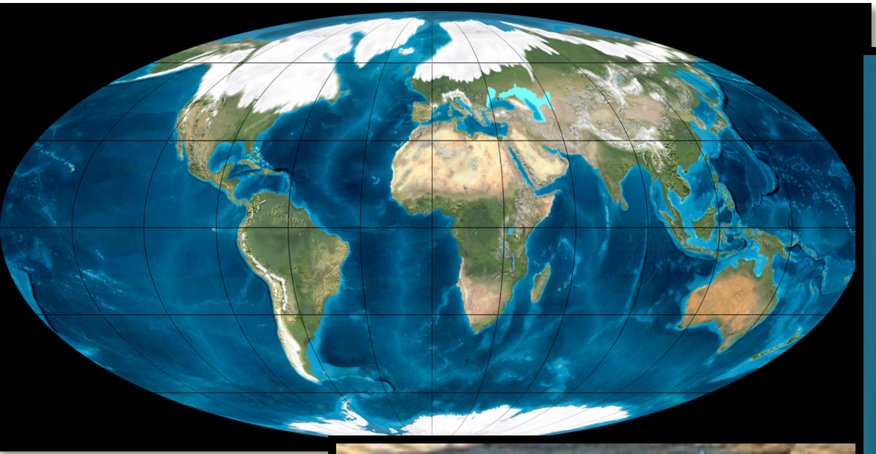
Glaciation

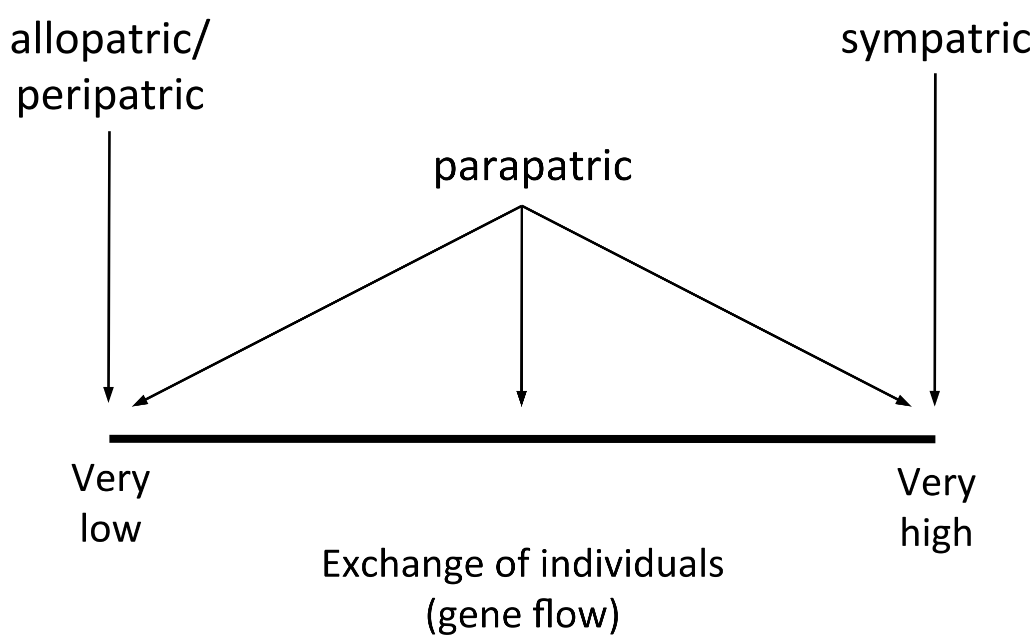


Recall the modes of speciation

Allopatric speciation – occurs when populations are geographically isolated throughout the entire process of differentiation
~ very low or no gene flow

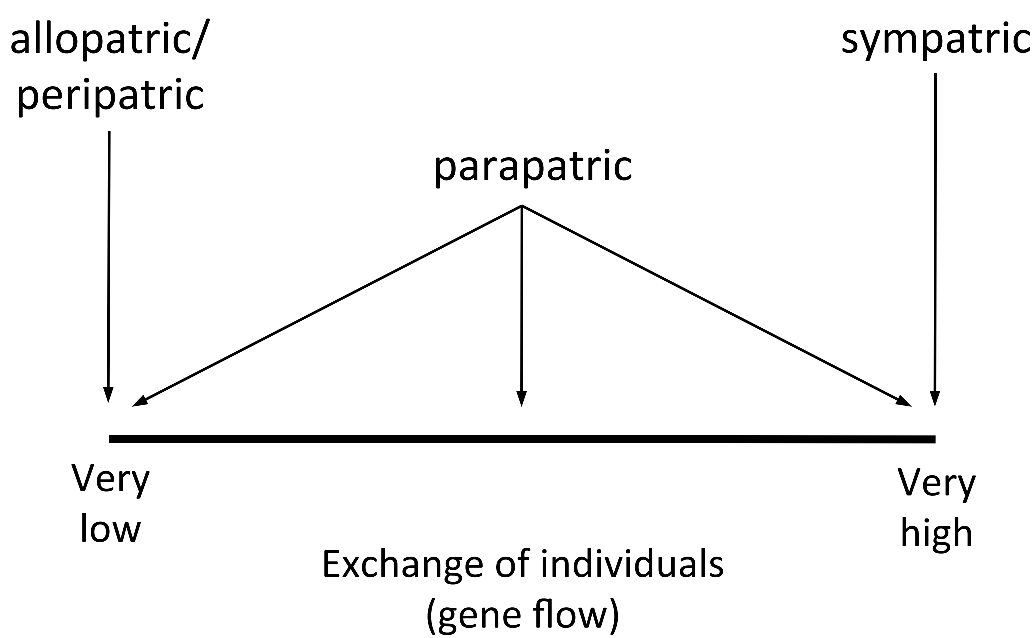
Parapatric speciation – Populations are largely allopatric but overlap in a narrow zone of contact ~ gene flow is limited in contact zone

Sympatric speciation – Two populations overlap extensively in their distributions ~ high potential for gene flow



Recall the modes of speciation

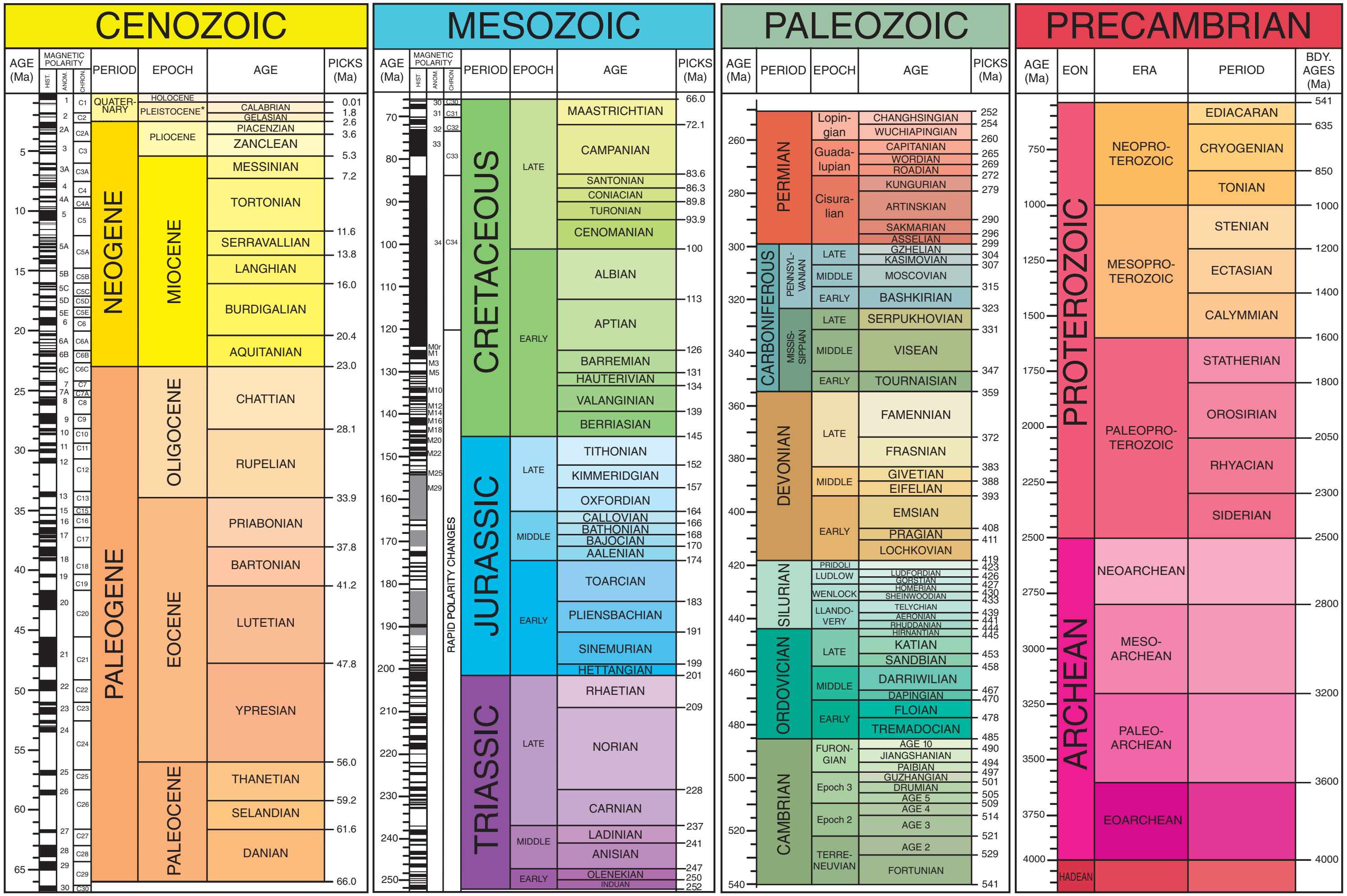
Glaciation and continental drift greatly affected species distributions in terrestrial and marine landscapes, providing opportunities for isolation (and connection) of populations = lots of chances for **allopatric speciation**



Goals and Learning Objectives

1) Familiarize yourself with the geologic time scale, and where the Pleistocene fits into this perspective of time
2) Understand how the Milankovitch cycles and feedback mechanisms relate to glaciation cycles
3) Appreciate how these cycles affected the extent of isolation of populations and the generation of refugia in the temperate zone (and influenced patterns of speciation)
4) Understand the (controversial) views for the role of refugia for speciation in the tropics during the Pleistocene

A geological perspective on time…



*The Pleistocene is divided into four ages, but only two are shown here. What is shown as Calabrian is actually three ages—Calabrian from 1.8 to 0.78 Ma, Middle from 0.78 to 0.13 Ma, and Late from 0.13 to 0.01 Ma.

Walker, J.D., Geissman, J.W., Bowring, S.A., and Babcock, L.E., compilers, 2012, Geologic Time Scale v. 4.0: Geological Society of America, doi: 10.1130/2012.CTS004R3C. ©2012 The Geological Society of America.

The Cenozoic, Mesozoic, and Paleozoic are the Eras of the Phanerozoic Eon. Names of units and age boundaries follow the Gradstein et al. (2012) and Cohen et al. (2012) compilations. Age estimates and picks of boundaries are rounded to the nearest whole number (1 Ma) for the pre-Cenomanian, and rounded to one decimal place (100 ka) for the Cenomanian to Pleistocene interval. The numbered epochs and ages of the Cambrian are provisional.

THE GEOLOGICAL SOCIETY OF AMERICA®

REFERENCES CITED Cohen, K.M., Finney, S., and Gibbard, P.L., 2012, International Chronostratigraphic Chart: International Commission on Stratigraphy, www.stratigraphy.org (last accessed May 2012). (Chart reproduced for the 34th International Geological Congress, Brisbane, Australia, 5–10 August 2012.)

Gradstein, F.M, Ogg, J.G., Schmitz, M.D., et al., 2012, The Geologic Time Scale 2012: Boston, USA, Elsevier, DOI: 10.1016/B978-0-444-59425-9.00004-4.

http://www.geosociety.org/science/timescale/

Continental Drift

The Geological Time Scale – Various methods used to estimate the age of deposits and timing of events…

Time scale described by dating stratigraphic layers of rock with uniform composition and marine fossils that had wide geographic distributions (known as index or guide fossils).

Ages of deposits estimated by using knowledge of radioactive element and isotope decay

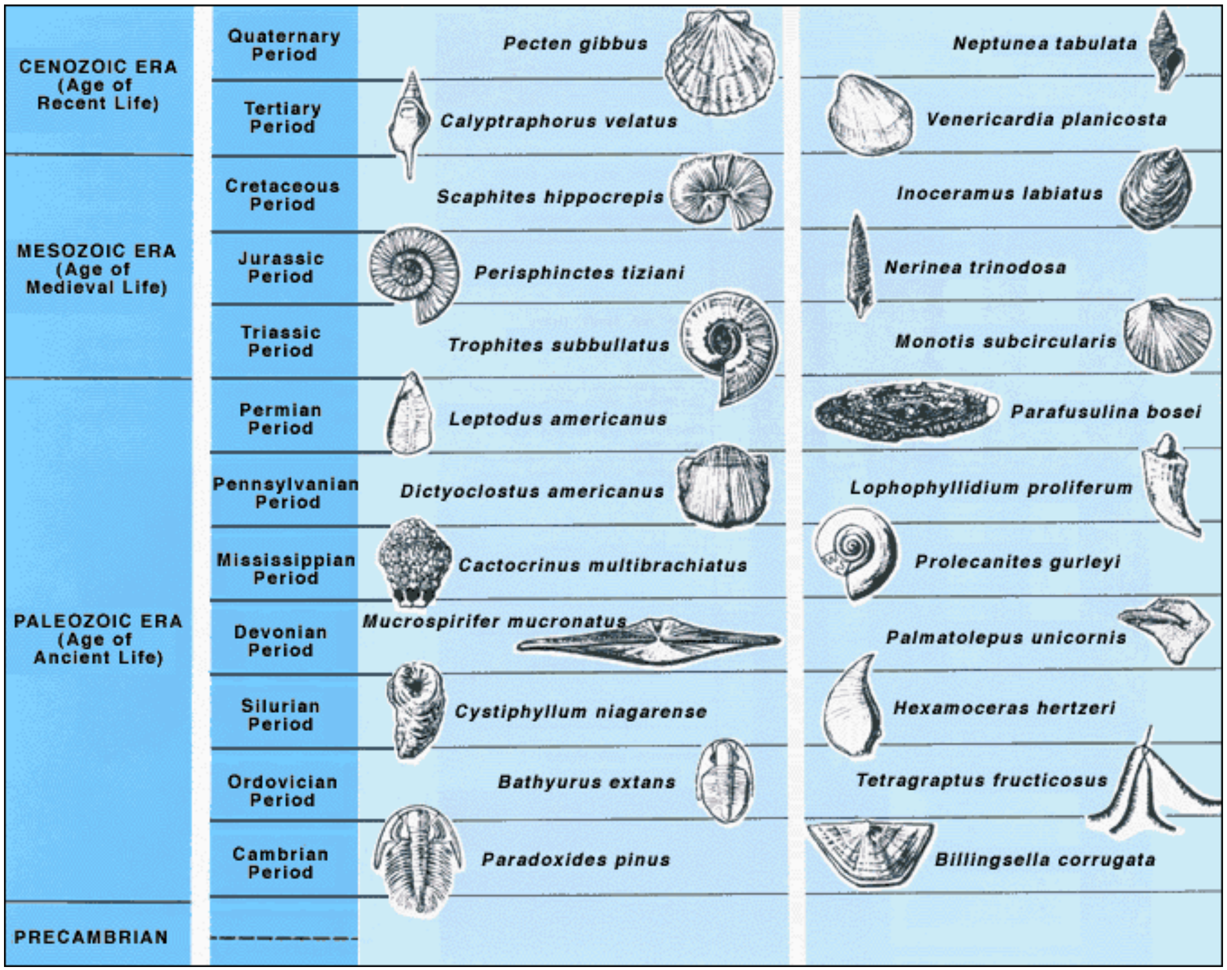
Isotopes of uranium decay to a stable end product of lead, with half-lives ~500 million years, provided the current estimate of the earth's age of about 4.6 billion years.

