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The western palaearctic species of *Nephrotoma* Meigen, 1803 (Diptera, Tipulidae), Part 5, Phylogeny and Biogeography

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ABSTRACT

The phylogeny and biogeography of the western Palaearctic species of *Nephrotoma* are analyzed. Phylogeny is dealt with in a cladistic sense. Briefly outlined are criteria developed for polarity decisions as well as the rôle assigned to parallelisms. Representatives of fourty-one Holarctic (sub)genera were examined in order to establish the sistergroup of *Nephrotoma*. The internal hypopygial stuctures of these taxa are discussed and the following cluster of closely related taxa is recognized: *Dolichopeza* s. str., *Oropeza*, *Nesopeza*, *Prionocera*, *Trichotipula*, *Scamboneura*, and *Nephrotoma*. The two last-mentioned taxa are considered sistergroups.

The western Palaearctic *Nephrotoma* species are assigned here to four monophyletic groups: *cornicina* group, *dorsalis* group, *brevipennis* group, and *crocata* group.

In the section dealing with biogeography, an attempt is made to correlate the phylogeny of the *cornicina* and *crocata* groups with glacial-interglacial cycles. In a further account the distribution patterns of all Palaearctic species are discussed in relation to Pleistocene and Holocene climatic fluctuations.

The origin of the genus is situated in early Tertiary East Asia. The *brevipennis* group, restricted to Madeira, is assumed to date back from at least Pliocene times. The *dorsalis* group, widespread throughout the Holarctic, apparently achieved its present range before the late Pliocene. It is intimated that the Pleistocene climatic oscillations had little effect on speciation within groups adapted to northern temperate or even cooler climates. This in contrast to the southern temperate and Mediterranean species groups such as the *flavescens* and *crocata* subgroups. The relative success of these two subgroups in post-Cromerian times may well be associated with their shift to more open habitats.

CONTENTS

PHYLOGENY

INTRODUCTION

The genus *Nephrotoma* has a world-wide distribution and contains about 430 species. In the present paper an attempt is made to reconstruct the evolutionary history of the species occurring in the western Palaearctic. Their relationships are analyzed according to the phylogenetic principles of Hennig (1966); viz. species are assigned to monophyletic groups based on synapomorphous characters. A detailed discussion of these principles, applied here to tipulids for the first time, is beyond the scope of this paper. Some general comments about the evaluation of characters and the rôle of parallelisms are made under methods; pertinent reviews on the phylogenetic approach are found in Bonde, 1977; Hecht & Edwards, 1977; Cracraft & Eldredge, 1979. The characters themselves are discussed in four sections: out-group comparisons, phylogeny of the species groups, autapomorphous and inconsistent characters.

METHODS

The basal concepts of the phylogenetic, or as it is frequently named, cladistic approach are:

— characters can be interpreted as primitive (plesiomorph, plesiotypic) or derived (apomorph, apotypic);

— restriction of a derived character to a set of taxa within a larger taxon indicates inheritance of this character from a common ancestor;

— derived characters restricted to and at the same time shared by all members of a taxon form the principal base for considering this taxon monophyletic; such characters are named synapomorph.

— a monophyletic group comprises all the progeny of a common ancestor and only these.

The most crucial points in phylogenetic analysis are the discrimination between primitive and derived character states, and the evaluation of the extent to which characters contribute to a reconstruction of the phylogeny.

A host of criteria has been developed to distinguish derived states from primitive ones. Of relevance to the group under study are criteria applicable to morphological characters. Such criteria can be arranged into three groups:

I. distribution of character states (pattern analysis);
II. deviation from a basic plan (process analysis);
III. correlation of transformation series.

These criteria are discussed in footnote 1. Criteria I and III are considered here to be the most reliable.

There are in fact no satisfactory criteria to separate phylogenetically important characters from unimportant characters. The reliability of a character can sometimes be estimated by its range of variability within the out-groups, viz. groups related to the group under study. Furthermore, frequently "group trends" sensu Ross (1974) occur. Characters associated with such trends are likely to have evolved parallelly in different lines of descent. In most instances character states are interpreted as parallelisms when the distribution of these states does not correspond with the distribution of synapomorphous characters (criterium III). With regard to parallelisms quite different opinions are held concerning their rôle in phylogenetic reasoning. The "unique insideparallelisms" sensu Brundin (1966, 1976) are considered by some authors as comparable to synapomorphous characters for the delimitation of monophyletic groups. Parallelisms are discussed in more detail in footnote 2. In this paper characters interpreted as synapomorphies are given more weight than parallelisms (see footnote).

The phylogenetic trees presented here are cladograms; they do not account for absolute time or degree of differentiation. Character states are indicated by open or solid rectangles, circles or triangles. Rectangles represent so-called strong characters, circles so-called weak characters. For several reasons the latter are assumed to have low weight. Character states not known for all members of a group are considered weak (e.g., females of *ramulifera, spatha* and *antithrix* were not examined). Furthermore, in-group parallelisms (e.g., inner margin of male sternite nine with reduced appendages) as well as out-group parallelisms (e.g., male claws not pectinate) are given low weight. Finally, colour pattern characteristics are considered a weak argument for the monophyly of a group.

Transformation series are sometimes not continuous but interrupted by specific character expressions found in single species. Triangles indicate such character expressions. These discontinuous series form a weak element in the phylogenetic analysis presented. Therefore, I have refrained from referring to such series as far as possible. However, the lack of other, well-defined synapomorphies, necessitates their use in certain instances.

Footnotes

1. Criteria upon which decisions about the polarity of characters can rely are discussed by Hennig, 1950, 1966; Maslin, 1952; Simpson, 1961; Colless, 1967; Kluge & Farris, 1969; Mayr, 1969; Schlee, 1969; Crowson, 1970; Liem, 1970; Marx & Rabb, 1970; Kluge, 1971; Peters & Gutmann, 1971; Munroe, 1974; Ross, 1974; Ball, 1975; Hecht & Edwards, 1976; Ekis, 1977; de Jong, 1980. The paleontological method (Hennig, 1966: 140—145) and the parasitological method (l.c.: 107—113) are not applicable to the group under study. The chorological method (l.c.: 133—139), cannot in my opinion be used as an aprioristic device in phylogenetic reasoning. The weakness of the chorological method is clear from Hennig's own supportive examples (l.c.: 134). He refers to the opinion of Kiriakoff (1956) that the monophyly of the lycaenid subfamily Brephidiinae is improbable because "recent investigations have shown almost irrefutably that no land connection between South America and Africa across the south Atlantic existed, at least during Middle Mesozoic or later". Hennig proceeds after this reference to state that "there is no need to give further examples", but in my view it is questionable whether Kiriakoff's opinion is justifiable on geological data only, as if the Brephidiinae would become monophyletic again as soon as geologists come up with a more recent opening of the southern Atlantic (see Sclater et al., 1977).

Another example used by Hennig concerns the ranges and femur colour patterns of the subspecies of the micropezid (tylid) *Mimegralla albimana* (l.c.: fig. 39, subtitling incorrect, subspecies revised by Hennig, 1935). This example is intended to demonstrate the progression rule ("the ever present parallelism between morphological and chorological progression", Brundin, 1972b: 74) but fails to do so. The progression rule is given an extra dimension by Brundin by stating that it is ever present (as cited above). Hennig was well aware of the restricted applicability of this rule (e.g., Hennig, 1960: 250—251).

The criteria for polarity decisions can be arranged in the following groups:

I. Distribution of character states (pattern analysis). This criterium can be applied to the in-group (the taxon under study) and to the out-group (taxa related to the in-group at a higher hierarchical level).

IA. In-group comparison. A general assumption is that within a taxon, character states with a restricted occurrence represent the apomorphous condition. Needless to say, limited occurrence may reflect inheritance of a character state from the basal stock, for example, the apterous condition of entognathous insects.

IB. Out-group comparisons. Here the assumption is that a character state is likely to be plesiomorphous when it is shared with the out-groups. The value of this criterium largely depends on the available information about the related taxa. A further assumption is that the related taxa "should not be actually derivable from members of the first group [the in-group]" (Crowson, 1970: 106); in other words, the monophyly of the in-group is a presumption, arrived at by a preliminary evaluation of all characteristics of the in-group as well as the out-groups.

II. Deviation from a basic plan (process analysis). The basic tenet of this criterium is outlined by Ekis (1977) as follows: "It involves a search for plesiotypic states, particularly of transformation series, of structurally rich characters that in aggregate are considered the basic ancestral plan. It is assumed that the relatively apotypic states of extant descendants ultimately evolved from that plan". In line with this criterium are judgements about characters with a correlated adaptive significance (Liem, 1970; Marx & Rabb, 1970; Peters & Gutmann, 1971). To enable these judgements, Munroe (1974) suggests "to accumulate more knowledge about biological events to allow more rigorous interpretations of the evidence, and more probably correct inferences should result".

III. Correlation of transformation series. The distribution of character states very often coincides. Transformation series with an already established polarity provide a means to interpret the direction of correlated series for which there are no effective arguments with respect to their polarity. Hennig (1966: 86—101) gives a detailed account of this criterium. Platnick (1979) interprets it as identical to out-group comparison but this is incorrect.

The different approaches towards polarity decisions range from not necessary at all (e.g., Gaffney, 1979), based on out-group comparison only (e.g., Andersen, 1979), to based on adaptational interpretations only (e.g., Gutmann, 1977). In the present study out-group comparison is considered the most reliable criterium (cf. de Jong, 1980), because in my view it is very reasonable to follow Andersen (1979), who states: "phylogenetic relationships are hypothesized without the need of prior assumptions about evolutionary processes. If adaptational arguments are used to reconstruct phylogenies, the progress of adaptation itself cannot be studied in the light of these phylogenies".

2. Parallel evolution is "the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry" (Simpson, 1961). Cladistic analyses of the most diverse groups have shown that parallelisms are very frequent. They are the result of group-trends which occur as an "expression of the canalized evolutionary potential of a monophyletic group" (Brundin, 1972a). This canalization is, according to Riedl (1977), the only real explanation of all macro-evolutionary phenomena ("one consequence is the cementation of structures, functions, and pathways, one more is the high probability that, if a species is to survive, the accessibility of adaptive niches is narrowly circumscribed", Riedl, 1977: 363—364).

Parallelisms are frequently applied in cladistic analyses. Outspoken proponents are Brundin (1966, 1976) and Saether (1977, 1979a, b), whereas Griffiths (1972), Andersson (1977), and Schlee (1975, 1978) are very much inclined to reject parallelisms from cladistic inferences.

Brundin (1976) discusses the applicability of parallelisms by referring to out-group parallelism and in-group parallelisms. Out-group parallelisms are parallelisms not restricted to the group under study. If all species in family A possess an apomorph character x and none of the genera inside A is more closely related to groups outside A than to other members of A, then we are entitled to regard character x as a true synapomorphy for all species in A, regardless of the parallel evolution of x in other families. The procedure of applying out-group parallelisms is also followed by Hennig (Hennig, 1970, 1972; see Saether, 1979b).

In-group parallelisms are parallel developments of derived characters within a supposed monophyletic group. Such parallelisms are named "underlying synapomorphies" by Saether (1979b) after Tuomikoski (1967), who states: "Parallel apomorphies may sometimes be used as evidence of monophyly and are then better comparable to synapomorphies than to convergent similarities. More precisely, in these cases the underlying synapomorphy is the agreement in capacity to develop parallel similarity".

In the present treatment of *Nephrotoma* monophyletic groups are based on what I consider strict synapomorphies. Some of the synapomorphies listed here might well represent out-group parallelisms, but not recognized as such because only a part of all known *Nephrotoma* species was examined. However, in those instances in which characters evolved apparently in parallel they were added to the cladogram in so far as they strengthen the monophyly of a group; the monophyly was not based on these characters. Although synapomorphous characters might well represent undetected out-group parallelisms, they never represent in-group parallelisms (by definition parallelly evolved). Hence, the latter cannot be interpreted as underlying synapomorphies (Saether, 1979b), or given equal weight than strict synapomorphies (Brundin, 1976). The "agreement in capacity to develop parallel similarity" (Tuomikoski, 1967), is an

obscure base for monophyly. The problem is how to be aware of this capacity in those taxa that dit not develop parallel similarity. Moreover, agreement is not only difficult to measure, but also difficult to achieve and to agree about.

OUT-GROUP COMPARISONS

In order to trace the sistergroup of the *Nephrotoma* species under study, many congeneric species from outside the western Palaearctic were examined. I found that all these species could be assigned to already established, western Palaearctic species groups. Hence, the sistergroup was to be looked for not in *Nephrotoma,* but among other tipulid taxa. The relationship between these taxa and *Nephrotoma* is not clear from the literature. The first attempt towards grouping of mainly European genera and subgenera was made by Theowald (1957). Based on larval and pupal characteristics, Theowald recognized among others the following groups:

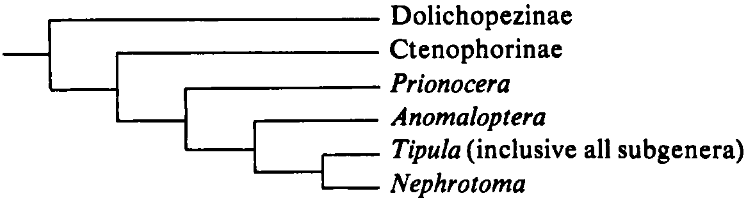
- *Dolichopeza* complex
  - *Dolichopeza* unit
    - *D. albipes* group
- *Ctenophora* complex
  - *Ctenophora* unit
    - *Ctenophora* group
    - *Tanyptera* group
  - *Nephrotoma* unit
    - *Nephrotoma* group
    - *Schummelia* group ? (subgenus of *Tipula*)
    - *Nigrotipula* group ?

Frommer (1963) presented, as a result of gross morphological studies on the reproductive system in twenty-one North American genera and subgenera, among others the following clusters of taxa:

cluster 1, subcluster 1.1 *Nephrotoma* and *Dolichopeza*
subcluster 1.2 *Tipula (Trichotipula)*
subcluster 1.3 *Tipula (Nobilotipula)* and *Tipula (Schummelia)*
cluster 2, subcluster 2.1 *Tipula (Nippotipula)*
subcluster 2.2 *Ctenophora, Tanyptera, Holorusia, Prionocera* and *Tipula (Arctotipula)*

These clusters "indicate relationship as suggested by resemblance but should not be regarded as a phylogenetic tree" (Frommer, 1963: 576).

The relationship of the Palaearctic Tipulidae, as illustrated by Savchenko (1966: fig. 44), can be represented as follows:



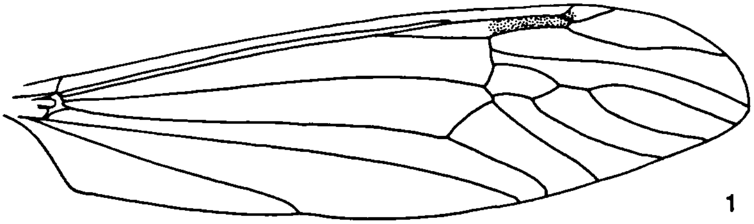
Finally, Alexander (1971) regarded *Nephrotoma* and *Scamboneura*, known from the Philippines, Indonesia, and New Guinea, as subgenera of a single genus, stating "the venation and male hypopygial structure are very similar in the two groups and likewise show a close relationship with *Dolichopeza*" (Alexander, 1971: 271).

In the classifications cited above, *Nephrotoma* is treated as a separate taxon, but its sistergroup remains questionable. In Savchenko's view it is the genus *Tipula*, whereas Frommer and Alexander suggest *Dolichopeza*. Furthermore, both Frommer and Theowald, in contrast to Alexander and Savchenko, assume that certain subgenera of *Tipula* show a closer "relationship" with *Nephrotoma* than with *Tipula*. The examination of representatives of 41 Holarctic (sub)genera confirms the latter opinion, especially when the internal structures of the male post-abdomen are taken into account. In studies dealing with the taxonomy or relationships of Tipulidae these structures are usually largely neglected (exceptions are Rees & Ferris, 1939; Neumann, 1958; Byers, 1961; Frommer, 1963); the present study shows that they are very important with respect to phylogenetic analysis.

Among the taxa examined the following cluster can be recognized (see for species names appendix 1): *Nephrotoma, Dolichopeza (Dolichopeza), Dolichopeza (Oropeza), Dolichopeza (Nesopeza), Tipula (Trichotipula), Scamboneura,* and *Prionocera*. This cluster is based on similarity. Certain character states are restricted to this group, but I refrain from calling them synapomorphies because information comes from the Holarctic Tipulidae (6 genera with about 60 subgenera) only. Very little information is available on the Tipulidae of the Southern Hemisphere (20 genera with about 27 subgenera). Moreover, of the 41 taxa mentioned above, usually only one or two representatives were studied. They have been compared with data from the literature, especially with those given by Frommer (1963), who examined many more species in each (sub)genus. Nevertheless, the conclusions presented here are very preliminary.

The major features of the male hypopygium of the Holarctic taxa are discussed below, together with some other characters. Special emphasis is given to the characters delimiting the cluster of taxa presented above.

Basistyle. The ninth segment of most lower Diptera bears ventrally two, two-segmented genital forceps. The basal segment is usually called basistyle (basimere, coxite), and the apical segment dististyle (gonocoxite, coxopodite). The dististyles are usually divided in an outer dististyle (od) and an inner dististyle (id). Among the lower Diptera the infraorder Tipulomorpha, comprising the families Trichoceridae, Cylindrotomidae, Limoniidae and Tipulidae, in all probability is the sistergroup of the remaining Diptera (Hennig, 1973). Except for the majority of Tipulidae, the basistyle in these families are elongate, cone-shaped appendages with the id and the od inserted at the apex (fig. 4). In the majority of Tipulidae the



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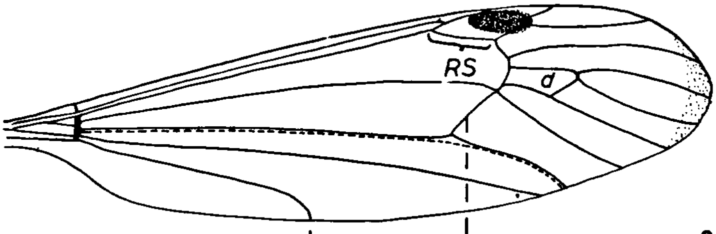

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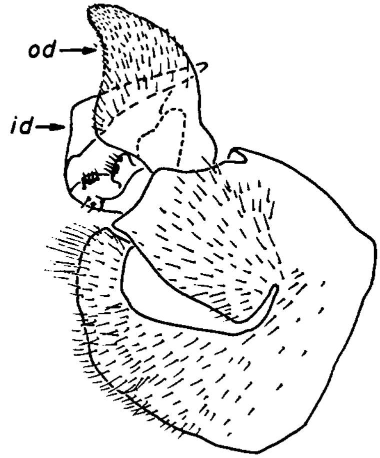

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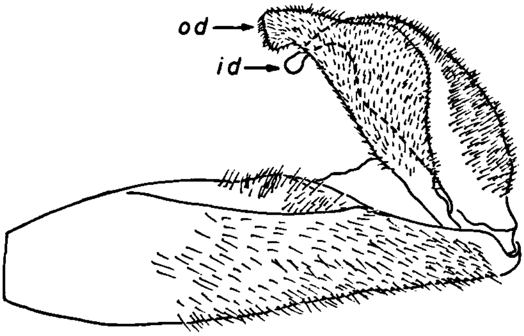

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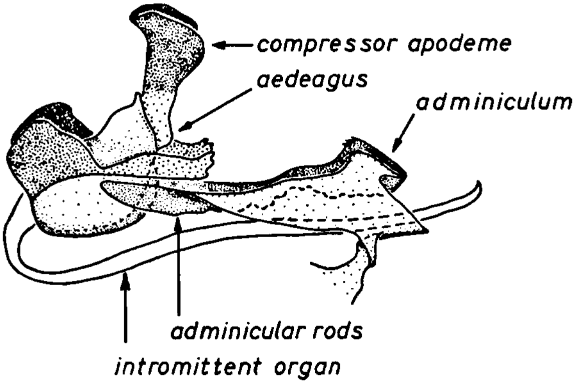

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Fig. 1: Wing of *Tipula* (*Savtshenkia*) *subsignata*. Fig. 2: wing of *Nephrotoma aculeata*, d = discal cell. Fig. 3: hypopygium of *Nephrotoma lundbecki*, side view. Fig. 4: hypopygium of *Longurio testaceus*, side view. Fig. 5: intromittent organ and associated structures in *Prionocera turcica*, side view.

basistyles are much shorter and usually semi-globular with the id and the od in a dorsal position (fig. 3). In practically all Tipulidae with this kind of basistyle there is a curved cleft just above the middle of the basistyles. An elongate, cone-shaped basistyle is considered the plesiomorphous condition in Tipulomorpha: first of all because it is found in Trichoceridae, the presumed sistergroup of the other three families (Hennig, 1973), and secondly because it is much more wide-spread among Tipulomorpha than the shorter type of basistyle. A few genera of Tipulidae also possess a plesiomorphous basistyle. They are mainly restricted to the Tropics and the Southern Hemisphere. Representatives of these phylogenetically primitive groups are very scarce in the Holarctic: *Longurio, Megistocera,* and *Brachypremna* reach the southern states of the U.S.A. and only three species are distributed as far north as Illinois, New Jersey, and New York.

Intromittent organ. The intromittent organ of Tipulidae is usually tubular throughout its length and runs from the aedeagus (semen pump, vesica) to the adminiculum (fig. 5 & 6). In this, Tipulidae differ from Trichoceridae (Neumann, 1958) and Limoniidae (Savchenko, 1966). The former group is devoid of an adminiculum and in the latter it is fused with the aedeagus. In its retracted position the intromittent organ lies with its tip inside the adminiculum. During copulation it is pushed outside the hypopygium by rotation of the aedeagus and by contraction of the membranous pouch (a continuation of the genital chamber) in which the organ is situated. It enters the bursa copulatrix of the female as far as the anterior end where the three spermathecal ducts begin. The lengths of the intromittent organ and the bursa copulatrix are in all probability correlated. In *Oropeza* both are longer than in *Dolichopeza* s. str. (Byers, 1961).

The length of the intromittent organ varies in the examined out-groups from 0.25 mm (*Brachypremna*) to 16.40 mm (*Schummelia*) (see appendix 1). In *Nephrotoma* it varies from 1.66 mm to 40.16 mm (see appendix 2). It is assumed that a short intromittent organ represents the plesiomorphous condition in Tipulidae: firstly because it seems to be a new development within Tipulomorpha that the aedeagus and the adminiculum are separated with the intromittent organ in-between; secondly, because a short organ is found especially among primitive groups. Lengthening as well as secondary shortening has occurred in the out-group taxa but also within *Nephrotoma.*

Usually the intromittent organ curves from the aedeagus forwards, then loops downwards along the floor of the eight segment and so through the adminiculum (fig. 5). In species with a long organ the loop can be as far cephalad as the anterior end of the abdomen. In some species of the *Nephrotoma dorsalis* group the cephalad and caudad directed parts are very near to each other and together spirally coiled inside the abdomen. In *Schummelia* the course of the intromittent organ is extremely complicated with alternating lateral loops (fig. 6).

Aedeagus. The aedeagus has a midventral position inside segment eight and is connected with the other parts of the postabdomen by muscles. In a

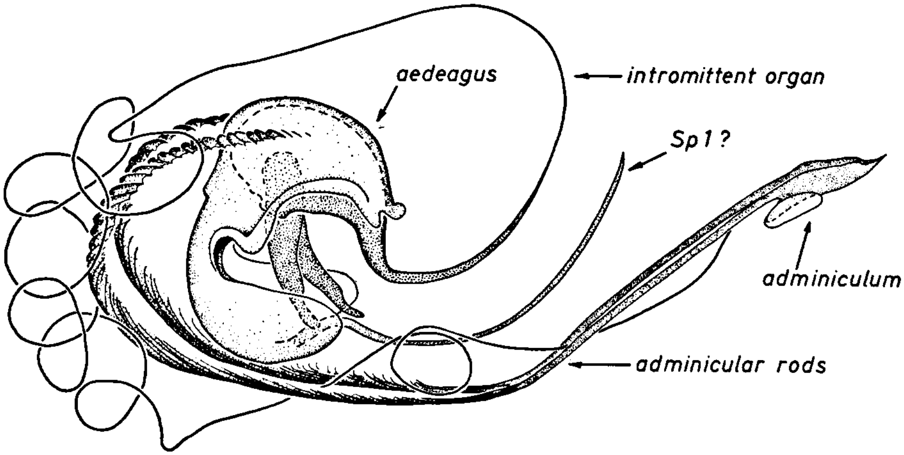


Fig. 6: Intromittent organ and associated structures in *Schummelia variicornis*, side view.

number of taxa sclerotized connections between aedeagus and adminiculum are present. Tjeder (1948) interpreted the presence of these connections in *Prionocera* (fig. 5) as representing an intermediate condition between the fused aedeagus-adminiculum of Limoniidae and the free aedeagus of Tipulidae. However, these connections, or adminicular rods sensu Byers (1961), were not found in such primitive tipulid genera as *Longurio, Brachypremna,* and *Megistocera.* They are present in *Prionocera, Nesopeza, Oropeza, Dolichopeza* s. str., *Schummelia,* and *Nephrotoma.* In the three last-mentioned taxa the rods are not connected with the aedeagus, and in *Nephrotoma* they are loose at both ends (X in fig. 18).

The aedeagus bears three sets of appendages: two anterolateral ones, two posterior ones and the dorsal, usually bifid compressor apodeme. These appendages are very variable in shape throughout the out-groups. In *Nephrotoma* it is especially the shape of the compressor apodeme which varies. The muscles surrounding the aedeagus attach at these appendages. With the aid of these muscles the aedeagus is able to rotate in the sagittal plane. Rotation takes place just before copulation to push the intromittent organ outside the hypopygium and amounts to about 180°. In the primitive genera *Longurio* and *Brachypremna* rotation amounts to about 90°, in *Schummelia* about 270°.

Adminiculum. The adminiculum consists of two sclerotized modifications, derived from the mid-dorsal margin of sternite nine. Its major function is to guide the intromittent organ during copulation. Usually it bears two lateral appendages which ascertain the correct position in-between the female cerci and hypovalvae. In its simplest form, found in *Brachypremna, Longurio, Holorusia, Vestiplex, Platytipula, Eumicrotipula, Pterelachisus,* the adminiculum is flat with a median longitudinal groove. In the majority of the examined taxa the two halves form an elongate, cone-shaped tube. In

Prionocera, Nesopeza, and *Dolichopeza* the shape of the adminiculum is very similar.

Genital bridge. The genital bridge, sensu Dobrotworsky (1968), is a strongly sclerotized plate which runs from one side of the hypopygium to the other side. It is situated underneath the anal (tenth) segment and posterior to the aedeagus. Vane-Wright (1967) stated that "a bridge structure is associated with hypopygia of a more robust nature", but this is an incorrect statement. In my view the presence of a bridge represents the plesiomorphous condition in Tipulidae because it seems to be homologous with the Fp-Fp connection mentioned by Neumann (1958) for Trichoceridae; furthermore, the various stages of reduction of the bridge must be considered derived from a complete bridge. Species of the following taxa possess a complete bridge: *Longurio, Dolichopeza, Dendrotipula, Sinotipula, Arctotipula, Holorusia, Lindneria, Vestiplex, Platytipula, Tipula, Yamatotipula.* In a number of taxa the central part of the bridge is isolated from the lateral parts. The central parts are named Sp1, the lateral parts Sp2 (after Neumann, 1958). Sp1 is the epimere of Rees & Ferris (1939), erroneously homologized by them with the adminicular rods. In the following taxa the Sp1 is no longer connected with the Sp2: *Schummelia* (?, fig. 6), *Emodotipula, Eumicrotipula, Lunatipula, Pterelachisus, Acutipula, Hesperotipula, Eremotipula, Setitipula, Tanyptera.* In all other taxa examined only the Sp2 are present. It is not known whether the genital bridge disappeared in these taxa through the Sp1 stage. For example, in *Odonatisca* the Sp2 are very elongate and almost in contact just posterior to the aedeagus. The Sp2 of *Nephrotoma, Prionocera, Nesopeza, Trichotipula,* and *Scamboneura* are very similar.

