Ecology and Management of the African Buffalo

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2 · *The Evolutionary History of the African Buffalo: Is It Truly a Bovine?*

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Introduction

If one sees an African buffalo (*Syncerus caffer*) for the first time after seeing many water buffalo (*Bubalus bubalis*), one could easily believe they are closely related. In 1758, Carolus Linnaeus named the water buffalo scientifically, but he did not classify the African buffalo. The first formal mention is by Anders Sparrmann (1779), a pupil of Linnaeus, who classified the species as *Bos caffer*, just as his mentor had classified the Asian species as *Bos bubalis*. A military artist named Charles Hamilton Smith coined the Latin genus name *Bubalus* for the Asian buffalo in 1827. A nineteenth-century taxonomist, Brian Hodgson, elevated the African buffalo to its own genus, namely, *Syncerus* Hodgson, 1847. What justifies the separation of these two 'buffalo' into distinct genera? Strangely enough, two fundamental characters: namely, in *Syncerus* the vomer and the palate are not fused, and the nuchal hair-stream is not reversed (Groves, 1969). Groves states: 'Consequently the generic separation of *Bubalus* from *Syncerus* seems thoroughly justified, and some at least of the similarity between them (such as that in the shape of the horn cores) must be put down to parallelism.' Whether these two fundamental traits have any ecological meaning is unknown, but the case for parallelism is intriguing.

A systematic classification is in principle based on diagnosable (often morphological, thus not necessarily functionally important) characters, mainly of extant species (see Zachos, 2018 for a review). Systematicists decided that the African buffalo should not be classified into one genus with the Asian buffalo, but does the fossil material combined with DNA-based phylogenies provide enough clues to establish the evolutionary history of the African buffalo? Our analysis will show that there is quite some doubt as to whether the African buffalo is related to the Asian buffalo species swarm, or to the larger one comprising wild cattle, yak and bison. The question that arises, of course, is whether taxonomy and systematics have any bearing on ecology and management. We believe it does if, by having knowledge on related species, one can more safely generalize; if not, then systematics at the level of the genus or higher is irrelevant. Indeed, conservation is about species – not genera, families or tribes.

The African buffalo is a large bovid. Mammals are classified as 'bovid' if they have, at least in the adult male, two or rarely four unforked horns. These are composed of bone cores protruding from their skull after 'horn buds' which are covered by a permanent layer of keratin start growing in the skin and fuse with the skull (Davis et al., 2014). Bovids emerged some 18.5 Myr ago (Vrba and Schaller, 2000) or even slightly more recently (Bibi, 2013). Some studies refer to an older emergence of the Bovidae based on material from Mongolia in the Middle Oligocene, thus 26 Myr ago (Trofimov, 1958; see Thomas, 1984), but this is now questioned (Métais et al., 2003). The mammals classified as Bovidae are thought to be related to each other, and the common trait of unforked horns is taken to be a shared, derived character, common between ancestor and descendants. Modern molecular techniques allowed this assumption to be put to the test, resulting in updated insights about the classification of the ~140 bovid species within the approximately 40 genera (Grubb, 1993). Within this group of Bovidae, African buffalo are classified with the subfamily Bovinae, within the tribe Bovini. The other two tribes in that subfamily are the Tragelaphini and the Boselaphini. All other bovids are classified within the subfamily Antilopinae.

Modern molecular techniques show that the subfamily Antilopinae as classified by morphologists has a very different evolutionary, and thus classificatory, structure than previously thought (Ropiquet and Hassanin, 2005; Hassanin, 2014). Enough reasonably well-dated fossils are available to pinpoint some major bifurcations between tribes in time. These phylogenies all suggest that the tribe Bovini is nested together with the Tragelaphini and the Boselaphini in one 'proper' subfamily, the Bovinae (Bibi, 2013; Druica et al., 2016). At first sight, the message about the evolution of the Bovini does not appear to have changed much since publications by Sinclair (1977) and Gentry and Gentry (1978). Yet there is now perhaps more reason to consider the

Bovini as a heterogeneous (non-monophyletic) group, the African buffalo not being closely related to either the water buffalo of Asia (*Bubalus*) or oxen, bisons and yaks. Perhaps it deserves a special tribe, Syncerini, but the evolution of the Bovini is still shrouded in much uncertainty. Five insights play havoc. First, phylogenies based on molecular markers rely heavily on available genetic material. For bovids, to date this material has been taken from living and thus contemporary specimens; fossil material does not yet play a role, except for some very recently extinct species. This means that for extinct tribes or even subfamilies there is no genetic information that has the potential to upset phylogenies that are based on parsimonious calculus (cf. Frantz et al., 2013; Table 2.1). Second, the phylogeny based on mitochondrial DNA shows a short period around 18–15 Myr in which the Boselaphini, Tragelaphini and Bovini separated (Hassanin, 2014; Zurano et al., 2019). It should be realized, however, that the phylogenetic trees based on DNA suggest such divergence to have taken place some 10 million years before the oldest finds of Tragelaphini (second half Late Miocene, *c.*7 Myr) or Bovini (*c.*8 Myr). Furthermore, the calibration of the molecular-based phylogeny is based on fossils from other families mainly (see Zurano et al., 2019 for details) while fossil Boselaphini may be hard to identify, because early forms had few distinctive features. Third, the fossil material itself may indicate that Bovini evolved from Boselaphini several times and not just once (Gentry, 2010). In fact, evidence for this is very slender, but this may nevertheless still be true because there is no evidence that early African Bovini (which are rare and poorly known) are derived from Asian forms. It is quite possible that they derived directly from African Boselaphini (close to *Tragoportax*; see Figure 2.1). Fourth, the number of Bovid species recognized in the fossil material is strongly determined by sampling effort, and there are many more sites for some periods than for others (Patterson et al., 2014). Lastly, within the Bovini tribe there is a worrying lack of clarity about not only the proper naming of species and genera in the fossil material, but also whether particular fossil species and their living descendants should be taken to belong to a particular genus or to another. Much dust has been stirred up on the systematic position of *Pelorovis*. Was it a distinct genus? Did it belong to the genus *Bos*? Did it belong to the genus *Syncerus*? Yet if animal populations cannot be classified into valid species and allocated precise generic status, then concepts like ‘competitive exclusion’ or ‘niche differentiation’ become very difficult to apply.

