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Review

The progressive evolution of cold-adapted species

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The evolution of cold-adapted terrestrial species underwent two main phases. First, the genera of cold-adapted taxa appeared during the Late Pliocene to Early Pleistocene. The modern day and Late Pleistocene cold-adapted species then arose during and after the Middle Pleistocene Transition. These species evolved through one or more of the following processes: out of the temperate zone, evolving *in situ*, or through montane preadaptation. Palaeogenetic studies are greatly contributing to our understanding of the timings and modes of evolution of cold-adapted species as well as when their specialised traits evolved. The evolution of polar plant and beetle species is claimed to show greater stasis than that of vertebrates, but could instead reflect morphological conservatism that can be tested with palaeogenetics.

Highlights

Cold-adapted vertebrate taxa underwent different phases of evolution during the last 3 million years. The first is the early appearance of some of the genera in the Pliocene to Early Pleistocene. There followed the appearance of many of the cold-adapted species after the time that glaciations more than doubled in length during the Middle Pleistocene. Since then there has also been climate-related species formation due to endemism through isolation, and when plant population range changes led to hybrid species.

Three different modes have been proposed for the evolution of cold-adapted taxa: the 'out of the temperate zone' hypothesis, the 'evolving *in situ*' hypothesis, and the 'montane preadaptation' hypothesis, all of which may have happened in different taxa at different times.

Palaeogenetic evidence has improved the precision of the timing of species origination as well as when and how species acquired their adaptations to the cold.

The difference in the rates of evolution between vertebrates and other taxa (plants and beetles) may be overstated, and the absence of evidence may be masking similar evolutionary trends in rates and modes of evolution.

The cold as a novel environment

The cold-adapted plant and animal species found in polar and subpolar regions of the northern and southern hemispheres are amongst the species most vulnerable to ongoing climatic warming [1–3]. If we are to best understand the vulnerabilities of these cold-adapted organisms it is important to investigate their evolutionary origins and histories.

Cold-adapted terrestrial plant and animal taxa can be considered as organisms that expand their distributions during cold episodes such as the **glacial** (see Glossary) phases of **Milankovitch cycles** [4]. These taxa, by contrast, contract into refugia during warm **interglacials** [5]. However, because species are individualistic, the different cold-adapted taxa cannot be described as having identical adaptations, and some contract to higher latitudes and/or higher altitudes while others, the continental-adapted taxa, contract towards the centre of continents [4]. An alternative definition of cold-adapted taxa is based on their specific phenotypic traits. These include anatomical, physiological, and behavioural characteristics related to the cold itself, such as increased fat storage, increased thermal insulation, and more efficient oxygen transport, or other factors related to features of cold environments such as white hair or plumage [6]. Apart from the extinct taxa whose remains have been found in the permafrost [7], until recently it was usually only the living cold-adapted species whose phenotypic traits could be considered in terms of their relationship to the cold. However, with the advent of **palaeogenetics**, which uses **ancient DNA (aDNA)** to examine functional pathways encoded in animal and plant genomes, it has become possible to consider the evolution of cold adaptations through time in living and extinct taxa [8,9].

However, cold-adapted animal and plant species are a relatively recent phenomenon during the **Cenozoic**. This suggests that these taxa are likely to have evolved from more warm-adapted organisms. The likely timing of this evolution is in part limited by the timing of the initiation of permanent ice in the Arctic, which began in the late Miocene (ca. 10 million years ago, Ma) [10]. This process was reinforced during the **Pleistocene** when land ice became especially prevalent during the cold glacials of the **Quaternary** [11].

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The terrestrial biomes that we associate today with cold climates are found towards the poles and at relatively high altitudes, namely the Tundra and the boreal Taiga forest. Some components of tundra are thought to have been present during the **Pliocene** [12], although the tundra biome was not yet in its present form [13]. During the Middle to Late Pleistocene glaciations, these cold biomes expanded from the poles and together with the dry continental grasslands (steppe) that expanded towards the oceanic areas they formed a largely extinct biome: the Steppe Tundra (mammoth steppe) of the **Palaearctic** and **Nearctic** [14].

Herein we review and compare the palaeontological and palaeogenetic evidence for how and when cold-adapted terrestrial taxa evolved. This review concentrates on northern hemisphere terrestrial vertebrates (mammals and one bird genus) that constitute modern boreal and tundra species as well as two Steppe Tundra species of the Pleistocene glaciations. Finally, we compare the vertebrate record with records of plants and beetles, which are thought to have different tempos and modes of evolution to cold adaptation.