Male sternite nine. Practically all Tipulidae have the ninth sternite divided in two by a membranous area that stretches from the midventral part to the region bearing the adminiculum. In a number of tipulid taxa and species groups of *Nephrotoma* this membrane projects beyond the hypopygium and in *Prionocera, Nesopeza,* and *Dolichopeza* the shape of the membrane resembles that of *Nephrotoma.* In a number of species groups within *Nephrotoma* the membrane bears sclerotized plates. These plates are ventrally fused, forming an elongate connection with the midventral part of the inner margin of sternite nine (figs. 9 and 10). The presence of these plates is interpreted as plesiomorphous within *Nephrotoma* because similar plates are found in *Trichotipula* and *Scamboneura.* Moreover, the reduced state of these characters found in *Nephrotoma* indicates that the presence of these plates is the ancestral condition.

Male tergite nine. The extension of the male tergite nine bears small spines in all *Nephrotoma* species studied. Similar spines were found in *Scamboneura, Nigrotipula, Tipula, Yamatotula,* and *Acutipula.*

Inner dististyles. The inner dististyles assume widely different shapes throughout the Tipulidae, but are usually of fairly constant shape within smaller species groups and subgenera (Alexander, 1965). In the taxa

Nephrotoma, Prionocera, Nesopeza, Oropeza, Dolichopeza, Nobilotipula, Trichotipula, and *Scamboneura* they show much overall resemblance. The lateral shell of the id has an upright lateral margin in *Scamboneura* and in the *brevipennis* and *crocata* groups of *Nephrotoma.*

Wing venation. *Nephrotoma, Dolichopeza, Oropeza, Nesopeza, Trichotipula,* and *Scamboneura* show much resemblance in wing venation (fig. 2). Vein Rs is short, vein MCu is shifted in the direction of the wing base (except in *Oropeza,* but compare Byers, 1961, fig. 40—47: variation in wing venation of *Oropeza tridenticulata*) and the hind margin of the wing is obtusely angled underneath vein A2. It is noteworthy that the discal cell (cell IstM2) is absent only in taxa belonging to the above cluster, namely *Nesopeza, Dolichopeza,* and *Scamboneura.*

Colouration. *Nephrotoma* species are yellow with brown to black spots or stripes on the head, thorax, and abdomen. This colour pattern is widespread in *Nobilotipula, Trichotipula,* and *Scamboneura.* It is not, however, restricted to these taxa, but also occurs among smaller species groups of tipulid, limoniid, and cylindrotomid taxa.

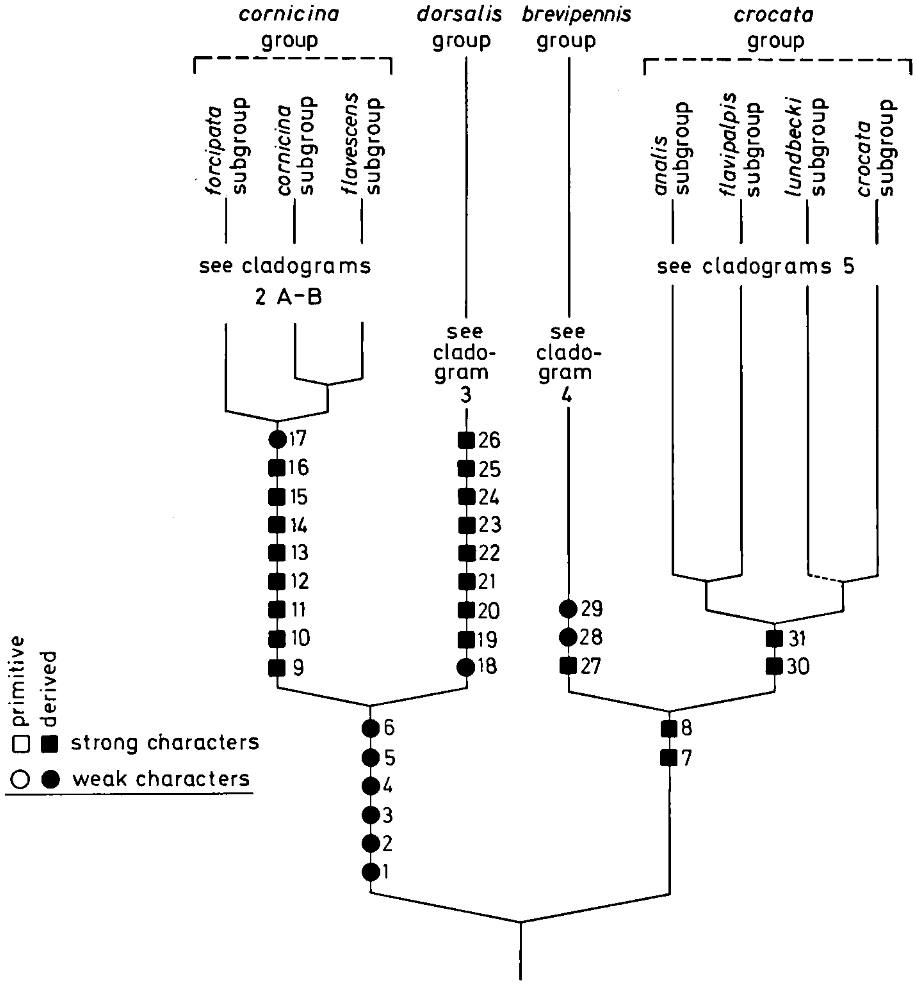
Tibial spurs. The number of apical spurs on the tibiae is usually 1 (front leg), 2 (middle leg), 2 (hind leg). It is 1, 1, 2, in *Nephrotoma, Dolichopeza, Oropeza, Nesopeza, Scamboneura, Nobilotipula, Emodotipula, Angarotipula, Dendrotipula, Sinotipula, Sinotipula* formerly *Bellardina.* In *Yamatotipula* the tibial spur formula is either 1, 2, 2, or 1, 1, 2.

Oosterbroek (1978) defined the genus *Nephrotoma* on wing venation. The combination of wing venation characteristics enables the recognition of tipulids as *Nephrotoma,* but each character in itself is not a synapomorphy for the genus. In fact there is at present only one such character recognized: the presence of free adminicular rods (fig. 18). *Trichotipula* and *Scamboneura* apparently are the closest allies of *Nephrotoma. Scamboneura* is very probably the sistergroup of *Nephrotoma,* based on synapomorphies of the inner dististyles.

PHYLOGENY OF THE SPECIES GROUPS

Introduction

The *Nephrotoma* species occurring in the western Palaearctic are here assigned to four speciesgroups. The presumed phylogeny of these groups is presented in cladograms 1 (basal phylogeny), 2A-B (*cornicina* group), 3 (*dorsalis* group), 4 (*brevipennis* group), and 5 (*crocata* group). Synapomorphous characters are numbered 1-n in all (set of) cladograms. Autapomorphous characters and characters whose distribution does not correspond to the presented phylogeny are discussed at the end of this section.



Cladogram 1: Basal phylogeny of the species groups.

Basal phylogeny (cladogram 1)

The *cornicina* and *dorsalis* groups are considered sistergroups. The monophyly of this pair of sistergroups is based on six, so-called weak characters. Both groups are founded on many synapomorphous characters apparently due to divergence from the basic plan in *Nephrotoma*, reducing the possibility of recognizing strong derived characters shared by members of both groups.

The sister group pair *brevipennis* group — *crocata* group shows much less divergence from the basic plan. For this reason only a few synapomorphous characters are available to establish the monophyly of the sister pair and that of its individual speciesgroups.

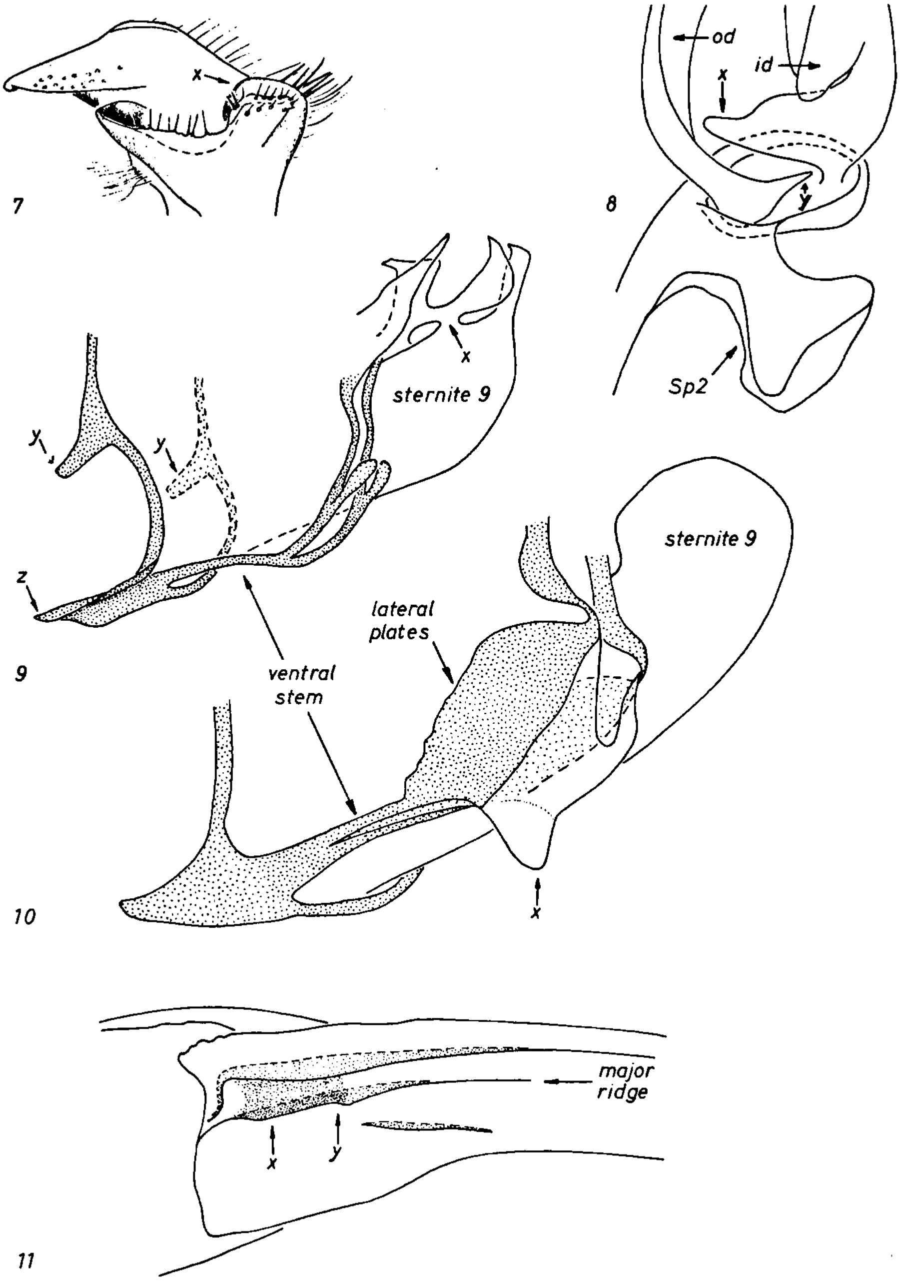


Fig. 7: Left inner dististyle (id) of *N. analis*, outside view. Fig. 8: dorsal margin of right half of sternite nine in *N. dorsalis*, dorsal view. Fig. 9: medisternal sclerotizations in *N. dorsalis*, lateroposterior view. Fig. 10: medisternal appendage in *N. croceiventris*, lateroposterior view. Fig. 11: anterior part of right hypovalva in *N. analis*, inside view.

The numbers 1—31 in cladogram 1 refer to the following:

1. The presence of a midventral projection on the medisternal sclerotizations is considered apomorph. The projection is absent in the *brevipennis*, *crocata*, and out-groups examined. In the *dorsalis* group the projection is inserted at the region between the lateral sclerotizations and the ventral stem. In the *cornicina* group the ventral stem is reduced and the projection thereby shifted towards the hind margin of the eighth sternite. The weakness of the character stems from the dissimilarity of the character states and the lack of intermediate states.

2. Out-group as well as in-group comparisons reveal that an elongate od, as found in the *dorsalis* group and in the phylogenetically primitive members of the *cornicina* group, should be considered apomorph. This character is given low weight because of its variability in the *cornicina* group.

3. In the *cornicina* and *dorsalis* group the abdominal spots are longitudinally arranged. The other two species groups have the abdomen banded or possess an abdominal colouration in which this pattern can be recognized. The former condition is considered derived as a result of out-group comparisons. Colour pattern characters are given low weight throughout this paper.

4. Usually the lateral appendages of the adminiculum are simple blades, directed caudad (fig. 59). This is the case in many of the out-groups and in the *brevipennis* and *crocata* groups. In the *dorsalis* group and the phylogenetically primitive members of the *cornicina* group the appendages are modified and directed dorsally. Dissimilarity of the respective states gives this character low weight.

5. The absence of a rugosity on the inner surface of the hypovalvae, just above the anterior part of the major ridge (X in fig. 11), is interpreted as a synapomorphy for the *dorsalis* and *cornicina* group. The rugosity is present in the other species groups and in *Scamboneura.*

6. The lateral shell of the id has an upright outer margin in the *brevipennis* and *crocata* groups and in *Scamboneura* (fig. 7). This condition is assumed to be plesiomorphous in *Nephrotoma* and the absence of such a margin synapomorphous for the *cornicina* and *dorsalis* groups.

7. The strengthening of the outer part of the id (X in fig. 7) is considered derived. The id of the *brevipennis* and *crocata* group shows much resemblance with the id of *Scamboneura*, but in this genus and in the other species groups of *Nephrotoma* the outer part is not strengthened.

8. The major ridge on the inner surface of the hypovalvae shows a smal bend at the edge of the rugosity (Y in fig. 11) in all species of the *brevipennis* and *crocata* group and in none of the other species examined. Although this is only a minor character, it is considered a strong synapomorphy for the respective groups because of its constancy.

The monophyly of the *cornicina* group is based on the following:

9. The ventral stem of the medisternal sclerotizations is reduced and the sclerotizations themselves are no longer fused with each other basally (fig.

87). The reverse condition apparently belongs to the ground plan in *Nephrotoma* (see preceding section).

10. The midventral projection of the medisternal sclerotizations is shifted to the hind margin of sternite eight (compare character 1).

11. The aedeagus possesses a midposterior appendage (Y in fig. 18). This appendage was found only among members of the *cornicina* group. Within this group there is a strong tendency towards reduction of the appendage (see *cornicina* group, character 14).

12. The crest on the id extends posteriorly (fig. 15). In all taxa examined the crest is either absent or restricted to the dorsal part of the id.

13. The extension of the male tergite 9 possesses lateral shells in the *cornicina* group only.

14. The female cerci of tipulids are usually blunt and elongate. In the *cornicina* group they are pointed (see *cornicina* group, character 1).

15. The female hypovalvae are reduced (see *cornicina* group, characters 2 & 16).

16. The female hypovalvae possess only one ridge on the inner surface (fig. 19). In all other tipulids examined there are two ridges.

17. The inner margin of the male sternite nine has a reduced midventral appendage. This character is discussed in the final section.

The monophyly of the *dorsalis* group is based on the following:

18. The fused valvulae are usually connected with sternite nine by elongate sclerotizations. In the *dorsalis* group, but also in *malickyi* and in *lundbecki* the connection is membranous. This character is given low weight because it is not entirely restricted to the *dorsalis* group. Furthermore, the female of the phylogenetically most primitive member of the *dorsalis* group, *ramulifera*, was not examined during this study.

19. The male sternite nine is lengthened caudad beyond the base of the od and id. In other tipulids the male sternite nine (basistyle) is usually semiglobular.

20. The id has a narrow prolongation at its base (X in fig. 8), found in all species of the *dorsalis* group and not outside the group.

21. The od also possesses a narrow prolongation at its base (Y in fig. 8), found in all species of the group and not outside the group.

22. The base of the id and od is surrounded by a sclerotized ring in practically all tipulids. Except for the *dorsalis* group this ring is strongly bent inside the hypopygium.

23. The lateral appendages of the adminiculum are basally broad with upcurved tips, further modified in *dorsalis* and *lunulicornis* (compare character 4).

24. The lateral appendages of the adminiculum are confluent with sternite nine at their lower posterior corners (X in fig. 9). In all other tipulids examined the lateral appendages are free from sternite nine.

25. The male sternite eight is medially incised. This character state is restricted to the *dorsalis* group.

26. The posterior appendages of the aedeagus are convergent. In all other *Nephrotoma* species the appendages are parallel or divergent.

For the *brevipennis* group only character 27 can be given much weight, as it is found in all three species. Characters 28 and 29 are good characters too, very likely to be uniquely derived. However, the female of *antithrix* remains unknown and, concerning 29, I am not sure whether the observed part of the

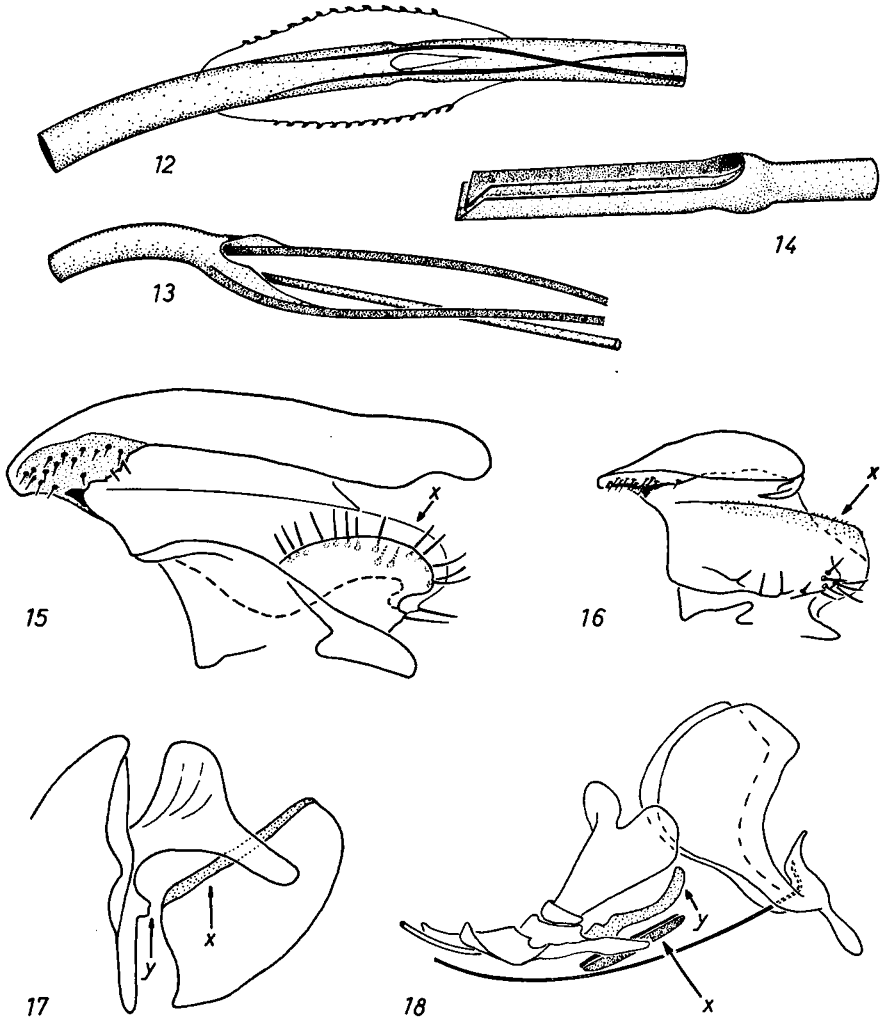


Fig. 12: Part of intromittent organ in *N. brevipennis*. Fig. 13: part of intromittent organ in *N. guestfalica*. Fig. 14: part of intromittent organ in *N. flavipalpis*. Fig. 15: left inner dististyle (id) in *N. appendiculata*, outside view. Fig. 16: left inner dististyle in *N. flavescens*, outside view. Fig. 17: adminiculum and right half of sternite nine in *N. flavescens*. Fig. 18: aedeagus, adminiculum, and intromittent organ (in part) in *N. aculeata*, side view.

intromittent organ in the holotype of *antithrix* (the only known specimen of this species), represents the entire organ in this species.

27. The adminiculum has small shells between the central part and the lateral appendages.

28. The dorsal edge of the female sternite eight is bipartite towards the hypovalvae.

29. The intromittent organ possesses a serrate membrane (fig. 12).

The *crocata* group is defined by two characters of the extension of the male tergite nine:

30. The extension bears lateral projections. In *lamellata* and *semiflava* these projections are further modified.

31. The extension possesses medial protuberances (see final section).

The cornicina group (cladograms 2A & 2B)

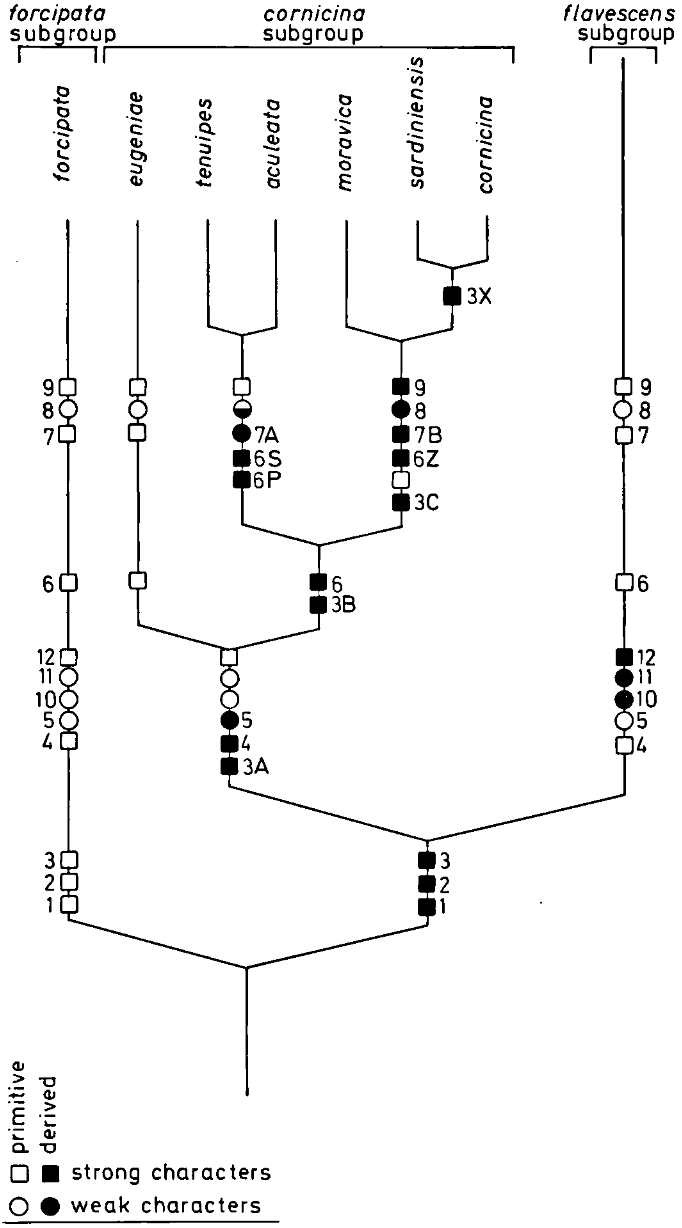
The *cornicina* group is a well-defined monophyletic group. It comprises the species treated in part 1 of the revision and *eugeniae* from part 4. These species are assigned to three subgroups: the *forcipata* subgroup, the *cornicina* subgroup, and the *flavescens* subgroup. Extreme variation occurs in many characters especially within the last-mentioned group. Because of the variability only a few reliable characters were recognized, but even among these problems arose from the individual character expressions found in several species. The result is a rather unbalanced phylogeny for the *flavescens* subgroup, a phylogeny based on few characters and containing several uncertainties. Nevertheless, the adopted phylogeny fits as well as possible, I hope, the encountered distribution of characters.

The numbers 1—12 in cladogram 2A refer to the following:

1. The female cerci of the species of the *cornicina* group are pointed, except in *forcipata.* In the latter species they are blunt and in length and shape intermediate between those of the *cornicina* group and the elongate blunt cerci found in the majority of Tipulidae and in the other speciesgroups within *Nephrotoma.* In *eugeniae, schaeuffelei,* and *quadrifaria* further reduction of the cerci occurred.

2. All species of the *cornicina* group show reduction of the hypovalvae (fig. 19) compared to the broad, elongate hypovalvae in other *Nephrotoma* species. Within this reductional trend, *forcipata* shows the most plesiomorphous condition (fig. 19A).

