Introduction

Mario Melletti and James Burton

This is the first comprehensive work combining the state of knowledge of every known wild cattle species. It covers the biology, taxonomy, evolution, conservation status and management of all 13 species. This book is addressed to researchers, conservationists and anyone with an interest in wild cattle. We hope the work will inform and inspire greater interest and passion for this group of species to help in our understanding of them and in their successful conservation.

Wild cattle belong to an amazing group of animals that have fascinated humans since ancient times. There are species that are very well known and charismatic, such as the American bison (*Bison bison*), but also species that are very little known to humans, living in remote forest areas, such as the saola (*Pseudoryx nghetinhensis*) in Vietnam and Lao PDR and the anoas species (*Bubalus depressicornis* and *Bubalus quarlesi*) on the island of Sulawesi, Indonesia (see also Table 1).

The link between wild cattle and humans has existed for thousands of years. Five species of wild cattle have been domesticated in the last 7000 years, including the wild water buffalo and the yak. This domestication has provided many benefits to humans, from meat and milk to draught animals (see Chapter 3 for more details). They are therefore valuable today as a genetic pool for ensuring that domestic breeds can adapt to changing pressures, such as climate and disease. Also, some species may have key roles in their natural ecosystems. They are not only an important prey species for predators, but also play an interesting role in maintaining ecosystems by grazing and wallowing. For instance, wild yak at high densities may change grassland community (Qiao *et al.* 2009). It is also known that some other species, such as American bison and African buffalo (*Syncerus caffer*), similarly to yak, may increase grass species diversity in the prairies and savannas, respectively. Thus, these species play an important role in ecosystem management. So wild cattle deserve further investigation in the future and greater effort to preserve them and the ecosystems they are an integral part of. Conversely, some introduced species need management, such as the feral water buffalo in Australia, which has completely altered the coastal ecosystem and so needs proper management (Werner 2013).

The future survival of many of these species is of great concern, considering that almost one-fifth of extant vertebrate species are classified as Threatened (Hoffmann *et al.* 2010). Furthermore, the distribution ranges of many large mammals have recently contracted substantially in tropical Asia alongside further reductions in diversity (Schipper *et al.* 2008). The region has little tradition of effectively managed protected areas. Consequently, many Southeast Asian species will become extinct in the near future if current trends continue (Duckworth *et al.* 2012). The declining conservation status of many wild cattle species shows the pressures they face and highlights the urgent need for greater effective conservation action. Twelve of the 13 species of the tribe Bovini are threatened to some degree; one is already extinct (aurochs); and another is possibly extinct (kouprey; see Table 1 for the IUCN categories). Asia is the most important and the richest region in terms of wild cattle species. Nine of the 12 species in the world are found in this continent, where there is a need for proper conservation and management measures (see Figure 1 and Table 1 for the distribution by country of all wild cattle species).

Conserving these species is often a challenge, especially in certain regions. This is the case due to our poor knowledge on account of their behaviour, being shy, solitary, nocturnal, wide-ranging or occurring at low densities (Gray 2012). For example, the saola was only discovered by the scientific community in 1992 and was one of the most spectacular and surprising zoological discoveries of the twentieth century (see also Chapter 19). It is now restricted to a small geographic area between Lao PDR and Vietnam, and is highly threatened by illegal hunting. The saola is facing immense pressure in all locations where it is found and without scaling up conservation initiatives this species is likely to be driven to extinction in the coming years, as has probably happened to the kouprey (*Bos sauveli*) in Southeast Asia.

Many steps can be taken to prevent species and habitat loss. For example, efforts should concentrate on increasing effectiveness of protected-areas management where remaining populations of threatened species still persist. For example,

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Table 1 Worldwide occurrences by country and conservation status of wild cattle according to the 2013 IUCN Red List of Threatened Species (for more details on the species distribution, see the related chapters in this book)

Species	Status (IUCN)	Occurrence	
American bison *Bison bison*[1]	Near Threatened	North America	Canada (Alberta, British Columbia, Manitoba, Northwest Territories, Saskatchewan, Yukon Territory); USA (Alaska, Arizona, California, Colorado, Iowa, Idaho, Illinois, Kansas, Kentucky, Minnesota, Missouri, Montana, Nebraska, North Dakota, Oklahoma, South Dakota, Texas, Utah, Wisconsin, Wyoming)
		Central America	Mexico
European bison *Bison bonasus*[2]	Vulnerable	Europe	Belarus, France, Germany, Lithuania, Poland, Romania, Russia, Slovakia, Ukraine
Gaur *Bos gaurus*	Vulnerable	Asia	Bangladesh, Bhutan, Cambodia, China, India, Lao PDR, Malaysia, Myanmar, Nepal, Thailand, Vietnam
Wild yak *Bos mutus*	Vulnerable	Asia	China, India
Banteng *Bos javanicus*	Endangered	Asia	Borneo, Cambodia, China?, Java, Lao PDR, Malaysia, Myanmar, Thailand, Vietnam
Kouprey *Bos sauveli*	Critically Endangered (possibly Extinct)	Asia	Cambodia, Lao PDR, Thailand, Vietnam
Wild water buffalo *Bubalus arnee*	Endangered	Asia	Bangladesh, Bhutan, Cambodia, India, Myanmar, Nepal, Thailand
Anoa *Bubalus depressicornis/quarlesi*	Endangered	Indonesia	Sulawesi and Buton Islands
Tamaraw *Bubalus mindorensis*	Critically Endangered	Philippines	Mindoro Island (Philippines)
Saola *Pseudoryx nghetinhensis*	Critically Endangered	Asia	Lao PDR, Vietnam
African buffalo *Syncerus caffer*	Least Concern	Africa	Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Democratic Republic of Congo, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea, Guinea-Bissau?, Kenya, Ivory Coast, Lesotho, Liberia?, Malawi, Mali?, Mozambique, Namibia, Nigeria, Niger, Republic of Congo, Rwanda, Senegal, Sierra Leone?, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Uganda, Zambia, Zimbabwe

