INTERSEXES AND THE HOMOLOGY OF GENITAL STRUC-TURES IN TIPULIDAE (DIPTERA)

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Abstract

Examination of the terminalia of intersexes of *Nephrotoma aculeata* (Loew) and *N. cornicina* (Linnaeus) corroborates the homology of the posterior extension of male sternite 8 and the female hypogynial valves, and the homology of the male gonocoxite and gonostylus with the posterior process of female sternite 9. It further reveals that the spinous structure at the posterior margin of tergite 9 in male Tipulidae which is usually regarded as a secondary extension of the tergite is a true secondary extension in its dorsal part, but can include elements of tergite 10 in its ventral portion. Details of the terminalia of male, female, and intersex *N. aculeata* and *N. cornicina* are illustrated. The *Nephrotoma* species are compared with *Bittacus weelei* Esben-Petersen (Mecoptera, Bittacidae) and *Tipula* (*Sinotipula*) *tessellatipennis* Brunetti (Diptera, Tipulidae) of which the male terminalia are illustrated.

INTRODUCTION

The correct interpretation of certain structures in the adult male postabdomen of Tipulidae still poses problems. It is generally accepted that nine abdominal segments can be distinguished externally in adult male Tipulidae (MCALPINE, 1981). The genital structures are located at the ninth segment, while adaptations of the eight sternite involved in copulation are commonly found.

The posterior margin of male tergite 9 is often provided with processes, the homology of which still is not satisfactorily clarified. Most recent authors interpreted the processes of tergite 9 as secondary extensions of this tergite (e.g., BYERS, 1961;

FROMMER, 1963; OOSTERBROEK, 1978, et seqq.; TANGELDER, 1983, et seqq.).

However, BRODO (1987: 9), in her monograph on the genus *Prionocera* Loew, stated that "(t)hese processes appear to be secondary extensions of the 9th tergite, but it is possible that in *Prionocera* the more ventrally situated single median lobe and/or the paired apical processes are remnants of a 10th tergite."

What is generally considered the ninth tergite and its posterior secondary extensions, is regarded as syntergite 9-10 in some of my publications (DE JONG 1993, 1994a, 1994b, 1995a, 1995b). This inter-

pretation was inspired by the striking resemblance and relative position of sclerotizations at the base of the proctiger in certain species of Tipulidae with well developed male cerci and corresponding structures in Mecoptera, especially Bittacidae (see discussion below).

According to WOOD (1991), one-segmented cerci are present in the groundplan of the male terminalia of Diptera. On the authority of HENNIG (1973: 210), the notion appears to be widely established that male Tipulomorpha are distinguished by the lack of cerci, a contention repeated by GRIFFITHS (1990) and more recently by OOSTERBROEK & COURTNEY (1995). Under character 89, OOSTERBROEK & COURTNEY listed the absence of male cerci as a synapomorphy for their clade Trichoceridae + Tipulidae s.l. (i.e., the Tipulomorpha sensu Hennig, containing the families Trichoceridae, Pediciidae, Cylindrotomidae, Tipulidae s. str., and Limoniidae sensu Stary 1992). However, my own observations show that distinct male cerci occur in all major lineages of Tipulomorpha with the exception of the Trichoceridae [e.g., Pediciidae: *Dicranota* (*Paradicranota* Alexander); Cylindrotomidae: *Cylindrotoma* Macquart; Tipulidae: *Tipula* (*Acutipula* Alexander), *Tipula* (*Sinotipula* Alexander); Limoniidae: *Austrolimnophila* (*Austrolimnophila* Alexander), *Dactylolabis* (*Dactylolabis* Osten Sacken), and *Phyllolabis* Osten Sacken]. MCALPINE (1981, figs. 2.113-2.115) presented illustrations of the male of the Nearctic *Trichocera garretti* Alexander (Trichoceridae) showing structures that were labelled as cerci lying posteriorly of a separate tergite 10. It is not clear whether McAlpine interpreted these structures correctly, as other Trichoceridae apparently are devoid of cerci in the male (KRZEMINSKA, pers. comm.). Considering the distribution of male cerci in other families of Diptera, their appearance in some of the major clades of the Tipulomorpha could well indicate that male cerci were present at the origin of the Tipulomorpha. [As already noted by BRODO (1987), an earlier publication giving illustrations of male cerci in Tipulidae s. str. is DOBROTWORSKY's 1968 introductory paper to the Australian Tipulidae, where he illustrated the cerci of the Australian *Leptotarsus* (*Macromastix*) *tortilis* Alexander ('anal style' in his figs. 6 I, K)].