Table 2.1 *Interplay between palaeontology and genetics to deduce a reliable phylogeny. The trade-off one makes between knowledge from genetics and palaeontological knowledge is not straightforward. It may upset established phylogeny, yet it may also strengthen it. If knowledge from palaeontology and genetics (if these have been reached independently) overlap, inference about the past is very strong. If there are mismatches between the two fields of enquiry, a research strategy can be formulated once one realizes the mismatch.*

		Genetics		
		Species that have been allotted an unquestionable place in a phylogeny, thus '*knowns*'	Species of which the place in a phylogeny *depends on a priori choices*	Species of which the genetics has not yet been carried out, thus '*unknowns*'
Palaeontology	*Knowns* (i.e. species that have been found and have been classified with confidence)	If there is match, we have reached a true justified belief (the hallmark of good science). If the two do not match, both fields of knowledge have to actively work together to solve the issues. Exciting new insights can arise: e.g. on the origin of *Bison bonasus* as a possible hybrid species of *Bison priscus* and *Bos primigenius*	Genetics should follow palaeontology and recalculate phylogenies. Bayesian approaches should incorporate prior knowledge from palaeontology	Here future progress in palaeo-DNA will perhaps make very unexpected changes
	Uncertain (i.e. species that have been found but about which the classification is unsure)	Palaeontology should incorporate knowledge from genetics to decide on the best place of such a species in an existing phylogeny	Danger exists that there is false certainty in published phylogenies by geneticists	A general state of ignorance predominates
	Unknowns (i.e. species that have not yet been found or identified)	Phylogenies based on absent species may give a false sense of certainty	Phylogenies based on absent species may give a false sense of certainty	'Unknown unknowns', which may upset any established phylogeny

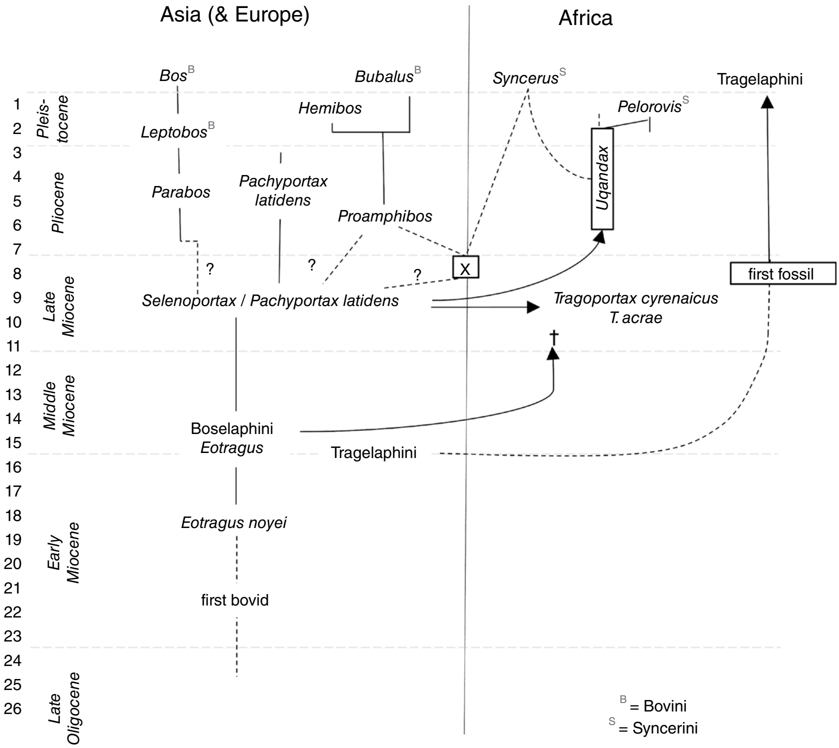

Figure 2.1 Phylogeny of the Bovini and Syncerini. During the Pleistocene members of the genus *Bos* ventured into Africa too (see text). The separation between Boselaphini and Bovini or Syncerini is very unclear.

The Genus *Pelorovis* and the *Syncerus antiquus* Conundrum

We start with *Pelorovis* and the issues surrounding its phylogenetic position to better understand the evolution of *Syncerus*. The most important insight that emerges is that there was a second species of *Syncerus*, namely *S. antiquus*, in much of Africa that went extinct only very recently, in the last two millennia. It overlapped in space and in time with the extant African buffalo.

Hans Reck started the excavations in Olduvai (Tanzania) and found the remains of a large mammal, which he named *Pelorovis* ('frightful sheep'). Later, Gentry (1967) classified *Pelorovis* with the Bovini, but thought it to be very distantly related to the Asian Bovini. *Pelorovis* may have been derived from *Simatherium* (Geraads, 1992) like the African buffalo *Syncerus*. The difficulty of Bovini classification is well underscored by the struggle palaeontologists have in allocating the different species of

Pelorovis to their classificatory nook: does a fossil belong to *Pelorovis* or to *Bos* or *Syncerus*, and, alternatively, should the genus *Pelorovis* be seen as an independent genus, or do the species of this genus better fit in *Bos* or *Syncerus*? Indeed, an identical specimen may be classified as *Pelorovis* or as *Simatherium* (Gentry, 2010), showing the opaqueness of the systematics and phylogeny of the Bovini (see Table 2.1).

