Paleogenomics of Animal Domestication

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Abstract Starting with dogs, over 15,000 years ago, the domestication of animals has been central in the development of modern societies. Because of its importance for a range of disciplines – including archaeology, biology and the humanities – domestication has been studied extensively. This chapter reviews how the field of paleogenomics has revolutionised, and will continue to revolutionise, our understanding of animal domestication. We discuss how the recovery of ancient DNA from archaeological remains is allowing researchers to overcome inherent shortcomings arising from the analysis of modern DNA alone. In particular, we show how DNA, extracted from ancient substrates, has proven to be a crucial source of information to reconstruct the geographic and temporal origin of domestic species. We also discuss how ancient DNA is being used by geneticists and archaeologists to directly observe evolutionary changes linked to artificial and natural selection to generate a richer understanding of this fascinating process.

Keywords Ancient DNA · Archaeology · Domestication · Entomology · Evolution · Genomics · Zoology

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1   Introduction

The domestication of plants and animals was one of the most significant transformations in human history. Domestication was central to the emergence of settled agricultural communities (Larson et al. 2014). The advent of farming and pastoralism, during the Neolithic transition, lead to massive social, economic, religious and demographic changes (Zeder 2012a). It supported vastly increased human population sizes (Bocquet-Appel 2011) and laid the foundation for the development of complex civilisations (Larson and Burger 2013). Ultimately these changes transformed the biosphere and ushered in the age of the Anthropocene (Smith and Zeder 2013).

The study of animal domestication is a broad endeavour, which draws in expertise from archaeology, genetics, ecology and physical sciences (Zeder et al. 2006; Vigne 2011; Larson et al. 2012, 2014; Zeder 2016; MacHugh et al. 2017). This multidisciplinary approach has provided the power to address the critical questions of when, where and how animal domestications took place (Larson et al. 2014), as well as to help elucidate the biological basis for animal domestication (Jensen 2014). More recently, the study of animal domestication has been transformed by the revolution in modern and ancient genome sequencing (Larson and Burger 2013; Larson and Bradley 2014; Gerbault et al. 2014).

This chapter will review how paleogenomics has informed, and will continue to inform, our understanding of animal domestication. We will discuss how paleogenomic approaches applied to domestic species have been used to resolve their geographic and temporal origin, to track human migration, and to understand how animal genomes have been shaped by changes in human culture and technology.

2   Sequencing Ancient DNA

Early ancient DNA (aDNA) studies were constrained by the high cost and low yield of the sequencing technology which was available at the time. The first aDNA study, which recovered DNA from an extinct quagga (Higuchi et al. 1984), used molecular cloning to amplify target DNA molecules, by ligating them into plasmids and replicating them within bacteria (Maniatis et al. 1982). This approach was rapidly superseded by the discovery of the polymerase chain reaction (PCR) (Saiki et al. 1985; Mullis and Faloona 1987), which allowed researchers to efficiently amplify predetermined genomic loci, for sequencing using the Sanger chain-terminating method (Sanger et al. 1977). In vitro amplification (PCR) also had its limitations as it required a priori knowledge of the loci being targeted, which restricted analyses to species and genes which had already been sequenced in modern populations. PCR targets the intended locus using a pair of primers (forward and reverse) which flank the target region. As aDNA is highly fragmented – mostly less than 100 base

pairs (bp) (Sawyer et al. 2012) – the loci targeted by the PCR primers need to be shorter than the average length of endogenous molecules in an ancient sample, or the experiment might fail.

These early PCR-based studies focused primarily on the recovery of a single gene locus from the mitochondrial DNA (mtDNA). The most commonly targeted regions were highly variable loci, such as cytochrome *b* and the mtDNA control region, which were used extensively for resolving molecular phylogenies (Irwin et al. 1991; Meyer 1994). Unlike the nuclear genome, which has only two copies in each cell, there can be many thousands of copies of the mitochondrial genome in each cell (Reynier et al. 2001). This greater relative abundance of mtDNA improves the likelihood of retrieving any particular locus via PCR amplification. Whilst mtDNA is easier to recover, its information content is more limited than nuclear autosomal DNA. Autosomal DNA is inherited equally from both parents, in contrast to mtDNA which is uniparentally inherited, along the maternal line only. Consequently, mtDNA may not reflect the broader evolutionary history of the species as a whole (reviewed in Ballard and Whitlock 2004). Discrepancies between mtDNA and nuclear DNA analysis can be particularly acute when there are sex-biased processes, population replacement or gene flow occurring at the population level, such as those documented in horses (Vilà et al. 2001; Lippold et al. 2011b), pigs (Frantz et al. 2013b) and cattle (Hanotte et al. 2002).

The advent of high-throughput or 'next-generation sequencing' (NGS) platforms in the mid-2000s (Margulies et al. 2005; Bentley et al. 2008) dramatically reduced the cost of sequencing and massively increased the volume of throughput (reviewed in Goodwin et al. 2016). For paleogenomics, NGS technology was instrumental in the sequencing of the first ancient whole genomes, beginning with a ~40,000-year-old woolly mammoth (*Mammuthus primigenius*) (Miller et al. 2008) and shortly followed by a similarly aged Neanderthal (*Homo neanderthalensis*) (Green et al. 2010). In the years since then, ancient whole genomes have been published for several non-human mammalian taxa, including the horse (Orlando et al. 2013; Schubert et al. 2014; Librado et al. 2015), Przewalski's horse (Der Sarkissian et al. 2015; Gaunitz et al. 2018), quagga (Jónsson et al. 2014), auroch (Park et al. 2015), mammoth (Palkopoulou et al. 2015; Lynch et al. 2015), wolf (Skoglund et al. 2015), dog (Frantz et al. 2016b; Botigué et al. 2017; Ní Leathlobhair et al. 2018) and goat (Daly et al. 2018). Whilst ancient whole genomes have yet to be published for domestic pigs, cattle, sheep or chicken, sequences for these taxa will likely be forthcoming in the near future.

Sequencing ancient genomes, however, even with NGS technologies remains challenging – the primary constraint being the poor preservation of endogenous aDNA in subfossil remains recovered from archaeological sites. It is not uncommon for the endogenous DNA fraction of an NGS sequencing run to be below 1% (Carpenter et al. 2013). This problem is particularly acute in geographic regions with warm climates (Hofreiter et al. 2015), where most domestic animals originated. Many factors contribute to the degradation of ancient DNA, including time, temperature, humidity, soil pH and microbial action. Despite decades of research, however, the decay kinetics of DNA degradation are still not well understood (Allentoft et al.

2012). In practice, the heterogeneity of DNA degradation makes preservation infeasible to accurately predict.

Recent studies have shown that aDNA preservation is also highly variable across different archaeological samples – awareness of which has led to dramatic improvements in aDNA recovery by focusing research on samples with higher endogenous yields. The petrous portion of the temporal bone can contain up to 183 times the concentration of endogenous DNA found in less dense bone (Gamba et al. 2014; Pinhasi et al. 2015). Tooth cementum has also been shown to contain comparably high levels of endogenous DNA content (Adler et al. 2011; Higgins et al. 2013; Damgaard et al. 2015). In experiments comparing petrous bones and tooth cementum, recovered from corresponding skeletons, the petrous bone was found to contain higher endogenous yields in only one tested assemblage, with the majority showing no systematic difference in yield (Hansen et al. 2017). As teeth are often over-represented in archaeological assemblages (Lam et al. 1999), they are an ideal target for aDNA recovery. In addition, teeth are great markers of domestication in multiple species, including pigs (Evin et al. 2013), horses (Cucchi et al. 2017) and dogs (Ameen et al. 2017).

Even with these strong constraints, genome-wide datasets have recently been published for early Neolithic farmers from sites across the Near East, including Anatolia, the Levant and Zagros Mountains (Broushaki et al. 2016; Gallego-Llorente et al. 2016; Lazaridis et al. 2016; Kılınç et al. 2016). Comparable sequences for domestic animals from the region have so far been limited to goats (Daly et al. 2018). Given the great importance of the Near East as a centre for domestication, it is likely that more genome-wide sequences from ancient domestic animals will be forthcoming in the near future. Recovery of nuclear aDNA will be crucial to our understanding of the underlying process of domestication.

3   Pathways to Animal Domestication

When, where and how animals were domesticated are central questions to our understanding of human civilisation. The current consensus amongst archaeologists and geneticists is that most domestic animals originated in a small number of 'core' zones, from whence they were dispersed across the globe (Larson and Fuller 2014). As such, animal domestication is thought to be a rare process. Ancient DNA has been key to establish (as well as to challenge) our perception of the geographical and temporal origin of many species and to test the idea that domestication is a rare phenomenon.

The idea that domestication is rare is also based on current theoretical perspective that depict domestication as a non-linear, diffuse and long-term process that requires specific conditions to occur (Conolly et al. 2011; Vigne et al. 2011). The complexity and nuance of these processes have informed the development of two new theoretical models of animal domestication, by Vigne (2011) and Zeder (2012b), which have cast off the anthropocentrism of many previous models.

Vigne's (2011) model described animal domestication as the ultimate phase of intensification in the relationship between animal and human populations. This multistage model proposes a continuum of intensification, progressing through phases of (1) anthropophily, (2) commensalism, (3) control in the wild, (4) control of captive animals, (5) extensive breeding, (6) intensive breeding and ultimately (7) pet keeping (Vigne 2011). Not all domestic animals, however, progressed through each of these stages. By focusing on the shared phases of intensification between different groups of domestic taxa, Zeder's (2012b) model has proposed three main pathways to domestication. This model describes animal domestication as a mutualistic process, with progressive intensification of animal-human relationships; however, it further distinguishes between three distinct evolutionary trajectories: a (1) commensal pathway, a (2) prey pathway and a (3) directed pathway (Zeder 2012b) (Fig. 1).

3.1 The Commensal Pathway

Under the commensal pathway, wild animals were firstly attracted to, and then entangled by, elements of the human constructed niche (Zeder 2012b). The attraction occurred as wild animals were drawn to food sources available on the margins of human occupation – such as refuse scavenging (e.g. wolves and wild boars), food stores (e.g. mice or chickens) or increased prey availability (e.g. cats). These commensal animals would have been subjected to subtle selection favouring individuals who were more adapted to exploit the human niche. Over time this human-animal relationship intensified, ultimately leading to a full domestic partnership. This commensal pathway implies no intentionality or forethought on the part of the human partners during most of the process but rather describes a slowly evolving beneficial relationship (Zeder 2012b).