Together with the Siphonaptera, the Mecoptera (including the family Nannochoristidae; WILLMANN, 1989) are generally considered to be closely related to the Diptera (BYERS, 1996; HENNIG, 1981; KRISTENSEN, 1991; WILLMANN, 1989; WOOD & BORKENT, 1989). Associated with their parasitic way of life, the Siphonaptera are morphologically highly specialized, while the Mecoptera, and especially the phylogenetically primitive family Bittacidae, show more generalized structures. The genital structures of the Bittacidae are remarkably similar to those of the Tipulidae and are used here as a point of reference for the below discussion.

SEXUAL TERATOLOGY IN
TIPULOMORPHA

In Imms' General Textbook of Entomology, RICHARDS & DAVIES (1977) distinguish three abnormal forms of sexual differentiation, viz., gynandromorphy, intersexuality, and hermaphroditism. Gynandromorphs or sex-mosaics are individuals in which some parts of the body show female characteristics while the remaining parts are male. Intersexes are forms which are more or less intermediate between the two sexes. Hermaphroditism occurs in individuals that are externally similar to either the male or female, but possess gonads that produce both spermatozoa and eggs. Gynandromorphs may be caused by the loss of a sex-chromosome in one of the

early cleavage nuclei of the embryo, by double fertilization of abnormal eggs possessing two nuclei, or by mosaic-like incidence of male-producing parthenogenesis at unusual high temperatures. Intersexuality results of the disturbance of the normal balance of epistatic relationships between male- and female-determining genes, caused by a diversity of stress factors ranging from high temperatures to parasitism. Under natural conditions, intersexes are only rarely encountered. The intersexes of *Nephrotoma cornicina* dealt with below were collected at Birmensdorf, Zürich, Switzerland, in a light trap from 7 July till 3 August 1980. The locality at Birmensdorf lay at a compound where newly developed pesticides were tested (DUFOUR, pers. comm.). Most probably, the environmental stress caused by the chemicals is the reason why a series of ten intersexes could be obtained over a longer period of time.

There are relatively few records on sexual deformation in Tipulomorpha. EDWARDS (1938) mentioned gynandromorphs of *Molophilus* Curtis and *Trichocera* Meigen, in which female cerci were present in combination with the normal terminalia of the male. A similar form of *Dicranomyia (Dicranomyia) mitis* Meigen, showing fully developed male structures combined with female cerci, was described and illustrated by GEIGER (1983). STARY (1969) described and illustrated a gynandromorph of *Dicranomyia (Numantia) fusca* Meigen, of which the left side of the terminalia showed fully developed male structures, while the right side contained partly developed female cerci and hypogynial valves. YOUNG (1987) described and illustrated what he considered a gynandromorphic specimen of *Tipula (Papuatipula) koiari* Young that showed a well-developed male-like left wing, a brachypterous female-like right wing, and terminalia that consisted dorsally of a female cercus on the right side, vaguely defined male parts on the left side, and hypogynial valves ventrally. Considering the intermediate state of development of some of the characters, the specimen might in fact represent an intersex.

Besides the above mentioned specimens and the intersexes of *Nephrotoma aculeata* and *N. cornicina* discussed below, sexual teratology in Tipulidae is known in *Nephrotoma pilicauda* (Savchenko) and in *Tipula (Savtshenkia) hartigiana* Theowald, Dufour & Oosterbroek. Independent of each other, OOSTERBROEK and PODENAS (pers. comm.) arrived at the conclusion that the holotype of *N. pilicauda* represents an intersex (cf. SAVCHENKO, 1973: 167-168, fig. 103). I have not examined *N. pilicauda* [holotype preserved in the collection of the Zoological Institute of the Academy of Sciences, St. Petersburg; cf. SAVCHENKO & KANDYBINA (1987)] and it remains to be solved to which species it actually belongs. According to THEOWALD, DUFOUR & OOSTERBROEK (1982), the description of *T. (S.) hartigiana* was based on five males and two females. However, the "female" paratype of *T. (S.) hartigiana* preserved in the collection of the Zoological Museum, Amsterdam is an intersex. As this specimen does not contribute much to the establishment of homologies in the terminalia of the Tipulidae it is not included in the present discussion.

I am not aware of the existence of hermaphroditism in Tipulomorpha.

