

# The impact of Quaternary Ice Ages on mammalian evolution

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The Quaternary was a time of extensive evolution among mammals. Most living species arose at this time, and many of them show adaptations to peculiarly Quaternary environments. The latter include continental northern steppe and tundra, and the formation of lakes and offshore islands. Although some species evolved fixed adaptations to specialist habitats, others developed flexible adaptations enabling them to inhabit broad niches and to survive major environmental changes. Adaptation to short-term (migratory and seasonal) habitat change probably played a part in pre-adapting mammal species to the longer-term cyclical changes of the Quaternary. Fossil evidence indicates that environmental changes of the order of thousands of years have been sufficient to produce subspeciation, but speciation has typically required one hundred thousand to a few hundred thousand years, although there are both shorter and longer exceptions. The persistence of taxa in environments imposing strong selective regimes may have been important in forcing major adaptive change. Individual Milankovitch cycles are not necessarily implicated in this process, but nor did they generally inhibit evolutionary change among mammals: many evolutionary divergences built over multiple climatic cycles. Deduction of speciation timing requires input from fossils and modern phenotypic and breeding data, to complement and constrain mitochondrial DNA coalescence dates which appear commonly to overestimate taxic divergence dates and durations of speciation. Migrational and evolutionary responses to climate change are not mutually exclusive but, on the contrary, may be synergistic. Finally, preliminary analysis suggests that faunal turnover, including an important element of speciation, was elevated in the Quaternary compared with the Neogene, at least in some biomes. Macroevolutionary species selection or sorting has apparently resulted in a modern mammalian fauna enriched with fast-reproducing and/or adaptively generalist species.

**Keywords:** Quaternary mammals; speciation; ecophenotypic flexibility; macroevolution; evolutionary rates

## 1. INTRODUCTION

Many striking examples of evolutionary change in the Quaternary have come from studies of mammals, especially those from northern regions permanently or periodically in the periglacial zone. It is evident that both among the living fauna (e.g. reindeer, musk-ox, polar bear) and among those recently extinct (e.g. mammoth, woolly rhinoceros), species have evolved with adaptations tuned to the peculiar environments of the Quaternary.

For mammals in particular, a common supposition is that evolution accelerated during the Quaternary. If true, this could be expressed in three possible ways:

- (i) the origin of new lineages (cladogenesis);
- (ii) the phenotypic divergence (especially when adaptive) of lineages; and
- (iii) the relative success of lineages, in terms of their survival, multiplication and extinction, producing broader changes of a macroevolutionary nature.

Recent interest in macroevolution has resulted in an emphasis on speciation as the main index of evolutionary

activity. However, phenotypic divergence, especially if adaptive, must be regarded as an equally important element of the evolutionary legacy of the Quaternary, and will be emphasized in the present treatment.

Although a period of major environmental perturbation, the Quaternary has been a relatively short interval of time. Any attempt to examine the evolutionary legacy of this period must ask whether the nature or amount of evolutionary change was different from equivalent intervals of time, the obvious point of comparison being the preceding Tertiary period. Features of the Quaternary period that have been thought to stimulate evolutionary activity include the following overlapping categories. Not all of these are exclusive to the Quaternary, and the examples given are slanted towards terrestrial mammals of northern latitudes.

- (i) The origin of novel environments (or at least, combinations of environmental parameters) imposing novel selective regimes, for example: permafrost; tundra; 'mammoth steppe'; and ice floes.
- (ii) Changes in the geographical distribution of environments, altering the selective regime in a given area, for example: climatic zones; vegetation types; and animal species in a competitive, predatory or prey relationship.

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- (iii) The repeatedly alternating nature of the environmental changes, selecting for generalist adaptations or flexibility: Milankovitch cycles, principally at 100 kyr, 41 kyr and 23 kyr periodicity; and millennial-scale or shorter events.
- (iv) The division of populations by environmental barriers, promoting allopatric speciation: ice sheets; seaways; vegetational belts and deserts; and lake formation, fission and fusion.
- (v) The contraction of populations, promoting divergence by founder effect and other means: on islands, as a result of sea-level change; and in refugial areas on the mainland.

These factors are principally abiotic, with direct influence on evolution and adaptation, but they also produce major changes in the biotic environment which may act in turn as proxy forcing factors in evolution (Barnosky 2001; Rothschild & Lister 2003). An obvious example is climatically induced changes in global vegetation patterns which influence herbivorous animals.

However, arguments have been raised to suggest that Quaternary conditions did not, or on theoretical grounds should not be expected to, encourage evolutionary change, or may even have depressed it (Coope 1979; Bennett 1990; Klicka & Zink 1997; Dynesius & Jansson 2000). These arguments include:

- (i) the short-term reversible nature of the environmental change leaves too little time in each cycle for speciation;
- (ii) selective regimes would go into reverse each time the environment reverts; and
- (iii) genetic changes could not accumulate because of migrations and resulting interbreeding of nascent species.

To the extent that we observe evolutionary change in mammals or any other group of organisms, we may therefore ask whether these changes occurred because of, or in spite of, the major environmental changes triggered by Milankovitch cycles. More broadly, the Quaternary provides a high-resolution perspective on the importance of abiotic versus biotic factors in mammalian evolution. Considering the whole Tertiary–Quaternary period, some (e.g. Janis 2003) have championed the importance of abiotic factors, such as tectonics and climate change, whereas others (e.g. Alroy *et al.* 2000) have reached the opposite conclusion and, largely by elimination, assume that purely biotic factors (i.e. those intrinsic to the animal or its biotic environment) are dominant. Barnosky (2001) and Jablonski (2003) provide a synthetic discussion of the two factors. Barnosky (2001), based on studies of Miocene mammals, believes that biotically driven ('Red Queen') evolution is predominant at short (sub-Milankovitch) time-scales, whereas abiotic factors act as evolutionary drivers if they operate over longer time-scales ( $10^5$  years or more), although shorter-term abiotic changes could have an effect if they are extremely violent.

In summary, the following questions can be posed.

- (i) Do mammals show adaptive changes triggered by peculiarly Quaternary conditions?

- (ii) Is there a higher rate of speciation, or faunal turnover generally, in the Quaternary than in previous episodes?
- (iii) Do the chronological patterns of change indicate that they are responding to Milankovitch or other cycles of environmental change?
- (iv) Have these changes left an imprint on the modern biota?

## 2. MAMMALIAN ADAPTATIONS IN THE QUATERNARY: THE 'MAMMOTH STEPPE' COMMUNITY

The existence of a relatively uniform fauna of large mammals adapted to the open environments of temperate and northern Eurasia and North America during Late Pleistocene 'cold stages', is well-attested (Guthrie 1990; Kahlke 1999). The various species by no means occupied identical niches, but in their differing ways all were adapted to environments peculiar to, or greatly expanded during, the Quaternary. Moreover, in almost all cases the origins of these species and/or their adaptations can be placed within the Quaternary itself. This combination of facts strongly suggests that it was Quaternary environments that shaped their evolution. Thus, Kahlke (1999, table 4) lists more than 20 large mammal species forming what he terms the 'mammoth–woolly rhinoceros faunal complex' of the Late Pleistocene in northern Eurasia. In every case the first fossil record of the species is within the Middle to Late Quaternary (from *ca.* 800 ka onwards). Including small mammals as well, Sher (1986a) listed more than 80 taxa (species or genera) known from the Beringian region, all to a greater or lesser extent adapted to the conditions of the far north, and all making their first appearance in the fossil record since *ca.* 2.5 Ma.

For example (table 1), the great expansion in area of ice-sheets and ice-floes provided the environmental setting for the origin of the polar bear. True tundra, to which species such as musk-ox and reindeer are primarily adapted, is unknown in the palaeobotanical record until *ca.* 2.5 Ma; this corresponds to the earliest well-proven presence of low-temperature permafrost, although the latter could have developed even earlier (Sher 1986b). The dry northern grassland known as 'tundra-steppe' or 'mammoth steppe' (Guthrie 1990), to which species including woolly mammoth, woolly rhinoceros and steppe bison became adapted, was a peculiarly Quaternary phenomenon. This does not necessarily mean that all the adaptations of these species evolved in the northern 'steppe-tundra' biome. Kahlke (1999) and A. V. Sher (personal communication) have suggested for the woolly rhinoceros *Coelodonta antiquitatis*, whose immediate forebears are found in the Early Pleistocene of Transbaikalia and central China, that some of their adaptations to cold and grass-eating may have arisen there in a partly steppic landscape and strongly continental climate. The same may be true of other species that ultimately became adapted to the northern biome.

Arguably the most detailed account of adaptive evolution and speciation is provided by the Eurasian representatives of the mammoth genus, *Mammuthus*. An early stage in the sequence, from *M. meridionalis* to

Table 1. Examples of mammalian species that arose in the Quaternary and show adaptations to peculiarly Quaternary conditions. First appearances are based on the fossil record, with the exception of *Ursus maritimus*, where it is based on mitochondrial DNA coalescence with *U. arctos*.

taxon	first appearance	location of first record	adaptations	precursor	references
<i>Mammuthus trogontherii/primigenius</i> (steppe/woolly mammoth)	2.0–1.3 Ma ( <i>M. trogontherii</i> ); 0.7 Ma ( <i>M. primigenius</i> )	China ( <i>M. trogontherii</i> ); northeast Siberia ( <i>M. primigenius</i> )	grazing dentition, high skull and mandible, fur, short ears and tail	<i>Mammuthus meridionalis</i> , open woodland feeders	Lister & Bahn (2000); Lister & Sher (2001)
<i>Coelodonta antiquitatis</i> (woolly rhinoceros)	ca. 0.8–0.5 Ma	central Europe	high crowned teeth, low-slung head, wide muzzle, fur	<i>Coelodonta tologojensis</i> (Transbaikalia; China), steppe/wooded steppe	Guerin (1980); Kahlke (1999)
<i>Bison priscus</i> (steppe bison)	?1.5–1.0 Ma, China; 0.5 Ma, Europe	Yushe, China; Europe	large, stocky body, low-slung head, hypsodont teeth, heavy fur	<i>Eobison/Bison</i> spp., probably woodland dwellers	Sher (1997)
<i>Alopex lagopus</i> (arctic fox)	0.7–0.2 Ma	northeast Siberia; Europe	white coat, small ears, strongly carnivorous dentition	<i>Vulpes</i> spp.: less carnivorous dentition, less arctic faunal association	Sher (1986b); Bonifay (1971)
<i>Rangifer tarandus</i> (reindeer/caribou)	1 Ma	Alaska	bunodont teeth for lichen and moss, antifreezes, wide splayed hooves	unknown neocervine deer	Guthrie & Matthews (1971); Kahlke (1969)
<i>Ovibos moschatus</i> (musk ox)	0.6 Ma	northeast Siberia; Germany	heavy outer fur, fine underwool (qiviut) eight times warmer than sheep's wool, large, hard hooves, social structure	probably a Beringian population of mixed <i>Praeovibos/Ovibos</i> morphology	Kahlke (1963); A. V. Sher, personal communication
<i>Ursus maritimus</i> (polar bear)	0.5–0.25 Ma	Holarctic, unknown	white coat, large size, carnivorous dentition, webbed feet	<i>U. arctos</i> (brown bear)	Talbot & Shields (1996); Barnes <i>et al.</i> (2001)