^{14}C decays to ^{12}C, half-life ~5800 years, useful for dating more recent events within 50,000 years.

Radiocarbon dates can be calibrated with tree rings analysis within 10,000 years.

The Geologic Time Scale

Index (guide) fossils used by paleontologists to chronologically correlate rock strata from different geographic localities

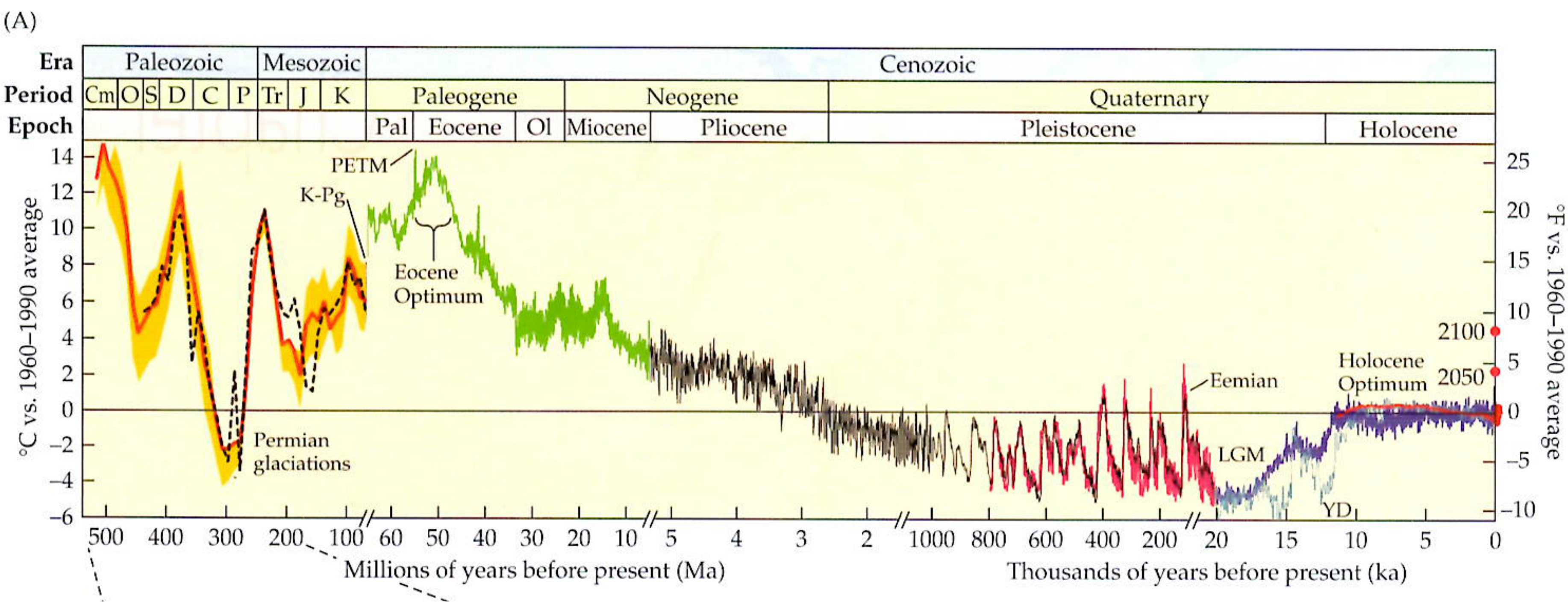


Cambrian/Ordovician trilobite

Jurassic ammonite

Reconstruction of global air temperatures

Compared to the global average air surface temperature from 1960 – 1990 (black line)



Based on oxygen and hydrogen isotope data from marine organisms and ice cores

(from Lomolino et al. 2017)

Glaciation

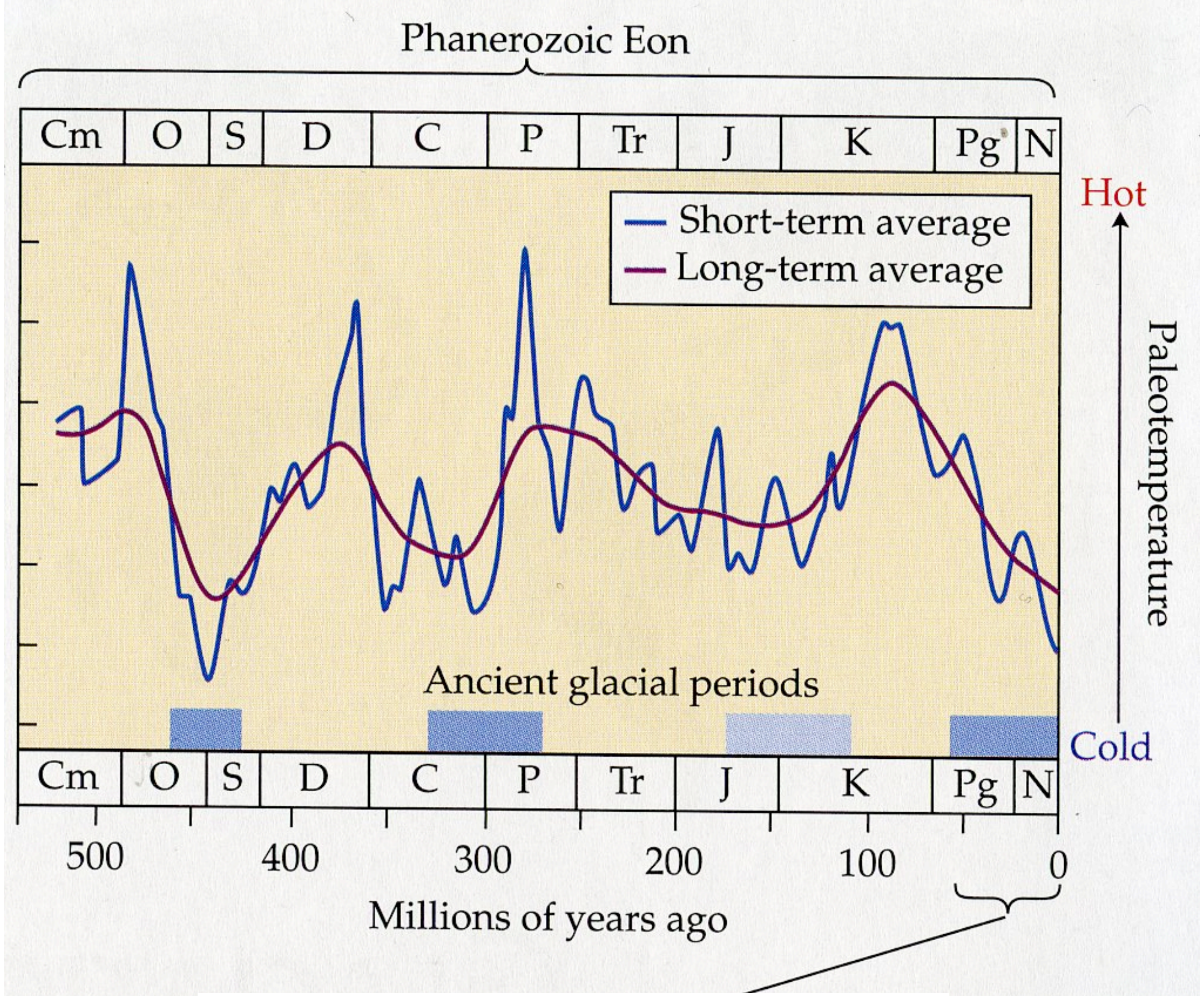
Glaciers form when the build-up of ice during cold, snowy periods exceeds melting of ice during warmer periods.

Movement occurs due to gravity (i.e., on a slope) and/or compression force (the minimum thickness for the latter mechanism appears to be about 50 m).

Glacier: a perennial mass of ice that moves, or is capable of movement, over land.

Glaciation

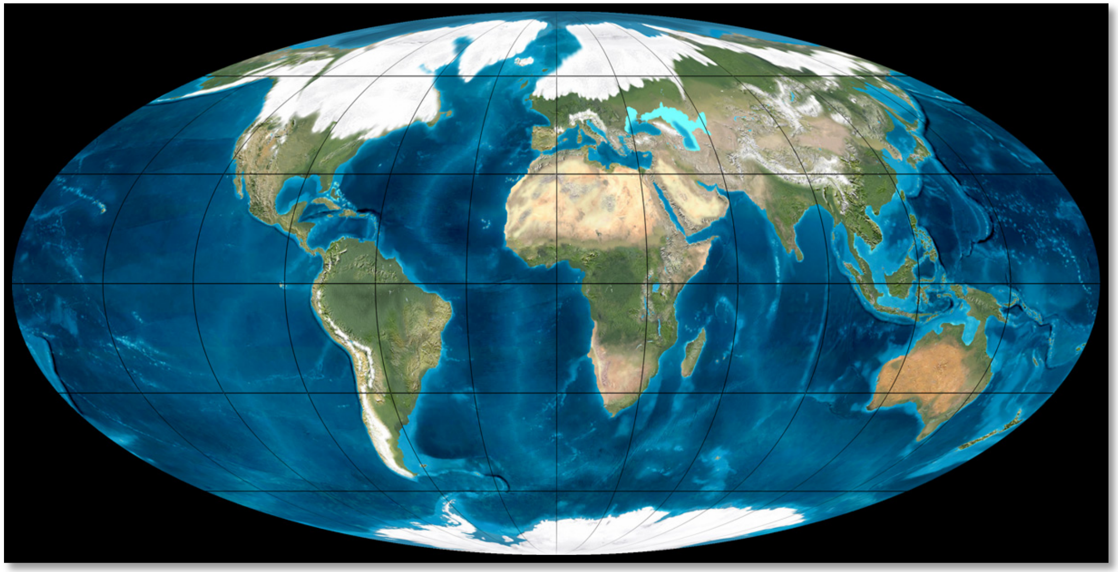
Glacial events have occurred several times over long time periods

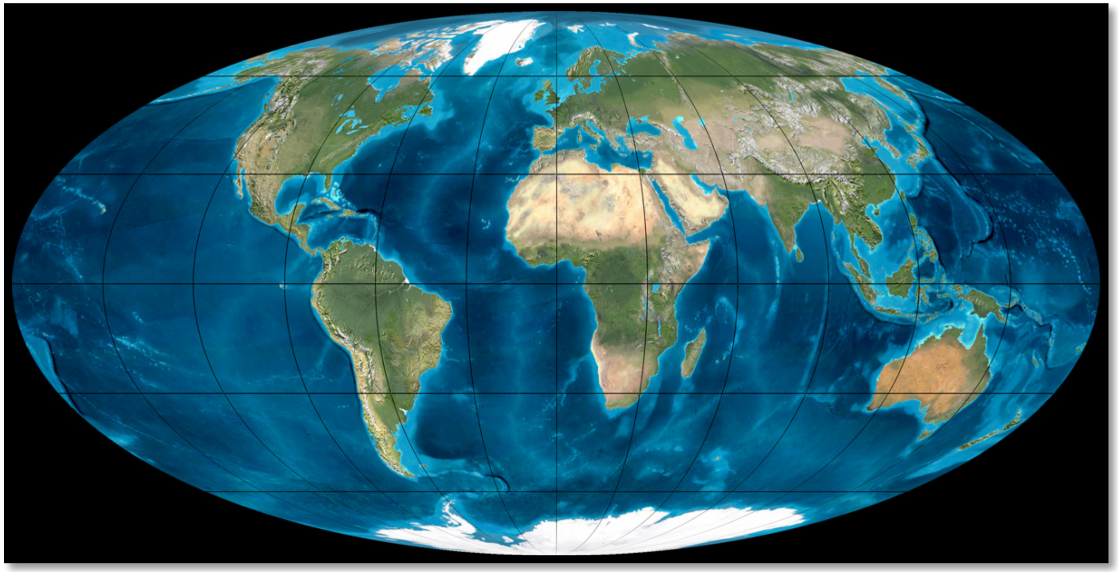


Cenozoic Era (66 mya to present)

(from Lomolino *et al.* 2010)

Glaciation



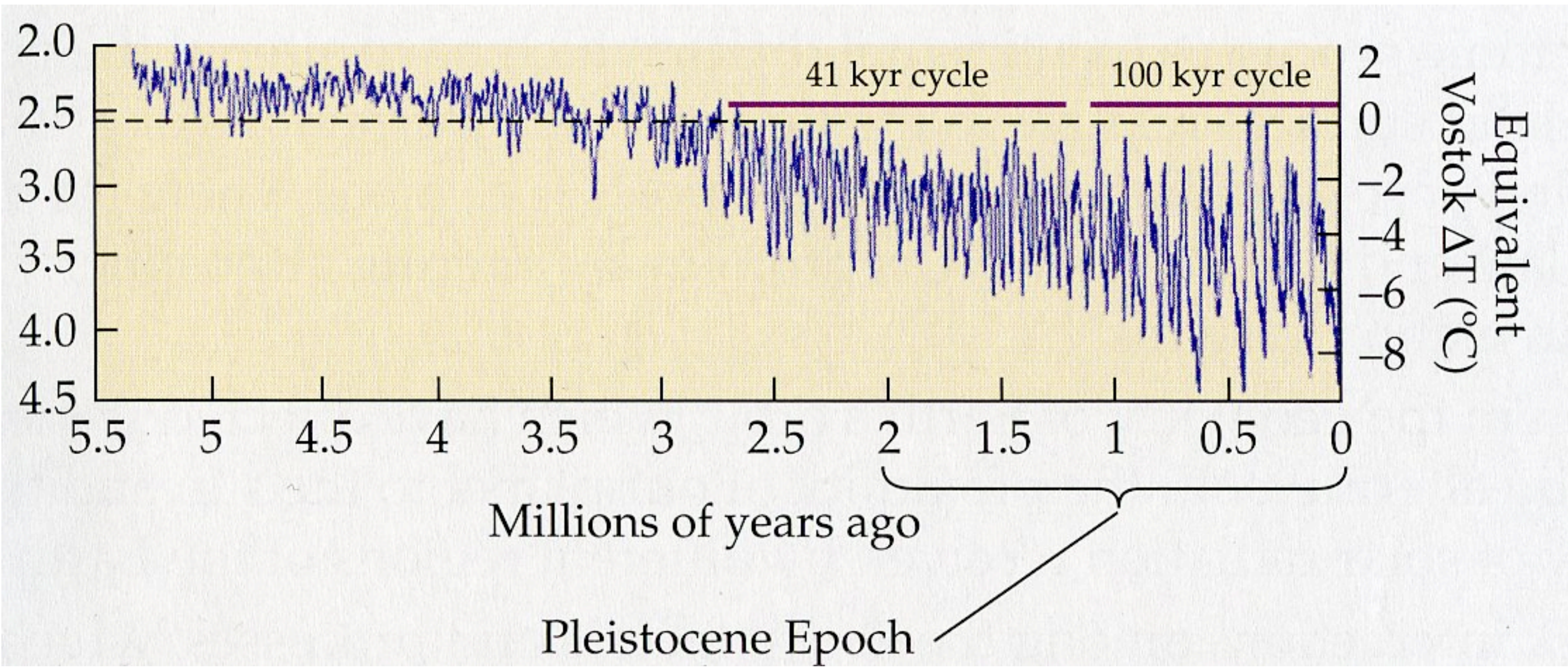


maps from: http://jan.ucc.nau.edu/~rcb7/globaltext2.html

Glaciation

We will focus on Pleistocene glaciations (roughly the last 2 million years)

