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Palaeoentomology of the Kap København Formation, a Plio-Pleistocene sequence in Peary Land, North Greenland

Jens Böcher

Geoscience

33 · 1995

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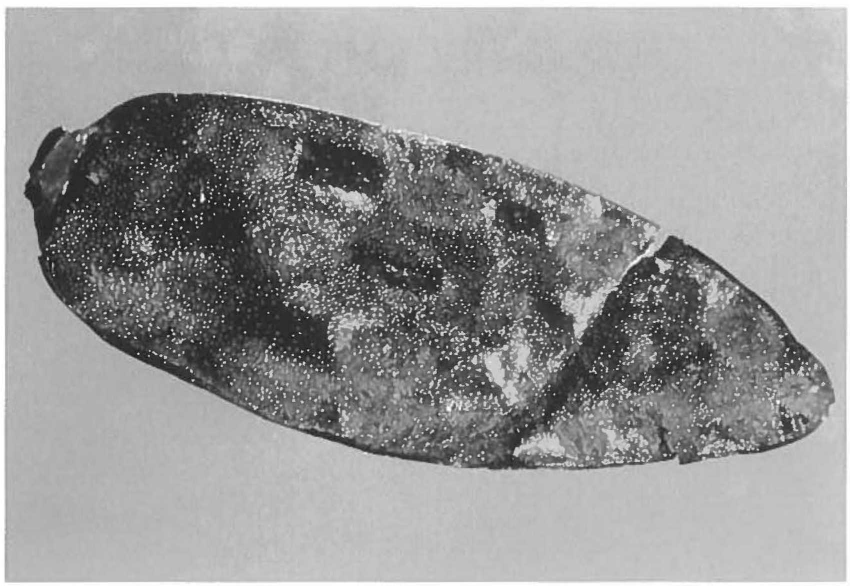

MEDDELELSER OM GRØNLAND, GEOSCIENCE 33 · 1995

Contents

The illustration on page 1 is a left elytron of the carabid *Elaphrus tuberculatus* Mäklin, 1877, from the Kap København Formation. The specimen is photographed in alcohol which adds to the brightness of the colours. Geert Brovad phot.

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The Kap København Formation in eastern Peary Land, latitude 82°30', is dated to the Plio-Pleistocene transition period, *c.* 2 million years B.P. The shallow water marine sediments contain abundant remains of terrestrial and limnic insects, in particular beetles (Coleoptera). The insect fauna is diverse, comprising 155 named species, of which 140 are beetles. The Coleoptera are dominated by ground beetles (Carabidae), rove beetles (Staphylinidae) and weevils (Curculionidae). Apart from three unknown and possibly extinct species, including *Diacheila matthewsi* n. sp. described herein, all the insect taxa are extant. Most are extralimital forms of the recent circumpolar subarctic/boreal fauna. However, a high number of fossils represent taxa which are today either nearctic or palaearctic, in some cases with modern occurrences in northeastern Asia or western North America. Many species are hygrophilic (20 %), aquatic (16 %) or riparian (18 %), thereby showing the existence of a great variety of freshwater wetland biotopes. Another large group (14 %) are either dependent on trees for food or are obligate forest dwellers and therefore indicate forest environments. Still other species suggest arctic/alpine living conditions (14 %), and a few are indicative of steppe environments. The fossil insect fauna thus strongly supports and elaborates previous palaeobotanical results showing that Peary Land at the beginning of the Quaternary epoch was covered by a rich and varied vegetation, in the lowlands with trees and probably small forests. The palaeoclimate was boreal and humid, with a July mean temperature of at least 8-11°C, but considerably warmer (13-19°C) in lowland areas or during certain time periods. There are indications of a shift in climate from subarctic to more southern boreal conditions during the deposition of the upper member (B) of the Kap København Formation.

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Introduction

A distinctive landscape with elongate, barren sandy hills rising up to 230 m above sea level is formed by the Kap København Formation in eastern Peary Land, North Greenland, at latitude 82°30'N (Fig. 1). This geological sequence was discovered and a type section described in detail in 1979 during mapping for the Geological Survey of Greenland (Funder & Hjort 1980). In 1980 samples were collected for palaeomagnetic studies and the type section was re-examined. In 1983 a geological-biological expedition investigated most of the area covered by the formation and subsequently the Kap København Formation was formally named (Funder *et al.* 1984). In 1986 Ole Bennike and the author supplemented the earlier work. In addition to Bennike's stratigraphical and palaeobotanical investigations a number of samples for palaeoentomological analyses were obtained in the 1986 field season.

Present climate, flora and fauna

Eastern coastal Peary Land has an extreme high arctic climate. No records exist, but undoubtedly the climate of the Kap København area closely resembles that of Station Nord, about 100 km to the southeast. Here the mean temperature for the warmest month (July) is *c.* 4°C, the mean for the coldest month (March) is *c.* -32°C,

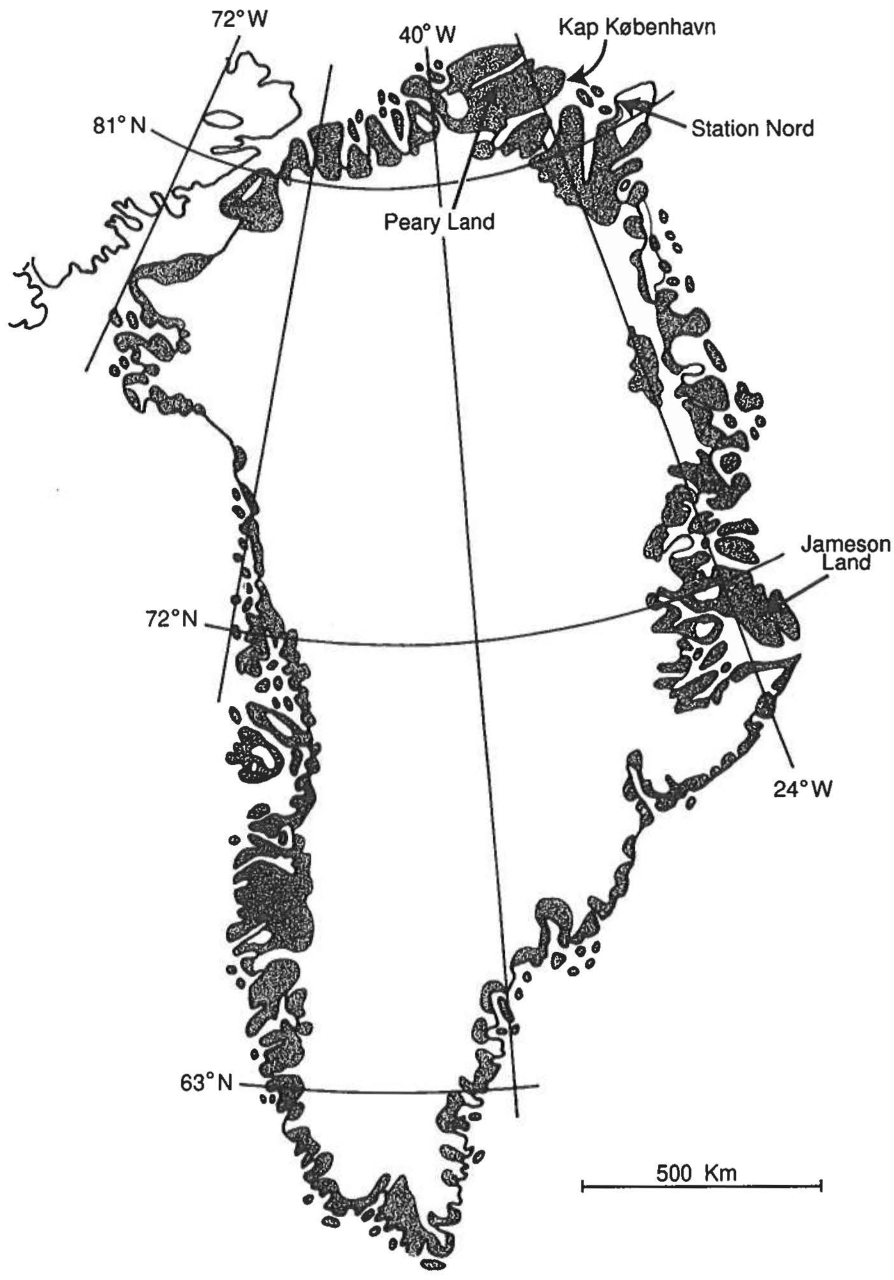


Fig. 1. Map of Greenland showing position of localities mentioned.

and the mean yearly precipitation is *c.* 200 mm (Fristrup 1981, Bay 1992). In spite of the low precipitation, conditions are comparatively humid along the Arctic Ocean; fog is frequent and the soil is generally moist. In the most continental parts of Peary Land precipitation is much lower, possibly around 25 mm per year (Fristrup 1952), and almost all of it falls as snow, which during winter is redistributed and deposited in drifts, leaving much of the landscape snow-free.

The low precipitation means that lakes, ponds and streams are few in number; however, numerous brooklets originate in the local snow drifts and constitute, together with melting permafrost, the most important source of water during the growth season.

The vegetation of Peary Land is high arctic, with a zonal development from the coast inland. In the coastal district, less than 10 km from the coast, the cold, humid summer climate is detrimental to plant growth. Here true polar desert occurs with an extremely low diversity of vascular plants and total absence of woody plants, Pteridophyta and Cyperaceae. The living plant biomass consists mainly of cyanobacteria, algae (in particular

Fig. 2. Landscapes with muskoxen at Kap København. a) Relatively luxuriant vegetation along a meltwater brook. *Dryas octopetala* and *Salix arctica* are found in the drier parts, mosses, sedges and *Ranunculus sulphureus* dominate the marshy margins of the watercourse. b) Typical barren "fell-field" vegetation. Practically the only species of vascular plants is *Dryas octopetala*.

a

b

Nostoc), lichens and mosses which almost cover the humid, patterned ground. Common herbs are *Saxifraga oppositifolia* and *Papaver radicatum*. The most unstable ground is totally without plant life.

A much higher diversity of vascular plants is found in central Peary Land, where the summers are sunny and warmer. Within about 10 km inland, *Salix arctica* and *Dryas octopetala* appear (Fig. 2). Here also small areas with closed vegetation, heaths of *Cassiope tetragona* and sedge meadows with *Carex stans* and *Eriophorum* occur, as an example in sheltered areas between the hills of the Kap København Formation and Kim Fjelde (Bennike 1990; Bay 1992).

In spite of marginal foraging conditions, a surprisingly large population of muskoxen exists in Peary Land (Klein & Bay 1990). Also the collared lemming and predatory birds and mammals associated with this species may be numerous. However, the insect fauna is very poor in both taxonomic diversity and number, especially in the coastal areas, where only chironomid midges, *Tipula arctica* and other flies (Empididae, Piophilidae, Anthomyidae, Muscidae, Calliphoridae) and a single species of lycosid spider (*Arctosa asperans*) are to be seen. Even biting mosquitos (*Aedes nigripes*) are fairly scarce. In sunny weather the high arctic fritillary butterfly, *Clossiana polaris*, and the arctic bumblebee, *Bombus polaris*, are conspicuous, and a few noctuid and geometrid moths (e.g. *Entephria polata*) are active

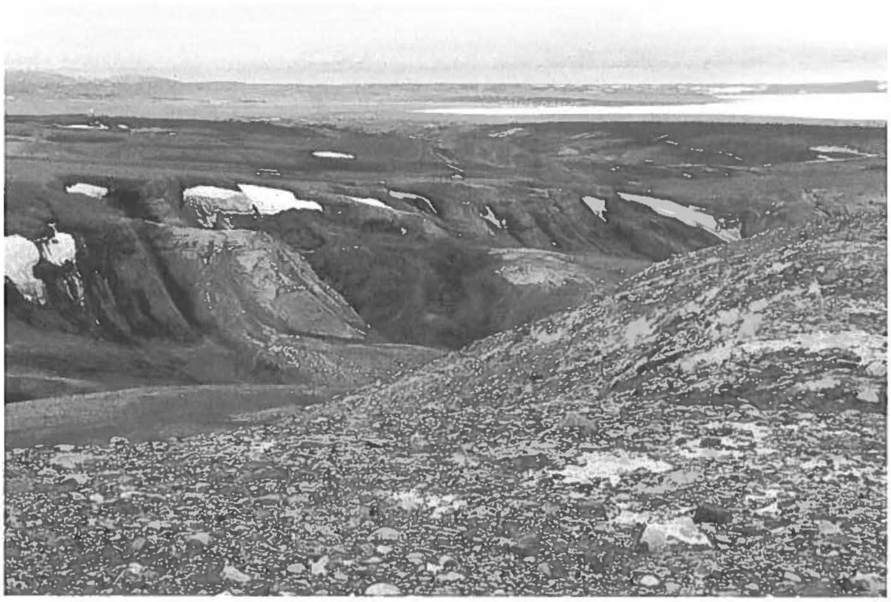


Fig. 3. The type section (locality 50) of the Kap København Formation. a) View over the area in a northerly direction towards the frozen Arctic Ocean.

b) The portion rich in organic detritus of unit B1 where entomological samples were taken.

throughout the constant "day". The arctic woolly moth *Gynaephora groenlandica* is present, and parasitoids of Lepidoptera (Ichneumonidae) are relatively numerous.

Not a single species of Coleoptera has been found in the Kap København area, and in central Peary Land only two species of beetles have been recorded, namely *Hydroporus morio* and *Gnypeta cavicollis* (Böcher 1988). *H. morio* (Dytiscidae) has a wide range in Greenland, from the southernmost point northwards along the entire west coast, but along the east coast it disappears north of 66°N. *G. cavicollis* (Staphylinidae) is one of the very few, truly high arctic beetles. In Greenland it is restricted to the northeastern coastland and therefore has a southern distributional limit at the low arctic-high arctic transition (Böcher 1988). Another species once reported from central Peary Land is the seed-bug *Nysius groenlandicus* (Heteroptera) which is almost ubiquitous in Greenland, but markedly xerophilic and thermophilic (Böcher 1972, 1976).

Geology of the Kap København Formation

The geological setting of the Kap København Formation and the region in which it occurs is discussed in a number of works dealing with the lithology, structural geology, stratigraphy, correlation, age and palaeobotany (Funder & Hjort 1980; Fredskild & Røen 1982; Funder *et al.* 1984, 1985; Mogensen 1984; Abrahamsen & Marcussen 1986; Bennike 1990; Feyling-Hanssen 1987, 1990; Bennike & Böcher 1990; Brouwers et al. 1991; Penney 1993).

Fig. 4. Landscapes from the northern part of the Kap København Formation. a) The cliff eroded by Ladegårdsåen clearly shows the division in the two members A (lower) and B (the arrow points to the transition). b) View over the Kap København Formation in a southerly direction from a position close to locality 119.

a

b

The Kap København Formation is a shallow water deposit of unconsolidated marine sediments, covering an area of *c.* 300 km^2 and with a thickness of at least 100 m. Two distinctive sedimentary members are evident in all parts of the area (Figs 3, 4). The lower member, A, consists of finely laminated, red or grey clay and silt. The upper member, B, subdivided into units 1, 2 and 3, consists mainly of sand, with the exception of unit B2, which is composed mainly of silt. Member B is distinguished by its layers and lenses with organic detritus containing abundant and well preserved remains of terrestrial and limnic plants and animals. The sediments of the Kap København Formation are tectonically disturbed, probably by glaciers overriding the area after their deposition.

To the north the sediments terminate abruptly on the southern bank of the river Ladegårdsåen (Fig. 4a), which rises in Kim Fjelde, an area of low mountains of Silurian sandstone to the north. Towards the west and south the Kap København Formation gradually disappears under glacial and Holocene sediments along the coast.

The lowest part of the Kap København Formation, Member A, was deposited in a low energy marine environment below storm wave base, and contains a sparse fauna of high arctic molluscs. In the overlying Member B, unit B1 was deposited in a shallow marine

a

b

Fig. 5. Locality 77. a) View from the north. The arrow points to the big lens, which is positioned about 100 m a.s.l. b) The lens of organic detritus, looking east.

environment of medium energy close to the shore and contains only few mollusc shells and shell fragments. Unit B2 mostly consists of bioturbated mud, dominated by the burrows of deposit feeding bottom invertebrates (presumably polychaete worms). Foraminifera, ostracode and mollusc faunas are rich and diverse (Símonarson *et al.*, in press). Like member A, unit B2 was deposited in a low energy environment, below storm wave base on the inner shelf. Unit B3 is rather heterogeneous, but like B1 it is dominated by coastal and nearshore sand. Marine molluscs are fairly sparse.

Accumulations of organic detritus occur especially in unit B3, in some cases forming peat-like layers. Trunks and branches of small trees, probably transported by rivers, are also characteristic for this unit. Bennike (1990) suggests that the lower part of unit B3 was deposited in an environment of medium energy, probably at the shoreface. The upper, driftwood bearing part was deposited in the beach zone, in the foreshore or backshore (Bennike 1990).

Units B1 and B3 thus clearly indicate that the Arctic Ocean coastline was free of ice, at least seasonally. This is also shown by the foraminifer faunas (Feyling-Hanssen 1990).

Taphonomy

In addition to the remnants of various marine organisms occurring *in situ* in the sediments (Foraminifera, marine Mollusca and Ostracoda, burrows of Polychaeta), the Kap København Formation is characterised by its abundant allochthonous remains of limnic and terrestrial plants and invertebrates, the latter dominated by insects. All of these fossils occur in 5-20 cm thick beds or in connection with wavy bedding from wave ripples in units B1 and B3 of member B. However, only a few accumulations of organic detritus have been found in unit B1 (Fig. 3,b). In some

Fig. 6. Close up of the surface of a layer of organic detritus from locality 77, showing well preserved leaves of *Salix* spp.

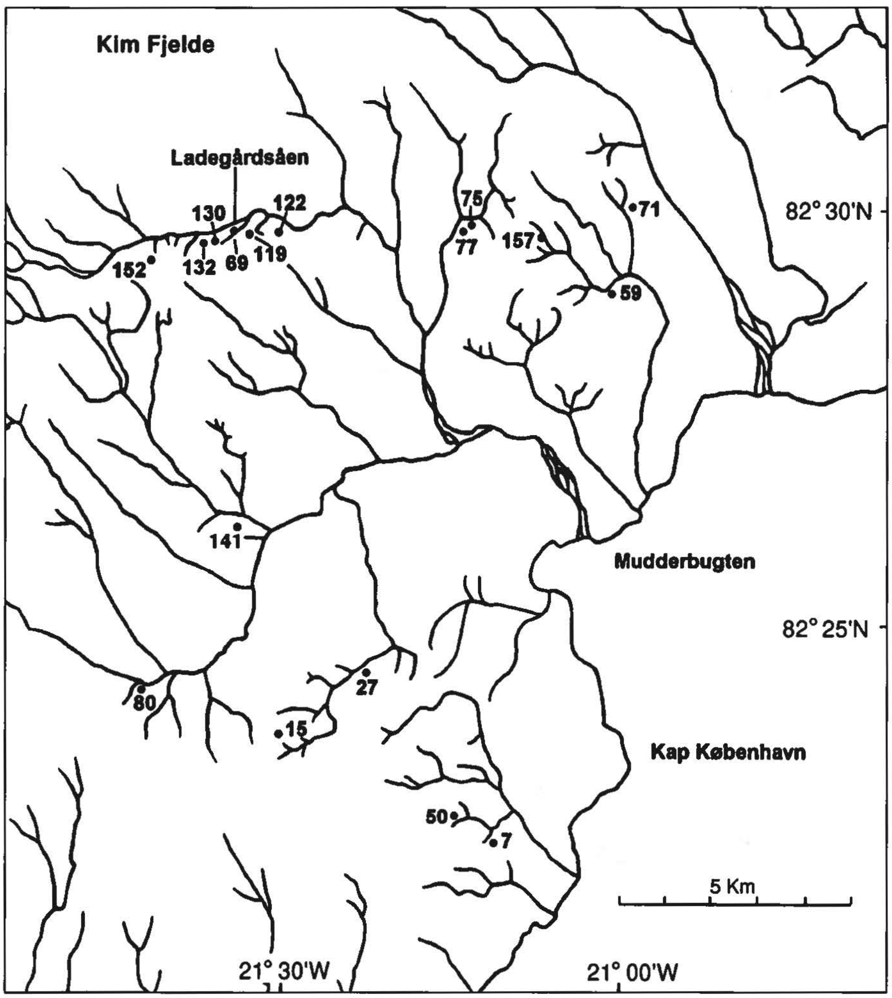


Fig. 7. The Kap København area showing field localities. Locality numbers according to Funder (1983) and Bennike (1986). The map is based on orthophotos and redrawn from Bennike (1990).

places within unit B3 organic detritus forms impressive lenses with thicknesses up to 1 m (Fig. 5). Most of the organic material is made up of mosses, but with plentiful remains of higher plants and arthropods as well (Fig. 6).

The terrestrial and limnic floral and faunal elements were deposited in marine, littoral environments, probably in protected bays, estuaries or river deltas, and transported there by rivers. The large lenses may originate from detritus filled holes in the foreshore made by stranded icebergs. Therefore, the samples of flora and fauna from the Kap København Formation represent the biota of the entire catchment area of the rivers that formerly drained eastern Peary Land.

Table 1. Survey of localities, entomological samples from 1986 ("ent"), and botanical samples from which insect remains have been obtained (1980, 1983, 1986: years of collection). The numbering of samples follows Funder (1983) and Bennike (1986). Regarding position of localities, see Fig. 7.

Locality No.	Sample No.	Unit	Origin
7	197171	B1	1980
15	56606	B1	1983
27	64914	B2	ent
50	64902-04	B3	ent
50	64905-07	B1	ent
50	64908-11	B3	ent
50	64912-13	B1	ent
50	197117	B1	1980
50	197118-19	B2	1980
50	197123-25	B1	1980
50	197127	B1	1980
50	197128	B2	1980
50	197129	B1	1980
50	197149	B2	1980
50	197153-54	B3	1980
50	197156	B3	1980
50	197158-63	B3	1980
50	197182	B2	1980
59	56653	B1	1983
69	53280	B3	1986
69	64939-40	B3	ent
71	56655	B3	1983
75	53261-62	B3	1986
75	53280	B3	1986
77	56666-67	B3	1983
77	64922-31	B3	ent
77	64933-38	B3	ent
77	64988-91	B3	1986
80	56710	B3	1983
119	53203	B3	1986
119	56688	B3	1983
119	56690	B3	1983
119	56692-93	B3	1983
119	64915-17	B3	ent
119	64919	B3	ent
119	64921	B3	ent
122	53214	B3	1986
130	53286	B3	1986
132	53263-65	B3	1986
141	64956	B3	1986
152	64972	B3	1986
157	64976	B3	1986

Age

The age of the Kap København Formation has been assessed by a number of independent methods. Stratigraphical work based on Foraminifera located the Pliocene-Pleistocene boundary in unit B2 (Funder *et al.* 1985; Feyling-Hanssen 1987, 1990). Mammalian remains from unit B3 of the extinct lagomorph genus *Hypolagus* and of the extant *Lepus* indicate an age of 2.2-1.9 million years (Repenning & Brouwers 1992). These biostratigraphical correlations support palaeomagnetic measurements from member B (Abrahamsen & Marcussen 1986) and amino acid analyses of bivalve shells (Funder *et al.* 1984, Funder 1989), all of which suggest that Member B of the Kap København Formation was laid down during a warm stage following the first major glaciation in the Northern Hemisphere, within the interval from *c.* 1.8 to 2.2 Ma (Brigham-Grette & Carter 1992; Repenning & Brouwers 1992; Penney 1993; Símonarson *et al.*, in press).

Palaeobotany

The fossil vascular flora of the Kap København Formation has been studied by Fredskild & Røen (1982) and Bennike (1990; see also Funder *et al.* 1985; Bennike & Böcher 1990). Seeds, fruits and leaves of about 60 taxa show that the area was vegetated by forest-tundra growing in a humid subarctic climate. Of the driftwood from unit B3, the dominant tree was *Larix groenlandii* which may have formed small woodlands and coppices together with *Picea mariana*, *Thuja occidentalis*, *Taxus* sp., *Betula alba*, *Alnus* cf. *crispa* and the shrubs *Myrica arctogale*, *Cornus stolonifera* and *Viburnum edule*. Such fossils are found in the same deposit with remains of present day widespread arctic species, including *Dryas octopetala*, *Oxyria digyna*, *Betula nana*, *Salix reticulata* and *Vaccinium uliginosum* ssp. *microphyllum*. The Kap København Formation also yielded a diverse flora of wetland and limnic plants, most of them with a modern boreal distribution (*e.g.*, *Nuphar lutea*, *Ranunculus* spp., *Hippuris vulgaris*, *Menyanthes trifoliata*, five species of *Potamogeton* and the *Sparganium angustifolium* type).

The mosses of the Kap København Formation have been studied by Mogensen (1984).

Palaeozoology

In addition to insects, a number of other terrestrial/limnic animal taxa occur in the Kap København Formation. Most numerous are oribatid mites, the rich material of which has been handed over to Peter Gjelstrup, University of Århus, for identification and treatment. Of other Arachnida only a few fragments of Araneae have been found (one carapax, two chelicera, a few doubtful leg joints). The Crustacea are fairly well represented, with twelve species of Cladocera (Røen 1988), and mandibles of *Lepidurus* sp. (Notostraca) are fairly frequent in unit B3. Also common in unit B3 are statoblasts of the bryozoans *Cristatella mucedo*, first reported from the formation by Fredskild & Røen (1982), and *Plumatella* sp. (Bennike 1990). Less frequent are egg capsules of Lumbricidae (earth worms) and Nematoda.

The few finds of mammals have been briefly mentioned see Repenning *et al.* 1987, Bennike 1990, Repenning & Brouwers 1992).

Fredskild & Røen (1982) reported on the macrofossils found in two samples collected during the discovery of the Kap København Formation in 1979 when the sediments were considered of interglacial age. In addition to three species of Crustacea, also three insect taxa were named (*Bembidion grapii*, *Gyrinus opacus*, cf. *Phyllodecta* sp. However, there seems to be disagreement between the fragments illustrated and the names of taxa given. Unfortunately the material has disappeared, and it has thus been impossible to confirm the identifications.

Based on the first identifications of the material collected in 1983 and 1986, I published preliminary lists of insect taxa (Böcher 1989a, Bennike & Böcher 1990). When comparing those lists with the present (Table 3) the reader will note a number of discrepancies. These are due to later revisions.

Material and methods

A relatively small part of the fossil insect material discussed here originates from the samples collected during the interdisciplinary expedition to Kap København in 1983. Instead most fossils come from collections made during the expedition in 1986.

The palaeoentomological samples, each comprising about four litres of sediment, were taken from layers with a high content of organic detritus. Only a single entomological sample comes from unit B2 in which organic detritus is rare. Five samples derive from unit B1, all taken in the type section (Locality 50); the remaining (30) samples are from unit B3. By far the majority of samples and insect remains originate from a single locality (77) where the organic detritus constitutes a large lens (Figs 5, 6). The samples are listed in Table 1. Regarding location of the sampling localities, see Fig. 7. For description of localities and details of sedimentology, see Bennike (1990).

The preservation of the insect fragments varies, but is in general surprisingly good, with hairs and scales retained (Figs 23, 26). Articulated sceletal parts were rarely found, a feature which is typical of allochthonous material (Matthews 1983). However, some partially articulated specimens are fairly common, e.g., head and prothoraces in *Hydroporus* and *Helophorus*, metasterna with metacoxae in Dytiscidae, femur+tibia and fused elytra in Curculionidae (Fig. 16,c) and generally sternites 1+2 in Carabidae.

The fossil insect material is deposited in the Zoological Museum, University of Copenhagen (ZMUC). All fragments which are identified to some extent, both mounted and in alcohol, are entered into a database comprising *c.* 3000 pieces.

Laboratory technique

The samples were processed at the ZMUC. Wet sieving was performed through a 40 cm diameter sieve with mesh width 0.6 mm. This is a coarser sieve than recommended by Coope (1986) and Elias (1994) but in accordance with Matthews (1974a). After sieving, the arthropod remains were concentrated by means of the kerosene flotation method (Coope 1986, Elias 1994) and subsequently washed with detergent and sieved through a 0.25 mm sieve. Almost all animal remains were picked out in alcohol under a dissecting microscope and stored in 70 % alcohol (Fig. 8). Sorting was facilitated by use of nine centimeter diameter petri dishes containing two concentric circles and one radial line engraved. The field of vision by 12.5 times magnification corresponds to the width of the circular rings. Most of the identifiable fragments were later mounted dry on cardboard rectangles on insect pins.

Two pieces of *Larix*-wood with a high concentration of insect fly-holes were split and examined for insect remains. In one case nothing was found, whereas the other (sample no. 53287; Figs 24, 25,a,b) yielded four mandibles from cerambycid larvae and a few unidentifiable fragments.

Identification

Identification of fossil insect remains is notoriously difficult and time consuming (see Elias 1994 for details). One of the reasons for this is that identification keys are of limited value when the fragments do not include, as is often the case, the diagnostic features. One fortunate example is constituted by a species of *Aegialia* which is common in the Kap København Formation, but for which the numerous fragments (elytra) possess few if any species-diagnostic features. However, one front leg of *Aegialia* was found, with a unique and diagnostic shape (Fig. 21,f) which unambigously relates it to *A. terminalis* Brown, 1931 – and because the other *Aegialia*-fragments (heads, pronota) also exactly fit Brown's description, the identification of the non descript specimens was further substantiated.

In most cases, however, the only really satisfactory way to identify fossils is to compare with securely identified modern material in museums and private collections. It must be admitted, however, that only exceptionally have all members of a genus been checked by such comparisons. Very often this is not necessary because at a certain stage the identification appears sufficiently certain.

No single collection is complete, not even the exten-

Fig. 8. Part of a rich sample (64925) from the big lens at locality 77. Species of *Bembidion*, *Pterostichus* (*Cryobius*) and Dytiscidae dominate. In the centre a metallic green pronotum of *Chrysomela populi*, immediately to the left of this elytra of *Hydroporus* sp. and *Elaphrus tuberculatus*.

sive one at the ZMUC. Supplementary studies have been undertaken at other museums and collections: Zoological Institute, University of Lund, Sweden; Zoological Museum and Institute, St. Petersburg, Russia; Department of Geological Sciences, University of Birmingham, U.K.; Agriculture Canada, and Geological Survey of Canada, Ottawa.

In some cases descriptions and figures (scanning electron micrographs) in the literature are complete and detailed enough to allow a reliable identification (such as Goulet's work on *Elaphrus* (1983) and Campbell's works on Staphylinidae).

It is generally a combination of size and shape and more subtle characters, like microsculpture (Figs 13, 14, 19) that provide the best basis for the identification. Colours, if not structural interference colours, are not reliable, since fossil insect fragments generally are darker than their modern counterparts.

The reliability of identifications varies greatly from case to case. Some taxonomic groups are so difficult, such as the carabid genus *Bembidion*, that a convincing and conclusive identification is usually impossible without reference to male genitalia, no fossils of which occur among the material studied for this paper. This means that the identifications of the multitude of *Bembidion*-fragments necessarily are uncertain, but to a varying degree. The situation is even worse considering the subgenus *Cryobius* of *Pterostichus*. In the absence of genitalia one has to rely exclusively on the shape and structure of pronota; the elytra, which are common in the Kap København sediments, are of little use as basis for species determinations.

In some cases an identification may seem hazardous, for instance that of *Cicindela* cf. *hybrida* L. which is based on a single head (Fig. 11,a). There are numerous palaearctic and in particular nearctic species in this genus, and the dimensions, structure and microsculpture of the heads are surprisingly homogenous throughout the genus. On the other hand, when the microsculpture of frons and clypeus are studied in detail, a large number of species can be eliminated as options, and it becomes probable that the fossil specimen belongs to *Cicindela* sensu strictu. One character is highly variable in this subgenus, namely the number of setae on the head. In several species there are many setae surrounding the compound eyes and medially on frons. The setae have disappeared on the fossil, but the setal sockets are conspicuous. There are very few, namely one at the upper

Table 2. Diagrammatic presentation of the relationship between summer temperatures of fairly oceanic areas, climatic zones and subzones, and characteristic vegetation (simplified and modified after Köppen 1936)

Mean July temperature (C°)	Climatic subzones	Climatic zones	Characteristic vegetation	
0				
	High Arctic		Polar desert	Fell-fields
5		ARCTIC		Dwarf-shrub heaths
	Low Arctic		Herb slopes	Marshes and tundras
			Copses	
10	Subarctic			Birch/conifer forests
	Boreal			Coniferous forests (taiga)
15		TEMPERATE		
	Southern temperate			Deciduous forests
20		SUBTROPICAL		

front margin of the eye and a prominent one further back, and also a few small sockets medially foremost on the frons (Fig. 11,a). One of the key characters of the highly variable and extremely widespread northern palaearctic *C. hybrida* is the small number of setae, which also fits in with the size, general morphology and microsculpture of the fossil head. Nevertheless, due to the large number of similar species regarding head characters, the identification must be considered tentative.

Identification of fossils from the Kap København Formation is particularly difficult because the fauna potentially contains elements of the entire circumpolar fauna, representing climatic zones varying from the High Arctic to the northern temperate regions. Table 5 shows that the fossil fauna has an almost equal share of modern nearctic and palaearctic species, meaning that faunal elements today restricted to either of these zones must be considered when attempting to identify the fossils.

The MCR method

The "Mutual Climatic Range method" developed by G. Russell Coope and collaborators (Atkinson *et al.* 1986, 1987) was employed for a relatively small part of the beetle material from the Kap København Formation. The method provides a means of reconstructing ancient temperature regimes and is based on temperature records from the limits of the present geographical ranges of the species found in an assemblage of fossil insects. When these temperature limits are superimposed, a "mutual climatic range" (MCR) of temperature regime (mean July temperature, mean January temperature) appears which is regarded the best approximation to the palaeotemperature conditions.

Terminology

Biogeographically the northern continents are subdivided in the PALAEARCTIC (Europe and northern Asia) and NEARCTIC (North America) Regions. CIRCUMPOLAR denotes a taxon found all the way round the North Pole, whereas a HOLARCTIC taxon has important gaps in the circumpolar distribution.

Greenland is traditionally included in the Nearctic Region, implying that the occurrence of a species in Greenland automatically renders it nearctic. In accordance with Böcher (1988, p. 5), Greenland is here considered a zoogeographical unit of its own, and consequently palaearctic species occurring in Greenland are not defined as holarctic.

The simplified climatic zonation used is based on a combination of temperature zones and vegetation zones (Table 2). The ARCTIC zone is defined by a mean temperature in warmest month (July) below 10°C. In the HIGH ARCTIC subzone it is below 5°C, and in the LOW ARCTIC subzone 5-10°C. The northernmost part of the boreal subzone of the TEMPERATE zone is called the SUBARCTIC. Here the mean temperature in warmest month is just above 10°C allowing open, stunted tree growth, which is absent from the Arctic. The most important subarctic tree genus is birch (*Betula*), most often in combination with different conifers (*Larix*, *Picea*, *Pinus*). The BOREAL subzone is characterized by dense coniferous forests.

ALPINE species are found in mountains above the tree limit, SUBALPINE species in the transition between real alpine and coniferous forest, most often characterized by species of treebirch (*Betula*). BOREO-ALPINE species have a disjunct distribution: a northern main area and a number of isolated occurrences in southern mountains.

