



# Evolution and domestication of the Bovini species

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## Summary

Domestication of the Bovini species (taurine cattle, zebu, yak, river buffalo and swamp buffalo) since the early Holocene (ca. 10 000 BCE) has contributed significantly to the development of human civilization. In this study, we review recent literature on the origin and phylogeny, domestication and dispersal of the three major *Bos* species – taurine cattle, zebu and yak – and their genetic interactions. The global dispersion of taurine and zebu cattle was accompanied by population bottlenecks, which resulted in a marked phylogeographic differentiation of the mitochondrial and Y-chromosomal DNA. The high diversity of European breeds has been shaped through isolation-by-distance, different production objectives, breed formation and the expansion of popular breeds. The overlapping and broad ranges of taurine and zebu cattle led to hybridization with each other and with other bovine species. For instance, Chinese gayal carries zebu mitochondrial DNA; several Indonesian zebu descend from zebu bull × banteng cow crossings; Tibetan cattle and yak have exchanged gene variants; and about 5% of the American bison contain taurine mtDNA. Analysis at the genomic level indicates that introgression may have played a role in environmental adaptation.

**Keywords** bison, cattle, hybridization, introgression, taxonomy, yak

## Introduction

The domestication of cattle and other species of the tribe Bovini played a key role in the development of human civilization. Largely fed on grass that is indigestible by humans, they provide meat, milk, leather and other products in addition to transportation and traction. Because of their impact on agricultural production, their size and powerful appearance, cattle have in most cultures a higher status than other domestic animals, with horse being the possible exception.

Like other livestock species, scientific investigations of the bovine species are keeping pace with technological

advances. *De novo* WGSs for most of the bovine species and several genome resequencing projects (Table 1) have revealed numerous unpredicted findings on the evolution and domestication of bovines (Taylor & Larson 2019). In this review, we survey the domestic and wild Bovini species and summarize the advancements based on the molecular evidence on phylogeny and evolution (Section The bovine species). For taurine cattle, zebu and yak, which are the most numerous cattle species, we review recent literature on the domestication, dispersal and differentiation of breeds (Section Phylogeny and evolution). Finally, we discuss hybridization between the interfertile bovine species as related to adaptation (Section Domestication, dispersal and differentiation of breeds).

## The bovine species

The bovine species form the tribe Bovini, which depending on the different classifications comprises four to seven genera and 14–18 species (Hassanin & Douzery 1999; Robinson & Ropiquet 2011): saola (*Pseudoryx nghetinhensis*, discovered only in 1992), African buffalo (*Syncerus caffer*), wild water buffalo (*Bubalus arnee*), the domestic river-type (*Bubalus bubalis bubalis*) and swamp-type (*Bubalus bubalis*

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Accepted for publication 03 June 2020

**Table 1** WGSs of Bovini species.

| Species   | Sex                         | Size (Gb)         | Assembly level                        | N50 (Mb) | Reference                        |
|---|-----------------------------|-------------------|---------------------------------------|----------|----------------------------------|
| <i>A. De novo assembled genomes</i>   |                             |                   |                                       |          |                                  |
| Taurine cattle  | Male, female <sup>1,2</sup> | 2.49              | Chromosome                            | 6.09     | Elsik <i>et al.</i> (2009)       |
|   | Male, female <sup>1,3</sup> | 2.54              | Chromosome                            | 6.49     | Zimin <i>et al.</i> (2009, 2012) |
|   | Female <sup>4</sup>         | 2.7               | Chromosome                            | 110      | Rosen <i>et al.</i> (2020)       |
| Zebu  | Male (Nelore) <sup>5</sup>  | 2.49              | Chromosome                            | 106.3    | Canavez <i>et al.</i> (2012)     |
|   | Male (Gir)                  | 2.55              | Chromosome                            | 104.3    | Assembly ASM29337v1              |
| Taurindicine  | Male                        | 2.50              | Chromosome                            | 99.63    | Koren <i>et al.</i> (2018)       |
|   | Male                        | 2.40              | Chromosome                            | 98.00    | Koren <i>et al.</i> (2018)       |
| Gayal   | Female                      | 2.61              |                                       | 2.74     | Mei <i>et al.</i> (2017)         |
|   | Female                      | 2.85              |                                       | 28.7     | Wang <i>et al.</i> (2017b)       |
| Yak   |                             | 3.00              |                                       |          | Mukherjee <i>et al.</i> (2019)   |
|   | Female                      | 2.46              | Scaffold                              | 1.34     | Qiu <i>et al.</i> (2012)         |
|   | Female                      | 2.13              | Chromosome                            | 98.2     | Unpublished                      |
|   | Male                        |                   | Chromosome                            | 114.4    | Assembly BosGru3.0               |
| Wild yak  | Female                      | 2.83              | Scaffold                              | 16.3     | Liu <i>et al.</i> (2020)         |
| American bison  | Male                        | 2.63              | Scaffold                              | 6.86     | Dobson (2015)                    |
| Wisent  | Male                        | 2.58              | Scaffold                              | 4.70     | Wang <i>et al.</i> (2017a)       |
| River buffalo   | Female                      | 2.65              | Chromosome                            | 112.00   | Mintoo <i>et al.</i> (2019)      |
|   | Female                      | 2.58              | Chromosome                            | 116.1    | Luo <i>et al.</i> (2020)         |
| Swamp buffalo   | Female                      | 2.57              | Chromosome                            | 117.3    | Luo <i>et al.</i> (2020)         |
| African buffalo   | Female                      | 2.64              | Scaffold                              | 1.35     | Glanzmann <i>et al.</i> (2016)   |
| Species   | Sex                         | Number of animals | Reference                             |          |                                  |
| <i>B. Major resequencing projects</i>   |                             |                   |                                       |          |                                  |
| Taurine   | Male                        | 432               | Chung <i>et al.</i> (2017)            |          |                                  |
| Taurine, composite  | Male                        | 379               | Stothard <i>et al.</i> (2015)         |          |                                  |
| Taurine, zebu   | Male                        | 2703 <sup>6</sup> | Hayes & Daetwyler (2019)              |          |                                  |
| European taurine  |                             | 155               | Mielczarek <i>et al.</i> (2018)       |          |                                  |
| French taurine  |                             | 274               | Boussaha <i>et al.</i> (2016)         |          |                                  |
| Iberian taurine   |                             | 48                | Da Fonseca <i>et al.</i> (2019)       |          |                                  |
| German Fleckvieh  |                             | 43                | Jansen <i>et al.</i> (2013)           |          |                                  |
| Southern Europe taurine   |                             | 19                | Upadhyay <i>et al.</i> (2019a, 2019b) |          |                                  |
| African taurindicine  |                             | 48                | Kim <i>et al.</i> (2017)              |          |                                  |
| East Asian taurine, zebu  |                             | 49                | Chen <i>et al.</i> (2018)             |          |                                  |
| Korean Hanwoo   |                             | 126               | Lee <i>et al.</i> (2016)              |          |                                  |
| Chinese taurine, taurindicine   |                             | 46                | Mei <i>et al.</i> (2017)              |          |                                  |
| Ancient taurine   |                             | 67                | Verdugo <i>et al.</i> (2019)          |          |                                  |
| Aurochs   | Male                        | 1                 | Park <i>et al.</i> (2015)             |          |                                  |
| Aurochs   |                             | 6                 | Verdugo <i>et al.</i> (2019)          |          |                                  |
| Pakistani zebu  | Male                        | 20                | Iqbal <i>et al.</i> (2019)            |          |                                  |
| Yak   |                             | 69                | Qiu <i>et al.</i> (2015)              |          |                                  |
| Wild yak  |                             | 15                | Qiu <i>et al.</i> (2015)              |          |                                  |
| Wisent  |                             | 7                 | Wecek <i>et al.</i> (2017)            |          |                                  |
| River buffalo   |                             | 25                | Whitacre <i>et al.</i> (2017)         |          |                                  |
| River and swamp buffalo   |                             | 98                | Sun <i>et al.</i> (2020)              |          |                                  |
| River buffalo   |                             | 132               | Luo <i>et al.</i> (2020)              |          |                                  |
| Swamp buffalo   |                             | 98                | Luo <i>et al.</i> (2020)              |          |                                  |
| Taurine, zebu and taurindicine (60), Bali cattle (8), gayal (23), American bison (1), wisent (11) |                             | 103               | Wu <i>et al.</i> (2018)               |          |                                  |

<sup>1</sup>Hereford Dominette female (major component) plus her father Domino.<sup>2</sup>Assembly UMD 3.1 (updated).<sup>3</sup>Assembly Btau 5.0 (updated).<sup>4</sup>Assembly ARS-UCD 1.2; Hereford Dominette female.<sup>5</sup>Assembly Bos\_indicus\_1.0.<sup>6</sup>These may included from sources that are listed in this table.

