

The Fossil Record and Evolution of Bovidae: State of the Field

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ABSTRACT

This paper presents a summary of the current state of knowledge on the evolution and fossil record of Bovidae and identifies topics and problems for further study. The earliest records of the different bovid tribes are reviewed, along with their geographic locations. Future work on the fossil bovid record should focus on: the reinvestigation of osteological characters that might distinguish early bovids from stem taxa; the late Miocene fossil record with respect to the evolutionary origins and biogeography of the living bovid tribes; and improved methodologies for reconstructing bovid phylogeny using morphology. This paper reflects the main themes discussed at the meeting of the Revealing Hominid Origins Initiative Bovid Analytical Working Group in Addis Ababa, Ethiopia.

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INTRODUCTION

Bovids are diverse herbivorous mammals that inhabit a wide spectrum of habitats and occur naturally over much of the globe. Ranging from the enigmatic and elusive forest antelopes of South East Asia and Central Africa to the ubiquitous cattle and other livestock common to most world cultures, and from the Himalayan goat to the desert oryx to the North American bison, bovids represent an example of a clade that owes its success to its capacity to diversify in the face of selective pressures. The evolutionary history of Bovidae is known to have taken place in the Miocene to Recent, or within the last 23 Ma (Figure 1). The Miocene fossil record is both rich and geographically extensive, and as a result the reconstruction of the evolutionary history of Bovidae promises to provide one of the most complete such histories for any large mammal group.

Between August 4 and 8, 2008, the Bovid Analytical Working Group of the Revealing Hominid Origins Initiative (National Science Foundation, USA) met in Addis Ababa for a conference on the fossil record and evolution of Bovidae with special emphasis on the late Miocene to early Pleistocene. A summary of the main themes, findings, and recommendations of the conference follows.

BOVID ORIGINS

Recognition of the earliest fossil bovids is not straightforward, nor for that matter is recognition of early or stem members of the different bovid subclades. Bovidae is diagnosed by the presence of permanent and unbranched horn cores with a permanent and unbranched horn sheath (Janis and Scott 1988). Sheaths are rarely preserved as fossils, so the recognition of an early bovid in the fossil record relies on the presence and morphology of the bony horn core alone. This proposition is problematic, however, given that members of other pecoran groups also bear a very similar horn-core structure (both fossil and living species, e.g., *Antilocapra americana*) and given the potential absence of horns in female individuals. Dental and other cranial and postcranial osteological characters of potential use for distinguishing the earliest bovids and stem bovids should be further investigated. Teeth and cranial characters of certain species of *Eotragus*, long considered the earliest bovids, may indicate that certain of these species are basal to (i.e., precede on the cladogram) the last common ancestor of all the living Bovidae. *Eotragus artensis* (Ginsburg and Heintz 1968;

France, MN4 in Gentry et al. 1999; ca.18–17Ma in Steininger 1999) has been proposed as a stem bovid (see also Azanza and Morales 1994), as has *E. noyei* (ca.18Ma, Pakistan, Solounias et al. 1995). *Eotragus minus*, from the early Miocene of Pakistan, may be even older than *E. noyei*, and possibly more primitive in morphology (Ginsburg et al. 2001).

Other taxa worth further consideration in relation to stem bovids include *Andegameryx*, *Amphimoschus*, *Namibiomeryx*, *Namacerus*, *Pseudoeotragus*, and *Homoiodorcas*. Taxa included in Hypsodontinae (Köhler 1993) might be diphyletic to (i.e., the sister group of) the remainder of Bovidae (Gentry et al. 1999). Various Miocene taxa have been referred to Hypsodontinae (Köhler 1987). The group is in need of revision, having never been treated in much detail, and its phylogenetic status remains unclear.

TRIBAL ORIGINS AND RADIATIONS

Bovids have long been classified among a dozen or so higher taxa, typically tribes. Simpson's (1945) classification divided bovids among 13 tribes in five subfamilies. Since that time, work on bovid systematics (morphological, behavioral, and molecular) has revealed a deep bifurcation within Bovidae separating the Bovinae from all the remaining bovids (Kingdon 1982; Lowenstein 1986), and has condensed the number of tribes to around 10 (e.g., Hassanin and Douzery 1999b).

