

**COMPARATIVE ANATOMY OF THE FEMALE GENITALIA OF GENERA
AND SUBGENERA IN TRIBE AEDINI (DIPTERA: CULICIDAE).
PART VIII. GENUS *VERRALLINA* THEOBALD**

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Abstract. A comparative, morphological analysis of the female genitalia of the subgenera of genus *Verrallina* Theobald was conducted. Based on the analysis, the female genitalia of *Verrallina* are characterized and a key to the included subgenera (i.e., *Harbachius* Reinert, *Neomacleaya* Theobald, and *Verrallina*) is provided. The female genitalia of the three currently recognized subgenera are described. Treatment of the genital morphology of each subgenus includes a composite description, detailed description and illustration of the type species, description of subcategories, list of the species examined, list of published illustrations of species with their citations, and a discussion. The discussion section contains a list of the most distinctive features of the subgenus, a comparison with other subgenera, and other pertinent information.

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INTRODUCTION

This is the eighth in a series of papers by the author that describes the female genitalia of the genera and subgenera included in tribe Aedini of family Culicidae. Part I of the series

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(Reinert 2000a) included a brief historical background of published papers dealing with the subject and provided an introduction to the series, part II (Reinert 2000b) dealt with genus *Psorophora* Robineau-Desvoidy, part III (Reinert 2000c) with genus *Udaya* Thurman, part IV (Reinert 2000d) with genus *Zeugomyia* Leicester, part V (Reinert 2000e) with genus *Aedes* Meigen, part VI (Reinert 2001a) with genus *Ayurakitia* Thurman, and part VII (Reinert 2001b) with genus *Opifex* Hutton. This paper covers genus *Verrallina* Theobald and the three included subgenera: *Harbachius* Reinert, *Neomacleaya* Theobald, and *Verrallina*.

MATERIALS AND METHODS

A comparative, morphological analysis of the female genitalia of the subgenera of *Verrallina* was conducted, a characterization of the female genitalia of the genus is given, and a key to the included subgenera is provided. The genitalia of the three currently recognized subgenera of the genus are described. The format used for each subgenus includes a composite description, a detailed description and illustration of the type species, a description of Assemblages in subgenus *Verrallina*, a list of the species examined, a list of published illustrations of species with their citations, and a discussion including the most distinctive features, and other items of note.

Within the subgenus *Verrallina*, the term Assemblage is used to avoid confusion with other reported informal categories. Assemblage, as used here, refers to a collection of species with similar morphological features of the female genitalia. The term is not meant to be a designated taxon; however, in the case of subgenus *Verrallina* it encompasses the same species as the Series of Reinert (1999).

Female genitalia of genus *Verrallina* are considered here to include all structures caudad of abdominal segment VII. Segment VIII is included since its tergum and sternum are often modified in development and shape, and possess specialized setae.

Terminology used in the descriptions and illustrations follows Reinert (2000a) and the abbreviations used are found in the "List of Abbreviations Used in the Text and/or Figures" that precedes the figures. Morphological descriptions are based on slide-mounted genitalia that were dissected from nonliving, dried females. Measurements and descriptions of female genital structures are based on specimens that were cleared, dissected, arranged in a dorsoventrally flattened position, and mounted in Canada balsam under glass cover slips on microscope slides. The method of preparation of specimens follows Reinert (2000a). Ranges given in the key and descriptions are based on the species (listed under "species examined" section of each subgenus) and the specimens that I have examined, therefore for a specific subgenus some variation may occur in species not seen. A phase contrast microscope was used because this was usually necessary to determine some structures of the spermathecal eminence on the roof of the vagina. Measurements of structures (e.g., length and width of tergum VIII, sternum VIII, cercus, etc.) include only the pigmented and sclerotized areas and were made at 400X magnification using an ocular micrometer having a linear scale of 100 divisions that had been calibrated using a stage micrometer. The scales used in the illustrations are in millimeters.

FEMALE GENITALIA OF GENUS *VERRALLINA* THEOBALD

Genus description. *Segments VII and VIII.* More or less dorsoventrally flattened. *Tergum VIII.* Proximal 0.10-0.70 retracted into segment VII; covered with minute spicules; moderately to heavily pigmented; short to moderately long; moderately wide to wide; base usually

slightly concave; apex gently convex, straight, or slightly concave; numerous short and moderately long setae scattered over distal 0.24-0.88; numerous broad scales on distal 0.50-0.84; basolateral seta present or absent (some species with small bulla instead of seta); VIII-Te index 0.35-0.80; VIII-Te/IX-Te index 1.05-6.84; length 0.16-0.35 mm; width 0.27-0.86 mm. **Sternum VIII.** Covered with minute spicules; moderately to heavily pigmented; length shorter than width; base concave mesally; apex with shallow to moderately deep, median emargination separating small lobe on each side of midline; setae on lobe slender or stout; numerous short and moderately long setae scattered over most of surface; numerous broad scales covering much of distal 0.78-0.96; apical, intersegmental membrane nonpigmented; VIII-S index 0.47-0.80; length 0.17-0.32 mm (0.37-0.45 mm in *Ve. yerburyi* (Edwards)); width 0.27-0.53 mm (0.65-0.76 mm in *Ve. yerburyi*). **Tergum IX.** Covered with minute spicules; moderately to heavily pigmented; very short or short (except few species); wide or very wide; ribbon-like or band-like; setae normally absent (several setae present in *Ve. gibbosa* (Delfinado) and *Ve. yusafi* (Barraud) and rarely one seta on one side in few other species); IX-Te index 0.12-0.83; length 0.03-0.15 mm (0.26-0.33 mm in *Ve. yerburyi*); width 0.14-0.46 mm. **Insula.** In subgenera *Neomacleaya* and *Verrallina* ill-defined, small, nonpigmented, with 2-7 small tuberculi (each usually with minute spicule); or in subgenus *Harbachius* insula absent and apparently replaced by median, apical, U- or V-shaped portion of lower vaginal sclerite; setae absent. **Lower vaginal lip.** With spicules at least on basal portion (normally restricted to hinge area in *Neomacleaya*); moderately to heavily pigmented; narrow (median, apical area apparently absent in *Harbachius*); with or without small, heavily pigmented, median projection caudally; lower vaginal sclerite lightly to heavily pigmented, variable in development, shape and number of sclerites. **Upper vaginal lip.** With spicules usually confined to posterior margin; 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*); upper vaginal sclerite moderately to heavily pigmented, variable in shape and development, very large, often covering much of vaginal roof. **Spermathecal eminence.** Well defined; heavily pigmented; depth shallow to deep; simple to complex; with or without spermathecal spicules; heavily pigmented spicule-lined pouch present (subgenus *Harbachius*) or absent (subgenera *Neomacleaya* and *Verrallina*). **Postgenital lobe.** Covered with minute to short spicules; short to moderately long; narrow to moderately wide; apex rounded or with small to very deep, median emargination; 5-29 setae distally on each side of midline, 11-57 total setae; ventral PGL/Ce index 0.24-0.61; dorsal PGL index 0.47-1.30; ventral PGL index 0.43-2.13; ventral length 0.06-0.16 mm. **Proctiger.** Membranous; with minute spicules. **Cercus.** Covered with minute to short spicules; more or less triangular in outline; short to moderately long; usually broad at base; apex acute; dorsal surface with number of short and moderately long setae scattered over most of surface, few long setae at apex, usually with numerous broad scales; ventral surface with several short to moderately long setae along outer margin and becoming more numerous distally; cercus index 1.76-4.27; Ce/dorsal PGL index 2.42-5.71; length 0.18-0.38 mm; width 0.05-0.13 mm. **Spermathecal capsules.** One large, one medium, and one small; 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.** Basal area nonpigmented to moderately pigmented.

