicel dark brown with few small pale brown scales mesally, flagellomere 1 with basal 0.65-0.80 pale and with several small brown scales near middle, flagellar whorls with 6 dark setae; clypeus dark brown; maxillary palpus with blackish-brown scales, 4-segmented, 0.19-0.21 length of proboscis; proboscis with blackish-brown scales, 1.05-1.19 length of femur I; eyes well separated dorsally; ocular setae blackish-brown, moderately long; head with scales broad, decumbent and blackish-brown except for few short erect forked blackish-brown scales on occiput and very few similar ones caudad of ocular setae, interocular space covered with broad silvery scales, similar scales extending caudally onto vertex for very short distance and laterally short distance on ocular line, broad silvery scales also forming broad stripe from area in front of antepnotum to ocular line on upper lateral surface, postgenal scales pale brown. *Thorax*. Scutal integument dark brown; scutum covered with curved narrow reddish-black scales except for small patch of curved narrow white scales on anterior promontory area, few similar scales on antedorsocentral and lateral scutal fossal areas and at scutal angle; prescutellar space bare; scutellum with patch of curved narrow white scales on each lobe, median lobe also with few curved narrow brown scales basally; dark reddish-black setae on following areas: 2-4 anterior promontory, acrostichal (anterior and posterior), few antedorsocentral, numerous dorsocentral (anterior and posterior), scutal fossal (few anterior, 4-8 lateral and 1,2 posterior), numerous antealar and supraalar, 4,5 posterior medial scutal, 1 parascutellar and scutellar (5-8 long and 3-5 short on lateral lobe, 4-6 long and 4 short on median lobe); pleural integument dark brown; antepnota widely separated, with broad silvery scales, 9-12 long and short dark setae; postpronotum with 5-8 posterior golden-brown setae; proepisternum with patch of broad silvery scales and 6-8 golden setae on upper area; subspiracular area, paratergite, mesomeron and metameron bare; postspiracular area with patch of broad silvery scales, 3-5 golden setae; mesokatepisternum with upper and lower patches of broad silvery scales, 6-8 golden setae; prealar area with 6-12 golden setae; mesepimeron (Fig. 14) with large patch of broad silvery scales near middle, 8-11 golden setae dorsad of scale patch. *Legs*. Coxae I-III with several broad pale scales and few short pale setae; femora I,II each with anterior surface brown-scaled and with white scales forming narrow basal band, I with white scales also on dorsobasal area, II also with narrow longitudinal stripe of white scales extending from base to near apex, III with anterior and posterior surfaces white-scaled with dorsoapical area brown-scaled, I,II with posterior surfaces white-scaled

and with narrow longitudinal brown-scaled stripe from base to apex, stripe ventral on I and dorsal on II; tibiae I-III dark brown-scaled, I also with posteroventral longitudinal white-scaled stripe extending from base to apex, II also with posterior surface white-scaled; tarsi I-III dark brown-scaled; posttarsi (Fig. 20) I-III each with 2 unguis, I-III with unguis equal in size, each with 1 tooth. *Wing*. Dorsal and ventral veins brown-scaled, costa also with few white scales at base, remigium with few white scales and 1 seta on posterior margin; alula with several narrow brown scales on margin; upper calypter with several golden setae on margin. *Halter*. Pedicel pale; capitellum dark brown-scaled. *Abdomen*. Terga with blackish-brown scales, I with large rectangular patch of white scales basolaterally, II-VII each with large basolateral patch of white scales extending slightly onto tergal surface; sterna white-scaled, III-VII also with broad apical band of brown scales, VII with white-scaled area reduced; terga and sterna with numerous golden setae. *Genitalia* (Fig. 2). Tergum VIII moderately pigmented, base slightly concave, apex straight, several short and moderately long setae apically, numerous short setae scattered over apical 0.77-0.88, basolateral seta absent, covered with minute spicules, numerous broad scales covering apical 0.50-0.65, basal 0.2-0.7 retracted into segment VII, VIII-Te index 0.70-0.79, VIII-Te/IX-Te index 2.67-2.85; sternum VIII moderately pigmented with apical 0.35-0.39 darker, base concave mesally, apex with moderately deep median indentation with small lobe on each side of midline, numerous short stout setae on lobes, numerous short and few moderately long setae scattered over entire surface except basal 0.09-0.14 and small basolateral area, numerous broad scales forming lateroapical patches, apical intersegmental fold unpigmented, VIII-S index 0.67-0.73; tergum IX moderately pigmented with basomedian area lightly pigmented, wide, short, base concave, apex with wide moderately deep median indentation and with 1-4 (usually 3,4) short setae apically on each side of midline, IX-Te index 0.46-0.49; insula absent but replaced with median apical U-shaped portion of lower vaginal sclerite that apparently serves in capacity of insula since it is situated in normal position of insula and lies in space between apical median lobes of sternum VIII; lower vaginal lip lightly to moderately pigmented, forming narrow band along basal 0.75 of area, apical 0.25 not developed, base attached near midpoint of lateral portion of upper vaginal lip, covered with small spicules, lower vaginal sclerite forming heavily pigmented ribbonlike strip attached to lower vaginal lip, extending around lower vaginal membrane and fused at apex forming projected wrinkled U-shaped structure, sclerite apparently replacing apical 0.25 of lower vaginal lip and insula, base of sclerite articulates with lateral winglike projection of spermathecal eminence "pouch"; upper vaginal lip moderately pigmented, narrow, median posterior portion lightly pigmented at base and projecting into large heavily pigmented cephalic shield covering posterior portion of spermathecal eminence, ventral surface of shield attached to caudal surface of spermathecal eminence, upper vaginal sclerite moderately pigmented, very large, well developed, base attached along entire lateral margin of upper vaginal lip and with heavily pigmented apodeme extending from posterolateral margin of upper vaginal lip to anterior mesal area; spermathecal eminence heavily pigmented, shallow in depth, egg-shaped in dorsal outline, heavily pigmented cephalad produced pouch attached to anterior tergal portion of spermathecal eminence, pouch with inner surface lined with numerous hairlike spicules and with basolateral winglike structure on each side; postgenital lobe short, relatively narrow, apex flat or broadly rounded, 8-10 setae on each side of midline, 16-18 total setae, dorsal PGL index 0.96-1.24, ventral PGL index 1.69-1.96; proctiger membranous with minute spicules; cercus more or less triangular in outline, moderately long, broad at base, apex acute, dorsal surface with numerous moderately long and few short setae on apical 0.91-0.95, ventral surface with few short setae along outer area, numerous (12 or more) broad scales on apical 0.75-0.84 of dorsal surface, cercus index 3.10-3.28, cercus/dorsal PGL index 3.10-3.65; 3 sperm-

athecacapsules, 1 large, 1 medium and 1 small in size, heavily pigmented, nearly spherical, few spermathecal capsule pores near orifice; accessory gland duct base lightly to moderately pigmented.

**MALE.** Similar to female in general habitus but with the following differences. *Head.* Antenna plumose, whorls with 8 setae, 1.15-1.27 length of proboscis; maxillary palpus 0.15-0.17 length of proboscis; proboscis 1.01-1.11 length of femur I. *Thorax.* Scutellum with curved narrow brown scales on each lobe, setae (4,5 long and 2,3 short on lateral lobes, 4 long and 2,3 short on median lobe); 5-9 anteprenotal setae; 3-5 postpronotal setae; 4,5 upper proepisternal setae; 1,2 postspiracular setae; 4,5 posterior mesokatepisternal setae; 4-7 prealar setae; 3-7 mesepimeral setae dorsad of scale patch. *Legs.* Tibiae I-III dark brown-scaled; posttarsi (Fig. 20) I-III with 2 unguis, I,II each with unguis unequal in size, larger unguis with 1 tooth, III with unguis equal in size, 1 unguis with 1 tooth. *Wing.* Costa and remigium without white scales. *Abdomen.* Terga with basolateral white-scaled patches smaller; sterna II-VII pale-scaled, VII brown-scaled. *Genitalia* (Fig. 6). Tergum IX heavily pigmented, forming moderately broad band mesally and expanding laterally on each side into triangular lobe, fused with tergum X, setae absent, connected laterally to sternum IX by narrow heavily pigmented band; gonocoxite short, broad, heavily pigmented, basotergal portion of mesal surface membranous with minute spicules, dorsal surface with few short and moderately long setae, 1,2 long setae near area of gonostylus attachment, ventral surface produced into large apicomeral lobe that is heavily pigmented on both sternal and tergal areas, apex expanded into small fingerlike loblet bearing 1 short seta near apex and 4,5 short setae at base, sternal area of lobe with 2 long stout setae at base of outer margin and several short setae over remainder of area, several broad scales on lateral and ventral surfaces of gonocoxite; gonostylus heavily pigmented, moderately long, approximately 0.6 length of gonocoxite, basal 0.28 moderately broad, middle 0.38 expanded and with 44-54 short setae, apical 0.34 narrow, recurved and with apex very heavily pigmented, gonostylar claw absent, attached subapically to gonocoxite; basal mesal lobe broad, moderately pigmented, covered with small spicules, 26-28 very short setae near center of lobe, 2 heavily pigmented short stout spinelike structures near middle of sternomesal margin, lobes connected mesally by broad band (aedeagal guide) forming shallow trough ventrad of distal portion of prosophaallus, sternomesal and outer margins of basal mesal lobe fused with gonocoxite; proctiger with paraproct heavily pigmented, forming long arm that is moderately broad basally and with apical 0.45 acuminate and curved slightly mesad, dorsal surface with few small spicules on basal 0.4 and with small heavily pigmented lump near middle at point of cercus attachment, basosternal area of paraproct forming small broad projection extending ventrad and articulates at point on the dorsomesal surface of basal piece near base of opisthophallus, proctiger strongly fused with tergum X, cercus membranous and without cercal setae; tergum X heavily pigmented, forming plate between proctiger and caudolateral portion of tergum IX, not connected mesally; phallosome complex, opisthophallus--consisting of moderately pigmented tergal transverse bridge between basal pieces, base attached to dorsomesal extension of caudal outer portion of basal piece, located dorsad of phallus and prosophaallus and ventrad of proctiger, phallus--consisting of pair of short, heavily pigmented, narrowly separated aedeagal sclerites joined mesally at bases by sternal bridge, sternolateral area of base with moderately long projections extending at approximately right angles and fused with tergomesal portion of prosophaallus base, apex of phallus forming tergal penis filament consisting of pair of long bars extending cephalad from phallus apex, bars connected by narrow transverse bridge near middle, apical 0.5 of bars curved dorsad and attached to sternal surface of opisthophallus, prosophaallus--consisting of pair of long heavily pigmented acuminate sclerites with bases widely separated and apices contiguous, base of sclerite attached to tergomesal portion of paramere and located ventrad and laterad of phallus, apical portion of sclerite projecting caudad and dorsad of phallus, prosophalic sclerite approximately 2.63 length

of aedeagal sclerite (measured along midline of phallus), paramere--heavily pigmented, broad, long (approximately 2.32 length of aedeagal sclerite), articulates at 2 points near middle with caudal area of basal piece, most inner point of basal piece attached to basosternal area of prosophallic sclerite, basal piece--moderately to heavily pigmented, very long (approximately 1.68 length of paramere), attached near middle of outer surface with moderately broad basotergal apodeme of gonocoxite; sternum IX heavily pigmented throughout, large, broad, strongly attached along lateral surfaces to sternomesal areas of gonocoxites, 2-8 short setae near center of caudal area.

**PUPA** (Fig. 10). Setal branching as recorded in Table 1. *Cephalothorax*. Lateralialia with area of well developed cuticular facets of compound eye; metanotum and areas of cephalothorax heavily pigmented. *Trumpet*. Moderately pigmented; short; hairlike spicules on distal 0.40-0.43 of inner surface; index 3.00-4.13, mean 3.58. *Abdomen*. Seta 6,9-VII weakly developed; 4-VIII with 2-4 branches; 9-VIII single or 2-branched. *Paddle*. Ovoid; with serrations on most of basal 0.85 of outer margin, minute proximally and well developed distally; with minute spicules on distal 0.15 of outer and distal 0.09 of inner margins; midrib reaching apex; seta 1-Pa weakly developed, moderately long, single; index 1.27-1.47, mean 1.34.

**FOURTH-INSTAR LARVA** (Fig. 14). Setal branching as recorded in Table 5. *Head*. Seta 4-C with 3,4 branches; 5-C single or 2-branched; 6-C with 2,3 branches; 7-C with 2-4 branches; 13-C single to 3-branched (rarely single). *Mouthparts*. Dorsomentum with 29-34 teeth. *Antenna*. Short, lightly pigmented, with several small scattered spicules; seta 1-A short, thickened, single; 2-A long; 3-A short, 0.27-0.31 length of 2-A; 4-A moderately long, 0.56-0.62 length of 2-A; 6-A short, 0.22-0.37 length of 2-A. *Abdomen*. Seta 6-I single (rarely 2-branched); 7-I single; 3-IV with 3,4 branches; 1-VIII with 2,3 branches; 5-VIII with 5,6 branches; 2-X with 3,4 branches, approximately equal in length; ventral brush (4-X) with 8 setae on grid and 2 precratal shorter ones, all multiple-branched; 4 moderately long anal papillae; comb consisting of 8-12 scales arranged in single slightly curved irregular row, each scale with stout median apical spine and small denticles basolaterally. *Siphon*. Moderately pigmented; acus well developed; index 1.58-2.08, mean 1.82; pecten on basal 0.56-0.58 of siphon, consisting of 11-15 (usually 14) spines, apical 1,2 spines longer and wider spaced than remainder, each spine long, slender and with small stout denticle basoventrally; seta 1-S short, with 2-4 branches, base attached on basal 0.67-0.68 of siphon distad of last pecten spine.

**EGG**. Unknown.

#### SPECIES INCLUDED IN SUBGENUS *HARBACHIUS*

- |  |  |
|--|--|
| 1. <i>Ve. (Har.) abdita</i> (Barraud)        | 8. <i>Ve. (Har.) ramalingami</i> (Reinert)   |
| 2. <i>Ve. (Har.) consonensis</i> (Reinert)   | 9. <i>Ve. (Har.) robertsi</i> (Laffoon)      |
| 3. <i>Ve. (Har.) fragilis</i> Leicester      | 10. <i>Ve. (Har.) srilankensis</i> (Reinert) |
| 4. <i>Ve. (Har.) hamistylus</i> (Laffoon)    | 11. <i>Ve. (Har.) stunga</i> (Klein)         |
| 5. <i>Ve. (Har.) indecorabilis</i> Leicester | 12. <i>Ve. (Har.) uniformis</i> (Theobald)   |
| 6. <i>Ve. (Har.) nobukonis</i> (Yamada)      | 13. <i>Ve. (Har.) yusafi</i> (Barraud)       |
| 7. <i>Ve. (Har.) pahangi</i> (Delfinado)     |  |

SUBGENUS *NEOMACLEAYA* (THEOBALD), NEW STATUS

- Neomacleaya* Theobald, 1907:238 (type species: *Neomacleaya indica* Theobald, 1907:238; monobasic).
- Aioretomyia* Leicester, 1908:185 (type species: *Aioretomyia Varietas* Leicester, 1908:185; first of 6 new species, selected by Brunetti 1914:55).
- Skusea* in part of Theobald 1907:544, 1910a:32, 1910b:488; Brunetti 1914:55.
- Verrallina* in part of Leicester 1908:197; Brunetti 1912:492.
- Neomacleaya* of Theobald 1908:291, 1910b:243; Brunetti 1912:458, 1914:66.
- Aioretomyia* of Brunetti 1912:490 (in part).
- Aedes* of Edwards 1913:229 (in part), 1922a:264 (in part), 1922b:264 (in part); Brunetti 1920:142 (in part); Senior-White 1923:53 (in part); Stojanovich and Scott 1965:11 (in part), 1966:47 (in part); Stone et al. 1966:50 (in part); Darsie et al. 1991:41.
- Culex* of Brunetti 1914:66.
- Aedes* (*Aedes*) of Edwards 1917:221 (in part), 1922a:272, 1922b:468 (in part), 1928:273, 1932:175 (in part); Dyar and Shannon 1925:79 (in part); Edwards and Given 1928:344 (in part); Barraud 1928:364 (in part), 1931:613 (in part), 1934:282 (in part); Borel 1930:283 (in part); Brug 1931:249, 1932:79 (in part); Taylor 1934:21 (in part); Bohart 1945:65 (in part); Laffoon 1946:235 (in part); King and Hoogstraal 1947:119 (in part); Carter 1950:89 (in part); Menon 1950:139; Wijesundara 1951:173 (in part); Knight and Hull 1951:214 (in part), 1953:472 (in part); Stone and Knight 1956:220 (in part); Stone 1956:339, 1958:69, 1967:210; Iyengar and Menon 1956:791 (in part); Stone et al. 1959:204 (in part); Iyengar 1960:69 (in part); Qutubuddin 1960:136; Kurihara 1965:21; Army Mosquito Project 1965:33 (in part); Knight and Stone 1977:70 (in part).
- Aedes* (subgenus ?) of Belkin 1962:422.
- Aedes* (*Verrallina*) of Steffan 1966:213 (in part); Huang 1968:41 (in part); Stone 1970:153 (in part); Basio 1971:32 (in part); Reinert 1974:12 (in part), 1976:206 (in part), 1978:225, 1984:11 (in part), 1999a:78 (in part); Tenorio 1976:54 (in part); Knight and Stone 1977:168 (in part); Sasa et al. 1977:159 (in part); Knight 1978:34 (in part); Miyagi and Toma 1979:16 (in part); Tanaka et al. 1979:443 (in part); Jayasekera and Chellian 1981:12 (in part); Rattanarithikul 1982:176 (in part); Tsukamoto and Horio 1985:494 (in part); Apiwathnasorn 1986:14 (in part); Lee et al. 1987:251 (in part); Tewari and Hiriyani 1988:28, 1994:36; Lu et al. 1988:51 (in part); Evenhuis and Gon 1989:203 (in part); Townsend 1990:36 (in part); Darsie and Pradhan 1990:108; Ward 1992:191 (in part).
- Aedes* (*Neomacleaya*) of Delfinado 1967:3 (in part), 1968:2 (in part); Stone 1970:153 (in part); Basio 1971:21 (in part); Klein 1973:2 (in part); Tanaka and Mizusawa 1973:625; Stone and Delfinado 1973:302 (in part); Hochman and Reinert 1974:7 (in part); Harrison et al. 1974:153 (in part); Tenorio 1976:54; Knight and Stone 1977:115 (in part); Kaur 1992:373 (in part).

The following are primary features of the subgenus.

**ADULTS.** *Head.* Eyes contiguous dorsally or nearly contiguous. *Thorax.* Mesepimeron with fine hairlike setae posteriorly and/or ventrally to scale patch (some species with numerous setae extending to near ventral margin of mesepimeron). *Legs.* Posttarsus III of both female and male with ungues simple.

**FEMALE GENITALIA.** *Lower vaginal sclerite.* Large, heavily pigmented, well developed, not contiguous with lower vaginal lip, usually spiculate. *Postgenital lobe.* Relatively narrow, with apex having deep to very deep median indentation. *Insula.* Ill-defined, small, with few tiny tuberculi. *Spermathecal eminence.* Complex, deep, with numerous well developed spicules (less developed in *Ve. incerta*, *Ve. panayensis* (Ludlow) and *Ve. rara*), without spinelined pouch cephalad. *Upper vaginal lip.* With median posterior area developed into large vertical shield caudad of spermathecal eminence. *Tergum VIII.* Short, noticeably wider than long, index about 0.35-0.57, nearly entire surface covered with numerous broad scales. *Sternum VIII.* With numerous thin setae on pair of median apical lobes, much of surface covered with broad scales.

**MALE GENITALIA.** *Gonocoxite.* Basotergal apodeme moderately broad. *Proso-phallus.* Consisting of pair of moderately long to long, narrow, heavily pigmented sclerites separated apically, approximately equal in length to phallus. *Phallus.* Consisting of pair of moderately long to very long aedeagal sclerites joined mesally at bases by sternal bridge and with narrow, moderately long projection basolaterally extending at approximately right angles. *Opisthophallus.* Short, caudal margin flat or concave mesally. *Paramere.* Moderately long, approximately equal in length to phallus. *Basal piece.* Short to moderately long.

**PUPAE.** *Cephalothorax.* Lateralia with area of moderately developed cuticular ocular facets of compound eye. *Trumpet.* Usually with apical portion expanded. *Abdomen.* Seta 2-IV-VI (in most species) thin, with bases more caudad than bases of seta 4-IV-VI; seta 9-VIII usually single or 2-branched.

**FOURTH-INSTAR LARVAE.** *Head.* Seta 7-C usually with 7-14 (range 5-17) branches; seta 8-C branched (Delfinado 1967, Fig. 3 of *Ve. atrius* shows 8-C single); seta 13-C short, usually with 3-5 (range 2-6) branches. *Antenna.* Seta 1-A with 3-6 branches (rarely 2-branched in *Ve. indica*). *Abdomen.* Seta 7-I long, with 2,3 branches; seta 2-X multiple-branched (with 5 or more branches); comb scales with stout median apical spine and smaller denticles on basolateral areas.

### *Verrallina (Neomacleaya) indica* (Theobald)

(Figs. 3, 7, 11, 14, 15, 18, 20)

*Verrallina indica* is the type species of subgenus *Neomacleaya* and is completely described below.

