

Fig. 3 Geological model for the OI thrust in which the fault actually dips 29° and displaces the Moho at 33 km. The Flannan thrust dips at 33° . Velocities were smoothed from interval velocities obtained by BIRPS during processing of the data⁶, and are in km s^{-1} . Although these velocities are relatively high, the sediments comprising the NL basin are believed to be mainly Palaeozoic (D. K. Smythe, personal communication).

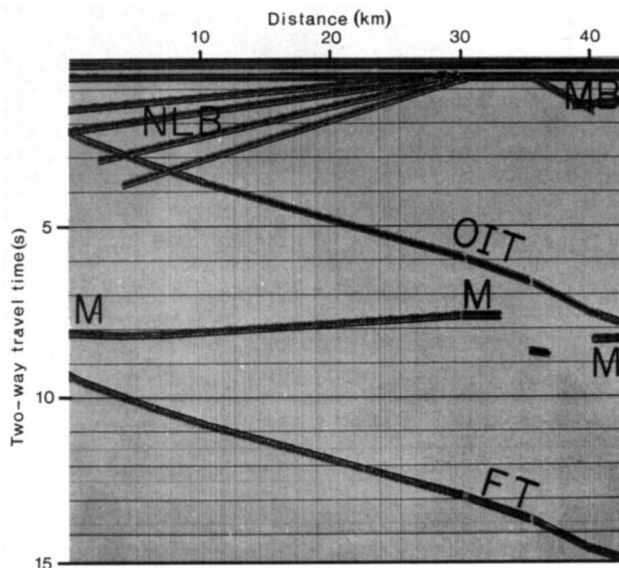


Fig. 4 Synthetic seismic section for the model in Fig. 2. Although the OI and Flannan fault planes dip at 29° and 33° , respectively, their reflections dip only $20\text{--}22^\circ$ on the seismic section. If the NL basin did not overlie the OI thrust, the reflection from the fault would dip at 26° on the unmigrated seismic section.

Three-dimensional control of these structures is provided by MOIST, a previous BIRPS survey¹, parallel to WINCH-1, but extending much further east, and by WINCH-2, which intersects MOIST in the Minch basin (Fig. 1). The OI thrust reflection dips at $20\text{--}22^\circ$ on MOIST and $24\text{--}25^\circ$ on WINCH-2. The observation that the NL basin is less well developed on WINCH-2 agrees well with its steeper dip on this line. All three seismic lines are as close as possible to dip lines, based on unpublished shallow data (D. K. Smythe, personal communication). Similar modelling suggests that a Moho displacement is associated with the OI thrust on both MOIST and WINCH-2. However, the displacement is obscured on MOIST and WINCH-2 by velocity pull-down associated with the Minch basin, which is much thicker on these lines than on WINCH-1. The OI and Flannan thrusts are most successfully modelled on MOIST by dips of

29° and $32\text{--}33^\circ$, respectively, as for the parallel WINCH-1.

The OI thrust reflection ends at a much shallower depth on MOIST than on WINCH-1, where it can be traced almost completely through the crust. The termination of the OI thrust reflection corresponds in each case to the beginning of the Minch basin at the surface, suggesting that the absence of a reflection from the OI thrust in the lower crust is owing to complications associated with the Minch basin sediments, rather than the termination of the fault at different crustal levels on the two lines.

Brewer and Smythe^{7,8} have proposed that the OI thrust displaces the Moho on MOIST, based on the intersection of the Moho with an extrapolation of the migrated OI thrust fault-plane reflection. However, because the apparent dip of the migrated fault reflection ($22\text{--}23^\circ$) differs from the dip of the fault plane by $6\text{--}7^\circ$, through pull-down, these extrapolations lead to an intersection ~ 20 km east of the displacement identified here. The apparent Moho displacements seen on MOIST at these other locations are caused by velocity pull-down from overlying basins; it is simply coincidental that the distorted OI thrust reflection projects into one of these apparent displacements.

In conclusion, the new modelling indicates that the OI thrust does not end in a ductile zone in the lower crust, but continues completely through the crust into the uppermost mantle. Although this result does not preclude the existence of a ductile lower crust, it does demonstrate that localized zones of deformation are likely to exist at these depths.