During the Pleistocene Epoch there were up to 20 glacial advances and retreats or "glacial-interglacial cycles"



In the last ~ 2 million years, we can use a range of methods to study Earth's history that would not be available for studying more ancient periods (e.g., tree rings, pack rat middens, pollen deposits in lake sediments)

(from Lomolino *et al.* 2010)

Glaciation

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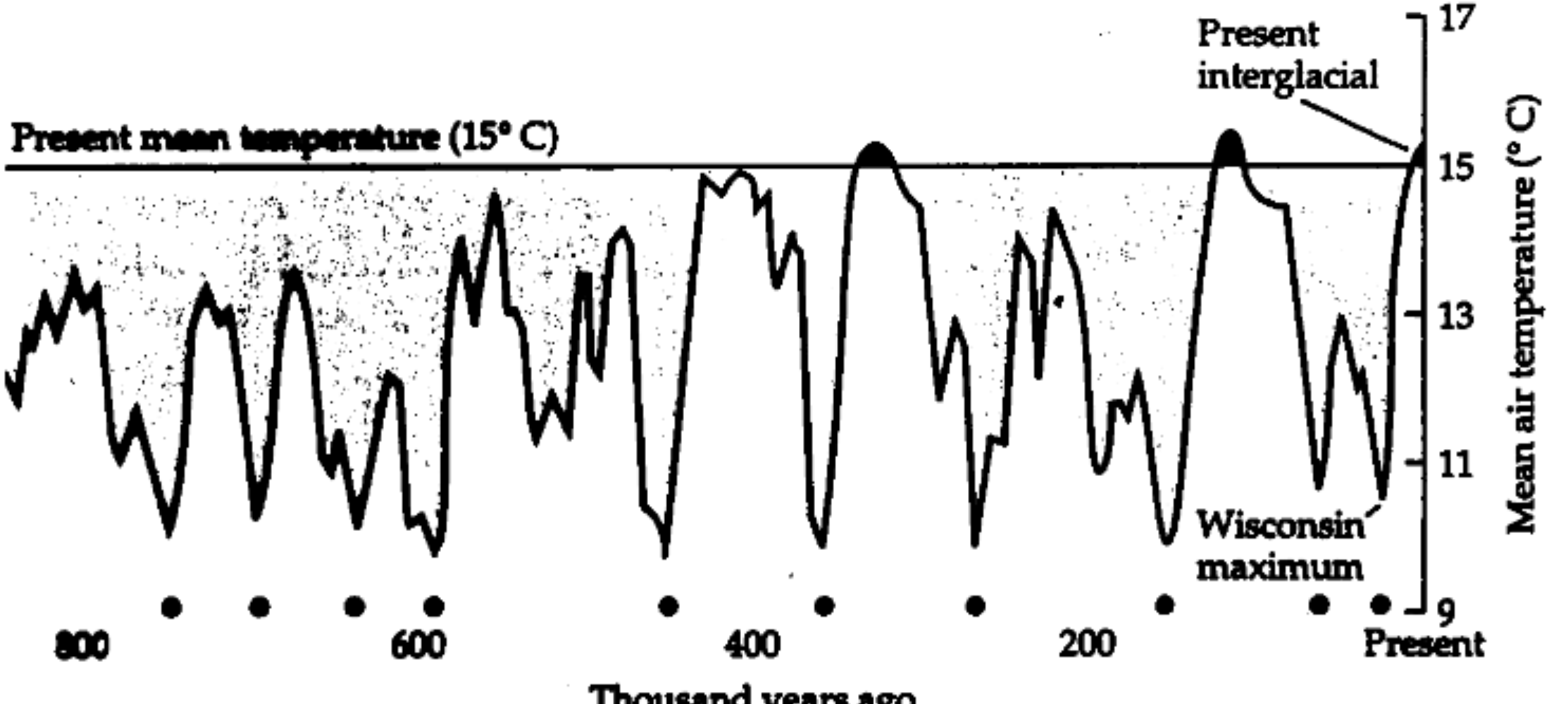


Zooming in to visualize cycles over 100,000 years…

(from Gates 1993)

Glaciation

Outline of topics in this section:

1) Causes of glaciation

2) Pleistocene glaciation

3) Changes associated with glaciation

4) Biogeographic consequences

5) Evolutionary consequences

6) Extinctions

Causes of Glaciation

Pre-Pleistocene Glaciations

Climatic cooling driven by:

Continental coalescence (generating huge continental areas)

Continental drift into far southern latitudes (near the south pole)

Not enough time for appreciable drift during the Pleistocene

Volcanic activity resulting in particulate matter in the atmosphere

Not associated with cooling in the Pleistocene

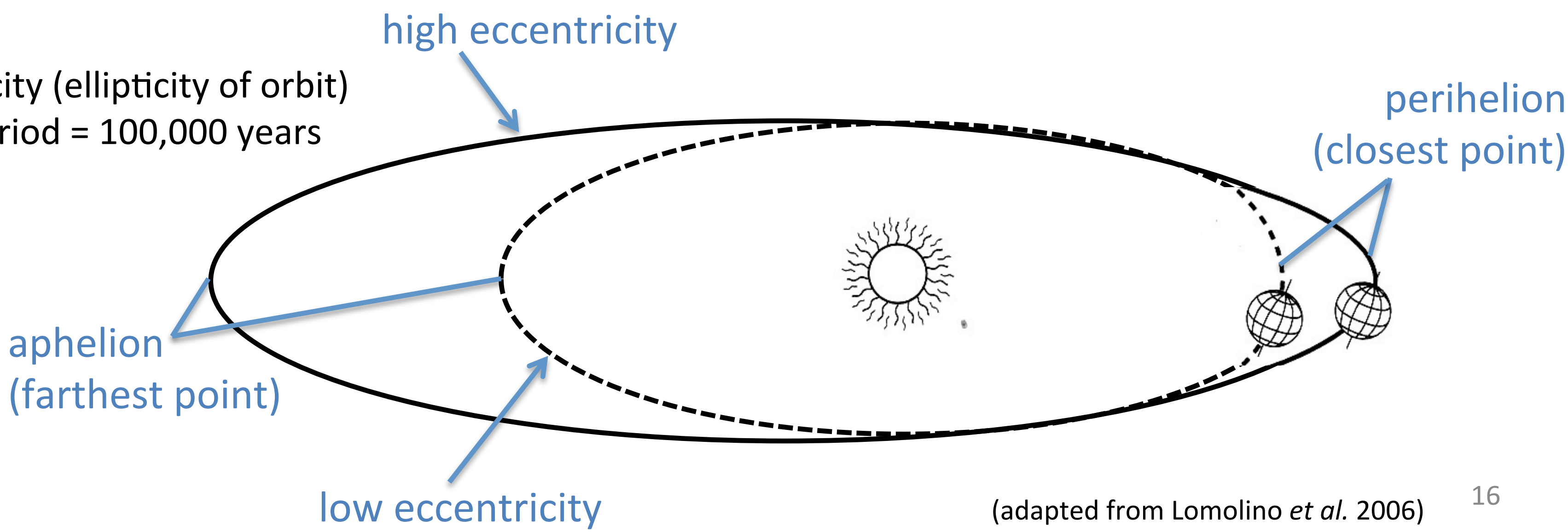
Causes of Glaciation

Pleistocene Glaciations

Milankovitch Cycles: variation in the Earth's eccentricity, axial tilt and precession comprise three dominant cycles, collectively known as Milankovitch cycles. The three cycles impact *the seasonality and location of solar energy* around the Earth, thus influencing Earth's climate system and the advance and retreat of glaciers.

Eccentricity: The shape of the Earth's orbit around the sun (ellipticity of orbit). When the orbit is most elliptical, the Earth receives 20-30% more solar radiation at the perihelion (closest point) than at the aphelion (farthest point). Today the orbit has low eccentricity (~6% difference in solar radiation between the perihelion and aphelion).

Eccentricity (ellipticity of orbit)
Cyclic period = 100,000 years



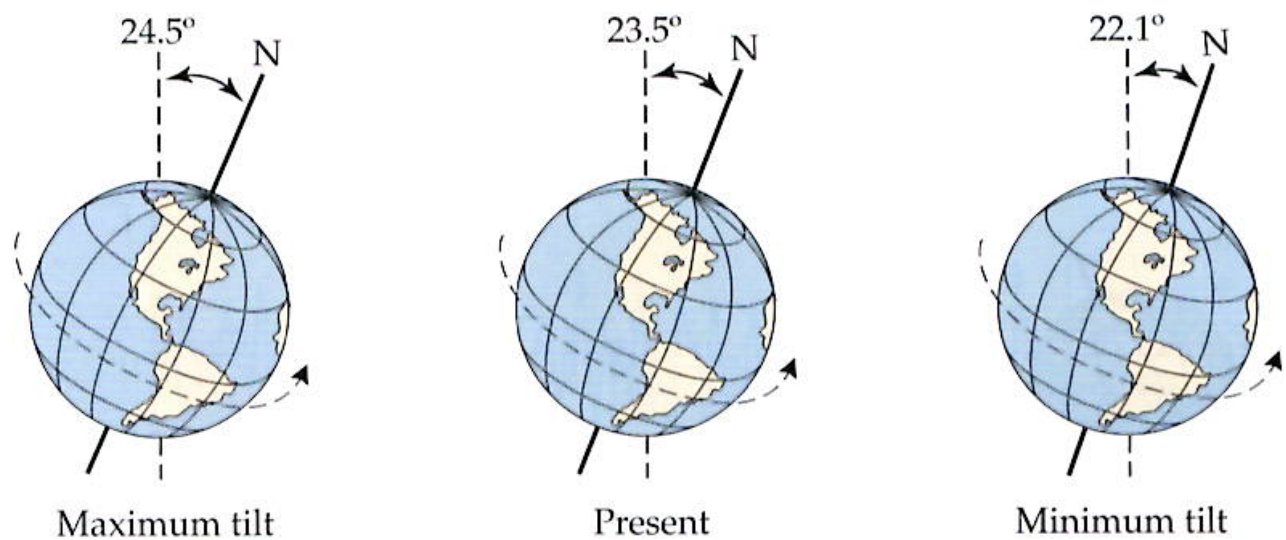
(adapted from Lomolino *et al.* 2006)

Causes of Glaciation

Pleistocene Glaciations

Milankovitch Cycles: variation in the Earth's eccentricity, axial tilt and precession comprise three dominant cycles, collectively known as Milankovitch cycles. The three cycles impact *the seasonality and location of solar energy* around the Earth, thus influencing Earth's climate system and the advance and retreat of glaciers.

Axial tilt (*obliquity*): Inclination of the Earth's tilt in relation to its plane of orbit around the sun. With minimum tilt, solar radiation is more evenly distributed across seasons (warmer winters/cooler summers). One hypothesis is that minimum tilt could promote growth of ice sheets (more snow with warmer winter, less opportunity for melt during cooler summer).



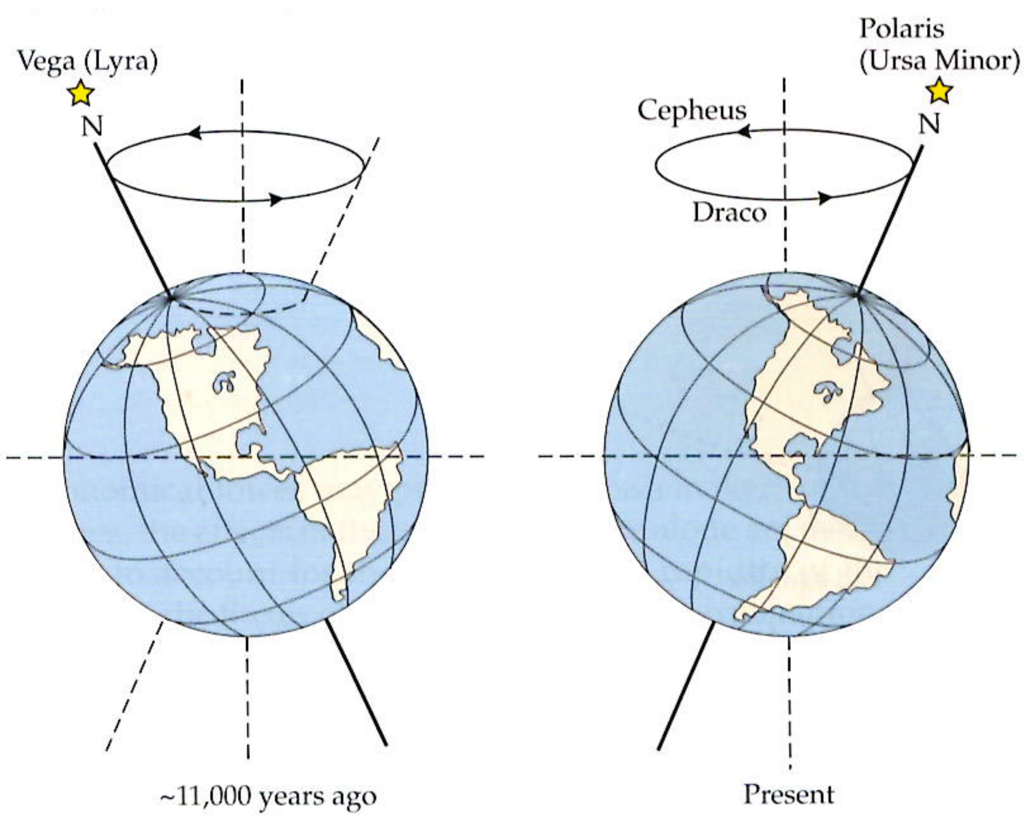
Axial tilt (obliquity)
Cyclic period = 41,000 years

(Lomolino *et al.* 2017)

Causes of Glaciation

Pleistocene Glaciations

Milankovitch Cycles: variation in the Earth's eccentricity, axial tilt and precession comprise three dominant cycles, collectively known as Milankovitch cycles. The three cycles impact *the seasonality and location of solar energy* around the Earth, thus influencing Earth's climate system and the advance and retreat of glaciers.