Seven species of *Pelorovis* have been named. *Pelorovis oldowayensis* is the best-known form; it has long, regularly curved horncores, first emerging almost posteriorly but recurving forwards, with a total span that can reach 2 m. It is best represented in Olduvai, but also in other Eastern African sites and in Israel (Geraads, 1986). *Pelorovis turkanensis* has shorter horns; it overlaps in time with the former species, but appears earlier. The North African '*Bos*' *bubaloides*, '*Bos*' *praeafricanus* and *Pelorovis howelli* (Hadjouis and Sahnouni, 2006) are almost certainly identical with one or the other East African forms. *Pelorovis kaisensis* from Uganda and perhaps Ethiopia differs in its virtually straight horns (Geraads and Thomas, 1994; Alemseged et al., 2020). The origin of the genus is unclear, especially because the distinction between the earlier African *Ugandax* and *Simatherium* dwindled recently with the discovery of more fossils. The last species to go extinct was *Pelorovis antiquus* (a.k.a. *Homoiceras antiquus*, *H. baineii* or *H. nilsonii*: Rossouw, 2001). However, this species may be better understood as *Syncerus antiquus*. Neither Gentry (2010) nor Klein (1994) were convinced that this was correct, but at present the leading verdict is that one could accept this view. *S. antiquus* had a wide distribution, and survived in northern Africa till recent times (Figure 2.2). A very late drawing of it may have been from Egypt just prior to the first Pharaoh from the so-named Amratian Civilization (~3600 BCE; see Childe, 1958, figure 1.9). Lovely rock art from the desert of Algeria shows scenes, including bulls fighting (e.g. Brodrick, 1948, p. 37).

In the Early Pleistocene beds in Arabia, a very large bovid has been found that is classified as *Pelorovis* cf. *oldowayensis* (Thomas et al., 1998). This may be an early proof of an outward migration of members of the genus *Pelorovis*, together with the 'Ubeidiya occurrence. Intriguingly, it had very large feet apparently adapted to move on soft substrates' (Thomas et al., 1998). The case shows how nomenclature intertwines with dating: the finds described by Thomas et al. (1998), and interpreted on the basis of morphological data as being close to *P. oldowayensis*, were later re-interpreted because the beds from which the fossils were extracted were dated later in time and were thus allocated to *Syncerus antiquus* (Stewart et al., 2019). This latter approach to classification is, in our opinion, incorrect. Similarly, molars of a smaller species that looked like those

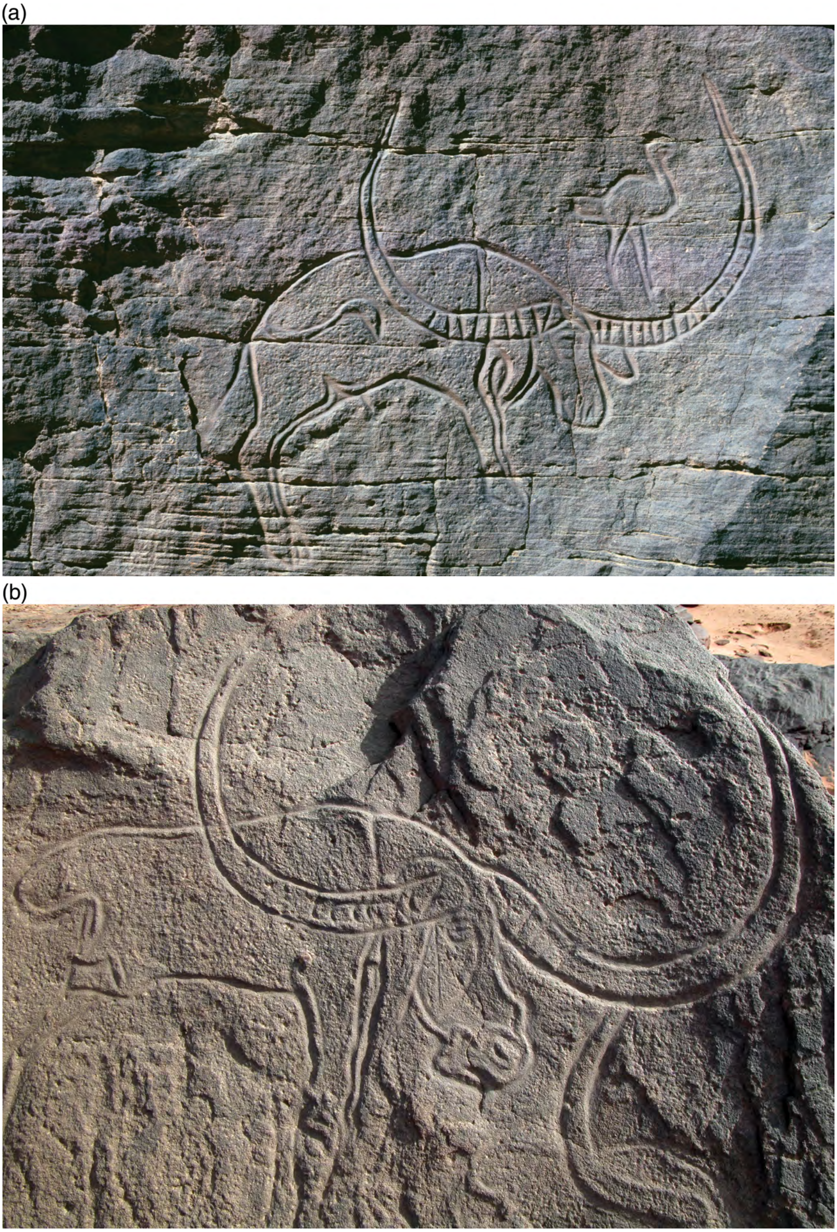

Figure 2.2 In rocky massifs in the Sahara, petroglyphs (engravings in the rock) of animal species are quite widespread. This rock art was made when the Sahara was covered by savannas or steppes, and thus shows many species that are now only known from the Sahel or East Africa. Among these are depictions of *Syncerus* (or *Pelorovis*) *antiquus*, which is now extinct but was once widespread. (a) *S. antiquus* from I-n-Habeter, Mesāk, Libya. Photo Jean-Loïc Le Quellec. (b) Rock engraving of *S. antiquus* from Tilizzāɣen, Mesāk, Libya. Photo Jean-Loïc Le Quellec (used with permission).