3. The extension of the male tergite nine is variously shaped within *Nephrotoma.* A widely V-shaped extension is considered the plesiomorphous condition in *Nephrotoma* (see final section). The medial part of the extension shows a distinct transformation series towards narrowing within the *cornicina* subgroup. In *forcipata* the extension is still widely V-shaped (fig. 21). In *eugeniae* it is V-shaped with medial swellings (fig. 20). In the sistergroup of *eugeniae* the medial swellings are large and prolonged ventrally (fig. 22). This ventral part distinctly curves towards the lateral shell in *moravica, sardiniensis*



Cladogram 2A: Phylogeny of the *cornicina* group and the *cornicina* subgroup.

and *cornicina* (fig. 23.). The monophyly of *cornicina* and *sardiniensis* is based on character 3X: central spines on lateral shell inserted on a swelling (fig. 23).
4. All members of the *cornicina* subgroup possess a triangular-shaped sclerotization on the outer margin of the id. It is considered a strong

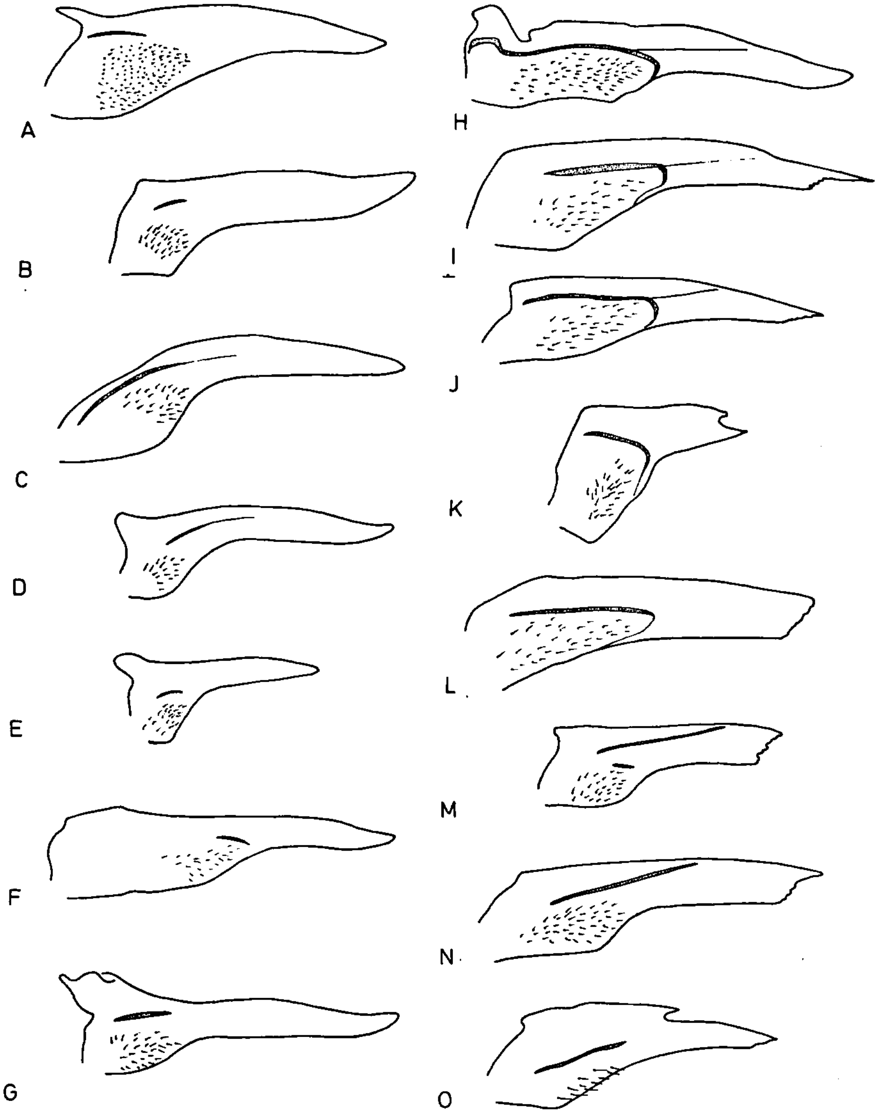


Fig. 19: Right hypovalva, inside view; A, *N. forcipata*; B, *N. tenuipes*; C, *N. aculeata*; D, *N. cornicina*; E, *N. eugeniae*; F, *N. schaeuffelei*; G, *N. nasuta*; H. *N. saccai*; I, *N. beckeri*; J, *N. fontana*; K, *N. quadrifaria*; L, *N. appendiculata*; M, *N. exastigma*; N, *N. flavescens*; O, *N. guestfalica*.

synapomorphy because occurrence is restricted to this subgroup.
5. The lateral shell of the id bears an upright projection posteriorly. This character is given less significance as similar but smaller projections are found in *schaeuffelei* and *spatha*.
6. In species comprising the sistergroup of *eugeniae* the medial projection at

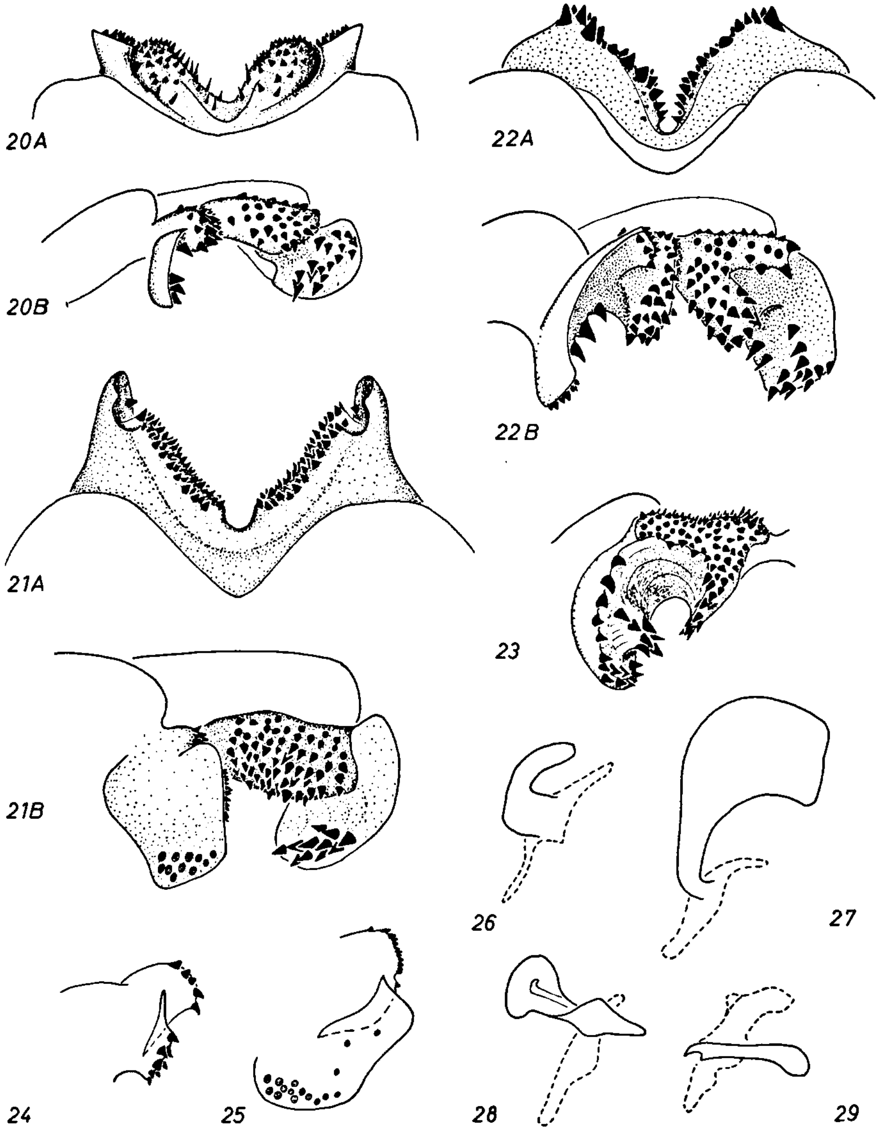


Fig. 20—25: Posterior extension of male tergite nine; 20, *N. eugeniae*, A: dorsal view, B: lateroposterior view; 21, *N. forcipata*, A: dorsal view, B: lateroposterior view; 22, *N. tenuipes*, A: dorsal view, B: lateroposterior view; 23, *N. cornicina*, rear view of left half; 24, *N. exastigma*, side view; 25, *N. fontana*, side view.

Fig. 26—29: Left lateral appendage of adminiculum: 26, *N. tenuipes*; 27, *N. aculeata*; 28, *N. cornicina*, 29, *N. minuscula*.

the hind margin of the male sternite eight is elongate and not dorsoventrally compressed as in the other species of the *cornicina* group. In *tenuipes* and *aculeata* the projection has no pubescence (6P) and is very slender and acute

(6S). The species *moravica, sardiniensis*, and *cornicina* possess a more robust projection with a knob-like end (6Z). All these character states are considered strong synapomorphies because of their restricted occurrence. 6S and 6Z do not apparently form a transformation series, but should be considered different expressions of the medial projection.

7. The lateral appendage of the adminiculum is very characteristic in *tenuipes* and *aculeata* (fig. 26 & 27) and in *moravica, sardiniensis*, and *cornicina* (fig. 28). Although 7A and 7B seem to represent quite different expressions of the character, 7B might well be derived from 7A. The latter, therefore, is given less significance.

8. The medisternal sclerotizations are entirely absent in *moravica, sardiniensis*, and *cornicina*. This character is considered weak because reduction of these plates also occurs in the *brevipennis* group and in several of the species of the *flavescens* subgroup.

9. The crest of the id is pubescent dorsally in the species *moravica, sardiniensis*, and *cornicina* only.

10. The dorsal margin of the male sternite nine is flattened (X in fig. 17) in all species of the *flavescens* subgroup except in *nasuta* and *spatha*. This character was not observed in any of the out-groups or remaining species groups within *Nephrotoma*.

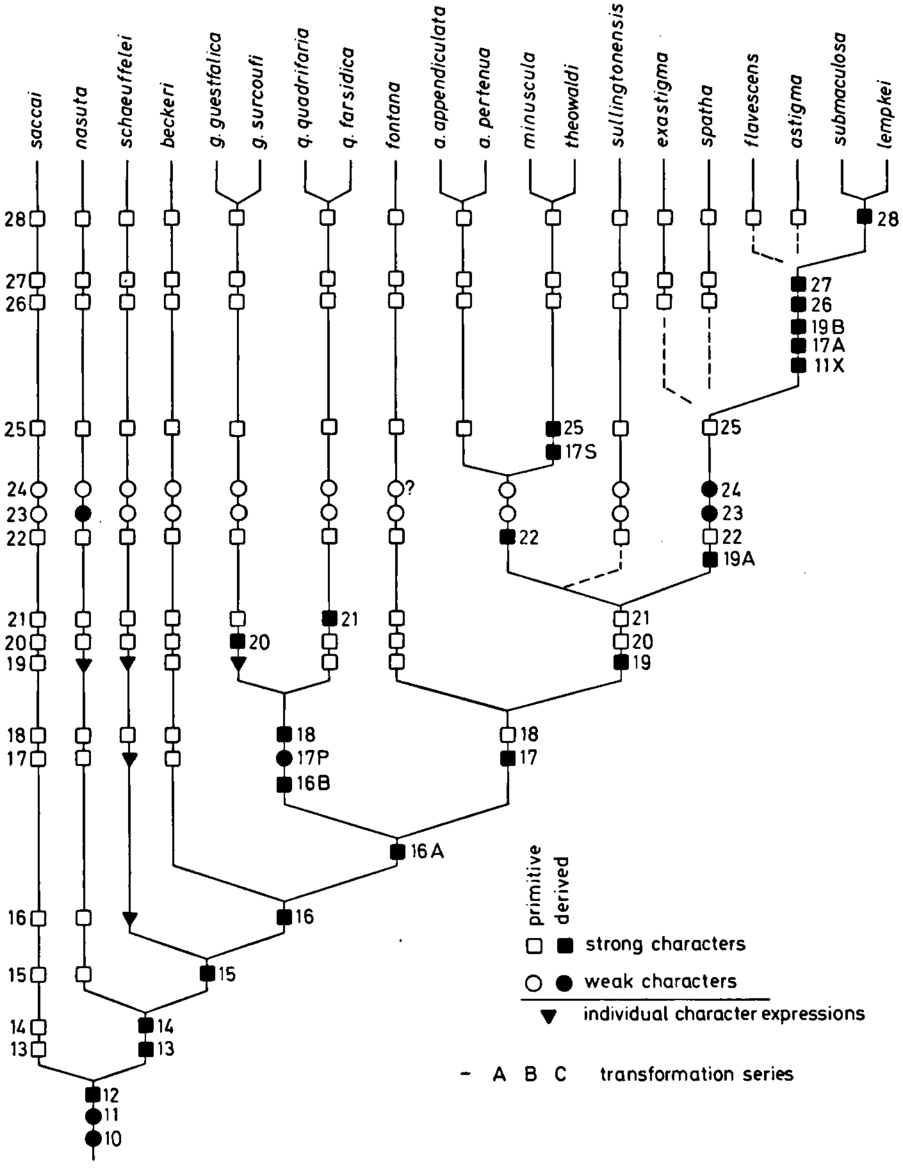
11. The posterior part of the id forms a membranous ridge underneath the free part of the crest (X in fig. 15 & 16) in all species of the *flavescens* subgroup except in *nasuta* and *guestfalica*. 11X in cladogram 2B refers to the short pubescence of this ridge in *flavescens, astigma, submaculosa*, and *lempkei* (fig. 16).

12. In all members of the *flavescens* subgroup the adminicular rods (X in fig. 18) are absent. Very slight remnants of these rods were found in one of the five *saccai* males examined (only eight *saccai* males are known).

The numbers 13—28 in cladogram 2B refer to the following:

13. The apical part of the intromittent organ consists of two filaments with a thin interjacent tube (fig. 13). The different types of intromittent organs found in *Nephrotoma* are discussed in the final section.

14. One of the synapomorphous characters for the *cornicina* group is the presence of a midposterior appendage at the aedeagus (Y in fig.18). Curiously enough there is a strong tendency towards reduction of this appendage in the *flavescens* subgroup. The species *schaeuffelei* and *beckeri* possess a reduced appendage while it is absent in *nasuta* and in species comprising the sistergroup of *beckeri*. Presence of this appendage could easily be interpreted as a synapomorphy for a smaller section of the *cornicina* group, but such an interpretation does not correspond with the distribution of the other synapomorphous characters. Furthermore, absence in most members of the *flavescens* subgroup is interpreted as reduction because traces of this appendage were found in several species, most distinct in *appendiculata*.



Cladogram 2B: Phylogeny of the *flavescens* subgroup.

15. In the sistergroup of *nasuta* the lateral appendages of the aedeagus are small, about half the size of the appendages in the other *Nephrotoma* species studied.

16. The species comprising the sistergroup of *schaeuffelei* have the distal margin of the hypovalvae serrate, as if the tip is broken off (fig. 19 I—O). The species *beckeri* has only the extreme tip reduced, in its sistergroup the entire apical part of the hypovalvae is reduced (16A) with extreme reduction in *guestfalica* and *quadrifaria* (16B). Very short and narrow hypovalvae are found in *schaeuffelei*, probably independently achieved from the broken-off phase. The similarity in shape between the hypovalvae of *beckeri* and *fontana* is secondary; in *fontana* reduction has proceeded beyond the stage figured for *appendiculata*.

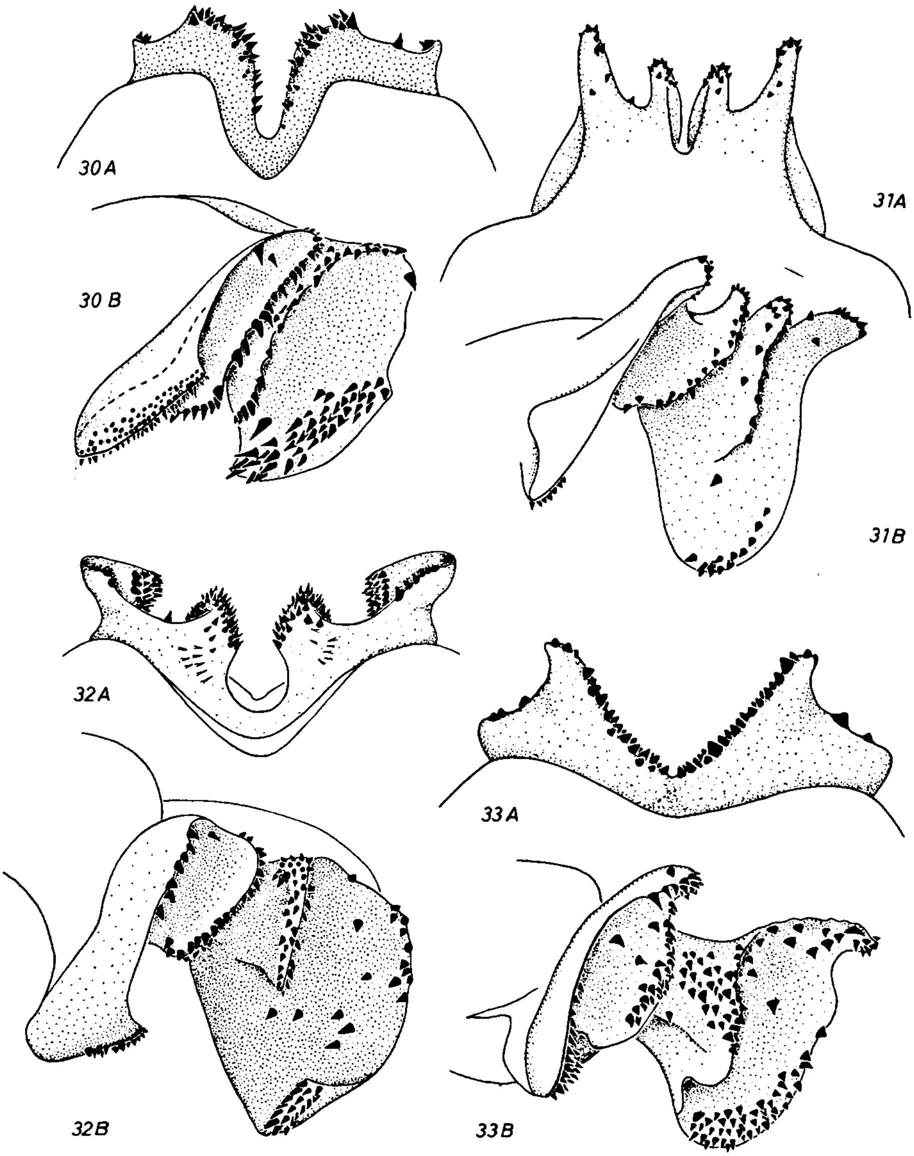


Fig. 30—33: Posterior extension of male tergite nine, A: dorsal view, B. lateroposterior view; 30, *N. saccai*; 31, *N. nasuta*; 32, *N. beckeri*; 33, *N. quadrifaria*.

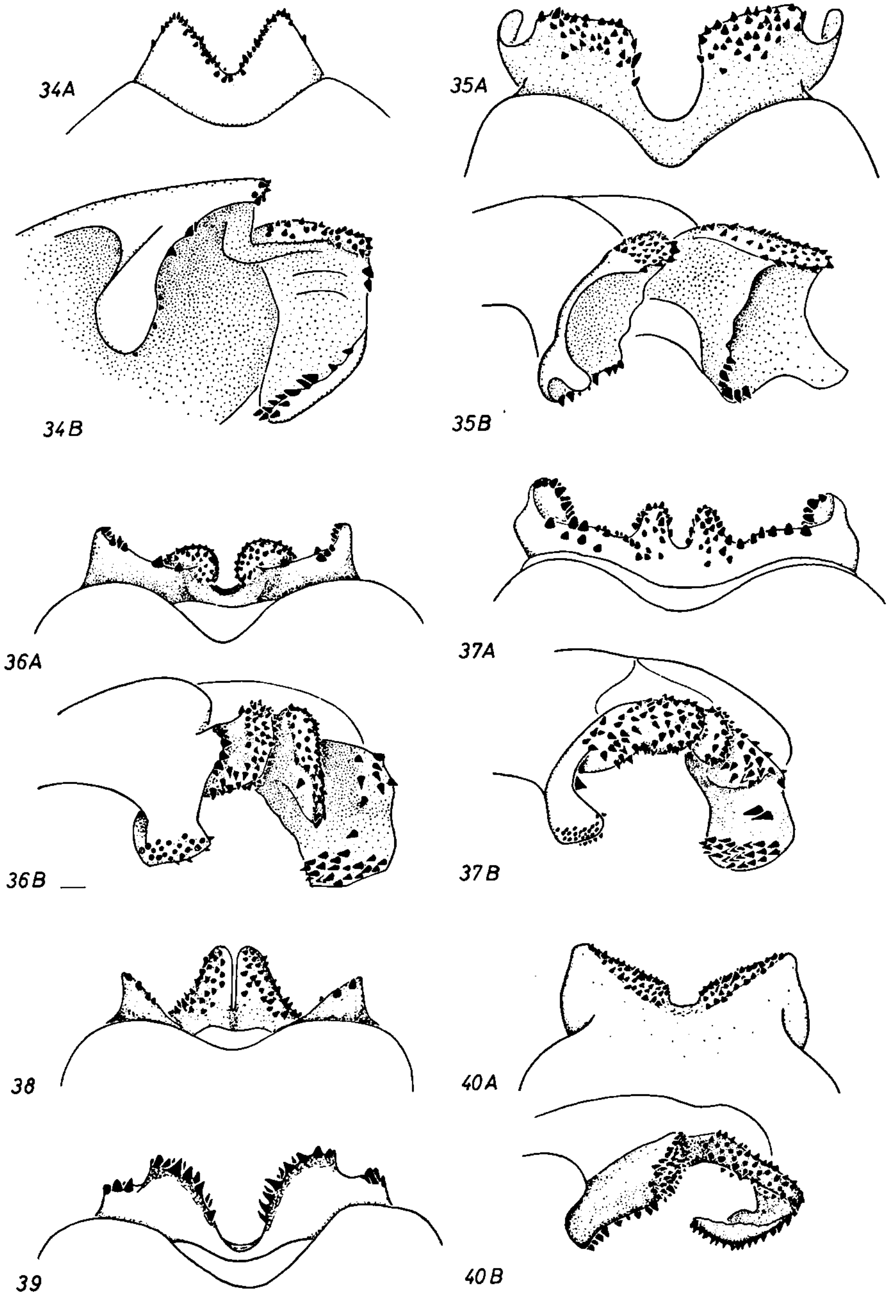


Fig. 34—40: Posterior extension of male tergite nine, A: dorsal view, B: lateroposterior view, 34, *N. schaeuffelei*; 35, *N. guestfalica*; 36, *N. sullingtonensis*; 37, *N. flavescens*; 38, *N. minuscula*, dorsal view; 39, *N. exastigma*, dorsal view; 40, *N. spatha*.

17. Character 17 refers to the shape of the extension of the male tergite nine. This shape apparently is correlated with the reduction of the hypovalvae (during copulation the hypovalvae are situated between the lateral parts of the extension). In *saccai* (fig. 30), *nasuta* (fig. 31), and *beckeri* (fig. 32) the extension is large with elongate spiny ridges underneath and extended lateral shells. In the species group *fontana* to *lempkei* (fig. 36—40) the extension is much smaller and shorter. In both *guestfalica* (fig. 35) and *quadrifaria* (fig. 33) the extension consists of two, posteriorly directed parts in which the central ridges and lateral shells are incorporated (17P). Both species have extremely short hypovalvae. 17P is considered weak because of the dissimilarity between the extensions of these two species. Very short hypovalvae are also found in *schaeuffelei*. The extension of this species has reduced central ridges (fig. 34). The species *flavescens, astigma, submaculosa,* and *lempkei* (fig 37) have very short and rounded central ridges (17A). In *spatha* (fig. 40) and *exastigma* (fig. 39) these ridges are apparently confluent with the dorsal margin, thereby broadening the medial incision. In *minuscula* (fig. 38) and *theowaldi* the central part of the extension is distinctly prolonged (17S).

18. The species *guestfalica* and *quadrifaria* are the only two among the *Nephrotoma* species examined which have bristles on the neala of the wing (Oosterbroek, 1979c: fig. 87).

19. The ridge on the inner surface of the hypovalvae (fig. 19) is curved downwards at the distal end in *saccai, beckeri, quadrifaria,* and *fontana*. This is assumed to be the plesiomorphous condition within the *flavescens* subgroup by parsimony and correlation with other transformation series. Absence of the downcurved part is considered synapomorphous for the *appendiculata-lempkei* group. The absence in *nasuta, schaeuffelei,* and *guestfalica* is correlated with the peculiar shape of the hypovalvae in these species (in *nasuta* the dorsal margin is modified anteriorly; the hypovalvae of *schaeuffelei* are extended inside sternite eight; in *guestfalica* the ridge changed position but is apparently homologous with the original ridge and not with the one discussed below). 19 is, in spite of the aforementioned character states, considered a strong character because of the uniform character expression in the *appendiculata-sullingtonensis* group, and because of the transformation series from this state to that in the *flavescens-lempkei* group. In the species of the latter group a new ridge has developed, running from the setose area towards the dorsal margin (19B). This ridge is also found in *exastigma* next to a small vestige of the original ridge (19A). The shape of the ridge in *spatha* is unknown as this species is known from males only.

20/21. For *guestfalica* and *quadrifaria* a number of autapomorphous characters can be listed. Both species possess a peculiar shaped extension of the male tergite nine. The lateral appendages of the adminiculum as well as the id are very characteristic in both species.

22. The *appendiculata-theowaldi* group is characterized by very short posterior appendages of the aedeagus.

23. The basal as well as the apical part of the intromittent organ are very short in *exastigma, spatha, flavescens, astigma, submaculosa,* and *lempkei,* but also in *nasuta.* Characters relating to the length of the intromittent organ are given low weight (see final section).

24. The male claws are not pectinate in the *exastigma-lempkei* group. In all other species of the *cornicina* group the male claws are pectinate (the character state remains unknown in *fontana*). In the other species groups pectinate as well as non-pectinate claws are found with the latter condition always restricted to smaller, monophyletic groups.

25. A synapomorphy for *minuscula* and *theowaldi* is the downcurved position of the apical part of the lateral appendages of the adminiculum (fig. 29). This character state is restricted to these two species and probably represents the last stage in a trend within the *cornicina* group to change the position of the appendage from dorsal to posterior.

26. In the *flavescens-lempkei* group the ventral appendages of the adminiculum are distinctly separated from sternite nine (Y in fig. 17). In the other *Nephrotoma* species these two parts are connected with each other or lie very close.

27. The remnants of the posteriorly reduced crest of the id are incurved (fig. 16) in the *flavescens-lempkei* group only.

28. The lateral appendages of the adminiculum have incurved anterodorsal margins in *submaculosa* and *lempkei.* In the other species of the *fontana-lempkei* group the anterodorsal margin is straight or reduced.

The species *sullingtonensis* does not share any synapomorphy with the *appendiculata-theowaldi* group or the *exastigma-lempkei* group. It is tentatively assigned to the sistergroup position of the former group, especially because of similarity in colour pattern. In the members of this group and in *sullingtonensis* the dark spots are distinctly enlarged. The *exastigma-lempkei* group can be characterized by having all dark spots reduced in size.

The dorsalis group (cladogram 3)

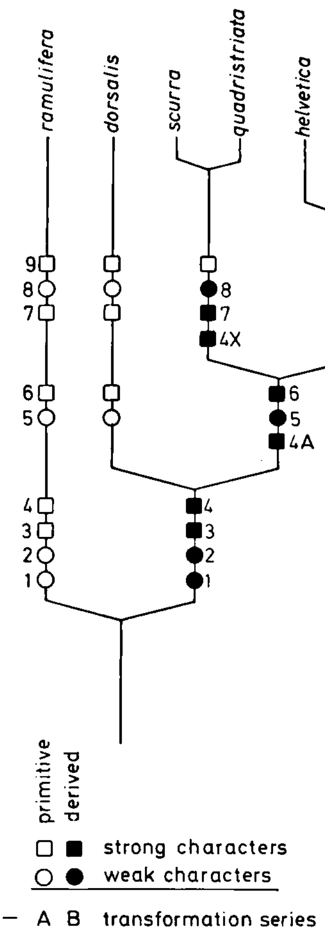
Seven taxa belonging to the *dorsalis* group occur in the western Palaearctic. Another eighteen taxa are known from the eastern Palaeartic and the group is represented in the Nearctic by about 25 taxa. The *dorsalis* group is a well-defined monophyletic group. Discussed here are the species treated in part 3 of the revision and *ramulifera,* treated in part 4.

The numbers 1—9 in cladogram 3 refer to the following:

1. The occipital marking is usually broad and basally rounded in *Nephrotoma.* In the sistergroup of *ramulifera* it is elongate and narrow. Colour characters are given low weight throughout this paper.

2. The male claws are not pectinate in the sistergroup of *ramulifera.* This character is discussed under the *cornicina* group: character 24.

3. The male sternite eight has a large medial incision in the sistergroup of *ramulifera.* In the latter species the incision is small. An incised sternite eight is considered synapomorphous for the *dorsalis* group.



Cladogram 3: Phylogeny of the *dorsalis* group.

4. The extension of the male tergite nine shows a distinct trend towards narrowing of the lateral parts and towards narrowing of the medial incision. In *ramulifera* (fig. 41) the two lateral halves are broad and the incision is widely V-shaped. *N. dorsalis* (fig. 42) shows small invaginations at the anterior margin of the lateral parts. In the sistergroup of *dorsalis* the invaginations become larger (4A), ultimately narrowing the lateral parts to about half the length of the central parts (4B) in *helvetica* (fig. 45), *austriaca* (fig. 46), and *lunulicornis* (fig. 47). 4X refers to the small medial incision in *scurra* (fig. 43) and *quadristriata* (fig. 44). 4Y refers to the inwardly directed lateral rods in *austriaca* and *lunulicornis*.

5. The inner margin of the male sternite nine has no lateral projections in the sistergroup of *dorsalis*. This character is discussed in the final section.

6. The species comprising the sistergroup of *dorsalis* have the central part of

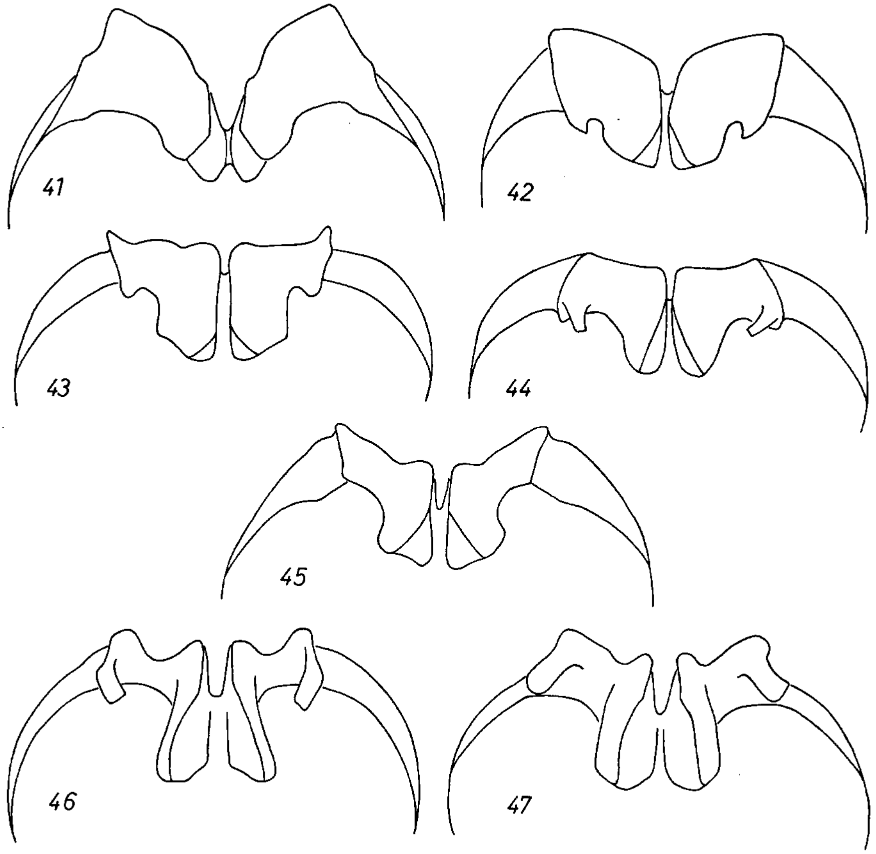


Fig. 41—47: Outline of posterior extension of male tergite nine, ventral view; 41, *N. ramulifera*; 42, *N. dorsalis*; 43, *N. scurra*; 44, *N. quadristriata*; 45, *N. helvetica*; 46, *N. austriaca*; 47, *N. lunulicornis*.

the adminiculum modified (fig. 48—53). The central part is winged in *scurra, quadristriata,* and *austriaca;* both *helvetica* and *lunulicornis* show further modifications.