Discussion. The type species, *butleri*, of genus *Verrallina* was originally described by Theobald (1901) in genus *Aedes* Meigen. Theobald (1903) described *Verrallina* as a new genus and included *butleri* in it along with two other species (the latter two species were later transferred to other genera). In 1907, Theobald described genus *Neomacleaya* and included in it a single

species, *indica* Theobald. Leicester (1908) described genus *Aioretomyia*. Edwards (1913) synonymized *Verrallina*, *Neomacleaya*, and *Aioretomyia* with genus *Aedes* and later (1917) he transferred the species previously included in *Verrallina*, *Neomacleaya*, and *Aioretomyia*, along with several additional species, to subgenus *Aedes* of *Aedes*. Belkin (1962) resurrected *Verrallina* as a subgenus of *Aedes* and provisionally included *Neomacleaya* and *Aioretomyia* as synonyms. Delfinado (1967) removed *Neomacleaya* from synonymy with *Verrallina*, resurrected it as a subgenus of *Aedes*, and included in it primarily Oriental species previously included in *Aedes*, *Aioretomyia*, *Neomacleaya*, and *Verrallina*. However, Huang (1968) followed Belkin (1962) and placed in subgenus *Verrallina* the species occurring in the Papuan Subregion. Reinert (1974) presented a new interpretation of subgenus *Verrallina* that included the separation of the subgenus into two sections (i.e., A and B) and divided the first section into three series (i.e., Butleri, Carmenti, and Indicus Series). He included *Neomacleaya* and *Aioretomyia* as synonyms of subgenus *Verrallina* of genus *Aedes*. In 1984, Reinert gave a slightly revised description of subgenus *Verrallina* and included the species occurring in Sri Lanka. Reinert (1999) restored *Verrallina* to generic rank in tribe Aedini and provided rationale for this action. He included in the genus three subgenera (i.e., *Neomacleaya*, *Verrallina* (with Butleri Series and Carmenti Series), and *Harbachius* (described as new)) and 94 named species. Reinert's (1999) arrangement is followed here.

The following combination of features is most distinctive for genus *Verrallina*: lower vaginal sclerite is present; insula is ill-defined, small, and has a few tiny tuberculi in subgenera *Neomacleaya* and *Verrallina* or the insula is absent in subgenus *Harbachius* and apparently replaced by an U- or V-shaped, median, apical, sclerotized portion of the lower vaginal sclerite, and setae are absent; spermathecal eminence is well defined and heavily pigmented; three heavily pigmented spermathecal capsules are present and each is different in size and usually has a short neck; tergum IX is short or very short (except for a few species, see under *Neomacleaya*), wide or very wide, and normally is without setae (except two species with a few setae and occasionally one seta in a few other species); upper vaginal sclerite is very large, it normally covers a large area of the vaginal roof, and it is moderately to heavily pigmented; cercus is more or less triangular in outline and usually has numerous broad scales on the dorsal surface; and tergum VIII and sternum VIII each normally has numerous broad scales that often cover much of the surface.

Verrallina is very different from all other genera of Aedini, as well as the other genera of Culicidae, in the remarkably complex development of the female and male genitalia. Barraud (1928) was the first to recognize the importance of the female genitalia for separating species of the genus. However, he apparently did not realize the significance of these uniquely developed structures at higher taxonomic levels. Development of the female genitalia of *Verrallina* differ in many important respects from species of the other genera of Aedini as noted above.

KEY TO SUBGENERA BASED ON FEMALE GENITALIA

1. Spermathecal eminence with cephalad, spicule-lined pouch; insula absent but replaced with U- or V-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 minute to small tuberculi; upper vaginal lip otherwise2

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 Assemblage)*Verrallina*

FEMALE GENITALIA OF SUBGENERA OF *VERRALLINA*

SUBGENUS *HARBACHIUS* REINERT

(Fig. 1)

Subgenus description. *Tergum VIII.* Moderately long; moderately wide; scaled area reduced and more distal; VIII-Te index about 0.58-0.80; VIII-Te/IX-Te index 2.00-3.03; length 0.16-0.23 mm; width 0.27-0.40 mm. *Sternum VIII.* With numerous stouter setae on pair of median, apical lobes; scaled areas smaller; VIII-S index 0.47-0.73; length 0.17-0.25 mm; width 0.33-0.40 mm. *Tergum IX.* Short and wide; IX-Te index 0.30-0.49; length 0.07-0.09 mm; width 0.14-0.26 mm. *Insula.* Absent but apparently replaced with median, apical, U- or V-shaped projection of lower vaginal sclerite; without tuberculi or setae. *Lower vaginal lip.* Restricted to lateral and basal areas, with minute spicules; sclerite forming pair of heavily pigmented, ribbon-like plates along floor of vagina and attached to lower vaginal lip throughout entire length, fused at apex and developed into median, U- or V-shaped projection, sclerite without spicules. *Upper vaginal lip.* With median, posterior area produced into large, horizontal shield extending anteriorly over or around spermathecal eminence. *Spermathecal eminence.* Relatively simple; shallow; few tiny spicules; with heavily pigmented, cephalad directed, spicule-lined pouch. *Postgenital lobe.* Relatively narrow; apex with shallow, median emargination or broadly rounded; ventral PGL/Ce index 0.36-0.58; dorsal PGL index 0.96-1.24; ventral length 0.07-0.11 mm. *Cercus.* Cercus index 2.84-4.27; Ce/dorsal PGL index 3.00-3.80; length 0.18-0.24 mm; width 0.05-0.07 mm.