MATERIAL, METHODS, AND TERMS

This study is based on the examination of males of the Mecopteron *Bittacus weelei* Esben-Petersen (originating from Malawi), normal specimens of *Tipula (Sinotipula) tessellatipennis* Brunetti (originating from Tajikistan), *Nephrotoma aculeata* (Loew), and *N. cornicina* (Linnaeus), plus two intersexes of *N. aculeata*

and ten intersexes of *N. cornicina* (all *Nephrotoma* specimens originating from Switzerland). Most material is dry-pinned, with the exception of the intersexes, which are stored in 70% alcohol. Most material discussed here is deposited in the collection of the Department of Entomology of the Zoological Museum, Amsterdam, with the exception of the intersexes of *N. aculeata* which are preserved in the collection of the Muséum d'Histoire Naturelle, Neuchâtel.

To examine the external and internal structures, the tip of the abdomen was removed and macerated in nearly boiling 10% KOH for a few minutes. The preparations were examined in glycerol using a Wild stereo-microscope magnifying up to 100 X. Illustrations were made with the aid of a drawing-tube attached to the microscope.

The terminology adopted for *B. weelei* follows the studies on the morphology and phylogeny of the Mecoptera by WILLMANN (1981a, 1981b, 1989) (fig. 1). The terms used to denote the morphological structures in the Tipulidae are in accord with MCALPINE (1981), with a few additions for the postgenital segments that correspond with Willmann's terms for the Mecoptera (fig. 2). DAHL'S (1980) particular interpretation of the terminal structures based on the postembryonic development of Trichoceridae and Limoniidae is not followed here, partly because equivalent studies on Mecoptera are not available, which prevents inter-order comparison. I consider the basistylus of Mecoptera the homologue of the gonocoxite of Diptera, the dististylus of Mecoptera the homologue of the inner and outer gonostyli of Diptera, and the penisfilum of Mecoptera the possible homologue of the combined aedeagus and aedeagal guide of Diptera.
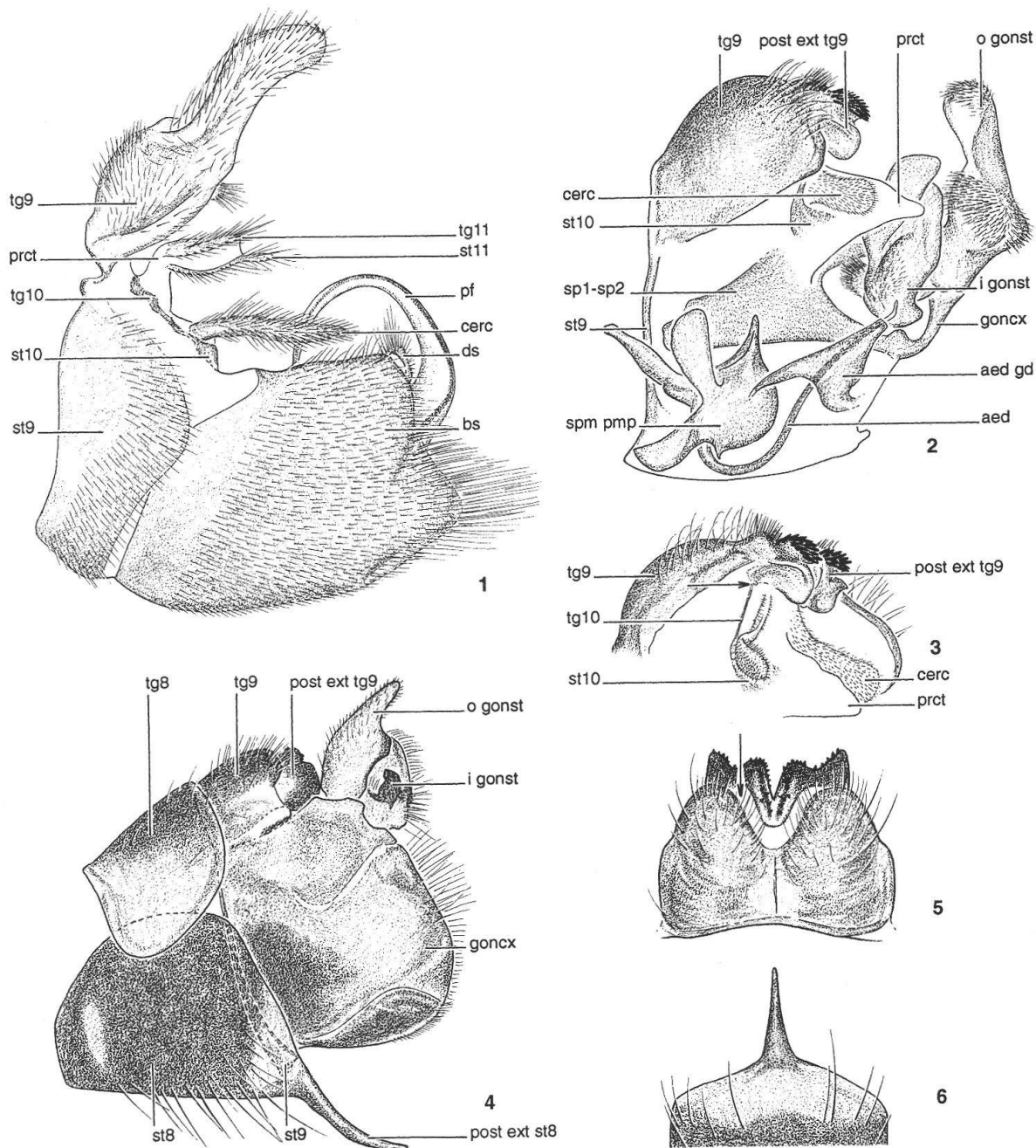
RESULTS
Bittacus weelei (fig. 1)

