

# Zitteliana

An International Journal  
of Palaeontology and Geobiology

Series B/Reihe B  
Abhandlung der Bayerischen Staatssammlung  
für Paläontologie und Geologie

# 31

International Conference on  
Ruminant Phylogenetics Munich 2013

03.–06. September 2013

Programme and Abstracts



Munich 2013

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Paläontologie  
& Geobiologie  
LMU München



Bayerische  
Staatssammlung  
für Paläontologie und Geologie



GeoBio-  
Center  
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## CONTENTS

PREFACE, ORGANISATION AND SPONSORS	4
FLOOR PLAN	5
PROGRAMME	6
ABSTRACTS	11
LIST OF ALL AUTHORS	37
LIST OF ALL PARTICIPANTS	39

Zitteliana	B 31	48 Seiten	München, 01.09.2013	ISSN 1612-4138
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## PREFACE

Ruminants are the most abundant (over 3 billion individuals) and diverse (up to over 300 distinguished species) group of ungulates. They include most of the agriculturally, environmentally, economically and culturally important species on earth. Ruminants display a fascinating spectrum of adaptations allowing them to successfully inhabit nearly every terrestrial biome. Yet, the evolutionary history of ruminants remains unresolved. The fossil record documents 43 million years of diversification including several key radiations, marking important steps in ruminant cladogenesis. This long time of radiations and extinctions makes ruminants an ideal group in which to study many aspects of evolutionary theory, like selection and speciation.

Ruminant phylogenetics has been a subject of scientific interest since the initial Linnean classification in 1735. Many competing phylogenetic hypotheses have been advanced since then, linking the many extinct and the six surviving ruminant families in almost every possible manner. For 250 years, these hypotheses were based on comparative studies of diverse phenotypic traits in a wide array of disciplines. In the last 20 years, advances in genome sequencing, developmental genetics, and computational phylogenetics have brought new forms of data and methodologies to bear on these questions. In some cases, this has helped to resolve phylogeny. In others, it has added to the confusion. Both phenomic and genomic data from fossil and extant species accumulate at an ever increasing rate. Expertise from specialists in all of these diverse disciplines is needed to make a coherent and logical synthesis of this enormous amount of data.

The International Conference on Ruminant Phylogenetics is the first of its kind and aims to provide an interdisciplinary meeting environment, promoting interaction of leading experts in diverse aspects of comparative ruminant (palaeo)biology. It includes reviews of critical disciplines by recognised experts, presentation and discussion of the most recent research results by participants and working group sessions on special topics and issues. It is designed to produce a stimulating atmosphere for intensive debate on crucial issues leading to the recognition of critical deficiencies and the initiation of collaborative efforts to resolve them.

We wish all participants a memorable conference with a fruitful outcome and the beginning of a new era in ruminant phylogenetics. Welcome to Munich!

Gertrud Rössner      William Silvia      Grégoire Métais      Brian Beatty      Eva Bärmann      Gert Wörheide

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Monday, September 2, 2013: 4 pm - 7 pm

Tuesday, September 3, 2013: 7:30 am - 6 pm

Wednesday, September 4, 2013: 7:30 am - 7 pm

Thursday, September 5, 2013: 7:30 am - 5 pm

Friday, September 6, 2013: 7:30 am - 5:30 pm

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Room 108 & Room 106

Access open

Monday, September 2, 2013: 3 pm - 10 pm

Tuesday, September 3, 2013: 8 am - 8 pm

Wednesday, September 4, 2013: 8 am - 8 pm

Thursday, September 5, 2013: 8 am - 8 pm

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Data encryption No encryption

TCP/IP Obtain an IP address automatically

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Do not specify Network Authentication or any encryption. For TCP/IP Properties choose 'Obtain an IP address automatically'. You get a worldwide valid IP Address, no Proxy Server is needed.

All Internet applications except Microsoft File and Printer sharing should work.

## PROGRAMME: TUESDAY, SEPTEMBER 3, 2013

Time	Speaker	Title
8:00 am - 8:30 am	Wörheide, Haszprunar, N. N., Rössner	Welcoming, organisational issues
<b>Session 1: Exploring Ruminant Phylogenetics - Reviews on Involved Disciplines</b>		
8:30 am - 9:10 am	Groves	Current taxonomy and diversity of crown ruminants above the species level
9:10 am - 9:50 am	Taylor	Genomics
<i>9:50 am - 10:30 am Coffee break</i>		
10:30 am - 11:10 am	Roberts	Developmental genetics
11:10 am - 11:50 am	Ianuzzi	Cytogenetics
11:50 am - 12:40 pm	Janis & Theodor	Skeletodental morphology
<i>12:40 pm - 2:00 pm Lunch break</i>		
2:00 pm - 2:40 pm	Clauss	Soft tissue biology
2:40 pm - 3:20 pm	Deleporte	Behavioural biology
<i>3:20 pm - 4:00 pm Coffee break</i>		
<b>Session 2: Mining and Recycling Ruminant Phylogeny Estimates - Reviews on the Outcome</b>		
4:00 pm - 4:40 pm	Bininda-Emonds	Rocks versus clocks or rocks and clocks: how can we solve the riddle of ruminant relationships?
4:40 pm - 5:20 pm	Hernández Fernández	Ruminant macroevolution: a phylogenetic approach based on extant faunas

## PROGRAMME: WEDNESDAY, SEPTEMBER 4, 2013

Time	Speaker	Title
8:20 am - 8:30 am	Rössner	Organisational issues
<b>Session 3: Phylogenetic Patterns in Ruminantia</b>		
8:30 am - 8:50 am	Koyabu	Phylogenetic patterns and diversity of embryonic skeletal ossification in Cetartiodactyla
8:50 am - 9:10 am	Asher	Dental eruption in ruminants and other mammals
9:10 am - 9:30 am	Green	Characterization of the gene family encoding for the pregnancy associated glycoproteins in ruminant ungulates
9:30 am - 9:50 am	Klisch	Morphological aspects of the evolution of the ruminant placenta
9:50 am - 10:10 am	Silvia	A comparison of vestigial zeugopodal and autopodal elements in ruminants and their potential use in establishing phylogenetic relationships
10:10 am - 10:30 am	Beatty	Histological insights into the deep homology of ruminant cranial appendages
<i>10:30 am - 11:00 am Coffee break</i>		

## PROGRAMME: WEDNESDAY, SEPTEMBER 4, 2013 (CONTINUATION)

Time	Speaker	Title
<b>Session 4: Phylogenetic Implications from Basal Hornless Ruminantia</b>		
11:00 am - 11:20 am	<b>Theodor</b>	Basicranial and ear morphology characters among basal ruminants
11:20 am - 11:40 am	<b>Métais</b>	Eocene-Oligocene selenodont artiodactyls from Asia and their bearing on the phylogeny and paleobiogeography of early ruminants
11:40 am - 12:00 pm	<b>Mennecart</b>	Reassessment of early European Ruminantia: implications for the diversity and evolution of the group
12:00 pm - 12:20 pm	<b>Barry</b>	The fossil tragulids of the Siwalik Formations of southern Asia
12:20 pm - 12:40 pm	<b>Sánchez</b>	Phylogeny of the Tragulidae (Mammalia, Cetartiodactyla, Ruminantia)
12:40 pm - 1:00 pm Group picture		
1:00 pm - 2:20 pm Lunch break		
2:20 pm - 2:40 pm	<b>Aiglstorfer</b>	New insights into tragulid phylogeny of Europe: <i>Dorcatherium nauyi</i> from the latest Middle Miocene of Austria
<b>Session 5: Phylogenetics in Cervidae</b>		
2:40 pm - 3:00 pm	<b>Lister</b>	Systematics of the endemic Pleistocene deer of Mediterranean islands
3:00 pm - 3:20 pm	<b>Azanza</b>	Fossil taxa and molecular clock calibrations in Cervidae phylogeny: the challenge of the middle-late Miocene muntjac-like deer
3:20 pm - 3:40 pm	<b>Heckeberg</b>	A revision of cervid phylogeny using a total evidence approach
3:40 pm - 4:00 pm	<b>Schulz</b>	Separating phylogenetic signals from trophic convergence in cervid dentition – implications from tooth morphology and 3D surface texture analysis
4:00 pm - 4:20 pm	<b>Zhang</b>	Late Miocene <i>Cervavitus novorossiae</i> (Cervidae, Artiodactyla) from Lantian, Shaanxi Province
4:20 pm - 4:50 pm Coffee break		
4:50 pm - 5:10 pm	<b>Ghaffar</b>	Fossil remains of family Cervidae from the Siwaliks of Pakistan
5:10 pm - 5:30 pm	<b>Croitor</b>	Deer from Plio-Pleistocene of Western Eurasia: matching fossil record and molecular phylogeny data
5:30 pm - 5:50 pm	<b>van der Geer</b>	Morphology of articular surfaces can solve a phylogenetic issue: one instead of two ancestors for <i>Candiacervus</i> (Mammalia: Cervoidea)
5:50 pm - 6:10 pm	<b>Doan</b>	Extinction-recolonization events in Crimean red deer populations during Late Pleistocene
6:10 pm - 6:30 pm	<b>Kubo</b>	Geographic variation in body size of Japanese sika deer: Bergmann's rule revisited



## PROGRAMME: THURSDAY, SEPTEMBER 5, 2013

Time	Speaker	Title
8:20 am - 8:30 am	Rössner	Organisational issues
<b>Session 6: Phylogenetic Relationships of Basal Pecora, Palaeomerycidae, Giraffidae, and Moschidae</b>		
8:30 am - 8:50 am	Rössner	On the phylogenetic position of the hornless pecoran <i>Amphimoschus</i> – an example of arising challenges with the incorporation of fossils in extant combined frameworks
8:50 am - 9:10 am	Costeur	The petrosal bone and inner ear of <i>Micromeryx</i> (Moschidae, Miocene)
9:10 am - 9:30 am	Beatty	New Late Miocene North American dromomerycine artiodactyl from the Amazon Basin: implications for interchange dynamics
9:30 am - 9:50 am	Solounias	The interrelationships of the Giraffidae
9:50 am - 10:10 am	Grossmann	New giraffoid fossils from the later Early Miocene Lothidok Formation (West Turkana, Kenya): implications for early giraffoid diversity
10:10 am - 10:30 am	Athanassiou	<i>Mitilanotherium</i> (Artiodactyla: Giraffidae) skull from the Lower Pleistocene locality of Sésklo (SE Thessaly, Greece)
10:30 am - 11:00 am Coffee break		
<b>Session 7: Phylogenetics in Bovidae</b>		
11:00 am - 11:20 am	Bärmann	The Evolution of body size, horn shape and social behaviour in crown Antilopini - an ancestral character state analysis
11:20 am - 11:40 am	Zhang	Neogene Bovidae from China: A review
11:40 am - 12:00 pm	Wolf	The anatomy and paleoecology of the boselaphine <i>Miotragocerus pannoniae</i> from the late Miocene Höwenegg locality (Hegau, Germany)
12:00 pm - 12:20 pm	Kostopoulos	Horn development in living boselaphines and their fossil relatives; implications for phylogenetic reconstructions
12:20 pm - 2:00 pm Lunch break		
2:00 pm - 2:20 pm	Andrés	The phylogenetic relationships of the Mio-Pliocene gazelles of Europe
2:20 pm - 2:40 pm	Fack	Revision of the Ovibovini Gill 1872 (Bovidae, Caprinae) through a cladistic analysis based on morphological characters
2:40 pm - 3:00 pm	Rozzi	Evolutionary patterns in insular fossil bovids
3:00 pm - 3:30 pm Coffee break		
3:30 pm - 3:50 pm	van der Made	Morphological evidence on the origin of <i>Bison</i> and the Cephalophini
3:50 pm - 4:10 pm	Brink	The evolutionary meaning of <i>Raphicerus</i> -like morphology in the dentitions and postcrania of <i>Antidorcas bondi</i> (Antilopini)
4:10 pm - 4:30 pm	Moodley	The possible role of hybridization in adaptive radiations
4:30 pm - 4:50 pm	Lenstra	Geographic differentiation of domestic ruminants
Guided Tour Tierpark Hellabrunn, 6:00 pm-7:30 pm; bus will be leaving 5:30 pm corner Richard-Wagner-Str./Briennerstr.		
Conference Dinner Gasthaus Siebenbrunn 8:00 pm-11:00 pm; bus will be leaving 11:30 pm for City Centre		

## PROGRAMME: FRIDAY, SEPTEMBER 6, 2013

Time	Speaker	Title
8:50 am - 9:00 am	Rössner	Organisational issues
<b>Session 8: Related Aspects and Future</b>		
9:00 am - 9:20 am	Zachos	Taxonomic inflation in ruminants and its bearing on evolutionary biology and conservation
9:20 am - 9:40 am	Alcalde	Evolutionary relationships between environments and locomotion in extant ruminants
9:40 am - 10:00 am	Cantalapiedra	Evolutionary rates for ruminants based on fossils and phylogenies
10:00 am - 10:20 am	Bibi	Toward a phylogeny of ruminants: combining morphology, molecules, fossils, and living taxa
10:20 am - 10:40 am	Hofreiter	Phylogenomics and adaptive genomics of ruminants
<i>10:40 am - 11:00 am Coffee break</i>		
11:00 am - 12:30 pm	Work group meetings	
<i>12:30 pm - 2:00 pm Lunch break</i>		
2:00 pm - 3:00 pm	Work group meetings	
<i>3:00 pm - 3:30 pm Coffee break</i>		
3:30 pm - 5:00 pm	Work group reports & final discussion	
8:00 pm - 0:00 am Farewell Party		



Atrium of the Paläontologisches Museum München with *Gomphotherium* aff. *steinheimense* as centerpiece

## ABSTRACTS

### INVITED REVIEWS

#### Soft tissue biology

Marcus Clauss

*University of Zurich, Switzerland; mclauss@vetclinics.uzh.ch*

There is a basic conflict of interest: Functional anatomists want to study those aspects of soft tissue morphology that are most likely related to their function and hence necessarily, at the same time, most likely subject of convergent evolution. Phylogenists need catalogues of unique characteristics that are best not subject to convergent evolutionary modification (and also not to immediate environmental/dietary/husbandry modification). However, it is exactly the measuring of such latter characters that functional anatomists usually avoid. A typical example of this dichotomy is the volume of a certain organ of the digestive tract (which is a measure of evident functional relevance), as opposed to its detailed shape (which is a measure that does not have functional relevance but might be interesting for phylogenetic studies). A general problem in using measures of functional anatomy is that they commonly describe features that scale with body mass; a difference in function is then often linked to differences as described by the quantitative measure relative to body mass between species. For phylogenetic studies, such quantitative measures may be of limited value unless clear thresholds are evident that can be used to categorize species.

Soft tissue anatomy of ruminants has been comparatively well studied, mainly in the context of adaptations to feeding niches in the frugivore-browser-grazer continuum. It has also been recorded in larger comparative studies on mammals, for example to relate kidney function to habitat. In many more recent studies, comparative analyses have included accounting for the phylogenetic structure of the dataset (using a variety of available, or specially-produced, phylogenetic trees), in order to test for convergence. While convergence, in particular with respect to feeding type, could be demonstrated in various characters, there is usually considerable scatter in the data – part of which could potentially be explained by the phylogenetic history of the species investigated.

Studies that have actually used soft tissue measures to solve phylogenetic questions are rare. Generally, such an approach was followed, rarely in a systematic manner, by 19th-century anatomists, but appears to have been mostly abandoned since. Remarkably, more recent studies using soft tissue anatomy rely on reports from those anatomy pioneers, which makes many claims difficult to trace. Assumed differences in soft tissue anatomy mostly follow known taxonomic boundaries and are not used to decide cases of unsolved phylogenies on a detailed level. For example, gross forestomach anatomy separates tragulids (which lack an omasum) from pecora (which have an omasum); similarly, tragulids lack a carotid rete (brain cooling mechanism) that pecora have. Among pecora, bovini are distinct in terms of exceptionally large omasum size (but

with a convergence in *Ovibos moschatus*), and also in terms of exceptionally low large intestine size and corresponding unformed faeces. Bovini (except for anoas) are also distinct in terms of a macroscopically lobed kidney. Special cases exist, like the additional rumen pillar of *Bubalus* spp., or the edged ruminal papillae of *Rangifer tarandus*. Such singular cases raise the question how valid the practice is to include similar characteristics for one-genus clades, such as Moschidae, as phylogenetic criteria. The probably most often-cited soft tissue character in ruminant phylogeny is the gall-bladder, which is present in tragulids, antilocaprids, moschids and in most bovini (with the notable exception of the Cephalophinae), absent in most cervids, and of irregular appearance in the giraffids. The conflicting evidence in giraffids raises the question how reliable such indicators are, and how many individuals need to be investigated to reach a conclusive answer. Other features mentioned in the literature, such as the number of colic coils, or the presence/absence of an ileo-caecal gland, should be viewed with extreme caution. For example, it has been stated that cervids lack an ileo-caecal gland, but literature reports on findings in both moschids and cervids exist, and the number of colic coils varies distinctively within ruminant families. Various traits of the gastrointestinal tract and its mesenteries, such as the transition from the rumen to the reticulum, or the shape of the last centrifugal colic coil (the ‘supra-Meckelian fold’), have been suggested to be of phylogenetic relevance, but this remains to be investigated systematically. Lung anatomy, which has been used extensively to reconstruct phylogeny in other mammalian lineages, has not been studied in detail in ruminants. Similarly, kidney anatomy probably is an unused source of phylogenetically relevant information. The presence of various skin glands has been used for phylogeny mainly within cervids. The major problem in the use of these characters is that assumptions for a whole family are often made on very sparse species records.