Type species description (Fig. 1). *Verrallina yusafi* (Barraud) is the type species of subgenus *Harbachi* and is completely described here. *Tergum VIII.* Proximal 0.20-0.70 retracted into segment VII; covered with minute spicules; moderately pigmented; length shorter than width; base slightly concave; apex straight; several short and moderately long setae apically; numerous short setae scattered over apical 0.77-0.88; numerous broad scales covering apical 0.50-0.65; basolateral seta present; VIII-Te index 0.70-0.79; VIII-Te/IX-Te index 2.67-2.85; length 0.21-0.23 mm; width 0.27-0.30 mm. *Sternum VIII.* Covered with minute spicules; moderately pigmented with apical 0.35-0.39 more darkly pigmented; length shorter than width; base concave mesally; apex with moderately deep, median emargination separating small lobe on each side of midline; numerous short, stout setae on lobes; numerous short and few moderately long setae scattered over distal 0.86-0.91 except for small, basolateral area; numerous broad scales forming lateroapical patches; apical, intersegmental membrane nonpigmented, moderately long; VIII-S index 0.67-0.73; length 0.22-0.25 mm; width 0.33-0.35 mm. *Tergum IX.* Covered with minute spicules; moderately pigmented but basomedian area more lightly pigmented; short and wide; base concave; apex with wide, moderately deep, median emargination and with 1-4 (usually 3,4) short setae apically on each side of midline; 2-8 total setae; IX-Te index 0.46-0.49; length 0.07-0.08 mm; width 0.14-0.17 mm. *Insula.* Absent but replaced with median, apical, V-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.** Covered with minute spicules; 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; lower vaginal sclerite forming heavily pigmented, ribbon-like strip attached to lower vaginal lip, extending around outer margin of vaginal floor and fused at apex, apical portion forming wrinkled, V-shaped structure and apparently replaces apical 0.25 of lower vaginal lip and insula, base of sclerite articulates with lateral, wing-like projection of spermathecal eminence "pouch". **Upper vaginal lip.** Few minute spicules along posterior margin; moderately pigmented; narrow; median, posterior portion lightly pigmented at base and projecting anteriorly as 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 spicules and with basolateral, wing-like structure on each side. **Postgenital lobe.** Covered with minute spicules; short; relatively narrow; apex flat or broadly rounded; 8-10 setae distally on each side of midline, 16-18 total setae; ventral PGL/Ce index 0.46-0.49; dorsal PGL index 0.96-1.24; ventral PGL index 1.69-1.96; ventral length 0.10-0.11 mm. **Proctiger.** Membranous; with minute spicules. **Cercus.** Covered with minute spicules; more or less triangular in outline; moderately long; broad at base; apex acute; dorsal surface with numerous moderately long and few short setae on distal 0.91-0.95, numerous (12 or more) broad scales on distal 0.75-0.84; ventral surface with few short setae along outer area; cercus index 3.10-3.28; Ce/dorsal PGL index 3.06-3.80; length 0.21-0.23 mm; width 0.06-0.07 mm. **Spermathecal capsules.** One large, one medium, and one small; heavily pigmented; nearly spherical; few spermathecal capsule pores near orifice. **Accessory gland duct.** Basal area lightly to moderately pigmented.

Species examined. *Verrallina abdita* (Barraud), *Ve. fragilis* Leicester, *Ve. hamistylus* (Laffoon), *Ve. indecorabilis* Leicester, *Ve. nobukonis* (Yamada), *Ve. pahangi* (Delfinado), *Ve. robertsi* (Laffoon), *Ve. srilankensis* (Reinert), *Ve. stunga* (Klein), *Ve. uniformis* (Theobald), and *Ve. yusafi*.

Discussion. The following combination of features is most distinctive for subgenus *Harbachius*: tergum VIII has the scaled area reduced in size and located more distal; VIII-S has numerous stouter setae on the median, apical lobes and the scaled area is reduced; insula is absent but it is apparently replaced with a median, apical, U- or V-shaped projection of the lower vaginal sclerite; lower vaginal lip is restricted to a narrow, spiculate strip on the basal and lateral areas, and the lower vaginal sclerite forms a pair of heavily pigmented, nonspiculate, ribbon-like plates along the floor of the vagina, it is fused at the apex and developed into a median, U- or V-shaped projection, and it is attached to the lower vaginal lip throughout most of its length; upper vaginal lip has the median, posterior area produced into a large, horizontal shield that extends anteriorly over or around the spermathecal eminence; and spermathecal eminence is relatively simple, shallow, nonspiculate, and has a heavily pigmented, spicule-lined pouch that is produced cephalad.

Ochlerotatus (Geoskusea) fimbripes (Edwards) possesses a lower vaginal sclerite that extends along the inner margin of the lower vaginal lip, but it is differently developed than those of *Harbachius*.

Published illustrations of female genitalia. Barraud (1928), *Ve. uniformis*; Barraud (1931), *Ve. abdita* and *Ve. yusafi*; Barraud (1934), *Ve. abdita*, *Ve. uniformis*, and *Ve. yusafi*; Laffoon (1946), *Ve. hamistylus* and *Ve. robertsi*; Bohart (1956), *Ve. nobukonis* (= *ishigakiensis* (Bohart)); Hara (1957), *Ve. nobukonis*; Delfinado (1967), *Ve. indecorabilis*; Delfinado (1968), *Ve. fragilis*, *Ve. hamistylus*, *Ve. nobukonis* (= *ishigakiensis*), *Ve. pahangi*, *Ve. robertsi*, and *Ve. yusafi* (= *siamensis* (Delfinado)); Klein (1973), *Ve. fragilis*, *Ve. indecorabilis*?, and *Ve. stunga*; Reinert (1974), *Ve. abdita*, *Ve. fragilis*, *Ve. hamistylus*, *Ve. indecorabilis*, *Ve. nobukonis*, *Ve. pahangi*, *Ve. robertsi*, *Ve. stunga*, *Ve. unifomis*, and *Ve. yusafi*; Tanaka et al. (1979), *Ve. nobukonis*; Reinert (1984), *Ve. srilankensis* and *Ve. uniformis*; and Reinert (1999), *Ve. yusafi*.

SUBGENUS *NEOMACLEAYA* THEOBALD

(Fig. 2)

Subgenus description. *Tergum VIII.* Short; noticeably wider than long; much of surface covered with numerous broad scales; VIII-Te index about 0.35-0.57; VIII-Te/IX-Te index 1.67-6.84 (1.05-1.35 in *Ve. yerburyi*); length 0.22-0.35 mm; width 0.46-0.86 mm. *Sternum VIII.* With numerous slender setae on pair of median, apical lobes; much of surface covered with broad scales; VIII-S index 0.56-0.70; length 0.26-0.45 mm; width 0.36-0.76 mm. *Tergum IX.* Usually very short and very wide (except longer and wider in few species, e.g., *Ve. harrisonicus* (Reinert), *Ve. yerburyi*); IX-Te index 0.12-0.49 (0.65-0.83 in *Ve. yerburyi*); length 0.03-0.15 mm (0.26-0.33 mm in *Ve. yerburyi*); width 0.18-0.46 mm. *Insula.* Ill-defined; small; with few tiny tuberculi; setae absent. *Lower vaginal lip.* Normally without spicules, few when present and often confined to basal area; sclerite large, heavily pigmented, well developed, not contiguous with lower vaginal lip, usually spiculate. *Upper vaginal lip.* With median, posterior area developed into large, vertical shield caudad of spermathecal eminence. *Spermathecal eminence.* Complex; deep; with numerous well developed spicules (less developed in *Ve. incerta* (Edwards), *Ve. panayensis* (Ludlow), and *Ve. rara* (Delfinado)); without cephalad, spicule-lined pouch. *Postgenital lobe.* Relatively narrow; apex with deep to very deep, median emargination; ventral PGL/Ce index 0.25-0.61; dorsal PGL index 0.47-1.30; ventral length 0.07-0.16 mm. *Cercus.* Cercus index 1.76-4.23; Ce/dorsal PGL index 2.42-5.71; length 0.20-0.38 mm; width 0.09-0.13 mm.