The synthetic seismic sections presented here were calculated using the Advanced Interpretive Modelling System (AIMS, Gequest International) on the Megaseis (Seiscom Delta) seismic computing system operated by the Consortium for Continental Reflection Profiling at Cornell. The research was supported by NSF grants EAR82-12445 and EAR83-13378. These results were presented at the International Symposium on the Deep Structure of the Continental Crust at Cornell University, 26-28 June 1984. I thank Simon Klempner, David Smythe, Larry Brown and Michael Warner for comments. Contribution 805 of Department of Geological Sciences, Cornell University.

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Palaeoclimate of Baffin Bay from 300,000-year record of foraminifera, dinoflagellates and pollen

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Several different models¹⁻⁵ have attempted to relate Quaternary marine and terrestrial records of ice-sheet growth in the North Atlantic region. The models are derived from either discontinuous terrestrial records, including marine fossils in raised shorelines^{1,2}, or from deep-sea calcareous microfossils^{3,4}. This study correlates Arctic marine and terrestrial data directly by comparing $\delta^{18}\text{O}$, foraminiferal, dinoflagellate and pollen records from a core taken in Baffin Bay. The core contains an almost continuous sequence of sediments deposited during isotope stages 1-10. Subarctic foraminifera and Atlantic dinoflagellates in early isotope stages

2, 4, 6 and 8 show that subarctic water entered southern Baffin Bay before the glacial maxima. Boreal-subarctic pollen suggest that Atlantic air flowed into Baffin Bay during the ice sheet growth phases. These data support models which postulate that open water in the Labrador Sea had an important role in supplying moisture to Laurentide and Greenland ice sheets.

Data for this study of ocean-atmosphere interaction during the late Quaternary were obtained from core 77-027-017 taken from a water depth of 935 m on the northern slope of Davis Strait at 66° 54.1'N, 58° 17.7' W (Fig. 1). The core includes a thin surface layer of brown diatomaceous mud overlying detrital carbonate-rich gravelly sand and ~10 m of partially bioturbated olive-grey sandy or silty mud. Planktonic and benthic foraminifera were studied in the >63 µm fraction using standard procedures⁶ to provide a biostratigraphical and palaeoceanographic record. Previous studies in Baffin Bay⁷ indicate that calcium carbonate dissolution limits the information content of calcareous microfossils; therefore, pollen and dinoflagellate cysts were also studied in core 017, using extraction methods⁸ suitable for clayey muds. Pollen and spores in marine sediments provide a link between terrestrial and oceanic environments and, off eastern Canada, pollen assemblages show a strong correlation with onshore climatic zones⁸. Most dinoflagellate cysts are spores of planktonic algae and, in marine sediments, they are proxy-indicators of surface water conditions^{9,10}.

The oxygen isotope composition of planktonic foraminifera in core 017 (Fig. 2) shows a typical isotopic record extending into stages 10 as defined by Emiliani¹¹. Calcareous foraminifera are absent from the top of the core because of the present shallow lysocline⁷. Gastropod shells from ~50 cm depth yielded a ¹⁴C age of 10,530 yr BP, confirming the isotope stage 1-2 transition between 60 and 70 cm. From 75 to 300 cm, high δ¹⁸O values represent isotope stages 2, 3 and 4. At 300 cm, a large (2.5%) shift in δ¹⁸O marks the top of stage 5. Stage 6 (465-515 cm) is rather compressed. Stage 7 (515-630 cm) has several light isotopic peaks, and a thermoluminescence (TL) age of 281,000 ± 20% yr BP on silt from 625 to 627.5 cm generally agrees with the age¹¹ of 251,000 yr BP for the base of stage 7. Stages 8 and 9 contain two light peaks. Below 810 cm, the record lies within stage 10.