The tempo of cold adaptation evolution in terrestrial vertebrates

The evolution of cold-adapted vertebrate species appears to take place over a protracted period, possibly concentrated during two main phases (Table 1, Figure 1). First, the evolution of some of the earliest members of the genera that would evolve into cold-adapted species took place in the Late Pliocene to Early Pleistocene when the Milankovitch cycles caused significant ice sheet expansions during glacial phases [11]. This time period included the earliest species of mammalian genera – such as mammoths (*Mammuthus* [15]), woolly rhinoceros (*Coelodonta* [16]), reindeer (*Rangifer* [17]), wolverines (*Gulo* [18]), and true lemmings (*Lemmus* [19]) – that either are associated with the tundra and/or boreal forest biomes of today or are extinct taxa that were adapted to the Steppe Tundra of the Late Pleistocene. This timing might suggest that the tundra biome first appeared in the Early Pleistocene and was a prerequisite for some faunal components of the tundra to become cold-adapted [15]. However, there is evidence that the tundra may not have been in its present form at this time [13]. Furthermore, the Steppe Tundra may have been in existence by the Early Pleistocene, although potentially at a more southerly latitude [20], and that the grass-based ecosystems became dominant during the Middle Pleistocene [21].

Towards the end of the Early Pleistocene, the intensity and duration of glacials increased relative to interglacials during a period known as the Middle Pleistocene Transition (MPT), ~1.25 Ma to 700 thousand years ago, ka (Figure 1) [10,22,23]. The latter part of the MPT (~920–640 ka) was when many of the cold-adapted vertebrate species that comprised the Steppe Tundra fauna first appear in the fossil record (Figure 1, Table 1) [15,17]. This might suggest a causal role for longer glacial cycles in the evolution of many cold-adapted species. We note that the earliest fossil occurrence of cold-adapted vertebrate species is generally in the North and East of the Palaearctic, and that their occurrence in Europe is later in the Middle Pleistocene (Table 1). The MPT is also the time during which the precursor of the Steppe Tundra fauna is first seen [17], although a recent claim for Early Pleistocene Steppe Tundra in China has been made [20].

The other general pattern is that if a direct ancestral species has been identified in the fossil record it is likely to have had a more ambiguous adaptation to the cold. This is especially manifested by taxa such as the mammoth occurring in both warm interglacial and cold glacial stages during the Middle Pleistocene of Europe [24]. Furthermore, the oldest members of some cold-adapted genera – such as the mammoth *Mammuthus rumanus*, wolverine *Gulo sudorus*, bear *Ursus arctos*, and ptarmigan *Lagopus* sp. – are found in the south during the Pliocene or Early Pleistocene (Table 1) [15,18,25,26]. In other cases, it is the immediate ancestors to the cold-adapted genera that originated in the south, such as *Plioctomys* (ancestral to the true lemmings) and *Praeovibos*

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(ancestral to the muskox) [17,19,27]. In addition to their southern range, these precursors to cold-adapted taxa are often found in deposits that include non-analogue associations with temperate and cold-adapted taxa [28]. However, this is not the case for the reindeer genus, which first appears in the Late Pliocene–Early Pleistocene and is associated with boreal ecological elements in the far north [13,17]. The collared lemming is similar, as its immediate precursor *Predicrostonyx* first appears in Alaska in the Early Pleistocene in what looks like a modern tundra [29]. The arctic fox precursor is hard to document with the fossil record due to difficulties in recognising its ancestors, although the earliest claimed ancestor, *Vulpes qiuzhudingi*, is from the Pliocene of Tibet (but see later) [30]. Finally, the woolly rhinoceros genus first appears in the Tibetan Plateau during the Pliocene which is at a relatively low latitude although at high altitude (Figure 1, Table 1) [16].

Theories for the origin of cold-adapted species

Three major hypotheses have been proposed for the evolution of cold-adapted species. These are not necessarily mutually exclusive and may be taking place simultaneously according to biogeographic circumstances and the nature of the taxa involved. Indeed, it is not always clear how distinct the hypotheses are (Table 2).

The 'out of the temperate zone' hypothesis

This posits that temperate species, potentially with preadaptations, expanded northwards during an interglacial and that part of the expanded population became exposed to cold climates, leading to adaptation to the cold conditions [4]. The most often cited example of this process is the polar bear that split from the brown bear, its phylogenetic ancestor, during the Middle Pleistocene [31,32], and that this may have happened in a northern area, perhaps in refugia such as Beringia or in **cryptic refugia**, so that brown bears could be exposed to the cold, thereby providing a stepping-stone to cold adaptation [4,33]. Sher *et al.* [34] proposed a similar scenario for the woolly mammoth, whereby an allopatric population was isolated in the cold xeric grasslands of Beringia from where it spread to occupy its eventual total range, including North America and Europe. These species would have switched from expanding and contracting from the warm in the south to doing so from the cold in the north [35]. The adoption of a new refugium would therefore lead to allopatric speciation.