Whether comparative data such as the papillation index, the size of the salivary glands, masseter muscle, forestomach compartments, intestinal lengths, or detailed measures of certain forestomach structures such as reticular crest height, rumen pillar thickness or omasal leaf count or surface, for which comparatively large datasets exist, can actually make a valuable contribution to phylogenetic analyses remains to be tested. The potentially most promising set of existing information is the standardized depiction of the ruminant forestomach by Hofmann, which could allow a categorization of shapes and proportions of different forestomach parts in a large number of species; for example, Cephalophinae have a markedly different forestomach shape than other very small ruminants; in those deer species depicted, Telemetacarpalia differ from Plesiometacarpalia in the number of ruminal blind sacs. For most soft tissue parameters, however, new dissection data will be indispensable.

## Behavioural biology

Pierre Deleporte<sup>1</sup>, Henri Cap<sup>2</sup>

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The use of behavioural characters in phylogenetics has a long and controversial history. Early approaches were clearly behaviour-based phylogenetic inferences, or mere self-contained macro-evolutionary scenarios. Decisive conceptual and methodological improvements in phylogeny inference led to a renewed interest in behavioural phylogenetics. Modern phylogenetics are best construed as a historical science, both for 'phylogeny making' and for 'phylogeny use' in comparative studies. Very contrasting views have emerged regarding the use of behaviour in such approaches. Is behaviour generally too plastic to carry reliable phylogenetic information? Should behavioural traits be used to establish phylogenetic relationships, or just mapped on an already made phylogeny based on supposedly more reliable grounds?

Such problems invite analyses of the requirements for characters to be used in phylogenetics. Both phylogenetic inference and testing of evolutionary scenarios on a phylogeny require reliable homology assessment. If we don't think that characters are likely homologous, we should not force them into a single evolutionary scenario, be it before or after phylogeny construction. The desirable criteria for establishing reliable hypotheses of homology involve special structure, connections, development and functions, as exemplified in the analysis of some behavioural characters of ruminants.

Accurate resolution of phylogenetic relationships requires the use of all relevant evidence, analyzing data sets separately or simultaneously. Ideally, the relative reliability of different kinds of characters needs to be recognized and incorporated in any analysis to effectively combine different topologies produced from separate analyses or to produce topologies based on different types of characters (molecular, morphological, behavioral) analyzed simultaneously. This is particularly important for the integration of behavioural analyses in phylogenetics. Relying on only one kind of character (e.g. molecular) is a popular but arbitrary solution. The notion of relative reliability of characters questions the evolutionary laws of character evolution (if any...), like possible differential probabilities of some character changes, or concerted versus independent evolutionary processes for similar characters in different phylogenetic lineages.

These concepts are illustrated in comparative studies of behaviour in ruminants. We examined stereotyped courtship behaviours in Cervidae. We found that behavioural-based phylogenetic relationships revealed similar relationships to those based on morphological or molecular characters. The primary separation of Cervinae from Capreolinae/Odocoileinae was strongly supported. Our behavioural approach failed to resolve relationships among some clades but these were typically where other approaches show similar problems. This may be indicative of real phylogenetic polytomies due to rapid specific radiation. The question of when to stop phylogenetic investigations in cases of suspected 'true polytomy' is well

worth being treated seriously to avoid possible arbitrary over-resolution of phylogenetic relationships and corresponding macroevolutionary scenarios.

Behavioural characters have some particularities, just as other phenotypic characters, when compared to molecular ones: existing in a range of more or less precisely defined states, being more diverse and hence potentially resistant to saturation than molecular characters, while being less easy to delineate and classify. But they are not so difficult to classify as to be discarded from phylogenetic analysis. A major difficulty consists in documenting the behavioural repertoire of numerous species with sufficient completeness and precision. Exhaustive field studies are very demanding, and the available literature may be of doubtful reliability for some less well-studied species. Ideal investigations should discriminate between species-specific, stable differences and plastic, context-dependent, intraspecific behavioural variants. The potential epigenetic objections are not acceptable as a general argument against any comparative behavioural study, but should be considered as a reason to investigate behavioural plasticity. This often necessitates extensive, specialized field work or experimental work. This has been a major limitation in the use of behavioral characters in phylogenetic studies, much more so than objections based on the quality of behavioural characters per se. Behavioural phylogenetics is not unsound. It is intellectually attractive, but it requires a lot of work to be valid.

Recently, we have seen impressive technical developments in the computing programs for phylogenetic analysis, including the capacity to treat ever enlarging sets of characters and taxa, and the growing possibility of implementing different evolutionary 'models' for different kinds of characters in a simultaneous analysis. In my view, these model-based approaches invite us to concentrate our theoretical reflections on our evolutionary biological assumptions, in an attempt to make them more explicit than implicit. Clearly, phylogenetic inferences cannot be made without implementing some notions of evolutionary processes. What do we know about such evolutionary processes, which allows us to interpret characters in a historical phylogenetic perspective? If our knowledge is limited, we must recognize the extent of our ignorance and remain correspondingly cautious regarding the risk of over-resolution of weakly supported phylogenetic relationships. I do not view this as a reason to renounce these analyses but rather as a way to improve our use and interpretation of all possible phylogenetic information. Given the present mix of success and continued difficulties in ruminant phylogenetics, macroevolutionary studies on this group provide a stimulating field of investigations for pushing forward the very young science of phylogenetics.

### Current taxonomy and diversity of crown ruminants above the species level

Colin P. Groves

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Linnaeus gave us the idea of systematics, with each taxon of

lower rank nested inside one of higher rank; Darwin showed that these taxa are the result of evolution; Hennig demonstrated that, if they are to mean anything, all taxa must represent monophyla. He also proposed that, to bring objectivity into the system, each taxonomic rank should be characterised by a particular time depth, but this is not easy to bring about: genera such as *Drosophila* and *Eucalyptus* have a time-depth comparable to hold orders among mammals! Within restricted groups of organisms, however, time-depths do tend to vary within limits: we will not do too much violence to current usage if we insist that a modern genus must have a time-depth of about 5 million years, i.e. going back at least to the Miocene-Pliocene boundary, and a modern family must have a time-depth of about 25 million years, i.e. going back to the Oligocene-Miocene boundary.

Molecular studies show that living ruminants present examples where the 'traditional' classification (in the main laid down in the mid-20th-century, and all too often still accepted a standard even today) violates Hennigian principles. Among Bovidae, the genera *Bos*, *Tragelaphus*, *Gazella* and *Hemitragus* are paraphyletic, and so, among Cervidae, are the genera *Cervus* and *Mazama*. I will discuss what we can do about these, and will then present, with commentary, a classification of living ruminants.

### **Rocks versus clocks or rocks and clocks: how can we solve the riddle of ruminant relationships?**

Lisa Helbig<sup>1</sup>, Samantha Price<sup>2</sup>, Olaf R.P. Bininda-Emonds<sup>1</sup>

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Much has been written about the conflict between molecular and morphological data in phylogenetic systematics, both in terms of the evolutionary relationships they indicate as well as the divergence-time estimates they provide. A cogent example on both counts is provided by the placental mammals and, closer to the theme of this conference, the placement of whales (Cetacea) relative to the even-toed ungulates ('Artiodactyla'). Even though it is now widely accepted that the former taxon now nests within the latter (together comprising Cetartiodactyla), a conflict still remains insofar as molecular estimates of the timing of the cetacean radiation vastly underestimate those provided by the fossil record. Another phylogenetic problem area within Cetartiodactyla is Ruminantia, where higher-level relationships within the group continue to be controversial beyond a sister-group relationship between Tragulidae and the remaining families. Using a supertree framework to explicitly visualize and resolve potential 'gene-tree heterogeneity' (i.e., conflicts between individual data sets), we sought to determine the root causes of this disagreement. Is there a fundamental conflict between molecular and morphological data or perhaps also within each of these data sources as well? By estimating and including divergence-time information in our analyses, we also examine the possibility of a basal adaptive radiation within the group, an evolutionary scenario that is known to confound phylogenetic analysis. Finally, we also examine for

congruence (or lack thereof) between fossil-based divergence-date estimates and those derived from molecular data. Together, our 'gene-tree' focussed approach provides much greater resolution regarding the conflict within Ruminantia and will help point the way towards resolving it in the future.

### **Ruminant macroevolution: a phylogenetic approach based on extant faunas**

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Combination of morphological, ethological and molecular information allowed for the reconstruction of the first complete estimate of the phylogenetic relationships among all extant ruminants. Such composite tree was derived by applying matrix representation using parsimony to previous partial estimates, and was remarkably well resolved. The ages of over 80% of the clades in the tree were estimated from information in the literature (including both fossil and molecular data); all the other nodes were calibrated indirectly in order to allow further macroevolutionary studies. This supertree has become a useful framework for comparative and evolutionary biologists interested in studies involving ruminants, including works on ecology, sexual selection, sociobiology, parasitology, domestication, fossil preservation, etc. As an example, here we present some studies based on the environmental and geographical context of ruminant macroevolution.

First, we tested some of the expectations derived from the resource-use hypothesis, which predicts that specialist species have higher speciation and extinction rates than generalists because they are more susceptible to environmental changes and vicariance. We used the biomic specialization index (BSI) of each species, which is based on its distribution within different biomes, and ran 10000 Monte Carlo simulations of our data in order to get a null distribution of BSI values against which to contrast the observed data. Additionally, we drew on the supertree of the ruminants and a phylogenetic likelihood-based method (QuaSSE) for testing whether the degree of biomic specialization affects speciation rates in ruminant lineages. Our results are consistent with the predictions of the resource-use hypothesis, which foretells a higher speciation rate of lineages restricted to a single biome (BSI = 1) and higher frequency of specialist species in biomes that underwent high degree of contraction and fragmentation during climatic cycles. Nevertheless, bovids and deer present differential specialization across biomes, which might be the result of divergent physiological constraints as well as a different biogeographic and evolutionary history.

We also explored the role of global abiotic change and ecological flexibility as two major factors influencing rates of speciation across clades. We connected past climate to changes in diet and diversification dynamics of ruminant mammals. Using multi-state speciation and extinction (MuSSE) models, we examined the most likely scenarios for evolutionary transitions among diets, and ask whether ruminant lineages with

different feeding styles (browsing, grazing and mixed feeding) underwent differential rates of diversification concomitant with global temperature change. The best model of trait change had transitions from browsers to grazers via mixed feeding, with appreciable rates of transition to and from grazing and mixed feeding. Diversification rates in mixed-feeder and grazer lineages tracked the paleotemperature curve, exhibiting higher rates during thermal maximums. The origination of mixed diet and grazing states triggered two adaptive radiations, during the Oligocene-Miocene transition and the Middle-to-Late Miocene. These results highlight the importance of dietary innovations in the success of ruminants during the Neogene. Finally, the geographical context appears as another important factor for the development of macroevolutionary processes. In this sense, phylogenetic community structure metrics were applied to faunal assemblages on four different hierarchical levels, which helped us to understand how macroecological and macroevolutionary processes shape assemblages at large geographical scales, providing a new insight into ruminant biogeography and evolution. Phylogenetic relatedness indexes were calculated for 59 ruminant assemblages on the landscape scale and their respective climatic dominions (continuous patches of biomes). This was done using both the global species pool and the biogeographic realms's species pool to build null observations. Non-random patterns were also tested for biogeographic realms within the global ruminant species pool. Our results suggest that the distribution of ruminant faunas is mainly limited to the boundaries of the respective biogeographic realm. Nonetheless, the diversification of some clades was found to be restricted to some extremely arid climatic dominions in the Sahara and Arabic regions. The random pattern exhibited by other extreme climatic dominions may reflect phylogenetically heterogeneous filling of less biome-specialized lineages in the dominions outside Africa.

These studies highlight the importance of an exhaustive phylogenetic information for the development of macroevolutionary studies. Due to the long tradition in phylogenetic works with ruminants, this group may be taken as a model for the study of the interactions between ecology and evolution. The next step in this field of study should be the integration of information from extinct species within the general context of the ruminant phylogeny. This new task must integrate all the known species in order to represent a complete view of the high ecological and evolutionary variability within ruminants. This will allow a deeper knowledge of the timing and causes of biotic events in this group.

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## Cytogenetics

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During species evolution the most important mutations have accumulated at the chromosome level. Thus chromosomes are interesting material to study the phylogenesis of species. The suborder Ruminantia belongs to the Cetartiodactyla order which groups 332 species. It consists of six families: Tragulidae, Antilocapridae, Giraffidae, Moschidae, Cervidae, and Bovidae, the latter five families being grouped into the infra-order Pecora and called 'true ruminants'. Comparison among various species using chromosome banding techniques, chromosome painting probes and detailed comparative FISH-mapping (gene order) allows prior chromosome rearrangements to be clarified, thereby differentiating ruminants from Cetartiodactyla and the various family species among this important sub-order. In particular, the pecoran ancestral karyotype (PAK) appears relatively similar to the more ancient ruminant ancestral karyotype (RAK). Indeed, PAK differs from RAK by seven fissions, two fusions and 12 inversions.

The Bovidae are the main family of ruminants not only for the number (approximately 250) but also because some of them are economically important and have an almost worldwide distribution, such as the cattle, zebu, water buffalo, sheep and goat. In bovids while the diploid number differs from 38 to 60, the fundamental number (FN) (number of chromosome arms) differs only between 58 to 62 (with only three exceptions) due to the widespread use, at the autosome level, of centric fusion translocations which have reduced the diploid number but not the chromosome arms. This hypothesis was later confirmed by using both chromosome banding and FISH-mapping techniques which not only revealed a high degree of conserved chromosome banding patterns but also the same gene order with only one exception: a proximal region moved from 'Bovinae' chromosome 9 to 'Caprinae' chromosome 14 by a simple translocation event (and inversion), as demonstrated by both linkage map and FISH-mapping techniques.

Contrasting with the autosomes, sex chromosomes have shared a more complex evolution. In particular, X-chromosomes of all bovids can be grouped into three different types: the submetacentric cattle X, the acrocentric eland or water buffalo type, and the acrocentric caprine type (with visible p-arms). The different shape and size is due to the different position of the centromeres (which moved along Xs by centromere transposition or centromere repositioning) and constitutive heterochromatin (C-banding) variations, respectively. However while the Bovinae type (i.e., cattle, water buffalo, eland) have conserved the same banding pattern and gene order, when comparing the Bovinae X with Caprinae X at least four transpositions (one of which involves the centromeres) occurred during the karyotype evolution of bovids, differentiating noticeably the Xs (and gene order) of these two subfamilies. Also the Y chromosome differs in shape (due to inversion and centromere transposition) and size (due to HC-variation). However, when comparing the chromosomes of Bovinae species with those of the remaining bovid subfamilies, it was

possible to conclude that ‘Bovinae’ subfamily is ancestral to the remaining ones. Indeed, chromosomes 9 and 14, as well as the X-Bovinae type, are only found in the Bovinae subfamily, the remaining ones showing both ‘Caprinae’ chromosome 9 and 14, as well as the ‘Caprinae’ X-type. This hypothesis is also confirmed when looking at other ruminants. Indeed, Bovinae chromosomes 9, 14 and X have been conserved with the same banding patterns also in the Giraffidae, Antilocapridae and Cervidae families of the Cetartiodactyla order and conserved the synteny with human chromosomes 6 and 13, respectively. Thus, Bovidae Ancestral Karyotype (BAK) should have 60 chromosomes all acrocentrics with autosomes similar to those of cattle and sex chromosomes similar to those of river buffalo. Thus, Bovinae subfamily is the only one with a karyotype very close to that of BAK, the remaining ones differing both at the autosome (i.e. chromosomes 9 and 14) and sex chromosome (i.e. X-chromosome) levels from BAK, although clear data (banded karyotypes) are available only in the subfamilies Caprinae, Hippotraginae, Reduncinae, Alcelaphinae, Antilopinae and Cephalophinae. This agrees with the mitochondrial tree reported recently with two different main branches in Bovidae family: Bovinae and Antilopinae, the latter including Aepycerotini, Neotragini, Antilopini, Reduncini, Cephalophini, Alcelaphini, Hippotragini and Caprini.

