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THE BIOGEOGRAPHY OF THE HOLARCTIC *NEPHROTOMA DORSALIS* SPECIES-GROUP (DIPTERA, TIPULIDAE)

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ABSTRACT

A biogeographic analysis is presented for the Holarctic *Nephrotoma dorsalis*-group in relation to the palaeogeographic, climatic and floristic history of the Holarctic region in the Cenozoic. Holarctic intercontinental connections across the Atlantic and by way of Beringia are discussed as well as the biogeographic developments in both the Palaearctic and Nearctic regions. Much attention is paid to a comparison with other insect groups. It is concluded that the history of the *dorsalis*-group was enacted largely in the Tertiary, besides Pleistocene influences on diversity and distribution. The early Tertiary origin of the group is located in the eastern Palaearctic, and its members are supposed to have reached Europe not prior to the late Miocene. It is concluded that exchange between the Palaearctic and Nearctic was entirely by way of Beringia where two vicariance events are postulated, namely in the Oligocene and in the late Pliocene. Other vicariances within the *dorsalis*-group could be correlated with the formation of the Japanese Sea (Miocene), the Himalayan Orogeny (middle Miocene), the development of boreal habitats (middle to late Miocene), the separation of eastern and western North America by climatic and orogenic factors (middle to late Miocene) and the Pleistocene glaciations. Late Pleistocene range extensions across Beringia in both directions are apparent in two species of the group.

CONTENTS

INTRODUCTION

Organisms of the Northern Hemisphere have been the subjects of biogeographic studies for some time past. Initially these studies focussed especially on the Quaternary history of the Holarctic region and its fauna, because it was thought that the Pleistocene glaciations "changed the whole underlying pattern of plant and animal distribution in northern parts of the north-temperate zone" (Darlington, 1957) and also that the Ice-ages had profound effects on evolution (De Lattin, 1967). Recently growing attention has been paid to the Tertiary background of faunal developments in the Holarctic. But if, as stated by Gressitt (1974), "the Holarctic is the result of Tertiary migrations between Laurentia and Angara", and if

the Insect fauna achieved many of its present characteristics during the Tertiary (Matthews, 1979), this fauna nevertheless is perhaps the major one that suffered from the negative effects of the Pleistocene glacial periods (De Lattin, 1967). This remains a serious complicating factor in the analysis of the biogeographical patterns in the Holarctic region.

Previous to this study, a taxonomic revision and a phylogenetic analysis were published of the *dorsalis*-group (fig. 1), a 47 species rich Holarctic group (map 2) of the worldwide crane-fly genus *Nephrotoma* Meigen, 1803 (Tangelder, 1983, 1984, 1985). The methodology for studying biogeography of organisms includes, among others, detailed knowledge of distributions and the cladistic analysis of the group under study. As stressed by Noonan (1986) there is a strong need for biogeographical studies of temperate Holarctic groups, based on cladistics, vicariance biogeography and geological data, to increase our understanding of the origin of Insect groups in the Northern Hemisphere. This study tries to fulfil these conditions and thereby to contribute to this understanding.

After a brief discussion about methods, a concise summary of the relevant geological history is presented, in order to confine the biogeographical chapters with short references to this summary. A short section treats the dispersal abilities of members of the *dorsalis*-group, because an understanding of a group's vagility is a prerequisite for any biogeography study (Noonan, 1985). The origin of the monophyletic Nearctic *macrocera*-group is the subject of a discussion concerning Holarctic intercontinental connections. Next the zoogeography of both the Palaearctic and Nearctic groups within the *dorsalis*-group is treated.
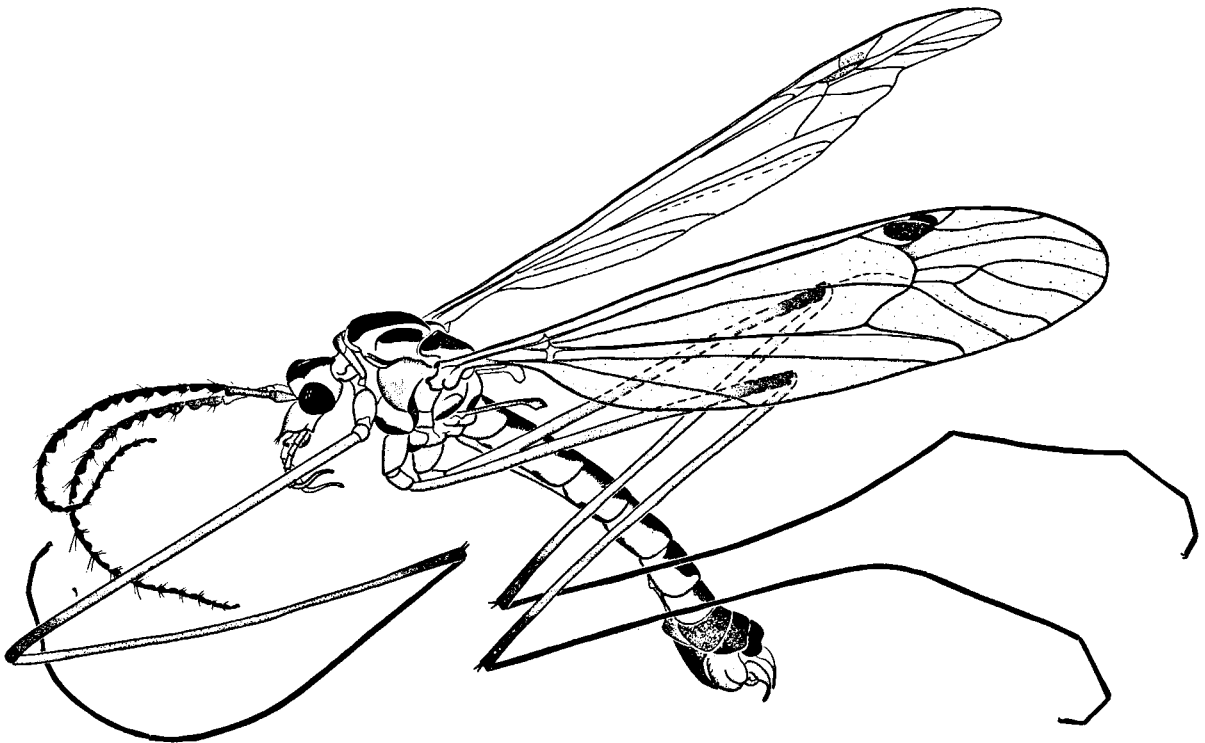

Fig. 1. *Nephrotoma dorsalis* (Fabricius, 1781), male.

ANALYTICAL PRINCIPLES

Historical biogeography attempts to explain present distributions of organisms by reference to past origin, evolution and distributions of organisms as well as past changes in landscapes (Müller, 1974). It recognizes that each group has its own history (Andersen, 1982) but that a "useful biogeographic explanation is not a search for unique explanations of unique events, but a search for congruency of biological and geological area cladograms" (Rosen, 1978). The aim is thus to seek general patterns and general explanations (Patterson, 1983).

Four prerequisites must be satisfied for meaningful historical biogeographical studies. First, the group being studied must be monophyletic. As noted by Erwin & Kavanaugh (1981) the three other prerequisites are: (1) it must be possible to formulate a hypothesis of the phylogenetic relationships of members of the group; (2) the geographical ranges of the extant species must be adequately known; and (3) the pool of included taxa must be large enough. Knowledge about the species of the *dorsalis*-group, as presented in Tangelder (1983, 1984, 1985) fulfils the four prerequisites.

To study the historical biogeography of this group I use the principles of the vicariance model as discussed by authors such as Platnick (1976b), Platnick & Nelson (1978), Rosen (1978), Morse & White (1979), Nelson & Platnick (1981) and Wiley (1981). This method superimposes the geographical distributions of groups upon cladograms to produce area cladograms. The resulting area cladograms for various species-groups are then compared with each other and with cladograms of other organisms to elucidate information about general vicariance and historical biogeography patterns of organisms. See Wiley (1981: 291-305) for a concise description of procedures employed in the vicariance model.

The subject of this study is a single Holarctic species-group of Tipulidae. However, much attention is paid to the comparison with what is known of the biogeography of other taxa, especially insect groups. The results of this study may be of use in future area-cladistic treatments of Holarctic biotas.

GEOLOGY OF THE NORTHERN HEMISPHERE

To understand the historical biogeography of the *dorsalis*-group one must first understand the past land configurations and climates. The following summary is based upon data in Nalivkin, 1973; King, 1977; Matthews, 1979; Ager, 1980; Adams, 1981; Barron et al., 1981; Hallam, 1981; Smith, Hurley & Briden, 1981; and Rögl & Steininger, 1983.

The Palaearctic

The Cretaceous and to a lesser degree the Palaeogene were characterized by worldwide marine transgressions. These transgressions in Europe consistently came from the direction of the opening Atlantic to the west, frequently changing a large part of the continent into a pattern of islands around some relatively stable continental blocks, with the maximum Tertiary transgression occurring in the Oligocene. In Siberia the marine transgressions mainly occupied the eastern pacific part of the continent (Kamchatka, Sakhalin, Primorye) and the Western Siberian Lowlands, just east of the Urals. These lowlands were nearly completely drowned in the Upper Cretaceous from the Arctic Ocean to the Tethys Sea (the Turgai Strait). At the end of the Cretaceous the sea began to withdraw to the north (Obik Sea) and a small land connection between Siberia and Europe was re-established in the Palaeocene. This land connection again was interrupted throughout the Eocene, by way of the Obik Sea and Turgai Strait (map 1), and restored in the Upper Oligocene, about 30 m.y. ago. The large central part of Siberia remained above sea level from the Mesozoic onward (Siberian Platform, Central Angara), and the north-eastern part including Chukotki remained continental from the Upper Cretaceous. The Scandinavian Platform and the central and southern European

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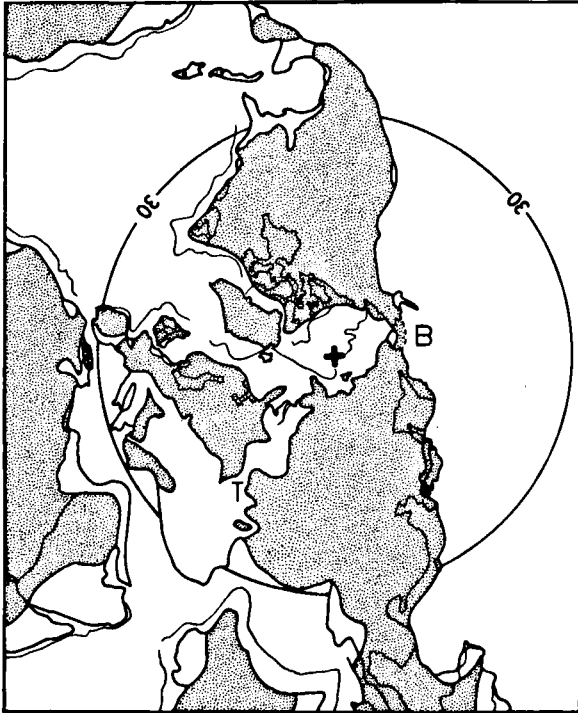
Map 1. Land configurations of the late Eocene (40 m.y.ago). Past land denoted by shaded areas. + = North Pole, T = Turgai Strait, B = Beringia. After Barron e.a. (1981).

islands united in the Miocene, although large parts of the present continent were still covered by the sea.

The separation of Japan from Asia by opening of the Japanese Sea is postulated in the late Cretaceous / early Tertiary (75-65 m.y ago) by Uyeda & Miyashiro (1974), but the current opinion is that the Japanese Sea was formed during the Oligocene / early Miocene (Barron et al., 1981) and that Japan was exposed to increasing insularity since the middle Miocene (Tanai, 1972).

The Ural Mountains were formed at the end of the Palaeozoic and remained above sea level from that time; the system was only weakly affected by orogenies in the Upper Cretaceous and the end of the Palaeogene. The mountain-systems in central and south Siberia are also of Upper Palaeozoic age, while later orogenies in the Upper Cretaceous and Tertiary mostly affected the southern ranges. The Himalayas

were formed by the tectonic collision of India with Asia, starting about 40 m.y. ago and with the most intense orogenic phase in the middle Miocene. The mountain systems of central and southern Europe were formed during the Alpine Orogeny, starting in the Upper Mesozoic, with the most important phases during the Tertiary, e.g. in the central Alps at the end of the Eocene with an important uplift in the Pliocene, and simultaneously also in the Carpathian Mountains.

Large ice-masses covered northern Europe several times during the Pleistocene, they were confined to higher latitudes in Asia (see "Climates"). Some authors (Zarina et al., 1964; De Lattin, 1967; Müller, 1974) supposed that from late Pliocene time onward Europe and central and east Asia were separated several times because of the strongly enlarged Aralo-Caspian Sea and the West Siberian Ice-lake between the Ural Mountains and the Yenisey. According to Frenzel (1968) the floral fossils are in contradiction with this, although the ice was strongly extended southward in the West Siberian lowlands during the last two glaciations (CLIMAP, 1976), with similar effects on the separation of Europe and Asia (Theowald & Oosterbroek, 1985). Temporary land connections were formed during the glaciations between the Asian mainland and the Japanese islands (De Lattin, 1967).

The Nearctic

A broad Midcontinental Seaway completely divided the North American continent from the Gulf of Mexico to the Canadian Arctic along the eastern side of the Cordilleran Region between 100-70 m.y. ago. This seaway disappeared at the end of the Cretaceous when the whole Cordillera System had transformed into a mountain range. This late Cretaceous / early Tertiary orogeny affected the whole range from Yukon south to the Sierra Madre in Mexico, although the Rocky Mountain region stood at low elevations. The crustal movements continued during most of the Tertiary and Quaternary. The Alaska Range rose in the Miocene,

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while a regional uplift in Pliocene/Quaternary was responsible for much of the present height of the central and southern Rocky Mountains. The Appalachians are of Palaeozoic age; a crustal uplift during the Pliocene considerably affected the system. Tertiary transgressions occurred in parts of the southeastern coastal plain and Mississippi embayment (map 1), while the Hudson Bay was filled with water also from time to time. The remainder of North America was continental during the Tertiary. The Pleistocene glaciations brought large ice-sheets over the northern parts of the continent (see "Climates"). Florida was separated from the mainland by marine transgressions during each interglacial.

Intercontinental connections

Trans-atlantic

The initial seafloor spreading in the Atlantic was about 165 m.y. ago, but the opening of the North Atlantic between Newfoundland and Ireland started about 90-95 m.y. ago. Europe, Greenland and North America were still contiguous then. Opening of the Norwegian Sea commenced in the Palaeocene (60-63 m.y. ago), while the Greenland Sea began to form after the end of the Eocene (38 m.y ago). It is generally accepted that a North Atlantic land continuity existed until at least about 49 m.y. ago (Kurtén, 1966; Pitman & Talwani, 1972; McKenna, 1975; Matthews, 1979, 1980). This continuity of Euramerica may have lasted another 10 m.y. and must have been situated north of Baffin Bay, which was a substantial barrier for faunal exchange from the Mesozoic (McKenna, 1975; Lindroth, 1979) or early Tertiary (Leg 105, 1986). A very narrow and apparently not always continuous North Atlantic land bridge, the so-called Greenland-Faroes-route, may have been in existence until the Miocene (Matthews, 1979, 1980; Eldholm & Thiede, 1980).