Precession (pole wandering)
Cyclic period = 22,000 years

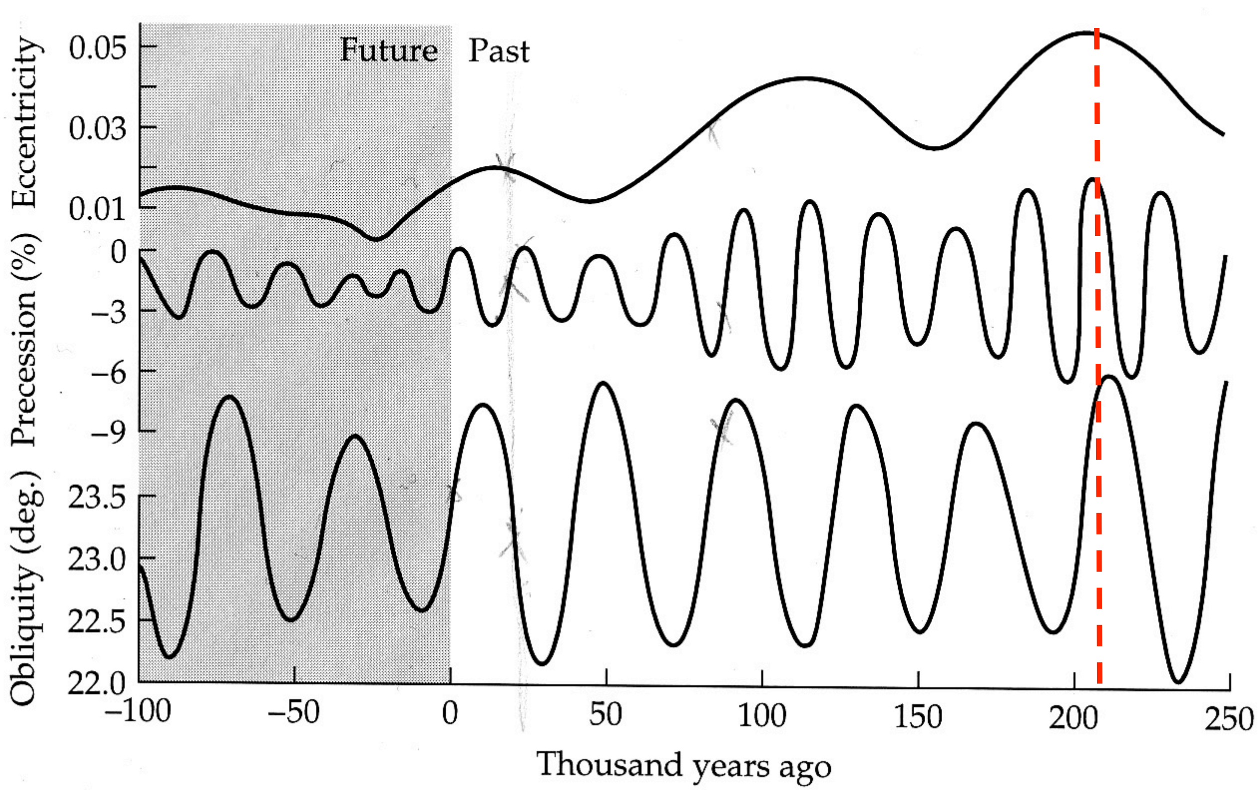
Precession: When axis is tilted towards Vega, the position of the Northern Hemisphere winter solstice coincides with the aphelion (farthest point from sun) and the summer solstice with the perihelion (closest point to sun), resulting in greater seasonal contrasts. Currently, Earth experiences perihelion close to the winter solstice.

(Lomolino *et al.* 2017)

Causes of Glaciation

Pleistocene Glaciations

Milankovitch hypothesized that when some parts of the cyclic variations are combined and occur at the same time, they are responsible for major changes to Earth's climate (even ice ages). Proposed in early 1900s, but empirical evidence supporting theory demonstrated in 1970s with deep sea sediment cores (Hays et al. 1976)



Causes of 100,000 yr cycles remain unclear – a topic of ongoing research:

Suggested combination of Milankovitch cycles and internal feedbacks

See Abe-Ouchi et al. 2013 *Nature*

(from Lomolino *et al.* 2006)

Causes of Glaciation

Pleistocene Glaciations – Likely generated by several factors and feedback effects

Summer temperatures are a critical factor that determine whether ice sheets retreat or grow. Ice sheets grow in the winter, and cooler summers cause less ice sheet retreat than warm summers.

Pleistocene glaciations driven by reduction in interception and absorption of solar radiation owing to Milankovitch cycles.

Feedback mechanisms contribute to rate of cooling and warming

Growing ice sheets:

- eliminate plant and animal life over large areas
- natural production of greenhouse gases declines
- more white surfaces increase the Earth's albedo

Retreating ice sheets:

- increasing plant and animal life
- increased production of greenhouse gases
- albedo decreases

Causes of Glaciation

Pleistocene Glaciations

Feedback mechanisms:

Strong correspondence among global temperature and natural changes in greenhouse gases over last 150,000 years.

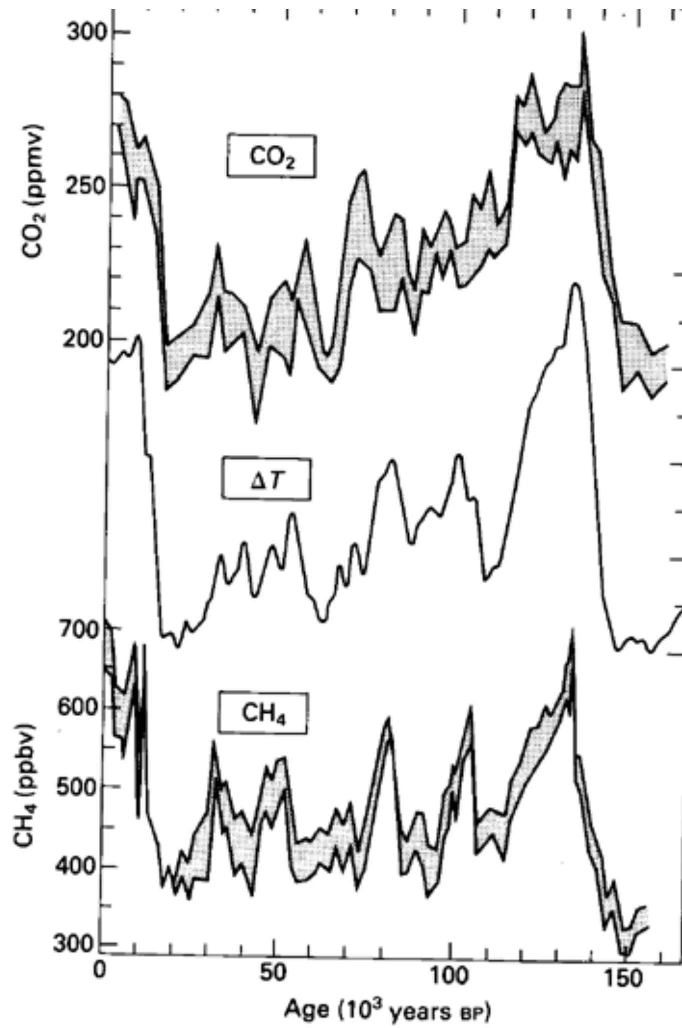


Fig. 10.14 Analyses of gas bubbles in an ice core taken from the Antarctic ice cap. These are regarded as fossil samples of the ambient atmosphere of the past. The concentrations of carbon dioxide (upper) and methane (lower) are shown together with a reconstruction of temperature change derived from oxygen isotope studies of the same area (middle). From Lorius *et al.* [14].

Pleistocene Glaciation

Pleistocene glaciations – additional noteworthy observations:

Most Pleistocene glaciations had the same range and extent.

Glacial sheets consisted of massive ice formations up to 4 km thick and covered up to one-third of Earth's land mass.

Much more extensive in the northern hemisphere (more land mass, more continental climate).

In the southern hemisphere, glaciation occurred in mountainous areas of New Zealand, southeastern Australia, eastern Africa, and South America.

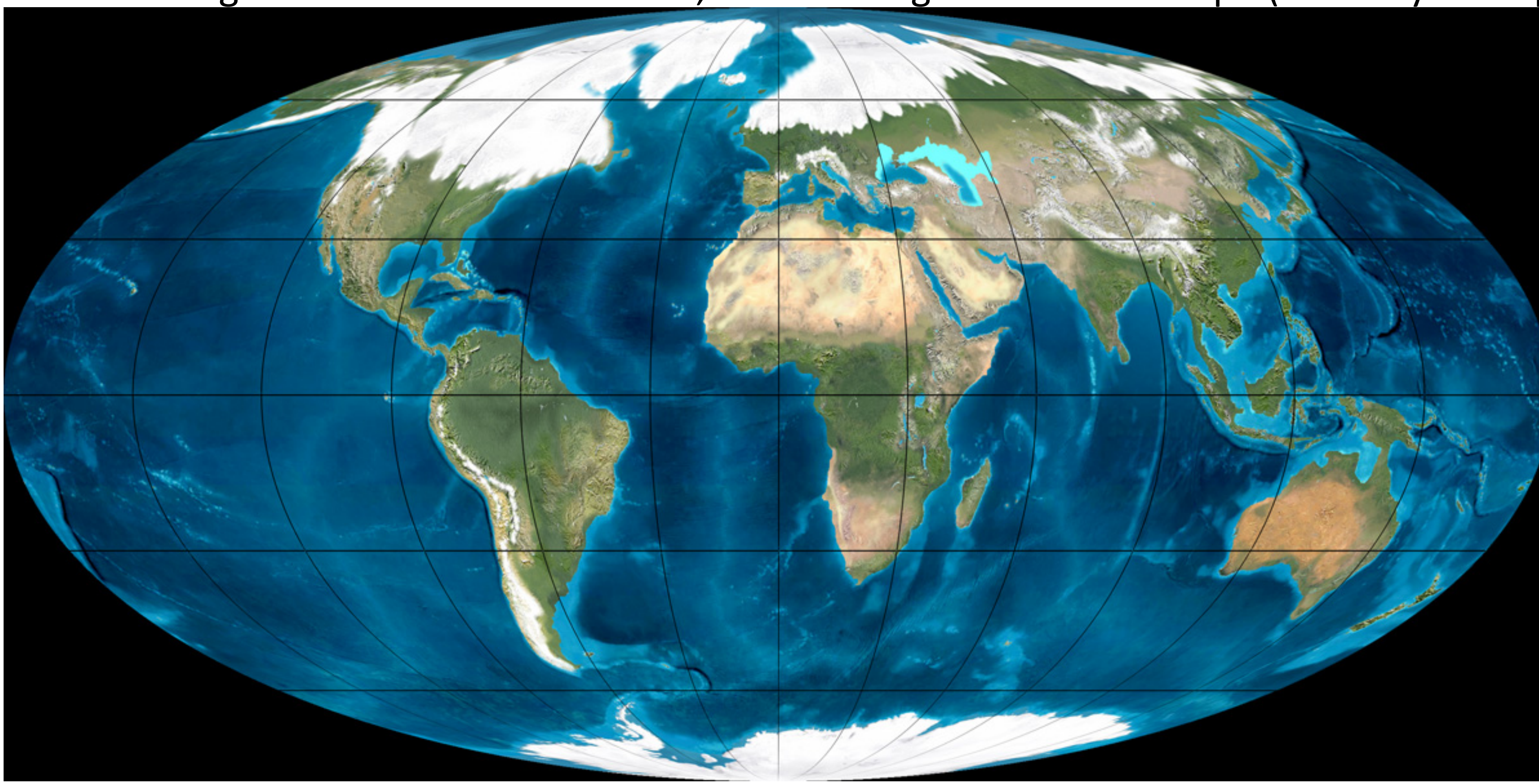
Greater extent in North America than Eurasia. For example, in the last glacial advance, 80% of the northern ice mass was in North America.

Little growth into the oceans.

Pleistocene Glaciation

Maximum extent of the last glacial advance in the northern hemisphere

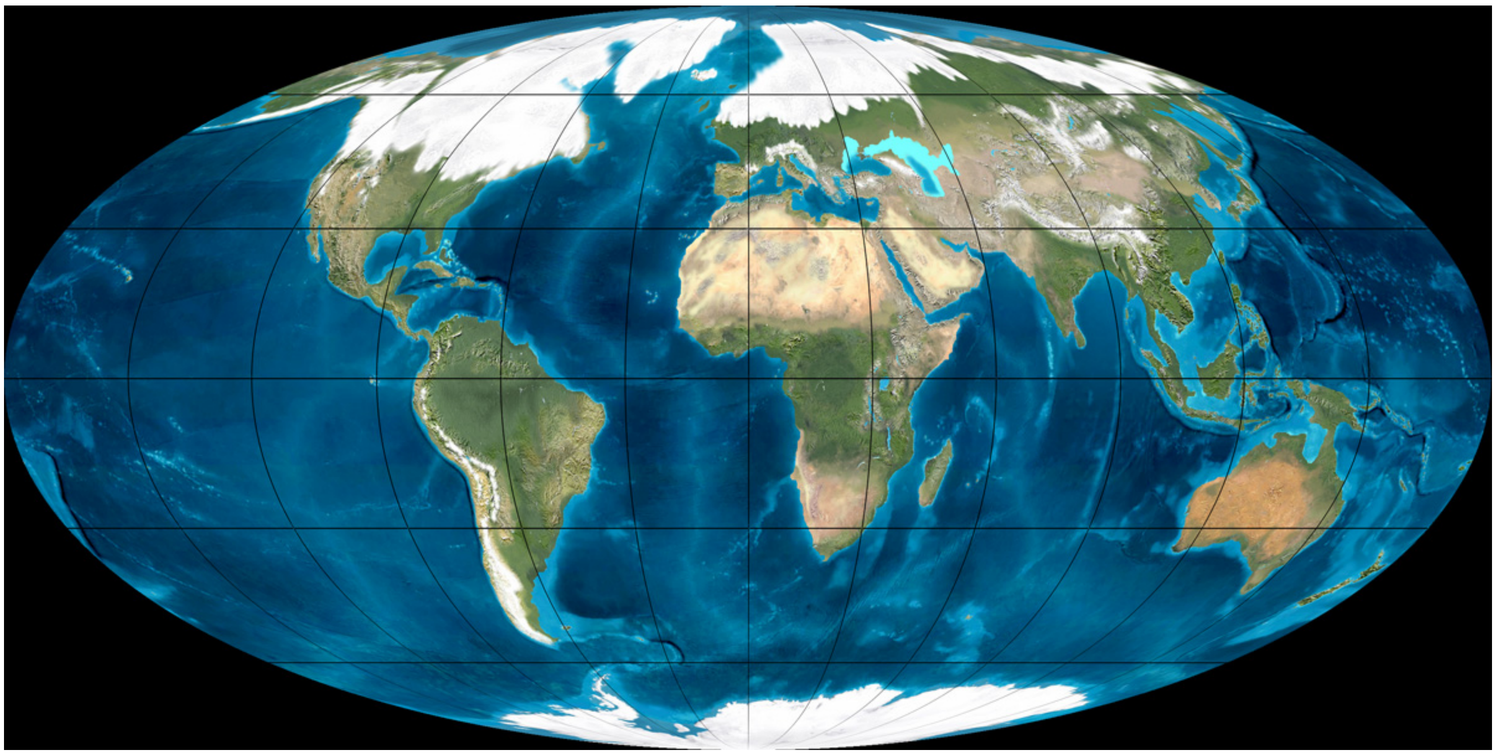
The *Wisconsin* glaciation in North America, and *Würm* glaciation in Europe (50 000 years bp)



Changes Associated with Glaciation

1) Elimination of Terrestrial Habitat

At the height of the last glaciation, the area of the ice sheets was estimated to cover about 33% of the earth's terrestrial area.