Although the number and diversity of planktonic and benthic foraminifera in core 017 (Fig. 2) are low, there are cyclical variations in their percentage abundance. Stage 1 contains only arenaceous benthic foraminifera, typically *Textularia earlandi*, *Trochammina inflata*, *T. nana*, *Eggerella advena* and *Reophax arctica*, with abundant diatoms and radiolaria. In the Canadian Arctic, this benthic assemblage is generally confined to areas of cool saline bottom waters¹², and is often associated with carbonate dissolution⁶. Benthic foraminifera in stages 3, 5, 7 and 9 are mostly calcareous species dominated by *Cassidulina reniforme*, *Elphidium excavatum* and *Fursenkoina fusiformis*. This fauna characterizes silty sediments below cold and low-oxygen waters. Planktonics are almost all *Neogloboquadrina pachyderma* (sinistral) with abundant diatoms and radiolaria. Calcareous foraminifera in stages 3, 5, 7 and 9 are largely lost to dissolution⁷. Benthics in stages 2, 4, 6, 8 and 10 are predominantly calcareous, mainly *Islandiella teretis*, *Nonionella labradorica*, *Buccella frigida*, *Astronion gallowayi* and *E. excavatum*. This fauna presently occupies deep basins with relatively warm bottom water on the eastern Canadian margin¹².

Planktonic foraminifera in core 017 include *N. pachyderma* (sinistral and dextral), *Globigerina quinqueloba* and *G. bulloides*, with up to 15% subarctic species. Modern distributions of subarctic planktonics are confined to warmer (4-10°C) surface waters; beneath the West Greenland Current, *G. quinqueloba* and *G. bulloides* make up to 25% of the planktonic fauna. The presence of subarctic foraminiferal peaks in the early glacial stages of core 017 suggests significant advection of subarctic surface water into northern Labrador Sea at these times (refs 6, 13, and manuscript in preparation). This would occur if the Arctic Island channels were largely blocked by ice, thereby reducing Arctic water outflow to the North Atlantic. Decreased

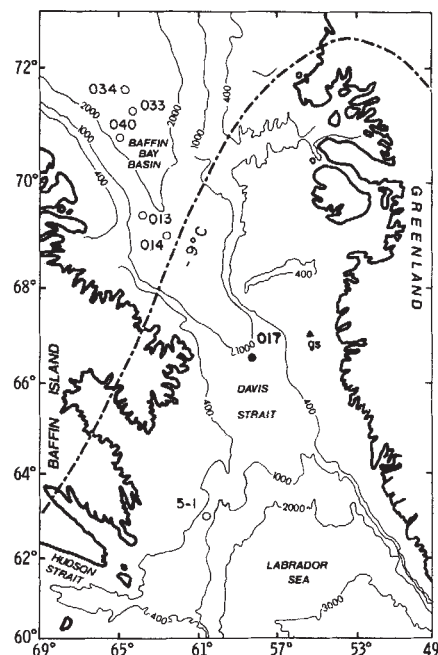


Fig. 1 Bathymetry of Baffin Bay (contours in m) showing the location of core 017 and other cores (ref. 13 and work in preparation) with detailed oxygen isotope, microfossil and/or palynological data; gs, grab sample used for isotopic data at the top of core 017 (see Fig. 2). The -9°C mean annual air isotherm (---) marks the average position of the Atlantic-Arctic air front.

surface runoff and reduced north-east Atlantic inflow would also result in a weaker Baffin Land Current during glacial periods⁶, thus allowing northward penetration of subarctic waters.

Data from core 017 and other cores from Davis Strait^{6,13} show that the interglacial strata are depleted in planktonic foraminifera but rich in siliceous/arenaceous microfossils, whereas the opposite is true for glacial strata. Alternation of predominantly siliceous/arenaceous and calcareous microfossils is typical of areas where carbonate cycles are a function of dissolution cycles⁷. Therefore, acid-resistant palynomorphs were studied in 42 samples taken as closely as possible to the foraminiferal sample intervals.

Figure 3 shows that Quaternary dinoflagellates are common although the numbers generally decrease downcore. The Atlantic dinoflagellates are species which presently have maximum percentage abundances in the temperate North Atlantic¹⁰, particularly beneath the North Atlantic Drift. These species include *Operculodinium centrocarpum*, *Nematosphaeropsis labyrinthea*, *Spiniferites ramosus*, *S. elongatus*, *S. bulloides* and *S. membranaceus*. Their modern distribution in Baffin Bay⁹ is confined to deep-water areas beneath the relatively warm (2-5°C) West Greenland Current. In Core 017, these species occur mainly in the interglacial stages 1, 5 and 7, but they also occur in glacial isotopic stage 2 and in the lower parts of stages 4, 6 and 8. The most common species in core 017 is *Multispinula minuta* which dominates the Canadian Arctic dinocyst assemblage⁹ found in modern sediments below the cold Baffin Land and Labrador Currents. In core 017, however, *M. minuta* dominates only in the glacial stages 6, 10 and upper 8, where it is associated with *Brigantidium simplex*, *Peridinium faeroense* cysts and a *Leiosphaera* species⁹ which is presently abundant in Arctic channels north of Baffin Bay.