Type species description (Fig. 2). *Verrallina indica* (Theobald) is the type species of subgenus *Neomacleaya* and is completely described here. *Tergum VIII.* Proximal 0.40-0.65 retracted into segment VII; covered with minute spicules; moderately pigmented with lightly pigmented, median, basal area; length shorter than width; base slightly concave; apex gently convex; numerous short and moderately long, slender setae at apex and similar ones scattered over distal 0.50-0.74; numerous broad scales on distal 0.59-0.76; 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.* Covered with minute spicules; moderately pigmented; length shorter than width; base concave mesally; apex with shallow (0.04-0.06 of VIII-S length), median emargination separating 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 distal 0.76-0.92; numerous broad scales covering most of distal 0.75-0.87; apical, intersegmental membrane nonpigmented, moderately long; VIII-S index 0.57-0.68; length 0.30-0.33 mm; width 0.36-0.55 mm. *Tergum IX.* Covered with minute spicules; moderately pigmented; very short and very wide, ribbon-like; 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; nonpigmented; with 3-7 small tuberculi, each with minute to

small spicule. **Lower vaginal lip.** Without spicules except few on outer margin of hinge area; heavily pigmented; with small, caudally projecting, heavily pigmented, median structure; lower vaginal sclerite comprised of pair of sigmoid-shaped, heavily pigmented sclerites mesolaterally on elevated portion of membrane extending over area between vaginal lip. **Upper vaginal lip.** Few spicules only along posterior margin; 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; 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 nonpigmented, cephalic arm very large and forming continuous, broad, wrinkled band around anterior of spermathecal eminence, 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 vaginal roof with heavily pigmented structures. **Postgenital lobe.** Covered with minute spicules; short; narrow; apex with moderately deep (0.11-0.29 of dorsal length), median emargination; 5-15 setae distally on each side of midline, 11-28 total setae; ventral PGL/Ce index 0.25-0.38; dorsal PGL index 0.89-1.78; ventral PGL index 1.06-1.70; ventral length 0.08-0.13 mm. **Cercus.** Covered with minute spicules; triangular in outline; moderately long; broad at base; apex acute; dorsal surface with numerous moderately long and few short setae scattered over distal 0.87-0.94, numerous (usually 14 or more) broad scales; ventral surface with several short and moderately long setae on outer 0.40-0.50; cercus index 2.95-3.97; Ce/dorsal PGL index 3.64-4.63; length 0.30-0.36 mm; width 0.08-0.10 mm. **Spermathecal capsules.** One large, one medium, and one small; heavily pigmented; elliptical; each with moderately broad, pigmented neck. **Accessory gland duct.** Basal area nonpigmented to lightly pigmented.

Species examined. *Verrallina adusta* (Laffoon), *Ve. agrestis* (Barraud), *Ve. andamanensis* (Edwards), *Ve. atrius* (Barraud), *Ve. campylostylus* (Laffoon), *Ve. cauta* (Barraud), *Ve. clavata* (Barraud), *Ve. comata* (Barraud), *Ve. comosa* (Reinert), *Ve. cretata* (Delfinado), *Ve. cyrtolabis* (Edwards), *Ve. gibbosa*, *Ve. harrisonicus*, *Ve. hispida* (Delfinado), *Ve. incerta*, *Ve. indica*, *Ve. johnsoni* (Laffoon), *Ve. johorensis* (Reinert), *Ve. lankaensis* (Stone and Knight), *Ve. latipennis* (Delfinado), *Ve. leicesteri* (Edwards), *Ve. macrodixoa* (Dyar and Shannon), *Ve. margarsen* (Dyar and Shannon), *Ve. neomacrodixoa* (King and Hoogstraal), *Ve. nigrotarsis* (Ludlow), *Ve. notabilis* (Delfinado), *Ve. panayensis*, *Ve. petroelephantus* (Wijesundara), *Ve. philippinensis* (Delfinado), *Ve. phnoma* (Klein), *Ve. pseudomediofasciata* (Theobald), *Ve. rara*, *Ve. sabahensis* (Reinert), *Ve. unca* (Theobald), *Ve. vallistris* (Barraud), *Ve. varietas* (Leicester), *Ve. virilis* Leicester, and *Ve. yerburyi*.

Discussion. The following combination of features is most distinctive for subgenus *Neomacleaya*: tergum VIII and sternum VIII each has most of the surface covered with scales; tergum IX is usually very short and wide; lower vaginal lip is narrow and it is usually without spicules (few spicules when present and often confined to the basal area), and the sclerite is large, heavily pigmented, well developed, usually spiculate, and is not connected with the lip; upper vaginal lip has the median, posterior area developed into a large, vertical shield caudad of the spermathecal eminence; and spermathecal eminence is complex, deep, normally with well developed spicules, and it is without a spicule-lined pouch.

Published illustrations of female genitalia. Barraud (1928), *Ve. andamanensis*, *Ve. atriis*, *Ve. cauta*, *Ve. indica*, *Ve. pseudomediofasciata*, *Ve. unca* (= *hirsutipleura* (Barraud)), and *Ve. vallistris*; Barraud (1931), *Ve. agrestis* and *Ve. comata*; Barraud (1934), *Ve. agrestis*, *Ve. andamanensis*, *Ve. atriis*, *Ve. cauta*, *Ve. comata*, *Ve. indica*, *Ve. pseudomediofasciata*, *Ve. unca*, and *Ve. vallistris*; Bohart (1945), *Ve. margarsen*, *Ve. nigrotarsis*, *Ve. panayensis*, and *Ve. unca*; Laffoon (1946), *Ve. campylostylus*, *Ve. johnsoni*, *Ve. macrodixoa*, *Ve. nigrotarsis*, *Ve. panayensis*, and *Ve. unca*; Wijesundara (1951), *Ve. lankensis* (= *ceylonicus* (Edwards)), *Ve. petroelephantus*, *Ve. spermathecus* (Wijesundara), and *Ve. yerburyi*; Delfinado (1967), *Ve. andamanensis*, *Ve. atriis*, *Ve. cauta*, *Ve. clavata*, *Ve. cretata*, *Ve. gibbosa*, *Ve. hispida*, *Ve. incerta*, *Ve. indica* (= *phnoma* (Klein)), *Ve. latipennis*, *Ve. notabilis*, *Ve. unca*, and *Ve. vallistris*; Delfinado (1968), *Ve. campylastylus*, *Ve. johnsoni*, *Ve. macrodixoa*, *Ve. margarsen*, *Ve. neomacrodoxia*, *Ve. nigrotarsis*, *Ve. panayensis*, *Ve. philippinensis*, *Ve. singularis* (Leicester), and *Ve. varietas*; Klein (1973), *Ve. cyrtolabis* and *Ve. rara* (= *dermajoensis* and *khmerus* (Klein)); Tanaka and Mizusawa (1973), *Ve. atriisimilis* (Tanaka and Mizusawa); Reinert (1974), *Ve. agrestis*, *Ve. andamanensis*, *Ve. atriis*, *Ve. campylostylus*, *Ve. cauta*, *Ve. clavata*, *Ve. comata*, *Ve. comosa*, *Ve. cretata*, *Ve. cyrtolabis*, *Ve. gibbosa*, *Ve. harrisonicus*, *Ve. incerta*, *Ve. indica*, *Ve. johorensis*, *Ve. lankaensis*, *Ve. latipennis*, *Ve. leicesteri*, *Ve. macrodixoa*, *Ve. margarsen*, *Ve. neomacrodoxia*, *Ve. nigrotarsis*, *Ve. notabilis*, *Ve. panayensis*, *Ve. petroelephantus*, *Ve. pseudomediofasciata*, *Ve. rara*, *Ve. sabahensis*, *Ve. unca*, *Ve. vallistris*, *Ve. varietas*, *Ve. virilis*, and *Ve. yerburyi*; Tanaka et al. (1979), *Ve. atriisimilis*; Reinert (1984), *Ve. indica*, *Ve. lankaensis*, *Ve. petroelephantus*, *Ve. pseudomediofasciata*, *Ve. spermathecus*, and *Ve. yerburyi*; Reinert (1999), *Ve. indica*.