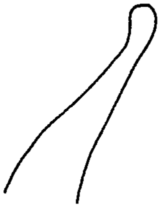
7. The midventral projection of the medisternal sclerotizations is absent in *scurra* and *quadristriata* only.

8. The stigma of the wing is faint in *scurra* and *quadristriata*; in the other species of the *dorsalis* group it is distinct.

9. The lateral shell of the id is directed almost vertically in *helvetica, austriaca,* and *lunulicornis,* whereas it is more or less horizontal in the other *Nephrotoma* species.

The brevipennis group (cladogram 4, fig. 54)

The three species from Madeira, viz.*brevipennis, lucida* and *antithrix,* form a monophyletic group. *N. antithrix,* known from the male holotype only, is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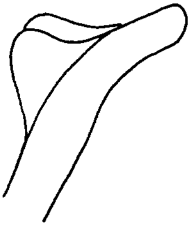
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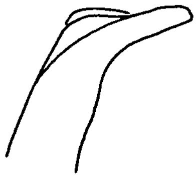
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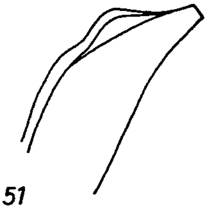
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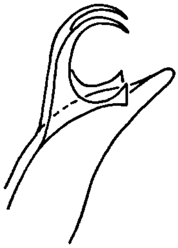
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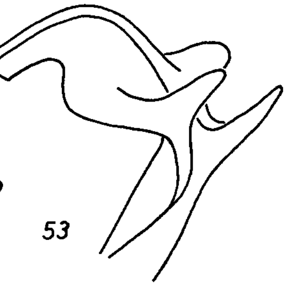
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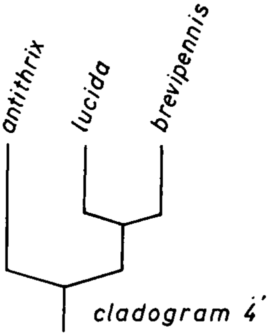

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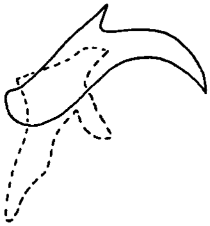
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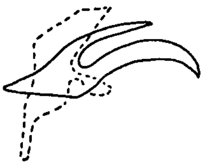
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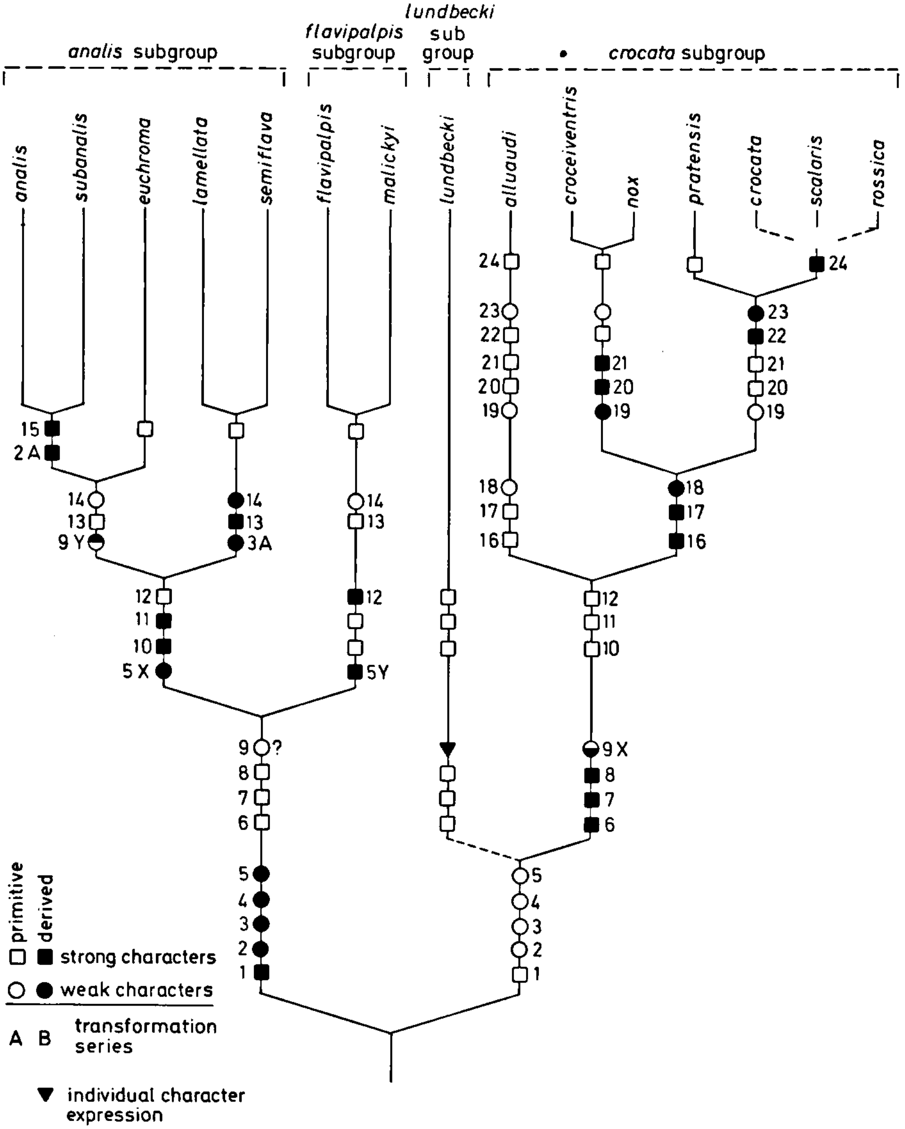
Fig. 48—53: Central part of adminiculum; 48, *N. dorsalis*; 49, *N. scurra*; 50, *N. quadristriata*; 51, *N. austriaca*; 52, *N. helvetica*; 53, *N. lunulicornis*. Fig. 54: presumed phylogeny of the *brevipennis* group. Fig. 55—57: lateral appendage of adminiculum; 55, *N. antithrix*; 56, *N. lucida*; 57, *N. brevipennis*.

interpreted as the sister species of the other two. This is merely based on similarity. The differences between *brevipennis* and *lucida* are small, whereas in *antithrix* the hypopygium is of a very peculiar shape, clothed with adversely directed hairs. A seemingly distinct transformation series is found in the lateral appendages of the adminiculum from a simple structure in *antithrix* (fig. 55) to a bifid structure in *brevipennis* (fig. 57). Given the highly derived hypopygial structures of *antithrix* it is not unlikely that the direction of this series is from *brevipennis* towards *antithrix* or from *lucida* (fig. 56) in two different directions. The closest ally of the Madeiran species is likely to be the Nearctic *ferruginea*. With respect to the characters 1—8 and 27—31 in



Cladogram 5: Phylogeny of the *crocata* group.

cladogram 1 it must be considered the sister species of the Madeiran ones. With them it shares character 27 but not 28 and 29. In *ferruginea* the lateral appendage is of the same shape and length as in *antithrix* but also slightly bifid as in *lucida.*

The crocata group (cladogram 5)

The *crocata* group consists of four subgroups: the *analis* subgroup (*analis* group sensu Oosterbroek, 1979a, 1979c), *The flavipalpis* subgroup, the *lundbecki* subgroup, and the *crocata* subgroup (*crocata* group sensu Oosterbroek, 1979a, 1979c). The adopted phylogeny of the group is given in cladogram 5. *N. lundbecki* is tentatively regarded here as the sister species of the *crocata* subgroup. Cladogram 5 does not account for the phylogeny of the species assemblage *crocata-scalaris-rossica.* Omitted from this cladogram are the subspecies of *croceiventris, pratensis, crocata,* and *scalaris.* Apart from the characters 16—24, these taxa merely differ in colouration. Such differences are given low weight throughout this paper and with regard to the above mentioned taxa they are of no significance at all. For example, within the species assemblage *crocata-scalaris-rossica,* the first two taxa show much resemblance in colouration but the same degree of resemblance is found between *pratensis eepi* and *croceiventris lindneri.*

The numbers 1—24 in cladogram 5 refer to the following:

1. The extension of the male tergite nine has the dorsal margin triangular between the lateral and medial protuberances. This character is restricted to the *analis* and *flavipalpis* subgroups. Its absence in *analis* and *subanalis* is considered a synapomorphy for these two species (2A).

2. The inner margin of the male sternite nine has a reduced midventral appendage. This character is discussed in the final section.

3. The Sp2 are triangular with a bulbous outgrowth. In *semiflava* the outgrowth is small and in *lamellata* it is absent (3A). This character is discussed in the final section.

4. The abdominal tergites have the lateral margins not darkened as in the other *Nephrotoma* species, but possess infuscated stripes well above the margins. In the melanistic *semiflava* the lateral margins are darkened.

5. The apical part of the intromittent organ is bifid, except in *lamellata.* 5X refers to the *analis* subgroup (fig. 62 & 63), where the bifid part is very short, less than 1% of the total lenght of the organ. 5X is given less significance because of its absence in *lamellata.* In the *flavipalpis* subgroup (5Y) the bifid part is very characteristic. It consists of two V-shaped filaments and accounts for about 75% of the total length (fig. 14). Number 5 itself is given low weight because it is not known whether the two different states 5X and 5Y are correlated. The different types of intromittent organs found in *Nephrotoma* are discussed in the final section.

6. All members of the *crocata* subgroup possess a small spine on the ventral surface of the intromittent organ (fig. 64). Within *Nephrotoma* this character is restricted to the *crocata* subgroup.

7. The Sp2 is dish-shaped. See for discussion final section.

8. The sclerotized rods between the fused valvulae and tergite nine usually end at the fused valvulae. In the *crocata* subgroup they are continued into the valvulae (fig. 60).

9. The extension of the male tergite nine is very characteristic in all four subgroups. In the *crocata* subgroup the extension possesses horn-like lateral projections (9X). *N. lundbecki* has distally directed projections bearing apical

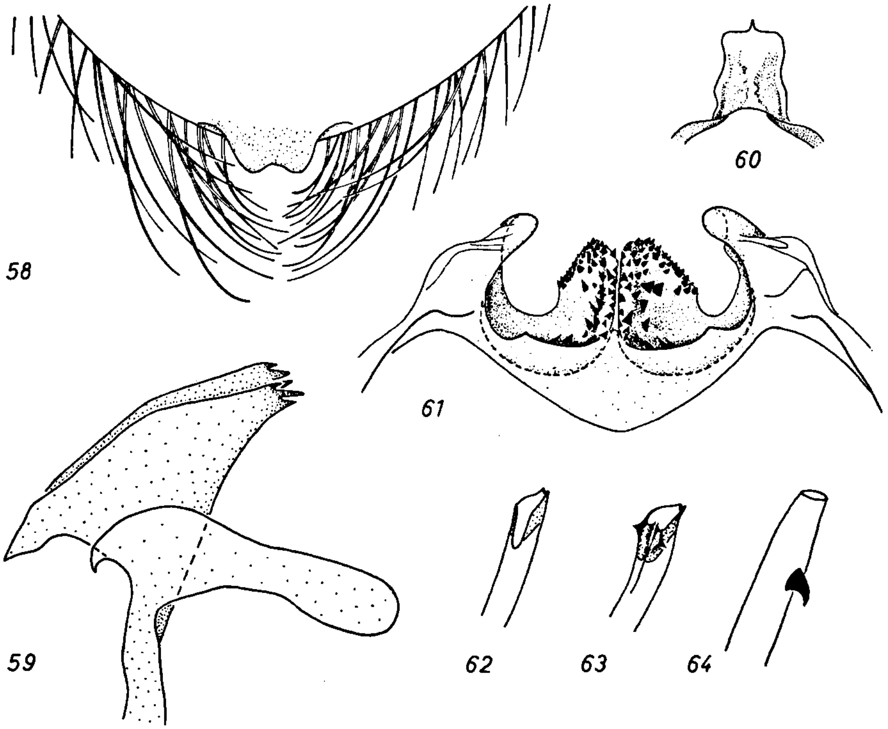


Fig. 58: Hind margin of male sternite eight in *N. croceiventris*, rear view. Fig. 59: adminiculum of *N. croceiventris*, lateral view. Fig. 60: fused valvulae of *N. alluaudi*, dorsal view. Fig. 61: extension of male tergite nine in *N. lamellata*, dorsal view.
Fig. 62—64: Apical part of intromittent organ; 62, *N. analis*; 63, *N. semiflava*; 64, *N. croceiventris*.

spines. In *flavipalpis* they are irregular shaped blades. In *malickyi* the lateral projections are reduced. The extension of *lamellata* and *semiflava* is entirely differentiated (see character 13). In *analis* and its relatives, the lateral projections are thin and curved upwards (9Y). The different states of this character cannot be interpreted as a transformation series; it is most feasible to regard them as different expressions of the same character. However, the possibility remains that either condition 9X or 9Y represents the plesiomorphous condition for the *crocata* group.

10. In practically all *Nephrotoma* the anterior beak of the id is pointed ventrally. The members of the *analis* subgroup have the ventral margin of the beak straight, running from the tip of the beak towards the lateral shell (fig. 7).

11. The posterior margin of the id is oblique in all species of the *analis* subgroup (fig. 7) whereas it is more rounded and extended posteriorly in the other *Nephrotoma* species.

12. Both *flavipalpis* and *malickyi* possess medisternal sclerotizations instead of a medisternal appendage as found in the other members of the *crocata* group.

13. The extension of the male tergite nine consists of two larger, rounded shells (fig. 61). The species *lamellata* and *semiflava* are very dissimilar in colouration. They are assumed to be monophyletic due mainly to the very characteristic extension.
14. The intromittent organ is lengthened (see final section).
15. In *analis* and *subanalis* the dorsal margin of the hypovalvae is narrowed at the anterior part whereas it is broad or even extended laterally in the other species of the *crocata* group.
16. All members of the *crocata* subgroup have the tip of the adminiculum dentate, except *alluaudi*. This character was not observed in any other *Nephrotoma* species.
17. The medisternal appendage has a midventral projection (X in fig. 10) in all members of the *crocata* subgroup except in *alluaudi*.
18. The intromittent organ is very short in the species of the *crocata* subgroup, except in *alluaudi* (see final section).
19. All species of the *crocata* group have pectinate male claws, except *croceiventris* and *nox* (compare *cornicina* group: character 24).
20. The furca is distinctly broadened at the apex in *croceiventris* and *nox* but not in the other species of the *crocata* group.
21. The hypovalvae of the *croceiventris* and *nox* females do not taper towards the tip as in the other species of the *crocata* subgroup.
22. The female cerci of the *pratensis-rossica* group are about 1.5 times as broad as the cerci in the other species of the *crocata* group.
23. The hairs along the hind margin of the male sternite eight are curved inwards throughout the *crocata* group (fig. 58), with the exception of *subanalis, lamellata,* and the *pratensis-rossica* group.
24. In the sistergroup of *pratensis* the membrane, concealing the midventral part of the male sternite eight, is not bilobed as in the other species of the *crocata* group (fig. 58).

No synapomorphous characters are recognized for the sistergroup relation between the *lundbecki* and *crocata* subgroups. With regard to the distribution and interpretation of character states throughout the *crocata* group, *lundbecki* is likely to be the sisterspecies of the *crocata* subgroup. Extensive dusted grey darkening of the body is found in *lundbecki* and in several species of the *crocata* subgroup only.

Autapomorphous characters

A list of autapomorphous characters is given below. For a number of species no such characters were recognized. In the majority of the other species usually several autapomorphies are present but only one is mentioned for every taxon. The sequence of the taxa is as in cladograms 2—5.
forcipata: inner margin of od sclerotized.
eugeniae: ventral blade of cerci very broad basally.

tenuipes: wing tip with numerous macrotrichiae.
aculeata: lateral appendage of adminiculum enlarged dorsally.
moravica: membrane connecting the two parts of the male sternite nine projects beyond the hypopygium.
sardiniensis: projection on lateral shell of id enlarged.
cornicina: no autapomorphous characters recognized.
saccai: furca reduced.
nasuta: dorsal margin of hypovalvae modified anteriorly.
schaeuffelei: membrane on posterior part of id enlarged. In part 1 of the revision the membrane was erroneously interpreted as the crest of the id.
beckeri: shape of the id.
g. guestfalica: no autapomorphous characters recognized.
g. surcoufi: crest on the id absent.
q. quadrifaria: no autapomorphous characters recognized.
q. farsidica: medial projection on male sternite eight directed dorsally.
fontana: no autapomorphous characters recognized.
a. appendiculata: protuberances on extension of male tergite nine shifted towards dorsal margin.
a. pertenua: no autapomorphous characters recognized.
minuscula: central part of adminiculum winged.
theowaldi: crest of id twisted outward along its longitudinal axis.
sullingtonensis: prescutal stripes in contact with each other.
exastigma: lateral prescutal stripes straight.
spatha: hairs on vertex very short.
flavescens: medial prescutal stripes with dull lateral margins.
astigma: no autapomorphous characters recognized.
submaculosa: no autapomorphous characters recognized.
lempkei: medial projection on male sternite eight slender.
ramulifera: midventral projections of the medisternal sclerotizations furcate.
dorsalis: midventral projection of the medisternal sclerotizations bilobed.
scurra: abdominal dorsal stripes very narrow.
quadristriata: first flagellar segment of the female lengthened.
helvetica: region between occipital marking and eyes extensively darkened.
austriaca: male and female with fourteen antennal segments.
lunulicornis: furca very large and bifurcate.
antithrix: hairs on the hypopygium adversely directed.
lucida: no autapomorphous characters recognized.
brevipennis: no autapomorphous characters recognized.
analis: no autapomorphous characters recognized.
subanalis: in *subanalis* the narrowing of the dorsal margin of the hypovalvae has proceeded further than in *analis*.
euchroma: lateral shell of the id pointed anteriorly.
lamellata: hypovalvae distinctly lengthened inside sternite eight.
semiflava: intromittent organ dentate apically (fig. 63).
flavipalpis: female sternite eight with two sclerotized shells in front of the

hypovalvae.
malickyi: medial protuberances of the extension of the male tergite nine curved outwards.
lundbecki: male sternite eight with incurved bristles at the posterior corners.
alluaudi: membranous part of medisternal appendage not invaginated.
c. croceiventris, c. lindneri: no autapomorphous characters recognized.
nox: abdomen steel-grey on anterior parts of tergites.
p. pratensis, p. eepi, c. crocata, c. luteata, s. scalaris, s. terminalis, rossica: no autapomorphous characters recognized.

Inconsistent characters

Not all characters investigated during this study contributed to the phylogenetic analysis of the species groups. Several characters turned out to be very variable throughout the groups, for example the shape of the compressor apodeme of the aedeagus. Other characters, although less variable, show a large discrepancy between their distribution and the adopted phylogeny. The most important of these characters are discussed below. The distribution of their respective states is exemplified in relation to the basal phylogeny of the species groups (fig. 65).

1. The genital bridge is reduced in *Nephrotoma* to the Sp2 state, situated at the dorsal margin of the male sternite 9 just in front of the od and id. The Sp2 is very characteristic in most species groups. In the *cornicina* group (fig. 66-80) it is triangular in shape except in *eugeniae*, *saccai*, and *quadrifaria*. A large rounded and folded Sp2 is found in the *dorsalis* group (fig. 85). In the *brevipennis* group and in *lundbecki* (fig. 84) it is short. The *flavipalpis* subgroup and most species of the *analis* subgroup possess a triangular shaped Sp2 with a bulbous outgrowth (fig. 82 & 83); in *semiflava* and *lamellata* the outgrowth is small or lacking (fig. 86). All members of the *crocata* subgroup have the Sp2 dish-shaped (fig. 81). The different shapes of the Sp2 cannot be placed into a transformation series. The elongate triangular shape as found in the *cornicina* group is interpreted as the less derived state.

2. The intromittent organ is tubular throughout its length in the majority of the out-groups and species groups of *Nephrotoma*. Three species groups of *Nephrotoma* possess a differently shaped organ. In the *flavescens* subgroup the apical part consists of two filaments and a thin interjacent tube in the sistergroup of *saccai* (fig. 13). Two V-shaped filaments comprise the apical part of the organ in the *flavipalpis* subgroup (fig. 14). In *brevipennis* and *lucida* the organ shows an interruption over a short distance (fig. 12); the same interruption, but more extended is found in the presumed sisterspecies of the *brevipennis* group, the Nearctic *ferruginea*. The distribution of these modifications throughout *Nephrotoma* suggests that they developed independently. The dissimilarity between the different states supports such an interpretation. Independent modifications of the intromittent organ are known to occur in other Diptera groups as well (Peus, 1952; Hennig, 1973). Two of the out-group species also possess an apically modified intromittent

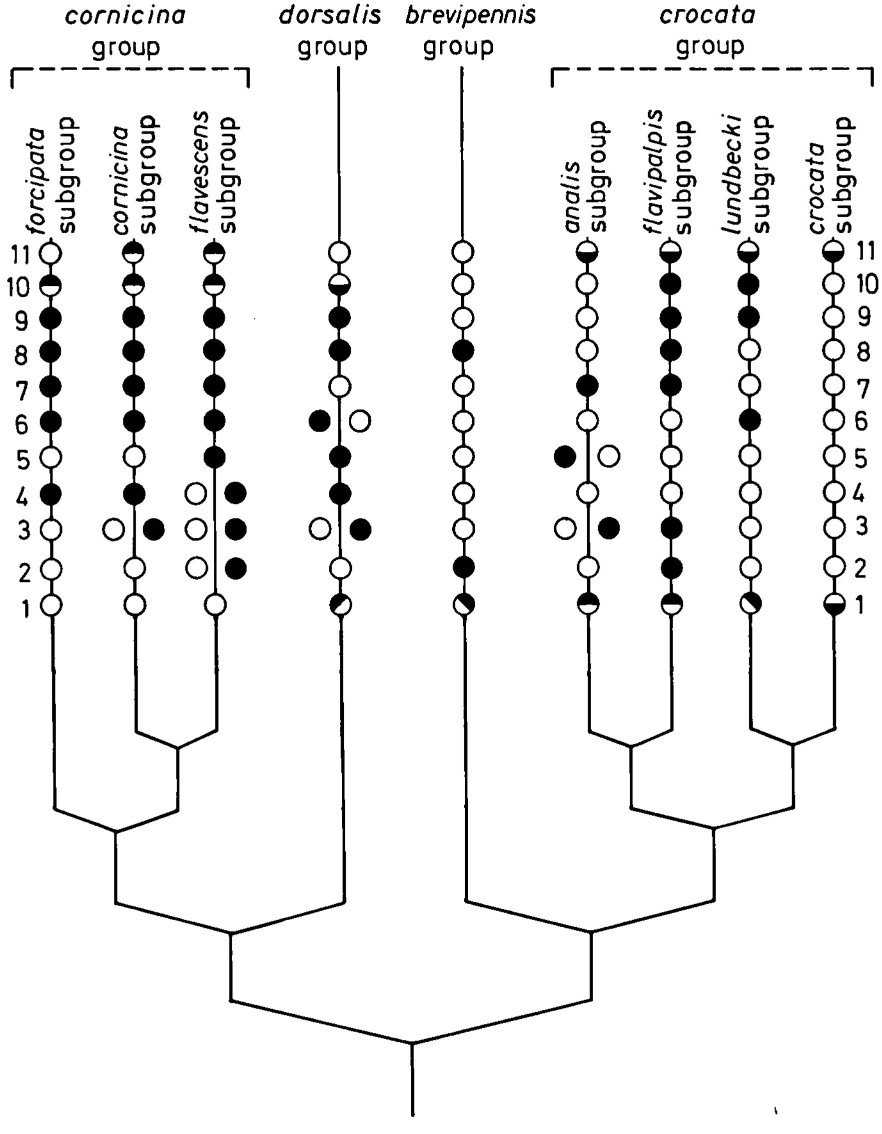


Fig. 65: Basal phylogeny of the species groups and distribution of inconsistent characters.

organ. In *Odonatisca juncea* the apical part is tripartite and in *Trichotipula oropezoides* it is bipartite with a stout, dorsally directed rod at the bifurcation (an organ tubular throughout was found in *Trichotipula cf. cahuilla).*

3. The length of the intromittent organ is fairly constant within a species or subspecies but varies considerably within the species groups (diagram 1A; see for data appendix 2; the absolute length ranges from 1.66 mm in *antithrix* to 40.16 mm in *helvetica*, about four times the abdominal length in *helvetica*; corrected for tergite two = 100, the length ranges from 1.63 mm to 25.10

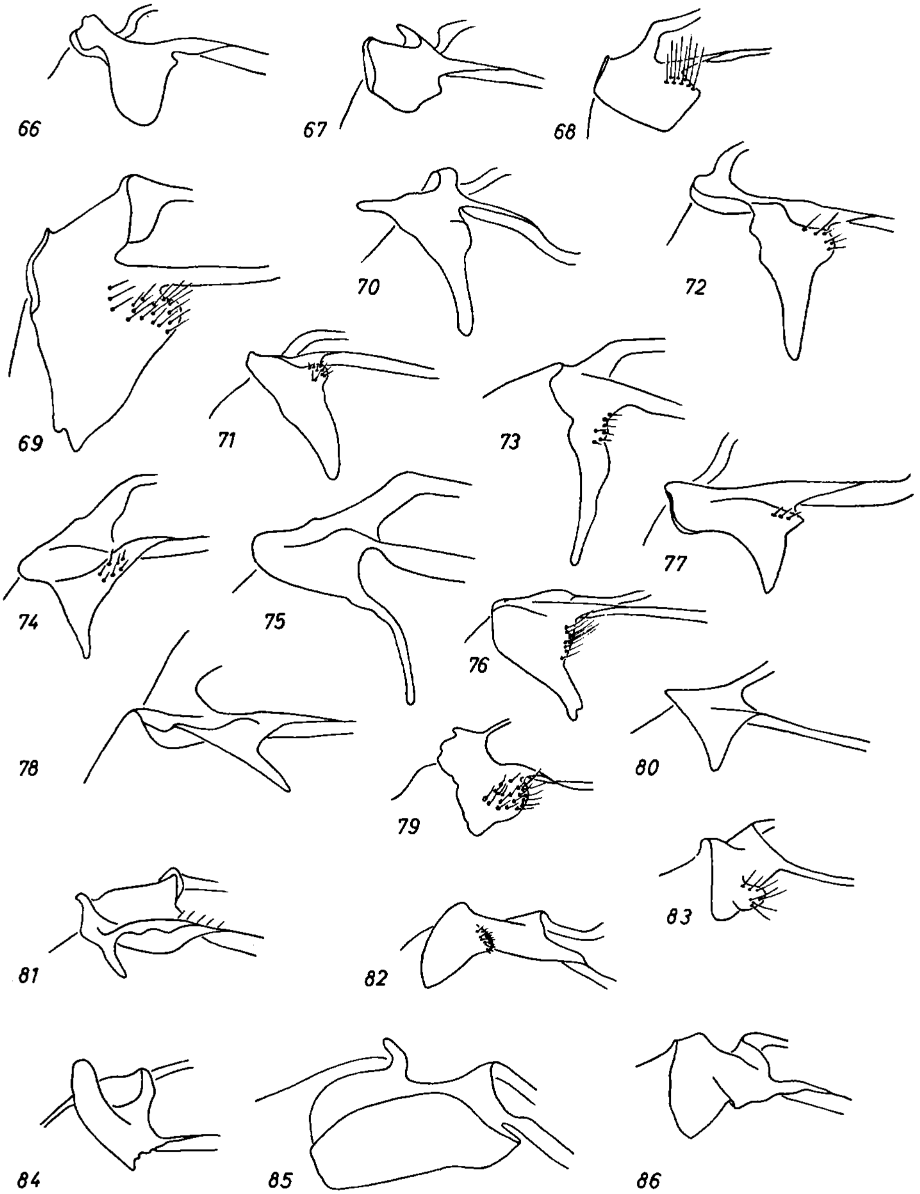


Fig. 66—86: Sp2 on dorsal margin of right sternite nine, inside view; 66, *N. quadrifaria*; 67, *N. saccai*; 68, *N. spatha*; 69, *N. schaeuffelei*; 70, *N. beckeri*; 71, *N. flavescens*; 72, *N. aculeata*; 73, *N. sullingtonensis*; 74, *N. nasuta*; 75, *N. appendiculata*; 76, *N. guestfalica*; 77, *N. tenuipes*; 78, *N. forcipata*; 79, *N. eugeniae*; 80, *N. cornicina*; 81, *N. alluaudi*; 82, *N. analis*: 83, *N. malickyi*; 84, *N. lundbecki*; 85, *N. ramulifera*; 86, *N. lamellata*.

mm; the variability within a species or subspecies is indicated in diagram 1 by triangles). Out-group comparisons revealed that a short intromittent organ represents the plesiomorphous condition in Tipulidae. With respect to *Nephrotoma* a length between 1 and 7 mm is considered plesiomorph. Comparison of the lengths in diagram 1A with the phylogeny of the species groups shows that in the majority of the groups the length of the organ does not show any correlation with the adopted phylogeny. Striking examples are the species-pairs *saccai-nasuta* and *helvetica-austriaca*. Therefore, low weight is given to synapomorphies referring to the length of the intromittent organ.

