C. R. Biologies 338 (2015) 494–501

Contents lists available at ScienceDirect

Comptes Rendus Biologies

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Evolution/Évolution

The role of Pleistocene glaciations in shaping the evolution of polar and brown bears. Evidence from a critical review of mitochondrial and nuclear genome analyses

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ARTICLE INFO

Article history:
Received 13 March 2015
Accepted after revision 18 April 2015
Available online 27 May 2015

Keywords:
Ursidae
nuDNA
mtDNA
Genome
Molecular dating
Introgression
Quaternary
Climatic changes

ABSTRACT

In this report, I review recent molecular studies dealing with the origin and evolution of polar bears (*Ursus maritimus*), with special emphasis on their relationships with brown bears (*U. arctos*). On the basis of mitochondrial and nuclear data, different hypotheses have been proposed, including rapid morphological differentiation of *U. maritimus*, genetic introgression from *U. arctos* into *U. maritimus*, or inversely from *U. maritimus* into *U. arctos*, involving either male- or female-mediated gene flow. In the light of available molecular and eco-ethological data, I suggest, firstly, that all divergences among major clades of large bears can be linked to glacial periods, secondly, that polar bears diverged from brown bears before 530 thousand years ago (ka), during one of the three glacial marine isotope stages (MIS) 14, 15.2 or 16, and, thirdly, that genetic introgression had occurred from female polar bears into brown bear populations during at least two glacial periods, at 340 ± 10 ka (MIS 10) in western Europe, and at 155 ± 5 ka (MIS 6) on the ABC islands of southeastern Alaska, and probably also in Beringia and Ireland based on ancient DNA sequences.

1. Introduction

The polar bear (*Ursus maritimus*) lives in the Arctic Circle (Fig. 1), where its preferred habitat is the sea ice along the coast and on the islands [1]. Like other mammals of the region, such as the Arctic fox (*Vulpes lagopus*) and Arctic hare (*Lepus arcticus*), the polar bear developed adaptations specific to sea ice habitat that distinguish it from its congeners living in milder conditions, the brown bear (*U. arctos*) and black bear (*U. americanus*). A thick layer of fat covered with dense white fur ensures thermal insulation and a perfect camouflage. The ears are small, which reduce heat loss due to cold temperatures. But unlike most other Arctic taxa, which have a more compact body compared to closely related species of lower latitudes (Allen's rule), the polar bear is more slender in appearance, with a longer neck and a smaller head [2]. These physical characteristics have probably been selected because of its semi-aquatic life, its survival greatly depending on its ability to hunt both on land and in water.

The first molecular phylogenies, based on mitochondrial DNA (mtDNA) sequences of the cytochrome *b* gene, indicated that *U. maritimus* and *U. arctos* are closely related species [3,4], in agreement with the paleontological scenario of Kurtén [5] and subsequent phylogenetic studies of the family Ursidae based on nuclear data [6–8]. However, the mitochondrial paraphyly of *U. arctos*, due to the inclusive position of *U. maritimus* (Fig. 2), had suggested from the beginning that the mitochondrial phylogeny does not reflect the true species tree [3]. Indeed, the mtDNA sequences of brown bears of Alaska's ABC

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http://dx.doi.org/10.1016/j.crvi.2015.04.008
1631-0691/

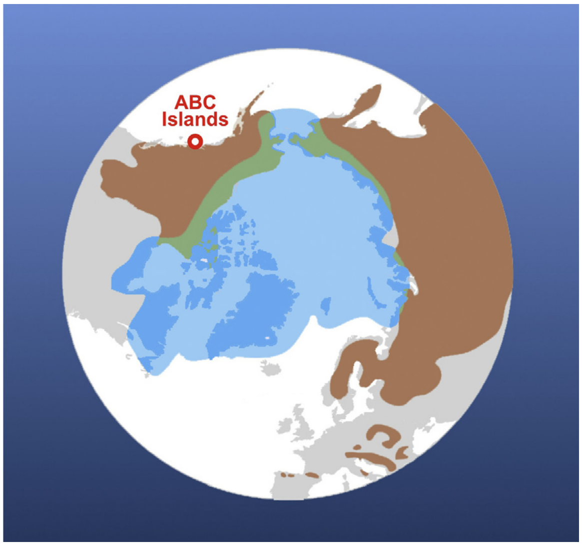

Fig. 1. Current geographical distributions of the polar bear (*Ursus maritimus*, in light blue) and brown bear (*Ursus arctos*, in brown). The map was modified from Liu et al. [20]. The position of ABC islands is indicated in red. Both species can meet occasionally on the lands of the Arctic Circle, in western North America and eastern Siberia (in green). For interpretation of the references to colour in this figure caption, please see the online version of this article.

