

BEAUFORTIA

INSTITUTE OF TAXONOMIC ZOOLOGY (ZOOLOGICAL MUSEUM)
UNIVERSITY OF AMSTERDAM

Vol. 35, no. 8

December 20, 1985

PHYLOGENY OF THE *NEPHROTOMA DORSALIS* SPECIES-GROUP (DIPTERA, TIPULIDAE), MAINLY BASED ON GENITAL CHARACTERS

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ABSTRACT

A reconstruction of the phylogenetic relationships is presented for the holarctic *Nephrotoma dorsalis*-group, comprising 47 species. Their relationships are analyzed according to the principles of Hennig (1966), briefly outlined under 'Methods'. Discussed are the outgroups of *Nephrotoma* and of the *dorsalis*-group, their sister groups however could not be established yet. The copulation-mechanism of crane flies is described, followed by a discussion of the structures involved in both sexes, allowing a better understanding of the observed character changes. A total of 99 characters was used to work out the phylogeny. The monophyly of the *dorsalis*-group and of most species-groups could therefore be based on more than one synapomorphy. The most primitive members of the *dorsalis*-group are found in the eastern Palaearctic. Remarkable is the monophyletic origin of all the nearctic species (the *macrocera*-group). The phylogeny of the group will be the base for a biogeographic analysis, dealt with in a forthcoming paper.

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INTRODUCTION

For an analysis of the faunal exchange between the Palaearctic and Nearctic regions well-

known and species-rich holarctic taxa which are also suitable for phylogenetic reconstructions are required. The *dorsalis*-group, a species-group of the worldwide crane fly genus *Nephrotoma* Meigen, fulfils these conditions: it is a rather large and recently revised (Tangelder, 1983, 1984) holarctic species-group with 20 representatives in the Nearctic and 29 in the Palaearctic, with an overlap of 2 species. As stressed by several authors, classification or phylogenetic reconstruction has to precede (historical) biogeographic investigations (e.g. Ball, 1976; Nelson & Platnick, 1981). The phylogeny of the *dorsalis* species-group is presented here in anticipation of a biogeographical study of the group, to be dealt with in a forthcoming paper, in which special attention will be paid to the faunal exchange between Eurasia and North America.

Tipulidae in general are well suited for phylogenetic reconstructions. They are considered to belong to the more primitive Diptera (Hennig, 1973; Savchenko, 1966) which makes it easier to homologize the different structures. Moreover, they possess a great variety of good distinguishing characters, mainly genital, which are indispensable for such an analysis. To facilitate a good understanding of these characters and their (presumed) function, the copulation-mechanism of crane flies is briefly described, followed by a discussion of the structures involved. That mainly genital characters are used in the analysis may be directly related to their role in the reproduction of the species. Eidetic characters (e.g. colour-patterns, pilosity, degree of gloss) seem to be subject to strong reticulate developments and are therefore not usually of great value in phylogenetic analysis.

The *dorsalis*-group comprises 47 species which are subdivided into smaller groups, each named after the senior species of the group involved (underlined in the cladograms). The *dorsalis*-group s.s. refers to only three species (*dorsalis*, *sachalina* and *spicula*). All drawings are original, partly taken from Tangelder (1983, 1984).

With respect to the classification of the crane flies some differences exist in the literature: In most papers of American and English authors (e.g. McAlpine, 1981) the family Tipulidae (Superfamily Tipuloidea) is subdivided into three subfamilies: Tipulinae, Limoniinae and Cylandrotominae, while these taxa are treated as families (Tipulidae, Limoniidae and Cylandrotomidae) in the continental European literature. This last approach is followed in this paper.

ABBREVIATIONS

a.c.	antecosta
adm.	adminiculum
ant.	antennae
fig(s).	figure(s)
f. valv.	fused valvulae
gon.	gonapophysis
hypov.	hypovalva
id	inner dististyle
int. sh.	internal shell
lat. sh.	lateral shell

l. beak	lower beak
maj. r.	major ridge
med. ap.	medisternal appendage
med. t.	mediotergite
mem. ar.	membranous area
occ. m.	occipital marking
od	outer dististyle
post. ap.	posterior appendage
post. m.	posterior margin
proj.	projection
rostr. ext.	rostral extension
rug.	rugosity
sem. p.	semen pump
sp2	sclerotized clasp, lateral part of genital bridge
St	Sternite
T	Tergite
ZMA	Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam, The Netherlands

METHODS

When a phylogenetic reconstruction of a particular group of organisms is presented, it is important to be clear about the methodological basis of the analysis, in order to allow subsequent evaluation of the approach followed.

The procedure adopted for the reconstruction of the phylogenetic relationships of the species of the *dorsalis*-group is the method originally developed by Hennig (1966), in its contemporary versions as presented in recent textbooks (Ross, 1974; Bonde, 1977; Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981 and Ax, 1984). The aim of phylogenetic research is to show how species are related through descent. It starts from the idea that historical events (speciation) can be reconstructed from a study of their products (the species), because heritable features are passed on from ancestral species to their descendants and therefore (some) shared characters are indicative of common ancestry. Modifications of characters provide features, unique to a given lineage. Phylogenetic relationships are inferred from the distribution of characters among the species being studied. Characters to be used have to be homologous and a distinction has to be made between primitive (plesiomorphic) or derived (apomorphic) character(states). Only the uni-

quely derived characters, restricted to and shared by all the members of a taxon (synapomorphies of Hennig) are indicative of closer relationships between taxa. Similarities in primitive character(states) (symplesiomorphies) convey no phylogenetic information. Fundamental in the procedure is the recognition of monophyletic groups, characterized by synapomorphies. By definition, these groups include all and only the descendants of one ancestral species; these are the only groups of species to be considered 'natural' in the phylogenetic sense, viz. groups existing "in nature as a result of a unique history of descent" (Wiley, 1981). Two (or more) monophyletic groups having an ancestor exclusive to them are called sister groups, together constituting a more comprehensive monophyletic group. The phylogenetic system in this way becomes structured like a hierarchy, and relationships are measured by relative recency of common ancestry, determined by the sequence of splitting events in phylogeny (cladogenesis). The construction of a branching cladogram is done by formulation of three-taxa-statements, hypotheses about the most recent common ancestor of two groups, relative to a third group. The resulting cladogram is the simplest type of phylogenetic hypothesis, which carries no implications for time or degree of differentiation.

The following methodological procedure was followed:

1. Monophyletic groups can be recognized only on the basis of synapomorphies: uniquely shared, derived character states.
2. A (dichotomous) branching diagram forms the best expression of a sequence of cladogenetic events.
3. The above sequence is reconstructed by arranging monophyletic terminal taxa into progressively more comprehensive monophyletic groups based on synapomorphies at a given level of analysis.
4. The evolutionary polarity of character states is assigned largely on the basis of outgroup analysis, which seems to be the only generally applicable criterion for assessing relative apo- c.q. plesiomorphy of character states (De Jong, 1980; Stevens, 1980). The criterion is that "if a character occurs in more than one state in a monophyletic group, the state that occurs also outside the group is likely to be the plesiomorphous state" (De Jong, 1980). Some authors (De Jong, 1980; Ax, 1984) consider the only prerequisite the presence of the relevant character outside the group, while others (e.g. Ross, 1974; Stevens, 1980; Nelson & Platnick, 1981; Watrous & Wheeler, 1981; Wiley, 1981) argue that the outgroup comparison should be made with a closely related group. However, selection of the wrong outgroups may have considerable impact on the acquired assumptions, so it is better to search for the most closely related groups and to give a reasoning for the selection of the outgroup.
5. Outgroup comparisons are applicable at all levels of a cladogram or to all monophyletic groups (Watrous & Wheeler, 1981). This implies that problems are reduced to smaller functional-group levels, a procedure applicable in some cases of homoplasy (= parallelism and convergency). The outgroup is then reduced to that group of species with the closest relationship with the group under study (see also Borkent, 1984).
6. In cases where the outgroup analysis failed, the criterion of correlation of transformation series (Hennig, 1966; De Jong, 1980) was used.
7. Cases of conflict between two or more apomorphies were solved by the assumption that losses occur many times more frequently than the formation of new characters.
8. The criterion of parsimony attends to the simplest explanation of a phenomenon or pattern. It was applied as a principle, minimizing the number of ad hoc statements necessary to explain a given distribution of character states. Parsimony is not a test of the hypothesis, but may be a useful expedient in the analysis.
9. Inconsistent characters, showing inter-specific differences fluctuating inside what

clearly seem monophyletic groups are not used in the analysis.

The results of the phylogenetic analysis of the *dorsalis* species-group are presented here in the form of a cladogram, accompanied by a discussion of the synapomorphous characters on which the monophyletic groups are based. They are treated in the sequence of the supposed underlying cladogenetic events, that is to say by splitting up the whole species group into smaller monophyletic units down to the species level. Weighting of characters is not applied which means that no distinction is made between strong or weak characters, because this would merely be a matter of interpretation. Moreover, the monophyly of the groups is founded where possible on more than one synapomorphy.

The advantage of the phylogenetic approach is that it results in a hypothesis which can be evaluated critically. Falsification of the presented cladogram is possible by additional characters or species discoveries and by a reinterpretation of character-polarity and compatibility of characters.

OUTGROUPS

Within the large family Tipulidae about 110 genera and subgenera are recognized. Several authors have tried to arrange some of these taxa according to their relationships. Theowald (1957) based a grouping of mainly western palaearctic taxa on larval and pupal characters; Frommer (1963) used gross morphological studies of the reproductive system in nearctic taxa, Savchenko (1966) both pre-imaginal and imaginal characters and Oosterbroek (1980) similarity, both mainly dealing with holarctic taxa. All these authors came to quite different conclusions and it is impossible to infer from this literature any general conclusions about the relationship of the genus *Nephrotoma* with other Tipulid-taxa. The systematic confusion is also clearly illustrated by the problems concerning the monophyly of the genus *Tipula* (see Frommer, 1963; Savchenko, 1966; Oosterbroek, 1980).

Oosterbroek & Theowald (in prep.) are currently working out the phylogenetic relationships within the family Tipulidae on the basis of pre-imaginal characters, while Van der Hut (in prep.) is trying to add new information by study of the egg-larvae. On the supra-generic level it is at the moment impossible to construct a reliable phylogeny on the basis of the adults only. This is largely due to the fact that a great number of higher taxa are paraphyletic groups, based on symplesiomorphous characters. For an analysis on a lower level, one is nearly completely bound to adult characters. Oosterbroek & Theowald (in prep.) conclude that the genus *Nephrotoma* is characterized by some distinct synapomorphous characters and rather separated from other taxa. From their studies, the following cluster comes forward as the sister group of *Nephrotoma*: Ctenophorinae (comprising *Ctenophora*, *Cnemoncosis*, *Dictenidia*, *Phoroctenia* and *Tanyptera*), *Nigrotipula* and *Tipula* (*Dendrotipula*). Not included in the analysis because of lack of immature material is the oriental genus *Scamboneura*, considered by Oosterbroek (1980) as the sister group of *Nephrotoma*; Alexander (1971) regarded both as subgenera of a single genus, and they might be closely related, but it is too early to speak of sister groups.

The outgroup comparisons with the above mentioned taxa are important in order to get a picture of the relationships within the genus *Nephrotoma*, comprising more than 400 species and subspecies distributed throughout the world. Oosterbroek (1980) distinguished four species-groups, exclusively based on western palaearctic material (52 species and subspecies). The revisions of the nearctic non-*dorsalis* species (Oosterbroek, 1984) and the Japanese *Nephrotoma* species (Oosterbroek, 1985) and the examination of many congeneric species from other parts of the world revealed that several more species-groups than those four already established can be distinguished within *Nephrotoma*. In his phylogenetic reconstruction of the western palaearctic species, Oosterbroek (1980, p. 323) designated the 'cornicina-group' as the sister group of the *dorsalis*-group, based on the synapomorphy of six so-called weak

characters. After thorough examination of those characters I came to the conclusion that they are no proper base for the assumed sister group relationship (see p. 154). In my opinion the *dorsalis*-group does have more affinities with the *brevipennis*-group, the *crocata*-group and some as yet undesignated oriental species-groups, because of, among other things, the completely medially incised posterior extension of tergite 9 of the male (figs. 16-19) and the presence of two ridges on the internal surface of the female hypovalvae (this last character-state is considered plesiomorphous by Oosterbroek, 1980, p. 326; for further discussion see p. 151). A final designation of the sister group of the *dorsalis* species-group is not yet possible; a taxonomic revision of the complete genus seems necessary before this can be done.

The genus *Nephrotoma* is defined by wing-venation (Meigen, 1818, as a separate section of the genus *Tipula*; Oosterbroek, 1978; Tangelder, 1983). However, the study of some new species which are *Nephrotoma*-like in genital characters but deviating in wing-venation throws some doubts upon this criterion. For example *N. distans* Edwards, 1928, a species from Tibet, does possess rather primitive characters compared to other *Nephrotoma* species. It has a wing-venation deviating from the general pattern (anterior corner of the discal cell fused with m-cu (Edwards, 1928)), although in one male (ZMA), one of the wings has a venation as usual in *Nephrotoma*. This species might be a real (primitive) *Nephrotoma* or otherwise very close to it, and therefore appropriate for outgroup comparison.

For the purpose of the phylogenetic analysis presented, outgroup comparisons are made with several non-*dorsalis* species and species-groups within the genus *Nephrotoma*, with the supposed sister group taxa of *Nephrotoma* (the Ctenophorinae, *Nigrotipula* and *T. (Dendrotipula)*) and with *Scamboneura*.

THE COPULATION-MECHANISM OF CRANE FLIES

Because the phylogenetic reconstruction of the

dorsalis-group presented here is mainly based on male and female genital characters, an outline will be given of the copulation-mechanism of crane flies and of the different structures involved (for more details see Neumann, 1958; Frommer, 1963). The terms 'tergum' and 'sternum' are used for the complete respective parts of the segments, while 'tergite' and 'sternite' refer only to the sclerotized parts (see McAlpine, 1981). See for terminology also figs. 1-3.

During the copulation the male and female genitalia are rotated some 180 degrees with respect to each other. The female hypovalvae are maneuvered into the male genital cavity (figs. 4-7), in which tergite 9 of the male serves as a guide, pressing against the ventral groove of sternite 8 of the female. The inner surface of tergite 9 is usually provided with median and lateral thickenings, frequently set with numerous black, sclerotized spines, which presumably serve a tactile-function (fig. 5). The inner dististyles move inside and hitch into the sclerotized folds on the inner surface of the hypovalvae, which are pressed against tergite 9 of the male. The result is a firm mutual anchorage of male and female genitalia; Neumann (1958) supposes a real, species-specific lock- and key-mechanism. The outer dististyles envelop the hypovalvae like an embrace; according to Neumann (1958) they have no special function other than protection, because males of *Tipula paludosa* were able to copulate normally without their outer dististyles.

The central portion of the adminiculum is directed caudad till its top opposes the opening of the bursa copulatrix of the female, situated in the intersegmental membrane between sternites 8 and 9, that is to say just ventral to the fused valvulae and dorsal to the furca. The fused valvulae rest towards the ventral side of the adminiculum during copulation. The gonapophyses presumably have a function in ascertaining the correct position of the adminiculum between the cerci and hypovalvae. Byers (1961) supposes the gonapophyses to force the tenth tergum and cerci of the female

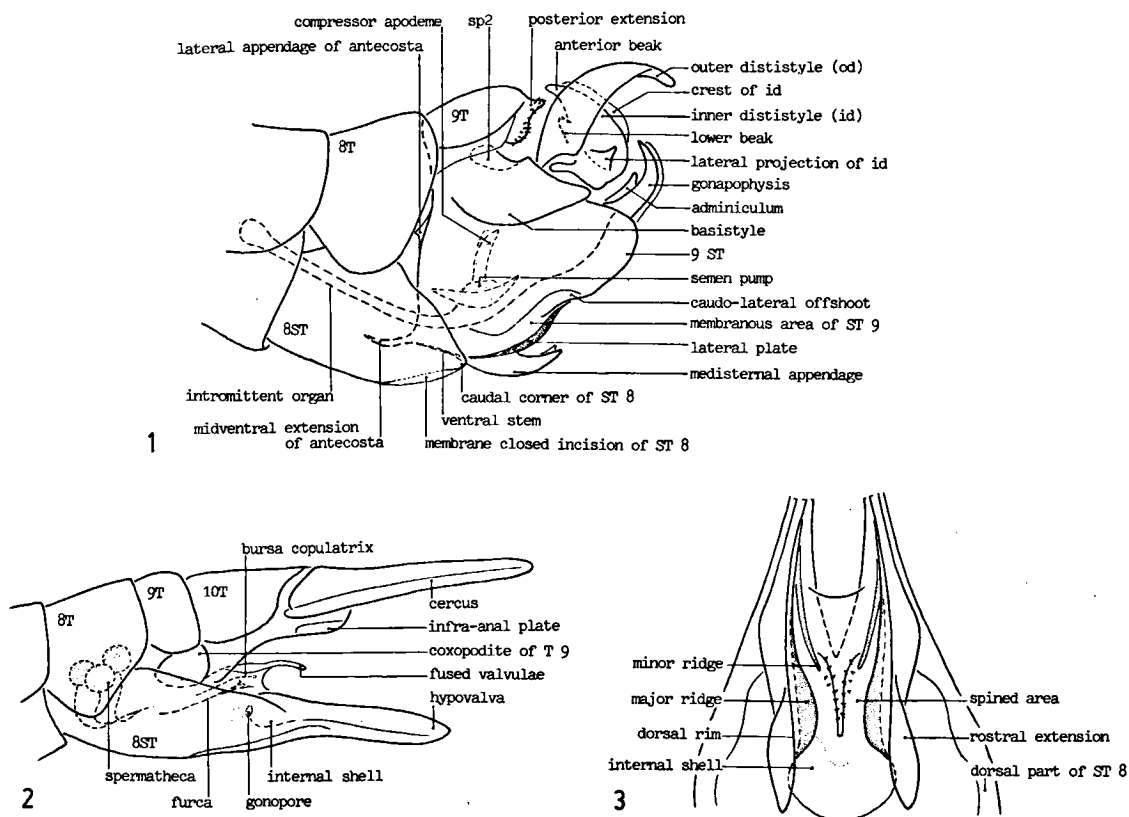


Fig. 1. Generalized drawing of the hypopygium, lateral view. Fig. 2. Generalized drawing of the ovipositor, lateral view. Fig. 3. Generalized drawing of the hypovalvae, dorsal view.

apart from the hypovalvae in *Dolichopeza* ssp. In the *dorsalis*-group, among others, the gonapophyses presumably also have a function in fixation, because of their upcurved, pointed tips (fig. 7, see arrow). The adminiculum supports and guides the intramittent organ into the bursa copulatrix of the female.

The intramittent organ emanates basally from the semen pump. This organ, situated inside segment 8 or 9 in a midventral position (figs. 1, 4), possesses lateral and posterior appendages and dorsally the movable compressor apodeme, where muscles attach in order to make rotation of the semen pump possible. By such a rotation in the sagittal plane and contraction of the membranous pouch in which the semen pump and intramittent organ are situated, the intramittent organ is pushed caudally outside the hypopygium into the bursa copulatrix, which branches in three long and

winding tubes each running out into a spermatheca. Movements of the compressor apodeme apparently cause a change in the volume of the semen pump, through which it functions as a real pump and semen is expelled (Frommer, 1963). The spermatozoa are stored in the three spermathecae of the female until the time of oviposition. According to Byers (1961) storage of spermatozoa in *Dolichopeza* occurs in a pouch which joins the bursa copulatrix nearby the attachment of the spermathecal ducts and presumably not in the small and reduced spermathecae itself.

