



## Genetics of domestication and world-wide introduction of *Bos indicus* (Zebu) and *Bos taurus* (Taurine) cattle

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### ABSTRACT

Neolithic people who had already domesticated crops such as barley and wheat, domesticated cattle more than 8,500 years ago. This development transitioned human populations from hunter-gatherers to sedentary complex societies. Modern cattle comprise mainly of two species (or types) *Bos taurus* (taurine) and *Bos indicus* (zebu or Indicine) which are distributed world-wide; and some minor species of cattle, including *Bos grunniens* (yak), *Bos frontalis* (gayal/mithun) and *Bos javanicus domesticus* (Bali banteng) are also important in East and Southeast Asia. Neolithic period onwards cattle have been deployed to plough land for efficient agriculture; yield milk, meat and leather and for making yoghurt, cheese and ghee from milk; transport people and goods in carts. Historical accounts of 10000 years and archaeological findings of Neolithic period have been complemented by recent mitochondrial and nuclear genetical-genomical evidences to understand the pre- and post- domesticated history of cattle. Analyses of nuclear and mitochondrial genome sequences for polymorphism at DNA markers in ancient (extinct) and modern cattle has revealed the parentage of cattle species, approximate dates and places of their domestication, approximate dates and routes of their migration to new habitats on different continents, and times and places of introgression from wild aurochs in Europe and Africa and admixture between species. Cattle have undergone natural and strong artificial selection for adaptation to varied environments, fertility, social behaviour, milk and meat yields, milk quality and aesthetic morphological features which have had pronounced effect on cattle genome, causing reduction in genetic variability. Here a brief review is presented about genetical evidence on above aspects and future research directions are also identified.

**Key words:** African taurine, Ancient cattle DNA, Banteng, Fertile crescent, Gaur, Indus valley, Mithun, Neolithic farmers, Yak

The interaction between domestic cattle and humans is an example of symbiotic relationship. There are five domesticated species (types) of the bovine genus *Bos* (family, Bovidae; subfamily, Bovinae; tribe, Bovini; 2n = 58+XY): Taurine and zebu are present world-wide; and banteng, gayal and yak are distributed in parts of Southeast Asia (Table 1). Domestication of cattle followed the advent of agriculture in the Neolithic period (Fuller *et al.* 2006, 2014; Fuller and Murphy 2014). Since their domestication 2,500 to 10,500 years ago (ya), cattle have served human civilizations as draught animals for ploughing of agricultural fields and wheeled transportation and as sources of milk, meat, skin, hide, leather and dung-fuel/fertilizer; and as the earliest form of capital. Cattle owners provided care and water, feed, housing and shelter from prey to the retained cattle. There are now more than 800 recognized breeds of cattle (>30 in India) in the world, in addition to non-descript

hybrids between different breeds and types of cattle (Felius 1995, Felius *et al.* 2014, Hongo 2011). Modern breeds of cattle yield on average basis 20l milk/day, containing 650 g milk protein and 750 g fat (Pehrsson *et al.* 2000). The world-wide yearly milk and meat production from cattle in 2015 was, 636 million tonnes (61 million tonnes in India) and 58.4 million tonnes (4.2 million tonnes in India) respectively, yearly yield of milk from other livestock-buffaloes, goats, sheep, camels, equines and yak was~ 125 million tonnes (dairy.ahdb.org.uk/market-information/supply; beef2live.com/story-world-beef production-ranking). In 2015, a cattle population of 965 million (301 million in India; beef2live.com/story-world-cattle-inventory-ranking) was able to meet the cow dairy requirements of 7.39 billion world population of humans (1.29 billion in India; www.worldmeters.info/world-population). Clearly, domestication of cattle was one of the most important developments for the cultural, demographic and economic advancement of human society, and acquirement of health promoting alleles by humans (Reich *et al.* 2009, Curry 2014, Mathieson *et al.* 2015, Kumar and Kumari 2016).