Table 3. Named insect species from the Kap København Formation
U, units of Member B of the Kap København Formation: B1, B2, B3. **G**, present geographical ranges: N, nearctic; WN, western nearctic; EN, eastern nearctic; P, palaearctic; WP, western palaearctic, EP, eastern palaearctic. **C**, present climatic ranges: A, arctic; HA, high arctic; LA, low arctic; SA, subarctic; B, boreal; T, southern temperate; ST, subtropical. **E**, ecological groups: A, aquatic; H, hygrophilic; R, riparian; T, tundra; S, forest and arboreal; X, xerophilic; E, eurytopic terrestrial; P, phytohagous; D, fungivorous; C, scavengers (see also legend to Table 12)

	U	G	C	E
COLEOPTERA				
Carabidae				
Trachypachus zetterstedtii (Gyllenhal, 1827)	B3	P	B	S
Nebria cf. *rufescens* (Ström, 1768)	B3	C	LA-SA	T
Nebria cf. *nivalis* (Paykull, 1790)	B3	C	LA-SA	T
Opisthius richardsoni Kirby, 1837	B3	WN	B	R
Notiophilus aquaticus (Linnaeus, 1758)	B1B3	C	LA-T	X
Notiophilus cf. *biguttatus* (Fabricius, 1779)	B3	WP	B-T	S
Cicindela cf. *hybrida* Linnaeus, 1758	B3	P	B-T	X
Blethisa multipunctata (Linnaeus, 1758)	B3	C	B-T	R
Blethisa catenaria Brown, 1944	B3	WN+EP	LA-SA	T
Diacheila polita (Falderman, 1835)	B3	WN+P	LA-SA	T
Diacheila matthewsi Böcher, 1995	B3	-	-	-
Elaphrus lapponicus Gyllenhal, 1810	B3	C	SA	H
Elaphrus sibiricus Motschulsky, 1846	B3	EP	B	R
Elaphrus cf. *olivaceus* LeConte, 1863	B3	N	B-T	R
Elaphrus lecontei Crotch, 1876	B3	WN	T	R
Elaphrus tuberculatus Mäklin, 1877	B1B2B3	WN+P	B	T
Elaphrus angusticollis F. Sahlberg, 1844	B3	WN+P	SA	R
Dyschirius cf. *varidens* Fall, 1910	B3	WN	T	R?
Miscodera arctica (Paykull, 1798)	B3	C	LA-B	X
Patrobus stygicus Chaudoir, 1871	B3	EN	B	H
Asaphidion alaskanum Wickham, 1919	B3	WN	LA-SA	T
Bembidion levettei Casey, 1918	B3	N	B	R
Bembidion alaskense Lindroth, 1962	B3	WN	B	R
Bembidion cf. *velox* (Linnaeus, 1761)	B1B3	P	B-T	R
Bembidion cf. *lapponicum* Zetterstedt, 1828	B3	WN+P	LA-SA	T
Bembidion cf. *balli* Lindroth, 1962	B3	WN	B	R
Bembidion cf. *vitiosum* Gemminger & Harold, 1868	B3	EP	-	-
Bembidion dyschirinum LeConte, 1861	B1B3	WN	B	X
Bembidion lampros Herbst, 1784	B3	P	B-T	X
Bembidion cf. *fellmanni* Mannerheim, 1823	B1B2B3	P	LA-SA	T
Bembidion cf. *difficile* (Motschulsky, 1844)	B3	P	B	R
Bembidion cf. *arcticum* Lindroth, 1963	B1B3	WN+EP	LA-SA	T
Bembidion planatum LeConte, 1848	B3	N	B	R
Bembidion cf. *planiusculum* Mannerheim, 1843	B1B3	WN	B	R
Bembidion cf. *gebleri* Gebler, 1833	B1B3	WN+P	B	R
Bembidion salebratum LeConte, 1848	B3	WN	B	R
Bembidion cf. *mckinleyi* Fall, 1926	B3	WN+P	SA	R
Bembidion cf. *lenae* Csiki, 1928	B1	WN+EP	LA-SA	T
Bembidion cf. *grapii* Gyllenhal, 1827	B3	C	LA-B	X
Bembidion cf. *yukonum* Fall, 1926	B1B3	C	SA	X
Bembidion cf. *bimaculatum* Kirby, 1837	B3	N	B-T	R
Bembidion cf. *sordidum* Kirby, 1837	B1B2B3	N	B	R
Pterostichus stygicus Say, 1823	B3	N	B-T	S
Pterostichus nigrita (Paykull, 1790) s.l.	B3	P	B-ST	H
Pterostichus cf. *corvinus* Dejean, 1828	B3	N	B-T	R
Pterostichus cf. *caudicalis* Say, 1823	B3	N	B-T	R
Pterostichus cf. *arcticola* Chaudoir, 1868	B3	N	LA-SA	T

Pterostichus cf. *planus* J. Sahlberg, 1887	B3	WN	SA	T
Pterostichus cf. *pinguedineus* Eschscholtz, 1823	B3	WN+EP	LA-B	T
Pterostichus riparius Dejean, 1829	B3	WN	B	S
Pterostichus brevicornis Kirby, 1837	B1B3	N+WP	LA-SA	T
Pterostichus vermiculosus Ménétries, 1851	B2B3	WN+P	LA-SA	T
Pterostichus cf. *agonus* Horn, 1880	B3	WN+EP	LA	T
Pterostichus haematopus Dejean, 1831	B3	N+EP	LA-B	T
Agonum cf. *consimile* Gyllenhal, 1810	B3	C	SA	H
Agonum cf. *exaratum* Mannerheim, 1853	B3	WN+P	LA-SA	T
Amara cf. *apricaria* (Paykull, 1790)	B3	C	B-ST	X
Amara cf. *glacialis* Mannerheim, 1853	B3	C	LA-SA	T
Amara cf. *quenseli* (Schönherr, 1806)	B3	C	SA-T	X
Amara cf. *brunnea* (Gyllenhal, 1810)	B3	WN+P	B-T	S
Amara cf. *pseudobrunnea* Lindroth, 1968	B3	N	B	H
Chlaenius cf. *interruptus* Horn, 1876	B3	WN	B-T	R
Dromius cf. *angusticollis* J. Sahlberg, 1880	B3	P	B	S
Noteridae				
Noterus crassicornis (Müller, 1776)	B3?	P	B-T	A
Dytiscidae				
Hydroporus cf. *morio* Aubé, 1838	B3	C	A-B	A
Hydroporus cf. *striola* Gyllenhal, 1827	B3	N	B	A
Oreodytes cf. *sanmarkii* (Sahlberg, 1826)	B3	WN+P	LA-T	A
Oreodytes alpinus (Paykull, 1798) /*laevis* Kirby, 1837	B2B3	C	LA-B	A
Agabus cf. *affinis* (Paykull, 1798)	B3	P	B-T	A
Agabus clavicornis Sharp, 1882	B3	WN+EP	LA-B	A
/*serricornis* Paykull, 1799	B3	P	LA-B	A
Agabus bifarius (Kirby, 1837)	B3	N	B-T	A
Agabus cf. *anthracinus* Mannerheim, 1852	B3	N	B-T	A
Ilybius vittiger (Gyllenhal, 1827)	B3	C	LA-B	A
Hydrophilidae				
Helophorus cf. *khnzoriani* Angus, 1970	B3	EP	T	A
Helophorus tuberculatus Gyllenhal, 1808	B3	C	B-T	H
Megasternum obscurum (Marsham, 1802)	B3?	WP	B-ST	D
Leiodidae				
Agaricophagus cephalotes Schmidt, 1841	B3	WP	B-T	D
Anisotoma cf. *castanea* (Herbst, 1792)	B3	WP	B-T	S
Silphidae				
Thanatophilus baicalicus Motschulsky, 1860	B3	EP	T	C
Heterosilpha ramosa (Say, 1823)	B3	WN	B-T	C
Agyrtidae				
Pteroloma forsstromii (Gyllenhal, 1810)	B1B3	WP	SA-T	R
Staphylinidae				
Stenus melanarius Stephens, 1833	B3	P	LA-T	H
Stenus cf. *canaliculatus* Gyllenhal, 1827	B3	C	LA-T	H
Stenus vinnulus Casey, 1884	B3	EN+WP	B-T	H
Stenus assequens Rey, 1884	B1	C	B-ST	E
Stenus hyperboreus J. Sahlberg, 1876	B3	N+WP	LA-B	H
Stenus cf. *carbonarius* Gyllenhal, 1827	B3	WP	B-T	H
Stenus pubescens Stephens, 1843	B1	C	B-T	R
Stenus cf. *pinguis* Casey, 1884	B3	WN	B-ST	H
Stenus sordidus Puthz, 1988	B3	N	LA-B	H
Stenus cf. *mammops* Casey, 1884	B3	N	EP	H
Stenus scrupeus Casey, 1884	B3	N	B-T	H
Kalissus nitidus LeConte, 1874	B3	WN	T	R
Pycnoglypta cf. *lurida* (Gyllenhal, 1813)	B1B3	C	SA-B	H
Micralymma cf. *brevilingue* Schiödte, 1845	B3	C	A	T

Olophrum boreale (Paykull, 1792)	B3	C	B	H
Olophrum consimile (Gyllenhal, 1810)	B3	C	SA-B	H
Olophrum cf. *rotundicolle* (Sahlberg, 1830)	B3	C	SA-B	H
Eucnecosum cf. *tenue* (LeConte, 1863)	B3	C	SA-B	H
Eucnecosum cf. *brunnescens* (J. Sahlberg, 1871)	B3	C	SA-B	H
Acidota quadrata (Zetterstedt, 1838)	B3	C	B	H
Coryphium angusticolle Stephens, 1834	B3	WP	B-T	S
Bledius cf. *litoralis* Heer, 1839	B3	P	B-T	R
Bledius cf. *arcticus* J. Sahlberg, 1890	B1B3	P	LA-SA	T
Bledius cf. *talpa* (Gyllenhal, 1810)	B3	P	LA-T	R
Tachyporus cf. *rulomus* Blackwelder, 1936	B1	N	B	H
Tachyporus cf. *borealis* Campbell, 1979	B1	N	B	H
Tachinus elongatus Gyllenhal, 1810	B3	C	LA-T	H
Scarabaeidae				
Aegialia terminalis Brown, 1931	B3	N	B	X
Cantharidae				
Podabrus cf. *alpinus* (Paykull, 1798)	B3	WP	LA-T	S
Elateridae				
Hypnoidus rivularius Gyllenhal, 1808	B3	P	LA-B	E
Byrrhidae				
Simplocaria cf. *metallica* (Sturm, 1807)	B3	N+WP	LA-B	R
Simplocaria cf. *elongata* J. Sahlberg, 1903	B3	C	LA-SA	T
Simplocaria basalis J. Sahlberg, 1903	B3	EP	LA-B	-
Morychus cf. *aeneus* (Fabricius, 1775)	B3	P	B-T	X
Arctobyrrhus subcanus (LeConte, 1878)	B3	N	SA-B	X
Curimopsis cf. *moosilauke* Johnson, 1986	B3	N	B	X
Derodontidae				
Laricobius cf. *caucasicus* Rost, 1893	B3	WP	T	P?
Anobiidae				
Cacotemnis cf. *carinatus* (Say, 1823)	B3	N	B	S
Coccinellidae				
Calvia quatuordecimguttata (Linnaeus, 1758)	B3	C	SA-T	P
Myrrha octodecimguttata (Linnaeus, 1758)	B3	P	B-ST	P
Colydiidae				
Orthocerus clavicornis (Linnaeus, 1758)	B3	P	B-T	X
Chrysomelidae				
Hydrothassa cf. *hannoveriana* (Fabricius, 1775)	B3	WP	SA-T	H
Chrysomela populi Linnaeus, 1758	B3	P	B-ST	S
Curculionidae				
Cyriophthalmus variegatus (Motschulsky, 1846)	B3	EP	B	P
Sitona cf. *ovipennis* Hochhuth, 1851	B3	EP	T	P
Grypus equiseti (Fabricius, 1775)	B2B3	C	SA-T	H
Grypus cf. *brunneirostris* (Fabricius, 1792)	B3	C	B-T	H
Notaris cf. *acridulus* (Linnaeus, 1758)	B3	P	B-T	H
Dorytomus cf. *imbecillus* Faust, 1882	B3	EN+EP	LA-B	S
Pseudostyphlus pillumus (Gyllenhal, 1836)	B3	WP	T	P
Anoplus cf. *plantaris* (Naezen, 1794)	B3	WP	B-T	S
Rhyncolus cf. *brunneus* Mannerheim, 1843	B3	N	B-T	S
Magdalis cf. *violacea* (Linnaeus, 1758)	B3	P	B-T	S
Lepyrus cf. *arcticus* Paykull, 1792	B3	P	LA-SA	S
Litodactylus leucogaster (Marsham, 1802)	B3	WP	B-T	A
Micrelus cf. *ericae* (Gyllenhal, 1813)	B3	WP	SA-T	P
Scolytidae				
Tomicus piniperda (Linnaeus, 1758)	B3	C	B-ST	S
Scolytus piceae (Swaine, 1934)	B3	N	B	S
Trypophloeus cf. *bispinulus* Eggers 1927	B3	WP	B	S

HYMENOPTERA				
Siricidae				
Urocerus cf. *gigas* (Linnaeus, 1758)	B3	C	B	S
Formicidae				
Camponotus cf. *herculeanus* (Linnaeus, 1758)	B3	C	SA-T	S
DIPTERA				
Chironomidae				
Corynocera ambigua Zetterstedt, 1840	B3	C	LA-B	A
TRICHOPTERA				
Hydropsychidae				
Arctopsyche ladogensis (Kolenati, 1859)	B3	C	SA-B	A
Hydropsyche nevae Kolenati, 1858	B3	P	B	A
Phryganeidae				
Agrypnia pagetana Curtis, 1835	B3	C	LA-T	A
Agrypnia straminea Hagen, 1873	B3	N	LA-T	A
Banksiola cf. *crotchi* Banks, 1944	B3	N	B	A
Brachycentridae				
Brachycentrus americanus Banks, 1899	B3	N+EP	LA-T	A
Limnephilidae				
Apatania crymophila McLachlan, 1880	B3	WN+EP	LA-B	A
Apatania cf. *nigra* Walker, 1852	B3	EN	B-T	A
Halesochila taylori (Banks, 1904)	B3	WN	B-T	A
Dicosmoecus obscuripennis Banks, 1938	B3	WN+P	B	A
HEMIPTERA				
Pentatomidae				
Eusarcoris punctatus (Linnaeus, 1758)	B3	P	B-T	H
Drepanosiphidae				
Chaitophorus cf. *salijaponicus* Mordvilko, 1929	B3	P	B-ST	S

A number of ecological terms are used. HABITAT denotes the physical space occupied by a species, whereas BIOTOPE means a certain, fairly homogenous living place for a number of species. STENOTOPIC species have a narrowly defined habitat, contrary to EURYTOPIC species which are found in a broad range of biotopes. HYGROPHILIC and XEROPHILIC denote species preferring either damp or dry biotopes, respectively; THERMOPHILIC species prefer high temperatures. RIPARIAN species are found on shores, SILVICOLOUS species are forest dwellers, ARBOREAL species live on or in trees. MONOPHAGOUS and OLIGOPHAGOUS species are specialized on one or a few food items, whereas POLYPHAGOUS species are fairly indiscriminate. PHYTOPHAGOUS taxa are plant-eaters, while FUNGIVOROUS species devour fungi.

Taxonomical part

A survey of all named species, including information on occurrence in the units of Member B, present geographical distribution, present climatic distribution, and ecological group is found in Table 3.

The taxonomy and nomenclature of North European species of Coleoptera follow Silfverberg (1992).

Information on modern distribution and habitat of the nominal species is given whenever possible. Regarding climatic distributions, "temperate" always means southern temperate and "boreal" does not include "subarctic" (cf. above).

The list of other fossil occurrences is restricted to late Tertiary-early Quaternary records provided by John V. Matthews (personal communication 1994; Matthews, in press). Figs 31 & 32 show the localities mentioned.

Abbreviations used: B1, B2, B3 followed by numbers: stratigraphic units of Member B and locality-numbers (see Table 1 and Fig. 7).

n.s.: nominal species.

A number of colleagues have taken part in the identification:

Insects in general: John V. Matthews, Ottawa, Canada; G. Russell Coope, Birmingham, U.K.

Coleoptera in general: Michael Hansen, ZMUC, Denmark

Elaphrus (Carabidae): Henri Goulet, Ottawa, Canada

Dromius (Carabidae), ***Ptinus*** (Ptinidae): Boris Kataev, St. Petersburg, Russia

Dytiscidae: Anders Nilsson, Umeå, Sweden

(overview): Mogens Holmen, Hillerød, Denmark

Helophorus (Hydrophilidae): Robert Angus, Egham, U.K.

Staphylinidae (overview): Viggo Mahler, Århus, Denmark

***Stenus*:** Volker Puthz, Schlitz, Germany
***Coryphium*:** Anthony Davies, Ottawa, Canada
***Bledius*:** Lee H. Herman, New York, U.S.A.
***Tachyporus*, etc.:** Scott A. Elias, Boulder, Colorado, U.S.A.
Byrrhidae: Paul J. Johnson, Madison, Wisconsin, U.S.A.
Curculionidae: Robert S. Anderson, Ottawa, Canada; Boris A. Korotyaev, St. Petersburg, Russia
***Scolytus*:** Stephen L. Wood, Provo, Utah, U.S.A.
Wood-boring Coleoptera: Matti Nuorteva, Helsinki, Finland
Hymenoptera in general: Ole Lomholdt, ZMUC, Denmark
Wood- and seed-boring Hymenoptera: Broder Bejer, Copenhagen, Denmark
Chironomidae: Wolfgang Hofmann, Plön, Germany
Trichoptera: Nancy Williams, Toronto, Canada
Aphidoidea: Ole E. Heie, Copenhagen, Denmark

References to the literature on identification, distribution and ecology of the species are generally not included. The most important works used are:
Arctic insects: Danks (1981).
Coleoptera in general: Arnett (1983); Böcher (1988); Brundin (1934); Dillon & Dillon (1961); Fjellberg (1972); V. Hansen (1908-1973, 1964); Holdhaus & Lindroth (1939); Horion (1941-74); Larsson & Gigja (1959); Poppius (1910); Schenkling (1926-1940); Silfverberg (1992); Strand (1946).
Carabidae: Ball (1966); Goulet (1983); Lindroth (1945a-b, 1949, 1954, 1961-69, 1985-86); Thiele (1977).
Dytiscidae: Balfour-Browne (1940, 1950); Larson (1975); Nilsson & Holmen (1995).
Hydrophiloidea: Balfour-Browne (1958); Angus (1970); M. Hansen (1987).
Staphylinidae: Campbell (1968, 1973, 1979, 1982, 1983, 1984); Herman (1986); Palm (1948, 1961).
Scarabaeidae: Brown (1931); Landin (1957).
Coccinellidae: Gordon (1985).
Chrysomelidae: Brown (1956); Silfverberg (1994).
Hymenoptera: Krombein *et al.* (1979).
Formicidae: Collingwood (1979).

COLEOPTERA

Carabidae

Trachypachus zetterstedtii (Gyllenhal, 1827)
Material: Two elytra (B3: 75, 77).
Distribution: Boreal Eurasia from Norway to E Siberia; rare species with scattered occurences.
Habitat: Indigenous to the conifer region, in dense, mixed forest with a rich herb vegetation and a thick layer of litter.
Fossil occurrences: Matthews (1979a, in press) show several types of *Trachypachus* both from Lava Camp, Seward Peninsula, Alaska (Late Miocene: 5.7 Ma) and from different Beaufort Formation localities, including Meighen Island (Pliocene). Some of these may represent *T. zetterstedtii* (John V. Matthews, personal communication 1995).

Nebria* cf. *rufescens (Ström, 1768)
Material: Two pronota, five elytra (B3: 77, 132).
Distribution (n.s.): Circumpolar, low arctic to subarctic, in Europe boreo-alpine. SW Greenland.
Habitat (n.s.): Almost confined to gravelly shores of streams and lakes with cold water, in Greenland especially along brooks surrounded by vigorous vegetation and in marshy areas. The preferred temperature is about 8°C (Krogerus 1960).

Nebria* cf. *nivalis (Paykull, 1790)
Material: Eight elytra (two fragments) (B3: 77, 119, 122).
Distribution (n.s.): Circumpolar, low arctic to subarctic; mainly alpine.
Habitat (n.s.): Sparsely vegetated mountain areas, usually near glaciers, along meltwater streams and on the shores of lakes with cold water. The species prefers even lower temperature than *N. rufescens* (Krogerus 1960).
Fossil occurrences (n.s.): Lava Camp, Seward Peninsula, Alaska (Late Miocene: 5.7 Ma).

Opisthius richardsoni Kirby, 1837
Material: Fragments of one head and one elytron (B3: 77).
Distribution: NW North America, boreal.
Habitat: Confined to clayish, sparsely vegetated banks of rivers and brooks where the larvae dig burrows, as a rule in company with *Bledius* spp.
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene).

Notiophilus aquaticus (Linnaeus, 1758)
Material: Two elytra (B1: 50); one elytron (B2: 27); one head, five elytra (B3: 77, 119, 130).
Distribution: Circumpolar, low arctic (subalpine) to temperate; polytypic species.
Habitat: Eurytopic in open, fairly dry biotopes, e.g. dwarf shrub heaths, forest edges, grassland.
Note: In combination with elytra the head may be identified by means of the arrangement of furrows on the clypeus.

Notiophilus* cf. *biguttatus (Fabricius, 1779)
Material: Two pronota (B3: 77).
Distribution (n.s.): Europe, subarctic to temperate.
Habitat (n.s.): Woodlands, mainly in clearings with fairly dry, sun-exposed ground and sparse vegetation; in humid climates also just above forest limit, and in Iceland most frequent on dry and sandy ground with a sparse herbaceous vegetation.

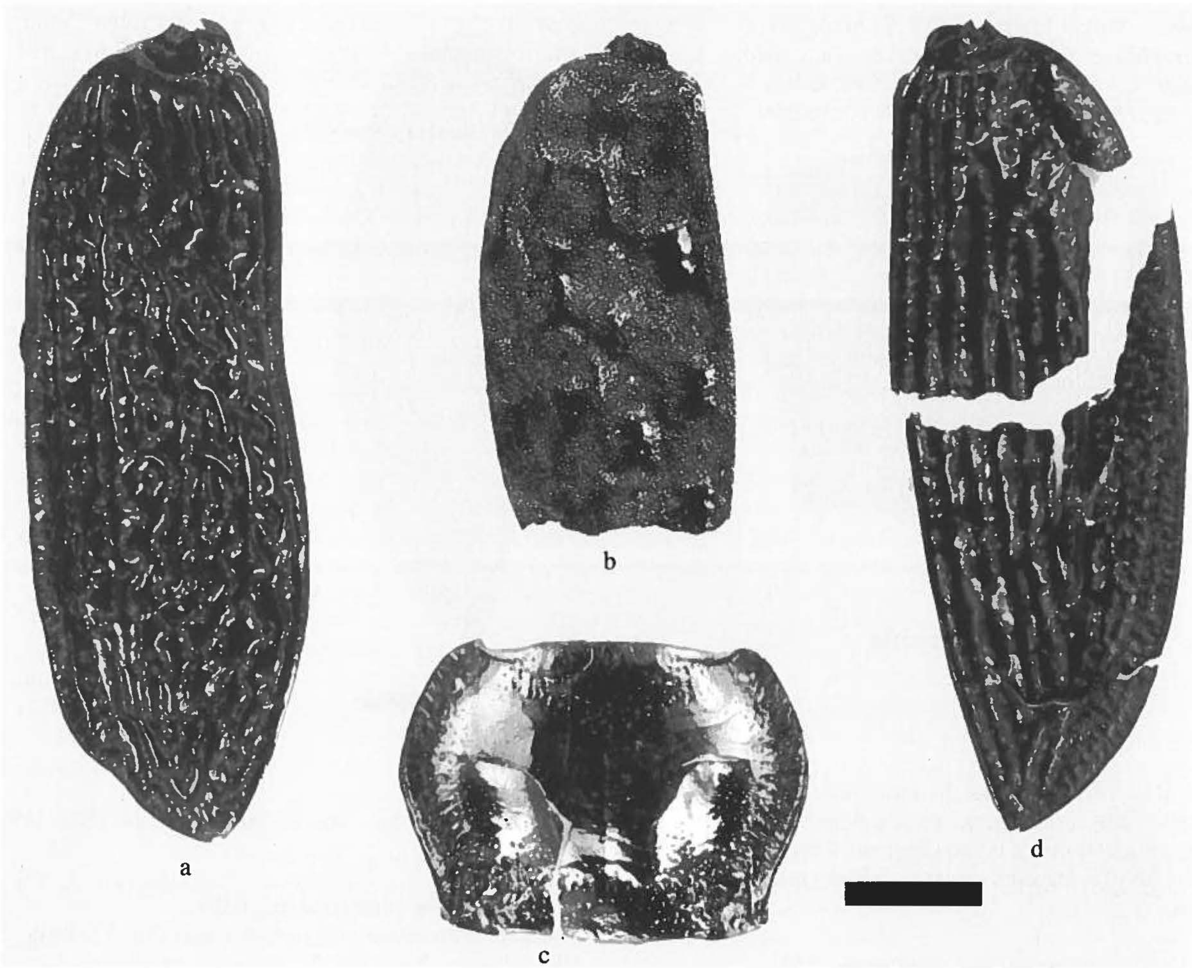


Fig. 9. a) *Pterostichus vermiculosus*, left elytron (64933); b) *Elaphrus tuberculatus*, left elytron (64936); c,d) *Blethisa catenaria*, pronotum (64924) and right elytron (64925). Scale: 1 mm.

Note: Pronota of *N. biguttatus* and *N. reitteri* Spaeth are almost identical, but the side margin is evenly curved in *reitteri*, somewhat angulate in *biguttatus*.

Notiophilus spp.
Material: Two elytra (B1: 50); one elytron (B2: 27); one pronotum (fragment), five elytra (B3: 50, 77).
Note. The elytra have all two preapical punctures, but the second elytral interval is less dilated than normally in the genus. The proportion, second interval : third+fourth intervals, is about 1.1 (in *N. aquaticus* about 1.4) and these elytra may represent a single, unknown species. However, one elytron from Locality 77 (unit B3) differs in having this proportion as small as 0.9 which is only found in one extant species, namely *Notiophilus aeneus* Herbst, 1806. This elytron might thus represent *N. aeneus* or a closely related extinct species. Similar elytra, referred to *N. aeneus*, are known from a number of late Miocene and Pliocene sites in Alaska (Lava Camp: cf. *aeneus*, and Lost Chicken placer mine), Yukon (Bluefish River near Old Crow), and the Canadian Arctic Archipelago (Banks Island, Meighen Island, Ellesmere Island) (Matthews, in press).

N. aeneus is presently distributed in temperate E North America and found in moss or among dead leaves in damp places in deciduous forests.

Cicindela cf. ***hybrida*** Linnaeus, 1758
Material: One head (B3: 132). Fig. 11,a.
Distribution (n.s.): Eurasia, boreal to southern temperate; polytypic.
Habitat (n.s.): Open, sun-exposed biotopes such as dry, sandy grass areas and dunes. Highly thermophilic species.
Note: The identification is tentative, based on the combination of size, general morphology, microsculpture, and the small number of setal sockets (two) inside the margin of the eyes (Fig. 11,a). See also p. 12-13.

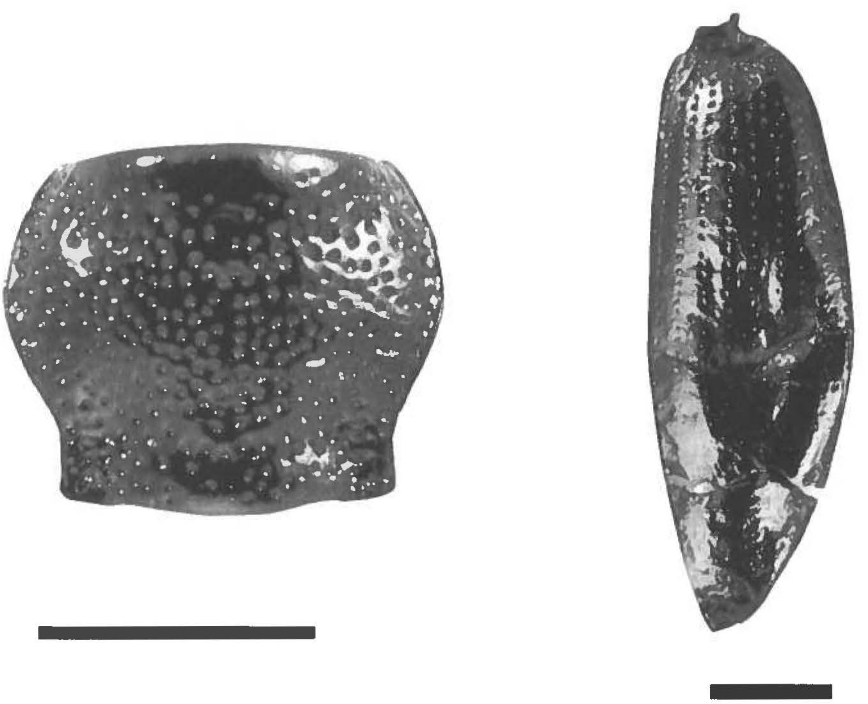


Fig. 10. *Diacheila mattewsi*, pronotum (53214) and right elytron (64924). Scales: 1 mm.

It is remarkable that the only find of the genus was of this relatively southern species, which in Scandinavia is not found north of central Finland. This might mean that the fossil represents an extinct sister species to *C. hybrida*.

Blethisa multipunctata (Linnaeus, 1758)
Material: Two pronota (B3: 77).
Distribution: Circumpolar, boreal to temperate.
Habitat: Marshy, sun-exposed ground in fens with a rich vegetation of Cyperaceae and mosses at the margins of lakes and slowly running rivers.
Fossil occurrences: Prince Patrick Island & Meighen Island, Beaufort Formation (Pliocene).

Blethisa catenaria (Brown, 1944)
Material: Three pronota, five elytra, six elytral fragments (B3: 77). Fig. 9,c,d.
Distribution: NE Siberia, few localities in Canada west of Hudson Bay and Alaska; low arctic to subarctic.
Habitat: Muddy margins of small tundra pools with vegetation of *Eriophorum angustifolium* and mosses.
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene); Beaver Peat & Strathcona Fiord, Ellesmere Island (early Pliocene?); Kutuyakh suite, E Siberia (late Pliocene); Olyor suite, E Siberia (early Pleistocene).

Blethisa spp.
Material: One head, one elytron fragment (B3: 119, 130).

Diacheila polita (Faldermann, 1835)
Material: Four elytra, one metasternum (B3: 77, 119).
Distribution: NW North America, Kola Peninsula through Siberia to Kamchatka; low arctic to subarctic.
Habitat: Both fairly dry heaths with e.g. *Betula nana* and *Vaccinium uliginosum* and the margins of small tundra pools with *Carex* spp. Also reported from well drained tussock tundra with shrubs of *Salix* and *Betula glandulosa* (in Brooks Range, Alaska; Schwert *et al.* 1992).

Diacheila matthewsi n. sp.
Material: One prothorax (B3: 122); one prosternal fragment (B3: 119); four elytra (B3: 77, 119). Figs 10, 11,b,c.

In addition to what is undoubtedly *D. polita*, the material comprises fragments of another species of *Diacheila*, which can not be referred to any of the known species.

Four elytra are smaller (average 4.2 mm in length, 1.5 mm in width; only two are complete) than the elytra of *D. polita* and *D. arctica* (Gyllenhal), but of the same size as the elytra of *D. fausti* Heyden. The known species have all more or less distinct, nearly isodiametric microsculpture on the elytra, whereas the elytra of the new species are without any trace of microsculpture.

One complete and very well-preserved prothorax is

Table 4. Comparison of selected body parts of four species of *Diacheila* Motschulsky, 1845 (Carabidae). The measurements are averages from five *arctica*, six *polita*, two *fausti*, and from one prothorax and five (three complete) elytra of *matthewsi*

	arctica	*polita*	*fausti*	*matthewsi*
Pronotum:				
Length (mm):	1.8	1.8	1.4	1.5
Width (mm):	2.1	2.1	1.8	1.8
Punctation:	fine	fine	fine	coarse
Carina:	strong	absent	trace	trace
Hind angels:	obtuse	right	acute	right
Sides:	slightly concave	sinuate	sinuate	sinuate
Prosternum:				
Punctation:	fine	fine	coarse	coarse
Microsculpture:	distinct	absent	distinct	absent
Elytra:				
Length (mm, from shoulder):	5.7	5.3	4.1	4.2
Greatest width (mm):	2.0	1.9	1.6	1.5
Microsculpture:	strong isodia-metric	weak isodia-metric	strong isodia-metric	absent

referred to the same species as the small elytra (Fig. 10). The pronotum is characterized by a very coarse and irregular punctation and has only a suggestion of a lateral carina inside the hind angles. The black, somewhat shiny prosternum has coarse, shallow punctures. The prothorax and elytra of the four species are compared in Table 4.

Matthews (1979a, 1979b, in press) described and figured a pronotum of a *Diacheila* species from the Beaufort Formation on Meighen Island. Later this *Diacheila polita* Type A has been found in several other sites, both of the Beaufort Formation and on the mainland of Canada (Matthews, in press). Matthews considered the species very close to *D. polita*, but the pronotum appears to be indistinguishable from the pronotum of *D. matthewsi*. It is accordingly assumed that the pronota from both the Canadian sites and Kap København belong to the same species, *Diacheila matthewsi*, which is further characterized by the small, smooth elytra (see Table 4 and the following description). The species is presumably extinct.

Fossil occurrences (of *Diacheila polita* Type A): Lost Chicken placer mine, Fortymile District, Alaska (middle Pliocene: 2.9 Ma.); Niguanak Site, N Alaska (Pliocene?); Bluefish River near Old Crow, Yukon Territory (Pliocene?); Ballast Brook, Banks Island & Prince Patrick Island & Meighen Island, all belonging to the Beaufort Formation (Pliocene); Beaver Peat, Strathcona Fiord & Riediger Site, Vendom Fiord region, both Ellesmere Island (early Pliocene?).

Description of a new species of Coleoptera: Carabidae *Diacheila matthewsi* n.sp.

Type material

One prothorax, one prosternal fragment, three right elytra, one left elytron.

The material is deposited in the Zoological Museum, University of Copenhagen, Denmark.

Holotype. Prothorax together with right elytron A, labelled KKF 53214 and KKF 64924, respectively.
Paratypes. Prosternal fragment labelled KKF 64917; right elytron B labelled KKF 64930; right elytron C (incomplete, anterior three fourths) labelled KKF 64936; elytron D labelled KKF 53203.