The evolution of cold-adapted taxa from more temperate ones is similar to the idea that temperate organisms evolved from tropical ones, known as the 'out of the tropics' (OTT) hypothesis which is used to explain the latitudinal diversity gradient [36,37]. The diversity gradient also exists between the temperate and cold biotas today [38,39], so similar processes may have taken place.

The 'evolving *in situ*' hypothesis

Kahlke [17] made a strong case that the evolution of some modern circumpolar tundra belt mammals evolved in the arctic region *in situ* as the climate cooled, rather than after expanding into the cold environment. Species such as the reindeer, muskox, and arctic fox are thought to have evolved in the northern tundra. This hypothesis is consistent with records in north Greenland of cold taxa such as reindeer at the onset of the Late Pliocene–Quaternary cooling [13]. This could signify that these taxa evolved *in situ* as cold climates increased in the Arctic region, in a manner similar to what has been suggested for many plants (see later) (e.g., [40]).

The 'montane preadaptation' hypothesis

This hypothesis suggests that organisms acquired cold adaptations in the high-altitude mountainous areas to the south during the Cenozoic, and subsequently expanded to lower altitudes and then across long distances to northern latitudes when climates cooled. This hypothesis

Glossary

Ancient DNA (aDNA): DNA that is in a degraded state and recovered from ancient organic remains.

Cenozoic: the current Era that includes the Palaeocene to the present day (66 to 0 Ma).

Cryptic refugia: areas often determined by topography where organisms survived in a scattered distribution beyond their main range during adverse climatic conditions.

Endemism: characterises a species that is found only in a solitary defined location, such as on an island or in a country.

Glacials: episodes when the Earth had large ice sheets driven by the Milankovitch cycles.

Interglacials: times without large ice sheets driven by the Milankovitch cycles.

Milankovitch cycles: the long-term climatic cycles caused by a combination of the variations of the Earth's orbit and position relative to the Sun.

Nearctic: the biogeographic realm that includes Greenland and North America as far south as Mexico.

Neogene: the Period that includes the Miocene and Pliocene that lasted from 23 to 2.6 Ma.

Palaearctic: the biogeographic realm that includes Europe, northern Africa, and Asia north of southeast Asia and the Indian subcontinent.

Palaeogenetics: the scientific field of recovering, analysing, and interpreting ancient DNA data.

Pleistocene: the major Epoch of the Quaternary characterised by glacial–interglacial cycles, and lasting from 2.6 Ma until 11.7 ka.

Pliocene: the last Epoch of the Neogene that lasted from 5.3 to 2.6 Ma.

Quaternary: the current Period that includes the Pleistocene to the present day (2.6 to 0 Ma).

Sedimentary ancient DNA (sedaDNA): ancient DNA that is recovered from sediments and other environmental contexts.

Table 1. First occurrence dates of fossils of cold-adapted terrestrial vertebrate species in Europe and globally, and the oldest global records of their genera