Beringia

An oceanic barrier between Asia and North America existed in Beringia till about 70 (McKenna, 1975) or 60 m.y. ago (Pitman & Talwani, 1972), which disappeared with the convergence of Asia and Alaska because of the opening of the Atlantic. A land connection between north-eastern Asia and North America was established during the largest part of the early and middle Tertiary (Hopkins, 1967; Matthews, 1980; map 1). From Oligocene times onward the relation between both continents was characterized by alternating 'make or break' situations (Hallam, 1981). Rögl & Steininger (1983) situated the formation of a Bering land bridge in the early Miocene (22 m.y. ago) and again in the late Miocene (about 10 m.y. ago), in relation with a worldwide regression every 12 million years. According to Matthews (1979) the geological evidence suggests that some type of Asian-Alaskan land connection existed from the late Cretaceous until the Pliocene. The paleontological evidence in support of a Miocene seaway across Beringia was misinterpreted according to Hopkins (pers. comm. in Matthews, 1979: 42). The Beringian transgression opened the Bering Strait in the late Pliocene (about 3.5 m.y. ago, Hopkins, 1967; Matthews, 1979), although the land connection was re-established several times during the Pleistocene, for example during the Illinoian and Wisconsin glaciations, when without doubt a broad land bridge existed over Beringia (Hopkins, 1967; Lindroth, 1979).

CLIMATES
(Mainly based on Frakes, 1979 and Hambrey & Harland, 1981)

The Cretaceous in the Holarctic Region was characterized by warm and dry conditions, followed by a general climatic deterioration during the Tertiary, culminating in the rapid oscillations of the late Tertiary and Quaternary glaciations. According to Hallam (1981) the climatic influence on biogeographic changes became increasingly significant through the Cenozoic.

The decline of hot and dry conditions near the end of the Cretaceous continued through the Palaeogene, giving rise to the development

of boreal climates. The great increase of global precipitation in the late Palaeocene continued through much of the Eocene, accompanied by a period of warmth; regions north to 45° had true tropical climates (Matthews, 1979). At the end of the Eocene there was a precipitous cooling followed by a time of comparatively low temperatures in the Oligocene, with two significant warmings in the early and late Oligocene. The middle Oligocene marked the end of high-latitude 'subtropical' assemblages. The climates in the Miocene were significantly warmer and wetter than at present, but midway through the Miocene climates deteriorated markedly, becoming cooler and drier. Other major intervals of cooling are recorded in the late Miocene and in the Pliocene. Estimates of mean annual temperature in the London Basin indicate a fall from 21° C in the Eocene, through 18° C in the Upper Oligocene and 16° C in the Miocene, to 14° C in Pliocene times, compared with 10° C at present. Further climatic changes were induced in the late Cenozoic by an increase in continental relief, with as a consequence the formation of extensive arid zones as has been recognized in western North America (Hallam, 1981).

The late Neogene saw the development of cyclicity over 100,000 year periods, with rapid warmings and more lengthy coolings. These glacial-interglacial cycles started in the late Pliocene; about 10 glacial periods have been recorded for the last one million years (Van der Hammen, 1979). The large ice-masses made their first advance to low mid-latitudes at the beginning of the Pleistocene and they seem to have been most widespread during the Kansan-Mindel and Illinoian-Riss glacial stages. During the last glaciation (Wisconsin-Würm) the ice-sheets covered, at their maximum extent, the North American continent almost entirely as far south as Kentucky (map 7) and extended in Europe across the whole of Scandinavia and the northern USSR south over the northern European lowlands, while large ice-fields developed in the Alps. Beringia stayed largely ice-free during the Wisconsin and Illinoian glaciations, but the glaciers formed a

barrier between Alaska and other parts of North America. The situation of pre-Illinoian glaciations is not exactly known (Hopkins, 1967). The Asian continent was not covered by continuous ice-sheets; during the last glaciation the ice was fragmented and confined to higher latitudes and mountainous areas (CLIMAP, 1976).

FLORISTIC HISTORY

(Graham, 1964; Wolfe & Leopold, 1967; Hopkins et al., 1971; Van der Hammen et al., 1971; Wright, 1977; Matthews, 1979, 1980; Wolfe, 1980).

Europe

Middle Eocene assemblages indicate a boreotropical flora for Europe. A warm temperate forest prevailed during the Upper Oligocene and Miocene in western and north-western Europe. Nalivkin (1973) reported such forests with big marshes, lakes and rivers at the Russian Platform in the Miocene. In the biota of northwestern Europe a progressive cooling in the first half of the Tertiary is illustrated (Hambrey & Harland, 1981), while presumably there also was a distinct cooling in Europe at the middle-late Miocene boundery. Many elements disappeared from northwestern Europe in the Upper Miocene, the flora indicates a cool-temperate to boreal climate between 6 to 10 m.y. ago in this area (Van der Hammen et al., 1971). The dominant vegetation in the Pliocene was a temperate mixed mesophytic forest, alternated with pine forests during the cooler phases. The forests were strongly impoverished during the first cold-period of the Pleistocene, about half the species of the rich Pliocene flora became extinct (Wright, 1977). The history of the tundra biome extends at least to the Miocene, but a single circumpolar tundra-zone may not have come into existence until the late Pliocene (Matthews, 1979). During the many Pleistocene climate-cycles profound changes of life conditions came across central and western Europe: an advance of tundra and cold-steppe

vegetation far to the south during the glacia-
tions and successive replacements by pine
forests and temperate deciduous trees during
the interglacials. The biotas were moved
southward by the advancing glaciers and
pressed against the east-west oriented mountain
ranges, which hindered the refuge-routes to the
south, as distinct from the situation in North
America. This may have had severe effects on
the extinction and speciation rates of the respec-
tive biotas (Warnecke, 1958; Howden, 1969;
Noonan, 1973).

Asia

The present-day treeless steppes of the mid-
USSR were covered by woodland during most
of the Tertiary, first containing evergreen
tropical species, but after the late Eocene cool-
ing giving way to deciduous forests and mixed
coniferous-deciduous forests (Hambrey &
Harland, 1981); which were also present in
northern West Siberia during the Oligocene
and Miocene. Temperate sclerophyllous
vegetation formed a broad, nearly continuous
belt across the continent in the late Palaeogene
(Axelrod, 1975). Lowland boreal forests
appeared during the middle to late Miocene
and the steppe floras only turned up near the
end of the Miocene. The Eocene floras of Japan
were largely subtropical to warm-temperate;
from the Oligocene onward the floras got a
more temperate aspect (Tanai, 1972). Other-
wise as in Europe and North America the ter-
restrial biota in eastern Siberia suffered only
partly from the Quaternary ice-ages and largely
preserved their own nature (Johansen, 1955).

North America

A boreotropical flora covered the northern part
of the continent during the early Tertiary, while
more (sub)tropical conditions prevailed south of
this. By the late Palaeogene, temperate
sclerophyllous vegetation formed a broad,
nearly continuous belt across the continent,
which became restricted by the spreading of
drier and colder climates by the mid-Oligocene
(Axelrod, 1975). A rich coniferous forest

existed across northern Canada after the mid-
Miocene, while south of it mixed mesophytic
forests were prevalent. By the late Miocene the
interior part of North America was grassland,
but prairies in the usual sense did not develop
until the Pliocene (Lehmkuhl, 1980). The floras
of the Pacific Northwest maintained their
temperate Asiatic aspect during most of the
Tertiary (Leopold & Macginitie, 1972), while
the late Tertiary orogenies and concomitant
alteration in climate are considered responsible
for the increasing aridity of the western and
central Cordilleras; conditions that spread to
the whole western part of the continent and
changed the vegetation from deciduous forests
in the Miocene to mainly deserts and semi-
deserts in the Pleistocene (Graham, 1972;
Schwartzbach, 1974). The floras of (south)-
eastern North America changed from tropical
to temperate from Eocene to Pliocene. The
glacial/interglacial cycles of the Pleistocene are
represented in the north-southward vegeta-
tional and faunal shifts; the refuge routes to the
south were not blocked by mountain ranges as
in Europe. These shifts are best studied for the
Late- and Postglacial, which started with a
broad boreal forest south of the Laurentide Ice-
sheet that shifted far to the north till the present
position (Delcourt & Delcourt, 1984). Tundra
environments south of the ice were sparse and
disappeared there completely with the retreat of
the ice (Coope, 1970; Matthews, 1979; Morgan
& Morgan, 1980).

The North Atlantic land continuity

This region, although situated in the high arc-
tic, permitted the exchange of warm-temperate
or temperate biota in the Palaeogene
(Mckenna, 1975, 1980; Wolfe, 1980; Hambrey
& Harland, 1981). The suggestions range from
cool-temperate to warm climates, while "mixed
conifer-hardwood and deciduous hardwood
forests blanketed the arctic region", including
Svalbard (Spitsbergen) and Ellesmere Island, in
the Palaeocene and Eocene (Axelrod, 1984).
"Direct migration between Europe and eastern
North America following the early Palaeogene

was by increasingly cooler temperate biota as the North Atlantic widened" (Raven & Axelrod, 1974).

Beringia

The floristic history of northeast Siberia and Alaska is essentially the same. A warm-temperate mixed mesophytic forest was thought to be continuous from Japan to eastern North America from the early Tertiary until the middle Miocene, according to the exploded Arcto-Tertiary Geoflora concept. In Matthews (1980) opinion such a forest never existed in Beringia, but a tropical or subtropical forest was present near the land bridge from Palaeocene till mid-Eocene. Hambrey & Harland (1981) speak of palms in Palaeogene Alaska. According to Wolfe (1980) broad-leaved evergreen vegetation extended to well above latitude 61° N (southern Beringia) in the Eocene, with north of it a boreo-tropical flora. After the climatic deterioration at the end of the Eocene, large regions of the northern Hemisphere were occupied by temperate broad-leaved deciduous and coniferous forests. The first occurrence of mixed mesophytic vegetation in Beringia was by the late Oligocene. Trans-beringian exchange of warm-temperate biota was probably possible in the Oligocene and Miocene. After the strong decline of summer temperatures in mid-Miocene, Beringia and presumably all of northern Canada were dominated by a diverse coniferous forest. A gradual impoverishment of this rich boreal forest during the Pliocene resulted in Pleistocene forests around the northern Pacific similar to the present-day forests there. Treeless conditions were imposed on the land bridge in the late Miocene and Pliocene. Tundra, if existing in the Pliocene, must have been situated far to the north. According to Wolfe (1980) and Thorne (1978) the Beringian area was a major floristic link between North America and Eurasia during the Palaeogene, but not during the Neogene. In the Quaternary a severe climate prevailed at Beringia, this area presumably was not forested during the

Pleistocene (Lindroth, 1979). During the last glaciation Beringia supported a dry and cold steppe tundra (Colinvaux, 1985), where only cold-hardy organisms could live (Lindroth, 1979). In the Holocene, woodland elements returned to the Bering region.

BIOGEOGRAPHY OF THE *DORSALIS*-GROUP

BIOLOGY AND VAGILITY

Craneflies are not directly connected with plant-associations, rather respond primarily to the hydrological regime of the soil and the micro-climate (Zinovjev & Savchenko, 1962). The absence of a clearly defined zonality according to plant formation in the distribution of the genus *Nephrotoma* is apparently due to the larval stage living and feeding on divergent substrates and vegetation (Savchenko, 1973).

The limited knowledge about the biology of the *dorsalis*-group is presented in Tangelder (1983, 1984). The precise larval substrate is known only for a few species of the group. But, as for most species of *Nephrotoma*, the larvae probably live mainly in humus-rich, more or less damp soil (Oosterbroek et al., 1976). The *dorsalis*-group largely occurs in the temperate zone, ranging between latitudes 27° to 70° N, with a few representatives in the subtropical regions and some members in the alpine and subarctic zones (map 2). Most species have one generation a year with only a few bivoltine exceptions. Elevations with specimens range from sea-level to 4300 meter. The adults of most species can be found in moist to wet mesophytic habitats such as deciduous or mixed forests, meadows, swamps and banks of streams. Only a few species are adapted to dryer conditions (e.g. *N. ramulifera*, *N. scurra*, *N. sublunulicornis*).

Mating takes place at or very soon after females emerge in most species. The females fly close to the ground when gravid and oviposit immediately or soon after mating (Pritchard, 1983). Their dispersal potential is therefore probably low, but apparently sufficient for large
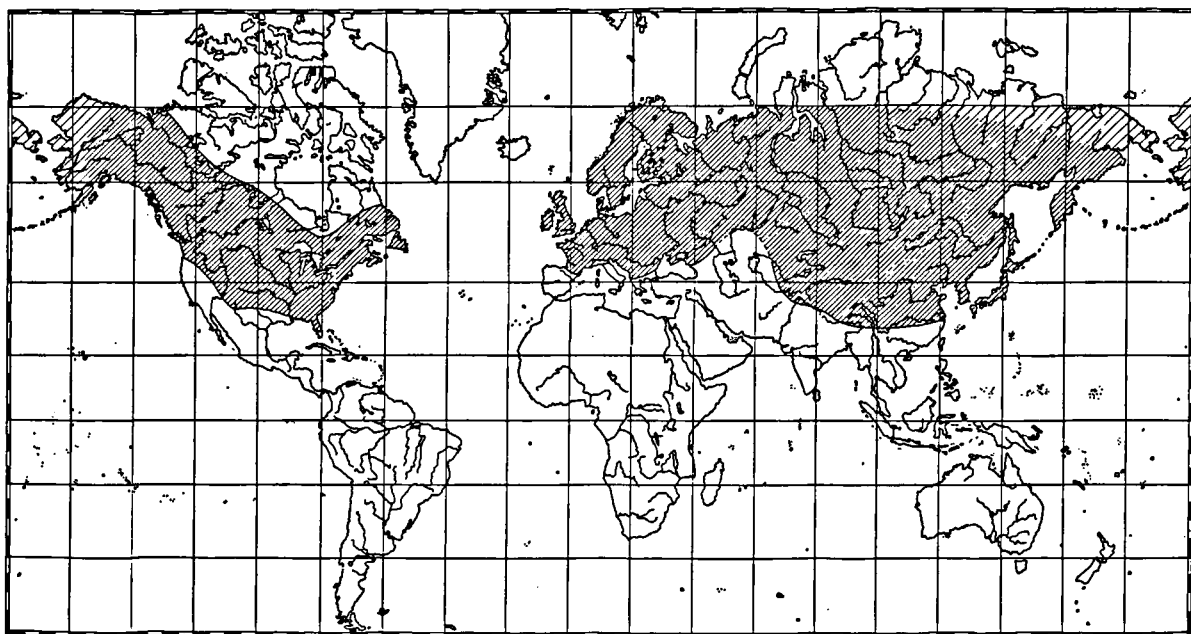
Map 2. Distribution of the *dorsalis* species-group.

distance dispersal over long periods of time, as shown by the many species now occupying extensive areas covered with ice during the last glaciation. This dispersal presumably did not exceed several hundreds of meters per year. With their heavy bodies, craneflies are not easily dispersed by wind (Gressitt, 1974). Although their vagility may be modest in flat and suitable habitats, craneflies probably fail to cross serious barriers such as mountainous areas and (large) water-surfaces. Theowald & Oosterbroek (in prep.) discuss data suggesting low vagility of Tipulidae.