Other interesting chromosome sites which evolved partially independently of chromosome arm conservation are the nucleolus organizer regions (NORs). Indeed, NOR-chromosomes differ in bovids not only in number (from 3 to 6) but also in their position, size and activity.

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### Skeletodental morphology

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Ruminants have traditionally been classified by a combination of plesiomorphic and homoplastic features. Cranial appendages were thought to unite pecorans, hornless forms were allied with the tragulids. The pecoran families were primarily defined by tooth crown height (e.g. cervids and giraffids brachydont, bovids and antilocaprids hypsodont), presence of the lateral digits (retained in cervids, lost in the others), and the form of the cranial appendages (e.g., presumed ossicones uniting bovids and giraffids), while basicranial features were used to separate them from other artiodactyls. In combination these features can be used to characterize the families, but while the form of cranial appendages may be diagnostic at the family level, neither tooth crown height nor the condition of the side toes can be used to define any of the extant families, to unite them in any combination, nor to assign relationships of extinct families. Both the Paleogene traguloid radiation and the Neogene pecoran radiation are plagued with parallelism in cranial and postcranial anatomy, relating to parallel changes in ecomorphology in the various

families (acquisition of a more fibrous diet and the development of more cursorial forms of locomotion).

In evaluating morphological features that may be useful in ruminant phylogeny, two important issues must be considered: possible functional value and variability. The morphological features used to unite the Ruminantia are fusion of the cuboid and navicular, the loss of the upper incisors, and an incisiform lower canine. Only the first is diagnostic: while it may indeed have a functional component, it is invariable within the suborder. Small upper incisors and less modified lower canines are retained in a diversity of early traguloids, and protoceratids may have acquired these derived features convergently with ruminants. Postcranial features have been proposed to define the Pecora, but many (e.g. the parallel-sided astragalus, a clearly functional feature) can be seen to have been evolved in parallel within more derived members of traguloid lineages. Of the more recently proposed synapomorphies, both cranial (e.g., a double lacrimal orifice) and postcranial (e.g., a closed metatarsal gully) have been shown to be highly variable both within and among taxa. Certain dental features may have a limited distribution, (e.g. the bilobed lower canine of giraffoids), and thus be useful for assigning extinct taxa to an extant lineage. However, others (an entostyle or a *Palaeomeryx*-fold) may be characteristic of brachydont forms, but are lost with the simplification of dental morphology in hypsodont members of the same lineage. Likewise, various cranial features (the posterior orbit, the length of the face or the basicranium) can be shown to be correlated with increasing hypsodonty, and cannot be treated as independent characters.

Basicranial characters have a long history of use in studies of artiodactyls. Numerous characters were used to delineate various groups, based primarily on the character states found among extant taxa (e.g. exposure of the mastoid), but fossil taxa preserve combinations of these characters which confound the simpler scenarios based on living taxa. The characters that have been used include the depth of the subarcuate fossa, shape and position of exposure of the mastoid, position and shape of the mastoid foramen, foramen ovale, postglenoid foramen, supraglenoid foramen, suprêmeatal fissure, the shape and location of the tympanohyal vagina, and the absence of the stapedia and promontory arteries. Many of these features appear to be useful in diagnosing clades within Ruminantia, but they are not necessarily exclusive to ruminants. The shallow subarcuate fossa and loss of the stapedia artery have been used as pecoran synapomorphies, but the distribution of the characters across the artiodactyls is more complex. A shallow subarcuate fossa is known among pecorans, except *Dremotherium*, and traguloids, hypetragulids and leptomerycids show the primitive deep fossa condition. However, suoids also show a shallow subarcuate fossa, presumably convergently, and so do the protoceratids. Loss of the stapedia artery in most pecorans has generally been inferred by the lack of a promontorial groove on the petrosal. However, transpromontorial grooves have been observed in *Bos*, *Antilocapra* and *Moschus*, and such grooves may also reflect the course of nerves, so the interpretation of the character is challenging and requires more complete study through dissection. Thus, although basicranial characters appear to be promising characters for ruminant phylogeny, detailed work on variability of these features across the extant and extinct taxa is needed to better assess their utility.



These problems might suggest that morphology be abandoned in favour of molecular data for phylogenetic studies. However, while molecular features may be used to establish a phylogeny of the living forms, the affinities of the extinct families remain elusive, especially the large diversity of Paleogene hornless forms (both traguloids and pecorans). Eighty-nine percent of described artiodactyl genera are extinct, which suggests that even a complete sampling of extant ruminants for both molecular and morphological characters would be woefully inadequate to resolve a complete phylogeny. Extinct taxa can play a critical role in establishing the phylogeny of extant taxa: the extensive fossil record of the Antilocapridae can be used to understand character polarities and break up long branches, whereas molecular information from the single extant species without information from the fossil forms may result in anomalous placement in a phylogeny. It becomes a challenge to determine anatomical features that might reflect phylogeny rather than function (and this is of course where basicranial features may play an important role when their distribution and variability has been more fully assessed).

### Developmental genetics

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Whole genome sequencing studies across a wide range of mammalian species has indicated that the highest divergence rates are associated with genes involved in reproduction, especially ones linked to placental function, and in providing immunity. Although a well developed placenta, with young born at an advanced stage of development, are hallmarks of eutherians, the placenta is arguably the most diverse of mammalian organs, with differences extending from gross morphology to the extent to which trophoblast penetrates the uterine endometrium and interacts with the maternal blood supply. I describe several genetic changes that have accompanied the evolution of the diffuse, epitheliochorial type of placentation encountered in all Cetartiodactyla, although I focus primarily on the more specialized cotyledonary placentas of pecoran species. Despite the fact that the uterine epithelium remains intact during pregnancies of these species, it is now generally accepted that the epitheliochorial state is not primitive, but a derived condition that is highly efficient and provides precocial young born after a long pregnancy. Although a non-invasive state may endow some major advantages, such as minimizing damage to and subsequent scarring of the maternal uterine wall, minimizing pathogen trafficking, and affording protection against maternal immune attack, there are also potential disadvantages that must be overcome in not having direct access to maternal blood. For example, adaptations with regard to nutrient acquisition and allocation, and fetal-maternal signaling must have occurred. I describe a series of large gene families, including those encoding growth hormone and prolactin-related proteins, the pregnancy-associated glycoproteins (PAG), the trophoblast Kunitz-domain proteins (TKDR), the syncytins, and type 1 interferons (IFN), that appear to have evolved unusually rapid-

ly in the lineage leading to even-toed ungulates and whales and have likely contributed to the success of the epitheliochorial state. I close with a discussion of the adaptive pressures that might have driven the remarkable diversity of placental genetic change yet preserved the main essentials of placental function. This project was supported by Agriculture and Food Research Initiative Competitive Grant no. 2011-67015-20070 from the USDA National Institute of Food and Agriculture.

### Genomics

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The pecorans (higher ruminants) are believed to have rapidly speciated in the Mid-Eocene, resulting in five distinct extant families: Antilocapridae, Giraffidae, Moschidae, Cervidae, and Bovidae. Due to the rapid radiation, the pecoran phylogeny has proven difficult to resolve, and 11 of the 15 possible rooted phylogenies describing ancestral relationships among the Antilocapridae, Giraffidae, Cervidae, and Bovidae have each been argued as representations of the true phylogeny. We have demonstrated that a genome-wide single nucleotide polymorphism (SNP) genotyping platform designed for one species can be used to genotype ancient DNA from an extinct species and DNA from species diverged up to 29 million years ago and that the produced genotypes can be used to resolve the phylogeny for this rapidly radiated infraorder. We used a high-throughput assay with 54,693 SNP loci developed for *Bos taurus taurus* to rapidly genotype 678 individuals representing 61 pecoran species. We produced a highly resolved phylogeny for this diverse group based upon 40,843 genome-wide SNP, which represents five times as many informative characters as have previously been analysed. We also established a method to amplify and screen genomic information from extinct species, and placed *Bison priscus* within the Bovidae. Using genotypes from 47,282 autosomal SNP markers, we evaluated the population structure of 134 domesticated bovid breeds and facilitate inferences concerning the history of domestication and breed formation. Patterns of geographic dispersal resulting from cattle exportation are recognizable in phylograms and phylogenetic networks calculated from FST values. Hybridization occurring after exportation is evident from principal component and admixture analysis. We also identify a cline of *Bos taurus taurus*/*Bos taurus indicus* hybridization in Asia. Iberian, Anatolian, Italian, and East Asian cattle were all found to have introgression from African taurine. Additionally, we demonstrate that three 400 year old teeth found in a Spanish well in St. Augustine, Florida come from an animal with Iberian ancestry and that was closely related to American Criollo breeds. Exportation, admixture, and selection have all been important forces in shaping bovine genomic variation.

## CURRENT RESEARCH PRESENTATIONS

### New insights into tragulid phylogeny of Europe: *Dorcatherium nauti* from the latest Middle Miocene of Austria

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While modern Tragulidae are restricted to Africa and Asia, the fossil record of the family shows a much wider distribution. Exclusively represented by the genus *Dorcatherium* the family is a frequent element in Miocene faunas from Europe. It comprises Early to Middle Miocene species (*Dorcatherium crassum*, *D. vindebonense*, *D. peneckeï* and *D. guntianum*) and Late Miocene species (*D. nauti*, *D. puyhauberti*, and *D. jourdani*). Although *D. nauti* is generally considered a typical Late Miocene species, rare findings prove its existence also for the late Middle Miocene. One of these oldest records is *D. nauti* from the locality Gratkorn (Austria), a surprisingly rich Central European terrestrial vertebrate fauna of the late Middle Miocene (12.2–12.0 Ma). It provides further support for an already wide distribution of the species from Spain (Abocador de Can Mata) to Poland (Przeworno) at this time. The origin and phylogenetic relationships of the species within European *Dorcatherium* is not understood yet due to scattered and incomplete findings. *D. nauti* is abundant at the locality of Gratkorn and provides more detailed information on the early representatives of the species, in contrast to the sites of Abocador de Can Mata and Przeworno, where it is a rare element. It shows morphometric and morphologic accordance with the type material from Eppelsheim (e.g. selenodont teeth, bicuspid p2) and the rich Late Miocene site Atzelsdorf (Austria). Based on distinct morphological differences (e.g. tricuspid p2 in *D. crassum*) the often assumed hypothesis of *D. nauti* deriving from the similar-sized bunoselenodont *D. crassum* is not supported, but *D. nauti* must be considered part of a selenodont lineage. As *D. nauti* shares with the other selenodont European species, *D. guntianum*, profound dental and skeletal characters, like e.g. the bicuspid p2 and unfused tibia and malleolar, a close phylogenetic relation of both can be supposed. Now proven occurrences of *D. nauti* in the late Middle Miocene close the long time reported gap in the late Middle Miocene between both species. According to the described morphological differences two European *Dorcatherium* lineages (selenodont including *D. guntianum*, *D. nauti*, *D. puyhauberti*, and *D. jourdani*; bunoselenodont including *D. crassum*, *D. vindebonense* and *D. peneckeï*) have often been assumed and are recently strengthened by newly described findings, even pointing to a diphyletic origin of European species. With the early representatives of *D. nauti* from Gratkorn more extensive evidence has been found for the selenodont lineage.

### Evolutionary relationships between environments and locomotion in extant ruminants

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Among the most important aspects conditioning ruminant lifestyle and habitat selection are climate, substrate or locomotion. The proper knowledge of how these variables relate among them within a phylogenetic context is essential to understand the ecology of this group. We encoded these aspects in extant species for using them as qualitative variables in comparative analyses. Eco- and ethological categories were grouped under criteria of bioclimatic conditions, vegetation, substrate, body size and types of locomotion displayed under stress. To determine the associations established among all these variables, we carried out both non-phylogenetic and phylogenetic comparative analyses. Firstly, we checked the relations by means of a non-parametric test ( $\chi^2$ ). Secondly, we tested for correlated character evolution using Pagel's maximum likelihood correlation method. The most interesting positive associations, common for both analyses, are those relating locomotor categories: gallop and stotting (type I), zigzagging and bounding gallop (type II), and climbing (type III). Additionally, gallop is tightly associated with open woodlands and grasslands. Other positive associations for both tests are: (1) forested biomes-dense forests; (2) snowy substrates-steppe; and (3) steep reliefs-taiga. Results regarding exclusively to the  $\chi^2$  analyses show that the locomotion is closely related to the environment. Locomotion type I appears strongly associated with species living in open areas, such as wooded plains and sandy and stony substrates, as those present in savannahs, deserts or Mediterranean environments. Type II is, by contrast, correlated to dense forests, like tropical rain/seasonal forests. Our results also show that gallop is the preferred type of locomotion of large size ruminants, whereas the small ones tend to move in a zigzagging style. The phylogenetic analyses reveal that type I very likely evolved in basal pecorans, being wide spread among giraffids, bovids — except cephalophines — and cervids — except muntiacines. Positive associations have been found between gallop and wetlands and scrublands, and stotting is associated with clear substrates. Type II was estimated as basal for the crown ruminants and featured in moschids, besides very common and evenly distributed among cervid groups. This type II evolved secondarily in lineages leading to kudus, wildebeests, dikdikis, cephalophines, reuduncines and neotragines. Zigzagging has also been related to wetlands and open woodlands. Type III (climbing) evolved during the Middle-Late Miocene and is mainly restricted to caprines. Results among environmental variables show tight relationships between wetlands and bushy areas, stony substrates and open woodland/scrublands, and tropical deciduous forests and grasslands. All these results are congruent with the observations in nature and, for the first time, statistically tested in the complete set of extant species of the suborder Ruminantia.

## The phylogenetic relationships of the Mio-Pliocene gazelles of Europe

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The gazelles are a diverse and widespread antilopine bovid group living in a variety of habitats like savannahs, deserts, mountains and hilly areas in North Africa and Asia. Their taxonomy and phylogenetic relationships are far from being resolved, but the currently recognised genera - *Gazella*, *Eudorcas* and *Nanger* - and the monophyly of the group are recently supported by both morphological and molecular phylogenies. Despite *Gazella* s.l. has been recorded in Middle Miocene deposits of Kenya, gazelles do not form a common component in African faunas until the Pliocene. By contrast, gazelles are common in Eurasia from the Late Miocene onward. In Europe, *Gazella* s.l. was represented by several species from the Late Miocene to the Lower Pleistocene, but the relationships with the living gazelles were never tested in a phylogenetic analysis.

We performed a cladistic analysis based on cranial, horn and teeth characters to explore the phylogenetic relationships of the European fossil gazelles with the extant antilopines. The Plio-Pleistocene *G. borbonica*, by far the best-known species, was the only one clearly related to living gazelles. A close relationship between *G. borbonica* and living *G. spekei* was detected in this study, but this result needs to be tested by further analyses as the relationships between living gazelles are not fully resolved by the data. The poorly known Pliocene *G. baturra* is also resolved as a close relative of the living gazelles but this result was not robust probably because of missing data. However, the Pliocene *G. soriae* and the Late Miocene *G. deperdita* are included within Antilopini but are not closely related to the living gazelles. Finally, the Greco-Iranian Late Miocene gazelles (*G. capricornis*, *G. dorcadoides* and *G. lydekkeri*) appear to belong to the stem-group of Antilopini. This result suggests they form part of an early radiation of antilopines. As a consequence, these Miocene gazelles should be removed from the genus *Gazella*.

## Dental eruption in ruminants and other mammals

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In contrast to the continuously erupting teeth commonly found in diapsids, actinopt, amphibians, and other vertebrates, mammals typically have only two generations of teeth. Generally speaking, mammals exhibit deciduous premolars, canines, and incisors which are replaced from below by their permanent successors, and such replacement is usually completed by sexual maturity and the attainment of adult body size. However, many variations occur on this theme. For example,

many soricids, talpids, cetaceans, and pinnipeds lack a deciduous generation. Ruminants, on the other hand, have been characterized as possessing three generations of teeth based on the timing of their eruption during ontogeny (but not on the number of teeth per locus). Other mammals (e.g., crown proboscideans) replace teeth horizontally (i.e., from behind, not below), and while not as developed as in elephants, certain species of ruminants also exhibit some degree of horizontal tooth replacement. In addition, the eruption sequence may vary across mammals; for example, most non-ruminant artiodactyls erupt posterior premolars before m3, whereas ruminants typically erupt m3 prior to posterior premolars. Finally, eruption may be 'late', i.e., takes place after the attainment of adult body size. This has been described as a shared, derived feature of endemic African mammals, but it also occurs across artiodactyls, including ruminants. Delaying the eruption of the permanent dentition may serve to maximize the amount of time during which a given animal is capable of efficient mastication. It also may result from phylogenetic, developmental, and/or physiological factors, and not be of immediate, adaptive relevance for a given species.