Bovinae (Bovini+Tragelaphini+Boselaphini)

Bovinae is the sister group to all remaining living bovids and is characterized by numerous morphological, behavioral, and molecular synapomorphies (e.g., Kingdon 1982; Hassanin and Douzery 1999b; Vrba and Schaller 2000; Bibi 2009). *Eotragus sansaniensis* (15.2Ma, France, Sen 1996), *E. noyei* (ca.18Ma, Pakistan), and an unnamed species from the Vihowa Formation (ca.18Ma, Pakistan) have been tentatively proposed as early or stem Bovinae (Solounias and Moelleken 1992; Azanza and Morales 1994; Solounias et al. 1995). These fossils would suggest that the cladogenetic event separating the Bovinae from the remainder of Bovidae must have occurred in the early Miocene, or certainly by 18Ma.

Stem Bovini were likely present in southern Asia (Siwaliks) by 9Ma, as represented by *Selenoportax* (Bibi 2007). After this time, early bovines dispersed first to Africa then to Europe. It is not clear when or where exactly the crown clade origi-

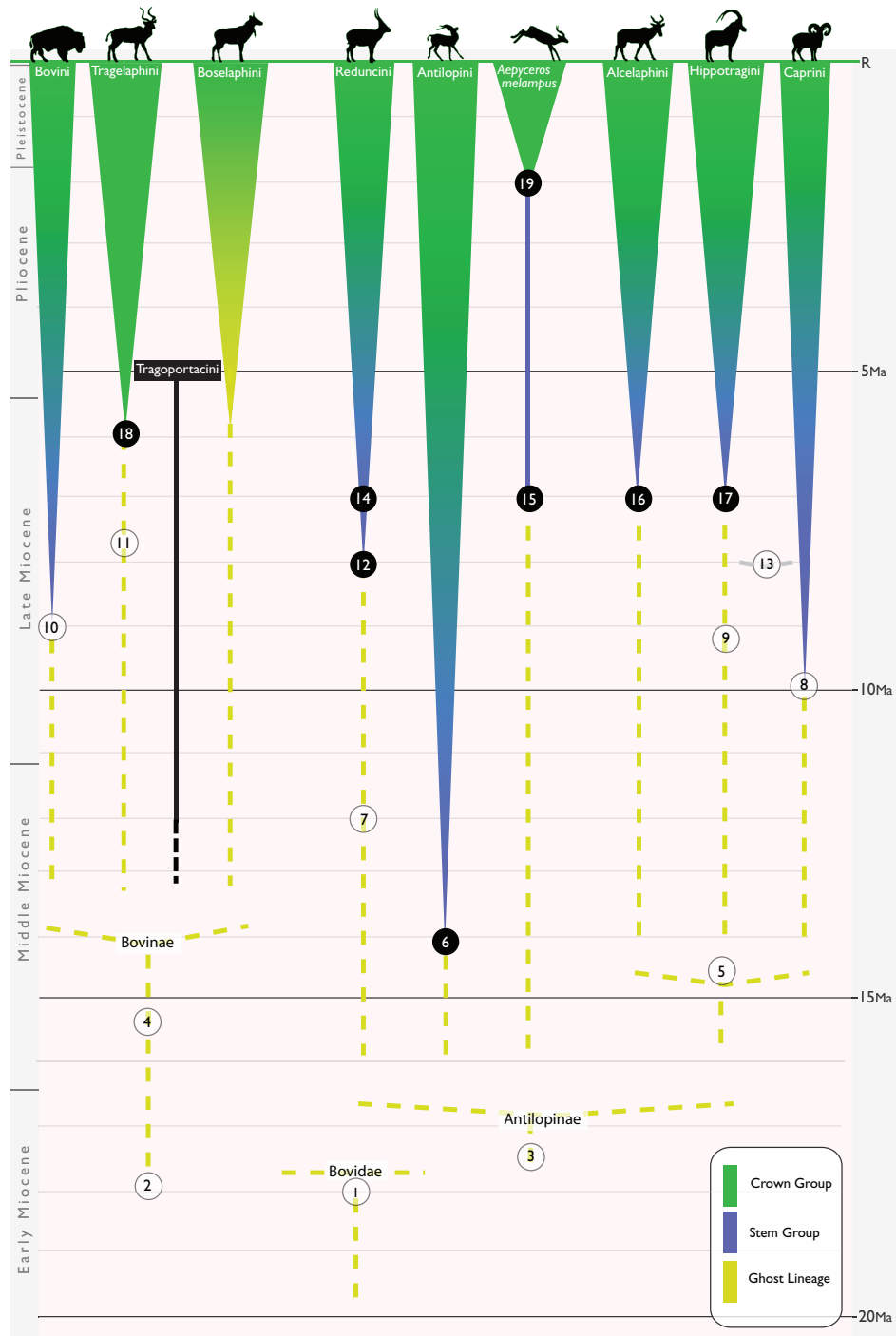


FIGURE 1. Phylogenetic diagram charting the evolution of the major bovid clades. Solid numbered circles represent fossils assignable to crown or stem groups, while open circles represent fossil taxa of potential phylogenetic affinity. Numbers refer to the following: **1**, *Eotragus artensis*, *Eotragus noyei*, *Eotragus minus*; **2**, *Eotragus noyei*, Vihowa Bovidae indet.; **3**, *Pseudoeotragus seegrabensis*; **4**, *Eotragus sansaniensis*; **5**, *Caprotragoides*, *Gentrytragus*, *Tethytragus*; **6**, Fort Ternan *Gazella* sp.; **7**, Ngorora '*Pachytragus* aff. *solignaci*'; **8**, *Pachytragus solignaci*; **9**, Djebel Krechem Hippotragini? indet.; **10**, *Selenoportax*; **11**, *Pheraios