As an example of male terminalia in Mecoptera, Bittacidae, fig. 1 depicts the terminalia of *Bittacus weelei*. WILLMANN (1989: 75-81) discussed the male postgenital segments, i.e., segments 10 and 11 throughout the distinguished families of Mecoptera. Segments 10 and 11 constitute the so-called proctiger. According to Willmann, there is a tenth segment in front of the male cerci. Tergite 10 shows a variety of forms in the distinguished families of the Mecoptera, being present as a single well developed structure in the oldest lineages, viz., the Nannochoristidae and Bittacidae, while it is usually partly or entirely reduced in the more derived families. Tergite 10 in Bittacidae is present either as a plate or as a slender strip (the latter situation is found in *B. weelei*). Willmann considered a medially separated sternite 10, as found in most families including the Bittacidae, the plesiomorphic condition in Mecoptera. Posterior to the tenth segment, the eleventh segment contains a sclerotized tergite and sternite that lie respectively dorsally and ventrally of the anal opening. The eleventh segment is rather constantly shaped throughout the Mecoptera.

Tipula (Sinotipula) tessellatipennis (figs. 2, 3)

Figs. 2 and 3 depict the terminalia of the male of *Tipula (Sinotipula) tessellatipennis*, a representative of the Tipulidae with well-developed cerci in the male. Adopting WILLMANN'S (1989) terminology for the postgenital structures, the sclerotizations at the base of the proctiger in front of the cerci represent the tenth segment. *T. (S.) tessellatipennis* has a distinct, ventrally separated sternite 10, which continues dorsally into a strip-like tergite 10. Dorsally, tergite 10 is fused with the ventral portion of the process at the posterior margin of

Figures. 1-6: 1, *Bittacus weelei* Esben-Petersen, male terminalia, lateral view (tergite 9 somewhat folded back); 2, 3, *Tipula (Sinotipula) tessellatipennis* Brunetti, male terminalia; 2, lateral view (left part of sternite 9, left part of genital bridge, and left gonocoxite and appendages removed); 3, tergite 9 and proctiger, ventrocaudal 3/4 view; 4-6, *Nephrotoma aculeata* (Loew), male terminalia; 4, lateral view; 5, tergite 9 and posterior extension, dorsal view; 6, posterior margin of sternite 8 and posterior extension, ventral view.

Abbreviations: aed: aedeagus; aed gd: aedeagal guide; bs: basistylus; cerc: cercus; ds: dististylus; goncx: gonocoxite; i gonst: inner gonostylus; o gonst: outer gonostylus; pf: penisfilum; post ext st8: posterior extension of sternite 8; post ext tg9: posterior extension of tergite 9; proc: proctiger; spm pmp: sperm pump; sp1- sp2: genital bridge sensu Dobrotworsky 1968; st9 - st11: sternite 9 - sternite 11; tg9 - tg11: tergite 9 - tergite 11.

tergite 9 (fig. 3, arrow). A similar connection between the dorsal part of tergite 10 and the ventral part of the process at the posterior margin of tergite 9 can be found in other species of Tipulidae. There are no traces of an eleventh segment in *T.* (*S.*) *tessellatipennis*.

