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Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys

Ole A. Sæther

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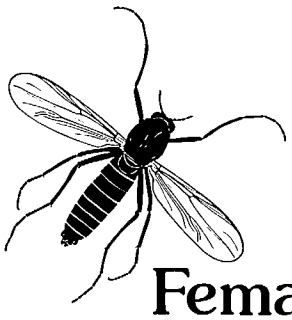

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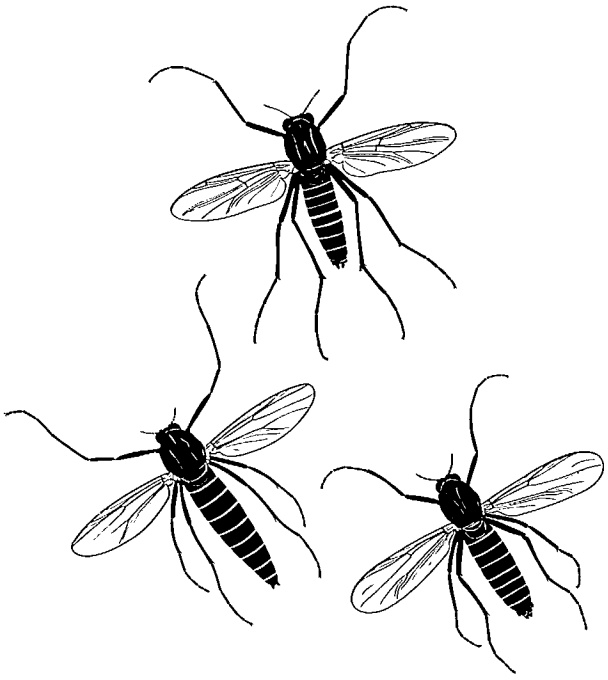

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BULLETIN 197

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ABSTRACT

SÆTHER, O. A. 1977. Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. Bull, Fish. Res. Board Can. 197: 209 p.

Elements of abdominal segments VIII–X or XI form the female genitalia in Diptera. Major genital elements include tergites (T) and sternites (S) VIII and IX, gonocoxites (Gc) VIII and IX (which may bear a gonostylus), gonapophyses (Gp) VIII and IX (which form a notum and rami), cerci, seminal capsules, and spermathecal ducts. Their development in various dipteran families (Nematocera and Brachycera) is discussed, the theoretical progenitor of the Diptera illustrated, and the female genitalia of 17 families of Diptera described (including 33 nonchironomid species representing 24 genera). Of the Chironomidae, 189 species representing 123 genera have been illustrated and a few additional species examined.

Within the Chironomidae, T VIII is reduced in the Telmatogetoninae only. Gc VIII is perhaps present in *Afrochlus harrisoni* Freem., but otherwise absent. Gonocoxapodemes (Gca) VIII are present in Diamesinae, Orthocladiinae, and Chironominae. Gp VIII is, in the basic design, simple and well developed; it is divided into a dorsomesal and a ventrolateral lobe in some Diamesinae, Prodiamesinae, most Orthocladiinae, and most Chironominae; occasionally it bears an apodeme lobe in the same subfamilies. Gc IX carries a gonostylus in Telmatogetoninae only, and is fused with T IX forming gonotergite IX in Tanypodinae, Aphroteniinae, and Podonominae. T IX is partly or fully divided into two setigerous protrusions in some Diamesinae, Prodiamesinae, Orthocladiinae, and in *Lauterborniella* (Chironominae). In Telmatogetoninae there are no seminal capsules, but there are two or three in the remaining subfamilies.

Within the Chironomidae, the Telmatogetoninae forms the sister group of the other subfamilies which can be divided into two sister groups of subfamilies: Tanypodinae + Aphroteniinae + Podonominae, and Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae.

Keys and diagnoses are given to subfamilies, tribes, genera, and some species of some genera of female Chironomidae. The phylogeny of each subfamily is discussed and synapomorphic diagrams presented for the Orthocladiinae and Chironominae using characteristics for males, pupae, and larvae, in addition to those of the females. In the Orthocladiinae, *Diplocladius* Kieff. probably forms the sister group of the remaining genera. In the Chironominae the tribes Tanytarsini and Pseudochironomini (new tribe) apparently form the sister group of the Chironomini.

RÉSUMÉ

SÆTHER, O. A. 1977. Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. Bull. Fish. Res. Board Can. 197: 209 p.

Des éléments des segments abdominaux VIII–X ou XI forment les organes génitaux femelles des Diptera. Les principaux éléments génitaux comprennent les tergites (T) et les sternites (S) VIII et IX, les gonocoxites (Gc) VIII et IX (pouvant porter un gonostyle), les gonapophyses (Gp) VIII et IX (formant un notum et rami), les cerques, les capsules séminales et les conduits des spermatophores. L'auteur analyse leur développement chez diverses familles de Diptera (Nematocera et Brachycera), figure le progéniteur théorique des Diptera et décrit les organes génitaux femelles de 17 familles de Diptera (y compris 33 espèces autres que des Chironomidae, représentant 24 genres). Parmi les Chironomidae, 189 espèces représentant 123 genres sont figurées, et quelques autres espèces sont examinées.

Chez les Chironomidae, T VIII n'est réduit que chez les Telmatogetoninae. Gc VIII est peut-être présent chez *Afrochlus harrisoni* Freem., mais est absent dans les autres cas. Les gonocoxapodèmes (Gca) VIII sont présents chez les Diamesinae, les Orthocladiinae et les Chironominae. Gp VIII, dans sa forme basale, est bien développé; il est divisé en lobes dorsomésal et ventrolatéral chez certains Diamesinae, Prodiamesinae, la plupart des Orthocladiinae et la plupart des Chironominae; dans ces mêmes sous-familles, il porte parfois un apodème. Gc IX ne porte un gonostyle que chez les Telmatogetoninae, et il se fusionne avec T IX pour former le gonotergite IX chez les Tanypodinae, les Aphroteniinae et les Podonominae. T IX est partiellement ou complètement divisé en deux excroissances sétigères chez certains Diamesinae, Prodiamesinae, Orthocladiinae et chez *Lauterborniella* (Chironominae). Chez les Telmatogetoninae il n'y a pas de capsules séminales, mais il y en a deux ou trois dans le reste des sous-familles.

Parmi le Chironomidae, les Telmatogetoninae constituent le groupe sœur des autres sous-familles, pouvant se diviser en deux groupes sœurs de sous-familles: Tanypodinae + Aphroteniinae + Podonominae et Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae.

L'auteur donne des clés et des diagnoses des sous-familles, tribus, genres et de quelques espèces de certains genres de Chironomidae femelles. Il discute de la phylogénie de chaque sous-famille et présente des diagrammes synapomorphes des Orthocladiinae et des Chironominae, se servant des caractéristiques des mâles, des pupes et des larves, en plus de celles des femelles. Chez les Orthocladiinae, *Diplocadius* Kieff. constitue probablement le groupe sœur des autres genres. Chez les Chironominae, les tribus Tanytarsini et Pseudochironomini (nouvelle tribu) constituent apparemment le groupe sœur des Chironomini.

INTRODUCTION

According to Smith (1969) components of external genitalia in both sexes of ectognathous insects are homologous in all orders. It is, therefore, possible to devise a uniform terminology for both sexes in all orders. Sæther (1971b, 1974) revised the male and female genitalia in accordance with the terminology of Smith. (See, however, Sæther (1975b p. 368, 1976b p. 5) for modifications of the terminology used by Sæther (1971b).) This Bulletin is an extension of the paper by Sæther (1974). However, in addition to diagnoses and descriptions of the female genitalia of a much higher number of genera and species of the Chironomidae, representatives of other nematocerous Diptera have also been examined and comparisons made between these, chironomids, and higher Diptera. This has made it possible to support the phylogenetic analysis of the Diptera as a whole as presented by Hennig (1968, 1969, 1973), to present synapomorphic diagrams or revise existing ones for the Chironomidae, and to form keys to subfamilies, tribes, genera, and some species of the Chironomidae.

MATERIALS AND METHODS

The mounting procedure is outlined by Sæther (1969 p. 1). The method does not allow for a close examination of the ovaries, oviducts, and muscles of the female terminalia, and these parts are treated only superficially.

Most chironomid workers have made slide preparations showing the female genitalia in lateral aspect. However, a ventral view is more fruitful in most cases. In some instances, particularly when the cerci are of taxonomic importance, a lateral aspect is also desirable. The slides were examined by a Zeiss Universal microscope, equipped with phase contrast and Nomarski interference contrast, and with a Wild M20 microscope with phase contrast. A Wild drawing tube was used to make all drawings.

The serial sections of *Chironomus* (*Camptochironomus*) *tentans* Fabr. were made by Mr B. R. Hobden. Specimens were dehydrated, imbedded in paraffin, serial sections of 10 μm thickness made, and mounted unstained in Permount for examination. Dr D. P. Scott used a Reichert Zetopan microscope with Reichert automatic camera and Nomarski interference contrast illumination, to photograph the sections.

In all drawings showing ventral aspects of the genitalia the ventral surface is shown to the left, outlines and internal parts to the right.

Most of the material originates from the collection at the Freshwater Institute, but much was supplied by a number of colleagues listed in the acknowledgments. The systematic division of the Diptera into suborders, infraorders, superfamilies, and families follows Hennig (1973).

ABBREVIATIONS

The following abbreviations are in the figures, and those marked with an asterisk are also in the text:

Acc	accessory gland
AG	accessory gonopore
An	anus
ApL	apodeme lobe of gonapophysis VIII
Ce	cercus (i)
Ce 1, 2	basal segment of cercus — distal segment of cercus
CO	compressor muscle of the common oviduct
*Csa	coxosternapodeme IX
D	dorsal muscle
DmL	dorsomesal lobe of gonapophysis VIII
DO	dilator muscle of the common oviduct
F	fulcrum (pivot) of gonocoxite IX or gonotergite IX
Fl	floor under vagina
G	gonopore
*Gc VIII	gonocoxite VIII
*Gc IX	gonocoxite IX
*Gca	gonocoxapodeme VIII
*Gp VIII	gonapophysis (es) VIII
*Gp IX	gonapophysis (es) IX
*Gs	gonostylus IX
Ig	intergonocoxal connective
K	knob on gonocoxapodeme against fulcrum
L	labium (a)
LVL	lower vaginal lip possibly representing fused and reduced gonapophyses VIII
Mb	membrane or sclerotic hinge connecting gonapophyses VIII to each other
MT	malphigian tubule
No	notum
O	oviduct, common or lateral
P	proctodaeum or hindgut
PgP	postgenital plate
R	ramus(i) (dorsal ramus of gonapophysis IX)
Re	rectum
*S	sternum, sternite, gonosternite
SCa	seminal capsules
SDu	spermathecal duct
SE	spermathecal eminence
SG	spermathecal gland
Spt	spermatheca(e)
SSC	special secretory cells of the spermathecal duct
*T	tergum, tergite, gonotergite
V	ventral muscle
Va	vagina
VlL	ventrolateral lobe of gonapophysis IX
X	segment X or proctiger

MORPHOLOGY OF FEMALE GENITALIA IN INSECTA AND DIPTERA

The external genitalia of ectognathous insects (i.e. insects other than Collembola and Protura) consist primarily of mesal extensions and lateral projections on limb bases of segments VIII and IX. The principal origins ascribed to the genital appendages (gonopods) are outlined by Smith (1969 p. 1051). According to one theory, they are homologous with limbs of other segments and are derived from the endopodites or exopodites of the coxopodite and/or telopodites (see Crampton 1929, 1942; Walker 1919; Tanner 1927; Nel 1929; Snodgrass 1931; Rees and Ferris 1939; Herting 1957; Sharov 1966). According to Gustafson (1950) they are composite structures with appendicular as well as papillary components, whereas Snodgrass (1933, 1957) argues they may be in either or both of the above theories but that the corresponding structures of different sexes or taxa are not necessarily homologous. Matsuda (1958) found that evidence was in favor of accepting the theory of Heymons (1899), that the external genitalia were sternal outgrowths. (For a review of the different theories see Nel (1929), Gustafson (1950), Matsuda (1958), Sharov (1966), and Smith (1969).)

According to Smith (1969; 1970a, b) all are correct in part. The external genitalia are a complex of limb bases, adjacent sternites, and coelomoducal ampullae, and appendages provide the major components. The components primitively consist of presumed telopodites (gonostyli) and possible endites (gonapophyses) borne on gonocoxites (Gc) of abdominal segments VII and IX. In the basic pattern of female pterygote insect genitalia an inverted pair of gonapophyses (Gp) IX is fused along a strengthening bridge (notum), and interlocked with a pair of Gp VIII by a sliding interlock (olistheter), on a dorsal apodeme (ramus), of Gp IX.

Smith (1969) divided the female genitalia into three major types: (1) Gp VIII moves on the stationary Gc IX and Gp IX; (2) both Gp IX move together in one direction and both Gp VIII move synchronously in the other; (3) all four gonapophyses move forward and back as a unit. Number 3, which is dominant among the higher holometabolous taxa including all Diptera, makes the sliding interlock obsolete. Insects of this type have separate gonapophyses and one or occasionally both pairs are reduced or absent.

In the Diptera the reduced (occasionally absent) Gp VIII enclose the inverted Gp IX (which also may be reduced or absent). Gonocoxite (Gc) VIII are present only in the Psychodidae (Fig. 4D, G), Sciaridae (Fig. 10C, D), and probably in *Afrochlus* Freem. (Podonominae; Chironomidae) (Brundin 1966 fig. 414). They are reduced to a pair of apodemes or internally thickened ridges along the caudolateral margins of the eighth sternum (gonocoxapodemes; Sæther 1974 p. 217), in Trichoceridae (Fig. 2B–D), Blephariceridae (very weak, Fig. 3A), some Chironomidae, and Bibionidae (Fig. 8A). According to Smith (1969) the articulation of Gc VIII has, in nearly all female insects, shifted from tergite (T) VIII to tergite (T) IX and this articulation is apparent in many chironomids, in the Psychodidae, and possibly the Ptychopteridae, with a knob on the gonocoxapodeme against a fulcrum or pivot (K and F in Fig. 4A, G) on Gc IX, gonotergite IX, or gonosternite IX. Gc VIII and gonocoxapodemes have apparently fused with coxosternite VIII in all other Diptera to form a gonosternite VIII. Gp VIII is primitively long and simple. In the Psychodidae (Fig. 4D, G) the Gp VIII are not separate from Gc VIII, but may be represented as caudolateral projections of Gc VIII. In the Blephariceridae (Fig. 3B, C) and Deuterophlebiidae (Fig. 3E) the Gp VIII are long and fused. In the Chaoboridae and Dixidae Gp VIII are absent, although they may be fused and represented by the so-called lower vaginal lip in the Culicidae (LVL in Fig. 6). The Gp VIII are apparently fused and reduced in the Cecidomyiidae (Fig. 9A, B). The only family with secondarily divided Gp VIII appears to be the Chironomidae.

Gp IX is best developed in the Tipulomorpha (Fig. 2), Ptychopteridae (Fig. 4A), Thaumaleidae (Fig. 7B), Chironomidae, Simuliidae (Fig. 7A), and Sciaridae (Fig. 10C, D). They are strongly

reduced in the Cecidomyiidae (Fig. 9), only part of the rami remains in the Ceratopogonidae (Fig. 7E), and Gp IX is practically or completely absent in the Scatopsidae, Chaoboridae, Culicidae, and Dixidae.

Gc IX may be distinct and relatively well developed. More often, however, they are strongly reduced, difficult to distinguish, and may be fused either with sternite IX (S IX), to form a gonosternite IX, as in the Tipulidae (Fig. 2A), the Psychodidae (Fig. 4D, E, G), and the Ptychopteridae (Fig. 4A); or with T IX, to form a gonotergite IX, as in some Chironomidae, apparently in the Cecidomyiidae (Fig. 9A, B) and probably most Cyclorrhapha where, however, S X also may be fused with the gonosternite (Crampton 1942; Hennig 1968). Gc IX bears a relatively long but slender gonostylus IX (Gs) possibly in some Nymphomyiidae, in Sciaridae (Fig. 10A, B) (apparently misnamed sternite X in Hirvenoja (1973 fig. 17)), and in Telmatogetoninae (Chironomidae). In all other families and chironomid subfamilies the gonostyli are absent. Smith (1969 p. 1963), who apparently examined a *Tipula* L., states only that the gonostyli usually are misnamed the cerci. He apparently overlooked the small gonosternite IX in *Tipula* and thus did not realize that the cerci originate from the apparent segment X, not from segment IX (Fig. 2A).

The Brachycera often have all gonopods reduced, accompanied either by desclerotization and telescoping of the caudal abdominal segments, including genital, or by having the apparent segment VII form a strongly sclerotized tube into which the fused terminal segments and apical cerci (often fused) can be withdrawn (such as in the Otitoidea, Micropezoidea, Lonchaeidae, and Agromyzidae (Hennig 1973 p. 219)). It is clear that this corresponds to the antovipositor defined by Smith. However, most lower Diptera do not possess true ovipositors in the sense of Smith either, as they usually consist of Gp VIII and the cerci, not of Gp VIII and IX and Gs IX. The only possible exception is the Sciaridae (Fig. 10C–E).

T VII and VIII are usually unmodified in the nematocerous Diptera. In the Telmatogetoninae (Chironomidae), however, T VIII is strongly reduced. In taxa such as the Anophelinae (Culicidae) (Fig. 6A), Scatopsidae (Fig. 8E), and Cecidomyiidae (Fig. 9) T VIII is slightly modified.

S IX usually is desclerotized and membranous. Only in the Tipulidae (Fig. 2A) and Psychodidae (Fig. 4D, E, G) is gonosternite IX nonmembranous. In the Bibionidae (Fig. 8A), Scatopsidae (Fig. 8C), Chaoboridae (Fig. 5A, B), and Culicidae (Fig. 6), S IX consists partly of a more or less sclerotized band connecting the Gc IX. In many of the remaining nematocerous Diptera the apodemes of coxosternites IX or the coxosternapodemes (Sæther 1974 p. 219), which sometimes connect with the rami of Gp IX and caudolaterally to Gc IX, are the only remaining sclerotized parts of S IX. The two gonocoxites are often connected by a weak membranous strap probably representing the intergonocoxal connective of Smith (1969).

T IX among nematocerous Diptera apparently is membranous in the Mycetophilidae only (Fig. 10B). It may, however, be reduced to a sclerotized strap and often hidden by T VIII as in Thaumaleidae (Fig. 7B), or hidden by T VII and VIII as in the Scatopsidae (Fig. 8E). In the Cecidomyiidae (Fig. 9) and in Tanypodinae, Podonominae, and Aphroteniinae (all Chironomidae), T IX is fused with Gc IX to each side to form a gonotergite. In the Tanypodinae this gonotergite is reduced to a narrow strap. A gonotergite may also be present in the Culicidae (Fig. 6), Chaoboridae (Fig. 5), and Dixidae, although rudiments of a gonocoxite appear to be present. T IX may be partially divided into two setigerous protrusions as in most Diamesinae, Prodiamesinae, and Orthocladiinae (Chironomidae). It may also be completely divided as in the Asilidae, Mydidae, Apioceridae, Therevidae, and Dolichopodidae (Crampton 1942 p. 83; Hennig 1973 p. 218). In the Ptychopteridae (Fig. 4A) T IX is fused with T VIII and T X.

Segment X of the Diptera is often not differentiated into tergites and sternites, but is continuous around the whole segment. Often the segmentation behind the genital segments is poorly defined and the entire complex formed by the telson and the postgenital segments is called the proctiger. In the present paper, however, the postgenital segments are divided into an apparent segment X, and a postgenital plate presumably represents an 11th sternite.

The cerci are generally regarded as appendages of segment XI but, because of the often reduced nature of XI, they frequently appear to belong to segment X. (Crampton (1929 p. 456), however, regards them as appendages of segments X.) The cerci, in the basic dipteran design (composed of characters present in both archetypes and present-day species), are two-segmented. They are thus reduced by one segment relative to the basic design of the Antliophora (Hennig

1973 p. 218). The two-segmented cerci are retained in the Deuterophlebiidae (with both segments reduced), at least some Nymphomyiidae, Tanyderidae, at least some Ptychopteridae (with the apical segment strongly reduced), some Cecidomyiidae, Ditomyiidae, Mycetophilidae (and probably Mycetophiloidea in general), Sciaridae, Stratiomyidae, some Rhagionidae, and in *Chrysogaster pulchella* Will. (Syrphidae) (Metcalf 1921) (where the two-segmented cerci, however, are probably of a secondary nature (Hennig 1973 p. 219)). In the remaining families the cerci are apparently one-segmented. When the segments posterior to VII are fused, forming an antovipositor, the cerci sometimes are fused, as in the Otitoidea and Pallopteroidea (Hennig 1973 p. 219). In some Diptera the cerci bear sensory organs. These have been examined only in *Phormia regina* Meig. (Wallis 1962), and *Musca autumnalis* De Geer (Hooper et al. 1972), but are apparently very well developed in the Blephariceridae also (Fig. 3A, B).

According to Smith (1969 p. 1071) the paired gonads of both sexes of ectognathous insects originally opened separately on papillae between coxites and coxosternites of somite VIII. Exits of these ducts were the gonadal gonopores. The two papillae on IX carried openings of the accessory glands, the accessory gonopores. The spermathecae are ectodermal invaginations around the distal end of the gonadal gonoduct. In modern insects the gonadal gonopores are usually united into a median aperture and often coalesce with the united accessory gonopores. In female Diptera the accessory gonopore usually remains separate from the gonadal gonopore, but both terminate in an ectodermal pocket, the vagina. The common oviduct of most insects is also mainly or entirely an ectodermal tube derived from segment VIII. The theoretical boundary between it and the vagina is often called the gonopore, but there is no practical criterion for distinguishing between the vagina and the common oviduct, which can be applied to all insects that are said to have both (Laffoon and Knight 1971 p. 40). As the spermathecae are ectodermal invaginations around the distal end of the gonadal gonoduct, the spermathecal eminence may represent remains of the papillae originally carrying the gonadal gonopore. Remains of the papillae of the accessory gonopore are, in the Diptera, clearly visible as membranous lobes (labia), caudal of the spermathecal eminence at each side of the accessory gonopore.

The ovaries and oviducts are not distinguishable with the method used here for clearing specimens. A review of these structures can be found in Hennig (1973 p. 229–230).

The accessory glands with their ducts are distinct only in some specimens examined. There are normally two accessory glands, but in some Culicidae (Brelje 1924) and at least in the chironomids *Chironomus* (Wensler and Rempel 1962) and *Hydrobaenus* (Sæther 1976b fig. 37), there is only one. The labia are recognizable as membranous lobes more or less connected to the caudal end of Gp IX in many Diptera. In the Sciaridae (Fig. 10C, D) they are completely or partly fused with the caudal end of the rami. The labia are often united to form a single lobe and sometimes have a caudal notch as in the Tipulidae (Fig. 2A), Trichoceridae (Fig. 2B–D), Culicidae (Fig. 5), and apparently Mycetophilidae (Fig. 10A). Sometimes they are distinct and carry microtrichia or spinules, more often they are absent or at least not detectable with my mounting technique.

The spermathecal eminence is usually situated directly oral of the labia and carries the opening(s) of the spermatheca(e). Spermatheca is used here for the entire caecum including the seminal capsule, spermathecal gland, and spermathecal duct when these are differentiated as parts of the spermatheca (see Laffoon and Knight 1971 p. 39. Sæther 1974 p. 219). According to Downes (1968) and Hennig (1973 p. 230) three spermathecae with independent openings, corresponding to three penis filaments in the male, is the basic design in female Diptera. In several groups of Diptera, and often within the same family, the numbers of seminal capsules and spermathecal ducts are frequently reduced independently. The seminal capsules may be completely absent and the spermathecal ducts apparently function as seminal storage organs as in the Telmatogetoninae of Chironomidae. In the Mycetophilidae (Fig. 10A) and Cecidomyiidae (Fig. 9) two seminal capsules are probably present but they are completely unsclerotized and, therefore, not distinguishable in the preparations examined. In some Acalyptratae one seminal capsule is divided in two, making four seminal capsules (Hennig 1968 p. 21, 1973 p. 231). The three separate spermathecal ducts with independent openings (primitive) may form a common duct with a common opening or be reduced to one or two ducts. However, even when only one seminal capsule remains there may still be three spermathecal ducts such as in the Simuliidae (Fig. 7A). Probably all Chironomoidea (Thaumaleidae, Simuliidae, Ceratopogonidae, Chironomidae) and

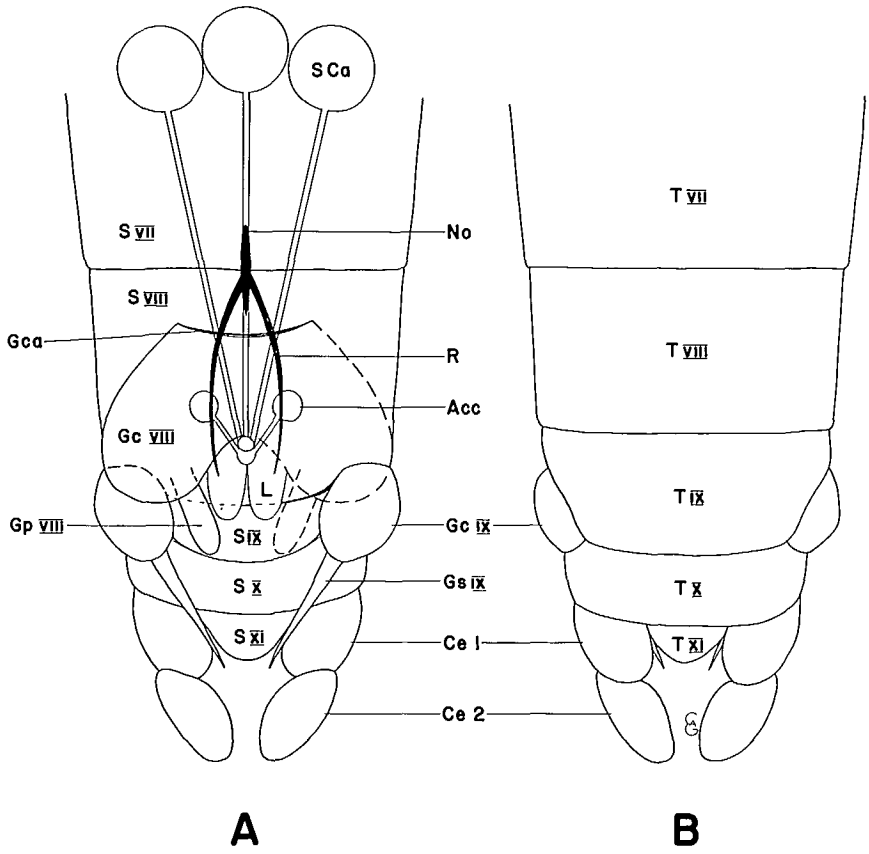

FIG. 1. Generalized female genitalia of the theoretical progenitor of the Diptera. A, ventral. B, dorsal.

Glossina Wied. (Glossinidae) have sperm transfer by means of a spermatophore, i.e. unlike other Diptera (Hennig 1973 p. 231; Nielsen 1959, for chironomids). A conspectus of the spermathecae and the accessory glands is given by Sturtevant (1925–26) and additional references by Hennig (1973 p. 229).

Hennig (1973 p. 3–4) outlines an archetype of the Diptera, a theoretical progenitor containing the synapomorphous and the most plesiomorphous characters of the order. For the female genitalia three characters are given: strongly shortened ovarioles, three spermathecae, and two-segmented cerci. The female genitalia of such a theoretical progenitor is illustrated in Fig. 1. Both Gc VIII and Gc IX are present. Gs IX (but not Gs VIII) is present but weak. Gp VIII is single, elongate, and well developed. Gp IX is distinct and well developed and most likely the notum is short. S IX is small, but still discernible as a sternite. T IX is well developed and similar to preceding tergites. S X and T X are probably still separate from each other. S XI is represented by a postgenital plate and there may be a T XI. The cerci are well developed and two-segmented. There are probably

two small accessory glands opening between well-developed labia. The three spermathecae have three spherical well sclerotized seminal capsules, three separate and straight spermathecal ducts with separate openings, and probably no spermathecal gland. All in all the female genitalia of this theoretical archetype, with the exception of the efferent system, is surprisingly similar to that of present-day Sciaridae. The female genitalia, including the efferent system of the theoretical progenitor of Chironomidae (Fig. 15) is also very close to that of the Diptera as a whole. However, no single present-day chironomid has retained all the primitive features.

In the following diagnoses of the female genitalia, a few species representing different groups and families of Diptera other than Chironomidae are given. It is not the purpose of this paper to give a complete picture of the female genitalia of any of these groups. To do that, one family at a time would have to be treated. Thus, the species treated may not be fully representative of their respective families. The references given are not meant to be complete and some may have been overlooked.

FEMALE GENITALIA OF DIPTERA OTHER THAN CHIRONOMIDAE

Infraorder Tipulomorpha

According to Hennig (1968, 1969, 1973) it is possible and even likely that the Tipulomorpha form the sister group (Polyneura) of all other groups of Diptera (Oligoneura). The infraorder is clearly monophyletic.

The female genitalia of Tipulomorpha appear to be relatively uniform. Both Gp VIII and Gp IX are well developed and long. Gc IX is either fused with S IX to form a gonosternite, or digitiform and separate. There are no gonostyli. Segment X and the postgenital plate are well developed. The cerci are characteristically long and slender, but may be secondarily reduced slightly. The labia are probably always fused. There are 3 seminal capsules. Possible synapomorphous characters for the Tipulomorpha may be the very long notum, the fused labia, and the shape of the cerci.

For descriptions of female genitalia see Dufour (1851), Snodgrass (1903), Keuchenius (1917), Tokunaga (1930, Limoniidae), Rees and Ferris (1939), Peus (1952, Cylindrotomidae), and Frommer (1963).

Fam. Trichoceridae
(Fig. 2B–D)

Species examined: *Trichocera regulationes* (L.), *Trichocera columbiana* Alex., *Trichocera borealis* Lack.

S VIII narrower than T VIII. Gp VIII simple, well developed, with indication of a basal gonocoxapodeme. Gp IX well developed, with very long notum. Gc IX placed ventrally, digitiform, without microtrichia, with a few setae, and no gonostylus. Segment X well developed. Postgenital plate well developed, usually without microtrichia, with a few setae. Cerci very long, slender, one-segmented.

Labia fused without microtrichia, with caudal notch. 3 sclerotized seminal capsules with separate ducts and separate or partly common openings.

The narrow S VIII and membranous or absent S IX are probably synapomorphous features for the family, compared with the Tipuloidea. The well-developed Gc IX and lack of a common spermethecal duct are symplesiomorphies.

Fam. Tipulidae
(Fig. 2A)

Species examined: *Tipula* sp.

Gp VIII simple, well developed. Gonocoxapodeme not apparent. Gp IX well developed with long notum. Gc IX fused with S IX to form a gonosternite IX. No gonostyli. Segment X and postgenital plate well developed. Cerci one-segmented, typically very long and well developed, occasionally short and rounded.

2 accessory glands with common opening. Labia fused, with caudal notch, with microtrichia. 3 heavily sclerotized seminal capsules, with long spermathecal ducts and a long common duct.

Gonosternite IX and the long, common spermathecal duct are synapomorphous features, compared with the Trichoceridae.

Infraorder Psychodomorpha

The monophyly of this group is doubtful. Representatives of Blephariceridae, Deuterophlebiidae, Ptychopteridae, and Psychodidae have been examined. Descriptions of female genitalia in the Nymphomyiidae can be found in Tokunaga (1935), Ide (1965), and Cutten and Kevan (1970); of the Tanyderidae in Williams (1933).

The female genitalia differ greatly from family to family and it is difficult to recognize any basic design or any synapomorphies for the Psychodomorpha as a whole. Ide (1965 p. 498) stated there are no cerci in *Palaeodipteron walkeri* Ide (Nymphomyiidae), but a "gonopod" with "coxite" and "style" is present. It seems more likely that this "gonopod" represents a two-segmented cercus (Cutten and Kevan 1970 p. 17). Cutten and Kevan suggest that the Nymphomyiidae perhaps are most closely related to the Deuterophlebiidae. There are not many similarities between the female genitalia of the 2 families. Both, however, have at least some species with very long Gp VIII and two-segmented cerci.

Fam. Blephariceridae
(Fig. 3A–D)

Species examined: *Agathon elegantulus* Röd.

GP VIII long, lobelike, fused along median line, but separated caudally by a notch. Gca VIII absent or barely indicated. Gp IX with short transverse notum and widely diverging rami. Gc IX well developed, situated ventrally orolaterad of Gp VIII; no gonostylus. S X membranous. Postgenital plate with a few strong caudal setae. T IX and X separate. Cerci one-segmented, large, complex, with numerous, apparently sensory setae.

Labia weak, fused with a few microtrichia. 3 oblong seminal capsules with separate spermathecal ducts but partly common opening.

Synapomorphous characters for the Blephariceroidea (Blephariceridae plus Deuterophlebiidae) may be the large fused Gp VIII and general shape of Gp IX. The complex one-segmented cerci and fused labia may be synapomorphies for the Blephariceridae, compared to the Deuterophlebiidae. The position of Gc IX relative to Gp VIII in the Blephariceridae resembles that found in the Tanyderidae (Williams 1933 fig. 15).

Fam. Deuterophlebiidae
(Fig. 3E–G)

Species examined: *Deuterophlebia nielsoni* Kenn.

Gp VIII large, fused with each other along median line, fused with rudiments of Gc IX laterally and with base of segment X caudally, i.e. segments VIII–X and their parts not clearly distinct from each other ventrally. T VIII–X, however, separated dorsally. Gp IX with a triangular notum and widely diverging rami. Cerci strongly reduced, 2-segmented.

Labia large, separate, with oromedian microtrichia. Spermathecae not observed.

Probable synapomorphous features for the family are the fusion of S VIII–X and the reduced cerci.

Fam. Ptychopteridae
(Fig. 4A–C)

Species examined: *Bittacomorpha clavipes* (Fabr.)

Gp VIII relatively large. Gp IX well developed, with long notum and short rami. Gc IX reduced and apparently fused with membranous but large S IX. T VIII, T IX, and T X fused

together. Postgenital plate large and well developed. Cerci 2-segmented, but with apical segment strongly reduced.

Labia complex, with microtrichia. 2 or 3 (3 according to Hennig (1972 p. 5)) weakly sclerotized seminal capsules with separate spermathecal ducts and openings.

The fused T VIII–X, the shape of S IX and the labia may be synapomorphous features for the family.

FAM. PSYCHODIDAE
(Fig. 4D–G)

Species examined: *Psychoda limicola* Vaill., *Psychoda elegans* Kinc.

Gc VIII fused, large, platelike, with anterior transverse gonocoxapodeme and caudal projections possibly representing Gp VIII. Gp IX reduced, consisting of a thin notum without distinguishable rami. Gc IX fused with T IX to form a gonotergite IX; no gonostylus. S IX platelike, partly or fully covered by Gc VIII. Postgenital plate apparently absent. T X sclerotized. Cerci one-segmented.

Labia membranous. 2 complex seminal capsules.

Interpretation of the different parts is somewhat uncertain. The fused Gc VIII are usually called the subgenital plate and said to be S IX (Quate 1955; Jung 1956; Vaillant 1971–72, 1973). However, as pointed out by Hennig (1972 p. 34) this can hardly be correct. Hennig thinks that the wrong numbering of this plate is a result of miscounting the segments. There does, however, seem little doubt that this plate is actually covering a S IX and that the error consists in not regarding the "subgenital plate" as an appendix of S VIII.

There are several potential synapomorphies for the family, or at least for the subfamily Psychodinae, including the fused platelike Gc VIII, the reduction of Gp IX, the fusion of Gc IX with T IX, the absence of a postgenital plate, and the complex seminal capsules. Strong plesiomorphies are the presence of Gc VIII and of a platelike S IX.

Infraorder Culicimorpha

The Culicimorpha are undoubtedly monophyletic with 2 clear sister groups, the superfamilies Culicoidea and Chironomoidea. The only apparent synapomorphies are the sperm transfer by spermatophores and the one-segmented cerci.

SUPERFAMILY CULICOIDEA

There are a number of synapomorphous features present in the female genitalia of this undoubtedly monophyletic superfamily: the fused and strongly reduced or absent Gp VIII (lower vaginal lip in the Culicidae), the small S IX, the completely reduced Gp IX, and the fused and reduced, or absent, labia.

FAM. DIXIDAE
(Peters and Cook 1966 fig. 13, 61–72, 106–119)

Gp VIII either absent or perhaps consisting of 2 caudolateral indistinctly separated lobes on S VIII. Gp IX apparently absent. Gc IX present and frequently distinct and lobelike. S IX usually a small triangular plate. Postgenital plate fused with S X. Cerci one-segmented.

One seminal capsule only, sclerotized, infrequently with small, sclerotized neck.

The presence of only one seminal capsule is a synapomorphous character, compared to the remaining families of the Culicoidea. The presence of weak Gp VIII, of an often distinct Gc IX, and of a relatively distinct S IX are symplesiomorphies for the family not shared by the Culicidae.

FAM. CHAOBORIDAE
(Fig. 5)

Species illustrated: *Mochlonyx* sp., *Chaoborus (Edwardsops) magnificus* Lane, *Chaoborus (Sayomyia) punctipennis* (Say), *Chaoborus (Sayomyia) brasiliensis* (Theob.), *Chaoborus (Chaoborus) flavicans* (Meig.), *Chaoborus (Chaoborus) crystallinus* (De Geer)

Gp VIII and IX absent. Gc IX barely indicated as part of a membranous gonosternite IX. Postgenital plate more or less fused with segment X. Cerci one-segmented.

Labia apparently absent. 3 seminal capsules with 3 spermathecal ducts separate for most of their length, but 2 joined a relatively long distance before opening and all 3 joined before common opening. Synapomorphies for the family are mentioned under the Culicidae.

Other figures for the female genitalia include Cook (1956 fig. 10, 15), Sæther (1970b fig. 5; 1972 fig. 6; 1976a fig. 1, 3).

FAM. CULICIDAE
(Fig. 6)

Species illustrated: *Anopheles (Anopheles) earlei* Varg., *Coquillettidia perturbans* (Walk.), *Aedes (Ochlerotatus) idahoensis* (Theob.)

Gp VIII fused and reduced, apparently forms so-called lower vaginal lip. Gp IX absent. Gc IX strongly reduced and partly fused with reduced membranous S IX. Postgenital plate relatively well developed. Cerci one-segmented.

Labia fused, reduced, or relatively distinct. 1–3 sclerotized seminal capsules. Spermathecal ducts either single (when one seminal capsule), or 2 with a partially common duct and common opening, and third with separate duct and opening (when 3 seminal capsules).

There are no certain synapomorphies, for the family as a whole, in culicid female genitalia compared with the Chaoboridae.

Synapomorphies for the Chaoboridae and Culicidae combined are the fused and reduced Gp VIII and the reduced Gc IX, S IX, and labia. In the Chaoboridae, Gp VIII and the labia apparently are completely absent, i.e. synapomorphies for this family compared with the Culicidae.

Female genitalia of the Culicidae are treated among others by Dufour (1851), Christophers (1923), Brelje (1924), Sturtevant (1925–26), Gerry (1932), Coher (1948), Giglioli (1963), and Laffoon and Knight (1971).

SUPERFAMILY CHIRONOMOIDEA

Although this superfamily is undoubtedly monophyletic there are no apparent synapomorphies in the female genitalia compared to the Culicoidea. There are, however, a number of symplesiomorphies, as the segments posterior to VII are never fused, a postgenital plate is always distinguishable, and at least vestiges of S IX and Gc IX are present.

FAM. THAUMALEIDAE
(Fig. 7B)

Species examined: *Thaumalea major* Bezzi

Gp VIII well developed. Gp IX well developed, with long notum and short rami. Gc IX well developed. T X often covered by T VIII. S IX apparently membranous, covered by S VIII and Gp VIII. Postgenital plate mostly large. Cerci one-segmented.

Labia membranous, relatively large. Spermathecae not observed.

The position of T IX as an interior sclerotized strap may be synapomorphous for the Thaumaleidae compared to the family group Chironomoidea (Simuliidae, Ceratopogonidae, Chironomidae).

Edwards (1929b) figured lateral views of the female genitalia of a number of species. Vaillant (1970) shows ventral views of the genitalia of 2 species.

Fam. Simuliidae
(Fig. 7A)

Species illustrated: *Simulium (Simulium) verecundum* Stone et Jamnb.

Gp VIII well developed. No Gc VIII or gonocoxapodeme. Gp IX well developed, notum long, rami fused with Csa IX. Gc IX fused with T IX to form a gonotergite IX, no gonostylus. S IX membranous with a sclerotized coxosternapodeme. Postgenital plate absent or fused with segment X. Cerci one-segmented.

2 accessory glands with common opening. Labia reduced, membranous. One large seminal capsule, but 3 spermathecal ducts with separate or partly common openings.

Synapomorphous features of female genitalia include: fusion of the rami and Csa IX to form a "gonofurca" together with the notum; a single seminal capsule; and absence of a postgenital plate. However, in the Ceratopogonidae, remains of the rami are fused with the coxosternapodeme and Gc IX, which are also fused with T IX to form a gonotergite; in the basic design of Chironomidae the rami remain separate from the coxosternapodemes, and Gc IX are separate and well developed. The female genitalia thus indicate that Ceratopogonidae alone is the sister group of the Simuliidae, not Ceratopogonidae plus Chironomidae as suggested by Hennig (1973 p. 27).

Female genitalia of the Simuliidae have been extensively and admirably used in taxonomy (e.g. Rubzov 1964).

Fam. Ceratopogonidae
(Fig. 7C–H)

Species illustrated: *Mallochohelea mallochi* Wirth, *Heteromyia fasciata* Say, *Bezzia pulverea* (Coq.), *Dasyhelea* sp., *Isohelea* sp.

Gp VIII well developed. No Gc VIII or gonocoxapodeme. Notum absent; only part of rami, fused with Csa IX, remaining of Gp IX. Gc IX fused with T IX to form a gonotergite IX; no gonostylus. S IX membranous, with sclerotized coxosternapodeme. Postgenital plate well developed. Cerci one-segmented.

Labia reduced, membranous. Spermathecae variable, consisting of 1–3 sclerotized seminal capsules of differing sizes and shapes and reduced to varying degrees. Spermathecal ducts apparently always joined before common opening.

The absence of a notum is a clear synapomorphy compared with other families of the Chironomoidea. However, Gp IX is completely reduced in the Culicoidea. If Chironomidae is regarded as the sister group of Ceratopogonidae then the fusion of the ramus with Csa IX, the fusion of Gc with T IX, and absence of a gonostylus are synapomorphous for the family compared with the basic design of the Chironomidae. However, as stated above the Simuliidae have these same characteristics.

Although several descriptions of female genitalia can be found (see particularly Chan and LeRoux (1965) and more general descriptions by Wirth (1952), Wirth and Dow (1972), Dow and Wirth (1972), Wirth and Ratanaworabhan (1972a, b), Grogan and Wirth (1975), Dow and Turner (1976)), a more complete synopsis has apparently never been attempted. The spermathecae especially lend themselves to systematic studies.

Infraorder Bibionomorpha

According to Hennig (1973 p. 30) there are never more than 2 spermathecae present in the females of this infraorder. Dufour (1851) and Sturtevant (1925–26), however, reported 3 spermathecae in the Bibionidae (Fig. 8A). Only a few scattered descriptions of female genitalia exist, including Abul-Nasr (1950) (Anisopodidae and Mycetophilidae), Munroe (1974) (Ditomyiidae), and Hirvenoja (1973 fig. 17) for *Bradysia ocellaris* (Comst.) (Sciaridae). No synapomorphous characters for the Bibionomorpha as a whole can be found in the female genitalia.

Fam. Bibionidae
(Fig. 8A, B)

Species examined: *Philia* cf. *tibialis* (Loew), *Philia stigmatera* (Say), *Bibio* sp.

Gp VIII relatively well developed. Gca VIII present. Gp IX relatively weakly sclerotized, with broad anteriorly rounded notum and weak rami. Gc IX weak, indistinct, fused with the sclerotized straplike S IX to form a gonosternite IX; no gonostylus. Postgenital plate very large. Segment X small. Cerci one-segmented.

Labia possibly fused, relatively large, with microtrichia. 3 seminal capsules with 3 separate spermathecal ducts with separate openings.

The presence of 3 separate spermathecal units is probably a plesiomorphy compared to all other Bibionomorpha.

Fam. Scatopsidae
(Fig. 8C–E)

Species examined: *Scatopse fuscipes* Meig.

Gp VIII large, fused along median margin, overreaching cerci. Gp IX apparently absent. S VIII small, partly covered by S VII. S IX membranous with sclerotized coxosternapodeme. Gc IX well developed, no gonostylus. T VIII reduced, partly covered by T VII. T IX a sclerotized strap completely covered by T VII and T VIII. Postgenital plate absent. Cerci one-segmented, short.

Labia membranous, fused. One seminal capsule with very thin spermathecal duct; later widens to a broad duct clothed with interior microtrichia and with a diverticulum.

There are a number of potential synapomorphies present in the female genitalia. However, more members of the family and its sister group need to be studied.

Fam. Cecidomyiidae
(Fig. 9A–C)

Species examined: *Mayetiola rigidae* (Ost. Sack.), *Aphidoletes thompsoni* Möhn.

Gp VIII fused and reduced or absent. Gp IX absent or strongly reduced. Gc IX fused with T IX to form a nearly tubular gonotergite IX. S IX reduced. Postgenital plate relatively well developed. Segment X strongly reduced or perhaps fused with gonotergite IX. Cerci one-segmented, separate, or fused.

Gonopore situated anterior on or caudad of gonotergite IX. Vulva situated at apex of gonotergite IX with an "eversible bursa" (Prasad and Grover 1964) opening immediately caudad. Labia membranous or sclerotized, but without microtrichia, forming part of the so-called "genital funnel" of Prasad and Grover (1964). Seminal capsules absent or completely unsclerotized. 2 spermathecal ducts joined shortly before common opening or at least with a common opening.

Metcalfe (1934) studied the structure and development of the female genital system in *Dasyneura leguminicola* Lint., and Prasad and Grover (1964) studied the female genitalia of *Aschistonyx baranii* Grov.

The position of the gonopore posterior to segment VIII and the eversible bursa almost certainly are synapomorphies. The tubular gonotergite IX also is a probable synapomorphy within the Bibionomorpha, but similar gonotergites can be found in several Brachycera.

Fam. Mycetophilidae
(Fig. 10A, B; Abul-Nasr 1950 fig. 25, 26)

Species examined: *Rymosia* sp.

Gp VIII well developed. Gp IX distinct in Mycetophilinae, apparently absent in Exechiinae (*Rymosia,* Fig. 10A, B). Gc IX strongly reduced, apparently fused with membranous S IX to form a gonosternite IX. T IX reduced to a narrow sclerotized strap in the Mycetophilinae, apparently membranous in the Exechiinae. Segment X divided or partly divided, carrying 2-segmented cerci. Postgenital plate very long, well developed, reaching or nearly reaching apex of cerci.

Labia membranous. 2 weakly sclerotized or unsclerotized seminal capsules with separate ducts and openings.

The female genitalia of *Rymosia* Winn. (Fig. 10A, B) and of *Mycetophila cingulum* Meig. (Abul-Nasr 1950 fig. 25, 26) are quite different and there are apparently no synapomorphous features.

Fam. Sciaridae
(Fig. 10C–E; Sæther 1970a fig. 10; Hirvenoja 1973 fig. 17)

Species examined: *Bradysia* sp. *A*, *Bradysia* sp. *B*

Gp VIII and Gc VIII well developed. Gp IX distinct, with short notum and strong rami. Gc IX small, but with long gonostylus. S IX membranous, with weak coxosternapodeme. Segment X well developed. S XI and T XI apparently present. Cerci large, 2-segmented.

Labia with apodeme, connected with rami, well developed. 2 very large seminal capsules; spermathecal ducts very long, with common opening.

The Sciaridae possesses more plesiomorphous features in the female genitalia than any other family of Diptera. The only possible synapomorphies may be found in the spermathecae.

Suborder Brachycera

No Brachycera have been examined here. The female genitalia have been investigated in several groups or families. References include Crampton (1942), Herting (1957), Oldroyd (1964), Kim and Cook (1966), Hennig (1971), Lehrer (1971), Mühlenberg (1971) and, for the various families, various parts of Linder (1924–). Internal structures are treated among others by Keuchenius (1917), Sturtevant (1925–26), Bonhag (1958), and Hori (1960).

Summary

Elements of abdominal segments VIII–X or XI form the female genitalia in Diptera. In Psychodidae and Sciaridae sternite VIII (S VIII) bears a gonocoxite VIII (Gc VIII), whereas in other Diptera Gc VIII is fused with S VIII. However, rudiments of Gc VIII are detectable as a gonocoxapodeme in Trichoceridae, Blephariceridae, and Bibionidae. Gc VIII or S VIII caudally bears the gonapophyses VIII (Gp VIII) which, in the basic design of Diptera, are long and simple. In Chaoboridae and Dixidae Gp VIII are absent, but are reduced and may be fused in Culicidae and Cecidomyiidae. Gonapophyses IX (Gp IX) in Diptera form a notum orally with caudolateral arms as rami. Gp IX are best developed in Tipulomorpha, Ptychopteridae, Thaumaleidae, Simuliidae, and Sciaridae; they are strongly reduced in Cecidomyiidae; only part of the rami remains in Ceratopogonidae; and Gp IX are practically absent in Scatopsidae, Chaoboridae, Culicidae, Dixidae, and most Brachycera. In the basic design gonocoxite (Gc) IX is distinct and well developed. Often Gc IX is more or less reduced and may be fused with sternite (S) IX to form a gonosternite IX (as in Tipulidae, Psychodidae, Ptychopteridae, and probably most of the Cyclorrhapha where S X may also be part of a gonosternite IX); or it is fused with tergite (T) IX to form a gonotergite IX (as in Culicidae, Chaoboridae, Dixidae, and apparently Cecidomyiidae). Gc IX bears a gonostylus IX possibly in some Nymphomyiidae, and in Sciaridae. T IX is membranous in Mycetophilidae; hidden by T VIII in Thaumaleidae; hidden by T VII and VIII in Scatopsidae, divided in Asilidae, Mydidae, Therevidae, and Dolichopodidae; fused with T VIII and X in Ptychopteridae; or all segments posterior of VII are fused to form an antovipositor, as in many Brachycera. In the basic dipteran design, the cerci are two-segmented. This condition persists in Deuterophlebiidae, Tanyderidae, Ditomyiidae, Mycetophilidae (and probably Mycetophiloidea), Sciaridae, Stratiomyidae; in some Nymphomyiidae, Ptychopteridae, Cecidomyiidae, and Rhagionidae; and secondarily in *Chrysogaster pulchella* Will. of Syrphidae.

There normally are two accessory glands, but in some Culicidae there is only one. The labia, or the remains of the papillae of the accessory gonopore, are usually recognizable as membranous lobes more or less connected to the caudal end of Gp IX. The labia are fused with the rami in the Sciaridae, united and form a single lobe in the Tipulidae, Trichoceridae, Culicidae, and apparently in Mycetophilidae; they carry microtrichia or spinules in at least some Tipulidae, Blephariceridae, Deuterophlebiidae, Ptychopteridae, and Bibionidae; they are strongly reduced in Ceratopogonidae and some Culicidae; and are apparently absent in Chaoboridae. There are three sclerotized seminal capsules with three separate spermathecal ducts with separate openings in the basic design of Diptera, and in Trichoceridae, Bibionidae, and some Ptychopteridae. The seminal capsules are often reduced to two or one or occasionally none; in some Acalyptratae, however, one of the three seminal capsules is divided into two, making four seminal capsules. In the Mycetophilidae and Cecidomyiidae the seminal capsules are either absent or completely unsclerotized. In the Dixidae, Simuliidae, Scatopsidae, and in some Culicidae and Ceratopogonidae, there is only one seminal capsule. The three separate spermathecal ducts with independent openings (primitive) may meet to form a common duct with a common opening, or be reduced to one or two ducts. Probably all Chironomoidea and *Glossina* Wied. (Glossinidae) have sperm transfer by means of a spermatophore.

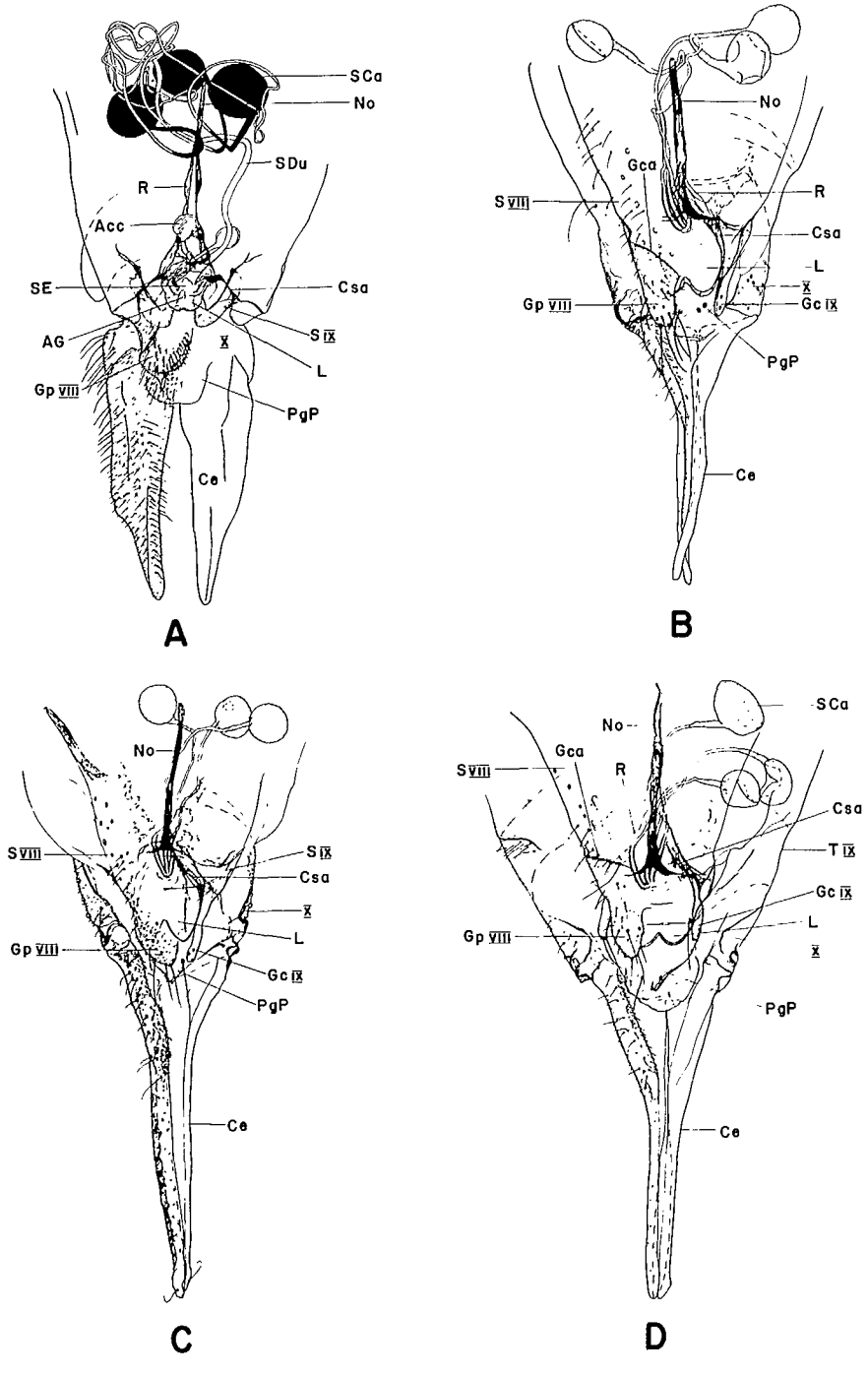

FIG. 2. Female genitalia of Tipulomorpha (ventral). A, Tipulidae, *Tipula* sp. B–D, Trichoceridae: B) *Trichocera regulationes* (L.); C) *Trichocera columbiana* Alex.; D) *Trichocera borealis* Lack.

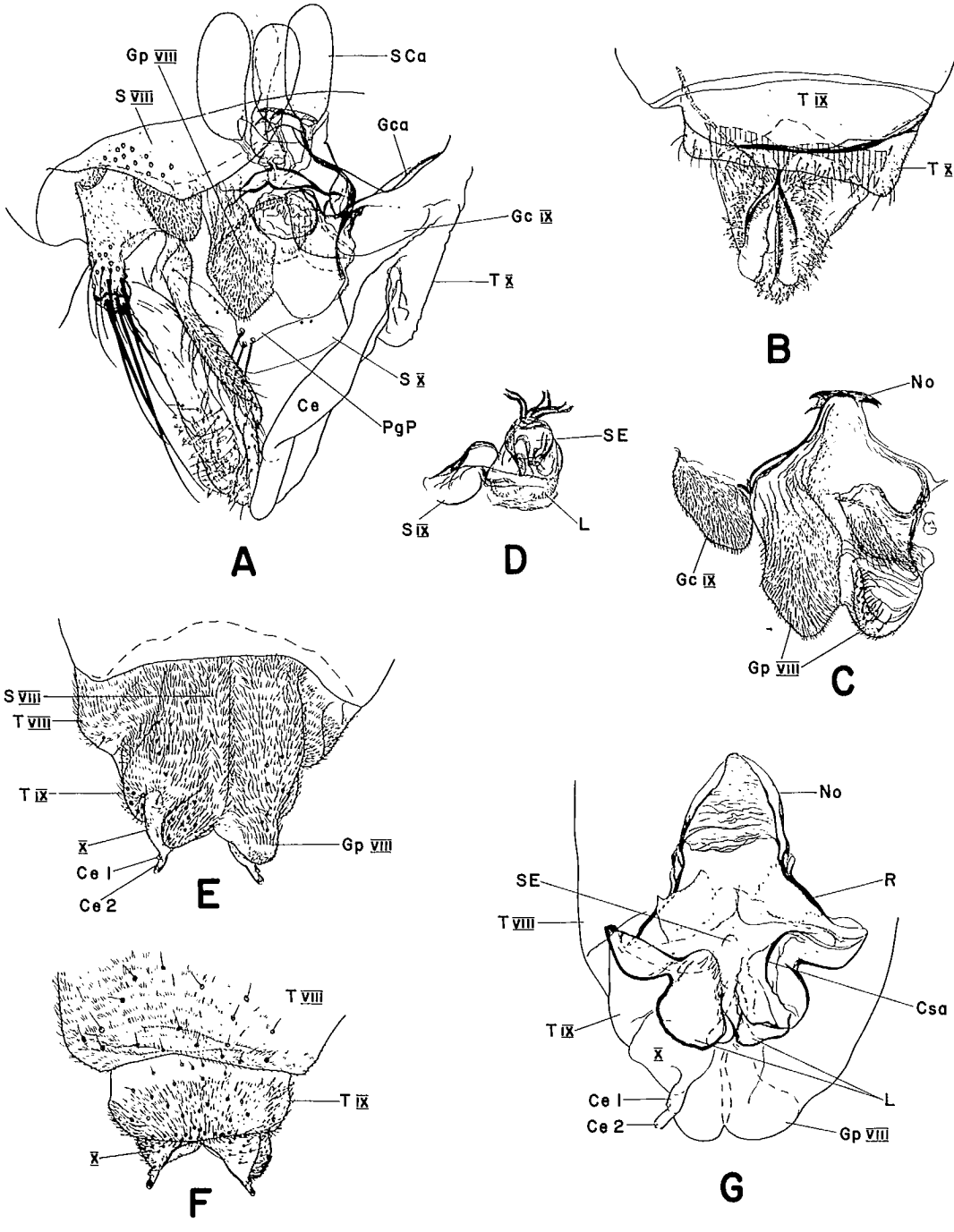

FIG. 3. Female genitalia of Psychodomorpha. A–D, Blephariceridae, *Agathon elegantulus* Röd.: A) ventral; B) dorsal; C) details of Gp VIII and Gc IX; D) details of S IX, spermathecal eminence (SE) and labia (L). E–G, Deuterophlebiidae, *Deuterophlebia nielsoni* Kenn.: E) ventral; F) dorsal; G) interior parts.

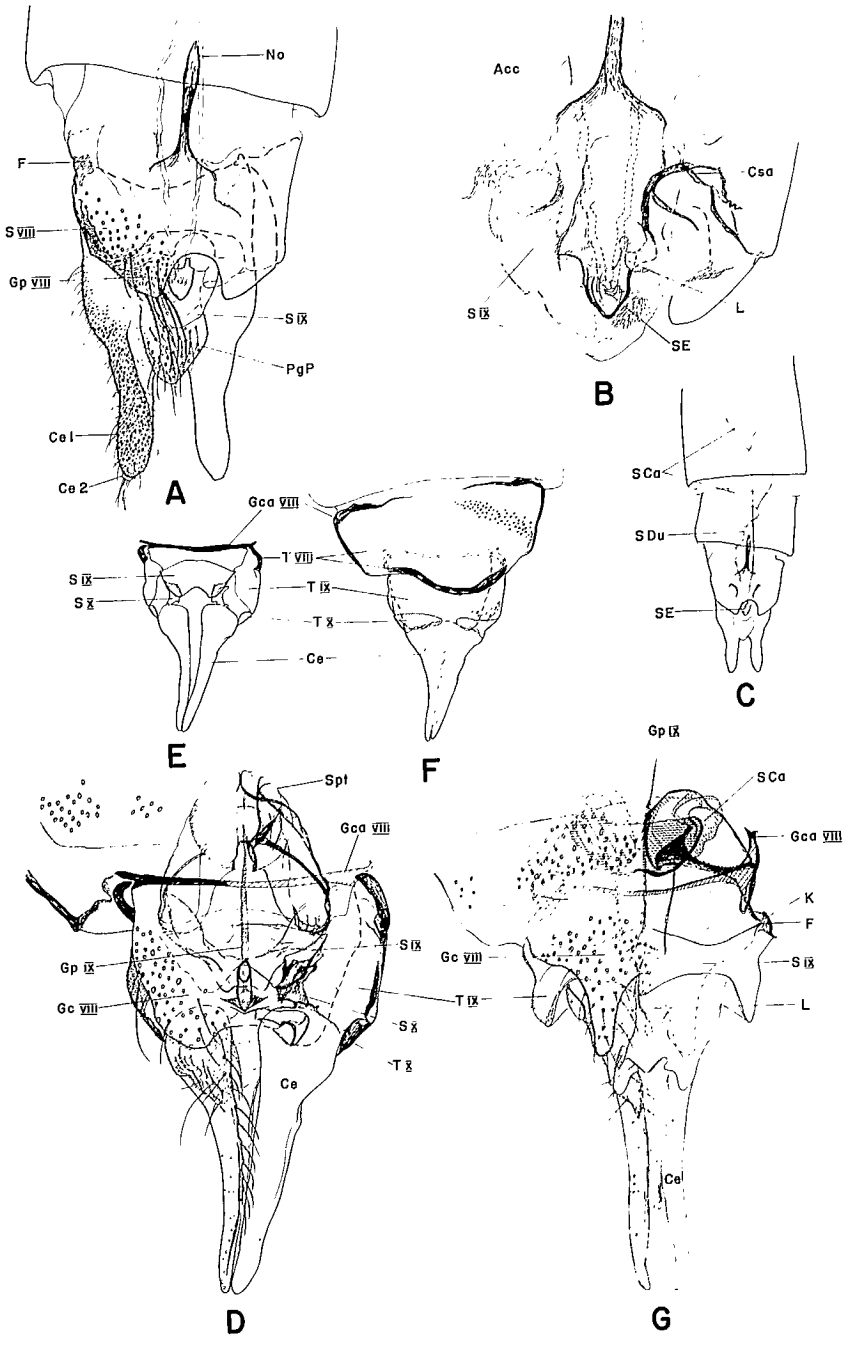

FIG. 4. Female genitalia of Psychodomorpha. A–C, Ptychopteridae, *Bittacomorpha clavipes* (Fabr.): A) ventral; B) detail of interior; C) abdomen showing spermathecae. D–G, Psychodidae: D–F) *Psychoda* sp.n. near *elegans* Kinc.; D) ventral; E–F) sternites and tergites; G) *Psychoda limicola* Vaill., ventral.

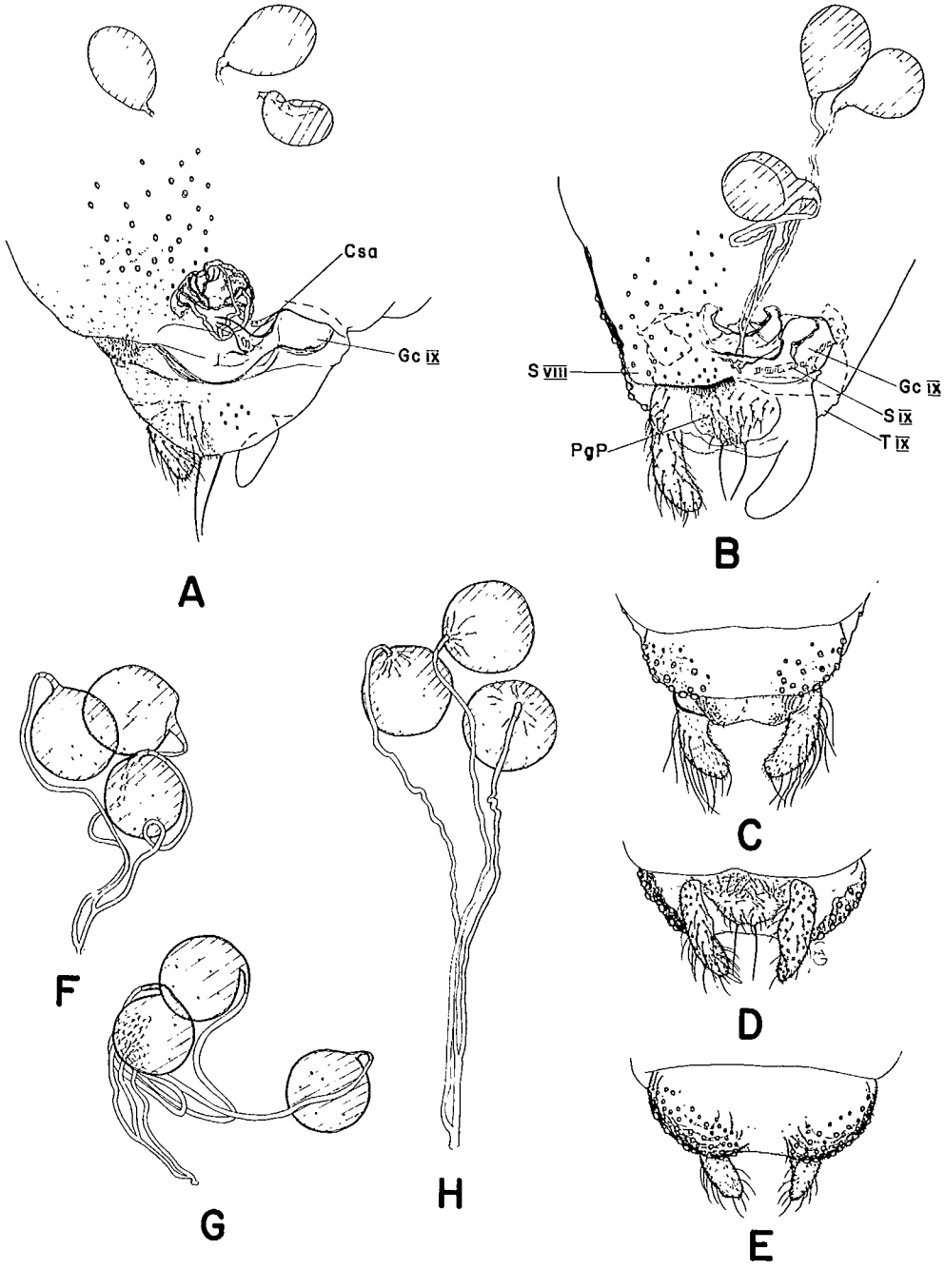

FIG. 5. Female genitalia of Chaoboridae. A, *Mochlonyx* sp. B–C, *Chaoborus (Edwardsops) magnificus* Lane: B) ventral; C) dorsal. D–E, *Chaoborus (Sayomyia) punctipennis* (Say): D) ventral; E) dorsal. F, *Chaoborus (Chaoborus) crystallinus* (De Geer), spermatheca. G, *Chaoborus (Chaoborus) flavicans* (Meig.), spermatheca. H, *Chaoborus (Sayomyia) brasiliensis* (Theob.), spermatheca.

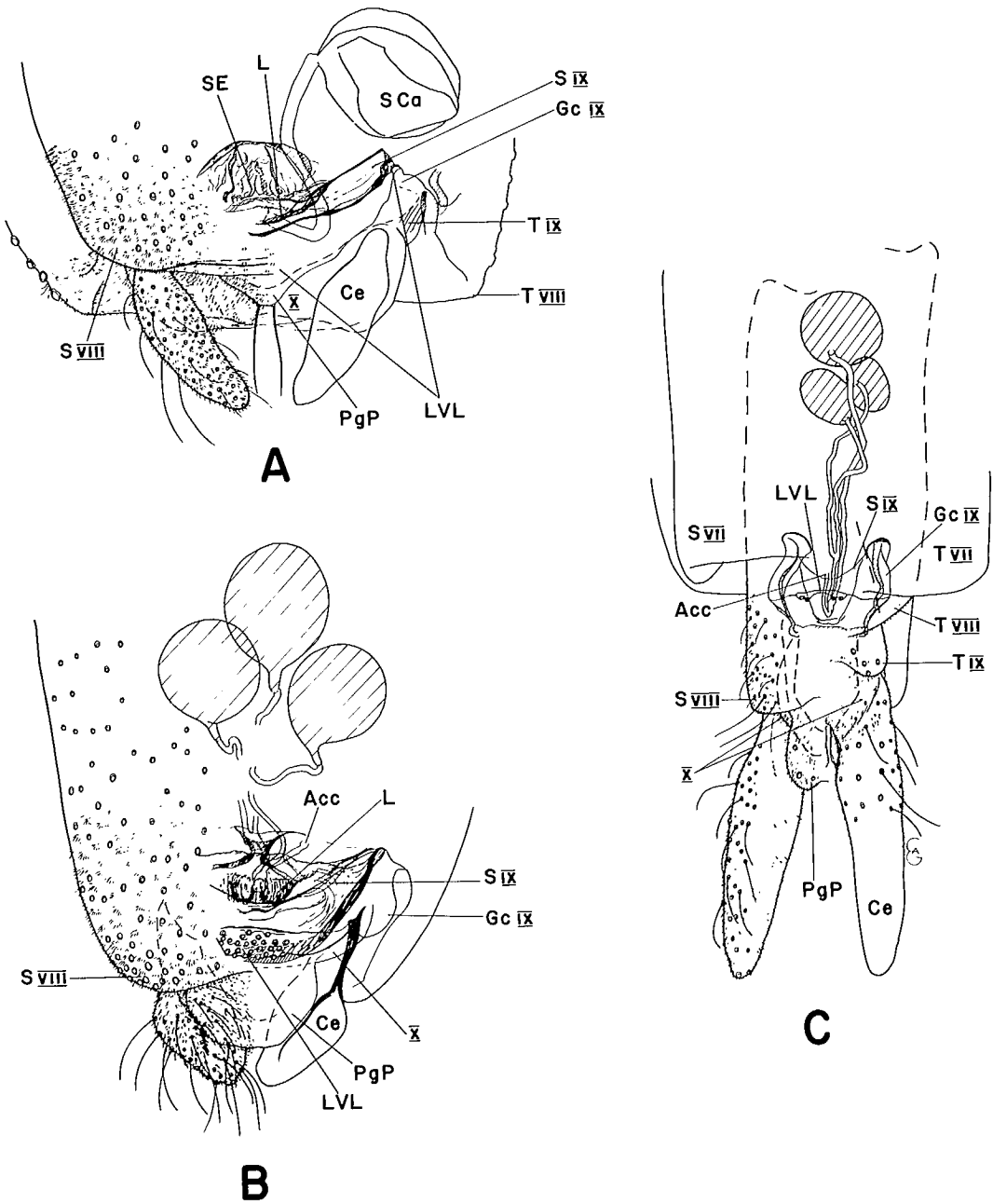

FIG. 6. Female genitalia of Culicidae, ventral view. A, *Anopheles (Anopheles) earlei* Varg. B, *Coquillettidia perturbans* (Walk.). C, *Aedes (Ochlerotatus) idahoensis* Theob.

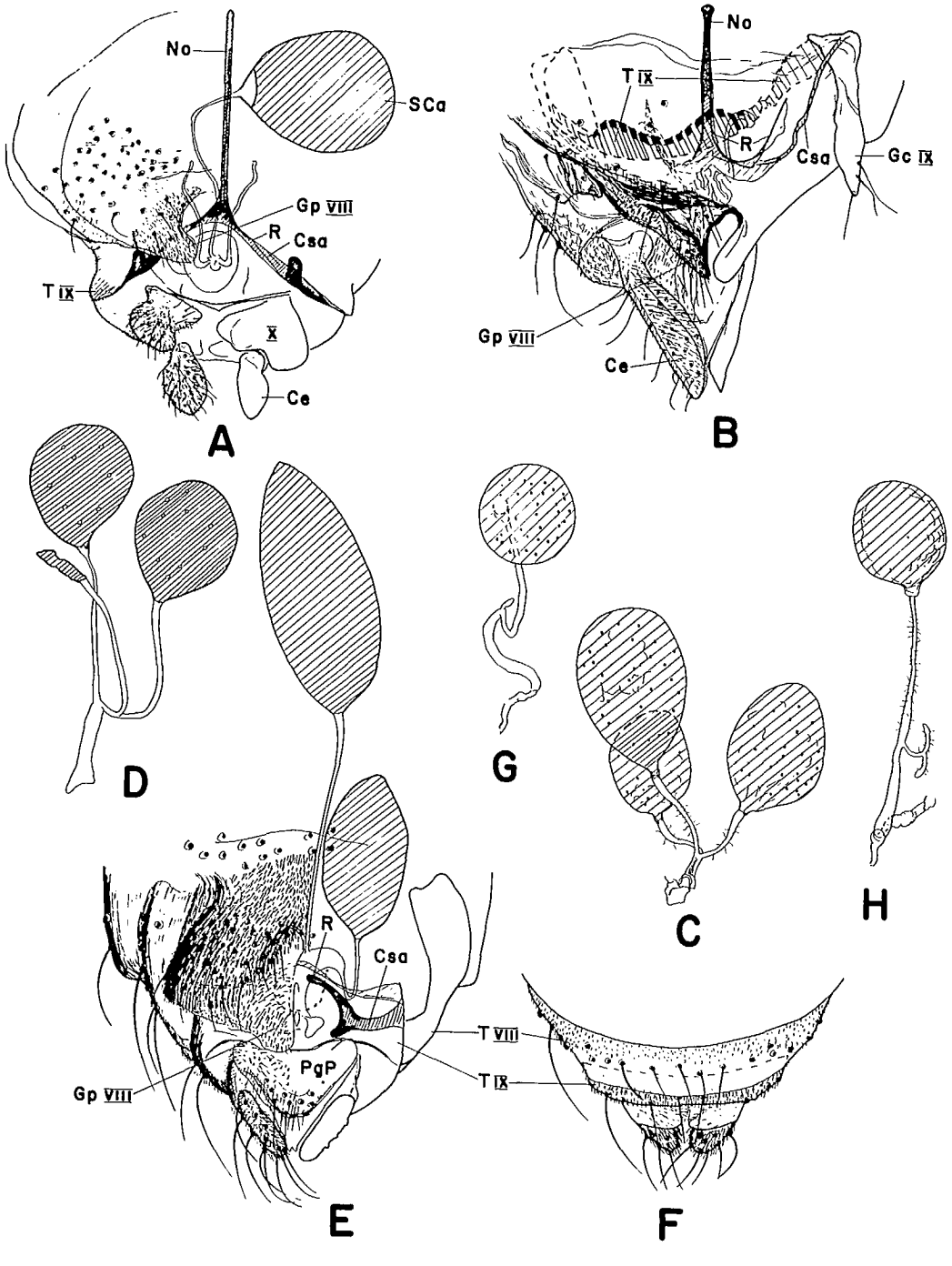

FIG. 7. Female genitalia of Culicimorpha. A, Simuliidae, *Simulium (Simulium) verecundum* Stone et Jamnb., ventral. B, Thaumaleidae, *Thaumalea major* Bezzi, ventral. C–H, Ceratopogonidae: C) *Mallochohelea mallochi* Wirth; D) *Heteromyia fasciata* Say, spermatheca; E) *Bezzia pulverea* (Coq.), ventral; F) *Bezzia pulverea* (Coq.), dorsal; G) *Dasyhelea* sp., spermatheca; H) *Isohelea* sp., spermatheca.

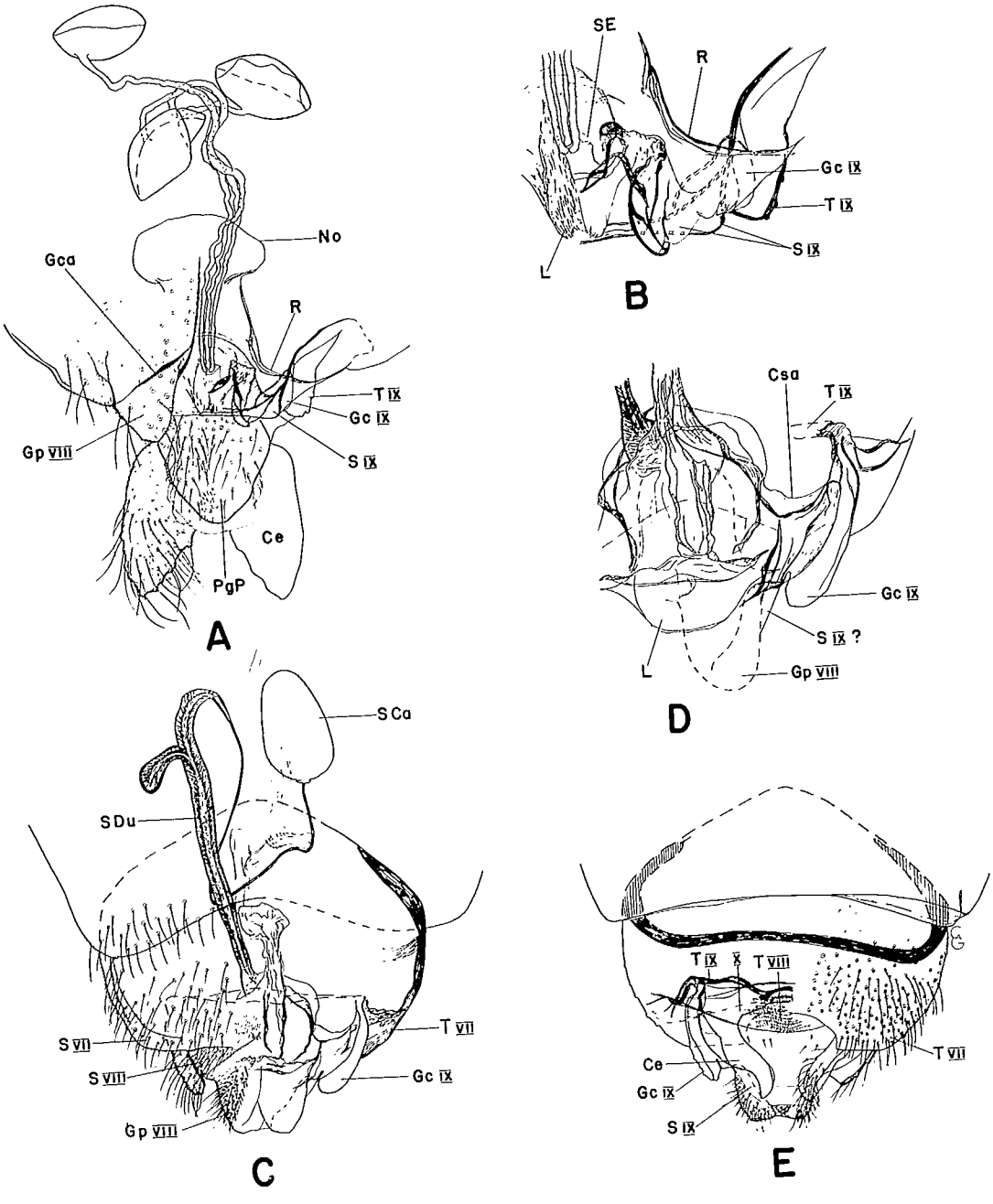

FIG. 8. Female genitalia of Bibionomorpha. A–B, Bibionidae, *Philia* cf. *tibialis* (Loew): A) ventral; B) details, ventral. C–E, Scatopsidae, *Scatopse fuscipes* Meig.: C) ventral; D) details, ventral; E) dorsal.

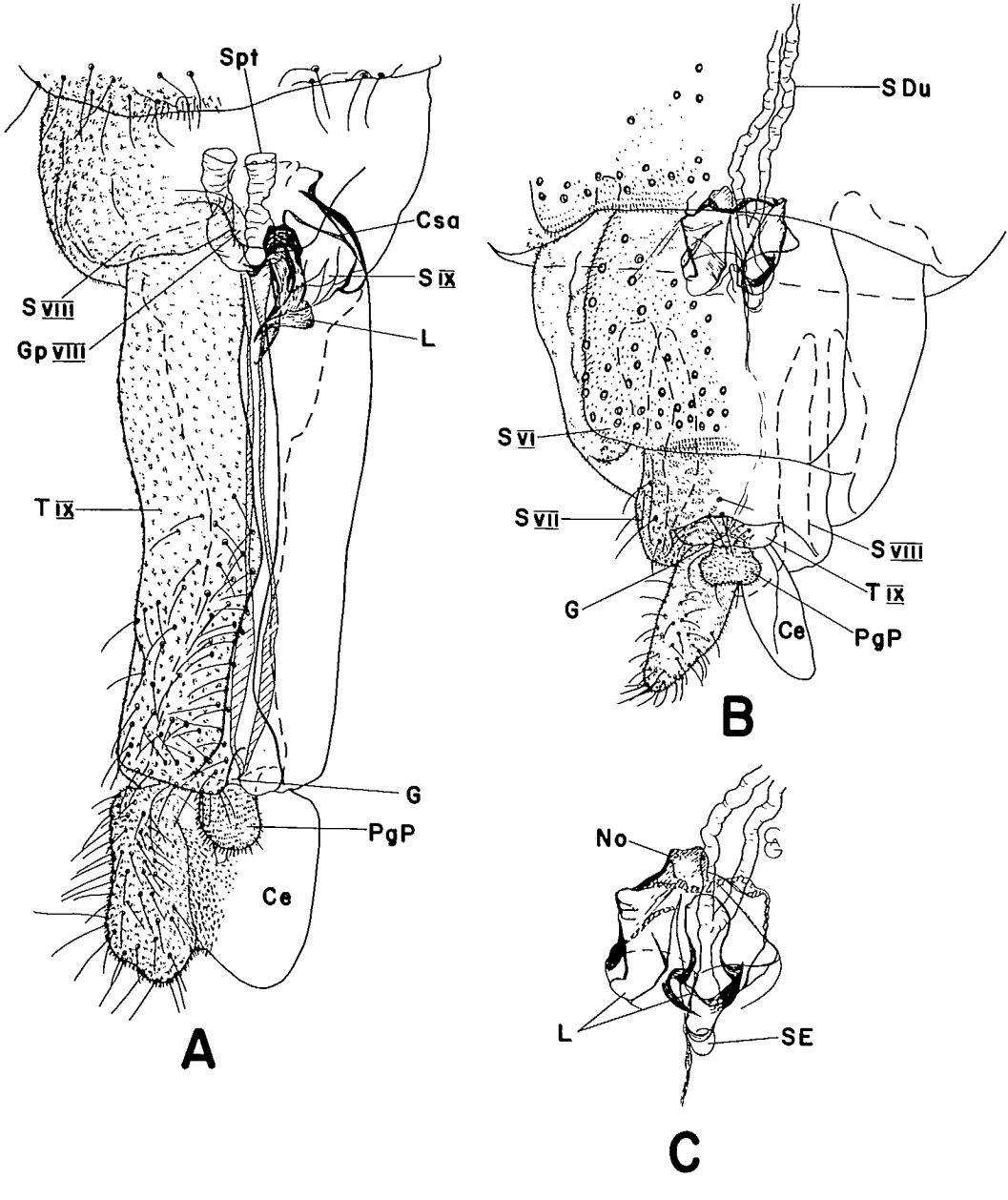

FIG. 9. Female genitalia of Cecidomyidae. A, *Mayetiola rigidae* (Ost. Sack.), ventral. B–C, *Aphidoletes thompsoni* Möhn: B) ventral; C) details of Gp IX, labia, and spermathecal eminence.