4. Number 4 stands for the diameter of the intromittent organ just beyond the aedeagus (diagram 1C, see for data appendix 2). There is no correlation between this character and the length of the organ. Out-group comparisons suggests that a thick intromittent organ (more than 22 µm) represents the plesiomorphous condition in *Nephrotoma*. The apomorphous condition is restricted to the *dorsalis* and *cornicina* groups. A thick intromittent organ apparently reappears within the *flavescens* subgroup in correlation with a modified apical part of the organ.

5. In two species groups the adminicular rods are absent. Reduction in the length of these rods is found in all other species groups, especially in *lamellata*, *flavipalpis*, *malickyi*, and *lundbecki*; in *semiflava* of the *analis* subgroup the rods are entirely absent.

6/7. The inner sclerotized margin of the male sternite nine has three appendages: two lateral ones (Y in fig. 9) and one midventral (Z in fig. 9). The lateral ones (character 6) are reduced in the *cornicina* group, the *lundbecki* subgroup, and the *dorsalis* group (*ramulifera* and *dorsalis* excepted). The ventral one (character 7) is reduced in the *cornicina* group and in both the *analis* and *flavipalpis* subgroups. Appendages as such were not observed in any of the out-groups. Nevertheless, presence of these appendages is assumed to be the plesiomorphous condition in *Nephrotoma* because the appendages are clearly reduced in the above-mentioned taxa.

8/9. During copulation the female cerci lie alongside the male hypopygium and are guided by special features of this structure. The members of the *crocata* group, except those of the *flavipalpis* subgroup, possess a protuberance on sternite nine, the medisternal appendage (fig. 10). The cerci are guided by means of a medial projection on sternite eight in the *cornicina* group and by a medially incised sternite eight in the *dorsalis* group and the *lundbecki* subgroup. It is assumed that the incurved bristles on the mediodistal part of sternite eight, as found in the *flavipalpis* subgroup, have a similar guiding function. Character 8 accounts for the absence of a medisternal appendage (●). Character 9 stands for the involvement of sternite eight during copulation (●). The distribution of these characters shows that there are only two exceptions to the rule that either sternite nine or sternite eight possesses the major guiding function. In the *brevipennis* group there are apparently no special features on the eighth or ninth sternite whereas in the *lundbecki* subgroup both sternites are involved. Out-group

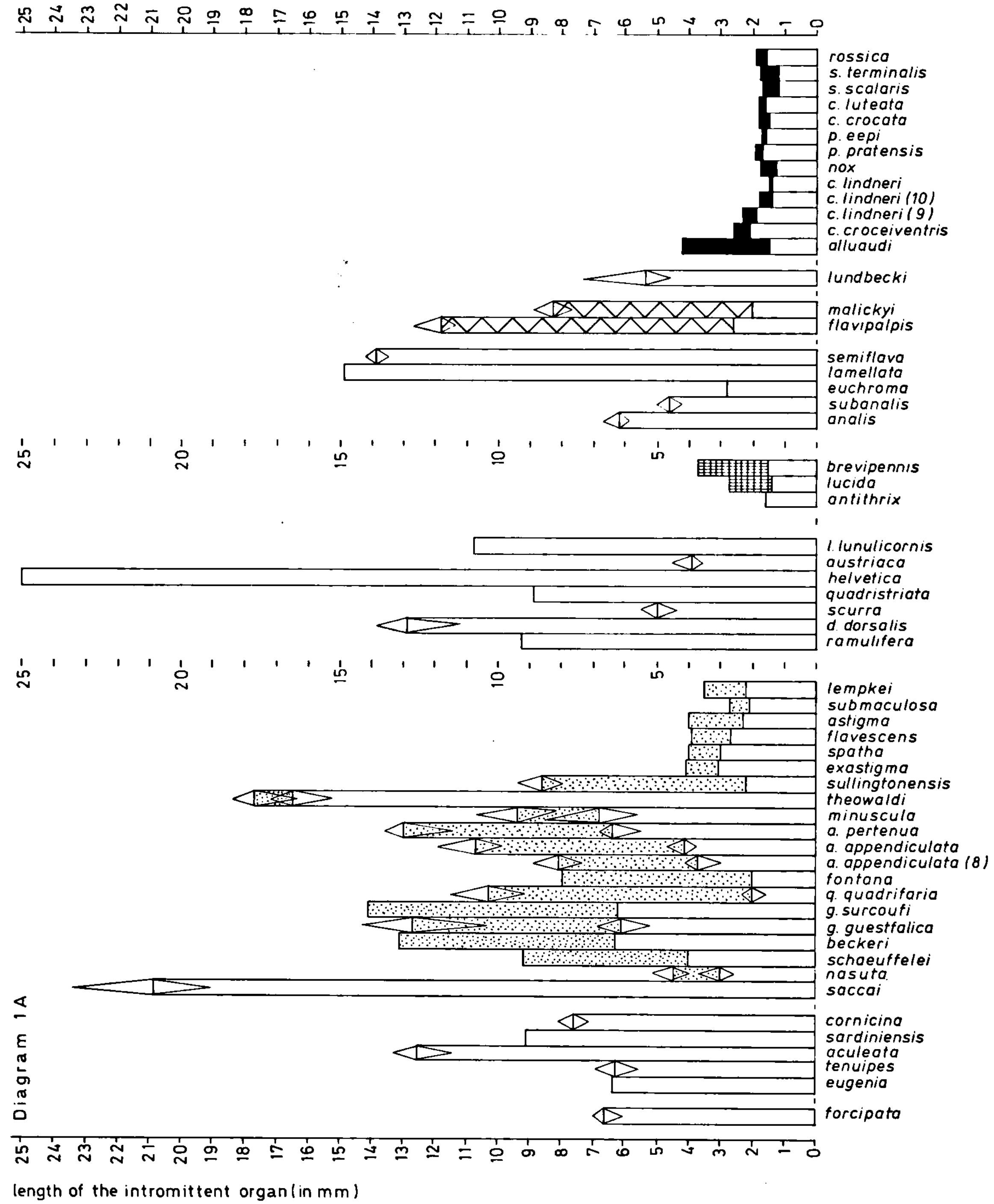


Diagram 1A

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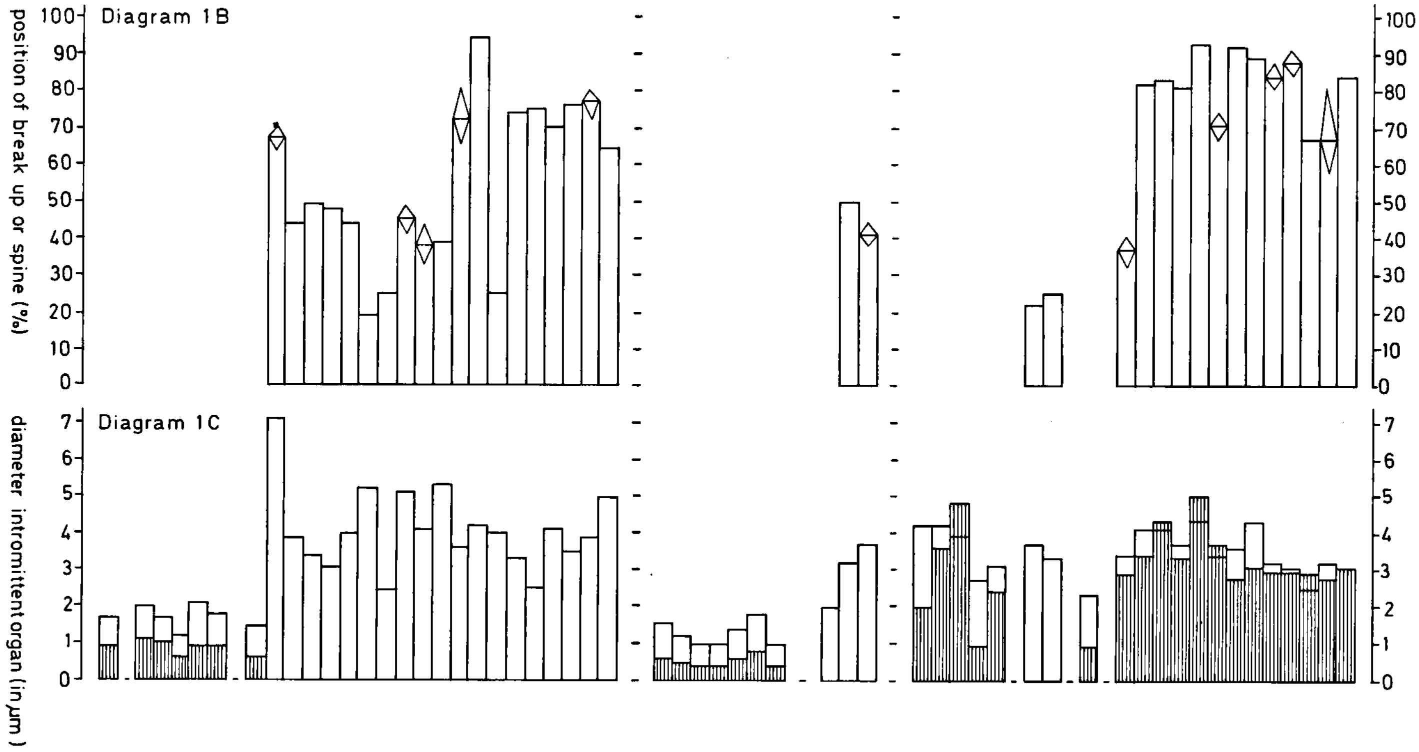
rossica
s. terminalis
s. scalaris
c. luteata
c. crocata
p. eepi
p. pratensis
nox
c. lindneri
c. lindneri (10)
c. lindneri (9)
c. croceiventris
alluaudi
lundbecki
malickyi
flavipalpis
semiflava
lamellata
euchroma
subanalis
analis
brevipennis
lucida
antithrix
l. lunulicornis
austriaca
helvetica
quadristriata
scurra
d. dorsalis
ramulifera
lempkei
submaculosa
astigma
flavescens
spatha
exastigma
sullingtonensis
theowaldi
minuscula
a. pertenua
a. appendiculata
a. appendiculata (8)
fontana
q. quadrifaria
g. surcoufi
g. guestfalica
beckeri
schaeuffelei
nasuta
saccai
cornicina
sardiniensis
aculeata
tenuipes
eugenia
forcipata
length of the intromittent organ (in mm)



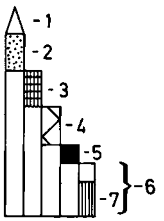


Diagram 1: length and diameter of the intromittent organ; A: length, corrected for tergite 2 = 100 (appendix 2B: 2 & 3); B: position of break-up or spine (appendix 2A: 9); C: diameter corrected for tergite 2 = 100 (appendix 2B: 4 & 5). 1: variability in length or percentage, indicated when it exceeds 0.3 mm or 3% respectively. 2: intromittent organ as in fig. 13. 3: intromittent organ as in fig. 12. 4: intromittent organ as in fig. 14. 5: black accounts for part beyond spine in the *crocata* subgroup. 6: diameter just beyond aedeagus. 7: diameter just in front of adminiculum (in some instances 7 exceeds 6). 8: *a. appendiculata* from Sardinia. 9: *c. lindneri* from eastern Turkey (type A, Oosterbroek 1979a). 10: *c. lindneri* from eastern Turkey (type B, Oosterbroek, 1979a).

comparisons revealed that a medisternal appendage belongs to the basic plan in *Nephrotoma*. This is also apparent from the distribution within the genus. In those groups in which sternite eight is involved, reduction of the medisternal appendage has occurred. This is also the case in the *lundbecki* subgroup. The only exception here is the *brevipennis* subgroup where reduction of the appendage is not associated with special features on sternite eight. The presumed sisterspecies of the *brevipennis* subgroup, the Nearctic *ferruginea*, possesses a medisternal appendage. Reductional trends within *Nephrotoma* are the flattening and narrowing of this appendage, whereby it comes in line with sternite nine, this conditon is here termed medisternal sclerotization (fig. 9). Further reduction is found in the *cornicina* group (fig. 87) where the ventral stem is absent.

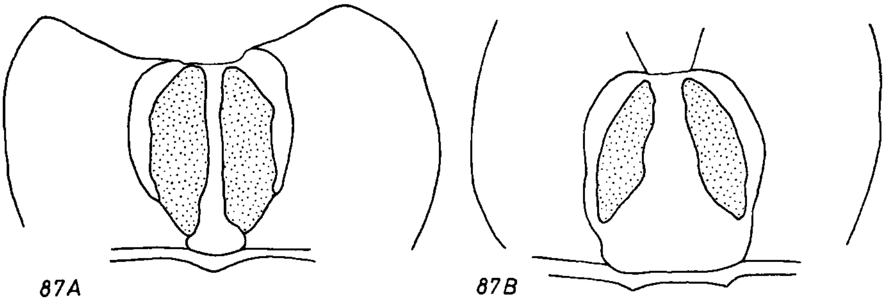


Fig. 87: Sternite nine, ventral view; A, *N. saccai*; B, *N. theowaldi*.

10. A dorsal crest on the id is found in the *flavipalpis* and *lundbecki* subgroups and in the *dorsalis* group. Posterior extension of the crest is a synapomorphy for the *cornicina* group (fig. 15). Presence of a crest is considered derived, but secondary reduction occurs frequently.

11. The extension of the male tergite nine is widely V-shaped without medial modifications in the *forcipata* subgroup, *ramulifera* of the *dorsalis* group and in the species of the *brevipennis* group. The distribution of this character among the *Nephrotoma* species under study suggests that a widely V-shaped extension is the basic plan for *Nephrotoma*. Modifications clearly serve the purpose of improving the grip on the hypovalvae during copulation. In the *dorsalis* group this is achieved by narrowing the extension. Species of both the *cornicina* and *crocata* group have developed differently shaped medial protuberances, accompanied by lateral shells, directed ventrally (*cornicina* group) or lateral projections, directed distally (*crocata* group).

BIOGEOGRAPHY

PHYLOGENETIC BIOGEOGRAPHY

The distribution of the taxa dealt with in this paper, is largely influenced by the Pleistocene glacial cycles and modern forms are likely to have evolved during isolation in glacial or interglacial refugia.

In the *cornicina* and *crocata* groups, both mainly restricted to the western Palaearctic, the reconstruction of the spatial history is based on the adopted phylogeny. This procedure is not followed in the *brevipennis* and *dorsalis* groups; the former group is restricted to Madeira and the latter group has about 40 representatives outside the western Palaearctic.

As in pollen diagrams which illustrate the alternating appearance and disappearance of plant taxa, periods of area restriction (R-phases) and area expansion (S-phases) are postulated for the *cornicina* group (fig. 88) and the *crocata* group (fig. 89). In both figures S1 is correlated with the present postglacial (Holocene), R1 is interpreted as the latest glacial period (Würm or Weichselian, 90.000—14.000 years B.P.). It is feasible to relate S2 to the Eemian (Riss-Würm interglacial of northern Europe, 110.000—90.000 years B.P.; towards the south inclusive the Brørup and Odderade interstadials, —60.000 years B.P.). R2 can be referred to the Saalian (Riss, 300.000—110.000 years B.P.). Further correlation is rendered impossible because of the great number of major glaciations recognized nowadays (Fink & Kukla, 1977: seventeen glaciations since the beginning of the Quaternary, 1.6 million years B.P.; see for Pleistocene dating West, 1977; Hantke, 1978; Lowe et al., 1979) The width of the bands in figures 88 and 89 is dictated by the cladograms and does not take account of the time-interval of the different phases. In order to facilitate reference to the different lines of descent, they are numbered 1—61 in figure 88, and 1—44 in figure 89.

The cladograms are correlated with Pleistocene climatic fluctuations under certain premises with respect to modes of speciation, speciation rates, glacial biogeography, and similarity.

Modes of speciation. It is assumed that speciation within *Nephrotoma* in allopatric, predominantly by vicariance. Host specialism, the main prerequisite for sympatric speciation, is not known within *Nephrotoma*, not are there geographically restricted species flocks. Semi-geographic or parapatric speciation might occur but no research in that direction has been undertaken in Tipulidae; parapatric contact zones, however, are extremely rare within the family.

Speciation rates. The period of isolation in glacial or interglacial refugia is considered of sufficient length to generate speciation. Recent studies on holometabolous insects have shown a pronounced difference in speciation rates between continental and insular patterns of isolation. In the former speciation may take one or several million years (Coope, 1970, 1979; Matthews, 1979a, 1979b) whereas the latter may lead to speciation in approximately 10.000 years (Whitehead, 1976; Dennis, 1977; Kavanaugh, 1979; Wheeler, 1979). The major glacial and interglacial periods lasted much longer than 10.000 years (climatic curves in Van der Hammen et al., 1971; Zagwijn, 1975). Following Whitehead Pleistocene cycles must have led to patterns of species differentiation, superimposing insular differentiation patterns on the evolution of continental biotas.

Glacial biogeography. Glacial refugia and their bearing on the present day Palaearctic fauna are discussed in detail by De Lattin (1967) and Varga (1977). Their reasoning largely follows the ecoclimatic rule of Larson (1957), which states that correlations between environmental features and breeding ranges allow the grouping of ranges with respect to their environmental characteristics for the present as well as for the past geological epochs. This view is also followed here unless reasonable doubt precludes its application. The major weakness of this method is twofold. In the first place actual distribution patterns cannot always be correlated with certain refugia. A particular taxon might no longer inhabit its former refugia. In several of these instances new refugia are postulated (e.g. Beirne, 1947, for the British Isles; see Dennis, 1977). Such additions to the classical set of refugia must be regarded with scepticism, especially when paleoenvironmental data are lacking. Their principle foothold is the estimated lack of vagility of taxa whereas, to cite Coope (1970) "it is evident that even the most sedentary species of Coleoptera adjusted their ranges on a grand scale during Wisconsin and Illonian glaciations and their associated interglacials". Other taxa presumably occupied more than one refugium. De Lattin (1967), for example, mentions a number of taxa at present widely distributed throughout the Palaearctic including the Manchurian refugium. From this he concludes that these taxa have spread from this refugium, occupying the Palaearctic from the east. Although there is not much evidence that this occurred on a large scale (Johansen, 1955) a number of taxa have certainly behaved this way. However, other taxa apparently dispersed into the Palaearctic simultaneously from different refugial sites; trans-Palaearctic distributed taxa especially are very often polycentric (Varga, 1977).

Secondly, recent palynological studies have shown that during full glaciation the Mediterranean area was characterized by extreme dryness and steppe vegetations with more humid environments confined to North-West Africa (Peterson et al., 1979) and the Levant (Farrand, 1971). Meanwhile, very little forest remained, restricted to riverbanks, marshes, and, at higher elevations, narrow zones between 500—900 metres, mainly on southern slopes. Similar belts of montane forests, intercalated between steppe and alpine vegetations, are at present found in the southern Siberian mountains (see for Spain: Florschütz et al., 1971; for Italy: Bortolami et al., 1977; Grüger, 1977; Bottema, 1978; for the Balkan, Greece, and the Near East: Farrand, 1971; Bottema, 1978). This picture is very much in contrast with the almost continuous chain of arboreal refugia postulated by De Lattin (1967: 321, 322). According to him extended forest refugia, characterized by humidity, existed in the Mediterranean area and the Near East (see also vegetation maps in Frenzel, 1968; Flint, 1971; Schwarzbach, 1974). However, arboreal refugia and in particular forests were apparently very local. As will be shown later, the fragmentation of the once widespread interglacial forests into small local zones did not effect speciation among typical forest species groups within *Nephrotoma*. The majority of what are considered modern species prefer more open habitats.

Similarity. In general it can be stated that within a monophyletic group closely related species will be more similar to each other than to other taxa (De Jong, 1980). Furthermore, in such groups degree of similarity probably reflects the relative time of origin; species which are very similar apparently evolved more recently than less similar species.

The cornicina group (fig. 88)

The phylogeny of the *cornicina* group, as given in cladograms 2A and 2B, is represented in figure 88, with the addition of an as yet undescribed sistertaxon of *beckeri* from Crete (Oosterbroek, 1981), and of *appendiculata* from Sardinia. The distributions of the members of the group are given in maps 1—7. All members, except *tenuipes, aculeata* and *cornicina*, are restricted to the western Palaearctic. Only one eastern Palaearctic species, *saghaliensis* Alexander from the Amur region, Japan, Sakhalin, and southern Kamchatka, is referable to the group, apparently as the sisterspecies of *cornicina* and *sardiniensis*.

The *flavescens-lempkei* group (56—61). Speciation events within this group are assigned to the R1 phase for two reasons. Firstly, the taxa are very similar; it is only due to sympatry that they are given species rank instead of subspecies rank. Secondly, the distribution of the taxa does not imply that they evolved earlier. The present day distribution of *flavescens* strongly suggests that 57 was restricted to the Iberian Peninsula during R1. The species *submaculosa* is at present widely distributed in Iberia and Italy; 58 can be postulated to have occurred in either one of these areas. An argument in favour of the Iberian Peninsula is the sistergroup relation between *submaculosa* and *lempkei*. The latter species is known from Mallorca and Menorca, two islands connected during R1 but isolated from Ibiza and the mainland. Occupation of these islands therefore presumably occurred during R1 from Spain. An argument against the former occurrence of 58 in Italy is the absence of *submaculosa* in Yugoslavia. Both *submaculosa* and *flavescens* are sympatric in the major part of their distribution areas. See for *astigma*: *guestfalica-lempkei* group.

The *sullingtonensis-theowaldi* group (46—55). The speciation events in this group are entirely contained in phase R1. Differentiation between 46 (West European taxon) and 47 (East European taxon) could also be referred to an earlier R-phase. However, the overall similarity, which is of the same nature as within the *flavescens-lempkei* group, favours R1. The first speciation event is between 46 in southwestern Europe and 47 in southeastern Europe including Italy and Turkey, followed by isolation of 49 in southern Turkey. The presence of *a. appendiculata* in Sardinia suggests that vicariance between 52 and 53 was preceded by isolation of the Sardinian populations. It seems unlikely that *a. appendiculata* reached the island after formation of the subspecies *a. pertenua*. From this it follows that during R1 taxon 53 was restricted either to Italy, or to both Italy and Iberia. It was apparently not

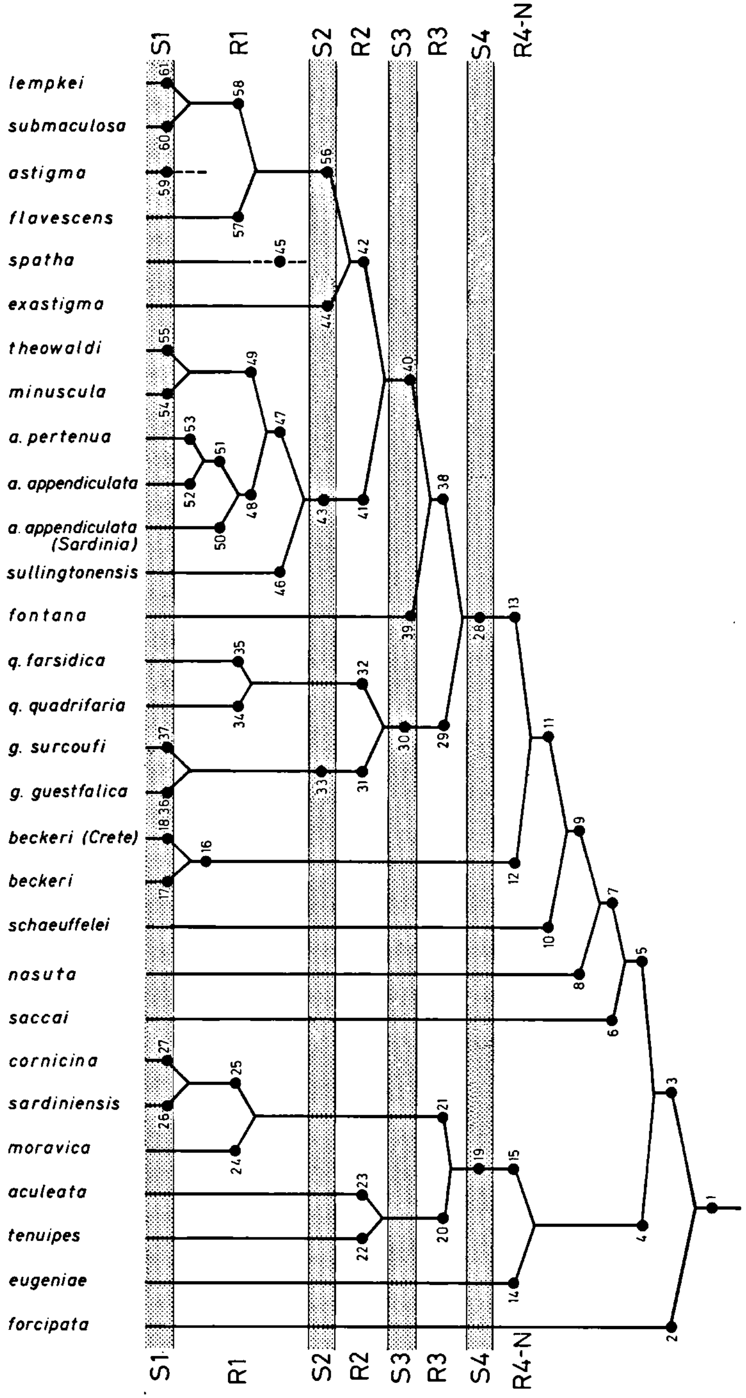


Fig. 88: Presumed phylogeny of the *cornicina* group in correlation to glacial (R) and interglacial (S) periods.

confined to the Iberian Peninsula alone because there is no reason to assume that *appendiculata* became extinct in Italy at some time during R1. Another explanation is to postulate 52 in the Balkan, northern Italy, and Sardinia, and 53 in southern Italy. Subsequently the South Italian populations dispersed to the north, dislocating *a. appendiculata* from the Italian mainland.