Nephrotoma aculeata
Normal specimens (figs. 4-10)

Figs. 4 to 6 show details of the terminalia of normal males of *Nephrotoma aculeata*, figs. 7 to 10 illustrate the female terminalia of the same species; the labelling is self-explanatory. The following features should be noted: as in other species of *Nephrotoma* and other Tipulidae, male tergite 9 and its spinous posterior extension are separated by a membranous suture (fig. 5, arrow); male sternite 8 medially carries a single, slender posterior extension (figs. 4, 6); male sternite 9 is slender and is followed by a broad gonocoxite that apically carries the inner and outer gonostyles (fig. 4); (the male proctiger is devoid of any sclerotizations and does not carry cerci); the female has distinct tergites 9 and 10, and well-developed cerci (figs. 7, 8); female sternite 8 posteriorly carries a pair of hypogynial valves (figs. 7, 9); female sternite 9 has broad sides, its medial part is slender and medially carries a posterior extension (figs. 7, 10); female sternite 10 is present as a flat, semi-circular blade (fig. 7).

Intersexes (figs. 11-14)

The two intersexes of *N. aculeata* are structurally fairly similar and show relatively well-developed female character states in the dorsal parts of the terminalia: the shape of tergite 9, tergite 10 provided with a medial longitudinal septum, relatively well-developed female cerci and sternite 10 (figs. 11, 12). The ventral parts show some male characteristics: posteriorly, sternite 8 carries a rudimentary single midventral extension (figs. 11, 13),

while sternite 9 is posteriorly extended over its entire width (fig. 14). No internal genital structures of either male (aedeagus, aedeagal guide, genital bridge, sperm pump) or female (genital fork, spermathecae) were found in the intersexes examined.
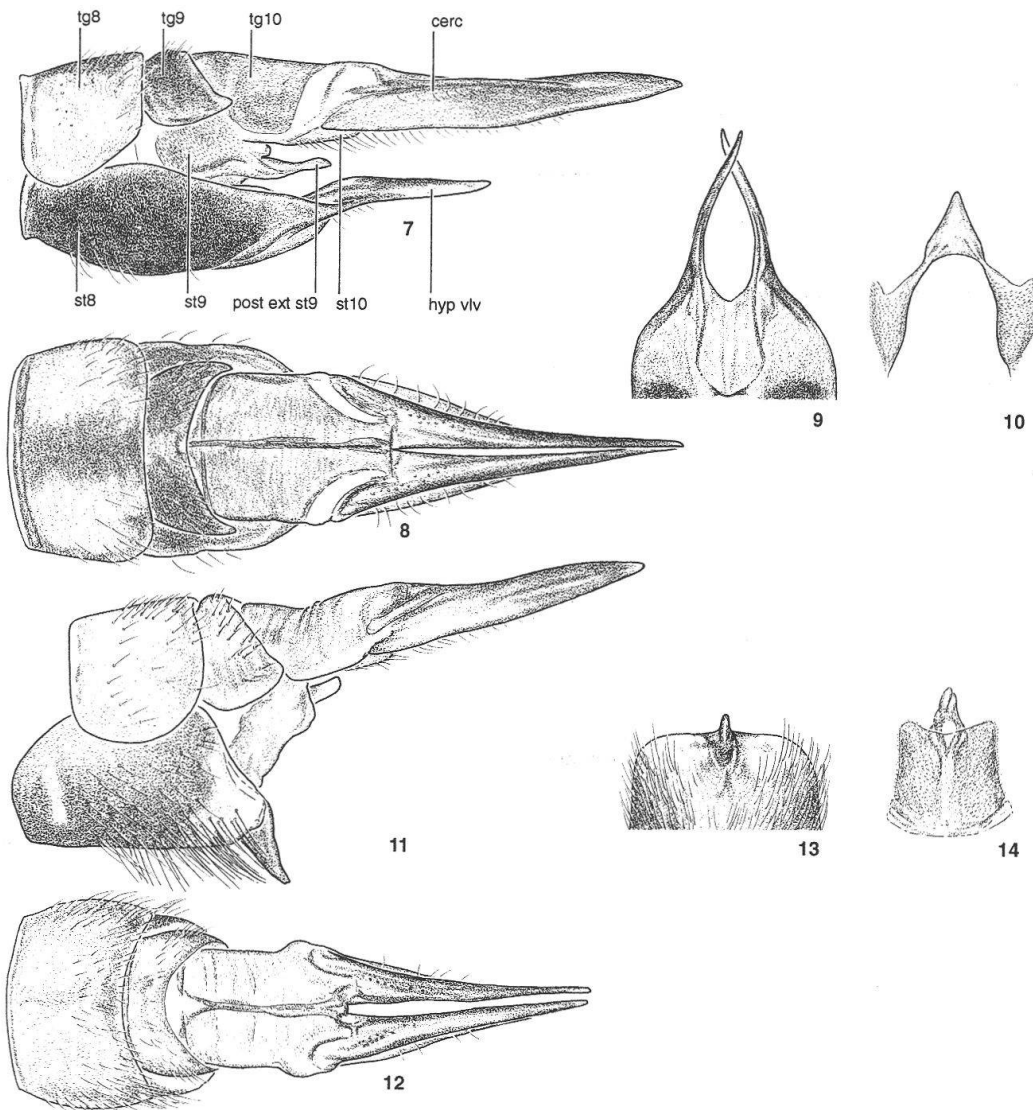
Nephrotoma cornicina
Normal specimens (figs. 15-21)