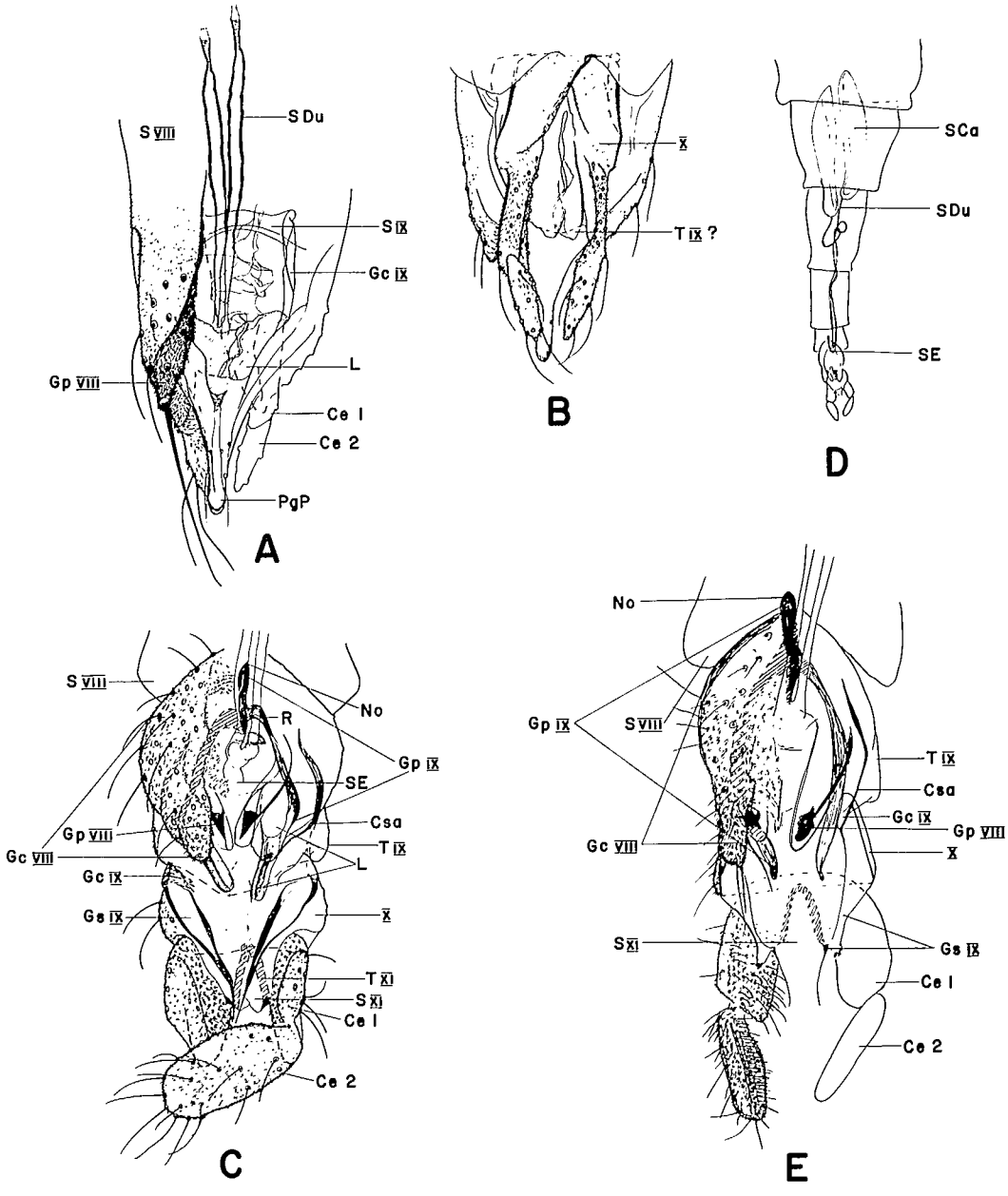

FIG. 10. Female genitalia of Bibionomorpha. A–B, Mycetophilidae, *Rymosia* sp.: A) ventral; B) dorsal. C–E, Sciaridae: C) *Bradysia* sp. *A*, ventral; D–E) *Bradysia* sp. *B;* D) abdomen showing spermatheca, E) ventral.

FEMALE GENITALIA OF CHIRONOMIDAE

The general morphology and terminology of female genitalia in the Chironomidae was outlined by Sæther (1974). Only a short review is necessary here. The different terms used by authors such as Miall and Hammond (1900), Tokunaga (1932), Abul-Nasr (1950), Wensler and Rempel (1962). Frommer (1967), Emden and Hennig (1970), Reiss (1966, 1969, 1971), and Rodova (1967; 1968; 1969a, b; 1970; 1971a, b; 1972a, b, c; 1974a, b), with their present equivalents, is given in Sæther (1974) and glossary of more general terms is given in Smith (1969) and Tuxen (1970).

Normally in the Chironomidae T VIII is unmodified. In the Telmatogetoninae (Fig. 27, 28), however, T VIII is strongly reduced. Gc VIII is apparently always absent except perhaps in *Afrochlus harrisoni* Freem. (Brundin 1966 fig. 414), where two transverse club-shaped lobes may be the rudiments of Gc VIII and Gp VIII. The Gca VIII, however, are represented in some Tanypodinae, the Diamesinae, Orthocladiinae, Prodiamesinae, and Chironominae as internally thickened ridges along the caudolateral margins of S VIII. Gp VIII is simple and well developed in the basic design. Within the Diamesinae (Fig. 29–34), Prodiamesinae (Fig. 35), Orthocladiinae (Fig. 37–61), and Chironominae (Fig. 63–90), however, there is a tendency for Gp VIII to split into 2 or 3 lobes, 2 principal lobes and an apodeme lobe (Sæther 1974 p. 218). This tendency to split, but not the splitting itself, is undoubtedly a synapomorphous feature for these subfamilies (see below). A membrane or sclerotized hinge appears to connect the 2 Gp VIII. Gp IX is well sclerotized, with distinct notum and rami in all chironomids. Gc IX is present and well developed in the basic design. In the Telmatogetoninae (Fig. 27, 28) it is strongly reduced, but bears a distinct Gs IX. In Tanypodinae (Fig. 17–24), Aphroteniinae (Fig. 25), and Podonominae (Fig. 26), Gc IX is fused with T IX to form a gonotergite IX, undoubtedly a synapomorphous feature. In the Tanypodinae, T IX is reduced to a narrow sclerotized strap without or with very few setae. In the Diamesinae, Prodiamesinae, Orthocladiinae, and *Lauterborniella* Bause (Fig. 73E) (Chironominae) there is a tendency for T IX to become partly or completely divided into 2 setigerous protrusions. Again the tendency, but not the actual division, is a synapomorphous feature for these families, i.e. as the division of Gp VIII. S IX is always reduced and membranous with a sclerotized coxosternapodeme and a membranous intergonocoxal connective. Segment X is not differentiated into tergites and sternites, but is continuous around the whole segment, except in the Podonomini where only S X appears to be present. It carries setae in most Podonominae, Tanypodinae, and Chironomini, and some Diamesini, but is void of setae in all Telmatogetoninae, Prodiamesinae, Orthocladiinae, Tanytarsini, and Pseudochironomini. The postgenital plate is usually small but distinct. Cerci are one-segmented.

There is one large, single accessary gland (Acc in Fig. 14, 15, 16) opening between the labia (Wensler and Rempel 1962 fig. 34; Sæther 1976b fig. 37). The membranous labia are bare or in some species, genera, or groups of genera, furnished with minute microtrichia or spinules. The labia are fused in the Podonominae, Telmatogetoninae, and the Corynoneura group only. The ovaries are about the same size as the large accessory gland. The ovaries are described by Miall and Hammond (1900 p. 111–115) and Abul-Nasr (1950) for *Chironomus dorsalis* Meig., and by Keuchenius (1917 p. 26–27, as *C. annularis* De Geer?) and Wensler and Rempel (1962 p. 214–216) for *C. plumosus* (L.). Some details of the early development of the genital organs are mentioned by Grimm (1871) and Hasper (1911) among others. The common oviduct is a wide flat tube joining the lateral oviducts to the vagina, whereas the lateral oviducts are very short, broad tubes joining the ovaries to the common oviduct (Fig. 11; Wensler and Rempel 1962 p. 213, fig. 34, 35, 38). In the Telmatogetoninae (Fig. 27, 28) there are no seminal capsules. The 2 spermathecal ducts are very broad and apparently function as seminal storage organs. In the remaining subfamilies there are 2 or 3 sclerotized seminal capsules. The spermathecal ducts are sometimes completely

separate with separate openings, sometimes joined for a longer or shorter distance, and sometimes have a common opening only. The spermathecal ducts are surrounded by special secretory cells shown in the transverse section of *Chironomus (Camptochironomus) tentans* Fabr. (SCC in Fig. 11).

Because of the rather derived character of the female genitalia in Diptera it is not possible to homologize any of the muscles found in the genitalia with those of the generalized insect used by Smith (1969). In the serial sections of *C. (C.) tentans,* the muscle terminology used by Wensler and Rempel (1962) is, therefore, followed. The compressor and dilator muscles of the common oviduct, as well as the dorsal and ventral muscles, are all recognizable in Fig. 11.

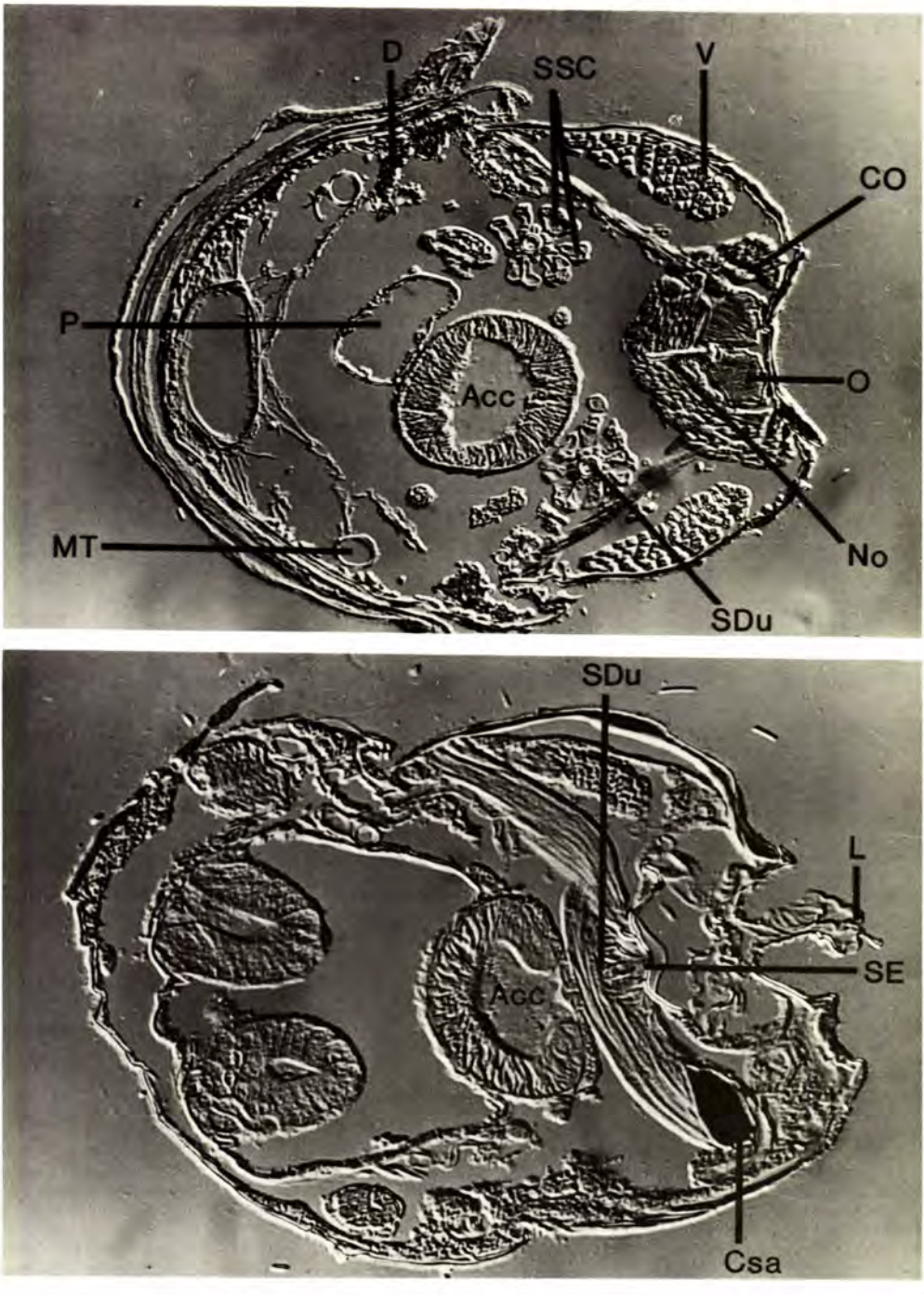

FIG. 11. Transverse section through notum posterior of seminal capsules of *Chironomus (Camptochironomus) tentans* Fabr. FIG. 12. Oblique section through seminal capsules, spermathecal eminence and labia of *C. (C.) tentans* Fabr.

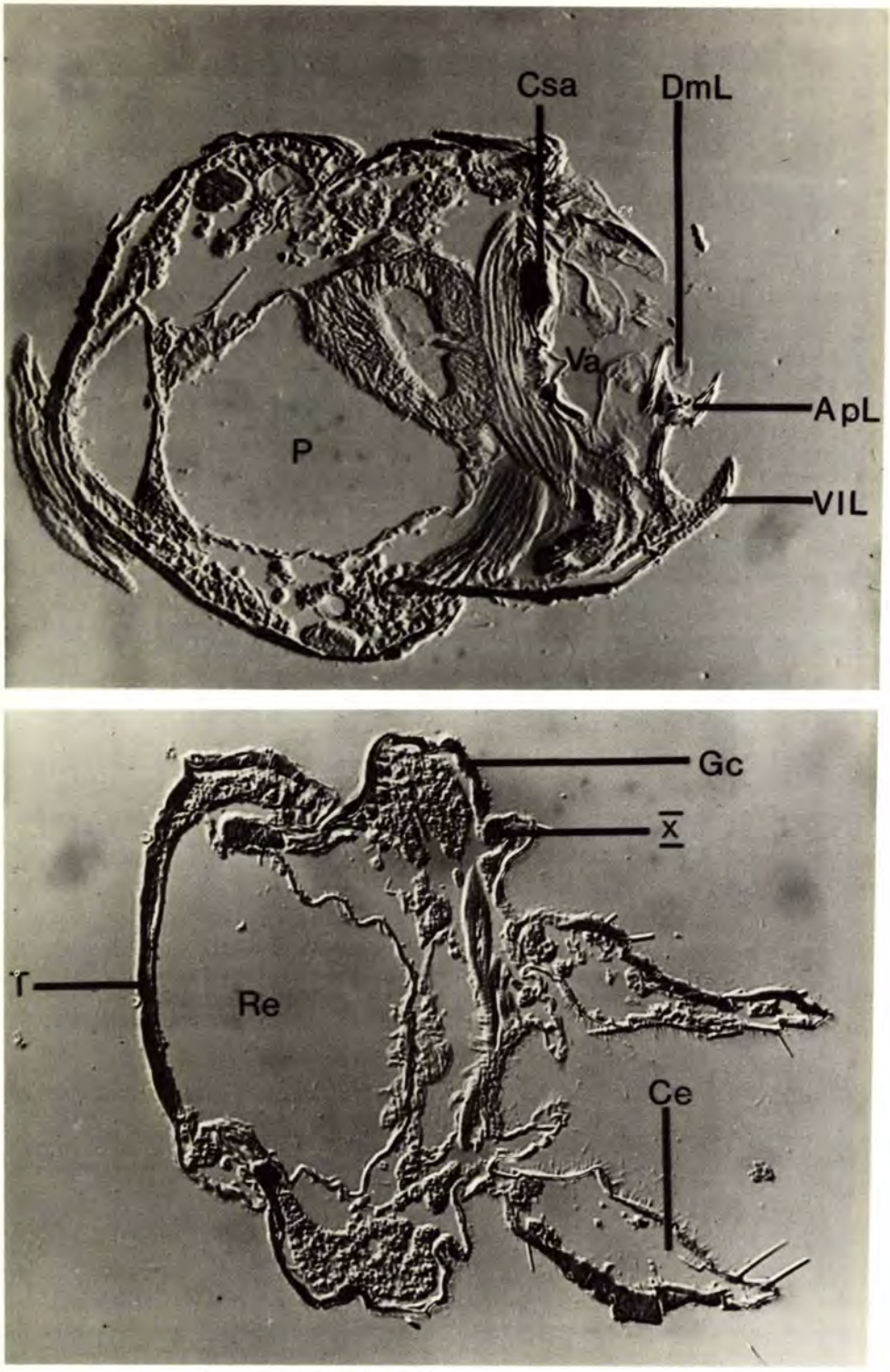

FIG. 13. Transverse section through lobes of Gp VIII of *C. (C.) tentans* Fabr. FIG. 14. Transverse section through Gc IX and cerci of *C. (C.) tentans* Fabr.

Phyletic Relationships within Chironomidae

The female genitalia of an archetype of the Chironomidae, a theoretical progenitor showing the assumed basic design, with features synapomorphous for the family and the most plesiomorphous characteristics, is illustrated in Fig. 15. This basic design is not realized within any of the recent chironomids although the Telmatogetoninae possesses several features, including a single lobelike Gp VIII and a Gs IX. Several characters, however, are more plesiomorphous within other subfamilies.

To recognize phylogenetic relationships (monophyletic groups) Hennig (1950, 1957, 1966) developed a theoretical synapomorphic diagram.

The criticism of Brundin (1966) by Schlee (1975) is justified only in part[1]. His main criticism is centered on Brundin's use of parallel trends as an indication of relationships. However, as stated by Tuomikoski (1967 p. 141): "Parallel apomorphies may sometimes be used as evidence of

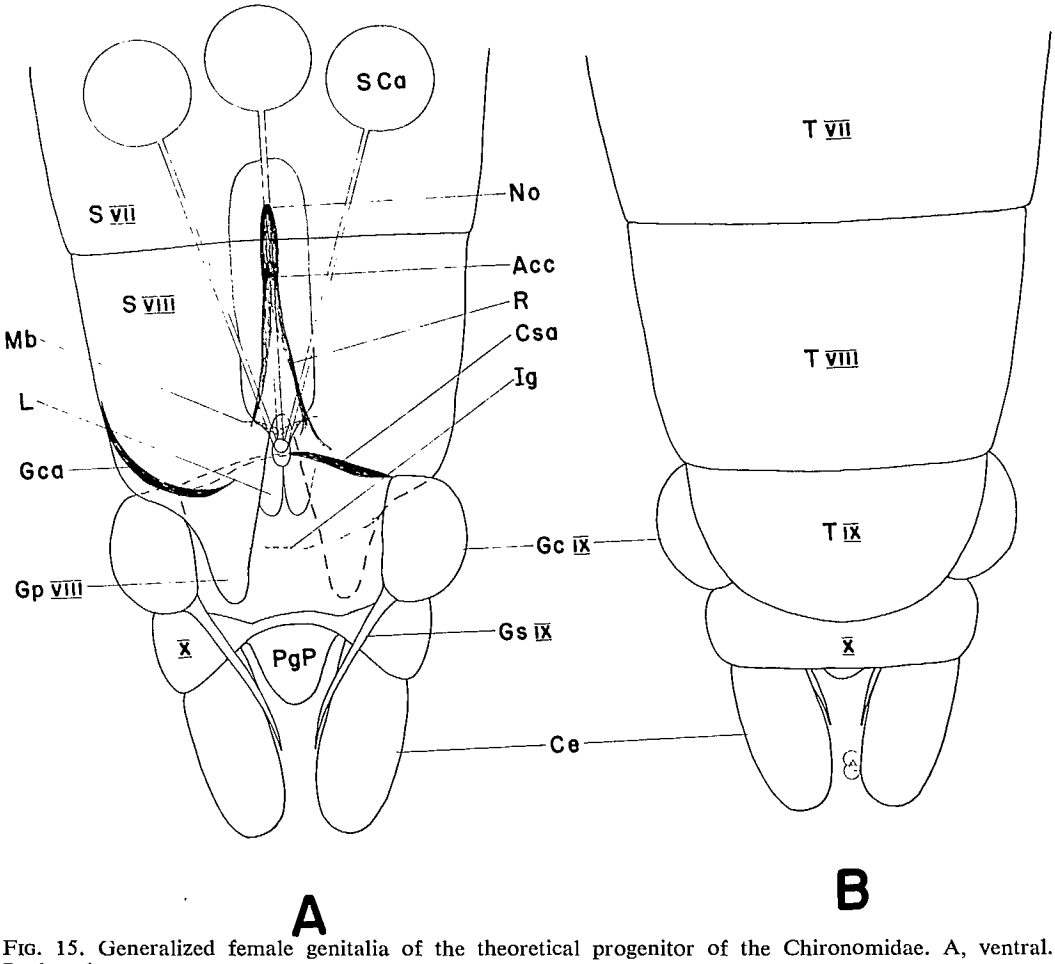

FIG. 15. Generalized female genitalia of the theoretical progenitor of the Chironomidae. A, ventral. B, dorsal.

[1]Brundin 1976 (A Neocomian chironomid and Podonominae — Aphroteniinae (Diptera) in the light of phylogenetics and biogeography. Zool. Scripta 5: 139–160) met Schlee's criticism on every point of pertinence and confirmed the conclusions reached by Brundin (1966) as well as the conclusions based on trends 9–14 in this publication.

monophyly and are then better comparable to synapomorphies than to convergent similarities. More precisely, in these cases the underlying synapomorphy is the agreement in capacity to develop parallel similarity." Crampton (1929 p. 484–485) also was aware of this: "... a modificational tendency ... may occur in some members of an 'ancestral' or more primitive group ... and again reappear in some members of a 'derived' or more specialized group ... despite the fact that all (or even most) of the members of both groups may not give any indication of such a tendency in their structural modifications, due to the fact that the tendency in question (or its genes) may be 'latent' in them and will manifest itself only upon the proper combination of genes, or what not, which will enable it to make itself 'patent.' In such cases, similar results produced by similar tendencies are not the result of 'convergent' development, but are the result of the operation of similar genes inherited from a common ancestry. The operation of such tendencies ... is very evident to one whose studies lead him to consider wide ranges of forms; but entomologists in general do not take kindly to this idea, and the time is apparently not ripe for its development."

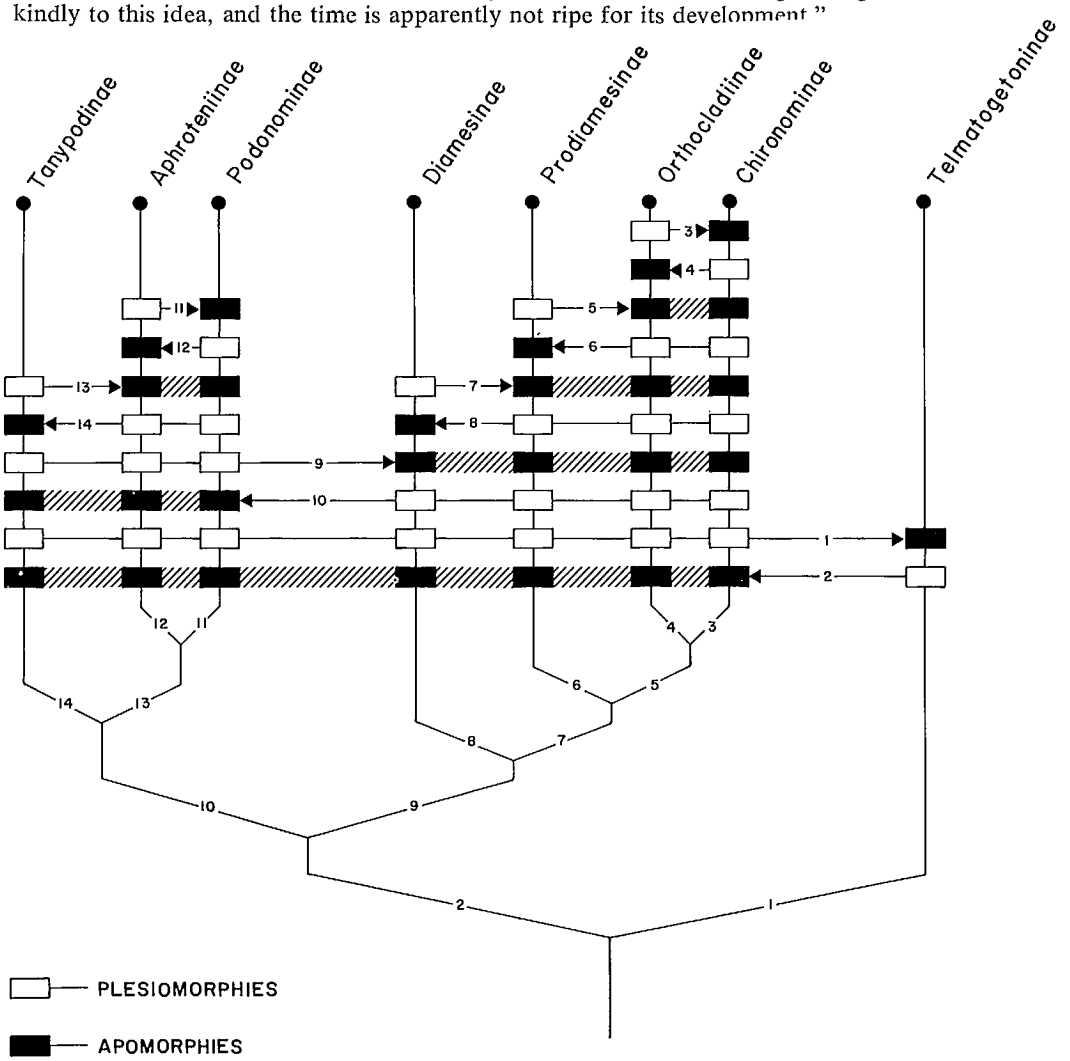

FIG. 16. Scheme of argumentation delineating the kladogenesis of the subfamilies of the Chironomidae by means of trends 1–14 (p. 31–32).

Hennig (see for instance Hennig 1966 p. 117–128) apparently partly agrees with the above, but does not recommend its usage. Schlee (1971 p. 23, 1975 p. 319) gives two minimum criteria for asserting that a character is synapomorphous: (a) It should be a principal (not gradual) deviation present within the whole group, but not found in the same formation in any taxon outside the group. (b) The homologous character alternative should be present not only in the sister group, but also uniformly in distant related groups, to show that this character alternative is plesiomorphous, thus implying that alternative (a) is derived. There are some cases of parallel development which fulfill all the above criteria of synapomorphies. (The only exception is they are not present within the whole group.) In the female genitalia, such parallelisms, and the underlying synapomorphy (the capacity or tendency to develop parallel similarity) are: the division of Gp VIII found in some Diamesinae, Orthocladiinae, Chironominae, and all Prodiamesinae, but not present in the other subfamilies or in any other family of the Diptera; the presence of an apodeme lobe in most Orthocladiinae, all Chironominae, a few Diamesinae, and all Prodiamesinae, but not in any other subfamily or in any other family; and the division of T IX into two setigerous protrusions again present in many Diamesinae, Prodiamesinae, and Orthocladiinae, and in *Lauterborniella* (Chironominae), but absent in other subfamilies and other dipterous families except for faint indications in the Chaoboridae. Such parallel apomorphies must indeed be more comparable to synapomorphies than to convergent similarities, but their usage should, if possible, be restricted to cases where the synapomorphy of the tendency to develop parallel similarity can be clearly demonstrated.

Delineation of the kladogenesis of chironomid subfamilies is attempted using a scheme of argumentation (Fig 16) and by the following trends (a = apomorphous, p = plesiomorphous):

Trends 1 — T VIII of female reduced (a), well developed (p).
— Gc IX of female reduced (a), well developed (p).
— Labia of female genitalia fused (a), separate (p).
— Seminal capsule reduced, spermathecal ducts serve as seminal storage organs (a); seminal capsules present and well developed (p).
— Tentorium long and cylindrical, cibarial pump heart-shaped (Sæther 1971b, fig. 3, 4) (a); tentorium and cibarial pump normal (p).

Trends 2 — Gp VIII relatively short, single, or divided (a); very large, elongate (p).
— Gs IX absent (a), present (p).

Trends 3 — Costa-extension absent, costa forms rounded angle with R_{4+5} (a); costa-extension distinguishable or, if secondarily absent, costa and R_{4+5} form acute angle (p).
— Claws of male single-pointed (a), with several apical teeth (p).
— Spurs modified into combs (a); spurs unmodified with combs absent or consisting of separate, stiff setae (p).
— Metatarsus of front leg longer than tibia (a), shorter (p).
— Gonostylus of male directed more or less rigidly backward (a), gonostylus folded inwards, joint with gonocoxite flexible (p).
— Anal macrosetae of pupa absent (a), present (p).
— Pupa with spurs on VIII (a), without (p).
— Setae underneath ventromental plates incorporated in plates and forming striations (a); ventromental plates with or without setae underneath, no striations (p).
(For a discussion of these trends see Sæther (1976b p. 10).)

Trend 4 — Volsellae reduced or absent (a), well developed (p) (see Sæther 1976b p. 12).

Trend 5 — MCu absent (a), present (p).

Trend 6 — Rami parallel-sided in free portion (a), converging (p).

Trends 7 — Fork of Cu below or distad of RM (a), proximad (p).
— Notum of female long (a), relatively short (p).
— Anal lobe of pupa with fringe of long setae (occasionally secondarily reduced) (a), without (p).

— Large ventromental plates present in larva (often secondarily reduced in Orthocladiinae) (a), ventrementum not or barely extending lateral of mentum (p).
— Ventromental plates either with setae underneath (on cardo) or setae incorporated in plates as striation (a), without setae underneath (p).
(For a discussion of trends 7 see Sæther (1976b p. 10).)

Trend 8 — Larval prementum with dense hair brushes divided into 3 groups (occasionally secondarily reduced or altered) (a), without hair brushes (p).

Although Brundin (1966 p. 368) regarded this trend as an evident synapomorphy for the Diamesinae, the trend could possibly go in the opposite direction. Sæther (1976b p. 12) used this trend to try to show the monophyly of the Diamesinae plus Telmatogetoninae as suggested by Brundin (1966 p. 370–373). In the Telmatogetoninae, however, there is just one undivided dense hair brush.

Trends 9 — Gp VIII shows capacity for division into 2 principal lobes (a), never shows such a capacity (p).
— Capacity for development of an apodeme lobe present (a), apodeme lobe never present (p). (For a discussion of these trends see above.)
— T IX shows capacity for division into 2 setigerous protrusions (a), does not show this capacity (p).
— Male with 11–13 or occasionally fewer flagellomeres (a), with 14 or 15 flagellomeres (p).
— Pupal thoracic horn without porous plate (a), with (p).
— Procerci of larva less than 2.5 times as long as wide (a), more than 2.5 times as long as wide (p).

Trends 10 — Gc IX of female reduced and fused with T IX to form a gonotergite IX (a), Gc IX not reduced or if reduced not fused with T IX (p).
— Larval premandibles absent or strongly reduced (a), present and well developed (occasionally secondarily reduced) (p).

Brundin (1966 p. 424) mentioned that in the males of the Tanypodinae, Podonominae, and Aphroteniinae, T IX also forms a simple annulus. Schlee (1975 p. 322, 336) who criticized the use of this character as a synapomorphy, stated that the same fusion occurs in other subfamilies. This may be correct; however, the fusion is at least less pronounced in other subfamilies and, together with the clear-cut presence of a gonotergite IX in the females, the character is not without significance. In the same way the importance of the reduction of the premandible and of the free-living habit of the pupae is dismissed too easily by Schlee (1975 p. 336).

Trends 11 — Labia of female genitalia fused (a), separate (p).
— Body of larvae without sclerotized plates bearing setae (a), with (p).

Trends 12 — Segment X of female reduced (a), well developed (p).
— Common opening of spermathecal duct conspicuously wide (a); openings separate or if common, opening narrow (p).
— Crossvein MCu absent (a), present (p).

Trends 13 — Gca VIII absent (a), indicated (p).
— R_{2+3} absent (a), present (p) (see, however, Schlee 1975 p. 321, 336–337).

Trends 14 — Gonotergite IX reduced to a narrow strip without or with very few setae (a); well developed, hood-shaped, with numerous setae (p).
— Glossae of larva fused, forming a large, sclerotized ligula which is more conspicuous than the mentum (a); glossae small, inconspicuous, not forming a large, sclerotized ligula (p) (see also Fittkau 1962 p. 58; Schlee 1975 p. 337–339).

Sæther (1976b p. 13) regarded the Telmatogetoninae as the sister group of the Diamesinae in accordance with Brundin (1966 p. 370–373). This assumption was based on only one possibly synapomorphous trend, the presence of dense hair brushes on the larval prementum, together with the series of possible parallel trends mentioned by Brundin. Further studies on the female

genitalia of the Chironomidae and other families has, however, clearly shown the uniqueness of the female genitalia in Telmatogetoninae, compared to the other subfamilies. In fact, if the females are regarded separately, there is ample justification to give the subfamily full family rank. The following monophyletic groups appear well established: Telmatogetoninae; all subfamilies minus Telmatogetoninae; Chironominae; Chironominae + Orthocladiinae + Prodiamesinae; Chironominae + Orthocladiinae + Prodiamesinae + Diamesinae; Tanypodinae; Podonominae; and Tanypodinae + Aphroteniinae + Podonominae. The remaining monophyletic unities are still not well established. The subfamily placement of the genus *Buchonomyia* Fittk. (Fittkau 1955) is uncertain. It does, however, belong to the monophyletic unit Chironominae + Orthocladiinae + Prodiamesinae + Diamesinae. Although some alternatives to the synapomorphic diagram outlined here exist, it at least appears to fit the present knowledge better than any of the alternatives.

Key to females of subfamilies and tribes of Chironomidae

1 Seminal capsules absent, spermathecal duct swollen, serves as seminal receptacle; T VIII reduced; T IX well developed with posterior lobes; gonostyli present, and together with posterior lobes of T IX, the elongated cerci, and the large Gp VIII form an ovipositor ..... Subfamily Telmatogetoninae (p. 59)

2 or 3 seminal capsules; T VIII not reduced; T IX reduced to well developed; gonostylus absent, no ovipositor 2

2 Gc IX reduced and fused with T IX to form a gonotergite IX which is either reduced and straplike or large, hood-shaped, and undivided; Gp VIII simple; crossvein MCu usually present (except Aphroteniinae) 3

Gc IX small to well developed, not completely fused with T IX, when apparently partly fused crossvein MCu absent; T IX often more or less completely divided into 2 setigerous protrusions; Gp VIII simple or more commonly divided into 2 or 3 lobes of which the larger one may cover the others; crossvein MCu present or absent 10

3 Gonotergite IX well developed, hood-shaped, with numerous setae, occasionally with posterior lobes; 2 or 3 seminal capsules; segment X usually without setae; vein R_{2+3} absent 8

Gonotergite IX reduced, straplike, usually without setae, at most with 2–10 setae; nearly always 3 seminal capsules; segment X nearly always with setae; vein R_{2+3} present ..... Subfamily Tanypodinae (p. 44) 4

4 Seminal capsule blackish, oval, with a distinct collar at spermathecal duct; tibial spurs spinelike with scattered spinules along and around shaft; wing membrane with apical setae only ..... Tribe Anatopyniini (p. 45)

Seminal capsule light to black, shape variable, never with a distinct collar; tibial spurs with a distinct lateral row of teeth; wing membrane without setae, with scattered setae, or apical setae only 5

5 Rudiments of Gc IX often indicated as caudolateral projections of gonotergite IX in dorsal view; ta_1 cylindrical; fork of Cu either petiolate with petiole at least 0.5 times as long as Cu_1 (subtribe Procladiina), or sessile with costa produced about twice the length of RM beyond R_{4+5} (subtribe Macropelopiina); seminal capsule fully or partly blackish, ovoid to bell-shaped[2] ..... Tribe Macropelopiini (p. 45)

[2] Seminal capsule ovoid to bell-shaped with widest end at mouth of spermathecal duct in Procladiina; oblong, ovoid, oval, or spherical, with widest portion almost never at mouth of spermathecal duct in Macropelopiina.

Gonotergite IX in dorsal view without any caudolateral projections; ta_4 chordate or cylindrical; fork of Cu either petiolate with petiole less than 0.3 times as long as Cu_1 or sessile with costa not produced or at most produced the length of RM beyond R_{4+5}; seminal capsule pale to dark 6

6 Fork of Cu petiolate; gonotergite IX without or with more than 2 setae 7

Fork of Cu sessile; gonotergite IX without or occasionally with 1 or 2 setae ..... Tribe Pentaneurini (p. 48)

7 Gp VIII triangular; segment X with setae; ta_4 chordate; wing membrane without setae ..... Tribe Coelotanypodini (p. 44)

Gp VIII tongue-shaped; segment X without setae; ta_4 cylindrical; wing membrane with setae at least at apex ..... Tribe Tanypodini (p. 45)

8 Crossvein MCu absent; segment X more or less reduced ..... Subfamily Aphroteniinae (p. 54)

Crossvein MCu present; segment X well developed ..... Subfamily Podonominae (p. 56) 9

9 Three seminal capsules except in *Boreochlus thienemanni* Edw.; only S X but not T X present, with or without setae; 13–15 flagellomeres, when only 13 (as in *Boreochlus)* apical portion of ultimate flagellomere forms an angle with basal portion ..... Tribe Boreochlini (p. 57)

Two seminal capsules except in *Podochlus* Brund. and *Parochlus chiloensis* group; segment X visible in dorsal view, probably always with setae; 7–13 flagellomeres, apical portion of ultimate flagellomere not bent ..... Tribe Podonomini (p. 56)

10 Three seminal capsules, or if only 2 (as in *Diamesa* Waltl), MCu present and T IX divided into 2 setigerous protrusions 11

Two seminal capsules or if 3 (as in *Diplocladius* Kieff. and *Brillia* Kieff. in part), MCu absent and T IX undivided 17

11 MCu absent ..... Subfamily Diamesinae in part, Tribe Harrisonini (p. 64)

MCu present 12

12 Gp VIII clearly divided into dorsomesal and ventrolateral lobes with ventrolateral lobe pencillike and about same size as dorsomesal lobe; segment X without setae; rami parallel-sided; T IX not distinctly divided into setigerous protrusions; FCu below or distad to RM; ta_4 not cordiform ..... Subfamily Prodiamesinae (p. 73)

Gp VIII simple or when divided ventrolateral lobe more or less rounded and much broader than dorsomesal lobe; segment X with or without setae; rami not parallel-sided; T IX undivided or strongly divided; FCu proximal to RM or when below RM, ta_4 cordiform ..... Subfamily Diamesinae (except Harrisonini) (p. 60) 13

13 T IX distinctly divided into 2 setigerous protrusions; Gp VIII divided with the dorsomesal lobe small and often covered by ventrolateral lobe; 2 or 3 seminal capsules; segment X with or without setae ..... Tribe Diamesini (p. 64)

T IX undivided or when faintly divided Gp VIII simple; always 3 seminal capsules; segment X at most with 1 seta 14

14 Notum much shorter than free part of rami; T IX with few setae and 2 caudolateral triangular projections; Gp VIII simple, elongated; labia large with marginal microtrichia; segment X without setae ..... Tribe Boreoheptagyini (p. 64)

Notum longer than free part of rami; T IX with more numerous setae and without caudolateral projections; Gp VIII simple or divided, not elongated; labia much smaller; segment X at most with 1 seta 15

15 T IX large, clearly less than twice as wide as long; Gp VIII divided, but divisions not obvious on specimens with closed vagina; segment X with conspicuous, curved, orally directed, ventral extensions ..... Tribe Protanypodini (p. 73)

T IX smaller, more than twice as wide as long; Gp VIII divided or undivided, vagina not closable; segment X without curved, orally directed, ventral extensions 16

16 Gp VIII a broad single lobe; T IX faintly divided into 2 setigerous protrusions; labia without microtrichia; segment X without setae ..... Tribe Lobodiamesini (p. 64)

Gp VIII divided into a large ventrolateral and a smaller dorsomesal lobe; T IX undivided, but setae may be concentrated on each side; labia nearly always with distinct microtrichia; segment X without or with 1 seta ..... Tribe Heptagyini (p. 63)

17 T IX small to large, usually more or less divided into 2 setigerous protrusions, when undivided T IX either shorter than 1.5 times as long as Gc IX, large and triangular, or with setae reduced in number and concentrated along posterior margin, or with 3 seminal capsules; segment X always without setae; tibial spurs not comblike ..... Subfamily Orthocladiinae (p. 76)

T IX large, nearly always more than 1.5 times as long as Gc IX, hood-shaped, undivided, or when faintly divided segment X with setae; setae of T IX evenly distributed at least on posterior half; segment X with or without setae; tibial spurs comblike ..... Subfamily Chironominae (p. 130) 18

18 S VIII forms a small to relatively large floor under oral part of vagina; segment X without setae; squama without setae; wing membrane usually at least with apical setae ..... Tribe Tanytarsini (p. 138)

S VIII does not form a floor under oral part of vagina (except in *Manoa* Fittk. of the Pseudochironomini); segment X with or without setae; squama usually with setae; when without, wing membrane without setae 19

19 Apex of front tibia with a spur with lateral denticles forming a comb; Gp VIII undivided or with vestigial and far lateral ventrolateral lobe; segment X without setae ..... Tribe Pseudochironomini n.tr. (p. 154)

Apex of front tibia with a scale, with or without a spine, never with comblike spur; Gp VIII simple or usually divided into 2 distinct lobes; segment X nearly always with setae ..... Tribe Chironomini (p. 156)

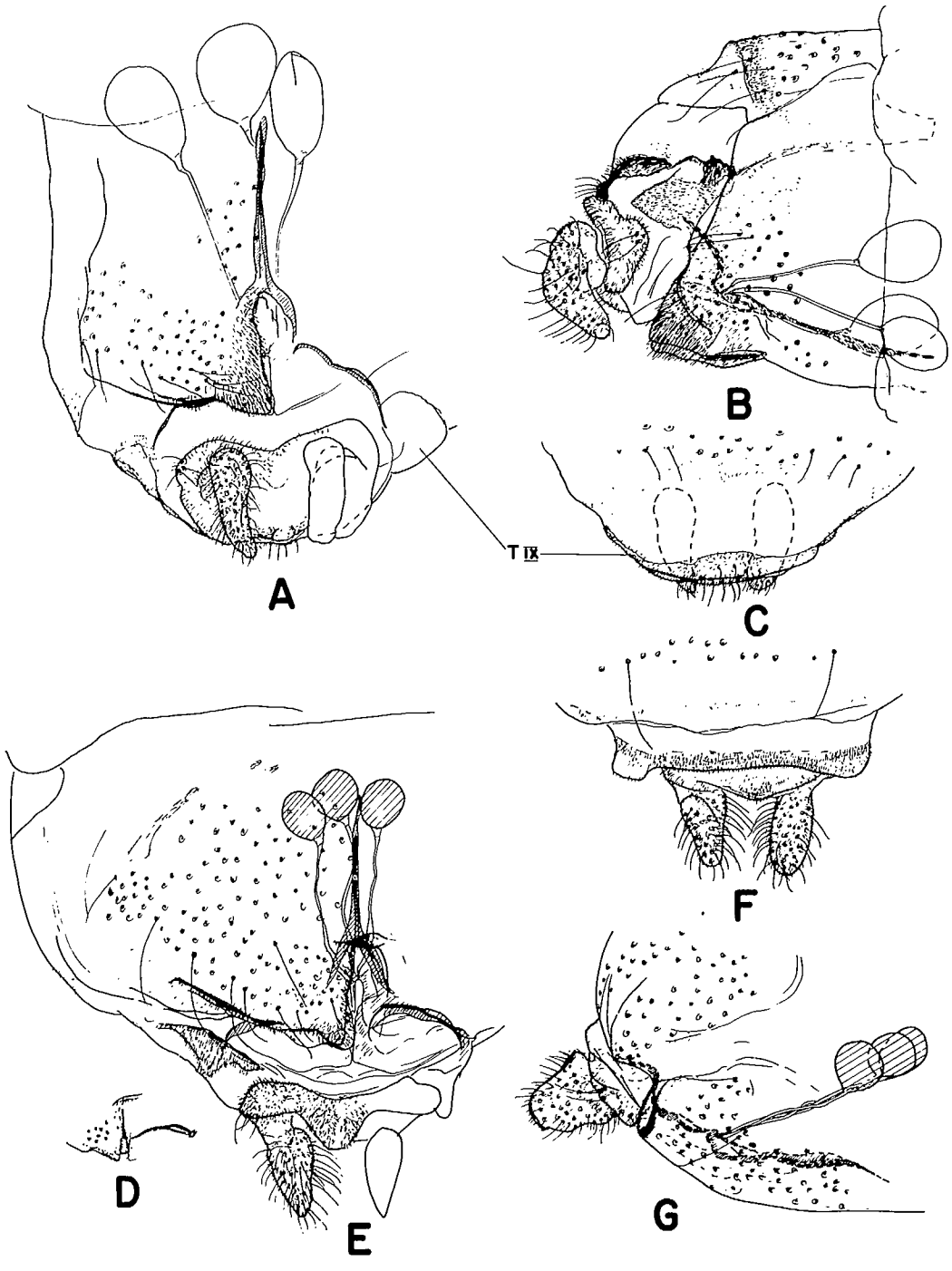

FIG. 17. Female genitalia of Tanypodinae. A–C, *Clinotanypus (Clinotanypus) pinguis* (Loew): A) ventral; B) lateral; C) dorsal. D, *Psectrotanypus (Psectrotanypus) eumorpha* (Subl.), detail of Gp VIII and coxosternapodeme. E–G, *Psectrotanypus (P.) dyari* (Coq.): E) ventral; F) dorsal; G) lateral.

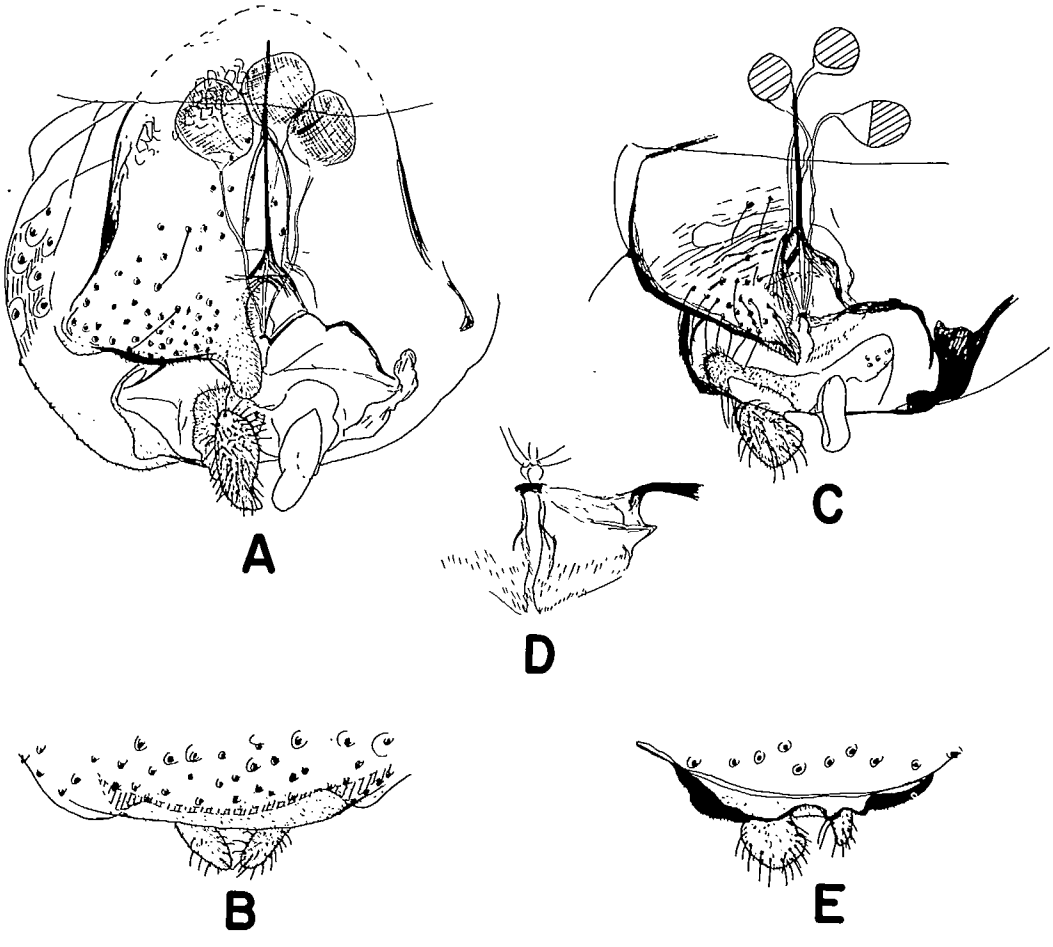

FIG. 18. Female genitalia of Tanypodinae. A–B, *Tanypus (Tanypus) stellatus* (Coq.): A) ventral; B) dorsal. C–E, *Coelotanypus scapularis* (Loew): C) ventral; D) labia; E) dorsal.

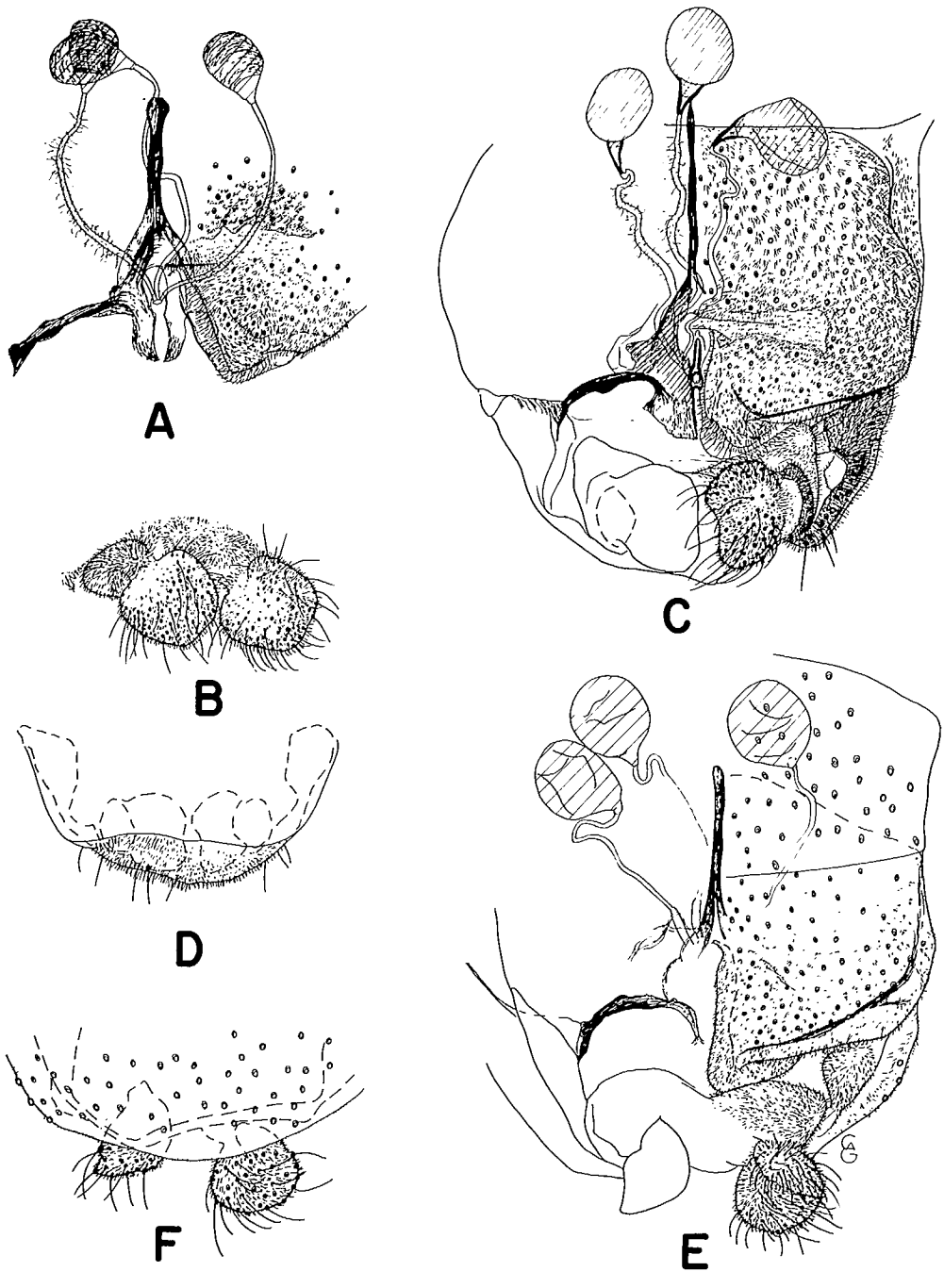

FIG. 19. Female genitalia of Tanypodinae. A–B, *Derotanypus aclines* (Subl.): A) Gp VIII, Gp IX, coxosternapodeme, and spermatheca; B) cerci, dorsolateral. C–D, *Alotanypus venustus* (Coq.): C) ventral; D) dorsal. E–F, *Natarsia baltimoreus* (Macq.): E) ventral; F) dorsal.

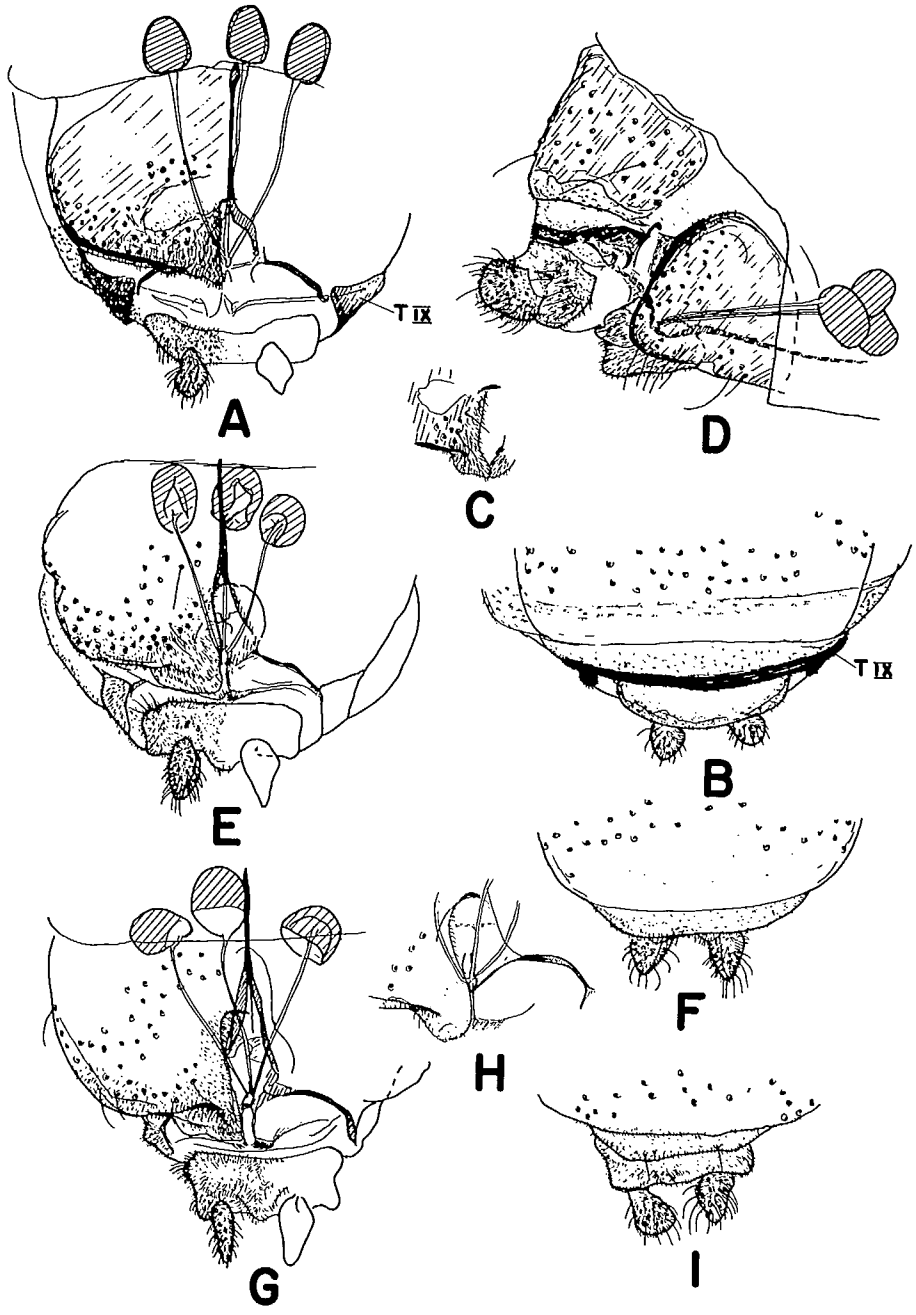

FIG. 20. Female genitalia of Tanypodinae. A–B, *Procladius (Procladius) denticulatus* Subl.: A) ventral; B) dorsal. C, *Procladius (Psilotanypus) bellus* (Loew), Gp VIII. D, *Procladius (Procladius) culiciformis* (L.), lateral. E–F, *Thienemannimyia* sp.: E) ventral; F) dorsal. G, I, *Conchapelopia (Conchapelopia) goniodes* (Subl.) var. *trifida* Rob.: G) ventral; I) dorsal. H, *Conchapelopia (Conchapelopia) rurika* (Rob.), Gp VIII, labia, and coxosternapodeme.

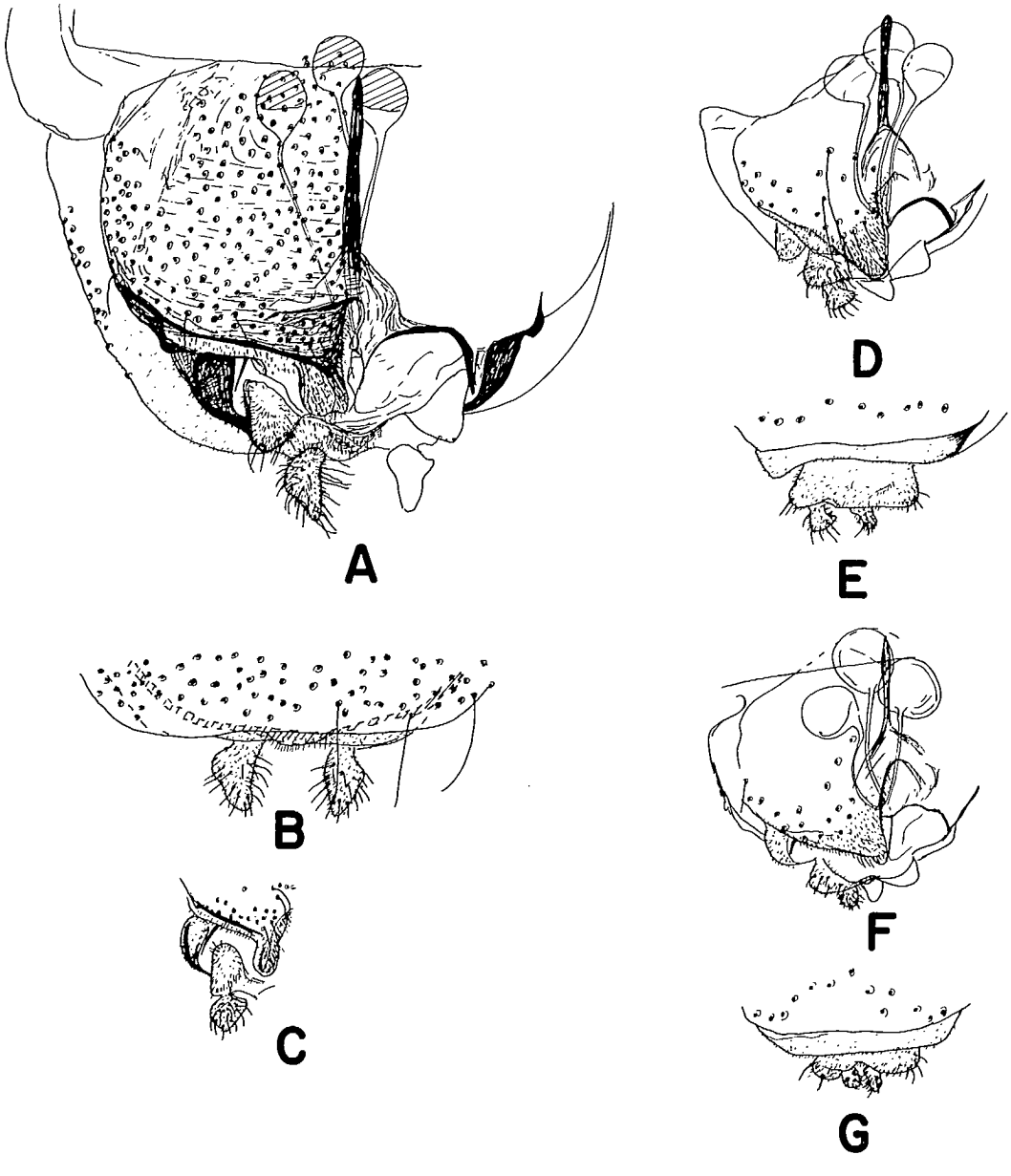

FIG. 21. Female genitalia of Pentaneurini, Tanypodinae. A–B, *Ablabesmyia (Ablabesmyia) annulata* (Say); A) ventral; B) dorsal. C, *Ablabesmyia (Ablabesmyia) basalis* (Wall.), ventral. D–E, *Monopelopia* sp.: D) ventral; E) dorsal. F–G, *Paramerina anomala* Beck et Beck: F) ventral; G) dorsal.

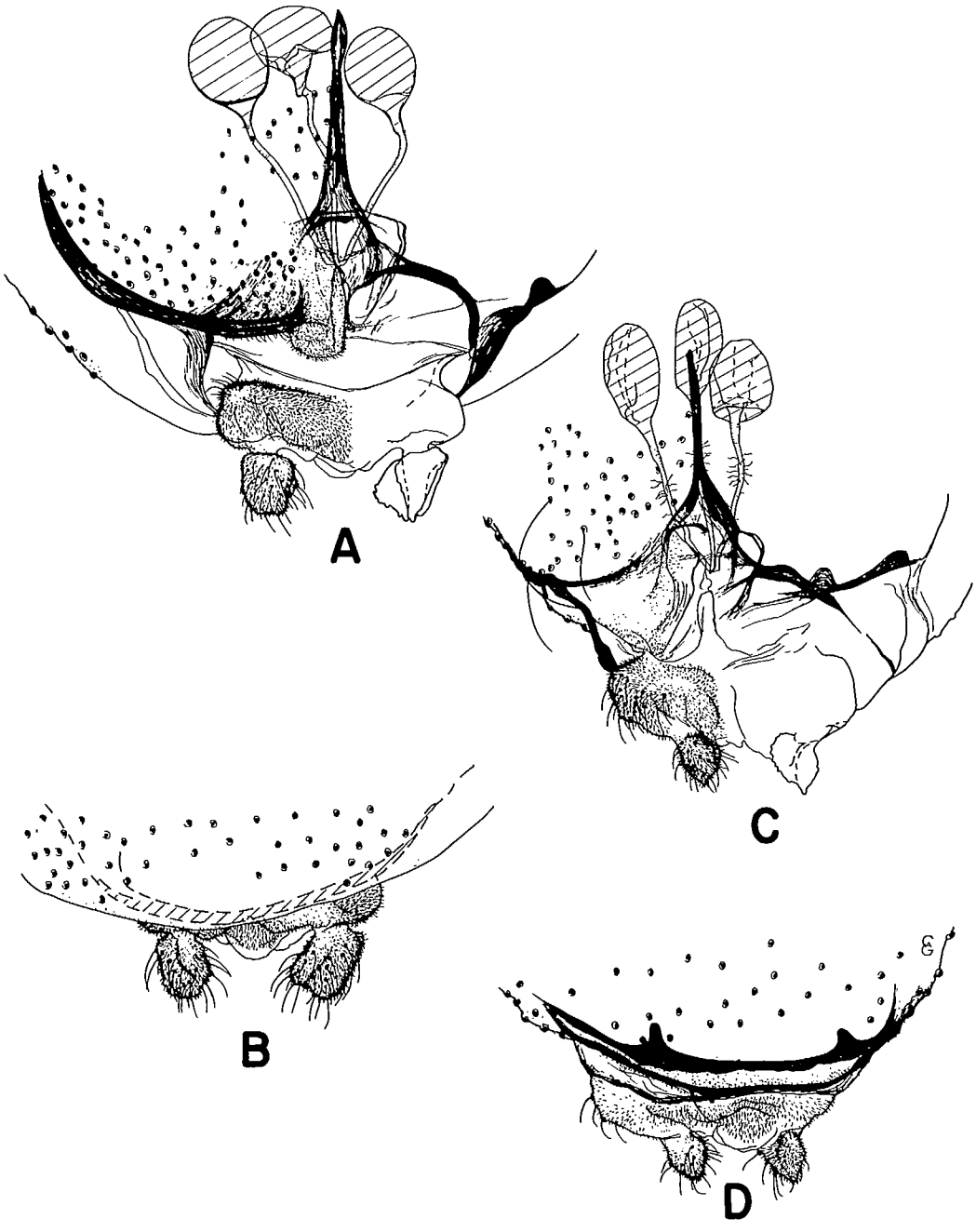

FIG. 22. Female genitalia of Pentaneurini. A–B, *Arctopelopia (Arctopelopia) griseipennis* (v.d. Wulp): A) ventral; B) dorsal. C–D, *Trissopelopia longimana* (Staeg.): C) ventral; D) dorsal.

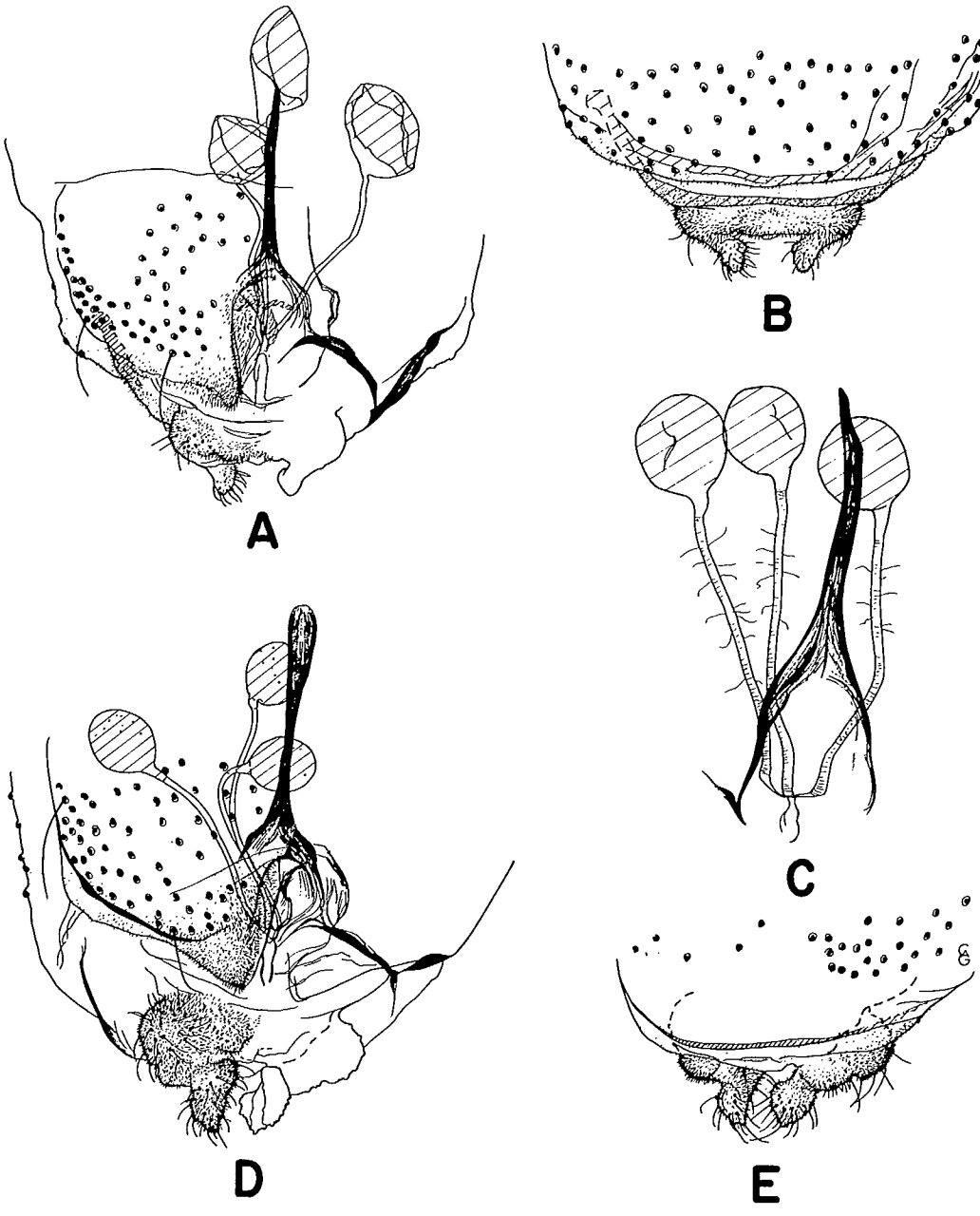

FIG. 23. Female genitalia of Pentaneurini. A–B, *Zavrelimyia signatipennis* (Kieff.): A) ventral; B) dorsal. C, *Zavrelimyia* sp., Gp. IX, and spermatheca. D–E, *Xenopelopia falcigera* (Kieff.): D) ventral; E) dorsal.

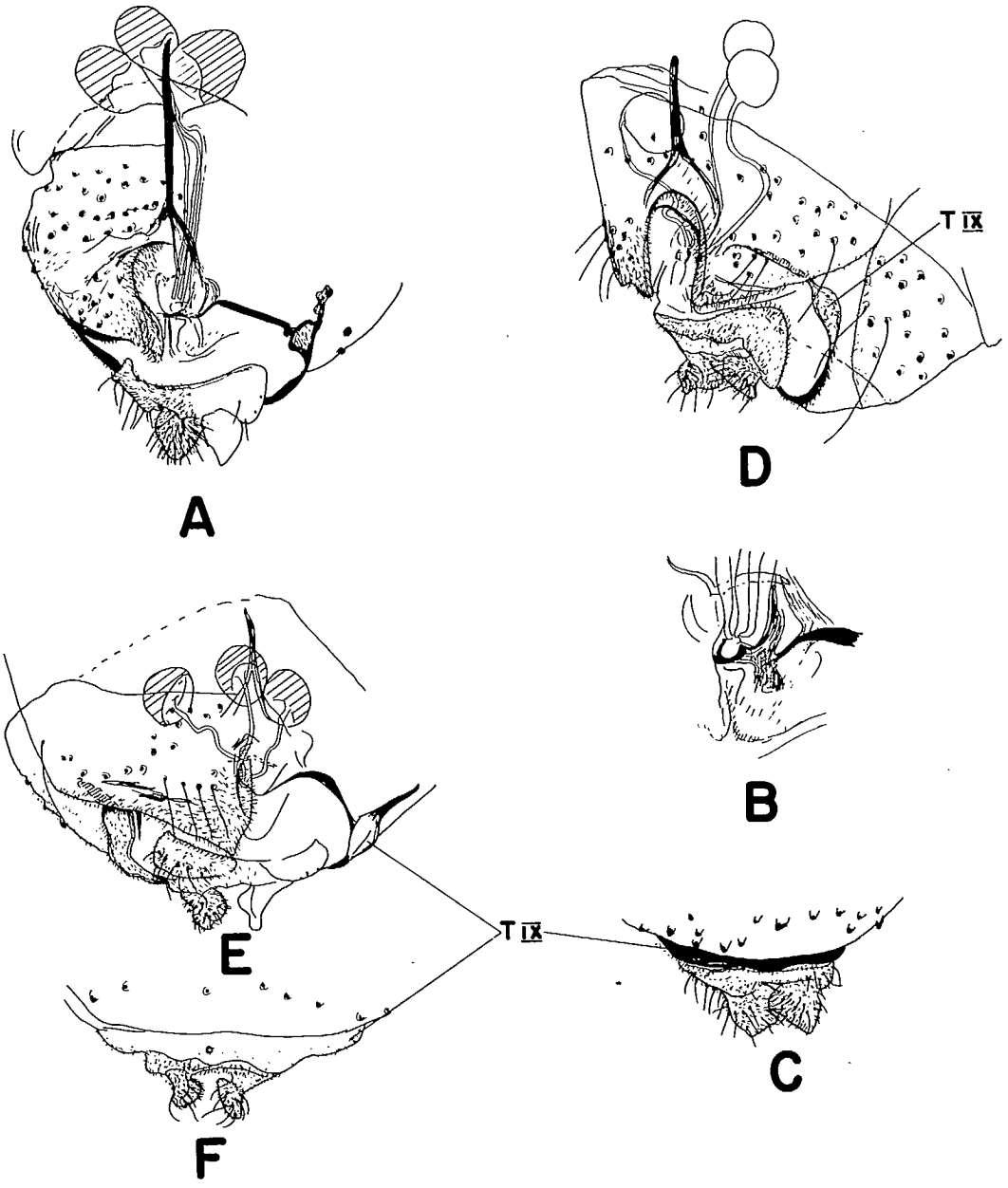

FIG. 24. Female genitalia of Pentaneurini. A–C, *Guttipelopia currani* Beck et Beck: A) ventral; B) labia and spermathecal eminence; C) dorsal. D, *Larsia* sp., ventrolateral. E–F, *Pentaneura inconspicua* (Mall.): E) ventral; F) dorsal.

SUBFAMILY TANYPODINAE
(Fig. 17–24)

T VIII normal. Gca VIII mostly weak. Gp VIII simple (Rodova (1974a fig. 33), however, indicates a minute secondary ventrolateral lobe in *Ablabesmyia phatta* Egg.), usually triangular, sometimes tongue-shaped with parallel margins, occasionally weak and somewhat semicircular; membrane weak, but present. Gp IX usually well developed; notum long, usually longer than free part of ramus, occasionally both rami and notum reduced as in *Pentaneura* Phil. (Fig. 24E). T IX narrow, straplike, completely fused with Gc IX to form a gonotergite IX. Rudiments of Gc IX mostly small, sometimes large, and occasionally visible in dorsal view as caudolateral protrusions of gonotergite IX. Gonotergite IX nearly always without setae (except in *Clinotanypus* Kieff. (Fig. 17A), *Alotanypus* Rob. (Fig. 19D), possibly *Derotanypus* Rob. (Fig. 19B), and *Conchapelopia* Fittk. (Fig. 20I)). Intergonocoxal connective present. Coxosternapodeme simple, straight to curved. Segment X with setae except in *Larsia* Fittk. (Fig. 24D), strongly constricted on both sides of postgenital plate to not constricted. Postgenital plate reduced to large. Cerci small to medium in size, rounded to pediform.

Labia separate, relatively well developed, sometimes with microtrichia. 3 seminal capsules, except *Telmatopelopia* Fittk. with 2 only (Rodova 1971b fig. 8). Spermathecal ducts completely or nearly straight, open separately on spermathecal eminence.

As in the Aphroteniinae and Podonominae, Gc IX is fused with T IX to form a gonotergite IX, a synapomorphous feature for these subfamilies. However, in contradiction to the other two subfamilies, T IX in the Tanypodinae is strongly reduced and consists only of a straplike band nearly always void of setae. Other characteristics are the general plesiomorphous-type. A closer examination of *Djalmabatista* Fittk. from the Amazon area (Fittkau 1968b) may yield additional information on the relationships between the Tanypodinae, Aphroteniinae, and Podonominae. According to Fittkau (1968b fig. 27) gonotergite IX in that genus is relatively long.

TRIBE COELOTANYPODINI
(Fig. 17A–C, 18C–E)

Gonotergite IX with rudiments of Gc IX large, much wider than the narrow rudiments of T IX, without or with a few setae. Gp VIII triangular. Gp IX well developed.

Labia with or without microtrichia.

Key to females of Coelotanypodini

1 Vein R_2 short and distinctly connected to R_3; 13 flagellomeres; antepronotum large ..... *Coelopynia* Freem. (Australia)

Vein R_2 not connected to R_3; 12 flagellomeres or when 13, antepronotum nearly always reduced 2

2 Gonotergite IX with a few setae; Gp VIII triangular with caudomesal angle of about 60°; labia without apical microtrichia; seminal capsules pale and longer than half the length of notum ..... *Clinotanypus* Kieff. (p. 45)

Gonotergite IX without setae; Gp VIII triangular with caudomesal angle of about 45°; labia with apical microtrichia; seminal capsules darker in apical half and shorter than ½ the length of notum ..... *Coelotanypus* Kieff. (p. 45)

Clinotanypus Kieff.
(Fig. 17A–C; Roback 1971a fig. 2)

Species examined: *C.* (*C.*) *pinguis* (Loew)

Gp VIII triangular with caudomesal angle of about 60°. Rudiments of Gc IX large, triangular in lateral view (Fig. 17B), relatively light colored. Gonotergite IX with a few median setae. Coxosternapodeme weak and nearly straight. Cerci relatively large, about as large as the large seminal capsules.

Labia without apical, but perhaps with a few weak basal microtrichia. Seminal capsules pale, longer than ½ the length of notum.

Coelotanypus Kieff.
(Fig. 18C–E; Roback 1971a fig. 31, 54)

Species examined: *C. scapularis* (Loew)

Gp VIII triangular with caudomesal angle of about 45°. Rudiments of Gc IX relatively large and blackish sclerotized. Gonotergite IX void of setae. Coxosternapodeme strongly curved. Cerci small, about as large as the small seminal capsules.

Labia with apical microtrichia. Seminal capsules dark in anterior half, smaller than ⅓ the length of notum.

TRIBE TANYPODINI
(Fig. 18A, B)

Tanypus Meig.
(Fig. 18A, B; Roback 1971a fig. 68, 102)

Species examined: *T.* (*T.*) *stellatus* Coq.

Gp VIII tongue-shaped with parallel sides. Gonotergite IX without setae. Coxosternapodeme weak. Segment X without setae.

Seminal capsules relatively light, reticulated by 2 sets of lines perpendicular to each other.

TRIBE ANATOPYNIINI

Anatopynia Joh.

Seminal capsule (Fittkau 1962 fig. 9) blackish, oval, with distinct collar.

TRIBE MACROPELOPIINI
(Fig. 17D–G, 19, 20A–D)

Gp VIII usually triangular with caudomesal angle of 60–90°. Gonotergite IX with or without setae, rudiments of Gc IX often indicated in dorsal view as caudolateral projections. Coxosternapodeme nearly straight. Segment X with setae. Cerci small to large.

Seminal capsules fully or partly dark sclerotized, oblong, spherical, or oval to bell-shaped, usually relatively small.

Preliminary key to females of Macropelopiini

1 Most gonotergite IX blackish sclerotized, without setae, rudiments of Gc IX in dorsal view very small; cerci as small as seminal capsules or smaller; seminal capsules blackish, bell-shaped to ovoid, with widest portion near mouth ..... *Procladius* Skuse (p. 47)

Gonotergite IX not blackish, with or without setae, rudiments of Gc IX in dorsal view larger or not apparent; cerci about as large as, to larger than, seminal capsules; seminal capsules partly or fully black or brown, oval, ovoid, or oblong, but widest portion almost never near mouth (except *Macropelopia* Thien. in part) 2

2 Gonotergite IX with about 6–8 relatively strong setae; neck of seminal capsule placed slightly asymmetrically on capsule, capsule including neck nearly as large as cerci ..... *Alotanypus* Rob. (p. 47)

Gonotergite IX with at most 2–4 setae; neck of seminal capsule not placed asymmetrically or when placed asymmetrically capsules clearly smaller than cerci 3

3 Gonotergite IX occasionally with 1–4 setae; seminal capsule ovoid to oval, anterior portion brown, and the wide funnel-shaped neck light and slightly rugulose ..... *Derotanypus* Rob. (p. 47)

Gonotergite IX probably always without setae; seminal capsule spherical, ovoid, oval, or oblong, always fully brownish or blackish 4

4 Seminal capsules oblong, widest portion just above the funnel-shaped neck (Fittkau 1962 fig. 30) ..... *Macropelopia* Thien. in part

Seminal capsules spherical to ovoid, widest medially 5

5 Rudiments of Gc IX visible in dorsal view as relatively large caudolateral portions of gonotergite IX ..... *Psectrotanypus* Kieff. (p. 47)

Rudiments of Gc IX not apparent in dorsal view ..... *Natarsia* Fittk. (p. 47)

(*Macropelopia* not keying to couplet 5 will key out either together with *Psectrotanypus* or with *Natarsia* (Fittkau 1962 fig. 31; Tokunaga 1937 fig. 46, 47, 49, 50; Roback 1971a fig. 130))

Derotanypus Rob.
(Fig. 19A, B; Roback 1971a fig. 146, 159)

Species examined: *D.* (*D.*) *aclines* (Subl.)

Gp VIII triangular with caudomesal angle of nearly 90°. Gonotergite IX apparently with 2 setae (examined specimen damaged), rudiments of Gc IX probably not visible in dorsal view. Coxosternapodeme straight (Fig. 19A) or slightly curved (Roback 1971a fig. 146, 159). Segment X with only one pair of setae. Postgenital plate apparently small.

Labia without microtrichia, but with longitudinal reticulation. Seminal capsules (Fig. 19A; Roback 1971a fig. 146, 159) rugulose, ovoid to oval, with anterior portion brown and the wide, funnel-shaped neck light; capsules about ½ as long as notum and about ⅔ as long as cerci.

Alotanypus Rob.
(Fig. 19C, D; Roback 1971a fig. 173)

Species examined: *A. venustus* (Coq.)

Gp VIII rounded at caudomesal angle. Gonotergite IX with about 6–8 relatively strong setae, rudiments of Gc IX not apparent as caudolateral projections in dorsal view. Coxosternapodeme very slightly curved. Segment X with several setae. Postgenital plate reduced.

Labia apparently with microtrichia and possibly with longitudinal lines. Seminal capsules (Fig. 19C; Roback 1971a fig. 173) with neck placed asymmetrically on capsule, capsule more than ½ as long as notum, and nearly as long as cerci.

Psectrotanypus Kieff.
(Fig. 17D–G; Sæther 1974 fig. 3)

Species examined: *P.* (*P.*) *dyari* (Coq.), *P.* (*P.*) *eumorpha* (Subl.)

Gp VIII triangular with caudomesal angle of about 60°. Rudiments of Gc IX visible in dorsal view as relatively large caudolateral projections of gonotergite IX, the latter without setae. Coxosternapodeme very slightly curved. Segment X with a few setae. Postgenital plate triangular with rounded apex.

Labia with a few weak microtrichia. Seminal capsules (Fig. 17E, G; Tokunaga 1937 fig. 52) spherical with short neck placed slightly to one side; capsules dark sclerotized, only slightly more than ⅓ as long as notum and smaller than cerci.

Natarsia Fittk.
(Fig. 19E, F)

Species examined: *N. baltimoreus* (Macq.)

Gp VIII triangular with caudomesal angle of about 60°. Gonotergite IX without setae, rudiments of Gc IX not apparent as caudolateral projections in dorsal view. Coxosternapodeme slightly curved. Segment X with several setae. Postgenital plate reduced.

Seminal capsules oval with short neck, about ¾ as long as notum and as long as cerci.

Procladius Skuse
(Fig. 20A–D; Roback 1971a fig. 313, 325, 353)

Species illustrated: *P. (Psilotanypus) bellus* (Loew), *P. (Procladius) culiciformis* (L.), *P. (Procladius) denticulatus* Subl.

Gp VIII either triangular with caudomesal angle of about 60° (*Procladius* s. str.), or more tongue-shaped (subgen. *Psilotanypus* Kieff.). Gonotergite IX blackish sclerotized, void of setae, rudiments of Gc IX visible in dorsal view as small circular caudolateral projections. Coxosternapodeme nearly straight. Segment X with a few to numerous setae. Postgenital plate very weak or nonapparent.

Labia without apical microtrichia. Seminal capsules (Fig. 20A, D; Tokunaga 1937 fig. 34, 45) dark, bell-shaped to oval, with widest part near the short neck; capsules ⅓–½ as long as notum and of about same size as the small cerci.

Key to some Nearctic females of *Procladius* Skuse

1 Gp VIII tongue-shaped; wing membrane without setae; segment X with 7–22 setae ..... *Procladius (Psilotanypus) bellus* (Loew)

Gp VIII triangular; wing membrane with setae; segment X with 16–58 setae ..... subgen. *Procladius* Skuse 2

2 Abdomen with indication of banding; anepisternum II without setae; segment X with about 25 setae; about 9–14 sensilla chaetica proximally on each metatarsus of middle and hind leg ..... *P. (P.) freemani* Subl.

Abdomen not banded; anepisternum II with or without setae; segment X with 16–18 or 20–58 setae; 3–14 sensilla chaetica on each metatarsus of middle and hind leg 3

3 Segment X with about 16–18 setae; anepisternum II without setae; about 3–10 sensilla chaetica proximally on each metatarsus of middle and hind leg ..... *P. (P.) sublettei* Rob.

Segment X with 20–58 setae; anepisternum II usually with setae; 3–14 sensilla chaetica 4

4 Segment X with about 56–58 setae; anepisternum II with 0–5 setae; about 9–14 sensilla chaetica on each metatarsus of middle and hind leg ..... *P. (P.) denticulatus* Subl.

Segment X with about 20–40 setae; anepisternum II with 3–15 setae; about 3–14 sensilla chaetica 5

5 Segment X with 20–30 setae; anepisternum II with 6–8 setae; 3–8 sensilla chaetica on each metatarsus of middle and hind leg ..... *P. (P.) culiciformis* (L.)

Segment X with about 34–40 setae; anepisternum II either with about 3 or 15 setae; either 4, 5, or 10–14 sensilla chaetica on each metatarsus of middle and hind leg 6

6 Anepisternum II with about 15 setae; about 10–14 sensilla chaetica on each metatarsus of middle and hind leg ..... *P. (P.)* ? *paragretis* Rob.

Anepisternum II with about 3 setae; about 4 or 5 sensilla chaetica on each metatarsus of middle and hind leg ..... *Procladius (P.)* ? sp.n.

TRIBE PENTANEURINI
(Fig. 20E–I, 21–24)

Gca VIII mostly weak, occasionally strong and conspicuous (in *Ablabesmyia* Joh. (Fig. 21A) and *Arctopelopia* Fittk. (Fig. 22A)). Gp VIII mostly triangular, occasionally tongue-shaped or weak and rounded. Gp IX well developed or occasionally reduced (in *Pentaneura* Phil., Fig. 24E); notum at least as long as free part of rami, usually twice as long. Gonotergite IX usually without setae, with 1 or 2 setae in *Conchapelopia* Fittk. (Fig. 20I) or with an annular sensilla in *Pentaneura* Phil. (Fig. 24F); rudiments of Gc IX not visible as caudolateral projections in dorsal view. Coxosternapodeme straight to strongly curved. Segment X with setae except in *Larsia* Fittk. (Fig. 24D). Postgenital plate reduced. Cerci small.

Labia with or without microtrichia. 3 seminal capsules, except *Telmatopelopia* Fittk. (Rodova 1971b fig. 8) with 2 only. Spermathecal ducts straight to slightly curved.