3.2 The Prey Pathway

Under the prey pathway, wild animals were firstly exploited for their meat and hides before demographic pressures led humans to take an ever-greater role in herd management (Zeder 2012b). Where hunting pressures may have changed the size and composition of prey herds, humans responded by adjusting their hunting strategies to maintain sufficient prey availability – such as preferential targeting of young males (Zeder 2006). Over time, these hunting strategies developed progressively through more advanced systems of herd management and captive breeding through to directed breeding for favourable behavioural and phenotypic traits. In this way, the early stages of the prey pathway can be seen as just as unintentional as the commensal pathway. In contrast, however, the latter stages of the prey pathway are characterised by an intensification of human intervention, in an attempt to maintain supply of a diminishing resource (Zeder 2012b).
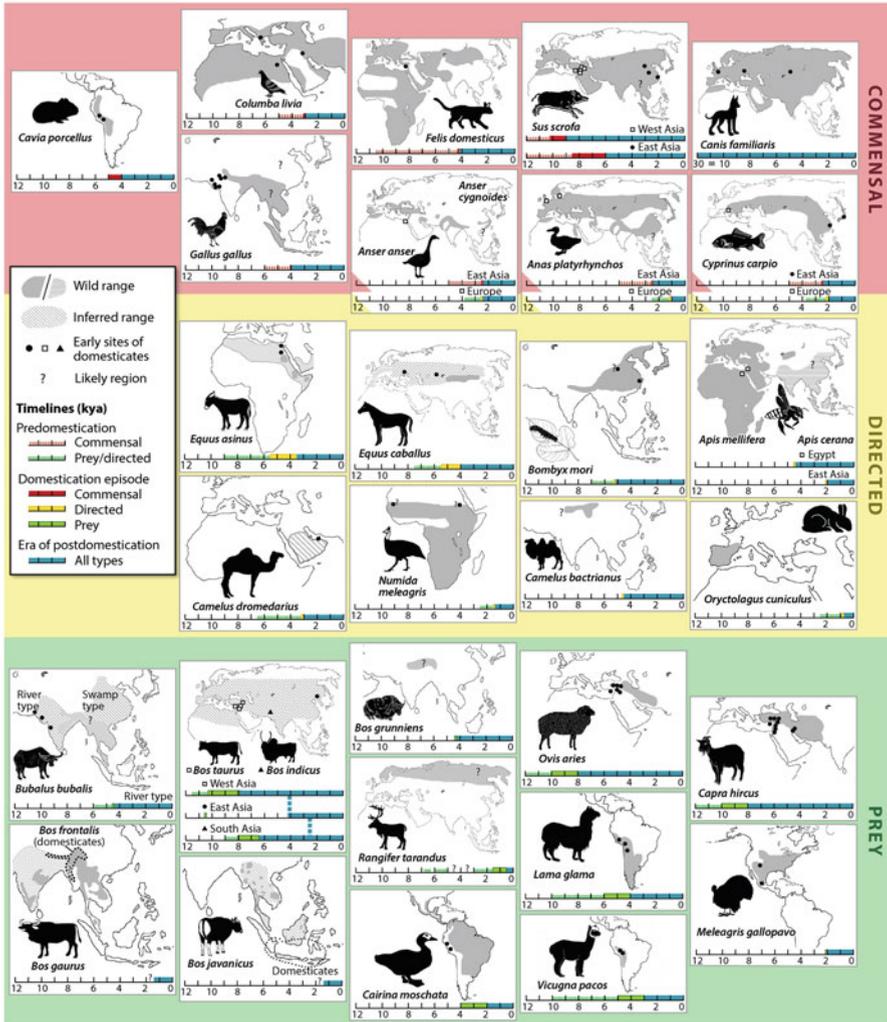
Fig. 1 Geographical/chronological time frame of domestication and potential pathways for major domestic animals. The timelines are in ky (1,000 years) increment. Adapted after Larson and Fuller (2014)

3.3 The Directed Pathway

Under the directed pathway, humans leveraged their prior experience with domestic animals, and their emergent understanding of directed breeding, to capture wild animals and intentionally bring them under increasing levels of human control (Zeder 2012b). The directed pathway describes the route taken for almost all recently domesticated taxa – particularly the exponential increase in aquatic species – but was

of much lesser importance in the distant past. A recent meta-analysis found that 97% of all aquatic domesticates have been domesticated in the past hundred years, including more than 100 species in the preceding decade alone (Duarte et al. 2007). This recent prevalence of the directed pathway, coupled with modern intensive breeding practices, has been formative in the minds of many researchers and obscured a clearer understanding of early animal domestications. The idea of the directed pathway as the preeminent mode of domestication is typified by the theories of Galton (1865) and Clutton-Brock (1994), amongst many others, in which domestication is seen as the logical outcome of the intentional taming of wild animals.

4 When, Where and Which Pathway

The domestication of animals began more than 15,000 years ago, with the domestication of the grey wolf (*Canis lupus*) by nomadic hunter-gatherers (Larson et al. 2012). It was not until much later (beginning around 11,000 years ago) that people in the Near East intensified their relationships with wild populations of sheep, goat, aurochs and boar, such that incipient domestication processes began to emerge (Conolly et al. 2011). By 10,000 years ago, these four elements of the so-called Neolithic package had spread extensively throughout Southwest Asia and the Eastern Mediterranean (Vigne 2008). Despite the later ubiquity of these domesticates across the region, detailed zooarchaeological studies have revealed the complex non-linear nature of these domestication processes, complete with ebbs and flows in tempo in response to the local environment and conditions (Conolly et al. 2011; Vigne et al. 2011).

In the following section, we will briefly review what is known about the domestication of a range of key mammalian, avian and insect species – with a particular focus on paleogenomic contributions to our understanding of these domestications. The species profiles are grouped by the pathways they each took towards domestication, to highlight shared elements of the underlying process.

4.1 Commensal Domesticates

4.1.1 Dogs

The first animal likely to have followed the commensal pathway to domestication was the grey wolf (*Canis lupus*) (reviewed in Thalmann and Perri 2018). It has been theorised that wolves which were naturally less wary of people would have been drawn to human encampments to scavenge refuse left by hunters (Thalmann and Perri 2018). Where, when and how many times wolves were domesticated remains a contentious issue, due to the sparsity of evidence and conflicting interpretations of both the archaeology and genetics (Germonpré et al. 2009; Larson and Bradley

2014; Skoglund et al. 2015; Frantz et al. 2016b; Botigué et al. 2017; Ní Leathlobhair et al. 2018).

The earliest widely accepted archaeological dog remains date to about 15,000 years ago (Thalmann and Perri 2018). Earlier canid remains, dating back to over 30,000 years ago (Germonpré et al. 2009), were recently described as dogs, but their status (as dogs or wolves) remains highly controversial (Perri 2016). Paleogenomic data has provided additional information about the potential time frame for dog domestication. In particular, analyses of genome-wide data from an ancient Siberian wolf (Skoglund et al. 2015) and an ancient Irish dog (Frantz et al. 2016b) together with radiocarbon dates have provided the means to estimate a reliable mutation rate for canids and to obtain an estimate of the divergence time between extant wolves and dogs of 20,000–40,000 years ago. This timing, which represents an upper bound for dog domestication, needs to be interpreted with caution as the ancestor of dogs may have become extinct (Thalmann et al. 2013; Freedman et al. 2014; Frantz et al. 2016b). This would mean this time instead represents the time of divergence between extant wolves and the ancestor of dogs, rather than the time at which dogs were domesticated.

Over the years, genomic (including paleogenomic) studies have provided conflicting information about the geographical origin of dogs, with papers suggesting that dogs originated in East Asia (Pang et al. 2009; Wang et al. 2015), Central Asia (Shannon et al. 2015), the Middle East (von Holdt et al. 2010) and Europe (Thalmann et al. 2013). Additional genome-wide paleogenomic studies, however, have provided novel clues on the geographical origin of dogs. For example, studies based on ancient genomes from European dogs have suggested that modern Western Eurasian populations (including Africa, Europe and Middle East) were most likely imported from Asia, over 7,000 years ago (Frantz et al. 2016b; Botigué et al. 2017). Based on additional archaeological data and multiple ancient mtDNA sequences, the authors of one of these studies suggested that populations that inhabited Europe and the Middle East, prior to the arrival of dogs from East Asia, had been domesticated independently (Frantz et al. 2015). This hypothesis, which implies that the dogs that were present prior to the arrival of East Asian dogs are now extinct, remains to be tested.

4.1.2 Pigs

Although they were hunted like other ungulate species (sheep, goat, cattle, etc.), the omnivorous lifestyle of pigs provided them with the ability to consume human waste, suggesting that they were potentially domesticated via a commensal pathway (Larson and Fuller 2014). Interestingly, pigs are the only animals for which we have unequivocal, genetic and archaeological evidence for two independent domestication processes, from two different subspecies of *Sus scrofa*, in China and Anatolia, respectively (Larson et al. 2005). Ancient DNA studies have played a key role in unravelling a complex domestication history marked by frequent population replacements.

The Western Eurasian domestic pigs were most likely first domesticated in Anatolia, over 10,000 years ago, as suggested by zooarchaeological evidence of selection and culling from long-term occupation sites such as the Çayönü Tepesi (Hongo and Meadow 1998; Ervynck et al. 2001). Ancient DNA evidence suggests that they were then transported, from the Near East into Europe as part of the Neolithic package (Larson et al. 2007a), around 9,000 years ago (Conolly et al. 2011). Evidence for such an early human-mediated dispersal of pigs, from the Near East into Europe, however, is absent from modern DNA sequences (Larson et al. 2005). Lack of Near Eastern ancestry in modern domestic breeds is most likely the result of a population turnover resulting from long-term gene flow between European wild boars and domestic pigs (Frantz et al. 2015), a process that likely started as soon as pigs were introduced in Europe (Larson et al. 2007a).