Details of the terminalia of normal males of *Nephrotoma cornicina* are given in figs. 15 to 17, while the female terminalia are shown in figs. 18-21. Basically, the terminalia of both sexes are similar to those of *N. aculeata*. As in the male of *N. aculeata*, tergite 9 and its spinous posterior extension are separated by a suture (fig. 16, arrow); the medial extension at the posterior margin of male sternite 8 is more robust than in *N. aculeata* and terminates in a blunt tip (figs. 15, 17); as in *N. aculeata*, the male proctiger also is entirely membranous and devoid of cerci.

Intersexes (figs. 22-28)

As in the intersexes of *N. aculeata*, the intersexes of *N. cornicina* show relatively well-developed female structures dorsally: tergite 10, cerci, and sternite 10 (figs. 22, 23). Compared to the female, the intersexes of *N. cornicina* have tergite 10 crumbled and reduced in size. Male features can be found ventrally: sternite 8 posteriorly carries a single midventral extension that, depending on the specimen, attains various stages of development ranging from rudimentary (fig. 25) to relatively well-developed (figs. 22, 27). When the male-like posterior extension of sternite 8 is not or only weakly developed, sternite 9 and its appendages (fig. 26) are more similar to that of the normal female (fig. 21), while a well-developed male-like posterior extension of sternite 8 is always associated with a blade-like sternite 9 (fig. 28).
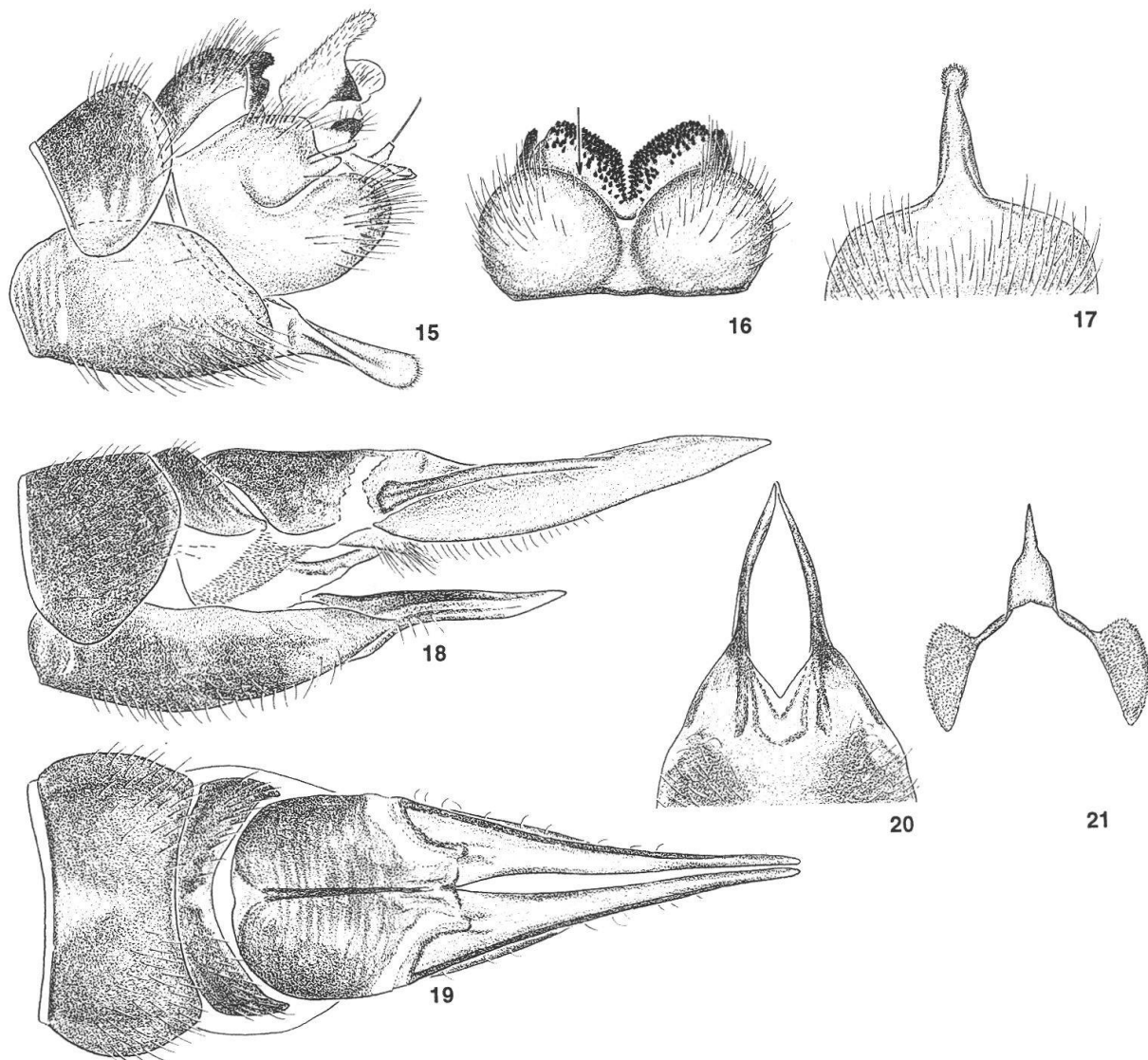
Figures 7-14: *Nephrotoma aculeata* (Loew). — 7-10, female terminalia; 7, lateral view; 8, dorsal view; 9, posterior margin of sternite 8 and hypogynial valves, ventral view; 10, sternite 9 and posterior extension, ventral view; 11-14, intersex terminalia; 11, lateral view; 12, dorsal view; 13, posterior margin of sternite 8 and posterior extension, ventral view; 14, sternite 9 and posterior extension, ventral view.
Abbreviations: cerc: cercus; hyp vlv: hypogynial valve; post ext st9: posterior extension of sternite 9; st8 - st10: sternite 8 - sternite 10; tg8 - tg10: tergite 8 - tergite 10.