PHYLETIC RELATIONSHIPS WITHIN PENTANEURINI

There seem to be several morphological features of phylogenetic importance present in the female genitalia. The genitalia of *Ablabesmyia* Joh. (Fig. 21A, B) and *Arctopelopia* Fittk. (Fig. 22A, B) are strikingly similar and quite different from the remaining genera. The tongue-shaped Gp VIII, the well-developed Gca VIII, and the strong and strongly curved coxosternapodeme all, however, appear to be plesiomorphous characters. Fittkau (1962 p. 70) believes that the presence of a complex of volsellae or endomeres (aedeagus) at the base of the male gonocoxite in the Tanypodinae is an apomorphous character, and Brundin (1966 p. 425) appears to agree with him. However, as indicated by Sæther (1971b p. 1247–1251) and shown by Hirvenoja (1973 p. 23–29) (see also Sæther 1976b p. 12), the presence of well-developed endomeres and/or volsellae clearly is a plesiomorphous feature with the lowest anagenetic step represented by *Protanypus* Kieff., some *Podonominae,* and probably *Ablabesmyia.* Further evidence is presented here where just the females of the genera with well-developed endomeres or volsellae are shown to possess the most plesiomorphous genitalia. *Ablabesmyia* shares the presence of well-developed volsellae with the *Thienemannimyia* group (sensu Fittkau 1962) including *Xenopelopia* Fittk. and *Telopelopia* Rob. (*Thienemannimyia* group sensu Roback 1971a p. 237). The larvae of these genera and larvae of *Trissopelopia* Kieff. and *Guttipelopia* Fittk. share the apparently apomorphous feature of having the apex of the first lateral teeth of the ligula directed slightly outward. In the genera *Ablabesmyia, Guttipelopia* and *Conchapelopia* Fittk. 1–4 claws of posterior parapods are dark. The thoracic horn and comb of the pupa are the same type in *Ablabesmyia* and *Guttipelopia.* In the female genitalia the *Thienemannimyia* group (sensu Roback 1971a) and *Guttipelopia* are the only Pentaneurini to carry microtrichia on the labia. It is not clear whether this is a plesiomorphous feature or an apomorphous feature subject to parallelism although the latter seems to be most likely. The coxosternapodeme is straight in *Guttipelopia, Thienemannimyia* Fittk., and *Xenopelopia* Fittk., apparently a synapomorphous feature. (It appears to be straight also in *Trissopelopia,* but is, however, of a different shape.) Gonotergite IX carries 1 or 2 setae in *Conchapelopia,* a plesiomorphous characteristic. The tibial spurs of *Ablabesmyia,* the *Thienemannimyia* group, and *Guttipelopia* all fall in the types shown by Fittkau (1960 fig. 2) or the start of his "Orthoclad type."

The morphological evidence of the female genitalia, taken in conjunction with previous evidence, suggests that *Ablabesmyia* forms the sister group of the *Thienemannimyia* group plus *Guttipelopia* and probably *Krenopelopia* Fittk., *Monopelopia* Fittk., and *Nilotanypus* Kieff. These 2 sister groups combined form the sister group of the remaining genera of the Pentaneurini. *Xenopelopia, Telopelopia, Thienemannimyia,* and *Guttipelopia* appear to form a monophyletic unit perhaps with *Krenopelopia, Monopelopia,* and *Nilotanypus* as their apomorphic sister group. The sister group of the last 2 groups combined is *Conchapelopia,* and of *Conchapelopia* plus these groups, *Arctopelopia.* An examination of female genitalia of the few remaining genera as well as a better study particularly of the larval mouthparts may confirm or contradict some of the above findings. It seems clear, however, that *Ablabesmyia* and *Arctopelopia* are more plesiomorphic than previously suggested and that the *Thienemannimyia* group (neither sensu Fittkau 1962 nor sensu Roback 1971a) is a monophyletic unit.

Preliminary key to females of Pentaneurini

(Of the excluded genera only the females of *Labrundinia* Fittk. and *Nilotanypus* Kieff. are known.)

1 Legs clothed with flattened scalelike setae, tarsi whitish with dark rings ..... *Lepidopelopia* Harr. (Africa)

Legs without scalelike setae, tarsi banded only in *Ablabesmyia* Joh. 2

2 Two seminal capsules ..... *Telmatopelopia* Fittk. (p. 53)

Three seminal capsules 3

3 Gp VIII tongue-shaped with parallel margins; Gca VIII pronounced, continuing to base of Gp VIII 4

Gp VIII triangular to rounded, never with parallel margins; gonocoxapodeme mostly weak or absent 5

4 Segment X strongly constricted ventrally on both sides of postgenital plate; seminal capsules much less than ½ as long as notum and usually distinctly darker in apical half than in basal half; labia without or perhaps with some very indistinct microtrichia ..... *Ablabesmyia* Joh. (p. 51)

Segment X almost without constriction orolaterad of postgenital plate; seminal capsule more than ½ as long as notum and only slightly darker in apical half; labia with relatively distinct microtrichia ..... *Arctopelopia* Fittk. (p. 51)

5 Labia with fine microtrichia; coxosternapodeme straight medially or when slightly curved, gonotergite IX with 1 or 2 setae; seminal capsule ½ as long as notum or slightly longer 6

Labia apparently without microtrichia; coxosternapodeme usually curved, when straight seminal capsules about ⅓ as long as notum; gonotergite IX without setae, but may have central annular sensilla 8

6 Gonotergite IX with 1 or 2 setae; coxosternapodeme evenly curved; labia with apical fine brush of microtrichia ..... *Conchapelopia* Fittk. (p. 52)

Gonotergite IX without setae; coxosternapodeme essentially straight medially; labia with scattered microtrichia near apex or also at mesal margin 7

7 Gp VIII rounded at apex, broadly triangular, with caudal and mesal margin forming angle of about 80°; coxosternapodeme weak; labia with scattered microtrichia at apex ..... *Thienemannimyia* Fittk. (p. 52)

Gp VIII more pointed at apex, with the straight caudal and the convex mesal margin forming angle of about 45°; coxosternapodeme strong; labia with very weak microtrichia at apex and along mesal margin ..... *Guttipelopia* Fittk. (p. 52)

8 Seminal capsule small, about ⅓ as long as notum; notum apparently widened at anterior end; coxosternapodeme straight; Gp VIII strong ..... *Xenopelopia* Fittk. (p. 52)

Seminal capsule larger, at least ½ as long as notum; notum not widened at anterior end; coxosternapodeme usually curved, when straight, Gp VIII weak 9

9 Gp VIII weak and rounded, with weak microtrichia; coxosternapodeme approximately straight in the middle; seminal capsules more than ⅔ as long as the normally developed notum ..... *Trissopelopia* Kieff. (p. 53)

Gp VIII better developed, triangular, with stronger microtrichia; coxosternapodeme curved; seminal capsules less than ⅔ as long as notum, or longer 10

10 Notum approximately as long as seminal capsules and only slightly longer than the small cerci; gonotergite IX with a median annulus ..... *Pentaneura* Phil. (p. 54)

Notum clearly longer than seminal capsules and cerci; gonotergite IX without annulus 11

11 Seminal capsules more than ⅔ as long as notum and much larger than cerci ..... *Paramerina* Fittk. (p. 53)

Seminal capsules about ½ as long as notum, much longer than or of about same size as cerci 12

12 Segment X apparently without setae; seminal capsules only slightly longer than cerci ..... *Larsia* Fittk. (p. 53)

Segment X with several setae; seminal capsules much longer than cerci 13

13 Gp VIII relatively large, covering part of segment X; segment X in dorsal view large, nearly twice as long as the cerci in dorsal view; seminal capsules nearly ⅔ as long as notum ..... *Monopelopia* Fittk. (p. 52)

Gp VIII relatively small, not reaching segment X; segment X in dorsal view about as long as cerci; seminal capsules shorter to slightly longer than ½ length of notum ..... *Zavrelimyia* Fittk. (p. 53)

Ablabesmyia Joh.
(Fig. 21A–C; Sublette 1964 fig. 7, 8; Rodova 1974a fig. 31, 33)

Species illustrated: *A. (A.) basalis* (Wall.), *A. (A.) annulata* (Say)

Gca VIII well developed, continues onto base of tongue-shaped Gp VIII. Secondary ventrolateral lobe of Gp VIII occasionally indicated as in *A. (A.) phatta* (Egg.) (Rodova 1974a fig. 33). Gp IX well developed, notum more than twice as long as ramus. Gonotergite IX very narrow. Coxosternapodeme strongly curved. Segment X strongly constricted to each side of base of weak postgenital plate.

Labia apparently without microtrichia. Seminal capsules (Fig. 21A; Rodova 1974a fig. 31, 33) small, less than ½ as long as notum and about same length as cerci, darker in oral half.

Arctopelopia Fittk.
(Fig. 22A, B)

Species examined: *A. (A.) griseipennis* (v.d. Wulp)

Gca VIII well developed, continues onto base of tongue-shaped Gp VIII. Gp IX well developed, notum not quite twice as long as ramus. Coxosternapodeme strong and curved. Segment X not constricted to each side of postgenital plate.

Labia with apical brush of numerous microtrichia. Seminal capsules relatively large, longer than ½ length of notum and longer than cerci.

Conchapelopia Fittk.
(Fig. 20G–I)

Species illustrated: *C. (C.) goniodes* (Subl.) var. *trifida* Rob., *C. (C.) rurika* (Rob.)

Gca VIII very weak. Gp VIII triangular with rounded caudomesal angle. Gp IX well developed, but notum only about as long as ramus. Gonotergite IX relatively well developed, with 1 or 2 setae (at least in examined species). Coxosternapodeme curved. Segment X well developed.

Labia with brush or apical microtrichia. Seminal capsules more than ½ as long as notum, longer than cerci, darker in oral half.

Xenopelopia Fittk.
(Fig. 23D, E)

Species examined: *X. falcigera* (Kieff.)

Gca VIII moderately developed. Gp VIII triangular. Gp IX well developed, notum more than twice as long as ramus and widened at oral end. Gonotergite IX narrow. Coxosternapodeme straight. Segment X well developed.

Labia without microtrichia. Seminal capsules ⅓ as long as notum, about same size as cerci, perhaps with a few microtrichia.

Thienemannimyia Fittk.
(Fig. 20E, F)

Species examined: *Thienemannimyia (T.)* sp.

Gca VIII not apparent. Gp VIII triangular. Gp IX with notum only slightly longer than ramus. Gonotergite IX relatively well developed. Coxosternapodeme weak and straight. Segment X well developed.

Labia with scattered microtrichia at apex. Seminal capsules about ½ as long as notum and slightly longer than cerci.

Guttipelopia Fittk.
(Fig. 24A–C)

Species examined: *G. currani* Beck et Beck

Gca VIII present. Gp VIII pointed, triangular, with straight caudolateral and convex mesal margin. Gp IX with notum slightly less than twice as long as ramus. Coxosternapodeme straight. Segment X normal.

Labia with scattered microtrichia. Seminal capsules more than ½ as long as notum, longer than cerci, darker in oral half.

Monopelopia Fittk.
(Fig. 21D, E)

Species examined: *Monopelopia* sp.

Gca VIII very weak. Gp VIII very large, triangular, with rounded apex. Gp IX with notum less than twice as long as ramus. Coxosternapodeme curved. Segment X large, conspicuous in dorsal view.

Labia without microtrichia. Seminal capsules large, between ½ and ⅔ as long as notum, longer than the small cerci.

Telmatopelopia Fittk.
(Rodova 1971b fig. 8)

Gp VIII triangular. Gp IX well developed. Gonotergite IX apparently well developed, apparently without setae. Coxosternapodeme slightly curved. Segment X relatively large.

Only 2 seminal capsules, much larger than the small cerci.

Zavrelimyia Fittk.
(Fig. 23A–C)

Species examined: *Z. signatipennis* (Kieff.), *Zavrelimyia* sp.

Gca VIII not apparent. Gp VIII somewhat triangular with rounded apex. Gp IX with notum twice as long as ramus. Coxosternapodeme curved. Segment X relatively well developed.

Labia without microtrichia. Seminal capsules slightly less to distinctly longer than ½ as long as notum, much longer than the very small cerci.

Paramerina Fittk.
(Fig. 21F, G)

Species examined: *P. anomala* Beck et Beck

Gca VIII not apparent. Gp VIII triangular. Gp IX weak, notum longer than ramus. Gonotergite IX relatively well developed. Coxosternapodeme weak, curved. Segment X of moderate size.

Labia without microtrichia. Seminal capsules longer than ⅔ as long as notum and more than 3 times as long as the very small cerci.

(*Lepidopelopia* Harr. (Harrison 1970) from Africa, judging from the male genitalia, apparently is close to *Paramerina*. However, scalelike setae on legs are unique in the Tanypodinae.)

Larsia Fittk.
(Fig. 24D)

Species illustrated: *Larsia* sp.

Gca VIII apparently absent. Gp VIII triangular, with blunt caudomesal angle. Gp IX well developed, notum slightly longer than ramus. Gonotergite IX partly sclerotized, slightly widened laterally. Coxosternapodeme curved. Segment X well developed, apparently without setae. Cerci very small.

Labia without microtrichia. Seminal capsules pale, spherical to ovoid, about ½ as long as notum and only slightly longer than cerci.

Neither the specimen illustrated (*Larsia* sp.) nor the other specimen examined, belonging to *L. berneri* Beck et Beck, are good specimens. However, *L. berneri* appears to have even smaller cerci than the illustrated species.

Trissopelopia Kieff.
(Fig. 22C, D)

Species examined: *T. longimana* (Staeg.)

Gca VIII relatively strong. Gp VIII rounded, weak, without or with very weak apical microtrichia. Gp IX well developed, notum longer than ramus. Gonotergite IX partly sclerotized. Coxosternapodeme approximately straight, strong in mesal part, weak laterally. Segment X well developed.

Labia widely rounded on inner margin, without microtrichia. Seminal capsules oblong, more than ⅔ as long as notum and twice as long as cerci, brown.

Pentaneura Phil.
(Fig. 24E, F)

Species examined: *P. inconspicua* (Mall.)

Gca VIII present. Gp VIII triangular, with relatively sharp caudomesal angle. Gp IX reduced, notum about as long as ramus. Gonotergite, at least in *P. inconspicua,* with central annulus. Coxosternapodeme strongly curved. Segment X weak, narrow at reduced postgenital plate.

Labia without microtrichia. Seminal capsules about as long as the short notum, slightly longer than cerci, darker in oral half.

Subfamily Aphroteniinae
(Fig. 25)

T VIII normal. S VIII without gonocoxapodeme. Gp VIII simple, with or without microtrichia, membrane present but indistinct. Gp IX well developed. Gc IX fused with T IX to form a very large gonotergite IX which is hood-shaped, undivided, with posterior concavity, or slightly emarginated between caudolateral corners, setae evenly distributed. Intergonocoxal connective not apparent. Coxosternapodeme well developed, wide. Segment X small to reduced, without setae. Postgenital plate weak to well developed. Cerci rounded, small to medium in size.

Labia separate, without microtrichia. 2 or 3 seminal capsules. Spermathecal ducts with loops or bends, with common opening on wide spermathecal eminence.

Female genitalia show mostly plesiomorphous characteristics such as large gonotergite IX, simple Gp VIII, and separate labia. However, the Gc IX are fused with T IX to form a gonotergite IX, a synapomorphous feature for this subfamily plus Podonominae and Tanypodinae. Other apomorphous features are the absence of gonocoxapodemes, reduction of segment X, and absence of setae from segment X.

The phyletic relationships within the subfamily are outlined by Brundin (1966 p. 334–338) who also gives a key to the adults.

Aphrotenia Brund.

Cerci very small, rounded, cup-shaped (Brundin 1966 p. 341); 3 small seminal capsules without neck (Brundin 1966 fig. 468).

Aphroteniella Brund.
(Fig. 25A, B; Brundin 1966 fig. 489, 490)

Species examined: *A. filicornis* Brund.

Gp VIII simple, apparently without microtrichia, membrane present. Gp IX well developed. Gonotergite IX with posterior concavity, however, without any emargination in the outline. Coxosternapodeme wide. Segment X with 2 large ventrolateral concavities with microtrichia apparently covered by a membrane. Postgenital plate relatively well developed, nearly as large as small cerci.

Labia large, triangular, pointed. 2 seminal capsules with neck and collar. (Brundin (1966 fig. 490) overlooked the collar.) Spermathecal ducts with loop, with unusual wide common opening on distinct spermathecal eminence.

Paraphrotenia Brund.
(Fig. 25C, D; Brundin 1966 fig. 508, 509)

Species examined: *P. excellens* Brund.

Gp VIII simple, covered with microtrichia, membrane not apparent. Gp IX with rami and notum more heavily sclerotized and wider than in *Aphroteniella.* Gonotergite IX with slight

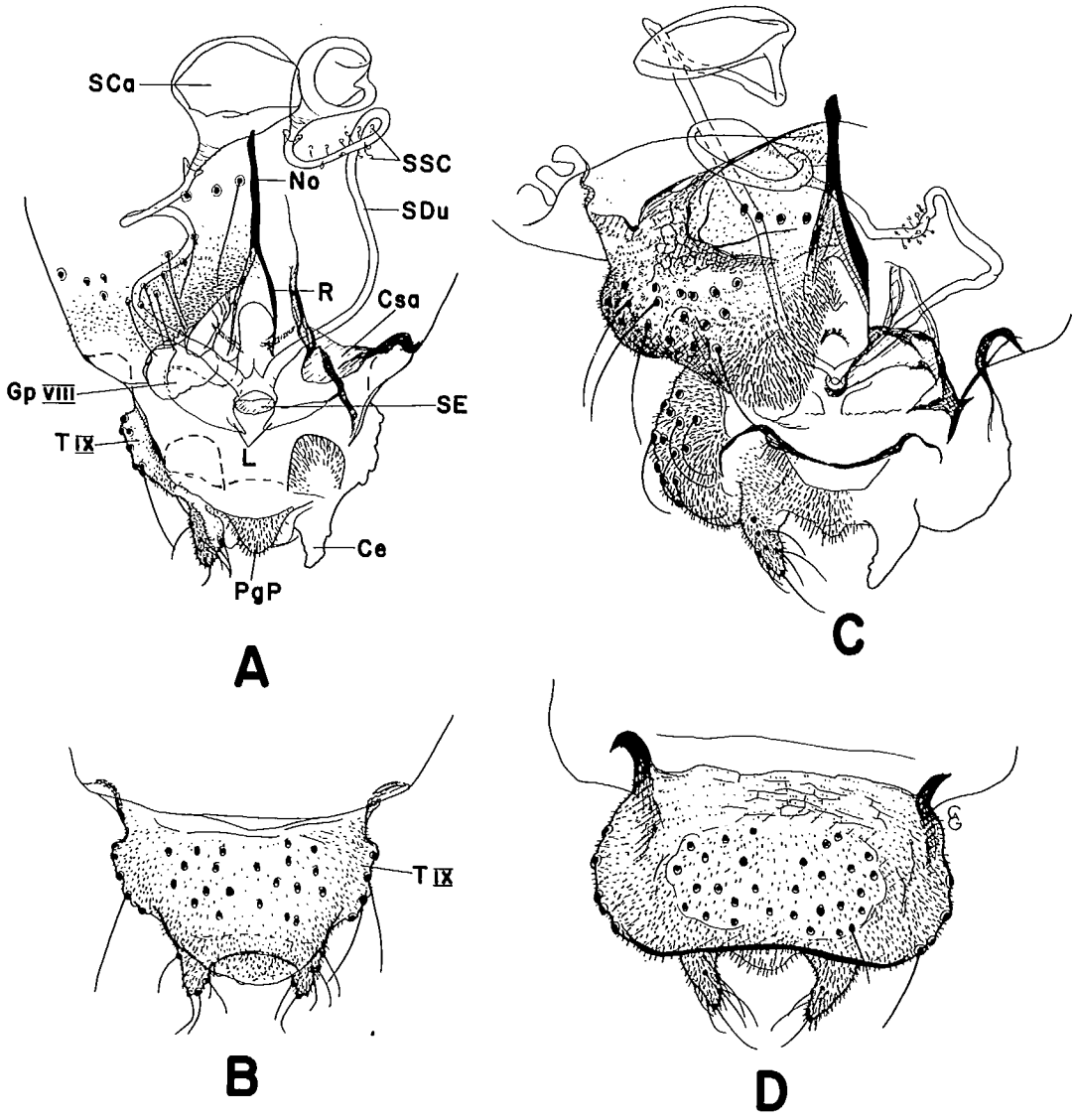

FIG. 25. Female genitalia of Aphroteniinae. A–B, *Aphroteniella filicornis* Brund.: A) ventral; B) dorsal. C–D, *Paraphrotenia excellens* Brund.: C) ventral; D) dorsal.

posterior emargination. Coxosternapodeme wide. Segment X relatively well developed, with sclerotized anterior ventral margin. Postgenital plate barely indicated, not separate from segment X.

Labia beak-shaped. 2 large, pale, transversely oblong, seminal capsules.

SUBFAMILY PODONOMINAE
(Fig. 26)

T VIII normal. Gc VIII absent or perhaps present in *Afrochlus* Freem. (see p. 57). S VIII without gonocoxapodeme. Gp VIII simple, undivided, rounded to tongue-shaped, sometimes with strong apical microtrichia; membrane not evident. Gp IX well developed, notum slightly shorter than rami to twice as long as rami. Gc IX fused with T IX to form a gonotergite IX. Gonotergite IX large, hood-shaped, undivided, occasionally with posterior lobes which may represent rudiments of Gc IX. Intergonocoxal connective apparently present. Coxosternapodeme well developed, often strongly widened in the middle. Segment X reduced to a well-developed sternite X or present also dorsally, with or without setae. Postgenital plate usually not distinctly separable from the large segment X, occasionally apparently well developed (see *Podonomus* Phil.). Cerci small to medium, generally simple and rounded, with microtrichia and numerous short setae of equal size, occasionally with one to several longer and stronger setae.

Labia small, apparently fused, without microtrichia. 2 or 3 relatively small seminal capsules. Spermathecal ducts straight or nearly straight; joined for a short distance, with common opening, or opening separately.

Female genitalia in general show mostly plesiomorphous features such as the large undivided gonotergite IX, well-developed segment X, and simple Gp VIII. However, as in Aphroteniinae and Tanypodinae, Gc IX is fused with T IX to form a gonotergite IX, a synapomorphous character for these subfamilies. The fused labia is a clear synapomorphous character for the subfamily. Although the labia are fused also in Telmatogetoninae, they are of a quite different type here. Doubts about the monophyly of the Podonominae raised by Schlee (1975) can thus be discounted.

The intergeneric relationships in the Podonominae are discussed by Brundin (1966 p. 98–104, fig. 634) and by Schlee (1975). Brundin (1966 p. 104) also gives a key to the adults.

TRIBE PODONOMINI
(Fig. 26A–C)

Only S X present, no T X or dorsal part of segment X. S X probably always with setae.

Generally 2 seminal capsules with 3 only in *Podochlus* Brund. and in *Parochlus chiloensis* group (sensu Brundin). Spermathecal ducts joined for a short distance before common opening (at least in *Parochlus kiefferi* (Garr.)).

The formation of segment X with only S X present is a clear synapomorphous feature with no parallelisms observed among any Diptera.

Parochlus End.
(Fig. 26A–C; Brundin 1966 fig. 51, 122, 152–154; Wirth and Gressitt 1967 fig. 2)

Species examined: *P. kiefferi* (Garr.)

Gp VIII more or less triangular with rounded apex. Gp IX with notum 1.0–1.5 times as long as rami. Gonotergite IX moderately large to large. Coxosternapodeme with a few curves, not as wide mesally as in other examined genera of the subfamily. S X well developed, with 3–12 setae on each side. Postgenital plate absent or barely indicated. Cerci more or less oval in form, sometimes arched or concave, usually with short setae, occasionally with one longer seta.

2 (most species) or 3 (*P. chiloensis* group) seminal capsules.

Podonomus Phil.
(Brundin 1966 fig. 181, 182, 214–237)

Gonotergite IX normal. S X well developed, with setae. Postgenital plate reduced to apparently very long (according to Brundin 1966 fig. 214–237). Cerci simple, squarish or oval; triangular and tapering, or more or less deeply excavated and divided.

2 seminal capsules.

Brundin (1966 p. 187) divides the species into 3 types based on the cerci. Also within each type the species can be separated on the basis of the cerci.

Podochlus Brund.
(Brundin 1966 fig. 321)

Gonotergite IX occasionally with hyaline, digitiform caudolateral lobe on each side (Brundin 1966 p. 241). Segment X with a few setae. Cerci simple and oval, with 1 or 2 longer and numerous short setae.

3 seminal capsules.

Rheochlus Brund.
(Brundin 1966 fig. 359, 360)

Gonotergite IX normal. Segment X with a few setae. Cerci with 1 or 2 longer and several short setae.

2 seminal capsules.

Podonomopsis Brund.

Gonotergite IX with hyaline, caudolateral lobes perhaps except in the *P. brevipalpis* group (sensu Brundin 1966 p. 273).

2 seminal capsules.

TRIBE BOREOCHLINI
(Fig. 26D–H)

Segment X normal, continuous around whole segment with large or small dorsal portion, with or without setae. Coxosternapodeme strongly widened in the middle.

Generally 3 seminal capsules, but with 2 only in *Boreochlus thienemanni* Edw. (although Brundin (1966 p. 104) mentions there are always 3 seminal capsules in the tribe). Spermathecal ducts open separately on spermathecal eminence.

The wide coxosternapodemes may possibly be a synapomorphous feature for the tribe, but too few species have been described to say if this character is consistently present.

Archaeochlus Brund.

Gp VIII aparently simple and as in *Lasiodiamesa brusti* Sæth. (Fig. 26D) according to Brundin (1966 p. 289). Cerci simply rounded.

3 seminal capsules.

Afrochlus Freem.
(Brundin 1966 fig. 414)

Rudiments of Gc VIII possibly present and form a club-shaped lobe together with Gp VIII. Gonotergite IX hyaline, forms a roof over cerci, strongly constricted subapically, straight-cut at well-sclerotized, setose, apical margin. Segment X without setae. Cerci crescent-shaped.

3 seminal capsules.

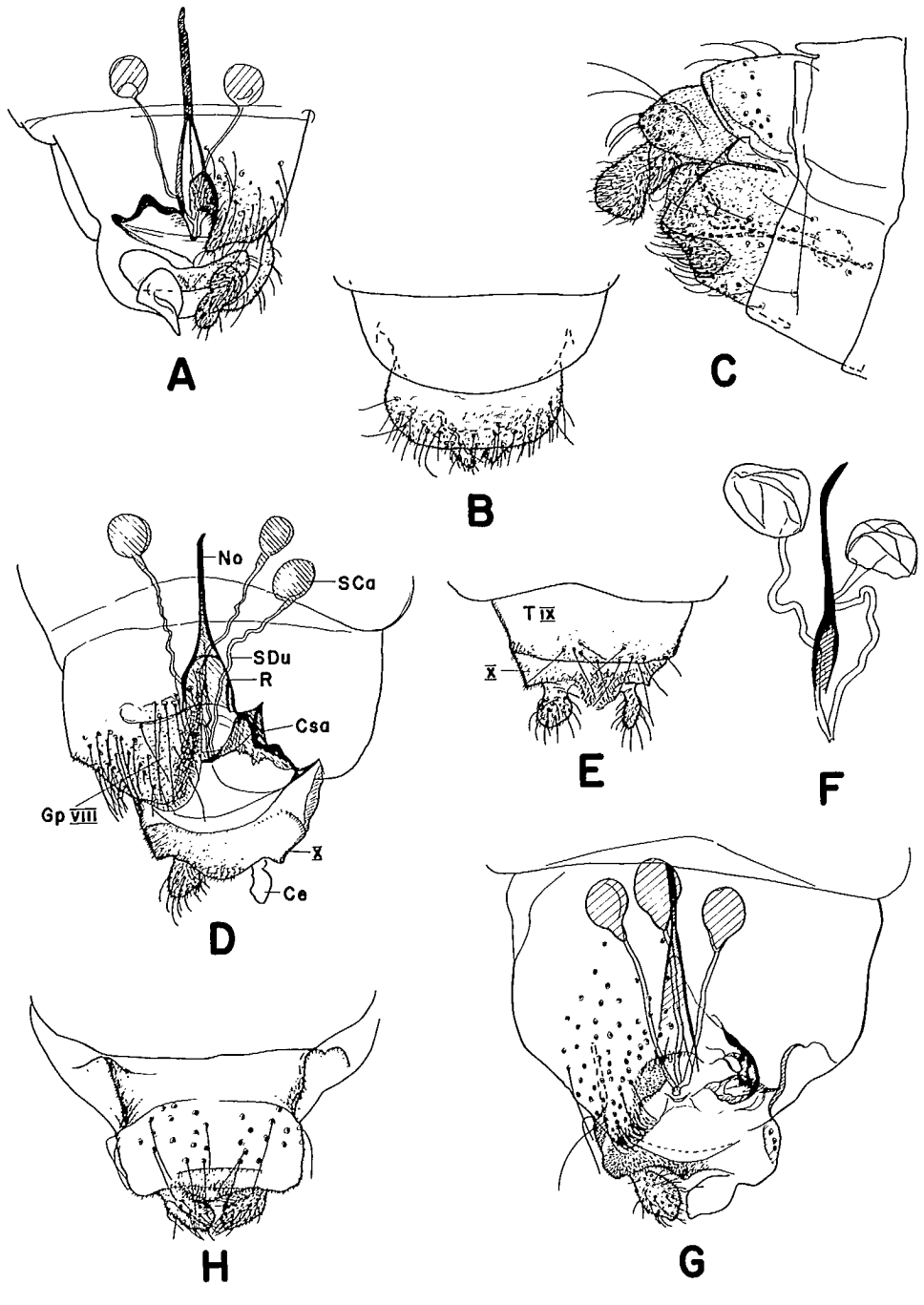

FIG. 26. Female genitalia of Podonominae. A–C, *Parochlus kiefferi* (Garr.): A) ventral; B) dorsal; C) lateral. D–E, *Lasiodiamesa brusti* Sæth.: D) ventral; E) dorsal. F, *Boreochlus thienemanni* Edw., spermatheca and notum. G–H, *Trichotanypus posticalis* (Lundb.): G) ventral; H) dorsal.

Boreochlus Edw.
(Fig. 26F; Brundin 1966 fig. 435)

Species examined: *B. thienemanni* Edw., damaged specimen

Segment X with setae. Cerci small, rounded, with distinct proximal stalk.

2 *B. thienemanni*, 3 (other species), seminal capsules. Spermathecal ducts open separately or have a partly common opening.

Trichotanypus Kieff.
(Fig. 26G, H; Brundin 1966 fig. 437; Wirth and Sublette 1970 fig. 4)

Species examined: *T. posticalis* (Lundb.)

Gp VIII wide, with caudolateral brush of strong microtrichia. Gp IX well developed, with rami longer than notum. Gonotergite IX rectangular. Coxosternapodeme complex, very wide medially. Segment X without setae. Postgenital plate barely indicated. Cerci small, rounded, with short stalk.

3 pear-shaped seminal capsules. Spermathecal ducts straight, with separate openings.

Lasiodiamesa Kieff.
(Fig. 26D, E; Brundin 1966 fig. 436)

Species examined: *L. brusti* Sæth.

Gp VIII broad, rounded, with hyaline margin. Gp IX well developed, notum about 1.5 times as long as ramus, rami parallel-sided. Gonotergite IX rhomboid, with setae concentrated near caudal margin. Coxosternapodeme complex, wide medially. Segment X well developed, with or without setae. Postgenital plate not clearly set off from segment X, rounded. Cerci small, rounded.

3 seminal capsules with distinct neck. Spermathecal ducts open separately.

Subfamily Telmatogetoninae
(Fig. 27, 28)

T VIII strongly reduced, with or without setae. S VIII large, with or without setigerous caudal projection between Gp VIII. Gonocoxapodemes lacking. Gp VIII simple, elongate, lobelike, covered with microtrichia; membrane not apparent. Gp IX somewhat reduced, notum about 2.5 times as long as ramus. T IX large, undivided, with 2 caudal lobes. Coxosternapodemes short, narrow, straight. Gc IX reduced, without setae. Gs IX present, long, tapering, with narrow apodeme, void of microtrichia. Intergonocoxal connective not apparent. Segment X reduced, divided in 2 lateral parts, void of microtrichia or setae. Postgenital plate absent. Cerci usually very long, slender, and tapering distally, occasionally small and bluntly rounded, densely covered by short, fine setae and microtrichia to form an ovipositor together with Gp VIII and gonostyli.

Labia small, fused, without microtrichia. Seminal capsules absent. 2 very wide spermathecal ducts with common opening apparently functioning as seminal storage organs.

On the basis of female genitalia alone, Telmatogetoninae could well be regarded as a family separate from Chironomidae. A number of features are unique to this subfamily, some plesiomorphous, others apomorphous. The large S VIII and T IX, simple Gp VIII, and the presence of a gonostylus are clearly plesiomorphous characters; while the strongly reduced T VIII, reductions of Gp IX, coxosternapodemes, Gc IX, and T X, the fused and reduced labia, the absence of seminal capsules with the widening of the spermathecal ducts are clearly synapomorphous characters. The presence of Gc IX as separate entities, although reduced, indicates that Telmatogetoninae may be closer to the Diamesinae, Prodiamesinae, Orthocladiinae, and Chironominae than to the remaining 3 subfamilies. This is, however, a plesiomorphous character and as shown on p. 31 Telmatogetoninae form the sister group of the remaining subfamilies.

Wirth (1949 p. 156) gives a key to the adults of the subfamily.

Thalassomya Schin.
(Wirth 1947a fig. 13–15, 1949 fig. 4)

S VIII with patch of long yellowish to dark setae caudally between Gp VIII. Cerci long, tapering, occasionally abruptly expanded at base.

Telmatogeton Schin.
(Fig. 27; Saunders 1928 fig. 6; Hesse 1934 fig. 3; Wirth 1947b fig. 7, 1949 fig. 5; Hashimoto 1973a fig. 15, 16)

Species examined: *T. japonicus* Tok.

S VIII with a small patch of long setae arising from sclerotized base between Gp VIII (in *T. williamsi* Wirth and *T. fluviatilis* Wirth, Wirth (1947b p. 163, 166)), with a few strong setae at base of Gp VIII (in *T. japonicus*), with a patch of fine setae (in *T. torrenticola* (Terry) (Wirth 1947b p. 157)), or with practically no setae (in *T. minor* Kieff. (Hesse 1934 p. 36, fig. 3), *T. hirtus* Wirth (Wirth 1947b p. 159), *T. latipennis* Wirth (Wirth 1949 p. 174), and *T. australicus* Wom. (Hashimoto 1973a fig. 15, 16)). S VIII long or shortened (in *T. hirtus* Wirth and *T. abnormis* (Terry) (Wirth 1947b p. 159, 169)). Gc IX and segment X strongly reduced (more so than in *Paraclunio* Kieff. and *Halirytus* Eat.). Cerci long or small and bluntly rounded (in *T. hirtus* Wirth and *T. abnormis* (Terry) (Wirth 1947b p. 159, 169)).

Paraclunio Kieff.
(Fig. 28; Hashimoto 1973b fig. 7; Sæther 1974 fig. 1)

Species examined: *P. alaskensis* (Coq.)

S VIII with a few strong setae on sclerotized tubercle between bases of Gp VIII. T IX in lateral view narrow, distinctly more narrow than the wide S VIII, equally wide anteriorly as posteriorly, or wider anteriorly. Gc IX and segment X better developed than in *Telmatogeton*, less developed than in *Halirytus*.

Halirytus Eat.
(Brundin 1962 fig. 2)

S VIII with stronger setae than in other genera of the subfamily, but without setae between bases of Gp VIII. Gp VIII shorter than in other genera of the subfamily. T IX in lateral view wider posteriorly than anteriorly. Gc IX and segment X apparently better developed than in *Telmatogeton* and *Paraclunio*.

Subfamily Diamesinae
(Fig. 29–34)

T VIII normal. S VIII with gonocoxapodemes. Gp VIII simple and undivided or divided into 2 principal lobes and sometimes a more or less well-developed apodeme lobe covered by principal lobes; membrane always present. Gp IX well developed, notum short to long. T IX undivided or more or less completely divided into 2 setigerous protrusions, not fused with small to large Gc IX. Intergonocoxal connective apparently always present. Coxosternapodeme well developed, simply curved, usually without distinguishing features. Segment X usually without setae. Postgenital plate small to reduced. Cerci small to large, always covered with microtrichia and short setae.

Labia separate, with or without microtrichia. 3 seminal capsules except *Diamesa* Waltl and *Pseudokiefferiella* Zavř. with 2, capsules with or without microtrichia. Spermathecal ducts straight or with small loops or bends, open separately on spermathecal eminence.

There appears to be no synapomorphous features of the female genitalia present in the

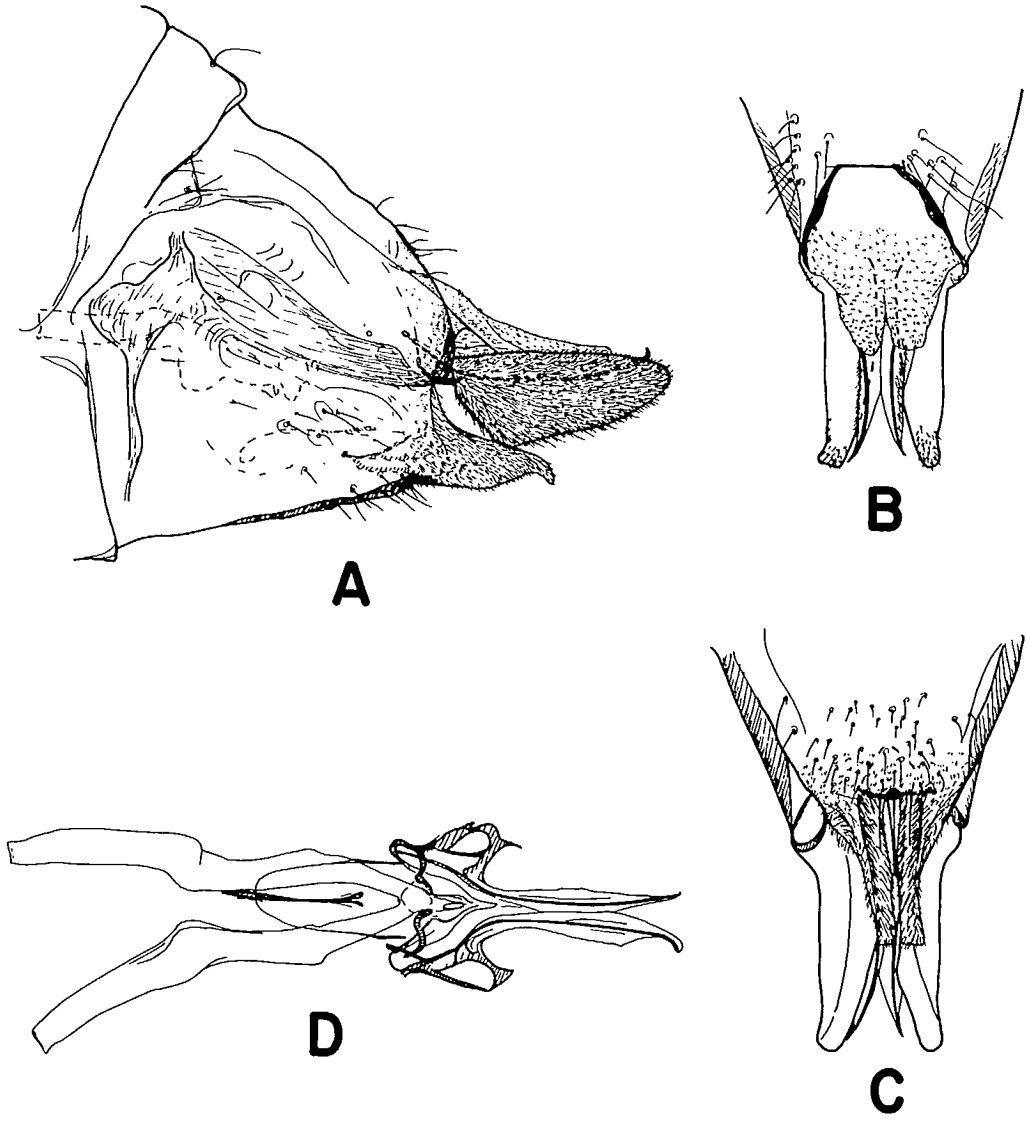

FIG. 27. Female genitalia of *Telmatogeton japonicus* Tok., Telmatogetoninae. A, lateral. B, dorsal. C, ventral. D, Gp IX, Gc IX, gonostylus, segment X, and spermatheca.

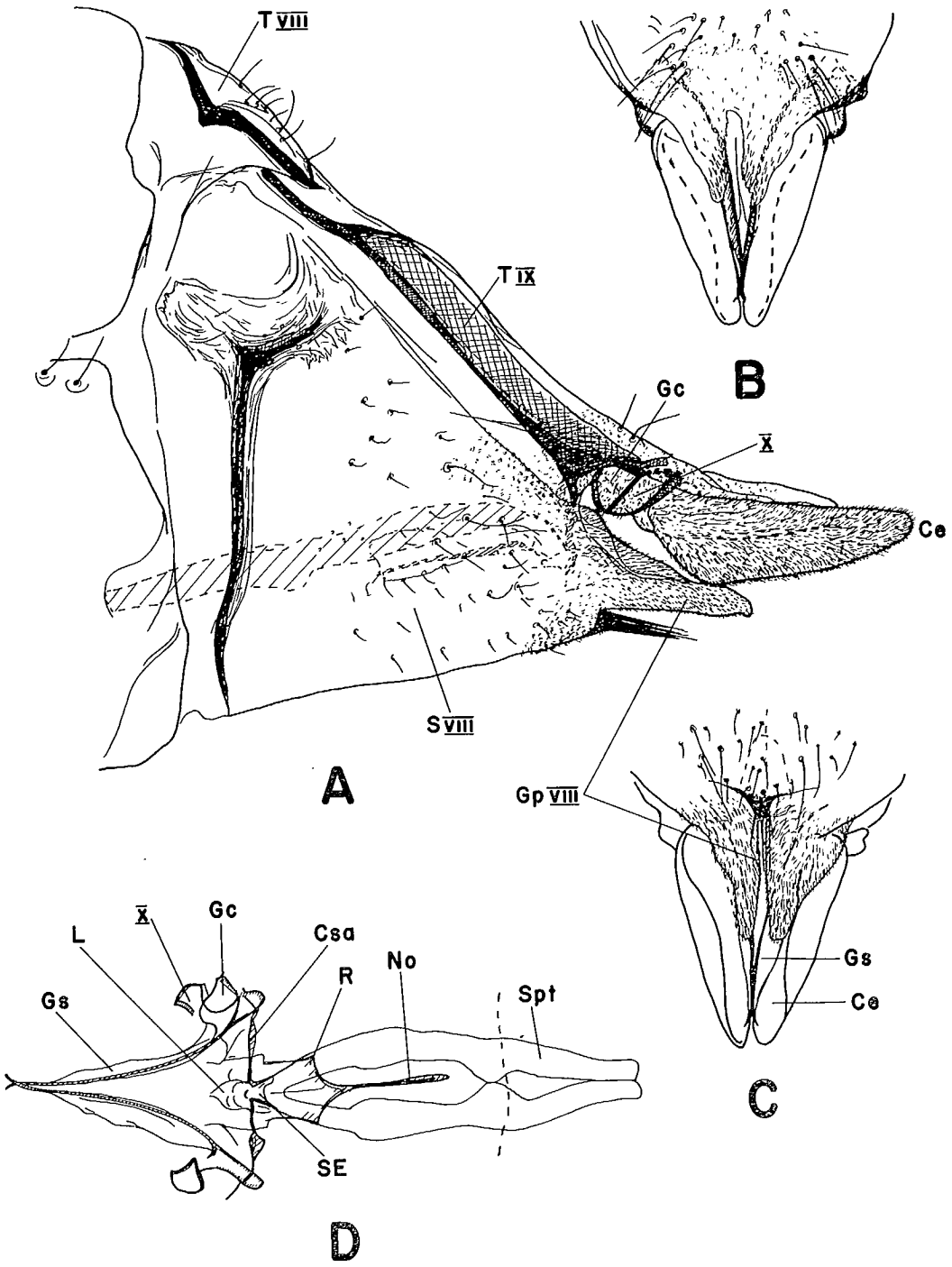

FIG. 28. Female genitalia of *Paraclunio alaskensis* (Coq.), Telmatogetoninae. A, lateral. B, dorsal. C, ventral. D, Gp IX, Gc IX, gonostylus, segment X, and spermatheca.

subfamily as a whole. Segment X is nearly always bare; exceptions are Diamesini with several setae, and *Paraheptagyia cinerascens* Edw. (Fig. 29A) with one seta on each side. Symplesiomorphous characters consist of the presence of Gca VIII, Gc IX as separate entities, unfused labia, the presence of intergonocoxal connective and membrane, and the fact that the spermathecal ducts open separately on the spermathecal eminence.

Buchonomyia Fittk. (Fittkau 1955 p. 403–414) will, in the key to subfamilies and tribes, probably key out to Diamesinae. Whether this placement is correct or not can only be shown by the unknown immatures and female. However, the male appears to show more affinities with the Prodiamesinae (see p. 74).

Brundin (1966 p. 362–373, 447–449) gives an account of diamesan phylogeny.

TRIBE HEPTAGYINI
(Fig. 29, 30)

Gp VIII divided into 2 principal lobes with the ventrolateral lobe covering the relatively well-developed apodeme lobe. Ventrolateral lobe large, more or less rounded; dorsomesal lobe tongue-shaped; apodeme lobe with or without microtrichia, with or without small tubercles. Gp IX well developed, with long notum, and short rami. T IX undivided, setae concentrated on posterior half or on lateral parts, occasionally with large caudolateral lobes (or large Gc IX ? (Brundin 1966 p. 404)). Segment X without or with at most one seta on each side. Postgenital plate small. Cerci medium sized.

Labia usually with microtrichia. 3 seminal capsules. Spermathecal ducts straight or nearly straight.

Brundin (1966 p. 374–378) gives an account of the intrinsic relationships within the tribe and a key to imagines.

Paraheptagyia Brund.
(Fig. 29A–C)

Species examined: *P. cinerascens* (Edw.)

Ventrolateral lobe of Gp VIII, at least in *P. cinerascens*, with both a caudal and an oral basal protuberance. Apodeme lobe without microtrichia or small tubercles. T IX with setae in posterior half, not concentrated laterally. Segment X with one seta on each side, at least in *P. cinerascens*. Postgenital plate relatively distinct.

Labia with minute microtrichia on apex, with longer microtrichia along inner margin.

Auracania Brund.
(Fig. 29D–F)

Species examined: *A. antiqua* Brund.

Ventrolateral lobe of Gp VIII rounded without basal protuberances. Apodeme lobe without microtrichia; with small, rounded tubercles. T IX with setae along caudal and lateral margin, occasionally with long caudolateral lobes (or long Gc IX ? (Brundin 1966 p. 404)). Segment X without setae. Postgenital plate vestigial. Labia with microtrichia. Seminal capsules (Fig. 29D; Brundin 1966 fig. 540) with distinct neck.

Limaya Brund.
(Fig. 30D–F)

Species examined: *L. longitarsis* Brund.

Ventrolateral lobe of Gp VIII rounded with microtrichia of differing sizes and thickness. Apodeme lobe with a few microtrichia. T IX with setae at posterior margin, more numerous laterally. Segment X without setae. Postgenital plate not separate from segment X.

Labia with distinct microtrichia. Seminal capsules with neck.

Maoridiamesa Pag.
(Fig. 30A–C)

Species examined: *M. stouti* Brund.

Ventrolateral lobe of Gp VIII rounded with microtrichia of differing sizes. Apodeme lobe with a few microtrichia. T IX with setae concentrated on lateral parts. Gc IX indistinct, perhaps partly fused with T IX. Segment X without setae. Postgenital plate distinct.

Labia without or possibly with a few very weak microtrichia along inner margin. Seminal capsules oblong, with neck.

TRIBE LOBODIAMESINI
(Fig. 31D–G)

Lobodiamesa Pag.
(Fig. 31D–G)

Species examined: *L. campbelli* Pag., monotypic

Gp VIII apparently undivided, covering indistinct apodeme lobe. Apodeme lobe without microtrichia. Gp IX with relatively short notum about as long as ramus. T IX faintly divided into 2 setigerous protrusions. Segment X well developed, without setae, with ventral group shagreenation of microtrichia. Postgenital plate not separate from segment X.

Labia without microtrichia. Seminal capsules large, spermathecal ducts curved.

TRIBE BOREOHEPTAGYINI
(Fig. 31A–C)

Boreoheptagyia Brund.
(Fig. 31A–C)

Species examined: *Boreoheptagyia* sp.

Gp VIII simple, tongue-shaped, elongate. Gp IX with very short notum, rami about 2.5 times as long as notum. T IX undivided; with sharp, triangular, caudolateral projections; with a few posterior setae. Segment X without setae. Postgenital plate small, rounded. Cerci rounded.

Labia very large, with distinct marginal microtrichia. Seminal capsules ovoid.

TRIBE HARRISONINI

Harrisonina Freem.

Seminal capsules bell-shaped (Freeman 1956 fig. 6).

TRIBE DIAMESINI
(Fig. 32, 33)

Gp VIII large and divided with the large ventrolateral lobe partially or fully covering small dorsomesal lobe. Membrane weak or absent. Apodeme lobe absent or vestigial. Gp IX well developed, notum medium long to short. T IX divided into 2 setigerous protrusions. Gc IX well developed and distinct. Segment X with or without setae. Postgenital plate usually not set off from segment X. Cerci medium to large in size, usually pediform in outline with rounded "heel" and more or less elongated "toe."

Labia usually without microtrichia. 2 or 3 seminal capsules. Spermathecal ducts with small bends or loops.

The intrinsic relationships within the tribe are discussed by Serra-Tosio (1971 p. 298–302).

Key to females of Diamesini

(Females of the first three genera are not sufficiently known. They have, however, been included to complete the key.)

1 Antepronotum with median and lateral setae; eyes hairy; acrostichals present (female unknown) ..... *Hesperodiamesa* Subl.

Antepronotum either completely covered with strong setae or with lateral setae only; eyes usually naked; acrostichals usually absent 2

2 Claws very long, ta_1 shorter than ta_5; eyes without dorsal elongation; dorsocentrals in 1 or occasionally 2 rows posteriorly (female inadequately described) ..... *Onychodiamesa* Pag.

Claws normal; ta_1 shorter to longer than ta_5; eyes not, to strongly extended; dorsocentrals in 1–5 rows 3

3 Weak acrostichals present; temporals in several rows anteriorly; dorsocentrals in a single row except close to scutellum (female unknown) ..... *Lappodiamesa* Ser.-Tos.

When acrostichals present and temporals in several rows; dorsocentrals in 2–5 rows 4

4 Segment X with numerous setae; 3 seminal capsules 5

Segment X without setae; 2 or 3 seminal capsules 6

5 T IX short, setigerous protrusions narrow with only a few setae; antepronotum completely covered with setae ..... *Pagastia* Ol. (p. 66)

T IX large, setigerous protrusions oval with numerous setae; antepronotum with lateral setae only ..... *Pseudodiamesa* Goetgh. (p. 66)

6 Two seminal capsules 7

Three seminal capsules 8

7 Gc IX a small, square lobe with about 10 setae; seminal capsules spherical; cerci circular in lateral view ..... *Pseudokiefferiella* Zavřel (p. 66)

Without above combination of characters ..... *Diamesa* Waltl (p. 66)

8 Gp VIII very large, reaching past basal half of cerci in lateral view; temporals in several rows; dorsocentrals in 2–4 rows ..... *Syndiamesa* Kieff. (p. 66)

Gp VIII smaller, not reaching base of cerci; temporals in single row; dorsocentrals in 1 row medially 9

9 Plate present orally of well-developed postgenital plate and between Gp VIII partially closing the vagina caudally; lateral portions of segment X not darkened; eyes not or very shortly extended dorsally ..... *Potthastia* Kieff. (p. 73)

If a similar plate is present it is not between Gp VIII; lateral portions of segment X dark; eyes with a moderate dorsal extension ..... *Sympotthastia* Pag. (p. 73)

Pagastia Ol.
(Fig. 32A–D; Oliver 1959 fig. 3)

Species examined: *P. orthogonia* Ol.

Gp VIII with rounded, moderately large ventrolateral lobe and narrow dorsomesal lobe surrounding vagina anterior of labia. Apodeme lobe apparently absent. Gp IX well developed. Segment X with a few setae. Postgenital plate weak. Cerci large, pediform with long "toe."

Labia without microtrichia, tongue-shaped. 3 seminal capsules with weak microtrichia.

Reduction of T IX in *Pagastia* compared to *Pseudodiamesa* appears to be an additional synapomorphy in the synapomorphic diagram constructed by Serra-Tosio (1968 pl. 12, 1971 pl. 142).

Pseudodiamesa Goetgh.
(Fig. 33D, E; Oliver 1959 fig. 8, 11, 14, 17, 18; Serra-Tosio 1971 pl. 10 fig. 1)

Species examined: *P. (Pachydiamesa) arctica* (Mall.)

Gp VIII with large, rounded ventrolateral lobe and small dorsomesal lobe surrounding vagina anterior of spermathecal eminence. Apodeme lobe apparently absent. Gp IX with short notum. T IX large, divided into 2 transversely oval protrusions with numerous setae. Segment X large, with lateral setae. Postgenital plate weak. Cerci large, pediform, with long "toe."

Labia with a few indistinct microtrichia. 3 large to moderately large, oblong to ovoid, seminal capsules.

A key to females of the genus is given by Oliver (1959 p. 54).

Syndiamesa Kieff.
(syn. *Parapotthastia* Ser.-Tos., Cranston 1975 p. 88) (Serra-Tosio 1971 pl. 24 fig. 15)

Gp VIII apparently very large, reaching middle of cerci in lateral view. T IX with small setigerous protrusions with few setae (Serra-Tosio 1971 p. 86). Segment X without setae. Postgenital plate small. Cerci triangular.

3 relatively small, oval seminal capsules.

Diamesa Waltl
(Fig. 33A–C; Oliver 1965 fig. 3; Sæther 1968 fig. 11; Serra-Tosio 1969 fig. 12, 1970 fig. 10, 1971 pl. 38 et seq., 1972 fig. 4, 1974 fig. 6)

Species examined: *Diamesa* spp.

Gp VIII with large ventrolateral lobe partly hiding smaller dorsomesal lobe surrounding vagina anterior of labia. Apodeme lobe present. Gp IX well developed, notum slightly shorter than ramus. T IX medium to large, setigerous protrusions of variable size and shape. Gc IX small and digitiform to large and rectangular, with few to numerous short to long setae. Segment X medium to small, without setae. Postgenital plate small to undifferentiated. Cerci circular, triangular, or pediform.

Labia rounded to pointed, without microtrichia. 2 oval to spherical seminal capsules. Spermathecal ducts with loop, at least in examined specimens.

Pseudokiefferiella Zavř.
(Serra-Tosio 1971 pl. 118)

T IX medium large, setigerous protrusions approximately transversely oval. Gc IX small, square, with few setae. Segment X without setae. Cerci circular in lateral view.

2 spherical seminal capsules.

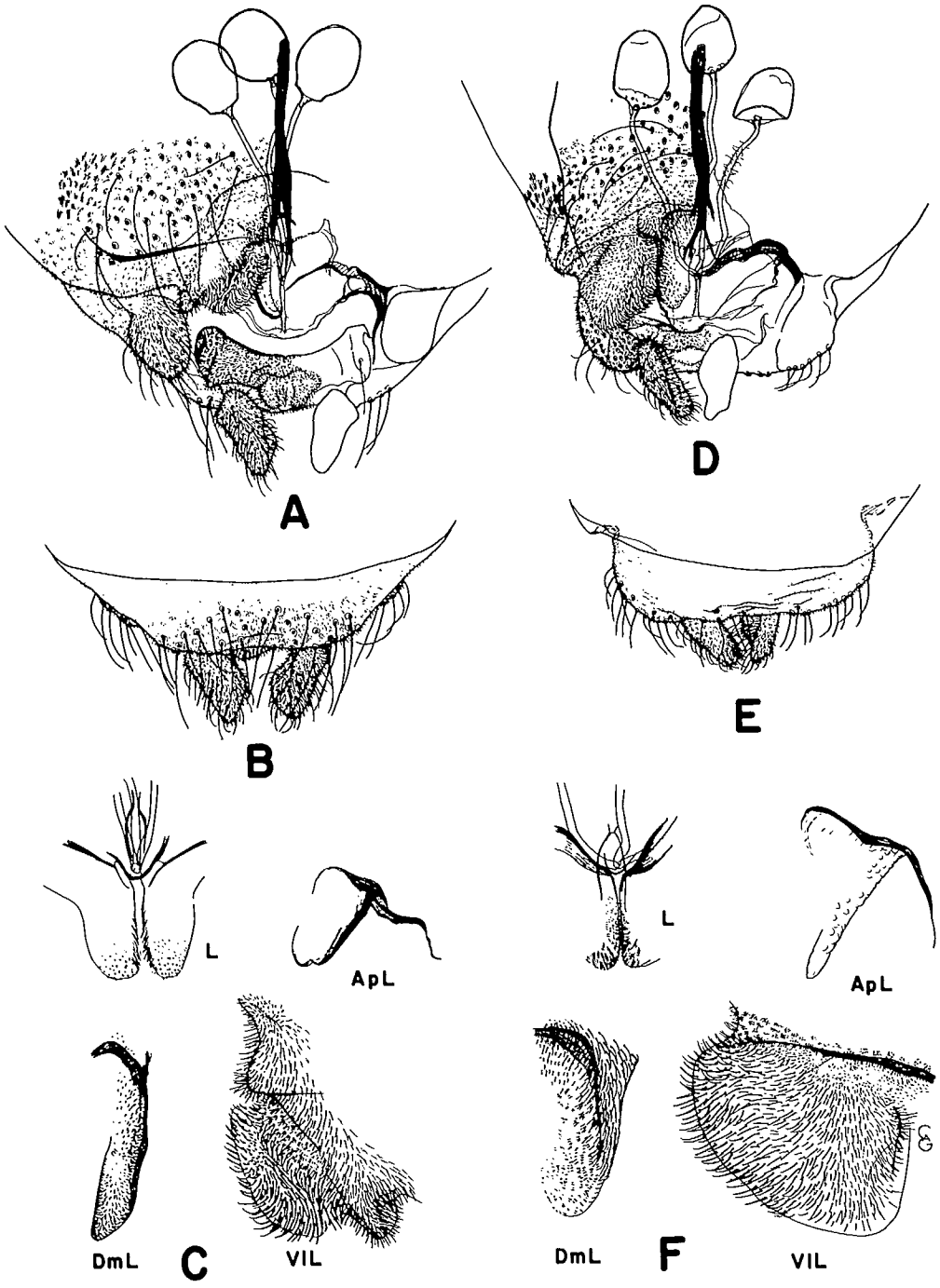

FIG. 29. Female genitalia of Heptagyini, Diamesinae. A–C, *Paraheptagyia cinerascens* (Edw.): A) ventral; B) dorsal; C) lobes of Gp VIII and labia. D–F, *Auracania antiqua* Brund.: D) ventral; E) dorsal; F) lobes of Gp VIII, and labia.

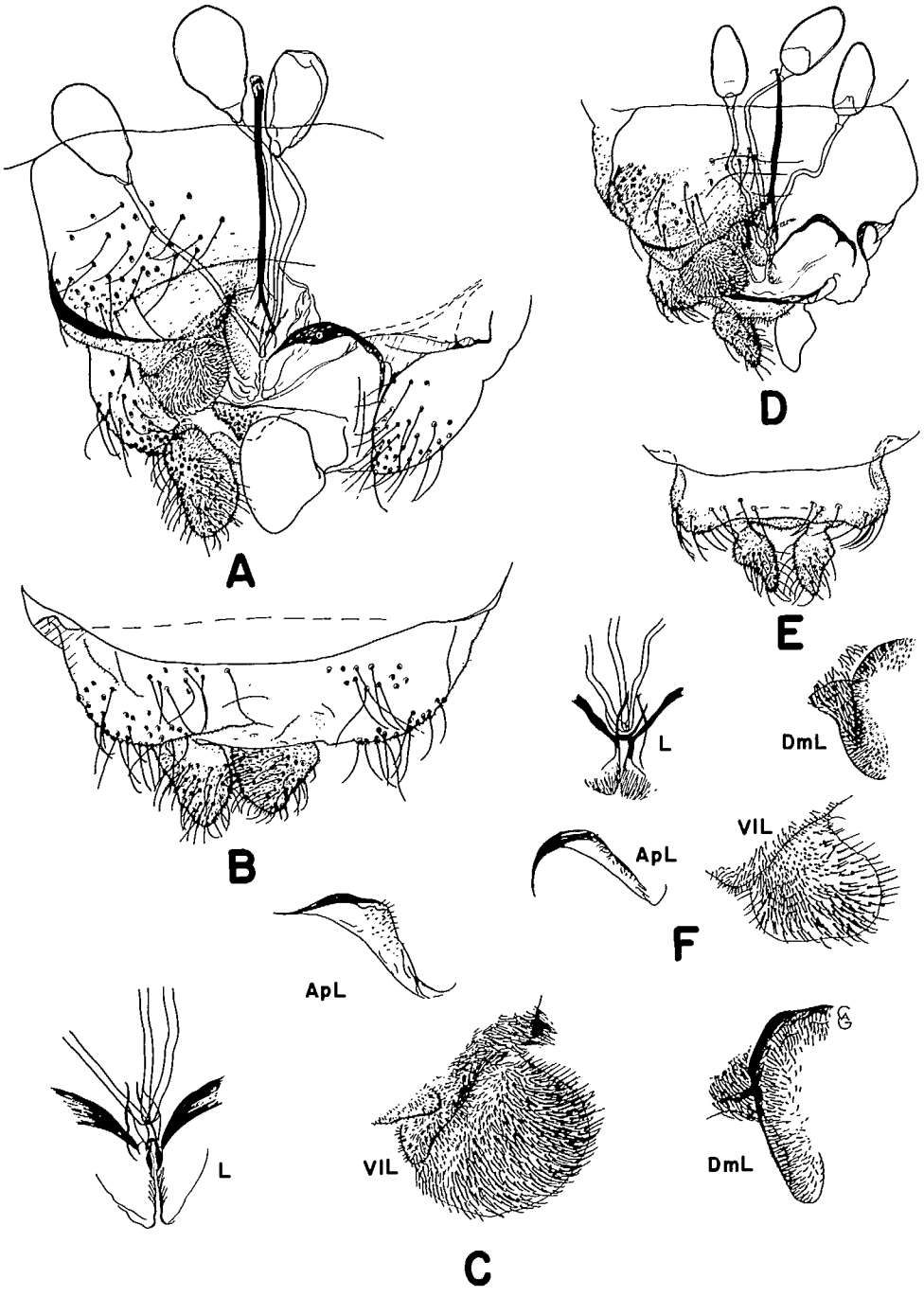

FIG. 30. Female genitalia of Heptagyini. A–C, *Maoridiamesa stouti* Brund.: A) ventral; B) dorsal; C) lobes of Gp VIII, and labia. D–F, *Limaya longitarsis* Brund.: D) ventral; E) dorsal; F) lobes of Gp VIII, and labia.

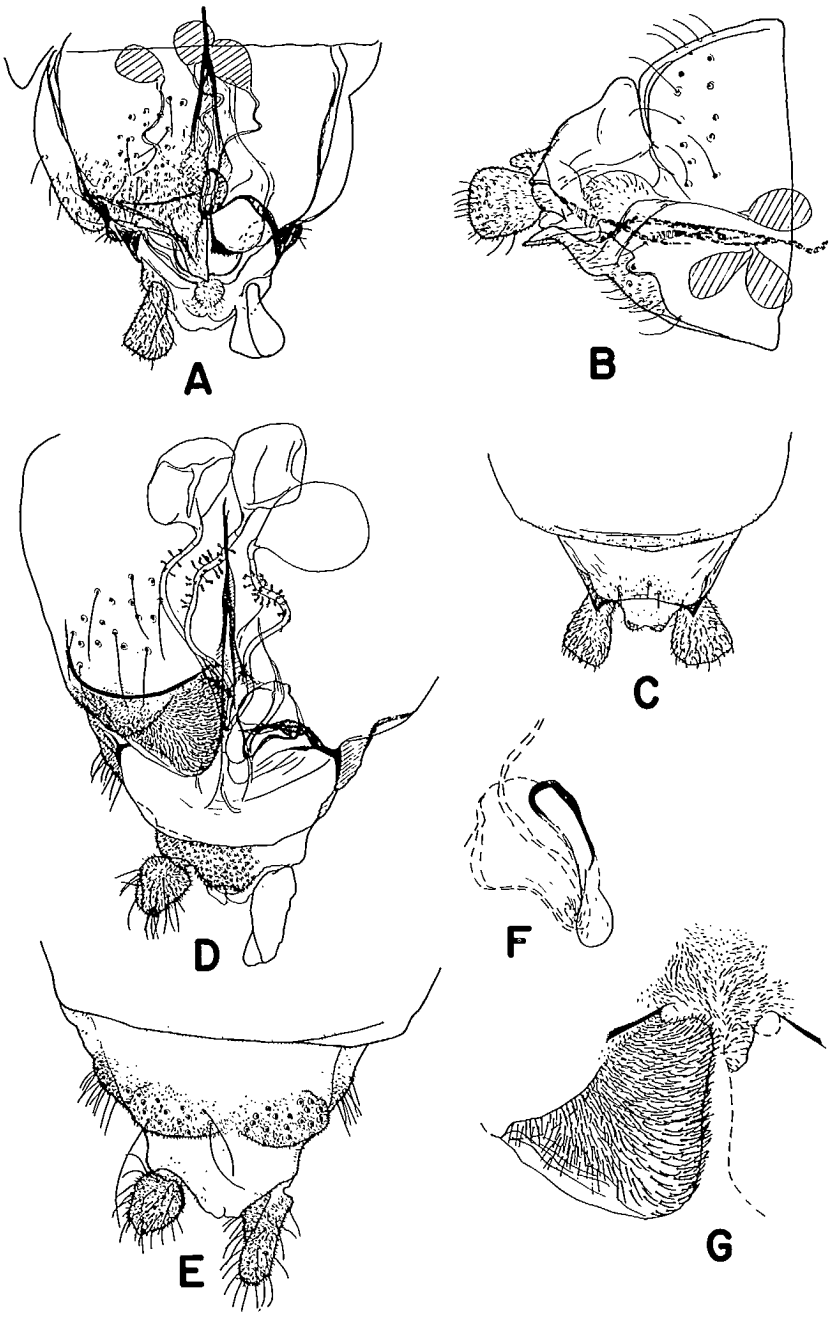

FIG. 31. Female genitalia of Diamesinae. A–C, *Boreoheptagyia* sp., Boreoheptagyini: A) ventral; B) lateral; C) dorsal. D–G, *Lobodiamesa campbelli* Pag., Lobodiamesini: D) ventral; E) dorsal; F) apodeme lobe; G) Gp VIII.

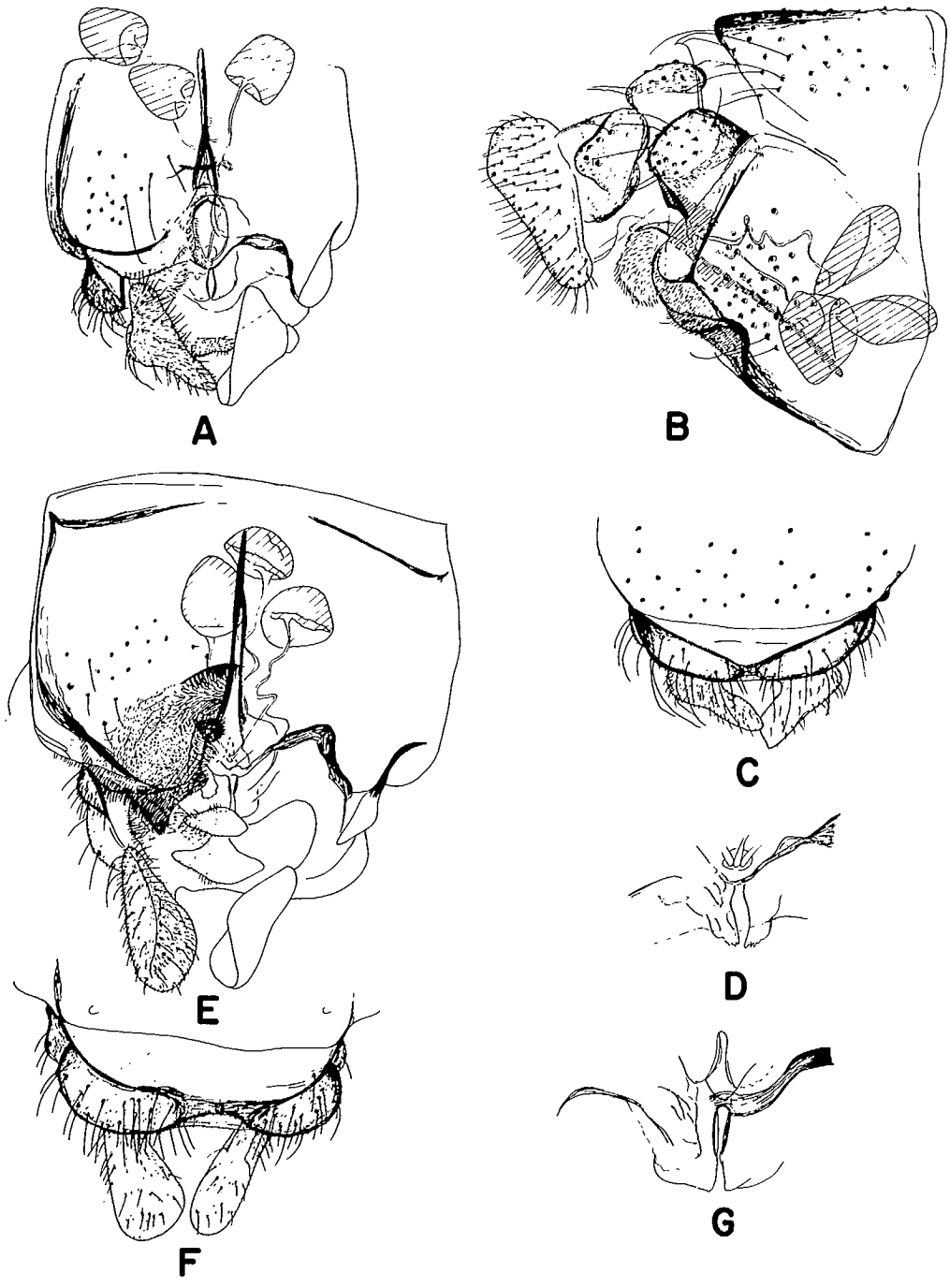

FIG. 32. Female genitalia of Diamesini, Diamesinae. A–D, *Pagastia orthogonia* Ol.: A) ventral; B) lateral; C) dorsal; D) labia. E–G, *Potthastia longimanus* Kieff.: E) ventral; F) dorsal; G) labia.

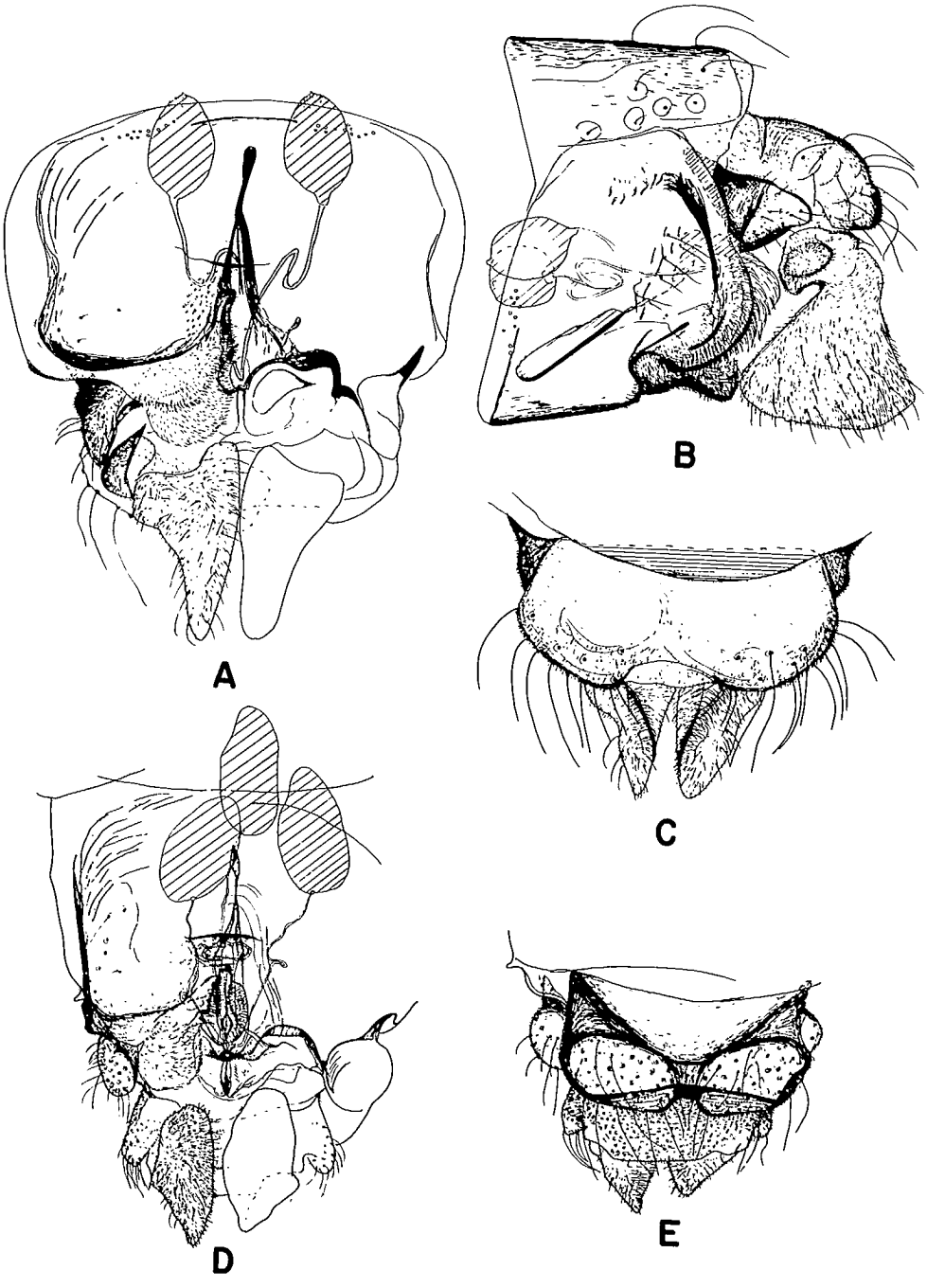

FIG. 33. Female genitalia of Diamesini. A–C, *Diamesa* sp.: A) ventral; B) lateral; C) dorsal. D–E, *Pseudodiamesa (Pachydiamesa) arctica* (Mall.): D) ventral; E) dorsal.

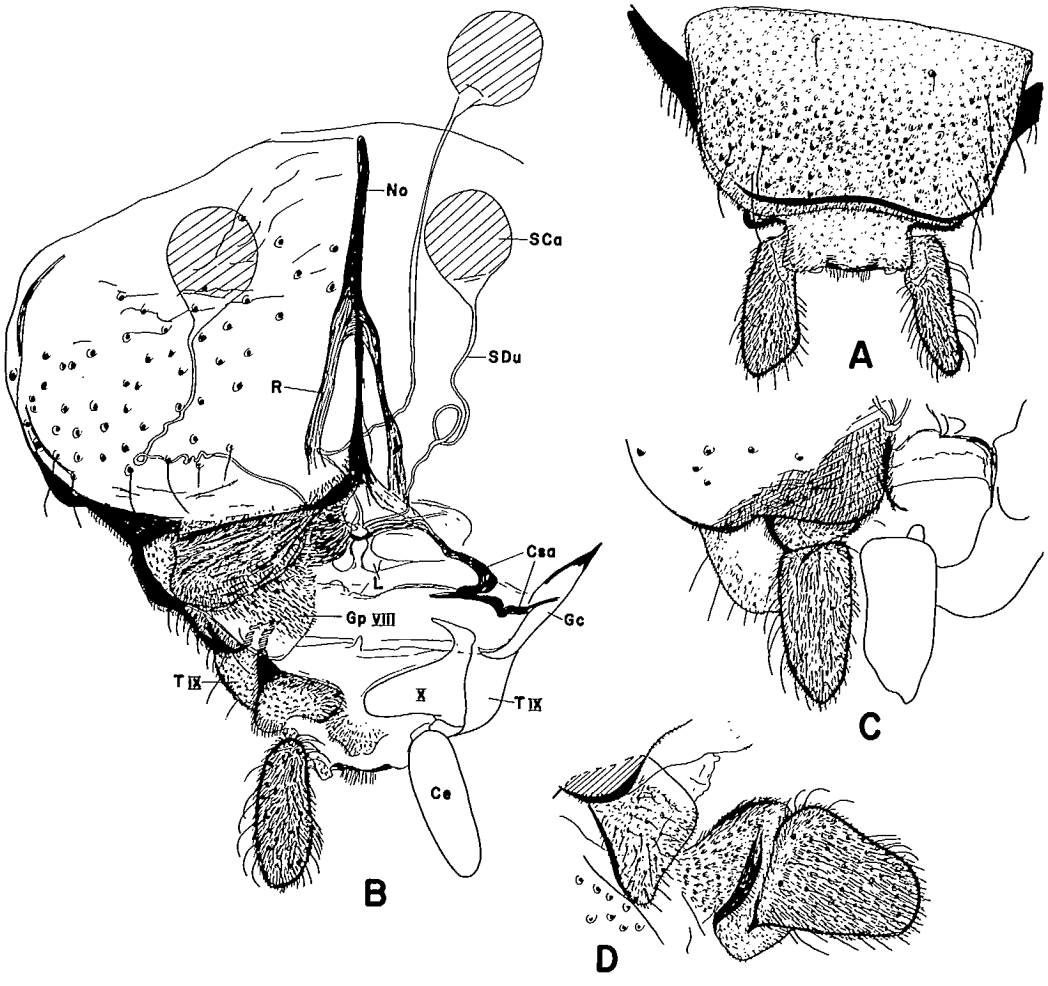

FIG. 34. Female genitalia of *Protanypus* sp. prob. *caudatus* Edw., Protanypodini, Diamesinae. A, dorsal. B, ventral. C, ventral view with vagina closed. D, Gc IX, segment X, and cercus in lateral view.

Sympotthastia Pag.
(Serra-Tosio 1971 pl. 124)

T IX apparently large. Gc IX large. Segment X without setae, lateral parts dark sclerotized. Postgenital plate apparently well developed. Cerci hexagonal with approximately equal sides.

3 oval seminal capsules.

Potthastia Kieff.
(Fig. 32E–G)

Species examined: *P. longimanus* Kieff.

Gp VIII large with ventrolateral lobe emarginated on caudomesal margin and partly covering dorsomesal lobe. Apodeme lobe vestigial. Gp IX well developed; notum very short, less than half as long as ramus. T IX of medium size, setigerous protrusions transversely oval. Transversely, approximately oval plate anterior of postgenital plate partly closes vagina caudally. Segment X without setae. Postgenital plate well developed, characteristically shaped. Cerci relatively large.

Labia broadly tongue-shaped, without microtrichia. 3 seminal capsules with weak microtrichia. Spermathecal ducts with weak curves.

TRIBE PROTANYPODINI
(Fig. 34)

Protanypus Kieff.
(Fig. 34; Sæther 1975b fig. 2; Wiederholm 1975 fig. 1)

Species examined: *P. ramosus* Sæth., *P.* ? *caudatus* Edw., *Protanypus* sp.n.

Gp VIII large to medium large, undivided but with mesal notch and anterior group of stronger microtrichia, membrane not apparent. Gp VIII can close under vagina and then appear simple and rounded (Fig. 34C). Gp IX well developed, notum about as long as ramus. T IX very large, rectangular, undivided, often with stronger sclerotized caudal margin. Gc IX apparently without setae. Coxosternapodeme with a strong median bend when vagina open, more evenly curved when vagina closed. Segment X with long, more or less curved orolateral projection, separated oral of small postgenital plate. Cerci simple, relatively large.

Labia simple, rounded, without microtrichia. 3 dark, ovoid seminal capsules with pale and more or less distinct funnel-shaped neck.

Very large undivided T IX of Protanypodini is of a more plesiomorphous nature than in other Diamesinae. On the other hand, characters such as the closable vagina, the coxosternapodemes, and orolateral extensions of segment X, probably are synapomorphous features of the tribe.

SUBFAMILY PRODIAMESINAE
(Fig. 35)

T VIII normal. S VIII with weak gonocoxapodeme. Gp VIII with narrow, mostly pencillike ventrolateral lobe not covering the about equally large dorsomesal lobe. Apodeme lobe present between and dorsad of principal lobes, indistinct to relatively distinct, sometimes with microtrichia. Membrane not evident. Gp IX well developed, rami parallel-sided, notum about as long as ramus. T IX of medium size, very faintly divided into setigerous protrusions with setae also sometimes present between protrusions. Gc IX well developed, separate from T IX, with several setae. Coxosternapodeme well developed, simply curved. Intergonocoxal connective always present. Segment X without setae. Postgenital plate small to well developed. Cerci more or less pediform.

Labia separate, tongue-shaped to rounded, without microtrichia. 3 seminal capsules covered with fine, short or long microtrichia. Spermathecal ducts long with bends or loops.

The shape of the Gp IX with parallel-sided rami is unique within Chironomidae and undoubtedly a synapomorphous feature of Prodiamesinae. A similar shape of Gc IX and T IX is found both within Diamesinae and specially within Orthocladiinae, although other formations are more common within both. A small pencillike ventrolateral lobe not covering any part of an equally large dorsomesal lobe is found in some Orthocladiinae and some Chironominae, but never within Diamesinae. The apex of the apodeme lobe is visible between the 2 principal lobes as in many Orthocladiinae and most Chironominae, but only in Heptagyini of Diamesinae. The apodeme lobe carries microtrichia at least in some *Monodiamesa*, a feature otherwise found only in *Limaya* Brund. and *Maoridiamesa* Pag. (Heptagyini), some *Psectrocladius* Kieff. (Orthocladiinae), *Rheotanytarsus* (Tanytarsini), and *Dicrotendipes* Kieff., *Glyptotendipes* Kieff., *Chironomus* Meig., *Kiefferulus* Goetgh., and *Einfeldia* Kieff. (Chironomini). As in most Diamesinae, there are 3 seminal capsules, although in the Orthocladiinae only some *Brillia* Kieff. and *Diplocladius* Kieff., are known to have 3. Among Diamesinae only *Pagastia* Ol. appears to have some fine microtrichia on the seminal capsules but all Prodiamesinae and several Orthocladiinae possess microtrichia. The spermathecal ducts open separately as in all Diamesinae and some Orthocladiinae.

Buchonomyia Fittk. (Fittkau 1955 p. 403–414) may belong here or in Diamesinae (see p. 63).

Key to females of Prodiamesinae

1 Gc IX in lateral view distinctly shorter than T IX; cerci with relatively short tapering "toe" ..... *Prodiamesa* Kieff. (p. 74)

Gc IX in lateral view nearly as large as or larger than T IX; cerci with long parallel-sided or tapering "toe" 2

2 Gc IX in lateral view larger than T IX; cerci pediform with parallel-sided "toe" ..... *Odontomesa* Pag. (p. 76)

Gc IX in lateral view nearly as large as T IX, cerci pediform with tapering "toe" ..... *Monodiamesa* Kieff. (p. 74)

Prodiamesa Kieff.
(Rodova 1969a fig. 2; Serra-Tosio 1964 fig. 3)

Ventrolateral lobe of Gp VIII with long microtrichia curved toward mesal apex. Gp IX with notum as long as ramus. Gc IX in lateral view shorter and smaller than T IX. Postgenital plate well developed, with parallel lateral margins. Cerci pediform with large rounded "heel," with apical point and short tapering "toe."

Monodiamesa Kieff.
(Fig. 35A–D; Brundin 1947 fig. 78)

Species examined: *M. tuberculata* Sæth., *Monodiamesa* sp.

Ventrolateral lobe of Gp VIII with rounded apex, microtrichia straight, directed mesad; dorsomesal lobe with oromesal protuberance; apodeme lobe relatively distinct, at least sometimes with apical microtrichia. Gp IX with notum slightly shorter than ramus. Gc IX in lateral view about as long and large as T IX. Postgenital plate well developed, elongate. Cerci pediform with pointed "heel" and long tapering "toe."

Seminal capsules with fine, relatively long, scattered microtrichia (Sæther 1973b p. 672).

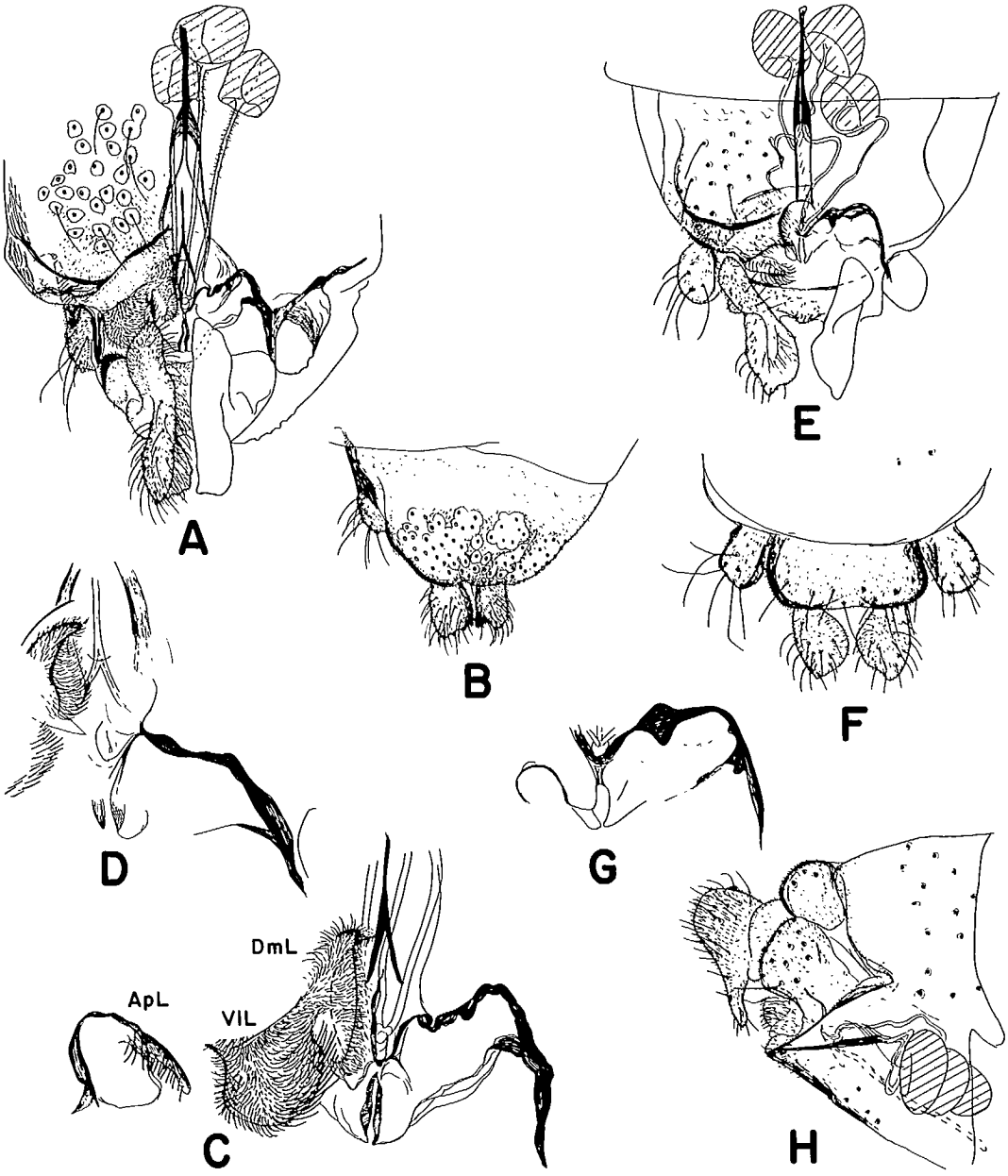

FIG. 35. Female genitalia of Prodiamesinae. A–C, *Monodiamesa* sp.: A) ventral; B) dorsal; C) coxosternapodeme, Gp VIII, and labia. D, *Monodiamesa tuberculata* Sæth., mesal part of Gp VIII, coxosternapodeme, and labia. E–H, *Odontomesa* cf. *fulva* (Kieff.): E) ventral; F) dorsal; G) coxosternapodeme and labia; H) lateral.