The female cerci lie alongside the ventral region of the male hypopygium during copulation (figs. 4, 6). The membranous midventral and midcaudal regions of sternum 9 of the male are unfolded and the different structures of the sternite, such as the bristles of hair on the caudo-lateral corners and the medisternal ap-

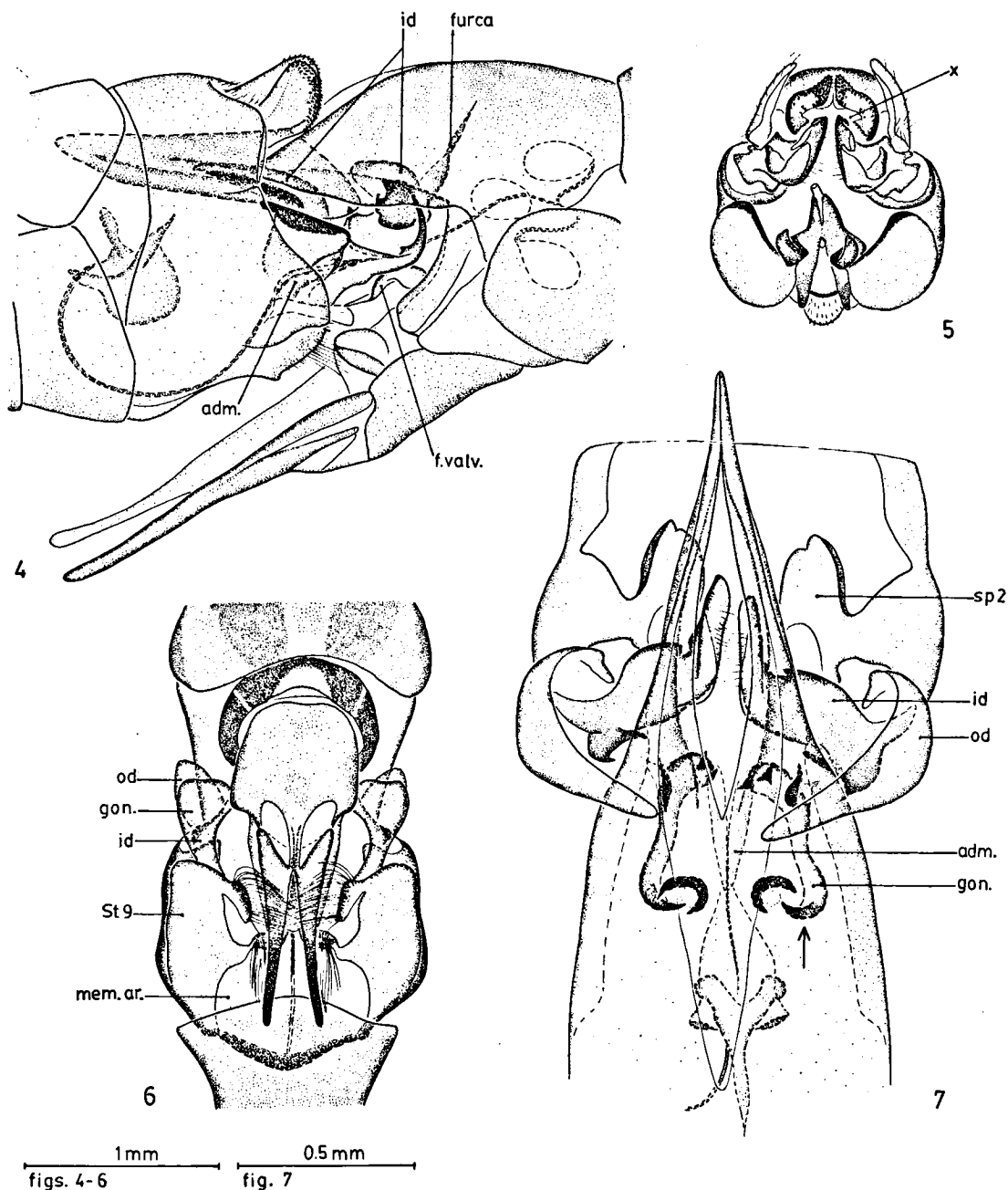


Fig. 4. *T. (Tipula) oleracea*, copula, lateral view, od removed. Fig. 5. *Nephrotoma appendiculata*, hypopygium after copulation, caudal view, x = entrance to genital cavity. Fig. 6. *T. (Yamatotipula) quadrivittata*, copula, ♂ from ventral, ♀ from dorsal view. Fig. 7. *Nephrotoma tenuis*, copula, ♂ from dorsal view with T9 removed, ♀ from ventral view.

pendage, presumably have a major guiding function, in which the male sternite 8 might also be involved (Oosterbroek, 1980). The top of the infra-anal plate of the female may stir the

membranous area of sternite 9 of the male, the bristles of which touch the base of the infra-anal plate (fig. 4).

GENITAL STRUCTURES

Males

The structures of the male genitalia possess a wide variety of characters, many of which are important for phylogenetic analysis (fig. 1). The term 'hypopygium' is frequently limited to the modified ninth segment, also called the genital segment, of the male (Snodgrass, 1904; Crampton, 1942; Neumann, 1958; Byers, 1961; Frommer, 1963); but others have used

the term as a synonym of 'terminalia', including the eighth abdominal segment (if modified) and the succeeding ones (e.g. Westhoff, 1882; Edwards, 1938; Mannheims, 1951; Alexander, 1965). This last approach is followed here, in order to have a general term which comprises all the genital and terminal structures. The ninth segment is the last distinctly recognizable one and there is no visible separation of the tenth and eleventh segments (Frommer, 1963).

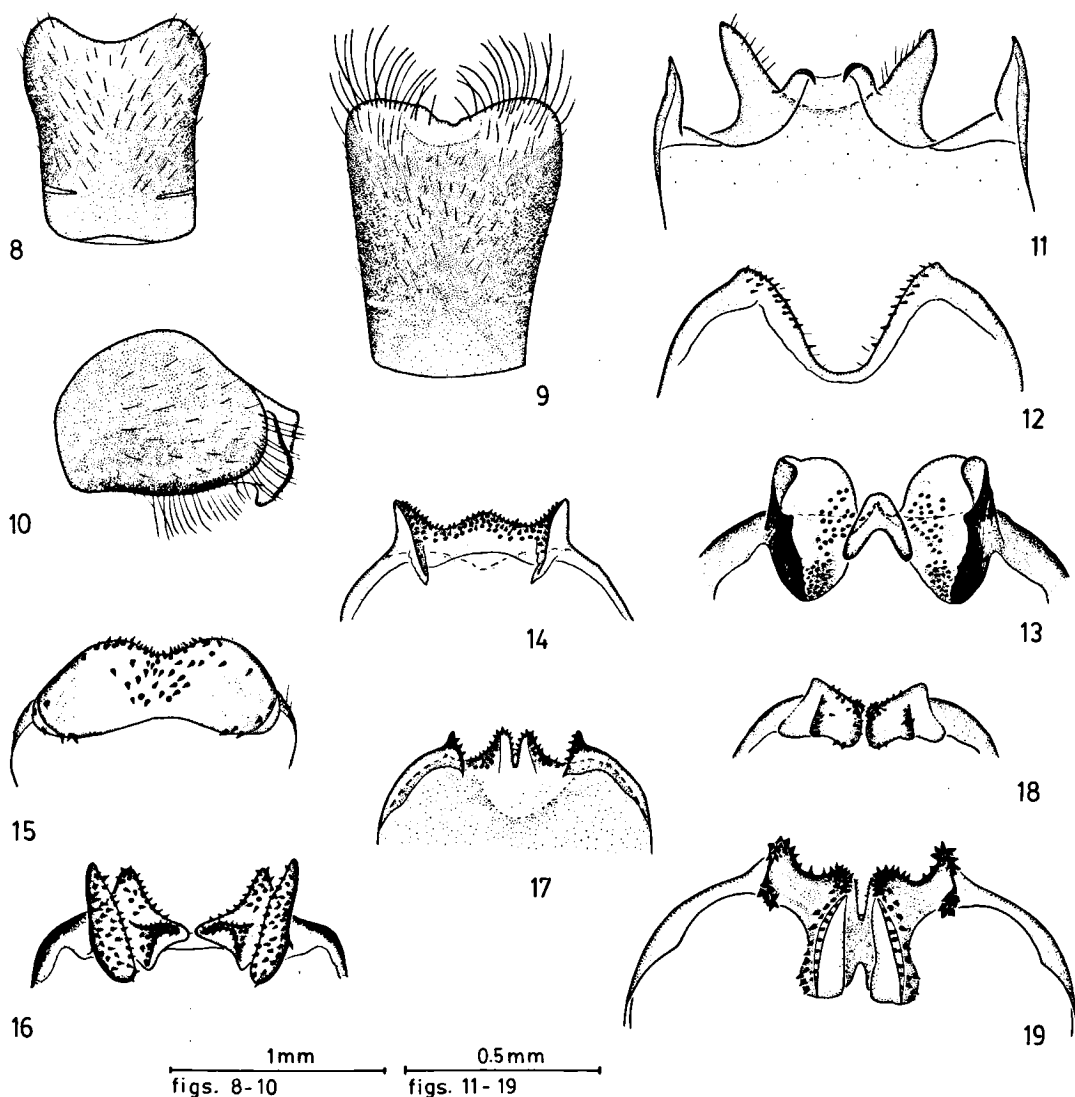


Fig. 8. *Scamboneura vittifrons*, St 8 of ♂, ventral view. Fig. 9. *Nephrotoma analis*, St 8 of ♂, ventral view. Fig. 10. *N. speculata*, St 8 of ♂, lateral view. Fig. 11. *Prionocera turcica*, T 9 of ♂, inside. Fig. 12. *T. (Trichotipula) cf. caluilla*, idem. Fig. 13. *Scamboneura vittifrons*, idem. Fig. 14. *Nephrotoma rectispina*, idem. Fig. 15. *N. distans*, idem. Fig. 16. *N. fuscescens*, idem. Fig. 17. *N. analis*, idem. Fig. 18. *N. albonigra*, idem. Fig. 19. *N. austriaca*, idem.

1. Sternum 8

In the greater part of the Tipulidae, including the closely related outgroups of *Nephrotoma*, sternite 8 of the male is unmodified (fig. 8), that is to say with a straight hind margin, which is clearly an ancestral condition as it is also found in the Limoniidae and Trichoceridae (see also Savchenko, 1966). In several species-groups within *Nephrotoma* (figs. 9, 10) sternite 8 shows modifications, such as medial projections, the development of long and dense bristles of hair or membrane covered incisions, and as pointed out by Oosterbroek (1980) these modifications indicate the involvement of sternite 8 in guiding the female cerci, which are lying alongside the ventral region of the hypopygium during copulation. Within the *dorsalis*-group sternite 8 is variously modified.

2. The genital ring

Tergum 9 and sternum 9, which in many Nematocera are joined laterally, together form the genital ring or basal ring, and in some taxa the sclerites are fused to form a complete ring. In *Nephrotoma* the tergite and sternite of the ninth segment are separated.

3. Tergum 9

The posterior extension of tergite 9 functions as a conductor when the female hypovalvae move inside the hypopygium, by which it is firmly pressed against the ventral groove of the female sternite 8 (fig. 5). Within *Nephrotoma* this extension is usually fitted with lateral and/or median thickenings on the inner surface, and in all the *Nephrotoma*-species examined this extension bears small, sclerotized spines. The hypovalvae push between these median and lateral thickenings inside the hypopygium; the spines are presumably sense-organs. The posterior extension of tergite 9 is variously structured throughout the Tipulidae (Frommer, 1963), ranging from hardly modified to intricately developed, and with or without spines (figs. 11-19). The origin of sensory spines is apparently a parallel development in various genera and subgenera (e.g. in *Nigrotipula*, *Scam-*

boneura, *T. (Trichotipula)*, *T. (Tipula)*, *T. (Yamatotipula)*, *T. (Savtshenkia)* and *T. (Acutipula)*). Going by outgroup comparison the simple structure of this extension, without a median incision, without median swellings and with (weak) lateral thickenings on the ventral side as found in for example *N. distans* and *N. rectispina* (figs. 14, 15), must be regarded as plesiomorphous, while the development of a complete median incision, median swellings, modified lateral thickenings and further modifications such as the prolonged median thickenings and sublateral invaginations (figs. 16-19) must be regarded as apomorphic conditions within *Nephrotoma*.

4. Sternum 9

During copulation the ventral region of the male hypopygium is covered by the female cerci, which are guided by the special features of the male sternites involved (fig. 6). In practically all Tipulidae the ninth sternite is divided into two by a midventral membranous area (Frommer, 1963; Oosterbroek, 1980; figs. 20-25). According to Neumann (1958) this median membrane ends caudally in the genital groove ('genitalmulde' in *Tipula paludosa*), which is deeply subsided at rest and folds out completely in copulating males, through which the adminiculum is drawn caudad. In many taxa (as in *Nephrotoma*) this membranous area is frequently caudo-laterally shooted and often bears two longitudinally arranged sclerotized plates (figs. 23-25). These plates can be fused ventrally, forming the ventral stem, connected with the antecosta of sternite 9. Within *Nephrotoma* as well as in the closely related outgroups (Ctenophorinae, *Nigrotipula*, *T. (Dendrotipula)* and *Scamboneura*) the membranous area frequently bears a midventral protuberance, the so-called medisternal appendage (figs. 22, 24, 75). This appendage is usually situated inbetween the plates and can be membranous or completely sclerotized; the shape ranges from slightly and narrowly projected to strongly extended or swollen with a bifid apex. The position of this appendage can be midventral (as in *Scamboneura* and many *Nephrotoma* species-groups) or shifted

towards the antecosta of sternite 9 or the hind margin of sternite 8 (as in *Nigrotipula nigra* and the *cornicina*-group (Oosterbroek, 1980)). However, the dissimilarity of this appendage in the different groups raises questions about the supposed homology of this structure in these taxa. Outgroup comparison reveals that both presence and absence of the plates as well as the medisternal appendage frequently occur within the Tipulidae and the reduced state of these structures as found in many species of *Nephrotoma* indicates that the presence of these plates and appendage does represent the ancestral condition (see also Oosterbroek, 1980, p. 352 "a medisternal appendage belongs to the basic plan in *Nephrotoma*"). Some taxa of Tipulidae possess strong bristles of hair at the midcaudal portions of sternite 9, which also serve in guiding or stirring the cerci (fig. 6). In *Nephrotoma* these bristles are frequently short and weakly developed.

The anterior margin or antecosta of sternite 9, called the bridge of sternite 9 by Rees & Ferris (1939), is usually distinctly sclerotized and sometimes bears a midventral and two lateral appendages (figs. 21, 25). These projections are usually found in a more or less pronounced state within *Nephrotoma*, but they are more scarce, especially the lateral ones, in the other Tipulid-taxa. The presence is assumed to be the plesiomorphous condition in *Nephrotoma* (Oosterbroek, 1980), because they are clearly reduced in some species-groups within *Nephrotoma* and because all the three appendages are clearly distinct in for example *T. (Dendrotipula) flavolineata*, a species belonging to one of the closely related outgroups of *Nephrotoma* (fig. 21).

5. The basistyle

According to McAlpine (1981), the basic pattern of the male terminalia of the Diptera comprises: "a pair of primitively two-segmented arms, the gonopods, arising postero-laterally on sternite 9 and consisting of a basal gonocoxite (basimere, basistyle) and a distal gonostylus (dististyle)". According to Snodgrass (1957) the basi- and dististyles develop from the lateral lobes of the phallic organs, which probably

originate from a pair of penes on the coxae of some legs and not from the legs itself. The gonostylus in its primitive form is single and simple (as in *Trichocera*, Edwards, 1938; fig. 26). In the great majority of the Tipulidae the dististyle is double, being more or less completely divided into an outer and an inner dististyle. The basi- and dististyles together were called parameres by Snodgrass (1957) and Frommer (1963). Oosterbroek (1980) supposes that an elongate, cone-shaped basistyle has to be considered the plesiomorphous condition in Tipulomorpha and the much shorter, usually semi-globular basistyle as found in the majority of Tipulidae the apomorphous one. In all *Nephrotoma* species examined the basistyle is fused with sternite 9 towards the antecosta and separated from it by a curved cleft more apically (fig. 25). A reduction in size of the basistyle, for example the narrowing in some members of the *dorsalis*-group (figs. 134, 135), must be regarded apomorphous (Frommer, 1963; Savchenko, 1966).

6. The inner dististyle (*id*)

This structure, inserted at the inner apex of the basistyle, has a major function in the attachment of the male and female genitalia during copulation. For that purpose they hook into the sclerotized folds on the inner surfaces of the female hypovalvae (figs. 4, 7). Oosterbroek (1980) stated: "the inner dististyles assume widely different shapes throughout the Tipulidae, but are usually of fairly constant shape within smaller species-groups and subgenera". According to Alexander (1965) they are of primary importance and are valid for the separation of subgenera. It is usually a more or less laterally flattened body, anteriorly extended into a sclerotized lobe or point (called the beak by Alexander, 1965), sometimes dorsally elevated into a thin plate or blade, the dorsal crest, frequently with a second projection on the anterior margin, the lower beak (Alexander, 1965), which is connected with the more or less extended lateral shell. In several taxa the inner dististyle is fitted with a variously modified lobe or spine at the outer base, called

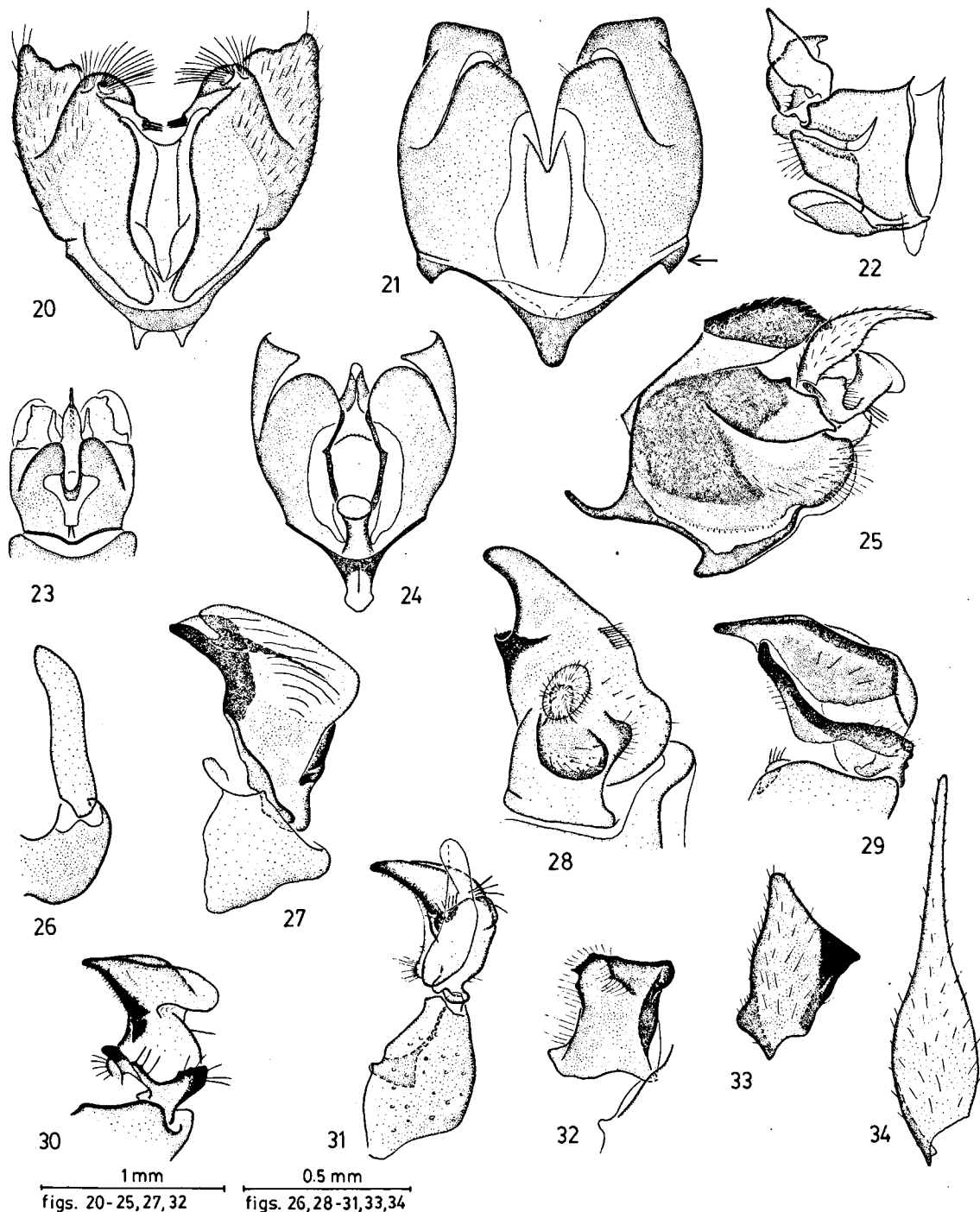


Fig. 20. *T. (Tipula) oleracea*, St 9, ventral view. Fig. 21. *T. (Dendrotipula) flavolineata*, St 9, ventral view. Fig. 22. *Scamboneura vittifrons*, St 9, lateral view. Fig. 23. *Nephrotoma distans*, St 9, ventral view. Fig. 24. *N. crocata*, St 9, ventral view. Fig. 25. *N. violovitshi*, St 9, lateral view. Fig. 26. *Trichocera annulata*, gonostyle, dorsal view. Fig. 27. *T. (Lunatipula) subcava*, id, outside. Fig. 28. *Tanyptera atrata*, id, outside. Fig. 29. *Scamboneura vittifrons*, id, outside. Fig. 30. *Nephrotoma cornicina*, id, outside. Fig. 31. *N. distans*, id and od, outside. Fig. 32. *Ctenophora flaveolata*, od, outside. Fig. 33. *Nephrotoma cornicina*, od, outside. Fig. 34. *N. nigrohalterata*, od, outside.

the 'outer basal lobe' by Alexander (1965); it is completely absent in *Nephrotoma*. Savchenko (1966) considered the 'simply built id' as the plesiomorphous condition and the 'complexely built id' as the apomorphous one. The inner dististyle as found in the closely related outgroups of *Nephrotoma* is more or less simply built: usually without a dorsal crest, with a hardly developed to distinct lateral shell and without further modifications (figs. 27-29). The lateral shell of the inner dististyle is variously modified within *Nephrotoma* (figs. 30, 31, 85, 136), while the development of a dorsal crest apparently is an apomorphous acquisition within *Nephrotoma*, although it is also found in some other genera and subgenera (e.g. *T. (Lunatipula)* (fig. 27), *T. (Beringotipula)*, *T. (Schummelia)*, *T. (Triplicitipula)*). Because of the part they play in copulation, the constructions of the inner dististyle and the female hypovalvae are presumably joined in a way, so the relatively simple structure of the inner dististyle as found in the outgroups, might be correlated with the lack of sclerotized ridges in the female hypovalvae (see also p.).