Species	Oldest occurrence of the species in Europe	Oldest occurrence of the species globally	Oldest occurrence of the genus
Woolly mammoth (*Mammuthus primigenius*)	*M. primigenius*; *c.* 190 ka; Europe [24]	*M. primigenius*; *c.* 700 ka; Siberia [15]	Early mammoth (*M. rumanus*); 3.5–2.5 Ma; first occurrence in Eurasia – Europe and China [15]
Woolly rhinoceros (*Coelodonta antiquitatis*)	*C. antiquitatis praecursor*; *c.* 270 ka; La Fage, France [96]	*C. antiquitatis praecursor*; *c.* 270 ka; La Fage, France [96]	Tibetan woolly rhinoceros (*Coelodonta thibetana*); *c.* 3.7 Ma; Tibetan Plateau [16]
Reindeer (*Rangifer tarandus*)	*R. tarandus stadelmanni*; *c.* 640–620 ka; Süssenborn, Germany [17]	*Rangifer* ex gr. *tarandus*; 1.2–0.6 Ma; Western Beringia [17]	Early reindeer (*Rangifer* sp.); Cape Deceit, Alaska [17]; *c.* 1.5–1.4 Ma [8,17,97]
Muskox (*Ovibos moschatus*)	*O. moschatus suessenbornensis*; *c.* 640–620 ka; Süssenborn, Germany [17]	*O. moschatus suessenbornensis*; *c.* 640–620 ka; Süssenborn [17]	No ancestral species in *Ovibos* but closely related early muskox *Praeovibos*. *P. priscus*; 900–400 ka; Palaearctic incl. Beringia. *P. beringensis*; 1.2–0.8 Ma; Beringia [17]
Polar bear (*Ursus maritimus*)	*U. maritimus*; 130–110 ka; Svalbard [98]	*U. maritimus*; 130–110 ka; Svalbard [98]	Oldest brown bear *Ursus arctos*, sites such as Loc. 9 and 13 Zhoukoudian, 620 ka [99]
Wolverine (*Gulo gulo*)	*Gulo gulo*; 1.7–1.3 Ma; e.g., Zabia Cave, Poland [100]	*Gulo gulo*; 1.7–1.3 Ma; e.g., Zabia Cave, Poland [100]	Early wolverine (*Gulo sudorus*) the Gray Fossil Site, Tennessee, 4.9–4.5 Ma [18]
Arctic fox (*Vulpes lagopus*)	*V. lagopus*; 400 ka; Pan European [101]	*Vulpes* aff. *Alopex* sp.; 700 ka; NE Siberia [17]	Early fox (*V. praeglacialis*) (not thought ancestral); various European sites 1.2–0.4 Ma [17]; *Vulpes qiuzhudingi*; Tibet, 5.08–3.60 Ma [30]
True lemmings (*Lemmus* spp.)	*L. lemmus*; c. 100–32 ka identified using aDNA [50]; no early records of other *Lemmus* species	No early records of other actual *Lemmus* species	Early true lemming (*L. sheri*); Eurasia; 1.65 and 0.45 Ma [19]. There are also records of unspecified *Lemmus* sp. from Cape Deceit at 1.5–1.4 Ma [8,97]
Arctic collared lemming (*Dicrostonyx torquatus*)	c. 250 ka; Ariendorf 1, Germany and Rybinsk, Russia [102]	c. 250 ka; Ariendorf 1, Germany and Rybinsk, Russia [102]	No ancestral species in *Dicrostonyx* but closely related ancestral collared lemming (*Predicrostonyx*). *P. hopkinsi*; Cape Deceit, Alaska; 1.5–1.4 Ma [8,97]. *Dicrostonyx* sp. Kärlich, Germany; *c.* 650 ka [103,104]
Willow ptarmigan (*Lagopus lagopus*)	*c.* 750 ka, Betfia 5, Romania and Kozi Grzbiet, Poland[25]	c. 750 ka, Betfia 5, Romania and Kozi Grzbiet, Poland[25]	Ptarmigan (*Lagopus* sp.), Węże, Poland and Csarnota 2, Hungary, 4.2–3.2 Ma [25]. *L. atavus*, Rebiolice Krolewskie, Poland and Beremend 5, Hungary, 3.2–2.5 Ma [25]
Rock ptarmigan (*Lagopus mutus*)	300–243 ka; La Fage, France [25]	300–243 ka; La Fage, France [25]	Ptarmigan (*Lagopus* sp.), Węże, Poland and Csarnota 2, Hungary, 4.2–3.2 Ma [25]. *L. atavus*, Rebiolice Krolewskie, Poland and Beremend 5, Hungary, 3.2–2.5 Ma [25]

was first applied to the evolution of arctic plants, many of which are thought to have evolved from montane ancestors to the south during the **Neogene** [41–44].

More recently, the hypothesis has been applied to how animals evolved to be cold-adapted as the 'third pole' or 'out of Tibet' hypothesis. This states that species such as the arctic fox and woolly rhinoceros became adapted to cold environments at lower latitudes but higher altitudes, such as in the Himalayas or the Tibetan Plateau, and subsequently moved north [16,30,45]. Wang *et al.* [45] suggested that the woolly rhinoceros evolved in the Tibetan Plateau in the cold, high-altitude grasslands which acted as a 'habituation ground' (or stepping-stone), allowing preadaptation during the Pliocene to the ensuing cold of the Pleistocene.

The molecular evidence in vertebrates

Ancient DNA analysis has revolutionised mammalian palaeontology by providing taxonomic accuracy and precision that was not previously available [46]. Included in this have been the