Odontomesa Pag.
(Fig. 35E–H)

Species examined: *O.* cf. *fulva* (Kieff.)

Ventrolateral lobe of Gp VIII with long microtrichia rising perpendicularly to lobe and curving mesad; dorsomesal lobe without oral protuberance, apparently without apical microtrichia. Gp IX with notum slightly longer than ramus. Gc IX in lateral view longer and larger than T IX. Postgenital plate barely differentiated, sides not parallel. Cerci pediform with long, partly parallel-sided "toe."

Labia tongue-shaped, curved mesad. Seminal capsules with very short and fine microtrichia.

Subfamily Orthocladiinae
(Fig. 37–61)

T VIII well developed, normal. S. VIII with gonocoxapodeme. Gp VIII simple or divided; apodeme lobe absent or present and distinct, covered or not covered by principal lobes; membrane present. Gp IX well developed, notum slightly shorter to somewhat longer than ramus. T IX large and well developed to relatively small or occasionally reduced; undivided, with caudal notch, cavity, or emargination, faintly divided, or strongly divided in setigerous protrusions; always with setae. Gc IX never fused with T IX, large to small, occasionally long and lobelike, and occasionally reduced; always with at least one seta. Coxosternapodeme well developed, usually simply curved, occasionally nearly straight or with several curves or bends, and in *Corynoneura* Winn. and some *Thienemanniella* Kieff. (Fig. 61) with one or several oral lamellae. Intergonocoxal connective apparently always present, but often very indistinct. Segment X normal, never with setae. Postgenital plate usually small to reduced, occasionally large. Cerci small to large, but mostly of moderate size.

Labia separate or occasionally fused and sclerotized *(Corynoneura* group, Fig. 61), without microtrichia except perhaps in *Heterotrissocladius* Spärck. 2 seminal capsules except in *Diplocladius* Kieff. (Fig. 37) and some *Brillia* Kieff. (Fig. 39D) where there are 3; with or without microtrichia. Spermathecal ducts straight, with bends or loops, occasionally extremely long *(Orthocladius* subgen. *Eudactylocladius* Thien., Fig. 46A); openings separate or common; with or without bulbs before opening; ducts usually not joined before common opening; occasionally joined for short or longer distance.

Phyletic Relationships within Orthocladiinae

There are a number of features in the orthoclad female genitalia of fundamental phylogenetic importance.

S VIII in *Metriocnemus* v.d. Wulp (Fig. 52A, E) and some *Nanocladius* Kieff. apparently form a minute floor under the anterior part of the vagina, somewhat similar to that found in Tanytarsini.

The Gp VIII in its most plesiomorphous form among Chironomidae is simple, long, and tongue-shaped. In Orthocladiinae the most plesiomorphous form is broader, more rounded. In the genera examined only *Chasmatonotus* Loew, *Abiskomyia* Edw., *Cardiocladius* Kieff., *Eukiefferiella* Thien., *Heterotanytarsus* Spärck, *Thienemanniella* Kieff., and *Corynoneura* Winn. are without any sign of a dorsomesal lobe. (In *Thienemanniella* there is a structure which may be a sclerotized and fused pair of vestigial dorsomesal lobes.) In *Diplocladius* Kieff., *Brillia* Kieff., *Metriocnemus, Thienemannia* Kieff., *Parorthocladius* Thien., *Chaetocladius* Kieff., *Limnophyes* Eat., *Clunio* Hal., *Camptocladius* v.d. Wulp, and *Pseudosmittia* Goetgh. there is a vestigial dorsomesal lobe consisting of a fine line with microtrichia surrounding the vagina anterior of the spermathecal eminence. The dorsomesal lobe is equally small, or nearly as small, in a few other genera, but more readily visible as it is not completely covered by the ventrolateral lobe, or because it has a small anterior projection. Finally, several genera have a dorsomesal lobe which is nearly

as large or, in *Zalutschia* Lip. (Fig. 51F), even larger than the ventrolateral lobe. In some genera it is difficult to observe that the Gp VIII is in fact double as the 2 lobes are equally long and overlapping (for instance *Hydrobaenus johannseni* (Subl.) Fig. 51C), whereas in others the 2 lobes are very distinct (as in *Heterotrissocladius* Spärck, Fig. 55A, D). From the above it will be clear that the principal lobe of Gp VIII is the ventrolateral lobe, and that the dorsomesal lobe develops from a line surrounding the vagina. In Chironominae the dorsomesal lobe is the principal lobe and the ventrolateral lobe develops from a lateral projection of Gp VIII. In other words, the ventrolateral and dorsomesal lobes of the 2 subfamilies are not directly homologous, and the division of Gp VIII in the 2 subfamilies is different and not parallel trends. The end result, however, may be very similar, and the capacity for division of Gp VIII is unique for Chironomidae (see p. 31, 131). In *Diplocladius*, the starting point both for Orthocladiinae, with a small linelike lobe around the vagina, and for Chironominae, with very small far lateral lobe, can be found.

T IX in its most plesiomorphous form among Chironomidae is very large and hood-shaped. In the Orthocladiinae this shape is fully realized only in *Diplocladius*. A very large T IX can be found in a number of plesiomorphic genera, but the shape is either rectangular, triangular, or of a more rounded triangular shape. The next steps in the evolution of T IX appear first as a caudal notch or weak emargination, followed by at first faint, later strong and complete division of the tergite into 2 setigerous protrusions. The wide and rounded caudal emargination in *Cardiocladius* (Fig. 39B), in *Chasmatonotus unimaculatus* Loew (Fig. 38E), and perhaps in *Ichtyocladius* Fittk., however, appear to be of a different nature and is interpreted here as a parallelism or a homoiology.

A reduction in size and number of setae on Gc IX often takes place simultaneously with a reduction of T IX, although in a few cases Gc IX is small and T IX is still large, or vice versa. The conspicuously long lobelike Gc IX in *Cardiocladius* (Fig. 39A, B) may be of a plesiomorphous nature although it seems more likely that they are a secondary development.

The coxosternapodeme is of phylogenetic importance mostly at the species level. Exceptions are *Zalutschia* (Fig. 51F) which has developed several curves and bends on the apodeme, *Corynoneura* (Fig. 61D, F), and part of *Thienemanniella* (Fig. 61A) which have weak to distinct lateral lamellae on the apodeme.

Segment X and the postgenital plate show little of phylogenetic importance. In *Metriocnemus*, however, sharply pointed caudolateral corners of segment X are developed, and *Psectrocladius* Kieff. often has mesally curved, sclerotized, ventral projections on segment X.

Size and shape of the cerci are of limited value.

Seminal capsules primitively carry microtrichia. These are present in a number of genera such as some *Brillia, Abiskomyia, Baeoctenus* Sæth., most *Hydrobaenus* Fries, *Nanocladius* Kieff., some *Orthocladius* v.d. Wulp, some *Cricotopus* v.d. Wulp, *Limnophyes*, and *Parakiefferiella* Thien. The presence and absence of the microtrichia within the same genus and their presence within unrelated genera show that the reduction of microtrichia as a trend is subject to numerous parallelisms and thus of minor importance.

Although *Diplocladius* obviously takes a plesiomorphic position within Orthocladiinae it possesses one strongly apomorphous feature, the fusion of 2 of the 3 spermathecal ducts for a relatively long distance. The common duct is longer than in any other examined chironomid although *Parochlus kiefferi* (Fig. 26A) has a relatively distinct common duct and some other Orthocladiinae have the ducts joined for a very short distance. The spermathecal ducts open separately (plesiomorphous) in *Brillia, Abiskomyia, Thienemannia, Cardiocladius, Rheocricotopus* Thien. et Harn., *Parorthocladius, Orthocladius* (some), *Halocladius* Hirv., *Cricotopus* (some), *Oliveria* Sæth., *Zalutschia* (some), *Chaetocladius, Bryophaenocladius* Thien., *Parakiefferiella* (some), and perhaps in *Phycoidella* Sæth.; there is a common opening (apomorphous) in the other examined genera. The presence of a common opening is also a trend subject to numerous parallelisms. The ducts are straight or nearly straight in a number of relatively plesiomorphic genera such as *Brillia, Heterotanytarsus, Psectrocladius, Baeoctenus* Sæth., *Paratrissocladius* Zavř., and *Synorthocladius* Thien. However, in some genera such as *Orthocladius, Cricotopus*, and *Parakiefferiella*, some species have straight ducts and others have one or several loops and bends. Again the lengthening of the duct is a trend which can be used only with caution because of the tendency to parallelism. The ducts of some genera and species *(Metriocnemus, Thienemannia* (weak), *Synorthocladius, Orthocladius* (some), *Halocladius, Cricotopus* (most), *Hydrobaenus*

(most), *Zalutschia* (most), *Chaetocladius, Limnophyes, Heterotrissocladius, Parametriocnemus, Parakiefferiella,* and possibly *Phycoidella)* have weak to strong bulbs before the opening or openings. Development of these bulbs is a useful trend for some groups and within some genera, but is also subject to numerous parallelisms.

Attempts to delineate the kladogenesis of phylogenetic branching of the Orthocladiinae genera by means of a scheme of argumentation or theoretical synapomorphic diagram (Hennig 1950, 1957, 1966) are presented in Fig. 36. To facilitate such a diagram, several genera have, in some cases, been grouped. These groups are mainly modifications of the groups used by Brundin (1956). For some genera or groups of genera the phyletic relationships have been shown in previous papers (Strenzke (1960) for the *Smittia–Clunio* group, Schlee (1968) for the *Corynoneura* group, Sæther (1975c) for the *Heterotrissocladius* group, Sæther (1976b) for the *Hydrobaenus* group). Some genera are placed very tentatively and are shown in parentheses in the diagram. Other genera cannot for the moment be placed even tentatively. This is primarily due to lack of knowledge of the female genitalia and immatures. In cases such as *Symbiocladius* Kieff. and *Ichtyocladius* Fittk. the extreme adaptation to a very specialized life obscure the interpretation of morphological details. The absence of an apical spine on the male gonostylus, the very large T IX, the apparently simple Gp VIII of the female, and the presence of a well-developed labral pecten of the larva indicate that *Ichtyocladius* (see Fittkau 1974), although showing several apomorphous and aberrant features, occupies a position near *Brillia, Abiskomyia,* or *Cardiocladius* and *Eukiefferiella. Petalocladius* Subl. et Wirth (Sublette and Wirth 1972 p. 1–4) appears to occupy a similar position perhaps most closely related to *Abiskomyia* and is, together with the Australian *Nasuticladius* Freem. (Freeman 1961 p. 650), tentatively placed together with *Abiskomyia* in the synapomorphic diagram. To simplify the scheme of argumentation, trends showing the same direction are grouped. Numbers in the diagram may refer to one or to several trends and parallelisms are not indicated. The following trends are used (a = apomorphous, p = plesiomorphous):

Trends 1 — Labia very large, strongly and completely sclerotized (a); small or large, never completely sclerotized (p).
— Coxosternapodeme with one to several well-developed lateral lamellae (a), with none or at most with one weak lateral lamella (p).
— Apodeme lobe large (a), small (p).
— Gp VIII short and rounded (a), longer, more lobelike and triangular (p).
— Larval antenna with 4 segments (a), with 5 (p).

Trend 2 — With a structure which may represent sclerotized and fused vestigial dorsomesal lobes (a), such structures not apparent (p).

Trends 3 — T IX and Gc IX of female reduced (a), well developed (p).
— Labia of female genitalia sclerotized and fused (a), separate (p).
— Apodeme lobe fully sclerotized (a), with a thin apodeme (p).
— R_{4+5} fused with costa (a), not fused (p).

Trends 4 — Dorsomesal lobe present (a), absent (p) (or possibly secondarily present and fused in *Thienemanniella).*
— T IX of male relatively small, not extending far caudally (a); relatively large, extending far caudally (p).
— Anal lobe of pupa without 3 lateral macrosetae, or when all macrosetae apparently lateral, placed at base of long projections and no fringe of setae present (a); anal lobe with 3 lateral macrosetae, fringe of setae and pair of mesal setae, anal lobe rounded (p).
(For trends 1–4 see also Schlee (1968 p. 84–107).)

Trends 5 — Costa shortened, R_{4+5} thickened (a); costa well developed, R_{4+5} not thickened and shortened (p).
— Larval antenna about ½ as long as mandible or shorter (a), longer (p).
(Some members of the group to the right *(Camptocladius,* some *Pseudosmittia)* show a division of T IX of the female but others have no caudal emargination.)

Trend 6 — Either marine or fully terrestrial (a), semiterrestrial or secondarily in fresh water (p).

Trends 7 — Ventrolateral lobe with a strong basal constriction (a), without (p).
— Wings of both sexes vestigial (a); well developed in male, reduced or vestigial in female (p).

Trends 8 — T IX of female with a wide caudal concavity (a), truncate (p).
— T IX visible in ventral view, cerci not visible in dorsal view (a); T IX not visible in ventral view, cerci visible in dorsal view (p).

Trend 9 — Palp 2-segmented (a), 5-segmented (p).

Trend 10 — Wing of both sexes reduced, halteres absent (a); wing and haltere well developed in male (p). (Parallel reduction takes place in *Tethymyia* Wirth.)

Trend 11 — Halteres absent in female (a), present (p).

Trend 12 — Wing of male without veins (a), with veins (p). (Parallel reductions take place both in *Belgica* Jac. and in *Tethymyia.)*

Trend 13 — Female with wing absent or reduced (a), well developed (p).

Trend 14 — Spermathecal duct strongly curved, with a far orally reaching loop (a); shorter (p). (This trend is somewhat doubtful because only descriptions of the spermathecal ducts in *Clunio* and *Thalassosmittia* Strenzk. et Remm. exist.)

Trends 15 — Anal tubules absent (a); present, although often reduced (p).
— Marine (a), terrestrial (p).

Trends 16 — Male antenna with black, stiff apical seta (a), without (p).
— Larva with 4 antennal segments or if with 5 segments, 3–5 minute (a); with 5, segments 3–5 distinct (p).
— Posterior parapods small and fused (a); separate (p).

Trends 17 — Integuments of pupa ventrally and dorsally with rows of spinules (a), without (p).
— Larval antenna strongly reduced, with only 4 segments (a); antenna about as long as mandible with segments 3–5 minute (p).
— Anterior parapods with only 3–5 longer claws (a), claws more numerous (p).

Trend 18 — Wing without setae on membrane (a), with (p).
(For trends 7–18 see also Strenzke (1960 p. 22–25) and Wirth (1949 p. 153–155).)

Trends 19 — Cu_1 strongly curved (or occasionally apical portion of Cu_1 absent) (a); slightly curved (p). *(Orthosmittia* Goetgh. has a straight Cu_1. This may be a result of the short cubital fork, absence of apical portion of Cu_1 as in some *Pseudosmittia,* or a secondary development. However, the immatures of *Orthosmittia* are unknown and the placement is tentative.)
— Wing without coarse punctation of microtrichia or setae (a), with (p).
— Squama without setae (a), with setae at least in female (secondarily reduced in some species) (p).
— Larval antenna reduced or 4-segmented or at least with segments 3–5 minute (a), well developed with segments 3–5 distinct (p).

Trends 20 — Anterior thoracic area of pupa with dense and coarse spines (a), smooth or with scattered spinules (p).
— Larval preanal segment bent so that anal segment and posterior parapods are directed ventrally at right angles to long axis of body (a), not bent (p).
— Short cylindrical anal segment and posterior parapods of larva can be completely withdrawn into preanal segment (a), cannot be withdrawn (p).

Trends 21 — Seminal capsules without microtrichia (a), with (p).
— Squama with few or no setae (a), fully fringed (p). (Parallel reduction takes place in *Heleniella* Gow. and in *Parakiefferiella* group.)

— Segment IX of pupa without 3 terminal setae (a), with well-developed short to long macrosetae (p).
— Procerci absent (a), present (p).
— Posterior parapods absent or reduced (a), well developed (p).

Trends 22 — Spermathecal ducts with distinct bulbs before common opening (a), without (p).
— Spermathecal duct with long loop reaching far orad (a), loop absent or shorter (p). (The loop can possibly be nearly as long in *Thalassosmittia.)*
— Tergites I, II, or III–VIII of pupa with anal row of spines (a); without spines or these present on fewer tergites (p). (Parallel development can be found in *Camptocladius.*)

Trends 23 — Terrestrial, marine, or secondarily in fresh water (a); in fresh water (p).
— Thoracic horn of pupa absent (a), present (p). (Parallel reductions take place in some species of several other genera to the left of Trends 23.)

Trends 24 — T IX of female strongly divided into 2 setigerous protrusions or at least setae only on lateral portions with a strong, caudal, square-cut emargination (a); T IX undivided or with a very weak caudal emargination or notch, sometimes with lateral concentrations of setae (p). (Parallel division takes place in *Camptocladius* and perhaps in some other genera of the same grouping in the diagram.)
— Dorsomesal lobe well developed, lobelike or when more linelike at least long and reaching caudad to labia (a); dorsomesal lobe small, linelike, surrounding anterior part of vagina (p). (Parallelly the lobe can be as large as in *Parametriocnemus* Goetgh., in *Gymnometriocnemus* and some *Smittia* Holmgr.)

Trends 25 — Acrostichals absent (a) (dorsocentrals may, however, meet posteriorly giving the impression of posterior acrostichals); acrostichals present, but reduced to a central tuft of weak setae (p).
— Blade at apex of basal antennal segment of larva almost twice as long as segments 2–5 combined (a), shorter than segments 2–5 combined (p).
— Ventromental plate of larva narrow (a), broad and distinct at least in more plesiomorphic species (p).

Trends 26 — Ventrolateral lobe reduced, not or only slightly larger than dorsomesal lobe (a); well developed, broad, rounded, much larger than the relatively well-developed dorsomesal lobe (p).
— Spermathecal ducts with bulbs before opening (a), without (p).
— Antepronotum with lateral setae only (a), covered with setae (p).
— Preepisternum and anepimeron without setae (a), with (p).
— Anal lobe of pupa sharply pointed, often produced into apicolateral projections (a); rounded (p).

Trends 27 — Squama without setae (a), with (p).
— Wing membrane without setae or strong microtrichia (a); with, at least in female (p).
— Cu_1 strongly and distinctly curved (a), less strongly (p).

Trends 28 — Setae of anal point of male conspicuously short and weak (a); strong, but often reduced in number (p).
— Pupal wing sheath with row of "pearls" (a), without (p). (Lindeberg (1962 p. 9) regarded this as a plesiomorphous character and Schlee (1968 p. 105) regarded it as apomorphous.)

Trends 29 — Vein R_{4+5} ends proximal of end of M_{3+4} (a), ends above end of M_{3+4} (p).
— Pedes spurii B "normal" or reduced (a), very long (p).
— Anal lobe of pupa without fringe of setae (a), with (p).
— Anal lobe of pupa without normal anal macrosetae (a), with (p).

Trends 30 — Gonocoxite of female with setae more than twice as long as cerci (a); of normal length, i.e. about as long as cerci (p).
— Tergites of pupa with strong posterior spines (a), without (p).

Trends 31 — Vein R_{4+5} ends above or proximal of end M_{3+4} (a), ends distinctly distad of end of M_{3+4} (p).
— Costa extended (a), not extended (p).

Trends 32 — Ventrolateral lobe of about same size as dorsomesal lobe (a), much larger (p).
— Antenna of larva with hairlike vestigial seventh segment (a); without (p). (A similar seventh segment is characteristic for several *Parakiefferiella*.)
— Lauterborn organs absent or vestigial (a), present and large (p).

Trends 33 — Spermathecal duct with angle or loop (a), straight or nearly straight (p).
— Pecten epipharyngis of larva consists of 3 weakly sclerotized, small, serrated scales (a); consists of 3 dark, sclerotized, smooth spines (p).

Trend 34 — Wing membrane with strong microtrichia (a); with setae, at least at apex in female, (p). (For trends 29–34, see also Sæther (1975c).)

Trends 35 — Spermathecal ducts with common or only slightly and indistinctly separate openings (a), with distinctly separate openings (p).
— Cu_1 distinctly curved (a), straight (p). (This trend is regarded of major importance here and not subject to parallelism. However, Cu_1 may be secondarily straight in *Orthosmittia* and in a few *Pseudosmittia*.)
— Larva without distinct labral scales between S I (a), with (p).

Trends 36 — Ventrolateral lobe with large, rounded oromesal projection (a), without (p). (A smaller projection is developed as a parallelism in *Gymnometriocnemus*.)
— Anal macrosetae of pupa strong and short, at most ½ as long as anal segment (a), longer, or secondarily absent (p). (Secondarily *Psilometriocnemus* Sæth. (Sæther 1969 p. 105–108) has similar macrosetae.)

Trends 37 — T IX of female either divided, with caudal notch or emargination, or at least with setae concentrated along caudal margin or on lateral portions (a); T IX undivided, large and triangular, or small and somewhat rectangular (p).
— Apodeme lobe small, but often distinct and visible between principal lobes (a); apodeme lobe minute, never distinct, not visible between principal lobes (p).
— Larval labrum without broad serrated plate between S I or between S I and S II, although sometimes with serrated scales or narrow plates (a); larval labrum with broad sclerotized plate with apical serration (sometimes secondarily reduced) (p).
— Larval premandible without or with small or reduced brush (a); with very strong brush (p).
(There are a number of other symplesiomorphies for *Metriocnemus* and *Thienemannia* such as the densely and completely hairy wings, long and strong acrostichals, numerous dorsocentrals, and densely haired abdominal tergites. However, all these characters can also be found in a few more apomorphic genera.)

Trends 38 — Anal point of male weak and narrow, sharply pointed, without setae or microtrichia (a); anal point when present and weak and sharply pointed, with microtrichia and/or setae at least at base (p).
— T II–VIII of pupa with caudal rows of blunt tubercles (a), tergites with caudal row of spines or unarmed (p).
— Larval mandible with seta interna consisting of conspicuously broad and plumose setae (a), setae less broad (p).
— Apex of larval prementum ventrally with 2 pairs of broad, right-angled plates with apical teeth covering prementum (Strenzke 1950 fig. 18) (secondarily reduced in several species) (a); lamelles of prementum of different form (p).

Trend 39 — Larval antennal segment 3 small, smaller than or as large as segment 4 when antenna well developed, vestigial together with segment 4 or 4 and 5 when antenna reduced (a); larger than segment 4 (p).

Trend 40 — Larval labrum without apically serrated plates or scales between S I (a); with apically serrated plates or scales, although often secondarily reduced (p).
(Trends 39 and 40 are somewhat ambiguous and the position of *Metriocnemus* and *Thienemannia* uncertain. However, trends 37 and 38 seem to be secure and the 2 genera show several common features with some of the more plesiomorphic genera to the right.)

Trends 41 — Ventrolateral lobe of Gp VIII much smaller than dorsomesal lobe (a), as large or larger (p).
— Coxosternapodeme with several curves or bends (a), at most with one strong bend (p). (These 2 trends will separate *Zalutschia* from all other Orthocladiinae. Although the female of *Trissocladius* Kieff. has not been examined, the genus is included here because these trends will be either synapomorphous for species of *Zalutschia* or for the genera *Trissocladius* and *Zalutschia* combined.)
— Oral projections of male sternapodeme well developed, rounded, transverse sternapodeme straight or concave (a); projections absent or narrow, triangular, transverse sternapodeme convex (p).
— Tergites of pupa with elevated patches of spinules (a), tergites flat (p).
— Chaetulae laterales of larva serrated (a), smooth (p).

Trends 42 — Acrostichals absent (a), present (p).
— Cu_1 distinctly but weakly curved (a), very slightly curved apically or straight (p).
— Setae absent underneath ventromental plates of larva (a), present (p).

Trends 43 — Tergite IX of male including anal point with less than 40 setae (a); with more than 40 setae, or occasionally number secondarily reduced (p).
— Median lobes of antepronotum at most meeting at a point anterior of scutum (a), joined along a broad or a very narrow suture (p).
(The first 2 trends under Trends 41 may also belong here as mentioned above.)

Trends 44 — Spermathecal duct with distinct bends, curves, or loops (a); nearly straight or with only weak bends or curves (p).
— Sensilla chaetica absent on middle leg in both sexes (a), usually present on middle leg in both sexes (p).
— Shagreenation reduced on T II–VIII of pupa (a), very extensive (p).
— Fringe of anal lobe of pupa short and reduced (a), setae and fringe long and well developed (p).
— Anterior chaeta of larval maxilla longitudinally curled, often forms a nearly complete cylinder (a); not curled, bladelike (p).

Trends 45 — Seminal capsule ovoid or oblong (a), spherical (p).
— Spermathecal ducts with common opening (a), separate openings (p).
— Pulvilli absent (a); small, but distinct (p).
— Sternapodeme of male with well-developed oral projections (a), oral projections absent or very small (p).

Trends 46 — T IX of female small (a); large, well developed (p).
— Clypeus wider than pedicel (a), narrower (p).
— Tarsal pseudospurs present on front leg (a), absent (p). (This trend may possibly go in the opposite direction.)
— T IX of male with heavy black appendages (a), without (p).
— Genital sac of pupa large, swollen, overreaching anal lobe (a); normal (p).
— Some chaetulae laterales of larval palatum serrated (a), all smooth (p).
(For trends 41–46 see also Sæther (1976b).)

Trend 47 — Dorsomesal lobe well developed, broadly triangular, with broad base, slightly smaller to much larger than ventrolateral lobe although often overlapping with this, ventrolateral lobe brushlike (a); dorsomesal lobe less well developed, either a narrow line with microtrichia surrounding anterior part of vagina or narrow triangular with a narrow point, usually much less wide at base than ventrolateral lobe, at most equally wide at base, but then with a secondary oromesal projection (p).

Trend 48 — Apodeme lobe with well-developed apodeme sometimes visible between principal lobes (a), apodeme lobe with very weak apodeme not visible between principal lobes (p).

Trends 49 — Pedicel of both sexes without setae (a), female pedicel with setae (p).
— Larval premandibular brush absent or when present vestigial (a), present and large or reduced to small serrated lamellae (p).

Trends 50 — Anal macrosetae of pupa at most ⅓ as long as anal segment (a), longer (p).
— Thoracic horn absent (a), present (although occasionally secondarily reduced) (p).
— Lauterborn organ of larval antenna absent (a), present (p).

Trends 51 — Lobes of Gp VIII do not form a distinct oral concavity (a), lobes form an oral concavity (p).
— Verticals not present in pupa (a), present (p).
— Apical tooth of larval mandible shorter than combined width of remaining teeth (a), longer (p).

Trends 52 — Anterior prealars (anterior notopleural setae) absent (a), present (p). (Parallel reductions take place in most *Halocladius* and *Cricotopus*.)
— Pupal thorax dorsally with blunt spines (a), rugulose or smooth (p).

Trend 53 — Dorsocentrals short and decumbent (a); normal, erect (p).

Trend 54 — Seta interna of larval mandible absent (a), present (p).

Trends 55 — Frontal setae of pupa absent (a), present (p).
— S I bifid (a), with more branches or when bifid each branch partly plumose (p).

Trends 56 — Postorbitals absent (a), present (p).
— Premandible of larva with 1 apical tooth (a), with 2 (p).

Trends 57 — Ventrolateral lobes cover vagina and meet at midline (a), do not meet at midline (p).
— Antepronotal lobes meet at a point or a short suture anterior of scutal projection (a), meet at a long suture (p).
— Anal point of male absent or strongly reduced (a), present and mostly well developed (p).

Trends 58 — Ventrolateral lobe not completely covering dorsomesal lobe (a), completely covering dorsomesal lobe (p).
— T IX of female completely and strongly divided into 2 setigerous protrusions (a), faintly divided (p).
— Eyes naked (a), hairy (p).
— Inner spur of metatibia with S-bend (a), without (p).
(For trends 49–58 see also Hirvenoja (1973 p. 55–68).)

Trend 59 — Ventromental plates without setae underneath (a), with (p).

Trends 60 — Ventrolateral lobe small and brushlike, not larger than dorsomesal lobe including anteriomesal projection (a); much larger than dorsomesal lobe (p).
— S I of larva (secondarily) simple (a), bifid (p).

Trend 61 — Dorsomesal lobe with anteriomesal rounded or occasionally pointed projection (although often covered by ventrolateral lobe) (a), without anteriomesal projection (p).

Trends 62 — T II of pupa without posterior row of recurved spines or spinules (a), with weak to strong row of recurved spines (p).
— Tooth part of larval mandible reduced relative to total length of mandible (a), well developed (p).
— Seta interna of larval mandible absent (a), present (or secondarily lost in *Acricotopus* Kieff. and *Paratrichocladius* Sant. Abr.) (p).

Trends 63 — None or small pulvilli (a), well-developed pulvilli (p).
— Anal lobe of pupa without fringe of setae (a), with (p).
— S I of larva simple or bifid (occasionally further split, but bifid nature still visible) (a); S I plumose or palmate (occasionally secondarily reduced) (p).

Trends 64 — Ventrolateral lobe broadly rounded, often slightly shortened, not covering any part of dorsomesal lobe and only base of distinct apodeme lobe (a); ventrolateral lobe covering all apodeme lobe and part of dorsomesal lobe (except *Synorthocladius* with secondarily reduced brushlike ventrolateral lobe and dorsomesal lobe with anteriomesal projection) (p).
— Larval procerci with spurs (secondarily reduced in some species) (a), without spurs (p).

Trends 65 — Apodeme lobe present and often distinct (a), absent (p). (Parallelly developed in *Diplocladius.*)
— Dorsomesal lobe present, although often minute (a); absent (p). (Parallelly there is a small dorsomesal lobe in *Diplocladius* and in *Brillia.*)
— Larval antenna without large alternating Lauterborn organs (a), with (p).

Trends 66 — Spermathecal ducts with common and very broad opening (a); spermathecal ducts primitively open separately (when secondarily with common opening as in most genera, opening less wide) (p).
— T IX of female strongly divided (a); undivided or secondarily divided (p).
— Two lateral setae of T II–VI of pupa short, thick, and spinelike (a); not spinelike (p).

Trend 67 — There apparently are no nonambiguous trends here. However, except for *Metriocnemus, Thienemannia,* and *Bryophaenocladius,* all genera to the right have T IX of female faintly to strongly divided into 2 setigerous protrusions, or at least a division indicated by a caudal notch or weak emarginations or by a concentration of setae on lateral portions. Genera to the left have T IX large and undivided and no indications of setigerous protrusions. However, a secondarily developed wide U-shaped emargination is present in *Cardiocladius* and some *Chasmatonotus.*

Trend 68 — S I of larva simple (secondarily split in some species of *Eukiefferiella)* (a), plumose or bifid (secondarily simple in a few species) (p).
(*Cardiocladius* and *Eukiefferiella* appear to differ in several particulars. The genus *Tokunagaia* Sæth. (syn. *Adactylocladius* Sæth, pro parte), however, with males not clearly separable from *Eukiefferiella* and with immatures clearly of *Cardiocladius* type, show that these 3 genera are closely related. Furthermore, the male genitalia of some species of all 3 genera are of identical type.)

Trends 69 — Male gonostylus with apical spine and additional preapical tooth, point, or crista dorsalis (secondarily reduced in a few species) (a); male gonostylus without apical spine, but with an apical point, tooth, or crista dorsalis (p). (Schlee (1975 p. 340) regards this and the following trend as going in the opposite direction.)
— Hind tibia with a comb of setae or at least with some stronger apical setae or 1 strong apical seta (a), without any trace of comb or stronger setae (p).
— Outer spur of hind tibia less than $\frac{2}{3}$ as long as inner spur (a), more than $\frac{2}{3}$ (p).
— Ventromental plates vestigial to moderately large, but never of Chironominae shape (a); of Chironominae shape (p).

Trends 70 — Anal lobe of pupa without any setae, with caudolateral pointed projections, and shallow U-shaped emargination between projections (a); anal lobe with setae (occasionally secondarily reduced), without caudolateral projections (or projections secondarily present), emargination between caudolateral parts of anal lobe less shallow (p).
— Larval antennal tubercle with prominent apical spur (a), without (p). (The last trend may possibly go in the opposite direction.)

Trends 71 — Two seminal capsules (a), 3 seminal capsules (although often secondarily reduced) (p).
— Wings not distinctly patterned (a), heavily marked with black (or often secondarily without markings) (p).
— Volsellae reduced to relatively well developed (a), volsellae strongly developed (p).
— Male gonostylus with apical spine, tooth, and/or crista dorsalis (a); without spine, crista dorsalis, or tooth, occasionally with strong apical setae (p). (The apparently minute apical spine in *Brillia par* Coq. (Sublette 1966b fig. 7, 1967b fig. 7) is only one of several apically situated thick setae.) (Schlee (1975 p. 340), however, regards the last trend as going in the opposite direction.)

Trend 72 — Pupal thoracic horn bifid at apex (a), not bifid (p).
(This trend has to be more closely examined as only the pupae of *Brillia* and *Propsilocerus* Kieff. are presently known. The 2 females of *Brillia* examined have also quite different types of seminal capsules. The species with 2 seminal capsules of differing size may possibly be *Brillia par*. The larva of this species has the second antennal segment only slightly shorter than the third, and the apical strong spinelike setae of the male gonostylus mentioned above separates the male from other species of *Brillia*. *B. par* may deserve generic rank and the apical setae of the gonostylus may be a feature synapomorphous with *Eurycnemus* v.d. Wulp and a first step toward the development of an apical spine (see Brundin 1956 p. 49 fig. 22).)

Trends 73 — T IX modified (divided, notched, triangular, reduced, etc.) (a); T IX large, hood-shaped (p).
— Gp VIII without indication of a far lateral lobe (a), with (p).
— Ventromental plates reduced to large, when very large without long and strong setae underneath (a); plates very large, with very strong and long setae underneath (p).

Trend 74 — Spermathecal ducts joined for a long distance (a); ducts primitively with separate openings, secondarily with common opening or occasionally joined for a very short distance (p).

Although most present findings of the phyletic relationships within Orthocladiinae appear to be well established by numerous trends, a number of parallelisms and ambiguous trends can also be found. Most in doubt are the general positions of *Chaetocladius*, *Metriocnemus* plus *Thienemannia*, and *Corynoneura* plus *Thienemanniella*. The exact position of *Heleniella* plus the genera grouped together with *Parakiefferiella* may also be different from the one shown here. The lack of knowledge of female genitalia and immatures prevents placement of some genera and others are placed only tentatively. The diagram thus can only be regarded as preliminary, and should be subject to further improvements and additions by future research. A project such as a comparative morphology of the larval mouthparts, particularly the maxilla, labrum, palatum, and prementohypopharyngeal complex certainly would throw additional light on the phyletic relationships of Orthocladiinae. Nevertheless, it seems clear that although Brundin (1956) in most cases was correct about the relative plesiomorphy or apomorphy of the different genera and about their relationships, his division of Orthocladiinae into two tribes, Orthocladiini and Metriocnemini, does not hold up. The Metriocnemini sensu Brundin minus *Thienemanniella* and *Corynoneura* and with the addition of *Heterotrissocladius* and *Paratrissocladius* do, however, appear to be a monophyletic unit. The Orthocladiini sensu Brundin, however, is not monophyletic. If Orthocladiinae were to be divided into tribes following the present scheme of argumentation, 8 tribes or subtribes would be needed to give the division practical value, namely: Diplocladiini, Eurycnemini, Abiskomyini, Cardiocladiini, Heterotanytarsini, Orthocladiini, Metriocnemini, and Corynoneurini, or with the last 4 tribes regarded as subtribes of Orthocladiini (Heterotanytarsina, Orthocladiina, Metriocnemina, Corynoneurina). However, if one accepts the view that the lack of a hind tibial comb and lack of an apical spine at the apex of the male gonostylus are apomorphies rather than plesiomorphies, then "Diplocladiini", "Eurycnemini", and "Abiskomyini" as used above would form a monophyletic unit, the Eurycnemini. In view of the preliminary nature of the present argumentation, it is better at present to keep the subfamily undivided.

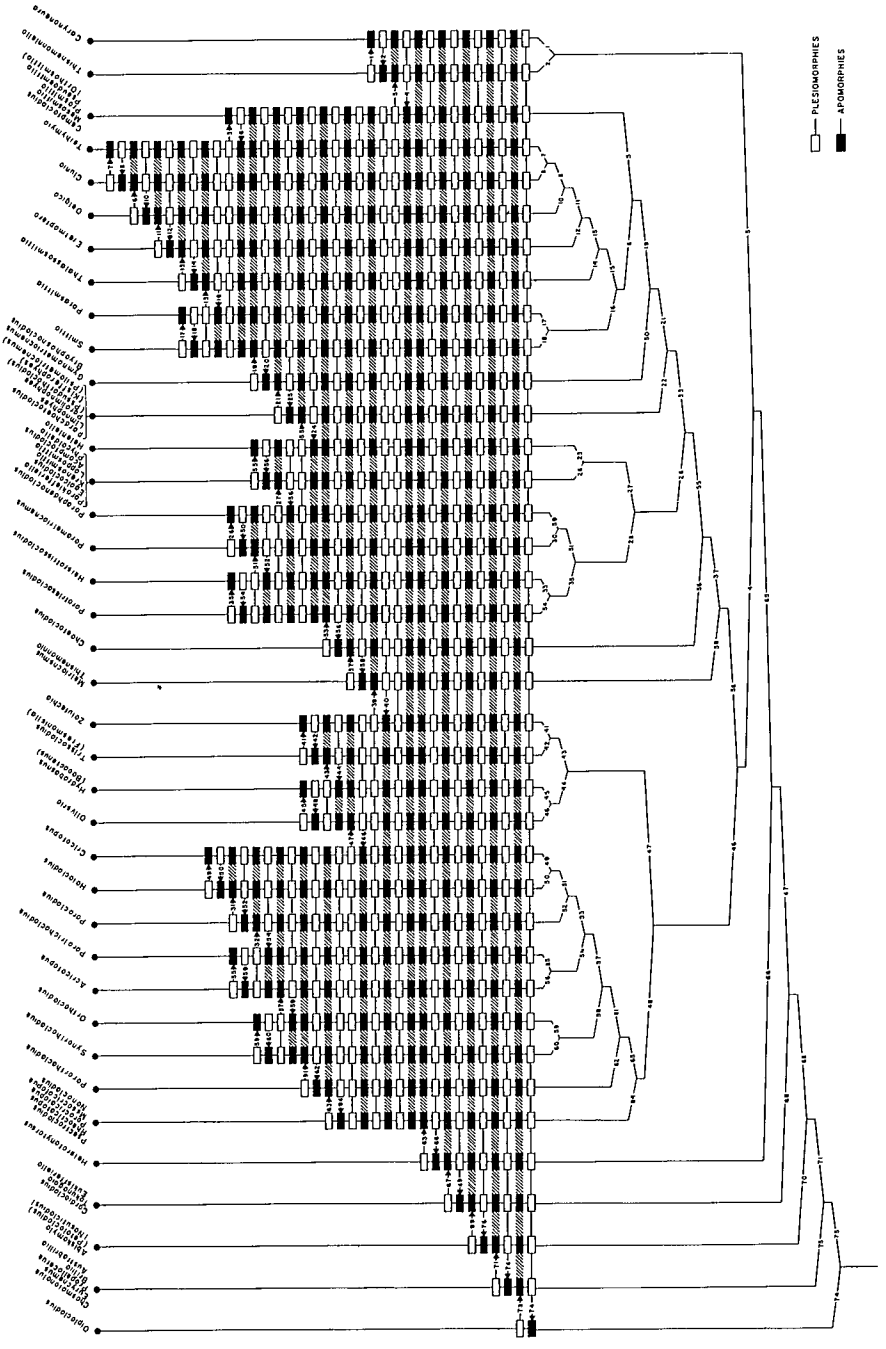

FIG. 36. Scheme of argumentation delineating the kladogenesis of genera of the Orthocladiinae by means of trends 1–74 (p. 78–85). Genera in parentheses tentatively placed.

Preliminary key to females of Orthocladiinae

(In the following key most genera of Orthocladiinae have been included even if the female genitalia have not been examined. However, some genera are placed tentatively together with others in a couplet and a few mainly exotic ones cannot be placed for the moment. The distribution is noted only for genera occurring outside the Holarctic region.)

1 Wings nearly always heavily marked with black, when not, clypeus produced as a short proboscis, or antepronotum with median group of setae, and squama and eyes bare 2

Wings never distinctly patterned; clypeus not produced as a short proboscis; when antepronotum with median group of setae either setae on squama, or eyes hairy 4

2 Pulvilli present; antepronotum with median group of setae; Gp VIII undivided; T IX either triangular and undivided, or with a deep, wide caudal emargination and with caudolateral corners ..... *Chasmatonotus* Loew (p. 95)

Pulvilli absent; antepronotum without median group of setae; Gp VIII at least sometimes divided; T IX probably always large and undivided 3

3 Eyes hairy; clypeus not produced ..... *Diplocladius* subgen. *Stictocladius* Edw. (South America, Australia, New Zealand)

Eyes bare; clypeus produced as a short proboscis ..... *Nasuticladius* Freem. (Australia)
(*Allometriocnemus coloensis* Freem., will also key here but has setae at apex of wing membrane.)

4 Mouth parts greatly elongated to form a sucking tube sometimes as long as whole body; wing membrane with setae ..... *Rhinocladius* Edw. (South America, Australia)

Mouth parts not produced into long tube; wing membrane with or without setae 5

5 Wings absent or strongly reduced 6

Wings well developed 9

6 Palp 2-segmented; hind tibial comb absent; halteres absent 7

Palp 5-segmented; hind tibial comb reduced to distinct; halteres present or absent 8

7 Gp VIII with large rounded or triangular ventrolateral lobe and linelike dorsomesal lobe; cerci situated ventrally, not visible in dorsal view; T IX visible in ventral view, with wide caudal emargination; ta_2 of hind leg shorter than ta_3 ..... *Clunio* Hal. (p. 103)

Gp VIII with ventrolateral lobe constricted at base; cerci situated caudally; T IX not visible in ventral view, caudally truncated; ta_2 of hind leg about as long as ta_3 ..... *Tethymyia* Wirth (p. 103)

8 Halteres absent; flagellum 6-segmented; Gp VIII undivided or with linelike dorsomesal lobe ..... *Belgica* Jac. (Antarctica) (p. 103)

Halteres present; flagellum 3-segmented; Gp VIII unknown ..... *Eretmoptera* Kell.

9 Hind tibial comb absent, vestigial, or consisting of only 1–4 setae 10

Hind tibial comb present and distinct with more than 5 setae 18

10 No true spurs present on front and middle tibia, hind tibial comb of 4 spines; T IX very large, covering most of cerci and all segment X in dorsal view, rectangular with wide posterior emargination; Gp VIII simple ..... *Ichtyocladius* Fittk. (South America) (p. 95)

Front and middle tibia with spurs, hind tibial comb absent, not separated from more basal spiniform setae or consisting of 1 heavy spine; T IX probably always smaller; Gp VIII simple or divided 11

11 Wing membrane with setae at least at apex; small to large pulvilli present; palp 5-segmented 12

Wing membrane without setae; pulvilli absent or very small; palp 4- or 5-segmented 13

12 Antepronotum with lateral and median setae; scutum conically produced; pulvilli large ..... *Eurycnemus* v.d. Wulp

Antepronotum with lateral setae only; scutum not produced; pulvilli small ..... *Heterotanytarsus* Spärck (p. 96)

13 Palp 4-segmented or when 5-segmented, acrostichals either strong and starting in front at antepronotum, or absent and brachiolum with less than 40 sensilla campaniformes and no single heavy spiniform seta forming hind tibial comb 14

Palp 5-segmented; acrostichals either a few in a lighter median area of scutum, or absent and brachiolum with more than 40 sensilla campaniformes and 1 heavy spiniform seta forms vestigial hind tibial comb 17

14 Acrostichals strong, starting in front at antepronotum; squama with less than 10 setae ..... *Bryophaenocladius* Thien., pro parte (p. 103)

Acrostichals absent or present only in center of scutum; squama with 10 or more setae 15

15 Middle and hind tibia each only with 1 spur; wing membrane without punctation of microtrichia ..... *Symbiocladius* Kieff.

Middle and hind tibia each with 2 spurs; wing membrane with fine to moderately heavy punctation of microtrichia 16

16 Small pulvilli present; wing membrane with fine punctation of microtrichia; palp 4-segmented ..... *Propsilocerus* Kieff.

Pulvilli absent; wing membrane with moderately heavy punctation of microtrichia; palp 4- or 5-segmented ..... *Trissocladius* Kieff.

17 T IX rectangular; Gp VIII simple; seminal capsules more than twice as large as cerci; a few long acrostichals in lighter median area of scutum ..... *Abiskomyia* Edw. (p. 95)

T IX triangular, faintly divided; Gp VIII divided into ventrolateral and dorsomesal lobes of about same size; seminal capsules small; acrostichals absent ..... *Baeoctenus* Sæth. (p. 100)

18 Eyes hairy; squama with setae or when without setae pulvilli well developed 19

Eyes bare, at most pubescent with longest microtrichia shorter than height of ommatids, or, when hairy, squama without setae and pulvilli absent or vestigial 30

19 Dorsocentrals short and decumbent; T IX faintly divided into 2 setigerous protrusions or at least with setae concentrated on lateral portions; Gp VIII with large ventrolateral lobe which completely covers dorsomesal lobe 20

Dorsocentrals long and erect; T IX undivided to strongly divided; Gp VIII simple to double, dorsomesal lobe when present vestigial to as large as ventrolateral lobe 22

20 Anterior portions of dorsomesal and ventrolateral lobes together with mesal portion of Gca VIII form an oral cavity with dark sclerotized margins; T IX very faintly divided or undivided but with setae concentrated on lateral portions ..... *Paracladius* Hirv. (p. 98)

No distinct oral cavity; T IX faintly to relatively strongly divided into 2 setigerous protrusions 21

21 Anterior prealars present; paratergites without setae; spermathecal ducts always with loops ..... *Halocladius* Hirv. (p. 99)

Anterior prealars usually absent, when present paratergites with setae; spermathecal ducts usually with loops, occasionally straight ..... *Cricotopus* v.d. Wulp (p. 99)

22 Pulvilli present and well developed; T IX probably always strongly divided or with square-cut caudal emargination; dorsomesal lobe probably always well developed and about as large as ventrolateral lobe 23

Pulvilli absent; T IX divided or undivided; dorsomesal lobe present, vestigial, or absent 25

23 Two short acrostichals in center of scutum; seminal capsule oblong with neck situated near anterior end of long side; T IX with square-cut caudal emargination or faintly divided into 2 setigerous protrusions ..... *Nanocladius* Kieff. (syn. *Microcricotopus* Thien. et Harn.) pro parte (p. 97)

Acrostichals short to moderately long, starting in front near antepronotum; seminal capsule with weak neck situated at caudal end; T IX probably always strongly divided into setigerous protrusions 24

24 Setae of abdominal tergites in median and anal transverse, regular rows; Gp VIII and spermatheca not known ..... *Paracricotopus* Thien. et Harn.

Setae of abdominal tergites irregularly scattered; ventrolateral, dorsomesal, and apodeme lobes well developed and distinct, but ventrolateral lobe short and wide at base; spermathecal ducts open separately without any bulbs before opening ..... *Rheocricotopus* Thien. et Harn. (p. 97)

25 Two short acrostichals in center of scutum; T IX probably always divided at least by caudal emargination 26

Short to long acrostichals starting in front at antepronotum; T IX divided or undivided 27

26 Prealars absent; Gc IX with caudomesal pointed projection ..... *Nanocladius* subgen. *Plecopteracoluthus* Steff. pro parte

Prealars present; Gc IX probably without projection ..... *Mesocricotopus* Brund.

27 Dorsocentrals numerous, in double to multiple row; T IX probably always undivided; dorsomesal lobe probably always vestigial and linelike or absent 28

Dorsocentrals few, in 1 row; T IX at least faintly divided; dorsomesal lobe developed, but hidden by large ventrolateral lobe 29

28 Acrostichals long; squama with about 2 setae; T IX undivided; dorsomesal lobe vestigial, linelike ..... *Thienemannia* Kieff. (p. 100)

Acrostichals short; squama with about 8–10 setae; T IX and dorsomesal lobe not known ..... *Petalocladius* Subl. et Wirth

29 Cerci with a group of longer ventral setae; temporals absent; palp short ..... *Acricotopus* Kieff. (p. 98)

Cerci without differentiated ventral setae; temporals present; palp normal ..... *Paratrichocladius* Sant. Abr. (syn. *Syncricotopus* Brund.) (p. 98)

30 Long acrostichals present, starting at antepronotum; costa extended; wing membrane usually with setae; Cu_1 distinctly curved; squama with setae 31

When long acrostichals present, costa not extended, wing membrane without setae or Cu_1 straight; squama with or without setae 33

31 Distinct pulvilli present; wing membrane with or without setae ..... *Pseudorthocladius* Goetgh.

(Cranston 1975 p. 89, however, shows that the formally correct name is *Pseudokiefferiella* Laur. nec Zavř.)

Pulvilli absent or vestigial; wing membrane with setae 32

32 R_{4+5} ends proximal to end of M_{3+4} ..... *Paraphaenocladius* Thien.

R_{4+5} ends above M_{3+4} ..... *Parametriocnemus* Goetgh. (p. 101)

33 Third reduced seminal capsule present with separate duct and opening (Fig. 37B), 2 remaining seminal capsules with spermathecal ducts joined for a distance almost $\frac{2}{3}$ as long as capsules; eyes hairy; squama without setae ..... *Diplocladius* subgen. *Diplocladius* Kieff. (p. 94)

Third seminal capsule absent, ducts at most joined for a very short distance; eyes bare or hairy; squama with or without setae 34

34 T IX large, at least as long as cerci in dorsal view, triangular, semicircular, or rectangular, never strongly divided into setigerous protrusions and with posterior emargination or notch only when triangular; eyes mostly bare; wing membrane with setae or bare with fine punctation of microtrichia 35

T IX usually smaller, when longer than cerci more or less strongly divided into 2 setigerous protrusions or with a posterior emargination, never triangular or semicircular, when as long as cerci, eyes hairy or wing membrane with coarse punctation of microtrichia 39

35 T IX triangular or semicircular; spermathecal ducts with common opening; Gc IX small or large; Gp VIII divided, dorsomesal lobe vestigial or well developed 36

T IX approximately rectangular; spermathecal ducts with common or separate openings; Gc IX large; Gp VIII simple or with vestigial dorsomesal lobe 37

36 T IX triangular with apical notch; Gp VIII divided into ventrolateral and dorsomesal lobes of about equal size; segment X without pointed caudolateral corners; cerci very large; wing membrane without setae; acrostichals short ..... *Hydrobaenus* Fries pro parte (*H. lugubris* group Sæther 1976b) (p. 99)

T IX triangular to semicircular without apical notch; ventrolateral lobe large, dorsomesal lobe vestigial; segment X with pointed caudolateral corners; cerci of moderate size; wing membrane with setae; acrostichals very long ..... *Metriocnemus* v.d. Wulp (p. 100)

37 Spermathecal ducts straight or nearly straight, with separate openings; 2 or 3 seminal capsules, when 2, 1 capsule distinctly larger than the other; wing membrane with setae ..... *Brillia* Kieff. (p. 95)
(And probably *Austrobrillia* Freem. from Australia (Freeman 1961 p. 640) which do not have setae on wing membrane.)

Spermathecal ducts with large loop and probably always common opening; 2 seminal capsules of equal size; wing membrane without setae 38

38 Setae of T IX reduced to a few along posterior margin; Gc IX usually with more than 6 setae; squama with setae or when without eyes hairy ..... *Eukiefferiella* Thien. (p. 96)
(*Tokunagaia* Sæth. will probably also key here.)

Setae of T IX numerous; Gc IX with less than 6 setae; squama without setae; eyes naked ..... *Thalassosmittia* Strenzk. et Remm. (p. 103)
(Syn. *Saunderia* Subl. (Sublette 1967a p. 318). See also couplet 57.)

39 T IX reduced, with only a few setae and with posterior emargination; Gc IX reduced; Gp VIII apparently simple; labia sclerotized and fused; seminal capsules much larger than cerci; R_{4+5} fused with costa 40

T IX and Gc IX well developed; Gp VIII simple or double; labia never sclerotized or fused; seminal capsules usually at most as large as cerci; R_{4+5} not fused with costa 41

40 Apodeme lobe small; labia small or large, but not completely sclerotized; coxosternapodeme simple or with 1 lateral lamella; eyes usually hairy ..... *Thienemanniella* Kieff (p. 104)

Apodeme lobe and labia large and strongly sclerotized; coxosternapodeme with 1 to several lateral lamellae; eyes bare ..... *Corynoneura* Winn. (p. 104)

41 Dorsomesal lobe much larger and wider than the brushlike ventrolateral lobe; T IX very faintly divided into 2 setigerous protrusions ..... *Zalutschia* Lip. (p. 100)

Dorsomesal lobe at most about as large as ventrolateral lobe; T IX either strongly and completely divided into 2 setigerous protrusions, undivided, or with weak to strong caudal emargination or cavity 42

42 T IX strongly and completely divided into 2 setigerous protrusions 43

T IX with none to strong caudal emargination 56

43 Dorsomesal and apodeme lobes present and distinct, not fully or partially covered by ventrolateral lobe 44

Ventrolateral lobe covers most of vestigial to distinct dorsomesal lobe and all apodeme lobe 49

44 Dorsomesal lobe only slightly shorter and narrower than ventrolateral lobe, both lobes finger-shaped 45

Ventrolateral lobe usually broadly rounded, usually broader at base than dorsomesal lobe; dorsomesal lobe often as long as or longer than ventrolateral lobe but then narrower apically 46

45 Spermathecal ducts with small bulbs before common opening; wing membrane at least with apical setae ..... *Heterotrissocladius* Spärck (p. 101)

Spermathecal ducts without bulbs; wing membrane without setae, but with strong microtrichia ..... *Paratrissocladius* Zavř. (p. 101)

46 Pulvilli large; segment X often with ventral, oromesally curved projections; setigerous protrusions of T IX relatively large with numerous setae; ventrolateral lobe large, much wider than dorsomesal lobe at base ..... *Psectrocladius* Kieff. (p. 96)

Pulvilli present or absent; segment X without ventral projections; setigerous protrusions of T IX relatively small with few setae; ventrolateral lobe less well developed, about as wide as dorsomesal lobe at base 47

47 Oral half of seminal capsules triangular; squama with setae ..... *Synorthocladius* Thien. (p. 97)

Seminal capsules rounded orally; squama without setae 48

48 Seminal capsules without microtrichia; cerci very long, elongation reaches labia in ventral view; pulvilli distinct ..... *Phycoidella* Sæth. (p. 102)
(And probably *Lapposmittia* Thien. with short palp, *Acamptocladius* Brund. with a scutal hump, and *Mesosmittia* Brund. with a few setae on squama.)

Seminal capsules with microtrichia; cerci very long to normal, pulvilli absent or vestigial; R_{2+3} close to or fused with R_{4+5} ..... *Parakiefferiella* Thien. (p. 101)
(And probably *Epoicocladius* Zavř. with R_{2+3} in the middle between R_1 and R_{4+5}, *Krenosmittia* Thien. without lateral setae on antepronotum, and possibly *Ancylocladius* Subl. et Wirth.)

49 Dorsomesal lobe reduced and narrow, linelike but distinct, less than ½ as long as ventrolateral lobe; squama without setae; eyes naked; pulvilli present ..... *Camptocladius* v.d. Wulp (p. 104)

Dorsomesal lobe well developed, at least ½ as long as ventrolateral lobe, but often indistinct since covered by ventrolateral lobe; squama with setae or when without, eyes hairy; pulvilli absent or small 50

50 Dorsomesal lobe with a rounded oral projection; spermathecal ducts at least usually with separate openings; acrostichals relatively well developed, start in front at antepronotum ..... *Orthocladius* v.d. Wulp (p. 98) 51

Dorsomesal lobe without rounded oral projection; spermathecal ducts usually with common opening; acrostichals absent or weak and starting some distance from antepronotum 54

51 Anal lobe very strongly protruding ..... *Orthocladius* subgen. *Pogonocladius* Brund.

Anal lobe at most slightly protruding 52

52 Spermathecal ducts extremely long, folded into several loops, reaching far anteriorly, with wider portions and very distinct bulbs before separate openings ..... *Orthocladius* subgen. *Eudactylocladius* Thien. (p. 98)

Spermathecal ducts straight or nearly straight, with or without weak bulbs before openings 53

53 Dorsomesal lobe nearly as wide at apex as at base; seminal capsule oval with distinct neck and with microtrichia in oral half; spermathecal duct straight ..... *Orthocladius* subgen. *Euorthocladius* Thien. (p. 98)

Dorsomesal lobe much wider at base than at the tapering apex; seminal capsule long and ovoid without distinct neck or microtrichia; spermathecal duct with small curves ..... *Orthocladius* subgen. *Orthocladius* v.d. Wulp (p. 98)

54 Setigerous protrusions of T IX narrowly separated; apex of dorsomesal lobe free; seminal capsules without microtrichia; squama without setae; eyes hairy; antepronotum covered with setae ..... *Heleniella* Gow. (p. 102)

Setigerous protrusions of T IX strongly and widely separated; apex of dorsomesal lobe covered by microtrichia at apex of ventrolateral lobe; seminal capsules usually with microtrichia; squama with setae; eyes bare or strongly pubescent; antepronotum not covered by setae 55

55 Setigerous protrusions of T IX very small; spermathecal ducts open separately; eyes pubescent; minute pulvilli present ..... *Oliveria* Sæth. (p. 99)

Setigerous protrusions of T IX large; spermathecal ducts with common opening; eyes bare; pulvilli absent ..... *Hydrobaenus* Fries, pro parte (excluding *H. lugubris* group, couplet 36) (p. 99)

56 Gc IX very long and lobelike; T IX deeply U-shaped emarginated on caudal margin; Gp VIII simple ..... *Cardiocladius* Kieff. (p. 96)

Gc IX normal; T IX with or without shallow caudal notch or emargination; Gp VIII divided, but dorsomesal lobe often consisting of a thin line surrounding vagina anterior of labia or spermathecal eminence 57

57 Seminal capsules oblong, at least ¾ as long as notum, dark sclerotized with a small but distinct, dark neck; ventrolateral lobe does not cover any part of the distinct dorsomesal and apodeme lobes; squama without setae; costa strongly extended ..... *Smittia* Holmgr. (p. 103)

(*Thalassosmittia* Strenzk. et Remm. may key here instead of to couplet 38. It differs by having spherical seminal capsules and more numerous setae on T IX. *Parasmittia* Strenzk. may key here or to couplet 59. It can be separated from both *Smittia* and *Pseudosmittia* by the presence of setae on the wing membrane.)

Seminal capsules spherical to ovoid, dark to pale; neck when present longer, funnel-shaped, and paler than oral part of capsule; ventrolateral lobe usually covers at least part of dorsomesal lobe; squama with setae or when without, costa not or barely extended or strongly extended 58

58 Wing membrane heavily punctated by microtrichia, sometimes also with setae; either apicolateral denticles of tibial spurs slightly or strongly enlarged or preepisternum with setae 59

Wing membrane at most finely punctated by microtrichia, bare; no enlarged apicolateral denticles of tibial spurs; precpisternum never with setae 62

59 Ventrolateral lobe with distinct anteriomesal or weak mesal projection; dorsomesal lobe and apodeme lobe only partly covered by ventrolateral lobe; either apicolateral denticles of tibial spurs strongly enlarged or wing membrane with setae 60

Ventrolateral lobe without projections, large, covering most or all of dorsomesal and apodeme lobes; apicolateral denticles of tibial spurs not or only slightly enlarged; wing membrane without setae 61

60 Gc IX large; ventrolateral lobe with distinct anteriomesal, rounded projection; spermathecal ducts with weak bulbs before separate openings; apicolateral denticles of tibial spurs enlarged, wing membrane without setae ..... *Chaetocladius* Kieff. (p. 101)

Gc IX small; ventrolateral lobe with weak mesal, fingerlike lobe; spermathecal ducts without bulbs before common opening; apicolateral denticles of tibial spurs not enlarged; wing membrane with setae ..... *Gymnometriocnemus* Goetgh. (p. 102)

61 T IX with caudal emargination; seminal capsules with microtrichia; spermathecal ducts with long loop and with distinct bulbs before common opening; preepisternum with setae ..... *Limnophyes* Eat. (p. 102)
(And probably *Paralimnophyes* Brund. with a less strongly developed antepronotum.)

T IX without caudal emargination; seminal capsules without microtrichia, spermathecal ducts with short loop and without bulbs before partly separate openings; preepisternum without setae ..... *Bryophaenocladius* Thien. (p. 103)

62 Gc IX long, relatively narrow, its margin against T IX broad, sclerotized; cerci much smaller than seminal capsules; seminal capsules with transverse striations; squama without setae ..... *Pseudosmittia* Goetgh. (p. 104)
(And probably *Orthosmittia* Goetgh. which may be a synonym of *Pseudosmittia* at least in part, because, for instance, the 1 examined female of *Pseudosmittia* reared from pupa has a somewhat shortened and straight Cu_1.)

Gc IX normal, without sclerotized margin against T IX; cerci about as large as the large unstriated seminal capsules; squama with setae ..... *Parorthocladius* Thien. (p. 97)
(And probably *Kiefferophyes* Freem. from Australia which, however, probably has genitalia more similar to those of *Limnophyes*, but key here because of the finer punctation of microtrichia on the wing membrane.)

Diplocladius Kieff.
(Fig. 37)

Species examined: *Diplocladius cultriger* Kieff.

Gca VIII weak. Gp VIII with rudimentary far lateral ventrolateral lobe, large central lobe (i.e. as in *Pseudochironomus* Mall. and *Manoa* Fittk. (Pseudochironomini) and *Lauterborniella* Bause (Chironomini)), and with small linelike dorsomesal lobe surrounding vagina (i.e. as in most Orthocladiinae). T IX large, undivided, with caudomesal point (i.e. as in several Tanytarsini). Gc IX large, with several setae. Segment X well developed. Postgenital plate triangular, relatively well developed. Cerci long, pediform, with elongated parallel-sided "toe."

Labia without microtrichia, curved mesad. 3 spherical seminal capsules with distinct neck. One capsule slightly reduced, with longer neck and separate duct and opening. 2 remaining capsules normal with spermathecal ducts joined and widened for relatively long distance (about as long as one ramus) before common opening.

Diplocladius shows several signs of relationships with Chironominae, such as the presence of a far ventrolateral lobe and of an apical point on T IX in the female genitalia, and several details of the males and immatures. The presence of a vestigial linelike dorsomesal lobe, however, indicates more relationship with Orthocladiinae. A closer examination of the subgenus *Stictocladius* Edw. (Edwards 1931 p. 279; Freeman 1959 p. 415, 1961 p. 640), known from South America, Australia, and New Zealand, may well elucidate the phylogenetic position of this genus.

Chasmatonotus Loew
(Fig. 38)

Species examined: *C. unimaculatus* Loew, *C. bimaculatus* Ost. Sack.

Gp VIII large, rounded, undivided, without any sign of dorsomesal lobe. T IX large, either wide with a very wide caudal concavity and caudolateral projections, or more narrow and approximately triangular. Gc IX well developed, with several setae. Segment X normal. Postgenital plate absent or vestigial. Cerci very small.

Seminal capsules large, spherical, dark in oral $\frac{4}{5}$, with oblique and weak neck. Spermathecal ducts curved, with partly separate openings.

Brillia Kieff.
(Fig. 39D–F)

Species examined: *Brillia* sp. *A*, *Brillia* sp. *B*

Gp VIII with large, rounded ventrolateral lobe and very small linelike dorsomesal lobe surrounding vagina anterior of spermathecal eminence. T IX large, rectangular, undivided, with numerous setae. Gc IX large, with numerous setae. Segment X normal. Postgenital plate broad, triangular with rounded apex. Cerci pediform, well developed.

Either 3 spherical seminal capsules covered with strong microtrichia, or 2 oblong capsules of unequal size, void of microtrichia. Spermathecal ducts nearly straight, open separately.

Chasmatonotus, Brillia, Eurycnemus v.d. Wulp. (Brundin 1956 p. 69), *Propsilocerus* Kieff. (Botnariuç and Albu 1956), and *Austrobrillia* Freem. (Freeman 1961 p. 640) probably form a group of related very plesiomorphic genera within the Orthocladiinae. A closer study of these and other exotic genera such as *Petalocladius* Subl. et Wirth (Sublette and Wirth 1972 p. 2) from the West Indies, *Nasuticladius* Freem. (Freeman 1961 p. 650) from Australia, and *Rhinocladius* Edw. (Edwards 1931 p. 368, Freeman 1961 p. 662) from Patagonia, South Chile, and Australia, will be an important step in confirming or disproving the synapomorphic diagram developed here.

Abiskomyia Edw.
(Fig. 40A–C)

Species examined: *A. virgo* Edw., *Abiskomyia* sp.n.

Gp VIII undivided, rounded, with microtrichia concentrated on central part. T IX large, rhomboid, undivided, with setae most numerous in caudal half and some setae in pale spots. Gc IX large, longer than T IX in lateral view. Segment X normal. Postgenital plate weak. Cerci rounded, of moderate size.

Seminal capsules large, spherical, dark, with minute but dense microtrichia. Spermathecal ducts open separately.

Ichtyocladius Fittk.
(Fittkau 1974 fig. 1, 3)

Gp VIII apparently undivided. T IX very large, covering all segment X and most of cerci in dorsal view, with wide caudal emargination. Gc IX large, elongate. Segment X normal. Postgenital plate not apparent. Cerci normal.

Seminal capsules ovoid, with oral neck. Spermathecal ducts apparently with separate openings.

Cardiocladius Kieff.
(Fig. 39A–C; Tokunaga 1939 fig. 50–52)

Species examined: *Cardiocladius* sp.

Gp VIII large, undivided, rounded, with strong but short microtrichia. T IX relatively large, with wide, deep, U-shaped caudal emargination. Gc IX very long, lobelike, nearly reaching middle portion of cerci. Coxosternapodeme nearly straight. Segment X, postgenital plate, and cerci normal.

Seminal capsules large, ovoid, darker in oral half. Spermathecal ducts with wide bend, with separate openings, no bulbs before openings.

Eukiefferiella Thien.
(Fig. 40D, E)

Species illustrated: *E. claripennis* (Lundb.)

Gp VIII very large, undivided, with caudomesal protuberance. T IX large, rectangular, undivided, with only a few caudal setae. Gc IX large. Segment X well developed. Postgenital plate weak. Cerci normal.

Seminal capsules ovoid, darker in oral half, without microtrichia.

Heterotanytarsus Spärck
(Fig. 40F–H; Sæther 1975a fig. 5)

Species examined: *H. nudalus* Sæth.

Gp VIII undivided, rounded. T IX divided into 2 setigerous protrusions. Gc IX well developed. Segment X normal. Postgenital plate weak. Cerci normal.

Seminal capsules ovoid. Spermathecal ducts nearly straight with wide triangular common opening.

Psectrocladius Kieff.
(Fig. 41, 42)

Species illustrated: *P. (P.) barbimanus* Edw., *Psectrocladius (P.)* sp. *A*, *Psectrocladius (P.)* sp. *B*, *P. (Allopsectrocladius) flavus* (Joh.)

S VIII usually reticulate or rugulose in orolateral portion. Gp VIII divided into a rounded ventrolateral lobe and a distinct narrow, triangular, pointed dorsomesal lobe. Apodeme lobe distinct, visible between principal lobes, occasionally with microtrichia. T IX strongly divided into 2 setigerous protrusions. Gc IX large. Segment X often with mesally curved oral projections. Postgenital plate well developed, rounded-triangular. Cerci pediform, relatively large.

Seminal capsules ovoid, with pale neck. Spermathecal ducts nearly straight or with very slight curve, without bulbs before common opening.

Good specific characters are: the size and shape of the principal lobes of Gp VIII and the apodeme lobe; the presence or absence and eventual shape of the ventral projections of segment X; and the size and shape of the cerci.

Rheocricotopus Thien. et Harn.
(Fig. 43)

Species examined: *R. effusus (Walk.), R. eminellobus* Sæth.

Gp VIII divided into low, rounded ventrolateral lobe; narrow, but distinct dorsomesal lobe with long microtrichia. Apodeme lobe distinct between principal lobes of Gp VIII, with straight apodeme. T IX strongly divided into 2 relatively small setigerous protrusions. Gc IX well developed. Segment X normal. Postgenital plate well developed, triangular. Cerci normal.

Seminal capsules ovoid, with or without distinct neck. Spermathecal ducts with bend, but seldom with complete loop, openings separate.

Nanocladius Kieff.
(syn. *Microcricotopus* Thien. et Harn.; *Plecopteracoluthus* Steff.,
see Sæther 1977) (Fig. 44D–G; Steffan 1965 fig. 10;
Sæther 1977 fig. 3, 5, 7, 9, 11, 14, 15, 18, 22)

Species illustrated: *N.* cf. *bicolor* (Zett.)

S VIII sometimes forms floor under anterior part of vagina. Gp VIII divided into broad, triangular to more rounded, large to medium, ventrolateral lobe; narrow, distinct dorsomesal lobe. Apodeme lobe weak, with nearly straight apodeme, usually visible between principal lobes. T IX with caudal square-cut emargination or faintly divided into setigerous protrusions. Gc IX large, longer than T IX in lateral view, occasionally with caudomesal point. Segment X normal. Postgenital plate well developed, rounded-triangular. Cerci relatively small to large.

Seminal capsules oblong, with spermathecal ducts placed on oral portion of mesal long side, with a few weak microtrichia. Spermathecal ducts with weak bend or loop, with or without bulbs before common opening.

A preliminary key to females is given by Sæther (1977).

Parorthocladius Thien.
(Fig. 45A, B)

Species examined: *P. nudipennis* (Kieff.)

Gp VIII divided, but dorsomesal lobe consists only of a fine line with microtrichia and covered by large, triangular ventrolateral lobe. Apodeme lobe not apparent. T IX small, with weak caudal emargination. Gc IX well developed. Segment X normal. Postgenital plate weak. Cerci relatively large.

Seminal capsules large, ovoid with weak oral point. Spermathecal ducts with loop, openings separate.

Synorthocladius Thien.
(Fig. 45C–E)

Species examined: *S. semivirens* (Kieff.)

Gp VIII divided into brushlike, small ventrolateral lobe curved mesad, and equally large dorsomesal lobe with rounded oromesal projection. Apodeme lobe relatively distinct, uncovered. T IX completely divided into 2 small setigerous protrusions. Segment X normal. Postgenital plate normal, triangular. Cerci relatively large.

Seminal capsules triangular in oral half, rounded caudally and with distinct neck. Spermathecal ducts nearly straight, with small bulbs near common opening.

Orthocladius v.d. Wulp
(Fig. 44A–C, 45F–H, 46; Hirvenoja 1973 fig. 28)

Species illustrated: *O. (O.) obumbratus* Joh., *O. (Euorthocladius)* sp., *O. (Eudactylocladius)* sp.

Gp VIII divided into large, rounded ventrolateral lobe covering part or most of dorsomesal lobe, and dorsomesal lobe with oral rounded projection. Apodeme lobe covered by ventrolateral lobe. T IX completely or nearly completely divided into 2 large setigerous protrusions. Gc IX large. Segment X normal. Postgenital plate relatively large, triangular. Cerci large.

Seminal capsules pear-shaped without distinct neck (subgen. *Orthocladius*); spherical with distinct neck, microtrichia, and darker in oral half (subgen. *Euorthocladius* Thien.); or very large and spherical, without distinct neck (subgen. *Eudactylocladius* Thien.). Spermathecal ducts nearly straight with separate openings (subgen. *Orthocladius*); straight with wide common opening (subgen. *Euorthocladius*); or extremely long with several loops and bends, widened portions, and distinct bulbs before separate openings (subgen. *Eudactylocladius*).

Acricotopus Kieff.
(Fig. 47A; Hirvenoja 1973 fig. 35, 36)

Species examined: *A. senex* (Joh.)

Gp VIII divided into large ventrolateral lobe and small dorsomesal lobe apparently almost completely covered by ventrolateral lobe and with pointed oral projection. T IX apparently divided into setigerous protrusions. Gc IX well developed. Segment X well developed. Cerci large, pediform with long "toe," "toe" with a few conspicuously stronger setae before apex.

Seminal capsule ovoid to pear-shaped. Spermathecal ducts slightly curved, apparently with common opening.

Paratrichocladius Sant. Abr.
(syn. *Syncricotopus* Brund.) (Fittkau 1954 fig. 9)

According to Hirvenoja (1973 p. 88) the female genitalia of *Paratrichocladius* appear to be the same type as in other genera of the *Cricotopus* group, i.e. with Gp VIII divided, ventrolateral lobe covering dorsomesal lobe, and dorsomesal lobe with oral projection.

Paracladius Hirv.
(Fig. 47 B–D; Hirvenoja 1973 fig. 44, 48, 51)

Species examined: *P. quadrinodosus* Hirv.

Gp VIII divided into large ventrolateral lobe and small dorsomesal lobe nearly completely covered by ventrolateral lobe. Dorsomesal lobe with curved, pointed oral projection; fused with ventrolateral lobe at projection. Anterior portion of lobes and mesal part of Gca VIII form concavity. Apodeme lobe completely covered by ventrolateral lobe. T IX undivided, but with setae concentrated on lateral portions and direction of microtrichia indicating a median dividing line. Gc IX normal or relatively small. Segment X normal. Postgenital plate distinct. Cerci pediform, normal.

Seminal capsules spherical to ovoid, with or without distinct neck. Spermathecal duct with one loop or bend, very slightly widened before common opening.

A key to the females of the genus is given by Hirvenoja (1973 p. 93).

Halocladius Hirv.
(Hirvenoja 1973 fig. 58, 62, 64, 66, 67, 69)

Gp VIII divided with ventrolateral lobe covering dorsomesal lobe, lobes fused at oral projection of dorsomesal lobe. Ventrolateral lobes in broad contact at midline. T IX not illustrated by Hirvenoja, but probably of *Cricotopus* type, i.e. faintly divided into setigerous protrusions. Gc IX relatively small. Cerci pediform, normal.

Seminal capsules ovoid to pear-shaped with more or less distinct neck. Spermathecal ducts with long to moderately long loop or bend, with bulbs before common opening.

A key to females of the genus is given by Hirvenoja (1973 p. 114).

Cricotopus v.d. Wulp
(Fig. 48, 49; Roback 1960 fig. 18, 19, 25, 26, 32; Sublette 1964 fig. 17, 18, 26; Sæther 1971c fig. 4; Hirvenoja 1973 fig. 74 et seq.)

Species illustrated: *C. (C.) slossonae* Mall., *C. (C.)* cf. *triannulatus* (Macq.), *C. (C.) bicinctus* (Meig.), *C. (C.) trifascia* Edw., *C. (Isocladius) sylvestris* (Fabr.)

Gp VIII divided into large, rounded ventrolateral lobe and dorsomesal lobe with oral projection. Ventrolateral lobes cover dorsomesal lobes and in broad contact. T IX faintly to distinctly divided into 2 setigerous protrusions. Gc IX small to large. Segment X normal. Postgenital plate weak to well developed, rounded-triangular. Cerci pediform, of moderate size.

Seminal capsules spherical, ovoid to pear-shaped; with or without small or large neck; occasionally with microtrichia. Spermathecal ducts usually with loop or bend, occasionally straight, usually with bulbs before separate or common opening(s).

Keys to females are given by Hirvenoja (1973 p. 135 et seq.). In *C. (Isocladius) sylvestris* (Fabr.), as identified according to the keys of Hirvenoja, there are 2 types of coxosternapodemes (Fig. 49G, I) possibly signifying 2 different species.

Oliveria Sæth.
(Fig. 50A–D; Sæther 1976b fig. 10)

Species illustrated: *O. tricornis* (Ol.)

Gp VIII divided into large ventrolateral lobe and smaller dorsomesal lobe, former covers part of latter. Apodeme lobe relatively large, but weakly sclerotized. T IX completely divided into 2 small setigerous protrusions. Gc IX small. Segment X small. Postgenital plate weak. Cerci normal.

Seminal capsules spherical, with microtrichia. Sphermathecal ducts curved, with small bulbs before funnel-shaped separate openings.

Hydrobaenus Fries
(syn. *Trissocladius* Brund. pro parte nec Kieff.)
(Fig. 51A–D; Sæther 1976b fig. 14, 15, 27, 33, 36, 37, 38, 40, 43, 45)

Species illustrated: *H. lugubris* Fries, *H. johannseni* (Subl.)

Gp VIII divided into moderately large to large ventrolateral lobe and dorsomesal lobe of equal to smaller size. Apodeme lobe indistinct, but apex usually visible between principal lobes. T IX either large and triangular with caudal notch (*H. lugubris* group), or strongly divided into 2 relatively large, setigerous protrusions. Gc IX normal. Segment X normal. Postgenital plate weak to well developed. Cerci large, pediform.

Seminal capsules ovoid to elongate, darkly sclerotized in oral $\frac{3}{5}$–$\frac{4}{5}$, usually with microtrichia. Spermathecal ducts usually with loop or strongly curved, common opening often distinctly widened and triangular.

A key to females is given by Sæther (1976b p. 73).

Baeoctenus Sæth.
(Fig. 50E–G)

Species examined: *B. bicolor* Sæth.

Gp VIII about equally divided into small ventrolateral and dorsomesal lobes. Apodeme lobe well developed, but only weakly sclerotized. T IX very large, triangular, with caudal notch, faintly divided into setigerous protrusions. Gc IX relatively large. Segment X and postgenital plate well developed. Cerci large.

Seminal capsules ovoid, relatively small, dark, sclerotized in oral half, with distinct microtrichia. Spermathecal ducts straight, with common opening.

Zalutschia Lip.
(syn. *Trissocladius* Brund. pro parte nec Kieff.)
(Fig. 51E, F; Sæther 1976b fig. 52, 53, 63, 65, 70)

Species illustrated: *Z. tornetraeskensis* (Edw.)

Gp VIII divided into small brushlike ventrolateral lobe and much larger, bluntly triangular dorsomesal lobe. Apodeme lobe indistinct, but visible between principal lobes. T IX very faintly divided into 2 setigerous protrusions or at least with caudal concavity. Gc IX normal. Coxosternapodeme with sharp curves or bends at least indicated by heavier sclerotization. Segment X, postgenital plate, and cerci normal.

Seminal capsules ovoid; with well-developed, triangular neck; without microtrichia. Spermathecal ducts with loops or bends or occasionally nearly straight, with or without bulbs before opening, occasionally with separate or nearly separate openings, occasionally ducts joined for a short distance.

A key to females is given by Sæther (1976b p. 188).

Metriocnemus v.d. Wulp
(Fig. 52; Reiss 1971 fig. 4, 5)

Species examined: *M. knabi* Coq., *Metriocnemus* sp.n.

S VIII forms small to minute floor under anterior part of vagina (i.e. as in the Tanytarsini). Gp VIII divided into large ventrolateral lobe, rounded, or with small apical projection, and linelike dorsomesal lobe. T IX large, pointed, triangular to semicircular, undivided. Gc IX well developed, with numerous setae. Segment X with orolateral extensions and pointed or rounded triangular caudolateral projections. Postgenital plate relatively well developed, triangular, pointed, mostly void of microtrichia. Cerci well developed, pediform.

Seminal capsules spherical, darker in oral ¾. Spermathecal ducts slightly curved, with distinct bulbs before common opening. (Reiss (1971 fig. 4), however, shows no such bulbs.)

Thienemannia Kieff.
(Fig. 53I–K)

Species examined: *T. gracilis* (Kieff.)

Gp VIII divided into large triangular ventrolateral lobe with rounded apex and weak linelike dorsomesal lobe surrounding vagina anterior of labia. T IX small, undivided. Gc IX large. Segment X normal. Postgenital plate small. Cerci normal.

Seminal capsules ovoid, void of microtrichia. Spermathecal ducts with loop, open separately, with very weak bulbs before opening.

Chaetocladius Kieff.
(Fig. 54A–C)

Species illustrated: *Chaetocladius* sp.

Gp VIII divided into large ventrolateral lobe with oromesal projection and small linelike dorsomesal lobe partially covered by ventrolateral lobe. Part of apodeme lobe visible between principal lobes. T IX undivided, but with caudal concavity. Gc IX well developed. Segment X and postgenital plate relatively well developed. Cerci normal.

Seminal capsules spherical, without neck. Spermathecal ducts with weak bend, with weak bulbs before separate openings.

Paratrissocladius Zavř.
(Sæther 1976b fig. 78)

Gp VIII divided into long, narrow, tongue-shaped ventrolateral lobe and dorsomesal lobe of nearly same length and shape. Apodeme lobe visible between principal lobes. T IX strongly and completely divided into 2 large setigerous protrusions. Gc IX normal. Segment X well developed. Postgenital plate well developed, triangular. Cerci relatively small.

Seminal capsules ovoid with distinct neck. Spermathecal ducts nearly straight, without bulbs before common opening.

Heterotrissocladius Spärck
(Fig. 55; Sæther 1974 fig. 2; 1975c fig. 2, 8, 13)

Species illustrated: *H. hirtapex* Sæth.

Gp VIII divided into long, narrow, tongue-shaped ventrolateral lobe and slightly shorter dorsomesal lobe about the same shape. Apodeme lobe visible between principal lobes. T IX strongly and completely divided into 2 setigerous protrusions of moderate size. Gc IX normal. Segment X well developed. Postgenital plate well developed, triangular with rounded apex. Cerci pediform, relatively small.

Labia with indication of microtrichia. Seminal capsules ovoid to pear-shaped, darker in oral half, with indication of weak neck. Spermathecal ducts with loop or strong angle, with bulbs before common opening.

A key to females is given by Sæther (1975c p. 6–7)

Parametriocnemus Goetgh.
(Fig. 53A–D)

Species illustrated: *P. lundbecki* (Joh.)

Gp VIII divided into large ventrolateral lobe and narrow dorsomesal lobe. Apodeme lobe visible between principal lobes, relatively distinct. T IX with deep, square-cut caudal emargination nearly dividing tergite into 2 setigerous protrusions. Gc IX normal, but with some extremely long setae far overreaching the relatively small cerci. Segment X well developed. Postgenital plate weak.

Seminal capsules ovoid, without distinct neck. Spermathecal ducts with loops or angles, with small bulbs before common opening.

Parakiefferiella Thien.
(Fig. 56A–E, I–L)

Species examined: *P. (P.) torulata* Sæth., *P. (P.)* sp.n. near *bathophila* Kieff., *P. (P.) coronata* (Edw.)

Gp VIII divided into relatively small, rounded to tongue-shaped ventrolateral lobe, and slightly larger dorsomesal lobe. Apodeme lobe visible between principal lobes. T IX strongly

divided into 2 setigerous protrusions. Gc IX normal, with some long setae reaching posterior parts of cerci. Segment X normal. Postgenital plate small, often sharply pointed. Cerci small to large.

Seminal capsules ovoid to pear-shaped, with microtrichia. Spermathecal ducts nearly straight or with loops, with bulbs before separate or nearly separate openings.

Phycoidella Sæth.
(Fig. 56F–H; Sæther 1971c fig. 10)

Species examined: *P. dentolatens* Sæth.

Gp VIII divided into small ventrolateral lobe and larger dorsomesal lobe. Apodeme lobe visible between principal lobes. T IX strongly divided into setigerous protrusions. Gc IX relatively long, but narrow. Segment X large, rounded, clearly visible in dorsal view. Postgenital plate small, sharply pointed. Cerci large.

Seminal capsules spherical, without neck or microtrichia. Spermathecal duct not visible in specimen examined.

Heleniella Gow.
(Fig. 57A–D; Serra-Tosio 1967 fig. 8)

Species examined: *H. ornaticollis* (Edw.)

Gp VIII divided into large, rounded ventrolateral lobe and relatively well developed, tongue-shaped dorsomesal lobe partly covered by ventrolateral lobe. Apodeme lobe covered by principal lobes. T IX divided into 2 setigerous protrusions with long setae. Gc IX normal, with long setae, longest reaching caudal half of cerci. Segment X, postgenital plate, and cerci normal.

Seminal capsules ovoid, with wide, pale neck. Spermathecal ducts with loops or bends, widened for a relatively long distance before common opening, but without bulbs.

Limnophyes Eat.
(Fig. 54D–K; Reiss 1966 fig. 4; Sæther 1975d fig. 4, 10)

Species illustrated: *L.* poss. *minimus* (Meig), *L.* ? *pilicistulus* Sæth.

Gp VIII divided into large ventrolateral lobe and small linelike dorsomesal lobe, hidden by ventrolateral lobe, and surrounding vagina anterior of spermathecal eminence. Apodeme lobe weak, with nearly straight apodeme. T IX undivided, with caudal notch or concavity. Gc IX normal. Segment X normal. Postgenital plate weak. Cerci small.