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Each cell of a cattle contains mitochondria possessing 103 copies of their DNA genome and a nucleus which contains 2 copies each of 29 autosomes and XX (in females) or XY (in males) sex chromosomes (Kieffer and Cartwright 1968). DNA sequences of mitochondrial and nuclear chromosomes of taurine and zebu cattle are known (Heindler *et al.* 2008, Zimm *et al.* 2009, Canavez *et al.* 2012). The cells of both cattle types carry genetic information about evolution of the cattle, in the form of mitochondrial genome haplotypes and frequencies of nuclear autosomal and Y chromosomal sequence alterations (alleles) and selective sweeps. Whereas the mitochondrial haplotypes are inherited through females, the nuclear markers are contributed to progeny by both male and female parents. Genetic variation accumulates with time/over generations, therefore, early domesticates are expected to carry less DNA sequence variation than their modern descendants. Archaeological skeletons (bones and teeth) of ancient cattle discovered in India, China, Southeast Asia, Middle East, Africa and Europe were used for DNA sequence analyses to elicit paleogenetic information about cattle ancestry, domestication and post-domestication movement. Comparative analysis of polymorphism in many thousand nuclear genome DNA markers and several mitochondrial DNA markers among hundreds of ancient cattle and thousands of extant cattle, later of breeds common in different parts of world, has generated information about the complex evolutionary history of cattle populations, including times and geographic locations of domestication events for different types of cattle and times and routes of their initial introduction from areas of domestication to parts of different continents (Loftus *et al.* 1999, Christian 2000, Copley *et al.* 2003, Freeman *et al.* 2004, Baig *et al.* 2005, Beja-Pereira *et al.* 2006, Bollongino *et al.* 2006, 2013, Edwards *et al.* 2007, Chen *et al.* 2010, Larson and Burger 2013, McTavish *et al.* 2013, 2014, Stock and Gifford-Gonzalez 2013, Magee *et al.* 2014, Decker *et al.* 2014, Schibler *et al.* 2014, Orlando 2015, Park *et al.* 2015, Scheu *et al.* 2015). Here, we briefly reviewed the results of these archaeozoological-cum-genetic-cum-historiogeographic studies.

#### *Origin of domestic taurine and zebu (indicine) cattle*

Cattle-like fiercely wild animals of huge size belonging to the taxa *Bos primigenius* or aurochs, descendant of *Bos acutifrons*, were the progenitor of major domestic cattle species (Perkins 1969, Epstein and Nason 1984, McKenna and Bell 1997, Bradley *et al.* 1998, Lenstra and Bradley 1999, Clutton-Brock 1999, Mona *et al.* 2010, McTavish *et al.* 2013, Felius *et al.* 2014, 2015, Orlando 2015, Park *et al.* 2015). From several million years ago (mya), *Bos primigenius* was endemic to a vast geographical area, including the grass plains of Asia (India), Central Asia (Steppes = Ukraine, Russia, Kyrgystan, China, Mongolia), Middle East, North Africa and Europe (Mona *et al.* 2010). Fossilized remnants of the species dating back to two mya have been discovered in India (Van Vuure 2001).

Paleogenetic evidence has further established that about 250,000 ya, aurochs had genetically diverged into sub-species, 2 of which were *Bos primigenius primigenius* that ranged in Northeast Asia and Europe (Eurasia), and *Bos primigenius namadicus* which ranged in India (Van Vuure 2001, Mona *et al.* 2010, Orlando 2015). The domesticated descendants of these species, now extinct, were the main resource of genetic variability present in the modern cattle in the world (Lenstra and Bradley 1999, Troy *et al.* 2001, Lenstra and Felius 2014).