The *guestfalica-lempkei* group (28—61). Number 28 represents a widespread European taxon, most probably of southeastern European origin (see below). Restriction during R3 resulted in vicariance between 29 and 38. Neither taxon 29, nor its descendents 31 and 32, can be assigned to a particular region as both *guestfalica* and *quadrifaria* were apparently polycentric during R1. It is for this reason that separation between 31 and 32 is referred to phase R2. The dissimilarity of the two species is also in favour of R2 or even R3. The area of restriction of taxon 38 is likely to be South West Europe and North Africa (39). Spread by 40 into Europe during phase S3 was followed by vicariance between 41 in southeastern Europe and 42 in southwestern Europe and northern Africa (44). During S2 43 became distributed throughout Europe and 56 throughout western Europe.

Differentiation of a North African isolate is found in *g. surcoufi* (37), *fontana* (39), *exastigma* (44), and *astigma* (59). Dispersal into North Africa by the immediate ancestors of these taxa probably occurred during the respective R-phases when temperate and humid conditons prevailed in that area (Peterson et al., 1979). The actual differentiation of these taxa is correlated with the boundaries of the respective glacial-interglacial periods.

The relative time of origin of *spatha* remains obscure. The species is known from Lugo, one of the most humid regions of Spain.

The *tenuipes-cornicina* group (19—27). The species *tenuipes*, *aculeata*, and *cornicina* are the only species of the *cornicina* group distributed throughout the Palaearctic. The area occupied by *aculeata* is an extension of the quite disjunct range of *tenuipes*, and *cornicina* shows a further extension of the *aculeata* range. *N. moravica* is known from Czechoslovakia and is sympatric with the above-mentioned species. The only allopatric species is *sardiniensis* from Sardinia. The speciation events 20—21, 22—23, 24—25, and 26—27 are correlated with the respective R-phases by dissimilarity of the species. The present day distributions of *tenuipes*, *aculeata*, and *cornicina*, imply that these species already existed, and were polycentric, during R1 (see also p. 371).

The *beckeri* group (16—18). The species *beckeri* is known from Taurus Cilic (Turkey) and Cyprus, and has a sistertaxon on Crete. In the biogeographical literature concerning Crete two different opinions are encountered with respect to the isolated nature of this island. Several authors, especially botanists (see Strid (1971) and Davis, Harper, & Hedge (1971)), postulate that Crete remained isolated from the Turkish mainland throughout the Pleistocene. Kuss (1973), working on Pleistocene mammals of the East Mediterranean islands, and Storch (1977), dealing with the present day distribution of mammals especially on Crete, both conclude that active spread from Turkey towards Crete occurred during Pleistocene glacial periods. A eustatic lowering of the sea-level by 100 metres (Milliman & Emery, 1968; Flint, 1971) cannot account for a land bridge connecting Turkey with Crete by way of Rhodos and Karpathos. The interjacent sea-depths amount to at least 500 metres. According to Storch (1977) the southern Aegean was under such tectonic stress that vertical movements may have had their part in building up the land bridge. These movements are estimated by Meulenkamp (1971) to have amounted to about 700—800 metres and, locally, to more than 1000 metres during the Pleistocene on Crete. The same picture, as presented by Storch for Crete, is given by Spitzenberger (1979) for Cyprus. With respect to *beckeri* and its sistertaxon on Crete it is assumed that their ancestor (16) was more widely distributed in at least southern Turkey during R1, thereby spreading to Cyprus as well as to Crete with subsequent speciation at the beginning of S1. The assignment of 17 and 18 to S1 results from the similarity of the two taxa. Furthermore, the same fundamental pattern of speciation is found in 54 and 55. The species *minuscula* is known from southeastern Turkey and Cyprus and its sistertaxon *theowaldi* from southwestern Turkey and Rhodos.

The remaining species (1—15). The taxa represented by the lineages 1—15 are considered to be the late Pliocene or early Pleistocene representatives of the *cornicina* group. The phylogeny of these taxa does not reflect any progression from west to east or otherwise. The present day distribution of their offspring does not correlate with recent reconstructions for the plate tectonics of the Mediterranean area (Van den Berg, 1979). The apparently complicated history of these taxa seems to be determined mainly by the late Pliocene and early Pleistocene climatic events. In all probability only a few taxa survived the deterioration of the climate from Miocene times onwards. The gradual extinction of the tropical and subtropical floras in central and northern Europe is well documented (Van der Hammen et al., 1971; West, 1977). By Cromerian times, (= Günz-Mindel interglacial, about 600.000 years B.P.), the flora apparently consists largely of modern European taxa. At about the same time the terrestrial vertebrate fauna is characterized by modern genera with extinct species (West, 1977). All taxa with a postulated origin later than S4 in figure 88 can be regarded as modern European taxa and those related to R4-n as relicts of pre-Cromerian times.

The crocata group (fig. 89).

The adopted phylogeny for the *crocata* group is represented here in figure 89 with addition of the subspecies not dealt with in the cladogram of the group. On zoogeographical grounds *rossica* and *crocata* are considered sisterspecies. The distributions of the taxa, given in maps 13—19, show that about 50% are widely distributed in Europe or Eurasia.

The *analis* subgroup (3—11). The distribution of *analis* suggests that its immediate ancestor was restricted to several areas during R1, viz. North Africa, the Iberian Peninsula, the Balkan, the Caucasus and southern

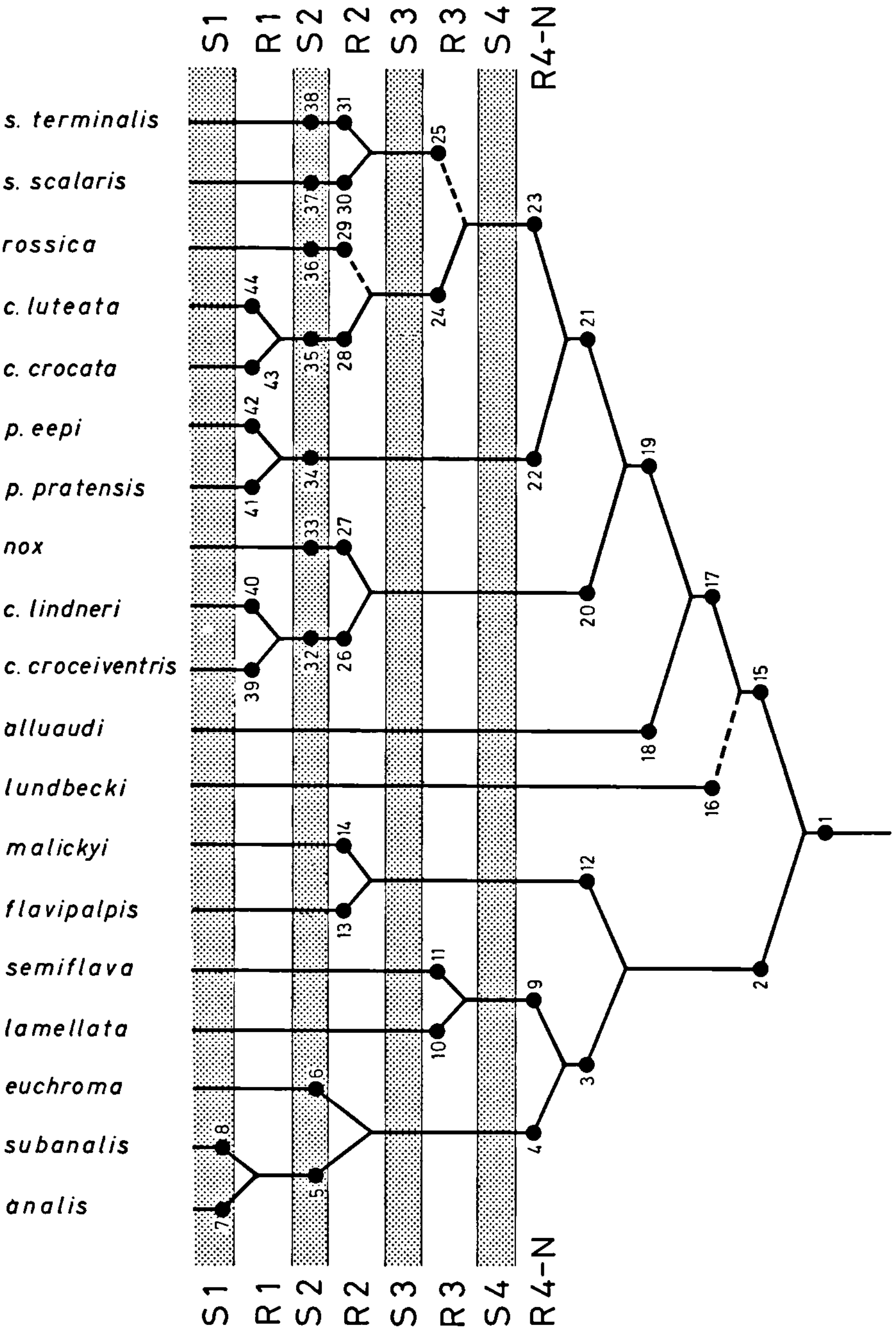


Fig. 89: Presumed phylogeny of the *crocata* group in correlation to glacial (R) and interglacial (S) periods.

Siberia. The species *analis*, *subanalis*, and *euchroma* are very similar. Therefore it appears reasonable to add Italy, where *euchroma* occurs, to the areas postulated above. This would, however, probably be incorrect. *N. analis* and *subanalis* are phylogenetically more advanced than *euchroma* and the advanced characters must have been present before restriction of *analis* into widely disjunct refugia occurred. The speciation events 5—6 and 7—8 are referred to the boundary of the respective R- and S-phases because of their north-south orientation.

The differentiation between *lamellata* and *semiflava* is referred to R3. This is tentative in so far as it might well be referable to R4-n, whereas assignment to R2 or R1 is very unsatisfactory. In the first place the two species are very dissimilar. Secondly, the distribution of *lamellata* implies that the species already existed during S2 with subsequent restriction in several areas. Furthermore, *lamellata* possesses a sistertaxon in the Nearctic: the species *alterna*. Examination of *lamellata* specimens from the Kurile revealed that *alterna*, the mainland populations of *lamellata* and the Sakhalin populations of *lamellata*, together comprise the sistergroup of the Kurilean *lamellata* populations. The differentation between *lamellata* and *semiflava* must have taken place prior to the events separating *lamellata*, *alterna*, and the Kurilean populations. The type of distribution of *lamellata* in Primorye and Sakhalin also suggests differentiation between *lamellata* and *semiflava* in R3 or earlier (see next section).

The *flavipalpis* subgroup (12—14). The assignment of the speciation event between *flavipalpis* and *malickyi* to R2 is based only on the dissimilarity of the two species. The distribution pattern of the species could not be correlated with well dated geological or climatic events.

The *crocata* subgroup (17—44). The presence of subspecies of *croceiventris*, *pratensis*, and *crocata* in the Iberian Peninsula implies that these species were already distributed south of the Pyrenees during S2 or that they became restricted there during R1. The differences between the subspecies concern mainly characters of colour. The areas of restriction are postulated as follows: 39, Iberia; 40, the Balkan (and Turkey?); 41, the Caucasus; 42, Iberia; 43, the Balkan and/or the Caucasus (and Italy?); 44, Iberia; the two subspecies of *scalaris* were apparently both restricted to several areas during R1. From this it follows that during S2 the following taxa were more or less widely distributed: 32, Europe; 34, Europe; 35, Europe or Eurasia; 37, Europe; 38, southern Russia. Because of the extent of these distributions further correlation of earlier speciation events is highly speculative. It seems reasonable nevertheless to assume an Asia Minor origin of the *croceiventris-scalaris* group and to postulate the majority of the speciation events in that area. The only geographically restricted species referable to the group is *nox*, known from south of the Caucasus. The refugia of the present-day widely distributed species also focus around Asia Minor. The presence of three subspecies, with an apparently recent origin, together with the absence of less recent endemics in the Iberian Peninsula, suggests that southwestern

Europe was not occupied by the group before S2. Thus, in a rough outline of the history of the *croceiventris-scalaris* group, taxon 19 is postulated in Asia Minor. The numbers 20 and 21 may represent disjunction and differentiation south (20) and north (21) of the Caucasus. Another north-south disjunction is apparently found in the taxa 24 (north) and 25 (south). All the other differentiations have an east-west orientation.

The species *rossica* and *crocata* are considered sisterspecies by parsimony and because *rossica* is sympatric with *crocata*. Within *Nephrotoma* closely

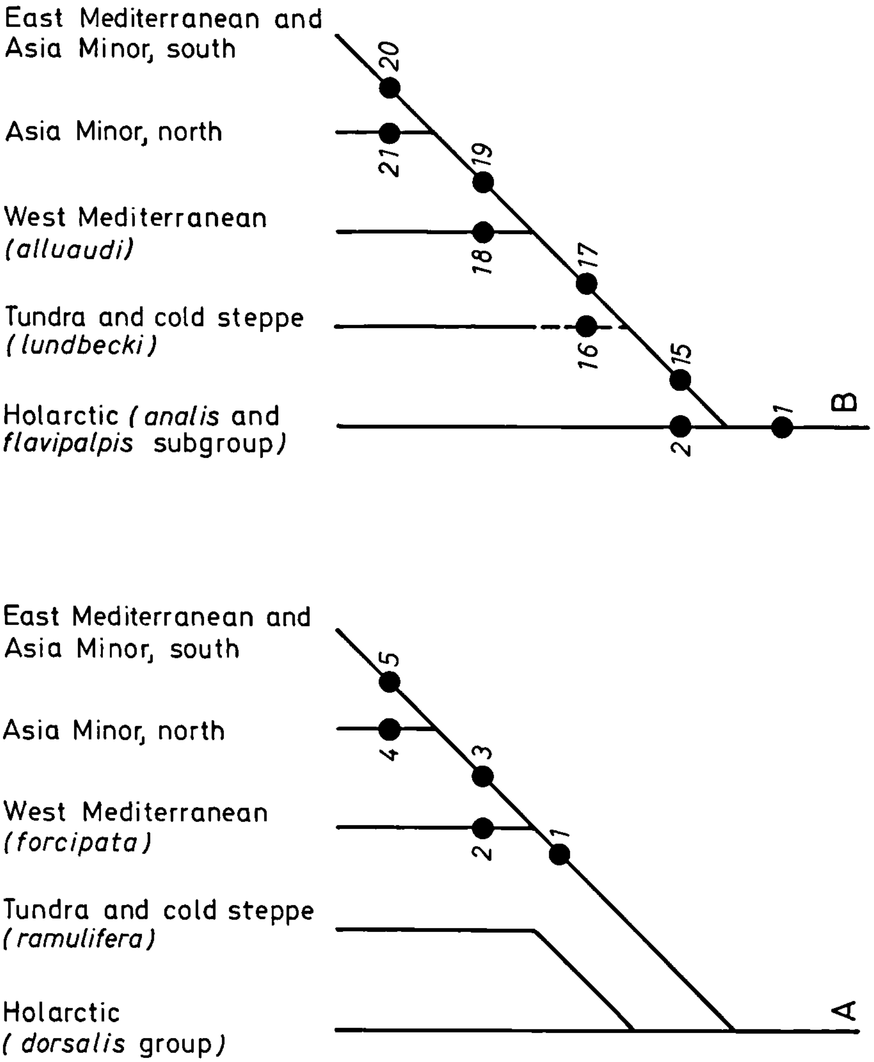


Fig. 90: Postulated pre-Cromerian phylogeny of the *dorsalis* and *cornicina* group (A), and the *crocata* group (B).

related species which are not vicariant are often sympatric (e.g., *flavescens-submaculosa*; *tenuipes-aculeata-cornicina*; these species are very frequently found in the same habitats; see also Den Boer, 1980: 228: "Taxonomically closely related (carabid) species are also ecologically closely related and will thus more often than not be found coexisting in the same habitats").

Similar to the *cornicina* group, taxa assigned to earlier than S4 may well be considered the pre-Cromerian representatives of the *crocata* group.

Comparison of the two groups

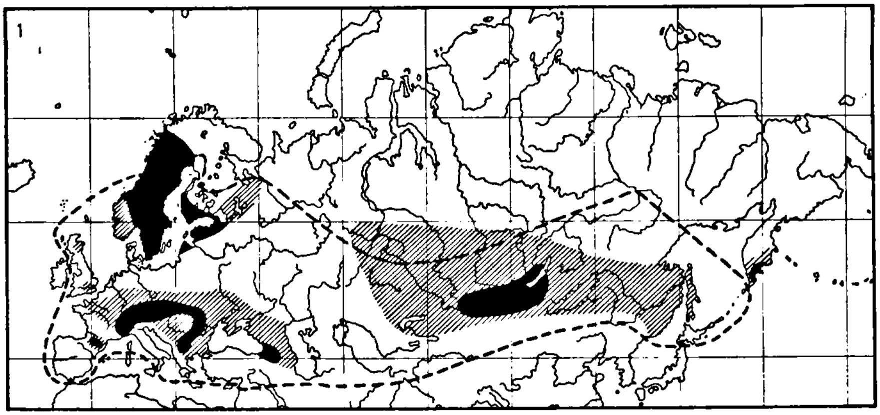
The *cornicina* and *crocata* groups show many differences in their general patterns of distribution. Moreover, speciation rates have been faster within the *cornicina* group, especially in the *flavescens* subgroup. This corresponds with the degree of differentiation from the ground plan, which is much greater in the *cornicina* group than in the *crocata* group (see basal phylogeny). In spite of these differences there are a few striking similarities with regard to the pre-Cromerian phylogeny of both groups. Figure 90A illustrates the basal phylogeny of the *cornicina* group together with the *dorsalis* group (the numbers refer to fig. 88). An almost identical pattern is found in figure 90B, representing the pre-Cromerian phylogeny of the *crocata* group (the numbers refer to fig. 89). In both instances a Holarctic group forms the sistergroup of a mainly western Palaearctic group. The only two *Nephrotoma* species inhabiting tundra and cold steppe vegetations are phylogenetically primitive members of a Holarctic group (*ramulifera*) or a western Palaearctic group (*lundbecki*, position not sustained by synapomorphous characters). The more primitive members of the mainly western Palaearctic groups are found in the eastern Mediterranean area and Asia Minor, except for the most primitive one, which is West Mediterranean in both the *cornicina* group (*forcipata*) and the *crocata* subgroup (*alluaudi*). Furthermore, widespread Eurasian taxa apparently originated in the north of Asia Minor in both groups.

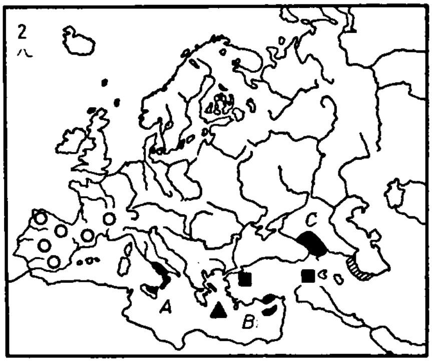
DISTRIBUTION PATTERNS

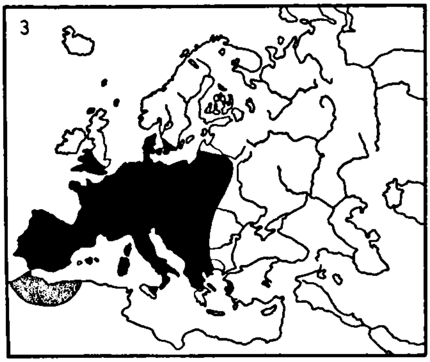
The present-day ranges

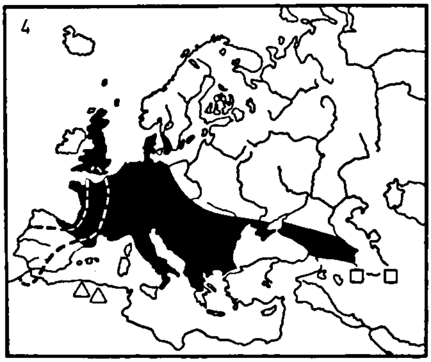
To give a more comprehensive picture of the Palaearctic *Nephrotoma* fauna, all taxa known from this region, except those endemic to China, are listed below. They are arranged into groups and subgroups on the basis of their distribution. The relationships of the eastern Palaearctic species have not yet been analyzed. Therefore, their distribution patterns are briefly outlined only, whereas those of the taxa treated in this paper are discussed in more detail in the next sections.

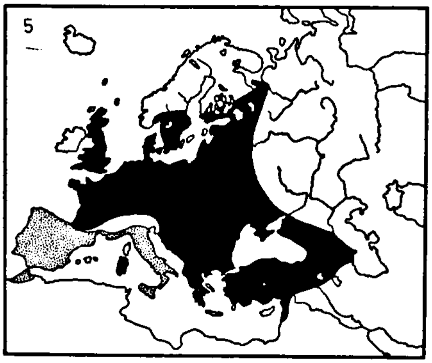
A. Species from the Far East (Japan, Sakhalin, Kurile, Primorye, Amur, and adjacent regions).











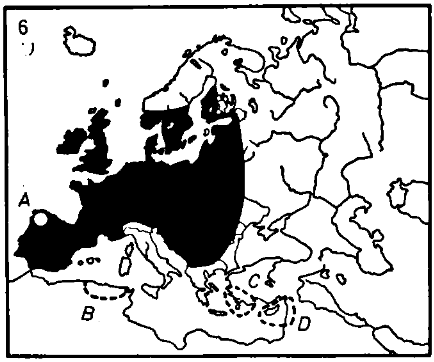
Map 1. Distribution of *N. tenuipes* (black), *N. aculeata* (black and diagonal hatching), and *N. cornicina* (broken line).

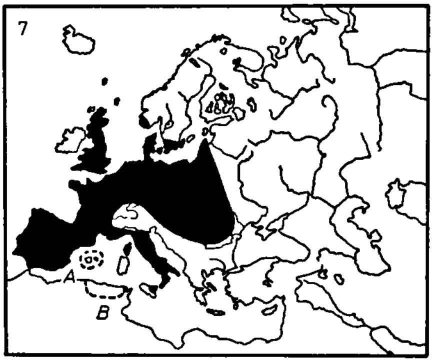
Map 2. Distribution of *N. forcipata* (circles), *N. saccai* (black A), nov. spec. cf. *beckeri* (triangle), *N. beckeri* (black B), *N. nasuta* (rectangles), *N. eugeniae* (black C), and *N. schaeuffelei* (diagonal hatching).

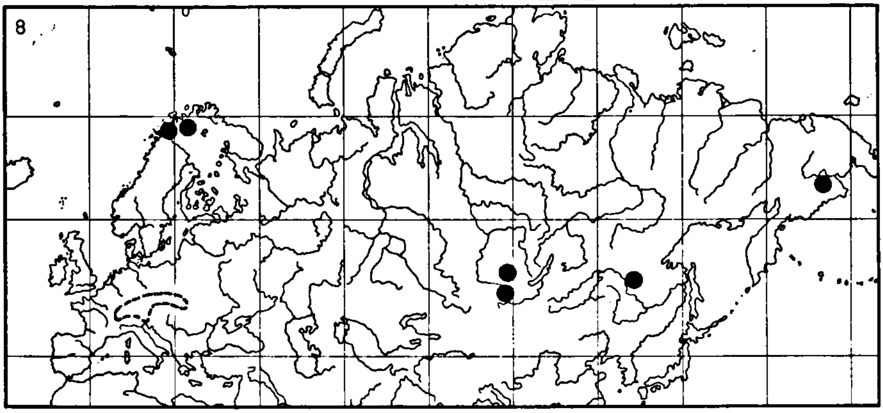
Map 3. Distribution of *N. g. guestfalica* (black), and *N. g. surcoufi* (stippled).

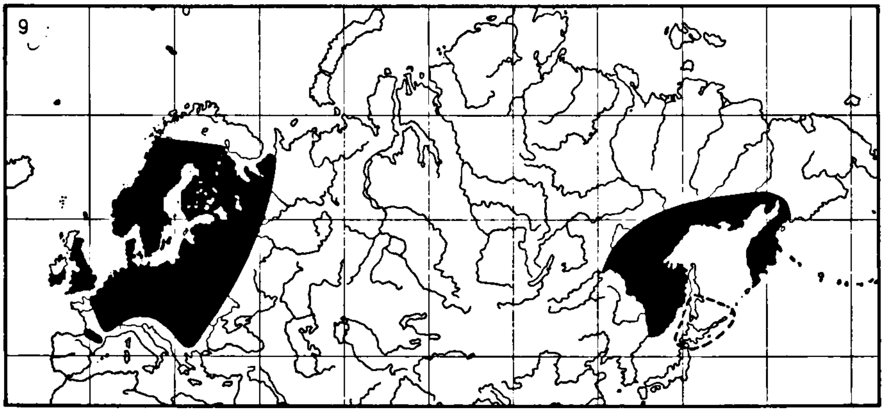
Map 4. Distribution of *N. q. quadrifaria* (black), *N. q. farsidica* (rectangles), *N. fontana* (triangles), and *N. sullingtonensis* (broken line).

Map 5. Distribution of *N. a. appendiculata* (black), and *N. a. pertenua* (stippled).







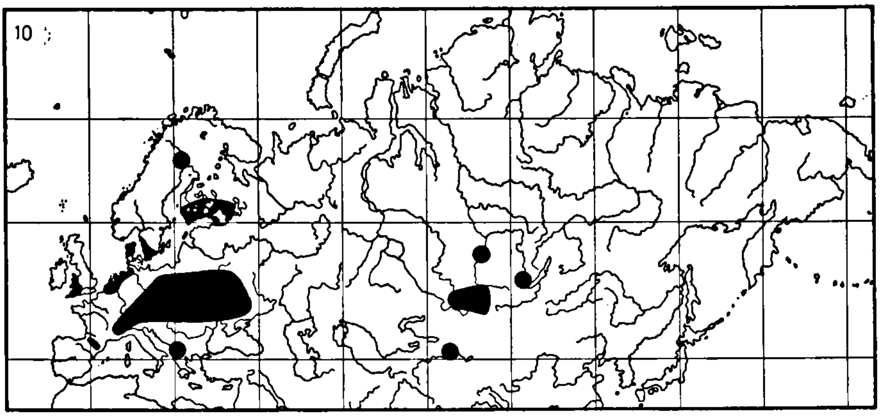


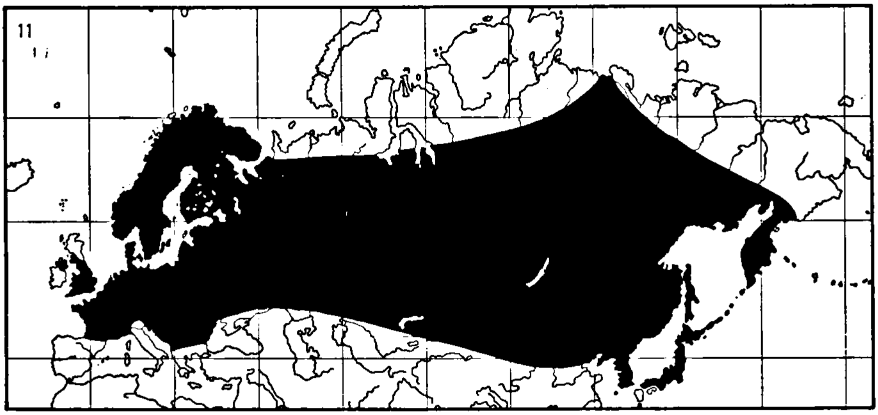
Map 6. Distribution of *N. flavescens* (black), *N. spatha* (white dot at A), *N. exastigma* (broken line B), *N. theowaldi* (broken line C), and *N. minuscula* (broken line D).

