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?

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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 (incuding 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