In the Neolithic period, about 10,500 ya, hunter gatherers who had converted to sedentary pastoralism (Diamond 2002, Ellis *et al.* 2013), located in fertile crescent in the boundary region of present day Turkey and Syria, domesticated *Bos taurus* or taurine cattle from among the *Bos primigenius primigenius* aurochs of the area (Troy 2001, Peters *et al.* 2005, Ho and Shapiro 2011, Hongo 2011, Vigne 2011, Schibler *et al.* 2014). Genetic analysis of ancient and modern taurine cattle showed that there was genetic bottleneck in the domestication process since only 80 or 81 female aurochs were the founding ancestors of extant taurine cattle (Ajman-Marson *et al.* 2010, Bollongino *et al.* 2012, Lenstra *et al.* 2014, Lenstra and Felius 2014, Scheu *et al.* 2015). The taurine cattle inherited from their founding mothers at least 6 types of mitochondrial haplogroups T, T1, T2, T3, T4 and T5 (a haplogroup structure is characterized by sequence of a 240 bp hypervariable mitochondrial (mt) DNA control region, variation in which is due to insertional and point mutations, base substitutions, deletions and additions) (Troy *et al.* 2001, Achilli *et al.* 2009). Domesticated in Eurasia, the taurine cattle are well adapted to temperate climatic conditions. Their other domestication attributes included tamed docile behaviour in human presence, ability to efficiently utilize grass and leaves as feed, faster rate of growth, smaller size, shorter lifespan and reduced sexual dimorphism as compared to aurochs, and ability to breed in captivity (Turner 1980, Felius 1995, Taberlet *et al.* 2011, Lenstra and Felius 2014).

Further domestication of *Bos primigenius namadicus* aurochs resulted into *Bos indicus* or zebu (indicine) cattle by the Indus valley farmers about 8,500 ya. The zebu domesticates inherited from their female parents I1 mt DNA haplogroup (Naik 1978, Loftus *et al.* 1994, Baig *et al.* 2005, Bradley *et al.* 2006, Fuller 2006, Jarrige 2006, Zeder *et al.* 2006, Singh 2008, Heindler *et al.* 2008, Armone-Marson 2010, Chen *et al.* 2010, Murray *et al.* 2010, Colledge *et al.* 2013, Magee *et al.* 2014). Another independent domestication of indicine cattle is proven to have occurred in the Indo-Gangetic plains area about 4000 ya. These domesticates carried I2 mt DNA haplogroup (Chen *et al.* 2010, Murray *et al.* 2010, Magee *et al.* 2014). The domesticated zebu cattle had some of the same traits as in domestic taurine cattle. However, zebu cattle is different from taurine cattle morphologically, anatomically and physiologically. Zebu domesticated in semi-temperate conditions bore smoother coat, a hump over shoulders, flapped rather than erect ears, more pendulous dewlap and

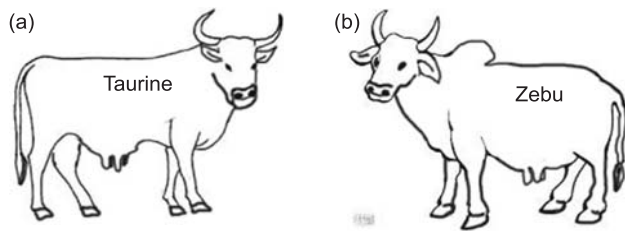


Fig. 1. Diagrammes of *Bos taurus* (Taurine) and *Bos indicus* (Zebu or Indicine) cattle. Taurine is humpless and bears erect ears. Contranstringly Zebu has a hump at shoulders and bears drooping ears.

larger sweat glands, and had predominance of intramuscular fat rather than subcutaneous fat, lower metabolic rate, late maturity and tolerance towards ticks (insects) and intestinal parasites (protozoa), water-stress, feed-stress, high humidity and high temperature (Utech *et al.* 1978, Hansen 2004, Bahbahani *et al.* 2015), European taurine and Indian zebu can both tolerate low temperatures (say  $-13^{\circ}\text{C}$ ) equally well, however taurines barely tolerate  $25^{\circ}\text{C}$  whereas zebu can tolerate temperatures beyond  $42^{\circ}\text{C}$  (Frisch and Vercoe 1977, Turner 1980, Grigson 1991, Hall 2004, Lenstra and Felius 2014). Beta casein in the milk of taurine called A1 beta casein has histidine at 67th position in the 209 amino acid (aa) long sequence. Corresponding position in the beta casein called A2 beta casein in zebu has proline. This mutation in taurine beta casein (A1) results in production of a 7 (aa) long digestion product called beta casomorphin-7 (BCM 7), which has been intriguingly implicated as a cause of several human disease conditions resulting from consumption of the taurine's milk (Beales *et al.* 2002, Hill 2003, Woodford 2009, Sodhi *et al.* 2012).