Here, I survey how patterns of dental eruption are distributed across mammals, including a diverse sample of ruminant artiodactyls, and attempt to correlate such patterns with potential phylogenetic, dietary, and physiological factors. In particular, I investigate the extent to which diet, physiology, and phylogeny compete to best explain differences in patterns of mammalian dental eruption.

## A *Mitilanotherium* (Artiodactyla: Giraffidae) skull from the Lower Pleistocene locality of Sésklo (SE Thessaly, Greece)

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Despite their taxonomic diversity and wide geographical range during the Miocene, the family Giraffidae experienced a dramatic species loss at the beginning of the Pliocene. In Western Eurasia only one genus, *Mitilanotherium* Samson & Radulesco, 1966, seems to have survived till the Early Pleistocene, as indicated by the close morphological and metrical resemblance among the scarcely available giraffid samples. Due to its rarity, the morphology of *Mitilanotherium* is not known in detail. A recently discovered skull, excavated in 2009 at the Lower Pleistocene (MN17) locality of Sésklo and described here, provides a more complete picture of the genus' cranial characters.

The specimen is fairly complete, lacking its rostral part (anterior of the premolars) and its zygomatic arches. It is long and rather low, being extremely wide at the level of the orbits. The ossicones are long and widely separated, with pointed apices uncovered by skin during life; they emerge supraorbitally, initially inclined rostrally and then curving mediocaudally. The cranial roof is nearly flat caudally, but becomes markedly concave between the ossicone bases. The dentition is brachyodont with moderately rugose enamel, prominent styles and weak lingual cinguli in the molars.

Compared to already known Eurasian fossil giraffids, *Mitilanotherium* is morphologically very similar to *Palaeotragus*, though somewhat larger, and it is considered as a close relative of it.

### Fossil taxa and molecular clock calibrations in Cervidae phylogeny: the challenge of the Middle-Late Miocene muntjac-like deer

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Recent advances in molecular clock procedures provide further opportunity to infer time-scales of organismal evolution. Such calibrations use paleontological data, assuming that the age of the oldest fossil attributed to a node is a good approximation of its minimum age. However, dates produced from such procedures are frequently incongruent with those estimated by the fossil record itself. In Cervidae phylogeny, this discrepancy is especially striking because the fossil record of cervids is relatively continuous and well-documented, thereby providing a good idea of both their evolutionary history and the origin of crown cervids. Molecular clock calibrations may produce highly spurious dates if i) fossil taxa are not adequately selected or their phylogenetic position is not precisely known, ii) the estimated ages of fossil taxa are wrong, iii) the selected nodes are very scarce, and iv) the distinction between dating crown and total clades is neglected. All these problems are observed in the molecular clock calibrations of the cervid phylogenies proposed to date. Only five taxa (*Procervulus*, *Cervavitus*, *Muntiacus leilaoensis*, *Pavlodaria* and *Eocoileus*) are recurrently used to calibrate the reference Cervidae, Cervinae, Cervini, Muntiacini (=Muntiacinae) and Rangiferini (=Odocoileini) nodes. Here we discuss the age of these taxa and their suitability for dating these nodes.

The node Muntiacini (=Muntiacinae) is particularly arguable since muntjac-like deer are common from the Middle Miocene onwards. Their taxonomic assignment to Muntiacini challenges the recent molecular dates of the origin of crown Cervidae around the Middle/Late Miocene boundary. Recent findings of Middle and Late Miocene cranial and postcranial remains of Spanish muntjac-like deer provide further evidence for the discussion of the primitive vs. derived condition of characters (e.g., lateral-postorbital position and backwards orientation of long pedicles, simple antlers and sabre-toothed upper canines, as well as their occurrence in tropical forested habitats) in extant muntjacs and tufted deer. Our study evidences that the phylogenetic relationships of Muntiacini, and, as a result, the evolutionary history of all crown cervids, require a more thorough analysis of fossil muntjac-like taxa.

### The evolution of body size, horn shape and social behaviour in crown Antilopini - an ancestral character state analysis

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The earliest known bovids, commonly placed in the genus *Eotragus*, are small species with short straight horns located above the orbits. Among living bovids there are several species that show a similar horn morphology. These dwarf antelopes were historically united in the group 'Neotragini', which is now known to be a polyphyletic assemblage, as the species of the genera *Ourebia*, *Raphicerus*, *Dorcatragus*, *Madoqua*, *Oreotragus*, and *Neotragus* are scattered across the bovid phylogeny. Nevertheless, their shared similarities, not only in body size and horn length but also in their social organization, are usually interpreted to represent shared plesiomorphic traits that were present in the most recent common ancestor of Antilopinae, a group comprising all bovids that are more closely related to sheep and goats than to cows.

This long-held hypothesis about bovid evolution can be tested using ancestral states reconstruction. The method builds on the fact that the evolutionary process creates a pattern of character change along the branches of a phylogeny. The pattern is preserved in the variation of characters among the tips of the phylogeny. Therefore it is sufficient to know the variation at the tips and the phylogeny for inferring the evolutionary process and for estimating character states at ancestral nodes.

In this study, I reconstruct the ancestral character states of body mass, horn length, territoriality, and female group size for basal nodes within Antilopini, including the most recent common ancestor of this group. Antilopini comprises gazelles and their allies, and includes most of the dwarf antelopes, i.e. the genera *Ourebia*, *Raphicerus*, *Dorcatragus*, and *Madoqua*. The phylogenetic basis of the analysis is a set of 2000 trees from a combined Bayesian analysis of molecular and morphological data. This allows for taking phylogenetic uncertainty into account, as neither the relationships of dwarf antelopes with other species in Antilopini nor the root of this taxon are currently known with confidence. The results show that while the social organization of the dwarf antelopes should be regarded as primitive, the small body size and short horns of *Ourebia*, *Raphicerus*, *Dorcatragus*, and *Madoqua* are most likely derived traits. The habitus of the ancestor of Antilopini was probably very similar to modern gazelles, consistent with the placement of the earliest fossil Antilopini in the genus *Gazella*.

## The fossil tragulids of the Siwalik Formations of Southern Asia

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Tragulids are an important component of the Late Oligocene through Pliocene Siwalik faunas of the Indian Subcontinent. Large collections of Siwalik fossils have recently been made by collaborative projects from Harvard University, the University of Arizona, the Geological Survey of Pakistan, and the Pakistan Museum of Natural History. Those collections as well as material in the Yale Peabody Museum and American Museum of Natural History, together comprise over 3700 specimens, including dental, cranial, and post-cranial elements. Most of this fossil material is from northern Pakistan and southwestern Punjab and comes from 451 sites in well-dated stratigraphic sections. The oldest specimens are from the Late Oligocene Chitarwata Formation and are around 26 to 26.5 Ma, while the youngest are in the Pliocene Tatrot Formation and are 3.3 Ma.

The fossil tragulids of the Siwaliks differ from the extant species in a number of ways. Importantly, they have a much wider range of body sizes. The smallest species is estimated to be just over 1 kg, while at least four species are over 25 kg, with the largest specimen estimated to be nearly 76 kg. Consequently the small species overlap with the smallest species of *Tragulus*, while the large species are much larger than individuals of *Hyemoschus* and approach medium size of bovids and cervids. Siwalik tragulids are also species rich, with typically at least four co-occurring species. This contrasts to extant tragulids, but compares to the five to seven co-occurring species of bovids. Finally, Siwalik tragulids are relatively common in the fossil collections, which is presumably related to their relative abundance in the living parent communities. Tragulids are most abundant between 18 and 10 Ma, making up nearly 40% of the fossil ruminants in the 1 to 200 kg body size range. Subsequently, however, their relative abundance is much diminished, being only 19% between 10 and 8 Ma and 7% between 8 and 6 Ma.

The history of the southern Asian tragulids can be related to documented environmental changes. The Siwaliks formed in a large fluvial system, with the depositional settings most productive of fossils being the lithologically mixed fills of the smaller floodplain channels. Many paleosols are present and although some may have formed under waterlogged, grassy vegetation the low relief floodplains were mostly forested or wooded with abundant cover and fruit. Isotopic analyses of tooth enamel and soil carbonates indicate the vegetation was dominated by C3 plants until ca 10 - 9 Ma, after which there were significant changes in precipitation with a shift to a more seasonally dry monsoon climate. The carbon isotope record shows that at ca. 8 Ma there was considerable C4 grass on the floodplains and by ca. 7 Ma extensive C4 grasslands. At the same time predominantly C3 communities became less common, which undoubtedly accounts for the change in the relative abundance of tragulids.

## Histological insights into the deep homology of ruminant cranial appendages

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The interrelationships of ruminant families are partly problematic because of two extant families, the Antilocapridae and the Giraffidae. Molecular phylogenies find that these two families are strongly supported as sister groups or at least nested together in a polytomy with a third clade of all remaining ruminants. Part of the problem with sorting out these relationships using the fossil record is that all of these groups have cranial appendages in their earliest recognized members, and it is unclear where the homology in these cranial appendages lies. Likewise, there are many extinct clades of ruminants that appear to fit in between these two modern clades when fossils are included in analyses.

To better assess the homology relationships between these tissues, we sectioned cranial appendages from *Merycodus*, a common Early Miocene merycodontine, a modern *Okapia*, and a *Kobus ellispriymnus*. *Merycodus* has an extension of the frontal that forms the horn shaft, and an external ossification in the form of a ring of porous bone that surrounds the shaft near its base. *Okapia* has a very small extension of the frontal that is capped by an external ossification made of porous bone (what is typically called the ossicone). *Kobus ellispriymnus* has an extension of the frontal that is long, and is surrounded by a thin separate layer of porous bone on which the keratinized sheath of horn is attached. We propose that the separate ring of porous bone in *Merycodus*, the ossicone in *Okapia* (known thus far only from the apex), and the external layer of porous bone in the *Kobus ellispriymnus* are homologous tissues, just as the extensions of the frontal are in each taxon. The extensions of the frontal can typically be identified by having a smooth external texture. Perhaps if all ruminant cranial appendage characters were revisited with the homology of these tissues in mind, a better understanding of character equivalents among the families could be achieved.

## Toward a phylogeny of ruminants: combining morphology, molecules, fossils, and living taxa

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Genomic analyses have revolutionized phylogenetic systematics, providing a powerful tool for the reconstruction of highly resolved phylogenies of extant species. A central challenge of phylogenetics now is the incorporation of ever increasing amounts of genomic information with organism-level (phenomic, e.g. morphological, behavioral) traits, and the simultaneous consideration of both extant and fossil taxa.

Ruminantia is a clade that exemplifies aspects of the progress and challenges facing the synthesis of genomic and organ-

mal approaches. Genomic analyses have helped resolve many ambiguous and controversial parts of the ruminant tree, but have also introduced competing hypotheses based on different genetic histories (e.g. mitochondrial vs. nuclear) and conflicts between genetic and morphological approaches. I provide examples from my work on Bovidae, the largest family of ruminants, to illustrate how fossil taxa may be incorporated into combined genomic-phenomic analyses, how phenomic character sets may be used to resolve conflicting gene trees, and how fossil taxa will be necessary in order to fully resolve certain deep time relationships within Ruminantia.

I also identified 16 areas of the fossil record that can be used as calibrations for molecular age estimations. I applied these to a re-analysis of a full mitochondrial data matrix of over 100 ruminant species. The results provide new (younger) age estimates for ruminant evolution, but also illustrate the wide variation in ages obtainable based on choice of calibration point. Using just one or a few calibrations, as studies to date have done, is probably insufficient to overcome molecular rate variations in such large trees, and a dense-calibration approach, using probability distributions and soft bounds, is argued to be better. This work also helps identify areas of conflict between genomic and phenomic approaches to taxonomic classification (e.g. the saola), and provides examples of how deep-time reconstruction of evolutionary rates, biogeography, and paleoecology can be misleading when conducted on trees of living taxa alone and without consideration of the fossil record.

I report on ongoing work to incorporate fossil ruminants together with existing mitochondrial and nuclear genomic datasets in a single total evidence analysis. This approach promises to immensely increase the accuracy of phylogenetic reconstruction, and aims to produce a synthetic evolutionary history that neither a molecular nor a fossil-based approach could arrive at alone.

### The evolutionary meaning of *Raphicerus*-like morphology in the dentitions and postcrania of *Antidorcas bondi* (Antilopini)

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*Antidorcas bondi* was a springbok, unusually adapted to a highly specialised grazing niche. During the Middle and Late Pleistocene it occurred in abundance throughout central southern Africa, from the north-eastern Karoo in the south to southern Zimbabwe in the north. It was the smallest of a range of six specialised grazing ungulates that became extinct towards the end of the Late Pleistocene. However, unlike the semi-arid adapted modern springbok, it was associated with wetland indicators, such as hippos, waterbuck and lechwe, which today occur in the Okavango area of Botswana and in southern Zambia as a relict fauna. There was a marked morphological shift in the dentitions of *A. bondi* from the end-Early Pleistocene to the Middle and Late Pleistocene, which we demonstrate by

non-destructive micro-focus X-ray Tomography ( $\mu$ XCT). A distal shift in the emphasis of mastication, a response to its adaptation as a small-bodied specialist grazer, caused a reduction of the premolar row and an increase in hypsodonty and enamel volume of the third molar. In earlier, less specialised forms, the ancestral state of *A. bondi* is clearly evident. The underived morphology seen in these dentitions, but also in the postcrania, shows marked similarities with the genus *Raphicerus* and we propose that in its ancestral state *A. bondi* would have resembled the living steenbok. We speculate that as geologically older fossils of *A. bondi* are found, predating the end-Early Pleistocene, there will be an increasing resemblance to steenbok and that *A. bondi* probably evolved from a *Raphicerus*-like ancestor. If supported by future evidence, this will have bearing on our understanding of the evolution of the tribes Antilopini, Alcelaphini and Caprini.

### Evolutionary rates for ruminants based on fossils and phylogenies

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The study of evolutionary rates and the temporal pattern of speciation and extinction rates is of major importance for the understanding of evolution. Such information can be recovered from both fossils and calibrated phylogenetic trees of extant species. In some cases we are limited to one of the two approaches – fossils or trees. Such is the case with extinct or severely impoverished groups or those lacking an adequate fossil record. Nevertheless, in those groups in which both comprehensive fossil and phylogenetic information is available, the comparison of the two proxies is desirable. Exploring and contrasting the outcome of both methods may help us to overcome their particular limitations. Additionally, such comparison might shed some light on the particular processes behind tree shape, beyond the pure fitting of evolutionary models. In the present work we focus on the evolutionary rates of the ruminant mammals at the global scale, comparing the signal of these rates on their fossil record (~1200 extinct and extant species) and the complete species level phylogeny of this suborder of cetartiodactyls (~200 extant species). Initial positive diversification rates were recovered from the fossil data during the Middle Eocene (~47 Ma), but there is no signal of these events in the extant species phylogeny. A first diversification pulse was estimated from the phylogeny during the late Eocene (~38 Ma). A remarkable turnover pulse – with both origination and extinction of fossil taxa – in the Eocene-Oligocene transition (~34 Ma) rendered accelerating speciation rates in the lineages leading to living ruminants. Net diversification rates were moderately negative during the Oligocene – low speciation and higher extinction –, although lineages leading to living ruminants underwent

accelerating diversification towards the end of this period. Indeed, the Oligocene-Miocene boundary (~23 Ma) witnessed a remarkable turnover episode in which both extinction and, especially, speciation rates peaked. From this moment until the latest Miocene both fossil and phylogenetic data depict speciation rates largely exceeding those of extinction. The Miocene-Pliocene transition (~5 Ma) brought about a new severe turnover pulse where extinction rates surpassed those of speciation. Net diversification rates recovered along the Pliocene and especially the Plio-Pleistocene limit (~2.6 Ma). During the last 1 myr, extinction rates increased again, rendering a diversity loss in the fossil record and a detectable slowdown in the diversification rate shown by the phylogeny. We conclude that the calibrated complete phylogenetic tree of the living ruminants holds abundant information about the evolutionary history of the group, especially from the late Oligocene onwards. Thus, such information is valuable when using the ruminant phylogeny in comparative methods, e.g. the study of trait evolution – and co-evolution – or trait-dependent diversification.