SUBGENUS *VERRALLINA* THEOBALD

(Figs. 3, 4)

Subgenus description. *Tergum VIII.* Short to moderately long; moderately wide; much of surface covered with broad scales; VIII-Te index 0.44-0.70; VIII-Te/IX-Te index 2.04-4.58; length 0.24-0.31 mm; width 0.30-0.50 mm. *Sternum VIII.* With numerous slender setae on pair of median, apical lobes; much of surface covered with broad scales; VIII-S index 0.47-0.85; length 0.19-0.29 mm; width 0.27-0.39 mm. *Tergum IX.* Short and wide; IX-Te index 0.31-0.44; length 0.06-0.09 mm; width 0.15-0.23 mm. *Insula.* Ill-defined; small; not pigmented; with few minute tuberculi; setae absent. *Lower vaginal lip.* Covered with minute spicules; sclerite small to moderate, lightly pigmented and somewhat poorly developed (except see description of Butleri Assemblage below), not contiguous with lower vaginal lip, usually without spicules. *Upper vaginal lip.* With median, posterior area narrow to moderately broad and not produced into vertical or horizontal shield. *Spermathecal eminence.* Relatively simple, comprised of pair of comma-shaped plates, without spicules (except Butleri Assemblage with spicules); without cephalad, spicule-lined pouch. *Postgenital lobe.* Moderately broad; apex broadly rounded, flat or occasionally with shallow, median emargination; ventral PGL/Ce index 0.24-0.46; dorsal PGL index 0.63-1.17; ventral length 0.06-0.09 mm. *Cercus.* Cercus index 2.38-3.08; Ce/dorsal PGL index 2.60-4.22; length 0.19-0.25 mm; width 0.06-0.09 mm.

Type species description (Fig. 3). *Verrallina butleri* (Theobald) is the nominotypical species of the Butleri Assemblage and the type species of *Verrallina* and is completely described here. *Tergum VIII.* Proximal 0.10-0.35 retracted into segment VII; covered with minute spicules; moderately to heavily pigmented; length shorter than width; base and apex both nearly straight; lateral margins slightly convex; several moderately long, moderately stout setae apically and few

short ones scattered over distal 0.39-0.57; numerous broad scales covering distal 0.59-0.77; 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.** Covered with minute spicules; moderately to heavily pigmented; length shorter than width; base concave; apex with moderately deep (0.10-0.14 of VIII-S length), median emargination separating small lobe on each side of midline; numerous short and moderately long setae scattered over distal 0.75-0.87, setae somewhat stouter on apical margin and lobes, more numerous on latter; numerous broad scales covering distal 0.78-0.90 except for small, median area; apical, intersegmental membrane nonpigmented, moderately long; VIII-S index 0.62-0.69; length 0.23-0.26 mm; width 0.34-0.39 mm. **Tergum IX.** Covered with minute spicules; moderately pigmented; short and wide; band-like; base with short, broad, median emargination; 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; nonpigmented; with 4,5 small tuberculi, each with minute spicule. **Lower vaginal lip.** Covered with minute spicules; moderately pigmented; with small, heavily pigmented, median arm projecting caudally; lower vaginal sclerite comprised of basal pair of oblong, moderately pigmented structures covered with small spicules and situated on elevated portion of membrane between vaginal lip, and with small, subapical, heavily pigmented, transverse bar. **Upper vaginal lip.** Posterior margin and posterolateral lobe with minute spicules; narrow to moderately broad; posterolateral area produced into small lobe; 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 basal portion of posterior area, sclerite bifurcate with anterior branch wide, moderately pigmented and attached to cephalic portion of spermathecal eminence, posterior branch wide and 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; comprised 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.** Covered with minute spicules; short; wide; apex broad, flat or with small (0.10 of dorsal length), median emargination; 14-19 setae distally on each side of midline, 29-36 total setae; ventral PGL/Ce index 0.30-0.41; dorsal PGL index 0.82-1.10; ventral PGL index 1.11-1.23; ventral length 0.07-0.09 mm. **Cercus.** Covered with minute spicules; triangular in outline; moderately long; broad at base; apex acute; dorsal surface with numerous long, moderately long and few short setae on distal 0.84-0.94, numerous (12 or more) broad scales; ventral surface with few short setae along outer area; cercus index 2.38-2.72; Ce/dorsal PGL index 2.91-3.43; length 0.20-0.24 mm; width 0.07-0.10 mm. **Spermathecal capsules.** One large, one medium, and one small; heavily pigmented; spherical; each with short, pigmented neck. **Accessory gland duct.** Basal area moderately pigmented.

Species assemblages within the subgenus based on morphological characters of the female genitalia.

I. Butleri Assemblage. **Lower vaginal sclerite.** Comprised of pair of moderately to heavily pigmented, variously shaped plates, usually with spicules. **Spermathecal eminence.** With spicules.

Description. See above for the description of *Ve. butleri*.

II. Carmentis Assemblage. **Lower vaginal sclerite.** Comprised of pair of lightly pigmented, somewhat wrinkled, ribbon-like plates, without spicules. **Spermathecal eminence.** Without spicules.

Description. (Fig. 4). *Verrallina carmentis* (Edwards) is the nominotypical species for