Zebu and taurine cattle (Fig. 1) were found to be fully interfertile. Only difference in their karyotypes is that Y chromosome is metacentric in taurine cattle and acrocentric in zebu cattle. Their F1 hybrids demonstrate high levels of heterosis (McDowell *et al.* 1996). Despite bottlenecks in the domestication events of cattle from among violently hostile aurochs and subsequently during introduction to distant lands thousands of years ago (Felius *et al.* 2014), the sustained zebu and taurine possessed considerable genetic variability. Their progeny responded to a wide variety of selection criteria, including adaptation to diverse agroclimates (Chan *et al.* 2010) and variety of feeds (Church 1984); coat colour (Schmitz 2014); stature (Randhawa *et al.* 2015); body weight (Pinheiro *et al.* 2012); strength and vigour for draught (Joshi *et al.* 2005); tolerance towards pests and diseases (Francis 1966, Qureshi *et al.* 1996, [ftp.fao.org/docrep/fao/](http://ftp.fao.org/docrep/fao/)); polledness and horn size (Schmitz 2013); high milk yield (Kiplagat *et al.* 2012, IAEA-TECDOC-1670); high content of protein (Zhou *et al.* 2015) and fat (Winter *et al.* 2002, Kaupe *et al.* 2004, Kuhn *et al.* 2004, Glaser *et al.* 2010) in the milk (Ibeagha *et al.* 2007); and high meat yield (Pinheiro *et al.* 2012, O'Rourke *et al.* 2013, Publication 8130 ANR Univ Cal). The major genes controlling certain important traits linked to positive selection sweeps in cattle include the following: *POLL* for

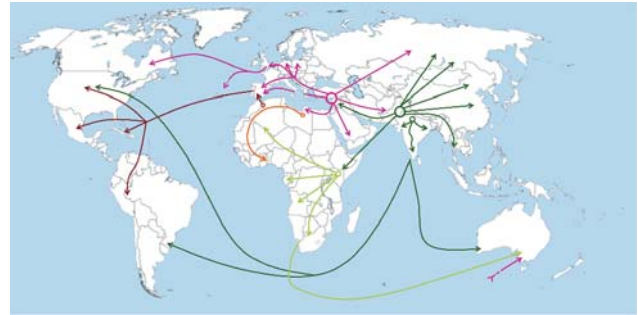


Fig. 2. Diagrammatic representation of centres of origin (domestication) and approximate migration routes of *Bos taurus* (Taurine) and *Bos indicus* (Zebu) cattle. Red and green circles respectively depict Fertile Crescent (Near East) area, the centre of origin of Taurines and Greater Indus valley/Indian subcontinent centres of origin of Zebus. The migration routes of Zebu to parts of Indian subcontinent, Southeast Asia, China, Mongolia, Near East, Africa, Americas and Australia are shown by arrows of green colour. Red coloured arrows show the migration routes of taurine to different parts of Europe via Mediterranean coast and Danube basin, Russia, Northeast Asia, India, Africa, North America and Australia. Light green coloured arrows show migratory routes of Taurine introgressed with zebu in Africa and movement into Australia. Orange coloured arrows depict the route of Aurochs introgressed Taurine or African Taurine in Africa. The entry of African Taurine  $\times$  zebu introgressed cattle into Portugal and Spain and from there to America is shown by brown coloured arrows.