Description

Pronotum. Length 1.48 mm; width 1.75 mm. The sides are moderately sinuate, with greatest width two fifths from anterior angles. Hind angles approximately right and with a weak latero-basal carina. Punctures very coarse, highly variable in width (on average about 0.03 mm) and irregularly disposed, frequently with mutual distances more than twice the diameter. The integument black and shining. Microsculpture absent.
Prosternum. Sculpture similar to pronotum, with very

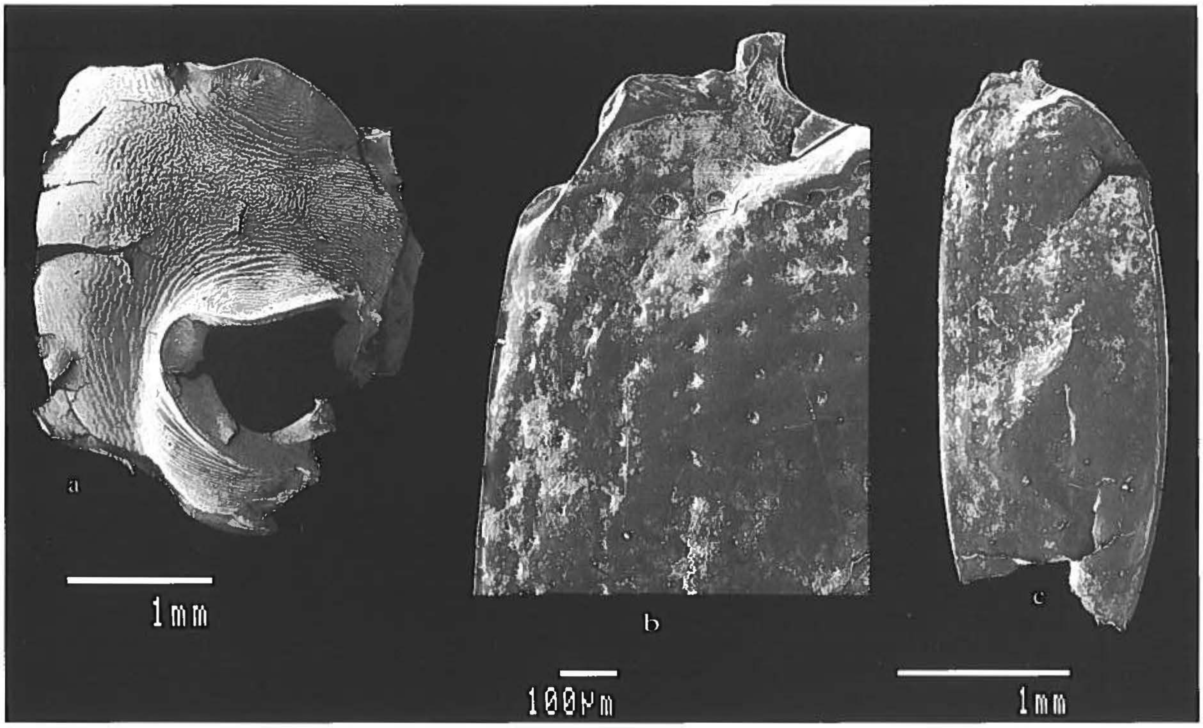


Fig. 11. a) *Cicindela* cf. *hybrida*, head (53265); b,c) *Diacheila matthewsi*, right elytron (64936). Scanning electron micrographs.

coarse, shallow punctures. Microsculpture absent. Colour shining black.

Elytra. A: Length (from shoulder) 4.25 mm, greatest width (at middle) 1.50 mm. B: Length 4.00 mm, greatest width 1.48 mm. C: Greatest width 1.40 mm. D: Length 4.25 mm, greatest width 1.60 mm. Microsculpture entirely absent. Colour shining, uniformly black (except in elytron D which is dull, brownish and less well preserved).

The generic assignment is evident from the evenly dispersed punctation of pronotum, which has a thin, anteriorly missing, raised margin; and from the elytra, which have an incomplete basal border and striae represented by more or less irregular rows of punctures, on third interval disturbed by a number of foveate dorsal punctures.

The species is distinguished from the other species of the genus by the small size (except *D. fausti*), the coarse and comparatively irregular punctation of prothorax, and the absence of microsculpture on both prothorax and elytra (see the comparison in Table 4).

Geographical distribution

The species is only known as fossils from unit B3 of the Plio-Pleistocene Kap København Formation, Peary Land, Greenland, and is probably extinct. It is, however, possible that this species is identical with "*Diacheila polita* Type A" of John V. Matthews which has been found widespread in Pliocene sediments from the Canadian Arctic (Matthews 1979a, 1979b, in press).

Derivation of specific epithet

Named after John V. Matthews Jr., Ottawa, Canada, pioneer investigator of North American Late Tertiary and Quaternary insect and plant fossils.

Elaphrus lapponicus Gyllenhal, 1810

Material: Three pronota, 12 elytra (2 fragments) (B3: 77, 119, 132).

Distribution: Circumpolar, subarctic (subalpine).

Habitat: Small, vigorous, sun-exposed fens with *Carex*, *Eriophorum* and mosses (e.g. *Paludella*), often near wells and streams. The preferred temperature (about 13°C) is higher than typical of most other alpine and subalpine carabid species (Krogerus 1960).

Fossil occurrences: Bluefish River near Old Crow, Yukon Territory (Pliocene?); Meighen Island, Beaufort Formation (Pliocene).

Note. The fossil specimens are typical of the species, though in many specimens the punctures are washed out (Henri Goulet, personal communication 1991).

Elaphrus sibiricus Motschulsky, 1846

Material: One pronotum (B3: 75).

Distribution: E Siberia to Kamchatka and N Japan; boreal.

Habitat: River banks and lake shores.

Elaphrus cf. ***olivaceus*** LeConte, 1863

Material: One elytron (B3: 77).
Distribution (n.s.): Transcontinental in North America, boreal to temperate.
Habitat (n.s.): Sun-exposed, organic mud flats, e.g., in *Typha*-marshes and in *Carex*-swamps along ponds and rivers.
Note. The fossil elytron appears to be more strongly punctate than in modern specimens (Henri Goulet, personal communication 1991).

Elaphrus lecontei Crotch, 1876
Material: One elytron (B3: 77).
Distribution: Almost confined to the prairie region of western North America; temperate.
Habitat: Sparsely vegetated mud flats close to the water at the shores of alkaline lakes and ponds ("halobiont").

Elaphrus tuberculatus Mäklin, 1877
Material: Three elytra (B1: 50), one elytron (B2: 50), three pronota, nine elytra and one mesosternum (B3: 69, 77, 119). P. 1; Figs 8, 9b.
Distribution: Holarctic (in North America not recorded east of Mackenzie River); low arctic to subarctic.
Habitat: In North America exclusively found on silt beaches along large rivers, especially in vegetation of *Equisetum fluviatile* in front of the willow zone. In Europe the species seems to be more eurytopic (but see note).
Note. Lindroth (1945a, 1961, 1985) regarded *E. tuberculatus* a northern form of *E. riparius* (Linnaeus). The fossil fragments are typical of *E. tuberculatus* in being heavily microsculptured and less densily punctured in the elytral intervals (Henri Goulet, personal communication 1991).

Elaphrus angusticollis F. Sahlberg, 1844
Material: One pronotum, four elytra (B3: 77, 119).
Distribution: Holarctic (in North America not found east of Mackenzie River, absent from Scandinavia); subarctic.
Habitat: Along rivers at some distance from the water, on sand-mixed clay in moderately dense vegetation, e.g. under bushes.
Note. The fossils are very close to modern *E. angusticollis*, but punctures are denser and slightly smaller in elytral pits, and the pronotal epipleuron is less punctate. It is definitely not *E. purpurans* Hausen (Henri Goulet, personal communication 1991).

Elaphrus spp.
Material: One metepisternum (B1: 50); four heads, two prosterna, four elytron fragments, one mesepisternum+epimeron, one metepisternum (B3: 69, 77, 119).

Dyschirius cf. ***varidens*** Fall, 1910
Material: One elytron (B3: 77).
Distribution (n.s.): W North America (from Washington south to California and Idaho); temperate.
Note. The elytron, which is without apex, has marginated base inside the shoulder and apparently three subhumeral fovea. This combination precludes all N and C European species and seems to limit the possibilities to three North American species, all found west of the Rocky Mountains (*D. varidens* Fall, *D. tridentatus* LeConte, *D. patruelis* LeConte). The small size and the shallow elytral striae effacing towards the apex definitely point at *D. varidens* (Lindroth 1961, Bousquet 1988).
Fossil occurrences (n.s.): Niguanak Site, N Alaska (Pliocene?). Fossils belonging to this species group (the *tridentatus* group, subgenus *Dyschiridius* Jeannel) have also been found on Meighen Island, Beaufort Formation (Pliocene).

Dyschirius spp.
Material: One elytron (B1: 50); one pronotum, 13 elytra (B3: 50, 69, 75, 77, 119).
All elytra are smooth and have 2-3 subhumeral fovea, but due to differences in size and shape represent at least two species.

Miscodera arctica (Paykull, 1798)
Material: One elytron (B3: 77).
Distribution: Circumpolar, low arctic to boreal (a few occurrences in temperate Europe are probably glacial relicts).
Habitat: Fairly dry, sandy localities, e.g. heaths with *Calluna* and *Empetrum*, and also alpine grass heaths and sparsely vegetated high mountain areas. As a rule the species is found together with species of Byrrhidae, the larvae of which it probably preys upon.

Patrobus stygicus Chaudoir, 1871
Material: Two heads, three pronota, seven elytra (B3: 77, 119).
Distribution: Transcontinental in North American (Alaska, Canada), boreal.
Habitat: The border of lakes, ponds and slowly running rivers and in marshes with high and dense vegetation (e.g. *Carex* spp., *Comarum* (= *Potentilla palustris*), *Menyanthes*, mosses), where the species has almost amphibious habits.

Asaphidion alaskanum Wickham, 1919
Material: One pronotum, five elytra (B3: 77).
Distribution: NW North America, low arctic to subarctic.
Habitat: Banks of rivers and brooks, but in considerable distance from the water, on sandy soil with sparse vegetation.
Fossil occurrences: Bluefish River near Old Crow, Yukon Territory (Pliocene?); Banks Island, Prince Patrick Island & Meighen Island, all Beaufort Formation (Pliocene).

Bembidion (Chrysobracteon) levettei Casey, 1918
Material: Five elytra (B3: 69, 77, 119).

Distribution: Transcontinental in North America, boreal.
Habitat: Clayish or sandy soil with sparse vegetation at the border of streams.
Fossil occurrences: Ballast Brook, Banks Island, Beaufort Formation (Pliocene).

Bembidion (Chrysobracteon) alaskense Lindroth, 1962
Material: One elytron (B3: 119).
Distribution: Confined to boreal Alaska.
Habitat: Presumably barren lake shores.

Bembidion (Chrysobracteon) cf. ***velox*** (Linnaeus, 1761)
Material: One pronotum (B1: 50), one elytron (B3: 69).
Distribution (n.s.): N and C Europe, Siberia; boreal to temperate.
Habitat (n.s.): Barren, firm, moist sand close to the water on river and lake shores and by the sea.

Bembidion (Chrysobracteon) cf. ***lapponicum*** Zetterstedt, 1828
Material: One pronotum (B3: 77).
Distribution (n.s.): Almost circumpolar (in North America only west of Hudson Bay); low arctic to subarctic (alpine).
Habitat (n.s.): Sparsely vegetated or barren shores of lakes and rivers, preferably on slightly moist sand.

Bembidion (Chrysobracteon) cf. ***balli*** Lindroth, 1962
Material: One elytron (B3: 77).
Ditribution (n.s.): Known only from the type locality in Alberta (Fort McMurray), boreal Canada.
Habitat (n.s.): Found on bare mud flats on a river shore.

Bembidion (Chrysobracteon) spp.
Material: Two heads, three elytron fragments (B3: 77, 119).

Bembidion cf. ***vitiosum*** Gemminger & Harold, 1868
Material: One pronotum (B3: 77).
Distribution (n.s.): E Siberia.
Note. The identification is somewhat tentative. There is no doubt as to the subgenus *Eurytrachelus* Motschulsky (= *Eudromus* Kirby), of which the nearctic species can be excluded and also the western palaearctic *laticolle* Duftschmid. Of the few remaining, mostly Siberian species, I have only seen one specimen of *vitiosum* (ZMUC). The fossil pronotum is a little broader, but otherwise very much like that of *vitiosum*, apart from the meshes of the microsculpture, which are isodiametric in the fossil and clearly transversal in the modern *vitiosum* studied.

Bembidion dyschirinum LeConte, 1861
Material: One elytron (B1: 50), four elytra (B3: 75, 77, 119).
Distribution: The western mountains of boreal North America; subalpine.
Habitat: Open, hilly country on sandy soil (moraine) with scattered bush vegetation (*Alnus*).
Fossil occurrences: Prince Patrick Island & Meighen Island, Beaufort Formation (Pliocene); Beaver Peat & Strathcona Fiord, Ellesmere Island (early Pliocene?).

Bembidion lampros (Herbst, 1784)
Material: One elytron (B3: 69).
Distribution: Europe and Siberia, introduced in North America; boreal to temperate.
Habitat: Highly eurytopic on open, sun-exposed ground with sparse vegetation, often with dry, sandy soil.

Bembidion (Plataphodes) cf. ***fellmanni*** Mannerheim, 1823
Material: Nine elytra (B1: 50), one elytron (B2: 50), three pronota and 19 elytra (B3: 50, 77, 119).
Distribution (n.s.): N Europe to E Siberia, in Europe boreo-alpine; low arctic to subarctic (alpine-subalpine).
Habitat (n.s.): Gravelly shores of streams, lakes and the sea and also subalpine meadows.
Note. The microsculpture of the elytra consists of fairly characteristic transverse meshes (fig. 210 in Lindroth 1985).

Bembidion (Plataphodes) cf. ***difficile*** (Motschulsky, 1844)
Material: Two pronota (B3: 77).
Distribution (n.s.): N Europe to Siberia and Mongolia, in Europe boreo-alpine; boreal forest region.
Habitat (n.s.): Mainly sparsely vegetated moist soil along streams, notably somewhat shady sites, e.g. under *Salix* bushes; less frequently lake- and seashores.
Note. The pronota resemble very much those referred to *B.* cf. *arcticum*, but are significantly larger.

Bembidion (Plataphodes) cf. ***arcticum*** Lindroth, 1963
Material: Two pronota, one elytron (B1: 50), five pronota, five elytra (B3: 77).
Distribution (n.s.): NW North America (Yukon, Alaska), E Siberia; low arctic to subarctic.
Habitat (n.s.): Barren banks of gravel and stones close to the water along streams; also at the margin of ponds and pools on the tundra.
Note. Elytra referred to this species are smaller than those of *B. fellmanni* and have microsculpture with almost isodiametric meshes.

Bembidion (Plataphodes) sp.
Material: Three elytra (B1: 50); four elytra (B3: 77), probably representing a single, small, unidentified species.

Bembidion (Plataphus) planatum LeConte, 1848
Material: Six elytra (B3: 77, 119).
Distribution: Disjunct in boreal E and W North America.

Habitat: Close to the water on barren, stony and gravelly banks of streams.
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene).

Bembidion (Plataphus) cf. ***planiusculum*** Mannerheim, 1843
Material: One elytron (B1: 50), ten elytra (B3: 77, 119).
Distribution (n.s.): Western coastland of boreal North America.
Habitat (n.s.): Barren, gravelly banks of streams, especially small creeks.
Note. Elytra referred to this species are often rufinistic and with a distinct carina in the interval outside 5. stria, close to the apex; the microsculpture consisting of transverse, irregular, rectangular meshes. Almost no punctures in striae.

Bembidion (Plataphus) cf. ***gebleri*** Gebler, 1833
Material: Two elytra (B1: 50), six elytra (B3: 77, 119).
Distribution (n.s.): Holarctic, from W Siberia to NW North America; boreal (and subalpine).
Habitat (n.s.): Barren, gravelly banks of streams, mostly large rivers.
Note. Elytra referred to this species have small size with largest width distally to the middle, obtuse apex and isodiametric microsculpture.

Bembidion (Plataphus) spp.
Material: One elytron (B1: 50); one elytron (B3: 77).

Bembidion salebratum LeConte, 1848
Material: Three elytra (B3: 77).
Distribution: Boreal North America east of Rocky Mountains.
Habitat: Fairly eurytopic, usually barren banks of quite small streams.
Note. Among nearctic species *B. salebratum* is the only possibility. The palaearctic *B. hirmocaelum* Chaudoir has denser, transversal microsculpture, and 7. stria is not visible to the apex.

Bembidion cf. ***mckinleyi*** Fall, 1926
Material: Five pronota, 17 elytra (B3: 50, 77, 119, 152).
Distribution (n.s.): Canadian Rocky Mountains, Scandinavia, Baical area (Siberia); subarctic (subalpine).
Habitat (n.s.): Exposed or somewhat shaded, barren sandy-stony banks of small rivers.
Note. Due to their dark, bluish-metallic coloration, most of the elytra can probably be referred to the subspecies *mckinleyi* s. str. (see Lindroth 1963). The elytra may be difficult to separate from those of *B. sordidum*, but the meshes of the microsculpture are weaker, more irregular and approximately isodiametric. – It is very difficult to distinguish the pronota of *B. mckinleyi*, *B. yukonum*, *B. bimaculatum* and *B. sordidum* and the identifications of pronota of these species are accordingly much more tentative than of elytra.

Bembidion cf. ***lenae*** Csiki, 1928
Material: One pronotum (B1: 50).
Distribution (n.s.): E Siberia and NW North America, low arctic to subarctic.
Habitat (n.s.): Dry, sandy sites on river banks in considerable distance from the water, usually in the shelter of *Alnus* bushes.
Note. The pronotum is very similar to that of *B. grapii*, but smaller, less cordiate, and with weaker carina at hind angles.

Bembidion cf. ***grapii*** Gyllenhal, 1827
Material: One elytron (B3: 77).
Distribution (n.s.): Circumpolar, low arctic to boreal (alpine-subalpine). Widely distributed in subarctic and low arctic Greenland. (Note: The find of *Bembidion grapii* in high arctic Northeast Greenland, quoted in Böcher 1988, is probably a mistake).
Habitat (n.s.): Fairly warm and dry situations, usually among sparse vegetation on south facing slopes, but close to richer vegetation, such as along brooks or at the edge of forests.
Fossil occurrences (n.s.): Beaver Peat & Strathcona Fiord, Ellesmere Island (early Pliocene?).
Note. The elytron is very similar to those of *B. yukonum*, but significantly smaller and with more marked transverse "lines" (rows of stretched meshes) in the microsculpture.

Bembidion cf. ***yukonum*** Fall, 1926
Material: Four elytra (B1: 50), five pronota and 24 elytra (B3: 69, 77, 119).
Distribution (n.s.): Almost circumpolar (not found in W Siberia), subarctic (mainly alpine).
Habitat (n.s.): Confined to barren, cracked, clayish soil, both on river banks and far from water.
Note. The elytra have weakly developed microsculpture consisting of long, transversal meshes arranged in rows and giving the impression of a faint cross-striping.

Bembidion cf. ***bimaculatum*** Kirby, 1837
Material: Seven elytra (B3: 77, 119).
Distribution (n.s.): C, W and NW North America, boreal to temperate.
Habitat (n.s.): Moist clayish soil with sparse vegetation, frequently along large rivers, but in some distance from water.
Fossil occurrences (n.s.): Meighen Island, Beaufort Formation (Pliocene).
Note. The microsculpture of the elytra is similar to that of *B. sordidum*, but with weaker, more stretched meshes. I am unable to distinguish pronota of *bimaculatum* and *sordidum*; accordingly some pronota referred to *sordidum* might be from *bimaculatum*.

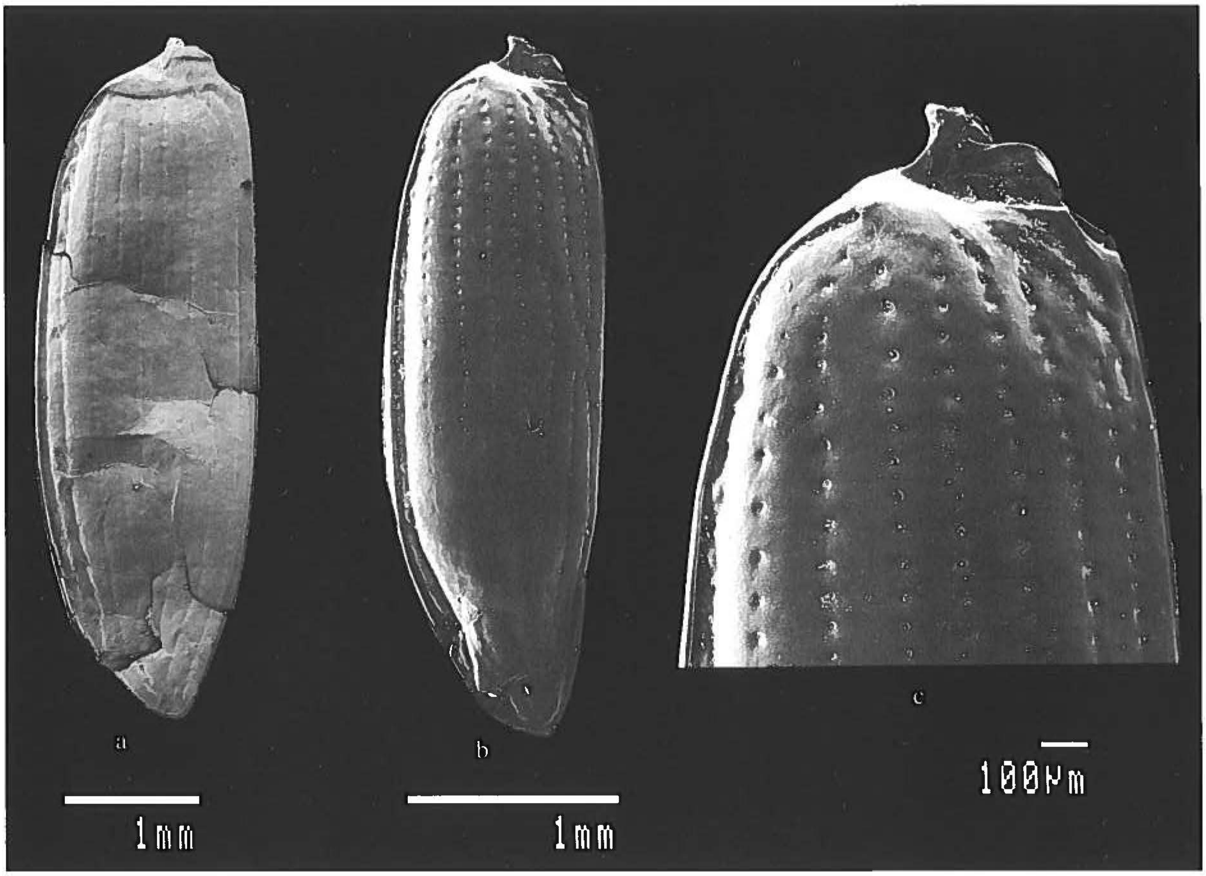


Fig. 12. a) *Pterostichus* (*Cryobius*) sp., left elytron (64937); b,c) *Bembidion* cf. *sordidum*, left elytron (64965). Scanning electron micrographs.

Bembidion cf. ***sordidum*** Kirby, 1837
Material: One pronotum (B1: 50), one elytron (B2: 27), ten pronota, 15 elytra (B3: 50, 75, 77, 119). Figs 12,b,c, 13.
Distribution (n.s.): Boreal North America.
Habitat (n.s.): Almost confined to shaded river banks.
Fossil occurrences (n.s.): Prince Patrick Island, Beaufort Formation (Pliocene); Green Bay beds, Prince Patrick Island (Late Pliocene?); Riediger site, Vendom Fiord region, Ellesmere Island (early Pliocene?).
Note. The elytra are brownish, without metallic hue; microsculpture strong, dense and fairly regular with meshes about twice as long as broad and arranged in transverse rows.

Bembidion spp.
Material: One pronotum, five elytra (B1: 50); three elytra (B2: 27, 50); one head, three pronota, 29 elytra (plus numerous elytron fragments) (B3: 50, 69, 75, 77, 119). Three elytra have distinctive characters and represent three (unknown) species (B3: 77, 119).

Pterostichus stygicus Say, 1823
Material: Two pronota (B3: 69, 77).
Distribution: Eastern North America, boreal to temperate.
Habitat: Hardwood forests or adjoining meadows with rich vegetation.

Pterostichus nigrita (Paykull, 1790) s.l.
Material: One pronotum (B3: 77).
Distribution: Europe, N and W Asia, Morocco; subarctic to subtropical.
Habitat: Confined to very humid biotopes, usually the shores of ponds, lakes and rivers on clayey, humus-rich soil with vigorous vegetation, also in forest swamps.

Pterostichus cf. ***corvinus*** Dejean, 1828
Material: One pronotum (B3: 77).
Distribution (n.s.): Almost transcontinental in North America (not reaching the Pacific coast); boreal to temperate.
Habitat (n.s.): The border of small, standing waters with soft soil and rich vegetation (grasses, *Carex* spp. etc.).
Fossil occurrences: ("cf. *corvinus*") Lava Camp, Seward Peninsula, Alaska (Late Miocene: 5.7 Ma).

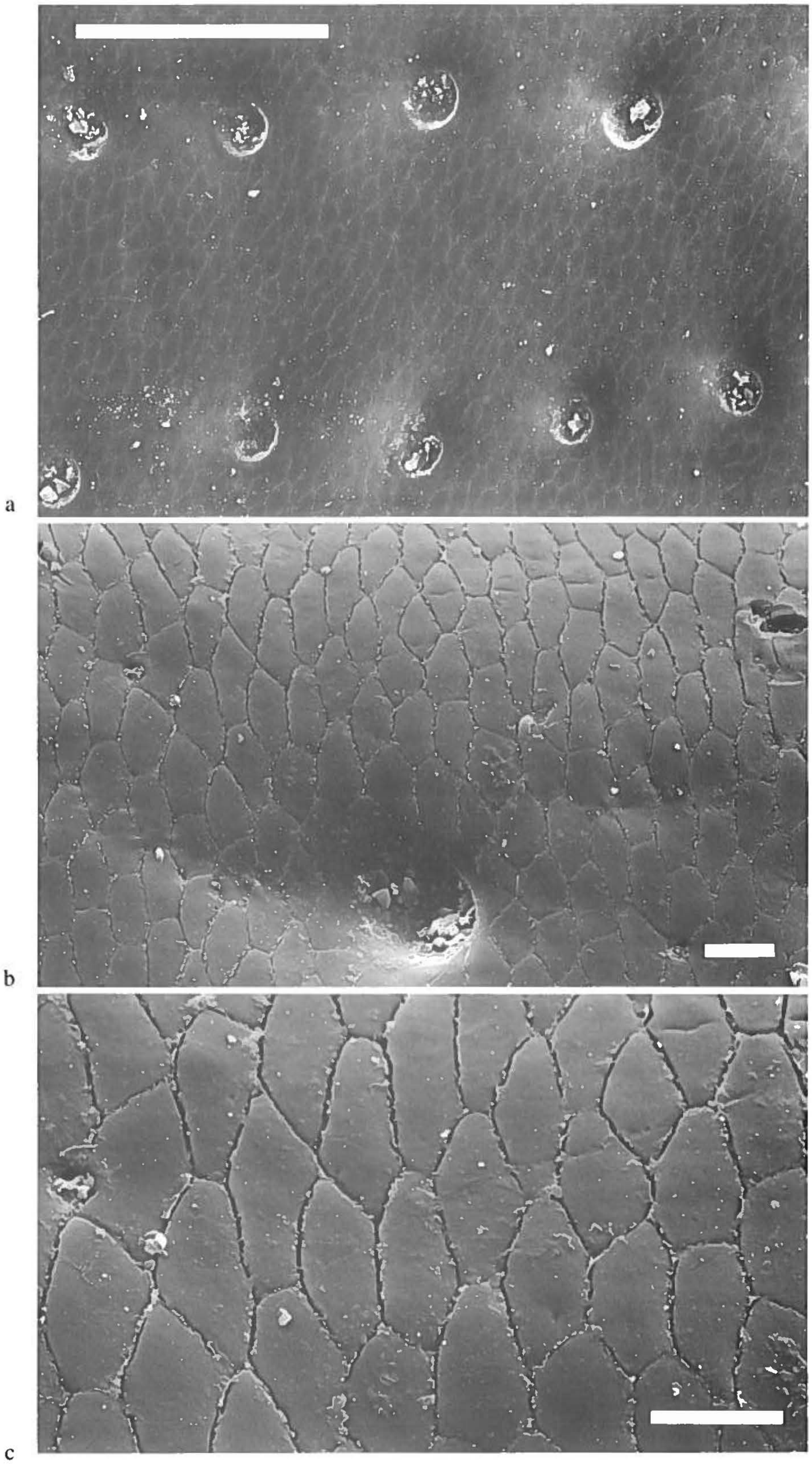


Fig. 13. *Bembidion* cf. *sordidum*, left elytron (64965), showing microsculpture at various magnifications. Scales: a) 100 µm; b,c) 10 µm. Scanning electron micrographs.

Pterostichus cf. ***caudicalis*** Say, 1823
Material: One pronotum (B3: 77).
Distribution (n.s.): Almost transcontinental in North America (not reaching the Pacific coast); boreal to temperate.
Habitat (n.s.): The border of shady eutrophic pools and ponds with soft, humus-rich soil.
Note. The pronota tentatively referred to this species and also to *P. corvinus* are small compared with recent material, but can not belong to any species of subgenus *Cryobius*, nor to a number of small, northern palaearctic species which have been checked.

Pterostichus (Cryobius) cf. ***arcticola*** Chaudoir, 1868
Material: One pronotum (B3: 77).
Distribution (n.s.): Almost transcontinental in North America, low arctic to subarctic (boreo-alpine).
Habitat (n.s.): In Labrador found on meagre coastal tundra.
Fossil occurrences (n.s.): Plateau Cap gravels, Northwest Territories (Late Pliocene).

Pterostichus (Cryobius) cf. ***planus*** J. Sahlberg, 1887
Material: Two elytra (B3: 50).
Distribution (n.s.): Alaska; probably alpine.
Note. The identification is based on size and the characteristic lengthy shape. The microsculpture should be rather weak and with transverse meshes but is barely visible on the fossil.

Pterostichus (Cryobius) cf. ***pinguedineus*** Eschscholtz, 1823
Material: Two pronota (B3: 77, 119).
Distribution (n.s.): Siberia east of Yenissei, North America west of Hudson Bay; low arctic to boreal (boreo-alpine in North America).
Habitat (n.s.): Rich vegetation on the tundra and wet meadows; below tree limit mostly under leaves on river banks.
Fossil occurrences (n.s.): Plateau Cap gravels, Northwest Territories (Late Pliocene); Olyor suite, E Siberia (early Pleistocene).

Pterostichus (Cryobius) riparius Dejean, 1829
Material: Two pronota, one elytron (B3: 77).
Distribution: North America west of Hudson Bay, boreal.
Habitat: Shady, somewhat moist places in forests, often near water; just above the forest limit in mountains. According to Lindroth (1966) the least cold-adapted of the North American species of subgenus *Cryobius*.

Pterostichus (Cryobius) brevicornis Kirby, 1837
Material: Two pronota (B1: 50); one pronotum, nine elytra (B3: 50, 69, 77, 119).
Distribution: N Russia, North America (transcontinental, boreo-alpine); low arctic to subarctic.
Habitat: Among grass and leaves in heaths, grasslands and forests close to the forest limit.
Fossil occurrences: Fosheim Dome sites, Fosheim Peninsula & Riediger Site, Vendom Fiord region, all Ellesmere Island (early Pliocene?).

Pterostichus (Cryobius) spp.
Material: One pronotum, four elytra (B1: 50); six elytra (B2: 27, 50); more than 50 elytra and elytron fragments (B3: 50, 69, 77, 119, 132, 152). On account of differences in size, shape and microsculpture, the elytra represent at least eight species. Fig. 12,a.

Pterostichus vermiculosus Ménétries, 1851
Material: One pronotum, one elytron (B2: 27, 50); three elytra, three elytron fragments (B3: 69, 77). Fig. 9,a.
Distribution: N Russia, N Siberia, North America west of Hudson Bay; low arctic to subarctic.
Habitat: Open tundra, probably not hygrophilic.
Fossil occurrences: Lava Camp, Seward Peninsula, Alaska (late Miocene: 5.7 Ma) ("*cf. vermiculosus*"); Niguanak Site, N Alaska (Pliocene?); Plateau Cap gravels, Northwest Territories (Pliocene?); Prince Patrick Island & Meighen Island, Beaufort Formation (Pliocene); Fosheim Dome sites, Fosheim Peninsula & Beaver Peat, Strathcona Fiord, all Ellesmere Island (Pliocene?); Olyor suite, E Siberia (early Pleistocene).

Pterostichus cf. ***agonus*** Horn, 1880
Material: Three elytra (B3: 77, 119).
Distribution (n.s.): NE Siberia, North America west of Hudson Bay; low arctic.
Habitat (n.s.): Moist tundra vegetation (with e.g. *Eriophorum scheuchzeri, Carex aquatilis, Saussurea alpina*).
Note. The apices of the elytra are more pointed than in modern specimens.

Pterostichus haematopus Dejean, 1831
Material: Two pronota (B3: 77, 141).
Distribution: N Siberia, North America; low arctic to boreal (boreo-alpine).
Habitat: Acording to Lindroth (1966) one of the most characteristic carabids on the tundra, occurring also in the northern coniferous region.
Fossil occurrences: Niguanak Site, N Alaska (Pliocene?); Meighen Island, Beaufort Formation (Pliocene); Beaver Peat, Strathcona Fiord, Riediger Site & Rochon Site, Vendom Fiord region, all Ellesmere Island (early Pliocene?); Olyor suite, E Siberia (early Pleistocene).

Pterostichus spp.
Material: One elytron (B1: 50); one head (B2: 27); one head (B3: 119).

Agonum cf. ***consimile*** (Gyllenhal, 1810)
Material: One pronotum (B3: 69).
Distribution (n.s.): Circumpolar, subarctic (subalpine).

Habitat (n.s.): Mires rich in mosses, *Carex* and *Eriophorum* spp.
Fossil occurrences (n.s.): Meighen Island, Beaufort Formation (Pliocene); Riediger Site & Vendom Fiord region, Ellesmere Island (early Pliocene?).

Agonum cf. ***exaratum*** (Mannerheim, 1853)
Material: One pronotum (B3: 77).
Distribution (n.s.): From Kola Peninsula through Siberia to North America west of Hudson Bay; low arctic to subarctic, but rarely below the tree limit.
Habitat (n.s.): Soft, marshy ground at the margin of ponds and pools with mosses, *Carex* and *Eriophorum* spp.

Agonum spp.
Material: Two pronota, two elytra (B3: 77, 119), probably representing two species.

Amara cf. ***apricaria*** (Paykull, 1790)
Material: One pronotum (B3: 119)
Distribution (n.s.): Almost circumpolar, but probably introduced in North America; subarctic (subalpine) to temperate.
Habitat (n.s.): Eurytopic on moderately dry soil in open country.

Amara cf. ***glacialis*** Mannerheim, 1853
Material: One pronotum (B3: 59).
Distribution (n.s.): North America, Siberia west to Yenissei; low arctic to subarctic.
Habitat (n.s.): Flat, fairly dry, sandy banks of rivers with scattered vegetation (e.g. *Chamaenaerion latifolium*).
Fossil occurrences (n.s.): Meighen Island, Beaufort Formation (Pliocene); Fosheim Dome sites & Fosheim Peninsula, Ellesmere Island (early Pliocene?).

Amara cf. ***quenseli*** (Schönherr, 1806)
Material: Three pronota (B3: 77).
Distribution (n.s.): Circumpolar, in Europe boreo-alpine; subarctic to temperate.
Habitat (n.s.): Open, sandy soil with sparse vegetation, e.g. seashore dunes with *Ammophila* and *Elymus*, but also characteristic of dry alpine and subalpine grasslands and dwarf-shrub heaths (together with *Miscodera arctica*).
Note. The fossil pronota are almost devoid of microsculpture and the punctation is denser than in modern specimens. However, these differences may not be significant considering the extensive variability of this species.

Amara cf. ***brunnea*** (Gyllenhal, 1810)
Material: Three pronota (B3: 77, 132).
Distribution (n.s.): N Eurasia, NW North America; subarctic (alpine-subalpine) to temperate.
Habitat (n.s.): Eurytopic in shady, fairly humid localities, most typically among dead leaves and vegetation in open birch forests, but also in peat bogs and dwarf-shrub heaths above the tree limit.