of *S. caffer* were classified as *S. antiquus* because *S. antiquus* is known from south-west Asia but *S. caffer* is not (Stewart et al., 2019). However, Geraads (1986) also identified *Pelorovis oldowayensis* from the Early Pleistocene in a nearby area, namely Israel, and later Martínez-Navarro et al. (2012) confirmed the identification, but assigned the species to *Bos*.

This raises the issue of the relationships of *Pelorovis* with *Bos*, a mostly Eurasian genus that includes, besides the modern cattle and aurochs, several wild, endangered southern Asian species and fossil species in the same area. In Africa, unquestionable early representatives of the genus are *Bos buiaensis* from Eritrea, dated to 1 Myr (Martínez-Navarro et al., 2010), a Middle Pleistocene *B. primigenius* from Tunisia dated to 0.7 Myr (Martínez-Navarro et al., 2014) and a species from the lower Awash Valley of Ethiopia, which is close to the southern Asian extinct species *B. acutifrons* (Geraads et al., 2004).

The Tunisian find is almost certainly a Eurasian immigrant (*pace* Martínez-Navarro et al., 2014), while the fact that the Eastern African forms were found close to the Aden straits strongly suggests that they are Asian immigrants. Detailed studies of the geology of the Bab-al-Mandab (the entry to the Red Sea from the Gulf of Aden) show that the straits between the Horn of Africa and the Hadhramaut, where a shallow sill is positioned (the Hanish Sill), remained submerged during the Pleistocene (Al-Mikhlafi et al., 2018). Yet during glacial periods, the straits were 'sufficiently narrow for both sides of the channel to have been visible at all times' and only about 1–3 km wide (Lambeck et al., 2011), thus making it feasible that Asian species of *Bos* crossed here into Africa. Note that the occurrence of *S. c. nanus* until a century ago on Bioko Island, some 35 km off the mainland in the Gulf of Guinea, cannot be taken as an example of buffalo being able to cross such a distance at sea, because Bioko Island was linked to the mainland until the beginning of the Holocene (Ceríaco et al., 2020). Nevertheless, buffalo are good swimmers, and are able to cross wide rivers like the Nile and the Zambesi.

By contrast, Martínez-Navarro et al. (2007, 2010) envisage an evolutionary line of the genus *Bos* starting as *Bos (P.) turkanensis* (Late Pliocene), *B. (P.) oldovayensis* (Early Pleistocene), *B. (P.) buiaensis* (Early Pleistocene) and thence *Bos primigenius* (the Aurochs) and also *Bos planifrons* (which more often is taken as the direct ancestral form of *Bos primigenius namadicus* – the Indian form of the aurochs which developed into *Bos indicus*, the zebu). The important consequence of accepting this interpretation is that the direct ancestors of cattle and zebu evolved in Africa and not in Asia. This would agree with the parsimony analysis on morphological characters performed by Geraads (1992), which showed them to be close on the cladograms. However, the detailed study by Gentry (1967) showed that the cranial morphology of *P. oldowayensis* is very different from that of *Bos*, and it is likely that their closeness on cladograms results from parallelisms. Furthermore, the contemporaneity of the last representatives of the former species with *Bos buiaensis* make an ancestral–descendant relationship extremely unlikely (Geraads, 2018). Moreover, this reasoning sits very uncomfortably with studies that base their reasoning on genetics: *B. primigenius*, cattle and zebu all fit snugly within the phylogenies of the other Asian *Bos* species (cf. Van der Made, 2013). After carefully considering the arguments and fossil material, Tong et al. (2018) conclude that *B. primigenius* was not derived from species that have been classified as *Pelorovis*, and support the view that *B. primigenius* evolved in South Asia, as does Van der Made (2013). Likewise, Bar-Yosef and Belmaker (2016) maintain the position that *B. primigenius* appeared in southwestern Asia as early as 1.2 Myr BP, and it continually occurred in this region until the Late Pleistocene. They recognize *B. buiaensis* in the Jordan Valley much later, namely 0.5–0.8 Myr, but as stated, this could well have been a *Pelorovis*. Indeed, many authors have stated that *Pelorovis (Syncerus) antiquus* was part of the mammal assemblage of the Pleistocene Levant.