horn development, *MSTN*, *AKA* and *GDF8* genes for muscular hypertrophy, *KIT* and *MC1R* for coat colour pattern, *PDGFRA* and *KDR* for fertility, *NCAPG-LCORN* and *PLAG1-CHCHD7* genes for stature, *R3HDM1*, *ZRANB3* genes for feed efficiency, *ABCG2*, *DGAT1* and *GHR* genes for milk yield and its protein quality and *HSPA9*, *CD14*, *ARAP3* and *PCDM* genes for immune response (Randhawa *et al.* 2016). Complementary nature of their characters allowed worldwide spread of taurine, zebu and their hybrids. However, cattle populations of taurine and zebu breeds in Eurasia and Asia remained susceptible to rinderpest transmission (Yadav 2011).

Following their origin, taurine and zebu cattle were dispersed in ancient times in different directions, via their co-migration with farmers and explorers moving to new farmable areas for greater opportunities. In recent times, cattle have been traded between different countries. Thus cattle got introduced to wherever human populations came to reside on different continents and islands. Discussed below is the paleogenetical and/or historiogenetical evidence about the times and routes of initial dispersal of zebu, taurine and their admixed lines to various parts of continents and to islands of human habitation (Fig. 2).

#### Introduction of taurine into Europe, Africa and Northeast Asia from Fertile Crescent

Starting from  $\sim 10,000$  ya, Neolithic farmers rapidly distributed the domesticated taurines world over. There is evidence that bulk of the taurines from Fertile Crescent were

taken away by the then farmers to different parts of Europe, resided hitherto by hunter gatherers (Evershed *et al.* 2008). Cattle were transported by boat to southwestern areas of Europe lying along the Mediterranean coast. Land route along the Danube river was used to reach the cattle to areas of central and northern Europe. Neolithism and cattle finally reached western Europe and England + Ireland around 6,000 ya. Genetic variability among the cattle, progressively introduced westwards and northwards, decreased among the onwards moving cattle. There was no gene flow from taurine cattle left in Fertile Crescent to taurine cattle moved towards Europe, from about 7,000 ya. The cattle that arrived in Europe from Fertile Crescent were predominantly the T3 haplogroup derivatives of the taurine domesticates (Lanstra and Bradley 1999, Troy *et al.* 2001, Balasse and Tresset 2002, Kuhn *et al.* 2004, Arbuckle and Makarewicz 2009, Decker *et al.* 2014, Felius *et al.* 2014, Orzoco-ter Wengel *et al.* 2015, Scheu *et al.* 2015). Taurine had introgression from aurochs in Europe. Ancient taurine cattle of P haplogroup and R haplogroup (originating from matings of European auroch females and taurine males) have been respectively found in Slovakia, Spain, Switzerland and Italy (Bollingino *et al.* 2006, Achilli *et al.* 2009, Ajmone-Marson *et al.* 2010, Bonfiglio *et al.* 2010, Schibler *et al.* 2014). It is also known that significant gene flow occurred from male aurochs to taurine females in England and Ireland (Orlando 2015, Park *et al.* 2015). Application of breeding procedure, from about 250 ya, on all of genetic variability accumulated in Europe has made the genetic base of modern European cattle much broader, thus somewhat overcoming the founding bottlenecks faced during introduction of taurine cattle into Europe (Felius 1995, Felius *et al.* 2014, Felius *et al.* 2015, Scheu *et al.* 2015).

Taurine cattle of T1 haplogroup (a variant of T3 haplogroup) migrated to Africa from Fertile Crescent (Bonfiglio *et al.* 2012b). Taurine cattle entered, along with southward migrating farmers, into Africa from an area near Suez in northeast of continent ~ 8,500 ya. Before the taurines spread in Africa, the introduced taurines inter-bred with males of *Bos primigenius africanus* (Linseele 2004), the African aurochs, which were genetically variant from European and Indian aurochs. The European taurines possessing high level of aurochs introgression are called African taurines. Because of introgression from aurochs, the African taurines acquired a very important trait, resistance towards trypanosomiasis (Stewart 1951). African taurines spread from northeast to west and central parts of Africa (Epstein and Mason 1984, Payne and Hoges 1997, Lenstra and Bradley 1999, Blech and McDonald 2000, Troy *et al.* 2001, Hanotte *et al.* 2002, Ajmone-Marson *et al.* 2010, Decker *et al.* 2014, Felius *et al.* 2014, 2015, Lenstra *et al.* 2014, Magee *et al.* 2014). Further, it has been ascertained that although rare, there are pure European/Fertile Crescent type taurines present in Africa (Decker *et al.* 2014).

