

Morphology and taxonomic value of the female external genitalia of Syrphidae and some other Diptera by new methodology

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In addition to the rough external morphology of the female genital segments the copulatory structures normally invaginated into abdominal segment 8, descriptively called the copulatory pocket, were examined. Without dissecting any part the copulatory pocket can be inverted and extruded from segment 8 so that all of its interior surface is exposed. This kind of preparation lends itself to stereoscopic examination and permits the mutual relationships of different structures to be easily observed and understood. In Syrphidae the copulatory pocket is variable in its dimensions and in many structural details. It is either membranous, submembranous, or includes various sclerotizations which often are true interarticulating sclerites. In all cases the detailed structure of the copulatory pocket is complicated. Species can be distinguished by the structural details of the copulatory pocket and characters for supraspecific taxonomy can be demonstrated. A short review of the morphology and taxonomic value of all the female external genital structures of Syrphidae is presented and documented by illustrating the genitalia of 26 species. The applicability of the inverted copulatory pocket method was also tested in other families of Diptera. It was found useful in a number of cases and a structural variation similar to Syrphidae is apparent in many groups. Examples of female genitalia from the following families are illustrated: Conopidae, Sciomyzidae, Muscidae, Asilidae, Therevidae, Stratiomyidae, Psychodidae and Sciaridae.

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1. Introduction

Since Metcalf's (1921) work on the morphology and taxonomic value of the male genitalia of Syrphidae the study of these structures has gradually become an almost standard method for estimating the taxonomic status of populations being studied and for the identification of specimens. Moreover, the male genitalia have provided an indispensable set of characters for supraspecific taxonomy.

The female genitalia of Syrphidae are still largely unknown. The general opinion has been that these structures are simple and greatly similar in different species and that they would not have any great taxonomic importance, at least on lower taxonomic levels. Some rough characters of the postabdomen and spermathecae have sometimes been described for different groups (e.g. Borisova

1981, 1982, 1985) and a few notes concerning Syrphidae are included in papers concerning other groups of Diptera (e.g. Henning 1973, Herting 1958, Saether 1977). Nayar (1965) published an important paper on the reproductive system and external genitalia of *Episyrphus balteatus* (De Geer) but was unable to demonstrate the important structures within segment 8. Recently Thompson & Torp (1982) applied the characters of segment 8 in the female for distinguishing two species of *Orthonevra*, and also illustrated part of the structures within the segment. It seems that only Shatalkin (1981) has earlier realized the wide taxonomic importance of the copulatory structures which are concealed within segment 8. By methods he did not describe he studied these structures and also attempted to use them for classifica-

tion, but even he was unable to produce a reasonable picture of the female external genitalia and he failed to fully document the decisions he made.

Having studied the female genitalia of Syrphidae for many years, I have developed a method by which all the important external structures can be made visible and easily interpreted and by which they can be stereoscopically studied and illustrated. The female genitalia have proved to offer a set of characters as important as those of the male genitalia: they are complex in structure, they are interspecifically variable and intraspecifically constant and they offer characters applicable at all taxonomic levels.

The primary aim of the present paper is to describe a new method for the study of the female external genitalia of Syrphidae, to describe their different structural types, and to give examples and demonstrations of their taxonomic value at different levels to encourage workers to make use of these structures. Secondly, in order to test the applicability of my method to the other groups of Diptera and in order to obtain a foundation for deducing the polarity of different character states, or in order to reveal the ground plan condition in the Syrphidae, representatives of a number of other dipteran families were also studied.

2. Material and methods

The material for this work consists of normal dry museum specimens. Respecting Syrphidae, the species described have been chosen from the world fauna with the following objectives in mind: to give a general idea about the structure and structural variation of the female genitalia within the family, to furnish examples of the interspecific variation between closely related species, and to give examples of their value in supraspecific taxonomy. A comprehensive review of the female genitalia of Syrphidae is not attempted. Concerning other families of Diptera, only a few examples have been chosen to serve as a methodological demonstration. The internal anatomy of the female genital system has been excluded.

The illustrations have been made by the aid of a camera lucida attached to a stereomicroscope (Wild M-5 microscope and Zeichentubus combined with movable Leiz mirror) from specimens freely in fluid — any compression of the specimen usually makes the structures totally incomprehensible. The verbal description of the parts illustrated is intentionally restricted to a minimum. According to common practice, the segments posterior to segment 7 are termed the female external genitalia, or simply the genitalia (cf. e.g. Saether 1977).

The following abbreviations are used in the Figures:

at8 — apodeme of tergum 8
at10 — apodeme of tergum 10
ce — cercus

cp — copulatory pocket
e — place of eminences of spermathecae and the accessory glands
gx8 — gonoxa 8
pgp — post genital or subanal plate
sd — spermathecal ducts
s7—s8 — sterna 7—8
t8—t10 — terga 8—10

3. Techniques for study of female genitalia

The female genitalia are not readily visible. The genital segments in the rest position are telescoped with the other parts of the postabdomen into the tip of the preabdomen so that usually only cerci, if anything at all, are visible. A convenient way of starting the preparation of the genitalia is to remove the entire apical part of the abdomen at a point between segments 4 and 5 or 5 and 6. At this stage it is best to macerate and clear the part which has been removed by the usual means of soaking or brief boiling in potassium hydroxide and to then expand it to its maximal length so that the segments are freely visible. Of the genital structures in this kind of preparation, sternum and tergum 8 and the cerci are exposed, and by careful expanding also tergum 10 and the subanal or post genital plate (Figs. 1A, 3B), but the most important structures remain hidden. Functionally and taxonomically the most important structures of the female external genitalia, morphologically mainly corresponding to the sternal areas of segments 9 and 10 and associated connectives, form a pouch-like structure invaginated into the interior of segment 8 with the aperture (gonotreme of e.g. Nayar 1965) at the apical end of sternum 8 (Fig. 1A, 3B). On the dorsal wall of this pocket or cavity are situated the accessory gonopores (eminences of the accessory glands and spermathecae) (Fig. 3B), in the ventral part near the apex of sternum 8 the gonadal gonopore (eminence of the oviduct), which is very difficult to pinpoint by this method. For the whole of the invagination discussed I use the descriptive term *copulatory pocket*. This is morphologically composed of very different elements and during copulation the whole apical part of the male hypandrium is inserted into the pocket (see Shatalkin 1981, Fig. 1A).