chryssomallos*; **12**, Siwalik Reduncini; **13**, *Protoryx/Pachytragus*; **14**, Lothagam Reduncini; **15**, Lothagam *Aepyceros*; **16**, Lothagam Alcelaphini; **17**, Toros Menalla & Lothagam Hippotragini; **18**, Lukeino *Tragelaphus* cf. *spekii*; **19**, Omo & Koobi Fora *Aepyceros melampus*. Bovid silhouettes adapted from Kingdon (1982).

nated as the fossil taxon closest to the most recent common ancestor of all living bovines has not yet been identified. The earliest African record of a bovine is at Toros-Menalla (Vignaud et al. 2002), Chad, at around 7Ma. By the end of late Miocene, several western Eurasian “boselaphines” begin to exhibit morphology suggestive of the bovine condition but the earliest European record of a bovine is in the early Pliocene (Gromolard 1980). The ability to confirm with certainty a southern Asian origin of Bovini is hampered by the poor African fossil record between 10 and 7Ma, whereby the absence of Bovini from Africa during this time may be a result of preservation bias. Once Bovini had originated, multiple bovine lineages become evident but good hypotheses of between- and within-lineage relationships are lacking. The water buffalo *Bubalus* most likely emerged from the Pliocene *Proamphibos* (Pilgrim 1939) and the African *Syncerus* from a *Ugandax* (Gentry and Gentry 1978) though the precise limits of the latter genus, along with that of *Simatherium*, are still unclear. The origins of *Bos* and *Bison* and the interrelationships of the many fossil species seemingly relevant to them remain problematic. The hypothesis that *Pelorovis* gave rise to *Bos* (Martínez-Navarro et al. 2007) requires further evidence.