*carabensis*) water buffalo, lowland anoa (*Bubalus depressicornis*), mountain anoa (*Bubalus quarlesi*), tamaraw (*Bubalus mindorensis*), European bison or wisent (*Bison bonasus*),

American bison (*Bison bison*), yak (*Bos grunniens*), wild yak (*Bos mutus*), banteng (*Bos javanicus*), gayal (*Bos frontalis*), gaur (*Bos gaurus*), kouprey (*Bos sauveli*), taurine cattle (*Bos*

*taurus*) and zebu (*Bos indicus*; Wilson & Reeder 2005). Although alternative taxonomic designations exist (e.g. *B. taurus indicus* or *Bos primigenius taurus*), in this article we follow the nomenclature more frequently used in the literature, which relies less on cross-fertility and reproductive isolations, and more on aspects related to genome divergence and domestication. All *Bos* and *Bison* species are cross-fertile (Table 2) and fertility is maintained in all female F1 hybrids and in male hybrid F1 offspring from matings of wild with domestic yak, American with European bison and taurine with zebu (Lenstra *et al.* 2012).

Five bovine species have been domesticated, are kept in large domestic populations and have been subject to strong human-directed selection. At present, around 0.75 billion taurine cattle ([www.fao.org/faostat/en/](http://www.fao.org/faostat/en/)) are raised around the world (Scherf & Pilling 2015). About the same number of zebus lives in the tropical regions (Utsunomiya *et al.* 2019). Both taurine cattle and zebu descend from the extinct aurochs. Approximately 135 million river-type buffaloes are kept at low altitudes in the tropical and subtropical regions ([www.fao.org/faostat/en/](http://www.fao.org/faostat/en/)). Most of these (94%) live in Asia (Luo *et al.* 2020). The swamp-type buffaloes are used in China and south-east Asia (35 million) as draft animals. A limited number of wild individuals still exist in India and Thailand (Zhang *et al.* 2020a, 2020b). Most of the about 14 million yaks are raised on the high-altitude Qinghai-Tibet Plateau (QTP). Their wild ancestor, the wild yak, maintains a population of around 15 000 in the north-western part of the QTP.

In contrast, Bali cattle and gayals have a restricted distribution range in south-east Asia close to the original range of their wild ancestor (Fig. 1). Although both are adapted to the human environment, they have not been subject to intense selective breeding. A population of more than 2 million Bali cattle are kept as draft and meat cattle

on Bali, other islands in eastern Indonesia and elsewhere in isolated herds (Wilson & Reeder 2005). They were introduced for farming on the Cobourg peninsula in northern Australia and after being abandoned established a large feral population (Bradshaw *et al.* 2007). Bali cattle still strongly resemble the endangered wild banteng, have a high fertility and thrive on low-quality fodder. Wild banteng may be still present in Java, possibly on Bali, and in Kalimantan (Indonesian Borneo), Sabah (part of Malaysian Borneo), Myanmar, Thailand, Cambodia and, probably, Laos and Vietnam (Gardner *et al.* 2016). The semi-feral gayals (about 300 000) are not kept in a farm environment and are used for ritual slaughtering. Like their wild ancestor, the gaur and gayal are both large animals but they have clearly different horns.

The other bovine species only live in the wild: American bison and European bison being kept in reservations in North America and Europe respectively; African or Cape buffalo in tropical Africa; and the three Bubalina lowland anoa, mountain anoa and tamaraw, the kouprey (now probably extinct) and the saola in south Asia (Fig. 1).

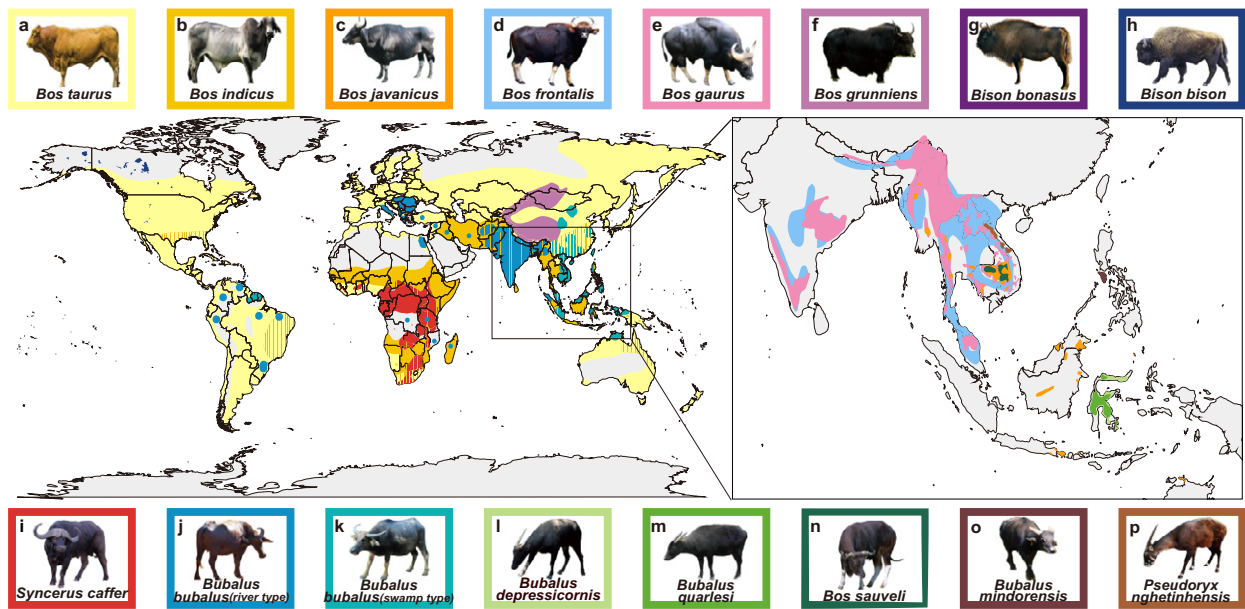
## Phylogeny and evolution

Sequences of ribosomal and mitochondrial DNAs and differences in karyotypes indicate three subtribes within the tribe Bovini (Tanaka *et al.* 1996; Hassanin & Douzery 1999). The Pseudorygina subtribe contains only the genus *Pseudoryx* with the only species saola; the Bubalina comprise the genera *Syncerus* and *Bubalus* containing the African and Asian buffaloes respectively; whereas the Bovina subtribe consists of the genera *Bison* and *Bos* (Fig. 2). The Bovina and Bubalina diverged 10–15 million years ago (Mya; MacEachern *et al.* 2009; Hassanin *et al.* 2013; Hassanin 2014). Molecular analyses suggested a close relationship of saola and the Bovina (Hassanin & Douzery 1999; Gatesy & Arctander 2000; Hassanin & Ropiquet 2004), but cytogenetic analyses linked saola to the Bubalina (Nguyen *et al.* 2008; Robinson & Ropiquet 2011).