The interior of the copulatory pocket is complicated, being composed of membranous, submembranous or interarticulating sclerotized lobes or of different combinations of these. It is practically impossible to obtain

an idea of these structures without further preparation. The whole copulatory pocket may be dissected free and further separated into pieces (e.g. dorsal and ventral halves), but the structure as a whole is very difficult to understand after such an operation. Instead of this I have applied a method which may be called an *inverted copulatory pocket method* which means that the copulatory pocket is extruded from inside segment 8 without dissecting any part and is moreover wholly inverted so that all the interior surface is exposed. Technically this can be accomplished by dissecting the genital segments from the rest of the postabdomen and by pushing with suitable tools (e.g. an angled or hooked pin) through the anterior end of segment 8 (Figs. 1A, B, C). It often happens that the copulatory pocket is extruded in an only partly inverted state (Fig. 1B) and the final inversion must be made by simultaneous manipulation through the interior of segment 8 and from outside the segment. When the copulatory pocket is short and is composed of sclerotized parts the work is rather easy, but when it is long and largely membranous it is more difficult and painstaking. In the latter case the work resembles the inversion of a stocking which must be started from the foot end. In most cases there is a fixed end point to the extrusion and inversion, this being similar within a species and usually also within more or less wide supraspecific groups. Only in those cases where the copulatory pocket is almost wholly membranous and very long is the final result not in all cases automatically identical (e.g. Fig. 5E). With a little practice the entire operation is usually neither more difficult nor more time consuming than the dissecting of the male aedeagus without seriously damaging other associated structures.

Although in a preparation made by the inverted copulatory pocket method the parts are partially in an artificial position, I regard the method as superior to any other I can imagine: all the parts of the external genitalia are in one piece and retain their mutual association and they are easily studied stereoscopically and can also be easily understandably illustrated. As in the case of male genitalia, I regard the lateral aspect as the most informative if it is desired to obtain a general idea of the whole genital system using one illustrated aspect only.

By the methods described above the internal genital structures can be studied only in part. Spermathecae and the spermathecal ducts, as

well as the accessory glands, are usually well preserved. If special care is not taken, however, the spermathecae are often left within the preabdomen when dissecting the postabdomen and must then be teased out separately. Instead, the ovaries and oviducts will be totally destroyed.

4. Female genitalia of Syrphidae: morphology and taxonomic value

4.1. Segment 8

Segment 8 varies from short to greatly elongated, the general shape being usually constant throughout larger supraspecific taxa, but e.g. in *Milesia* species groups may differ in this respect (Figs. 3D, E, 4A–D). The tergum and sternum are usually subequal in size, but sometimes conspicuously unequal (Figs. 1A, D–G, 5B, C, 6B). These characters usually apply at generic or higher taxonomic levels; in *Paragus*, *Paragus* (*Paragus*) and *P. (Pandasymphthalmus)* conspicuously differ in this respect (Figs. 6A, B). Tergum 8 is either almost wholly and uniformly sclerotized, or partly submembranous. In the latter case sclerotization tends to be lost more or less broadly laterally, especially on the posterior half (e.g. Figs. 3A, D, E, 4A–D, 6E), on the submedian or sublateral stripes (Figs. 2C, 6D), or there may be a submembranous median line (Fig. 5C). All these sclerotization patterns are characters of wide supraspecific groups. Strong modifications of tergum 8 are rare (Figs. 1D, 5C). In some cases it is unusually flat (Figs. 1A, D–G). At least in some species of *Leiogaster* (not figured) there is a variably strong median tubercle on the flattened tergum 8. Tergum 8 is hairy or setose throughout excepting the extreme anterior marginal area, or the hairs are more or less extensively absent on the lateral and anterior areas (e.g. Figs. 2B, 5B, 6E). Only in a few cases do the hairs tend to be strongly reduced, as e.g. in the genus *Orthonevra* (Fig. 1), in which species or individuals lacking all the hairs occur. The hairs on tergum 8 vary in strength and length between different groups. They are all more or less similar, or in some cases there are strong and very long setae among the shorter and finer ones; in the species of *Palumbia* and *Milesia* (Figs. 3B, D, E, 4A–D) the number and position of such differentiated setae has proved to be a good indicator of species groups.

As with tergum 8 also sternum 8 may be practically wholly uniformly sclerotized (e.g. Figs. 3B, 5A–E), but in most groups it is more or less extensively submembranous on the posteroventral part, often also on the lateral margin. In some cases the whole ventral area is submembranous (e.g. Fig. 2C). In other cases the lateral sclerotized stripe is broken into patches (Fig. 6C) or sternum 8 is practically entirely submembranous (Fig. 6E). The extreme apicoventral part of sternum 8 usually forms a well distinguished hairy area which sometimes includes a distinct sclerite (e.g. Figs. 2C, 5E) and which I interpret as a rudiment of the gonocoxite. As in tergum 8 the sclerotization pattern of sternum 8 is usually similar in wide supraspecific groups.

Striking modifications of sternum 8 are uncommon, but they are found here and there in widely different groups (Figs. 1A, D–G, 2E, 5C, D, 6B); in *Orthonevra* (Fig. 1) there is a general tendency to have slightly, and in different species a differently modified sternum 8. *O. stackelbergi* (Figs 1D, E) has one of the most modified forms of sternum 8 that I have seen. Sternum 8 is often almost entirely hairy, but different types of reduction also occur (Figs. 1A, D, F, 5B). Outstanding hairs or setae deviating from other hairs are found in an infraspecifically constant pattern in some groups (Figs. 3B, D, E, 4A–D, 6E).

4.2. Segment 9

Segment 9 is strongly transformed. The sternal parts and probably also part of the tergal structures belong to the copulatory pocket and are at present not identifiable. In some cases there is a distinct sclerotized hairy plate lateroventrally from tergum 10 (Fig. 2C) which I interpret as tergum 9: this interpretation is based on a comparison with some orthorrhaphous Diptera (e.g. Figs. 8A, B). In some syrphids there is a hairy patch in the homological place, which most probably corresponds to tergum 9 (e.g. Figs. 2A, D, E, 3A, D). These distinctly interpretable rudiments of tergum 9 are delimited in some groups of Milesiinae (Eristaliinae) in the broad sense and represent a distinct plesiomorphic character state in Syrphidae; total reduction (apomorphy) has apparently occurred several times.

4.3. Segment 10

As in segment 9 the sternal parts of segment 10 are apparently included in the copulatory pocket. In most Syrphidae tergum 10 is well developed and has an apparent position of tergum 9 between tergum 8 and the cerci. In some groups the sclerite tends to be reduced and in some genera it is entirely or practically entirely absent (e.g. Figs. 6A, B, E). In a few cases the sclerite is apically bilobed or medially divided (Figs. 2A, D, 6C). The length of the sclerite varies greatly (compare e.g. Figs. 5C, 6C, D). Surface modifications of tergum 10 are rare (Fig. 2E). When developed, the sclerite is hairy or setose; in the studied species of *Merodon* (Fig. 5E) the hairs are needlelike. Tergum 10 usually has well developed long basoventral apodemes, which in different groups are different in shape and relative size (compare e.g. Figs. 2A, C, E); the apodemes may be practically absent even if other parts of the sclerite are well developed (e.g. Figs. 2E, 5E).