Further ancient DNA evidence suggests that European domestic pigs, lacking Near Eastern ancestry, were later introduced back into the Near East (Anatolia), during the Iron Age where they replaced pigs with Near Eastern ancestry (Ottoni et al. 2013). More recently, Chinese pigs, which were domesticated from a highly divergent subspecies (Frantz et al. 2013b, 2016a), were imported in Europe to improve production traits during the industrial revolution (White 2011; Bosse et al. 2014a). This process dramatically affected the genetic (Bosse et al. 2014b) and phenotypic make-up (Bosse et al. 2014a) of European populations.

In East Asia, the first unequivocal evidence of pig domestication dates back to ~8,600 years ago at the site of Jiahu near the Yellow River (China) (Cucchi et al. 2011). Similar to the process seen in Europe, ancient mtDNA evidence suggests that East Asian domestic pigs were transported from their domestication centre to Island Southeast Asia, Papua and Polynesia where they were later replaced by pigs of European decent (Larson et al. 2010; Linderholm et al. 2016). During their human-mediated dispersal throughout Island Southeast Asia, domestic pigs encountered a high diversity of wild suid species (and subspecies) which readily interbreed with domestic pigs (Frantz et al. 2013b, 2014; Ai et al. 2015). Future ancient nuclear DNA will be able to assess whether deliberate interbreeding with wild stock may have allowed for adaptation of domestic pigs to the wide range of habitat they encountered in Europe, Asia and Polynesia (Frantz et al. 2016a).

4.1.3   Cats

Cats (*Felis catus*) also became domesticated via the commensal pathway; however, despite their worldwide popularity, relatively little is known about the origins of the domestic cat (reviewed in Geigl and Grange 2018). The archaeological and genetic evidence points to both the Near East and Egypt as important regions for the domestication of the cat (Vigne et al. 2004; Driscoll et al. 2007; Ottoni et al. 2017). The wild progenitor of the domestic cat (*Felis catus*) is the Near Eastern wildcat (*Felis silvestris lybica*), which has a natural range spanning North Africa and the Near East (Driscoll et al. 2007). Archaeological remains of wildcats in the Near East point to a long history of commensal relationship with early farming

communities, where they are thought to have predated on invasive rodent populations (Vigne et al. 2004, 2012). This relationship persisted for thousands of years before the appearance of any classic domestication traits – such as reduction in overall body size and the emergence of novel coat colours (Vigne et al. 2016). The dispersal of domestic cats around the world was aided by their role on ships and trade vessels as protection against rodents. This is reflected in their patterns of dispersal, which mirror major trade routes (Lipinski et al. 2008; Ottoni et al. 2017).

A worldwide phylogenetic study of modern cats, using a fragment of the mitochondrial genome (mtDNA) and microsatellite markers, has shown that the Near Eastern wildcat (*F. s. lybica*) is more closely related to the domestic cat than other subspecies of wildcat (Driscoll et al. 2007). Based on the current distribution of wildcats, the authors concluded that cats were most likely domesticated in the Near East. Of the 979 analysed samples, they identified 15 wildcats from Israel, the United Arab Emirates, Bahrain and Saudi Arabia with mtDNA and microsatellite markers consistent with those found in modern domestic cats (Driscoll et al. 2007). Further research, using microsatellite markers to analyse the phylogeographical structure of modern domestic cats, also found support for a Mediterranean basin origin for their dispersal (Lipinski et al. 2008).

A recent ancient mtDNA study of 209 archaeological cat remains has shown that mitochondrial lineages from both the Near East and Egypt contributed to worldwide domestic cat populations at different times (Ottoni et al. 2017). Their analysis showed that domestic cats are drawn from five deeply divergent mtDNA subclades (IV-A to IV-E) of *F. s. lybica* and that the relative proportions of domestic cat haplogroups have shifted over time. The IV-A and IV-B subclades were identified as originating in the Near East and represent the first wave of domestic cats which spread across the Old World. The IV-C subclade originated in Egypt and was found in the majority of Egyptian cat mummies. Despite a supposed ban on the export of Egyptian cats (Zeuner 1963), the Egyptian subclade increased in frequency outside Egypt, such that during the first millennium AD in western Anatolia, it had expanded to twice the frequency of the local Near Eastern subclade (Ottoni et al. 2017). The authors speculated that the cause of this increase might have been due to more desirable behavioural characteristics of the Egyptian cats.

The same study also looked at the history of the tabby coat trait, one of the most widely used markers for identifying domestic cats (Ottoni et al. 2017). Their analysis found that the coat-colour variant responsible for the derived blotched tabby marking only reached high frequency after the Middle Ages, around the time that cat pelts were being traded for clothing. Coupled with the relatively small changes in overall size of domestic cats, this suggests that directed breeding of cats for morphological novelty was a very late phenomenon (Ottoni et al. 2017).

4.1.4   Chickens

Genetic data from modern domestic chickens and wild junglefowl have established that the red junglefowl (*Gallus gallus*) is the primary wild ancestor of the domestic

chicken (Liu et al. 2006; Miao et al. 2013). Studies of nuclear genetic data have demonstrated, however, that the yellow skin allele found in domestic chickens was not inherited from red junglefowl but was instead inherited from the grey junglefowl (*Gallus sonneratii*) demonstrating that the genome of modern domestic chickens combines elements of at least two junglefowl species (Eriksson et al. 2008).

An initial review of the archaeological evidence argued that chicken domestication had begun by the third millennium BC, since the first robust evidence for poultry farming has been recovered in the Indus Valley ~2,600–1,900 BC, before chickens were then translocated to the Near East, Africa and Europe during the first millennium BC (Zeuner 1963). Based on an analysis of osteological evidence that attested to the presence of chickens during the Middle Neolithic (~6,000–4,000 BC) in the Yellow River basin, West and Zhou (1988) concluded that chickens were domesticated in the Southeast Asian native range of red junglefowl prior to 6,000 BC before being dispersed westwards along a northern route through Central and Western Eurasia. Two subsequent studies (Berke 1995; Peters 1997) questioned whether the Chinese specimens actually belonged to domestic chickens since they possessed morphological features typical of other galliform birds including pheasants. Despite these critiques, a mid-Holocene origin of domestic chickens has been frequently claimed in the literature.

A recent ancient DNA analysis of galliform bone specimens from Early and Middle Neolithic sites in the Yellow River basin reinforced the claims for an early domestication of chickens (Xiang et al. 2014). This study suggested that red junglefowl dispersed naturally to Northern China following the Younger Dryas where they were then domesticated during the early Neolithic. This assertion has since been questioned. An independent morphological re-evaluation of galliform bones from Northern Chinese Neolithic sites concluded that the bones in question belonged primarily to the common pheasant (*Phasianus colchicus*) (Peters et al. 2016; Eda et al. 2016). In addition, several lines of evidence including an assessment of associated wild mammalian faunas and high-resolution climate and precipitation records from temperate Holocene East Asia suggested that the (sub-)tropical forest habitat conducive to thermophilic red junglefowl did not extend into Northern China during the mid-Holocene climatic optimum (Peters et al. 2016). Lastly, multiple studies of modern domestic chickens have suggested that red junglefowl from peninsular Southeast Asia is the likely initial population from which domestic chickens were derived, and a recent genetic study of complete mitochondrial genomes has cast doubt on the likelihood that chickens were domesticated in Northern China (Huang et al. 2018). Future archaeological and genomic studies of modern and ancient chickens are necessary to reveal not only the spatial and temporal pattern of chicken domestication but also the process which led to the close association between chickens and people.

4.2 Prey Domesticates

4.2.1 Goats

Goats (*Capra hircus*), along with sheep (*Ovis aries*) and cattle (*Bos taurus*) all followed the prey pathway to domestication in the Fertile Crescent region of the Near East (Zeder 2012b). Archaeological and genetic evidence has established that goats were domesticated from the bezoar ibex (*Capra aegagrus*), a species of wild goat inhabiting the mountainous region spanning southwestern Turkey to central Afghanistan and southern Pakistan (Zeder and Hesse 2000; Naderi et al. 2008).

Detailed zooarchaeological studies of wild goat assemblages have allowed researchers to reconstruct the age and sex-specific harvest profiles employed by hunters prior to domestication. These harvest profiles reveal incipient herd management strategies, in which hunters transitioned from targeting of prime age males, which maximised short-term meat return, towards selective culling of subadult males and older adult females, to promote growth in herd sizes (Zeder and Hesse 2000; Zeder 2006, 2008). These management strategies of wild ranging goats gradually intensified from herding towards a fully domestic relationship, and domestic phenotypes appear in archaeological goat assemblages around 10,500 years ago at multiple sites across Southeastern Anatolia, the Zagros Mountains and Cyprus (Conolly et al. 2011).

Domestic goats were subsequently brought into Europe as part of the Neolithic package; however, unlike with pigs and cattle, there were no extant wild populations for the incoming domestic population to admix with (Scheu et al. 2012). Studies of modern mitochondrial DNA in domestic goat populations have revealed unusually high levels of genetic diversity coupled with low levels of geographical structuring (Luikart et al. 2001; Naderi et al. 2007, 2008). This diversity has been attributed to population structure in the region of domestication, followed by extensive trade and transport of domestic goats. Modern goat populations comprise six maternal haplogroups (A, B, C, D, F and G), with most domestic goats belonging to haplogroup A (Naderi et al. 2007). The first ancient DNA study of goats established that haplogroups A and C were both present in the Early Neolithic in France, with moderately high genetic diversity, a result that the authors interpreted as potential evidence for two independent domestications with subsequent gene flow between populations (Fernández et al. 2006).

Recently, the diverse origins of domestic goats were further investigated in the first genome-wide study of ancient caprids (Daly et al. 2018). The authors selectively targeted petrous bones to retrieve genome-wide data from 51 ancient goats and used mtDNA capture to retrieve complete mtDNA genomes for 83 ancient goats. Their analyses of nuclear genomes provided evidence for variable proportions of ancestry shared between pre-domestic wild goats and early domestic goat populations, which suggested local recruitment of divergent wild populations during domestication (Daly et al. 2018). This was mirrored by the mtDNA data, which showed that multiple highly divergent haplogroups were involved in the domestication process

and have differentially contributed to the genetic make-up of modern populations. This study also revealed that, in contrast to modern populations (Naderi et al. 2008), mtDNA haplogroups were highly structured in ancient populations (Daly et al. 2018). Interestingly, the collapse in haplogroup structure happened relatively early in their evolutionary history (~7,000 years ago), when haplogroup A replaced most others to become the dominant haplogroup across the region (Daly et al. 2018).