**FEMALE** (Fig. 18). *Head.* Antenna dark brown, 0.98-1.06 length of proboscis, pedicel dark brown with few small dark scales and short fine dark setae mesally, flagellomere 1 with basal 0.65 pale and with several small dark scales near middle; clypeus dark brown; maxillary palpus with blackish-brown scales, 0.16-0.20 length of proboscis; proboscis with blackish-brown scales, 1.14-1.26 length of femur I; eyes nearly contiguous dorsally; vertex with broad dark brown decumbent scales except for few curved narrow white scales on interocular space, ocular line with curved narrow white scales, coronal suture with row of curved narrow white scales on each side and extending from occiput to near ocular line; ocular setae dark brown, well developed; occiput with numerous short brown erect forked scales and few broad and curved narrow decumbent white scales; postgena with narrow stripe of broad white scales extending from area in front of antepnotum to ocular line, lower area with broad cream-colored scales. *Thorax.* Scutal integument dark brown; scutum covered with curved narrow dark reddish-brown scales except for curved narrow white scales on anterior promontory area, antedorsocentral area, supraalar area and along lateral margins of prescutellar area; prescutellar area bare; dark reddish-black setae on following areas: 2-5 on anterior promontory, numerous acrostichals (anterior and posterior), few

antedorsocentral, numerous dorsocentral (anterior and posterior), scutal fossal (few anterior, 3-8 lateral, 1-3 median and 2-5 posterior), several prescutellar, numerous antealar and supraalar, 5-7 posterior medial scutal; scutellum with patch of curved narrow white scales on each lobe, few similar brown scales basally on median lobe, 10-17 dark setae on lateral lobe, 10-14 dark setae on median lobe; pleural integument dark brown; antepronotum without scales, 13-24 long and short dark setae; postpronotum with curved narrow brown scales on upper area, several similar white ones on posterior area cephalad of setae, 4-8 dark setae; proepisternum with patch of broad white scales and 8-20 setae on upper area; postspiracular area with several curved narrow and occasionally few moderately broad white scales, 6-10 dark setae; paratergite occasionally with few curved narrow white scales laterally; mesokatepisternum with upper and lower patches of broad white scales, 3,4 upper and 9-15 lower dark setae; prealar area with 1-3 long moderately broad scales in some specimens, 9-14 dark setae; mesepimeron (Fig. 14) with median patch of broad white scales, dorsal ones longer and somewhat narrower, 10-20 setae (several short and fine) dorsad of scale patch (also few long scales usually dorsad of setae), 2-4 short fine hairlike golden setae along posterior margin of scale patch; other pleural areas bare. *Legs.* Coxae I-III with several dark setae, I with broad brown scales and small dorsal patch of broad white scales on anterior surface, II,III with patch of broad white scales on outer area of anterior surfaces; trochanters I-III with few short setae and few broad pale scales; femora I,II with anterior surfaces brown-scaled, I with scales paler brown, II also with narrow longitudinal anteroventral pale-scaled stripe, III also with most of basoanterior area pale-scaled, I-III also with few white scales on anterior and posterior surfaces apically, posterior surfaces mainly pale-scaled, I with narrow longitudinal posteroventral brown-scaled stripe, II,III with posterodorsal longitudinal brown-scaled stripe narrower basally and broader apically; tibiae I-III dark brown-scaled, I,III also with broad posteroventral longitudinal pale-scaled stripe, II with posterior surface pale-scaled; tarsi I-III dark brown-scaled; posttarsi (Fig. 20) I-III with 2 ungues, I,II each with ungués equal in size, each with 1 tooth, III with ungues equal in size, both simple. *Wing.* Dorsal and ventral veins dark brown-scaled; alula with several moderately broad and few narrow brown scales on margin; upper clypter with several pale setae on margin; 1-3 remigial setae. *Halter.* Pedicel pale; capitellum with creamy-white scales and with dorsal scales pale brown. *Abdomen.* Terga with blackish-brown scales and white-scaled markings as follow: I with few scales on dorsomedian area and basolateral patch, II-VII with narrow basolateral patch, II-IV and occasionally V also with dorsomedian transverse band extending cephalad onto lateral margin and joined to basolateral patches, VIII with number of scattered scales; sterna brown-scaled with basolateral pale-scaled areas; terga and sterna with numerous golden seta, mostly along posterior margins. *Genitalia* (Fig. 3). Tergum VIII with numerous broad scales on apical 0.59-0.76, basal 0.40-0.65 retracted into segment VII, moderately pigmented with lightly pigmented median basal area, wide, base slightly concave, apex gently convex, numerous short and moderately long thin setae at apex and similar ones scattered over apical 0.50-0.74; basolateral seta present; VIII-Te index 0.54-0.60, VIII-Te/IX-Te index 3.87-6.84, length 0.29-0.34 mm, width 0.50-0.59 mm; sternum VIII with numerous broad scales covering most of apical 0.75-0.87, moderately pigmented, wide, base concave mesally, apex with shallow (0.04-0.06 of length) median indentation and with small lobe on each side of midline, numerous moderately long setae apically, more numerous and slightly stouter on apical lobes, numerous short and few moderately long setae scattered over apical 0.76-0.92, apical intersegmental fold unpigmented, VIII-S index 0.57-0.68, length 0.30-0.33 mm, width 0.36-0.55 mm; tergum IX moderately pigmented, very wide and short, ribbonlike, setae absent, IX-Te index 0.14-0.29, length 0.05-0.09 mm, width 0.28-0.35 mm; insula ill-defined, short, unpigmented, with 3-7 small tuberculi, each with minute to small spicule; lower vaginal lip heavily pigmented, without spicules except few on outer margin of hinge area, with small caudally

projecting heavily pigmented median structure, lower vaginal sclerite consisting of pair of sigmoid-shaped heavily pigmented sclerites lateromesally on elevated portion of membrane extending over area between vaginal lip; upper vaginal lip heavily pigmented, complex, lateral surfaces forming wide parallel plates produced into sharp posterior angles and curved sternally and then mesally to form continuous band, stout arm extending mesally from near midpoint of dorsal surface of lateral area and forming large continuous upright shield surrounding posterior portion of spermathecal eminence, spicules only along posterior margin of upper vaginal lip, upper vaginal sclerite heavily pigmented, extremely large and complex, base attached along entire lateral margin of upper vaginal lip except for short posterior portion, large caudal arm extending mesally and forming crown around posterior portion of spermathecal eminence, posterior area of sclerite unpigmented, cephalic arm very large and forming continuous broad band around anterior of spermathecal eminence, band wrinkled, fenestrated and with mesal transverse slit; spermathecal eminence heavily pigmented, large, deep, ovoid in dorsal outline, long spicules with lateral projections attached to cephalic area; combined spermathecal eminence, upper vaginal lip and upper vaginal sclerite covering nearly entire upper vaginal wall with heavily pigmented structures; postgenital lobe short, narrow, apex with moderately deep (0.11-0.29 of dorsal length) median indentation, 5-15 setae on each side of midline, 11-28 total setae, dorsal PGL index 0.89-1.78, ventral PGL index 1.06-1.70, ventral length 0.08-0.13 mm; cercus triangular in outline, moderately long, broad at base, apex acute, with numerous (usually 14 or more) broad scales scattered over dorsal surface and with numerous moderately long and few short setae scattered over apical 0.87-0.94, ventral surface with several short and moderately long setae on outer 0.4-0.5, cercus index 2.95-3.97, cercus/dorsal PGL index 3.64-4.63, cercus length 0.30-0.36 mm; 3 spermathecal capsules, 1 large, 1 medium and 1 small in size, heavily pigmented, elliptical, each with moderately broad pigmented neck; accessory gland duct base unpigmented to lightly pigmented.

**MALE.** Essentially as in the female but with the following differences. *Head.* Antenna plumose, 10,11 setae in whorls, 0.98-1.14 length of proboscis; maxillary palpus 0.12-0.18 length of proboscis; proboscis 1.06-1.24 length of femur I; vertex without narrow scales on coronal suture. *Thorax.* Setal differences as follow: 2-4 on anterior promontory, scutal fossal (few anterior, 4,5 lateral, 1,2 median and 2-4 posterior), scutellum with 6-10 on lateral lobe and 6-12 on median lobe, 7-11 on antepronotum, 3-5 on postpronotum, 7-10 on upper proepisternum, 2,3 on postspiracular area, 2,3 upper and 7-10 lower on mesokatepimeron, 5-8 on prealar area; mesepimeron with 5-9 dorsad of scale patch and 1,2 fine hairlike setae posterior to patch. *Legs.* Posttarsi (Fig. 20) I-III with 2 ungues, I,II each with ungues unequal in size, larger unguis with 1 tooth, III with ungues equal in size, both simple. *Abdomen.* Terga with basolateral white-scaled patches usually extending slightly onto dorsal surfaces. *Genitalia* (Fig. 7). Tergum IX heavily pigmented, band-like with lateral areas broad, cephalic margin evenly concave, outer caudal margin fused to tergum X, broadly connected laterally to sternum IX; gonocoxite with apex of dorsal surface extending into long broad flattened lobe bearing 2-5 short setae arranged in small patch on basomesal area, several short and long stout setae on apical 0.8, ventral surface with several short and long stout setae on apical 0.6, several broad scales on ventral and lateral surfaces; gonostylus moderately pigmented, moderately long (approximately 0.73 length of gonocoxite minus apical lobe), narrow, curved, base with small lobe, apex pointed and tip recurved, 1-3 short thin setae subapically; basal mesal lobe moderately pigmented, consisting of proximal area bearing 11-19 short thin setae dorsally and 10-22 short stout flattened acuminate setae on mesal surface, broad flat area extending onto mesal membrane of gonocoxite bearing 4-10 short fine setae and minute spicules, and apical long curved arm resembling gonostylus in form; proctiger with paraproct forming heavily pigmented long slender slightly curved acuminate arm with basal area expanded and connected to tergum IX, base of

proctiger lightly fused with tergum X; tergum X heavily pigmented, consisting of small rectangular plate laterad of paraproct base and extending ventrad from caudal margin of tergum IX; phallosome complex, opisthophallus--consisting of lightly to moderately pigmented tergal transverse bridge between basal pieces, caudal margin slightly indented mesally, basosternal area attached to basotergal portion of outer area of prosophallus, phallus--consisting of pair of moderately long aedeagal sclerites joined together by narrow basal bridge, sternolateral area of base with moderately long projection extending laterally at approximately right angles and fused to basotergal portion of prosophalic sclerite, apex of phallus forming tergal penis filament and consisting of small lightly pigmented sclerotized lobe produced cephalad, prosophallus--consisting of pair of moderately long acuminate prosophalic sclerites, each sclerite with distal portion heavily pigmented and slightly curved, proximal portion lightly pigmented, forming broadly rounded area and attached to tergomal portion of paramere, prosophalic sclerite approximately equal in length to aedeagal sclerite, paramere--approximately equal in length to aedeagal sclerite, articulating at point approximately 0.65 from base with caudal area of basal piece, basal piece--moderately to heavily pigmented, moderately long, attached to moderately broad apodeme of gonocoxite; sternum IX with lateroapical areas rounded, 13-19 short and moderately long setae in elongate patch along caudal margin.

**PUPA** (Fig. 11). Setal branching as recorded in Table 2. *Cephalothorax*. Moderately to heavily pigmented; lateralia with area of moderately developed cuticular ocular facets of compound eye; seta 5-CT with 3-5 branches. *Trumpet*. Heavily pigmented; index 2.53-3.45, mean 2.88. *Abdomen*. Terga moderately pigmented; seta 1-II with 4-7 (usually 6,7) branches; 2-II laterad of 3-II; 1-III with 3,4 branches; 5-IV with 2,3 branches; 1-V single to 3-branched (usually 2-branched); 1-VI with 2-4 (usually 2) branches; 3-VII with 2-6 (usually 2-4) branches; 9-VIII single or 2-branched. *Paddle*. Ovoid; with minute serrations on most of basal 0.68-0.72 of outer margin; with minute spicules on apical 0.35-0.38 of outer and apical 0.13-0.15 of inner margins; seta 1-Pa single, moderately long; index 1.43-1.68, mean 1.56.

**FOURTH-INSTAR LARVA** (Fig. 15). Setal branching as recorded in Table 6. *Head*. Moderately to heavily pigmented; patch of small spicules over compound eye; seta 4-C with 2-5 (usually 4,5) branches; 5-C with 3 branches; 6-C with 1 branch noticeably longer than others; 7-C with 7-12 branches; 13-C with 3-5 branches. *Mouthparts*. Dorsosentrum with 35-40 teeth. *Antenna*. Moderately long; moderately pigmented; several small spicules scattered over entire shaft; seta 1-A with 2,3 (usually 3) branches, moderately long. *Thorax*. Seta 8-P with 2 branches; 3-M single to 3-branched (usually single); 11-M with 2,3 branches. *Abdomen*. Seta 6-I with 3,4 branches; 7-I with 2 branches, occasionally 3-branched; 3-IV with 5-7 branches; 1-VIII with 2-5 branches; 1,2-VIII attached to small common sclerite; 5-VIII with 7-12 branches; 2-X with 7-11 branches; comb consisting of 8-12 (usually 8 or 10) scales arranged in single curved irregular row, each scale with stout median apical spine and small denticles on basolateral areas; 4 anal papillae, moderately long. *Siphon*. Moderately to heavily pigmented; index 1.68-2.37, mean 1.88; pecten on basal 0.56-0.65 of siphon, consisting of 11-15 (usually 12-14) spines, distal 2 spines longer and more widely spaced than remainder, each spine long, slender and with 1-3 small stout denticles basoventrally; seta 1-S with 3-6 branches, short, attached on basal 0.70-0.77 of siphon distad of last pecten spine.

**EGG**. Unknown.

SPECIES INCLUDED IN SUBGENUS *NEOMACLEAYA*

1. *Ve. (Nma.) adusta* (Laffoon)
2. *Ve. (Nma.) agrestis* (Barraud)
3. *Ve. (Nma.) andamanensis* (Edwards)
4. *Ve. (Nma.) atriisimilis* (Tanaka and Mizusawa)
5. *Ve. (Nma.) atrius* (Barraud)
6. *Ve. (Nma.) campylostylus* (Laffoon)
7. *Ve. (Nma.) cauta* (Barraud)
8. *Ve. (Nma.) clavata* (Barraud)
9. *Ve. (Nma.) comata* (Barraud)
10. *Ve. (Nma.) comosa* (Reinert)
11. *Ve. (Nma.) cretata* (Delfinado)
12. *Ve. (Nma.) cyrtolabis* (Edwards)
13. *Ve. (Nma.) gibbosa* (Delfinado)
14. *Ve. (Nma.) harrisonicus* (Reinert)
15. *Ve. (Nma.) hispida* (Delfinado)
16. *Ve. (Nma.) incerta* (Edwards)
17. *Ve. (Nma.) indica* (Theobald)
18. *Ve. (Nma.) johnsoni* (Laffoon)
19. *Ve. (Nma.) johorensis* (Reinert)
20. *Ve. (Nma.) komponga* (Klein)
21. *Ve. (Nma.) lankaensis* (Stone and Knight)
22. *Ve. (Nma.) latipennis* (Delfinado)
23. *Ve. (Nma.) leicesteri* (Edwards)
24. *Ve. (Nma.) macrodixoa* (Dyar and Shannon)
25. *Ve. (Nma.) margarsen* (Dyar and Shannon)
26. *Ve. (Nma.) neomacrodixoa* (King and Hoogstraal)
27. *Ve. (Nma.) nigrotarsis* (Ludlow)
28. *Ve. (Nma.) notabilis* (Delfinado)
29. *Ve. (Nma.) nubicola* (Laffoon)
30. *Ve. (Nma.) panayensis* (Ludlow)
31. *Ve. (Nma.) petroelephantus* (Wijesundara)
32. *Ve. (Nma.) philippinensis* (Delfinado)
33. *Ve. (Nma.) phnoma* (Klein)
34. *Ve. (Nma.) prioekaensis* (Brug)
35. *Ve. (Nma.) protuberans* (Delfinado)
36. *Ve. (Nma.) pseudodiurna* (Theobald) (?)
37. *Ve. (Nma.) pseudomediofasciata* (Theobald)
38. *Ve. (Nma.) pseudovarietas* (Reinert)
39. *Ve. (Nma.) rami* (Barraud)
40. *Ve. (Nma.) rara* (Delfinado)
41. *Ve. (Nma.) sabahensis* (Reinert)
42. *Ve. (Nma.) seculata* (Menon)
43. *Ve. (Nma.) singularis* (Leicester)
44. *Ve. (Nma.) sohni* (Reinert)
45. *Ve. (Nma.) spermathecus* (Wijesundara)
46. *Ve. (Nma.) torosa* (Delfinado)
47. *Ve. (Nma.) unca* (Theobald)
48. *Ve. (Nma.) vallistris* (Barraud)
49. *Ve. (Nma.) varietas* (Leicester)
50. *Ve. (Nma.) virilis* Leicester
51. *Ve. (Nma.) yerburyi* (Edwards)

SUBGENUS *VERRALLINA* THEOBALD

*Verrallina* Theobald, 1903:295 (type species: *Aedes Butleri* Theobald, 1901:230; first of 3 included species, selected by Blanchard 1905:417).

*Aedes* of Theobald 1901:230 (in part); Giles 1902:481; Brunetti 1907:367, 1920:143 (in part); Edwards 1913:229 (in part), 1922a:264 (in part); Senior-White 1923:53 (in part); Mattingly 1956:794; Stojanovich and Scott 1965:11 (in part), 1966:47 (in part); Russell 1996:55 (in part).

*Verrallina* in part of Blanchard 1905:417; Leicester 1908:196; Theobald 1910b:494; Brunetti 1912:491.

*Aedes* (genus uncertain) of Theobald 1905:35.

*Skusea* of Blanchard 1905:417 (in part); Theobald 1907:542 (in part), 1910a:32 (in part), 1910b:488 (in part); Bancroft 1908:55; Taylor 1914a:465.

*Pseudoskusea* of Taylor 1912:27.

*Uranotaenia* of Brunetti 1914:73.

*Lepidotomyia* of Taylor 1914b:191.

*Aedes* (*Aedes*) of Edwards 1917:222 (in part), 1922b:468 (in part), 1932:175 (in part); Dyar and Shannon 1925:81 (in part); Edwards and Given 1928:345 (in part); Barraud 1928:365 (in part), 1934:294 (in part); Paine *in* Paine and Edwards 1929:309; Borel 1930:287 (in part); Brug 1932:79 (in part), 1934:512; Taylor 1934:21 (in part), 1944:76; Bonne-Wepster and Brug 1937:41; Causey 1937:414; Bohart 1945:65 (in part), 1957:65; Laffoon 1946:233 (in part); Bohart and Ingram 1946:29; King and Hoogstraal 1947:115 (in part); Bonne-Wepster 1948:320, 1954:244; Penn 1949:62; Carter 1950:89 (in part); Wijesundara 1951:175 (in part); Knight and Hull 1951:215 (in part), 1953:472 (in part); Stone and Knight 1956:227 (in part), 1977:71 (in part); Iyengar and Menon 1956:789 (in part); Chu 1958:112; Stone et al. 1959:204 (in part); Iyengar 1960:68 (in part); Assem and Bonne-Wepster 1964:102; Army Mosquito Project 1965:33 (in part); Stone et al. 1966:50; Knight and Stone 1977:71 (in part).

*Aedes* (?*Skusea*) of Edwards 1921:76.

*Aedes* (*Skusea*) of Brug 1924:437.

*Aedes* (*Verrallina*) of Belkin 1962:412; Stone 1963:131, 1970:152 (in part); Army Mosquito Project 1965:29; Stone et al. 1966:50; Steffan 1966:213 (in part); Huang 1968:1 (in part); Basio 1971:32 (in part); Marks 1973:66; Stone and Delfinado 1973:310; Reinert 1974:11 (in part), 1976:206 (in part), 1984:10 (in part), 1999a:78 (in part); Hochman and Reinert 1974:8; Matsuo et al. 1974:440; Tenorio 1976:53 (in part); Knight and Stone 1977:167 (in part); Sasa et al. 1977:159 (in part); Knight 1978:34 (in part); Taylor and Maffi 1978:212; Miyagi and Toma 1979:14 (in part); Tanaka et al. 1979:442 (in part); Jayasekera and Chelliah 1981:6; Rattanarithikul 1982:175; Tsukamoto 1982:305; Tsukamoto and Horio 1985:494 (in part); Apiwathnasorn 1986:15 (in part); Lee et al. 1987:251 (in part); Lu et al. 1988:51; Evenhuis and Gon 1989:203 (in part); Townsend 1990:52 (in part); Linley et al. 1991:593; Ward 1992:190 (in part); Reinert and Harbach 1992:253.

*Aedes* (*Neomacleaya*) of Delfinado 1967:4 (in part), 1968:2 (in part); Stone 1970:153 (in part); Basio 1971:21 (in part); Klein 1973:5 (in part); Tanaka and Mizusawa 1973:633 (in part); Stone and Delfinado 1973:302 (in part); Hochman and Reinert 1974:7 (in part); Knight and Stone 1977:116 (in part); Lu and Li 1982:34; Lu and Su 1987:30.

The following are primary features of the subgenus.

**ADULTS.** *Head.* Eyes contiguous dorsally. *Thorax.* Mesepimeron with fine hairlike setae posteriorly and/or ventrally to scale patch. *Legs.* Posttarsus III of both female and male with unguis simple (except male of *Ve. prioekaensis* with tooth on one unguis).

**FEMALE GENITALIA.** *Lower vaginal sclerite.* Small, lightly pigmented and somewhat poorly developed (except see description of Butleri Series below), not contiguous with lower vaginal lip, sclerites usually without spicules. *Postgenital lobe.* Moderately broad, with apex broadly rounded, flat or occasionally with shallow median indentation. *Insula.* Ill-defined, small, unpigmented, with few tiny tuberculi. *Spermathecal eminence.* Relatively simple, consisting of pair of comma-shaped plates, without spicules (except Butleri Series with spicules), without spinelined pouch cephalad. *Upper vaginal lip.* With median posterior area narrow to moderately broad and not produced into vertical shield. *Tergum VIII.* Short to moderately long, moderately

wide, index about 0.44-0.70, much of surface covered with broad scales. *Sternum VIII*. With numerous thin setae on pair of median apical lobes, much of surface covered with broad scales.