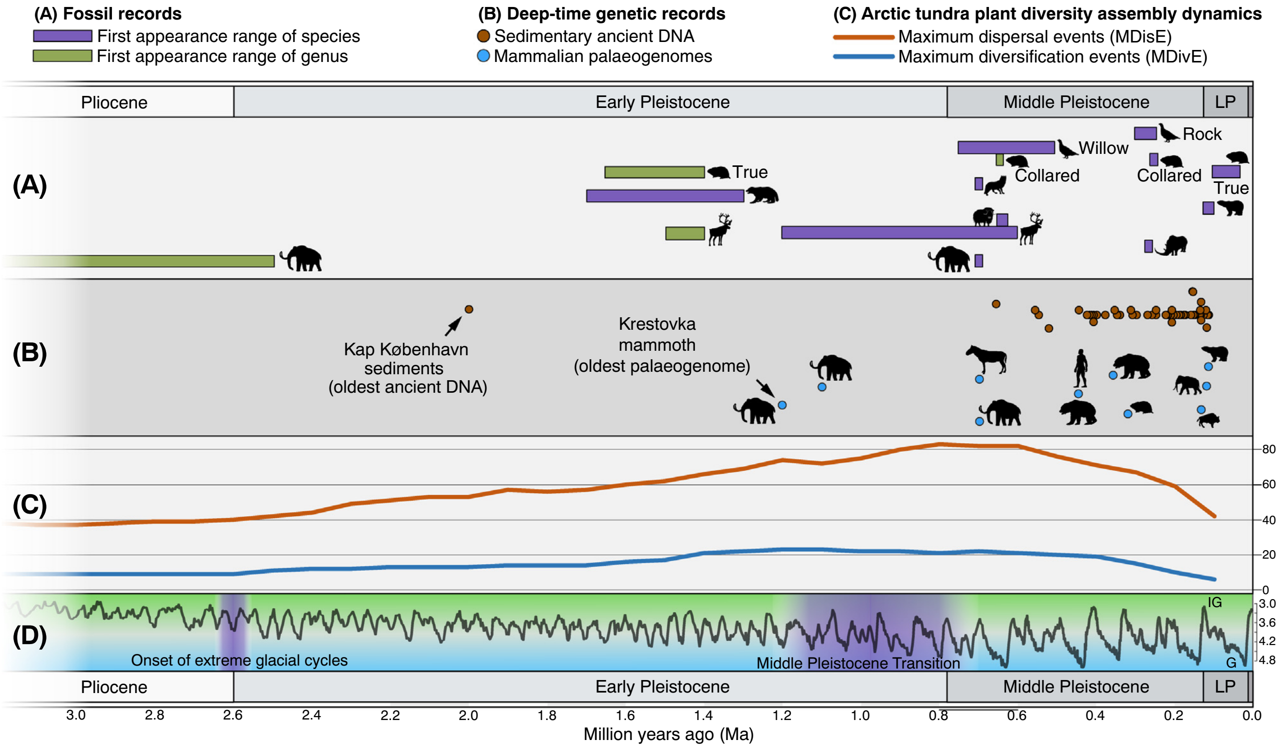

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Figure 1. Timeline for the evolution of cold-adapted vertebrate and plant taxa. (A) The first occurrences of cold-adapted species and genera in the vertebrate fossil record. The first appearance range of the genus for seven species is older than 3.0 Ma (see also Table 1). (B) The availability of Early and Middle Pleistocene ancient DNA records (adapted with permission from [105], with data from [106,107]) that could be used to test the three hypotheses for the evolution of cold-adapted species. (C) Plant phylogenetic records document the maximum counts of arctic plant species arrival or *in situ* speciation events in 100 ka time bins (replotted from [80]). (D) Climatic cycles alternated between warm interglacials (IG, green shading) and cold glacials (G, blue shading) (adapted from [105] with LR04 oxygen isotope curve data from [108]). Purple shading denotes the timing of major climatic transitions associated with the evolution of cold adaptation. Animal silhouettes are from phylopic.org and represent taxa listed in the same order as Table 1 (from mammoth to rock ptarmigan) in panel A and deep-time mammalian palaeogenomes in panel B (see also [105] and references therein).

recognition of species that, in some cases, were entirely cryptic, such as the discovery of the Denisovan hominins in southern Siberia [47] and the Krestovka mammoth lineage in northeastern Siberia [8]. There has also been confirmation that morphologically disparate taxa may be more closely related than their anatomy might suggest, such as the ancestor of the muskox, *Praeovibos*, whose mitochondrial DNA sequences fall within the diversity of the modern *Ovibos* species [48]. In addition, this increased precision has led to the identification of subspecific populations that were not visible in the morphology of fossils, some of which have been lost in the Late Pleistocene (e.g., muskox [49], true lemming [50], and collared lemming [51–53]). By contrast, the

Table 2. The dominant hypotheses for the evolution of cold-adapted species with possible examples of where they took place

Hypothesis	Description	Examples	Refs
Out of the temperate zone	Temperate species expand towards the pole in an interglacial, and the expanded population becomes exposed to cold climates and evolves cold adaptation	Brown bear, Woolly mammoth	[4,31–34]
Evolving *in situ*	Polar species evolved in the Arctic region *in situ* as global climates cooled after the Late Pliocene	Reindeer, Various arctic plants	[13,17,40]
Montane preadaptation (also known as 'third pole' or 'out of Tibet')	Cold adaptations are acquired by species in mountainous areas to the south of the polar region during the Cenozoic before expanding to lower altitudes and northwards as climates cooled	Arctic plants, Woolly rhinoceros, Arctic fox	[16,30,41–43,45]

two European ptarmigan species exhibit continuity without loss [54]. This has led to revisions of accepted phylogeographic histories, including that of the brown bear, which represents one of the three paradigms of European postglacial colonisation patterns [55–57]. This increased precision also revealed a greater level of dynamism in past populations than was previously known, which appears to have been caused by climate-driven vegetation change [51].

