Forest-Tundra Neighbouring the North Pole: Plant and Insect Remains from the Plio-Pleistocene Kap København Formation, North Greenland

O. BENNIKE[1] and J. BÖCHER[2]

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ABSTRACT. The Kap København Formation in northeast Peary Land, Greenland, is believed to be 2.0-2.5 million years old, i.e., from the Plio-Pleistocene transition. The dating is primarily based on biostratigraphical correlation of lower marine fauna and a few fragments of terrestrial mammals. Although deposited in marine and coastal environments, the sediments contain abundant remains of terrestrial and limnic organisms. This paper examines macroscopic plant and insect remains. About 60 taxa of vascular plants and 120 insect taxa have so far been identified. Nearly all of the named insect species are extant, extralimital forms, generally of a recent subarctic/boreal and more or less circumpolar distribution. The species composition shows that upland areas were covered with forest-tundra and heathland and that mesotrophic, well-vegetated lakes and a number of other wetland localities existed in the area. The presence of arctic plants in the formation puts some time constraints on their origin.

Key words: Plio-Pleistocene, North Greenland, palaeoecology, forest-tundra

RÉSUMÉ. La Formation de Kap Kobenhavn dans le nord-est de la terre de Peary, au Groenland, daterait de 2,0 à 2,5 Ma, c'est-à-dire de la transition du Plio-Pléistocène. La datation repose essentiellement sur une corrélation biostratigraphique de la faune marine inférieure et aur quelques fragments de mammifères terrestres. Même s'ils se sont déposés dans des milieux marins et côtiers, les sédiments contiennent d'abondants vestiges d'organismes terrestres et limniques. La présente communication examine des vestiges macroscopiques de plantes et d'insectes. Environ 60 taxons de plantes vasculaires et 120 taxons d'insectes ont jusqu'à ce jour été identifiés. Presque toutes les espèces d'insectes identifiés sont des formes exotiques existantes qui ont en général une distribution subarctique/boréale et plus ou moins circumpolaire récente. La composition des espèces indique que les terres hautes étaient recouvertes de forêt-toundra et de lande, et que la région était parsemée de lacs mésotrophes à végétation abondante et de plusieurs autres terres humides. La présence de plantes arctiques dans la formation en précise l'origine dans le temps.

Mots clés: Plio-Pléistocène, Groenland septentrional, paléoécologie, forêt-toundra

РЕФЕРАТ. Формация Кап Кёбенхавн в северо-восточной части Земли Пири, Гренландия, насчитывает, предположительно, 2-2,5 миллиона лет, т. е. относится ко времени плио-плейстоценового перехода. Эта датировка основана главным образом на биостратиграфической корреляции низшей морской фауны и нескольких остатков наземных животных. Составляющие формацию осадки изобилуют остатками наземных и озерных организмов, хотя их накопление происходило в обстановке морских и прибрежных районов. В настоящей статье рассматриваются макроскопические остатки растений и насекомых. На настоящее время идентифицировано около 60 таксонов сосудистых растений и 120 таксонов насекомых. Почти все из идентифицированных насекомых относятся к ныне существующим, экстразональным формам, встречающимся в современную эпоху, как правило, в субарктиче-ских/северных и более или менее циркумполярных районах. Видовой состав указывает на то, что плоскогорья были покрыты в то время лесотундрой и вересковыми пустошами и что в этом районе существовали мезотрофные, заросшие растительностью озера и заболоченные земли. Присутствие в формации арктических растений накладывет на них некоторые временные ограничения.

Ключевые слова: плиоплейстоцен, Северная Гренландия, палеоэкология, лесотундра

INTRODUCTION

While Neogene and Early Pleistocene sediments (primarily the Beaufort Formation) containing evidence of the former terrestrial and limnic environments have been known for several decades in northern Canada (see review in Matthews, 1987; Matthews and Ovenden, 1990-this issue), similar sediments (the Kap København Formation) have only recently been located in Greenland (Funder and Hjort, 1980; Fig. 1). The Kap København Formation is of great significance with regard to Late Cenozoic high latitude biological and climatic evolution

This paper primarily discusses macroscopic remains of vascular plants and insects in the Kap København Formation, latitude 82°30′N (see also Böcher, 1989, and Bennike, in press). Other fossil terrestrial and limnic organisms present in the sediments include plants such as various thallophytes (Bennike, in press) and mosses (Mogensen, 1984) and animals such as cladocerans, freshwater bryozoans, notostracas, oribatid mites and vertebrates (Fredskild and Røen, 1982; Repenning *et al.*, 1987; this paper).

The Kap København Formation (Fig. 2), which covers about 300 km^2 and is exposed at elevations up to 230 m above sea level, is divided into two members (Funder *et al.*, 1984). The lower (A) is up to 50 m thick and rather homogeneous, consisting of laminated marine mud with scattered dropstones and lenses of non-sorted sediment (diamicton) interpreted as representing evidence for nearby glaciation. This member contains a sparse mollusc and Foraminifera fauna, indicating arctic/high arctic conditions. No macroscopic plant or insect remains are present; the pollen flora is depauperate and dominated by *Betula*.