[1] All bison herds managed for conservation purpose in North America are included.
[2] Free-ranging and semi-free populations included.
?: Probably Extinct.

the creation and the effective protection of many reserves and national parks along the Carpathian Mountains has allowed restoration of several populations of European bison from 1963 to today, with a trend that is still growing. This may secure the future viability of these populations (for more details, see Chapter 22). The involvement of local people is another crucial aspect that occurs when they are actively involved in conservation activities and understand the potential benefits of the species and the habitats they use for communities' sustainable resource use. An example comes from Vietnam, where a new approach was piloted using hired 'forest guards' coming primarily from communities surrounding the Thua-Thien Hue Saola Nature Reserve (see Box 19.1). The objective of this model is to provide intensive protection to the saola population of the reserve through the removal of direct threats.

One more aim of this book is to identify gaps in our knowledge, so that conservation practitioners can address those species and populations of highest priority for conservation efforts to prevent further declines. Greater global focus is beginning to occur on halting this decline in species, such as the Convention on Biological Diversity's Aichi target 12 – preventing extinctions – in its ten-year strategic plan (www.cbd.int/sp/targets).

Our intention for the book to inform those interested in wild cattle has three elements: (1) the book provides a comprehensive review of knowledge of all wild cattle species; (2) it gives a clear understanding of the conservation status of each