One of the most important areas in which aDNA research has contributed is the confirmation of the ages of the most recent common ancestors of living and extinct species. The genetic divergence between the woolly mammoth and the Asian elephant, the closest living relative, has been estimated at *c.* 2.5 Ma [58], although a 5 Ma date is more likely based on the fossil record [15,59], and the former date may reflect post-speciation gene flow between the two taxa after they both left Africa. Other taxa such as the woolly rhinoceros lineage tell a similar story, with the split from their extinct closest fossil sibling taxon, *Stephanorhinus*, occurring at 5.5 Ma based on whole-genome aDNA data [60]. A Middle Pleistocene divergence of the polar bear from its sibling species, the brown bear, is generally accepted [61] with an aDNA-based best estimate in the Middle Pleistocene [32], although much older and younger estimates have also been made [62,63]. The divergence between the brown bear and the polar bear is likely complicated by the apparent recurrent introgressive events between the two species driven by cyclical climate and range changes [64]. It is clear from genetic data [65] that the sibling taxa to the arctic fox are the swift fox (*Vulpes velox*) and kit fox (*Vulpes macrotis*) found south of the Arctic in North America. Although no molecular divergence estimate has been attempted, a similar sequence divergence, as observed in the aforementioned bears, might suggest a split during the Middle Pleistocene or slightly earlier [66]. This means that the hypercarnivorous nature of the arctic fox is a derived character that is likely a response to cold climates where a more omnivorous diet is less available. Therefore, the morphological similarity of the Pliocene *V. qiuzhudingi* from Tibet is probably convergent with the arctic fox rather than ancestral to it. The collared lemmings and true lemmings have both undergone species-level radiations as well as evolving cold adaptation (Box 1). Both genera have a number of species that appear to have arisen through a series of splits that are likely to have had allopatric origins in the Arctic due to climate-driven circumstances from the Middle Pleistocene onwards [53,67]. True lemmings are distinguished by having what may be the youngest speciation event of all during the last 100 ka, leading to the Norway lemming [50].

Recent whole nuclear genome analyses have been conducted on specimens dated to more than one million years old [8]. This includes a specimen on the woolly mammoth lineage and another divergent lineage that contributed to the hybrid North American Columbian mammoth (*M. columbi*). The woolly mammoth lineage was morphologically similar to its steppe mammoth ancestor (*M. trogontherii*) and had already acquired most of the protein-coding changes thought to be associated with cold adaptation by 1 Ma [8]. The woolly mammoth lineage continued to evolve after 700 ka with changes to other traits such as those related to hair and skin, fat storage, metabolism, and decreased ear size [9].

Other taxonomic groups

Many other groups either have a limited fossil record, such as soft-bodied organisms that are often not preserved over geological time, or do not have lineages of species documenting their evolution. For the latter category, it is important to examine the similarities and differences between vertebrates and such groups – with the best documented being plants and beetles – to better understand the ecological circumstances of the evolution of cold-adapted species.

Plants

Plants adapted to cold environments are an important precondition for arctic food webs. There are 2218 arctic vascular plant species [68,69], most of which are also found further south, with

Box 1. Lemming radiations detected by ancient DNA

Genetic data for the true lemmings suggest that modern species of *Lemmus* diverged *c.* 2.1 Ma, when the Palaearctic and Nearctic species were separated [67]. Within the Palaearctic *Lemmus* species, there were two phases of diversification, with the western and eastern Palaearctic clades splitting at c. 1 Ma and a second division occurring between Eastern Palaearctic clade of Siberian lemming (*L. sibiricus*) and Amur lemming (*L. amurensis*) at *c.* 680 ka. Meanwhile the split between the Norway lemming (*L. lemmus*) (Figure I) and the western clade of *L. sibiricus* was thought to have taken place later, around 310 ka [67] or before the Last Glacial Maximum ~100–32 ka [50]. The latter would make the Norway lemming one of the youngest mammalian species alive today.