The upper member (B) is up to at least 70 m thick, rather heterogeneous but dominated by coastal and nearshore sand (units B1 and B3). It also contains an offshore silt unit (B2) at about 100 m above sea level with abundant and diverse *in situ* marine faunas (molluscs, foraminifers [Feyling-Hanssen, in press] and ostracodes [Brouwers *et al.*, unpubl. ms]). The bivalve mollusc *Cyrtodaria kurriana* may point to a nearby output of fresh water.

That rivers did indeed enter the area is clearly shown by accumulations of detrital organic matter in parts of member B. Only a few smaller such accumulations have been located below unit B2 (the silt unit), while above the silt unit, in unit B3, organic-rich lenses and layers are widespread. They include logs of small, stunted trees.

At present the Kap København area supports a flora of about 70 species of vascular plants (Bennike, unpubl.). The

[1]Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark
[2]Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

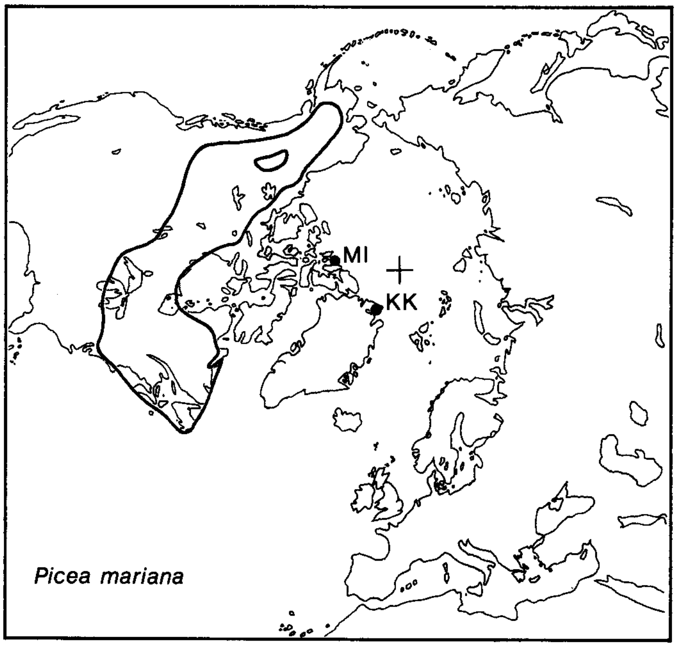

FIG. 1. The location of the Kap København Formation (KK) in North Greenland and the present range of *Picea mariana* (black spruce) (modified after Little, 1971). Also shown is the location of Meighen Island (MI).

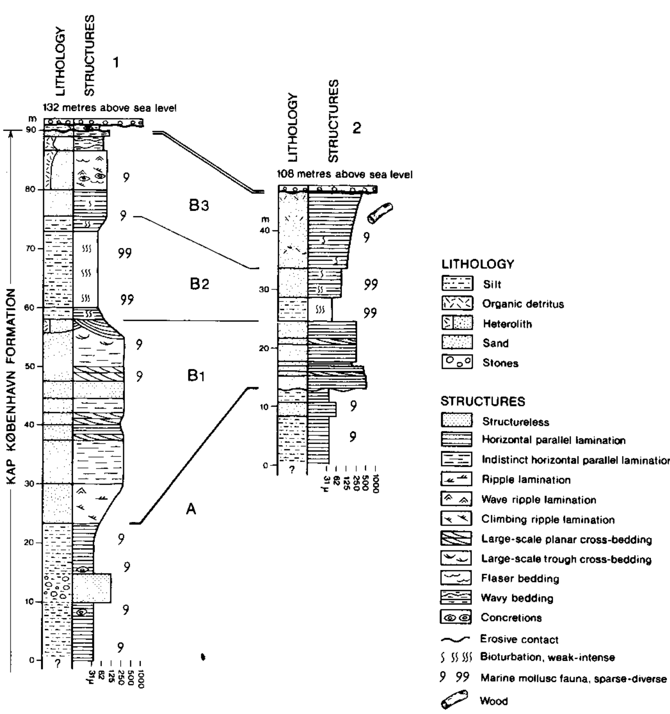

FIG. 2. Stratigraphy of the Kap København Formation to the southeast (left) and north (right) (adapted from Funder *et al.*, 1984, with permission).

only woody plants are *Salix arctica*, *Dryas* and *Cassiope tetragona*. The latter forms small patches of heath in a sheltered area. Along the coast no woody plants can thrive, and the vegetation is dominated by *Papaver radicatum* and *Saxifraga oppositifolia*. There are no climatic data from the area, but as judged from the vascular plant flora the mean temperature for the warmest month is 3.5-4°C in the sheltered area with *Cassiope* heaths (Edlund, 1983). The present insect fauna is dominated by chironomids and flies. In spite of intensive hunting, no beetles were caught in the area. The lakes of the area are ultra-oligotrophic.