4.4. Cerci and postgenital (subanal) plate

The cerci and subanal plate are always present and well developed and greatly similar in all groups; there are rather small differences in shape and small differences in sclerotization or the pattern of the weakly and more strongly sclerotized parts. Only in a few cases is the cercus distinctly more modified (Figs. 2E, 5B, 6B); in *Paragus* (Figs. 6A, B) the "cercus" may include elements of tergum 10. In all cases the cercus of the female is one-segmented even where it is two-segmented in the male (some *Chrysogaster* and some Cerioidini), which suggests that the two-segmented condition in the male is apomorphic in relation to the ground plan condition of Syrphidae (cf. Henning 1973). Both sclerites are always hairy, with only slight differences between different groups; in the studied species of *Merodon* the hairs on the cercus are needle-like.

4.5. Copulatory pocket

An important land mark for orientation in regard to the structures of the copulatory pocket, either inverted or uninverted, is the position of eminences of the accessory glands and spermathecae. These are situated on or at

a more or less distinct prominence or process (marked "e" in Figs.) and are often associated with sclerotized parts. The eminences themselves are not always easily detected except by following their ducts. In two closely related genera, *Merapioidus* and *Brachymyia*, the eminences are surrounded by longitudinal lip-like lobes (Figs. 2A, D).

The copulatory pockets of Syrphidae can roughly be divided into two principal or extreme types: the membranous type and the sclerotized type. In the membranous type the copulatory pocket is composed of a more or less complicatedly folded thinner or thicker membrane, but often with more or less distinct sclerotization at the accessory gonopores and near the median line (Figs. 2A, C, D, 3A, 4D, 5C, E, 6A, C–E). The sclerotized type is characterised by many interarticulating, often strong sclerites lying in various positions (Figs. 1B–G, 2E, 3B–D). These two types are not clearly differentiated, more or less intermediate types occurring (e.g. Figs. 2B, 3E, 4C, 5A, B, 6B). The basic structural type is constant in more or less wide taxa. In Syrphinae (including Pipizini) the copulatory pocket belongs to the membranous type; only in the species of *Paragus* (*Pandasyophthalmus*) is there a large sickle-shaped basolateral sclerite (Fig. 6B). The other major units of the family are more heterogeneous in this respect. Some closely related genera are conspicuously different in the type of copulatory pocket, e.g. in *Orthonevra* the copulatory pocket includes many sclerotized parts (Fig. 1), but in two related genera, *Chrysogaster* and *Leiogaster*, it is membranous. In the closely related genera *Syrittoxylota* and *Palumbia* it includes a complex system of sclerites (Figs. 2E, 3C), in a related genus *Spilomyia* it is largely membranous (Fig. 3A), and in another related genus *Milesia* it is of either type (Figs. 3D, E, 4) — in *Milesia* the general structural type is a good indicator of different supraspecific groups (Hippa, in preparation).

I assume that the characters of the copulatory pocket will prove taxonomically important and useful in all cases at species level. I have studied the females of about 60 species of *Milesia* (a large part undescribed) and can distinguish all of them by the structure of the copulatory pocket (for a few examples, see Figs. 3D, E, 4). For another example I have chosen some species of *Orthonevra* (Fig. 1) — these also nicely demonstrate the usefulness of the characters of the copulatory pocket at species level.

Also in the genus *Sphaerophoria* (Fig. 6E), in which the females of many species are presently undistinguishable, the detailed structure of the membranous copulatory pocket seems to be in many respects dissimilar, but a completed study is not yet available.

The correlation of the female copulatory pocket with the structures of the male genitalia is still far from clear. As was mentioned above, the apical part of the whole male hypandrium seems to penetrate into the copulatory pocket. Accordingly, there must be a structural correspondance between the two copulatory apparatus, as can also be implied from some illustrations given by Shatalkin (1981). In my experience the general complexity of the male superior lobes and aedeagus is reflected in the complexity of the female copulatory pocket and vice versa (e.g. comparisons within the genus *Milesia* and between *Milesia*, *Palumbia*, *Syrittosyrphus* and *Spilomyia*, between *Orthonevra*, *Chrysogaster* and *Leiogaster*, and within Microdontini) and I presume there is a close key and lock system even if I cannot at present demonstrate it.

The use of the characters of the copulatory pocket for cladistic analysis of Syrphidae has proved very difficult. I once tried to homologize the sclerites of the copulatory pocket with the gonopodes of segments 8 and 9 and sterna 9 and 10, following Saether's (1977) ideas of these structures in Nematocera, and even supposed I was able to identify some of the structures. Brundin's (1983) finds in *Chilenomyia* of the Chironomidae made me very uncertain and at present I do not venture to make any homologizations. Also, within the Syrphidae the true homologies, except in restricted groups, have proved very difficult to trace and also this kind of speculation is omitted as premature. The at least apparent similarity of some of the sclerotized type of copulatory pockets in Syrphidae with similar structural types in some orthorrhaphous Diptera (e.g. Figs. 8A, B) may suggest that this type of copulatory pocket would be the ground plan condition of Syrphidae. However, before the homologies are firmly documented this kind of hypothetization lacks firm foundations.

5. Female external genitalia of other Diptera

Mainly to test the applicability of the above described inverted copulatory pocket method, representatives of many families other than