7. The outer dististyle (od)

This structure, inserted at the outer apex of the basistyle, embraces the female hypovalvae during copulation, and according to Neumann (1958) it protects the more intricate inner dististyle against damage. It is variously modified in the different groups (figs. 31-34), sometimes being a simple cylindrical lobe, frequently broader and more flattened (Alexander, 1965) as in *Nephrotoma*. The outer dististyle is usually fleshy, but sometimes partly sclerotized; both conditions occur within *Nephrotoma*, the last one in members of the *cornicina*-group (fig. 33). In the closely related outgroups of *Nephrotoma* partly sclerotized outer dististyles are also found (fig. 32), while *Scamboneura*-species have fleshy ones. Further modifications within *Nephrotoma* such as an elongated outer dististyle (found in some members of the *dorsalis*-group) should be considered apomorphous (Oosterbroek, 1980), although this character shows a wide variation

within different species-groups (figs. 34, 79, 100, 120, 152).

8. The sp2

This structure, connected with the dorso-internal edge of the basistyle, is supposed to form a part of the so-called genital bridge (Dobrotworsky, 1968). This is a sclerotized curved rod which runs from one side of the hypopygium to the other, underneath the anal segment and posterior to the semen pump. According to Neumann (1958) it is a differentiation of the wall of the genital chamber (see no. 13); the central part was named sp1 and the two lateral parts sp2 (abbreviation of 'Sklerit-spangen'). A complete, undivided bridge is considered the plesiomorphous condition in Tipulidae by Oosterbroek (1980), who supposed it to be homologous with a structure in the Trichoceridae (the Fp-Fp connection in Neumann, 1958; fig. 35), which is the presumed sister group of the other three families of the infraorder Tipulomorpha (Cylindrotomidae, Limoniidae and Tipulidae) (Savchenko, 1966; Hennig, 1973). A complete bridge was found in some Limoniidae (e.g. *Pedicia rivos*a, fig. 36) and the parameres mentioned by Peus (1952) for the Cylindrotomidae presumably are homologous with parts of the genital bridge. A complete bridge appears to be a widespread character among the more primitive genera in the adopted phylogeny of Oosterbroek & Theowald (in prep.), e.g. in species of *Clytocosmus*, *Longurio*, *T. (Arctotipula)*, *Holorusia*, *T. (Tipula)*, *T. (Platytipula)*, *T. (Yamatotipula)*, *Dolichocheza*, *T. (Lunatipula)*, *T. (Vestiplex)*, *Prionocera*. The breaking up of the bridge in a central (sp1) and two lateral parts (sp2), as found in many genera, must be considered a reduction (Oosterbroek, 1980). In other taxa, including *Nephrotoma*, only the sp2 are present. In the closely related outgroups of *Nephrotoma* there is found a complete bridge in species of *T. (Dendrotipula)* (fig. 37) and only the sp2 in the other taxa (Ctenophorinae, *Nigrotipula* and *Scamboneura*; fig. 38).

The form of the sp2 can be rather variable within *Nephrotoma*, they frequently are more or

less hollow shell-like structures with small to large internal extensions, which are frequently fitted with some hairs (figs. 39-41). Observation of copulations suggests that the sp2 give some support at the hypovalvae, which are resting in the hollow surfaces during copulation (fig. 7). In the *dorsalis* species-group the sp2 are bald and largely V-shaped (figs. 66, 67).

9. The semen pump

Various terms have been applied to the basal part of the median phallic organ, such as 'vesica' (Edwards, 1938; Tjeder, 1948; Byers, 1961; Dobrotworsky, 1968), 'aedeagus' (Mannheims, 1958; Oosterbroek, 1980), 'Penisblase' (Neumann, 1958), 'Samenblase' (Savchenko, 1966), 'basal bulb of penis' (Rees & Ferris, 1939) and 'basiphallus' (McAlpine, 1981). Following the terminology used by Frommer (1963) and Hennig (1973) it is called here the semen pump. The frequently used term 'aedeagus' may cause confusion, because it has been used for different structures: frequently for the complete phallic organ including the semen pump, the intromittent organ and the adminiculum, but sometimes only for the semen pump or the semen pump with the intromittent organ.

In Tipulidae the semen pump, situated midventrally inside segment 8 or 9, is connected with other parts of the hypopygium by muscles, or in some taxa also by sclerotized connections (the adminicular rods, see no. 11). It bears three sets of appendages: a pair of lateral appendages, a pair of posterior ones and the unpaired, usually bifid and dorsally placed compressor apodeme (figs. 1, 42-44). These appendages vary in shape and size throughout the Tipulidae; according to Frommer (1963) there is a relative increase in the size of the appendages in *Nephrotoma*. The central vesicle of the semen pump is bulbously swollen in many of the outgroups (figs. 42, 43, 45, 46) and rather flat in most species of *Nephrotoma* (figs. 44, 47-49), a reduction according to Frommer (1963). Muscles attach at the appendages by which the semen pump is able to rotate in the sagittal plane, in order to push the intromittent

organ caudally outside the hypopygium. The degree of rotation varies: it amounts to about 90° in species of *Longurio* and *Brachypremna* (Oosterbroek, 1980), 180° in *Tipula paludosa* (Neumann, 1958) and about 270° in *T. (Schumelia)* (Oosterbroek, 1980). In a male of *Nephrotoma tenuis* captured in copula, no rotation of the semen pump could be observed, while in such a male of *Nephrotoma appendiculata* a rotation of about 120° was observed. The dorsal compressor apodeme is movable, which may cause a change in the volume of the central vesicle in order to expel the semen into the intromittent organ. The supply of semen passes through the seminal duct, which is connected to the testes.

10. The intromittent organ

From the semen pump, the penis or intromittent organ in Tipulidae arises rostrally, curves forward and downward within a membranous pouch and runs further caudad through the membranous floor of the genital chamber and out through the adminiculum (figs. 1, 4, 46-49). It is a flexible, tubular organ, usually throughout its length, presumably consisting of an inner and outer tube as observed in some taxa (Frommer, 1963), and sometimes branching in the apical part. Its primary function is to transfer sperm to the female reproductive system. In its retracted position the intromittent organ lies with its tip inside the adminiculum, from where it is pushed outside the hypopygium into the bursa copulatrix of the female during copulation, by rotation of the semen pump and contraction of the membranous pouch.

The length of the intromittent organ varies greatly, both in the outgroups (from 0.25-16.4 mm) as well as within *Nephrotoma* (1.66-40.16 mm) (Oosterbroek, 1980). The intromittent organ enters the bursa copulatrix as far as the anterior end where the three spermathecal ducts meet, and reaches according to Neumann (1958) even further into these ducts. Oosterbroek (1980) presumes that the length of the intromittent organ and that of the bursa copulatrix are probably correlated because of the fact that in *Oropeza* both are longer than in

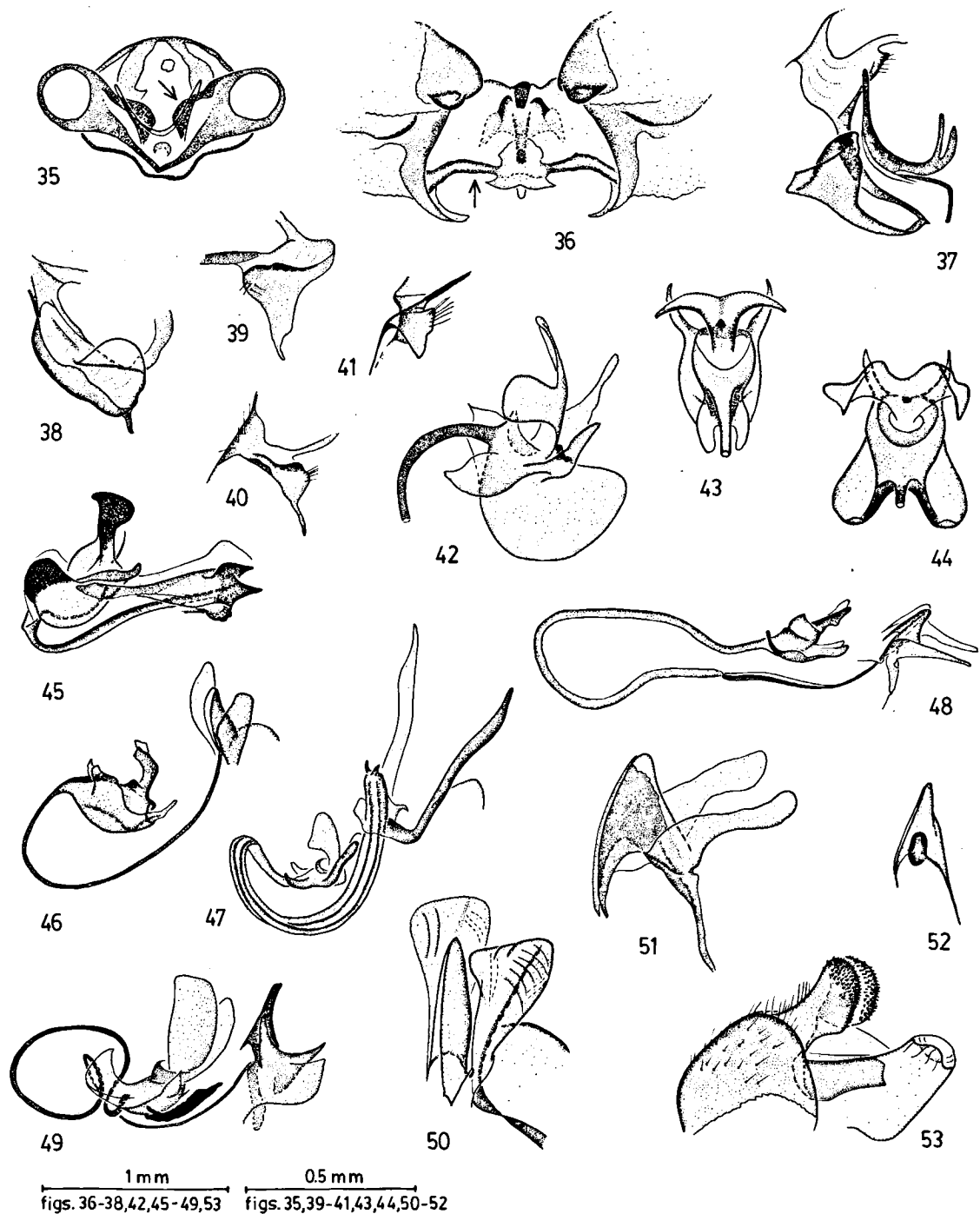


Fig. 35. *Trichocera annulata*, hypopygium, caudal view, gonostyle removed. Fig. 36. *Pedicia rivos*a, hypopygium, dorsal view, T 9 removed. Fig. 37. *T. (Dendrotipula) flavolineata*, genital bridge and adminiculum, lateral view. Fig. 38. *Ctenophora flaveolata*, sp2, inside. Fig. 39. *Nephrotoma rectispina*, sp2, inside. Fig. 40. *N. repanda*, sp2, inside. Fig. 41. *N. flavipalpis*, sp2, inside. Fig. 42. *Tanyptera atrata*, semen pump, lateral view. Fig. 43. *Scamboneura vittifrons*, semen pump, dorsal view. Fig. 44. *Nephrotoma analis*, semen pump, dorsal view. Fig. 45. *Prionocera turcica*, semen pump, intromittent organ and adminiculum, lateral view. Fig. 46. *Scamboneura spec.*, idem. Fig. 47. *Nephrotoma rectispina*, idem. Fig. 48. *N. flavescens*, idem. Fig. 49. *N. perincisa*, idem. Fig. 50. *Scamboneura vittifrons*, adminiculum and gonapophyses, lateral view. Fig. 51. *Nephrotoma crocata*, idem. Fig. 52. *N. scurroides*, idem. Fig. 53. *T. (Tipula) oleracea*, T 9 and anal cone, lateral view.

Dolichocheza s.s. (Byers, 1961), and he also assumes (as Frommer, 1963) that a short intromittent organ represents the plesiomorphous condition in Tipulidae. This is because the development of an intromittent organ inbetween the semen pump and the adminiculum seems to be a new development within the Tipulomorpha, being absent in the Trichoceridae and relatively short, uncurved and directed caudally in the Cylindrotomidae (Peus, 1952) and Limoniidae (Edwards, 1938; Savchenko, 1966). Lengthening of the intromittent organ, and possibly also secondary shortening, has occurred in different taxa. In the closely related outgroups of *Nephrotoma* a rather short intromittent organ can be found (fig. 46), while within *Nephrotoma* the length of the organ ranges from rather short to strongly lengthened and winding (figs. 47-49). Within the *dorsalis*-group the organ is tubular and unbranched throughout its length.

11. *The adminiculum*

This is a sclerotized structure situated on the middorsal margin of sternum 9 which serves as a support and guide for the intromittent organ. The commonly used name 'adminiculum', which means 'support', was introduced by Westhoff (1882) because of the form and function of this organ; it is frequently termed 'aedeagal guide'. The adminiculum is composed of two fused lateral elements, derived from the intersegmental membrane between segments 8 and 9 (Frommer, 1963). During copulation it is directed far caudally, its top reaching the genital opening of the female. In its simplest form the adminiculum is a flat, plate-like structure with a median groove which embraces and guides the intromittent organ; but in many taxa, for example in *Nephrotoma* and the closely related outgroups, it is a more or less cone-shaped tube (figs. 46-52) bearing in some species (e.g. in the *dorsalis*-group) anterior modifications. In some genera (e.g. *Prionocera*, *Dolichocheza*) a pair of distinct sclerotized connections run between the adminicular base and the semen pump (fig. 45), lying in the membranous

floor of the genital chamber. They were called adminicular rods by Byers (1961) and basal parts of the parameres by Tjeder (1948), who compared these connections in *Prionocera* with the fused semen pump-adminiculum in Limoniidae. In some taxa (*Dolichocheza* s.s., *T. (Schummelia)*) these rods are not connected with the semen pump; in many *Nephrotoma* species only small isolated rods are present (e.g. *cornicina*-group, *brevipennis*-group, *crocata*-group, fig. 49) or they are completely absent as in the *dorsalis*-group, which clearly may be considered a reduction. In the closely related outgroups of *Nephrotoma* no adminicular rods have been observed.

12. *The gonapophyses*

Articulating with the lateral base of the adminiculum and the middorsal margin of sternum 9 there is usually a pair of appendages, the gonapophyses, a term used by, among others, Snodgrass (1904), Alexander (1942) and Byers (1961). After the latter, "the gonapophyses of male insects are median projections in proximity to the gonopore". They ascertain the correct position of the adminiculum between the female cerci and hypovalvae, and serve as accessory structures for supporting and directing the intromittent organ and perhaps also for protecting the organ while in rest. These structures, called parameres by Edwards (1938) and McAlpine (1981) and lateral appendages of adminiculum by Oosterbroek (1978), are "surprisingly constant throughout the order of Diptera and only rarely are they indistinguishable or absent" (McAlpine, 1981). According to the latter author the parameres, or gonapophyses, are homologous throughout the Diptera; but Byers (1983) considers the gonapophyses in *Chionea* as probably not homologous with the gonapophyses of some other Tipulids, *Dolichocheza* for example. Within the genus *Nephrotoma* the shape of the gonapophyses varies from very small and unmodified (fig. 52) to bulbously thickened, elongated and/or with several extensions or modifications (figs. 47-49, 51). Within the *dorsalis*-group the broadened

and flattened gonapophyses do have dorsally directed upcurved tips, which distinctly is an apomorphous condition (figs. 68, 69).

13. *The genital cavities*

The membranous sac in which the intromittent organ is found is called the genital chamber; it is formed by an invagination of the intersegmental membrane between the ninth and tenth segment (Frommer, 1963). Sometimes the chamber is rostrally extended as a membranous pouch. The wall of the chamber is contiguous with the base of the semen pump and the dorsal wall may be more or less sclerotized as a part of the already mentioned genital bridge (see no. 8). This sclerotization is presumably the tegmen of Edwards (1938), and is called the epimere by Rees & Ferris (1939), unnamed by Frommer (1963) and named sp1 by Neumann (1958). The cavity in which the female hypovalvae are inserted during the copulation is formed by the invaginated anal cone (proctiger) and the connected blindsack (Neumann, 1958), sometimes also called genital chamber (Byers, 1961).

14. *The proctiger*

The cone-shaped, usually membranous proctiger or anus bearing region lies just beneath the apex of the ninth tergite. This structure is (tentatively) assigned to segments ten and eleven (Edwards, 1938; Rees & Ferris, 1939; Frommer, 1963), to the tenth segment (Snodgrass, 1904; Byers, 1961) or to the eleventh segment (McAlpine, 1981). In some taxa the proctiger is dorsally covered by two sclerotized anal plates (fig. 53), called the tenth tergite by Rees & Ferris (1939); within *Nephrotoma* the structure is completely membranous. Sclerotizations in the ventral wall of the proctiger are called hypoproct and assigned to the eleventh sternum by McAlpine (1981). During copulation the proctiger is invaginated rostrally in order to receive and hold the female hypovalvae (Neumann, 1958).

15. *General remarks*

Within the Tipulomorpha (Trichoceridae, Cy-

lindrotomidae, Limoniidae and Tipulidae) there seem to be a 'trend' towards increasing the mobility of the male hypopygium which arose in several lineages independently. This greater mobility of the hypopygial parts is achieved partly by the reduction of the genital bridge (see no. 8), the reduction of the sclerotized connection between the adminiculum and the semen pump (see no. 11), the reduction of the sclerotizations (plates and ventral stem) on the ventral surface of sternum 9 (see no. 4) and the separation of tergite 9 and sternite 9 (see no. 2).

Females

The structures of the female genitalia have up to now been frequently neglected or underrated in both phylogenetic and taxonomic work. This is only partly due to the lack of material and the difficulty in identification of female Tipulids (positive exceptions are Byers, 1961, 1983; Oosterbroek, 1978-80; Vermoolen, 1983). Snodgrass (1903) stated with respect to the abdomen of female Tipulids that "there is but one type of structure throughout the entire family, and that the generic and specific modifications of this type are but slight. The contrast between the males and the females in this respect is very striking. The modifications of the female parts are insignificant when compared with the enormous variety of hypopygial structure in the males". I do not agree with this statement. Although the male hypopygium usually shows more differentiated characters than the female, the structures found especially in the hypovalvae show distinct variations and are of significant importance for phylogenetic analysis. All the elements of the female terminalia, including the cerci, are often called the *ovipositor* in the Diptera, although as such it is not homologous with the true orthopteroid-type ovipositor (Crampton, 1942; McAlpine, 1981). The term 'ovipositor' however, rather refers to the function of oviposition (Byers, 1961). The eighth through eleventh segments of the female abdomen are modified to form the ovipositor (figs. 2, 3).

1. *The genital chamber*

The genital opening, situated in the inter-segmental membrane between sternites 8 and 9 (Frommer, 1963), leads to the genital chamber, that is the space between the dorsal surface of the eighth sternum and the ventral surfaces of the ninth and tenth segments (Snodgrass, 1903). It is the place where the eggs are fertilized. The posterior part is called the bursa copulatrix, an elongated cylindrical tube which branches more anteriorly into the three spermathecal ducts, which each run out into a round or oval spermatheca in which usually the spermatozoa are stored. The median or common oviduct, connected with the paired ovaries, terminates in the gonopore, the lower opening of the genital chamber, which rises slightly from the inner floor of the hypovalvae (Byers, 1961; Frommer, 1963; fig. 2).