On the other hand, over 2.8 million km^2 of ocean floor were exposed as new terrestrial habitat as sea levels dropped (Canada today covers about 10 million km^2).

Changes Associated with Glaciation

1) Elimination of Terrestrial Habitat

Resulted in the isolation of many species within *glacial refugia*.

Glacial Refugium: an area that has remained relatively unchanged while surrounding areas are glaciated, and which has thus served as a refuge for species displaced by the glacial advance.

Changes Associated with Glaciation

Glacial Refugia

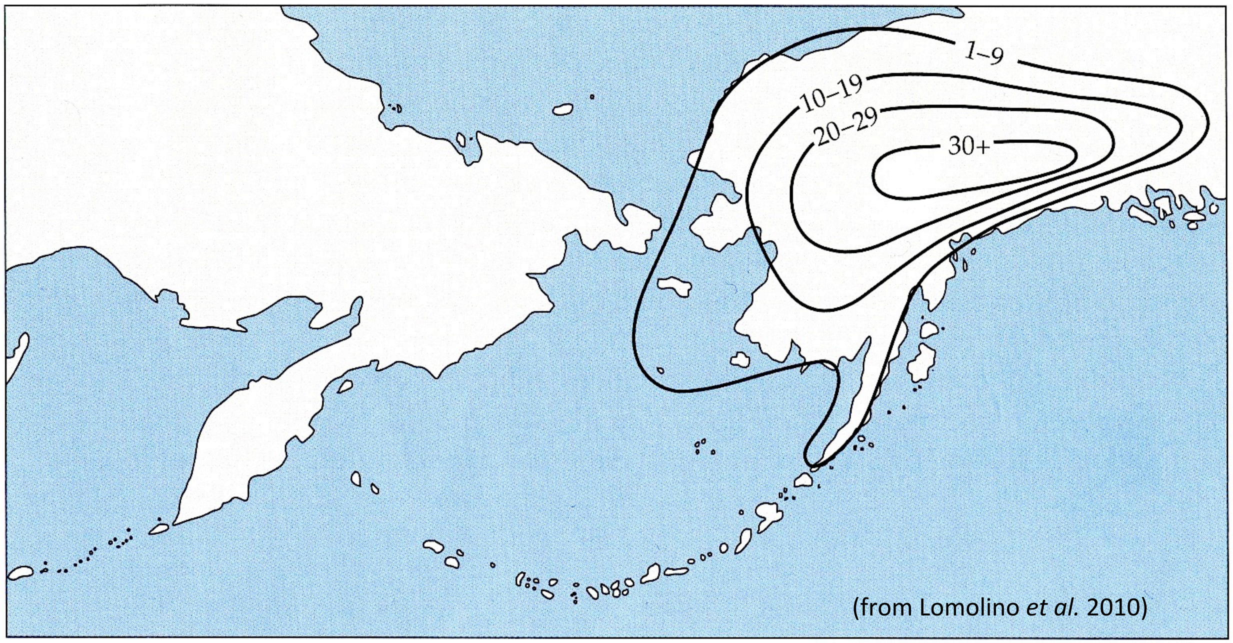
http://www.isgs.illinois.edu/maps-data-pub/publications/geonotes/graphics/wisc-glaciers.gif

Changes Associated with Glaciation

Glacial Refugia

Locations of refugia identified from centers of diversity or centers of endemism

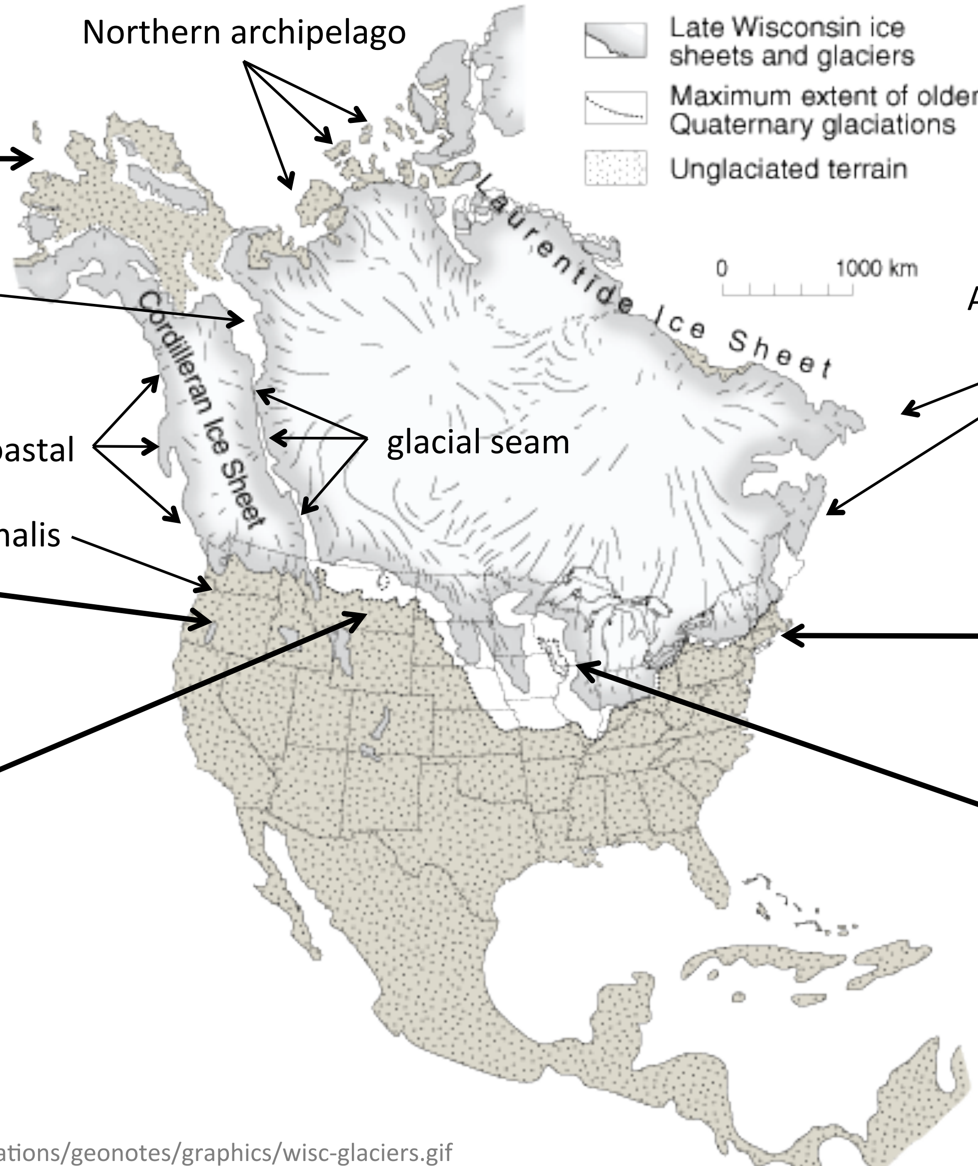
e.g., number of endemic plant species in Beringia



High frequency of endemic plant species used to put forward the idea that Beringia remained unglaciated and served as a refugium for Arctic forms during the Pleistocene.

Changes Associated with Glaciation

Other Glacial Refugia?



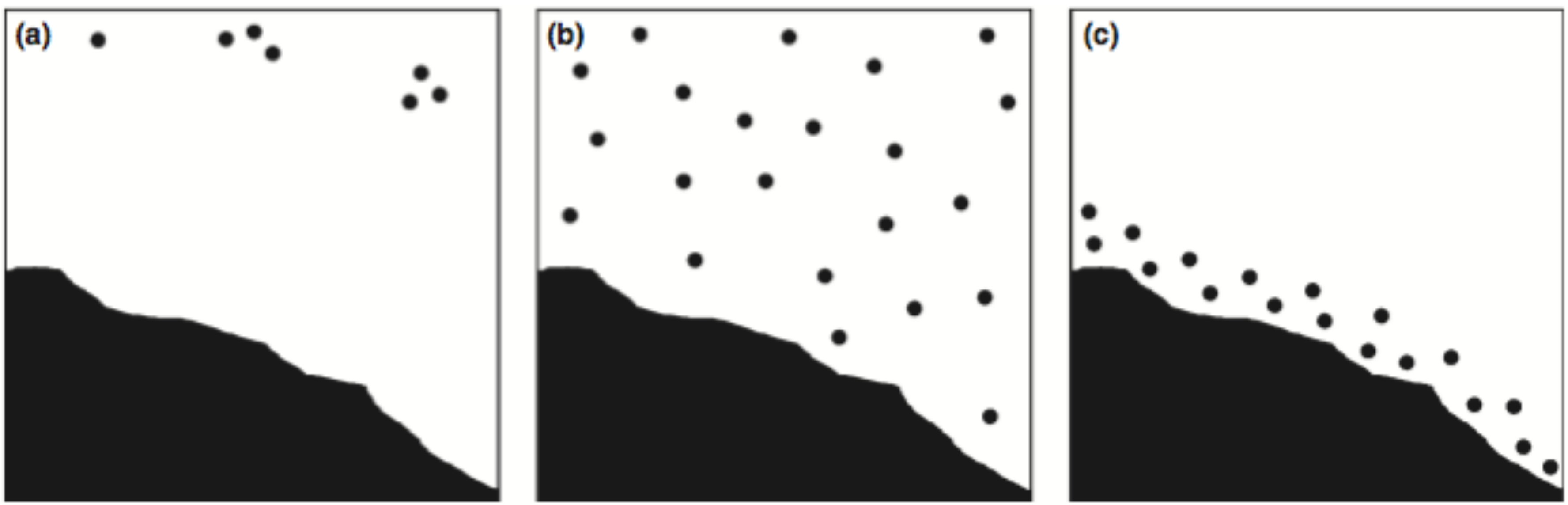
http://www.isgs.illinois.edu/maps-data-pub/publications/geonotes/graphics/wisc-glaciers.gif

Changes Associated with Glaciation

Glacial Refugia

Microrefugia: glacial refugia of smaller geographical area that may have been important to fewer species than larger main refugia (macrorefugia) for survival during glaciation (aka, cryptic refugia, interglacial refugia, northern refugia, relict isolates – see Rull 2009).

Distal or remote | Widespread or diffuse | Proximal or ecotonal



Three types of possible distribution patterns of isolated populations (i.e., microrefugia) according to relative position with respect to a larger refugium (i.e., macrorefugium)

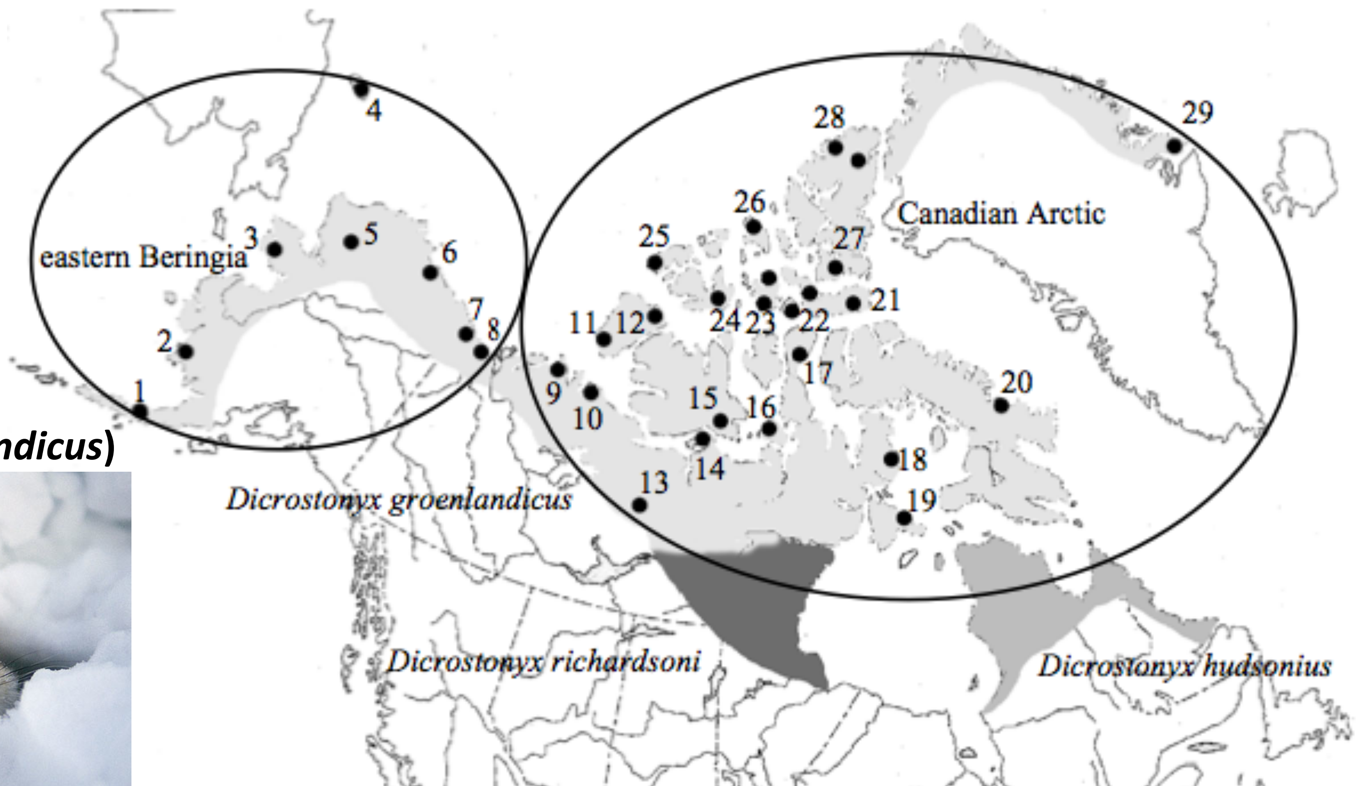
(Figure 1 from Rull 2009)

Changes Associated with Glaciation

Glacial Refugia

Microrefugia: glacial refugia of smaller geographical area that may have been important to fewer species than larger main refugia (macrorefugia) for survival during glaciation (aka, cryptic refugia, interglacial refugia, northern refugia, relict isolates – see Rull 2009).