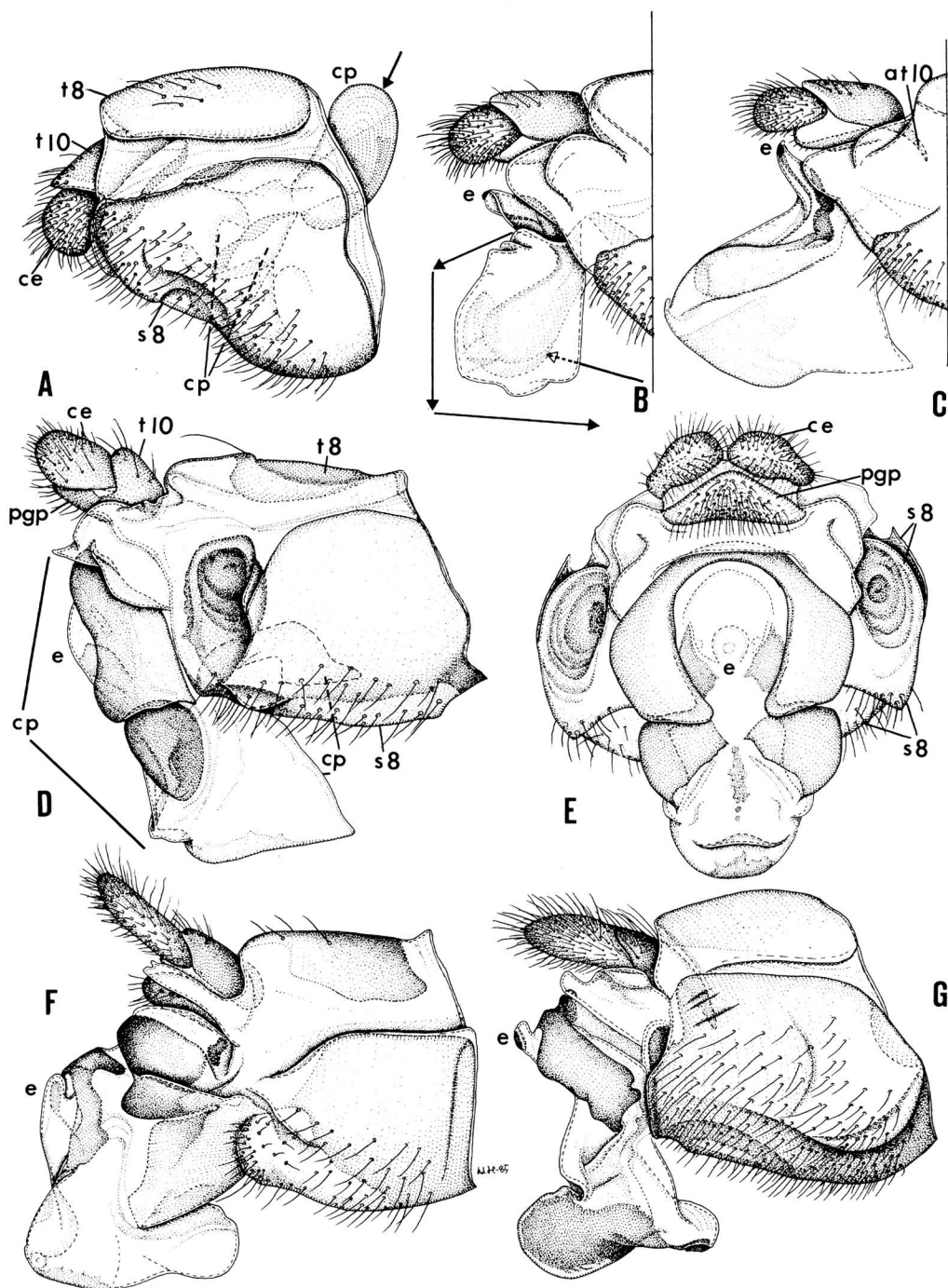


Fig. 1. Female genitalia of Syrphidae, lateral view (A–D, F, E) and posterior view (E). — A–C: *Orthonevra nobilis* (Fallén) (Finland). — D and E: *O. stackelbergi* Thompson & Torp (Finland). — F: *O. geniculata* (Meigen) (Finland). — G: *O. erythrogona* (Malm) (Finland). Series A–C describe different stages in extruding and inverting the copulatory pocket, the arrows indicating the necessary manipulation of the parts (see also text, p. 308–309).

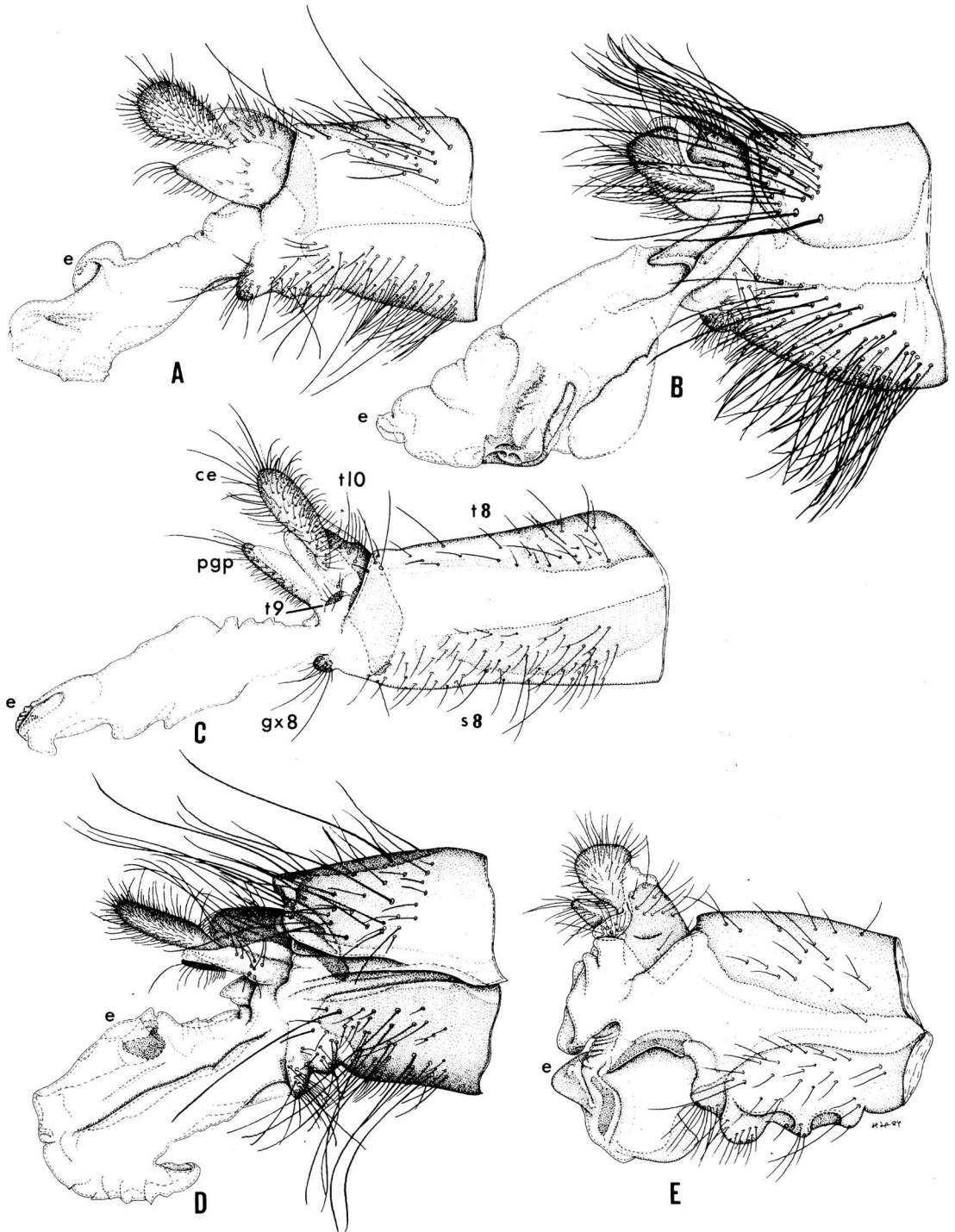


Fig. 2. Female genitalia of Syrphidae, lateral view. — A: *Merapioidus villosus* Bigot (Colorado). — B: *Volucella zonaria* (Poda) (Yugoslavia). — C: *Eristalis tenax* (Linnaeus) (Finland). — D: *Brachymyia nigripes* Williston (USA). — E: *Syrittosyrphus opacea* Hull (South Africa).