In the biogeographic analysis of the *dorsalis*-group is started from the constancy of ecological requirements of the species and from their modest vagility.

AGE AND ORIGIN OF THE *DORSALIS*-GROUP

The origin of the genus *Nephrotoma* dates back to the late Mesozoic according to Savchenko (1966, 1973), because this would be the only way in which its presence in Australia, South America and Madagascar can be explained. Oosterbroek et al. (1976) presumed an early Tertiary origin in east Asia, because of the lack of Mesozoic fossils of the genus. Other authors, studying other groups of organisms also reached the conclusion of a Mesozoic origin because of a worldwide distribution, e.g. Spence (1982, Coleoptera, Carabidae), Baumann (1975, Plecoptera), Meinander (1979, Neuroptera), Cranston et al. (1987, Diptera, Chironomidae) and Milner (1983, Salamanders). The conclusion of Savchenko seems most likely, and his argument of the worldwide distribution of the genus is illustrated more explicitly by the *brevipennis*-group, a monophyletic species-group within *Nephrotoma* (Oosterbroek, 1979). The distribution of this group comprises Africa, South America, Central and North America and one species in the eastern Palaearctic which is closely related to the Nearctic species (Oosterbroek, 1985). Although the phylogeny of this group is not worked out yet, one nevertheless can conclude that the distribution on either side

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of the southern Atlantic can best be explained by an origin of the *brevipennis*-group before both continents finally separated in the Upper Cretaceous (Dietz & Holden, 1970). A Mesozoic origin of the genus seems a more parsimonious explanation than postulating a later origin, dispersals across oceans and extinction of the groups in northern areas. The modest vagility of the crane flies, apparent from the distinct failure of some species to cross even slight watergaps (Theowald & Oosterbroek, in prep.) is a strong argument in favour of vicariance.

Given a Mesozoic age of the genus *Nephrotoma*, an (early) Palaeogene origin is proposed for the *dorsalis* species-group, probably synchronized with the development of boreal climates in the northern Hemisphere. The diversity of species-groups within the genus *Nephrotoma* (more than 15 in the Holarctic region, Oosterbroek, 1984, 1985) may also be an indication of the rather old age of the genus and the constituent species-groups. Unfortunately no identifiable fossils are available to support this idea, although there are fossils of Tipulidae reported from middle Eocene formations in British Columbia and Colorado (Wilson, 1978), and from the Oligocene in Europe (from Theowald & Oosterbroek, 1985).

All the monophyletic species-groups within the *dorsalis*-group, except the derived Nearctic *macrocera*-group (fig. 2), are (mainly) restricted to the eastern Palaearctic, while only two species are endemic to Europe (Tangelder, 1984). The sister group of the *dorsalis*-group is not known with certainty. The study of several undescribed oriental species of *Nephrotoma* reveals a close affinity of these species to the *dorsalis* species-group, which indicates that the sister group presumably can be found in the Oriental Region. Considering this, the 'region of origin' of the *dorsalis*-group had to be sought in the eastern Palaearctic, which also is supposed to be the region of origin of the genus (Oosterbroek et al., 1976; Oosterbroek, 1980). The phylogeny and distribution of the *dorsalis*-group, as outlined in the following chapters, also points in this direction.

SPECIATION RATES

Speciation rates of one to several million years are supposed for arctic and temperate insects with a continental pattern of isolation, especially Carabids, but slow rates of evolution are presumably widespread among insects (Coope, 1970, 1978; Matthews, 1980). A mean speciation rate of 3 million years is supposed for continental speciation in the Nearctic stock of *Schizogenius* (Coleoptera, Carabidae) (Whitehead, 1972). Kavanaugh (1979) suggested rates varying from 9,000 to 1.8 million years for speciation in *Nebria* (Coleoptera, Carabidae), and he concluded that the slower rates possibly apply to lowland forms. Noonan (1981) postulated speciation rates varying from an origin of species during the Pliocene and/or Pleistocene and an origin during the Pleistocene in *Anisotarsus* (Coleoptera, Carabidae). Wheeler (1979) suggested a speciation rate lying between 10,000 to 1 million years in *Anisotoma* (Coleoptera, Leiodidae), besides marking that this may be much faster than indicated in many Carabid groups. Liebherr (1986) concluded from electrophoretic data a speciation rate of several (1 or 2 to 4) million years in North American Platinini (Coleoptera, Carabidae), which was consistent with his scenario of the zoogeographic history of the species-group. According to Väisänen (1984) the rate of morphological differentiation of species of *Mycomya* (Diptera, Mycetophilidae) appears to have been slow, taking several million years. Gagné (1981) even postulated that species of fungus gnats (Diptera, Mycetophilidae) may have remained essentially unchanged since the early Tertiary.

A longest successive series of 15 speciation events, i.e. the maximum number of known dichotomies in a single lineage, can be inferred from the cladogram of the *dorsalis*-groups s.l. (numbered in figs. 2-6, from the base of the cladogram up to *sublunulicornis*). Within the derived Nearctic *macrocera*-group a longer successive series (12) is found than within the presumably older Palaearctic groups (at most 8). This fact possibly indicates that extinction

played a more important part in the Palaearctic than in the Nearctic region, although other causes also may have been responsible for this difference.

If we accept a speciation rate of one to several million years, then the *dorsalis*-group is at least of late Oligocene age (30 m.y. ago), but presumably older, also bearing in mind the possibilities of extinctions.

DISTRIBUTION OF THE
DORSALIS—GROUP (Maps 2-12)
(Based on Tangelder, 1983, 1984; Oosterbroek & Tangelder, 1987)

The *dorsalis*-group is composed of 47 species of which 27 are Palaearctic, 18 Nearctic and 2 Holarctic in distribution.

All monophyletic Palaearctic species-groups of the *dorsalis*-group s.l. (fig. 2) are completely or mainly eastern Palaearctic. The phylogenetically old ones, the *nigricauda*-group (3 species) and the *pamirensis*-group (5 species) are confined

to central and east Asia (map 3). *N. ramulifera* has a Holarctic distribution with a presumably Pleistocene introduction into the Nearctic (Alaska) and a sparse distribution in the tundra regions of Europe and Asia (map 6). The *dorsalis*-group s.s. (3 species), *lunulicornis*-group (6 species), *austriaca* and *scurra*-group (8 species), together composing the sister group of the Nearctic *macrocera*-group, are eastern Palaearctic in distribution (maps 4 and 5), but all with one or two representatives that occur, disjunct or uninterrupted, also in the western Palaearctic. Only two members of this compound sister group, namely *helvetica* (belonging to the *scurra*-group) and *austriaca* (uncertain sister species of *scurra*-group and/or *lunulicornis*-group) are endemic to Europe (map 5). Nine species of the Palaearctic stock, represented in four out of the five species-groups, occur in Japan, Sakhalin and/or the Kuril Islands, six of them endemic (maps 3, 4 and 5). Two species (*kaulbacki* and *libra*), both primitive members of the phylogenetically older groups, are found in
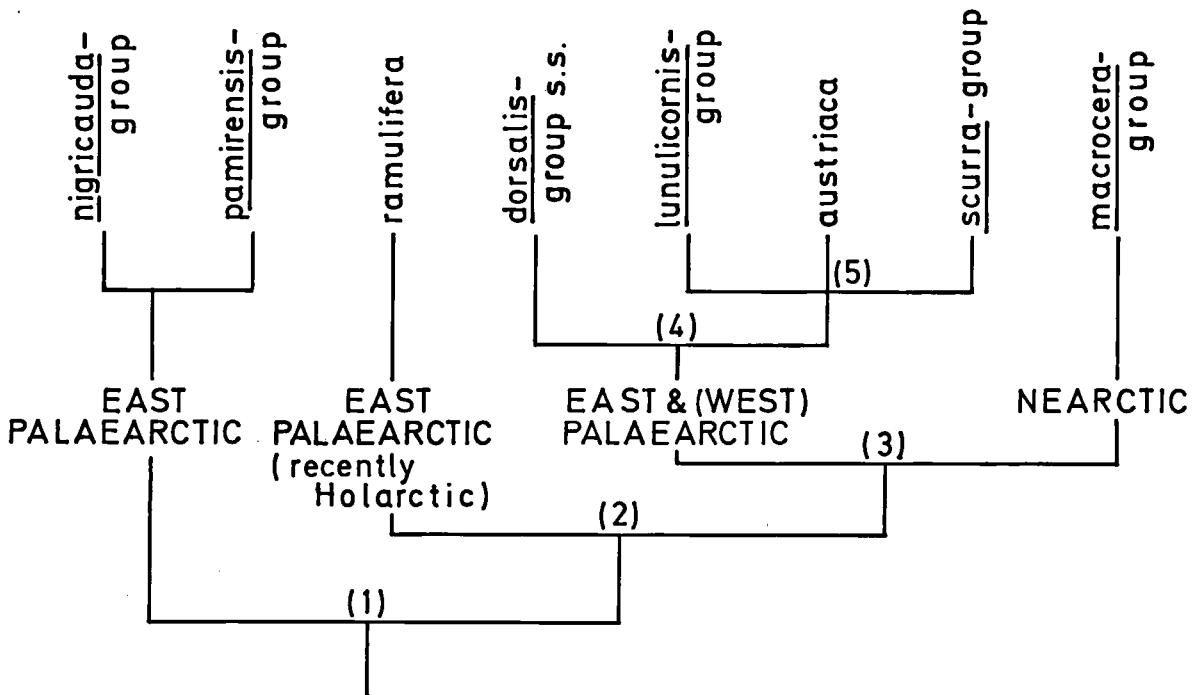

Fig. 2. Cladogram of the species groups within the *dorsalis* group s.l. Numbers indicate successive speciation events in a single lineage.

the Himalayas and two species (*perobliqua* and *profunda*) are known from China (maps 3 and 5). From this distribution pattern an eastern Palaearctic origin of the *dorsalis*-group can be inferred on account of parsimony.

All 20 Nearctic species of the *dorsalis*-group, except for the Holarctic *ramulifera* but including the eastern Palaearctic *sublunulicornis*, belong to the monophyletic *macrocera*-group (fig. 2). Twelve species are confined to the eastern part of North America, ranging from New-foundland to Florida and not stretching westward beyond Longitude 100°W (maps 7-11). The phylogenetically oldest member of the group, *sodalis*, is transcontinental, however with all the (north) western localities situated in an area formerly completely covered by the Wisconsin Ice-sheets (map 7), so this transcontinental distribution presumably is a postglacial attainment. The same may be said of the narrowly westward ranging northern distribution of *penumbra* (map 8), covering New England up to Labrador and narrowly ranging into northern British Columbia. Only the members of the derived *occipitalis*-subgroup are partly or completely concentrated in the central and northern Cordilleran region (map 12). Three are confined to the western mountains, one (*breviorcornis*) ranges from Colorado eastward to the Atlantic and one (*occipitalis*) is northern transcontinental and also found in Kamchatka and central Asia (map 6). The only Palaearctic member of this subgroup (*sublunulicornis*) occurs in central Asia (map 6). This distribution pattern justifies the conclusion that evolutionary radiation apparently took place from the eastern side of the continent, as also will be discussed below.

INTERCONTINENTAL CONNECTIONS

The *dorsalis* species-group can be divided into a Palaearctic and a Nearctic stock. The Palaearctic stock comprises several monophyletic species-groups, three of which form the sister group of the derived monophyletic Nearctic stock (fig. 2). This sister group is eastern Palaearctic with some representatives in

Europe. The Nearctic species-group is essentially concentrated at and apparently has its evolutionary radiation from the eastern side of the continent. No members of the *dorsalis*-group are found in the south-western part of North America.

One of the interesting questions in the biogeography of the *dorsalis*-group applies to the time and way whereby the monophyletic Nearctic *macrocera*-group developed in North America. Does it concern a trans-atlantic or a Beringian faunal exchange?

1. Trans-atlantic

The first possibility concerns the North Atlantic faunal exchange and the subsequent vicariance of eastern North America and Europe because of the final separation of Euramerica by opening of the North Atlantic in the early Eocene (or somewhat later according to some authors). Noonan (1986) reported that "a survey of biogeographical literature on all insect orders reveals more than 20 groups with biogeographical patterns suggesting that Euramerican ancestors were split by the opening of the North Atlantic". The following studies do suggest such a vicariance, based on (cladistic) sister group relationships between taxa of Europe and eastern or mainly eastern North America. The vicariance relationships range from the species-level to genera or even subfamilies. In many cases warm to temperate species are concerned, and most authors suppose the vicariance of their groups to have taken place before the mid-Eocene. The studies mentioned are: Insects, Plecoptera: Ross & Ricker (1971, vicariance on the genus-level, *Allocapnia*); Neuroptera: Meinander (1979, vicariance on the genus-level, Aleuropteryginae); Homoptera: Richards (1965, vicariance on genus- and species-group level, Callaphidini); Hemiptera: Schaefer & Calabrese (1980, amphi-atlantic species-pairs, Gerridae); Coleoptera: Noonan (1973, vicariance on the subgenus-level, Carabidae, Anisodactylini), Allen (1980, vicariance between genera, Carabidae, Myadi), Clark

(1978, vicariance on the species-level, Curculionidae, *Tychius*), Roughly & Pengelly (1981, vicariance between species-groups, Dytiscidae, *Hydaticus*); Diptera: Marshall & Roháček (1984, vicariance on the species-group level, Sphaeroceridae, *Telomerina*), Väisänen (1984, vicariance relations between sister species, Mycetophilidae, *Mycomya*); Araneae: Platnick (1976a, vicariance between species-groups, Laroniinae); Amphibians: Case (1978, vicariance between species-groups, *Rana*), Milner (1983, vicariance on the subfamily-level, Salamanders). Gagné (1981, Diptera, Mycetophilidae) even postulates a Holarctic, amphi-North Atlantic distribution of species, resulting from a North Atlantic contact in the Eocene. Freitag & Ball (1969) suggested for the ancestor of *Evarthrus* (Coleoptera, Carabidae) an early Tertiary Beringian exchange from Europe/Asia into North America and the subsequent extinction of ancestral stocks in Asia and in western North America. But according to Noonan (in press), it is much more parsimonious to assume that the lineage was once present across Euramerica and was divided when the North Atlantic opened.