4.2.2 Sheep

Sheep (*Ovis aries*) also followed a prey pathway to domestication in the Fertile Crescent, around 10,500 years ago, with the Asiatic mouflon (*Ovis orientalis*) as the most likely wild progenitor (Conolly et al. 2011). Both the urial (*Ovis vignei*) and the argali (*Ovis ammon*) have also been suggested as potential ancestors; however, no mitochondrial lineages from either species have been observed in domestic sheep populations (Meadows et al. 2011). The European mouflon (*Ovis aries musimon*) is a feral descendent of a primitive domestic population (Bruford and Townsend 2006), and a recent genome-wide analysis revealed widespread bidirectional admixture between European mouflon and modern domestic sheep (Barbato et al. 2017).

Domestic sheep populations comprise five maternal haplogroups (A, B, C, D and E), with most modern sheep belonging to haplogroups A, B and C (Meadows et al. 2011). Two major Y-chromosome patrilines have also been identified, showing limited geographic structure (Meadows and Kijas 2009). Similar to the pattern seen in domestic goats, the maternal haplogroups diverged long before domestication, suggesting that multiple divergent lineages were involved in the domestication process (Pedrosa et al. 2005; Meadows et al. 2011). The relative abundance of these haplogroups has changed over time, with haplogroups A and B dominating the initial expansion into Europe, followed by haplogroup C around 3,000 years ago (Tapio et al. 2006). This first wave of domestic sheep, bred primarily for meat production, was replaced by a second wave of domestic stock carrying improved production traits for wool and milk (Chessa et al. 2009; Demars et al. 2017).

Recently, a genome-wide study of selection in modern sheep and goats found 90 selective sweep regions which segregated between domestic and wild populations of *Capra* and *Ovis* (Alberto et al. 2018). A gene ontology enrichment analysis (reviewed in Huang et al. 2009) identified significant enrichment for genes involved in nervous system, immunity and productivity traits (Alberto et al. 2018). Interestingly, this analysis identified only 20 regions under selection which were common to both *Capra* and *Ovis*, suggesting that convergent phenotypes in goats and sheep were primarily established by selection on non-homologous gene regions.

4.2.3 Cattle

Cattle (*Bos taurus* and *Bos indicus*) also followed the prey pathway to domestication; however, there is ongoing uncertainty about how many times cattle were

domesticated (Loftus et al. 1994; Troy et al. 2001; Hanotte et al. 2002; Beja-Pereira et al. 2006; Chen et al. 2010; Pitt et al. 2018). Large genome-wide studies of modern domestic cattle have shown that they form three deeply divergent groups: (1) Eurasian and (2) African taurine cattle (*Bos taurus*) and (3) Asian indicine cattle, or zebu (*Bos indicus*) (Gibbs et al. 2009; Decker et al. 2014).

The earliest cattle domestication occurred in the Fertile Crescent, approximately 10,500–10,000 years ago, where Eurasian taurine cattle were domesticated from wild Eurasian aurochs (*Bos primigenius*) (Hanotte et al. 2002; Helmer et al. 2005; Hongo et al. 2009; Conolly et al. 2011). The domestication of Asian indicine cattle occurred in South Asia, approximately 8,000–7,500 years ago, and was the product of either an independent domestication process or admixture between domestic taurine cattle and Asian aurochs (*Bos primigenius namadicus*) (Meadow 1983; Loftus et al. 1994; Chen et al. 2010; Larson and Burger 2013). Current archaeological and genetic evidence is consistent with an independent domestication process; however, without ancient genome-wide data, admixture between Asian aurochs and domestic taurine cattle cannot be ruled out as the potential source of indicine cattle domestication (Larson and Burger 2013). Uncertainty around a hypothesised independent domestication of African aurochs (*Bos primigenius africanus*) (Bradley et al. 1996; Hanotte et al. 2002; Wendorf and Schild 2005; Stock and Gifford-Gonzalez 2013), in the Western Desert of Egypt, has been largely resolved following reanalysis of the archaeological material (Brass 2018) and explicit model-based testing of the genetic data (Pitt et al. 2018), which found no evidence for an independent African domestication.

A recent study published the first whole-genome sequence of an extinct Eurasian aurochs (*Bos primigenius*), recovered from a 6,750-year-old British specimen (Park et al. 2015). Analysis of the genome-wide data revealed localised nuclear gene flow into the ancestors of British and Irish taurine cattle, contrary to previous mtDNA studies, which found no evidence of introgression (Edwards et al. 2007). Model-based testing of ancient genetic data suggests that the matrilineal founding population of taurine cattle may have been as low as just 80 individuals (Bollongino et al. 2012; Scheu et al. 2015). As taurine cattle migrated from the Near East into Europe, their mtDNA genetic diversity decreased along the axis of migration, and intercontinental migration continued up until ~7,000 years ago (Scheu et al. 2015). When whole-genome sequences of early domestic cattle become available, we will be able to better resolve the role of introgression between Eurasian domestic cattle and wild aurochs.

Within Asia, the evolutionary history of the *Bos* genus is characterised by reticulate admixture between domestic cattle populations and other *Bos* species (Wu et al. 2018). East Asian cattle populations show a mosaic of ancestry components, including an ancestral East Asian taurine component, a later Eurasian taurine component and a deeply divergent Chinese indicine component (Chen et al. 2018). Cattle populations from Tibet also show signs of adaptive introgression of yak (*Bos grunniens*) genes, in the response-to-hypoxia pathway, likely supporting an adaptation to high altitude (Chen et al. 2018; Wu et al. 2018) – similar to the adaptive introgression from Denisovans into Tibetans (Huerta-Sánchez et al. 2014) and Tibetan wolves into Tibetan mastiffs (Miao et al. 2017).

4.2.4 New World Camelids

In South America, llamas (*Lama glama*) and alpacas (*Vicugna pacos*) likely also followed a prey pathway. Archaeological evidence suggests the domestication of llamas and alpacas from their potential wild progenitors, vicuñas (*Vicugna vicugna*) and guanacos (*Lama guanicoe*), began ~6,000 years ago (Diaz-Lameiro 2016) within their overlapping native ranges in the mountainous regions of Bolivia, Chile and Peru and the central Andes Mountains (Barreta et al. 2013). There are two current hypotheses for how the domestication of these two species took place. The first is that both llamas and alpacas are domesticated forms of guanacos. Alternatively, alpacas may be a domesticated form of vicuñas, while llamas were derived from guanacos.

Both these hypotheses have support from genetic data. Ancient mitochondrial DNA sequenced from llama and alpaca remains from pre-Columbian South American sites (Cerro Narrio, Ecuador and Iwawi, Bolivia) demonstrated that the ancient alpacas and llamas clustered together within a well-supported monophyletic group more closely related to guanacos than to vicuñas, thus suggesting that both species were domesticated from guanacos in the northern South American Andes (Diaz-Lameiro 2016). The second hypothesis is supported by a study using modern nuclear data, which suggested that alpacas and llamas are more closely related to vicuñas and guanacos, respectively (Kadwell et al. 2001; Wheeler et al. 2006). Though this second study based upon a larger number of nuclear and mitochondrial loci has more weight, the large observed differences between the wild species may be partly due to a strong bottlenecking in the recent past. For instance, the vicuña population in the 1960s had a population size of only 2,000 across South America (Barreta et al. 2013), and guanaco populations have been small over the past century. The biases associated with these recent demographic shifts may have had an effect on the interpretation of these datasets. Understanding the origins and domestication history of these two species will be much more clearly understood through the generation and interpretation of ancient nuclear DNA datasets derived from archaeological material across the spatio-temporal range of the wild and domestic species.

4.3 Directed Domesticates

4.3.1 Horses

The earliest suggested case of an animal following the directed pathway to domestication is that of the horse (*Equus ferus caballus*) (Zeder 2012b), which may have been domesticated to assist steppe pastoralists in hunting wild horses (Levine 1999; Olsen 2006a). Identifying horse domestication in the archaeological record is difficult because many of the classic markers of domestication show no discernible variation between early wild and domestic populations – e.g. morphological changes (Eisenmann and Mashkour 2005) and mortality profiles (Olsen 2006a, b). The

earliest evidence for horse domestication (reviewed in Orlando 2018) comes from Central Asia, around ~5,500 years ago, where skeletal pathologies indicate horses were bridled and probably ridden and stable isotope analysis of lipid residues in pottery indicate processing of mare's milk (Outram et al. 2009).

Modern horse populations comprise 18 major maternal haplogroups (A–R), 17 of which are found in domestic horses and 1 of which (haplogroup F) is found only in Przewalski's horses (*Equus ferus przewalskii*) (Achilli et al. 2012). This high number of mtDNA haplogroups, which diverged long before the start of domestication, has been interpreted as evidence of extensive restocking of wild mares during the domestication process (Vilà et al. 2001; Lippold et al. 2011b). In contrast, modern Y-chromosome patrilines have an extreme lack of diversity (Lindgren et al. 2004), likely caused by a strong bottleneck in male horses. The timing of this bottleneck is not clear, however, as aDNA studies have revealed that ancient domestic horses had greater Y-chromosome diversity than modern horses (Lippold et al. 2011a; Librado et al. 2017). The recent publication of the first complete assembly of the horse Y-chromosome should assist in future aDNA studies of male-biased processes in horse domestication (Janečka et al. 2018).

A recent genome-wide aDNA study of 14 ancient domestic horses has also challenged the traditional view that the high rate of deleterious mutations found in modern horses can be attributed to a male population bottleneck during domestication (Librado et al. 2017). The 'cost of domestication' hypothesis (reviewed in Moyers et al. 2018) argues that the process of domestication leads to increased levels of deleterious mutations in domestic animals – principally via population bottlenecks and strong artificial selection. In the case of horses, however, aDNA has revealed that ancient domestic horses had high rates of genetic diversity, and an analysis of the fitness consequences of that diversity found that the mutational load of ancient horses was less than that of both modern horses and pre-domestic horses (Librado et al. 2017). This implies that current levels of deleterious mutations are most likely a product of subsequent breeding practices, rather than a consequence of the domestication process itself.