2. *Sternum 8 with the hypovalvae*

In contrast with the unmodified tergum 8, sternum 8 is elongated and reaches far beyond its tergum. From the distal end it is projected posteriorly in the form of a pair of blade-like processes, the hypovalvae, also called egg-guides (figs. 61, 62). During copulation the hypovalvae are inserted into the male genital cavity (formed by the invaginated proctiger and blindsack) and are firmly held there by means of a mutual anchorage (figs. 4, 7). In Tipulids the inner surfaces of the hypovalvae are usually rough or pubescent and/or possess one or two sclerotized longitudinal folds (major and minor ridges), which the males inner dististyles can seize during copulation, and which also function in oviposition. Between the bases of the hypovalvae a cup-like cavity (internal shell) is usually formed, where the eggs pass by just before oviposition (Oosterbroek, 1978). The basal median area is fitted with small, more or less sclerotized spines (the spined area) in all the Tipulids examined (fig. 3).

The hypovalvae were considered as 'gonapophyses' (Rees & Ferris, 1939) or 'appendages' (Snodgrass, 1903) of the eighth segment, but Frommer (1963) considered them rather a modified portion of the sternal region. They

vary throughout the Tipulidae from developed, elongate and sclerotized to very small and fleshy. Several authors consider the small hypovalvae as reduced (Savchenko, 1966; Oosterbroek, 1980 for the *cornicina*-group) or rudimentary (Frommer, 1963), that is to say as the apomorphous condition. The presence of longitudinal ridges on the inner surfaces of the hypovalvae is variable: no ridges present (observed in for example species of *Prionocera*, *Nigrotipula*, *Ctenophora*, *Tanyptera*, figs. 54, 59), only a major ridge distinct (in for example *T. (Dendrotipula)* and the *cornicina*-group, figs. 55, 57), or a major and minor ridge present (in for example *Scamboneura*, *T. (Tipula)* and most species of *Nephrotoma*, figs. 56, 58, 60, 93). Oosterbroek (1980, p. 326) considered the presence of only one ridge in the *cornicina*-group as an apomorphous character versus the plesiomorphous condition of two ridges. In view of the conditions observed in the closely related outgroups of *Nephrotoma* (no ridges or only a major ridge, except in *Scamboneura*, where two ridges are present), it is more likely that the presence of two developed sclerotized ridges represents the derived condition in *Nephrotoma*.

3. *The furca*

This structure, also called the vaginal apodeme (Frommer, 1963), is a small sclerotization in a membranous area of the eighth sternum. According to Snodgrass (1903), it is possibly the fused and rudimentary anterior gonapophyses, a view rejected by Frommer (1963). It lies directly above the common oviduct and ventral of the genital opening and is, according to Frommer (1963) equipped with no muscles of any sort, although Byers (1983) mentions muscles at the furcal base in *Chionea*. The furca is composed of a pair of sclerites of the eighth sternite, which may unite to form a bifid plate (Crampton, 1942). Shape and size may vary within the different genera; the structure is frequently more or less forked (figs. 63-65).

4. *Segment 9, the fused valvulae*

The ninth segment is partly modified into the ovipositor in Tipulidae. Tergum 9 shows no

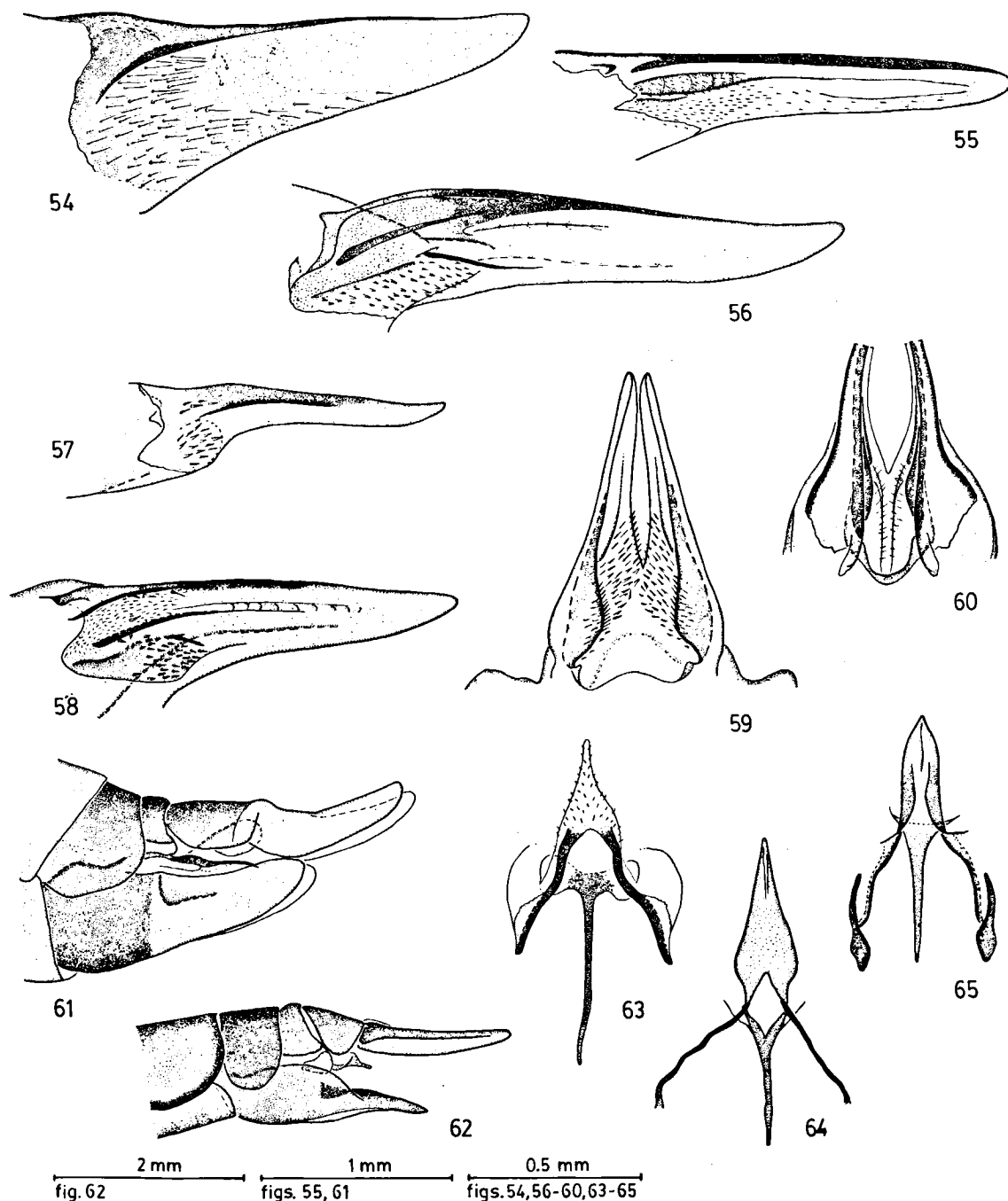


Fig. 54. *Nigrotipula nigra*, right hypovalva, inside. Fig. 55. *T. (Dendrotipula) flavolineata*, right hypovalva, inside. Fig. 56. *Scamboneura* spec., right hypovalva, inside. Fig. 57. *Nephrotoma cornicina*, right hypovalva, inside. Fig. 58. *N. spec.*, *brevipennis*-group, right hypovalva, inside. Fig. 59. *Prionocera turcica*, hypovalvae, dorsal view. Fig. 60. *Nephrotoma fletcheriana*, hypovalvae, dorsal view. Fig. 61. *Ctenophora flaveolata*, ovipositor, lateral view. Fig. 62. *Nephrotoma forcipata*, ovipositor, lateral view. Fig. 63. *Nigrotipula nigra*, fused valvulae and furca, dorsal view. Fig. 64. *Nephrotoma flavescens*, fused valvulae and furca, dorsal view.

special modifications, although it is usually more or less reduced in size. In many taxa the ninth tergite is connected with a chitinized plate at its lower posterior corner, called the coxopodite of tergite 9 (Rees & Ferris, 1939) and considered a separate piece of this tergite (Frommer, 1963). The sternal part of the segment forms the roof of the genital chamber; the median portion, generally called the 'fused valvulae', is sclerotized and usually connected with the coxopodite of the ninth tergite by sclerotized converging arms. The fused valvulae are situated just dorsally of the genital opening; they rest towards the ventral side of the male adminiculum during copulation. This paired structure is generally considered as the ninth sternum (Snodgrass, 1903; Rees & Ferris, 1939; Crampton, 1942; Byers, 1961; Frommer, 1963); it is erroneously called the furca in McAlpine (1981). Snodgrass (1903) considered the two free caudal processes of this structure found in *Tipula angustipennis* as rudimentary second gonapophyses, an unwarranted term according to Frommer (1963). Byers (1961) regarded the fused valvulae in *Dolichopeza* as a modification of the sclerotized anterior ring (antecosta) of the ninth sternum. The shape and size of the fused valvulae vary among the different taxa and they may provide phylogenetically important characters. In the closely related outgroups of *Nephrotoma* the fused valvulae are completely fused to a more or less triangular structure and connected with the coxopodite of tergite 9 by means of more or less sclerotized rods. In species of *Nigrotipula* and *T. (Dendrotipula)* the posterior portion of the structure is fitted with short hairs (fig. 63). Within *Nephrotoma* the fused valvulae are bare and triangular and within different species-groups the sclerotizations are reduced to small separate plates (figs. 64, 65). The connection with the coxopodite of tergite 9 is sclerotized in most species-groups of *Nephrotoma*; except for *sodalis* this connection is largely or completely membranous in members of the *dorsalis*-group.

5. The cerci

The paired cerci are the dorsal terminal pro-

cesses of the ovipositor. Several authors consider them derived from the eleventh segment, although usually no distinct fragments of tergum 11 can be found in female Tipulids and the cerci do arise at the apex of the tenth tergum. Moreover the muscles associated with the cerci largely arise from the tenth tergite (Frommer, 1963). No sclerotized tenth sternal plate can be found in female crane flies (Frommer, 1963). During copulation the cerci lie alongside the ventral region of the male hypopygium, and they do not seem to serve a special function in this, although Neumann (1958) reports that females of *Tipula paludosa* from time to time do brush the cerci along the lateral parts of the male hypopygium, which induces a new contraction of the dististyle-muscles. The cerci are usually more associated with oviposition, when the tip of the abdomen is thrust into the substrate in which the eggs are deposited.

The cerci are primitively two-segmented in female Diptera, but are independently reduced to one segment in many groups, for example in all Tipulomorpha (Hennig, 1973). They are usually well developed and elongate in Tipulidae (figs. 61, 62), sometimes reduced to fleshy lobes (Frommer, 1963). The elongate and blunt cerci found in the majority of the Tipulidae are considered plesiomorphous by Oosterbroek (1980), while the pointed cerci found in the *Nephrotoma cornicina*-group represent the apomorphous condition. Within the different species groups there is less variability in the structure of the cerci.

6. The infra-anal plate

The infra-anal plate, situated below the bases of the cerci and directly below the anus, is generally considered to be the remnant of the tenth and/or eleventh sternum. It is usually a fleshy, flap-like appendage, frequently more or less divided into two and set with short to long hairs. During copulation this plate is moving, and touches the membranous median area of the males sternite 9 with its tip (Neumann, 1958, for *Tipula paludosa*). This structure hardly varies between the different taxa.

THE PHYLOGENY OF THE NEPHROTOMA DORSALIS-GROUP

Introduction

Oosterbroek (1978-80) revised the western palaearctic species of *Nephrotoma* and designated four species-groups:

1. the *cornicina*-group: a palaearctic species-group with only one, presumably introduced species (*cornicina*) in the Nearctic;
2. the *brevipennis*-group: a species-group distributed from Africa, the Macronesian Islands and South-, Central- and North America to the eastern Palaearctic, from where one species is known;
3. the *crocata*-group: a species-group occurring in the palaearctic and nearctic regions and probably also in the oriental region;
4. the *dorsalis*-group: a species-group with a holarctic distribution, represented by 20 species in the Nearctic and by 29 species in the Palaearctic.

Besides these four species-groups several others can be recognized especially among the many species of the tropical regions, but a revision is needed before these groups can be formalized. This makes it difficult to establish the sister group of the *dorsalis* species-group. As already mentioned, the sister-group relationship of the *cornicina*- and *dorsalis*-groups as proposed by Oosterbroek (1980, p. 325) is not followed here. Examination of a great number of *Nephrotoma* species revealed that the six so-called weak characters on which the sister-group relation was based, could not be retained as synapomorphies, at least not on this level of analysis: Character 1 refers to the "presence of a mid-ventral projection", which is the same structure as the medisternal appendage of sternite 9, which is present in members of the *crocata*-group as well. An elongate od (character 2) is only found in some subgroups within the *dorsalis*-group, while it is also found in members of other groups. Longitudinally arranged abdominal spots (character 3) are not limited to the *cornicina* and *dorsalis* species-groups. The orientation of the gonapophyses (character 4) is

strongly variable in most species-groups. The rugosity on the inner surface of the hypovalvae (character 5) is also present in the primitive members of the *dorsalis*-group as well as in (some) members of the *cornicina*-group, so the absence cannot be a synapomorphy for those groups. The lateral shell of the id (character 6) can be strongly variable; in members of most species-groups, including the *cornicina* and *dorsalis* groups, the presence of an upright outer margin, which is considered plesiomorphous by Oosterbroek (1980), does occur, so the absence cannot be a synapomorphy for both groups.

In my view the *dorsalis*-group is more related to the *brevipennis*- and *crocata*-groups, because of the possession of two ridges on the internal side of the hypovalvae and the completely medially incised posterior extension of tergite 9 of the male, both considered apomorphous (see p. 143, 151). How the supplementary species-groups will fit in the phylogenetic system of the genus *Nephrotoma* is still unknown, so outgroup comparisons for the purpose of the phylogenetic analysis of the *dorsalis*-group will be made with all the non-*dorsalis* species examined.

Monophyly of the *dorsalis*-group

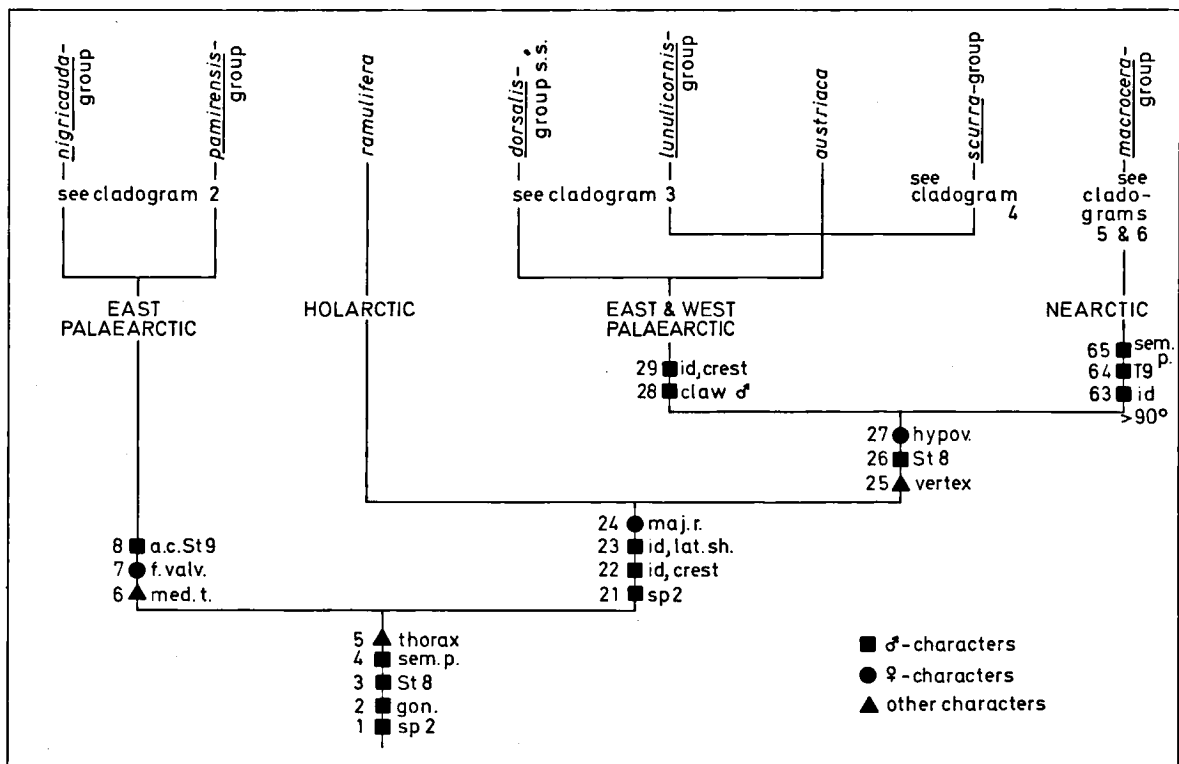
Oosterbroek (1980) examined the western palaearctic species of *Nephrotoma* and assigned 7 species to the *dorsalis*-group, the monophyly of which he based on nine synapomorphies. Examination of all the present known species of the group (47) showed that three characters could be retained for the entire group, whereas the others were either not distinguishable in all the members of the group (no. 18, membranous connection of the fused valvulae with tergite 9; no. 24, gonapophyses confluent with sternite 9) or found outside the *dorsalis*-group as well (no. 19, caudal lengthening of the male sternite 9; no. 20, narrow prolongation at the base of the id; no. 21, narrow prolongation at the base of the od; no. 22, sclerotized ring around the bases of the id and od not strongly bent).

The monophyly of the *dorsalis*-group is based on the next five synapomorphous characters:

1. In the *dorsalis*-group the sp2 (a supposed

remnant of the genital bridge) is large, rounded and folded, without hairs and with variable transparent extensions along the base (figs. 66, 67). A largely unfolded sp2, usually partly fit with hairs, as found in the non-*dorsalis* species of *Nephrotoma* and outside the genus has to be considered the plesiomorphous condition (figs. 38-41). This character for the *dorsalis*-group was already mentioned by Oosterbroek (1980, p. 346), although not as a synapomorphy.

2. The gonapophyses are basally broad and have dorsally directed, upcurved tips (figs. 68, 69), with further modifications in the *dorsalis*-group s.s., the *lunulicornis*-group and the *macrocera*-group except *sodalis*. This character-state is restricted to the *dorsalis*-group s.l. and apparently a condition derived from the small and unmodified gonapophyses found within and outside *Nephrotoma* (Oosterbroek, 1980, p. 326, character no. 23).
3. The male sternite 8 is medially incised in all the members of the *dorsalis*-group, ranging from weakly to deeply incised (figs. 70, 71, 78). An unmodified sternite 8 with a straight hind margin is clearly the plesiomorphous condition (see p. 143). The modifications of sternite 8 found in other species-groups within *Nephrotoma* (e.g. the deep and wide membrane-covered incisions in some members of the *crocata*-group) are supposed to be parallel developments (Oosterbroek, 1980, p. 326, character no. 25).
4. The posterior appendages of the semen pump are more or less convergent in all the members of the *dorsalis*-group (fig. 72). They are sometimes parallel and usually divergent in other species of *Nephrotoma* and outside the genus (Oosterbroek, 1980, p. 327, character no. 26).
5. A completely shining thoracic surface, including the pleural parts, is found in the



Cladogram 1. Basal phylogeny of the species-groups.

dorsalis-group only and must be considered a derived condition within *Nephrotoma*. The species of the *nigricauda*-group form an exception with their partly shining thoracic surface with limited opaque areas, which is supposed to be a relapse into a more primitive condition (5.1).