The main features of the dinoflagellate stratigraphy are (1) peaks of Atlantic species which often correspond to decreases in subarctic foraminifera; (2) changes in the ratio of the warm water indicator *O. centrocarpum* to the Arctic indicator *M. minuta*, with peaks of *O. centrocarpum* often inversely related to the subarctic foraminiferal peaks; and (3) large increases in dinoflagellate concentrations which mostly correspond to

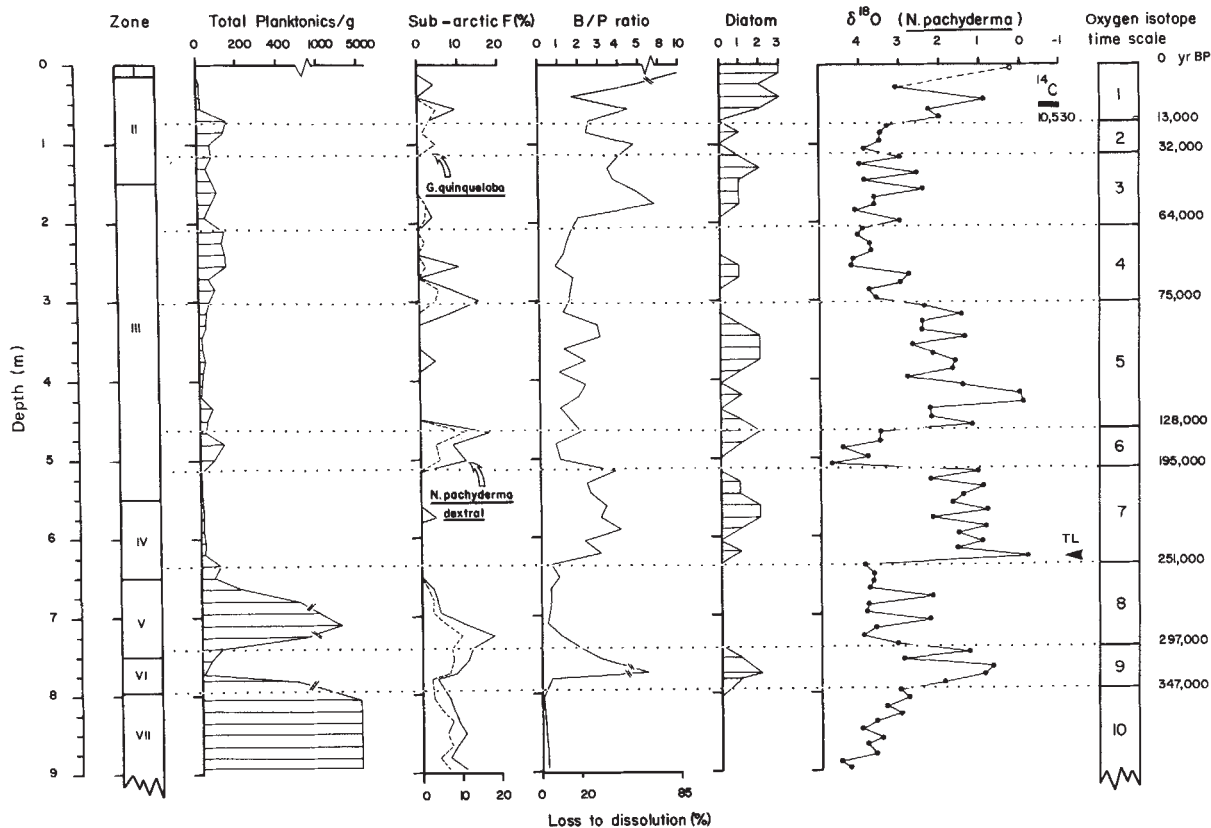


Fig. 2 Foraminiferal zones, planktonic foraminiferal totals per gram sediment, subarctic foraminiferal species (percentage total planktonics), large diatoms (>63 μm) per gram sediment on a scale from 0 (absent) to 3 (abundant, >10,000), and δ¹⁸O record of *Neogloboquadrina pachyderma* (*sinistral*) in core 017. Oxygen isotope time scale refers to ref. 11. ¹⁴C, radiocarbon data; TL, thermoluminescence data; B/P ratio is the ratio of total benthic to total planktonic foraminifera. Dashed line at top of the isotope record was obtained from the grab sample shown in Fig. 1.

