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Broad maternal geographic origin of domestic sheep in Anatolia and the Zagros

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Abstract

We investigated the controversial origin of domestic sheep (*Ovis aries*) using large samples of contemporary and ancient domestic individuals and their closest wild relatives: the Asiatic mouflon (*Ovis gmelini*), the urial (*Ovis vignei*) and the argali (*Ovis ammon*). A phylogeny based on mitochondrial DNA, including 213 new cytochrome-b sequences of wild *Ovis* confirmed that *O. gmelini* is the maternal ancestor of sheep and precluded mtDNA contributions from *O. vignei* (and *O. gmelini* × *O. vignei* hybrids) to domestic lineages. We also produced 54 new control region sequences showing shared haplogroups (A, B, C and E) between domestic sheep and wild *O. gmelini* which localized the domestication center in eastern Anatolia and central Zagros, excluding regions further east where exclusively wild haplogroups were found. This overlaps with the geographic distribution of *O. gmelini gmelini*, further suggesting that the maternal origin of domestic sheep derives from this subspecies. Additionally, we produced 57 new CR sequences of Neolithic sheep remains from a large

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area covering Anatolia to Europe, showing the early presence of at least three mitochondrial haplogroups (A, B and D) in Western colonization routes. This confirmed that sheep domestication was a large-scale process that captured diverse maternal lineages (haplogroups).

KEYWORDS

ancient DNA, animal domestication, area of early domestication, maternal genetic origins, mitochondrial DNA, phylogeny, sheep ancestor, wild sheep

The earliest archaeological evidence for the presence of domesticated sheep was found in the Taurus mountains, Southeastern Anatolia and dates to 10,500 years BP (International Council for Archaeozoology et al., 2005; Zeder, 2008), making this region a putative area of sheep domestication. Sheep later spread over the Old World during the Neolithic, following human migration routes. Toward Europe, they took two major trajectories: the Danubian route across continental Europe and the Mediterranean route, crossing the sea to large islands such as Cyprus and Sardinia from the ninth to the sixth millennia BP (Tresset & Vigne, 2007, 2011; Vigne et al., 2012). Toward Asia, the most likely hypothesis is colonization through Turkmenistan and Mongolia (Flad et al., 2007; Lv et al., 2015; Vigne, 2015). In the eastern part of the spread, the earliest evidence of sheep is to be found at around 9500–9000 years BP in central and southern Zagros (Daujat & Mashkour, 2017; Kamjan et al., 2018; Roustaei & Mashkour, 2016) and at about the same dates in the north-east of Iran (Roustaei et al., 2015) and southern central Asia (Dobney & Jaques, 2010). The presence of domestic sheep is documented much later in China, around 4500–4000 years BP (Flad et al., 2007).

Based on genetic studies, several wild Asiatic species have been proposed as the ancestor of domestic sheep (Nadler et al., 1973; Pedrosa et al., 2005). These are the argali, *Ovis ammon*, the Asiatic mouflon, *Ovis gmelini* (often previously named *orientalis* following the nomenclature of Nadler et al., 1973) and the urial, *Ovis vignei*. Cytogenetic (Nadler et al., 1973) and archaeozoological (Clutton-Brock, 1981; Uerpmann, 1987) data have suggested the elimination of *O. ammon* and *O. vignei* as potential ancestors, leaving *O. gmelini* as the best candidate wild species from which sheep were domesticated. However, fluctuations in the nomenclature (Rezaei et al., 2010), the occurrence of a hybrid zone between *O. gmelini* and *O. vignei* and putative domestication events in the lower Indus valley (Meadows, 1984) raise the possibility of genetic contributions from other wild species. Thus, we aimed to confirm the hypothesis of a unique maternal *O. gmelini* origin, and to localize the domestication area by finding the present wild populations representing the most direct descendants of domesticated matrilineages. We also sought to identify the first maternal lineages of domestic sheep entering Europe during the Neolithic spread.