The difference between the *dorsalis*-group and all the above-cited examples is that the sister group of the mainly eastern Nearctic *macrocera*-group has an eastern Palaearctic distribution, with only a few (derived) forms in the western Palaearctic. It may have become possible for eastern Palaearctic ancestors to spread into Europe by way of a relatively narrow land connection which was re-established between Siberia and Europe in the Palaeocene, and through this even further across the North Atlantic land continuity which existed until the early Eocene. This was possible also with respect to the climate and vegetation. However, the sister group relatives of the Nearctic *macrocera*-group must then have become extinct in the western Palaearctic. And although the turbulent Cenozoic history of Europe somewhat accomodates this idea, it is remarkable that complete extinction apparently did not happen to the European faunas of all the groups cited above, and according to Savchenko (1983)

complete extinction has not been the case for the Tipulid faunas of Europe. According to Coope (1978) there certainly is no evidence for extinction on a large scale in temperate and cool-temperate groups during the Quaternary, while extinction may be of minor importance during the Tertiary. Milner (1983) discussed the alternative possibility of a Palaeocene 'window', by which cryptobranchid salamanders from Asia could have reached North America via Europe, but rejected it, because no members of the group are recorded from Europe prior to the Oligocene and because this Palaeocene connection between Asia and Europe appears to have been relatively tenuous and intermittent. Savchenko (1983) holds the view that trans-atlantic connections were of minimal importance in the formation of the Palaearctic and Nearctic Tipulid faunas. The endemic distributions of *austriaca* and *helvetica* in Europe do indicate a Tertiary exchange between eastern and western Palaearctic faunas, although much later in time than the developments discussed above (see "the Palaearctic species-groups").

2. *Trans north-pacific (Beringia)*

The second option deals with the spread of ancestral biota from eastern Asia to North America by way of Beringia and the subsequent vicariance of both areas by the appearance of a barrier in Beringia. Although a land bridge between both continents existed during most of the Tertiary, a barrier apparently arose repeatedly to interrupt the faunal exchange across the connection. Simpson (1947) concluded from an analysis of fossil mammal faunas that there was a break in faunal exchange between Eurasia and North America in the middle Eocene and again in middle to late Oligocene. This last break presumably can be attributed to the Bering area. From Oligocene times onward barriers for faunal exchange probably existed several times. Such barriers were climatic rather than physical (Matthews, 1980), for slight (e.g. climatic) obstacles can prevent the spread of some animals for long periods of time (Illies, 1983).

Several examples of a Palaeogene exchange and subsequent vicariance in Beringia can be found in the literature:

Platnick (1976a) explained the distribution of related spider faunas (*Callilepis*, Laroniinae) in North America and Eurasia by the vicariance event of separation of Asiamerica in the Oligocene. Byers (1961) suggested the break up of a widespread range of *Dolichopeza* (Diptera, Tipulidae) in the northern parts of Europe, Asia and North America sometimes in the Oligocene, when the cooling displaced their forests southward. Ball & Negre (1972) postulated for the Nearctic species of *Calathus* (Coleoptera, Carabidae) seven dispersal-waves emanating from the Old World by way of Beringia; the original invaders appeared in the Nearctic in the early to middle Tertiary. Faunal exchanges across a Bering land bridge in the early Tertiary were also supposed for the Odontiinae (Lepidoptera, Pyralidae) by Munroe (1975), the Psylloidea (Homoptera) by Hodkinson (1980), the Fanniinae (Diptera, Muscidae) by Chillcott (1960), the Lucanidae (Coleoptera) by Ratcliffe (1984) and the Chrysolampinae (Hymenoptera, Chalcidoidea) by Darling (1986), all compatible with an interruption of the connection in the Oligocene. Goulet (1983) suggested an extension of numerous temperate Asiatic elements into North America from middle Oligocene until early Miocene in Carabidae (Coleoptera). According to Case (1978) western North American *Rana* diverged in the Oligocene from an Eurasian ancestor which probably crossed Beringia. Milner (1983) supposed the dispersal from Asia to North America over Beringia by the ancestor of two genera of Salamandrids, appearing in the Oligocene and Miocene of North America respectively, which indicates vicariance in about the mid-Oligocene. These examples concern taxa living under warm to temperate conditions. They all are mainly or partly represented in the western Nearctic. A distribution pattern similar to that of the mainly eastern Nearctic *macrocera*-group and her eastern Palaearctic sister group is less easily found in the literature. The following examples comply to this pattern:

Ross (1974) discussed the distribution pattern of a species-group of the Caddisfly genus *Wormaldia*, which is completely eastern Palaearctic with one member in the eastern Nearctic. He explained this pattern by a dispersal from Asia across Beringia, presumably as far east as the Appalachians, a disruption of the intercontinental distribution by the extinction of the widespread ancestor in the northern part of the range and the evolution of the isolated populations. As observed by Patterson (1983) this explanation is vicariance rather than dispersal, although no timing for the sequence of events is specified. Lindquist (1986) mentioned several poorly known taxa of Tarsonemidae (Acari, Heterostigmata), which apparently have disjunct distributions, with one area in south-eastern North America and the other either in Japan, or more widely spread in Eurasia, but no further zoogeographic conclusions were drawn. The floristic affinities between the mixed mesophytic forests of eastern Asia and eastern North America (Graham, 1972; Szafer, 1975) were previously explained as remnants of a Tertiary continuous forest belt in the Northern Hemisphere. However, according to Wolfe (1972) the history of this forest type is much more complex and has developed largely independently in several regions from depauperate late Oligocene vegetation.

Within the Nearctic *macrocera*-group a longest successive series of 12 speciation events in one lineage can be inferred from the cladogram, after the vicariance with the Palaearctic sister group (figs. 5, 6). Given the age of the *dorsalis*-group, the presumed speciation rate and the evolutionary development of the Nearctic stock, the isolation of their ancestor in North America is supposed to have taken place sometime in the early Tertiary. The tropical or subtropical forests occupying Beringia during the Eocene presumably were unsuitable for the (warm)temperate members of the *dorsalis*-group. The temperate forests found in large regions of the Northern Hemisphere after the late Eocene cooling, presumably facilitated the extension of the range of the ancestor of the

Nearctic group from Asia over the land bridge into the New World, probably a transcontinental extension up to the eastern side. Savchenko (1983) also considered a faunal exchange of warm-temperate Tipulid faunas in Beringia in the early Oligocene possible. During the early Oligocene, the Cordillera System was already formed from Yukon to Mexico, and although the mountains were not nearly as high as at present, they may have prevented the expansion of the range to the south-western part of the continent. A vicariance of Palaearctic and Nearctic faunas in middle to late Oligocene may be inferred from several examples in the literature. Whether or not a physical barrier in Beringia was involved, the isolation of both faunas was intensified by the mid-Oligocene spreading of drier and colder climates, which restricted the formerly continuous temperate sclerophyllous vegetation (and with that possibly also the members of the dorsalis-group) to the Appalachian area and the west coast (where it was exterminated later, Axelrod, 1975). Subsequent events which prevented members of the group from spreading south-westward and forced them into eastward direction or eliminating them from the western parts may have been: the strong decline in summer temperatures in mid-Miocene Beringia and northern Alaska, which made this area unsuitable for the temperate members of the dorsalis-group and the increasing aridity that spread to the whole western part of the continent in the late Tertiary, changing deciduous forests into (semi)deserts (see "Floristic History").

I therefore postulate the Beringian vicariance of Palaearctic and Nearctic stocks of the dorsalis-group and the transcontinental crossing of the last one across the northern Nearctic in middle to late Oligocene, after which faunal expansion and subsequent speciation occurred at the eastern side of the continent.

THE PALAEARCTIC SPECIES-GROUPS

As already mentioned, the origin of the dorsalis-group has to be sought in the eastern Palaearctic, presumably in the early Tertiary. 27 Species are known from the Palaearctic region and all belong to exclusively Palaearctic groups, except ramulifera which is also known from Alaska, and sublunulicornis, a member of the otherwise completely Nearctic macrocera-group. While much zoogeographic literature is available for the Nearctic region, much less is available for the eastern Palaearctic region, as also observed by Noonan (1986). Many papers about organisms of the eastern Palaearctic (cf. De Lattin, 1967; Varga, 1977; Oosterbroek, 1980) focussed on the glacial history, while others (Savchenko, 1973; Beschovski, 1984) lacked a cladistic analysis. A valuable, general zoogeographic paper about Palaearctic Tipulidae is the one by Savchenko (1983). In his paper Savchenko described 14 fundamental zoogeographic complexes of Palaearctic Tipulidae, defined as associations of forms convergently adapted to life conditions, with identical ecological potency as well as similar geological age, geographic origin and taxonomic relationships. In the discussion below reference will be made to the following complexes:

1. The Central Asian complex consists of species inhabiting the central Asian mountain regions. It is dominated by unspecialized elements, dates back to the Upper Palaeogene and is considered to be in a more or less relict state.

2. The Palaearchaearctic complex is composed of zoogeographic elements from east and central-east Asia. In historical aspect it is an intermediate between the Oriental and Boreal zoogeographic complexes and dates back to the Miocene or even the Oligocene. It is ecologically related to hygrophylous or mesophytic environments.

3. The Boreal complex can be considered as a continuation of the Palaearchaearctic complex and has changed in the direction of a higher specialization. It is related to the temperate forests and forest-steppes and has its origin in the late Miocene.

The dorsalis-group (as well as the genus Nephrotoma) is thought to have originated and

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differentiated in the eastern Palaearctic, and the same is supposed for many other Tipulid taxa, such as the Ctenophorinae and many subgenera of *Tipula* (Theowald & Oosterbroek, 1983). The ancient Angara (central Asia today) was considered to have had favourable conditions for faunal evolution for millions of years and a great influence on the present fauna of the Palaearctic (Warnecke, 1958; Povolný, 1966). A uniform vegetation suitable for Tipulids existed in large parts of Angara in the Oligocene, together with the conditions for a zonal differentiation of the fauna, which also counted for the mountain-areas of Angara and the north-eastern Bering-area (Savchenko, 1983). A first differentiation of the temperate *dorsalis*-group in the ancient Angara in the late Eocene/early Oligocene seems to fit with the contemporary cooling and development of deciduous forests in this area and with the distribution of the phylogenetically old *pamirensis-nigricauda*-groups.

Species such as the members of the *pamirensis*-group (fig. 3, map 3), all montane species, are considered by Savchenko (1983) as part of the Central Asian Tipulidae complex which has its roots in the Upper Palaeogene. They all have very limited distributions in the central Asian mountain areas: the Pamir-region (*pamirensis* and *pjotri*), the Min-shan Mountains (*perobliqua*), the Tuva region (*violovitshi*) and the Himalaya (*libra*); according to Varga (1977) representing a state of refugial isolation. The members of its sister group (fig. 3, map 3) are distributed in the Himalaya (*kaulbacki*) and Japan (*electripennis* and *nigricauda*). The phylogenetically oldest species of each group, *libra* and *kaulbacki*, are both endemic to the Himalayas, and their origin may be related with the Himalayan Orogeny which had its most intense phase in the middle Miocene. The vicariance event which separated the Japanese species *electripennis* and *nigricauda* from their continental sister species *kaulbacki*, must have been
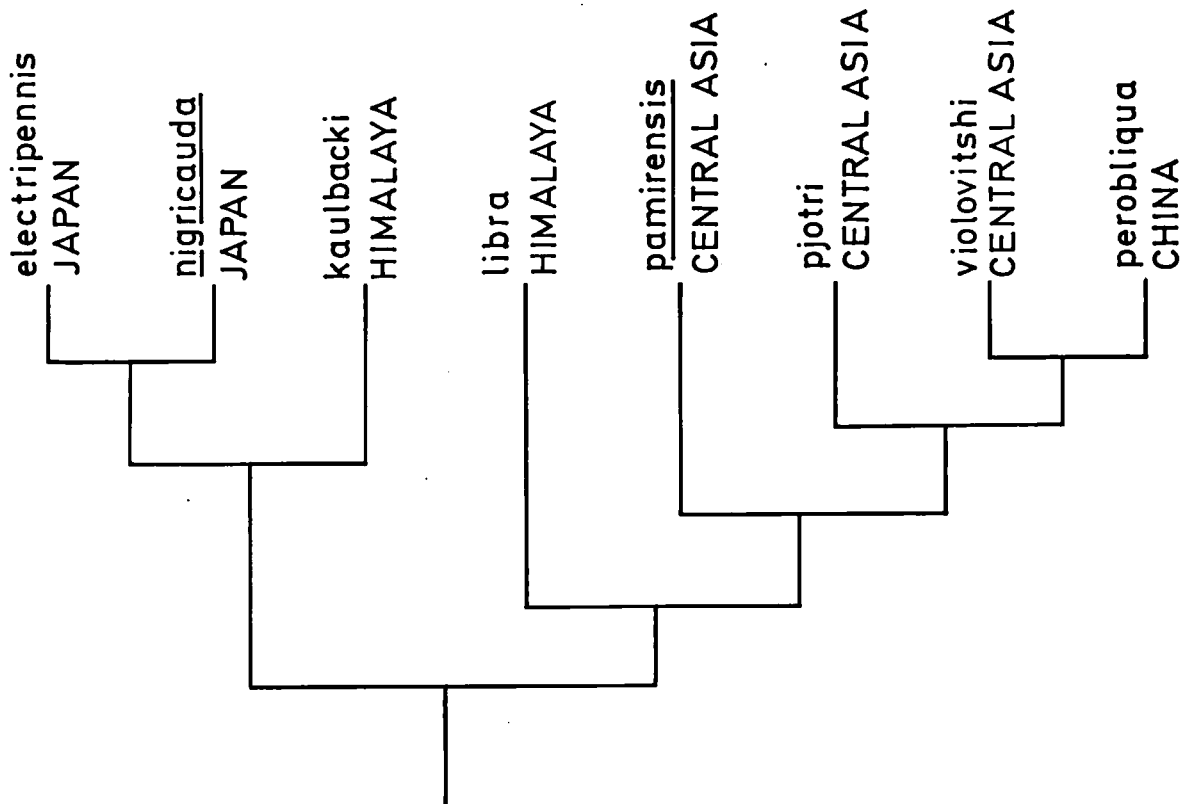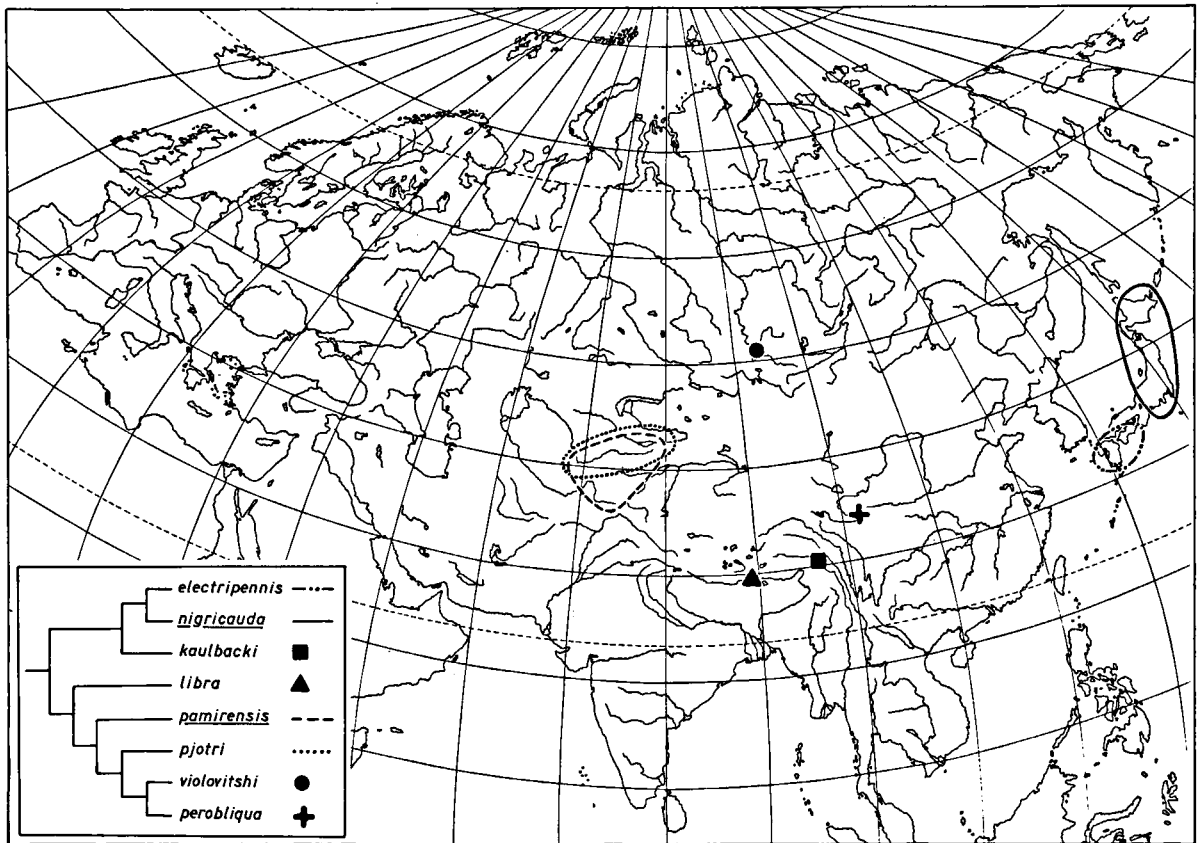

Fig. 3. Cladogram of the *nigricauda*-group and the *pamirensis*-group.