Neolithic pastoralists of Fertile Crescent took taurine

cattle of T2, T3 and T4 haplogroup (latter a subgroup of T3) to Northeast Asia (North China and Mongolia) about 5000 ya. During bronze age (4000–2700 ya) taurine were exclusive cattle in Northern China. From North China, taurine cattle migrated to Japan 1,800 ya via Korean peninsula. T4 haplogroup taurine cattle are present only in Siberia, Mongolia, China, Korea and Japan (Mannen *et al.* 2004, Ajmone-Marson *et al.* 2010, Li *et al.* 2013, Cai *et al.* 2014, Lenstra *et al.* 2014, Magee *et al.* 2014, Yonesaka *et al.* 2015).

#### *Zebu introgressed African Taurine spread in Africa and entered Southwest Europe*

Spread of cattle in highly diverse agro-environments of African continent, such as hot and dry, temperate to tropical, became possible with the derivation of African Taurine × zebu hybrids (Lenstra and Bradley 1999, Ajmone-Marson *et al.* 2010, Magee *et al.* 2014, Mwai *et al.* 2015). Zebu cattle were introduced into Africa from India in waves, first 4000 ya, second 1300 ya and third 128 ya (Epstein and Mason 1984, Felius 1995, Payne and Hoges 1997, Hanotte *et al.* 2002, MacHugh *et al.* 1997, Marshall 1989, Ajmone-Marson *et al.* 2010, Decker *et al.* 2014, Mwai *et al.* 2015, Orzoco-ter Wengel *et al.* 2015). Pure zebu cattle do not occur in African continent (Decker *et al.* 2014, Mwai *et al.* 2015). The zebu introgressed African taurine carry T1 mt DNA suggesting that zebu males were crossed with African taurine females to obtain Taurine × zebu hybrids (Troy *et al.* 2001, Edwards *et al.* 2007). Absence of zebu mt DNA in zebu admixed African taurines is intriguing and requires an explanation. The zebu introgressed cattle are distributed all over Africa, but with varying zebu content. Zebu introgression is poorly represented in West and South-Africa, it is predominant in East and Central-Africa (McHugh *et al.* 1997, Payne and Hoges 1997, Freeman *et al.* 2004).

Zebu introgressed African taurine cattle (carrying genes from Fertile Crescent taurine, African aurochs and Indian Zebu) were introduced into Portugal and Spain, from Morocco via the strait of Gibraltar, during Moorish occupation (1300 ya); such cattle also reached Italy from Spain (Cymbrom *et al.* 1999, 2005, Beja-Pereira *et al.* 2006, Decker *et al.* 2014, Mwai *et al.* 2015). Zebu introgressed African taurine perhaps served as a source of indicine genes into European and American cattle (Orzoco-ter Wengel *et al.* 2015).

#### *Zebu and taurine cattle admixture in Middle- and Near-East and in India*

The cattle present in the Fertile Crescent Area of Near East/Middle East are not the original taurine domesticates since the migratory Neolithic farmers had spread most of the genetic variability of the taurines domesticated in Fertile Crescent into Europe, North Africa and Northeast Asia (Ajmone-Marson *et al.* 2010, Decker *et al.* 2014). Over time cattle of the entire area from Italy to Iran through Fertile Crescent got admixed with African taurine and Zebu genetic

variability. Zebu cattle had reached the region by 6500 ya (Decker *et al.* 2014). Both males and females participated in contributing the zebu gene flow into taurines of the area (Loftus *et al.* 1994, Lenstra and Bradley 1999, Troy *et al.* 2001, Edwards *et al.* 2007, Ajmone-Marson *et al.* 2010, Akis and Oztabak 2013, Ozsensoy and Kurar 2014). Reciprocally, taurine cattle reached Indus Valley 6200 ya and introgressed with zebu. Important zebu breeds have been shown to possess taurine genes (Naik 1978, Kumar *et al.* 2003, Baig *et al.* 2005, Magee *et al.* 2014).