Based on mitogenomic data, the estimated divergence timing of the basal split of the three modern collared lemming species, with arctic collared lemming (*Dicrostonyx torquatus*) on the one hand and the North American lineages – northern collared lemming (*D. groenlandicus*) and Ungava collared lemming (*D. hudsonius*) – on the other, dates to >200 ka [53]. The subsequent split between the North American collared lemmings was early in the last glacial (~110 ka). These divergences may have been caused by a high sea level in the Bering Sea causing the initial divergence and dense forest separating the two North American species lineages [53]. However, analysis of collared lemming nuclear genomes has uncovered alternative phylogenetic relationships between the three species, with the arctic and northern collared lemmings recovered as sibling lineages to the exclusion of the Ungava collared lemming [109]. Resolution of collared lemming evolutionary history is therefore an active area of research.

Figure I. A Norway lemming (*Lemmus lemmus*), nicknamed Kurt, from Sarek National Park, Sweden. Photo by Love Dalén.

only 5% **endemism** in the region. Thus, as for vertebrates, we are dealing with cold-adapted species that also thrive well in boreal, and for some also temperate and/or steppe, climates and represent a phylogenetically clustered and filtered subset of the northern hemisphere flora [70]. The arctic flora is characterised by high ploidy levels, large distribution ranges (50% having a circumpolar distribution), and a high degree of selfing and asexual reproduction [71,72]. It should be noted that there is not a single life-history trait that is specific for arctic plants [73]. Beringia and high-altitude regions at lower latitudes are assumed to be glacial refugia for the arctic flora [74], by contrast with the amphi-Atlantic region where repeated glaciation, long-distance dispersal, and *in situ* evolution occurred [40,75]. The arctic plants have their origins in the Cenozoic boreal forest, alpine flora of Asian and American mountains, and the Asian steppe [76].

The Late Pliocene–Early Pleistocene flora of the Arctic is poorly known because fossils are rare [13,77]. The longest record, Lake El´Gygytgyn in northeastern Siberia, dates back to 3.6 Ma, and fossil pollen shows a significant change from larch forest to treeless steppe and tundra *c.* 2.6 Ma [78,79]. Macrofossils, pollen, and aDNA show a diverse mixture of arctic and boreal flora in northern Greenland around 2 Ma, with the aDNA revealing ancestors of current birches

(*Betula*) and willows (*Salix*) [13]. The taxonomic resolution of arctic plant palaeorecords are often low (genus level and above). Therefore, much of what we know about the evolution of the arctic flora is based on phylogenetic and biogeographic inference, and as with vertebrates, we find examples that support all three aforementioned hypotheses.

The largest phylogenetic study of 548 arctic plant species belonging to 16 families shows that dispersal into the Arctic, and diversification within the Arctic, exhibit comparable temporal patterns [80]. These trends began around 10–9 Ma, increased rapidly around 2.6 Ma, and reached their peak between 1.0 and 0.7 Ma (Figure 1). There were four times as many dispersal events than *in situ* diversifications. The mean age of arctic endemic species is 1.6 Ma, thus considerably younger than the mean age of 2.66 Ma found for the total number of arctic species analysed. The likely source regions were the lowland and alpine areas south of the Arctic, which is concordant with studies based on biogeographical patterns [81] and an earlier review of phylogenies [82], but western North America stood out as the single most important source region [80]. Examples of a western North American origin include bog bilberry (*Vaccinium uliginosum*) [83] and crowberry (*Empetrum nigrum*) [84], whereas mountain sorrel (*Oxyria digyna*) and purple saxifrage (*Saxifraga oppositifolia*) originated in the Himalayas [85,86]. Furthermore, there are examples of Pleistocene *in situ* origins having developed mainly through divergent evolution or successive higher-level polyploidisations after hybridisation, as exemplified by arctic poppies (*Papaver*), whitlow-grasses (*Draba*) and mouse-ear chickweeds (*Cerastium*) [72,75,87].

There are no known arctic plant extinctions [68,69] during the Quaternary, which may be related to the lower taxonomic resolution of pollen and plant macrofossils. However, a recent study using **sedimentary ancient DNA (sedaDNA)** suggests that extinction has occurred for arctic plants, although extinction rates have been low [88]. Thus, arctic plants may be resilient to climate fluctuations, possibly due to their high dispersal ability [89–91] and high ploidy levels carrying functional traits of several ancestral genomes [72,76].

Beetles

Quaternary fossil beetles are generally attributed to modern species, and this has been interpreted as signifying that they underwent minimal evolution during the Quaternary [92,93]. This means that there are few series of ancestor–descendants and suggests that living beetle species evolved during the Neogene (>2.6 Ma). Some evolution has been documented in, for example, the ground beetle *Asaphidion* where an extinct species and later fossils may represent stages in the evolution of the modern species *A. yukonense* [94]. Other beetles with possible ancestor–descendant lineages include the precursor to the water scavenger beetle *Helophorus tuberculatus*, and stages in the loss of flight in both the rove beetle *Tachinus apterus* and the pill beetle *Morychus viridis* [94].