Reconnaissance field work was carried out at Kap København in 1979 and 1980. More detailed work was conducted in 1983 (Funder *et al.*, 1984) and in 1986 by the present authors (Bennike, 1987).

METHODS

Most of the plant and animal remains were isolated by washing the samples through two sieves (plants: meshes of 0.42 and 0.21 mm; insects: meshes of 0.6 and 0.35 mm). Most samples dispersed well in water, but a few were treated with cold 5% KOH. After sieving, the insect remains were concentrated by flotation with kerosene and subsequent washing with detergent (Coope, 1986). Plant and insect remains were sorted out under a dissecting microscope. The plant material and part of the insect material is kept in 70% alcohol, but a large fraction of the identifiable insect fragments are mounted dry on standard cardboard rectangles on insect pins.

Both plant and insect remains are represented by fragments, which are generally well preserved. Small and thin-walled seeds and fruits are poorly preserved and presumably under-represented. The same is the case with fragile insects (e.g., Diptera and Lepidoptera).

RESULTS

A preliminary list of plant and insect remains in the Kap København Formation is presented in Appendices 1 and 2. Some plant and insect remains are shown in Figures 3, 4 and 5.

All but the following three of the plant remains are classified as extant species. The larch *Larix groenlandii* is closely related to *Larix occidentalis* (western larch) of the Rocky Mountains. *Myrica arctogale* is closely related to the extant species *M. gale* (sweet gale) and the extinct species *M. eogale* described from the Neogene of Siberia (V.P. Nikitin, 1976). Two fossils are classified as *Aracites globosa*. These extinct plants are described in Bennike (in press).

As usual regarding subfossil assemblages, beetles (Coleoptera) dominate the insect record due to the highly

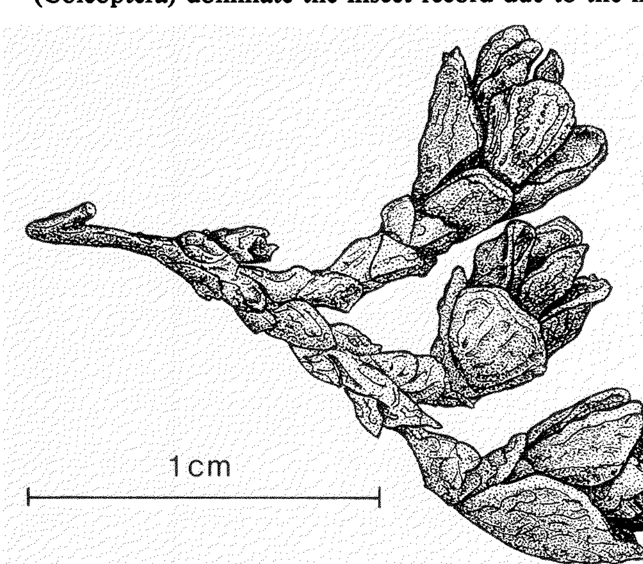

FIG. 3. Twig of *Thuja occidentalis* (white cedar) with scaly leaves and three small cones.

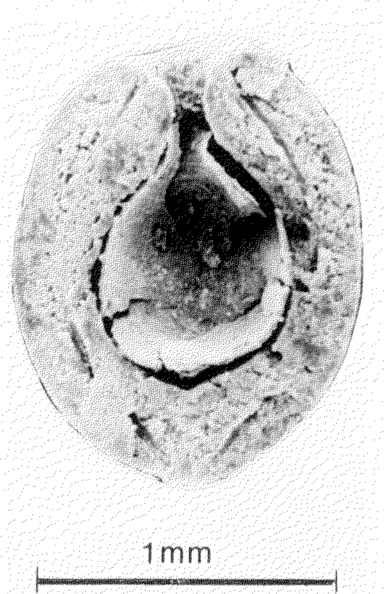

FIG. 4. SEM photo showing internal view of sectioned specimen of *Aracites globosa*.