One of the most striking features in the intersexes of *N. cornicina* is found in the structure of tergite 9 (figs. 22-24) which is relatively long and narrow, more corresponding with that of the male (fig. 16) than with the transverse tergite 9 of the female (figs. 18, 19). The intersexes studied show various developmental stages of spinous lobes at the posterior margin of tergite 9.

Tergite 9 and its posterior processes are entirely separate from the following tergite 10 in the intersexes.

As in the intersexes of *N. aculeata*, no internal genital structures of either male or female were found in the intersexes of *N. cornicina*.
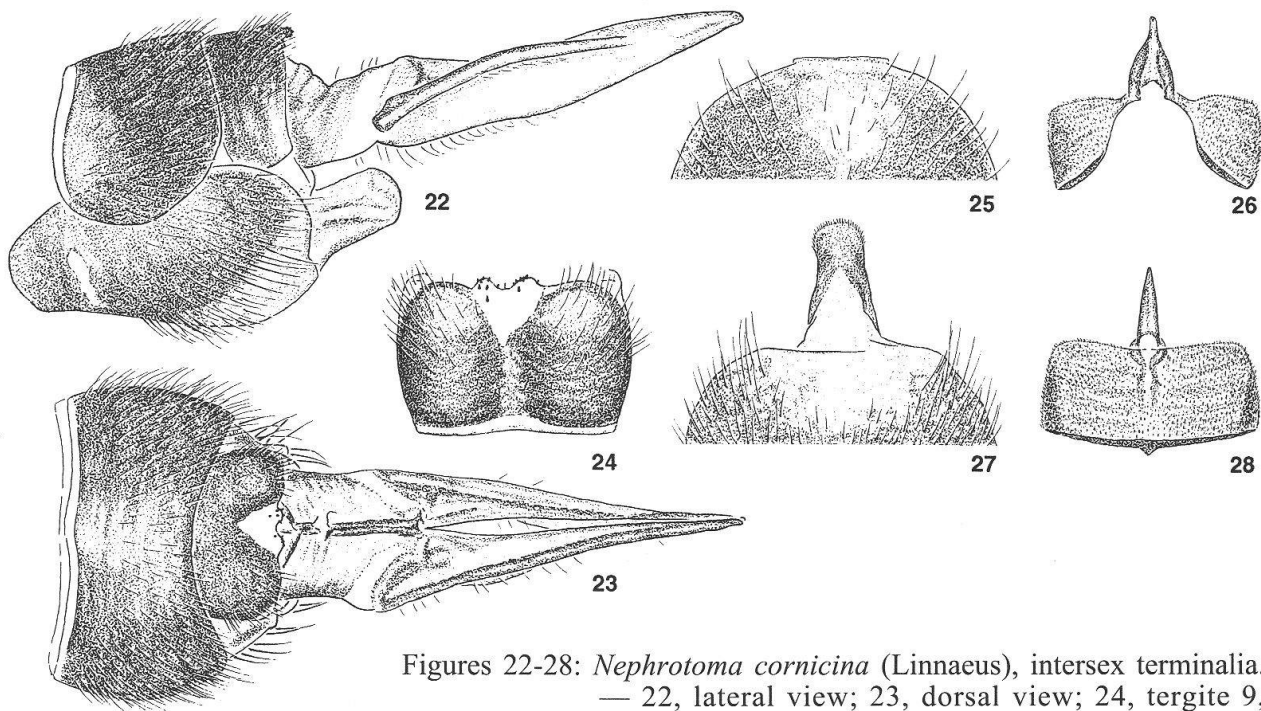
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Figures 15-21: *Nephrotoma cornicina* (Linnaeus). — 15-17, male terminalia; 15, lateral view; 16, tergite 9 and posterior extension, dorsal view; 17, posterior margin of sternite 8 and posterior extension, ventral view; 18-21, female terminalia; 18, lateral view; 19, dorsal view; 20, posterior margin of sternite 8 and hypogynial valves, ventral view; 21, sternite 9 and posterior extension, ventral view.