Phylogeny of the *dorsalis*-group

Cladogram 1 shows the basal phylogeny of the *dorsalis*-group, the other cladograms (2 to 6) show the detailed phylogeny of the subgroups; the numbers refer to the following characters:

6. The mediotergite usually bears a dark median stripe on the anterior part in species of *Nephrotoma* (fig. 73). In the *nigricauda*- and *pamirensis*-groups this anterior stripe is completely lacking, which must be considered a reduction. In the nearctic species *rogersi*, *macrocera* and *gnata* a similar reduction of this stripe can be found. Another and correlated primitive feature of the mediotergite is the presence of darkened lateral sides, found in *kaulbacki*, *pamirensis*, *pjotri* and *perobliqua*.
7. The fused valvulae of the female are usually fused into a sclerotized structure within *Nephrotoma* and in the outgroups. In some subgroups (e.g. the *nigricauda*- and *pamirensis*-groups, but also the *crocata*-group s.s. this structure is reduced to smaller separate plates (figs. 74, 103, 154), clearly a parallel development but a synapomorphy on the subgroup-level (see also characters 38, 48 and 88). However, the females of *libra*, *violovitshi* and *perobliqua* are unknown, so the synapomorphy is partly an interpretation. The separate plates are characteristically sickle- to oval-shaped in the *nigricauda*- and *pamirensis*-groups (fig. 74).
8. As mentioned before (p. 144) the presence of two distinct lateral appendages on the antecosta of sternite 9 is considered plesiomorphous within *Nephrotoma* (fig. 75). These appendages are reduced in the *nigricauda*- and *pamirensis*-groups (fig. 76), a condition also observed in the *macrocera*-group and the *lunulicornis*- and *scurra*-groups (see character 40).
9. The caudal corners of male sternite 8 are distinctly extended beyond the hind margin (figs. 70, 78) in the *nigricauda*-group, clearly a unique and derived condition within the *dorsalis*-group and incomparable with the modifications of sternite 8 in the *dorsalis*-group s.s. (character 35).
10. The anterior margin of the gonapophyses is distinctly curved in the members of the *nigricauda*-group (fig. 77), a condition not found elsewhere within the *dorsalis*-group or in other *Nephrotoma* species.
11. The posterior margin of the od is characteristically curved and the tip slenderly elongated in the *nigricauda*-group (fig. 79); these are derived modifications.
12. A reduction of the basistyle in the *nigricauda*-group (fig. 76), which will be further discussed under character 68.
13. The male sternite 8 bears black spines on the top or just underneath the caudal corners in *electripennis* and *nigricauda* (figs. 70, 78), a distinctly unique acquisition, indicating the involvement of sternum 8 in the copulation.
14. The lateral thickenings on the inner surface of the posterior extension of tergite 9 are ridge-like (fig. 80) in members of the *pamirensis*-group.
15. The posterior extension of male tergite 9 bears a deep V- to U-shaped median incision in *pamirensis*, *pjotri*, *violovitshi* and *perobliqua* (figs. 81, 82), a synapomorphous character at this subgroup-level.
16. The occipital marking is characteristically onion-shaped in all the four species of this subgroup (fig. 83).
17. Within the *dorsalis*-group the basal shape of the main body of the id is a more or less rectangular plate, anteriorly prolonged at its apex into the upper beak, and more or less with a right angle between the dorsal margin and the straight posterior margin (fig. 84). It is hardly possible to submit this character to outgroup comparisons, because of the strong variation of the id in

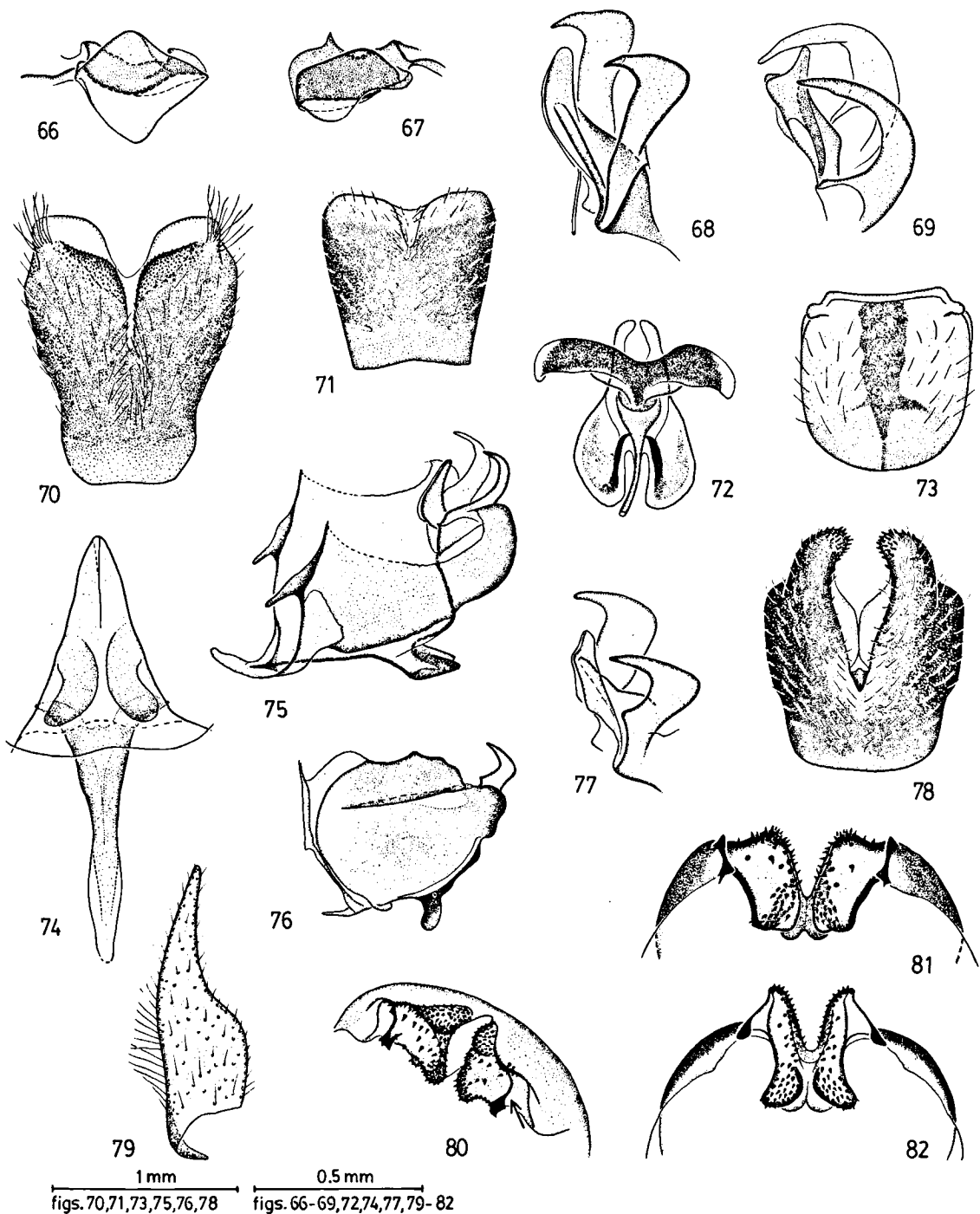
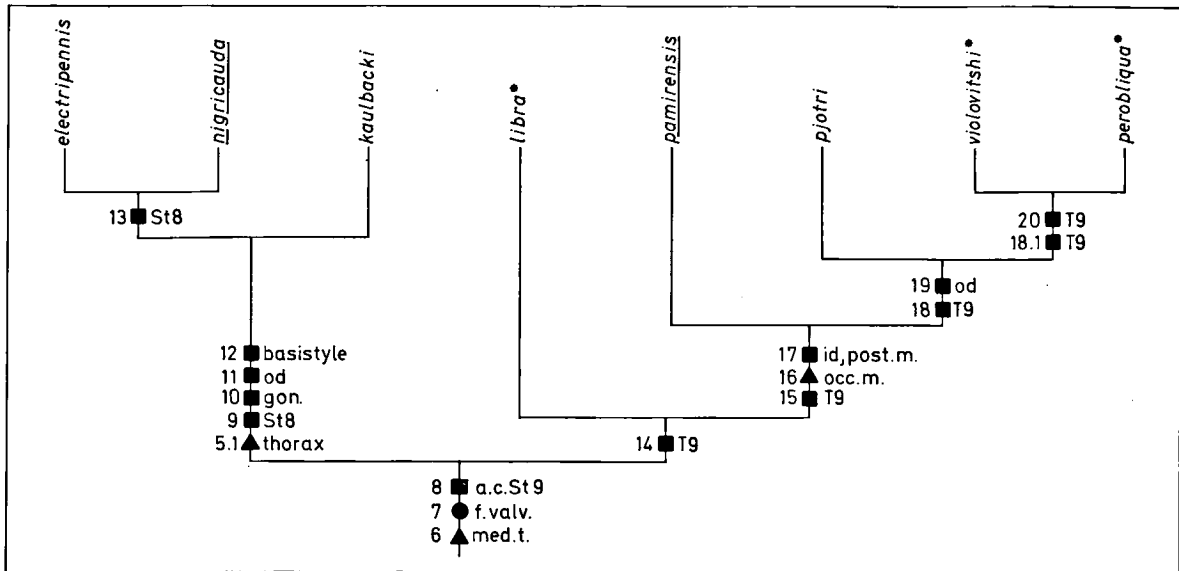


Fig. 66. *Nephrotoma electripennis*, sp2, inside. Fig. 67. *N. ramulifera*, sp2, inside. Fig. 68. *N. pjotri*, adminiculum and gonapophyses, lateral view. Fig. 69. *N. excelsior*, idem. Fig. 70. *N. electripennis*, St 8 of ♂, ventral view. Fig. 71. *N. perobliqua*, St 8 of ♂, ventral view. Fig. 72. *N. violovitshi*, semen pump, dorsal view. Fig. 73. *N. cirrata*, mediotergite, dorsal view. Fig. 74. *N. pjotri*, fused valvulae and furca, dorsal view. Fig. 75. *N. ramulifera*, St 9, dorso-lateral view. Fig. 76. *N. electripennis*, St 9, lateral view. Fig. 77. *N. electripennis*, adminiculum and gonapophyses, lateral view. Fig. 78. *N. nigricauda*, St 8 of ♂, ventral view. Fig. 79. *N. nigricauda*, od, outside. Fig. 80. *N. pamirensis*, T 9 of ♂, caudo-latero-ventral view. Fig. 81. *N. pjotri*, T 9 of ♂, inside. Fig. 82. *N. violovitshi*, T 9 of ♂, inside.



Cladogram 2. Phylogeny of the *nigricauda*-group and the *pamirensis*-group. *Female unknown.

the different groups. The posterior margin of the id of *pamirensis*, *pjotri*, *violovitshi* and *perobliqua* is distinctly curved (fig. 85), which may be considered apomorphic.

18. The median protuberances on the inner surface of the posterior extension of male tergite 9 show a tendency to elongate in anterior direction in *pjotri* (fig. 81), this elongation being more strongly developed in *violovitshi* and *perobliqua* (18.1; fig. 82). Short median protuberances clearly represent the plesiomorphous condition within *Nephrotoma*, as they were found in all the non-*dorsalis* species examined. In the *dorsalis*-group elongation of the median parts of the posterior extension occurs within different groups (e.g. the *nigricauda*-group and the *lunulicornis*- and *scurra*-groups, see character 41).
19. The outer dististyles have somewhat elongated tips and long hairs along the anterior margin in *pjotri*, *violovitshi* and *perobliqua* (fig. 86).
20. The posterior extension of male tergite 9 has strongly produced lateral corners in *violovitshi* and *perobliqua* (fig. 82).
21. In the *nigricauda*- and *pamirensis*-groups the sp2 is folded but not completely V-shaped,

while it is distinctly V-shaped in all the other species of the *dorsalis*-group, a condition considered apomorphic (see also character 1, figs. 87-89). Moreover, in the *nigricauda*- and *pamirensis*-groups the internal flap-like extension at the base is large and triangular, a condition frequently seen in the outgroup (e.g. the *crocata*-group, the *brevipennis*-group, the *cornicina*-group) and considered the less derived state by Oosterbroek (1980, p. 346). This flap is reduced in the other members of the *dorsalis*-group. So the completely V-shaped sp2 with a more or less reduced internal flap is considered a synapomorphy for *ramulifera* up to and including the *macrocera*- and *scurra*-groups (figs. 89, 117).

22. The crest of the id is more or less limited to the dorsal region of the dististyle, while it is also distinctly lobed basally in *ramulifera* up to and including the *macrocera*- and *scurra*-groups (figs. 89, 96, 118, 161). This type of crest is considered a synapomorphy for this group. The plesiomorphous condition, a crest not basally lobed and extended along the dorsal and upper posterior region of the id, is found in the *nigricauda*- and *pamirensis*-groups and many non-*dorsalis* species of *Nephrotoma* (figs. 84, 85, 87, 88).

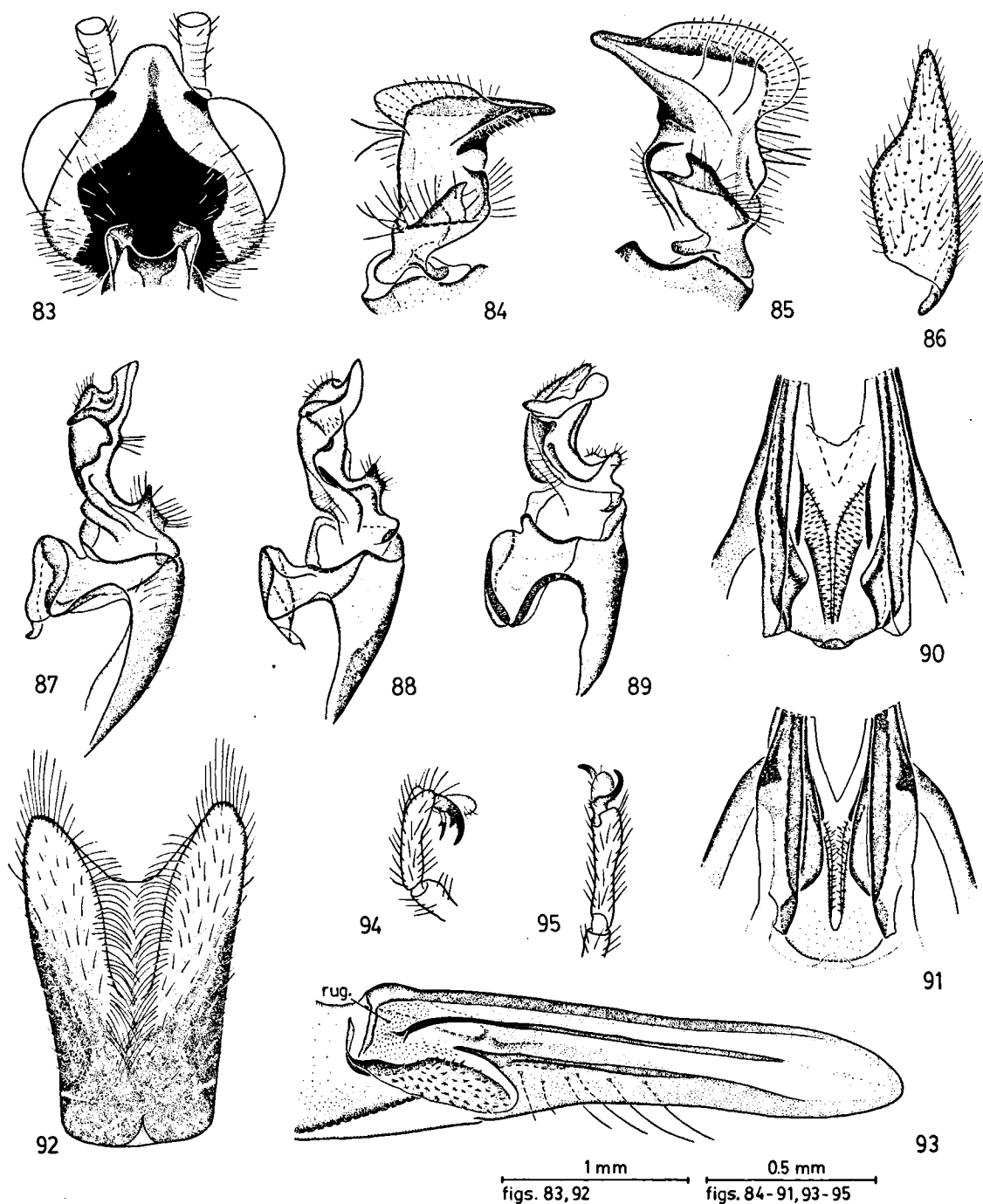
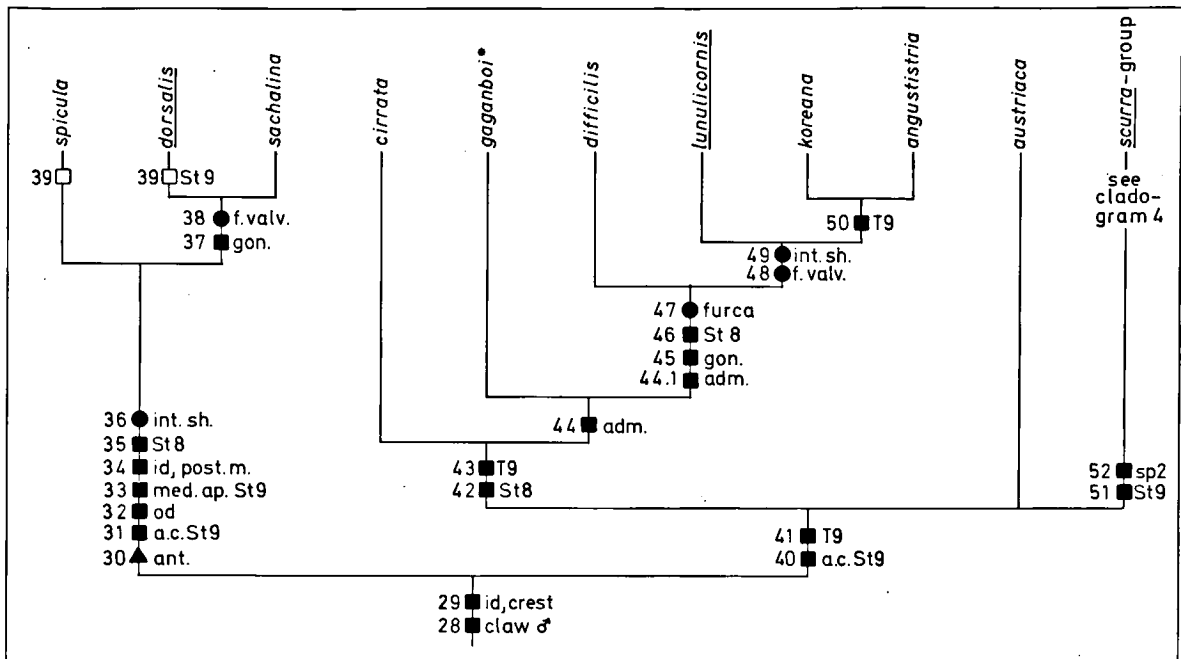


Fig. 83. *Nephrotoma pjotri*, head, dorsal view. Fig. 84. *N. kaulbacki*, id, outside. Fig. 85. *N. pamirensis*, id, outside. Fig. 86. *N. perobliqua*, od, outside. Fig. 87. *N. electripennis*, id, anterior view. Fig. 88. *N. pamirensis*, id, anterior view. Fig. 89. *N. ramulifera*, id, anterior view. Fig. 90. *N. pjotri*, hypovalvae, dorsal view. Fig. 91. *N. cirrata*, hypovalvae, dorsal view. Fig. 92. *N. laticrista*, St 8 of ♂, ventral view. Fig. 93. *N. pjotri*, right hypovalva, inside. Fig. 94. *N. ramulifera*, tarsal claw ♂. Fig. 95. *N. spicula*, tarsal claw ♂.

23. The lateral shell of the id has a more or less horizontal orientation, a synapomorphy for *ramulifera* up to and including the *macrocera*- and *scurra*-groups, as concluded from outgroup comparison (fig. 89).
24. The major ridge at the internal side of the hypovalvae has a rather narrow and curved basal part in the *nigricauda*- and *pamirensis*-groups (fig. 90), while this base is more bulbous and elongated in the other species of the *dorsalis*-group (figs. 91, 101, 126), which is considered the apomorphous condition on the basis of outgroup comparison.
25. The surface of the vertex is completely shining or subshining in the *macrocera*-group up to and including the *scurra*-group, a condition only rarely found in other species of *Nephrotoma*.
26. An unmodified sternite 8 in the male, as found in the largest part of Tipulidae, is supposed to be the ancestral condition (see p. 143). In the *pamirensis*-group and *ramulifera* sternite 8 is simple and only weakly medially incised, while in the *nigricauda*-group sternite 8 is uniquely modified (characters 9 and 13). In the *macrocera*-group up to and including the *scurra*-group there is a tendency towards deepening and widening of the median incision of the hind margin (fig. 92), sometimes attended by further modifications (see characters 35, 42, 56, 78, 87). In this group we also see the presence of hairbrushes on the caudal corners of sternite 8 (with a few exceptions: *sodalis*, *cirrata*, *microcera*, *barbigera*). These brushes are absent in *ramulifera* and in the *nigricauda*- and *pamirensis*-groups except for *electripennis*.
27. Presence of a rugosity on the inner surfaces of the hypovalvae, around the base of the major ridge (fig. 93), is a plesiomorphous character, found in all species-groups of *Nephrotoma* and outside the genus. This rugosity is absent in the *macrocera*-group up to and including the *scurra*-group.
28. Within most species-groups of *Nephrotoma* pectinate as well as non-pectinate tarsal claws in the male are found, but the latter apomorphous condition is always restricted to smaller monophyletic groups (Oosterbroek, 1980, p. 337). In the majority of Tipulidae-taxa the male claws are pectinate (fig. 94). In the *dorsalis*-group s.s. up to and including the *scurra*-group the tarsal claws of the male are untoothed (fig. 95), a condition also found in the *macrocera*-group (character 66) except for *sodalis*, the most primitive member of the group. This clearly has to be considered a parallel reduction within those sister groups.
29. The crest of the inner dististyle is slightly to distinctly crenated in the *dorsalis*-group s.s. up to and including the *scurra*-group (figs. 96, 118, 119).
30. The antennae of both males and females of the *dorsalis*-group s.s. are polymerous, with more than the basic 13 antennal segments of other *Nephrotoma*. Polymerous antennae in both males and females occur in other *Nephrotoma*, but are always restricted to smaller monophyletic groups or single species (e.g. the *eucera*-group, character 89).
31. The midventral extension of the antecosta of sternite 9 in males is rather long and spatula-shaped in members of the *dorsalis*-group s.s.; it is more developed than in other species of *Nephrotoma* (fig. 97). A more or less similar condition is also found in the nearctic species *cingulata*.
32. The apex of the od is strongly and slenderly elongated, clearly a derived modification (fig. 100).
33. The medisternal appendage of sternite 9 is characteristically modified into a bilobed extension (fig. 99).
34. The posterior margin of the id bears a small but distinct sclerotized thickening in the species of the *dorsalis*-group s.s., from which some long bristles arise (fig. 96). It is a unique derivation, incomparable with the thickenings found in members of the *scurra*-group (character 54).
35. The male sternite 8 has strongly extended, lobe-shaped and upcurved caudal corners in the *dorsalis*-group s.s., which clearly is a unique acquisition (fig. 98).