The number of the Bubalina species varies according to the author (Wilson & Reeder 2005; Groves & Grubb 2011; Rasmus *et al.* 2013). For the Asian buffaloes, we tentatively acknowledge six species: river buffalo, swamp buffalo, wild buffalo and three other wild species (see above, Fig. 1; Wilson & Reeder 2005). The river buffalo ( $2n = 50$ ) and swamp buffalo ( $2n = 48$ ) have different karyotypes (Fischer & Ulbrich 1967), but are interfertile and have formed hybrid populations in south China and Bangladesh (Luo *et al.* 2020; Zhang *et al.* 2016). MtDNA and Y-chromosomal sequences indicate that the swamp and river buffalo are at least as divergent as taurine and zebu cattle (Yindee *et al.* 2010) and have been domesticated separately (Sun *et al.* 2020). Selection targeting the dairy production of the river buffalo and the draught power of the swamp buffalo is likely

**Table 2** The fertility of hybrid offspring between bovine species.

| Parental combination      | Female offspring | Male offspring | Reference   |
|---------------------------|------------------|----------------|---|
| Cattle × American bison   | Fertile          | Infertile      | Boyd (1915)   |
| Cattle × European bison   | Fertile          | Infertile      | <a href="http://www.zubry.com/zubron">http://www.zubry.com/zubron</a> |
| Cattle × gaur             | Fertile          | Infertile      | Abdullah <i>et al.</i> (2009)   |
| Cattle × gayal            | Fertile          | Infertile      | He <i>et al.</i> (2015)   |
| Cattle × yak              | Fertile          | Infertile      | Wiener <i>et al.</i> (2006)   |
| Cattle × zebu             | Fertile          | Fertile        | Lenstra <i>et al.</i> (2012)  |
| Yak × American bison      | Fertile          | Infertile      | Deakin <i>et al.</i> (1935)   |
| Yak × bison-cattle hybrid | Fertile          | Infertile      | Deakin <i>et al.</i> (1935)   |
| Zebu × banteng            | Fertile          | Infertile      | Vadhanakul <i>et al.</i> (2004)                                       |
| Zebu × gaur               | Fertile          | Infertile      | Vadhanakul <i>et al.</i> (2004)                                       |
| Zebu × gayal              | Fertile          | Infertile      | Winter <i>et al.</i> (1986)   |
| Zebu × yak                | Fertile          | Infertile      | Wiener <i>et al.</i> (2006)   |



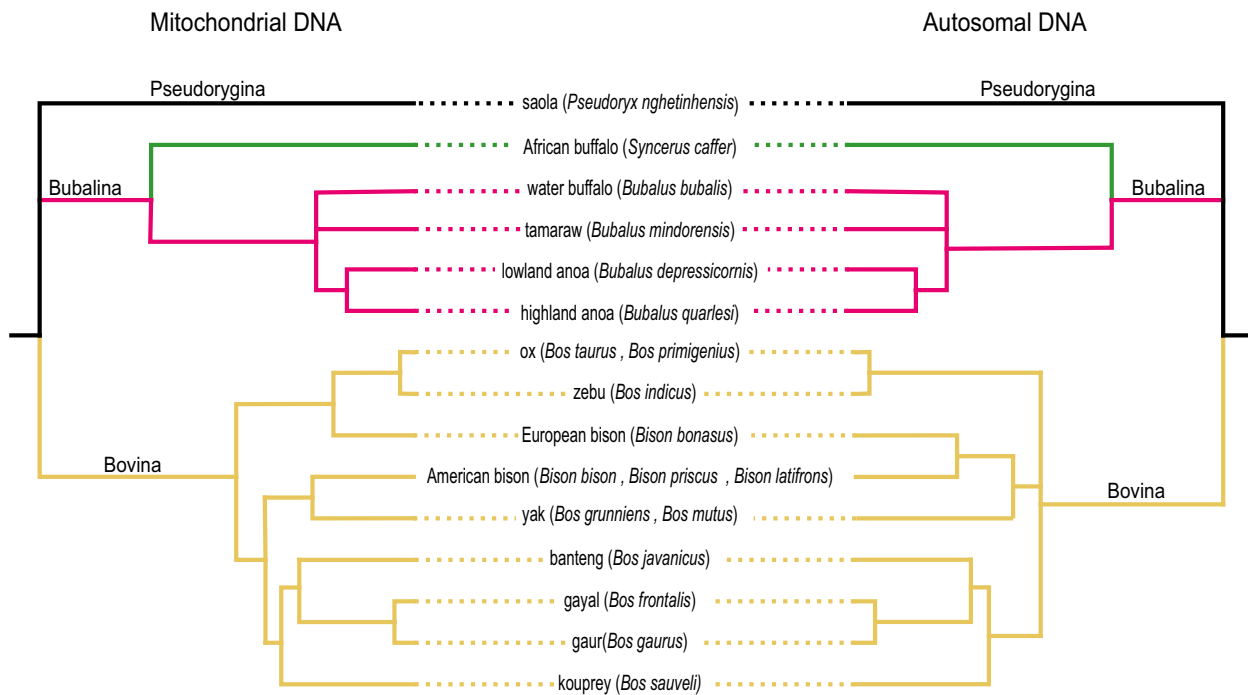
**Figure 1** Bovine species are widespread throughout the world. The map shows the locations of 16 bovine species. The areas with alternating stripes indicate the overlapping ranges of two or three species. In this map, we combined wild Asian buffalo with domesticated buffalo and wild yak with domesticated yak. (a) Cattle are found everywhere except on in deserts and in the polar regions. Most cattle are raised at mid and low altitudes (<1500 m) but the Peru Criollo lives at an altitude of more than 3000 m. (b) Zebu cattle are kept in tropical regions in India, Indochina, Indonesia, south China (Yunnan, Guangxi, Hainan), east Africa, Brazil, USA and Australia (www.fao.org/faostat/en/, Felius *et al.* 2014). (c) Wild banteng live on Java, probably in Laos and Vietnam and possibly in Bali, Kalimantan, Sabah, Myanmar, Thailand and Cambodia (Gardner *et al.* 2016). (d) Gayal is a domestic relative of gaur living in east India and in Yunnan. (e) Gaur still occur in scattered areas in Bhutan, Cambodia, China, India, Laos, peninsular Malaysia, Myanmar, Nepal, Thailand and Vietnam (Duckworth *et al.* 2016). (f) Yaks live on the Qinghai–Tibet Plateau, including Gansu, Sichuan, Xinjiang, Tibet and Qinghai, in Outer Mongolia and in Ladak (north India and in Nepal (Buzzard & Berger 2016). (g) European bison now live in free-ranging and semi-free herds in Poland, Lithuania, Belarus, Russian Federation, Ukraine, Slovakia and several reservations in western Europe (Olech 2008). (h) The original North American range for *Bison bison* is situated between northern Mexico, Alaska and central Alberta in Canada (Aune *et al.* 2017). (i) African buffaloes are distributed throughout sub-Saharan Africa (Group 2008). (j) Domestic river-type buffaloes are found in India, Sri Lanka, Pakistan, south Iraq, several Balkan countries, Italy, Egypt and Brazil (Mason & Cockrill 1974; Luo *et al.* 2020). (k) The range of domestic swamp-type water buffaloes includes the Yangtze river basin in China, south China, Indochina, Nepal, Indonesia, the Philippines and Brazil, whereas small wild populations of the wild water buffaloes are found in India, Sri Lanka, Bhutan, Nepal, Myanmar and Thailand (Hedges *et al.* 2014; Felius *et al.* 2014; Luo *et al.* 2020; Kaul *et al.* 2019). (l, m) The lowland and mountain anoa are found only in Indonesia on Sulawesi and Buton islands (Burton *et al.* 2016a,b). (n) The historical distribution of kouprey was Cambodia, southern Laos, south-east Thailand, and western Vietnam (Timmins *et al.* 2016a). (o) The Tamaraw is endemic to Mindoro Island in Philippine, where it is limited to the mountainous interior of the Island (Boyles *et al.* 2016). (p) Saola occur only in the Annamite Mountains region of Laos and Vietnam (Timmins *et al.* 2016b).

to have led to divergent domestication traits (Luo *et al.* 2020). There are only few data on the similarities between domestic and wild buffaloes (Zhang *et al.* 2020a; Luo *et al.* 2020) and there may have been domestic introgression into the wild populations and vice versa.

Doubts on the separate species status of the gayal (Payne 1970) were dispelled after analysis of the mtDNA and Y-chromosomal DNA (Verkaar *et al.* 2004) and WGSs (Wu *et al.* 2018). Gayal is often considered as the domestic form of gaur. These two species indeed have similar mtDNA (Verkaar *et al.* 2004) and Y-chromosomal sequences (Nijman *et al.* 2008). However, gaur ( $2n = 56$ ) and gayal ( $2n = 58$ ) have different karyotypes and also different horn shapes. Wu *et al.* (2018) observed a large difference between their WGSs and proposed that gayal descended from a different (sub)species. On the other hand, the divergence of the gaur and gayal may have been

increased by the recent zebu introgression into the gayal from the Yunnan population, which is known to harbour zebu mtDNA (Gou *et al.* 2010). In addition, gaur and gayal share the t2/28 Robertsonian translocation (Chi *et al.* 2005; Qu *et al.* 2012), whereas the t1/29 translocation (Mamat-Hamidi *et al.* 2012) in gaur was not found in Indian gaur and in at least part of the Thai gaurs (Chaveerach *et al.* 1988; Gallagher & Womack 1992) and is thus polymorphic. So gayal and gaur are closely related, if clearly diverged, species and hybrid offspring must be rare.