**MALE GENITALIA.** *Gonocoxite*. Basotergal apodeme broad. *Prosophallus*. Consisting of pair of moderately long sclerites developed into series of lightly pigmented, overlapping, flattened, leaf-like plates apically, sclerites separated apically, more or less equal in length to phallus (*Ve. lugubris* with single leaf-like plate). *Phallus*. Consisting of pair of moderately long aedeagal sclerites joined mesally near midlength by narrow sternal bridge, apices of sclerites contiguous and legs angled outward presenting A-shaped appearance. *Opisthophallus*. Short to moderately long, with caudal margin gently concave mesally. *Paramere*. Short, noticeably shorter than length of phallus. *Basal piece*. Short to moderately long.

**PUPAE.** *Cephalothax*. Lateralial without or with small area of very poorly developed cuticular ocular facets of compound eye. *Trumpet*. Usually with more or less uniform width throughout length. *Abdomen*. Setae 2-IV-VI (in most species) somewhat thicker and with bases more cephalad than bases of setae 4-IV-VI; seta 9-VIII usually with 3-6 branches (except some species in Butleri Series).

**FOURTH-INSTAR LARVAE.** *Head*. Seta 7-C with 5-14 branches; 8-C single (Carmentis Series) or branched (Butleri Series); seta 13-C single, moderately long (*Ve. butleri*, *Ve. iriomotensis* and *Ve. lugubris* of Butleri Series with 13-C shorter and with 2-4 branches). *Antenna*. Seta 1-A usually with 3-6 (range 3-9) branches. *Abdomen*. Seta 7-I long, single; seta 2-X with 2,3 branches (except with 4-8 branches in few species, e.g., *Ve. butleri*, *Ve. dux*, *Ve. iriomotensis*, *Ve. lineata*, *Ve. variabilis*; single in *Ve. cuccioi*); comb scales rounded apically, with uniformly developed short denticles on lateral and apical margins (*Ve. dux* and *Ve. iriomotensis* with longer median spine).

### BUTLERI SERIES

**FEMALE GENITALIA.** *Lower vaginal sclerite*. Consisting of pair of moderately to heavily pigmented, variously shaped plates, usually with spicules. *Spermathecal eminence*. With spicules.

**MALE GENITALIA.** *Gonocoxite*. Occasionally without but usually with dorsoapical or ventroapical lobes or fleshy projections, without subapical spiniforms on sternomesal area (*Ve. butleri* with spiniform but also with apical projections). *Basal mesal lobe*. Consisting of small plate bearing several short to moderately long thin setae and one or more stout spiniform(s) or lobe(s).

**PUPAE.** *Abdomen*. Seta 9-VIII usually single (*Ve. iriomotensis* single or 2-branched; *Ve. lugubris* with 3-6 branches).

**FOURTH-INSTAR LARVAE.** *Head*. Seta 8-C branched; seta 13-C branched (*Ve. dux* single or 2-branched).

#### *Verrallina (Verrallina) butleri* (Theobald)

(Figs. 4, 8, 12, 14, 16, 19, 20)

*Verrallina butleri* in the nominotypical species of the Butleri Series and the type species of the genus and subgenus *Verrallina* and is completely described below.

**FEMALE** (Fig. 19) *Head*. Antenna dark brown, 1.01-1.11 length of proboscis, pedicel dark brown with few small dark scales and short fine setae mesally, flagellomere 1 with basal 0.25

pale and with several small dark scales near middle; clypeus dark brown; maxillary palpus with blackish-brown scales, 0.17-0.21 length of proboscis; proboscis with blackish-brown scales, 1.17-1.24 length of femur I; eyes contiguous dorsally; vertex covered with broad blackish-brown decumbent scales but with double row of broad white decumbent scales on midline extending anteriorly nearly to ocular line (some specimens with only few white scales); interocular space with 6-8 curved narrow white scales (some specimens with these scales pale brown); ocular setae blackish-brown and well developed; postgena with blackish-brown scales and narrow stripe of white scales extending from area in front of antepnotum to ocular suture; occiput with patch of short erect forked scales, mesal ones dark, lateral ones paler. *Thorax*. Scutal integument dark brown; scutum covered with curved narrow reddish-black scales except for small patch of curved narrow white scales on anterior promontory area; prescutellar area bare; dark reddish-black setae on following areas: 2-4 on anterior promontory, numerous on acrostichal (anterior and posterior), few on antedorsocentral, numerous on dorsocentral (anterior and posterior), scutal fossal (few anterior, 4,5 lateral, 2 posterior), several on prescutellar, numerous on antealar and supraalar, 6 on posterior medial scutal; scutellum with patch of curved narrow reddish-black scales on each lobe, 8-10 setae on lateral lobe and 9-11 setae on median lobe; pleural integument dark brown; antepnotum without scales, 11-17 long and short dark setae; postpronotum with dorsal patch of curved narrow reddish-black scales, 5-8 dark posterior setae; proepisternum with patch of broad white scales and 9-12 dark setae on upper area; postspiracular area without scales, 3-8 dark setae; mesokatepisternum with upper and lower patches of broad white scales, several scales of upper patch with brownish tinge, 4,5 upper and 14-16 posterior dark setae, few (3-6) short fine hairlike setae cephalad of upper scale patch near subspiracular area; prealar area with 9-12 dark setae; mesepimeron (Fig. 14) with median patch of broad white scales, 13-15 setae (several short and fine) dorsad of scale patch, several short fine hairlike setae on areas caudad and ventrad of scale patch but not extending onto lower area; other pleural areas bare. *Legs*. Coxae I-III with several dark setae, I with broad brown scales and small dorsal patch of white scales on anterior surface, II,III with patch of broad white scales on anterior surfaces; trochanters I-III with few short setae and few broad pale brown scales; femora I,II with anterior surface dark brown-scaled, I also with broad posterodorsal longitudinal stripe of pale brownish scales, II also with broad posteroventral longitudinal stripe of pale brownish scales, remainder of posterior surfaces of I,II dark brown-scaled, III dark brown-scaled with anteroventral broad longitudinal stripe of cream-colored scales from base to near apex, posterior surface with broad longitudinal pale brownish-scaled stripe ventrally; tibiae I-III and tarsi I-III with blackish-brown scales; posttarsi (Fig. 20) I-III with 2 ungues, I,II each with ungues equal in size, each with 1 tooth, III with ungues equal in size, both simple. *Wing*. Dorsal and ventral veins with blackish-brown scales; alula with several moderately broad dark brown scales on margin; upper calypter with several pale brown setae on margin; 1 remigial seta. *Halter*. Pedicel pale; capitellum dark brown-scaled. *Abdomen*. Terga with blackish-brown scales, I with small basolateral patch of white scales, II-VII each with small lateral white-scaled patch, extreme lateral portion of patches basal; sterna brown-scaled with basolateral white-scaled spot, V,VI also with few pale scales on mesal areas. *Genitalia* (Fig. 4). Tergum VIII with numerous broad scales covering apical 0.59-0.77, basal 0.10-0.35 retracted into segment VII, moderately to heavily pigmented, wide, base and apex both nearly straight, lateral margins slightly concave, several moderately long stout setae apically and few short ones scattered over apical 0.39-0.57, basolateral seta usually present, VIII-Te index 0.54-0.66, VIII-Te/IX-Te index 3.11-3.83, length 0.23-0.27 mm, width 0.37-0.47 mm; sternum VIII with numerous broad scales covering apical 0.78-0.90 except for small median area, moderately to heavily pigmented, wide, base concave, apex with moderately deep (0.10-0.14 of length) median indentation and with small lobe on each side of midline, numerous short and

moderately long setae scattered over apical 0.75-0.87, setae somewhat stouter on apex and submedian lobes, more numerous on the latter, apical intersegmental fold unpigmented, VIII-S index 0.62-0.69, length 0.23-0.26 mm, width 0.34-0.39 mm; tergum IX moderately pigmented, wide, short, band-like, base with short broad median indentation, apex slightly concave, setae absent, IX-Te index 0.32-0.40, length 0.07-0.09 mm, width 0.20-0.23 mm; insula ill-defined, short, unpigmented, with 4,5 small tuberculi each with minute spicule; lower vaginal lip moderately pigmented, covered with minute spicules, with small caudally projecting heavily pigmented median arm, lower vaginal sclerite consisting of basal pair of oblong moderately pigmented structures covered with small spicules and situated on elevated portion of membrane extending over area between vaginal lip, and with small subapical heavily pigmented transverse bar; upper vaginal lip narrow to moderately broad, posterolateral area produced into small lobe, posterior and posterolateral lobe covered with minute spicules, upper vaginal sclerite very large, well developed, base attached to basal half of lateral area of upper vaginal lip and with heavily pigmented projection on basoposterior area, sclerite bifurcate with anterior branch wide, moderately pigmented and attached to cephalic portion of spermathecal eminence, posterior branch wide, heavily pigmented with caudally produced, heavily pigmented, mesally curved arm connected with its mate by small membranous strip and forming crown around spermathecal eminence; spermathecal eminence heavily pigmented, shallow, consisting of pair of comma-shaped lateral structures connected caudally and produced into fleshy, very lightly pigmented, cephalic projection, moderately long spicules on lateral and cephalic areas; postgenital lobe short, wide, apex broad, flat or with small (0.1 of dorsal length) median indentation, 14-19 setae on each side of midline, 29-36 total setae, dorsal PGL index 0.82-1.10, ventral PGL index 1.11-1.23, ventral length 0.07-0.09 mm; cercus triangular in outline, moderately long, broad at base, apex acute, dorsal surface with numerous (12 or more) broad scales and numerous long, moderately long and few short setae on apical 0.84-0.94, ventral surface with few short setae along outer area, cercus index 2.38-2.72, cercus/dorsal PGL index 2.91-3.43, cercus length 0.20-0.24 mm; 3 spermathecal capsules, 1 large, 1 medium and 1 small in size, heavily pigmented, spherical, each with short pigmented neck; accessory gland duct base moderately pigmented.

**MALE.** Essentially as in the female but with the following differences. *Head.* Antenna plumose, 0.97-1.09 length of proboscis; maxillary palpus 0.11-0.14 length of proboscis; proboscis 1.09-1.11 length of femur I; vertex with only 2,3 broad white scales on midline. *Thorax.* Scutellum with 6-8 setae on lateral lobe and 8-10 setae on median lobe; 9-11 anteprenotal setae; 4 postpronotal setae; 4-6 upper proepisternal setae; 2,3 postspiracular setae; 5-7 prealar setae; mesepimeron with 6-8 setae dorsad of scale patch. *Legs.* Posttarsi (Fig. 20) I-III with 2 ungues, I with ungues unequal in size, each with tooth, II with ungues unequal in size, larger ungue simple and smaller ungue with 1 tooth, III with ungues equal in size, both simple. *Abdomen.* Tergum VIII wide, caudolateral area produced into lobe bearing patch of very long stout curved setae and median caudal area bearing patch of moderately long to long stout setae. *Gentitalia* (Fig. 8). Tergum IX moderately to heavily pigmented, band-like with median caudal margin slightly concave and strongly fused to tergum X, narrowly connected laterally to sternum IX; gonocoxite with sternal surface strongly produced ventrally, tergal surface with few very long stout setae on apicolateral area, ventral surface with apex slightly produced caudally and bearing 2 long broad heavily pigmented longitudinally striated setae with bases nearly contiguous and apices bluntly pointed and 1 longer narrower stout lanceolate seta slightly ventrad of other 2, mesal subapical area with small moderately to heavily pigmented bulla bearing moderately long sternal arm, short proximal conical tergal projection and small distal lump, 1 moderately long seta between bulla and 2 broad apical striated setae, remainder of ventral surface with numerous short thin setae and few broad scales, lateral surface with several long stout

setae on apical area and few broad scales on basal area; gonostylus moderately pigmented, long (approximately 1.1 length of gonocoxite), basal area forming large lobe with minute spicules and bearing 8-10 short, moderately long and long stout setae, apical portion bifid, produced into ventral shorter striated bladeliike structure with few minute spicules, and dorsal narrow arm thicker distally and terminating in short pointed hook, distal area bearing 3-5 short thin setae and basal area of arm bearing 3 moderately long stout setae, attached to apex of gonocoxite; basal mesal lobe lightly to moderately pigmented, consisting of small proximal area bearing 8-13 short thin setae, each arising from tubercle and small distal lightly pigmented indistinct area on mesal membrane of gonocoxite bearing 1-3 very short setae, lobe connected mesally with its mate by narrow moderately pigmented band (aedeagal guide) covered with minute spicules and located ventrad of prosophallus and phallus; proctiger moderately pigmented, continuous tergally, paraproct not separated but restricted to very heavily pigmented strip along sternal margin of proctiger, apex with 3-6 small heavily pigmented teeth; tergum X moderately to heavily pigmented, strongly fused to caudal margin of tergum IX and base of proctiger, margins indistinct but fusion lines wrinkled; phallosome complex, opisthophallus--consisting of moderately pigmented tergal transverse bridge between basal pieces, lateral surface curved ventrad, caudal margin with outer area produced into cuplike lobe, base attached to dorsomesal extension of caudal portion of basal piece, phallus--consisting of pair of moderately long aedeagal sclerites joined near midlength by narrow sternal bridge, apices of sclerites contiguous and legs angled outward presenting A-shaped appearance, base of sclerite attached to inner tip of paramere, tergal area of sclerite basad of sternal bridge strongly fused to inner basosternal portion of prosophallus, apex of phallus with loosely attached tergal penis filament consisting of small moderately pigmented U-shaped structure produced cephalad, prosophallus--consisting of pair of prosophallic sclerites each with bulbous base fused to basotergal area of phallus and tergomesal portion of paramere, apical 0.4-0.5 produced into several lightly pigmented and flattened contiguous leaf-like structures having apices fused into single flattened plate and positioned between laterosternal surface of opisthophallus and lateral margin of phallus, prosophallic sclerite approximately equal in length to aedeagal sclerite, paramere--moderately long, approximately 0.67 length of aedeagal sclerite, articulated at point near middle of outer margin with caudal area of basal piece, basal piece--moderately to heavily pigmented, moderately long, attached to broad basotergal apodeme of gonocoxite; sternum IX with apicolateral areas rounded, 6-11 short and moderately long setae in small patch near middle of caudal margin.

**PUPA** (Fig. 12). Setal branching as recorded in Table 3. *Cephalothorax*. Moderately pigmented; lateralia without or with small area of very poorly developed cuticular ocular facets of compound eye; seta 5-CT with 4-7 branches. *Trumpet*. Heavily pigmented; index 4.13-5.60, mean 4.83. *Abdomen*. Terga I-III moderately pigmented; seta 1-II with 17-27 branches; 2-II laterad of 3-II; 1-III with 4-10 branches; 5-IV single or 2-branched; 1-V with 3-5 (usually 3,4) branches; 1-VI with 4-6 branches; 3-VII with 4-9 (usually 5-7) branches; 6-VII with 4-8 branches; 9-VIII single. *Paddle*. Ovoid; with minute serrations on distal portion of basal 0.62 of outer margin; with minute spicules on apical 0.38-0.41 of outer and apical 0.28-0.35 of inner margins; seta 1-Pa single, moderately long; index 1.17-1.58, mean 1.33.

**FOURTH-INSTAR LARVA** (Fig. 16). Setal branching as recorded in Table 7. *Head*. Moderately pigmented; seta 4-C with 3-6 (usually 4,5) branches; 5-C with 2-4 (usually 3) branches; 7-C with 5-7 (usually 5,6) branches; 13-C with 2-4 branches. *Mouthparts*. Dorsosentum with 21-26 teeth. *Antenna*. Moderately long; lightly pigmented; several small spicules scattered over entire shaft; seta 1-A with 6-8 branches, moderately long. *Thorax*. Seta 8-P single; 3-M with 3 branches. *Abdomen*. Seta 6-I with 2,3 (usually 2) branches; 7-I single; 3-IV with 4-6 (usually 5,6) branches; 1-VIII with 3-5 branches; 5-VIII with 9-15 branches; 2-X with 6-8 branches; comb consisting of

9-14 (usually 11,12) scales arranged in single curved irregular row, each scale with 1,2 slightly stouter and longer median apical spines and smaller denticles on basal and lateral areas; 4 short anal papillae. *Siphon*. Moderately pigmented; index 2.32-2.82, mean 2.53; pecten on basal 0.52-0.56 of siphon, consisting of 9-12 (usually 10 or 12) spines, distal 2,3 spines longer and wider spaced than remainder, each spine long, slender and with 1,2 small stout denticles basoventrally; seta 1-S with 4-7 branches, short, attached on basal 0.64-0.71 of siphon distad of last pecten spine; 6-S single, short; 8-S with 3-6 branches, short.

**EGG.** Description adapted from Matsuo et al. (1974:440). *Shape*. Apparently fusiform; anterior end gradually tapered. *Chorion*. Viewed with scanning electron microscope at 500x on upper (ventral) surface as follows: reticulation composed of pattern of anteroposteriorly elongated polygonal cells, each cell with 1-5 large rounded hemispherical papillae, small papillae between large papillae and ridge and often confluent with them; and reticulation of inner chorion with same pattern as outer chorion but with papillae absent.

#### SPECIES INCLUDED IN SUBGENUS *VERRALLINA*, BUTLERI SERIES

- |   |  |
|---|--|
| 1. <i>Ve. (Ver.) butleri</i> (Theobald)       | 4. <i>Ve. (Ver.) iriomotensis</i> (Tanaka<br>and Mizusawa) |
| 2. <i>Ve. (Ver.) cunninghami</i> (Taylor) (?) |  |
| 3. <i>Ve. (Ver.) dux</i> (Dyar and Shannon)   | 5. <i>Ve. (Ver.) lugubris</i> (Barraud)                    |

#### CARMENTI SERIES

**FEMALE GENITALIA.** *Lower vaginal sclerite*. Consisting of pair of lightly pigmented, somewhat wrinkled, ribbonlike plates, without spicules. *Spermathecal eminence*. Without spicules.

**MALE GENITALIA.** *Gonocoxite*. Without dorsoapical or ventroapical lobes or fleshy projections, with one or more subapical spiniform(s) on sternomesal area (except absent in *Ve. leilae* and *Ve. simplus*). *Basal mesal lobe*. Consisting of small broad plate bearing number of short to moderately long thin setae.

**PUPAE.** *Abdomen*. Seta 9-VIII usually with 3-6 branches.

**FOURTH-INSTAR LARVAE.** *Head*. Setae 8-C and 13-C single.

#### *Verrallina (Verrallina) carmenti* (Edwards)

(Figs. 5, 9, 13, 14, 17, 20)

*Verrallina carmenti* is the nominotypical species for the Carmenti Series and is completely described below.

**FEMALE.** *Head*. Antenna dark brown, 0.76-0.83 length of proboscis, pedicel dark brown with few small dark scales and short fine setae mesally, flagellome 1 with basal 0.3 pale and with several small dark scales near middle, flagellar whorls with 6 dark setae; clypeus dark brown; maxillary palpus with blackish-brown scales, 4-segmented, 0.11-0.13 length of proboscis; proboscis with blackish-brown scales, 1.50-1.55 length of femur I; eyes nearly contiguous dorsally; ocular setae blackish-brown and well developed; head with decumbent scales all broad and blackish-brown except row of curved narrow pale brown scales on ocular line, narrow stripe of broad white scales on lateral surface extending from ocular line to point anterior of anteprenotum, and numerous

moderately long dark brown erect forked scales on occiput. *Thorax*. Scutal integument dark brown; scutum covered with curved narrow reddish-black scales except for curved narrow golden-white scales forming small patch on anterior promontory, antedorsocentral area, supraalar area near base of wing and along anterior and lateral margins of prescutellar space; prescutellar space bare; scutellum with patch of curved narrow reddish-black scales on each lobe; dark blackish-brown setae on following areas: 4,5 on anterior promontory, numerous on acrostichal (anterior and posterior), few on antedorsocentral, numerous on dorsocentral (anterior and posterior), scutal fossal (few anterior, 6,7 lateral and 2 posterior), numerous on antealar and supraalar, 7,8 on posterior medial scutal, 1 parascutellar and scutellar (8-11 long and 4-6 short on lateral lobe, 6-10 long and 5-7 short on median lobe); pleural integument dark reddish-brown; antepnota widely separated, scales absent, 18-28 long and short dark setae; postpronotum with curved narrow reddish-black scales on upper area and few moderately broad brown ones below, 6-10 long and short dark posterior setae, patch of short hairlike setae ventrad of scale patch and cephalad of posterior setae; proepisternum with patch of broad white scales and 15-19 long and short dark setae on upper area; subspiracular area, paratergite, mesomeron and metameron bare; postspiracular area with 6-12 setae; mesokatepisternum with upper patch of broad pale brown scales (few posterior ones white) and lower patch of broad white scales, 4-7 upper and 15-19 posterior dark setae, patch of short fine hairlike golden setae cephalad of upper scale patch near subspiracular area; prealar area with 11-15 dark setae; mesepimeron (Fig. 14) with patch of broad white scales near center, 21-31 dark setae dorsad of scale patch, several brown hairlike setae along posterior and ventral margins of scale patch and becoming more numerous posteroventrally but not extending onto lower 0.25 of sclerite. *Legs*. Coxae I-III each with several dark setae, I with anterior surface with broad brown scales on middle and small dorsal and ventral patches of white scales, II,III with patch of broad white scales on outer area of anterior surface; trochanters I-III with broad pale brown scales; femora I,II each with anterior surface dark brown-scaled, III with anterior surface white-scaled and with dorsal longitudinal stripe of dark brown scales extending from base to apex and forming narrow apical band, I with posterior surface pale-scaled with ventral longitudinal stripe of dark brown scales extending from base to apex, II,III each with posterior surface pale-scaled and with narrow dorsal longitudinal stripe of dark brown scales extending from base to apex, stripe broader distally and forming band on apical 0.12-0.20; tibiae I-III and tarsi I-III each with blackish-brown scales; posttarsi (Fig. 20) I,II each with 2 ungues, I with ungues equal, each with 1 tooth, II with ungues equal, one unguis with 1 tooth, III with ungues equal, both simple. *Wing*. Dorsal and ventral veins with blackish-brown scales; alula with several narrow brown scales along margin; upper calypter with several pale setae on margin; 1,2 remigial setae. *Halter*. Pedicel pale; capitellum brown-scaled but with pale scales dorsally. *Abdomen*. Terga with blackish-brown scales, I with rectangular patch of white scales basolaterally, II-VII each with lateral white-scaled spot, extreme lateral portion of spot basal; sterna with dark brown scales, II-VII also each with basolateral white-scaled patch; terga and sterna with numerous golden setae, mostly along posterior margins. *Genitalia* (Fig. 5). Tergum VIII moderately pigmented, wide, base and apex slightly concave, several short and moderately long setae on apical 0.46-0.60, few long setae along apical margin, basolateral seta absent but with small bulla in this location, numerous broad scales covering apical 0.74-0.83, basal 0.3-0.5 retracted into segment VII, VIII-Te index 0.63-0.70, VIII-Te/IX-Te index 3.68-4.09; sternum VIII moderately pigmented, wide, base slightly concave, apex with moderately deep median indentation with very small lobe on each side of midline, numerous short and moderately long setae scattered over apical 0.86-0.83, numerous broad scales covering most of apical 0.90-0.94, apical intersegmental membrane unpigmented, VIII-S index 0.75-0.80; tergum IX moderately pigmented, wide, short, band-like, base with short median indentation, setae absent, covered with

minute spicules, IX-Te index 0.33-0.39; insula ill-defined, short, unpigmented, covered with minute spicules, with 4,5 small tuberculi each with minute spicule; lower vaginal lip moderately pigmented, narrow, covered with minute spicules, lower vaginal sclerite consisting of pair of very lightly pigmented small plates, without spicules and somewhat wrinkled; upper vaginal lip lightly to moderately pigmented, moderately broad laterally and narrow posteriorly, posterolateral margin evenly rounded and not lobed, minute spicules on posterior margin, upper vaginal sclerite moderately pigmented, well developed, base attached to basal 0.5 of inner portion of upper vaginal lip, sclerite bifurcate with anterior branch small, lightly pigmented and attached to cephalic portion of spermathecal eminence, posterior branch wide with caudally produced, lightly pigmented, mesally curved arm connected with its mate and forming crown around spermathecal eminence; spermathecal eminence heavily pigmented, shallow, consisting of pair of comma-shaped lateral structures connected caudally and produced into fleshy, very lightly pigmented small cephalic projection, spicules absent; postgenital lobe short, wide, apex broad with moderately deep median indentation, 11-15 setae on each side of midline, 23-29 total setae, completely covered with minute spicules, dorsal PGL index 0.88-1.08; proctiger with minute spicules; cercus triangular in outline, moderately long, broad at base, apex acute, base concave, dorsal surface with numerous short and moderately long setae on apical 0.84-0.90 and few (1-9) broad scales, few long setae at apex, ventral surface with few short and moderately long setae along outer margin and apical area, index 2.64-2.97, cercus/dorsal PGL index 3.46-3.84; 3 spermathecal capsules, 1 large, 1 medium and 1 small in size, heavily pigmented, spherical, each with short narrow heavily pigmented neck, few tiny spermathecal capsule pores near orifice; accessory gland duct base moderately pigmented.