Seminal capsules with distinct microtrichia, pear-shaped with large neck. Spermathecal ducts with very long loop and bulbs before common opening, occasionally joined a short distance before opening.

Gymnometriocnemus Goetgh.
(Fig. 53E–H)

Species examined: *Gymnometriocnemus* sp., *Gymnometriocnemus* sp.n.

Gp VIII divided into large ventrolateral lobe with small mesal branch, and small relatively narrow dorsomesal lobe. Apodeme lobe weak, but visible between principal lobes. T IX undivided, but with caudal concavity. Gc IX relatively small. Segment X and postgenital plate normal. Cerci very small.

Seminal capsules ovoid to pear-shaped. Spermathecal ducts with bends, without bulbs before common opening.

Bryophaenocladius Thien.
(Fig. 57E–G; Sæther 1973a, fig. 2)

Species examined: *Bryophaenocladius* sp.; *B. productus* (Freem.)

Gp VIII divided into large, rounded ventrolateral lobe and small, relatively narrow dorsomesal lobe. Ventrolateral lobes in contact at midline. Apodeme lobe weak, covered by principal lobes. T IX undivided, without caudal concavity or emargination; setae concentrated on caudal fourth. Gc IX relatively small. Segment X and postgenital plate normal. Cerci moderately large.

Seminal capsules ovoid to pear-shaped, with pronounced funnel-shaped neck. Spermathecal ducts with distinct loop, without bulbs before partly separate openings.

Smittia Holmgr.
(Fig. 58, 59; Oliver 1970 fig. 16, 18)

Species examined: *Smittia* sp. *A*, *Smittia* sp. *B*, *Smittia* sp. *C*, *Smittia* sp. *D*, *Smittia* sp. *E*

Gp VIII divided into small to large ventrolateral lobe and mostly narrow, distinct dorsomesal lobe. Apodeme lobe visible between principal lobes. T IX undivided, but usually with weak caudal concavity or emargination. Gc IX small to moderately large. Segment X and postgenital plate weak to very weak. Cerci small to very small.

Seminal capsules heavily sclerotized, elongate, ovoid, with short, but distinct, square, sclerotized neck. Spermathecal ducts with loops and common opening.

Thalassosmittia Strenzk. et Remm.
(Syn. *Saunderia* Subl., Sublette 1967a p. 318 syn. nov.) (Strenzke and Remmert 1957 fig. 7)

T IX undivided, at least not with strong caudal concavity (Strenzke and Remmert 1957 p. 265), setae concentrated on lateral portions.

Seminal capsules spherical, heavily sclerotized. Spermathecal ducts with loop reaching far orally.

Belgica Jacobs
(Wirth and Gressitt 1967 fig. 1)

According to Wirth and Gressitt (1967 p. 199) the female genitalia appear to be close to those of *Clunio* Hal., but with the cerci and T IX placed in normal position.

Clunio Hal.
(Strenzke 1960 fig. 19, 20; Roback 1971b fig. 9, 11)

Gp VIII divided into large ventrolateral lobe and linelike dorsomesal lobe surrounding anterior part of vagina. T IX with wide caudal concavity or emargination, setae concentrated on lateral portions; T IX visible in ventral view. Gc IX well developed. Segment X and postgenital plate small. Cerci small and placed ventrally, not visible in dorsal view.

Seminal capsules ovoid. Spermathecal ducts with loop.

Tethymyia Wirth
(Wirth 1949 fig. 2)

Gp VIII divided into large ventrolateral lobe with strong basal constriction and distinct, but apparently linelike dorsomesal lobe. T IX caudally truncated, not visible in ventral view. Gc IX

well developed. Postgenital plate large, triangular, with truncate caudal end. Cerci subovoid, of medium size.

Seminal capsules oval, sclerotized.

Camptocladius v.d. Wulp
(Fig. 60A–C)

Species examined: *C. stercorarius* (De Geer)

Gp VIII divided into large, rounded ventrolateral lobe mostly covering very small, linelike dorsomesal lobe. Apodeme lobe weak, covered by principal lobes. T IX divided into 2 setigerous protrusions. Gc IX normal. Segment X weak. Postgenital plate not apparent. Cerci of moderate size.

Seminal capsules ovoid, with funnel-shaped pale neck. Spermathecal ducts with loop and common opening.

Pseudosmittia Goetgh.
(Fig. 60D–F; Thienemann and Strenzke 1940 fig. 5)

Species examined: *P.* sp.n. near *restricta* Brund.

Gp VIII divided into large ventrolateral lobe partly or fully covering small linelike dorsomesal lobe. Apodeme lobe relatively distinct, but small. T IX undivided, but probably mostly with a very weak caudal notch and setae concentrated on lateral portions. (According to Strenzke and Remmert (1957 p. 265) there may even be a strong caudal concavity in some species.) Gc IX long, but relatively narrow, in broad sclerotized contact with T IX. Segment X normal. Postgenital plate weak or absent. Cerci small.

Seminal capsules ovoid, with transverse striations (at least in specimens examined). Spermathecal ducts relatively wide, with loops, slightly widened before common opening.

Thienemanniella Kieff.
(Fig. 61A–C)

Species illustrated: *Thienemanniella* sp.

Gp VIII apparently undivided, large; however, with a structure which may represent fused and sclerotized dorsomesal lobes. Apodeme lobe covered by Gp VIII, fully sclerotized, small compared with that of *Corynoneura* Winn. T IX reduced, with weak caudal concavity, only about 2 setae on each side. Gc IX reduced, narrow, but relatively long, with 1 seta. Coxosternapodeme with or without anterior lamella. Segment X normal. Postgenital plate well developed, triangular. Cerci small. Labia fused and fully sclerotized, small or large. Seminal capsules large, ovoid, with funnel-shaped neck. Spermathecal ducts nearly straight, joined a short distance before common opening.

Corynoneura Winn.
(Fig. 61D–F)

Species illustrated: *Corynoneura* sp. *A*, *Corynoneura* sp. *B*

Gp VIII large, undivided. Apodeme lobe very large, fully sclerotized. T IX reduced, with strong caudal concavity, about 2 setae on each side. Gc IX reduced, narrow but long, with one seta. Coxosternapodeme with one to several partly sclerotized lamellae. Segment X and postgenital plate well developed. Cerci small.

Labia fused and sclerotized, very large. Seminal capsules very large, spherical to oval, without distinct neck, mouth placed orally. Spermathecal ducts not distinct in specimens examined.

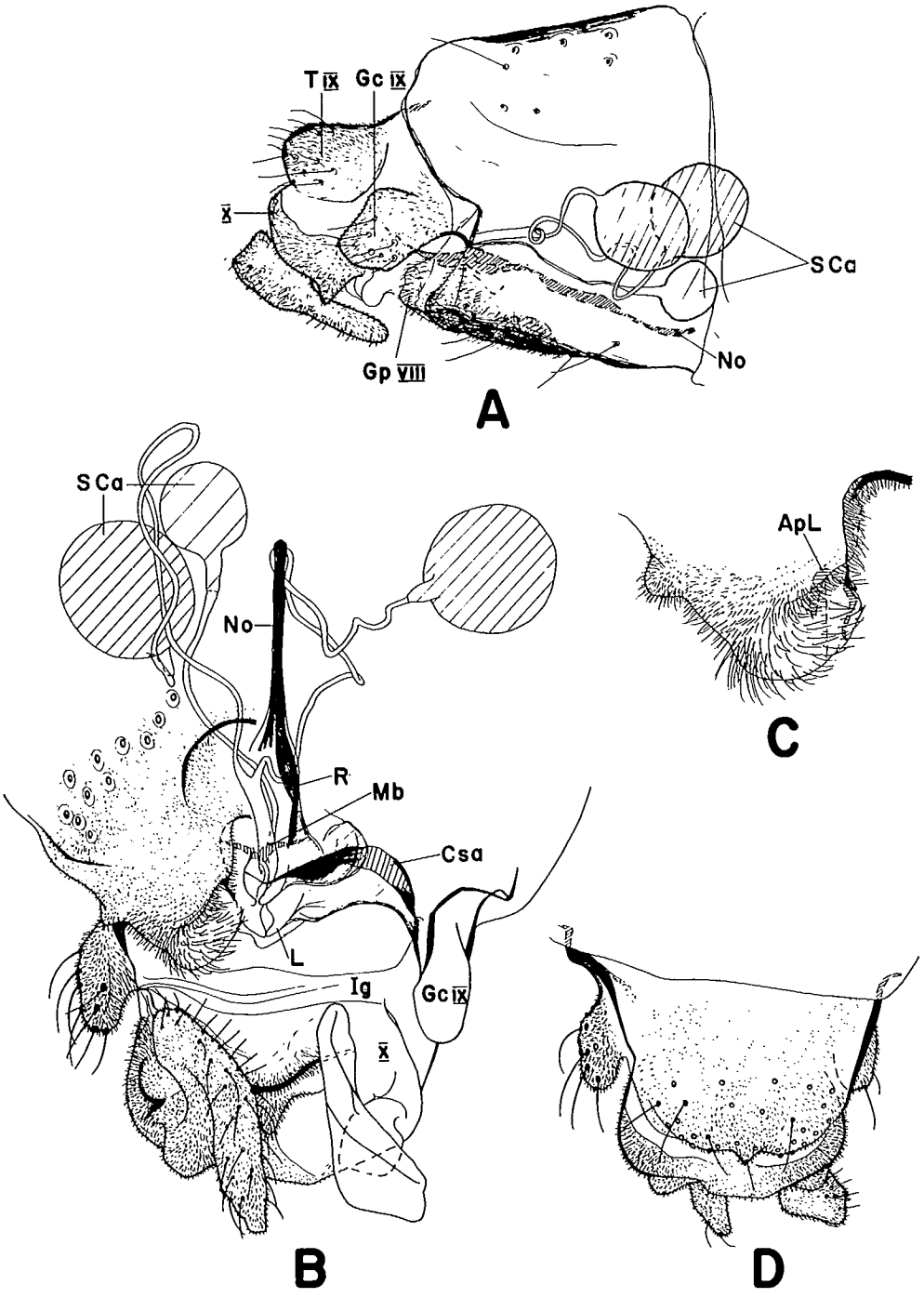

FIG. 37. Female genitalia of *Diplocladius (Diplocladius) cultriger* Kieff., Orthocladiinae. A, lateral. B, ventral. C, Gp VIII. D, dorsal.

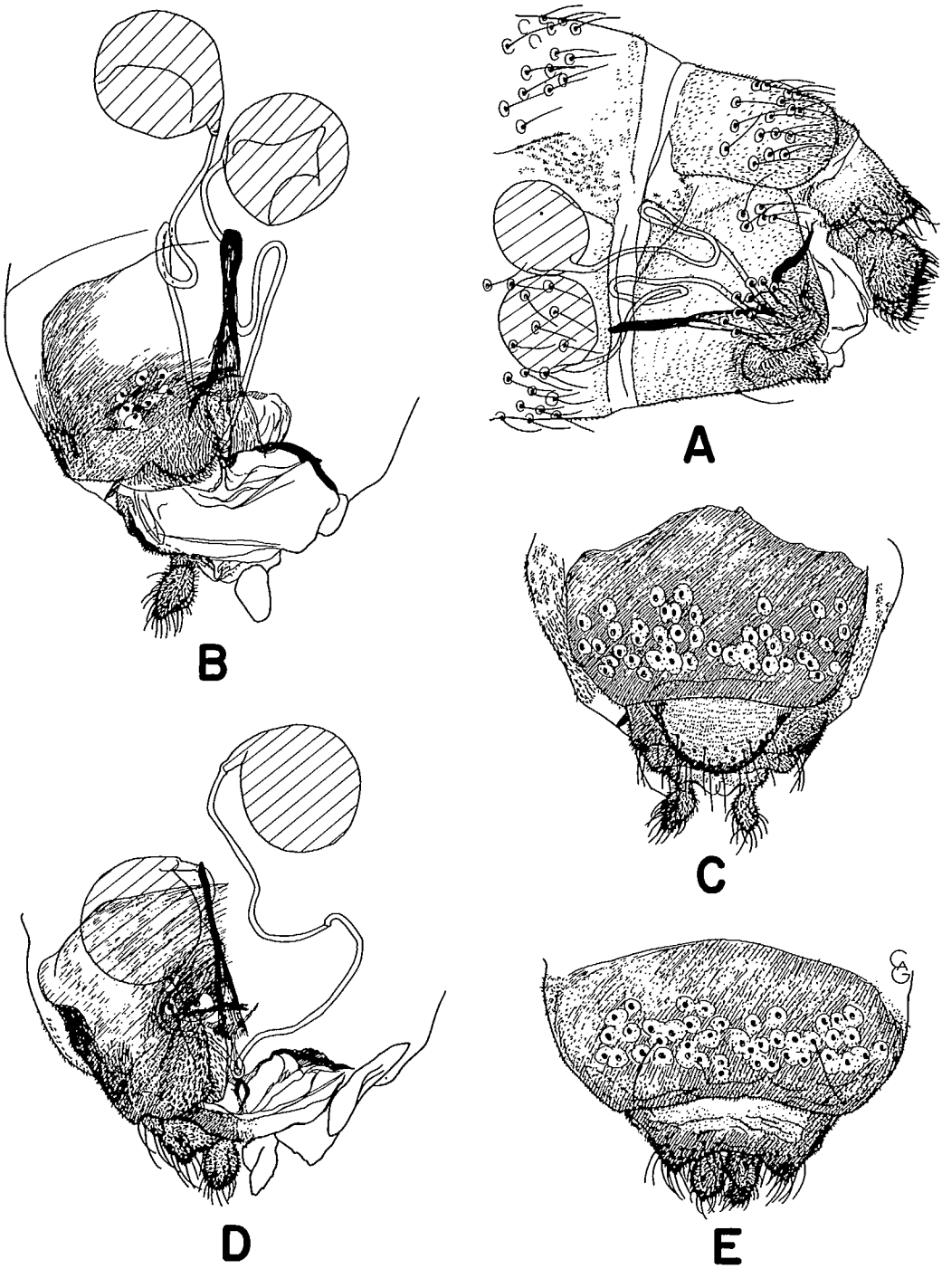

FIG. 38. Female genitalia of *Chasmatonotus* spp., Orthocladiinae. A–C, *C. bimaculatus* Ost. Sack.: A) lateral; B) ventral; C) dorsal. D–E, *C. unimaculatus* Loew: D) ventral; E) dorsal.

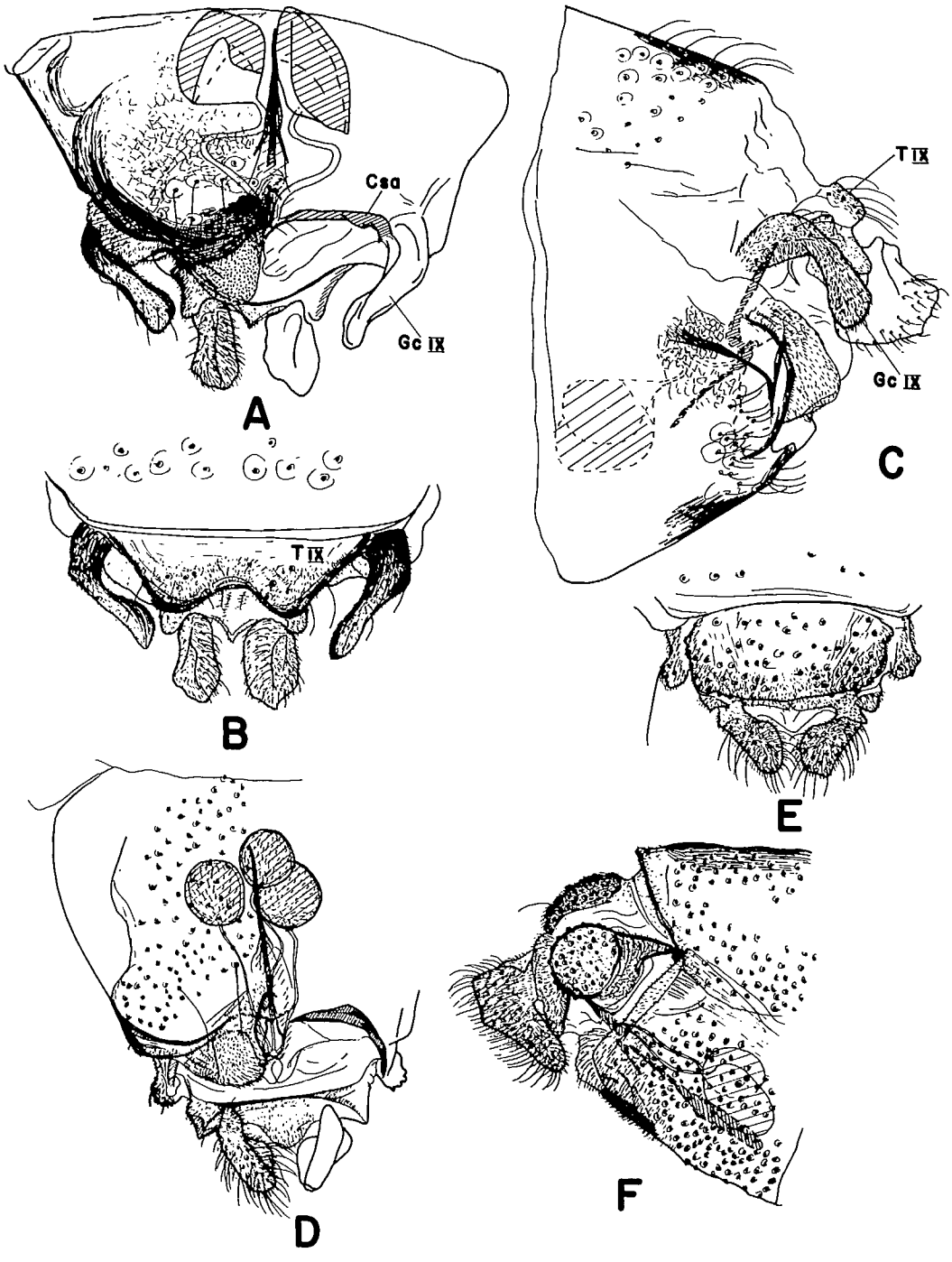

FIG. 39. Female genitalia of Orthocladiinae. A–C, *Cardiocladius* sp.; A) ventral; B) dorsal; C) lateral. D–E, *Brillia* sp. *A*; D) ventral; E) dorsal. F, *Brillia* sp. *B*, lateral.

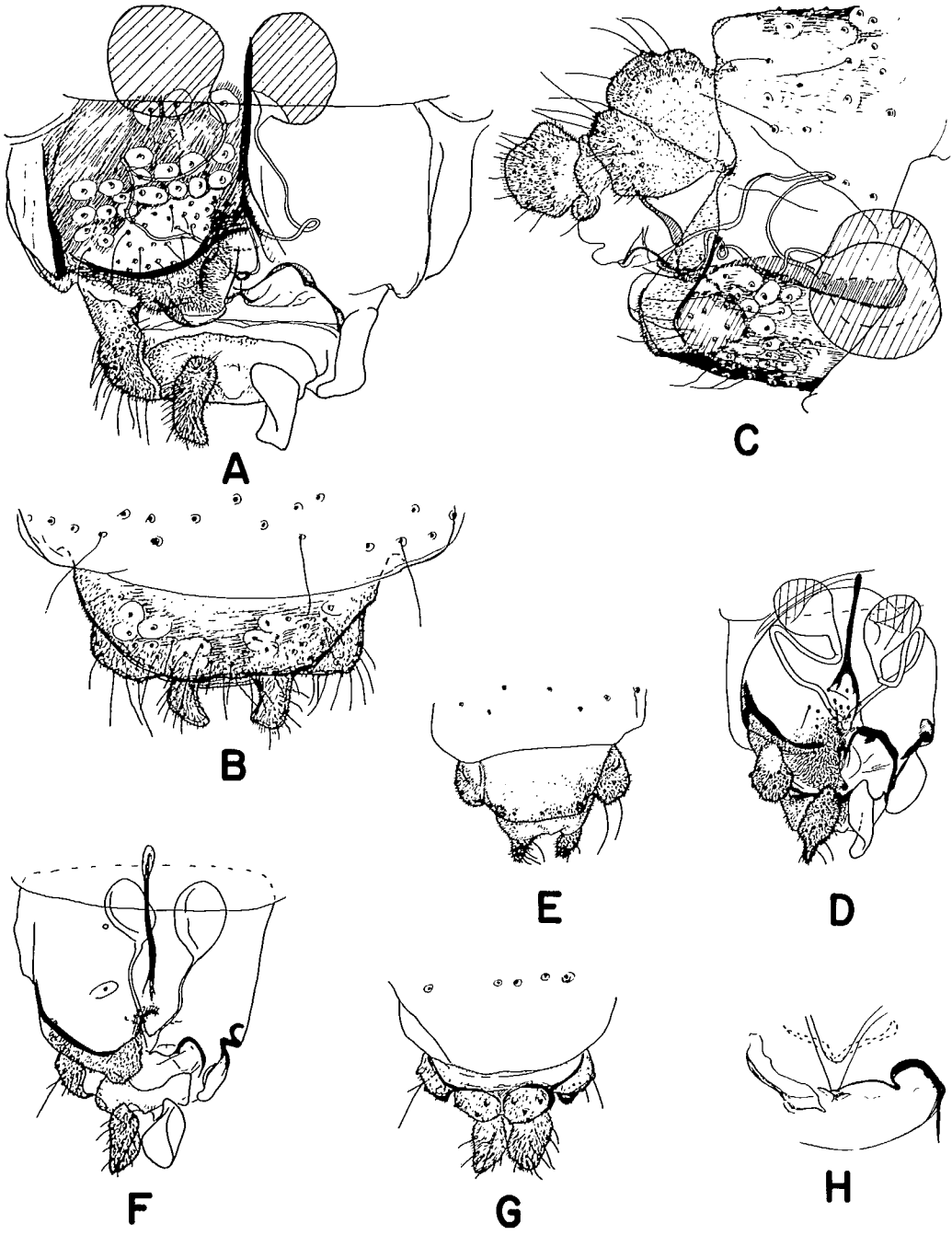

FIG. 40. Female genitalia of Orthocladiinae. A–C, *Abiskomyia virgo* Edw.: A) ventral; B) dorsal; C) lateral. D–E, *Eukiefferiella claripennis* (Lundb.): D) ventral; E) dorsal. F–H, *Heterotanytarsus nudalus* Sæth.: F) ventral; G) dorsal; H) coxosternapodeme, labia, and spermathecal eminence.

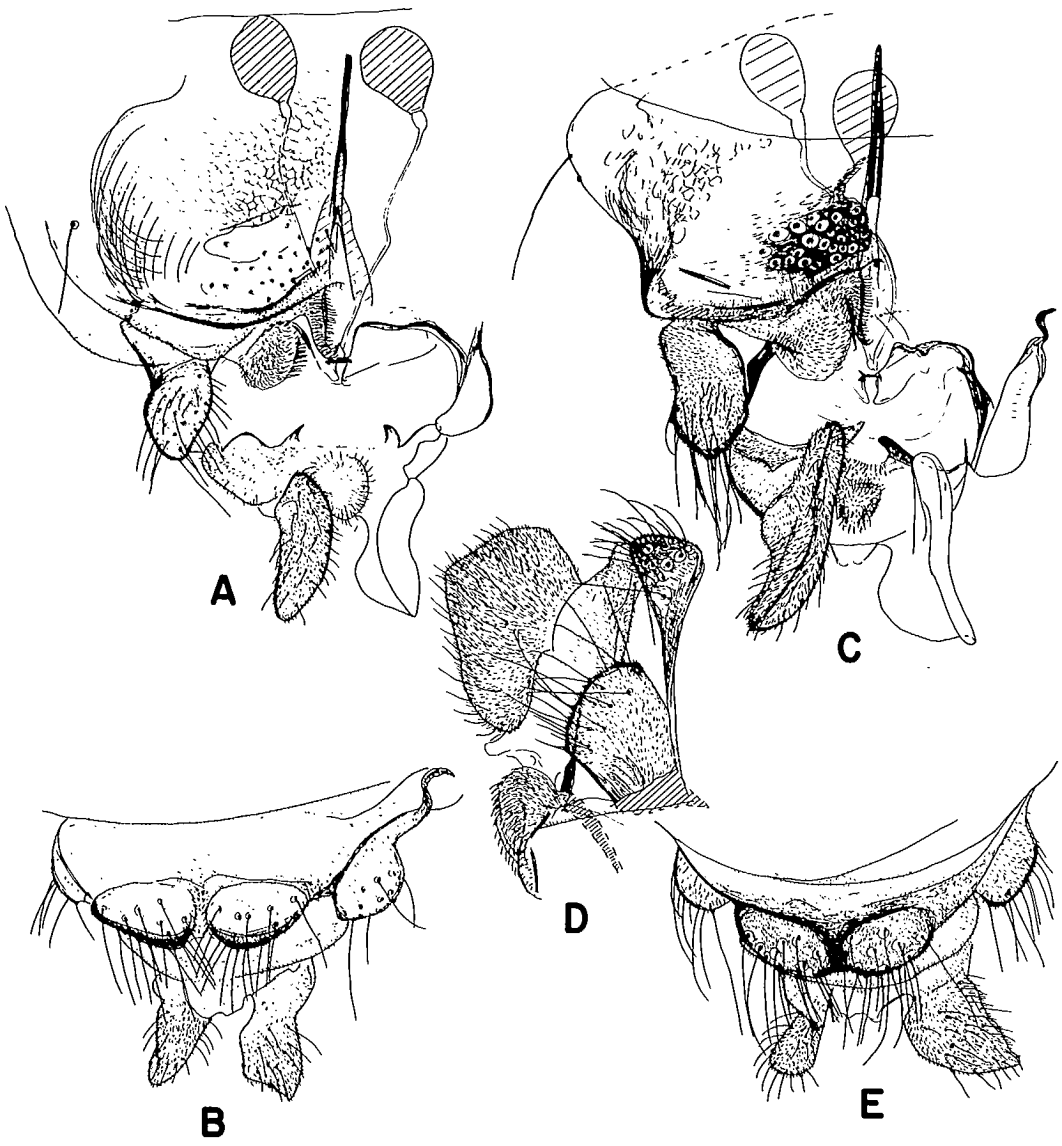

FIG. 41. Female genitalia of *Psectrocladius* spp., Orthocladiinae. A–B, *P. (P.) barbimanus* (Edw.): A) ventral; B) dorsal. C–E, *P. (Allopsectrocladius) flavus* Joh.: C) ventral; D) lateral; E) dorsal.

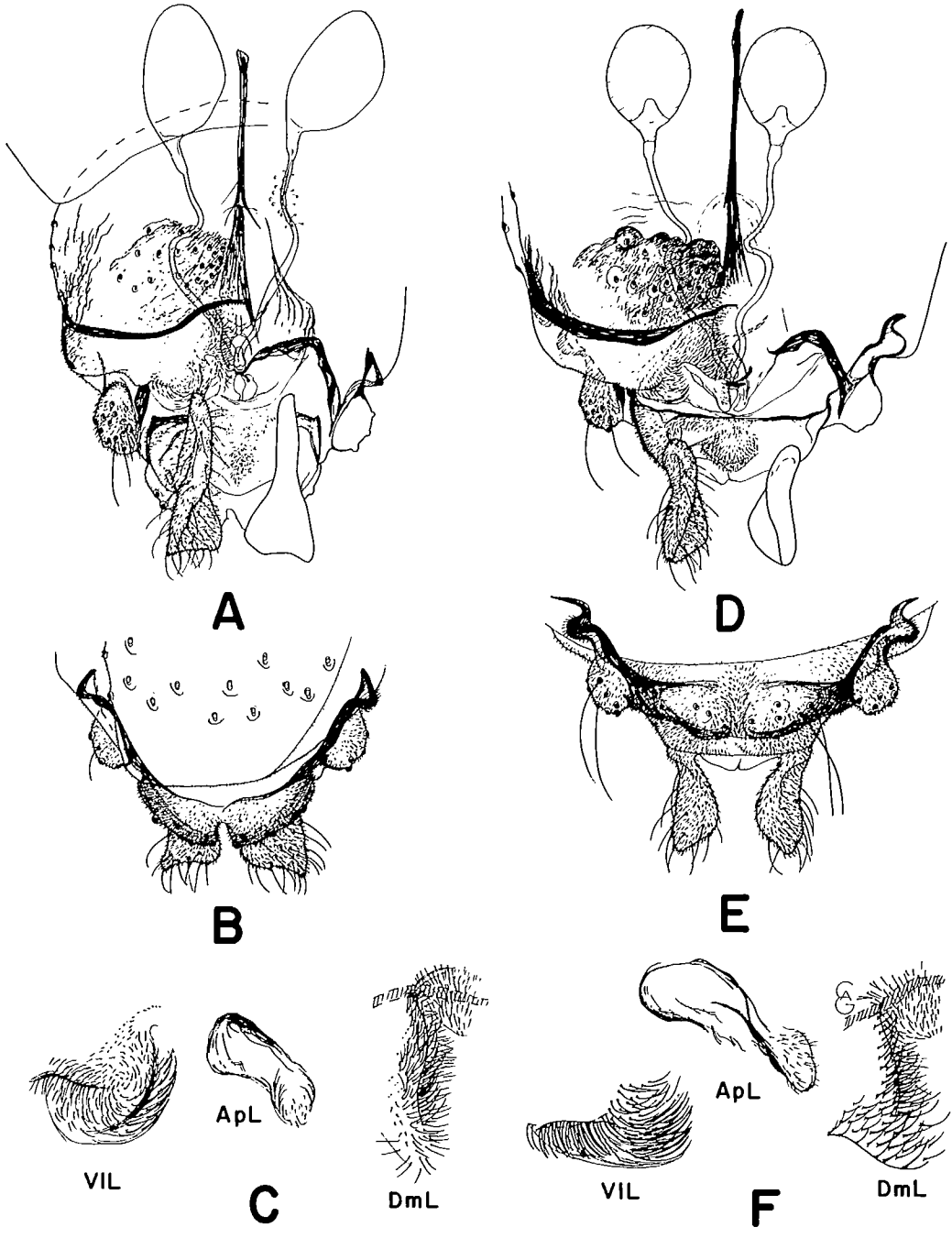

FIG. 42. Female genitalia of *Psectrocladius (Psectrocladius)* spp., Orthocladiinae. A–C, *Psectrocladius (P.)* sp. *A:* A) ventral; B) dorsal; C) lobes of Gp VIII. D–F, *Psectrocladius (P.)* sp. *B:* D) ventral; E) dorsal; F) lobes of Gp VIII.

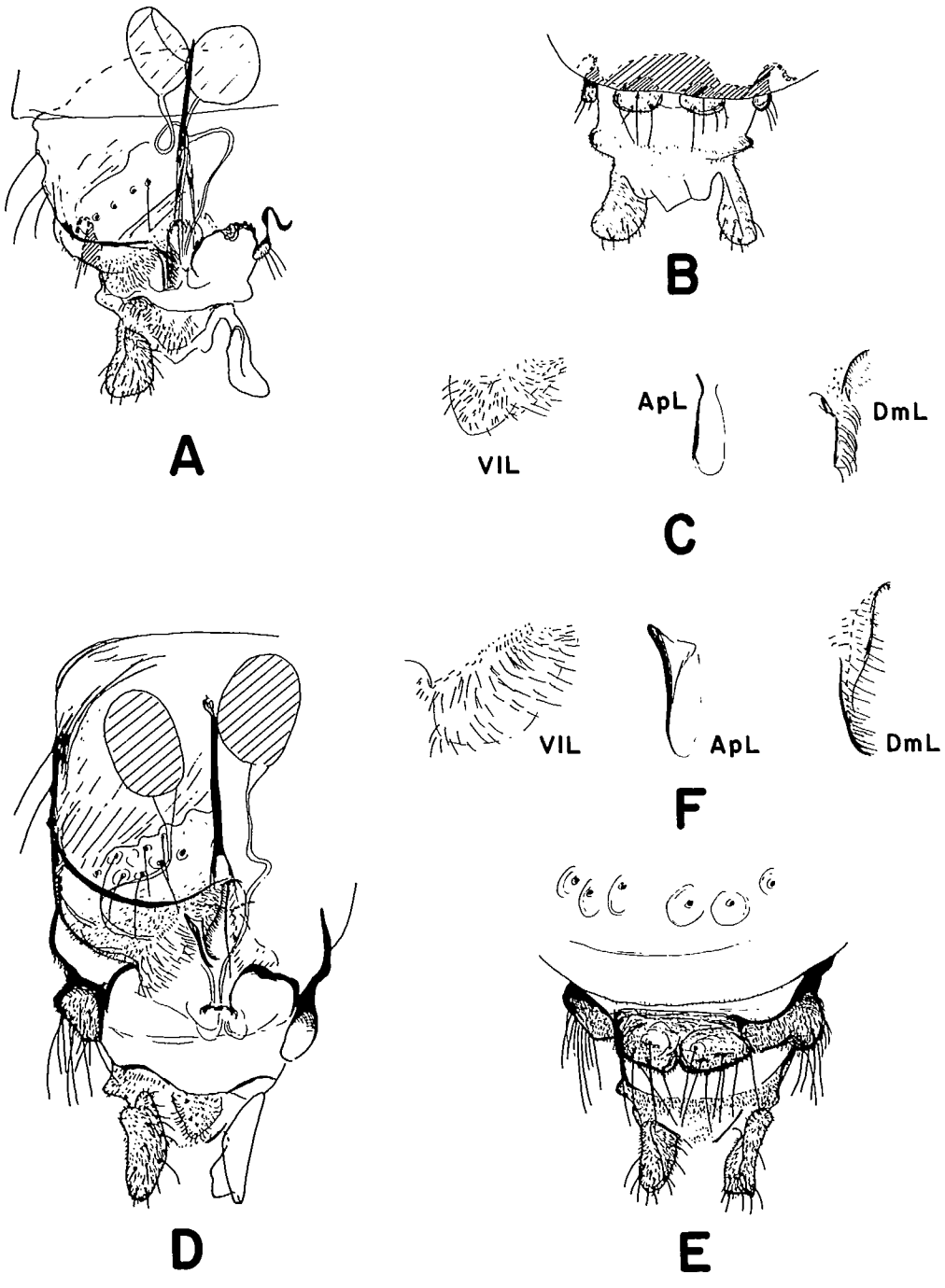

FIG. 43. Female genitalia of *Rheocricotopus* spp., Orthocladiinae. A–C, *R. eminellobus* Sæth.: A) ventral; B) dorsal; C) lobes of Gp VIII. D–F, *R. effusus* (Walk.): D) ventral; E) dorsal; F) lobes of Gp VIII.

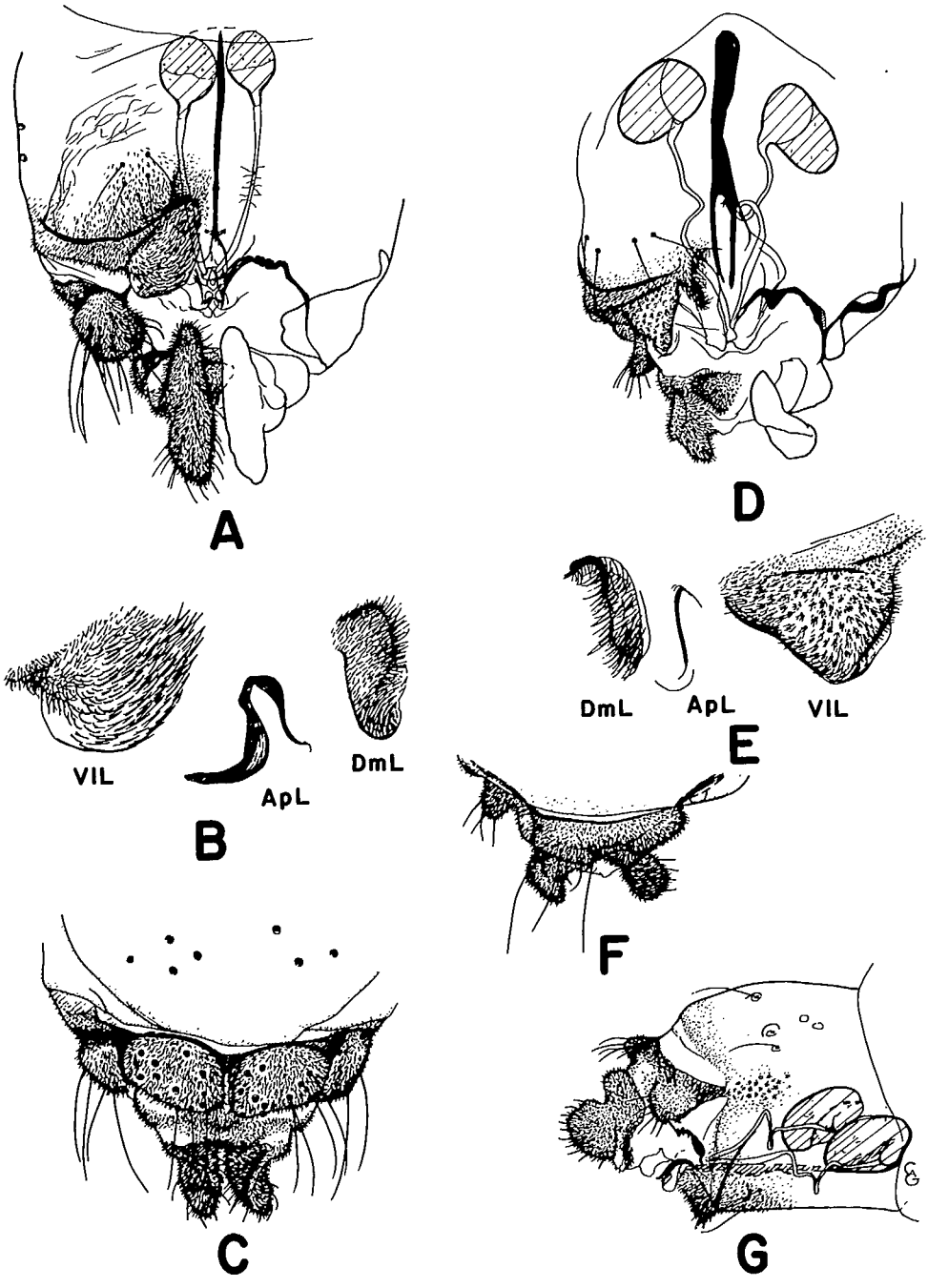

FIG. 44. Female genitalia of Orthocladiinae. A–C, *Orthocladius (Euorthocladius)* sp.: A) ventral; B) lobes of Gp VIII; C) dorsal. D–G, *Nanocladius (Nanocladius)* cf. *bicolor* (Zett.): D) ventral; E) lobes of Gp VIII; F) dorsal; G) lateral.

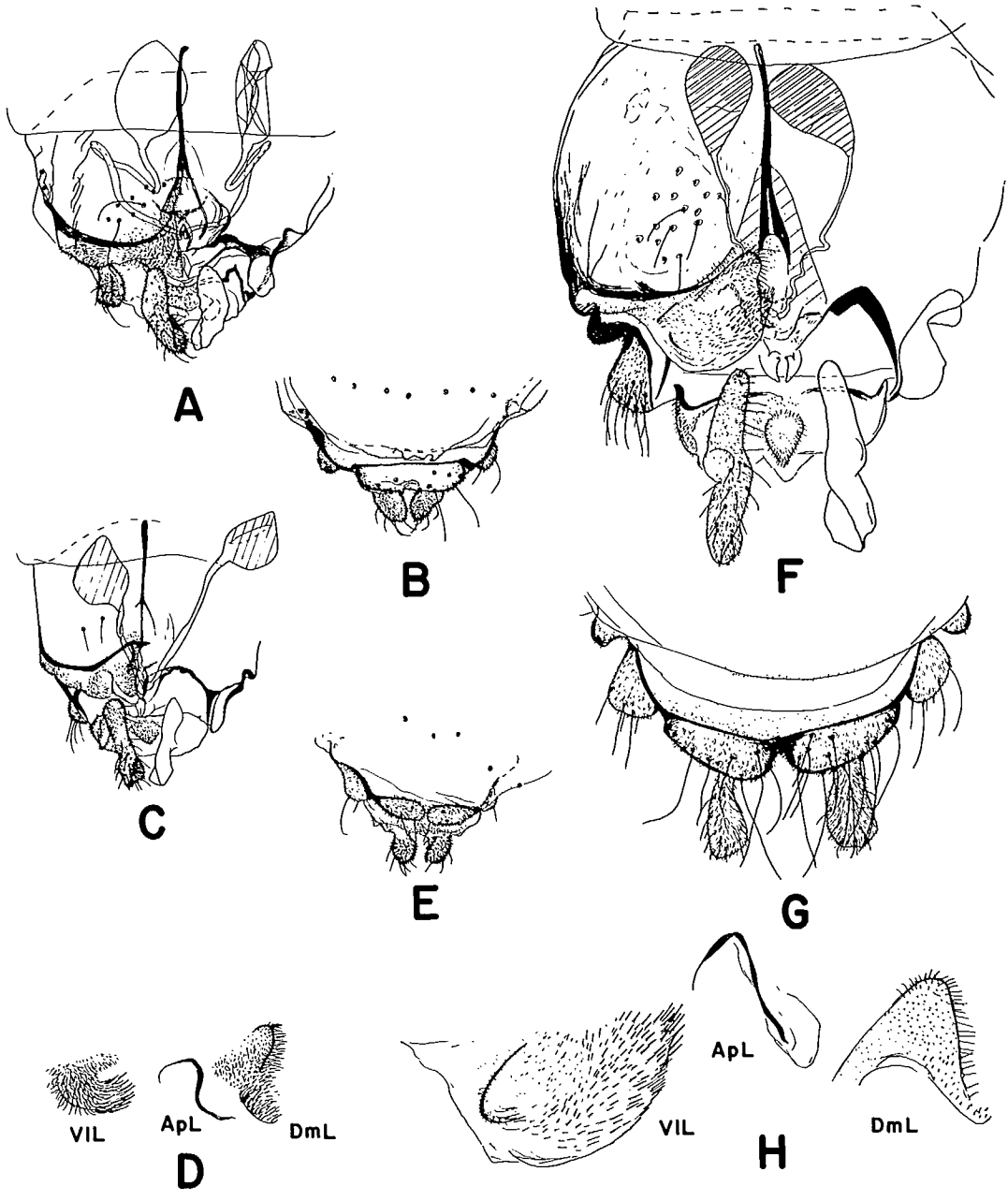

FIG. 45. Female genitalia of Orthocladiinae. A–B, *Parorthocladius nudipennis* (Kieff.): A) ventral; B) dorsal. C–E, *Synorthocladius semivirens* (Kieff.): C) ventral; D) lobes of Gp VIII; E) dorsal. F–H, *Orthocladius (Orthocladius) obumbratus* Joh.: F) ventral; G) dorsal; H) lobes of Gp VIII.

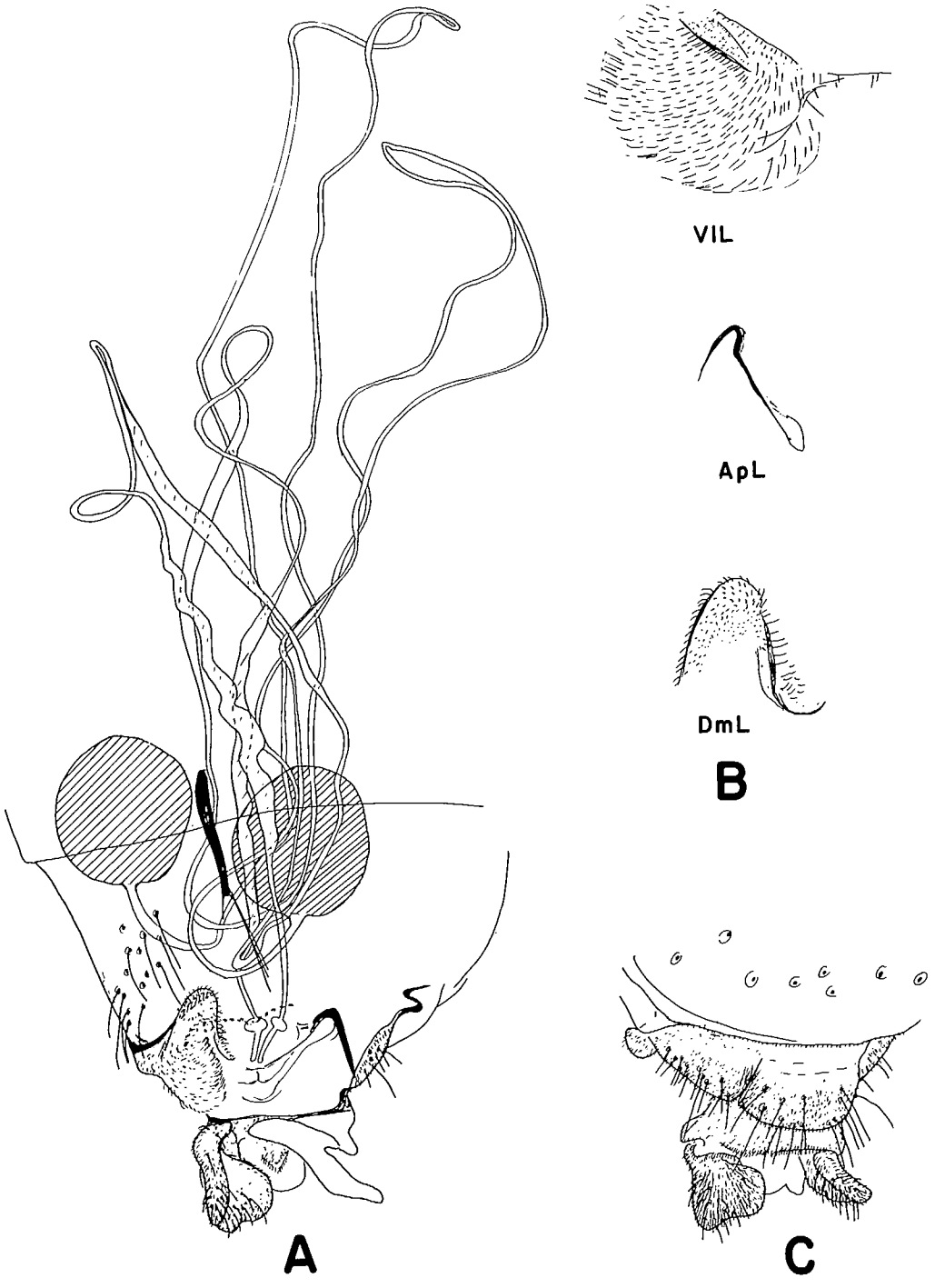

FIG. 46. Female genitalia of *Orthocladius (Eudactylocladius)* sp., Orthocladiinae. A, ventral. B, lobes of Gp VIII. C, dorsal.

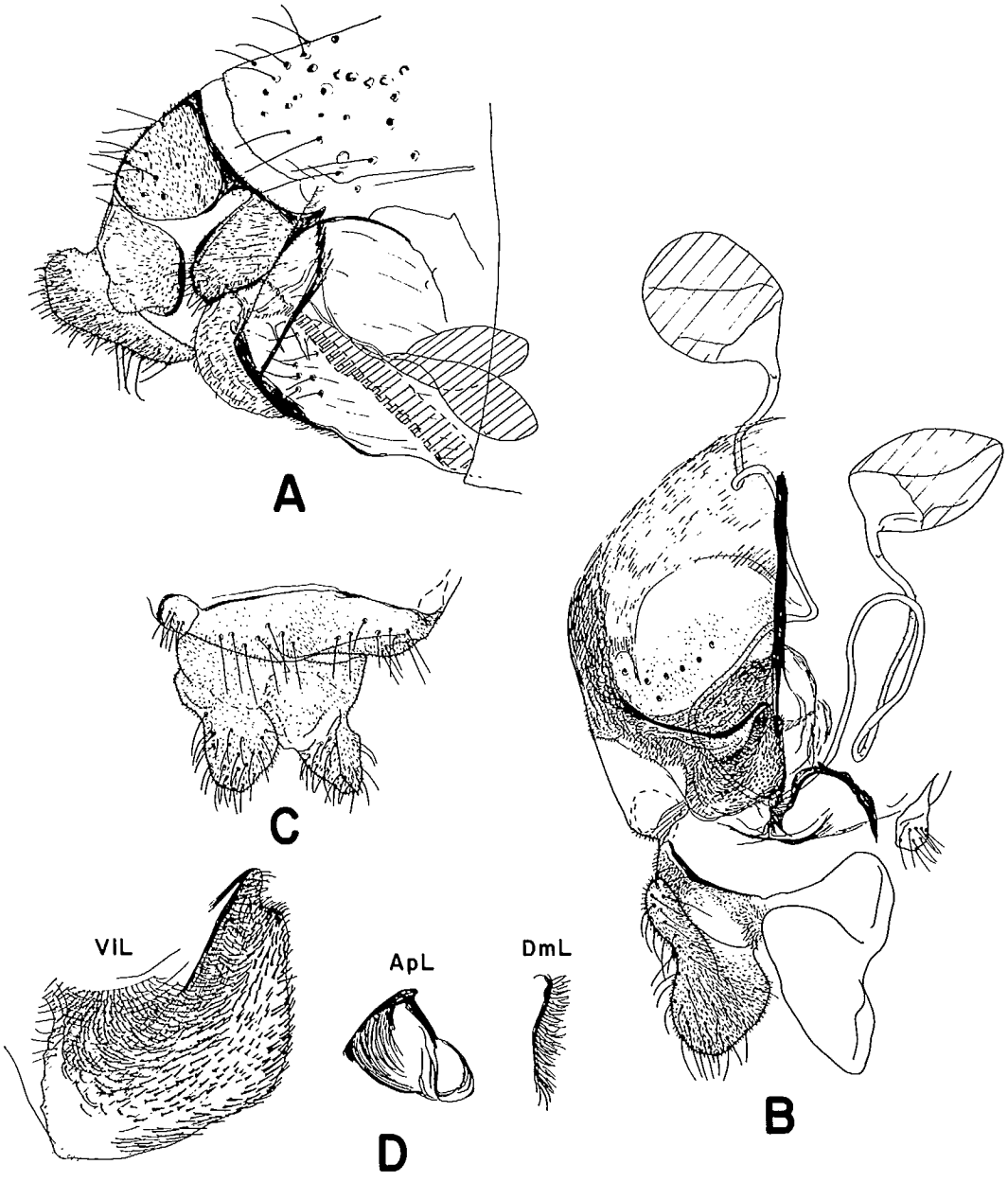

FIG. 47. Female genitalia of Orthocladiinae. A, *Acricotopus* cf. *senex* (Joh.), lateral. B–D, *Paracladius quadrinodosus* Hirv.: B) ventral; C) dorsal; D) lobes of Gp VIII.

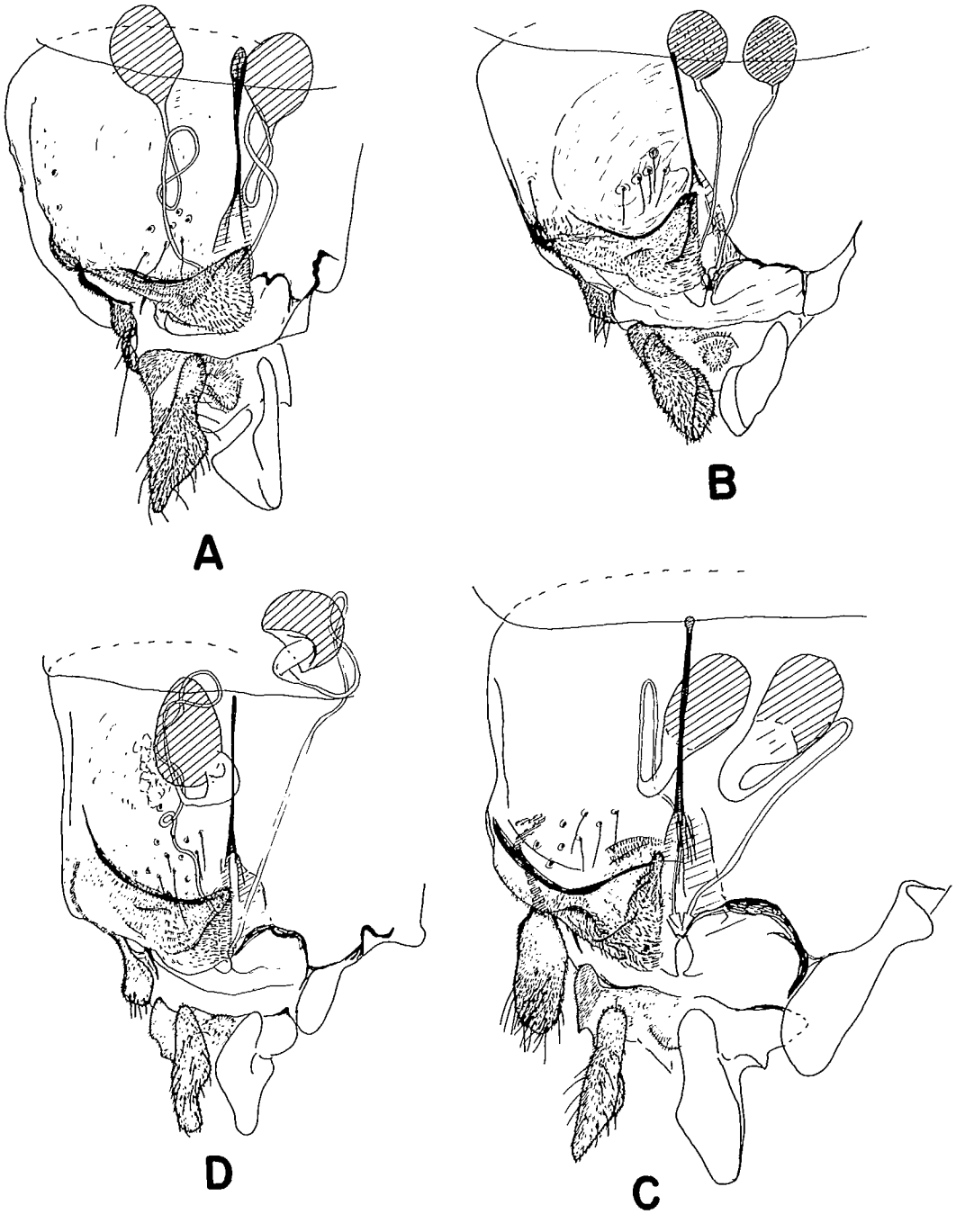

FIG. 48. Female genitalia of *Cricotopus* spp., Orthocladiinae, ventral views. A, *C. (C.) slossonae* Mall. Coq. B, *C. (C.) bicinctus* (Meig.). C, *C. (C.) trifascia* Edw. D, *C. (Isocladius) sylvestris* (Fabr.).

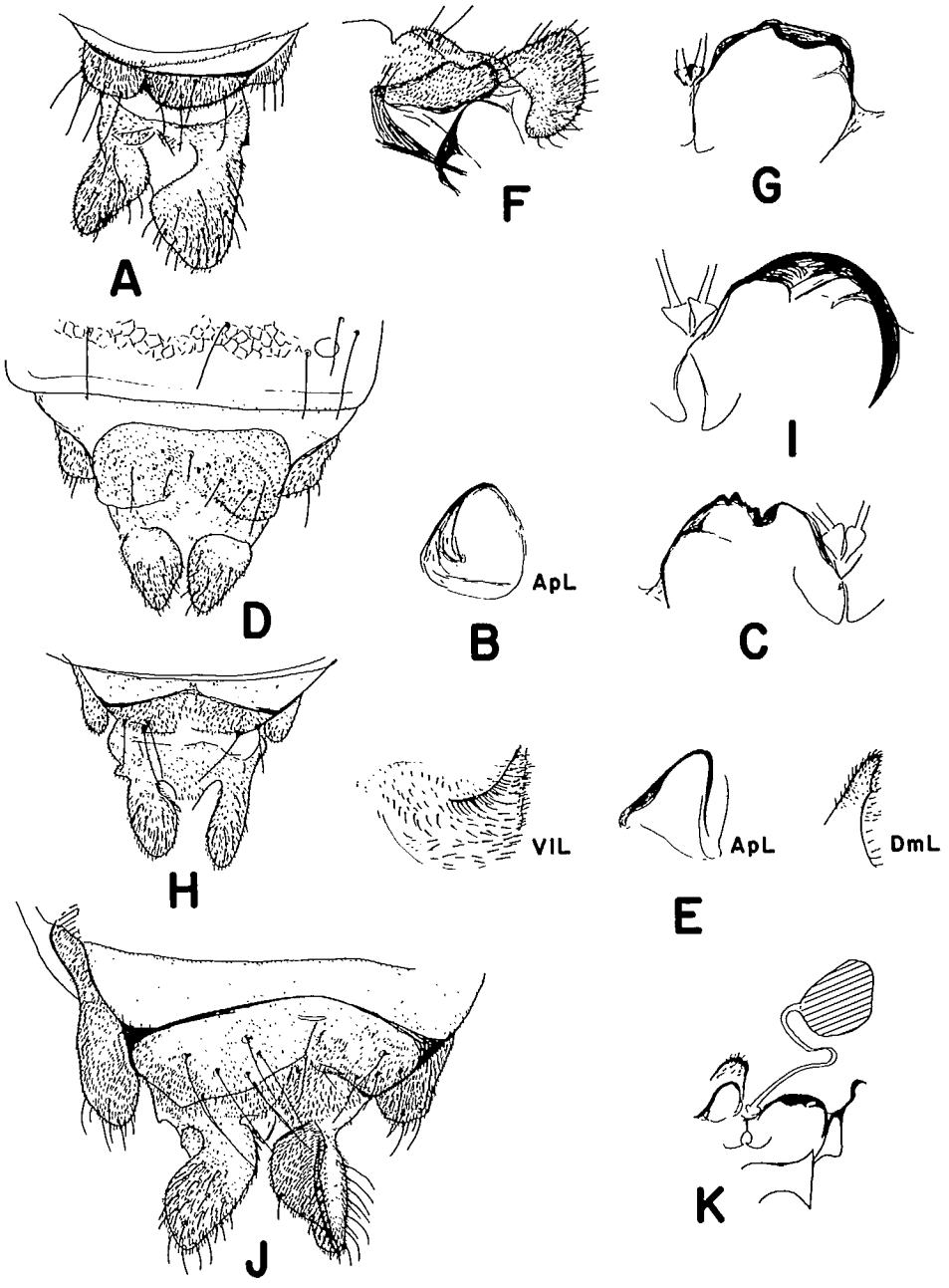

FIG. 49 Female genitalia of *Cricotopus* spp., Orthocladiinae. A–C, *C. (C.) slossonae* Mall.: A) dorsal; B) apodeme lobe; C) coxosternapodeme, labia, and openings of spermathecal ducts. D–E, *C. (C.) bicinctus* (Meig.): D) dorsal; E) lobes of Gp VIII. F–H, *C. (Isocladius) sylvestris* (Fabr.) type 1: F) lateral; G) coxosternapodeme, labia, and openings of spermathecal ducts; H) dorsal. I, *C. (Isocladius) sylvestris* (Fabr.) type 2; coxosternapodeme, labia, and openings of spermathecal ducts. J, *C. (C.) trifascia* Edw. dorsal. K, *C. (C.)* cf. *triannulatus* (Macq.), dorsomesal lobe, coxosternapodeme, labia, and spermatheca.

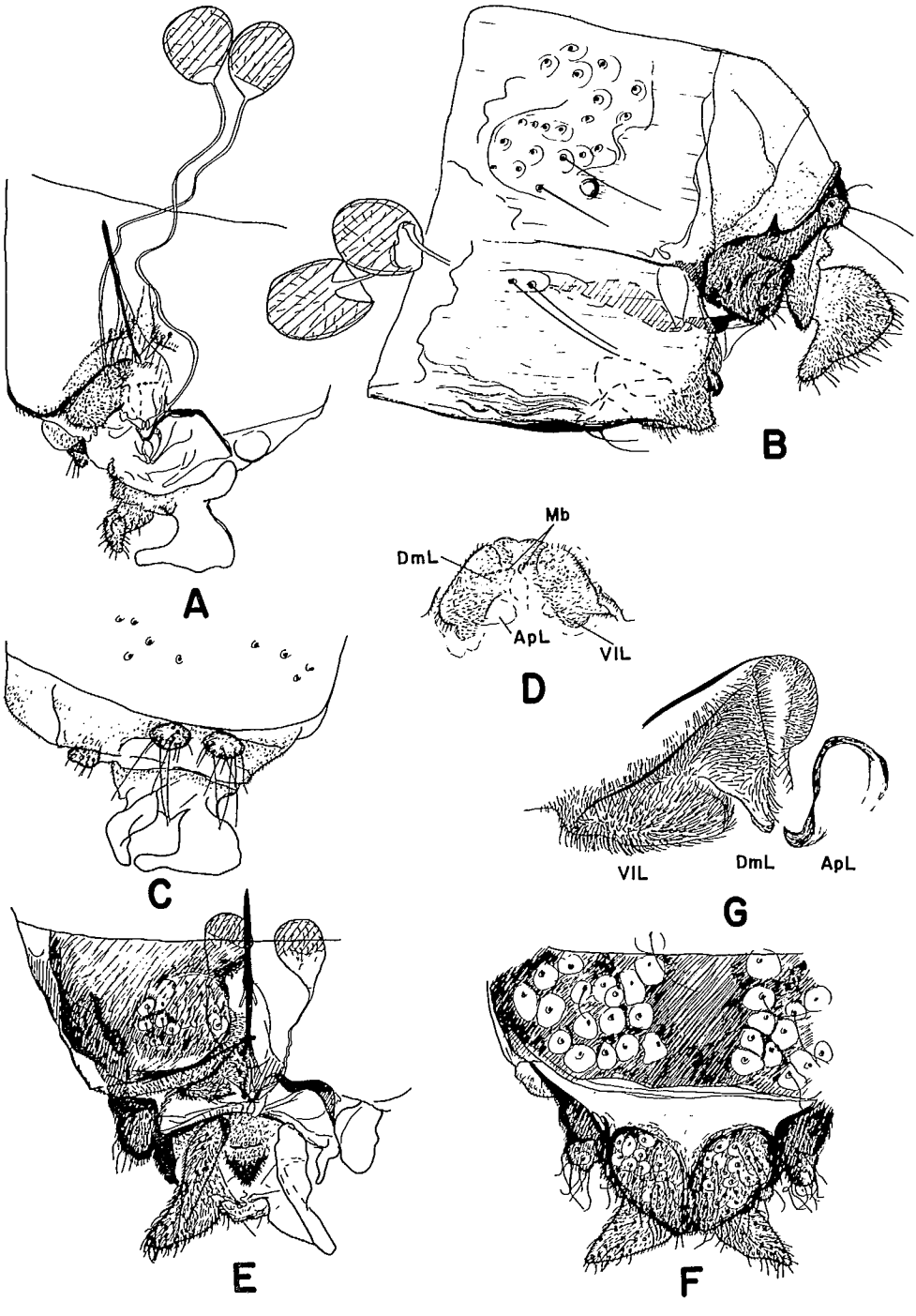

FIG. 50. Female genitalia of Orthocladiinae. A–D, *Oliveria tricornis* (Ol.): A) ventral; B) lateral; C) dorsal; D) lobes of Gp VIII. E–G, *Baeoctenus bicolor* Sæth.: E) ventral; F) dorsal; G) Gp VIII.

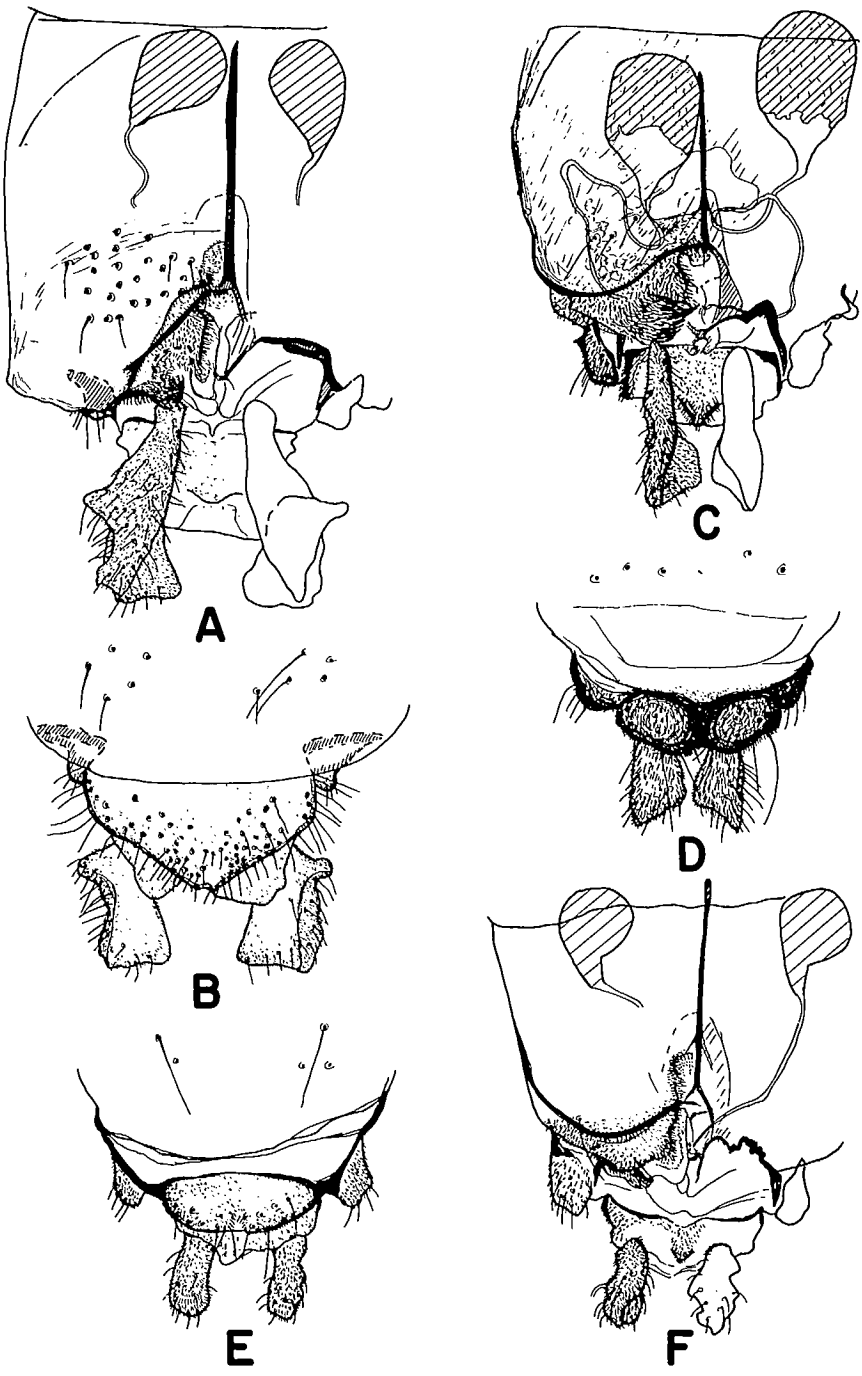

FIG. 51. Female genitalia of Orthocladiinae. A–B, *Hydrobaenus lugubris* Fries: A) ventral; B) dorsal. C–D, *Hydrobaenus johannseni* (Subl.): C) ventral; D) dorsal. E–F, *Zalutschia tornetraeskensis* (Edw.): E) dorsal; F) ventral.

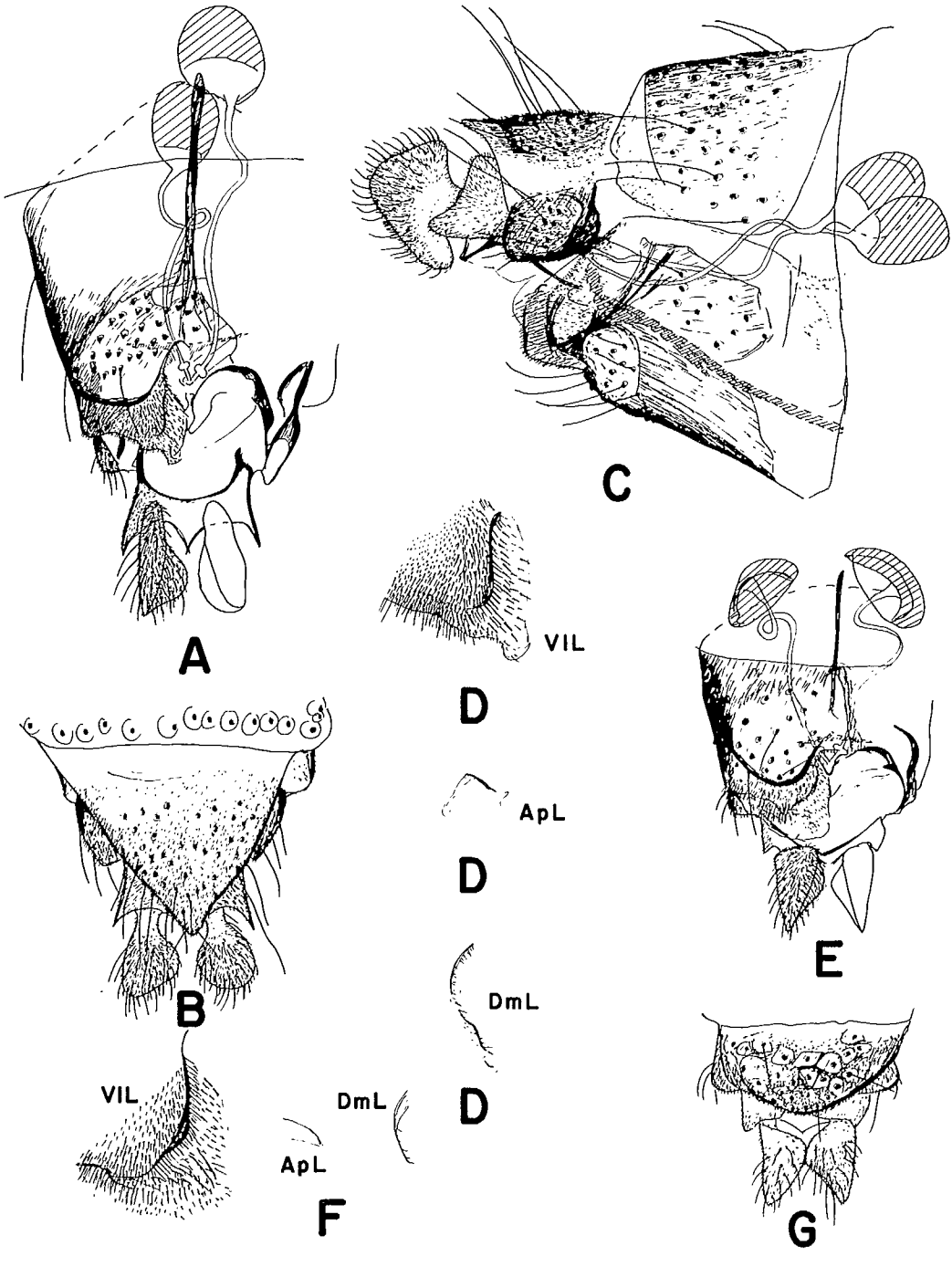

FIG. 52. Female genitalia of *Metriocnemus* spp., Orthocladiinae. A–D, *M. knabi* Coq.: A) ventral; B) dorsal; C) lateral; D) lobes of Gp VIII. E–G, *Metriocnemus* sp.n.: E) ventral; F) lobes of Gp VIII; G) dorsal.

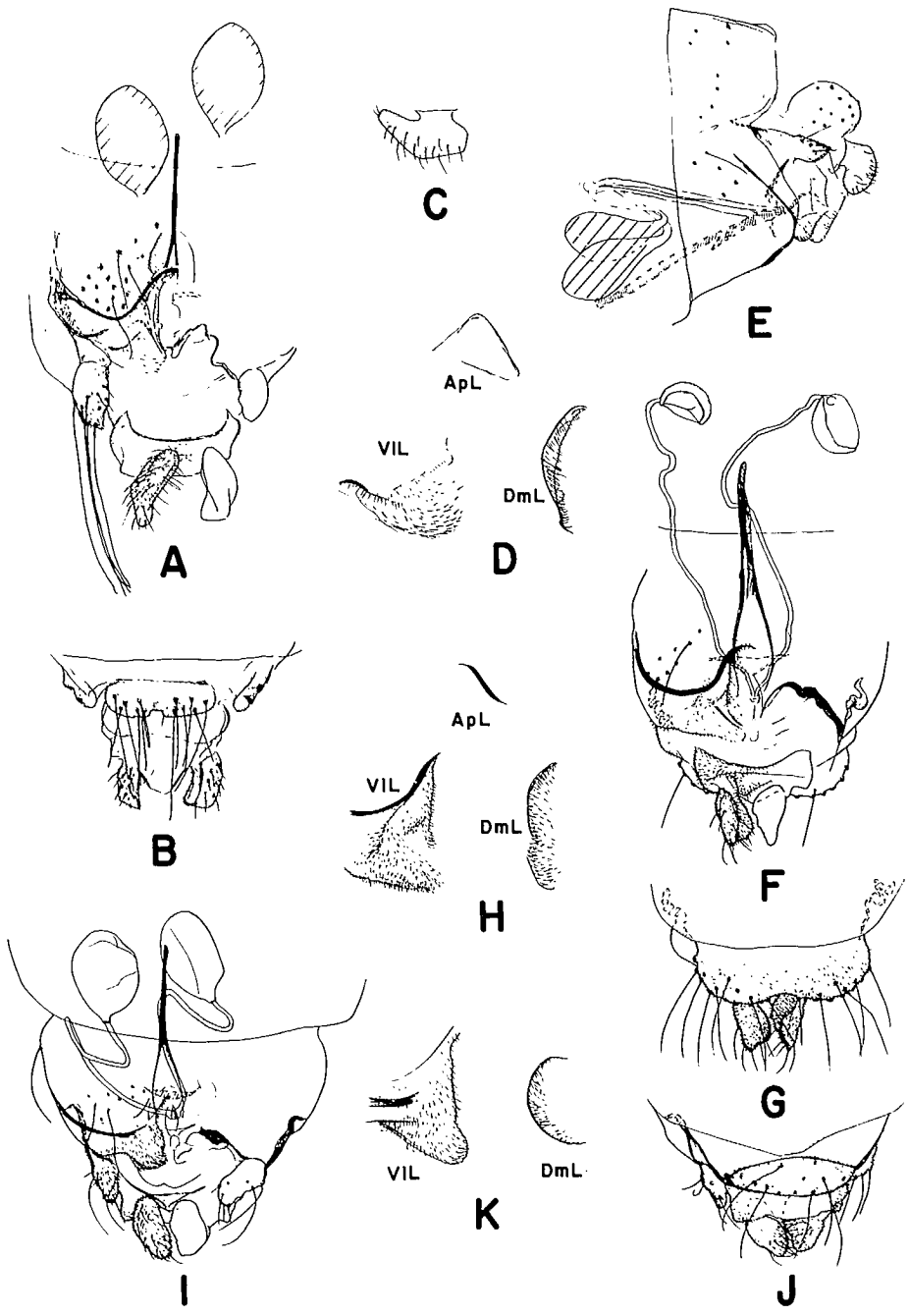

FIG. 53. Female genitalia of Orthocladiinae. A–D, *Parametriocnemus lundbecki* (Joh.): A) ventral; B) dorsal; C) cercus, lateral; D) lobes of Gp VIII. E, *Gymnometriocnemus* sp., lateral. F–H, *Gymnometriocnemus* sp.n.: F) ventral; G) dorsal; H) lobes of Gp VIII. I–K, *Thienemannia gracilis* (Kieff.): I) ventral; J) dorsal; K) lobes of Gp VIII.

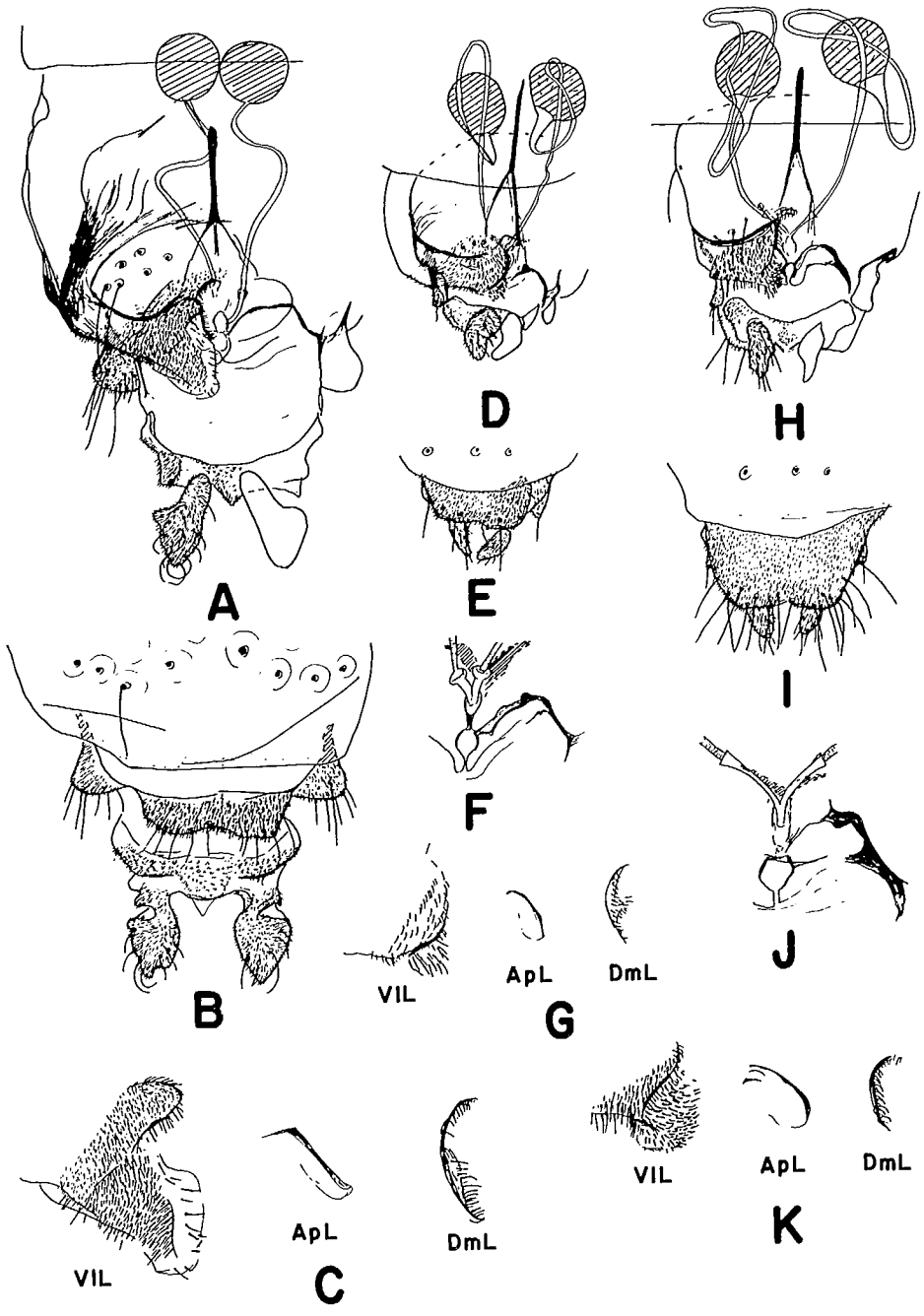

FIG. 54. Female genitalia of Orthocladiinae. A–C, *Chaetocladius* sp.: A) ventral; B) dorsal; C) lobes of Gp VIII. D–G, *Limnophyes* poss. *minimus* (Meig.): D) ventral; E) dorsal; F) coxosternapodeme, labia, membrane, and opening of spermathecal ducts; G) lobes of Gp VIII. H–K, *Limnophyes pilicistulus* Sæth.?: H) ventral; I) dorsal; J) coxosternapodeme, labia, membrane, and opening of spermathecal ducts; K) lobes of Gp VIII.

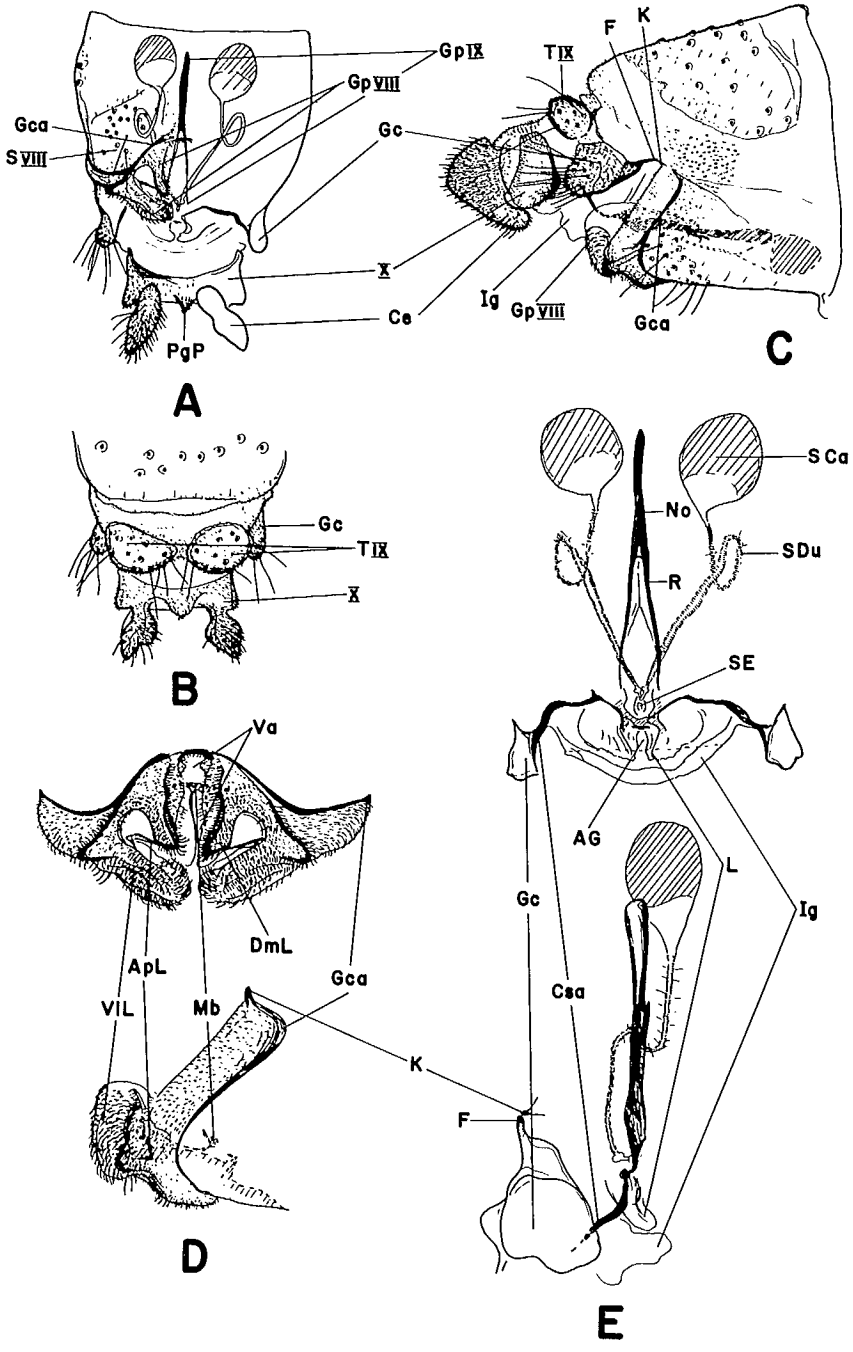

FIG. 55. Female genitalia of *Heterotrissocladius hirtapex* Sæth., Orthocladiinae. A, ventral. B, dorsal. C, lateral. D, Gp VIII, Gca VIII, and membrane in ventral (top) and lateral (bottom) views. E, Gc IX, coxosternapodemes, Gp IX, labia, and spermathecae in ventral (top) and lateral (bottom) views.

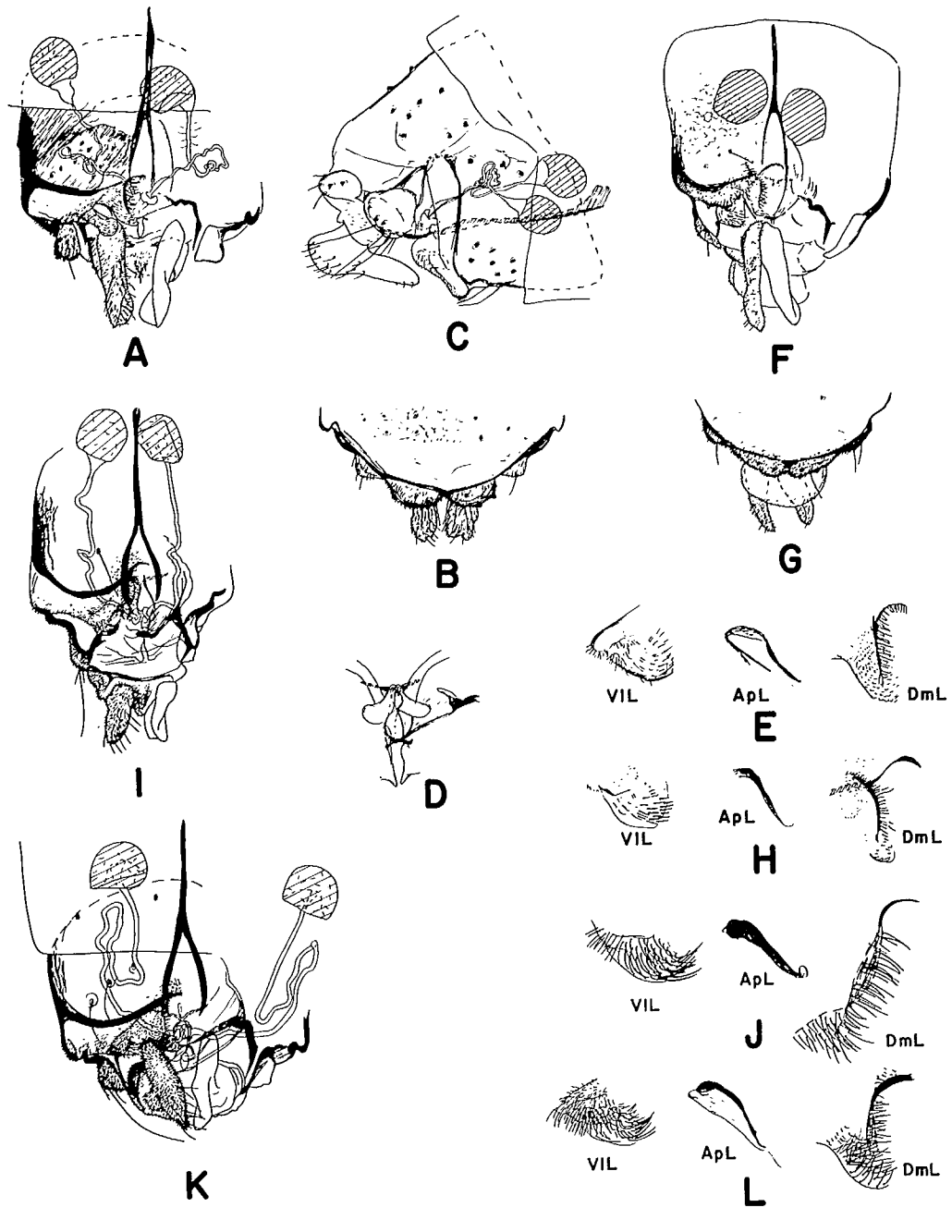

FIG. 56. Female genitalia of Orthocladiinae. A–E, *Parakiefferiella torulata* Sæth.: A) ventral; B) dorsal; C) lateral; D) labia and openings of spermathecal ducts; E) lobes of Gp VIII. F–H, *Phycoidella dentolatens* Sæth.: F) ventral; G) dorsal; H) lobes of Gp VIII. I–J, *Parakiefferiella coronata* (Edw.): I) ventral; J) lobes of Gp VIII. K–L, *Parakiefferiella* sp.n. near *bathophila* Kieff.: K) ventral; L) lobes of Gp VIII.