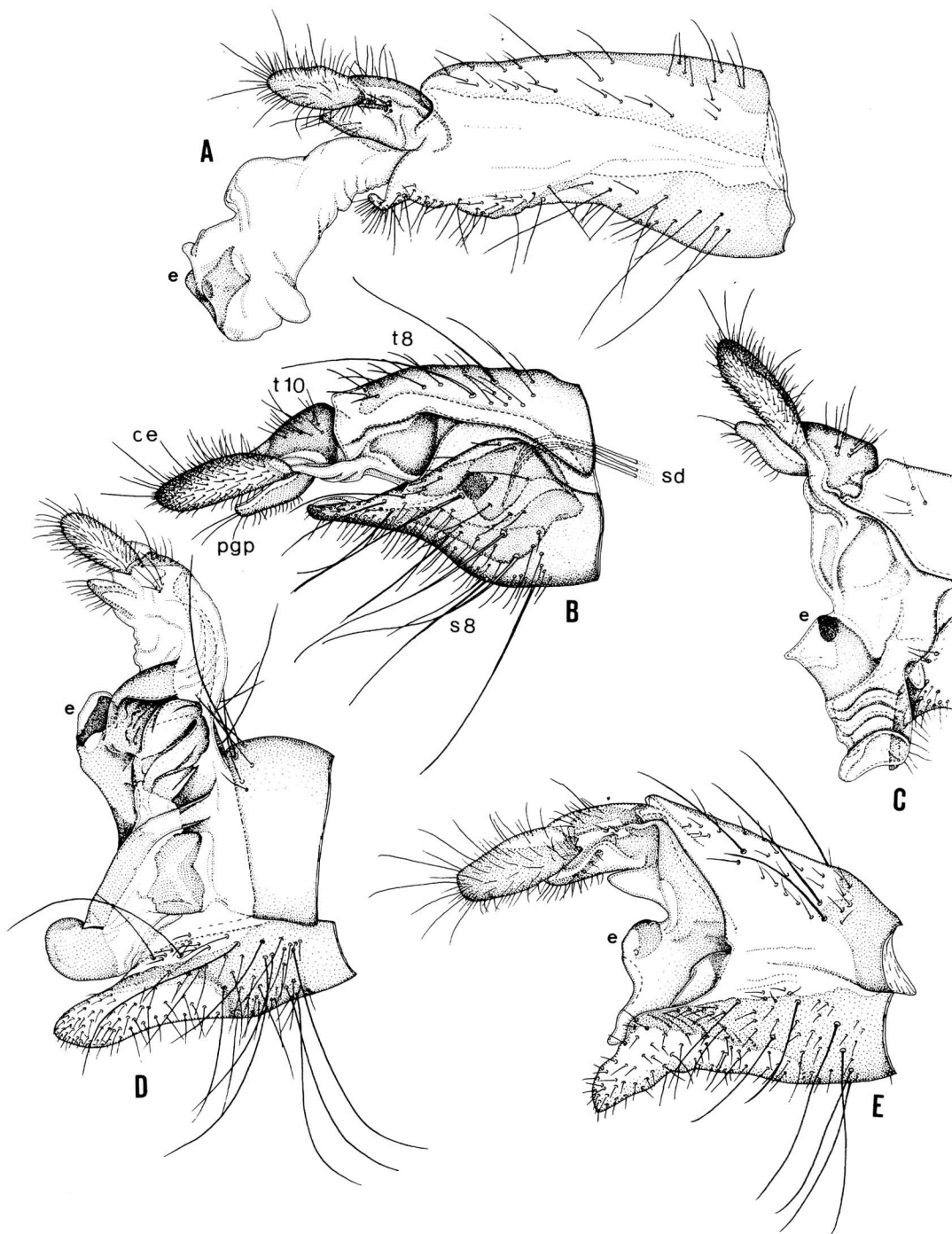


Fig. 3. Female genitalia of Syrphidae, lateral view; B and C the same specimen with the copulatory pocket uninverted (B) and inverted (C). — A: *Spilomyia fusca* Loew (Tennessee). — B and C: *Palumbia (Korinchia) simulans* De Meijere (Java). — D: *Milesia* sp. af. *balteata* Kertész (Malaysia). — E: *M. semiluctifera* (Villeneuve) (Turkey).