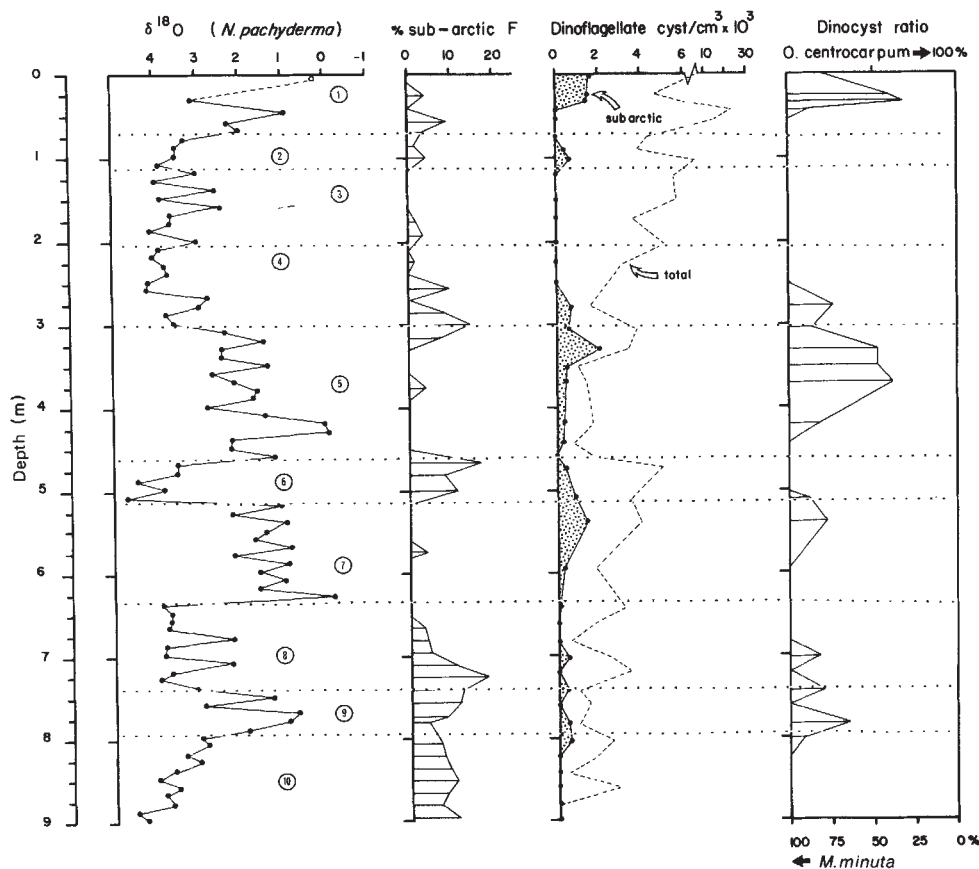


Fig. 3 Summary of dinoflagellate cysts in core 017, compared with the δ¹⁸O record and percentage total subarctic planktonic foraminifera. See text for explanation of subarctic (=Atlantic) dinoflagellates and the Dinocyst ratio. Circled numbers refer to isotopic stages.