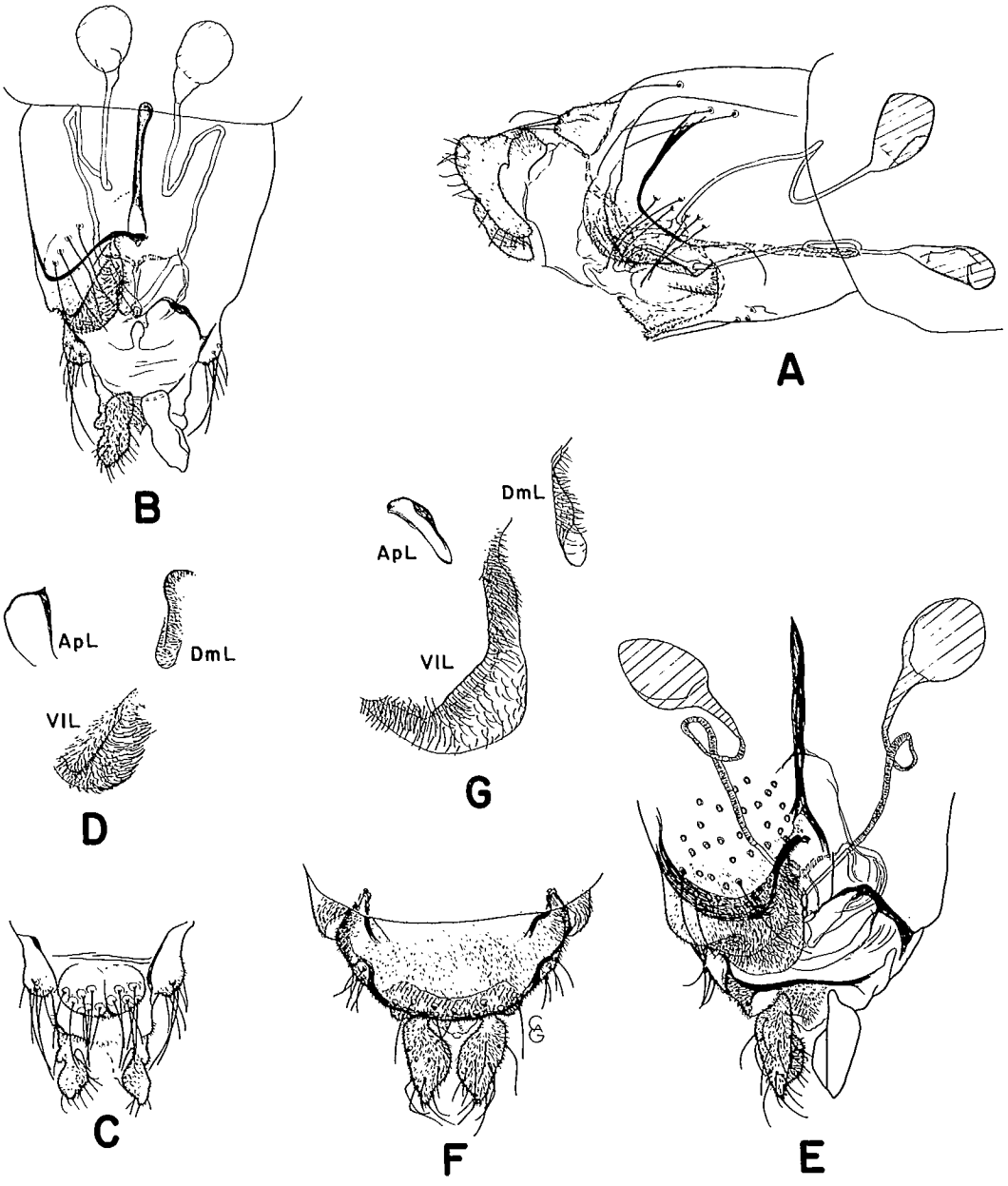

FIG. 57. Female genitalia of Orthocladiinae. A–D, *Heleniella ornaticollis* (Edw.): A) lateral; B) ventral; C) dorsal; D) lobes of Gp VIII. E–G, *Bryophaenocladius* sp.: E) ventral; F) dorsal; G) lobes of Gp VIII.

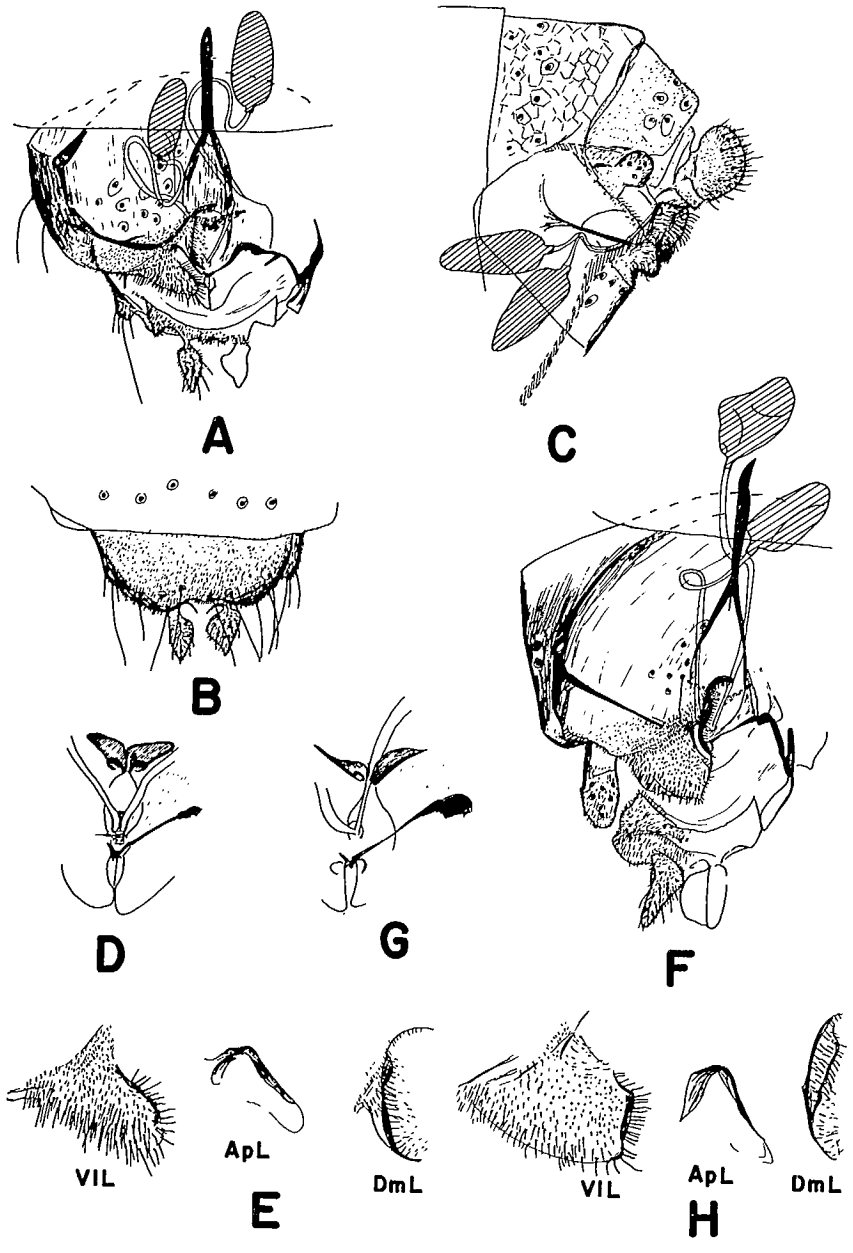

FIG. 58. Female genitalia of *Smittia* spp., Orthocladiinae. A–E, *Smittia* sp. *A:* A) ventral; B) dorsal; C) lateral; D) membrane, labia, and spermathecal eminence; E) lobes of Gp VIII. F–H, *Smittia* sp. *B:* F) ventral; G) membrane, labia, and spermathecal eminence; H) lobes of Gp VIII.

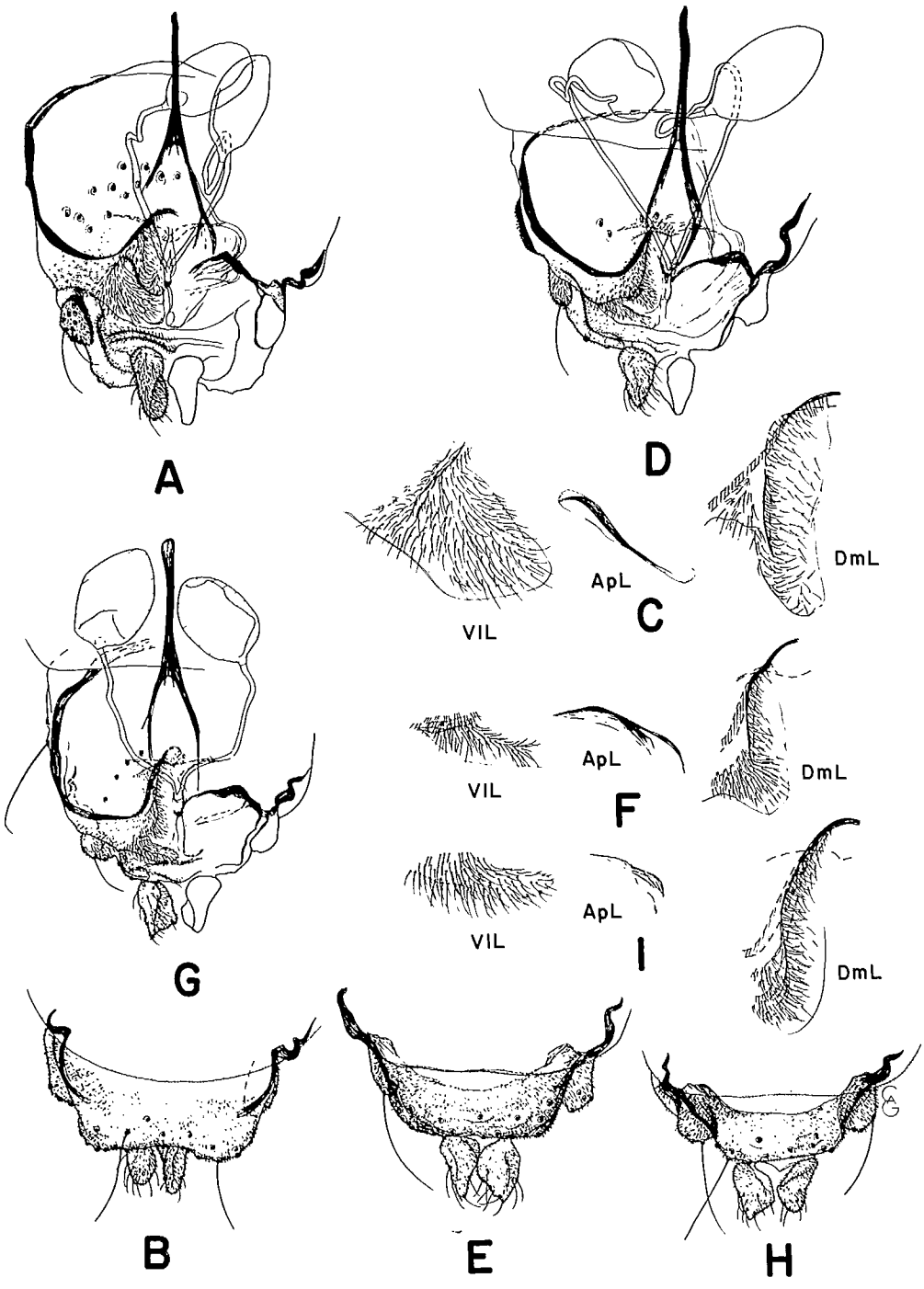

FIG. 59. Female genitalia of *Smittia* spp., Orthocladiinae. A–C, *Smittia* sp. *C:* A) ventral; B) dorsal; C) lobes of Gp VIII. D–F, *Smittia* sp. *D:* D) ventral; E) dorsal; F) lobes of Gp VIII. G–H, *Smittia* sp. *E:* G) ventral; H) dorsal; I) lobes of Gp VIII.

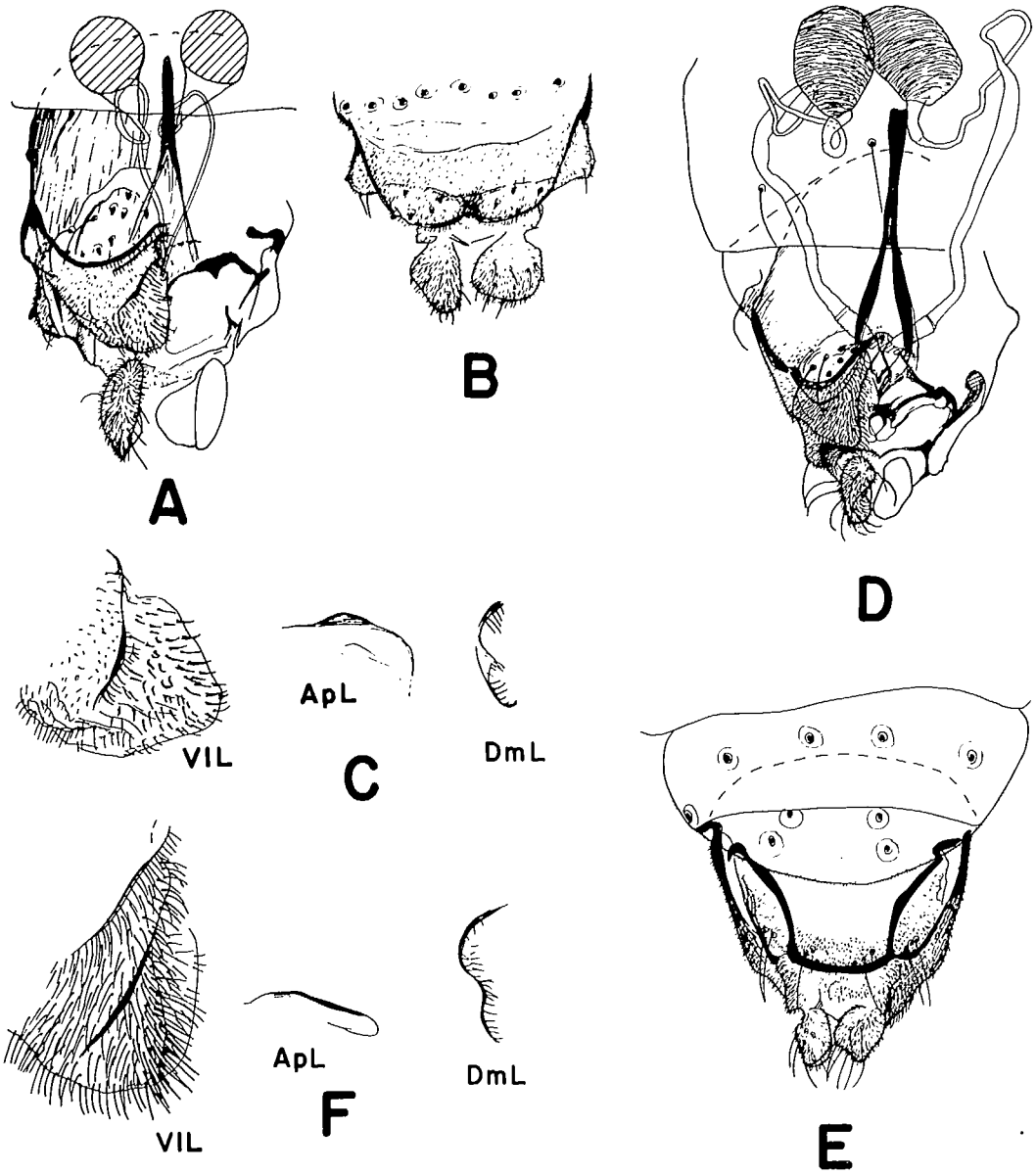

FIG. 60. Female genitalia of Orthocladiinae. A–C, *Camptocladius stercorarius* (De Geer): A) ventral; B) dorsal; C) lobes of Gp VIII. D–F, *Pseudosmittia* sp.n. near *restricta* Brund.: D) ventral; E) dorsal; F) lobes of Gp VIII.

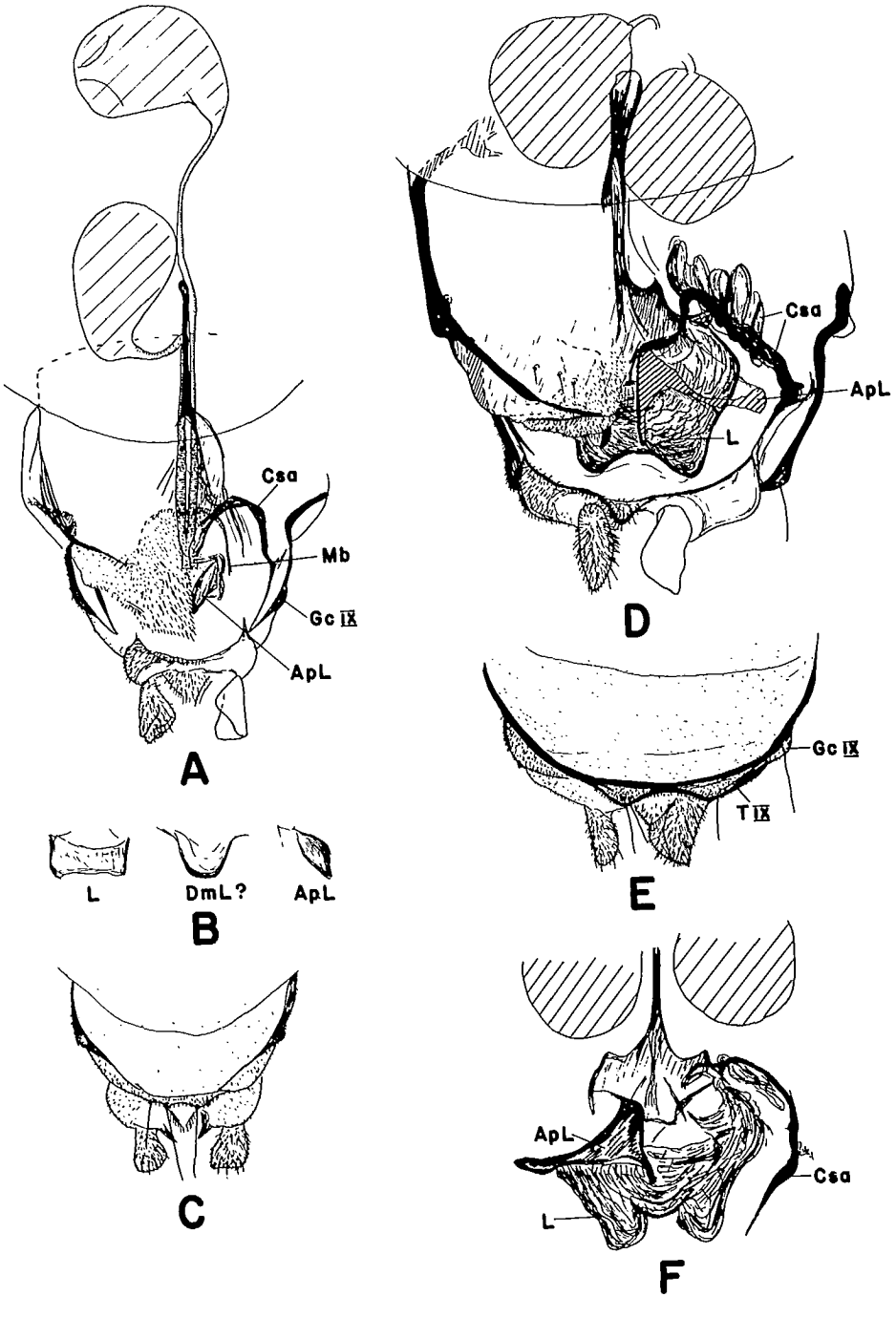

FIG. 61. Female genitalia of Orthocladiinae. A–C, *Thienemanniella* sp.: A) ventral; B) possible fused dorsomesal lobes of Gp VIII, fused labia, and apodeme lobe; C) dorsal. D–E, *Corynoneura* sp. *A:* D) ventral; E) dorsal. F, *Corynoneura* sp. *B*, Gp IX, coxosternapodeme, apodeme lobe, and labia.

Subfamily Chironominae
(Fig. 63–90)

T VIII well developed, normal. Gca VIII always well developed laterally, sometimes joined mesally anterior of vagina, sometimes rounded caudally, often with branch running out on base of Gp VIII. S VIII forms a floor under anterior part of vagina in the Tanytarsini, under more lateral parts in *Manoa* Fittk. (Fig. 71A) (Pseudochironomini), and does not form a floor in the remainder. Gp VIII simple, broad, and usually caudally rounded in *Paratendipes* Kieff. (Fig. 72A), *Microtendipes* Kieff. (Fig. 72C, D), *Nilothauma* Kieff. (Fig. 73A) (Chironomini), and in *Zavrelia* Kieff. (Fig. 63A, C), *Stempellinella* Brund. (Fig. 63E, G), *Stempellina* Bause (Fig. 63J, L), *Thienemanniola* Kieff. (Lehmann 1973 fig. 19), *Tanytarsus* v.d. Wulp (Fig. 64A, C, E, G; 65A), *Corynocera* Zett. (Fig. 65D), *Pontomyia* Edw. (Tokunaga 1932 fig. 34), *Nimbocera* Reiss, *Cladotanytarsus* Kieff. (Fig. 66B, C), and *Lenziella* Kieff. (Fig. 66G) (Tanytarsini). Gp VIII divided into large dorsomesal lobe and a slight indication of a far lateral ventrolateral lobe in Pseudochironomini and *Lauterborniella* Bause (Fig. 73D, F). Ventrolateral lobe in remaining genera of Chironomini small and brushlike, long and narrow, broad and triangular, or rectangular; smaller than dorsomesal lobe except in *Stictochironomus* Kieff. (Fig. 77F, G), *Goeldichironomus* Fittk. (Fig. 78C, D), *Nilodorum* Kieff. (Fig. 79D, E), and *Chironomus* subgen. *Camptochironomus* Kieff. (Fig. 82A, C). (In *Stictochironomus* and *C. (Camptochironomus)*, however, the dorsomesal lobe is secondarily reduced.) Dorsomesal lobe with oral group shagreenation in *Xenochironomus* Kieff. (Fig. 83A, B) and in the *Harnischia* complex. Apodeme lobe always present, sometimes with microtrichia, occasionally vestigial and nonapparent. Membrane always present. Gp IX well developed, notum always more than 1.5 times as long as ramus in Pseudochironomini and Chironomini, about as long to twice as long as ramus in Tanytarsini. T IX large, well developed, nearly always hood-shaped and undivided; divided into setigerous protrusions by a reticulated median area only in *Lauterborniella* (Fig. 73E). T IX in Tanytarsini often more triangular and with distinct orolateral shoulders. Gc IX moderately large to very small, never fused with T IX, mostly with several setae, often with only 1 or 2 setae, or void of setae. Coxosternapodeme nearly straight, simply curved, or with 2 curves. Intergonocoxal connective always present. Segment X normal, without setae in Tanytarsini, Pseudochironomini, and in some *Microtendipes, Nilothauma, Xenochironomus (Xenochironomus)*, and *Cryptotendipes* Lenz; in *Fleuria* Kieff. (Fig. 78A) segment X with elongate, flat, caudolateral extensions forming a collar around cerci. Postgenital plate mostly triangular, pointed or rounded, and relatively large, occasionally weak or reduced. Cerci generally large to medium size and pediform in Pseudochironomini and Chironomini, usually smaller and more rounded in Tanytarsini.

Labia with microtrichia in *Manoa, Paralauterborniella,* some *Stictochironomus, Nilodorum, Xenochironomus,* and in the *Harnischia* complex. 2 seminal capsules, nearly always moderately to relatively large in size, oval or ovoid, pale, and without microtrichia, extremely large in *Corynocera* (Fig. 65D); neck placed caudally except in *Stictochironomus* (Fig. 77C, F) where it is situated more laterally. Spermathecal duct usually straight or nearly straight, with distinct loops or bends in some or all species of *Zavrelia, Stempellinella, Stempellina, Tanytarsus, Corynocera, Rheotanytarsus* Bause, the Pseudochironomini, *Phaenopsectra* Kieff., *Pagastiella* Brund., *Graceus* Goetgh., *Polypedilum* subgen. *Pentapedilum* Kieff., *Tribelos* Town., and *Chironomus* Meig. Spermathecal ducts always with common opening, never fused, or with bulbs before opening.

Phyletic Relationships within Chironominae

In the female genitalia of this subfamily there are, once more, many features of fundamental phylogenetic importance.

The branching of Gca VIII onto the base of Gp VIII as well as straight gonocoxapodemes are both probably apomorphies.

The floor formed by S VIII under the anterior part of the vagina in the Tanytarsini is a clear synapomorphous feature for the tribe. Although a floor is present also in *Manoa,* the floor covers more lateral parts of the vagina and may have developed independently. However, the capacity of S VIII to form a vaginal floor may be a synapomorphy for Tanytarsini and Pseudochironomini

combined, as similar well-developed floors are not present in any other chironomids or Diptera examined. (A very small floor, however, is indicated in some *Metriocnemus* and *Nanocladius*.)

The Gp VIII in its most plesiomorphous form is, among the Chironominae, a simple, broad, and usually caudally rounded lobe. Division of the Gp VIII into 2 principal lobes is different from that of the Orthocladiinae (except *Diplocladius* where both types of divisions are indicated), where the margin of the vagina develops into a dorsomesal lobe. In the Chironomini the most lateral part of Gp VIII first forms a minute ventrolateral lobe such as in the Pseudochironomini and *Lauterborniella*. This lobe develops first to a small ventrolateral lobe with long apical microtrichia which makes it look like a little brush (as in most genera of the "Chironomariae connectens" grouping of Lenz (1954–62)). The lobe may become long and narrow as in some genera of the *Harnischia* complex or it may become broad and more triangular or rectangular as in *Goeldichironomus, Nilodorum, Xenochironomus, Cryptochironomus* Kieff., and *Demicryptochironomus* Lenz. In *Goeldichironomus* and *Nilodorum* both lobes are well developed, with the dorsomesal lobe larger than the ventrolateral lobe, a synapomorphous feature for the 2 genera. In *Stictochironomus* and *Chironomus (Camptochironomus)* the dorsomesal lobe is independently reduced. From the above it is obvious that the main lobe of Gp VIII in this subfamily is the dorsomesal lobe while in the Orthocladiinae it is the ventrolateral lobe; the division of Gp VIII into 2 principal lobes is not a homologous trend in the 2 subfamilies. The capacity for division of Gp VIII, however, is, as stated on p. 32, a synapomorphy for the Diamesinae, Prodiamesinae, Orthocladiinae, and Chironominae combined. In *Xenochironomus* and the *Harnischia* complex the dorsomesal lobes have oromesal group shagreenation, a feature not found in other chironomids, and thus a clear synapomorphous feature. The apodeme lobe carries microtrichia only in *Dicrotendipes* Kieff., *Glyptotendipes* Kieff., *Chironomus*, *Kiefferulus* Goetgh., and *Einfeldia* Kieff., a clear synapomorphous feature for these genera.

T IX is nearly always large and undivided, i.e. in its plesiomorphous form. However, the division found in *Lauterborniella* shows that this capacity is also preserved in the subfamily. The triangular T IX with orolateral shoulders found in many Tanytarsini is an apomorphy, but apparently is not synapomorphous for the tribe.

Reduction in size and number of setae on Gc IX both are apomorphous characteristics subject to parallelisms.

The coxosternapodemes appear to be of phylogenetic importance mostly at the species level. A simply curved coxosternapodeme is probably the plesiomorphous form.

The absence of setae on segment X is a synapomorphous feature for the Tanytarsini plus Pseudochironomini. Parallel reductions, however, take place in some *Microtendipes, Nilothauma, Xenochironomus (Xenochironomus)*, and *Cryptotendipes*. The collar formed around the cerci by segment X in *Fleuria* is a clear synapomorphy for the genus.

The presence of microtrichia on the labia in *Xenochironomus* and the *Harnischia* complex is apparently a synapomorphous feature for these groups combined. Parallelly, however, microtrichia can be found on the labia of *Manoa, Paralauterborniella,* some *Stictochironomus*, and *Nilodorum*.

The seminal capsules and spermathecal ducts are of phylogenetic importance only in a few genera and at the species level.

The kladogenesis is delineated by means of a scheme of argumentation or a theoretical synapomorphic diagram (Fig. 62). The following trends are used (a = apomorphous, p = plesiomorphous):

Trends 1 — Postgenital plate nearly parallel-sided at base (a), normal, triangular (p).
— One S-seta of larval labrum extremely long, thick, and bladelike, the others reduced (a); 1 S-seta long, but not thickened and bladelike (p).
— Larval antenna with 7 segments (a), with 5 (p). (6 segments probably is plesiomorphous within the subfamily as a whole.)
(The placement of *Robackia* Sæth. is highly tentative (see Sæther 1977).)

Trends 2 — Gca VIII nearly straight from middle of base of ventrolateral lobe to orally of vagina (a), curved caudally between bases of principal lobes of Gp VIII (p).
— Posterior tentorial pit large (a), small (p).
— Anal comb or spur of pupa vestigial or absent (a), present (p).

Trends 3 — Ventrolateral lobe very large with broad base, triangular to rectangular, nearly as wide as long (a); lobe smaller, clearly longer than wide (p).
— Gc IX with 0 or 1 seta (a), with 2 or more setae (p).
(See also Sæther (1971a, 1977) for these and the following trends in the *Harnischia* complex.)

Trends 4 — Ventrolateral lobe without microtrichia on caudolateral margin (a), microtrichia along margin numerous (p).
— Postgenital plate rounded (a), triangular (p).

Trends 5 — Posterior portion of tentorium short (a), long (p). (Parallel development takes place in *Cladopelma* Kieff.).
— Annular organ on larval antenna $\frac{2}{3}$–$\frac{3}{4}$ from base (a), $\frac{1}{6}$–$\frac{1}{3}$ from base (p).

Trend 6 — Ventrolateral lobe partly hidden by dorsomesal lobe (a), not hidden (p). (Trend not examined for *Acalcarella* Shil.).

Trend 7 — Ventromental plates of larvae with very strong and distinct striations (a), striations weak or possibly absent (?) (p).
(The placement of *Beckia* Sæth, is highly tentative (see Sæther 1977).)

Trend 8 — Median tooth of larval mentum triangular, pointed, pale (a); median tooth not triangular or pointed, often pale (p).
(The position of *Acalcarella* Shil. is not quite certain. The labral sensilla (Shilova 1955 fig. 25), however, indicates that the genus at least belongs to the group consisting of *Paracladopelma* Harn., *Beckia*, *Cyphomella* Sæth., *Harnischia* Kieff., *Chernovskiia* Sæth., *Cryptochironomus*, *Robackia* Sæth., *Gillotia* Kieff., and *Demicryptochironomus*. *Cyphomella* has a pupa of the same type as in *Acalcarella*, as in some *Parachironomus* Lenz. The male genitalia, however, resemble *Paracladopelma* more (Sæther 1977 fig. 37).)

Trends 9 — Labral sensilla of larva elongate, with 3 "segments" (a); relatively small or absent, with not more than 2 "segments" (p).
— Median pair of larval chaetulae laterales broad, distinctly serrated (a); simple, slender, unserrated, or very indistinctly serrated (p).
— Larval premandible with 4–6 teeth (a), with 2 or 3 teeth (p).
— Mentum with broad colorless median tooth or at least with lighter median teeth (a), median teeth of mentum as dark as lateral teeth (p).

Trend 10 — The only trend mentioned here (Sæther 1971a) is the shape of the male volsellae. However, because *Harnischia cuneata* Townes has been found to be a *Demicryptochironomus* and not a *Microchironomus* Kieff. (see Sæther 1977), this trend is now ambiguous.

Trends 11 — Pecten epipharyngis of larva a comb with several teeth (a); consisting of 3 small scales fused at base, sometimes serrated (p).
— Seta interna of mandible absent (a), present (p).

Trends 12 — Posterior tentorial pit relatively large (a), small (p).
— Four or less L-setae on pupal segment VIII (a), 5 (p).
— Anal spur of pupa single, long, slender, and relatively light colored (a); not so (p).
— Larval mentum with lateral-most 2 or 3 teeth more or less clearly set off (a), not set off (p).

Trends 13 — Microtrichia of labia secondarily reduced (a), present but often weak (p).
— Apical microtrichia of ventrolateral lobe very long, nearly half as long as the lobe (a); microtrichia shorter (p).
— Gonocoxapodeme with 2 strong curves (a), simply curved or with weak curves or bends (p).
— Antennal blade of larva extending beyond tip of antenna (a), not extending beyond tip (p).

Trends 14 — Tergite VI or several tergites of pupa with tubercles (a), tergites without tubercles (p).
— Larval mentum with lateral 2 or 3 teeth enlarged and distinctly set off from the others (a), less clearly enlarged and set off (p).
(In Sæther (1971a fig. 10) *Cladopelma* is said to form the sister group of *Cryptotendipes* and *Microchironomus* combined. A reexamination of the trends used there and new evidence of the female genitalia, however, suggest that the present interpretation is more likely.)

Trends 15 — Segment X without setae (a), with (p).
— Seminal capsules small, distinctly shorter than cerci (a), seminal capsules well developed, clearly longer than cerci (p).
— Thoracic horn of pupa very elongate (a); not elongate (p).

Trends 16 — Volsella of male gonocoxite vestigial (a); strongly reduced, but not vestigial (p).
— Cephalic tubercle of pupa with spinules, without apical seta (a); smooth, with strong apical seta (p).
(For trends 1–16 see also Sæther (1971a).)

Trend 17 — One pair of male volsellae reduced (a), both pairs well developed (at least in *Xenochironomus* subgen. *Anceus* Rob.) (p).

Trends 18 — Antepronotum, as seen from above, completely interrupted mesally by a narrow notch (a); antepronotum not interrupted mesally, although usually distinctly notched (p).
— Cephalic tubercle of pupa reduced, broad and flat (a); present and conspicuous (p).
— Ventromental plates joined, or separated by less than width of median mental tooth (a), more widely separated (p).

Trends 19 — Dorsomesal lobe with weak or strong oromesal group shagreenation of microtrichia (a), no group shagreenation (p).
— Labia with microtrichia (secondarily reduced in *Microchironomus*) (a), without microtrichia (p).

Trend 20 — Larva with at least one pair of blood-gills (secondarily reduced in many species and in the genus *Dicrotendipes*, although a larva seen by the author which appears to belong to this genus does have a weak pair of blood-gills) (a); blood-gills never present (p).

Trend 21 — Apodeme lobe and part of ventrolateral lobe covered by dorsomesal lobe (a); apodeme lobe only partially covered, ventrolateral lobe not covered (p).
(There may be several other trends belonging here or to trend 22, but a closer study of the genera included in the 2 groups is needed. Even trends 21 and 22 may be shown not to be valid.)

Trend 22 — Spermathecal duct distinctly but weakly curved (a), straight or very indistinctly curved (p).

Trend 23 — Apical microtrichia of ventrolateral lobe very long, the longest ½–¾ as long as lobe (a); apical microtrichia although strong, much shorter (p).

Trends 24 — Tergites IV–VI of pupa with a macelike process or with a patch of coarse dark spines near the anterior margin (a), without process or patch (p).
— Ventromental plate of larva very long (a), shorter (p).

Trend 25 — Apodeme lobe well developed, with distinct microtrichia (a); weak, with very indistinct microtrichia (p).

Trend 26 — Ventromental plate of larva short, only 1.0–1.5 times as long as wide (a); long, usually at least 3 times as long as wide (p).
(Short ventromental plates are plesiomorphous within Chironomidae as a whole and probably also within Chironominae. However, long ventromental plates are characteristic for the genera from *Goeldichironomus* to *Einfeldia* in the synapomorphic diagram, so a reversal apparently has taken place in *Dicrotendipes*.)

Trend 27 — Apodeme lobe with microtrichia (a), without (p).

Trends 28 — Ventrolateral lobe large, distinctly larger than the well-developed dorsomesal lobe (a); ventrolateral lobe at most as large as the dorsomesal lobe, or when larger dorsomesal lobe reduced (p).
— Gc IX of female with 0 or 1 seta (a), with 2 or more setae or occasionally number secondarily reduced (p).

— Seta subdentalis of larval mandible long (Fittkau 1965 fig. 25, 1968a fig. 22; Beck and Beck 1970 fig. 5; Reiss 1974b fig. 10, 14, 17) (a); shorter (p).
— Comb of larval mandible with long setae (see above references) (a), with shorter setae (p).
— Ventromental plates of larvae strongly down-curved mesally and separated from one another by less than width of trifid median tooth (see above references) (a); more widely separated, less down-curved (p).
(Lipiniella Shil. (Shilova 1961, 1963; Rodova 1969b p. 200–202) appears, on the basis of the immatures, to form the sister group of *Goeldichironomus* and *Nilodorum* combined. The imagines, however, appear to be more closely related to *Glyptotendipes.*)

Trends 29 — Ventrolateral lobe of Gp VIII with reticulations (a), without (p).
— Labium with a few very weak microtrichia (a), without (p).
— Membrane with a few microtrichia (a), without (p).
— Palp segments reduced, only 1.5 times as long as wide (a), normal (p).
— Blood-gills of larva absent (a), present (p). (The presence of blood-gills may be plesiomorphous or apomorphous. It is, however, certainly symplesiomorphous or synapomorphous for the group of genera from *Goeldichironomus* to *Einfeldia* in the synapomorphic diagram.)

Trend 30 — Seta subdentalis of larval mandible long, broad and serrated (a); long, but narrower and smooth (p). (See references, trends 28.)

Trend 31 — There are no clear synapomorphous trends for the genera to the right of *Fleuria* compared with *Fleuria.* The position of *Fleuria* (and of *Lenziola* Kieff. if it is a valid genus) is thus uncertain. The imagines of the genus (or genera) are very aberrant and probably adapted to copulation on the ground.

Trends 32 — Gc IX without setae (a), with (p). (Secondarily reduced in some genera.)
— Apodeme lobe fused with dorsomesal lobe (a), separate (p).
— Segment X with elongate, flat caudolateral extensions forming a collar around basal half of cerci (a); without such extensions (p).
— Male with 7–9 flagellomeres (a), with 11 (p).
(A number of additional trends can be found in the male hypopygium and probably in the immatures.)

Trends 33 — Ventrolateral lobe of Gp VIII well developed, nearly as large as to larger than dorsomesal lobe, occasionally secondarily reduced (a); ventrolateral lobe smaller than dorsomesal lobe (p). (Parallel development takes places in *Stictochironomus* where, however, the dorsomesal lobe is reduced.)
— Male with 11 or less flagellomeres (a), with 13 flagellomeres (p).
— Apex of front tibia on inner side with a low rounded scale, not distinctly projecting (a), with a distinctly projecting subtriangular spine or scale (p). (Parallel reduction takes place in *Paralauterborniella).*

Trends 34 — Ventrolateral lobe secondarily reduced, nearly vestigial (a); ventrolateral lobe larger (p). (That the ventrolateral lobe is secondarily reduced and not of a plesiomorphous small character, can be seen by the deep concavity between the principal lobes.)
— Gca VIII straight, ending on base of dorsomesal lobe (a); curved (p).
— Spermathecal duct with small loop or strong curve (a), straight or weakly curved (p).
(A large number of other trends synapomorphous for the genus *Stenochironomus* Kieff. can be found particularly in the immatures (see Lenz 1954–62 p. 179–181).)

Trend 35 — Larval pecten epipharyngis fused at base and forms 1-toothed plate (a), pecten epipharyngis consists of 3 separate scales each with 1 to several teeth (p).

Trend 36 — Segments V and VI of pupa with 0–3 filamentous L-setae (a), both with 4 filamentous L-setae (p).

Trends 37 — Dorsomesal lobe reduced (a), well developed (p).
— Ventrolateral lobe very large (a); smaller, brushlike (p).
— Gca VIII straight, ends between principal lobes of Gp VIII (a); curved, with or without branch on dorsomesal lobe (p).
— Spermathecal duct placed laterally on seminal capsule (a), placed caudally (p).

Trends 38 — Larval pecten epipharyngis with 2 to several layers of teeth (a), with simple teeth (p).
— Larval antenna with 5 segments, without large Lauterborn organs (a); with 6 segments and large Lauterborn organs (p).

Trends 39 — Segment V and VI of pupa without filamentous L-seta (a), with 3 filamentous L-setae (p).
— Anal lobes of pupa with caudomesal tuft of setae in addition to lateral fringe (a), without tuft (p).
— Pecten epipharyngis of larva with several layers of teeth (a), with 2 layers (p) (see Stewart and Loch 1973 fig. 17).

Trends 40 — Dorsomesal lobe very long, extending distinctly caudad of labia (a); shorter (p).
— Gca VIII with branch on base of dorsomesal lobe (a), without (p).
— One spine only on middle and usually on hind tibia (a), 2 spines on both (p).

Trend 41 — Thoracic horn of pupa with 20 to more than 300 branches (a), with less than 12 branches (p).

Trends 42 — Gca VIII either straight and ending on base of dorsomesal lobe, or nearly straight with a distinct branch ending on base of dorsomesal lobe (a); Gca VIII rounded caudally, at most with weak indication of indistinct branch ending between principal lobes (p). (In *Stictochironomus* it is straight, but ends between the principal lobes and is much shorter and weaker than in *Phaenopsectra* and related genera).
— Ventrolateral lobe curved mesally, with long apical, parallel microtrichia forming a small brush (a); ventrolateral lobe not brushlike (p). (Parallel development of brushlike ventrolateral lobe takes place in *Tribelos* and *Endochironomus*.)
— Tibia of midleg with 0 or 1 spine (a), with 2 (p). (Parallel reductions take place in *Stictochironomus*, *Parvitergum* Freem., *Tribelos*, and *Imparipecten* Freem.)

Trends 43 — Segment V and VI of pupa each with 3 filamentous L-setae (a), with 4 (p).
— Larval antenna with 5 segments (a), with 6 (p).

Trends 44 — Labia of female genitalia with microtrichia (a), without (p).
— Squama without setae (a), with (p).
— Pulvilli absent or vestigial (a), well developed (p).
— Median tooth of larval mentum pale (a), dark (p).

Trends 45 — Ventrolateral lobe well developed (a), very small (p).
— Lauterborn organs of larval antenna vestigial or absent (a), present and well developed (p).

Trends 46 — T IX divided by caudal emargination and central reticulated area (a); undivided, normal, hood-shaped (p).
— Gc IX without setae (a), with 1–10 setae (p). (In *Graceus* these setae are secondarily reduced.)
— Seminal capsule with distinct, sclerotized, darker neck (a); without distinct neck, indication of neck not darkly sclerotized (p).
— Larval abdominal segment VIII with prominent dorsal projection (a), without (p).
— Larval abdominal segment VIII with lateral tubules (a), without (p).

Trends 47 — Ventrolateral lobe small to well developed (a), Gp VIII undivided (p).
— Pecten epipharyngis of larva either fused to form a single plate or consists of 3 toothed scales (a); consists of 3 separate, simple teeth (p). (Lenz (1954–62 fig. 357) showed that the pecten epipharyngis of *Polypedilum* Kieff. can have 3 simple teeth. In the text, however, Lenz (p. 238) mentioned that the epipharyngeal pecten have 12–18 teeth. I have not seen any *Polypedilum* larvae with only 3 teeth and even if it should be true for some species it probably would be a secondary reduction.)

Trend 48 — Mentum of larva with one or more very small median teeth (secondarily reduced in some *Microtendipes* and overlooked although usually present, but reduced to a notch, in *Omisus* Town. (Beck and Beck 1970 fig. 1)) (a); mentum with larger median teeth (p).

(This trend is ambiguous and doubtful. *Microtendipes, Omisus,* and *Paratendipes* all have a 6-segmented larval antenna with large alternating Lauterborn organs. The alternating placement of the Lauterborn organs may be apomorphous, with the opposing Lauterborn organs in *Nilothauma* representing the plesiomorphous state, but then parallel development takes place in *Lauterborniella* and *Stictochironomus*. According to the literature *Microtendipes, Omisus,* and *Paratendipes* each have only 3 filamentous L-setae on segment V of the pupa, an apomorphous feature. However, *Paratendipes basidens* Town. and an undescribed species of *Microtendipes* in our collection both have 4 filamentous L-setae on V, and a new species of *Paratendipes* has 8–10 filamentous L-setae on segments V–VII, and 5 on VIII. *Paratendipes* also is variable in the number of setae in the fringe on the squama and the number of spines on the combs of the midleg and hind leg (0–2 on midlegs, 1 or 2 on hind legs). Higher variability appears to be characteristic for relatively plesiomorphic genera.)

Trends 49 — Anterior margin of T VIII and S VIII of male subtriangularly produced medially (a), rounded or subtruncate (p). (Parallel development takes place in *Polypedilum.*)
— T IX of male with 1 or 2 median, dorsal, hornlike processes (a); without (p).
— Segment X without setae (a), with one or more setae on each side (p). (Parallel reduction however, takes place within *Microtendipes.*)
— Squama without setae (a), with (p).
— Pulvilli vestigial (a), well developed (p).
— Cephalic tubercles of pupa lacking (a), present (p).
— Larval antenna with 5 segments and small Lauterborn organs (a), with 6 segments and large Lauterborn organs (p).

Trends 50 — Front tibia either without a spine or with spine about 0.8 times as long as tibial diameter (a), spine about 1.5 times as long as tibial diameter (p).
— Hind tibia with 1 spine (a), with 2 (p).

Trends 51 — Gp VIII broad and rounded (a), bluntly triangular (p).
— Coxosternapodeme nearly straight (a), simply curved (p).
— Gonocoxite without volsella 2a (a), with (p).
— Larval mentum with 2 minute median teeth between 2 larger teeth (minute median teeth secondarily reduced in some specimens of some species of *Microtendipes,* reduced to a notch in *Omisus*) (a); median tooth slightly larger, not between larger teeth (p).
(Gca VIII is straight and ends on Gp VIII in *M. rydalensis* (Edw.), *Microtendipes pedellus* (DeGeer), and in *Nilothauma* sp.n, but not in *Microtendipes chloris* (Meig.). Although a straight gonocoxapodeme is apomorphous it is, therefore, not synapomorphous for the 2 genera. The capacity to develop straight gonocoxapodemes may, however, be synapomorphous. The female genitalia of *Nilothauma* and *Microtendipes* are essentially identical. Brundin (1949 p. 840) states that Edwards (1929a p. 396) was certainly wrong in placing *Nilothauma* near *Microtendipes* and *Paratendipes* and agrees with Townes (1945 p. 34) that the genus is more closely related to *Polypedilum.* The evidence of the female genitalia, however, strongly suggests that Edward's placement of the genus is correct.)

Trends 52 — Seminal capsules ovoid, slightly pointed orally (a); spherical to oval, not pointed (p).
— Spermathecal duct slightly curved outward before opening (a), straight (p).

Trends 53 — Front tibia without true spur (a), with (p).
— Thoracic horn of pupa divided in 6 to more than 300 branches (a), simple or at most with 2 branches (p).

Trends 54 — Segment X of female without setae (a), with setae (p). (Parallel reductions take place in some *Microtendipes, Nilothauma, Xenochironomus (Xenochironomus),* and *Cryptotendipes*).
— Front tibia with comb (secondarily reduced in most Tanytarsini, but present at least in *Goetghebueria* Kieff. and some species of *Paratanytarsus* Bause) (a); without comb (p).
— Larval antenna with 5 segments (a), with 6 in plesiomorphic genera although secondarily reduced in several genera (p).

Trend 55 — Pulvilli absent (a), present or secondarily reduced (p).
(There are no nonambiguous trends for *Megacentron* Freem. compared with other Pseudochironomini.)

Trends 56 — No true anal point present, T IX of male, however, large, hood-shaped, with numerous setae (a); true anal point present (p).
— Volsella 2a absent or reduced (a), well developed (p).

Trends 57 — Female with 5 flagellomeres (a); with 6 or secondarily reduced to 5 in some *Riethia* Kieff. (p).
— Thoracic horn of pupa divided into 2 branches (a), probably always simple (p).
— Cephalic tubercles of pupa reduced (a), probably always well developed (p).

Trends 58 — Caudomesal portion of S VIII forms a deeply divided floor under anterior part of vagina (at least in *Manoa)* (a), does not form a floor (p). (Parallel development takes place in the Tanytarsini. The floor, however, appears quite different.)
— Pars ventralis (sensu Hirvenoja 1973 p. 23) absent (a), present (p).
— Antepronotum reduced (a), well developed (p).

Trend 59 — No clear apomorphous feature for *Riethia,* compared to *Manoa,* can be found from the descriptions.

Trends 60 — Eyes without distinct dorsal elongation (a), with (p).
— Squama apparently without setae (a), with (p).

Trends 61 — Wing membrane without setae (a); with, although occasionally secondarily reduced (p).
— Larval antenna with reduced Lauterborn organs (a), Lauterborn organs well developed (p).
— Ventromental plates elongate, nearly meet at midline, narrow, with parallel striations (a); wider and less elongate, clearly separated, striations not parallel (p). (Parallel development of ventromental plates takes place in the subtribe Tanytarsina.)

Trends 62 — Caudomesal portion S VIII forms a small to large floor under anterior part of vagina (a), does not form a floor (p). (Parallel development takes place in *Manoa;* the floor, however, is a different shape (see trends 58).)
— Larval antenna situated on high tubercle with or without apical spur (a), no high tubercle (p).
— Abdominal segments of larva with plumose setae (a), without (p).

Trends 63 — Ventrolateral lobe large, about as large as dorsomesal lobe (a); small to well developed, but distinctly smaller than dorsomesal lobe (p).
— Spurs of middle and hind tibial combs absent (a), present (p). (In *Himatendipes* Tok. the combs are reduced but rudimentary spines are still present.)
— Lauterborn organs of larva small, on long pedicels (a); slightly to much larger, on short pedicels (p).

Trend 64 — Apodeme lobe relatively distinct (a), indistinct (p).

Trends 65 — Gp VIII clearly divided into distinct ventrolateral and dorsomesal lobes (a), undivided (p).
— Gca VIII straight or nearly straight, ends on base of dorsomesal lobe (a); caudally curved (p).
— Notum long (1.5–2.5 times as long as seminal capsule) (a), notum distinctly shorter (p).
— Apodeme lobe apparent, although often inconspicuous (a); not apparent (but probably always present) (p).

Trends 66 — Gca VIII weak and often not apparent (a), strong and distinct (p).
— Floor under vagina very large to moderately large (a), moderately large to minute (p).

Trend 67 — Volsella 2a of male with branched setae (a), without (p).

Trends 68 — Gca VIII absent or vestigial (a); weak, but relatively distinct (p).
— Lauterborn organs of larva small and on long pedicels (a); larger, on short pedicels (p).

Trends 69 — Anal point of male with crests or keel, usually with spines, occasionally keels and spines secondarily reduced (a); simple, without crests, keels, or spines (p).
— Ventromental plates of larva narrow, elongate, nearly meet at midline, generally rounded at inner apices, with parallel striations (a); well separated, broader, pointed at inner apices, striations not quite parallel (p). (Parallel development takes place in the Pseudochironomini, see trends 61.)

Trends 70 — Anal lobes of pupa without dorsal setae (a), with (p).
— Larval antennal tubercle with large distalmedian simple or palmate projection (a), without (p). (Parallel development of projection, although smaller, takes place in *Micropsectra* Kieff. and some *Tanytarsus*.)

Trends 71 — S VIII forms very large floor under anterior part of vagina (a), smaller floor (p).
— Gonocoxite of male with an appendix in addition to volsellae 1, 1a, 2, and 2a (a); without (p).
— Anal lobe of pupa with short, rigid, comblike setae (a); with fringe of long setae (p).
(A number of other synapomorphies for *Thienemanniola* will be apparent from Lehmann (1973). The statement by Lehmann (1973 p. 412), that *Thienemanniola* and *Corynocera* are probably derived from plesiomorphous Orthocladiinae and his indication that the Tanytarsini are not a monophyletic unit, is contradicted by the present findings. *Corynocera* clearly is close to *Tanytarsus*, and *Thienemanniola* clearly forms the sister group of *Zavrelia* Kieff., *Stempellinella*, *Stempellina*, and *Constempellina* Brund. combined. Both *Corynocera* and *Thienemanniola* are typical Tanytarsini in the structure of their female genitalia.)

Trend 72 — Volsella of male gonocoxite absent (a), present (p).

Trends 73 — Floor formed by S VIII under anterior part of vagina with median suture (a), without (p).
— Scutum with median protuberance (a), without (p).
— Pupal thoracic horn short (0.2–0.3 mm) (a), long (0.6–0.7 mm) (p).
— Larval mandible with 3 outer teeth (a), with 4 (p).

Trend 74 — Lauterborn organs alternating (a), opposite (p).

Most phyletic relationships within the Chironominae are well established; better so than within the Orthocladiinae. The tribe Tanytarsini is a distinctly monophyletic unit whose sister group consists of the new tribe Pseudochironomini. The Tanytarsini falls into two fairly distinct groups, the new subtribes Zavreliina (Sectio Tanytarsariae connectens) and Tanytarsina (Sectio Tanytarsariae genuinae). The Pseudochironomini cannot be shown to be quite as clearly monophyletic, mainly because of lack of knowledge about the immatures and female genitalia of *Riethia* and *Megacentron*. The last genus has some characteristics in common with *Paratendipes* and related genera, and may perhaps belong to the tribe Chironomini which is apparently monophyletic. However, some of the lesser known genera listed with *Paratendipes* in Fig. 62 may possibly be more closely related to *Megacentron* and may, together with this genus, deserve a fourth tribe. Within the Chironomini, minor adjustments of the scheme of argumentation, in all likelihood, will be necessary; however, the main groupings of genera appear well established by nonambiguous synapomorphies. The sequence of genera from the more plesiomorphic to the more apomorphic is surprisingly similar to the sequence found in Townes (1945) and different from that used by Lenz (1954–62). Although Sectio Chironomariae genuinae sensu Lenz apparently is monophyletic, his Sectio Chironomariae connectens is not. It does not seem practical to divide the Chironomini into subtribes, so names for genus groups or complexes are used.

TRIBE TANYTARSINI
(Fig. 63–70)

S VIII forms a small to large floor, at least under anterior part of vagina; posterior margin of floor sinuate or concave, occasionally with a median suture. Gp VIII simple or divided into distinct ventrolateral and dorsomesal lobes. Microtrichia of ventrolateral lobe, or caudolateral and caudal

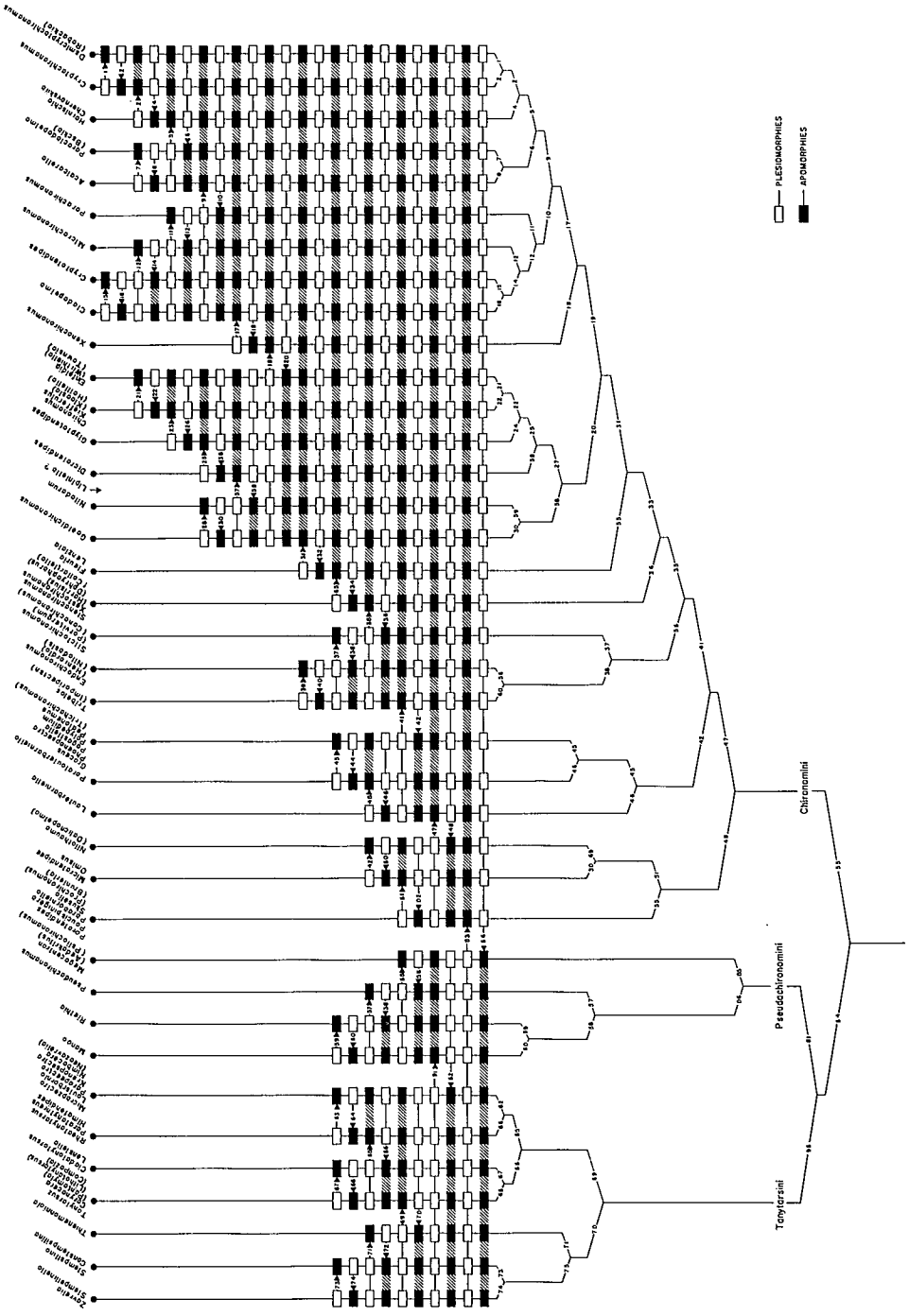

FIG. 62. Scheme of argumentation delineating the kladogenesis of the genera of the Chironominae by means of trends 1–74 (p. 131–138). Genera in parentheses tentatively placed. (It is now recognized that *Gillotia* belongs with *Demicryptochironomus*, and *Cyphomella* with *Acalcarella*.)

margins of Gp VIII when undivided, long, often conspicuously so. Apodeme lobe usually indistinct, occasionally distinct and with indication of microtrichia. Membrane without microtrichia. T IX large, mostly subtriangular with weak or strong lateral shoulders, sometimes with sharply triangular mediocaudal projection and triangular shoulders, sometimes almost semicircular with no indication of shoulders. Gc IX moderately to strongly developed, usually with setae. Notum short to long. Segment X always without setae. Postgenital plate triangular to semicircular, nearly always present and distinct. Cerci small to moderately large.

Labia without microtrichia. Seminal capsules mostly ovoid. Spermathecal ducts straight, nearly straight, or with distinct curves or loops, with common opening.

Preliminary key to females of Tanytarsini

1 Tibial combs absent or rudimentary; wings either without setae on membrane or crumpled at apex with a tuft of apical setae, sometimes absent or reduced 2

At least a weak comb of free spines present, wing membrane nearly always with at least apical setae, wing not crumpled at apex or absent 7

2 Female vermiform, without front legs, with vestigial middle and hind legs; Gp VIII apparently undivided ..... *Pontomyia* Edw. (p. 144)

Female with wings and front legs, middle and hind legs often shortened and thickened, but not vestigial; Gp VIII divided or undivided 3

3 Middle and hind tibiae with distinct simple apical spurs 4

Middle and hind tibiae without spurs, sometimes with rudimentary combs of minute spines 6

4 Front legs long, slender; middle and hind legs shortened, thickened, with 1 or 2 dark and smooth apical spurlike spines; palp short, with 4 or 5 segments 5

Legs similar in appearance, all tibiae with a relatively long, pale, spurlike spine; palp well developed, 5-segmented ..... *Biwatendipes* Tok. (Japan)

5 Gp VIII with rounded caudomesal angle, with long microtrichia; caudolateral angles of T IX very large, rounded, reaching as far caudad as smaller mesocaudal projection; wings with apical tuft of long setae ..... *Corynocera* Zett. (p. 144)

Gp VIII with pointed caudolateral angle, with short microtrichia; caudolateral angles of T IX pointed, not reaching as far caudad as equally large and pointed mesocaudal projection; wings without apical tuft of setae ..... *Thienemanniola* Kieff. (p. 143)

6 Tibia of middle and hind legs with apical lobe bearing a tuft of setae, without rudimentary comb; Gp VIII undivided ..... *Lenziella* Kieff. (p. 144)

Tibia of middle and hind legs without apical lobe, but with rudimentary combs of minute spinules; Gp VIII probably divided ..... *Himatendipes* Tok. (Kashmir)

7 Front tibia with a comb of 4–10 distinct spines, no tibial spurs ..... *Goetghebueria* Kieff. (probably a heterogeneous genus)

Front tibia without a comb, or when a comb of 2–4 teeth present (as in some *Paratanytarsus*) at least 1 tibial spur present on middle or hind legs 8

8 Tibial combs reduced to some free or nearly free spines, no tibial spurs 9

Tibial combs normal, with or without spurs 11

9 Scutum with tubercle; wing membrane with dense setae on apical half, with a few setae extending almost to wing base ..... *Constempellina* Brund.

Scutum without tubercle; wing membrane with setae at most near apex and along posterior margin 10

10 Wing membrane with less than 10 setae at apex; R_{4+5} ends distad of M_{3+4}; Gp VIII divided ..... *Parapsectra* Reiss, pro parte (p. 154)

Wing membrane with more numerous setae at apex and along posterior margin; R_{4+5} ends proximad of M_{3+4} ..... *Yuasaiella* Tok. (Japan)

11 Middle and hind tibial combs without spurs; Gp VIII divided 12

Middle and/or hind tibial combs with at least 1 spur, or when without spurs Gp VIII undivided 14

12 Middle and hind tibial combs contiguous or overlapping, occupying more than half apical circumference of tibia, or when separate eyes hairy and few or no setae on wing membrane 13

Middle and hind tibial combs narrowly separate; eyes bare; wing membrane fully haired ..... *Krenopsectra* Reiss

13 Ventrolateral lobe of Gp VIII long, lobelike, situated far laterad; eyes reniform ..... *Parapsectra* Reiss, pro parte (p. 154)

Ventrolateral lobe of Gp VIII shorter, rounded, and situated more mesally; eyes with dorsal extensions ..... *Micropsectra* Kieff. (p. 145)

14 Eyes ellipsoid or teardrop shaped, hairy, or when bare R_{4+5} ends proximad of M_{3+4} or over M_{3+4} with R_{2+3} weakly developed; scutum without tubercle 15

Eyes with dorsal extensions or when without, eyes bare; when R_{4+5} ends proximad of M_{3+4} scutum with tubercle; when R_{2+3} weakly developed or absent, eyes with long dorsal extensions, and R_{4+5} ends distad of M_{3+4} 16

15 Eyes hairy; R_{4+5} ends proximad of M_{3+4}; Gp VIII simple ..... *Zavrelia* Kieff. (p. 142)

Eyes bare or when hairy R_{4+5} ends over or distad of M_{3+4}; Gp VIII probably divided ..... *Neozavrelia* Goetgh.

16 Eyes with long dorsal extensions; frontal tubercles absent; antepronotum reduced, not visible from above; wing densely haired, R_{2+3} nearly fused with R_{4+5}; only outer combs of middle and hind legs with spur; pulvilli lacking ..... *Camposia* Reiss (Chile)

Without the above combination of characters 17

17 Front tibia with weak serrated scale; wing slightly reduced with a few apical setae; Gp VIII undivided ..... *Nimbocera* Reiss (Chile, Argentina) (p. 154)

Front tibia without serrated scale; wings not reduced, usually with numerous setae; Gp VIII divided or undivided 18

18 Gp VIII clearly divided into ventrolateral and dorsomesal lobes; floor under vagina small to medium; notum 1.0–2.5 times as long as seminal capsules 19

Gp VIII undivided or very indistinctly divided; floor under vagina medium to large; notum less than 1.5 times as long as seminal capsules 21

19 Notum more than 2.5 times as long as seminal capsules; apodeme lobe distinct, apparently with weak microtrichia; R_{2+3} indistinct or absent; tibial combs small and separate ..... *Rheotanytarsus* Bause (p. 144)

Notum 1.0–2.0 times as long as seminal capsules; apodeme lobe less distinct, without microtrichia; R_{2+3} distinct; tibial combs contiguous to slightly separated, occupying about ½ apical circumference 20

20 Notum less than 1.5 times as long as seminal capsules ..... *Lauterbornia* Kieff. (p. 145)

Notum 1.5–2.0 times as long as seminal capsules ..... *Paratanytarsus* Bause (p. 145)

21 Floor under anterior part of vagina with a median suture; scutum with tubercle .... *Stempellina* Bause (p. 143)

Floor without suture; scutum without tubercle 22

22 Apex of ventrolateral lobe approximately rounded, with very long, nearly straight microtrichia directed caudomesad; floor under vagina moderately large to very large; neck of seminal capsule placed caudally; eyes usually with distinct and strong dorsal elongation ..... *Tanytarsus* v.d. Wulp (p. 143)
(and probably *Lithotanytarsus* Thien.)

Ventrolateral lobe with straight caudomesal margin, with medium long microtrichia either curved oromesad or directed caudad; floor under vagina moderately large; neck of seminal capsule placed caudally or laterally; eyes ellipsoid 23

23 Caudal margin of floor under vagina sinuate; neck of seminal capsule placed caudally; apical microtrichia of ventrolateral lobe not curved oromesad; spermathecal ducts with strong bend or loop ..... *Stempellinella* Brund. (p. 142)

Caudal margin of floor evenly concave; neck of seminal capsule placed laterally; apical microtrichia of ventrolateral lobe curved oromesad; spermathecal ducts usually straight or nearly straight ..... *Cladotanytarsus* Kieff. (p. 144)

Zavrelia Kieff.
(Fig. 63A–D)

Species examined: *Zavrelia* sp.

Gca VIII strong, rounded caudally. S VIII forms large floor under anterior part of vagina, posterior margin of floor sinuate, floor without suture, with 2–4 setae. Gp VIII simple, with relatively long caudal microtrichia. Apodeme lobe not apparent. Notum short, about as long as seminal capsules, rami slightly diverging. T IX pointed, triangular. G IX small, with few setae. Postgenital plate rounded triangular, wide at base. Cerci about as large as seminal capsules.

Seminal capsules ovoid, with relatively large funnel-shaped neck. Spermathecal ducts with bends.

Stempellinella Brund.
(Fig. 63E–H)

Species examined: *S.* sp.n. near *brevis* (Edw.)

Gca VIII weak. S VIII forms relatively large floor under anterior part of vagina, posterior margin of floor sinuate, floor without suture. Gp VIII simple, with straight caudal margin, caudolateral point, and long caudally directed caudal and caudolateral microtrichia. Apodeme lobe not apparent. Notum short, about as long as seminal capsules; rami nearly parallel for most of their length. T IX bluntly triangular without or with very weak shoulders. Gc IX normal, with a few setae. Postgenital plate triangular, wide at base. Cerci about as large as seminal capsules.

Seminal capsules ovoid, with relatively large funnel-shaped neck. Spermathecal ducts with strong bends.

The species examined differs from other *Stempellinella* by having pulvilli. However, in other details of all stages it is a good member of the genus.

Stempellina Bause
(Fig. 63I–P)

Species examined: *S.* sp.n. near *almi* Brund., *S.* near *subglabripennis* (Brund.), *Stempellina* sp.

Gca VIII rounded caudally. S VIII forms relatively large floor under anterior portion of vagina, floor with median and sometimes lateral sutures. Gp VIII simple, weak, with long caudal microtrichia. Apodeme lobe not distinguishable. Notum short, about as long as seminal capsules, rami not parallel. T IX relatively small, broadly and bluntly triangular, occasionally with sharp caudal point. Gc IX with 0 or 1 seta. Postgenital plate short. Cerci slightly larger than seminal capsules.

Seminal capsules ovoid, without distinct neck. Spermathecal ducts weakly curved.

S. sp.n. near *almi* has 3 sutures in the floor under the vagina and one seta on Gc IX; whereas *S.* sp. near *subglabripennis* has one suture, no setae on Gc IX, and a sharp caudal point on T IX. The third species has one median suture in the floor, one seta on Gc IX, and no sharp caudal point on T IX.

Thienemanniola Kieff.
(Lehmann 1973 fig. 19–21)

Gca VIII weak. S VIII forms very large floor under most of vagina. Gp VIII simple, with pointed caudomesal corner, without conspicuously long microtrichia. T IX very large, with sharply triangular caudomesal projection, and triangular shoulders. Gc IX apparently weak and without setae. Postgenital plate weak. Cerci relatively small.

Tanytarsus v.d. Wulp
(Fig. 64, 65A–C; Wülker 1961 fig. 5; Reiss 1966 fig. 1)

Species illustrated: *T. holochlorus* Edw., *T.* prob. sp. near *nemorosus* Edw., *T.* prob. sp.n. near *debilis* (Meig.), *Tanytarsus* sp. *A*, *Tanytarsus* sp. *B*

Gca VIII weak or apparently absent. S VIII forms large to very large floor under anterior part of vagina. Gp VIII simple, rounded, with very long caudal, and caudolateral nearly straight microtrichia. Notum relatively short. T IX medium to large; bluntly triangular, semicircular, or low and rounded; with or without sharp caudal point or rounded shoulders. Gc IX without or with 1–8 setae. Postgenital plate triangular, distinct. Cerci moderately large.

Seminal capsules ovoid, with indistinct neck. Spermathecal ducts with curve or loop.

There are several sharp differences between the female genitalia of the species examined. Particularly the size and shape of T IX, the number of setae on Gc IX, the size of the floor under the vagina, and the shape of the coxosternapodeme will, in all likelihood, provide valuable taxonomic characteristics. However, all species examined are either tentatively identified or belong to undescribed species.

Corynocera Zett.
(Fig. 65D, E; Rodova 1967 fig. 2)

Species examined: *C. ambigua* Zett.

Gca VIII not distinguishable. S VIII forms a very large floor with straight caudal margin under part of vagina. Gp VIII simple, rounded, with very long caudal and caudolateral, nearly straight microtrichia. Notum relatively short. T IX with very large rounded shoulders and caudomesal projection absent or nearly absent. Gc IX nearly hidden in ventral view by the extended caudolateral corners of S VIII, hidden in dorsal view by T IX, without setae. Postgenital plate triangular. Cerci normal.

Seminal capsule extremely large, with neck. Spermathecal duct with loops or curves.

Pontomyia Edw.
(Tokunaga 1932 fig. 34)

Gca VIII distinct. S VIII apparently forms a large floor under vagina. Gp VIII simple. T IX apparently semicircular. Gc IX apparently weak and without setae. Postgenital plate not apparent. Cerci small, situated caudolaterally.

Seminal capsules very small, with characteristically swollen neck. Spermathecal ducts straight or nearly straight.

Cladotanytarsus Kieff.
(Fig. 66A–D)

Species illustrated: *Cladotanytarsus* sp.

Gca VIII nearly straight, ends at base of dorsomesal lobe. S VIII forms a moderate size floor without setae under anterior part of vagina. Gp VIII simple, with straight caudomesal margin, apical microtrichia curved oromesad. Notum of medium length. T IX broadly triangular to semicircular, rounded apically, occasionally with pale, orolateral spurlike projections. Gc IX with 1 or 2 setae. Postgenital plate broad and rounded. Cerci small.

Seminal capsules small, neck placed laterally. Spermathecal ducts nearly straight.

Lenziella Kieff.
(Fig. 66E–G)

Species examined: *L. cruscula* Sæth.

S VIII forms a moderate size floor bearing several (about 8) setae under vagina. Gp VIII simple, with straight caudomesal margin, but with indication of caudolateral corner. Notum relatively short. T IX semicircular with spurlike orolateral shoulders. Gc IX with 2 setae. Cerci small.

Seminal capsules small, neck placed orolaterally. Spermathecal ducts nearly straight.

The specimen examined was damaged and Gp VIII broken up. Fig. 66G represents a reconstruction of Gp VIII and may be slightly incorrect.

Rheotanytarsus Bause
(Fig. 67)

Species examined: *R. nigricauda* Fittk., *Rheotanytarsus* sp.

Gca VIII straight or nearly straight, ends on base of dorsomesal lobe of Gp VIII. S VIII forms a moderate size floor under anterior part of vagina. Gp VIII divided into small to moderately large ventrolateral lobe with long apical microtrichia and well-developed dorsomesal lobe. Apodeme lobe distinct, apparently with apical microtrichia. Notum very long, more than 2.5 times as long as seminal capsules. T IX bluntly triangular to low and semicircular, with weak or moderately strong shoulders. Gc IX without or with a few setae. Postgenital plate triangular. Cerci normal.

Seminal capsules ovoid, without neck. Spermathecal ducts with sharp curves.

Although the 2 species examined differ sharply in several details, the long notum and the distinct apodeme of the apodeme lobe makes them easily distinguishable from other Tanytarsini with divided Gp VIII.

Paratanytarsus Bause
(Fig. 68, 69; Botnariuç and Albu 1971 fig. 6–16)

Species illustrated: *P.* sp.n. near *natvigi* (Goetgh.), *Paratanytarsus* sp. *A–D*

Gca VIII nearly straight, ends on base of dorsomesal lobe of Gp VIII. S VIII forms a very small to moderate size floor under anterior part of vagina. Gp VIII divided, apical microtrichia of ventrolateral lobe curved oromesad. Apodeme lobe present, but inconspicuous. Notum long, 1.5–2.0 times as long as seminal capsules. T IX mostly semicircular, sometimes with orolateral pale spinelike projections. Gc IX with few setae. Postgenital plate triangular. Cerci normal.

Seminal capsules ovoid, without neck. Spermathecal ducts nearly straight or with weak curves.

The 5 species illustrated can be separated from each other by the numbers of setae of Gc IX, the presence or absence of an orolateral pale spine on T IX, the shape of Gp VIII, and the length of the notum. *Paratanytarsus* sp. *A* would have fallen into the genus *Lundstroemia* Kieff. synonymized with *Paratanytarsus* by Reiss (1974a p. 207). *Paratanytarsus* sp. *B* is a parthenogenetic form cultured at the Freshwater Institute, Winnipeg, Man.

Micropsectra Kieff.
(Fig. 70A–C; Rodova 1970 fig. 2)

Species illustrated: *M. contracta* Reiss, *Micropsectra* sp.

Gca VIII straight in mesal portion, ends on base of dorsomesal lobe of Gp VIII. S VIII forms a small floor under anterior part of vagina. Gp VIII divided; apical microtrichia of ventrolateral lobe short to moderately long, curved oromesad. Apodeme lobe present, but inconspicuous. Notum long, 1.5–2.0 times as long as seminal capsule. T IX mostly semicircular. Gc IX with a few setae. Postgenital plate weak, triangular. Cerci normal.

Seminal capsules ovoid, with or without distinct neck. Spermathecal ducts straight or nearly straight.

Lauterbornia Kieff.
(Fig. 70E, F)

Species examined: *L. sedna* Ol.

Gca VIII weak. S VIII forms small floor under vagina. Gp VIII divided; apical microtrichia of ventrolateral lobe relatively short, curved oromesad. Notum about as long as seminal capsules. T IX apparently semicircular. Gc IX apparently without setae. Postgenital plate weak, rounded triangular. Cerci normal.

Seminal capsules large, with funnel-shaped neck. Spermathecal ducts straight.

The examined specimen is a mature female pupa and some details such as the coxosternapodemes, Gc IX, and T IX were indistinct.

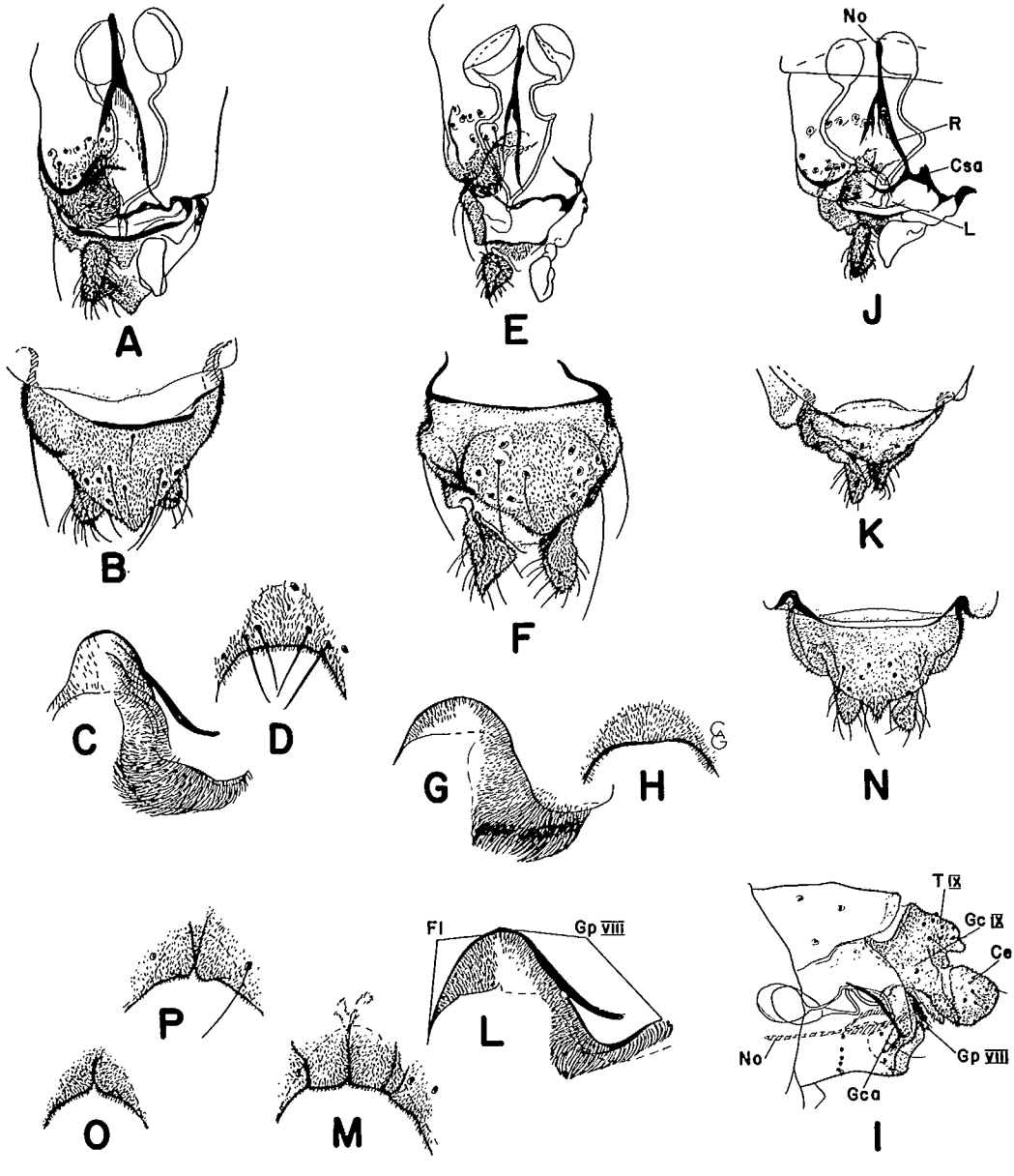

FIG. 63. Female genitalia of Zavreliina, Tanytarsini, Chironominae. A–D, *Zavrelia* sp.: A) ventral; B) dorsal; C) Gp VIII and floor under vagina (dorsal); D) floor, ventral. E–H, *Stempellinella* sp.n. near *brevis* (Edw.): E) ventral; F) dorsal; G) Gp VIII and floor under vagina (dorsal); H) floor, ventral. I–M, *Stempellina* sp. near *almi* Brund.: I) lateral; J) ventral; K) dorsal; L) Gp VIII and floor under vagina (dorsal); M) floor, ventral. N–O, *Stempellina* near *subglabripennis* (Brund.): N) dorsal; O) floor, ventral. P, *Stempellina* sp., floor, ventral.

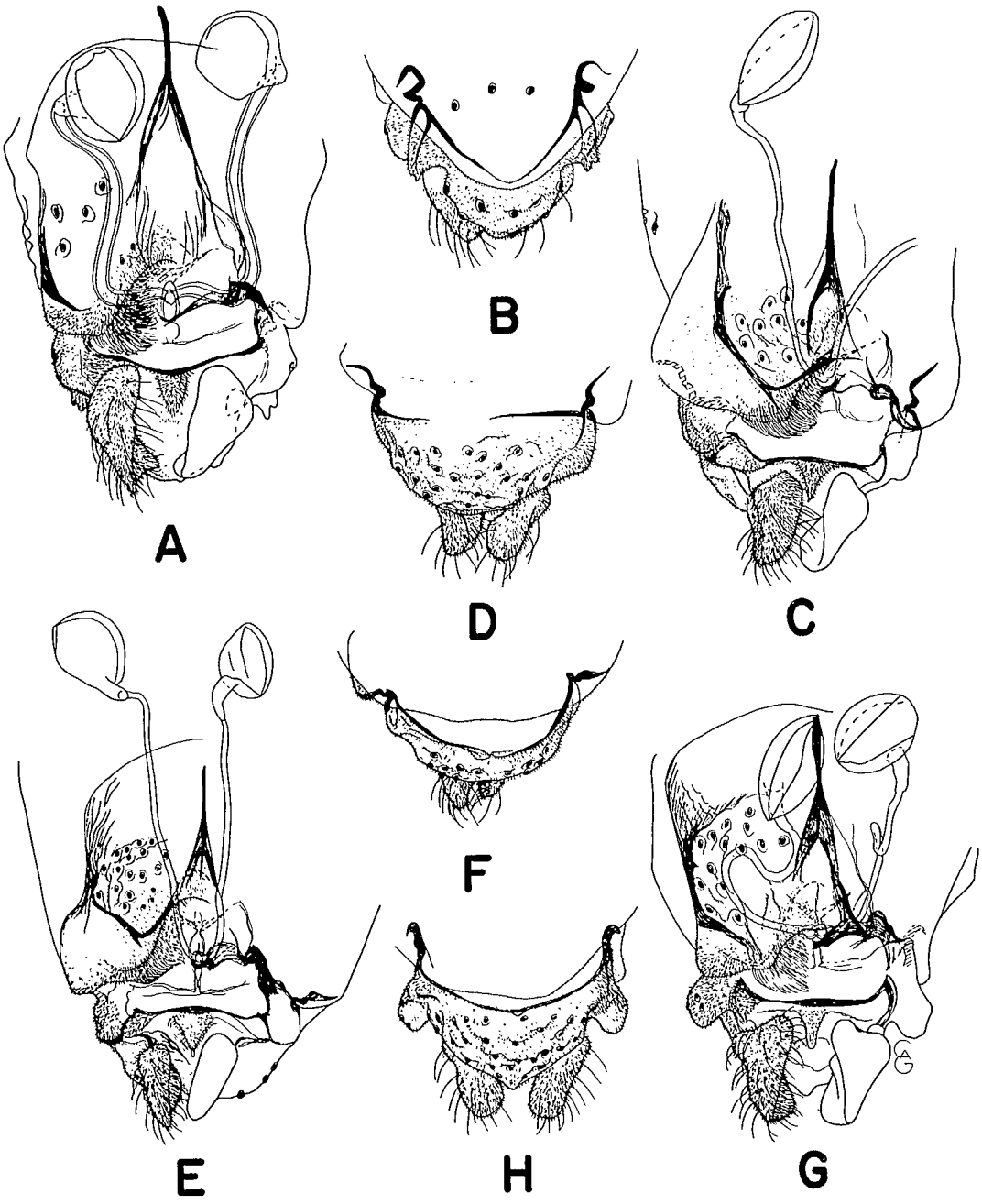

FIG. 64. Female genitalia of *Tanytarsus* spp., Tanytarsina, Tanytarsini, Chironominae. A–B, *T. holochlorus* Edw.: A) ventral; B) dorsal. C–D, *T.* cf. sp. near *nemorosus* Edw.: C) ventral; D) dorsal. E–F, *T.* cf. sp.n. near *debilis* (Meig.): E) ventral; F) dorsal. G–H, *Tanytarsus* sp. *A*, Lake Winnipeg: G) ventral; H) dorsal.