Kouprey was discovered as a separate species only in 1937. Wild populations were recorded in Cambodia, southern Laos, south-east Thailand, and western Vietnam (Wilson & Reeder 2005). However, it has not been sighted since 1970 (Timmins *et al.* 2016a). Again, molecular analysis removed doubts on the species status (Galbreath



**Figure 2** Phylogeny of the tribe Bovini. The suggested three subtribes (Wilson & Reeder 2005), taxonomical treatments and maximum-likelihood phylogenetic relationships of the Bovine species based on the mitochondrial genomes (Robinson & Ropiquet 2011; left) and the nuclear genomes (unpublished and Wang *et al.* 2018) (right). For mtDNA trees that differentiate swamp and river water buffalo, see Bibi (2013) and 2012 Hassanin *et al.* (2012).

2006; Hassanin & Ropiquet 2007a; Hassanin & Ropiquet 2007b). Ancient mtDNA analysis revealed its similarity to the continental banteng (*Banteng javanicus birmanensis*; Hassanin & Ropiquet 2007a; Hassanin & Ropiquet 2007b). Because this mtDNA deviates from the mtDNA of the Indonesian banteng (*Banteng javanicus javanicus*) or its domestic derivative Bali cattle, it was proposed that kouprey mtDNA has been introgressed into the continental banteng (Hassanin *et al.* 2006).

Continental ( $2n = 56$ ) and Indonesian ( $2n = 60$ ) banteng are considered as the same species, although they have different karyotypes as a consequence of the same t1/29 and t2/28 Robertsonian translocations (Robinson & Ropiquet 2011), which are also observed in gaur (see above). In addition, Indonesian bulls do not have the same fawn color as the females, but are dark brown.

Although wild yaks were suggested to comprise a separate species, morphological and genetic evidence suggest a close interaction of wild and domestic populations (Guo *et al.* 2006). Only 209 genes of domestic yak were found to be influenced by selection, whereas most genomic regions do not show wild–domestic differentiation (Qiu *et al.* 2015). In addition, gene flow between domestic and wild yaks is more frequent than between the domestic yak and two domestic breeds with morphological features deviating from both wild and domestic yak. Plausibly, domestic yaks emerged by multiple domestications of the wild yak (Guo

*et al.* 2006), as has been proposed for taurine cattle (Verdugo *et al.* 2019).

Because of their morphological distinctiveness, American bison (*B. bison*) and European wisent (*B. bonasus*) have been placed in a separate monophyletic genus within the Bovina (Simpson 1945; Wilson & Reeder 2005). In phylogenetic analyses of genome sequences (Fig. 2), these two *Bison* species are linked to yak (Wang *et al.* 2018; Wu *et al.* 2018). However, mitochondrial genomes link the European wisent to the root of the taurine-indicine branch clearly separate from American bison, the extinct steppe bison (*Bison priscus*), yak and the other four *Bos* species (Hassanin & Ropiquet 2004; Wang *et al.* 2018). This has been explained by either a hybrid origin of the wisent (Verkaar *et al.* 2004; Soubrier *et al.* 2016) or by incomplete lineage sorting (Lenstra *et al.* 2016; Massilani *et al.* 2016). The latter explanation is the most compatible with an appreciable heterogeneity of the nuclear gene tree topologies of the bovine species (Wang *et al.* 2018). Ancient DNA analysis revealed that the wisent mtDNA is closely related to the mtDNA of a taxon denoted as ‘Bb1’ (Massilani *et al.* 2016) or ‘X-clade’ (Soubrier *et al.* 2016). Subsequently, this taxon was identified as the extinct woodland bison (*Bison schoetensacki*), which emerged about 1 Mya and is thus a sister species of the wisent (Palacio *et al.* 2017).

Where and when did the tribe Bovini originate? Bovini fossils dated at 8.9 Mya in the late Miocene have been found

in southern Asia in the lowlands south of the Himalayas, where the Bovini emerged as a lineage of the Boselaphini (Bibi 2007). This tribe within the subfamily Bovinae comprises two extant species, the Indian nilgai and the four-horned antelope in India and Nepal respectively, both near the origin region of the Bovini. Still in the late Miocene, the Bovini grew in size and acquired their typical robust dentition as a response to an increase in seasonal aridity (Bibi 2007). From the subtribe Pseudorygina only the saola survived. Within the subtribe Bubalina, the ancestor of African buffalos migrated through Europe to Africa (Hasanin 2014). Predecessors of the African buffalo are the *Pelorovis antiquus* or giant buffalo, which lived from 2.5 Mya to 4000 years ago (Martínez-Navarro *et al.* 2007), and the late Pleistocene *Ugandax* (Museum *et al.* 1978). The Asian late Pleistocene *Proamphibos* (Abbas *et al.* 2018) is probably ancestral to Asian buffalos, which subsequently evolved into the current water buffalo (Gautier *et al.* 2016; Zhang *et al.* 2020a, 2020b). The common ancestor of the subtribe Bovina may have been related to the fossil genus *Selenoportax* living in Siwaliks around 9 Mya (Bibi 2007). A more recent fossil Bovini species was *Leptobos* (Cherin *et al.* 2019), which lived around 2 Mya .

The subtribe Bovina comprises three subclades containing respectively: (i) yak, American bison and wisent; (ii) gaur, gayal and banteng; and (iii) taurine and zebu (Fig. 2). Divergence of these subclades is supposed to have taken place between 3 and 5 Mya, but estimates on the basis of recent genomic data range from 0.5 to 1.7 Mya (Gautier *et al.* 2016; Wang *et al.* 2018; Wu *et al.* 2018). The yak diverged from the bison–wisent lineage around 1.8–2.5 Mya and became adapted to the high altitude of the QTP (Flerow 1980). Most bison-like fossils from the Pliocene–Pleistocene dated at 1.7–2 Mya were found in Europe (Martínez-Navarro *et al.* 2007). Therefore, bison and wisent probably diverged within the early Pleistocene in Europe or northern Asia. Bison arrived in North America via the Bering Strait during the late Pleistocene: 135 000–195 000 years ago and again 45 000–21 000 years ago as testified by numerous fossils near the Strait and adjacent regions (Froese *et al.* 2017).

The *Bos* subclade most likely split into the taurine–zebu and kouprey–banteng–gayal–gaur lineages during the late Pliocene (Bibi 2007). After the divergence of taurine and zebu cattle within the Pleistocene, the wild cattle or aurochs (*B. primigenius*) from the taurine lineage became widespread in Europe between the Middle Pleistocene to Holocene.

## Domestication, dispersal and differentiation of breeds

### General aspects of domestication

For a better understanding the domestication of the Bovini species, it is relevant to summarize a few new and general

insights into the domestication process. Domestication of both animals and plants has been highly important during the history of our civilization and has been beneficial in several ways. First, domesticated animals provide a stable source of food and other animal products such as hides and wool. Second, before the mechanization of agriculture, large livestock such as cattle and horses supplied the labor force for transport, plowing and riding. In addition, dogs guard human settlements as well as livestock and assist during hunting; cats protect grain stores from rodents; domestic pets provide company; and several species, but especially the bovines, are used in a variety of games and rituals.

Domestication implies breeding in captivity for several generations and adaptation to human management (Larson & Burger 2013; Loftus *et al.* 2014). It provides to the animal shelter, food and protection against predators (Mignon-Grasteau *et al.* 2005). Domestication has been successful for those mammalian and avian species that were able: (i) to attenuate aggression and fear while retaining strong social instincts; (ii) to breed in captivity; and (iii) to grow fast growth on food not suitable for human consumption, e.g. grass, acorns, rodents and wastes (Diamond 2002). It has been proposed that domestication via a slight reduction in neural crest cells affects animal behavior and alters morphological and physiological traits associated with domestication, such as a smaller brain and a marked docility (Wilkins *et al.* 2014).

Three plausible modes of domestication have been proposed (Larson & Burger 2013): (i) the commensal approach for species that were attracted to human settlements and were captured and bred; (ii) the prey route for most domestic artiodactyls, which initially were used as source of food; and (iii) a directed pathway for species able to accomplish specific tasks, such as horses for riding.

All bovines most likely were domesticated via the prey pathway. The volume of scientific literature on the different bovine species in fact mirrors their respective population sizes. In the following sections, we focus on the domestication and subsequent dispersal of the three *Bos* species that have established the largest populations, taurine cattle, zebu and yak. For the domestication of two other highly successful bovines, the river and the swamp buffalo, we refer to Zhang *et al.* (2020a), Sun *et al.* (2020) and Luo *et al.* (2020). A more detailed account of the domestication of zebu has been presented by Utsunomiya *et al.* (2019).