Cladogram 3. Phylogeny of the *dorsalis*-group s.s. and the *lunulicornis*-group. *Female unknown.

36. The internal shell at the base of the female hypovalvae is usually a cup-like cavity surrounded by a more or less sclerotized rim, the internal arch. In the three species of the *dorsalis*-group s.s. the internal shell is strongly broadened, a condition not found elsewhere within the *dorsalis*-group s.l. (fig. 101).
37. The gonapophyses (see also character 2) bear large antero-basal extensions in *dorsalis* and *sachalina* which are intricately shaped, especially in *sachalina* (fig. 102). It is a unique acquisition within *Nephrotoma*.
38. The fused valvulae of the female are reduced to narrow, elongated separate plates in *dorsalis* and *sachalina* (fig. 103; see also character 7).
39. Another unique feature, found in *dorsalis* and *spicula*, is the tooth-like or pointed-tapering projection on the caudo-dorsal corners of sternite 9 (figs. 104, 105), which is absent in *sachalina*. A parallel development of this structure in both species can be assumed, although a reduction of this projection in *sachalina* seems more likely.
40. The lateral appendages of the antecosta of sternite 9 are reduced in the *lunulicornis*- and *scurra*-groups and in *austriaca* (see discussion character 8).
41. The median protuberances at the inner surface of the posterior extension of male tergite 9 are characteristically prolonged in anterior direction, accompanied by a distinct narrowing of the median incision in the *lunulicornis*-group, *austriaca* and *scurra*-group (figs. 106-108) (see also discussion character 18).
42. The hind margin of male sternite 8 is deeply incised, while the membrane covering this incision is entirely or partly set with short hairs (figs. 112, 113), in the members of the *lunulicornis*-group (see also character 26).
43. In the species of the *lunulicornis*-group the posterior extension of male tergite 9 is very deeply invaginated between the lateral and the elongated median protuberances at the inner surface (figs. 106, 107).
44. The central part of the adminiculum bears a peculiar anterior extension in *gaganboi*

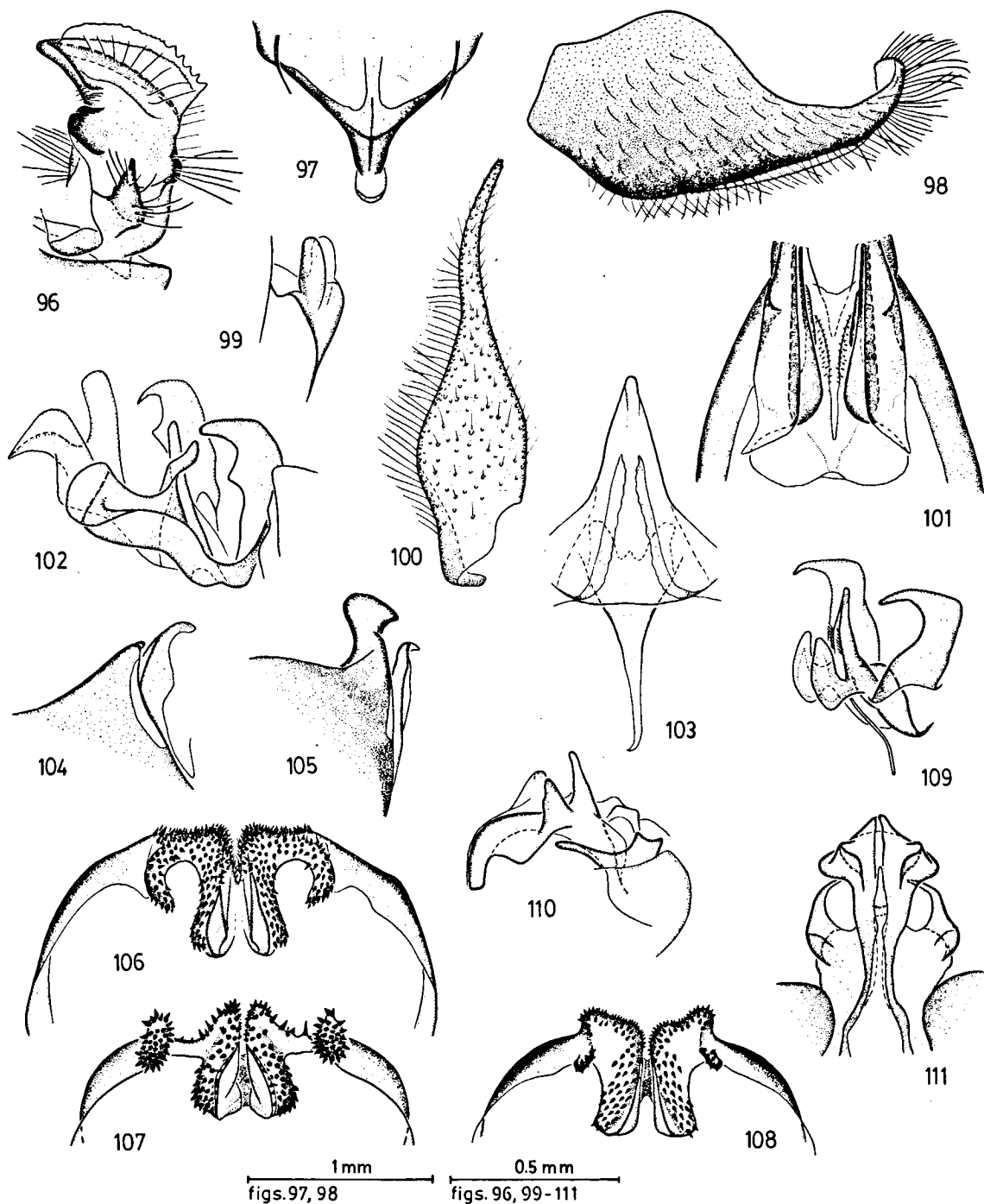
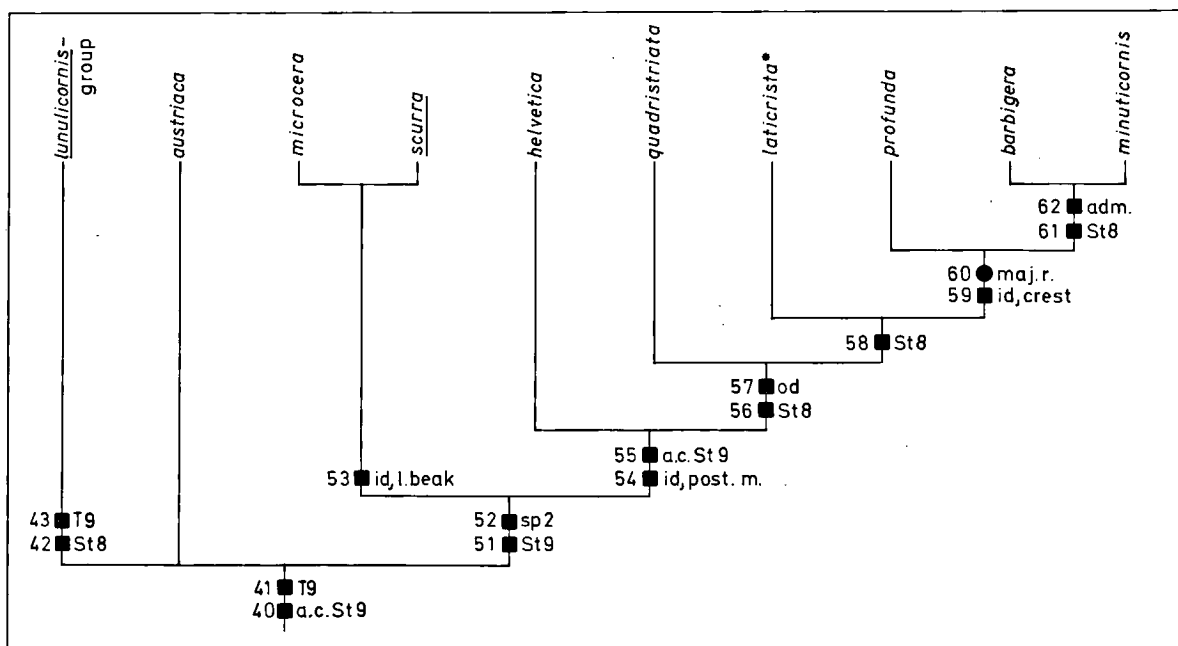


Fig. 96. *Nephrotoma spicula*, id, outside. Fig. 97. *N. dorsalis*, antecosta of St 9, inside. Fig. 98. *N. sachalina*, St 8 of σ , lateral view. Fig. 99. *N. spicula*, medisternal appendage of St 9, lateral view. Fig. 100. *N. sachalina*, od, outside. Fig. 101. *N. dorsalis*, hypovalvae, dorsal view. Fig. 102. *N. sachalina*, adminiculum and gonapophyses, lateral view. Fig. 103. *N. sachalina*, fused valvulae and furca, dorsal view. Fig. 104. *N. spicula*, caudo-dorsal corner of St 9 with left gonapophysis, caudal view. Fig. 105. *N. dorsalis*, idem. Fig. 106. *N. cirrata*, T 9 of σ , inside. Fig. 107. *N. koreana*, T 9 of σ , inside. Fig. 108. *N. laticrista*, T 9 of σ , inside. Fig. 109. *N. gaganboi*, adminiculum and gonapophyses, lateral view. Fig. 110. *N. lunulicornis*, adminiculum and gonapophyses, lateral view. Fig. 111. *N. angustistria*, adminiculum and gonapophyses, caudal view.

- (fig. 109). This extension is much larger and more intricate in *difficilis*, *lunulicornis*, *koreana* and *angustistria* (figs. 110, 111), a strong synapomorphy for these four species (44.1).
45. The gonapophyses usually have dorsally directed and upcurved tips in members of the *dorsalis*-group (character 2). In the four remaining species of the *lunulicornis*-group the upcurved parts of the gonapophyses are reduced, while the bases are pointedly extended anteriorly (figs. 110, 111).
 46. The membrane which covers the incision of male sternite 8 has short hairs lined along the margins (fig. 113) in *difficilis* up to and including *angustistria*, which must be considered a reduction of the entire hair as found in *cirrata* and *gaganboi* (character 42). The condition found in the *eucera*- and *occipitalis*-groups has to be considered a parallel development (character 87).
 47. The furca is relatively large with a strongly developed bifurcation in the four species (fig. 115).
 48. The fused valvulae are reduced to elongated separate plates in *lunulicornis*, *koreana* and *angustistria* (fig. 115; see also character 7).
 49. The internal shell at the base of the hypovalvae is usually sclerotized, but in *lunulicornis*, *koreana* and *angustistria* it is reduced to a more or less membranous structure (fig. 114).
 50. The anterior margin of the posterior extension of male tergite 9 is bulging on both sides of the median incision in *koreana* and *angustistria* (fig. 107).
 51. The caudal corners of male sternite 9 are rather angular in members of the *scurra*-group, a condition most distinctly expressed in *quadristriata* up to and including *minuticornis* (figs. 116, 123, 124). In lateral view these corners are distinctly extended beyond the basistyle and somewhat upcurved. In all the other species of the *dorsalis*-group and in the outgroup these corners are rounded (fig. 112).
 52. The sp2 is large and V-shaped in the *dorsalis*-group (character 1) and is linked up with the dorso-internal edge of the basistyle. Near the connection of the inner flap of the sp2 with the apical ring of the



Cladogram 4. Phylogeny of the *scurra*-group. *Female unknown.

- basistyle, which surrounds the bases of the id and od, there is a characteristic membranous gap in the sclerotization found in all the members of the *scurra*-group (fig. 117). However, this condition is also found in *sodalis*, the most primitive member of the *macrocera*-group, where it must be considered a parallel development.
53. The lower beak of the id, that is the anterior projection connected with the lateral shell, is acutely extended in *microcera* and *scurra* (fig. 118). The rounded-off lower beak found in most species of the *dorsalis*-group and in the outgroup is apparently the plesiomorphous condition. In some species (e.g. *helvetica*, *minuticornis*, *penumbra*, *tenuis*, *gracilicornis*) the lower beak is angular but not acutely extended.
 54. The posterior margin of the id bears a distinct bulge where long bristles are inserted, in *helvetica* up to and including *minuticornis* (fig. 119). It is a unique acquisition for this group and rather weak in *laticrista* only.
 55. The antecosta of sternite 9 shows a striking crack on both sides of the midventral extension in *helvetica* up to and including *minuticornis* (figs. 121, 122), while in all the other species of the *dorsalis*-group the antecosta curves more smoothly.
 56. The hind margin of male sternite 8 is very deeply incised and bears long curving bristles along this incision and on the midventral surface in *quadristriata* up to and including *minuticornis* (figs. 92, 116, 123, 124; see also character 26).
 57. The apex of the od is slenderly elongated in *quadristriata* up to and including *minuticornis* (fig. 120).
 58. The male sternite 8 is distinctly elongated in *profunda*, *laticrista* and *minuticornis* (figs. 92, 123, 124), and somewhat less distinctly in *barbigera*. The ancestral condition is a short eighth sternite.
 59. The crest of the id is somewhat extended along the posterior margin in *profunda*, *barbigera* and *minuticornis* (fig. 119). It is considered a derived condition here, incom-
 - parable with the plesiomorphous state as found in the *nigricauda*- and *pamirensis*-groups (see character 22).
 60. The base of the major ridge of the hypovalvae is bulbously thickened in *profunda*, *barbigera* and *minuticornis* (fig. 126), a condition clearly derived from the usually narrow base of the major ridge. The female of *laticrista* is unknown.
 61. The incision of the hind margin of male sternite 8 is covered by a membrane which bears a midventral finger-like extension in *barbigera* and *minuticornis* (fig. 124); a unique acquisition.
 62. An unmodified cone-shaped central part of the adminiculum as found in most species-groups within *Nephrotoma* and also in the primitive members of the *dorsalis*-group (e.g. the *nigricauda*-group, the *pamirensis*-group, *ramulifera*, the *dorsalis*-group s.s.) has to be considered the plesiomorphous condition. Most members of the *lunulicornis*-, *scurra*- and *macrocera*-groups, and *austriaca*, have anterior thickenings (figs. 109-111, 146, 147, 162), which can be strongly extended and/or modified in different subgroups (e.g. character 44). In *barbigera* and *minuticornis* the central part of the adminiculum bears two long, flat anterior extensions (fig. 125), a condition more or less similar to that in *sodalis* and considered a parallel development.
 63. In the phylogenetically more primitive species of the *dorsalis*-group the main body of the id is a more or less rectangular plate, anteriorly prolonged at its apex into the upper beak and more or less with a right angle between the dorsal margin and the straight posterior one (figs. 84, 85, see character 17). In the *macrocera*-group the angle between the dorsal and posterior margins is more than 90 degrees, although this is rather weak in *sodalis* and *rogersi*, the most primitive species of the group (figs. 127, 136, 137, 156, 161). This condition of the id is also weakly present in some members of the *scurra*-group.
 64. The presence of lateral protuberances at the