Map 3. Distribution of the *nigricauda*-group and the *pamirensis*-group.

the formation of the Japanese Sea in the Oligocene/early Miocene which caused increasing insularity of Japan in the mid-Miocene. *N. violovitshi* may be a Tertiary relict from the Tuva region, probably ranging back to the early Pliocene or even Miocene (Savchenko & Violovich, 1967).

N. ramulifera is a phylogenetically old boreal species from tundra and mountain-steppe, the sister species of all the remaining species-groups (fig. 2). Its evolution must have been associated with the development of steppe floras and tundra, from late Miocene/Pliocene onward. The species presumably spread from the eastern Palaearctic to the west in the Pleistocene, or somewhat earlier. The distribution of tundra elements, and that of *ramulifera* too (map 6), is disjunct because the tundra suffered from a strong suppression to the north and a narrow-

ing of its living area in the Postglacial (De Lattin, 1967; Varga, 1977). Extension of the range of *ramulifera* into the extreme north-western Nearctic across Beringia most probably occurred during the last glaciation, parallel with the extension of the Nearctic *occipitalis* into Siberia (see next chapter).

The sister group of the Nearctic *macrocera*-group is composed of the *dorsalis*-group s.s., the *lunulicornis*-group, the *scurra*-group and *austriaca* (fig. 2). Within these three species groups the same (reduced) zoogeographical pattern can be observed. Fig. 4 shows the reduced area-cladograms of the three groups (using the methodology of Allen, 1983: taxa and areas outside the regions concerned are indicated by dashed lines and identical areas that are juxtaposed to one another in a single monophyletic lineage are combined). It seems likely to pro-
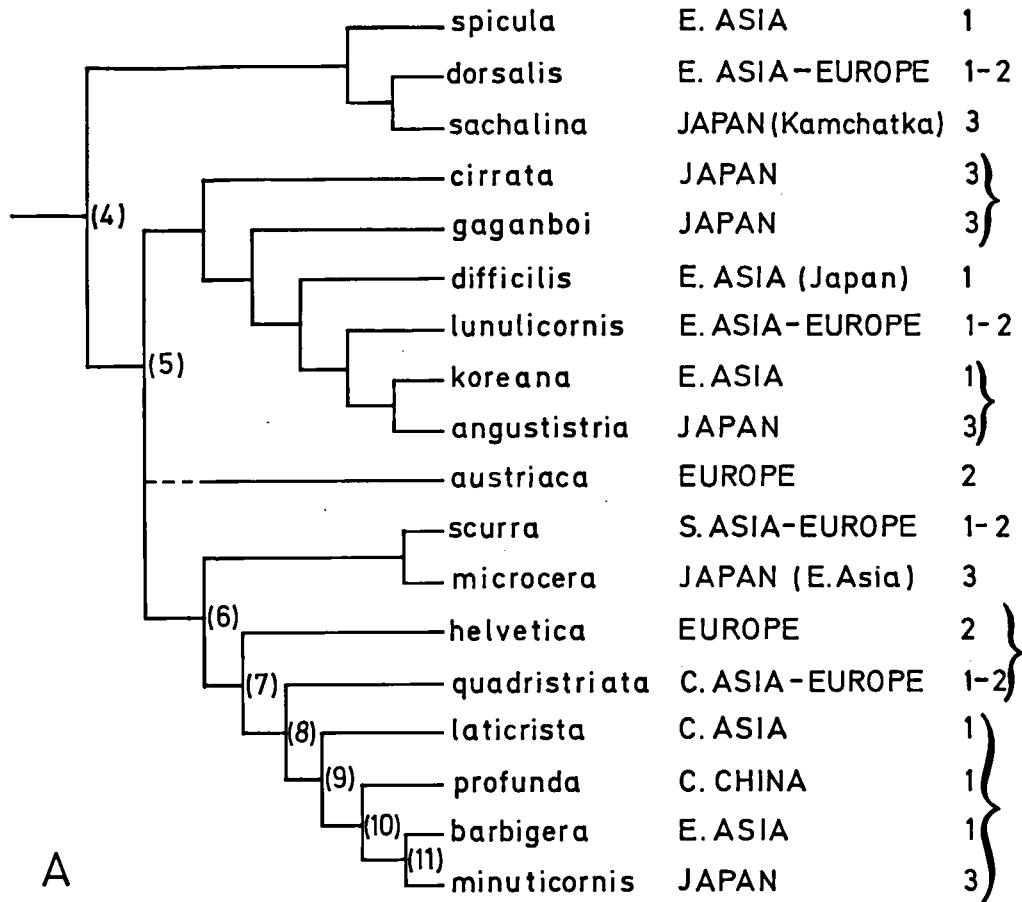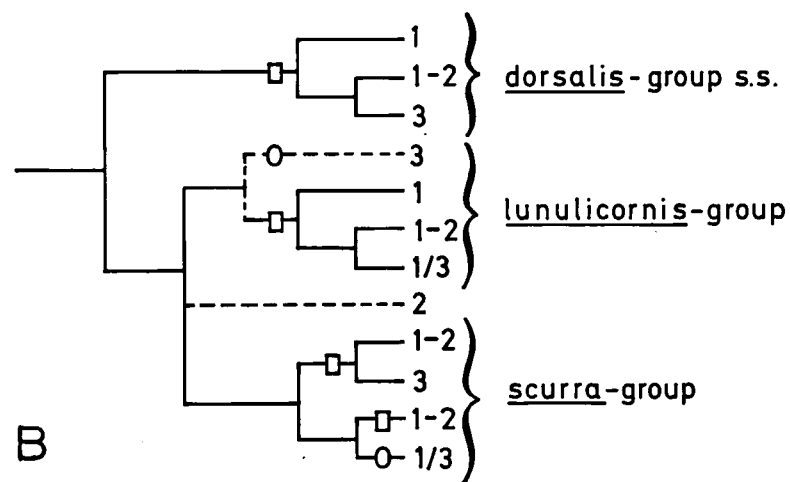
Fig. 4. A: Cladogram of the Palaearctic *dorsalis*-group s.s., *lunulicornis*-group, *austriaca* and *scurra*-group. B: Reduced area cladogram of the same groups. 1 = Asia (continental), 2 = Europe, 3 = Japan. O = Palaearchaearctic lineage, □ = Boreal lineage. Numbers between brackets indicate successive speciation events in a single lineage. For further explanation see text.

pose that the same palaeogeographic events are responsible for the parallel developments within these groups.

The east Asia-Eurasia-Japan pattern (1/1-2/3' in fig. 4) is clear within the three closely related species of the *dorsalis*-group s.s. and the four derived, also closely related, species of the *lunulicornis*-group. Within the *scurra*-group the Eurasia-Japan lineage (1-2/3 in fig. 4) is formed by the closely related sister species *scurra* and *microcera*, while the other lineage shows a different Eurasia-central and east Asia pattern (1-2/1 in fig. 4). The species of these (east Asia)-Eurasia-Japan lineages mainly can be considered as part of the Boreal complex as defined by Savchenko (1983), who dated it back to the late Miocene. Its development parallels the ecological changes in forest-types within temperate latitudes of Eurasia. Their sister lineages can be considered as part of the Palaearchaearctic complex (*cirrata, gaganboi*), of which the age is dated back to the Miocene or even the Oligocene (Savchenko, 1983), or as part of the mixed Palaearchaearctic/Boreal complex (*helvetica* up to *minuticornis*). The separation of both lineages and the development of the (east Asia)-Eurasia-Japan complexes presumably were correlated with a differentiation in ecological requirements, which may have been associated with the mid-Miocene cooling and allied appearance of lowland boreal forests in Asia. Brown (1987) recognized species pairs consisting of a deciduous forest and a boreal forest member in Nearctic Phoridae (Diptera). The three Eurasian species (*dorsalis, lunulicornis* and *scurra*) are abundant and widely distributed because of a wide ecological tolerance, which enabled them to spread into Japan when the circumstances were allowed. Such an expansion from the Asian mainland into Japan was not possible from the early to middle Miocene, when the Japanese Sea was formed, until the Pleistocene glaciations, when repeated lowering of the sealevel restored the connection between eastern Asia and Japan (De Lattin, 1967). So the vicariance of the Eurasian and Japanese species most probably is of Pleistocene age. In all three

cases it concerns very closely related sister taxa (*dorsalis/sachalina*; *lunulicornis/angustistria-koreana*; *scurra/microcera*).

Within the *dorsalis*-group s.s. (fig. 4), the east Asian lineage is formed by *spicula*, distributed in North Korea, Primorye and eastern Manchuria. The Eurasian species is the disjunct *dorsalis* and its sister species the Japanese *sachalina*, also occurring in Sakhalin and the Kuril Islands, and which presumably recently has extended its range towards Kamchatka (map 4).

The Palaearchaearctic lineage of the *lunulicornis*-group (fig. 4) is composed of the two Japanese species *cirrata* and *gaganboi*. Their isolation in Japan must have preceded the development of the Boreal complex, and is considered to be related to the forming of the Japanese Sea and the increasing insularity of Japan in the middle Miocene.

The Boreal lineage is formed by four closely related species: the eastern Palaearctic *difficilis*, the disjunct Eurasian *lunulicornis* and the sister species *angustistria* (Japan) and *koreana* (Korea, Primorye and eastern Manchuria) (map 4). The speciation events within this subgroup have to be of late Pliocene and Pleistocene age, because the last two dichotomies are related to the alternating connections between Japan and the mainland during the Pleistocene glaciations.

The Boreal lineage of the *scurra*-group (fig. 4) comprises only the Eurasian *scurra* and the Japanese *microcera*; the latter having extended its range into Korea presumably during one of the last glaciations (map 5). The mixed Palaearchaearctic-Boreal lineage of the *scurra*-group comprises four eastern Palaearctic species, while an Eurasian species (*quadristriata*) and an European endemic (*helvetica*) form the first branchings (fig. 4). Another European endemic (*austriaca*) forms an unresolved trichotomy with the *lunulicornis*- and *scurra*-groups (fig. 4). All three belong to the Boreal complex, so they are supposed to have developed more or less in parallel with the other Boreal Eurasian species. The four remaining species of the Palaearchaearctic lineage are
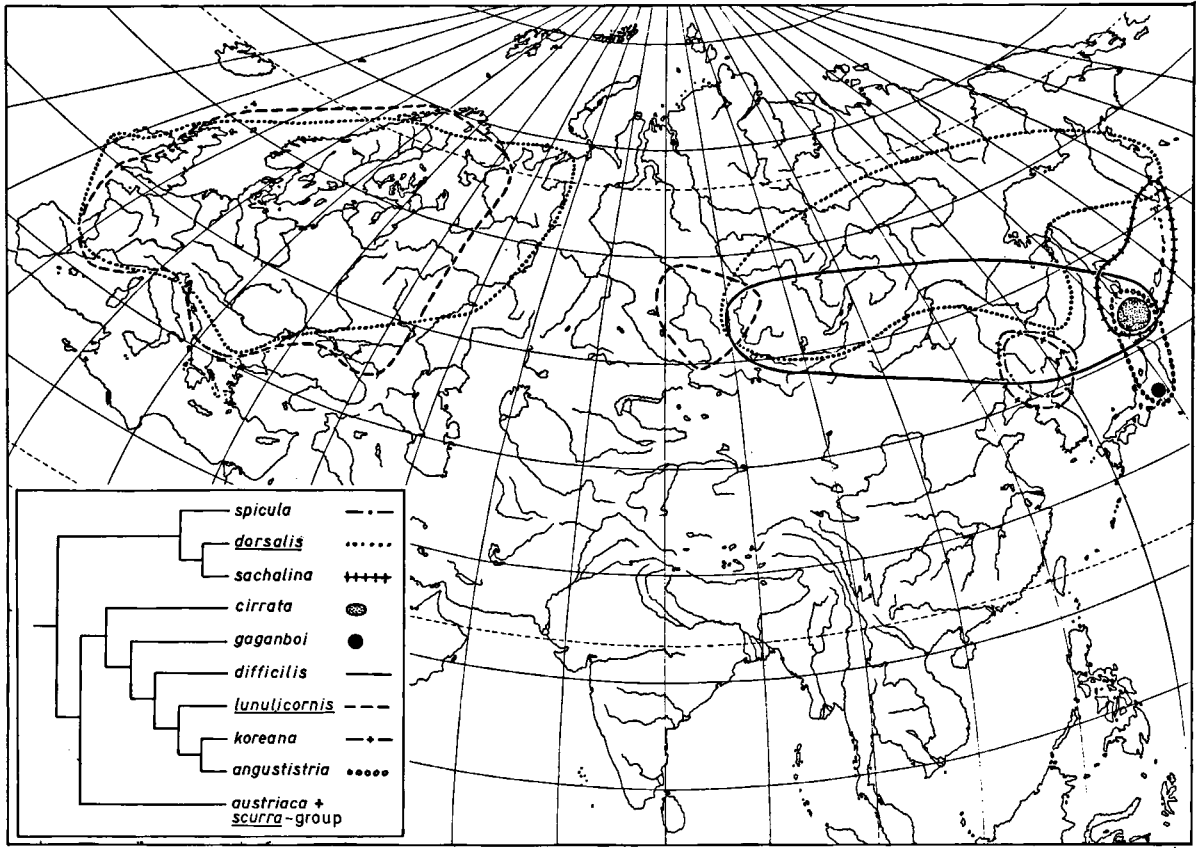
Map 4. Distribution of the *dorsalis*-group s.s. and the *lunulicornis*-group.

disruptedly distributed in the eastern Palaearctic, from southern Siberia (Kirkiz SSR, *laticrista*) and central China (Sichuan, *profunda*) to central and east Siberia (*barbigera*) and Japan (*minuticornis*) (map 5). The vicariance between *barbigera* and *minuticornis* presumably is of Pleistocene age.