*M. trogontherii*, appears to have taken place in the latest Pliocene to Early Pleistocene of eastern Asia, probably in China, in response to continental climate and partly steppic habitat (Wei *et al.* 2003; Lister *et al.* 2004). Further specialization to produce the woolly mammoth, *M. primigenius*, can be traced through a series of samples indicating that the genesis of this cold-adapted, grazing species took place in the Beringian region (Lister & Sher 2001). Importantly, adaptation to grazing (seen in dental features) progressed over a million years or more, through several stages that are observable in the fossil record between *ca.* 1.2 Ma and *ca.* 50 ka. The transitions from *M. trogontherii* to early *M. primigenius* in the interval 1.2–0.7 Ma, and thence to late *M. primigenius* by 0.4 Ma, each time with an increase in grazing adaptation of the molars, appears to have taken place in northeast Siberia, presumably in semi-isolated populations. Like *M. trogontherii* before it, *M. primigenius* later migrated into Europe, where their successive immigrations were formerly perceived as *in situ* evolution (Lister & Sher 2001).

Northern Siberia as the locus of origin of the woolly mammoth makes sense in terms of the environmental selective regime (Sher *et al.* 2003). The permafrost environment has been present there since at least 2.5 Ma, with a peculiar, extremely continental climate of very cold winters and short but relatively warm and dry summers. Plant and insect studies indicate that this environment supported a largely treeless, grass- and herb-dominated vegetation with xerophilous and steppe elements. Importantly, fossil insect assemblages indicate similar environmental conditions for all horizons in which the evolving mammoth populations have been found (Kiselyov 1981; Sher *et al.* 2003). Periods of decreased continentality and increased moisture were relatively short, and may have reduced the range of tundra–steppe communities but did not obliterate them entirely until the Holocene. The terrestrial environmental effects of Milankovitch oscillations, although undoubtedly felt in these regions, were not as extreme as in, for example, western and central Europe. As a result, mammoth populations in northeast Siberia experienced environmental conditions that had two key characteristics resulting in profound adaptive evolution: (i) they imposed a strong selective regime; and (ii) they were almost constantly present over the *ca.* 1.2 Myr period during which mammoths have been recorded. Whether such long-term constancy has been a required pattern for significant adaptive change among Quaternary mammals in general is unknown, but it indicates that not all species originating during a series of Milankovitch oscillations need to be able to cope with strongly varying conditions. An alternative possibility is that oscillating conditions, such as Milankovitch cycles, could theoretically have a ‘ratcheted’ cumulative effect on directional evolution, periodically imposing the appropriate selective pressure (e.g. steppic vegetation for grazing mammals) while leaving the species in stasis at other times (see West-Eberhard 2003, p. 518).

Similarly detailed examples of substantial change through the Quaternary have been adduced for many small mammal (especially rodent) lineages; for reviews see Martin (1993) for North America and Maul *et al.* (1998) for Europe.

### 3. FLEXIBLE ADAPTATION

Although some species have evolved specialist adaptations to specific habitats, others have developed flexible adaptations, i.e. features allowing them to survive variable or varying environments. In view of the inconstancy of Quaternary environments in time and space, the possibility that this type of adaptive response has been particularly common in the Quaternary is worthy of examination. Flexible adaptation can be achieved in several ways:

- (i) fixed, but broad-use adaptations;
- (ii) behavioural flexibility; and
- (iii) ecophenotypic plasticity.

The red deer/wapiti (*Cervus elaphus/C. canadensis*), a highly successful ungulate with wide Holarctic distribution, provides examples of all three. A fixed adaptation is the presence of so-called ‘mesodont’ teeth: medium crown height allowing the animal to take a mixture of browse (soft leaves of trees and shrubs) or graze (more abrasive grass and other low-growing plants). In the case of red deer/wapiti, populations differ greatly in the proportions of these foods taken, both now and in the Quaternary (Lister 1984). Behavioural flexibility is shown by the ability of red deer to seek food in unusual circumstances, for example the use of seaweed by island populations, including timing of feeding to match low tides (Conradt 2000). Finally, ecophenotypic plasticity is shown in the adaptive changes in rumen morphology of red deer raised on different diets: on grass, they develop the open rumen with small papillae characteristic of grazing ruminants, whereas on browse they develop the large, flat papillae typical of browsers; accommodation occurs within two to three weeks (Hofmann *et al.* 1976; Hofmann 1983). A combination of all these features, together with its propensity for forming locally adapted populations or subspecies (see § 4), goes a long way to explaining not only the broad distribution and varied habitat of the red deer at the present day, but also its persistence through varied habitats in the Quaternary, including cool, open, grassy environments, intermediate savannahs, and temperate wooded habitats (Lister 1984). Moose (*Alces*) and roe deer (*Capreolus*), by contrast, which have more restricted ecological ranges today, and in the Quaternary were found only in wooded phases (Lister 1984; Lister *et al.* 1998), are physiologically incapable of consuming large quantities of grass (Hofmann 1985).

There are other examples of phenotypic effects in living mammals that seem likely to have been a legacy of their Quaternary history. Weaver & Ingram (1969) showed experimentally that domestic swine raised at 5 °C developed short, stocky limbs and thicker coats than their siblings raised at 30 °C. Because short and stocky limbs are regarded as one form of adaptation to cold climate according to Allen’s rule, and a mammal’s coat is one of its chief thermoregulatory devices, the response seen in swine could be not merely a non-adaptive developmental effect, but an example of adaptive phenotypic flexibility moulded by natural selection. Another example is the propensity of mice to grow shorter tails when reared under cold conditions (Falconer 1981), protecting against heat

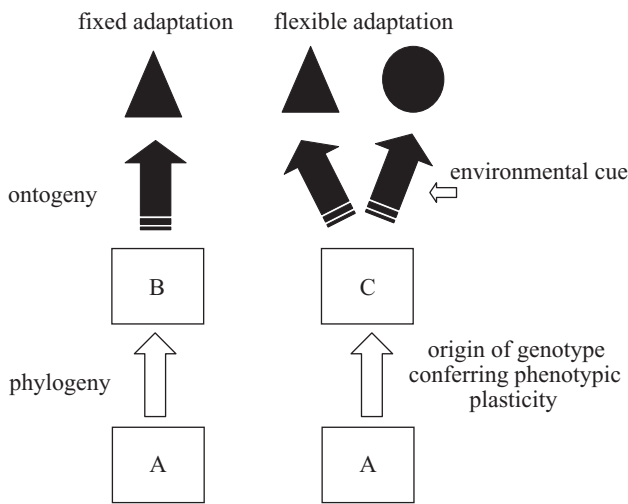


Figure 1. The origin and operation of adaptive phenotypic plasticity. A is the ancestral genotype, conferring a fixed phenotypic adaptation. In the lineage on the left, A evolves into B, still conferring a fixed phenotypic adaptation (triangle). In the lineage on the right, A evolves into C, a genotype capable of producing two alternative adaptive phenotypes (triangle and circle), depending on an environmental cue. The cue can operate once, during ontogeny, fixing one adult phenotype, or during the life of the animal, allowing adaptive remodelling of adult phenotype.

loss as well as frostbite. It is hard to be certain that such responses evolved as adaptations, but at least they have potential current survival value (i.e. they are 'aptations' *sensu* Gould & Vrba (1982)). An evidently adaptive effect that can be seen in the wild is the seasonal phenotypic plasticity of the bog lemming, *Synaptomys borealis*, where the middle claws are enlarged during winter, apparently an adaptation to living in ice and snow (Jones & Birney 1988).

Although environmentally triggered phenotypic changes themselves do not qualify as 'evolution', the propensity to respond in this way must itself have evolved (figure 1). Lister (1984) suggested that the oscillating vegetational environment to which the red deer was subjected during the Quaternary may itself have selected for a genotype capable of responding ecophenotypically, thus obviating the need for further genetically based evolutionary change. As a matter of fact, all three aspects of flexible adaptation in red deer, mentioned above, may be plesiomorphic: mesodonty is a general feature of *Cervus* species; phenotypically flexible rumens are found in many other ruminants (Forsyth & Fraser 1999); and animals as diverse as sheep and reindeer will eat seaweed (Conradt 2000). Nonetheless, the red deer species, *C. elaphus*, evolved in the Quaternary utilizing this package of adaptations, and became one of the most successful inhabitants of its varied environments.

The idea of selection by and for varying conditions has been particularly developed by Potts (1998*a,b*), who has coined the term 'variability selection', especially in relation to the evolution of cognitive abilities and the ability to solve problems: adaptations that are flexible in the extreme sense of allowing the organism to respond to novel or unpredictable environments. In this model, as in

Lister (1984) on red deer, it is the variability of the environment *per se* that eventually selects for individuals capable of flourishing in all conditions. Potts (1998*a,b*) points to the increase in amplitude of Milankovitch cyclicity after *ca.* 750 ka as the key stimulus to this 'time-integrated selective process'. However, there are problems with models of this type. Natural selection can operate only at the current moment. If we imagine an environment switching between 'cold' and 'warm' conditions, during a 'cold' phase individuals adapted to cold will be favoured; during a 'warm' phase individuals adapted to warmth will be favoured. In both phases, individuals with a 'general' adaptation allowing them to fare passably well in either environment will be selectively inferior to the appropriate narrowly adapted ones and their genotypes will not spread.