**MALE.** Similar to female in general habitus but with the following differences. *Head.* Antenna plumose, 0.76-0.84 length of proboscis; maxillary palpus 0.11-0.12 length of proboscis; proboscis 1.39-1.56 length of femur I. *Thorax.* Anterior promontory with 3,4 setae; scutal fossal (few anterior, 2-4 lateral and 1 posterior) setae; 14-21 anteprenotal setae; 4-6 postprenotal setae; 14-18 upper proepisternal setae; 5-7 postspiracular setae; 8-10 prealar setae; mesepimeron with 14-18 setae dorsad of scale patch. *Legs.* Posttarsi (Fig. 20) I-III with 2 ungues, I,II each with ungues unequal, each with 1 tooth, III with ungues equal, both simple. *Genitalia* (Fig. 9). Tergum IX moderately pigmented, caudal margin concave mesally, strongly fused to tergum X, setae absent, narrowly connected laterally to sternum IX; gonocoxite short, broad, heavily pigmented, mesal surface membranous with minute spicules, dorsal and ventral surfaces with several short and few moderately long setae scattered over most of surfaces, few long stout setae on apical 0.6 of outer margin of dorsal and lateral surfaces, ventral surface also with short heavily pigmented spiniform on apicomeral area and arising from short tubercule, short stout seta basad and moderately long seta distad of tubercule, several broad scales on basal area becoming more numerous laterally and extending onto lateral surface; gonostylus moderately pigmented, moderately long (approximately 0.68 length of gonocoxite), basal 0.4 expanded and bearing 10-12 short setae, apical 0.6 narrow, curved and tapered to point, apex slightly recurved; basal mesal lobe lightly to moderately pigmented, consisting of somewhat triangular plate situated on membranous basal mesal area of gonocoxite and bearing 7-13 short setae and with small apical area with 8-11 short setae, sternal margin of plate strongly fused to basomesal margin of ventral surface of gonocoxite, lobe connected mesally to its mate by narrow moderately pigmented band (aedeagal guide) covered with minute spicules and located ventrad of prosophaallus and phallus; proctiger continuous tergally, moderately pigmented, paraproct indistinct, not separated or free arm, base with small short sternal projection articulating at point on the dorsomesal surface of basal piece near base of opisthophallus, cercal setae absent; tergum X moderately pigmented, strongly fused to median caudal margin of tergum IX and base of proctiger, margins indistinct but fusion lines somewhat wrinkled; phallosome

complex, opisthophallus--consisting of moderately pigmented narrow transverse bridge tergally between basal pieces, lateral surface curved ventrad, caudal margin slightly concave to truncate, base attached to dorsomesal extension of caudal portion of basal piece, located dorsad of phallus and prosophallus and ventrad of proctiger, phallus--consisting of pair of moderately long heavily pigmented aedeagal sclerites joined near midlength by narrow sternal bridge, apices of sclerites contiguous and legs angled outward presenting A-shaped appearance, base of sclerite attached to inner tip of paramere, tergal area of sclerite (basad of sternal bridge) strongly fused to inner basosternal portion of prosophallus, apex of phallus with loosely attached tergal penis filament consisting of large moderately pigmented U-shaped structure projected cephalad, prosophallus--consisting of pair of sclerites with bulbous base fused to basotergal area of phallus and tergomesal portion of paramere, apical 0.5-0.6 produced into several lightly pigmented flattened contiguous leaf-like structures with apices fused into single plate and extending caudad of posterior margin of opisthophallus, base positioned between laterosternal surface of opisthophallus and lateral margin of phallus, prosophallic sclerite approximately equal in length to aedeagal sclerite, paramere--heavily pigmented, short, approximately 0.46 length of aedeagal sclerite, articulates at point near middle of outer margin with caudal area of basal piece, basal piece--moderately pigmented, moderately long, outer surface attached to broad basotergal apodeme of gonocoxite; sternum IX moderately pigmented throughout, large, broad, apicolateral areas rounded, 9-12 short and moderately long setae in elongate patch near middle of caudal margin.

**PUPA** (Fig. 13). Setal branching as recorded in Table 4. *Cephalothorax*. Lateralia with area of moderately developed cuticular ocular facets of compound eye. *Trumpet*. Heavily pigmented; with hairlike spicules on distal 0.54-0.60 of inner surface; index 3.19-4.28, mean 3.81. *Abdomen*. Setae 6,9-VII weakly developed; 4-VIII with 2-4 branches; 9-VIII with 3-6 branches. *Paddle*. Ovoid; with minute serrations on distal portion of basal 0.57 of outer margin; with minute spicules on apical 0.43 of outer and apical 0.3 of inner margins; midrib not reaching apex; seta 1-Pa moderately long, single or 2-branched; index 1.14-1.55, mean 1.38.

**FOURTH-INSTAR LARVA** (Fig. 17). Setal branching as recorded in Table 8. *Head*. Seta 4-C with 6-10 branches; 5-C with 3-7 branches; 7-C with 8-14 branches; 13-C single. *Mouthparts*. Dorsomentum with 36-41 teeth. *Antenna*. Moderately long, lightly to moderately pigmented, with small spicules scattered over shaft, more numerous on basal area; seta 1-A with 3-5 branches; 2-A long, with subapical constriction; 3-A short, 0.20-0.31 length of 2-A; 4-A moderately long, 0.57-0.74 length of 2-A; 6-A short, 0.27-0.35 length of 2-A. *Abdomen*. Seta 6-I with 3 branches; 7-I single; 3-IV with 4-8 branches; 1-VIII with 5-8 branches; 5-VIII with 7-11 branches; 2-X with 3 branches, 1 branch longer than others; ventral brush (4-X) with 10 setae on grid and 2 precratal shorter ones, all multiple-branched; saddle moderately pigmented, incompletely rings segment X, acus absent; 4 moderately long anal papillae; comb consisting of 10-14 (usually 12-14) scales arranged in single curved irregular row, each scale with small uniformly developed denticles on lateral and apical margins. *Siphon*. Moderately pigmented; acus well developed; index 3.00-3.49, mean 3.29; pecten on basal 0.59-0.64 of siphon, consisting of 12-16 (usually 13-15) spines, apical 3 spines longer and wider spaced than remainder, each spine long, slender and with 1,2 small stout denticles basoventrally, distal 2-4 spines with or without denticles; seta 1-S short, with 2-4 branches, base attached on basal 0.70-0.72 of siphon distad of last pecten spine; 6-S short, single; 8-S short, with 2-5 branches.

**EGG**. Description adapted from Huang (1968:21, Fig. 25). *Shape*. Elongate; pronounced narrowness relative to length; somewhat curved; 5.9-6.0 times as long as wide, 845 microns x 141 microns. *Chorion*. Dark; chorionic cells different on ventral, lateral and dorsal surfaces.

**SPECIES INCLUDED IN SUBGENUS *VERRALLINA*, CARMENTI SERIES**

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| 1. <i>Ve. (Ver.) azureosquamata</i><br>(Bonne-Wepster)     | 14. <i>Ve. (Ver.) obsoleta</i> (Huang)                       |
| 2. <i>Ve. (Ver.) bifoliata</i> (King and<br>Hoogstraal)    | 15. <i>Ve. (Ver.) parasimilis</i> (King and<br>Hoogstraal)   |
| 3. <i>Ve. (Ver.) carmentis</i> (Edwards)                   | 16. <i>Ve. (Ver.) pipkini</i> (Bohart)                       |
| 4. <i>Ve. (Ver.) cuccioi</i> (Belkin)                      | 17. <i>Ve. (Ver.) quadrifolium</i> (Brug)                    |
| 5. <i>Ve. (Ver.) embiensis</i> (Huang)                     | 18. <i>Ve. (Ver.) quadrispinata</i> (King and<br>Hoogstraal) |
| 6. <i>Ve. (Ver.) foliformis</i> (King and<br>Hoogstraal)   | 19. <i>Ve. (Ver.) reesi</i> (King and<br>Hoogstraal)         |
| 7. <i>Ve. (Ver.) funerea</i> (Theobald)                    | 20. <i>Ve. (Ver.) sentania</i> (King<br>Hoogstraal)          |
| 8. <i>Ve. (Ver.) killertonis</i> (Huang)                   | 21. <i>Ve. (Ver.) similis</i> (Theobald)                     |
| 9. <i>Ve. (Ver.) leilae</i> (King and<br>Hoogstraal)       | 22. <i>Ve. (Ver.) simplus</i> (King and<br>Hoogstraal)       |
| 10. <i>Ve. (Ver.) lineata</i> (Taylor)                     | 23. <i>Ve. (Ver.) trispinata</i> (King and<br>Hoogstraal)    |
| 11. <i>Ve. (Ver.) mccormicki</i> (Belkin)                  | 24. <i>Ve. (Ver.) vanapa</i> (Huang)                         |
| 12. <i>Ve. (Ver.) milnensis</i> (King and<br>Hoogstraal)   | 25. <i>Ve. (Ver.) variabilis</i> (Huang)                     |
| 13. <i>Ve. (Ver.) multifolium</i> (King and<br>Hoogstraal) |  |

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**FIGURE ABBREVIATIONS****Female genitalia**

AGDB	= Accessory gland duct base	SCA	= Spermathecal capsule
BMA	= Basal median apodeme	SCaP	= Spermathecal capsule pore
BLS	= Basal lateral seta	SE	= Spermathecal eminence
Ce	= Cercus	SES	= Spermathecal eminence spicule
DPGL	= Line of attachment of proctiger to dorsal surface of PGL	Tu	= Tuberculus
H	= Hinge	UVL	= Upper vaginal lip
I	= Insula	UVS	= Upper vaginal sclerite
IX-Te	= Tergum IX	VIII-S	= Sternum VIII
LVL	= Lower vaginal lip	VIII-Te	= Tergum VIII
LVS	= Lower vaginal sclerite	VT	= Ventral tuft
PGL	= Postgenital lobe	1-4-S	= Setae 1-4-S of VIII-S

**Male genitalia**

AeS	= Aedeagal sclerite	IX-Te	= Tergum IX
AeG	= Aedeagal guide	OP	= Opisthophallus
AG	= Apodeme of Gc	Par	= Paramere
BML	= Basal mesal lobe	PF	= Penis filament
BP	= Basal piece	PO	= Prosophallus
Gc	= Gonocoxite	Ppr	= Paraproct
Gs	= Gonostylus	Pr	= Proctiger
IX-S	= Sternum IX	X-Te	= Tergum X

**Pupa**

CT	= Cephalothorax	Mr	= Midrib
GL	= Genital lobe	Mtn	= Metanotum
I-VIII	= Abdominal segments I-VIII	Pa	= Paddle
		T	= Trumpet

**Fourth-instar larva**

A	= Antenna	Mx	= Maxilla
C	= Cranium	P	= Prothorax
CS	= Comb scale	PS	= Pecten spine
Dm	= Dorsomentum	S	= Siphon
I-VIII,X	= Abdominal segments I-VIII,X	T	= Metathorax
M	= Mesothorax	VmCS	= Ventromedian cervical sclerite

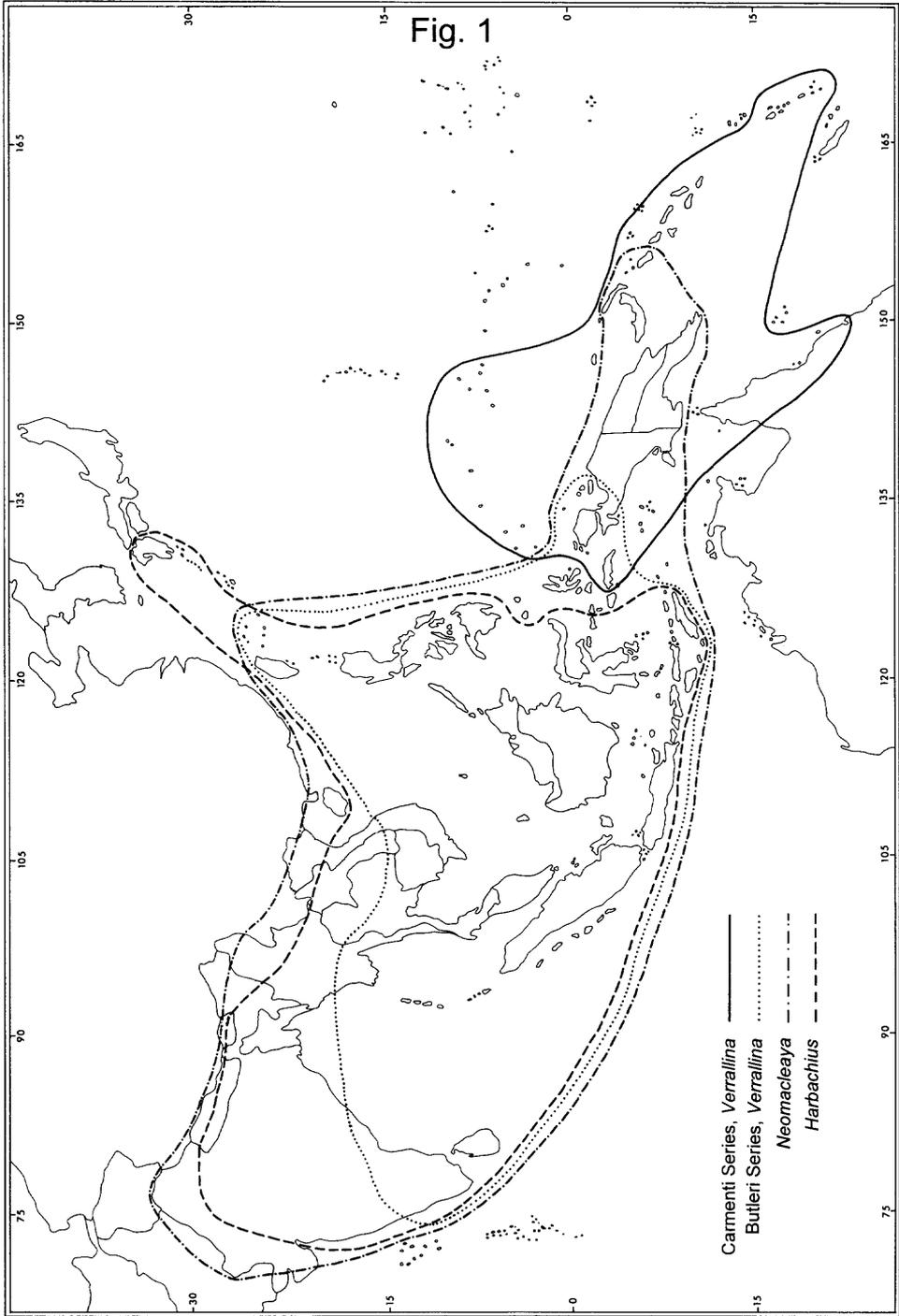
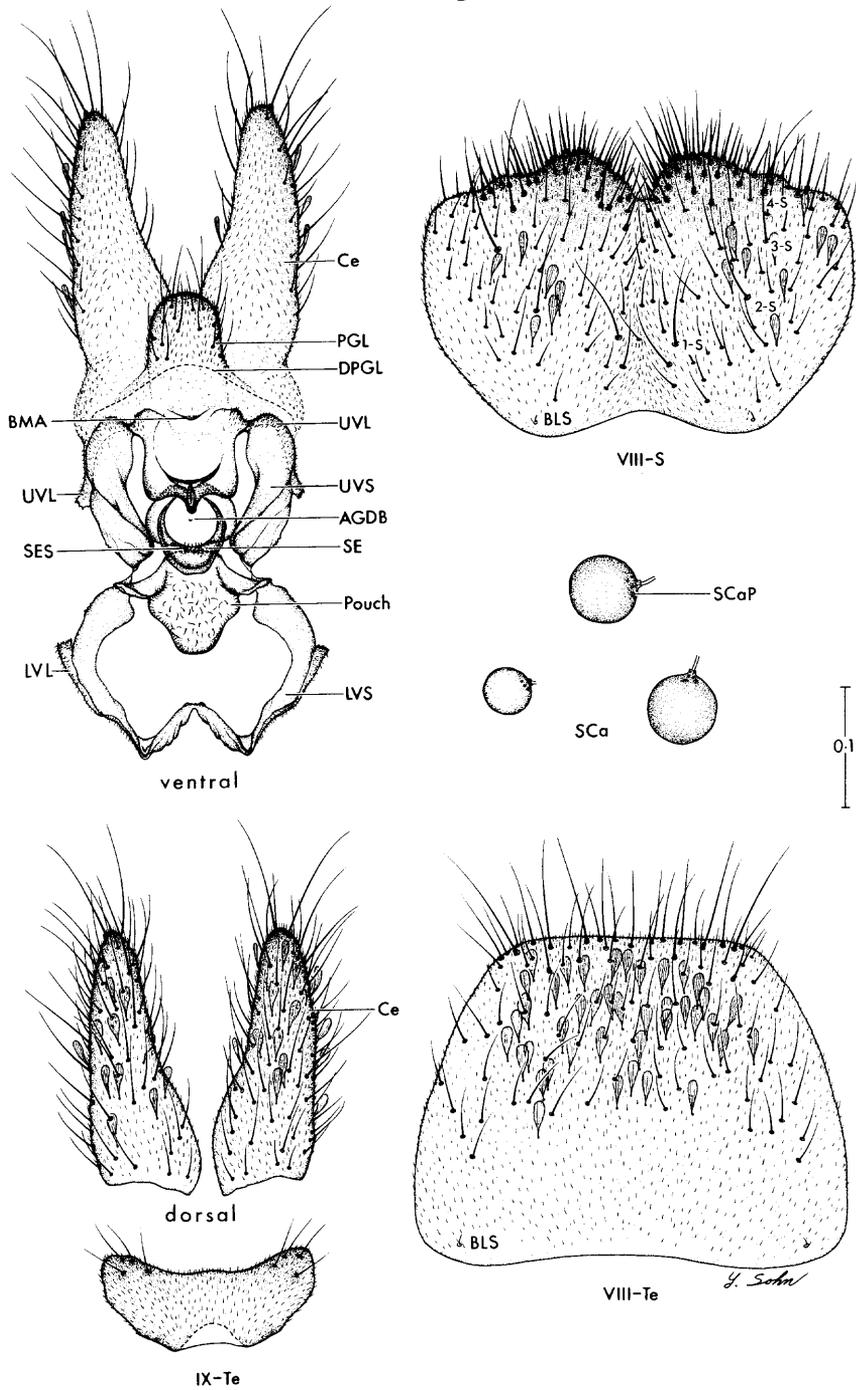
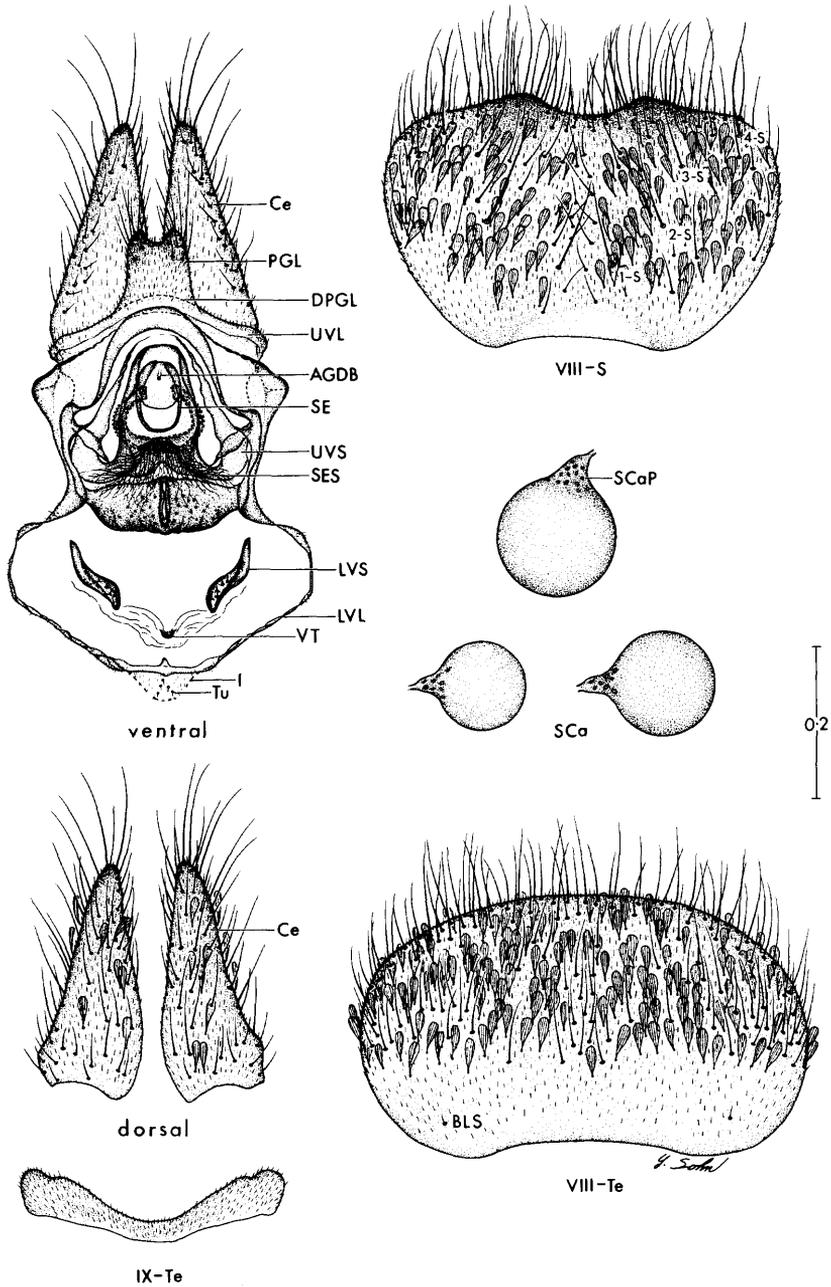