Mitochondrial DNA (mtDNA) has been extensively and successfully used to describe the genetic diversity of domestic animals and to study their origins and histories. Indeed, it allows the identification of the maternal evolutionary relationships with wild relatives because it is evolutionarily well conserved, yet sufficiently variable to capture genetic structure (Bruford et al., 2003; Zeder, 2006). Fragments of the non-coding *Control Region (CR)* or *Cytochrome b (Cytb)* gene have been used to show the existence of five different haplogroups in domestic sheep, designated as A–E (Arora et al., 2013; Chen et al., 2006; Demirci et al., 2013; Guo et al., 2005; Hermes et al., 2020; Hiendleder et al., 2002; Horsburgh & Rhines, 2010; Ibrahim et al., 2020; Kolosov et al., 2021; Meadows et al., 2007; Pedrosa et al., 2005; Resende et al., 2016; Rezaei et al., 2010; Singh et al., 2013; Tapio et al., 2006; Zhao et al., 2011). Analysis of complete mitochondrial genomes (Meadows et al., 2011) confirmed the validity of such mtDNA fragments for discriminating among haplogroups and tracing the history of maternal lineages.

We built two datasets, one to compare modern domestic and wild sheep and another to compare modern and ancient domestic sheep (see Table S1). For the first one, we carried out an extensive non-invasive sampling of wild *Ovis* corresponding to 132 wild sheep, including three *O. ammon*, 85 *O. gmelini*, 15 *O. vignei*, one *Ovis musimon* and 28 hybrids *gmelini* × *vignei*. Samples originated from 55 geographic localities representing most of their distribution area and encompassing the putative region of domestication according to archaeological data (see Table S2, Appendix S1). Moreover, we collected samples from 81 domestic sheep from 28 different countries as representative of the mtDNA worldwide domestic diversity (Table S2, Appendix S1). We sequenced 1217 bp of the *Cytb* locus for these samples and retrieved 421 supplementary sequences from GenBank (Table S2, Appendix S1). We built the second dataset on 120 bp of the more variable *CR* sequence to analyze intra-specific diversity (corresponding to the most recent divergences). Data for 1283 present-day sheep were collected from GenBank, and we sequenced 54 modern *O. gmelini* (Table S3) and 57 ancient domestic samples mostly distributed in Europe and dating back around 8000 and 5000 years BP (Figure 1b, Tables S4 and S5, Appendix S1).

We built maximum likelihood and neighbor-joining (Saitou & Nei, 1987) trees using IQTREE (Nguyen et al., 2015) and the R package APE (Paradis et al., 2004), respectively (Appendix S1), to infer the phylogenetic relationships between the Middle East wild species and 362 *Ovis aries* representative of worldwide domestic diversity. Both phylogenies showed the monophyly of each of the three wild species (i.e. *O. gmelini*, *O. vignei* and *O. ammon*). All *O. aries* fall within the *O. gmelini* clade, confirming that domestic sheep evolved from ancestral matrilineages of the Asiatic mouflon (Bunch et al., 2006; Demirci et al., 2013; Hiendleder et al., 1998, 2002; Meadows et al., 2007, 2011; Tapio et al., 2006). This latter clade was divided into two clusters, both containing haplotypes from wild and domestic sheep (Figure 2), showing the early divergence between A/B haplogroups and C/E haplogroups (Meadows et al., 2007). Interestingly, individuals from the *O. gmelini* × *vignei* hybrid zone in central Iran had either an *O. gmelini* or an *O. vignei* maternal origin, as already shown by Demirci et al. (2013). None of them fell into a clade containing domestic sheep (Figure 2), precluding the contribution of hybrid populations to domestics. However, urial Y-chromosome haplotypes, found in several Asiatic mouflons (Deng et al., 2020), support a partial paternal contribution of the urial.