Is there good reason to accept the view that *Pelorovis antiquus* should be considered as *Syncerus antiquus* as deduced by Peters et al. (1994) but rejected by Klein (1994)? The predecessor (but not necessarily ancestor) of *P. antiquus* was *P. oldovayensis*. This species was already present in the Levant (Bar-Yosef and Belmaker, 2016) and perhaps in Arabia (Thomas et al., 1998) in the Early Pleistocene. Yet, Martínez-Navarro and Rabinovich (2011) argue to classify this species as *S. antiquus*; however, their publication does not present arguments other than opinion. The original argument put forward by Peters et al. (1994) to view *P. antiquus* merely as a form of *S. caffer*, or as a separate species *S. antiquus*, was mainly based on the observation that the postcranial skeleton hardly differed from *S. caffer* (Peters et al., 1994). However, this is a weak argument, because 'The similarity in the postcranial skeleton known from *Bos*, *Bison* and *Bubalus arnee* is surprising considering that, according to an analysis of mitochondrial DNA, the separation of the *Bubalus–Syncerus* clade from the *Bos–Bison* clade goes back to the Middle Miocene' (Van der Made et al., 2016; see also Von Koenigswald et al., 2019). The main argument of Klein (1994) was that the two species coexisted for a long time, and if both were to be viewed as *Syncerus*, then that would not have been possible. This is, however, based on an old ‘rule’ of competitive exclusion formulated by Charles Darwin but for which there is no firm evidential support (Prins and Gordon, 2014a, 2014b). Note that species of the same genus can very well coexist, as exemplified by Lechwe and Puku or Plains Zebra and Grevy’s zebra in Africa, or for that matter by the many different *Anas* spp., *Anser* spp., *Corvus* spp., etc. in the Boreal zone.

Yet we also have not read convincing arguments to accept the view that *Pelorovis antiquus* was merely another African buffalo or even a more drought-adapted subspecies of the present-day African buffalo (cf. Peters et al., 1994). Indeed, the stance one takes with respect to the systematic position of *P. antiquus* affects the way the evolutionary history of *S. caffer* is interpreted. Note that this has little to do with accepting or rejecting the narrow species concept proposed by Groves and Grubb (2011, p. 1 ff.). However, Gentry (2010) takes *P. antiquus* (grudgingly) as *S. antiquus*, even though he does not present arguments for (or against) this view. However, this evidence is murky, because it depends so much on interpretation in the case of the fossil Bovini material. This implies that one has to consider two alternative scenarios in the evolution of *Syncerus*: namely, one with *S. antiquus* as a species coexisting with *S. caffer* and living in the same area as *B. primigenius* in northern Africa, and the other in which *Syncerus* never reached the areas to the north of the Sahara but that the relevant ‘buffalo’ species in that area was *P. antiquus*.

Miocene Origins of the African Buffalo

How far back in time can one trace the ancestry of the African buffalo? It may have appeared reasonably clear 50 years ago (Sinclair, 1977, p. 22), but the crucial issue is whether the African buffalo really fits into the Bovini (together with the Asian buffalo and the wild cattle swarm). On the basis of DNA, it can be deduced that the last common ancestors of the Bovini and the Tragelaphini (species like the present-day kudu, bushbuck and eland antelope) lived some 18 Myr (Bibi et al., 2009) or 15 Myr ago (Zurano et al., 2019), but the first fossil material comes from *Eotragus*, which is classified as a Boselaphine (like the present-day nilgai). Between the oldest species, *E. noyei* from Pakistan (18 Myr), and the next species, *E. sansaniensis* from France (15.2 Myr), there is a gap of 3 million years, which is as long as the duration of the entire Pleistocene (Solounias and Moelleken, 1992). Then there is another enormous time gap of some 6 million years to a genus named *Selenoportax/Pachyportax*, again from Pakistan (9 Myr; Bibi et al., 2009). An ancestral relation between *Pachyportax* and *Parabos* (thought to be ancestral to *Leptobos*, *Bos* and *Bison* and perhaps to *Proamphibos* leading to *Bubalus*) has been surmised, but the evidence is weak. From *Pachyportax* onwards, the fog of the fossil record lifts a bit. But just when one seemed to be back on firm footing, Gentry (2010) dropped a bombshell by pointing out that there is a fair chance that the Bovini are not even monophyletic. Indeed, Geraads (1992) had already shown that the relationship between Asian and African buffalo is not well supported. In other words, after decades of hard field work and thinking, the early history of the Bovini is not yet clear regardless of what phylogenies based on present-day DNA seem to suggest. Later we will show that cross-fertilization data between African and Asian buffalo also point to a very weak relationship within the group of organisms that are classified as Bovini.

The genus *Eotragus* was a long-lived one with a very wide distribution, ranging from Europe to China, Pakistan and Israel to Kenya (Solounias et al., 1995). The genus *Tethytragus* was similar to *Eotragus*, but evolutionary perhaps not a Boselaphine, and even though *T. langai* still falls within the class of brachydont herbivores, it was more hypsodont than *Eotragus* and may already have been a grazer (DeMiguel et al., 2011, 2012). Yet it appears that the early 'invasion' of Africa by Boselaphini at the beginning of the Middle Miocene did not lead to today's Bovini in Africa. They may have arisen from a second 'invasion' of Boselaphini at the end of the Middle Miocene (Thomas, 1984; Gentry, 2010).

The next genus to consider is *Pachyportax*, which lived during the end of the Miocene. The genus has also been classified within the Boselaphini, but it appears that the Boselaphini are not a homogeneous tribe (Bibi et al., 2009). *Pachyportax latidens* was a large Boselaphine during the Late Pliocene (7–3.5 Myr) of the Siwalik Hills of Pakistan with strongly developed molars for chewing roughage (Ikram et al., 2017). At the same time, there was another Boselaphine in the Siwaliks with less hypsodont molars, which was of the genus *Tragoportax*. European *Tragoportax* at least are large forms, and have rather long legs (perhaps similar to the nilgai). There were quite a number of other putative Boselaphini species at that time in the Siwalik mammal assemblage (Batool et al., 2016), but whether they were truly Boselaphine is uncertain (Bibi et al., 2009). Miocene Bovini show mesowear patterns that are similar to present-day browsers and mixed-feeders, and the molars were not yet very hypsodont (Bibi, 2007). Indeed, Solounias and Dawson-Saunders (1988) elegantly showed how masticatory morphology features relating to intermediate feeding and grazing adaptations evolved in parallel several times and independently from primitive browsing conditions. According to these authors, this did not happen in a savanna-type landscape but in the broad-leaved forests and woodlands there (in Greece). Bibi's (2007) palaeoecological reconstruction is that these early Bovini started utilizing open C_3 vegetation with C_3 grasses. Indeed, C_4 grasses became important only later (Barry et al. 2002), and Bibi (2007) speculates that because the hypsodont index only reached values indicating pure grazing around 8 Myr ago, this behaviour started with the emergence of C_4 grassland at that time. However, the abrasion patterns of the molars do not support this (Bibi, 2007). The driving evolutionary force may have been the strengthening of the monsoonal system due to the uplift of the Tibetan Plateau (Searle, 2017) leading to resource scarcity during the dry season (Bibi, 2007). The fire-dominated and grazer-induced grasslands came into existence only about 2 Myr ago in Africa (Spencer, 1997).