Fig. 2



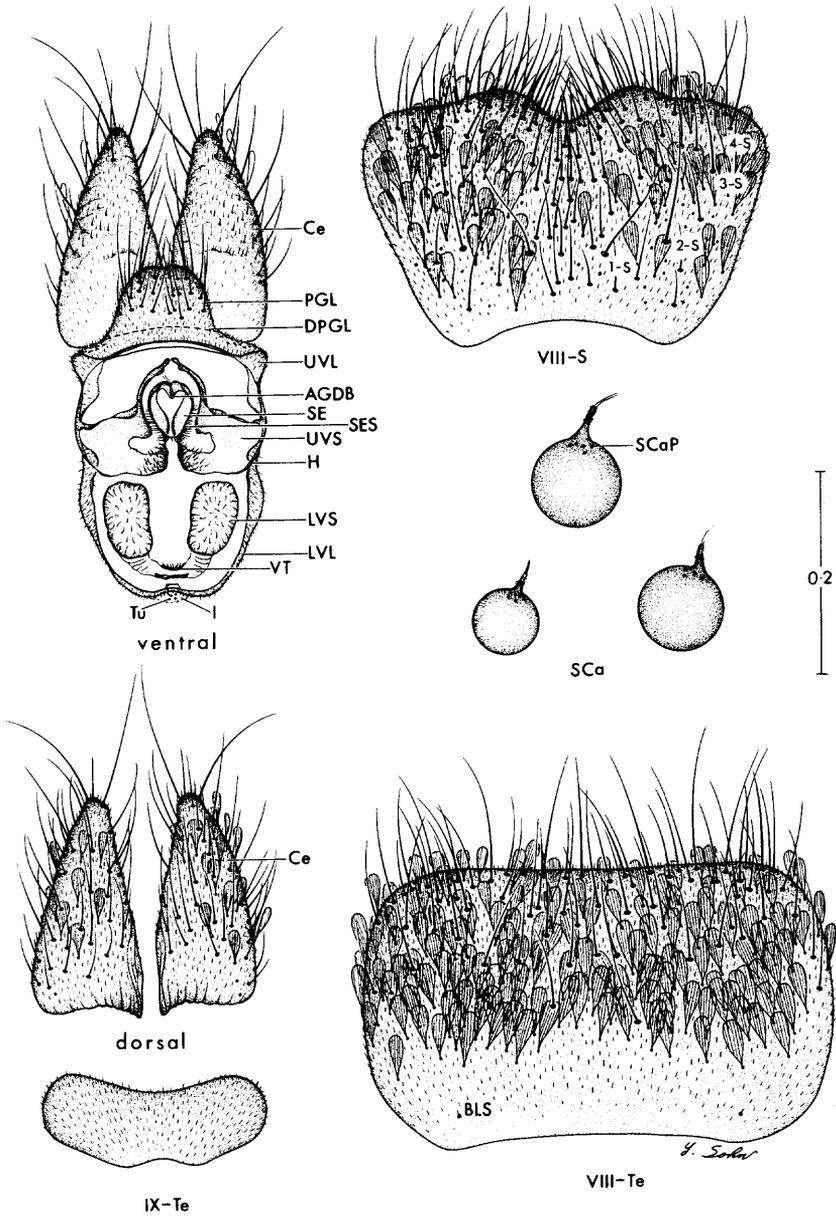
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Fig. 3