Especially for ecophenotypic adaptation, the outcome in such situations depends crucially on the relative lengths of environmental cycles and the animals' generation time. Only if an individual animal experienced both kinds of climate during its lifetime, or its offspring experienced a different sort from itself, would there be selection for flexible adaptation (Moran 1992; Scheiner 1993; Pigliucci 2001, ch. 9). Selection of this kind is hardly ever likely to occur with Milankovitch cycles of the order of  $10^4$ – $10^5$  years. Among living organisms, the most reliable cues, which have led to the evolution of reversible flexibility, are seasonal, for example in the growth of a winter white coat in mammals such as the snowshoe hare. The longer the time between environmental switches, and the more irregular their occurrence, the less likely that flexible adaptations will evolve: the reading of environmental cues, and the matching of phenotype to environment, will lose precision because of attenuation of selective scrutiny (Moran 1992; Rollo 1995, pp. 243, 393), and selection will favour fixation of a single phenotype (Scheiner 1993).

Flexible behaviour and advanced cognition of the type envisaged by Potts may be a special case, in that the ability to respond creatively to new challenges could be selectively advantageous over a fixed response both in the environment in which it originally evolves, and in a second, changed environment, eventually coming to supplant fixed adaptations to either (Potts 1998*b*).

A more general explanation of the origin of flexible adaptation in the Quaternary, however, is that it arises in response to fine-scale temporal or spatial environmental variability, as a result of which the organism is then pre-adapted to cope with longer-scale change. Selection in spatially heterogeneous environments has been extensively explored both in theory and reality (Scheiner 1998). If an animal moves between different regions of landscape and vegetation during the course of days, months or years, or its offspring disperse into environments varying among themselves or from that of the parent, then selection can favour flexible adaptation. Many species undertake migratory movements that fulfil these criteria. Turning to temporal variation, its principal expression in many environments today is seasonal change, which in terms of temperature, at least, is far greater in many parts of the world today than average glacial–interglacial differences in the Pleistocene. Temporal variations on short time-scales can lead to the evolution of flexible adaptation, including phenotypic flexibility (Gomulkiewicz & Kirkpatrick 1992).

The flexible adaptations gained in response to seasons would then allow the species to survive changes on longer time-scales, such as those induced by Milankovitch cycles, provided at least some of the key environmental varying factors were the same. Potts (1998*b*) envisages a graded spectrum of environmental variability, with cycles such as sunspot activity (tens of years) and Heinrich events (hundreds to thousands of years) forming a bridge between annual and Milankovitch cycles, the whole spectrum integrating into variability selection. These ideas would benefit from simulation modelling.

Further, it is possible that flexible adaptations could have evolved by selection between taxonomic lineages, rather than between individuals, if the genotype conferring a flexible response were fixed (perhaps by founder effect) in one lineage but not in another. In particular this could provide a mechanism for the genesis of flexible adaptation across longer-term cycles. Lineages fixed for the flexibility genotype would survive multiple shifts of climate whereas those fixed for adaptation to one climatic regime or the other would become extinct when the 'wrong' regime returned. Along similar lines, Barnosky (2001) suggested that, if speciation in mammals typically takes more than  $10^5$  years, only incipient species capable of surviving Milankovitch-scale fluctuations (of cyclicity less than or equal to  $10^5$  years) will survive. Such models have the usual disadvantage of 'weak' inter-lineage selective power compared with selection on individuals (Maynard Smith *et al.* 1985), but Rollo (1995, p. 162) considered that it could work between lineages at a relatively low taxonomic level.

It is very likely that some of the morphological differences we observe between fossil samples of Quaternary mammal species represent the operation of ecophenotypic responses (Lister 1992). The most obvious are the ubiquitous shifts in body size, though the experiments described above with pigs indicate that this could also in theory apply to body proportions. In practice it is hard to determine from the fossil record whether such observed differences were due to genetic or ecophenotypic changes. They are most likely to have been ecophenotypic in response to spatial or short-term temporal environmental heterogeneity. Over the longer term, for more complex features, and especially at an inter-species level, they are more likely to reflect genetically fixed changes in morphology.

Ecophenotypic effects may have wider significance, especially in the origin of fixed genetic attributes, by the process known as 'genetic assimilation' (Waddington 1942): that is, selection for individuals showing the strongest response until the morphology develops even without the environmental cue. Given the propensity for mammals to show direct (ecophenotypic) changes in body size depending on nutrition, it is likely that many cases of size change, such as dwarfing on islands, began in this way, to be supplanted and enhanced by genetic change as time progressed (Roth 1992; Lister 1996). Noting the ability of mice reared in a cold environment to grow shorter tails (see above), Rollo (1995, p. 224) suggests that short-tailed northern rodents such as lemmings and field voles (*Microtus*) may have evolved by genetic assimilation of this capability. Pigliucci (2001, p. 293) summarizes other important potential evolutionary roles for phenotypic plasticity.

#### 4. SPECIATION AND SUBSPECIATION

The degree to which the genesis of individual Quaternary species and their adaptations can be traced varies greatly with the quality of the fossil record (table 1). In some instances, the immediate precursors of Quaternary species are quite unknown, as in the reindeer, *Rangifer tarandus*, known to be a sister-group to certain other living New World deer (Webb 2000), but with no close fossil or living relatives. In others, congeneric likely precursors or close sister-groups to the species that were adapted to the ice-age can be identified. An example is the Middle (*ca.* 780–120 ka) to Late Pleistocene (*ca.* 120–10 ka) steppe bison, *Bison priscus*, where species of the subgenus *Eobison* are known from the Early Pleistocene (*ca.* 1.8–0.78 Ma), and are thought from their morphology to be woodland-adapted species (Sher 1997). However, here as in many other cases, we have no detailed information on the transformation. Even for the mammoth lineage, where the fossil record has pinpointed Early to Middle Pleistocene China and northeast Siberia as likely areas of speciation (see § 2), the duration of the individual allopatric events is known only within broad limits.

In other cases, where resolution allows, the time-course of subspeciation and speciation can be examined. Two main questions are of interest. First, when did the species originate? Second, how long did the speciation process take? These questions are intertwined, because if speciation is a slow, cumulative process, a sharply defined 'date' for it cannot be given (Avice 2000). Various lines of evidence have been brought to bear on these issues, including the fossil record, palaeogeography, morphology of modern forms, and increasingly, molecular data. Problems of conflict between these data sources, and the need for a complementary approach (Conroy & van Tuinen 2003), will be stressed in the following account.

The examples given below are summarized in table 2. Starting at the 'short' end of possible time-scales, Lister & Rawson (2003) examined divergence in northern mammalian species separated between Siberia and Alaska at the last flooding of the Bering Strait, *ca.* 10 ka (Elias *et al.* 1996). Many species are found on both sides of the Strait (termed 'amphiberingian' by Hoffman (1981)), for example the arctic fox, *Alopex lagopus* (figure 2*a*); but no example of sibling species could be found, and even nominal subspecies pairs across the Strait are often barely divergent: the duration of isolation was presumably too short. A good example is provided by moose, *Alces americana*, which is not only generally similar in karyotype, morphology and behaviour between eastern Siberia and North America (see below), but the nominal subspecies of northeasternmost Siberia, *A. a. buturlini*, and that of Alaska, *A. a. gigas*, are particularly alike in large size and dark coloration (Heptner *et al.* 1961; Boeskorov 2001). This example is corroborated by radiocarbon data, indicating that the species did not enter the Beringian region, and cross into Alaska, until very shortly before the breaching of the Bering Strait *ca.* 10 ka (Guthrie (1995); R. D. Guthrie, personal communication). The northeast Siberian and Alaskan populations are nonetheless in different mtDNA haplogroups, which Hundertmark *et al.* (2002) interpret as evidence for different founding populations and the convergence of morphology; but the biogeographical

Table 2. The timing and duration of speciation and subspeciation among Quaternary mammals: examples mentioned in the text. The examples have been roughly ordered by degree of taxonomic separation, based on traditional features such as morphology, behaviour or karyotype; the categories are to some extent arbitrary. The examples illustrate the difficulty of separately estimating 'date' and 'duration' of taxonomic divergence, and the variable level of congruence between fossil and mtDNA estimates of time since common ancestry.

region	taxa	common name	map reference	level of taxonomic differentiation	fossil and modern history	molecular data	timing of taxonomic divergence	references
Alaska/northeast Siberia	<i>Lemmus trimucronatus</i>	brown lemming	figure 2b	none (across Bering Strait)	separated since 10 ka (based on sea-level history)	mtDNA estimate of expansion <i>ca.</i> 163 ka	none in 10 kyr	Fedorov <i>et al.</i> (2003)
Alaska/northeast Siberia	<i>Alces americana</i>	moose	figure 2f	none (across Bering Strait)	species entered the region shortly before separation of Bering Strait 10 ka	northeast Siberian and Alaskan populations are in different mtDNA haplogroups, implying either mtDNA lineage sorting or convergent morphology	none in 10 kyr	Boeskorov (2001); Hundertmark <i>et al.</i> (2002)
Jersey	<i>Cervus elaphus jerseyensis</i>	dwarf red deer	figure 3a	subspecies (extinct)	parent species ( <i>C. elaphus</i> ) fossil record 400 ka to present; on Jersey at <i>ca.</i> 126 ka; dwarf present 6 kyr later (dated by sea-level history)		subspecies diverged in $\leq 6$ kyr	Lister (1995)
Florida Keys	<i>Odocoileus virginianus claviium</i>	Key deer	figure 3b	subspecies	parent species ( <i>O. virginianus</i> ) known as fossil <i>ca.</i> 2 Ma to present. Islands separated <i>ca.</i> 5 ka		subspecies diverged in $\leq 5$ kyr	Lister (1995)
North America	<i>Marmota flaviventris</i>	yellowbelly marmot	figure 2d	subspecies, minor divisions	isolated since 10 ka, based on fossils and biogeography	two samples have 1.6% mtDNA divergence in <i>cyt b</i> (coalescence <i>ca.</i> 750 ka)	subspecies probably diverged in past 10 kyr	Polly (2003); Steppan <i>et al.</i> (1999)
North America	<i>Marmota caligata</i>	hoary marmot	figure 2d	subspecies, minor divisions	isolated since 10 ka, based on fossils and biogeography		subspecies probably diverged in past 10 kyr	Polly (2003)

(Continued.)