Europe is depauperate in species of the *dorsalis*-group, both in endemic species (2) and in transcontinental ones (5). This may be explained by the relatively late arrival of the group in Europe, and the more or less destructive effects of the Pleistocene glaciations.

An expansion of the fauna from Asia into Europe was possible after the restoration of the land connection between both continents in the late Oligocene. However, the formation of a common Tipulid fauna for Eurasia presumably started in the Miocene, when the European

islands were united and rich deciduous forests became indigenous in the western Palaearctic (Povolný, 1966; Savchenko, 1983; Theowald & Oosterbroek, 1983). A subsequent separation of Asian and European biotas in the Miocene is suggested by Allen (1983) from the distribution-patterns of several Arthropods. The spread of boreal species to Europe presumably paralleled the formation of boreal forests at temperate latitudes in Eurasia in the late Miocene/early Pliocene (Savchenko, 1983). The only two European endemics, *austriaca* and *helvetica*, both have a limited distribution in the Alpine region (map 5). According to Theowald & Oosterbroek (1985) there are only a few western Palaearctic montane species belonging to eastern Palaearctic groups and they suppose a northern tundra/taiga route to Europe for these species. A late Miocene or early Pliocene

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arrival in Europe is supposed for the ancestors of both alpine species, and their development may be related to the Pliocene uplift of the central Alps (*helvetica*) and the Carpathians (*austriaca*); old elements of the central European fauna are presumed to have inhabited this territory since the end of the Tertiary (Povolný, 1966; Savchenko, 1983). The extension of favourable habitats between Europe and central and east Asia was broken several times in the late Pliocene and Pleistocene because of a drying and cooling (Beschovski, 1984) and the alternating efficiency of the West Siberian barrier (Theowald & Oosterbroek, 1983). The spread of the boreal Eurasian species of the *dorsalis*-group s.l. from the eastern Palaearctic to Europe presumably occurred in the Pleistocene, but before the last glaciation (Theowald & Oosterbroek, 1983).

The east-west Palaearctic disjunctions shown by three out of the four Eurasian species (*dorsalis*, *lunulicornis* and *quadristriata*, while the range of *scurra* is more or less continuous, maps 4, 5) must be the result of the West Siberian barrier during the last glaciation. Four other *Nephrotoma*-species outside the *dorsalis*-group show this pattern of disjunction (Oosterbroek, 1980). They survived the Würm glaciation in both an eastern and western Palaearctic refugium and their transpalaearctic ranges may be considered polycentric (Varga, 1977; Oosterbroek, 1980; Theowald & Oosterbroek, 1983, 1986). There are no morphological differences between the disjunct populations. It is rather unlikely that the continuous transpalaearctic species *scurra* spread to Europe from an eastern centre during the Postglacial period (Theowald & Oosterbroek, 1983).
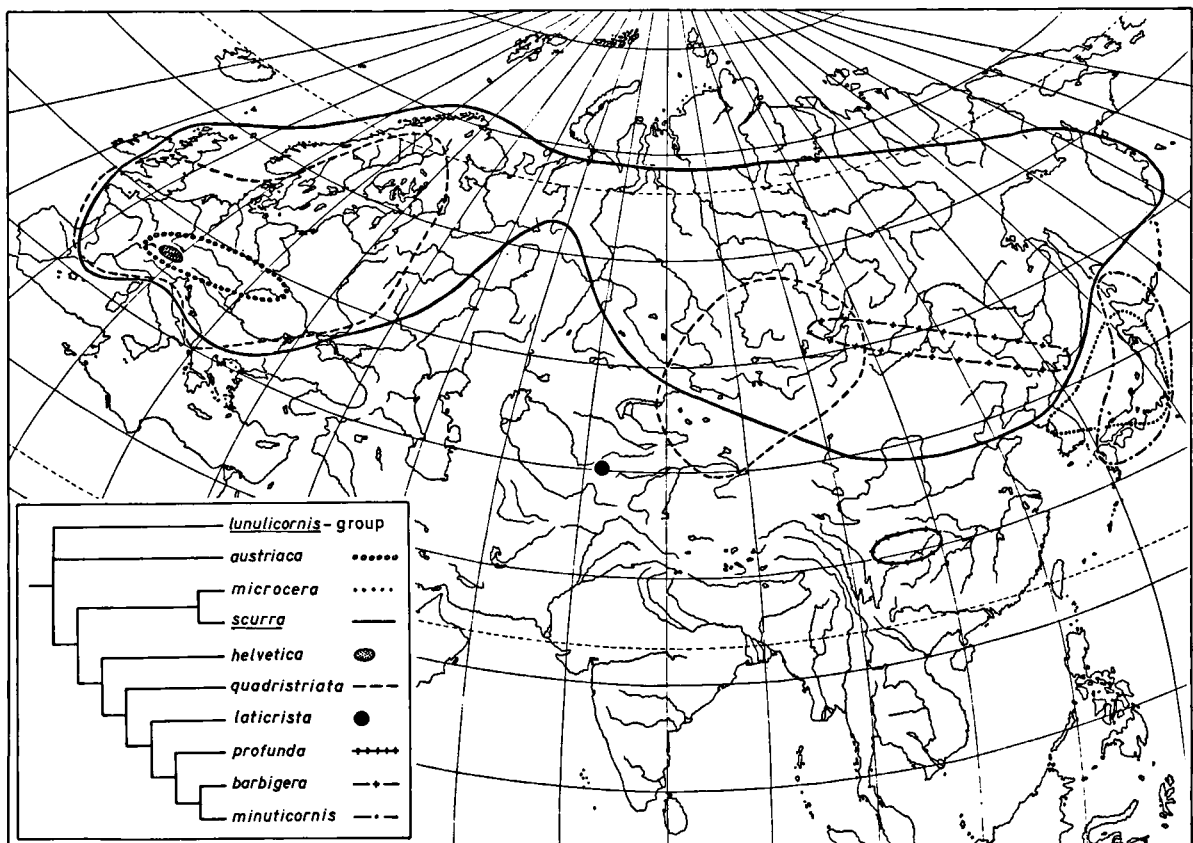
Map 5. Distribution of *austriaca* and the *scurra*-group.

Presumably the euryecious *scurra* was already able to fill the gap. The old and rather low Ural Mountains presumably did not affect the *dorsalis*-group, either as a cause of isolation, or as a barrier for expansion.

According to Savchenko (1973, 1983) the Eurasian fauna experienced profound changes at the end of the Neogene, which he termed a time of crisis in the history of the temperate latitudes of Eurasia. In contrast with North America, the Tertiary faunal diversity, including the genus *Nephrotoma*, was strongly impoverished in Europe and northern Asia; there surely was not complete extinction, but rather a shift in composition and location. Several authors have supposed large-scale extinctions and extensive speciation during the Pleistocene glacial-cycles (Warnecke, 1958; Povolný, 1966; De Lattin, 1967; Oosterbroek, 1980; Theowald & Oosterbroek, 1983, 1985). This contrasts with the conclusions of, for example, Coope (1970, 1978) and Matthews (1977) from the fossil record, that there is no evidence of any morphological evolution during the last half million years at least and that extinction played a very minor part in the development of our present day insect fauna. However, this accounts for faunas of the temperate and cool Northern Hemisphere, while the picture for more southerly distributed groups may be different (Oosterbroek, 1980). Within the *dorsalis*-group, the speciation rate was not perceptibly accelerated because of the glacial periods; the number of new Pleistocene species more or less equals the expected speciation over this period of time. Thus, although extinction may have been a certain factor in minimizing the *dorsalis*-group in Europe, the Pleistocene glaciations probably did not play a dominant part, either in creating new species, or in causing large scale extinction. The influence on the entomofauna of Siberia was probably even slighter (Savchenko, 1983).

The effects of the Pleistocene glaciations on the distribution ranges of the species of the *dorsalis*-group can be summarized as follows:
1. The already discussed disjunction of the Eurasian species, which are all considered polycentric. After the last glaciation the species occupied Europe from the Balkan Peninsula refugium (Theowald & Oosterbroek, 1983).
2. An extension of the range from Japan to the mainland (Korea) by *microcera* and the reverse, from the mainland to northern Japan and Sakhalin by *difficilis*, probably during one of the last glacial periods.
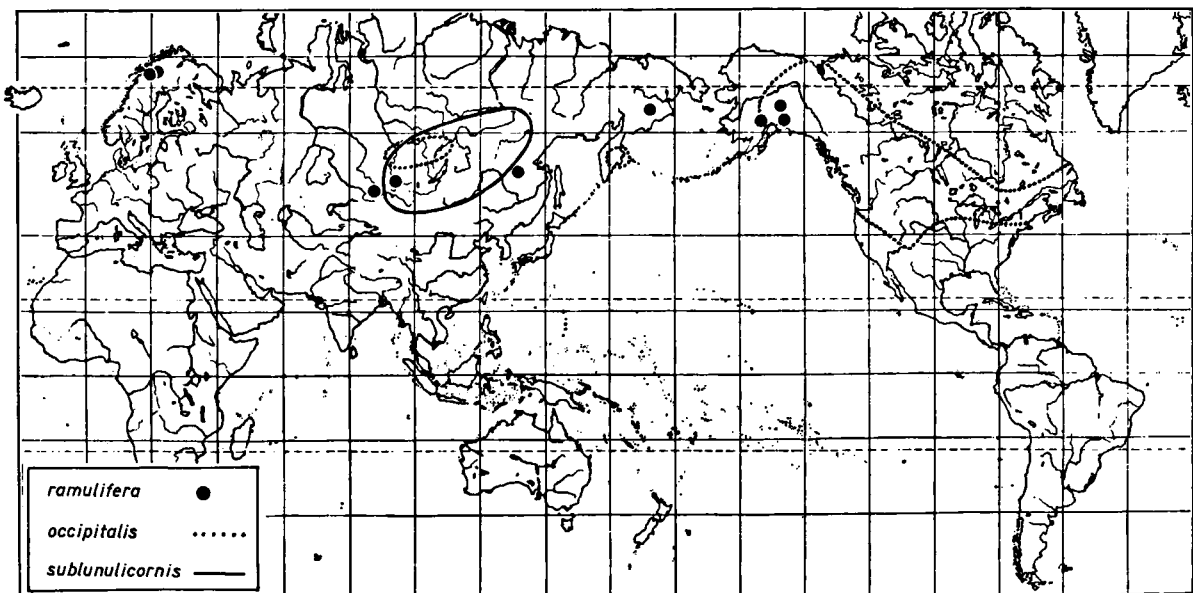
Map 6. Distribution of *ramulifera*, *occipitalis* and *sublunulicornis*.

3. The retraction of species into refugia; many oreal and oreotundral species still are in a state of refugial isolation (Varga, 1977); for the *dorsalis*-group apparent in *kaulbacki, libra, pamirensis, pjotri, violovitshi, perobliqua, ramulifera, austriaca, helvetica* and *laticrista*.

4. Finally the exchange of cold-resistant elements across Beringia, including the extension from north-east Siberia to Alaska by *ramulifera* and the reverse from North America to east and central Siberia by *occipitalis*.

THE NEARCTIC *MACROCERA*-GROUP

Up to now 37 species of *Nephrotoma* are recorded from the Nearctic region, 20 of them belonging to the *dorsalis*-group and all except *ramulifera* being part of the *macrocera*-group (Tangelder, 1983), while the remaining 17 are members of 7 other species groups (Oosterbroek, 1984). The *dorsalis*-group thus may be considered the most diverse and possibly one of the oldest species-groups of *Nephrotoma* in the Nearctic. As seen in the previous chapter, the ancestor of the *macrocera*-group was probably isolated in North America in middle to late Oligocene. Given the distribution of the nearctic species: all except the most derived *occipitalis*-group ranging into or confined to the eastern part of the continent, we can state that most evolutionary radiation took place and presumably is correlated with palaeogeographic events in this part of the continent.

Because of extensive sympatry (cf. Lafontaine, 1982) it is impossible to trace and date all the individual speciation events responsible for the origin of most of the eastern species. The original distribution ranges have been strongly influenced by the effects of the Pleistocene Ice Ages, which caused alteration of the geographical ranges possibly on an enormous scale as shown by the fossil record (Coope, 1978; Morgan & Morgan, 1980) and by the sweeping clean of large areas by the ice. Even so, according to Savchenko (1973) the genus *Nephrotoma* preserved practically its total Tertiary diversity in North America. Belicek (1976) also concluded that the influence of the

Pleistocene glaciations on the composition of the (Coccinellid) fauna of North America was relatively insignificant, but that the effects on distribution were profound. All species of the Nearctic *macrocera*-group are largely or partly distributed on previously ice-covered land (maps 7-12), except four south-eastern species (ice-limits according to Prest, 1969, map 7).

Vicariance events which led to speciation in the eastern Nearctic are possibly related to Tertiary events such as the fluctuations of epicontinental seas in the south-eastern United States, the encroaching seas which sporadically filled the Hudson Bay, orogenic activity in the Appalachian system and climatic and vegetational changes, and to some extent possibly the Pleistocene events. Similarly, Freitag & Ball (1969) suggested that the history of *Evarthrus* (Coleoptera) is related to the geological and biotal history of eastern North America. Ross & Ricker (1971) supposed the evolution of the entire sequence of ancestral types of *Allocapnia* (Plecoptera), with a minimum of 8 speciation-pulses, in the Appalachian System. According to Campbell (1980) and others (Freitag & Ball, 1969; Coope, 1970, 1978; Matthews, 1977) their is no evidence of Pleistocene speciation in any group of north temperate or arctic Coleoptera. As concluded for the beetle fauna by Campbell (1980), the *dorsalis*-group is depauperate in the arctic, possibly because they already completed their latest major speciation in the late Tertiary at a time when the tundra was just evolving and spreading. Few dichotomies in the cladogram can be correlated with concrete palaeogeographic events, while many biogeographical conclusions cannot predate the Pleistocene glaciations because of their profound influence, especially the last one which more or less obliterated the effects of the previous ones (Dosdall & Lehmkuhl, 1979).