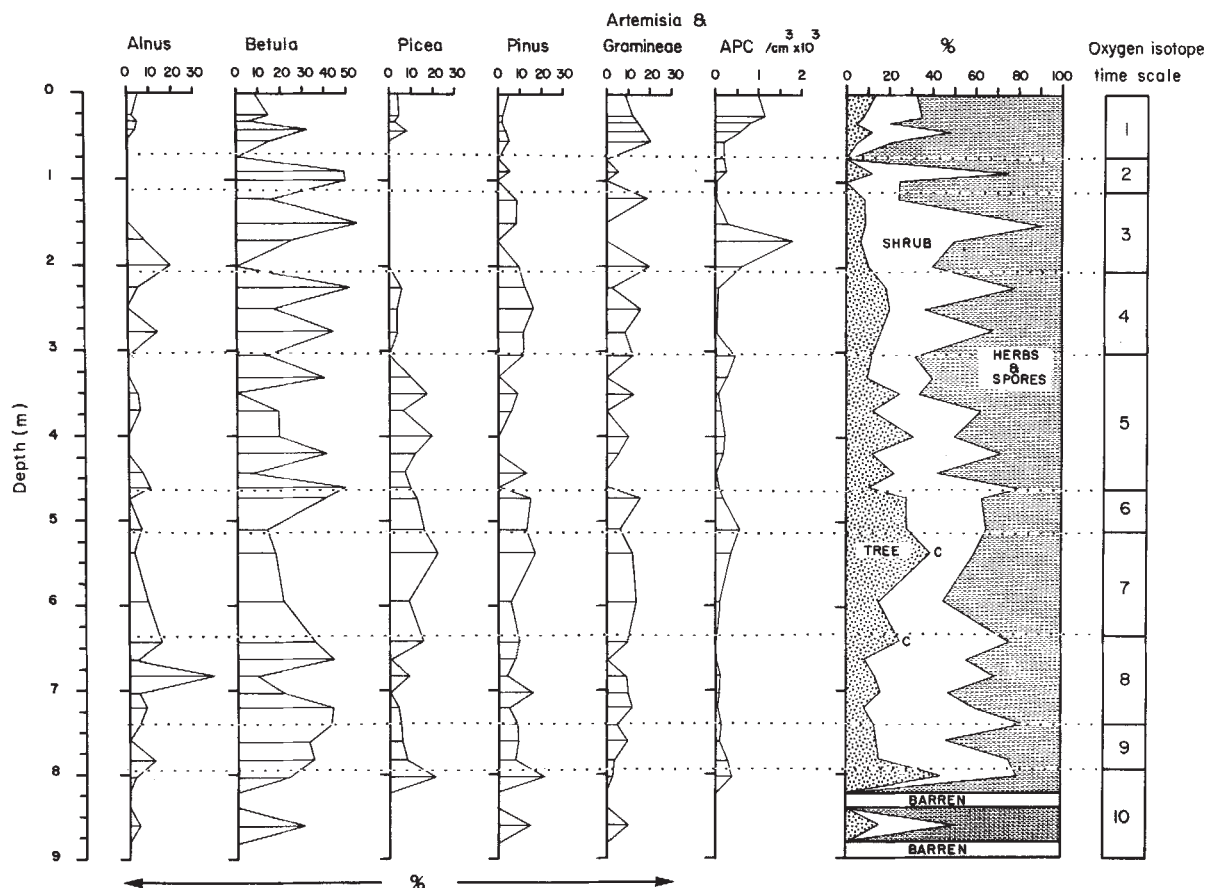


Fig. 4 Pollen percentage diagram for main tree, shrub and herb taxa in core 017, total concentrations of Quaternary pollen and spores (APC) and cumulative percentages of conifer tree, 'shrub' (*Alnus* and *Betula*) and herb pollen plus moss spores. C, *Carya* pollen present.

interglacial stages and are correlated with diatom peaks. These features indicate that maximum primary productivity during the late Quaternary is associated with interglacial stages of relatively warm, open summer water in southern Baffin Bay. The productivity peaks may account for the greater dissolution (20%) of planktonic foraminifera during interglacials than during glacial stages (<10% dissolution)⁷. However, the presence of Atlantic dinoflagellates in stages 2 and lower stages 4, 6 and 8 also implies relatively warm surface water at the core site during early parts of glacial stages, providing independent confirmation of the palaeotemperatures suggested by the subarctic foraminifera.