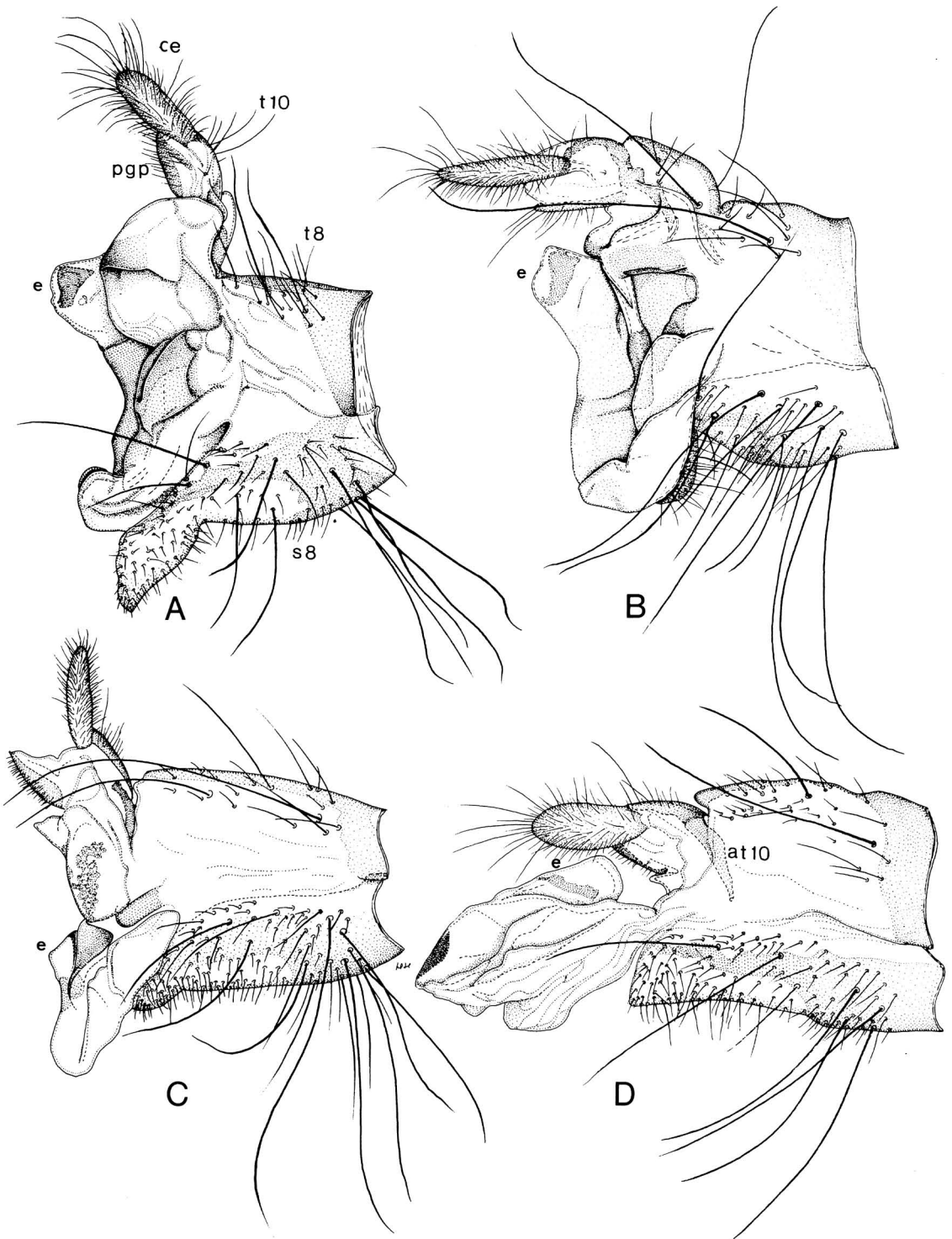


Fig. 4. Female genitalia of Syrphidae, lateral view. — A: *Milesia variegata* Brunetti (Thailand). — B: *Milesia conspicua* Curran (Malaysia). — C: *M. apicalis* Snellen van Vollenhoven (Java). — D: *M. undulata* Snellen van Vollenhoven (Japan).

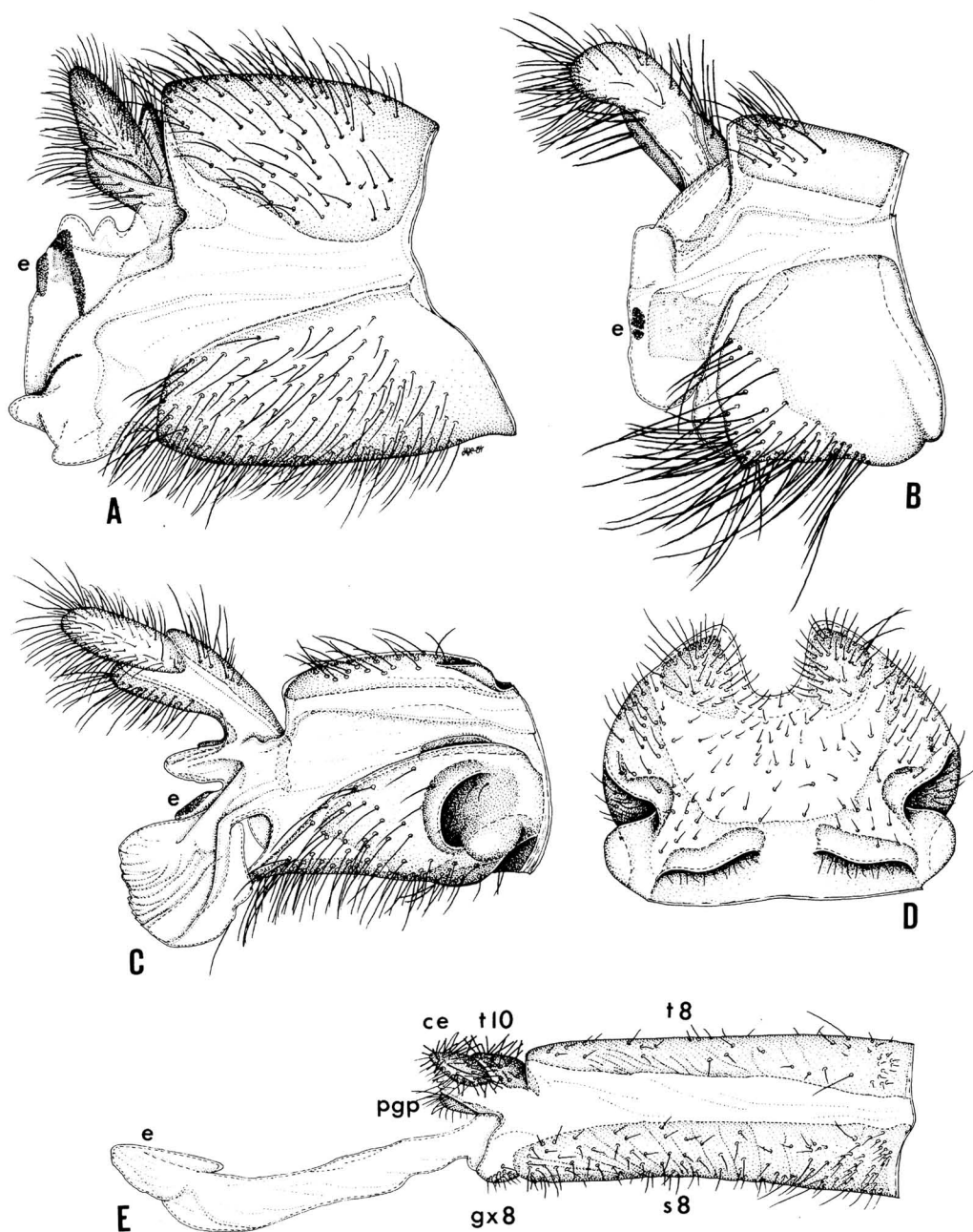


Fig. 5. Female genitalia of Syrphidae, lateral view (A, B, C, E) and sternum 8, ventral view (D). — A: *Spheginobaccha* sp. (Madagascar). — B: *Argentinomyia prima* (Curran) (Brazil). — Cand D: *Mixogaster* sp., probably *conopsoides* Macquart (Brazil). — E: *Merodon clavipes* (Fabricius) (Spain).