Generally, however, there appears to be a consensus that beetles have been stable taxonomically, ecologically, and physiologically since the Pliocene, and that they can therefore be used to reconstruct Early Pleistocene climate variables [95]. This is because there is no evidence for assemblages with thermally contradicting associations when the modern climate envelopes for the species are considered [95]. Although this appears to be contradicted by a sedaDNA study of the Kap København formation in northern Greenland, which suggests an ecosystem that has no modern analogue and implies a lack of agreement of the climate indicators across organisms [13]. We note that the results do, however, agree with Elias and Matthews [95] that the ecology at this high latitude site 2 Ma was that of a lower latitude boreal forest today, albeit with some arctic elements [13].

Concluding remarks

Many cold-adapted vertebrates, unlike other groups, have a reasonable fossil time series documenting the evolution of species lineages through the late Cenozoic and especially the Pleistocene. These lineages have been based primarily on morphological comparative analysis of skeletal and dental remains, which show evolutionary changes that represent adaptations to the environments in which they lived. This signifies that their evolution is understood from the tangible physical adaptations of the organisms themselves.

There appear to be different patterns in the mode and tempo of the evolution of the varied cold-adapted terrestrial vertebrate species. The timings may have involved two broad phases, with an early phase during the Late Pliocene–Early Pleistocene when the first indications of cold-adapted taxa may have been established. There followed a phase after the MPT when many of the modern and Late Pleistocene cold-adapted species originated. Later species evolution has taken place during the last 100 ka and involves the various plant hybrid speciation events as well as the evolution of the isolated Norway lemming.

The ways in which cold-adapted species evolved may have been taxon-specific. Some seem to have originated *in situ*, have longer histories in the northern latitudes, and evolved as climates cooled during the late Cenozoic. Others may have involved a stepping-stone whereby higher altitude or cryptic northern refugial populations acquired traits that favoured survival in cold conditions. The latter would cause exposure to cold climes where the species eventually switched from expanding and contracting from the warmer south to doing so from the cold in the north [35]. The adoption of a new refugium would therefore lead to allopatric speciation.

Evidence coming from palaeogenetics of tissue remains and sediments has confirmed some of what was concluded from traditional palaeontological methods, although unexpected results have also been revealed with the population-level studies showing us the likely underlying processes taking place. The advent of functional analyses of palaeogenomes has started to reveal cold-adapted traits that were not visible before, which allows for the timing of such traits to be related to climate and environmental records. This research area is in its infancy but will likely revolutionise our understanding of how the evolution to cold adaptation took place.

It may be that the apparent differences between the evolution of terrestrial vertebrates on the one hand, and the apparent evolutionary stasis of plants and beetles during the Quaternary on the other, have been overstated due to reliance on fossil morphology. With palaeogenetics, direct measurement of plant and beetle evolutionary rates will allow for exploration of biogeographic histories, divergence timings, and modes and timings of morphological and physiological trait acquisitions. This will aid our understanding of the past ecologies of plants and beetles, and may have implications for their use in the reconstruction of past environments (see Outstanding questions).

The earliest ecologies described in the far north seem to include many boreal elements, non-analogue associations, and some extinct or ancestral taxa [13]. This would suggest that the modern arctic tundra ecology had not yet been assembled at between 2.6 and 1.8 Ma, and that relatively few tundra species were present. The differences are caused by inherent limitations of the study of the distinct taxonomic groups. This begs the question as to where the full range of modern arctic species came from, and the non-analogue nature of the ecosystem may signify that more evolution of the constituent species has taken place than has been generally accepted [28]. Although we here use examples from northern terrestrial ecosystems, comparable investigation of other biomes, such as the southern high-latitudes and the marine realm, will provide a more comprehensive understanding of the evolution of Earth's cold-adapted biota.

Outstanding questions

Did different taxonomic groups evolve at different rates during the Quaternary?

If there are differences in evolutionary rates between groups, is this reflected in deeper divergence between insect and plant sister sibling species compared with vertebrates?

Do plant and insect species need smaller areas in which to originate than large vertebrates?

If there is greater evolution than is visible in the morphology of plants and animals, where does this leave the use of these organisms as proxies for past environments?

To what extent can rates of evolution in different groups be tested using aDNA and sedaDNA methodologies?

Does the timing of taxonomic evolution for species identified from morphology coincide with adaptations to the environment identified in animal and plant genomes?

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Declaration of interests

No interests are declared.

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