Przewalski's horses are often described as the only extant wild horses (e.g. Der Sarkissian et al. 2015), after they were rescued from extinction in the wild following a captive breeding programme involving 12 wild-caught individuals (Volf et al. 1991). A recent genome-wide aDNA study of ancient domestic and Przewalski's horses, from the domestication centre in Central Asia, however, showed that Przewalski's horses are not truly wild but are instead the feral descendants of the first domestic horses (Gaunitz et al. 2018). This study revealed that it was the ancestors of modern Przewalski's horses which were first domesticated ~5,500 years ago and that by ~4,000 years ago, there had been a nearly complete genetic turnover amongst domestic horses, coinciding with the dramatic population expansion associated with the Yamnaya culture during the Early Bronze Age (Allentoft et al. 2015; Gaunitz et al. 2018). The exact timing of this turnover, and the geographic origin of the population, which gave rise to all modern domestic horses, remains unknown. Whilst there is still much to discover about the evolutionary history of horses, this study highlights the incredible insights that paleogenomics can bring to our understanding of the history of domestication.

4.3.2 Rabbits

The European rabbit (*Oryctolagus cuniculus*) is often reported to have been domesticated via the directed pathway. In the most widely cited historical account, rabbits were supposedly domesticated by Catholic monks in France, circa AD 600, when they were granted a dispensation to eat foetal rabbits during Lent (Zeuner 1963; Clutton-Brock 1981). The practice of eating *laurices* – newborn or foetal rabbits – goes back to at least the first century AD, when Pliny the Elder describes the Spanish delicacy of cutting foetal rabbits from the belly of their mother and eating them whole and uneviscerated (*Naturalis Historia*, 8.55). It follows that by granting permission to consume *laurices* during the many fasting days of the mediaeval calendar, French monks were suddenly motivated to move the breeding of rabbits above ground to obtain a reliable supply of newborn rabbits. First put forward by Nachtsheim (1936), this account has its origins in a widely miscited text from the late sixth century by St Gregory of Tours (Gregory 1969). Through successive retellings, the account became incrementally embellished, such that consumption of *laurices* became especially popular amongst the monks during Lent (Nachtsheim 1936), then permitted by the Church because they were not considered meat (Zeuner 1963), and ultimately that the dispensation was granted by Pope Gregory the Great (Carneiro et al. 2011), an unrelated contemporary of St Gregory of Tours. In fact, there is no evidence that eating *laurices* was ever commonplace nor that they were not considered meat, and the timing and nature of rabbit domestication remains unknown (Irving-Pease et al. 2018).

Despite this, European rabbits have a well-resolved geographic origin, in Southwest France, and the presence of an extant wild progenitor makes it comparatively easy to obtain modern genomic samples from which to model the process of selection during domestication (Carneiro et al. 2011, 2014, 2015). A recent study compared genome-wide data from six breeds of domestic rabbits and wild rabbits from across their native range, to scan for segregating signatures of selection (Carneiro et al. 2014). The authors found more than 100 selective sweep regions distinct to domestic rabbits, and a gene ontology enrichment analysis identified significant enrichment for genes involved in brain and neuronal development (Carneiro et al. 2014). Interestingly, the authors found very few fixed derived alleles in the domestic breeds, suggesting that domestication was achieved via changes in allele frequencies at hundreds of loci, each with low effect size. When ancient genome-wide data becomes available for European rabbits, it should be possible to test the timing of selection at these loci, to better elucidate the process of rabbit domestication.

4.3.3 Old World Camels

The progenitor of modern Old World camels reached Eurasia ~3 million years ago (Gauthier-Pilters and Dagg 1981; Köhler 1981; Peters 1997). By the Middle

Pleistocene, Old World camels ranged from China and Mongolia over Central Asia to the Arabian Peninsula, including parts of North Africa and Eastern Europe (Köhler 1981; Titov 2008). By the end of the Pleistocene, the range of wild camelids had contracted dramatically (Gaulthiers-Pilters and Dagg 1981; Kozhamkulova 1986; Titov 2008), and several wild camel species became extinct leaving only the species *Camelus ferus*.

The distribution of the small extant wild population is restricted to China and Mongolia (Bannikov 1976; Hare 1997; Reading et al. 1999; Mix et al. 1997, 2002), though the domestic form, *Camelus bactrianus*, has spread throughout Central Asia and is now found from Northeast China, Mongolia, South Russia and Central Asia. In Asia Minor, its distribution overlaps with that of the dromedary. The one-humped dromedary camel, probably once found as a wild animal throughout the Arabian region but known with certainty only in the domestic or feral state, is now widespread in the hot deserts of North Africa and Arabia (Walker 1964).

Archaeological records show evidence for a relationship between people and the Bactrian camel ~5,000 years ago (Bulliet 1975; Benecke 1994), and the earliest records of camel bones come from sites Turkmenistan and Iran (Kuzmina 2008). Given the presence of camel bones in Bronze Age strata from sites in Iran and southern Turkmenistan, it has been hypothesised that the inhabitants of the Iranian Plateau and the Kopet Dagh foothills area played a major role in the domestication of the two-humped camel (Benecke 1994).

Due to their use as pack animals, the modern populations of dromedary camels do not possess significant phylogeographic structure (Almathen et al. 2016). A recent study of dromedary camels (Almathen et al. 2016) successfully recovered DNA from ancient dromedary remains. The authors concluded that the founders of the modern domestic dromedary camels were likely a population of wild camels present in the southeastern corner of the Arabian Peninsula and that domestic populations were routinely hybridised with wild individuals with novel mtDNA haplotypes.

4.3.4 Insects

Two domesticated insect species likely followed the directed pathway: silkworms (*Bombyx mori*) and honeybees (*Apis mellifera*). People probably began selectively breeding moths for silk production ~5,000 years ago (Bisch-Knaden et al. 2014). The extreme changes in morphology and their reliance on humans for survival and reproduction have led to the recognition of the domestic form as a unique species, *B. mori*. Recent genetic analyses of complete mitochondrial sequences from different geographic regions (Li et al. 2010) and a mixture of mitochondrial and nuclear loci (Sun et al. 2012) now suggests that silkworm domestication began in China, in line with fossil, historical and archaeological lines of evidence (Sun et al. 2012).

Though there is a clear genetic distinction between wild and domestic silkworm lineages, *B. mori* retain ~83% of the genetic variance of its wild relatives.

Xia et al. (2009) interpreted this observation as evidence for a short domestication process with a large starting population. Yang et al. (2014) used coalescence simulations and approximate Bayesian computation (ABC) methods on 29 nuclear loci to suggest that domestication began ~7,500 years ago with a subsequent bottleneck ~4,000 years ago. Though the genetic architecture of domestication remains uncertain, several studies have identified genes and phenotypes that have been selected during domestication, including loci related to the olfactory system (Xiang et al. 2013), orphan genes (Sun et al. 2015) (reviewed in Tautz and Domazet-Lošo 2011) and epigenetic changes (Xiang et al. 2013).

The genus *Apis* has ten distinct species, nine of which are confined to Asia which suggests that the domesticated species, *A. mellifera*, also originated in Asia. This is supported by the fact that the closest species to *A. mellifera*, *Apis cerana,* is found in Western and Central Asia. Unlike domestic silkworms however, there is a range of subspecies of domesticated honeybee, and these are phenotypically distinct in different geographic regions. Because these species are adapted to their environment of origin, the basis for this phenotypic variation is largely unknown (Wallberg et al. 2014). These subspecies fall into four categories supported by morphometric and genetic studies: A are subspecies found throughout Africa, M from Western and Northern Europe, and C Eastern Europe and O includes species from Turkey and the Middle East (Han et al. 2012). Despite the parsimonious explanation of an Asian origin, an early paper using 1,136 nuclear SNPs suggested Africa as the origin of *A. mellifera* due to the unexpected rooting of their phylogenetic tree in the African clade (Whitfield et al. 2006). More recent studies have questioned this conclusion. One study demonstrated that some of the analysed subspecies were actually recent hybrids, and by removing these species from the analyses, the root of phylogenetic trees did not fall unequivocally into the A clade (Han et al. 2012). A similarly ambiguous conclusion was drawn when trees were built using 8.3 million SNPs (Wallberg et al. 2014). As a result, Asia remains the most likely origin of *A. mellifera*.

Harpur et al. (2012) found that honeybees exhibit unusually high levels of genetic diversity, as domestic bees are more genetically diverse than wild populations in Europe. This high level of diversity is believed to be maintained by the crossing of queens from diverse locations to produce more diverse hives. De la Rúa et al. (2013) pointed out that backcrossing with the local populations may be reducing the overall variation in the global honeybee population. Interbreeding between wild and domestics may be reducing the number of individuals with local adaptations that may be advantageous in a changing environment.

Relative to domestic mammal species, it is far more difficult to identify domestic insects in the archaeological record. As a result, investigations into the early process of domestication will have to rely upon genetic and morphological insights derived from museum specimens of silkworm and honeybees (e.g. Cridland et al. 2018).

5 The Biological Architecture of Domestication

Given its importance for our understanding of evolution, domestication has been extensively studied by experimental biologists and geneticists. These studies have focused on characterising the nature of the specific biological changes underlying the differences between domestic and wild species, as well as the interspecific similarities amongst domestic animals (known as the 'domestication syndrome'; Fig. 2). Paleogenomics has an enormous potential to address many questions regarding the biological underpinning of domestication by, for example, providing time-series data that can help detect artificial selection in the genome. Here we review how studies have, and will continue to, leverage the power of paleogenomics to answer fundamental questions in domestication.

5.1 Theories and Experiments

The evolutionary basis of animal domestication is one of the most enduring questions in evolutionary biology. Shortly after Charles Darwin (1859) published the theory of evolution by natural selection, he turned his attention to the study of domestication. Darwin's (1868) seminal work on the topic, *The Variation of Animals and Plants under Domestication*, examined in extensive detail the remarkable phenotypic similarity shown by a diverse range of domestic animals. Darwin's observations on the role of selection during domestication distinguished between two phases of artificial selection: termed 'unconscious' and 'methodical'. Darwin argued that the initial phase of domestication would have involved people unknowingly selecting for domestication traits by, for example, choosing the more productive cattle to breed and the less productive to eat (Darwin 1868). Over time, these unconscious selective pressures formed the many regional landraces of animals. More recently, he theorised people began practising conscious or methodical selection, in which animals were bred with a specific phenotypic outcome in mind – a view largely informed by the animal husbandry practices of the nineteenth century (Marshall et al. 2014). This perspective on animal domestication placed central focus on the role of human intent in the development of domestication traits and reproductive isolation from wild populations to preserve them.