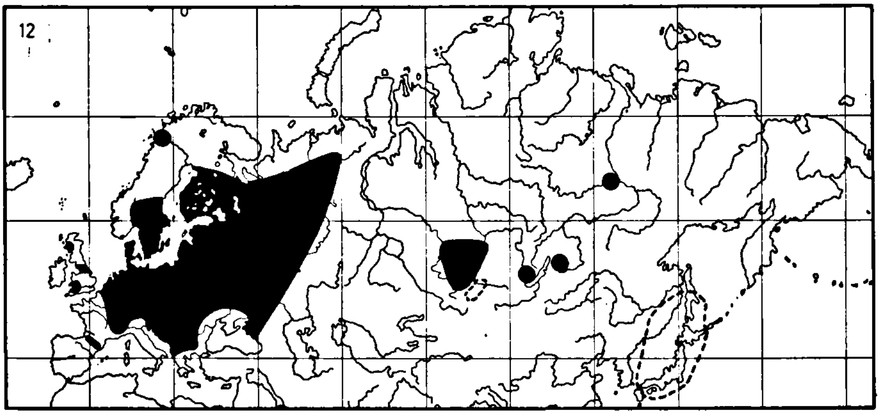
Map 7. Distribution of *N. submaculosa* (black), *N. lempkei* (broken line A), and *N. astigma* (broken line B).

Map 8. Distribution of *N. ramulifera* (black dots), and *N. austriaca* (broken line). *N. helvetica* is known from Wallis, Switzerland only.

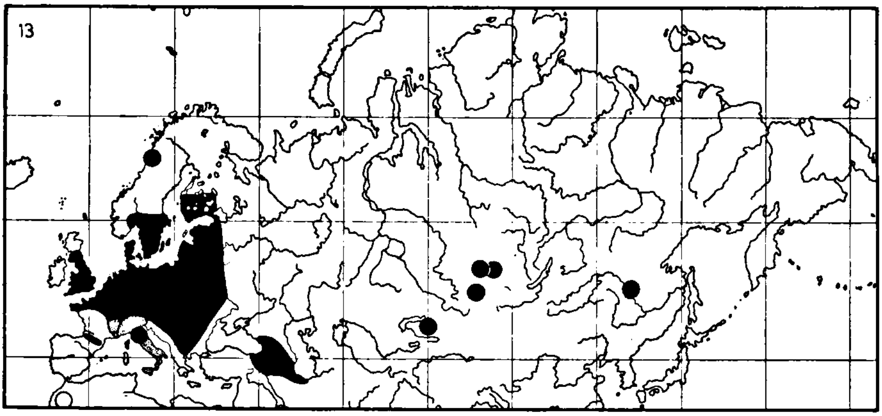
Map 9. Distribution of *N. d. dorsalis* (black), and *N. d. sachalina* (broken line).

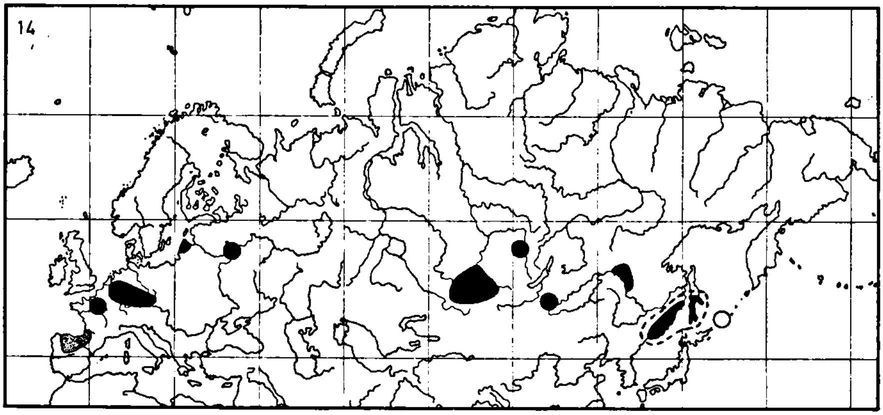


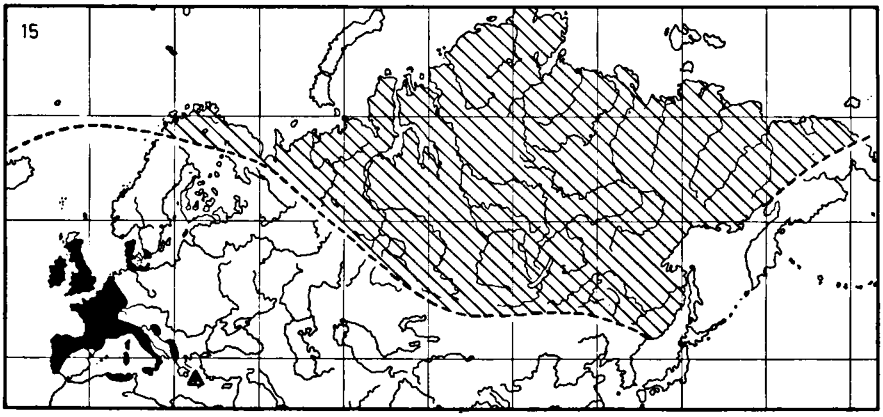




Map 10. Distribution of *N. quadristriata*.
Map 11. Distribution of *N. scurra*.
Map 12. Distribution of *N. l. lunulicornis* (black), and *N. l. angustistria* (broken line).



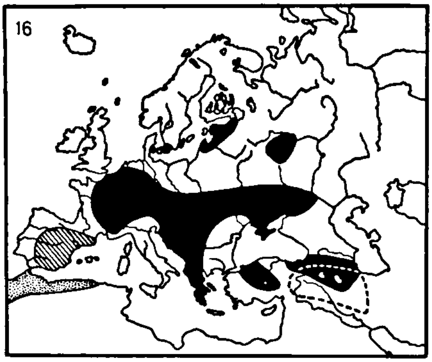


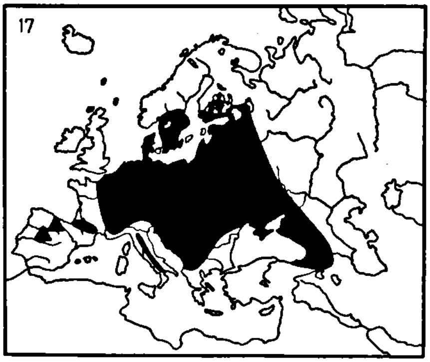


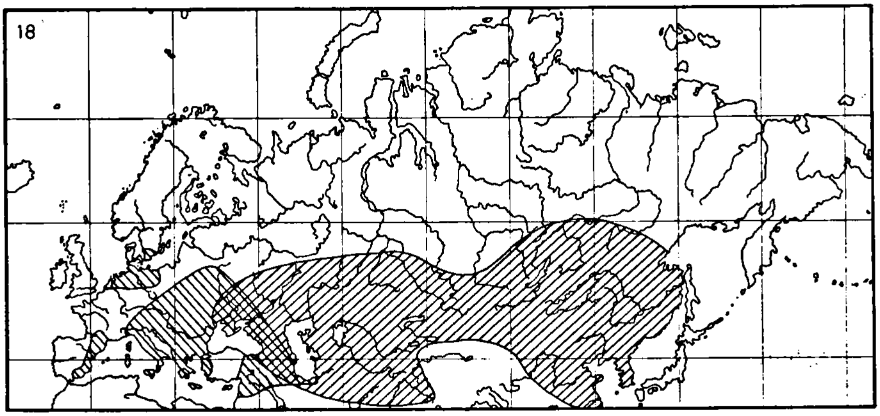
Map 13. Distribution of *N. analis* (black), *N. euchroma* (stippled), and *N. subanalis* (circle, Haut Atlas, Morocco).

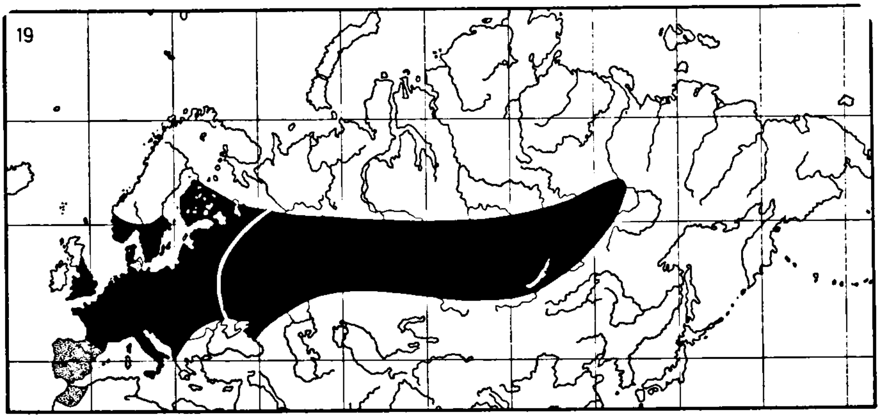
Map 14. Distribution of *N. l. lamellata* (black), *N. l. sublamellata* (broken line), *N. l.* subsp. nov. (circle), and *N. semiflava* (stippled).

Map 15. Distribution of *N. lundbecki* (diagonal hatching, circumpolar), *N. flavipalpis* (black), and *N. malickyi* (triangle).









Map 16. Distribution of *N. c. croceiventris* (diagonal hatching), *N. c. lindneri* (black), *N. nox* (broken line), and *N. alluaudi* (stippled).

Map 17. Distribution of *N. p. pratensis* (black), and *N. p. eepi* (triangles).

Map 18. Distribution of *N. s. scalaris* (diagonal hatching Europe), and *N. s. terminalis* (diagonal hatching Eurasia).

Map 19. Distribution of *N. c. crocata* (black), *N. c. luteata* (stippled), and *N. rossica* (east of white line).

A1. The species *akitae, contrasta, daisensis, elektripennis, geminata, iyoensis, ozenumensis*, and *subpallida* are endemic to Japan. All eight species are known from Honshu, two of them have also been recorded from Shikoku.

A2. Distributed from Japan southwards are: *flavonota* (Japan, coast of China to about 22° N), *palloris* (Japan, Formosa), *sinensis* (Japan, Primorye, Korea, coast of China to about 22° N, Formosa, Hai-nan), and *virgata* (Japan, Primorye, Korea, Formosa, Java). These four species, together with the circumpolar *lundbecki* and the southern Palaearctic *scalaris terminalis*, are the only Palaearctic *Nephrotoma* taxa distributed outside this region. Thus, the recent *Nephrotoma* fauna of the Palaearctic region seems very isolated from those of the surrounding regions. Recent exchange with the Oriental region apparently took place along the coastal region of China. A connection between the southern Siberian mountains and the central or southern Chinese mountains is established by the ranges of *consimilis* and *trilobulata* (see below). Such connections might turn out to be more common when the relationships of the eastern Palaearctic and Oriental taxa are investigated in more detail.

A3. Eighteen taxa are distributed from the Kurile and Japan westwards. The following taxa are limited to Japan, Sakhalin, Kurile and Primorye: *autumnalis, bifusca, dorsalis sachalina, esakii, flammeola, lamellata sublamellata, minuticornis, neopratensis, nigricauda, pullata, repanda*. They occupy at least two of the four areas listed above; six of them are recorded from two of these areas, one from all four, and two are not known from Japan. Extension of the range farther west to the Amur and/or Baikal region is shown by: *barbigera, erebus, hirsuticauda, lunulicornis angustistria, martynovi, parvirostra parvirostra*, and *saghaliensis*. All seven taxa are known from Primorye, all but one from Japan, and all but one from Sakhalin; three are recorded from the Kurile.

A4. The following seven taxa show limited distributions in Korea (1 taxon), Primorye, or the Amur region; two of them are known from both the Primorye and Amur regions: *atrostyla, biappendiculata, chosensis, fuscescens, mannheimsi, parvirostra serristyla, pilicauda*.

B. Species from the southern Siberian mountains.

B1. Three taxa, *parvirostra relicta, trilobulata*, and *violovitshi*, are confined to the Altai, Tuva, and Baikal regions. According to Savchenko (pers. comm., 1978), *trilobulata*, formerly treated as a synonym of *consimilis* (widely distributed in the Himalayas), is a good species, replacing *consimilis* in southern Siberia.

B2. Extension of the range as under B1 is found in *sublunulicornis* (northeast to river Jena), *rubriventris* (northeast to river Kolyma), *stackelbergi* (northeast to river Lena, west to southern Ural), *stejnegeri* (east to Kamchatka), and *ligulata* (southwest to Pamir).

B3. Restricted to the Pamir region are *laticrista* and *pamirensis*.

C. Western Palaearctic species.

C1. Three species are endemic to Madeira: *antithrix, brevipennis*, and *lucida.*

C2. Endemic to North West Africa are *alluaudi, astigma, exastigma, fontana, guestfalica surcoufi*, and *subanalis.*

C3. Distributed in the western Mediterranean area (including Italy): *appendiculata pertenua, crocata luteata, croceiventris croceiventris, euchroma, forcipata, lempkei, pratensis eepi, saccai, sardiniensis, semiflava*, and *spatha.*

C4. The following taxa are distributed in the eastern Mediterranean area (inclusive Asia Minor): *beckeri*, nov. sp. Crete cf. *beckeri, eugeniae, malickyi, minuscula, nasuta, nox, quadrifaria farsidica, schaeuffelei*, and *theowaldi.*

C5. The species *austriaca, helvetica*, and *moravica*, have a limited distribution in central Europe.

C6. Restricted to western Europe are *flavipalpis* and *sullingtonensis.*

C7. The following taxa are widely distributed in Europe: *appendiculata appendiculata, croceiventris lindneri, flavescens, guestfalica guestfalica, pratensis pratensis, quadrifaria quadrifaria, submaculosa, scalaris scalaris.*

D. Palaearctic species.

D1. Two taxa, *rossica* and *scalaris terminalis*, are predominantly distributed in northern Asia, not farther west than the Black Sea.

D2. A disjunct or fragmented distribution throughout the Palaearctic is found in : *aculeata, analis, dorsalis dorsalis, lamellata lamellata, lunulicornis lunulicornis, quadristriata, tenuipes.*

D3. Taxa with an uninterrupted distribution throughout the Palaearctic are: *cornicina, crocata crocata*, and *scurra.*

D4. Both *lundbecki* and *ramulifera* are restricted to the Arctic and the southern Siberian mountains.

Refugia and Endemism

Southern Europe, North Africa, and Madeira, together account for 29 endemic *Nephrotoma* taxa: in total 67% of the western Palaearctic fauna. Relatively few of them can be considered old endemics: the three species of Madeira and *forcipata, eugeniae, saccai, nasuta, schaeuffelei*, and *alluaudi.*

The six North African endemics are of different ages. *N. alluaudi* is apparently of early Pleistocene age, whereas the other endemics are of a later origin. Exchange between North Africa and Europe took place from Europe to North Africa, either by way of southern Italy and Sicily, or via Gibraltar. Six taxa occur in Morocco and West Algeria, viz. *alluaudi, crocata luteata, subanalis, appendiculata pertenua, guestfalica surcoufi*, and *sullingtonensis.* Except for *alluaudi*, these taxa are considered recent immigrants which apparently arrived in North Africa by way of Gibraltar. Of the taxa occurring in East Algeria and Tunisia, viz. *astigma, exastigma, fontana*, and *flavipalpis*, the first-mentioned is apparently the most recent. These four species inhabit the humid woodlands of the area. Braun Blanquet (1953) maintains that the European elements of the Kroumerie woodlands in

North-West Tunisia arrived in North Africa by way of Gibraltar. Furthermore, Davis and Hedge (1971) state that for plant taxa the Spain-Morocco route certainly seems to have been used far more frequently than the Sicilian route and that the former route was presumably most effective during glacial periods. Similar conclusions were reached by Theowald and Oosterbroek (1980) with regard to the total North African tipulid fauna. The majority of the *Nephrotoma* taxa apparently also arrived in North Africa via Gibraltar. Braun Blanquet's (1953) assumption that exchange occurred during the Mindel (Elster) glaciation only, might be correct for plant taxa but is not followed here for *Nephrotoma* (compare figure 88).

Seven taxa are endemic to the Iberian Peninsula and, apart from *forcipata* and *semiflava*, apparently of late Pleistocene origin. About the same number of taxa occurred south of the Pyrenees during the latest glacial period and became re-established in Europe afterwards.

The Balkan and Greece possess no endemic *Nephrotoma* taxa, and the rôle of these regions as a glacial refugium for present-day widely distributed taxa is obscured by the absence of a great number of these taxa in Greece and towards the Black Sea (see table 1 below). Present climatic, as well as vegetational conditions, together with the lack of sufficient knowledge of Bulgarian and Rumanian Tipulid fauna, are presumably responsible for the number of species known from southeastern Europe. The refugial character of this area must have been at least as important as the Iberian Peninsula. The absence of a barrier to the north accounts to a large extent for the lack of endemics.

Italy, bordered to the north by a very effective barrier, has one older endemic, *saccai*, and only two more recent ones. Apparently only one non-endemic taxon, *appendiculata pertenua*, occupied Italy during the latest glacial period. The composition of the Italian fauna, and in particular the paucity of recent endemics, is difficult to explain. Certainly the Alps were a more effective barrier during deterioration of the environmental conditions than were the Pyrenees. However, the interglacial *Nephrotoma* fauna of Italy probably was in a similar proportion to the European fauna as that of present day Italy. Nevertheless, isolation of this interglacial fauna did not occur, or did not lead to differentiation, on a scale comparable to that in the Iberian Peninsula. The explanation for this could be the north-south orientation of the Apennines in contrast to the east-west orientation of the Spanish and Portuguese Sierras. Moreover, a broad land connection over the northern half of the Adriatic existed between Italy and Yugoslavia during glacial periods. Traces of the effect of such a connection are not discernable in the present-day distribution of the European *Nephrotoma* fauna, but are apparent from a study of the Italian Tipulidae (Theowald & Oosterbroek, 1981).

Eight endemic taxa are known from Asia Minor. Three of these are considered old endemics of at least early Pleistocene origin. The area played an important rôle throughout the Pleistocene in the maintenance of the western Palaearctic fauna.

Three species, *moravica*, *helvetica*, and *austriaca*, are restricted to central Europe. These species belong to speciesgroups which are widely distributed throughout the Palaearctic. *N. moravica* is known from a few localities in Czechoslovakia; *helvetica* is a thermophilous relict, occurring in the Rhône valley in Switzerland; *austriaca* occurs at altitudes between 500 and 1500 metres in the Alps and the Carpathians. The origin of these three species must be referred back to at least the penultimate glacial period. *N. moravica* is phylogenetically more primitive than *cornicina* and the latter species apparently already possessed its derived characters in the latest interglacial. The presumed sisterspecies of *austriaca*, *stejnegeri*, is distributed in eastern Asia. East-west disjunctions, such as between these two species, are dated below as of at least glacial origin and *N. helvetica* is phylogenetically more primitive than *austriaca*.

Disjunctions

The zoogeographical separation between the western and eastern Palaearctic *Nephrotoma* fauna is very distinct. Out of the 104 taxa, 47 belong to the east and 43 to the west. Of the remaining 14 taxa, two, *lundbecki* and *ramulifera*, are restricted to the north in Europe and more widespread in Asia. Another five taxa are widely distributed in Eurasia without disjunctions. The remaining Eurasiatic species are disjunct and occur mainly west of the line Arkhangelsk-Caspian Sea as well as east of the Yenissey river and in the southern Siberian mountains. This pattern of disjunction is identical to the one separating the western and eastern Palaearctic species. From the Urals, situated in the middle of this area, only eight taxa are known, the five widely distributed ones together with *lundbecki*, *stackelbergi*, and *aculeata*.

Johansen (1955) correctly attributes an ecological nature to the Yenissey faunal barrier. This explains to a certain extent why a number of taxa did not spread farther west or east, but not how others became distributed on either side of the large area. Usually disjunctions of this kind are dated back to the latest glacial period (e.g., Thienemann, 1950). In the present case, there is some evidence supporting this interpretation rather than to postulate a postglacial origin. This evidence is found in the distribution of the eastern Palaearctic taxa, assigned to the group A3 above. These taxa indicate that Primorye, Sakhalin, northern Japan, and the southern Kurile islands, together form a distinct faunal region. Eustatic lowering of the sea level during glacial periods resulted in land connections between these areas. During the latest glacial period, with a drop in sea level of about 100 metres, Sakhalin was connected with the mainland along its northern half only. The distribution range of practically all the taxa in group A3 is situated south of this connection and must have been further south when the connection was actually in existence. The establishment of this faunal region, therefore, cannot be dated back to the latest glacial period, but rather to periods

		NORTH SWEDEN	NORTH NORWAY	KAMCHATKA	EURASIATIC	DISJUNCT IN EURASIA	PYRENEAN POPUL. ISOLATED	LIMIT IN FRANCE FROM NW TO SE	NOT TO WEST COAST OF BLACK SEA	CENTRAL & SOUTH. SPAIN	CENTRAL & SOUTH ITALY	GREECE	GR. BRITAIN, SOUTH	GR. BRITAIN, CENTRAL	GR. BRITAIN, NORTH	IRELAND	TURKEY	CAUCASUS
PALAEARCTIC TAXA	*cornicina*	x	x	(x)	x					x	x	x	x	x	x		x	x
	scurra	x	x	x	x								x	x		x		
	d. dorsalis	x	x	x	x	x	x	x	x				x	x	x	x		
	aculeata	x	x	x	x	x	x	x					x		x			x
	tenuipes	x	x	x	x	x	x		x									x
	analis		(x)		x	x	x	x	x				x	x			x	x
	l. lunulicornis		(x)		x	x	x	x	x				x	x	x			
	quadristriata	(x)			x	x	x	x	x					x				
	l. lamellata				x	x		x	x									
	c. crocata				x				x	0	x		x	x				
EUROPEAN TAXA	*p. pratensis*						x	x	x	0	x						x	x
	c. lindneri							x	x	0		x					x	x
	s. scalaris				0					x	x	x					x	x
	a. appendiculata								0	0	x	x	x	x		x	x	
	flavipalpis								x	x	x		x	x	x	x		
	flavescens								x	x			x	x	x	x	x	
	submaculosa								x	x	x		x	x	x			
	q. quadrifaria										x	x	x	x	x			x
	g. guestfalica								x	x	x	x	x				x	

Table 1. Distribution characteristics of the taxa, widespread in Europe. For discussion see text.

preceded by warmer conditions than at present, resulting in a more northerly distribution of the species than today. According to West (1977: 383) rise of temperature above the present-day level occurred during the latest interglacial. A more northerly distribution can also be inferred from the presence of many representatives of the *dorsalis* group in the Nearctic region. It was apparently during these warmer periods that a number of species became widespread throughout the Palaearctic and Holarctic, with subsequent restriction to several separate areas.

Widespread European taxa

The major distributional features of the nineteen taxa, widely distributed in Europe, are listed in table 1. The upper half of the table contains the taxa with a Palaearctic distribution. Of these, *crocata* is apparently the only postglacial immigrant to western Europe.

At the top of the table five taxa are listed, occurring far into the north of Scandinavia. Both *cornicina* and *scurra* occupy a very large range and show no central Russian disjunction. It is noteworthy that four out of these five taxa are also known from Kamchatka, whereas the fifth, *cornicina*, has been recorded from islands bordering the peninsula. In total Kamchatka accounts for only five *Nephrotoma* species (incl. *stejnegeri*).

All Palaearctic taxa, except *cornicina* and *scurra*, score very high in the next three categories of the table: the Pyrenean populations are isolated; the limit in France runs from northwest to southeast and well north of the Mediterranean coast; they do not reach the west coast of the Black Sea. It is less feasible to interpret these characteristics as the actual state of expanding or retracting distribution areas because they are shared by a number of taxa. The distribution in France, with isolated populations in the Pyrenees, presumably dates back to shortly after the younger Dryas (11.000—10.500 years B.P.). During this colder phase of the Holocene, distribution areas shifted southwards, and taxa not already inhabiting the Pyrenees were able to occupy these mountains. The present disjunctions north of the Pyrenees were established by the subsequent amelioration of the climatic conditions. Logically, these disjunctions are restricted to the more temperate European taxa, not distributed in the southern refugia (*pratensis* seems to be an exception but occurs in the Sierras and Apennines only). That re-establishment into Europe took place immediately after the late Dryas period is a well known fact (De Lattin, 1967; Rose, 1972; Dennis, 1977). The third characteristic, not distributed to the west coast of the Black Sea, probably has an environmental base, and lack of sufficient knowledge of Bulgaria and Rumania may also contribute. This pattern is shared with a number of mainly western European taxa, not distributed as far east as the Black Sea.

N. analis, *l. lunulicornis*, and *quadristriata* are each known from localities in northern Scandinavia. The relevant data were taken from Lackschewitz (1933, 1935) and Tjeder (1955), and can be considered reliable. These data show that these species had a more northerly distribution, most probably during the Atlantic climatic optimum (7000—5000 years B.P.) when the treeless tundra of North Eurasia almost disappeared (Schwarzbach, 1974). Similar hypsothermic relicts are the isolated populations of *forcipata* (Lyon), *sullingtonensis* (Sussex), *quadristriata* (entire range fragmented), *euchroma* (Lyon), *lamellata* (Estland), *c. lindneri* (entire range fragmented), and *s. scalaris* (northwestern Europe).

Except for *cornicina* and *c. crocata*, none of the Palaearctic species are known from the three southern European refugia; neither are they replaced there by subspecies. This is in contrast to the European species which are usually widely distributed in Spain, Italy or Greece, or represented there by subspecies (circles in table 1). The refugia of the Palaearctic species were presumably situated to the north of those inhabited by the European species. The localisation of these refugia is highly speculative because most Palaearctic species prefer deciduous forests or mountainous areas. The members of the *dorsalis* group were probably restricted to southern France and/or the Balkan because all four widespread taxa of this group occur in Great Britain whereas none has been recorded from the Caucasus. The species *analis* or its immediate ancestor apparently also had a refugium in southwestern Europe because of the presence of *analis* in Great Britain and *subanalis* in southern Morocco. The European members of the *crocata* subgroup had their refugia in Turkey and/or the Caucasus. This easterly position might well be responsible for the fact that only one member, the widespread *c. crocata*, reached the British Isles. The connection between Great Britain and the continent lasted until some time in the Boreal stade (about 8000 years B.P., Dennis, 1977; West, 1977; about 7.500 years B.P., Rose, 1972; Wheeler, 1977).

Only four species are recorded from Ireland compared with fourteen from Great Britain. Probably the number of species recorded from Ireland will increase, as is shown by a comparison of the British and Irish taxa in other groups (plant taxa: 2200 against 1260, West, 1977; butterflies: 56 against 26, Dennis, 1977; Bumblebees: 26 against 21, Alford, 1975; mammals: 41 against 21, West, 1977).

BIOGEOGRAPHY OF THE GENUS

The origin of *Nephrotoma* is dated back to Mesozoic Pangaea by Savchenko (1973). According to Savchenko it is only in this way that the presence of the genus in Australia, South America, and Madagascar, as well as the separation of these faunas from those of Asia and Africa at the transition of the Mesozoic and Cenozoic, can be explained.

A different opinion is presented by Oosterbroek, Schuckard & Theowald (1976), who presumed an early Tertiary origin in East Asia, with dispersal into southeastern Asia, Indonesia and the Holarctic. Subsequent spreading into Africa and South America occurred after adaptation of the Holarctic fauna to the warm temperate conditions of the late Palaeogene Northern Hemisphere (climatic curves in Matthews, 1979). South America has only few species, mainly restricted to the north (Oosterbroek & Schuckard, 1976). The African fauna is largely confined to high mountainous areas, resembling the African distribution of the comparatively recent European subgenus *Tipula* (Oosterbroek, Schuckard & Theowald, 1976; Theowald, 1977). The postulated East Asian origin is supported by the sistergroup relation between *Nephrotoma* and *Scamboneura*. The latter genus is distributed in the Philippines, Indonesia, and New Guinea.

At present four monophyletic species groups are recognized in the western Palaearctic. Phylogenetic analyses of the species of the other regions are still lacking. Hence, a detailed account of the Holarctic history of the genus cannot be given and is only briefly outlined below.

The *brevipennis* group, with three species on Madeira, might well be considered a warm temperate relict of at least Pliocene origin. Its sisterspecies is the Nearctic *ferruginea*, according to Frommer (1963) "the supposed prototype" of the Nearctic *Nephrotoma* fauna. The *brevipennis* group, together with *ferruginea*, forms the sistergroup of the *crocata* group.

The latter group was apparently already widely distributed in the Palaearctic during early Pleistocene times (compare fig. 90B). According to Mitchell-Thomé (1976) the island of Madeira has an early Miocene origin ("coral relief testifies to uplift, the building of a Miocene bioherm in a warm neritic environment").