Assuming that the boundaries of the current distribution of wild species are similar to those at the time of domestication (Uerpmann, 1987), the exclusion of *O. ammon*, *O. vignei* and *O. vignei* × *O. gmelini* hybrids as possible ancestors precludes hypotheses that the Central Iranian Plateau, the Lower Indus Valley and even more eastern locations contributed to domestication. Based on archaeozoological data, the cradle for sheep domestication would extend from central Anatolia to northern and central Zagros (International Council for Archaeozoology et al., 2005; Zeder, 2008, 2011). This is confirmed by mtDNA data, as the highest nucleotide diversity was found in this region (Table S6) where, moreover, the mtDNA haplogroups carried by modern Asiatic mouflon were the closest to those of the domestics (Figure 1b'). This region overlaps the current distribution of the subspecies *O. gmelini gmelini*, whereas *O. g. isphahanica* and *O. g. laristanica* are spread further east and south, respectively (Figure 1a; Michel & Ghoddousi, 2020). The strong bottleneck experienced (even recently) by the Cyprus mouflon (*Ovis ophion*), which is close to *O. g. gmelini* (Sanna et al., 2015) and results from the early transportation of individuals from the continent (Vigne et al., 2014), makes it very difficult to assess its potential contribution to the domestic diversity. Besides that, the presence of some haplotypes similar to those of domestic sheep in modern *O. g. gmelini* populations offers evidence that the latter gave rise to the domestic haplogroups without excluding later introgression of domestic stock into wild populations.

We used CR sequences from 1283 modern and 57 ancient domestic sheep to investigate global sheep mitochondrial diversity. Most modern sheep (56%) were from the B haplogroup, followed by the A (34%), C (9%) and D and E (<0.5%) (Figure S2). These proportions are similar to those of other studies (Demirci et al., 2013; Kandoussi et al., 2020; Lv et al., 2015; Meadows et al., 2007; Sanna et al., 2015). As already shown (Handley et al., 2007; Kijas et al., 2009; Meadows et al., 2005), sheep showed very weak genetic differentiation at the continental scale (no between-continent $F_{ST} > 0.02$). The A and B haplogroups have a worldwide distribution that is not homogeneous, with more than 78% of the A haplogroup located in Asia. In northern and southern Europe, A and B haplogroups were detected with a high preponderance of the B haplotypes (above 90%) and some rare C haplotypes (Table S6; Demirci et al., 2013; Deng et al., 2020; Lv et al., 2015).

The genotyping of 57 ancient samples showed that there were at least three haplogroups present in Neolithic European domestic sheep, with the B haplogroup already predominant (i.e. 55 B, 1 A and 1 D haplotypes; Appendix S1, Tables S5 and S6). We probably did not detect other low-frequency haplogroups from that area. However, this result indicates that the A and D haplogroups have been present since the beginning of western sheep diffusion during the Neolithic. This predates by several millennia the first evidence of the A haplogroup in Europe, as it was already detected in medieval sheep from Finland but not in the oldest samples from the Iron period (Demirci et al., 2013; Niemi et al., 2013; Rannamäe et al., 2016). Thus we confirm the hypothesis of a very early presence of this haplogroup in Europe, and support the idea that a later introduction of A haplotypes from Spanish populations during the sixteenth century is unlikely as these importations concerned mainly rams (Niemi et al., 2013).

Combining genetic data from *O. aries* and its closest wild relatives with archaeozoological data makes it possible to propose a subspecies of the Asiatic mouflon, *O. gmelini gmelini*, as the maternal origin of domestic sheep. The current distribution of the Asiatic mouflon and the geographic pattern of its genetic diversity are consistent with domestication first taking place in eastern Anatolia and in northern and central Zagros, as supported by archaeozoological data (Clutton-Brock, 1981; International Council for Archaeozoology et al., 2005; Uerpmann, 1987). They preclude more eastern independent domestication centers, especially in the Indus Valley, as well as the contribution of *O. gmelini* × *O. vignei* hybrids. Studies on the diversity of chromosome Y have given valuable insights into the demographic history of sheep (Deng et al., 2020), but have not provided information on the geographic origin. However, studies on chromosome Y (Li et al., 2020) and whole genome data (Barbato et al., 2017) brought evidence for the occurrence of post-domestication introgressions from the wild toward domestic sheep. At least three different haplogroups (B, A and D) diverged before domestication