### Taurine and zebu cattle

The wild auroch ancestors of the taurine cattle became extinct in 1627, well after domestication. The Indian aurochs ancestral to zebu disappeared from Uttar Pradesh of India around 1800 years ago (Chen *et al.* 2009). Paleontological studies have indicated that domestic forms of the aurochs were kept in the Middle Euphrates Valley 10 800–10 300 years ago (Helmer *et al.* 2005; Conolly

*et al.* 2011; Bollongino *et al.* 2012; Koren *et al.* 2018), in the High Tigris Valley around 10 200 years ago (Bollongino *et al.* 2005) and in western Anatolia and south-eastern Europe around 8800 years ago. A taurine cattle fossil found in eastern Sahara near the Nubian Nile originated from 6500–5500 years BC (Chenal-Vélarde 1998). Archaeological evidence for zebu domestication was found in India in the middle or late Holocene (Naik 1978).

Remarkably, a bovine mandible fossil (belonging to the taurine species lineage) with obvious signs of artificial breeding from north-east China was dated to between 10 756 and 10 565 years ago (Zhang *et al.* 2013), but there is no other evidence for the establishment of a domestic population. Furthermore, molecular markers link the present cattle in this region to the domesticates from the Fertile Crescent. Therefore, if domestication took place in north-east China, it did not persist.

Molecular evidence for domestication and the subsequent dispersal over the Old World has been derived from the uniparental mitochondrial (Lenstra *et al.* 2012) and Y-chromosomal markers (Edwards *et al.* 2011) and from autosomal variation (Decker *et al.* 2014; Verdugo *et al.* 2019). In general, mtDNA sequence variations may link domestic animals to their wild ancestors. In addition, they often differentiate livestock animals from different continents or subcontinents as the result of major migrations. MtDNA divides most of the current cattle into six major haplogroups: taurine T1, T2, T3 and T4 and indicine I1 and I2 (Troy *et al.* 2001; Magee *et al.* 2007; Chen *et al.* 2009; Bollongino *et al.* 2012; Lenstra *et al.* 2012). All T haplogroups diverged 11 000–16 000 years ago (Achilli *et al.* 2009; Di Lorenzo *et al.* 2016). Analysis of ancient DNA indicated that T1, T2 and T3 originated from the first domestic cattle in south-west Asia and led to an estimate of 80 female founders (Bollongino *et al.* 2008). T1 is predominant in Africa (Troy *et al.* 2001; Bonfiglio *et al.* 2012). Its occurrence in Spain and southern Italy probably indicates admixture of African cattle (Decker *et al.* 2014; Da Fonseca *et al.* 2019). An African sub-haplogroup T1c1 is well represented in Brazil and Paraguay, providing evidence for direct migration from Africa to South America (Ginja *et al.* 2019). The T3 haplogroup occupies around half of the populations in south-west Asia (Lenstra *et al.* 2012; Di Lorenzo *et al.* 2016). Most cattle from the Neolithic age in Europe carry T3 haplogroup (Lari *et al.* 2011; Lenstra *et al.* 2012). An Italian aurochs sequence has also been reported (Lari *et al.* 2011), but this T3 sequence is remarkably close to modern sequences. Therefore, contamination via the presence of bovine serum albumin in the reagents may not have been rigorously excluded (Champlot *et al.* 2010). The T4 haplogroup derived from T3 has only been found in China, Korea (Achilli *et al.* 2009) and Japan (Mannen *et al.* 2004) and in Yakutian cattle from Siberia (Kantanen *et al.* 2009). A bovine fossil dating back to 4500 years ago in eastern China was found to carry T4 (Cai *et al.* 2014).

The zebu haplogroups I1 and I2 most likely originated in India (Chen *et al.* 2009). Haplogroup I1 became predominant in zebus from China and Indochina (Magee *et al.* 2007; Jia *et al.* 2010; Gao *et al.* 2017). Several Chinese cattle carry Y1A, a derivative of Y1 (Chen *et al.* 2018; Xia *et al.* 2019).

In addition to the major T haplogroups, eight rare haplogroups have been found in current or ancient cattle: T5, T6 (for two different haplogroups), E, P, Q, R and C (Achilli *et al.* 2009). In the phylogenetic tree of haplogroups, T5 resulted from an early split-off in the T haplogroups and has been found in Italian Valdostana cattle (Bonfiglio *et al.* 2010). T6 first designated a haplogroup in Balkan cattle (Hristov *et al.* 2017), but its phylogenetic position separate from the other T haplogroups has not been supported by a complete mitogenome sequence, and its occurrence in Balkan ancient cattle and aurochs has not been confirmed (Scheu *et al.* 2015). T6 has also been used to designate a haplogroup in Chinese Yunling cattle, which appeared to split independently from the root of T1, T2 and T3 (Xia *et al.* 2019).

In a haplotype trees, the haplogroups diverge in the order I (zebu) - R - E - P before the most recent split of Q and T (Achilli *et al.* 2009). Haplogroup E has so far only been observed in one German Neolithic sample. The P haplogroup has been found in most aurochs samples. It has been reported for a few taurine mtDNA entries in the nucleotide sequence database (Achilli *et al.* 2008; Achilli *et al.* 2009), for a taurine fossil in Switzerland (Schlumbaum *et al.* 2006) and, remarkably, in the Korean Hanwoo (Noda *et al.* 2018). This suggests that auroch introgression into domestic cattle did occur, but rarely. WGSs of ancient auroch DNA have indeed indicated low level of auroch introgression (Park *et al.* 2015; Upadhyay *et al.* 2017, Verdugo *et al.* 2019).

Haplogroup Q, similar to haplogroup T, has been found in both ancient and modern taurine cattle from different locations in Europe and North Africa (Bonfiglio *et al.* 2010; Olivieri *et al.* 2015; Scheu *et al.* 2015; Niemi *et al.* 2015), suggesting that it was also present in the earliest domesticates (Edwards *et al.* 2007b). Haplogroup R has only been found in a few Italian cattle (Bonfiglio *et al.* 2010). The deviating haplogroup C was present in Late Pleistocene cattle with the domestication signal in north-east China mentioned above (Zhang *et al.* 2013).

In contrast to the maternally inherited mtDNA, Y-chromosomal DNA is informative for the paternal origin and male introgression. Y-chromosomal SNP loci identified two taurine chromosome haplogroups, Y1 and Y2, and one zebu haplogroup, Y3 (Svensson & Götherström 2008). Haplogroup Y1 is mainly found in northern European and northern Spanish cattle (Edwards *et al.* 2011) and Y2 is predominant in cattle from central and southern Europe, western Asia and Africa (Edwards *et al.* 2011; Lancioni *et al.* 2016). The initial finding of Y1 in ancient auroch DNA

(Götherström *et al.* 2005) appeared not to be reproducible and all wild aurochs in Europe and Africa analyzed so far carry haplogroup Y2 (Bollongino *et al.* 2008; Pérez-Pardal *et al.* 2010).

On the basis of WGSs, Chen *et al.* (2018) differentiated Y2a was present in European and north- and central-Chinese bulls and Y2b was mainly found in Chinese bulls. However, Álvarez *et al.* (2017) used Y2a to indicate an African haplogroup identified on the basis of Y-chromosomal microsatellites. There is a similar conflicting nomenclature for a subdivision of Y3. On the basis of WGS results, Y3a has been defined as the major Chinese Y3 haplotype and Y3b as the haplotype of Indian zebu bulls (Chen *et al.* 2009). On the basis of microsatellites, an African–south Asian Y3<sub>A</sub>, an African Y3<sub>B</sub> and a south Asian Y3<sub>C</sub> were further suggested (Pérez-Pardal *et al.* 2018).

The large difference between taurine and zebu mitogenomes and their Y-chromosome haplogroups is also reflected by their autosomal DNAs (Porto-Neto *et al.* 2014; Decker *et al.* 2014; Upadhyay *et al.* 2017; Chen *et al.* 2018; Utsunomiya *et al.* 2019). On the basis of molecular evidence, additional domestication sites have been proposed in Africa for taurine cattle and in south-east China for zebus. Cattle from both regions have distinctly different autosomal DNA (Decker *et al.* 2014; Flori *et al.* 2014; Gao *et al.* 2017; Chen *et al.* 2018; Zhang *et al.* 2018a, 2018b; Pitt *et al.* 2019b). However, Pitt *et al.* (2019a) conclude on the basis of 50K SNP profiles and approximate Bayesian calculations that there was no separate domestication in Africa and that gene flow from African aurochs explains the additional genetic variation of African taurine cattle. With the currently available evidence, the separate position of south-east Chinese cattle with an estimated divergence since 36.6–49.6 kya (Chen *et al.* 2018) may be the result of either a separate domestication or a complete turnover of immigrated domestic cattle by introgressive capture of local aurochs. The latter scenario would be similar to the history of European domestic pigs (Frantz *et al.* 2019).