These ideas were further developed by Francis Galton (1865, 1883), based on ethnographic observation of pet keeping in hunter-gatherer communities. Galton argued that the domestication of animals was a direct consequence of the human desire to capture and tame wild animals. All animals would be exposed to this process, but only those with a natural predisposition towards domestication would be permanently tamed. These anthropocentric views of domestication proved very influential, placing human intent at the heart of many contemporary definitions of domestication (Bökönyi 1989; Ducos 1989; Clutton-Brock 1994).

	increased tameness	decreased brain size	decreased heart weight	shorter muzzle	reduced tooth size	increased variability of vertebrae count*	change in caudal vertebrae count**	more frequent oestrus cycles	floppy ears	curly tail	supernumerary toes	disproportionate dwarfism***	depigmentation	increased skin area; skin folds	hairlessness	wool	curly hair
	occur in all individuals/have occurred in early domesticated forms of a species								occur in some varieties/breeds of a species								
dog	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
silver fox	X	x (?)		X				X	X	X			X				
ferret	X	X	X										X				
mink	X	X											X				
cat	X	X		X			X		X	X		X	X		X	X	
donkey	X	X							X				x (?)				
horse	X	X			X				X		X	X	X		X		
buffalo	X												X				
cattle	X	X		X					X		X	X	X	X			X
zebu	X								X				x (?)	X			
yak	X	X											X				
goat	X	X		X				X	X			X	X		X		X
sheep	X	X		X			X		X			X	X	X	X	X	X
reindeer	X												X				
pig	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X
camel	X	X											X				
dromedary	X	X											X				
llama	X	X	X								X		x (?)			X	
alpaca	X	X	X									X	X	X		X	
rabbit	X	X	X						X				X	X	X	X	X
guinea pig	X	X	X						x (?)				X				X
chinchilla	X												x (?)				
hamster	X												X				
mouse	X			X	X	X	X						X		X		X
rat	X	X	X				X						X				
gerbil	X	X					X						x (?)				

Fig. 2 Multiple traits, commonly referred to as 'domestication syndrome', and their occurrence in different mammalian species. Adapted after Sánchez-Villagra et al. (2016)

Darwin's (1868) study of domestication identified a series of behavioural, physiological and morphological traits shared by domestic animals, but not by their wild progenitors. These shared traits subsequently became known as the 'domestication syndrome' (Hammer 1984). Amongst domestic animals, these traits are now considered to include increased docility and tameness, reduction in body mass and brain size, novel coat colours and patterns, altered tails and floppy ears, smaller teeth and

shorter snouts, prolonged physical and behavioural neoteny, more frequent and nonseasonal reproductive cycles as well as changes in hormonal and neurotransmitter expression (Darwin 1868; Hammer 1984; Wilkins et al. 2014). The prevalence of these traits amongst domestic animals, including birds, fish and mammals, suggests that domestic animals respond similarly to artificial selection. The resultant domestication syndrome (Fig. 2) has been hypothesised to result from a disruption in developmental process of the neural crest (Wilkins et al. 2014; Sánchez-Villagra et al. 2016).

Experimental studies of animal domestication have played a key role in our understanding of how the domestication syndrome develops. The earliest experiments involved domestication of the brown rat (*Rattus norvegicus*) (King and Donaldson 1929; Castle 1947); however, the most informative experiments involved the silver fox – a melanistic form of the red fox (*Vulpes vulpes*). Beginning in 1959 at the Institute of Cytology and Genetics in Novosibirsk, Dmitry Belyaev established an experimental breeding programme which selectively bred silver foxes, brown rats and European mink (*Mustela lutreola*) for tameness (Belyaev 1969; Trut et al. 2004, 2009). Captive silver foxes were sourced from fur farms, where they had been selectively bred for their unique coat pigmentation (Belyaev 1969). Their level of aggression towards humans was tested by attempting to hand feed, stroke or handle the foxes, and those which exhibited the least aggressive response were chosen for subsequent breeding (Trut et al. 2004). The selective pressures in each generation were very high, with only 3% of males and 8–10% of females permitted to breed (Trut et al. 2004). Within 30 generations, almost half of the experimental foxes had behavioural relationships with humans that were analogous to domestic dogs. Interestingly, they also exhibited classic symptoms of the domestication syndrome – changes in coat colour and snout length, floppy ears and altered developmental timing (Trut et al. 2004).

Whole-genome sequences for tame, aggressive and conventional foxes raised under these experimental conditions have recently been published (Kukekova et al. 2018). Analysis of this data identified more than 100 regions showing signatures of selection in one or more of the experimental populations, and the *SorCS1* gene was identified as a strong candidate gene for tame behaviour.

5.2 Genetic Changes During Domestication

Many researchers have investigated the genetic basis for the phenotypic and behavioural changes seen in the domestication syndrome (Dobney and Larson 2006; Trut et al. 2009; Albert et al. 2009; Driscoll et al. 2009; Axelsson et al. 2013; Jensen 2014; Wilkins et al. 2014; Carneiro et al. 2014). With regard to plant domestication, good progress has been made in identifying genes linked to domestication and crop improvement (reviewed in Doebley et al. 2006; Olsen and Wendel 2013); however, the identification of similar genes linked to animal domestication has been more elusive. Increasingly, research has suggested that the phenotypic

diversity found in domestic animal populations is based on complex genetic architectures involving hundreds of genes and regulatory regions, each with small effect sizes (Larson et al. 2014; Wilkins et al. 2014; Carneiro et al. 2014).

Evidence drawn from across the range of domestic taxa, and phenotypic traits, suggests complex pleiotropic, polygenic and epistatic effects (Reissmann and Ludwig 2013; Wilkins et al. 2014; Wright 2015). For example, pleiotropy – in which single genes affect multiple discrete phenotypic traits – has been putatively identified in behavioural, morphological, life history and sexual ornament traits in domestic chickens (*Gallus gallus*) (Wright et al. 2010; Johnsson et al. 2012). Polygenic traits – in which single phenotypic traits are controlled by multiple genes – are most clearly evident in pigmentation traits for hair, skin and eyes, where more than 125 causal genes have been identified in domestic mice (*Mus musculus*) (Bennett and Lamoreux 2003). Epistasis – in which the expression of a genetic variant is dependent on the effect of one or more variants in modifier regions (Cordell 2002) – has been putatively identified in more than a dozen epistatic pairs effecting tameness, flight and startle responses, body weight and other traits, in experimentally domesticated brown rats (Albert et al. 2009). Amongst domesticated crops, where the architecture of domestication traits is better understood, epistasis is thought to play a key role in phenotypic expression (reviewed in Doust et al. 2014).

The identification of genes involved in animal domestication and their mapping to complex traits has been achieved via two main approaches: (1) quantitative trait locus (QTL) mapping (reviewed in Mackay et al. 2009) and (2) genome-wide association studies (GWAS) (reviewed in McCarthy et al. 2008). Both techniques have been critical in identifying candidate genes associated with traits that differentiate domestic populations (Goddard and Hayes 2009). This work has been aided by the development of online databases, cataloguing known gene associations. The Animal QTLdb now contains more than 57,000 trait mappings (Hu et al. 2007, 2016), and the Online Mendelian Inheritance in Animals (OMIA) database (Nicholas 2003; Lenffer et al. 2006) catalogues thousands of monogenic traits in domestic animals. QTL mapping and GWAS studies, however, often focus on traits that are important for economic productivity rather than traits that differentiate wild and domestic populations.

Population genomic studies that focus on identifying signatures of selection in genome-wide sequence data from wild and domestic populations have also identified numerous candidate genes putatively involved in animal domestication. This approach has recently been used to identify putative selection in polygenic loci involved in brain and neuronal development traits in domestic rabbits (*Oryctolagus cuniculus*) (Carneiro et al. 2014) and digestion and nervous system development traits in dogs (Axelsson et al. 2013). Genome-wide sequencing data has also been used to test the hypothesis of gene loss as a driver of rapid evolutionary change (Olson 1999), which has been discounted as an important process in the domestication of dogs (Freedman et al. 2016), chickens (Rubin et al. 2010), pigs (Rubin et al. 2012) and rabbits (Carneiro et al. 2014).

## 5.3   Temporal Pattern of Genetic and Morphological Changes

Identifying the genetic basis of animal domestication based solely on modern DNA, however, can be problematic (Larson and Burger 2013). In order to identify the genetic basis of traits that are associated with the early stages of the domestication process, it is necessary to dissociate these traits from changes that happened during later stage of the process (Vigne 2011). This can be problematic as domestic animals bear little direct resemblance to their early forbears, due to thousands of years of artificial selection, divergent environmental conditions and introgression with populations unrelated to the initial domestication. More recently, this has been further complicated by intensive breeding practices which have made reconstructing the early stages of domestication much harder (Larson and Burger 2013).

Recently, a genome-wide selection scan identified a putative domestication locus in the thyroid-stimulating hormone receptor (*TSHR*) gene in domestic chickens (Rubin et al. 2010). Thyroid hormone metabolism has previously been suggested as a key factor in animal domestication (Crockford 2002; Dobney and Larson 2006), and the *TSHR* gene has been shown to play an important role in metabolic regulation and control of seasonal reproduction in birds (Nakao et al. 2008) and mammals (Hanon et al. 2008). Single nucleotide polymorphisms (SNPs) from the *TSHR* sweep region, including a candidate causal missense mutation, were genotyped in hundreds of domestic chickens, from dozens of geographically dispersed populations. The missense mutation was found to be almost completely fixed in the domestic population, with an allele frequency of 0.987 (Rubin et al. 2010). The same SNPs were typed in more than 50 red junglefowl (*Gallus gallus*) – thought to be the primary wild ancestor of the domestic chicken (Eriksson et al. 2008). The missense mutation was found with an allele frequency of 0.35, which the authors attributed to introgression from domestic chickens into zoo populations of red junglefowl (Rubin et al. 2010).