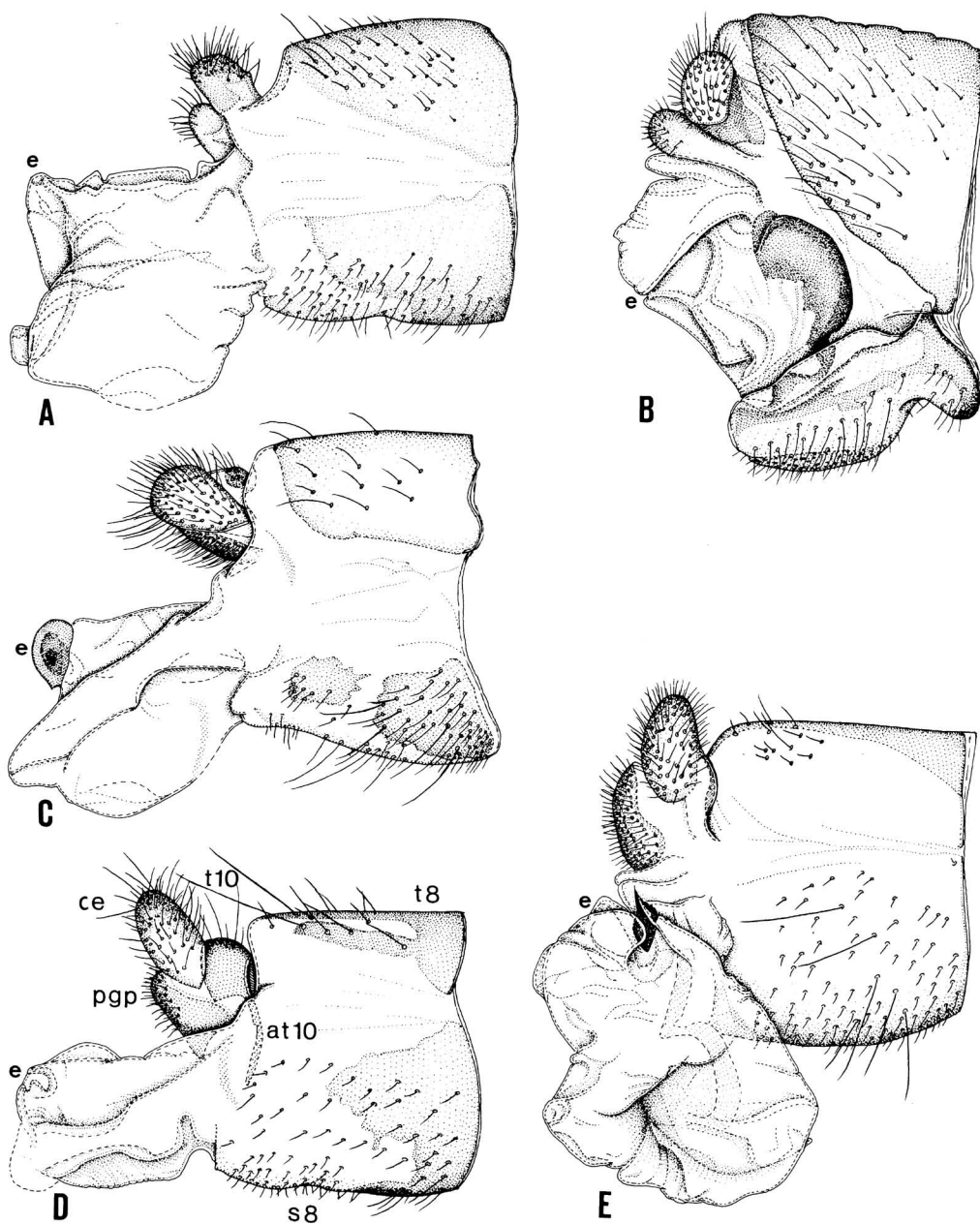


Fig. 6. Female genitalia of Syrphidae, lateral view; in E the copulatory pocket is only partly inverted. — A: *Paragus* (*Paragus*) *tibialis* Fallén (USSR). — B: *P. (Pandasyophthalmus) finitimus* Goeldlin (Finland). — C: *Didea alneti* (Fallén) (Finland). — D: *Xanthandrus comtus* (Harris) (Finland). — E: *Sphaerophoria* sp., probably *abbreviata* Zetterstedt (Finland).