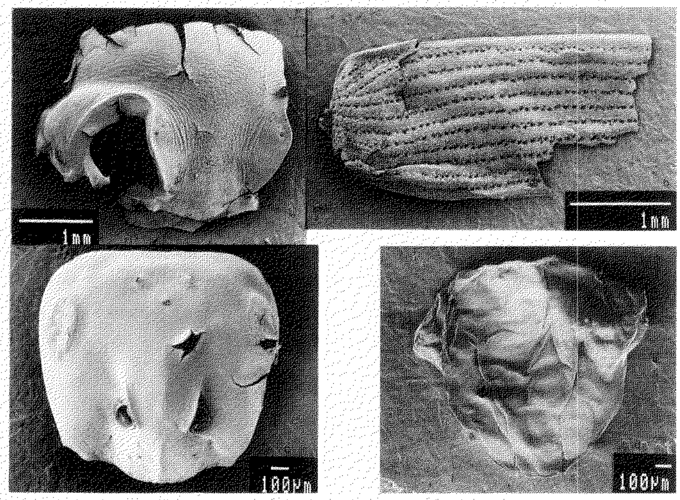

FIG. 5. SEM photos of some insect remains from the Kap København Formation: a) head of a *Cicindela* species (tiger beetle); b) left elytron of a *Hedrobregmus* species (death watch beetle) probably closely related to *H. pertinax* (L.), but with smaller and more dense strial punctures and more coarse, warty-spiny surface structure; c) head of *Camponotus* cf. *herculeanus* (L.) (carpenter ant); d) head of a leaf hopper (Cicadellidae gen. and sp. indet.).

resistant exoskeleton of most species. Among the Coleoptera the ground beetles (Carabidae) are prevalent. It is not apparent from the list that the rove beetles (Staphylinidae) are at least as well represented, but until now only a minor part of the numerous fragments have been identified. This is also true to some degree with the predaceous diving beetles (Dytiscidae).

It has so far been possible to identify 38 species and 65 genera (27 families, 6 orders) of insects. All fossil species are classed with extant species, but unidentified material might include extinct taxa.

Only a few logs exceed 12 cm in cross section and a few metres in length (maximum is 18 cm in cross section and 460 cm in length). Growth rings are extremely narrow, about 0.3 mm in width on average, but highly variable. Logs of *Larix* (n=76), *Picea* (n=22) and *Betula* (n=1) have been identified. A number of insects (*Hadrobregmus*, *Pissodes*, *Rhyncolus*, *Scolytus*, *Pityophthorus*, *Camponotus herculeanus*) are intimately associated with trees. *Camponotus herculeanus* (carpenter ant) is confined to forests or at least to the presence of trees. It avoids the dark and cool interior of forests, preferring sunny edges and stony slopes. The nest is almost exclusively built in living or dead trees, both in conifers and hardwoods (Larsson, 1943; Collingwood, 1979). *Hadrobregmus* is confined to dead, dry wood.

Fly holes and galleries in wood reveal the presence of still more arboricolous forms (Cerambycidae, Buprestidae, *Urocerus*, *Megastigmus*). A few species prefer woodland but are not dependent on trees (*Notiophilus biguttatus*, *Bembidion grapii*) (Lindroth, 1961-69, 1985-86).

In addition to *Larix groenlandii* and *Picea mariana*, boreal upland plants include *Thuja occidentalis* (Fig. 3), *Taxus* sp., *Cornus* spp. and *Viburnum* cf. *edule*. Common dwarf shrubs are *Betula nana*, *Dryas octopetala* and *Vaccinium uliginosum*. Insect species such as *Notiophilus aquaticus*, *Blethisa catenaria*, *Diacheila polita*, *Miscodera arctica*, *Pterostichus brevicornis*, *P. vermiculosus* and *Agonum exaratum* prefer open tundra or fairly xeric heathland (Lindroth, 1961-69, 1985-86).

The upland vegetation during the sedimentation of the formation was dominated by forest-tundra and heaths, and an increase of summer temperatures of *c.* 7°C as compared to the present day is implied from floral composition and growth ring analyses (Bennike, in press).

The trees probably grew in sheltered areas with rather heavy snow cover during the winter period. Where basal parts of branches are preserved they are always bent downwards as a result of loading by snow.

It is remarkable that none of the insect species from the Kap København Formation occurs in the High Arctic today and only one species (*Pterostichus vermiculosus*) is confined to the (Low) Arctic. However, a number of species (14) extend into the Low Arctic but are found as well in subarctic environments (Danks, 1981). By far the majority of the named species (90%) are mainly or partly found in the subarctic zone. Some species are temperate-boreal, extending into the subarctic zone (e.g., *Notiophilus biguttatus* and *Grypus equiseti*), and some are today boreo-alpine (*Nebria rufescens*, *Tachyporus nimbicola*, *T. rulomus* and *Camponotus herculeanus*).

Modern tree lines are made up of only one or two tree species, but the Kap København Formation contains remains of four or five species. The dominating tree was larch, which presently forms the tree line in Siberia, while in North America today spruce is the dominating conifer of the boreal forests.

Although upland plants and insects are well represented in the Kap København Formation, wetland organisms are undoubtedly heavily overrepresented, because their remains are the most likely to be dispersed by streams. Seeds and fruits of the water plants *Menyanthes trifoliata*, *Hippuris vulgaris* and *Potamogeton* spp. are very common. Remains of freshwater invertebrates include statoblasts of freshwater bryozoans (*Cristatella mucedo* and *Plumatella* spp.), ephippia, head shields and shells of Cladocera, mandibles of *Lepidurus* sp. and egg cocoons of Turbellaria. Aquatic insects are represented by head capsules of chironomid larvae, fragments of larval Trichoptera and fragments of at least 23 species of beetles (many Dytiscidae and some species of Gyrinidae and Hydrophilidae). Overall these aquatic organisms confirm the picture of a subarctic climate and indicate the presence of an abundance of different freshwater biotopes in the ancient landscape, notably that well-vegetated, mesotrophic lakes were present. Especially interesting in this connection is the concise description by Larson (1975:367) of the typical habitat of *Agabus bifarius* as: "shallow temporary ponds situated in rough fescue prairie or in parkland areas. These ponds are typically shaded, at least in part, by willow, aspen and emergent vegetation as well as dense accumulations of *Carex* and grass stalks."