Islands (Admiralty, Baranof and Chichagof; see Fig. 1) were found to be very similar to those of polar bears, but more distant from those of other brown bears [3,4,9,10].

In the past five years, multiple molecular studies have led to various interpretations of the evolutionary origin of the polar bear. In this paper, all recent hypotheses are reviewed, and a new scenario is proposed in the light of available molecular and eco-ethological data.

2. Molecular hypotheses proposed for the origin of the polar bear

2.1. A rapid and recent morphological differentiation of U. maritimus?

In 2010, Lindqvist et al. [9] sequenced the mitochondrial genome of the oldest polar bear fossil, which is a specimen from the Svalbard Archipelago in Norway, dated at 120 ± 10 ka. Using this ancient sequence, it was possible to date more precisely the timing of divergence events in the mitochondrial tree of bears [9–11] (Fig. 2, tree A): 566–490 ka for the most recent common ancestor (MRCA) of brown and polar bears, 336–310 ka for the MRCA of "clade P", which is composed of clade 1 (brown bears from western Europe) and clade 2 (polar bears and ABC islands brown bears); 162–152 ka for the MRCA of clade 2; 136–134 ka for the divergence between the fossil from Svalbard and modern polar bears (clade 2b); and 52–41 ka for the MRCA of extant polar bears. Based on these time estimates, Lindqvist et al. [9] concluded that there was a rapid and recent morphological differentiation of the polar bear, i.e., between 162–152 and 136–134 ka. Davison et al. [12] agreed with such a recent split between *U. maritimus* and *U. arctos*, and made the ad hoc assumption that the mitochondrial paraphyly of *U. arctos* is due to incomplete lineage sorting of mtDNA haplotypes. However, all these assumptions imply that the mitochondrial history was not too much distorted by possible hybridization events between polar and brown bears.

2.2. An Irish origin for the modern polar bear matriline?

In 2011, Edwards et al. [13] sequenced a D-loop fragment of ~ 300 bp in brown and polar bears from various geographic and temporal origins (38 ka to present). Their analyses suggested that the haplogroup of modern polar bears was more closely related to extinct Irish brown bears than to the polar bear fossil from Svalbard. Based on the apparent paraphyly of extinct Irish brown bears with respect to modern polar bears, Edwards et al. [13] concluded in favour of the hypothesis involving mitochondrial introgression from Irish brown bears into polar bears. However, this conclusion was poorly supported by the data, as most nodes of the tree, including the paraphyletic pattern, were found to be unstable (posterior probability < 0.85). Such a lack of robustness can be explained by three factors: (1) an alignment of very short DNA sequences (< 300 bp) containing only a few informative sites; (2) a large amount of missing data (the alignment of the 22 prehistoric sequences, accession numbers JF900154–JF900175, contains 32% of missing nucleotides on the total length of 295 bp); (3) a significant proportion of exclusive autapomorphies, which might suggest sequencing errors in the dataset.

Apparently, the only robust node was the one grouping modern and extinct polar bears, modern ABC islands brown bears, and extinct Irish brown bears.

2.3. Are polar bears an old and distinct bear lineage, which has been recently introgressed by ABC islands brown bears?

In 2012, Hailer et al. [14] sequenced 14 independent introns (representing an alignment of 9116 nucleotides) in 45 individuals of polar, brown, and black bears. They found that brown bears constitute a monophyletic group that separated from polar bears at 603 ka (Fig. 2, tree B). This study was strongly criticized by Nakagome et al. [15,16], who revealed that, of the 13 loci analysed (one locus, LRGUK, was excluded due to high frequencies of recombinants), only one supported the monophyly of brown bears, four did not provide any resolution, and eight were in agreement with the paraphyly of brown bears. To this, Hailer et al. [17] responded that the analyses of Nakagome et al. [15,16] did not take into account the effect of incomplete lineage sorting, as well as the possible impact of gene flow (introgression) between polar and brown bears.

Miller et al. [11] performed deep sequencing of the nuclear genome for five bears, including one polar bear, three brown bears from Alaska (two from ABC islands and one from Kenai Peninsula), and one black bear. They also sequenced about 12 million nuclear genome SNP markers in 22 additional modern polar bears and the fossil from Svalbard. The results supported the monophyly of both *U. maritimus* and *U. arctos*; the Svalbard's fossil being