Collared Lemming
(*Dicrostonyx groenlandicus*)



(from Federov and Stenseth 2002)

Changes Associated with Glaciation

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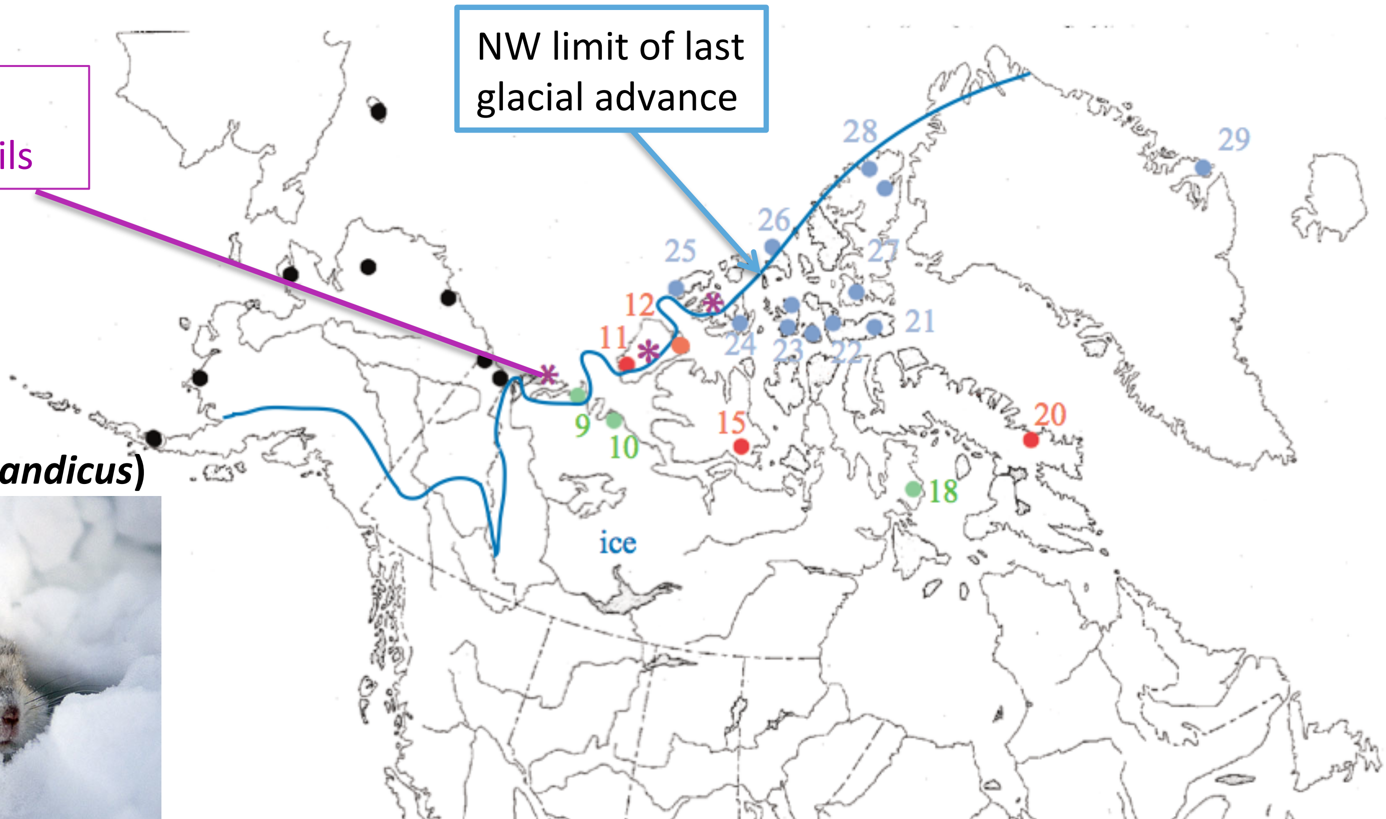
* Location of vertebrate fossils

NW limit of last glacial advance



(from Federov and Stenseth 2002)

Collared Lemming
(*Dicrostonyx groenlandicus*)

Changes Associated with Glaciation

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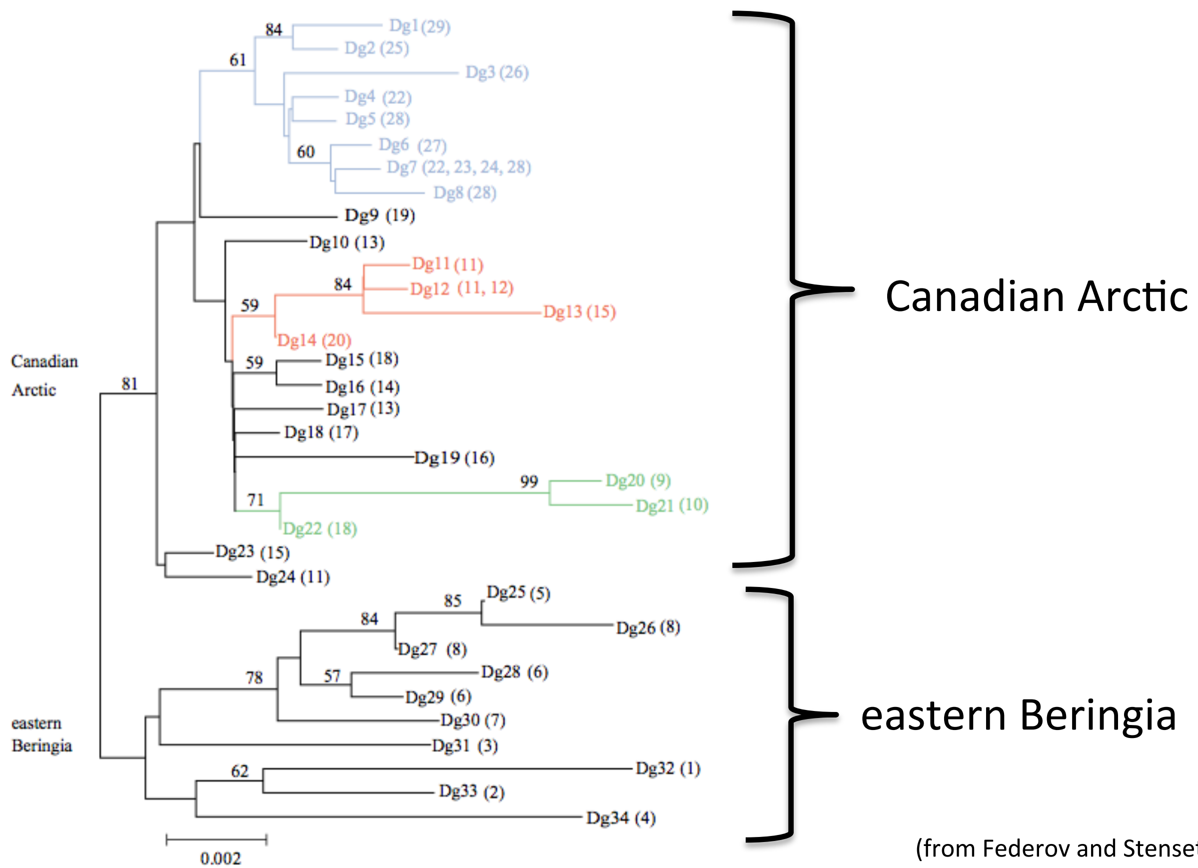
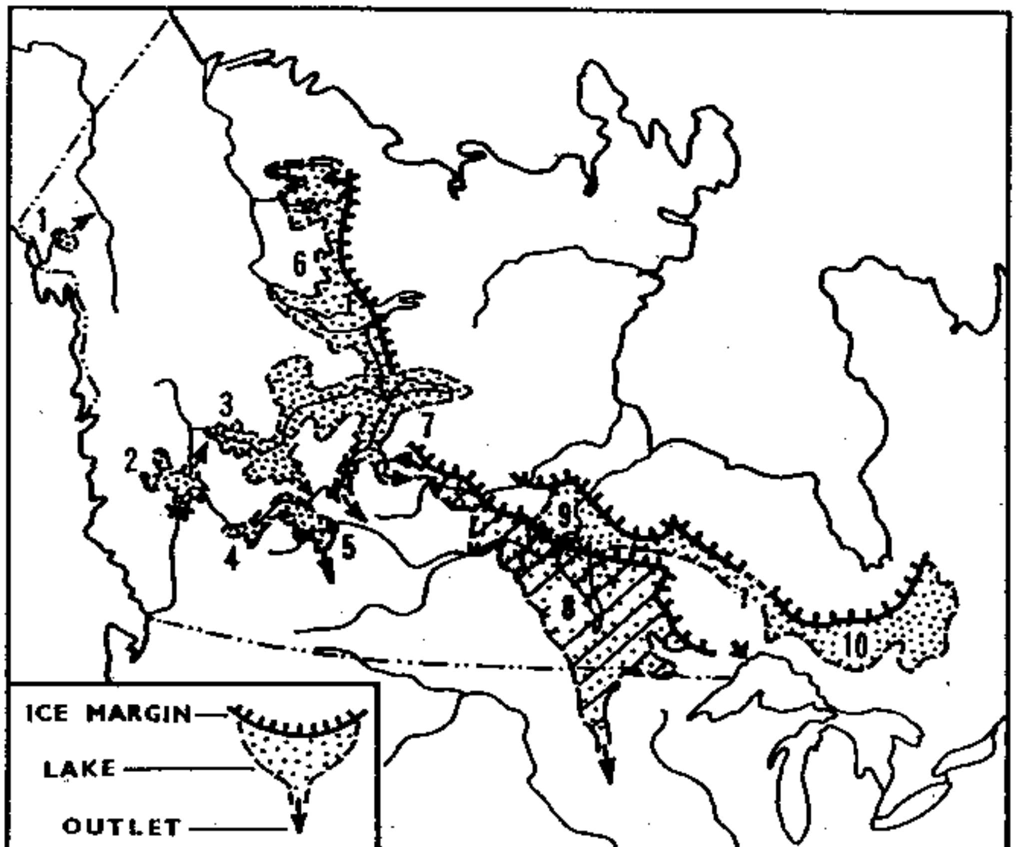


(from Federov and Stenseth 2002)

Changes Associated with Glaciation

Many areas also became more interconnected with proglacial lakes
(i.e., lakes that form just beyond frontal margin of advancing or retreating glacier)

Proglacial lakes (c. 8000 - 9000 yrs. bp)



Proglacial Lakes (did not necessarily exist at the same time):

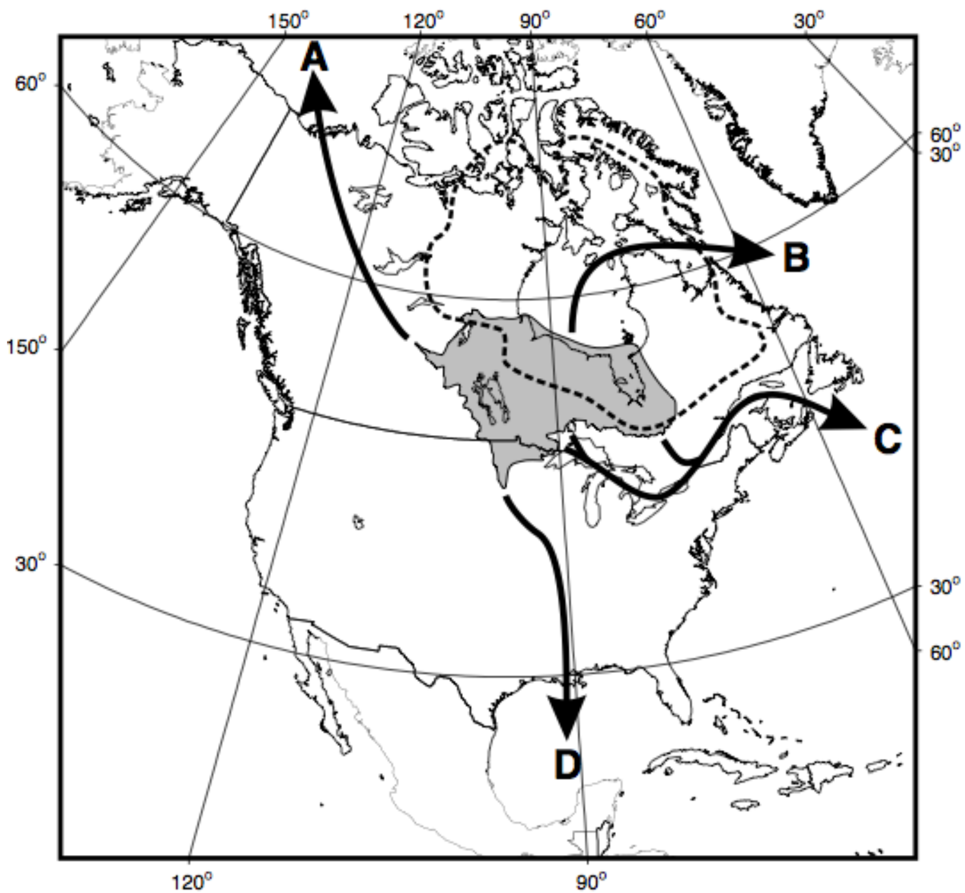
1. Dezadeash Lake
2. Prince George Basin
3. Lake Peace
4. Miette Lake
5. Lake Edmonton
6. Lake McConnell
7. Lake Tyrell
8. Lake Agassiz, Campbell phase
9. Lake Agassiz, Gimli phase
10. Lake Barlow-Ojibway

(from McPhail and Lindsey 1970)

Changes Associated with Glaciation

Many areas also became more interconnected with proglacial lakes
(i.e., lakes that form just beyond frontal margin of advancing or retreating glacier)

Proglacial lakes (9000 yrs. bp)



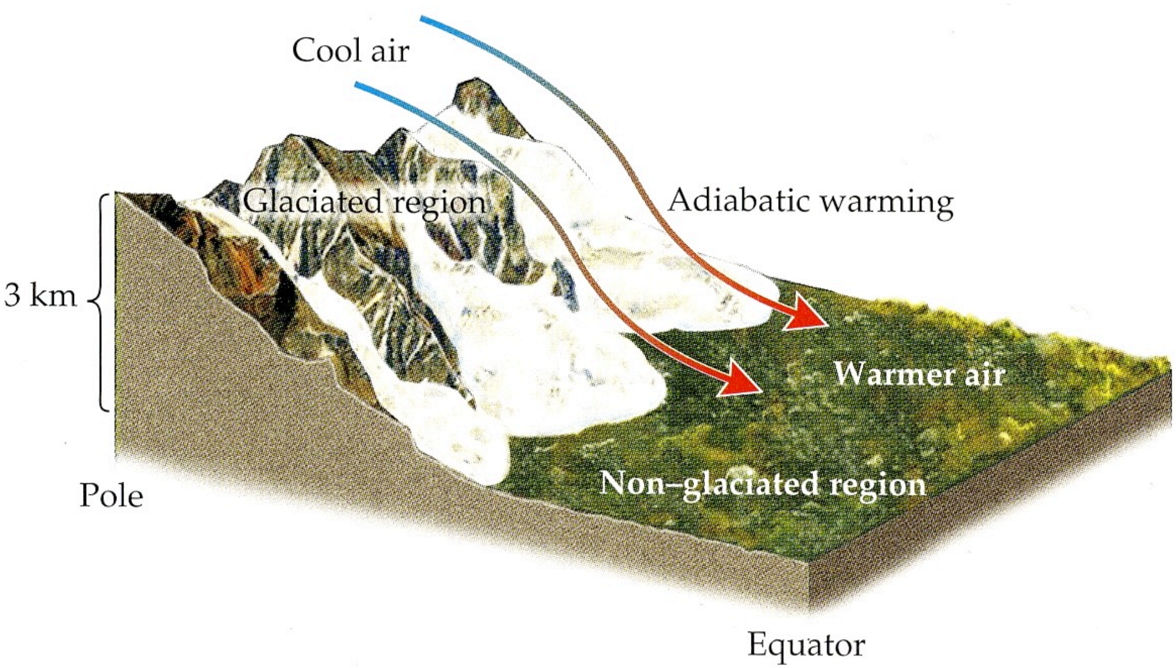
(from Teller *et al.* 2002)

Changes Associated with Glaciation

2) Shifts in Climate Regimes

Large changes in distribution of biomes, especially due to changes in precipitation.