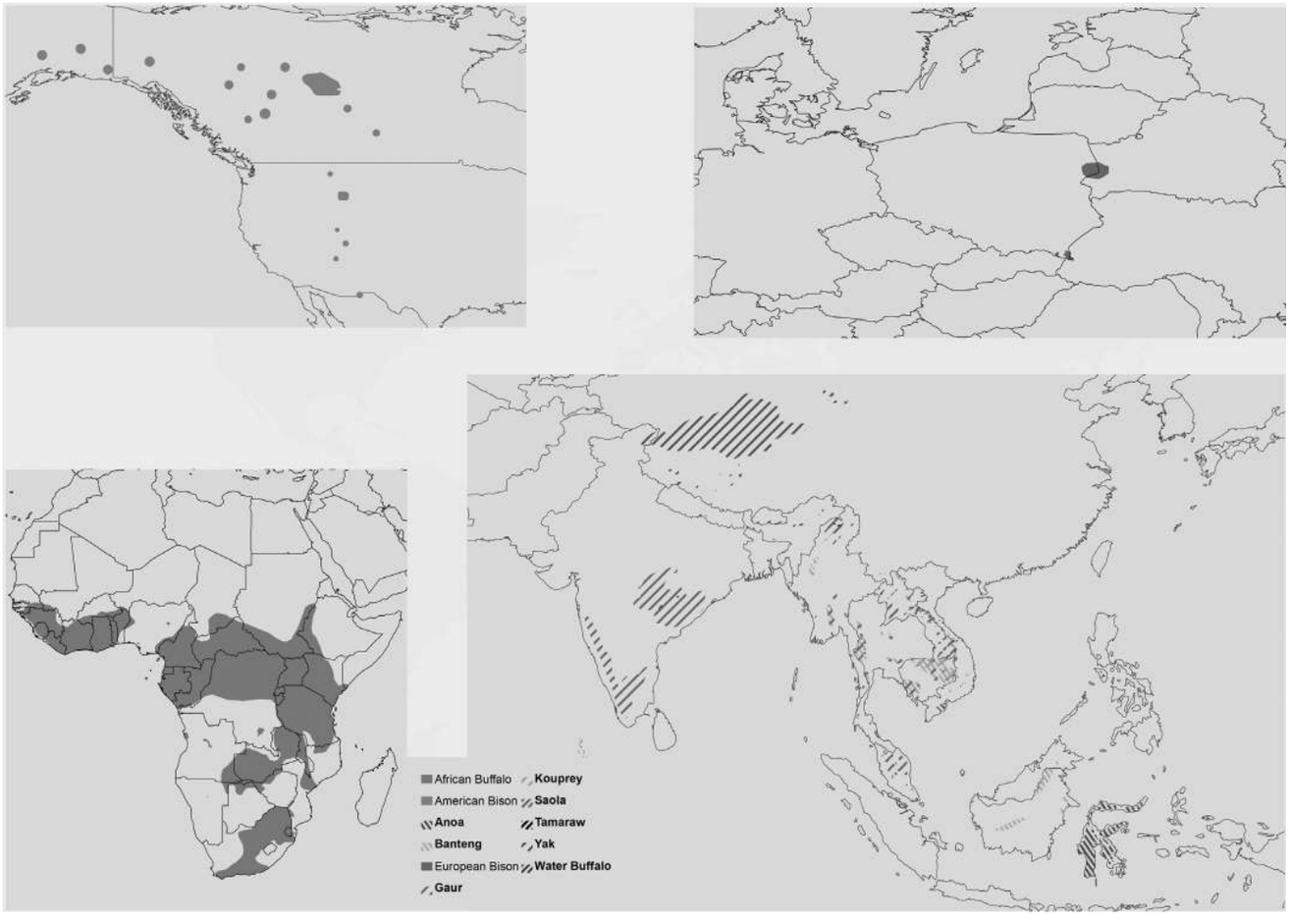

Figure 1 Worldwide distribution map of wild cattle according to the 2008 IUCN Red List of Threatened Species.

species and gaps in current knowledge; (3) it includes a number of case studies of conservation activities, including some of the most threatened and poorly understood species. These three aspects will hopefully contribute towards the conservation and management of wild cattle and their habitats.

General background

The initial stages of the work were begun in 2009, when one of the editors (Mario Melletti) set out to put together a basic idea and a collection of all the major papers and books on wild cattle. This huge amount of information gave an indication that there were so many important gaps in our knowledge of the tribe Bovini that at the beginning the book seemed almost impossible. However, after a year of collecting information, it started to look like the project could get under way, although the work would have to be considerable. The second step was to involve a second editor (James Burton), and work together to build up a suitable group of leading world experts. The third step was to form a team of artists: Francesco Rinaldi, who drew the colour plates of each species; and Luciano Toma and Enrico Chiarelli, who drew the black and white illustrations. This was a long process that occupied the artists for 18 months in an attempt to draw the most realistic animals. The fourth step was to involve a GIS expert, Piero Visconti of the Global Mammal Assessment Programme (University of Rome 'La Sapienza') to build up the distribution maps for all species on the basis of IUCN Red List data. From the beginning, the success of the book has depended on all the various contributors, located in many different countries, affiliated with many institutions including, among others, IUCN SSC, IUCN/SSC Asian Wild Cattle Specialist Groups (AWCSG) and AfBIG (African Buffalo Initiative Group ASG/SSC IUCN. This three-year study involved 70 experts from 21 countries.

It should be stated that this book is not a definitive taxonomic reference. We follow the most traditionally accepted version, such as the work of Wilson & Reeder (2005), *Mammal Species of the World*. For some species, for example the African buffalo, the recent work of Groves & Grubb (2011) separates them into more species – four in the case of the African buffalo. However, this taxonomic complexity remains to be resolved with further molecular studies; currently the editors, the authors and the available literature suggest that there is no

strong genetic evidence to split the African buffalo into four species. Yet, current debates about the bison raise serious implications for their conservation. In fact, some biologists consider European and American bison to be the same species. If broadly accepted, this would result in a down-listing by the IUCN Red List and a change in conservation priorities; it would complicate management of the European (three subspecies) and American bison (two subspecies) at the subspecies level. Again in this case we prefer to adhere to the conventions used by Wilson & Reeder (2005) and the IUCN Red List of Threatened Species (2013), considering the genus *Bison* as comprising two species: European bison (*Bison bonasus*) and American bison (*Bison bison*).

The aurochs, although extinct, was included because it represents the ancestor of most modern domestic cattle and because it was a relatively recent extinction.

The structure of the book

Although we have attempted to be consistent, the style and content of the chapters may vary somewhat from author to author. Some accounts on forest-dwelling species are limited because of the lack of information compared to better-known species.

The layout of the book follows a detailed organisation in four sections consisting of 27 chapters. It begins with 'Systematic, Ecology and Domestication', followed by 'Evolution, Anatomy and Function', then 'Species Accounts' and 'Conservation and Management' sections.

Systematic, ecology and domestication

In this part of the book, the following are covered:

- Chapter 1: the ancient and recent hypotheses of interspecific relationships and the systematic position of the tribe Bovini are presented.
- Chapter 2: the role of Bovini as keystone species and landscape architects are presented.
- Chapter 3: the ecology and cultural aspects of domestication through millennia and across different regions of the world are described.

Evolution, anatomy and function

In this part of the book the main characteristics of some anatomical aspects of Bovini are discussed, such as mammary glands, digestive system, horns and teeth in the context of evolution and function. The chapters included within this part are as follows:

- Chapter 4 gives a review of what is known on the skeletal evolution of the entire Bovini tribe.
- Chapter 5 provides an overview of mammary development, anatomy and function.
- Chapter 6 is focused mainly on the general anatomy and morphophysiological adaptation of the digestive system in cattle.
- Chapter 7 describes a generalised bovine post-canine dental anatomy, placing this in the context of the adaptation of grazing dentitions to dietary function.
- Chapter 8 offers a unified review of what is known of the evolution, anatomy and development of bovid horns.