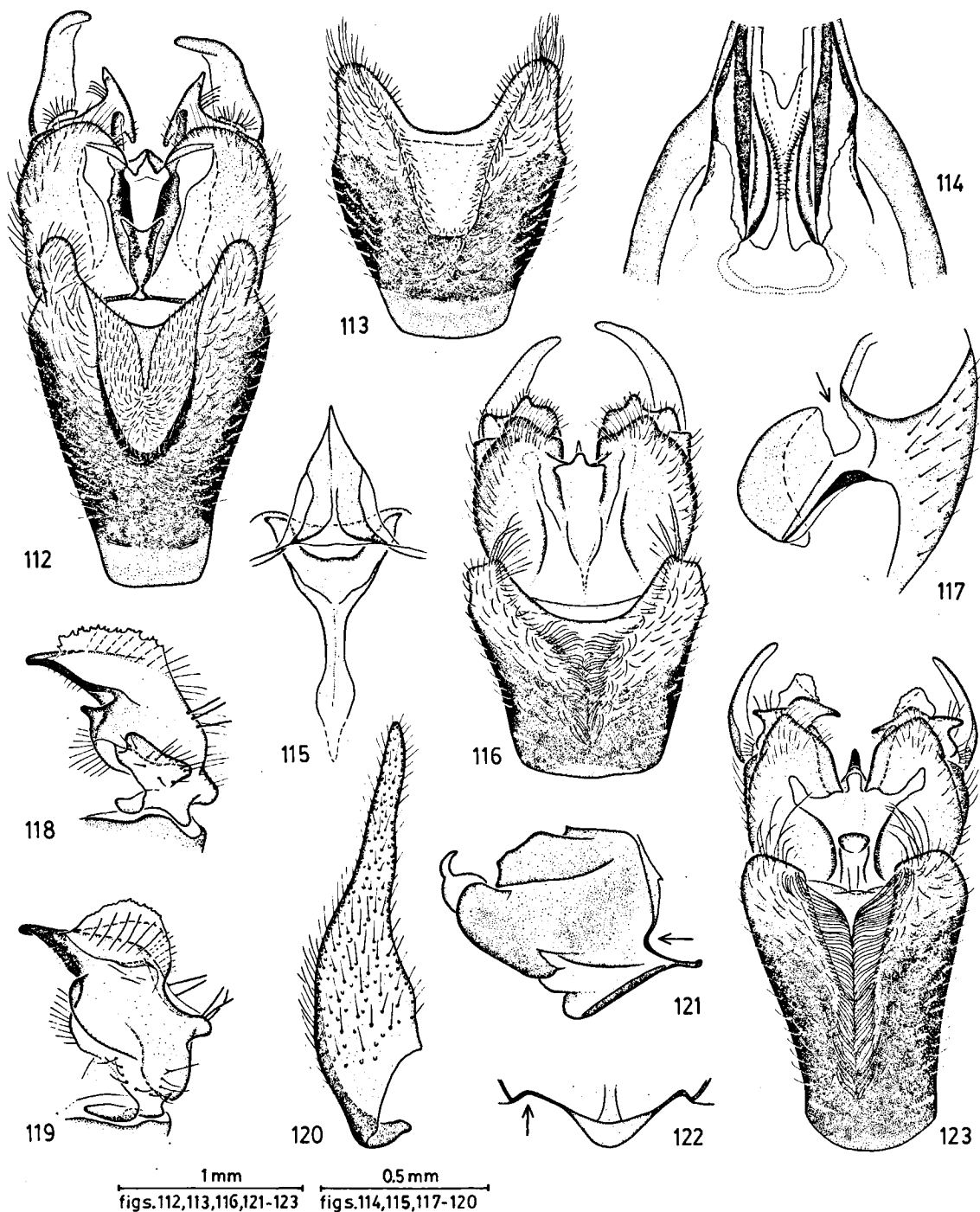


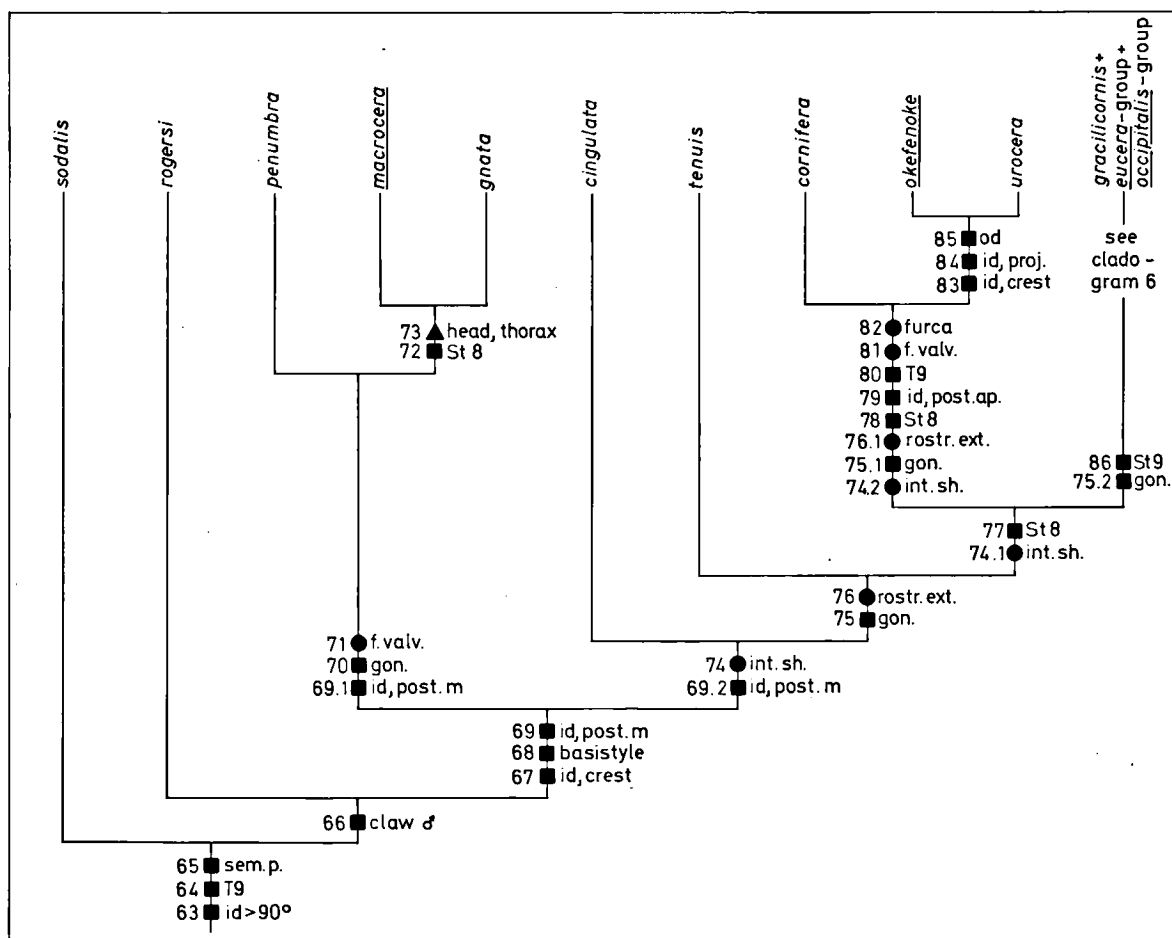
Fig. 112. *Nephrotoma cirrata*, hypopygium, ventral view. Fig. 113. *N. difficilis*, St 8 of σ , ventral view. Fig. 114. *N. lunulicornis*, hypovalvae, dorsal view. Fig. 115. *N. angustistria*, fused valvulae and furca, dorsal view. Fig. 116. *N. quadristriata*, hypopygium, ventral view. Fig. 117. *N. scurra*, sp2, dorsal view. Fig. 118. *N. scurra*, id, outside. Fig. 119. *N. profunda*, id, outside. Fig. 120. *N. quadristriata*, od, outside. Fig. 121. *N. helvetica*, St 9, lateral view. Fig. 122. *N. minuticornis*, antecosta of St 9, inside. Fig. 123. *N. profunda*, hypopygium, ventral view.

inner surface of the posterior extension of male tergite 9 is considered plesiomorphous, as it is found within nearly all species-groups of *Nephrotoma* and also outside the genus (c.f. *Scamboneura*, fig. 13). In the species of the *macrocera*-group these lateral protuberances are reduced, and in several species of the group they are replaced by small sublateral anterior extensions (figs. 131, 132, 158, 159). In the most primitive member of the group, *sodalis*, both presence and absence of these sublateral extensions occur (Tangelder, 1983: figs. 199a, b).

65. The compressor apodeme of the semen pump is, in its basic form, composed of a median, usually invaginated partition, with two wings at the lateral ends, giving each

half of the apodeme a three-lobed aspect (fig. 128). In the *macrocera*-group both halves of the compressor apodeme are arranged more or less on a level, with each wing consisting of only two lobes (figs. 129, 130), although this is weakly so in the *okefenoke*-group. This condition also occurs in a few other species of the *dorsalis*-group (*gaganboi*, *microcera* and *minuticornis*) and also in some other species-groups within *Nephrotoma*.

66. The most primitive member of the *macrocera*-group, *sodalis*, has the tarsal claws of the male toothed, a plesiomorphous condition. In all the other species of the *macrocera*-group the claws are non-pectinate. The same condition occurs in the sister group (*dorsalis*-group s.s., *lunulicornis*-group,



Cladogram 5. Phylogeny of the *macrocera*-group, first part, including the *macrocera*-group s.s. and the *okefenoke*-group.

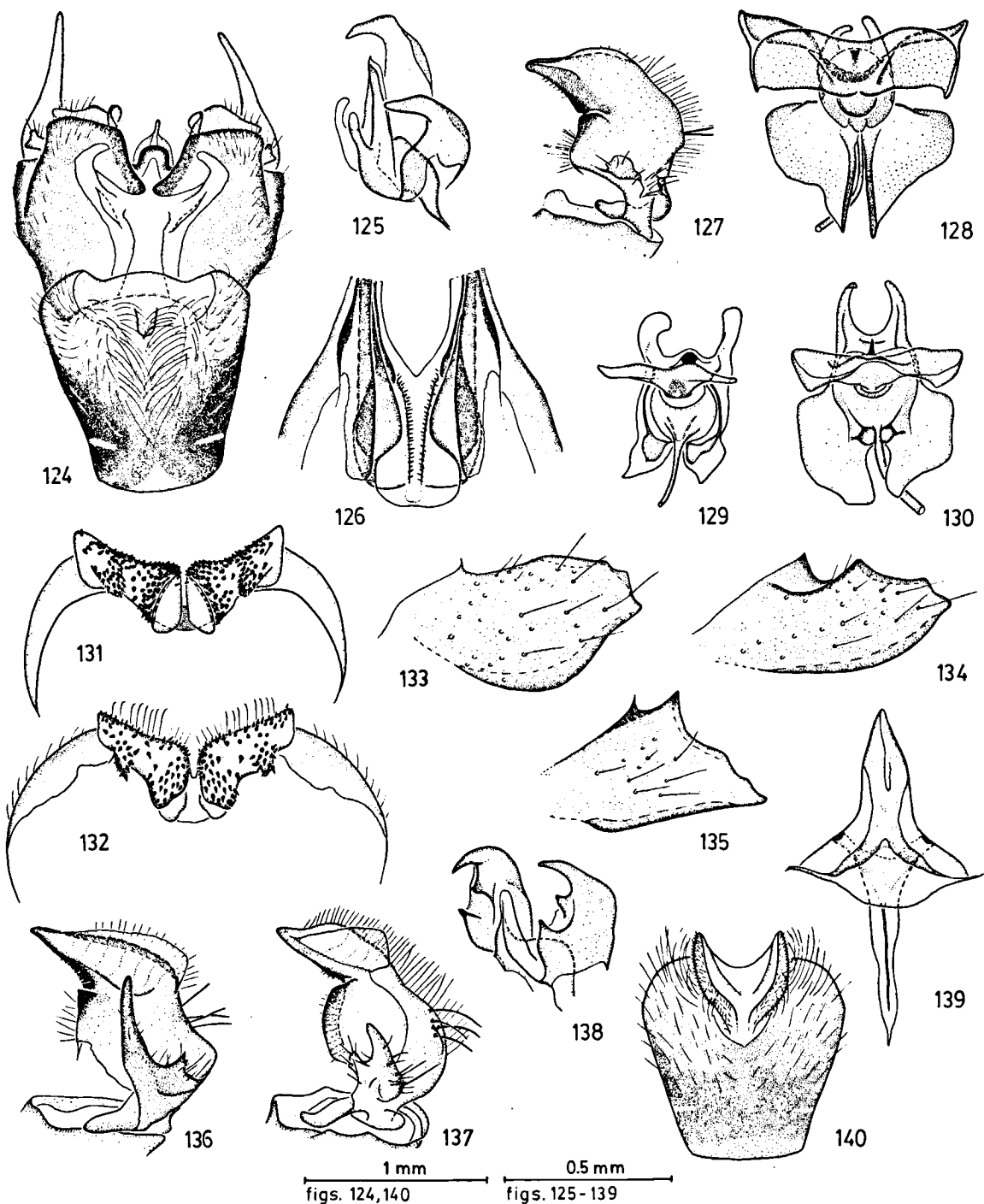


Fig. 124. *Nephrotoma barbiger*, hypopygium, ventral view. Fig. 125. *N. minuticornis*, adminiculum and gonapophyses, lateral view. Fig. 126. *N. minuticornis*, hypovalvae, dorsal view. Fig. 127. *N. sodalis*, id, outside. Fig. 128. *N. ramulifera*, semen pump, dorsal view. Fig. 129. *N. rogersi*, semen pump, dorsal view. Fig. 130. *N. cingulata*, semen pump, dorsal view. Fig. 131. *N. sodalis*, T 9 of σ , inside. Fig. 132. *N. penumbra*, T 9 of σ , inside. Fig. 133. *N. sodalis*, basistyle, lateral view. Fig. 134. *N. tenuis*, basistyle, lateral view. Fig. 135. *N. gracilicornis*, basistyle, lateral view. Fig. 136. *N. penumbra*, id, outside. Fig. 137. *N. cingulata*, id, outside. Fig. 138. *N. macrocera*, adminiculum and gonapophyses, lateral view. Fig. 139. *N. macrocera*, fused valvulae and furca, dorsal view. Fig. 140. *N. gnata*, St 8 of σ , ventral view.

- austriaca* and *scurra*-group), considered a parallel reduction (see character 28).
67. The crest of the id is broadly extended dorsally in the *macrocera*-group s.s. up to and including the *occipitalis*-group, while it is not extended in the two primitive species *sodalis* and *rogersi* (figs. 136, 137, 156, 161).
 68. The basistyle is, in its primitive form, rather short and broad and semiglobular in the majority of Tipulidae (Oosterbroek, 1980, p. 317) and in *Nephrotoma* (fig. 133). A reduction in size, such as the narrowing of the basistyle in the *macrocera*-group s.s. up to and including the *occipitalis*-group (figs. 134, 135), has to be regarded apomorphic (Frommer, 1963; Savchenko, 1966). A parallel reduction of the basistyle has occurred in the *nigricauda*-group (see character 12).
 69. The posterior margin of the id, which is straight in its plesiomorphous condition, is distinctly curved in the *macrocera*-group s.s. up to and including the *occipitalis*-group. In the *macrocera*-group s.s. long bristles are inserted at the concave upper part of the posterior margin (fig. 136; 69.1), while in the remaining groups long bristles are inserted at the convex bulge of this posterior margin (figs. 137, 156, 161; 69.2). However, the interpretation of this character in the *okefenoke*-group is difficult because of the strong modification of the id in the three species of this group (fig. 149).
 70. The gonapophyses are characteristically shaped in the *macrocera*-group s.s.: they are broad, with an acute subbasal extension and acutely curved tips, and internally prickled or set with some thorns (fig. 138).
 71. The sclerotization of the fused valvulae in the female is typically X-shaped in the *macrocera*-group s.s. (fig. 139).
 72. The hind margin of male sternite 8 bears two hairy median lobes in *macrocera* and *gnata*, a unique acquisition within the *dorsalis*-group (fig. 140).
 73. The dorsal surface of both head and thorax of *macrocera* and *gnata* is completely (sub)opaque, a condition apparently derived from the complete shining head and thorax found in all the other species of the *dorsalis*-group except the most primitive ones (*nigricauda*-group, with opaque areas on head and thorax, and *pamirensis*-group and *ramulifera*, with opaque areas on the head only); see also character 25.
 74. The internal shell between the bases of the hypovalvae shows a tendency to narrowing and prolongation in anterior direction in *cingulata* up to and including *sublunulicornis*, an apparently derived condition which is more strongly developed in the *okefenoke*-, *eucera*- and *occipitalis*-groups and *gracilicornis* (figs. 141, 143, 144; 74.1). It is modified into a broad and strongly sclerotized cup-shaped structure in the *okefenoke*-group (fig. 142; 74.2).
 75. In *tenuis* up to and including *sublunulicornis* the gonapophyses are modified into more or less tapering crook-shaped structures (figs. 145-147, 162). The tips are more or less blunt in the *okefenoke*-group (fig. 146; 75.1), while the crooks are curving like a cow's horn in *gracilicornis* and the *eucera*- and *occipitalis*-groups (figs. 147, 162; 75.2).
 76. The dorsal margins of the hypovalvae are anteriorly prolonged into the sclerotized rostral extensions in *tenuis* (as a disconnected semi-circular structure), the *okefenoke*-group (transformed into blade-like sheets, 76.1, fig. 142), *gracilicornis* (rather weak), the *eucera*-group (distinct and strongly elongated in *eucera* and *euceroidea*, 76.2, fig. 143) and the *occipitalis*-group (club-shaped sclerotizations, 76.3, fig. 144). These are unique acquisitions within the *dorsalis*-group.
 77. The caudal corners of male sternite 8 are more or less pronounced and acuminate in the *okefenoke*- up to and including the *occipitalis*-groups (figs. 148, 157, 160, 163).
- The *okefenoke*-group, consisting of three species, is characterized by several uniquely and strongly derived synapomorphies (74.2, 75.1, 76.1 and 78 to 82):
78. The hind margin of male sternite 8 has a

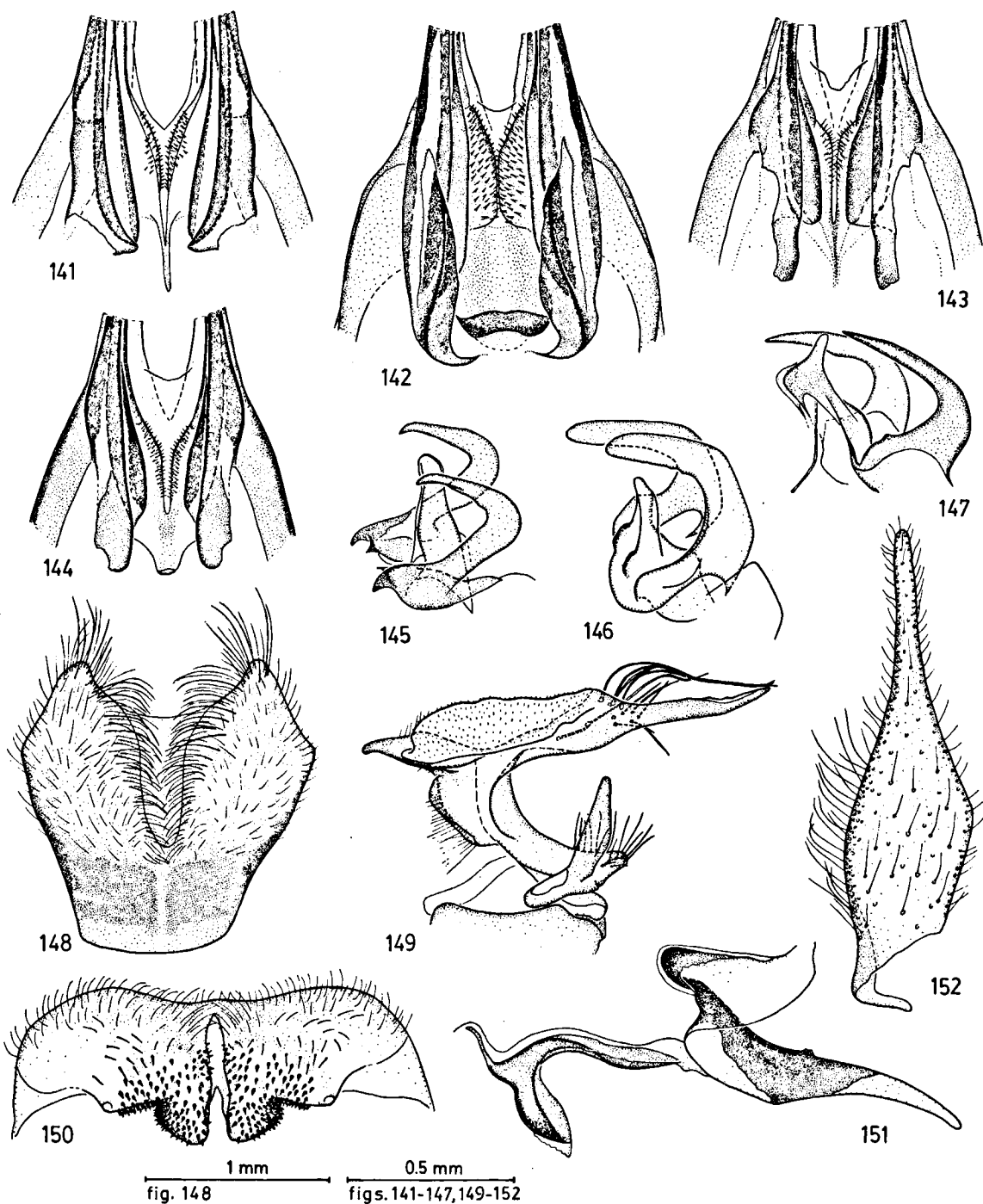
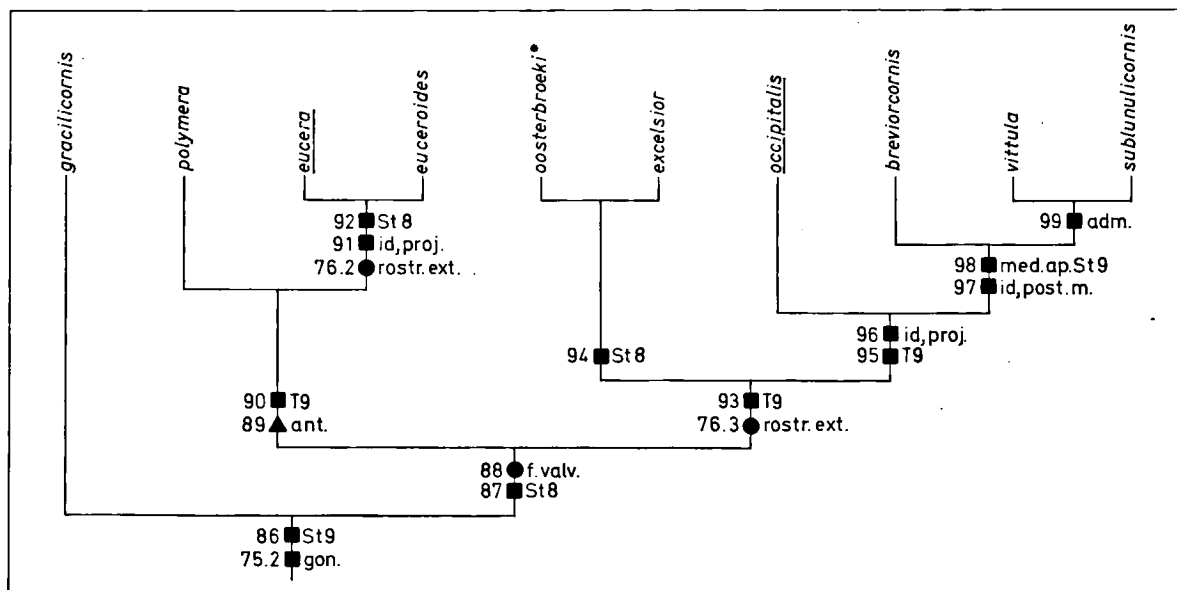


Fig. 141. *Nephrotoma gracilicornis*, hypovalvae, dorsal view. Fig. 142. *N. okefenoke*, hypovalvae, dorsal view. Fig. 143. *N. euceroideis*, hypovalvae, dorsal view. Fig. 144. *N. vittula*, hypovalvae, dorsal view. Fig. 145. *N. tenuis*, adminiculum and gonapophyses, lateral view. Fig. 146. *N. okefenoke*, idem. Fig. 147. *N. oosterbroeki*, idem. Fig. 148. *N. cornifera*, St 8 of σ , ventral view. Fig. 149. *N. okefenoke*, id, outside. Fig. 150. *N. okefenoke*, T 9 of σ , caudal view. Fig. 151. *N. urocera*, fused valvulae and furca, lateral view. Fig. 152. *N. urocera*, od, outside.