Domestication has been followed by a number of major migrations of cattle, which have reached all inhabited continents (Feliuss *et al.* 2014). This created a huge diversity of breeds and adaptations to various, often extreme environments. The most consequential migrations were the following:

- 1 The Neolithic colonization of Europe from 6000 to 4000 BC introduced cattle as well as other livestock and crop species. WGS studies of ancient taurine and auroch DNA samples between the fertile crescent and the Balkan regions showed influence of local aurochs on the domestic samples (Verdugo *et al.* 2019). This is in line with a detectable affinity of a British auroch sample with modern British and Irish breeds (Park *et al.* 2015). Although there is only scarce documentation on the diversity of European cattle until the eighteenth century, it is plausible that local developments led to a

number of distinct types that existed as early as the Middle Ages: the primitive Balkan Busha cattle, the Podolian steppe cattle, the Alpine spotted cattle (*Fleckvieh*) such as the Simmental, the Alpine brown cattle, the German Red dairy cattle and since the eighteenth century the Dutch black- and red-pied dairy cattle. Cattle from Spain, south France, Great Britain and the Nordic countries are phenotypically diverse, but breeds originating from the same country or region are relatively closely related (Feliuss *et al.* 2011). Since the eighteenth century the differences between local types of cattle have increased by the formation of breeds with explicit breeding objectives (Feliuss *et al.* 2014, 2015). Relationships between these breeds can be studied at the genomic level using SNP bead arrays (Decker *et al.* 2014) or whole-genome sequencing (Chung *et al.* 2017; Hayes & Daetwyler 2019). Analysis of genetic diversity typically uses three complementary analysis tools: coordination analysis, genetic distances and model-based clustering. The several studies published so far target either worldwide panels of breeds (Decker *et al.* 2014; Orozco-terWengel *et al.* 2015; Chung *et al.* 2017) or breeds from the same region or country: central Europe (Kukučková *et al.* 2018), northern Europe (Stronen *et al.* 2019), north-west Europe (Kelleher *et al.* 2017), north-west and southern Europe (Upadhyay *et al.* 2017), southern Europe (Upadhyay *et al.* 2019a, 2019b), the Mediterranean area (Flori *et al.* 2019), the Balkans (Simčić *et al.* 2015; Ramljak *et al.* 2018), Belgium and the Netherlands (François *et al.* 2017), France (Gautier *et al.* 2010), Ireland (Browett *et al.* 2018), Italy (Mastrangelo *et al.* 2018; Barbato *et al.* 2020), the Netherlands (Van Breukelen *et al.* 2019), Russia (Yurchenko *et al.* 2017; Sermyagin *et al.* 2018), Sardinia (Cesarani *et al.* 2018), Sicily (Mastrangelo *et al.* 2014), northern Spain (Cañas-Álvarez *et al.* 2015), Spain and Portugal (Da Fonseca *et al.* 2019), Sweden (Upadhyay *et al.* 2019a, 2019b) and Switzerland (Signer-Hasler *et al.* 2017). The European diversity pattern reflects the geographic origin of the breeds, but also a number of breed expansions (Feliuss *et al.* 2014). During the first half of the nineteenth century, the English Shorthorn was a popular breeding sire in Belgium and northern France. The French beef breed Rouge de Prés (or Maine-Anjou) is closely related to the Shorthorn, which also has influenced the dairy breeds Belgian Blue and Normande and the beef breed Charolais. Later in the same century, black-pied, red-pied and red dairy breeds spread over northern Europe. The export of Dutch black-pied cattle to the USA eventually led to the development of the Holstein, now the most productive breed of dairy cattle. Another dairy breed, the hardy Scottish Ayrshire, had a major influence on several Norwegian, Swedish and Finnish breeds (Li & Kantanen 2010), whereas modern



- dairy breeds have been crossed into Danish Red (Zhang *et al.* 2018a, 2018b). The dispersal of these dairy breeds largely accounts for the north-west European range of the Y-chromosomal haplogroup Y1. In central Europe, the dual-purpose Swiss Simmental and related *Fleckvieh* breeds as well as the Swiss Alpine brown cattle influenced several breeds, the brown cattle mainly in mountainous areas. A consistent finding based on genome-wide SNP studies (Gautier *et al.* 2010; Decker *et al.* 2014; Ramljak *et al.* 2018) suggests a major cluster of central European breeds that consists of distinct subclusters of Alpine spotted (Simmental-like), Alpine brown and southern-French beef breeds respectively. This cluster is separate from both the northern (British, northern-continental, Scandinavian) and Mediterranean (Iberian, Podolian) breeds. A few breeds (Jersey, Guernsey, Charolais, Piedmontese, Mallorquina) appear to have been developed separately from other cattle breeds, which might be the combined effect of a mixed origin and genetic isolation. Simmentals are now more and more influenced by Holstein-Friesian cattle (Frkonja *et al.* 2012). Admixture analysis shows the influence of zebu breeds on Mediterranean cattle (Decker *et al.* 2014; Barbato *et al.* 2020). The Italian Podolian breeds emerged from documented massive imports from the fifteenth to eighteenth centuries of east-European steppe cattle (oxen as well as fertile animals) via the Adriatic ports of Zadar and Venice (Feliuss *et al.* 2014). Several studies were focused on two potential sources of phenotypic variation: the ROHs (Purfield *et al.* 2012; Ferenčaković *et al.* 2013a, 2013b; Kim *et al.* 2013; Šidlová *et al.* 2015; Zhang *et al.* 2015) and the CNVs (Bickhart *et al.* 2016; Boussaha *et al.* 2016; Letaief *et al.* 2017; Upadhyay *et al.* 2017; Mielczarek *et al.* 2018). Different algorithms have been used to localize in the genome those regions that have been targeted by selection, as indicated by a relatively low diversity and/or more pronounced differences in allele frequencies between breeds (Utsunomiya *et al.* 2015). Selection signatures have been reported for several European breeds (Utsunomiya *et al.* 2013; Mancini *et al.* 2014; Zhao *et al.* 2015; Boitard *et al.* 2016; Cesarani *et al.* 2018; Eusebi *et al.* 2018; Yurchenko *et al.* 2018). For the POLLED (hornless) trait, four genetic variants have been identified in an intergenic region of BTA1 (Aldersey *et al.* 2020). Another widespread and consequential gene variant is the PLAG1 Q allele, which led to the recovery of stature of cattle in the sixteenth to eighteenth centuries (Utsunomiya *et al.* 2017).
- 2 Taurine cattle immigrated into Africa after 4800 BC (Hanotte *et al.* 2002; Stock & Gifford-Gonzalez 2013), where they have probably been influenced by local aurochs (see above). Although many taurine cattle have been influenced by zebu, several taurine breeds still persist (Gautier *et al.* 2009; Flori *et al.* 2012, 2014; Jemaa *et al.* 2015; Boushaba *et al.* 2019). The trypanotolerant taurine cattle near the West African coast have remained relatively free from zebu introgression because of the local occurrence of tse-tse flies causing trypanosomiasis (Bradley *et al.* 1996). Gautier *et al.* (2009) report selection signatures in west African cattle. Flori *et al.* (2012) linked the *slick* hair coat locus to thermotolerance.
  - 3 An eastward migration of taurine cattle reached east Asia between 3000 and 2000 BC (Flad *et al.* 2009; Cai *et al.* 2014; Choi *et al.* 2014; Lee *et al.* 2014, 2016; Sharma *et al.* 2016; Gao *et al.* 2017; Mei *et al.* 2017; Chen *et al.* 2018; Zhang *et al.* 2018a, 2018b), including Siberia, with its extremes of temperature (Iso-Touru *et al.* 2016).
  - 4 After 3200 BC climate change caused a westward migration of zebu from the Indus Valley to the Fertile Crescent and resulted in a turnover of the cattle in the Fertile Crescent. This was partially male-mediated as revealed by the taurine/indicine ratios for mtDNA, Y-chromosomes and autosomes (Edwards *et al.* 2007a; Karimi *et al.* 2016; Verdugo *et al.* 2019). In India and Pakistan, several specialized zebu breeds have emerged (Liao *et al.* 2013; Gajjar *et al.* 2018; Iqbal *et al.* 2019; Dixit *et al.* 2020). Crossbreeding with taurine dairy breeds enhances dairy production (Wakchaure *et al.* 2015).
  - 5 The import of zebu bulls into Africa started as early as 4000 years ago and after AD 700 was stimulated by the Islamic conquest (Hanotte *et al.* 2002; Murray *et al.* 2013; Mbole-Kariuki *et al.* 2014; Taye *et al.* 2018; Utsunomiya *et al.* 2019). Crossbreeding with local taurine populations generated so-called 'taurindicine' hybrids with a variable taurine/zebu genomic composition (McTavish & Hills 2014), which were better adapted to the tropical conditions than the original taurine cattle. Sanga cattle (Makina *et al.* 2014, 2016) remained mostly of taurine origin and around 1500 AD were the dominant cattle in east and south Africa. However, at the end of the nineteenth century Sanga was, together with several taurine breeds, largely replaced by indicine cattle, which suffered less than taurine cattle from the rinderpest epidemic (Feliuss *et al.* 2014). All African zebu cattle have retained the taurine mtDNA from their ancestor along the maternal lineage. Admixture of modern dairy breeds into African zebu breeds has been reported by Kim & Rothschild (2014). Selection signatures have been identified by Bahbahani *et al.* (2015), Kim *et al.* (2017) and Taye *et al.* (2018).
  - 6 After 1000 BC zebu migrated to Indochina and China (Naik 1978). Contacts with earlier imports of taurine cattle in China resulted in a taurine-indicine cline from north to south. The intermediate taurindicine breeds exhibit different combinations of taurine and zebu