In Libya, *Tragoportax cyrenaicus* lived about 7 Myr ago; the species was perhaps derived from the West Eurasian form (Gentry, 2010). From South Africa, *T. acrae* has been reported (also known as *Mesembriportax acrae*, but cladistically sitting more comfortably with *Tragoportax*: Spassov and Geraads, 2004). *Tragoportax* had a very large range, from Spain to China, and from southern Asia to southern Africa (Batool et al., 2016). In the Siwaliks, the lineage of *Tragoportax* changed from a C_3 browser at 8 Myr to a C_4 grazer at 7.5 Myr. By 6.5 Ma, most frugivores and/or browsers had disappeared even though areas of C_3 vegetation remained until at least 4.5 Myr on the flood plain (Patnaik, 2013; cf. Saarinen, 2019).

Sinclair (1977, p. 22), based on Pilgrim (1939) and Thenius (1969, cited in Sinclair, 1977), suggested that *Parabos* was the ancestor of the African Bovini (*Pelorovis*, *Syncerus*) but also of the Eurasian *Bos* and *Bubalus*. The fact that much older Bovini have been found in Pakistan, namely some 8 Myr ago (Bibi, 2007), and that no *Parabos* has been found outside Europe and the Middle East, pleads against accepting the genus *Parabos* as ancestral to modern Bovini. This is reinforced by the fact that it seems to be seen better as belonging to the Boselaphini than to the Bovini (Gromolard, 1980; Gromolard and Guerin, 1980; Geraads, 1992). Moreover, *Parabos* still occurred much later in time than the separation of *Syncerus* and *Bubalus*. It appears that Boselaphines disappeared from the African continent at the end of the Miocene (Gentry, 1990; Bibi, 2007 – the Miocene ends 5.3 Myr), unless there was a lineage leading to the present-day African buffalo.

The Pliocene Ancestors of *Syncerus*

Genetic data suggest a separation of *Bubalus* and *Syncerus* some 8.8 Myr ago (Hassanin, 2014) or even a million years earlier (Zurano et al., 2019), or (on the basis of cytochrome-c analyses) some 6 Myr ago (Druica et al., 2016), thus in the Miocene. Among the oldest African Bovines, *Ugandax* cf. *gautieri* (see Thomas, 1984) has been reported from Lukeino, as early as about 6 Myr (Pickford and Senut, 2001); this species had much morphological similarity with *Simatherium demissum* from South Africa (Thomas, 1984; cf. Geraads, 1992). *Ugandax* may have been derived from the *Selenoportax–Pachyportax* lineage from the Siwaliks (Thomas, 1984; Gentry, 2010), but Bibi (2009, p. 332) states that it was also very similar to *Proamphibos lachrymans* (the putative ancestor of the Asian buffalo). Bibi (2009, p. 339) poses that *Proamphibos lachrymans* was the last common ancestor of the African and Asian buffalo. *Proamphibos* was substantially larger than *Pachyportax* (Bibi, 2009, p. 339).

There was a suite of species within the genus *Ugandax* or closely related (*U. [S.] demissum* from Early Pliocene South Africa; *U. coryndonae* from the Middle Pliocene, Ethiopia; *U. gautieri* from Uganda, of about 5 Myr; *Simatherium kohllarseni* from the Middle Pliocene of Tanzania and Kenya; and *S. shungurense* from the Late Pliocene of Ethiopia; Geraads et al., 2009a). Yet the evolutionary link between *Ugandax–Simatherium* and *Syncerus* also is not well supported by cladistic analyses (Geraads, 1992).

Ugandax coryndonae is perhaps the best known of the Pliocene African Bovini, represented by a large number of specimens from Ethiopia (Gentry, 2006; Geraads et al., 2009b, 2012). This species may have lived until the Pleistocene, 2.5 Myr ago (Bibi, 2009, p. 335). In other words, the notion that *Ugandax* could have given rise to *Syncerus* (Gentry, 2006) is not well supported by cladistic analysis, and is further undermined by the earliest records of *Syncerus* perhaps overlapping in time with those of *Ugandax* (Gentry, 2010; Bibi et al., 2017).

The deduction that a Middle Pliocene emigration took place by a *Syncerus*-type buffalo from Africa into the Caucasus (Vislobokova, 2008), and from there to Eastern Europe (Evlogiev et al., 1997), by a species classified as *Eosyncerus ivericus* is most likely not justified because the material appears to be Caprine (Bukhsianidze and Koiava, 2018).