The phylogenetically oldest member of the Nearctic group, *sodalis* (fig. 5), has a transcontinental distribution in the northern United States and Canada, with southern extensions in the Rocky Mountains and the Appalachians (map 7). It may be considered a species with less restricted ecological requirements, which is
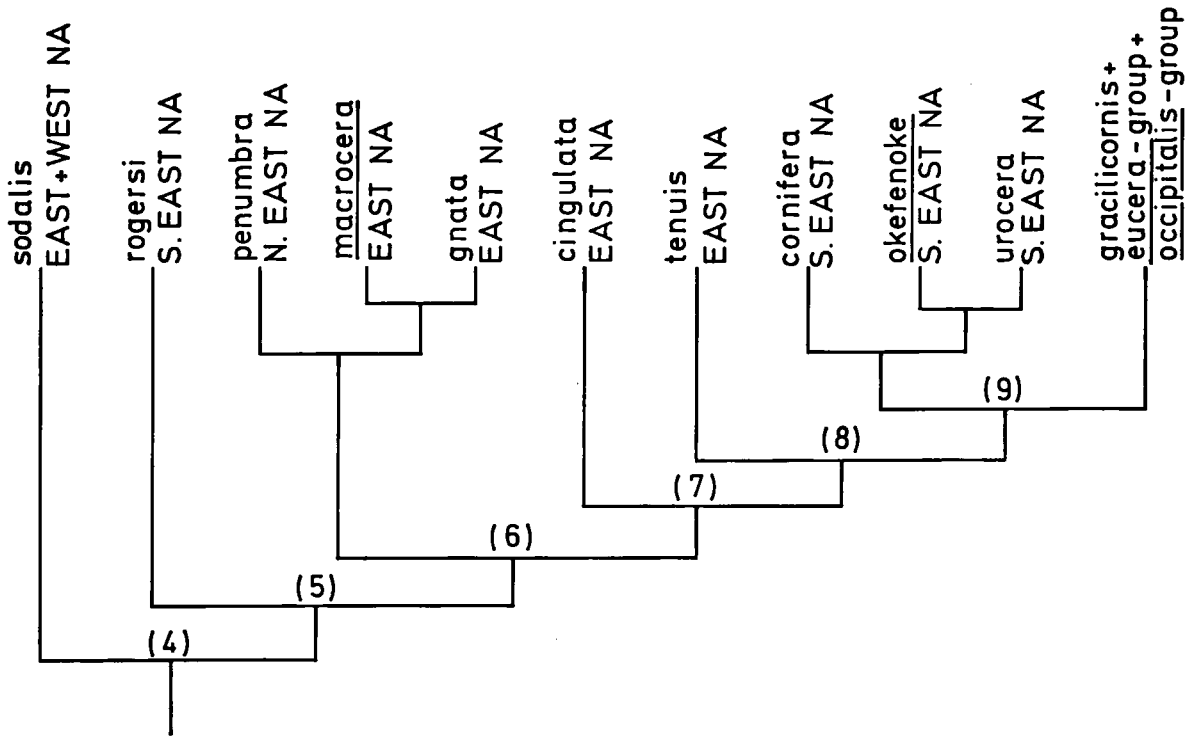
Fig. 5. Cladogram of the Nearctic *macrocera*-group, first part.
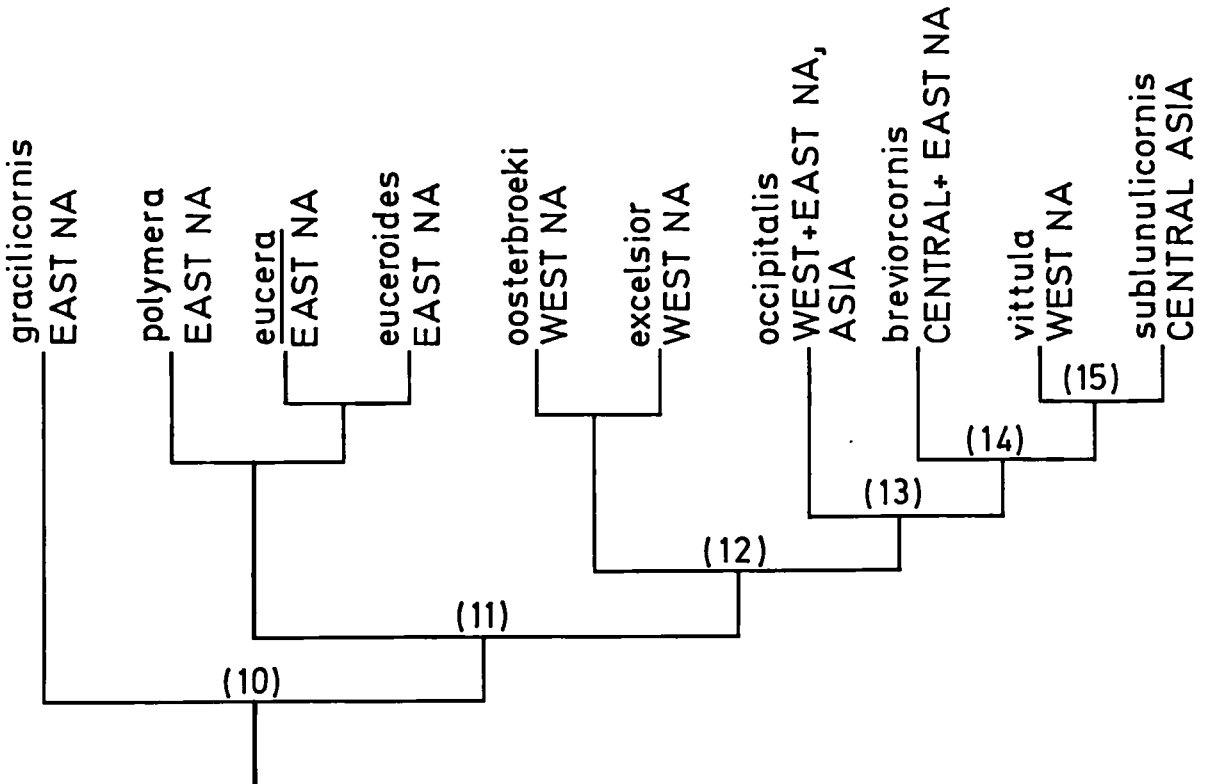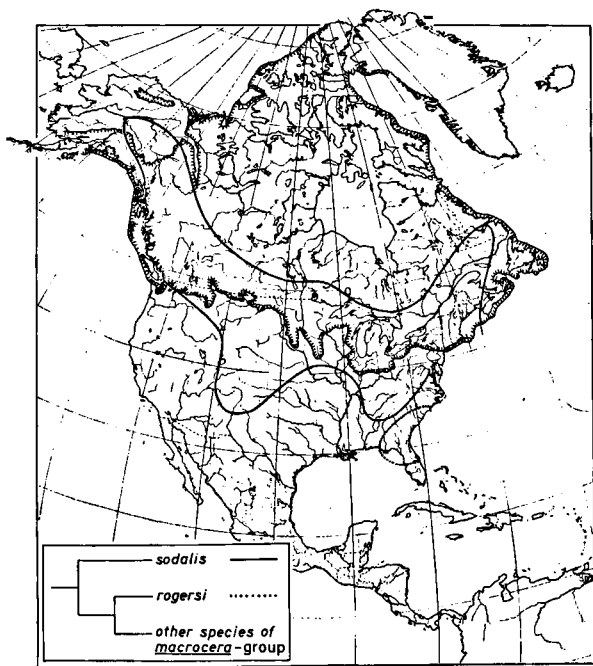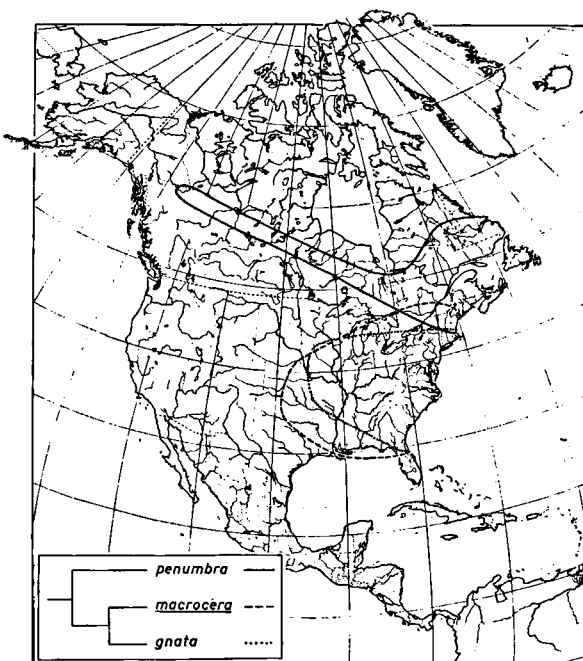

Fig. 6. Cladogram of the Nearctic *macrocera*-group, second part. Numbers indicate successive speciation events in a single lineage. NA = North America.

able to occur in a combination of range types (Campbell, 1980), namely the boreal, eastern and Cordilleran ranges as defined by Munroe (1956). All the north-western localities (except one in Alaska) are situated in previously ice-covered areas, indicating that the range was essentially eastern and possibly Cordilleran, and that the boreal transcontinental distribution apparently is a post-glacial acquisition, derived from southern refugia in east and west (Larson, 1975; Dorsdall & Lehmkuhl, 1979). *N. sodalis* is thought to have originated in the eastern part of the continent, as is presumed for most species of the *macrocera*-group. They largely fit the eastern ranges described by Munroe (1956) as related to the deciduous forest formation.

Both the phylogenetically old *rogersi* as well as the derived *okefenoke*-group (3 species) (fig. 5) occur in the south-eastern United States including Florida (maps 7, 10). Their speciation may be related to the Tertiary and Pleistocene transgressions in this area, as also thought by Roughly & Pengelly (1981) who


Map 8. Distribution of the *macrocera*-subgroup.

related the vicariance of two south-eastern species of Dytiscidae (Coleoptera) to these sea-level fluctuations in the Pliocene and Pleistocene. Speciation within the *okefenoke*-group possibly took place in Florida refugia during (early) Pleistocene interglacials, when Florida was isolated from the mainland by water barriers, as also supposed by Freitag & Ball (1969) for *Evarthrus*-species (Coleoptera, Carabidae).
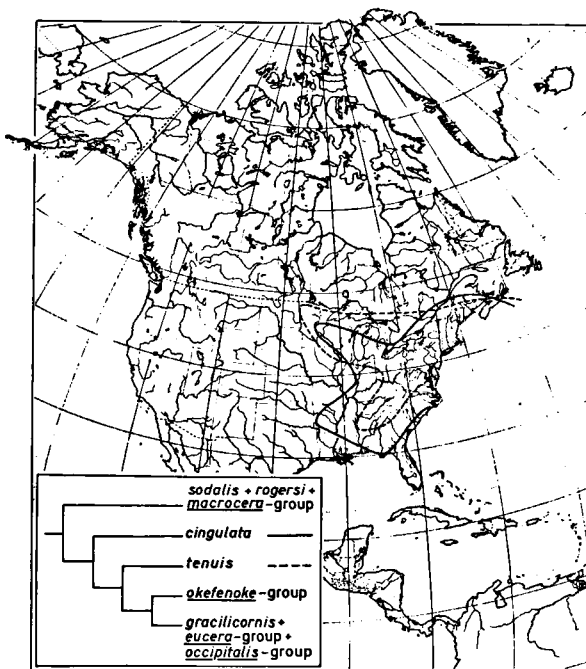
The range of *penumbra* is completely situated on previously ice-covered land (map 8). It resembles more or less the subarctic north-eastern range described by Munroe (1956) and Campbell (1980), who postulated an off-shore eastern coastal refugium on the emergent continental shelf. The remaining eastern species (*macrocera, gnata, cingulata, tenuis, gracilicornis* and the *eucera*-group, 3 species) are all largely sympatric (maps 8-11); their speciation presumably is correlated with orogenic events in the Appalachian system (most intense in the Pliocene), and the considerable changes in climate and vegetation during the Tertiary. They must have survived glaciations in the south-eastern United States, where a con-

Map 7. Distribution of *sodalis* and *rogersi*. Shaded line indicates the maximum extent of the Wisconsin Ice, after Prest (1969).

siderable intrusion of northern species occurred during the glacial maxima, particularly along high elevations in the Appalachians (Campbell, 1980). All are known from localities in the southern Appalachians, and especially the ranges of *tenuis* (map 9) and *euceroides* (map 11) stretch southward along the axis of the eastern mountain chains. *N. macrocera* and *gnata* are closely related and morphologically only slightly different species. However their present sympatry (map 8) indicates that their differentiation occurred before Recent times.
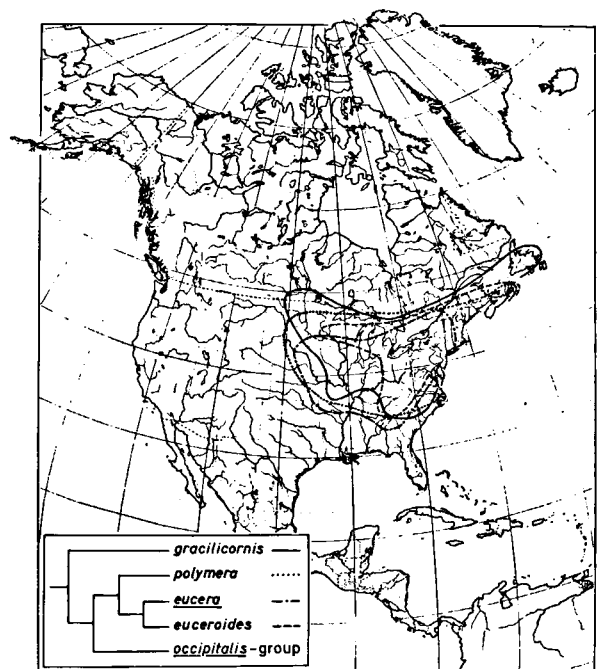
.The *occipitalis*-group, the most derived Nearctic species-group (fig. 6), is the only one with members distributed in the western part of the continent. They all occur in the Rocky Mountains and/or Cascade Ranges, while two species (*occipitalis* and *breviorcornis*) also extend to the eastern parts (map 12). The ancestor of this group probably became isolated in the western cordillera region and separated from the eastern sister group (the *eucera*-group) by the development of grassland in the interior part of North America in middle to late Miocene. Erwin & Kavanaugh (1981) also concluded that the

cornifera ——
okefenoke —·—
urocera ······
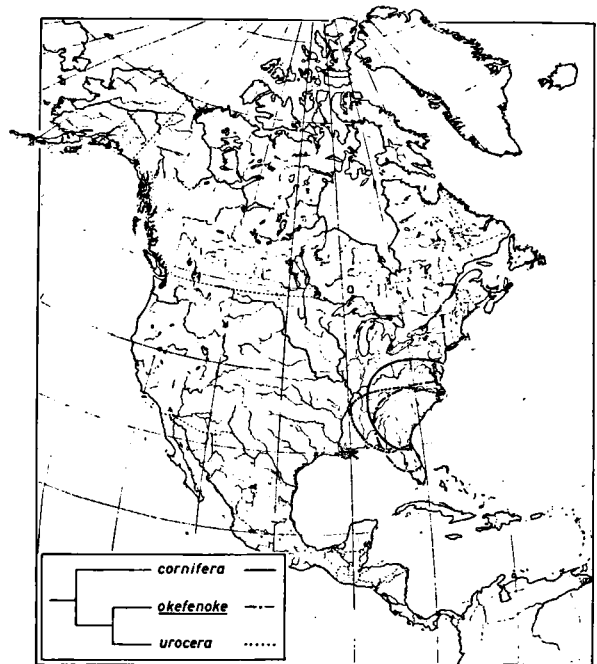
Map 10. Distribution of the *okefenoke*-group.

sodalis + rogersi +
macrocera-group
cingulata ——
tenuis ————
okefenoke-group
gracilicornis +
eucera-group +
occipitalis-group

Map 9. Distribution of *cingulata* and *tenuis*.

gracilicornis ——
polymera ······
eucera —·—
euceroides ———
occipitalis-group

Map 11. Distribution of *gracilicornis* and the *eucera*-group.