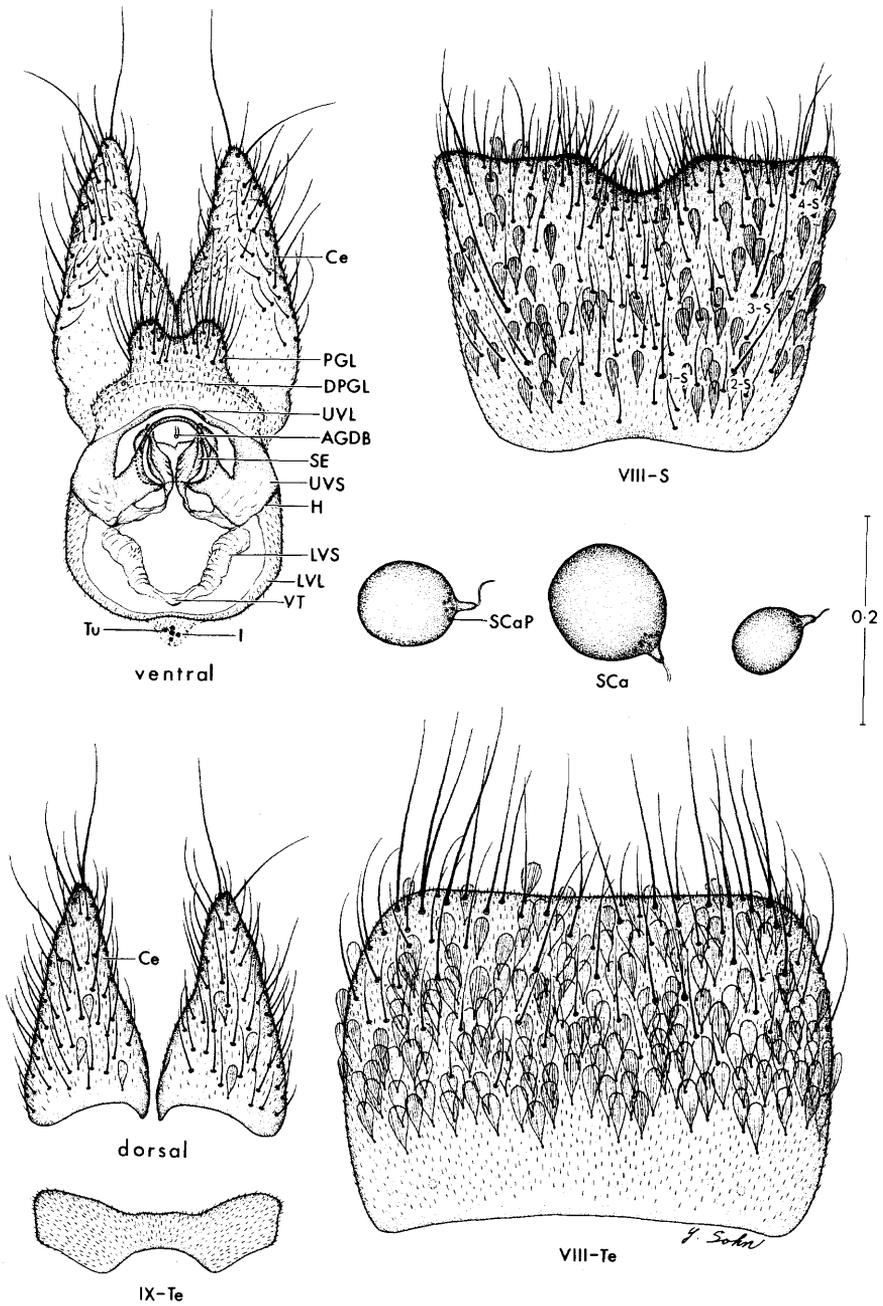
*Verrallina (Neomacleaya) indica*

Fig. 4



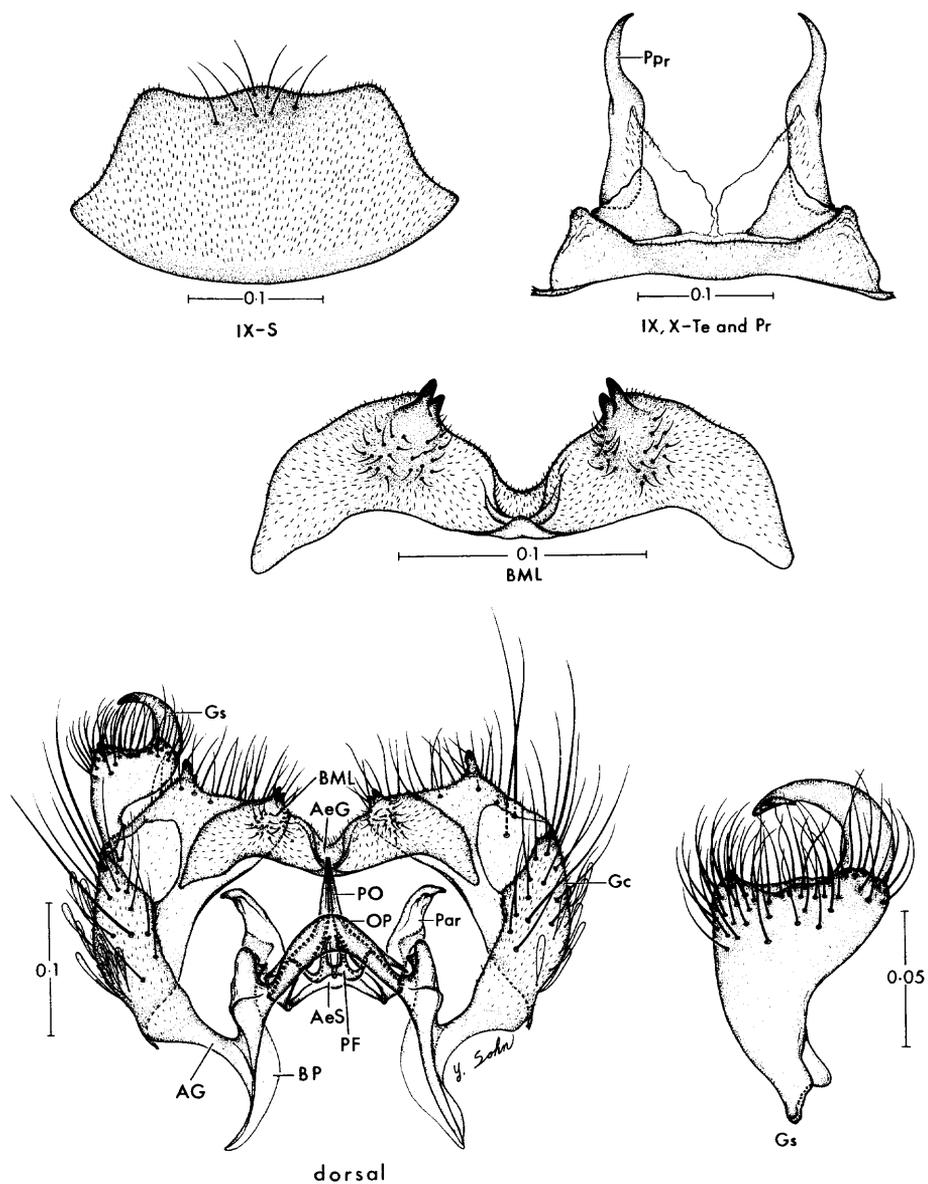
*Verrallina (Verrallina) butleri*

Fig. 5



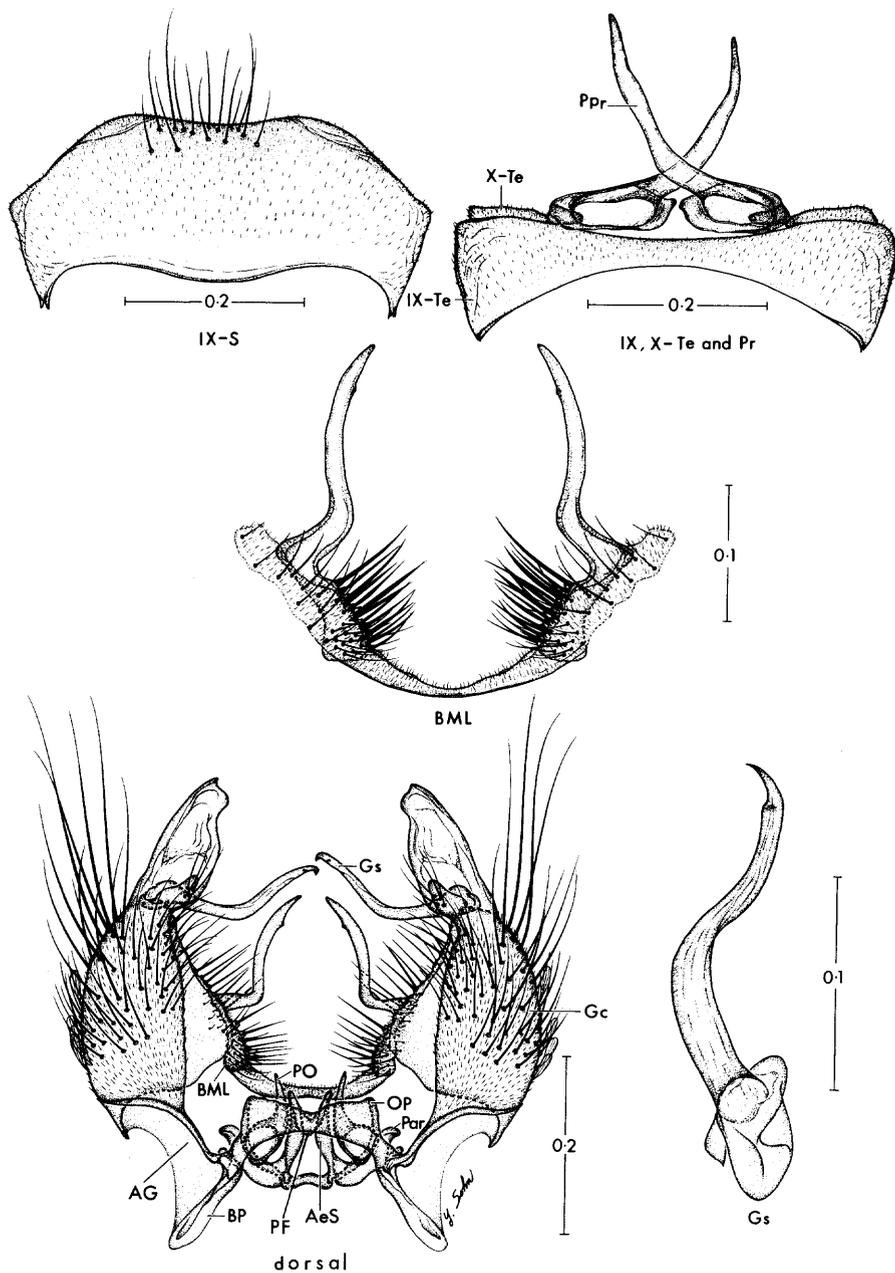
*Verrallina (Verrallina) carmenti*

Fig. 6



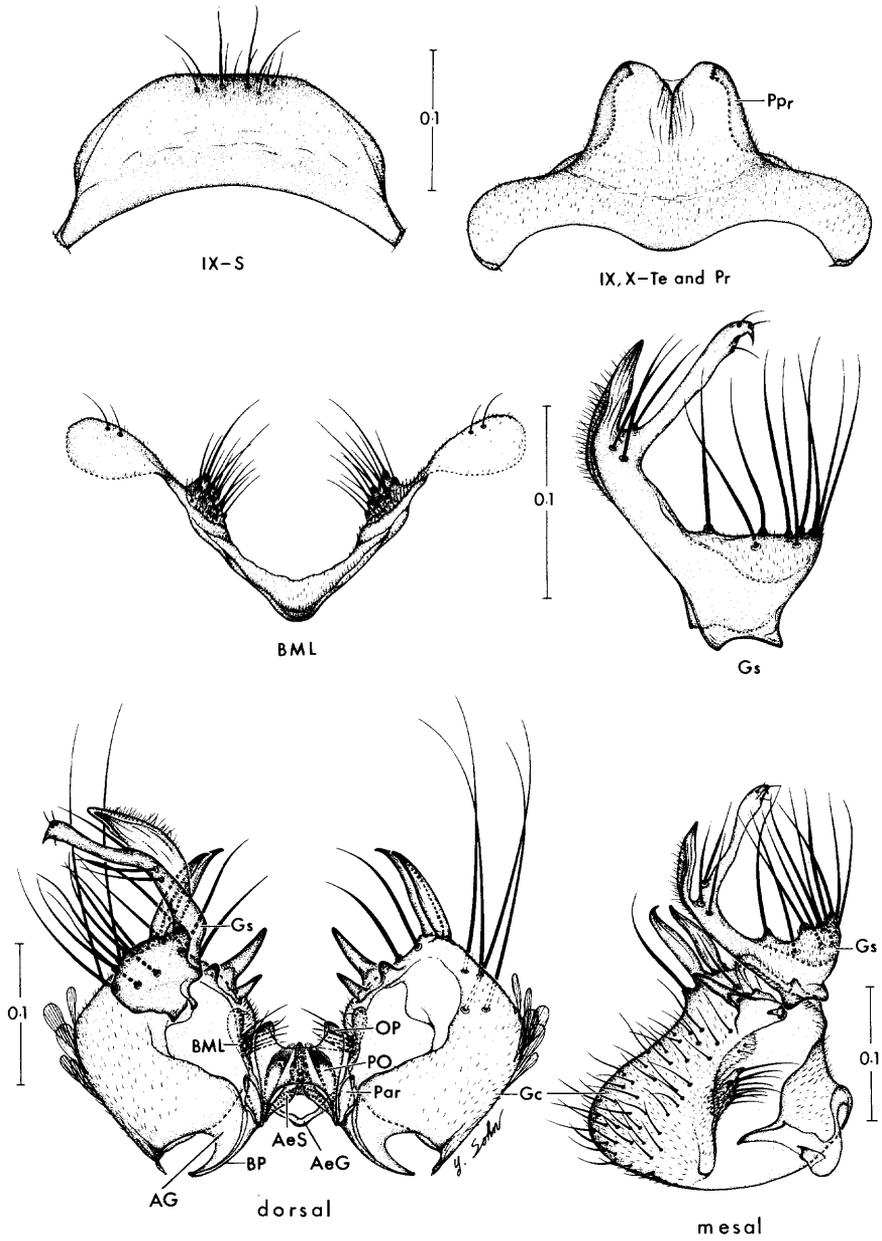
*Verrallina (Harbachius) yusafi*

Fig. 7



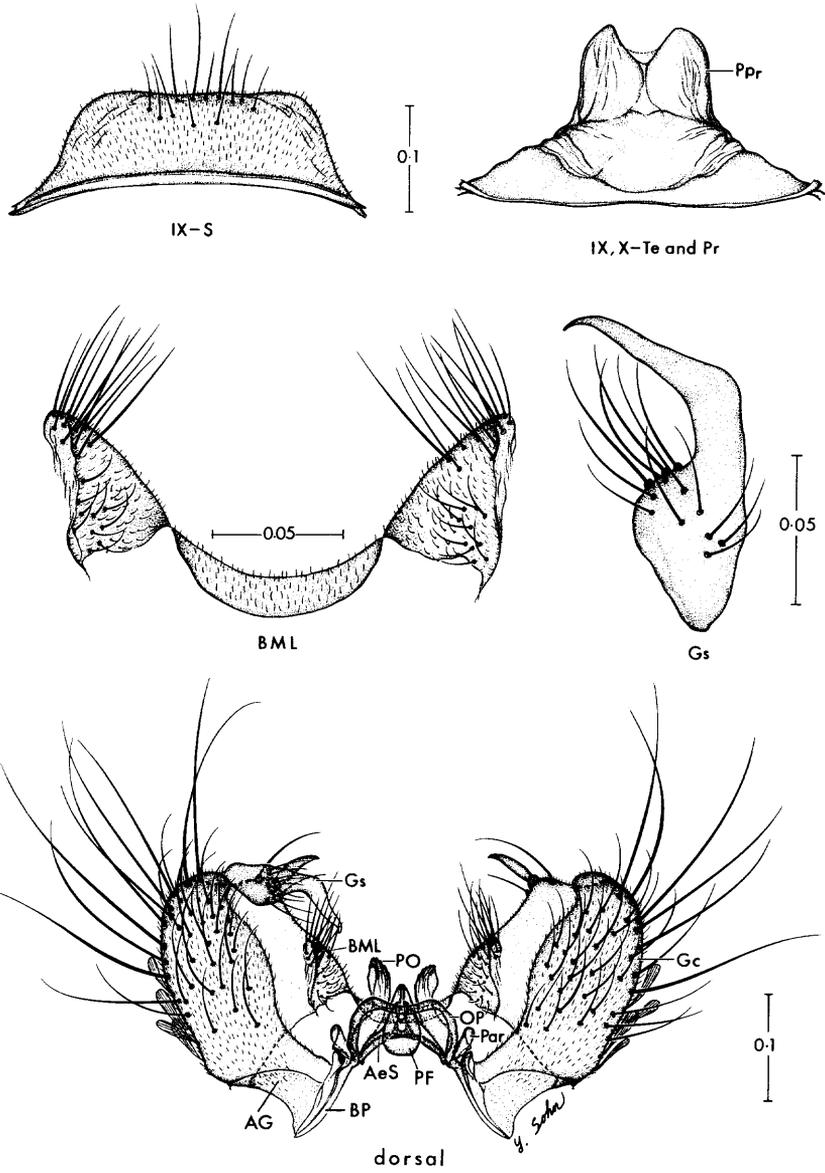
*Verrallina (Neomacleaya) indica*

Fig. 8



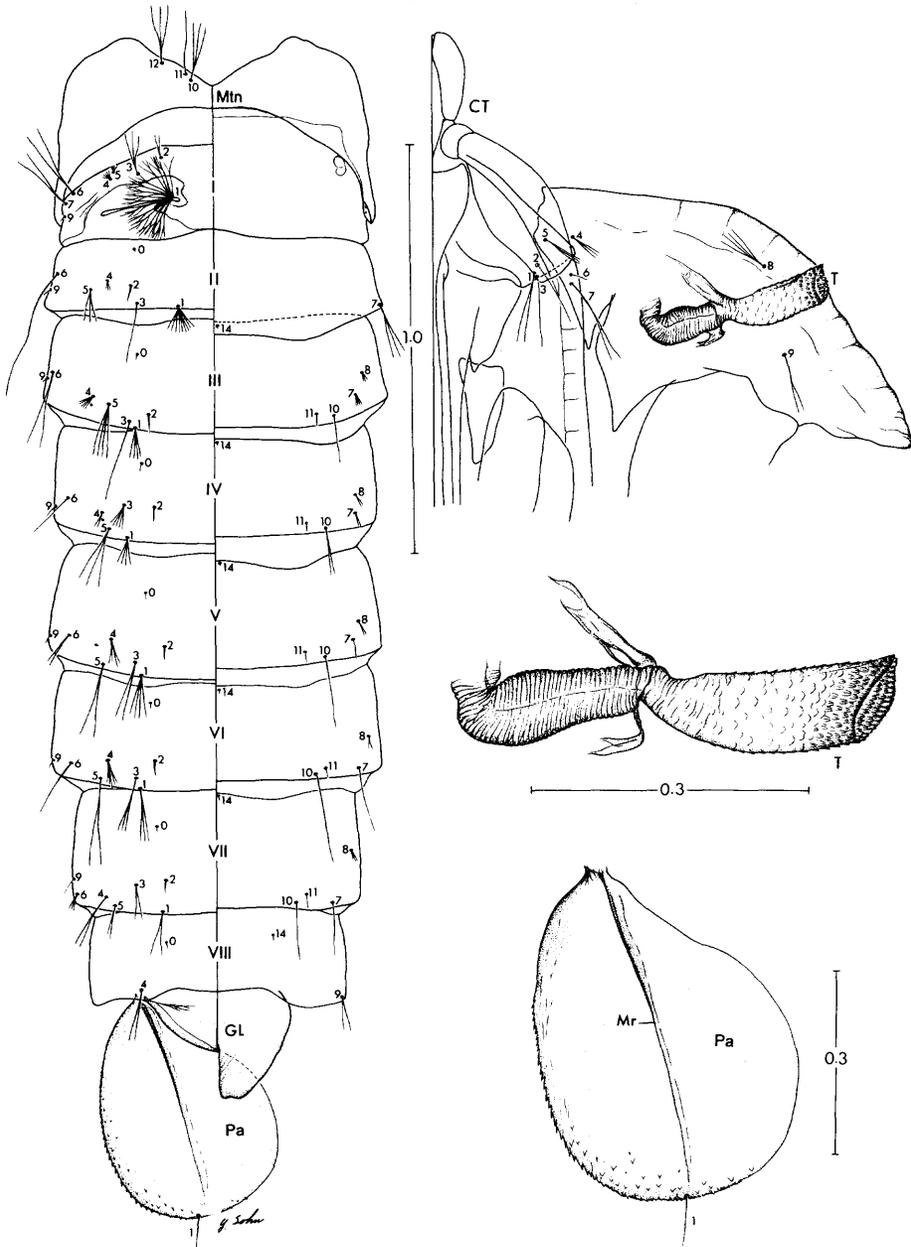
*Verrallina (Verrallina) butleri*

Fig. 9



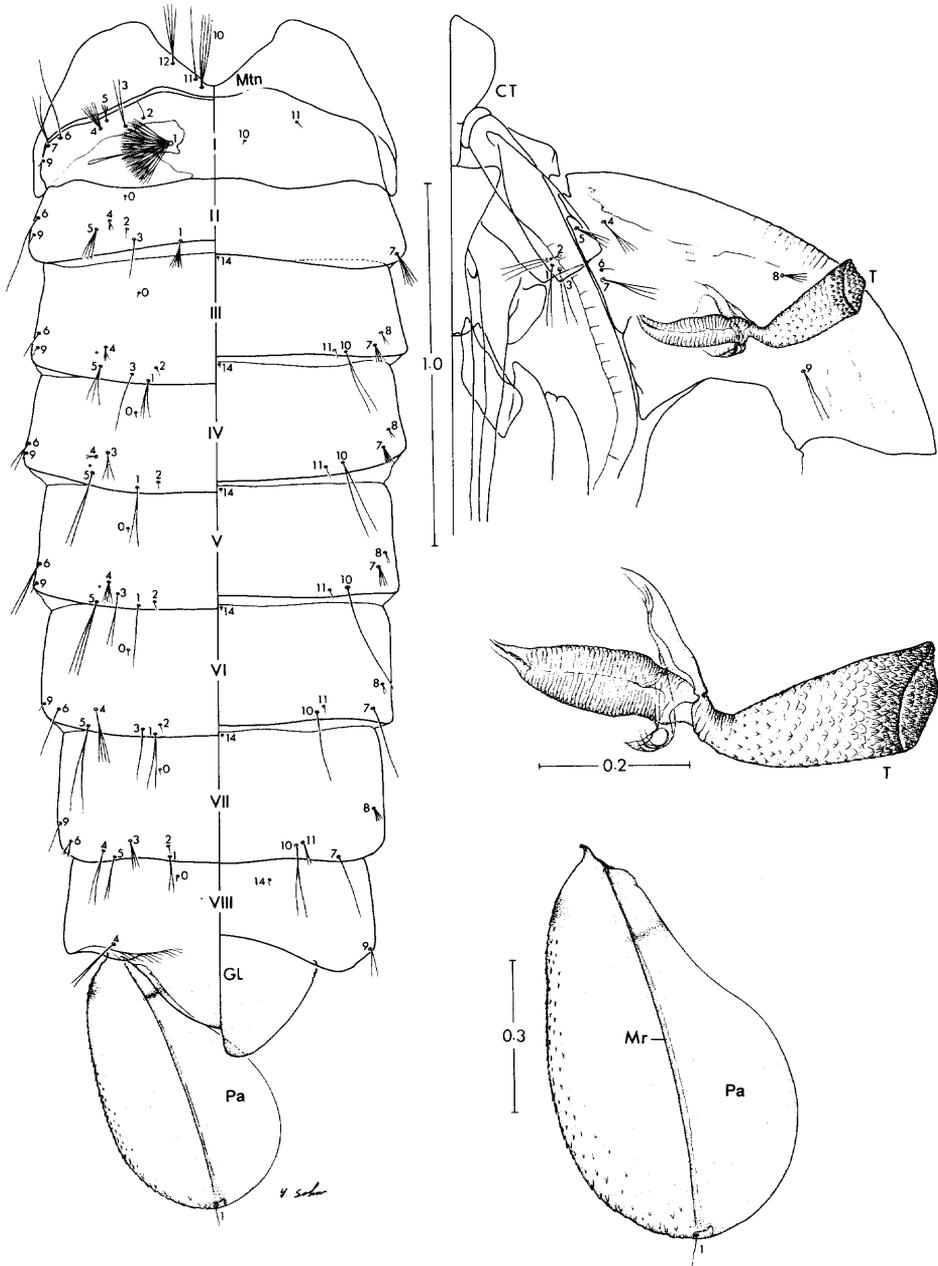
*Verrallina (Verrallina) carmenti*

Fig. 10



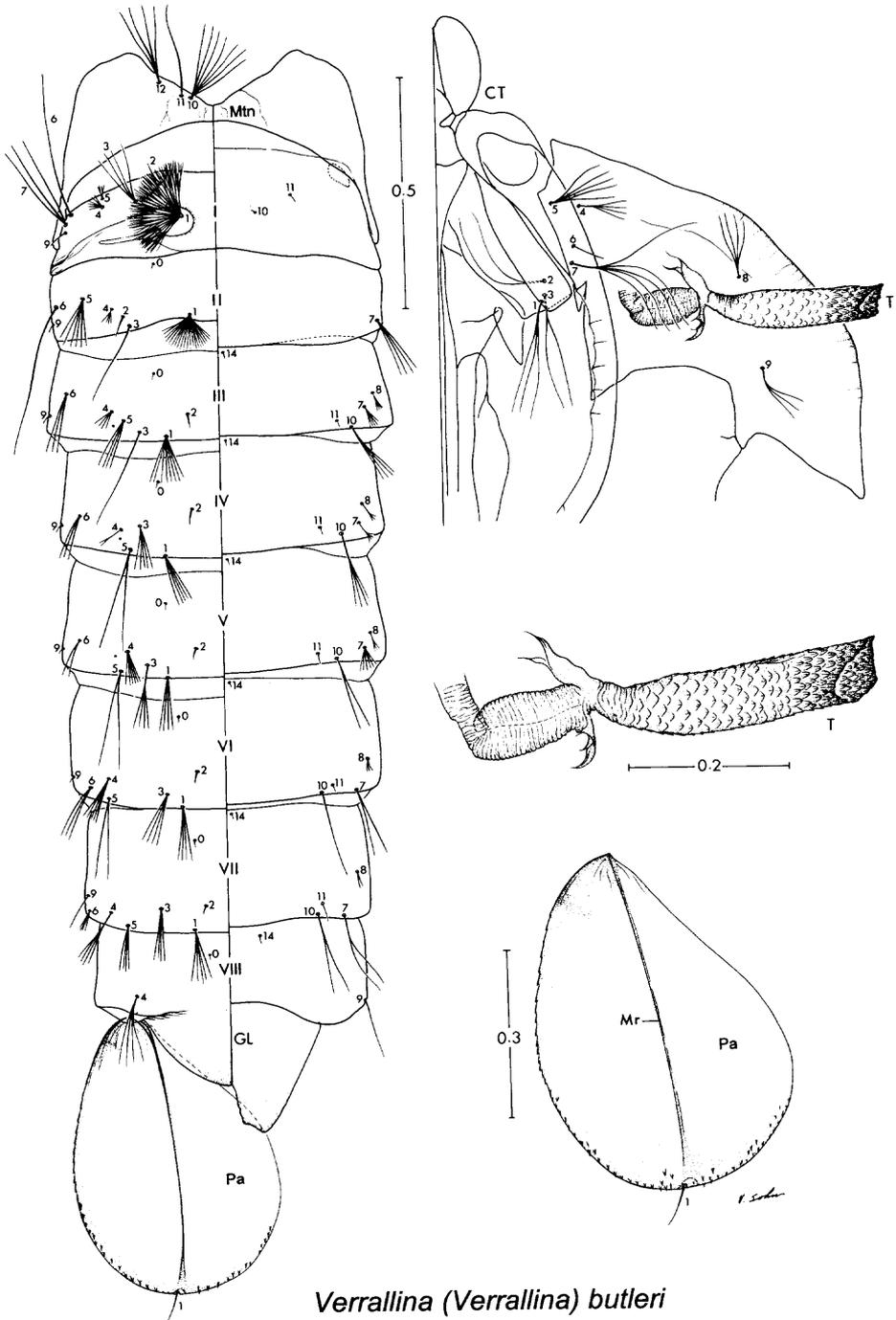
*Verrallina (Harbachius) yusafi*

Fig. 11



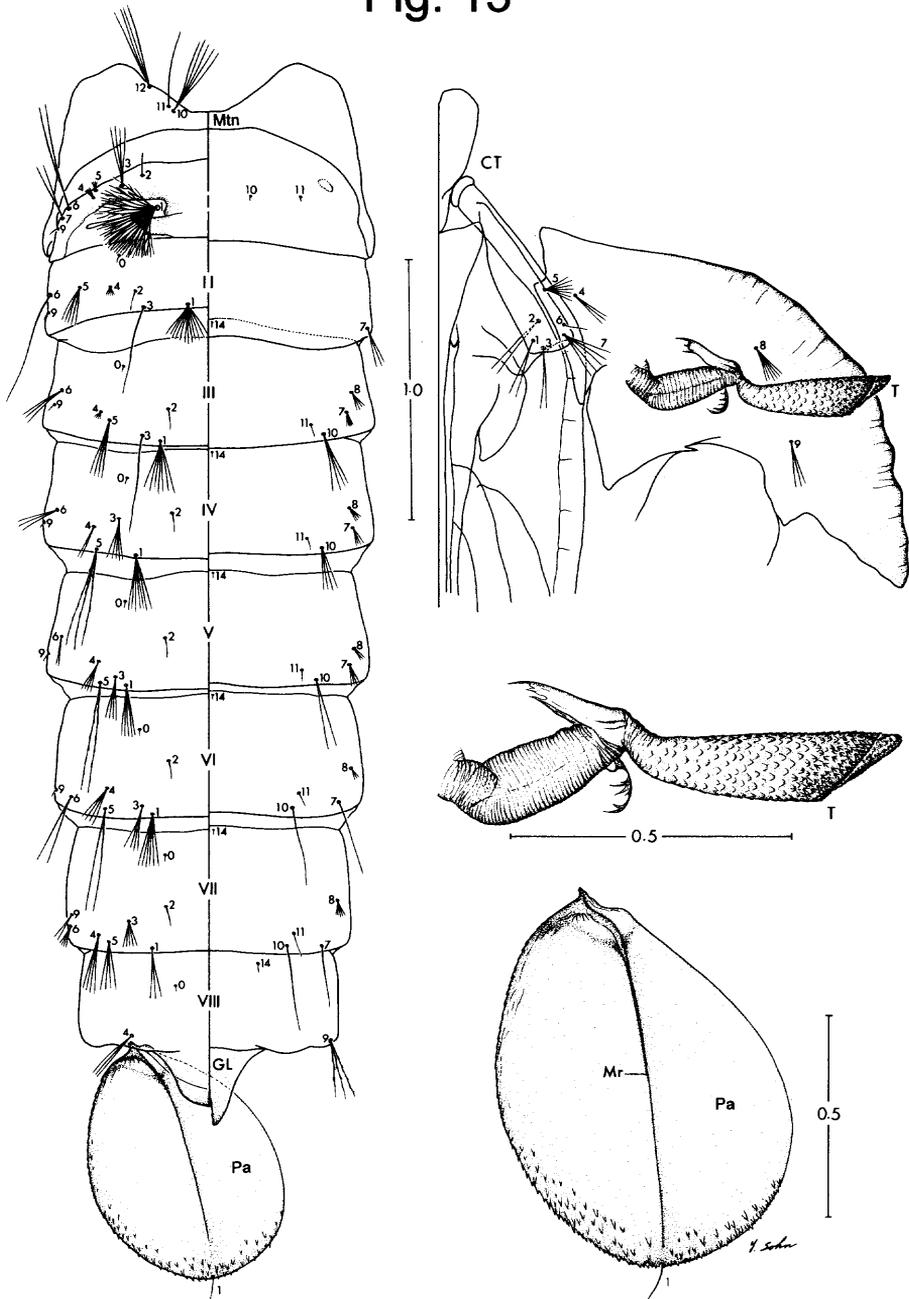
*Verrallina (Neomacleaya) indica*

Fig. 12



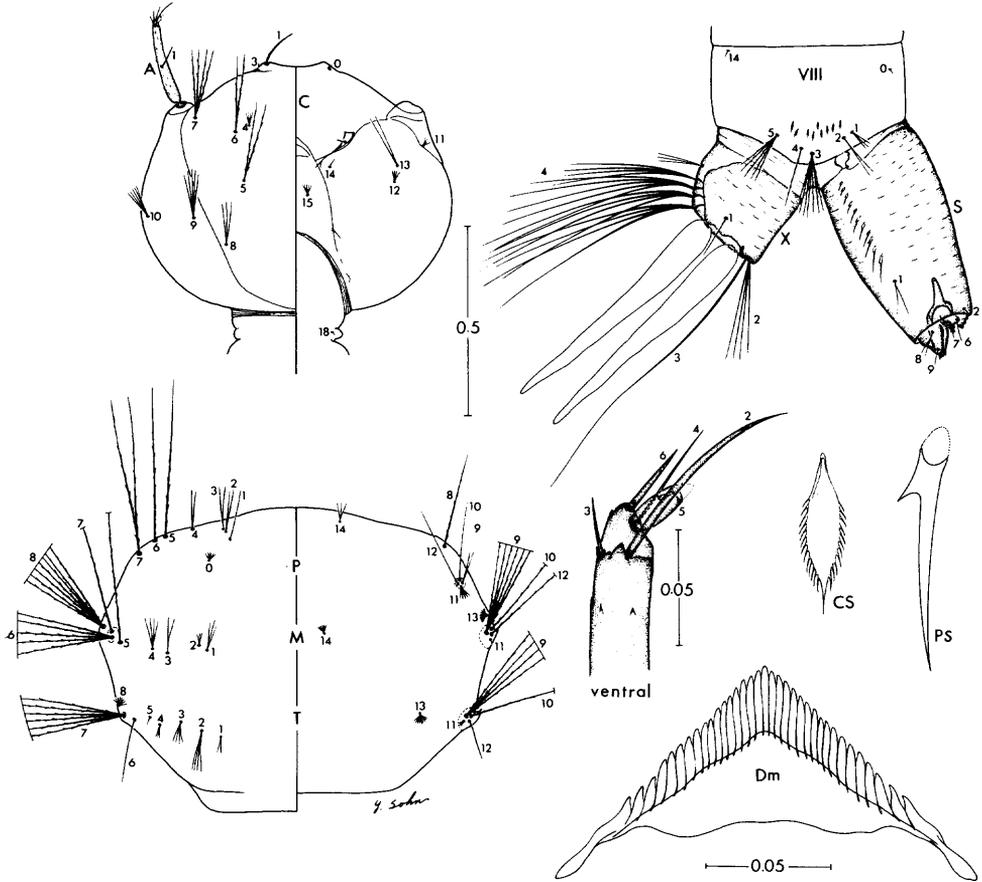
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Fig. 13