The history of the Tragelaphini as known so far is almost entirely African. The earliest tragelaphine that is probably a crown group member (i.e., not a stem representative) is recognized from the Lukeino Formation (Thomas 1980), Kenya, dated to between 6.56–5.72Ma (Deino et al. 2002). Tragelaphini are entirely absent from the fossil record of Chad (Geraads et al. 2001; Vignaud et al. 2002) and not well represented in the North African record (Geraads et al. 1998). The Lukeino tragelaphine already bears the main horn core synapomorphies of the group, and no consensus was reached on the possible existence of any stem group lineages or potential ancestors for Tragelaphini. The stem tragelaphine lineage may have evolved either in Africa or Eurasia. *Pheraios chrysomallos* (Kostopoulos and Koufos 2006), from the late Miocene of Greece, has been proposed as a possible stem tragelaphine.

Boselaphini is a large, diverse, and, as currently understood, non-monophyletic group. A revision of the systematics of taxa variously grouped as Boselaphini is warranted. The crown clade—i.e. the two living boselaphines, *Boselaphus tragocamelus* and *Tetracerus quadricornis*, along with their immediate ancestors—is most likely separate from the majority of Miocene fossil forms generally

referred to “Boselaphini.” Crown Boselaphini has a poor fossil record, with a handful of Asian localities of imprecise Plio-Pleistocene age yielding fossil *Boselaphus* and *Proboselaphus* (Rütimeyer 1878; Matsumoto 1918; Pilgrim 1939). We know of no fossil record for *Tetracerus*. The Miocene fossils traditionally attributed to “Boselaphini” may be divided among independent clades and stem groups of one or more living bovid tribes (Pilgrim 1939; Moyà-Solà 1983; Thomas 1984b; Bibi 2007). The dominant late Miocene fossil “boselaphines,” both in terms of diversity and geographic range, are species of the genera *Miotragocerus* and *Tragoportax*. Interrelationships between *Tragoportax* and *Miotragocerus* remain unclear, with diagnoses so far proposed to distinguish the two genera being difficult to consistently apply in a wide context. Species of these genera range throughout the late Miocene, and are found across Eurasia from China to Spain, in the Siwaliks, and to the far south of South Africa. *Tragoportax*, *Miotragocerus*, and other taxa such as *Protragocerus*, have been united under the name *Tragocercina* or *Tragocercini* (Sokolov 1953; Korotkevich 1981; Thomas 1984a, 1984b). However, by the rules of the International Code on Zoological Nomenclature (Article 39), a family-group taxon name may not be based on a genus found to be a junior homonym—in this case *Tragocercus*, previously occupied for a beetle. As a result we adopt for this fossil group the name *Tragoportacini*, appropriately based on *Tragoportax*—this being the genus in which we now place the old type species *T. amalthea*, of *Tragocercus*—for a fossil group uniting *Tragoportax*, *Miotragocerus*, and allies.

Antilopinae/Aegodontia

The clade including all bovids that are not Bovinae is known as either Antilopinae (Kingdon 1982; Hassanin and Douzery 1999b) or Aegodontia (Schlosser in Zittel 1911:499, sensu Vrba and Schaller, 2000). The former term is more appropriate in the context of phylogenetic nomenclature but is problematic for the Linnean system, as it would incorporate other subfamilial designations (e.g., Caprinae). ‘Antilopinae’ (sensu Simpson 1945) has also been previously used to unite the Antilopini + Neotragini, but the non-monophyly of the latter group (see below) means such a designation is now probably unnecessary, leaving the name available for redefinition as the sister-group to Bovinae. Aegodontia has been recently redefined, but is ambiguous in that this group would include bovids that are not ‘aegodont’ (‘goat-toothed’) as originally

diagnosed. This clade is supported by numerous morphological, behavioral, and molecular synapomorphies (e.g., Kingdon 1982; Hassanin and Douzery 1999b; Vrba and Schaller 2000; Bibi 2009).

Pseudoeotragus seegrabensis from Austria may be an early stem member of Antilopinae (Azanza and Morales 1994 figs. 7-8), with an age of 18–17Ma (MN4, Made 1989; Agustí et al. 2001).