The presence of *Tolypella* cf. *nidifica* (Characeae) oospores may indicate that ion-rich waters were also present in the general area.

A large fraction of the beetles are hygrophilous species living in damp, luxuriant places close to the water (e.g., *Nebria rufescens*, *Patrobus stygicus*, *Bembidion transparens*, *Olophrum* spp., *Tachyporus* spp. and *Tachinus* spp.) (Lindroth, 1961-69, 1985-86; Campbell, 1973, 1979). However, a similar fraction occurs exclusively on open, sandy or gravelly shores and banks of lakes and streams. These are generally thermophilous, diurnal and highly active predators hunting by means of vision and, accordingly, dependent on a high incidence of sunshine during the active season (species of *Elaphrus*, *Asaphidion*, *Bembidion*, *Notiophilus*, *Cicindela* and *Stenus*). Also *Aegialia* spp. are intimately connected with sandy areas, especially seashores.

The majority of the identified insect species today exhibit a circumpolar or holarctic distribution (56%), while 26% are nearctic and 18% palaearctic. Some are presently found far away from Greenland: *Elaphrus sibiricus* is distributed from central Siberia and Mongolia eastwards to northeast China, Japan and Kamchatka (Goulet, 1983); *Asaphidion alaskanum* is restricted to Alaska, the Northwest Territories and Yukon (Canada) (Lindroth, 1961-69); *Bembidion planiusculum* is restricted to the northwestern coastland of North America (Alaska and British Columbia) (Lindroth, 1961-69) and *Helophorus niger* to northwestern Siberia (Angus, 1970). Only two species, *Nebria rufescens* and *Bembidion grapii*, are found in Greenland today (Böcher, 1988).

NOTES ON *PICEA*

Picea (spruce) remains include three cones and numerous needles. The cones are small, broadly elliptic in outline and compare well with modern *P. mariana* (black spruce) cones. However, the needles show rather large morphological variability, from short, thick ones with rounded apexes to longer, more slender needles with acute apexes.

According to some students, needles of northern North America spruces can be identified by their anatomy: needles of *P. mariana* and *P. rubens* (red spruce) have two lateral resin channels, while needles of *P. glauca* (white spruce) only have resin sacs or no resin cavities (Durell, 1916; Duman, 1957; J.H. McAndrews, pers. comm. 1987; Birks, 1976:402 [unpubl. appendix II cited]). Others consider this character unreliable (R.G. Baker, pers. comm. 1987; J.V. Matthews, pers. comm. 1987; H.E. Wright, pers. comm. 1987; Marco, 1932).

Studies of modern reference material were in complete agreement with Duman's results: *P. mariana* and *P. rubens* needles have two resin channels, a feature never observed in *P. glauca* needles. The resin sacs of the latter, if paired, may however easily be confused with the resin channels of *P. mariana* and *P. rubens* if the needles are not cleared or are only sectioned at a few levels. While *P. mariana* and *P. glauca* cannot be separated by their morphology, *P. rubens* needles are generally larger than *P. mariana* needles. Twenty spruce needles of different morphology from the Kap København Formation were sectioned transversely at about 20 different levels. They all had two resin channels and are referred to *P. mariana* on account of this character and their size.

NOTES ON *ARACITES*

Two fossils of the mysterious extinct plant *Aracites globosa* are present in the material (Fig. 4). They are identical to the fossils named *Aracispermum* sp. by Matthews (1987) and *Aracites Johnstrupii* by Matthews (1989).

There is a great deal of confusion about the names *Aracites*, *Aracites johnstrupii* (Hartz) Nikitin and *Aracispermum*. The names were originally proposed by the Russian palaeobotanist P.A. Nikitin in the late 1940s. He died in 1950, but his main works were not published until later (P.A. Nikitin, 1957, 1965). The fossils described as *Carpolithes Johnstrupii* by Hartz (1909) belong to the genus *Myrica* (Kircheimer, 1938, 1957; Friis, 1985). Dorofeev (1963) transferred *Aracites johnstrupii* to the genus *Aracispermum*, a genus name first proposed by P.A. Nikitin in 1947 but not formally established until 1965 (P.A. Nikitin, 1965). However, V.P. Nikitin (1979) proposed to keep the two genera separate, a view adopted here. P.A. Nikitin (1957) proposed that the fossils are seeds belonging in the family Araceae. Apparently, Reid and Reid (1915) were the first to describe this fossil type. They classified it as fruits of an extinct *Hippuris* species. Furthermore, Katz and Katz (1964) proposed that *Aracites* belong in the family Cucurbitaceae.