As for the foraminifera, the number and diversity of quaternary pollen and spores in core 017 (Fig. 4) are low, as expected for oceanic sediments north of the treeline in eastern Canada^{8,9}, but again there are cyclical variations in 'absolute' pollen concentrations (APC) and percentage abundance of indicator species which are correlated with oxygen isotope stages. The top of stage 1 (0–50 cm) is characterized by boreal-subarctic shrub (*Alnus*) and tree pollen percentages (*Pinus*, *Picea*) similar to those found in surface sediments of Baffin Bay⁹, south of the summer position of the Atlantic–Arctic air front (Fig. 1). About 75% of the *Betula* pollen are the small *B. minor* type typical of tundra shrubs. Gramineae dominate the herb pollen, with other taxa including *Artemisia*, *Oxyria*, Rosaceae and Saxifragaceae. The interval from 50 to 325 cm is marked by rare *Picea* and by large fluctuations in *Betula*. Stage 2 contains low APC and variable percentage *Pinus*, Gramineae, *Artemisia*, *Sphagnum* and *Polytrichum*, as presently found in marine sediments⁹ north of the Atlantic–Arctic air front. *Betula* percentages are similar to those found in the Devon Island ice core for the same time interval¹⁴. Stage 3 is marked by higher APC and *Alnus* occurs at the base, suggesting some influx of southern air¹⁵. Stages 4,

8 and 10 contain very low APC but *Alnus* and *Picea* suggest sporadic influx of Atlantic air. Stage 5 is marked by higher tree pollen percentages and peaks in *Picea* and *Alnus*; the assemblages are similar to those in stage 1, but higher percentage *Betula* suggests a wider shrub distribution than presently found on Baffin Island. This agrees with pollen in peat below the Kogalu marine sediments¹⁶, with an age of ~130,000 yr BP.

Tree pollen in stage 6 suggest a strong influx of Atlantic air, but sampling control is poor for this interval in core 017, and data from other cores (Fig. 1) show that this is true only for sediments near the stage 6–7 transition. Interglacial stages 7 and 9 show slight increases in APC and percentage tree pollen; the presence of *Carya* also marks stage 7 in core 017 and other Davis Strait cores¹³.

Overall, the combined palynological and foraminiferal data from core 017 provide palaeoclimatic evidence which supports models^{1–3} that attribute North Atlantic continental ice sheet growth to increased northward flow of warm water during early glacial stages. The present relatively warm climate and sea-surface temperatures in southern Baffin Bay result from (1) high latitude penetration of warm cyclonic air fronts; (2) inflow of Atlantic water through the West Greenland Current. Meridional air flow accounts for boreal tree and shrub pollen in modern Baffin Bay sediments^{9,15} and during older interglacial stages. Lower pollen concentrations and diversity during glacial stages suggest a southward shift of the Arctic air front and stronger zonal flow of polar air characterized by *Betula*, *Artemisia*, Gramineae and other herbs, in addition to ubiquitous *Pinus* grains. However, the presence of boreal tree/shrub taxa in glacial stages 4, 6, parts of 8 and 10 indicate influx of Atlantic air during all initial and some later phases of ice-sheet growth. Presence of Atlantic dinoflagellates during early glacial stages also

supports the foraminiferal data indicating increased water mass transport from the south. Furthermore, the persistent presence of pollen and dinoflagellates during glacial maxima implies extensive areas of summer open water (for example, more than the present ice covered Arctic Ocean north of Ellesmere Island¹⁷), although production of dinoflagellates and large (>63 µm) diatoms is low. Heterotrophic peridinioid dinoflagellates like *M. minuta* (= *Protoperidinium pellucidum* cyst form) can survive under ice up to 2 m thick, but they are very rare or absent in continuously ice covered regions¹⁷.

We conclude that both palynological and foraminiferal studies of core 017 provide palaeoclimatic data which contradict models requiring continuous sea-ice cover in Baffin Bay/Labrador Sea during glacial stages⁵ but are compatible with models based on orbital changes in summer insolation, with very rapid initial glaciation¹⁻³ and subsequent limited sea ice, the continental ice sheets being maintained by precipitation transported northwards from the south-west along storm tracks directed by strong land-sea thermal gradients.

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Inheritance of stereotyped gibbon calls

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Little is known about how vocal patterns develop in non-human primates, mainly because suitable controlled experiments are difficult to carry out on these animals¹. Results of isolation experiments²⁻⁴ and observations of interspecific hybrids^{1,5} suggest no greater role for vocal learning than exists in many other vertebrates⁶⁻⁹, and less than has been found in birds¹⁰⁻¹³. We have now studied vocal patterns of hybrids between white-handed gibbons (*Hylobates lar*) and pileated gibbons (*Hylobates pileatus*) in natural mixed-species groups, in a zone of interspecies contact in central Thailand, and in some captive mixed-species groups. We find that in female hybrids, the patterns of the loud and stereotyped 'great-calls' show no evidence of learning from parents, and appear to be under strong genetic control. Daughters maturing in groups with genetically unlike parents develop great-calls unlike those of their mothers, even though these calls develop only while the daughters sing simultaneously with their mothers.