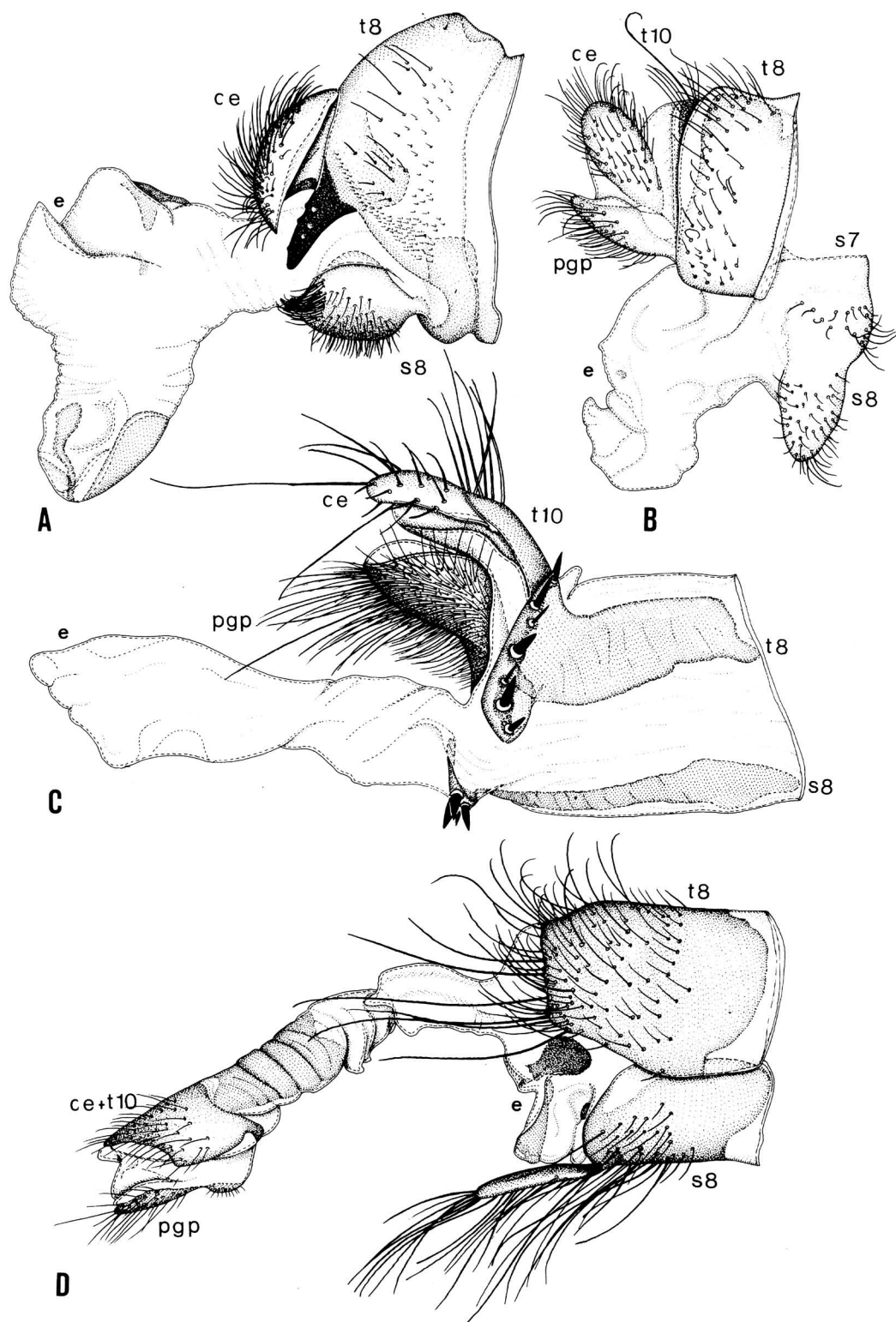


Fig. 7. Female genitalia of Conopidae (A), Sciomyzidae (B), Muscidae (C) and Asilidae (D), lateral view. — A: *Conops vesicularis* Linnaeus (Finland). — B: *Tetanocera ferruginea* Fallén (USSR). — C: *Mesebrina mystacea* (Linnaeus) (Finland). — D: *Laphria flava* (Linnaeus) (Finland).

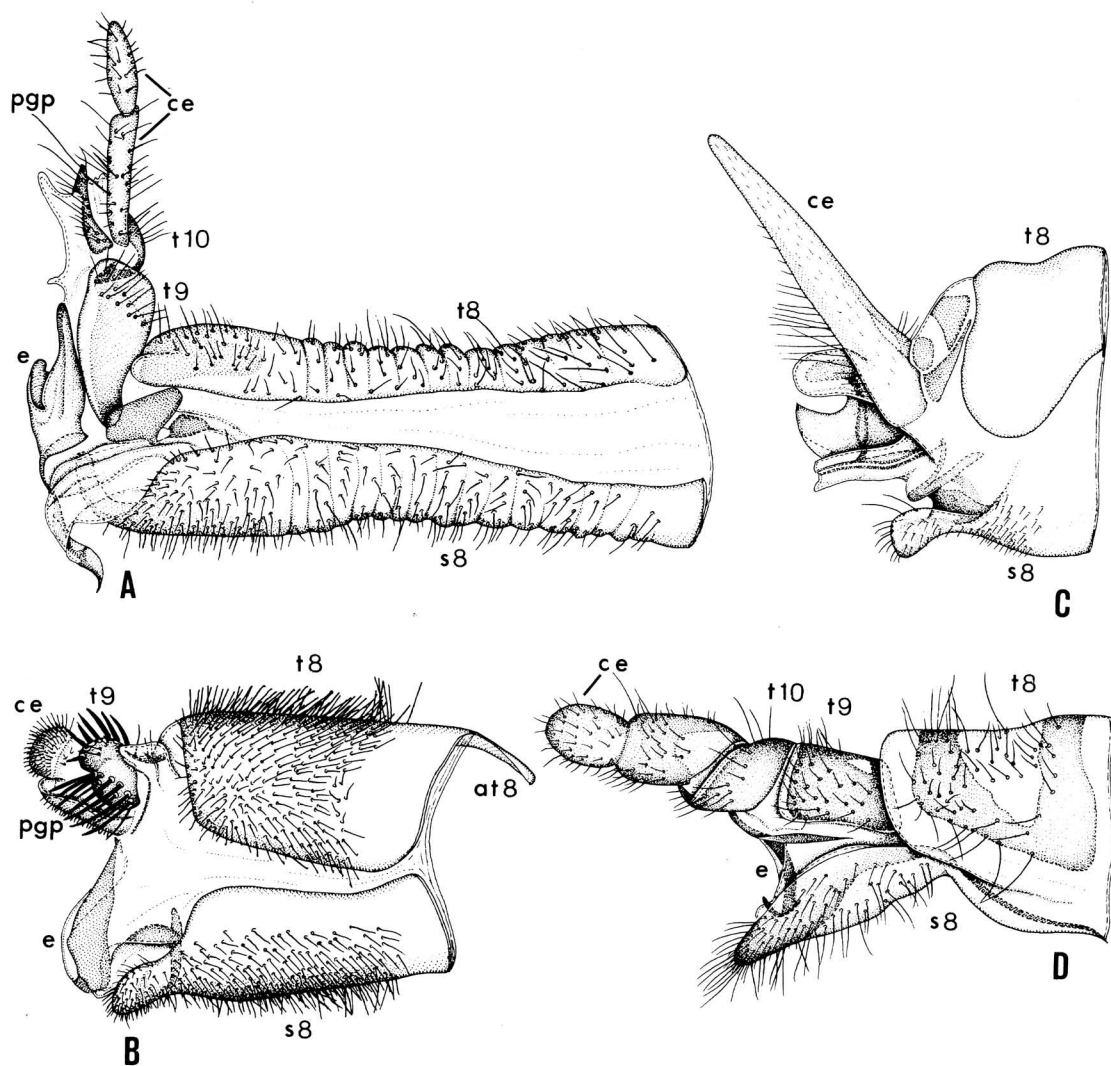


Fig. 8. Female genitalia of Stratiomyiidae (A), Therevidae (B), Psychodidae (C) and Sciaridae (D), lateral view. — A: *Hermetia* sp. (Brazil). — B: *Psilocephala eximia* (Meigen) (Finland). — C: *Psychoda* sp. (Japan). — D: *Sciara thomae* (Linnaeus) (Finland). In *Psychoda* (C) the copulatory structures could further be extruded and inverted on the median part.

Syrphidae were studied. In Brachycera, both in orthorrhaphous families and in Cyclorrhapha, the basic structural types occurring in Syrphidae can be found. In most Cyclorrhapha I studied the copulatory pocket is extensive and its inversion may be technically difficult; it was also most often of the membranous type (Figs. 7B, C), but those with sclerites or sclerotized parts do also occur (Fig. 7A, see also Andersson 1984, Figs. 42, 43). In orthorrhaphous families (Figs. 7D, 8A, B) the copulatory pocket is usually smaller, shorter, and in most cases easily inverted. At least in many Empidoidea the peculiar structure of the copulatory pocket prevents the extruding and inverting process. The structural types vary from complicated sclerite-bearing ones (Figs. 7D, 8A, B) to membranous. At least in some families, e.g. Stratiomyidae, the variation is great and resembles that above described for Syrphidae. Also in many groups of Nematocera

the extruding of the copulatory structures open a quite new aspect in which the relationship of the different parts is more easily understood than from the usual slide preparation. Especially in those cases in which these structures are extremely complicated, as in Psychodidae (Fig. 8C), their correct understanding without manipulation and stereoscopic study may be extremely difficult. In other cases where there are strong rami and a narrow sclerotized notum (see Saether 1977) the true inversion of the copulatory structures is not possible (Fig. 8D). The large membranous copulatory pocket found in many Brachycera I have never seen in Nematocera.

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