AGE ESTIMATE AND CORRELATION

The Kap København Formation is primarily dated by its remains of mammals, molluscs, foraminifers and ostracodes, and secondly by palaeomagnetic and amino acid studies.

At the 18th International Geological Congress in London, in 1948, it was recommended to place the Plio-Pleistocene boundary at the base of the Calabrian Stage in Italy (King and Oakley, 1949). The age of the boundary thus defined is presently dated to *c.* 1.6 Ma (Backman *et al.*, 1983; Tauxe *et al.*, 1983). However, in the Netherlands and in other parts of northwest Europe the boundary is usually placed at 2.3 or 2.5 Ma (e.g., Zagwijn and Hager, 1987; Mangerud, 1986; Watts, 1988). Because of this discrepancy it is important to try to put an age on deposits in this time range.

The simultaneous occurrence in the uppermost part of the formation of the extinct rabbit *Hypolagus* and the extant hare *Lepus* suggests an age of *c.* 2.0 Ma (Repenning *et al.*, 1987). The Foraminifera faunas (Funder *et al.*, 1985; Feyling-Hanssen, 1986, 1987, in press) include some extinct species, among which is *Cibicides grossa*, from the lower part of the formation. In the North Sea area this species became extinct slightly before the Reuverian/Praetiglian boundary (King, 1983), dated to about 2.3 Ma by palaeomagnetic studies (Montfrans, 1971).

The marine molluscan fauna includes a number of species that originated in the Pacific Ocean and first entered the Arctic Ocean and the North Atlantic by the first opening of the Bering Strait about 3 Ma ago (Albertsson, 1978; Gladenkov, 1979). The molluscan fauna correlates best with the lower part of the Gubik Formation in northern Alaska, having such species as *Macoma balthica*, *Cyrtodaria kurriana* and *Trichotropis bicarinata* in common (Bennike, 1989; Marincovich, pers. comm. 1987). The lower part of the Gubik Formation is dated to the Late Pliocene (Repenning, 1983; Nelson and Carter, 1985).

Only minor parts of the Kap København Formation have been studied palaeomagnetically. These parts show reverse polarity (Abrahamsen and Marcussen, 1986) and were deposited prior to the Brunhes/Matuyama boundary at *c.* 0.7 Ma. Unfortunately, no reversals have been detected in the sedimentary sequence.

We conclude that the Kap København Formation is probably between 2.5 and 2.0 Ma old.

The fossil flora and insect fauna show closest resemblance to those from the Beaufort Formation on Meighen Island (Matthews, 1974b, 1977, 1979, 1987). The flora from Meighen Island also contains a mixture of boreal and arctic species, many of which are the same as those from Kap København. A conspicuous common feature is the predominance of the two carabid genera *Bembidion* and *Pterostichus*. However, the presence on Meighen Island of the plants *Pinus*, *Picea banksii*, *Comptonia*, *Claytonia* and *Physocarpus* led Matthews (1987) to suggest that the Meighen Island flora and fauna is somewhat older than the Kap København Formation. Recent $^{87}Sr/^{86}Sr$ analyses on *Arctica* sp. shell fragments suggest an age between 2.5 and 5.1 Ma (Matthews and Ovenden, 1990-this issue).

It is suggested that the warm climate in North Greenland was primarily a North Atlantic phenomenon. Evidence for a similar large temperature increase is recorded from England (Jenkins and Houghton, 1987) and from the Vörring Plateau off Norway (Eldholm *et al.*, 1987). On the other hand, a similar climatic warming in this late time interval is not seen in the Krestovka section of northeast Siberia (Sher *et al.*, 1979), in the Late Cenozoic sequences of Yukon (C. Schweger, pers. comm. 1987) or in the Cape Deceit sequence of western Alaska (Matthews, 1974a; Repenning, 1980).

CONCLUSIONS

The flora and fauna found in northernmost Greenland at the Tertiary-Quaternary boundary were indeed very different from those at present. Most notable is the occurrence of tree species in the area. Only 33 species of modern native beetles are known from all of Greenland, just two of which occur in North Greenland, where they are restricted to the warmer, interior parts (Böcher, 1988). This is in striking contrast to the fossil record of at least 120 species of Coleoptera from the Kap København Formation. No ants exist in Greenland today, but at least three species are found as fossils. The great majority of the named fossil insect species are today found in the subarctic zone and thus confirm the picture of a forest-tundra environment derived from the floral remains.

Altogether the flora and fauna of the Kap København Formation account for a fairly detailed picture of the palaeoecological conditions: a varied environment, very much characterized by a diversity of freshwater localities, in some places bordered by rich vegetation, in other places with open, sunny and sandy shores. Trees and possibly small forests were present in sheltered places, separated by tundra vegetation and more xeric heath areas.