Species accounts

The aim of this part of the book is to give detailed and current data on the species. It summarises most of the published and grey literature available from the recent past. In Chapters 9–20 the 13 wild cattle species are described in detailed accounts prepared by one or more specialists. The chapters treat the following topics: *names*; *taxonomy*; *subspecies and distribution*; *descriptive notes*; *habitat*; *movements and home range*; *activity patterns*; *feeding ecology*; *reproduction and growth*; *behaviour*; *parasites and diseases*; *status in the wild and status in captivity*. Each species has been illustrated in colour and in black and white. The aim of the drawings is not to produce the age/sex classes as in a field guide, but to illustrate only the adult males of each species in their environment. Moreover, we also use pictures to illustrate most species and their habitats. In addition, two boxes are included: Box 16.1, in the wild water buffalo account, presents an interesting overview on the genetics of this species and the potential threats to the whole population by introgression with domestic buffalo. Box 19.1 describes the new approach for Vietnam using hired 'forest guards' in Thua-Thien Hue Saola Nature Reserve to provide intensive protection to the saola population.

Species accounts are arranged as follows:

Names: This section starts with the English and scientific names. Names are also given in French, German, Spanish and Italian. Where available, names in other languages are also provided. Common and scientific names generally follow the work of Wilson & Reeder's *Mammals Species of the World* (2005). Montgelard *et al.* (1997) proposed placing all species of Artiodactyla and Cetacea into the same order, called Cetartiodactyla, to render the classification compatible with the molecular phylogeny. We follow this classification, which is also adopted by the IUCN Red List of Threatened Species (2013).

Taxonomy: Taxonomic issues are discussed and, where genetic information is available, species relationships are assessed on the basis of the molecular and genetics studies.

Subspecies and distribution: In this section the global distributions of the species are described and changes from the past ranges are discussed. Where available, detailed information for each country is provided. The subspecies universally recognised are described and, in some cases, such as the African buffalo and banteng, the most recognised are treated in detail. For the distribution maps we used a combination of IUCN (2013) maps with the addition of data from the IUCN-SSC/AWCSG (2010) report. The maps cover the world distribution of the species. The information provided in the maps should always be taken in conjunction with this section, which often gives details on the distribution by countries or

geographical features that may help to determine the location of the species.

Descriptive notes: The main morphological characteristics are summarised, including body, horns and hair characteristics (e.g. geographical variation in body/horns size, coat colour) and lifespan (e.g. maximum age recorded in the wild and in captivity, if known). The dental formula is provided as I = incisors, C = canines, P = premolars, M = molars. The numbers refer to the upper and lower side of the half of the jaw as described in this example: I 0/3 C 0/1 P 3/3 M 3/3 (×2) = 32.

Habitat: This section provides a description of the broad ecological requirements of the species and the factors affecting its distribution and the habitat used are discussed.

Movements and home range: In this section movement and home range are described and, when data are available in relation to age/sex classes, food resources, season and habitat type, these are provided.

Activity patterns: The general activity patterns and variation according to age/sex classes, food resources, period of day, seasons and habitat type are discussed.

Feeding ecology: This section describes the main feeding requirements of the species and, when available, the list of plant species eaten are given.

Reproduction and growth: Some aspects of reproduction and growth are analysed, at least for the most known species.

Behaviour: This section focuses on certain behavioural traits of the species, such as herd and individual behaviour, agonistic behaviour, sexual behaviour and sexual segregation.

Parasites and diseases: The most common diseases are described, including foot and mouth disease (FMD) and bovine tuberculosis (BTB). Where information is available, the most common parasite infections are briefly discussed.

Status in the wild: The status and conservation of the species worldwide is one of the main themes of this book, thus considerable efforts have been made to provide informative and up-to-date information. The current status of species and subspecies are described. This section also provides examples of the conservation measures, *in situ* and *ex situ*, that can be adopted to secure the survival of the species. In addition, information on legislation and classification within the IUCN Red List is given.

Status in captivity: This section discusses the status of the species that are kept in zoos, their breeding success and the size of the captive populations. Most information is obtained from the World Zoo and Aquarium Conservation Strategy (WZACS) and members of the European Association of Zoos and Aquaria (EAZA).

Reference: Each chapter aims to include most of the important literature in the form of papers, books, monographs, published and unpublished reports, grey literature, doctoral and master's theses. One of the aims of the reference section is to provide the reader with an idea of how much information is currently available on each species and give an overview of the state of our knowledge.

Conservation and management

In this section we have arranged a set of accounts, including some case studies, giving an overview on conservation, management, genetics and disease ecology.

In Chapter 21 the status of 'wild' plains bison in Canada is addressed in response to the questions: what is a wild plains bison, and are there any wild plains bison in Canada?

In Chapter 22 the amazing history of European bison restoration in the Carpathian Mountains is described.

In Chapter 23 the first project to capture and translocate gaur, conducted in India, is presented.

In Chapter 24 a conservation and management strategy of the only remaining small population of possibly pure wild water buffalo in Koshi Tappu Wildlife Reserve, Nepal, is presented.

Chapter 25 describes the genetic structure of the African buffalo on a continental scale, giving an interesting scenario on the complex relationships between different subspecies.