Table 2. (Continued.)

region	taxa	common name	map reference	level of taxonomic differentiation	fossil and modern history	molecular data	timing of taxonomic divergence	references
northwest Europe	northwest European part of <i>Sorex araneus</i> complex	common shrew	figure 2h	groups of karyotypic races (equivalent to subspecies with major divisions)	<i>Sorex araneus</i> population, probably ancestral to modern groups, at ca. 150–100 ka (based on morphology); modern divergence seen at 15–14 ka		groups diverged within ca. 135 kyr interval 150–15 ka	Polly (2001)
North America	<i>Marmota monax</i>	woodchuck	figure 2d	subspecies, major divisions	fossil species known since 1.0–0.7 Ma; subspecies were separated during the last glacial cycle (i.e. since 100 ka)	three samples have 1.6% mtDNA divergence in cyt <i>b</i> (coalescence ca. 750 ka)	subspecies diverged within 100 kyr	Polly (2003); Steppan <i>et al.</i> (1999)
Holarctic	<i>Alces alces</i> (Europe and West Asia)/ <i>A. americana</i> (East Asia and North America)	elk/moose	figure 2f	incipient species	likely ancestor <i>A. latifrons</i> known as fossil until ca. 400 ka; <i>A. alces/americana</i> stock appeared ca. 100 ka; separation of the species definitely attested only since ca. 10 ka	mtDNA coalescence 85 ka	incipient species diverged some time in 390 kyr interval 400–10 ka	Boeskorov (2001); Hundertmark <i>et al.</i> (2002)
Holarctic	<i>Cervus elaphus</i> (Europe and West Asia)/ <i>C. canadensis</i> (East Asia and North America)/ <i>C. nippon</i> (East China and Japan)	red deer/wapiti/sika deer	figure 2g	incipient species	likely ancestor <i>C. acoronatus</i> known as fossil until ca. 600 ka; differentiated species appear ca. 400 ka (European <i>C. elaphus</i> and Chinese <i>C. nippon</i> ); ca. 100 ka (North American <i>C. canadensis</i> )	range of mtDNA coalescent dates depending on calibration point: 5.0–0.75 Ma	incipient species diverged in ca. 500 kyr interval 600–100 ka	Lister (1984); Kuwayama & Ozawa (2000); Randi <i>et al.</i> (2001)

(Continued.)



Table 2. (Continued.)

region	taxa	common name	map reference	level of taxonomic differentiation	fossil and modern history	molecular data	timing of taxonomic divergence	references
Holarctic	<i>Ursus maritimus</i> / <i>U. arctos</i>	polar and brown bears	figure 2e	species	<i>Ursus arctos</i> known from fossils ca. 500 ka to present; <i>Ursus maritimus</i> poor fossil record ca. 50 ka to present	mtDNA coalescence ca. 250–200 ka. mtDNA tree topology and modern biology indicates <i>U. arctos</i> is immediate (paraphyletic) progenitor of <i>U. maritimus</i>	species diverged within past 250 ka	Talbot & Shields (1996)
Holarctic	<i>Lynx lynx</i> (Eurasia)/ <i>L. canadensis</i> (North America)	lynx	figure 2c	species	common ancestor <i>L. issidorensis</i> known as fossil from ca. 1 Ma; extant forms from ca. 100 ka	4% mtDNA divergence between species, suggesting coalescence 3.2 Ma	species diverged in 0.9 Myr interval ca. 1 Ma to 100 ka	Kurten & Anderson (1980); Johnson & O'Brien (1997)
Holarctic	<i>Lemmus trimucronatus</i> , <i>L. lemmus</i> and <i>L. sibiricus</i>	brown, Norway and Siberian lemmings	figure 2b	species (taxonomy is contentious)	<i>Lemmus</i> known from at least 1 Ma in northern Siberia and North America. Earliest dates of modern species unclear	4–7% mtDNA divergence between species	species presumably diverged over several hundred thousand years, at least	Kurten & Anderson (1980); Zazhigin, (1997); Fedorov <i>et al.</i> (2003)
Alaska/northeast Siberia	<i>Marmota flaviventris</i> and <i>M. camtschatica</i>	Alaska and black-capped marmots	figure 2d	species	Bering Strait formed ca. 10 ka	mtDNA divergence 15–16% and not sister-taxa	divergence much longer than since last separation of Bering Strait (> 10 kyr)	Steppan <i>et al.</i> (1999)
Bering Sea	<i>Sorex jacksoni</i> (St Lawrence Is.), <i>S. pribilofensis</i> (Pribilof Is.) and <i>Microtus abbreviatus</i> (St Matthew Is.)	endemic shrews and vole	figure 3d	species	known from modern forms only. Bering islands separated ca. 10 ka	<i>M. abbreviatus</i> , very closely related to mainland Alaskan <i>M. murus</i> on cyt b	assumed to have evolved in ≤10 kyr based on sea-level history, but this presumes the species evolved on the islands	Hoffmann (1981); Conroy & Cook (2000)

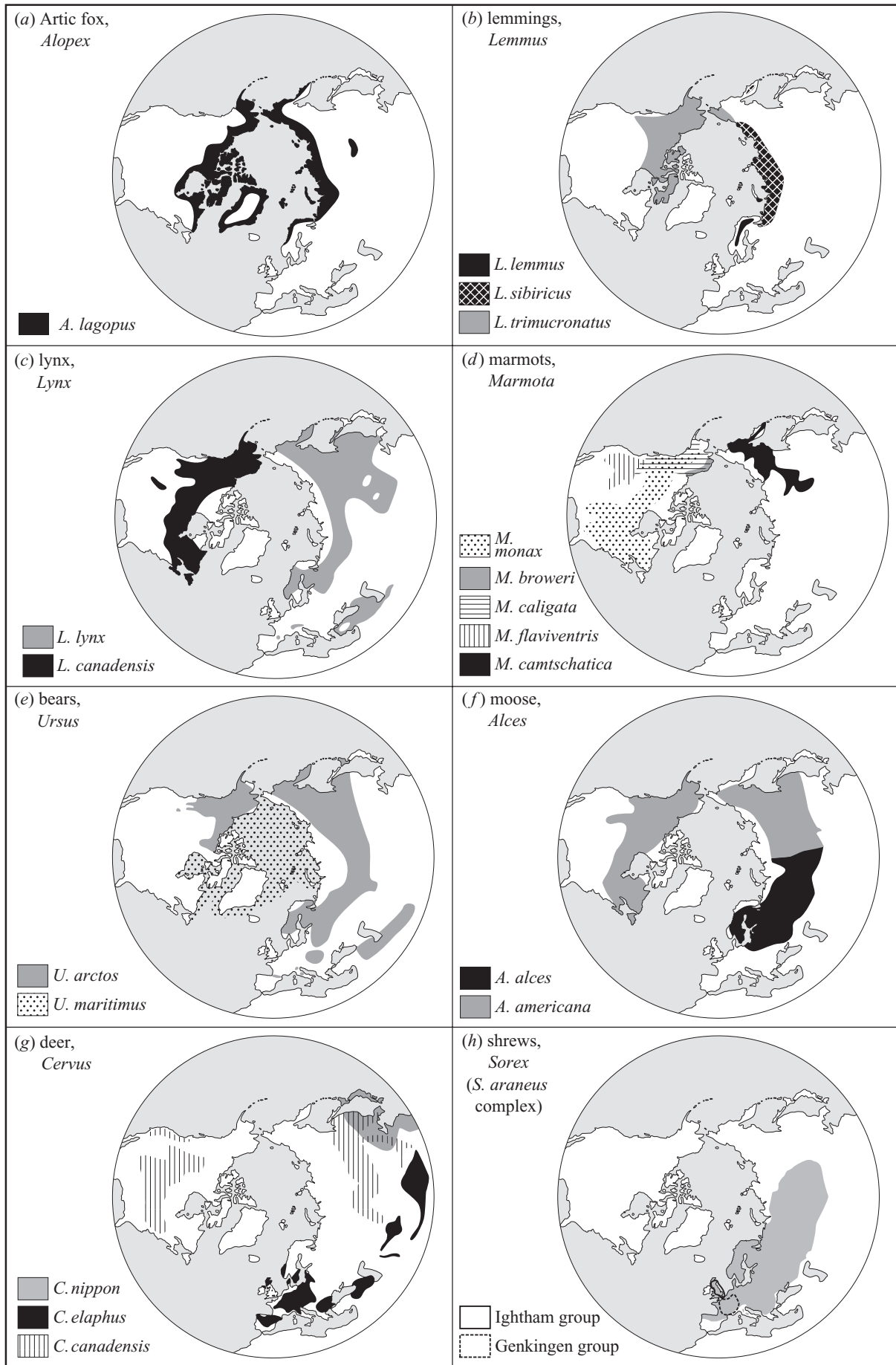


Figure 2. (Caption opposite.)

Figure 2. Modern distributions of mainland taxa discussed in the text and summarized in table 2. (a) Arctic fox, *Alopex lagopus*. (b) Lemmings: *Lemmus trimucronatus*, brown lemming; *L. lemmus*, Norway lemming; and *L. sibiricus*, Siberian lemming. (c) Lynx: *Lynx lynx* and *Ly. canadensis*. (d) Marmots: *Marmota flaviventris*, yellowbelly marmot; *M. caligata*, hoary marmot; *M. monax*, woodchuck; *M. broweri*, Alaska marmot; and *M. camtschatica*, black-capped marmot. (e) Bears: *Ursus arctos* brown/grizzly bear; and *U. maritimus*, polar bear (range extends somewhat inland). (f) elk/moose: *Alces alces* and *A. americana*. (g) Deer: *Cervus elaphus*, red deer; *C. canadensis*, wapiti; and *C. nippon*, sika deer. (h) Shrews, *Sorex araneus* group (selected northwest European morphotypes: see text).

history makes mtDNA lineage sorting between small founder populations a likely alternative explanation. Another interesting example has been provided by Fedorov *et al.* (2003) in their study of lemmings (*Lemmus*). This group shows strong phylogeographical division into four haplogroups around the Holarctic (see below), but a single haplogroup of *L. trimucronatus* straddles the Bering Strait (figure 2b).

In various other taxa, 'species pairs' occur on either side of the Bering Strait (Hoffman 1981), but events much earlier than 10 ka are implicated, even though the longer-term alternating flooding and rejoining of the Bering Strait may have been involved. Some of these species pairs are Quaternary in origin, for example the lynx. This genus is represented by *Lynx lynx* in Eurasia and *Lynx canadensis* in North America (figure 2c), but the fossil form *Lynx issiodorensis* was spread across both continents in the Early Pleistocene (*ca.* 1 Ma) and is a likely progenitor to both (Kurtén & Anderson 1980), even though mtDNA divergence of 4% suggests a deeper coalescence of haplotypes, at *ca.* 3.2 Ma (Johnson & O'Brien 1997). In another example, the marmots *Marmota broweri* in Alaska and *M. camtschatica* in northeast Siberia were long considered sister-species (figure 2d). However, an mtDNA phylogeny of the genus shows that they are not closely related (Steppan *et al.* 1999). This indicates the danger of assuming recent vicariance from present-day distributions.