In general climatic zones shifted toward the Equator during glacial periods, but patterns of shifts are complicated by configuration of land and large bodies of water and the glaciers themselves.



As cool air descends down the face of glaciers (2-3 km), the air warms as pressure increases (adiabatic heating).

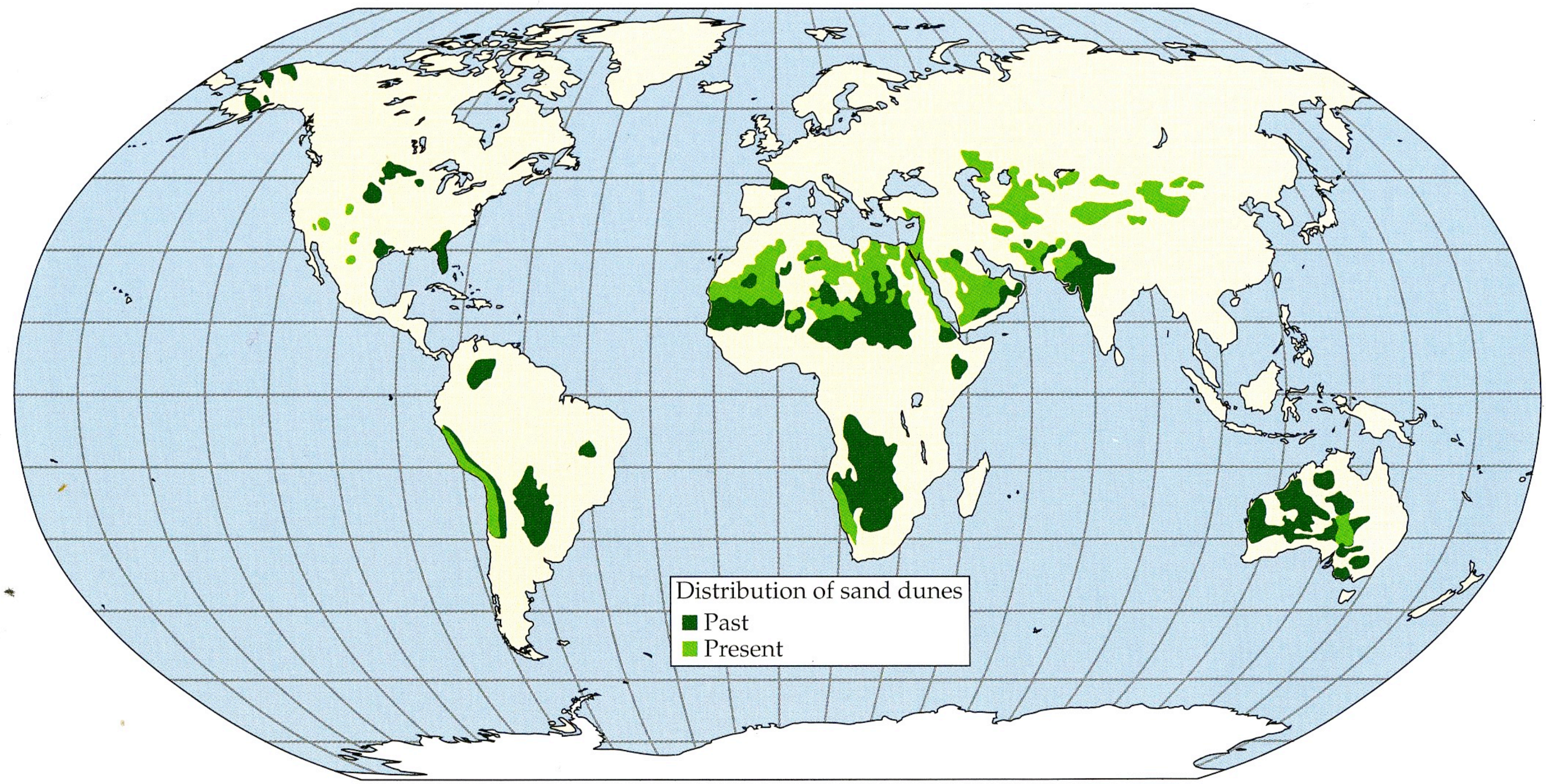
The warm dry air makes environments near glacial margins fairly moderate in temperature and relatively dry.

(from Lomolino *et al.* 2010)

Changes Associated with Glaciation

2) Shifts in Climate Regimes

General decrease in evaporative input of moisture into the air caused global aridification and expansion of deserts and other xeric ecosystems

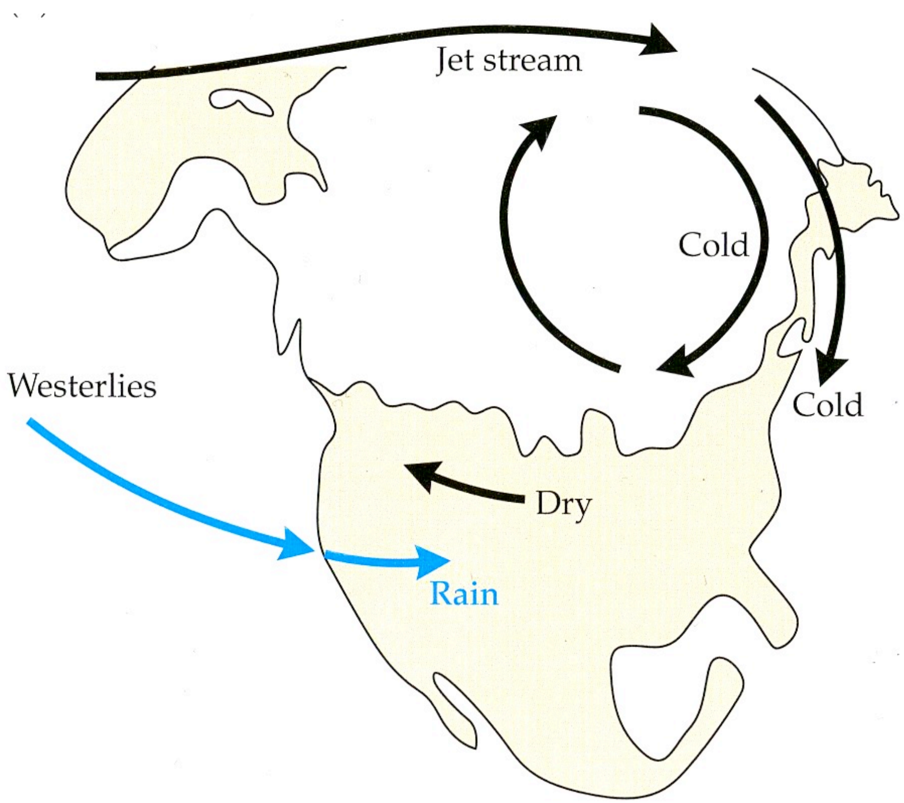


(from Lomolino *et al.* 2010)

Changes Associated with Glaciation

2) Shifts in Climate Regimes

North American ice sheets caused splitting of jet stream and southward deflection of westerlies



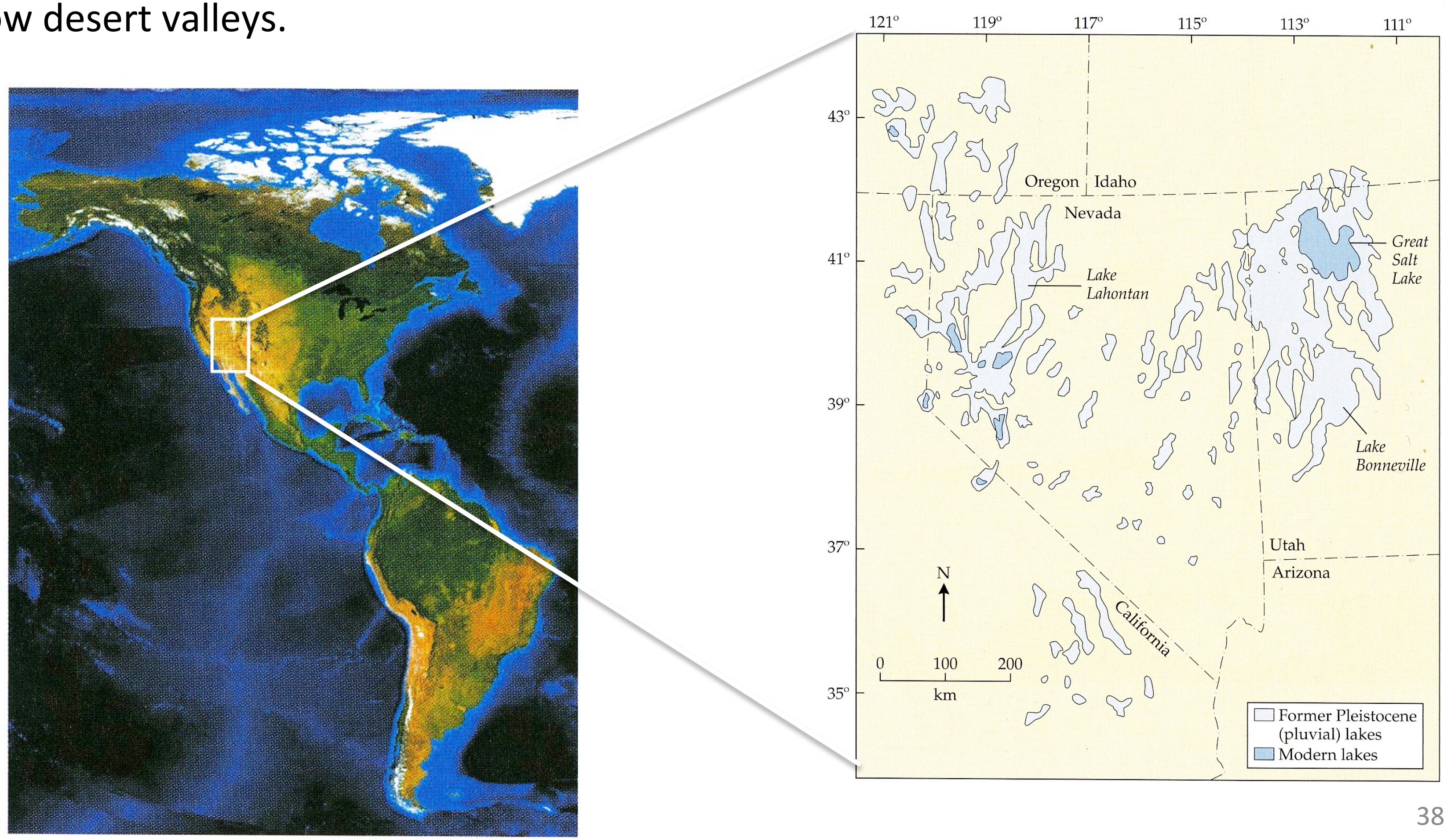
Resulted in dry easterly winds and desiccation of lakes near glaciers,
but saturated ocean air masses brought precipitation to American southwest and elevated water levels in lakes.

(from Lomolino *et al.* 2010)

Changes Associated with Glaciation

2) Shifts in Climate Regimes

Distribution of pluvial lakes in western NA during the LGM. Many arid regions of the continent experienced wetter, cooler climates, and lakes and marshes filled what are now desert valleys.



(from Lomolino *et al.* 2010)

Changes Associated with Glaciation

2) Shifts in Climate Regimes

Distribution of pluvial lakes in western NA during the LGM. Many arid regions of the continent experienced wetter, cooler climates, and lakes and marshes filled what are now desert valleys.

Lahontan cutthroat trout (*Oncorhynchus clarki*)

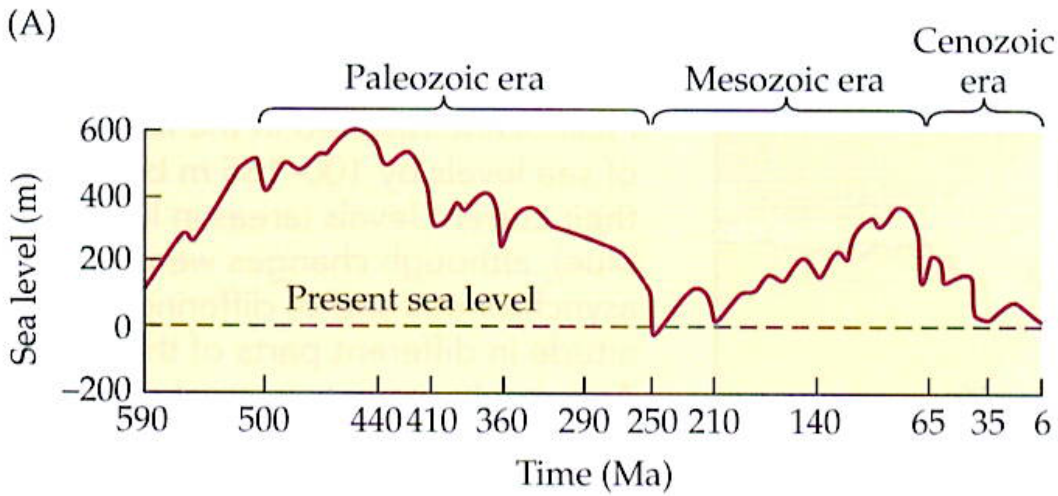
e.g., The Lahontan cutthroat trout evolved in the resulting huge *pluvial lakes* and fed on an endemic forage fish known as tui chub (*Gila bicolor*).

Tui chub (*Gila bicolor)*

Pyramid Lake

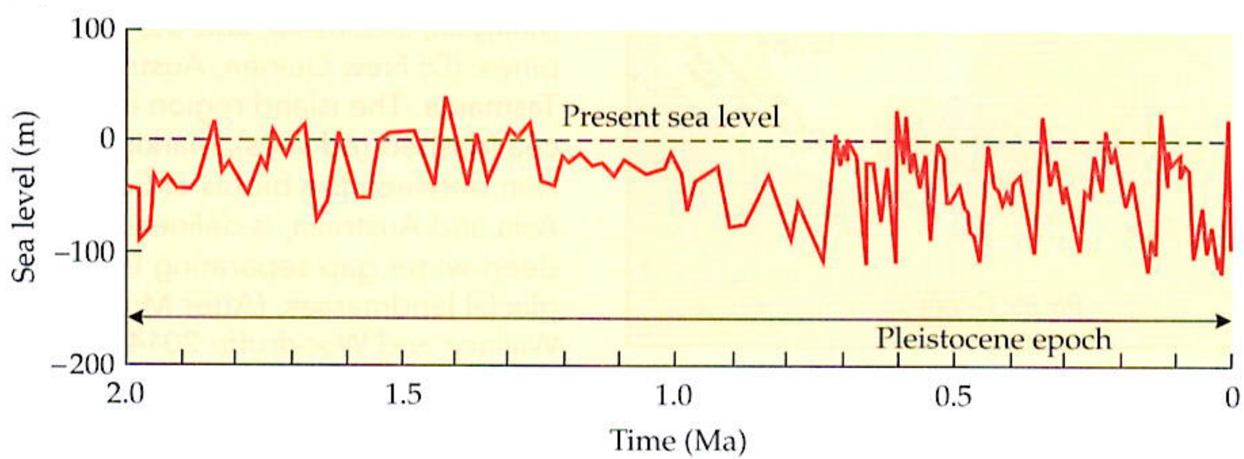
Changes Associated with Glaciation

3) Changes in sea level across timescales - Global changes that occur in all oceans at the same time are known as *eustatic* changes.