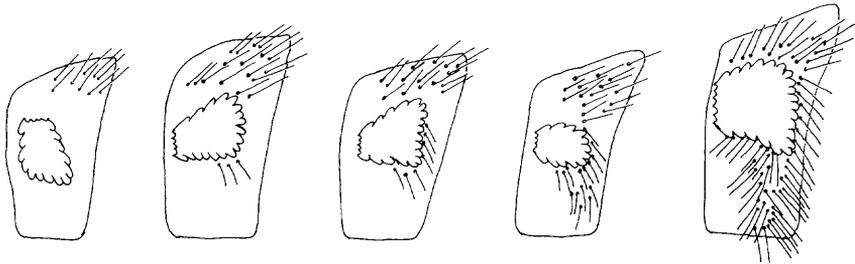


*Verrallina (Verrallina) carmenti*

Fig. 14



*Verrallina (Harbachius) yusafi*



*yusafi* ♀

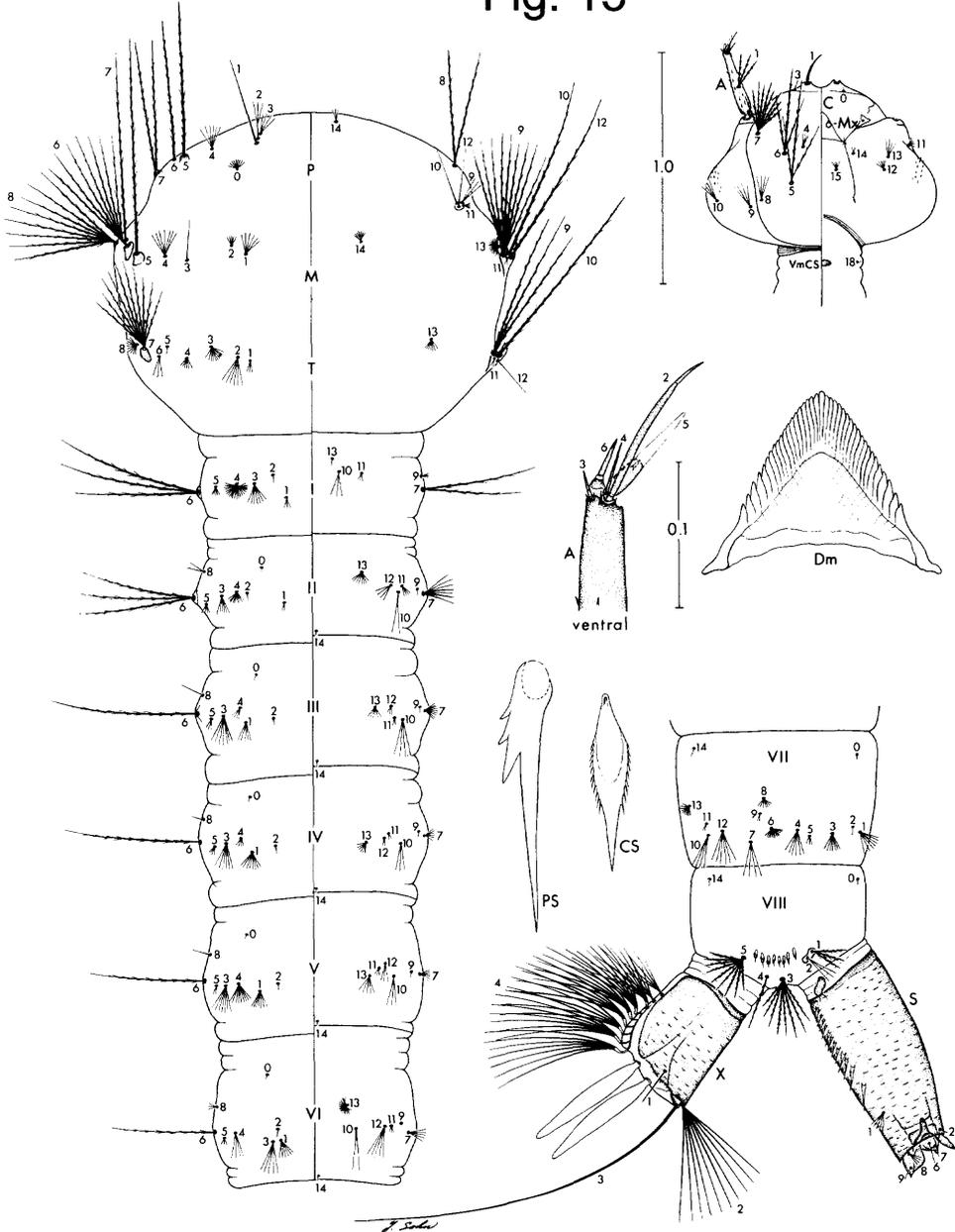
*indica* ♀

*carmenti* ♀

*butleri* ♀

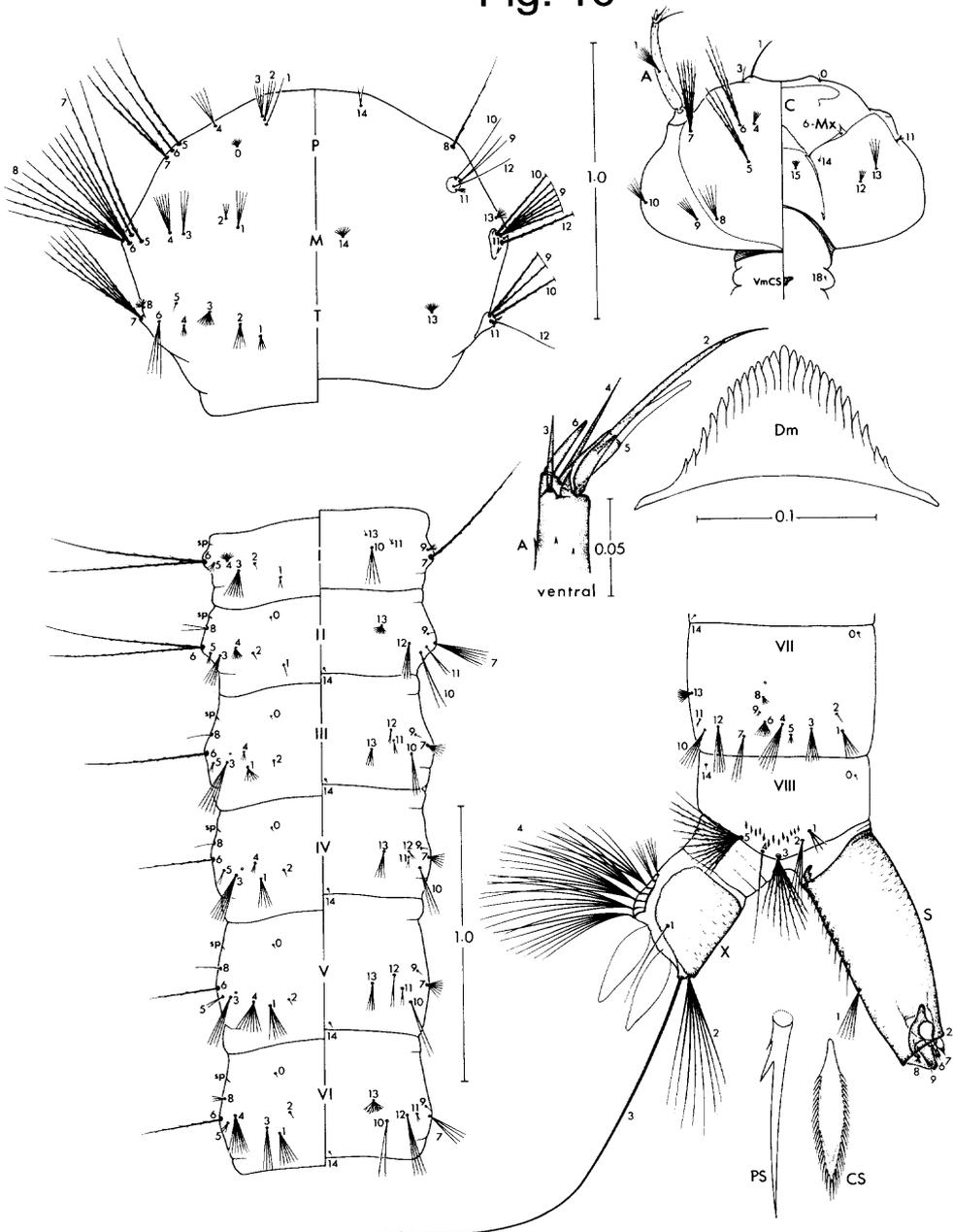
*unca* ♀

Fig. 15



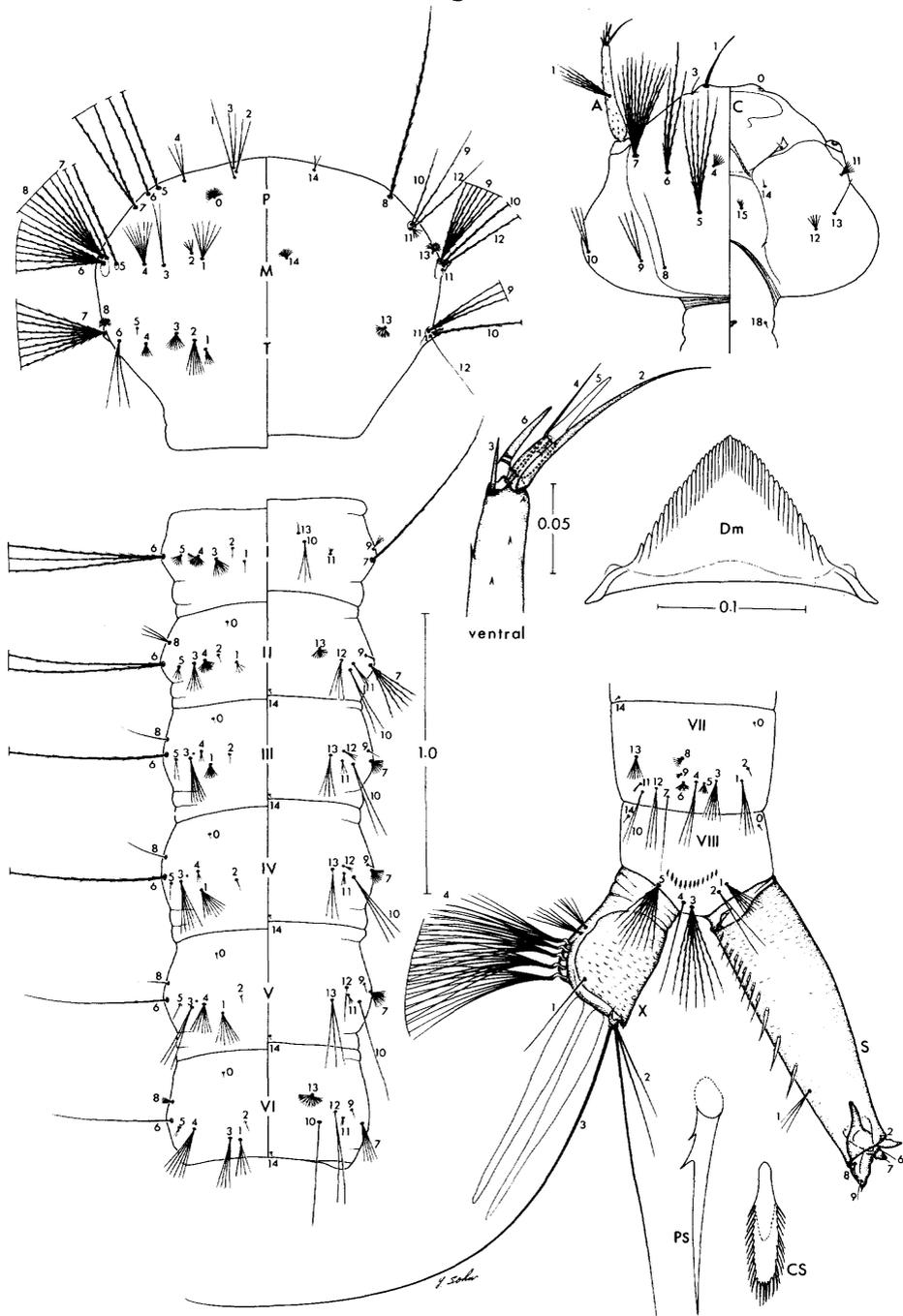
*Verrallina (Neomacleaya) indica*

Fig. 16



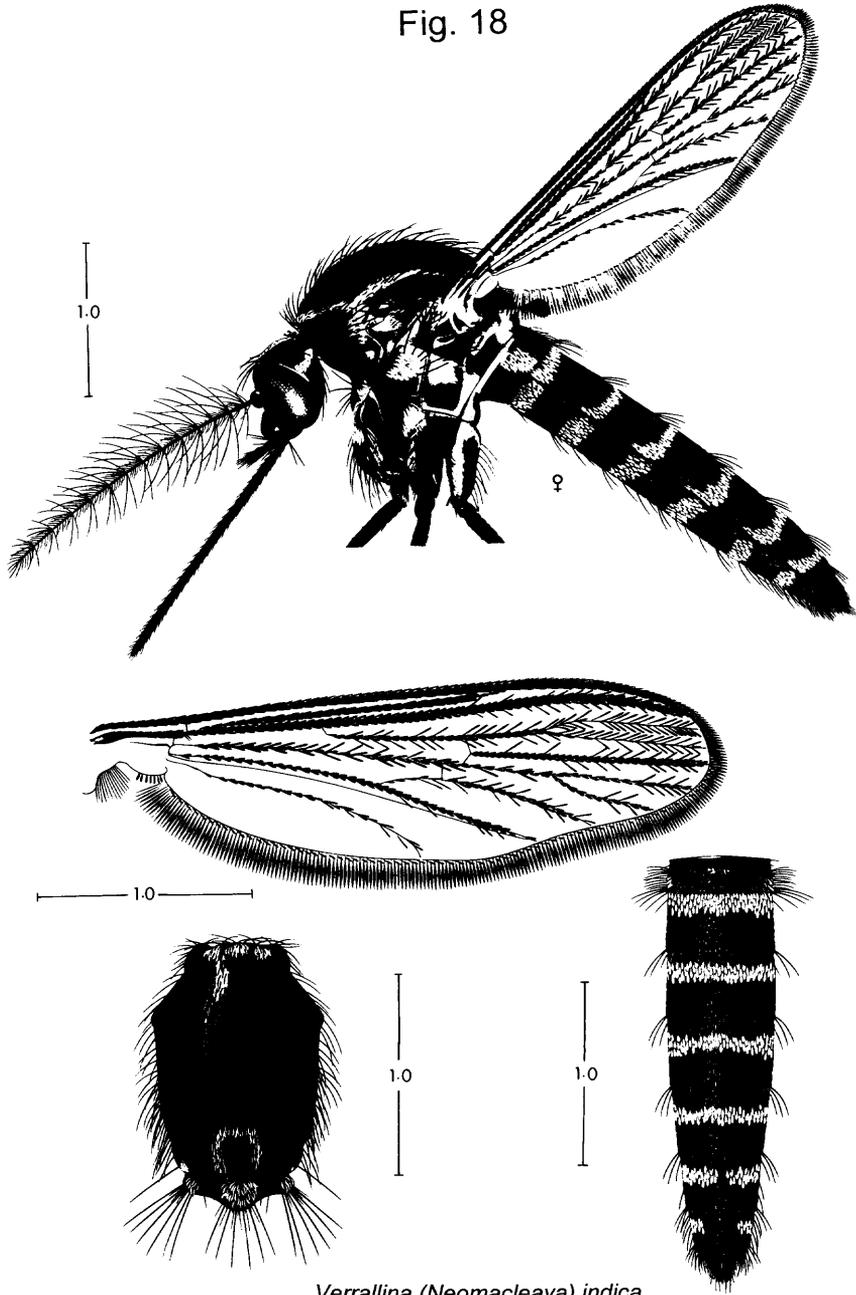
*Verrallina (Verrallina) butleri*

Fig. 17



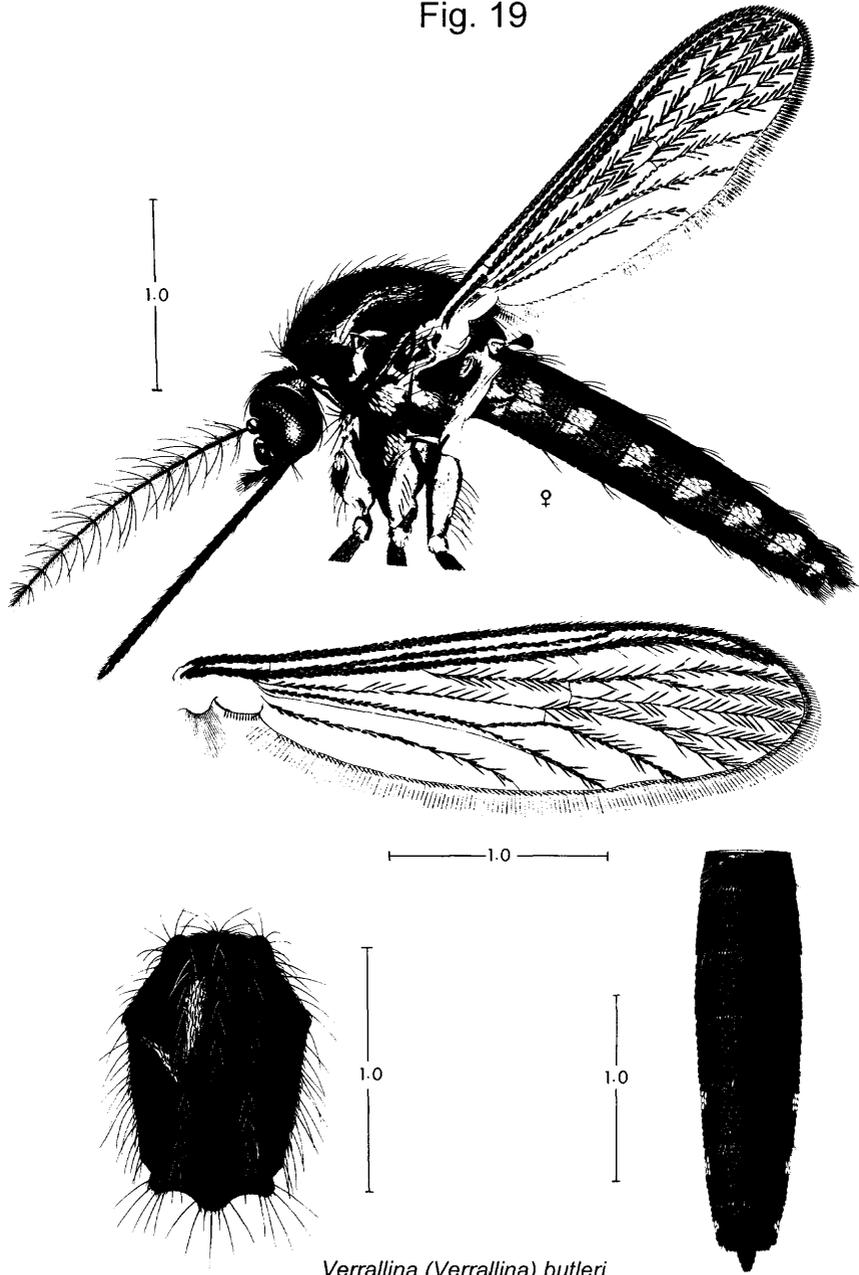
*Verrallina (Verrallina) carmentis*

Fig. 18



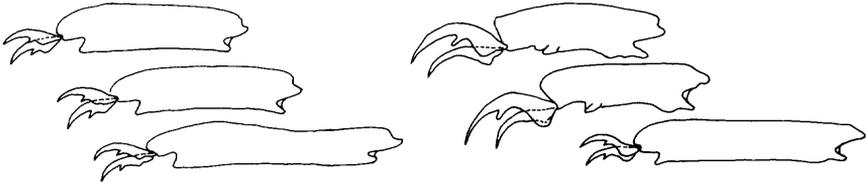
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Fig. 19

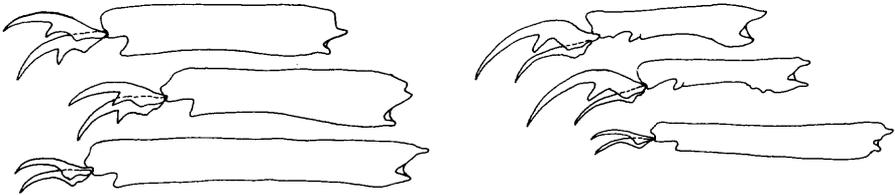


*Verrallina (Verrallina) butleri*

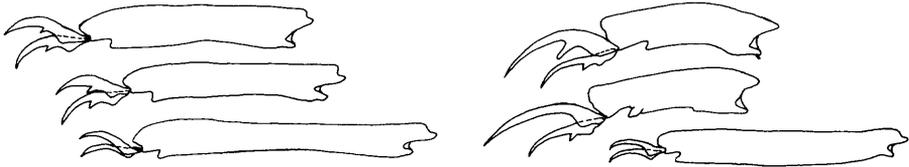
Fig. 20



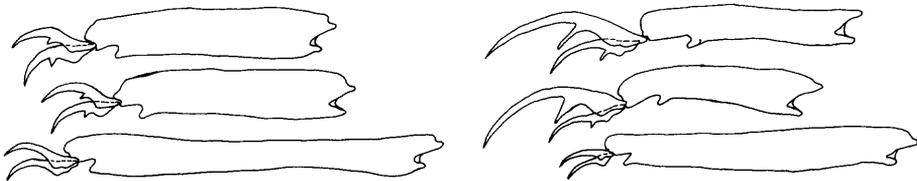
♀ *Verrallina (Harbachius) yusafi* ♂



♀ *Verrallina (Neomacleaya) indica* ♂



♀ *Verrallina (Verrallina) butleri* ♂



♀ *Verrallina (Verrallina) carmenti* ♂

— 0.2 —

Table 1. Observed branching of setae on pupae of *Ve. (Har.) yusafi* (9 specimens).