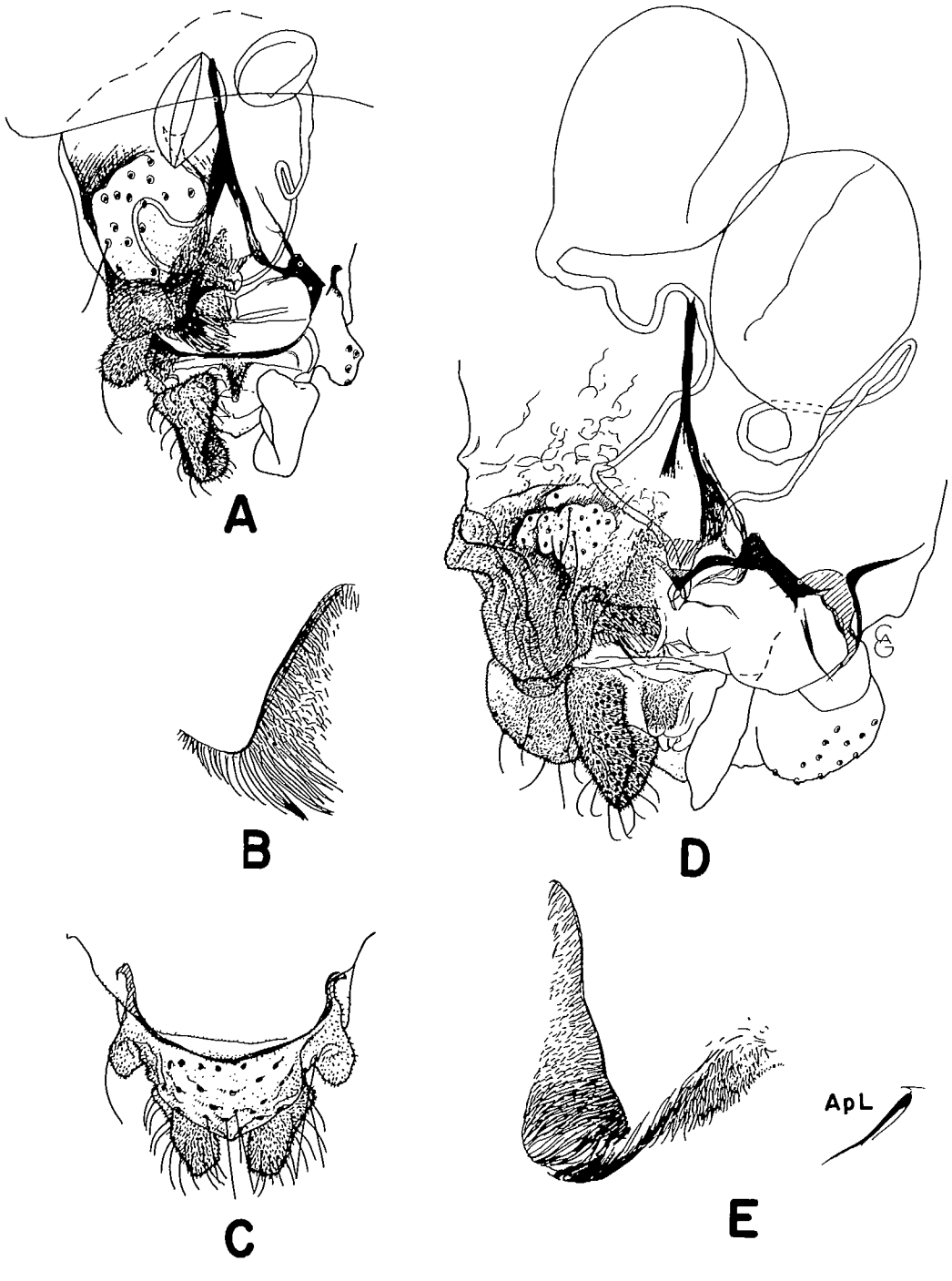

FIG. 65. Female genitalia of Tanytarsina. A–C, *Tanytarsus* sp. *B:* A) ventral; B) Gp VIII; C) dorsal. D–E, *Corynocera ambigua* Zett.: D) ventral; E) lobes of Gp VIII.

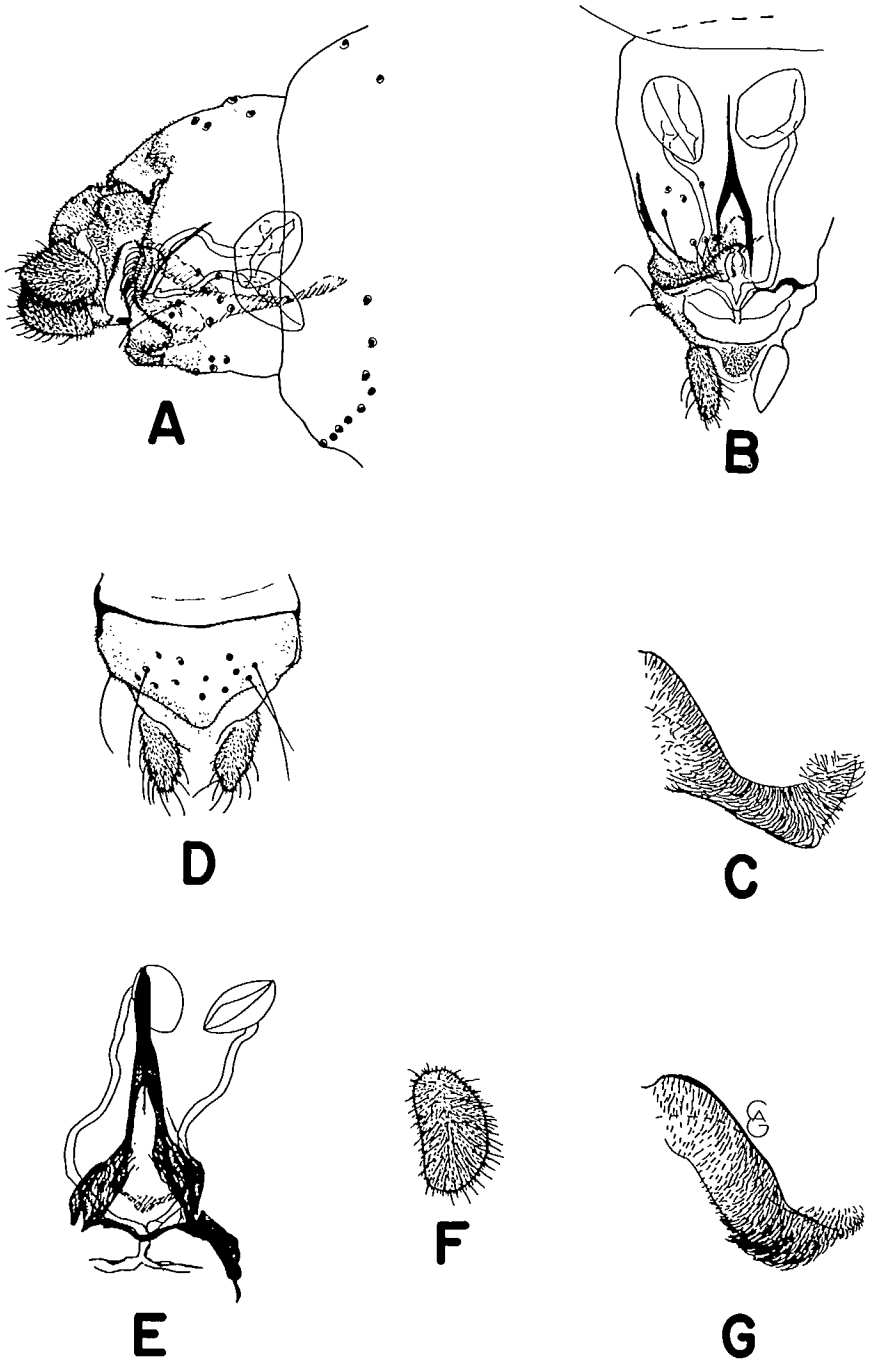

FIG. 66. Female genitalia of Tanytarsina. A–D, *Cladotanytarsus* sp.: A) lateral; B) ventral; C) Gp VIII; D) dorsal. E–G, *Lenziella cruscula* Sæth.: E) Gp IX, membrane, coxosternapodeme, and spermatheca; F) cercus, ventral; G) Gp VIII.

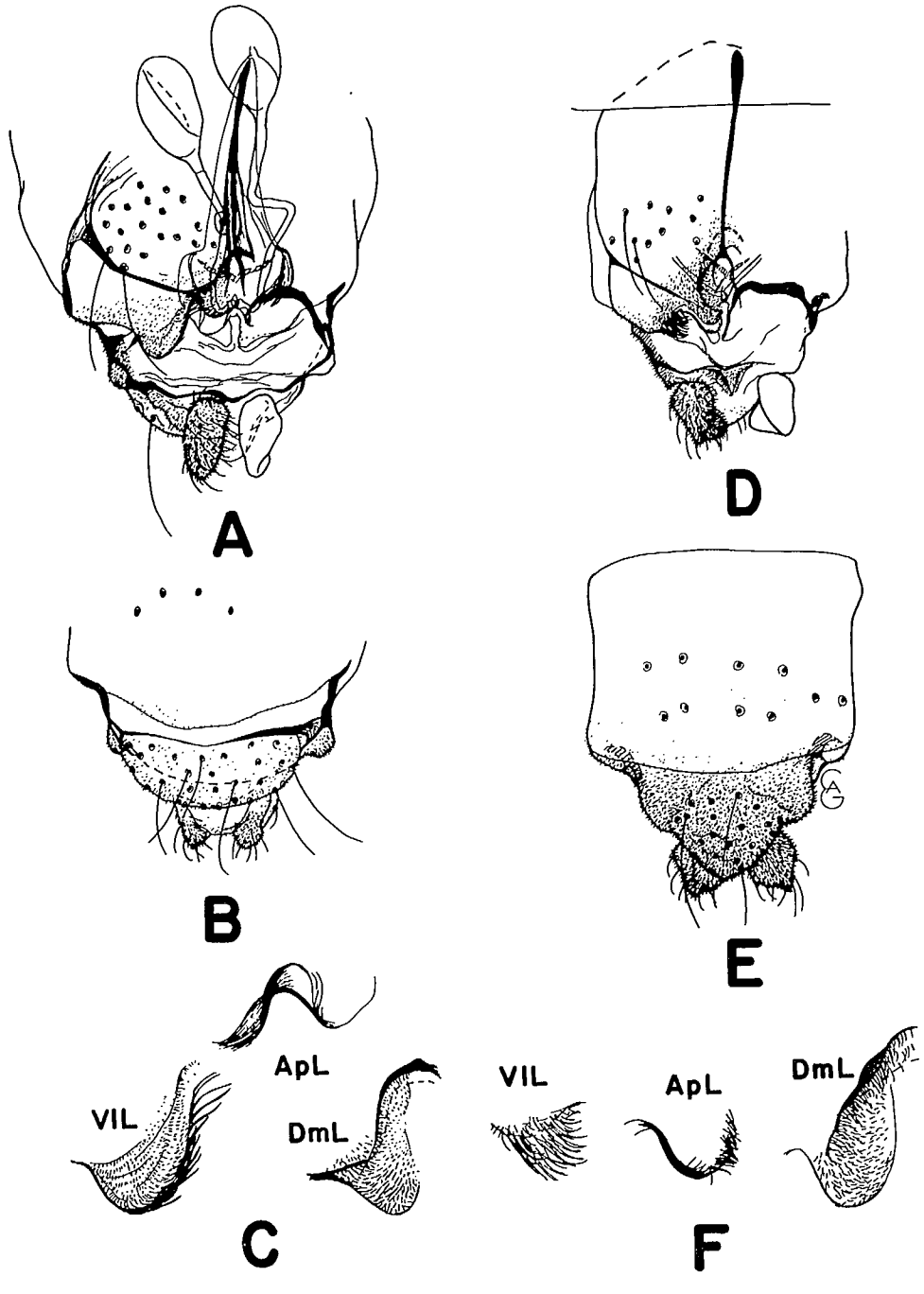

FIG. 67. Female genitalia of *Rheotanytarsus* spp., Tanytarsina. A–C, *R. nigricauda* Fittk.: A) ventral; B) dorsal; C) lobes of Gp VIII. D–F, *Rheotanytarsus* sp.: D) ventral; E) dorsal; F) lobes of Gp VIII.

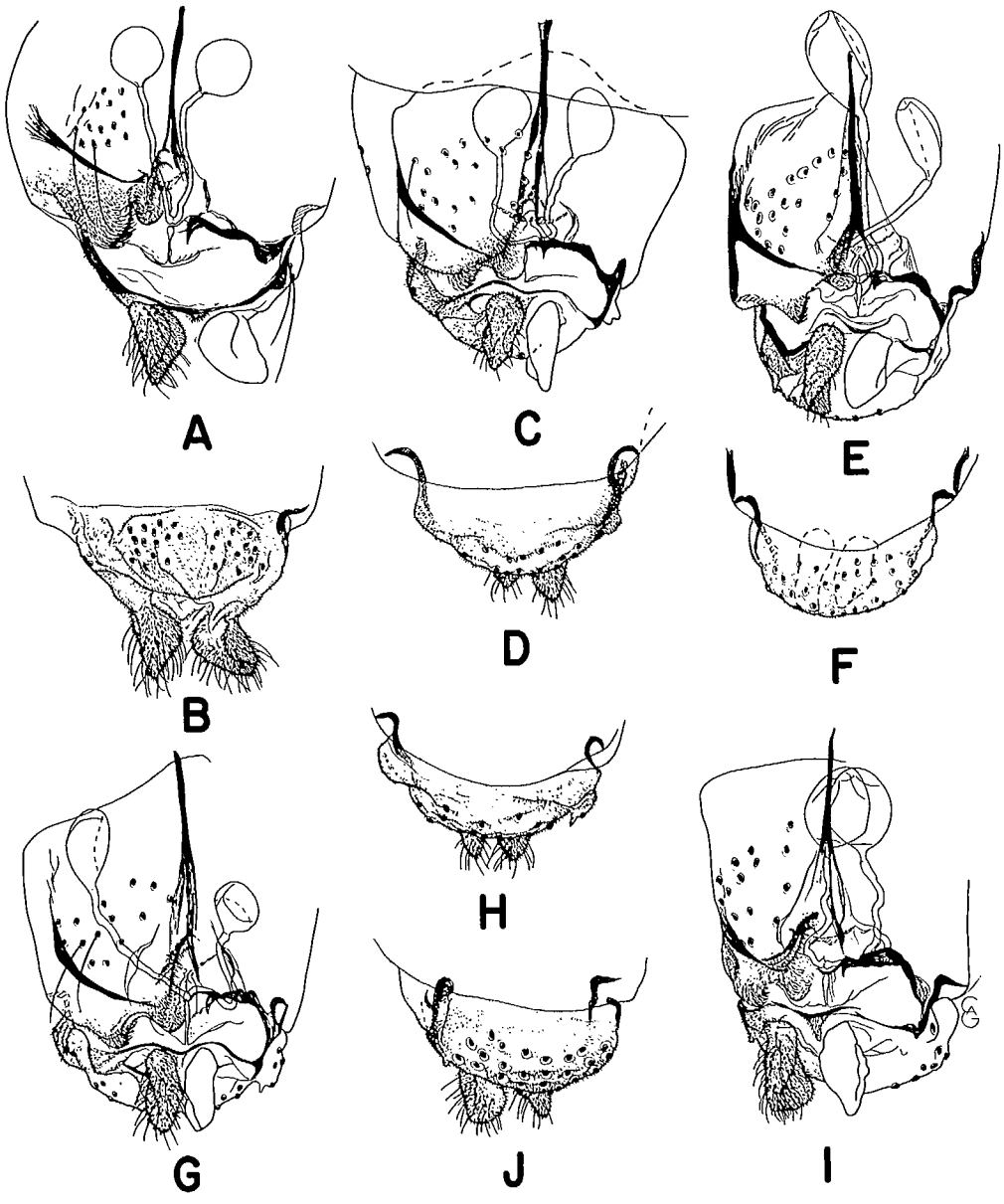

FIG. 68. Female genitalia of *Paratanytarsus* spp., Tanytarsina. A–B, *Paratanytarsus* sp. *A:* A) ventral; B) dorsal. C–D, *Paratanytarsus* sp. *B:* C) ventral; D) dorsal. E–F, *Paratanytarsus* sp. *C:* E) ventral; F) dorsal. G–H, *Paratanytarsus* sp. *D:* G) ventral; H) dorsal. I–J, *P.* sp.n. near *natvigi* (Goetgh.): I) ventral; J) dorsal.

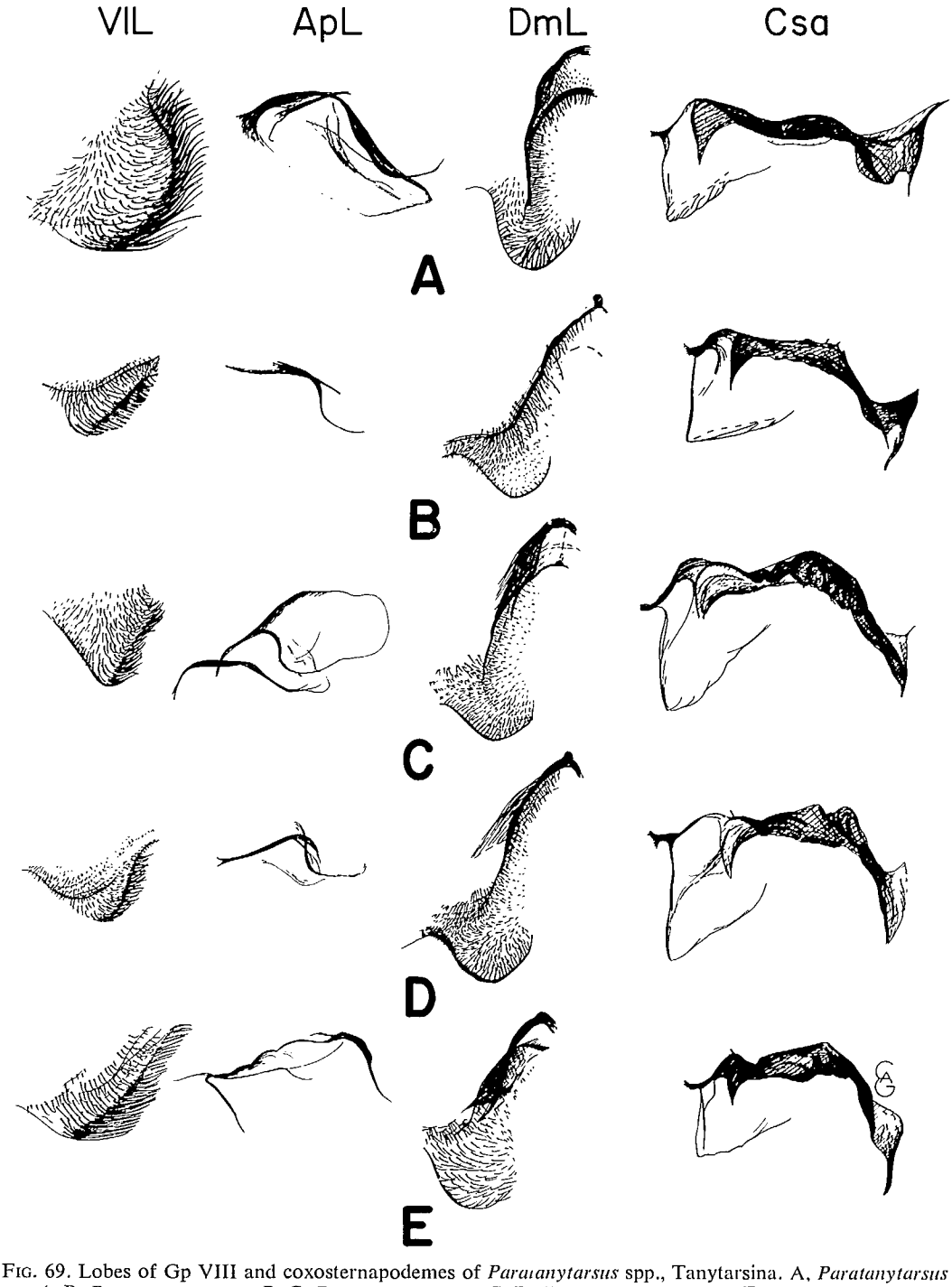

FIG. 69. Lobes of Gp VIII and coxosternapodemes of *Paratanytarsus* spp., Tanytarsina. A, *Paratanytarsus* sp. *A*. B, *Paratanytarsus* sp. *B*. C, *Paratanytarsus* sp. *C*. D, *Paratanytarsus* sp. *D*. E, *P*. sp.n. near *natvigi* (Goetgh.)

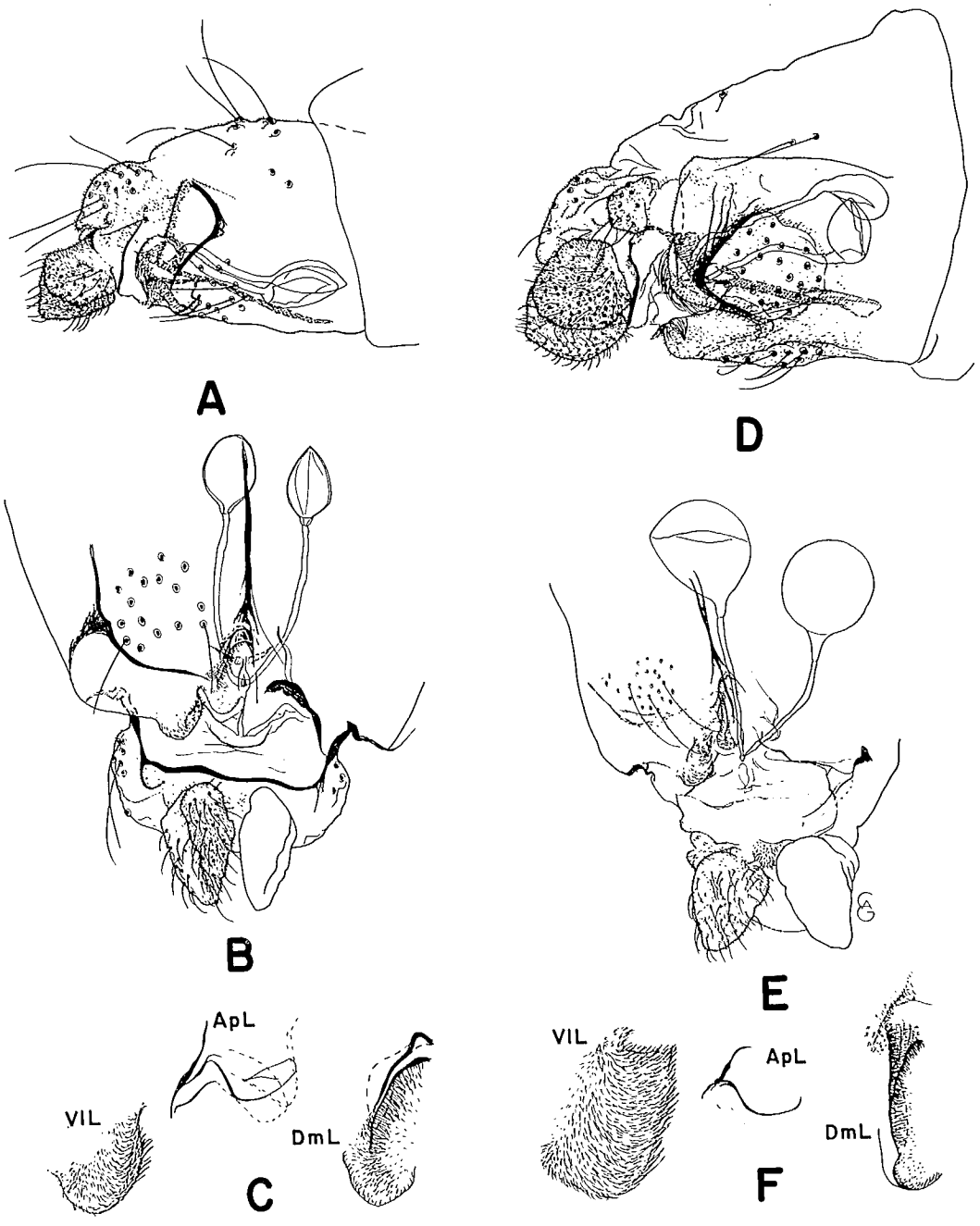

FIG. 70. Female genitalia of Tanytarsina. A, *Micropsectra* sp., lateral. B–C, *Micropsectra contracta* Reiss: B) ventral; C) lobes of Gp VIII. D, *Nimbocera patagonica* Reiss, lateral. E–F, *Lauterbornia sedna* Ol.: E) ventral; F) lobes of Gp VIII.

Parapsectra Reiss
(Reiss 1969 fig. 7)

Gca VIII straight in more mesal portion, ends on base of dorsomesal lobe of Gp VIII. S VIII forms a small floor under anterior part of vagina. Gp VIII divided; apical microtrichia of ventrolateral lobe long, directed oromesad, mesad, and caudomesad; ventrolateral lobe situated far laterad. Notum long, apparently more than 1.5 times as long as seminal capsules. T IX semicircular. Gc IX with a few setae. Postgenital plate triangular, Cerci small.

Seminal capsules ovoid, neck indistinct. Spermathecal ducts with one weak curve.

Nimbocera Reiss
(Fig. 70D)

Species examined: *N. patagonica* Reiss

Gca VIII rounded caudally. S VIII forms relatively small floor under vagina. Gp VIII simple, with long caudal microtrichia apparently as in *Tanytarsus*. Notum short. T IX bluntly triangular. Gc IX well developed, with about 10 setae. Cerci relatively large.

Seminal capsules small, with indistinct neck. Spermathecal ducts nearly straight.

TRIBE PSEUDOCHIRONOMINI (NEW TRIBE)
(Fig. 71)

S VIII does or does not form floor under anterior and mesal portions of vagina. Gp VIII simple or with far lateral indication of ventrolateral lobe. Apodeme lobe weak. T IX large, hood-shaped, undivided. Gc IX relatively large, with a few setae. Segment X without setae. Cerci medium to large.

Seminal capsules ovoid to spherical, with relatively large funnel-shaped neck. Spermathecal ducts not completely straight.

Key to adults of Pseudochironomini

1 Antepronotum strongly reduced, not visible from above; pulvilli usually absent or vestigial; male without volsella 2a; no true anal point 2

Antepronotum well developed, collarlike; pulvilli absent or well developed; male at least with rudiments of volsella 2a or with all volsellae reduced; true anal point present or absent 3

2 Eyes without dorsal elongation; pulvilli absent; squama apparently without setae; S VIII of female forms a floor under vagina ..... *Manoa* Fittk. (Brazil) (p. 154)

Eyes with dorsal elongation; pulvilli present or absent; squama with setae ..... *Riethia* Kieff. (Australia, New Zealand, South Chile)

3 True anal point absent in male; eyes without distinct dorsal elongation; female with 5 flagellomeres ..... *Pseudochironomus* Mall. (p. 156)

True anal point present in male; eyes with distinct dorsal elongation; female probably always with 6 flagellomeres ..... *Aedokritus* Rob. (South America), *Megacentron* Freem. (Argentina, Australia), and *Psilochironomus* Subl. (South America) (p. 156)

(The male of the last genus can be distinguished by the lack of volsellae (Sublette 1966a p. 19), while *Aedokritus* Rob. (Roback 1958, 1960 p. 99–100) can possibly be separated from *Megacentron* Freem. (Freeman 1961 p. 676) by means of the spotted or banded wings and the simple, not bifid, setae on volsella 2 of the former.)

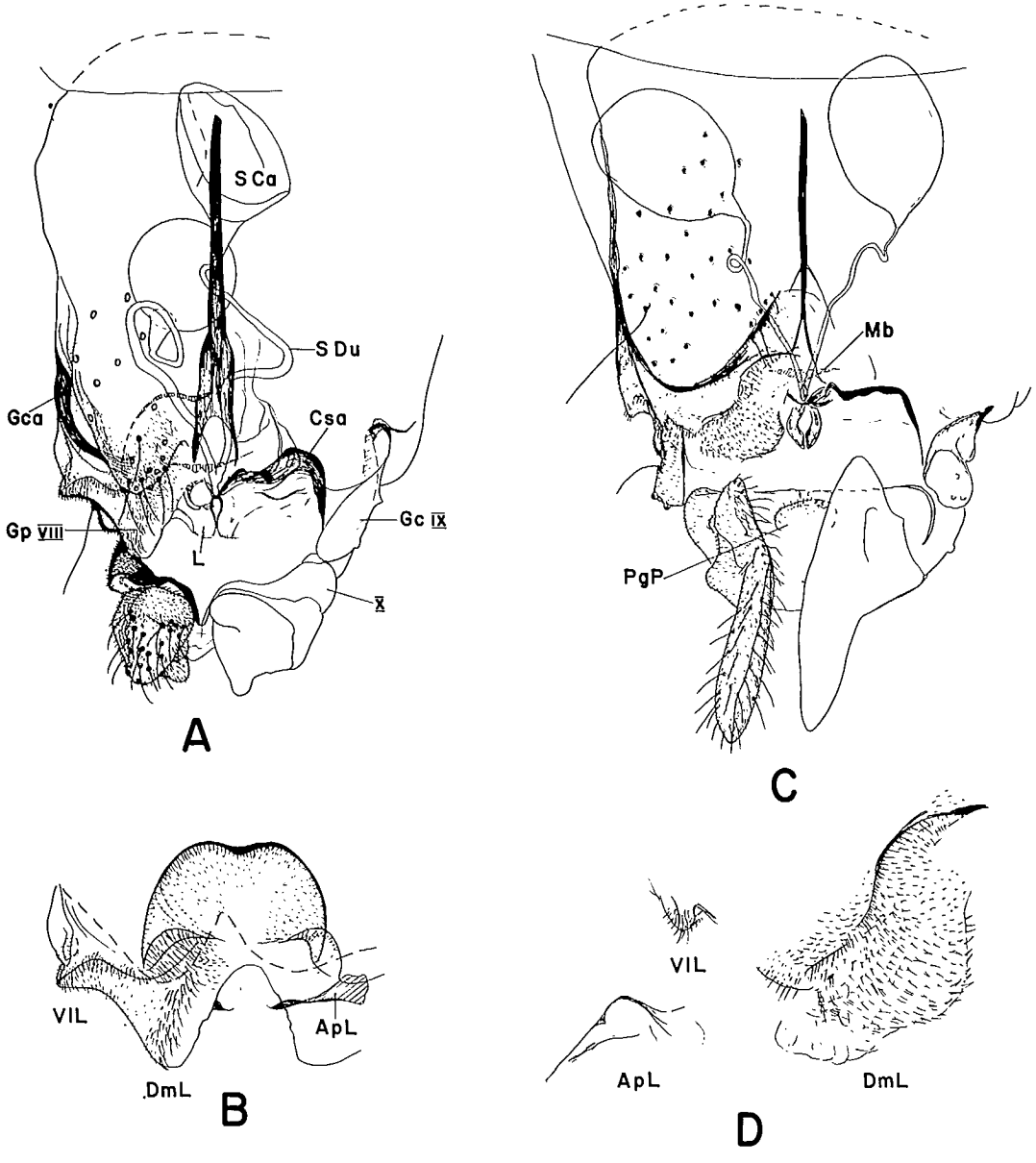

FIG. 71. Female genitalia of Pseudochironomini, Chironominae. A–B, *Manoa obscura* Fittk.: A) ventral; B) Gp VIII. C–D, *Pseudochironomus fulviventris* (Joh.): C) ventral; D) lobes of Gp VIII.

Manoa Fittk.
(Fig. 71A, B; Fittkau 1963 fig. 12, 13)

Species examined: *M. obscura* Fittk.

Gca VIII strong, rounded posteriorly. S VIII forms floor carrying numerous setae (about 30) under anterior and lateral parts of vagina; floor with deep, triangular, caudomesal incision. Gp VIII with large, triangular dorsomesal lobe and far lateral indication of a ventrolateral lobe. Notum slightly longer than seminal capsules. T IX large. Gc IX moderately large, with about 3 setae. Postgenital plate triangular. Cerci of medium size.

Seminal capsules large, spherical, with pronounced funnel-shaped neck. Spermathecal ducts with loop.

Pseudochironomus Mall.
(Fig. 71C, D; Sæther 1977 fig. 28D)

Species illustrated: *P. fulviventris* (Joh.)

Gca VIII relatively strong, rounded posteriorly, very weakly joined medially. S VIII does not form floor under vagina. Gp VIII with large, rounded dorsomesal lobe and far lateral, very weak indication of ventrolateral lobe. Notum about as long as seminal capsules. Gc IX moderately large, with about 3 setae. Postgenital plate rounded. Cerci large.

Seminal capsules ovoid, large, with funnel-shaped neck. Spermathecal ducts with small loop or bend.

Aedokritus Rob.
(Roback 1958 fig. 9, 10)

Gca VIII apparently absent. Gp VIII apparently simple, large, and triangular. Cerci large.

Aedokritus Rob. (Roback 1958, 1960 p. 99–100), *Megacentron* Freem. (Freeman 1961 p. 676), which is possibly a synonym of *Aedokritus*, and *Psilochironomus* Subl. (Sublette 1966a p. 19) show several similarities with *Paratendipes* Kieff. (the first 2 in the male hypopygium) and should perhaps be placed at the base of the Chironomini, or in a fourth tribe together with *Paratendipes* and related genera. The justification both for the placement of these genera and for the erection of this new tribe will have to be confirmed by an examination of the immatures and the female genitalia of all 6 genera.

TRIBE CHIRONOMINI
(Fig. 72–90)

S VIII never forms floor under vagina. Gp VIII simple or more often divided into ventrolateral and dorsomesal lobes. Dorsomesal lobe always well developed, never linelike (i.e. different from most Orthocladiinae where the main lobe is the ventrolateral), sometimes with oral group shagreenation of minute microtrichia (*Xenochironomus* Kieff. and the *Harnischia* complex), occasionally dorsomesal lobe ventral of ventrolateral lobe (as in *Paracladopelma laminata* Kieff. Fig. 88A, B). Ventrolateral lobe small to large, often brushlike, usually smaller than dorsomesal lobe. Apodeme lobe always present, sometimes well developed, with more or less distinct microtrichia. Membrane occasionally with microtrichia (*Nilodorum* Kieff. Fig. 79D, E). Gp IX normal, well developed. T IX large, hood-shaped, completely undivided except in *Lauterborniella* Bause (Fig. 73E); occasionally with small, triangular, caudal projection (*Microtendipes chloris* (Meig.) Fig. 72E). Gc IX small to medium; never completely fused with T IX; usually with a few setae, but often with only 1 or 2 setae or without setae. Segment X usually with a few setae, occasionally with only 1 or 2 setae on each side or without setae. Postgenital plate small to large. Cerci medium to large.

Labia sometimes with microtrichia. Seminal capsules small to large. Spermathecal ducts usually straight or nearly straight, occasionally with loop or sharp bend, always with common opening.

Preliminary key to females of Chironomini

1 Palp reduced, with 2–4 very short segments 2

Palp normal or when reduced (*Graceus* Goetgh., *Nilodorum* Kieff.) with 5 segments 3

2 Antepronotum reduced, not visible from above; body with tufts of long setae ..... *Collartiella* Goetgh. (Africa)

Antepronotum well developed, visible from above; body without tufts of long setae ..... *Halliella* Kieff. (syn. *Bacotendipes* Kieff.)

3 Combs of hind tibia without spurs; 6 flagellomeres; Gp VIII divided, ventrolateral lobe brushlike; Gc IX without setae; spermathecal duct with loop ..... *Graceus* Goetgh. (p. 164)

Hind tibia with at least 1 spur; usually 4 or 5 flagellomeres; Gp VIII divided or simple, ventrolateral lobe brushlike or not brushlike; Gc IX without or usually with setae; spermathecal duct usually without loop 4

4 Anterior femora swollen apically to form a slight club; middle and hind tibia each with 1 spur; either squama bare and front tibia with apical spine, or squama with 4 or 5 setae and scale of front tibia rounded; 4 flagellomeres, or wing spotted, or legs with adpressed scales 5

Anterior femora not apically swollen; when middle and hind tibia each with 1 spur either squama fully fringed or wings clear; female with more than 4 flagellomeres; legs without scales 7

5 Front tibia with distinct spur; legs without scales; squama bare; antepronotum without lateral tubercles 6

Front tibia with smooth scale; legs with scales; squama with 4 or 5 setae; antepronotum with lateral tubercles ..... *Lepidopodus* Freem. (Africa)

6 Wings spotted; 5 or 6 flagellomeres; pulvilli well developed ..... *Lauterborniella* Bause, pro parte (subgen. *Zavreliella* Kieff. which perhaps should be regarded only as a synonym) (p. 164)

Wings at most slightly smoky; 4 flagellomeres; pulvilli vestigial ..... *Kribiodosis* Kieff. (Africa)

7 Squama without setae; pulvilli vestigial or hairlike 8

Squama with setae, or when without pulvilli well developed 11

8 Front tibia with an apical spine which, including its base, is at least as long as tibial diameter 9

Front tibia with an apical spine which, including its base, is not more than 0.6 times as long as tibial diameter, or without a spine 10

9 Hind tibia with 2 spurs; Gp VIII undivided; segment X without setae; 6 flagellomeres ..... *Nilothauma* Kieff. (p. 164)

Hind tibia with 1 spur; female unknown ..... *Dolichopelma* Kieff.

10 Gp VIII divided, labia with microtrichia; front tibia without apical spine ..... *Paralauterborniella* Lenz (p. 164)

Gp VIII undivided, labia without microtrichia; front tibia with apical spine ..... *Paratendipes* Kieff., pro parte (p. 163)

11 Scutum extending moderately to far forward beyond reduced antepronotum; middle and hind tibia each with 2 spurs; female genitalia probably always as in *Stenochironomus* Kieff. (Fig. 77F, G) 12

Scutum not extending beyond antepronotum or, when extending moderately beyond antepronotum, at least middle tibia with only 1 spur; female genitalia probably never as in *Stenochironomus* 14

12 Anterior tibia with a mucronate scale; head with group of long coarse setae projecting forwards between antennae ..... *Ophryophorus* Freem. (New Zealand)

Anterior tibia with rounded scale; head without long setae projecting forward between antennae 13

13 Wing membrane with setae; Gp VIII not described ..... *Harrisius* Freem. (New Zealand)

Wing membrane without setae; Gp VIII with deep concavity between well-developed dorsomesal lobe and vestigial ventrolateral lobe ..... *Stenochironomus* Kieff. (p. 167)
(And *Xestochironomus* Subl. et Wirth which has a less strongly produced scutum.)

14 Pulvilli absent, vestigial or small; middle and hind tibia each with 1 spur or, when 2 or none, front tibia with an apical spine which, including its base, is about 0.6 times as long as tibial diameter 15

Pulvilli well developed; middle and hind tibia each with 1 or 2 spines; front tibia with or without apical spine 19

15 Front tibia without apical spine 16

Front tibia with apical spine 17

16 R_{4+5} and costa reach apex of wing, only slightly separated from apically upturned M_{1+2} ..... *Paucispinigera* Freem. (New Zealand)

R_{4+5}, costa, and M_{1+2} normal ..... *Paraborniella* Freem. (Australia, female not known)

17 Wings with dark pattern; middle and hind tibiae each with 1 spur; Gp VIII not described 18

Wings at most with pale greyish pattern; middle and hind tibia usually each with 2 spines; Gp VIII undivided ..... *Paratendipes* Kieff., pro parte (p. 163)

18 Wings broad, FCu far distad of RM; pulvilli present, but inconspicuous ..... *Kribiothauma* Kieff. (Africa)

Wings normal, FCu below or very slightly distad of RM; pulvilli vestigial ..... *Kribiocosmus* Kieff. (Africa)

19 Setae on squama absent or greatly reduced in number; middle tibia with 1 apical spine; hind tibia with 1 apical spine or, when with 2, squama bare and T IX divided by median reticulation; apex of front tibia with a distinctly projecting rounded or mucronate scale 20

Squama fully fringed or when setae absent or reduced in number, 1 or both middle and hind tibia with more than 1 spine, or apex of front tibia with a low rounded scale which is not distinctly projecting; T IX never partially divided 21

20 Apex of front tibia with mucronate scale; squama bare; T IX partially divided, with median reticulation; ventrolateral lobe minute, but brushlike ..... *Lauterborniella* Bause, pro parte (p. 164)

Apex of front tibia with rounded scale; squama bare or with a couple of setae; female not known ..... *Skusella* Freem. (Australia)

21 Gp VIII simple; middle and hind tibia each with 1 apical spine 22

Gp VIII divided; middle and hind tibia each with 1 or 2 apical spines 23

22 Acrostichals absent; front tibia truncate, without scale or spine ..... *Microtendipes* Kieff. (p. 163)

Acrostichals present; front tibia with apical mucronate scale ..... *Omisus* Town.

23 Apex of front tibia with low, rounded scale, not distinctly projecting[3]; middle tibia nearly always with 2 spines; dorsomesal lobe with indication of oromesal group shagreenation of microtrichia, or labia or membrane or apodeme lobe with microtrichia, or ventrolateral lobe larger than dorsomesal lobe, or segment X with caudolateral projections forming a partial collar around cerci 36

Apex of front tibia with a distinctly projecting rounded or mucronate scale; middle tibia nearly always with 1 spine (except *Endochironomus* Kieff., *Nilodosis* Kieff., *Henrardia* Goetgh., and *Conochironomus* Freem.); dorsomesal lobe without group shagreenation; labia or membrane nearly always without microtrichia; apodeme lobe without microtrichia; ventrolateral lobe smaller than dorsomesal lobe except in *Stictochironomus* Kieff.; no caudolateral projections of segment X 24

24 T IX produced caudad as a curved fingerlike process longer than cerci; front tibia with a very long spine which, with its broader base, is longer than apical width of tibia; middle and hind tibia each with 2 spurs ..... *Nilodosis* Kieff. (Africa)

T IX normal; front tibia without or with short spine or scale; middle tibia usually with 1 spur 25

25 Outer comb of middle tibia with 4 spurs, inner comb with 1 spur; hind tibia with 2 spurs ..... *Henrardia* Goetgh. (Africa)

Middle and hind tibia each with 1 or 2 spurs 26

26 Six flagellomeres; middle tibia with 2 spurs except in *Imparipecten* Freem.; hind tibia with 2 spurs 27

Five flagellomeres; middle tibia with 1 spur; hind tibia with 1 or 2 spurs 29

[3] Goetghebuer (1937–54 p. 50) mentions that *Fleuria* Kieff. has a spine on front tibia. According to the examined specimen and Rodova (1968 p. 142, fig. 22) there is no spine.

27 Acrostichals absent; scale at apex of front tibia without spine ..... *Conochironomus* Freem. (Africa, Australia)

Acrostichals present; scale at apex of front tibia mucronate 28

28 Middle tibia with 1 spur ..... *Imparipecten* Freem. (Australia)

Middle tibia with 2 spurs ..... *Endochironomus* Kieff. (p. 166)

29 Ventrolateral lobe not brushlike, much larger than dorsomesal lobe; labia at least sometimes with fine microtrichia ..... *Stictochironomus* Kieff. (syn. *Allochironomus* Kieff.) (p. 166)
(And probably *Parvitergum* Freem. from Australia, known only from males.)

Ventrolateral lobe more or less brushlike, distinctly smaller than dorsomesal lobe; labia apparently never with microtrichia 30

30 Dorsomesal lobe narrow and very long, extending caudad of ventrolateral lobe and labia; Gc IX with 1 or 2 setae; segment X with few setae ..... *Tribelos* Town. (p. 166)

Dorsomesal lobe shorter or, if nearly as long, setae on Gc IX and segment X more numerous 31

31 Gc IX with 1 seta; squama with 0–3 setae ..... *Pagastiella* Brund. (p. 165)

Gc IX with at least 3 setae; squama with at least 6 setae 32

32 Wing membrane with setae; spermathecal duct with angle 35

Wing membrane without setae; spermathecal duct straight or nearly straight 33

33 Four flagellomeres; pulvilli not bilobed ..... *Pedionomus* Subl. (p. 166)

Five flagellomeres; pulvilli bilobed ..... *Polypedilum* Kieff., pro parte (p. 165)

34 Dorsomesal lobe parallel-sided, extending caudad of well-developed ventrolateral lobe about to apex of labia ..... *Polypedilum* subgen. *Tripodura* Town. (p. 165)

Dorsomesal lobe not parallel-sided, extending caudad to about same level as ventrolateral lobe, or ventrolateral lobe reduced ..... *Polypedilum* subgen. *Polypedilum* Kieff. (p. 165)

35 Front tibia with a pointed scale ending in a conspicuous spine; inner comb of middle tibia and outer comb of hind tibia with a spine, the other combs unarmed ..... *Polypedilum* subgen. *Pentapedilum* Kieff. (p. 165)

Front tibia with an apically rounded scale or sometimes with a minute apical spine or scale; middle tibia with 1 spine and hind tibia with 2 spines, inner spine very small or (in some specimens of *P. albescens* Town.) absent ..... *Phaenopsectra* Kieff. (syn. *Sergentia* Kieff. and *Lenzia* Kieff.) (p. 164)

36 Segment X with caudolateral extensions form a collar around cerci; Gc IX without setae; apodeme lobe apparently secondarily fused with dorsomesal lobe ..... *Fleuria* Kieff. (p. 167)

Segment X without collarlike extensions; Gc IX usually with at least 1 seta; apodeme lobe distinct or indistinct, never fused with dorsomesal lobe 37

37 Dorsomesal lobe with oromesal group shagreenation, sometimes very indistinct and possibly absent in some *Xenochironomus* subgen. *Anceus* Rob.; labia nearly always with microtrichia, when absent seminal capsules at least as large as cerci, or dorsomesal lobe covering part of ventrolateral lobe in ventral aspect; apodeme lobe and membrane without microtrichia 38

Dorsomesal lobe without oromesal group shagreenation; labia without microtrichia or, when these indicated, membrane also with microtrichia; seminal capsules smaller than cerci; dorsomesal lobe never covering part of ventrolateral lobe; apodeme lobe with or without microtrichia 48

38 Antepronotum as seen from above completely interrupted medially so the 2 halves are distinctly separated by a narrow notch; Gc IX without setae ..... *Xenochironomus* Kieff. 39

Antepronotum not interrupted medially although often notched; Gc IX usually with at least 1 seta 40

39 Ventrolateral lobe rounded; segment X with 0–2 setae on each side ..... *Xenochironomus* subgen. *Xenochironomus* Kieff. (p. 171)

Ventrolateral lobe triangular; segment X with 2 or more setae on each side ..... *Xenochironomus* subgen. *Anceus* Rob. (p. 171)

40 Ventrolateral lobe large and broad, about as wide as long; Gc IX with 0 or 1 seta 41

Ventrolateral lobe smaller and more narrow or, when long, clearly longer than wide; Gc IX usually with 1 or more setae 42

41 Ventrolateral lobe with distinct mesal concavity and with notch on lateral margin ..... *Demicryptochironomus* Lenz (p. 173)

Ventrolateral lobe approximately triangular with nearly straight mesal margin and slightly convex outer margin ..... *Cryptochironomus* Kieff. (p. 173)

42 Segment X without setae ..... *Cryptotendipes* Lenz (p. 171)

Segment X with setae 43

43 Labia without microtrichia; ventrolateral lobe narrow in ventral aspect with long apical microtrichia lying in the longitudinal direction of lobe ..... *Microchironomus* Kieff. (p. 172)

Labia with at least indication of weak microtrichia; ventrolateral lobe wider with some apical microtrichia lying partly perpendicular to lobe, occasionally ventrolateral lobe reduced 44

44 Ventrolateral lobe without caudal and caudolateral microtrichia; Gc IX usually with 2 setae 45

Ventrolateral lobe covered with microtrichia or reduced; Gc IX usually with 0 or 1 seta 46

45 Ventrolateral lobe with only a few short and weak caudomesal microtrichia; Gca VIII weak ..... *Harnischia* Kieff. (p. 173)

Ventrolateral lobe with numerous, but short oral, oromesal, and caudomesal microtrichia; Gca VIII relatively strong ..... *Chernovskiia* Sæth. (p. 173)

46 Ventrolateral lobe relatively broad, only slightly longer than wide; microtrichia of labia very indistinct ..... *Cladopelma* Kieff. (p. 171)

Ventrolateral lobe about 1.5–3.0 times as long as wide or strongly reduced; microtrichia of labia very distinct to indistinct 47

47 Ventrolateral lobe small, but not vestigial, partially hidden by dorsomesal lobe; Gc IX without setae; labia with weak microtrichia ..... *Paracladopelma* Harn. (p. 172)
(Probably *Acalcarella* Shil., and possibly *Cyphomella* Sæth. See Sæther 1977.)

Ventrolateral lobe either long and well developed with long apical microtrichia or vestigial, never partially hidden by dorsomesal lobe; Gc IX with 0–3 setae; labia with strong or weak microtrichia ..... *Parachironomus* Lenz (p. 172)
(*Acalcarella and Cyphomella* Sæth. may possibly key here instead of to *Paracladopelma*.)

48 Ventrolateral lobe distinctly larger than dorsomesal lobe; apodeme lobe without microtrichia; Gc IX weak, with 0 or 1 seta 49

Ventrolateral lobe usually distinctly smaller than dorsomesal lobe, when larger apodeme lobe with distinct microtrichia; Gc IX normal to weak, with 2 or more setae 50

49 Ventrolateral lobe with reticulations; membrane with microtrichia, labia apparently with indications of microtrichia; Gc IX without seta; palpal segments about 1.5 times as long as wide ..... *Nilodorum* Kieff. sensu E. C. Beck (p. 168)

Ventrolateral lobe without reticulations; membrane and labia without indications of microtrichia; Gc IX with or without seta; palpal segments longer ..... *Goeldichironomus* Fittk. (syn. *Siolimyia* Fittk.) (p. 168)

50 Antepronotum deeply notched mesally, interrupted by scutum in dorsal view 51

Antepronotum not interrupted mesally although usually distinctly notched 54

51 T III–VI without median, basal, scarlike impressions; frontal tubercles present 52

T III–VI with median, basal, scarlike impressions; frontal tubercles present or absent ..... *Glyptotendipes* Kieff., pro parte (p. 169) 53

52 Thorax either black with acrostichals, or pale greenish marked with orange brown, and without acrostichals; 5 or 6 flagellomercs; each comb of middle and hind legs with 1 spur ..... *Glyptotendipes* subgen. *Demeijerea* Krus. (p. 169)

Thorax greenish with orange brown markings and with acrostichals; 6 flagellomeres; each comb of middle and hind legs with 1 or 2 spurs ..... *Lipiniella* Shil. (p. 168)

53 Six flagellomeres; T II with median, basal, scarlike impression; frontal tubercles distinct ..... *Glyptotendipes* subgen. *Phytotendipes* Goetgh. (p. 169)

Five flagellomeres; T II without median, basal, scarlike impression; frontal tubercles absent or vestigial ..... *Glyptotendipes* subgen. *Glyptotendipes* Kieff. (p. 169)

54 Apodeme lobe narrow, with very indistinct microtrichia ..... *Dicrotendipes* Kieff. (syn. *Limnochironomus* Kieff.) (p. 168)

Apodeme lobe relatively distinct, with distinct microtrichia 55

55 Frontal tubercles vestigial or absent; antepronotum uniformly narrowed toward center, not produced or notched medially; wing membrane occasionally with setae .... *Kiefferulus* Goetgh. (p. 170)

Frontal tubercles usually present and well developed; antepronotum somewhat narrowed toward center, but medially more or less produced, usually with a broad, but weak median notch; wing membrane without setae .... *Chironomus* Meig. (p. 169), *Einfeldia* Kieff. (p. 170) 56
(and probably *Kloosia* Krus. and *Halliella* Kieff.)

56 Dorsomesal lobe reduced, with a sclerotized edge, smaller than ventrolateral lobe .... *Chironomus* subgen. *Camptochironomus* Kieff. (p. 169)

Dorsomesal lobe larger than or as large as ventrolateral lobe, no sclerotized edge 57

57 Gca VIII joined mesally anterior of vagina; large dorsomesal lobe partially covering small ventrolateral lobe; apodeme lobe covered by principal lobes .... *Einfeldia* Kieff. (p. 170)

Gca VIII not joined mesally; dorsomesal lobe usually not covering part of ventrolateral lobe; at least part of apodeme lobe not covered by principal lobes .... *Chironomus* subgen. *Chironomus* Meig. (p. 169)
(and probably *Chironomus* subgen. *Chaetolabis* Town.)

Paratendipes Kieff.
(Fig. 72A, B; Rodova 1972c fig. 3)

Species examined: *P. albimanus* (Meig.)

Gca VIII strong, rounded at posterior margin, meet mesally, with indication of small branch running out on Gp VIII. Gp VIII simple, rounded at caudolateral angle, with few or no mesal microtrichia. Apodeme lobe very weak. T IX normal. Gc IX normal, with about 2 setae. Segment X with 1 seta on each side. Postgenital plate large (see Rodova 1972c fig. 3), in Fig. 72A postgenital plate slightly distorted. Cerci relatively long.

Seminal capsules ovoid, somewhat pointed orally, with short neck. Spermathecal ducts nearly straight.

This genus together with *Paucispinigera* Freem. (Freeman 1959 p. 428) from New Zealand, *Paraborniella* Freem. (Freeman 1961 p. 717) from Australia, *Skusella* Freem. (Freeman 1961 p. 718) from Australia and Africa, and perhaps *Prochironomus* Kieff. and *Brunieria* Kieff. (Goetghebuer 1937–54 p. 69, 72) form a group of plesiomorphic Chironomini which shows several similarities with *Megacentron* of the Pseudochironomini; they may perhaps deserve a fourth tribe (see p. 138, 156).

Microtendipes Kieff.
(Fig. 72C–E; Pinder 1976 fig. 3)

Species examined: *M. pedellus pedellus* (De Geer), *M. chloris* (Meig.)

Gca VIII strong, straight posteriorly, ends on Gp VIII. Gp VIII simple, but with strong microtrichia in more than one layer. Apodeme lobe very weak. T IX normal or with a small, triangular, caudal projection. Gc IX with 0–2 setae. Coxosternapodeme nearly straight. Segment X with (*M. rydalensis* (Edw.) Pinder 1976 fig. 2) or without setae. Postgenital plate large. Cerci relatively long.

Seminal capsules small, spherical to oval. Spermathecal ducts straight.

Nilothauma Kieff.
(Fig. 73A–C)

Species examined: *Nilothauma* sp.n.

Gca VIII straight, ends on Gp VIII. Gp VIII simple, broad, and rounded or straight caudally. Apodeme lobe very weak. T IX normal. Gc IX with a few setae. Coxosternapodeme nearly straight. Segment X without setae. Postgenital plate relatively large, triangular. Cerci of moderate size.

Seminal capsules relatively small, oval with distinct cylindrical neck. Spermathecal ducts straight.

Lauterborniella Bause
(Fig. 73D–F)

Species examined: *L. varipennis* (Coq.)

Gca VIII strong, but short, ends on Gp VIII. Gp VIII with well-developed dorsomesal lobe and vestigial and far lateral ventrolateral lobe. Apodeme lobe weak, but relatively long. T IX partly divided by caudal emargination and central reticulation. Gc IX without setae. Segment X with several setae. Postgenital plate well developed. Cerci of moderate size.

Seminal capsules oval, with distinct, more darkly sclerotized neck. Spermathecal ducts straight.

The species examined will fall in the subgenus *Zavreliella* Kieff. However, as mentioned by Townes (1945 p. 20) the division into subgenera does not seem to hold up.

Paralauterborniella Lenz
(Fig. 74A–C; Rodova 1972a fig. 3)

Species examined: *P. nigrohalterale* (Mall.)

Gca VIII nearly straight, ends on base of Gp VIII. Gp VIII divided into well-developed dorsomesal lobe and small, brushlike ventrolateral lobe. T IX normal. Gc IX with 1–3 setae. Segment X with 0 or 1 seta on each side. Postgenital plate wide, triangular. Cerci normal.

Labia with microtrichia. Seminal capsules ovoid. Spermathecal ducts straight.

Graceus Goetgh.
(Fig. 74D–G)

Species examined: *Graceus* near *ambiguus* Goetgh.

Gca VIII nearly straight laterally, with small branch on base of dorsomesal lobe of Gp VIII, weakly connected mesally. Gp VIII divided into large, rounded dorsomesal lobe, and small, brushlike ventrolateral lobe. T IX normal. Gc IX without setae. Segment X with several (6–12) setae on each side. Postgenital plate triangular, large, distinct. Cerci normal.

Seminal capsules spherical, relatively small. Spermathecal ducts with loop.

On the basis of the female genitalia this genus is very close to *Phaenopsectra* Kieff.

Phaenopsectra Kieff.
(syn. *Lenzia* Kieff., *Sergentia* Kieff.)[4] (Fig. 75A–C, Rodova 1972b fig. 3)

[4] Kieffer (1921b p. 274, 275), in his first description of the genus *Phaenopsectra*, included two species, *P. connectens* Kieff. and *P. leucolabis* (Kieff.). (Sublette and Sublette (1965 p. 174) overlooked the second species.) Both Goetghebuer (1937–54 p. 80), and Townes (1945 p. 71), apparently independently, selected *P. leucolabis* as the generic type and showed that this species is a junior synonym of *Phaenopsectra flavipes* (Meig.). The latter is a typical *Lenzia* Kieff. sensu Lenz and included in that genus by Lenz (1954–62 p. 248). Thus, even if *Phaenopsectra* sensu Lenz (containing *P. connectens* only) should deserve generic rank the name would have to be changed because *Phaenopsectra* Kieff. is the senior synonym of *Lenzia* Kieff. Whether *Sergentia* Kieff. deserves subgeneric or even generic rank is worth further study. The differences, however, appear to be too small to justify a separation.

Species examined: *P. obediens* (Joh.), *P. coracina* (Zett.), *P. punctipes* (Wied.)

Gca VIII with small branch on base of dorsomesal lobe of Gp VIII; gonocoxapodeme strong laterally, weakly connected mesally. Gp VIII divided into large dorsomesal lobe and small brushlike ventrolateral lobe. Apodeme lobe weak, but its apodeme relatively distinct. T IX normal. Gc IX with about 3–6 setae. Segment X with several (6–18) setae on each side. Postgenital plate triangular, large, distinct, or indistinct. Cerci normal.

Seminal capsules spherical to ovoid. Spermathecal ducts nearly straight, with bend or small loop.

The species examined differ from one another in the presence or absence of a bend or loop on the spermathecal ducts, the number of setae on Gc IX and segment X, and the shape of the principal lobes of Gp VIII.

Pagastiella Brund.
(Fig. 75E)

Species examined: *P. ostansa* (Webb)

Gonocoxapodeme straight, on base of dorsomesal lobe of Gp VIII. Gp VIII divided into large dorsomesal lobe and small brushlike ventrolateral lobe. Apodeme lobe weak. T IX normal. Gc IX with 1 or 2 setae. Segment X with about 4 or 5 setae on each side. Postgenital plate triangular, normal. Cerci normal, relatively small.

Seminal capsules oval. Spermathecal ducts with weak curve.

Polypedilum Kieff.
(Fig. 76; Rodova 1974a fig. 14, 17, 19, 21; Sæther and Galloway 1976 fig. 2)

Species illustrated: *P. (P.) nubeculosum* (Meig.), *P. (P.) illinoense* (Mall.), *P. (Pentapedilum) tritum* (Walk.), *P. (Tripodura) simulans* Town.

Gca VIII with main branch on dorsomesal lobe of Gp VIII and more or less distinct connection mesally, anterior of vagina. Gp VIII divided into large dorsomesal lobe and smaller brushlike ventrolateral lobe. Apodeme lobe weak. T IX normal. Gc IX with 1–10 setae. Segment X with 3–10 setae on each side. Postgenital plate triangular, usually pointed at apex, occasionally rounded. Cerci normal.

Seminal capsules spherical to oval, relatively small. Spermathecal ducts straight, nearly straight, or with about a 90° bend.

Three subgenera are recognized here, *Polypedilum* s.str., *Pentapedilum* Kieff., and *Tripodura* Town. *Tripodura* has a long parallel-sided dorsomesal lobe clearly overreaching the ventrolateral lobe and attaining the posterior margin of the labia (Fig. 76E, F; Rodova 1974a). The spermathecal ducts are completely straight or nearly straight. *Polypedilum (Tripodura) scalaenum* (Schrank) (Rodova 1974a) and *Polypedilum (Tripodura) bicrenatum* Kieff. have 1 or 2 setae on Gc IX and about 4 setae on each side of segment X; *Polypedilum (Tripodura) pullum* (Zett.) has about 4 setae on Gc IX and about 5 setae on each side of segment X; and *Polypedilum (Tripodura) simulans* Town. has about 6 setae on Gc IX and about 7 setae on each side of segment X. *Polypedilum (Pentapedilum) tritum* (Walk.), the only member of this subgenus examined, has a shorter dorsomesal lobe than the subgenus *Tripodura*, spermathecal ducts with a sharp bend, and 9 or 10 setae both on Gc IX and on each side of segment X. *Polypedilum (Polypedilum) nubeculosum* (Meig.) as described by Rodova (1974a) appears to be a different species from the *P. (P.) nubeculosum* drawn here (Fig. 76A, B), differing both in the shape of the principal lobe of Gp VIII and in the number of setae on Gc IX and segment X (segment X with 2 or 3 setae on each side in Rodova, 6–9 setae in the specimens examined here). However, in both cases the postgenital plate is rounded posteriorly and the dorsomesal lobe different from that of *Tripodura*. *Polypedilum (Polypedilum) illinoense* (Mall.) can be separated from the other species by the reduced ventrolateral lobe and the sharply bent spermathecal ducts.

Pedionomus Subl.
(Sublette 1964 fig. 86, 87)

Gc IX with about 8 setae. Segment X with about 8 setae on each side. Cerci normal.

Tribelos Town.
(syn. *Endotendipes* Lenz) (Fig. 75D)

Species examined: *T.* cf. *protextus* (Town.)

Gca VIII rounded posteriorly, joined mesally, with small branch on base of dorsomesal lobe. Gp VIII divided into very long, tonguelike dorsomesal lobe and relatively large, brushlike ventrolateral lobe. Apodeme lobe weak. T IX normal. Gc IX only with 1 or 2 setae. Segment X only with about 2 setae on each side. Postgenital plate triangular, relatively small. Cerci normal.

Seminal capsules ovoid. Spermathecal ducts nearly straight or with small bend.

The female genitalia of this genus shows similarities with *Phaenopsectra* and even more with *Polypedilum*. Lenz (1954–62 p. 185) placed the genus as a subgenus of *Endochironomus*, and Hamilton et al. (1969 p. 32) regarded it as a subgenus of *Phaenopsectra*. The pupa, however, shows that the genus probably should be placed near *Endochironomus* and *Stictochironomus*.

Endochironomus Kieff.
(Fig. 77A, B; Rodova 1968 fig. 12, 16, 17, 20; 1974a fig. 24; Sæther and Galloway 1976 fig. 1)

Species examined: *E. nigricans* (Joh.)

Gca VIII strong, rounded caudally, joined anterior of vagina. Gp VIII divided into large dorsomesal lobe and smaller but well developed, more or less brushlike ventrolateral lobe. Apodeme lobe weak. T IX normal. Gc IX with one to several setae. Segment X with several setae. Postgenital plate triangular, moderately to very long. Cerci long.

Seminal capsules spherical to oval with weak indistinct neck. Spermathecal ducts straight or nearly straight.

Endochironomus donatoris Shil. (Rodova 1974a) can be separated from the other described females on the bases of the shorter postgenital plate, the broader more brushlike ventrolateral lobe, the stronger microtrichia on the dorsomesal lobe, and the presence of only one seta on Gc IX. The female genitalia of *Endochironomus nigricans* (Fig. 77A, B) and *Endochironomus subtendens* (Town.) are practically identical. However, the former has 6–8 setae on Gc IX and 8 or 9 setae on each side of segment X, whereas the latter has 3–6 and 5–7 setae, respectively. These 2 Nearctic species appear to be separable from the 3 species described by Rodova (1968) by the ventrolateral lobe and the longer postgenital plates. *Endochironomus tendens* (Fabr.) (Rodova 1968 fig. 12) has about 10 setae on Gc IX but *Endochironomus albipennis* (Meig.) and *Endochironomus impar* (Walk.) (Rodova 1968) have about 6 and 4 or 5 setae, respectively.

The genera *Henrardia* Goetgh. (Freeman 1957 p. 408), and *Nilodosus* Kieff. (Freeman 1957 p. 406), both from Africa, are probably closely related to *Endochironomus*, and both, together with *Tribelos*, *Stictochironomus*, and related genera, probably form an old and relatively plesiomorphic group.

Stictochironomus Kieff.
(syn. *Allochironomus* Kieff.) (Fig. 77C–E; Reiss 1971 fig. 1–3; Rodova 1974a fig. 26, 28)

Species examined: *S. rosenschoeldi* (Zett.), *S. crassiforceps* (Kieff.)

Gca VIII straight, ends between principal lobes of Gp VIII. Gp VIII divided into small, tonguelike dorsomesal lobe and large, well-developed ventrolateral lobe. Apodeme lobe very weak. T IX normal. Gc IX with a few setae. Segment X with several setae. Postgenital plate long, but narrow. Cerci long.

Labia occasionally with very weak microtrichia. Seminal capsules ovoid, neck weak and placed laterally.

Stictochironomus crassiforceps (Kieff.) (syn. *Allochironomus crassiforceps* Kieff.) has a few very weak microtrichia on the labia (Fig. 77E), but otherwise has identical female genitalia to *Stictochironomus rosenschoeldi* Zett. (Fig. 77C, D) and *Stictochironomus histrio* (Fabr.) (Rodova 1974a fig. 26). The only remaining significant difference between *Stictochironomus* and *Allochironomus* is the 3 pairs of volsellae in male *Allochironomus* which are judged here as a plesiomorphous feature. *Allochironomus* should, therefore, in accordance with Shilova (1964 p. 735) and Rodova (1974a p. 186), be regarded as a junior synonym of *Stictochironomus*.

Parvitergum Freem. (Freeman 1961 p. 716) from Australia and *Conochironomus* Freem. (Freeman 1961 p. 701) from Africa and Australia appear closely related to *Stictochironomus*. Although the adult of *Conochironomus* has 2 spines on each comb of the middle and hind tibia and thus appears closer to *Endochironomus*, the larva, according to Martin (1975 p. 22), shows that the genus is closer to *Stictochironomus*.

Stenochironomus Kieff.
(Fig. 77F, G; Rodova 1971a fig. 5)

Species examined: *S. taeniapennis* (Coq.)

Gca VIII straight, main branch ends on Gp VIII, but smaller branches join anterior of vagina. Gp VIII with a deep concavity between a well-developed dorsomesal lobe and a vestigial ventrolateral lobe. Apodeme lobe with distinct apodeme. T IX normal. Gc IX with a few setae (about 3–7). Coxosternapodeme nearly straight. Segment X with a few setae. Postgenital plate broad and well developed. Cerci normal.

Seminal capsules ovoid. Spermathecal ducts with curve or small loop.

Stenochironomus gibbus Fabr. (Rodova 1971a p. 135) has only 3 setae on Gc IX and about 6 on each side of segment X. *Stenochironomus fascipennis* (Zett.) (Rodova 1971a p. 136) and *Stenochironomus taeniapennis* (Coq.) (Fig. 77F, G) both have about 7 setae on Gc IX and 3 setae on each side of segment X.

As in the preceding 2 genera, this genus also has some probable exotic relatives including *Xestochironomus* Subl. et Wirth (Sublette and Wirth 1972 p. 7) from the West Indies, *Harrisius* Freem. (Freeman 1959 p. 426, 1961 p. 704) from New Zealand and Australia, *Ophryophorus* Freem. (Freeman 1959 p. 427) from Australia, and *Collartiella* Goetgh. (Freeman 1957 p. 418) from Africa.

Fleuria Kieff.
(Fig. 78A, B; Rodova 1968 fig. 23)

Species examined: *F. lacustris* Kieff.

Gca VIII rounded caudally, without branches and not joined anterior of vagina. Gp VIII divided into dorsomesal lobe and slightly smaller ventrolateral lobe. Apodeme lobe apparently fused with dorsomesal lobe. T IX hood-shaped, triangular, with anterior concavity. Gc IX without setae. Segment X with elongate, flat, caudolateral extensions forming a collar around basal half of cerci, setae present on extensions but not on basal parts of segment X. Postgenital plate small, triangular. Cerci complexly folded.

Seminal capsules ovoid. Spermathecal ducts straight.

Goetghebuer (1937–54 p. 50) mentions that *Fleuria* Kieff. has a spine on the front tibia. On the specimen examined and according to Rodova (1968 p. 142 fig. 22) this spine is absent. Goetghebuer also regards *Lenziola* Kieff. as a synonym of *Fleuria*, but Lenz (1954–62 p. 167) keeps them separate. Although the 2 genera are probably related, the apparent reason for Goetghebuer's synonymizing, the reduction in numbers of male flagellomeres, is primarily an aberrant character resulting from specialized behavior, such as mating on contact, and is not necessarily a generic character.

Goeldichironomus Fittk.
(syn. *Siolimyia* Fittk.) (Fig. 78C, D; Fittkau 1968a fig. 12, 13)

Species examined: *G. holoprasinus* (Goeldi)

Gca VIII weak to relatively strong, curved caudolaterally, meeting anterior of vagina. Gp VIII divided into small dorsomesal lobe and large ventrolateral lobe. Apodeme lobe weak. T IX normal. Gc IX weakly separated from T IX, with 0 or 1 seta. Segment X large with about 7 to more than 30 setae on each side. Postgenital plate triangular with rounded apex. Cerci normal.

Seminal capsules oval, with short neck. Spermathecal ducts straight. *Goeldichironomus amazonicus* (Fittk.) (syn. *Siolimyia amazonica* Fittk., Reiss 1974b p. 113) differs from *Goeldichironomus holoprasinus* by lacking a seta on Gc IX and having more than 30 setae (as opposed to about 7) on each side of segment X.

Nilodorum Kieff. sensu E. C. Beck
(Fig. 79D, E)

Species examined: *N. devineyae* E. C. Beck

Gca VIII rounded caudolaterally, joined mesally. Gp VIII divided into relatively small dorsomesal lobe and very large ventrolateral lobe with reticulation on caudolateral surface. Membrane with a few microtrichia. T IX normal. Gc IX very small, without setae. Segment X with about 15 setae on projections on each side. Postgenital plate relatively small, triangular. Cerci normal.

Labium apparently with a few very weak microtrichia. Seminal capsules spherical with weak funnel-shaped neck. Spermathecal ducts straight.

The genus used by Beck (1961 p. 126–127) is not necessarily the same as *Nilodorum* Kieff., defined by Kieffer (1921a p. 30, 1921b p. 272, 1922 p. 45) and Freeman (1957 p. 374).

Lipiniella Shil.
(Rodova 1969b fig. 5)

Gca VIII rounded caudally. Gp VIII divided into dorsomesal lobe and slightly smaller ventrolateral lobe. T IX normal. Gc IX well developed, with about 10 setae. Segment X with several setae. Cerci normal.

Seminal capsules oval, with funnel-shaped neck. Spermathecal ducts nearly straight.

Dicrotendipes Kieff.
(syn. *Limnochironomus* Kieff. Fig. 79A–C)

Species examined: *D.* cf. *modestus* (Say), *D. botaurus* (Town.)

Gca VIII rounded caudally, joined mesally. Gp VIII divided into relatively large dorsomesal lobe and smaller ventrolateral lobe. Apodeme lobe narrow, with very weak and indistinct microtrichia. T IX normal. Gc IX small, with 1 or 2 setae. Segment X with about 2–7 setae on each side. Postgenital plate triangular, relatively large. Cerci normal.

Seminal capsules spherical to oval, with weak indication of neck.

The 2 species examined are easily separable by the shape of the ventrolateral and apodeme lobes and the more numerous setae on each side of segment X in *D. modestus* (6 or 7 compared with 2 or 3 in *D. botaurus*).

Glyptotendipes Kieff.

(Fig. 80; Rodova 1969b fig. 6, 1974a fig. 3, 5, 8, 10, 11; Sæther and Galloway 1976 fig. 8)

Species illustrated: *G. (Phytotendipes) paripes* (Edw.), *G. (P.) barbipes* (Staeg.), *G. (P.) lobiferus* (Say), *G. (Demeijerea) brachialis* (Coq.)

Gca VIII rounded caudally, joined mesally. Gp VIII divided into well-developed dorsomesal lobe and ventrolateral lobe of nearly same size to much smaller. Apodeme lobe well developed, with distinct microtrichia. T IX normal. Gc IX small to well developed, with about 2–12 setae. Segment X with setae (about 4–16) on each side. Postgenital plate triangular, narrow to broad at base, relatively large. Cerci normal.

Seminal capsules oval. Spermathecal ducts straight or nearly straight.

Three subgenera of *Glyptotendipes* are recognized here in accordance with Hamilton et al. (1969 p. 28) and Lenz (1954–1962 p. 170–171) who, however, uses the names *Prophytochironomus* Lenz for *Demeijerea* Krus. and *Phytochironomus* Kieff. for *Glyptotendipes* s.str. *Glyptotendipes (Demeijerea) rufipes* L. has about 10 setae on Gc IX and about 5 setae on each side of segment X (Rodova 1969b fig. 8), and *Glyptotendipes (Demeijerea) brachialis* (Coq.) has about 5 setae on Gc IX and about 10 setae on each side of segment X. *Glyptotendipes (Glyptotendipes) varipes* Goetgh. and *Glyptotendipes (Glyptotendipes) imbecillis* Walk. (Rodova 1974a) both have 2 or 3 setae on Gc IX, however *G. (G.) varipes* has only 4 setae on each side of segment X and *G. (G.) imbecillis* has 9–12 setae. The species in the subgenus *Phytotendipes* Goetgh. where the female genitalia are sufficiently known can be placed in the following key:

Key to sufficiently known females of *Glyptotendipes* subgen. *Phytotendipes* Goetgh.

1 Gc IX with about 11 setae; segment X with about 21 setae on each side ..... *Glyptotendipes (Phytotendipes) glaucus* (Meig.) (Rodova 1974a fig. 5)

Gc IX with 2–6 setae; segment X with 8–16 setae on each side 2

2 Ventrolateral lobe reduced, shorter than apodeme lobe; segment X with 14–16 setae on each side; Gc IX with 4–6 setae; ta_2 of front leg 1.3–1.4 times as long as ta_3 ..... *Glyptotendipes (Phytotendipes) lobiferus* (Say) (syn. *G. (P.) gripekoveni* Kieff.) (Fig. 80)

Ventrolateral lobe not reduced, longer than apodeme lobe; when segment X has 14–16 setae on each side, Gc IX with less than 4 setae; ta_2 of front leg 1.0–1.2 times as long as ta_3 3

3 Ventrolateral lobe smaller than dorsomesal lobe; postgenital plate narrow at base; segment X with about 8 setae on each side; ta_2 of front leg about 1.1–1.2 times as long as ta_3 ..... *Glyptotendipes (Phytotendipes) paripes* (Edw.) (Fig. 80A, B; Rodova 1974a fig. 3)

Ventrolateral lobe slightly larger than dorsomesal lobe; postgenital plate broad at base; segment X with about 15 setae on each side; ta_2 of front leg about as long as ta_3 ..... *Glyptotendipes (Phytotendipes) barbipes* (Staeg.) (Fig. 80 C, D)

Chironomus Meig.

(Fig. 81, 82A–E; Rempel 1936 fig. 6; Wülker 1961 fig. 3, 6, 1964 fig. 3; Götz 1964 fig. 5; Frommer 1967 fig. 143, 144, 146; Rodova 1968 fig. 5, 6, 9, 1969b fig. 2, 3, 1974b fig. 2; Sæther and Galloway 1976 fig. 5)

Species illustrated: *C. (C.)* cf. *atrella* (Town.), *C. (C.) plumosus* L. forma *semireductus* Lenz, *C. (C) decorus* Joh., *C. (C.) halophilus* Kieff., *C. (Camptochironomus) tentans* Fabr., *C. (Camptochironomus) pallidivittatus* Mall.

Gca VIII strong, rounded caudally, not joined mesally. Gp VIII divided into small to relatively large dorsomesal lobe and usually smaller, but well-developed ventrolateral lobe. Apodeme lobe distinct, with distinct microtrichia. T IX normal. Gc IX relatively well developed, with 0–20 setae. Segment X with 4–20 setae on each side.

Postgenital plate well developed, triangular, pointed, or rounded at apex. Cerci large.

Seminal capsules ovoid to oval. Spermathecal ducts slightly curved.

Of the 3 subgenera recognized here, *Chaetolabis* Town., *Camptochironomus* Kieff., and *Chironomus* s.str., only the last 2 have been examined. *Camptochironomus* is recognizable by the characteristic and somewhat reduced dorsomesal lobe. *C. (Camptochironomus) pallidivittatus* Mall. (Fig. 82D) has only one seta on Gc IX and about 20 on each side of segment X, but Rodova's drawing (Rodova 1969b fig. 2) shows 7 and 12 setae, respectively. However, in other species of *Chironomus* there also appears to be a considerable variation in the number of these setae, more so than in other genera. In *Chironomus (Chironomus) decorus* Joh. for instance there are 2 groups, one with 1–3 setae on Gc IX and 4–7 setae on each side of segment X, and the other with 3–7 and 12–15 setae, respectively. Specimens from both groups, however, have been taken together in the same sample at the same date and the characteristic markings of the species make the identification relatively certain. *C. pallidivittatus,* however, appears to be separable from *Chironomus (Camptochironomus) tentans* Fabr. (Fig. 82A–C; Rodova 1969b fig. 3) by the shape of the ventrolateral lobe; it also has less than 50 sensilla chaetica on the metatarsi of both hind leg and midleg, whereas *C. tentans* has 160–250 sensilla chaetica on both legs.

It is premature to attempt an identification key even to the sufficiently described females of the subgenus *Chironomus* based on the genitalia. However, good diagnostic features appear to be present in most species. *Chironomus halophilus* Kieff. (Fig. 81H) has a characteristic small, black apodeme lobe. *Chironomus plumosus* L. (Fig. 81D, E; Rodova 1968 fig. 4) and *Chironomus pilicornis* Fabr. (Rodova 1974b fig. 2) have 13–18 setae on Gc IX and the others have 0–7 setae. *C. plumosus* also has 130–252 sensilla chaetica on each metatarsus of midleg and hind leg (about the same number as in *Chironomus (Chironomus) crassicaudatus* Mall.), *C. decorus* has 88–122, and *C. atrella, Chironomus (Chironomus) atritibia* Mall., and probably the majority of the remaining species have 34–65 sensilla chaetica on each metatarsus.

Kiefferulus Goetgh.
(Fig. 82F, G)

Species examined: *K. dux* (Joh.)

Gca VIII rounded caudally, not joined mesally. Gp VIII divided into relatively large dorsomesal lobe and small, but well-developed ventrolateral lobe apparently with fewer microtrichia than in *Chironomus.* Apodeme lobe distinct, with microtrichia. T IX normal. Gc IX small, with about 2 setae. Segment X with several setae. Postgenital plate triangular, broad at base. Cerci relatively large.

Seminal capsules oval. Spermathecal ducts slightly curved.

Einfeldia Kieff.
(Fig. 78E, F; Rodova 1971a fig. 11, 12, 17; Oliver 1971 fig. 7)

Species examined: *E. pagana* (Meig.)

Gca VIII rounded caudally, joined mesally anterior of vagina. Gp VIII divided into relatively large dorsomesal lobe and smaller ventrolateral lobe partially covered by dorsomesal lobe. Apodeme lobe covered by principal lobes, but well developed, with distinct microtrichia. T IX normal. Gc IX normal, with 2–6 setae. Segment X with about 5–9 setae on each side. Cerci normal.

Seminal capsules oval. Spermathecal ducts nearly straight.

Xenochironomus Kieff.
(Fig. 83)

Species examined: *X. (X.) xenolabis* (Kieff.), *X. (Anceus) scopula* Town.

Gca VIII strong, rounded caudolaterally, weakly joined mesally anterior of vagina. Gp VIII divided into about equally large dorsomesal and ventrolateral lobes; dorsomesal lobe with distinct (subgenus *Xenochironomus)* to very indistinct (subgenus *Anceus* Rob.) orsomesal group shagreenation. Apodeme lobe relatively distinct, without microtrichia. T IX normal. Gc IX without setae. Segment X without setae in subgen. *Xenochironomus*, with a few on each side in subgen. *Anceus*. Cerci relatively large.

Labia with many distinct microtrichia in subgen. *Xenochironomus*, fewer and less distinct in subgen. *Anceus*. Seminal capsules ovoid. Spermathecal ducts straight.

Cladopelma Kieff.
(syn. *Cryptocladopelma* Lenz) (Fig. 84A–C)

Species examined: *C. viridula* (L.)

Gca VIII rounded caudally, joined mesally. Gp VIII divided into narrow dorsomesal lobe with oromesal group shagreenation and broad ventrolateral lobe. Apodeme lobe very weak. T IX normal. Gc IX normal, with one seta. Segment X with 1 or 2 setae on each side. Postgenital plate weak. Cerci normal.

Labia with very few, indistinct apical microtrichia. Seminal capsules ovoid. Spermathecal ducts straight.

Cryptotendipes Lenz
(Fig. 85)

Species examined: *C. casuarius* (Town.), *C. pseudotener* (Goetgh.), *C. darbyi* (Subl.)

Gca VIII rounded caudally, joined mesally. Gp VIII divided into dorsomesal lobe with distinct oromesal group shagreenation and well developed, elongate ventrolateral lobe with or without group shagreenation. Apodeme lobe very weak to more distinct. T IX normal. Gc IX with 1–3 setae. Segment X without setae. Postgenital plate triangular, relatively well developed. Cerci normal.

Labia with microtrichia. Seminal capsules very small, spherical to ovoid. Spermathecal ducts straight.

Key to examined females of *Cryptotendipes*

1 Ventrolateral lobe with distinct group shagreenation, about as wide at apex as dorsomesal lobe (Fig. 85D, E); apodeme lobe with basally branched apodeme; coxosternapodeme narrow with a mesal curve ..... *Cryptotendipes darbyi* (Subl.)

Ventrolateral lobe without distinct group shagreenation, as wide as or narrower than dorsomesal lobe at apex; apodeme lobe with simple apodeme; coxosternapodeme wider, sometimes with sharp angle or bend 2

2 Ventrolateral lobe distinctly more narrow than dorsomesal lobe at apex; coxosternapodeme strong, heavily sclerotized, with sharp anterior angle (Fig. 85G) .... *Cryptotendipes pseudotener* (Goetgh.)

Ventrolateral lobe at most slightly more narrow than dorsomesal lobe (Fig. 85A–C); coxosternapodeme moderately strong, nearly straight .... *Cryptotendipes casuarius* (Town.)

Microchironomus Kieff.
(syn. *Leptochironomus* Pag.) (Fig. 84D, E; Sæther 1977)

Species examined: *M. nigrovittatus* (Mall.)

Gca VIII curved caudally, joined mesally. Gp VIII divided into dorsomesal lobe with oromesal group shagreenation, and long, narrow, ventrolateral lobe with long apical microtrichia lying in longitudinal direction of lobe. (If ventrolateral lobe is turned it will, however, appear quite wide.) Apodeme lobe very weak. T IX normal. Gc IX with one seta. Segment X with about 2 setae on each side. Postgenital plate normal, triangular. Cerci small.

Labia without microtrichia. Seminal capsules oval. Spermathecal ducts straight.

Parachironomus Lenz
(Fig. 86, 87)

Species illustrated: *P. frequens* (Joh.), *P. bacilliger* (Kieff.), *P. abortivus* (Mall.), *P. potamogeti* (Town.), *Parachironomus* sp. *A*, *Parachironomus* sp. *B*

Gca VIII rounded caudally, occasionally with weak branch at base of dorsomesal lobe of Gp VIII, usually weak and not joined mesally, occasionally meets mesally. Gp VIII divided into dorsomesal lobe with distinct oromesal group shagreenation and usually long, well-developed ventrolateral lobe with indication of group shagreenation of microtrichia; ventrolateral lobe occasionally reduced and with very few microtrichia. Apodeme lobe usually weak. T IX normal. Gc IX with 0–3 setae, usually without setae. Segment X with 2 to several setae on each side. Postgenital plate normal, triangular. Cerci normal.

Labia with indistinct and few, to very distinct and many microtrichia. Seminal capsules ovoid to oval. Spermathecal ducts straight or nearly straight.

Parachironomus bacilliger (Kieff.), *Parachironomus abortivus* (Mall.), *Parachironomus carinatus* (Town.), *Parachironomus potamogeti* (Town.), *Parachironomus frequens* (Joh.), and *Parachironomus* sp. *A* all have essentially the same type principal lobes of Gp VIII; however, the apical microtrichia of the ventrolateral lobe are considerably shorter in *P. frequens* and the whole lobe is apparently shorter in *P. carinatus* (not a good specimen). *P.* sp. *A* has one seta on Gc IX, *P. potamogeti* 0 or 1, and the others none. *P. potamogeti* and *P. frequens* have about 6 setae on each side of segment X and the others have 2. *Parachironomus* sp. *B.* differs from the other species by having a strongly reduced ventrolateral lobe, 2 or 3 setae on Gc IX, and 3 or 4 setae on each side of segment X. Its pupa is a typical *Parachironomus* of the *varus* group in the sense of Lenz (1954–1962 p. 201). Its presumed larva (Fig. 87G), however, is very atypical and shows some relationship with *Paracladopelma*. The species possibly deserves subgeneric rank.

Paracladopelma Harn.
(Fig. 88)

Species illustrated: *P. laminata* (Kieff.), *P.* cf. *undine* (Town.)

Gca VIII strong, characteristic. Gp VIII divided into dorsomesal lobe with oromesal group shagreenation, and ventrolateral lobe partially hidden by dorsomesal lobe. Apodeme lobe weak. T IX normal. Gc IX without setae. Segment X with 2–6 setae on each side. Postgenital plate triangular with broad base. Cerci normal.

Labia with weak microtrichia. Seminal capsules relatively small, oval. Spermathecal ducts straight.

The 2 species illustrated have nearly identical female genitalia and very similar male genitalia (Goetghebuer 1937–54 fig. 112; Townes 1945 fig. 168), but differ in coloration.

The genera *Acalcarella* Shil. (Shilova 1955 p. 319–322) and possibly *Cyphomella* Sæth. (Sæther 1977) probably form the sister group of *Paracladopelma* and possibly *Beckia*, Sæth. However, the females of all genera except *Paracladopelma* remain undescribed. The exact placement of these genera, as well as a number of larval and pupal types of the *Harnischia* complex with unassociated adults, remains uncertain.

Harnischia Kieff.
(Fig. 89A, B)

Species examined: *H. curtilamellata* (Mall.)