As pointed out earlier, about 50% of the Nearctic fauna belongs to the *dorsalis* group. Most probably, the rest of this fauna will have, in part at least, an East Asian origin. Monophyletic taxa, distributed on either side of the northern Pacific, are fairly frequent among Tipulidae (maps in Savchenko. 1961, 1964). According to Matthews (1979) transberingian exchange of warm temperate plants (and animals) probably did occur during the Miocene, when mixed mesophytic forests were prevalent in North America and Asia. The land connection between Alaska and Asia was in existence throughout the Tertiary until the Pliocene (appr. 3 million years B.P.), and again during glacial periods. Examination of Nearctic members of the *dorsalis* group indicates that all four major phyletic lines, recognized in cladogram 3, are represented in the Nearctic. Dating the exchange by way of Beringia is not yet possible, but apparently such an exchange already occurred in Pliocene times, taking into account the amount of Nearctic taxa, belonging to the *dorsalis* group. The glacial-interglacial cycles did not result in differentiation of the group to an extent comparable with the *flavescens* and *crocata* subgroups. The northern distribution of the group as a whole is apparently responsible for this (see below).

Modern European taxa of Cromerian or later origin are predominant in the *flavescens* and *crocata* subgroups. In contrast with the remaining species groups, open habitats are preferred by the members of these two subgroups and especially in the *crocata* subgroup river banks are favourite sites. Of all species discussed, only a small number, *cornicina, submaculosa, sullingtonensis*, *pratensis*, *croceiventris*, *quadristriata*, and *scurra*, can inhabit dry places, but in this they are usually not very consistent. For example, *submaculosa* shows a clear preference for sandy areas in the Netherlands and Great Britain, but is found farther south in damp localities as well. Furthermore, species such as *cornicina* and *scurra* can be found in a wide variety of habitats, ranging from open sandy heath to dry coniferous forests or very moist deciduous forests. For a number of phylogenetically primitive taxa the habitat preference is not known (*beckeri*, *saccai*, *schaeuffelei*, *nasuta*), and only a few species are confined to special environments (e.g., *sullingtonensis*: dry pine woods or dry *Cistus* vegetations). In spite of this a comparison of habitats with the respective cladograms indicates that moist deciduous forests formed the primeval environment for the early evolution of *Nephrotoma* within the Holarctic. Species with a distinct preference for forests are: *forcipata*, *eugeniae*, *analis*, *lamellata*, *flavipalpis*, *dorsalis*, *lunulicornis*, and *helvetica*. As pointed out by Oosterbroek, Schuckard and Theowald (1976), comparison of present day distribution patterns reveals that most species prefer moist temperate climates, thus showing a correlation with the zone of deciduous forests.

The phylogenetically primitive *ramulifera* and *lundbecki* inhabit the tundra and cold steppes. In both instances this might well mark a shift from woody environments to more open habitats. In this the sistergroup of *lundbecki*, the *crocata* subgroup, was successful, whereas *ramulifera* is the only Palaearctic species of its group adapted to open environments. At what time tundra was added to the environments inhabited by *Nephrotoma* remains uncertain. Since tundra vegetations were already present in the Miocene (Matthews, 1979), the time is not necessarily recent (compare discussion of fig. 90 A & B).

With respect to the postulated origin for members of the *flavescens* and *crocata* subgroups as Cromerian or later, an interesting view is presented by Coope (1970, 1979, referring among others to Matthews, 1976a, b). According to Coope, modern work by widely scattered investigators on fossil Coleoptera of the Northern Hemisphere has revealed neither evidence of morphological change during the later Quaternary, nor is there reason to believe that many species became extinct. A hint of evolutionary change is found in early Pleistocene fossils, probably dating from over a million years.

The investigations by Coope, Matthews, and others, have dealt up to now with the faunas of the temperate and cool Northern Hemisphere with bias in favor of open, lowland areas (see Kavanaugh, 1979). Climatic conditions started to fluctuate soon after the beginning of the Pliocene (5 million years B.P.) with about seventeen major glaciations during the Pleistocene. No doubt the present northerly distributed Holarctic faunas are largely qualified to cope with the effects of these climatic fluctuations. Extinction of those taxa which failed to do so might have been in part a gradual process, but presumable was most severe at the beginning of the environmental deterioration.

The picture presented by Coope and others does not differ much from the one given here for the northerly distributed species groups. However, within more southerly distributed groups many taxa are confined to one particular area. The amount of taxa, presumably restricted to one area during the latest glacial period, is not allusive for an early Pleistocene origin, the more so because these areas are located in southern Europe. Isolation of smaller populations than to the north must have had its effect on speciation. This, for example, is very clear in the Holarctic subgenus *Lunatipula*; eighty percent of the about 260 western Palaearctic *Lunatipula* species is restricted to the Mediterranean subregion.

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ERRATA TO PARTS 1—4

Part 1 (Beaufortia, 27: 1—137)

page 1, line 4: *sardiniensis* i.s.o. *sardegniensis*.
page 6, fig. 4 lateral appendage of ADM i.s.o. posterior appendage.
page 7, fig. 5: fused valvulae i.s.o. sternum 9 (see part 2: 58—59).
page 56, line 3: posterior extension i.s.o. median projection.
page 73, line 17: Riedel, 1919b i.s.o. Riedel, 1919.
page 87, line 20: tergite 7 i.s.o. sternite 7.
page 88, line 27: Pierre, 1919b: 18 i.s.o. Pierre, 1919b: 618.
page 93, line 25: Zoological Museum i.s.o. Entomological Department.
page 100, line 30: Riedel, 1919b i.s.o. Riedel, 1919.
page 104, line 3: absent i.s.o. small.
page 111, line 14: Aritzo i.s.o. Afrika.
page 114, line 24: add after dull: or at least less shining than stripes themselves.
page 120, line 7, tergite 7 i.s.o. sternite 7.
page 133, line 11: Savchenko, 1966, is referred to throughout part 1 as Savchenko, 1966b; the paper should be referred to as: E. N. Savchenko & G. O. Krivolutzkaya, 1966.
page 135, line 4: The paper by Stubbs, 1974, appeared in Ent. Gaz., 25: 127—136 (not Ent. monthly Mag., 25: 127—236).

Part 2 (Beaufortia, 28: 57—111).

page 84, map 4: *terminalis* i.s.o. *terminals*.

Part 3 (Beaufortia, 28: 157—203).

page 178, line 17: Lackschewitz, 1935b i.s.o. Lackschewitz, 1935)
page 182, Figs 25—29: 25, *N. profunda* i.s.o. *N. profunda*.
page 190, line 17: 15-segmented i.s.o. 13-segmented.

Part 4 (Beaufortia, 29: 129—197).

page 136, line 38: 1865 i.s.o. 1965.

Appendix 1. Length and diameter of the intromittent organ in Holarctic taxa.

1. Taxon	2. Country or region	3. Length Tergite 2 (T2)	4. Total length intr. organ (mm)	5. Diameter intr. organ beyond aedeagus (µm)	6. Diameter intr. organ before adminiculum (µm)	7. 4, corrected for T2 = 100	8. 5, corrected for T2 = 100	9. 6, corrected for T2 = 100
Brachypremna dispellens Walker	U.S.A. (S. Carolina)	178	0.25	3.2		0.14	1.8	
Nesopeza spec. 1	India (Madras)	115	0.52	5.2		0.45	4.5	
Nesopeza spec. 2	India (Madras)	125	0.95	7.1		0.76	5.7	
Nobilotipula nobilis Loew	U.S.A. (Maine)	115	0.94	3.8		0.81	3.3	
Vestiplex scripta Meigen	Netherlands	148	1.08	3.6		0.73	2.4	
Sinotipula chimaera Savchenko	U.S.S.R. (Kazakhstan)	182	1.29	7.4		0.71	4.1	
Odonatisca juncea Meigen	Netherlands	166	1.56	9.8		0.94	5.9	
Platytipula luteipennis Meigen	Netherlands	167	1.61	2.6	0.8	0.96	1.6	0.5
Longurio testaceus Loew	U.S.A. (Pennsylvania)	317	1.64	4.6		0.52	1.5	
Angarotipula tumidecornis Lundström	U.S.S.R. (?)	153	1.67	2.8	1.5	1.09	1.8	1.0
Eumicrotipula spec.	Mexico	190	1.70	6.7		0.89	3.5	
Prionocera turcica Fabricius	Netherlands	123	1.70	5.6		1.38	4.6	
Arctotipula salicetorum Siebke	Norway	153	1.86	3.6	2.3	1.21	2.4	1.5
Sinotipula subcinerea Doane (formerly *Bellardina*)	U.S.A. (Colorado)	148	1.93	10.4		1.31	7.0	
Dolichopeza albipes Ström	Netherlands	154	2.06	8.1	1.3	1.34	5.3	0.8
Pterelachisus varipennis Meigen	Netherlands	157	2.18	5.1		1.39	3.2	
Holorusia spec.	Indonesia (Sumatra)	254	2.22	4.5		0.87	1.8	
Emodotipula obscuriventris Strobl	Spain	138	2.25	3.4	1.3	1.63	2.5	0.9
Dictenidia bimaculata Linnaeus	Netherlands	122	2.31	3.0		1.89	2.5	
Nigrotipula nigra Linnaeus	Netherlands	129	2.93	1.7		2.27	1.3	
Scamboneura vittifrons Walker	Indonesia (Buru)	179	2.96	2.6	1.4	1.66	1.5	0.8
Mediotipula stigmatella Strobl	Greece	120	2.99	3.0	1.6	2.50	2.5	1.3
Oropeza venosa Johnson	Canada (Toronto)	136	3.59	9.6	3.5	2.64	7.1	2.6

Appendix 1, continued

1.	2.	3.	4.	5.	6.	7.	8.	9.
Ctenophora flaveolata Fabricius	Netherlands	190	4.80	3.3	2.3	2.53	1.7	1.2
Yamatotipula lateralis Meigen	Netherlands	162	4.89	2.2	0.7	3.02	1.4	0.4
Trichotipula spec. cf. *cahuila* Alexander	U.S.A. (California)	97	4.99	5.3	2.1	5.15	5.5	2.2
Trichotipula oropezoides Johnson[1])	U.S.A. (Michigan)	140	5.15	3.3	1.8	3.68	2.4	1.3[1])
Acutipula maxima Poda	Netherlands	283	5.44	10.0		1.92	3.5	
Tanyptera atrata Linnaeus	Netherlands	141	5.80	8.0	0.8	4.11	5.7	0.6
Lindnerina subexcisa Lundström	Sweden	157	5.89	4.5	2.0	3.75	2.9	1.3
Tipula paludosa Meigen	Netherlands	193	5.89	1.4		3.05	0.7	
Dendrotipula flavolineata Meigen	Netherlands	191	6.04	5.0	1.3	3.16	2.6	0.7
Beringotipula unca Wiedemann	Netherlands	175	6.05	4.0	1.2	3.46	2.3	0.7
Lunatipula livida v. d. Wulp	Netherlands	172	6.83	4.2	0.9	3.97	2.4	0.5
Tipulodinodes lacteipes Alexander	U.S.A. (California)	149	7.18	2.1	0.6	4.82	1.4	0.4
Lunatipula vernalis Meigen	Netherlands	190	7.73	3.7	0.5	4.07	1.9	0.3
Hesperotipula circularis Alexander	U.S.A. (California)	126	10.34	3.7	0.6	8.20	2.9	0.5
Savtshenkia marmorata Meigen	Netherlands	128	12.30	2.7	0.9	9.61	2.1	0.7
Setitipula trichophora Alexander	U.S.A. (California)	114	12.36	3.5	1.1	10.84	3.1	0.8
Eremotipula spec.	U.S.A. (Utah)	179	13.80	2.9	0.7	7.71	1.6	0.4
Schummelia variicornis Strobl	Netherlands	145	16.40	4.0	1.0	11.30	2.8	0.7

[1]): In *Trichotipula oropezoides* the bifid apical part comprizes 54% of the total length; number 9 accounts for the diameter just before the break-up.

Appendix 2. Length and diameter of the intromittent organ in western Palaearctic *Nephrotoma* species; 2A: absolute length and diameter; 2B: data corrected for tergite 2 = 100 (presented in diagram 1).

Appendix 2A

1. Taxon	2. Number 1) of specimens	3. Countries or regions	4. Length tergite 2	5. Length 2) basal part (mm)	6. Total length (mm)	7. Diameter beyond aedeagus (µm)	8. Diameter before adminiculum (µm)	9. $\frac{\text{Basal length}}{\text{Total length}} \times 100$
forcipata	2	5	123 ±8		8.02 ±.07	20±2	11	
eugeniae	2	15	91 ±2		5.83 ±.03	19±2	10 ±1	
tenuipes	2	9	134 ±4		8.41 ±.62	23±3	11 ±2	
aculeata	4	6, 9, 10, 25	136 ±10		$17.07^{-2.37}_{+2.22}$	16^{-3}_{+1}	8 ±1	
sardiniensis	2	8	106 ±3		9.66 ±.16	23±1	10 ±2	
cornicina	6	5, 9, 20, 21, 25	120 ±4		$9.15^{-.71}_{+.67}$	21±2	10 ±3	
saccai	3	9	126 ±2		$26.28^{-2.65}_{+3.41}$	19^{-5}_{+3}	8	
nasuta	3	13	117^{-7}_{+9}	$3.50^{-.25}_{+.42}$	$5.18^{-.29}_{+.39}$	82±7		67±3
schaeuffelei	2	17	105 ±2	4.19±.10	9.63 ±.03	41±3		44±1
beckeri	1	14	110	6.93	14.39	37		48- 1
g. guestfalica	5	5, 18, 25	114^{-6}_{+10}	$6.92^{-.90}_{+.60}$	$14.43^{-2.23}_{+1.27}$	36^{-4}_{+6}		48_{+2}
g. surcoufi	2	1	105 ±3	$6.54^{-.07}_{+.05}$	$14.82^{-.10}_{+.09}$	42±1		44
q. quadrifaria	5	5, 19, 20, 25	133^{-11}_{+12}	$2.60^{-.31}_{+.28}$	$13.62^{-.61}_{+.77}$	69^{-1}_{+4}		19±1
fontana	1	2	97	1.93	7.79	56		25
a. appendiculata (Sardinia)	3	8	110^{-9}_{+7}	$3.98^{-.44}_{+.13}$	$8.79^{-.13}_{+.23}$	56±3		45±4
a. appendiculata	7	10, 11, 13, 25	131^{-9}_{+13}	$5.30^{-.46}_{+.72}$	$13.89^{-1.92}_{+1.28}$	54^{-4}_{+6}		38^{-5}_{+6}
a. pertenua	5	5, 9, 18	118 ±16	$7.50^{-1.48}_{+1.13}$	$15.34^{-2.59}_{+2.19}$	63^{-7}_{+12}		49^{-2}_{+1}
minuscula	3	13, 14	97^{-9}_{+12}	$6.72^{-1.47}_{+2.78}$	$9.18^{-1.29}_{+2.44}$	35^{-3}_{+2}		72^{-6}_{+10}
theowaldi	3	11, 13	93^{-8}_{+7}	$15.36^{-.97}_{+1.84}$	$16.44^{-1.07}_{+1.94}$	39±4		94±1
sullingtonensis	5	5	100^{-9}_{+6}	$2.14^{-.24}_{+.47}$	$8.52^{-1.15}_{+1.49}$	39^{-4}_{+6}		25^{-2}_{+1}

Appendix 2A, continued

1.	2.	3.	4.	5.	6.	7.	8.	9.
exastigma	2	2,3	105 ±1	3.20±.24	4.32 ±.26	35±1		74±1
spatha	1	5	102	3.07	4.10	26		75
flavescens	7	5, 10, 18 24, 25	120^{-5}_{+7}	$3.27^{-.17}_{+.22}$	$4.68^{-.33}_{+.31}$	49^{-5}_{+3}		70±2
astigma	3	2	102^{-3}_{+6}	$2.37^{-.14}_{+.09}$	$3.12^{-.20}_{+.14}$	35±3		76±1
submaculosa	7	5, 18, 25	116^{-11}_{+15}	$2.46^{-.43}_{+.35}$	$3.18^{-.37}_{+.36}$	45^{-7}_{+6}		77^{-5}_{+3}
lempkei	2	7	90 ±7	2.02±.10	3.17 ±.20	45±1		64±1
ramulifera	1	27	143		13.34	23	8	
dorsalis	4	20, 25	133^{-8}_{+4}		$17.15^{-1.98}_{+.97}$	16±1	7 ±1	
scurra	6	9, 18, 25, 26, 28	167 ±5		$8.35^{-.94}_{+1.15}$	17^{-4}_{+1}	6 ±1	
quadristriata	2	9, 25	134 ±9		11.80 ±.69	13±2	5	
helvetica	1	20	160		40.16	23	9	
austriaca	3	9, 21	131 ±8		$5.14^{-.60}_{+.74}$	23^{-2}_{+4}	11 ±3	
lunulicornis	2	25	141 ±3		15.17	14	6	
antithrix	1	4	102		1.66	20		
lucida	2	4	128	1.72	3.43	40±3		50
brevipennis	4	4	102 ±10	$1.52^{-.10}_{+.20}$	$3.75^{-.35}_{+.14}$	38±7		41±3
analis	5	6, 9, 18, 20, 25	139^{-3}_{+2}		$8.65^{-.44}_{+.69}$	58^{-3}_{+4}	27^{-3}_{+2}	
subanalis	4	1	129 ±2		$5.94^{-.56}_{+.60}$	55^{-5}_{+7}	46^{-3}_{+2}	
euchroma	4	9	137^{-3}_{+5}		$3.84^{-.18}_{+.36}$	53^{-3}_{+4}	66^{-7}_{+18}	
lamellata	2	25, 34	142 ±3		21.10 ±.17	34±4	13 ±1	
semiflava	3	5	128 ±2		$17.83^{-.30}_{+.48}$	40^{-2}_{+1}	30^{-3}_{+5}	
flavipalpis	5	9, 25	131^{-4}_{+5}	$3.38^{-.24}_{+.22}$	$15.44^{-.92}_{+.91}$	48^{-4}_{+3}		22^{-2}_{+1}
malickyi	2	12	130 ±5	2.62±.13	10.73 ±.40	43±2		25±1
lundbecki	12	28, 33, 35 36, 37	128 ±15		$6.87^{-1.10}_{+3.60}$	29^{-3}_{+9}	10 ±3	

Appendix 2A, continued

1.	2.	3.	4.	5.	6.	7.	8.	9.
alluaudi	5	1	131^{-9}_{+15}	$2.00^{-.29}_{+.42}$	$5.47^{-.33}_{+.65}$	43^{-5}_{+7}	39^{-3}_{+4}	37^{-5}_{+3}
c. croceiventris	3	5	135^{-7}_{+9}	$2.81^{-.24}_{+.23}$	$3.42^{-.27}_{+.25}$	55^{-5}_{+4}	46^{-1}_{+2}	82±1
*c. lindneri*3)	3	13	139 ±6	2.68±.26	3.25 ±.20	56^{-9}_{+12}	59 ±3	83±2
*c. lindneri*4)	3	13	126^{-12}_{+6}	$1.79^{-.07}_{+.08}$	2.22 ±.12	46±1	42 ±4	81±1
*c. lindneri*5)	7	10, 11 13, 22	147^{-17}_{+10}	2.00±.11	2.14 ±.10	63^{-7}_{+11}	73^{-13}_{+6}	93±2
nox	3	13,17	144^{-10}_{+6}	1.88±.10	2.65 ±.04	49^{-11}_{+7}	53 ±7	71^{-4}_{+3}
p. pratensis	4	18, 21, 25	141^{-7}_{+12}	$2.43^{-.09}_{+.21}$	$2.65^{-.08}_{+.20}$	51^{-6}_{+4}	39^{-4}_{+2}	92±1
p. eepi	3	5	131 ±2	$2.05^{-.12}_{+.17}$	$2.28^{-.12}_{+.18}$	56±1	41 ±1	89±1
c. crocata	5	9, 18, 25	136 ±10	$2.10^{-.32}_{+.27}$	$2.50^{-.35}_{+.39}$	43+7	40 ±4	$84^{-2}_{+3.}$
c. luteata	5	5	121^{-10}_{+12}	$1.95-^{-.28}_{+.23}$	$2.22^{-.25}_{+.28}$	38^{-4}_{+5}	36^{-6}_{+5}	88^{-4}_{+2}
s. scalaris	4	10, 25	137^{-4}_{+3}	1.59±.06	$2.39^{-.05}_{+.03}$	34^{-2}_{+4}	39 ±5	67^{-2}_{+1}
s. terminalis	4	16, 17, 31, 32	132^{-14}_{+19}	$1.63^{-.35}_{+.40}$	$2.41^{-.19}_{+.09}$	42±3	37 ±1	67^{-9}_{+14}
rossica	2	29,30	119 ±6	1.89±.06	2.25 ±.08	36	36	84

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1) The numbers refer to the following countries or regions: 1, Morocco; 2, Algeria; 3, Tunisia; 4, Madeira; 5, Spain; 6, Andorra; 7, Mallorca; 8, Sardinia; 9, Italy; 10, Yugoslavia; 11, Greece; 12, Crete; 13, Turkey; 14, Cyprus; 15, Abkhazskaya ASSR (Caucasus); 16, Azerbaydzhan SSR (Caucasus); 17, Iran; 18, France; 19, Luxemburg; 20, Switzerland; 21, Czechoslovakia; 22, Austria; 23, Rumania; 24, Ireland; 25, Netherlands; 26, Poland; 27, Sweden; 28, Finland; 29, Moscow; 30, Veloniki (U.S.S.R.); 31, Kazakhstan SSR (U.S.S.R.); 32, Mongolia; 33, Kokchetav (U.S.S.R.); 34, Primorye (U.S.S.R.); 35, Magadan (U.S.S.R.); 36, Greenland; 37, Canada.

2) The basal part is the part in-between the aedeagus and the break-up or (*crocata* subgroup) the ventral spine.

3) Aberrant populations from eastern Turkey (described as type A in part 2).

4) Aberrant populations from eastern Turkey (described as type B in part 2).

5) Inclusive populations from western Turkey only.

Appendix 2B: data given in appendix 2A are corrected for tergite 2=100.

1. Taxon	2. Length basal part (2A: 5)	3. Total length (2A: 6)	4. Diameter beyond aedeagus (2A: 7)	5. Diameter before adminiculum (2A: 8)
forcipata		6.55±.48	17±1	9±1
eugeniae		6.41±.17	20±2	11±1
tenuipes		6.29±.65	17±2	10±2
aculeata		$12.56^{-1.03}_{+.79}$	12^{-3}_{+1}	6±1
sardiniensis		9.12±.11	21±1	9±2
cornicina		$7.61^{-.41}_{+.44}$	18^{-2}_{+1}	9±2
saccai		$20.85^{-1.79}_{+2.71}$	15^{-4}_{+2}	6
nasuta	$3.02^{-.44}_{+.54}$	$4.46^{-.42}_{+.60}$	71^{-4}_{+7}	
schaeuffelei	3.99 ±.17	9.18±.21	39±2	
beckeri	6.30	13.08	34	
g. guestfalica	$6.07^{-.88}_{+.80}$	$12.67^{-2.24}_{+1.60}$	31^{-4}_{+5}	
g. surcoufi	6.22 ±.07	14.08±.21	40±2	
q. quadrifaria	$1.97^{-.37}_{+.33}$	$10.30^{-1.15}_{+1.21}$	52^{-5}_{+8}	
fontana	1.99	8.03	58	
a. appendiculata (Sardinia)	$3.66^{-.63}_{+.45}$	$8.05^{-.65}_{+.88}$	51^{-3}_{+5}	
a. appendiculata	$4.07^{-.35}_{+.60}$	$10.66^{-.78}_{+1.28}$	41^{-4}_{+7}	
a. pertenua	$6.36^{-.91}_{+.43}$	$13.02^{-1.48}_{+.61}$	53±3	
minuscula	$6.81^{-1.25}_{+1.91}$	$9.38^{-1.14}_{+1.28}$	36±2	
theowaldi	$16.52^{-1.21}_{+.68}$	$17.69^{-1.34}_{+.69}$	42^{-7}_{+4}	
sullingtonensis	$2.15^{-.15}_{+.31}$	$8.55^{-.52}_{+.89}$	40^{-5}_{+6}	
exastigma	3.05 ±.20	4.11±.21	33±1	
spatha	3.01	4.02	25	
flavescens	$2.73^{-.15}_{+.19}$	$3.91^{-.19}_{+.20}$	41^{-4}_{+3}	

Appendix 2B, continued

1.	2.	3.	4.	5.
astigma	$2.32^{-.06}_{+.10}$	$3.04^{-.08}_{+.11}$	35^{-3}_{+2}	
submaculosa	$2.12^{-.21}_{+.34}$	$2.74^{-.36}_{+.37}$	39^{-5}_{+10}	
lempkei	2.25 ±.08	3.53±.07	50±4	
ramulifera		9.33	16	6
dorsalis		$12.92^{-.60}_{+.99}$	12±1	5±1
scurra		$5.00^{-.64}_{+.53}$	10±2	4±1
quadristriata		$8.85^{-.05}_{+.04}$	10±1	4
helvetica		25.10	14	6
austriaca		$3.94^{-.33}_{+.60}$	18±2	8±2
lunulicornis		10.80±.19	10	4
antithrix		1.63	20	
lucida	1.35	2.69	32	
brevipennis	1.50 ±.19	$3.69^{-.21}_{+.10}$	37^{-7}_{+5}	
analis		$6.22^{-.36}_{+.50}$	42±3	20^{-3}_{+1}
subanalis		4.60±.40	42^{-2}_{+5}	36^{-2}_{+1}
euchroma		$2.80^{-.11}_{+.27}$	39^{-3}_{+4}	48^{-4}_{+3}
lamellata		14.91±.15	27±3	9±1
semiflava		$13.90^{-.42}_{+.29}$	31^{-2}_{+1}	24^{-3}_{+5}
flavipalpis	$2.58^{-.11}_{+.19}$	$11.80^{-.37}_{+.87}$	37±3	
malickyi	2.02 ±.18	8.28±.63	33	
lundbecki		$5.35^{-.77}_{+1.97}$	23^{-4}_{+5}	8^{-3}_{+2}
alluaudi	$1.52^{-.18}_{+.14}$	$4.17^{-.33}_{+.14}$	34^{-5}_{+7}	29^{-1}_{+3}
c. croceiventris	$2.09^{-.14}_{+.19}$	$2.55^{-.17}_{+.32}$	41^{-3}_{+5}	34^{-3}_{+2}
c. lindneri [2A: 3)]	$1.93^{-.19}_{+.10}$	$2.34^{-.22}_{+.18}$	41^{-9}_{+10}	43^{-3}_{+4}

Appendix 2B, continued

1.	2.	3.	4.	5.
c. lindneri$^{\text{2A: 4)}}$	$1.43\,^{-.13}_{+.21}$	$1.77^{-.17}_{+.28}$	37^{-1}_{+2}	33±3
c. lindneri$^{\text{2A: 5)}}$	$1.37\,^{-.08}_{+.15}$	$1.47^{-.10}_{+.15}$	43^{-6}_{+9}	50^{-7}_{+9}
nox	$1.31\,^{-.12}_{+.09}$	$1.84^{-.06}_{+.09}$	34^{-6}_{+4}	37±3
p. pratensis	$1.73\,^{-.20}_{+.16}$	$1.89^{-.21}_{+.15}$	36^{-2}_{+4}	28±3
p. eepi	$1.57\,^{-.10}_{+.15}$	$1.75^{-.10}_{+.16}$	43±1	31±1
c. crocata	$1.54\,^{-.13}_{+.08}$	$1.83^{-.12}_{+.16}$	32^{-4}_{+5}	30^{-5}_{+4}
c. luteata	$1.61\,^{-.16}_{+.18}$	$1.83^{-.09}_{+.16}$	31±2	30±3
s. scalaris	$1.16\,^{-.06}_{+.07}$	$1.74^{-.03}_{+.08}$	25±2	29^{-3}_{+2}
s. terminalis	$1.23\,^{-.15}_{+.34}$	$1.83^{-.13}_{+.11}$	32±2	28^{-3}_{+4}
rossica	1.59 ±0.3	1.89±.03	31±2	31±2