Seta No.	Cephalothorax		Abdominal Segments		
	CT	I	II	III	IV
0			1	1	1
1	1-3(2)	10-20(16)	8-13(8)	3-5(4)	3-5(4)
2	1,2(2)	1,2(1)	1	1	1
3	1-3(2)	2-4(3)	1	1	2-5(4)
4	2-5(3)	3-5(4)	2-5(3)	2-5(3)	2,3(2)
5	3-5(4)	2-4(2)	3-5(3)	2-4(3)	2,3(3)
6	1,2(1)	2,3(2)	1,2(2)	2,3(2)	1-3(2)
7	2,3(2)	2,3(3)	2,3(2)	1-4(2)	1,2(2)
8	2-4(4)			1-3(2)	1,2(2)
9	2,3(3)	1	1	1	1
10	2-5(3)			1-3(2)	1-3(2)
11	1			1	1
12	2-4(3)				
14				1	1

Seta No.	Abdominal Segments				Paddle Pa
	V	VI	VII	VIII	
0	1	1	1	1	
1	2-4(3)	2-4(3)	2-4(2)		1
2	1	1	1		
3	2,3(2)	2-4(2)	2-4(3)		
4	3-5(4)	2-5(4)	2,3(2)	2-4(2)	
5	1,2(2)	1-3(2)	2		
6	1,2(2)	1,2(1)	2-4(3)		
7	1-4(2)	1	1		
8	2,3(2)	1-3(2)	1-3(2)		
9	1	1	1	1,2(1)	
10	1	1	1		
11	1	1	1		
12					
14	1	1	1	1	

**Table 2. Observed branching of setae on pupae of *Ve. (Nma.) indica* (10 specimens).**

Seta No.	Cephalothorax		Abdominal Segments		
	CT	I	II	III	IV
0			1	1	1
1	2,3(2)	12-25(20)	4-7(6)	3,4(4)	1-4(2)
2	2,3(2)	1,2(1)	1	1	1
3	1-3(2)	1-4(2)	1,2(1)	1,2(1)	3-6(4)
4	2-5(3)	5-10(6)	3-5(4)	2-5(4)	2-4(2)
5	3-5(3)	2-5(3)	2-5(4)	3-6(4)	2,3(2)
6	1	1	1	1-3(1)	1-3(2)
7	2-4(3)	2-5(3)	2-5(2)	2-4(3)	2-4(2)
8	2-5(4)			2-4(3)	2,3(2)
9	2,3(2)	1	1	1	1
10	3-9(4)	1		1-3(2)	1-4(2)
11	1	1		1,2(1)	1,2(1)
12	2-4(2)				
14				1	1

Seta No.	Abdominal Segments				Paddle Pa
	V	VI	VII	VIII	
0	1	1	1	1	
1	1-3(2)	2-4(2)	1-5(3)		1
2	1	1	1		
3	1-5(2)	1-4(2)	2-6(3)		
4	3-7(4)	2-5(4)	2,3(2)	1-4(3)	
5	2,3(2)	2,3(2)	2,3(2)		
6	1-4(2)	1-3(2)	2-5(4)		
7	1-5(3)	1,2(1)	1,2(1)		
8	1-4(3)	2-5(3)	2-4(3)		
9	1	1	1,2(1)	1,2(2)	
10	1-3(1)	1	1,2(1)		
11	1,2(1)	1-3(1)	1,2(1)		
12					
14	1	1	1	1	

**Table 3. Observed branching of setae on pupae of *Ve. (Ver.) butleri* (10 specimens).**

Seta No.	Cephalothorax		Abdominal Segments		
	CT	I	II	III	IV
0			1	1	1
1	2-5(3)	14-23(20)	17-27(20)	4-10(8)	4-7(5)
2	1,2(2)	1	1	1	1
3	1-3(2)	3-5(4)	1	1	4-8(5)
4	2-5(4)	6-9(6)	4-8(4)	4-6(4)	2-4(2)
5	4-7(5)	4-9(4)	3-7(6)	4-7(4)	1,2(2)
6	1	1	1	2-4(3)	2-4(3)
7	3-7(5)	1-4(3)	3-6(4)	4-8(5)	2-4(4)
8	4-7(4)			3-6(4)	2-4(3)
9	2-4(3)	1,2(1)	1	1	1
10	7-13(7)	1		3-6(4)	3-5(4)
11	1	1,2(1)		1	1
12	3-5(4)				
14				1	1

Seta No.	Abdominal Segments				Paddle Pa
	V	VI	VII	VIII	
0	1	1	1	1	
1	3-5(4)	4-6(4)	4-6(5)		1
2	1	1	1		
3	3-5(4)	3-6(4)	4-9(6)		
4	4-7(6)	4-8(5)	3-6(4)	3-5(4)	
5	1-3(2)	2-4(2)	2-4(4)		
6	2,3(2)	2-4(3)	4-8(4)		
7	4-7(6)	1-3(2)	1-3(2)		
8	2-4(3)	2-5(3)	2-4(4)		
9	1	1	1,2(1)	1	
10	2-4(2)	1,2(1)	1-3(2)		
11	1	1	1		
12					
14	1	1	1	1	

**Table 4.** Observed branching of setae on pupae of *Ve. (Ver.) carmentis* (9 specimens).

Seta No.	Cephalothorax		Abdominal Segments		
	CT	I	II	III	IV
0			1	1	1
1	2,3(2)	19-36(22)	12-16(13)	6-11(7)	5-8(5)
2	2,3(2)	1	1	1	1
3	1,2(1)	2-4(4)	1	1	5-10(7)
4	3-5(3)	5-9(8)	5-10(6)	3-7(5)	2,3(2)
5	5-10(6)	4-7(4)	4-6(5)	3-6(5)	2,3(3)
6	1	1-3(3)	1	2-5(3)	3,4(3)
7	2-7(5)	2-5(4)	3-5(3)	4,5(5)	2-4(3)
8	6-10(7)			4,5(4)	2-4(3)
9	3-6(3)	1-3(1)	1	1	1
10	4-10(7)	1		4,5(4)	4,5(4)
11	1	1		1	1
12	4-7(5)				
14				1	1

Seta No.	Abdominal Segments				Paddle Pa
	V	VI	VII	VIII	
0	1	1	1	1	
1	2-6(4)	3-6(4)	2-5(4)		1
2	1	1	1		
3	3-6(4)	3-5(4)	3-6(4)		
4	4-10(5)	4-9(6)	3-5(4)	2-4(3)	
5	2	2,3(2)	3-5(4)		
6	2-4(3)	2,3(2)	3-6(4)		
7	4-7(6)	1	1,2(1)		
8	2-4(3)	3,4(3)	4-6(4)		
9	1	1	2,3(2)	3-6(6)	
10	1-3(2)	1	1-3(1)		
11	1	1	1		
12					
14	1	1	1	1	

**Table 5. Observed branching of setae on larvae of *Ve. (Har.) yusafi* (3 specimens).**

Seta No.	Cranium		Thorax		Abdominal Segments		
	C	P	M	T	I	II	III
0	1	5-7(6)				1	1
1	1	1	2,3(3)	2,3(2)	1	1,2(2)	2-4(4)
2		1,2(2)	2,3(3)	4-6(4)	1	1	1
3	1	1,2(2)	1,2(2)	4-7(4)	4,5(5)	3	2,3(3)
4	3,4(3)	1,2(2)	4	2-4(2)	6-11	4,5(5)	2,3(3)
5	1,2(1)	1	1,2(1)	1	3	2,3(2)	2
6	2,3(2)	1	5,6(6)	1	1,2(2)	1	1
7	2-4(3)	2,3(2)	1	5-8(7)	1	5,6(5)	5-7(6)
8	3,4(3)	1	6-8(6)	7-9(8)		2,3(2)	1
9	4,5(4)	2,3(2)	6-9(9)	2-4(3)	3-5(3)	1	1
10	4,5(4)	1	1	1	2,3(2)	1	1,2(1)
11	2-5(4)	3-5(4)	1	3	2	2,3(3)	2-4(2)
12	1-4(3)	1	1	1	1,2(1)	1-3(2)	2,3(2)
13	1-3(2)		8-12(8)	9		4-6(4)	4,5(4)
14	1	2,3(3)	4-8			1	1
15	4,5(4)						

Seta No.	Abdominal Segments						Siphon S
	IV	V	VI	VII	VIII	X	
0	1	1	1	1	1		
1	3,4(4)	3,4	2-4(2)	2,3(3)	2,3(3)	1	2-4(2)
2	1	1	1	1	2	3,4(4)	1
3	3,4(3)	2	2	2,3(2)	4-8(7)	1	
4	2-4(3)	4,5(5)	2-4(3)	2	1		
5	1,2(2)	1,2	2	2-4(2)	5,6(5)		
6	1	1	1,2(1)	5,6(6)			1
7	2-5(2)	4-6(4)	2,3(2)	1,2(2)			1
8	1	1,2(1)	2-5(3)	4-6(6)			2
9	1	1	1	2			1
10	1,2(1)	1	1	1			
11	2,3(2)	2,3(2)	2,3(2)	1,2(2)			
12	2	1,2(1)	1,2	1,2(1)			
13	3-5(4)	4,5(4)	9-16(9)	4-6(6)			
14	1	1	1	1	1		

**Table 6. Observed branching of setae on larvae of *Ve. (Nma.) indica* (12 specimens).**

Seta No.	Cranium		Thorax		Abdominal Segments		
	C	P	M	T	I	II	III
0	1	6-13(7)				1	1
1	1	1	3-7(5)	2-5(2)	1-5(3)	1-3(2)	5-10(7)
2		2-4(3)	2-6(3)	3-8(5)	1	1	1
3	1	2-5(4)	1-3(1)	3-14(11)	5-9(7)	5-9(6)	4-8(6)
4	2-5(4)	4-7(6)	5-10(7)	3-6(6)	14-22(15)	6-15(8)	3-5(3)
5	3	1	1,2(1)	1	2-5(3)	2-4(4)	2-5(2)
6	2-4(3)	1	4-9(7)	2-5(3)	3,4(3)	2-4(3)	1,2(1)
7	7-12(8)	2,3(2)	1	8-12(10)	2,3(2)	4-10(6)	7-15(9)
8	2-5(4)	2	6-10(8)	8-19(11)		2	1
9	3-5(4)	2-5(2)	7-12(9)	3,4(3)	3-5(4)	1,2(1)	1
10	2-5(4)	1	1	1,2(1)	3,4(4)	2-6(3)	3-6(5)
11	3-6(6)	2-6(5)	2,3(2)	2	2-4(3)	2-5(3)	2-5(3)
12	3-9(4)	1	1	1		3-6(4)	2-6(4)
13	3-5(4)		11-18(14)	6-12(10)	1	8-14(8)	3-7(5)
14	1-4(1)	2-4(3)	7-10(7)			1	1
15	4-8(5)						

Seta No.	Abdominal Segments						Siphon S
	IV	V	VI	VII	VIII	X	
0	1	1	1	1	1		
1	5-11(5)	5-11(6)	5-8(5)	3-7(7)	2-5(3)	1	3-6(5)
2	1	1	1	1	2-4(3)	7-11(9)	1
3	5-7(7)	5-7(5)	5-8(5)	5-12(9)	6-11(7)	1	
4	2-5(3)	7-11(8)	4-7(6)	2-7(6)	1		
5	2-4(2)	2-4(2)	2-4(3)	2-5(3)	7-12(9)		
6	1,2(1)	1	1	5-14(10)			1,2(1)
7	5-13(7)	4-15(7)	3-6(4)	3,4(3)			1
8	1,2(1)	1,2(1)	3-7(4)	2-8(7)			3-5(4)
9	1	1	1	1-4(3)			1
10	2-6(4)	2-6(3)	1-3(2)	2-5(4)			
11	2-4(3)	2-4(3)	2-4(3)	2-4(3)			
12	2,3(3)	2-4(3)	3-6(4)	4-7(5)			
13	4-8(6)	4-7(5)	21-28(25)	7-14(9)			
14	1	1	1	1	1		

**Table 7. Observed branching of setae on larvae of *Ve. (Ver.) butleri* (10 specimens).**

Seta No.	Cranium		Thorax		Abdominal Segments		
	C	P	M	T	I	II	III
0	1	9-15(9)				1	1
1	1	1	2-4(4)	2-5(2)	1-3(2)	1-3(1)	4-7(6)
2		2,3(3)	2-5(3)	4-8(5)	1	1	1
3	1	2-4(3)	3	6-10(9)	4-7(5)	4-9(5)	4-6(4)
4	3-6(4)	3-5(4)	4-7(6)	4-6(5)	9-18(9)	6-12(8)	2-5(3)
5	2-4(3)	1	1	1	3,4(4)	2-4(3)	1-3(2)
6	3,4(3)	1	3-7(5)	3,4(3)	2,3(2)	1,2(2)	1
7	5-7(6)	1-3(2)	1	4-8(8)	1	4-6(6)	5-8(6)
8	3-5(4)	1	4-8(7)	7-12(9)		2	1
9	3-5(4)	1,2(2)	6-8(7)	2	3-5(4)	1	1
10	3-5(4)	1	1	1	3,4(4)	1,2(2)	2-4(3)
11	2-5(2)	2-6(4)	1,2(2)	2,3(3)	1,2(2)	2	2,3(2)
12	4,5(4)	1	1	1		3-5(3)	2,3(2)
13	2-4(3)		7-17(10)	6-9(6)	1,2(2)	7-12(8)	3-5(4)
14	1	2,3(2)	5-10(8)			1	1
15	5-7(5)						

Seta No.	Abdominal Segments						Siphon S
	IV	V	VI	VII	VIII	X	
0	1	1	1	1	1		
1	4-6(4)	4-6(5)	4-7(6)	4-7(5)	3-5(3)	1	4-7(5)
2	1	1	1	1	3-5(4)	6-8(7)	1
3	4-6(6)	4-8(4)	4-6(4)	5-7(7)	5-11(7)	1	
4	2-4(2)	7-10(8)	4-8(8)	4-6(5)	1		
5	1-3(2)	1-3(2)	1-4(2)	3-6(4)	9-15(10)		
6	1	1	1	7-11(10)			1
7	6-11(6)	6-10(7)	4,5(4)	2,3(2)			1
8	1	1,2(1)	3-5(3)	3-7(5)			3-6(5)
9	1	1	1	1,2(2)			1
10	3,4(3)	1,2(2)	1-4(2)	3-5(4)			
11	2	2,3(2)	2,3(2)	1-3(2)			
12	2,3(2)	1-3(2)	2-5(4)	4-6(5)			
13	2-4(4)	3-5(3)	13-20(20)	6-10(9)			
14	1	1	1	1	1		

**Table 8. Observed branching of setae on larvae of *Ve. (Ver.) carmentis* (10 specimens).**

Seta No.	Cranium		Thorax		Abdominal Segments		
	C	P	M	T	I	II	III
0	1	14-25(18)				1	1
1	1	1	4-8(6)	4-7(5)	1	3-6(4)	6-11(8)
2		2,3(2)	3-7(4)	6-9(7)	1	1	1
3	1	2	2-4(3)	10-16(10)	5-11(6)	5-9(7)	5-9(6)
4	6-10(7)	3-6(5)	6-9(7)	6-9(7)	17-27(24)	10-17(11)	2-5(3)
5	3-7(5)	1	1	1	5-9(6)	2-6(4)	1-3(2)
6	3	1	5-10(6)	2,3(3)	3	2,3(2)	1
7	8-14(11)	2	1	6-10(7)	1	3-8(5)	7-12(10)
8	1	1,2(1)	6-8(8)	18-27(22)		2-4(3)	1
9	2-4(3)	1	6-11(10)	3	3-5(3)	1-4(1)	1
10	2-4(3)	1	1	1	2-4(3)	2,3(2)	2,3(2)
11	5-8(6)	3-6(5)	2,3(3)	2,3(3)	3-5(3)	2-4(3)	2,3(3)
12	3-6(5)	1	1	1		3-5(4)	2-4(3)
13	1		18-40(24)	14-23(15)	1,2(1)	12-24(15)	3-7(4)
14	1	1,2(2)	13-20(15)			1	1,2(1)
15	5-11(5)						

Seta No.	Abdominal Segments						Siphon S
	IV	V	VI	VII	VIII	X	
0	1	1	1	1	1		
1	5-10(8)	5-9(7)	3-6(4)	4-6(4)	5-8(6)	1	2-4(3)
2	1	1	1	1	2	3	1
3	4-8(7)	2-4(3)	3-5(4)	5-9(6)	6-11(8)	1	
4	2-5(3)	6-12(7)	3-7(6)	2-4(3)	1		
5	1,2(1)	1,2(1)	2-4(2)	4-8(6)	7-11(9)		
6	1	1	1	10-16(11)			1
7	8-13(10)	8-15(12)	4-7(5)	1			1
8	1	1	5-8(5)	6-9(7)			2-5(2)
9	1	1	1,2(1)	2-4(4)			1
10	2,3(3)	1	1	2,3(2)			
11	2,3(3)	2-4(3)	2-4(3)	2-4(2)			
12	2-4(3)	1,2(1)	2,3(2)	2,3(3)			
13	2-4(3)	2-4(3)	22-40(30)	6-11(7)			
14	1	1,2(1)	1	1-3(1)	1		

APPENDIX A. Current status of life stages/structures of species in genus *Verrallina*.

Species	♀	♀g	♂	♂g	P	L	E
<i>abdita</i>	X	X*					
<i>adusta</i>	X*		X*	X*	X*	X*	
<i>agrestis</i>	X	X*	X	X*	X*	X*	
<i>andamanensis</i>	X*	X*	X*	X*	X*	X*	
<i>atriisimilis</i>	X*	X*	X*	X*		X*	
<i>atrius</i>	X*	X*	X*	X*	X*	X*	
<i>azureosquamata</i>	X*	X*					
<i>bifoliata</i>			X	X*			
<i>butleri</i>	X*						
<i>campylostylus</i>	X*	X*	X*	X*	X*	X*	
<i>carmenti</i>	X*	X*	X*	X*	X*	X*	
<i>cauta</i>	X	X*	X	X*			
<i>clavata</i>	X*	X*	X*	X*	X*		
<i>comata</i>	X	X*					
<i>comosa</i>	X*	X*					
<i>consonensis</i>			X	X*	X*	X*	
<i>cretata</i>	X*	X*	X*	X*	X*	X*	
<i>cuccioi</i>	X*	X*	X*	X*	X*	X*	
<i>cunninghami</i>	X*		X				
<i>cyrtolabis</i>	X*	X*	X*	X*	X*	X*	
<i>dux</i>	X*						
<i>embiensis</i>			X*	X*			
<i>foliformis</i>	X*	X*	X*	X*	X*	X*	
<i>fragilis</i>	X*	X*	X	X*			
<i>funerea</i>	X	X*	X	X*	X	X*	X*
<i>gibbosa</i>	X	X*	X*	X*	X*	X*	
<i>hamistylus</i>	X*	X*	X*	X*		X*	
<i>harrisonicus</i>	X	X*					
<i>hispida</i>	X	X*					
<i>incerta</i>	X*	X*	X*	X*	X*	X*	
<i>indecorabilis</i>	X	X*	X*	X*			
<i>indica</i>	X*	X*	X*	X*	X*	X*	
<i>iriomotensis</i>	X*	X*	X*	X*	X*	X*	
<i>johnsoni</i>	X*	X*	X*	X*	X*	X*	
<i>johorensis</i>	X*	X*					
<i>killertonis</i>	X	X*	X*	X*			
<i>komponga</i>			X*	X*			
<i>lankaensis</i>	X*	X*	X*	X*			
<i>lateipennis</i>	X*	X*	X	X*	X*	X*	
<i>leicesteri</i>	X*	X*	X*	X*	X*	X*	
<i>leilae</i>			X	X*			
<i>lineata</i>	X*						

## APPENDIX A (continued)

Species	♀	♀g	♂	♂g	P	L	E
<i>lugubris</i>	X*	X*	X*	X*	X*	X*	
<i>macrodixoa</i>	X*	X*	X*	X*	X*	X*	
<i>margarsen</i>	X*	X*	X*	X*	X*	X*	
<i>mccormicki</i>	X*	X*	X*	X*	X*	X*	
<i>milnensis</i>	X	X*	X*	X*			
<i>multifolium</i>	X	X*	X*	X*	X*	X*	
<i>neomacrodixoa</i>	X*	X*	X*	X*	X*	X*	
<i>nigrotarsis</i>	X*	X*	X*	X*	X*	X*	
<i>nobukonis</i>	X*	X*	X*	X*	X*	X*	X*
<i>notabilis</i>	X*	X*					
<i>nubicola</i>			X	X*			
<i>obsoleta</i>	X		X*	X*			
<i>pahangi</i>	X	X*					
<i>panayensis</i>	X*	X*	X*	X*			
<i>parasimilis</i>	X*		X*?	X*?	X	X*	X*
<i>petroelephantus</i>	X	X*					
<i>philippinensis</i>	X	X*	X	X*			
<i>phonoma</i>	X	X*	X*	X*			
<i>pipkini</i>	X*	X*					
<i>prioekanensis</i>			X*	X*			
<i>protuberans</i>			X	X*			
<i>pseudodiurna</i>			X	X*			
<i>pseudomediofasciata</i>		X*	X*	X*	X*	X*	X*
<i>pseudovarietas</i>			X*	X*			
<i>quadrifolium</i>	X	X*	X*	X*	X*		
<i>quadrispinata</i>	X*	X*	X*	X*	X	X	
<i>ramalingami</i>			X*	X*			
<i>rami</i>			X*	X*			
<i>rara</i>	X*	X*	X*	X*			
<i>reesi</i>	X*		X*	X*			
<i>robertsi</i>	X*	X*	X*	X*	X*		
<i>sabahensis</i>	X*	X*					
<i>seculata</i>			X*	X*			
<i>sentania</i>	X*	X*	X*	X*	X	X*	
<i>similis</i>	X		X*?	X*?	X*	X*	
<i>simplus</i>			X	X*			
<i>singularis</i>	X*	X*	X*	X*			
<i>sohni</i>			X*	X*			
<i>spermathecus</i>	X	X*					
<i>srilankensis</i>	X*	X*	X*	X*			
<i>stunga</i>	X*	X*					
<i>torosa</i>			X*	X*	X*	X*	

## APPENDIX A (continued)

Species	♀	♀g	♂	♂g	P	L	E
<i>trispinata</i>	X*	X*	X*	X*	X*	X*	
<i>unca</i>	X*	X*	X*	X*	X*	X*	
<i>uniformis</i>	X*	X*	X	X*			
<i>vallistris</i>	X*	X*	X*	X*	X*	X*	
<i>vanapa</i>	X*		X*	X*	X*		
<i>variabilis</i>	X*	X*	X*	X*	X*	X*	
<i>varietas</i>	X*	X*	X	X*			
<i>virilis</i>	X*	X*	X*	X*			
<i>yerburyi</i>	X*	X*	X*	X*	X*	X*	
<i>yusafi</i>	X*	X*	X*	X*	X*	X*	

X = Stage/structure has been described.

\* = Portion of stage/structure has been illustrated. Many of the adult ♀ and ♂ illustrations are of the posttarsi only.

? = Not a positive association.

♀ = Female.

♀g = Female genitalia.

♂ = Male.

♂g = Male genitalia.

P = Pupa.

L = Fourth-instar larva.

E = Egg.

**APPENDIX B. Conspectus of Taxonomic Changes.**

**New Taxa**

*Harbachius* Reinert, new subgenus of genus *Verrallina* Theobald

**Changes in Taxonomic Status**

*Harbachius* Reinert, included species as listed on page 22

*Neomacleaya* Theobald, revalidated as subgenus of *Verrallina* with  
included species as listed on page 28

*Verrallina* Theobald, resurrected from subgenus of genus *Aedes* Meigen

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Valid taxa are in Roman type, synonyms are italicized. Boldface page numbers are those which began the primary treatment of the taxon. Figure numbers are in parentheses.

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