Amara cf. ***pseudobrunnea*** Lindroth, 1968
Material: One pronotum (B3: 77).
Distribution (n.s.): Almost transcontinental in North America, though not reaching the Pacific coast; boreal.
Habitat (n.s.): Among leaves under bushes on sandy moraine.
Note. The pronotum has punctures along the sides to the front margin; this is mentioned as a rare case by Lindroth (1968).

Amara spp.
Material: One head (B1: 50); two heads, one pronotum, 26 elytra (B3: 50, 69, 75, 77, 119, 132).
Due to differences in size and shape, the elytra represent at least three species.

Chlaenius interruptus Horn, 1876 (***C. alternatus*** Horn, 1871)
Material: One pronotum (B3: 77).
Distribution: Pacific coastland of North America, boreal to temperate.
Note. *C. interruptus* is probably only a western form of *C. alternatus*, which is distributed transcontinentally in North America east of, and thus allopatric with, *C. interruptus* (Lindroth 1969). However, the shape, size, colour and punctation of the fossil pronotum agrees with the western form.
Habitat (both forms): Among rich vegetation on shores of ponds, lakes and slowly flowing rivers.

Dromius cf. ***angusticollis*** J. Sahlberg, 1880
Material: One elytron (B3: 119).
Distribution (n.s.): Ural, Siberia, (boreal?).
Habitat: Probably arboreal like other species of *Dromius* s.str.
Fossil occurrences: A similar species, *D. piceus* Dejean, occurs at Meighen Island, Beaufort Formation (Pliocene).

Carabidae gen. et sp. indet.
Material: Three heads, one elytron fragment, three mesosterna, seven sternites 1+2, tergites/sternites (B1: 50); one sternites 1+2 (B2: 27); 31 heads, several mandibles, a large number of elytron fragments, sterna, sternites 1+2, tergites/sternites (B3: 50, 69, 71, 75, 77, 119, 122).

Haliplidae

Haliplus sp.
Material: Two elytra (B3: 69, 77).
Habitats: Most species of this genus feed on algae in clean, nutrient-rich, vegetated ponds and lakes.

Fossil occurrences: This genus has also been found in the Beaufort Formation on Meighen Island (Pliocene).

Noteridae

Noterus crassicornis (Müller, 1776)
Material: One meso- and metasternum (probably from unit B3).
Distribution: Europe, N Asia; boreal to temperate.
Habitat: Eurytopic in permanent stagnant waters among decaying submerged vegetation.

Dytiscidae

Hygrotus sp.
Material: One elytron (B3: 77).
Habitats: Small, stagnant waters of different type.

Hydroporus acutangulus-group
Material: Two elytra, two metasterna with coxae (B3: 77).
Note. According to Anders Nilsson (personal communication 1994) this group in addition to the palaearctic *H. acutangulus* Thomson comprises two arctic nearctic species: *H. polaris* Fall and *H. subvirescens* Fall, plus a few Siberian species.

Hydroporus cf. ***morio*** Aubé, 1838
Material: Three heads, one thorax, five pronota, 29 elytra (B3: 69, 77, 80, 119).
Distribution (n.s.): Circumpolar, high arctic to boreal. In West Greenland north to *c.* 80°N, but not found north of 66°N along the east coast.
Habitat (n.s.): Eurytopic in stagnant waters, preferably small vegetated ponds and temporary pools.

Hydroporus cf. ***striola*** (Gyllenhal, 1826)
Material: One elytron (B3: 77).
Distribution (n.s.): Circumpolar, boreal to temperate.
Habitat (n.s.): Shallow stagnant water, temporary or permanent, usually with large amounts of plant debris and emergent vegetation (e.g. *Carex*-marshes).
Note. The identification is based on the characteristic colour pattern in combination with the size (Anders Nilsson, personal communication 1991).

Hydroporus oblitus-group
Material: One head + pronotum (B3: 77).
Note. According to Anders Nilsson (personal communication 1994) this group comprises five nearctic and one palaearctic species.

Hydroporus spp.
Material: One elytron (B2: 27); three heads, six pronota, more than 30 elytra and elytron fragments, eight metasterna+coxae (B3: 69, 77, 119, 122, 132).

Oreodytes cf. ***sanmarkii*** (Sahlberg, 1826)
Material: One metasternum with coxae (B3: 119).
Distribution (n.s.): Europe through Siberia to Kamchatka, in North America known only from two localities in the western Low Arctic (Larson 1975); low arctic to temperate, montane in the south.
Habitat (n.s.): Mainly streams and rivers on hard bottoms among sand and gravel, but also along exposed lake shores.
Note. The fossil has stronger punctation than modern specimens.

Oreodytes alpinus (Paykull, 1798)/***laevis*** Kirby, 1837
Material: One elytron, one metasternum with sternites 1-2 (B2: 27); two heads, one pronotum, 13 elytra, 16 metasterna (15 with coxae) (B3: 69, 75, 77, 132).
Distribution: *alpinus*: Fennoscandia to NW Siberia, low arctic (subalpine) to boreal. *laevis*: NW North America, boreal to temperate (subalpine).
Habitat: *alpinus*: oligotrophic rivers and lakes with clear, cool water, on sandy or gravelly bottom without vegetation. *laevis*: Cool or cold silt- or gravel-bottomed pools adjacent to cold, usually swift creeks and rivers or quiet portions of such streams. Frequently associated with silt-laden water of glacial melt-streams (Larson 1975).
Note. According to Nilsson & Holmen (in press), *O. alpinus* and *O. laevis* may belong to the same, circumpolar species.

Oreodytes spp.
Material: Three elytron fragments (B3: 77).

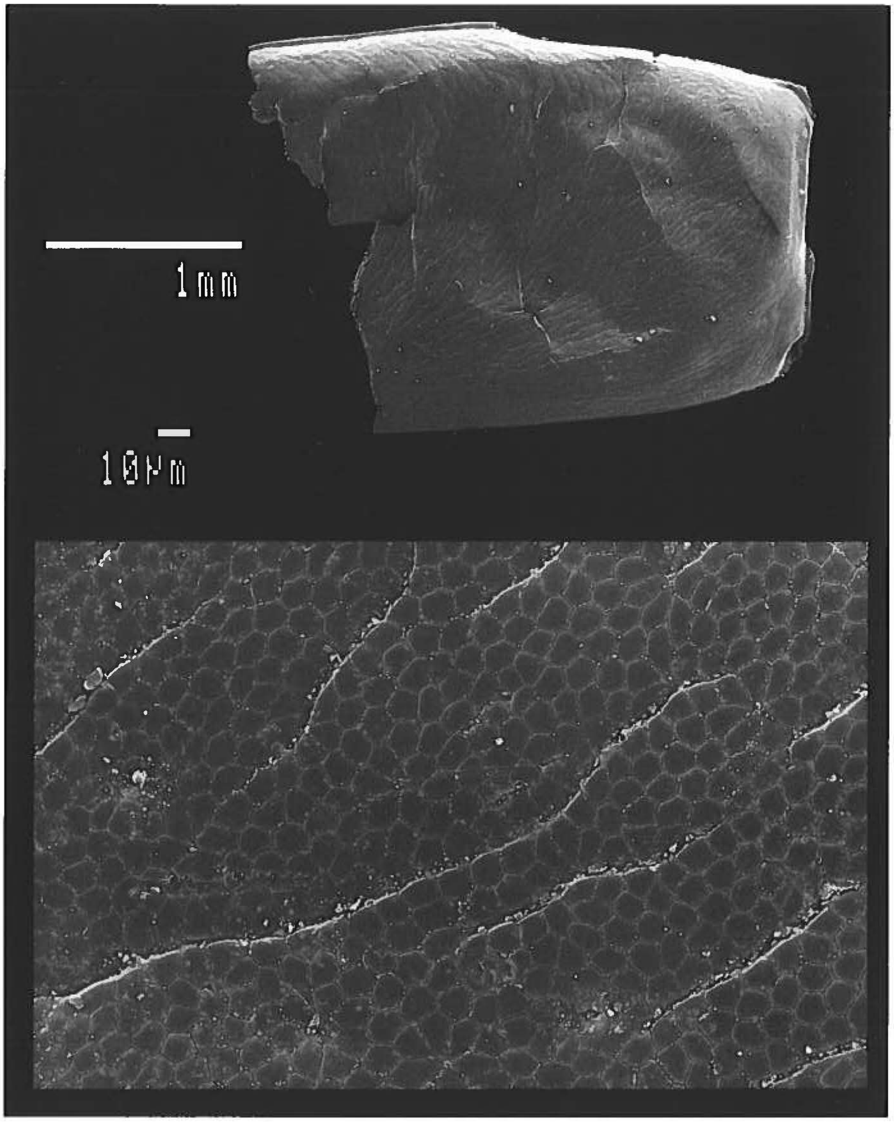
Hydroporinae gen. et sp. indet.
Material: One head, one pronotum, one elytron (B3: 77, 119, 132).

Agabus cf. ***affinis*** (Paykull, 1798)
Material: Two elytra, one metasternum with coxae (B3: 77, 119).
Distribution (n.s.): Eurasia, boreal to temperate.
Habitat (n.s.): *Sphagnum* pools, acid marshes, forest fens.

Agabus affinis-group
Material: Four pronota, eight elytra, two metasterna with coxae (B3: 75, 77, 119, 132).
Note. According to Anders Nilsson (personal communication 1994) this group comprises seven palaearctic and three nearctic species.

Agabus clavicornis Sharp, 1882/***serricornis*** Paykull, 1799
Material: Six elytra, one metasternum with coxae (B3: 77, 132).
Distribution: *clavicornis*: North America west of of Hudson Bay, E Siberia and N Mongolia; low arctic to temperate; *serricornis*: Fennoscandia to N Siberia, low arctic to boreal.

Fig. 14. *Agabus bifarius*, left elytron (fragment) and elytral microsculpture (64933). Scanning electron micrographs.



Habitat: Eutrophic ponds and lakes with a rich vegetation (both species).
Note. According to Anders Nilsson (personal communication 1991) it is not possible to separate these two species on elytron or metasternum characters.

Agabus bifarius (Kirby, 1837)
Material: One head, three pronota, eight elytra, one metasternum with coxae, sternites 1+2 (B3: 69, 77, 122, 141). Fig. 14.
Distribution: Almost transcontinental in North America, boreal to temperate.
Habitat: Eurytopic in permanent and temporary ponds in both prairie and forest areas. Most typical of shallow, temporary ponds in rough fescue prairie or in parkland areas. These ponds are typically shaded by *Salix* spp., *Populus tremula* etc. and with dense vegetation of *Carex* spp. and grasses (Larson 1975).
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene); Beaver Peat, Strathcona Fiord & Riediger Site, Vendom Fiord region, both Ellesmere Island (early Pliocene?).

Agabus cf. ***anthracinus*** Mannerheim, 1852
Material: One pronotum, one metasternum with coxae (B3: 77, 119).
Distribution (n.s.): Boreal and temperate North America.
Habitat (n.s.): Eurytopic in shallow stagnant or slow-flowing water with dense emergent vegetation and mats of plant debris, e.g. *Carex*-marshes.

Agabus spp.
Material: Two heads, four pronota, two elytra, three

metasterna+coxae, three metacoxae, several metafemora and sternites (B3: 69, 75, 77, 122, 132). The elytra are probably from the same species.

Ilybius vittiger (Gyllenhal, 1827)
Material: One elytron (B3: 77)
Distribution: Circumpolar, low arctic to boreal.
Habitat: Small stagnant water bodies shaded by trees or boulders and often with *Sphagnum* spp.

Ilybius sp.
Material: One head, four pronota, seven elytra, three metasterna+coxae (B3: 50, 69, 77, 119, 132), possibly representing only one species.

Agabus/Ilybius spp.
Material: Elytron fragments, sternites (B3: 77).

Agabini spp.
Material: One head, two elytra, four sternites (B1: 50; B3: 77, 119).

Colymbetes sp.
Material: One metasternum with coxae, one metacoxa, one metafemur (B3: 77).
Habitats: Lakes and ponds.
Note. Due to differences in microsculpture and other characters the fragments can not stem from the circumpolar, arctic *C. dolabratus* (Paykull), which is widely distributed in Greenland today.

Dytiscidae gen. et sp. indet.
Material: Larval mandibles; sternites; numerous fragments of pronota, elytra, sterna etc. (B3: 69, 75, 77, 119).

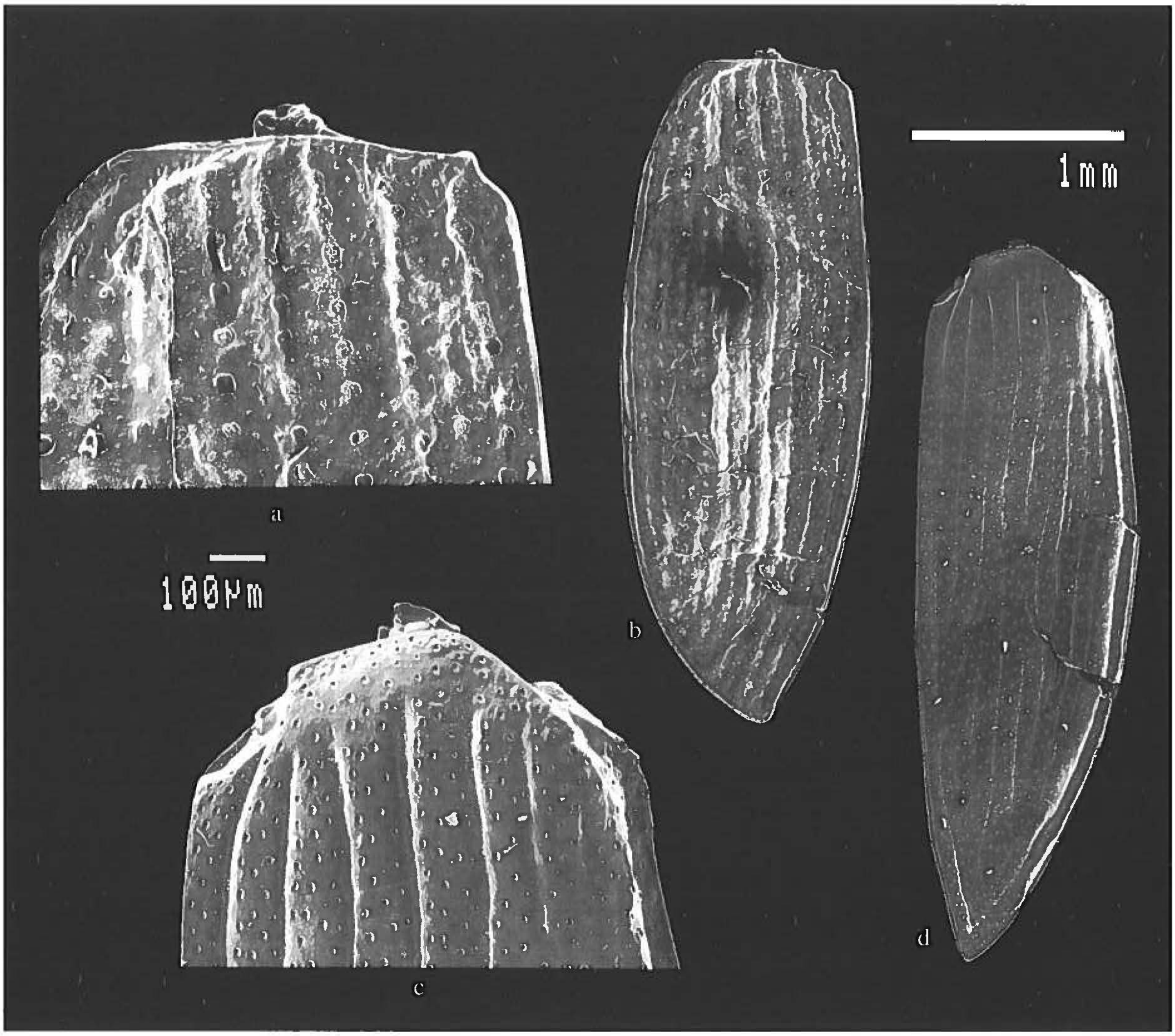


Fig. 15. a,b) *Helophorus* cf. *khnzoriani*, left elytron (64928); c,d) *Hypnoidus rivularius*, right elytron (64930). Scanning electron micrographs.

Gyrinidae

Gyrinus sp.
Material: Two elytra (B3: 77, 132).
Habitats: The species are swift carnivors hunting on the surface of ponds, lakes and slowly flowing streams.
Fossil occurrences: Ballast Brooks, Banks Island, Beaufort Formation (Pliocene); Remus Creek site, Fosheim Peninsula & Beaver Peat, Strathcona Fiord, all Ellesmere Island (early Pliocene?).

Hydrophilidae

Helophorus cf. ***khnzoriani*** Angus, 1970.
Material: one head+pronotum, four pronota, 28 elytra (B3: 77, 119, 132). Fig. 15,a,b.
Distribution (n.s.): Altai (Kasakhstan and Mongolia); temperate (alpine).
Habitat (n.s): Alpine waters (about 2500 m above sea level).
Note. According to Robert B. Angus (personal communication 1994) a firm identification can not be done without examination of the adeagophore. The size of the elytra is too small for the closely related *H. niger* J. Sahlberg. The species is easily distinguished from all known species (except *H. niger*) by its dark colour and reduced sculpture of the head and pronotum (Angus 1970). The scutellary striae are reduced to one or two punctures, a feature matched by some recent *H. khnzoriani*. The species has to be palaearctic or extinct, because there are no indigenous nearctic species of *Helophorus* s. str. with scutellary striae.

Helophorus tuberculatus Gyllenhal, 1808
Material: One elytron (B3: 77).
Distribution: Circumpolar, boreal to temperate.

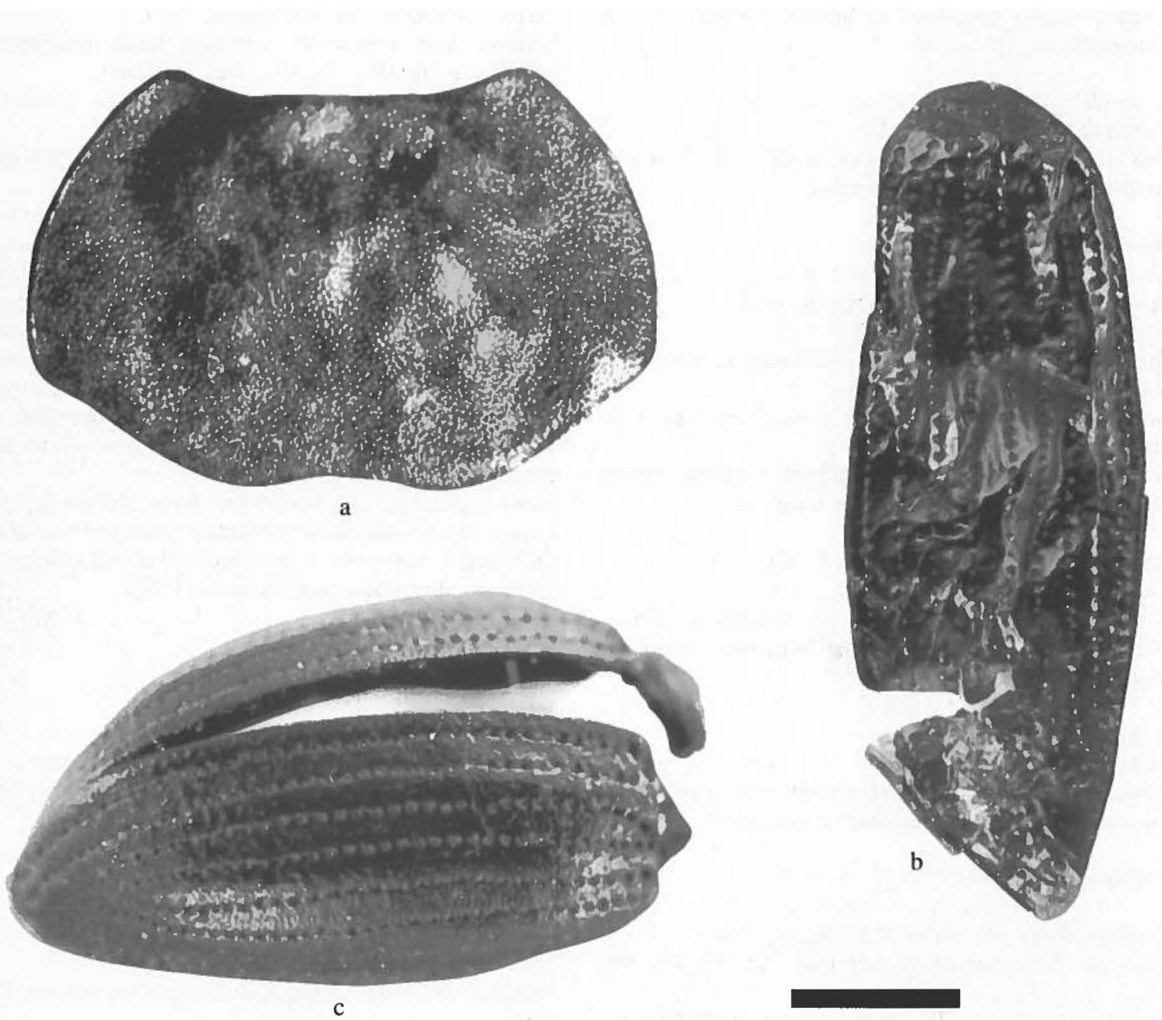


Fig. 16. a) *Thanatophilus* cf. *baicalicus*, pronotum (64928); b) *Pteroloma forsstromii*, right elytron (64931); c) *Cyriophthalmus variegatus* partly fused elytra (56692). Scale: 1 mm.

Habitat: Among wet mosses in *Sphagnum*-bogs and at the banks of oligotrophic-acid moor pools.
Fossil occurrences: The very similar *H. meighensis* Matthews is reported from the Beaufort Formation on Meighen Island, Beaufort Formation (Pliocene) and at several Pliocene sites on Ellesmere Island. *H. tuberculatus* has not been found at any of the Pliocene sites in the Canadian Arctic. *H. meighensis* is regarded the extinct sister species of *H. tuberculatus* (Matthews 1976).

Helophorus spp.
Material: One head, one pronotum, 13 elytra, several elytra and elytron fragments in poor condition (B3: 77, 119).

Megasternum obscurum (Marsham, 1802)
Material: One elytron, probably from B3.
Distribution: Europe, N Africa, the Caucasus (introduced in North America); subarctic to subtropical.
Habitat: Highly eurytopic, in all kinds of decaying organic matter.

Laccobius sp.
Material: One elytron (B3: 77).
Habitats: The species are found in all kinds of limnic biotopes and also in brackish water.

Leiodidae

Agaricophagus cephalotes Schmidt, 1841
Material: One elytron (B3: 119).
Distribution: C Europe (north S Scandinavia, south to C Italy); boreal to temperate.
Habitat: Subterranean, probably living from fungal hyphae.
Note. The elytra are easily identifiable from the characteristic, delicate cross stripes anteriorly.

Anisotoma cf. ***castanea*** (Herbst, 1792)
Material: One elytron (B3: 77).
Distribution (n.s.): N and C Europe, boreal to temperate.
Habitat (n.s.): In fungi associated with decaying wood of deciduous trees.

Anisotoma spp.
Material: Two elytra (B3: 77).
Note. The elytra clearly originate from two species of different size, both smaller than *A. castanea*.

Silphidae

Thanatophilus baicalicus Motschulsky, 1860
Material: Two pronota, one elytron (B3: 69, 77). Fig. 16,a.
Distribution: Siberia: Baikal-Amur area, temperate.
Note. The identification is based on general (fairly small) size, shape, pilosity and microsculpture, especially the very coarse punctures of both pronotum and elytron. *T. dispar* Herbst is very close, but has smaller punctures.

Heterosilpha ramosa (Say, 1823)
Material: One pronotum (fragment), one elytron (B3: 75).
Distribution: Boreal and temperate W North America, south to Baja California and Mexico (in the south apparently represented by the alleged subspecies *H. r. cervaria* Mannerheim, 1843; Arnett 1983).
Habitat: Feeds probably on carrion (small mammals, birds) as well as on other insects.
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene).

Agyrtidae

Pteroloma forsstromii (Gyllenhal, 1810)
Material: One elytron (B1: 50); one head, one pronotum, five elytra (B3: 77, 119, 152). Fig. 16,b.
Distribution: N and C Europe (boreo-alpine), subarctic to temperate (subalpine in the south).
Habitat: Shady shores of lakes and streams, often found among moss and plant litter.
Note. According to Brown (1933) the elytra of *Pteroloma nebrioides* Brown are seven-tenths as wide as long, a relation which readily precludes this species (0.34-0.40 in the fossils). The third species to be considered, *P. sibiricus* Szekessy, is according to the description very similar to *P. forsstromii*, the most important difference being found in the male genitalia. However, the elytra are more narrow, behind middle barely broader than in front of middle (Szekessy 1935). The fossil elytra are clearly broadest behind middle.
Fossil occurrences: A poorly preserved elytron of *Pteroloma* has been found in the older (Pliocene?) levels of the TAGLU borehole in the Mackenzie Delta (John V. Matthews, personal communication 1995).

Cholevidae

Catops sp.
Material: One elytron (B3: 77).
Habitats: Most species are found at decaying animal or vegetable substances, e.g. carcasses, or in mammal burrows.

Colonidae

Colon sp.
Material: One elytron (B3: 119).
Habitats: Probably living from fungal mycelia in the soil.

Staphylinidae

Philonthus/Quedius spp.
Material: Two heads, five pronota, six elytra (B3: 50, 69, 75, 77, 119, 132).
Note. It does not seem possible to separate the two genera on the basis of head-, pronotum- or elytron characters.

Cf. ***Lathrobium*** sp.
Material: One elytron (B3: 77).
Habitats: Most species are hygrophilic and found in decaying plant debris.

Stenus melanarius Stephens, 1833
Material: One elytron (B3: 77).
Distribution: Circumpolar, subarctic to temperate.
Habitat: Marshy shores of lakes, ponds and streams with a rich vegetation, also in *Sphagnum*-bogs in forests, humid meadows and on loamy-sandy beaches.

Stenus cf. ***canaliculatus*** Gyllenhal, 1827
Material: One metasternum (B3: 77).
Distribution (n.s.): Circumpolar, low arctic to temperate.
Habitat (n.s.): Highly eurytopic in fairly humid biotopes, e.g. grass fields and meadows, under plant litter in *Salix*-scrubs; also sandy river and lake shores, and plant communities above forest limit.

Stenus vinnulus Casey, 1884 (syn. ***confusoides*** Renkonen, 1935)
Material: Two elytra, one metasternum (B3: 69, 77, 119).
Distribution: Fennoscandia, E North America; boreal to temperate.
Habitat: Fairly eurytopic, e.g. marshy lake shores with *Carex-Sphagnum* swamp and below decaying plant material in scrubs with rich vegetation.

Stenus assequens Rey, 1884 (syn. ***simillimus*** L. Benick, 1949)
Material: One elytron (B1: 50).
Distribution: Circumpolar, boreal to subtropical.
Habitat: Highly eurytopic, e.g. in coniferous forest litter, in moss and on sandy margins of ditches and pools.

Stenus hyperboreus J. Sahlberg, 1876
Material: One elytron (B3: 77).
Distribution: Transcontinental in North America, N Fennoscandia to W Siberia; low arctic to boreal, alpine in western U.S.A.

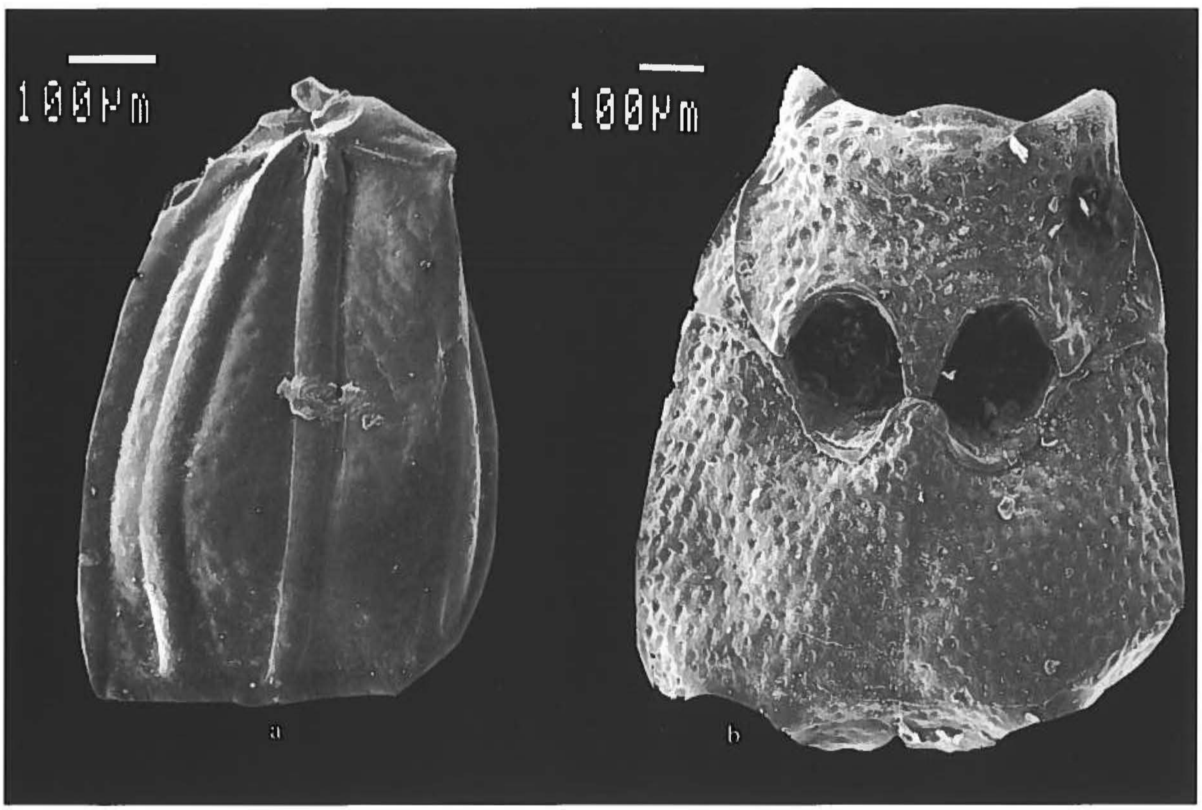


Fig. 17. a) *Kalissus nitidus*, left elytron (64925); b) *Stenus* n. sp.?, mesosternum + metasternum (64917). Scanning electron micrographs.

Habitat: Different humid biotopes: *Sphagnum*-bogs, sedge meadows and vegetated shores of rivers and ponds.

Stenus cf. ***carbonarius*** Gyllenhal, 1827
Material: One elytron (B3: 77).
Distribution (n.s.): N and C Europe, W Siberia; subarctic to temperate.
Habitat (n.s.): Eurytopic in humid biotopes: *Betula*-woodland, *Salix*-scrubs, meadows, shores of rivers and lakes; also marshes and slopes with rich vegetation above tree limit.
Note. The metasternum of *S. carbonarius* has a unique character: a posterior-median carina (Volker Puthz, personal communication 1993).

Stenus pubescens Stephens, 1833
Material: One metasternum (B1: 50).
Distribution: Probably circumpolar, boreal to temperate.
Habitat: Vegetated banks of lakes and rivers, also running or swimming on the water surface.
Note. According to Volker Puthz (personal communication 1992), *S. fraternus* Casey is the nearctic subspecies of *S. pubescens*.

Stenus cf. ***pinguis*** Casey, 1884
Material: One elytron (B3: 119).
Distribution (n.s.): W North America (British Columbia to California); boreal to subtropical.
Habitat (n.s.): Humid sedge meadows at lake shores and ponds.

Stenus sordidus Puthz, 1988
Material: Two elytra, three metasterna (B3: 77, 119).
Distribution: North America, low arctic to boreal.
Habitat: Swamps, humid sedge meadows.

Stenus cf. ***mammops*** Casey, 1884
Material: One elytron, one metasternum (B3: 77, 119).
Distribution (n.s.): Transcontinental in North America,

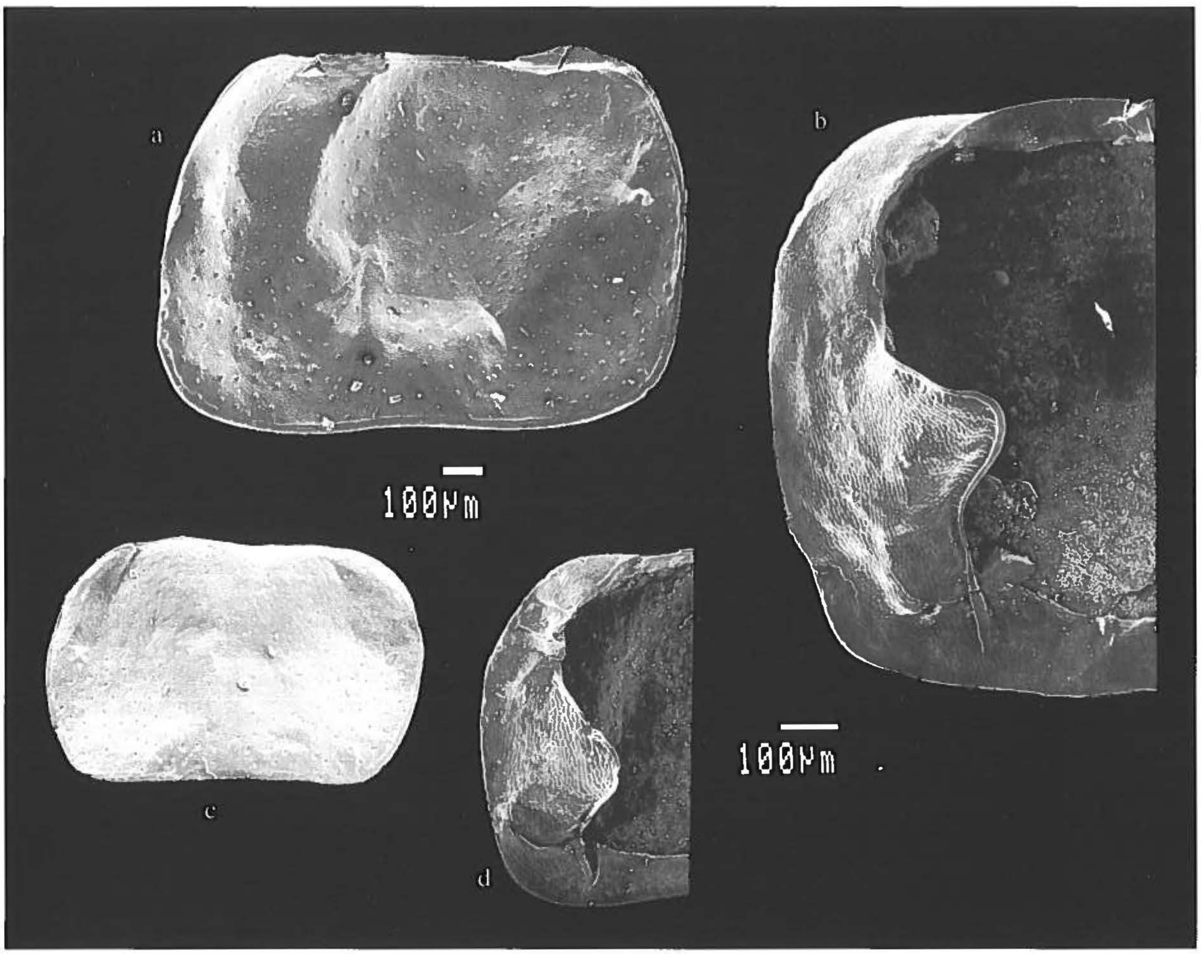


Fig. 18. a,b) *Eucnecosum* n. sp.?, pronotum (64938, 64926); c,d) *Eucnecosum* cf. *brunnescens*, pronotum; (64923, 64926); b) and d) are viewed from the under side. Scanning electron micrographs.