The polar bear, *Ursus maritimus* (tables 1 and 2; figure 2e), was envisaged as evolving in the Middle Pleistocene from a coastal population of brown bears that took to feeding on marine mammals (Kurtén 1964), but the fossil record is extremely poor. Recent mtDNA studies have confirmed Kurtén's supposition, however, showing that the polar bear evolved from within the range of brown bear populations, the process beginning some time in the interval 200–250 ka, or perhaps a little earlier (Talbot & Shields 1996; Barnes *et al.* 2001). Because polar bear is nested within brown bear in the mtDNA phylogeny, it is evident that the brown bear is the direct ancestor of polar bear, not just its closest surviving sister-group, so their comparison provides direct evidence on the origin of the species.

Other mammals show stages in the process of speciation. Two lineages of large deer, elk and moose (*Alces*) and red deer and wapiti (*Cervus*), each have a complex chain of subspecies around Eurasia and North America, but in each case the chain is divided into two major phylogeographical groups, east and west (figure 2f,g). The

similarity between eastern Siberian and North American moose has already been mentioned. For reasons that are unclear, the major division in each genus occurs further west, within central Asia, and presumably represents secondary contact of populations which initially diverged in allopatry to the east and west. In each case, however, the two major groups differ in size, coat, antlers, behaviour and ecology, and in the case of the elk/moose, in karyotype (Heptner *et al.* 1961; Boeskorov 2001; Randi *et al.* 2001; Hundertmark *et al.* 2002; Lister 2004). The status of these groups as subspecies, semispecies or species has long been debated, with current opinion tending to regard them as incipient species *C. elaphus/C. canadensis* and *A. alces/A. americana* (Boeskorov 2001; Randi *et al.* 2001). Moreover, the sika deer, *C. nippon* of Japan, eastern China and the Russian Far East is part of this *Cervus* complex as it appears to be the sister-group of *C. canadensis* (Kuwayama & Ozawa 2000; Randi *et al.* 2001).

For elk and moose, recent data indicate low mtDNA diversity and a coalescence date for the current worldwide diversity of no more than 85 ka (Hundertmark *et al.* 2002). The fossil record of this lineage indicates a widespread progenitor species *A. latifrons* between *ca.* 700–400 ka, and the spread of the *A. alces/A. americana* stock from *ca.* 100 ka, but unfortunately no clear indication of the timing or duration of origin of the latter in the intervening period, despite some suggestive morphologically intermediate fossils *ca.* 200–100 ka (Sher 1987; Kahlke 1990; Lister 1993). By the same token, the date at which *A. alces* and *A. americana* began to diverge is uncertain. The 85 kyr coalescence could correspond to the younger bound provided by the fossil record (100 ka). However, if the modern species arose deeper in the 'fossil gap' 400–100 ka, the young mtDNA coalescence of modern haplotypes would suggest that there were earlier-originating populations of the species which are no longer extant (cf. Barnes *et al.* (2001) on bears).

For *Cervus*, by contrast, a much deeper mitochondrial coalescence date of *ca.* 5.2–6.8 Ma has been obtained for the split between the 'incipient species' red deer and wapiti/sika (Randi *et al.* 2001). However, this appears to pre-date the origin of these groups, because the fossil record of the whole lineage does not begin until *ca.* 700 ka in Eurasia, possibly a little earlier in North America, before which an array of clearly different *Cervus* species is found (Guthrie & Matthews 1971; Kurten & Anderson 1980; Lister 1984). The richness of this fossil record makes it highly unlikely that a 5–6 Myr 'ghost range' for *C. elaphus/C. canadensis/C. nippon* has been missed. After the establishment of this lineage, the fossil record indicates that the characteristic antler differences between modern European *C. elaphus* and Asian/North American *C. canadensis/C. nippon* had arisen by *ca.* 400 ka (Lister 1984, 1986). Again, this is notably different from the mtDNA dates of 1.9–2.8 Ma and 3.7–5.0 Ma for the two groups, respectively (Randi *et al.* 2001). Today, these taxa are on the verge of qualifying as biological species so, taking the fossil record literally, the process of speciation appears to have taken several hundred thousand years.

The mismatch between the fossil record and the mitochondrial data for *Cervus* is likely to be due to a combination of two factors. First, an inappropriate calibration point for the mtDNA calculations: Randi *et al.* (2001) use

a very high estimate of 15.0–16.7 Ma for the palaeontological origin of the Cervinae (the subfamily to which *Cervus* belongs), but if an alternative estimate of 6–8 Ma is used (Miyamoto *et al.* 1990), the origin of the *C. elaphus/C. canadensis/C. nippon* stock shrinks to *ca.* 2.0–2.7 Ma, of *C. elaphus* to 1.0–0.75 Ma, and of *C. canadensis/C. nippon* to 1.5–2.0 Ma (calculated from data in Randi *et al.* 2001), much closer to their earliest fossil occurrences. Kuwayama & Ozawa (2000) obtained an even younger divergence date of 0.8 Ma for the divergence of *C. elaphus* and *C. canadensis/C. nippon*, but this is based on an improbable calibration point of only 1.6 Ma for the split between *Cervus* and *Dama* (fallow deer). The second factor contributing to the mismatch between fossil and mitochondrial dates may be the divergence of mitochondrial haplotypes before cladogenesis at a population level, the conventional point of taxonomic division when phenotypic differences can begin to accumulate (see below).

The precise outcome of Quaternary changes on mammalian metapopulations will have depended on the palaeogeographical and other circumstances particular to each taxon. This is illustrated by the dental morphology of marmots in North America, described by Polly (2003). *Marmota monax* (figure 2*d*) inhabits forest, and its patchy range during the last glaciation extended along, and was probably broken up by, the long southern margin of the ice sheet. This has resulted in deep morphological divisions that have been only partly homogenized during the Holocene when the populations expanded and became contiguous. For the related *M. flaviventris* and *M. caligata*, the inverse applies: inhabiting alpine vegetation, expansion of these habitats during the long glacial episodes led to greater homogenization among populations: the modern subspecies have been isolated (in various mountain ranges) only for the few thousand years of the Holocene and are less dentally divergent (Polly 2003). The differences in dental divergence between the *Marmota* species are not reflected in available mtDNA distances (table 2), but current molecular sample sizes are insufficient for reliable comparison. Similar arguments on population subdivision and fusion were used for the chipmunk (*Tamias*) species complex in western North America (Hoffmann 1981). Among birds, Stewart (2002) suggests that Quaternary environmental changes altered migratory patterns, leading to the effective reproductive isolation of different populations, and thereby to speciation in some cases. An example is in the origin of the spotless starling, *Sturnus unicolor*, in the Iberian peninsula, which adopted a more sedentary lifestyle than the common starling, *S. vulgaris*, to the north and east.

The position of the boundaries or hybrid zones between the extant species or phylogroups will depend on both the location of refugia and any natural barriers to colonization. For example, in the case of the lemmings (*Lemmus*) mentioned above (figure 2*b*), the Holocene distribution of species and phylogroups across northern Siberia and North America arose by migration, from southern refugia, into previously glaciated terrain, although the phylogeographical divisions are clearly deeper than the last glaciation (Fedorov *et al.* 2003). Divisions between mtDNA haplogroups correspond to major rivers—the Mackenzie and Lena—and in the case of the latter, also to a former ice-sheet on the adjacent Verkhoyansky mountain ridge. A

further division, between *L. sibiricus* and *L. trimucronatus*, occurs at the Kolyma river, and is marked by karyological differences and a breeding barrier as well (Jarrell & Fredga 1993); Fedorov *et al.* (2003) suggest that this split might have originated from ‘vicariant separation by intermittent inundation of the Bering Strait’ over several glacial–interglacial cycles, with a subsequent westward shift of the species boundary.

For several of the species discussed above (*M. monax*, *C. elaphus/C. canadensis/C. nippon*, *Lemmus sibiricus/trimucronatus*), the diverging intraspecific clades have survived not only several 100 kyr Milankovitch climatic cycles, but also extensive range changes in response to them, and the formation of hybrid zones where they meet on expansion, without homogenization or losing their momentum towards speciation. This corresponds to examples in other taxa described by Hewitt (1999, 2003). The weight of evidence therefore indicates that significant divergence generally accumulates over several glacial–interglacial cycles. In a few cases significant differences can be seen within a single 100 kyr Milankovitch cycle, as in shrews of the *Sorex araneus* complex in Europe (figure 2*h*). Two groups identified by Polly (2001) show not only morphological and genetic differentiation, but also karyotypic differences, which appear to have accumulated between populations since the last interglacial. The same may be the case for the division between *A. alces* and *A. americana* (see above), but further dating evidence is required. In a recent study tracing the sagebrush vole (*Lemmiscus curtatus*) through a detailed 800 kyr sequence in western North America, Barnosky & Bell (2003) found that morphological change accumulated across several glacial–interglacial cycles, and was not particularly promoted by individual cycles except for the warmest, driest interglacial in the sequence, which saw the most pronounced morphological change.

These examples highlight some general issues relating to the estimation of dates of species origin, or the time taken by the speciation process. First, the estimated date of common ancestry to the closest surviving modern relative (the living sister-species), whether determined from molecular or phenotypic data, can long pre-date species’ origins if that relative is not the original sibling species (the species from which the study species originally split, or the other daughter species resulting from that split). Working in the other direction is the possibility that the most anciently diverged populations of the study species are missing from the fossil record, or in the case of DNA studies, are no longer extant, causing the most recent common ancestry of available populations to underestimate the date of species origin. This is probably the case for elk and moose, where fossils indicate a deeper ancestry than extant mtDNA. This problem can in some cases be circumvented by the inclusion of ancient DNA from extinct fossil populations (Barnes *et al.* 2001). The identification of the true sibling species is likely if one species nests within another in the tree (as in the case of the polar bear and brown bear), or if biological and fossil data indicate a very close relationship (as in red deer, wapiti and sika).

Second, mitochondrial polymorphism can originate before the actual splitting of biological populations, the resulting mitochondrial lineages only later becoming

sorted into descendant sister-taxa, so the time of division of the taxa themselves may be overestimated by mitochondrial coalescence dates (Avice 2000; Nichols 2001). This may be a contributing factor in the red deer/wapiti clade (see above), where mitochondrial coalescence long predates the first appearance in the fossil record of both the common ancestor of *C. elaphus/C. canadensis*, and the two daughter species themselves. The remainder of the mismatch is probably accounted for by a further general confounding factor: an inappropriate fossil calibration point for attributing absolute ages to mtDNA coalescent events (see above, and Conroy & van Tuinen (2003) for discussion).