- deeply U-shaped incision which is bordered by long and curved hairs (fig. 148).
79. The id bears a peculiarly formed posterior appendage (fig. 149).
 80. The posterior extension of male tergite 9 has thick median protrusions and no lateral ones (fig. 150).
 81. The fused valvulae are strongly sclerotized and basally upcurved into a baggy extension (fig. 151).
 82. The furca, a small and flat sclerotization in all other *Nephrotoma* species examined, is a twofold structure in the *okefenoke*-group (fig. 151).
 83. The crest of the id is pubescent in *okefenoke* and *urocera* (fig. 149), a character-state not found elsewhere in the *dorsalis*-group except for *ramulifera*, which has the inner lobe of the crest pubescent.
 84. The lateral-posterior part of the id bears an upright extension in *okefenoke* and *urocera* (fig. 149).
 85. The apex of the od is distinctly and slenderly elongated in *okefenoke* and *urocera* (fig. 152).
 86. The caudo-median plates of male sternite 9, situated between the lateral offshoots of the membranous area and the medio-caudal (genital) groove, are concavely curved, a unique derivation in *gracilicornis*, the *eucera*-group and the *occipitalis*-group (fig. 153).
 87. The membrane, closing the deep incision of the hind margin of male sternite 8, is lined with long hairs in all the species of the *eucera*- and *occipitalis*-groups (figs. 157, 160, 163). It is a derived acquisition and presumably a parallel development to the condition found in the *lunulicornis*-group (see characters 26 and 46).
 88. The fused valvulae are more or less reduced to elongated separate plates in the *eucera*- and *occipitalis*-groups (fig. 154; see also character 7).
 89. The antennae of both males and females of the *eucera*-group are polymerous, possessing more than the basic number of antennal segments (13 in *Nephrotoma*, see character 30).
 90. The posterior extension of male tergite 9 protrudes distinctly beyond the caudal margin of this tergite (fig. 155) in all the three species of the *eucera*-group.
 91. The id bears a lateral ridge or projection in



Cladogram 6. Phylogeny of the *macrocera*-group, second part, including the *eucera*-group and the *occipitalis*-group.
*Female unknown.

the majority of the *dorsalis*-group and in other species-groups of *Nephrotoma*. This projection is completely reduced in *eucera* and *euceroideis* (fig. 156).

92. In *eucera* and *euceroideis* the median incision of the hind margin of male sternite 8 is deeper as in *polymera* and more or less V-shaped (fig. 157).

93. The posterior extension of male tergite 9 bears small sublateral protrusions on the inner surface (character 64), which are shifted in median direction in the members of the *occipitalis*-group compared to the other species of the *macrocera*-group (figs. 158, 159).

94. The bundles of hair on the median mem-

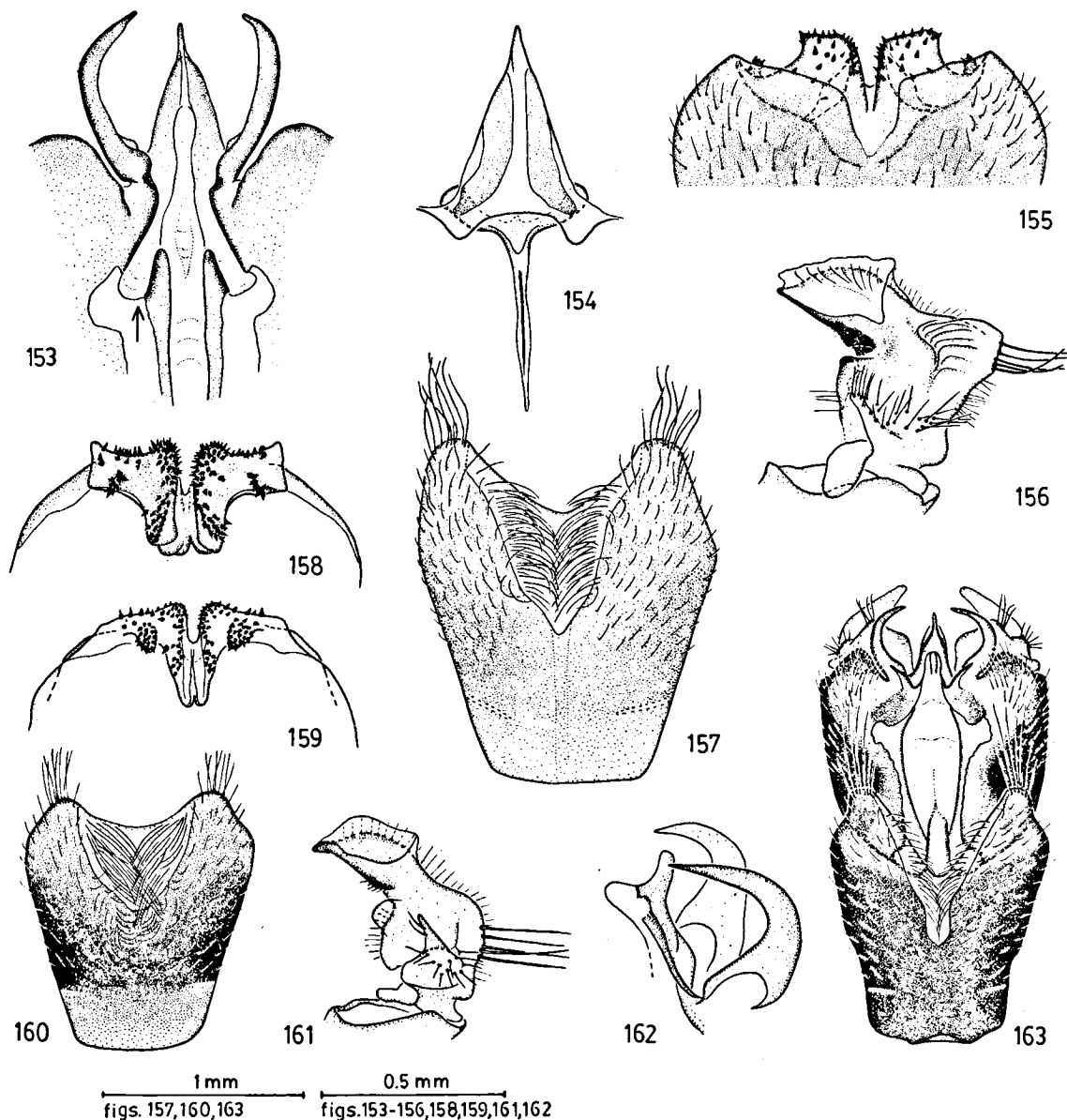


Fig. 153. *Nephrotoma occipitalis*, caudo-median region of St 9 and adminiculum, caudo-ventral view. Fig. 154. *N. polymera*, fused valvulae and furca, dorsal view. Fig. 155. *N. euceroideis*, T 9 of ♂, outside. Fig. 156. *N. eucera*, id, outside. Fig. 157. *N. eucera*, St 8 of ♂, ventral view. Fig. 158. *N. excelsior*, T 9 of ♂, inside. Fig. 159. *N. occipitalis*, T 9 of ♂, inside. Fig. 160. *N. oosterbroeki*, St 8 of ♂, ventral view. Fig. 161. *N. brevioricornis*, id, outside. Fig. 162. *N. vittula*, adminiculum and gonapophyses, lateral view. Fig. 163. *N. sublunulicornis*, hypopygium, ventral view.

brane of male sternite 8 are rather long and abundant in *oosterbroeki* and *excelsior* (fig. 160).

95. The hind margin of the posterior extension of male tergite 9 has more or less acutely extended lateral corners in the majority of the *macrocera*-group (figs. 131, 132, 158). These corners are flattened in *occipitalis*, *breviorcornis*, *vittula* and *sublunulicornis* (fig. 159).
96. The lateral projection of the id is typically spine-shaped in *occipitalis*, *breviorcornis*, *vittula* and *sublunulicornis* (fig. 161).
97. The posterior margin of the id is typically curved in an S-shape in *breviorcornis*, *vittula* and *sublunulicornis* (fig. 161).
98. The presence of a medisternal appendage and lateral plates at the mid-membranous area of male sternite 9 is considered plesiomorphous (see p. 144). Reduction of these structures has occurred within several small species-groups and individual species (e.g. *microcera*, *quadristriata*, *barbigera*; *sodalis*, *rogersi*, *macrocera* and *gnata* and the *okefenoke*-group). Such a reduction of both the medisternal appendage and the sclerotized lateral plates is also found in *breviorcornis*, *vittula* and *sublunulicornis*, which on this level is considered a synapomorphy for these three species (fig. 163).
99. The central part of the adminiculum has anterior thickenings or extensions in most members of the *macrocera*-group (see also discussion character 62). These thickenings are more strongly extended in *vittula* and *sublunulicornis* than in the other species of the *occipitalis*-group (fig. 162), which on this level is considered a synapomorphy for these two species.

DISCUSSION

Reconstruction of the phylogeny of a species-group frequently meets with problems of homoplasy (parallel and convergent developments). For the more closely related the organisms are, the greater the possibility for parallel variation because of their common genetic background

(De Jong, 1980). Within the *dorsalis*-group several characters subject to parallel developments were recognized. Some of these characters were considered to provide useful arguments for the phylogenetic analysis on the subgroup level (Watrous & Wheeler, 1981), although the monophyly of the species-groups was only rarely based on such characters alone:

- the reduction of the lateral appendages on the antecosta of sternite 9 (characters 8 and 40)
- the reduction of the basistyle (characters 12 and 68)
- elongation of the tip and sometimes other modifications of the od (characters 11, 19, 32, 57 and 85)
- the elongation of the median protuberances at the inner surface of the posterior extension of male tergite 9 (characters 18 and 41)
- the reduction of the pectination of the male tarsal claws (characters 28 and 66)
- the polymeric condition of the antennae (characters 30 and 89)
- the reduction of the fused valvulae into separate plates (characters 7, 38, 48 and 88)
- the presence of pilosity on the median membrane of male sternite 8 (characters 42 and 87).

Some other characters are distinctly inconsistent within the *dorsalis*-group and were therefore not useful in the analysis, except for some relationship-decisions on the species level, given the acquaintance of the evolutionary polarity of the character states, for example:

- the reduction of the lateral plates and the medisternal appendage of male sternite 9 (character 98)
- the presence and size of the anterior thickenings on the central part of the adminiculum (characters 62 and 99)
- the presence and shape of the lateral projection of the id (characters 91 and 96).

Much depends on the interpretation of characters and character states, and in this there will always be an element of subjectivity, which can however be limited by thorough study and comparison with those characters in the outgroups. The basing of most mono-

phyletic groups on more than one synapomorphy enlarges the reliability of the analysis. However, some obscurities and uncertainties still remain, such as the precise place of *austriaca* in the cladogram. Differences in interpretation may result in some alternative options for parts of the presented phylogeny, such as a closer relationship of the *macrocera*-group with the *scurra*-group or a sister-group relation between the *dorsalis*-group s.s. and the *lunulicornis*-group. On the basis of the available information, however, the presented cladogram is considered the most reliable and parsimonious one.

The most primitive members of the *dorsalis*-group, the *nigricauda*- and *pamirensis*-groups, are found in the eastern Palaearctic. This is consistent with the presumed origin of the genus *Nephrotoma* in East Asia (Oosterbroek *et al.*, 1976) and with the supposition that the sister group of the *dorsalis*-group must be sought in the oriental region. An interesting conclusion of the analysis is the monophyletic origin of all the nearctic species, the *macrocera*-group, which is the sister group of the *dorsalis*-, *lunulicornis*-, *austriaca* and *scurra*-(sub)groups together, all palaearctic groups; while *ramulifera*, the sister species of both the nearctic *macrocera*-group and the palaearctic groups, has a holarctic distribution. The biogeography of the whole *dorsalis*-group, with questions concerning the faunal exchange between the palaearctic and nearctic regions, will be dealt with in a forthcoming paper.

ACKNOWLEDGEMENTS

For valuable advice and critical discussion I am much indebted to Pjotr Oosterbroek and Theowald van Leeuwen. Furthermore I wish to thank Bruce Townsend for checking the English. The investigations were supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for the Advancement of Pure Research (ZWO). A grant, which facilitated the publication of this study was thankfully received from the Uyttenboogaart-Eliassen Foundation (Amsterdam).

REFERENCES

- ALEXANDER, C. P., 1942. Family Tipulidae. In: Guide to the Insects of Connecticut, Part 6. The Diptera or true flies of Connecticut. Bull. Conn. St. geol. nat. Hist. Surv., 64: 196-486. (Reprinted 1966).
- , 1965. New subgenera and species of crane-flies from California (Diptera: Tipulidae). Pacific Insects, 7: 333-386.
- , 1971. New or insufficiently known Australasian crane-flies (Dipt. Tipulidae). Studia Entomologica, 14: 267-318.
- AX, P., 1984. Das Phylogenetische System: 1-349 (Gustav Fischer Verlag, Stuttgart, New York).
- BALL, I. R., 1976. Nature and formulation of biogeographical hypotheses. Syst. Zool., 24: 407-430.
- BONDE, N., 1977. Cladistic classification as applied to Vertebrates. In: Hecht, Goody & Hecht (Eds), Major patterns in vertebrate Evolution; Nato Advanced Studies Institute, Plenum Press, New York, 14: 741-804.
- BORKENT, A., 1984. The systematics and phylogeny of the Stenochironomus complex (Xestochironomus, Harrisius, and Stenochironomus) (Diptera: Chironomidae). Mem. ent. Soc. Canada, 128: 1-161.
- BYERS, G. W., 1961. The Crane Fly genus Dolichopeza in North America. Univ. Kans. Sci. Bull., 42: 665-924.
- , 1983. The Crane Fly genus Chionea in North America. Univ. Kans. Sci. Bull., 52: 59-195.
- CRAMPTON, G. C., 1942. The external Morphology of the Diptera. In: Guide to the Insects of Connecticut, Part 6. The Diptera or true flies of Connecticut. Bull. Conn. St. geol. nat. Hist. Surv., 64: 10-165 (reprinted 1966).
- DOBROTOWSKY, N. V., 1968. The Tipulidae (Diptera) of Australia. I. A review of the genera of the subfamily Tipulinae. Aust. J. Zool., 16: 459-494.
- EDWARDS, F. W., 1928. Some nematocerous Diptera from Yunnan and Tibet. Ann. Magn. nat. Hist., (10) 1: 681-703.
- , 1938. British short-palped craneflies. Taxonomy of adults. Trans. Soc. British-Ent., 5: 1-168.
- ELDRIDGE, N. & J. CRACRAFT, 1980. Phylogenetic Patterns and Evolutionary Process. Method and Theory in Comparative Biology: i-viii, 1-349 (Columbia University Press, New York).
- FROMMER, S. I., 1963. Gross morphological studies of the reproductive system in representative North American Crane-flies (Diptera: Tipulidae). Univ. Kans. Sci. Bull., 44: 535-626.
- HENNIG, W., 1966. Phylogenetic Systematics: 1-263 (University Illinois Press, Urbana).
- , 1973. Diptera (Zweiflügler). In: Kükenthal, W., Handbuch der Zoologie, 4: (2) 2/31, Lief. 20: 1-337.
- HUT, R. M. G. VAN DER, (in preparation). The first-instar larvae of Tipulidae.
- JONG, R. DE, 1980. Some tools for evolutionary and phylo-

- genetic studies. *Z. zool. Syst. Evolut.-forsch.*, **18**: 1-23.
- MANNHEIMS, B., 1951. Tipulidae. In: Lindner, E., *Die Fliegen der Palaearktischen Region*, **15**: 1-64.
- McALPINE, J. F., 1981. Morphology and terminology. In: McAlpine, J. F. et al. (Eds), *Manual of Nearctic Diptera*, **1**: 9-63 (Biosyst. Res. Inst. Monograph 27, Ottawa).
- MEIGEN, J. W., 1818. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. **1**: i-xxxvi, 1-333, pls. 1-11 (F. W. Forstmann, Aachen).
- NELSON, G. & N. PLATNICK, 1981. Systematics and biogeography. Cladistics and vicariance: i-xi, 1-566 (Columbia University Press, New York).
- NEUMANN, H., 1958. Der Bau und die Funktion der männlichen Genitalapparate von *Trichocera annulata* Meig. und *Tipula paludosa* Meig. (Dipt. Nematocera). *Dt. ent. Z.*, **5**: 235-298.
- OOSTERBROEK, P., 1978. The western palaearctic species of *Nephrotoma* Meigen, 1803 (Diptera, Tipulidae), Part 1. *Beaufortia*, **27**: 1-137.
- , 1979a. idem, Part 2. *Beaufortia*, **28**: 57-111.
- , 1979b. idem, Part 3. *Beaufortia*, **28**: 157-203.
- , 1979c. idem, Part 4, including a key to the species. *Beaufortia*, **29**: 129-197.
- , 1980. idem, Part 5, Phylogeny and Biogeography. *Beaufortia*, **29**: 311-393.
- , 1984. A revision of the crane fly genus *Nephrotoma* Meigen, 1803, in North America (Diptera, Tipulidae). Part II: the non-dorsalis species-groups. *Beaufortia*, **34**: 117-180.
- , 1985. The *Nephrotoma* species of Japan (Diptera, Tipulidae). *Tijdschr. Ent.*, **127**: 235-278.
- OOSTERBROEK, P., R. SCHUCKARD & BR. THEOWALD, 1976. Die *Nephrotoma*-Verbreitung in der Welt (Diptera, Tipulidae). *Bull. zool. Mus. Univ. Amsterdam*, **5**: 111-123.
- OOSTERBROEK, P. & BR. THEOWALD, (in preparation). A re-assessment of genera of Tipulidae based on preimaginal characters.
- PEUS, F., 1952. *Cylindrotomidae*. In: Lindner, E., *Die Fliegen der palaearktischen Region*, **17**: 1-80.
- REES, B. E. & G. F. FERRIS, 1939. The morphology of *Tipula reesi* Alexander (Diptera: Tipulidae). *Microentomology*, **4**: 143-178.
- ROSS, H. H., 1974. *Biological Systematics*: i-vi, 1-345 (Addison-Wesley Publishing Company, Reading, Massachusetts).
- SAVCHENKO, E. N., 1966. Phylogenie und Systematik der Tipulidae. *Fauna Ukraini*, **14**, part 1: 63-88 (Ukrainian). German translation by Theowald, Br. & G. Theishinger, *Tijdschr. Ent.*, **122** (1979): 91-126.
- SNODGRASS, R. E., 1903. The terminal abdominal segments of female Tipulidae. *Jl N.Y. ent. Soc.*, **11**: 177-183.
- , 1904. The hypopygium of Tipulidae. *Trans. Am. ent. Soc.*, **30**: 179-236.
- , 1957. A revised interpretation of the external reproductive organs of male insects. *Smithsonian Misc. Coll.*, **135**: 1-60.
- STEVENS, P. F., 1980. Evolutionary polarity of character states. *Ann. Rev. ecol. Syst.*, **11**: 333-358.
- TANGELDER, I. R. M., 1983. A revision of the crane fly genus *Nephrotoma* Meigen, 1803, in North America (Diptera, Tipulidae). Part I: the dorsalis species-group. *Beaufortia*, **33**: 111-205.
- , 1984. The species of the *Nephrotoma dorsalis*-group in the Palaearctic (Diptera, Tipulidae). *Beaufortia*, **34**: 15-92.
- THEOWALD, BR., 1957. Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera). Insbesondere der West-Palaearktischen Arten. *Tijdschr. Ent.*, **100**: 195-308.
- TJEDER, B., 1948. The Swedish Prionocera (Dipt. Tipulidae). *Opusc. ent.*, **13**: 75-99.
- VERMOOLEN, D., 1983. The *Tipula* (*Acutipula*) *maxima* group. I. Taxonomy and Distribution. *Bijdr. Dierk.*, **53**: 49-81.
- WATROUS, L. E. & Q. D. WHEELER, 1981. The outgroup comparison method of character analysis. *Syst. Zool.*, **30**: 1-11.
- WESTHOFF, F., 1882. Ueber den Bau des Hypopygiums der Gattung *Tipula* Meigen. Erster Theil. Inaugural-Dissertation, Münster: 1-62, Taf. I-VI.
- WILEY, E. O., 1981. *Phylogenetics. The theory and practice of Phylogenetic Systematics*: i-xv, 1-439 (J. Wiley and Sons, New York, Toronto).

Received: September 4, 1985.