Siberia east of Lena and Amur, Kamchatka, Hokkaido; boreal.
Habitat (n.s.): Eurytopic in humid biotopes: swamps, *Sphagnum*-bogs, mosses and lichens in humid forests, leaf litter of *Alnus* and grasses.

Stenus scrupeus Casey, 1884
Material: One head, two elytra (B3: 77, 119).
Distribution: North America, boreal to temperate.
Habitat: Forest swamps, *Carex*-meadows at the edge of ponds.

Stenus n. sp.?
Material: One pronotum, one elytron, four metasterna (♀, ♂) (B3: 77, 119). Fig. 17,b.
Note. According to Volker Puthz (personal communication 1991, 1994) these fragments have striking characters, but can not be referred to any known species. They probably represent an unknown species close to *S. jacuticus* Poppius and *S. sordidus* Puthz, which are both found in low arctic regions.

Stenus spp.
Material: One elytron, one metasternum (B1: 50); four heads, four pronota, six elytra, five metasterna (B3: 50, 69, 77, 119).

Kalissus nitidus LeConte, 1874
Material: Three elytra (B3: 77, 119). Fig. 17,a.
Distribution: Only known from westernmost, temperate North America (the coast of British Columbia, Vancouver Island and Seattle, Washington), but according to the distribution of Quaternary fossils in northern Canada, its present range probably extends much further north (J.V. Matthews, personal communication 1995).
Habitat: The holotype was collected on the pebbly margins of a small lake (on Vancouver Island).
Fossil occurrences: Lava Camp, Seward Peninsula, Alaska (late Miocene: 5.7 Ma); Bluefish River near Old Crow, Yukon Territory (Pliocene); Prince Patrick Island, Beaufort Formation (Pliocene).

Pycnoglypta cf. ***lurida*** (Gyllenhal, 1813)
Material: Five elytra (B1: 50); 11 elytra (B3: 50, 69, 77, 119).
Distribution (n.s.): Circumpolar, subarctic to boreal.
Habitat (n.s.): Eurytopic in humid biotopes, e.g., among rich vegetation in marshes, in *Sphagnum*-bogs, and under decaying plant material in *Salix*-scrubs.
Fossil occurrences (n.s.): Meighen Island, Beaufort Formation (Pliocene).
Note. The elytra are indistinguishable from those of *P. lurida*, but I have not seen the remaining four species of the genus (three from E Siberia, one from E North America; Campbell 1983).

Phyllodrepa sp.
Material: Two pronota (B3: 77).
Habitats: The species probably feed on fungal hyphae and are found in association with decaying organic substances (e.g. in compost, dung, bird nests and mammal dens).

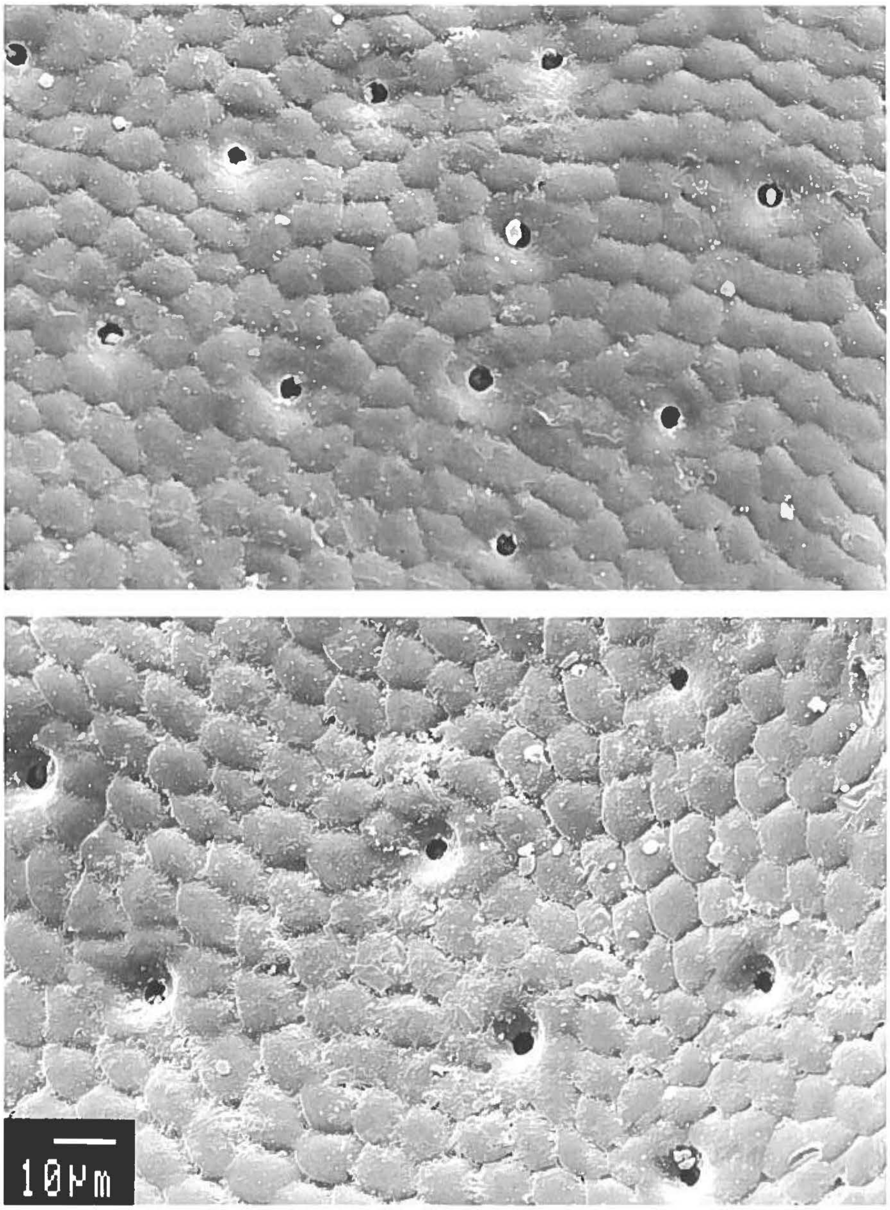
Omalium spp.
Material: Three elytra (B3: 77).
Habitats: The species are associated with decaying vegetable and animal matter.

Micralymma cf. ***brevilingue*** Schiödte, 1845
Material: One head (B3: 77).
Distribution (n.s.): Circumpolar, arctic. Widely distributed in Greenland, north to the southern High Arctic.
Habitat (n.s.): Fairly eurytopic in humid biotopes, including the upper part of the tidal zone on sandy seashores.
Fossil occurrences (n.s.): Matthews (1974a) reported the species abundantly from the early Pleistocene Cape Deceit Formation in W Alaska, which was deposited far from the sea, and also (1968) from late Pleistocene sites in interior Alaska, apparently in fairly xeric environments. Fossils presumed to be from this or a closely related species also occur at a number of Pliocene sites in the Canadian and Alaskan Arctic (See *Micralymma* sp., Appendix 2, in Matthews, in press).

Olophrum boreale (Paykull, 1792)
Material: Three heads, three pronota and five elytra (cf.) (B3: 77).
Distribution: Circumpolar, boreal (In North America boreo-alpine).
Habitat: Edges of lakes, ponds, bogs and streams with luxuriant vegetation (*Equisetum*, *Typha*, mosses, shrubs); also in leaf litter, particularly of *Alnus* and *Salix*, and in moist meadows above the tree limit.
Fossil occurrences: Beaver Peat, Strathcona Fiord, Ellesmere Island (early Pliocene?).
Note. The heads are identified on the basis of abrupt constriction behind the eyes, isodiametric microsculpture behind this, irregular, coarse punctation, and the development of the subocular ridge (Campbell 1983, fig. 34).

Olophrum consimile (Gyllenhal, 1810)
Material: Three pronota (B3: 77, 119, 122).
Distribution: Circumpolar, subarctic to boreal (boreo-alpine).
Habitat: Similar to *O. boreale*.
Fossil occurrences: Beaver Peat, Strathcona Fiord, Ellesmere Island (early Pliocene?).

Olophrum cf. ***rotundicolle*** (Sahlberg, 1830)
Material: One pronotum (B3: 119).
Distribution (n.s.): Circumpolar, subarctic to boreal (in Europe boreo-alpine).
Habitat (n.s.): Similar to *O. boreale*.



a

b

Fig. 19. Pronotal microsculpture of *Eucnecosum* spp. (at same magnification). a) cf. *brunnescens* (64923); b) n. sp.? Scanning electron micrographs.

Olophrum spp.
Material: One head, 35 elytra and elytron fragments (B3: 69, 77, 119, 132). The elytra at least represent three species.

Eucnecosum* cf. *tenue (LeConte, 1863)
Material: Five heads and three pronota (B3: 69, 77).
Distribution (n.s.): Circumpolar, subarctic to boreal (boreo-alpine).
Habitat (n.s.): In moist deciduous plant litter, in particular of *Alnus* and *Salix*; also in vegetation at the edge of bogs, on shallow lake margins, streams and moist meadows.

Eucnecosum cf. ***brunnescens*** (J. Sahlberg, 1871)
Material: Two heads and 35 pronota (B3: 69, 75, 77, 119, 157). Figs 18,c,d, 19,a.
Distribution (n.s.): Circumpolar, subarctic to boreal (in North America boreo-alpine).
Habitat (n.s.): Similar to *E. tenue*.
Note. It is difficult to identify pronota of *Eucnecosum* on the basis of Campbell (1984), but in some cases the different disposition of punctures appears evidently. It is easier to separate the heads on basis of the SEM photos.

Eucnecosum n. sp.?
Material: 10 pronota (two halves) (B3: 75, 77). Figs 18,a,b, 19,b.
Note. These pronota are large compared to other species of *Eucnecosum*, average 0.91 mm in length and 1.39 mm in width ("normal" *Eucnecosum*: 0.7 mm and 1.0 mm), but otherwise very similar to those of that genus concerning shape, isodiametric microsculpture and punctation (Figs 18,a,b, 19,b). It has as yet not been possible to refer the pronota to any known species, and most probably they represent an unknown (extinct?) species of *Eucnecosum* or of a closely allied genus.

Eucnecosum spp.
Material: 10 elytra (B1: 50); five heads, 11 pronota, 57 elytra (B3: 69, 75, 77, 119, 132).

Acidota quadrata (Zetterstedt, 1838)
Material: Four pronota and five elytra (B3: 69, 77).
Distribution: Circumpolar, boreal (in North America boreo-alpine).
Habitat: Eurytopic in humid biotopes, similar to *Eucnecosum.*

Coryphium angusticolle Stephens, 1834
Material: Two pronota (B3: 77).
Distribution: N and C Europe, subarctic to temperate.
Habitat: Under bark of both deciduous and coniferous trees, living as well as dead.

Carpelimus (Trogophloeus) sp.
Material: Three pronota (B3: 77, 119).
Habitats: Soil surface, probably feeding on algae.

Omaliinae gen. et sp. indet.
Material: 15 elytra (B3: 69, 77).

Bledius cf. ***litoralis*** Heer, 1839
Material: One pronotum and (possibly) one elytron (B3: 77).
Distribution (n.s.): Europe, Caucasus, E Siberia, Mongolia; in Europe boreo-alpine; boreal to temperate.
Habitat (n.s.): Humid, loamy and muddy sand on shores of rivers and brooks.

Bledius cf. ***arcticus*** J. Sahlberg, 1890
Material: Two pronota (B1: 50); 12 pronota (B3: 77).
Distribution (n.s.): From N British Isles and Scandinavia to the Lena River (Siberia); low arctic to subarctic.
Habitat (n.s.): Sandy, sparsely vegetated shores of rivers.
Note. The pronotum is characteristic by the rough, in some cases crenelated or even serrate side margins, which are almost parallel anteriorly. The elytra of *B. arcticus* are very short, brownish, and with fairly dense and blurred punctation. Most of the unidentified *Bledius*-elytra can probably be referred to this species.

Bledius cf. ***talpa*** (Gyllenhal, 1810)
Material: Six pronota (B3: 69, 77).
Distribution (n.s.): N and C Europe, Siberia; low arctic to temperate (alpine in the south).
Habitat (n.s.): Sandy lake- and river shores without vegetation.

Bledius spp.
Material: One head, 11 elytra (B1: 50); four heads, 46 elytra (B3: 50, 69, 75, 77, 119).

Oxytelinae gen. et sp. indet.
Material: One pronotum (B3: 77).

Mycetoporus sp.
Material: One pronotum, one elytron (B3: 77, 152).
Habitats: Mouldy places, e.g. under mosses or decaying plant material.

Bolitobius sp.
Material: One elytron (B3: 77).
Habitats: In toadstools and fungi or under loose bark feeding on fungal hyphae.

Tachyporus cf. ***rulomus*** Blackwelder, 1936
Material: One pronotum (B1: 50).
Distribution (n.s.): Transcontinental in North America, boreo-montane.
Habitat (n.s.): Eurytopic in wet biotopes.
Note. The specific identifications of *Tachyporus* is highly tentative, based on chaetotaxy (Campbell 1979) which is difficult to observe in fossil material.

Tachyporus cf. ***borealis*** Campbell, 1979
Material: One pronotum (B1: 50).
Distribution (n.s.): Transcontinental in North America, boreal.
Habitat (n.s.): Eurytopic in moist places, most often found in coniferous leaf litter at the edges of streams, ponds, or lakes.

Tachinus elongatus Gyllenhal, 1810
Material: One head, seven pronota, eight elytra, one 5. tergite, five 8. tergites (3♀, 2♂) (B3: 69, 77, 119, 132).
Distribution: Circumpolar, low arctic to temperate (in North America boreo-alpine).
Habitat: Highly eurytopic in damp places (stream banks, meadows, wet moss on tree trunks, various decaying matter, e.g. under seaweed on seashores).

Tachinus spp.
Material: Two pronota, nine elytra (B3: 69, 77, 119) representing at least two species.

Atheta spp.
Material: Five elytra (B1: 50); two elytra (B3: 77, 119).

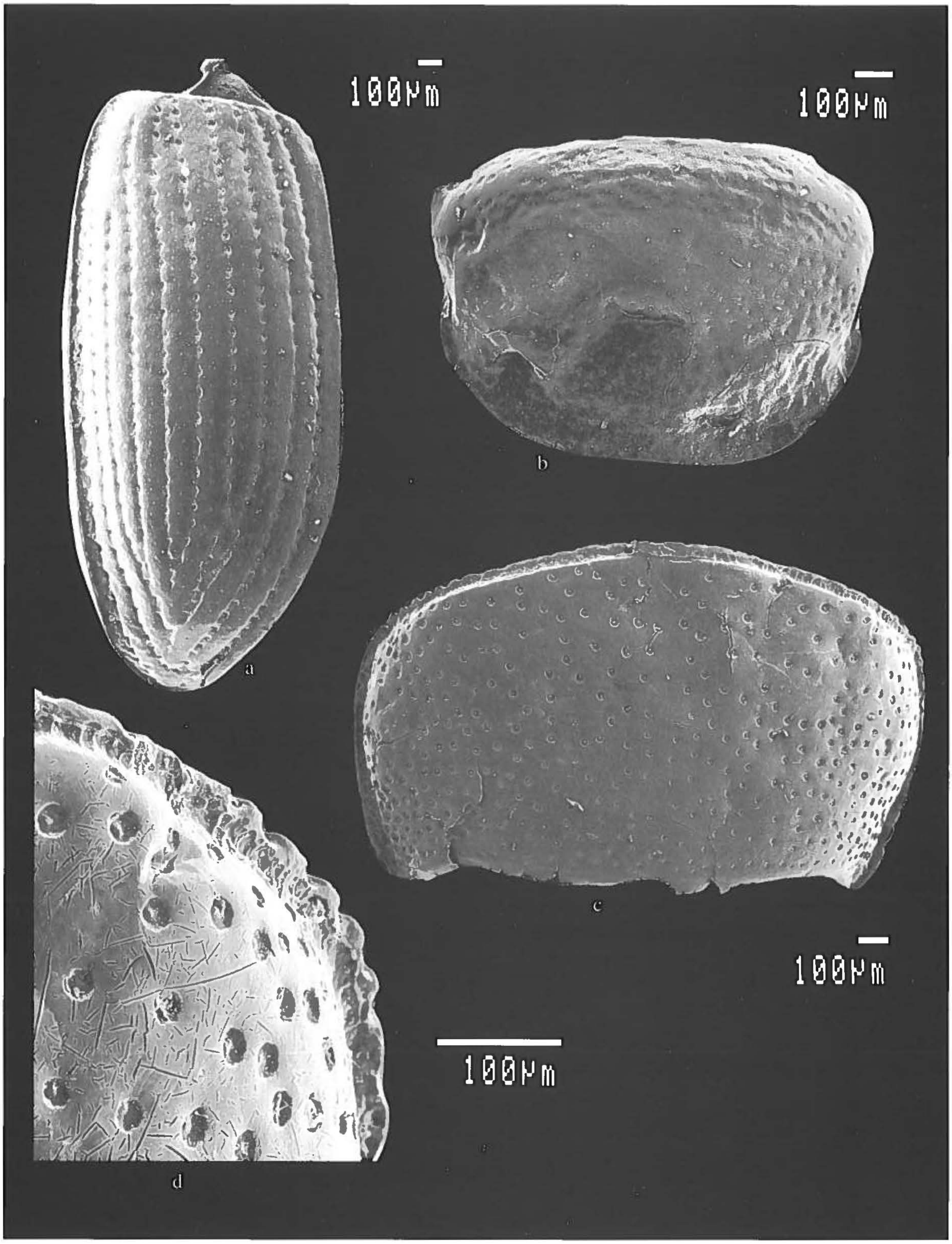


Fig. 20. *Aegialia terminalis*. a) Left elytron (52263); b) head (64915); c,d) pronotum (64915). Scanning electron micrographs.

Fig. 21. *Aegialia terminalis.* a,d) right and left elytron; c) left elytron from under side; b) hind wing from c) (all 64935); e) metasternum (64924); f) front femur+tibia (64924); g) *Laricobius* cf. *caucasicus* (64931). Scale: 1 mm.

Aleocharinae gen. et sp. indet.
Material: Two pronota, seven elytra, five metasterna (B1: 50); one elytron (B2: 50); five pronota, 12 elytra (B3: 50, 77, 119).

Staphylinidae gen. et sp. indet.
Material: Seven elytra (B1: 50); three heads, nine elytra, five metasterna, one abdomen, sternites, tergites (B3: 50, 77, 119, 132).

Scarabaeidae

Aegialia terminalis Brown, 1931
Material: Six heads, 15 pronota, more than 100 elytra (in some cases with hind wings), one metasternum, one anterior femur + tibia (B3: 50, 69, 75, 77, 119, 122, 132, 141, 152). Figs 20, 21,a-f.
Distribution: C boreal Canada (Alberta, Saskatchewan), Colorado.
Habitat: Probably sandy areas along shores of rivers and lakes; the species of the genus most probably feed on plant roots.
Note. The fossil species clearly belongs to the subgenus *Psammoporus* Thomsen, 1863 (in which *A. sabuleti* (Panzer) is the type species). According to Brown (1931) *A. terminalis* differs from all others of the subgenus by the weakly developed punctation and sculpture of the head and by the shape of the anterior tibiae (Figs 20,b, 21,f).

Aphodius sp.
Material: One pronotum (B3: 77).
Habitats: Almost all species live in and from mammalian dung.

Cantharidae

Podabrus cf. ***alpinus*** (Paykull, 1798)
Material: One head (B3: 77).

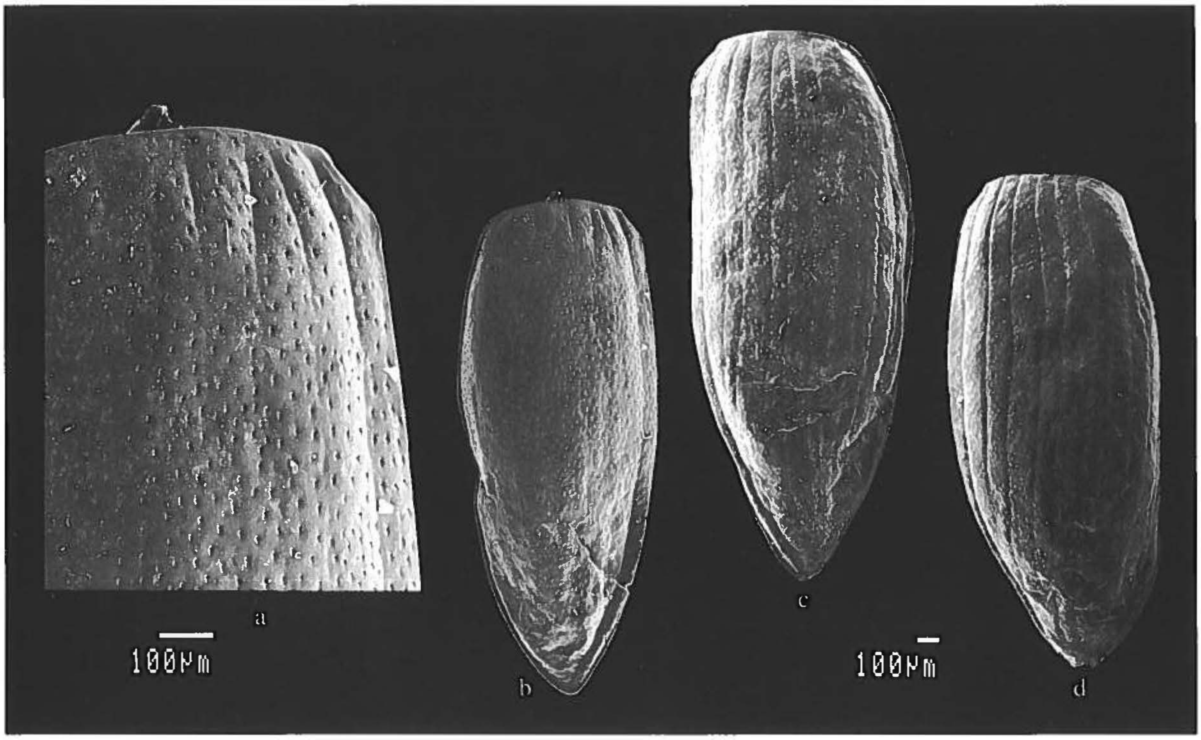


Fig. 22. a,b) *Simplocaria basalis*, left elytron (64917); c) *Simplocaria* cf. *elongata*, right elytron (64933); d) *Simplocaria* cf. *metallica*, right elytron (64933). Scanning electron micrographs.

Present distribution (n.s.): N and C Europe (alpine in the south), Siberia; low arctic to temperate.
Habitat (n.s.): On deciduous trees and shrubs, and in meadows.

Elateridae

Hypnoidus rivularius Gyllenhal, 1808
Material: 18 elytra, one prosternum, one metasternum (B3: 77, 119). Fig. 15,c,d.
Distribution: Scandinavia through Siberia, boreo-alpine in Europe; low arctic (subalpine) to boreal.
Habitats: Highly eurytopic; most often found under stones in scrubs, heaths and meadows.
Note. Several species of *Hypnoidus* are identifiable on the arrangement of minute spines on the shoulder of the elytra in combination with other elytral characters.

Buprestidae

Gen. et sp. indet.
Material: Galleries and exit holes in *Larix* wood (B3).
Distribution: The family is predominantly tropical with only comparatively few and rare boreal species.
Fossil occurrences: The family is represented in the Beaufort Formation on Meighen Island (Pliocene).

Byrrhidae

Simplocaria* cf. *metallica (Sturm, 1807)
Material: Four elytra (B3: 77). Fig. 22,d.
Distribution (n.s.): Europe, North America (in Europe boreo-alpine); low arctic to boreal. Low arctic and subarctic W and S Greenland.
Habitat (n.s.): Eurytopic, most often in the vicinity of water (moss-feeder).

Simplocaria* cf. *elongata J. Sahlberg, 1903
Material: 19 elytra (B3: 50, 77). Fig. 22,c.
Distribution (n.s.): Circumpolar, low arctic to subarctic. One record from low arctic W Greenland.
Habitat (n.s.): Under mosses in humid places.

Simplocaria basalis J. Sahlberg, 1903
Material: 31 elytra (B3: 69, 77, 119). Fig. 22,a,b.
Distribution: Siberia: Yenissei and Lena areas, Baikal area; boreal.
Note. In the material two types of *Simplocaria*-elytra are evident: one with very short striae which is referred to *S. basalis*, and one with striae almost throughout the elytron. The type with long striae can be further divided into two length classes, of which the long one is referred to *elongata*, the short one to *metallica*. The *S. basalis*-type also has more distinct, denser and deeper punc-

tures, and in several instances there are remains of a reddish pubescence (Sahlberg 1902-1903).

Simplocaria spp.
Material: Six pronota, four elytra, metasternum+sternites 1+2 (B3: 69, 77, 119).
Fossil occurrences: Undetermined fragments of *Simplocaria* have been found in many late Tertiary sites from Alaska to Yukon and the Canadian Arctic Islands.

Morychus cf. ***aeneus*** (Fabricius, 1775)
Material: One head (B3: 77).
Distribution (n.s.): N and C Europe, Siberia, Tibet; boreal to temperate.
Habitat (n.s.): Under stones and mosses in sandy areas, especially on freshwater shores and seashores.

Arctobyrrhus (=Tylicus) subcanus (LeConte, 1878)
Material: Two heads, one elytron, one elytron fragment, one metasternum (B3: 75, 77, 119).
Distribution: North America and SW Greenland, subarctic to boreal.
Habitat: Fairly eurytopic in moderately xeric places (mossfeeder).
Note. According to Paul J. Johnson (personal communication 1992) *Tylicus* Casey is synonymized with *Arctobyrrhus* Münster, and *Morychus dovrensis* (Münster, 1802) and *Tylicus subcanus* LeConte, 1878 should be recombined as sister-species in this genus.

Byrrhus sp.
Material: Sternites 1+2 (B3: 77).
Habitats: The species are generally associated with fairly dry, sandy ground (moss-feeders).

Curimopsis cf. ***moosilauke*** Johnson, 1986
Material: One elytron (B3: 119).
Distribution (n.s.): Transcontinental in boreal North America, mostly alpine (Johnson 1986).
Habitat (n.s.): In particular beneath small stones resting on a moss-surface on sandy soil (Johnson 1986).

Derodontidae

Laricobius cf. ***caucasicus*** Rost, 1893
Material: One right elytron (B3: 77). Fig. 21,g.
Note. The identification is doubtful. Only four species of the genus are known, namely besides *L. caucasicus* the

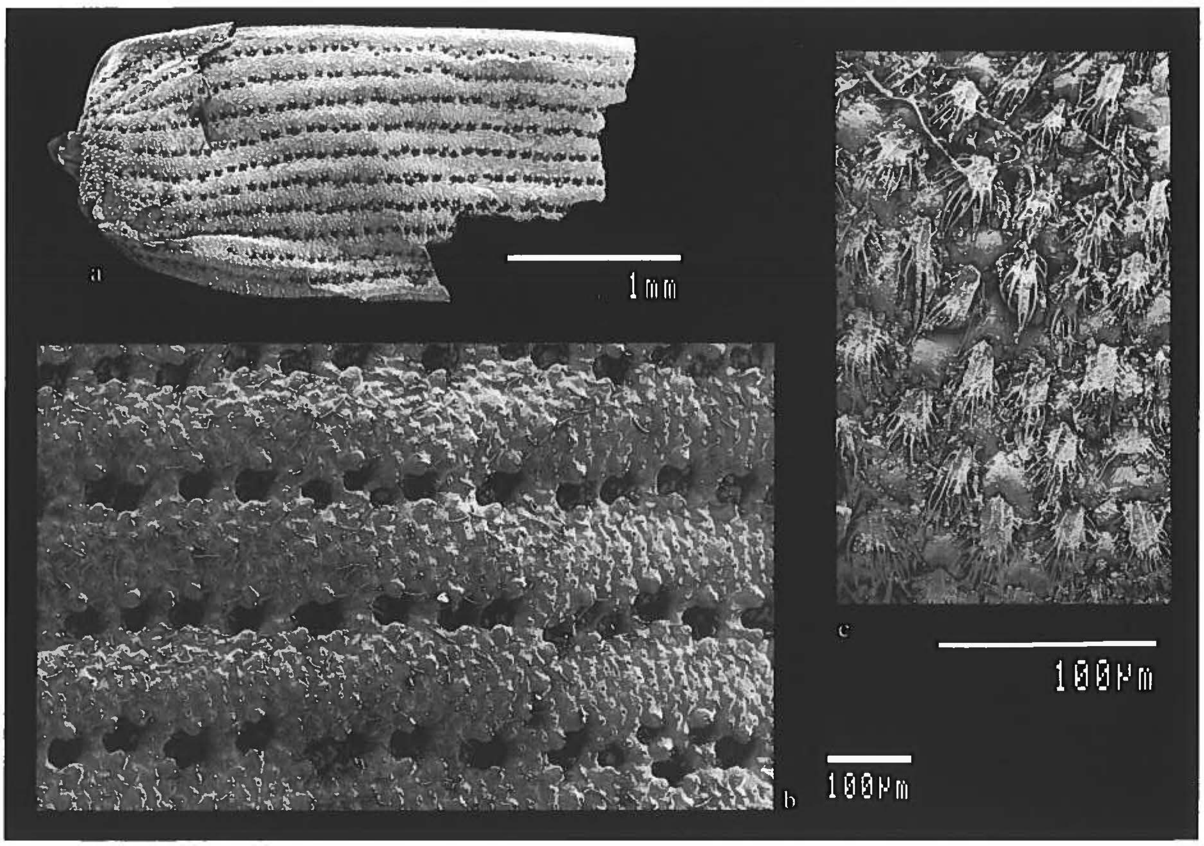


Fig. 23. a,b) *Cacotemnis* cf. *carinatus*, left elytron (64927); c) *Grypus equiseti*, elytral scale covering (53266). Scanning electron micrographs.

widespread, circumpolar *L. erichsoni* Rosenhauer, *L. sahlbergi* Reitter, which is only known from one locality (Fatjanowsk) in arctic W Siberia, and the newly described *L. kovalevi* Nikitsky, 1994, collected in the Magadan district, Siberia. These species have all smooth elytra with only trace of microsculpture; the striae have coarse punctures, and the striae are separated from one another by about the width of the punctures. The fossil elytron has very fine, isodiametric microsculpture and smaller punctures, the rows of which are separated by two to three times their width. It has been impossible to trace material of *L. caucasicus*, and even the type specimens appear to have vanished. However, according to the description (Rost 1893) and the key in Reitter (1894), the smaller size of the elytral punctures is a key character for this species. Thus, if not belonging to *L. caucasicus*, the fossil elytron represents an unknown, possibly extinct species.
Distribution (n.s.): W. Caucasus.
Habitat: *L. erichsoni* is both as larva and adult a predator of aphids on different species of conifers.

Anobiidae

Cacotemnis (=Hadrobregmus) cf. ***carinatus*** (Say, 1823)
Material: One elytron (B3: 119). Fig. 23,a,b.
Distribution (n.s.): Boreal North America.
Habitat (n.s.): Usually in logs of *Fagus* and *Acer* in moist woods.

Ptinidae

Ptinus sp.
Material: One mesosternum+metasternum (♀) (B2: 50B).
Habitats: The species feed on a variety of (dry) plant and animal substances.

Dasytidae

Amecocerus sp.
Material: Three elytra (B3: 77).
Habitats: The larvae of most Dasytidae live in dry-rotten wood, while the imagines are often found on flowers.
Note. *Amecocerus* is a large, primarily nearctic genus that also includes a few South American species.

Nitidulidae

Nitidula sp.
Material: One elytron (B1: 50).
Habitats: Most species are associated with dry carcasses.

Cryptophagidae

Atomaria sp.
Material: Two pronota (B3: 119).
Habitats: The species probably feed on fungal hyphae (moulds) and are found in compost, dung and rotting fungi.

Coccinellidae

Scymnus/Nephus spp.
Material: Seven elytra (B3: 77, 119).
Habitats: The species have concealed habits and prey mainly on different Hemiptera, e.g. Coccoidea spp.

Calvia quatuordecimguttata (Linnaeus, 1758)
Material: Six elytron fragments (B3: 119).
Distribution: Circumpolar, subarctic to temperate (montane in S Europe).
Habitat: On deciduous trees and shrubs, also on flowering herbs in dry grassland.
Note. The species is extremely variable in colour and pattern. The fragments all originate from a form with light markings on a dark background.

Myrrha octodecimguttata (Linnaeus, 1758)
Material: One elytron and three elytron fragments (B3: 77).
Distribution: Europe, Siberia, C Asia; boreal to subtropical.
Habitat: On trees (in particular conifers) and shrubs.

Latridiidae

Corticaria spp.
Material: One pronotum, four elytra (B3: 77, 119).
Habitats: The species are found in association with decaying plant material, feeding on moulds.

Latridiidae gen. et sp. indet.
Material: Two elytron fragments (B3: 77, 119).

Cisiidae

Cis spp.
Material: Three elytra (B3: 77) from two species.
Habitats: The species are found in, and living from, tinder fungi (mostly *Polyporus* spp.) which grow on weak or dying trees.

Colydiidae

Orthocerus clavicornis (Linnaeus, 1758)
Material: One elytron (B3: 77).
Distribution: N and C Europe, the Caucasus, Siberia; boreal to temperate.
Habitat: Under stones, lichens and mosses on sandy soil.

Cerambycidae

Gen. et sp. indet.

Fig. 24. Fragment of tree trunk of *Larix groenlandii* with galleries and fly holes of Cerambycidae spp. (right). At left the lower middle part is shown at greater magnification. Scale: 25 cm.

Material: One small elytron (B3: 77); four larval mandibles from galleries in *Larix* wood (sample 53287, Fig. 24). Fig. 25,a,b. The mandibles probably represent three species, of which one might be a *Hylotrupes* sp. (Fig. 25,b). Galleries and fly holes in *Larix* wood (B3). Fig. 24.

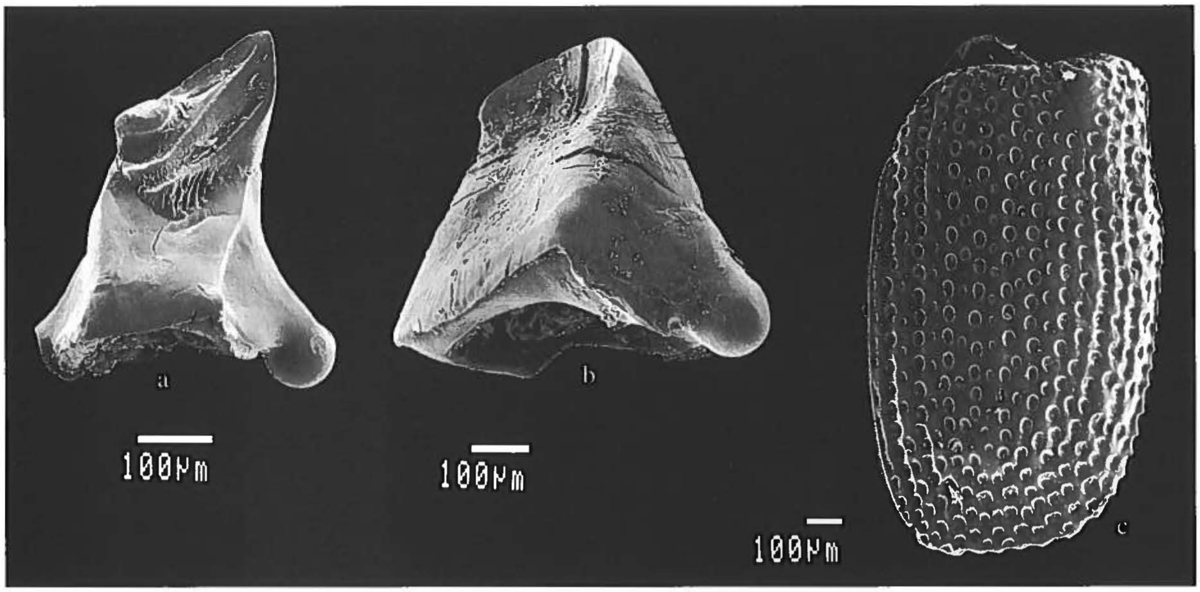


Fig. 25. a,b) mandibles of Cerambycidae larvae found in the piece of *Larix* wood shown in Fig. 24 (53287). b) is possibly from a *Hylotrupes* sp.; c) *Scolytus piceae*, right elytron. Scanning electron micrographs.