The oldest substantiated African occurrences of Reduncini occur at Lothagam (Harris 2003) and Toros-Menalla (Vignaud et al. 2002). These may prove younger than the earliest occurrence in the Siwaliks, which may be 8Ma or older (Barry et al. 2002). The cranium attributed to *Pachytragus* aff. *solignaci* from the late middle or early late Miocene of Ngorora, Kenya (Thomas 1981), deserves re-examination as a possible reduncine. The problem of the relatively poor African late Miocene fossil record is again pertinent here.

In line with recent phylogenetic studies, it was agreed that “Neotragini” is not monophyletic. The majority of “Neotragini” are paraphyletic with respect to Antilopini (Gentry 1992; Rebholz and Harley 1999). The most species-rich and widespread antilopine is *Gazella*. Fossils attributed to this taxon go back to the late mid-Miocene of Fort Ternan, Kenya (ca. 14Ma, Gentry 1970; Shipman et al. 1981).

The origins of the impala, *Aepyceros*, remain unknown. The impala is first known from late Miocene African localities, with the oldest secure records coming from Lothagam and Toros-Menalla (Harris 2003; Geraads et al. 2008). A study of impala origins should investigate a possible connection with European and North African spiral-horned antilopines. The living species, *A. melampus*, is first recorded in the latest Pliocene, at Koobi Fora (Harris 1991) and possibly Omo (Gentry 1985).

The Hippotragini + Alcelaphini + Caprinae together form a monophyletic clade, substantiated by numerous recent phylogenetic studies (e.g., Vrba and Schaller 2000; Ropiquet and Hassanin 2005). Fossil taxa such as *Protoryx* and *Pachytragus*, debated to be either caprine or hippotragine (Bosscha Erdbrink 1988; Gentry 2000) may actually lie closer to a common ancestor of both these clades. Taxa such as *Tethytragus*, *Gentrytragus*, and *Caprotragoides* may also lie in various positions in, or close to, the stem group of the larger clade Caprini+Hippotragini+Alcelaphini (Azanza and Morales 1994; Gentry 2000). The relationships of these three genera to one another are still not known, particularly of *Tethytragus* to the other two.

The old name Pseudotragini (sensu Solounias and Moelleken 1992) has been proposed as a paraphyletic group that includes possible stem caprines. *Pachytragus solignaci* (Tunisia, MN9/10 in Geraads 1989; ca.10Ma in Steininger 1999) has more specifically been proposed as a potential early crown caprine (Solounias and Moelleken 1992). “Ovibovini” is non-monophyletic, with phylogenetic studies partitioning *Budorcas* and *Ovibos* among Caprinae, (Bouvrain and de Bonis 1984; Ropiquet and Hassanin 2005).

The earliest confirmed hippotragines are known from Toros-Menalla, Chad, aged to about 7Ma (Geraads et al. 2008). The Chadian fossils demonstrate that hippotragines present a mix of derived and primitive characters that suggestively place them at the stem of the hippotragine clade. The maximal age of the most recent common ancestor of all living Hippotragini (crown clade) is as a result set to around 7Ma.

The oldest Alcelaphini are known from between about 7.5–6.5Ma from Lothagam, Kenya (Harris 2003; McDougall and Feibel 2003). Alcelaphini are virtually absent at Toros-Menalla, and not recorded from Mpesida (Thomas 1980) and Mio-Pliocene Middle Awash deposits (Haile-Selassie et al. 2004; Haile-Selassie et al. 2009). Vrba’s (1997) phylogenetic study suggests the origins of crown Alcelaphini are to be found prior to 5Ma.

APPROACHES TO SYSTEMATICS

Bovids, being diverse animals that inhabit a spectrum of habitats from arid environments to wetlands, present an excellent resource with which to formulate and test evolutionary and paleoecological hypotheses. At the same time, their great diversity presents a serious challenge to morphological systematics. Homoplasy in bovid evolution is evidently rampant (Gentry 1992), and the application of comprehensive morphological cladistic methods to bovid systematics requires much more work, particularly as concerns the difficult task of character formulation and coding. Over recent years, morphological cladistic analyses using a selective set of characters and taxa (in contrast to ‘total’ methods) have had greater success in producing phylogenies commensurate with the fossil and molecular data (e.g., Vrba 1997; Geraads et al. 2008). Future phylogenetic work would benefit greatly from increased incorporation of ontogenetic data (e.g., Vrba et al. 1994).