So, back to *Proamphibos*. During the Pliocene, this large bovine lived in the foothills of the Himalayas and the floodplains of the Indus and Ganges (Khan et al., 2009). Two species have been distinguished, namely, the less advanced form (with regards to skull and horn morphology) *P. lachrymans* and the more advanced *P. kashmiricus* (Pilgrim, 1939; Khan and

Akhtar, 2011). The body mass of *Proamphibos* was about 200 kg (Dennell et al., 2005). Later (i.e. younger) finds of *P. lachrymans* have been reclassified as *Damalops palaeindicus*, not belonging within the Bovini but to the Alcelaphini (the hartebeest group); the presence of *Proamphibos* as late as 0.8 Myr ago is thus factually refuted. Apparently, it did not co-occur with *Hemibos* (neither with *H. acuticornis* nor with *H. triquetricornis*) and also not with *Bubalus* in Siwalik deposits (Badam, 1977: his table 2; also, in figure 17.11 of Patnaik, 2013). The genus *Proamphibos* is thus considered to be more ancient than the genus *Hemibos* (cf. Bibi, 2009, p. 338). The genus *Hemibos* was considered to include the direct ancestor of *Bubalus*, and perhaps especially of the Anoa of Sulawesi (Groves, 1976). Evidence of co-occurrence of *Hemibos* with *Bubalus*, however, pleads against this. There is no evidence that members of the genus *Hemibos*, which appears to have derived from *Proamphibos*, migrated to Africa or were involved in any way in the evolution of African Bovini and *Syncerus* in particular.

An independent lineage, not leading to *Syncerus* but perhaps related, was present in northern Africa in the form of *Leptobos syrticus*. Gentry (1990), Duvernois (1992) and Geraads (1992) concluded that it should not be maintained within the genus *Leptobos*; they prefer to not assign it to a genus, but conclude a similarity with *Syncerus*. '*Leptobos*' *syrticus* may be related to *Jamous kolleensis* from Pliocene Chad, but this latter species does not show clear affinity with *Syncerus* (Geraads et al., 2009a). *Jamous kolleensis* was a medium-sized bovine, still with rather primitive molars (Geraads et al., 2009a). Because the Eurasian genus *Leptobos*, so important for understanding the evolution of *Bos* including *Bison*, apparently did not otherwise play a role in the evolution of *Pelorovis* or *Syncerus*, we do not deal with it in this chapter.

Thus, *Proamphibos*, or less likely *Ugandax*, is perhaps the link between Asian and African buffalo that geneticists identified to have lived some 8 Myr ago. Cladistic analysis of many fossil forms, modern *Bubalus* and modern *Syncerus* do not well support a strong relationship between Asian and African buffalo (Geraads, 1992). A putative separation some 8 Myr ago is an ancient one for mammals in contrast to birds because the former have prezygotic and postzygotic barriers and the latter prezygotic ones only. These postzygotic barriers are confirmed through embryo transfer experiments (see below), so the genetic distance is really to be reckoned in millions of years. On the basis of a careful analysis of karyotype evolution, it also appears that African and Asiatic buffalo evolved along two different and independent routes, as their centric fusions involved different homoeologous chromosomes (Iannuzzi et al., 2009).

African Buffalo *Syncerus caffer* – Pleistocene and Holocene Fossil Material

So, neither a cladistic analysis of many fossil and modern forms nor studies on nuclear DNA and embryology support a strong relationship between African and Asian buffalo. The ancestry of Asian buffalo, through its descending from *Hemibos*, which was derived from *Proamphibos*, appears reasonably well-founded. The ancestry of the African buffalo is shrouded in opacity. As sketched out, the Pliocene forms *Ugandax* led to *Simatherium* and may have led from there to *Syncerus*, but this link is not well supported by cladistic analyses (Geraads, 1992). Fossil *Syncerus*, such as at Shungura and Olduvai, had no large basal bosses (as the modern Cape buffalo *Syncerus c. caffer*) (Gentry, 1990). Gentry even states that these *Simatherium* were small and short-horned similar to the forest buffalo *S. c. nanus* of today. Whether they form an unbroken lineage to the present forest buffalo is not known, but this is very unlikely given the way that *S. c. nanus* is genetically nested within the other living African buffalo (Van Hooft et al., 2002). Recent genetic studies (reviewed in Prins and Sinclair, 2013) suggest that *S. c. nanus* is the older form and *S. c. caffer* only arose some 150,000 years ago. Whether the two forms (a *nanus*-like one and a *caffer*-like one), as suggested by Gentry (1990), really have been present for a long time seems to be contradicted by genetic analyses (see e.g. Van Hooft et al., 2002). In Chapter 8, Prins, Ottenburghs and Van Hooft revise their opinion, and conclude that *S. c. nanus* is a derived form, while *S. c. aequinoctialis* may be closest to the ancestral form.

The first species that can be classified as *Syncerus* may have been *Syncerus acoelotus*. Geraads et al. (2009a) state that it was as large as the modern *S. caffer* but with less-advanced horns. However, because fossils are not plentiful and the remains are fragmentary, classification remains fraught with issues. Indeed, Gentry (1985) compared Shungura Member C (~2.7 Ma) *Syncerus* horn cores to those of *Syncerus acoelotus*, named from the much younger Olduvai Bed II (~1.5 Ma), but later, Gentry (2010) referred to them as *Simatherium shungurense*. Bibi et al. (2017) re-examined some of the Shungura material and state that they prefer Gentry's (1985) opinion, so they choose to see these fossils again as *Syncerus acoelotus*. A possible very early find of *S. caffer* is from northern Sudan near Dongola; the authors were convinced it was not a *Pelorovis (S.) antiquus* but a true African buffalo (Chaix et al., 2000), but the age of the site is poorly supported. We are not aware of any palaeontological material that can be ascribed to some of the other existing forms of *S. caffer*, to wit *S. c. mathewsi* or *S. c. brachyceros*. Unless material is unearthed, one has to rely on genetic analyses to reconstruct the history of the morphological differentiation within the species. The scant sample sizes on morphology that Groves and Grubb (2011, p. 122 ff.) rely on to distinguish *S. brachyceros* or *S. mathewsi* as separate species are certainly not convincing.