Chrysomelidae

Donacia spp.
Material: Six elytron fragments, femur+tibia (B3: 77, 119).
Habitats: On different aquatic plants; the larvae are limnic.

Cf. ***Chrysolina*** spp.
Material: One pronotum fragment, 28 elytron fragments, femur+tibia (B2: 27; B3: 69, 77, 119, 132).
Habitats: On different herbaceous plants.
Note. Species of *Chrysolina* are characteristic of subarctic and low arctic areas (Silfverberg 1994) and well represented in Beringian early Pleistocene sediments (Matthews 1974a; Sher *et al.* 1979).

Hydrothassa cf. ***hannoveriana*** (Fabricius, 1775)
Material: One elytron (B2: 27); one elytron (B3: 77).
Distribution (n.s.): N and C Europe, W Siberia; subarctic to temperate.
Habitat (n.s.): On *Caltha palustris* on wet ground.
Note. The identification is based on the colour pattern.

Chrysomela populi Linnaeus, 1758
Material: One pronotum (B3: 77). Fig. 8.
Distribution: Whole of Palaearctis, boreal to subtropical.
Habitat: On *Populus* and (more rarely) *Salix* spp.
Note. According to Brown (1956) no nearctic species has got a similar pronotum. That of *C. lapponica* Linnaeus is fairly close, but differs in shape of hind angles, punctation and microsculpture.

Cf. ***Galerucella*** sp.
Material: One elytron (B3: 119).
Habitats: On different herbaceous plants and deciduous trees.

Chrysomelidae spp. (incl. cf. Chrysomelidae spp.)
Material: Two sternites (B1: 50); four heads, one pronotum, one sternum fragment, several elytron fragments, femora (B3: 50, 69, 77, 119).

Curculionidae

Cf. ***Phyllobius*** sp.
Material: One elytron (B3: 77).
Habitats: Both trees and herbaceous plants; the larvae are subterranean and feed on roots.

Cyriophthalmus (=Lepidosoma) variegatus (Motschulsky, 1846)
Material: Two heads, one prothorax, 20 elytra (six articulated), two sternites 1+2 (B3: 69, 75, 77, 119, 132). Fig. 16,c.
Distribution: Found in a narrow coastal zone from the Magadan-area (E Siberia) south to N Korea; boreal to temperate.
Habitat: Found on *Rosa* sp. along rivers. In Kamchatka

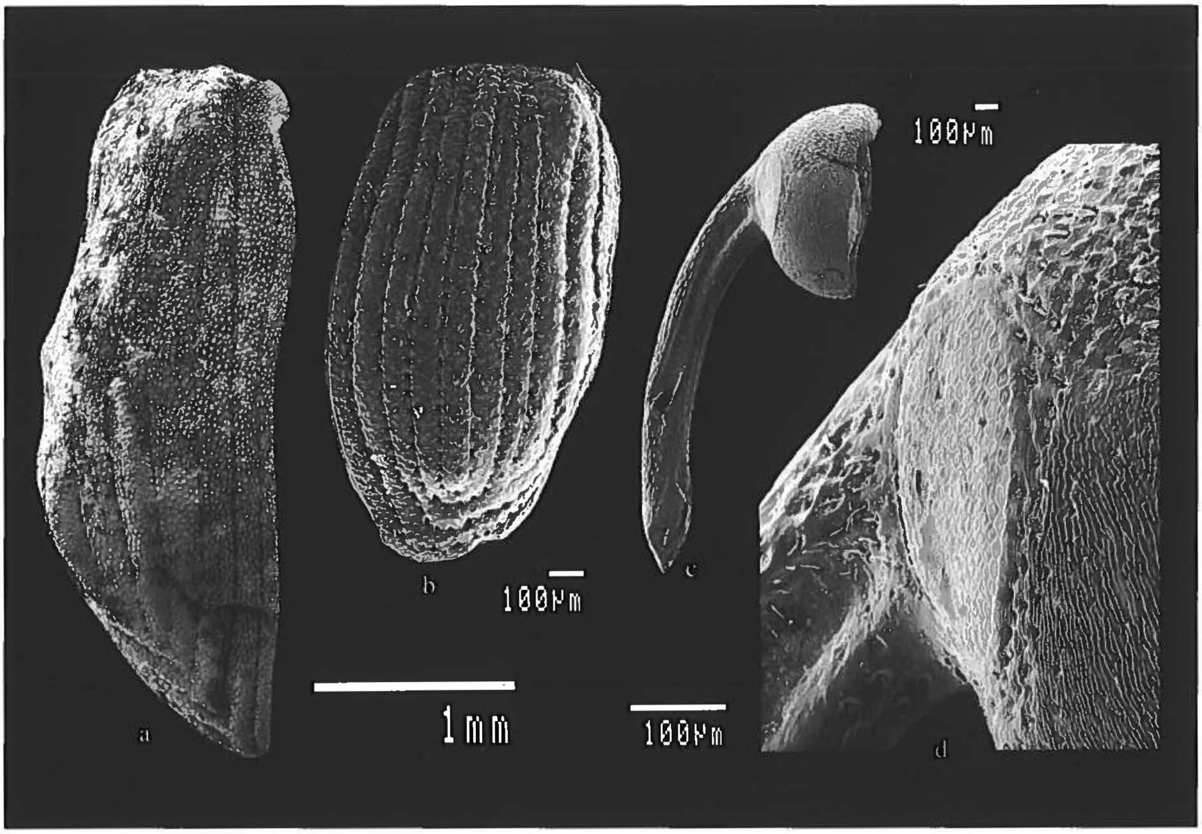


Fig. 26. a) *Grypus equiseti*, left elytron (53266); b) *Litodactylus leucogaster*, right elytron (64940); c,d) *Notaris* cf. *acridulus*, head (64925). Scanning electron micrographs.

sparse birch forest in flooded lands is the usual habitat (Boris Korotyaev, personal communication 1994).

Sitona cf. ***ovipennis*** Hochhuth, 1851
Material: One head, one prothorax (B3: 119).
Distribution (n.s.): S Russia through Siberia to the Amur area; temperate.
Habitat (n.s.): On *Hedysarum* spp. growing on gravelly slopes with herb vegetation. The larva feeds on the roots.
Note. Boris Korotyaev (personal communication 1993) referred the material to *Sitona* cf. *ovipennis borealis* Korotyaev, 1979 – a subspecies restricted to Taimyr, Kolyma basin and Chukotka. Korotyaev (personal communication 1994) now regards this a distinct species, in the Pleistocene apparently with a wide distribution from arctic to temperate regions.

Cf. ***Hypera*** sp.
Material: One prothorax (B3: 119).
Habitats: The species are found on herbaceous plants, in most cases Fabaceae.

Grypus equiseti (Fabricius, 1775)
Material: One prothorax, one elytron (B2: 27); two prothoraces, more than 50 elytra and elytral fragments, two sternites 1+2 (B3: 77, 119, 122, 132, 152). Figs 23,c, 26,a.
Distribution: Circumpolar, subarctic to temperate.
Habitat: The larva bores in stalk and root of *Equisetum* spp.
Fossil occurrences: Niguanak Site, N Alaska (Pliocene?); Prince Patrick Island & Meighen Island, Beaufort Formation (Pliocene); Remus Creek site & Fosheim Peninsula, Ellesmere Island (early Pliocene?).

Grypus cf. ***brunneirostris*** (Fabricius, 1792)
Material: One elytron fragment (B3: 77).
Distribution (n.s.): Circumpolar, boreal to temperate.
Habitat (n.s.): The larva bores in *Equisetum arvense* and *E. fluviatile*.
Note. The fossil is only the front half of a right elytron in a fairly bad condition. However, the size, the characteristic, dented shape, the bristles and reddish brown scales allow a tentative identification.

Notaris cf. ***acridulus*** (Linnaeus, 1758)
Material: Two rostra, six heads, seven prothoraces, nine elytra, one mesosternum, one metasternum, 10 sternites 1+2 (B3: 69, 77, 119, 122, 130, 132). Fig. 26,c,d.

Distribution (n.s.): Europe through Siberia to Mongolia, subarctic to temperate.
Habitat (n.s.): The larva bores in stalk and root of different marsh plants, e.g. *Glyceria maxima*.

Dorytomus cf. ***imbecillus*** Faust, 1882
Material: One prothorax (B3: 77).
Distribution (n.s.): Siberia, NE North America, SW Greenland; low arctic to boreal.
Habitat (n.s.): The larva feeds on catkins of *Salix* spp.

Dorytomus sp.
Material: Two elytra (B3: 77).
Habitats: The larvae feed on the catkins of *Salix* and *Populus* spp.

Pseudostyphlus pillumus (Gyllenhal, 1836)
Material: One elytron (B3: 77).
Distribution: C and S Europe, temperate.
Habitat: The larva bores in flower heads and roots of *Matricaria* spp.

Anoplus cf. ***plantaris*** (Naezen, 1794)
Material: Four elytra (B3: 77, 119).
Distribution (n.s.): Europe, subarctic to temperate.
Habitat (n.s.): The larva mines leaves of *Betula* and *Alnus* spp., rarely of *Salix* spp.

Rhyncolus cf. ***brunneus*** Mannerheim, 1843
Material: Two elytra (B3: 77, 119).
Distribution (n.s.): Transcontinental in North America, boreal to temperate.
Habitat (n.s.): Both larva and adult bore in wood of dying or dead, in general deciduous, trees.

Rhyncolus spp.
Material: Three elytra (B3: 77, 119) probably from two species.
Habitats: Both larvae and adults spend their whole life in living or dead wood.

Magdalis cf. ***violacea*** (Linnaeus, 1758)
Material: One elytron (B3: 119).
Distribution (n.s.): Europe, Asia Minor, Siberia; subarctic to temperate.
Habitat (n.s.): On *Pinus*, *Picea* and *Abies* spp. The larva bores in the wood of young branches, the adult feeds exteriorly on the bark.

Lepyrus cf. ***arcticus*** Paykull, 1792
Material: One pronotum fragment, eight elytra (fragments), sternites 1+2 (B3: 77, 119, 132).
Distribution (n.s.): Fennoscandia through Siberia, low arctic to subarctic.
Habitat (n.s.): On *Salix* spp. The larva gnaws the roots, the adult feeds on the leaves.
Note. The identification is based on large size in combination with coarse sculpture (mostly scale sockles), which renders the elytral apices almost serrate.

Litodactylus leucogaster (Marsham, 1802)
Material: Seven elytra (B3: 69, 77). Fig. 26,b.
Distribution: Europe, boreal to temperate.
Habitat: On *Myriophyllum verticillatum* in eutrophic, stagnant waters; limnic both as larva and adult.

Micrelus cf. ***ericae*** (Gyllenhal, 1813)
Material: One prothorax (B3: 77).
Distribution (n.s.): Europe, subarctic to temperate.
Habitat (n.s.): Both larva and adult feed on the flowers of *Calluna vulgaris* and *Erica tetralix*.
Note. The prothorax differs from modern material studied by being less collar-like swollen anteriorly, where the two small spines are also placed more apart than in modern specimens.

Isochnus sp.
Material: One elytron (B3: 119).
Habitats: The species generally feed on *Salix* and *Populus* spp. (Anderson 1989).

Curculionidae gen. et sp. indet.
Material: Pronota, elytra, sterna, sternites, legs, small fragments. Only one mesosternum from unit B1 (50), the remainder from unit B3 (69, 75, 77, 119, 132). The elytra represent at least seven species.

Scolytidae

Tomicus piniperda (Linnaeus, 1758)
Material: One elytron (B3: 77).
Distribution: Circumpolar, subarctic to subtropical.
Habitat: Stumps and living trunks of *Pinus* spp., more rarely *Picea* spp.
Note. The species is distinguished from *T. minor* (Hartig) by means of the arrangement of scale-like spines on the frontal margin of elytra and between 6. and 7. stria.

Scolytus piceae (Swaine, 1934)
Material: Four elytra (B3: 77, 119). Fig. 25,c.
Distribution: North America, subarctic to boreal (northern U.S.A. to northern limit of tree growth in Alaska and Canada).
Habitat: Shaded-out dying branches or dying seedlings of *Picea* spp.
Note. According to Stephen L. Wood (personal communication 1993) the Kap København specimens have the strial punctures distinctly larger than in modern specimens. Although this character varies in the species, a geographical race could be based on the Kap København material.

Trypophloeus cf. ***bispinulus*** Eggers, 1927
Material: One pronotum (B3: 119).

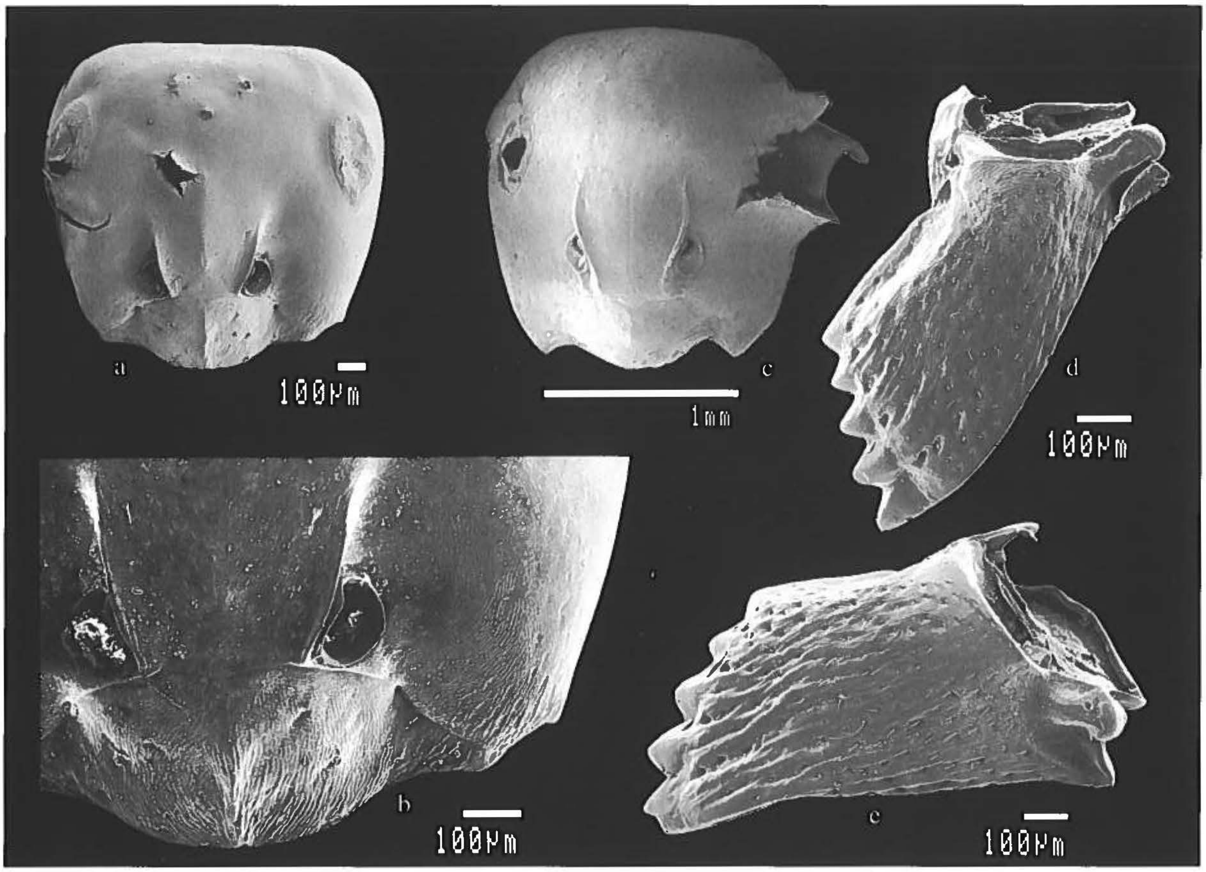


Fig. 27. a,b) *Formica* sp., head (56666); c) *Camponotus* cf. *herculeanus*, head (64972); d,e) *Camponotus* sp., mandibles (64936). Scanning electron micrographs.

Distribution (n.s.): Boreal Europe.
Habitat (n.s.): The larva bores in *Populus tremula* and other species of *Populus*.
Note. The pronotum differs from those of *Pityophthorus* spp. only by more scattered punctation and a distinct microsculpture. (*T. asperatus* (Gyllenhal) is very much alike, but has small warty spikes behind the garlands of "scales").

Pityophthorus sp.
Material: Galleries in *Larix* wood.

HYMENOPTERA

Tenthredinidae

Dolerus sp.
Material: One head (B3: 122).
Habitats: The larvae feed on Poaceae, Cyperaceae and Juncaceae.

Tenthredinidae gen. et sp. indet.
Material: One head (B3: 119).

Siricidae

Urocerus cf. ***gigas*** (Linnaeus, 1758).
Material: Fly holes and tunnels in *Larix* wood (B3).
Distribution (n.s.): Circumpolar, boreal to temperate.
Habitat (n.s.): The larva bores in wood of conifers (*Picea, Abies, Larix, Pinus, Pseudotsuga*).
Note. Two subspecies have been described, the palaearctic *U. g. gigas* (L.) and the nearctic *U. g. flavicornis* (Fabricius).

Ichneumonidae

Banchus sp.
Material: One head (♂) (B3: 77).
Habitat: The species are primarily parasitoids on *Bombus* spp.

Pimplinae
Gen. et sp. indet.
Material: One tergite (B1: 50), one thorax fragment (B3: 132).
Habitats: The species are parasitoids on Lepidoptera larvae.

Ichneumonidae gen. et sp. indet.
Material: One propodeum (B1: 50); nine heads (B3: 75, 77, 119).

Torymidae

Megastigmus sp.
Material: Bore holes in *Larix* seeds (B3) (Bennike 1990, fig. 340).
Habitats: The larvae live in and from seeds of *Larix* spp.

Chalcidoidea

Fam., gen. et sp. indet.
Material: One head (B1: 50); two heads (B3: 77, 122).

Proctotrupoidea

Fam., gen. et sp. indet.
Material: Two heads (B3: 77, 119).
Habitat: The species are generally parasites of insect eggs.

Diapriidae (Proctotrupoidea)
Gen et sp. indet.
Material: One head (B3: 119).

Formicidae

Myrmica sp.
Material: Two heads, petiolus (B3: 77, 119).
Habitats: Relatively small colonies nesting in stumps, under stones or in banks.

Leptothorax sp.
Material: One head (B3: 69).
Habitats: Small communities under stones, in rock crevices, under bark, in twigs or in peat.

Camponotus cf. ***herculeanus*** (Linnaeus, 1758)
Material: Five heads, one scutellum, one propodeum, (B3: 77, 119, 122, 141, 152). Two heads are from workers, one head, the propodeum and scutellum from queens. Fig. 27,c.
Distribution (n.s.): Circumpolar, subarctic (subalpine) to temperate (boreo-montane in Europe).
Habitat (n.s.): Shaded, chiefly coniferous forests, nesting in rotten stumps and logs, occasionally mining in living trees, especially conifers. Probably the dominant ant in the forests of boreal and alpine North America.

Camponotus spp.
Material: 12 mandibles, ten heads and head fragments, two prothoraces, four pronota, one meso+metathorax, two thorax fragments, two coxae (B3: 77, 105, 119). Fig. 27,d,e.
Note. Two heads (from males) are certainly not from *C. herculeanus*, the remainder of the fragments could as well be from that species.

Formica sp. (due to the size: the *Formica rufa*-group).
Material: Two heads, one abdomen (B3: 77). One head is from a queen. Fig. 27,a,b.
Habitats: Generally forming huge societies in boreal and subalpine forests.

Formicinae
Gen. et sp. indet.
Material: One mandible, two heads (B3: 77, 122).

DIPTERA NEMATOCERA

Tipulidae

Tipula spp.
Material: One larval mandible (B1: 50); one larval mandible, one larval head, one female cercus (B3: 77, 119).
Habitats: The hygrophilic larvae are found in soil or freshwater; the food is generally plant roots.

Simuliidae

Gen. et sp. indet.
Material: Seven larval head capsules (B3: 119).
Habitats: The occurrence of larvae of Simuliidae indicates fast running water conditions.

Chironomidae
(larval head capsules)

Tanypodinae
Gen. et sp. indet.
Material: One (B3: 122).

Cf. ***Diamesa*** sp.
Material: Four (B3: 122).
Habitats: Larvae of *Diamesa* are known to prefer cold, fast running water, and high abundances may be found in glacial meltwater brooks (Alm & Willasen 1993).

Diamesinae
Gen. et sp. indet.
Material: Four (B3: 119).

Axarus sp.
Material: Two (B1: 50; B3: 119).
Note. According to Wolfgang Hofmann (personal communication 1993), *Axarus* is a strange taxon with only

one doubtful species in Europe, four in North America and several in South America. The larvae occur in soft littoral sediments of lakes and rivers.

Chironomus sp.
Material: Two (B3: 69, 119), five of *Chironomus*-type (B3: 122, 132).

Chironomini spp.
Gen et sp. indet.
Material: Three (B3: 122, 132).

Micropsectra sp.
Material: One (B3: 132).
Habitats: The larvae of most *Micropsectra* species live in cold water and are especially associated with muddy deposits in slowly flowing streams (Alm & Willasen 1993).

Cf. ***Endochironomus*** sp.
Material: Two (B3: 122, 132).

Corynocera ambigua Zetterstedt, 1838
Material: Four (B3: 122, 132).
Distribution: Circumpolar, low arctic to boreal.
Habitat: Lakes.
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene).

Cf. ***Orthocladius*** sp.
Material: Eight (B3: 122, 132).

Cf. ***Psectrocladius*** sp.
Material: One (B3: 122).

Orthocladiinae
Gen. et sp. indet.
Material: Five (B3: 122, 132).

DIPTERA BRACHYCERA

Calyptratae

Gen. et sp. indet.
Material: One head (B1: 50); one head, seven puparia (B3: 69, 77, 119).

Calliphoridae

Gen. et sp. indet.
Material: Eight puparia (B3: 77, 119).
Habitats: The larvae live in and from vertebrate carcasses.

LEPIDOPTERA

Gen. et sp. indet.
Material: One larval mandible, three larval heads (B3: 77, 122).

TRICHOPTERA

(larval sclerites)

Hydropsychidae

Arctopsyche ladogensis (Kolenati, 1859)
Material: 22 frontoclypei, 32 parietals, four mandibles, 106 pronota, 10 meso/metanota (B3: 69, 75, 77, 119, 132).
Distribution: Circumpolar, subarctic to boreal.
Habitat: Cool streams and rivers with solid bottom; a netspinner feeding mainly on other insects and diatoms.
Fossil occurrences: Meighen Island, Beaufort Formation (Pliocene).

Hydropsyche nevae Kolenati, 1858
Material: One frontoclypeus, 27 parietals, 34 pronota, two mesonota, two coxa (B3: 77, 119, 132).
Distribution: Scandinavia through N Russia, Siberia and C Asia to Kamchatka; boreal.
Habitat: Solid bottom (stones and wood) in rivers and streams with rapids in hills and foothills; often together with *Arctopsyche ladogensis*.

Phryganeidae

Agrypnia pagetana Curtis, 1835
Material: One frontoclypeus, 12 pronota, one coxa (B3: 77).
Distribution: Circumpolar, low arctic to temperate.
Habitat: Among vegetation in stagnant and slowly flowing water.

Agrypnia straminea Hagen, 1873
Material: One frontoclypeus, 13 pronota (B3: 77).
Distribution: N North America (except Alaska); low arctic to temperate.
Habitat: Stagnant and slowly flowing waters.

Banksiola cf. ***crotchi*** Banks, 1944
Material: One pronotum (B3: 77).
Distribution (n.s.): Transcontinental in North America, boreal.
Habitat (n.s.): Lakes, ponds, rivers, streams.

Phryganeidae gen. et sp. indet.
Material: Two parietals, one mandible, one adult mesonotum (B3: 69, 77).

Brachycentridae

Brachycentrus americanus Banks, 1899
Material: One frontoclypeus, five pronota (B3: 77).
Distribution: Circumpolar in N and mountainous North America and N Asia from N Kazakhstan and Mongolia through E Siberia to Kamchatka, Sakhalin and Japan; boreal to temperate.
Habitat: Cold, running water; omnivorous, but mainly feeding on diatoms.

Limnephilidae

Apatania crymophila McLachlan, 1880
Material: One parietal, three pronota (B3: 77, 119).
Distribution: N Urals through Siberia to Kamchatka, C North America (Manitoba); low arctic to boreal.
Habitat: Stony bottom in cool springs (below *c.* 12°C in summer) and shallow parts of rivers and rivulets, feeding on diatoms.

Apatania cf. ***nigra*** Walker, 1852
Material: Ten pronota, three parietals (B3: 77, 119).
Distribution (n.s.): E North America (James Bay area and Maine); boreal to temperate.
Habitat (n.s.): Diatom scraper on stones in streams.

Anabolia sp.
Material: Four parietals, four pronota (B3: 77).
Habitats: Standing and slowly flowing waters; detrital feeders.

Cf. ***Clistoronia*** sp.
Material: One frontoclypeus, two parietals (B3: 69, 77).
Distribution: Nearctic genus.
Habitats: Ponds and small lakes, usually at higher elevations; detrital feeders.

Psychoglypha sp.
Material: One parietal, three pronota, one mesonotum (B3: 77).
Distribution: Nearctic genus.
Habitats: Standing and running waters.

Limnephilus sp.
Material: One frontoclypeus, seven pronota, three mesonota (B3: 77, 119).
Habitats: Standing and slowly flowing waters; detrital feeders.

Halesochila taylori (Banks, 1904)
Material: Two parietals, two pronota (B3: 77).
Distribution: NW North America (Alaska to Oregon); boreal to temperate.
Habitat: Small lakes and ponds, feeding largely on plant detritus.

Cf. ***Pycnopsyche*** sp.
Material: One parietal, one pronotum (B3: 77).
Distribution: Nearctic genus.
Habitats: Cool streams and rivers; detrital feeders.

Dicosmoecus obscuripennis Banks, 1938
Material: One parietal, one pronotum (B3: 77).

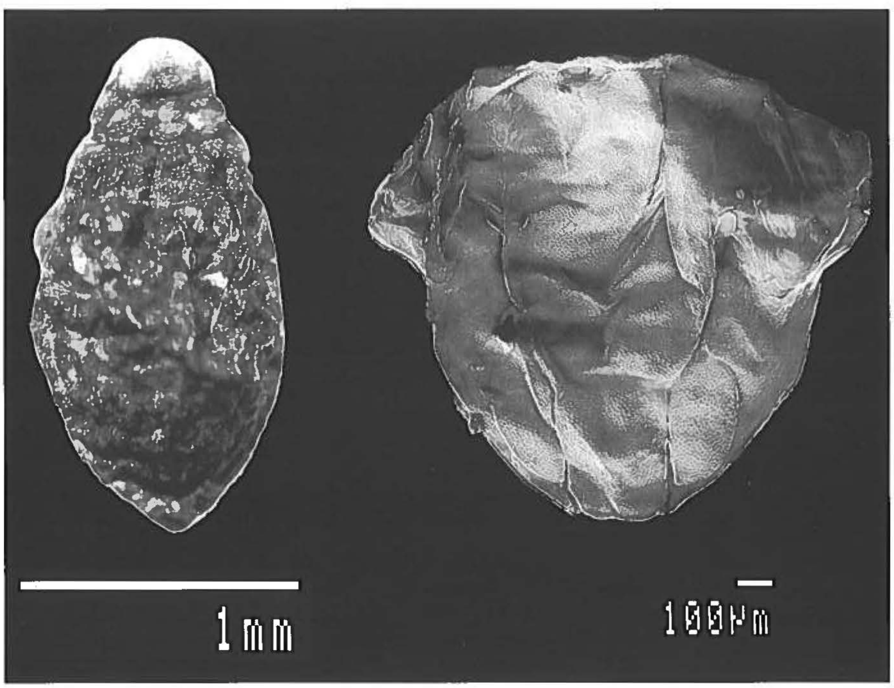


Fig. 28. a) *Chaitophorus* cf. *salijaponicus niger*, body except appendages (63934) (Ole Heie phot.; b) Cicadellidae sp., head (64935), scanning electron micrograph.

Distribution: NW North America (Alaska, Yukon, Northwest Territories), NE Russia through Siberia to Kamchatka; boreal.
Habitat: Stones and solid sand in lakes and rivers, feeding on detritus.

Limnephilidae gen. et spp. indet.
Material: Four frontoclypei, eight parietals, 37 pronota, three mesonota, one adult mesonotum (B3: 77, 119).

Molannidae

Molanna sp.
Material: One pronotum (B3: 77).
Habitats: Sand and mud substrates in standing and running waters.

HEMIPTERA HETEROPTERA

Pentatomidae

Eusarcoris (Rhacognathus) punctatus (Linnaeus, 1758)
Material: Four scutella (fragments) (B3: 69, 77).
Distribution: Europe through Siberia to Japan; subarctic to temperate (montane in the south).
Habitat: Damper parts of heaths, also mentioned from shrubs of *Betula* and *Populus tremula*.

Elasmucha sp.
Material: One scutellum (B3: 77).
Habitats: The few species (one nearctic, four palaearctic) are found on different shrubs and trees, in particular species of *Betula* and *Alnus*. The females exhibit parental care for eggs and young nymphs.

Pentatomidae gen. et sp. indet.
Material: One scutellum (B3: 77).

Lygaeidae

Peritrechus sp.
Material: One head (B3: 77).
Habitats: The species are found in dry, sandy areas. Seedfeeders.

Saldidae

Saldula spp.
Material: Two pronota (probably representing two species) (B3: 77).
Habitats: Most species are found on mud flats at the margin of ponds, rivers or estuarines.

HEMIPTERA HOMOPTERA

Cicadoidea

Gen. et sp. indet.
Material: One head (B3: 77).

Cicadellidae

Gen. et sp. indet.
Material: Three heads (B3: 69, 77). Fig. 28,b.
Habitats: The species generally feed on grasses.

Aphidoidea: Drepanosiphidae

Chaitophorus cf. ***salijaponicus niger*** Mordvilko, 1929
Material: One entire body except antennae and legs. Fig. 28,a.
Distribution (n.s.): Europe to C Asia; boreal to subtropical.
Habitat (n.s.): In small colonies feeding on different species of *Salix*, sometimes visited by ants in the spring (Heie, 1982).
Note. Heie (1995) describes the specimen and presents the argumentation in favour of the identification.

Palaeoecological part

This part treats the results from the taxonomical section. It is a prerequisite that my general confidence in the many inconclusively identified species ("cf.") allows a treatment as if they were in fact the nominal species.

Zoogeography

The present geographical distributions of the fossil species appear from Table 3 and the taxonomical part and is summarized in Tables 5 & 6.

The modern biogeographical position of Greenland has been very much discussed (Böcher 1988). Greenland today has an intermediary position between the Nearctic and the Palaearctic Regions, but the share of nearctic and palaearctic taxa differs highly from one group of organisms to another. For instance, the Greenland Trichoptera have marked American affinities with six nearctic and two holarctic species, whereas among the Coleoptera the palaearctic species by far outnumber the nearctic with one nearctic versus twelve palaearctic species (Böcher 1988). However, in most taxonomical groups the number of circumpolar/holarctic species dominate in the Greenland flora and fauna.

From Table 5 it is evident that the insect fauna of the Kap København Formation was perfectly intermediate between what are nowadays nearctic and palaearctic faunal elements, but that the modern circumpolar plus holarctic component was dominant. Considering the distributions in more detail by dividing the Nearctic and Palaearctic Regions in western and eastern subregions, some surprising facts appear (Table 6). Many more of the Kap København species are today confined to the western Nearctic and the western Palaearctic subregions than to the other two subregions.

Only two species (*Patrobus stygicus*, *Apatania* cf. *nigra*) are exclusively found in the eastern Nearctic subregion, which is closest to Greenland, and of the 26 species with different holarctic distributions (in frame, Table 6), eleven are missing only in the eastern Nearctic subregion (WN+P). This situation is probably caused by the Pleistocene glaciations which affected the North American continent differently, with survival centers in the Northwest (Alaska-Yukon) and in the south (Schwert & Ashworth 1988).

Table 7 lists the 40 species which are today confined to only one geographical subregion. A strange taxonomical/biological distribution is apparent, with no less than 13 species of Carabidae nowadays confined to the western Nearctic and a number of phytophagous species, in particular Curculionidae, confined to the western or eastern Palaearctic.

Table 5. Present geographical distribution of 158 insect species from the Kap København Formation (154 named species plus four representatives of nearctic genera: *Amecocerus*, *Clistoronia*, *Psychoglypha*, *Pychnoglypha*). The ranges of both *Agabus clavicornis* and *A. serricornis* are included.

Geographic regions	No. species	%
Circumpolar	38	24.1
Holarctic	26	16.5
Nearctic	46	29.1
Palaearctic	48	30.4
Total:	158	

Table 6. Matrix showing the present geographical distributions of 158 insect species from the Kap København Formation (154 named species plus four representatives of nearctic genera; see Table 4). Symbols: P, palaearctic; WP, western palaearctic, EP, eastern palaearctic; N, nearctic; WN, western nearctic; EN, eastern nearctic. The combination P+N is tantamount to circumpolar (C), whereas the eight combinations within the frame denote holarctic species

		P	WP	EP
		26	15	7
N	28	38 (C)	3	3
WN	16	11	0	7
EN	2	0	1	1

Table 7. Insect species from the Kap København Formation at present confined to only one geographic subregion. Symbols: WN, western nearctic; EN, eastern nearctic; WP, western palaeartic; EP, eastern palaearctic. Phytophagous species are marked with *.

Species	WN	EN	WP	EP
Opisthius richardsoni	x			
Notiophilus cf. *biguttatus*			x	
Elaphrus sibiricus				x
Elaphrus lecontei	x			
Patrobus stygicus		x		
Asaphidion alaskanum	x			
Bembidion alaskanum	x			
Bembidion cf. *balli*	x			
Bembidion cf. *vitiosum*				x
Bembidion dyschirinum	x			
Bembidion cf. *planiusculum*	x			
Bembidion salebratum	x			
Pterostichus cf. *planus*	x			
Pterostichus riparius	x			
Chlaenius interruptus	x			
Helophorus cf. *khnzoriani*				x
Megasternum obscurum			x	
Agaricophagus cephalotes			x	
Anisotoma cf. *castanea*			x	
Thanatophilus baicalicus				x
Heterosilpha ramosa	x			
Pteroloma forsstromii			x	
Stenus cf. *carbonarius*			x	
Stenus cf. *pinguis*	x			
Kalissus nitidus	x			
Coryphium angusticolle			x	
Podabrus alpinus			x	
*Simplocaria basalis**				x
Laricobius cf. *caucasicus*			x	
Hydrothassa cf. *hannoveriana**			x	
*Cyriophthalmus variegatus**				x
Sitona cf. *ovipennis borealis**				x
*Pseudostyphlus pillumus**			x	
Anoplus cf. *plantaris**			x	
*Litodactylus leucogaster**			x	
Micrelus cf. *ericae**			x	
Trypophloeus cf. *bispinulus**			x	
Apatania cf. *nigra*		x		
Halesochila taylori	x			
Totals:	15	2	15	7

Habitat requirements

A small number of species (*Diacheila polita*, *Stenus assequens*, *Hypnoidus rivularius*, *Simplocaria metallica*) appear to be fairly eurytopic in that they do not even clearly prefer either damp or dry biotopes. In other respects these species are ecologically different. *S. metallica* is to some extent riparian, *D. polita* is predominantly a tundra species. In terms of their climatic distribution, *D. polita* is low arctic-subarctic, *S. metallica* and *H. rivularius* are low arctic-boreal, and *S. assequens* boreal-subtropical. Many more species are eurytopic, but to a varying degree xerophilic (14 species) or hygrophilic (30 species).