Molecular systematics has over the last 20 years provided significant insight into the evolutionary history of, and interrelationships within, Bovi-

dae. Molecular systematic work provided strong evidence for the existence of Antilopinae/Aegodontia (Lowenstein 1986; Hassanin and Douzery 1999b), the polyphyly of Neotragini (Hassanin and Douzery 1999b; Matthee and Robinson 1999; Rebolz and Harley 1999) and Ovibovini (Groves and Shields 1997; Hassanin et al. 1998; Ropiquet and Hassanin 2005). Molecular phylogenetic work has also advanced knowledge of living but enigmatic bovid species. Notable among these is the case of the saola, *Pseudoryx nghetinhensis*, a goat-like antelope living in the forests of Vietnam and Laos, only first described in 1993 (Dung et al. 1993; Kemp et al. 1997). Morphological comparisons (Thomas 1994) suggested inclusion within the Caprini while molecular work proposed affinity to Bovinae and Bovini (Dung et al. 1993; Hassanin and Douzery 1999a). A 'total evidence' approach using both morphological and molecular characters supported the previous contentions of the molecular evidence, that the saola was in fact a member of Bovinae and even nested deep within Bovini (Gatesy and Arctander 2000). *Pseudonovibos spiralis*, the linh duong, is another recently described bovid (Peter and Feiler 1994) of uncertain status. *Pseudonovibos spiralis* is known only from a number of horn sheaths collected from Vietnam, and controversy has raged over whether the characteristically spiraled and annulated horns are indeed indicative of a new species, or whether they are simply modified horn sheaths of cattle, *Bos taurus*. Molecular phylogenetic studies have made a strong case that *Pseudonovibos spiralis* is simply a synonym of *Bos taurus* (Peter and Feiler 1994; Olson and Hassanin 2003 and references therein).

BIOGEOGRAPHY

The wide geographic range of Bovidae, and the fact that many bovid clades are restricted in their distributions, makes this group ideal for biogeographic investigation. The Miocene evolution of Bovidae took place against the backdrop of major climatic and physiographic changes, including the closure of the Tethys Gateway (Berggren 1972), opening of the East African and Red Sea rift valleys (Ghebream 1998), gradual global cooling (Zachos et al. 2001), the Messinian salinity event (Hsü et al. 1973), and the global expansion of C₄ grasslands at low latitudes (Cerling et al. 1997). As such, the search for correspondence between global environmental changes and major biogeographic events in the evolutionary history of Bovidae is a main focus of any synthetic treatment of the bovid fossil record.

Bovids are diagnostic components of biogeographic zones defined on the basis of whole fossil faunas. For example, the fossil bovids from the late Miocene Baynunah Formation (United Arab Emirates, Gentry 1999) suggest an overlapping of the North African, Greco-Iranian (=Sub-Paratethyan), and Oriental (south Asian) Provinces. These traditional biogeographic provinces, outlined for the late Miocene by Bernor (1984), continue to remain relevant for discussion today, as do the topics addressed by past syntheses of bovid paleobiogeography (Gentry 1968; Thomas 1984a).

Systematic and paleontological work of the last two decades has significantly improved the resolution at which bovid paleobiogeography can formulate and test hypotheses. For one, the production of more robust phylogenies, particularly by way of molecular methods, has allowed for the rapid development of phylogeographic studies. Such studies have worked to reconstruct ancestral areas for higher clades (e.g., Hassanin and Ropiquet 2004) as well as the geographic range expansions and contractions of individual species (e.g., Arctander et al. 1999). Additionally, the fossil record has been sufficiently improved to allow for new appraisal of late Miocene biogeographic trends. Higher resolution paleobiogeographical studies are now possible that reveal developing zoogeographies both among and within biogeographic provinces in the late Miocene. For example, marked differences appear to have differentiated the Southern Balkan vs. Anatolian faunas of the late Miocene Greco-Iranian Province (Kostopoulos 2009).