- mtDNA and Y-chromosomes (Gao *et al.* 2017; Mei *et al.* 2017; Chen *et al.* 2018; Lwin *et al.* 2018; Zhang *et al.* 2018a, 2018b; Li *et al.* 2019; Utsunomiya *et al.* 2019; Xu *et al.* 2019). Yang *et al.* (2017) and Xu *et al.* (2019) studied CNVs and selection signatures in Chinese zebu as well taurine cattle. CNVs in Chinese cattle have been proposed to be involved in high-altitude adaptation (Zhang *et al.* 2020a, 2020b).
- 7 Import of zebu to Indonesia probably started 1500 years ago. Several Indonesian zebu breeds have retained traces or even mtDNA of banteng origin (Mohamad *et al.* 2009; Decker *et al.* 2014; Wangkumhang *et al.* 2015; Hartati *et al.* 2015).
  - 8 Cattle were imported into North and South America from Europe and Africa from 1492 (Gautier & Naves 2011; McTavish *et al.* 2013; Felius *et al.* 2014; Pitt *et al.* 2019a). A large variety of well-adapted Criollo breeds (Ginja *et al.* 2019) are mainly of Iberian and African origin. In contrast, most cattle imported into the USA and Canada and later to Australia and New Zealand originated from north-west Europe (Felius *et al.* 2014; Stothard *et al.* 2015). The Chirikof island cattle in Alaska combined Siberian Yakut with north-west European ancestry (Decker *et al.* 2016). The Mexican Lidia (fighting cattle) with a high level of inbreeding (total ROH coverage 68%) is a genetically distinct population largely separate from the Spanish Lidia (which has an even higher genomic ROH coverage of 74%) and from the Criollo breeds (Eusebi *et al.* 2017).
  - 9 The import of large numbers of Indian zebras to Brazil included mostly bulls but also cows (Ajmone-Marsan *et al.* 2010; Perez-O'Brien *et al.* 2015; Campos *et al.* 2017; Utsunomiya *et al.* 2019). From Brazil zebras were exported to other American countries, including the USA (Villalobos-Cortés *et al.* 2015). As with the African taurine cattle, several Criollo breeds are partially of indicine origin (Ginja *et al.* 2019). In the USA, the import of zebu led to the development of the popular transboundary Brahman zebu breed, which has taurine mtDNA as well as an autosomal taurine ancestry of 9% (Koufariotis *et al.* 2018). Zavarez *et al.* (2015) and Peripolli *et al.* (2018) reported an average genomic coverage of ROHs (>1 Mb) in Nelore (5%) and Gyr (7%) respectively. These values are clearly lower than those found for taurine breeds (for instance, 16% for Criollo cattle, Eusebi *et al.* 2017).
  - 10 In the nineteenth and twentieth centuries, the productive 'cosmopolitan' breeds, most of which originated from Europe, started to spread worldwide (Felius *et al.* 2015). Nowadays, the most important and highly productive transboundary breeds include the dairy black-pied Holstein-Friesian and Jersey, the beef breeds Angus, Hereford, Charolais and Limousin and the Brahman zebu. In America and Australia, this has led to the formation of several synthetic breeds by combining taurine and/or indicine cattle from different origins (Felius *et al.* 2014). Artificial selection has been most intense for Holstein cattle (Kim *et al.* 2013; Ma *et al.* 2019) and is now being accelerated by genomic selection.

## Yak

The domestication of yaks is considered to have been essential for the human habitation of the QTP. The existence of domestic yaks 4500 years ago has been documented (Wiener *et al.* 2006; Meyer *et al.* 2009), but so far there is no fossil evidence for an earlier domestication.

Sequence variations in the mtDNA D-loop region from domestic yaks identified two lineages, which diverged more than 100 000 years ago (Guo *et al.* 2006). Both lineages and one additional lineage are present in wild yaks (Wang *et al.* 2010). These lineages may have resulted from allopatric differentiation of subpopulations separated by the Pleistocene glaciation, which became reunited during post-glacial migrations. After the glacial period, the distributional range of wild yaks shrank owing to the expansion of the human population (Wang *et al.* 2010). These events may also explain the presence of three well-diverged Y-chromosomal haplotypes YH1, YH2 and YH3 (Li *et al.* 2014).

On the basis of sequence variation, domestic mtDNA clades are estimated to have expanded since 6000 and 12 000 years BP (Guo *et al.* 2006; Wang *et al.* 2010). This roughly agrees with a domestication of yaks 7300 years ago on the basis of WGSs (Qiu *et al.* 2015). Furthermore, these WGS data indicated a sixfold expansion of the domestic yak population around 3600 years ago. These two expansion datings are consistent with two large-scale human population expansions in the QTP, 10 000–7000 years ago during the early Neolithic and 4000–3000 years ago during the late Holocene (Qiu *et al.* 2015). The first expansion was explained by the domestication of yaks, which in the absence of agricultural settlements was accomplished by nomadic herders (Qiu *et al.* 2015). The second expansion of the yak population coincided with the introduction of the cultivation of barley on the QTP between 4000 and 3000 years, which may well have allowed the human population expansion (Chen *et al.* 2015). However, this expanded human population also increased the requirement for protein-rich food, hides, fuel and transportations, which could all be provided by the expanding domestic yak population.

Genomic comparisons between yak and cattle identified an expansion in yaks of gene families related to sensory perception and energy metabolism, as well as an enrichment of protein domains involved in sensing the extracellular environment and hypoxic stress (Qiu *et al.* 2012). Furthermore, positively selected and rapidly evolving genes in the yak are significantly related to hypoxia and nutrition

metabolism. Domestication of yaks probably relaxed selective constraints and allowed an accumulation of deleterious mutations (Wang *et al.* 2010; Hu 2012; Qiu *et al.* 2015; Xie *et al.* 2018). Several of these genes are related to smell perception and chemical stimuli (Hu 2012). Although this may well be explained by the environmental requirement to be able to find scarce food, olfactory receptor genes often give false positives in GWAS studies as a consequence of their abundance and dynamic evolution (Lawrence *et al.* 2013).

Breed-level differentiation is weak, but the white Tianzhu yaks have a clearly distinct appearance with several selection signatures (Qiu *et al.* 2015; Xin *et al.* 2019). Genomic approaches to adaptation have been complemented by microRNA (Guan *et al.* 2017) or transcriptome studies (Wang *et al.* 2017a; Lan *et al.* 2018; Qi *et al.* 2018; Xin *et al.* 2019), which identified for several genes a higher or lower expression than in taurine cattle. However, the inferred involvement of genes in adaptation needs to be tested further by functional studies.