Most of the eurytopic xerophilic species are commonly found in sandy heath and dune areas. These species

Table 8. The number of insect species from the Kap København Formation associated with different freshwater shores, including a number of species placed in other ecological groups than group R (riparian species, cf. Table 12)

	Exposed	Shaded	Eurytopic	Totals
Lake shores	3	5	1	9
River shores	13	2	1	16
Shores	9	12	1	22
Totals:	25	19	3	47

Table 9. Simplified modern ecological distribution of the taxa of Trichoptera from the Kap København Formation. *D. obscuripennis* is found on stones and solid sands, *Molanna* spp. on sand and mud bottom, both taxa in running as well as standing waters. (By courtesy of Nancy Williams, Toronto)

	Running water		Standing water	
Species	Swift, cool, stony	Slow, vegetated	Ponds and small vegetated lakes	Lakes
Arctopsyche ladogensis	x			
Hydropsyche nevae	x			
Agrypnia pagetana		x		
Agrypnia straminea		x	x	x
Banksiola crotchi	x	x	x	x
Brachycentrus americanus	x			
Apatania crymophila	x			
Apatania nigra	x			
Anabolia sp.		x	x	
Clistoronia sp.			x	
Psychoglypha sp.		x	x	
Limnephilus sp.		x	x	
Halesochila taylori			x	
Pycnopsyche sp.	x			
Dicosmoecus obscuripennis	x		x	
Molanna sp.	x		x	

are apparently quite independent of the vicinity of water. *Amara pseudobrunnea* has been found under bushes on sandy moraine and may belong in this group of species. The pentatomid bug *Eusarcoris punctatus* is another heath species, but prefers the damper portions and shrubs.

Open biotopes also comprise tundra, which in the broad sense simply denotes all the arctic plant communities north of the forest limit. The marked tundra species (totally 22) include xerophilic as well as hygrophilic species; the common criterion is their prevailing arctic affinity, probably as a consequence of a low temperature range preferred. Seventeen of the tundra species today occur in both low arctic and subarctic environments.

A large fraction of the named species are associated with limnic biotopes, either as more or less riparian (30 %; Table 8), hygrophilic (20 %), or as true aquatic species (16 %). Trichoptera and most Nematocera (Chironomidae, Simuliidae) are here considered aquatic since the species spend most of their lives as larvae and pupae in water. The dominance of taxa associated with limnic biotopes in the fossil record may be exaggerated because these are the most likely to be carried along with watercourses and sedimented.

Hygrophilic taxa are in some cases semi-aquatic, living in very humid surroundings, like mosses and vigorous vegetation on shores of ponds and streams (*Helophorus tuberculatus*, *Acidota quadrata*, species of *Olophrum*, *Eucnecosum* and *Tachyporus*).

Many riparian species are hygrophilic predators, most often found beneath luxuriant vegetation (e.g. *Blethisa multipunctata*, *Elaphrus lapponicus*, *Patrobus stygicus*, *Pterostichus nigrita*, *Chlaenius interruptus*, several species of *Stenus*). Others are herbivores associated with different swamp plants (*Donacia* spp., *Notaris acridulus*) or are monophagous on swamp plants (*Grypus equiseti*, *G. brunneirostris* on *Equisetum* spp., *Hydrothassa hannoveriana* on *Caltha palustris*).

One very prominent ecological group occurs exclusively on open, sandy or gravelly, sun-exposed shores of lakes and rivers. These are mainly species of *Bembidion* (14, four of the subgenus *Chrysobracteon*), but also of *Asaphidion*, *Opisthius*, *Elaphrus* and the shore bug genus *Saldula*. *Cicindela hybrida* might as well occur in this association of thermophilic, diurnal and highly active predators, which hunt by means of vision and accordingly are dependent on a high incidence of sunshine during the active season. Species of *Cicindela* prefer microclimatic temperatures of 30-40°C and are unable to fly at temperatures below 30°C (Thiele 1977). The sand-dwelling *Aegialia terminalis*, the tunnelling *Bledius* species and their predators, *Dyschirius* spp., also belong in this kind of biotope. It is obviously necessary to envisage extensive stretches of sandy shores, possibly including dune areas and the seashore, in order to account for this large ecological group.

A couple of species indicate even more xeric conditions, namely the "halobionts" associated with saline ponds and their shores in a steppe environment, *Elaphrus lecontei* and *Agabus bifarius*. Such biotopes were probably found at some distance from the coast in a more continental climate. In this connexion it is significant that Bennike (1990) found *Artemisia*-pollen as a minor, but consistent element in his pollen analyses.

The aquatic Coleoptera are dominated by pond and lake species with only one exclusively rivuline species (*Oreodytes sanmarkii*). The larval Trichoptera indicate a wide range of freshwater biotopes, from cool, stony mountain streams to vegetated ponds (Table 9). Most stagnant water species are found in vegetated ponds, the larva of the chironomid *Corynocera ambigua* exclusively in deep lakes. The limnic weevil, *Litodactylus leucogaster*, feeds on *Myriophyllum verticillatum*.

A significant fraction of insects, 14 % of named species, are more or less obligate forest species (Table 10), either as dependent on some general, possibly micro-cli-

Table 10. Insect taxa from the Kap København Formation associated with forest environment or trees and shrubs

		Arboreal			
	Forest environment	Leaf feeders etc.	Wood borers	Fungivores	Carnivores
Trachypachus zetterstedtii	x				
Notiophilus biguttatus	x				
Pterostichus stygicus	x				
Pterostichus riparius	x				
Amara brunnea	x				
Dromius angusticollis					x
Anisotoma castanea				x	
Anisotoma spp.				x	
Coryphium angusticolle				x	
Podabrus alpinus					x
Buprestidae spp.			x		
Laricobius cf. *caucasicus*					x
Cacotemnis carinatus			x		
Amecocerus sp.			x?		
Calvia quatuordecimguttata					x
Myrrha octodecimguttata					x
Cis spp.				x	
Cerambycidae spp.			x		
Chrysomela populi		x			
Dorytomus imbecillus		x			
Dorytomus sp.		x			
Anoplus plantaris		x			
Rhyncolus brunneus			x		
Rhyncolus spp.			x		
Magdalis violacea			x		
Lepyrus arcticus		x			
Isochnus sp.		x			
Tomicus piniperda			x		
Scolytus piceae			x		
Trypophloeus bispinulus			x		
Pityophthorus sp.			x		
Urocerus gigas			x		
Megastigmus sp.		x			
Myrmica sp.	x				
Leptothorax sp.	x				
Camponotus herculeanus	x				
Camponotus spp.	x				
Formica sp.	x				
Elasmucha sp.		x			
Chaitophorus salijaponicus					
Total taxa 39	10	8	12	4	5

matic, ecological features in the forest environment or because they are intimately associated with trees, such as the wood-boring beetles (Anobiidae, Cerambycidae, Scolytidae). These phytophagous insects thus are more indicative of the presence of trees than of the existence of forest. However, the carpenter ant, *Camponotus herculeanus*, is a true indicator of forest, both stenotopically occurring inside shaded forests and dependent on tree trunks and stumps for residence. Also the species of the *Formica rufa*-group are decidedly silvicolous, and even the members of the other ant-genera (*Myrmica* and *Leptothorax*) may nest in stumps and under bark. Also a number of carabids, in particular *Trachypachus zetterstedtii* and *Pterostichus stygicus*, are obligate forest species, whereas other carnivorous beetles, e.g. *Dromius angusticollis* (Carabidae), *Calvia quatuordecimguttata*, *Myrrha octodecimguttata* (Coccinellidae) and *Podabrus alpinus* (Cantharidae) may be termed arboreal. Some taxa which are included in Table 10 and associated with *Salix* and *Populus* (*Dorytomus* spp., *Lepyrus arcticus*, *Isochnus* sp.) are not true forest species, but inhabit low arctic and subarctic coppice.

It is interesting that "*Diacheila polita* type A", probably identical with *D. matthewsi*, occurred in the independently dated Lost Chicken site (2.9 Ma), eastern central Alaska. Here the associated abundant plant fossils suggest a dense forest environment – quite unlike the open arctic/subarctic biotopes preferred by the extant species of *Diacheila* (Matthews, in press). If *Notiophilus aeneus* is present in the Kap København Formation

Table 11. Oligophagous phytophagous insect taxa from the Kap København Formation

Insect taxa	Plant taxa
Grypus equiseti	*Equisetum*
Grypus brunneirostris	*Equisetum*
Scolytus piceae	*Picea*
Tomicus piniperda	*Pinus, Picea*
Magdalis violacea	*Pinus, Picea, Abies*
Hydrothassa hannoveriana	*Caltha palustris*
Cyriophthalmus variegatus	*Rosa*
Sitona ovipennis	*Hedysarum*
Litodactylus leucogaster	*Myriophyllum verticillatum*
Dorytomus imbecillus	*Salix*
Lepyrus arcticus	*Salix*
Chaitophorus salijaponicus	*Salix*
Chrysomela populi	*Salix, Populus*
Isochnus sp.	*Salix, Populus*
Trypophloeus bispinulus	*Populus tremula*
Anoplus plantaris	*Betula, Alnus*
Cacotemnis carinatus	*Fagus, Acer*
Micrelus ericae	*Calluna, Erica*
Pseudostyphlus pillumus	*Matricaria*

it also belongs in this company of obligate forest-dwellers.

A number of fungivorous species are mainly silvicolous because they are connected with the fungi and toadstools parasitizing trees, e.g. species of *Cis* in *Polyporus* spp. (tinder fungi) and of *Anisotoma*. *Coryphium angusticolle* lives under bark, probably from fungal hyphae. *Agaricophagus cephalotes* and *Colon* spp. are subterranean, probably living from fungal mycelia.

The fossil plant material also bears evidence of the activity of insects. In a large fraction of the wood of *Larix groenlandii* are found galleries, tunnels and exit holes of wood-boring insects (Fig. 24). Large, round fly holes are probably made by wood wasps (*Urocerus gigas*), whereas more oval holes of different sizes stem from the exit of longhorn beetles (Cerambycidae, Fig. 25,a,b). A few galleries in the wood-surface probably are bored by larvae of the predominantly tropical beetle family Buprestidae, and also a few of the characteristic galleries of bark beetles were found (possibly *Pityophthorus* sp.). Some seeds of *Larix* have exit holes of a seed wasp (*Megastigmus* sp., Torymidae; Bennike 1990, fig. 34).

The monophagous or oligophagous herbivorous species are presented in Table 11. The habitat of these species is thus defined by the habitat of their host plants, and their presence in the Kap København Formation indicate the simultaneous occurrence of their host plants. In a number of cases (*Salix*, *Betula*, *Alnus*, *Picea*, *Equisetum*) these genera are known from macrofossils (Bennike 1990). However, *Populus*, *Fagus*, *Acer*, *Myriophyllum*, *Matricaria*, *Calluna*/*Erica* and *Caltha* have not been reported. One explanation is that remains of the plants concerned have not yet been discovered. Another possibility is that the feeding habits of the insects in question are inadequately known, or that they formerly had other feeding habits and were less specialized. For instance, it is easy to imagine *Micrelus ericae* feeding on other ericaceous genera in addition to *Calluna* and *Erica*, e.g. *Cassiope*, *Ledum* or *Andromeda* which are found in the Kap København Formation, or that *Hydrothassa hannoveriana* besides *Caltha* could feed on some species of *Ranunculus*, which are also present.

In addition to the specialists mentioned, all the members of the Byrrhidae are moss feeders, and numerous species of bryophytes are known from the Kap København Formation, where mosses of Amblystegiaceae often dominate the organic detritus (Mogensen 1984). Other phytophagous groups include the Chrysomelidae, Curculionidae, Lepidoptera (larvae), Lygaeidae, Cicadellidae, the members of which may be fairly polyphagous. Larvae of crane flies (*Tipula*) are polyphagous root-feeders.

Species of the genus *Bledius* (and probably *Carpelimus*) devour algae growing in humid sand. A number of taxa are fungivorous (Leiodidae, Colonidae, Latridiidae, Cryptophagidae, Cisiidae, many Staphylinidae, e.g. *Mycetoporus*, *Bolitobius*). These species are associated with decaying vegetable and animal substances, and a number of other species have the same affinities although their precise feeding biology is unknown (*Megasternum obscurum*, *Catops*, *Coryphium*, *Phyllodrepa*, *Omalium*).

Only very few remains of terrestrial vertebrates are known from the Kap København Formation (*Lepus*, *Hypolagus*; Repenning *et al.* 1987; Repenning & Brouwers 1992; Bennike 1990), but the insect fauna in different ways indicate their existence. *Aphodius* spp. live in and from mammalian dung. In this context it is interesting to note that droppings of hares or rabbits have been reported from the Kap København Formation (Bennike 1990). The silphids (*Thanatophilus*, *Heterosilpha*) and the larvae of Calliphoridae (blowflies) eat vertebrate carcasses; when these are mummified, they serve as food for *Catops*, *Nitidula* and *Ptinus* spp.

A large fraction of the limnic taxa (Chironomidae, Simuliidae, most Trichoptera) consume organic detritus.

Ecological groups

Matthews (1983; Hughes *et al.* 1981) suggested a method for comparison of northern fossil insect assemblages. Some samples from the Kap København Formation have been treated in a similar way (Tables 12-15). Because of the limited and highly varied knowledge of the autecology of the different species, it is merely a simple and practical division in groups of species sharing some important ecological feature.

Admittedly, this is a rough and unsatisfactory division, because the criteria of the grouping are not consistent. For instance, the tundra group (T) is based on geographic distributions, whereas Group H is based on a preference for damp environments, and Group R on the association with a physical feature, namely freshwater

Table 12. Total insect taxa in alphabetical order from the richest sample, No. 64924 (Locality 77, unit B3) of the Kap København Formation. For each taxon is given the number of fragments, the minimum number of individuals, and the ecological group. Symbols: **Group A**, aquatic species; **Group H**, hygrophilic species, including phytophagous species on plants growing in humid places; **Group R**, shore species; **Group T**, species with main distribution north of the forest limit (tundra species); **Group S**, forest species and species feeding on shrubs and trees; **Group X**, xerophilic species (species from dry environments, independent on the vicinity of water); **Group E**, eurytopic terrestrial species; **Group P**, phytophagous species (except those on swamp plants, shrubs and trees), including their specialized predators (e.g. ladybird beetles); **Group D**, species associated with decaying vegetable matter, in most cases fungus-eaters; **Group I**, parasitoids; **Group C**, species feeding on carrion. - The four first mentioned groups are chiefly made up by carnivores.

Taxon	Number of fragments	Minimum number of individuals	Ecological group
Acidota quadrata	3	1	H
Aegialia terminalis	15	6	X
Agabus affinis	1	1	A
Agabus affinis group	3	1	A
Agabus bifarius	1	1	A
Agabus sp.	2	1	A
Agonum sp.	1	1	H
Agrypnia pagetana	4	3	A
Agrypnia straminea	8	7	A
Aleocharinae sp.	1	1	-
Amara sp.	1	1	-
Anabolia sp.	3	3	A
Anisotoma sp.	1	1	S
Apatania nigra	4	4	A
Arctobyrrhus subcanus	1	1	X
Arctopsyche ladogensis	34	21	A
Bembidion cf. *difficile*	1	1	R
Bembidion cf. *fellmanni*	1	1	T
Bembidion cf. *mckinleyi*	3	1	R
Bembidion cf. *planiusculum*	2	1	R
Bembidion cf. *sordidum*	1	1	R
Bembidion cf. *yukonum*	3	1	X
Bembidion (Plataphus) sp.	1	1	-
Bembidion sp.	2	1	-
Bledius cf. *arcticus*	1	1	T
Bledius spp.	4	3	R
Blethisa catenaria	2	2	T
Blethisa multipunctata	1	1	H
Brachycentrus americanus	2	1	A
Camponotus sp.	2	1	S
Chrysolina sp. (cf.)	1	1	P
Cis sp.	1	1	S
Corticaria sp.	2	1	D
Diacheila matthewsi	2	1	-
Dicosmoecus obscuripennis	1	1	A
Donacia sp.	2	1	H
Dyschirius sp.	2	1	R
Elaphrus angusticollis	1	1	R
Elaphrus tuberculatus	1	1	T
Elaphrus sp.	1	1	-
Eucnecosum cf. *brunnescens*	5	5	H
Eucnecosum spp.	15	8	H
Formicoidea sp.	1	1	S
Grypus equiseti	6	2	H
Helophorus cf. *khnzoriani*	6	4	A
Helophorus spp.	4	2	A
Hydroporus cf. *morio*	1	1	A
Hydroporus oblitus group	1	1	A
Hydroporus spp.	9	3	A
Hydropsyche nevae	31	17	A
Hygrotus sp.	1	1	A
Hypnoidus rivularius	1	1	E
Ilybius spp.	2	1	A
Litodactylus leucogaster	1	1	A
Notaris cf. *acridulus*	2	1	H
Notiophilus sp.	1	1	-
Olophrum cf. *boreale*	2	1	H
Olophrum spp.	2	1	H

Omalium sp.	1	1	D
Oreodytes alpinus/laevis	3	1	A
Patrobus stygicus	1	1	H
Phyllodrepa sp.	1	1	D
Podabrus cf. *alpinus*	1	1	S
Psychoglypha sp.	1	1	A
Pteroloma forsstromii	1	1	R
Pterostichus riparius	2	1	S
Pycnoglypta cf. *lurida*	1	1	H
Rhacognathus punctatus	2	1	H
Rhyncolus cf. *brunneus*	1	1	S
Scolytus piceae	1	1	S
Scymnus/Nephus sp.	1	1	P
Simplocaria basalis	2	1	-
Simplocaria cf. *metallica*	1	1	R
Simplocaria spp.	2	2	-
Stenus hyperboreus	1	1	H
Stenus sordidus	1	1	H
Stenus spp.	3	1	-
Tachinus cf. *elongatus*	1	1	H
Tachinus spp.	3	1	-
Tipula sp.	1	1	H
Tomicus piniperda	1	1	S
Total: 81	247	157	
Named species: 47			

Table 13. Numbers of taxa, fragments and minumum numbers of individuals of ecological groups in three samples from a lens of organic detritus at Locality 77, uppermost (64922), in the middle (64924) and lowermost (64937). For explanation of ecological groups, see Table 12

a) Sample 64922

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	8	44.4	11	52.4	8	44.4
H	3	16.6	3	14.3	3	16.6
T	1	5.6	1	4.8	1	5.6
S	2	11.1	2	9.5	2	11.1
X	2	11.1	2	9.5	2	11.1
P	1	5.6	1	4.8	1	5.6
I	1	5.6	1	4.8	1	5.6
Total:	18		21		18	

b) Sample 64924:

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	22	31.4	123	53.9	77	53.1
H	17	24.3	47	20.6	29	20
R	9	12.8	14	6.1	11	7.6
T	4	5.7	7	3.1	5	3.5
S	9	12.8	11	4.8	9	6.2
X	3	4.3	19	8.3	8	5.5
E	1	1.4	1	.4	1	.7
P	2	2.9	2	.9	2	1.4
D	3	4.3	4	1.8	3	2.1
Total:	70		228		145	

c) Sample 64937:

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	14	29.8	26	37.1	16	30.8
H	12	25.5	16	22.9	13	25
R	6	12.8	6	8.6	6	11.5
T	5	10.6	7	10	5	9.6
S	4	8.5	4	5.7	4	7.7
X	3	6.4	8	11.4	5	9.6
E	1	2.1	1	1.4	1	1.9
P	2	4.2	2	2.9	2	3.8
Total:	47		70		52	

Table 14. Numbers of taxa, fragments and minumum numbers of individuals of ecological groups in three samples from Locality 119. Samples 64915 & 64916, in coarse detritus, are from one metre above 64917. For explanation of ecological groups, see Table 12

a) Samples 64915+64916:

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	5	22.7	8	24.2	5	20.8
H	3	13.6	3	9.1	3	12.5
R	1	4.5	1	3.0	1	4.2
T	3	13.6	4	12.1	3	12.5
S	1	4.5	2	6.1	1	4.2
X	2	9.1	4	12.1	2	8.3
E	1	4.5	5	15.2	3	12.5
P	5	22.7	5	15.2	5	20.8
I	1	4.5	1	3.0	1	4.2
Total:	22		33		24	

b) Sample 64917:

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	12	20	28	21.5	17	20.7
H	17	28.3	32	24.6	23	28.0
R	8	13.3	10	7.7	8	9.8
T	4	6.7	6	4.6	4	4.9
S	5	8.3	13	10	8	9.8
X	4	6.7	24	18.5	8	9.8
E	1	1.7	5	3.8	3	3.7
P	4	6.7	7	5.4	6	7.3
D	4	6.7	4	3.1	4	4.9
C	1	1.7	1	.8	1	1.2
Total:	60		130		82	

Table 15. Numbers of taxa, fragments and minimum numbers of individuals of ecological groups in the entomological samples from units B3 and B1 at Locality 50. For explanation of ecological groups, see Table 12

a) Locality 50, unit B3 (samples 64902-04, 64908-11):

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	1	9.1	1	7.1	1	7.7
H	1	9.1	1	7.1	1	7.7
R	2	18.2	3	21.4	3	23.1
T	5	45.4	7	50	6	46.2
X	1	9.1	1	7.1	1	7.7
P	1	9.1	1	7.1	1	7.7
Total:	11		14		13	

b) Locality 50, unit B1 (samples 64905-07, 64912-13):

Ecological groups	Number of taxa	%	Number of fragments	%	Minimum number of individuals	%
A	2	8.3	4	8	2	5.1
H	6	25	20	40	15	38.5
R	5	20.8	6	12	6	15.4
T	5	20.8	12	24	9	23.1
X	2	8.3	3	6	3	7.8
E	1	4.2	1	2	1	2.6
P	1	4.2	2	4	1	2.6
I	2	8.3	2	4	2	5.1
Total:	24		50		39	

Table 16. Comparison of total insect taxa from units B1 and B2 with the samples from unit B3 taken at Locality 50 (other samples from this unit appear from Table 3). Symbols: LA, low arctic; SA, subarctic; B, boreal; T, southern temperate; A, aquatic; H, hygrophilic; R, riparian; T, tundra; S, forest and arboreal; X, xerophilic; E, eurytopic terrestrial; P, phytophagous; D, fungivorous; I, parasitoids; C, scavengers (see also legend to Table 12)

Insect taxa	Unit: B1	Unit: B2	Unit: B3 (Loc.50)	Climatic zone	Ecological group
Notiophilus aquaticus	x	x		B-T	X
Notiophilus spp.	x	x	x	-	-
Elaphrus lapponicus	x			SA	H
Elaphrus tuberculatus	x	x		LA-SA	T
Elaphrus sp.	x			-	-
Dyschirius sp.	x		x	-	R
Bembidion cf. *velox*	x			B-T	R
Bembidion dyschirinum	x			B	X
Bembidion cf. *fellmanni*	x	x	x	LA-SA	T
Bembidion cf. *arcticum*	x			LA-SA	T
Bembidion cf. *planiusculum*	x			B	R
Bembidion cf. *gebleri*	x			B	R
Bembidion (*Plataphodes*) spp.	x			-	-
Bembidion (*Plataphus*) sp.	x			-	-
Bembidion cf. *mckinleyi*			x	SA	R
Bembidion cf. *lenae*	x			LA-SA	T
Bembidion cf. *yukonum*	x			SA	X
Bembidion cf. *sordidum*	x	x	x	B	R
Bembidion spp.	x	x	x	-	-
Pterostichus cf. *planus*			x	SA?	T
Pterostichus brevicornis	x	x	x	LA-SA	T
Pterostichus (*Cryobius*) spp.	x	x	x	-	-
Pterostichus vermiculosus		x		LA-SA	T
Pterostichus spp.	x	x		-	-
Agonum sp.			x	-	-
Amara spp.	x		x	-	-
Carabidae spp.	x	x	x	-	-
Hydroporus sp.		x		-	A
Oreodytes alpinus/laevis		x		LA-B	A
Ilybius sp.			x	-	A
Agabini sp.	x			-	A
Pteroloma forsstromii	x			SA-T	R
Philonthus/Quedius sp.			x	-	-
Stenus assequens	x			B-ST	E
Stenus pubescens	x			B-T	R
Stenus spp.	x		x	-	-
Pycnoglypta cf. *lurida*	x		x	SA-B	H
Eucnecosum sp.	x			-	H
Bledius cf. *arcticus*	x		x	LA-SA	T
Bledius spp.	x		x	-	-
Tachyporus cf. *rulomus*	x			B	H
Tachyporus cf. *borealis*	x			B	H
Atheta sp.	x			-	H
Aleocharinae spp.	x	x	x	-	-
Staphylinidae spp.	x		x	-	-
Aegialia terminalis			x	B	X
Simplocaria cf. *elongata*			x	LA-SA	T
Ptinus sp.		x		-	D
Nitidula sp.	x			-	C
Chrysolina sp.		x		-	P
Hydrothassa cf. *hannoveriana*		x		SA-T	H
Chrysomelidae spp.	x		x	-	P
Grypus equiseti		x		SA-T	H
Curculionidae sp.	x			-	-
Pimplinae sp.	x			-	I
Chalcidoidea sp.	x			-	I
Ichneumonidae sp.	x			-	I
Hymenoptera spp.	x			-	-
Tipula sp.	x			-	H
Axarus sp.	x			-	A
Calyptratae sp.	x			-	-
Number of named species:	20	9	9		
Number of named genera:	16	10	13		
Total taxa:	47	18	23		

Table 17. Ecological groups of units B1 and B3. Symbols: A, aquatic; H, hygrophilic; R, riparian; T, tundra; S, forest and arboreal; X, xerophilic; E, eurytopic terrestrial; P, phytophagous; D, fungivorous; I, parasitoids; C, scavengers (see also legend to Table 12)

Ecological groups	Unit B1 Taxa	%	Unit B3 Taxa	%
A	2	6.5	50	23.1
H	7	22.6	32	14.8
R	7	22.6	30	13.9
T	6	19.4	20	9.3
X	3	9.7	16	7.4
E	1	3.2	1	.5
S	-	-	35	16.2
P	1	3.2	14	6.5
D	-	-	9	4.2
I	3	9.7	6	2.8
C	1	3.2	3	1.4
Total:	31		216	

shores. However, the ecological grouping allows a better overview and facilitates a quantitative comparison of different assemblages based on minimum numbers of individuals in each group.

Fig. 29 comprises the 227 taxa from the Kap København Formation which can be placed in one of the ecological groups. Taxa more or less associated with freshwater biotopes (A+H+R) dominate (totally 52 %). Next come forest taxa (15 %) and tundra taxa (10 %). Of the last mentioned about two thirds are hygrophilic or usually found on freshwater shores.

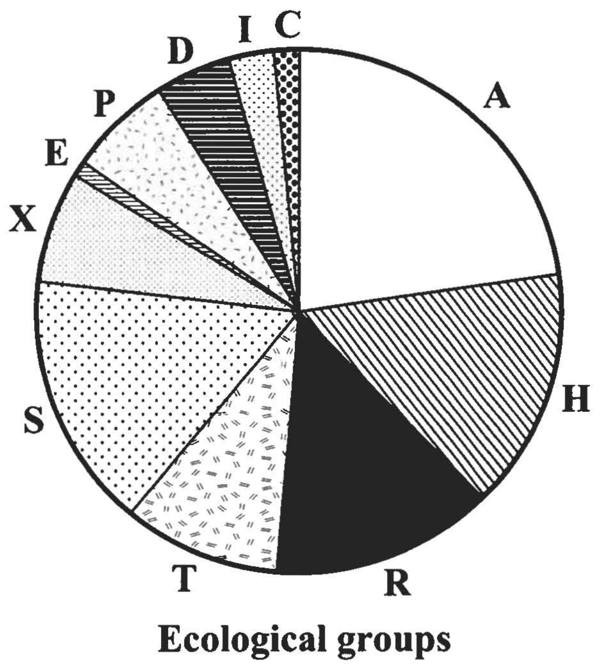


Fig. 29. Pie-diagram showing the modern distribution in ecological groups of 227 insect taxa from the Kap København Formation. Symbols: A, aquatic; H, hygrophilic; R, riparian; T, tundra; S, forest and arboreal; X, xerophilic; E, eurytopic terrestrial; P, phytophagous; D, fungivorous; I, parasitoids; C, scavengers (see also legend to Table 12).

Tables 12 and 13,b show the taxonomical and ecological composition of the sample with the highest diversity: unit B3, Locality 77, No. 64924. Here aquatic, hygrophilic and shore taxa together make up 69 %, 81 % of the number of fragments, and 81 % of the minimum number of individuals. Other samples from Locality 77 contain a varying amount of fossils, but ecologically they conform closely to the distribution in sample 64924 (Table 13,a,c).

Table 14 compares the ecological grouping in samples from Locality 119 (B3). Two samples (64915, 64916) are from a layer with coarse detritus mostly consisting of small twigs and sticks, whereas sample 64917 is from a thin layer with fine detritus about one metre below the coarse layer. The assemblage from the lower layer is similar to sample 64924, Locality 77, whereas the upper samples are very different, with low diversity and unusually numerous tundra and phytophagous taxa. These differences stress the importance of taphonomic factors.

Table 15 compares the ecological groups in units B1 and B3 from locality 50, the type section (only entomological samples). There is a general scarcity of aquatic taxa in these samples and a total lack of forest taxa in unit B1. All these samples, and especially those from unit B3, are very poor in insect remains, both regarding number of fragments and diversity. As to the ecological grouping, the assemblages from the two units are fairly similar, and thus quite unlike the picture seen in other samples from unit B3 (Tables 12-14). All representatives of forest fauna are absent, and in both B1 and B3 only one fragment of an aquatic beetle (Agabini sp. and *Ilybius* sp., respectively) was found.

However, the taxonomical composition of the two units from Locality 50 is somewhat different (Table 16, where the total collections from B1 and B3 at locality 50 are considered). In other samples from B3 fragments of *Aegialia* and *Simplocaria* are very characteristic and numerous. These genera, together with representatives of *Amara* and *Agonum*, are also present in B3 of Locality 50 and absent from B1.

It can thus be stated that when the samples from units B1 and B3 are compared, the insect faunas from the two units are very different, both regarding diversity and ecological composition (Table 17). However, the difference is not apparent at Locality 50, where a meagre fauna devoid of forest species and almost without aquatic elements is found in both units (Tables 15,16). It is difficult to explain this situation. Possibly the solution has to do with local sedimentation conditions. Taphonomical factors might explain the similarity of the assemblages from the two units at Locality 50, for instance if the streams that brought the sediments to the area primarily drained treeless upland areas with few stagnant waterbodies.

Climate

Palaeobotanical indications of climate

The arctic tree line nowadays roughly follows the 10°C July isotherm, and the modern northern limit of the most warmth demanding plants and also of the freshwater bryozoan *Cristatella mucedo* found in the Kap København Formation approaches the arctic tree line (Fredskild *et al.* 1975). Presence of forest-tundra in the Kap København area thus implies a July mean temperature above 10°C. On the other hand, tree ring measurements show that conditions were marginal for tree growth (Bennike 1990), indicating that summer temperatures were *c.* 10°C. Because the ranges of few species are confined by winter temperatures, these are more difficult to assess. However, a few of the southern taxa from the Kap København Formation (*Thuja occidentalis*, *Taxus* sp.) are unable to endure mean January temperatures below -17°C (Bennike 1990).

Studies of the moss flora of the Kap København Formation point to a precipitation higher than today (Mogensen 1984), and the modern distribution of *Thuja occidentalis* is limited by a minimum yearly precipitation of about 500 mm (Bennike 1990). In some of the fossil, stunted trees, the branches evidently have been deformed by heavy snow load, and several of the Kap København plant species require a covering of snow during winter (Bennike 1990).

Bennike (1990) concluded that the climate during the deposition of the Kap København Formation was subarctic and fairly oceanic. Mean July temperature was 10-11°C, 7-8°C higher than today. January mean temperature was presumably between -10°C and -15°C, 15-20°C higher than today. Precipitation was probably at least 500 mm per year, two times that of today, with winters rather rich in snow.

Present climatic range of fossil insects

Of the 33 indigenous species of Coleoptera occurring in Greenland today (Böcher 1988), eight have been found in the Kap København Formation, although six of them with uncertain identification: *Nebria rufescens*, *Bembidion grapii*, *Hydroporus morio*, *Micralymma brevilingue*, *Simplocaria metallica*, *Simplocaria elongata*, *Arctobyrrhus (=Tylicus) subcanus* and *Dorytomus imbecillus*. *H. morio* and *M. brevilingue* are widespread in Greenland and reach the High Arctic, *B. grapii* nearly reaches the High Arctic, whereas the other species are restricted to low arctic and subarctic Southwest Greenland. None of the identified species from the Kap København Formation belonging to other orders occur in Greenland today.

In the taxonomical part I have attempted to assign the modern climatic distribution of the species. This is not easy in many cases when the range is little known and vaguely described in the literature. Fig. 30,a,b shows,

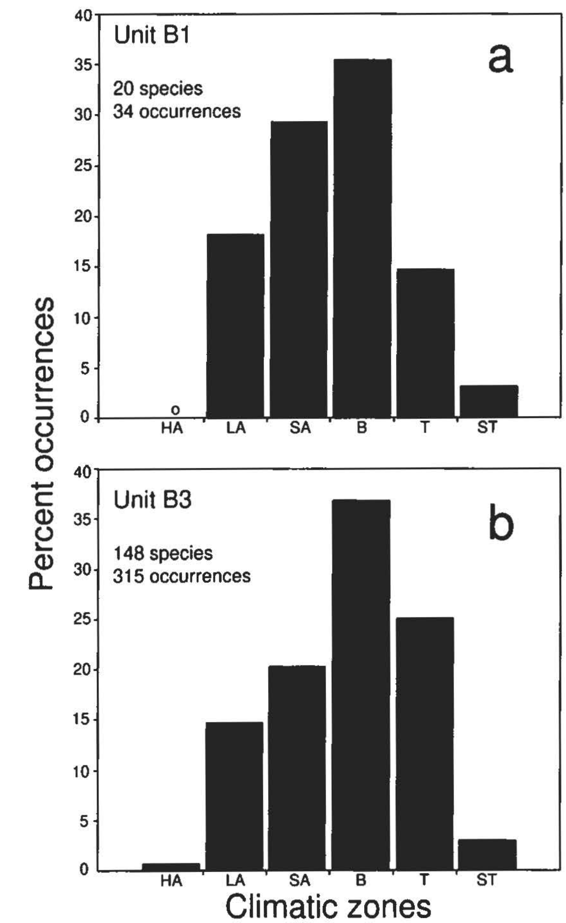


Fig. 30. Histograms showing the percentage of modern occurrences in different climatic zones of named insect species from the Kap København Formation. a) unit B1; b) unit B3. Symbols: HA, high arctic; LA, low arctic; SA, subarctic; B, boreal; T, southern temperate; ST, subtropical.