In Chapter 26 the importance of sanitation at buffalo–cattle interfaces is described for Africa in the face of intense agricultural and human development.

Finally, Chapter 27 describes the various roles that ex situ populations of wild cattle play in conservation of these species. An overview of wild cattle held in zoological collections and background on the status of these populations is discussed.

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Part I Systematic, ecology and domestication

Chapter 1

Systematic and evolution of Bovini

Alexandre Hassanin

Introduction

According to the IUCN (2013), 13 species are currently recognized in the taxonomic group to which wild cattle belong (tribe Bovini): aurochs (now only represented by domestic breeds), banteng (in Southeast Asia), gaur (in India and mainland Southeast Asia), kouprey (in northern and eastern Cambodia and adjacent countries), yak (throughout the Tibetan Plateau), American bison (in the western half of North America), European bison (now confined to Eastern Europe), African buffalo (in sub-Saharan Africa), Asian water buffalo (only a few small populations in India and mainland Southeast Asia), lowland anoa and mountain anoa (both found only on Sulawesi and Buton Island), tamaraw (endemic to the Philippine island of Mindoro) and saola (in the Annamite Mountains of Vietnam and Laos).

The most fascinating aspect in the evolution of Bovini is that at least five species have been domesticated during the Holocene: aurochs, banteng, gaur, yak, Asian buffalo, and maybe the kouprey. As a result, their recent evolutionary history has been severely disrupted by the migration and explosive growth of human populations throughout the world. Before the Neolithic, populations of wild cattle were very successful and widely distributed across Europe, Africa, Asia and North America. Today, most wild species are restricted to small and isolated populations in a few countries, whereas domestic forms are present on all arable land on Earth. The aurochs, which was the ancestor of most breeds of domestic cattle, became extinct in 1627 (Tikhonov 2008). Field scientists have reported no living specimen of kouprey in the open deciduous dipterocarp forests of Southeast Asia since the 1980s, suggesting that it is possibly extinct (Timmins *et al.* 2008). All other wild species but the American bison are listed as Critically Endangered (CR), Endangered (EN) or Vulnerable (VN) in the IUCN Red List of Threatened Species (IUCN 2013).

In this chapter, I describe the systematic position of the tribe Bovini, and I review ancient and recent hypotheses of interspecific relationships. Then, I propose a biogeographic scenario to explain their past and current geographic distributions.

Systematic position of the tribe Bovini

Wild cattle belong to the order Cetartiodactyla (Figure 1.1), which is the second most diversified order of large mammals after Order Primates (IUCN 2013). Members of this taxonomic group were originally divided into two different orders: Artiodactyla and Cetacea. Artiodactyls are even-toed ungulates, including ruminants, pigs, hippos and camels. They were originally present on all continents, except the Australian region and Antarctica, and most domestic livestock come from this group, including cattle, sheep, goat, pig and camel. They are characterized by two main limb features: a paraxonic foot, which means the axis of the limb support passes between the third and fourth digits; and in the ankle, the astragalus is 'double-pulleyed', i.e. with a trochlea for the tibia and an opposing trochlea for the navicular, which enhances hindlimb flexion and extension, and allows very limited lateral rotation of the foot. Cetaceans include whales and dolphins. All are marine animals except for a few species of freshwater dolphins. The common ancestor of Cetacea acquired many adaptations to an aquatic life, such as a fusiform body, forelimbs modified into flippers, no hindlimbs or rudiments and a tail fin (fluke) used for propulsion. Molecular studies have recovered a sister-group relationship between cetaceans and hippos, indicating that Artiodactyla is paraphyletic (Irwin & Arnason 1994; Gatesy *et al.* 1996; Montgelard *et al.* 1997). To render the classification compatible with the molecular phylogeny, Montgelard *et al.* (1997) proposed placing all species of Artiodactyla and Cetacea into the same order, called Cetartiodactyla. After several years of controversy between molecular biologists and morphologists, a paraxonic foot and a double-pulley astragalus were found in Eocene whales (Gingerich *et al.* 2001), confirming that cetaceans evolved from terrestrial cetartiodactyls.

Wild cattle belong to the suborder Ruminantia (Figure 1.1), which is the most diversified group of Cetartiodactyla, with 215 species related to goat, sheep, deer, pronghorn, giraffe and chevrotains. All ruminants are able to digest cellulose through the action of various microorganisms (bacteria and eukaryotes, such as ciliates and fungi) that are contained in the rumen, the