Great-calls are the most spectacular sounds in the repertoires of gibbons. They are sung by females at intervals of 2-4 min

during morning song bouts, and last approximately 14-24 s. In most species, females are accompanied by their mates in a ritualized duet¹⁴⁻²⁰; in a few species, females sing solo near their mates^{16,20-22}. The songs are believed to function in territory advertisement^{5,14,16,23} and in maintaining the monogamous pair bond^{15,19,24-26}.

The acoustic patterns of great-calls are highly species-specific^{16,27,28}. The great-calls of *H. lar* and *H. pileatus* have similar length and frequency range, the major differences being in the shapes and number of notes (Fig. 1). Great-calls of *lar* average 8.4 notes (s.d. 1.66; $n = 14$ individuals recorded in Khao Yai Park, Thailand, one call randomly selected from each) and *pileatus* great-calls average 72.8 notes (s.d. 9.61; $n = 19$ individuals, recorded from three locations in Thailand)²⁹. Comparison of sound spectrograms of *lar*, *pileatus* and hybrid calls shows that the number of notes per s uttered at the end of the call varies relatively less than the total number of notes. For *lar*, the number of notes per s in the last quarter of the call (including no less than three notes) averages 0.49 (s.d. 0.054; $n = 14$) compared with an average of 9.6 (s.d. 0.51; $n = 19$) for *pileatus*²⁹.

Most of our recordings of wild gibbons were made in a small zone of overlap and hybridization between *H. lar* and *H. pileatus* in Khao Yai National Park, central Thailand^{27,29,30}. About 215 groups were identified and mapped in this zone during 1976-80, and 23 groups were found to contain mated adults of different species or hybrids, most of which have been tape recorded. All tape-recorded hybrids have been frequently studied closely with binoculars.

Despite their close relationship, body colour patterns provide unambiguous separation of the species and recognition of their hybrids²⁹. The major pelage differences are the presence of a complete ring of white fur around the face in *lar*, compared with white eyebrows and a black cap in *pileatus*; also a white scrotal tuft of fur in *pileatus* males, and a black 'vest' and greyish body in *pileatus* females, compared with the solid buff or brownish-black body coloration in *lar*. *H. pileatus* is sexually dichromatic whereas *lar* is asexually dichromatic in Khao Yai. Hybrids have various odd or intermediate colour patterns. No individuals with normal *lar* or *pileatus* call types have been found to have odd or atypical coloration, but a few individuals with *lar*-like coloration (for example, females CW7 and TO1, Fig. 1) have slightly more rapid emission of notes than is typical of *lar*.

Great-call patterns of clear phenotypic hybrids tend to be intermediate between those of *lar* and *pileatus* in nearly all respects. Those hybrids that resemble one species more than the other (Fig. 1g, h, l)²⁹ show a corresponding resemblance in great-call pattern. One feature that is somewhat more variable in hybrids than in *lar* or *pileatus* is the length of the call; some have fairly short calls (for example, HE2). In respects other than acoustic pattern, such as frequency and time of singing, duet structure and loudness, the hybrids have not been found to differ significantly from normal *lar* or *pileatus*, although in some respects they are intermediate between the species (our unpublished data).

The relatively rigid territoriality and monogamy of gibbons³¹ allows the identification of mother-daughter pairs in the wild with a high degree of certainty. Juvenile or sub-adult females in the family group frequently sing along with their mother's great-calls, the mother and daughter usually beginning their calls within 1 s of each other^{15,18,22,32-34}. This suggests that the young may have to learn or practise the song³⁵, which does not seem to serve any important function before adulthood.

Three groups with genetically unlike parents (as determined by pelage) had 4-5-year-old daughters who sang with their mothers. The pelage of the daughters was intermediate between that of parental types, providing further evidence of parentage²⁹. Sonagrams of two of these pairs of females are shown (Fig. 1q, r). In all three cases the adult females were hybrids, with call patterns and pelage about half-way between *lar* and *pileatus*. In two cases (CW6 and HS3), the adult male was a *lar*; in the