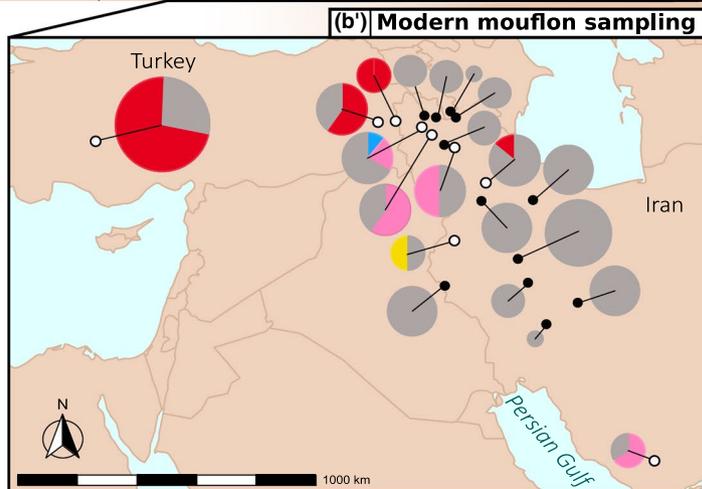
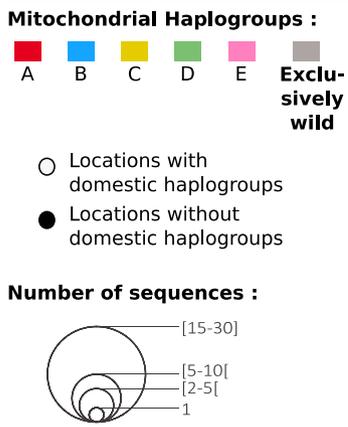
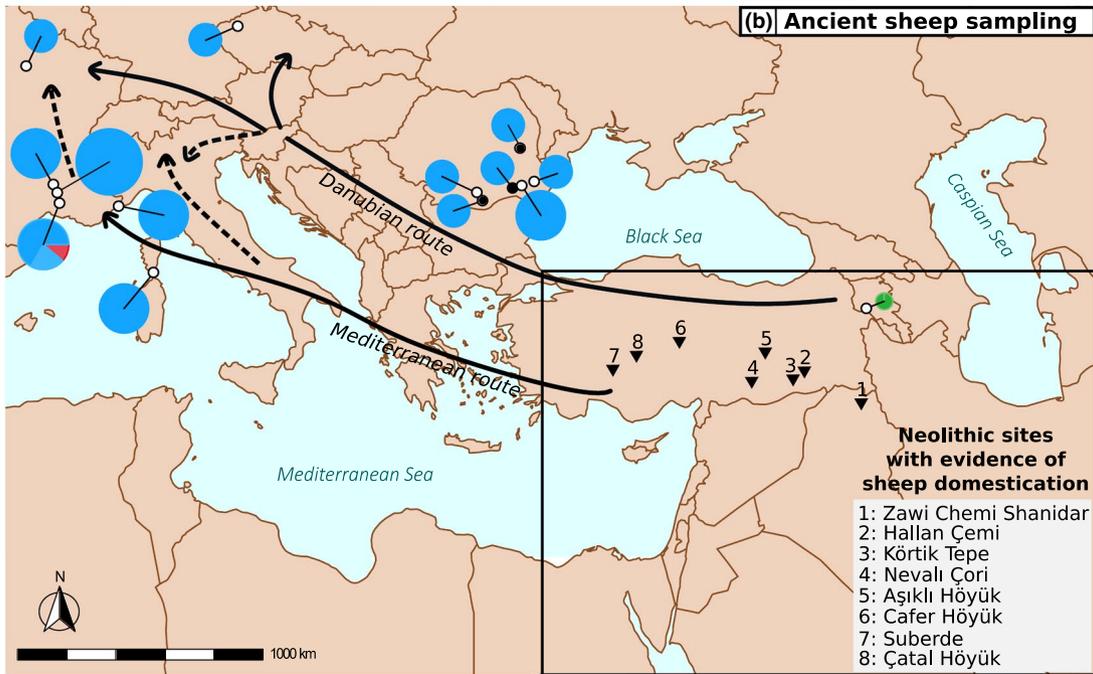
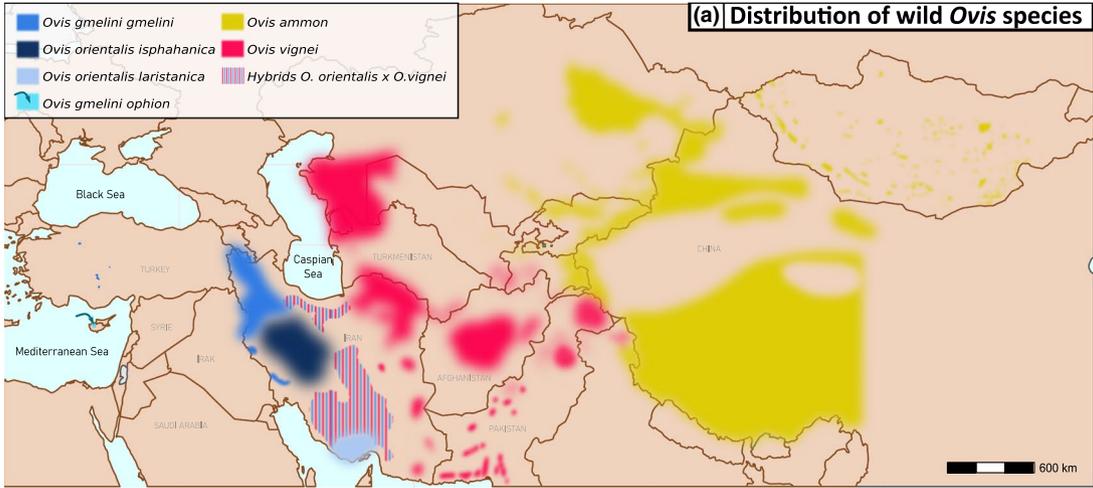