Gca VIII weak, rounded caudolaterally, not clearly joined mesally. Gp VIII divided into dorsomesal lobe with extensive oromesal group shagreenation, and ventrolateral lobe with only a few weak caudomesal microtrichia. Apodeme lobe normal. T IX normal. Gc IX with 2 setae. Segment X with about 2–4 setae on each side. Postgenital plate rounded, not triangular. Cerci relatively small.

Labia with distinct microtrichia. Seminal capsules ovoid. Spermathecal ducts straight.

Chernovskiia Sæth.
(Fig. 88C–E; Sæther 1977 fig. 41)

Species examined: *C. amphitrite* (Town.)

Gca VIII relatively strong, rounded caudally, not clearly joined mesally. Gp VIII divided into dorsomesal lobe with oromesal group shagreenation, and ventrolateral lobe without caudolateral microtrichia, but with numerous oral, oromesal, and caudomesal microtrichia. Apodeme lobe normal. T IX normal. Gc IX with 2 setae. Segment X with 1 or 2 setae on each side. Postgenital plate small, rounded. Cerci relatively small.

Labia with distinct microtrichia. Seminal capsules ovoid. Spermathecal ducts straight.

Cryptochironomus Kieff.
(Fig. 90A–D)

Species examined: *C.* cf. *digitatus* (Mall.), *C.* cf. *stylifera* (Joh.), *C. ponderosus* (Subl.)

Gca VIII rounded laterally, nearly straight at base of Gp VIII, joined mesally. Gp VIII divided into dorsomesal lobe with oromesal group shagreenation, and very broad long ventrolateral lobe nearly straight on mesal margin, slightly convex on outer margin. Apodeme lobe weak. T IX normal. Gc IX with 0 or 1 seta, with strong microtrichia. Segment X with several setae. Postgenital plate normal, triangular. Cerci relatively large.

Labia with a few microtrichia. Seminal capsules ovoid. Spermathecal ducts straight.

Of the 3 species examined, *Cryptochironomus* cf. *stylifera* (Joh.) (syn. *C. psittacinus* Town. nec Meig.) differs from *Cryptochironomus* cf. *digitatus* (Mall.) only by a seta on each Gc IX. *Cryptochironomus ponderosus* (Subl.) has a slightly different ventrolateral lobe (Fig. 90D) from the other 2 species.

Demicryptochironomus Lenz
(Fig. 90E, F)

Species examined: *D. vulneratus* (Zett.)

Gca VIII strong and straight laterally, rounded caudally, weaker, and joined mesally. Gp VIII divided into large dorsomesal lobe with oromesal group shagreenation, and large ventrolateral lobe nearly as wide as long with a mesal concavity and lateral notch. Apodeme lobe weak. T IX normal. Gc IX without setae. Segment X with several setae. Postgenital plate nearly parallel-sided at base, triangular at apex. Cerci large.

Labia with distinct microtrichia. Seminal capsules small, spherical, with short, funnel-shaped neck. Spermathecal ducts straight.

The immatures of *Robackia* Sæth. (Sæther 1977) indicate a relationship wih *Demicryptochironomus*. The males, however, seem to show closer relationship with *Paracladopelma* and *Parachironomus*, respectively. The undescribed female will probably resolve the problem of where to place this genus.

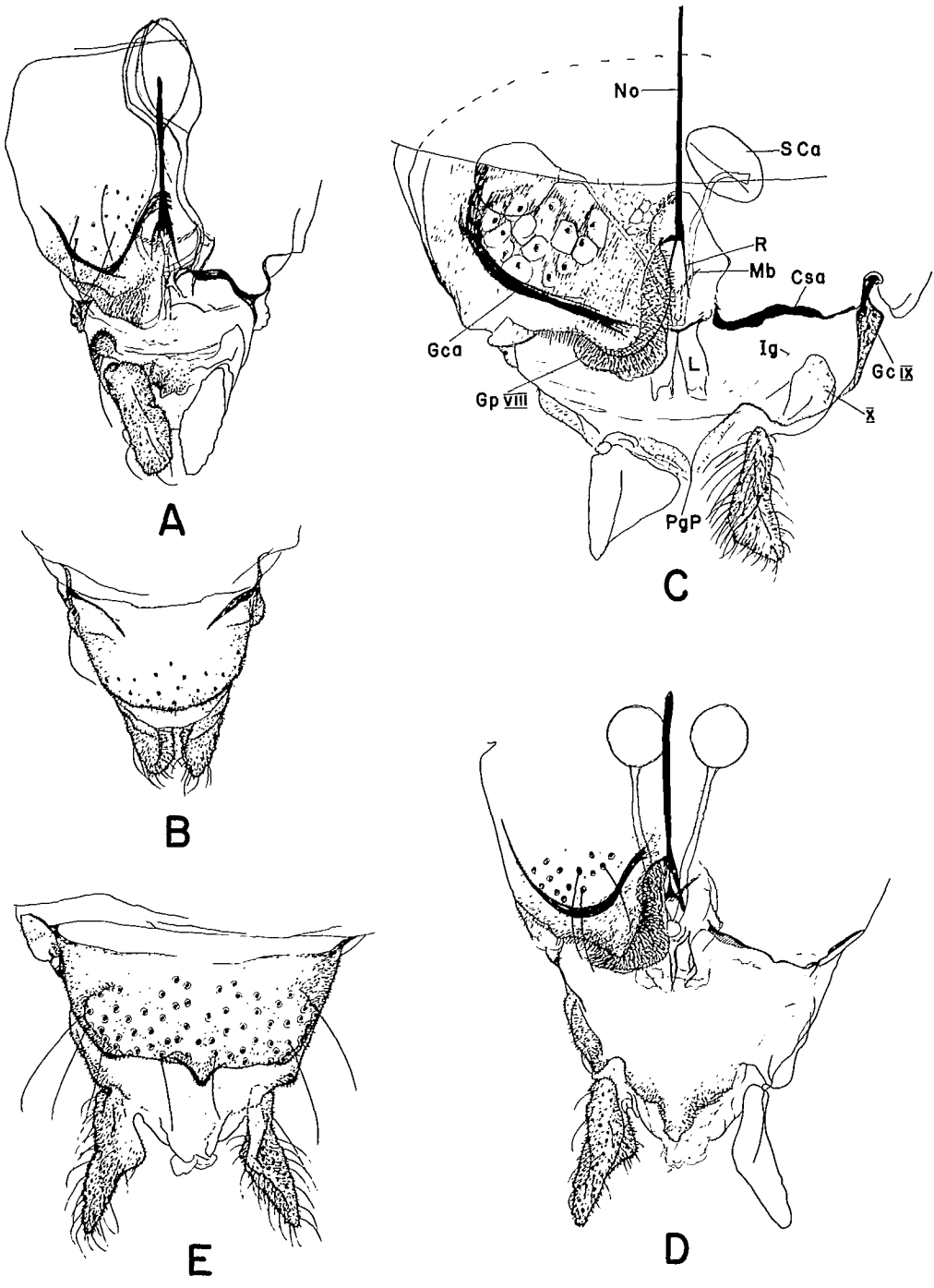

FIG. 72. Female genitalia of Chironomini, Chironominae. A–B, *Paratendipes albimanus* (Meig.): A) ventral; B) dorsal. C, *Microtendipes pedellus pedellus* (De Geer), ventral. D–E, *Microtendipes chloris* (Meig.): D) ventral; E) dorsal.

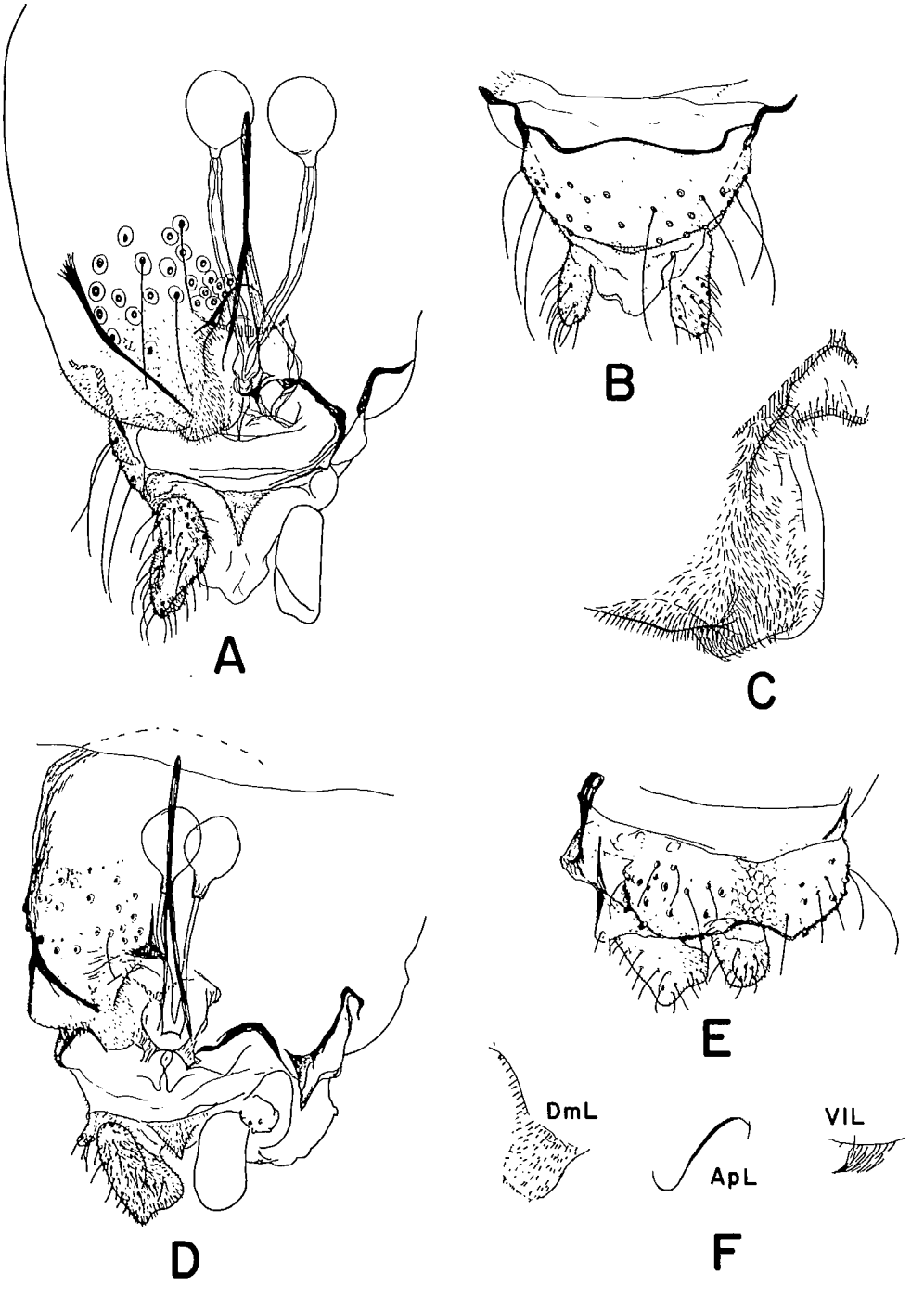

FIG. 73. Female genitalia of Chironomini. A–C, *Nilothauma* sp.n.: A) ventral; B) dorsal; C) Gp VIII. D–F, *Lauterborniella varipennis* (Coq.): D) ventral; E) dorsal; F) lobes of Gp VIII.

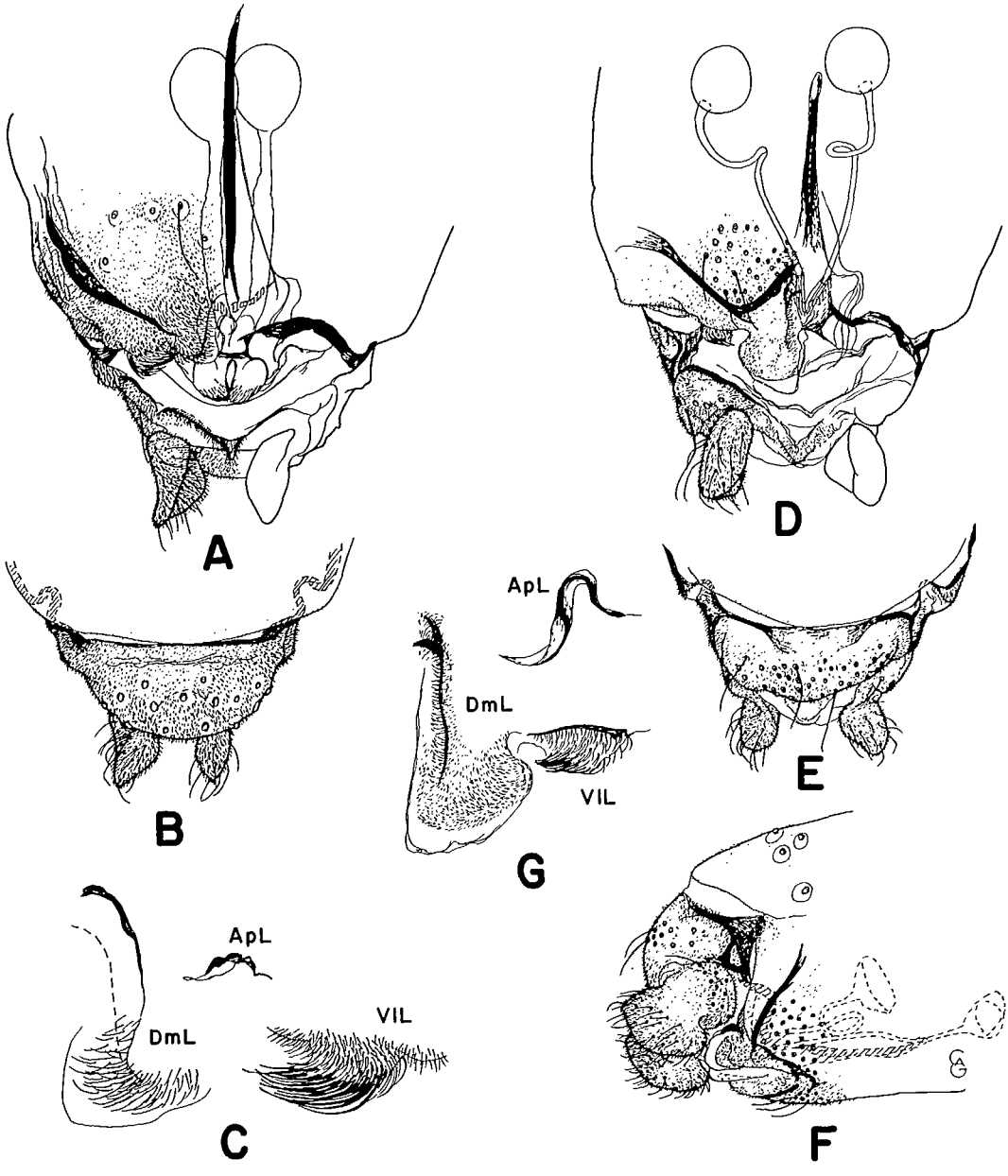

FIG. 74. Female genitalia of Chironomini. A–C, *Paralauterborniella nigrohalterale* (Mall.): A) ventral; B) dorsal; C) lobes of Gp VIII. D–G, *Graceus* near *ambiguus* Goetgh.: D) ventral; E) dorsal; F) lateral; G) lobes of Gp VIII.

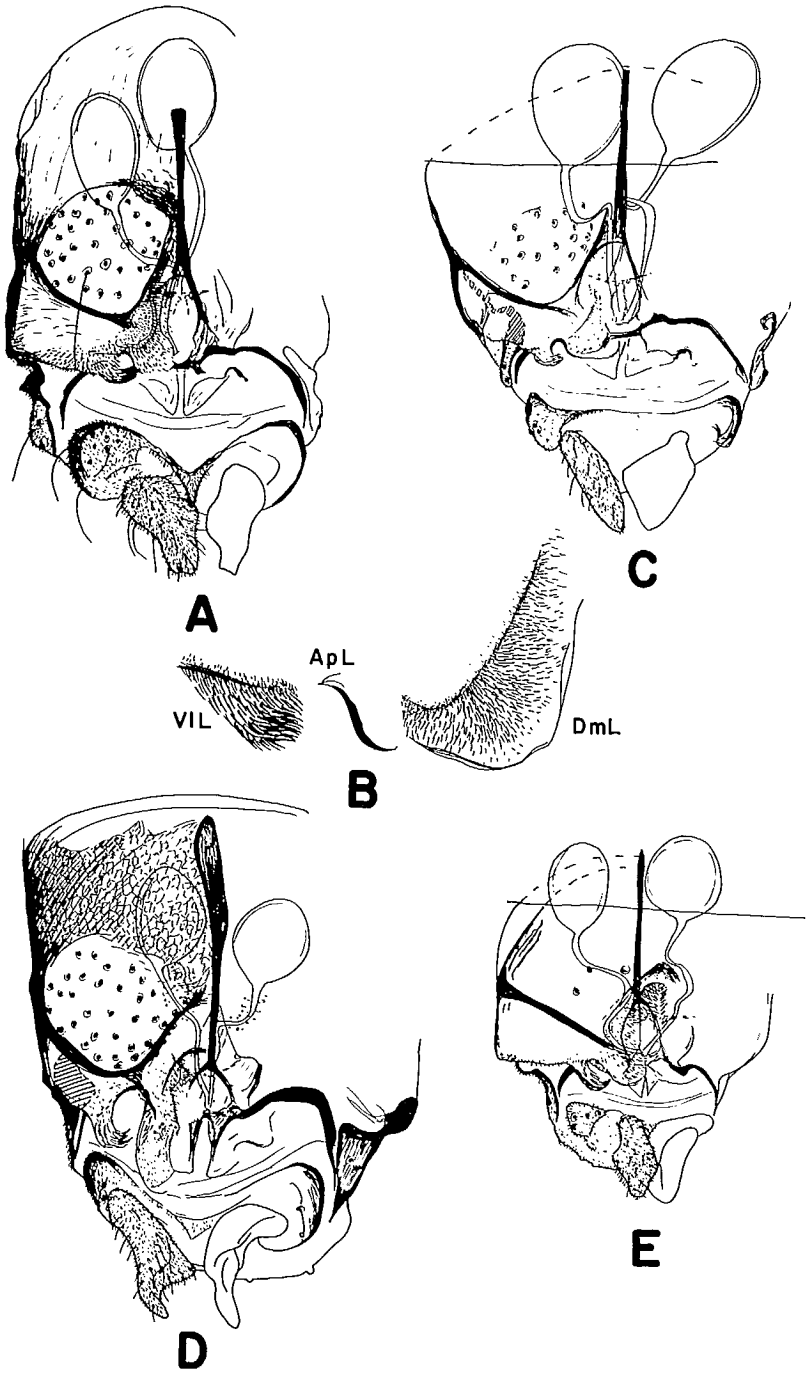

FIG. 75. Female genitalia of Chironomini. A, *Phaenopsectra obediens* (Joh.), ventral. B, *Phaenopsectra coracina* (Zett.), lobes of Gp VIII. C, *Phaenopsectra punctipes* (Wied.), ventral. D, *Tribelos* cf. *protextus* (Town.), ventral. E, *Pagastiella ostansa* (Webb), ventral.

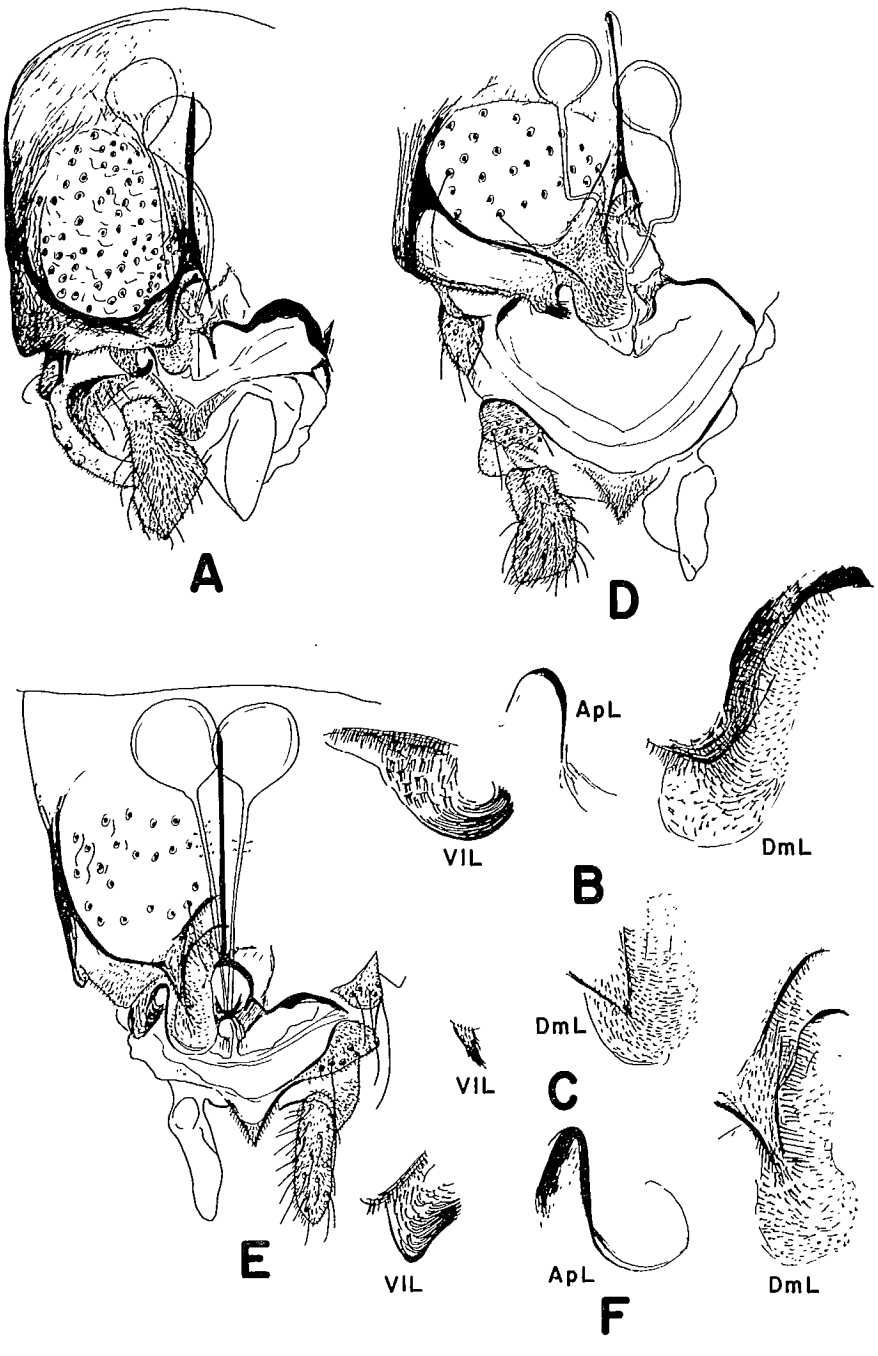

FIG. 76. Female genitalia of *Polypedilum* spp., Chironomini. A–B, *P. (P:) nubeculosum* (Meig.): A) ventral; B) lobes of Gp VIII. C, *P. (P.) illinoense* (Mall.), lobes of Gp VIII. D, *P. (Pentapedilum) tritum* (Walk.), ventral. E–F, *P. (Tripodura) simulans* (Town.): E) ventral; F) lobes of Gp VIII.

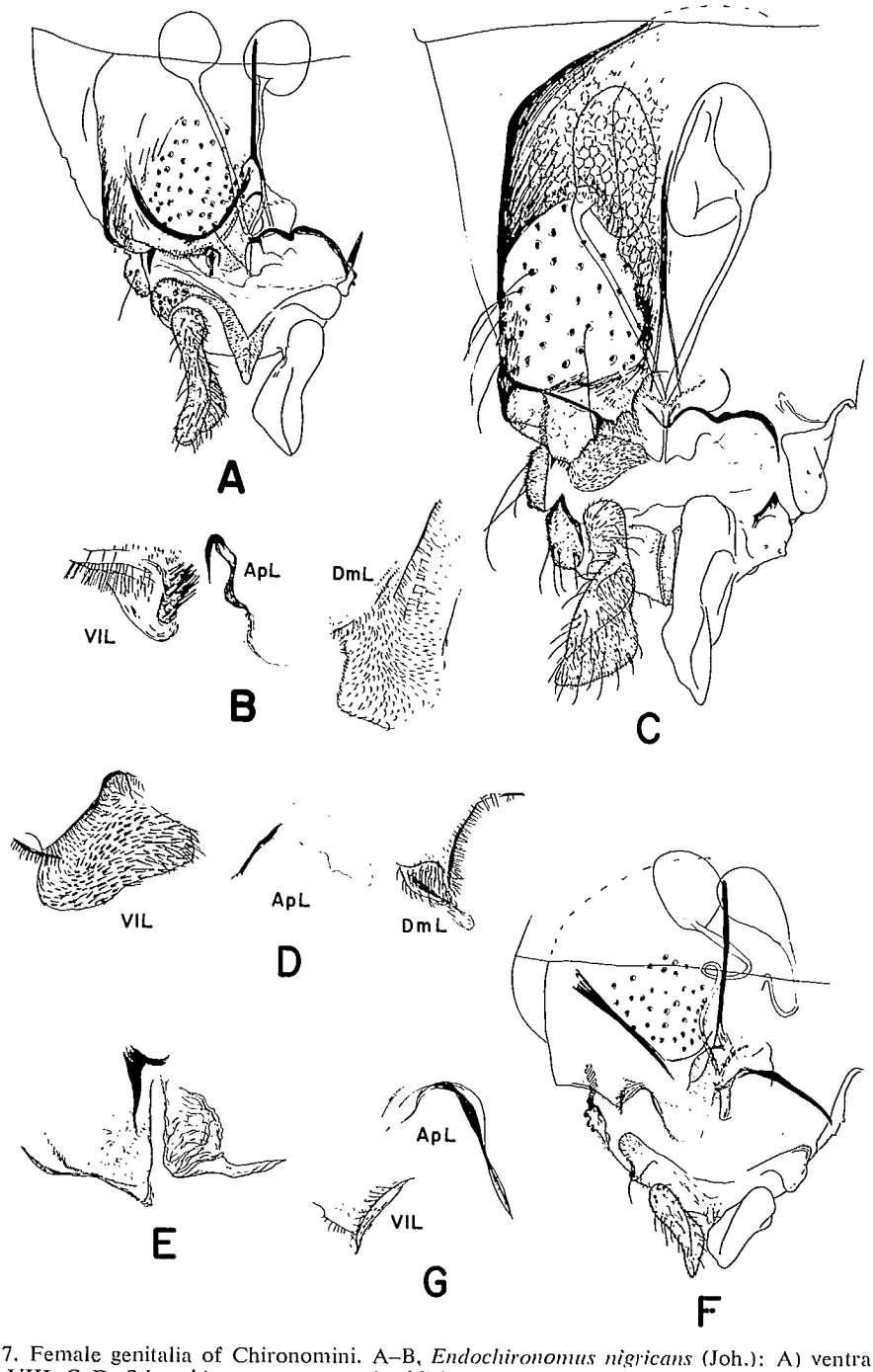

FIG. 77. Female genitalia of Chironomini. A–B, *Endochironomus nigricans* (Joh.): A) ventral; B) lobes of Gp VIII. C–D, *Stictochironomus rosenschoeldi* (Zett.): C) ventral; D) lobes of Gp VIII. E, *Stictochironomus crassiforceps* (Kieff.), labia. F–G, *Stenochironomus taeniapennis* (Coq.): F) ventral; G) ventrolateral and apodeme lobes of Gp VIII.

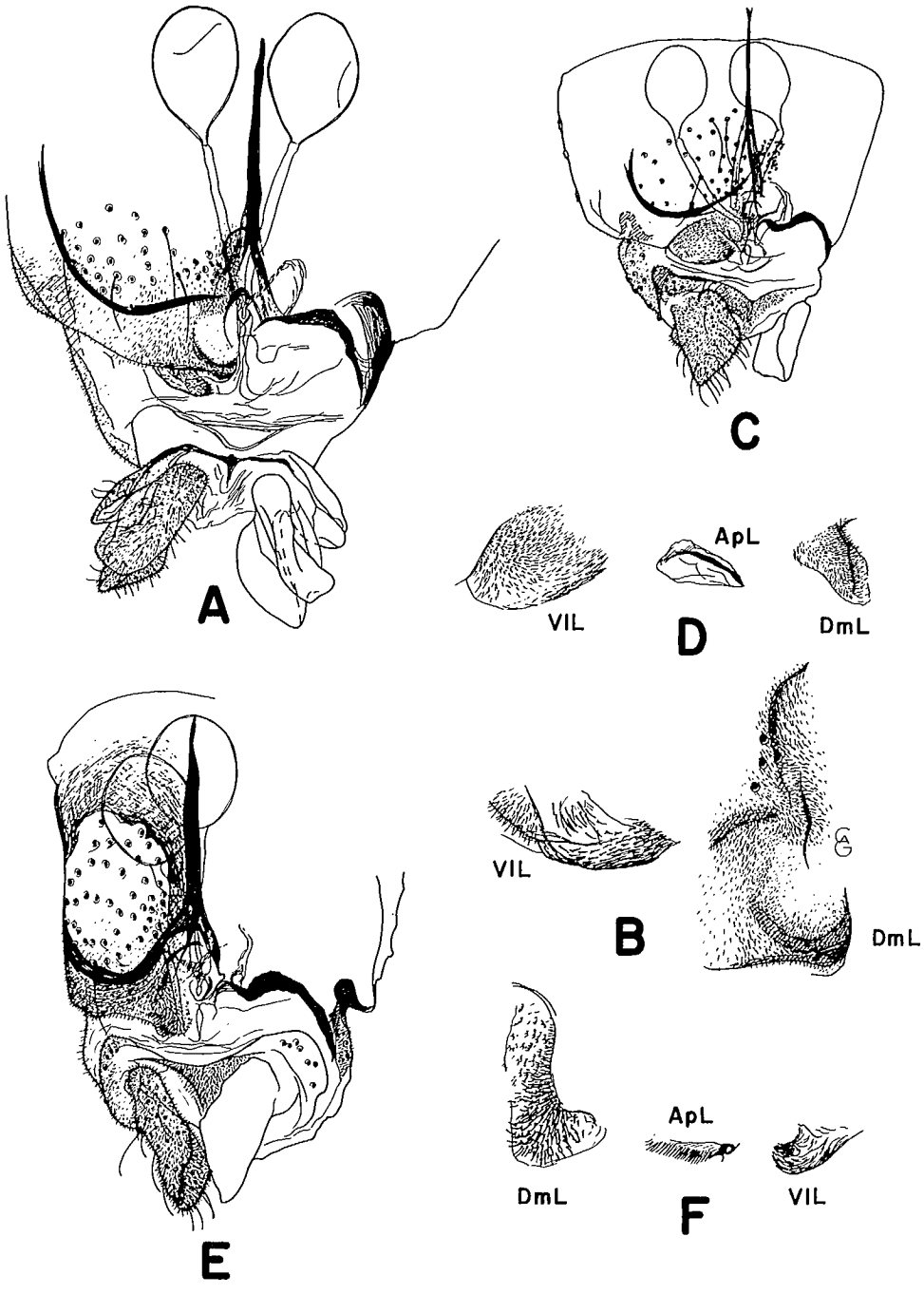

FIG. 78. Female genitalia of Chironomini. A–B, *Fleuria lacustris* Kieff.: A) ventral; B) lobes of Gp VIII. C–D, *Goeldichironomus holoprasinus* (Goeldi): C) ventral; D) lobes of Gp VIII. E–F, *Einfeldia pagana* (Meig.): E) ventral; F) lobes of Gp VIII.

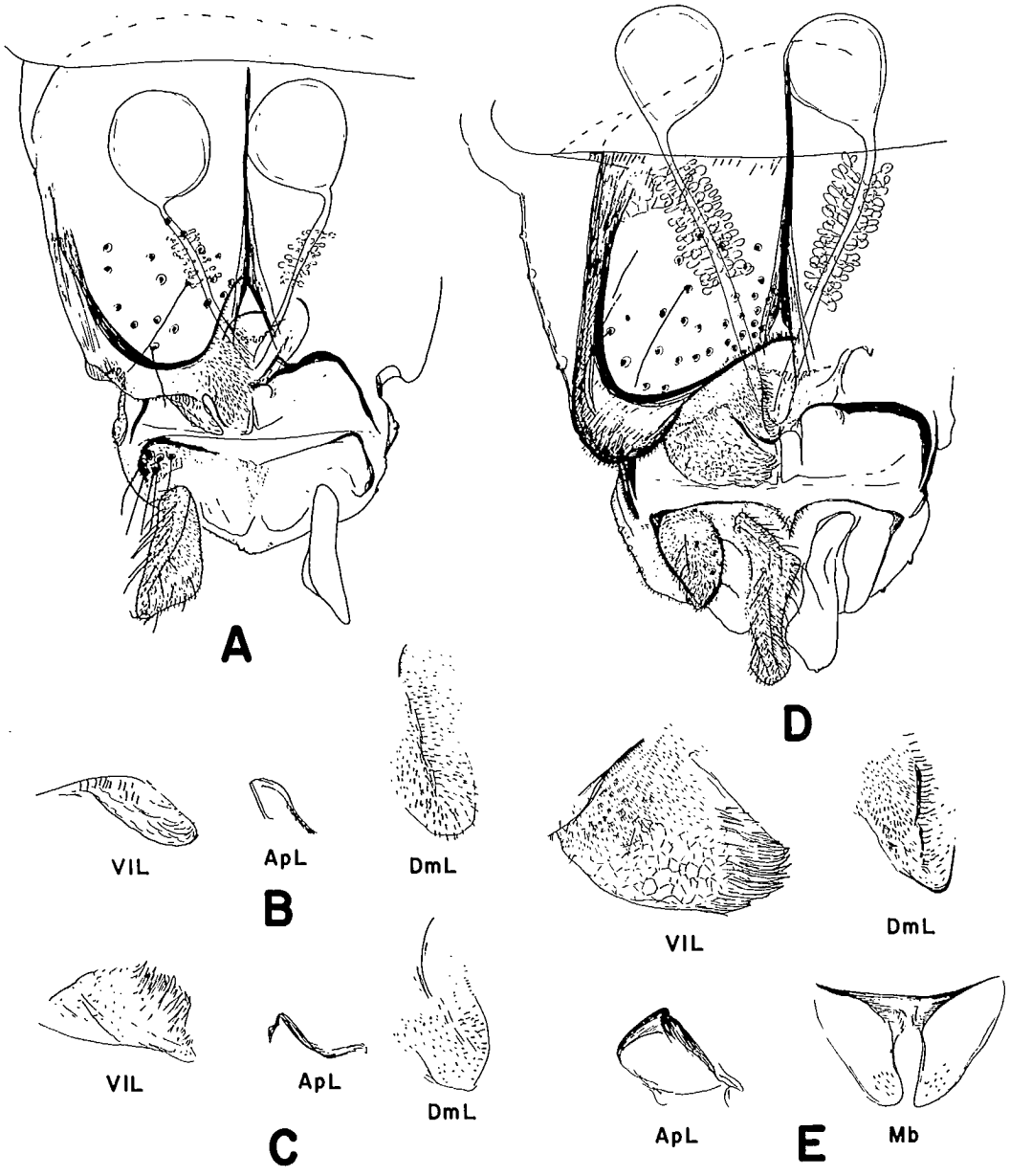

FIG. 79. Female genitalia of Chironomini. A–B, *Dicrotendipes* cf. *modestus* (Say): A) ventral; B) lobes of Gp VIII. C, *Dicrotendipes botaurus* (Town.), lobes of Gp VIII. D–E, *Nilodorum devineyae* E. C. Beck: D) ventral; E) lobes of Gp VIII.

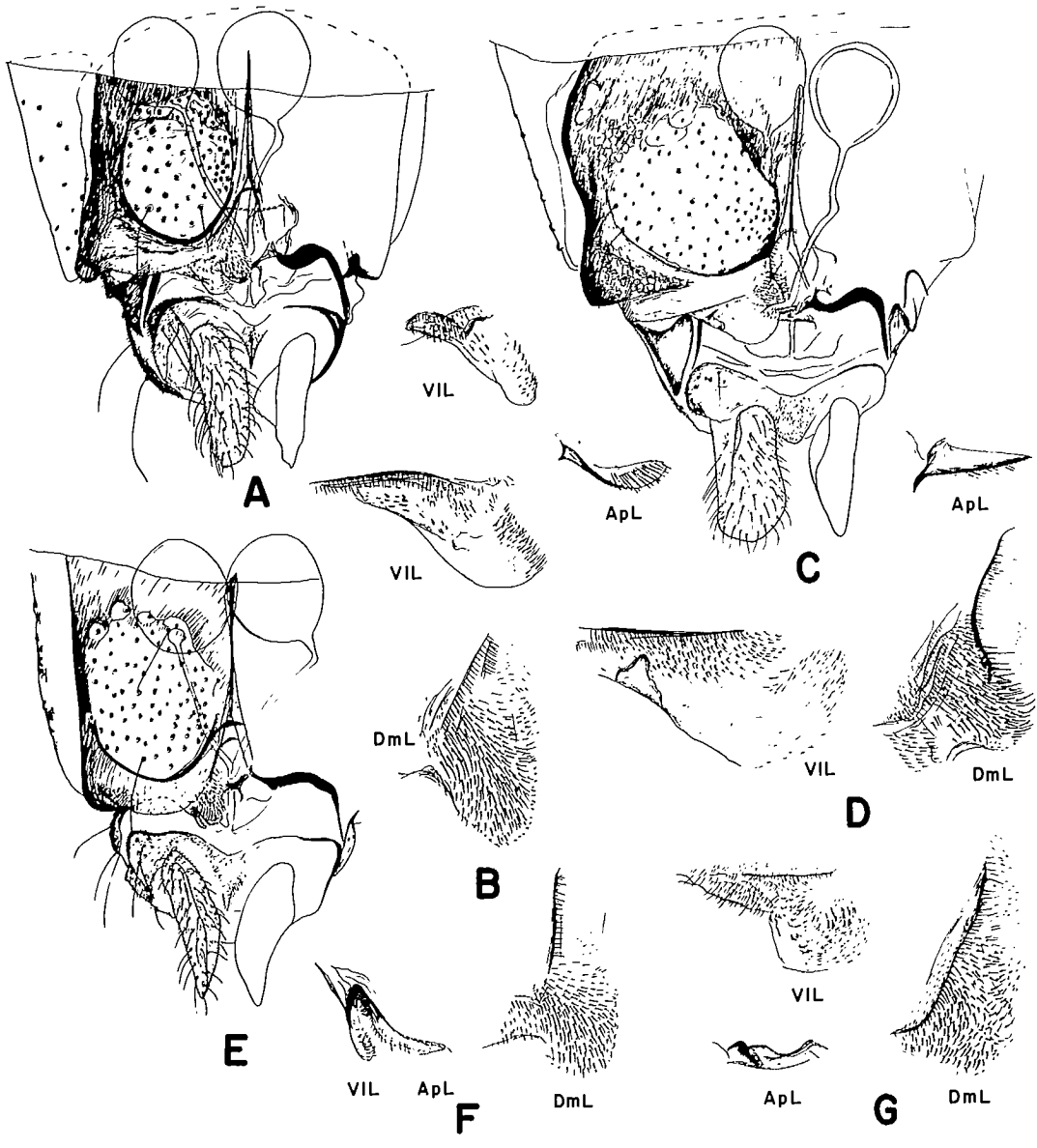

FIG. 80. Female genitalia of *Glyptotendipes* spp., Chironomini. A–B, *G. (Phytotendipes) paripes* (Edw.): A) ventral; B) lobes of Gp VIII, with variation of ventrolateral lobe partly caused by position. C–D, *G. (Phytotendipes) barbipes* (Staeg.): C) ventral; D) lobes of Gp VIII. E–F, *G. (Phytotendipes) lobiferus* (Say): E) ventral; F) lobes of Gp VIII. G, *G. (Demeijerea) brachialis* (Coq.), lobes of Gp VIII.

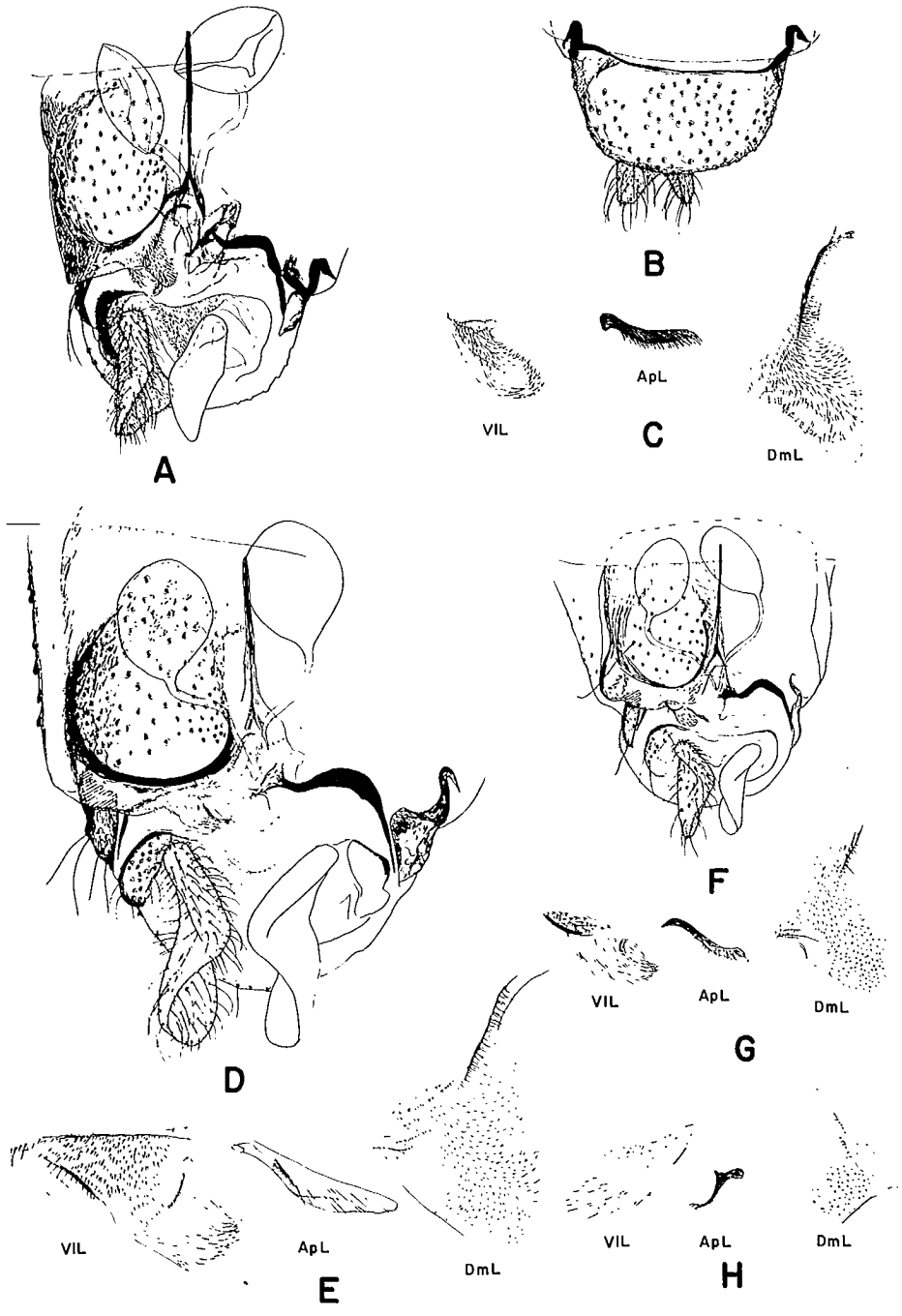

FIG. 81. Female genitalia of *Chironomus (Chironomus)* spp., Chironomini. A–C, *C. (C.)* cf. *atrella* (Town.): A) ventral; B) dorsal; C) lobes of Gp VIII. D–E, *C. (C.) plumosus* (L.) fa *semireductus* Lenz: D) ventral; E) lobes of Gp VIII. F–G, *C. (C.) decorus* (Joh.): F) ventral; G) lobes of Gp VIII. H, *C. (C.) halophilus* Kieff., lobes of Gp VIII.

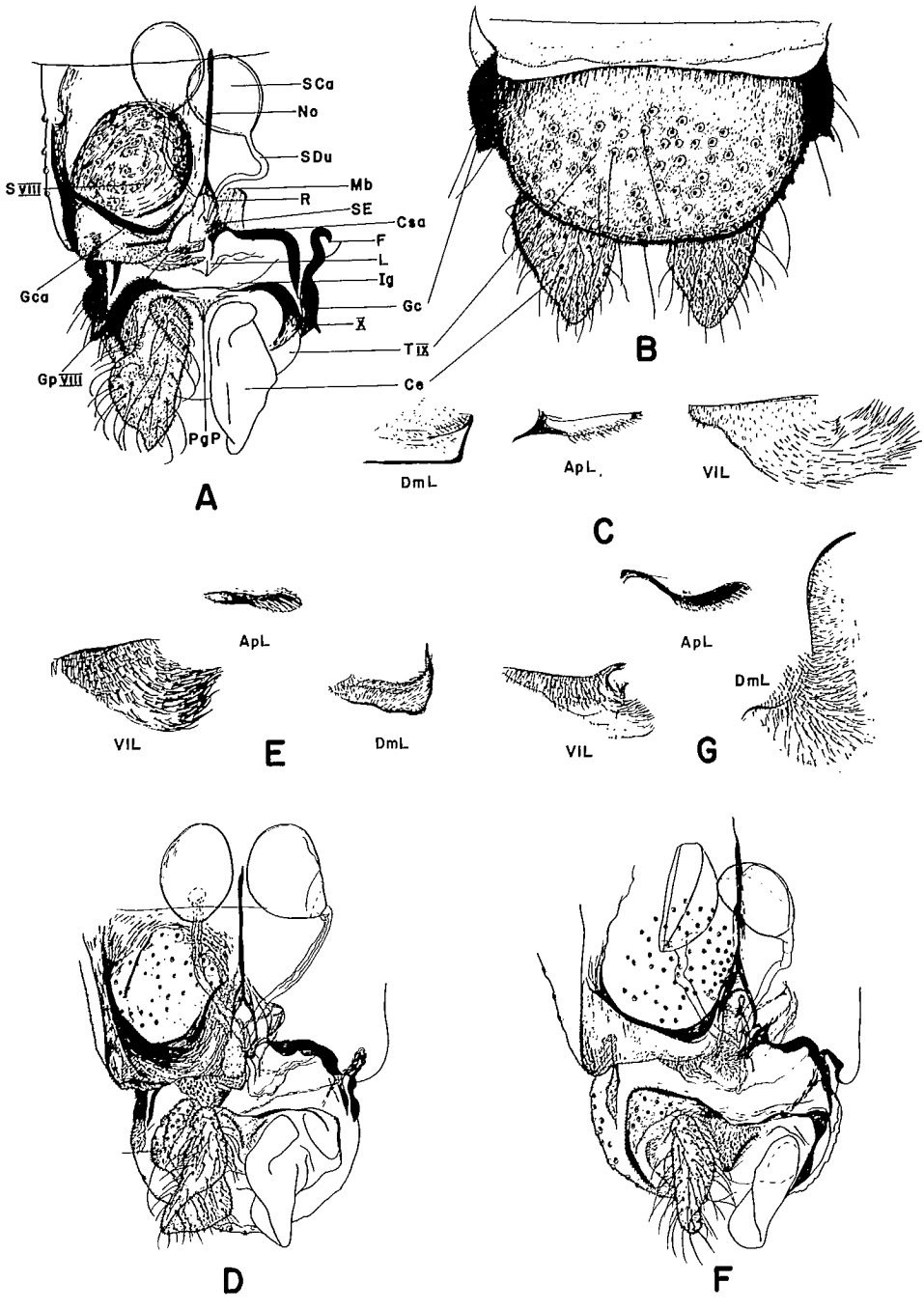

FIG. 82. Female genitalia of Chironomini. A–C, *Chironomus (Camptochironomus) tentans* Fabr.: A) ventral; B) dorsal; C) lobes of Gp VIII. D–E, *Chironomus (Camptochironomus) pallidivittatus* Mall: D) ventral; E) lobes of Gp VIII. F–G, *Kiefferulus dux* (Joh.): F) ventral; G) lobes of Gp VIII.

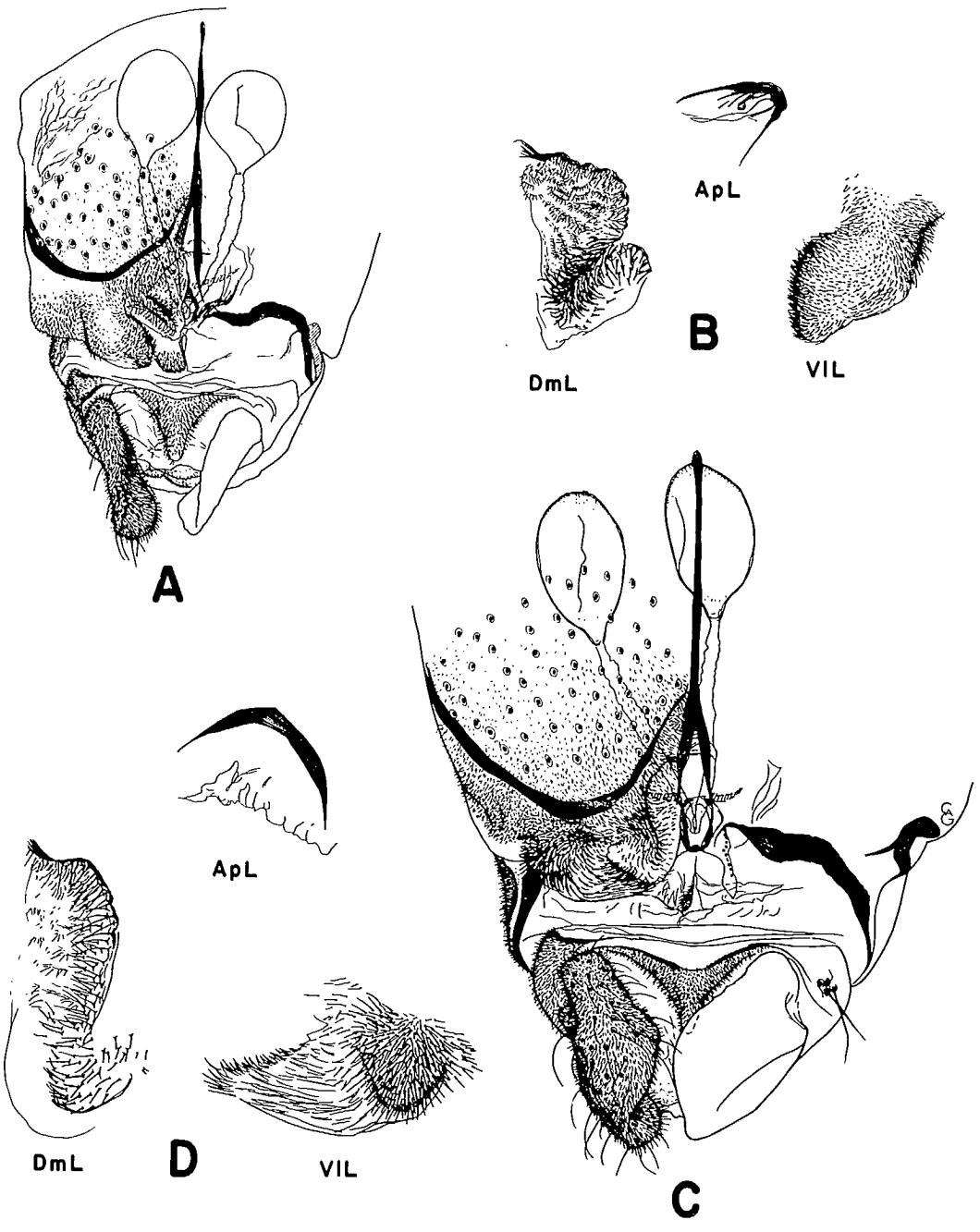

FIG. 83. Female genitalia of *Xenochironomus* spp., Chironomini. A–B, *X. (X.) xenolabis* (Kieff.): A) ventral; B) lobes of Gp VIII. C–D, *X. (Anceus) scopula* Town.: C) ventral; D) lobes of Gp VIII.

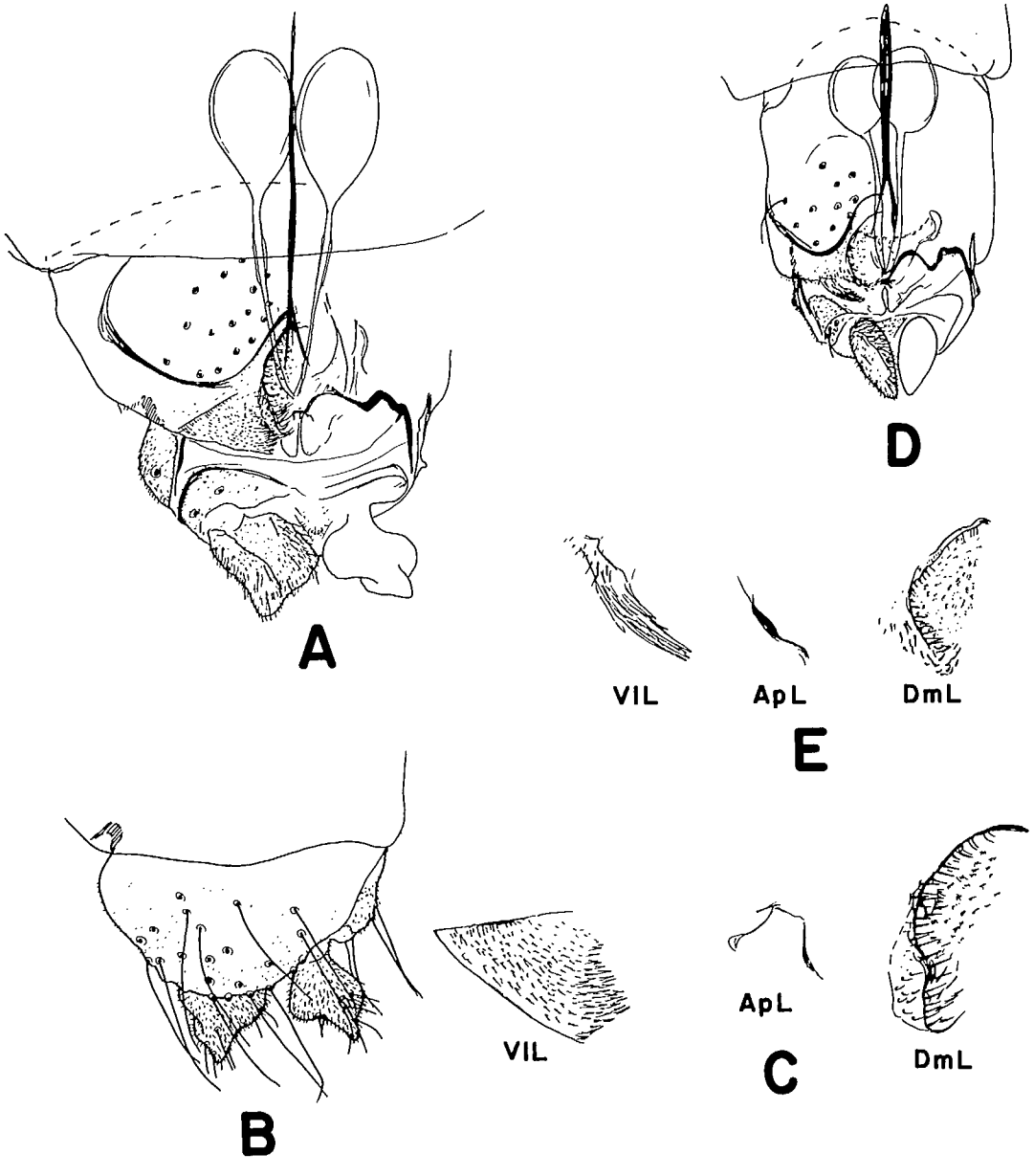

FIG. 84. Female genitalia of Chironomini. A–C, *Cladopelma viridula* (L.): A) ventral; B) dorsal; C) lobes of Gp VIII. D–E, *Microchironomus nigrovittatus* (Mall.): D) ventral; E) lobes of Gp VIII.

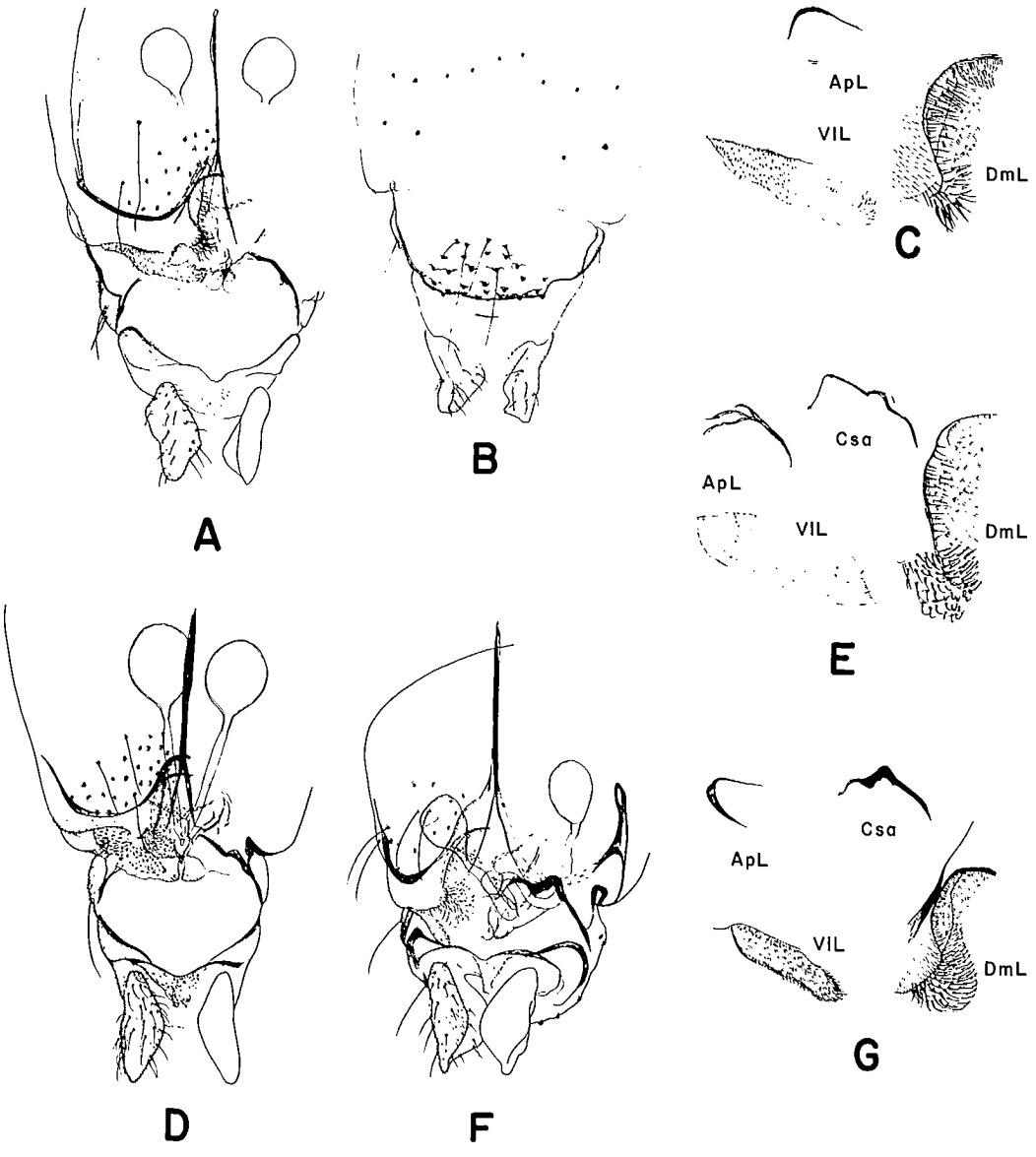

FIG. 85. Female genitalia of *Cryptotendipes* spp., Chironomini. A–C, *C. casuarius* (Town.): A) ventral; B) dorsal; C) lobes of Gp VIII. D–E, *C. darbyi* (Subl.): D) ventral; E) coxosternapodeme and lobes of Gp VIII. F–G, *C. pseudotener* (Goetgh.): F) ventral; G) coxosternapodeme and lobes of Gp VIII.

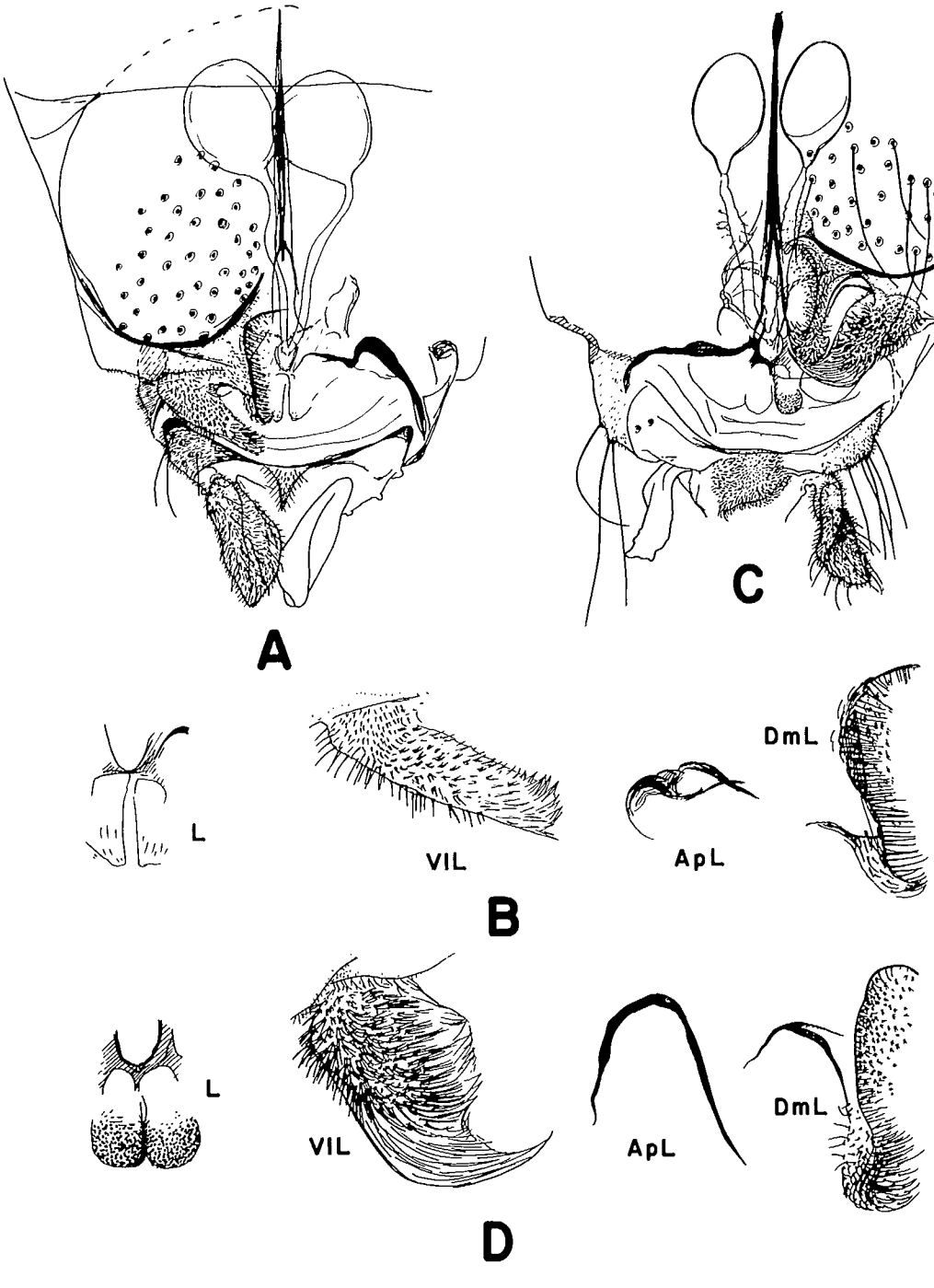

FIG. 86. Female genitalia of *Parachironomus* spp., Chironomini. A–B, *P. frequens* (Joh.): A) ventral; B) labia and lobes of Gp VIII. C–D, *P. bacilliger* (Kieff.): C) ventral; D) labia and lobes of Gp VIII.

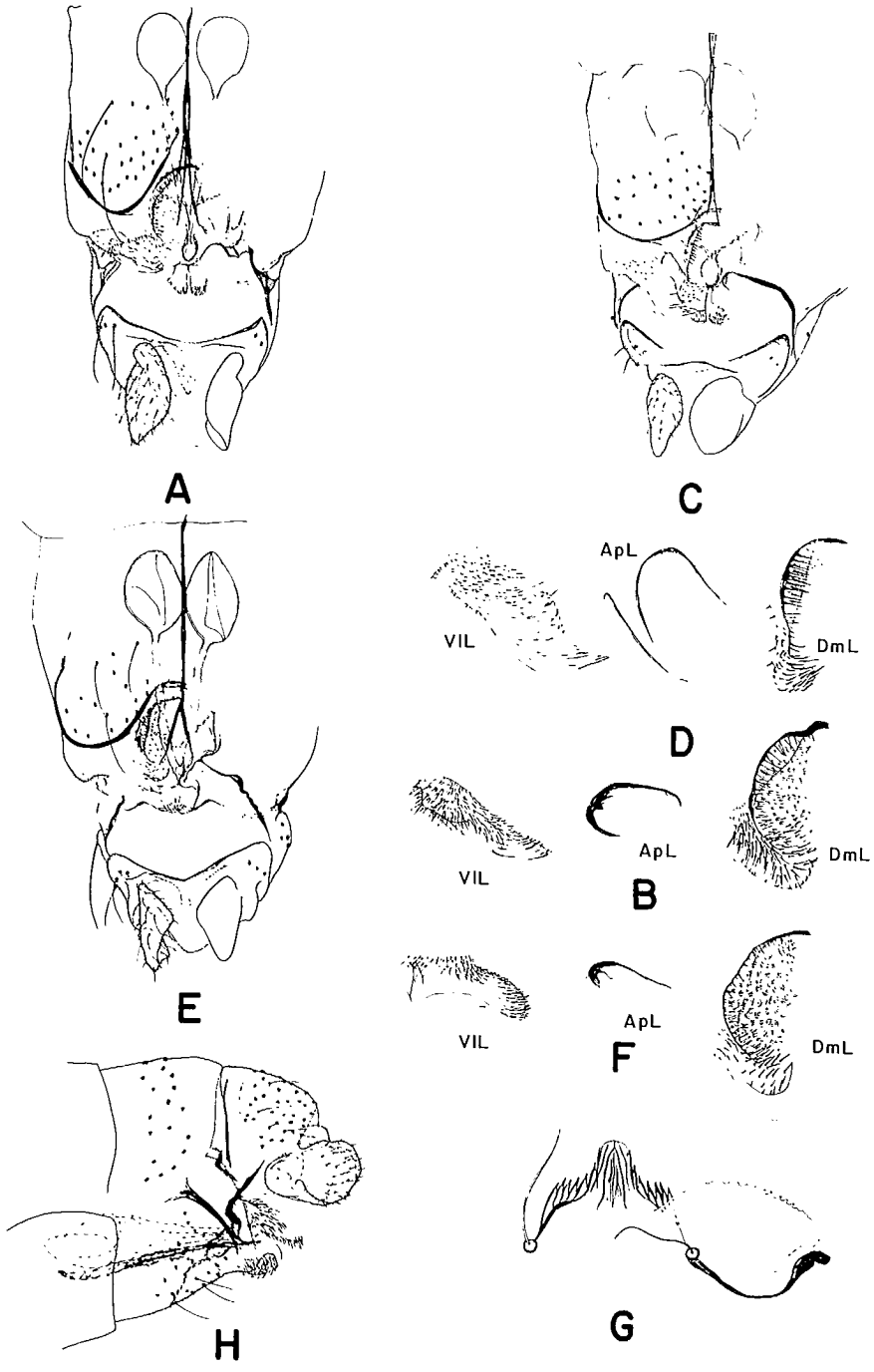

FIG. 87. *Parachironomus* spp., Chironomini. A–F, H, female genitalia. A–B, *P. abortivus* (Mall.): A) ventral; B) lobes of Gp VIII. C–D, *Parachironomus* sp. *A:* C) ventral; D) lobes of Gp VIII. E–G, *Parachironomus* sp. *B:* E) ventral; F) lobes of Gp VIII. G) larval mentum. H, *P. potamogeti* (Town.), lateral.

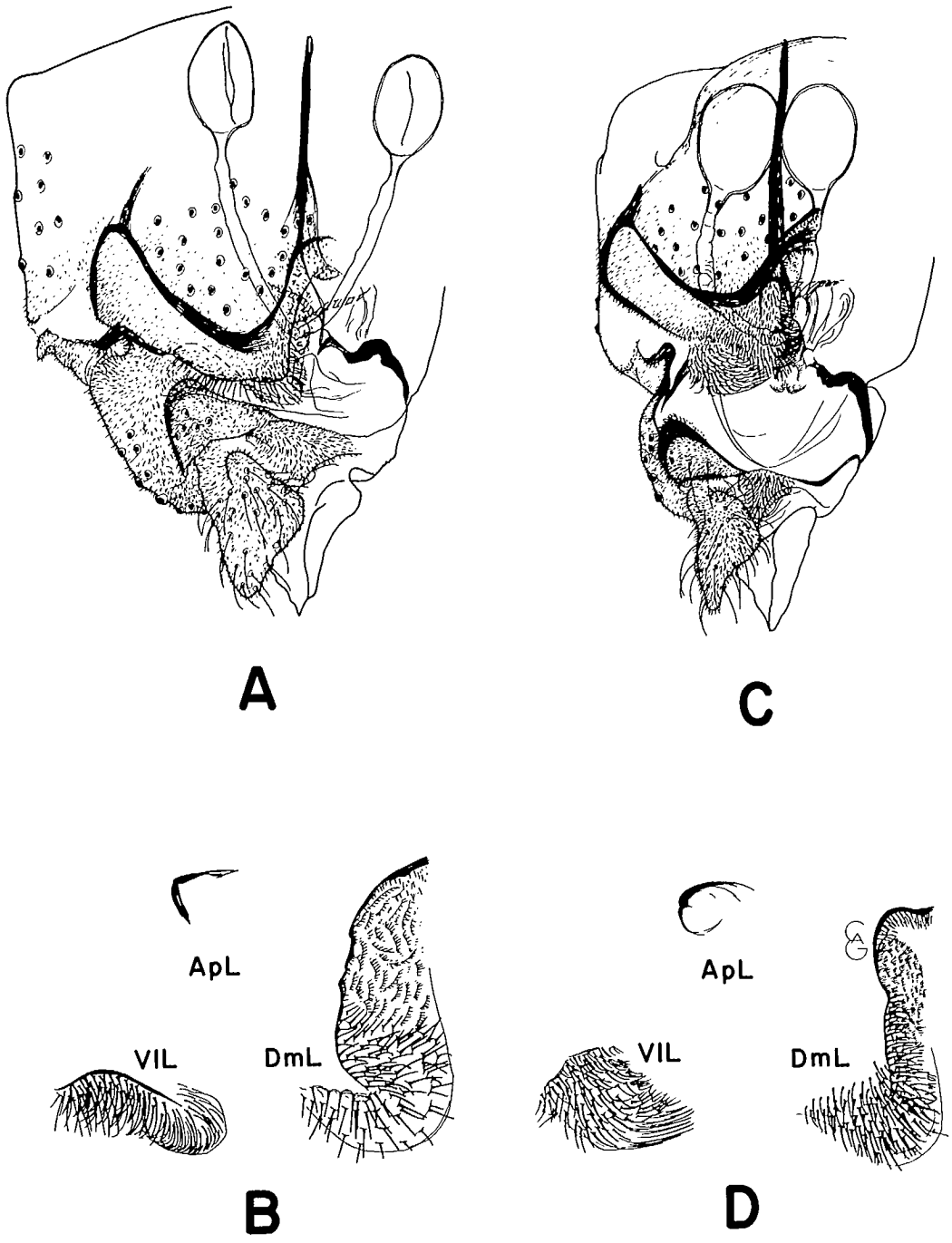

FIG. 88. Female genitalia of *Paracladopelma* spp., Chironomini. A–B, *P. laminata* (Kieff.): A) ventral; B) lobes of Gp VIII. C–D, *P.* cf. *undine* (Town.): C) ventral; D) lobes of Gp VIII.

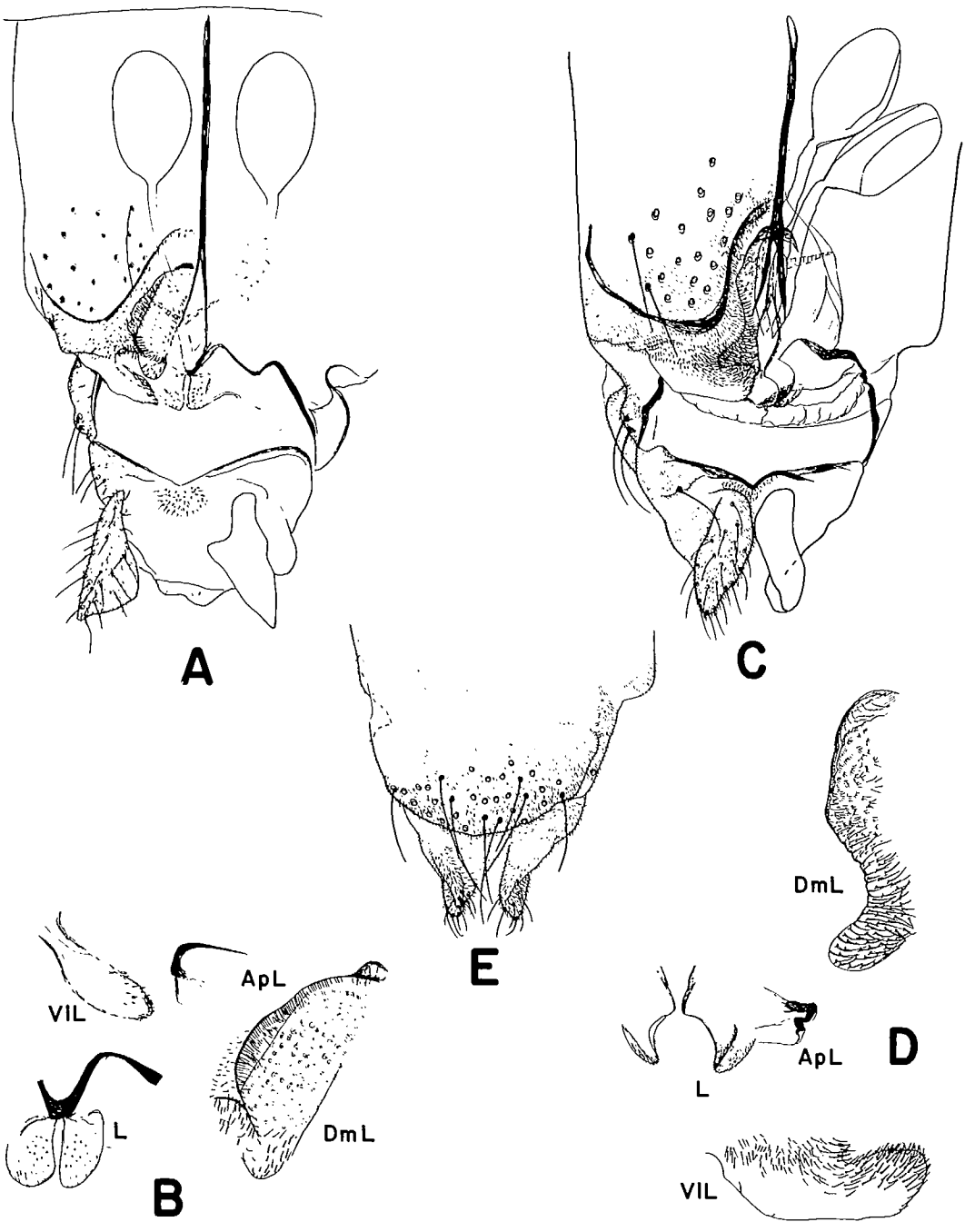

FIG. 89. Female genitalia of Chironomini. A–B, *Harnischia curtilamellata* (Mall.): A) ventral; B) lobes of Gp VIII and labia. C–E, *Chernovskiia amphitrite* (Town.): C) ventral; D) lobes of Gp VIII; E) dorsal.

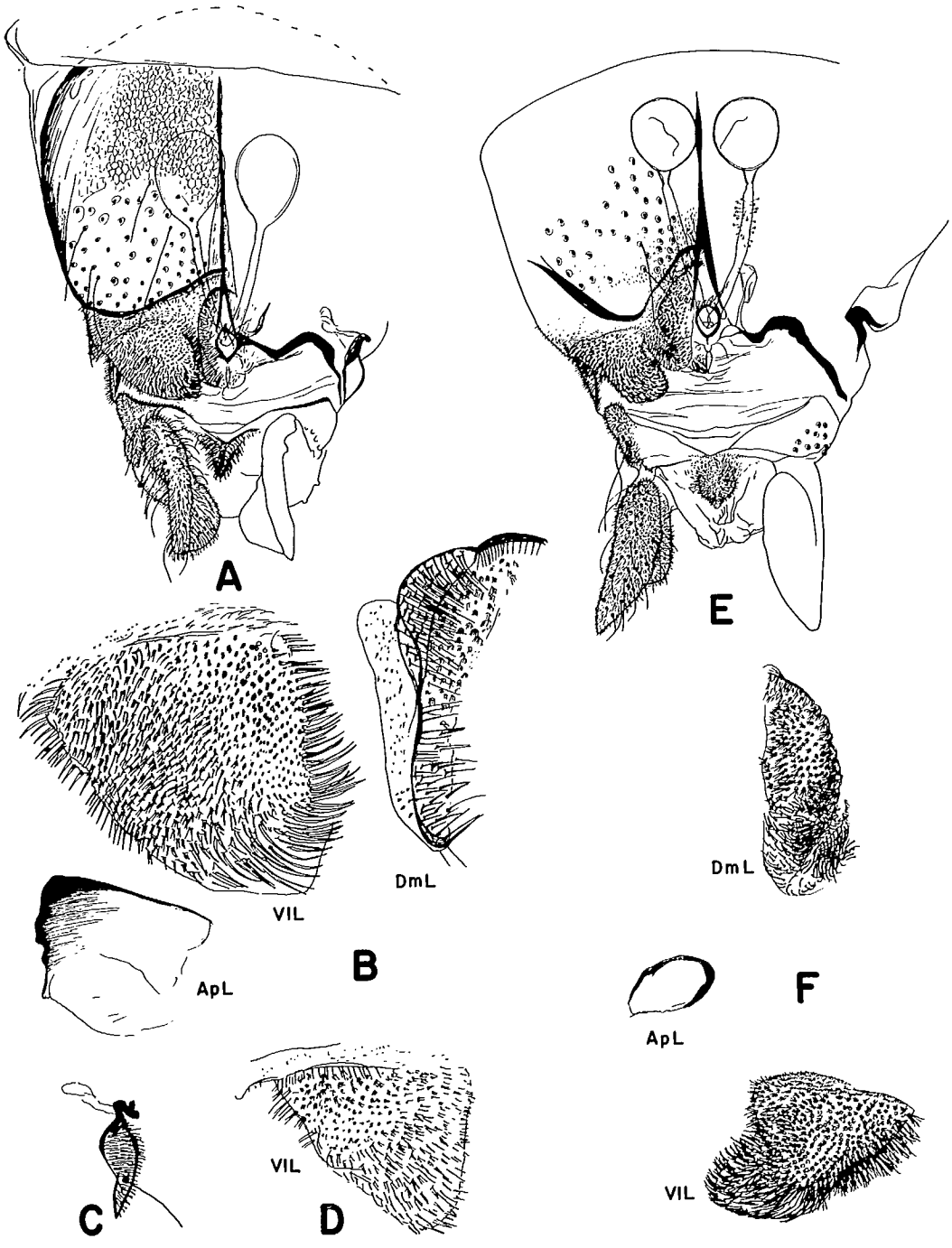

FIG. 90. Female genitalia of Chironomini. A–B, *Cryptochironomus* cf. *digitatus* (Mall.): A) ventral; B) lobes of Gp VIII. C, *Cryptochironomus* cf. *stylifera* (Joh.), Gc IX. D, *Cryptochironomus ponderosus* (Subl.), a ventrolateral lobe of Gp VIII. E–F, *Demicryptochironomus vulneratus* (Zett.): E) ventral; F) lobes of Gp VIII.

Summary

Normally T VIII is unmodified in Chironomidae. In the Telmatogetoninae, however, T VIII is strongly reduced. A floor formed by S VIII under the anterior part of the vagina can be found in *Nanocladius, Metriocnemus, Manoa,* and Tanytarsini. Only in *Afrochlus harrisoni* Freem. may S VIII possibly bear a gonocoxite (Gc VIII). However, Gc VIII is detectable as a gonocoxapodeme in Diamesinae, Orthocladiinae, Prodiamesinae, Chironominae, and some Tanypodinae. Gp VIII is, in the basic design, simple and well developed. It is still single and undivided in Tanypodinae, Aphroteniinae, Telmatogetoninae, Lobodiamesini, Boreoheptagyini, Protanypodini, *Chasmatonotus, Abiskomyia, Ichtyocladius, Cardiocladius, Eukiefferiella, Heterotanytarsus, Thienemanniella, Corynoneura, Paratendipes, Microtendipes, Nilothauma, Zavrelia, Stempellinella, Stempellina, Thienemanniola, Tanytarsus, Corynocera, Pontomyia, Nimbocera, Cladotanytarsus,* and *Lenziella.* In the remaining genera it is divided into two principal lobes, dorsomesal and ventrolateral, and occasionally an apodeme lobe. In the Orthocladiinae, the ventrolateral lobe usually is the largest and the dorsomesal lobe forms a narrow line around the vagina, whereas in the Chironominae the main lobe usually is the dorsomesal lobe and the ventrolateral lobe forms a small brush. The apodeme lobe is equipped with microtrichia in *Limaya, Maoridiamesa, Monodiamesa, Psectrocladius* (some), *Rheotanytarsus, Dictrotendipes, Glyptotendipes, Chironomus, Kiefferulus,* and *Einfeldia.* Gp IX is well developed throughout the family. In Tanypodinae, Aphroteniinae, and Podonominae Gc IX is fused and T IX forms a gonotergite IX. In the Tanypodinae, this gonotergite is reduced to a narrow strip. Gc IX carries a Gs IX in the Telmatogetoninae only. T IX is primitively undivided, but is partly divided in Lobodiamesini, Diamesini, Prodiamesinae, most Orthocladiinae (except *Diplocladius, Abiskomyia, Chasmatonotus, Ichtyocladius, Eukiefferiella, Paracladius, Metriocnemus, Thienemannia, Chaetocladius, Limnophyes, Gymnometriocnemus, Bryophaenocladius, Smittia, Thalassosmittia, Clunio, Tethymyia,* and *Pseudosmittia,* although some of the above do have a slight caudal concavity), and in *Lauterborniella.* The cerci are one-segmented throughout the family.

The accessory gland is simple, at least in *Hydrobaenus* and *Chironomus.* The labia, or the remains of the papillae of the accessory gonopore, are fused in Podonominae, Telmatogetoninae, and the *Corynoneura* group. They carry microtrichia in *Clinotanypus, Coelotanypus, Alotanypus, Psectrotanypus, Arctopelopia, Conchapelopia, Thienemannimyia, Guttipelopia,* Heptagyini (perhaps except *Maoridiamesa), Pseudodiamesa, Heterotrissocladius, Manoa, Paralauterborniella, Stictochironomus* (some), *Nilodorum, Xenochironomus,* and the *Harnischia* complex. In Telmatogetoninae the seminal capsules are absent and the wide spermathecal ducts apparently function as seminal storage organs. There are three seminal capsules in the Tanypodinae (except *Telmatopelopia), Aphrotenia, Podochlus, Parochlus chiloensis* group, Boreochlini (except *Boreochlus thienemanni),* Diamesinae (except *Diamesa* and *Pseudokiefferiella),* Prodiamesinae, *Diplocladius,* and some *Brillia;* remaining chiromomids have two seminal capsules. The seminal capsules carry microtrichia in *Xenopelopia* (weak), *Pagastia, Potthastia,* Prodiamesinae, *Brillia* (some), *Abiskomyia, Baeoctenus, Oliveria, Hydrobaenus* (most), *Nanocladius, Orthocladius* (some), *Cricotopus (some), Limnophyes,* and *Parakiefferiella.* The spermathecal ducts open separately on the spermathecal eminence in Tanypodinae, Boreochlini, Diamesinae, Prodiamesinae, *Brillia, Abiskomyia, Ichtyocladius, Cardiocladius, Rheocricotopus, Parorthocladius, Halocladius, Oliveria, Thienemannia, Chaetocladius, Bryophaenocladius, Parakiefferiella;* some *Orthocladius, Cricotopus,* and *Zalutschia;* and perhaps in *Phycoidella.* In the remaining chironomids the spermathecal ducts are joined for a short distance or have at least a common opening.

PROSPECTIVES

Attempts have been made in this monograph to examine the female genitalia of as many genera and species of Chironomidae as practically possible, and to compare them with each other and representatives of all common families of nematocerous Diptera. The result has been gratifying in as much as the female genitalia are proven as important a systematic tool as the male genitalia, and even more important phylogenetically. However, the investigation has also shown that in many cases it is not sufficient to examine one or two isolated genera of a family, subfamily, or tribe, or one or two species of a large genus, to give satisfactory diagnoses for the complete group. The Chironomidae as a whole offer a prime example of the importance of studying all groups before making a statement with phylogenetic implications: without examining the female genitalia of the Telmatogetoninae, the concept of the theoretical chironomid progenitor would have been fundamentally different. On the other hand, in some cases (within the well-known female genitalia of the Simuliidae) the variation is minimal. The comparisons made between the Chironomidae and other nematocerous families suffer from lack of knowledge of some families. Within the Chironomidae a closer examination of the exotic, particularly Neotropical and Australian, genera is desirable as these often occupy a key position in understanding the phylogeny and systematics of related genera. The preliminary nature of most diagnoses and the keys given here can only be improved by further investigations.

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