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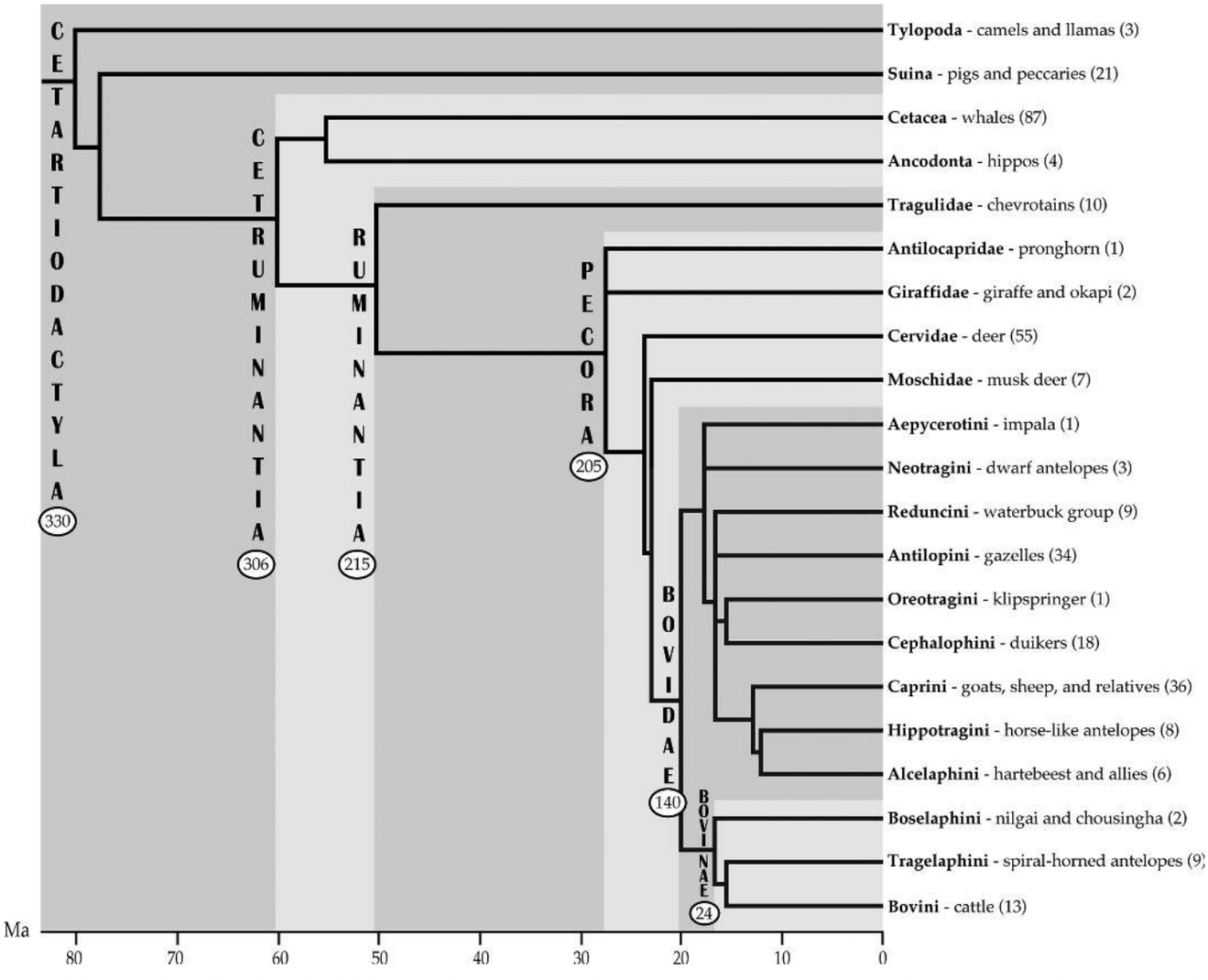

Figure 1.1 Systematic position of the tribe Bovini. The tree is a chronogram, which means that branch lengths are proportional to divergence times. A time scale is provided at the bottom. The ages were estimated using a DNA alignment of complete mitochondrial genomes (Hassanin *et al.* 2012). The number of species is indicated on the nodes for higher taxa, and between round brackets for terminal taxa (data extracted from the website of the IUCN).

most developed of the three or four compartments in their stomach. The compartmentalization of the ruminant stomach is probably the key innovation that explains their evolutionary success. In addition, ruminants have well-adapted teeth characterized by the presence of an incisiform lower canine, which is adjacent to lower incisors, and a horny pad that replaces the upper incisors. All modern and fossil representatives of the group are diagnosed by an osteological autapomorphy, which corresponds to the fusion of the cuboid and navicular bones in the tarsus. Molecular studies have confirmed the monophyly of Ruminantia, as well as the major division between Tragulina (composed of the family Tragulidae – African and Asian chevrotains) and Pecora (including all other ruminant families: Bovidae, Cervidae, Moschidae, Giraffidae and Antilocapridae) (Hassanin & Douzery 2003; Matthee *et al.* 2007; Hassanin *et al.* 2012). In addition, they have shown that Ruminantia, Cetacea and Hippopotamidae form a clade, named the Cetruminantia by Waddell *et al.* (1999) (e.g. Shimamura *et al.* 1997; Gatesy *et al.* 1999; Hassanin *et al.* 2012).