### The petrosal bone and inner ear of *Micromeryx* (Moschidae, Miocene)

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*Micromeryx* is one of the very few representatives of the Moschidae family to be known from the European fossil record. It first appeared in Europe in the late Early Miocene and is known until the Turolian in the early Late Miocene. It is a common genus and is recorded in many Miocene localities. Despite this commonness and the abundance of its remains in several well-known localities (e.g., Sansan, La Grive, and Steinheim all of Middle Miocene age), *Micromeryx* was never described in details until recent discoveries in Spain increased its species diversity and brought its skull to light. The Middle Miocene locality Steinheim in Germany yielded most parts of the skeleton of *Micromeryx flourensianus* including a well-preserved, although crushed skull (NMB Sth.833) and two isolated petrosal bones. This material has never been described before. I describe here the petrosal of *Micromeryx* for the first time. I compare it with the petrosal of *Moschus moschiferus*, the extant musk deer, and of the boselaphine *Tetracerus quadricornis* considered as one of the basalmost bovids to which moschids are possibly most closely related among ruminants. Among other characters, the fenestra cochleae is large and oval-shaped in *Micromeryx* while it is more rounded in *Tetracerus*; the promontorium is always hemi-ellipsoid but is less inflated and expanded in *Micromeryx* and *Moschus* than in *Tetracerus*. The secondary facial foramen is large and anteriorly positioned in the latter and in *Moschus* while it seems to be much smaller in *Micromeryx*. The fossa for the tensor tympani is deep and large in *Tetracerus* and less expanded, although also deep, in *Micromeryx* and *Moschus*. The subarcuate fossa is large and deep in *Micromeryx* and *Moschus*; it is large but shallow in *Tetracerus*. In addition, I performed CT-scans of the skull NMB Sth.833

and of the best preserved isolated petrosal. I reconstructed the bony labyrinth of *Micromeryx*. I compare the latter to that of another isolated fossil petrosal from La Grive which is most likely attributable to *Micromeryx flourensianus*. I also compare them to the bony labyrinths of *Tetracerus* and *Moschus*. The cochlea of *Micromeryx* shows 2 turns like that of *Moschus* while *Tetracerus* shows 2.5 turns. The cochlear canal in *Micromeryx* and *Moschus* are not as tightly coiled as in *Tetracerus* and are reminiscent of the situation seen in the tragulid *Moschiola meminna*. The first whorl does not strongly overlie the second one as it does in *Tetracerus*. The vestibule is bulkier in the moschids than in *Tetracerus*. A notable difference between *Micromeryx* and *Moschus* would be the stronger inflation of the anterior ampulla in the former. Some variability exists in the overall morphology of the bony labyrinth of *Micromeryx flourensianus*. The bony labyrinths of the isolated petrosals from Steinheim and La Grive look remarkably similar and slightly differ from that of the skull from Steinheim: e.g., the cochlear canal of the skull looks more vertical in lateral view.

### Deer from Plio-Pleistocene of Western Eurasia: matching fossil record and molecular phylogeny data

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The report proposes a revision of poorly known fossil cervid forms and a new look on Late Neogene cervid phylogeny with implications for known data from mitochondrial and nuclear genetic analysis. *Pliocervus matheroni* from the Late Miocene of Europe is poorly known with unclear systematic position. Some characters (parallel orientation of long pedicles situated very close to each other; antler shape, dental morphology, developed upper canines) place *P. matheroni* close to Late Miocene *Pavlodaria orlovi* from the *Hipparion* fauna of Kazakhstan. *Pliocervus* and *Pavlodaria* must be phylogenetically very close or even synonymous. Both *Pliocervus* and *Pavlodaria* share the same orientation and position of the pedicles on the skull as modern *Capreolus*. The analysis of cranial morphology and dentition of *Procapreolus moldavicus* revealed a set of primitive capreoline cranial characters, combined with orientation of pedicles as in modern *Odocoileus* and primitive *Muntiacus*-like characters (large upper canines, long pedicles, deep and large preorbital fossae). *Procapreolus moldavicus* stands closer to a forerunner of the stock that radiated to New World deer than to modern *Capreolus*. Apparently, several lineages of Capreolinae evolved in Northern Eurasia before the Mio-Pliocene boundary: the archaic *Procapreolus* lineage that does not have direct descendants in the modern fauna; the little known *P. loczii* that seems to be closer to the hypothesized forerunner of New World Capreolinae; and the *Pliocervus-Pavlodaria* lineage that may be close to modern *Capreolus* and *Hydropotes*. The dichotomy of Cervinae and Capreolinae, perhaps, is a consequence of the first expansion of Miocene ancestors of Capreolinae into the ecologically less favorable parts of Central and Boreal Asia. This may explain the generally more advanced degree of evolutionary specialization in Capreolinae, the development

of additional enamel folds in the molars (the *Palaeomeryx* fold and the protoconal fold), which are better developed in the Capreolinae, and a more advanced specialization of premolars in the Capreolinae, if compared to the Cervinae. The biogeographic expansion of Cervinae is recorded in Europe during the Early Pliocene. Apparently, this expansion coincides with the first successful radiation of the Old World deer that gave such fossil forms as *Arvernoceros ardei*, *Praeclaphus perrieri*, *Metacervoceros pardinensis* and possibly modern *Axis axis* and *Rucervus duvaucelii*. *A. ardei* and *R. duvaucelii* share the same plane of antler construction, so *Arvernoceros* and *Rucervus* may be closely related genera, or even synonymous. The second important radiation of Cervinae took place by the end of the Villafranchian, when appeared modern rich in forms *Cervus*, *Przewalskium*, and the extinct giant *Praemegaceros*, which together with *Eucladoceros*, apparently, also belong to the *Rusa-Cervus* stock. *Dama*, *Megaloceros*, and *Megaceroides* represent another stock of Cervinae that evolved in Western Eurasia and Mediterranean area.

### Extinction-recolonization events in Crimean red deer populations during Late Pleistocene

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Analyses of mitochondrial DNA sequences of contemporary red deer populations have shown that this species can be divided into two major groups that are geographically separated. The Western red deer group inhabits Europe, the Middle East and Africa while the Eastern group is present in Asia and North America. This pattern is probably caused by climatic and environmental changes during the Pleistocene. We performed analyses of ancient DNA from Crimean red deer remains to investigate the population history of this species. Red deer samples for ancient DNA analysis were collected mostly from Emine-Bair-Khosar cave situated on the north edge of the Lower Plateau of the Chatyrdag Massif (Crimean Mountains). Analyzed bones were radiocarbon dated and their ages ranged from ca. 1 to more than 45 cal kyr BP. Phylogenetic analyses indicated that during the Late Pleistocene the Crimean Peninsula was inhabited by specimens belonging to both Western and Eastern red deer group. Nowadays only European populations are present on the peninsula. Simulation analysis suggested that different extinction-recolonization events happened in red deer populations in the last glacial period.

### Revision of the Ovibovini Gill 1872 (Bovidae, Caprinae) through a cladistic analysis based on morphological characters

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The living musk ox (*Ovibos moschatus*) and takin (*Budorcas taxicolor*) are usually grouped together under the name Ovibovini, into the subfamily Caprinae. A lot of extinct taxa have been attributed to this tribe, such as: *Criotherium*, *Urmiatherium*, *Parurmiatherium*, *Tsaidamotherium*, *Kabulicornis*, *Plesiaddax*, *Mesembriaceros*, *Pliotragus*, *Megalovis*, *Hesperoceridas*, *Soergelia*, *Boopsis*, *Bootherium*, *Symbos* and *Euceratherium*. If the last four genera have always been considered as true Ovibovini closely allied to *Ovibos*, the phylogenetic positions of the other genera remain controversial.

Several of these taxa have been revised and are no longer attributed to Ovibovini. For example, *Criotherium* has been recently assigned to Antilopinae and *Urmiatherium* to Oiocerini. Thus, the content of this group has drastically changed during the last decades. But these changes are not restricted to extinct taxa. Indeed, considering only extant species, the affinities between *Ovibos* and *Budorcas* have been questioned during the last decades. Several molecular phylogenies have revealed that the musk ox and the takin do not form a monophyletic group. Some palaeontologists have also rejected the closeness of these two taxa. For example, *Budorcas* has recently been excluded from the Ovibovini. On the other hand, phylogenetic reconstructions based on morphological characters have shown the monophyly of Ovibovini.

In order to clarify the taxonomic content of this tribe and its definition in cladistics terms, a phylogenetic analysis of Bovidae based on dental, cranial and postcranial characters is realized. This analysis focuses mainly on Caprinae and includes most of the putative ovibovines described in the literature. Based on the resulting cladogram, the affinities between *Criotherium*, *Urmiatherium*, *Plesiaddax* and *Sinotragus* are exposed and thus, the first three genera are excluded from the Ovibovini. Finally, a list of apomorphies for the clade Ovibovini is presented, a clade that contains two living species: the musk ox and the takin.

### Fossil remains of family Cervidae from the Siwaliks of Pakistan

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Fossil remains of the family Cervidae are poorly known from the Siwalik continental deposits. Moreover, the earlier identifications are confused partly due to the incomplete original description of species and partly due to inadequate selection of diagnostic characters. Similarly the exact stratigraphic range of these fossils used for the original description



is unknown. As a result the number of species, taxonomy and validity, as well as the stratigraphic range of these species in the Siwaliks have been considered as exaggerated and needs precise paleobiogeographic and biochronologic studies. In this paper, new materials collected from the Middle - Upper Siwaliks are evaluated to confirm the taxonomic and stratigraphic biases of the tribe Cervini.

### Characterization of the gene family encoding for the pregnancy associated glycoproteins in ruminant ungulates.

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Among eutherians, there are many examples of gene families whose RNA and protein products are expressed only in the placenta. Ruminant ungulates are a particularly useful group in which to study such expanded gene families because several are known to be present in them. Examples include the pregnancy-associated glycoproteins (PAGs), the prolactin-related proteins (PRPs), the trophoblast Kunitz domain proteins (TKDPs) and the interferon tau (IFN $\tau$ ). Each of these families encode for secretory proteins that are expressed exclusively in trophoblasts – the epithelial cells of the placenta that interact with maternal uterine epithelia at the fetal-maternal interface. The PRPs, TKDPs and IFN $\tau$  are found only in the Ruminantia. The PAGs appear to be present in most artiodactyls, but not in other mammalian orders. The PAGs arose by duplication of an ancestral pepsinogen F gene and subsequently underwent a substantial expansion within the Ruminantia. There are more than 20 PAGs that have been described in domestic cattle and related species. These genes can be segregated into ‘ancient’ and ‘modern’ members based upon estimates of when they arose. Ancient PAGs have been identified in multiple species within Ruminantia, Suina and Cetacea. In contrast, most of the modern PAGs are found in Bovidae with only a few modern ones that have been identified and sequenced from other pecorans (e.g. Cervidae and Giraffidae). The expansion within the modern PAG grouping has been associated with positive selection for amino acid diversity – particularly in regions of surface loops. Furthermore, many of the ruminant PAGs are expressed only in unusual trophoblast giant (binucleated) cells. These cells have the capacity to fuse with maternal uterine epithelial cells to deliver their protein products to uterine connective tissue. Consequently, those PAGs produced by trophoblast binucleated cells can accumulate in the maternal uterine stroma and be taken up by maternal blood to circulate during pregnancy. Other PAGs are expressed by cytotrophoblasts and these tend to accumulate at the placenta-uterine interface and do not appear to enter the maternal circulation. Little is known about the function of the modern PAGs. In light of their regulated production and their abundant expression by trophoblasts, they probably are serving important roles that are unique to the synepitheliochorial placenta of ruminant ungulates.

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### New giraffoid fossils from the later Early Miocene Lothidok Formation (West Turkana, Kenya): Implications for early giraffoid diversity

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Excavations at Kalodirr and Moruorot (ca. 17 mya) in the West Turkana Region of Kenya have yielded several cranial appendages, dentitions and postcranial fossils. Some represent novel taxa, while others contribute new information for previously recognized taxa; all of which contribute to our understanding of the diversity of early Giraffoidea. We assign one cranial appendage to *Climacoceras* sp. nov. Another novel cranial appendage, unlike any previously described, is attributed to Climacoceratidae. It is most similar to *Climacoceras* in possessing small tines, but differs in its cranial base and curvature of the shaft. This appendage is detached from the skull opening new questions about the formation of the climacoceratid cranial appendages. For the Giraffidae: One ossicone is assigned to a new taxon. It bears some resemblance to *Prolibytherium* from Gebel Zelten, but also to *Giraffokeryx* from Fort Ternan, making it difficult to determine its exact relationships among the Giraffidae. We interpret three ossicones as a growth series and assign them to cf. *Canthumeryx* sp. These ossicones are oval, wide at their base and short even when from a young individual. They have a keel which is provisionally interpreted to be anterior. The ossicones appear to enlarge isometrically. This is the first time complete ossicones are attributed to *Canthumeryx*. *Canthumeryx* is well-known from Moruorot represented by a partial skeleton of a juvenile previously published. More dental material from Kalodirr and Moruorot most likely represents several adults of *Canthumeryx*, demonstrating slight population diversity in non-metric dental traits in this taxon. A referred metacarpal is simple and primitive but long as in all Giraffidae.

These new fossils demonstrate that by the end of the early Miocene in Africa the Giraffoidea included at least two diverse families. Climacoceratidae are distinct from the Giraffidae in having branching cranial appendages. These were not frontal bone expansions as in Bovidae, and differ from antlers in the shape of their base, suggesting that they were not deciduous as in Cervidae. By the latter part of the Early Miocene of Africa, the Giraffoidea include at least four genera, of which at least two are included in the Giraffidae as demonstrated by ossicones from West Turkana. This diversity is increased if *Prolibytherium* from Gebel Zelten is included in the Giraffidae.

## A revision of cervid phylogeny using a total evidence approach

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Cervidae are a popular and well-known family of ruminants, although many aspects of their evolutionary history remain enigmatic. Since their origin in the early Miocene (~20 mya) their capacity to adapt to a variety of environments has enabled cervids to thrive, leading to a rich diversity documented in the fossil record and with 53 extant species. Most cervid phylogenetic estimates have either been reconstructed from molecular data (extant species) or from morphological data (single fossil taxa or groups). The first option only includes representatives of the living crown group, resulting in trees that are typically fairly well resolved with reasonable node supports, but some discrepancies. The second option deals only with a reduced taxon sample and provides sufficient topologies, although often less well resolved and supported; however, morphology is the only data source available that links fossil and extant species. In many cases, resulting tree topologies of both approaches are controversial. Ideally, to provide an overall picture of cervid evolution, acquisition of as much information as possible from character and taxon sampling is desirable. A strong molecular backbone from extant cervids, combining mitochondrial and nuclear markers, and scoring of the morphology of extant and fossil taxa – in this study focusing on craniodental characters – connects fossil cervids with living species and facilitates the systematic positioning of the former. Other characters, such as soft tissue anatomy, behaviour and ecology, should also be considered. In reality, this optimal result is difficult to achieve. In the present study, in cases where only morphological data were available, the analyses often failed to place extant species close to their generic relatives. Conversely, for more recent fossil cervids (Pliocene and Pleistocene), the analyses found a connection to extant representatives. For Miocene cervids, however, the position varied from one analysis to another; these taxa form a polytomous stem group to all other cervids (with tragulids as the outgroup) or nest within crown group Capreolinae when five non-cervid outgroup taxa are added. This occurred under different optimisation criteria. These results demonstrate that accurate and reproducible scoring of observed morphological characters is essential to reduce these difficulties. For example, character format and software specifics are affected mutually and subjective assessment of characters and character states based on authors' individual experiences may bias outcomes. Total evidence approaches remain the method of choice when it comes to reconstructing evolution beyond genus level. Thus, when scoring defined morphological features, it is desirable to use standardised, non-ambiguous quantitative or presence/absence characters,

or to describe other more subjective characters as clearly as possible via documentation in public photographic databases.

## Phylogenomics and adaptive genomics of ruminants

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As stated in the backgrounds and aims of this conference, 'the evolutionary history of ruminants remains unresolved', while at the same time 'phenotypic and genomic data from fossil and extant species accumulate at an ever increasing rate'. With constantly decreasing DNA sequencing costs, the speed of data accumulation is likely to further increase. However, currently, these data accumulate in a relatively uncoordinated fashion. Here I suggest using this conference as an opportunity for initiating a ruminant genome project that aims at sequencing full genomes for all ruminant species for which DNA can be made available, including recently extinct species using ancient DNA technology, to provide the first full phylogenomic analysis for a taxonomic group on the species level. In addition, the project should have two additional goals. First, in contrast to many other genome projects it should aim at full annotation and assembly of the genomic data to enable analyses of functional adaptive changes on the DNA level. And second, morphological data, including from extinct species too old for obtaining ancient DNA should be included in the analyses with the aim to provide as complete a picture of ruminant phylogeny as possible. I will discuss the potential benefits and insights that could be gained from such a project.