the Carmenti Assemblage and is completely described here. **Tergum VIII.** Proximal 0.30-0.50 retracted into segment VII; covered with minute spicules; moderately pigmented; length shorter than width; base and apex slightly concave; several short and moderately long setae on distal 0.46-0.60; few long setae along apical margin; numerous broad scales covering distal 0.74-0.83; basolateral seta absent but with small bulla in this location; VIII-Te index 0.63-0.70; VIII-Te/IX-Te index 3.68-4.09; length 0.29-0.31 mm; width 0.47-0.50 mm. **Sternum VIII.** Covered with minute spicules; moderately pigmented; length shorter than width; base slightly concave; apex with moderately deep, median emargination separating very small lobe on each side of midline; numerous short and moderately long setae scattered over distal 0.86-0.83; numerous broad scales covering most of distal 0.90-0.94; apical, intersegmental membrane nonpigmented, moderately long; VIII-S index 0.75-0.80; length 0.28-0.29 mm; width 0.35-0.38 mm. **Tergum IX.** Covered with minute spicules; moderately pigmented; short and wide; band-like; base with short, median emargination; setae absent; IX-Te index 0.33-0.39; length 0.08 mm; width 0.21-0.23 mm. **Insula.** Covered with minute spicules; ill-defined; short; nonpigmented; with 4,5 small tuberculi, each with minute spicule. **Lower vaginal lip.** Covered with minute spicules; moderately pigmented; narrow; lower vaginal sclerite comprised of pair of very lightly pigmented, small plates, without spicules, and somewhat wrinkled. **Upper vaginal lip.** Minute spicules on posterior margin; lightly to moderately pigmented; moderately broad laterally and narrow posteriorly; posterolateral margin evenly rounded and not lobed; upper vaginal sclerite moderately pigmented, well developed, base attached to basal 0.50 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; comprised of pair of comma-shaped, lateral structures connected caudally and produced into fleshy, very lightly pigmented, small, cephalic projection; spicules absent. **Postgenital lobe.** Covered with minute spicules; short; wide; apex broad with moderately deep, median emargination; 11-15 setae distally on each side of midline, 23-29 total setae; ventral PGL/Ce index 0.36-0.40; dorsal PGL index 0.63-0.76; ventral length 0.08-0.09 mm. **Cercus.** Covered with minute spicules; triangular in outline; moderately long; broad at base; apex acute; base concave; dorsal surface with numerous short and moderately long setae on distal 0.84-0.90, 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; cercus index 2.64-2.97; Ce/dorsal PGL index 3.46-3.84; length 0.22-0.25 mm; width 0.08-0.09 mm. **Spermathecal capsules.** One large, one medium, and one small; heavily pigmented; spherical; each with short, narrow, heavily pigmented neck; few minute, spermathecal capsule pores near orifice. **Accessory gland duct.** Basal area moderately pigmented.

Species examined.

I. Butleri Assemblage. *Verrallina butleri*, *Ve. dux* (Dyar and Shannon), and *Ve. lugubris* (Barraud).

II. Carmenti Assemblage. *Verrallina azureosquamata* (Bonne-Wepster), *Ve. carmenti*, *Ve. cuccioi* (Belkin), *Ve. foliformis* (King and Hoogstraal), *Ve. funerea* (Theobald), *Ve. killertonis* (Huang), *Ve. lineata* (Taylor), *Ve. mccormicki* (Belkin), *Ve. milnensis* (King and Hoogstraal), *Ve. multifolium* (King and Hoogstraal), *Ve. obsoleta* (Huang), *Ve. parasimilis* (King and Hoogstraal), *Ve. pipkini* (Bohart), *Ve. quadrifolium* (Brug), *Ve. quadrispinata* (King and Hoogstraal), *Ve. reesi* (King and Hoogstraal), *Ve. sentania* (King and Hoogstraal), *Ve. similis* (Theobald), *Ve. trispinata* (King and Hoogstraal), *Ve. vanapa* (Huang), and *Ve. variabilis* (Huang).

Discussion. The two assemblages in subgenus *Verrallina* correspond to the two series of Reinert (1999). The nominotypical species for each of the assemblages is fully described above.

The following combination of features is most distinctive for subgenus *Verrallina*: tergum VIII and sternum VIII each has much of the surface covered with scales; tergum IX is short and wide; lower vaginal lip is narrow and covered with minute spicules and the sclerite is small to moderate, lightly pigmented and somewhat poorly developed in some species, and it is not contiguous with the lower vaginal lip; upper vaginal lip has the median, posterior area narrow to moderately broad and it is not produced into a vertical or horizontal shield; and spermathecal eminence is relatively simple, it is comprised of a pair of comma-shaped plates, and it is without a spicule-lined pouch.

Published illustrations of female genitalia. Barraud (1928), *Ve. butleri*, *Ve. dux* (= *sigmoides* (Barraud)), and *Ve. lugubris*; Barraud (1934), *Ve. butleri*, *Ve. dux* (= *sigmoides*), and *Ve. lugubris*; Bohart (1945), *Ve. dux* and *Ve. dux* (= *macrodixoa* ?); Laffoon (1946), *Ve. butleri* (= *umbrosus* (Brug)) and *Ve. dux*; Bonne-Wepster (1948), *Ve. azureosquamata*; Wijesundara (1951), *Ve. butleri* (= *carteri*); Iyengar and Menon (1956), *Ve. butleri* and *Ve. dux*; Bohart (1956), *Ve. pipkini*; Chu (1957), *Ve. dux*; Chu (1958), *Ve. dux*; Delfinado (1967), *Ve. dux*; Delfinado (1968), *Ve. lugubris*; Tanaka and Mizusawa (1973), *Ve. iriomotensis* (Tanaka and Mizusawa); Reinert (1974), *Ve. azureosquamata*, *Ve. butleri*, *Ve. carmenti*, *Ve. cuccioi*, *Ve. dux*, *Ve. foliformis*, *Ve. funerea*, *Ve. killertonis*, *Ve. lineata*, *Ve. lugubris*, *Ve. mccormicki*, *Ve. milnensis*, *Ve. multifolium*, *Ve. pipkini*, *Ve. quadrifolium*, *Ve. quadrispinata*, *Ve. sentania*, *Ve. trispinata*, and *Ve. variabilis*; Tanaka et al. (1979), *Ve. iriomotensis*; Reinert (1984), *Ve. butleri* and *Ve. lugubris*; Reinert (1999), *Ve. butleri* and *Ve. carmenti*.

ACKNOWLEDGMENTS

Appreciation is expressed to Donald R. Barnard and Herbert Oberlander (CMAVE) for providing facilities to complete this study; to Ralph E. Harbach (The Natural History Museum, London, United Kingdom), Richard C. Wilkerson (WRBU), Thomas J. Zavortink (Department of Biology, University of San Francisco, San Francisco, CA), and Richard F. Darsie, Jr. (Florida Medical Entomology Laboratory, Vero Beach, FL) for reviewing the manuscript; to Thomas V. Gaffigan (WRBU) for the loan of specimens; and to Young T. Sohn (illustrator assigned to an organization preceding the WRBU) for preparing the illustrations.

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Figure 2. Female genitalia of *Verrallina (Neomacleaya) indica*.