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western Nearctic *erasum*-group (*Bembidion*, Coleoptera, Carabidae) arose in that region no earlier than in Miocene time, in association with general cooling trends and contemporary orogenic events. Subsequent speciation may be related to the orogeny in the Rocky Mountains during the Miocene, Pliocene and early Pleistocene.

One member of the *occipitalis*-group, *sublunulicornis*, the sister species of the Cordilleran *vittula* (fig. 6), has its range in central Asia (map 6). This is assumed to be the result of expansion of the range of their common ancestor across Beringia and the subsequent vicariance by opening of Bering Strait about 3.5 million years ago (Hopkins, 1967). Several authors have suggested a faunal exchange across Beringia and subsequent speciation of sister taxa in the (late)Pliocene, such as Ball (1966), Ball & Negre (1972) and Goulet & Smetana (1983) (all Coleoptera, Carabidae), Clark (1978) and Bajtenov (1982) (both Coleoptera, Curculionidae), Chandler (1982, Coleoptera, Anthicidae) and O'Hara (1982, Diptera, Tachinidae).

Plotting the distributions of the Nearctic *occipitalis*-group on a single map (map 12) reveals that the small area of overlap of 4 out of the 5 component species is situated in the central Rocky Mountains (Colorado and Wyoming). This probably indicates the region of the Wisconsinan refugium for the members of this group. The distributions of *excelsior* and *vittula* cover an elongate area across the Rocky Mountains from Colorado northward to south and eastern Alaska. This distribution type, called 'extended Cordilleran range' by Munroe (1956), was also recognized in for example Trichoptera (Nimmo, 1971), Coleoptera (Coccinellidae, Belicek, 1976; Carabidae, Kavanaugh, 1980) and Lepidoptera (Pike, 1980; Lafontaine, 1982), and an external refugium south of the ice was suggested as the source area for species with this distribution type. These species spread northward as suitable habitats became available as the ice retreated. The presence of those taxa in the southern Rocky Mountains probably dates to
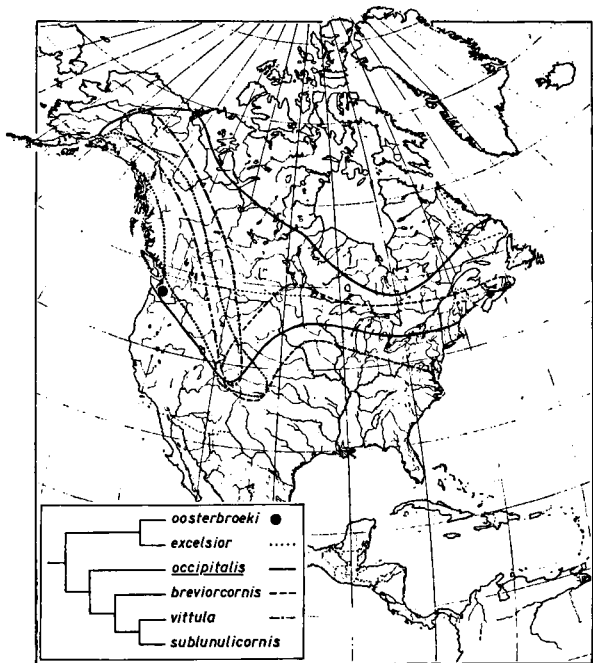
Map 12. Distribution of the *occipitalis*-group, except *sublunulicornis*.

pre-Wisconsin times (Pike, 1980). The Beringia refugium was probably unimportant as a source for montane species (Kavanaugh, 1980; Pike, 1980). *N. breviorcornis* ranges from the central Rocky Mountains to the Atlantic coast; it probably moved eastward from a central Cordilleran refugium across the broad boreal forest south of the retreating Laurentide Ice-sheet. Because of the rather limited distribution of *breviorcornis* near the Atlantic coast, spread from an eastern southern refugium is not very likely.

N. occipitalis shows a combined boreal and extended Cordilleran range with several localities in Alaska which were ice-free during the Wisconsin glaciation (map 12). Boreal species survived the last glacial period south of the ice-sheet, and in some cases in the Beringian refugium. *N. occipitalis* shows a variability in colour between northern and southern specimens (Tangelder, 1983), which may indicate that the species survived in both a Cordilleran refugium south of the ice and the Beringian refugium. According to Belicek (1976) some species of Coccinellidae survived the glaciations in different regions, suggested by

their geographic variation in colour and pattern (which is genetically fixed). Larson (1975) also suggested the possibility of a dual origin of Alberta-populations of Dytiscidae. According to Savchenko (1983) the darker coloration of northern specimens is a differentiation of melanistic forms which indicates a colder climate. The occurrence of *occipitalis* in Kamchatka and central Siberia (map 6) likewise points to a Beringian survival during one of the last glacial periods, because this Holarctic distribution presumably is the result of a faunal exchange across a temporary ice-free land connection, which was established in Beringia then. Many Holarctic distributions of Insect species are attributed to an exchange during one of the (last) Pleistocene glaciations (e.g. Moore & Ross, 1957; Chillcott, 1960; Baumann, 1975; Cuny, 1980; Hodkinson, 1980; O'Hara, 1982; Benhan-Pelletier & Norton, 1983 (Acari); Goulet, 1983; Goulet & Smetana, 1983). The same applies to the Holarctic distribution of another member of the *dorsalis*-group, *ramulifera* (see previous chapter). The ecological tolerance of the boreal *occipitalis* seems large enough to enable a survival in the cold and dry tundra existing in Beringia then.

DISCUSSION AND CONCLUSIONS

It becomes clear from the biogeographic analysis that the *Nephrotoma dorsalis*-group has essentially developed in parallel with Tertiary events, as supposed for the genus by Savchenko (1973). Many details of the biogeographic analysis are necessarily narrative and sometimes rather speculative, because the original distribution patterns are affected by dispersals, shifting of ranges, extinctions and so forth, which can make biogeographic patterns difficult to trace, and because of the lack of comparisons and certain palaeogeographic information. Nevertheless the present approach can clarify the understanding of the basal patterns and be valuable as comparison for future biogeographic studies of the Holarctic region. By an analysis down to the species-level it is possible to expose the most detailed patterns, which may be obscured in a higher taxa analysis that

implies the risk of jumping to incorrect conclusions. For example consider the overall distributions of the various subgroups, such as the mainly eastern Nearctic *macrocera*-group and its Eurasian sister group. This would lead to the conclusion of a North Atlantic exchange and vicariance of both groups instead of a Beringian history as is proposed in this paper.

For the *dorsalis* species-group an origin and first differentation is postulated in late Eocene/early Oligocene in central Asia (the ancient Angara). The Tertiary vicariances which could be correlated with geological and climatic events are summarized in fig. 7; the Pleistocene developments are presented in the text. These vicariances include the following events:

— A vicariance between an eastern Palaearctic and a Nearctic stock in Beringia in the Oligocene.

— The separation of Japan and the Asian mainland in the middle Miocene, causing vicariance of taxa in two species-groups (*nigricauda-* and *lunulicornis*-groups).

— The parallel vicariance of Himalayan and central Asian species because of the Himalayan orogeny in the middle Miocene (*nigricauda-* and *pamirensis*-groups).

— A middle to late Miocene vicariance of Boreal and Palaearchaearctic lineages because of a climatic cooling and concurrent development of lowland boreal habitats (*dorsalis-* s.s., *lunulicornis-* and *scurra*-groups).

— The development of grassland in central North America in the middle to late Miocene, causing the vicariance of eastern and western Nearctic stocks (*eucera*-group / *occipitalis*-group).

— A late Pliocene vicariance of western Nearctic and eastern Palaearctic species in Beringia (*vittula* / *sublunulicornis*).

— Pleistocene speciation events include the separation of Eurasian and Japanese species-pairs (*dorsalis/sachalina*; *lunulicornis/angustistria-koreana*; *scurra/microcera*; *barbigera/minuticornis*); the subsequent vicariance of *angustistria* (Japan) and *koreana* (east Asia); and possibly speciation within the Nearctic *okefenoke*-group and of *macrocera/gnata*.
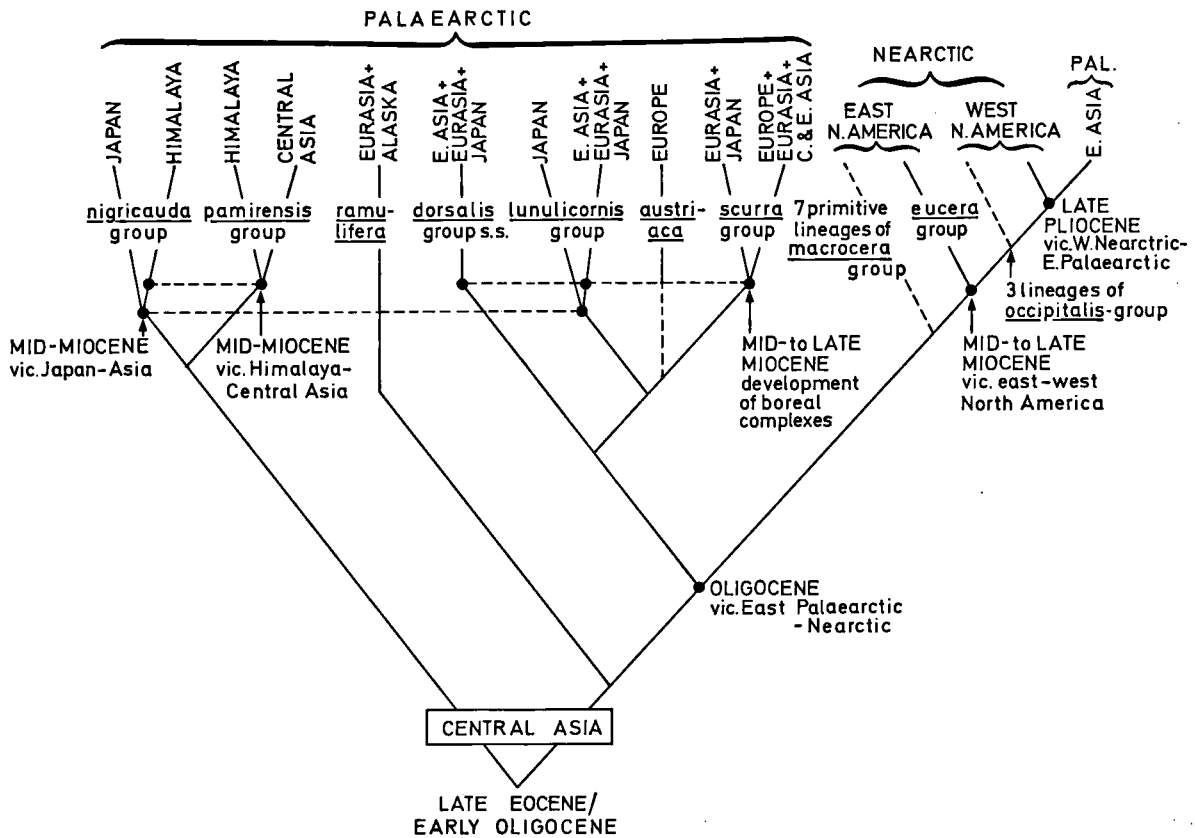
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Fig. 7. Area cladogram of the *dorsalis* species-group, with indication of Tertiary developments. vic. = vicariance, PAL. = Palaearctic.

The distribution patterns shown by the Holarctic *dorsalis*-group fit in general the schematic diagram of the history of North Temperate landmasses by Allen (1983), which is based on cladogram information of nine other Arthropod-taxa (fig. 8). This involves a break between Asia and North America in the Bering-area in the Oligocene and a separation of western and eastern North America in the Miocene. The history of Europe (reassociation with Asia in the Upper Oligocene and division in the Miocene), is assumed not to have played a part in the development of the *dorsalis*-group until the late Miocene.

The Bering land bridge and its history appears to be of great importance in the development of the Holarctic *dorsalis*-group. It was used several times by members of the group for extension of their ranges and subsequent
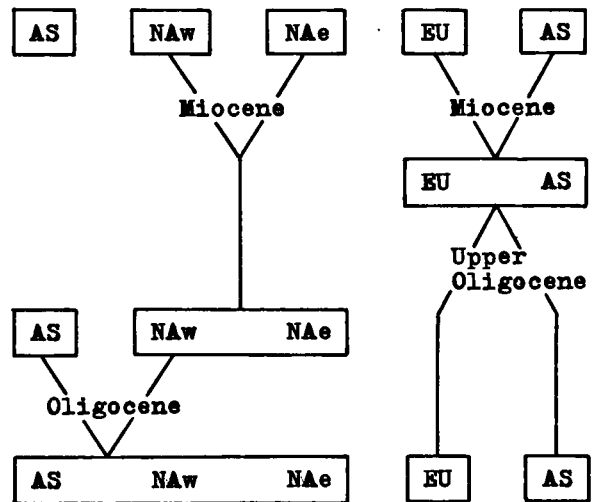

Fig. 8. Schematic diagram of the history of North Temperate landmasses, after Allen (1983, fig. 65, p. 626). AS = Asia, NAw = North America west, NAe = North America east, EU = Europe.

vicariances, under different ecological conditions, such as the Oligocene exchange and separation when temperate forests occupied Beringia and the late Pliocene exchange under treeless and boreal conditions. The Pleistocene extensions to both sides (*ramulifera*, *occipitalis*) were possible only for cold-hardy organisms. The fact that no Beringian exchange by members of the *dorsalis*-group could be established between the Oligocene and late Pliocene, presumably is associated with the existence of climatic barriers rather than physical ones (Matthews, 1980).

The overwhelming influence of the Pleistocene Ice-Ages on speciation and distribution of the Holarctic fauna as supposed by several authors cannot be recovered in the history of the *dorsalis*-group. There certainly was influence on diversity (speciations and extinctions) and distribution (e.g. alternating north-south movements, probably on a large scale), but the history of the group is distinctly rooted in the Tertiary.

Falsification of the presented hypothesis is possible for example by the discovery of fossils in Europe representing members of the *dorsalis*-group older than of late Miocene age, or by the detection of phylogenetically primitive species in Europe or even North America, or by the discovery of new species in eastern Asia. Falsification of course can also be done by a reinterpretation of the cladogram, for example by using a set of completely different characters such as biochemical or cytological ones.

ACKNOWLEDGEMENTS

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