## Morphological aspects of the evolution of the ruminant placenta

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The mammalian placenta shows a fascinating variability on the macroscopic, microscopic and molecular level. Here we review and analyse the character evolution in the ruminant placenta. The parsimony-based computer program MacClade was used to analyse morphological traits in species from all ruminant families as well as from non-ruminants such as pigs and camelids as outgroups to root the character evolution. A diffuse epitheliochorial placenta was identified as ancient condition or stem species pattern of ruminants. This condition was present in the Tragulidae (mouse deer). On the stem lineage to Pecora (higher ruminants) it was transformed into a cotyledonary type placenta, in which intense fetomaternal interdigitation concentrated in discrete areas, the placentomes. The stem species pattern of Pecora had a polycotyledonary placental type with a high number of placentomes (50-150). The placentomes were flat and had a simple branching pattern

of the fetal villi. These conditions were maintained in most families, but on the stem lineage of Cervidae and Moschidae a reduction to a oligocotyledonary type of placentation with only 5–8 placentomes took place. In addition, highly branched villi inside the placentomes developed independently in several taxa, as well as the occurrence of concave placentomes in *Ovis* and *Capra* and the independently evolved presence of stalked placentomes in *Bos* and the Cervidae. Binucleate trophoblast giant cells (BNCs) were found in all ruminant placentae. These cells produced several secretory proteins, partially with hormonal functions, which were delivered into the maternal organism after a fusion of the BNCs with maternal uterine epithelial cells to form trinucleate feto-maternal hybrid cells or larger syncytial plaques, the ‘synepitheliochorial’ condition. Functional interpretations of these findings were based on the ‘viviparity-driven conflict hypothesis’. It states that divergent interests of mother and offspring lead to a rapid antagonistic coevolution, which might be cause of the huge placental diversity. As part of this conflict several mammalian clades independently evolved mechanisms to release fetal hormones to the mother to increase the fetal endocrine influence on the maternal metabolism. BNC fusion with maternal cells is the ruminant specific mechanism to deliver fetal hormones into the dam. We hypothesise that the metabolic changes that were associated with the evolution of forestomach fermentation in Pecora were the main driving force behind other traits. The development of the cotyledonary placenta could be related to a diminished availability of glucose in ruminants. This might have promoted the evolution of the cotyledonary placenta that had a high feto-maternal exchange area, but a low conductivity for glucose. Thus, an arms race could have occurred in which the mother tried to restrict and the fetus tried to increase transplacental glucose flow.

### Horn development in living boselaphines and their fossil relatives: implications for phylogenetic reconstructions

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Nowadays, boselaphines are restricted to the Indian sub-continent represented by two distantly related and largely different species, *Boselaphus tragocamelus* and *Tetracerus quadricornis*. The ancestry of both living taxa can hardly be traced along the fossil record beyond a couple of Ma at the best, though molecular data set their common origin at 6–8My ago, a time period when bovids of a presumably boselaphine appearance strongly radiated and were widely distributed in the Old World. Nevertheless, building phylogenetic relationships between living boselaphines and their Miocene relatives has been proved to be an extremely hard task due mainly to the discontinuity and insufficiency of the fossil record, and the equivocal interpretation of many bovid skeletal characters.

Among anatomical features that have traditionally been used to link fossil bovid taxa with living boselaphines is the overall horn core configuration. Indeed, distinct horn core characters seen in the Indian *Boselaphus*, have been repeatedly observed

in various combinations in the fossil record, allowing different scenarios of boselaphine horn development and conflicting phylogenetic interpretations.

As part of a larger study concerning fossil boselaphine-like bovids, the status and value of some of these characters is re-examined in the light of the horn-development process in *Boselaphus*. The analysis exhibits that in both living and fossil boselaphines ca. 70% of the total adult horn length is reached during the first-to-the second growing season(s) as in other bovids, but the higher rates of *Boselaphus* horn thickening take place later in life, probably during the years males are actively involved in breeding. At the same time, thickening is not uniformly distributed on the horn surface but exaggerated along the antero-proximal part. As the horn grows, the zone of anterior horn thickening of *Boselaphus* migrates proximally on the sub-horizontal frontals engulfing the pedicle and resulting in successively less inclined top appositional bone surfaces that provide small successive proximal steps. Alternatives of this basic mechanism would explain most horn core shapes seen on extinct boselaphine-like bovids and in combination with other fossil evidences highly affect the interpretation of several horn and frontal features used in relevant phylogenetic analyses.

### Phylogenetic patterns and diversity of embryonic skeletal ossification in Cetartiodactyla

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There is enormous variation in the skeletal morphology reflecting a wide spectrum of ecological diversification of this clade. One major drive of skull diversification is heterochrony, changes in developmental timing which leads to differentiation of morphology between species. Although numerous examples of skeletal heterochrony among vertebrates are described to date, how heterochronic variation is related to changes in life history traits remains poorly understood. The more classic heterochronic studies have focused on quantifying changes in size and shape, whereas the study of ‘sequence’ heterochrony incorporates changes in the timing of discrete developmental events with many advantages in comparative studies. Here we provide the study on the embryonic ossification sequence of skeletal elements in Cetartiodactyla and related mammalian taxa.

Ossification sequence data of skeletal elements of embryonic *Bos*, *Ovis*, *Capra*, *Capreolus*, *Dama*, *Stenella*, *Sus* and *Camelus* was described and compared with that of other 97 mammalian species. We employed an enzymatic clearing and staining method and a high-resolution tomography ( $\mu$ CT) technique for detecting ossification. Some specimens were cleared and stained by a modified method of a standard enzymatic procedure, and the earliest appearance of ossifications were recorded based on uptake of alizarin red. As other species were historical museum specimens, the appearance of bones was also assessed noninvasively by acquiring shadow images taken by  $\mu$ CT at the University Museum, University of Tokyo and at the Anthropological Institute, University of Zurich. Three dimensional visualization and analysis of shadow images

were conducted in Avizo 6.1. We performed Parsimov-based Genetic Inference (PGi) to analyses heterochronic changes in the investigated taxa. PGi examines the sequence as one single, complex character and uses the Parsimov algorithm as an edit-cost function to optimise ancestral states and sequence heterochronies. The PGi analysis was computed eight times independently, and subsequently the shortest tree that was assumed to recover the most probable heterochronies was adopted.

We found that premaxilla, maxilla, jugal, and orbitosphenoid are accelerated in the onset of ossification timing in Cetartiodactyla compared to other mammals. Furthermore, we identified that Ruminantia is characterized by acceleration of alisphenoid and ectotympanic. Possible ecomorphological significance of these heterochronic shifts will be discussed in the presentation.

### Geographic variation in body size of Japanese sika deer: Bergmann's rule revisited

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There have been a number of studies investigating Bergmann's rule, a well-known pattern of increasing animal body size with increasing latitude. However, since species tested for Bergmann's rule usually have wide geographical range, it is possible that apparent correlation between latitude (or some ecological factors varying with latitude) and body size is merely reflecting a phylogenetic structure, the case often concerned in interspecific comparisons. In exploring factors responsible for latitudinal body size cline within species, Japanese sika deer (*Cervus nippon*) is an ideal species. The distribution extends from the northern to the southern islands (from 43° N to 26° N) and it exhibits considerable morphological variations among local populations including body mass, which ranges from around 40kg for male deer in southern islands to over 100kg for male deer in northern populations. This latitudinal variation in body mass has been mentioned as an example of Bergmann's rule. Based on external morphology and distribution, they have been generally classified into six subspecies. Molecular phylogenetics, however, have shown that there are only two genetically distinct groups of the Japanese sika deer, the northern and southern lineages, which diverged around 0.3-0.5 Mya. The northern lineage includes populations in northernmost island (Hokkaido) and most of the mainland (Honshu) except for the southwestern region of Honshu, whereas the southern lineage includes those in the south-western Honshu region and southwestern islands. Previously, Ozaki and colleagues reported morphological differentiation in mandible and teeth between the two lineages. Thus it is expected that body size also differs significantly between the lineages, irrespective to meteorological and/or ecological cline found among populations. We tested correlation between body size of sika deer and meteorological and ecological variables, taking intraspecific phylogeny into consideration. We found that body size negatively correlated with meteorological variables

in the same manner for the northern and southern lineage: i.e. the two lineages were on the same regression line contrary to the case for molar metrics. Thus rather than the historical backgrounds the two lineages experienced in the past, current meteorological/ecological factors may be responsible for the body size cline. By stepwise regression, we selected most influential factors. Body mass negatively correlated with cold index and annual precipitation for both sexes. In addition, residuals from a regression line of body mass against greatest length of cranium (i.e. relative weight) also negatively correlated with cold index. This indicates sika deer in colder areas are absolutely as well as relatively (to their skull size) heavier than those in warmer area. Heaviness may be related to amount of fat reserve, which is crucial for survival during food-scarce winter seasons in colder areas.

### Geographic differentiation of domestic ruminants

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Several factors control geographic patterns of genetic diversity in domestic populations: predomestic differentiation of wild ancestor populations, location(s) of the initial domestication, postdomestic introgression of wild populations and the serial founder effects of migrations, adaptation, human selection, breed formation, inbreeding and crossbreeding. We review and compare the phylogeographic patterns of taurine and indicine cattle, sheep, goat and the river and swamp types of water buffalo. Spatial clines of mitochondrial DNA diversity are weak for sheep and goat, stronger for taurine cattle and, in spite of the absence of morphological variation, most outspoken for the East-Asian swamp buffalo. Autosomal diversity patterns show a clear difference between the weak and strong genetic clines of sheep and goat, respectively, which can be explained by crossbreeding between sheep populations of different origin. Remarkably, geographic distributions of Y-chromosomal haplotypes from sheep, goat and cattle reveal for all three species within Europe sharp contrasts of northern and southern haplogroups. This may reflect adaptations to climate and landscape, but also differences in agricultural tradition.

### Systematics of the endemic Pleistocene deer of Mediterranean islands

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Endemic species of deer evolved on several Mediterranean islands in the Quaternary. A brief review will be given of the deer described from islands including Corsica/Sardinia, Sicily, Malta and Crete. The main candidate ancestors are deer of the genera *Cervus*, *Dama*, *Megaloceros* and *Praemegaceros*, all well-known from the continental European Middle to Late Pleistocene. In many cases, however, the island forms have

unusual, and sometimes highly variable, morphologies, so that their likely mainland ancestral species has been difficult to identify with certainty. We describe characters relevant to the systematics of these deer, and the results of new cladistic analyses attempting to place the island forms within the phylogenetic framework of mainland taxa.

### Morphological evidence on the origin of *Bison* and the Cephalophini

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Bisons are among the most abundant large mammals of the Pleistocene of Europe or even of the whole Palearctic. Their appearance in Western Europe occurred against a background of major climatic change.

West European bison are represented by three or four lineages. Important characters for distinguishing *Bison* species are horn chore and skull characteristics and the biometrics of the metapodials. These are described for the fossil and living West European *Bison* species (*B. menneri*, *B. voigtstedtensis*, *B. degiulii*, *B. schoetensacki*, *B. priscus*, *B. bonasus*, *B. priscus*). The observed morphological patterns are used for retracing the evolution of *Bison* and its biogeographical history, suggesting several dispersal events from Asia to Europe.

If truly a bison, *Bison palaeosinensis* might be the oldest bison. Its affinities and the minimum age of the *Bos*-*Bison* split will be discussed.

At present Cephalophini are believed to be strictly African. They have horn cores that are like short and simple spikes, which are situated well behind the orbits. In Bovini, Alcelaphini and some Caprini horn cores also moved backwards, but there tend to be extensive sinuses in this area of the skull and the horn cores are large and have more complex morphologies than in Cephalophini. Neotragini are small antelopes, that have spike-like horn cores, like the Cephalophini, but are easily differentiated, by the fact that in Cephalophini, the base of the horn core is entirely over the brain case, while in Neotragini it is partially over the orbit. This is a derived feature in the Cephalophini. Fossils having this morphology, were previously assigned to different tribes, including Neotragini, but are more likely Cephalophini and indicate a Eurasian record for this tribe that is at least as old as the African one.

### Reassessment of early European Ruminantia: implications for the diversity and evolution of the group

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It is commonly asserted that ruminants first appeared in Europe during the Late Eocene. Then, during the Oligocene,

a local evolution of 3 different Asiatic lineages (Lophiomerycidae, Bachitheriidae, and 'Moschidae' through those of Gelocidae) is assumed to have taken place until the Early Miocene. Based on the review of specimens from European localities, this study aims to discuss a new insight into the diverse evolutionary patterns of European ruminants from the Oligocene to the Early Miocene.

The previously known oldest European ruminants are only represented by isolated, often lost specimens of unclear provenience. The earliest undeniable European ruminants occurred after the 'Grande Coupure' (MP20/21, Oligocene, ca. 33.5 My). All these fossils are currently attributed to Gelocidae. Even if the primitive shape of the molars remains quite homogenous, those of the fourth lower premolar suggest the presence of several families. Originating from Asia, ruminants (e.g., Lophiomerycidae, Bachitheriidae, and Tragulidae) diversified throughout Europe until MP23. Swamps and forests dominated the landscape. At the beginning of MP24, global climate change, probably linked to the Oi2 glaciation, resulted in drier woodlands. Our thorough review of the fossil record indicates that the Gelocidae and the Tragulidae disappeared at this time, whereas only the larger species of Bachitheriidae and Lophiomerycidae survived, probably resulting in a local European speciation. At MP24/25 (ca. 29.2 My), Bachitheriidae diversified and *Mosaicomeryx* arrived. European mammal evolution was relatively quiet and steady until MP27. Around MP28, large changes occurred, probably caused by the latest Oligocene Warming. First a speciation resulted in ruminants adapted to more open habitats, followed by a rapid extinction, linked to new Asiatic immigrants (e.g., *Babameryx* and *Dremotherium*), causing a total renewal of the European fauna. The Oligo-Miocene transition (ca. 22.9 My) was marked by the Mi1 glaciation, which coincided with fragmentation of the environment resulting in a local speciation. At the end of MN2, a considerable diversity (at least 11 species) of hornless, saber-toothed ruminants is recorded in Europe. The familial attribution and phylogenic position of these ruminants is still debated, belonging to extinct families or being a member of an extant one, but too basal to be recognized as such. The beginning of the Proboscidean datum (MN3a, ca. 19.8 My) led to the disappearance of all these 'old taxa' and the emergence of the modern groups possessing, for example, appendages.

As opposed to the theory of a regional European evolution, that implies few immigrations, this study highlights European ruminant evolutionary patterns strongly related to global changes, that were emphasized in Europe by its dead end paleogeography, punctuated by repeated waves of immigration from Asiatic origin (from MP20, MP28, and MN3) and local speciation (during MP24 and MN1).

### Eocene-Oligocene selenodont artiodactyls from Asia: their role in understanding the phylogeny and paleobiogeography of early ruminants

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At present, there is little or no consensus regarding the phylogenetic relationships of Ruminantia within (cet)artiodactyls. Although tragulids are the only extant representatives of the basal radiation of ruminants, the scarce or unavailable fossil record for this group prior to the Miocene prevents reliable estimation of how deep into the Paleogene the tragulids and thus crown-ruminants may have originated. Available molecular evidence supports a relatively ancient (Early to Middle Eocene) dichotomy between tragulids and pecorans (horned ruminants). Moreover the phylogenetic relationships between Ruminantia and the other groups of cetartiodactyls remain unclear from both molecular and paleontological perspectives, and in all cases source of discrepancy and misunderstanding. One key for resolving discrepancies between morphological and molecular data is to better understand the basal radiation and phylogeny of what the ancient authors used to name 'dichobunoids'. This paraphyletic assemblage of tragulid-like bunodont to bunoselenodont artiodactyls inhabited the three Holarctic continents during the Early and Middle Eocene. Resolving the dichobunoids Gordian knot is hampered by the inadequacy of the Asian fossil record of these early 'selenodonts' (here envisaged as a grade) that probably bring many clues about the origin and early evolution of ruminants. Likewise, the comparatively sparse Eocene fossil record of Asia certainly contributes to the gap or ghost lineage involved by molecular trees.

In this context, I propose to focus on 3 Asian windows of the Paleogene fossil record that have yielded dichobunoid and/or ruminants: the Middle Eocene Shanghuang fissure fillings (coastal China), the Early Oligocene of the Bugti Hills (Central Pakistan), and the Late Oligocene Kizilirmak Formation of the Cankiri Basin (Central Turkey). Phylogenetically significant morphological characters are thought to be distributed among the skull and dentition, as well as in limb structure. Incompletely known fossil taxa may, therefore, be especially problematic for purposes of phylogeny reconstruction. Added to this difficulty is a substantial and well documented level of homoplasy within selenodont cetartiodactyls. However, in an attempt to decipher the affinities of these Paleogene Asian ruminants with their European and North American counterparts, a phylogenetic analysis including most of the available morphological features has been realized. The results stress the role of Asia in the origin and early diversification of Ruminantia, but also emphasize the need of more complete fossil data from the Middle-Late Eocene of southern Asia.