Presumably the rather similar fossil faunas and floras found at Kap København and in other parts of northern North America in the Late Tertiary constituted a coherent biota surrounding the Arctic Ocean. Extensive areas of lowland tundra did not yet exist, but arctic plants such as the widespread *Dryas* were well established. Other old records of *Dryas* come from Meighen Island (Matthews, 1987).

Some "neobotanists" have hypothesized that the arctic flora did not originate until the Quaternary (e.g., Tolmatchev, 1966), but the fossil records from northern North America and Greenland show that it must have existed already in the Late Tertiary.

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APPENDIX 1. VASCULAR PLANTS REPRESENTED BY MACROSCOPIC REMAINS IN THE KAP KØBENHAVN FORMATION

Equisetaceae
- *Equisetum* sp.

Selaginellaceae
- *Selaginella selaginoides* (L.) Link

Polypodiaceae
- gen. and sp. indet.

Pinaceae
- *Picea mariana* (Mill.) B.S.P.
- *Larix groenlandii* Bennike

Cupressaceae
- *Thuja occidentalis* L.

Taxaceae
- *Taxus* sp.

Nymphaeaceae
- *Nuphar lutea* type

Ranunculaceae
- *Ranunculus* spp.
- *Anemone* sp.

Papaveraceae
- *Papaver* sect. *Scapiflora* sp.

Betulaceae
- *Betula nana* L.
- *Betula alba* L. s. l.
- *Alnus* cf. *crispa* (Ait.) Pursh

Polygonaceae
- *Oxyria digyna* (L.) Hill.
- *Polygonum* sp.
- *Rumex acetosa* L.

Caryophyllaceae
- *Cerastium* cf. *arcticum* Lge./*alpinum* L.
- *Stellaria* sp.
- ?*Arenaria* sp.
- *Melandrium affine* J. Vahl/*angustiflorum* (Rupr.) Walp.

Violaceae
- *Viola* sp.

Cruciferae
- *Arabis* cf. *alpina* L.

Salicaceae
- *Salix reticulata* L.
- *Salix* spp.

Myricaceae
- *Myrica arctogale* Bennike

Ericaceae
- *Arctostaphylos uva-ursi* (L.) Spreng.
- *Cassiope tetragona* (L.) D. Don.
- *Ledum palustre* L.
- *Andromeda polifolia* L.

(continued)

APPENDIX 1. (continued)

Oxycoccus palustris Pers.
Vaccinium uliginosum L. ssp. *microphyllum* Lge.
Empetraceae
Empetrum nigrum L. s.l.
Crassulaceae
Sedum annuum L.
Fabaceae
Hedysarum sp.
Rosaceae
Potentilla palustris (L.) Scop.
Potentilla spp.
Dryas octopetala L.
Rubus chamaemorus L.
R. arcticus L./*saxatilis* L.
Hippuridaceae
Hippuris vulgaris L.
Geraniaceae
Erodium sp.
Cornaceae
Cornus stolonifera Michx.
C. canadensis L.
Cornus sp. A
Menyanthaceae
Menyanthes trifoliata L.
Caprifoliaceae
Viburnum cf. *edule* (Michx.) Raf.
Scrophulariaceae
?*Linaria* sp.
Potamogetonaceae
Potamogeton natans L.
P. cf. *perfoliatus* L/*richardsonii* (Benn.) Rydb.
P. cf. *gramineus* L.
P. alpinus Balb.
P. cf. *vaginatus* Turcz.
Juncaceae
Juncus sp.
?*Luzula* sp.
Cyperaceae
Carex spp.
Scirpus microcarpus Presl.
Gramineae
Gen. and sp. indet.
Sparganiaceae
Sparganium angustifolium type
Insertae sedis
Aracites globosa (Reid & Reid) Bennike
Carpolithes sp. A