DISCUSSION

Sternite 8 in all intersexes studied lacks the hypogynial valves of the female but in both intersexual specimens of *N. aculeata* and most intersexes of *N. cornicina* the sternite carries a single male-like extension at its posterior margin (figs. 11, 13, 22, 25, 27), thus supporting the homology of the female hypogynial valves and the male posterior extension of sternite 8.

In the intersexes of *N. aculeata*, the occurrence of a male-like extension at the posterior margin of sternite 8 (fig. 13) is accompanied by the presence of an elongate sternite 9 (fig. 14). The intersexes of *N. cornicina* either combine a weakly developed male-like posterior extension of sternite 8 (fig. 25) with a more female-like sternite 9 and appendages (fig. 26), or a well-developed male-like posterior extension of sternite 8 (fig. 27) with a blade-like

Figures 22-28: *Nephrotoma cornicina* (Linnaeus), intersex terminalia. — 22, lateral view; 23, dorsal view; 24, tergite 9, dorsal view; 25, 27, posterior margin of sternite 8 and posterior extension, ventral view; 26, 28, sternite 9 and posterior extension, ventral view.

sternite 9 (fig. 28). This observation concurs with MICKOLEIT's (1973) interpretation of the process of sternite 9 in female Mecopteroidea as the homologue of the male gonocoxite and gonostylus of sternite 9. It conflicts with DAHL's (1980) establishment of the homology of the male gonocoxite and gonostylus with the structure interpreted here as the female cercus. The homology established by Dahl is also contradicted by the references of EDWARDS (1938) and GEIGER (1983) of gynandromorphs that in the same individual showed the joint presence of a pair of completely developed male gonocoxites and gonostyles together with a pair of female cerci. The blade-like posterior extension of sternite 9 (figs. 14, 28) in intersexes with a well-developed male-like posterior extension to sternite 8 could be the result of male-like stretching of the sternite, although no typically male-structured gonocoxites or inner and outer gonostyles

in any stage of development were found in the intersexes.

As the extension at the posterior margin of tergite 9 in male Tipulidae is often separate from the disc of the tergite by a membranous area or a distinct suture (as for instance in species of *Nephrotoma*; figs. 5, 16, arrows), and the ventral side of the process in certain species of Tipulidae is connected with structures that must be interpreted as tergite 10 (as for instance in *T. (S.) tessellatipennis*; fig. 3), I previously concluded that the extension is homologous with tergite 10 and accordingly regarded the combined tergite 9 and its extension as syntergite 9-10.

The study of the range of intersexual forms of *N. cornicina* shows that the spinous extension of tergite 9 is a real appendage of tergite 9 that is separate from tergite 10, and analogously the spinous exten-

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sion of tergite 9 in the normal male should be interpreted as a secondary process of tergite 9. The observation however, that the ventral parts of the posterior extension of tergite 9 are connected with tergite 10 in certain species of Tipulidae, as for instance the non-spinous ventral parts of the posterior extension in *T. (S.) tessellatipennis* (figs. 2, 3), suggests that the posterior extension of tergite 9 may contain a combination of elements of both tergites 9 and 10, and may represent fragments of tergite 10 exclusively in Tipulidae with an unarmed extension.

ACKNOWLEDGEMENTS

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