Third, plausible evolutionary scenarios based on modern distributions, suggestive of past vicariance or other biogeographical events, should be treated as hypotheses requiring supplementary evidence. This point was made by Klicka & Zink (1997) in relation to bird species putatively formed by the interposition of the Laurentide ice sheet, and similarly applies to some north-south species pairs among North American mammals listed by Hoffmann (1981) such as the lynx, *Lynx canadensis*, and bobcat, *Lynx rufa*, or the Dall sheep, *Ovis dalli*, and big-horn sheep, *O. canadensis*. Some of the trans-Beringian species pairs mentioned earlier fall into the same category. This is not to deny that vicariant events operated in the formation of these species, but modern distributions may have shifted since species origins (Graham *et al.* 1996; Losos & Glor 2003), so dated palaeodistributional evidence of evolving populations, in conjunction with palaeo-environmental data, is ideally required.

Avice (2000) described a valuable framework for estimating the duration of species origins from modern mtDNA data. The coalescent date for living sister-species is taken as the maximum date for the initiation of their original split (i.e. the speciation event). From this can be subtracted the coalescent date for the phylogroups or subspecies into which the species are divided. Because the origin of these intraspecific entities must post-date the origin of the species themselves, the result is an estimate of the duration of the speciation event. Using this approach, Avice *et al.* (1998) found average coalescences for pairs of mammalian sister-species of *ca.* 3 Myr, and of their constituent phylogroups of *ca.* 1 Myr, leading to an estimate of *ca.* 2 Myr for a typical duration of speciation. Avice (2000) (see also Wake 1997) comments that although the coalescent dates of many living sister-species fall within the Pliocene, their speciation was often not completed until the Pleistocene, supporting the importance of Pleistocene conditions in converting initially intraspecific phylogroups into true species.

Although consistent with this perspective, the data of the fossil record suggest that the mtDNA dates may still be underestimating the importance of the Quaternary. In an ideal situation (with dense sampling of a lineage across its distribution in time and space), fossil data can produce estimates analogous to those used by Avice (2000) for mtDNA: the first occurrence of a species, its last occurrence before dividing into recognizably differentiated subspecies, and the first occurrences of those subspecies. As described above, and summarized in table 2, various Quaternary mammalian lineages fulfil these requirements to greater or lesser degrees. However, even the coarse data

available for most species have a direct bearing on the issue. The fossil record of Quaternary mammals of the Holarctic, at least, indicates that almost all living species make their first appearance in the past 2 myr, and that most had durations of much less than this (see examples above, and discussion of macroevolutionary data in § 7). This suggests that the mtDNA coalescent dates for living sister-species may frequently overestimate the date of initiation of speciation, and in consequence extend the apparent duration of the speciation process. Potential explanations for this have been given above: living 'sister species' are more distantly related than the (extinct) true sibling of each; and/or mitochondrial coalescence predates the division into separate breeding populations.

In summary, estimation of speciation dates and durations should ideally be based on all available lines of evidence, including molecular coalescences, morphological differentiation in the fossil record, and/or the distributions, phenotypes and interbreeding potential of living forms. Seeking a single 'date' for the origin of a species may be an inappropriate goal when speciation is a process taking a long time. Nonetheless, taking all the data together, the evidence suggests that the Quaternary has been of primary importance in creating and moulding most mammal species alive today.

## 5. ISLAND MAMMALS

A different situation, in which extensive speciation and adaptive evolution took place in Quaternary mammals, is in the origin of island endemics. This includes the dwarfing of various species of large mammals on many islands of the Mediterranean, southeast Asia and elsewhere. Although island endemics have evolved throughout mammalian history, in the Quaternary we have a sufficiently extensive fossil record to examine patterns and rates of change in relation to the palaeoenvironment. It is clear that, in part, the evolution of endemism has been triggered by sea-level changes, resulting in turn from the expansion and contraction of Quaternary ice-sheets (Lister & Rawson 2003).

A simple example is provided by Cyprus, where no terrestrial mammals are known from before the Quaternary, but lowered sea level apparently then allowed rare (so-called 'sweepstakes') dispersal from the mainland. Endemic dwarf hippopotamus and elephant then evolved there (Sondaar 1977). As pointed out by Sondaar, such faunas tend to be formed by species that are good swimmers, and the endemic forms show clear locomotory and other adaptations to island conditions. The cause of dwarfing itself is much debated, but its consistent occurrence and characteristics on many islands strongly suggest that it is a result of natural selection, whether as an adaptive response to resource limitation and reduced predation, or as a consequence of selection for rapid maturation and early reproduction (Roth 1992; Raia *et al.* 2003).

How long do such forms take to evolve? Unlike most continental examples, islands can provide an opportunity for pinning down the duration of allopatry, because of their known history of isolation in relation to changing sea-level. Lister (1996) compared island dwarfing in deer in two very different settings. In the first, sea-level rise in the last interglacial (*ca.* 120 ka) brought about the

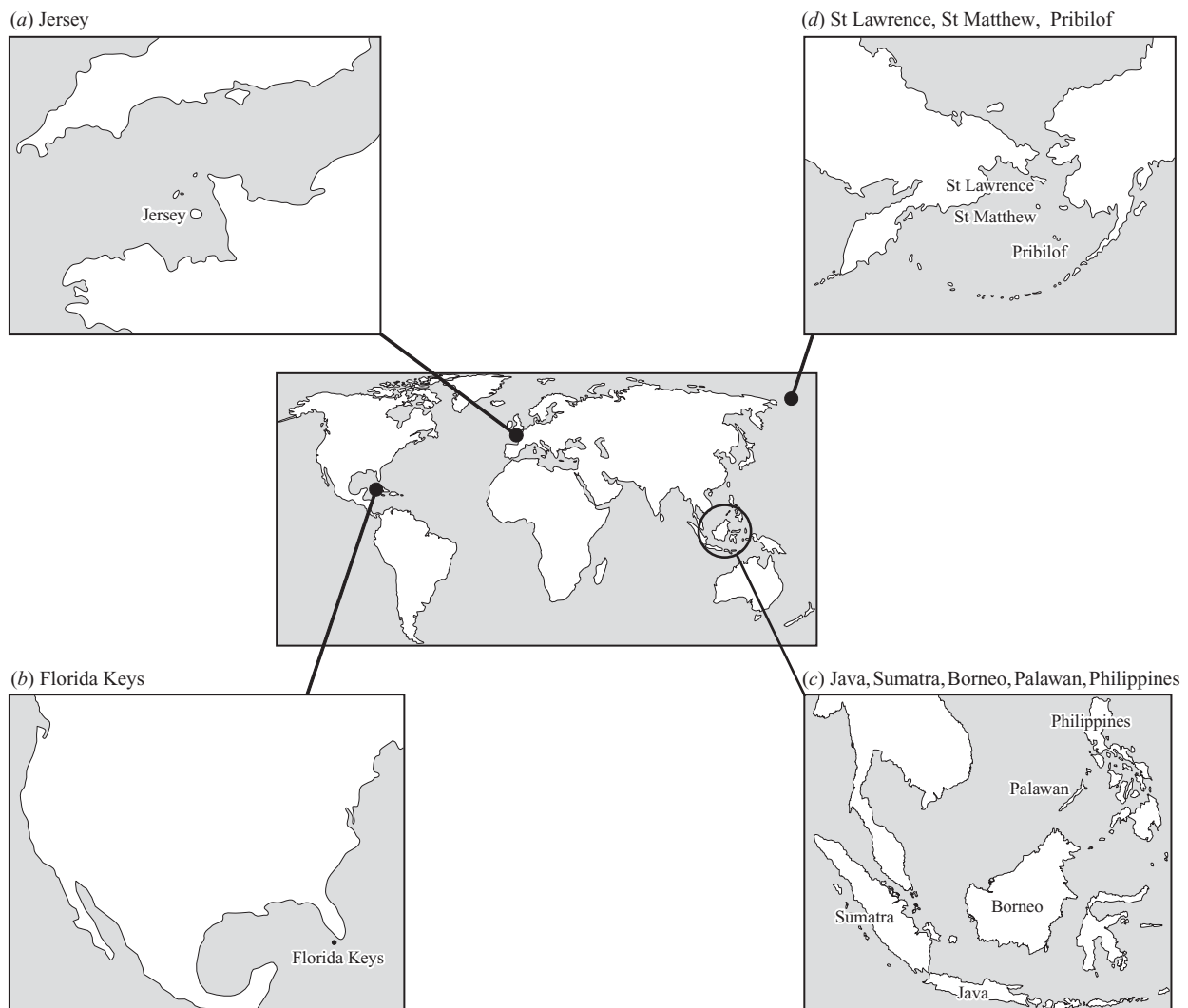


Figure 3. Distributions of island taxa discussed in the text and summarized in table 2. (a) Extinct dwarf red deer, *Cervus elaphus jerseyensis*; (b) Key deer, *Odocoileus virginianus clavium*; (c) islands of southeast Asia with varying degrees of endemism; and (d) islands in the Bering Sea with endemic shrews and rodents.

isolation of a population of red deer (*C. elaphus*) on Jersey, an island close to the northwest coast of France (figure 3a). Within 6 kyr, the population had become dwarfed to about one-sixth mainland body weight, but there were few other changes apart from the allometric consequences of size reduction (Lister 1996), and the animals appear to have been like an extreme example of small-bodied *C. elaphus* populations at the present day. They can therefore be regarded as a subspecies (*C. e. jerseyensis* Zeuner), and were soon lost as sea-level fell and reconnected Jersey to the mainland. Similar natural experiments have taken place in the Holocene; for example, the formation of a small-bodied subspecies of white-tailed deer (*Odocoileus virginianus clavium*) in roughly 5 kyr on the Florida Key islands, paralleled on other islands off the southeastern USA (Purdue & Reitz 1993; Lister 1995; figure 3b).

The longer-term experiment was provided by deer from Crete (de Vos 1984). That island was permanently separated from the mainland, and deer arrived by sweepstakes dispersal, diversifying over several hundred thousand years of the Middle and Late Pleistocene into seven or eight endemic forms. These have postcranial features (such as shortened distal limb elements), and unique antler

morphology (a species-specific recognition character), indicating species status (de Vos 1984; Lister 1996).