Eustatic sea levels were typically much higher than in recent past

Records through the Pleistocene show repeated and very rapid transitions in sea level between full glacial and interglacial conditions



(from Lomolino *et al.* 2017)

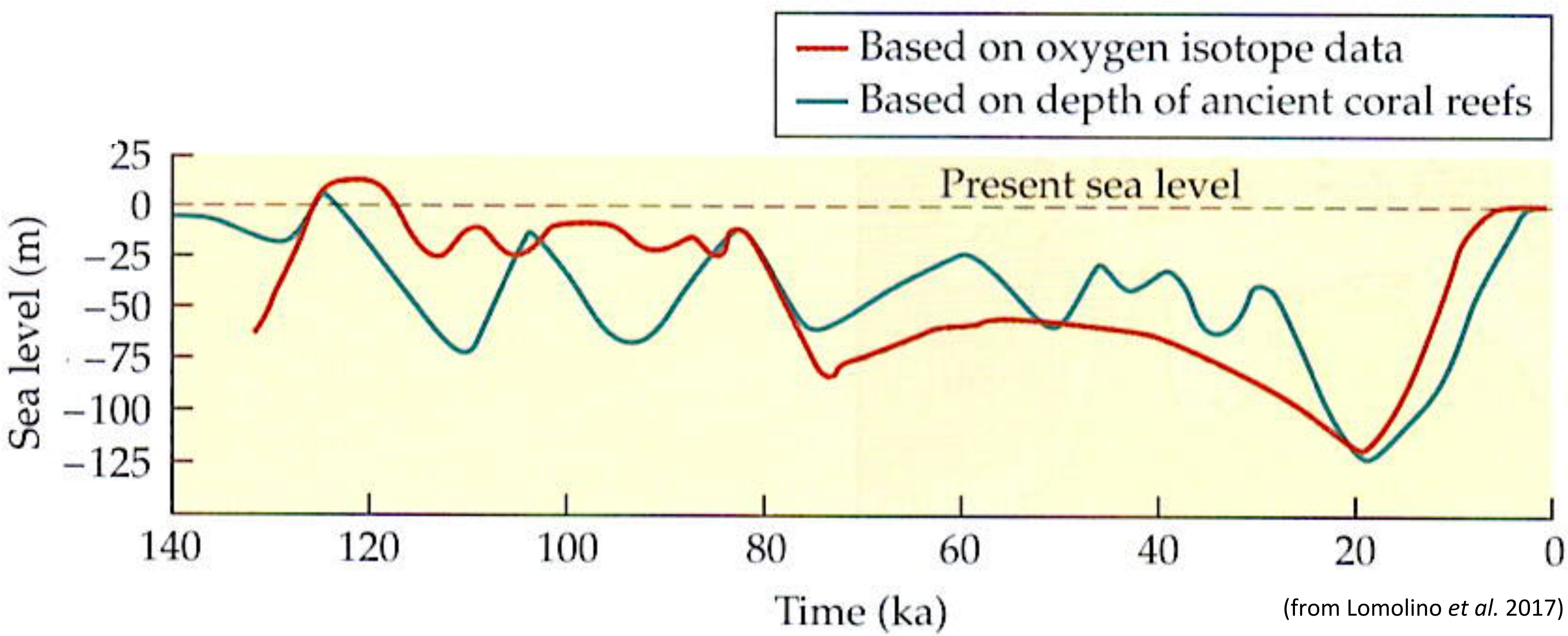
Changes Associated with Glaciation

3) Changes in sea level across timescales

Global changes were driven by the tremendous uptake of moisture as glaciers grew.

At the last glacial maximum (LGM) the total volume of ice was about 84 million cubic km! (It's currently 32 million cubic km.)

The average change was up to 130-135 m at the height of the last glaciation.



(from Lomolino *et al.* 2017)

Changes Associated with Glaciation

3) Changes in Sea Level

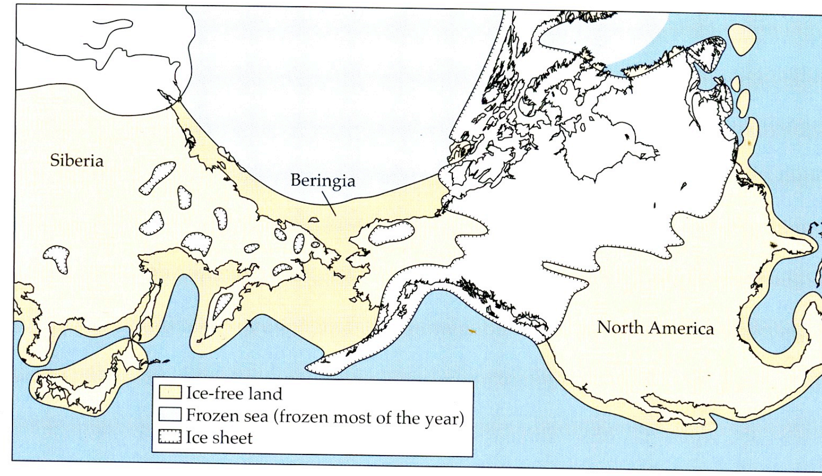
Drops in sea level caused the formation of land bridges between formally isolated land masses.

Beringia (top)

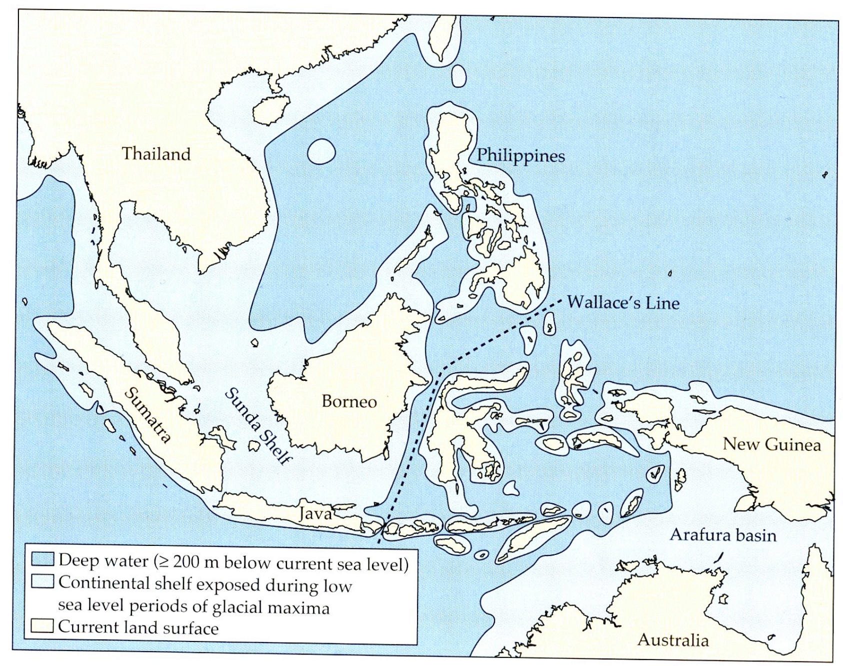
Southeast Asia and Australia (bottom)

Many terrestrial regions and associated biotas now isolated by oceanic barriers were connected

(though note the persistence of Wallace's line)



(B)



(from Lomolino *et al.* 2010)

Changes Associated with Glaciation

3) Changes in Sea Level – Local changes

In high northern latitudes, the mass of 2-3 km high glaciers caused a depression of land up to 300m in coastal areas

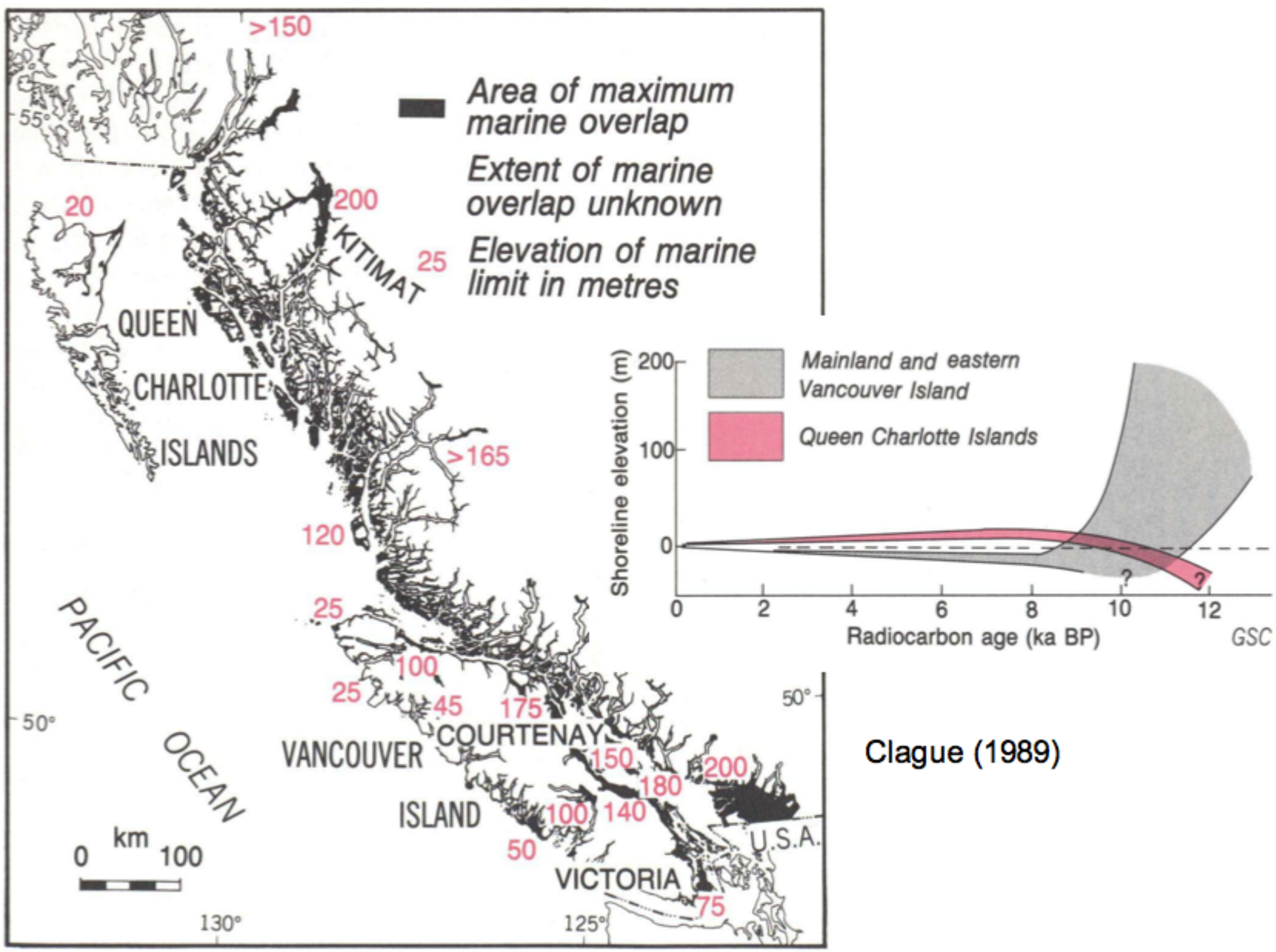
When ice sheets retreat, "rebound" of land takes much longer. This results in a massive inflow of marine waters that form wide expanses of shallow seas

Local changes in sea level, when global levels remain unchanged, are *isostatic* changes.

Changes Associated with Glaciation

3) Changes in Sea Level

In British Columbia, before *isostatic rebound* (c. 10 000 yrs. bp), parts of coastal BC were submerged > 200m below sea level.

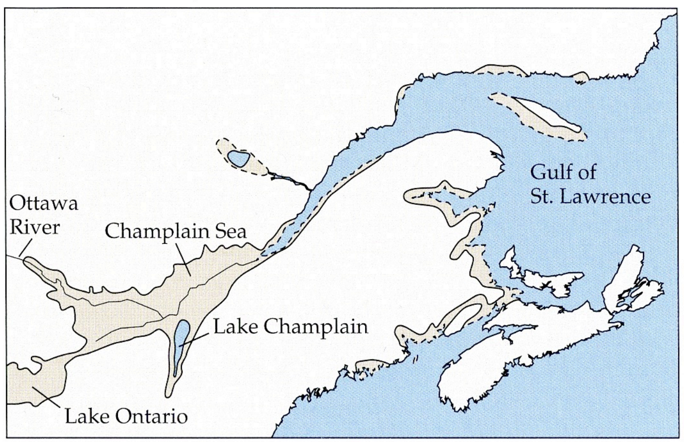


Clague (1989)

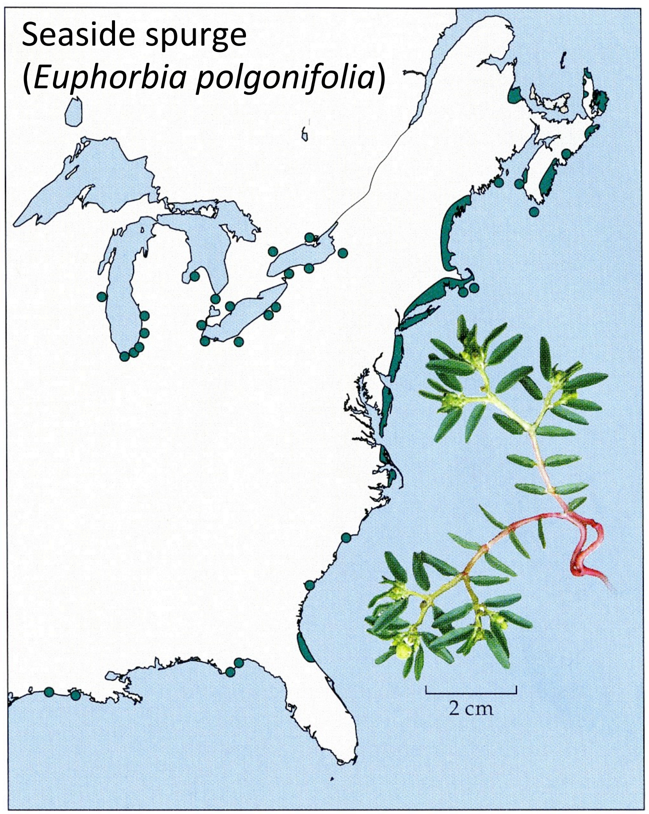
Changes Associated with Glaciation

3) Changes in Sea Level

In eastern North America, an influx of marine waters inundated the St. Lawrence River Valley such that large inland sea (The Champlain Sea) extended from the Atlantic coast to Lake Ontario.



Inland seas provided dispersal routes inland for marine, estuarine, and salt marsh species such as the "seaside" spurge (right), explaining current disjunct distribution.



(from Lomolino *et al.* 2010)