The presence of a monophyletic Caprini+Alcelaphini+Hippotragini (unnamed clade) provides a good opportunity for paleobiogeographic studies as the living Caprini are almost entirely Eurasian while recent Alcelaphini and Hippotragini are African (the latter are present in Arabia as well). On the basis of fossil and molecular phylogenetic evidence, Ropiquet and Hassanin (2005) proposed that Caprini originated on Mediterranean islands in the late Miocene. In addition to major cladogenetic and dispersal events, the record of rare and isolated occurrences of bovid taxa outside their expected geographic range is another important indicator of biogeographic interchange. For example, caprines have a very limited record of presence in Africa, and Plio-Pleistocene fossil caprines like *Bouria* and *Makapania* are taken to be immigrants southwards from Eurasia. The age of occurrence of these fossil caprines in Africa happens also to correspond to pronounced

global cooling events (Vrba 1995). Both Alcelaphini and Hippotragini have a limited Plio-Pleistocene record (Pilgrim 1939) outside of Africa, namely in the Siwaliks, and Alcelaphini may have also occurred in the late Miocene of Italy with *Maremmia* (e.g., Thomas 1984a). Additional possible African occurrences in Europe include possible reduncines from late Miocene Sicily and Turkey (Seguenza 1902; Köhler 1987; Gentry 1999). Late Miocene links between sub-Saharan Africa and southern Asia are also apparent in the shared presence of bovid taxa such as the reduncine *Kobus porrecticornis* (see Haile-Selassie et al. 2009). In light of the apparent barriers to exchange between southern Asia and the Greco-Iranian Province (Beden and Brunet 1986), shared occurrences of Bovidae between the Siwaliks and parts of Africa begs further investigation.

BOVIDS IN THE CONTEXT OF HOMINID ORIGINS

The oldest hominids known are *Sahelanthropus tchadensis* from Chad (ca.7Ma, Lebatard et al. 2008), *Ardipithecus kadabba* from Ethiopia (5.7Ma, WoldeGabriel et al. 2001), and *Orrorin tugenensis* from Kenya (ca.6Ma, Pickford and Senut 2001). Though these may be the three most popular actors on the late Miocene stage, it is on the basis of the remainder of the fossil fauna that the contextual picture (climatic, vegetational, and biogeographic) is drawn. A major impediment to increasing the resolution of the paleontological 'big picture' in the late Miocene is the limited nature of the African fossil record prior to 7Ma. Even with such limitations, Bovidae, often the most abundantly represented mammalian group in these fossil contexts, have the greatest potential to inform the biogeographic and climatic contexts of early hominid origins. For example, the absence of tragelaphines from the late Miocene and Pliocene Chadian fossil record (Geraads et al. 2001; Vignaud et al. 2002) hints at deep biomic discontinuities between the Lake Chad basin and the entire East African Rift Valley throughout this time. The abundance of *Tragelaphus* at the 4.4Ma Aramis hominid site provides a key indication that *Ardipithecus ramidus* inhabited a wooded environment (WoldeGabriel et al. 1994). Changing proportions of alcelaphines and antilopines at late Pliocene hominid sites provide a main support for the hypothesis that *Homo* and *Paranthropus* originated during a major drying trend between 2.8–2.0Ma (Vrba 1985; Bobe and Eck 2001).

The environmental and ecological dynamics responsible for the evolution and distribution of early hominid taxa are rarely to be reconstructed from the hominids themselves. That bovids are ecologically diverse and present in abundance at hominid sites means this clade provides some of the strongest evidence with which to propose and test hypotheses relating human evolution to environmental changes. To those interested in the context of early hominid evolution, these are interesting times as multiple independent fieldwork efforts, in Africa and elsewhere, target the period between 5 and 10Ma. This span of time is much better known from Europe and will soon be better understood from southern and central Asia with work currently in progress. The grand task of threading together the inter-continental picture of evolutionary, biogeographic, and climatic changes will prove to be a major objective of those working on bovid paleontology and systematics in the years to come.

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