The identification of the *TSHR* gene as a domestication locus relies on the assumption that selective pressure on the allele that is now almost fixed in domestic chickens took place during the early stage of the domestication process. This assumption was directly tested when another research group recovered aDNA from 80 domestic chickens, from a dozen sites across Europe, with a temporal range of approximately 2,000 years (Girdland Flink et al. 2014). The authors were able to genotype the SNP from the *TSHR* sweep region in 44 ancient samples. The missense mutation was found with an allele frequency of just 0.432, and only 18% of the samples were homozygous for the derived allele (Girdland Flink et al. 2014). This analysis clearly demonstrated that the fixation of the *TSHR* missense mutation was associated with later trait improvements rather than the initial domestication process (Fig. 3).

In a subsequent study, selection on the *TSHR* locus was revisited, with an expanded ancient DNA dataset and the application of a novel Bayesian statistical framework for modelling the strength of selection over time (Loog et al. 2017). The authors concluded that selection on the derived allele began around AD 920,

Fig. 3 Pie charts representing the allele frequency of variants at *TSHR* and *BCDO2* (affecting skin colour) in ancient chickens. This figure demonstrates that the variants at those genes, which are thought to influence traits in modern domestic chickens, were not found at high frequency in ancient chickens. Their rise in frequency is thought to be associated with breeding during the Middle Ages, but not with the domestication process (Loog et al. 2017). Adapted after Girdland Flink et al. (2014)
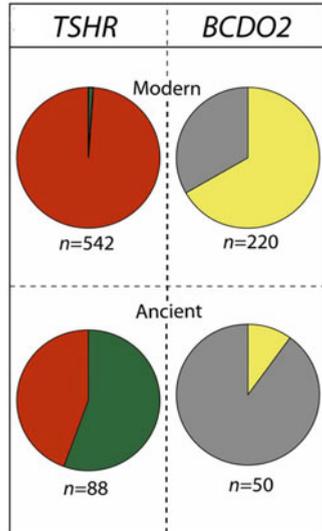
coinciding with mediaeval religious dietary reforms, which may have increased demand for both chicken and eggs (Loog et al. 2017). These findings are supported by zooarchaeological assemblages from England and Germany, spanning the mediaeval period, which show an increase in both the overall frequency of chickens and the relative proportion of adult hens – interpreted as sign of increased egg production (Serjeantson 2006; Sykes 2007; Holmes 2014). Functional genetic investigation of the pleiotropic effects of the *TSHR*-derived allele in chickens has shown that it is associated with increased egg production (Karlsson et al. 2016), decreased aggression and less fearful behaviours (Karlsson et al. 2015) – consistent with artificial selection for intensified egg production during the mediaeval period. Evidently, *TSHR* has played an important role in the evolutionary history of domestic chickens; however, its identification as a domestication locus is erroneous, and it can better be described as an improvement trait.

Similar cases, involving misidentified domestication genes, have been reported in domestic dogs and wheat. In the latter, a derived allele, fixed in modern populations of wheat, was identified as a putative domestication locus in the *NAM-B1* gene (Uauy et al. 2006). Ancient DNA recovered from herbarium seeds, however, established that the ancestral allele was still commonly found in cultivated populations as recently as 150 years ago (Asplund et al. 2010). Similarly, a recent genome-wide study of dogs demonstrated that most modern populations harbour a high number of copies of the *AMY2B* genes (Axelsson et al. 2013). This high copy number is almost fixed in modern dogs (Freedman et al. 2014) and allows them to better process starch (Axelsson et al. 2013). Ancient DNA studies, however, showed that these genetic variations only started to occur following the onset of farming, more than 7,000 years after dogs were domesticated (Arendt et al. 2016; Ollivier et al. 2016). More recent aDNA analysis further suggests that selection on *AMY2B*

copy-number variation did not begin until well after the advent of agriculture (Botigué et al. 2017).

These examples clearly demonstrate the importance of ancient DNA in verifying the timing of selection during the domestication process and the pitfalls inherent in inference based solely on modern DNA. As the number of aDNA studies increases, the geographic range and temporal resolution of these datasets will allow ever more detailed studies to investigate which loci were under selection during the early phases of domestication.

5.4 Genes as Domestic Markers

Genetic markers can potentially be used to evaluate whether animal remains belong to a wild or domestic individual; however, the use of genetics is controversial due to the disputed importance of genetic changes during the early phases of domestication (Zeder 2012a; Vigne 2015). These controversies stem from a general lack of consensus regarding the definition of domestication, particularly one which unifies both plants and animals. This lack of clear definition has recently been identified as one of the key challenges in domestication research (Zeder 2015). There are, however, some clear examples of genetic (and phenotypic) changes that are highly diagnostic of the domestication status of an animal. For example, multiple non-synonymous (protein changing) mutations have been found in the melanocortin 1 receptor (*MC1R*) gene of pigs which leads to a black coat colour, or black spotted colour, and loss of their wild-type camouflage coat pattern (Fang et al. 2009). At least three independent mutations, resulting in similar phenotypes, exist in pigs, one in European pigs, one in East Asian pigs and one in Hawaiian feral pigs (introduced during the Polynesian expansion; Fig. 4) (Linderholm et al. 2016). In modern European domestic pigs, this dominant allele, which leads to loss of camouflage, is found at very high frequency, while it is almost absent from wild populations (Koutsogiannouli et al. 2010; Frantz et al. 2013a). This suggests a strong negative selection in wild boars.

This European dominant black allele was recently found in four ~6,500-year-old pig remains from the site of Ertebølle (Mesolithic of northern Germany) (Krause-Kyora et al. 2013). These animals also had a mtDNA haplogroup originating in Near Eastern domestic populations, and geometric morphometric (GMM) analysis revealed they had molars with domestic shape characteristics and pathologies (Krause-Kyora et al. 2013). Their domestic status, however, conflicted with the cultural context in which they were found – Mesolithic hunter-gatherer rather than Neolithic farmers.

This sparked a controversy and led to several published replies (Evin et al. 2014; Rowley-Conwy and Zeder 2014a, b). The principle critique centred on the lack of evidence that humans at Ertebølle had a special relationship with these animals, distinct from that of wild boar (Rowley-Conwy and Zeder 2014a). The authors of the reply argued that domestication involves more than the phenotypic expression of
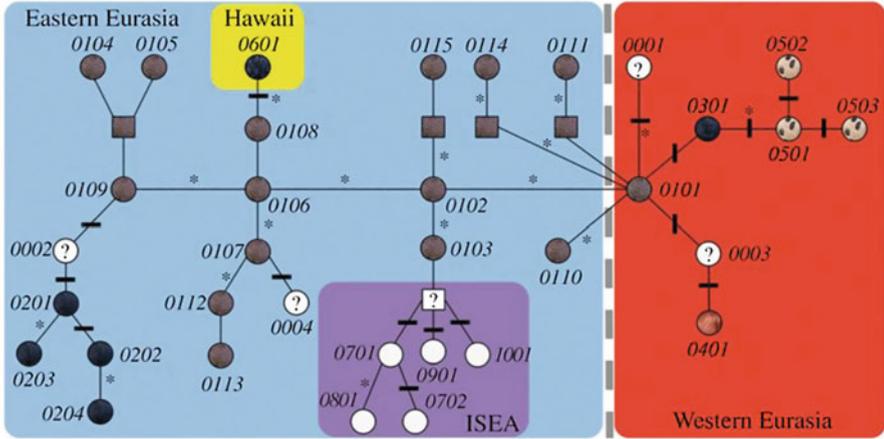
Fig. 4 Haplotype network for the MC1R gene coding region. This figure demonstrates the existence of three lineages of black pigs, in Hawaii, Europe and East Asia. Adapted after Linderholm et al. (2016)

genetic traits and requires a mutualistic relationship between the domestic and the domesticator. Therefore, even unambiguously domestic animals – with the complete set of behavioural and phenotypic traits – identified in this undifferentiated context would shed no light on the process of domestication or the adoption of agriculture in the region (Rowley-Conwy and Zeder 2014b). All together this highlights the fact that biological markers, even highly discriminative as those described above, cannot on their own provide the sole basis for a definition of domestication.

5.5 Introgression in Domestication

Animal domestication is often thought to be defined, not solely by genetic and phenotypic characteristics but also by population processes such as a strong bottlenecks, reproductive isolation from wild populations and directed breeding (Marshall et al. 2014). More recently, modern and ancient genomic datasets have revealed that these conditions were much less common than previously thought – revealing complex and varied patterns of introgression between wild and domestic pigs (Frantz et al. 2015), goats (Daly et al. 2018), cattle (Park et al. 2015), horses (Schubert et al. 2014), dromedary camels (Almathen et al. 2016), cats (Ottoni et al. 2017) and many other species (Marshall et al. 2014). As early farmers spread outwards from the major centres of domestication, the domestic animals that accompanied them frequently interbred with wild populations encountered along their routes of dispersal. Successive waves of gene flow over thousands of years have resulted in modern genomes which are complex palimpsests, containing traces of many different ancestral populations. For researchers that use DNA to re-trace the temporal and

geographic origin of domestic populations, introgression can be a double-edged sword. Patterns of admixture have been useful in untangling routes of animal dispersal and human migration (Larson et al. 2007b), but they have also led to misleading interpretations, based on limited mitochondrial datasets, for multiple independent domestications of cattle (Hanotte et al. 2002), pigs (Larson et al. 2005), goats (Luikart et al. 2001), sheep (Pedrosa et al. 2005) and horses (Vilà et al. 2001).

The specific patterns of introgression vary between different species, depending on the way domestic populations were managed, and the variety of wild populations which were encountered. For example, widespread introgression in European pigs has been attributed to loose herd management practices, in which free-ranging domestic pigs interbred freely with neighbouring wild boar populations, whose offspring were adopted into the loosely managed herds (Ottoni et al. 2013; Frantz et al. 2015). These patterns of introgression are highly asymmetric in pigs, with wild boars receiving little to no gene flow from domestic populations (Frantz et al. 2015). In general, the directionality of admixture is biased towards gene flow from local populations into migrant groups, especially with increasing distance from the source of the migration (Currat et al. 2008). Notable exceptions do occur, however, such as the *K*-locus variant introgressed from dogs into wolves (Schweizer et al. 2018) and *MITF* gene variants introgressed from cattle into yaks (Wu et al. 2018).