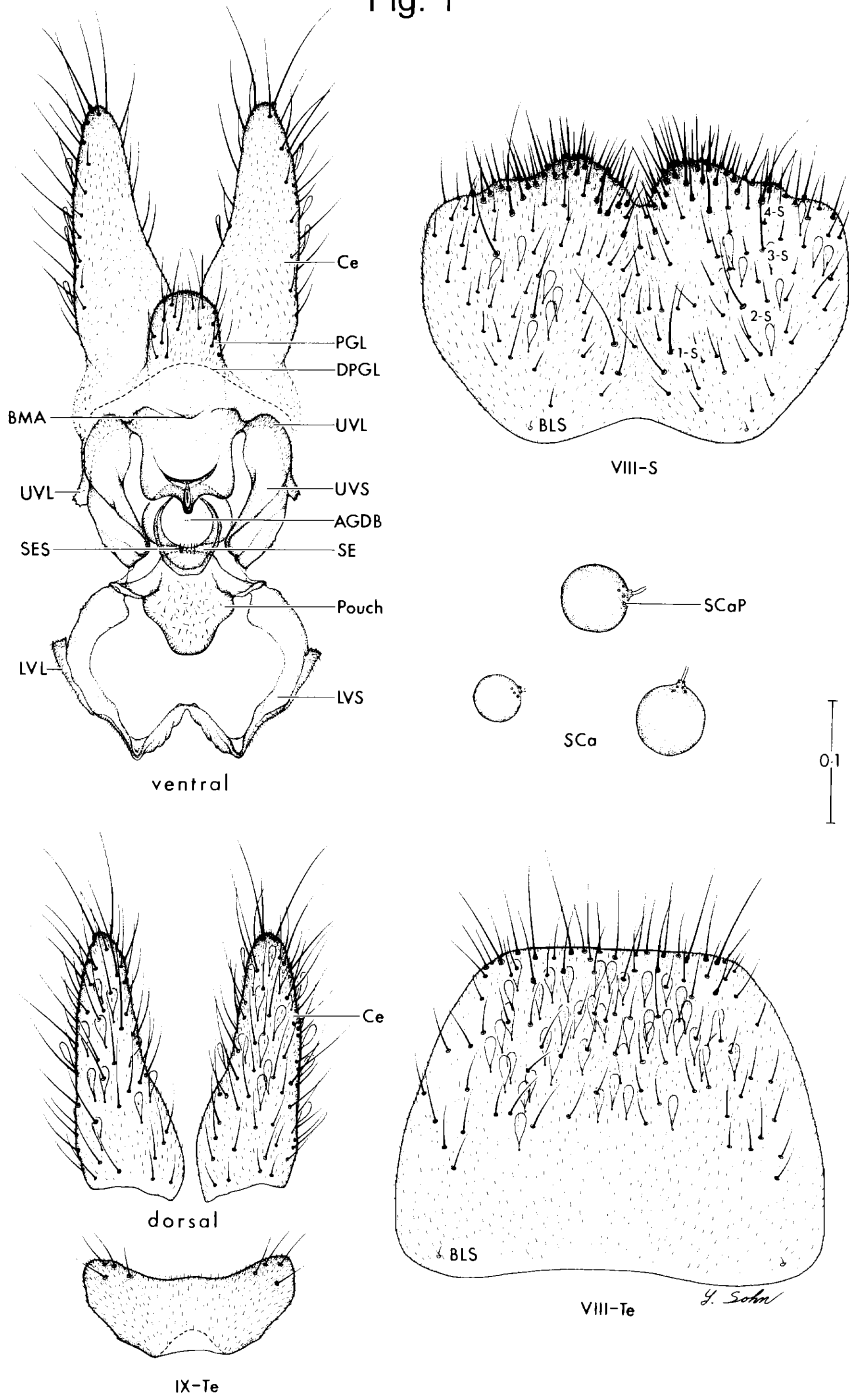
Figure 3. Female genitalia of *Verrallina (Verrallina) butleri*.

Figure 4. Female genitalia of *Verrallina (Verrallina) carmenti*.

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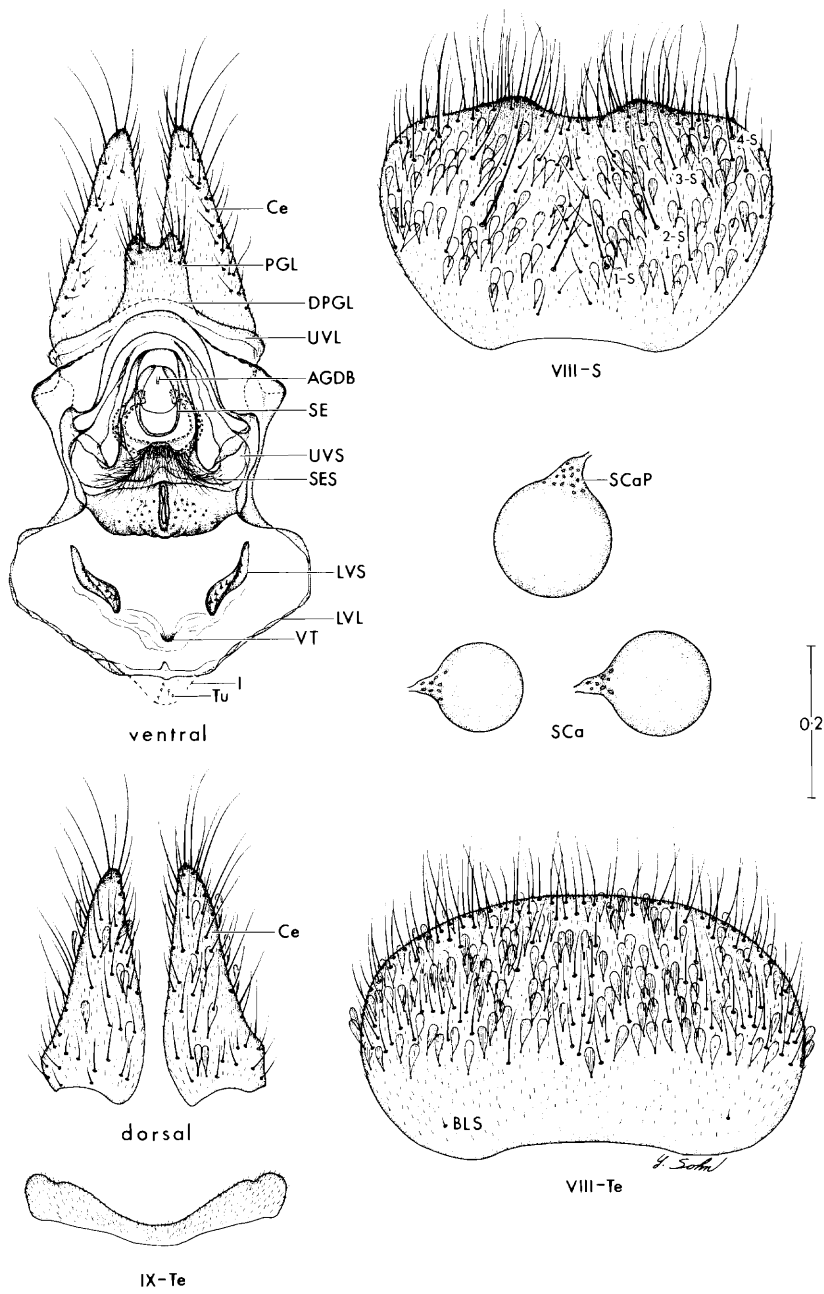
AGDB	= accessory gland duct base
BLS	= basal lateral seta
BMA	= basal mesal apodeme
Ce	= cercus
DPGL	= line of attachment of Pr to dorsal surface of PGL
H	= hinge
I	= insula
IX-Te	= tergum IX
LVL	= lower vaginal lip
LVS	= lower vaginal sclerite
mm	= millimeter
PGL	= postgenital lobe
Pr	= proctiger
SCa	= spermathecal capsule
SCaP	= spermathecal capsule pore
SE	= spermathecal eminence
SES	= spermathecal eminence spicule
Tu	= tuberculus
UVL	= upper vaginal lip
UVS	= upper vaginal sclerite
VIII-S	= sternum VIII
VIII-Te	= tergum VIII
VT	= ventral tuft
1-4-S	= setae 1-4 of sternum VIII