APPENDIX 2. FOSSIL INSECTS FROM THE KAP KØBENHAVN FORMATION

COLEOPTERA
Carabidae
Cicindela sp.
Carabus spp.
Nebria cf. *rufescens* (Ström, 1768)
Nebria spp.
Notiophilus cf. *aquaticus* (Linnaeus, 1758)
Notiophilus cf. *biguttatus* (Fabricius, 1770)
Blethisa cf. *catenaria* Brown, 1944
Diacheila polita (Faldermann, 1835)
Elaphrus lapponicus Gyllenhal, 1810
Elaphrus sibiricus Motschulsky, 1846
Elaphrus tuberculatus Mäklin, 1877
Miscodera arctica Paykull, 1798
Patrobus cf. *stygicus* Chaudoir, 1871
Patrobus spp.
Asaphidion alaskanum Wickham, 1919
Bembidion (Chrysobracteon) cf. *lapponicum* Zetterstedt, 1828
Bembidion (Chrysobracteon) sp.
Bembidion (Plataphus) cf. *planatum* Leconte, 1848
Bembidion (Plataphus) cf. *planiusculum* Mannerheim, 1843
Bembidion (Plataphus) spp.
Bembidion (Hirmoplataphus) sp.
Bembidion (Peryphus) cf. *mckinleyi* Fall, 1926
Bembidion (Peryphus) cf. *grapii* Gyllenhal, 1827
Bembidion (Peryphus) cf. *sordidum* Kirby, 1837
Bembidion (Diplocampa) cf. *transparens* Gebler, 1829
Pterostichus cf. *adstrictus* Eschscholtz, 1823
Pterostichus (Cryobius) cf. *brevicornis* Kirby, 1837
Pterostichus (Cryobius) spp.
Pterostichus cf. *vermiculosus* Menetries, 1851
Pterostichus haematopus Dejean, 1831
Agonum cf. *exaratum* Mannerheim, 1853
Amara cf. *glacialis* Mannerheim, 1853
Amara spp.
Dromius sp. (palaearctic)
Dytiscidae
Hydroporus spp.
Oreodytes spp.
Hydroporinae spp.
Agabus bifarius (Kirby, 1837)
Agabus spp.
Ilybius spp.
Colymbetinae spp.
Dytiscidae spp.
Gyrinidae
Gyrinus spp.
Hydrophilidae
Helophorus (Meghelophorus) cf. *niger* J. Sahlberg, 1880
Helophorus (Rhopalelophorus) cf. *frater* Smetana, 1985
Helophorus spp.
Hydrophilidae gen. and sp. indet.
Catopidae
cf. *Catops* sp.
Liodidae
cf. *Anisotoma* sp.
Silphidae
Heterosilpha ramosa (Say, 1823)
Staphylinidae
Philonthus sp.
Quedius sp.
Pycnoglypta sp.
Olophrum cf. *rotundicolle* (C. R. Sahlberg, 1834)
Olophrum cf. *consimile* (Gyllenhal, 1810)
Eucnecosum cf. *brachypterum* (Gravenhorst, 1802)
Eucnecosum spp.
Omaliinae spp.
Bledius spp.
Mycetoporus sp.
Tachyporus cf. *nimbicola* Campbell, 1979
Tachyporus cf. *rulomus* Blackwelder, 1936
Tachinus spp.
Stenus spp.
cf. *Atheta* sp.
Aleocharinae gen. and sp. indet.
Scarabaeidae
Aegialia cf. *sabuleti* (Panzer, 1797)
Aegialia spp.
Elateridae
Hypnoidus spp.
Buprestidae
Galleries and exit holes in *Larix* wood
Byrrhidae
Simplocaria spp.
Anobiidae
Hadrobregmus cf. *pertinax* (Linnaeus, 1758)
Lathridiidae
cf. *Corticaria* sp.
Lathridiidae gen. and sp. indet.
Cerambycidae
gen. and sp. indet. (galleries in *Larix* wood)
Chrysomelidae
Hydrothassa sp.
cf. *Graphops* sp.
cf. *Chrysomela* sp.
cf. *Galeruca* sp.
Chrysomelidae gen. and sp. indet.
Apionidae
Apion spp.
Curculionidae
cf. *Otiorhynchus* spp.
Pissodes sp.
Grypus equiseti (Fabricius, 1775)
Notaris sp.
Rhynchaenus sp.
Dorytomus sp.
Rhyncolus sp.
Curculionidae spp.
Scolytidae
Scolytus sp.
Pityophthorus sp.
gen. and sp. indet. (galleries in *Larix* wood)

HYMENOPTERA
Siricidae
Urocerus cf. *gigas* (Linnaeus, 1758) (fly holes in *Larix* wood)
Tenthredinidae
gen. and sp. indet.
Ichneumonidae:
cf. Pimplinae sp.
Ichneumonidae gen. and sp. indet.
Chalcididae
gen. and sp. indet.
Diapriidae
gen. and sp. indet.
Torymidae
Megastigmus sp. (bore holes in *Larix* seeds)
Formicidae
Camponotus cf. *herculeanus* (Linnaeus, 1758)

(continued)

APPENDIX 2. (continued)

Camponotus sp.
Formica sp.
Formicinae
gen. and sp. indet.
Hymenoptera
gen. and sp. indet.
DIPTERA
Chironomidae
Tanypodinae
gen. and sp. indet.
Orthocladius spp.
Psectrocladius sp.
Orthocladiinae
gen. and sp. indet.
cf. *Diamesa* sp.
Chironomus spp.
Endochironomus sp.
Microspectra sp.
Corynocera ambigua Zetterstedt 1840
Chironomini spp.
Brachycera
gen. and sp. indet.
Cyclorrhapha
Schizophora spp.
LEPIDOPTERA
gen. and sp. indet.
TRICHOPTERA
gen. and sp. indet.
HEMIPTERA
cf. Cicadellidae
gen. and sp. indet.

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