We mentioned earlier that phylogenies based on DNA do not take into consideration the DNA sequences of extinct species if genetic material is no longer available (see Table 2.1). So even where, for example, Bibi (2013) took into account three *Bubalus* species (when there are five or six) into his phylogeny, he did not (and could not) include a whole suite of recently extinct species (some 10 from China: Dong et al., 2014) or the three species that went extinct 2–1 Myr ago (from southern Asia: Van den Bergh et al., 2001; Patnaik, 2013). This relative 'blindness' may cause an optimally parsimonious phylogeny to be an imperfect reconstruction of evolution in reality. This is no criticism of such work, to the contrary, but a call for even better integrating palaeontology with genetics (Table 2.1).

The whole group of (wild) cattle and bison combines well, but ancestors of the wild South-East Asian cattle, bison and West Asian cattle apparently speciated at one short period of time, which cannot be resolved hierarchically (MacEachern et al., 2009). A major issue is extensive hybridization between the whole group of cattle, zebu, yak, gaur, banteng, wisent and bison. Indeed, closely related species (as established by genetic analyses) show hardly any or no barriers to cross-breeding. Species that diverged longer ago show infertility in the male offspring but none in the female offspring. Back-crosses are then very well possible, and this may explain the frequently observed introgression of genetic material in one species from another. Species that are only distantly related cannot cross-breed; in a number of cases, it has been found that in-vitro fertilization is then possible, but the embryo only survives briefly in vitro. These results are further supported by embryo transplantations of 'normal' embryos of one species implanted into a cow of another species.

As expected, this technique shows that embryos of *Bos taurus indicus* transferred to *B. t. taurus* cows result in fully normal parturitions (Summers et al., 1983). Likewise, *B. gaurus* embryos have been transferred to *B. taurus* cows without any problems (Stover et al., 1981). However, pregnancy of embryos of *Bison bison* that were transferred to *B. taurus* cows were terminated sometime between 60 and 100 days (Dorn, 1995). This does not mean that they are not frequently born, because they are, and are named 'beefalo'. Sanders (1925) already reported that male offspring of bison–cattle hybrids (at that time named catalo) frequently were either aborted, stillborn or died very young. Crosses between yak and cattle also often result in increased abortion (Zhang, 2000), yet the offspring that survives is valuable, because they are strong (personal observation).

Water buffalo and cattle are genetically much more distant. Indeed, the pregnancy of *Bubalus bubalis* embryos transferred to *B. taurus* cows terminated after 37 days (Drost et al., 1986). After in-vitro fertilization, embryos of crosses between cattle and water buffalo only survive to the blastocyst state (Kochhar et al., 2002), and to the morula state only in in-vitro fertilization of cattle with African buffalo sperm (Owiny et al., 2009). Indeed, African buffalo are more distantly related to the other Bovini than to Asian buffalo.

In other words, prezygotic barriers are nearly absent between the different species of *Bos* and *Bison*, but postzygotic barriers become increasingly severe with increasing genetic (and evolutionary) distance. We deduce from this that postzygotic barriers become an overwhelming barrier between Bovini that are separated by more than 5 Myr or more, and that prezygotic barriers become an issue after a divergence of some 2 Myr. This appears to be about the same as in wild pigs (*Sus*; Frantz et al., 2013), and very different from birds like ducks (Kraus et al., 2012) or geese (Ottenburghs et al., 2017), where postzygotic barriers do not play a (major) role against horizontal gene transfer (see also Syvanen, 2012; Stewart et al., 2019). Because the Bovini hold much interest in terms of livestock production, perhaps more is known about 'evolution in progress' with this species group than with nearly any other. The picture that emerges is not a simple evolutionary tree, but a system more akin to 'reticulated evolution' (Buntjer et al., 2002).

Using microsatellite data, Ritz et al. (2000) put forward that some 2.5 million years ago, water buffalo and African buffalo had a common ancestor. Their data show that the genetic distance between African buffalo and species of the genus *Bos* appears to be equal. More recent research not using microsatellites but nuclear genome sequences suggests that the groups (*Bubalus* plus Sync*erus*) and (*Bos* plus *Bison*) split very much earlier, namely around five to nine million years ago (Bibi, 2013). The findings of Ritz et al. (2000) are even more difficult to understand if one realizes that a short genetic distance can point to hybridization. Hybridization between *Syncerus* and *Bos*, however, is very unlikely given the outcome of the fertilization and transplantation experiments alluded to above. An alternative explanation is that because these two genera split relatively recently, the genetic makeup is so similar because of incomplete lineage sorting (MacEachern et al., 2009; Bibi, 2013).

Perhaps the true phylogenetic relationship must be derived through other techniques, as was done by Buntjer et al. (2002). They used amplified fragment length polymorphism (AFLP) to generate nuclear DNA fingerprints that display variation of loci dispersed over the nuclear genome of the different species. They did not use algorithms that necessitate solving a tree, and also think that a 'consequence of reticulation is that a tree topology is not adequate for representing the phylogeny'. The Bovini thus form a prime case of 'evolution in action' in which there is a hugely successful group of morphologically very distinct species through which exchange of adaptive or non-adaptive genes can move within the 'supra species' *Bos* (*sensu* Kraus et al., 2012). However, the African buffalo is not part of the species swarm of cattle, gaur, zebu, banteng, yak, wisent and bison that form the Bovini. It is evolutionarily so far removed from that group of Palaearctic and Oriental Bovini that it may be thought as a single surviving species in a tribe 'Syncerini'. Does that have any repercussions for understanding their ecology or management better? We seriously doubt this, because the amount of ecological knowledge garnered from wild Asian buffalo in their native environment is negligible. The wild Asian species is nearly extinct, and little progress has been made to reintroduce them into the wild. In other words, the African buffalo may be irreplaceable and for understanding it, one cannot plagiarize knowledge from other Bovini.

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