### The possible role of hybridization in adaptive radiations

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Changes in Africa's paleoclimate over the Pliocene-Pleistocene epochs promoted adaptive radiations that resulted in an overwhelming present-day mammalian diversity. The bovids in particular appear to have exploited productive paleoenvironments to their fullest potential, resulting in the most diverse

and abundant array of herbivores on earth. A remarkable amount of bovid diversity in ecological specialisation, size, life history, sexual dimorphism and social systems is captured within the nine tragelaphine (or spiral-horned) antelope species (Tribe Tragelaphini). Their fossil record shows that they radiated in several paleoclimatically-associated bursts from a common ancestor about six million years ago. Today, they are found throughout sub-Saharan Africa in almost every habitat type, with generalist species ranging widely and specialists restricted to arid, montane or rain-forest habitats. Paleodistributions show that specialist species once ranged more widely, suggesting evolutionary histories of range expansions and contractions, modulated by spatially and temporally variable paleo-environments. In this case, the classical view would predict that selective and demographic forces would promote either differentiation or homogenization, depending on the level of reproductive isolation between radiating populations. However, an increasing body of knowledge now suggests a key role for introgression (or hybridization) in tragelaphine speciation. Firstly, reproductive isolation mechanisms appear not to be fully developed in this tribe as several species produce fertile hybrids in captivity. Secondly, their level of phenotypic convergence is exceptional. Molecular studies have revealed paraphyly among species that were once assumed, on the basis of morphology, to be sister taxa. Intraspecifically, within the *Sylvaticus* super-lineage of the bushbuck (*Tragelaphus scriptus*) complex, the distinct large, dark and thickly coated phenotype inhabiting the isolated montane forests along the East African rift is known to have evolved independently at least four times - on the Ethiopian Highlands, the Imatong Mountains, Mt Elgon and the Gregory Rift. The frequency of convergent evolution at both the incipient and full species levels implies the adaptive advantage of certain phenotypes over others. Thirdly, hybrid zones between the bushbuck super-lineages *Sylvaticus* and *Scriptus* are common in central and eastern Africa. Lastly, the recent discovery of a cyto-nuclear phylogenetic dissociation provides the 'smoking gun' signature of an ancient hybridization event within this group. While a mitochondrial DNA phylogeny shows the two bushbuck super-lineages to be paraphyletic, species tree reconstruction with nuclear introns restores the bushbuck's monophyly. The unambiguous sorting of the slower-evolving nuclear loci effectively rules out incomplete lineage sorting as a basis for the mitochondrial DNA paraphyly. Only an ancient hybridization event - between a proto-nyala female and a proto-bushbuck male in the early stages of the radiation, during the early Pliocene - can reconcile mitochondrial and nuclear gene trees. I therefore suggest a key role for hybridization in mammalian speciation, especially in adaptive radiations, where the inevitable loss of genetic diversity during rapid differentiation may be offset by incompletely developed reproductive isolation mechanisms that allow the influx of hybrid genetic variation.

## New Late Miocene North American dromomerycine artiodactyl from the Amazon Basin: implications for interchange dynamics

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For decades, it was assumed that the Great American Biotic Interchange (GABI), wherein mammals from North America invaded the isolated island continent of South America and a few South American taxa migrated northward, occurred with the closure of the Isthmus of Panama in the late Pliocene, conventionally thought to have occurred about 3.0–2.5 Ma. A new dromomerycine palaeomerycid artiodactyl, *Surameryx acensis* new genus new species, from upper Miocene deposits of the Amazon Basin documents the first and only known occurrence of this Northern Hemisphere group in South America. Osteological characters place the new taxon among the earliest known dromomerycine artiodactyls, which lived in North America during the early to middle Miocene, 20–16 Ma. The presence of this North American dispersant in Amazonia is further evidence that terrestrial connections between North America and South America through Panama existed as early as the early Late Miocene, ~9.5 Ma, as previously indicated by approximately coeval specimens of proboscideans, peccaries, and tapirs in South America and ground sloths in North America. Although palaeomerycids apparently never flourished in South America, peccaries and tapirs diversified and still live there today, and proboscideans thrived there until the end of the Pleistocene.

## On the phylogenetic position of the hornless pecoran *Amphimoschus* – an example of arising challenges with the incorporation of fossils in extant combined frameworks

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The early diversification of Pecora, documented by the fossil record of the latest Oligocene and Early Miocene, comprises first representatives of crown pecorans (Antilocapridae, Giraffidae, Cervidae, Moschidae, Bovidae, extinct groups), and includes many taxa lacking cranial appendages. The systematic positions of the latter are discussed controversially. One of

those is *Amphimoschus* Bourgeois, 1873 from the Eurasian Early/Middle Miocene. Based mainly on dental characters, previous authors hypothesized moschid, cervoid, cervid, hoplitomerycid, bovid, or, most recently, bovoid origin. Recently, an extraordinarily well-preserved cranium of *Amphimoschus* was unearthed in Taiwan and is now providing substantial additional information for systematic discussions. Within a large morpho-molecular ruminant framework we reassess its phylogenetic position. For this purpose we compare a range of different tree-building algorithms and data-combination strategies (supermatrix, scaffold analysis), and assess the influence of different data partitions (e.g., dentition) on the outcome of phylogenetic analyses.

We performed morphological and combined analyses under Maximum parsimony, Maximum likelihood and Bayesian inference criteria of a data matrix comprising a wide range of extant Pecora, extinct Pecora indet., early Cervidae, extant Tragulidae, and Oligocene Tragulina. The sampling includes 120 craniodental characters, five nuclear loci and one mitochondrial gene (total of ~4800 bp).

Phylogenetic analyses predominantly group the *Amphimoschus* cranium with the extant *Moschus*. The phylogenetic position of the latter, and therewith of *Amphimoschus*, differs within Ruminantia dependent on the data partition and analysis method used. Exclusively morphological data sets place *Moschus* + *Amphimoschus* in a basal pecoran polytomy together with *Dremotherium* and the remaining crown-group taxa while combined analyses place *Moschus* + *Amphimoschus* as the sister group of Bovidae. This stands in contrast to the most recent assignment of *Amphimoschus* to Bovoidea, but the results provide strong support for a moschid origin as proposed back in 1873. However, since tree topologies of morphological and combined analyses differ essentially, the predominant position of *Amphimoschus* within Moschidae might be caused by superficial morphological similarity in the absence of DNA data. A further critical aspect is the importance of cranial appendages in the classification of crown genera, which might mask an early appendage-less evolution of crown pecoran families and necessarily groups hornless fossils with hornless representatives of living Pecora. The phylogenetic analysis of the exquisite Taiwanese *Amphimoschus* cranium is an excellent example of arising challenges in combined extant-extinct analyses, both in the morphological and morpho-molecular aspect, and allows for new interpretations of early pecoran phylogeny.

## Evolutionary patterns in insular fossil bovids

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Insular fossil bovids, ranging in age from the latest Miocene to the Holocene, are widely recorded in Asian and Western Mediterranean islands. Several taxa characterized by different levels of endemism, but no species with an entirely identical

adaptation, existed on different islands. Even considering that evolutionary processes, affecting size and morpho-functional features, mainly depend on inter- and intra-specific competition as well as on typology of free available niches, it is difficult to identify a dominant factor in the evolution of insular bovids. Moreover, highly modified insular biota show a mixture of apomorphic and plesiomorphic features that obscure their phyletic relationships, and make their origin and evolutionary patterns problematic to determine.

A few common evolutionary traits can however be detected. Body size trends of insular fossil bovids are in agreement with the island rule pattern showing a negative relationship between  $S_i$  (= mean mass of individuals from an insular population divided by  $M$ ) and  $M$  (= body mass of individuals of the mainland or ancestral form). The increased hypsodonty of molars (a quite common morphological trend in insular artiodactyls maybe related to an augment in the reproductive lifespan/longevity) is shared by most of insular bovids, including browsers such as the Javanese small boselaphine *Duboisia santeng*. A recurring pattern in insular bovids (although some exceptions exist) is the simplification of the horn cores, as shown by both living (e.g., *Bubalus depressicornis* and *Bubalus quarlesi*) and highly modified fossil taxa (e.g., *Duboisia santeng*, *Nesogoral* spp., *Myotragus*). Conversely, morphological traits related to the so called 'low-gear' locomotion, exhibited by few insular bovids and regarded as typical adaptations acquired by insular artiodactyls, mainly depend on the presence of predators on the island.

Assessing causal factors behind these modifications is not an easy task and a number of still unsolved issues need to be scrutinized, firstly to what extent phylogeny and bauplan might affect evolutionary patterns of insular bovids.

### Phylogeny of the Tragulidae (Mammalia, Cetartiodactyla, Ruminantia)

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The Tragulidae are the most basal of extant Ruminantia, and the only living remnants of an ancient radiation of ruminants that produced successive sister groups to the Pecora. They comprise the smallest living cetartiodactyls and survive today as Old World tropical relics: *Moschiola* in India and Sri Lanka, *Tragulus* in Southeast Asia and the Philippines, and *Hyemoschus* in Africa from Sierra Leona to Uganda. As the most primitive representatives of the extant Ruminantia, tragulids are less advanced than living pecorans in almost all of their morphological and physiological features.

The origin and early evolution of tragulids are still a mystery because their fossil record during the Paleogene is extremely scarce. However, tragulids were the only non-pecoran ruminant group that surpassed the Paleogene, showing an amazing radiation that produced several genera that spread out all over the Old World by the end of the Early Miocene: '*Dorcatherium*' (Africa, Asia, and Europe), *Dorcabune* (Asia),

*Siamotragulus* (Asia and Africa) and *Afrotragulus* (Africa).

We present the first large-scale cladistic analysis of the Tragulidae. In our study we include a large number of fossil and extant species, integrating the study of cranial, dental and postcranial morphological features with near 50 characters.

Our aim is to test several phylogenetic hypotheses on tragulid evolution: e.g. the extant disjunct distribution of the Tragulidae is related to phylogeny, that is, both an African and an Asian clade of tragulids do exist; *Hyemoschus* is closely related to *Dorcatherium*; *Dorcatherium* is a deeply paraphyletic taxon; and there was a still-unrecorded large-scale radiation event of tragulids previous to their first Miocene record. All of these hypotheses have been classically considered in the recent (and not so recent) works on Tragulidae. Our results not only give answers to these questions but also incorporate some interesting paleo-biogeographical interrogants that have to be explored in future works.

### Separating phylogenetic signals from trophic convergence in cervid dentition – implications from tooth morphology and 3D surface texture analysis

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Phylogenetic relationships of Cervidae have traditionally been reconstructed based mainly on cranial morphology and more recently by molecular analyses. Both approaches produced controversial results at every intrafamilial level. Generally only little is known about the diversity of the tooth morphology in extant and fossil Cervidae and its relevance for phylogenetic questions. Our study focuses on detailed scrutiny of tooth crown characters and separation between phylogenetic relevant homologies and convergences caused by trophic adaptation, in order to determine tooth crown character evolution. We compared the tooth morphology of the postcanine dentition of about 30 extant and 20 fossil cervid species, beginning with the earliest known cervid from the Early Miocene (20 million years ago) and covering mainly Eurasian localities. Approximately 50 indicative qualitative and quantitative characters were found, which can be used in phylogenetic analyses and enable us to detect tooth crown character evolution; e. g. development of lingual anterior and posterior metacristid on the lower fourth premolar. Additionally, occlusal surfaces of the dentition were investigated using 3D surface texture analysis. We used 46 industrial 3D surface texture parameters and tested their capability to robustly indicate specific functional traits and trophic adaptations. Our results clearly prove a spectrum of tooth morphologies from ancestral species in tropical regions to highly derived extant species in arctic regions. Apart from the well-known moderate increase



of cervid tooth crown height, we found modifications in the tooth crown elements, which are highly indicative for species differentiation. Furthermore, surface texture analysis is used to separately analyse texture related to micro-morphology, trophic adaptations and a combination of both. Correlation of the occlusal surface texture geometry with trophic adaptations in extant cervids, reveals large independence of tooth morphology, but a strong reflection of major food sources. Integration of the collected data in existing phylogenetic frameworks helps untangling the phylogenetic signal from convergent dietary adaptations. Hence, the diversity of tooth crown characters in Cervidae and their modifications through time, respectively, serve as primary phylogenetic signal. This allows us to use tooth morphology characters without the risk that the data are biased by convergence for cervids including their fossil representatives. Initial results showed that the three subfamilies, Capreolinae, Cervinae and Munticinae, can be supported by the analyses. Furthermore, monophyly for certain genera, i. e. *Axis*, *Cervus*, *Rucervus* and *Rusa*, could be proven, and for fossil species a link to their living representatives could be made. Combining all selected parameters provides a more comprehensive and detailed representation of tooth morphology, trophic adaptations and the functional integrity of the occlusal surface.

### A comparison of vestigial zeugopodal and autopodal elements in ruminants and their potential use in establishing phylogenetic relationships

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While the skeletal structure of the limbs of ruminants is quite derived from the ancestral eutherian state, there is considerable variation within the group. The limbs of most extant ruminants are adapted for cursorial locomotion, including the extreme reduction of the fibula, metapodials and phalanges for digits 1, 2 and 5. The nature and extent of the reduction is variable. Comparative analyses of zeugopodal and autopodal characters, including regressed elements, have been used to assist in the development of ruminant phylogenies. Recently, we have described a lateral 'splint bone' in North American moose (*Alces alces*). It was found fused to 75% of metatarsal specimens collected from mature animals on Isle Royale, MI, USA (n=366), to 95% of specimens from Alaska (n=132) and to 95% of specimens from other North American locations (n=22). It was also found in 94% of fossilized specimens from Alaska (n=49) and in 100% of fossil specimens of *Cervalces scotti* (n=5). Thus, it appears to be a very common feature in the Alceini. A lateral splint bone is also common in *Odocoileus virginianus* (94%, n=31) and *Odocoileus hemionus* (94%, n=17). It is much less common in *Rangifer tarandus* (reindeer: 54%, n=13; caribou: 50%, n=10). The only plesiometacarpal cervids examined thus far are *Cervus elaphus* (95%, n=21) and *Cervus canadensis* (76%, n=25). In Bovidae, the lateral splint is found in *Bos taurus* (35%, n=17) but not in *Ovis aries* (0%, n=6).

The form of the splint is consistent within species. It is large in *Alces alces*. It averages 3.5 mm wide and extends distally 85 mm from the proximal end of the metatarsal (22% of the length of the metatarsal). It is typically fused to the metatarsal at its proximal end but a distal free portion extends an average of 18 mm. It is much narrower and shorter in the other cervids, even when scaled for metatarsal length. In the vast majority of cases, it is very tightly apposed to the metatarsal over its complete length. The lateral 'splint bone' may result from the ossification of a fine, lateral homologue of the interosseous ligament. This ligament runs along the plantolateral edge of the metatarsal. It extends from the distal end of the splint towards the proximal phalanx of digit 5 (lateral dewclaw) in all ruminants examined. A small (fusiform, 3-7 mm long), calcified element was observed imbedded within the distal portion of the ligament in 3 of 4 adult moose during soft tissue dissection. An analogous calcified structure was found in 3 of 12 *O.v.*, 2 of 10 reindeer, 1 of 2 *C.c.* and 0 of 4 *B.t.* Similar evaluations of the medial metatarsal splint, metatarsal 1, the phalanges in digits 2 and 5, and the fibula have been initiated. The variability in occurrence and structure within species necessitates the examination of large numbers of individuals for accurate description. The utility of these characters in establishing phylogenetic relationships within the Ruminantia remains to be determined.