Wild cattle belong to the family Bovidae (Figure 1.1), which is the most successful family of the suborder Ruminantia (140 species). Bovids are characterized by the structure of the horns. Present in all males and sometimes females, these consist of a permanent bone core covered by a non-branched and non-deciduous sheath of keratin (Nowak 1999). The family is found on all continents except Australia, Antarctica and South America. Most ancient classifications recognize between five and eight subfamilies within the Bovidae (e.g. Simpson 1945; McKenna & Bell 1997; Grubb 2005), but molecular studies have concluded the existence of a major

division within the family Bovidae, separating the subfamily Bovinae from all other species of Bovidae (Hassanin & Douzery 1999a, 1999b; Matthee & Robinson 1999; Matthee & Davis 2001; Ropiquet *et al.* 2009; Hassanin *et al.* 2012). This result is consistent with the taxonomic view of Kingdon (1997, 1982), who defined only two bovid subfamilies on the basis of morphology and behaviour: the subfamily Bovinae includes the three tribes Bovini (cattle, bison, yak, buffalo and saola), Boselaphini (nilgai and four-horned antelope) and Tragelaphini (bongo, eland, bushbuck, kudu, nyala and sitatunga); the subfamily Antilopinae includes all other bovid tribes (Antilopini, Aepycerotini, Alcelaphini, Caprini, Cephalophini, Hippotragini, Neotragini, Oreotragini and Reduncini; Figure 1.1).

Phylogenetic relationships among species of Bovini

Classifications of the tribe Bovini based on morphology

In the popular classification of Simpson (1945), all species of wild cattle were arranged into a new tribe, named Bovini, which included six different genera at that time: *Bos* (aurochs, domestic cattle and yak), *Anoa* (anoa and tamaraw), *Bibos* (gaur and banteng), *Bison* (European bison and American bison), *Bubalus* (Asian buffalo) and *Syncerus* (African buffalo; Figure 1.2a). This view was largely followed by Bohlken (1958), with the exception of two taxa: the tamaraw was considered a dwarf buffalo and therefore relegated to a subspecific rank within *Bubalus arnee*, and, similarly, the European bison was treated as a subspecies of *Bison bison* (Figure 1.2b). Simpson (1945) did not mention the kouprey in his classification, whereas Bohlken (1958) interpreted the kouprey as a hybrid between banteng and domestic cattle. Three years later, Bohlken (1961) recognized, however, that the kouprey belongs to a distinct species closely related to the banteng, but he reduced *Bibos* to a subgeneric rank under *Bos*. In the morphological study of Groves (1981), the kouprey was grouped with the aurochs and the yak with the bison (Figure 1.2c). As a consequence, the genera *Bibos* and *Bison* were synonymized with *Bos*. The phylogenetic results of Geraads (1992) were very similar (Figure 1.2d), but both yak and bison were found to be the sister-group of the aurochs, banteng, gaur and kouprey. Consequently, two genera were retained by Geraads (1992) within the subtribe Bovina: *Bison* for the two first species, and *Bos* for the four other species. Two other subtribes were proposed by Geraads (1992): Bubalina, comprising the Asian buffalo and anoas; and Syncerina, including only the African buffalo.

In 1992 a new bovid species, the saola, was discovered in the jungles of the Annamite Range of Vietnam and Laos: *Pseudoryx nghetinhensis* (Dung *et al.* 1993). This enigmatic and very rare species was first referred to the tribe Boselaphini (nilgai and four-horned antelope) on the basis of a preliminary DNA analysis and some morphological characters, such as the presence of pre-orbital glands and white markings of the pelage (Dung *et al.* 1993). Based on the morphology of the skull and dentition, Thomas (1994) concluded a close relationship of the saola with serow and goral of Asia (*Capricornis* and *Naemorhedus*, tribe Caprini). Schaller and Rabinowitz (1995) noted, however, resemblances to Bovini and Tragelaphini. These contradicting conclusions probably explain why the saola was not included in Bovini in the classification of McKenna & Bell (1997; Figure 1.2e). Thereafter, two independent molecular studies provided robust evidence for the placement of the saola within Bovini (Hassanin & Douzery 1999a; Gatesy & Arctander 2000). In more recent classifications, such as that of Grubb (2005), *Pseudoryx* is therefore classified in the tribe Bovini (Figure 1.2f).

According to the IUCN (2013), the tribe Bovini includes the following thirteen species:

(1) *Bos gaurus* C. H. Smith, 1827 – gaur
(2) *Bos javanicus* d'Alton, 1823 – banteng
(3) *Bos mutus* (Przewalski, 1883) – yak
(4) *Bos primigenius* Bojanus, 1827– aurochs
(5) *Bos sauveli* Urbain, 1937 – kouprey
(6) *Bison bison* (Linnaeus, 1758) – American bison
(7) *Bison bonasus* (Linnaeus, 1758) – European bison
(8) *Bubalus arnee* (Kerr, 1792) – Asian buffalo
(9) *Bubalus depressicornis* (C. H. Smith, 1827) – lowland anoa
(10) *Bubalus mindorensis* Heude, 1888 – tamaraw
(11) *Bubalus quarlesi* (Ouwens, 1910) – mountain anoa
(12) *Pseudoryx nghetinhensis* Dung, Giao, Chinh, Touc, Arctander & MacKinnon, 1993 – saola
(13) *Syncerus caffer* (Sparrman, 1779) – African buffalo.