African cattle, which early genetic evidence suggested might have been independently domesticated (Hanotte et al. 2002), are now better explained by introgression between Near Eastern domestic cattle (*Bos taurus*), wild North African aurochs (*Bos primigenius africanus*) and successive waves of domestic Asian zebus (*Bos indicus*) (Mwai et al. 2015; Brass 2018; Pitt et al. 2018). In domestic chickens, the now ubiquitous yellow leg trait was acquired via introgression from the wild grey junglefowl (*Gallus sonneratii*) (Eriksson et al. 2008). For some species, introgression with wild populations continues to be an active process – particularly amongst reindeer (*Rangifer tarandus*) (Røed et al. 2008) and honeybees (*Apis mellifera*) (Harpur et al. 2012), which exhibit very high levels of genetic diversity.

An important, but limited, approach to investigating these complex histories is to use large genome-wide datasets to characterise the patterns of diversity and admixture seen in modern domestic populations – like cattle (Gibbs et al. 2009; Decker et al. 2014), sheep (Kijas et al. 2012), goats (Wang et al. 2016; Brito et al. 2017), pigs (Ai et al. 2013), horses (McCue et al. 2012; Petersen et al. 2013; Schaefer et al. 2017), chickens (Muir et al. 2008; Stainton et al. 2017), dogs (von Holdt et al. 2010; Shannon et al. 2015) and mice (Yang et al. 2011; Staubach et al. 2012). These large modern datasets benefit from the relative ease of sampling and low cost of data generation, compared to aDNA. The recent development of novel computational methods using phased haplotypes (Lawson et al. 2012; Hellenthal et al. 2014) has increased the precision with which the timing, direction and fraction of admixture can be resolved in these high-quality modern datasets.

The inferences which can be made from modern DNA alone, however, are limited by the use of modern genetic variation as a proxy for ancestral populations. Modern DNA can be blind to population replacement (e.g. Haak et al. 2015; Gaunitz

et al. 2018), because the extirpated populations made little contribution to modern genetic variation. Nor can modern DNA effectively detect or measure admixture from unsampled extinct species (e.g. Prüfer et al. 2014; Park et al. 2015), because the ancestral states of both species are unknown – although statistical methods have been developed to infer admixture from unsampled archaic populations (e.g. Plagnol and Wall 2006; Vernot and Akey 2014). The best approaches are those that combine both ancient and modern DNA with explicit testable models of evolutionarily processes (Gerbault et al. 2014). The recent development of novel Bayesian techniques for modelling serially sampled DNA holds particular promise to reveal important insights into the evolutionary process of domestication (Schraiber et al. 2016; Ferrer-Admetlla et al. 2016; Loog et al. 2017).

6   Future Perspectives

6.1   Ancient Epigenomes

The role of epigenetics in the domestication process, and in regulating domestic phenotypes, is a promising area of new research. For example, researchers working on the experimental domestication of the silver fox have suggested that observed differences in hormonal expression, associated with the domestication syndrome, may be linked to epigenetic modifications (Trut et al. 2009). A recent study comparing methylation patterns between dogs and wolves found 68 significantly differentially methylated sites across the two species, which included sites linked to the *GABRB1* and *SLC17A8* neurotransmitter genes, associated with a range of cognitive functions (Janowitz Koch et al. 2016). The role of epigenetics in a wide range of livestock phenotypes has also recently garnered a lot of attention (Feeney et al. 2014; Ibeagha-Awemu and Zhao 2015; Triantaphyllopoulos et al. 2016).

As our understanding of epigenetics improves, the ability to retrieve epigenetic information from ancient DNA will become increasingly important (reviewed in Hanghøj and Orlando 2018). Technical advances have recently made the recovery of ancient methylation maps possible (Briggs et al. 2010), which has resulted in the publication of the first genome-wide methylation maps for an ancient human (Pedersen et al. 2014), a Neanderthal and a Denisovan (Gokhman et al. 2014). Specialist computational tools for performing these analyses have also recently become available (Hanghøj et al. 2016). Presently, an equivalent ancient genome-wide methylation map has yet to be produced for domestic animals; however, as the number of ancient whole-genome sequences increase, it is only a matter of time before these become available.

6.2 Technical Advances

On the technical front, paleogenomics has benefited greatly from the development of increasingly cheaper and higher-throughput sequencing platforms. As development of these machines continues apace, we can expect the cost of DNA sequencing to continue to reduce. In some experimental designs, the limiting factor is no longer the cost of sequencing, but the costs of reagents and skilled labour for sample preparation (Rohland and Reich 2012). Protocols and laboratory equipment for automated library preparation, using liquid handling robots, are already available (Farias-Hesson et al. 2010; Lundin et al. 2010), and such approaches will likely become more commonplace in the future. As the cost of sequencing and sample preparation continues to drop, the number of samples and range of taxa which can be sequenced will increase concomitantly. Domestic animals are well represented in many archaeological sites, providing the potential for aDNA studies with fine-grained transects through time.

As paleogenomic studies scale up, increasingly sophisticated population genetic models will be necessary to interpret the process of animal domestication (Gerbault et al. 2014). Current methods for inferring patterns of admixture will need to be extended and improved to deal with more complicated models and larger datasets. Model-based clustering techniques, like *STRUCTURE* (Pritchard et al. 2000) and *ADMIXTURE* (Alexander et al. 2009), are very popular but widely over-interpreted (Lawson et al. 2018). Graph fitting approaches, like *TreeMix* (Pickrell and Pritchard 2012) and *MixMapper* (Lipson et al. 2013), are useful for inferring models of admixture but lack a formal statistical test of fit (Patterson et al. 2012). Formal models of admixture can be tested with *f*-statistics (Reich et al. 2009; Patterson et al. 2012) and *D*-statistics (Green et al. 2010; Durand et al. 2011), but these methods cannot resolve complex admixture topologies. Haplotype-based methods (Lawson et al. 2012; Hellenthal et al. 2014) work well on high-quality phased data, but are not suitable for low-coverage ancient data. Bayesian techniques, like *admixturegraph* (Leppälä et al. 2017), can test goodness of fit between models using Bayes factors, but computing these factors is computationally expensive, making automated model exploration very slow. As datasets continue to increase in size, the main constraint on genome analysis will be scaling computation to contend with the growth in sequence data (Muir et al. 2016).

6.3 Novel Substrates for aDNA

Paleogenomics is branching out into the recovery of aDNA from a range of novel substrates (reviewed in Green and Speller 2017). For example, the recent demonstration that aDNA can be successfully retrieved from historic parchments has opened up a whole new avenue for the study of domestic animals (Teasdale et al. 2015). Large numbers of historical parchments exist in archival and private

collections across Europe. These parchments represent an exceptionally well-dated source of aDNA for reconstructing the evolutionary history of regional landraces of sheep, goat and cattle (Teasdale et al. 2015). Ancient coprolites from domestic animals have also recently been shown to be a suitable substrate for the recovery of aDNA. Using a combination of microscopy and aDNA sequencing, a recent study of domestic dog coprolites was able to establish the major diet components of ancient Polynesian dogs (Wood et al. 2016). Additionally, ancient latrines have been shown to contain retrievable quantities of parasite aDNA, the host specificity of which can be used to infer the presence of domestic animal species (Søe et al. 2018).

Calcified dental plaque, known as dental calculus, has also recently been established as an important new substrate for aDNA recovery (Adler et al. 2013; Warinner et al. 2014, 2015; Weyrich et al. 2015). Archaeological studies of dental calculus in domestic animals have a long history, the earliest of which used light microscopy to study phytoliths trapped in dental calculus from cattle, sheep and horse teeth (Armitage 1975). Other early studies identified a broad range of organic substances in dental calculus (Dobney and Brothwell 1986) and developed a system for quantifying dental calculus in human, cattle and sheep teeth (Dobney and Brothwell 1987). More recently, paleogenomic studies of dental calculus have focused on changes in human health and diet. For example, a recent study used aDNA from dental calculus to establish that Mesolithic foragers in the Balkans were consuming domesticated plant foods (Cristiani et al. 2016). As paleogenomics broadens its focus away from human-centred studies, similar studies of animal diet and oral health will no doubt be applied to domestic taxa and their wild progenitors.

Environmental and sediment DNA are also showing strong potential for reconstructing the movement of domestic animals and their environmental impacts. A recent study used DNA metabarcoding of alpine lake sediments to build a high-resolution picture of agricultural land use since the Neolithic (Giguet-Covex et al. 2014). The authors were able to identify ancient sediment DNA from cattle, goats, sheep, horses and chickens and to correlate their abundance with changes in plant cover and erosion. The potential of environmental DNA, however, is moderated by the risk of vertical DNA movement through sediment stratigraphy. For example, one study identified sheep DNA in a New Zealand cave site from layers which predated European contact, demonstrating that DNA leaching can be problematic under some soil conditions (Haile et al. 2007). The inability to directly date environmental DNA from sediments which lack macrofossils is also a significant concern and has caused some to question the identification of the earliest domestic wheat in Britain, from an 8,000-year-old layer of a sediment core (Smith et al. 2015a, b; Bennett 2015).

7 Conclusion

The future of paleogenomics and its application to the study of animal domestication looks bright. Ten years ago, the retrieval of a single gene locus from few ancient samples was cause for celebration. Now, studies involving genome-wide data from

dozens (Haak et al. 2015; Fu et al. 2016; Lazaridis et al. 2016) or even hundreds (Mathieson et al. 2015; Lipson et al. 2017) of ancient samples are increasingly commonplace. So far, large paleogenomic studies have favoured retrieval of ancient human DNA, but similarly sized studies of domestic animals are certainly on the horizon. As our understanding of aDNA preservation (Hansen et al. 2017) and decay kinetics (Kistler et al. 2017) improves, more informed choice of skeletal elements and sampling locations will also permit the retrieval of aDNA from older time depths and warmer climates. We anticipate that the trend will be towards larger studies with many more samples and much older and finer temporal resolution.

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