### The interrelationships of the Giraffidae

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Giraffidae are distinguished by ossicones, a bilobed canine and are represented by eleven main lineages (a working hypothesis). First two groups are basal groups but are rather specialized and distinct from other Giraffidae (groups 3-11), which are more homogeneous. (1) In *Palaeomeryx* the metapodials fuse differently from other Giraffidae and other ruminants. They also have an occipital 'horn'. (2) *Prolibytherium* has specialized occipital condyles and specialized ossicones. (3) *Canthumeryx* is probably the most basal of Giraffidae. *Canthumeryx* is characterized by a neck of intermediate length, ossicones above the orbital margin and an open nasolacrimal canal. Only members of this early group (3) have narrow crania in relation to the width of the frontals and an open nasolacrimal canal. Group (3) are possibly known from deposits as early as 19 mya in Kenya, and certainly from deposits approximately 17.5 mya from Libya, Kenya and Greece. Lineages 3-11 are characterized by large-sized animals with large-longish metapodials. The rest of the groups (4-11) have wider crania and a closed nasolacrimal canal. (4) *Injanatherium* has specialized metapodials and may be near *Canthumeryx*. (5) Giraffokerycinae: *Giraffokeryx* has a distinct second anterior pair of ossicones. (6) Sivatheriinae are very large-sized with large frontal sinuses and shortened necks. *Sivatherium* is the more primitive in ossicone position but the metapodials are specialized (short). *Bramatherium* is the more specialized with

fusions of ossicones but with more generalized metapodials (long). (7) *Schansitherium* is intermediate with four ossicones as in Sivatheriinae but a Palaeotraginae-like skull shape (the ossicone apices are dead). (8) Palaeotraginae are united by a dead ossicone condition and various cranial features. *Sa-motherium* is more primitive than *Palaeotragus* in its larger size and ossicone position. *Palaeotragus* is derived by a size reduction and the repositioning of ossicones medially. (9) Bohlininae have a specialized metapodial condition; the deep posterior trough. A morphocline is observed: *Birgerbohlina* shortest metapodials, *Honanotherium* longer and *Bohlinia* longest. (10) Giraffinae: *Giraffa* is specialized with large head sinuses, posterior positioning of ossicones, long radius, long metapodials and neck. The junction of the neck to the thorax is specialized. *Giraffa* may be near Bohlininae or long necks have evolved independently twice. The oldest *Giraffa* is from the Siwaliks of Pakistan (7 mya). This is suggestive of *Giraffa* migrating into Africa. (11) Okapiinae: *Afrikanokeryx* has elongated canals inside the ossicones. *Okapia* displays dead apices on ossicones like Palaeotraginae and *Schansitherium* but large head sinuses like Sivatheriinae and Giraffinae. The neck is short. *Okapia* may be near Sivatheriinae.

### Basicranial and ear morphology characters among basal ruminants

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The modern family Tragulidae is often regarded as a primitive archetype for the earliest ruminants, as these are generally small-bodied selenodont taxa lacking cranial appendages. As a result, the basal ruminants have, until fairly recently, been placed within the Tragulina with little regard for the relationships among them, their monophyly or their morphological diversity. Increased diversity of Asian material and more explicit phylogenetic work has generated several testable hypotheses of relationship among basal ruminants, suggesting that the groups' ultimate origins are Asian, and the North American families, the Hypertragulidae and Leptomerycidae evolved independently from within Asian clades, immigrating separately to North America.

One current hypothesis unites the North American hypertragulids with the Asian praetragulids, as a basal offshoot of ruminants, but of the seven features suggested to unite them, only two (medial concavity of the posterior palate, and an enlarged orbital part of the lacrimal) represent potential synapomorphies. In this hypothesis the main ruminant stem is represented by the tragulids+lophiomerycid clade and an archaeomerycid(leptomerycid(bachitheriid+gelocid) clade. A number of basicranial features show unclear polarities or a high degree of variability (such as bullar mophology which is highly variable in early ruminants), while others can be argued to support this hypothesis. The occipital exposure of the mastoid, a feature of bachitheriids, archaeomerycids, gelocids, and leptomerycids; the closed postorbital bar, is present in bachitheriids, archaeomerycids, leptomerycids, and gelocids, and presumably evolved convergently among tragulids.

Many of the cranial characters do not clearly support this hypothesis. The shallow subarcuate fossa is shared by gelocids and Pecora. Anterior displacement of the stapedia muscle fossa is known in hypertragulids, leptomerycids and tragulids, which suggests a possible functional component driving parallel evolution. The enlarged, subcentral tympanohyal vagina is known in archaeomerycids and leptomerycids, but remains unknown for others. Detailed high-resolution CT of the ear region of *Hypisodus* shows a mix of derived and ancestral features. The medial petrosal carries the basicochlear groove, unlike other ruminants; the deep subarcuate fossa contains a large mastoid fossa within it, also known in basal tylopods. However, it also bears a sharp crest on the medial petrosal, a feature of more derived ruminants, raising the question of whether the degree of inflation of the bulla is correlated. Additional information remains to be identified using high-resolution CT studies; many basal artiodactyl taxa have recently been described using these techniques to better understand basicranial and petrosal features, and better documentation of basal ruminant taxa may allow considerable improvement in resolution by clarifying character states and homology assessments.

### Morphology of articular surfaces can solve a phylogenetic issue: one instead of two ancestors for *Candiacervus* (Mammalia: Cervoidea)

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During the Late Pleistocene, the insular deer of Crete underwent cladogenesis in isolation as a result of which it is represented by six to eight species (depending on the taxonomy followed). The body size range from the smallest (about 22 kg) to the largest species (about 316 kg) is impressive. For decades, this unusual broad range has given rise to much debate concerning the process of speciation. Two alternative hypotheses have been proposed. One assumes two invasions, expressed in various generic names for the different species (e.g. *Praemegaceros* for the smaller, and *Leptocervus* or *Pseudodama* for the larger species) and thus making the Cretan deer a polyphyletic group. The other hypothesis assumes one invasion and a subsequent evolutionary radiation or cladogenesis. In that view, the Cretan deer form a monophyletic group. Until now, this issue could not be satisfactorily solved because of the lack of any cranial and dental remains of the two largest species. Recent morphological and functional analysis of the articulations of the limb bones sheds new light on this issue. We found that both shape and absolute size of some articulations and the morphology of the vertebrae are remarkably similar among the size classes, suggesting a common origin for all species of Cretan deer. In particular, the limb bones of both dwarf and giant representatives of the Cretan deer deviate morphologically from those of similar-sized mainland deer, including their ancestors. The result is massive bones with

broad joints in the dwarf species and very slender bones with narrow joints in the giant species, whereas this is opposite in the mainland species when we disregard length. To conclude, this means firstly that the ancestor of the Cretan deer species must have had a morphology in between that of the dwarfed and giant species and secondly, that the Cretan deer are monophyletic and thus the name *Candiacervus* applies to all six or eight species, which are now sister species. Since, concerning the postcranial skeleton, the least derived *Candiacervus* species is the *Dama*-sized *C. cretensis*, we suggest that the most likely sister species to all Cretan deer is a mainland deer of that size. *Candiacervus* shares many characters with *Dama* and *Megaloceros* but most characters that distinguish these two genera are polymorphic in *Candiacervus* and can thus not be used. Based on size alone, we tentatively suggest *Dama* as ancestral to *Candiacervus*.

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### Late Miocene *Cervavitus novorossiae* (Cervidae, Artiodactyla) from Lantian, Shaanxi Province

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Fossil deer from the base of the Lantian Formation, Shaanxi Province, are described and assigned to *Cervavitus novorossiae* by its size, three-tined antlers, curved development of the beam, laterally flattened fork, long and curved brow tine, pedicles prolonged by a ridge on the frontals, the long span between the burr and first fork in young individuals etc. *Palaeomeryx*-folds on lower molars are present in European specimens but generally undeveloped or missing in Chinese ones. New biochronological data suggests the possible origination of *Cervavitus* in Europe, and subsequent migration to China. The differences of *C. novorossiae* with *C. shanxius* (Teilhard de Chardin and Trassaert, 1937; Dong and Hu, 1994) show that *C. novorossiae* might evolve into the latter in order to adapt to climatic and environmental changes. Overview of the pliocervines from China confirms five species of *Cervavitus* existed in China: *C. novorossiae* Khomenko, 1913, *C. shanxius* Dong & Hu, 1994, *C. huadeensis* Qiu, 1979, *C. ultimus* Lin, Pan & Lu, 1978, and *C. fenqiu* Han, 1987.

### The anatomy and paleoecology of the boselaphine *Miotragocerus pannoniae* from the late Miocene Höwenegg locality (Hegau, Germany)

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While the basal Boselaphini (or Tragoportacini) are known to be represented by a number of taxa in the late Miocene of Europe, the poor state of preservation of most early boselaphine remains makes it difficult to taxonomically define species and assess phylogenetic relationships among members of this tribe. Especially the interrelationships between two dominant genera in this context, *Miotragocerus* and *Tragoptax*, are poorly understood.

In contrast to most other late Miocene European fossil sites, the southern German Höwenegg locality (10.3 Ma; MN9) is known for the exceptional preservation and completeness of its numerous skeletons of various large mammals. Being represented by 24 complete or near-complete skeletons at present, *Miotragocerus pannoniae* is the most common mammal at this locality. No detailed description of the anatomy of Höwenegg *Miotragocerus* has as yet been published. This is surprising, given the sample's potential for helping in circumscribing the thus far proposed species of *Miotragocerus* as well as in taxonomically re-evaluating material allocated to other early boselaphines. A matter of particular interest in this regard is sexual dimorphism as evident in horn core morphology, given that such intraspecific variability causes much taxonomic confusion at localities where only disarticulated early bovid specimens are found.

Four recently discovered and prepared Höwenegg *Miotragocerus* skeletons housed in the Natural History Museums of Stuttgart and Karlsruhe have now been described in detail and compared to the remaining boselaphine material from this locality. In doing so, metric data for nearly all skeletal elements could be obtained. Furthermore, all currently accessible horn cores of Höwenegg *Miotragocerus*, some of which can securely be tied to female individuals in association with fetuses, were investigated. Measurements of horn core dimensions as well as morphological observations allowed the development of a thorough understanding of the extent and nature of cranial sexual dimorphism in this taxon. Our anatomical observations will aid in identifying morphological characters useful for future phylogenetic analysis of basal boselaphines.

We also analyzed the paleodiet of Höwenegg *Miotragocerus* using microwear and mesowear methods in order to assess the paleoecology of this species in particular and of the Höwenegg environment in general. The assessment generally indicates a browse-dominated diet for this boselaphine. Interestingly, while this is also true for the Höwenegg hipparion, *Hippotherium primigenium*, these equids must have preferred a diet slightly richer in grass, as is evident in the results of our microwear analysis. Further analysis of the functional anatomy of Höwenegg *Miotragocerus* based on postcranial elements will provide additional information on this boselaphine's paleoecology.

## Taxonomic inflation in ruminants and its bearing on evolutionary biology and conservation

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Recently, many ruminant ‘new’ species have been named, mostly by raising subspecies to species rank. This is primarily a consequence of the phylogenetic species concept (PSC) that has become very popular over the last few decades. It is argued that much of this taxonomic inflation is artificial due to shortcomings of the PSC and unjustified reliance on insufficient morphological and/or genetic data. Species splitting based on gene trees inferred from mitochondrial DNA only and phenetic analyses aimed at diagnosability produces particularly doubtful results that also create an unnecessary burden on the conservation of biodiversity because effective population sizes of already threatened species are further reduced and genetic rescue is hampered, potentially resulting in an increased risk of extinction. The main aim and rationale of defining diagnosability and/or monophyly as the main criteria for taxon delimitation by the PSC is the detection of natural units. However, equating these units with species is both evolutionarily misleading and detrimental to conservation. This will be demonstrated by both theoretical considerations and examples taken from ruminants that have recently been unwarrantedly split into various ‘species’, such as red deer (*Cervus elaphus*) and klipspringer (*Oreotragus oreotragus*).

## Neogene Bovidae from China: A review

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The study of Chinese fossil bovids dates back to the beginning of the last century. The period during the 1920’s and 1930’s witnessed the peak time of fossil collecting and describing. From the 1950’s on, not only some new bovid taxa have been reported, but also the systematic positions of some bovid genera have been revised by Chinese paleontologists.

Two Oligocene genera, *Palaeohypsodontus* and *Hanhainicus* were described from Ulanatal, Inner Mongolia. Recent comparison with Valley of Lakes, Mongolia shows *Palaeohypsodontus* occurred also from similar horizon (Biozone C, Early Late Oligocene). The status of *Palaeohypsodontus* as a bovid is still in dispute with only broken jaws and teeth found, *Hanhainicus* may be even more weakly supported.

In total, 30 genera belonging to 5 subfamilies of Bovidae (Hypsodontinae, Urmiatheriinae, Caprinae, Antilopinae, and Bovinae) are recognized from Chinese Neogene strata. Most of the genera were found from North China. There have been discovered a few taxa from the Late Miocene of Southwest China (e. g. *Selenoportax*).

The biochronological and geographical distribution of fossil bovids from China shows four turnover events during

the Neogene time:

The first event happened between the Early and Middle Miocene. *Sinopalaeocerus* went extinct, and there occurred *Turcocerus*, which is the dominant element during the Middle Miocene in North China. The Middle Miocene/ Late Miocene boundary witnessed the second remarkable turnover event of Bovidae. None of the Middle Miocene taxa survived into the Late Miocene. The third turnover event happened near the Miocene/Pliocene boundary. The diversified group Urmiatheriinae went extinct. The fourth turnover event is characterized by the occurrence of extant genera and species during and after the Late Pliocene.



## LIST OF ALL AUTHORS

<hr/>		<hr/>	
<b>A</b>		<b>G</b>	
Aiglstorfer, Manuela	17	Van der Geer, Alexandra A.	33
Alberdi, María T.	17	Ghaffar, Abdul	23
Alcalde, Gema M.	17	Green, Jonathan	24
Andrés Rodrigo, María	18	Grossman, Ari	24
Asher, Robert J.	18, 25, 30	Groves, Colin P.	12
Athanassiou, Athanassios	18		
Azanza, Beatriz	17, 18, 19, 21		
<hr/>		<hr/>	
<b>B</b>		<b>H</b>	
Bam, Lunga	21	Hamilton, Charles H.	32
Bärmann, Eva V.	18, 19, 30	Heckeberg, Nicola S.	25, 30, 31
Barry, John C.	20	Helbig, Lisa	13
Beatty, Brian L.	20, 30	Hernández Fernández, Manuel	13, 17, 21
De Beer, Frikkie C.	21	Hoffman, Jakobus	21
Bernor, Raymond L.	34	Hofreiter, Michael	25
Bibi, Faysal	20	Hou, Sukuan	32
Bininda-Emonds, Olaf R. P.	13		
Böhme, Madelaine	17		
Breda, Marzia	27		
Brink, James S.	21		
<hr/>		<hr/>	
<b>C</b>		<b>I</b>	
Campbell Jr., Kenneth E.	30	Iannuzzi, Leopoldo	14
Cantalapiedra, Juan L.	13, 17, 21		
Cap, Henri	12		
Chen, Guanfang	35		
Clauss, Marcus	11		
Costeur, Loïc	22		
Croitor, Roman	22		
<hr/>		<hr/>	
<b>D</b>		<b>J</b>	
Dalen, Love	23	Janis, Christine M.	15
Decker, Jared E.	16		
Deleporte, Pierre	12		
DeMiguel, Daniel	19		
Doan, Karolina	23		
Drinia, Hara	33		
<hr/>		<hr/>	
<b>E</b>		<b>K</b>	
Erpenbeck, Dirk	30	Klisch, Karl	25
		Kostopoulos, Dimitris S.	26
		Koyabu, Daisuke	26
		Kubo, Mugino	27
<hr/>		<hr/>	
<b>F</b>		<b>L</b>	
Fack, Fabrice	23	Lenstra, Johannes A.	27
Frailey, Carl D.	30	Lister, Adrian	27
		Lomolino, Mark V.	30
		Lyras, George	33
<hr/>		<hr/>	
		<b>M</b>	
		Van der Made, Jan	28
		Menecart, Bastien	28
		Mess, Andrea	25
		Métais, Grégoire	28
		Moodley, Yoshan	29
		Morales, Jorge	18, 21, 31
<hr/>		<hr/>	
		<b>P</b>	
		Palombo, Maria R.	30
		Price, Samantha	13
		Prothero, Donald R.	30

---

**Q**

Quiralte, Victoria 31

---

**R**

Ríos, María 31  
Roberts, R. Michael 16  
Rössner, Gertrud E. 17, 25, 30, 31  
Rozzi, Roberto 30

---

**S**

Sánchez, Israel M. 31  
Sandoval-Castellanos, Edson 23  
Schnabel, Robert D. 16  
Schulz, Ellen 31  
Semperebon, Gina M. 34  
Silvia, William F. 32  
Silvia, William J. 32  
Solounias, Nikos 20, 24, 32  
Stankovic, Ana 23

---

**T**

Takatsuki, Seiki 27  
Taylor, Jeremy F. 16  
Theodor, Jessica M. 15, 33

---

**V**

De Vos, John 33

---

**W**

Wang, Lihua 34  
Wolf, Dominik 34  
Wörheide, Gert 25, 30

---

**Z**

Zachos, Frank E. 35  
Zhang, Zhaoqun 34, 35

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