#### Introduction of cattle into Americas

Human colonization and dispersal of cattle were concurrent in Americas. Between 1493 and 1521 (28 calendar years), cattle were shipped in large numbers from Portugal, Spain and southern France and dispersed in areas of southern North America (state of Texas) and northern South America (Mexico, Columbia and Venezuela) (Rouse 1977, Barragy 2003). These cattle were either T3 mt DNA bearing European taurines or T1 mt DNA bearing Iberian taurines, the latter possessing tripartite genome with components of European taurine, African aurochs and Indian zebu, received in Portugal and Spain from Africa via strait of Gibraltar (Barragy 2003, McTavish *et al.* 2013, Decker *et al.* 2014, Magee *et al.* 2014). These cattle ranged freely in the wild for about 400 years and thus became naturally selected for adaptation to local conditions. Subsequently, breeds such as Corriente in Mexico, Longhorns in Texas and Romosinuano in Columbia emerged from them (Rouse 1977). The prime Indian zebu breeds were brought to Brazil in 1813 and these were redistributed to North America in 1880. Zebu breeds were brought directly from India to North America in 1906 and also European breeds were brought around that time from Europe continent (Hoyt 1982). Widespread crossing of taurine and zebu in Americas provided the genetic variability needed for adoption of cattle to environments in Americas varying from temperate to tropical (Magee *et al.* 2014).

#### Cattle introduction into Australia

Cattles are not indigenous to Australia, like they are to Eurasia. First batch of taurines and zebu types of cattle arrived, with first batch of European settlers in Australia in 1788, these cattle had been obtained from South Africa. This introduction was successful and animals thrived in the wild. A bigger batch of cattles were brought from India in 1795. Subsequently Australia imported most of the important breeds from America, Asia and Europe (darkenberger.com.au/...-us/history-of-beef-cattle).

#### Cattle in India and adjoining Southeast Asia

Climates in the Indian subcontinent (South Asia, areas of ancient Indus Valley Civilizations included) and Southeast Asia are as varied as alpine, montane, arid, semi-arid, semi-temperate, dry tropical and humid tropical. The parent species of *Bos indicus* (zebu/indicine) cattle, the

Indian aurochs *Bos primigenius namadicus* which ranged in Indian subcontinent was adapted to the climate associated with alpine, grassland, savanna and rainforest agro-ecological conditions. The wide environment adaptability of zebu cattle stemmed from its parentage. In addition to zebu cattle, the Neolithic farmers of the region domesticated several sister species viz. *Bos grunniens* (yak), *Bos frontalis* (mithun/gayal) and *Bos javanicus* (Bali-banteng). They experimented and successfully used interspecific hybrids of zebu (or taurine) as one parent and yak, mithun, wild yak (*Bos mutus*) or wild gaur (*Bos gaurus*) as the other parent and hybrids of wild gaur with mithun and banteng and of wild yak with domesticated yak (Table 1). Genetic variability present in the cattle of the region is enormous and awaits conservation and characterization.