FIGURE 1 Geographic distribution of wild *Ovis* species (a) and ancient domestic (b) and modern wild (b') haplogroups. We obtained species distributions from the IUCN database (see references below). For *Ovis gmelini* subspecies, we combined information from sites described in the detailed report and general distribution of the species to draw approximate ranges of continental subspecies

1. *Ovis ammon*: Reading, R., Michel, S. & Amgalanbaatar, S. 2020. *Ovis ammon*. The IUCN Red List of Threatened Species 2020: e.T15733A22146397. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T15733A22146397.en>.
2. *Ovis gmelini*: Michel, S. & Ghoddousi, A. 2020. *Ovis gmelini*. The IUCN Red List of Threatened Species 2020: e.T54940218A22147055. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T54940218A22147055.en>.
3. *Ovis vignei*: Michel, S. & Ghoddousi, A. 2020. *Ovis vignei*. The IUCN Red List of Threatened Species 2020: e.T54940655A54940728. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T54940655A54940728.en>.

The haplogroups of ancient sheep (*Ovis aries*) were determined based on *CR* sequences (120 bp). The related haplogroups of modern mouflon (*Ovis gmelini*) were determined based on *CR* sequences and confirmed by comparison with *Cytb* sequences (1217 bp). The Neolithic sites with evidence of sheep domestication were taken from the literature (International Council for Archaeozoology et al., 2005; Zeder, 2008, 2011)