Another excellent case study has been described by Heaney (1986), and summarized by Lister & Rawson (2003), in southeast Asia (figure 3c). Once again, we can contrast situations where isolation was cyclic on time-scales of only a few thousand years, with longer-term isolation. The Philippine archipelago, as a whole, is isolated by distance and deep seas from the rest of southeast Asia, and its mammal fauna thus has a very high proportion of endemic species and many endemic genera, which took millions of years to evolve. At the opposite extreme, islands of the continental shelf (Borneo, Java and Sumatra) were connected to the mainland at each low sea stand (most recently *ca.* 18 ka), and have relatively few endemic species. An intermediate condition is shown by Palawan. This is an island divided from Borneo by a channel *ca.* 145 m deep, greater than the 120 m sea-level drop of the Late Pleistocene, but indicating connection in the late Middle Pleistocene, *ca.* 160 ka, when global sea-level fell by 160 m. Palawan has a considerable number of endemic species, but few endemic genera (Heaney 1986). As in the mainland examples (§ 4), the implication is that

subspecies can form in a few thousand years, but that speciation typically requires one or a few hundred thousand years.

There are some apparent exceptions to this rule, in the existence of endemic species on islands that formed in the Holocene. Examples are provided by islands in the Bering Sea (figure 3*d*), where the shrews *S. jacksoni* on St Lawrence Island and *S. pribilofensis* on Pribilof Island, and the vole *Microtus abbreviatus* of St Matthew Island, have each differentiated to the point where their relationships to mainland species are not obvious (Hoffmann 1981). All of these islands were part of the Beringian land mass until sea-level rise cut them off *ca.* 10 ka. A possible alternative explanation for these 'endemics', however, is that they were formerly more widespread species that have survived as relicts on the islands and become extinct on the mainland. In that case, they might have had a more ancient origin. For *M. abbreviatus*, recent mtDNA evidence indicates a close relationship to, and presumably recent derivation from, the mainland Alaskan *M. miurus* (Conroy & Cook 2000). Further molecular, morphological and palaeontological exploration of these forms and potential mainland relatives is required.

## 6. MIGRATION 'VERSUS' EVOLUTION

It has often been stated that animal species survived Quaternary environmental changes in two main ways: by evolving adaptations to new habitats, or by 'migrating' (shifting their range) so as to track a favoured habitat. The term 'migration' is perhaps inappropriate, because in many cases ranges changed with little or no actual movement of animals (Lister 1997; Von Koenigswald 1999). Range expansion requires movement of founder individuals, but *in situ* population expansion then fills the new territory. Range contraction is by die-off not necessarily accompanied by migration.

It is certainly the case that many species responded to Quaternary changes with large range shifts. Examples include reindeer, from the Arctic to southern Europe between interglacials and glacials, and hippopotamus, from Africa to central Europe between glacials and interglacials (Stuart 1982). Graham *et al.* (1996) illustrated major changes in many mammal distributions in the Late Pleistocene of North America, including both expansion and contraction, and 'movement' of the entire range from one region to another, in keeping with climatic and vegetational change. To a degree, species showing dramatic range shifts tend to be those with narrow, specialized niches, such as steppe-living saiga antelope (*Saiga tatarica*) whose range repeatedly expanded into central and western Europe during dry, continental phases of the Quaternary, from a core range further east (Kahlke 1992). Other species, by contrast—often those with broader niches and flexible adaptations, such as red deer, described above, and many carnivores—stayed where they were (frequently over a wide area), or showed relatively minor expansions and contractions of their range boundaries.

The relationship of migration to evolution is not that of a simple alternative but a complex interaction. Dynesius & Jansson (2000) argued that regular migration depresses divergent speciation by truncating isolate persistence. However, there are several ways in which range shifts may

cause, or at least be correlated with, evolutionary change, so the major range shifts of the Quaternary may have provided as much of an opportunity for evolution as a dampener of it.

- (i) In the expansion of populations by 'pioneer' individuals or groups, founder effects alter their genetic composition (usually reducing diversity) (Ibrahim *et al.* 1996; Hewitt 1996). The newly founded populations will therefore have different genetic compositions from each other and from the 'parent' stock in the refugium. The extent to which such changes are cumulative across multiple Milankovitch-induced cycles, or are lost when populations re-contrast in the following cycle, will depend on factors particular to the case in question (Petit *et al.* 2003). Examples (such as for marmot species) have been given above (§ 4).
- (ii) In the contraction of range, areas in which population sizes are falling are, by definition, imposing strong selective pressure. There is potential for individuals to survive if they have appropriate adaptive traits: evolution will have occurred (Lister 1997).
- (iii) If by 'migrating', populations are held in a broadly similar habitat for long periods (even if its geographical location shifts), the resulting constancy of selective pressure may allow long-term adaptive change; an example is given by the mammoth, above (§ 2).
- (iv) In many cases, migrating species may be responding to certain environmental cues (such as temperature), but other parameters will differ in the new range. For example, animal species expanding their range from northern Siberia into central Europe during glacial stages must have experienced changed conditions of daylight, substrate, vegetation, and other species in a competitor or predator-prey relationship to them. All of these factors imply a changed selective regime (Reznick & Ghalambor 2001).

An example of the interaction between migration and evolution is provided by the stimulus to morphological change (dental adaptation to more abrasive vegetation) in water voles (*Arvicola terrestris*) when they expanded from southern to northern Europe after the retreat of the Saalian ice *ca.* 130 ka (Van Kolfschoten 1990; Lister 1997). For various ungulates, Geist (1971) has proposed that the large forms with elaborate antlers (e.g. *C. canadensis* and *A. americana*) arose by *r*-selection as they entered nutritionally rich, unpopulated areas after glacial retreat. Grubb (2000) expanded this idea, showing that geographical 'chains' of related mammalian species or subspecies are better explained by evolution during dispersal, than by gradual *in situ* divergence of vicariant populations. Grubb (2000, p. 166) comments: 'Dispersing organisms should evolve faster; evolutionary rates are likely to be speeded up at the dispersal front compared with the centre of origin, where conditions are more stagnant and selection adopts a stabilizing role. When populations forge ahead into new territory, they experience an upsurge of directional selection'.

## 7. MACROEVOLUTION

The term 'macroevolution' has been used in many ways, but here I refer to evolutionary trends within a clade, determined by the differential survival, extinction and multiplication of species (Stanley 1979). A prerequisite of this process is a significant degree of species turnover, without which 'higher level' processes of species sorting or selection (Vrba 1989) cannot operate. How does turnover in the Quaternary compare with episodes of similar length in the Tertiary? As well as its relevance to macroevolutionary trends, the answer to this question should provide additional evidence on the issue of Quaternary speciation rate, addressed in previous sections.

For any time interval, relative turnover can be calculated as the sum of first and last appearances divided by the total number of species, and has a possible range of 0 to 2. Fortelius *et al.* (1996) examined first and last appearances of mammal species through *ca.* 10 Myr of the Miocene, across six time intervals. Their data for their 'West Block', comprising western and central Europe, give an average value for relative turnover, across the six intervals, of *ca.* 0.9 per interval (range of 0.7–1.2). The intervals are of average length *ca.* 1.7 Myr which, coincidentally, is similar to the duration of the entire Quaternary, allowing direct comparison unaffected by interval length (cf. Foote 2000).

Lister (1997) pointed out that for the European Quaternary, virtually all mammal species present at the start had disappeared by its end, and, by the same token, no present-day species was present at the outset. This is confirmed by perusal of species lists for the start and end of the European Quaternary (Stuart 1982; Sardella *et al.* 1998), and implies a high rate of turnover (figure 4). Taking the Quaternary as a single time unit analogous to each of the Miocene intervals, all the species present at the start can be considered 'last appearances' (because they all became extinct during the Quaternary); all those at the end, 'first appearances' (because they all appeared during the Quaternary). Both of these subsets of species therefore have a relative turnover of 1.0. All other species must have both arisen and become extinct in the Quaternary; this subset by itself would give a maximal relative turnover of 2.0. The overall value must therefore lie between 1.0 and 2.0, depending on the relative proportions of these categories. Full faunal lists for the European Quaternary, using up-to-date taxonomy across all families and regions, have yet to be collated, but it is evident from partial lists (e.g. Sardella *et al.* (1998) on selected species for the Italian Quaternary) that half or more of all recorded species both arose and disappeared during the Quaternary, indicating an overall relative turnover value well over 1.0. Using Sardella *et al.*'s tabulation of large and small mammal species in intervals from the Tasso faunal unit (*ca.* 1.7 Ma) to present, a relative turnover value close to 1.5 can be calculated from their data (162 first or last appearances / 109 species). At present this can be taken as only a very general figure but it is well outside the range of the Miocene data and supports the notion of heightened levels of species turnover (origination and extinction) in the Quaternary. For both the Quaternary and the Miocene sequences, large and small mammals show approximately similar average figures, and 'turnover' is very roughly

comprised of an equal number of first and last appearances. Although, in a few cases, first and last appearances in the region may be due to migration, there is no doubt that turnover is predominantly an index of species origin and extinction.

It is possible that this result could be influenced by the greater stratigraphic resolution of the Quaternary compared with the Miocene, especially in allowing recognition of multiple replacing chronospecies within lineages (C. M. Janis, personal communication). But in the other direction, the Italian data exclude at least 40 species of endemic island forms (mostly Mediterranean (Mayhew 1977; Sondaar 1977; de Vos 1984)), all or almost all of which would increase relative turnover as they arose and disappeared during the course of the Quaternary. The Italian data also exclude a variety of species restricted to northern Europe (*Ovibos*, *Rangifer*, etc.). Further work is needed on this topic.

An elevated rate of species turnover in the Quaternary, deduced here from first and last appearance data across all taxa is, of course, concordant with the data on rapid rates of speciation and subspeciation observed in studies of individual lineages (§§ 4 and 5). An interesting perspective on the promotion of speciation and extinction by environmental disturbance was provided by McKinney & Allmon (1995), based on fossil invertebrate sequences. They suggest that speciation is maximized at 'intermediate' levels of disturbance. At low levels of disturbance, speciation rates are low because little within-species vicariance and population fragmentation occurs, whereas at high levels of disturbance, newly isolated populations do not persist long enough to speciate. The latter situation recalls Coope's (1979) and Bennett's (1990) view of the Quaternary, but the reality for northern mammals, at least, seems to be that the Quaternary imposed an 'intermediate' level of disturbance *sensu* McKinney & Allmon (1995). In part this may have been mediated by the ability of species and populations to avoid the most severe environmental perturbances by range shifts.