Of the two zebu domesticated populations, the I1 mt DNA carrying zebu population spread from the greater Indus valley eastwards. Migratory farmers brought the I1 haplotype zebu to Haryana, Uttar Pradesh, Bihar, Odisha and West Bengal states of the present Indian geography, Bangladesh, Myanmar and Thailand and adjoining mainland countries. Zebu cattle were present in Thailand 6000 ya (Wangkumhang *et al.* 2015), and had reached Indonesian islands before 1000 ya (Mohamad *et al.* 2009, 2012). Some Thai breeds of Zebu cattle have *Bos javanicus* admixture (Wangkumhang *et al.* 2015). Zebu were introduced from India into Central and Northern China and Mongolia and were present in Southern China 3500 ya (Naik 1978, Payne and Hoges 1997, Cai *et al.* 2014, Decker *et al.* 2014, Magee *et al.* 2014). The haplotype I2 of Zebu spread from the Indo-Gangetic plains southwards and became the main cattle of all parts of India and of Srilanka and Bangladesh (Edea *et al.* 2015). There are zebu or zebu × taurine breeds in all milk producing countries. India has 37 well characterized zebu breeds for milk (Sahiwal, Gir, Red Sindhi, Tharparkar and Rathi), milk and draught (Kankrej, Ongole and Haryana) and draught (29 breeds), selected by farmers in various parts of India over antiquity (Naik 1978, Baig *et al.* 2005, Decker *et al.* 2014, Felius *et al.* 2014, Magee *et al.* 2014, Sharma *et al.* 2015, allindiadairy.com/cattle-breeds). From the time of origin to present, different breeds have introgressed each other giving rise to non-descript cattle in India. In recent years many Indian zebu breeds have been introgressed with taurines to improve milk yield. Use of cattle as means of transportation and traction having declined, steps are needed to conserve the purity of prominent Indian zebu milk and milk and draught breeds in such a way that much sought combination of alleles for disease and pest tolerance, heat and water stress tolerance and effective utilization of low quality and rough material as feed in indigenous Indian zebu varieties are not eroded.

#### Concluding remarks

*Bos taurus* (taurine) and *Bos indicus* (zebu) domesticates inherited from *Bos primigenius* only a small fraction of genetic variability. Since their domestication 8500 ya, both taurine and zebu cattle have spread worldwide. There were

many bottlenecks in the process of introduction of domestic cattle to new geographic areas, and thus the genetic variability got reduced. The domesticates have undergone natural selection and artificial selection by their owners, based on the needs of the latter for various combinations of characters, including superior adaptation to local abiotic and biotic stresses, nature of feed, fertility, milk and meat production, draught power, docility, social behaviour, coat colour and size and shape of horns. In the last 250 years, production properties of cattle have been improved by application of general, molecular and biometrical genetic procedures for selections of progeny from crosses between pre-characterized parent animals, using conventional mating, artificial insemination, *in vitro* fertilization and embryo cloning and transfer procedure. Use of CRISPR/Cas 9 nuclease gene editing to mediate directed changes in specific genes has also begun. Following the application of strong selection criteria for specific trait(s) multiple times, cattle have been exposed to further depletion of genetic variability. To conserve all the prevailing alleles with large favourable effects, there is need to identify individual genes controlling such properties in the available genetic resources. Now that modern technologies of controlled reproduction are available, it has become possible to utilize worldwide genetic resources of cattle in any one place. Genomic information from minor cattle species and other mammals, including man, will be useful in this direction.

Pre- and post-domestication history of zebu cattle of Indian sub-continent is less understood than that of taurine cattle in Europe and Africa. Archaeological investigations in Indus valley areas of India in Himachal Pradesh, Haryana, Punjab, Uttar Pradesh and Rajasthan and in areas of Pakistan and Afghanistan are needed to recover any remnants of ancient cattle for their paleogenetic analysis and comparison with modern zebu breeds. The ancient cattle genomes need to be treated as reservoirs of novel genes/alleles for cattle improvement.

All the genetic analysis carried out so far, about cattle domestication process, distribution worldwide and breeds available in different countries, has shown the following with reference to properties in Zebu cattle. In antiquity (5000–10000 ya), the sedented Indian farmers located in the latitudinal areas of Sarswati-cum-Indo-gangetic plains domesticated the Indian aurochs *Bos primigenius* into *Bos indicus* cattle whose progeny had qualities of adapting to draught in climates of all the inhabited continents and islands of earth and producing milk that had health promoting properties.

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