Three taxa have sometimes been treated as subspecies rather than full species. For example, Bohlken (1958) proposed uniting *Bison bonasus* with *Bison bison*, *Bubalus mindorensis* with *Bubalus arnee* and *Bubalus quarlesi* with *Bubalus depressicornis* (Figure 1.2b). In addition, the two species of anoa are put into either the genus *Anoa* (Simpson 1945; Bohlken 1958; Geraads 1992; McKenna & Bell 1997) or the genus *Bubalus* (Groves 1981; Grubb 2005; IUCN 2013).

In the next section, domestic forms are treated as subspecies of the wild species name, in accordance with the stated aims of taxonomic freedom in the Code of Zoological Nomenclature (Gentry *et al.* 2004). Therefore, I use *Bos primigenius taurus* for the common cattle, *Bos primigenius indicus* for the zebu (or humped cattle), *Bos gaurus frontalis* for the mithan or gayal, *Bos mutus grunniens* for the domestic yak, *Bubalus arnee bubalis* for the river buffalo and *Bubalus arnee carabanesis* for the swamp buffalo.

Molecular phylogenies

Evidence for three divergent lineages within the tribe Bovini

Most phylogenetic studies based on DNA sequences have concluded the existence of three divergent lineages within the tribe Bovini, corresponding to the subtribes Bovina, Bubalina

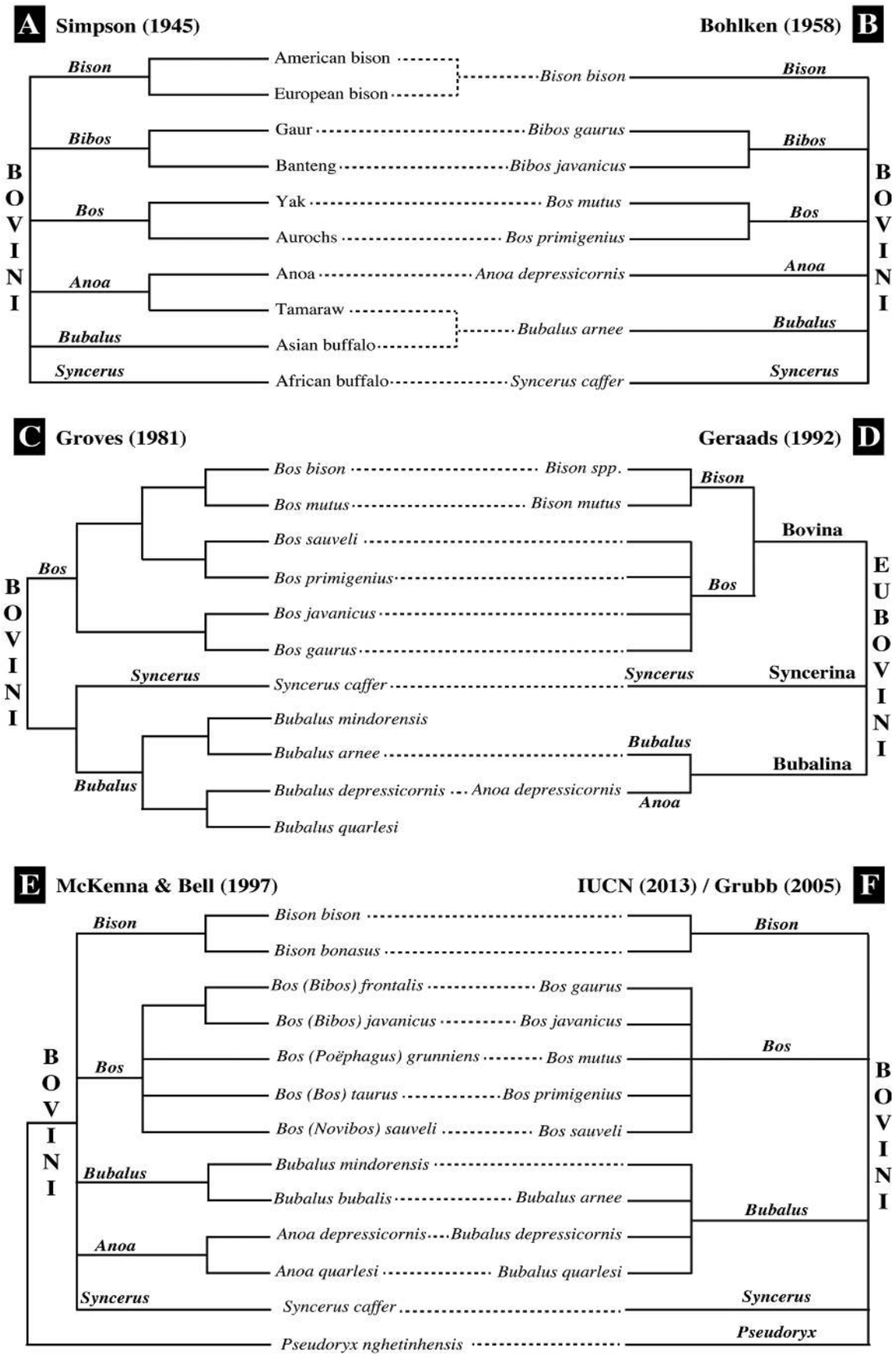

Figure 1.2 Classifications of Bovini based on the morphology.