### Interspecific hybridization

Species hybridization is often revealed by a discordance of the mtDNA-derived phylogeny with the phylogeny based on morphology, autosomal DNA and/or Y-chromosomal DNA. A more refined analysis may localize in the genome those parts that have been introduced by hybridization. We can discern three categories of interspecific hybridization.

- 1 incidental hybridization of wild or semi-feral species with domestic cattle;
- 2 hybridization of domestic species for breed improvement;
- 3 terminal crossing exploiting the unique performance of the hybrid offspring.

### Incidental hybridization

As discussed in the Introduction, the mtDNA of the mainland banteng differs from the mtDNA from Indonesian banteng and has descended since about 10 000 years from the mtDNA of the extinct kouprey (Hassanin & Ropiquet 2007a; Hassanin & Ropiquet 2007b). Likewise, the south-Chinese population of semi-feral gayals carries zebu mtDNA, which most likely resulted from spontaneous female introgression (Gou *et al.* 2010). A genomic scan of the differentiation of gayal and zebu across the gayal genome indicated a number of zebu autosomal sequences in the Chinese gayal sequence, which are proposed to play a role in adaptation (Wu *et al.* 2018).

Traces of taurine introgression have been found in wisent (Massilani *et al.* 2016; Wecek *et al.* 2017; Wang *et al.* 2018). This appears to be of recent origin, but occurred before the extinction of wisent in the wild. However, as discussed in the section 'The bovine species', the bovine-like mtDNA in wisent and the extinct woodland wisent

probably resulted from incomplete lineage sorting (Wang *et al.* 2018).

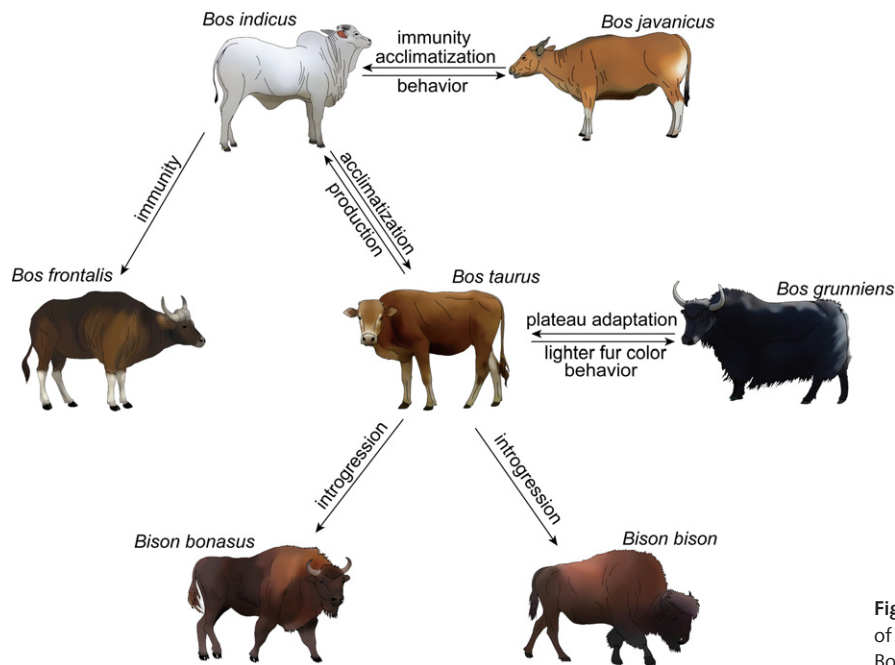
The maternal introgression of taurine cattle into American bison has resulted in an overall 5% frequency of taurine mtDNA (Ward *et al.* 1999) and a taurine origin of up to 1.8% of the autosomal genome (Halbert *et al.* 2005; Halbert & Derr 2006; Wang *et al.* 2018; Wu *et al.* 2018). This is thought to have occurred at the beginning of the nineteenth century during captive breeding of the bison prior to their release into the wild (Hedrick 2009). On the other hand, it has not been excluded that spontaneous contacts occurred between the still large bison population of the nineteenth century and cattle escaped from the large herds that were transported across the prairies. So far, there is no clear evidence that mtDNA from a related species affects an animal's appearance, viability and adaptation, and its relevance for conservation is arguable.

### Hybridization and breed improvement

Hybridization of cross-fertile species may serve the purpose of improving the adaptation or performance of breeds (Fig. 3). During their dispersal over the tropical zones of Asia, Africa and America (see above), zebu came into contact with south-west Asian, African, Chinese and American taurine populations respectively, which led to the emergence of several taurindicine breeds (Utsunomiya *et al.* 2019). Both south-west Asia (Edwards *et al.* 2007a; Verdugo *et al.* 2019) and central China (Lai *et al.* 2006; Lei *et al.* 2010; Gao *et al.* 2017; Chen *et al.* 2018) are now taurine-zebu transition zones. Remarkably, the level of zebu ancestry in China does not vary continuously, but has at increasing range values of 0–0.1, 0.25–0.35 or 0.6–1.0 from north to south China (Gao *et al.* 2017). Chinese zebu acquired taurine alleles associated with production traits, whereas zebu heat-acclimatization-related alleles were introgressed into taurine cattle (Chen *et al.* 2018).

In addition, zebu cattle in south China as well as Indonesia were found to contain traces of banteng (Mohamad *et al.* 2009; Decker *et al.* 2014; Gao *et al.* 2017; Chen *et al.* 2018). For the southern Chinese cattle, the banteng component amounts to 3% and contains genes related to sensory perception, immunity, heat-acclimatization and color pattern (Chen *et al.* 2018). Conversely, Wu *et al.* (2018) reported introgression of zebu into both banteng and gayal, which in both cases introduced genes involved in the nervous and immune systems.

The link between introgression and adaptation is most obvious in Tibetan cattle, which received 1.2% yak ancestry. This contains genes involved in smell perception, immunity and adaptation to hypoxia and high altitude (Chen *et al.* 2018; Wu *et al.* 2018). Conversely, introgression of taurine or zebu cattle into yak (Qi *et al.* 2010) introduced variants of genes involved in nervous system development (Medugorac *et al.* 2017) and coat color (Wu



**Figure 3** Gene flow and the likely adaptations of the introgressed genes between seven Bovine species.

*et al.* 2018). However, as mentioned in the section ‘Yak’, associations of olfactory receptor genes may be artifactual (Lawrence *et al.* 2013).

Beefalo is a recognized American breed that is claimed to maintain a domestic cattle/bison composition of 5:3 ([www.ctq2.org/beefalo/a-short-history-of-beefalo/](http://www.ctq2.org/beefalo/a-short-history-of-beefalo/)). Hereford and Charolais are often used as domestic ancestors, but beefalo bulls are fertile and can be bred within their population. Beefalo is advertised to give tender beef with more protein, one-fifth less fat and one-third less cholesterol than beef from normal cattle. However, the ancestry of the beefalo has not been verified by molecular analysis. The founder of the beefalo, ‘Basolo’, was said to be a bison × F1 backcross, but it has been reported to have a taurine Y-chromosome (Lenoir & Lichtenberger 1978).

Zubron ([en.wikipedia.org/wiki/zubron](http://en.wikipedia.org/wiki/zubron)) is a wisent–taurine hybrid, which was intended to be a hardy and productive alternative to cattle. So far it has remained an experimental breed.

### Terminal crossing

Terminal crossing offers a fast alternative to selective breeding and combines favorable alleles from different species. A well-known parallel in the Equini tribe is the case of the mule and hinny reciprocal crosses, which are obtained by hybridization between horses and donkeys. Thus, dzo, khainag or yakow denotes an F1 hybrid of yak and taurine or zebu cattle. They are reared in Tibet and Mongolia (Wiener *et al.* 2006). By hybrid vigor, these hybrids grow fast, reach a large sizes, have good disease resistance and are productive.

Another productive terminal crossbred is the selembu, kept since 1980 in Malaysia and generated by mating gaur bulls and taurindicine cows (Ismail *et al.* 2018). Selembu are used for both dairy and beef production.

### Conclusion

We have surveyed recent literature on evolution, domestication and hybridization of the Bovini, several of which are domestic and thus relevant for agricultural production. The tribe of the Bovini is remarkably versatile with respect to environmental range. Whole-genome sequencing identifies exchange of genes between the species. This is a source of information on the adaptation of cattle to specific environments, which remains to be tested on the functional level.

### Acknowledgements

This work was supported by the Ministry of Science and Technology of the People’s Republic of China (2010DFA34610), the Fundamental Research Funds for the Central Universities (lzujbky-2019) and International Collaboration 111 Programme (BP0719040).

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