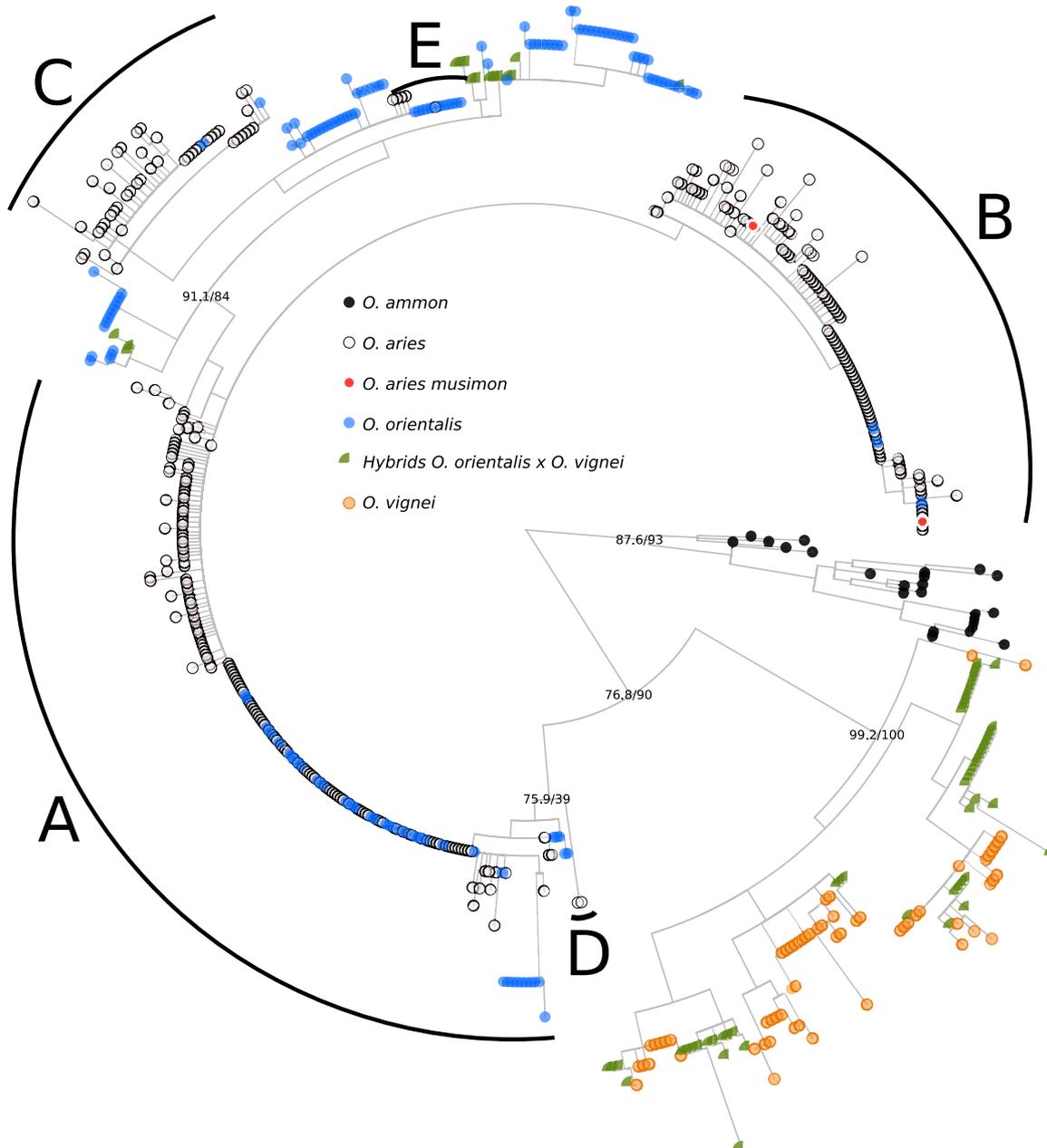


FIGURE 2 Phylogenetic relationships between the domestic sheep (*Ovis aries*) and its potential wild ancestors: the argali (*Ovis ammon*), the urial (*Ovis vignei*) and the Asiatic mouflon (*Ovis gmelini*). The phylogenetic tree was built using maximum likelihood methods implemented in IQTREE with *cytb* sequences (1217 pb). The numbers on the principal nodes correspond to support values (Ultrafast Bootstrap value/SH-aLRT value). The black circle arcs represent the different mitochondrial haplogroups

and underwent early diffusion toward Europe at the beginning of the Neolithic. Thus, our results globally indicate that sheep domestication was a process that occurred on a large geographical scale. It involved the capture of a wide genetic diversity over a large area, as already shown for other livestock species such as goats (Daly et al., 2018; Naderi et al., 2008), pigs (Bosse, 2018; Larson et al., 2007, 2010) and cattle (Götherström et al., 2005; McTavish et al., 2013).

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

All *Cytb* and *CR* sequences produced in this study have been published on GenBank under the accession numbers MW684398–MW684451, MW684452–MW684508 and MW677233–MW677445.

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