Fig. 1



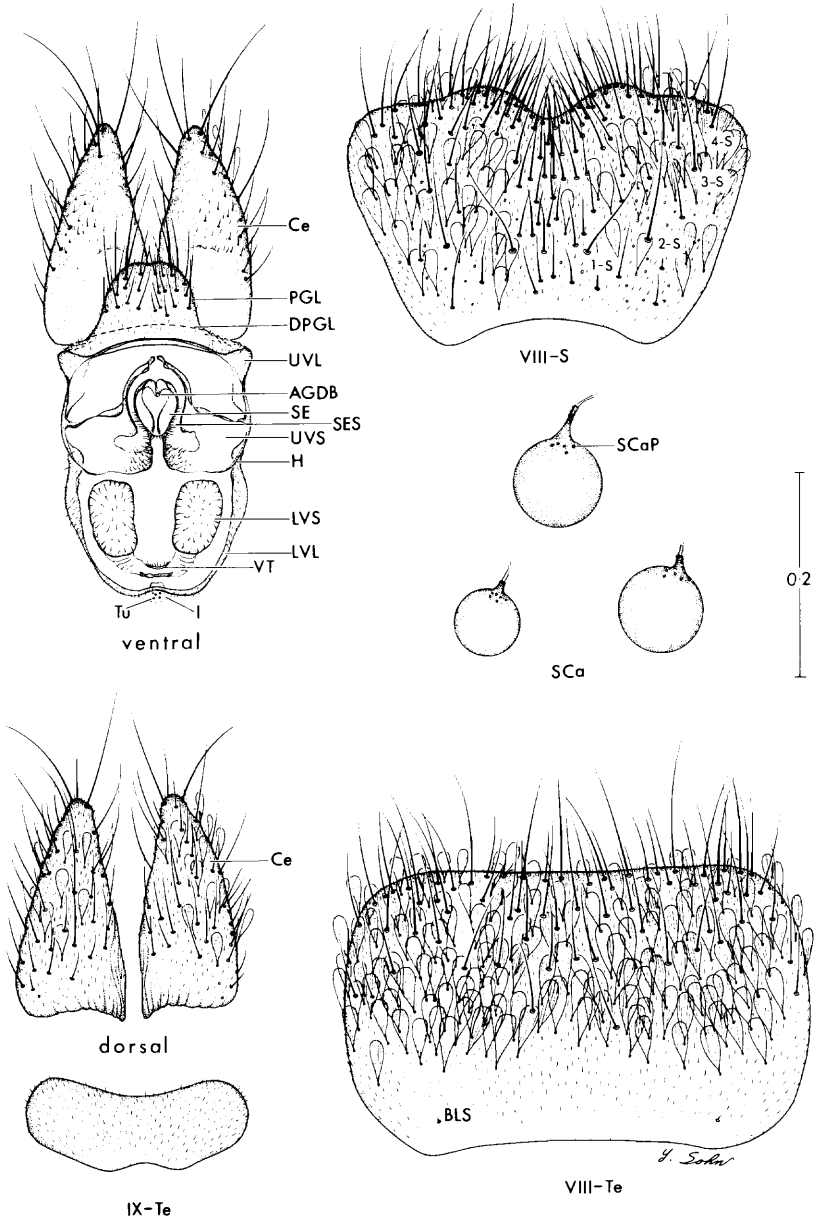
Verrallina (Harbachius) yusafi

Fig. 2



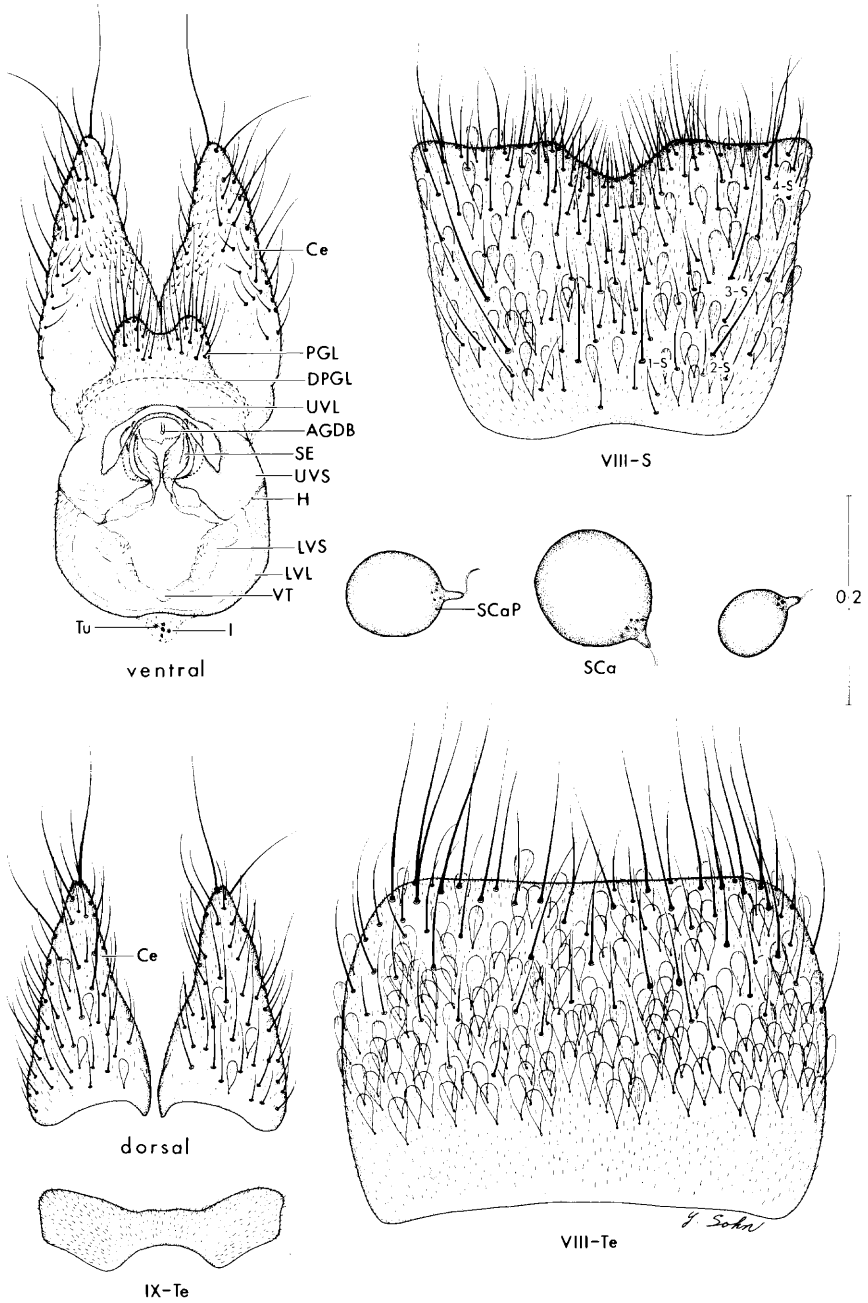
Verrallina (Neomacleaya) indica

Fig. 3



Verrallina (Verrallina) butleri

Fig. 4



Verrallina (Verrallina) carmenti

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