Two recent studies have suggested macroevolutionary consequences of Quaternary species turnover, owing to differential survival of species with particular attributes. Potts (1998*b*, table 2) compared species that had become extinct in East Africa during the Middle Pleistocene with closely related forms that survived. He suggests that species that became extinct tended to have highly specialized anatomies indicating narrow niche breadth, such as the zebra *Equus oldowayensis*, the hippopotamus *Hippopotamus gorgops* and the elephant *Elephas recki*. However, species surviving to the present day, such as the zebra *Eq. grevyi*, hippopotamus *H. amphibius*, and elephant *Loxodonta africana*, are more ecologically flexible in their diet, social structure or locomotion. He interprets this in terms of selection for coping with environmental change (see § 3). This recalls Barnosky's (2001) suggestion, cited earlier, that only species capable of surviving Milankovitch-scale climatic fluctuations would survive the Quaternary, although Barnosky believed that many of those that did not would barely make it into the fossil record at all. Dynesius & Jansson (2000) also see this environmental variability as promoting the evolution of generalism and also, interestingly, of vagility, although they do not explicitly invoke macroevolutionary processes.



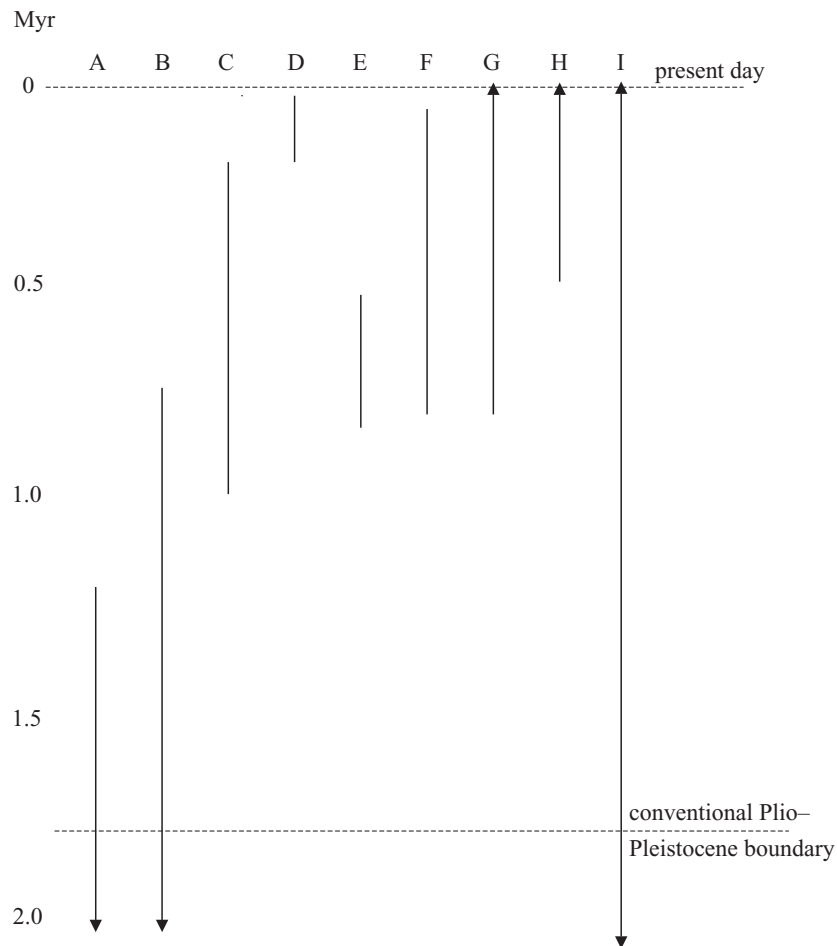


Figure 4. Examples of first and last appearance data contributing to species turnover estimates among European Quaternary mammals. A, *Equus stenonis*, zebra horse; B, *Mammuthus meridionalis*, ancestral mammoth; C, *M. trogontherii*, steppe mammoth; D, *M. primigenius*, woolly mammoth; E, *Megaloceros verticornis*, a giant deer; F, *Palaeoloxodon antiquus*, straight-tusked elephant; G, *Cervus elaphus*, red deer; H, *Ursus arctos*, brown bear; and I, hypothetical species spanning the entire Quaternary. A, B, G and H have a value of 1.0 for turnover calculation (first or last appearance in the Quaternary); C, D, E and F have a value of 2.0 (first and last appearance in the Quaternary); I has a value of zero.

In another study, Johnson (2002) examined the Late Quaternary extinction event across several continents, and showed that absolute fecundity, in offspring per year, was strongly related to survival, across all categories of body size. Johnson concluded that the modern world is depauperate in species with slow reproduction ('bradyfauna'), or to put it another way, there has been macroevolutionary selection in favour of fast reproducers. This fact is consistent with either a hunting or climatic cause of the Late Quaternary extinction (Cardillo & Lister 2002). Johnson (2002) further showed that species that 'bucked the trend', surviving the extinction event despite low fecundity, tended to inhabit 'cryptic' niches, by being, for example, arboreal, nocturnal, or inhabiting dense forests, high latitudes or high altitudes. The survival of a greater proportion of species in 'cryptic' niches is another legacy, which might reflect the demise of more conspicuous animals by human hunting (Johnson 2002).

### 8. CONCLUSION

Responses to the four questions posed at the outset can now be suggested.

**(a) Do mammals show adaptive change triggered by peculiarly Quaternary conditions?**

Many mammals of the northern Holarctic, both living and recently extinct, show adaptations to conditions (e.g. permafrost, tundra, steppe-tundra and ice-floes) that either originated, or became much more widespread, during the Quaternary. Other examples are provided by species isolated on islands by Quaternary sea-level changes, showing adaptations to the island habitat.

It is likely that not only fixed adaptations, but also adaptive ecophenotypic or behavioural flexibility, developed in many species during the Quaternary. Phenotypic effects may in turn have played a role in the origin of fixed differences. Examples include island dwarfing and the origin of short limbs and tails in some northern species.

**(b) Is there a higher rate of speciation, or faunal turnover generally, in the Quaternary than in previous episodes?**

The fossil record demonstrates that almost all modern mammal species, at least in Europe and northern Asia, are Quaternary in origin. Comparison between the Middle to

Late Miocene and the Quaternary suggests a significant increase in mammalian faunal turnover in Europe, at least partly owing to enhanced levels of speciation and extinction. Moreover, the prevalence of modern species with deep internal phylogeographic divisions, dating to the Quaternary, indicates that a 'head count' of species which have completed speciation will underestimate the generation of new species in the Quaternary, because the Quaternary is still continuing and with it, the process of speciation for many taxa.

**(c) Do the chronological patterns of change indicate that they are responding to Milankovitch or other cycles of environmental change?**

The examples of speciation, both on the mainland and in islands, show that although subspecies can form in a few thousand years, full speciation usually takes longer, typically one to several hundred thousand years. In a few cases, species have formed within the span of a single Milankovitch cycle (*ca.*  $10^4$ – $10^5$  years), but we do not know whether this cycle was itself the forcing factor. Importantly, however, the formation of many species over longer time-scales of  $10^5$ – $10^6$  years indicates that Milankovitch cyclicity has not universally inhibited speciation by continually 'returning the clock to zero'. In some cases, at least, this is achieved by range changes which keep the lineage in a quasi-constant strong selective environment, or which impose key differences encouraging altered adaptation. In other cases, environmental variability may have selected for broad-niche adaptations. In practice, mammals do not seem to have needed range constancy for gradual speciation through 'isolate persistence' (cf. Dynesius & Jansson 2000).

**(d) Have these changes left an imprint on the modern biota?**

As far as terrestrial mammals are concerned, the Quaternary has clearly left a strong evolutionary legacy. Many, perhaps most, living mammalian species arose in the Quaternary. Their adaptations, distributions and areas of endemism have been strongly shaped by Quaternary environments. The examples discussed here are admittedly largely drawn from northern biomes strongly affected by Quaternary environmental change. In proportion to the *ca.* 4600 living species of mammal, this is a relatively small group, and it is for future research to determine if these patterns are global in extent. Quaternary climatic cycles have certainly been implicated in vertebrate speciation and adaptation in other parts of the world. For example, the explosive radiation of the cichlid fishes in East African lakes is in part due to the periodic formation and evaporation of the lakes in keeping with Milankovitch cyclicity and Heinrich events (Johnson *et al.* 1996; Stager *et al.* 2002). As has been shown above, the diversity and distribution of mammals on southeast Asian islands has also been shaped by Quaternary conditions. However, Vrba (2000) suggests that, after a major burst of speciation at the onset of Quaternary conditions *ca.* 2.8–2.5 Ma, mammals in Africa did not show appreciably enhanced evolution above Tertiary levels, in marked distinction to the European results discussed above. A possible contributing factor is the greater intensity of Milankovitch effects at

higher latitudes although, paradoxically in the present context, Dynesius & Jansson (2000) see this as an inhibitor rather than a promoter of gradual speciation. Finally, macroevolutionary selection has filtered the species that survive to the present day, for example by increasing the proportion of species of high fecundity and generalist adaptations.

In summary, it is clear that Quaternary evolution is a complex, multifactorial process, in which different causal factors have produced a range of effects. The challenge now is to understand the underlying rules that determine evolutionary outcomes: across taxa, time-scales, geographical realms and changing environments. This will require careful attention to the nature of the data and the approach of researchers working in different areas. For example, tracing speciation rate or other macroevolutionary indices through the Cenozoic will have to take account of variations in stratigraphic resolution and the taxonomic practices of workers studying different time-intervals. Perhaps most challenging of all, we need to investigate to what extent the perceived lack of evolution in some Quaternary groups (such as beetles (Coope 1979) or marine invertebrates (Jackson & Johnson 2000)), or at least lack of increase in evolutionary rate or turnover (as described for birds by Klicka & Zink (1997)), compared with the riot of evolution evident among the mammals, may or may not be an artefact of different datasets, whether relating to methods of investigation or the inherent nature of the material. For example, many of the taxonomic divisions and evolutionary trends among mammals, cited in the present work, are based on fossil teeth and/or bony display organs such as horns or antlers. Birds, apart from having a much poorer fossil record generally, lack both these taxon-specific features; as Stewart (2002) has emphasized, feather coloration and song do not fossilize. A combination of molecular and morphological evidence, modern and fossil, is critical for constraining evolutionary tempo and mode. This may be more challenging to achieve in some groups than others, but will ultimately lead to a fuller understanding of species' origins and adaptation.

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## **Notice of correction**

Figure 2 is now presented in its correct form.

A detailed erratum will appear at the end of the volume.

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