Table 18. MCR reconstructions of ancient temperature regimes at Kap København. The figures in brackets in first column denote the number of samples. With the exception of Locality 50, all the samples originate from unit B3. t_n = number of taxa included in the calculation. »W« and »C« denote either warm (temperate) or cold (subarctic) temperature conditions

Samples	Locality	t_n	TMAX (°C) (mean July temperature)		TMIN (°C) (mean January temperature)
64923	77 (upper)	10	10 – 13		-18 – -8
64925	77 (middle)	12	10 – 11		-13 – -4
64936	77 (lower)	12	10 – 11		-19 – -9
(4)	77 (O-25 cm)	18	13 – 19	W	-24 – -1
	do.	-	8 – 11	C	-29 – -17
(6)	77 (25-50 cm)	20	10 – 11		-19 – -9
(6)	77 (50-80 cm)	20	13 – 19	W	-24 – -1
	do.	-	8 – 11	C	-29 – -17
(2)	69 (combined)	9	12 – 19	W	-19 – -9
	do.	-	7 – 11	C	-40 – -17
(5)	119 (combined)	11	10 – 11		-13 – -10
(5)	50 (unit B1)	4	11 – 13		-26 – -7
Total KKF samples		28	15 – 19	W	-15 – 1
do.		-	8 – 11	C	-29 – -17

separately for the units B1 and B3, the percentage of species occurring in each of the climatic zones. Presence in the boreal subzone dominates, and 33 species are confined to this subzone. Only two species are exclusively arctic: *Pterostichus agonus* and *Micralymma brevilingue*, while *M. brevilingue* and *Hydroporus morio* are the only species occurring in the High Arctic. The distributions of nine species include subtropical areas.

The dominance of temperate (boreal and southern temperate) insect taxa point to warmer conditions than the subarctic tree-line conditions suggested by the fossil flora (Bennike 1990). The overall impression of the Kap København insect assemblage is that of a boreal fauna similar to what is today found in areas such as Newfoundland and central Finland, where mean temperatures in warmest month are about 15°C and in coldest month about -10°C.

Palaeotemperature reconstruction by the MCR method

Only 28 of the named Kap København species are included in the existing data base used for the MCR reconstructions, which is mainly based on European beetle species. Table 18 presents MCR results based on single samples with a high representation of these species, and total samples from different sites and horizontal sections of sites.

Three single samples from the upper, middle and lower part of the large lens of organic detritus at Locality 77 (unit B3) indicate a mean July temperature of 10-11°C or 10-13°C and a mean January temperature between -19°C and -4°C. However, when all samples from the upper, middle and lower portion of the lens are combined, their MCR-calculated temperatures indicate a mixed origin for the faunas in the upper and lower portion, with one part of the fauna indicating temperate conditions (July 13-19°C) and another low arctic-subarctic conditions (July 8-11°C). The middle portion, however, indicates subarctic conditions similar to the single sample from the same sedimentary sequence.

The MCR method also showed Locality 69 (unit B3) to contain a heterogenous fauna, whereas the localities 119 (unit B3) and 50 (unit B1) both indicate a subarctic climate. When the total samples from the Kap København Formation are combined, the programme also divides the material in two parts reflecting either cold (July: 8-11°C; January: -17 – -29°C) or warm conditions (July: 15-19°C; January: -15 – +1°C).

The subarctic conditions (July temperature 10-11°C) indicated by some of the faunal elements match results from the fossil flora (Bennike 1990). But the MCR estimates reveal a marked heterogeneity in several of the samples and sampling localities.

One explanation could be rebedding of part of the material, causing insect fragments from older layers to be mixed with representatives of the fauna contemporaneous with the sediments. Speaking against this is the fairly uniform, excellent preservation of the material from all the samples, not least from the rich Locality 77.

Alternatively, the time resolution within the sampled sections might be so low that material from different climatic spells are combined. It is, however, difficult to imagine a number of climatic shifts during the deposition of the apparently very homogeneous large lens in locality 77.

A third explanation is offered by the marked allochthonous nature of the Kap København deposits. The heterogeneity of the assemblages could reflect a heterogeneous drainage area. It is easy to envisage both lowland areas with a rich boreal vegetation including forests and a variety of limnic biotopes, and also uplands with colder, subarctic-low arctic conditions in the drainage area; accordingly the rivers would bring debris from a mixture of biota to the depositional areas. Differences in the vegetation of different drainage basins would naturally result in assemblages with varying composition. This may be the reason why the fauna of unit B3 is so meagre and peculiar at Locality 50 (p. 62).

Although based on a limited number of beetle species, and irrespective of the interpretation, the MCR reconstructions clearly indicate that at least two different climatic regimes occurred during the formation of the upper member (B) of the Kap København Formation, one with arctic/subarctic conditions, another with temperate conditions. This result is different from the climatic interpretation based on the fossil vascular plants, from which only subarctic conditions have been inferred (Bennike 1990).

Incongruence of vegetation and insect fauna has been demonstrated several times during investigations of Quaternary sites and has been explained by the general higher mobility of insects compared to most plants (Coope 1977, 1987; Coope & Brophy 1972; Matthews 1975; Lemdahl 1988). During a period with rapidly rising temperatures, which might have been the case when Member B of the Kap København Formation was formed, the insect fauna thus more precisely indicates the temperature regime than the vegetation.

Comparison of the units

The taxa found in the two lowermost units, B1 and B2, are shown in Table 16. Only one sample (64914, Locality 27) was taken from B2 with supplementary material from six botanical samples, whereas five entomological samples with supplementary material from six botanical samples were taken from unit B1 (Table 1). This is part of the explanation of the much lower diversity in B2 compared with B1. It is none the less peculiar that exclusively beetles and no rove beetles apart from a single Aleocharinae elytron were obtained from unit B2.

Very marked differences also appear when the fauna of unit B1 is compared with that of unit B3 (Tables 3,12,16). Carabidae are highly dominant in B1 (80 % of named species), in particular the genus *Bembidion*, whereas a number of taxa which play an important role in unit B3 are completely or almost absent in B1 (Dytiscidae, Byrrhidae, *Aegialia*, Curculionidae, Formicidae, Trichoptera). A few taxa were found only in unit B1 (*Bembidion* cf. *lenae*, *Stenus assequens*, *S. pubescens*, *Tachyporus* spp., *Nitidula* sp.).

However, as already discussed (p. 62), a pronounced difference between the biota of units B1 and B3 is apparent only when the samples from B1 are compared with the samples from B3 as a whole. At the type section (Locality 50) the samples from B3 yielded a very poor fauna (Table 16), which in terms of ecological composition (Table 15) is similar to that of B1, although with tundra taxa relatively more prevalent.

The modern climatic range of the taxa from unit B1 shows a relatively higher percentage of occurrences in the cool low arctic-subarctic climates than when the total taxa from unit B3 are considered (Fig. 30). The difference, however, is not statistically significant.

The MCR reconstruction from unit B1 (July: 11-13°C; based on only four species) reflects colder conditions than the "warm" faunal fraction of some B3-samples, which show temperate summer temperatures (12-19°C).

The insect fauna of unit B1 is dominated by hygrophilic, rivuline and tundra taxa, but otherwise characterized by the scarcity of limnic taxa and the total absence of arboreal and forest taxa (Tables 15,16,17). This might point to an ecological situation with prevalence of open, treeless and possibly cool conditions, with scarcity of limnic biotopes.

Though not explicitly pointed out by Bennike (1990), this conclusion is in agreement with the palaeobotanical results. All remains of trees are restricted to unit B3, together with at least 23 species of shrubs and herbs with a modern boreal-temperate distribution. Two arctic-alpine species (*Melandrium affine*, *Arabis alpina*) are confined to unit B1, which is moreover dominated by typical and widespread arctic species like *Betula nana*, *Vaccinium uliginosum* and *Empetrum nigrum*. These play a prominent part in unit B3 as well.

The meagre flora of unit B2 is very much like that of B1, with an absence of tree fossils. However, the amount of tree pollen is similar in samples from B2 and B3 (Bennike 1990). Because unit B2 was deposited in deeper water than B1 and B3, the absence of tree remains, and possibly also the peculiar insect assemblage, might be caused by longer transport distance. Both the marine ostracod and mollusc fauna from B2 indicate relatively warm sea water conditions (Brouwers *et al.* 1991; Símonarson *et al.*, in press).

Seeds of *Menyanthes trifoliata* are markedly less common in the samples from unit B1 in comparison with B2 and B3, and seeds of *Hippuris* are common in B3, present in B2, but absent from B1. All the boreal aquatic species (*Nuphar*, *Potamogeton* spp., *Sparganium angustifolium*) are absent from B1, where only one species of water plant is found besides *Menyanthes*, namely *Potamogeton* cf. *vaginatus*, which preferably grows in deep, brackish water. The scarcity of aquatic plants in unit B1 supports the low frequency of limnic biotopes indicated by the insect fossils.

It is concluded, therefore, that units B1 and B3 were laid down under different climatic circumstances. During the deposition of unit B1 conditions were comparatively dry and cool and limnic biotopes, in particular stagnant waters, were scarce. Low precipitation might also be responsible for the absence of trees, but possibly summer temperatures were just below the limit for tree growth. Higher precipitation and higher summer temperatures in the lowlands were the prerequisites for the

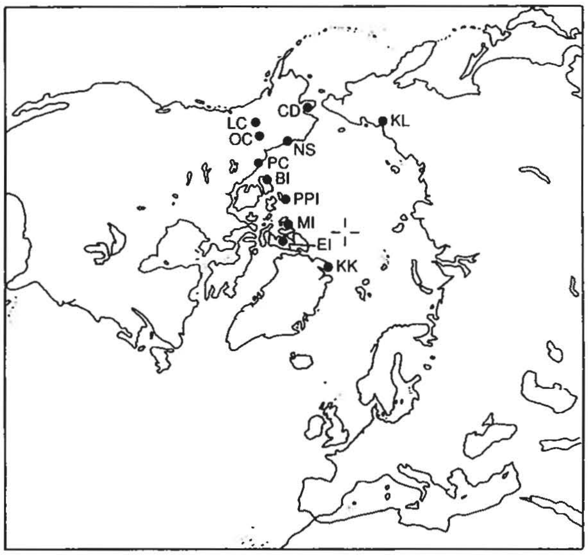


Fig. 31. Sites with fossil insects mentioned. BI: Banks Island (Worth Point, Ballast Brook); CD: Cape Deceit and Lava Camp, Seward Peninsula; EI: Ellesmere Island (Hvitland beds; Remus Creek site and Fosheim Dome on Fosheim Peninsula; Beaver Peat sites in Strathcona Fiord; Riediger Site and Rochon site in the Vendom Fiord region); KK: Kap København; KL: Kolyma Lowland; LC: Lost Chicken Site; MI: Meighen Island; NS: Niguanak Site; OC: Old Crow region, including Bluefish River; PC: Plateau Cap; PPI: Prince Patrick Island.

high diversity of wetland biotopes and for the existence of temperate woodlands during the deposition of unit B3. – The few insect fossils from unit B2 do not allow palaeoenvironmental conclusions.

Comparison with other fossil insect faunas

The late Tertiary Beaufort Formation in the Queen Elizabeth Islands and on Banks Island, arctic Canada, constitute the most obvious geological sequence to compare the Kap København Formation with. It is situated fairly close and almost as far north. As presently defined (Fyles 1990, Fyles *et al.* 1994) the Beaufort Formation is distributed from Banks Island northeast to Meighen Island (Figs 31, 32). It consists of unconsolidated fluvial sand with organic beds containing a wealth of well preserved plant and animal remains. The dating and chronology of the different exposures of the Beaufort Formation is difficult and has been the subject of much discussion (Brigham-Grette *et al.* 1987; Matthews 1989, in press; Matthews & Ovenden 1990; Matthews *et al.* 1990; McNeil 1990; Fyles *et al.* 1991, 1994). The age of the Beaufort Formation on Meighen Island is estimated at about 3 million years, and most of the Beaufort Formation may have approximately the same age, since differences in flora can be explained by differences in latitude and/or continentality (Matthews & Ovenden 1990).

The Beaufort Formation on Meighen Island thus possibly predates the Kap København Formation by 0.5 – 1 Ma (Repenning & Brouwers 1992). The fossil flora and insect fauna from Meighen Island has been studied intensively and is the best known biota of the Beaufort Formation (Kuc 1974; Matthews 1977, 1979a, 1979b, 1987, 1989, in press; Matthews & Ovenden 1990). The flora of trees is more diverse than that of the Kap København Formation, but otherwise the floras of the two formations show great similarity (Bennike 1990).

A pronounced similarity is also apparent when the two insect faunas are considered (Table 19; Matthews 1977; Matthews, in press). The dominance in both of the carabid genera *Bembidion* and *Pterostichus* is conspicuous. Notable is also the many common genera of Staphylinidae, Curculionidae and of different limnic and riparian insect groups, and that ants and leafhoppers are present in both faunas. Of the 80 genera of Coleoptera represented on Meighen Island, 49 are in common with the Kap København Formation.

There are, however, important differences as well, such as the presence of four species of *Carabus* and two species of *Harpalus* in the Beaufort Formation of Meighen Island, whereas no representatives of these genera have been found in the Kap København Formation. Carabid species like *Pelophila rudis* LeConte and *Platidiolus vandykei* Kurnakow from Meighen Island are absent from Kap København. On the other hand, the Kap København Formation has got a species of *Cicindela*, a genus entirely lacking in the Beaufort Formation, and a number of genera of Curculionidae in the Kap København Formation are absent from the Beaufort Formation (*Cyriophthalmus, Sitona, Anoplus, Rhyncolus, Litodactylus*). A peculiar absence from the Kap København Formation is that of *Amara alpina* (Paykull). *Amara* cf. *alpina* is common in the Beaufort Formation, and *A. alpina* was widespread in Greenland during the last interglacial (Böcher 1989b; Böcher & Bennike 1991, Bennike & Böcher 1992, 1994).

Contrary to the impression of a lower diversity in the Kap København Formation when the vascular floras are compared, the insect fauna from Kap København appears to be richer than that of the Beaufort Formation. For example, there are 21 named species of *Bembidion* from the Kap København Formation and only ten from the Beaufort Formation on Meighen Island, of which five are in common. There are about the same number of named species of *Pterostichus* (Kap København: 12, Meighen Island: 11, three in common). In both faunas are several species of *Elaphrus*, but once more Kap København outnumbers Meighen Island with six versus four species.

However, some of the differences between the Kap København and Meighen Island faunas result from a different level of identification. For example, *Elaphrus* spp. from Meighen Island may include several species, and no species have been identified of the staphylinid

Table 19. Insect species from the Beaufort Formation on Meighen Island in common with the Kap København Formation. »(BP)« indicates occurence also in the early Pliocene Beaver Peat sites, Ellesmere Island. The total number of named insect species is 155 from the Kap København Formation, 71 from Meighen Island including 13 species determined to "type" or species groups (Matthews, in press). The present geographical and climatic distributions and the ecological groups of the species are included. "(cf.)" indicates that the identification is uncertain in one or both of the sites; "(?)" indicates the possible identity of "*Diacheila polita* type A" with *D. matthewsi*. For explanation of other symbols, see Tables 6 & 12 and Fig. 30

Species	Geographical range	Climatic range	Ecological group
Opisthius richardsoni	WN	B	R
Blethisa multipunctata	C	B-T	R
Blethisa catenaria (BP)	WN+EP	LA-SA	T
Diacheila polita type (?) (BP)	-	-	-
Elaphrus lapponicus	C	SA	H
Asaphidion alaskanum	WN	LA-SA	T
Bembidion dyschirinum (BP)	WN	B	X
Bembidion planatum	N	B	R
Bembidion grapii (cf.) (BP)	C	LA-B	X
Bembidion bimaculatum (cf.)	N	B-T	R
Bembidion sordidum (cf.)	N	B	R
Pterostichus brevicornis (cf.)	N+WP	LA-SA	T
Pterostichus vermiculosus (BP)	WN+P	LA-SA	T
Pterostichus haematopus (BP)	N+EP	LA-B	T
Agonum consimile (cf.)	C	SA	H
Amara glacialis (cf.)	C	LA-SA	T
Agabus bifarius (BP)	N	B-T	A
Heterosilpha ramosa	WN	B-T	C
Pycnoglypta lurida (cf.)	C	SA-B	H
Grypus equiseti	C	SA-T	H
Corynocera ambigua	C	LA-B	A
Arctopsyche ladogensis	C	SA-B	A

genus *Stenus* (John V. Matthews, personal communication 1995; Matthews, in press).

A striking example of different diversity is seen in the Trichoptera (Nancy Williams, personal communication 1993, 1994). In the Beaufort Formation on Meighen Island three named species and two additional genera have been found. The assemblage from the Kap København Formation comprises ten named species and six additional genera of caddisflies. According to John V. Matthews (personal communication 1995) some of this difference is probably due to a sampling bias in the laboratory.

Matthews & Ovenden (1990: 388) and Matthews (in press) present an overview of known late Tertiary-early Quaternary sites with terrestrial fossils from arctic/subarctic localities (Fig. 32). The Beaufort Formation on Prince Patrick Island and Banks Island (Ballast Brook, Upper Unit) is considered slightly older than that on Meighen Island (Matthews & Ovenden 1990). The insect fauna of Prince Patrick Island is similar to that found on Meighen Island, but fewer taxa have been found. The Ballast Brook fauna, Banks Island (Fyles *et al.* 1994; Matthews, in press), is even less diverse and more different from the Kap København fauna, with presence of the carabid genera *Tachys*, *Tachyta* and *Trechus* and of three species of *Micropeplus*, Micropeplinae (Staphylinidae). However, there are also taxa in common with the Kap København Formation which have not been recorded from Meighen Island: *Bembidion (Chrysobracteon) levettei*, possibly *Bembidion (C.) balli*, and *Gyrinus* sp.

The Worth Point Formation on Banks Island is considered only slightly younger than the Kap København Formation (*c.* 1.9 Ma; Matthews 1989; Matthews *et al.* 1986; Matthews & Ovenden 1990; Vincent 1990). The fossil arthropod fauna is poor with only ten named species, of which *Elaphrus lapponicus* is in common with the Kap København Formation. Remarkable is the presence of *Carabus truncaticollis* Eschscholtz and the xerophilic weevils *Lepidophorus lineaticollis* Kirby and *Vitavitus thulius* Kissinger. Early Quaternary sites with fossil insects are also found in northern and western Alaska, northern Yukon, and mainland North West Territories (Matthews, in press).

The Lost Chicken placer mine in interior, eastern Alaska is well dated to 2.9 Ma (Ager *et al.* 1994; Matthews, in press). A comparison with the fossil insect fauna here shows little similarity, with only one named species, "*Diacheila polita* type A", in common, but with 57 % of the named genera from the Lost Chicken in common with the Kap København Formation.

A number of newly discovered sites on Ellesmere Island, presumably from early and middle Pliocene, have yielded plenty of insect fossils still under study (Matthews, in press). Nine named species from the Beaver Peat sites in Strathcona Fiord are in common with the Kap København Formation, namely – in addition to those indicated in Table 19 – *Olophrum boreale* and *O. consimile*, which are not known from the Beaufort Formation.

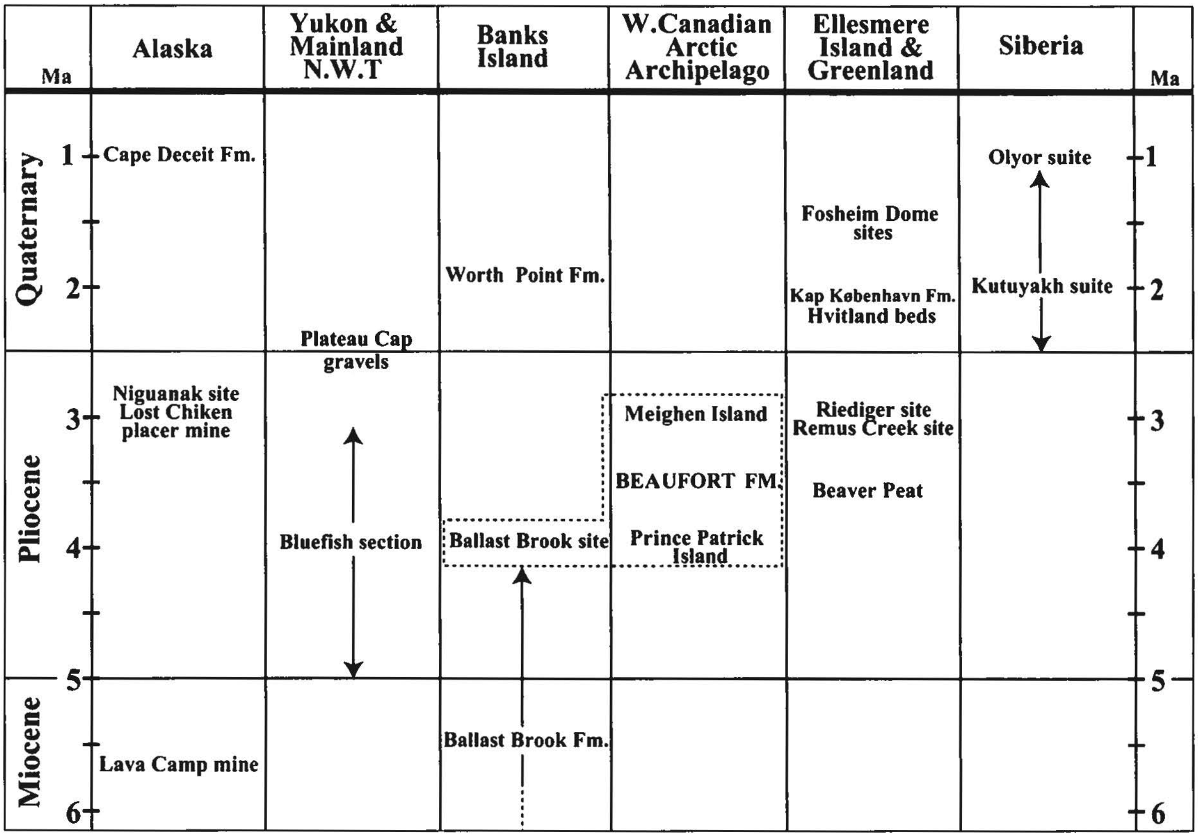


Fig. 32. Simplified correlation diagram showing the sites mentioned in the text. Fm.: formation; Ma: million years. Arrows indicate possible age ranges. (Modified after Matthews & Ovenden 1990 and Matthews, in press).

Of particular interest in the actual context are the recently studied nearshore marine Hvitland beds on northern Ellesmere Island, which are correlated with Member A of the Kap København Formation (John V. Matthews, personal communication 1995). Fossils of plants and insects are scarce. The most important plants are *Saxifraga oppositifolia* and *Dryas octopetala*, and the insects include a few fragments of the predominantly arctic subgenus *Cryobius* (*Pterostichus*), but not a hint of the diversity found at Kap København, even from the meagre unit B2. The climate accordingly was probably much colder (arctic) than during Kap København time, yet the Hvitland beds almost certainly fall in age between the Kap København Formation and the Beaufort Formation on Meighen Island (John V. Matthews, personal communication 1995).

According to Sher *et al.* (1979) and Matthews & Ovenden (1990) the Kutuyakh suite of the Krestovka key section from Kolyma Lowland, Eastern Siberia, includes layers equivalent to the Kap København Formation in age, approximately 1.8 to 2.8 Ma. The sparse insect fauna (Kiselyov, in Sher *et al.* 1979) reflects both tundra environments (*Amara alpina*, *Blethisa catenaria*, *Pterostichus costatus* Menetries, *Pterostichus* (*Cryobius*) spp.) and arboreal/shrub vegetation (*Pissodes irrorata* Reitter).

The Kutuyakh suite is unconformably overlain by the Olyor suite (Sher *et al.* 1979; Matthews & Ovenden 1990; Repenning & Brouwers 1992). The abundant insect remains in the sediments are dominated by both tundra species, which are in part in common with the Kap København Formation (*Blethisa catenaria*, *Pterostichus haematopus*, *P. vermiculosus*, *Pterostichus* (*Cryobius*) spp., including *P. (C.) pinguedineus*, *Amara alpina*) and xerophilic Siberian steppe taxa, which are entirely absent from the Kap København Formation – for instance several species of the weevil genera *Coniocleonus* and *Stephanocleonus* and a highly abundant pill beetle, *Chrysobyrrhulus rutilans* Motschulsky (Kiselyov in Sher *et al.* 1979; Matthews 1974b, 1983).

The Olyor suite is considered approximately contemporary with the *c.* 1,0 Ma Cape Deceit Formation of western Alaska (Matthews 1974a, 1974b, in press; Matthews & Ovenden 1990) and in many respects it reflects similar ecological conditions: tundra-steppe. The insect fauna is likewise characterized by a combination of tundra Carabidae, in particular the subgenus *Cryobius* of *Pterostichus*, and xerophilic taxa such as *Tachinus ap-*

terus Mäklin (Staphylinidae) and the weevils *Lepidophorus lineaticollis* and *Vitavitus thulius*. Otherwise the faunal composition of the Cap Deceit Formation has many similarities with the Kap København fauna, at least on the generic level.

General discussion and conclusions

Geological background and biogeography

There is geological evidence of a number of cold periods in Greenland during the latter part of the Pliocene (Larsen *et al.* 1994), with the first heavy glaciation occurring *c.* 2.5 Ma (Funder 1989, Funder & Larsen 1989, Jansen *et al.* 1990). A cold spell is indicated by Member A of the Kap København Formation (Funder *et al.* 1984, Bennike 1990, Feyling-Hanssen 1990) which is correlated with the Hvitland beds in northern Ellesmere Island (John V. Matthews, personal communication 1995). After this cold period a warm climate returned and Member B of the Kap København was deposited. The excellent preservation in permafrost of the fossils from Kap København indicates that the following cooling occurred shortly after their deposition. Since then the Kap København sediments have probably been permanently frozen, not even with interruptions during the Pleistocene interglacials.

When the Kap København Formation was formed, Greenland was placed approximately at the present position and was biogeographically as isolated as it is today (Rowley & Lottes 1988). Phytogeographically the formation was more closely allied with North America than with Eurasia (Bennike 1990). However, the composition of the Kap København fossil insect fauna is intermediate between what are today nearctic and palaearctic faunas, giving the impression of a vivid intermingling of the biota surrounding the Arctic Ocean. This situation was probably caused by the Arctic Ocean itself, which was partially free of ice, at least during summer (Funder *et al.* 1985, Funder 1989; Bennike 1990; Repenning & Brouwers 1992) and therefore acted as a means of transportation rather than as a barrier between the circumpolar biota along the borderlands of this sea. A high degree of resemblance between the Kap København insect fauna and the somewhat older fauna of the Canadian Beaufort Formation from Meighen Island is evident. A similar situation exists concerning the vascular plant flora of the Kap København Formation (Bennike 1990).

Moving south from Peary Land at the time when the Kap København Formation was formed, one would presumably meet boreal and even southern temperate forests with much higher biological diversity. During deposition of the Beaufort Formation in northern North America, the boreal zone had a latitudinal extent of at least 20° (Matthews, in press). Apart from pollen from ocean drillings (Vernal & Mudie 1989) no remains of such forests have been found in southern Greenland.

Longevity of species

The identification of the Kap København insect material showed that it was possible to refer almost all of the determinable fragments to modern taxa. Only two species are probably extinct (*Diacheila matthewsi* and *Stenus* sp.) and the unknown species of *Eucnecosum* may be extinct. However, because huge northern areas are still unexplored entomologically, it is difficult definitely to declare a species extinct. In the somewhat older Beaufort Formation Matthews (1977, 1979a) discovered a small number of probably extinct species; and from the well dated Lava Camp beds in western Alaska (5.7 Ma) only a minor fraction of the fragments could be referred to extant species (Hopkins *et al.* 1970; Matthews 1976, 1977, 1979a). Studying late Pleistocene material, G. Russel Coope was the first to demonstrate the longevity of beetle species, and constancy of insect species through most of the Pleistocene is now a well documented fact (Coope 1978, 1979, 1987; Buckland & Coope 1991). In general, the modern insect species were probably present by the end of the Tertiary (Matthews 1977, 1979a, 1979b; Coope 1979), and this is also shown by the present study. Most insect families existed already at the Cretaceous/Tertiary boundary (Labandeira & Sepkoski 1994).

In the survey of taxa it is stated when a species is known from other late Tertiary/early Pleistocene sites. The Kap København Formation collection represents the oldest record of 124 insect species.

Survey of the insect fauna

A very conservative estimate of the number of insect species found in the Kap København Formation add up to *c.* 275, of which 210 are Coleoptera, but probably about 300 are represented. The total number of named species is 155 of which 140 (90 %) are Coleoptera. The Coleoptera are highly dominated by Carabidae (45 % of species, 19 % of genera); next come Staphylinidae

Table 20. Named insect taxa from the Kap København Formation

Orders	Families	Genera	Species
Coleoptera	29	97	140
Hymenoptera	7	8	2
Diptera	4	9	1
Lepidoptera	0	0	0
Trichoptera	5	12	10
Hemiptera	5	5	2
Total: 6	50	131	155

Table 21. Named taxa of Coleoptera from the Kap København Formation

Families	Species	Genera
Carabidae	63	18
Haliplidae	-	1
Noteridae	1	1
Dytiscidae	9	6
Gyrinidae	-	1
Hydrophilidae	3	3
Leiodidae	2	2
Silphidae	2	2
Agyrtidae	1	1
Cholevidae	-	1
Colonidae	-	1
Staphylinidae	27	17
Scarabaeidae	1	2
Cantharidae	1	1
Elateridae	1	1
Buprestidae	-	-
Byrrhidae	6	5
Derodontidae	1	1
Anobiidae	1	1
Ptinidae	-	1
Dasytidae	-	1
Nitidulidae	-	1
Coccinellidae	2	3
Latridiidae	-	1
Colydiidae	1	1
Cerambycidae	-	-
Chrysomelidae	2	5
Curculionidae	13	15
Scolytidae	3	4
Total: 29	140	97

(19 % of species, 18 % of genera) and Curculionidae (9 % of species, 15 % of genera). Two genera dominate the Carabidae: *Bembidion* (21 species; 33 %) and *Pterostichus* (11 species; 17 %). One genus dominates the Staphylinidae: *Stenus* (11 species; 41 %). Surveys of named taxa are presented in Tables 3, 20 & 21.

The insect species most abundantly represented in the Kap København Formation are *Hydroporus* cf. *morio*, *Eucnecosum* cf. *brunnescens*, *Bledius* cf. *arcticus*, *Aegialia terminalis*, *Simplocaria basalis*, *Grypus equiseti* and *Arctopsyche ladogensis*.

Palaeoecology

A detailed environmental reconstruction is possible, based on the insect fauna from the Kap København Formation. However, this implies an assumption which might seem unlikely, namely that the taxa involved have kept their ecological niches unchanged for two million years, equivalent to about the same number of generations. Coope (1970, 1978, 1979) has discussed this problem thoroughly and convincingly, regarding Pleistocene insects. In spite of higher age, Coope's arguments can undoubtedly be extended to cover the Kap København insects as well. The main point in the argument is that far from giving rise to a high level of speciation, the climatic variability during the Pleistocene appears to have favoured constancy of insect species – in their morphology as well as in physiology and ecological position.

Compared with today we find odd combinations of species in the Kap København Formation, but it is still possible to combine them ecologically in a meaningful way and to envisage the ancient insect communities. Occurrence in the Kap København Formation of species which are today confined to Europe, or western North America, or eastern Siberia, may be astonishing. However, as late as during the last glacial cycle a number of insects occurred in Britain which are now confined to the Mediterranean area, or central Asia, thereby demonstrating the mobility of insects (Coope 1973, 1977; Buckland & Coope 1991). Large scale distributional shifts of a similar magnitude to those recorded by the Kap København Formation occurred several times during the late Pleistocene (Coope 1975, 1977, 1979; Morgan & Morgan 1980; Morgan *et al.* 1984; Schwert & Ashworth 1988).

The modern climatic distributions of the insects from the Kap København Formation together cover the range from the High Arctic to subtropical areas, but with a maximum of species occurring in the boreal subzone.

The palaeotemperatures indicated by some of the MCR reconstructions are similar to what is estimated for the fossil vascular flora (July mean temperature 10-11°C; Bennike 1990). However, the MCR values show a heterogeneous origin of some of the insect assemblages from both single samples and sites. This mixture of species indicating either "warm" or "cold" environments can be interpreted as caused by a heterogeneous drainage area with both temperate lowlands and subarctic-arctic highlands. The existence of temperate conditions, which is not indicated by the fossil plant remains, is one of the important conclusions derived from the fossil insect fauna.

There are both palaeobotanical and palaeoentomological indications that the climate during deposition of unit B3 was more humid and warmer than during deposition of unit B1. An alternative explanation of the entirely missing arboreal and forest taxa in unit B1, though not of the scarcity of limnic taxa, could be that these had yet not invaded the area from which they were eliminated during the preceding cooling, when Member A of the formation was formed.

Geographical differences are possibly indicated during the B3-period. In samples from the southern part of the area, at the type section (Locality 50), remains of forest and limnic taxa are rare compared to the abundance of these in samples from the area along Ladegårdsåen, *c.* 13 km north of Locality 50 (Fig. 7). This could be due to inland versus coastal ecological differences; geologically there is good evidence that the Kap København Formation was deposited at the coast. A maritime effect might also be responsible for the apparent contrast between the subarctic, treeline character of the flora and the generally more warmth demanding insect fauna. This might even explain the presence of some temperate plants, like *Taxus* and *Thuja*, that are out of place in a treeline context.

The fossil insect fauna tells about a varied, boreal landscape characterized by a multitude of different wetland biotopes. In sheltered lowland localities trees and small forests were found, whereas the low uplands were covered by heaths, meadows and mires. Along rivers and lakes luxuriant vegetation including scrubs alternated with sandy shores, and at Kap København the seashore was presumably also sandy with dune areas. The warm microclimates of such biotopes allowed the presence of thermophilic species like tiger beetles (*Cicindela*). At higher elevation in Kim Fjelde and further north a variety of plant communities similar to those found in the Arctic today were found together with barren fell fields and rapid, cool streams. Somewhere in the inland conditions were so dry that prairie environments and saline ponds existed.

No modern analogue to the Kap København fossil biota is found, but some similarity to extant subarctic environments is obvious, such as those in southernmost Greenland, Labrador and Scandinavia. According to Henri Goulet (personal communication 1991) the fauna of *Elaphrus* spp. from the Kap København Formation is similar to that at Inuvik, Northwest Territories, Canada; the ant fauna reported from the Mackenzie River Delta (Brown 1949) is almost identical to that of the Kap København Formation; and undoubtedly other points of resemblance may be found.

However, the mixture of nearctic and palaearctic, low arctic, boreal and southern temperate taxa, the odd composition of trees at the forest limit, and – most important – the many temperate plants and insects occurring at an extreme northern latitude, render the Kap København biota unique. The light regime at Kap København, with five months of the year completely without sunshine and five months with the sun constantly above the horizon, would not by itself present problems to boreal insects, provided the summer months were sufficiently warm and sunny to allow development and activity, and the winter rich in snow protecting the hibernating stages. Such climatic conditions are indeed indicated by the flora and insect fauna of the Kap København Formation, deposited 800 kilometres from the North Pole. Possibly the combination of high summer temperatures, moderate winter temperatures, high precipitation, and the polar light regime can explain the naturalness of what we today see as ecological and biological peculiarities.

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